

Geology and Paleontology
of the
Lee Creek Mine, North Carolina, III

Clayton E. Ray and David J. Bohaska

EDITORS

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ABSTRACT

Ray, Clayton E., and David J. Bohaska, editors. Geology and Paleontology of the Lee Creek Mine, North Carolina, III. *Smithsonian Contributions to Paleobiology*, number 90, 365 pages, 127 figures, 45 plates, 32 tables, 2001.—This volume on the geology and paleontology of the Lee Creek Mine is the third of four to be dedicated to the late Remington Kellogg. It includes a prodomus and six papers on nonmammalian vertebrate paleontology. The prodomus continues the historical theme of the introductions to volumes I and II, reviewing and resuscitating additional early reports of Atlantic Coastal Plain fossils. Harry L. Fierstine identifies five species of the billfish family Istiophoridae from some 500 bones collected in the Yorktown Formation. These include the only record of *Makaira purdyi* Fierstine, the first fossil record of the genus *Tetrapturus*, specifically *T. albidus* Poey, the second fossil record of *Istiophorus platypterus* (Shaw and Nodder) and *Makaira indica* (Cuvier), and the first fossil record of *I. platypterus*, *M. indica*, *M. nigricans* Lacépède, and *T. albidus* from fossil deposits bordering the Atlantic Ocean. Robert W. Purdy and five coauthors identify 104 taxa from 52 families of cartilaginous and bony fishes from the Pungo River and Yorktown formations. The 10 teleosts and 44 selachians from the Pungo River Formation indicate correlation with the Burdigalian and Langhian stages. The 37 cartilaginous and 40 bony fishes, mostly from the Sunken Meadow member of the Yorktown Formation, are compatible with assignment to the early Pliocene planktonic foraminiferal zones N18 or N19. The Pungo River fish fauna is dominated by warm water taxa; the Yorktown fauna includes warm and cool water species. These changes are attributed to increased upwelling waters in Yorktown time. The abundant fossils provide the basis for several changes in selachian taxonomy and for two new species of bony fishes. George R. Zug records 11 taxa of turtles from the Yorktown Formation: a sideneck (*Bothremys*); six sea turtles (*Caretta*, ?*Chelonia*, *Lepidochelys*, *Procolpochelys*, *Psephophorus*, *Syllomus*); a softshell turtle (trionychid); two pond turtles (probably *Pseudemys* and *Trachemys*); and a giant tortoise (*Geochelone*). Albert C. Myrick, Jr., records the crocodylian *Thecachampsa antiqua* (Leidy) on the basis of fragmentary float material from the Pungo River or Yorktown Formation, or both. Robert W. Storer describes a new species of grebe of the genus *Podiceps* from the Yorktown Formation. Storrs L. Olson and Pamela C. Rasmussen record some 112 species of birds from the Pungo River and Yorktown formations. Apart from an undetermined number of shearwaters, only a few species are thought to come from the Pungo River Formation. The marine species from the Yorktown Formation include three loons, two grebes, five albatrosses, at least 16 shearwaters and petrels, one pelican, two pseudodontorns, three gannets, two cormorants, 9–11 auks and puffins, one skua, three jaegers, five gulls, two terns, and 20 ducks, geese, and swans. The less common land and shore birds are represented by 29 species, including three cranes, one rail, two oystercatchers, one plover, four scolopacids, one flamingo, one ibis, one heron, three storks, one condor, five accipitrids, one osprey, one phasianid, one turkey, one pigeon, and one crow. The fauna is dominated by a radiation of auks of the genus *Alca*. The early Pliocene fauna is very modern in aspect, suggesting that most modern lineages of birds were already in existence.

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Dedicated to
Remington Kellogg
1892-1969

Geology and Paleontology of the Lee Creek Mine, North Carolina, III

Prodromus

Clayton E. Ray

Prodromus... a preliminary publication or introductory work.

WEBSTER'S THIRD NEW
INTERNATIONAL DICTIONARY, 1964

The archaic title is intended to reflect the antiquarian nature of this paper and to emphasize my conviction that our work on the Lee Creek Mine project, a quarter century of effort by many people, is decidedly preliminary. Publication began with volume I (Ray, 1983), which included papers on Remington Kellogg (to whom the series is dedicated), on the Lee Creek phosphate mine itself, and on stratigraphy and correlation, plants, and microfossils. The only paper specifically devoted to vertebrate fossils was that on otoliths of bony fish, included therein as "microfossils." That was primarily an unsuccessful effort to see the paper in print before the death of its senior author, John Fitch, who was then terminally ill. Volume II (Ray, 1987) was devoted exclusively to mollusks, the most conspicuously abundant and well-preserved fossils in the mine. Initially, it was planned that all vertebrate fossils, other than otoliths, would be included in a third, concluding volume (Ray, 1983:3); however, subsequent productive collecting, especially that by able and devoted amateurs, has resulted in great accumulation of more and better fossils. These have been subjected to thorough research by the contributors and, combined, expand the vertebrate papers beyond the reasonable confines of a single volume. The papers divide themselves conveniently into two sets, all groups other than mammals in this, volume III, to be followed by mammals, volume IV, which will include a tax-

onomic index to the publications of Remington Kellogg, predominantly on mammals.

This prefatory note continues the historical theme of those introducing volumes I and II, in which I attempted to review the early history of paleontological discovery and publication on the middle Atlantic Coastal Plain of British America. Having flattered myself that I had unearthed essentially everything, it is salutary to be reminded through several oversights that in antiquarian, as in paleontological, research one can never do too much digging. Returns in each are apt to be unpredictable and to be meager in relation to time invested (hardly "cost effective"), but there will always be something new, and, to comprehend it when found, one must be steeped in the subject. Thus, my primary objective is to rescue from obscurity or oblivion the additional early history that I have learned; not only to give credit to the pioneers, but to add to the foundation that may enable and inspire others to find out more, especially about American fossils surviving in European collections, and to dig further into the early literature. Thus, the present paper is an extension of those introducing volumes I and II and should be used in conjunction with them, as I have tried to avoid undue repetition of text and literature cited.

Although a full explication is beyond my scope herein and beyond my competence anywhere, I hope in reviewing these records to give some inkling of their importance, not only in the development of paleontology, but also in the broader intellectual concerns of the times. Fossils were more prominent in general scholarly discussions of the seventeenth and eighteenth centuries than at any time since. Although debate as to their na-

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ture and significance has long since dropped from the forefront of general investigation, we have by no means won the day. In western culture many educated people, including scientists, either ignore fossils or reject them as evidence of organic evolution, and humankind as a whole knows nothing of fossils (McIver, 1992; Lemonick, 1996).

No paleontologist can claim to be literate without thorough attention, not merely a perfunctory bow, to the role of fossils in western thought. Neglect of history is inexcusable in a historical science such as paleontology, but its literature in English is very skimpy, and that written by practicing paleontologists is generally narrow and shallow (although not universally so; e.g., see Ward, 1990), much devoted to "correcting" past mistakes and concepts in the light of present knowledge and fads. Of course we are obligated to correct objective errors in striving to approach truth ever more closely, but this is less and less specifically useful as we delve deeper into the ontogeny of our science. Much more satisfying is to understand the thoughts on fossils in the context and constraints of the times and the relevance of those thoughts to subsequent developments. The best primers on this subject in English are Rudwick (1976), especially the first 100 pages, and Drake (1996), the latter focused on Robert Hooke but with uncommon explication of context. Also very instructive are Challinor (1953), Morello (1979, 1981), and Young (1992). Davidson (2000:333) outlined the otherwise neglected role of Richard Verstegan in the early seventeenth century; however, she is mistaken in attributing the first published illustration, in 1605, of a shark's tooth to him. That distinction almost certainly belongs to Gesner (see Rudwick, 1976:30, fig. 1.9), who in 1558 even included a modern comparative specimen alongside his fossil. Davidson (2000:343) cited Gesner's work as probably available to Verstegan but mentioned neither Gesner's figure nor the work of Kentmann of 1565 in Gesner (see Rudwick, 1976:11–17).

These and other sources cited herein provide essential background on the principal players in the founding of paleontology, including, among others, da Vinci, Colonna, Scilla, Steno, and Hooke, and those in the interrelated development of collections, including Aldrovandi, Cospi, Giganti, Kircher, Mercati, Worm, and others. I refer to their work and its broader implications only in the course of resurrecting the primary reports on American fossils. These allusions should be sufficient to show that these reports are not mere curiosities of antiquarian delight but were integral to cutting-edge (see Maienschein, 1994, regarding this trendy term) intellectual concerns.

Although there is no universal agreement as to what or when the Renaissance was, few would disagree that it was earlier, stronger, wider, and deeper in Italy than it was anywhere else. It is no accident that Italian names, notably those mentioned above, dominate the earliest stages in the history of paleontology and museums, and that Italian influence extended strongly into northern Europe and the British Isles.

For example, Steno, or Niels Stensen, was a Danish cleric, but his scientific career was mostly Italian in locale, patronage, and material (Scherz, 1969, 1971); Olaus Worm, also Danish,

probably was influenced by Aldrovandi in forming his museum (Schepeleern, 1990:82); Aldrovandi's pioneering catalogs of his collection were emulated and cited frequently in much later catalogs in England (Grew, 1681; Sloane, see Thackray, 1994:125); and John Ray visited and was much impressed by Aldrovandi's collection (Torrens, 1985:206). Steno's work was immediately translated into English by Oldenburg, and it became the subject of great interest in the Royal Society (Eyles, 1958; Stokes, 1969:16). (Hooke accused Oldenburg and Steno of conspiring to plagiarize his ideas (Oldroyd, 1989:217); Drake (1996:116–117), especially, supported Hooke's claims, and, more importantly, documented his widely undersung contributions.)

It has been suggested (e.g., Rudwick, 1976:39–41; Torrens, 1985:207) that recognition of fossils as remains of once-living organisms occurred in Italy before it did in northern Europe and England because the Italian fossils were "easy," being geologically young, little altered, and close to the sea and to living relatives, whereas those elsewhere were much older, in deformed inland rocks, and the most conspicuous fossils were not closely related to living forms. Unfortunately, these factors can at best only partially explain away the Italian preeminence. Surely at least as important was the existence of an affluent society, with concomitant cultural sophistication, ready to underwrite research and to accept truth through logical argument. Gould (1997) presented a convenient and timely analysis of Leonardo's brilliant and prescient insights on fossils, well fixed in the context of time and place. Both geologic and human history preadapted Italy as the scene of these breakthroughs, and just as they were interwoven with a rich tapestry of culture, art, learning, and patronage, so also was the interrelated development of natural history collections. The literature in English reveals little comprehension of the fact that natural history museums developed (and survived in some cases) in continental Europe, especially in Italy, in some semblance of modern form, a century earlier than in the English-speaking world. It seems altogether too revealing that in 1995 I found the pages uncut in the Smithsonian Institution Library copy of MacGillivray's (1838) life of Aldrovandi. This neglect has been partially corrected in some excellent recent publications, including Impey and MacGregor (1985) and Findlen (1994). Ethnological and zoological objects from the Latin New World (then including Florida) have been well documented in these early collections (e.g., see Heikamp, 1976:458; Laurencich-Minelli, 1985), but to my knowledge no fossils have as yet been recognized. Nevertheless, the search for the beginnings of paleontology of the New World should begin in sixteenth century Italy, through direct examination of collections by appropriate specialists. The best hope might well be the collections of the great Ulisse (Latinized as Ulyssis) Aldrovandi (1522–1605), who was known to have had a strong interest in the New World (Heikamp, 1976:458; Laurencich-Minelli and Serra, 1988). His catalogs, largely compiled during his lifetime but published posthumously (Ambrosinus, 1648; Figure 1), remained a powerful influence long afterward in England (see above).



FIGURE 1.—Title page (much reduced) of Aldrovandi's 1648 monumental catalog of his museum. It was compiled and was widely known during his lifetime (1522–1605) but was published by Ambrosinus more than 40 years after Aldrovandi's death (Findlen, 1994:25).

Some Early Records

This brings me to the first instances to be added to early reports of fossils from the Atlantic coast of North America. As early as 1669 an allusion was made to natural history specimens from Virginia in a collection, long since forgotten and irretrievably lost, maintained by the East India Company at its headquarters in London (Hunter, 1985:162). The first explicit record to be added is that by Nehemiah Grew, who in 1681 published by subscription under auspices of the Royal Society a catalog of its collections, the title page of which is reproduced herein (Figure 2; see Hunter, 1989, especially p. 142 et seq., for genesis and nature of the catalog; see LeFanu, 1990, for Grew's life and contributions; see Clark, 1992, for an authoritative guide to histories of the society, its periodical publications, and indices thereto). Included are two entries for fossils specifically stated to have come from the New World.

A sort of MUSCULITES fill'd with Earth like *Tobacco-Pipe* Clay or Marle. Found amongst the earth of a Hill that was overturn'd at *Kenebank* in *New England*. (Grew, 1681:264)

A great petrify'd SCALLOP. Figur'd by *Ambrosinus* (*b*) with the Name of *Hippopectinites*. Given with several more of the same bigness, by Mr. _____ *Wicks*. 'Tis half a foot over. Many of the same kind were taken out of a great Rock in *Virginia*, forty miles from *Sea* or *River*. (Grew, 1681:262)

(*b*) Aldrov. Mus. Metall. (Grew, 1681:262, marginal citation)

The first of these undoubtedly was a mussel shell, common in the late Pleistocene marine clays of the Presumpscot Formation of coastal Maine, including the vicinity of Kennebunk (Stuiver and Borns, 1975; Thompson, 1982:212, 226). John Winthrop, Jr. (1606–1676), an original fellow and major contributor to the society's repository (Lyons, 1944:50, 64; Stearns, 1951:196, 212, 246, 1970:117–139), undoubtedly was the source of the specimen in question. In letters of 11 October 1670, printed in part in Birch (1756(2):473–474) and quoted in part by Stearns (1970:137), he alluded to "small shells" among the objects sent from a "hill near Kennebeck, Me, that turned over in summer last (June or July) into the River." The mysterious "blowing-up" of the hill was reported also by John Josselyn (1674:210; see also White, 1956:180).

The second entry is potentially of much greater interest. The marginal bibliographic citation is to Aldrovandi's monumental, classic illustrated catalog (Ambrosinus, 1648), which Grew cited repeatedly, in this case alluding to a giant pecten illustrated on page 832 of volume 4. This raised the intriguing possibility that Aldrovandi's specimen might conceivably be a previously unsuspected and much earlier example from the New World. Unfortunately, my limited investigation to date has revealed no positive evidence that the giant pecten or any of Aldrovandi's fossils came from America; rather, Grew's allusion seems to be only an obsolete, broadly conceived synonymy, understandable for the time. The specimen has not been found among surviving collections in Bologna, but it is thought to have come from the vicinity of the city (Sarti, in litt., 1993).

Returning to Grew's specimens from Virginia, I had previously been inclined to accept the argument that the specimen of

giant pecten, *Chesapecten jeffersonius*, described and illustrated by Lister, the first fossil so far known of any kind from the New World to be described and illustrated, probably had been collected by John Banister and sent directly to Lister, Petiver, or Sloane (see Ray, 1987:2), but now the Royal Society's Repository seems at least as likely. Not only was Lister's specimen "half a foot over," but also Lister (1639–1712) and Grew (1641–1712) coincided in their activities in the Society (Hunter, 1994:188–189), and Lister is known to have used other specimens from the repository.

The history of the repository is of great interest, not only in attempting to locate a potential historical treasure such as the giant pecten but also for its cautionary lessons to museologists in general. Early impetus to the establishment and support of the collection came from the need for a substantive rallying point for the struggling Royal Society and for a source of public prestige (Hunter, 1985, 1989:127, 128). Explicit and strikingly modern statements of the purposes of natural history collections were made by Grew (1681, preface), who advocated collections as an inventory of nature and as documentation of the ordinary, and by Hooke (1635–1703), who also took an active and at times official role in connection with the collections (see especially Hunter, 1989:125, 127, 139–141), and whose pioneering studies of fossil cephalopods stimulated his following statements (1705:338; also in Drake, 1996:236–237):

And indeed it is not only in the description of this Species of Shells and Fishes, that a very great Defect or Imperfection may be found among Natural Historians, but in the Description of most other things; so that without inspection of the things themselves, a Man is but a very little wiser. ... It were therefore much to be wish'd for and endeavour'd that there might be made and kept in some Repository as full and compleat a Collection of all varieties of Natural Bodies as could be obtained, where an Inquirer might be able to have recourse, where he might peruse, and turn over, and spell, and read the Book of Nature, and observe the *Orthography*, *Etymologia*, *Syntaxis* and *Prosodia* of Nature's Grammar, and by which, as with a *Dictionary*, he might readily turn to and find the true Figure, Composition, Derivation and Use of the Characters, Words, Phrases and Sentences of Nature written with indelible, and most exact, and most expressive Letters, without which Books it will be very difficult to be thoroughly a *Literatus* in the Language and Sense of Nature. The use of such a Collection is not for Divertisement, and Wonder, and Gazing, as 'tis for the most part thought and esteemed, and like Pictures for Children to admire and be pleas'd with, but for the most serious and diligent study of the most able Proficient in Natural Philosophy. And upon this occasion tho' it be a digression, I could heartily wish that a Collection were made in this Repository of as many varieties as could be produced of these kinds of Fossile-Shells and Petrifications, which would be no very difficult matter to be done if anyone made it his care.

Despite these and other resounding statements within the society, the reality (dictated largely by its dilettante membership) was that its collection continued to be much like that of a private cabinet of curiosities—devoted to the rare and bizarre rather than being a microcosm of what exists, ordinary as well as extraordinary (Hunter, 1989:150). This tension has yet to be resolved in museums, although the "inventory of nature" movement seems to be gaining ascendancy at last. Further, the society found that although establishing a museum is easy, maintaining it in the long term ("perpetuity") is almost impossible. From the beginning, much of the society's attention was

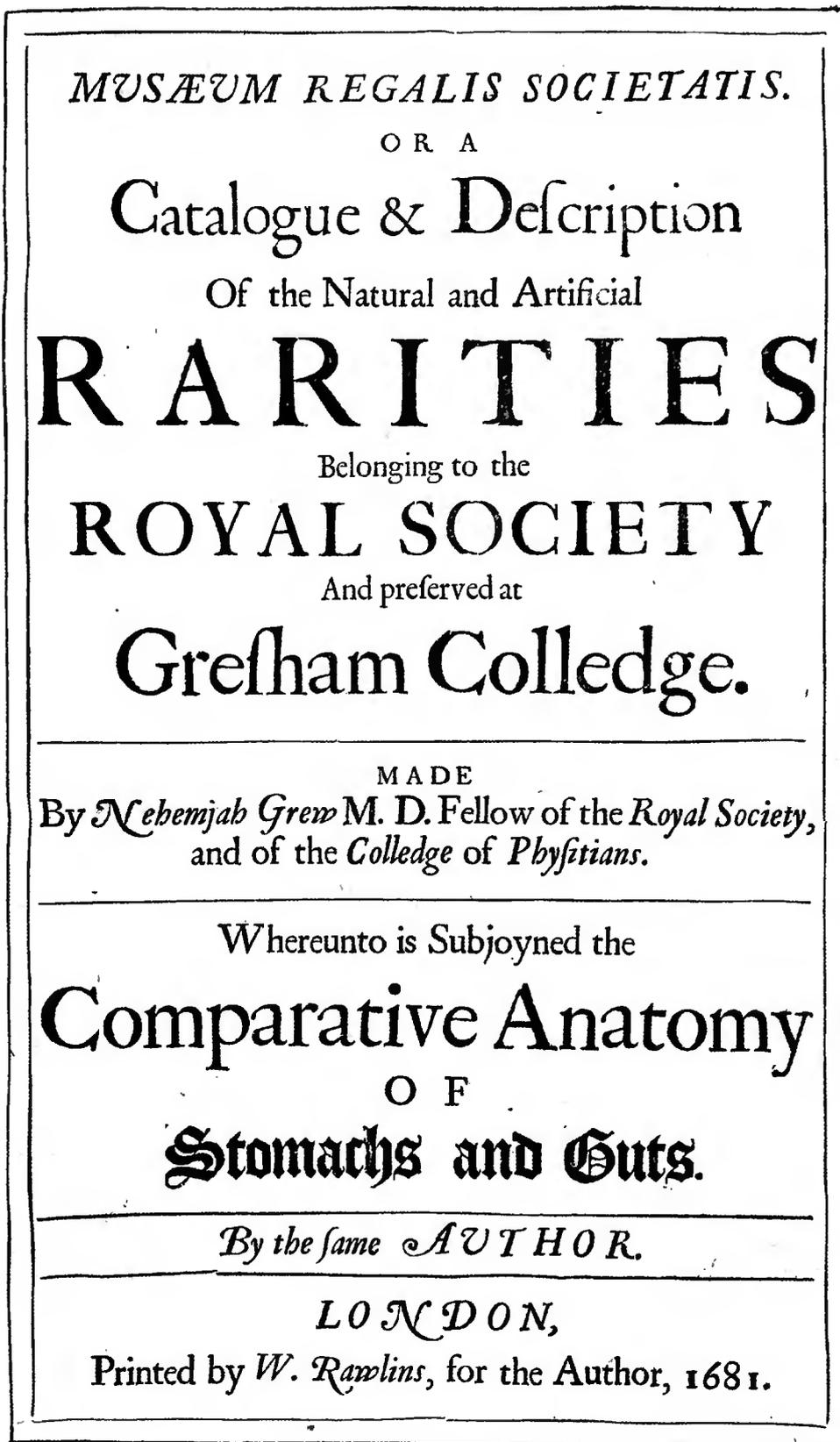


FIGURE 2.—Title page (reduced) of Grew's 1681 catalog of the repository of the Royal Society.

usurped by monetary problems, including difficulty in collecting dues and shortfall in funds to pay support staff. After years of vicissitudes in the care of its collections that entailed repeated efforts at revitalization, and finally faced with a critical problem in space to house the collection, the society offered its collections to the British Museum in 1779 (Hunter, 1989:153–155), which accepted in 1781 (Lyons, 1944:211). Now, a mere two centuries later, the heir to that collection, The Natural History Museum (BMNH), London, the Gibraltar of its kind, itself faces an uncertain future (e.g., see *Nature*, 1990), as do its counterparts elsewhere (Trescott, 1996; Butler, 1997).

In any case, the “several” giant pecten(s) from Virginia should have gone in 1781 to the British Museum. Although it seems unlikely that such large, conspicuous shells would have been lost, sold, or destroyed, even in the vandalous “cremations” of curator Shaw (Stearn, 1981:17), they have not as yet been recognized in the existing collections of BMNH (Nuttall, in litt., 1993).

The specimens in all probability represent *Chesapecten jefersonius* (see Ray, 1987), since 1993 the official fossil of the Commonwealth of Virginia (Anonymous, 1993) and thus of great historic and current interest if found.

This leaves only the matter of the donor, “Mr. ____ Wicks,” who turns out to be a subject of specific and general interest in spite of the paucity of information about him. The person in question undoubtedly is Michael Wicks, clerk of the Royal Society for at least 20 years (Thomson, 1812:15, lists his years in office as 23), from the first meeting of the council on 13 May 1663 (Birch, 1756(1):236) at least until 27 November 1683, when it was resolved that “Mr. Cramer be clerk to the society in Wicks’s place” and that “Mr. Wicks be told, that his attendance is of no farther use” (Birch, 1757(4):229). This resolution seems however not to have had the finality that it implied, as Mr. Wicks was given orders at the meeting of 2 April 1684, and the treasurer was ordered on 14 January 1685 to pay him “fifteen pounds for a year and a half’s salary” (Birch, 1757(4):277, 355). Robinson (1946:194–195) gave a summary of Wicks’ employment by the society, indicating that the last mention of him is that of 13 November 1695, when a gratuity was voted him by the Council; however, Hunter (1994:235) noted a substantial payment to him as late as 1696. It should be noted that Robinson refers to Wicks as “Weekes,” that he appears as “John Weeks” in Weld (1848:562), secondarily as “Weekes” in Hunter (1994:235), and is omitted altogether by Lyons (1940:344).

Apparently prior to Wicks’ appointment with the society, Dr. Jonathan Goddard (1617–1675, professor at Gresham College) had employed “Mr. Mich. Weekes, who looked to his stills” (Aubrey, 1898(1):268). In this case, the stills were for production of ingredients to various secret medicinal nostras. It is thought that Wicks got the job as clerk through Goddard’s influence (Robinson, 1946:194). This seems plausible in view of Goddard’s major role in the birth and early development of the society, from its unchartered gestation, beginning in 1645 (Copeman, 1960; McKie, 1960), through the turbulent period

of the Civil War, Commonwealth, and Protectorate (inauspicious for the founding of anything “Royal”).

In John Aubrey’s (1626–1697) notes (dated 12 March 1689) for his brief life of Walter Raleigh, in connection with Raleigh’s role in introducing tobacco to England, he states (Aubrey, 1898(2):181–182),

Mr. [Michael] Weekes, register* of the Royal Society and an officer of the custome-house, does assure me that the customes of tobacco over all England is four hundred thousand pounds per annum.

*Subst. for ‘clerk.’

There can be no doubt that Weekes and Michael Wicks are one and the same person. In response to my queries regarding Wicks, Mary Sampson (pers. comm., 1993), archivist to the Royal Society, found only one written communication by Wicks in the society’s unpublished Classified Papers series (CL. P. XXIV.56), a brief undated note of some 13 lines, addressed to Henry Oldenburg (his boss). I have been unable to decipher the handwritten note entirely, but the gist of it is that he put out some papers for Oldenburg stating, “I am sorry I could not wait upon you sooner, my business at Custome House being much more than ordinary.”

In 1993, Gillian Hughes, an independent researcher, undertook on my behalf a preliminary search in the Public Record Office for evidence of Michael Wicks in the Customs Establishment. The earliest certain indication found by her lists Michael Wicks as Receiver for the Plantations among officers of his majesty’s customes for 1673 and 1675 (PRO 30/32/15 and 17), and his name was last seen in those lists for 1693 (PRO, CUST 18/28). In the published *Calendar of Treasury Books* (Shaw, 1935:584), allusion is made under the date 17 April 1694 to “Mich. Wicks, late Receiver of the Plantation Duties and of the new impositions on tobacco and sugar... lately discharged from that service.” The *Calendar of Treasury Papers* (Redington, 1868:338) indicates “confusion in the accounts of Mr. Wicks,” and the Commissioners of Customs “describe their perplexities about his accounts, and that to prevent further enlargement they had dispensed with his attendance at the Custom House. ... Dated 5 Jan. 1693 [now 1694].”

Thus it seems clear that Michael Wicks (up to his dismissal under a cloud) was in an unusually favorable position for direct, frequent communication with merchant ships sailing to and from British America. At the meeting of the Royal Society on 13 June 1683, “Mr. WICKS was desired to procure from the East-India ships a quantity of the shining sand of St. Christopher’s and James river in Virginia” (Birch, 1757(4):209). This request would hardly have been made had it not been anticipated that Wicks could accommodate it.

Interestingly, this is the only instance in the long employment of Wicks by the society in which he was “desired” to do something, rather than “ordered” or “directed.” This is probably not accidental, but reflects a momentary deference to his position with the custom house. Otherwise, paid subordinates were addressed in the imperative, whereas the gentlemen Fel-

lows were “requested” or “desired” to do something. Pumfrey (1991:12–16; Drake, 1996:17–18, 104–105, not withstanding) has made a persuasive case for this distinction in connection with his study of Robert Hooke’s precarious position betwixt and between, which may have contributed to Hooke’s apparently atypical egalitarian attitude toward subordinates (e.g., see Shapin, 1989:269), as well as to his prickly attitude toward the establishment.

It should be recognized that the society’s treatment of Wicks was not cruel and unusual but was in general correct for the social system of the time and place. Even allowing for the free-wheeling attitude toward spelling in those days, it apparently was not important to get his name right or even to include it consistently in society records, nor perhaps was it important for Grew to remember or later insert Wicks’s given name in the manuscript for the society’s catalog.

The next explicit report of specimens from the Atlantic Coastal Plain is that of Sloane (1697). He borrowed the specimens from his friend, Dr. Tancred Robinson, who had just received them from Maryland (most likely from the Rev. Hugh Jones, who arrived there in 1696 and was accused by Woodward of sending specimens to “rogues and rascalls,” including Sloane, Petiver, Lister, and Robinson (Stearns, 1952:292, 306)). These specimens included at least three isolated tooth plates of the ray *Aetobatis*, illustrated in Sloane’s figs. 7–12; it is unclear from his text whether the articulated partial tooth battery shown in his figs. 13 and 14 also is from Maryland (see Figure 3). At least the fragmental plate shown in his figs. 7 and 10 is among the very small number of the founder’s specimens known to survive in BMNH, where it was featured in an exhibition on the history of paleontology (Edwards, 1931:61) and where it apparently is still to be found (Thackray, 1994:132). Obviously Robinson must have allowed Sloane to retain at least one of the fossils. Some or all of the others may be preserved in Woodward’s collection at Cambridge. In an appendix to his primary catalog of English “extraneous” fossils (catalog B of Price, 1989:94), however, Woodward (1728–1729) listed modern specimens preserved for comparison to his fossils, and on page 111, under his entry number 25, a modern ray dentition, he expressly stated that his ray tooth plates sent by Jones from Maryland “were digg’d up, together with those” reported by Sloane (see catalog B of Price, 1989).

Sir Hans Sloane (1650–1753) is best known as a prodigious collector who provided the foundation for the collections of the British Museum and its offshoots. He also was a man of parts who was a successful doctor of medicine, an olympian letter writer, and a major force in the Royal Society, although he was not without his detractors, most notably John Woodward (e.g., see MacGregor, 1994:19). Most have made light of his abilities as a thinker and researcher. Nevertheless, his little paper on the fossil ray plates is an elegant example of modernity produced before any pattern was established. He placed the isolated unknowns (considered by some to be bits of petrified mushrooms) alongside the most appropriate specimens of known identity, articulated and disarticulated modern ray tooth batter-

ies, found them to be similar in detail, illustrated them accurately in comparable orientations, and concluded that they derived from identical or closely related organisms. One’s first impulse today might be to dismiss this approach as routine, but it was not such in the context of the time. Although spectacular examples of brilliant comparative methodology are known here and there from the sixteenth century onward (note that Grew used the approach and the term, “comparative anatomy,” in 1681, see Figure 2), the techniques were not codified and universally applied until the nineteenth century under the influence of Cuvier, Owen, and Agassiz. This could not have occurred prior to the Age of Enlightenment/Reason, with the spread of the notion that all problems could be successfully solved through intensive inspection and that ordinary humans could rely on their own careful observations irrespective of authority. This approach was the cornerstone of the Royal Society. Until recently, this reliance was taken for granted, so much so that the sublime notion could be expressed profanely, if I may be permitted one homely example: Remington Kellogg, once asked by a colleague what criteria allowed him to conclude that a certain fragmentary whale vertebra was in fact identifiable to a particular species, immediately replied resoundingly, “because it looks like it, goddamit it!” He did not live to experience the postmodern entry of doubt introduced by phylogenetic systematics and social constructivism, in which we question the meaning of all our observations.

Further, Sloane’s (1697) note was written when the nature of fossils as vestiges of once-living organisms had by no means been universally accepted by serious scholars. This topic brings us conveniently to the next known report and illustration of fossils from the Atlantic Coastal Plain, that of a bone fragment and a shark tooth by Scheuchzer (1708), whose title page and figures are reproduced herein (Figures 4–6). Both specimens are preserved in the Paleontological Museum of Zürich (Leu, in litt., 1997; see also Furrer and Lev, 1998:33).

Johann Jacob Scheuchzer (1672–1733), little familiar to the English-speaking scientific community, is known primarily as an object of derision for his *Homo diluvii testis* faux pas, based on a fossil salamander (see Jahn, 1969, for this and for a good thumbnail biography of Scheuchzer in English). Scheuchzer was actually a very substantial scientist who translated Woodward into Latin and promoted his ideas (notably organic origin of fossils) on the continent. Scheuchzer was in close contact with Sloane and other leading naturalists of the Royal Society. His historical significance would unquestionably be better appreciated had Jahn’s (1975) promised bio-bibliography of Scheuchzer and translations of his major works materialized.

The bone fragment from Maryland was attributed by Scheuchzer (1708:22) to the acetabular region of the innominate bone of a mammal (“Animalis”), not a farfetched supposition. This fragment, however, matches very well the portion of a small cetacean atlas vertebra that characteristically remains after the vertebra breaks at the weak points and rolls on the beach; it is illustrated (Figure 5) alongside a typical float specimen and a well-preserved atlas from the Miocene of Ches-

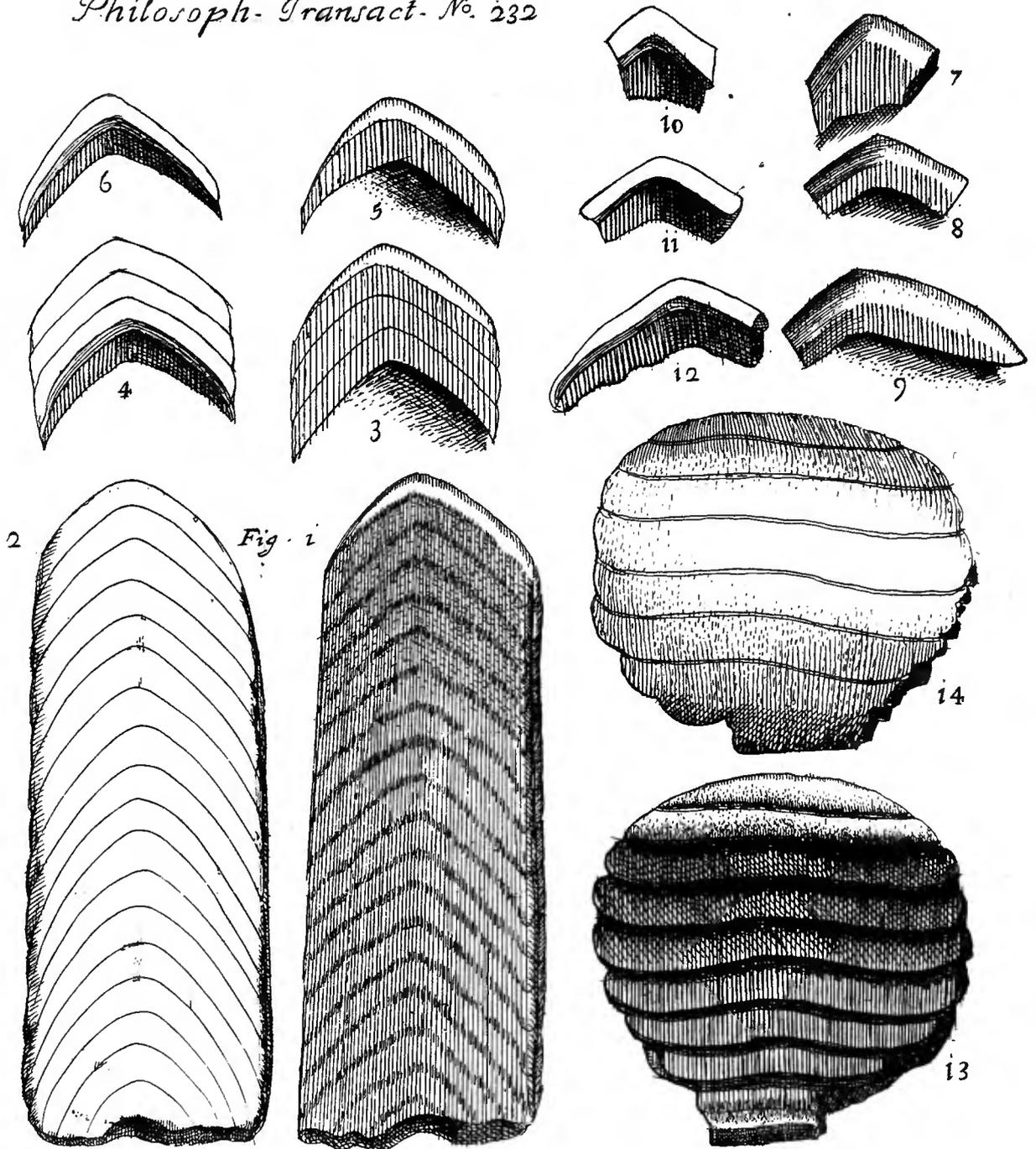
Philosoph. Transact. No. 232

FIGURE 3.—Plate accompanying Sloane's 1697 report on fossil ray teeth from Maryland ($\times 1$). His figures 1–6 are of modern species, figures 7–12 are of fossil species from Maryland, and figures 13–14 are of fossils from an unknown locality, possibly Maryland.

peake Bay in Maryland. This is probably the first cetacean (and mammalian) fossil from America to be illustrated.

This Maryland specimen, especially if received by Scheuchzer from Petiver, probably was sent by Hugh Jones.

Lhwyd (1660–1709) complained that Petiver and his pal Dooddy got aboard ship and rifled collections from Jones intended for him (Gunther, 1945:343, 462). Among specimens cataloged by Sloane that came to him in Petiver's collection were "shark

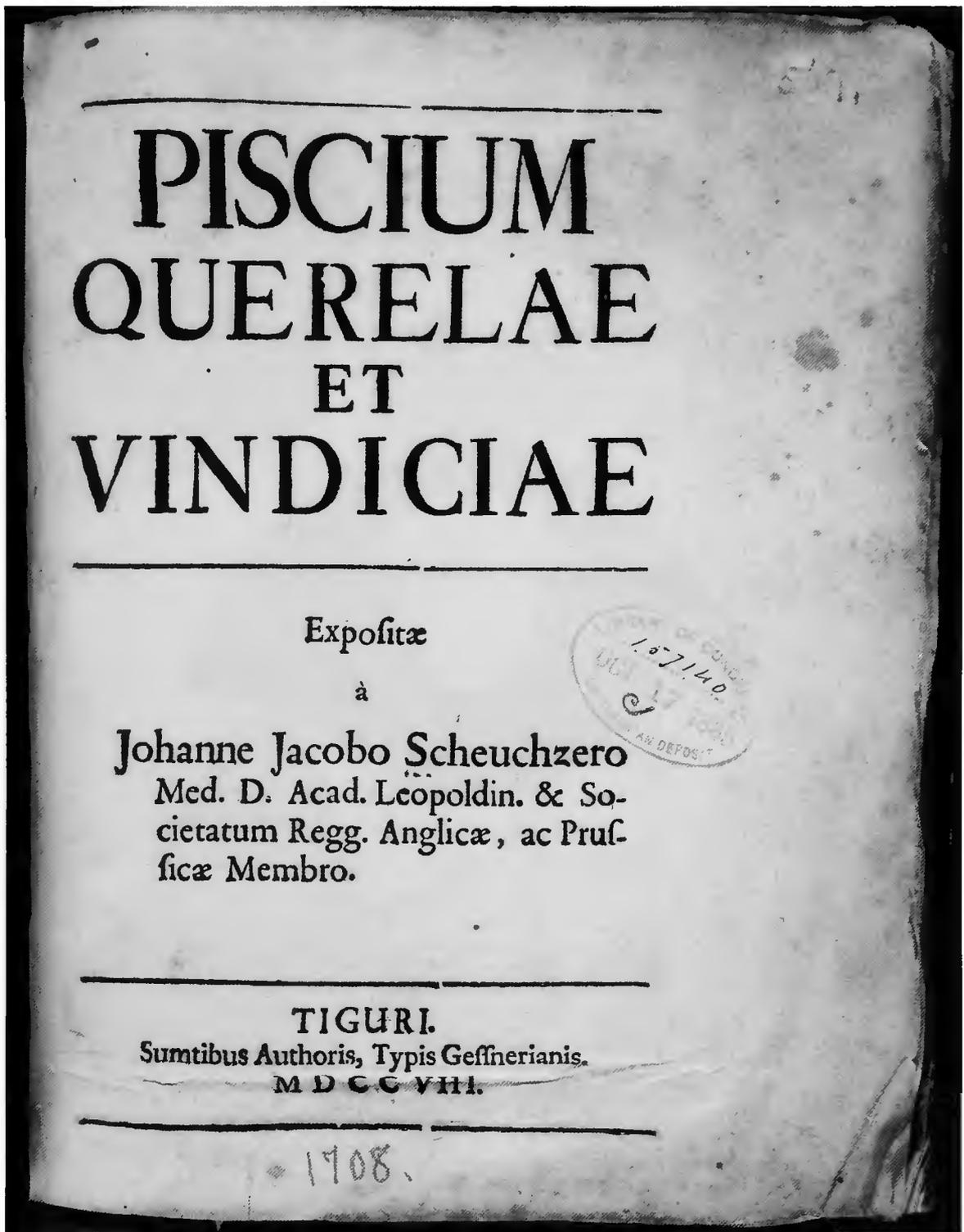


FIGURE 4.—Title page of Scheuchzer's 1708 classic, *Piscium Querelae et Vindiciae* (x1).

teeth and other fossils sent from Maryland by the Revd Hugh Jones" (Thackray, 1994:126). Jones communicated especially with Petiver and sent specimens from Maryland at least from 1696 to 1702, although he became ill in 1700. Jones had gotten

his job as chaplain to the governor of Maryland through the initial recommendation of Lhwyd, furthered by the Temple Coffee House group that included Sloane, Petiver, Doody, Lister, and Robinson (Stearns, 1952:292–294; Jessop, 1989).

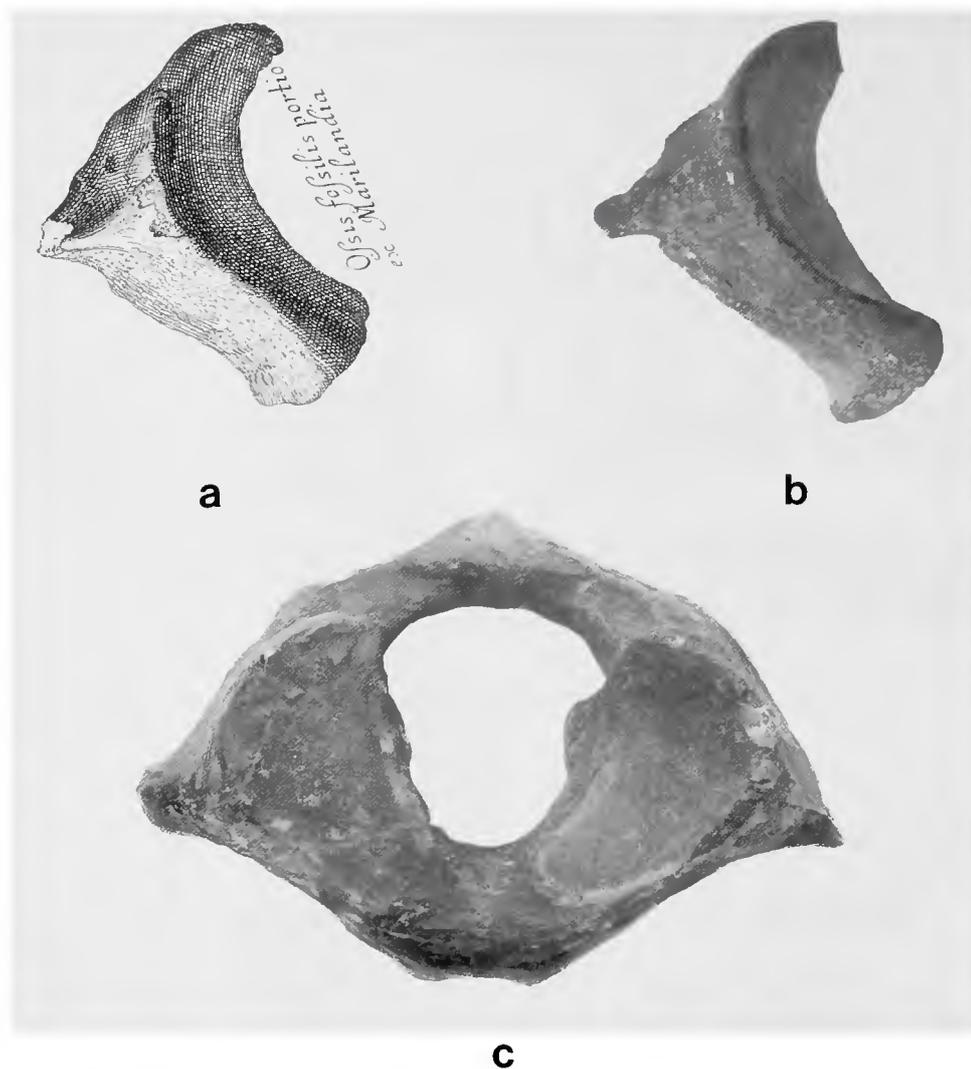


FIGURE 5.—Cetacean atlas vertebrae in cranial aspect ($\times 0.82$), *a*, Scheuchzer's figure reproduced; *b*, similar waterworn fragment, *Lophocetus* sp., probably collected on beach in Calvert County, Maryland, USNM 449525 (National Museum of Natural History, Smithsonian Institution, which houses collections of the former United States National Museum); *c*, complete atlas, Cove Point, Calvert County, Maryland, St. Marys Formation, collected by Francis Markoe, Jr., 1841, part of the holotype of *Lophocetus calvertensis* (Harlan), itself a historic specimen (Gilmore, 1941:311–312, 377; Simpson, 1942:162, 176). (Scale bar=1 cm.)

The second specimen, an incomplete tooth of *Carcharodon megalodon* Agassiz from the Carolinas (Figure 6*a*), is described by Scheuchzer (1708:20) as lacking serrations. The absence of serrations is of no taxonomic significance because the tooth is clearly waterworn and is typical of the rolled specimens so abundant in the lower reaches of several rivers in South Carolina.

Scheuchzer's comparison was to Luid number 1259, a similarly waterworn specimen from the British Crag (Figure 6*c*). The number refers to the collection of Edward Lhwyd, Latinized as Luid, among the many variations of the surname (see Gunther, 1945:vii) (see Roberts, 1989, for a succinct biography), whose specimen survives in the geological collections at the University Museum, Oxford (Powell, in litt., 1993).

Scheuchzer's inferred outline of his incomplete specimen is a very early example of paleontological restoration, however modest.

Jacob (or James) Petiver (?1663–1718), identified as the donor, was a London pharmacist and perhaps second only to Sloane as a natural history collector and letter writer (see Stearns, 1952, for the fullest account of Petiver). Of course, Lhwyd and Woodward outdid Petiver in their geological collections (Torrens, 1985).

Petiver's most productive correspondent in South Carolina was the Rev. Joseph Lord, who began sending him specimens in 1701 and continued at least until 1713 (Stearns, 1952:346, 362). Especially relevant may be Petiver's (1705:1960) account of two fossil shark teeth sent by Lord,

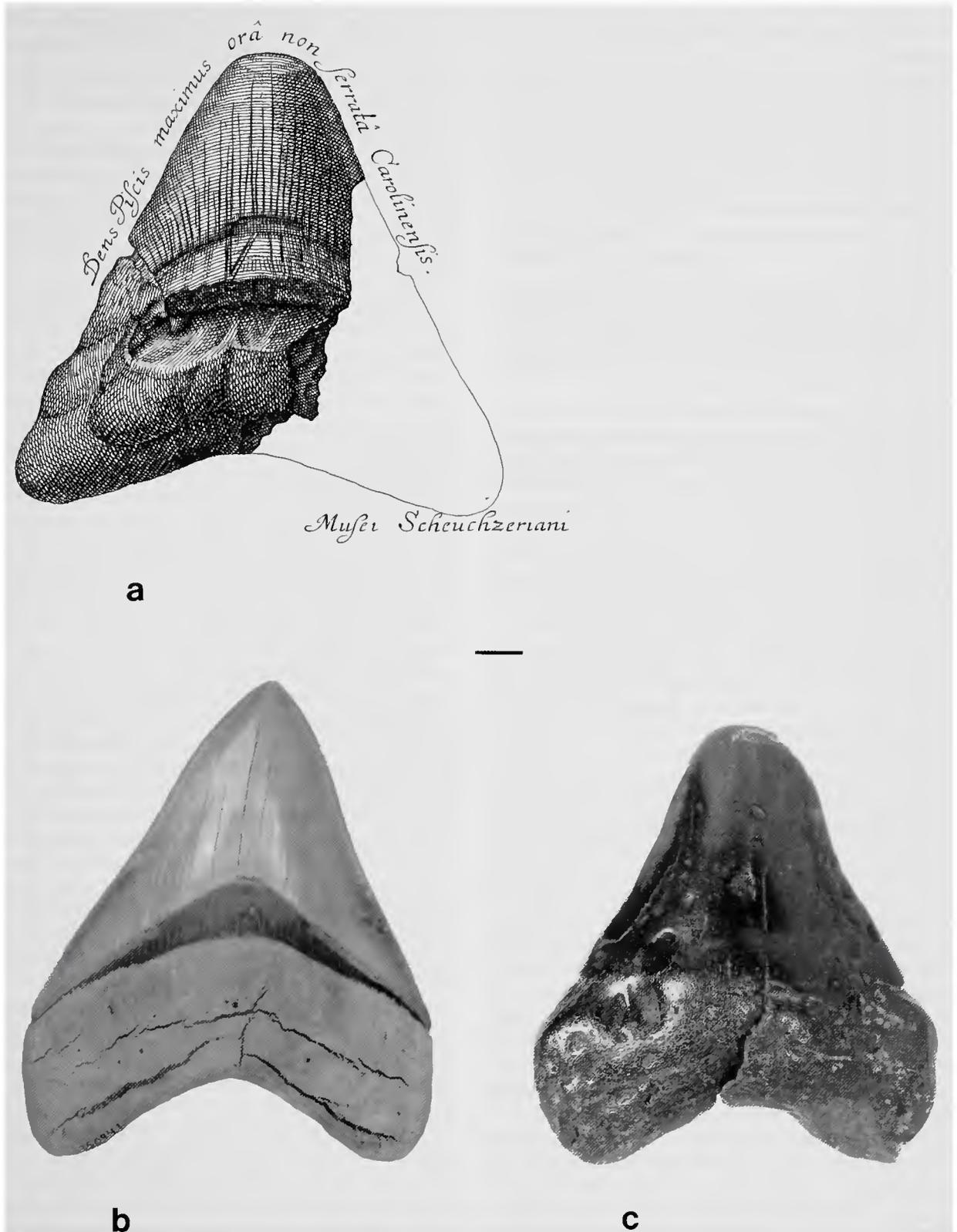


FIGURE 6.—Teeth of *Carcharodon megalodon* ($\times 0.82$), *a*, Scheuchzer's figure reproduced; *b*, well-preserved tooth, showing serrations, collected by P.J. Hamatuk, from Yorktown Formation spoil, Lee Creek Mine, North Carolina, USNM 350941; *c*, waterworn specimen, probably from the bone bed at the base of the Red Crag, Suffolk, England (H.P. Powell, in litt., 1993), Lhwyd collection number 1259, Oxford University Museum, photograph courtesy of Oxford University Museum of Natural History. (Scale bar=1 cm.)

the first of which could possibly be the very one illustrated by Scheuchzer.

Here may be mentioned what is probably the earliest allusion to a fossil of a bony fish from the New World, other than Winthrop's 1636 allusion to "Fishes' bones" from the James River (Ray, 1983:4). In a letter to Petiver from his home at Dorchester (this would have been old Dorchester on the Ashley River), South Carolina, dated 1 September 1707, Lord writes:

Herewith comes a small box with divers Fossils. ... In a part of my land where some were digging after a sort of Marl... a stone was digged, somewhat flat & broad, but looking like ye marl among which it lay, on which was ye tail of a small fish & ye body near as far as ye Navel, of a brown colour, shewing fins & scales very apparently, but all Stone; & it seemed so distinct that I had a conceit I might separate it from ye rest of ye Stone, which I endeavoured to no purpose, but in trying much defaced ye Impress; & since, only lying in my Study made it more obscure: but however I have put it into ye Box.

The letter was marked as received on 26 January 1708, as was presumably the accompanying small box. The original letter is preserved among the Sloane manuscripts (Sloane 4064, folio 150) in the British Library (permission to quote not required; Taylor, in litt., 25 April 1994) as a result of Sloane's having purchased Petiver's papers and collections after the latter's death (Stearns, 1952:244; MacGregor, 1994:23). The fossil fish should have been among the Sloane specimens that initiated the British Museum, but if it survives in the BMNH, it has not as yet been recognized (Thackray, 1994:132).

In striking contrast to the loss or unknown fate of most North American fossils from the colonial era is the survival of those in the Scheuchzer collection and in the incomparable collection of his correspondent, John Woodward (1665–1728), preserved essentially intact, with data, at the University of Cambridge. The essential background to this collection can be learned from Woodward's own catalogs (Woodward, 1728–1729), Gunther (1937:424–433), and especially Price (1989). A measure of its volume and significance can be gained from the catalog entries. The North American fossils are contained in catalogs K and M of Price's notation (1989:93–94; table 1). Of 655 catalog entries for foreign fossils (only fossils in the modern sense, excluding rocks and minerals), 74 are North American; these represent a minimum of 127 of the total 1210 specimens. Thus, the North American material constitutes more than 10 percent of both total catalog numbers and specimens. Of the 127 specimens, 74 are invertebrates, mostly mollusks, and 53 are vertebrates, mostly sharks' teeth. Of the 74 catalog entries, 51 are from Maryland and 23 are from Virginia. Among the Maryland entries, at least 27 are attributed to William Vernon, 18 to Hugh Jones, and three to David Krieg, the three most important names in seventeenth-century natural history collecting in Maryland. Although focused primarily on their botanical collecting, the account of their activities in Maryland by Frick et al. (1987) is a convenient and authoritative source (see also Stearns, 1970:264–274). Jones, as previously noted, spanned the years 1696–1702 but was largely incapacitated for the last two. Vernon and Krieg overlapped almost exactly in their brief visits, during the spring and summer of 1698. There was keen interest and competition, in part unfriendly, among British nat-

uralists for the specimens. Woodward, generally at odds with most of his contemporaries, boasted that "Mr. Doody had given him all or the greatest part of those fossils you [Jones] sent him" (Petiver to Jones, 10 March 1698; quoted in Frick et al., 1987:19; see also Stearns, 1970:265).

Of three catalog entries for Virginia specimens attributed to John Banister, two are explicitly stated to have been given by Doody, clearly a continuing benefactor of Woodward. Banister's collecting could not have been later than 1692, the year of his death (see Ewan and Ewan, 1970, for a definitive account of Banister).

All of the 20 North American entries (19 mollusks, 1 barnacle) in Woodward's additional list (catalog M of Price, 1989) pertain to what was probably a single locality near the James River, 20 miles (~32 km) above its mouth. One specimen was found "by Lyons-Creek" (now Lawnes Creek, reverting to the place names of Christopher Lawne's Plantation, established in 1619), which empties into the James River just below Hog Island, opposite Williamsburg, some 20 miles (~32 km) up the James. All are attributed to a "Mr. Miller," who is probably the Mr. Miller described by Hearne (Salter, 1915:148) as Woodward's "neighbor & particular Acquaintance for 30 years past, who often went abroad with him to gather Fossils, and assisted him often in packing up boxes, to be sent abroad to Professors & curious persons, & presented him himself with a Drawer or two from the West Indies."

With the possible exception of the Miller specimens from the James River, all North American specimens in the Woodward collection were collected prior to 1700. Judging from the identity of the collectors, their time, and Woodward's annotations, it seems highly probable that some of the specimens may have been studied or illustrated by Banister, Lister, Sloane, or contemporaries. Price's valuable studies, cut short by his untimely death, were only just beginning to reveal the value of this unique resource, and it has not been feasible to examine the collection firsthand for the present project. Close study of the specimens with relevant literature at hand could scarcely fail to yield interesting results. Some of the shark teeth have been examined recently by Shelton P. Applegate of the Universidad Nacional Autonoma de México.

The majority of the remaining entries for foreign fossils in Woodward's catalogs (catalogs K and M of Price, 1989) are from the extremely important collections of Scilla and Scheuchzer. Woodward appears to have been meticulous in citing their specimens, but as yet none of his entries for them can be identified as pertaining to North American specimens. The collection should, of course, be searched for them.

The next instance of early collecting that I wish to note is from a letter to Peter Collinson from John Custis of Williamsburg, Virginia, believed to have been written on 28 August 1737. In it Custis alludes to the extreme drought of that summer, which necessitated his digging a deep well to water his garden. The letter is quoted in part from Swem (1957:47):

As you are a very curious gentleman I send you some things which I took out of the bottom of A well 40 feet deep; The one seems to be a cockle petre-

fyd one a bone petrefyd; [this?] seems to have been the under beak of some large antediluvian fowl. Wish they may bee acceptable.

In a letter of 5 December 1737, Collinson thanked Custis for “the Curious Fossils that you sent Mee last year” (Swem, 1957:60); again, in a letter of 5 March 1741 (Swem, 1957:71), Collinson alludes to fossils sent by Custis as “shells that was found so Deep when you was Makeing the Mill Dam.” At least some of these fossils were on exhibit at Mill Hill School, on the site of Collinson’s home, near London, in the early 1930s, but they have been lost sight of since (Swem, 1957:172; Hume, 1994:22). Interestingly, the 1964 archaeological reexcavation of Custis’ 40-foot (~12 m) well in Colonial Williamsburg, Virginia, yielded fossil shells and whale bones (Hume, 1994:20, 22). All of these specimens undoubtedly derive from the Pliocene Yorktown Formation.

John Custis (1678–1749), educated in England, was a prominent citizen of Virginia and an avid horticulturist, which led to his association with Peter Collinson (Swem, 1957:11–20). Collinson (1694–1768) was a successful business man with extensive interests in the American colonies, including a lifelong avocation to botany (Swem, 1957:1–9). He was singled out by Stearns (1951:194–195) as one of the most active fellows of the Royal Society in encouraging North American naturalists. He is perhaps best known in North America in connection with the vertebrate fossils of Big Bone Lick, Kentucky (Jillson, 1936; Simpson, 1943). Although Collinson was especially active in adding to Sloane’s collection (Swem, 1957:3), no evidence has yet emerged to identify any fossils from Custis’ digging in Williamsburg in the surviving collections of BMNH.

Lastly, although much later than the other reports cited herein, I wish to supplement my earlier account (Ray, 1983:6–7) of Latrobe’s 1799 report of vertebrate fossils from Richmond, Virginia, including sharks’ teeth, fish vertebrae, a large bird femur, and a partial porpoise flipper. Latrobe (1809:283–284) returned to this subject as follows:

It was my intention then, to have offered to the [American Philosophical] Society, a series of geological papers, the materials of which I had collected, and of which this memoir [Latrobe, 1799] was the first. But my intention was delayed and partly defeated by the loss of a very large collection of all the principal fossils, necessary to elucidate my observations, in their passage by water, from Fredericksburg to Philadelphia.—This collection, intended for the American Philosophical Society, was made by the industry of my excellent friends, Mr. William Maclure now at Paris, of the late Dr. Scandella whose untimely death in 1798 science and friendship equally have to deplore, and of myself.—It consisted of specimens of loose and undecayed fossil shells, found on and near *the surface*, from the coast to the falls of the rivers of Virginia, of the shell rocks of York river, of the clays with impressions of shells in every fracture, but which shew no remaining evidence of any calcareous matter when subjected to chemical tests; of the exuviae of sea animals*, bones of fishes, sharks’ teeth, marsh mud, fossil wood and coral rock, dug from the deep wells about Richmond, of the marles of Pamunkey and Mattapony, of all the strata of the coal mines on James’s river, of the varieties of the granite of Virginia, of the free stone of James’s river and the Rappahannoc, with the vegetable petrefactions and coal belong to it; and of a variety of miscellaneous fossils. ... The loss of this collection dispirited me, and the occupations of a most labourious profession deprived me of time.

*Drawings of some of the exuviae accompanied my memoir, to which refer.—The bones of the foot there represented, are probably those of a sea tortoise....

Had those collections survived and become available for research in Philadelphia, paleontology of the Atlantic Coastal Plain might have been advanced by some decades. In the same report Latrobe went on to discuss other geologic phenomena including delineation of the fall line and its significance in relation to building stones. He was a practical man whose job at that time was “Surveyor of the Public buildings of the U. States,” (Latrobe, 1809:293), which makes his closing observation (Latrobe, 1809:292) regarding the geologic problems discussed all the more revealing:

It is fortunate that the solution of these aenigmas of nature are of no consequence whatever to our happiness, or of use to our enjoyments.—But the pleasures of investigation, and of *wonder*, the offspring of ignorance, are not without a charm, which often entices the mere speculative philosopher into researches that produce results beneficial to mankind.

We continue to vacillate in the unresolved and unresolvable stress between applied and pure research. In the most recent cycle, support for pure research probably reached a peak in the expansive mood of prosperity during the 1960s, when science could save us. We may hope that the retrenchment of the 1990s, with its demand for quick returns and the rise of pseudoscience, is the nadir of the curve and not the precipitous slope of descent into continuing decay and rejection of science (see Sagan, 1995, especially chapters 14, 23, and 25, and Gross et al., 1996, for timely, accessible examinations of the problem; see Maull, 1997, for an example of the widespread and disastrous confounding of science and scientists by social constructivists).

Conclusions

Review of these additional early publications on fossils from the Atlantic Coastal Plain leads to a few observations of seemingly wider relevance. These may be grouped conveniently for present purposes under the topics of “Firsts” for North America and for paleontology and of “Sharks’ Teeth.”

FIRSTS.—Simpson (1942, 1943) was among the very few practicing vertebrate paleontologists in the modern era to have looked seriously into the early history of the subject in North America. Here, too, should be mentioned the historical research by Helen Ann Warren, under the aegis of Henry Fairfield Osborn (in Osborn, 1931:ix, 1–33), which was similar in content and emphasis, if not in depth, to that of Simpson. Simpson was more than casually involved with preparation of the book (on Edward Drinker Cope) of which Warren’s work was part, overlapped completely with her at the American Museum of Natural History (Osborn, 1931:ix), and may have relied too heavily on her spadework. Be that as it may, he brought together a great deal of scattered information and quite correctly contrasted casual or inconsequent early finds (such as those by early Indians—interesting but not contributing to science) with those that were to become factors in the advancement of knowledge in western culture. In his words, “true discovery [is] that leading by a traceable route, however devious, to eventual elucidation of the problems concerned” (Simpson,

1942:135), and again, “merely seeing a fossil bone or picking it up in idle curiosity is hardly discovery....scientific discovery was that which initiated continuous consciousness and record of the occurrence of fossil animals in America and had the first scientific studies as its sequel” (Simpson, 1943:26–27).

Although these definitions are meaningful, Simpson was mistaken in every instance in applying them toward identification of firsts for North America, thus making his papers not the definitive work that he supposed (Simpson, 1943:26). Taking caution from his example, I do not propose that my candidates are in truth firsts, only that they are the earliest known to me (as indicated, I suspect, even hope, that there are still earlier ones, especially Italian, and thus I believe that the present account is not the last word). It must be emphasized that Simpson provides a large target only because he had the rare insight to see the value of history and the ability to draw so much together from scratch. His well-earned stature and authority make doubly important the correction of his objective errors. Further, those errors reflect what I believe to be a pervasive lack of comprehension among American paleontologists of the sophisticated nature of natural history investigations by western Europeans in the late seventeenth and early eighteenth centuries.

Simpson (1942:131) defined six periods in the history of vertebrate paleontology in America, the first two of which are of interest here.

1. *Pre-scientific Period*.—From the earliest times to about 1762. The first fossil discoveries were made. Toward the end of the period bones were collected and sent to Europe. No truly scientific study of them had been made.

2. *Proto-scientific Period*.—From about 1762 to about 1799. In 1762 Daubenton read a paper on American fossils treating them for the first time in what deserves to be called a scientific way.

In reference to Lord’s 1707 letter to Petiver about the fossil fish tail (see “Some Early Records,” above) Simpson stated (1942:135), “The incident is... unique for its date, and for a long time there after, in involving a *small* fossil vertebrate. Most of the eighteenth century naturalists overlooked bones of animals smaller than the mastodon. ...” Simpson (1943:27) regarded letters from Cotton Mather as the “first publication on American fossil vertebrates” (published in 1714 in the Royal Society’s *Philosophical Transactions*), and Simpson thought they probably were based on mastodon remains. In allusion to Catesby’s 1743 report of African slaves’ recognition of fossil proboscidean teeth, Simpson (1942:134) credited them with the “first technical identification of an American fossil vertebrate,” assuming the incident to have occurred prior to 1739. Based on the collection from Big Bone Lick, primarily of mastodon remains, Simpson stated (1942:135), “If Columbus discovered America in 1492, Charles Le Moyne, second Baron de Longueuil, discovered American fossil vertebrates in 1739.” Simpson (1942:144–145) added that “Guettard (1756, read in 1752) published the first illustration of an American vertebrate fossil... [and] a decade later Daubenton (1764, read in 1762)... [provided]... an excellent example of the comparative method... one of the four most basic... principles in the rise of

vertebrate paleontology and it may fairly be dated from Daubenton....” Both Guettard’s and Daubenton’s contributions stemmed from the 1739 Longueuil collection of mastodon remains.

Both Sloane (1697) and Scheuchzer (1708) conspicuously antedate Guettard for the first description and illustration of North American fossil vertebrates. Sloane’s paper in particular meets every possible criterion: the fossils reported were collected through a purposive scientific program (about which more beyond); Sloane was among the most prominent natural historians of his or any other era; he published in the premier scientific journal in English; his title alone reveals the significance of his subject; the specimens are small, and at least one survives today; and the paper is a model of comparative methodology.

The larger point to be emphasized is the nature of the natural history enterprise in western Europe in the late seventeenth and early eighteenth centuries, for present purposes especially in England, and especially centered among fellows of the Royal Society. Their sustained, intensive, extensive interest in North America is well recognized and is woven into the modern literature of zoology and especially of botany (Stearns, 1970, and Frick et al., 1987, are superb examples) but is reflected hardly at all in that of paleontology (among notable exceptions is Gernon et al., 1987), especially of vertebrates.

There was nothing in the least casual or chancy in the collection of North American fossils; rather, they resulted from a purposive campaign. In fact, it is a little surprising that the results were so meager for fossils in light of the effort expended. Much of the voluminous correspondence of Sloane, Petiver, Woodward, and others was devoted to creating and maintaining a network of collectors, not least in the New World.

A very good taste of the flavor of time and place can be had from Stearns’ (1952:293–303) account of how the group cooked up a collector in cleric’s clothing. The Bishop of London, in 1694, sought advice from Martin Lister in recommending a candidate for chaplain to the governor of Maryland. This eventuated in Edward Lhwyd’s putting forward his assistant, Hugh Jones, whose specific qualification was that he would be a worthy successor to John Banister. Jones was groomed in natural history, run hastily through religious orders, and rushed off to Maryland. Besides Lister and Lhwyd, James Petiver, Samuel Doody, Jacob Bobart, and Tancred Robinson are known to have had specific roles in the care and feeding of Jones; Petiver quite literally—besides equipment, supplies, and literature, he sent Jones a cheshire cheese and English beer, plus medicine and medical advice (Stearns, 1952:297, 299, 303).

John Woodward (1696) provided “brief instructions” to geological collectors (see Eyles, 1971:403; Price, 1989:93, footnote 7). Petiver also prepared instructions, which were sent out with travellers and to correspondents. These were highly sophisticated, even to the point of recommending the stomach contents of sharks, and other great fish, as a source of “divers strange animals not easily to be met with elsewhere” (Stearns,

1952:363). As to fossils (his “formed Stones), Petiver instructed, “These must be got as intire as you can, the like to be observed in marbled Flints, Slates, or other Stones, that have the Impression of Plants, Fishes, Insects, or other Bodies in them; these are to be found in Quarries, Mines, Stone or Gravel Pitts, Caves, Cliffs, and Rocks, on the Sea shoar, or wherever the Earth is laid open” (Stearns, 1952:364).

Thus, these natural historians knew exactly what they wanted and devoted much thought, energy, and money toward getting it. Much of their massive correspondence concerns details of instructing, inducing, exhorting, even bribing others to collect (e.g., see MacGregor, 1995, on Sloane’s correspondence and Stearns, 1952, on Petiver’s).

SHARKS’ TEETH.—Sharks’ teeth are the quintessential enigmas of nature, whose charm has inspired wonder, and finally researches, more widely and continuously than perhaps any other fossil. It would scarcely be possible to overemphasize their importance in cutting-edge debate on the meaning, nature, and definition of fossils in the sixteenth and seventeenth centuries. As indicated earlier, Rudwick (1976) has done a masterful job in laying out the major features of the story as it unfolded in the pioneering works of Colonna, Scilla, Steno, and Hooke; these need not be retold, but some essential points may be emphasized.

First, “fossil” continued for many years to encompass almost any, usually natural, object “dug-up” from the earth, notably mineral specimens. “Figured stones” was a common term for what we now understand as fossils. Until there was general acknowledgment that objects resembling living animals or plants actually were remains of once-living things, there was no logical basis to require a distinction from other interesting things dug up.

Sharks’ teeth, as glossopetrae or tongue-stones, were widely and deeply embedded in European pre-scientific culture, emanating especially from Malta, where the fossils are abundant and are conveniently intertwined with the religious and magical lore of St. Paul, serpents, and poison (for a sampling of this lore, see Zammit-Maempel, 1975, 1989, and Bassett, 1982).

From our present god-like heights of sophistication we have tended to dismiss the seeming wrongheaded reluctance to recognize sharks’ teeth and other fossils for what they are as the ridiculous ignorance of benighted times; however, these gentlemen were no simpletons but rather the greatest minds of that or any other age. Even after presentation of the careful, logical arguments of Steno and Hooke, widely circulated in the Royal Society, that community of scholars did not rise as one in acceptance. Instead, the subject was hotly contested for some 30 years before being laid to rest pretty much by the early 1700s. Grew, Hooke, Lhwyd, Woodward, Ray, Lister, Newton, and Scheuchzer all weighed in on the issue (e.g., see Stokes, 1969). Some, including Hooke, Woodward, and Scheuchzer, were decisive in their support of organic origin. In this group only Lister was adamant in his opposition. His views have been characterized as ridiculous in hindsight, but his problem, in part, may

have been that he knew too much. Lister knew mollusks as perhaps none other of the time, and demanded, but did not find, exact correspondence between fossil and living forms. He was no fool—witness his coming close to “inventing” geologic mapping (Lyons, 1944:99; Stearns, 1970:168). He might well be the Agassiz to Hooke’s Darwin in this debate. Further, recognition of fossils as such created serious problems in the frame of reference of the time. From it followed almost inevitably the problem of extinction of forms without modern counterpart, and this was unacceptable in a perfectly economical universe, whether divine or natural. It was in relation to this problem that fossil and modern natural history specimens from far off places, such as America, held special appeal. Locally extinct organisms might well survive elsewhere.

With the possible exception of Lister, it might be observed that the practices of those who equivocated on the nature of fossils made sense only if they in fact accepted their organic origin. For example, Grew (1681:257) extrapolated (pretty successfully) on the size of shark (36 feet; ~11 m) from which large glossopetrae originated; Sloane’s (1697) paper on ray teeth was based solidly on comparative methodology—his perfunctory allusion to God’s wisdom seems all too much like covering his flank. One is tempted to suspect persistence of a certain measure of accommodation to authority through lip service while proceeding operationally on the basis of persuasive new insights.

Another fascinating aspect in which sharks’ teeth illustrate how scientific discovery works is the fact that Steno, Scilla, Hooke, and Woodward were essentially coeval in their researches. Barring some more persuasive evidence of intellectual piracy than has thus far materialized, the interesting point is that this was an idea whose time had come. Hooke was a great and wide-ranging idea man, and there is no need to detract from his astounding originality. His geologic insights and priorities have at last been well presented (Drake, 1996). Nevertheless, he clearly had a tendency toward jealousy of priority—whatever the topic, he thought of it first (which contributed strongly to his irreparable schism with Newton). Even if Steno was aware of Hooke’s and/or Scilla’s ideas, he has to be accorded primacy because he developed the idea fully with step-by-step logical procedure, which has been brought out best by Scherz (1969, 1971). Woodward clashed with almost everyone, was a thoroughly unsympathetic character, and was accused of pirating Scilla’s ideas, but he probably was not a plagiarist (Jahn, 1972:210) (useful and accessible insights into Woodward’s activities and character may be found in Eyles, 1971, and Levine, 1977).

Another great truth illustrated by this history is that discoveries do not stay discovered; they must be tended like a garden. Scilla (1670) illustrated what turned out to be the first known specimen of a sharktoothed porpoise, family Squalodontidae, a nice piece of a mandible with three teeth. This historic specimen, preserved in the Woodward Collection at Cambridge, has since been the object of repeated attention in the paleontologi-

cal literature of the modern era. Although first formally described as a seal, and in one aberrant view regarded as a hippopotamus (Owen, 1840–1845:564–565, pl. 142: fig. 3), it has long since become securely and correctly embedded in the literature as a squalodont cetacean, the holotype of *Squalodon melitensis* (Blainville), where it has been alluded to and figured repeatedly (e.g., see McCoy, 1867:145; Kellogg, 1923:24; Gunther, 1937:433, unnumbered figure, p. 432; Fabiani 1949:26–29, figs. 9, 10; Rothausen, 1968:92). Then, in 1992, Gould (in Purcell and Gould, 1992:93–94, figs. 64, 65) misidentified the specimen as the jaw of a shark, invalid support for the valid interpretation of glossopetrae. Although as always we have a duty to correct objective mistakes, especially by contemporary and influential authorities (I wrote to Gould immediately upon discovering the error, 8 March 1993), the significant point is hardly that even the greatest living spokesperson for paleontology to the world at large is fallible, but that approach to truth is a fragile dynamic that requires continual vigilance. There may be some validity to Gould's (1996:110) claim that "persistent minor errors of pure ignorance are galling to perfectionistic professionals," but this has no bearing on the overriding requirement that each professional strive assiduously to get things right and never knowingly let even "minor errors" persist.

Finally, the history of sharks' teeth in relation to humans is a powerful cautionary tale against fashion in science. Fortunately, people in general have maintained a seemingly innate curiosity and interest in them throughout time. In professional paleontology, however, when I was a student some four decades ago at a prestigious university, only a naive beginner would risk being labelled childish, or worse, "amateurish," by betraying any interest in sharks' teeth (or dinosaurs). Now dinosaurs are the hottest topic in vertebrate paleontology, and even sharks are respectable subjects of investigation (Klimley and Ainley, 1996). Scientists are probably no more foolish as a group than the citizenry at large in lurching to extremes, but they may tend to appear so in retrospect because they put extreme views on record in emphatic terms. More reflective attention to the history of our science would undoubtedly tend to mitigate our most embarrassing emanations and perhaps damp down fadism. I hope that these few modest historical nuggets are enough to persuade readers that ancient specimens, many lost or mislaid, and the thinking and writing surrounding them are not mere quaint curiosities but are landmarks that can and should have meaning today.

Secord (1996:459) has made a forceful case for the value of history not merely as entertainment or nostalgia but as an active force in research, concluding:

Rather, a bold enquiry into the past can uncover the basic structures and large-scale patterns of change which lie behind our current dilemmas. We have inherited not just our institutions and practices, but our problems: and these can only be understood as products of history. A new culture of natural history will flourish only if it is effectively rooted in—and draws upon—a critical understanding of the past.

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Analysis and New Records of Billfish (Teleostei: Perciformes: Istiophoridae) from the Yorktown Formation, Early Pliocene of Eastern North Carolina at Lee Creek Mine

Harry L. Fierstine

ABSTRACT

Five species of the billfish family Istiophoridae (*Istiophorus platypterus* (Shaw and Nodder), *Makaira indica* (Cuvier), *M. nigricans* Lacépède, *M. purdyi* Fierstine, *Tetrapturus albidus* Poey) were identified from approximately 500 separate bones collected in the Yorktown Formation (early Pliocene) at Lee Creek Mine, North Carolina. This is the only record of *M. purdyi*, the first fossil record of the genus *Tetrapturus* (specifically *T. albidus*), the second fossil record of *I. platypterus* and *M. indica*, and the first record of *I. platypterus*, *M. indica*, *M. nigricans*, and *T. albidus* from fossil deposits bordering the Atlantic Ocean.

Identification was accomplished by converting length and width measurements of individual fossil elements to ratios (proportions), treating them as variables, and comparing them to ratios computed from a large series of bones from extant istiophorid species. Ratios of a fossil specimen that fell outside the range of ratios computed for extant species, or that were equivocal as to genus or species, were identified as one of the following: Istiophoridae, genus and species indeterminate; *Istiophorus* cf. *I. platypterus*; *Makaira* cf. *M. indica*; *M.* cf. *M. nigricans*; *M. purdyi*; cf. *Makaira* sp.; or *Tetrapturus* cf. *T. albidus*. Fifty-three percent of the fossil elements were identified as Istiophoridae, genus and species indeterminate, or as *M. nigricans*.

Significant differences ($P < 0.05$) exist between the prementary, rostrum, scapula, and vertebrae 1 and 23 of extant *Makaira nigricans* and *M. nigricans* from Lee Creek Mine. Features at the extremely significant level ($P < 0.001$) are prementaries that are deeper and rounder, rostra that have rounder cross sections and more ventrally placed nutrient canals, and first vertebrae that have a narrower transverse diameter anteriorly.

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A review of the natural history and zoogeography of the extant Istiophoridae was used to draw inferences about Lee Creek billfish. The presence of *Makaira indica* at Lee Creek Mine suggests that the Panama seaway may have been a migration route for billfish during the early Pliocene. The concentration of billfish at the mine supports the contention that the Yorktown Formation represents a tropical to warm temperate (21°–28°C) oceanic environment that was deposited at depths greater than 100 m. Using the width of the rostrum as an estimate of body size, *M. nigricans* at Lee Creek Mine probably had a sex ratio of a nonspawning population; therefore, I hypothesize that by Yorktown time *M. nigricans* had already established the present pattern of migrating northward in the western North Atlantic Ocean during the summer to feed after spawning in more southern waters.

The fossil history of billfish relevant to the Lee Creek Mine fauna is reviewed and in some cases specimens are reidentified. The family Istiophoridae has a fossil history from the middle Miocene to recent, with the qualification that "*Istiophorus*" *solidus* (Van Beneden) (late Eocene, Ghent, Belgium) may be an istiophorid. *Makaira belgicus* (Leriche) (middle Miocene, Anvers, Belgium), *I.* cf. *I. platypterus* (late Miocene, Eastover Formation, Virginia, United States), and *Tetrapturus albidus* (early Pliocene, Yorktown Formation, North Carolina, United States) are the oldest known species within their respective genera.

Introduction

Lee Creek Mine, located near Aurora, Beaufort County, eastern North Carolina, is a large phosphate deposit mined by Texasgulf, Inc. The Yorktown Formation (early Pliocene) at the mine has yielded the world's largest collection of fossils of the family Istiophoridae (billfish). Billfish are usually found as partial remains of one or two individuals at any one site (numerous references in Fierstine, 1990, and Schultz, 1987), but at Lee Creek Mine approximately 500 separate bones have been

collected (mostly segments of rostra and vertebral centra). Based on past studies, the fragmentary nature of Lee Creek specimens would be expected to contribute little to our knowledge of extant billfish. Recently, however, Fierstine and Voigt (1996) examined intra- and interspecific variation in recent billfish skeletons and demonstrated that adult billfish could be identified using rostral characters alone. They suggested that their technique of identification could be applied to partial rostra, whether fossil or recent. Herein I employ methods described in their paper to establish the presence of four species of extant billfish among the skeletal elements at Lee Creek Mine and to relate these data to the natural history and zoogeography of living billfish species.

ACKNOWLEDGMENTS.—Without the contributions of many visionary amateurs, especially Peter Harmatuk and Becky and Frank Hyne, who donated fossil specimens to the National Museum of Natural History (NMNH; containing collections of the former United States National Museum (USNM)), Smithsonian Institution, there would have been few specimens to study. R. Bisbee and family were gracious hosts during the 1995 Bisbee Black and Blue Marlin Tournament, Cabo San Lucas, Baja California Sur, Mexico. Special thanks are extended to the following individuals for allowing examination of specimens in their custody: B. Brown (American Museum of Natural History), D. Catania (California Academy of Sciences), R. Feeney (Los Angeles County Museum of Natural History), S. Jewett (NMNH), M. McGroutner (Australian Museum, Sydney), R. Purdy (NMNH), R. Rosenblatt (Scripps Institute of Oceanography, University of California, San Diego), V. Schneider (North Carolina State Museum), and J.D. Stewart (Los Angeles County Museum of Natural History). R.E. Weems (United States Geological Survey, Reston, Virginia) and L.W. Ward (Virginia Museum of Natural History, Martinsville) provided valuable information on the collection site of *Istiophorus calvertensis* Berry (= *I. platypterus*). R. Purdy led me on an informative field trip to Lee Creek Mine and was exceedingly helpful in sending me specimens and references and in keeping me informed on various aspects of the Lee Creek Mine project. M. Gottfried (Michigan State University Museum), J.D. Stewart (Los Angeles County Museum of Natural History), and D. Tyler (Smithsonian Institution Press) made valuable suggestions on an earlier version of the manuscript. L.G. Barnes (Los Angeles County Museum of Natural History) reviewed part of the paleogeographic section and brought *Metaxytherium arctodites* Aranda-Manteca, Domning, and Barnes to my attention. Finally, A. Fierstine deserves special recognition for her assistance and encouragement throughout this study.

MATERIALS AND METHODS

Following Fierstine and Voigt (1996), I use the scientific and common names of Robins et al. (1991) for recent species of fish, the institutional abbreviations of Leviton et al. (1985), and

a combination of the osteological terminology of Davie (1990), Gregory (1933), Gregory and Conrad (1937), Jollie (1986), Rojo (1991), and Schultz (1987). Linear measurements of bones or structures were made to the nearest 0.5 mm with dial calipers or metric rule.

LEE CREEK MINE SPECIMENS.—Billfish fossils were collected primarily by amateurs over the past 20 years from the weathered surface of spoil windrows from zones 1 and 2 (Yorktown Formation), a by-product of dredging operations. Gibson (1983) concluded that both zones were deposited in early Pliocene time, and Hazel (1983:97) dated both zones at 4.4–5.0 Ma based on planktonic foraminifers and radiometric dating of a stratigraphically equivalent site. Zone 1 contains sediments of open marine, inner- to middle-shelf environments that were deposited at depths of 80 to 100 m, and zone 2 contains sediments of regressive, marginal marine environments that accumulated at 30 m or less (Gibson, 1983).

Approximately 500 individual elements were examined, including 183 vertebrae (mostly centra), 97 rostral fragments, 51 prementaries, 30 scapulae, 28 quadrates, 26 first pectoral rays, 21 maxillaries, 18 articulars, 17 dentaries, 13 parasphenoids, six epurals, four pterygiophores, two median-fin spines, and one vomer. The material is housed at NCSM and NMNH.

RECENT COMPARATIVE SPECIMENS.—Whole and partial skeletons were examined. The number of specimens studied, their size range (length from lower jaw to fork of caudal fin, in mm), and the general collecting locality for each species are as follows. Sailfish, *Istiophorus platypterus* (Shaw and Nodder): 29 (1437–1830) western Atlantic Ocean, 16 (1770–2175) eastern Pacific Ocean, 5 (1365–2025) off eastern Australia; black marlin, *Makaira indica* (Cuvier): 3 (2457–3054) eastern Pacific Ocean, 8 (1325–2120) off eastern Australia; blue marlin, *Makaira nigricans* Lacépède: 41 (1727–3283) central Pacific Ocean, 1 (3280) Indian Ocean, 11 (2210–2432) western Atlantic Ocean, 1 (size and locality unknown); white marlin, *Tetrapturus albidus* Poey: 21 (1530–1765) western Atlantic Ocean; shortbill spearfish, *Tetrapturus angustirostris* Tanaka: 5 (1486–1619) central Pacific Ocean; striped marlin, *Tetrapturus audax* Philippi: 11 (1924–2463) eastern Pacific Ocean, 1 (2500) off eastern Australia, 2 (2420–2650) off New Zealand, 1 (1990) Indian Ocean, 1 (size and locality unknown); Mediterranean spearfish, *Tetrapturus belone* Rafinesque: 1 (size unknown) Mediterranean Sea; longbill spearfish, *Tetrapturus pfluegeri* Robins and de Sylva: 3 (1690–1740) western Atlantic Ocean. The material is housed at the following institutions: AMNH, AMS, CAS, GMBL, LACM, NCSM, UF, and NMNH.

FOSSIL COMPARATIVE SPECIMENS.—The museum number, osteological material, geological age, and locality are given in the text for each relevant, non-Lee Creek Mine fossil specimen. The material is housed at The Natural History Museum, London (which houses collections of the former British Museum (Natural History) (BMNH)), IRSNB, LACM, MNHNP, UCMP, and NMNH (collections are cataloged under USNM numbers).

CHARACTERS

The characters and their definitions for each bone or structure are as follows.

ARTICULAR (Figure 1a,b).—Five characters occur in the region of the socket (main jaw joint) for articulation with the quadrate bone: length from the anterior margin of the socket to the posterior edge of the articular (ASM); length of the socket from its anterior to its posterior margin (AL); length from the apex of the socket to the posterior margin of the socket (AAL); width of the socket region from the medial process to the outer margin of the socket (ATW); and width of the socket proper (AW).

DENTARY (Figure 2a).—Two characters are in the region of the interdental joint: depth from the anteriormost denticles perpendicular to the ventral margin of the dentary (not to the distalmost margin of the dentary, which often has a projection) (DAD); and length of the interdental joint from the mandibular foramen to the anteriormost denticles (DJL).

FIRST PECTORAL-FIN RAY (Figure 2e).—Two characters occur on the surface of the first pectoral-fin ray that articulates with the scapula: greatest width from the outer margin of the flange to the outer margin of the ray (FW); and width of FW that crosses the scapular facet (FAW).

MAXILLA (Figures 1e,f, 3a,c).—Five characters occur in the “triangular region” that articulates with the nasal, premaxilla,

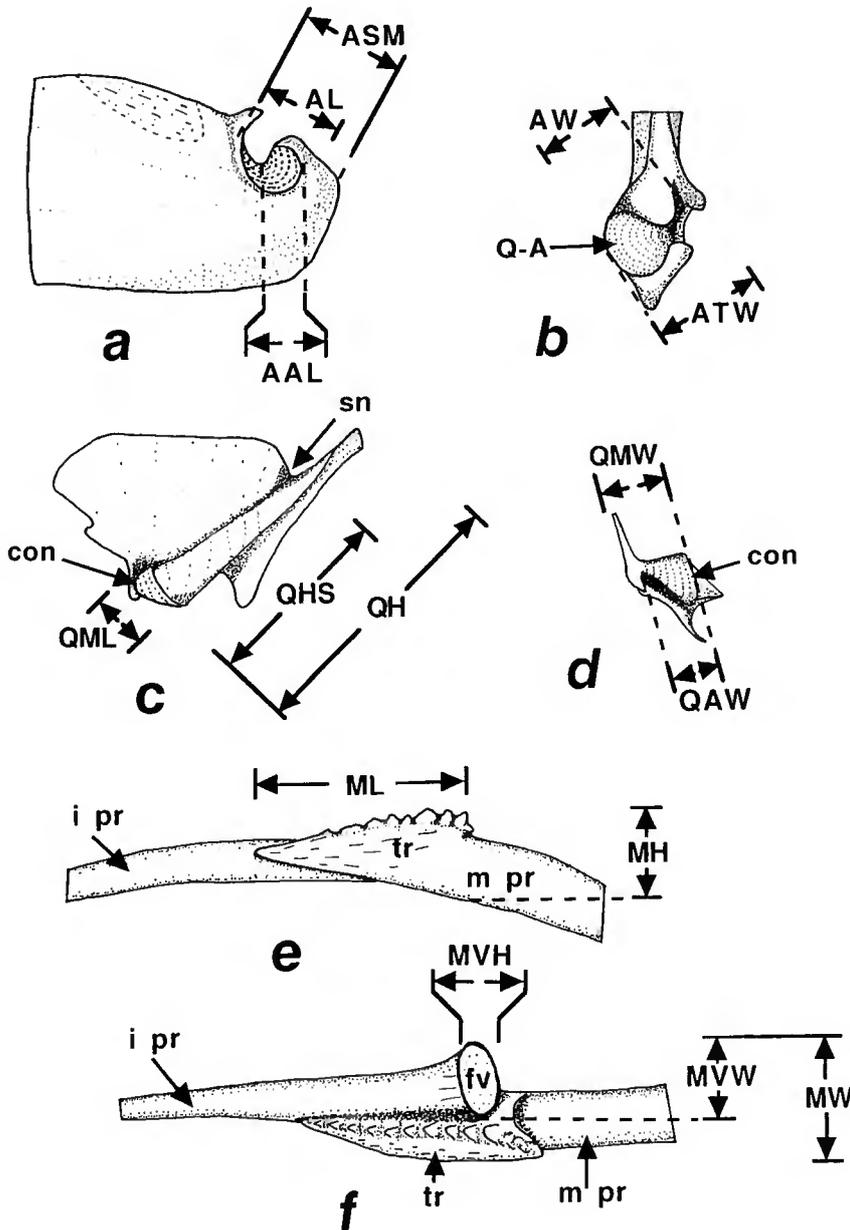
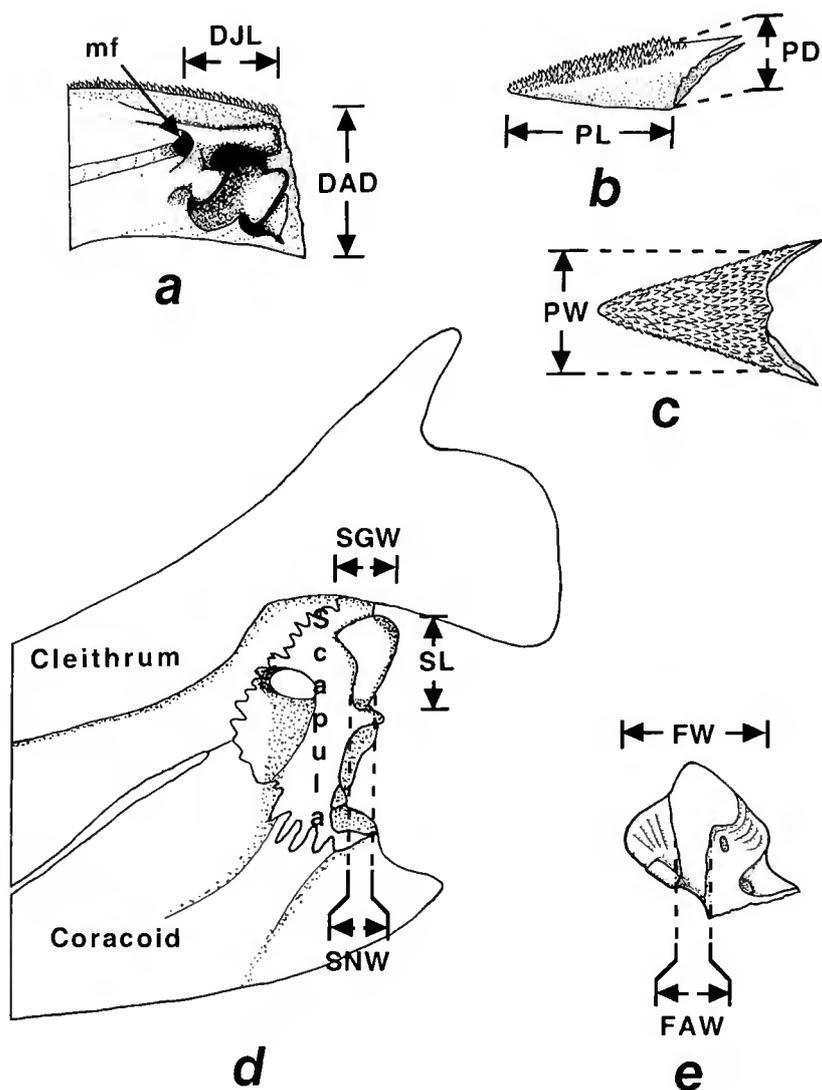


FIGURE 1.—Bones of a generalized istiophorid: *a*, left articular, lateral view of posterior region; *b*, left articular, dorsal view of joint with quadrate; *c*, left quadrate, lateral view; *d*, left quadrate, ventral view of joint with articular; *e*, left maxilla, lateral view of triangular region; *f*, left maxilla, dorsal view of triangular region. Abbreviations: con=condyle, fv=facet for articulation with vomer, i pr=internal process, m pr=maxillary process, Q-A=socket of quadrate-articular joint, sn=symplectic notch, tr=triangular region of maxilla. See “Characters” for definition of other abbreviations.

FIGURE 2.—Bones of a generalized istiophorid: *a*, left dentary, medial view of interdentary joint; *b*, predentary, left lateral view; *c*, predentary, dorsal view; *d*, left pectoral girdle, lateral view emphasizing articular surface for first pectoral-fin ray of scapula; *e*, left first pectoral-fin ray, proximal view emphasizing articular facet for scapula. Abbreviation: mf=mandibular foramen. See “Characters” for definition of other abbreviations.



prenasal, and vomer bones: length of the “triangle” (ML); height of the triangle (MH); width from lateral surface of the triangle to the medial margin of the facet for articulation with the vomer (MW); and height (MVH) and width of the facet (MVW) for the vomer.

Although the maxilla in whole specimens is an elongate bone with an anteromedially projecting internal process and a posterolaterally projecting maxillary process, only the triangular region was preserved in Lee Creek specimens.

PARASPENOID (Figure 5*a,b*).—Four characters are in the central region: distance between the left carotid foramen and the orbital margin of the left dorsal wing (PAF); width between the carotid foramina (PAFW); depth between the ventral margin of the parasphenoid and the notch posterior to the basisphenoid process (PAD); and narrowest width of the anterior process (PAW).

PREDENTARY (Figure 2*b,c*).—Three characters were measured: length along the ventral midline (PL); width across the

widest expanse of the denticulated surface (PW); and depth perpendicular to the long axis from the widest expanse of the denticulated surface to the ventral surface of the bone (PD). The posterior extensions of the predentary usually form wing-like processes that are wider than PW, but because the extensions often are missing in the fossils and broken in the recent specimens, this measurement was omitted.

QUADRATE (Figure 1*c,d*).—Five characters were measured: greatest height from the condyle for articulation with the articular to the tip of the dorsal process (QH); height from the condyle to the notch for the symplectic bone (QHS); greatest width (medial to lateral) in the region of the condyle (QAW); width of the condyle (QMW); and length of the condyle (QML).

ROSTRUM (Figures 3, 4).—Rostra were measured according to the methods of Fierstine and Voigt (1996). Two regions were emphasized in recent specimens: 0.5L, or one-half the distance between the distal tip and the orbital margin of the lat-

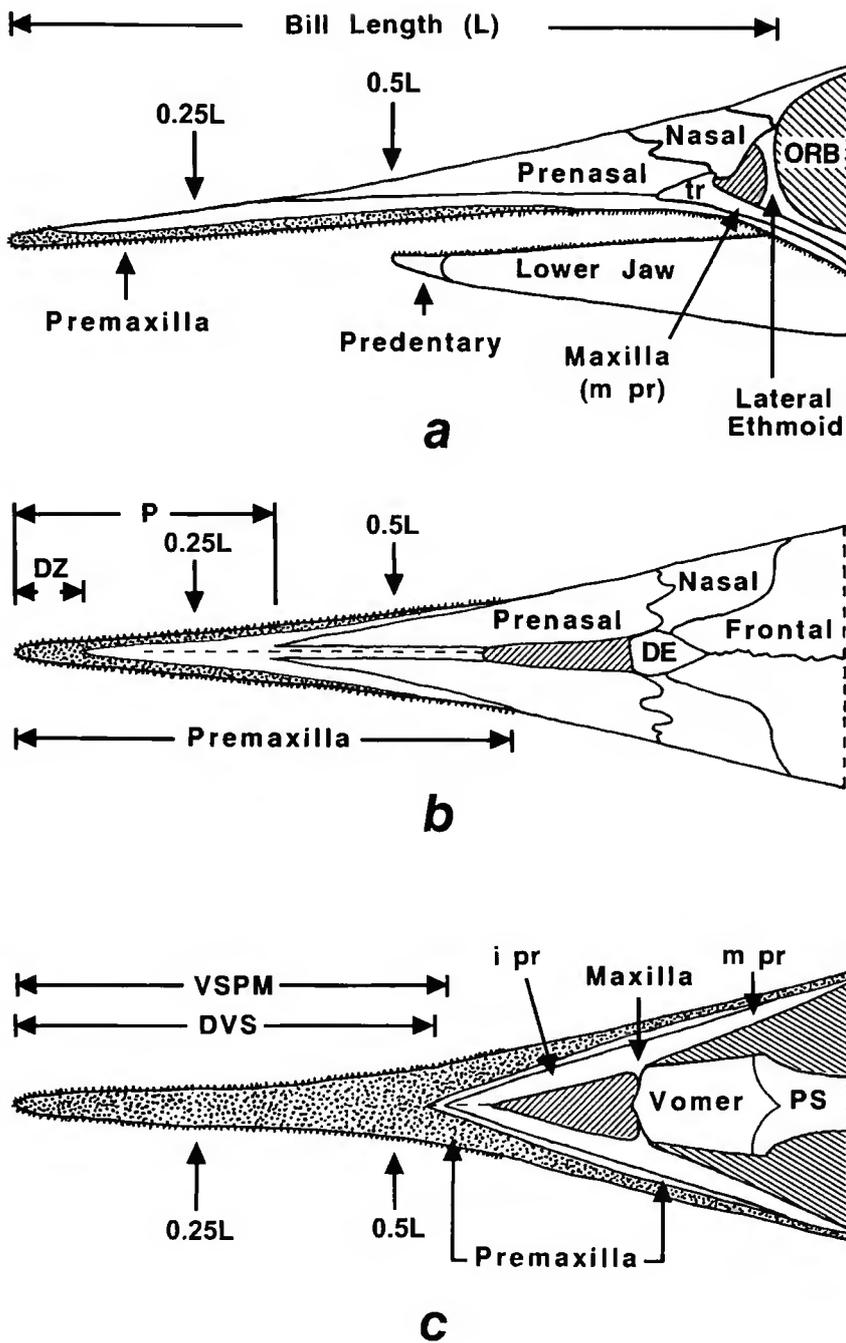


FIGURE 3.—A generalized istiophorid rostrum (modified from Fierstine and Voigt, 1996): *a*, left lateral view; *b*, dorsal view; *c*, ventral view. Abbreviations: DE=dermethmoid bone, i pr=internal process, m pr=maxillary process, ORB=orbital region, PS=parasphenoid bone, tr=triangular region of maxilla. See "Characters" for definition of other abbreviations.

eral ethmoid bone, and 0.25L, or one-fourth the distance between the distal tip and the orbital margin of the lateral ethmoid bone. Characters studied (Figures 3, 4) in each region (0.5L and 0.25L, respectively) were depth (D1, D2) and width (W1, W2) of the rostrum, height (H1, H2) of the left nutrient canal (as seen in cross section), and distance (DD1, DD2) of the nutrient canal from the dorsal surface (as seen in cross section). Characters studied without reference to region were distribution of denticles on the dorsal surface of the rostrum measured from the distal tip (DZ), length from the distal tip of the ro-

strum to the distal extremity of the prenasal bone (P), presence or absence of denticles on the prenasal bone, and length from tip to where the fused premaxillaries divide (VSPM) into separate bones.

In Lee Creek Mine specimens, the exact position of 0.5L or 0.25L was unknown, and cross sections were studied at the broken end(s). No transverse cuts were made. Using the technique of Fierstine and Crimmen (1996), a cross section was estimated to be at 0.5L if the prenasal bone was large and to be at 0.25L if the prenasal bone was tiny or absent. Characters

studied in each estimated region were identical to those studied in recent species.

SCAPULA (Figure 2*d*).—Three characters occur on the surface that articulates with the first pectoral-fin ray: length from the flange to the dorsal margin (SL); greatest width (SGW); and narrowest width (SNW). The articular surface also was judged to be “flat” or “curved.”

VERTEBRAE (Figures 5*c–f*, 6).—All members of the Istiophoridae have 24 vertebrae, with the genera *Istiophorus* and *Tetrapturus* having 12 precaudals and 12 caudals and the genus *Makaira* having 11 precaudals and 13 caudals (Nakamura, 1983, 1985). Most vertebral remains from Lee Creek Mine are incomplete, consisting only of centra without processes. Each vertebra's general position in the vertebral column (e.g., anterior or posterior caudal) usually can be determined, but not its specific position (e.g., first caudal). In contrast, the first, twenty-second, twenty-third, and twenty-fourth (hypural) vertebrae are distinctive enough to be identified consistently among the fossil vertebrae and, therefore, were chosen for detailed examination.

Eight characters occur on the first, twenty-second, and twenty-third vertebrae (Figure 5*c–f*): length from the anterior edge to the posterior edge of the centrum (CL); length from the anterior edge of the centrum to the anterior margin of the spinal foramen (AS); length from the posterior edge of the centrum to the posterior margin of the spinal foramen (PS); lateral diameter of the anterior surface of the centrum (LAD); dorsoventral diameter of the anterior surface of the centrum (VAD); lateral diameter of the posterior surface of the centrum (LPD); dorsoventral diameter of the posterior surface of the centrum (VPD); and narrowest width of the centrum as seen from the ventral surface (NW). An additional measurement was made of the greatest width across the articular surfaces for the exoccipital bones (ASW) on the first vertebra (Figure 5*f*).

Five characters occur on the hypural (Figure 6): length from the anterior edge of the centrum to the hypural notch (HL); dorsoventral diameter of the anterior surface of the centrum (HDD); length from the dorsal tip of the hypural plate to the ventral tip (HH); greatest width across the hypurapophyses (HW); and length of the hypural notch (HNL).

DATA ANALYSIS

SPECIES IDENTIFICATION AND COMPARISON.—This paper basically builds on methods developed by Fierstine and Voigt (1996) for identifying recent billfish using rostral characters. I believe ratios (proportions) help reduce size effects and facilitate identification of isolated bones or bone fragments; thus, ratios were used as variables rather than direct measurements. Ratios were usually formed by dividing a shorter measurement (e.g., width) by a longer measurement (e.g., length). For example, for the prementary bone (Figure 2*b,c*), width (PW) was divided by length (PL) to obtain the ratio PW/PL, depth (PD) was divided by length (PL) to obtain PD/PL, and depth (PD)

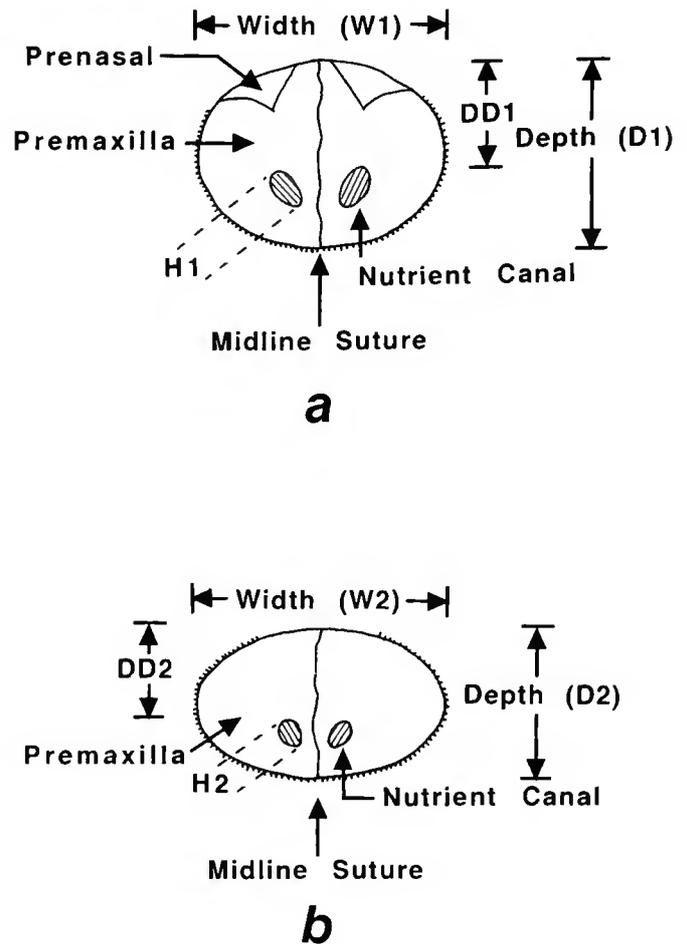


FIGURE 4.—A generalized istiophorid rostrum (modified from Fierstine and Voigt, 1996): *a*, cross section at one-half bill length (0.5L); *b*, cross section at one-fourth bill length (0.25L). See “Characters” for definition of abbreviations.

was divided by width (PW) to obtain PD/PW. A table of observed ranges for each ratio was constructed for each recent species (Tables 1, 2).

Each Lee Creek Mine specimen was measured, the measurements were converted to ratios (Tables 3, 4), and the ratios were compared to the observed ranges of recent species (see Table 5 for examples using selected prementary bones). If a ratio fell within the range of the recent species, then it was so scored. If a specimen had more scores of one species than another, it was identified as belonging to that species. A specimen was identified only to genus if its score overlapped two or more species of the same genus; it was identified to family if its score overlapped two or more genera. If some ratios fell outside the observed ranges for recent species, the specimen was identified as a variant of a known recent (e.g., cf. *Makaira* sp.) or fossil taxon.

Where possible, measurements of non-Lee Creek Mine fossil specimens were converted to ratios (Table 6) and were compared with both Lee Creek and recent specimens.

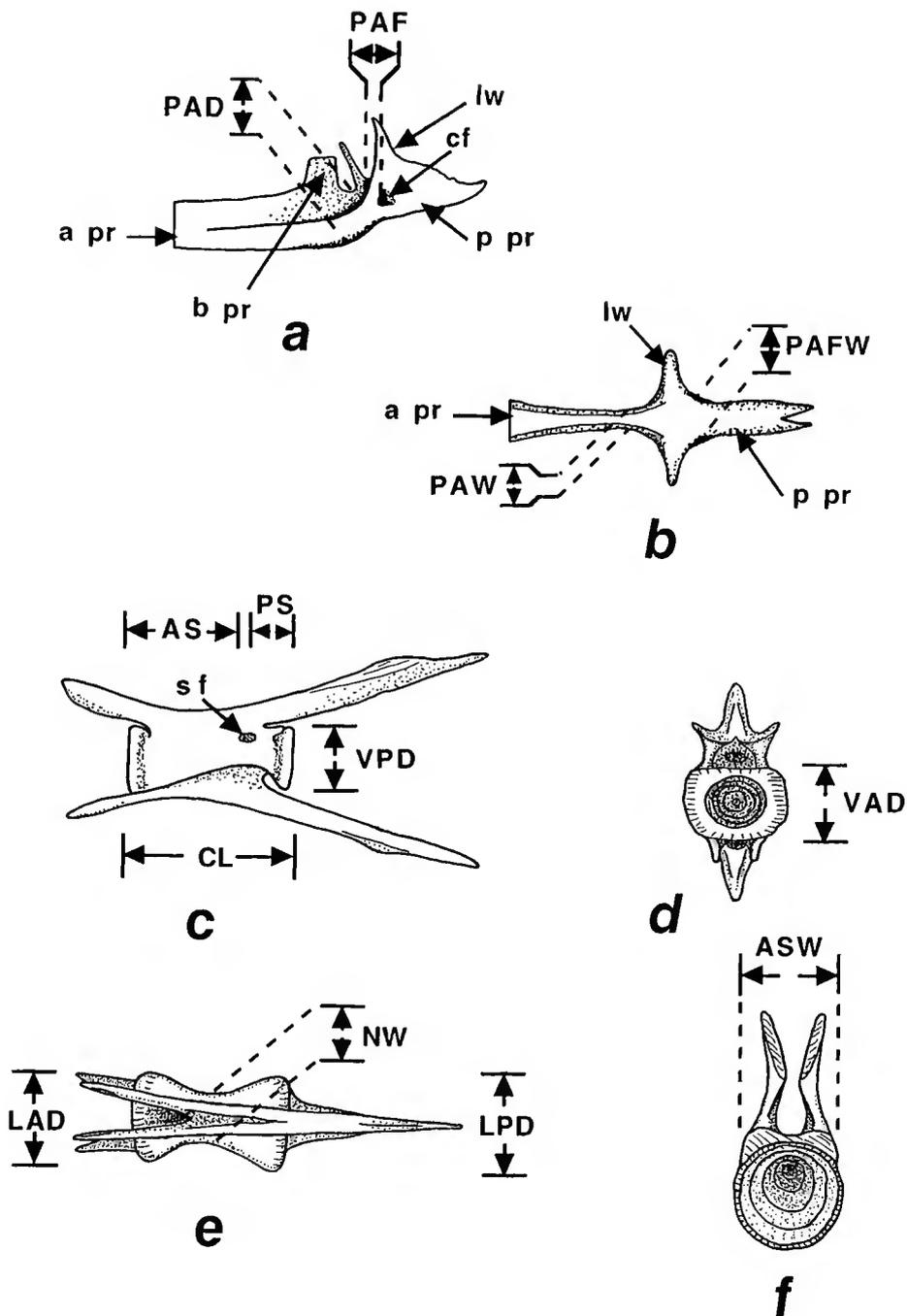


FIGURE 5.—Bones of a generalized istiothorid: *a*, parasphenoid, left lateral view of posterior region; *b*, parasphenoid, ventral view of posterior region; *c*, twenty-second vertebra, left lateral view; *d*, twenty-second vertebra, anterior view; *e*, twenty-second vertebra, dorsal view; *f*, first vertebra, anterior view. Abbreviations: a pr=anterior process, b pr=basisphenoid process, cf=carotid foramen, lw=lateral wing, p pr=posterior process, sf=spinal foramen. See "Characters" for definition of other abbreviations.

STATISTICAL METHODOLOGY.—As described above, simple descriptive statistics were used to identify fossil specimens, that is, each ratio from a Lee Creek Mine specimen was compared to the range of values for that ratio in all recent istiothorid species (Tables 1, 2). After the identifications were

finalized, the unpaired *t*-test (Welch's modification, InStat® statistical software (GraphPad Software, 1993)) was used to compare variables (ratios) of *Makaira nigricans* from Lee Creek Mine to those of recent *M. nigricans* (Table 7) and *M. indica* (Table 8). Other species from Lee Creek Mine were

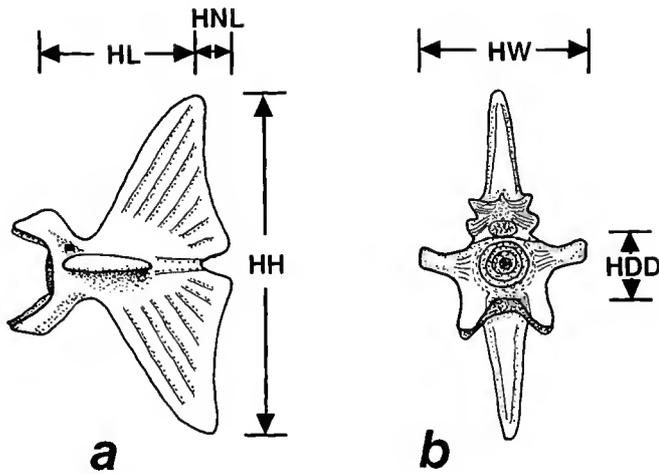


FIGURE 6.—Hypural of a generalized istiophorid: *a*, left lateral view; *b*, anterior view. See "Characters" for definition of abbreviations.

not included in the statistical analysis because of their small sample sizes.

Systematic Paleontology

Class ACTINOPTERYGII sensu Nelson, 1994

Division TELEOSTEI sensu Nelson, 1994

Order PERCIFORMES sensu Johnson and Patterson, 1993

Suborder SCOMBROIDEI sensu Carpenter et al., 1995

Family ISTIOPHORIDAE sensu Robins and de Sylva, 1960, genus and species indeterminate

PLATES 1a–k, 2a–j, 3d–h

MATERIAL.—14 articulars (NCSM 5576; USNM 284817, 284888, 290195, 291204, 475433, 481894, 481902, 481913, 481917, 488016, 488062, 488099, 488113); 8 dentaries (NCSM 2126; USNM 381941, 475394, 475417, 476373, 481980, 488025, 488084); 26 first pectoral-fin rays (NCSM 5297; USNM 284901, 284918, 284919, 290147–290149, 290202, 475435, 475436, 481904–481907, 488026, 488028, 488030–488032, 488041, 488053, 488054, 488061, 488083, 2 USNM uncataloged); 5 maxillae (USNM 475425, 481983, 481989, 488038, 488039); 1 parasphenoid (USNM 284815); 26 predentaries (USNM 286961, 286966, 286967, 286970, 286977, 475398, 475403, 475404, 475412–475414, 481952, 481953, 481955–481958, 481960, 481961, 481964–481966, 488010, 488012, 488013, 488015); 17 quadrates (NCSM 6966, 7901, 8324; USNM 475426, 475427, 475429–475432, 481915, 488042, 488051, 488081, 488090, 488108, 488114, 488115); 37 rostra (NCSM 2972, 8657, 11224; USNM 286900, 286947, 286994, 286995, 475400, 475409, 475422, 476329, 476331, 476332, 476334, 481934, 481939, 481945, 481946, 481950,

481951, 481970, 481975, 481978, 481984, 488017–488019, 488021, 488022, 488119, 7 USNM uncataloged); 12 scapulae (NCSM 7902; USNM 290205, 290206, 475428, 475434, 481925, 481926, 488034, 488109, 488111, 2 USNM uncataloged); 9 vertebra number 1 (NCSM 4914, 6920, 11187; USNM 286178, 488058, 488074, 488077, 488087, 1 USNM uncataloged); 1 vertebra number 23 (USNM 488094); 11 hypurals (USNM 282946, 283731, 290542, 290594, 481982, 488091, 488092, 488103, 488105, 2 USNM uncataloged).

REMARKS.—Specimens range in size from small to large and have the morphology of a generalized istiophorid with the exception that some specimens have one or more ratios that lie outside the range of values measured for extant istiophorids (Tables 1, 2). Some of these unique specimens are as follows: articular NCSM 5576 (Plate 1a,b), with an AAL/AL ratio (1.24) indicating an unusual-shaped socket for articulation with the quadrate; dentary USNM 488084 (Plate 1c), a very small specimen, with a DAD/DJL ratio (0.32) indicating a shallow interdentary joint; first pectoral-fin ray USNM 290202 (Plate 1d), with a FAW/FW ratio (0.80) demonstrating a large articular surface for the scapula; maxilla USNM 475425 (Plate 1f,g), with three unique ratios (MVW/MVH=0.66, MVW/MW=0.37, MVW/MH=0.43) indicating a very small articular surface for the vomer bone; predentary USNM 481956 (Plate 1j,k), with two ratios (PW/PL=1.54, PD/PL=1.02) indicating the bone is very short relative to its width and depth, yet it does not appear abnormally developed; quadrate USNM 481915 (Plate 2a,b), with a QAW/QHS ratio (0.55) indicating a wide surface for articulation with the articular; 17 rostra having either one or both ratios D1/W1, D2/W2 with values greater than 0.83, suggesting a rounder cross section; first vertebra USNM 286178, with three ratios (LAD/CL=0.36, LPD/CL=0.36, LAD/LPD=1.0) indicating a centrum having a small diameter for its length.

Parasphenoid bone USNM 284815 (Plate 1h,i) is provisionally placed here because it has a confusing array of ratios: one (PAF/PAD) scores only for *Tetrapturus albidus* and another (PAD/PAFW) scores only for *Makaira nigricans*. Several predentaries (e.g., USNM 286961, 481955, 481957, 481960, 481961) are from large individuals, much larger than any extant *Istiophorus platypterus* or *T. albidus* examined. Fifteen of the quadrates are so fragmentary that only two out of a possible five ratios can be used for identification. All scapulas have curved surfaces for articulation with the first pectoral-fin ray. Some specimens are larger than any scapulas examined of extant *I. platypterus* and *Tetrapturus* spp. (e.g., USNM 475428), whereas others are smaller (e.g., NCSM 7902, Plate 3d).

Nine of the 37 rostra have denticles on the prenasal bone (Table 3), whereas the remainder either do not have denticles or the presence or absence of denticles is unknown. Twelve of the rostra are so poorly preserved that they have only one ratio that can be used for identification. Rostrum USNM 481946 shares all of its ratios with extant *M. indica* as well as with one of the species of extant *Tetrapturus*. Several rostra (e.g.,

TABLE 1.—Mean (\bar{x}), observed range, and number of specimens examined (n) for each of 10 rostral variables (ratios), and presence (P) or absence (A) of denticles on the prenasal bone for six extant species of the family Istiophoridae. Abbreviations for ratios are explained in the text and in the legends to figures 3 and 4.

Character	<i>I. platypterus</i> (\bar{x}) (range) n	<i>M. indica</i> (\bar{x}) (range) n	<i>M. nigricans</i> (\bar{x}) (range) n	<i>T. albidus</i> (\bar{x}) (range) n	<i>T. angustirostris</i> (\bar{x}) (range) n	<i>T. audax</i> (\bar{x}) (range) n	<i>T. pfluegeri</i> (\bar{x}) (range) n
Ratio							
D1/W1	.68(.58-.78)31	.72(.66-.78)10	.70(.59-.80)41	.62(.56-.66)13	.64(.57-.70)3	.68(.59-.80)13	.62(.59-.64)2
H1/D1	.24(.15-.35)28	.16(.13-.20) 9	.14(.07-.20)36	.13(.09-.15) 7	—	.14(.10-.17) 8	—
DD1/D1	.32(.21-.41)28	.43(.38-.49) 9	.46(.33-.62)36	.40(.35-.45) 7	—	.11(.08-.14) 7	—
D2/W2	.64(.55-.75)30	.68(.58-.77)10	.64(.54-.83)41	.53(.47-.61)14	.61(.58-.64)3	.61(.52-.67)13	.65(.65)2
H2/D2	.18(.11-.26)28	.10(.08-.12) 9	.12(.06-.21)32	.12(.09-.14) 7	.11(.07-.14)2	.12(.09-.14) 8	—(.15)1
DD2/D2	.38(.28-.46)28	.46(.38-.51) 9	.47(.22-.64)32	.40(.32-.43) 7	.63(.62-.63)2	.46(.41-.55) 8	.49(.48-.50)2
D2/VSPM	.03(.03-.04)25	.06(.05-.08) 8	.04(.04-.05)35	.04(.03-.05)12	.15(.13-.19)3	.04(.03-.05)12	.05(.05-.06)2
W2/VSPM	.05(.04-.06)24	.09(.07-.10) 8	.07(.05-.08)35	.07(.06-.09)12	.24(.20-.30)3	.06(.05-.08)12	.08(.07-.09)2
P/VSPM	.58(.45-.83)17	.53(.48-.60) 8	.51(.38-.87)33	.53(.42-.66)11	.39(.30-.45)3	.48(.38-.57)12	.55(.55-.56)2
DZ/P	1.4(.76-2.5)18	.30(.10-.50) 9	.04(0-.11)37	2.4(1.5-3.3) 9	0(0)3	.93(.30-2.0) 9	0(0)2
Denticles on prenasal bone	(P/A) n (8/23) 31	(P/A) n (0/10) 10	(P/A) n (1/36) 37	(P/A) n (9/1) 10	(P/A) n (0/3) 3	(P/A) n (2/8) 10	(P/A) n (0/2) 2

USNM 286994, 476334, 481939) have a naturally shortened distal tip (Plate 2c,d). Two specimens have unequal-sized nutrient canals: USNM 475400 has the right canal more narrow than the left, and the left canal of USNM 475409 (Plate 2h) is larger in diameter than the right. The left prenasal of USNM 476329 extends more distally than the right.

Genus *Istiophorus* Lacépède, 1801

***Istiophorus platypterus* (Shaw and Nodder, 1792)**

PLATE 4a-k

MATERIAL.—2 maxillae (USNM 290198, 488082); 5 rostra (USNM 286949, 286972, 481967, 481968, 481973).

REMARKS.—Both maxillae are large and probably come from specimens of greater body length than any extant *Istiophorus platypterus* examined. In fact, maxilla USNM 290198 (Plate 4a,b) is much larger than any maxilla examined for *Makaira nigricans*. All rostra are small and fit within the body length expected for *I. platypterus*. All rostra have three or more ratios on which to base an identification and have ratios H1/D1 and H2/D2 within the range of extant sailfish. Rostrum USNM 481973 (Plate 4e) has asymmetrically sized nutrient canals.

***Istiophorus* cf. *I. platypterus* (Shaw and Nodder, 1792)**

PLATE 5a-e

MATERIAL.—1 rostrum (USNM 286950); 1 hypural (USNM 488093).

REMARKS.—Specimens are placed in this taxon because one or more ratios fall outside the range of values measured for extant istiophorids (Tables 1, 2), whereas other ratios fall within the characteristics of *Istiophorus platypterus*. Rostrum USNM 286950 (Plate 5c) has a H2/D2 ratio (0.27) greater than any extant *I. platypterus* examined (Table 1).

Genus *Makaira* Lacépède, 1802

***Makaira indica* (Cuvier, 1832)**

PLATE 5f-k

MATERIAL.—4 predentaries (USNM 475399, 475411, 488009, 488014); 2 scapulas (USNM 481927, 488112).

REMARKS.—The predentaries (Plate 5h-k) are distinguished by having PD/PL ratios that only encompass *Makaira indica* and *M. nigricans* and by having PD/PW ratios that fall outside the observed range for *M. nigricans* (>0.61) but within the range of other istiophorids. Both scapulas have a narrow, flat articular surface for the first pectoral-fin ray (Plate 5f,g). A narrow width with a flat articular surface is characteristic of *M. indica* (Wapenaar and Talbot, 1964) (SNW/SL, Table 2).

***Makaira* cf. *M. indica* (Cuvier, 1832)**

PLATE 5l

MATERIAL.—1 scapula (USNM 488100).

REMARKS.—Scapula USNM 488100 (Plate 5l) has a narrow, curved surface for articulation with the first pectoral-fin ray.

***Makaira nigricans* Lacépède, 1802**

PLATES 6a-m, 7a-m

MATERIAL.—4 dentaries (NCSM 2124, 2125; USNM 475396, 475423); 8 parasphenoids (NCSM 5159, 11248; USNM 2855370, 421526, 481990, 488047, 488048, 488050); 13 predentaries (USNM 25741, 291066, 291114, 475415, 481935-481938, 481954, 481959, 481962, 481963, 488011); 38 rostra (NCSM 2129; USNM 286973, 286986, 286996, 290614, 297407, 475397, 475401, 475405, 475406, 475408, 475410, 475419-475421, 476330, 476333, 481941-481943, 481947-481949, 481971, 481972, 481976, 481977, 488020, 488023, 488024, 8 USNM uncataloged); 5 scapulae (USNM

TABLE 2.—Mean (\bar{x}), observed range, and number of bones examined (n) for variables (ratios) on 12 bones of eight extant species of the family Istiophoridae. Abbreviations for ratios are explained in the text and in the legends to figures 1, 2, and 5.

Ratio	<i>I. platypterus</i>		<i>M. indica</i>		<i>M. nigricans</i>		<i>T. albidus</i>		<i>T. angustirostris</i>		<i>T. audax</i>		<i>T. belone</i>		<i>T. pfluegeri</i>			
	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n		
Articular																		
AL/ASM	.70(.59–.80)	22	.90(.85–.94)	2	.80(.66–.93)	23	.71(.58–.91)	15	–	.78(.68–.88)	9	–	–	–	–	–	–(.81)	1
AW/AL	.74(.53–.94)	22	.70(.69–.70)	2	.84(.68–1.1)	23	.91(.65–1.3)	15	–	.71(.58–.85)	9	–	–	–	–	–	–(.89)	1
AAL/AL	.74(.59–.92)	22	.59(.59–.60)	2	.68(.47–.91)	23	.70(.54–.97)	15	–	.66(.55–.79)	9	–	–	–	–	–	–(.29)	1
ATW/AL	1.1(.91–1.4)	21	.94(.94–.95)	2	1.2(.98–1.6)	22	1.3(.96–1.9)	15	–	1.1(.87–1.3)	9	–	–	–	–	–	–(1.1)	1
AW/ATW	.67(.54–.78)	26	.74(.74–.74)	2	.71(.55–.78)	22	.71(.57–.86)	15	–	.63(.58–.70)	10	–	–	–	–	–	–(.81)	1
Dentary																		
DAD/DJL	.44(.33–.55)	15	–(.86)	1	.76(.55–.89)	12	.53(.47–.60)	10	–	.56(.39–.74)	7	–	–	–	–	–	.26(.22–.30)	2
First pectoral-fin ray (dorsal segment)																		
FAW/FW	.65(.55–.71)	17	.27(.18–.37)	8	.65(.51–.72)	20	.66(.61–.72)	14	–(.62)	1	.62(.58–.67)	4	–(.72)	1	–	–	–(.65)	1
Maxilla																		
MW/ML	.39(.25–.57)	14	–	.64(.60–.70)	5	.47(.44–.51)	8	–	.47(.45–.49)	2	–	–	–	–	–	–	.24(.23–.24)	2
MH/ML	.33(.26–.47)	14	–	.43(.38–.49)	14	.38(.34–.45)	10	–	.37(.36–.37)	2	–	–	–	–	–	–	.33(.31–.34)	2
MVW/MVH	1.4(.95–2.4)	9	–	1.2(1.1–1.3)	3	1.2(.80–1.8)	3	–	1.2(.96–1.5)	2	–	–	–	–	–	–	–	–
MVW/ML	.22(.17–.36)	9	–	.36(.35–.37)	3	.20(.18–.24)	3	–	.28(.25–.31)	2	–	–	–	–	–	–	–	–
MVW/MW	.55(.48–.63)	9	–	.56(.53–.60)	3	.44(.40–.48)	3	–	.60(.51–.69)	2	–	–	–	–	–	–	–	–
MVW/MH	.64(.59–.75)	9	–	.90(.81–.96)	3	.54(.50–.58)	3	–	.77(.68–.85)	2	–	–	–	–	–	–	–	–
Parasphenoid																		
PAF/PAFW	.58(.39–.67)	9	–(.32)	1	.41(.32–.52)	8	.51(.45–.60)	9	–	.68(.63–.72)	2	–	–	–	–	–	–(.63)	1
PAF/PAD	.55(.47–.67)	9	–(.54)	1	.64(.57–.73)	8	.60(.47–.83)	9	–	.62(.57–.68)	2	–	–	–	–	–	–(.49)	1
PAD/PAFW	1.1(.74–1.4)	9	–(.59)	1	.63(.55–.79)	8	.86(.73–.98)	9	–	1.1(1.1–1.1)	2	–	–	–	–	–	–(1.3)	1
PAW/PAFW	.70(.62–.86)	9	–(.85)	1	.84(.67–1.0)	8	.53(.41–.73)	9	–	.58(.47–.68)	2	–	–	–	–	–	–(.89)	1
PAD/PAW	1.6(1.2–2.2)	9	–(.70)	1	.77(.62–.97)	8	1.7(1.0–2.1)	9	–	2.0(1.6–2.4)	2	–	–	–	–	–	–(1.5)	1
Prementary																		
PW/PL	.50(.23–.63)	21	.54(.48–.62)	5	.65(.45–1.1)	23	.41(.34–.57)	15	.60(.54–.69)	4	.42(.33–.51)	13	–(.59)	1	–	–	–(.65)	1
PD/PL	.27(.20–.37)	21	.38(.30–.41)	5	.36(.26–.58)	23	.24(.20–.33)	15	.59(.52–.69)	4	.26(.22–.30)	13	–(.53)	1	–	–	–(.60)	1
PD/PW	.56(.48–1.0)	21	.70(.63–.81)	5	.56(.48–.61)	23	.59(.53–.65)	15	.99(.97–1.0)	4	.60(.53–.72)	13	–(.90)	1	–	–	–(.92)	1
Quadrate																		
QAW/QH	.17(.15–.20)	11	.29(.28–.31)	2	.23(.19–.27)	22	.21(.18–.24)	17	–(.16)	1	.21(.20–.22)	4	–	–	–	–	–(.17)	1
QMW/QAW	.68(.58–.81)	11	.85(.83–.88)	2	.77(.57–.92)	22	.73(.48–.88)	18	–(.65)	1	.71(.67–.77)	4	–	–	–	–	–(.62)	1
QAW/QHS	.29(.24–.39)	11	.44(.44–.45)	2	.36(.30–.43)	21	.35(.30–.40)	18	–	.38(.37–.39)	2	–	–	–	–	–	–(.30)	1
QMW/QHS	.19(.17–.23)	11	.38(.38–.38)	2	.27(.22–.35)	21	.25(.19–.30)	18	–	.28(.27–.28)	2	–	–	–	–	–	–(.18)	1
QMW/QML	.73(.62–.80)	11	1.1(1.1–1.1)	2	.86(.63–1.0)	22	.83(.53–1.0)	18	–(.56)	1	.79(.65–1.0)	4	–	–	–	–	–(.71)	1
Scapula																		
SGW/SL	.67(.55–.81)	13	.44(.36–.53)	8	.58(.51–.76)	20	.64(.54–.72)	13	.70(.68–.71)	2	.63(.60–.64)	4	–	–	–	–	.64(.64–.64)	2
SNW/SL	.44(.30–.53)	13	.16(.11–.19)	8	.35(.22–.51)	20	.42(.30–.55)	13	.60(.53–.68)	2	.56(.49–.63)	4	–	–	–	–	.56(.54–.57)	2
SNW/SGW	.65(.53–.78)	13	.36(.26–.47)	8	.60(.37–1.0)	20	.67(.50–.84)	13	.87(.74–1.0)	2	.89(.82–1.0)	4	–	–	–	–	.87(.85–.90)	2
Vertebra 1																		
AN/CL	.61(.53–.69)	7	–	.64(.51–.74)	6	.67(.57–.77)	4	–	.64(.59–.70)	2	–	–	–	–	–	–	–(.65)	1
PN/CL	.46(.40–.52)	10	–	.41(.38–.47)	9	.37(.26–.42)	4	–	.43(.39–.45)	5	–	–	–	–	–	–	–(.41)	1
ASW/VAD	.82(.61–1.0)	9	–	1.0(.79–1.6)	9	.89(.85–.96)	4	–	.90(.81–.97)	5	–	–	–	–	–	–	–(.86)	1
ASW/CL	.62(.50–.78)	9	–	.95(.77–1.2)	9	.69(.64–.76)	4	–	.81(.76–.88)	5	–	–	–	–	–	–	–(.48)	1
LAD/CL	.68(.60–.77)	9	–	.92(.84–1.0)	9	.69(.62–.75)	4	–	.78(.70–.87)	5	–	–	–	–	–	–	–(.53)	1
VAD/CL	.77(.62–.91)	10	–	.94(.74–1.0)	9	.77(.74–.79)	4	–	.91(.82–.99)	5	–	–	–	–	–	–	–(.56)	1
VAD/LAD	1.1(.88–1.3)	9	–	1.0(.80–1.2)	9	1.1(1.1–1.2)	4	–	1.2(1.1–1.2)	5	–	–	–	–	–	–	–(1.1)	1
LPD/CL	.78(.72–.89)	10	–	1.0(.92–1.1)	8	.74(.69–.78)	4	–	.86(.80–.90)	5	–	–	–	–	–	–	–	–
VPD/CL	.76(.70–.83)	10	–	.95(.86–1.0)	9	.73(.69–.76)	4	–	.85(.78–.91)	4	–	–	–	–	–	–	–	–
VPD/LPD	.97(.93–1.0)	10	–	.93(.86–1.0)	8	.98(.97–1.0)	4	–	.98(.93–1.0)	4	–	–	–	–	–	–	–	–
LAD/LPD	.89(.82–.97)	9	–	.91(.86–.96)	8	.93(.91–.96)	4	–	.91(.88–.96)	5	–	–	–	–	–	–	–	–
VAD/VPD	1.0(.76–1.1)	10	–	.99(.76–1.1)	9	1.1(1.0–1.1)	4	–	1.1(1.1–1.2)	4	–	–	–	–	–	–	–	–
NW/CL	.37(.22–.47)	10	–	.63(.57–.74)	9	.41(.39–.47)	4	–	.45(.42–.52)	5	–	–	–	–	–	–	–(.22)	1
NW/LPD	.47(.30–.56)	10	–	.62(.55–.68)	8	.56(.51–.60)	4	–	.52(.47–.58)	5	–	–	–	–	–	–	–	–
Vertebra 22																		
AN/CL	.60(.57–.64)	11	–(.56)	1	.60(.57–.62)	7	.58(.55–.62)	5	–	.60(.59–.60)	2	–	–	–	–	–	–(.62)	1
PN/CL	.38(.32–.42)	11	–(.38)	1	.39(.36–.43)	7	.39(.36–.45)	5	–	.40(.40–.41)	2	–	–	–	–	–	–(.38)	1
LAD/CL	.58(.45–.66)	11	–(.68)	1	.77(.58–.87)	7	.58(.54–.63)	5	–	.61(.61–.61)	2	–	–	–	–	–	–(.48)	1
VAD/CL	.53(.47–.57)	11	–(.50)	1	.50(.42–.54)	7	.50(.46–.53)	5	–	.52(.51–.52)	2	–	–	–	–	–	–(.45)	1
VAD/LAD	.91(.78–1.1)	11	–(.73)	1	.66(.62–.73)	7	.87(.84–.92)	5	–	.85(.83–.87)	2	–	–	–	–	–	–(.94)	1
LPD/CL	.54(.48–.62)	10	–(.74)	1	.74(.56–.84)	7	.54(.51–.57)	4	–	.64(.63–.66)	2	–	–	–	–	–	–(.46)	1

TABLE 2.—Continued.

Ratio	<i>I. platypterus</i>		<i>M. indica</i>		<i>M. nigricans</i>		<i>T. albidus</i>		<i>T. angustirostris</i>		<i>T. audax</i>		<i>T. belane</i>		<i>T. pfluegeri</i>		
	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	
VPD/CL	.49(.45-.54)	11	-.50	1	.48(.45-.51)	7	.48(.46-.50)	4	-	-	.54(.51-.57)	2	-	-	-	-.40	1
VPD/LPD	.90(.80-.97)	10	-.68	1	.65(.60-.81)	7	.89(.83-.93)	4	-	-	.84(.77-.91)	2	-	-	-	-.87	1
LAD/LPD	1.1(.92-1.2)	10	-.92	1	1.0(.99-1.1)	7	1.0(.99-1.1)	4	-	-	.95(.93-.97)	2	-	-	-	-1.0	1
VAD/VPD	1.1(1.0-1.1)	11	-(1.0)	1	1.0(.94-1.1)	7	1.0(.98-1.1)	4	-	-	.96(.93-1.0)	2	-	-	-	-1.1	1
NW/CL	.32(.26-.42)	11	-.41	1	.49(.34-.56)	7	.32(.29-.34)	4	-	-	.33(.33-.34)	2	-	-	-	-.68	1
NW/LPD	.58(.54-.62)	10	-.55	1	.66(.59-.72)	7	.60(.53-.67)	4	-	-	.52(.51-.53)	2	-	-	-	-1.5	1
Vertebra 23																	
AN/CL	.69(.67-.75)	8	-.69	1	.59(.50-.68)	7	.58(.56-.94)	6	-.66	1	.61(.61-.62)	2	-	-	-	-.72	1
PN/CL	.28(.20-.31)	58	-.24	1	.36(.28-.47)	7	.32(.30-.35)	6	-.29	1	.31(.30-.31)	2	-	-	-	-.28	1
LAD/CL	.62(.56-.71)	9	-.83	1	.88(.64-1.1)	7	.64(.57-.71)	6	-.56	1	.72(.69-.75)	2	-	-	-	-.52	1
VAD/CL	.58(.48-.73)	10	-.56	1	.57(.52-.64)	7	.57(.53-.62)	6	-.53	1	.62(.60-.64)	2	-	-	-	-.48	1
LAD/LAD	.90(.82-.98)	9	-.68	1	.65(.57-.82)	7	.89(.86-.94)	6	-.94	1	.86(.81-.92)	2	-	-	-	-.92	1
LPD/CL	.56(.48-.82)	10	-.63	1	.68(.53-.83)	7	.57(.52-.66)	6	-.48	1	.65(.63-.67)	2	-	-	-	-.47	1
VPD/CL	.50(.42-.63)	10	-.50	1	.52(.44-.59)	6	.53(.48-.59)	6	-.43	1	.54(.52-.56)	2	-	-	-	-.42	1
VPD/LPD	.90(.76-.99)	10	-.79	1	.77(.71-.88)	6	.92(.88-.95)	6	-.89	1	.83(.77-.89)	2	-	-	-	-.91	1
LAD/LPD	1.2(1.1-1.2)	9	-(1.3)	1	1.3(1.2-1.4)	7	1.1(1.1-1.1)	6	-(1.2)	1	1.1(1.1-1.1)	2	-	-	-	-1.1	1
VAD/VPD	1.2(1.1-1.2)	10	-(1.1)	1	1.1(1.0-1.2)	6	1.1(1.0-1.2)	6	-(1.2)	1	1.2(1.1-1.2)	2	-	-	-	-1.1	1
NW/CL	.53(.38-.81)	10	-.53	1	.61(.44-.76)	7	.51(.46-.59)	6	-.41	1	.53(.51-.54)	2	-	-	-	-.45	1
NW/LPD	.95(.76-1.1)	10	-.84	1	.90(.83-.92)	7	.89(.84-.95)	6	-.86	1	.81(.80-.82)	2	-	-	-	-.97	1
Hypural																	
HDD/HL	.46(.38-.55)	10	-.34	1	.38(.29-.43)	6	.47(.44-.49)	6	-.47	1	.45(.41-.48)	3	-	-	-	-.44	1
HDD/HH	.24(.22-.26)	10	-.20	1	.21(.15-.25)	6	.26(.24-.28)	6	-.24	1	.24(.23-.25)	3	-	-	-	-.24	1
HDD/HW	.41(.36-.47)	10	-.36	1	.39(.28-.46)	6	.45(.44-.47)	5	-.46	1	.45(.40-.52)	3	-	-	-	-.44	1
HL/HH	.53(.47-.58)	10	-.58	1	.55(.52-.58)	6	.55(.52-.58)	6	-.51	1	.53(.51-.56)	3	-	-	-	-.55	1
HW/HL	1.1(.94-1.4)	10	-.96	1	.97(.89-1.0)	6	1.0(1.0-1.1)	5	-(1.0)	1	1.0(.94-1.1)	3	-	-	-	-1.0	1
HW/HH	.59(.51-.66)	10	-.55	1	.54(.50-.60)	6	.56(.54-.60)	5	-.51	1	.54(.49-.57)	3	-	-	-	-.55	1
HNL/HL	.37(.30-.47)	10	-.22	1	.28(.22-.31)	6	.34(.29-.40)	6	-.41	1	.32(.31-.33)	3	-	-	-	-.37	1

290197, 290211, 421527, 481929, 488110); 6 vertebra number 1 (USNM 481923, 488059, 488071, 488078, 488088, 1 USNM uncataloged); 8 vertebra number 22 (USNM 286181, 488056, 488066, 488076, 488089, 488098, 2 USNM uncataloged); 16 vertebra number 23 (USNM 286179, 288000, 488044, 488045, 488055, 488063, 488064, 488067, 488068, 488070, 488094-488096, 3 USNM uncataloged); 3 hypurals (NCSM 4938; USNM 488069, 488104).

REMARKS.—All specimens have one or more ratios only within the range of values measured for extant *Makaira nigricans* (Tables 1, 2). Seven of the eight parasphenoids have only one or two ratios out of a possible five used for identification. Most prementaries were assigned to this taxon on the basis of ratio PW/PL; however, four prementaries (USNM 475415, 481936 (Plate 6*g,i*), 481938, 488011) have two ratios (PW/PL, PD/PL) characteristic only of *M. nigricans* (Table 2). All scapulas have curved articular surfaces for the first pectoral-fin ray.

Eight of the 38 rostra have only one ratio (either D1/W1 or D2/W2) on which to base an identification. Two specimens have denticles on the prenasal bone, six lack denticles, and the presence or absence of denticles for the other 30 rostra is not known. Specimens range in size from moderate (USNM 475421) to huge (USNM 475405, 481941 (Plate 6*f,h,j*)). Some specimens (e.g., USNM 297407, 475406, 481943, 481949, 481976, 481977) have a naturally worn tip, sometimes with the nutrient canals exposed at the distal end (e.g., USNM 481976,

Plate 7*a-c*). USNM 290614 has a small abnormal growth (keel) on the dorsal tip of the bill.

All vertebrae 1, 22, and 23 have at least two or three ratios with values that are characteristic of *M. nigricans*.

Makaira cf. M. nigricans Lacépède, 1802

PLATES 8*a-j*, 9*a-f*

MATERIAL.—2 parasphenoids (USNM 488049, 488116); 3 quadrates (NCSM 6944; USNM 476372, 481903); 5 rostra (NCSM 7427; USNM 286958, 481944, 481974, 1 USNM uncataloged); 5 vertebra number 1 (USNM 481897, 481910, 488057, 488072, 488073); 5 vertebra number 22 (USNM 286177, 488033, 488079, 488080, 488086); 7 vertebra number 23 (USNM 476371, 481909, 488065, 488097, 3 USNM uncataloged); 4 hypurals (USNM 283735, 481979, 2 USNM uncataloged).

REMARKS.—Specimens having one or more ratios that lie outside the range of values measured for extant istiophorids (Tables 1, 2) are placed here because the values for some of the other ratios fall within the range characteristic of only *Makaira nigricans*. Some of these unusual specimens include the following: parasphenoid USNM 488116 (Plate 8*d,f*) with a PAF/PAD ratio of 0.94, indicating a shallower depth of the parasphenoid bone; quadrate NCSM 6944 (Plate 8*a,j*) with three ratios (QAW/QH=0.37, QAW/QHS=0.52, QMW/QML=1.1),

TABLE 3.—Mean (\bar{x}), observed range, and number of specimens examined (n) for each of eight rostral variables (ratios), and presence (P) or absence (A) of denticles on prenasal bone for seven istiophorid taxa from Lee Creek Mine. Abbreviations for ratios are explained in the text and in the legends to figures 3 and 4.

Character	Istiophoridae, gen. and sp. indeterminate	<i>Istiophorus platypterus</i>	<i>Istiophorus cf. I. platypterus</i>	<i>Makaira nigricans</i>	<i>Makaira cf. M. nigricans</i>	<i>Makaira purdyi</i>	<i>Makaira sp.</i>
	(\bar{x}) (range) n	(\bar{x}) (range) n	(\bar{x}) (range) n	(\bar{x}) (range) n	(\bar{x}) (range) n	(\bar{x}) (range) n	(\bar{x}) (range) n
Ratio							
D1/W1	.79(.65–.89)12	.73(.72–.75)3	–	.79(.77–.80) 3	–(.86)1	–	–
H1/D1	.17(.10–.24) 6	.22(.21–.23)3	–	.15(.09–.19)14	.14(.11–.19)3	–	–(.20)1
DD1/D1	.48(.39–.64) 6	.37(.35–.42)3	–	.52(.41–.59)14	.59(.47–.80)3	–	–(.43)1
D2/W2	.77(.61–.91)27	–(.69)1	–(.75)1	.76(.66–.83)36	.90(.86–1.0)4	(.95)1	.76(.73–.77) 5
H2/D2	.14(.09–.22)16	.24(.22–.25)2	–(.27)1	.15(.06–.22)16	.09(.06–.12)2	(.16)1	.17(.16–.17) 2
DD2/D2	.49(.32–.53)16	.44(.43–.45)2	–(.39)1	.52(.40–.62)16	–(.57)1	(.57)1	.51(.47–.55) 2
P/VSPM	–(.39)1	–	–	–	–	(.38)1	–
DZ/P	.31(.15–.41) 4	–	–	.49(.38–.59) 3	–(.81)1	(.14)1	–(.35)1
Denticles on prenasal bone	(P/A?) n	(P/A?) n	(P/A?) n	(P/A?) n	(P/A?) n	(P/A?) n	(P/A?) n
	(8/6/22) 36	(0/1/4) 5	(0/1/0) 1	(2/6/30) 38	(2/0/3) 5	(1/0/0) 1	(1/2/2) 5

quadrate USNM 476372 with two ratios (QAW/QH=0.37, QAW/QHS=0.54), and quadrate USNM 481903 with one ratio (QAW/QHS=0.51) indicating a wide surface for articulation with the articular; five rostra having either one or both ratios D1/W1, D2/W2, with values greater than 0.83, indicating a rounder cross section; five vertebra number 1 each with a NW/LPD ratio greater than 0.70, indicating a more hourglass-shaped centrum; five vertebra number 22 with a mixture of unique ratios, two with a NW/LPD ratio greater than 0.74, indicating a more hourglass-shaped centrum; seven vertebra number 23 with an array of unique ratios, including three with VPD/LPD ratios less than 0.69, two with LAD/LPD ratios greater than 1.39, and one with VAD/CL and VAD/LAD ratios less than any other istiophorids; and four hypurals (USNM 283735, 481979 (Plate 9*d,e*), 2 USNM uncataloged), have HL/HH ratios (0.72, 0.61, 0.63, and 0.62, respectively) indicating a shorter height from tip to tip.

All vertebrae 1, 22, and 23 have a minimum of two ratios (except one USNM uncataloged vertebra 23 with one ratio) with values that are characteristic of *M. nigricans*. Hypurals USNM 283735 and two USNM uncataloged specimens have only three ratios out of a possible seven on which to base an identification, and they have just one ratio characteristic of *M. nigricans*.

Makaira purdyi Fierstine, 1999a

PLATE 3*a–c*

MATERIAL.—1 rostrum (holotype, USNM 481933).

REMARKS.—The rostrum is morphologically distinct from any extant istiophorid in the following combination of characters: (1) the fused portion of the premaxillae is short and stout with denticles covering at least the distal one-half of its dorsal surface; (2) at 0.25L, the cross section is nearly round (D2/W2=0.95) (Fierstine, 1999a).

Makaira sp.

PLATES 9*g–i*, 10*a–d,g–i*

MATERIAL.—2 dentaries (USNM 286997, 475418); 1 pre-dentary (USNM 481931); 2 quadrates (USNM 488006, 488075); 5 rostra (NCSM 11223; USNM 285384, 475390, 481969, 1 USNM uncataloged); 1 scapula (USNM 290204); 1 vertebra 23 (USNM 290542); 2 hypurals (USNM 481981, 488102).

REMARKS.—These specimens have one or more ratios that fall within the observed range of values measured for both *Makaira indica* and *M. nigricans* (Tables 1, 2). Both dentaries are from large individuals. Predentary USNM 481931 (Plate 10*a,b*) is massive, much larger than any extant istiophorid examined. Four of the five quadrates have four of five possible ratios on which to base an identification, and all are from large individuals. Rostrum USNM 285384 has an eroded tip with both nutrient canals exposed. All rostra are from small- to moderate-sized individuals with the exception of USNM 475390 (Plate 9*g–i*), which came from a very large fish. The scapula has a curved articular surface and is from a very large-sized individual. The hypurals (USNM 481981 (Plate 10*h,i*), 488102) came from large-sized individuals and have HNL/HL ratios within the range of both *M. indica* and *M. nigricans*.

cf. Makaira sp.

PLATE 10*e,f,j–l*

MATERIAL.—2 dentaries (NCSM 2990; USNM 475395); 2 quadrates (USNM 481916, 481919); 1 hypural (USNM 488007).

REMARKS.—These specimens have at least one ratio near the observed ranges of values measured for *Makaira indica* and *M. nigricans*, but they have one or more ratios that lie outside the ranges of values measured for extant istiophorids (Tables 1, 2). Some of these unusual specimens include the following: dentaries NCSM 2990 (Plate 10*j*) and USNM 475395 with DAD/DJL ratios (0.96 and 1.04, respectively) indicating a

deep interdendry joint; quadrates USNM 481916 (Plate 10*k,l*) and 481919 with QAW/QHS ratios (0.47 and 0.53, respectively) indicating a wider joint surface for articulation with the articular; and hypural USNM 488007 (Plate 10*e,f*) with three ratios (HL/HH=0.71, HW/HL=0.85, HNL/HL=0.11) indicating both a longer centrum length and that it came from a small-sized specimen.

Genus *Tetrapturus* Rafinesque, 1810

Tetrapturus albidus Poey, 1860

PLATES 11*a-j*, 12*a-d*

MATERIAL.—3 articulars (USNM 290193, 488029, 488043); 7 maxillae (USNM 290203, 475393, 475402, 475424, 488036, 488037, 488040); 2 parasphenoids (USNM 488027, 488046); 2 quadrates (USNM 481908, 488008).

REMARKS.—I have reservations about recognizing *Tetrapturus albidus* at Lee Creek Mine because its identification is based on poorly preserved features of fragmentary material. Articulars USNM 290193 (Plate 11*a,b*) and 488043, all seven maxillae, both parasphenoids, and quadrate USNM 488008 are from individuals of greater body length than any extant species of *Tetrapturus* measured. Five of the seven maxillae are poorly preserved, with only two ratios available for identification. Both parasphenoids are incomplete and have only ratio, PAD/PAW, on which to base an identification. Quadrate USNM 481908 (Plate 12*a,b*) has a QAW/QH ratio (0.31) that falls only within the range of values for *Makaira indica*, but its QMW/QAW ratio (0.53) is only within the range of values for *T. albidus*. The other three ratios encompass an extant species of *Tetrapturus*. Quadrate USNM 488008 (Plate 12*c,d*) has two ratios (QMW/QAW=0.53, QMW/QML=0.61) characteristic only of values measured for *T. albidus*.

Tetrapturus cf. *T. albidus* Poey, 1860

PLATE 12*e,f*

MATERIAL.—2 maxillae (USNM 488035, 488085).

REMARKS.—Both maxillae have MVW/MH ratios (0.46 and 0.47, respectively) outside the range of values measured for extant istiophorids (Tables 1, 2); however, other ratios are within the observed range of values for *Tetrapturus albidus*.

Discussion

COMPARISON OF LEE CREEK SPECIMENS TO OTHER FOSSIL AND RECENT SPECIES.—Because fossil billfish have been reviewed previously (Fierstine, 1974, 1978, 1990; Schultz, 1987), only specimens with direct relevance to Lee Creek and recent istiophorids are discussed herein. There are three widely recognized families of billfishes, each defined in part by its rostrum. The Istiophoridae (marlin, sailfish, and spearfish) have an oval to round bill with paired nutrient foramina and have both fossil and recent representatives. The Xiphiidae (sword-

fish) have a flattened bill with paired nutrient canals as well as a central chamber and have both fossil and recent representatives. The extinct Xiphiorhynchidae have an oval to round bill with one or more pairs of nutrient foramina and a central canal.

Schultz (1987) recognized three questionable families of billfish, the extinct Blochiidae, extinct Paleorhynchidae, and extant Tetrapturidae. Too little is known about the first two families to determine if they are billfish (Fierstine, 1974), and the third should not be recognized (Fierstine and Voigt, 1996). Carroll (1988) placed many of these questionable billfish in the Xiphiidae, a decision that has no merit.

Most early workers (see references in Fierstine, 1978, and Schultz, 1987) placed fossil specimens of Istiophoridae into new or existing fossil species of *Istiophorus*. Perhaps other genera and extant species were not considered because the systematics of the recent Istiophoridae was poorly understood. Robins and de Sylva (1960, 1963), Nakamura et al. (1968), and Nakamura (1983, 1985) revised the extant Istiophoridae and recognized three genera, *Istiophorus*, *Makaira*, and *Tetrapturus*, although the number of species in *Istiophorus* and *Makaira* was equivocal. I follow Robins and de Sylva (1960, 1963) and Robins et al. (1991), and not Nakamura (1983, 1985), in treating both the sailfish and blue marlin as single, world-wide species (*I. platypterus* and *M. nigricans*, respectively) and not as separate Atlantic Ocean (*I. albicans* and *M. nigricans*) and Indo-Pacific Ocean (*I. platypterus* and *M. mazara*) forms. Genetic studies support the status of a single, world-wide species each of sailfish and blue marlin (Graves and McDowell, 1995).

Because most early workers placed fossil billfish of disparate morphologies in *Istiophorus* (sailfish genus), I have reclassified specimens into other genera where warranted. If data to make an accurate identification were lacking, I left the specimens in *Istiophorus* but put quotes around the generic name.

"*Istiophorus*" *robustus* (Leidy, 1860) (AMNH 5684, holotype, ?Pleistocene, Ashley River, South Carolina) is a short (140 mm) distal rostral fragment that was refigured by Hussakof (1908). Based on published accounts, the specimen is oval in cross section (long axis is dorsoventral) for most of its length. Nutrient canals were not discussed or figured. Denticles are probably restricted to the ventral surface (dorsal surface in Leidy's figure, but the specimen is probably upside down) (Fierstine, 1974). Schultz (1987) placed the specimen in *Aglyptorhynchus* Casier, 1967 (questionable billfish), and considered it to have been collected in the Eocene. Without reexamining the specimen I do not think it is relevant to Lee Creek istiophorids.

"*Istiophorus*" *rotundus* Woodward, 1901 (BMNH P8799, holotype, Tertiary phosphate beds of South Carolina), is a very stout and round rostral fragment that is extremely massive for its length (313 mm). Due to poor preservation, I measured the specimen's width and depth 95 mm distal from its proximal end (W=93.8 mm, D=78.5 mm, D/W=0.84). The rostrum has never been sectioned to determine the presence, number, position, and size of nutrient canals. No denticles or alveoli are visible, and I was unable to determine which sur-

TABLE 4.—Continued.

Ratio	Istiophoridae, gen. and sp. indet.		<i>I. platypterus</i>		<i>I. platypterus</i> cf. <i>I. platypterus</i>		<i>M. indica</i>		<i>M. indica</i>		<i>M. nigricans</i>		<i>M. nigricans</i>		<i>Makaira</i> cf. <i>M. nigricans</i>		<i>Makaira</i> sp. cf. <i>Makaira</i> sp.		<i>T. albidus</i>		<i>Tetrapturus</i> cf. <i>T. albidus</i>		
	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	(\bar{x})	(range) n	
VAD/CL	.86	(.67–.97) 8	—	—	—	—	—	—	—	—	—	.94	(.92–.95) 5	.97	(.94–1.0) 4	—	—	—	—	—	—	—	—
VAD/LAD	1.2	(1.1–1.3) 8	—	—	—	—	—	—	—	—	—	1.1	(1.0–1.2) 5	1.1	(1.1–1.1) 3	—	—	—	—	—	—	—	—
LPD/CL	.77	(.36–.89) 8	—	—	—	—	—	—	—	—	—	.95	(.90–1.1) 6	1.0	(.97–1.1) 5	—	—	—	—	—	—	—	—
VPD/CL	.83	(.66–.90) 7	—	—	—	—	—	—	—	—	—	.94	(.89–1.1) 4	.99	(.94–1.1) 4	—	—	—	—	—	—	—	—
VPD/LPD	1.0	(.99–1.0) 7	—	—	—	—	—	—	—	—	—	.99	(.95–1.0) 4	.99	(.95–1.0) 4	—	—	—	—	—	—	—	—
LAD/LPD	.89	(.79–1.0) 8	—	—	—	—	—	—	—	—	—	.88	(.85–.92) 5	.89	(.85–.96) 4	—	—	—	—	—	—	—	—
VAD/VPD	1.0	(.99–1.1) 7	—	—	—	—	—	—	—	—	—	.99	(.89–1.1) 4	.98	(.95–1.0) 4	—	—	—	—	—	—	—	—
NW/CL	.52	(.23–.66) 9	—	—	—	—	—	—	—	—	—	.64	(.56–.73) 6	.73	(.69–.76) 5	—	—	—	—	—	—	—	—
NW/LPD	.68	(.60–.76) 8	—	—	—	—	—	—	—	—	—	.67	(.62–.69) 6	.73	(.71–.76) 5	—	—	—	—	—	—	—	—
Vertebra 22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AN/CL	—	—	—	—	—	—	—	—	—	—	—	.58	(.55–.62) 6	.58	(.53–.65) 5	—	—	—	—	—	—	—	—
PN/CL	—	—	—	—	—	—	—	—	—	—	—	.43	(.35–.54) 7	.38	(.29–.42) 5	—	—	—	—	—	—	—	—
LAD/CL	—	—	—	—	—	—	—	—	—	—	—	.70	(.66–.77) 7	.75	(.64–.84) 5	—	—	—	—	—	—	—	—
VAD/CL	—	—	—	—	—	—	—	—	—	—	—	.49	(.44–.53) 7	.50	(.44–.59) 5	—	—	—	—	—	—	—	—
VAD/LAD	—	—	—	—	—	—	—	—	—	—	—	.69	(.62–.74) 7	.67	(.59–.73) 5	—	—	—	—	—	—	—	—
LPD/CL	—	—	—	—	—	—	—	—	—	—	—	.71	(.66–.75) 8	.73	(.69–.83) 5	—	—	—	—	—	—	—	—
VPD/CL	—	—	—	—	—	—	—	—	—	—	—	.46	(.43–.50) 7	.45	(.42–.49) 4	—	—	—	—	—	—	—	—
VPD/LPD	—	—	—	—	—	—	—	—	—	—	—	.65	(.58–.71) 7	.61	(.54–.71) 4	—	—	—	—	—	—	—	—
LAD/LPD	—	—	—	—	—	—	—	—	—	—	—	1.0	(.91–1.0) 7	1.0	(.88–1.2) 5	—	—	—	—	—	—	—	—
VAD/VPD	—	—	—	—	—	—	—	—	—	—	—	1.0	(.95–1.1) 6	1.1	(1.1–1.2) 4	—	—	—	—	—	—	—	—
NW/CL	—	—	—	—	—	—	—	—	—	—	—	.47	(.45–.51) 8	.57	(.46–.70) 5	—	—	—	—	—	—	—	—
NW/LPD	—	—	—	—	—	—	—	—	—	—	—	.67	(.61–.72) 8	.78	(.64–1.0) 5	—	—	—	—	—	—	—	—
Vertebra 23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AN/CL	—	(.65) 1	—	—	—	—	—	—	—	—	—	.60	(.51–.76) 12	.62	(.61–.64) 4	—	—	—	—	—	—	—	—
PN/CL	—	(.23) 1	—	—	—	—	—	—	—	—	—	.37	(.30–.46) 12	.34	(.31–.37) 4	—	—	—	—	—	—	—	—
LAD/CL	—	—	—	—	—	—	—	—	—	—	—	.76	(.61–1.0) 15	.89	(.79–.95) 7	—	—	—	—	—	—	—	—
VAD/CL	—	(.52) 1	—	—	—	—	—	—	—	—	—	.51	(.46–.59) 15	.53	(.42–.58) 7	—	—	—	—	—	—	—	—
VAD/LAD	—	—	—	—	—	—	—	—	—	—	—	.68	(.58–.77) 15	.59	(.47–.64) 7	—	—	—	—	—	—	—	—
LPD/CL	—	(.58) 1	—	—	—	—	—	—	—	—	—	.60	(.52–.75) 13	.70	(.60–.82) 7	—	—	—	—	—	—	—	—
VPD/CL	—	(.51) 1	—	—	—	—	—	—	—	—	—	.47	(.43–.53) 11	.48	(.44–.51) 4	—	—	—	—	—	—	—	—
VPD/LPD	—	(.87) 1	—	—	—	—	—	—	—	—	—	.77	(.71–.84) 10	.67	(.63–.75) 4	—	—	—	—	—	—	—	—
LAD/LPD	—	—	—	—	—	—	—	—	—	—	—	1.3	(1.2–1.4) 13	1.3	(1.2–1.5) 7	—	—	—	—	—	—	—	—
VAD/VPD	—	(1.0) 1	—	—	—	—	—	—	—	—	—	1.1	(1.0–1.2) 11	1.1	(1.1–1.1) 4	—	—	—	—	—	—	—	—
NW/CL	—	(.61) 1	—	—	—	—	—	—	—	—	—	.55	(.46–.69) 15	.69	(.61–.80) 7	—	—	—	—	—	—	—	—
NW/LPD	—	(1.1) 1	—	—	—	—	—	—	—	—	—	.94	(.87–1.1) 13	1.0	(.84–1.2) 7	—	—	—	—	—	—	—	—
Hypural	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HDD/HL	.40	(.36–.43) 10	—	—	—	—	—	—	—	—	—	.40	(.36–.45) 3	.32	(.29–.36) 3	.40	(.39–.42) 2	—	—	—	—	—	—
HDD/HH	.23	(.20–.27) 9	—	—	—	—	—	—	—	—	—	.22	(.20–.25) 3	.21	(.20–.22) 3	.22	(.21–.23) 2	—	—	—	—	—	—
HDD/HW	.41	(.38–.43) 4	—	—	—	—	—	—	—	—	—	.42	(.38–.46) 2	—	(.37) 1	.41	(.39–.43) 2	—	—	—	—	—	—
HL/HH	.56	(.49–.62) 10	—	—	—	—	—	—	—	—	—	.54	(.51–.57) 3	.65	(.61–.72) 4	.54	(.54–.54) 2	—	—	—	—	—	—
HW/HL	1.0	(.97–1.1) 4	—	—	—	—	—	—	—	—	—	1.0	(.99–1.0) 2	.93	(.89–.97) 2	.99	(.98–1.0) 2	—	—	—	—	—	—
HW/HH	.58	(.56–.60) 3	—	—	—	—	—	—	—	—	—	.54	(.53–.55) 2	.57	(.55–.59) 2	.54	(.52–.55) 2	—	—	—	—	—	—
HNL/HL	.27	(.21–.32) 5	—	—	—	—	—	—	—	—	—	.25	(.25–.26) 3	—	(.26) 1	.21	(.21–.22) 2	—	—	—	—	—	—

TABLE 5.—Sample score sheet for species identification of selected predatory bones from Lee Creek Mine. Species score code: 0=outlier, 1=*Istiophorus platypterus*, 2=*Makaira indica*, 3=*M. nigricans*, 4=*Tetrapturus albidus*, 5=*T. angustirostris*, 6=*T. audax*, 7=*T. belone*.

Catalog number	PW/PL		PD/PL		PD/PW		Species
	Value	Score	Value	Score	Value	Score	
USNM 291066	.83	3	.50	3	.60	1,3,4,6	<i>Makaira nigricans</i>
USNM 475399	.62	1,2,3,5	.40	2,3	.64	1,2,4,6	<i>Makaira indica</i>
USNM 475412	.59	1,2,3,5,7	.35	1,2,3	.59	1,3,4,6	Istiophoridae
USNM 481931	.58	1,2,3,5	.45	3	.76	1,2	<i>Makaira</i> sp.
USNM 481956	1.54	0	1.02	0	.67	1,2,6	Istiophoridae

face is dorsal or ventral. Schultz (1987) placed *I. rotundus* in *Xiphiorhynchus*, but it probably belongs to the genus *Makaira*. Until more is known about the morphology of *I. rotundus*, meaningful comparison with Lee Creek and recent istiophorids is fruitless.

"*Istiophorus*" *solidus* (Van Beneden, 1871) (IRSNB P643, holotype, late Eocene, Ghent, Belgium) is a poorly preserved rostral fragment with one pair of round nutrient canals that are placed more toward the lateral periphery than in other istiophorids. The specimen is 17 mm long, 27.3 mm wide, and 17.3 mm deep at its proximal end (D/W=0.63). The exact position and size of the nutrient canals have not been recorded. Paired grooves run the length of the dorsal surface and indicate the presence of paired prenasal bones. Schultz (1987) placed *I. solidus* in *Xiphiorhynchus*, but because of the lack of a central canal and the presence of prenasal bones, I believe the specimen is an istiophorid. Its morphology is unlike any species of recent billfish or billfish found at Lee Creek Mine, but the specimen is poorly preserved.

Istiophorus calvertensis Berry, 1917 (USNM 9344, holotype, late Miocene, Eastover Formation, Tar Bay, James River, Virginia), is a distal rostral fragment 310 mm long. Berry (1917) originally thought the specimen was collected in the Calvert Formation, but according to both R.E. Weems (pers. comm., 1996) and L.W. Ward (pers. comm., 1996) there is very little, if any, Calvert Formation at Tar Bay, and chances are very strong that it was collected in the late Miocene Eastover Formation of Ward and Blackwelder (1980). Both Weems and Ward admit, however, that the specimen could have been

collected in the Yorktown Formation, although it is unlikely due to the Yorktown Formation's minor presence at Tar Bay.

The specimen is 25.8 mm deep (D1) and 36.0 mm wide (W1) at its proximal end, which approximates 0.5L. A pair of nutrient canals are exposed, each measuring 7.0 mm high (H1) and located 11.0 mm from the dorsal surface of the rostrum (DD1). The anterior extension of the prenasal groove (P) is 170 mm from the distal tip; 0.25L is estimated to be 134 mm from the distal tip. The rostrum is 21.2 mm deep (D2) and 30.8 mm high (W2) at 0.25L. On the dorsal surface of the rostrum, denticles extend posteriorly from the distal tip for 57.3 mm (DZ).

Based on ratios computed from these measurements (Table 6) and on reexamination of the specimen (Fierstine, 1998), I identify this specimen as *Istiophorus* cf. *I. platypterus*. It has relatively large nutrient foramina (H1/D1) similar only to recent *I. platypterus* (Table 1), but the placement of the canals (DD1/D1) and area of the dorsal surface covered with denticles (DZ/P) are not sailfish-like. These latter two features are discounted because the dorsal denticular pattern may not have been completely preserved, and ratio DD1/D1 is nearly within the range of values for recent *I. platypterus*. Comparison of USNM 9344 to rostra from Lee Creek Mine (Table 3) shows that the D1/W1 ratio is similar to that in specimens identified as *I. platypterus*, the H1/D1 ratio is unlike that in any specimen studied, and the DZ/P ratio is similar to that in specimens identified as *Makaira* sp.

On the basis of its large nutrient canals, Schultz (1987) classified *I. calvertensis* in *Pseudohistiophorus* De Buen, 1950, a genus that Nakamura (1983) synonymized with *Tetrapturus*. Schultz made an erroneous decision because, as noted above,

TABLE 6.—Eight rostral variables (ratios) for six fossil istiophorid taxa from localities other than Lee Creek Mine. The presence or absence of denticles on the prenasal bone is unknown for these taxa. Abbreviations for ratios are explained in the text and in the legends to figures 3 and 4.

Ratio	<i>Istiophorus</i> cf. <i>I. platypterus</i> , type of <i>I. calvertensis</i> (USNM 9344)	<i>Makaira belgicus</i> , type specimen (IRSNB P1117)	<i>Makaira courcelli</i> , type specimen (MNHNP 250)	<i>Makaira panamensis</i> , type specimen (USNM 181710)	<i>Makaira teretirostris</i> , type specimen (depository unknown)	<i>Makaira nigricans</i> (LACM 17693)
	D1/W1	.72	—	.67	—	.87
H1/D1	.27	—	—	—	.10	—
DD1/D1	.43	—	—	—	.58	—
D2/W2	.69	.80	.66	.76	.84	.76
H2/D2	—	.15	—	.27	.11	.17
DD2/D2	—	.34	—	—	.56	.56
P/VSPM	—	—	—	—	—	—
DZ/P	.34	—	—	—	—	—

the size of the canals relative to the depth of the rostrum fits solely within the observed range of values for *I. platypterus* (Table 1). Fierstine (1990) thought critical review would synonymize *I. calvertensis* with *M. nigricans*; however, based on the information presented herein, the specimen belongs to the genus *Istiophorus*.

Istiophorus platypterus (Shaw and Nodder, 1792) was identified from a single, partial trunk vertebra (UCMP 125228) in upper Pliocene sediments, San Diego Formation, San Diego County, California, by Gottfried (1982). Until now, this vertebra was the only fossil record of a sailfish in the literature since the revision of the extant Istiophoridae (Robins and de Sylva, 1960, 1963; Nakamura, 1983, 1985). Because the specimen's exact position in the vertebral column is unknown, and because I studied only vertebrae from Lee Creek Mine that could be accurately identified to position 1, 22, 23, or 24 (hypural), I was unable to compare it to Lee Creek material.

Makaira belgicus (Leriche, 1926) (IRSNB P1117, holotype, middle Miocene, Anvers, Belgium) is a distal rostral fragment measuring 200 mm long, 32.3 mm wide (W2), and 25.9 mm deep (D2) at its proximal end. Prenasal bones are indicated by grooves, and paired nutrient canals are visible in cross section. Based on ratios in Table 6, the specimen falls within the range of values of recent *M. nigricans* (Table 1) and of *M. nigricans* from Lee Creek Mine (Table 3, except for the nutrient canals being closer to the dorsal surface of the rostrum (DD2/D2)).

Makaira courcellii (Arambourg, 1927) (MNHN 250, holotype, early Pliocene, Algeria) consists of two rostra and several fragments. One well-preserved rostrum is 287 mm long, with the following widths and depths in mm: D1=21.7, W1=32.6, D2=16.4, W2=24.8. Ratios for this specimen are listed in Table 6. The other rostrum is crushed at its proximal end and measurements were not taken. Each rostrum contains one pair of nutrient canals, but their size and position have not been measured. Denticles are restricted to the ventral and lateral surfaces of the well-preserved specimen, and paired prenasal grooves are present. Arambourg (1927) originally placed the specimens in *Xiphiorhynchus*; however, Schultz (1987) placed the specimens in *Makaira* and gave the age of the locality as late Miocene. Based on the ratios given in Table 6 and the distribution of the denticles, I agree with Schultz's identification. The lack of other morphological information precludes a meaningful comparison between *M. courcellii* and other fossil and extant istiophorids.

Makaira indica (Cuvier, 1832) was identified from a nearly complete head (including pectoral and pelvic girdles and fins) from the early Pleistocene, Cabatuan Formation, Luzon, Philippines, by Fierstine and Welton (1983). The specimen was identified by its rigid pectoral fin, a diagnostic feature of the black marlin. Until the present study, this specimen was the only record of a black marlin in the paleontological literature.

Makaira cf. *M. nigricans* Lacépède, 1802, was identified from an incomplete, disarticulated skull (USNM 375733) in the Eastover Formation, late Miocene, Virginia (Fierstine, 1998), and from a nearly complete rostrum (USNM 358534) in the

Gatún Formation, late Miocene, Panama (Fierstine, 1999b). The Eastover specimen is similar to recent *M. nigricans* in 15 of 19 ratios, but it is dissimilar in four, three of which are outside the observed range of all extant istiophorids. The Gatún specimen is similar to recent *M. indica* in 15 of 18 ratios, and it is similar to recent *M. nigricans* in 16 of 18 ratios. Two ratios that are similar to recent *M. indica*, but not *M. nigricans*, are discounted because they involve the denticular pattern on the dorsal surface of the rostrum, features that may have been incompletely preserved.

Makaira panamensis Fierstine, 1978 (USNM 181710, holotype, late Miocene or early Pliocene, Chagres Sandstone, Atlantic coast of Panama), was described from a large neurocranium with a poorly preserved rostrum attached. Except for its unique features (size of myodome, length of orbit, and relative size of nutrient canals), the specimen is most similar to recent blue marlin and black marlin; hence, the rationale for recognizing it as a new species of *Makaira*. If the rostrum without the neurocranium had been among material collected at Lee Creek, it would have been listed under "cf. *Makaira* sp." Fierstine (1978) believed the Chagres Sandstone was late Miocene based on Woodring (1957, 1970, 1973), but its age is now considered to be late Miocene or early Pliocene (Woodring, 1982) or Pliocene (Coates et al., 1992).

Makaira sp. was identified from several bones from late Miocene localities in Southern California. Fierstine and Applegate (1968) studied a distal rostrum (LACM 17693) and prementary bone (LACM 16074) from separate localities in Orange County, California, and Fierstine and Welton (1988) examined several associated bones (articular, dentary, preoperculum, pterygiophores) of a single individual marlin (UCMP 118559) from the San Mateo Formation, San Diego County, California. The specimens were originally identified as *Makaira* sp. because of a lack of recent comparative material, but now that skeletal material is available, I have reexamined them with the following results.

Extant *Makaira nigricans* (Table 1) is the common identification for all three ratios computed for the rostrum (Table 6). Because the ratios of the prementary (PW/PL=0.62, PD/PL=0.37, PD/PW=0.60) fall within the observed range of values (Table 2) for both *Istiophorus platypterus* and *M. nigricans*, it is identified as Istiophoridae, genus and species indeterminate.

Analysis of the articular and dentary bones separately, as in the Lee Creek fossils, yields an identification of Istiophoridae, genus and species indeterminate, for both; however, when they are considered as skeletal elements from a single fish, then *M. nigricans* becomes the obvious choice. The ratios of the articular are within the observed values for sailfish, blue marlin, and white marlin, whereas the ratio of the dentary is within the observed values for blue marlin and striped marlin; therefore, the common identification for the two bones is *M. nigricans*.

Makaira teretirostris (Van Beneden, 1871) (?middle Miocene, Belgium, exact locality unknown) is a large, distal rostral fragment (520 mm long) with paired nutrient canals and prenasal bones. Denticles and alveoli are neither mentioned nor

figured. The original description of the specimen was based on a cast and an artist's drawing, and disposition of the type is unknown. Schultz (1987) synonymized the specimen with *M. belgicus* and gave the type locality as southern France and the age as Pliocene. I made measurements from the drawing in Van Beneden (1871) and computed ratios (Table 6). Based on this analysis, *M. teretirostris* is slightly outside the observed range of ratios of recent *M. nigricans* (compare Tables 1, 6) but is within the range of values of *M. cf. M. nigricans* from Lee Creek Mine (Table 3). Without more information about the specimen, I recognize *M. teretirostris* and do not synonymize it with *M. belgicus*.

Lawley (1876) described a well-worn, elongate, slender rostrum from lower Pliocene rocks, Orciano, Italy, as *Brachyrhynchus vanbenedensis*. The specimen was redescribed, refigured, and placed into the living *Histiophorus herschelii* (Gray, 1838) by Barbolani (1910). Nakamura et al. (1968) synonymized *H. herschelii* with *M. nigricans*, and more recently Schultz (1987) placed *B. vanbenedensis* in synonymy with *M. teretirostris*. Until the specimen is studied further, I follow Schultz (1987).

In summary, the family Istiophoridae has a fossil history from middle Miocene to recent, with the qualification that "*Istiophorus*" *solidus* (late Eocene, Ghent, Belgium) may be an istiophorid. *Makaira belgicus* (middle Miocene, Anvers, Belgium), *Istiophorus cf. I. platypterus* (late Miocene, Eastover Formation, Virginia, United States), and *Tetrapturus albidus* (early Pliocene, Yorktown Formation, North Carolina, United States) are the oldest known species within their respective genera. The temporal distribution of the Istiophoridae is given in Figure 7.

INTERSPECIFIC AND INTRASPECIFIC VARIATION.—Any study of variation at Lee Creek Mine is dependent upon two factors: the number of fossil bones identified to species and the number of bones examined for each extant species. Only *Makaira nigricans* is sufficiently represented at Lee Creek to make a statistically meaningful comparison, and then only for a few bones.

Significant differences exist only between the predentary, rostrum, scapula, and vertebrae 1 and 23 of extant *M. nigricans* and *M. nigricans* from Lee Creek Mine (Table 7). The predentary in the Lee Creek specimens tends to be wider (PW/PL), deeper (PD/PL), and rounder in cross section (PD/PW). The rostra from Lee Creek tend to have rounder cross sections throughout their length, and the nutrient canals are smaller distally (H2/D2) and are more ventrally placed both proximally (DD1/D1) and distally (DD2/D2). In addition, the distal dorsal surface of the rostrum (DZ/P) is covered with more denticles than in the extant blue marlin. The scapulae from Lee Creek Mine have a narrower articular surface (SNW/SL, SNW/SGW). First vertebrae from Lee Creek Mine exhibit a narrower anterior articular surface (LAD/CL) and a more constricted centrum (NW/LPD) with respect to their length. Twenty-third vertebrae of the blue marlin from Lee Creek have centra that are less depressed anteriorly (VAD/CL) and more constricted (NW/LPD) with respect to their posterior width.

Blue marlin from Lee Creek Mine are more similar to extant black marlin than to extant blue marlin in two features (Table 8). The predentary bone in Lee Creek material is rounder (PD/PW) than in extant blue marlin, and the dorsal surface of the distal rostrum has more denticles (DZ/P). So few vertebrae of extant black marlin were examined that no meaningful comparison with Lee Creek specimens was undertaken.

TABLE 7.—Results of the unpaired *t*-test (Welch's modification) to determine significant differences between the means of variables (ratios) of the predentary, rostrum, scapula, and two vertebrae among *Makaira nigricans* from Lee Creek Mine and extant *M. nigricans*. Abbreviations for ratios are explained in the text and in the legends to figures 2–5. (*= $P < 0.05$; **= $P < 0.01$; ***= $P < 0.001$.)

Ratio	Extant <i>M. nigricans</i> compared with Lee Creek <i>M. nigricans</i>
Predentary	
PW/PL	*
PD/PL	***
PD/PW	***
Rostrum	
D1/W1	**
DD1/D1	***
D2/W2	***
H2/D2	**
DD2/D2	**
DZ/P	*
Scapula	
SNW/SL	**
SNW/SGW	*
Vertebra 1	
LAD/CL	***
NW/LPD	*
Vertebra 23	
VAD/CL	*
NW/LPD	*

TABLE 8.—Results of the unpaired *t*-test (Welch's modification) to determine significant differences in the means of the same variables (ratios) listed in Table 7 for the predentary, rostrum, and scapula among *Makaira nigricans* from Lee Creek Mine and extant *M. indica*. Abbreviations for ratios are explained in the text and in the legends to figures 2–5. (n.s.=not significant ($P > 0.05$); *= $P < 0.05$; **= $P < 0.01$; ***= $P < 0.001$.)

Ratio	Extant <i>M. indica</i> compared with Lee Creek <i>M. nigricans</i>
Predentary	
PW/PL	***
PD/PL	**
PD/PW	n.s.
Rostrum	
D1/W1	*
DD1/D1	***
D2/W2	***
H2/D2	***
DD2/D2	**
DZ/P	n.s.
Scapula	
SNW/SL	**
SNW/SGW	*

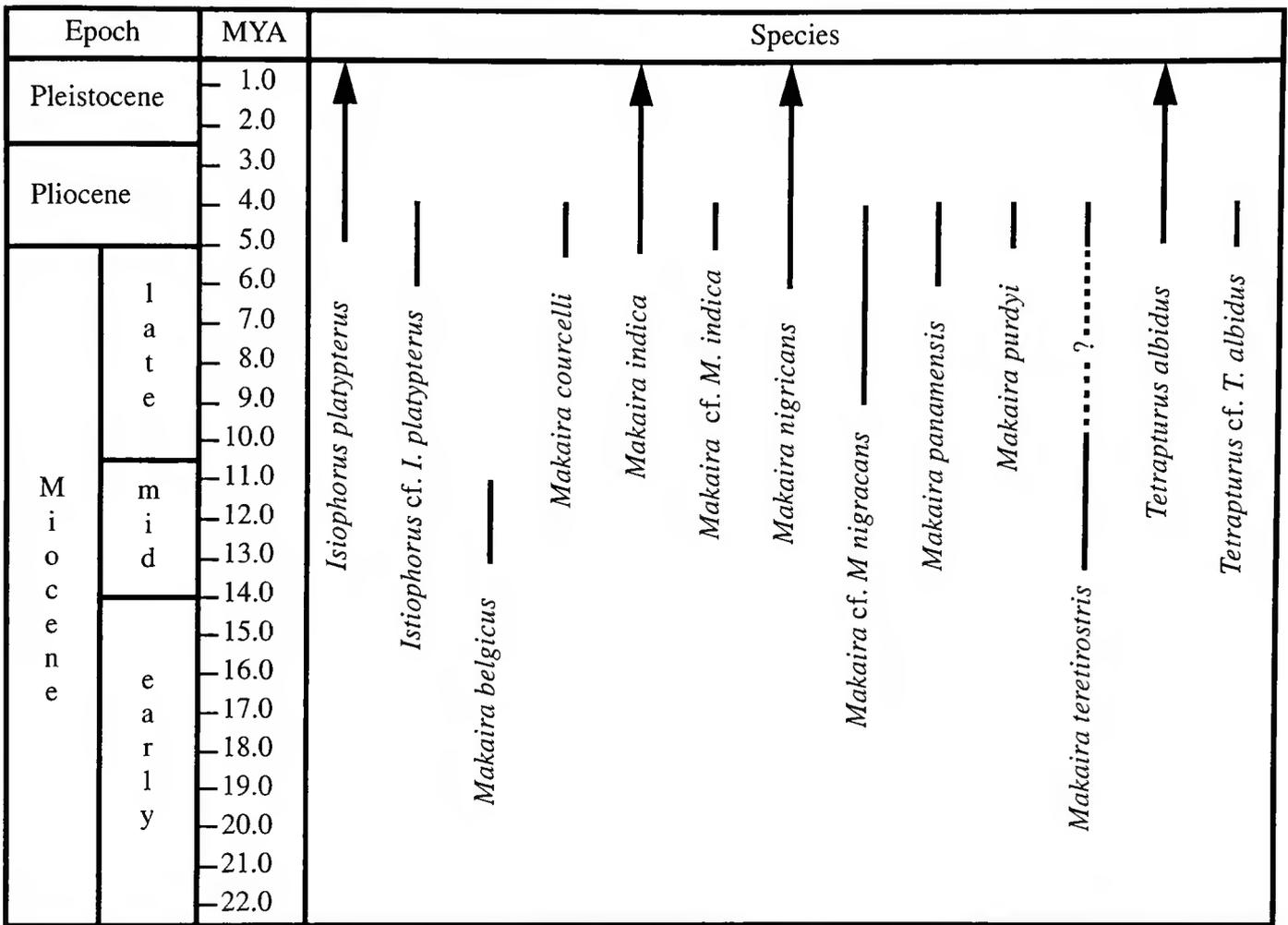


FIGURE 7.—Temporal distribution of the family Istiophoridae. Arrow indicates species that exist in recent time. Time scale is from Gibson (1983:38 (uncopyrighted)).

Some of the rostra at Lee Creek Mine demonstrate abnormalities found in extant billfish (Gudger, 1940; Morrow, 1951; Firerstone and Voigt, 1996). For example, rostrum USNM 481976 (Plate 7a-c) has a foreshortened tip with nutrient canals exposed distally, and rostrum USNM 475409 (Plate 2h) has unequal-sized nutrient canals. Rostrum USNM 481984 (Plate 2i,j) and a few others appear eroded, possibly by stomach acids after being consumed by a predator.

DISTRIBUTION AND LIFE HISTORY OF RECENT SPECIES.—The following information was taken liberally from Nakamura (1983, 1985) unless otherwise indicated. Emphasis is placed on species that inhabit the Atlantic Ocean and are found at Lee Creek Mine. In general, istiophorids are distributed throughout tropical and subtropical waters, some entering temperate climates. All are oceanic and epipelagic species that usually favor waters greater than 20°C. Sexes are separate and are indistinguishable externally. Each species has a distinct reproductive season and spawning ground, and mature individuals spawn

several times each season by broadcasting gametes (Hopper, 1986). Adults are opportunistic predators, consuming cephalopods (squids) and many different species of pelagic fishes, including members of the Carangidae (jacks), Clupeidae (herrings, pilchards, sardines), Coryphaenidae (dolphin-fish), Scombridae (mackerels, tunas, and allies), and Trichiuridae (snake mackerels, cutlass fishes). Although age estimates are given below for some species, aging of billfish is imprecise because of the difficulty in establishing annual growth patterns in calcified structures (Hill et al., 1989). Frazier et al. (1995) concluded the function of the rostrum was unclear. It may serve in one or more capacities, possibly in hydrodynamics, food capture (spearing/slashing), or defense/aggression, but the fish can get along without its bill because there are numerous records of apparently healthy billfishes with damaged, malformed, or missing rostra.

Istiophorus platypterus (sailfish) inhabits the Atlantic, Indian, and Pacific oceans, possibly the Mediterranean Sea, and

sometimes enters the Red Sea through the Suez Canal. It is considered to be the least oceanic of the billfishes, often migrating to near-shore waters. Its distribution is influenced by wind and water temperature, favoring temperatures of 21°–28°C. In the western North Atlantic and western Pacific oceans, *I. platypterus* migrates northward in an extension of warm water during the summer and migrates southward with the onset of cold weather to form loose schools of up to 30 individuals. The sailfish reaches a total length of around 3.2 m (tip of bill to tip of tail) and a weight of 58 kg in the Atlantic Ocean and reaches around 3.4 m total length and 100 kg in weight in the Indo-Pacific Ocean. Females are consistently larger than males (Jolley, 1974). Tagged sailfish are generally recaptured near their original release site; however, one specimen caught off Isla Mujeres, Mexico, in the Caribbean was recaptured 2596 km distant off La Guiria, Venezuela (National Marine Fisheries Service, 1994). De Sylva (1957) reported that sailfish grow rapidly, attaining a weight of 9.1 kg within one year and having an estimated life span of two to three years. Jolley (1974), using a different aging method, found that sailfish in the Atlantic Ocean reached an age of seven years, with ages two to four being the most numerous.

Makaira indica (black marlin) is restricted to tropical and subtropical waters of the Indian and Pacific oceans, except for occasional strays into the Atlantic Ocean via the Cape of Good Hope. It is found in waters with surface temperatures ranging from 15°–30°C and is often found as close to land masses as is *Istiophorus platypterus*. The distribution and abundance of *M. indica* off Natal are positively influenced by the presence of submarine canyons, some reaching a depth of 600 m within one km of shore (van der Elst, 1990). The black marlin reaches a total length of 4.48 m and a weight of 708 kg. Females grow more rapidly than males so that at any given age males are much smaller than females (Hopper, 1986). Fish tagged off northern Queensland, Australia, generally are recaptured north or south of their point of release. One specimen released off Baja California was recaptured north of New Zealand, thereby making a trans-Pacific and trans-equatorial migration of 5700 km (Pepperell, 1990).

Makaira nigricans (blue marlin) inhabits the tropical and temperate waters of the Atlantic, Indian, and Pacific oceans. It is the most tropical of all billfishes, favoring blue water (depths greater than 100 m) at surface temperatures around 24°C (22°–31°C). The blue marlin in the Atlantic Ocean reaches a total length of approximately 4.0 m and a weight of 580 kg, whereas in the Pacific Ocean it reaches a total length of approximately 4.5 m and a weight of 906 kg. Although most tagged blue marlin are recaptured near their point of release, one fish traveled at least 16,871 km from the North Atlantic Ocean off Delaware, across the equator to the Indian Ocean near Madagascar, presumably via the Cape of Good Hope (National Marine Fisheries Service, 1994). As in *M. indica*, females grow more rapidly than males, so that at the same age females are much larger than males (Hopper, 1986). Both sexes become sexually mature at around six to eight

years of age. During the reproductive season (usually summer), smaller males outnumber the larger females by as much as six to one (Hopper, 1990). Based on preliminary estimates from blue marlin caught off Kona, Hawaii, longevity is at least 18 years for males and at least 27 years for females (Hill et al., 1989).

According to Browder and Prince (1990), blue marlin are most abundant off the mid-Atlantic coast in the summer. May and June are probably spawning months for blue marlin off Florida and the Bahamas. Adult fish off Cape Hatteras in June appeared to have already spawned.

Tetrapturus albidus (white marlin) inhabits much of the Atlantic Ocean, including the Gulf of Mexico and Caribbean Sea, from 45°N to 45°S in the western South Atlantic and to 35°S in the eastern South Atlantic. A few individuals are known from the Mediterranean Sea and from off Brittany, France. The white marlin is usually found in blue water and favors surface temperatures greater than 22°C. Steep drop-offs, submarine canyons, and shoals are often scenes of important feeding concentrations. They migrate to subtropical waters to spawn, with peak spawning in the summer. Females become larger than males, and during the spawning season males outnumber females on the spawning grounds. Most tagged white marlin were recaptured nearby, some after two or more years at large. Individuals, however, can travel long distances. One fish released in the United States Virgin Islands in 1991 was recaptured one year later off Mohammedia, Morocco, a transoceanic and transequatorial movement of 5840 km (National Marine Fisheries Service, 1994). White marlin attain a maximum size of 2.0 m (lower jaw to fork of caudal fin) and a weight of 79 kg.

Tetrapturus audax (striped marlin) and *T. angustirostris* (shortbill spearfish) inhabit mainly the tropical, subtropical, and temperate waters of the Pacific and Indian oceans, occasionally straying into the Atlantic Ocean via the Cape of Good Hope. Striped marlin prefer more temperate water than other billfishes, and shortbill spearfish are more oceanic, favoring waters greater than 900 m in depth. *Tetrapturus belone* (Mediterranean spearfish) is limited in distribution to the Mediterranean Sea, and *T. pfluegeri* (longbill spearfish) is widely distributed in the Atlantic Ocean from approximately 40°N to 35°S. Striped marlin attain the largest size and weight of any species of *Tetrapturus*, reaching a length (tip of bill to fork of caudal fin) of 3.5 m and a weight of 200 kg. Maximum body lengths (tip of lower jaw to fork of caudal fin) and weights, respectively, are approximately 2.4 m and 70 kg for the Mediterranean spearfish, 2.0 m and 52 kg for the shortbill spearfish, and 2.0 m and 45 kg for the longbill spearfish. A striped marlin tagged off Cabo San Lucas, Baja California Sur, Mexico, was recaptured near Norfolk Island in the South Pacific, a distance of 9600 km (Squire and Suzuki, 1990). Movement patterns of spearfishes are poorly understood.

IMPLICATIONS OF DISTRIBUTION AND LIFE HISTORY OF RECENT SPECIES FOR LEE CREEK MINE FOSSILS.—The presence of *Makaira indica* at Lee Creek Mine is unexpected based on

its present distribution. During or prior to the early Pliocene, the black marlin may have had access to the North Atlantic Ocean via a more favorable environment than the Cape of Good Hope. According to Coates et al. (1992), the final closure of the Isthmus of Panama occurred around 3.5 Ma BP, 1.0–1.5 Ma after Yorktown time at Lee Creek (Hazel, 1983). Coates et al. (1992) also believed that depths prior to closure ranged from shallow to shallow inner shelf (<200 m) and upper slope (200–800 m) on the Caribbean side of Panama to a trench-slope environment on the Pacific side. *Makaira indica* is often found near land masses, islands, and coral reef areas (Nakamura, 1985). Therefore, during and prior to Yorktown time the Panama region was not a barrier but was a route for black marlin migrating between the Atlantic and Pacific oceans. Whitmore and Stewart (1965) believed the Canal Zone was the site of a narrow seaway throughout most of the Tertiary.

There is other evidence that the Panama seaway was a migration route for vertebrates. According to Purdy et al. (this volume), the sharks *Carcharhinus macloiti* and *Triaenodon obesus* are present at Lee Creek Mine. Both species inhabit only the tropical Indo-Pacific Ocean today (Compagno, 1984). Gillette (1984) concluded that the ichthyofauna of the Miocene Gatún Formation (Panama) resembles the marine faunas of North Carolina (Pungo Formation), Ecuador, and the Antilles. Finally, the presence of the sirenian *Metaxytherium calvertense* Kellogg in both the middle Miocene Calvert Formation (Maryland, United States) and the correlative Montera Formation in Peru (de Muizon and Domning, 1985) and the presence of *Metaxytherium arctodites* Aranda-Manteca, Domning, and Barnes, 1994, in Mexico and California, further suggests there were faunistic exchanges between the Atlantic and Pacific oceans during the mid-Neogene.

The presence of *Istiophorus platypterus*, *Makaira nigricans*, and *Tetrapturus albidus* at Lee Creek Mine fits the distribution of extant species in the northwestern Atlantic Ocean today. The blue marlin is much more abundant at Lee Creek Mine than are the other two species, but this may be due to collection bias or to difficulty in identifying isolated and fragmentary elements.

Recent *Makaira nigricans* and most other billfish favor blue water (>100 m depth) and water temperatures of 22°–31°C, so it is likely that billfish during Lee Creek time preferred the same environments. Based on Gibson's (1983) conclusion that zone 1 of the Yorktown Formation was deposited at water depths of 80 m to 100 m and zone 2 was deposited at depths of less than 30 m, I believe that most, if not all, adult billfish specimens were collected in zone 1 (basal Yorktown Formation).

If one assumes, based on my sample of 38 recent blue marlin where sex was known, that all fish with a rostrum width greater than 23.0 mm (measured at one-fourth bill length, or 0.25L) are female, then blue marlin at Lee Creek Mine have a sex ratio of approximately one male to two females. The ratio of males to females would be much larger in a spawning population (Hop-

per, 1990); therefore, I hypothesize that the present pattern of blue marlin migrating northward in the western North Atlantic Ocean during the summer to feed after spawning was established during Yorktown time or earlier.

Frazier et al. (1995) and Fierstine and Crimmen (1996) have reviewed the literature of extant istiophorids impaling inanimate and animate objects with their rostrum. They noted that healthy billfish have been captured with shortened bills and assumed damage occurred when the fish broke away from its impalement. Although the reasons for spearing behavior are unclear, foreshortened bills at Lee Creek Mine is evidence that the behavior was established during Yorktown times or earlier.

STUDY LIMITATIONS.—Purdy et al. (this volume) have pointed out many of the pitfalls that reduce understanding of the Lee Creek Mine fauna. They believed careful excavation of units 1–3 of the Yorktown Formation, rather than surface collecting from spoil piles, would have produced articulated skeletons and less fragmentary material. Strict stratigraphic control is critical for exploration of changes in species composition (seasonal or throughout Yorktown time) and for collecting paleoecological data. Partial or whole, articulated skeletons would have made identification more convincing because identification would have been based on measurements of several elements, not just those from one fragmentary bone. Also, more complete skeletal material from recent species, especially black marlin and most of the species of *Tetrapturus*, would have increased our knowledge of interspecific and intraspecific variation of the Istiophoridae and would have made comparisons more certain.

Conclusions

The identification of *Istiophorus platypterus*, *Makaira indica*, *M. nigricans*, *M. purdyi*, and *Tetrapturus albidus* at Lee Creek Mine is very significant. It is the only record of *Makaira purdyi*, the first fossil record of the genus *Tetrapturus*, specifically *T. albidus*, the second fossil record of *I. platypterus* and *M. indica*, and the first record of *I. platypterus*, *M. indica*, *M. nigricans*, and *T. albidus* from fossil deposits bordering the Atlantic Ocean.

The presence of *M. indica* at Lee Creek suggests that the Panama seaway may have been a migration route for billfish during the early Pliocene. The concentration of billfish at Lee Creek Mine supports the contention that the Yorktown Formation represents a tropical to warm temperate (21°–28°C) oceanic environment that was deposited at depths greater than 100 m.

Based on the size of isolated bones at Lee Creek Mine, *I. platypterus* and *T. albidus* are estimated to have reached much larger sizes and weights than their living representatives. *Makaira nigricans* from Lee Creek are more similar to extant *M. indica* than to extant *M. nigricans* in two features, a more round prementary and a greater area of denticles on the dorsal surface of the distal rostrum.

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Plates

PLATE I

Istiophoridae, genus and species indeterminate
Yorktown Formation, Lee Creek Mine

- a, b.* NCSM 5576, right articular: *a*, lateral view; *b*, dorsal view of joint with quadrate.
- c.* USNM 488084, left dentary, medial view of interdentary joint.
- d.* USNM 290202, first pectoral-fin ray, view of articular facet for scapula.
- e.* NCSM 5297, first pectoral-fin ray, view of articular facet for scapula.
- f, g.* USNM 475425, left maxilla: *f*, lateral view; *g*, dorsal view.
- h, i.* USNM 284815, parasphenoid: *h*, ventral view; *i*, left lateral view.
- j, k.* USNM 481956, predentary: *j*, right lateral view; *k*, dorsal view.

Each scale bar=2 cm

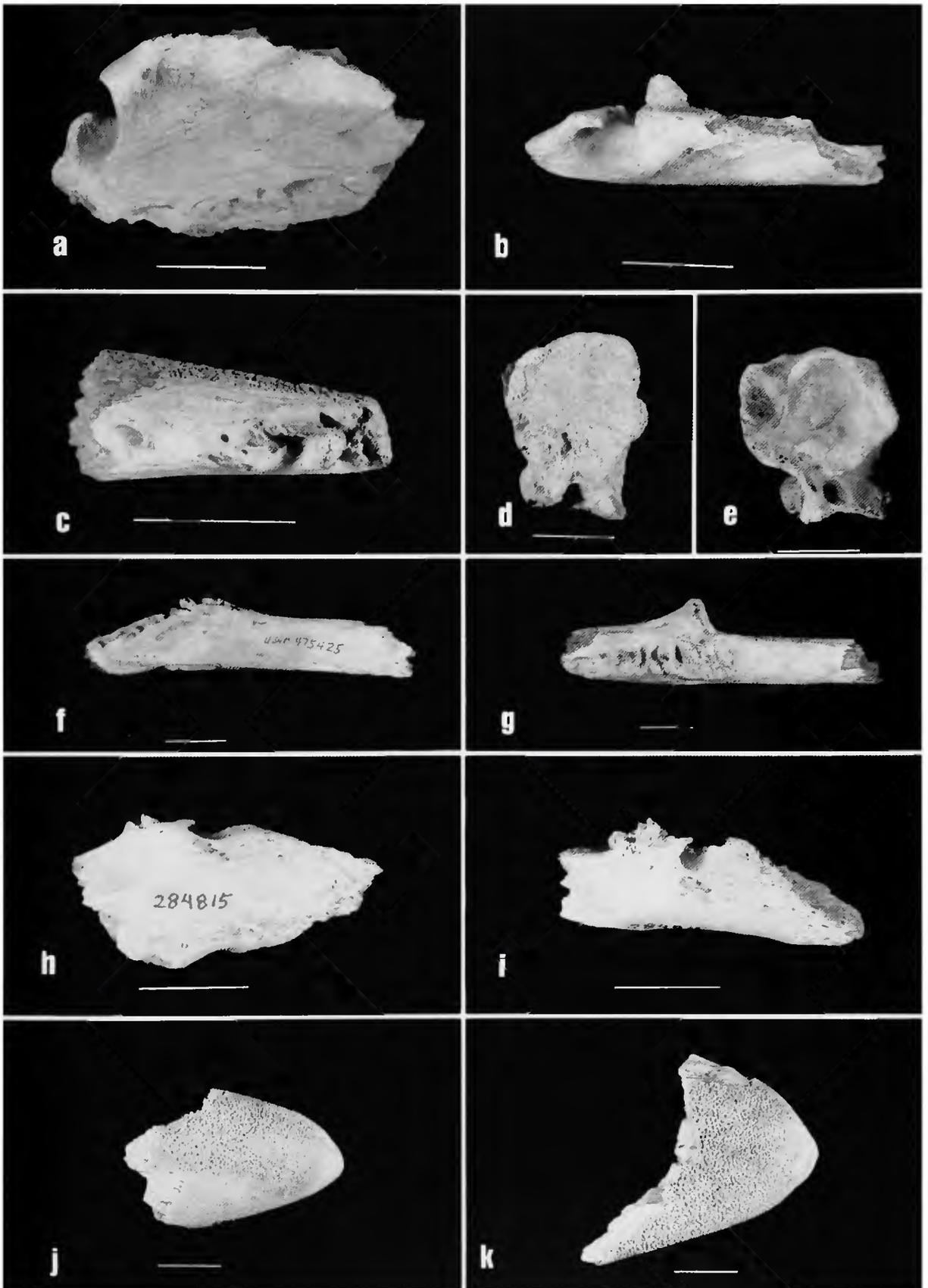


PLATE 2

Istiophoridae, genus and species indeterminate
Yorktown Formation, Lee Creek Mine

- a, b.* USNM 481915, left quadrate: *a*, lateral view; *b*, view of articular condyle for articular.
c–e. USNM 481939, rostrum: *c*, left lateral view; *d*, dorsal view; *e*, cross section.
f–h. USNM 475409, rostrum: *f*, left lateral view; *g*, dorsal view; *h*, cross section.
i, j. USNM 481984, rostrum: *i*, left lateral view; *j*, dorsal view.

Each scale bar=2 cm

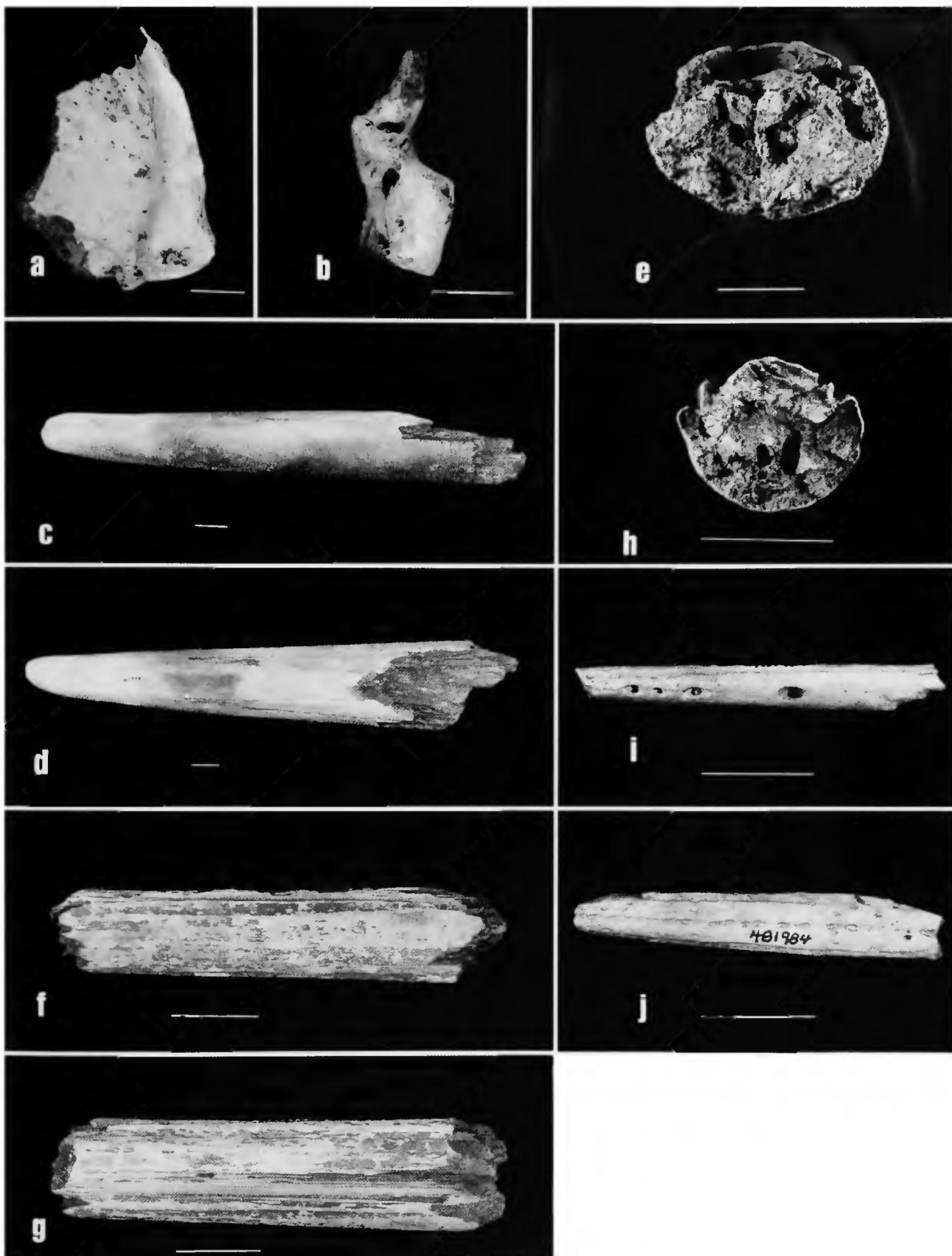


PLATE 3

Makaira purdyi Fierstine, 1999a
Yorktown Formation, Lee Creek Mine

a-c. USNM 481933 (holotype), rostrum: *a*, left lateral view; *b*, dorsal view; *c*, ventral view.

Istiophoridae, genus and species indeterminate
Yorktown Formation, Lee Creek Mine

d. NCSM 7902, right scapula, view of articular surface for first pectoral-fin ray.
e,f. NCSM 4914, vertebra 1: *e*, left lateral view; *f*, anterior view.
g,h. USNM 481982, hypural: *g*, left lateral view; *h*, anterior view.

Each scale bar = 2 cm

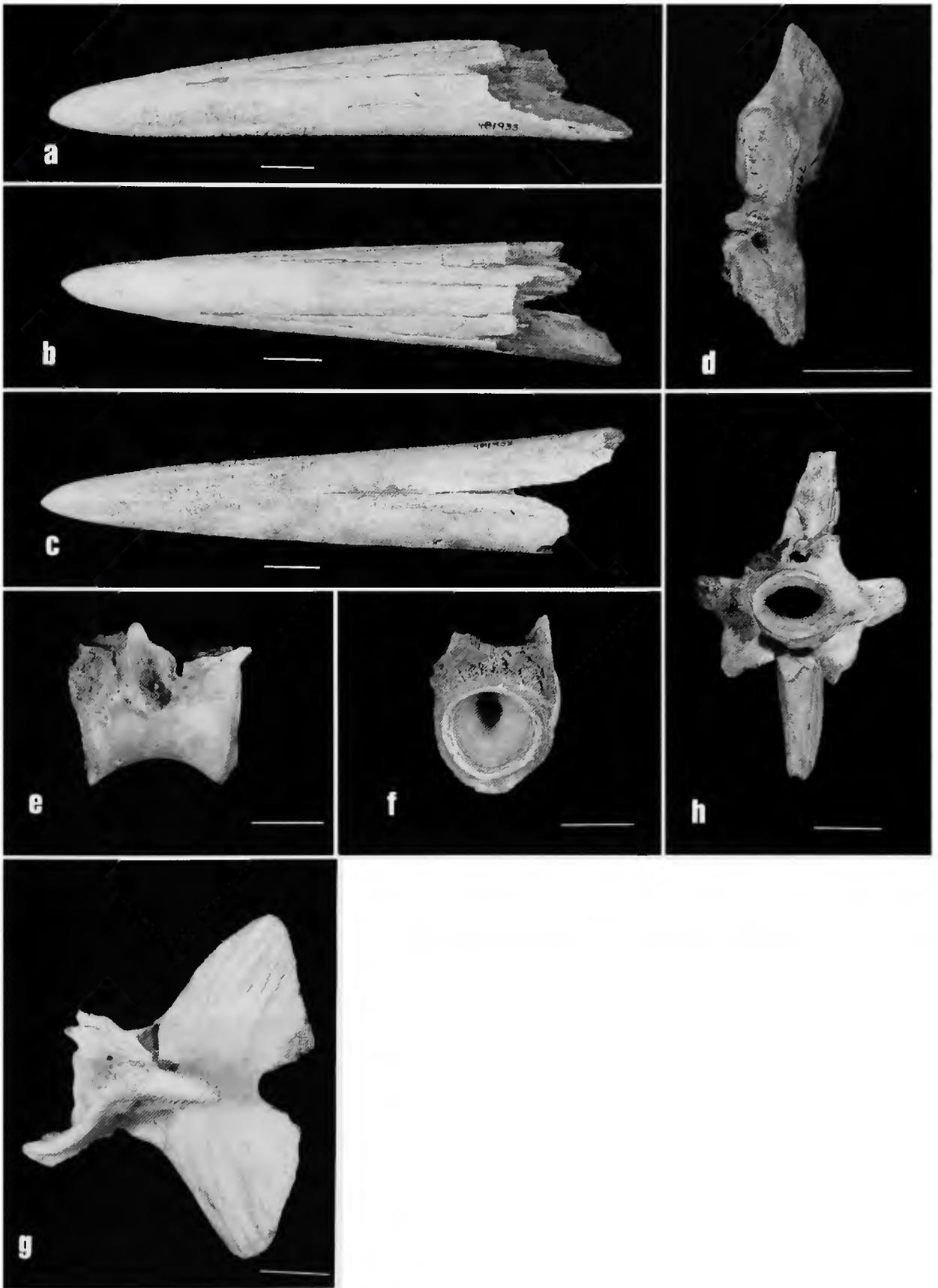


PLATE 4

Istiophorus platypterus (Shaw and Nodder, 1792)
Yorktown Formation, Lee Creek Mine

- a, b.* USNM 290198, left maxilla: *a*, dorsal view; *b*, lateral view.
c–e. USNM 481973, rostrum: *c*, left lateral view; *d*, dorsal view; *e*, cross section.
f–h. USNM 286949, rostrum: *f*, dorsal view; *g*, left lateral view; *h*, cross section.
i–k. USNM 481967, rostrum: *i*, left lateral view; *j*, cross section; *k*, dorsal view.

Each scale bar = 2 cm

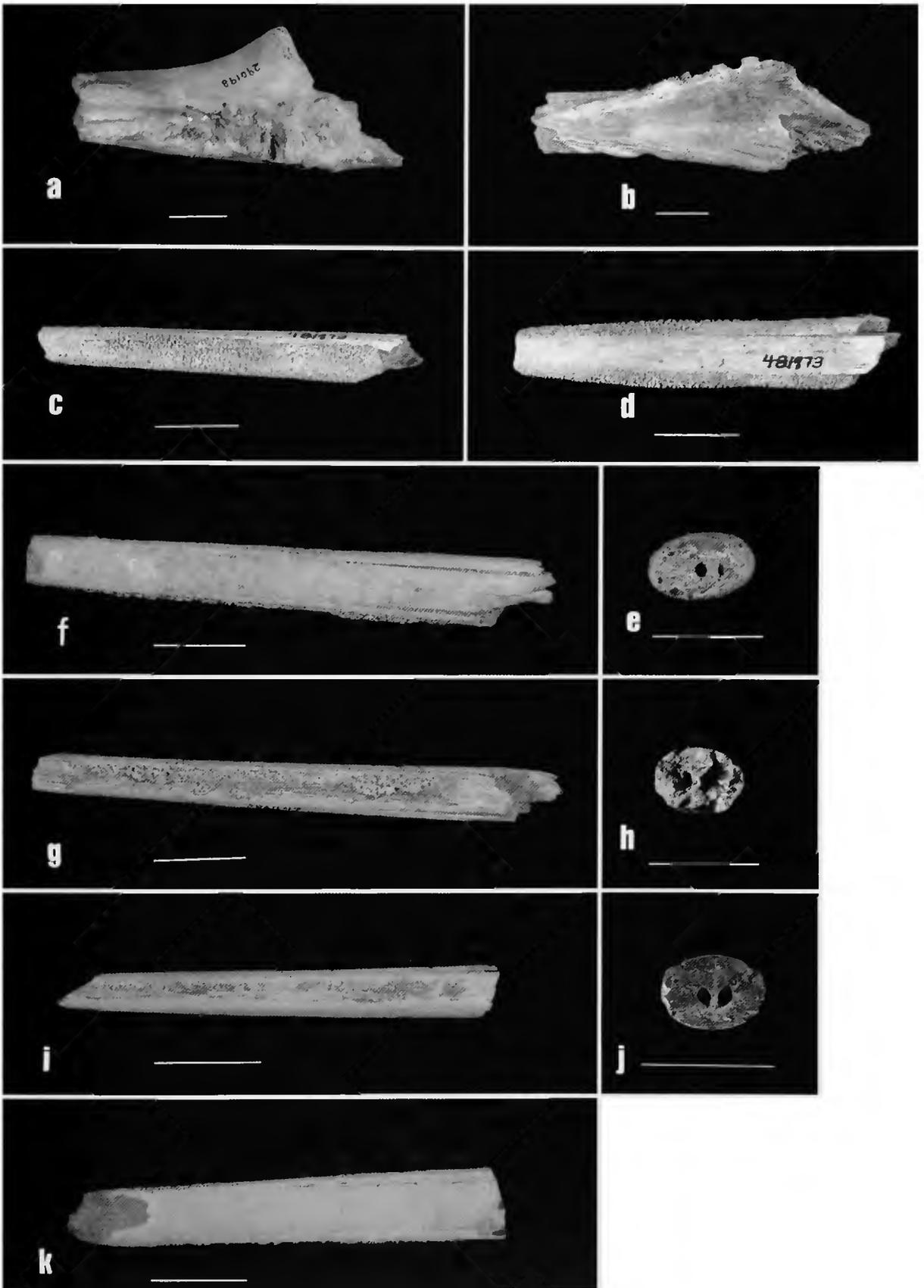


PLATE 5

Istiophorus cf. *I. platypterus* (Shaw and Nodder, 1792)
Yorktown Formation, Lee Creek Mine

- a-c.* USNM 286950, rostrum: *a*, left lateral view; *b*, dorsal view; *c*, cross section.
d,e. USNM 488093, hypural: *d*, left lateral view; *e*, anterior view.

Makaira indica (Cuvier, 1832)
Yorktown Formation, Lee Creek Mine

- f.* USNM 481927, right scapula, view of articular surface for first pectoral-fin ray.
g. USNM 488112, right scapula, view of articular surface for first pectoral-fin ray.
h,i. USNM 475399, predentary: *h*, right lateral view; *i*, dorsal view.
j,k. USNM 488009, predentary: *j*, right lateral view; *k*, dorsal view.

Makaira cf. *M. indica* (Cuvier, 1832)
Yorktown Formation, Lee Creek Mine

- l.* USNM 488100, left scapula, view of articular surface for first pectoral-fin ray.

Each scale bar = 2 cm

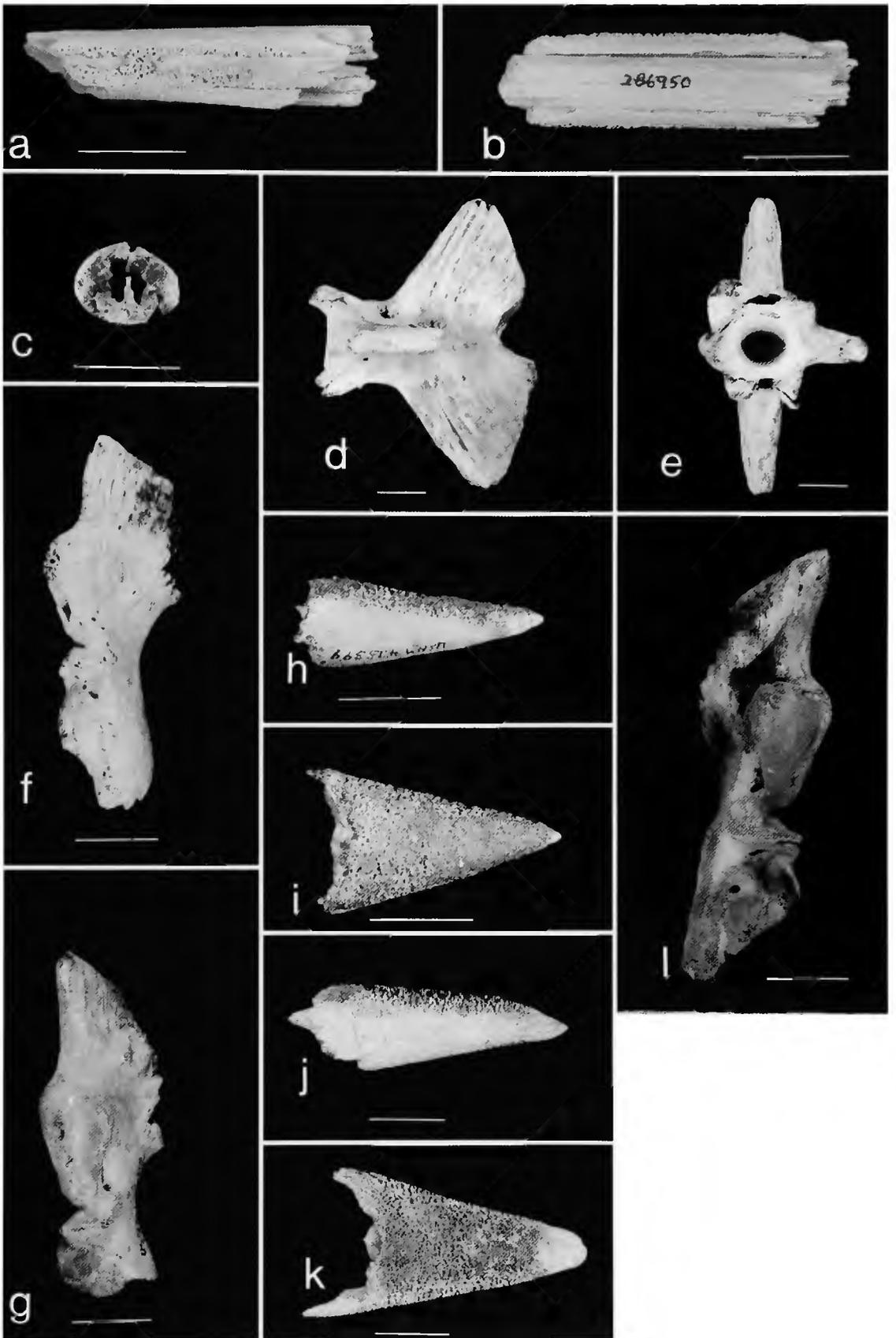


PLATE 6

Makaira nigricans Lacépède, 1802
Yorktown Formation, Lee Creek Mine

- a.* NCSM 2125, left dentary, medial view of interdental joint.
- b,d.* NCSM 5159, parasphenoid: *b*, left lateral view; *d*, ventral view.
- c,e.* USNM 291066, predentary: *c*, dorsal view; *e*, left lateral view.
- f,h,j.* USNM 481941, rostrum: *f*, left lateral view; *h*, dorsal view; *j*, cross section.
- g,i.* USNM 481936, predentary: *g*, dorsal view; *i*, left lateral view.
- k-m.* USNM 481943, rostrum: *k*, cross section; *l*, left lateral view; *m*, dorsal view.

Each scale bar = 2 cm

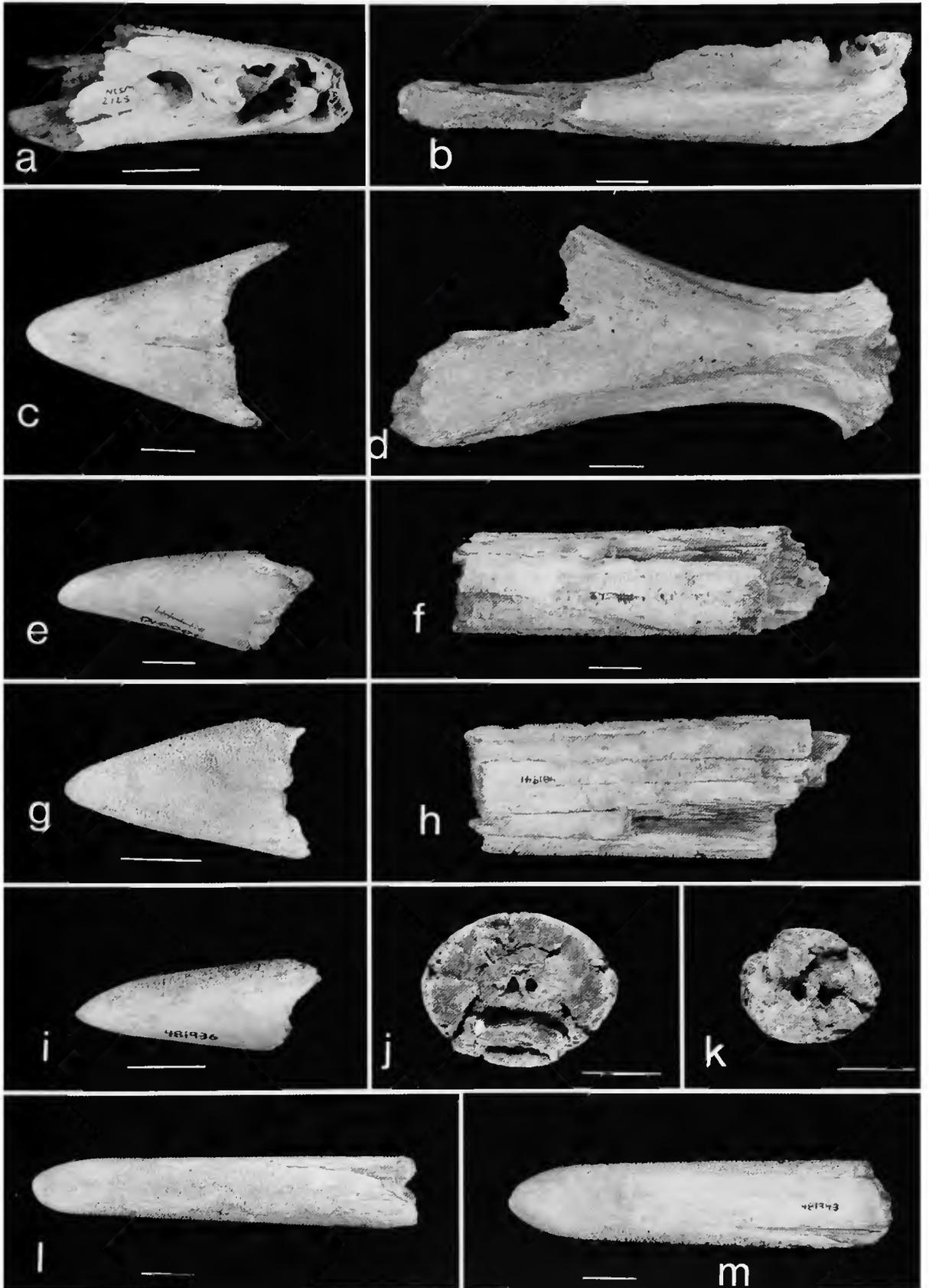


PLATE 7

Makaira nigricans Lacépède, 1802
Yorktown Formation, Lee Creek Mine

- a-c.* USNM 481976, rostrum: *a*, left lateral view; *b*, dorsal view; *c*, view of nutrient canals exposed at distal tip.
- d.* USNM 421527, right scapula, view of articular surface for first pectoral-fin ray.
- e.* USNM 290197, right scapula, view of articular surface for first pectoral-fin ray.
- f,h.* USNM 286179, vertebra 23: *f*, left lateral view; *h*, anterior view.
- g,l.* USNM 286181, vertebra 22: *g*, anterior view; *l*, left lateral view.
- i,k.* USNM 481923, vertebra 1: *i*, anterior view; *k*, left lateral view.
- j,m.* NCSM 4938, hypural: *j*, anterior view; *m*, left lateral view.

Each scale bar=2 cm

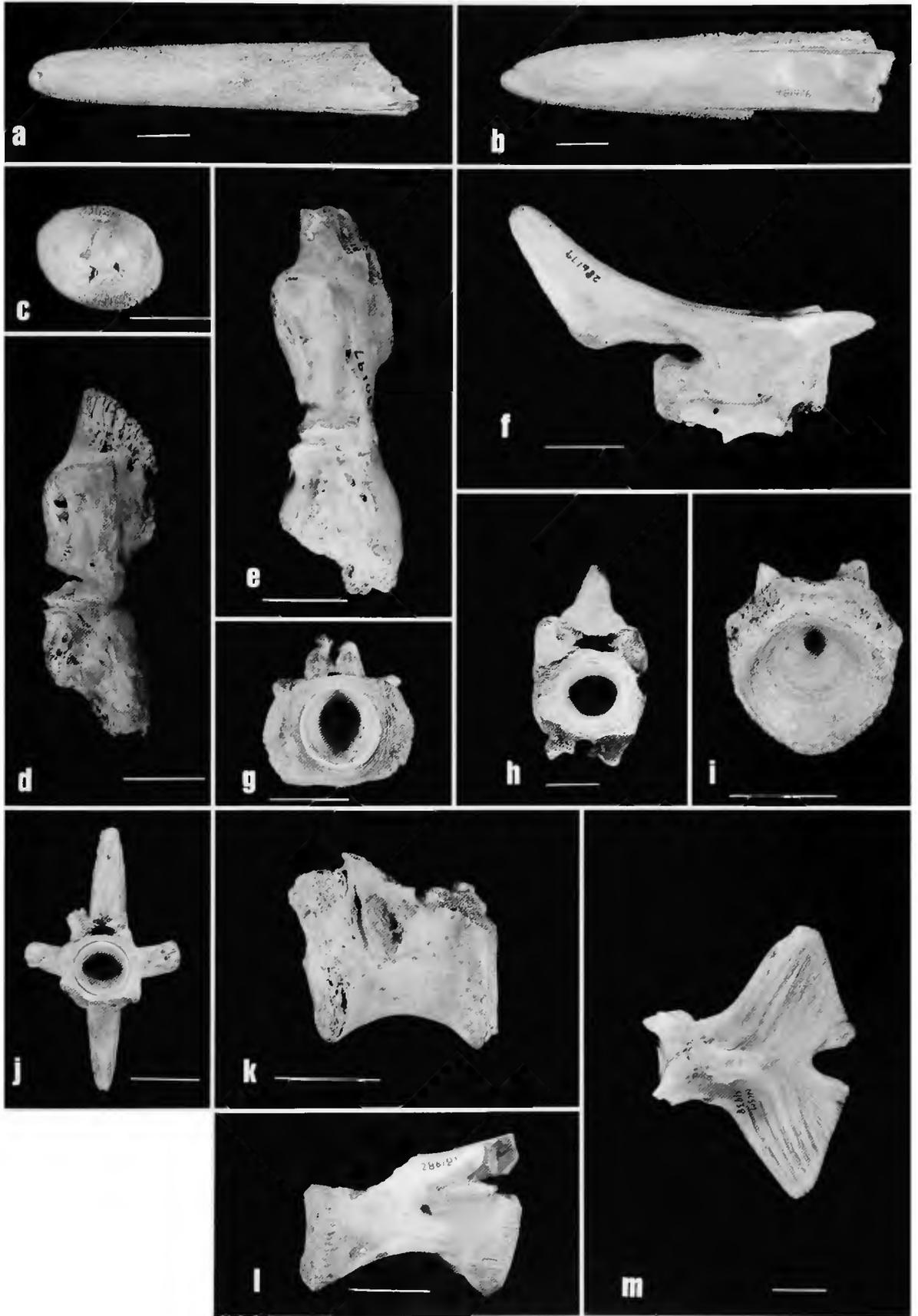


PLATE 8

Makaira cf. *M. nigricans* Lacépède, 1802
Yorktown Formation, Lee Creek Mine

- a,j.* NCSM 6944, left quadrate: *a*, lateral view; *j*, view of articular condyle for the articular.
b,c. NCSM 7427, rostrum: *b*, left lateral view; *c*, dorsal view.
d,f. USNM 488116, parasphenoid: *d*, right lateral view; *f*, ventral view.
e,g. USNM 481944, rostrum: *e*, left lateral view; *g*, dorsal view.
h,i. USNM 481897, vertebra 1: *h*, left lateral view; *i*, anterior view.

Each scale bar=2 cm

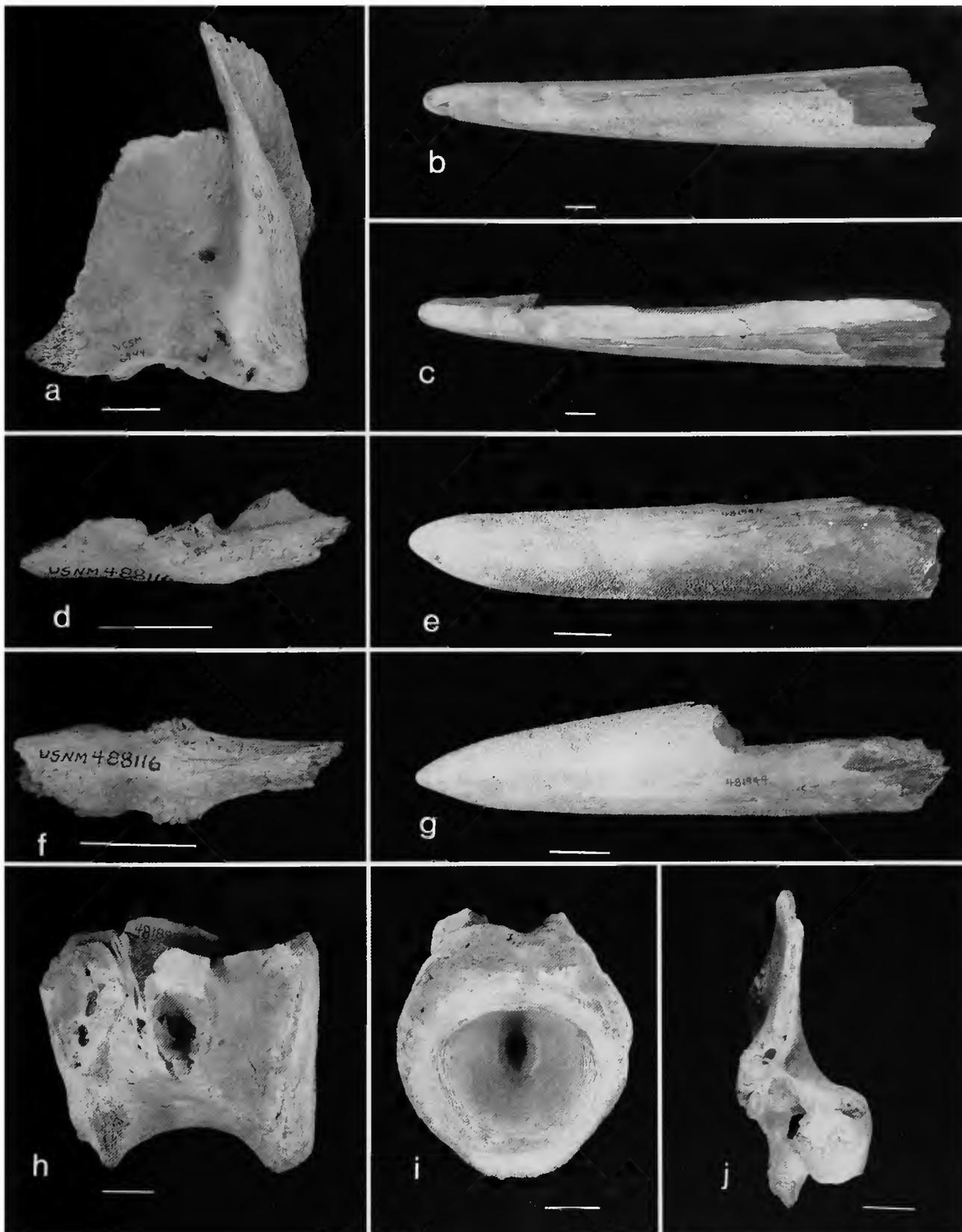


PLATE 9

Makaira cf. *M. nigricans* Lacépède, 1802
Yorktown Formation, Lee Creek Mine

- a, b.* USNM 286177, vertebra 22: *a*, left lateral view; *b*, anterior view.
c, f. USNM 481909, vertebra 23: *c*, left lateral view; *f*, anterior view.
d, e. USNM 481979, hypural: *d*, right lateral view; *e*, anterior view.

Makaira sp.
Yorktown Formation, Lee Creek Mine

- g-i.* USNM 475390, rostrum: *g*, dorsal view; *h*, cross section; *i*, left lateral view.
j, l. USNM 290542, vertebra 23: *j*, left lateral view; *l*, anterior view.
k. USNM 286997, right dentary, medial view of interdentary joint.

Each scale bar=2 cm

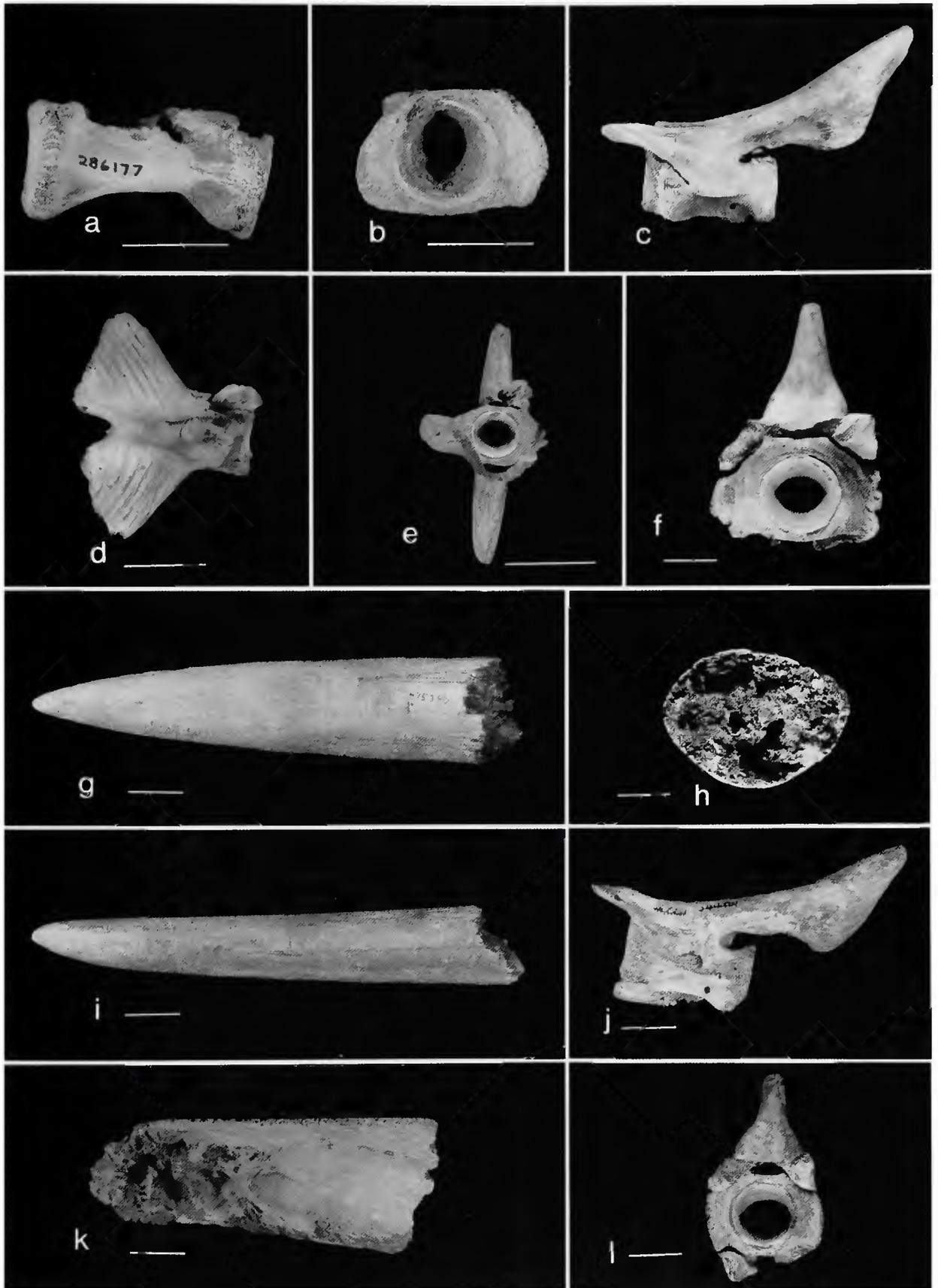


PLATE 10

Makaira sp.

Yorktown Formation, Lee Creek Mine

- a, b.* USNM 481931, predentary: *a*, left lateral view; *b*, dorsal view.
c, d. USNM 488006, left quadrate: *c*, view of articular condyle for articular; *d*, lateral view.
g. USNM 290204, left scapula, view of articular surface for first pectoral-fin ray.
h, i. USNM 481981, hypural: *h*, right lateral view; *i*, anterior view.

cf. Makaira indica sp.

Yorktown Formation, Lee Creek Mine

- e, f.* USNM 488007, hypural: *e*, left lateral view; *f*, anterior view.
j. NCSM 2990, right dentary, medial view of interdentary joint.
k, l. USNM 481916, left quadrate: *k*, view of articular condyle for the articular; *l*, lateral view.

Each scale bar=2 cm

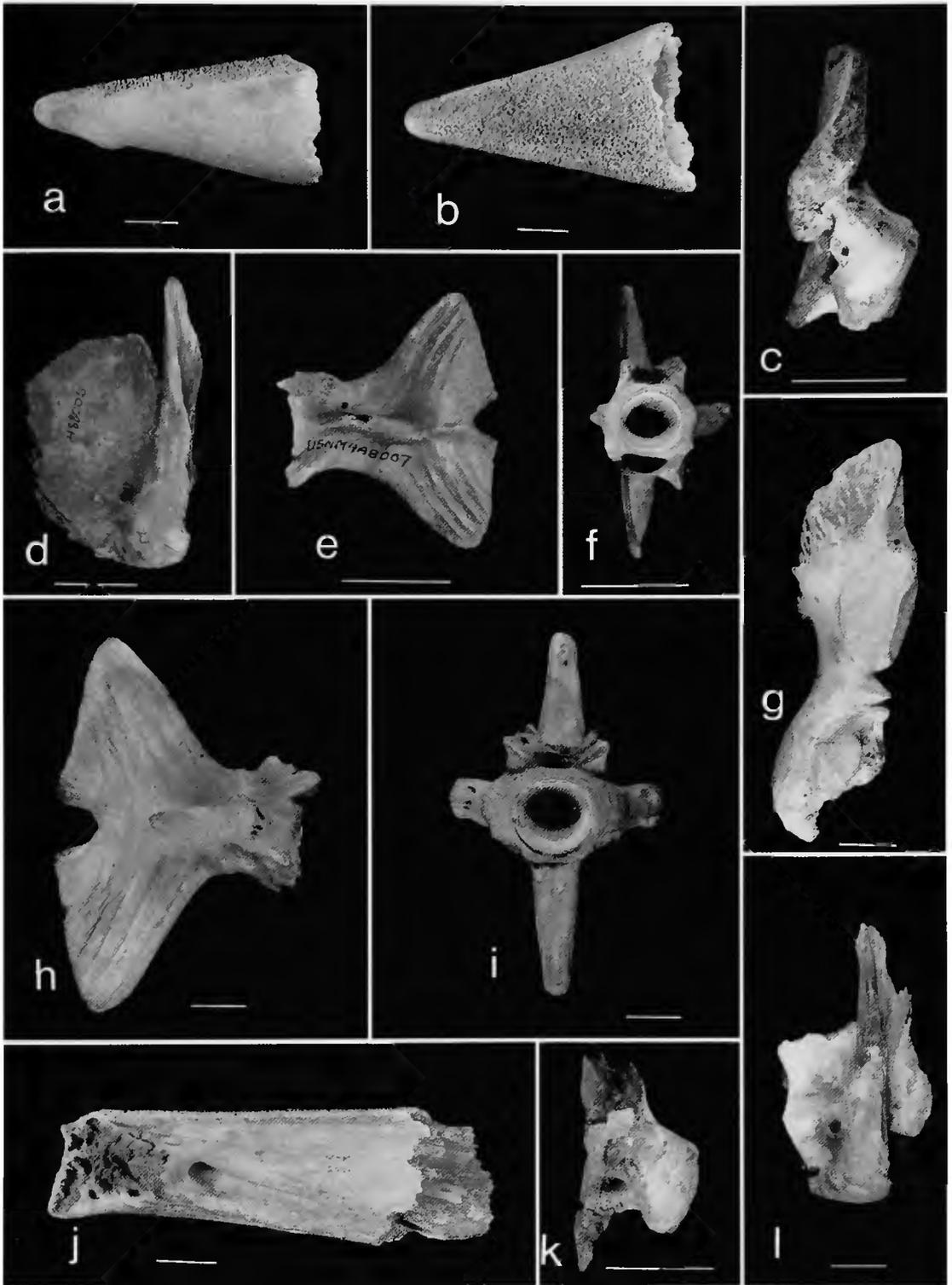


PLATE 11

Tetrapturus albidus Poey, 1860
Yorktown Formation, Lee Creek Mine

- a, b.* USNM 290193, left articular: *a*, lateral view; *b*, dorsal view of joint with quadrate.
c, d. USNM 475393, right maxilla: *c*, lateral view; *d*, dorsal view.
e, f. USNM 488046, parasphenoid: *e*, left lateral view; *f*, ventral view.
g, h. USNM 290203, right maxilla: *g*, lateral view; *h*, dorsal view.
i, j. USNM 488027, parasphenoid: *i*, left lateral view; *j*, ventral view.

Each scale bar = 2 cm

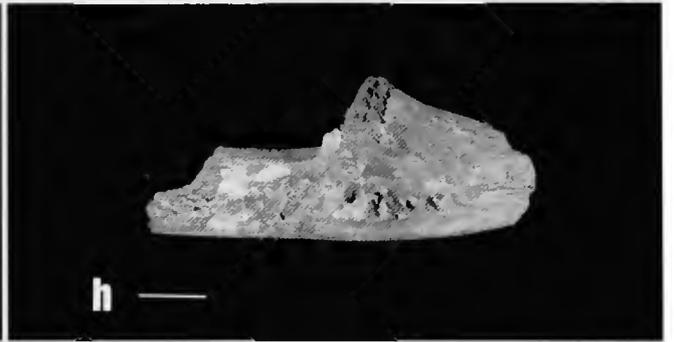
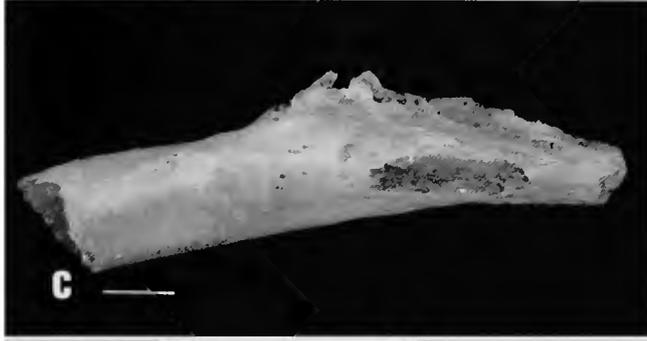
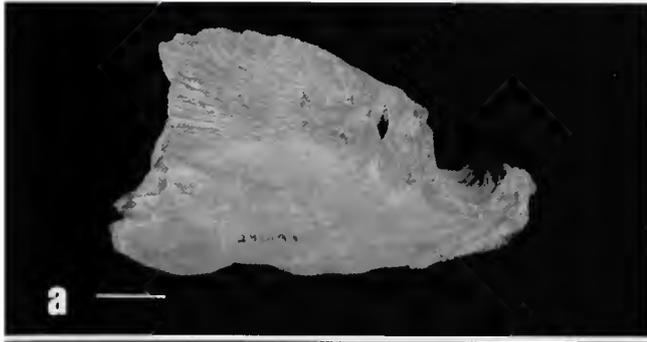


PLATE 12

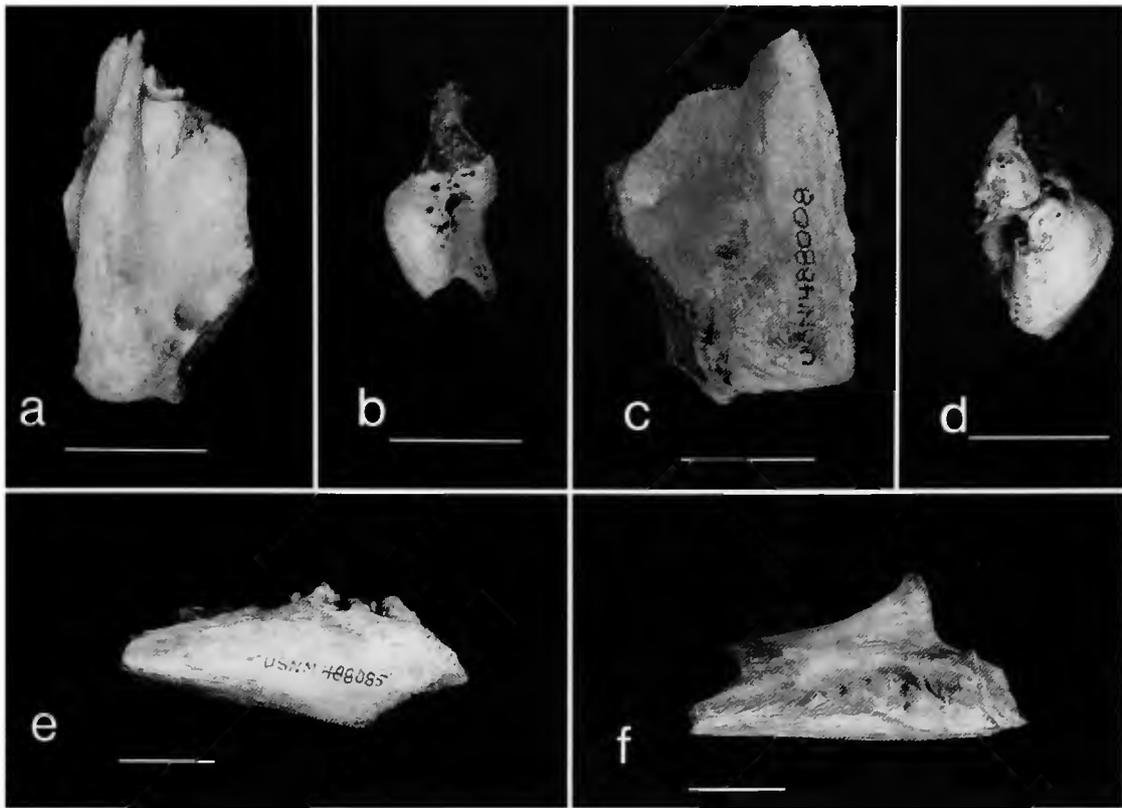
Tetrapturus albidus Poey, 1860
Yorktown Formation, Lee Creek Mine

a, b. USNM 481908, right quadrate: *a*, lateral view; *b*, view of articular condyle for the articular.
c, d. USNM 488008, left quadrate: *c*, lateral view; *d*, view of articular condyle for the articular.

Tetrapturus cf. *T. albidus* Poey, 1860
Yorktown Formation, Lee Creek Mine

e, f. USNM 488085, left maxilla: *e*, lateral view; *f*, dorsal view.

Each scale bar=2 cm



The Neogene Sharks, Rays, and Bony Fishes from Lee Creek Mine, Aurora, North Carolina

Robert W. Purdy, Vincent P. Schneider, Shelton P. Applegate,
Jack H. McLellan, Robert L. Meyer, and Bob H. Slaughter

ABSTRACT

The fish remains, including 104 species from 52 families, collected at the Lee Creek Mine near Aurora, Beaufort County, North Carolina, constitute the largest fossil marine fish assemblages known from the Coastal Plain of the eastern United States. The fish faunas came principally from the Pungo River Formation (Burdigalian, planktonic foraminifera zones N6–7) and the Yorktown Formation (Zanclian, planktonic foraminifera zone N18 and younger). A few specimens were obtained from the James City Formation (early–middle Pleistocene).

As an assemblage, the fishes found in the Pungo River Formation, including 44 species of selachians and 10 species of teleosts, are most similar to those from the “Muschelsandstein” of the Swiss Molasse.

The Yorktown Formation fish assemblage includes 37 species of selachians and 40 species of teleosts, derived mostly from the base of the Sunken Meadow Member.

Although the Pungo River Formation fish fauna is dominated by warm-water (18°–25°C) taxa, the Yorktown Formation fossil fish fauna includes warm and cool water species. Both fish assemblages occur with a cool-temperate invertebrate fauna.

The abundant remains in both faunas permit us to make the following interpretations concerning shark taxonomy. We reassign *Megascyliorhinus* to the family Parascyllidae and *Parotodus benedenii* (Le Hon) to the Lamnidae. Among the mako sharks, we designate the lectotype of *Isurus desori* (Agassiz) and synonymize it with *I. oxyrinchus* Rafinesque and separate *Isurus xiphodon* (Agassiz) from *I. hastalis* (Agassiz). *Palaeocarcharodon*, *Procar-*

charodon, *Megaselachus*, and *Carcharocles* are synonymized with *Carcharodon*. *Sphyrna laevis* (Cope) is synonymized with *S. zygaena* (Linnaeus), and *Galeocerdo triquetus* Cope is synonymized with *Alopias* cf. *A. vulpinus* (Bonnaterre).

This fauna produced four new records and two new species. Among the selachians, we note the first records of *Megascyliorhinus*, *Rhincodon*, *Megachasma*, and *Isistius* from the Atlantic Coastal Plain, and among the bony fishes, the first occurrences in the fossil record of *Caulolatilus* and *Pomatomus*. We also describe two new species of bony fishes, *Lopholatilus rayus* and *Pagrus hyneus*.

Introduction

The fossil faunas of both bony fishes and elasmobranchs at Lee Creek Mine are among the largest in the world, and the Pliocene remains represent one of the most abundant and diverse fossil vertebrate faunas yet recorded in the scientific literature (see Table 1). This fossil fish fauna consists of tens of thousands of selachian teeth (including six associated dentitions) and bony fish remains (including teeth, cranial fragments, an articulated skull, several associated skeletons, vertebrae, fin spines, otoliths). This fauna extends the record of many extant fishes into the Neogene of the United States. We identify more than 35 species not previously recognized from this province (excluding the otolith record; see Fitch and Lavenberg, 1983) and provide the first thorough account of this faunal diversity and its paleoecological implications.

PREVIOUS WORK.—The literature concerning fossil fishes of the Atlantic Coast of North America is rather meager. Leriche (1942) provided one of the most comprehensive accounts of the fossil fishes of the area with a list of 50 Miocene and Pliocene species, and he also reviewed work previous to his own. The most useful of these works are illustrated papers by Gibbes (1848–1849) and Leidy (1877), concerning the phosphate beds of South Carolina, and Eastman's (1904) summary of the fishes of the Chesapeake Group in Maryland.

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Fowler's (1911) lengthy work on the fossil fishes of New Jersey is useful as a catalog, but the specimen locality data are so poor that the informational value of the paper is seriously marred. Case's (1980) paper on the lower Miocene sharks of the Belgrade Formation is the only recent work about the Neogene fishes of the Atlantic Coast of North America.

North Carolina fossil fishes are especially poorly known. Emmons (1858) included some species now known to occur prolifically at the Lee Creek locality. Cope (1869, 1871, 1875) made additions to this fauna, and Leriche's (1942) Duplin Marl occurrences are primarily from North Carolina.

PROJECT HISTORY.—A first manuscript describing the fossil fish fauna of Lee Creek Mine was completed in the mid-1970s. It reflected largely the work of Robert L. Meyer (sharks and rays) and Bob H. Slaughter (bony fishes). In the early 1980s Jack H. McLellan revised the manuscript and added to it additional taxa that he and Robert W. Purdy had identified subsequent to the first manuscript. Due to other commitments, Meyer, Slaughter, and McLellan relinquished responsibility for final revisions to Purdy. Purdy, who revised the Chondrichthyes and the geological portions of the manuscript, sought the help of Vincent P. Schneider to do the fossil bony fishes.

Shelton P. Applegate reconstructed composite dentitions of the common Lee Creek shark taxa; he and Purdy subsequently refined these to reflect, as accurately as possible, the dentitions of these sharks. They are illustrated herein.

We must state here that Applegate disagrees with Purdy's assignment of *Parotodus* to the Lamnidae, Purdy's identification of the first upper anterior tooth of *Parotodus* and *Carcharodon* as the second anterior tooth, and Purdy's recognition of *Galeocerdo contortus* as a species separate from *G. aduncus* Agassiz (= *G. sp.* herein).

Since the completion of the McLellan manuscript in the early 1980s, much new information has been published about the paleoecology and paleoceanography of the Atlantic Coastal Plain, the ecology of extant fishes, and the taxonomy of fossil and extant fishes. Many additional specimens were added to the collections, including two associated dentitions of fossil sharks. Also, Gordon Hubbell made available to us his important collection of extant sharks' dentitions. This manuscript, therefore, represents a major revision of the earlier ones.

ACKNOWLEDGMENTS

We express special thanks to Peter J. Harmatuk and to Becky and Frank Hyne, who collected and generously donated several thousand specimens to the National Museum of Natural History (NMNH), Smithsonian Institution, including many of the specimens cited below. We extend special thanks as well to Wayne and Aura Baker, who also donated many specimens to the Smithsonian. The Hynes and the Bakers also were instrumental in encouraging collectors at the mine to donate important specimens to the Smithsonian. We also express gratitude to Kate and Gordon Hubbell, who graciously provided Bob Purdy

with room and board during his several visits to their home to study shark dentitions in the Hubbell collection.

R.W.P. extends sincere thanks to Jann Thompson and Clayton E. Ray for their encouragement and support of this research project.

For the presentation of specimens to the Smithsonian Institution we thank Wayne and Aura Baker, William Bean, Jim Bourdon, Tom and Pat Burns, Rann Carpenter, Gerard R. Case, Ralph Chamness, N.E. Cowell, Raymond Douglas, George C. Fonger, Harvey A. Franz, Jr., Tex Gilmore, David W. Grabda, Chris Harmatuk, Jack M. Hird, Jerry Hughes, Jeremy Jacobs, Geoffrey Keel, Royal H. and Gene Mapes, the late Earl M. Mason, Vance McCollum, Gregory McKee, Arnold Powell, George Powell, George Prinsen, Norm Riker, Judy Schneider, Clyde Swindell, the late Charles Wells, the late Edgar A. Womble, and many members of the Calvert Marine Museum Fossil Club, the Myrtle Beach Fossil Club, the National Museum of Natural History field parties, and the North Carolina Fossil Club.

Examination of collections or specimens of modern and fossil fishes was made possible with the assistance of Shelton P. Applegate and Camm Swift (Los Angeles County Museum of Natural History), Leonard Compagno (then at Stanford University), M.N. Feinberg, (Department of Ichthyology, American Museum of Natural History), W.I. Follett (Department of Ichthyology, California Academy of Science), Joseph Gregory (Department of Paleontology, University of California at Berkeley), Gordon Hubbell (Key Biscayne, Florida), Alvaro Mones (Museo Nacional de Historia Natural, Montevideo, Uruguay), Kazuhiro Nakaya (Hokkaido University), Dirk Nolf and Paul Sartenaer (Institut Royal des Sciences Naturelles de Belgique), Harold Wes Pratt, Jr. (National Marine Fisheries Service, National Oceanographic and Atmospheric Administration), Martin Sander (Paläontologisches Institut und Museum der Universität Zürich), Earl Shapiro (Academy of Natural Sciences of Philadelphia), Scott Snyder (Department of Geology, East Carolina State University), Toru Taniuchi (University of Tokyo), Giancarlo Tondi (Universita degli Studi di Roma "La Sapienza"), Stanley H. Weitzman and Victor Springer (Division of Fishes, NMNH), and Elizabeth Wing (Florida Museum of Natural History).

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We are grateful to the following individuals for translating into English papers in French, German, Italian, and Japanese:

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National Science Foundation Grant GB 28598-1 supported the Southern Methodist University's field work at Lee Creek Mine. National Science Foundation Grant GB 36727 and a Smithsonian Institution research grant supported travel to museums. Field work conducted by Smithsonian staff was supported by the Smithsonian Institution through the Walcott Fund and the Remington and Marguerite Kellogg Fund.

METHODS

The lack of adequate skeletal collections of extant western Atlantic fishes hampered our identification of the bony-fish remains. We identified the more tropical species of the fauna at the University of Florida, where Elizabeth Wing maintains an excellent synoptic skeletal collection of Florida fishes. One of us (V.P.S.), with the assistance of members of the North Carolina Division of Marine Fisheries, especially Fritz Rhode and Jim Franesconi, assembled a synoptic collection of the fishes presently living off the coast of North Carolina; this collection now resides in the North Carolina State Museum. Gordon Hubbell's extensive private collection of extant sharks' dentitions assisted in our identification of the fossil teeth. We also examined specimens from the private collections of Chris Harmatuk (Bridgeton, North Carolina) and Leonard Compagno (Cape Town, South Africa). These collections and the osteological specimens available in the Division of Fishes, NMNH, were used as the comparative basis for identifying the Lee Creek Mine material.

To avoid the erection and perpetuation of unnecessary taxa, Leriche (1905, 1910, 1936b) advocated using reconstructed tooth sets for the study of fossil shark species. For lamnoid sharks, Applegate (1965, in prep.) supplemented Leriche's work by refining Leriche's tooth terminology and by identifying the morphological characters of the anterior teeth. These characters identify them to jaw position even when they occur as isolated teeth. For taxa with dentitions that are not easily differentiated into anteriors and laterals, Applegate recommended that the dentitions of closely related extant taxa be used as models for the reconstructions. Leriche's and Applegate's methods were employed in our study of the Lee Creek Mine sharks.

The abundance and diversity of elasmobranch teeth in the Miocene and Pliocene sediments at Lee Creek Mine allowed us to reconstruct the dentitions of the common shark taxa. By comparing these reconstructions with the dentitions of extant sharks, we believe we have unraveled ambiguities that have plagued the study of fossil sharks.

The unrecognized high degree of variation in dental morphology in extant sharks fostered this ambiguity. Compagno (1988:26) noted that "the general scarcity of comparative data for teeth of living sharks has led to many errors in the paleontological literature. Unawareness of patterns of positional, devel-

opmental, and sexual heterodonty have led both paleontologists and neontologists astray." In our attempts to establish the identities of the Lee Creek Mine sharks, we examined as many dentitions of extant sharks as possible, both from different age groups and sexes and from different parts of the world. For most taxa, only a few specimens were available, and some of these were not sized or sexed and were from the same population.

At this time, cladistic analyses of the taxa are not possible because of the fragmentary nature of the material and the unavailability of comparative osteological data for phylogenetic analysis. Where possible we have identified potential synapomorphies, but we qualify them as tentative for the reasons given above.

The taxonomic classifications and nomenclature used in this paper follow Compagno (1977, 1984) and Carroll (1988). Descriptions of taxa are from these sources unless noted otherwise. Dates for taxa published by Agassiz (1833-1843) were taken from Jeannet (1928, 1929), who published a schedule of publication dates for Agassiz's work.

Synonyms are provided only for fossil taxa whose identifications are being changed.

Due to the great number of fossil fish specimens recovered at Lee Creek Mine, only figured or measured specimens were cataloged. Thus, although the total number of specimens referred to each taxon is cited, with few exceptions, only the cataloged specimens are listed. Figured specimens are from Lee Creek Mine unless otherwise noted.

All measurements were made in millimeters or centimeters. For shark teeth, tooth height was measured from the apex of the crown to a line tangential to the basal margin of the root, tooth width was measured at the greatest lateral extent of the tooth, and tooth thickness was measured in the area of the central foramen of the root. Total length is abbreviated as TL.

Because the specimens were not collected in place, we made special efforts to collect from spoil areas where there was the least chance of mixing taxa from different horizons. We sifted large quantities of the Pungo River Formation, particularly the ore zone (unit 3) and units 4 and 5. Our principal source for ore-zone material was the coarse tailings found at the mill, and even in this material we occasionally found waifs from the Yorktown or James City formations. Despite these problems of mixing, we believe our collection techniques were careful enough to allow us to decide the stratigraphic occurrence of most of the taxa in this study.

A field party from the Shuler Museum of Paleontology of Southern Methodist University undertook the initial bulk processing of sediments for fossils, especially microvertebrate remains. Subsequent bulk collecting was conducted by McLellan, Applegate, Schneider, and Purdy. We also collected on the spoil piles from areas that did not appear to be contaminated by mixed sediments and fossil invertebrates. Because we could not collect on the working face of the mine, we made special efforts to bulk sample uncontaminated piles of units 1 to 3 of

the Yorktown Formation. Some specimens were found in lumps of matrix or had matrix in cavities or grooves in the specimen; this associated material was submitted to Thomas G. Gibson (United States Geological Survey) for analysis of any foraminifera present. Gibson's reports helped us to stratigraphically place many of these specimens.

The Lee Creek Mine collection has accumulated since the opening of the mine test pit in 1963. Field parties under the direction of Clayton E. Ray (NMNH) began actively prospecting the locality in August 1971. Bob Slaughter and a party from Southern Methodist University, Dallas, Texas, collected bulk samples for screen washing in July 1972.

The cataloged specimens are housed in the collections of the North Carolina State Museum of Natural Sciences and the NMNH.

ABBREVIATIONS.—Institutional abbreviations used in the text are as follows.

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
CAS	California Academy of Science
CMM	Calvert Marine Museum
ETHGI	Paläontologisches Institut Universität Zürich
IG	Brussels Museum of Natural History
NCSM	North Carolina State Museum of Natural Sciences
TE-PLI	Staatliches Museum für Naturkunde Karlsruhe
UNIG	Universität Neuchâtel, Institut für Geologie
NMNH	National Museum of Natural History collections (including collections of the former United States National Museum), Smithsonian Institution

Stratigraphy

The section exposed at Lee Creek Mine includes more than 30 m of fossiliferous marine sedimentary rocks assigned to the Pungo River and Yorktown formations. Gibson (1967, 1983) described these exposures in detail; unless otherwise noted, stratigraphic units herein are those of Gibson.

The Pungo River Formation, a subsurface unit, is exposed in the lower part of the mine pit. The upper 3.7 m of this formation consists of thin limestone layers interbedded with thin phosphate sand layers (units 4–7). Below this lies the ore bed, a phosphate sand layer about 12 m thick (units 1–3). Within the ore bed, a thin but persistent indurated sand layer containing diatomite occurs (unit 2). Below the main ore layer, about 3 m of low-grade indurated phosphatic sand occurs that is not mined. This layer rests unconformably on the Castle Hayne Formation of middle Eocene age. Gibson's units 1 to 3 correlate with the lower Miocene Dunkirk beds of the Calvert Formation of the Chesapeake Group to the north, which are Burdigalian (Hoffman and Ward, 1989:55), and units 4 to 7 correlate with the Fairhaven Member of the Calvert Formation, which are Langhian (Hoffman and Ward, 1989:55).

The Yorktown Formation, which at Lee Creek Mine unconformably overlies the Pungo River Formation, consists of blue clayey, fossiliferous sand. Ward and Blackwelder (1980) subdivided the Yorktown Formation into four members; beginning

with the oldest, they are the Sunken Meadow Member, the Rushmere Member, the Morgarts Beach Member, and the Moore House Member. Only the first three members occur at Lee Creek Mine. Hazel (1983) presented evidence that the Yorktown Formation at the Lee Creek locality is planktonic foraminifera zone N19 (early Pliocene). Riggs et al. (1982), Gibson (1983), Snyder et al. (1983), and others have confirmed this age assignment. At Lee Creek Mine, the Sunken Meadow Member is the source of most of the vertebrate fossils.

SOURCES OF THE FISH FOSSILS

Vertebrate fossils occur in both the Yorktown and the Pungo River formations. A few fish fossils were found in situ, in exposures along the pit walls. Most specimens, however, were obtained by searching piles of overburden in mined-out parts of the pit. Other sources of fossils were the piles of ore waiting to be slurried and pumped to the mill, the residue of coarse rubble left behind at the ore pumping sites, and the reject piles at the mill.

The overburden consists of the Pleistocene sediments, Yorktown Formation, and the top 3.7 m or so of the Pungo River Formation. During mining the draglines cast the overburden aside into a previously mined cut, stacking this material in windrows or spoil piles. Rains wash finer sediments down the slopes of the spoil piles leaving the fossils behind. Fish teeth and bones and other fossils are common in this lag material.

As the draglines cast the overburden aside, inevitable mixing of the overburden layers occurs. Because, however, the dragline buckets are very large and the sediments are cohesive, large masses of homogeneous material from identifiable horizons survive the drop from the bucket onto the spoil piles.

PUNGO RIVER FORMATION.—Much of the Pungo River material studied herein was collected from the ore layers (units 1–3). We obtained this material at the active mining sites where the draglines stack thousands of tons of ore to await transport to the mill. By screening bulk samples of this unprocessed ore through size 30 mesh screens, we collected many small bones and teeth.

Smaller draglines move the ore to sumps; there it is mixed with water, screened to remove coarse particles, and pumped through pipelines to the mill. When all of the ore at a site has been pumped to the mill, large piles of particles too coarse for slurring remain. These piles yielded many fossils.

When the ore slurry reaches the washer section of the mill it is screened, and particles coarser than sand size are discarded. These piles of mill rejects, which we screened, also yield Pungo River fossils; the pumping and screening, however, abrades the specimens.

The upper 3.7 m of the Pungo River Formation (units 4–7) is cast upon the spoil piles along with the nonphosphatic Yorktown Formation. After weathering, these upper Pungo River sediments are easily recognized by their characteristic lithologies. Shark teeth and osteichthyan vertebrae occur embedded in

the thin limestone layers, but the phosphatic sands that alternate with the limestones (unit 4) are a more prolific source of fossils. It was from these sources that we obtained the Pungo River fish assemblage. Although we did not collect them in place, we assign them with some confidence to the lower and middle parts of the formation (units 1–3) and to the upper part (units 4–7).

YORKTOWN FORMATION.—The blue gray, silty sands containing some phosphate pellets, cetacean bone fragments, and *Placopecten clintonius* (Gibson, 1983), the invertebrate guide fossil for the basal part of the Yorktown Formation, identify sediments of the lowest 1.2 m of the Yorktown Formation. These sediments yielded many fish fossils.

In the basal layer of the Yorktown Formation, fish fossils occur in two states of preservation. They either are well preserved and unabraded or are blackened, broken, worn, and heavily etched. Intermediately worn specimens are uncommon.

The dark, worn specimens are themselves divisible into two groups: (1) fossils that are common in the Pungo River Formation and occur only in the basal layer of the Yorktown Formation as redeposited specimens, and (2) fossil teeth known to occur only in the basal layer of the Yorktown Formation. We believe they originated in post-Pungo River beds that were eroded completely before or during the Yorktown transgression.

The well-preserved component of the fossil fish assemblage accumulated after the initial high-energy transgression. We believe that most of the identifiable bony-fish remains found on the spoil piles came from the bottom 4 m of the Yorktown Formation (units 1–3). Sediments representing unit 3 occur only as small patches on the spoil piles, as the unit is only 0.6 m thick. These patches are readily identified by an abundance of fish otoliths, well-preserved small shark teeth, chalky crab chelae, and other characteristic fossils.

BIOSTRATIGRAPHIC IMPLICATIONS OF THE FISH FAUNAS

Based on fish remains alone, the biostratigraphic position of this fish fauna is difficult to assess. Many of the Lee Creek Mine taxa cannot be distinguished from the extant species.

Another problem is that many species of extant sharks segregate by size and/or by sex, and in some species the growth rates vary such that individuals of the same age in two different populations of the same species will be of measurably different sizes. The effects of these distributions and size differences on the fossil record of sharks have not yet been assessed. Until they are, we believe that the usefulness of fossil shark teeth as guide fossils is questionable.

The stratigraphic ranges of several large shark genera, such as *Galeocerdo* and *Carcharodon*, suggest the maximum ages of the deposits. *Galeocerdo* sp. (= *G. aduncus* of Agassiz, Cappetta, Leriche, and others) and *G. contortus*, frequently used as guide fossils, have broad stratigraphic ranges: Rupelian to Serravalian for the former and Chattian to Tortonian for the

latter (Cappetta, 1987:123). Based on specimens from a stratigraphically controlled collection he made from the Neogene of Belgium, Leriche (1926) extended the range of *Galeocerdo aduncus* into the Zancian; these teeth, however, may be from juveniles of *G. cf. G. cuvier*. De Stefano (1909) questionably referred a tooth from the Pliocene of Tuscany to *G. aduncus*; however, this is apparently referable to *G. cf. G. cuvier* and definitely is not *G. aduncus*. *Galeocerdo contortus* has a more restricted stratigraphic range than does *G. sp.*, and along with the presence of *Carcharodon subauriculatus*, which ranges from the Chattian to the Burdigalian and possibly the Langhian, it suggests a maximum age of Chattian for the Pungo River fauna.

In the Yorktown Formation the absence of *Galeocerdo* sp. and *G. contortus* and the presence of *G. cf. G. cuvier* corresponds with the occurrence of these sharks in Europe. The large *Galeocerdo* from the lower part of the Yorktown Formation is quite modern in aspect. The only fossil teeth that to our knowledge are similar are those from the Ashley phosphate beds of South Carolina (now thought to be of Pliocene age, Sanders, pers. comm., 16 Jun 1990) and the *Galeocerdo* from the Orciano beds of Pliocene age in Italy (Lawley, 1876; De Stefano, 1909). Espinosa-Arrubarrena and Applegate (1981) also reported the occurrence of this shark as *G. rosaliensis* in the basal late Pliocene of Baja California, which may also be a synonym of *G. capellini*. The absence of *Galeocerdo* sp. in the basal Yorktown Formation and the presence of the more modern *G. cf. G. cuvier* supports an early Pliocene age for these beds.

Fossil Shark Teeth

From the beginnings of shark paleontology, most paleontologists have identified the different morphotypes of shark teeth as belonging to different species, but within a species, tooth morphology varies considerably; the dentitions of one species may contain several different morphotypes. This practice for naming fossil shark species has led to much taxonomic confusion.

Agassiz (1833–1843) published the first extensive work on fossil shark teeth. Many of his species were based on incomplete teeth or on teeth from different jaw positions of species he described earlier in his work; nevertheless, his classic work laid the foundation for the study of fossil shark taxonomy.

Maurice Leriche, who studied fossil sharks for the first half of this century, revised many of Agassiz's species and those of other earlier workers. As the basis of his taxonomic studies, Leriche created artificial tooth sets for fossil species. He was the first fossil shark specialist to do this, and although many fossil shark specialists ignored Leriche's method of study, he made many significant contributions to the study of fossil sharks.

Despite Leriche's work, the naming of new species seemed to be more important than scientific accuracy. As a result of this, common fossil shark taxa have appeared in the literature many times under many different names. Today, a morass of

TABLE 1.—Faunal list of Lee Creek Mine fishes (1–6=stratigraphic unit, A=abundant, C=Common, U=uncommon, R=redeposited).

Taxon	Pungo River Formation						Yorktown Formation			James City Formation
	1	2	3	4	5	6	1	2	3	
Class CONDRICHTHYES										
HEXANCHIDAE										
<i>Notorynchus cepedianus</i>	C	C	C	C	C		C	C		
<i>Hexanchus</i> sp.							U	U		
ECHINORHINIDAE										
<i>Echinorhinus</i> cf. <i>E. blakei</i>				U	U		U	U		
SQUALIDAE										
<i>Squalus</i> sp.							U	U		
<i>Isistius</i> sp.							U	U	U	
PRISTIOPHORIDAE										
<i>Pristiophorus</i> sp.	U	U	U							
RHINOBATIDAE										
<i>Rhinobatos</i> sp.				C	C					
PRISTIDAE										
<i>Pristis</i> sp.							U?			
<i>P.</i> cf. <i>P. pectinatus</i>							U?			
RAJIDAE										
<i>Raja</i> sp.							U?			
DASYATIDAE										
<i>Dasyatis</i> <i>say</i>	C	C	C	C	C					
<i>D. centroura</i>							C	C		
<i>D.</i> cf. <i>D. americana</i>	U	U	U							
MYLIOBATIDAE										
<i>Pteromylaeus</i> sp.	U	U	U	U	U					
<i>Aetobatus</i> sp.				C	C		C	C		
RHINOPTERIDAE										
<i>Rhinoptera</i> sp.	C	C	C	C	C					
<i>Plinthiscus stenodon</i>	C	C	C	C	C	C				
MOBULIDAE										
<i>Mobula</i> sp.	C	C	C	C	C		R?			
<i>Manta</i> sp.							U	U		
SQUATINIDAE										
<i>Squatina</i> sp.				U	U		U	U		
PARASCYLLIDAE										
<i>Megascyliorhinus miocaenicus</i>	R									
GINGLYMOSTOMATIDAE										
<i>Ginglymostoma</i> sp.			R							
RHINCODONTIDAE										
<i>Rhincodon</i> sp.	A	A	A							
ODONTASPIDIDAE										
<i>Carcharias taurus</i>							C	C		U
<i>C. cuspidata</i>	A	A	A	A	A		C			
<i>C.</i> sp.	U	C	C	C	C					
<i>Odontaspis ferox</i>	U	U	U	U	U	U				
<i>O.</i> cf. <i>O. acutissimo</i>	C	C	C	C	C	U?				
MEGACHASMIDAE										
<i>Megachasma</i> sp.				U	U		U			
ALOPIIDAE										
<i>Alopias</i> cf. <i>A. superciliosus</i>			R							
<i>A.</i> cf. <i>A. vulpinus</i>				U	U		U	U		
CETORHINIDAE										
<i>Cetorhinus</i> sp.			C							
LAMNIDAE										
<i>Parotodus benedenii</i>							U	U		
<i>Isurus oxyrinchus</i>	C	C	C	C	C		C	C		
<i>I. hastalis</i>	A	A	A	A	A		A	A	C	
<i>I. xiphodon</i>							A	A		
<i>Lamna</i> sp.							U?			
<i>Corcharodon subauriculatus</i>	C	C	C	C	C					
<i>C. megalodon</i>			U	U	U		C			
<i>C. carcharias</i>							U			U

TABLE 1.—Continued.

Taxon	Pungo River Formation						Yorktown Formation			James City Formation
	1	2	3	4	5	6	1	2	3	
SCYLIIORHINIDAE										
<i>Scyliorhinus</i> sp.	C	C	C	C	C		R?			
TRIAKIDAE										
<i>Galeorhinus</i> cf. <i>G. affinis</i>	U	U	U	U	U		R?	R?		
<i>Hypogaleus</i> sp.	U									
<i>Mustelus</i> sp.	U	U	U	U	U					
HEMIGALEIDAE										
<i>Paragaleus</i> sp.	A	A	A	A	A		R?			
<i>Hemipristis serra</i>	A	A	A	A	A	C	C	C	U?	
CARCHARHINIDAE										
<i>Galeocerdo</i> sp.	A	A	A	A	A	C				
<i>G. contortus</i>	A	A	A	A	A	C				
<i>G.</i> cf. <i>G. cuvier</i>							A	C	U	
<i>Carcharhinus brachyurus</i>	A	A	A	A	A					
<i>C. falciformis</i>		U	U	U						
<i>C. leucas</i>	U	U	U	U	U		C	C	C	
<i>C. macloti</i>	A	A	A	A	C		R			
<i>C. obscurus</i>							C	C	C	
<i>C. perezii</i>			A	A	A		C			
<i>C. plumbeus</i>				U	U		U			
<i>Rhizoprionodon?</i> sp.	U	U	U	U	U					
<i>Negaprion brevirostris</i>				U	U		U	U		
<i>Triaenodon obesus</i>	U	U	U							
SPHYRNIDAE										
<i>Sphyrna lewini</i>										U
<i>S.</i> cf. <i>S. media</i>	C	C	C	C	C		U	U		
<i>S. zygaena</i>	U	U	U	U	U		U	U	U	
Class OSTEICHTHYES										
ACIPENSERIDAE										
<i>Acipenser</i> cf. <i>A. oxyrhynchus</i>							A	A		
LEPISOSTEIDAE										
<i>Lepisosteus asseus</i>										U
ELOPIDAE										
<i>Megalops</i> cf. <i>M. atlanticus</i>					U	U				
CONGRIDAE										
<i>Conger</i> cf. <i>C. oceanicus</i>							U			
CLUPEIDAE										
<i>Alosa</i> cf. <i>A. sapidissima</i>							U?			
ARIIDAE										
<i>Bagre</i> sp.				C	C		C	C		
BATRACHOIDIDAE										
<i>Opsanus tau</i>							U			
LOPHIIDAE										
<i>Lophius</i> cf. <i>L. americanus</i>							C?			
MERLUCCIDAE										
<i>Merluccius bilinearis</i>							A	A		
TRIGLIDAE										
<i>Prionotus</i> cf. <i>P. evolans</i>							C	C	C	
SERRANIDAE										
<i>Epinephelus</i> sp.							C	C		
<i>Mycteroperca</i> sp.							U			
BRANCHIOSTEGIDAE										
<i>Caulolatilus</i> cf. <i>C. cyanops</i>							U			
<i>Lopholatilus rayus</i>							A			
POMATOMIDAE										
<i>Pomatomus saltatrix</i>							C	C		
CARANGIDAE										
<i>Seriola</i> sp.							U	U		
SPARIDAE										
<i>Archosargus</i> cf. <i>A. probatocephalus</i>							C			
<i>Lagodon</i> cf. <i>L. rhomboides</i>		A	A	A	A	A	C?	C?		
<i>Pagrus hynemus</i>							C			

TABLE I.—Continued.

Taxon	Pungo River Formation						Yorktown Formation			James City Formation
	1	2	3	4	5	6	1	2	3	
<i>P. sp.</i>							C			
<i>Stenotomus cf. S. chrysops</i>							C	C?	C?	
SCIAENIDAE										
<i>Sciaenops sp.</i>							C	C		
<i>S. ocellatus</i>										U?
<i>Pogonias cf. P. cromis</i>				U	U		A	A		C?
LABRIDAE										
<i>Tautoga cf. T. onitis</i>							U	U		
URANOSCOPIDAE										
<i>Astroscopus sp.</i>							U			
SPHYRAENIDAE										
<i>Sphyraena cf. S. barracuda</i>		C	C	C	C	C	C	C		
SCOMBRIDAE										
<i>Sarda sp. aff. S. sarda</i>				C	C		A	A		C
<i>Auxis sp.</i>							U			
<i>Thunnus sp.</i>			C	C			A			
<i>Acanthocybium solandri</i>							C			
XIPHIIDAE										
<i>Xiphias gladius</i>							U			
ISTIOPHORIDAE										
<i>Istiophorus cf. I. platypterus</i>							U	U		
<i>Makaira cf. M. indica</i>							U	U		
<i>M. nigricans</i>							A	A		
<i>Tetrapturus cf. T. albidus</i>							U	U		
<i>Hemirhabdohynchus sp.</i>		U	U	U	U					
BOTHIDAE										
<i>Paralichthys sp.</i>							U	U		
MONACANTHIDAE										
<i>Aluterus sp.</i>				C	C	C	A	A		A
TETRAODONTIDAE										
<i>Sphoeroides hyperostosus</i>							A	A		A
DIODONTIDAE										
<i>Chilomycterus schoepfi</i>				U	U		A	A		A
MOLIDAE										
<i>Mola chelonopsis</i>							U			
Indeterminate										
Emmon's fish tooth										U

scientific names exists in shark paleontology, and more new fossil taxa are described each year.

Many of the type specimens for the species described in Europe during the nineteenth century have yet to be rediscovered. Some were destroyed by the ravages of wars; others remained in private collections, many of which have been lost or destroyed. Even the type specimens that were not lost were rarely redescribed and refigured. These problems have further hindered fossil shark taxonomy.

The lack of good museum collections of dentitions from extant sharks and the paucity of scientific papers describing dental variation in extant sharks also have hampered the study of fossil sharks. In extant species, the extent of dental variation remains undocumented. Without knowing the range of dental variation, paleontologists cannot make sound judgements about the taxonomy of fossil sharks.

In studying the Lee Creek Mine sharks, we attempted to make the most parsimonious interpretation possible of the fos-

sil evidence. We compared the fossil teeth with those of as many related extant species as possible, looking for characters to separate or synonymize the fossil species. Where studies of extant species indicated that great variability in dental morphology existed but that variability was not defined, we identified these taxa to genera only. In instances where no information exists about dental variability in the extant species, we identified the fossil teeth to the fossil species. For fossil teeth that we could not separate from those of the extant species, we give ecological information on the extant species and the probable total length of the fossil species. The latter we estimated from the measurements of the largest tooth in the upper jaw of extant sharks of known length.

TOOTH TERMINOLOGY

An extensive terminology, including many synonymous terms, has arisen for the description of shark teeth. Compagno (1988) called for a standardization of this terminology, and we

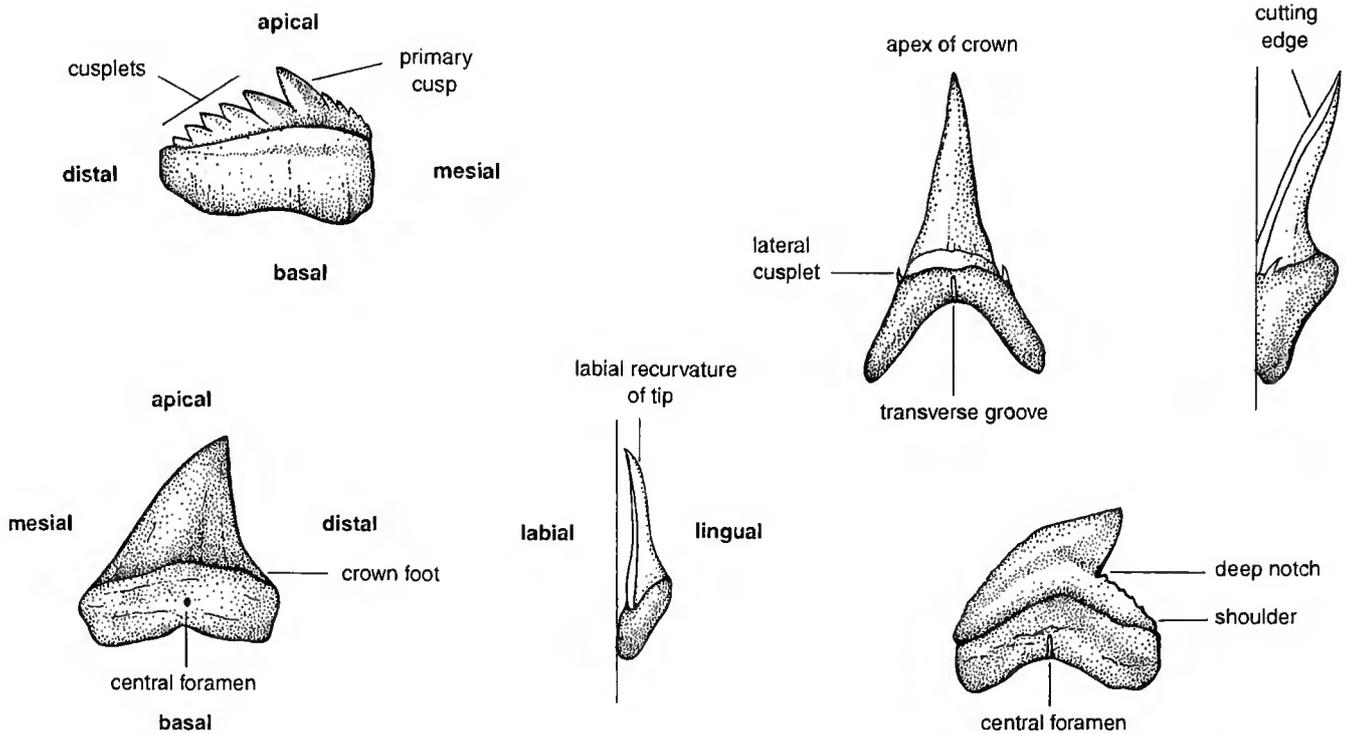


FIGURE 1.—Tooth terminology used in this paper.

use the terms he suggested, which incorporate those of Applegate (1965a, 1967). See Compagno (1988:27–30) and Figure 1 for the definitions of these terms. In view of the importance of reconstructing tooth sets of fossil shark species, Applegate and Compagno's tooth terminology is reviewed below.

Among the lamniform sharks, which include *Alopias*, *Carcharias*, *Carcharodon*, and *Isurus*, among others, several basic tooth types occur. Leriche (1905) and Applegate (1965a) identified these tooth types as median (medial), symphyssial, alternate, anterior, intermediate, lateral, and posterior (Figures 2, 5a; Compagno, 1988, fig. 3.4). These names indicate position in the shark's jaws. Compagno (1988:32–33) defined shark teeth that cannot be differentiated into anteriors and laterals as follows:

When anteriors are not differentiated (as is often the case in the lower jaw) but posteriors are, the more mesial teeth are termed ANTEROLATERALS; when posteriors are not differentiated but anteriors are, the more distal teeth are LATEROPOSTERIORs; and when neither anteriors or posteriors are differentiated, the parasymphyssial teeth are ANTEROPOSTERIORs.

Small symmetrical and asymmetrical teeth occur in the symphyssial region of many species of sharks; Applegate recognized three types of teeth in this region: median (medial), symphyssial, and alternate (definitions from Compagno, 1988; occurrence of teeth in taxa from Applegate, 1965a). The lamniform tooth types are described below.

UPPER AND LOWER TEETH.—The lower teeth are not as compressed as the upper teeth; their tips usually recurve toward

the more convex side of the tooth or lingually. A straight-edged area parallel to the long axis of the flat or labial face of the crown and tangent to the base of the crown facilitates seeing this relationship (in upper teeth as well). (Exceptions to this are the upper anterior teeth. Except in *Alopias*, the tips of these teeth bend lingually, but this lingual bend is not as great as that of the lower anterior teeth). In the area of the central foramen, in the lower anterior teeth and the first two or three laterals, the root possesses a noticeable bulge or torus. In the lower lateral teeth, the angle formed by the root lobes is not as obtuse as that in the upper laterals.

In the upper teeth, the tip of the crown in profile or lateral view is straight, or it may recurve labially, and the crown is more compressed or blade-like than are those of corresponding teeth of the lower jaw. The torus on the lingual face of the root is noticeably developed only in the anterior and intermediate teeth; the roots of the upper lateral teeth are flatter than those of the lowers.

Exceptions, however, do occur. In the extant *Lamna* and in *Isurus paucus* we observed upper lateral teeth with slight lingual bends, and in two juvenile *I. paucus* dentitions from the same locality, the same upper lateral tooth in each dentition has a strong lingual bend.

MEDIAL TEETH.—Medial teeth are small, often symmetrical but may be asymmetrical, and occur at the juncture of the left and right jaws. These teeth are found in the Scyliorhinidae, Tri-

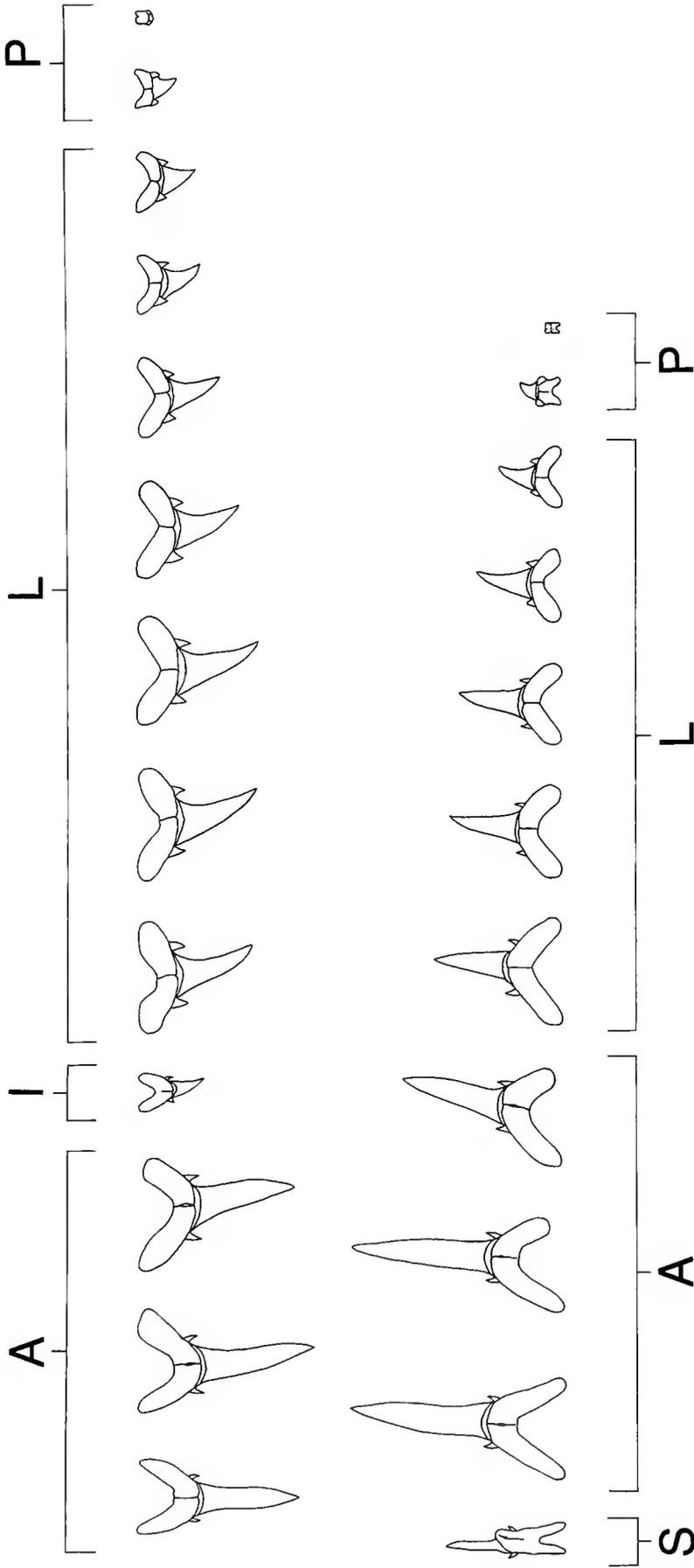


FIGURE 2.—Diagram of *Carcharias taurus* dentition showing tooth types: S=symphysial tooth; A=anterior teeth; I=intermediate tooth; L=lateral teeth; P=posterior teeth.

akidae, Pseudotriakidae, Carcharhinidae, Sphyrnidae, Hexanchidae, Squalidae, and Heterodontidae.

SYMPHYSIAL TEETH.—These teeth, which usually look like miniatures of the first anterior teeth, have asymmetrical roots and occur on either side of the symphysis. They are usually in the lower jaw but also may occur in the upper jaw. Symphysials are found in the Odontaspidae, Cretolamnidae, Carcharhinidae, Sphyrnidae, Hemigaleidae, and the Mitsukurinidae.

ALTERNATE TEETH.—These are “small teeth with asymmetrical crowns that form two interdigitated rows on the symphysis, with the cusps of each row hooked mesially towards the opposite row” (Compagno, 1988:32). They are found in the Carcharhinidae and Hemigaleidae. We did not recover alternate teeth at Lee Creek Mine.

ANTERIOR TEETH.—Two upper (three in *Carcharias* and *Mitsukurina*) and three lower anterior teeth occur in the dentitions of lamnoid sharks. These teeth usually have erect, awl-like crowns; their tips may curve slightly toward the corner of the jaw (distally). The width of an anterior tooth is less than 80% of the tooth's height. In *Odontaspis*, *Carcharias*, *Mitsukurina*, *Scapanorhynchus*, and small individuals of *Isurus*, the anterior teeth have a sigmoidal curvature in lateral view, but in upper teeth the sigmoidal curvature is not as great, and the root is not as thick in lateral view as it is in the lower anterior teeth (Figure 3). A shallow to deep hollowing of the labial face of the root occurs in these teeth to accommodate the torus of the next-forming tooth. This hollowing or concavity has its greatest development in the lower anterior teeth, which have the most prominent toruses, and in which the crown of the tooth overhangs the root. In upper anterior teeth, where the torus is less developed, the labial face of the root may be slightly recessed or flush with the labial face of the crown.

Some exceptions to these characters do occur. In the upper teeth of *Carcharodon*, *Isurus xiphodon*, and large individuals of *I. paucus*, the anterior teeth lose their awl-like appearance, and in *Carcharodon* and *I. xiphodon* the angles of the root lobes are broader than in those of other lamnoid species.

Because each anterior tooth exhibits a basic morphological pattern, the identification of the characters that define them is most important, but one of these characters alone, such as the angle formed by the root lobes, is not sufficient for identifying this tooth type. One of us (R.W.P.) measured the angles of the root lobes (see Table 2) of the anterior teeth in dentitions from extant



FIGURE 3.—Upper and lower anterior teeth in lateral view to show sigmoidal curvature of crown: a, upper; b, lower.

TABLE 2.—Variation in the angle of the root lobes in the first two upper (A1, A2) and lower (a1, a2) anterior teeth of extant lamnoid sharks. (n =number of specimens.)

Taxon	n	A1	A2	a1	a2
<i>Carcharias</i>	2	38°–40°	44°–92°	37°–51°	48°–67°
<i>Lamna nasus</i>	9	–	82°–143°	60°–120°	106°–141°
<i>L. ditropis</i>	3	–	86°–125°	83°–135°	100°–130°
<i>Isurus paucus</i>	8	–	86°–137°	34°–60°	74°–111°
<i>I. oxyrinchus</i>	4	–	76°–91°	30°–50°	45°–75°
<i>Carcharodon</i>	28	–	116°–156°	62°–108°	81°–115°

lamnoid species; he found that these angles broaden as the shark increases in size and that the angles differ noticeably for the same tooth position in the left and right jaws. In identifying anterior teeth, then, the attitudes of the crowns and the proportional development of the root lobes are the most constant and the most important features (Figure 4). Even these features are variable, and they should be used with prudence.

First Upper Anterior Tooth (Applegate's type A tooth): This is the most symmetrical tooth among the upper anteriors, and the root lobes are nearly equal in size and form an acute angle. The crown may appear to be symmetrical or slightly asymmetrical, but it remains erect.

Second Upper Anterior Tooth (Applegate's type C tooth): The root lobes of this tooth form a wide acute to right angle, and the lobes are not equal in size (the longer root lobe is usually on the mesial side of the tooth). The crown has a slight distal slant, and the mesial cutting edge is slightly to very convex.

Third Upper Anterior Tooth (Applegate's type E tooth): This is the shortest tooth in the upper anterior series. The mesial root lobe is longer than the distal lobe, and the crown leans distally; the distal cutting edge is slightly to very convex.

First Lower Anterior Tooth (Applegate's type B tooth): The root lobes of this tooth are nearly equal or equal in length, form an acute angle, and are almost U-shaped in appearance; one lobe may be somewhat flattened. The torus or swollen area surrounding the transverse groove and/or central foramen attains its greatest development in this tooth. In some species the roots of these teeth are elongated. The crown of this tooth, the most symmetrical of the lowers, has the least amount of distal curvature.

Second Lower Anterior Tooth (Applegate's type D tooth): The root lobes of this tooth form an acute to small obtuse angle, and the mesial lobe is usually longer than the distal lobe. The curvature of the crown is similar to that of the first lower anterior tooth. Except in *Carcharodon*, this tooth is usually the greatest in height.

Third Lower Anterior Tooth (Applegate's type F tooth): This is the shortest tooth in the lower anterior series. The root lobes form a right to obtuse angle, and the mesial root lobe is noticeably longer than the distal one and may be pointed. The torus is more noticeable in this tooth than it is in its upper

counterpart. The tooth's crown has a strong distal lean to it; its mesial edge is almost straight or is concave.

INTERMEDIATE TEETH.—Intermediate teeth occur in the upper jaws between the anterior and lateral teeth. Although they are usually small, they may be almost as large as the neighboring teeth. Two sharks of the same size and species can have intermediate teeth of markedly differing sizes. These teeth, except in *Carcharodon* and *Isurus xiphodon*, have U-shaped roots, and their crowns, except in *Carcharodon*, slant toward the corner of the jaws. The mesial edge of the crown is slightly concave to convex, and the distal edge is concave. In *Carcharodon* these teeth may be broad- or narrow-crowned, with root lobes that form right to obtuse angles. In *Isurus xiphodon* the intermediates have triangular crowns and have root lobes that form obtuse angles.

LATERAL TEETH.—The root lobes in the lateral teeth form obtuse angles. These angles are usually smaller in the lower teeth than they are in the corresponding upper teeth, which are usually more blade-like than the lower teeth. In the upper teeth the crowns curve toward the angle of the jaws, whereas in the lower teeth they usually tend to be erect; however, we have seen strongly curved lower lateral teeth in *Isurus oxyrinchus*.

POSTERIOR TEETH.—In the posterior teeth, the crowns are small and are not well developed.

Systematic Paleontology

Class CHONDRICHTHYES

Order HEXANCHIFORMES

Family Hexanchidae

(cowsharks, sixgill sharks, and sevengill sharks)

Maisey and Wolfram (1984:172) identified three dental characters that, in addition to nondental characters, they considered to unite the living hexanchids: (1) "teeth compressed labiolingually; lateral teeth bladelike but with several cusps in a rectilinear series along the cutting edge;" (2) "upper and lower teeth distinctly different, the lowers generally being longer and having more cusps;" and (3) "posteriormost upper and lower teeth are small button-like, unserrated and lacking cusps."

Maisey (1986:101) revised these characters and reduced the number of dental characters to one: "Labio-lingually flattened teeth, with the root and crown lying in the same plane and the basal surface enlarged to form the 'lingual' side of the root." His character, however, also may be applied to the Echinorhinidae.

Thies (1987:197) modified Maisey's dental character to read: "Lower lateral teeth flattened labiolingually and elongated mesiodistally, producing a sawblade-like appearance to the tooth (Maisey and Wolfram 1984, in part)." His modification restricts the application of this character to the Hexanchidae. Thies (1987:197) also added the following two additional den-

tal synapomorphies: "Main cusp of lower lateral teeth with a serration on the lower portion of its mesial edge or, alternatively, with mesial cusplets," and "tooth root of lateral teeth flattened labiolingually and rectangular in shape, with a straight basal edge."

Compagno (1984:13) also identified elongate, comb-like, lower lateral teeth, which he called anterolaterals, as a characteristic of the family. These dental synapomorphies define the family Hexanchidae.

Maisey and Wolfram (1984:173) stated that the lower medial tooth of *Notorynchus* has a vertical median cusp that is strongly inclined, whereas in *Hexanchus* it is almost vertical. The median teeth in three dentitions, however, two of *H. griseus* (USNM 176566, 188048) and one of *H. vitulus* (USNM 110900), all with strongly inclined median cusps, contradict their observations about this tooth; Thies (1987:195) also confirmed that their character is not taxonomically useful.

Using the lower anterolateral teeth, Applegate (1965b:124) identified characters for separating the genera of this family, stating, "*Hexanchus* possesses serrations on the front [mesial] edge of its most anterior crownlet. *Notorhynchus* [sic] has small unequal denticles [which increase in size apically] and the third genus in the family Hexanchidae, *Heptanchus* [sic] has one or two distinct narrow anterior denticles." Maisey and Wolfram (1984:173) and Compagno (1984:17, 19, 22) added that there are eight to 10 distal cusplets in the teeth of adult *Hexanchus*, five to six distal cusplets in the teeth of adult *Notorynchus*, and "an abruptly high cusp, and up to 7 or 8 distal cusplets" in the teeth of adult *Heptanchias*. Applegate did not identify the taxonomic characters of the upper anterolateral teeth.

Kemp (1978) was the first paleontologist to try to distinguish the upper anterolateral teeth of *Notorynchus* from those of *Hexanchus*, with the following observations: "Teeth [of *Notorynchus*] in first rows a little higher than broad ranging through to a little broader than high in last rows. Teeth of *Hexanchus* are lower and broader in comparison. Primary cusp similar to *H. griseus* but with fewer crownlets distally, ranging from only 1 in first row to 4 to 5 or 6 in the last row." In the dentitions of the extant hexanchid genera available to us, Kemp's relationship of tooth height to breadth was variable in both genera; the *Notorynchus* condition was found in the upper anterolaterals of *Hexanchus* and the converse in *Notorynchus*. In addition to Kemp's character of the number of distal cusplets, the upper teeth of *Notorynchus* are distinguished from those of *Hexanchus* by the presence of one or more cusplets on the mesial cutting edge of the anteriormost teeth and by the presence at the base of the mesial cutting edge of a small shoulder. Because only a small number of dentitions of the living species were available to us, we cannot ascertain the validity of these characters. Using these characters and those identified by Applegate (1965b), we

identified only the genera *Notorynchus* and *Hexanchus* among the Lee Creek Mine fossil teeth.

Herman et al. (1987:43–56), in their comparative morphological study of the posterior teeth of the Hexanchidae, found that these teeth possess characters that allow generic identification. These teeth, however, were not recovered at Lee Creek Mine.

In the Hexanchidae, ontogenetic variation is known to occur in two genera, *Hexanchus* and *Notorynchus*. In juveniles of *Hexanchus*, Bigelow and Schroeder (1948:82) reported that in the lower lateral teeth “the inner [mesial] margins [are] smooth in newborn specimens, but finely serrate in large, with intermediate sizes showing intermediate states.” Concerning *Notorynchus*, Kemp (1978) noted, “As in *Hexanchus* the number of crownlets, especially in the lower laterals and the degree of denticulation of mesial margin of all teeth increases with age, and thus the size of the tooth.”

According to Ward and Thies (1987), the dental formula for each upper jaw is one to two symphyisial, five to six anterolateral, and six to 13 posterior teeth; in the lower jaws it is one medial tooth; and in each jaw, it is five to six anterolateral and four to 12 posterior teeth. They did not mention, however, the upper medial tooth that is present in *Notorynchus* (Kemp, 1978). Kemp (1978) gave the dental formula for the upper jaw (one side) of *Notorynchus cepedianus* as two medial (one medial, one symphyisial), six to seven lateral (anterolateral), and 11 to 13 posterior teeth, and for the lower jaw (one side), one medial, six lateral (anterolateral), and eight to nine posterior teeth. He gave the dental formula for the upper jaw (one side) of *Hexanchus griseus* as two medial (both symphyisial), nine lateral, and eight posterior teeth, and for the lower jaw (one side), one medial, six lateral, and eight to nine posterior teeth.

Notorynchus cepedianus (Peron, 1807)

FIGURE 4

Notidanus plectrodon Cope, 1867:141 [Miocene, Maryland].

Notidanus primigenius Agassiz, 1843:303, pl. 27: figs. 6–8, 13–17 [Miocene, Switzerland].—Eastman, 1904:77, pl. 29: fig. 6 [Miocene, Maryland].—Leriche, 1942:63–64, pl. 4: figs. 7–9 [Miocene, Maryland].

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—Some 300 teeth, USNM 205296, 256290, 256312, 256315, 256316, 282771, 282776, 391921, 459874–459915, 474814–474857, 474871, 474872.

REMARKS.—Although these teeth are often assigned to the species *Notorynchus primigenius*, they are identical to those of the living *N. cepedianus* from the Pacific Coast of North America. Like the extant species, the attitudes of the primary cusps and cusplets range from almost erect to more recumbent, with the latter attitude being more predominant.

Figure 4a shows our reconstruction of this dentition. As noted above, the posterior teeth were not recovered at Lee Creek Mine. In the upper dentition, the first two mesial symphyisial teeth lack a shoulder at the basal extremity of the cutting edge, but in comparison to extant hexanchid dentitions, these teeth are most similar to those of *Notorynchus*. The first of these two teeth, the first symphyisial, has a squarish root in labial view; in *Hexanchus* the root of this tooth appears to be triangular to rhomboidal. As in *Notorynchus*, in the second of these two teeth the mesial and apical edges of the root form a right angle. In *Hexanchus* this angle is absent, and the slanted contour of the cutting edge continues down to the base of the root. The remaining teeth in the upper jaw are characteristic of *Notorynchus*.

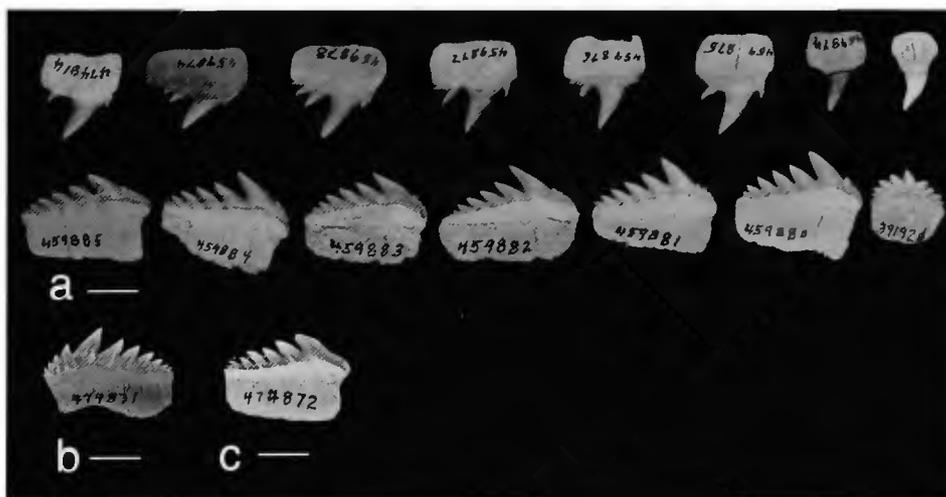


FIGURE 4.—*Notorynchus cepedianus*: a, lingual view of composite dentition; b, lingual view of lower lateral tooth, USNM 474871, with enlarged serrations on mesial edge; c, lingual view of lower lateral tooth, USNM 474872, with mesial serrations absent. (Scale bars=1.0 cm.)

In the lower jaw, the medial tooth has a nearly erect median cusp with lateral cusplets that are slightly recurved, which is characteristic of *Notorynchus* teeth rather than those of *Hexanchus*. All the other teeth in the dentition are identical to those of *Notorynchus cepedianus*.

In his review of the fossil Hexanchidae, Kemp (1978) identified the more erect primary cusp and cusplets as a character for separating the teeth of *N. primigenius* from those of *N. cepedianus*; however, Kemp's character occurs in the extant species (Guzman and Campodonico, 1976:208), and Agassiz (1833–1843, pl. 27: figs. 16, 17) included in his type suite two teeth with more recumbent primary cusps and cusplets, which Kemp stated was characteristic of the extant species. Kemp's characters, therefore, cannot be used for separating *N. primigenius* from *N. cepedianus*, and the fossil species is a junior synonym of the extant species.

Two teeth from Lee Creek Mine exhibit morphological variations not previously noted in *Notorynchus*. In USNM 474871 (Figure 4b) the recurved serrations on the mesial shoulder of the cutting edge are greatly enlarged, and in USNM 474872 (Figure 4c) the serrations are almost completely absent; at the mesial end of the shoulder of this tooth only three very small serrations are present. In Mesozoic deposits, specimens with enlarged mesial serrations, which are yet to be observed in the extant species, have been assigned to the genus *Notidaniodon* (Cappetta, 1975; Ward and Thies, 1987), but because this enlargement also occurs in the Lee Creek *Hexanchus* teeth (see below), we believe this enlargement of the mesial serrations may fall within the range of variation in the extant species and does not warrant generic separation.

Available lower anterolateral teeth range from 14 to 30 mm in length and from 19 to 21 mm in maximum height. The largest of these teeth are twice the size of those from two extant dentitions that we measured, which were from males 2 m in length. These larger fossil teeth came from individuals between 3 and 4 m TL.

According to Ebert (1986:439), *Notorynchus* inhabits relatively shallow (<100 m in depth), open coastal, temperate habitats. Compagno (1984:23) reported that they often occupy water less than 1 m in depth. They feed principally on sharks and rays, but marine mammals and bony fishes also are important prey, and they also eat mollusks and crustaceans (Ebert, 1986:444, 1991).

Hexanchus sp.

FIGURE 5

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—22 teeth, USNM 256275, 256289, 256313, 256314, 282780, 437771, 474859–474870.

REMARKS.—These teeth are so similar to those of the living *Hexanchus griseus* that specific segregation of the two is questionable. This applies as well to Sismonda's type specimen

(1861, fig. 13) of *H. gigas*. All of Leriche's (1926:391) criteria for distinguishing these two species, such as size of mesial serrations, point of maximum root height, and absolute size, are subject to ontogenetic variation and do not work with large samples, a problem also noted by Cione and Reguero (1994:6). Arambourg (1927:223) suggested one character, overlooked by Leriche and by Cione and Reguero, that may be sufficient to separate the fossil form. In the lower anterolateral teeth, the cusps of *H. gigas* are separated by notches that nearly reach the coronal-root boundary and thus make the cusps appear well developed and separate. These notches are much shallower in *H. griseus* and *H. vitulus* (e.g., see Bigelow and Schroeder, 1948, fig. 8; Kemp, 1978, pl. 12: fig. 5). Teeth with both types of notches occur in about equal numbers in the Pliocene sediments of Peru, where *Hexanchus* is more abundant than it is at Lee Creek Mine. Because adequate samples of *H. gigas* and the extant species were unavailable for this study, we cannot assess the taxonomic value of this character; therefore, we believe it is premature to assign the Lee Creek Mine teeth to a species.

Two forms of lower anterolateral teeth occur at Lee Creek Mine. In one the cusplets diminish gradually in size toward the distal end of the tooth (Figure 5a), and in the other the principal cusp is significantly higher than the distal cusplets (Figure 5b); Ward (1979:115) identified these forms as grisiform and vituliform, respectively, representing two evolutionary lines leading to the extant species. He based his definition of vituliform on a male dentition published by Bass et al. (1975d, pl. 2), which he must have assumed was characteristic for the species. In the dentition of the holotype of *H. vitulus* (a female) published by Springer and Waller (1969, fig. 2A), the lower anterolateral teeth are grisiform. According to David A. Ebert (pers. comm., 10 Dec 1990), this type of sexual dimorphism also occurs in *H. griseus*. The grisiform teeth are, therefore, those of females, and the vituliform teeth are those of males.

Lower anterolateral teeth in the Lee Creek Mine collection range from 42.7 to 55.0 mm in width and from 24.1 to 32.2 mm in maximum height. USNM 256289 (Figure 5e), from the Yorktown Formation, is the largest of these, with 11 distal cusplets; it measures 55 mm in width and 32 mm in height. This tooth is 20%–30% larger than the largest lower anterolateral tooth in the largest dentition available to us, USNM 188048 (female *Hexanchus griseus*, 433 cm TL), which measures 42.6 mm in width and 22.6 mm in height.

Another large specimen from this formation is a symmetrical lower medial tooth, USNM 474860 (Figure 5f), which measures 24 mm in width and 26 mm in height. As is often found in the medial teeth of the extant species of *Hexanchus*, the median cusp of this tooth is greatly developed, with shallow mesial and distal notches in the cutting edge; the mesial and distal shoulders are serrated with coarse, erect serrations. In some extant *Hexanchus* these serrations are large enough to be considered cusplets (height > 1.0 mm).

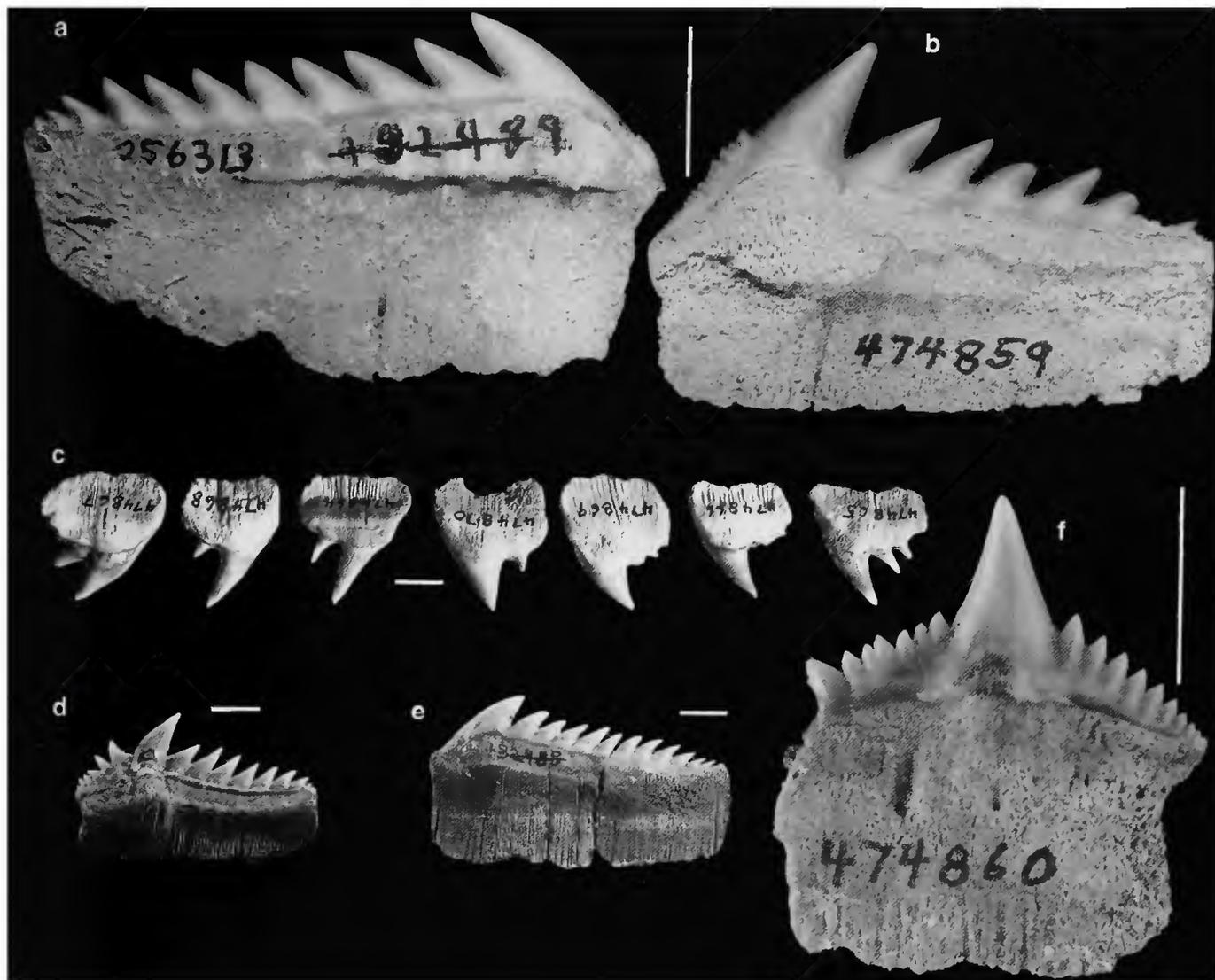


FIGURE 5.—*Hexanchus* sp.: a, USNM 256313, lingual view of lower anterolateral tooth with gradually diminishing distal cusplets; b, USNM 474859, lingual view of lower anterolateral tooth with principal cusp much taller than distal cusplets; c, lingual view of seven upper anterior teeth; d, USNM 437771, lingual view of lower lateral tooth with enlarged serrations on its mesial edge; e, USNM 256289, lingual view of largest lower anterolateral tooth from Lee Creek Mine in USNM collections; f, USNM 474860, symmetrical lower medial tooth. (Scale bars: a,b=0.5 cm; c-f=1.0 cm.)

Eight of the 22 teeth from Lee Creek Mine are from the anterior portion of the upper jaw; these teeth possess one to two distal cusplets (Figure 5c). In the extant *H. griseus* the first two teeth usually do not have distal cusplets; in the teeth that follow these, the number of distal cusplets varies from dentition to dentition. In USNM 188048 (female, 433 cm TL), these teeth possess two to three distal cusplets. Ebert (pers. comm., 10 Dec 1990, 17 Apr 1992) has a male dentition from an individual of 333 cm TL having upper teeth with one to two cusplets, and he has examined another dentition from a

female of 421 cm TL with two to three distal cusplets on the upper anterior teeth. As also noted by Kemp (1978), the number of distal cusplets increases as the shark grows larger. This variation in the number of distal cusplets evidently is ontogenetic and not sexually dimorphic.

In four comparative dentitions and in dentitions illustrated in published accounts of both extant species, we noticed significant variation in the morphology of the teeth. The tips of the cusplets are either straight or recurved, and the cusplets of some teeth appear to be more erect than are those of others. In

dentitions where the mesial and distal ends of the teeth do not abut, the mesial edges of the roots are straight rather than concave, and in abutting teeth this concavity ranges from slight to deep.

One fossil lower anterolateral tooth with eight distal cusplets (USNM 437771) exhibits a morphology that we have not observed in the teeth of the extant species; the mesial serrations, which are not recurved, are greatly enlarged, being as large as some of the distal cusplets (Figure 5*d*). Nothing about this tooth suggests that it is pathologic.

Compagno (1984:20, 21) reported that the extant species inhabit continental and insular shelves in temperate and tropical seas in water depths exceeding 90 m; they feed on other sharks, bony fishes, carrion, seals, and crustaceans. Ebert (1994:216) noted that in the extant species, the young feed principally on cephalopods, and that as they mature, bony fishes and chondrichthyans become an increasingly important part of their diet. The few individuals greater than 200 cm TL that he examined fed on cetaceans and on larger, more active teleosts, such as marlin and swordfish.

Order SQUALIFORMES

Family ECHINORHINIDAE (bramble sharks)

Echinorhinus blakei Agassiz, 1856

FIGURE 6

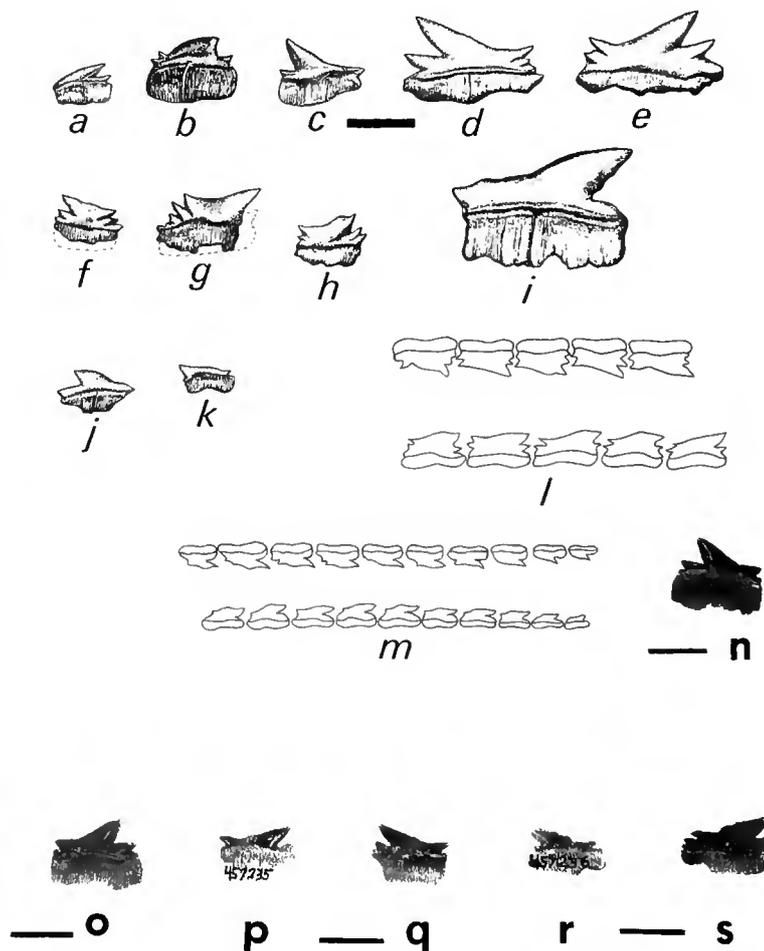
Echinorhinus blakei Agassiz, 1856:272, pl. 1: figs. 7, 8, 17 [Miocene, California].—[Not *Echinorhinus blakei* Jordan and Hannibal, 1923, pl. 4: figs. c,d.]

HORIZON.—Pungo River Formation (units 4, 5).

REFERRED MATERIAL.—13 complete teeth and fragments of teeth, USNM 207608, 207609, 280334, 281317, 281331, 287739, 287740, 412221, 457232–457236.

REMARKS.—The upper and lower teeth of bramble sharks are alike (dignathic homodonty). This small to medium-sized shark has smooth-edged teeth, with the strongly oblique central cusp sloping toward the corners of the mouth. In published dentitions of *Echinorhinus brucus* (Bigelow and Schroeder, 1948, fig. 102; Bass et al., 1976, pl. 11; Herman et al., 1989, pl. 1) this obliquity varies noticeably. The greatest obliquity occurs in Bigelow and Schroeder's dentition of an unsexed indi-

FIGURE 6.—*Echinorhinus blakei*: a, USNM 412221, posterolateral tooth, lingual view; b, USNM 207609, upper posterolateral tooth, lingual view; c, USNM 207608, posterolateral tooth. *Echinorhinus blakei*, Miocene, California: d,e, views of holotype. *Echinorhinus richiardi*, Pliocene, Tuscany: f–h, syntypes. *Echinorhinus caspius*, Oligocene, Armenia: i, lingual view. *Echinorhinus priscus*, Eocene, Morocco: j,k, lingual views. *Echinorhinus brucus*: l,m, outlines of partial dentitions of the extant Atlantic species, after Bigelow and Schroeder (1948); n, USNM 287739, lower posterolateral tooth, lingual view; o, same specimen, labial view; p, USNM 457235, upper posterolateral tooth, lingual view; q, same specimen, labial view; r, USNM 457236, upper posterolateral tooth, lingual view; s, same specimen, labial view. (Scale bars=1.0 cm.)



vidual, and the least occurs in Herman et al.'s dentition from a 228 cm female. In these dentitions the mesial edges of the teeth also exhibit noticeable variation; those of Herman et al.'s dentition are very convex, whereas in the other dentitions they are straight to slightly convex. In adults, one to three lateral cusplets may be present on the mesial side of the central cusp, and one to two lateral cusplets may be present on the distal side; some of these cusplets may occur unpaired. In juveniles only the main cusp is present (Compagno, 1984:25).

We refer 12 teeth from the Pungo River Formation to *Echinorhinus*. They show considerable variation in the number of accessory cusplets and in the degree of curvature of the edges of the central cusp (Figure 6n-s). One tooth (Figure 6n,o; cf. Figure 6d,e) strongly resembles the holotype of *E. blakei* from the Miocene Temblor Formation of California. Of two extant species recognized by Compagno (1984), *E. brucus* (Bonna-terre, 1788) and *E. cookei* Pietschmann, 1928, the fossil teeth bear a closer resemblance to those of the latter species; however, this comparison is based on the published dentitions of *E. brucus* cited above and on one of *E. cookei* (Garrick, 1960, fig. 3).

The earliest known echinorhinid teeth, *E. caspius* Glikman (1964) from the early Oligocene of Armenia (Figure 6i) and *E. priscus* Arambourg (1952) from the early Eocene of Morocco (Figure 6j,k), are simple, lacking well-developed cusplets. In the extant species, the juvenile teeth (Figure 6m) and the adult posterior teeth also lack cusplets (Garrick, 1960; Compagno, 1984; Herman et al., 1989), and the type specimens of Glikman and Arambourg are very similar to the juvenile teeth of the extant species. Without examining the types of the fossil species and many dentitions of the extant species, the affinities of these Paleogene species cannot be determined.

Echinorhinus richiardi from the Pliocene of Tuscany (Figure 6f-h), with well-developed lateral cusplets, may belong to the extant species *E. brucus*.

The teeth identified as *Echinorhinus blakei* by Jordan and Hannibal (1923) are fragmentary hexanchid teeth. The tooth in their pl. 4: fig. d is a median tooth of *Hexanchus*; the generic identity of the other tooth figured is indeterminate.

We provisionally assign the teeth from Lee Creek Mine to *E. blakei*; without an extensive series of dentitions from the extant species we cannot determine if the teeth of the fossil and extant species are separable. The fossil teeth may be identical to those of *E. cookei*, and this latter species may be a junior synonym of *E. blakei*.

The height of the teeth ranges from 9.4 to 11.8 mm, and the width ranges from 11.8 to 15.8 mm.

The living species of this shark (Compagno, 1984:26, 27) are bottom dwellers in temperate to tropical seas, sometimes occurring in shallow water but primarily in deep water. *Echinorhinus brucus* occurs in waters from 18 to 90 m deep, and *E. cookei* occurs in waters from 11 m to at least 424 m in depth. They feed on other sharks and on bony fishes, including catfish, hake, and flounder.

Family SQUALIDAE (dogfish sharks)

Squalus sp.

FIGURE 7a,b

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—1 tooth, USNM 207546.

REMARKS.—Unlike *Squalus acanthias*, the common North Atlantic dogfish, but like *S. almeidae*, this tooth is rather robust. Its cutting edges are smooth but irregular. On its labial face (Figure 7a) the crown foot is slightly convex and extends basally to form a peg; this peg extends well below the basal margin of the root. Like *S. almeidae*, the lateral edges of the peg converge but become parallel near the peg's basal end. Lateral to the peg the boundary between the crown foot and the root is sinuous.

On the lingual face of the tooth (Figure 7b), the crown foot extends basally to form a prominent process; this process has a deep central depression (also observable in *S. acanthias*), making it V-shaped. On either side of this process the root is excavated, and clearly marked foramina open into these depressions. The basal margin of the root forms a ridge, which is bisected by a transverse groove.

In the extant species the teeth are alike in both jaws, being low crowned, blade-like, interlocked teeth with a single cusp and a distal enamel shoulder on a low root; the cutting edges are smooth in living species but are serrated in some fossil species (Compagno 1984:109). Bass et al. (1976:13) noted that in *Squalus acanthias* "slight sexual dimorphism is apparent, the male having teeth with more erect and pointed cusps."

Although the teeth from Lee Creek Mine share characters with *Squalus almeidae* from the middle Miocene of Portugal, USNM 207546 differs from this species in the sinuosity of the mesial cutting edge, which is rectilinear in *S. almeidae*. Because at this time we cannot assess the taxonomic value of this character, we do not assign the Lee Creek Mine specimen to a species.

This specimen measures 2.9 mm in height and 4.2 mm in width; its size falls within the size range of the extant *Squalus acanthias*. According to Compagno (1984), the latter species ranges in size from 22 cm at birth to 160 cm TL.

The extant *Squalus acanthias* inhabits boreal to warm temperate waters from the intertidal zone to 900 m in depth. This shark feeds primarily on bony fishes (Compagno, 1984:112).

Isistius sp.

(cookiecutter sharks)

FIGURE 7f,g

HORIZON.—Yorktown Formation (units 1-3).

REFERRED MATERIAL.—5 teeth, NCSM 11287, 11288, 11291, 11292, USNM 475362.

REMARKS.—While bulk sampling a Yorktown Formation spoil pile, one of us (V.P.S.) recovered five lower teeth of this

species. These teeth compare favorably with those illustrated by Bigelow and Schroeder (1948:510). All of the teeth have broad, flat, triangular crowns with smooth, very thin, transparent cutting edges. Of the five teeth, NCSM 11287 (Figure 7f) and NCSM 11292 (Figure 7g) are nearly complete. NCSM 11287 is the largest, measuring 8.3 mm in height and 5.3 mm in width; a central foramen and shallow transverse groove are present on the lingual face of the root. In NCSM 11292 the root basal to the central foramen is missing; this tooth measures 3.7 mm in height and 2.4 mm in width.

These teeth compare favorably with the types of *Scymnus triangulus* (Probst, 1879:175), which Cappetta (1970) rightly referred to *Isistius*. The Lee Creek Mine teeth, however, differ from Probst's species and the living species in lacking the median groove. With the lack of ample comparative extant and fossil material, we cannot judge the validity of this character or the validity of *I. triangulus* Probst. Of the two living species, *I. brasiliensis*, which has moderately large teeth, and *I. plutodus*, which has enormous teeth (Compagno 1984:93–95), the Lee Creek Mine species appears to be more closely related to *I. brasiliensis*.

Although teeth of *Isistius* have been found in the Miocene and Pliocene sediments of Europe and South America (Ecuador) (Cappetta, 1987:64), the specimens from Lee Creek Mine represent the first occurrence of this taxon in North America.

According to Compagno (1984:94), the extant *I. brasiliensis* is a tropical, oceanic shark, epipelagic to bathypelagic in distribution. In addition to feeding on squid, gonostomatids, and crustaceans, this shark "has highly specialized suctorial lips and a strongly modified pharynx that allow it to attach to the sides of large bony fishes such as marlin, tuna, albacore, wahoo, and dolphinfishes, as well as dolphins and other cetaceans and even the megamouth shark (*Megachasma*). The shark then drives its razor-sharp sawlike lower dentition into the skin and flesh of its victim, twists about to cut out a conical plug of flesh, then pulls free with the plug cradled by its scooplike lower jaw and held by the hooklike upper teeth" (Compagno, 1984:94).

Order PRISTIOPHORIFORMES

Family PRISTIOPHORIDAE (saw sharks)

Pristiophorus sp.

FIGURE 7c

HORIZON.—Pungo River Formation (units 1–3).

REFERRED MATERIAL.—6 rostral teeth, USNM 207583, 299481, 467554–467556, 467587.

REMARKS.—We assign these teeth to this genus rather than to *Pliotrema* because their dorsoventrally compressed and enameled crowns are not serrated on the distal edges. In *Pliotrema* (Fowler, 1941:283) these distal edges are serrated. The largest tooth in this sample measures 19.2 mm in length



FIGURE 7.—*Squalus* sp.: a, USNM 207546, labial view; b, same specimen, lingual view. *Pristiophorus* sp.: c, USNM 207583, rostral spine, lateral view. *Rhinobatos* sp.: d, USNM 207544, lingual view; e, USNM 207545, lingual-occlusal view. *Isistius* sp.: f, NCSM 11287, lower tooth, lingual view; g, NCSM 11292, lower tooth, labial view. (Scale bars=0.25 cm.)

(Figure 7c). Because large samples of the dentitions of the extant species were not available, we believe it is not prudent to identify these specimens beyond genus.

According to Compagno (1984:137), the extant Atlantic species is "a little known, deep-water, tropical sawshark of the continental and insular slopes of the Bahamas region, occurring on or near the bottom at depths from 640 to 915 m." Its presence in the shallower Pungo River seas may have been through the excretions or the regurgitated hard parts from a predator shark.

Order RHINOBATIFORMES

Family RHINOBATIDAE
(guitarfishes)*Rhinobatos* sp.FIGURE 7*d,e*

HORIZON.—Pungo River Formation (units 4, 5).

REFERRED MATERIAL.—9 teeth, USNM 207544, 207545.

REMARKS.—In occlusal view, these teeth are oval to tetragonal (Figure 7*e*); a peg extends down from the lingual surface of the crown onto the surface of the root (Figure 7*d*), which is lingually deflected. A transverse groove bisects the root. Because the range of dental variation in the extant species is not yet known and because we were unable to examine any specimens of the extant species, we believe it is unwise at this time to attempt a taxonomic evaluation of the fossil species or to attempt a more precise identification of the Lee Creek Mine specimens.

The extant species, *Rhinobatos lentiginosus*, inhabits subtropical to tropical waters of the western Atlantic Ocean (Bigelow and Schroeder 1953:66–67); it occasionally reaches as far north as Cape Hatteras, North Carolina. Little is known about its range and habits.

Order PRISTIFORMES

Family PRISTIDAE
(sawfishes)*Pristis* sp.FIGURE 8*a,b*

HORIZON.—Yorktown Formation (unit 1?).

REFERRED MATERIAL.—3 rostral teeth, USNM 281389, 281390, 412220.

REMARKS.—These teeth may be those of juveniles because they lack a groove along their posterior edges; this condition also is found in an extant species with rostral teeth of similar form (*Pristis* sp., USNM 232696). All three specimens are slightly abraded, and their surfaces exhibit bite marks. Teeth from Lee Creek Mine are relatively short (23.5–25.5 mm in length) and thin (2.6–2.9 mm in thickness; ratio of width to thickness 2.1–2.7). They show no trace of a subbasal barb.

Bigelow and Schroeder (1953:28–29) reported that the extant common sawfish (*P. pectinatus*) inhabits warm temperate to tropical coastal waters and feeds on bony fishes and bottom-dwelling animals.

Pristis cf. *P. pectinatus* Latham, 1794FIGURE 8*c,d*

HORIZON.—Yorktown Formation (unit 1?).

REFERRED MATERIAL.—1 rostral tooth, USNM 412219.

REMARKS.—This rostral tooth does not differ appreciably from those of the extant *Pristis pectinatus*. The exerted part of

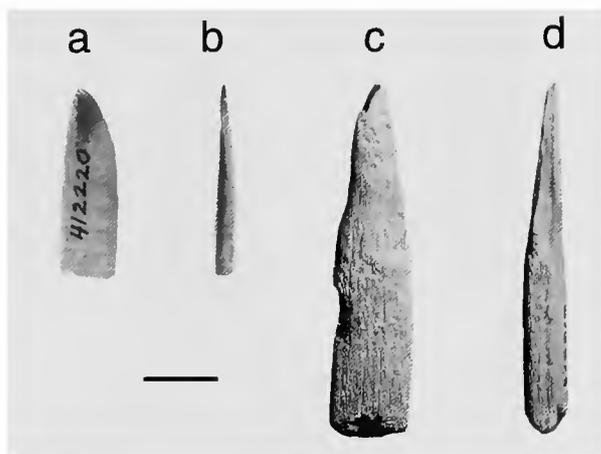


FIGURE 8.—*Pristis* sp.: *a*, USNM 412220, dorsal view; *b*, same specimen, distal view. *Pristis* cf. *P. pectinatus*: *c*, USNM 412219, dorsal view showing regularly tapering exerted portion; *d*, same specimen, posterior view showing position of groove. (Scale bar=1.0 cm.)

the tooth is moderately short, being about equal to the inserted part. The apex of the crown is aligned with the mesial axis rather than being displaced distally. On the exerted portion of the tooth, the distal margin is straight (Figure 8*c*), with a noticeable groove (Figure 8*d*) that extends to the tip of the tooth, rather than a cutting edge. On the inserted portion of the tooth the distal margin bends mesially. The outline of the mesial margin of the tooth is obliterated by wear and breakage, but the exerted portion was probably convex and rounded in cross section. The tooth is 52.7 mm in proximodistal length, 12 mm in anteroposterior length, and 7.5 mm thick at the proximal end, tapering to 2.0 mm at the worn apex.

Oral teeth, which also are important for the identification of fossil pristid remains, were not recovered at Lee Creek Mine.

Order RAJIFORMES

Family RAJIDAE
(skates)*Raja* sp.

FIGURE 9

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—2 teeth, USNM 476398, 476399.

REMARKS.—Two teeth recovered from the spoil piles of principally Yorktown matrix compare favorably with those in a dentition of a male of the extant species *Raja laevis* (USNM 110962). USNM 476398 (Figure 9*a,b*), from the anterior portion of the jaw, has an awl-like crown that inclines strongly lingually; the crown foot extends laterally, creating a shelf that circumscribes the crown. Basal to the crown foot the root is constricted but flares basally. On its labial side the root is flattened, which gives it a semicircular cross section. A deep

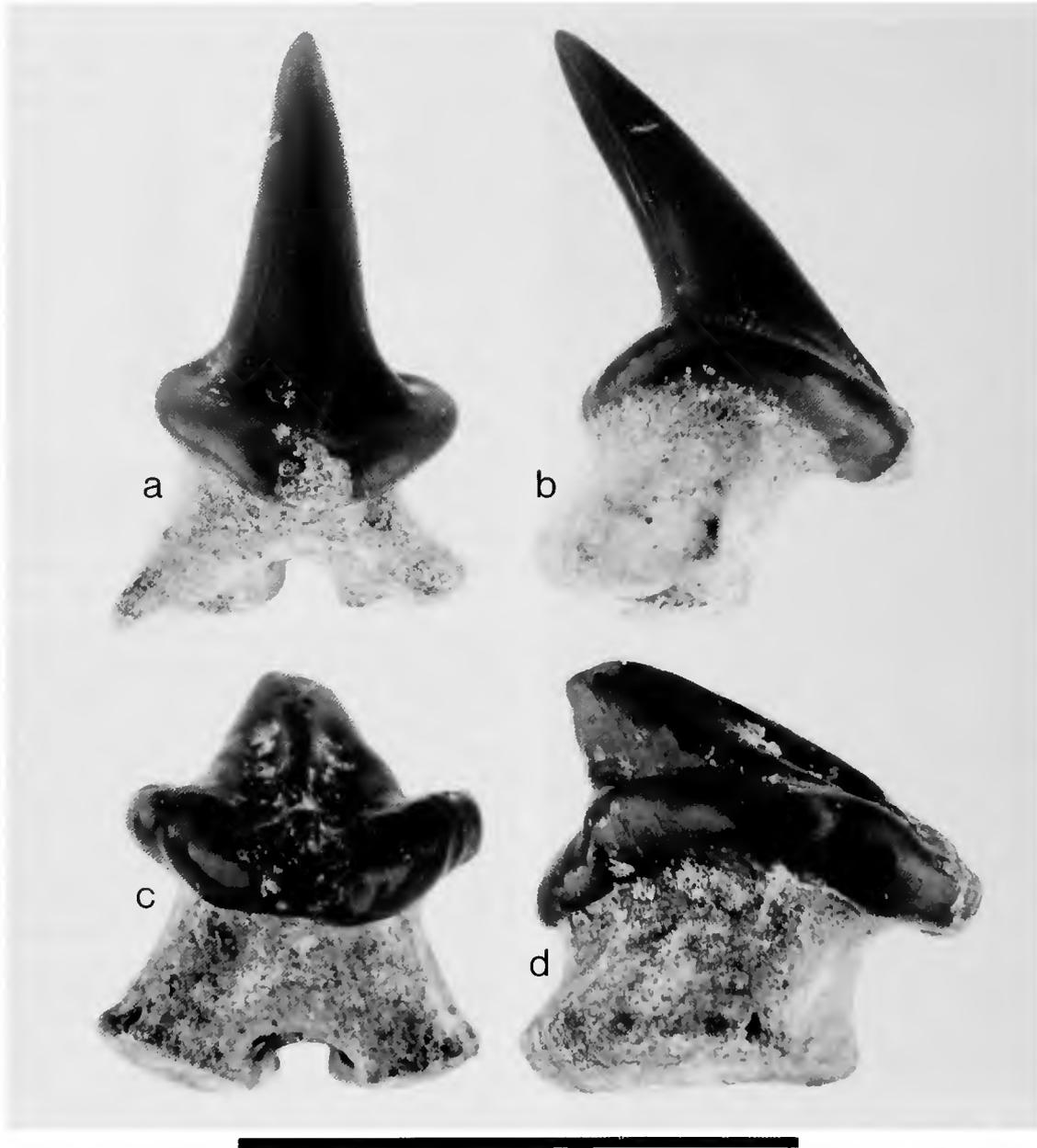


FIGURE 9.—*Raja* sp.: a, USNM 476398, labial view; b, same specimen, lateral view; c, USNM 476399, labial view; d, same specimen, lateral view. (Scale bar=0.1 cm.)

transverse groove bisects the root, giving it a bipedal appearance. This tooth measures 7.25 mm in height and 5.35 mm in width. In USNM 476399 (Figure 9c,d) the crown is stubby and rounded by wear; the root is similar to that of the above specimen. This tooth measures 5.20 mm in height and 5.40 mm in width.

The extant *Raja laevis* feeds chiefly on larger crustaceans, but it also eats bony fishes, including tautog and hake (Bigelow and Schroeder, 1953:223). According to McEachran and Musick (1975:119), this skate ranges from the Gulf of St. Lawrence to Cape Hatteras and occurs to depths of 375 m.

Order MYLIOBATIFORMES

Family DASYATIDAE (stingrays)

Dasyatis say (Lesueur, 1817)

FIGURE 10a-r

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—433 isolated teeth, USNM 207584–207588, 301684–302045.

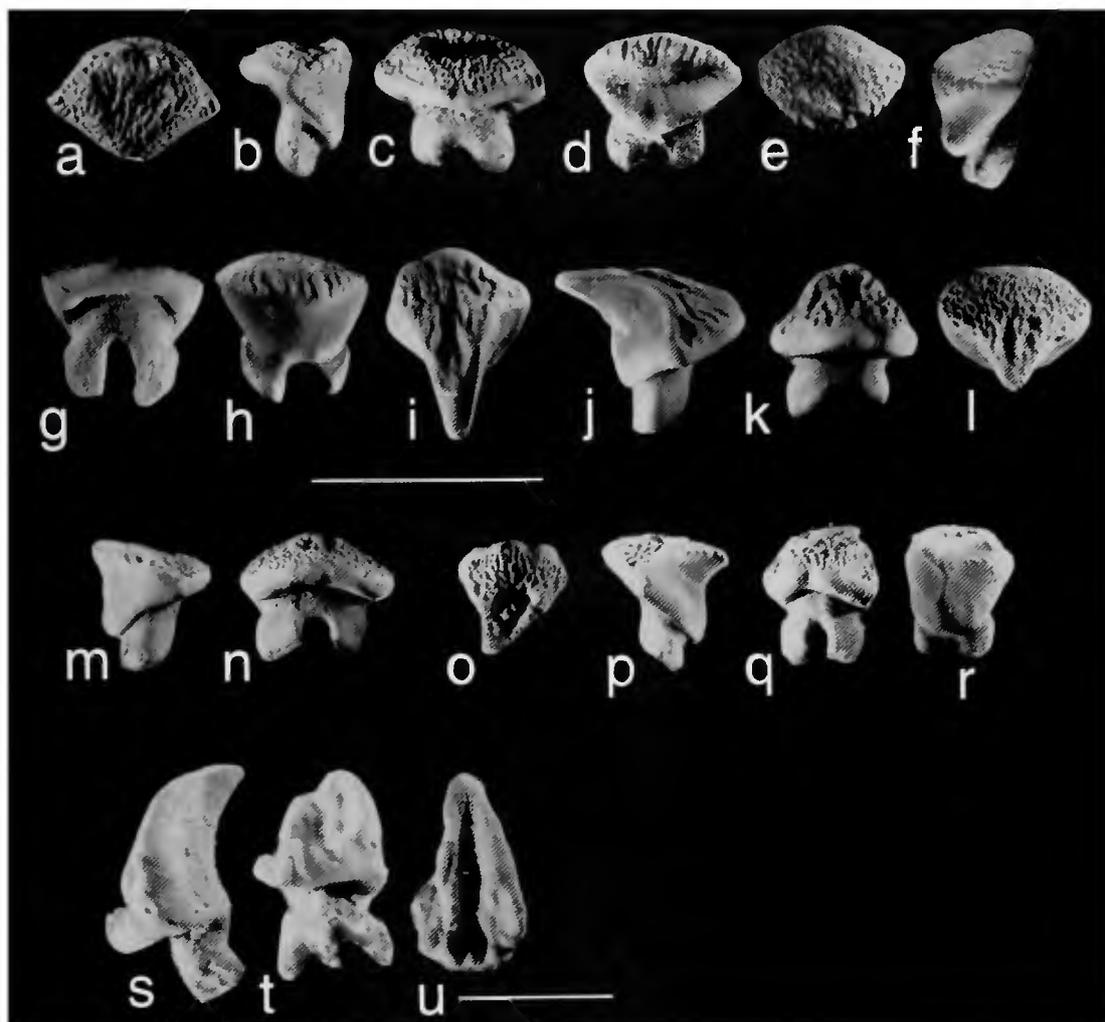


FIGURE 10.—*Dasyatis say*, male and female teeth: *a*, USNM 207584, Yorktown Formation, female tooth, occlusal view; *b*, same specimen, lateral view; *c*, same specimen, labial view; *d*, same specimen, lingual view; *e*, USNM 207585, Yorktown Formation, female lateral tooth, occlusal view (lingual side down); *f*, same specimen, lateral view; *g*, same specimen, labial view; *h*, same specimen, lingual view; *i*, USNM 207586, Yorktown Formation, male tooth, occlusal view; *j*, same specimen, lateral view; *k*, same specimen, labial view; *l*, USNM 207587, Pungo River Formation, male tooth, occlusal view; *m*, same specimen, lateral view; *n*, same specimen, labial view; *o*, USNM 207588, Pungo River Formation, male medial? tooth, occlusal view; *p*, same specimen, lateral view; *q*, same specimen, labial view; *r*, same specimen, lingual view. *Dasyatis* cf. *D. americana*, USNM 207548, Pungo River Formation: *s*, lateral view; *t*, labial view; *u*, occlusal view. (Scale bars: *a*–*r*=0.5 cm; *s*–*u*=0.25 cm.)

REMARKS.—The Lee Creek Mine teeth are morphologically identical to those of the modern *Dasyatis say*. They both display a punctate occlusal surface, a well-defined cutting edge dividing the occlusal surface and lingual apron, and abbreviated striations that extend a short distance down the lingual apron from the cutting edge.

Bigelow and Schroeder (1953:382) and Taniuchi and Shimizu (1993) reported that the teeth of *D. say* exhibit sexual dimorphism. The teeth of females and immature males are “quadrangular with blunted corners, about as broad (transversely) as long (anteroposteriorly), the functional surface weakly rounded or more or less irregular from wear; those of mature males with

low and broadly triangular cusps, largest in youngest rows” (Taniuchi and Shimizu, 1993:54). Teeth from both sexes occur at Lee Creek Mine; those of females are illustrated in Figure 10*a*–*h*, and those of males are illustrated in Figure 10*i*–*r*. The teeth range in height from 2.6 to 3.8 mm (mean=3.2 mm, *n*=5) and range in width from 2.8 to 3.9 mm (mean=3.3 mm, *n*=5).

Although the extant species normally inhabits subtropical to tropical waters, it ventures into more temperate waters during the summer. Bigelow and Schroeder (1953:358–359) reported that *D. say* “has been reported as deep as 6–20 fathoms; and some may summer where the depth is as great as 20–30 fathoms, if reports of their occurrence on Georges Bank are well

founded." The extant species probably feeds on crustaceans and mollusks.

Dasyatis centroura (Mitchill, 1814)

FIGURE 11a–d, g–i

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—About 350 dermal denticles, USNM 182122, 182123, 182129–182135, 182137, 182139,

182141, 280071–280305, 353680, 353684, 445534, 445544, 476402, 476403, 482224–482229.

REMARKS.—Numerous dermal denticles were recovered from the spoil piles, particularly in the Yorktown matrix, that are very similar to those found along the tail and back of the extant species *Dasyatis centroura*. These denticles are circular to oval in outline, with one or more centrally located conical points. Silas and Selvaraj (1985:252) reported that the sharpness of the conical points decreases as the base of the denticle

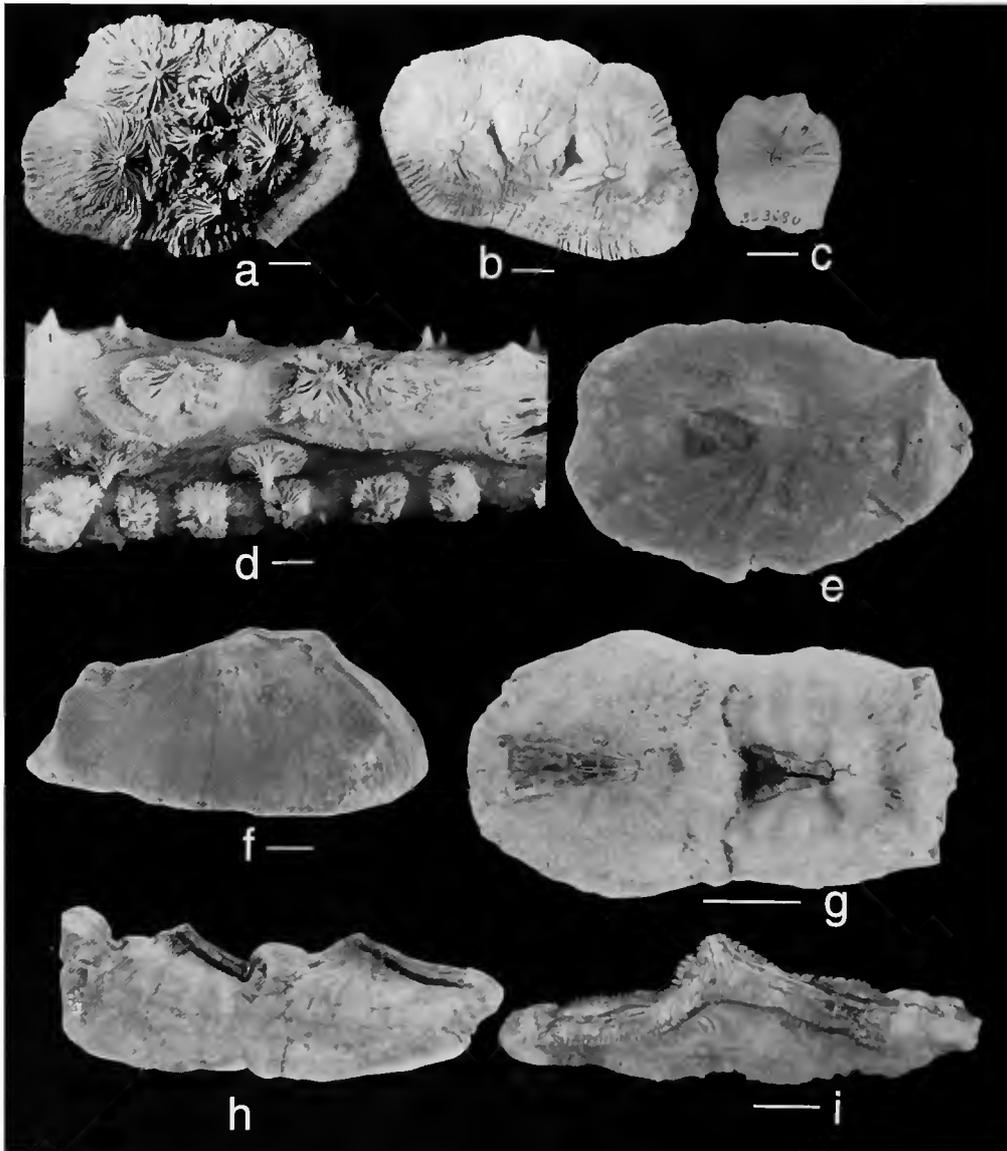


FIGURE 11.—*Dasyatis centroura*: a, USNM 353684, dorsal view of dermal denticle marked by radiating rugosities with enameloid caps missing; b, USNM 280071, dorsal view of dermal denticle with three conical points with enameloid caps preserved; c, USNM 353680, dorsal view of dermal denticle with triangular enameloid cap. Recent *D. centroura*: d, USNM 197504, dorsal view of caudal denticles. *Ceratopterus unios*, holotype, ANSP 8069, dermal denticle: e, dorsal view; f, lateral view. *Dasyatis centroura*: g, USNM 482224, dorsal view of dermal denticle; h, same specimen, lateral view; i, USNM 482225, dorsal view of dermal denticle with serrate enameloid cap. (Scale bars = 1.0 cm.)

increases in size. Unlike *D. centroura*, which is known to have denticles that support only two or three conical points (Bigelow and Schroeder, 1953:355), the Lee Creek Mine specimens support up to 10 conical points, which may be the result of the Lee Creek Mine denticles coming from specimens larger than those available to Bigelow and Schroeder.

The external surfaces of these denticles may have fragile, triangular (narrow to wide) to conical enameloid caps (Figure 11*b,c*) (terminology of Reif, 1979). Basal to these caps, the external surface of the denticle may be smooth to strongly striated. According to Bigelow and Schroeder (1953:355), those with striated bases occur only on the tail. On the dermal denticles of a tail of a recent *D. centroura* (USNM 197504) (Figure 11*d*) and in a Lee Creek Mine specimen (USNM 280071, Figure 11*b*), these striations extend under the enameloid cap. In Lee Creek Mine specimens that lack enameloid caps, these striations extend almost to the apex of the denticle (Figure 11*a*). Paleontologists (Larrazet, 1886; Zittel, 1887–1890; Reif, 1979) have identified fossil specimens without their enameloid caps as *Acanthobatis*; these should be referred to *Dasyatis*.

Figure 11*i* shows a narrow denticle, USNM 482225, that we believe also belongs to *Dasyatis centroura*. The edges of the enameloid cap are serrated in the same manner as the caudal spines.

According to Stehmann (1981), the extant species inhabits tropical latitudes, occurring in waters to depths of 300 m, and it feeds principally on bivalves, crustaceans, and worms.

***Dasyatis* cf. *D. americana* Hildebrand
and Schroeder, 1928**

FIGURE 10*s–u*

HORIZON.—Pungo River Formation (units 1–3).

REFERRED MATERIAL.—1 isolated tooth, USNM 207548.

REMARKS.—The root is dasyatid except that the specimen illustrated has two grooves rather than the usual one. The root constricts to one-third of the basal diameter at the crown-root boundary. Like most male dasyatid teeth, the crown is acuminate but asymmetrical, the occlusal surface is convex labially and divided into two ridges by a deep medial sulcus, and the basal margin is accentuated by a cingulum-like irregular ridge. The Lee Creek Mine specimen is 3.5 mm in maximum height and 1.9 mm in width (mesial-distal diameter).

Except for the tripartite root, this tooth, which has a medial sulcus on the occlusal surface, resembles those of the male *Dasyatis americana*.

According to Bigelow and Schroeder (1953:350–351), the extant species prefers warm-temperate to tropical coastal waters. It is not known to occur at the depths represented by the Pungo River Formation; their presence there may be the result of regurgitation by sharks that fed on them. The extant *Dasyatis americana* feeds on blue crabs, clams, shrimp, worms, and small bony fishes.

NOTA BENE

Leidy (1876:86) described as a new species of manta ray (*Ceratoptera unios*) a large, thick, dermal denticle (length=8.2 cm, width=5.4 cm, thickness=3.6 cm) of *Dasyatis*. The holotype (ANSP 8069), which Leidy mistook for a caudal spine, has an elongate, oval enameloid cap. Basal to this cap the denticle surface is striated. At one extremity of its long axis, a facet indicates that this denticle abutted another one. This specimen (Figure 11*e,f*), which was found in the phosphate beds along the Ashley River, South Carolina, and may be from the Pliocene, is more massive than any found at Lee Creek Mine. Two fused denticles from Lee Creek Mine, USNM 482224, which together measure 4.8 cm in length (width=2.4 cm, thickness=1.4 cm), are similar in morphology (Figure 11*g,h*). These fused denticles support our assignment of *Ceratoptera unios* to *Dasyatis*. At this time we cannot ascertain the specific identity of Leidy's holotype.

**Family MYLIOBATIDAE
(eagle rays)**

***Pteromylaeus* sp.**

FIGURE 12*a,k*

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—7 partial dental pavements, USNM 24758, 25448, 297760, 464159.

REMARKS.—These specimens may be indistinguishable from the extant species, *Pteromylaeus bovinus*, which is presently found in the eastern Atlantic Ocean and the Mediterranean Sea. With only one specimen of the extant species available to us, we cannot confirm the identity of the fossil species; thus, we identify the teeth from Lee Creek Mine to genus only. The largest specimen of this species from Lee Creek Mine is USNM 464159 (Figure 12*k*).

We refer the Lee Creek Mine specimens to *Pteromylaeus* because the length of the median teeth is seven times greater than their width, a character that McEachran and Capapé (1984:206) and Capapé and Quignard (1975:1335) used to separate the teeth of *Pteromylaeus* and *Myliobatis*. Garman (1913:438) characterized the teeth of *Pteromylaeus* as having three rows of very narrow lateral teeth; however, the width of the teeth appears to be variable because Capapé and Quignard (1975:1331) figured a dentition with lateral teeth that are identical to those of *Myliobatis*. Nishida (1990), who studied the phylogeny of the myliobatoids, stated that the size and shape of these teeth are highly variable. When large suites of dentitions of myliobatids become available for study, our generic assignment for the fossil species may have to be revised.

The extant species inhabits warm-temperate to tropical waters (McEachran and Capapé, 1984:205) and feeds on bottom-dwelling crustaceans and mollusks.

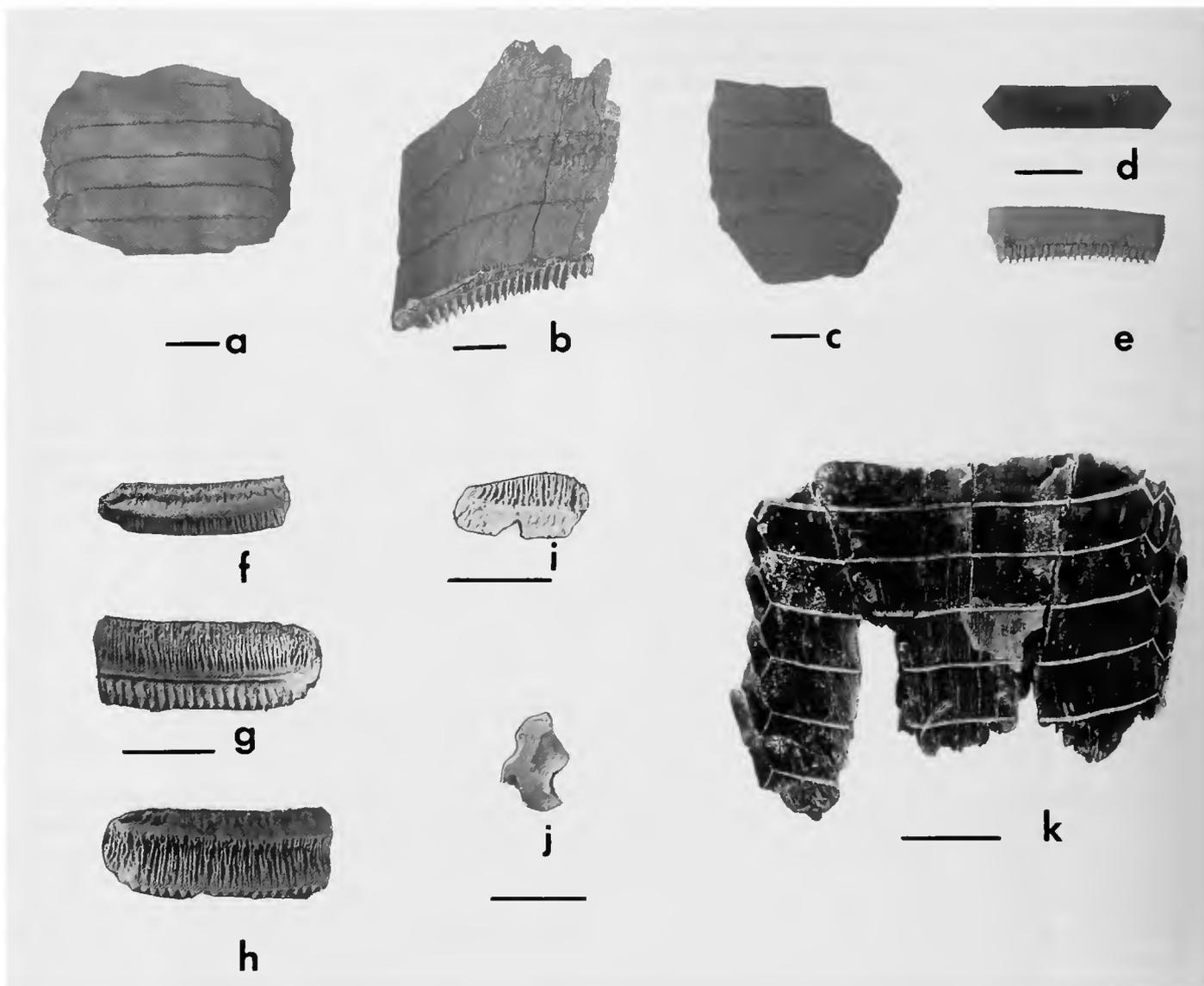


FIGURE 12.—*Pteromylaeus* sp.: a, USNM 24758, lower dental battery, occlusal view. *Aetobatus* sp.: b, USNM 312263, lower dental battery, occlusal view; c, USNM 312264, upper dental battery, occlusal view. *Rhinoptera* sp.: d, USNM 24745, lower medial tooth, occlusal view; e, same specimen, anterior view. *Plinthicus stenodon*: f, USNM 207591, incomplete medial tooth showing narrow occlusal surface; g, same specimen, lingual view showing bifurcating grooves on crown and multilobed root; h, same specimen, labial view; j, same specimen, lateral view. i, USNM 207592, lateral tooth, occlusal view. *Pteromylaeus* sp.: k, USNM 464159, lower dental battery, occlusal view. (Scale bars=1.0 cm.)

Aetobatus sp.

FIGURES 12b,c, 13

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—3 uncataloged incomplete upper dental plates (Pungo River Formation phosphatic limestone); numerous uncataloged incomplete isolated teeth; 2 lower and upper dental batteries, USNM 312263, 312264; cast of 1 restored upper dental pavement, USNM 489120 (Yorktown Formation).

REMARKS.—Most of the specimens from Lee Creek Mine are incomplete, isolated teeth. They include chevron-shaped lower teeth and gently arching upper teeth that are characteristic of *Aetobatus*. The largest and only specimen with complete teeth from Lee Creek Mine is in the collection of George W. Powell, Jr., who donated an excellent cast of this specimen to the Smithsonian Institution (USNM 489120, Figure 13). This specimen, which is 24.2 cm long and 12.5 cm wide, has the lingual portion of the dentition nearly complete; the labial portion of the dentition consists of teeth with large fragments missing.



FIGURE 13.—*Aetobatus* sp., USNM 489120, Yorktown Formation, cast of upper dental battery collected and restored by George W. Powell, Jr., occlusal view. (Scale bar=1 cm.)

In form, the teeth are gently arcuate, with no lateral tooth rows present, which is characteristic of the genus (Bigelow and Schroeder, 1953:452). On the right lateral extremity of the dentition, each tooth tapers to a rounded point. On the left side, the teeth are truncated and have rounded corners. Because dentitions from large individuals of the extant species of *Aetobatus* were not available to us, we believe that at this time it is prudent not to identify this specimen to species.

According Bigelow and Schroeder (1953:461), the extant species inhabits shallow to deep, warm temperate to tropical waters. It feeds on bivalve mollusks.

Family RHINOPTERIDAE
(cownose rays)

Rhinoptera sp.

FIGURE 12*d,e*

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—Approximately 200 fragments of teeth; 52 isolated teeth, USNM 24745, 284831, 312262.

Garman (1913), Gudger (1933), and Nishida (1990) reported that the size, shape, and number of rows of these teeth (5–19) are highly variable. Because sufficient samples of the dentitions of the extant species were unavailable to us, we believe it is premature to assign the Lee Creek Mine specimens to a fossil species or to evaluate the validity of the fossil species.

REMARKS (isolated teeth).—The crown height of unworn teeth is approximately equal to the width of the crown (crown height/width=0.9–1.3, mean=1.06, $n=6$). In medial teeth the crown heights are uniform from one side of the tooth to the other, but in the first rows lateral to the medial teeth, the crowns are higher on the mesial side than on the distal side. In unworn teeth, the occlusal surfaces either are smooth or are covered with faint and irregular depressions. The transverse edges of the crown show irregular vertical ridges; on the labial side of the tooth, the surface is smooth and shiny, but on the lingual side of the tooth, it usually has a finely pebbled texture. On this same side of the tooth just below the crown, a prominent transverse ridge extends the full length of the tooth.

The crown overhangs the root on all but the lingual side, where the root margin is even with or projects beyond the base of the crown. As the teeth grew, the number of grooves in the root decreased; for example, the number of grooves per cm (spacing of grooves) decreased from a maximum of 13.6 (small median tooth, transverse width=14 mm) to 7.5 (intermediate-sized upper medial tooth, transverse width=23 mm). The largest specimens have 7.5 to 8.5 grooves per cm.

The extant cownose ray inhabits coastal to deep, warm-temperate to tropical waters, but it migrates into more temperate waters during the summer (Rogers et al., 1990). It feeds on bivalve mollusks.

Plinthicus stenodon Cope, 1869

FIGURE 12*f-j*

HORIZON.—Pungo River Formation (units 1–6).

REFERRED MATERIAL.—Several hundred isolated teeth, USNM 207591, 207592.

REMARKS.—This species, known only from isolated teeth, is easily recognized. The occlusal face is concave and is covered with labiolingually oriented rounded ridges and grooves. On all specimens the width of the occlusal surface is about 2.5 mm, or about one-third the height of the medial teeth and about one-half the height of the teeth of the presumed second lateral row.

Labial and lingual articulating surfaces bear closely spaced (20 per cm) vertical ridges that often split and divide. When viewed laterally, the laminae on the root (which is the myliobatid type) are subcircular and are unusually thin (0.3 mm) and fairly widely spaced (6 per cm).

Three types of teeth are present in the sample: (1) asymmetrical teeth about 1 cm in length, higher mesially than distally; (2) symmetrical short teeth also about 1 cm in length; and (3) symmetrical long teeth. Teeth of the third type are almost always broken, but the contacting pieces of a complete tooth sometimes can be recovered by careful collecting. Two such teeth, each 42 mm in length, were collected from the sandy layers of units 4 and 5 of the Pungo River Formation. When arranged in a rhinopterid pattern, the short teeth of types one and two would represent the second and first lateral rows, respectively, and the long teeth of type three would represent the medial row. This series formed a rather coarsely ridged pavement that, judging from the seemingly little wear that appears on the occlusal surfaces, was not used for heavy-duty crushing.

Cappetta (1970, 1987) assigned *Plinthicus* to the mobulids because the tooth is high and thin and little wear appears on the occlusal surface and because of the osteodentine histology; however, his sample was too small to reconstruct the dentition. When we reconstructed the dentition of this ray, the teeth best fit in a typical *Rhinoptera* pattern, with a transversely convex upper pavement and a nearly flat or only slightly transversely concave lower pavement. Both of the dental pavements were longitudinally convex, the upper more so than the lower. Each dental pavement appears to have consisted of seven rows of teeth: three distinct sets of transversely elongated teeth, a medial and two lateral rows, and four rows of lateralmost teeth with nearly equal transverse and longitudinal widths, the condition in the extant species.

The specimens that Fowler (1911) attributed to *Plinthicus* belong in part to *Myliobatis* and in part to *Aetobatus*.

A few teeth with lower crowns were found in the same layers as the above specimens; these have a similar root pattern but a distinctly different occlusal surface. This surface is less rugose, and it inclines sharply downward toward the labial edge. It is uncertain if this represents a different form or is a result of wear. The occlusal surface does not appear to be abraded.

Family MOBULIDAE (manta rays)

Mobula sp.

FIGURE 14a-p

HORIZON.—Pungo River Formation (units 1–5); ?Yorktown Formation (unit 1, possibly redeposited).

REFERRED MATERIAL.—40 isolated teeth, USNM 207549, 207579–207582; 7 caudal spines, USNM 285372, 285381, 291226, 421695, 467584, 467585.

REMARKS.—Notarbartolo-di-Sciara (1987:9) reported that ontogenetic variation and sexual dimorphism occur in the teeth of *Mobula*, stating, “Heterodonty is one of the most salient mobulid characteristics. Sexual dental dimorphism, as well as ontogenetic, dignathic, and monognathic heterodonty, all occur in most *Mobula* species. One cause of such a high degree of variability may be that teeth often appear to grow in width, therefore increasing the number of cusps and of root lobes, prior to the branching of one row into two. As a consequence of the variety of tooth shapes which can be found within the same toothband, the use of tooth morphology as a systematic tool may be misleading in living forms, and quite problematical in palaeontological [sic] studies. An effort should be made of identifying tooth characters which remain constant within each species, if tooth morphology is to be used as a taxonomic aid in defining the systematics of the genus *Mobula*.”

In view of the above, we herein identify the three morphotypes that occur at Lee Creek Mine to genus only.

The teeth of the first morphotype (USNM 207549, 207579, 207580; Figure 14a–i) have flat, triangular, ovoid, or rectangular occlusal surfaces and one to four lingual cusplets. A row of tubercles may occur on the occlusal surface along the labial edge or along the labiolingually directed shallow striations. In sagittal section the root is wedge-shaped to trapezoidal and is basally divided into one to four grooves, the number of grooves increasing with an increase in the length of the tooth.

Teeth of the second morphotype (USNM 207581; Figure 14m–o) are small (1.5 mm total height), with a prominent, median, lingually directed cusplet bordered on either side by a pair of much shorter lateral cusplets. The occlusal surface is marked by relatively deep and labiolingually directed sulci that extend from the labial edge of the tooth, where they are best developed, partly onto the median cusplet. The lateral edges of the crown are usually higher than the middle of the occlusal surface, making the latter concave. The root is either bipartite or tripartite.

In the third morphotype (USNM 207582; Figure 14j–l), the teeth have broad, labiolingually compressed crowns. The labial and lingual faces appear corrugated, with strong, vertical ridges separated by deep grooves; the ridges may bifurcate or end part way up the crown face. The occlusal face is flattened; this surface is triangular in occlusal view on narrow specimens but zig-zags on more elongate specimens, an effect caused by the jagged lingual edge. The root is small and is divided basally into two to five lobes.

Seven caudal spines from the spoil piles at the Lee Creek Mine are referred to this genus. They compare favorably with the spine illustrated by Notarbartolo-di-Sciara (1987:58), except that just basal to where the exerted spine inserts into the bulbous base there are two thin, lobate structures (Figure 14p).

The extant species (Bigelow and Schroeder, 1953:493) inhabits warm temperate to tropical coastal waters, feeding on small shrimp and minnows.

Manta sp.

FIGURE 14g

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—30 osseous masses partially enclosing diminutive caudal spines, USNM 280595, 467557–467583.

REMARKS.—Holmes (1859) first described and published the only illustration of these caudal spines. In their discussion of the extant giant devil ray, *Manta birostris*, Bigelow and Schroeder (1953:504) noted that some specimens have one or two small caudal spines. Other specimens lack emergent spines but may have a prominent hard protuberance on the dorsal side of the base of the tail, close behind the dorsal fin. This knob is formed by a fusiform mass of bony material that is attached to the muscular tissue of the tail. On the sloping posterior surface of the bony mass, a stubby spine is often present, the spine and the bone being completely covered by skin.

A number of fusiform osseous masses, some with very small caudal spines, were collected at Lee Creek Mine from the lower beds of the Yorktown Formation (e.g., Figure 14g). These agree very closely with Holmes's description and figure.

Extant devil rays (Bigelow and Schroeder, 1953:501, 509–510) inhabit subtropical to tropical shallow waters, and they also may be found in deeper waters. Little is known about their feeding habits.

BATOIDEI

Genus and species undetermined

FIGURE 15a

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—1 caudal spine, USNM 476297; numerous uncataloged caudal spines.

REMARKS.—Imbricated caudal spines are common fossils at Lee Creek Mine, especially in Pungo River sediments. Although they are frequently referred to *Dasyatis* (stingray) in the Lee Creek fauna, at least four families of batoid fishes have members that bear one or more of these spines on the dorsal surface of the tail. It is not possible now to assign these spines to genus or species.

Order SQUATINIFORMES

Family SQUATINIDAE

(angel sharks)

Squatina sp.

FIGURE 15b–l

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—17 teeth, USNM 207541–207543, 475000; 14 vertebrae, USNM 464226–464240.

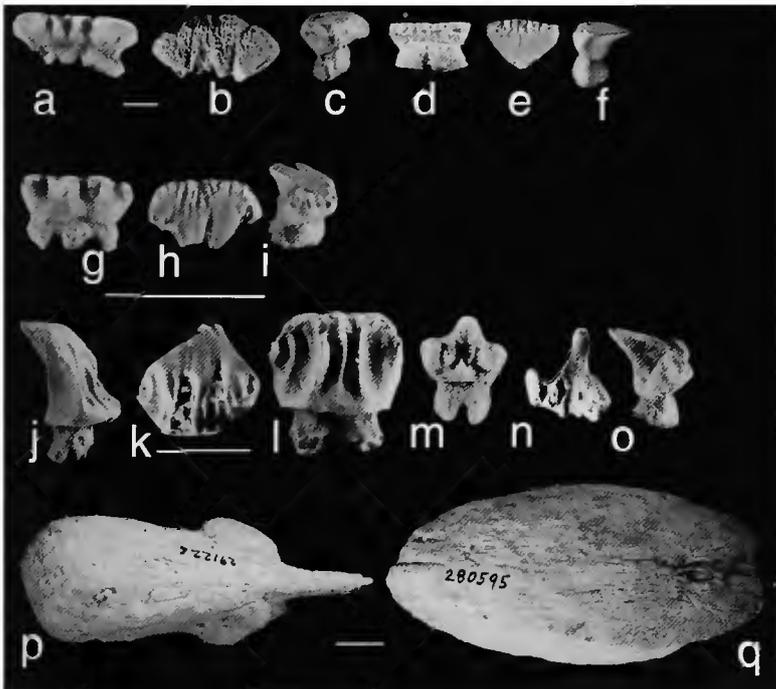


FIGURE 14.—*Mobula* sp., tooth type 1: a, USNM 207549, lingual view; b, same specimen, occlusal view; c, same specimen, lateral view; d, USNM 207579, tooth lacking posterior cusplets, labial view; e, same specimen, occlusal view; f, same specimen, lateral view; g, USNM 207580, tooth with prominent posterior cusplets and tripartite root, lingual view; h, same specimen, occlusal view; i, same specimen, lateral view. *Mobula* sp., tooth type 2: j, USNM 207581, lateral view of high-crowned tooth with bipartite root; k, same specimen, occlusal view; l, same specimen, lingual view. *Mobula* sp., tooth type 3: m, USNM 207582, labial view of anterolateral tooth; n, same specimen, occlusal view; o, same specimen, lateral view. *Mobula* sp., caudal spine: p, USNM 291226, dorsal view. *Manta* sp., caudal spine: q, USNM 280595, dorsal view. (Scale bars: a–f=0.25 cm; g–i=0.30 cm; j–o=0.20 cm; p,q=2.0 cm.)

REMARKS.—The teeth have broad roots that appear thin or very compressed when viewed labially or lingually. In basal view, the root is hollowed out and protrudes lingually, more so in the lower teeth than in the upper teeth. On the labial face of the crown, an enameloid peg extends basally; on the lingual face, the crown foot extends like an apron out onto the root. These dental characters are characteristic of *Squatina* (Cappetta, 1987).

An anterior tooth from the Pungo River Formation (USNM 207543, 6.8 mm high \times 6.5 mm wide) is distinctive because of the robustness of the crown relative to the root (Figure 15*h-j*). The crown is smooth on the labial face (Figure 15*i*), and it is slightly less convex on the labial face than on the lingual face. The mesial cutting edge of the crown is absent, possibly due to wear. Mesial and distal enamel shoulders are short and concave rather than convex toward the root. The root is marked basally by a deep sulcus.

USNM 207542 (5.8 mm high \times 1.1 mm wide; Figure 15*e-g*) and USNM 475000 (6.7 mm high \times 8.0 mm wide), from the Yorktown Formation, also are anterior teeth as indicated by their convex roots, which are concave in basal view. They differ from the other specimens in having a central, well-marked ridge on the lower half of the labial face of the crown, which forms an apron over the labial face of the root. The enamel shoulders extend almost to the lateral extremities of their roots.

A small Yorktown Formation specimen, USNM 207541 (3.5 mm high \times 3.7 mm wide; Figure 15*b-d*), shows a faint indication of the coronal ridge that characterizes the aforementioned Yorktown Formation specimens. It differs from both of the other teeth in having low but distinct lateral denticles on each enamel shoulder.

Fourteen vertebrae were found that are identical to those of the extant *Squatina squatina*. They are aseptate centra that in cranial or caudal view are oval in outline (Figure 15*k,l*). The largest centrum measures 18.2 mm in height and 24.9 mm in width.

The extant western Atlantic species, *Squatina dumeril*, inhabits temperate to subtropical waters (Compagno, 1984:146). It feeds on small bottom fishes, crustaceans, and shellfish.

Order ORECTOLOBIFORMES

Family PARASCYLLIDAE (collared carpetsharks)

Genus *Megascyliorhinus* Cappetta and Ward, 1977

When it was first described, *Megascyliorhinus* was assigned to the Scyliorhinidae. Later, Cappetta (1987:113) noted that the teeth of this genus lack a pulp cavity and possess a core of osteodentine in the lower half of the cusp and that this genus, therefore, may not be a scyliorhinid.

Pfeil (1984:112) erected a new family, Megascyliorhinidae, for this genus, noting that “the apico-basal transverse ridges of the lingual and labial crown faces and the morphology of the

root with its characteristic system of vascularisation” distinguish this family from the Scyliorhinidae. Because these characters occur in other orectolobiform families and do not establish a unique identity for Pfeil’s taxon, we believe his erection of a new family is incorrect.

Cione (1986) identified a new species, *Megascyliorhinus trelewensis*, from the late Oligocene–early Miocene sediments of Patagonia. His specimens differ, however, from all others assigned to this genus in two ways: (1) they lack an osteodentine core, and (2) the transverse groove of the root does not divide the basal face of the root into two “pedestals.” When we compared the illustrations of his type suite to the juvenile teeth of the extant species, the nature of the transverse groove, the position of the central foramen, and the occurrence of lateral foramina were very similar. We believe, therefore, that Cione’s species is not assignable to *Megascyliorhinus* and may be based on juvenile teeth of an already described species of *Hemipristis*, which in fossil form has orthodont teeth (Compagno, 1988:35).

Nishimoto and Karasawa (1991) noted that unlike the Scyliorhinidae, the root of *Megascyliorhinus miocaenicus* lacks labial marginal foramina, and it bears a pair of large, lingual marginal foramina. Further, the flattened basal face of the root with a central foramen and a pair of large, lingual marginal foramina suggested to them that this genus belongs in the Orectolobiformes, family indeterminate.

We agree with Nishimoto and Karasawa (1991) that this genus is an orectolobiform, but we also believe that it is a member of the family Parascyllidae. Of the orectolobiforms, only the teeth of the Parascyllidae have roots with broad, flat bases divided by median grooves. Also, in basal view, the roots of the teeth of *Megascyliorhinus* have the same shape as those of the parascyllids. Similarities between parascyllids (illustrated by Herman et al., 1992) and *Megascyliorhinus* also can be found in the crown, dentitions of both have teeth that are elongate, and both lack labial aprons or pegs. Unlike the teeth of the Parascyllidae, lateral cusplets are absent or are not as large as those in the extant members of this family, and the coronal-root boundary is not constricted. Despite these differences, we believe *Megascyliorhinus* should be assigned to the Parascyllidae.

Megascyliorhinus miocaenicus (Antunes and Jonet, 1969–1970)

FIGURE 15*p,r*

HORIZON.—Pungo River Formation (unit 1).

REFERRED MATERIAL.—1 tooth, USNM 475364.

REMARKS.—David Ward donated to the USNM one tooth of this species, which he recovered from the “basal black sand” of the Pungo River Formation, Gibson’s (1967) dark greenish brown phosphatic sands (unit 1). This tooth lacks its tip and lacks lateral cusplets, and the very convex labial face obscures the cutting edge. Unlike other teeth of this species, which are

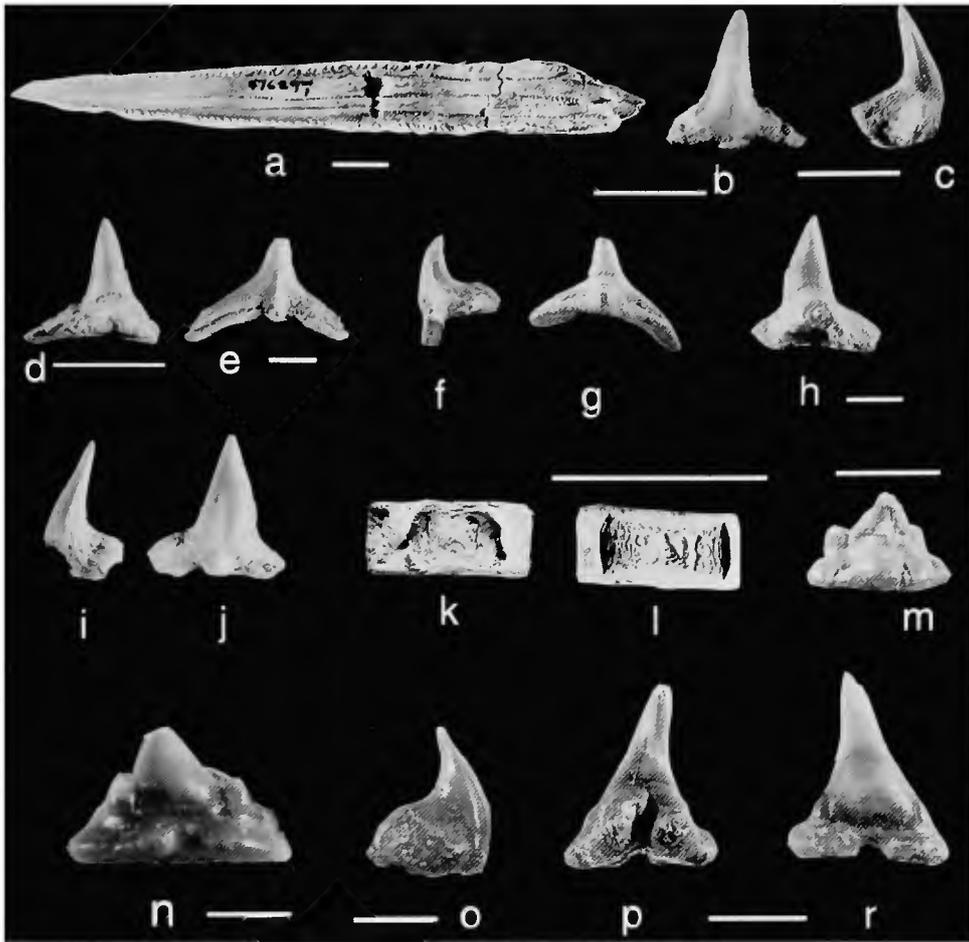


FIGURE 15.—Batoid: *a*, USNM 476297, caudal spine, dorsal view. *Squatina* sp.: *b*, USNM 207541, incomplete anterolateral tooth, labial view; *c*, same specimen, lateral view; *d*, same specimen, lingual view; *e*, USNM 207542, anterior tooth, labial view; *f*, same specimen, lateral view; *g*, same specimen, lingual view; *h*, USNM 207543, anterior tooth, lingual view; *i*, same specimen, lateral view; *j*, same specimen, labial view; *k*, USNM 464235, vertebra, dorsal view; *l*, same specimen, ventral view. *Ginglymostoma* sp.: *m*, USNM 457231, lingual view; *n*, same specimen, labial view. *Rhincodon* sp.: *o*, USNM 467537, lateral view. *Megascyliorhinus miocaenicus*, USNM 475364: *p*, lingual view; *r*, labial view. (Scale bars: *a*=1.0 cm; *b*–*d*, *h*–*j*, *m*, *p*, *r*=0.2 cm; *e*–*g*=0.9 cm; *k*, *l*=0.75 cm; *n*=0.15 cm; *o*=0.175 cm.)

striated on the labial and lingual faces, only the base of the labial crown foot has faint striations, and the lingual face is smooth. Striations, a primitive character, also are absent on the teeth of the extant species of this family. With the exception of the striations, this specimen compares favorably with the holotype of *Megascyliorhinus miocaenicus*. The tooth measures 7.2 mm in height and 6.4 mm in width.

Antunes and Jonet (1969–1970) assigned this species to *Rhincodon*, but Cappetta (1987:113) correctly assigned it to *Megascyliorhinus*.

The Lee Creek tooth is the first record of this genus from North America and is the first record of this species in the western Atlantic basin. *Megascyliorhinus miocaenicus* has been found in the Miocene and Pliocene sediments of France,

Tunisia, and Japan and in the Oligocene of Czechoslovakia (Cappetta, 1987:113).

From the Miocene–Pleistocene sediments of New Zealand and Australia, Keyes (1984) identified more elongate teeth with striated crowns that also lacked lateral denticles as *M. cooperi* Cappetta and Ward, a species previously known only from the Paleogene. In differentiating his specimens from *M. miocaenicus*, Keyes (1984:205) noted that the teeth of the latter species were “more robustly crowned with pronounced, elongate denticles.” His description does not agree with that of Antunes and Jonet’s holotype (1969–1970:153, fig. 205, pl. 9: figs. 42–44). This specimen has a stockier appearance than those illustrated by Keyes, and it lacks lateral denticles. In the extant parascyllids, the more slender teeth come from the an-

terior portions of the jaws. Antunes and Jonet's holotype probably came from a more distal position in the jaw than those illustrated by Kemp. Like the lamniform and carcharhiniform sharks, elongation of teeth also may be an intraspecific variation in Parascyllids. Kemp's basis for assigning the New Zealand and Australian Neogene teeth to *M. cooperi* seems tenuous.

Family GINGLYMOSTOMATIDAE
(nurse sharks)

Ginglymostoma sp.

FIGURE 15*m,n*

HORIZON.—Pungo River Formation (unit 3).

REFERRED MATERIAL.—1 tooth, USNM 457231.

REMARKS.—One tooth of a nurse shark was recovered from the Lee Creek Mine. It has a stocky principal cusp with one pair of lateral cusplets (Figure 15*m,n*). The root is well developed, and it is bisected by a transverse groove that penetrates its lingual edge. It measures 2.6 mm in height and 4.3 mm in width.

The teeth of *Nebrius*, which have more than two pairs of lateral cusplets and have cusplets that occur more apically along the cutting edge than in *Ginglymostoma*, have been misidentified as *Ginglymostoma* (see Arambourg, 1935, pl. 20: figs. 5, 6; Cappetta, 1970, pl. 7: figs. 1–6). According to Compagno (1984:207), the teeth of *Nebrius* are “more or less compressed in the sides of the jaws,” whereas those of *Ginglymostoma* are not.

Nurse sharks are inshore, bottom sharks (Compagno, 1984:206) that inhabit subtropical to tropical waters from less than 1 m to at least 12 m in depth. These sharks feed on bottom-dwelling invertebrates and on sea catfishes, mullets, puffers, and stingrays.

Family RHINCODONTIDAE
(whale sharks)

Rhincodon sp.

FIGURE 15*o*

HORIZON.—Pungo River Formation (units 1–3).

REFERRED MATERIAL.—17 teeth, USNM 467536, 467537, 467539–467553.

REMARKS.—Compagno (1984:209) characterized the minute teeth of this genus as “not strongly differentiated in jaws, with a medial cusp, no cusplets and no labial root lobes; tooth rows extremely numerous, in over 300 rows in either jaw of adults and subadults.”

The crown of the Lee Creek Mine tooth (Figure 15*o*) is sharp, slightly curved lingually, and has a perfectly smooth surface. It is compressed laterally, and the cutting edges are dis-

tinct but dull. A narrow and relatively long apron descends onto the lingual face of the root.

The roots of these teeth are bulbous and are wider at the mesial and distal sides than at the crowns, and they possess a well-marked central foramen and transverse groove. A pair of prominent lateral foramina are located high on the mesial and distal sides of the root, and the basal area of the root is marked by small, irregular vascular openings. These teeth are identical to those of the extant species, *Rhincodon typus* Smith.

The largest tooth collected has a maximum dimension of 6.3 mm; other specimens range in maximum dimension from 5.5 mm to 3.0 mm.

Cappetta (1987:81) reported the only other occurrence of *Rhincodon* in the fossil record as coming from the middle Miocene of southern France (see Cappetta, 1970, fig. 72A–C). The Lee Creek Mine specimens are the first occurrence of this genus in the Atlantic Coastal Plain.

According to Bigelow and Schroeder (1948), the extant whale shark reaches a length of 18.3 m TL, and may have over 3600 small teeth. A sampling of the ore reject gravels indicates that these fossil teeth are quite abundant.

According to Compagno (1984:210–211), the living whale shark is a “tropical and warm-temperate shark, often seen far offshore but coming close inshore and sometimes entering lagoons of coral atolls.... It apparently prefers areas where the surface temperature is 21° to 25°C with cold water of 17°C or less upwelling into it.... The whale shark is a versatile suction filter-feeder, and feeds on a wide variety of planktonic and nektonic organisms. Masses of small crustaceans are regularly reported, along with smaller and not so small fishes such as sardines, anchovies, mackerels, and even small tunas and albacore as well as squids.”

Order LAMNIFORMES

Compagno (1990a:370–372) identified synapomorphies for the Lamniformes, which include the following dental characters: (1) excluding *Cetorhinus* and *Megachasma*, teeth are differentiated into anteriors, intermediates, laterals, and posteriors; (2) excluding *Mitsukurina*, transverse ridges are lost on tooth cusps in the anterolateral teeth, and reduced ridges are sometimes present on basal ledges; (3) excluding *Mitsukurina* and *Carcharias*, the first upper anterior tooth is lost or replaced by a symphysial tooth; and (4) excluding *Mitsukurina* and the Odontaspidae, the third lower anterior tooth is reduced to the size and shape of a lateral tooth.

We amend these with the following. In associated dentitions of *Carcharodon subauriculatus* and *C. megalodon*, the third lower anterior tooth shows little or no lateralization. This condition often persists in the dentitions of *C. carcharias*, and this condition is not as great as that found in the two extant species of *Isurus* and in two associated dentitions of *Isurus xiphodon*, the putative precursor of *C. carcharias*.

Family ODONTASPIDIDAE
(sand tigers)

In the past, all species of Odontaspidae were assigned to the genus *Odontaspis*, but Compagno (1977) recognized characters to identify two genera in this family: *Odontaspis* and *Carcharias*. Because, however, the latter name had been suppressed by Opinion 723 of the International Commission on Zoological Nomenclature (1965), Compagno assigned *Odontaspis taurus* to the next available junior synonym of *Carcharias*, *Eugomphodus*. Cappetta (1987:91), using Rule 23b of the 1964 edition of the International Code of Zoological Nomenclature (ICZN), rejected *Eugomphodus* as a nomen oblitum, but he did so without the required approval of the International Commission on Zoological Nomenclature, and for the senior synonym he selected *Synodontaspis* White, 1931. With the publication of the 1985 edition of the ICZN, however, Rule 23b can no longer be used to suppress taxonomic names; therefore, Cappetta's (1987) suppression of *Eugomphodus* was unjustified. In 1986 Compagno and Follett's appeal for the conservation of *Carcharias* Rafinesque, 1810, was published and in 1987 the commission (Opinion 1459) conserved *Carcharias* (International Commission on Zoological Nomenclature, 1987).

Both *Carcharias* and *Odontaspis* occur at Lee Creek Mine. Compagno and Follett (1986:89–90) described the following dental characters, which separate these two genera:

[*Carcharias* with] three rows of upper anterior teeth on either side of the symphysis; heterodonty strong along jaws, lateral teeth compressed and bladelike, with flattened cusps, and posterior teeth strongly differentiated as carinate, molariform crushers; cusplets on anterior teeth short and strongly hooked and cusps stout and broad-tipped; teeth larger, second lower anterior tooth 1.3 to 1.5 times the height of comparable tooth in *Odontaspis*....

...[*Odontaspis* with] two rows of upper anterior teeth on either side of symphysis; heterodonty weaker along jaws, lateral teeth little compressed and not bladelike, with cusps little flattened, and posterior teeth not differentiated as molariform crushers; cusplets on anterior teeth long and straight or weakly curved, not hooked, and cusps slender and narrow-tipped; teeth smaller, second lower anterior tooth 0.6 to 0.8 times height of comparable tooth in *Carcharias*.

In the Lee Creek Mine fauna we identified three species of *Carcharias*: *C. taurus*, *C. cuspidata*, and *C. contortidens*; and we identified two species of *Odontaspis*: *O. ferox* and *O. cf. O. acutissima*.

Carcharias taurus Rafinesque, 1810

FIGURES 16, 17c,d

HORIZON.—Yorktown Formation (units 1, 2); James City Formation.

REFERRED MATERIAL.—About 200 teeth, USNM 453082–453084, 453086, 453087, 453089, 453091, 453092, 453094–453097, 453100–453107, 453110–453112, 453114–453116, 453118–453122, 453124, 453126–453130, 453133, 453135, 454400–454404, 454407, 454410–454412, 454414, 454416–454418, 476344–476346, 476348, 476349, 489143; 1 vertebra, USNM 464242.

REMARKS.—The anterior teeth (Figure 16) are identical to those of the extant *Carcharias taurus*. The main cusps of the teeth are slender and awl-like, with convex but slightly flattened lingual faces. On the lingual face of the crown, faint and irregular striae occur as they do in some teeth of *C. taurus* and in some specimens attributed to *Odontaspis acutissima* Agassiz. In the fossil teeth and in the dentition of the extant *Carcharias taurus*, the cutting edges of the lower first anterior tooth end higher (apically) on the crown (about one-third up



FIGURE 16.—*Carcharias taurus*, anterior teeth: a, USNM 476344, first upper anterior, lingual view; b, USNM 476345, first lower anterior, lingual view; c, USNM 476346, second upper anterior, lingual view; d, USNM 489143, second lower anterior, lingual view; e, USNM 476348, third upper anterior, lingual view; f, USNM 476349, third lower anterior, lingual view. (Scale bars: a–d,e,f=1.0 cm.)

the crown) than do those of the other anterior teeth; this condition of the lower first anterior tooth exists also in the anterior teeth of *Odontaspis*. In the second and third anterior teeth, the mesial and distal cutting edges are complete.

The lateral teeth of this species and those of the more abundant *Carcharias cuspidata* are identical. None of the lateral teeth from the Yorktown Formation are striated.

Two studies, one by Sadowsky (1970) and the other by Taniuchi (1970), provide some information about variation in the dentitions of the extant species. Sadowsky noted that one pair of lateral denticles was present in 93% of the dentitions he examined ($n=528$); the remaining dentitions had from zero to two pairs of lateral denticles. Other observations from his suite of specimens pertinent to the study of fossil shark teeth include the following: (1) the number of symphyseal tooth positions varies; the number of anterior tooth positions (three) is constant; (2) great variability exists in the number, size, and shape of the lateral teeth; (3) there is no sexual dimorphism in these dentitions; (4) embryonic teeth lack lateral denticles; and (5) the number of intermediate teeth varies from one to four.

Taniuchi, who studied 24 specimens, added (1) the number of lateral denticles correlates closely with the size of the shark; (2) in sharks under 100 cm TL, lateral denticles are absent; (3) in some specimens the first through fourth lateral teeth have two pairs of lateral denticles; and (4) the number of intermediate teeth varies from one to five. He also reported a fourth upper anterior in one specimen, but from his illustration, this tooth appears to be a symphyseal tooth, which may occur in upper jaws of *Carcharias taurus*.

In the living species, we observed the following variations in tooth morphology. A dentition from South Africa (Hubbell collection, ML102387) exhibits considerable variation in tooth morphology. The second upper anterior and the third lower anterior teeth (as well as the first and second upper laterals), on the labial faces, have shallow V-shaped depressions in the crown foot, and the lower first and second anteriors have deep V-shaped depressions in the crown foot, causing the enamel to overhang the root. On the labial face of the lower lateral teeth, starting with the first, the crown foot is adorned with vertical plications; these plications extend down onto the dentine of the basal groove. Leriche (1910:271) also noticed these plications and stated, "This character has no specific or even individual value." In contrast, in another adult specimen, USNM 110298, the V-shaped grooves in the crown foot are absent, and the plications are finer and are confined to the basal groove. In USNM 110939, from a juvenile, the plications are absent. These observations, based on a small number of dentitions, suggest that depressions and ornamentation on the labial face of the crown foot are variable and are taxonomically insignificant.

The anterior teeth range from 18.0 to 41.0 mm in total height (mean=31.9 mm, $n=51$), from 15.0 to 21.0 mm in maximum width (mean=18.0 mm), and from 2.4 to 1.4 in height to width ratio (mean=1.8).

One vertebra found on the spoil piles is identical to those of *Carcharias taurus* (Figure 17c,d). It is septate and of medium size, with thick rims; the oval ventral and dorsal foramina extend to the rims of the vertebra (Kozuch and Fitzgerald, 1989).

Compagno (1984:217) reported that this shark inhabits shallow, temperate to tropical waters from the surf zone to 191 m in depth. It feeds on a wide variety of bony fishes, including bluefish, bonitos, hakes, searobins, sea basses, and porgies, as well as on small sharks, rays, and invertebrates.

Carcharias cuspidata (Agassiz), 1843

FIGURES 17a,b, 18

HORIZON.—Pungo River Formation (units 1–3); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—331 teeth, USNM 207611, 451255, 451257–451273, 454631, 476350.

REMARKS.—Agassiz (1843:290) distinguished this species from *Carcharias elegans* by the smoothness of its labial and lingual tooth faces, and he distinguished it from other odontaspids by the greater development of the tooth's root. Of the specimens he figured (pl. 37a: figs. 43–50), the second upper anterior teeth in figs. 46 and 48 and a second lower anterior tooth in fig. 49 are of *Carcharias*; the teeth in his figs. 43–45, which were still in matrix at the time of illustration, also may belong to this genus, but the tooth in his fig. 47 is indeterminate. The tooth in his fig. 50 may belong to *Odontaspis*.

Leriche (1910:270) further characterized this species as follows:

The teeth of *Odontaspis cuspidata* ...are large and robust. Their crown is completely smooth, very sharp along the edges, flat on the external face, strongly convex on the internal face.

The lateral denticles are in the anterior teeth, relatively small and very acuminate. In the lateral teeth, they are much enlarged, becoming often very obtuse and sometimes seem to form a prolonging of the enamel of the crown. Their crest is itself denticulated. One observes generally an external, rather large denticle and, between this last and the crown, much smaller denticles.

The root is rather developed. The furrow in which the nutritive foramen opens, on the internal face, is shallow; it is hardly indicated in the anterior teeth. (Translated from French by R.W.P.)

Most of these characters occur in *C. taurus*; the two exceptions are the greater development of the root and the wider crowns of the anterior teeth, which do not occur in teeth of similar size in the living species.

Comparing anterior teeth of similar size, the crowns in *C. taurus* are more elongate and have a narrower appearance than in *C. cuspidata*, and the roots of the second upper anterior tooth of *C. cuspidata* are longer and the crown is shorter than in *C. taurus* (see Figure 17a,b, cf. Figure 16c).

Another character that may prove taxonomically significant is that the angle of the root lobes in the lower first anterior teeth is greater in *C. cuspidata* (mean=72°, range=63°–82°, $n=11$) than in *C. contortidens* (mean=63°, range=54°–70°, $n=18$) and in *C. taurus* (mean=62°, range 53°–75°, $n=11$). Before

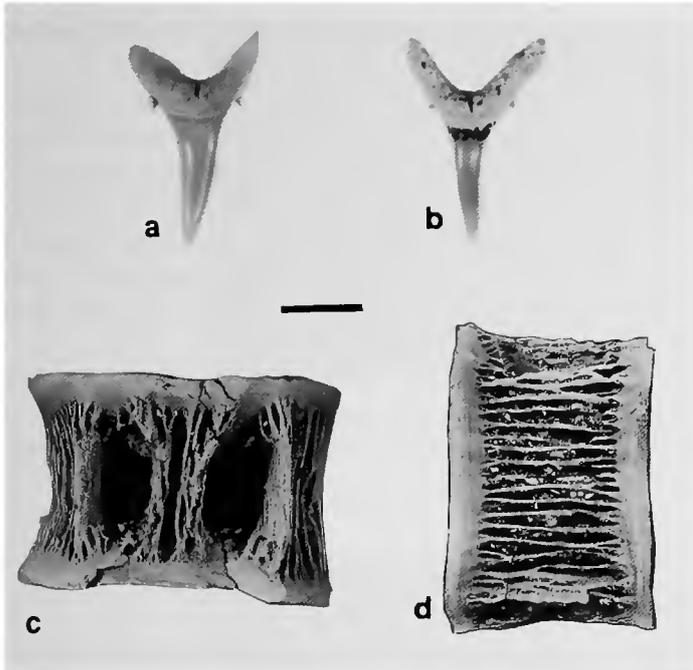


FIGURE 17.—*Carcharias cuspidata*: a, USNM 476350, second upper anterior tooth, lingual view; b, USNM 454631, second upper anterior tooth, lingual view. *Carcharias taurus*, vertebra, USNM 464242: c, slightly oblique dorsal view; d, lateral view. (Scale bar=1.0 cm.)

these angles can be used with confidence, they must be tested on larger populations of all three species.

In Figure 18a, using teeth from the Pungo River Formation, we reconstructed a composite dentition of this species. As mentioned earlier, because of their identical morphology, some of the lateral teeth may be those of *Carcharius taurus*.

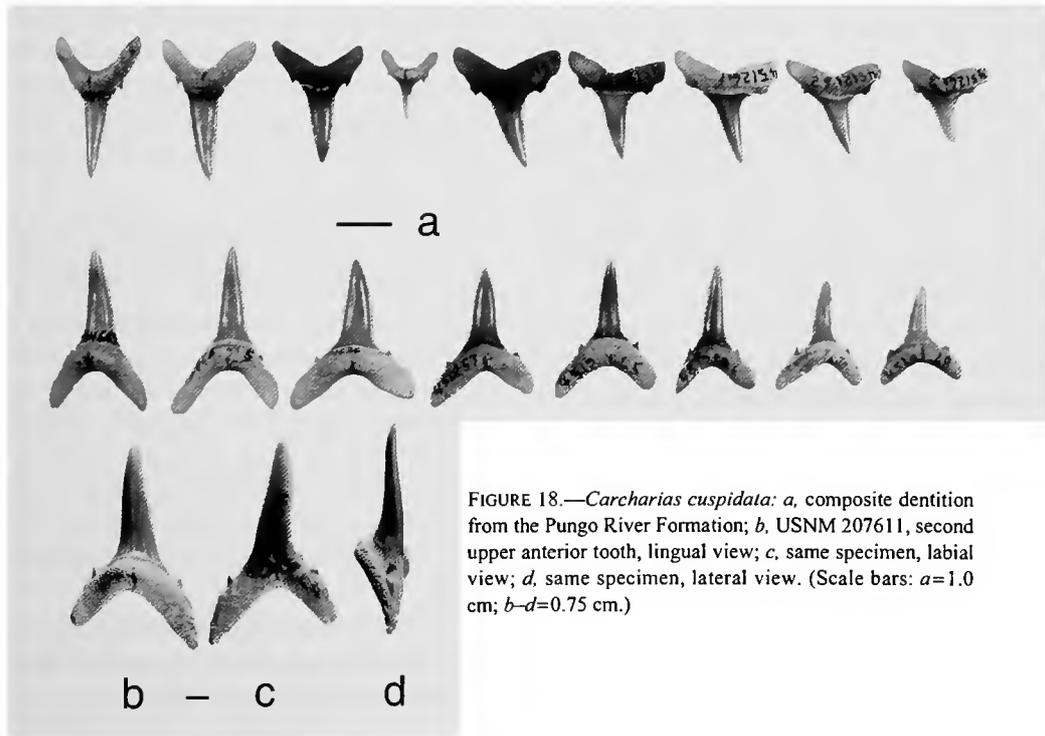


FIGURE 18.—*Carcharias cuspidata*: a, composite dentition from the Pungo River Formation; b, USNM 207611, second upper anterior tooth, lingual view; c, same specimen, labial view; d, same specimen, lateral view. (Scale bars: a=1.0 cm; b-d=0.75 cm.)

It is surprising to find *Carcharias cuspidata* as late as the early Pliocene (Figure 18b-d), but there is little doubt as to the identity of the Yorktown form, and the teeth are so well preserved that reworking from a lower horizon is very improbable. Only 11 teeth of this species were found in Yorktown sediments. Three of these are first lower anteriors and have a mean height of 3.2 cm (range=3.0-3.8 cm), a mean width of 2.0 cm (range=1.8-2.3 cm), and a mean root angle of 79° (range=69°-85°).

The first lower anterior teeth range from 2.4 to 3.2 cm in height (mean=2.8 cm, n=11), 1.6 to 2.1 cm in width (mean=1.8 cm, n=11), and 63° to 82° in root-lobes angle (mean=72°, n=11).

Carcharias sp.

FIGURE 19

HORIZON.—Pungo River Formation (units 1-5).

REFERRED MATERIAL.—About 100 teeth, USNM 454419, 454420, 454565-454571, 454573-454579, 454618, 454619, 454628, 454632-454635, 454643, 454651, 454655, 454657, 454689.

REMARKS.—The Lee Creek Mine specimens are very similar to those described by Agassiz (1843:294-295) as *Carcharias contortidens*. Of the specimens in his type suite, only those in his pl. 37a: figs. 21-23 have lateral cusplets and can be assigned to the genus *Carcharias*. The specimen in his fig. 21 appears to be an incomplete, second upper anterior tooth; those in figs. 22 and 23 are first lower and upper anterior teeth, respectively. Agassiz (1843:294-295) characterized a tooth of this species by "its subulate form, irregular and re-

curved inside; its internal face is distinctly folded, and the folds continue over all the length of the cone even near the tip, assuming the form of more or less undulated, small veins, very numerous and strongly distinct at the base of the enamel, but of which the number diminishes higher proportionally as they become mixed up." As in the teeth from Lee Creek Mine (Figure 19), the type teeth are more slender than those of *C. cuspidata* of similar size, and in comparison to *C. taurus*, the teeth of *C. contortidens* are striated or partially so on the lingual faces of their crowns, whereas in the living species they are usually smooth.

Leriche (1910) synonymized *C. contortidens* with *Odontaspis acutissima* Agassiz; he believed that these two species were based on teeth from different jaws of the same dentition. *Odontaspis acutissima*, however, is a separate species and belongs in the genus *Odontaspis* (see below).

The teeth of *C. contortidens* compare more favorably with those of *C. taurus* than do those of *C. cuspidata*. In the extant and fossil species, the range of dental variation is unknown; therefore, the validity of the characters used to identify the fossil species cannot be assessed as yet, and we believe it is not prudent to identify the Lee Creek Mine teeth to species.

The first lower anterior teeth of *C. contortidens* range from 2.8 to 3.7 cm in height (mean=3.3 cm, $n=18$), 1.4 to 1.9 cm in width (mean 1.6 cm, $n=18$), and 54° to 70° in root-lobes angle (mean= 63° , $n=18$).

Odontaspis ferox Risso, 1826

FIGURE 20a-c

HORIZON.—Pungo River Formation (units 1–6).

REFERRED MATERIAL.—35 teeth, USNM 278545, 453065, 453067–453081.

REMARKS.—The teeth of this species are rare in the Lee Creek Mine fauna; they are identical to those of the living *Odontaspis ferox*. As in the extant species, the cutting edges of the teeth do not reach the base of the crown. The lateral cusplets are longer than those in teeth of comparable size of *Carcharias*. In the extant and the fossil species, the number of pairs of lateral cusplets varies from one to three.

As in *Carcharias taurus*, the teeth of *O. ferox* exhibit morphological variations. In a dentition from an individual 2.75 m TL long and of unknown sex (Hubbell collection, MRD2), the anterior teeth have only one pair of lateral cusplets, whereas the lateral teeth have two pairs. In another dentition from a larger individual of unknown size and sex (Hubbell collection, MRD1), the anterior and lateral teeth possess two to three pairs of lateral cusplets. On the labial faces of the crowns of the upper and lower teeth of this latter dentition, plications occur on the crown foot basal to the lateral cusplets but not between them, but in the teeth of the 2.75 m individual, these plications are absent. The labial faces of these plicated teeth are moder-

ately convex, whereas those of the unplicated dentition are only slightly convex.

Only two first lower anterior teeth were found in the Pungo River Formation: USNM 453079, which measures 3.4 cm in height and 1.6 cm in width, and USNM 453065 (Figure 20a), which measures 3.0 cm in height and 1.5 cm in width. The Yorktown occurrence is represented by one first lower anterior tooth, USNM 278545 (Figure 20c), which measures 3.9 cm in height and 2.0 cm in width. These teeth are from individuals with total lengths of greater than 3 m TL.

Compagno (1984:220) reported that this little-known shark inhabits "deepish water in warm-temperate to tropical seas...at depths of 13 to 420 m.... It feeds on small bony fishes, squids and shrimps."

Odontaspis cf. *O. acutissima* (Agassiz, 1843)

FIGURE 20d-h

HORIZON.—Pungo River Formation (units 1–5, ?6).

REFERRED MATERIAL.—180 teeth, USNM 451147–451180, 454526–454538.

REMARKS.—We tentatively identify the small Pungo River odontaspid as *Odontaspis acutissima* (Figure 20d–h). The syntypes of this species have long lateral cusplets, which are characteristic of *Odontaspis*. The second tooth in the type suite (Agassiz, 1843, pl. 37a: fig. 34), from the Miocene of Switzerland, is embedded in matrix except for the tip of its crown, with only its labial face exposed. Agassiz (1843:294) provisionally assigned this specimen to *Lamna acutissima*. The first specimen (his fig. 33), a lower lateral tooth with elongate lateral cusplets of unknown provenance, therefore must be considered the holotype of this species. If this specimen still exists, it must be reexamined because it resembles a Paleogene form rather than one from the Miocene. The Miocene teeth identified as *O. acutissima* may have to be assigned to the next available junior synonym.

Agassiz characterized the teeth of this species as having distinct striations on the lingual faces of the crowns. In the Lee Creek Mine teeth, the striations are weakly developed, and they are best seen under magnification with a raking light. Because the taxonomic significance of these striations cannot now be assessed, we tentatively assign the teeth from Lee Creek Mine to a species. Questions about these teeth, such as whether they should be referred to juveniles of *O. cf. O. ferox* or whether they fall within the range of variation of the teeth of the extant species cannot be answered until large samples of teeth from the fossil and extant species are available for study.

The first lower anterior teeth of this species range from 1.5 to 1.9 cm in height (mean=1.7 cm, $n=10$) and from 0.8 to 1.2 cm in width (mean=0.9 cm, $n=10$).



FIGURE 19.—*Carcharias* sp., anterior teeth: *a*, USNM 454566, first upper anterior, lingual view; *b*, USNM 454573, first lower anterior, lingual view; *c*, USNM 454628, second upper anterior, lingual view; *d*, USNM 454643, second lower anterior, lingual view; *e*, USNM 454635, third upper anterior, lingual view; *f*, USNM 454632, third lower anterior, lingual view. (Scale bar=1.0 cm.)



FIGURE 20.—*Odontaspis ferox*, anterior teeth: *a*, USNM 453065, first lower anterior, lingual view; *b*, USNM 453078, second lower anterior, lingual view; *c*, USNM 278545, first lower anterior, lingual view. *Odontaspis* cf. *O. acutissima*: *d*, USNM 451148, second upper anterior, lingual view; *e*, USNM 451150, third upper anterior, lingual view; *f*, USNM 451147, first lower anterior, lingual view; *g*, USNM 451149, second lower anterior, lingual view; *h*, USNM 451151, third lower anterior, lingual view. (Scale bars: *a, b, d-h*=1.0 cm; *c*=1.4 cm.)

Family MEGACHASMIDAE (megamouth sharks)

Megachasma sp.

FIGURE 21

HORIZON.—Pungo River Formation (units 1–3); ?Yorktown Formation.

REFERRED MATERIAL.—9 teeth, NCSM 8796, 9560, USNM 457237, 457238, 459821, 459822, 464062, 475475, 482303.

REMARKS.—The larger specimens of this species are from the Yorktown Formation. The largest of these (NCSM 8796) is 17.0 mm high, 15.0 mm thick, and 11.9 mm wide (Figure 21*e, f*). It and the two following specimens were collected by Frank and Becky Hyne, who are experienced collectors at Lee

Creek Mine and who are familiar with the stratigraphy of the site. USNM 457237 is 15.2 mm high, 12.5 mm thick, and 13.1 mm wide (Figure 21*a, b*), and USNM 457238, a lower tooth, is 9.6 mm high, 5.2 mm thick, and 7 mm wide (Figure 21*g, h*). The Hynes are confident that they collected these specimens on the Yorktown spoil piles, where they concentrate most of their collecting effort. USNM 475475 (Figure 21*n-p*) is 14.3 mm high, 10.8 mm thick, and 16.1 mm wide; NCSM 9560 is 15.7 mm high, 10.0 mm thick, and 10.8 mm wide. With the exception of USNM 457238, these specimens have elongate, slender crowns. USNM 457238 is more like the Pungo River specimens, and it may be from that formation.

The Pungo River specimens are smaller (Figure 21*i-m*), with USNM 459821 measuring 8.1 mm in height, 6.2 mm in thickness, and 6.8 mm in width, and USNM 459822 measuring 8.7

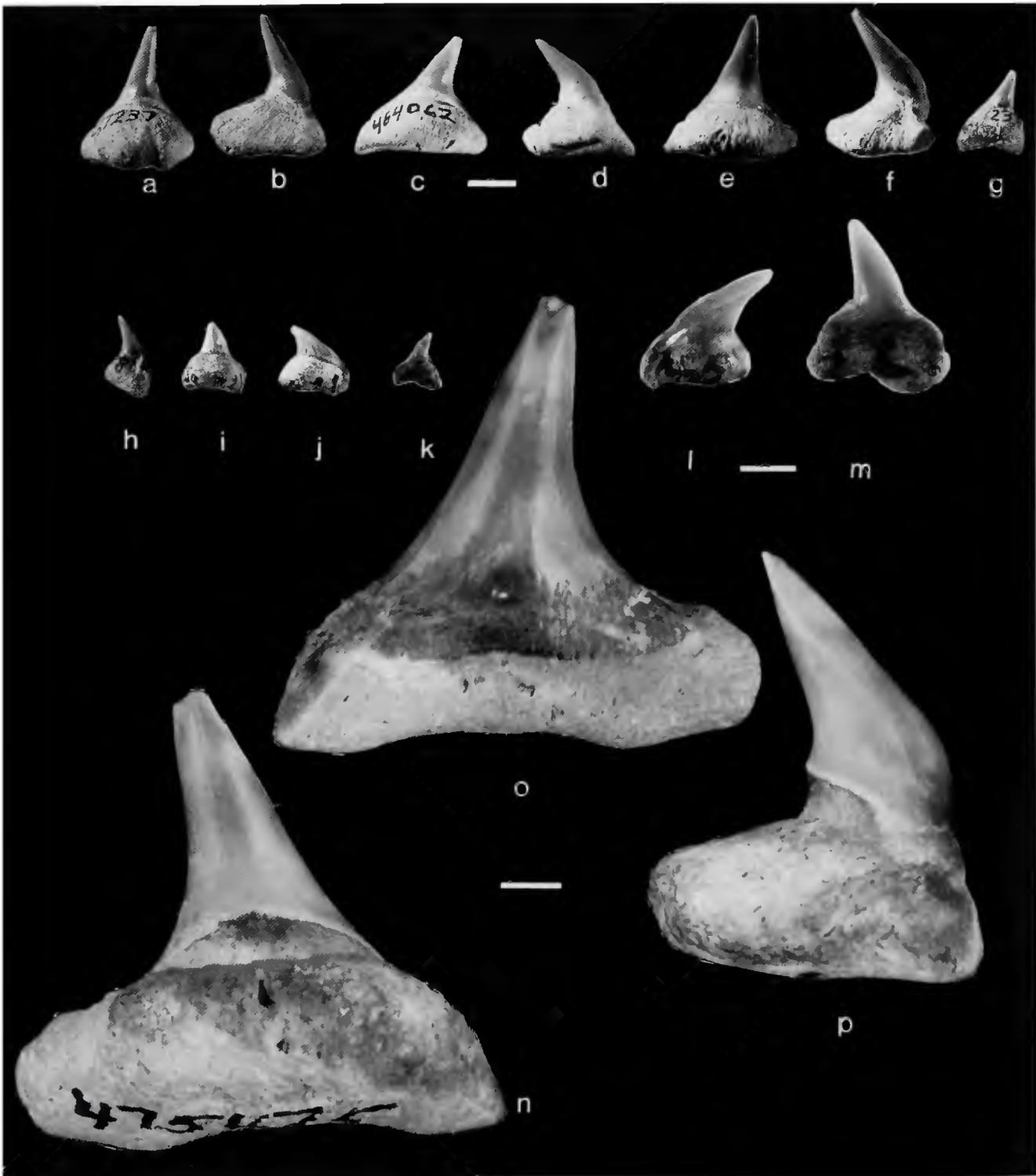


FIGURE 21.—*Megachasma* sp. teeth: *a*, USNM 457237, Yorktown Formation, lingual view; *b*, same specimen, lateral view; *c*, USNM 464062, Yorktown Formation, lingual view; *d*, same specimen, lateral view; *e*, NCSM 8796, Yorktown Formation, lingual view; *f*, same specimen, lateral view; *g*, USNM 457238, Yorktown Formation?, lingual view; *h*, same specimen, lateral view; *i*, USNM 459821, Pungo River Formation, lingual view; *j*, same specimen, lateral view; *k*, USNM 459822, Pungo River Formation, lingual view; *l*, same specimen, lateral view; *m*, same specimen, labial view; *n*, USNM 475475, ?Yorktown Formation, lingual view; *o*, same specimen, labial view; *p*, same specimen, lateral view. (Scale bars: *a*–*k*=1.0 cm; *l*,*m*=1.11 cm; *n*–*p*=1.25 cm.)

mm in height, 5.4 mm in thickness, and 7.0 mm in width. Unlike the Yorktown specimens, these teeth have stocky crowns. We do not know enough about the dentitions of the extant species to determine if these size differences are of ontogenetic or taxonomic significance.

The Lee Creek Mine specimens are similar to the teeth of the extant *Megachasma pelagios* (Compagno, 1990a:359, fig. 2; Herman et al., 1993:195, pls. 45–48) but differ from them in one respect. In two of the eight Lee Creek Mine specimens, the lateral edges of the roots protrude slightly more than those of the illustrated teeth of *M. pelagios*. They differ also from other megachasmid teeth from the Miocene of California by the lesser development of the lateral protrusion of the roots and by the absence of lateral cusplets, which also are present in some of the teeth of the extant species (Herman et al., 1993, pls. 45–47). The small sample size of teeth from Lee Creek Mine does not allow us to assess the taxonomic significance of these differences.

The teeth from Lee Creek Mine exhibit considerable morphological variation: crowns may have incomplete cutting edges, transverse grooves may be absent or in varying stages of development even though they appear to be functional teeth, a callosity on the labial crown foot may be smooth or grooved, and the size and the position of the central foramen on the torus of the root may vary. In the larger, Yorktown Formation specimens, the cutting edges of the crown are usually incomplete, but in one of these larger teeth (NCSM 8796), the cutting edges extend to the base of the crown. Punctae on the labial face of the root are present only on these larger teeth.

The living species is a slow-swimming plankton feeder that normally inhabits mesopelagic waters, but it may return to shallow waters to mate (Lavenberg, 1991).

Family ALOPIIDAE (thresher sharks)

Genus *Alopias* Rafinesque, 1810

In *Alopias* the third upper anterior tooth, second from the symphysis, is usually the largest anterior tooth, although in *A. superciliosus* the second upper anterior tooth is occasionally the largest. The lower anterior teeth are 10% to 20% smaller than the upper anteriors. In both jaws, the anterior teeth are not much larger than the first two lateral teeth, which Gruber and Compagno (1981:626) noted is characteristic of *Alopias*.

Two species of thresher shark have been found at Lee Creek Mine, *Alopias* cf. *A. superciliosus* (Lowe) and *A. cf. vulpinus* (Bonnaterre).

Alopias cf. *A. superciliosus* (Lowe, 1840)

FIGURE 22*h*

HORIZON.—Pungo River Formation (unit 3).

REFERRED MATERIAL.—1 tooth, USNM 475448.

REMARKS.—A tooth from the Pungo River Formation ore-coarse fraction is almost identical to some of the lower first anterior teeth found in males of the extant bigeye thresher shark. The crown is elongate, and on its lingual face the basal callosity is smooth. A shallow transverse groove is present on the lingual face of the root. This tooth measures 13 mm in height and 9 mm in width.

In the paleontological literature, this species has been identified from the lower Miocene of North Carolina (Case, 1980:83); from the middle Miocene of Maryland (Kent, 1994:72), Parma, Italy (Cigala-Fulgosi, 1983:224–226), and Lisbon, Portugal (Antunes, 1970); and from the Pliocene of Tuscany, Italy (Cigala-Fulgosi, 1988).

According to Compagno (1984:231), the extant species inhabits circumtropical coastal and oceanic waters from the surface to depths of at least 500 m. It feeds on bony fishes and squids.

Alopias cf. *A. vulpinus* (Bonnaterre, 1788)

FIGURE 22*a,b,f,g*

Galeocerdo triquetus Eastman, 1904:89, pl. 32: fig. 12 [holotype, ANSP 1214, Calvert Formation, Maryland].

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—About 70 teeth, USNM 282471, 289095, 289106, 297466, 312441, 312447, 324928, 421917, 421919, 421921, 437885, 451181–451211, 451328, 451329, 457241, 457242; 1 vertebra, USNM 464241.

REMARKS.—Middle Tertiary alopiid teeth have been assigned to two species, *Alopias exigua* (Probst, 1879) and *A. latidens* Leriche, 1908. Probst (1879), who did not give a diagnosis for his species, described as a new species of mako shark a suite of teeth that he believed were from different positions in the jaws. His figs. 20 and 21, which he identified as anterior teeth, represent incomplete teeth with erect, slender crowns and cannot be identified with confidence to genus; however, Leriche (1927:76) indicated that fig. 20 may represent a tooth of *Lamna cattica*. This tooth, which consists of only the crown, is not that of an *Alopias*. Probst's fig. 21 resembles the tooth of a carcharhinid rather than that of *Alopias*; nevertheless, the teeth in his figs. 22 to 25 possess roots that are more characteristic of *Alopias* than of *Isurus*. Because the location of Probst's type specimens is unknown, they cannot be compared with those of *A. vulpinus*; therefore, the validity of *A. exigua* cannot be determined.

Leriche (1908:379) separated *A. latidens* from *A. exigua* "by its greater size and stockier form," but stocky teeth occur in the extant *A. vulpinus*. In USNM 110941 (sex not indicated) the lower teeth are stockier than those of another individual of approximately the same size, USNM 232639; therefore, the stockiness of the crown, which also is a sexually dimorphic character in *A. superciliosus* (see Cigala-Fulgosi 1983), is not a useful character for separating species of *Alopias*.

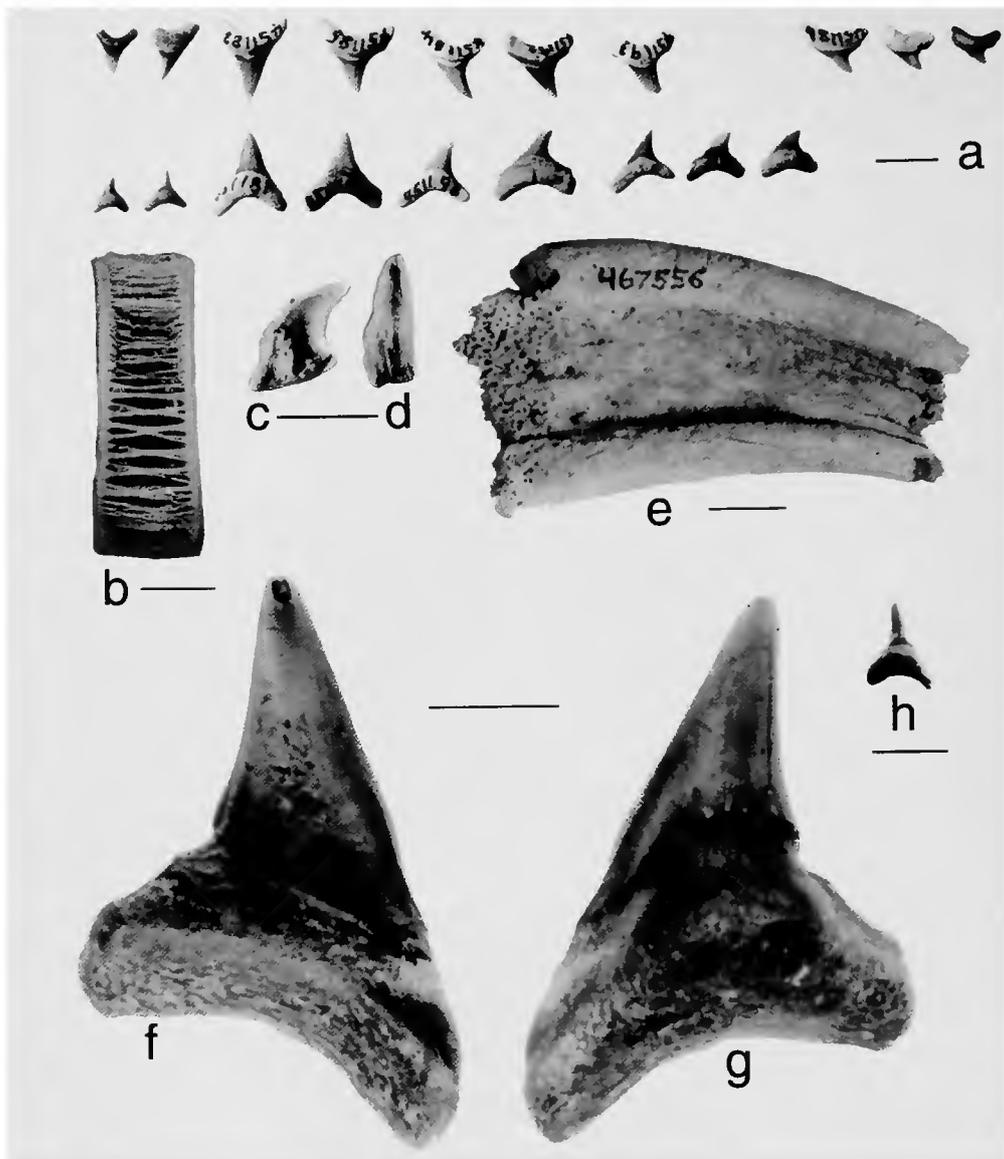


FIGURE 22.—*Alopias* cf. *A. vulpinus*: a, composite dentition, with intermediate tooth, fourth to sixth and tenth to seventeenth upper lateral teeth, third lower anterior tooth, and sixth to seventeenth lower lateral teeth missing; b, USNM 464241, vertebra. *Cetorhinus* sp.: c, USNM 312269, tooth, lateral view; d, same specimen, lingual view, e, USNM 467556, clasper spine, dorsal view. Holotype of *Alopias triqueter* (= *A.* cf. *A. vulpinus*), ANSP 1214: f, lingual view; g, labial view. *Alopias* cf. *A. superciliasus*: h, USNM 475448, tooth, lingual view. (Scale bars: a, b, e, h = 1.0 cm; c, d = 0.25 cm; f, g = 0.33 cm.)

Leriche (1927:76) and Cappetta (1970:23) also identified incomplete cutting edges as a character to distinguish *A. exigua* from *A. latidens*. In Probst's type suite for *A. exigua*, the two non-*Alopias* teeth are the only ones with incomplete cutting edges; therefore, both species have teeth with complete cutting edges.

The validity of *A. latidens* will have to await the restudy of Probst's types, if they still exist, study of Leriche's type specimens, and study of dental variation in a large population of *A.*

vulpinus and large, synchronous populations of the fossil specimens. In view of the above and the limited number of fossil and extant specimens, we cannot find characters to separate the Lee Creek Mine specimens from the extant species, and we believe the assignment of the Lee Creek Mine allopiid to a species is unwarranted at this time.

The teeth from Lee Creek Mine (Figure 22a) have wide, stocky crowns with complete cutting edges, and the callosity on the labial face of the crown foot is rounded, sometimes

forming a ridge, and is plicated. Of the three extant species of *Alopias*, these characters occur in the teeth of *A. vulpinus*.

In the five dentitions available to us, the teeth of *Alopias vulpinus* exhibit considerable variation and characters not noted in the paleontological literature. The lower medial tooth varies in size and may be absent. The lower anterior teeth are 10% to 20% smaller than the upper anteriors. Among the upper anterior teeth, the third upper anterior (second from the symphysis) tooth is the largest. The tips of the intermediate teeth bend lingually rather than labially or being straight. In the lower lateral teeth, the attitudes of the crowns range from inclined with a straight distal cutting edge to hooked with a concave distal cutting edge. The tips of some of the upper lateral teeth, in lateral view, do not curve labially but rather curve slightly lingually. Mesial and/or distal cusplets may be present.

Galeocerdo triquetus was established on the basis of an abraded lower anterior tooth. Eastman (1904:89) characterized the species as follows: "Teeth very robust, with elevated crowns, smaller and less twisted than those of *G. contortus*, and more faintly serrated along the coronal edges. Anterior margin only slightly arched, posterior notch inconspicuous." In examining the holotype of this species, ANSP 1214 (Figure 22*f,g*), we noticed that the faint serrations are confined to the basal portion of the distal cutting edge; the remainder of the cutting edge is smooth. We synonymize *Galeocerdo triquetus* with *Alopias* cf. *A. vulpinus* because the type specimen lacks the well-developed distal enamel shoulder characteristic of *Galeocerdo* and because there is a callosity on the labial face of the root that extends well onto the root. This tooth is almost identical to the first lower anterior tooth of *Alopias vulpinus*, and we believe it represents the same species as the specimens from Lee Creek Mine.

The anterolateral teeth from Lee Creek Mine range in height from 0.8 to 1.5 cm (mean=1.2 cm, $n=18$). These sharks were probably 4.5 to 6 m TL.

The vertebrae of this shark also are found at Lee Creek Mine. Their craniocaudal length is short (see Kozuch and Fitzgerald, 1989), and in side view they are septate, with the septa diverging toward the rims of the vertebrae (Figure 22*b*). Their dorsal and ventral foramina vary in shape from oval to rectangular. These vertebrae are identical to those of a specimen of *A. vulpinus* (USNM 110242).

Compagno (1984:233) reported that *A. vulpinus* inhabits coastal to oceanic temperate to tropical waters; the young are often found close inshore and in shallow bays. They feed mainly on schooling fishes, such as mackerels and bluefish.

Family CETORHINIDAE

(basking sharks)

Cetorhinus sp.

FIGURE 22*c-e*

HORIZON.—Pungo River Formation (unit 3).

REFERRED MATERIAL.—1 tooth, USNM 312269; 1 calcified clasper spine, USNM 467556.

REMARKS.—The single-cusped crown is nearly recumbent (Figure 22*c,d*); near the apex of the crown the labial face is almost parallel to the basal face of the root. In cross section, the crown is triangular basally to oval apically. The labial face forms the short side of this triangular crown foot; the lingual faces are wider than the labial face and meet at an acute angle near the crown-root boundary.

The root forms a pedestal for the crown. In basal view it has a triangular outline; a lingually placed central foramen occurs in a shallow transverse groove that bisects this face. The labial face protrudes somewhat, but it is flush with the crown; the labial end of the transverse groove divides this face. Both on the mesial face and the distal face of the root, three lateral canals open into a depression. The tooth measures 3.1 mm in total height, and the root is 3.3 mm in width, and 2.1 mm thick.

In morphology, except for its strongly lingually directed crown, this tooth compares well with adult teeth of extant *Cetorhinus maximus*, but it differs in its much smaller size, which is about half that of the extant species (compare with Herman et al., 1993, pl. 43). The strong lingual inclination of the crown is more characteristic of juvenile than of adult basking sharks (Herman et al., 1993:194–195), but unlike the teeth of the juveniles, the crowns of the teeth from Lee Creek Mine are unornamented. Sufficient specimens of the extant species have not been examined to determine if ornamentation is a variable character in juveniles.

In addition to the tooth, a calcified clasper spine (Figure 22*e*), was recovered from the spoil piles. This specimen is identical in morphology to those illustrated by Leriche (1926, fig. 195, pl. 37: figs. 6, 7).

The living basking sharks are plankton feeders and inhabit boreal to warm-temperate coastal to pelagic waters (Compagno, 1984:235). Along the Atlantic coast of North America they have been reported as far south as the Florida coast.

Family LAMNIDAE

(mackerel sharks, mako sharks, white sharks)

There are three extant genera in this family, *Carcharodon*, *Isurus*, and *Lamna*. Of these, *Lamna* has the most primitive teeth¹, which are very similar to those of *Cretolamna appendiculata*. *Lamna*, however, has teeth with reduced, tapered lateral cusplets and root lobes that are not very lobate, and it has a first anterior tooth with root lobes that form an angle of 90° or

¹In their phylogenetic analysis based on dental morphology, Long and Waggoner (1996) selected *Mitsukurina* as the outgroup. In comparison to *Hybodus* and *Cretolamna*, however, the teeth of *Mitsukurina* are very derived. Several of their synapomorphies, such as absence of diastem, short root lobes, multiple pairs of lateral cusplets, and moderate lateral cusplets, are plesiomorphic characters.

greater rather than the acute angle of those of *Cretolamna*. We identify these characters as autapomorphies for *Lamna*. For *Carcharodon* and *Isurus*, Compagno (1990a:372) identified as dental synapomorphies the characters "jaws and anterior teeth enlarged; lateral cusplets lost on teeth or present only in very young (?)," and as a synapomorphy of *Isurus*, he identified the flexed anterior teeth. This synapomorphy is absent in *Isurus xiphodon* (see below). Only one of the synapomorphies Compagno (1990a:372) identified for *Lamna* is found as a fossil: a calcified rostral node without lateral fenestra.

In addition to these genera, we tentatively assign, as Kemp (1991) did, *Parotodus* to this family. The teeth of this genus exhibit characters that prompted Cappetta (1980) to assign it to the Otodontidae. Our comparisons lead us to assign *Parotodus* to the Lamnidae for the reasons discussed below.

Cappetta (1980) included *Parotodus* in the Otodontidae because of its very globular root, particularly in the lateral teeth, and because of the presence, in the Oligocene form, of lateral denticles. These characters, however, are not taxonomically useful. As in other lamnids, the globular roots are confined to the lower teeth where the toruses are well developed. Lateral cusplets, a primitive character, also occur in *Lamna*, the Odontaspidae, the Alopiidae, *Triaenodon* (which have very broad lateral cusplets), and occasionally in the adult teeth of *Isurus* (Bass et al., 1975c:28) and *Carcharodon*. We did not find any derived characters to justify the assignment of *Parotodus* to the Otodontidae.

At first we assigned *Parotodus* to the Alopiidae because although some individuals of living makos may have stocky teeth, their anterior teeth are more elongate than their lateral teeth. In our sample of *P. benedenii*, however, the heights of the largest lateral teeth (5.6–6.0 cm) and those of the anterior teeth (5.8–6.6 cm) overlap. This overlap in height, which does not occur in extant *Isurus* or in *Otodus*, agrees with the observations on *Alopias* of Gruber and Compagno (1981:626): "Anterior teeth of threshers differ from lateral and posterior teeth in having narrower crowns relative to their height and more erect cusps, they are less well differentiated in *Alopias* than in lamnids, odontaspids, pseudocarchariids." Compagno (1990a:371) identified the reduced size of the anterior teeth as a synapomorphy of *Alopias*; this synapomorphy also pertains to *Parotodus*.

Other characters, however, suggest that *Parotodus* is not an alopiid. While examining the Lee Creek Mine specimens, Compagno (pers. comm., 14 Apr 1993) noted that the morphologies of the roots of *Parotodus* were like those of a mako rather than those of a thresher. We reexamined these teeth and those of *Isurus* and *Alopias* to verify his observation, and we found the following. (1) Unlike alopiids, in labial view, the lateral teeth of *Parotodus* do not have broad, shallow roots with enamel shoulders extending to the extremities of the root lobes. Like lamnids, in *Parotodus* the root lobes extend slightly beyond the basal boundary of the crown foot, and the roots are deep. (2) Like lamnids and unlike alopiids, the lower anterior teeth are not 10% to 20% smaller in height than the upper oc-

cluding teeth. (3) Like lamnids and unlike alopiids, the heights of the first three or four lateral teeth exceed their respective widths. These findings suggest to us that the less differentiated anterior teeth (see Compagno, 1990a:371) were derived independently of *Alopias*, and we assign *Parotodus* tentatively to the Lamnidae.

Genus *Parotodus* Cappetta, 1980

Until 1980, paleontologists assigned the sole species of this genus, *Parotodus benedenii*, to the genus *Isurus*; in that year Cappetta erected a new genus for this species, *Parotodus*, which he characterized as having "very great thickness of the crown and a very globular root" (Cappetta, 1980:35). We revise his diagnosis to read as follows: upper and lower laterals with hooked, mako-like crowns; heights of first three or four lateral teeth exceed their respective tooth widths; anterior teeth not well differentiated from lateral teeth.

Antunes and Jonet (1969–1970) and Antunes (1978) stated that the teeth identified as *Isurus benedenii* were the intermediate teeth of *Isurus hastalis*. Cappetta (1980), however, correctly argued that the teeth of *Parotodus benedenii* represented different jaw positions and that their thicknesses were proportionally greater than the intermediate teeth of *I. hastalis*.

Despite their stocky crowns, the teeth of *Parotodus* bear some similarities to *Isurus oxyrinchus*. Like *I. oxyrinchus*, the lower anterior teeth have well-developed toruses and robust crowns, which in the Lamnidae are peculiar to *Isurus oxyrinchus*. Also like *I. oxyrinchus*, the tips of the lower teeth, in lateral view, recurve labially. Unlike *I. oxyrinchus*, the sharply defined cutting edges on the anterior teeth extend to the crown foot. The roundness of the lingual crown foot, noticeable from the labial side in *I. oxyrinchus*, is not visible from this side. We do not believe, however, that these similarities warrant synonymizing *Parotodus* with *Isurus*.

Kuga (1985:14–16), apparently unaware of Cappetta's paper, erected the genus *Uyenoa* for this species, which he kept in the family Lamnidae; however, the senior name for this species is *Parotodus*.

Parotodus benedenii (Le Hon, 1871)

FIGURES 23, 24

Isurus moniwaensis Hatai, Masuda, and Noda, 1974:19–20, pl. 2: figs. 20, 22 [Miocene, Japan].

Uyenoya benedenii Kuga, 1985:14–16 [Neogene, Japan].

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—85 isolated teeth, USNM 24757, 279254, 279320, 281382, 282471, 283598, 289044, 289088, 289095, 289104, 289106, 293759, 293762, 297466–297468, 302442, 312441, 312447, 324928, 421612, 421629, 421917–421921, 437885, 454539–454563, 457258–457285.

REMARKS.—Le Hon (1871:6) characterized this species as follows: “Species of enormous thickness that resembles the Cretaceous *Oxyrhina crassidens* of Dixon. The neck of the tooth is very wide and the gum imprint exceedingly pronounced as in all teeth with thick roots. The crown is incurved more or less, and some curved and hooked teeth having the same characters it seems to me to have belonged to the same animal” (translated from French by R.W.P.). The type specimen that Le Hon illustrated is a second lower anterior tooth, which he noted was found in Pliocene sediments during the excavation of the fortifications around Anvers, Belgium.

Leriche (1910:281–283) reported the earliest occurrence of this species in the early Oligocene, Rupelian, of Belgium. These teeth are much smaller than those of the Pliocene form. In his suite of illustrated specimens, Leriche (1910) also included two teeth of *Lamna rupeliensis* (his pl. 16: figs. 5, 6), which he identified as *Oxyrhina benedenii*. Leriche (1910:282) noted that “the transformation of the heels of the crown into lateral cusplets is observed mainly in the lateral teeth of the upper jaw (Fig. 5, 6, 8, 9)” (translated from French by R.W.P.). Although the teeth in his figs. 5 and 6 were not found in association with the others, his identification of them was not challenged by subsequent workers.

The sample of 85 teeth from Lee Creek Mine permitted us to reconstruct the dentition of this shark (Figure 23). As in lamniform sharks, the upper and lower anterior teeth exhibit the same morphological characters that permit their differentiation: their crowns are more erect, and the angle formed by the root lobes is more acute than in the lateral teeth. In the lower anterior teeth there is a greater development of the torus.

Only the second and third upper anterior teeth are present from Lee Creek Mine. The first anterior tooth may be absent in this genus; no teeth were recovered that were nearly symmetrical and with root lobes forming an acute angle. In the second anterior tooth, the crown inclines distally, the distal cutting edge is concave, the root lobes intersect at a right or slightly obtuse angle, and the distal root lobe has a greater mass than the mesial one. In the third upper anterior tooth, along the mesial edge, the arc of the distal curvature is almost continuous from the tip of the crown to the base of the root. The distal cutting edge is nearly straight. The root lobes intersect at an obtuse angle, and as in the second anterior tooth, the distal root lobe has the greatest development.

We identified three intermediate teeth: USNM 289088, 293762, and 312447 (Figure 24a–e). As in the anterior teeth, these teeth are much higher than they are wide, but they are smaller than the anterior and lateral teeth in our suite of specimens. Their root lobes form an acute to right angle, and as in the third upper anterior, their crowns have a distal curvature and, in lateral view, a very pronounced labial curvature.

In the lower jaw, the anterior teeth possess toruses (lingual protusion of the root) (Figure 24f) with a much greater development than those of the lateral teeth. The first anterior tooth has an erect crown, with the root lobes forming an acute or right angle. In the second anterior tooth the erect crown has a slight distal curvature; the root lobes form a right or obtuse angle. In the third anterior tooth, which has a distally inclined crown, the mesial root lobe is longer than the distal one.

In *Parotodus*, except for their size, the lateral teeth of both jaws have hooked crowns very similar to those of two dentitions of an *Isurus oxyrinchus* in the Hubbell collection

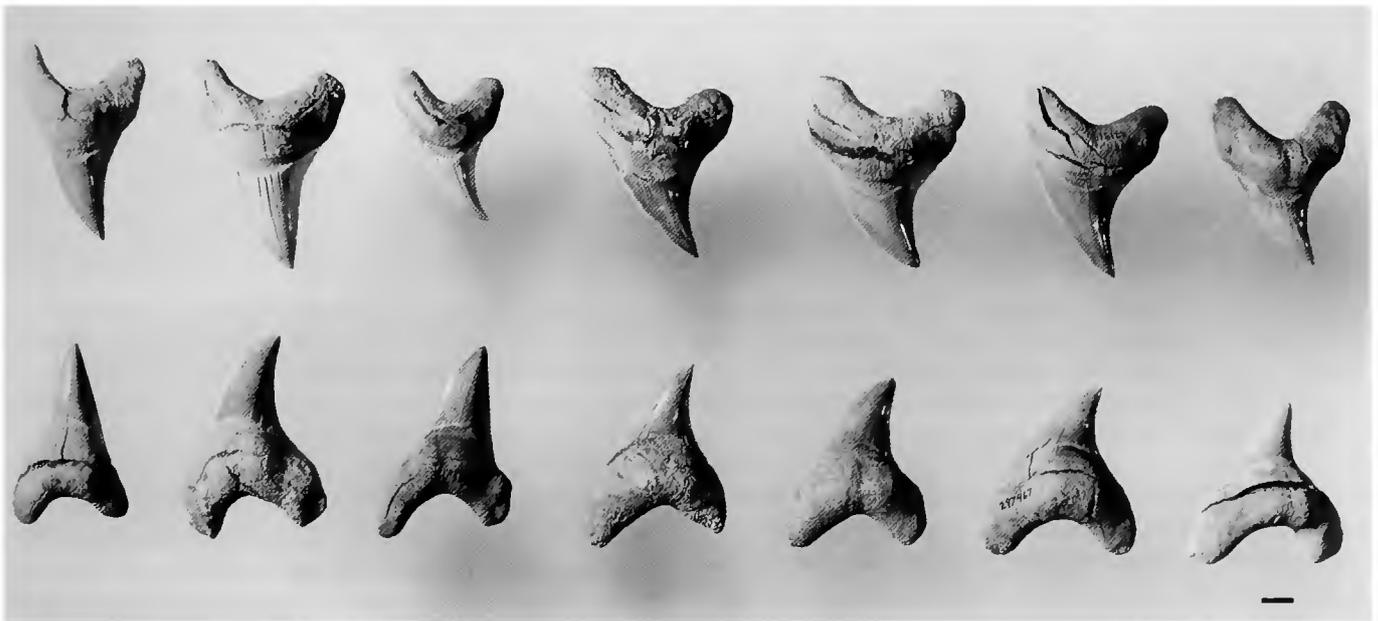


FIGURE 23.—*Parotodus benedenii*, composite dentition, lingual view. (Scale bar=1.0 cm.)



FIGURE 24.—*Parotodus benedenii*: a, USNM 289088, intermediate tooth, lingual view; b, USNM 293762, intermediate tooth, lingual view; c, USNM 312447, second lower intermediate tooth, lingual view; d, same specimen, lateral view; e, same specimen, labial view; f, USNM 457258, lower anterior tooth, lateral view showing development of torus. (Scale bars: a,b=1.0 cm; c-e=0.9 cm; f=0.5 cm.)

(DO52188, MD62287). In both species the lower teeth are more erect than the upper teeth.

Kemp (1991, pl. 32) noted and illustrated a specimen of this species consisting of 30 detached teeth in matrix from the early Miocene Batesford Limestone, Batesford, Australia, including the upper and lower anteriors and two symphyssial

teeth. The symphyssial teeth appear to be from the upper and lower jaws; the tooth in his fig. E1,2 is more compressed than the symphyssial tooth in his fig. D; therefore, we concur with Kemp's identification of them as upper and lower symphyssial teeth. We did not find any comparable teeth at Lee Creek Mine. The presence of symphyssial teeth in the Batesford spec-

imen may be the retention or reappearance of a primitive character.

Davis (1888:26–27) described the species *Oxyrhina vonhaastii* from the Oligocene of New Zealand and included in his type suite a mass of about 20 teeth in limestone. Although we have not seen his type suite, we believe that this species should be assigned to *Parotodus*, and it may be a junior synonym of *P. benedenii*.

In the fall of 1992, Clyde Swindell and George Powell recovered an associated, partial dentition of this shark from Lee Creek Mine (Kent and Powell, 1999). This dentition confirms the presence of two upper anterior teeth. Until this specimen can be compared with those from Australia and New Zealand, we believe it is premature to assess the relationship of this species to the Oligocene and early Miocene specimens and to other lamnids.

The anterior teeth of this shark range from 5.8 to 6.3 cm in height (mean=6.2 cm, $n=6$) and from 3.7 to 5.0 cm in width (mean=4.3 cm, $n=6$). Because their lateral and anterior teeth are not well differentiated by tooth height, there is no living lamnid that can be used as a model for estimating the total length of *Parotodus benedenii*, but we guess that large adults were between 6 and 7.5 m long.

Hatai, Masuda, and Noda (1974:19–20, pl. 2: figs. 20, 22) described a new species, *Isurus moniwaensis*, from the Miocene of Japan; their type specimen is identical to specimens identified herein as *Parotodus benedenii*.

Roux and Geistdoerfer (1988) reported the occurrence of teeth of this species in the Pleistocene deposits in the Indian Ocean off New Caledonia (see "*Carcharodon megalodon* (Agassiz, 1835)," below, for further discussion).

Compagno (pers. comm., 14 Apr 1993) suggested that this shark fed by grabbing prey, such as seabirds, porpoises, and seals, with its teeth and swallowing it whole.

Genus *Isurus* Rafinesque, 1810

The teeth of *Isurus* have smooth cutting edges, have smooth labial and lingual coronal faces, usually lack lateral cusplets, and the central foramen usually does not open into a well-defined transverse groove. In both jaws the teeth are differentiated into anteriors, intermediates (upper jaw only), laterals, and posteriors. Espinosa-Arrubarrena (1987:26) gave the formula for fossil and living makos as follows: (upper jaw) two anteriors, one intermediate, five to seven laterals, three to four posteriors; (lower jaw) three anteriors, five to seven laterals, three to four posteriors. Of these tooth types, the anteriors are the most important taxonomically; in the dentitions we have examined so far, they exhibit the least amount of variation within a species.

Ontogenetic heterodonty occurs in the extant species of *Isurus*. In individuals over 3 m TL, the teeth broaden and become thinner, even in the lower laterals, which normally have robust crowns, and the attitudes of the crowns may change

considerably, becoming strongly arched distally. Espinosa-Arrubarrena (1987) noted that lateral cusplets occurred in the lateral and posterior teeth of juveniles, but in the available juvenile dentitions of *I. oxyrinchus* (USNM 232652, TL=1901 mm?; USNM 232650, TL=1310 mm), *Isurus paucus* (USNM 196024, TL=1251 mm; USNM 196039, TL=1801 mm), and in numerous juvenile *I. xiphodon* teeth, we did not observe any lateral cusplets. Bass et al. (1975c:28), however, reported that in large individuals of *I. oxyrinchus*, minute lateral cusplets occur on the distal shoulder of the more posterior lateral teeth. To date no sexual heterodonty has been noted.

In the upper and lower jaws, differences in morphology exist between teeth of the same jaw positions. The upper teeth have broader, thinner crowns, and their roots are not as well developed as are their counterparts in the lower jaw. In the lower teeth, in the area of the central foramen, the torus is well developed; the greatest development of the torus occurs in the lower first anterior tooth and diminishes in each successive tooth until it is not discernible in the second or third lateral tooth.

Espinosa-Arrubarrena (1987:110–117) recognized three groups of makos based on the elongate and cylindrical shape of the crowns of the anterior teeth and on the lengths of the root lobes of the upper anterior teeth. To facilitate discussion, we call his groups the *oxyrinchus-paucus* group, the *desori* group, and the *hastalis* group.

He defined the *oxyrinchus-paucus* group as containing species with "small to medium-sized teeth, that have cylindrical to slightly flattened and very narrow crowns in the upper anterior teeth" (Espinosa-Arrubarrena, 1987:110–113). He subdivided this group into three lineages: the *I. oxyrinchus* lineage, the *I. paucus* lineage, and the *I. sp. D-I. sp. E* lineage. His *I. oxyrinchus* lineage is characterized by having anterior teeth "with root branches that are unequally long [the mesial side is longer]." His second subgroup, the *I. paucus* lineage, is characterized by having "root branches that are equally long," and his third subgroup, the *I. sp. D-I. sp. E* lineage, is characterized by unequal root branches but with the distal branch longer than the mesial one (Espinosa-Arrubarrena, 1987:113).

The *desori* group was defined as "isurid species with large and very robust teeth that represent an intermediate stage between the narrow or cylindrical crowns of the uppers of group one [*oxyrinchus-paucus* group] and the wide and totally flattened upper teeth of the *I. hastalis* and *I. planus* lineages. The species included in this category are *I. desori*, *I. retroflexus*, and *I. sp. F*. The upper anterior morphotypes in *I. desori* tend to be unequal (longer mesial side [root lobes]), and in *I. retroflexus* and *I. sp. F*, the same elements tend to be equal in size" (Espinosa-Arrubarrena, 1987:113–114).

Finally, his *hastalis* group was defined as "isurid species with wide crowns and totally labiolingually flattened upper teeth (triangular shaped crowns). The species groups of *I. hastalis* and *I. planus* (with *I. sp. G* and *I. sp. H* respectively) obviously represent the opposite end of the grasping-cutting se-

ries. These are teeth of very large size, the cylindrical (rounded cross section) shape of the crown has been completely lost. And the root branches of the upper anteriors are unequal in *I. hastalis* and very symmetrical (mesial and distal sides of the same size) in *I. planus*" (Espinosa-Arrubarrena, 1987:116–117). Espinosa-Arrubarrena and others have identified as *I. hastalis* teeth that Agassiz named *I. xiphodon*, which is not a junior synonym of *I. hastalis* (see below).

When we applied these characters to recent and Lee Creek Mine specimens, we found the following exceptions to Espinosa-Arrubarrena's groupings. (1) In a dentition from a 3.9 m TL female *I. paucus* (Hubbell collection, JG5379), the third upper left anterior tooth has a mesial root lobe that is longer than the distal one. In another dentition from a 4 m TL female of the same species (Hubbell collection, NA91690), in all of the teeth except the upper intermediate and the third through fifth upper laterals, the mesial root lobes are longer than the distal root lobes. (2) In a dentition of a large *I. oxyrinchus* of over 3.7 m TL (USNM 309253), the second upper anterior tooth has a distal root lobe that is longer than the mesial one. (3) In dentitions of *I. paucus* from individuals of over 3.7 m TL, the anterior teeth become broader and flatter, losing their cylindrical or rounded cross section. Compared to *I. paucus*, in *I. oxyrinchus* the compression of the anterior teeth occurs to a much lesser degree in some individuals (USNM 309253), and no compression occurs in others (LJVC 901119). (4) The teeth in the type suite for *I. desori* (Agassiz, 1843:282), in size and roundness of cross section, can only be assigned to Espinosa-Arrubarrena's *oxyrinchus-paucus* group. (5) The broadness and flatness of the holotype of *I. planus* falls within the range of variation occurring in the extant *I. oxyrinchus* and *I. paucus*, particularly in individuals of 3.7 m TL or more.

In summary, the lengths of the root lobes and the roundness of the crowns of the anterior teeth in cross section are characters that vary within a species.

We believe, however, that there are three species of mako sharks represented at Lee Creek Mine. Those with more flexuous, awl-like anterior teeth with a labial recurvature at the tips we identify as *I. oxyrinchus*; those with less flexuous anterior teeth with more compressed crowns and with straight-tipped lower anterior teeth we identify as *I. hastalis*; and those with triangular, compressed upper anterior teeth with tips that may become labially recurved as they become larger and with straight-tipped lower anterior teeth we identify as *I. xiphodon*.

Isurus oxyrinchus Rafinesque, 1810

FIGURES 25, 26

Oxyrhina desori Agassiz, 1843:282, pl. 37: figs. 8, 9 [figs. 10–13 indeterminate; lectotype: ETHG1 P145, selected herein; Miocene, Switzerland].—Leriche, 1927:68, pl. 10: figs. 1–10 [Miocene, Switzerland].

Oxyrhina desori Gibbes, 1848–1849:203, pl. 27: figs. 169, 170 [Pliocene, South Carolina].

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—115 teeth, USNM 207619, 207620, 207622, 207626, 207628–207630, 279119, 279136, 279155, 293736, 312442, 312443, 312448, 312449, 312452, 336759, 339897, 421619, 421884, 421983, 425494, 425502, 425558, 425851, 425856, 425862–425872, 452469, 452481, 452483, 452487, 452488, 452491, 452494–452497, 452499–452501, 452505–452507, 452510, 452512, 452514, 452530, 452541–452543, 452550, 452563, 452565, 452566, 452572–452574, 452579, 452583, 452612, 452620, 453142, 453146, 453147, 453152, 453153, 453156, 453158, 453160–453162, 453164, 453170, 453174, 453175, 453184, 454280, 454281, 454283, 454286, 454302–454304, 454336, 454355, 454358, 454360, 454378, 454383, 454385, 454387–454389, 474966–474975, 476296.

REMARKS.—Agassiz (1843:282) characterized *Oxyrhina desori* as follows: "Relative to their height, the teeth of our *Oxyrh. desori* are much less broad than those of *Oxyrh. hastalis*; moreover they are thicker and nearly semicylindrical; and the cone of the tooth, instead of being straight, curves at first a little to the outside in order to turn back next to the inside; and when the tip, from its side, recurves in turn to the outside, the profile of the tooth takes on a very wavy appearance, which contrasts with the straight form and uniform bend to the outside of *Oxyrh. hastalis*" (translated from French by R.W.P.).

Except for two, the syntypes are indeterminate, and Gibbes (1848–1849:203) related that Agassiz, subsequent to the publication of his opus, felt that *I. desori* was identical to *Lamna cuspidata*. Gibbes, therefore, named a new species of fossil mako as *O. desori* to preserve Agassiz's name; the three teeth of his type suite are referable to *Isurus oxyrinchus* and *I. xiphodon* (Gibbes, 1848–1849, pl. 27 figs. 169, 170, and fig. 171, respectively). *Oxyrhina desori* Gibbes, however, is a junior homonym of *Oxyrhina desori* Agassiz, and it is unavailable for use as a species name.

Leriche (1910) also considered the syntypes of Agassiz's species to be indeterminate. Rather than abandon the name, Leriche (1910, 1927) referred his own specimens to "*Oxyrhina desori*" as identified by Sismonda (1849), which is presumably, but not necessarily, also referable to *Oxyrhina desori* sensu stricto. Leriche's concept of this species, which is based on teeth that are similar to those of *I. paucus*, has prevailed until now even though, according to the rules of zoological nomenclature, his redefinition of the species was invalid.

Had Agassiz and Leriche been correct about the type suite of *O. desori*, this species would be a nomen dubium and would be unavailable as a species name; however, one of Agassiz's syntypes is a diagnostic anterior tooth of *Isurus*. We obtained casts of three of Agassiz's (1843) syntypes, the specimens figured in his pl. 37: figs. 8–10. Of the three, the tooth

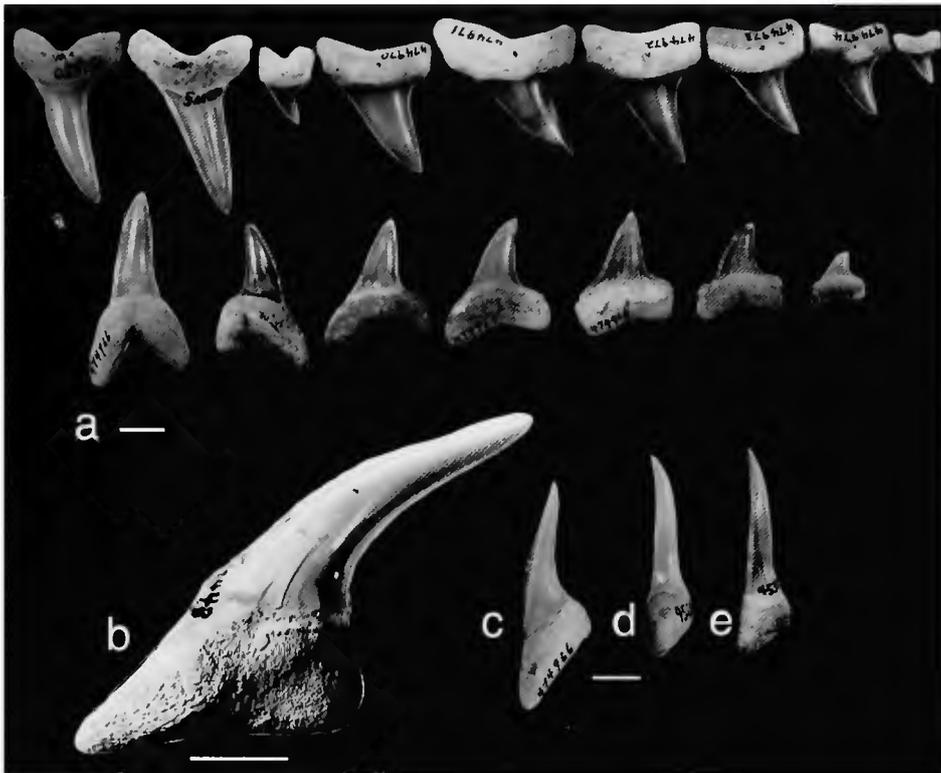


FIGURE 25.—*Isurus oxyrinchus*: a, composite dentition, lingual view; b, USNM 312443, first lower anterior tooth, lateral view; c, USNM 474966, second lower anterior tooth, lateral view; d, USNM 452530, second upper anterior tooth, lateral view; e, USNM 453175, third upper anterior tooth, lateral view. (Scale bars: a, c–e=1.0 cm; b=0.5 cm.)

in fig. 9 (ETHGI P145) is the second upper anterior of *Isurus*; this specimen lacks lateral cusplets and lacks any indication that they were ever present, and it possesses a sufficient portion of the root to show the absence of a well-developed transverse groove, which is present in odontaspids. Agassiz's fig. 8 also may be the same tooth of *Isurus*, but the tooth in fig. 10 and the teeth illustrated in figs. 11–13 are indeterminate. Because ETHGI P145 (Figure 26a–c) is the only tooth of the type suite that can be definitely identified as *Isurus*, we designate this specimen the lectotype, and *Oxyrhina desori* is not a nomen dubium.

Oxyrhina desori is, however, a junior synonym of *Isurus oxyrinchus* Rafinesque, 1810. The morphology of the lectotype is identical to a right, upper second anterior tooth of almost equivalent size in the dentition of *I. oxyrinchus* (USNM 309253). The widths of the crowns and the development of the distal cutting edges are the same in both. Therefore, we place *Oxyrhina desori* Agassiz in synonymy with *Isurus oxyrinchus*.

In the anterior teeth of *I. oxyrinchus* (Figure 25b–e), the tips of the crowns usually exhibit a labial recurvature; this is more noticeable in the upper anteriors. This recurvature also occurs

in the tips of the upper and lower lateral teeth, but it is not always present.

In the extant *I. oxyrinchus*, as in the Lee Creek Mine specimens, the upper anterior teeth exhibit morphological variation. The mesial cutting edge of the second upper anterior (first tooth in jaw) is straight to strongly convex, whereas the distal cutting edge may be gently sinuous to nearly straight. The root lobes intersect at acute to obtuse angles, and their lateral extremities may be pointed to rounded.

In the third upper anterior tooth, as in the second upper anterior, the mesial cutting edge is straight to strongly convex. These strongly convex cutting edges may not form the usual continuous arc with the mesial margin of the root. The root lobes intersect at right to obtuse angles.

Intermediate teeth have distally hooked crowns, and the root lobes are often pointed, with the basal margin of the root arcuate.

The lower anterior teeth are more robust and are more flexuous than those of similar-sized individuals of *Isurus paucus* and *I. hastalis*, and in labial view, the roundness of the crown foot obscures the definition of the mesial or distal (or both) cutting edges; this condition also exists in the upper anteriors.



FIGURE 26.—*Isurus oxyrinchus*, cast of ETHGI P145, lectotype of *Oxyrhina desori*, USNM 476355: a, lingual view; b, lateral view; c, labial view. *Isurus oxyrinchus*: d, USNM 452483, first lower anterior tooth with elongate root lobes, lingual view; e, USNM 312448, lower lateral tooth with mesial cusplet, labial view; f, USNM 476296, lower lateral tooth with broad lateral cusplets, labial view; g, USNM uncataloged, lower lateral tooth from extant species with lateral cusplets, labial view. (Scale bars=1.0 cm.)

These anterior teeth incline distally. In one dentition (Hubbell collection, 11191), plications are present on the labial crown feet of the lower anterior teeth. Like *I. hastalis* but unlike *I. xiphodon*, the teeth usually have elongate root lobes (Figure 26d), particularly in the first and second anterior teeth, that taper to a point, but they also may be rounded.

Garrick (1967:679) noted that in juveniles and small adults, the distal cutting edge of the second upper anterior and the first lower anterior teeth are incomplete. In larger adults these cutting edges are complete.

In the lateral teeth of the extant species (Figure 26g), the crowns are erect to strongly hooked. Often the enameloid does not extend down to the basal margin of the crown foot, giving the crown foot a dull appearance. Ridges may be present on the labial crown feet. In large adults, the crowns become very thin. The root lobes are angular to lobate. On the lingual surface a shallow transverse groove may occur, which also occurs in anterior teeth.

In addition to the above morphological variations, we note the following. In the first lower anterior tooth (USNM 452483, height of tooth=46.0 mm, labial height of root=20.2 mm), the root lobes are longer than those of a larger first anterior of the extant species (Compagno collection, LJVC-901119, height of tooth=50.8 mm, labial height of root=19.8 mm). Also, two lateral teeth exhibit a pair of broad, low, rounded lateral cusplets (USNM 312448, 476296, Figure 26e,f).

Anterior teeth from the Pungo River Formation ranged from 2.7 to 5.0 cm in height (mean=3.8 cm, $n=8$) and from 1.7 to 2.9 cm in width (mean=2.2 cm). Anterior teeth from the Yorktown Formation ranged from 2.8 to 5.8 cm in height (mean=3.9 cm, $n=50$) and from 1.1 to 3.2 cm in width (mean=2.2 cm). On the basis of measurements of teeth from extant sharks of this species of known size, the shortfinned makos of the Pungo River and Yorktown seas ranged in size from 2.4 to 4.6 m TL.

The extant shortfin mako shark (Compagno, 1984:243) is common in coastal and oceanic waters in warm-temperate and tropical seas. It feeds on a wide variety of bony fishes, including tunas, bonitos, carangids, sea basses, porgies, and swordfish, and on other sharks, sea turtles, and, occasionally, marine mammals.

Isurus hastalis (Agassiz, 1838)

FIGURES 27, 28a-c

Oxyrhina hastalis Agassiz, 1838: pl. 34: figs. 3, 5, 13, 16, 17; 1843:277 [figs. 4, 7-10, 12, 15, indeterminate; early Miocene, Switzerland].—Leriche, 1926:399, pl. 31: figs. 3, 4, 7, 8, 11, 12, 20-23; 1927:71, pl. 11: figs. 1-3, 5-7 [not fig. 4; early Miocene, Switzerland]; 1942:69-71, pl. 5: figs. 11-20 [Calvert Formation, Maryland].

Oxyrhina xiphodon Agassiz, 1838, atlas volume 3, pl. 33: figs. 11, 12.

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1–3).

REFERRED MATERIAL.—About 500 teeth, USNM 207632–207635, 278592, 281043, 293598, 293610, 293705, 336748, 336750, 336761, 421883, 421885, 425491, 425553, 425644, 425857, 425858, 425860, 425861, 425873–425880, 437446, 452431, 452468, 452482, 452484–452486, 452489, 452498, 452503, 452504, 452508, 452511, 452513, 452515, 452516, 452518–452529, 452532–452540, 452544–452549, 452551–452556, 452561–452564, 452578, 452580, 452582, 452591–452593, 452596, 452598, 452601, 452602, 452604–452607, 452609–452611, 452613, 452614, 452616–452622, 452625, 452626, 452628–452631, 452634, 452635, 452638–452640, 453140, 453141, 453143, 453145, 453149, 453153, 453155, 453159, 453165–453171, 453173, 453176–453183, 453185–453187, 454284, 454285, 454287–454289, 454314–454321, 454324, 454326, 454335, 454337–454339, 454342–454344, 454349–454354, 454356, 454357, 454359, 454361–454363, 454366, 454369, 454374–454377, 454379, 454380, 454382, 454393, 454520, 474976–474993.

REMARKS.—Agassiz's type suite (1838, pl. 34: figs. 3–13, 15–17) consists of mainly upper anterior teeth; his fig. 3 is a lower lateral, and his figs. 4 (UNIG 240), 5 (UNIG 243), and 7 are upper laterals. Although most of his remaining specimens are incomplete, the size and the broadness of the crowns suggest that they are all mako teeth. With the possible exceptions of the specimens in his figs. 6 and 11 (UNIG 244), these upper teeth all appear to belong to the same species. Agassiz (1843:277) characterized them as "teeth with rather great stature, elongated and in the form of a lance." The tips of the upper anterior teeth in the type suite exhibit a strong labial curvature, a character that we believe is taxonomically significant (see be-

low). Of Agassiz's syntypes, the specimen in his fig. 16, if it is still in the collections of the Universität Neuchâtel, should be declared the lectotype for this species.

In morphology, the teeth of *Isurus hastalis* (Figure 27) are almost identical to those from large individuals (TL=3.7–4.3 m) of *I. paucus*. The tips of the upper anterior teeth of the latter species, however (TL=2.3–4.2 m, $n=9$), usually lack the labial recurvature that is so well developed in *I. hastalis* (Figure 28a). In the small number of *I. paucus* dentitions available to us ($n=9$), only one dentition (Hubbell collection, JF91980, 2.6 m TL, female) had upper anterior teeth with tips that exhibited a strong labial recurvature. At present, we do not know how common this recurvature is in the extant species.

The upper anterior teeth of Leriche's (1910:275–280, figs. 78–86, pl. 16: figs. 16–31) sample of teeth from the Oligocene of Belgium, which he identified as *Oxyrhina desori* and *O. desori flandrica*, are identical to those of the extant *Isurus paucus*. They lack a labial recurvature. This suggests that *I. paucus* may be a junior synonym of *I. hastalis*, but because of the small number of dentitions available of *I. paucus*, we hesitate in synonymizing the two species.

In *I. hastalis* and *I. paucus*, the cutting edges of the anterior teeth are sharply defined to the base of the crown. The lower anterior teeth of these two species are difficult to distinguish, but in *I. paucus* the more prominent development of the lingual torus of the roots may prove to be a useful character; although its consistent occurrence in a large sample of this species cannot yet be determined. In *I. hastalis* the mesial cutting edges of the lower anterior teeth are convex, whereas they are straight in *I. xiphodon*, and the root lobes, particularly in the first anterior tooth, are more elongate and are not as massive as those of *I. xiphodon*.

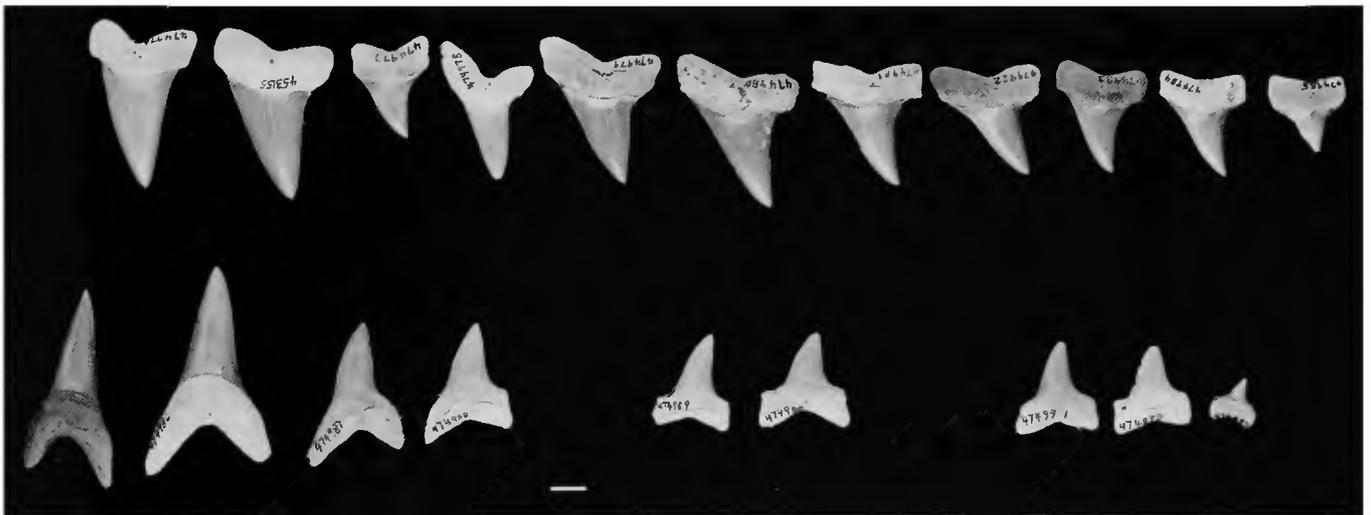


FIGURE 27.—*Isurus hastalis*, composite right dentition, lingual view. (Scale bar=1.0 cm.)

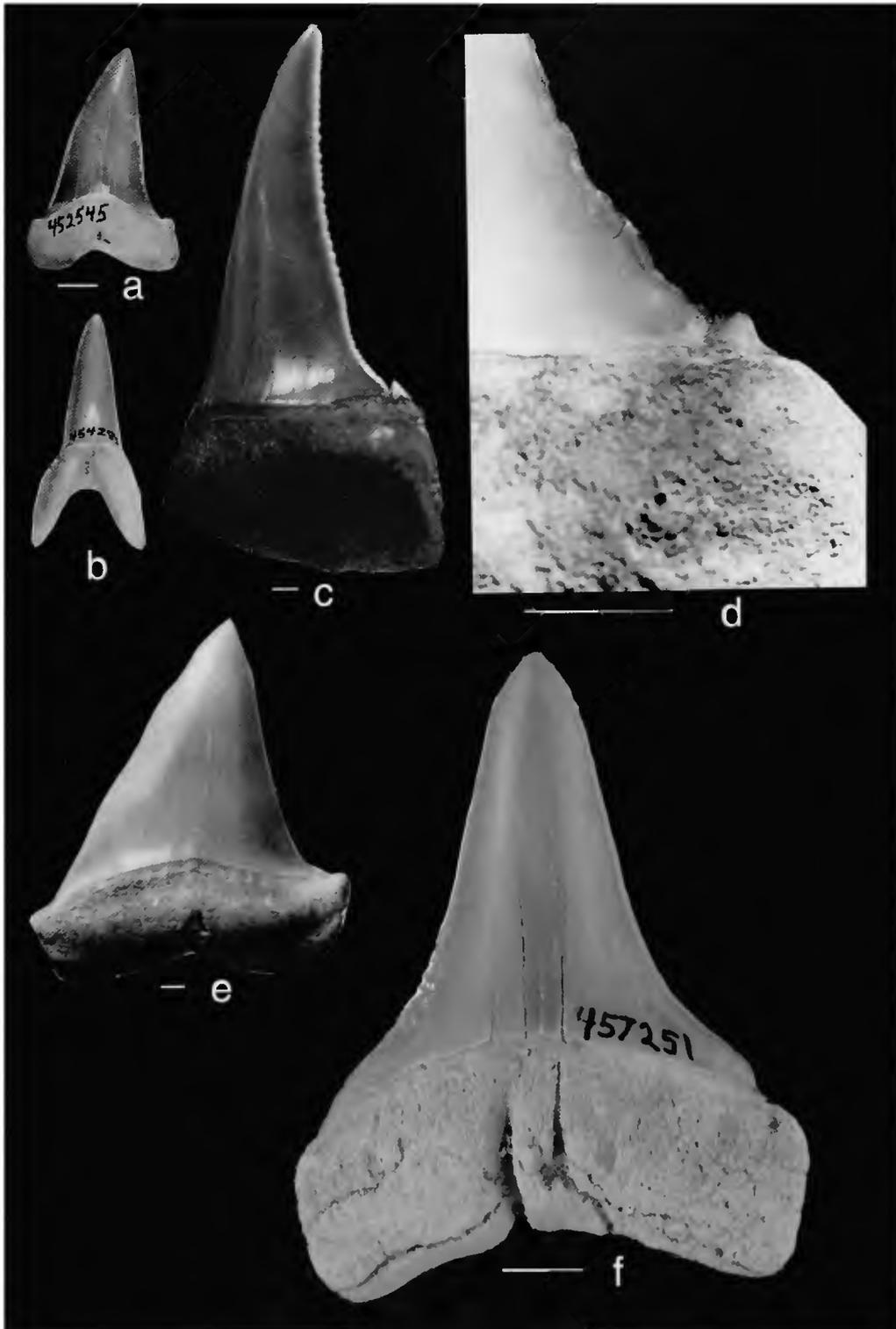


FIGURE 28.—*Isurus hastalis*: a, USNM 452545, second upper anterior tooth, lateral view showing labial recurvature; b, USNM 454285, first lower anterior tooth, lingual view showing rounded torus with transverse groove; c, IG 27385, lower Miocene, Antwerp, Belgium, close-up of serrated cutting edge. *Isurus xiphodon*: d, USNM 476356, Yorktown Formation, unit 4, close-up of mesial cutting edge with incipient serrations; e, USNM 457248, first upper lateral tooth, lingual view showing ear-like structures on root; f, USNM 457251, lower lateral tooth, lingual view showing transverse groove on root. (Scale bars: a,b=1.0 cm; c,f=0.33 cm; d=0.25 cm; e=0.5 cm.)

Unlike *Isurus oxyrinchus*, the upper and lower lateral teeth of *I. hastalis* have tips that lack the labial recurvature. Their crowns are usually broader than those of *I. oxyrinchus*, but the upper lateral teeth are not as broad as those of *I. xiphodon*. The lower lateral teeth are asymmetrical and are broader than those of *I. xiphodon*.

One morphological variation in the teeth of *I. hastalis* should be mentioned. In a first lower anterior tooth (USNM 454285), the torus of the root is bisected by a broadly rounded transverse groove (Figure 28b).

Isurus hastalis is the most common mako at Lee Creek Mine. The anterior teeth from the Pungo River Formation range from 2.3 to 5.2 cm in height (mean=4.1 cm, $n=58$) and from 1.3 to 3.8 cm in width (mean=2.6 cm, $n=58$). Those from the Yorktown Formation range from 1.7 to 5.7 cm in height (mean=4.1 cm, $n=76$) and from 1.1 to 3.8 cm in width (mean=2.6 cm, $n=75$). Anterior teeth within these size ranges in the extant *I. paucus* are found in individuals of 1.8 to 4.6 m TL.

Recently, dentitions from both species of extant makos over 3.7 m TL became available for study. Dental characters used to identify *I. retroflexa* also occur in these dentitions. The compressed tooth crown that Agassiz (1843:281) said distinguished *I. retroflexa* from all other species of *Isurus* is found in *I. oxyrinchus* (USNM 309253) and in *I. paucus* (Hubbell collection, JG5379). In a dentition from an *I. paucus* of 3.9 m, the compressed upper and lower teeth have rounded tips identical to those identified by Leriche (1926, 1927) and Cappetta (1970, pl. 6: fig. 1) as *I. retroflexa*. Agassiz's holotype and only specimen of *I. retroflexa*, an incomplete lower lateral with a rounded tip, lacks the labial recurvature that usually occurs in *I. oxyrinchus*. The nature of this specimen does not permit its assign-

ment with confidence to *I. hastalis*, *I. oxyrinchus*, or *I. paucus*; therefore, we consider *I. retroflexa* a nomen dubium.

Isurus xiphodon (Agassiz, 1838)

FIGURES 28d-f, 29-31

Oxyrhina trigonodon Agassiz, 1843:279, pl. 37: figs. 17, 18 [Neogene, Germany].

Oxyrhina plicatilis Agassiz, 1843:279, pl. 37: figs. 14, 15 [Neogene, Italy].

Oxyrhina crassa Agassiz, 1843:283, pl. 37: fig. 16.

Oxyrhina desori Gibbes, 1848-1849:203, fig. 171 [Pliocene, South Carolina].

Anotodus agassizii Le Hon, 1871:8-9 [Neogene, Belgium].

Oxyrhina hastalis Agassiz.—Leriche, 1926, pl. 31: figs. 5, 6, 9, 10, 13-19, 24, 26-30 [Neogene, Belgium].

Isurus hastalis (Agassiz).—Menesini, 1969:15-17, pl. 2: figs. 1-3, 5, 9, 11, 12.

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—About 400 teeth, USNM 278765, 278766, 278771, 278774, 278792, 278799, 278801, 278814, 279059, 279060, 279062, 279188, 279200, 279963, 279964, 279967, 287485, 287694, 293599, 293609, 293710, 293713, 293714, 302447, 312646, 324933, 336738, 336739, 336746, 421613, 421618, 421769-421772, 421776, 421777, 421910-421913, 421916, 421923, 421977, 425592, 425854, 425859, 437443, 437444, 437447, 452557, 452571, 452576, 452577, 452927-452930, 452937, 452945, 452946, 452948-452950, 452955, 453144, 453150, 453157, 454307, 454313, 454325, 454345, 454347, 454348, 454364, 454368, 454370, 454371, 457245-457251, 474918, 474919, 476356, 476416-476422, 482198-482211, 482214, 482218, 482219, 482221.

REVISED DIAGNOSIS.—Upper anterior and lateral teeth broad, triangular; juvenile teeth like those of adults in form;



FIGURE 29.—*Isurus xiphodon*, composite dentition of an adult, lingual view. (Scale bar=1.0 cm.)

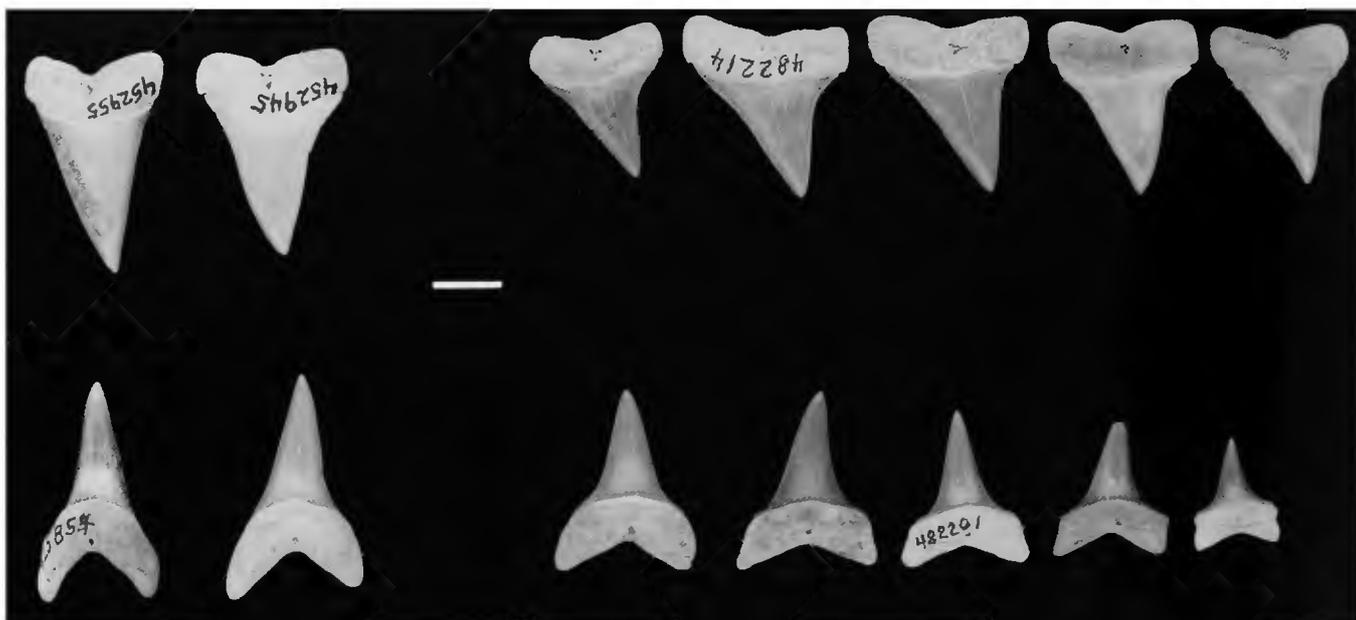


FIGURE 30.—*Isurus xiphodon*, composite dentition of a juvenile, lingual view. (Scale bar=1.0 cm.)

lower teeth with erect crowns; lower anterior teeth with short, massive root lobes.

REMARKS.—Agassiz (1843:278) separated this species from *Isurus hastalis* on the basis of a “noticeable flattening” of the lingual crown foot. This flattening, however, is not always present, and it is insignificant taxonomically. The broadness of the teeth of *I. xiphodon*, a character that Agassiz (1843:278) believed was too vague, does, however, separate the two species.

Two of the seven specimens in the type suite for *I. xiphodon* (Agassiz, 1838, pl. 33: figs. 11, 12) are teeth of *I. hastalis*. The remainder of the specimens, figured in pl. 33: figs. 14–17, are broad, triangular, upper-jaw teeth of *I. xiphodon*. The specimens in figs. 16 and 17 are anterior teeth, but only the specimen in fig. 17 is complete. If this specimen (listed by Agassiz as in the collection of “Mr. Bronn”) still exists, it should be designated the lectotype of this species.

Agassiz attributed two upper teeth and one lower tooth of this mako to three different species, *Oxyrhina trigonodon*, *O. plicatilis*, and *O. crassa*, respectively. Lawley (1878), on the basis of 140 associated teeth from the Pliocene of Tuscany, synonymized Agassiz’s species, which were based on upper teeth, with Le Hon’s newly described *A. agassizi*. Leriche (1926) synonymized *O. trigonodon*, *O. plicatilis*, and *O. crassa* with what he believed was the same species as the senior name, *I. hastalis*.

Lawley (1878, pl. 5: fig. 1) reconstructed from 140 associated teeth the first dentition of this species, but the upper anterior teeth are from the opposite jaw; their tips are pointing in the

wrong direction, and the positions of the first and second lower anterior teeth are reversed.

Based on unassociated teeth from the Neogene of Belgium, Leriche (1926, pls. 31, 32) published the first accurate reconstruction of this dentition, but he considered the broad, triangular teeth to be those of an old individual of *I. hastalis*. Because, however, the general form of the upper and lower teeth of juveniles and young adults of *I. xiphodon* are identical to those of large adults (Figures 29, 30), *I. xiphodon* cannot be synonymized with *I. hastalis*.

In addition to the above illustrated specimens, two associated dentitions were available to us, one nearly complete, from the Pisco Formation of Peru, and the other consisting of 27 teeth, including the anteriors, from the Calvert Formation of Maryland. Our reconstructions (Figures 29, 30) are based on these specimens.

The upper teeth have broad, triangular crowns that become more asymmetrical toward the corners of the mouth. Unlike any other species of mako, the upper anterior teeth have very broad, flattened crowns. In the second upper anterior tooth, which is the first tooth from the symphysis, the crown is usually asymmetrical, with a broadly convex mesial cutting edge and a concave distal cutting edge. The angle of the root lobes is smaller in the second upper anterior tooth, and the root lobes are almost equal in size. The crown is more asymmetrical in the third upper anterior tooth than in the second tooth, and the mesial root lobe is longer than the distal root lobe. In the morphology of the crown and in the angle of the root lobes, the intermediate tooth of our reconstruction compares

favorably with the form of those of other mako species. Its crown is erect, and it has a strong labial curvature. In the lateral teeth the mesial and distal root lobes form nearly a 180° angle.

The lower teeth have erect crowns that in labial or lingual view appear almost symmetrical. Unlike those in other species of mako, the lower anterior teeth exhibit very little distal curvature or labiolingual sinuosity. (Note that in our reconstruction (Figure 29), the undersized first and third anterior teeth were the only ones available to us for these tooth positions). In all the lower teeth, unlike in *I. oxyrinchus*, the tips are straight, which suggests that *I. xiphodon* is more closely related to *I. paucus*. As in the extant makos, the lower teeth of this mako often have compressed crowns; paleontologists often identify these as *I. retroflexa*.

In teeth identified as *Isurus hastalis*, from the late Miocene of Peru, Muizon and De Vries (1985:553–555) noticed that incipient to very fine serrations were present on the cutting edges, the latter type coming from youngest beds of the late Miocene. They interpreted this occurrence as documenting a transition from this species to *Carcharodon carcharias*, which is abundant in the early Pliocene. *Carcharodon carcharias* teeth, however, occur in the middle Miocene of Maryland, and white-shark teeth that may be from ancestors of *C. carcharias* were collected in older Tertiary sediments (Purdy, 1996:69). Does the Peruvian record represent a transition? We think not.

Serrations do occur in different mako species groups. Agassiz (1843) first noticed mako-type teeth with very fine serrations. His syntypes of *Carcharodon escheri* from the middle Miocene of Switzerland, an upper and a lower lateral tooth, compare more favorably with those of *Isurus oxyrinchus* than they do with those of *I. xiphodon*. In labial or lingual view the crown of the lower lateral tooth has a distal curvature, and the coronal tip exhibits a labial recurvature, which is characteristic of the lower laterals of *I. oxyrinchus*. The crown of the upper lateral syntype is characteristic of both *I. oxyrinchus* and *I. paucus*, but the tip of its crown also exhibits a labial recurvature, which is characteristic of the former species. *Carcharodon escheri*, therefore, is not a species intermediate between *I. xiphodon* and *C. carcharias*.

The teeth identified by Leriche (1926:409, pl. 33: figs. 1–8) as *Isurus hastalis escheri* from the early Miocene of Antwerp are teeth of *I. xiphodon* (his figs. 3, 6, 8) and *I. hastalis* (his figs. 1, 2, 4, 5). Figure 28c shows the partially serrated edges of the tooth in Leriche's fig. 5 and another tooth, a second upper anterior, both cataloged as IG 27385. Serrations, therefore, may appear in any of the three mako groups, and they are not useful for establishing phylogenetic relationships.

From the matrix of Gibson's (1967, 1983) zone 4 of the Yorktown Formation (Rushmere Member), one of us (J.H.M.) collected a tooth (USNM 476356) of *I. xiphodon* on which the basal third of the distal cutting edge bears incipient serrations (see Figure 28d).

Although the forms of *Isurus xiphodon* and *Carcharodon carcharias* are similar, differences exist between them to suggest that the former did not give rise to the latter. First, in *I. xiphodon*, the juvenile lower first anterior teeth possess root lobes of equal length (Figure 30), and the angle formed by them is acute; this character is present in seven of the teeth present in the USNM collections. In the same teeth in juvenile *Carcharodon carcharias*, however, the mesial root lobe is longer, and the angle between the root lobes is obtuse (Figure 33a). In juvenile dentitions in the Compagno and Hubbell collections, these two characters are consistent in teeth of *C. carcharias*. Second, unlike *C. carcharias*, which exhibits strong ontogenetic heterodonty, ontogenetic heterodonty was weak or absent in *I. xiphodon*. Third, unlike *Carcharodon*, in the two associated dentitions of *I. xiphodon* available to us, the second lower anterior is the largest tooth in the anterior series. The heights of the anterior teeth are as follows.

	Second lower anterior tooth	Second upper anterior tooth
CMM V-245	6.6 cm	6.3 cm
Hubbell/Peru	6.0 cm	5.8 cm

Finally, in his comparative analysis of mitochondrial DNA sequences of the Lamnidae, Martin (1996:52) estimated that the time of origin of *Carcharodon* occurred perhaps in the Paleocene or early Eocene; this estimate is supported by the fossil evidence (Purdy 1996:69).

In view of the above, we cannot agree with Casier (1960), Cappetta (1987), and Muizon and De Vries (1985) that *Carcharodon carcharias* evolved from *I. hastalis* (herein identified as *I. xiphodon*). We believe that the similar tooth morphologies of these two species are due to parallel evolution rather than to a direct phylogenetic relationship.

Several teeth from Lee Creek Mine exhibit morphological variations worth mentioning. Below the basal margin of the crown on the lingual face, ear-like structures occur on the roots of four upper teeth (USNM 454345, 457245, 457248, 457250) at their mesial and distal extremities (Figure 28e). In two lower teeth the roots appear swollen (USNM 457247, 457249; Figure 31b), and one of these, USNM 457247, has the appearance of buttocks, with a broad transverse groove. Another lower tooth, USNM 457251, the root of which is not swollen, has a deep transverse groove that is offset from the center of the lingual face of the root and which extends to the basal margin of the root (Figure 28f).

Although the teeth of this species have been recovered from the Calvert Formation (middle Miocene), we did not find them in the Pungo River Formation. We suspect that this may be due to the absence or rarity of pinnipeds and cetotheres in the Pungo River sea.

In Figure 31c–e, several examples of pathologic teeth are shown. One of them, USNM 457246, exhibits the same constriction of the crown that Uyeno and Hasegawa (1974:258) used to diagnose a new species, *Carcharodon akitaensis*. Causes of tooth pathologies in mako sharks are not yet known.

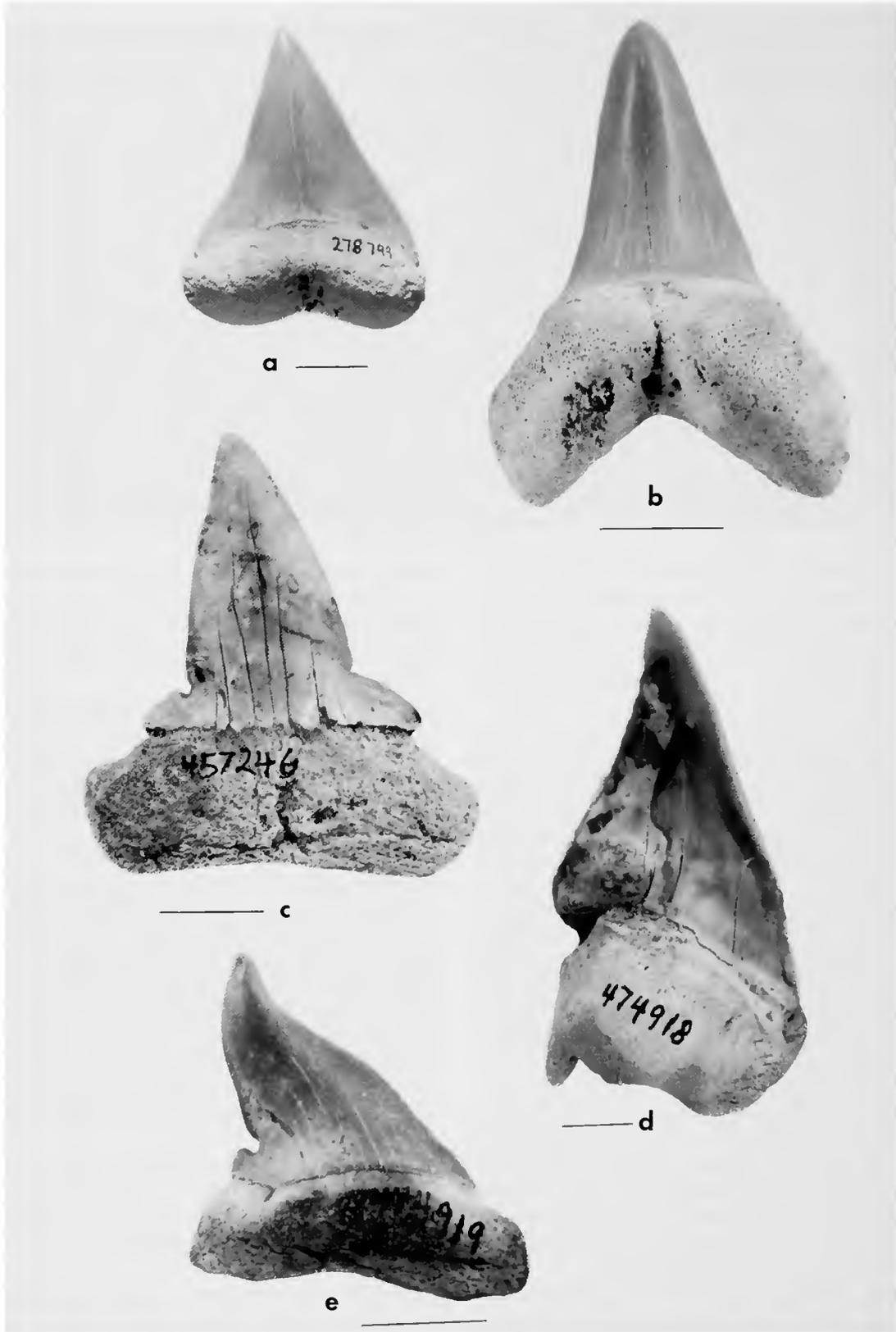


FIGURE 31.—*Isurus xiphodon*: a, USNM 278799, lingual view of right upper lateral tooth with swollen root; b, USNM 457247, lower lateral tooth with swollen root, lingual view; c, USNM 457246, pathologic upper lateral tooth, lingual view; d, USNM 474918, pathologic upper lateral tooth, lingual view; e, USNM 474919, pathologic upper lateral tooth, lingual view. (Scale bars=1.0 cm.)

The anterior teeth of this species range from 2.5 to 8.1 cm in height (mean=4.1 cm, $n=46$) and from 1.7 to 5.5 cm in width (mean=3.2 cm, $n=46$).

We thought we could use the relationship between tooth size and total length in *Carcharodon carcharias* to estimate the size of *I. xiphodon*. In the extant species, however, we discovered that in individuals of nearly the same size, the anterior teeth of *Isurus* are greater in height than those of *Carcharodon*; the teeth of a 3.96 m TL *I. oxyrinchus* (Compagno collection, LJVC-901119) are equivalent in height to those of a 5.2 m TL *Carcharodon carcharias* (Hubbell collection, X11384A). Therefore, on the basis of these data, we estimate that *I. xiphodon* at Lee Creek attained 6 to 7.6 m TL.

In one specimen of *Callophoca obscura* Van Beneden from the Yorktown Formation of Lee Creek Mine, USNM 467592, the distal portion of a right humerus exhibits long, straight, unserrated bite marks (Figure 31b), inflicted most likely by *I. xiphodon*. Could this shark have had a dietary preference for warm-water phocid seals?

Lamna sp.

FIGURE 32

HORIZON.—Yorktown Formation (?unit 1).

REFERRED MATERIAL.—6 rostral nodes, USNM 474994–474999.

REMARKS.—Six rostral nodes collected from the spoil piles at Lee Creek Mine compare favorably with those of *Lamna ditropis* (Matsubara, 1955:115, fig. 15A–C; Compagno, 1988:69, fig. 7.1A) and *L. nasus* (Parker, 1887, pl. 4: fig. 4, pl. 5: fig. 11; Garman, 1913, pl. 62). Concerning the Lee Creek Mine specimens, Compagno (pers. comm., 1982) stated that the calcification of these rostra is more characteristic of *Lamna ditropis* than of *L. nasus*, and that *L. nasus* has rostral cartilage less extremely developed than that of *L. ditropis*. Figure 32a shows the hypercalcified development of the rostrum in *L. ditropis* (USNM 313874); comparable specimens of *L. nasus* were not available to us. Therefore, we are reluctant to make a specific identification of these specimens at this time.

In more than 20 years of collecting at Lee Creek Mine, we have seen no teeth that can be identified definitely as *Lamna*, and in this time only six rostral nodes were found. Thus, this species is one of the rarest to occur here.

In comparison to carcharhiniform calcified rostra (Figure 61a–d), the only other group with tripodal rostra (Compagno, 1988:48), those of *Lamna* have dorsolateral rostral cartilages that, in dorsal view, attach to the anterior rostral node at a very acute angle rather than at a wide angle as in those of the carcharhiniform sharks, and on the dorsal surface of the rostral node, there is no median groove or fossa. These rostral nodes range in size (lateral width) from 1.9 to 3.6 cm.

The extant species of *Lamna* inhabit shallow to epipelagic, cold waters and feed on schooling fishes (Compagno, 1984:247–249).

Genus *Carcharodon* Smith in Müller and Henle, 1838

Carcharocles Jordan and Hannibal, 1923:56.

Procarcharodon Casier, 1960:13.

Palaeocarcharodon Casier, 1960:13.

Megaselachus Glikman, 1964:231.

Until recently, the genus *Carcharodon* included *C. carcharias*, the extant great white shark; *C. orientalis*, a small Paleocene species; and the group of very large white sharks, the giant-toothed species *C. auriculatus*, *C. angustidens*, and *C. megalodon*. The apparent absence of small-toothed species of *Carcharodon* from the end of the Paleocene to the middle Miocene suggested to Casier (1960) that the giant-toothed species and the extant species had separate origins in the Tertiary, and the origin of the extant species from *C. megalodon* did not seem plausible. He concluded that the *C. auriculatus*–*C. megalodon* line was not related to *C. carcharias*; therefore, he erected the genus *Procarcharodon* (type species *Carcharodon angustidens* Agassiz, 1835, Oligocene of Europe) for these large sharks with finely serrated teeth and the genus *Palaeocarcharodon* for the Paleocene species with coarsely serrated teeth. Casier (1960:13) characterized *Procarcharodon* as follows: “Teeth large and broad slightly compressed, with margins generally regularly serrated, sometimes pectinate; with denticles present in the Eocene and the Oligocene, disappearing as a rule in later forms. Root well developed.” His reason, however, for erecting these genera, the absence of small-toothed species in the middle Tertiary, was based on an inadequately sampled and biased fossil record.

In his scenario for the evolution of these forms, Casier considered the two most important characters to be the loss of lateral denticles and the appearance of marginal serrations. He stated (1960:15), “In their evolution one is assisted thus by the appearance, several times, of [these] two dental characters following in succession. . . . 1. In the branch of *Palaeocarcharodon*, where it [the appearance of marginal serrations] does not accompany the disappearance, nor even reduction of denticles; 2. in those of *Procarcharodon*, where it accompanies the loss of denticles, but only secondarily (the appearance of marginal serrations has preceded, in this case, the disappearance of lateral denticles); [and] 3. in the branch of *Carcharodon* s. str., where the appearance of marginal serrations has, on the contrary, been preceded by the loss of lateral denticles (already lost even in the ancestral form: *Oxyrhina hastalis*).”

Casier believed that two species, *Otodus obliquus subserratus* Agassiz and *Isurus hastalis escheri* (Agassiz), confirmed this hypothesis. The teeth of these species exhibit incipient marginal serrations, and both occur prior to the appearance in the fossil record of *C. auriculatus* and *C. carcharias*. Casier surmised, therefore, that these earlier species represented transitional forms, *O. o. subserratus* to *Carcharodon auriculatus* and *I. h. escheri* to *C. carcharias*.

Both of Casier’s characters, however, occur widely in the gauleomorph sharks. Applegate (1967:49) and Compagno (1988:28) reported that serrations have evolved several times in sharks (Paleozoic cladodonts, hexanchoids, squaloids, lam-



FIGURE 32.—*Lamna ditropis*: a, USNM 313874, extant species with calcified rostral node. *Lamna* sp.: b, USNM 474998, rostral node, lateral view; c, same specimen, ventral view. (Scale bars: a=2.0 cm; b,c=1.0 cm.)

noids, and carcharhinoids), and Compagno suggested that they may have evolved at least three times in the Carcharhiniformes. Likewise, among the lamnoid and carcharhinoid sharks, the loss of lateral cusplets represents a general evolutionary trend. Therefore, neither character can be used with confidence for developing phylogenetic scenarios.

In 1969 Janvier and Welcomme reviewed the phylogeny of these sharks. They restricted the definition of *Procarcharodon*, with no documentation for this change, to include only the Eocene *Carcharodon angustidens*, but they placed the Oligocene form of this species back in the genus *Carcharodon*.

Casier's concept of the genus *Procarcharodon* was challenged by Glikman (1964), who found a greater resemblance between *Otodus obliquus* Agassiz and *Carcharodon auriculatus* and *C. angustidens* (teeth with lateral cusplets) than between the latter two species and *C. megalodon*. Glikman (1964:231) proposed to include *C. auriculatus* and *C. angustidens* in *Otodus* and characterized the teeth as "smooth margined in Paleocene forms, sometimes serrate on the upper jaw of early Eocene forms and serrate on both jaws from the middle Eocene onwards. Neck well developed in the anterior and anterolateral teeth only. One pair of large accessory denticles." For teeth without lateral cusplets, he created the genus *Megaselachus*, type species *C. megalodon* Agassiz, characterized by having "all teeth with serrate crowns; neck well developed; [and] most teeth without accessory denticles" (Glikman, 1964:231). Well-developed neck areas also occur in the teeth of *Cretoxrhina mantelli*, *Parotodus benedenii*, *Carcharhinus leucas*, *C. longimanus*, *Carcharodon orientalis*, *C. auriculatus*, *C. angustidens*, *C. subauriculatus*, and, in a lesser degree of development, in the juvenile teeth of *C. carcharias* (see below). Accessory denticles occur in the juvenile teeth of *C. megalodon* and *C. carcharias* and may be retained in the teeth of adults. Glikman's characters are not useful for establishing the generic identity of these sharks.

We believe Glikman's inclusion of *Carcharodon auriculatus* (sensu lato) and *C. angustidens* in *Otodus* is unjustified. From a large suite of *Otodus obliquus* teeth from Morocco, one of us (R.W.P.) reconstructed a dentition of this shark and identified three upper anterior tooth positions, as opposed to two in *Carcharodon*. Also, unlike *Carcharodon* (including the giant-toothed species), the third lower anterior tooth points distally. A cast of a newly discovered associated dentition of this shark (Hubbell collection, uncataloged) from the Moroccan Eocene confirmed the presence of the first upper anterior tooth. In this dentition, one of us (R.W.P.) identified an intermediate tooth that points distally. This orientation is opposite to that found in *Carcharodon*, including the giant-toothed line. Rather than decreasing perceptibly in size, step fashion, as in *Carcharodon*, the second through sixth upper lateral teeth have similar heights, as they do in *Lamna*. Finally, the second lower anterior tooth is the largest tooth in the dentition. These characters of *Otodus* suggest that there is a greater morphological difference between teeth of *Otodus* and

Carcharodon than has been assumed by previous workers, and that *Otodus* is not the ancestor of *Carcharodon*.

Jordan and Hannibal (1923:56) created the genus *Carcharocles* with *Carcharodon auriculatus* (Blainville) as the type species, characterizing it as follows: "[Teeth] similar to *Carcharodon*, but with a strong denticle on each side on the base of the tooth. Teeth narrower and more erect than in *Carcharodon*, their edges finely serrated." These characters also occur in an associated dentition that we identify as *Carcharodon subauriculatus* and in some juvenile teeth of *C. megalodon*. Until recently, Jordan and Hannibal's genus was largely assumed to be a junior synonym of *Carcharodon*.

Finally, Cappetta (1987) synonymized *Procarcharodon* Casier (1960) and *Megaselachus* Glikman (1964) with *Carcharocles* Jordan and Hannibal (1923), which of these three is the senior name.

In two sets of associated teeth from the Rupelian of Belgium, Siverson (1989) observed two additional characters for separating *Carcharocles* from *Carcharodon*: the absence of dignathic heterodonty and the absence of an intermediate tooth. Dignathic heterodonty, however, is present in *Carcharodon auriculatus* (see Dockery and Manning, 1986, pls. 2, 3), and it is very marked in the associated tooth sets from Lee Creek Mine (see below), which are from young individuals of *Carcharodon subauriculatus*. Like *C. carcharias*, dignathic heterodonty in the giant-toothed line becomes less marked in older individuals.

In extant *Carcharodon* the intermediate teeth are highly variable in size and morphology (morphological variation is particularly evident in juveniles); they can range in height from about one-half to almost equal the height of the teeth in the adjacent tooth positions. Agassiz (1835, pl. F, 1843:91) and Leriche (1910:287, footnote 3, fig. 89) figured and described dentitions of *C. carcharias* with intermediate teeth the same size or almost the same size as the teeth of adjacent files. The form of the crown may range from being like that of a lower lateral tooth to like that of a broad, upper anterior tooth. Two characters, however, are consistent: the distal cutting edge is longer than the mesial one, causing the tip of the tooth to be erect or to point mesially rather than distally as in the lateral teeth, and the tooth has a strong labial curvature, stronger than any other tooth in the jaw. Uyeno et al.'s (1989, fig. 4) associated dentition shows the crown orientations of the teeth from the upper right jaw. Their tooth number three, which also is the position in the jaw of the intermediate tooth, has a tip that bends mesially. In their pl. 4, it also has a strong labial curvature. This tooth is undoubtedly an intermediate tooth (Gottfried et al., 1996, independently identified this character of the intermediate tooth as a synapomorphy for the genus *Carcharodon*). Also, in the associated tooth sets of *C. subauriculatus*, based on the above characters, we identified teeth that we are certain are intermediates. In detached tooth sets, these teeth may be mistaken for lower lateral teeth. In the Belgian specimens, the intermediate teeth may be absent or misidentified.

Several researchers have expressed opinions contrary to those of the above workers, synonymizing the genera of Casier, Glikman, Jordan, and Hannibal with *Carcharodon*. Keyes (1972:239–240) disputed Casier's erection of *Procarcharodon* for the large-toothed species of these sharks and the derivation of *C. carcharias* from *Isurus hastalis*, but he did not document his position.

Welton and Zinsmeister (1980:7) also questioned Casier's interpretations: "We do not find Casier's interpretations convincing, and we agree with Keyes (1972) that the similarities between *I. hastalis* and *Carcharodon* (in the restricted sense of Casier 1960) might be convergence rather than phylogenetic relationship. The phylogeny of *Carcharodon* is best interpreted through detailed analysis of tooth morphology and dental formulae using specimens collected only under conditions of demonstrable superpositional control. A detailed study of ontogenetic heterodonty in the living *C. carcharias* and *Isurus* spp. would be extremely useful in resolving these problems."

In 1983 Bendix-Almgreen stated that the structure of the coronoin fibrous architecture of *Carcharodon carcharias* and *C. megalodon* was too similar to be of divergent origins, and on the basis of this character, he synonymized *Procarcharodon* with *Carcharodon*. He did not, however, compare the coronoin of these sharks with that in the teeth of other lamnoids, and the usefulness of the coronoin fibrous architecture as a taxonomic tool for neoselachians has yet to be demonstrated.

Uyeno and Sakamoto (1984:52) noted the similarity between the juvenile teeth, particularly the serrations, of *Carcharodon megalodon* from the middle Miocene sediments in the Chichibu Basin, Japan, and those of *C. carcharias*. Although they did not elaborate on them, they found that the characters used to identify *Procarcharodon* also occur in *Carcharodon carcharias*. They reiterated Welton and Zinsmeister's (1980) call for an extensive study of recent and fossil *Carcharodon* teeth to help to resolve the problem.

In their report on *Carcharodon auriculatus*, Dockery and Manning (1986:16) stated that they did not use *Procarcharodon* "because it appears to have been erected on the basis of the shared primitive characters of its component species," adding that "despite its huge size, considered a unique derived character here, *C. megalodon* shares with *C. carcharias* a reduction of the accessory cusps that are so prominent in *C. auriculatus*." But, the loss of lateral cusplets has occurred in other lamniform and carcharhiniform sharks earlier in their histories; therefore, Dockery and Manning's shared character for these two species, the loss of lateral cusplets, cannot be considered to be unique to them.

Uyeno et al. (1989:83) reported on an associated dentition of *Carcharodon megalodon*, consisting principally of upper teeth, from the middle Miocene sediments of the Saitama Prefecture, Japan, and remarked, "In examining the teeth rows contained in the male great white shark (full length 3.9 meters), it can be seen that the teeth closely resemble *C. megalodon*." They did not illustrate, however, the teeth of the extant great white shark.

The foregoing shows the diversity of opinion that exists about the taxonomy of the extinct great white sharks. Of these opinions, we agree with Welton and Zinsmeister (1980) about the need for an extensive study of the dentitions of the living and extinct species. The abundance of *Carcharodon megalodon* at the Lee Creek Mine and Gordon Hubbell's excellent private collection of *C. carcharias* dentitions, including as well those of other lamnids, facilitated our study of this problem. Hubbell's collection and the collections of the CAS and the NMNH permitted us to study dental variation in 35 complete dentitions, ranging from neonates to very large adults, and in 28 partial dentitions consisting of anterior teeth. Although we would be more confident with larger samples of the living and fossil species, we believe that the specimens presently available to us in these collections provide sufficient evidence to suggest that the genera of Casier, Glikman, and Jordan and Hannibal are indeed junior synonyms of *Carcharodon*.

In the fossil and the extant species of *Carcharodon*, the juvenile and adult teeth of both lines share similarities suggesting that they belong to a single genus. First, unlike other galeomorph sharks, in both lines of *Carcharodon* the cutting edges of juvenile teeth are coarsely serrated, and they become finer in the larger replacement teeth. Second, unlike *Isurus* (including *I. xiphodon*), in a juvenile *C. carcharias* (CAS 40905), as in *C. megalodon*, the upper anterior teeth have on their lingual crown feet a chevron-shaped neck area (Figure 33a). This character, which also was observed in juvenile dentitions of *C. carcharias* in the Hubbell collection, is lost in later generations of teeth. Finally, the juvenile teeth of *C. carcharias*, with their coarse serrations and lateral cusplets, resemble closely those of *C. orientalis* (Figure 33b). These similarities are not found in *Isurus* and *Otodus* (see above).

In addition to these similarities, these two lines of *Carcharodon* share three derived characters that are not found in any other lamnids, including two associated dentitions of *Isurus xiphodon*. (1) The mesial cutting edge of the first tooth from the symphysis in the upper jaw, a second upper anterior, rather than being convex for 50% or more of its length, is straight or nearly so from the lateral extremity of the crown foot to the apex of the crown or to within one-eighth of its total length of the apex (it may be convex in this area). This straightness is unique to *Carcharodon*. (2) This second upper anterior tooth, rather than the second lower anterior, as in other lamnids, is the largest tooth in the dentition. (3) The intermediate tooth has a distal cutting edge that is longer than the mesial cutting edge, causing the tip to be erect or to point mesially rather than pointing distally. Thus, the tooth has a reversed appearance (Gottfried et al., 1996) that is unlike all other lamnoid intermediate teeth, which have longer mesial cutting edges and distally pointing crowns. These three characters were present in the associated fossil dentitions with complete sets of anterior teeth available to us, one of *C. subauriculatus* and two of *C. megalodon*, and in Uyeno et al.'s (1989, fig. 4) associated dentition of *C. megalodon*.

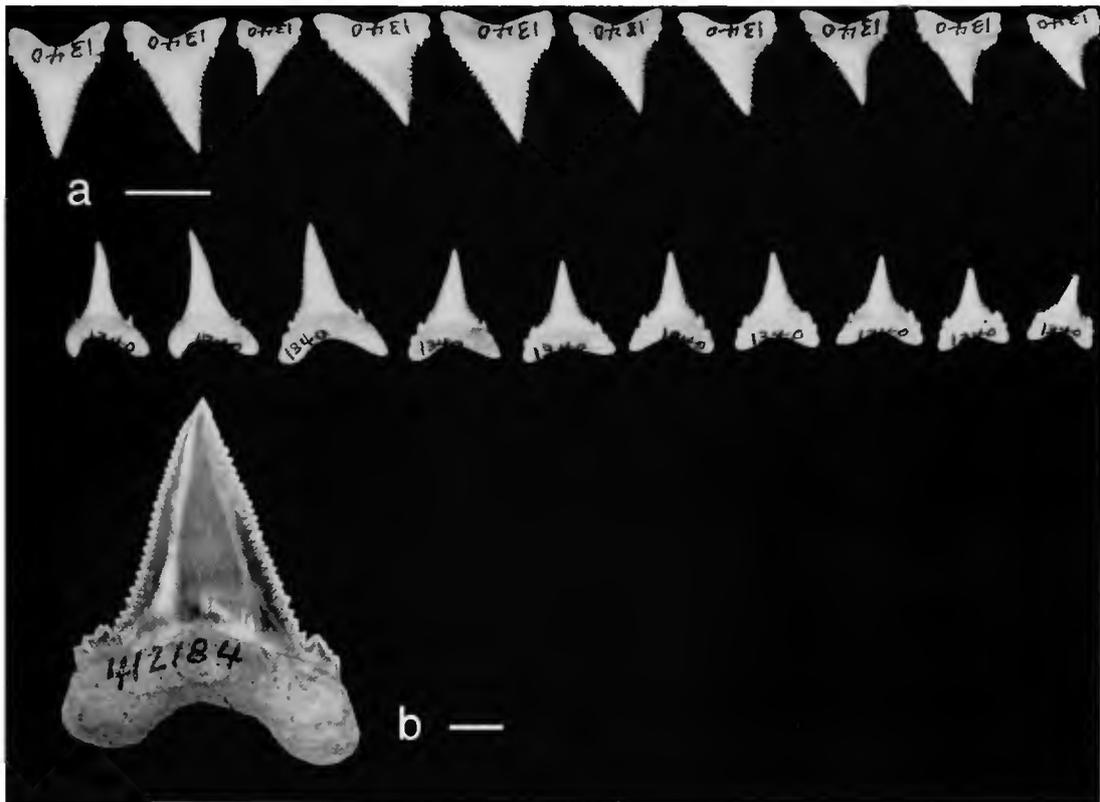


FIGURE 33.—*Carcharodon carcharias*: a, CAS 40905, dentition of juvenile. *Carcharodon orientalis*: b, USNM 412184, Aquia Formation, Prince Georges County, Maryland, upper anterior tooth, lingual view. (Scale bars=1.0 cm.)

In view of the above, *C. megalodon* and *C. carcharias* and their respective Tertiary predecessors, including *C. orientalis*, share more morphologic characters in common with one another than with any other lamnoid shark. Consequently, we believe that *Palaeocarcharodon*, *Procarcharodon*, *Megaselachus*, and *Carcharocles* are junior synonyms of *Carcharodon*.

The first upper anterior tooth, present in *Carcharias taurus*, is absent from the associated dentitions of *Carcharodon subauriculatus* and *C. megalodon* from Lee Creek Mine, the associated dentition of *C. megalodon* reported on by Uyeno et al. (1989), and another of this species, from the Bone Valley Formation, in the Hubbell collection.

In both the extant and the fossil species, a wide range of dental variation exists. In the anterior teeth, the first upper tooth (the second anterior) is predominantly symmetrical, but those of juveniles and sometimes those of adults are often slightly asymmetrical, and in the extant species, this asymmetry existed in 22 (35%) of the 63 dentitions that we examined². These asymmetrical teeth are prevalent in white sharks with narrow

teeth. Because these asymmetrical teeth exhibited morphological characters found in the second upper anterior teeth of *Carcharias taurus*, we disagree with Applegate and Espinosa-Arribarrena's (1996) assertion that this tooth is the first and not the second tooth position, which they stated is missing in *Carcharodon*. Our position that the first upper anterior tooth is actually a second upper anterior agrees with Compagno's (1990a) conclusion.

The intermediate teeth of both the giant-toothed and small-toothed *Carcharodon* may have slightly concave or straight distal cutting edges, with the mesial ones being convex or straight apically and concave or straight basally. In individuals of great size, the cutting edges may become nearly equal in length.

In the extant species, tooth width varies widely. For example, six second upper anterior teeth measuring 5.8 cm in height had widths ranging from 3.8 to 5.0 cm, and a 6.1 cm tooth had a width of 3.6 cm. These variations in width occur in both males and females, and they are present in the teeth of *Carcharodon megalodon*.

The number of central foramina in the teeth of *C. subauriculatus* and *C. megalodon* varies from one large foramen to four smaller foramina.

²Purdy (1996:69) identified the symmetry of this tooth as a synapomorphy, but in view of its variability in the living species, we think this is a weak character.

Compagno (1984:238) characterized the teeth of this genus as follows: "Flat, triangular, with broad, serrated, nearly straight cusps, and lateral cusplets only in juveniles below 2 m long (which may have at least some smooth-edged or partially smooth); intermediate teeth in upper jaw very large, over half height of upper anteriors." We would add that in early Tertiary species, lateral cusplets persist into adulthood.

In the Lee Creek Mine fauna we recognize three species of *Carcharodon*: *C. subauriculatus* from the Pungo River Formation, *C. megalodon* from the Yorktown Formation, and *C. carcharias* from the Yorktown and James City formations.

Carcharodon subauriculatus Agassiz, 1839

FIGURES 34–36

?*Carcharodon polygyrus* Agassiz, 1838, pl. 30: figs. 9–12 [Miocene, Switzerland]; 1843:253.

Carcharodon auriculatus de Blainville.—Ameghino, 1906:181–182, fig. 48 [Miocene, Argentina].

?*Carcharodon chubutensis* Ameghino, 1906:183, fig. 49 [Miocene, Argentina].

Carcharodon megalodon (Agassiz).—Leriche, 1926:412–422, pls. 35, 36 [Miocene, Belgium].

Carcharodon megalodon var. *chubutensis* Ameghino.—Leriche, 1927: 80, pl. 12, pl. 13: figs. 1–3 [Miocene, Switzerland].

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—2 associated dentitions, USNM 299832, 411881; several hundred teeth, USNM 244350, 256331, 256333, 256334, 280557, 280564, 282356, 282457, 295331, 295339, 298362, 336370, 339920, 348132, 348185, 348186, 348201, 348206, 348210, 348228, 348230, 348237, 356965, 356968–356971, 356974.

REMARKS.—We distinguished this species from *Carcharodon megalodon* by the presence of lateral cusplets on the anterior teeth of subadults and usually adults; these cusplets are not

separated from the crown by a deep notch as they are in *C. angustidens* and *C. auriculatus*. Juvenile, anterior teeth of *C. megalodon* may possess well-defined lateral cusplets.

Agassiz based *Carcharodon subauriculatus* on a suite of three anterior teeth, two of which (Agassiz, 1839, pl. 30a: figs. 11, 12) bear lateral cusplets. In the specimen in his fig. 11, the notches that separate the lateral cusplets from the crown have all but disappeared, and in the specimen in his fig. 12, a shallow notch separates the mesial lateral cusplet from the crown; the distal portion of the tooth is not shown. Agassiz described three other species to which the Pungo River teeth might be referred: *C. heterodon*, *C. polygyrus*, and *C. megalotis*. These species, however, are based on lateral teeth, which could belong to either *C. subauriculatus* or juvenile *C. megalodon*.

Leriche (1926:420) synonymized the teeth of *C. subauriculatus* with *C. megalodon*, and he assigned the early Miocene teeth with lateral cusplets to *C. chubutensis* Ameghino, which Ameghino (1906, fig. 49) based on a lateral tooth. Ameghino (1906, fig. 48) identified an anterior tooth as *C. auriculatus*, which Leriche (1926:420) synonymized with *C. chubutensis*. Both of these, however, are referable to *C. subauriculatus*, the senior name.

Peter J. Harmatuk recovered two sets of what appear to be associated teeth of this species, USNM 299832 (27 teeth) and USNM 411881 (106 teeth), concentrated in two separate small areas on the spoil piles. Both sets include the enameloid shells of partially formed teeth, and both sets possess morphological peculiarities that suggest they represent associated dentitions. All of the teeth in USNM 299832 possess small "denticles," composed of osteodentine rather than the orthodentine and enameloid of cusplets, on the lateral extremities of the roots at the base of the crown. In USNM 411881, on the

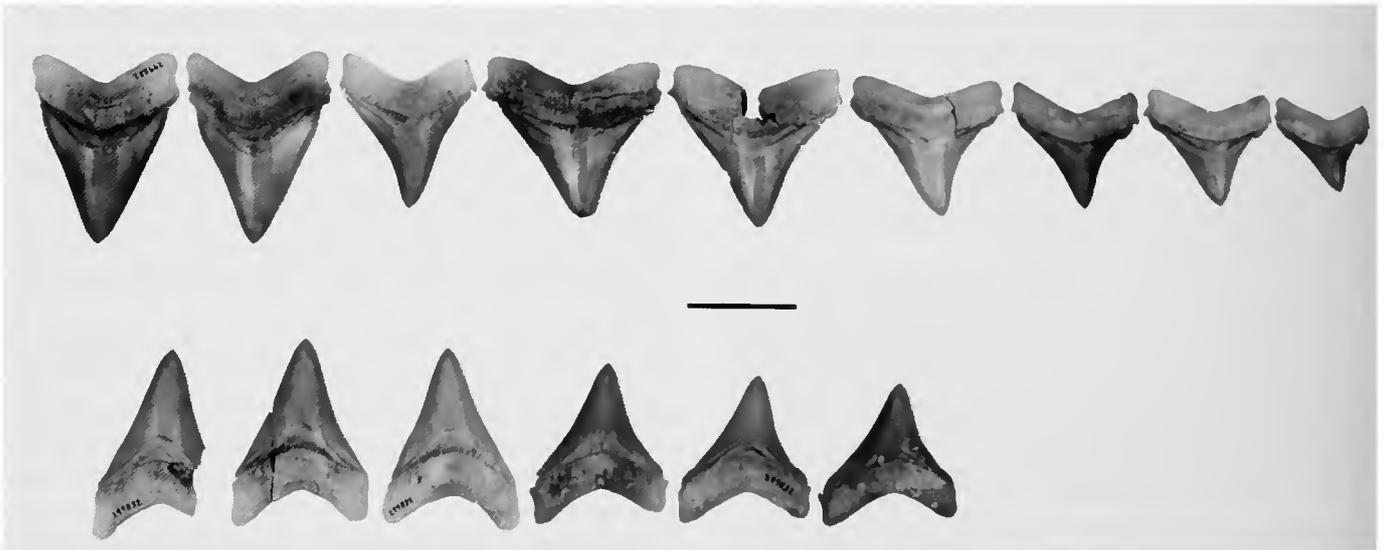


FIGURE 34.—*Carcharodon subauriculatus*, USNM 299832, Pungo River Formation, associated dentition from the right jaws, lingual view. (Scale bar=1.0 cm.)

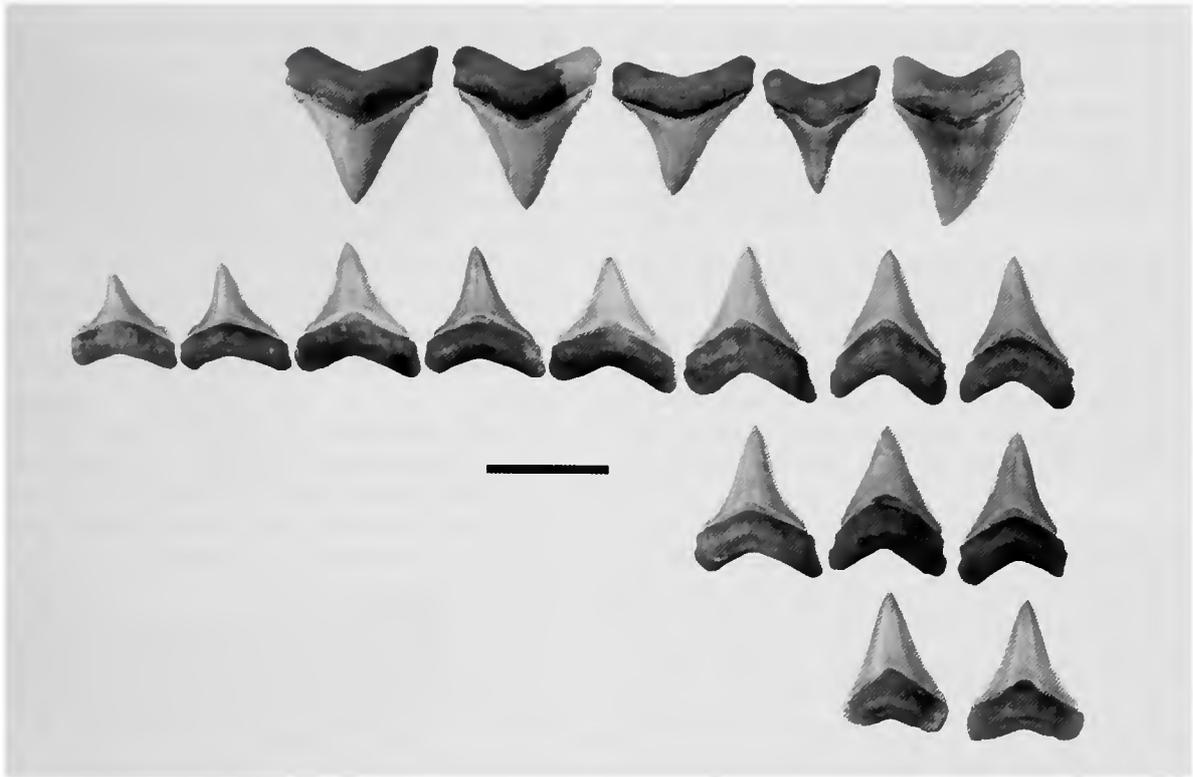


FIGURE 35.—*Carcharodon subauriculatus*, USNM 411881, Pungo River Formation, associated dentition from the left jaws, lingual view. (Scale bar=1.0 cm.)

lingual face of the root lobes, a small slit or slits occur in exactly the same positions on each tooth. Some teeth possess a slit on one lobe only, which may be either the mesial or distal lobe. In both sets these teeth fit the sizes anticipated for the different tooth positions in a dentition of *Carcharodon*. These features suggest strongly to us that these tooth sets represent associated dentitions.

Neither tooth set represents a complete dentition. In USNM 299832 (Figure 34), which consists of teeth from mainly the right side, the second upper anterior tooth, the upper intermediate tooth, and the lower right anterior teeth are present. From the upper jaws, the right second through fifth lateral teeth are present; from the lower jaws, the first through third lateral teeth from both sides and the left fourth through fifth lateral teeth are present.

In the second tooth set, USNM 411881 (Figure 35), the dentition from the left jaw is nearly complete; only the second upper anterior tooth and one upper and two lower posterior teeth are missing. From the right jaw, the dentition includes most of the upper lateral teeth, several lower lateral teeth, and an incomplete first anterior tooth.

These tooth sets furnished us with information not available from isolated teeth. Like *C. carcharias*, the height of the second upper anterior tooth in USNM 299832 (8.9 cm) is greater than the height of the second lower anterior tooth (8.5 cm). In USNM 411881, which is from a slightly smaller individual

(height of second lower anterior=6.8 cm), the second upper anterior tooth is missing; therefore, we were unable to make the same comparison for this specimen. Another similarity with *C. carcharias* is the nearly symmetrical second lower anterior tooth in each tooth set (Figures 34, 35).

In both tooth sets dignathic heterodonty is present. The upper teeth are broader than the lowers, the lower anterior teeth and the anteriormost lateral teeth have better-developed toruses than their upper-jaw counterparts, and the cutting edges of the lower teeth are more concave than those of the upper teeth.

In both tooth sets, the third lower anterior tooth is neither reduced in size nor is it the shape of a lateral. In an associated dentition of *C. megalodon* from the Bone Valley Formation in the Hubbell collection, this condition also exists. Uyeno et al. (1989) noted, however, that the third lower anterior tooth in their associated dentition of *C. megalodon* from Japan was almost the same size as the first lateral tooth, both teeth being only slightly smaller than the lower anterior teeth. At present, due to the very small number of associated tooth sets for these sharks, we cannot determine if the lack of lateralization of the third lower anterior tooth is a retention of a primitive character or a variable character in these sharks.

The second upper anterior tooth (present only in USNM 299832), which is the first tooth from the symphysis, is slightly asymmetrical. Its mesial cutting edge is nearly straight,

whereas the distal cutting edge is slightly concave. In this specimen the second and third upper anteriors are very similar, having only minor differences in tooth height and width, crown width, shape of the cutting edges, and shape of the root. In USNM 411881 the crown is strongly inclined distally; its mesial cutting edge is strongly convex, and the distal one is concave.

The intermediate teeth of both dentitions were easily identified by their strong labial curvature. With concave cutting edges, both of these intermediate teeth resemble lower lateral teeth, but their crowns, which point mesially, are wider than those of the lower laterals of their respective dentitions. In both intermediate teeth the lateral cusplets are almost lost, and on the lingual face of the root, they have three central foramina.

The upper lateral teeth of USNM 299832 (five present) are broader than those of USNM 411881 (eight present) and have nearly straight cutting edges, whereas the upper lateral teeth of USNM 411881 have concave cutting edges. In USNM 299832 the crowns of the upper lateral teeth are more erect than are those of USNM 411881. The first upper lateral tooth has a stronger labial curvature than in the other upper lateral teeth. This tooth is distally inclined, and its mesial cutting edge is straight, whereas the distal one is strongly concave. Its mesial root lobe is usually more tapered than its distal one. Of the upper lateral teeth, the second tooth usually has the greatest height in this series. Its crown is broader than that of the first lateral tooth, and the cutting edges are slightly concave to nearly straight, giving the tooth a symmetrical appearance. The width of this tooth is usually 85% to 95% of its height. In the remaining lateral teeth, the crowns diminish perceptibly in size and have a slight distal inclination.

The three lower anterior teeth have erect crowns. The mesial and distal cutting edges are slightly concave in the first and second teeth and are more so in the third, giving the crown of this tooth a narrower appearance than those of the first two. In USNM 299832 the distal root lobes of these anterior teeth are more rounded than the mesial lobes are, but in USNM 411881 the mesial and distal root lobes of the second tooth both are rounded, and in the third tooth, the mesial root lobe is tapered. In USNM 411881, the crown of this last tooth points straight

up, but in USNM 299832, it has a slight mesial bend. On the lingual face, in the central portion of the root, the torus is prominent in USNM 299832 and forms a ridge concentric to the basal edge in USNM 411881.

In both dentitions the width of the first lower lateral tooth slightly exceeds its height (Table 3), but in the Japanese (Uyeno et al., 1989), Peruvian, and Bone Valley associated dentitions, these teeth are higher than they are wide. Too few associated dentitions of these sharks are available to show whether or not this difference between the Lee Creek Mine teeth and those in the Japanese, Peruvian, and Bone Valley dentitions is ontogenetic.

In both sets the lateral cusplets are absent or are the least developed in the anterior teeth and are the most developed in the more posterior lateral teeth. In USNM 411881 the three teeth in upper lateral file number three show the transition from well-developed lateral cusplets to almost none (Figure 36), which indicates that they are lost quickly.

Among the various fossil faunas with *Carcharodon megalodon*-type teeth, teeth with lateral cusplets occur commonly in the Burdigalian, Aquitanian, and perhaps the Chattian stages. These teeth also are common in the Fairhaven Member of the Calvert Formation in Maryland and at the base of the Calvert Formation in Virginia. In the Chesapeake Group, the percentage of such teeth drops sharply above Zone 4 (Shattuck, 1904) of the Calvert Formation.

During the Chattian, *Carcharodon subauriculatus* may have had a nursery area in what is now South Carolina (Purdy, 1996, and in prep.). In a stratigraphically controlled sample recovered from the Chandler Bridge Formation (Sanders, 1980), juvenile teeth ($n=98$) of this shark are very common, with the anterior teeth ranging from 4.4 to 5.7 cm in height. Only five teeth from very large adults were recovered. Of these specimens, a first lower lateral tooth, the most anterior tooth in this size range found, measured 9.5 cm in height. This tooth is equivalent in size to those from the Yorktown Formation. These large teeth may be from females that came to the Chandler Bridge area, an area of subtropical waters during the Chattian, to bear their young.

We have not seen any large teeth from the Pungo River Formation. Anterior teeth from this area range in height from 1.8

TABLE 3.—Measurements (in cm) of associated dentitions of *Carcharodon subauriculatus* from Lee Creek Mine. (A2–A3=upper anterior teeth, I=intermediate tooth, L1–L9=upper lateral teeth, a1–a3=lower anterior teeth, I1–I9=lower lateral teeth, B=incomplete tooth, M=tooth missing from dentition.)

Specimen	Upper dentition												Lower dentition												
	A2	A3	I	L1	L2	L3	L4	L5	L6	L7	L8	L9	a1	a2	a3	I1	I2	I3	I4	I5	I6	I7	I8	I9	
USNM 299832																									
height	8.9	8.8	7.1	8.5	8.3	7.3	6.2	5.2	M	M	M	M	B	8.5	8.2	6.1	6.6	M	M	M	M	M	M	M	M
width	6.9	6.8	6.4	7.6	7.9	7.9	7.0	4.7	–	–	–	–	–	6.5	6.3	6.2	6.0	–	–	–	–	–	–	–	–
USNM 411881																									
height	M	7.1	6.5	6.7	6.6	5.9	5.5	4.6	4.0	3.2	2.2	M	6.2	6.8	6.4	5.3	5.7	5.4	4.6	M	M	M	M	M	M
width	–	5.6	6.3	6.3	6.4	6.2	5.8	5.1	4.5	3.7	2.9	–	4.9	5.0	5.3	5.4	5.4	5.2	4.7	–	–	–	–	–	–

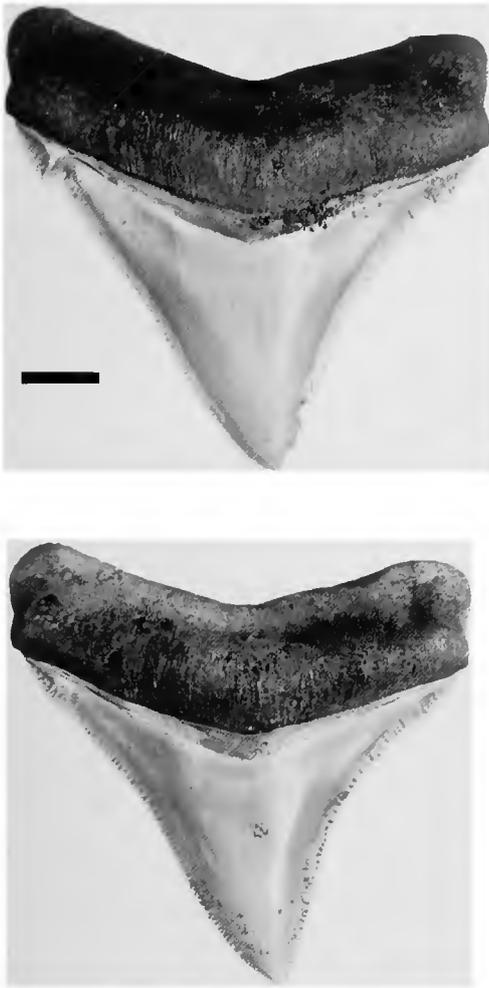


FIGURE 36.—*Carcharodon subauriculatus*, USNM 411881, lingual view of third upper lateral file showing loss of lateral cusplets. (Scale bar=1.0 cm.)

to 8.4 cm (mean=4.6 cm, $n=56$) and probably came from individuals between 3 and 10 m in total length.

In the extant *Carcharodon carcharias*, Klimley (1985) observed along the western coast of North America that adult females give birth to pups south of Point Conception, California, and then move north to their feeding areas where there is an abundance of pinnipeds. The young white sharks, which feed principally on fish, move northward as they grow larger. During the Neogene along the Atlantic coast of North America, *Carcharodon subauriculatus* may have pupped in the warm waters of the area of present-day Charleston, South Carolina, and as the juveniles increased in size, they may have moved northward to principal feeding areas where larger prey were probably more abundant. The distribution of *Carcharodon subauriculatus* in the Neogene of the Atlantic Coastal Plain, then, could have been governed by their size and the availability of prey. This might explain the absence of large *C. subauriculatus* in the Pungo River Formation.

Carcharodon megalodon (Agassiz, 1835)

FIGURES 37–42

Carcharodon akitaensis Uyeno and Hasegawa, 1974:257–260, figs. 1–3 [Miocene, Japan].

HORIZON.—Upper Pungo River Formation (units 4–6)?; Yorktown Formation (unit 1).

REFERRED MATERIAL.—1 associated dentition, NCSM 13073; several hundred isolated teeth, USNM 182108, 214947, 244350, 256331, 256333, 256334, 278515, 279338, 279353, 280509, 280557, 280564, 281392, 289087, 295331, 295339, 298362, 298368, 299766, 336257, 336370, 339917, 348169, 348178, 348247, 348265, 348338, 348344, 348366, 348375, 350923, 350924, 355736, 355762, 355766, 355822, 355884, 355888, 356965, 356968–356975, 356981–357010, 445500, 474915, 474916, 475360, 476358.

REMARKS.—We distinguish these teeth from those of *Carcharodon subauriculatus* by the lack of lateral cusplets on sub-adult and adult teeth and often on the anterior teeth of juveniles.

Agassiz (1835, pl. 29: figs. 1–6, 1843:247–248) founded this species on six teeth, three of which were from Malta; the provenance of the others is unknown. He characterized the species as follows: “Its general form is perceptibly equilateral.... The marginal serrations are uniform on each edge of the tooth. The enamel overlaps scarcely the root at the limit of the latter; it is indented at an almost right angle on the internal face (fig. 2), while it is simply concave on the external face (fig. 3). The thickness of the tooth is not very considerable (fig. 2a); the internal face is convex; the external face on the other hand is flat even a little concave. The root is very heavy; it forms alone more than a third of the total height of the tooth; in the other specimens these proportions are able to vary according to their position in the jaw” (Agassiz, 1843:247–248; translated from French by R.W.P.).

Agassiz’s (1835, pl. 29: figs. 2, 3) type specimen is a second upper anterior tooth preserved in the Staatliches Museum für Naturkunde in Karlsruhe, Germany (TE-PLI 18) (Figure 39d).

Teeth satisfying this description occur in the upper layers of the Pungo River Formation, but they may be examples of adult *C. subauriculatus* that lack lateral cusplets. Some of the dark, worn teeth from the basal Yorktown Formation may be redeposited from the Pungo River Formation or may be relicts from the hiatus. Other teeth from the lower Yorktown layer are beautifully preserved and are relatively light in color, and most certainly they are contemporaneous. These large teeth are the most sought-after fossils in the Lee Creek Mine, and collecting experience indicates that they are found only in the lower portion of the Yorktown Formation.

The associated dentition (NCSM 13073) consists of the second and third anterior teeth from both upper jaws, a right intermediate tooth, the first through fourth lateral teeth from both upper jaws (Figure 37), and three incomplete lower lateral teeth. Another tooth under this number (13073.23) is a third anterior tooth from a smaller individual.

The second anterior teeth (first tooth position) are nearly symmetrical, the right more so than the left. Their cutting edges are convex, and there are four central foramina on the lingual faces of the roots.

The third anterior teeth are asymmetrical; their mesial cutting edges are nearly straight but are convex apically, and their distal cutting edges are concave basally and convex apically. The crowns of these teeth have a labial curvature. There are three central foramina on the lingual faces of the roots. The mesial root lobes are rounded and are longer than the more lobate distal lobe.

The intermediate tooth has the proportions (height/width) of an intermediate tooth rather than those of a lateral tooth; its crown bends labially, and its tip points mesially, but only slightly. The mesial cutting edge is nearly straight, whereas the distal one is concave. Four central foramina are present on the

lingual face of the root. The mesial root is rounded, whereas the distal root is somewhat lobate.

The crowns of the lateral teeth are mainly asymmetrical with the exception of the tooth from the second position. On the lingual faces of the root lobes of these teeth, two to three central foramina are present. The mesial root lobes are usually rounded, whereas the distal ones are lobate.

The first lateral tooth has a nearly straight mesial cutting edge and a concave distal one. Its crown has a strong labial curvature.

The second lateral teeth, which are the largest of the lateral series, have crowns that are nearly symmetrical, and the teeth as a whole are equilateral. The crown has a slight labial curvature.

The third and fourth lateral teeth are similar to the first in general form.

Only incomplete lower lateral teeth were present in this dentition, and these had narrower crowns than did their upper

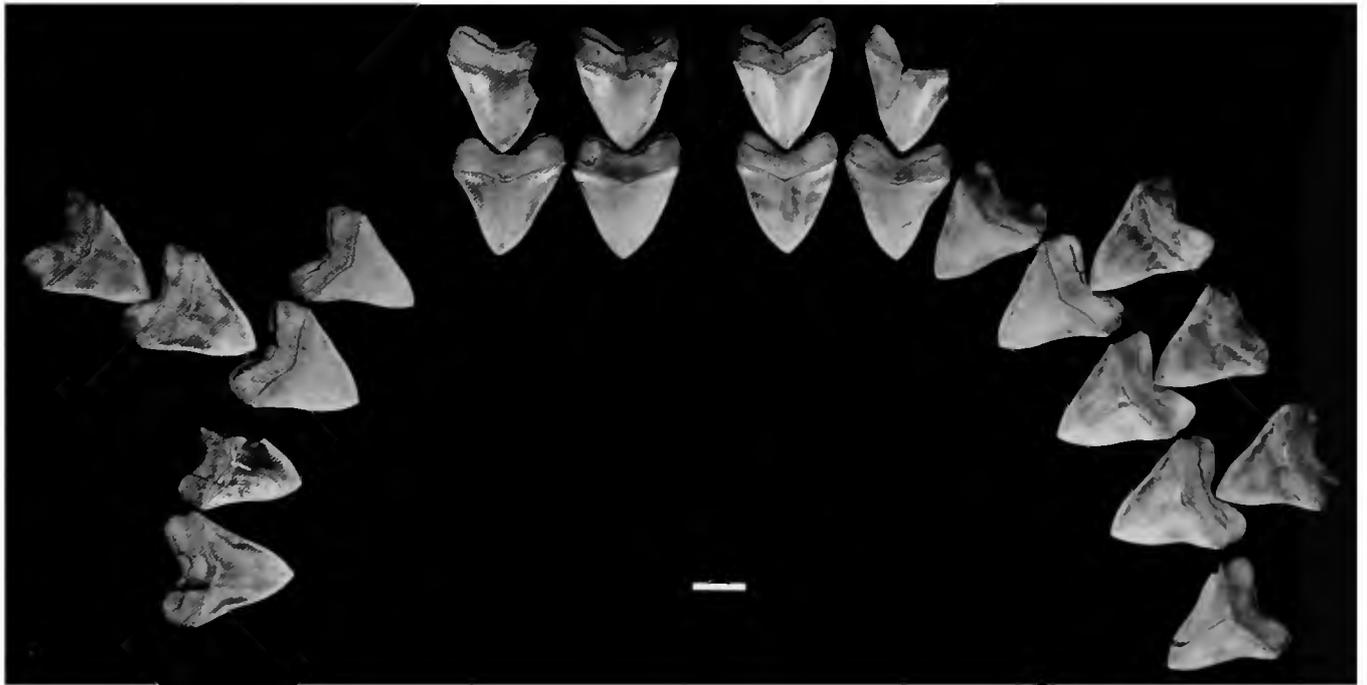


FIGURE 37.—*Carcharodon megalodon*, NCSM 13073, associated upper dentition, lingual view. (Scale bar=5.0 cm.)



FIGURE 38.—*Carcharodon megalodon*, composite lower dentition, lingual view. (Scale bar=5.0 cm.)



FIGURE 39.—*Carcharodon megalodon*: a, USNM 445500, heart-shaped fourth or fifth upper lateral tooth, lingual view; b, USNM 474915, same type of tooth, lingual view; c, USNM 355822, third upper anterior tooth with noticeable torus, basal view; d, USNM 476358, cast of holotype (Staatliches Museum TE-PLI 18), lingual view. (Scale bars=1.0 cm.)

counterparts. Their cutting edges were concave, and their roots were incomplete. These teeth were not measured.

As points of reference, we used some 40 dentitions of the living species, mostly uncataloged, in the USNM, CAS, and Hubbell collections; the two associated dentitions of *C. subauriculatus* (USNM 299832, 411881); and the associated dentition of *C. megalodon* from the Bone Valley Formation (Hubbell collection) to identify the lower teeth (Figure 38) among the isolated Lee Creek Mine teeth. The crowns of all lower teeth bend lingually, and in most lower teeth the mesial root lobe is pointed, and the distal one is lobate. The prominence of the root torus, which may be round or ridge-like, decreases progressively in more distal tooth positions.

The first anterior teeth are symmetrical, with concave to nearly straight cutting edges. The root lobes form a right or slightly obtuse angle.

The second anterior teeth are slightly asymmetrical, pointing distally, with concave cutting edges. The angle of the root lobes is slightly broader than that of the first anterior tooth.

In the third anterior tooth, the tip of the crown points mesially. Near the apex, the mesial cutting edge is more convex than the distal one. Below this point the cutting edges are straight to slightly concave. The angle of the root lobes is broader than that of the second anterior teeth.

Among the lateral teeth, the first or second is the largest; the remaining teeth decrease in size and become more asymmetri-

cal toward the angle of the jaws. The distal cutting edges are more concave than are the mesial ones. The root lobes form obtuse angles ranging from 114° to 140° .

We observed some tooth variations in *C. megalodon* that we have also observed in *C. carcharias*. The upper teeth are triangular (ranging from equilateral to isosceles) in outline. In some upper lateral teeth of *C. megalodon*, the mesial root lobe may be lobate, but this is not its usual form, which, unlike the distal lobe, is slightly tapered. The mesial cutting edge is convex (USNM 445500, 474915) (Figure 39*a,b*), which gives the teeth a heart-shaped appearance. The labial faces of the crowns of these teeth are convex, and the crown tips bend lingually slightly. Aside from their slightly pathologic appearance, these teeth agree in morphology with those of *C. carcharias* from the fourth and fifth upper lateral files. The torus is well developed (Figure 39*c*) on the lingual face of the root in a second upper anterior tooth (USNM 355822).

Pathologies occur in many of the teeth; examples of these are illustrated in Figure 40*a-c*. The tooth germs of the two teeth in Figure 40*a,b*, USNM 474916 and 339917, respectively, were injured on their distal edges; these injuries caused the teeth to buckle lingually and distally. In USNM 339917, which received the greater injury, the distal cutting edge is distorted. The tooth germ of the tooth in Figure 40*c*, USNM 475360, was injured near its apex, which distorted its distal cutting edge. Cadenat (1962) noted that these deformities are caused by inju-

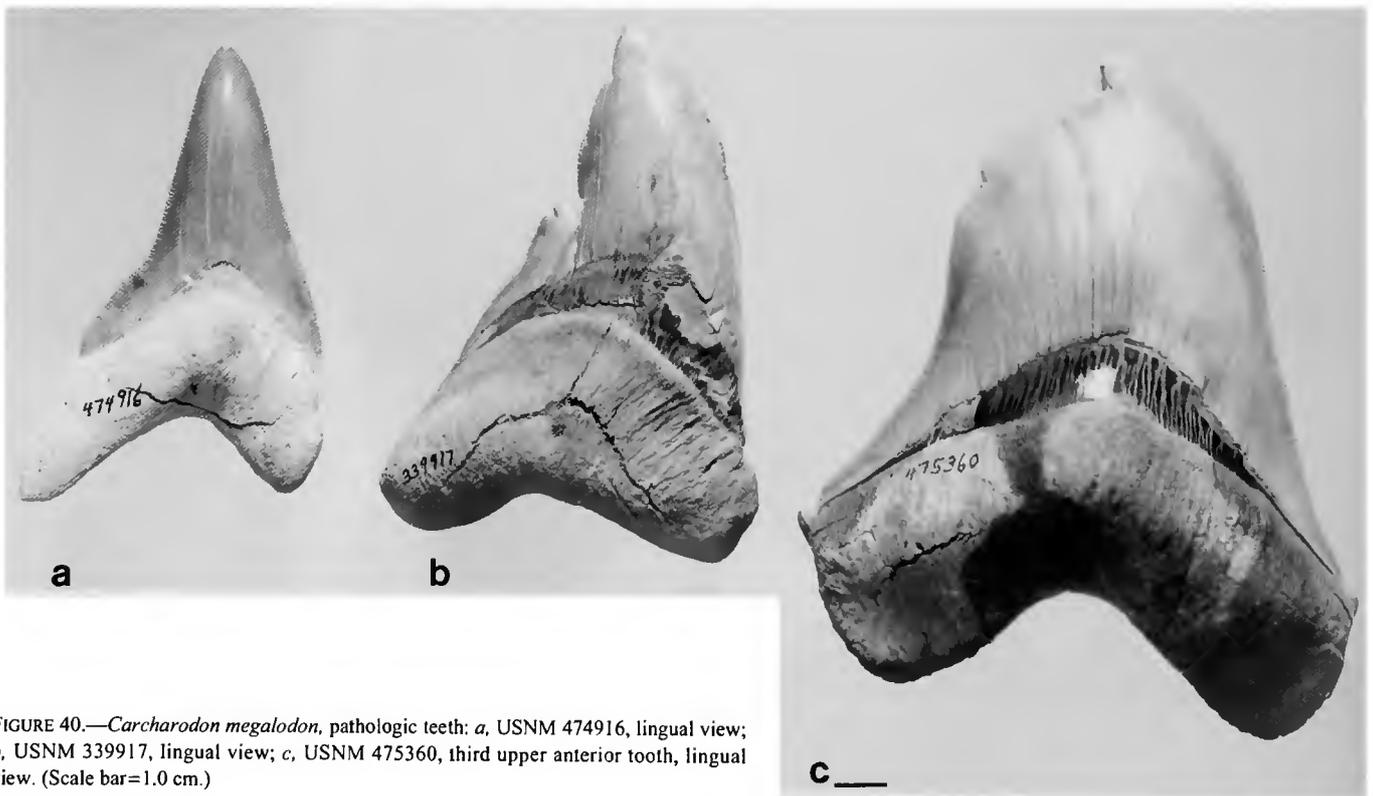


FIGURE 40.—*Carcharodon megalodon*, pathologic teeth: *a*, USNM 474916, lingual view; *b*, USNM 339917, lingual view; *c*, USNM 475360, third upper anterior tooth, lingual view. (Scale bar=1.0 cm.)

ries to the tooth germs on the insides of the jaws, usually caused by stingray spines or sea catfish spines. Once injured these tooth germs continually produce deformed teeth.

Uyeno and Hasegawa (1974) described *Carcharodon aki-taensis* on the basis of a pathologic tooth of *C. megalodon*. This type of pathology also occurs in *Isurus xiphodon*.

Another specimen worth noting is a tooth of this species with bite marks on it (USNM 336257, Figure 41a). When viewed under magnification (Figure 41b), it is clear that these bites were made by a serrated tooth. Is it evidence of a shark

eating a shark or of a loose tooth becoming lodged in the prey during feeding and then being bitten as the shark bit off a chunk of its prey?

In the USNM collections, the largest tooth (USNM 214947), a second upper anterior tooth from Lee Creek Mine, measures 15.0 cm (5.9 in) in height and probably came from a 15 m TL shark. Larger teeth have been found in the Yorktown Formation at New Bern (15.6 cm, Harmatuk collection, uncataloged) and from the Cooper River, South Carolina (16.2 cm, Hubbell collection, uncataloged). The teeth from the Yorktown Forma-

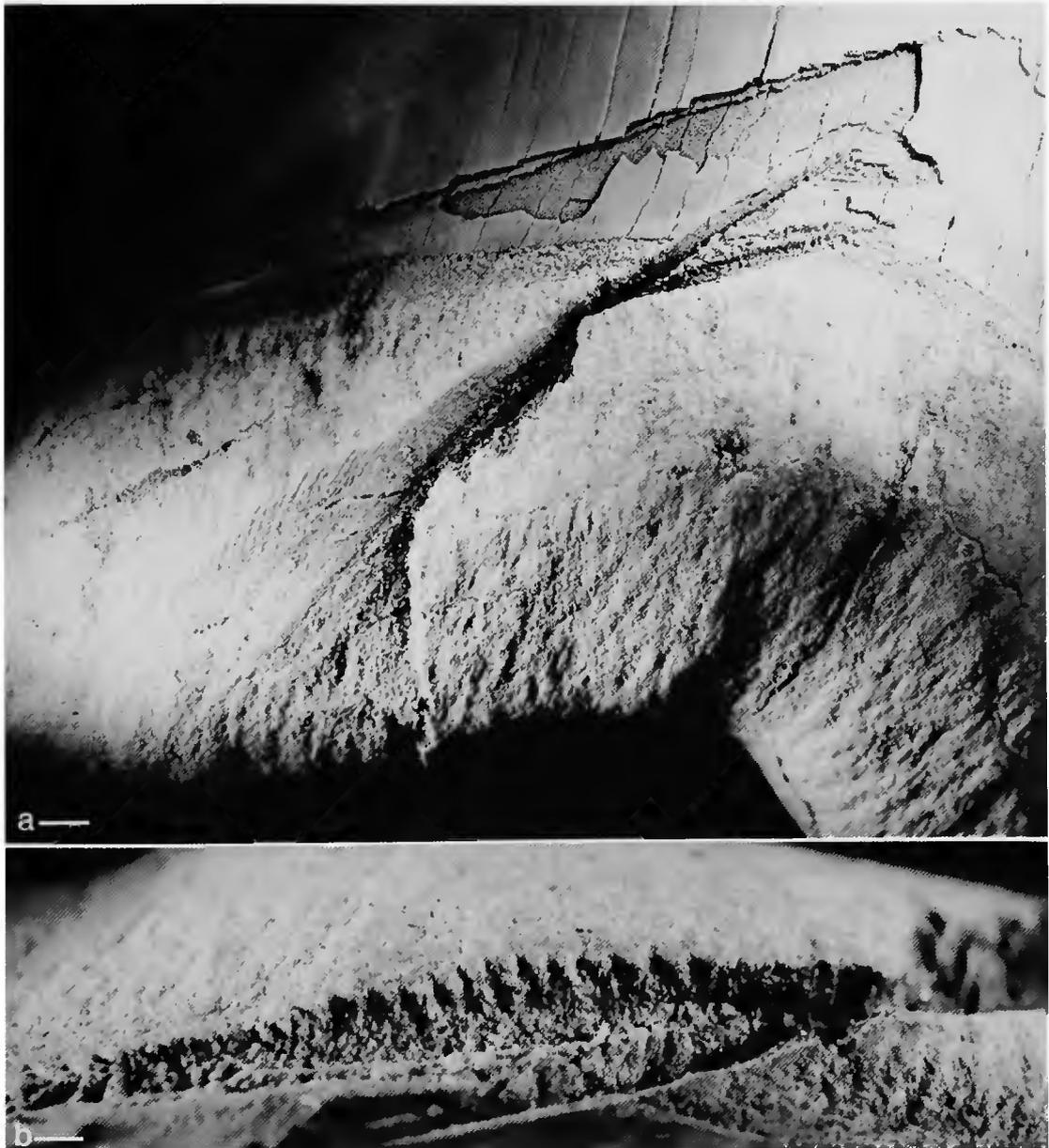


FIGURE 41.—*Carcharodon megalodon*, USNM 336257; a, lingual view of bitten tooth; b, close-up of bite mark showing serrations. (Scale bars: a=1.0 cm; b=0.3 cm.)



FIGURE 42 (opposite).—*Carcharodon megalodon*, composite dentition, USNM, reconstruction by John G. Maisey, AMNM. From left, top row: Robert J. Emry, Curator, Department of Paleobiology; Victor G. Springer, Curator, Department of Vertebrate Zoology; Peter J. Harmatuk, Collaborator, Department of Paleobiology; Ian G. MacIntyre, former Chairperson, Department of Paleobiology. Middle row: Sue Nell Voss, former Writer/Editor, Department of Exhibits; Clayton E. Ray, Curator, retired, Department of Paleobiology. Bottom row: Walter Erick Hock, Sr., former Modelmaker, Exhibits Central; Robert Purdy, Museum Specialist, Department of Paleobiology (all NMNH). (Photograph by Chip Clark, NMNH.)

tion at Lee Creek Mine range in size from 5.6 to 15.0 cm (mean=11.2 cm, $n=25$).

A reconstruction of the jaws of *C. megalodon* (Figure 42) includes as functional teeth specimens from Lee Creek Mine. The tooth in the left second lower anterior position is a left second upper anterior tooth. Several other teeth also are misplaced, including the right second lower anterior tooth, which is a right third upper anterior tooth; the right second lower and left third lateral teeth, which are upper intermediate teeth; and the right and left third lower anterior teeth, which are left third upper anterior teeth from a smaller individual. Gottfried et al. (1996) published a corrected dental reconstruction of this shark.

The earliest records of this species were reported from New Zealand, from the Oligocene sediments at Weka Pass (Davis, 1888:13) and from the early Oligocene sediments (Keyes, 1972:233). Keyes (1972:234) suggested that Davis' Weka Pass specimen was collected in the Pliocene "Greta Beds" that also occur at this locality. Many of the Oligocene specimens reported by Keyes were collected without precise stratigraphic data, and some of these are incomplete specimens, which in several instances lack the lateral cusplet area of the tooth; therefore, their stratigraphic position and in some instances their taxonomic identity cannot be ascertained. One specimen, however, with matrix adhering to it (Keyes, 1972: 235, figs. 10, 11), contains an imprint of a *Venericardia*, which Keyes matched with the sediments of the Chatton Marine Formation (middle Oligocene). This tooth, which is 12.0 cm in height, lacks the distal portion of the root and the mesial lateral cusplet, but we believe that it is from an adult *C. subauriculatus* and that other specimens from the Oligocene and early Miocene identified as *C. megalodon* also are *C. subauriculatus*.

Roux and Geistdoerfer (1988:137) reported manganese-enriched specimens in Pleistocene sediments dating from 20,000 to 120,000 years ago dredged in the Indian Ocean off Madagascar that may be the latest occurrence of *C. megalodon*. Based on the rates of accretion of manganese calculated by Burnett and Piper (1977), they estimated that the minimum age for these teeth is 10,000 years. Seret (1987) also reported dredged specimens from off New Caledonia in the southwestern Pacific Ocean; he estimated the age of these specimens at 1 Ma. Whether or not these specimens were continually exposed to conditions that permitted the accretion of manganese at a constant rate is not known, and they could be as old as Miocene or Pliocene.

Several large cetacean bones with large, serrated bite marks, collected at Lee Creek Mine, confirm that this shark preyed and/or scavenged on large whales (see Purdy, 1996).

Compagno (1990b:57) hypothesized that *Carcharodon megalodon* "may have been capable of preying on large baleen whales without the cooperative pack-hunting tactics that the smaller killer whale apparently needs to use to subdue difficult prey.... Various reconstructions of the jaws of *C. megalodon*... suggest that this shark had a predatory apparatus capable of inflicting mortal injuries on even a fin whale or blue whale."

Carcharodon carcharias (Linnaeus, 1758)

FIGURES 33a, 43

HORIZON.—Yorktown Formation? (unit 1); James City Formation.

REFERRED MATERIAL.—22 teeth, USNM 214465, 214466, 256337, 279304, 279311, 280579, 281051, 281055, 281059, 285623, 476340.

REMARKS.—These teeth are more compressed than are those of *Carcharodon megalodon* of equivalent size. The teeth of *C. carcharias* also have less massive roots and often have coarser serrations (Figure 43).

Teeth of the extant species exhibit considerable variation in their morphology. The serrations of the cutting edges range from fine, as in *Carcharodon megalodon*, to coarse, with the finer serrations being more evident in the teeth of adults. In the upper anterior teeth, the tips of the second anterior teeth may be symmetrical, point distally, or (sometimes) point mesially. The third anterior tooth also may be symmetrical or nearly so. In the lower anterior teeth, the root lobes may arch labially. The intermediate teeth may have symmetrical or asymmetrical crowns, and in the same dentition, the morphology of the right and left intermediate teeth can be very dissimilar. Like the intermediate teeth, the upper first lateral tooth may have a strong labial curvature. The attitudes of the crowns of the upper lateral teeth may be erect or distally inclined. In the lower lateral teeth the extremities of the root lobes may be straight or rounded.

Three juvenile dentitions of the extant species available to us for this study provided further information about variation in these teeth. In CAS 40905 (female, 1.6 m TL; Figure 33a) and in dentitions from a female (1.2 m TL) and a male (1.4 m TL) from the Hubbell collection, the upper teeth, rather than being erect, are inclined distally. The cutting edges of these teeth range from smooth near the tip to coarsely serrated basally. The cutting edges of the lateral cusplets range from smooth to coarsely serrated, particularly in the posterior lateral teeth. In all three dentitions the second upper anterior teeth are symmetrical; in the 1.2 m female, the distal root lobe tapers to a point and the mesial one is lobate, and in CAS 40905, the opposite condition exists. Unlike teeth of adults, the second lower anterior tooth is equivalent to or larger than the second upper anterior tooth

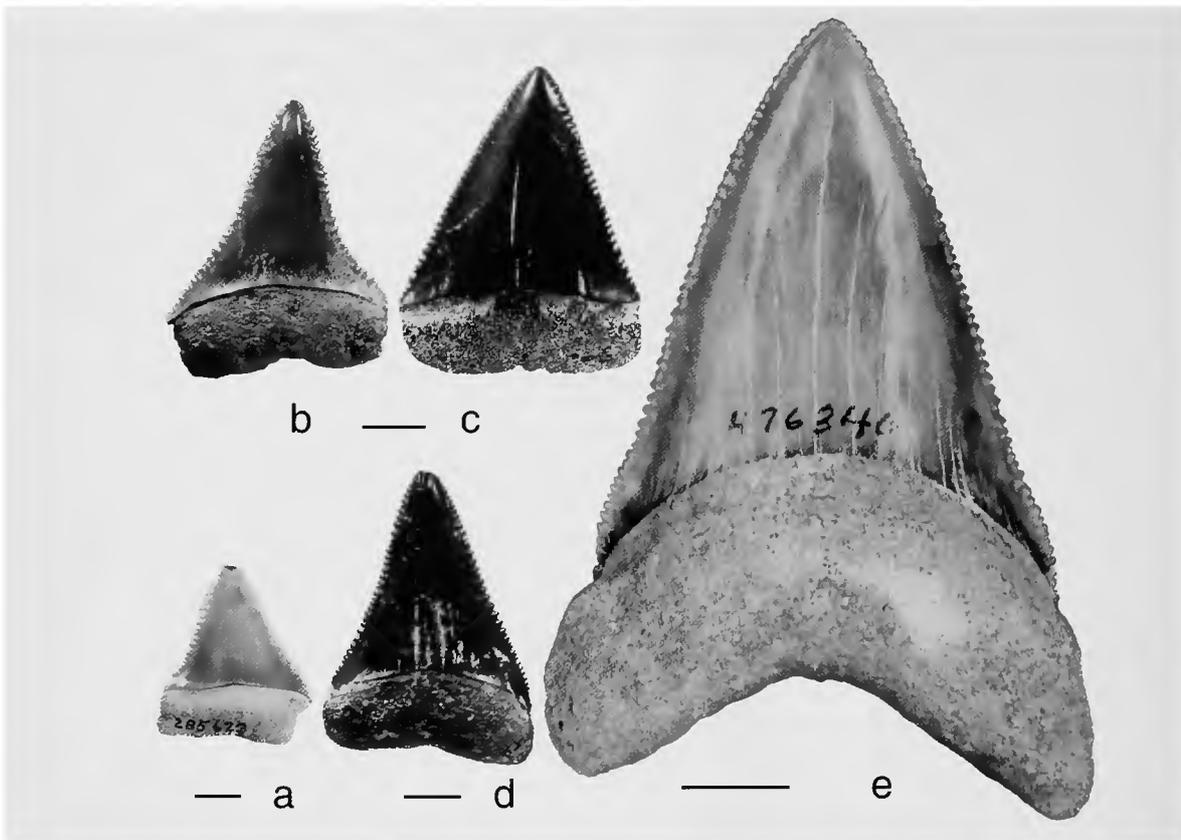


FIGURE 43.—*Carcharodon carcharias*: a, USNM 285623, Yorktown Formation?, upper lateral tooth, lingual view; b, USNM 279311, Yorktown Formation?, upper lateral tooth, lingual view; c, USNM 281055, James City Formation, upper lateral tooth, lingual view; d, USNM 281059, upper anterior tooth, lingual view; e, USNM 476340, second upper anterior tooth, lingual view. (Scale bars: a=1.0 cm; b–d=1.25 cm; e=0.5 cm.)

(CAS 40905 tooth heights: upper second anterior (A2)=1.56 cm, lower A2=1.61 cm; 1.2 m female, upper A2=1.48 cm, lower A2=1.54 cm; 1.4 m male, upper A2=1.66 cm, lower A2=1.66 cm). Among the intermediate teeth, the tip of the tooth points mesially in CAS 40905, is almost symmetrical in the 1.2 m female, and is erect but asymmetrical in the 1.4 m male.

At Lee Creek Mine, most specimens are jet black, and the roots are very corroded. On the spoil piles, these teeth were found intermingled with masses of large molluscan shells of the James City Formation. A few teeth, however, compare in preservation to those from the basal Yorktown Formation (Figure 43a,b). Because they have been found in early Pliocene beds elsewhere, this occurrence is not unusual (Leriche, 1936b:746; Muizon and De Vries, 1985:554).

Their rarity in the basal Yorktown Formation may be related to the abundance of large teeth of *C. megalodon*; at Peruvian localities of equivalent age where *C. megalodon* is uncommon, *C. carcharias* is abundant, and it is rare in Miocene sediments that yield the teeth of *C. megalodon*. Leriche (1927:82) also noted that *C. carcharias* “appears in the Miocene, where it is exceedingly rare. It is more widespread in the Pliocene, where it tends to replace *C. megalodon*.” In the late Pliocene sedi-

ments of Baja California, Espinosa-Arrubarrena and Applegate (1981) report that these two species do occur together. The stratigraphic resolution of the Baja California occurrence is not fine enough to determine if the two species occurred in the area at the same time of the year or at different times. With the exception of this last, these occurrences suggests to us that these two species may have had allopatric distributions (For further discussions of the distribution and paleoecology of *Carcharodon*, see Purdy, 1996).

In their study of white sharks from along the coast of California, Tricas and McCosker (1984:232–233) reported that “fish prey predominated in the diet of sharks [*Carcharodon carcharias*] approximately 3 m or less (TL), while pinnipeds and cetaceans predominated in those of larger sharks.” Casey and Pratt (1985:10) made similar observations about white sharks occurring off the east coast of the United States. Compagno (1984:240; see also Cliff et al., 1989) noted the following: “Larger white sharks above 3 m long tend to prey heavily on marine mammals, while smaller sharks below 2 m long feed heavily on bony fishes and small sharks, but even large sharks are capable of eating smaller prey such as the 150 crabs, salmonns, hakes, and rockfishes found in a 4.4 m specimen from

Washington State, USA. Pinnipeds may be especially important prey for white sharks where they occur together, but in tropical areas without these mammals the white shark is probably capable of subsisting on other sharks, bony fishes, turtles and cetaceans."

According to Compagno (1984:239–240), white sharks are primarily coastal and offshore inhabitants of continental and insular shelves. They are most commonly recorded in cold and warm-temperate seas.

The Lee Creek great white sharks were between 4 and 5 m in total length.

Order CARCHARHINIFORMES

Family SCYLIORHINIDAE

(cat sharks)

Scyliorhinus sp.

FIGURE 44a–h

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation? (unit 1? probably redeposited from underlying sediments).

REFERRED MATERIAL.—12 isolated teeth, 1 from Yorktown Formation, USNM 312266–312268.

REMARKS.—Compagno (1988:121) described the teeth of *Scyliorhinus* as follows: "[Teeth] similar in upper and lower jaws, cusps more oblique in upper jaw.... Sexual heterodonty absent or poorly developed.... Anterolateral teeth have erect or semioblique, moderately high cusps and mesial and distal cusplets, lower on posterior teeth; transverse ridges are confined to the basal ledges and do not extend onto the cusps." The Lee Creek Mine teeth match his description.

The teeth from Lee Creek Mine are small (mean total height 3.1 mm (Figure 44a–h); mean maximum mesial-distal length 2.5 mm) and have a prominent, lingually inclined central cusp bordered on either side by a single lateral cusplet. The central cusp is conical apically, but its lower part is divided into labial and lingual faces by mesial and distal cutting edges. These extend from one-third to one-half the height of the main cusp through a notch formed between the main cusp and the lateral cusplets, and then ascend onto the lateral cusplets. On the labial face, the main cusp and the lateral cusplets are moderately convex. This face of the crown is smooth apically, but it is sometimes striated along the crown-root boundary. These striations are usually absent on the convex, lingual face of the central cusp, but they may be present on the lateral cusplets. The root has a prominent planar basilar face divided by an open transverse groove.

The Lee Creek Mine specimens and those identified by Antunes and Jonet (1969–1970) and Cappetta (1970) as *Scyliorhinus distans* (Probst, 1879) may represent the same species, but because little is known about the dental morphology of the extant spotted cat sharks, of which there are 13 species, it is not prudent at this time to assign the fossil teeth to a species.

Compagno (1984:366) reported that the extant chain cat shark inhabits waters of 73 to 550 m in depth from off southern New England to Florida and from the northern Gulf of Mexico to Nicaragua; its feeding habits are unknown.

Family TRIAKIDAE

(tope sharks)

Galeorhinus cf. *G. affinis* (Probst, 1878)

FIGURE 44i–m

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2, possibly redeposited).

REFERRED MATERIAL.—37 teeth, USNM 207450, 207451, 207453, 207454, 312270–312272.

REMARKS.—For the genus *Galeorhinus*, Compagno (1988:248) described the teeth as exhibiting weak dignathic heterodonty, and except for two upper and lower medials, the anterior and posterior teeth cannot be differentiated (anteroposteriors). The medial teeth differ from the "anteroposteriors in having erect cusps and both mesial and distal cusplets, whereas anteroposteriors have oblique cusps and well-developed distal cusplets. Mesial cusplets are well developed in the fossil Eocene species *Galeus rectoconus* Winkler, 1873 [Cappetta assigned this species to his genus *Abdounia*], and occasional adults of the living *Galeorhinus galeus*. Pegs absent from tooth crowns. Tooth roots with strong transverse notches" (Compagno, 1988:248). In the seven dentitions of *Galeorhinus galeus* (Hubbell collection) available to us, the mesial edges are straight or dog-legged. In larger males, the teeth have broader crowns than do those of females, and the distal cusplets are saw-toothed. The teeth from Lee Creek Mine resemble those of females (Figure 44i–m).

Probst's (1878:139, pl. 1: figs. 64–67) type suite for *G. affinis* contains four teeth of two different genera; only the two teeth in his figs. 66 and 67 belong to *Galeorhinus*; the other two teeth (figs. 64, 65) appear to be symphysials of *Paragaleus*. The specimens in his figs. 66 and 67 are very close in morphology to those illustrated by Compagno (1988, pls. 20: fig. J, 21: fig. J) and Herman et al. (1988:106, pl. 13). Because Probst's type specimens are lost and a large sample of dentitions from the extant species is not available to us, we cannot at this time assess the validity of his species. If it is valid, then the Lee Creek Mine teeth, which resemble those in Probst's figs. 66 and 67, should be assigned to *Galeorhinus affinis*.

The Lee Creek Mine specimens are small; tooth height ranges from 2.0 to 7.5 mm, width ranges from 2.1 to 9.9 mm, thickness ranges from 0.9 to 3.0 mm, and the number of distal cusplets ranges from two to four. Compagno (1988:33) reported that the number of distal cusplets in *Galeorhinus* increases with the growth of the shark.

This shark no longer inhabits the coastal waters off eastern North America. It is found in cold to warm-temperate continen-

tal seas in the eastern Pacific, the eastern North Atlantic, the South Atlantic, and off southern Australia, where it frequents depths from 2 to 471 m. It feeds on bony fishes and invertebrates (Compagno 1984:387–388).

Hypogaleus sp.

FIGURE 44q

HORIZON.—Pungo River Formation (unit 1).

REFERRED MATERIAL.—1 tooth, USNM 207452.

REMARKS.—This tooth from the lower Pungo River Formation compares favorably with the lower teeth figured by Compagno (1988, pl. 21: fig. 1) and Herman et al. (1988, pl. 14). In the living species and in the Lee Creek specimen, the mesial edge of the crown is convex, and the distal cutting edge is concave on the apical half of the crown. This specimen measures 4.1 mm in height and 5.5 mm in width.

According to Compagno (1988:394), this shark inhabits deepish water in the tropical and subtropical western Indian and western North Pacific oceans; it eats bony fishes.

Mustelus sp.

FIGURE 44n–p

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—5 isolated teeth, USNM 207589, 207590.

REMARKS.—These diminutive durophagous teeth are convergently similar to those of certain rhinobatids and pristids.

The mesiodistal diameter (range=1–1.3 mm) is twice that of the labiolingual diameter and is one and one-half times the maximum tooth height; the labiolingual diameter is approximately equal to the medial height of the crown measured on the lingual side. In apical view, the occlusal surface is elliptical, more or less flattened, but rising slightly above the lingual peg and restricted from the lingual surface by a cutting edge. On the labial face (Figure 44o), the crown overhangs the root and is vertically striated. These striations, or more accurately, vermiculating ridges, continue a short distance onto the occlusal surface of unworn teeth. These ridges also occur on the lingual surface of the crown and extend higher there than on the labial surface. On the lingual face (Figure 44p) the medial portion of the crown foot expands to form a relatively prominent, rhinobatid-like process or peg. The root is bipartite, with a flattened attachment face that is inclined at about a 30° angle to the plane of the occlusal surface.

Compagno (1984:399), for purposes of identification, separated *Mustelus* into three groups, those with “cusps high on teeth,” those with “no cusps on teeth,” and those with “low blunt cusps present on teeth, crowns asymmetrical.” The Lee Creek Mine specimens belong to the last category, and they are similar to those of *M. canis*, which inhabits the temperate and tropical continental waters of the western Atlantic and the Gulf of Mexico (Compagno 1984:405). It is found from the intertidal zone to 200 m in depth and feeds mainly on crustaceans, although it also feeds on small bony fishes (Compagno 1984:406).



FIGURE 44.—*Scyliorhinus* sp.: a, USNM 312266, incomplete, anteroposterior tooth, labial view; b, same specimen, lingual view; c, USNM 312267, anteroposterior tooth, lingual view; d, same specimen, lateral view; e, same specimen, labial view; f, USNM 312268, anteroposterior tooth, lateral view; g, same specimen, lingual view; h, same specimen, labial view. *Galeorhinus* cf. *G. affinis*: i, USNM 312270, lower anteroposterior tooth, lingual view; j, USNM 312271, upper anterior anteroposterior tooth, labial view; k, USNM 312272, upper anterior anteroposterior tooth, lingual view; l, USNM 207450, upper medial tooth, labial view; m, USNM 207453, lower anteroposterior tooth, labial view. *Mustelus* sp.: n, USNM 207589, anteroposterior tooth, lateral view; o, same specimen, labial view; p, USNM 207590, anteroposterior tooth, lingual view. *Hypogaleus* sp.: q, USNM 207452, anterior tooth, lingual view. (Scale bars: a–e=0.3 cm; f–h=0.25 cm; i=0.5 cm; j–l=0.5 cm; m–q=0.1 cm.)

Family HEMIGALEIDAE
(weasel and snaggletooth sharks)

Paragaleus sp.

FIGURE 45

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (unit 1, probably redeposited).

REFERRED MATERIAL.—About 50 teeth, USNM 207455–207461, 475446, 475447, 476288–476292.

REMARKS.—Teeth from the Pungo River Formation (Figure 45) compare favorably with those of the extant species. Compagno (1988:258) described these teeth as follows: “Upper anterolateral teeth with moderately long cusps that are no-

ticeably longer than the distal cusplets. Lower anterolateral teeth slightly smaller than uppers. Cusps of lower anterolaterals short, stout, straight or slightly hooked, and differentiated from the crown foot by distal sometimes mesial notches. Some or almost all cusps on lower anterolaterals oblique or semioblique. Distal and sometimes mesial cusplets on some lower anterolateral teeth. . . . Ventral edges of root lobes and crown feet straight or nearly so and horizontal on anterolaterals of lower jaw, giving teeth an inverted T shape.” In his description, Compagno does not mention the mesial cusplets that may occur on the upper anterior tooth as illustrated by Bigelow and Schroeder (1948:277). Otherwise, the Lee Creek Mine teeth agree with Compagno’s description.

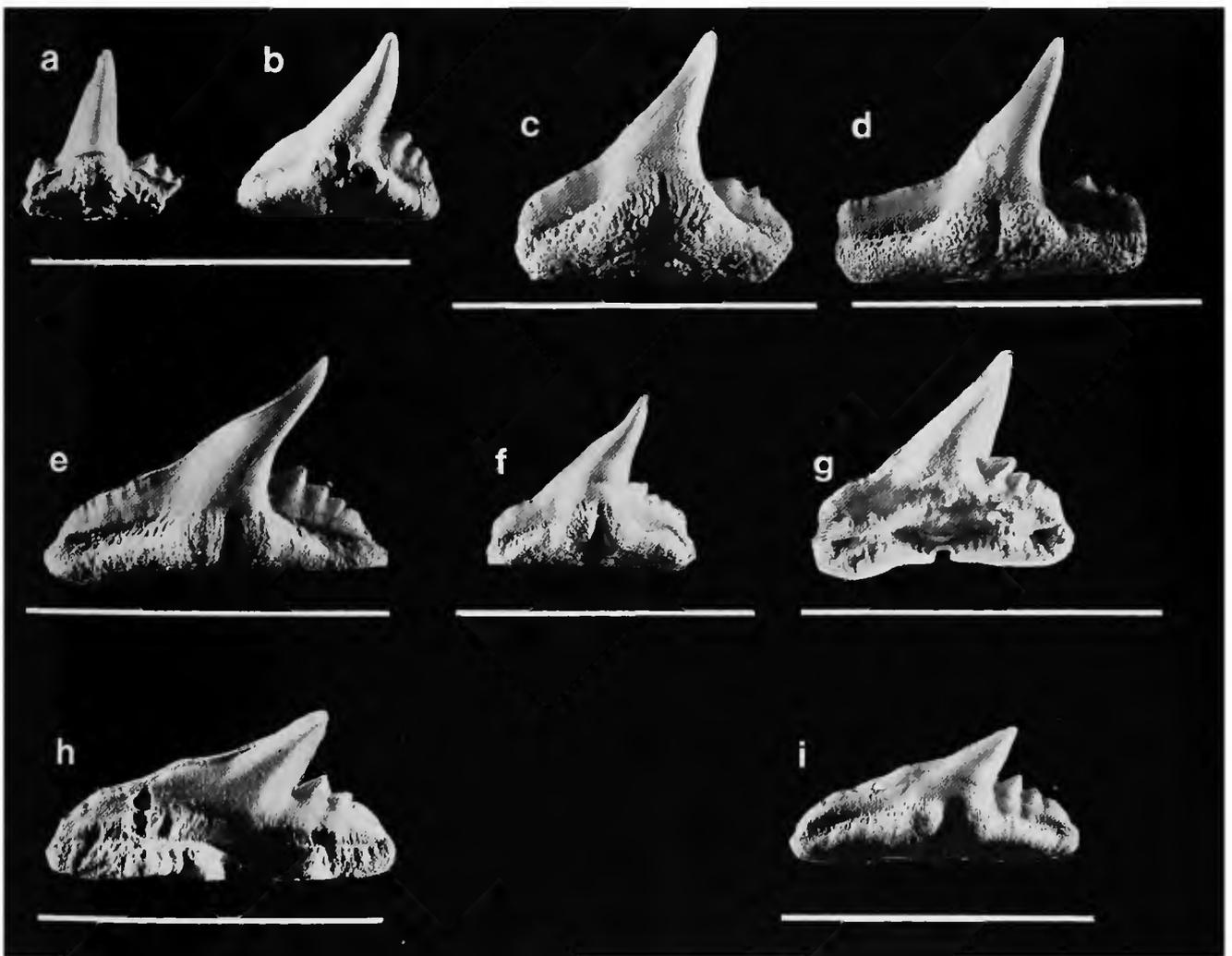


FIGURE 45.—*Paragaleus* sp., Pungo River Formation: *a*, USNM 207455, upper medial tooth, lingual view; *b*, USNM 207456, upper anterior tooth, lingual view; *c*, USNM 207457, lower anterior tooth, lingual view; *d*, USNM 207458, lower anterior tooth, lingual view; *e*, USNM 207459, lower anterolateral tooth, lingual view; *f*, USNM 207460, upper anterolateral tooth, lingual view; *g*, same specimen, labial view (reversed); *h*, USNM 207461, upper lateral tooth, labial view; *i*, same specimen, lingual view (reversed). (Scale bars = 0.25 cm.)

The upper teeth from Lee Creek Mine have crowns that incline distally, with smooth cutting edges that become serrated basally on the distal enamel shoulder; the shoulder is separated from the crown by a deep notch. Their crowns are elongate, with convex distal and concave mesial cutting edges. As in the extant species, often the tips of the crowns bend lingually but not as much as those of the lower teeth. The upper teeth have more compressed roots than do those of the lower teeth. On the lingual face of the root there is a well-developed transverse groove that penetrates the basal margin of the root.

In the lower jaw, the most anterior teeth lack the distal serrations, and their crowns may be slightly contorted. In the region of the transverse groove, their roots are thicker than those of occluding upper teeth. The more distal anterolateral teeth possess serrated enamel shoulders.

Although Jonet (1966:81–83; emended in Antunes and Jonet, 1969–1970:169–171) described a new species, *Paragaleus pulchellus*, for his specimens, insufficient specimens of the four extant species are available to assess the validity of Jonet's species; therefore, we refrain from identifying the Lee Creek Mine specimens to a species.

The anterolateral teeth from Lee Creek Mine are 6.4 to 8.5 mm in height (mean=7.4 mm, $n=6$) and 6.6 to 9.2 mm in width (mean=7.9 mm, $n=6$); they probably came from night sharks between 1.5 and 1.7 m in total length.

According to Compagno (1984:442–444), *Paragaleus* inhabits tropical and warm-temperate waters off western Africa, the northwestern India Ocean, and the western Pacific Ocean. *Paragaleus pectoralis* preferentially feeds on squids but will also take small bony fishes.

Genus *Hemipristis*, Agassiz, 1843

Compagno (1988:269–270) characterized the teeth of this genus as follows: "The medials are very small, clawlike teeth with very narrow roots and strongly hooked cusps; symphysials are similar but larger, with broader symmetrical roots. Upper anteriors are abruptly larger, broader, and flatter than the symphysials and differ from the laterals in having much narrower roots and crowns. The lower anteriors are very high, narrow, deep-rooted and hook-cusped teeth having serrations or cusplets, if any, confined to the crown foot, and form a spike-studded impaling pad. ... The lower anteriors grade into the laterals by becoming lower-crowned, broader, shorter-cusped, and by having serrations or fine cusplets extending onto the distal crown feet. Upper laterals are very broad, wide, triangular teeth, with compressed, horizontal-edged roots, broadly convex mesial edges, and arcuate distal edges having coarse serrations or cusplets. In small specimens the cusps of all the teeth are slightly more oblique than those of adults and subadults. In the young a few distal cusplets are present on upper laterals (five on fifth upper laterals of a 532 mm. specimen) but these become more numerous on adults and subadults (10 or more on fifth upper lateral) and turn into coarse serrations."

Hemipristis serra Agassiz, 1835

FIGURES 46–48a

HORIZON.—Pungo River Formation (units 1–6); Yorktown Formation (units 1, 2, 3?).

REFERRED MATERIAL.—About 700 teeth, USNM 278198, 435197, 444191, 451274–451327, 474917, 474920–474940; 6 vertebrae, USNM 467528–467532.

REMARKS.—The teeth of this species are among the most common large-selachian remains occurring at the Lee Creek Mine in both formations; their abundance permitted us to reconstruct their dentitions (Figures 46, 47).

The upper and lower symphysial teeth, the lower anterior teeth, and the first two laterals from the lower jaw are awl-like, with a few serrations or cusplets near the base of the crown. The more distal lower lateral teeth have coarsely serrated cutting edges and are much narrower than the upper lateral teeth. The upper anterior and lateral teeth are subtriangular, labiolingually compressed, broad, and with coarsely serrated cutting edges. One of the more characteristic features of these teeth and of *Hemipristis* is the prominent lingual torus of the root.

Hemipristis seems to increase in size through its evolutionary history as do some of the other large sharks of the Neogene. At Lee Creek Mine, the largest teeth of *Hemipristis*, which are 30% larger than those from the Pungo River Formation, occur in the lower Yorktown Formation. These teeth are the largest yet reported in the literature. In the Tertiary sediments of Baja California, Applegate (1986) also noticed this increase in tooth size in *Hemipristis*; his tooth sizes correspond with those from Lee Creek Mine and those (measured by R.W.P.) from the early Miocene to early Pliocene of Florida. But is this size increase an evolutionary change?

One exception to this increase in size through time does exist: the teeth of *Hemipristis*, collected in place with late Oligocene whales and invertebrates (Sanders, 1980), range in height from 12.2 to 25.8 cm (mean=19.4 cm, $n=21$). These teeth compare in size with those from the middle and late Miocene. We question, therefore, whether this size increase is related to the evolution of *Hemipristis*; it may be due to ecological changes favoring increasingly larger sharks, which in earlier epochs may have inhabited areas not represented in the available fossil record.

Are the Pungo River *Hemipristis* teeth those of juveniles? As noted above, Compagno (1988:269–270) reported the occurrence of ontogenetic variation in the upper lateral teeth of the extant species, namely, that the number of cusplets on the distal cutting edge increases with age. In comparing the fifth upper laterals of the reconstructed *Hemipristis* dentitions from the Pungo River (tooth height=2.04 cm) and the Yorktown (tooth height=3.41 cm) formations, both teeth possess 14 coarse, distal serrations. Therefore, the smaller, Pungo River *Hemipristis* teeth are from adults, possibly young adults. The apparent size difference between the Pungo River and York-



FIGURE 46.—*Hemipristis serra*, Pungo River Formation, composite dentition, lingual view; second symphyseal and last lateral tooth of upper series and last three lateral teeth of lower series missing. (Scale bar=2.0 cm.)

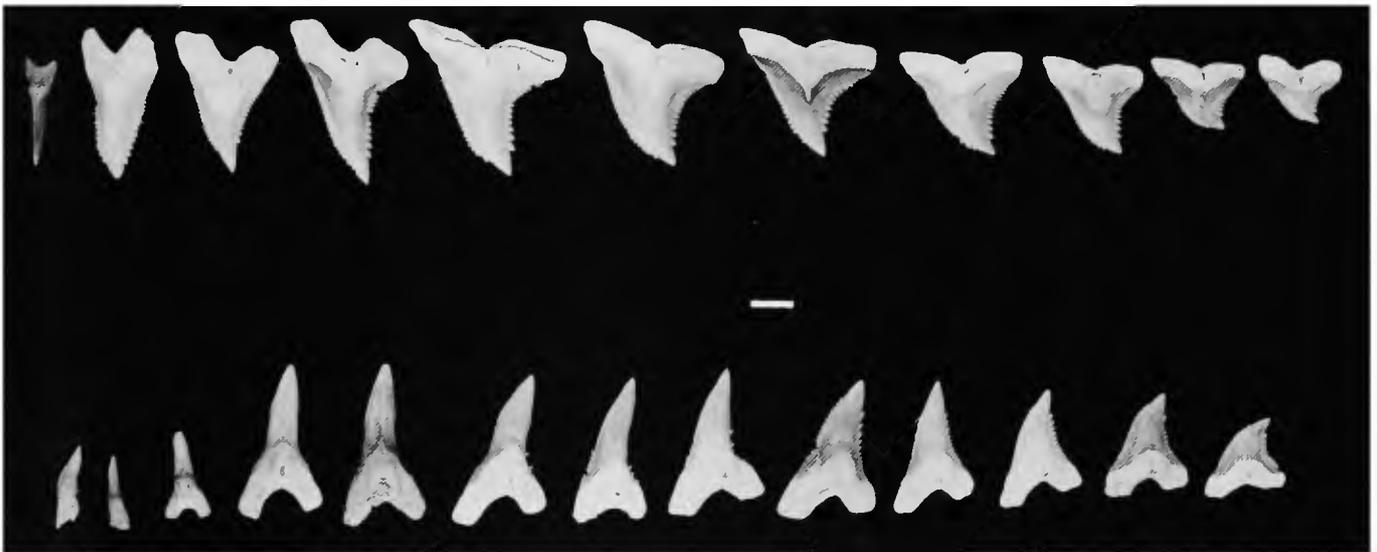


FIGURE 47.—*Hemipristis serra*, Yorktown Formation, composite dentition, lingual view; two symphyseals and two posterior lateral teeth of upper series and one symphyseal and 10 lateral teeth of lower series missing. (Scale bar=1.0 cm.)

town populations of this shark (see Branstetter et al., 1987) also may reflect different rates of growth.

Compared to the extant species, the crowns of the upper teeth in both fossil dentitions are more erect than are those of the adult female of *H. elongatus* illustrated by Compagno (1988, pl. 20N), whereas the attitudes of the crowns of the lower teeth of the fossil species are similar to those of *H. elongatus* in his pl. 21N.

The sizes of the *Hemipristis* teeth from the Pungo River and the Yorktown formations are contrasted below. Most of the Pungo River specimens are from the ore horizons, units 1–3, but some material from the upper Pungo River Formation is in-

cluded as well. The measured Yorktown specimens are from units 1 and 2.

	Range (mm)	Mean	Number
Pungo River Formation			
Height	14.1–29.1	20.3	20
Width	12.3–35.5	21.4	20
Yorktown Formation			
Height	16.4–41.0	29.1	27
Width	14.0–43.5	25.9	27

Six vertebrae (Figure 48a) from Lee Creek Mine are identical with those associated with a dentition of *Hemipristis serra* from the Calvert Formation. These are short, aseptate centra

with rectangular to suboval dorsal and ventral foramina; diagonal laminae bisect these foramina. In the vicinity of the foramina and along the rims of the centra, pores are usually present.

The extant species is a tropical coastal shark that inhabits waters from 1 to 30 m in depth in the Red Sea and Indian Ocean. It feeds on birds, sea catfish, mackerel, croakers, grey sharks, and other fish (Compagno, 1984:441).

Family CARCHARHINIDAE
(requiem sharks)

Genus *Galeocerdo* Müller and Henle, 1837
(tiger sharks)

Compagno (1988:279–280) described these teeth as follows: “Dignathic heterodonty weak, but monognathic heterodonty well-developed, with strongly differentiated medials and anteroposteriors in both jaws (anterolaterals grade into posteriors), and lower symphyseal. Sexual heterodonty absent. Ontogenetic heterodonty weak, with young having fewer cusplets, narrower, longer, and more oblique cusps, and more angular mesial edges on their anteroposterior teeth than adults. ... Anteroposterior teeth with characteristic cockscomb shape, with oblique primary cusps and strongly notched distal edges. Teeth secondarily anaulacorhizous, with no transverse groove and notch [in basal margin of root].”

We would modify the above because the “strongly notched distal edges” are not predominant in some fossil species (e.g., *Galeocerdo latidens*).

We tentatively identify three species of *Galeocerdo* from Lee Creek Mine: *Galeocerdo* sp. (identified by others as *G. aduncus*), *G. contortus*, and *G. cf. G. cuvier*. Our uncertainty regarding *G. sp.* and *G. cuvier* arises from the wide range of variability in tooth shape that exists in these sharks; our identification of *G. contortus* is uncertain because its anterior teeth are unlike those of *Galeocerdo*.

During the Tertiary history of *Galeocerdo*, two basic tooth forms reoccur and persist into the living species. In the earliest known form, *Galeocerdo latidens*, the distal notch of the cutting edge is not well developed. This tooth form, which is common in the middle Eocene, recurs in abundance in the early Miocene of Africa and in the late Miocene of Florida and occasionally in the teeth of the extant species (Hubbell, private collection; Alvaro Mones, pers. comm., 11 Jun 1991). The second tooth form, with a deeply notched distal cutting edge, occurs at widespread localities from the late Eocene (*G. clarkensis* White from Alabama) to the present; this tooth form is abundant in the late Oligocene of South Carolina, the middle Miocene of the Chesapeake Group, and most Pliocene marine deposits where *Galeocerdo* occurs. Rather than representing taxonomic differences, because both tooth types occur in the extant species, this patchwork distribution suggests to us that the teeth of the fossil species and possibly the extant species are highly variable in the development of the distal notch. Because of this variability, we believe that the taxonomy of this

genus needs revision and that the fossil species should be defined on the basis of the predominant tooth morphotype of several widely distributed, synchronous populations.

None of these tooth morphotypes, however, matches exactly that of the teeth from the Pungo River Formation at Lee Creek Mine, which have a well-developed distal notch and the lateral extremities of the roots turned apically as in *G. latidens*. This last character is not present in the teeth of *Galeocerdo* from younger sediments.

Concerning the Pliocene teeth that we identify as *G. cf. cuvier*, we believe that large samples of these teeth must be compared with large samples of teeth from the extant tiger shark, which are not presently available, to ascertain the identity of the Pliocene teeth; this also applies to ascertaining the validity of Applegate's *G. rosaliensis*.

Our uncertainty with *Galeocerdo contortus* concerns its generic identity. The teeth of *G. contortus* differ markedly from all other species of *Galeocerdo*. By comparing the teeth of *G. contortus* to those of *G. latidens* and *G. cuvier*, we can contrast these differences.

Like *Galeocerdo cuvier*, *G. latidens* has nearly homodont teeth, and on the lingual face of the root, the lower anterior teeth possess a slight but noticeable torus with a very shallow transverse groove; this character is harder to discern in the extant species. In *G. contortus*, however, the lower anterior teeth have well-developed toruses with deep transverse grooves (Figure 48d). Also, in the anterior anteroposterior teeth of *G. cuvier* and *G. latidens*, the width of the tooth exceeds its height, and in *G. contortus* the opposite is true. In morphology, the teeth of *G. contortus* do not fit the pattern for this genus.

Both Leriche (1942) and Applegate (1978) proposed that the teeth of *G. contortus* were the lowers of *G. aduncus*. If they are, for a carcharhinid, this shark had a very unusual dentition because the heights of the lower anteriors (mean=15.7 mm, $n=136$, range=12.0–19.4 mm) exceed those of the upper anteriors (mean=14.0 mm, $n=65$, range=10.7–16.8 mm), which is the opposite of the condition in *G. latidens* and *G. cuvier*, where the height of the upper teeth exceeds that of their lower counterparts.

Also, in screen-wash samples of shark teeth from the Eocene Castle Hayne Formation at Rose Hill, North Carolina, the teeth of *G. latidens* ($n=100$) exhibit the weak dignathic heterodonty seen in *G. cuvier*. Both uppers and lowers of the Eocene teeth can be identified, and no *G. contortus*-type teeth of comparable size (1.2–2.0 cm, anterolaterals) were found (*G. contortus* has not yet been found in the Eocene). Therefore, we cannot agree with the proposals of Leriche (1942) and Applegate (1978).

Cappetta (1980) placed teeth from the Paleocene and Eocene similar to those of *Galeocerdo contortus* in his new genus *Physogaleus* and assigned them to *P. secundus* (Winkler, 1874), which he made the type species of the genus. Unlike *Galeocerdo contortus*, Cappetta's (1980, fig. 5A) specimens possess a deep distal notch. Also, Winkler's two syntypes, which are illustrated in lateral view only, are quite different in morphology. Winkler's specimens possess orectilobiform rath-

er than carcharhiniform roots. Winkler described the root of the type specimen as "a wide and robust root, of a remarkable form: it presents a kind of a mound or a pyramid with three faces, and with a wide base, that forms below a triangle with rounded angles. In the middle of this lower face of the root one observes a circular depression, while the enamel of the crown forms a kind of ribbon, it terminates in a small tubercule on the internal face of the root." Winkler did not mention the presence of a transverse groove on the root, which is characteristic of carcharhiniform teeth, and his "enamel ribbon" may be the peg that is often found on the teeth of orectilobiform sharks. Until Winkler's syntypes are found, the identity of *Physogaleus* remains in doubt.

The characters of *G. contortus* are not characteristic of *Galeocerdo*, but we feel that generic reassignment of these teeth should await the discovery of an associated dentition and a more thorough study of the Paleogene forms.

Size is often used to separate fossil and extant species of *Galeocerdo* (Antunes, 1963; Antunes and Jonet, 1969–1970; Applegate, 1978, 1986). A recent study by Branstetter et al. (1987) found that two populations of the extant species, one in the Gulf of Mexico and the other in the Atlantic Ocean off the coast of the southeastern United States, had different rates of growth and that tiger sharks of known age from the Gulf of Mexico were larger than individuals of equivalent age from the Atlantic population. Also, Hubbell (pers. comm., 1990) noted that the largest individuals of this species do not come from these two populations but from the Pacific Ocean off Panama, an area of upwelling and high food availability. Another study by Lowe et al. (1996:209) indicated that tiger sharks segregate by size—smaller ones live in shallow, nearshore waters, whereas larger ones are more pelagic. If these distributions also were true for fossil tiger sharks, then, except for nursery areas, large teeth would occur in sediments deposited in pelagic waters, and small teeth would occur in sediments deposited in shallow, nearshore waters. If this hypothesis is correct, then the Neogene record of a size increase in tiger sharks may reflect an increase in water depth and in the availability of prey in the basins of deposition rather than an evolutionary change.

In identifying the Lee Creek Mine tiger shark teeth, we believe that there is a wide range of variation in tooth morphology within a species and that two species are represented in the Miocene and another in the Pliocene. More extensive sampling of Miocene and Pliocene shark tooth horizons may prove us wrong.

Galeocerdo sp.

FIGURES 48*b,e*, 49

HORIZON.—Pungo River Formation (units 1–6).

REFERRED MATERIAL.—About 200 teeth, USNM 451233–451251, 464118, 464119, 476376.

REMARKS.—Agassiz (1835, pl. 26: figs. 24–28, 1843:231) characterized *Galeocerdo aduncus* as having a greater con-

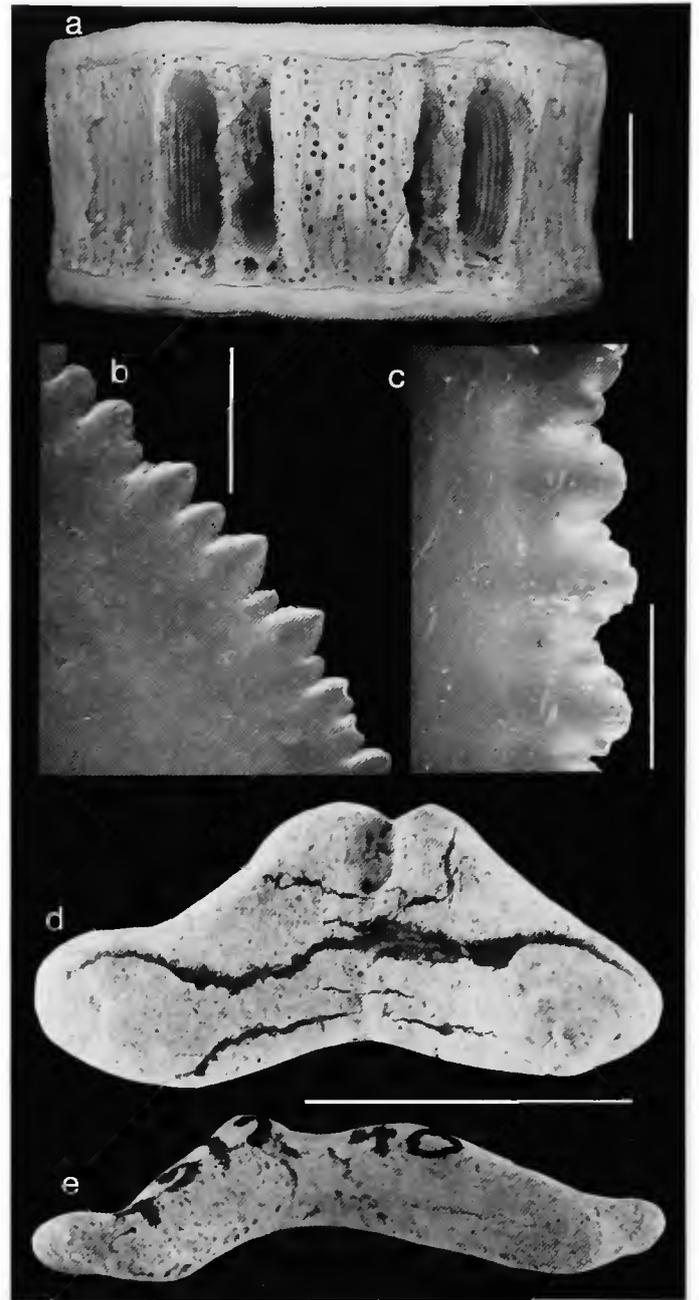


FIGURE 48.—*Hemipristis serra*: a, USNM 467531, vertebra, dorsal view. *Galeocerdo* sp.: b, USNM 476376, pointed serrations on mesial edge of tooth; e, USNM 451240, basal view of root. *Galeocerdo cuvier*: c, USNM 476377, pointed, compound serrations on mesial edge of tooth. *Galeocerdo contortus*: d, USNM 451226, basal view of lower anterior tooth showing well-developed torus. (Scale bars: a=0.5 cm; b,c=0.5 mm; d,e=0.33 cm.)

vexity in the distal enamel shoulder than exists in the living species; this character, however, is variable in the fossil and extant species. Cigala-Fulgosi and Mori (1979) described the only character that may separate middle Miocene teeth identified traditionally as *G. aduncus* (= *G. sp.* herein) from *G. cuvi-*

er; they noticed that unlike the extant species, on the basal half of the mesial edge of the tooth the serrations are simple rather than compound (cf. Figures 48*b*, 48*c*). Incipient compound serrations, however, may be present. We do not know if these compound serrations are present or absent on Agassiz's holotype, which was deposited at the Staatliches Museum für Naturkunde, Karlsruhe, but is now lost. According to Agassiz, the holotype was found in the Schwabia region of southwestern Germany, where marine sediments were deposited from the Burdigalian into the Zancian. Because the exact age of the type specimen cannot be determined, it may represent a juvenile of *G. cf. cuvier*, or it may be the species identified until now as *G. aduncus* by vertebrate paleontologists. Without examining the type specimen, the identity of *G. aduncus* cannot be ascertained. We believe, therefore, that *Galeocerdo aduncus* is a nomen dubium and is not available for use as a scientific name.

At this time, however, we hesitate to identify the next available junior synonym because the types of the subsequently described species are not now available to us, and we do not know their whereabouts. We believe that the resolution of this problem must await a major revision of the fossil species of this genus.

Figure 49 illustrates a reconstructed dentition of this species. For illustration purposes, these teeth were separated by spaces; the lingual recurvature of the lateral extremities of the roots indicates that these teeth overlapped (Figure 48*e*), a condition termed alternate-imbricate overlap by Compagno (1988:31). The crowns of the upper teeth have a strong labial curvature, and as in the extant species, they are slightly more elongate than their lower-jaw counterparts. In our reconstruction, the lower medial, an upper posterior, and a lower posterior tooth are missing; they were not found in the USNM collections.

Well-preserved specimens of this species are found embedded in the mold and cast limestones in the upper part of the Pungo River Formation. The species also is common in ore-sump residues and from the reject gravels screened from the

ore during processing. The condition of the few specimens found on spoil piles of lower Yorktown Formation sediments suggests that they were redeposited.

We have not seen the specimens described by Leriche (1942) as *Galeocerdo aduncus*, but on the basis of his illustrations (pl. 7: figs. 33–42), the teeth appear to be the same as *Galeocerdo contortus* Gibbs (see discussion of *G. contortus*).

The anterior and anterolateral teeth range from 10.7 to 16.8 mm in height (mean=14.0 mm, $n=65$) and from 12.4 to 20.0 mm in width (mean=16.2 mm, $n=65$). In the extant tiger sharks, teeth of these sizes are found in individuals of 1.8–3 m TL.

Galeocerdo contortus Gibbs, 1848–1849

FIGURES 48*d*, 50

Galeocerdo acutus Storms, 1894:81–82, pl. 6: fig. 18 [Rupelian, Belgium].

Galeocerdo triquetra Eastman, 1904:89, pl. 32: fig. 12 [Calvert Formation, Maryland].

Physodon triquetra Leriche, 1942:79 [Calvert Formation, Maryland].

Galeocerdo oduncus Agassiz.—Leriche, 1927:88, pl. 14: figs. 1–3, 6 [middle Miocene, Switzerland]; 1942:87–88, pl. 7: figs. 33–42 [Calvert Formation, Maryland].—Caretta, 1972:54–57, pl. 11: figs. 1, 2, 4 [middle Miocene, Italy].

HORIZON.—Pungo River Formation (units 1–6).

REFERRED MATERIAL.—About 600 teeth, USNM 451212–451232, 476386–476393.

REMARKS.—*Galeocerdo contortus* is distinguished from the other small tiger shark of the Pungo River Formation, *G. sp.* (see above), by the following criteria.

<i>Galeocerdo</i> sp.	<i>Galeocerdo contortus</i>
crown relatively thin, flat; margins nearly in same plane	crown thick, twisted; mesial margin warped
mesial margin of crown uniformly curved in profile	mesial margin of crown flexuous in profile
serrations on enamel shoulder compound, coarse	serrations on enamel shoulder simple, fine
apex angle of crown 35°–50° (mean=43°, $n=16$)	apex angle of crown 22°–40° (mean=31°, $n=40$)
root relatively thin; like <i>G. cuvier</i> , lacks prominent torus on lingual face	root thick, with prominent torus on lingual face as in <i>Hemipristis</i>
width of anterior anteroposterior teeth exceeds height of tooth	height of anterior anteroposterior teeth exceeds width of tooth

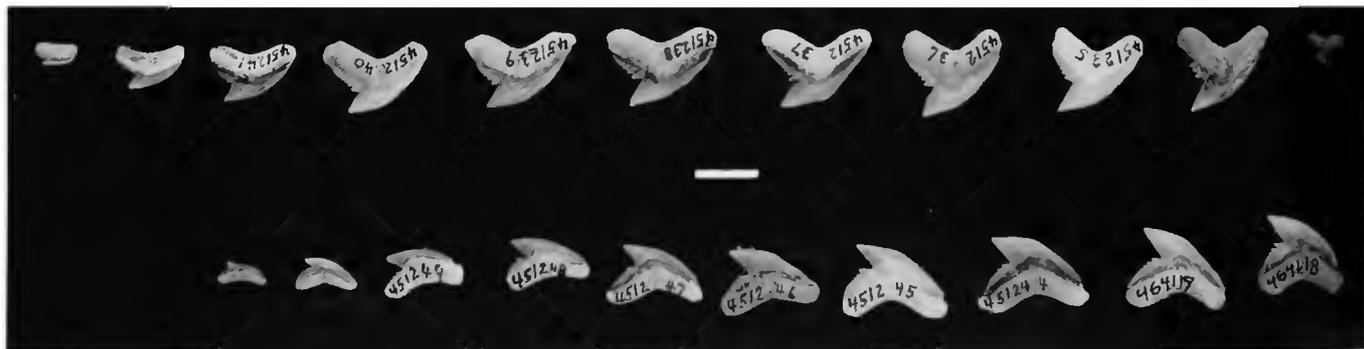


FIGURE 49.—*Galeocerdo* sp., composite dentition, lingual view. (Scale bar=1.0 cm.)

Galeocerdo contortus always occurs with *G. sp.* in Neogene localities on the East Coast of the United States. Counts of teeth collected by screen washing at Lee Creek Mine indicate it is twice as common as *G. sp.* This ratio has been constant in several separately collected samples.

Figure 50 represents a reconstructed dentition of this species. In sorting the teeth, we identified both uppers and lowers. In the lower teeth, a prominent, lingual torus is present, particularly in the more anterior teeth (Figure 48*d*), which becomes less prominent in the more posterior teeth. The tips of the crowns of these teeth exhibit the characteristic lingual bend. In the upper teeth, the root is more compressed, and the tips of the crowns have a noticeable labial curvature. Our reconstruction, based on *G. cuvier*, includes all tooth positions except the upper medial, if one is present, and one or two of the posterior teeth in each jaw.

Cappetta (1987:123) stated that this species does not occur in Europe, but specimens identified by Storms (1894) as *Galeocerdo acutus* and by Leriche (1927) and Caretto (1972) as *Galeocerdo aduncus* are the teeth of *G. contortus*.

In separating *Galeocerdo contortus* from *G. sp.* we asked ourselves how the Pungo River environment supported two such top predators. We compared the reconstructed dentition of *G. contortus* with those of other carcharhinids; the narrow upper teeth are similar to those of *Negaprion*, which feeds on bony fishes and rays. Unlike *G. sp.*, which has broad-bladed teeth for biting off chunks of flesh from larger animals, but like *Negaprion*, *G. contortus* had teeth for feeding on smaller bony fishes and rays. Therefore, the dentitions of *G. sp.* and *G. contortus* suggest that these two sharks did not compete for the same prey.

Tooth height of the anterior and anterolateral teeth ranges from 12.0 to 19.4 mm (mean=15.7 mm, $n=136$). Mesial-distal width of these teeth ranges from 12.0 to 19.5 mm (mean=15.5 mm, $n=136$). The average tooth size of *G. contortus* is larger than that of *G. sp.*

Galeocerdo cf. G. cuvier Peron and LeSueur, 1822

FIGURES 51, 52*a,b*

Galeocerdo arcticus.—Leriche, 1942:88, pl. 7: figs. 1, 2 [Ashley phosphates (=Goose Creek Formation), middle Pliocene].—[Not *G. arcticus* Faber, 1829=*G. cuvier* Peron and LeSueur, 1822.]

HORIZON.—Yorktown Formation (units 1–3).

REFERRED MATERIAL.—649 teeth, USNM 451213–451218, 451225–451230, 456327, 457287, 457288, 474941–474960; 1 vertebra, USNM 467534.

REMARKS.—These teeth are as large as some of those of the largest individuals of the extant species and are twice as large as those of *Galeocerdo aduncus* (= *G. sp.* herein). They are identical in many respects to the teeth of *G. cuvier*, but unlike those of the extant species, the basal and apical portions of the mesial cutting edge are straight; this edge presents a distinct obtuse angle. In the extant species (Compagno, 1988:279) this obtuse angle is predominant in the juveniles rather than in the adults.

Lawley (1876:16–17) erected *Galeocerdo capellini* on the basis of an isolated tooth from the Pliocene of Tuscany, Italy, but he did not illustrate the holotype. He first illustrated two teeth of this species from the type locality without referring to either of them as the holotype (Lawley, 1881:145–146, pl. 1: fig. 6, pl. 2: fig. 5). De Stefano (1909:578) synonymized this species with *G. aduncus*. The tooth, however, in Lawley's pl. 2: fig. 5, which is enlarged, has compound serrations on its mesial edge; therefore, it cannot be synonymized with *G. aduncus*. Landini (1976:115–116) and Cigala-Fulgosi and Mori (1979:125) noted that the *Galeocerdo* teeth from the Mediterranean Pliocene are indistinguishable from the extant species, and they synonymized the Pliocene species *G. capellini* with *G. cuvier*. A decision, however, about the synonymy of these two species must await the study of dental variation in a larger sample of *G. cuvier* from various parts of the world.

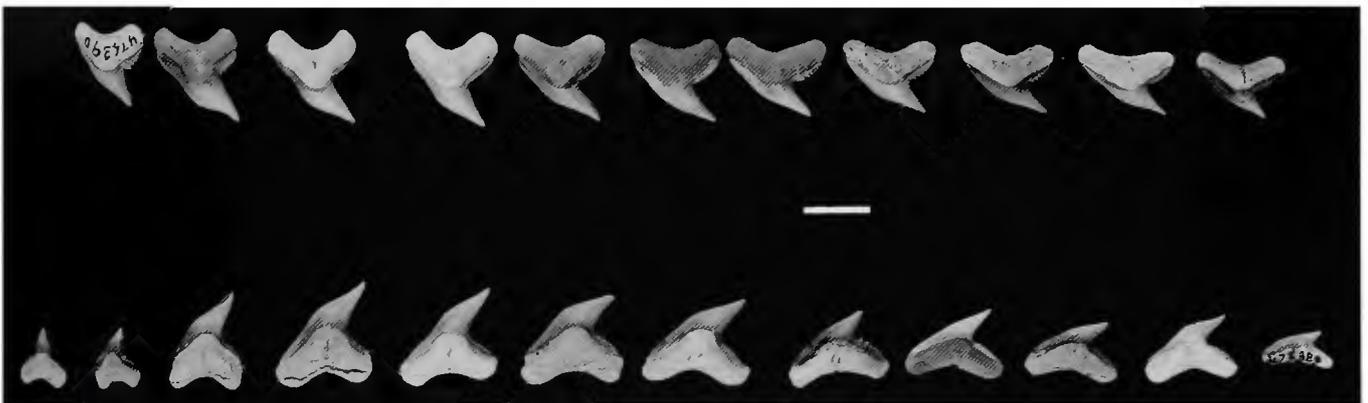


FIGURE 50.—*Galeocerdo contortus*, composite dentition, lingual view. (Scale bar=1.0 cm.)

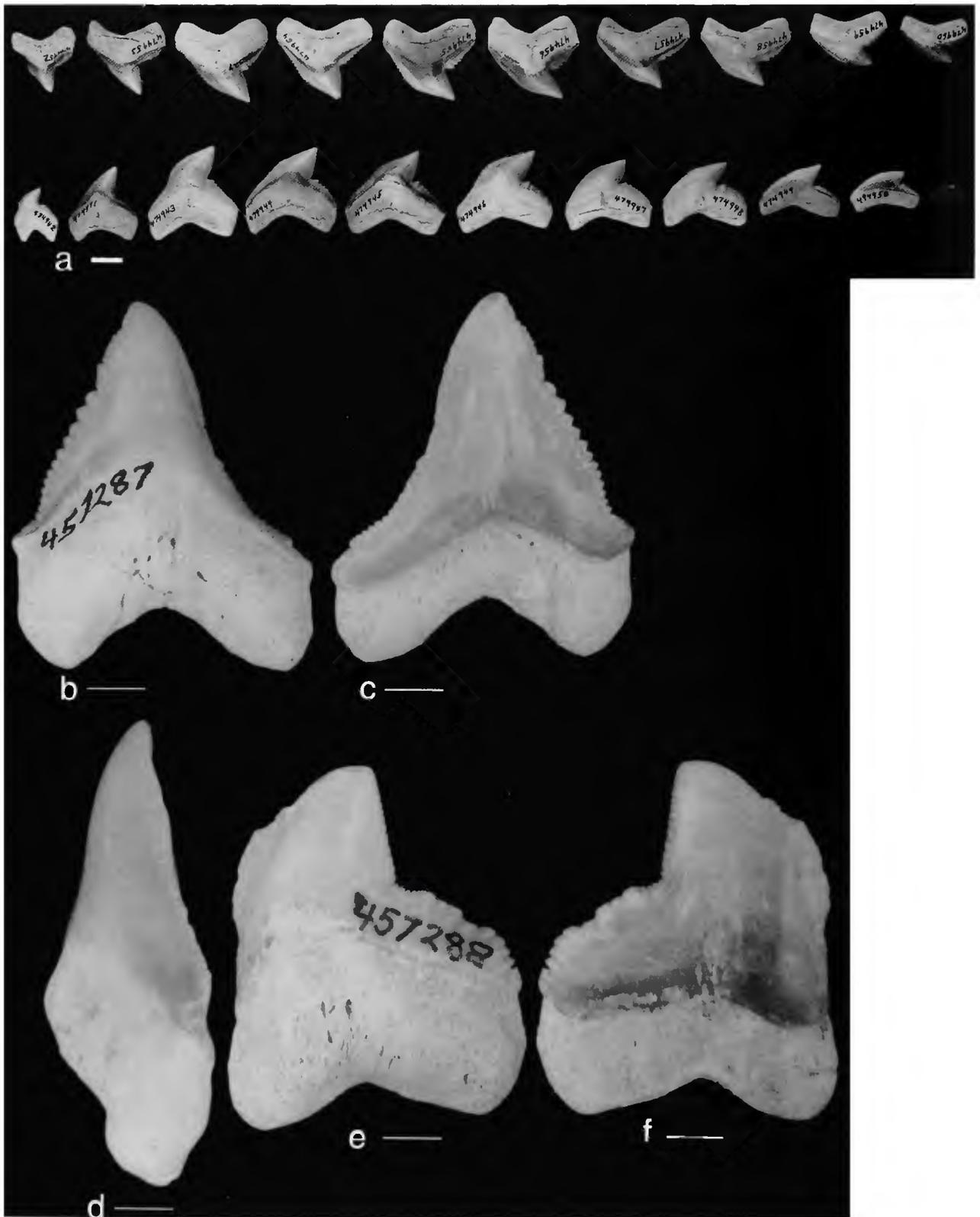


FIGURE 51.—*Galeocerdo* cf. *G. cuvier*: a, composite dentition, lingual view; b, USNM 457287, pathologic tooth, lingual view; c, same specimen, labial view; d, same specimen, lateral view; e, USNM 457288, pathologic tooth, lingual view; f, same specimen, labial view. (Scale bars: a=1.0 cm; b-f=0.33 cm.)

Applegate (1978) erected the species *Galeocerdo rosaliaensis* for Pliocene teeth from Baja California, Mexico, and stated that this species is distinguished "by having the combination of large size and shape similar to *G. cuvier*, but with the upper half of the anterior border flattened" (Applegate, 1978:59). These characters also occur in *G. capellini* and *G. cuvier*; therefore, we believe that Applegate's species is a junior synonym of *G. capellini* Lawley.

A reconstruction of a dentition of this species (Figure 51a) shows that, as in the extant species, the tips of the crowns of the lower teeth have a slight lingual bend, whereas the tips of the upper teeth have a noticeable labial curvature; however, this labial curvature is obscured in teeth that have convex, labial, coronal surfaces. In the lower teeth, a slightly developed torus is present on the lingual surface of the root, and the arch formed by the root is often asymmetrical (skewed distally), whereas the arch of an upper-tooth root is usually more symmetrical.

Two pathologic teeth, USNM 457287 and 457288, were collected by Frank and Becky Hyne (Figure 51b-f). Gudger (1937) and Cadenat (1962) noticed these pathologies in the extant species, but they were unable to identify their cause. In other species of sharks, Cadenat (1962) found that similar deformities were due to the tooth germs being damaged by stingray or sea catfish spines, and Compagno (1984:505) reported that tiger sharks prey on these animals.

Tooth height ranges from 13.5 to 29.1 mm (mean=22.2 mm, $n=38$). Mesial-distal width ranges from 24.4 to 33.0 mm (mean=28.9 mm, $n=38$). Apical angle, the angle between the mesial and distal margins at the apex, ranges from 45° to 65° (mean=52°, $n=33$).

One vertebra (Figure 52a,b) from Lee Creek Mine, probably from the Yorktown Formation, exhibits the characters identified by Kozuch and Fitzgerald (1989) as belonging to *Galeocerdo*. The centrum is aseptate with scattered pores, and the dorsal and ventral foramina are oval and do not extend to the rims of the centrum.

According to Compagno (1984:504), the extant tiger shark is a "wide-ranging coastal-pelagic tropical and warm-temperate shark. ... It often occurs in river estuaries, close inshore off wharves and jetties in harbours." He reported (1984:505) that it preys on a variety of fishes (including sea catfish, tarpon, mackerel, porcupine fishes, and puffers), marine reptiles, sea birds (including shearwaters, frigate birds, pelicans, and cormorants), marine mammals (including seals, monk seals, and odontocete whales), carrion, and mollusks. Compagno (1984:505) reported that "this shark takes marine reptiles more than any species, and frequently preys on sea turtles (green, loggerhead, and ridley turtles) and is one of the most important predators on sea snakes."

Genus *Carcharhinus* Blainville, 1816

Until recently, the taxonomic confusion that existed in the extant sharks of this genus hampered identification of the fossil teeth. Many paleontologists assigned the fossil teeth of *Carcharhinus* to different genera and assigned teeth now attributable to two or more species to one fossil species. Garrick (1982, 1985), however, revised the taxonomy of this genus and included descriptions and illustrations of the teeth of each species. Compagno's work (1984, 1988) also has added important information about the identity of these sharks on the basis of teeth. These works and the available dentitions of the extant species suggest that the differences in dental characters between species is often subtle.

Naylor and Marcus (1994) developed a morphometric method for analyzing the variation in the upper teeth of *Carcharhinus* that segregates the teeth of the many extant species of this genus, and at present Naylor is developing this technique for the study of fossil species of this genus. When developed, his method may facilitate the identification of the Lee Creek Mine species.

The tooth types present in this genus include upper and lower medials or alternates, usually lower symphysials, upper anteriors, upper lateroposteriors, lower anteroposteriors, and upper and lower posteriors. Compagno (1988:310) provided some generic characteristics for the teeth, noting,

[The anterior teeth of the lower jaw are] absent or poorly differentiated. Upper anteriors are usually abruptly narrower based than adjacent laterals. Sexual heterodonty usually absent or weak, ... ontogenic heterodonty very variable in different species. Teeth often have thicker, less oblique cusps, and more numerous, less coarse [sic], and stronger serrations in adults than young. Cusplets, where present, are often better developed in young than adults, where they may disappear entirely or become coarse serrations. [In adults] crowns moderately high and cusps variably short to very long on teeth of both jaws. Cusps variably erect or oblique on the upper teeth, usually more or less erect on lower teeth but oblique in some species. Most species have well-developed serrations along the entire edges of the upper teeth. Some either lack them at all stages (*C. macloiti*) or have them poorly developed or absent in young (*C. brevipinna*, *C. isodon* and *C. leiodon*) and poorly to well-developed in adults (*C. brevipinna* and *C. isodon*). Cusplets are entirely lacking from lower teeth but are variably developed on upper teeth. Some species have distal cusplets on their upper teeth when young but lose them when adult (*C. melonopterus*); in others these persist throughout life (*C. dussumieri*, *C. sealei*, *C. signatus* and *C. macloiti*). Mesial cusplets are sometimes present on upper teeth (as in *C. falciformis*, *C. signatus* adults, and *C. macloiti*). Roots of lower anterolateral teeth usually with nearly straight ventral edges but these are moderately to deeply arched in a few large-toothed species (such as *C. leucas* and *C. ambionensis*). Teeth usually holaulacorhizous, with transverse notches and grooves, but these are sometimes absent. Basal ledges and grooves are vestigial or absent on tooth crowns.

Hundreds of vertebrae assignable to this genus were found at the mine; five different morphotypes, which may be found in one or several species, are illustrated herein (Figure 52c-l). In cranial or caudal view, these aseptate vertebrae may be round or oval in outline; the ventral edge may be concave, and the dorsal edge may be slightly pointed (see Kozuch and Fitzgerald, 1989). The dorsal and ventral foramina also vary in shape, being square, rectangular, or oval. Too few speci-

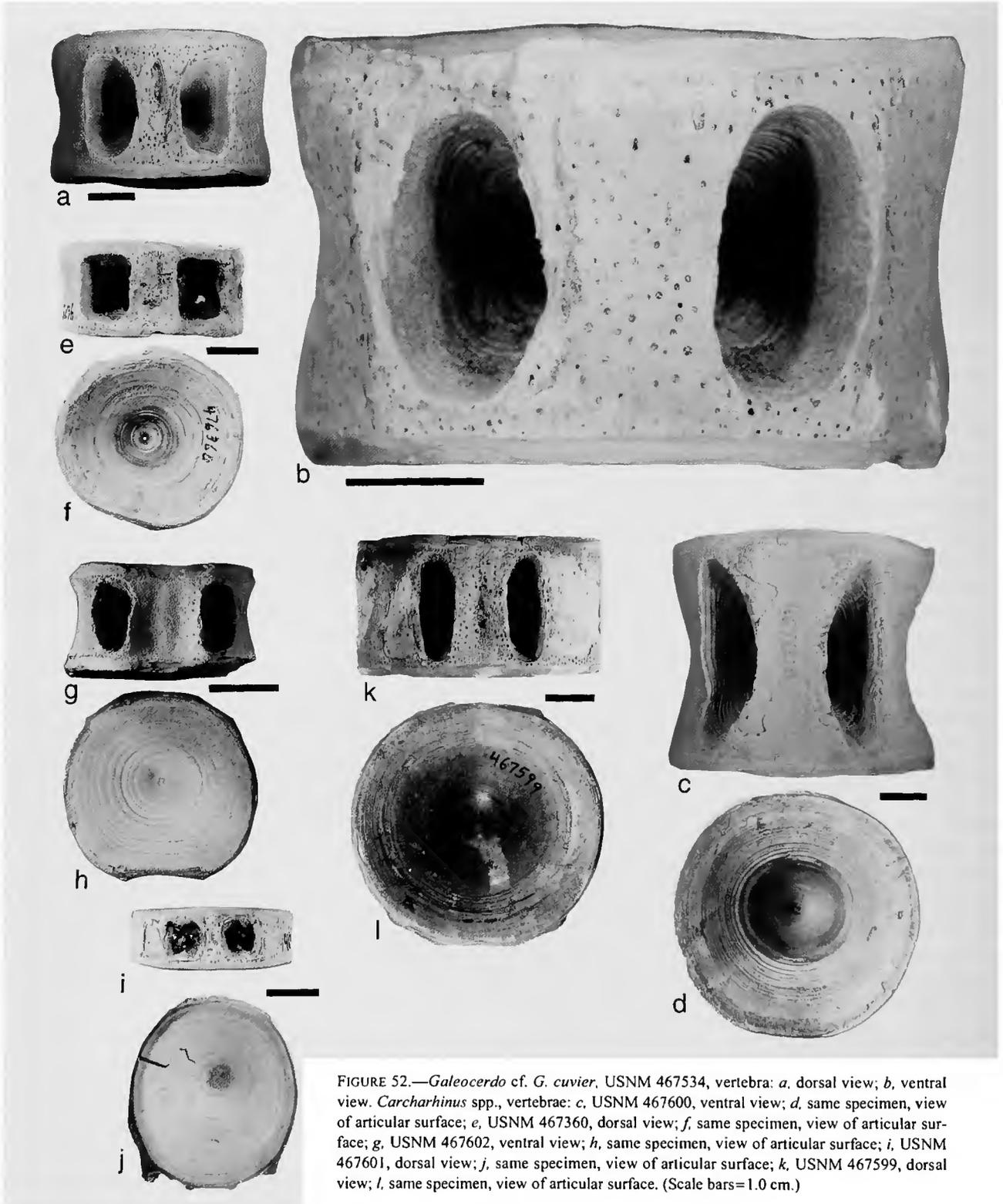


FIGURE 52.—*Galeocerdo* cf. *G. cuvier*, USNM 467534, vertebra: a, dorsal view; b, ventral view. *Carcharhinus* spp., vertebrae: c, USNM 467600, ventral view; d, same specimen, view of articular surface; e, USNM 467360, dorsal view; f, same specimen, view of articular surface; g, USNM 467602, ventral view; h, same specimen, view of articular surface; i, USNM 467601, dorsal view; j, same specimen, view of articular surface; k, USNM 467599, dorsal view; l, same specimen, view of articular surface. (Scale bars=1.0 cm.)

mens of the extant species are available to identify them to species.

At least seven species of *Carcharhinus* may be distinguished tentatively among the Lee Creek Mine teeth: *C. brachyurus*, *C. falciformis*, *C. leucas*, *C. macloiti*, *C. obscurus*, *C. perezi*, and

C. plumbeus. Because tooth morphology varies greatly in the small number of dentitions now available from the extant species, the characters that we use to identify them may, after examination of larger numbers of dentitions, fall within the range of intraspecific variation in two or more species.

Carcharhinus brachyurus (Günther, 1870)

FIGURE 53a

- Corax egertoni* Agassiz, 1843:228, pl. 36: fig. 6 [Miocene, Maryland].
Carcharhinus egertoni (Agassiz).—Antunes and Jonet, 1969–1970:189–190, pl. 15: figs. 110, 111 [middle Miocene, Portugal].
Carcharhinus priscus (Agassiz).—Cappetta, 1970:54–57, pl. 13: figs. 8–19 [middle Miocene, France].
Prionodon egertoni (Agassiz).—Leriche, 1942:80–82, pl. 7: fig. 4 [middle Miocene, Maryland].
Sphyrna americana Leriche, 1942:86, pl. 6: figs. 7, 8 [fig. 6=*C. cf. limbatus*; early Pliocene, South Carolina].
Sphyrna prisca eastmani Leriche, 1942:85, fig. 7, pl. 7: figs. 28–32a [middle Miocene, Maryland].

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—About 500 teeth, USNM 463978–463998, 474888–474902.

REMARKS.—These teeth (Figure 53a) compare favorably with those of mature females of the extant species. Compagno (1984:465) characterized the upper teeth of the living species as having “narrow, strongly serrated, semierect to oblique [crowns], high bent cusps and transverse roots.” All of these characters exist in teeth identified to this species from Lee Creek Mine. In our examination of dentitions (e.g., USNM 197665) from the recent species, we found that the upper teeth may be finely serrated rather than strongly serrated as indicated by Compagno. Although these teeth may be confused with those of *Carcharhinus perezii*, the convexity or angle of the mesial cutting edge gives the tooth a truncated appearance, and the teeth are narrower than those of *C. perezii*.

According to Bass et al. (1973:24), the upper teeth of “large males are distinctly hooked near the tips as compared to those of females.” Garrick (1982:175) added that compared to females, the upper teeth of males are proportionately longer and narrower, are more oblique to curved laterally, and have finer serrations. In females, hooked upper teeth do occur in the more posterior regions of the jaws but not in the anterior regions; it is in the posterior region of the jaw that this sexual dimorphism is more pronounced. None of the upper teeth of this species examined from Lee Creek Mine exhibit the characteristics found in the teeth of males.

Although the two syntypes of *Corax egertoni* were not available to us for this study, one of them (Agassiz, 1843, pl. 36: fig. 6) is identical to those of the extant *C. brachyurus*. According to Agassiz (1843:228), these specimens are from the Tertiary of Maryland. The teeth of *C. brachyurus* are common in the Calvert Formation of Maryland and Virginia.

At Lee Creek Mine, the anterolateral teeth range from 1.2 to 1.5 cm in height (mean=1.4 cm, $n=21$) and from 1.3 to 1.8 cm in width (mean=1.6 cm, $n=21$); in the extant species, teeth of this size are found in individuals of 2 to 3 m TL.

According to Compagno (1984:465), the extant species is poorly known; it inhabits inshore to offshore warm-temperate waters from the surfline to at least 100 m in depth. It eats a variety of bony fishes, including sea catfish, porgies, and hake, as well as spiny dogfish, rays, squid, and cuttlefish.

Carcharhinus falciformis (Bibron, 1841, in Müller and Henle, 1839–1841)

FIGURE 53b–f

- Prionodon egertoni* (Agassiz).—Leriche, 1942:80–82, pl. 7: fig. 3 [Pliocene, North Carolina, South Carolina].

HORIZON.—Pungo River Formation (units 2–4).

REFERRED MATERIAL.—5 teeth, USNM 476244–476248.

REMARKS.—Among the teeth from Lee Creek Mine (Figure 53b–f), we were able to identify only the uppers, which are identical with those of the extant species. On the lingual face of the root and penetrating its basal margin there is a well-developed transverse groove. The distal cutting edges of these moderately broad-bladed teeth have a shallow, angular notch; apical to this notch the cutting edge is perpendicular to a line tangent to the basal margin of the root; basal to this notch, there is an enamel blade, which is finely serrated like the apical portion of the cutting edge. On their mesial cutting edges, at about the midpoint between the tip and the base of the cutting edge, there is a gap in the serrations. Basal to this gap the serrations are larger and therefore coarser. With the exception of this gap, the mesial cutting edge is fairly straight from the base to the tip of the crown. This gap in serrations and the straightness of the mesial cutting edge are characteristic of *Carcharhinus falciformis*.

In the extant species, the upper teeth vary somewhat in morphology. In USNM 232776, from a 2 m TL female, the tips of the crowns are slightly hooked, and in USNM 196026, from a 2.27 m TL female, the teeth are not hooked but are more distally inclined. The mesial gap in the serrations is absent. In USNM 232780, from an unsized male, the mesial edge has a dog-leg turn as in *C. brachyurus*, and in USNM 112584, from 2.3 m TL male, the shallow, distal notch is rounded rather than angular.

Among the Lee Creek Mine specimens, the only anterior anterolateral tooth present measures 14.2 mm in height and 15.0 mm in width; it came from an individual of probably 3 m TL.

The extant silky shark inhabits warm, nearshore waters from depths of 18 to 500 m. It feeds primarily on bony fishes, including sea catfish, yellowfin tuna, albacore, and porcupine fish (Compagno, 1984:471–472).

Carcharhinus leucas (Valenciennes, 1839, in Müller and Henle, 1839–1841)

FIGURE 54a

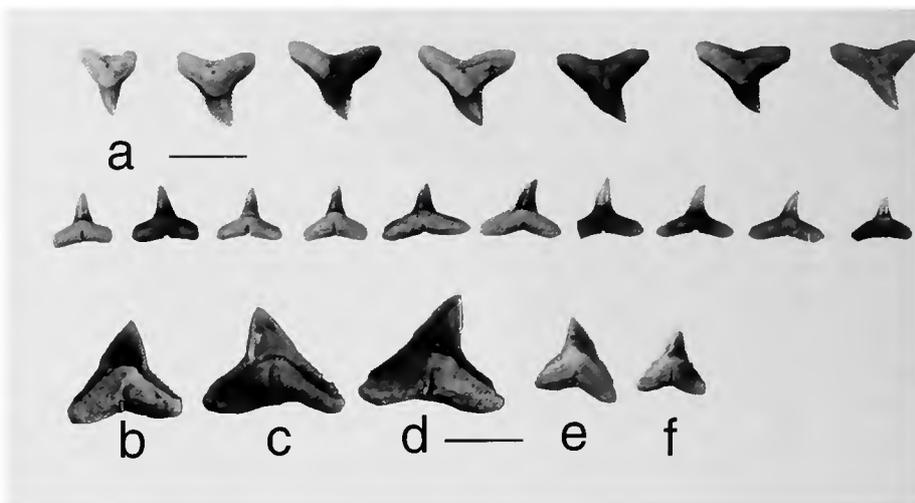
- Corax egertoni* Agassiz, 1843:228, pl. 36: fig. 7 [Miocene, Maryland].
Prionodon egertoni (Agassiz).—Leriche, 1942:80–82, pl. 7: figs. 11, 12.

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1–3).

REFERRED MATERIAL.—About 200 teeth, USNM 278376, 278379, 278381, 278386, 278398, 278411, 278428, 278436, 282953, 457079, 457084, 459778–459820, 474961.

REMARKS.—These teeth (Figure 54a), abundant in the Yorktown Formation and very rare in the Pungo River Formation at

FIGURE 53.—*Carcharhinus brachyurus*: a, composite dentition. *Carcharhinus falciformis*: b, USNM 476244, upper anterolateral tooth, lingual view; c, USNM 476245, upper anterolateral tooth, lingual view; d, USNM 476246, upper anterolateral tooth, lingual view; e, USNM 476247, upper anterior tooth, lingual view; f, USNM 476248, upper symphysial tooth, lingual view. (Scale bars: a=1.0 cm; b–f=1.0 cm.)



Lee Creek Mine, are identical to those of the extant species. The lower teeth have thick crowns and roots, and the cutting edges are finely serrated. In some lower teeth the transverse groove is well developed and penetrates the basal margin of the root so as to be visible from the labial side of the tooth; in others, which appear to be functional teeth, the transverse groove is only partially developed or is absent. The basal margin of the root is arcuate. Punctae may be present on the labial face of the root and also on the roots of the upper teeth.

The form of the upper teeth tends to be equilateral rather than elongate. Both cutting edges are finely serrated, with coarser serrations basally. The mesial cutting edge of the crown is straight, wavy, or slightly convex apically; the shallow, angular notch is absent. The distal cutting edge is usually concave, but a shallow, angular notch may be present. The basal margin of the root is usually arcuate but may be angular. In one recent dentition (USNM uncataloged, vertebrate paleontology synoptic collection) the roots of the upper teeth are nearly lobate.

The upper teeth of this species are very similar to those of *Carcharhinus longimanus*. Although the teeth of the latter species are usually more elongate than are those of *C. leucas*, one dentition (USNM 183804) has teeth that are equilateral in form, giving them a stocky appearance. These teeth, however, have broader crowns than do those of *C. leucas*, and in *C. leucas* the distal cutting edge in the area of the crown foot usually forms a noticeable blade.

The lower teeth also are similar to those of *C. longimanus*. In the latter species the crowns of the anteriors and the anterior laterals are asymmetrical; in *C. leucas* they are almost symmetrical, but for both species, these observations were made on a small number of dentitions, and in larger populations of these species they may not be valid.

One of Agassiz's two syntypes (1843, pl. 36: fig. 7) for *Coxax egertoni* compares favorably with a lateral tooth of *Carcharhinus leucas*.

The teeth identified and figured by Leriche (1942) as *Prionodon egertoni* represent several species of *Carcharhinus*, but

his figs. 11 and 12 of pl. 7 compare favorably with the teeth of the extant *C. leucas*.

Cappetta (1987:125–126, fig. 106D) identified a tooth from the Yorktown Formation at Lee Creek Mine as *Pterolamiops longimanus*; *Pterolamiops* is a junior synonym of *Carcharhinus* (Compagno, 1988), and Cappetta's tooth also may belong to *C. leucas*.

The anterolateral teeth from the Pungo River Formation range from 1.7 to 2.0 cm in height (mean height=1.9 cm, $n=8$) and from 1.6 to 2.2 cm in width (mean width=1.9 cm, $n=8$), which falls in the range of teeth sizes in the extant species from individuals of 2 to 3 m TL. Those from the Yorktown Formation range from 1.9 to 2.4 cm in height (mean height=2.1 cm, $n=16$) and from 1.9 to 2.5 cm in width (mean width=2.3 cm, $n=16$) and probably came from individuals of 2 to 4 m TL.

Compagno (1984:479) stated that the extant species inhabits shallow, tropical and subtropical waters "less than 30 m deep and occasionally less than a meter deep, but ranging into deeper water close to shore down to at least 152 m depth." The extant shark feeds on bony fishes, including tarpon, sea catfish, tuna, sea bass, and bluefish, and on sharks, rays, sea turtles, birds, whales, and invertebrates (Compagno, 1984:480).

Carcharhinus macloti (Müller and Henle, 1839)

FIGURE 54b

Hypoprion acanthodon (Le Hon).—Antunes and Jonet, 1969–1970:187, pl. 15: figs. 100–108 [Miocene, Portugal].

HORIZON.—Extremely abundant in the ore layers of the Pungo River Formation (units 1–3); less abundant but still the dominant carcharhinid in units 4 and 5; uncommon and probably redeposited in the base of the Yorktown Formation (unit 1).

REFERRED MATERIAL.—More than 400 isolated teeth, USNM 207464, 464164–464179, 464181, 464183–464185, 474903–474914.

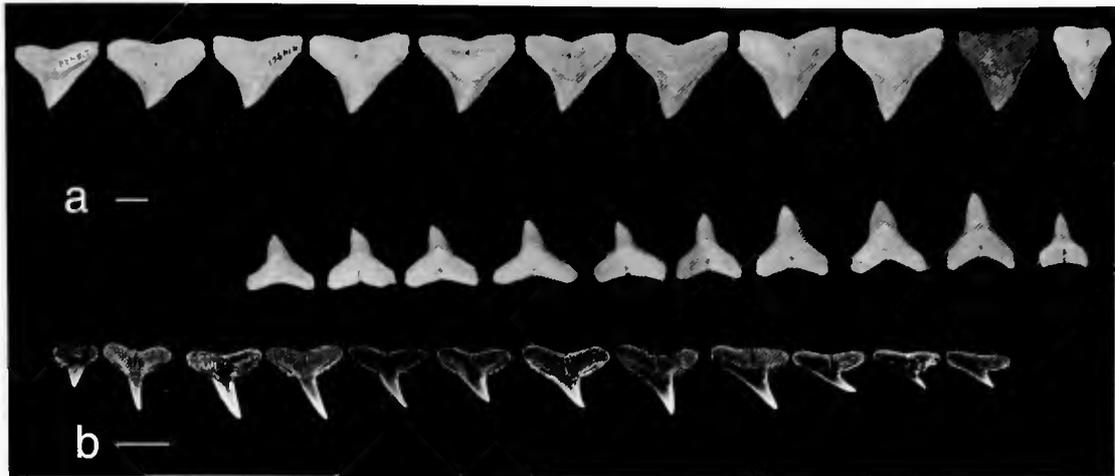


FIGURE 54.—*a*, *Carcharhinus leucas*, composite dentition; *b*, *Carcharhinus macloiti*, composite upper dentition. (Scale bars=1.0 cm.)

REMARKS.—Until recently this species was assigned to the genus *Hypoprion*, but Raschi et al. (1982) have shown that this genus is a junior synonym of *Carcharhinus*. Compagno (1984, 1988) and Garrick (1985) concurred with their decision.

The upper teeth (Figure 54*b*) are small (3–7 mm in height, 3–8 mm in width), triangular, acutely pointed, and, except on the mesial and distal enamel blades, have smooth cutting edges. In two-thirds of the sample, the mesial enamel blade is serrated with one to five cusplets (mean=1.6; $n=320$). These serrations, which are unevenly developed, range from distinct, well-differentiated cusplets to indistinct, wavy interruptions of the mesial cutting edge. The distal enamel blade is rounded or rectilinear, with one to seven poorly to well-developed cusplets (mean=3.1; $n=309$). The anterior teeth tend to be erect and bilaterally symmetrical, with short, convex, mesial and distal enamel blades. Toward the commissure of the jaws, the more posterior teeth become increasingly inclined, with a correlated deepening of the distal notch formed between the main cusp and its enamel blade. The root's rounded, lingual face is divided by a rather broad transverse groove, which penetrates the basal margin of the root.

According to Garrick (1985:17), the number of large serrations present on the upper teeth is variable; he reported that "in four juveniles and subadults (both sexes)... there were 1–2 serrae laterally and 0–1 medially, whereas in a mature female... there were up to 4 laterally and 3 medially; contrasting this with a mature male... [the male] had not more than 2 or 3 laterally (and these poorly defined) and 0 medially; the difference between these two adults may reflect either sexual dimorphism or geographic variation."

The lower teeth are smaller than the upper teeth and are symmetrical and broad based, have narrow principal cusps, and lack cusplets and serrations.

The anterolateral teeth of this species range from 5.0 to 7.3 mm in height (mean height=5.6 mm, $n=21$) and from 5.0 to

9.1 mm in width (mean width=6.6 mm, $n=21$). Although we did not have any dentitions from individuals of known size, these measurements fall within the size range for the extant species, 69–100 cm TL (Compagno 1984:487).

According to Compagno (1984:487), this tropical, little-known, inshore shark inhabits continental and insular shelves.

Carcharhinus obscurus (Le Sueur, 1818)

FIGURE 55*a*

HORIZON.—Yorktown Formation (units 1–3).

REFERRED MATERIAL.—About 110 teeth, USNM 456596–456635, 457077–457089.

REMARKS.—These teeth (Figure 55*a*) compare very closely with those of the extant species. The upper teeth of this species are identified by their vertical to almost vertical distal cutting edges and by their apically convex mesial cutting edges; the tip of the tooth appears to be deflected distally. We could not identify the lower teeth with certainty.

In three dentitions of the extant species, we observed the following morphological variations. The number of rows of symphyseal teeth varies from one to three in the lower jaws and from one to two in the upper jaws. In AMNH 89233 SD, in the anteriormost upper teeth near the apex, the mesial cutting edge is straight rather than convex. In both the upper and lower teeth of the same dentition, the root lobes of the teeth form obtuse rather than straight angles, and in the lower teeth the basal constriction of the cutting edges is absent. A juvenile dentition (AMNH 89269 SD) has lower teeth with smooth to incipiently serrated cutting edges and has upper teeth with incipient serrations present.

The upper anterolateral teeth from Lee Creek Mine range in height from 1.7 to 2.2 cm (mean=1.9 cm, $n=32$) and from 1.8 to 2.5 cm in width (mean=2.1, $n=32$). In the extant species, teeth of this size are found in sharks of 3 m TL.

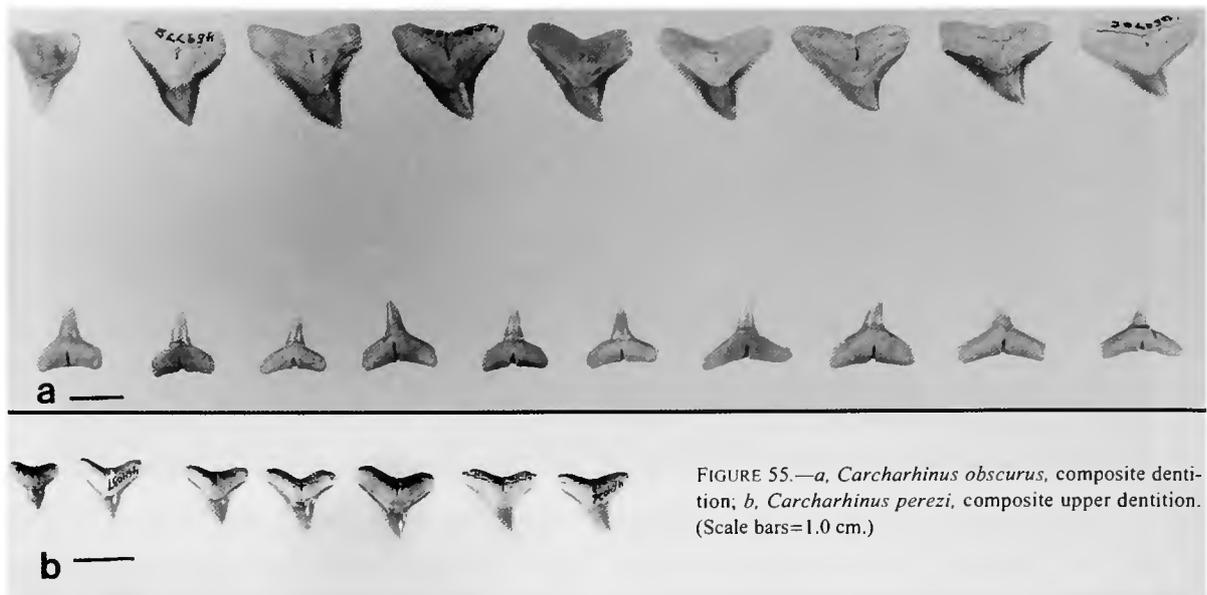


FIGURE 55.—*a*, *Carcharhinus obscurus*, composite dentition; *b*, *Carcharhinus perezii*, composite upper dentition. (Scale bars=1.0 cm.)

According to Compagno (1984:490–491), the extant dusky shark is “a common, coastal-pelagic, inshore and offshore warm-temperate and tropical shark of the continental and insular shelves and oceanic waters adjacent to them.” This species feeds on bony fishes, such as tunas, barracuda, jacks, and bluefish; sharks, as well as sawsharks, angelfish, and dogfish; and invertebrates.

Carcharhinus perezii (Poey, 1876)

FIGURE 55*b*

HORIZON.—Pungo River Formation (units 3–5); Yorktown Formation (unit 1).

REFERRED MATERIAL.—50 teeth, USNM 463977, 464007–464010, 464012, 464014–464026, 464028–464046, 474874–474887.

REMARKS.—The teeth from Lee Creek Mine (Figure 55*b*) compare favorably with those of the extant species. In the extant species, the crowns of the upper teeth are fairly narrow, and except for the teeth in the two anteriormost positions, they incline distally; the distal angular notch may be well developed, or it may be rounded. The mesial cutting edge ranges from being slightly convex to being nearly straight. In the lower teeth, the erect crowns have complete, smooth cutting edges. These same characters are found in the Lee Creek Mine teeth.

The Lee Creek Mine teeth range in height from 1.3 to 1.8 cm (mean=1.4 cm, $n=40$) and in width from 1.3 to 2.2 cm (mean=1.7 cm, $n=37$); in the extant species teeth of this size are found in individuals of about 2 m TL.

Compagno (1984:493) reported that this tropical shark is found inshore on “continental and insular shelves, at depths down to at least 30 m.” This shark eats bony fishes.

Carcharhinus plumbeus (Nardo, 1827)

FIGURE 56

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (unit 1).

REFERRED MATERIAL.—6 specimens, USNM 459788, 474962–474965, 476293.

REMARKS.—The upper teeth of this species are of moderate width; they are narrower and more elongate than those of *Carcharhinus obscurus*, and they lack the apical convexity of the cutting edge that characterizes the latter species. They may be confused with the elongate teeth of *C. albimarginatus*, but in this last species the tips of the teeth are hooked, and midway between the tip and the root on both cutting edges there is a noticeable, shallow notch. After the seventh tooth from the symphysis, the mesial notch is lost.

An amateur collector, Bill Heim, first identified a tooth from Lee Creek Mine that matches perfectly with the first upper anterolateral tooth in the dentition (Figure 56*a*) of the extant species. Five other teeth (Figure 56*b–e*) were recovered from the spoil piles; in one of these, which may not be a fully functional tooth, the transverse groove is absent.

The three teeth that are from the anterior part of the jaw measure 1.4 cm, 1.6 cm, and 1.9 cm in height. Extant sandbar sharks with teeth of this size are about 2 m in total length.

Compagno (1984:494) stated that the extant species is a “coastal-pelagic shark, of temperate and tropical waters, found on continental insular shelves and in deep water adjacent to them.” It feeds on “relatively small bottom fishes” (Compagno, 1984:495), including porgies and searobins, and on mollusks and crustaceans.

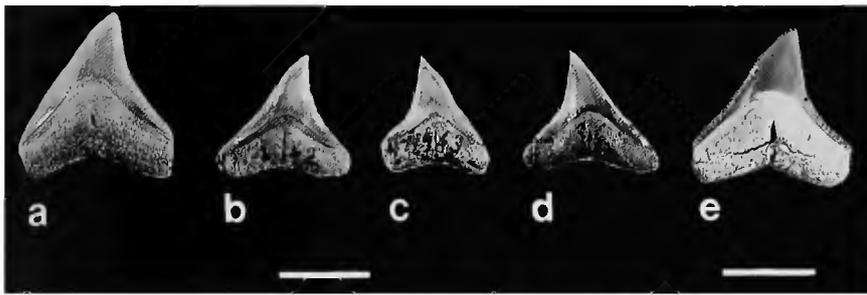


FIGURE 56.—*Carcharhinus plumbeus*, upper anterolateral teeth: a, USNM 459788, lingual view; b, USNM 474962, lingual view; c, USNM 474963, lingual view; d, USNM 474964, lingual view; e, USNM 476293, lingual view. (Scale bars: a–d=1.0 cm; e=1.0 cm.)

Rhizoprionodon? sp.

FIGURE 57a–g

HORIZON.—Pungo River Formation (units 1–5).

REFERRED MATERIAL.—About 50 isolated teeth, USNM 207535–207540.

REMARKS.—In the extant *Rhizoprionodon*, Compagno (1988:295–296) noted the following: “Dignathic heterodonty weak and best developed in anteroposteriors closest to the symphysis, these teeth having higher roots and crowns and more arched root edges in the upper jaw than in the lower. Upper laterals have slightly higher crowns, slightly stouter cusps, and less concave mesial edges than the lowers. Tooth row groups include small, weakly differentiated, and often double-bladed and erect-cusped medials, 2–3 rows of weakly differentiated upper anteriors, sometimes a lower symphyseal, and poorly differentiated posteriors. The anteriors differ from adjacent laterals in having narrower and higher crowns. . . Fine serrations present on teeth of adults of larger species. . . Tooth roots and crowns relatively low and deep. Teeth holaulacorhizous, with transverse notches and grooves. Basal ledges and grooves absent or poorly defined on teeth.”

Springer (1964) revised and redivided the genus *Scoliodon* into three genera: *Rhizoprionodon*, *Loxodon*, and *Scoliodon* sensu stricto. Each has very similar teeth, all of which are convergent or parallel to those of some species of *Sphyrna*. Consequently, Springer was pessimistic about identifying the isolated teeth of these genera.

Compagno (1984, 1988) included tooth characters in his diagnoses for the species of *Rhizoprionodon*, but with one exception, he also listed these as characters for *Scoliodon* and *Loxodon*. The one exception is the presence of serrations in the teeth of *Rhizoprionodon*. The Lee Creek Mine teeth, which have smooth or weakly serrated cutting edges, are identical in form to those Compagno (1988, pl. 22G, 23G) illustrated, but until more is known about the usefulness of these dental characters, we assign fossil teeth to this genus only tentatively.

These fossil teeth (Figure 57a–g) are characterized by a combination of concave mesial cutting edges both on upper and lower teeth, smooth or indistinctly serrated cutting edges, deeply notched distal cutting edges, erect crowns, and distinct

enamel shoulders. These characters, except for the notch on the distal enamel shoulder, are shared more or less by all species of *Sphyrna* with nonserrated teeth. Teeth from the lower jaw of these species of *Sphyrna* (e.g., *S. tiburo*) are similar to those from the upper jaw of *Rhizoprionodon*, but differences exist in their proportions. Relative to their width, the crowns in sphyrnid teeth are higher than those of *Rhizoprionodon*, and the primary cusp is relatively wider. The Lee Creek Mine teeth closely resemble the more distinctive lower teeth of the extant *Rhizoprionodon terraenovae*. We found no certain criteria to eliminate *Loxodon* or *Scoliodon*.

European Miocene representatives of the *Scoliodon* group have been referred to *Rhizoprionodon taxandriae* (Leriche, 1926; Antunes and Jonet, 1969–1970; Cappetta, 1970). Leriche’s (1926, pl. 28: figs. 7–10) specimens of *Carcharias* (*Scoliodon*) *taxandriae* are poorly preserved, and certainly not all of them are *Scoliodon* sensu lato. The specimen in Leriche’s fig. 7 is indeterminate; Cappetta (1970:62) thought it was *Galeorhinus affinis*. Leriche’s fig. 10 probably represents a small sphyrnid, and the specimens in his figs. 8 and 9 are either upper teeth of *Rhizoprionodon* or lower teeth from a smooth-toothed sphyrnid. Until these latter two specimens can be compared to the teeth of the extant species of *Rhizoprionodon* and *Sphyrna*, the validity of *R. taxandriae* remains in doubt.

Three of the fossil teeth are from the more anterior portion of the jaw; they range in height from 3.2 to 5.2 mm (mean=4.1) and in width from 4.3 to 5.7 mm (mean=4.3).

The extant species, *Rhizoprionodon terraenovae*, inhabits coastal warm-temperate to tropical seas from the intertidal zone to a depth of possibly 280 m (Compagno, 1984:533); it feeds on small bony fishes, including small jacks and tilefish.

Genus *Negaprion* Whitley, 1940 (lemon sharks)

Compagno (1988:342) characterized the teeth of this genus as follows: “Tooth row groups include upper and lower medials, lower symphysials [sic], upper anteriors, upper lateroposteriors, and lower anteroposteriors (or upper laterals, lower anterolaterals, and lower posteriors). Anteriors differ from adjacent laterals only in being smaller and narrower relative to their heights. Sexual heterodonty apparently little developed. Ontogenic het-

erodonty moderate: small specimens of 500–600 mm. total length have more oblique cusps, weaker mesial blades, and lack serrations on the blades of their upper lateroposterior teeth, but larger examples between 1–2 meters length have more erect cusps, stronger mesial blades and basal serrations.... Cusplets present on upper teeth of individuals below 650 mm. but lost in larger specimens. Roots of lower anterolateral teeth with nearly straight to slightly arched ventral edges. Teeth holaulacorhizous, with very weak transverse grooves and transverse notches weak or absent. Basal ledges very weak but faintly indicated even in teeth of adults, sometimes with nodular edge representing vestigial transverse ridges.”

Negaprion eurybathrodon (Blake, 1862)

FIGURE 57h–j

Carcharias collata Eastman, 1904:85–86, pl. 32: figs. 3–5 [Miocene, Maryland].

Carcharias magna (Cope).—Eastman, 1904:86, pl. 32: figs. 6, 7 [Calvert Formation, Maryland].

Sphyrna magna (Cope).—Leriche, 1942:85 [citation].

?*Aprionodon* cf. *collata* (Eastman).—Leriche and Signeux, 1957:35, pl. 11: figs. 12, 13 [Miocene, France].

Negaprion cf. *eurybathrodon* (Blake).—Antunes and Jonet, 1969–1970: 175–177, pl. 13: figs. 80, 81 [middle Miocene].

Negaprion kraussi (Probst).—Cappetta, 1970:52–53, pl. 15: figs. 1–10, ?11, 12, 14–17 [early Miocene, France].

HORIZON.—Pungo River Formation (unit 4 or 5; 1 tooth); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—31 teeth, USNM 207490–207492, 451333–451340.

REMARKS.—Blake (1862) described a Miocene tooth of this species as that of *Lamna eurybathrodon*. White (1955) observed that the carcharhinid tooth recorded by Blake was actually a *Negaprion* upper tooth and that teeth of the same general form were widely distributed in Miocene deposits. In the same paper he noted correctly that the teeth described by Eastman (1904) as *Carcharias collata* were the lower teeth of *Negaprion*, and that the teeth figured by Eastman (1904) and referred to *C. magna* (Cope) also should be referred to *Negaprion*, but he hesitated to synonymize *C. magna* and *N. eurybathrodon*. More recently, Antunes and Jonet (1969–1970) have rightly synonymized the two species. Cappetta (1970:52) referred his specimens of *Negaprion* to *N. kraussi* (Probst), but Antunes and Jonet (1969–1970:176) pointed out that the specimens that Probst described as *Carcharias (Scoliodon) kraussi* were in poor condition and may be either *Sphyrna* or *Negaprion*. If they are *Negaprion* they are a junior synonym of *N. eurybathrodon*; thus *N. kraussi* of Cappetta, but not necessarily *C. (Scoliodon) kraussi* Probst, is a junior synonym of *N. eurybathrodon* (Blake). If, however, these teeth are identical to those of *N. brevirostris* (Poey), as they appear to be, *N. brevirostris* must be synonymized with *Negaprion eurybathrodon*.

The anterolateral teeth from Lee Creek Mine range in size from 1.4 to 2.1 cm (mean=1.6 cm, $n=9$). In the extant lemon

shark, teeth in this size range are found in sharks of 2.1–3 m TL, which is the size range for mature adults (Compagno 1984:520).

According to Compagno (1984:519–520), this shark inhabits inshore, tropical waters from the intertidal zone down to at least 92 m; it feeds on bony fishes, including sea catfishes, jacks, and porcupine fishes, on stingrays, occasionally on sea-birds, and on invertebrates.

Genus *Triaenodon* Müller and Henle, 1837 (whitetip reef sharks)

In the extant species of this shark, the upper teeth can be differentiated into two medials, one symphyisial, three anteriors, 15 to 18 laterals, and one or two posteriors; in the lower jaw, aside from two medials, one symphyisial, and (sometimes) one or two posteriors, anterior and lateral teeth cannot be differentiated (Compagno 1988:352). When the posterior teeth can be identified, the remaining lower teeth are called anterolaterals, and when the posterior teeth cannot be differentiated, they are called anteroposteriors.

Compagno (1988:352) characterized the teeth of this genus as follows: “Sexual heterodonty apparently weak or absent. Ontogenic heterodonty moderately developed, with adults having narrower and more differentiated medials than young. Young also have mesial cusplets absent from a few more rows of teeth adjacent to the ends of the dental bands than adults and have slightly more oblique cusps.” Returning to the description of adult teeth, he continued, “Mesial edges differentiated into cusplets on most teeth except for a variable number of rows near the ends of the dental bands. Primary cusps present on all teeth, erect towards the symphysis but becoming oblique towards the ends of the dental bands. Primary cusps narrow-based and high. Distal edges strongly notched on all teeth, but serrations are absent. Tooth roots and crowns relatively high and moderately compressed. Teeth holaulacorhizous, with well-developed transverse grooves and notches. Basal ledges and grooves absent from teeth.”

Triaenodon obesus (Rüppell, 1835)

FIGURE 57k–n

Otodus callicus Philippi, 1846:24, pl. 2: figs. 5–7 [early Miocene, Cassel].

Lamna callica (Philippi).—Leriche, 1926:395–397, pl. 28: figs. 50–52 [“Bolderian,” Belgium]; 1927:65–68, pl. 7: figs. 12–15, 17, 18 [Miocene, Switzerland].—Cappetta, 1970:23–25, pl. 4: figs. 5–8 [Helvetian, France].

HORIZON.—Pungo River Formation (units 1–3).

REFERRED MATERIAL.—5 teeth, USNM 283497, 312434, 312436, 459824, 459825.

REMARKS.—The five teeth recovered from the Pungo River Formation (Figure 57k–n) are the typical upper lateral teeth of *Triaenodon*. These teeth are extremely labiolingually compressed and have tall, distally inclined and broad-based crowns that are bordered by lingually bent, large, lateral cusplets; at the

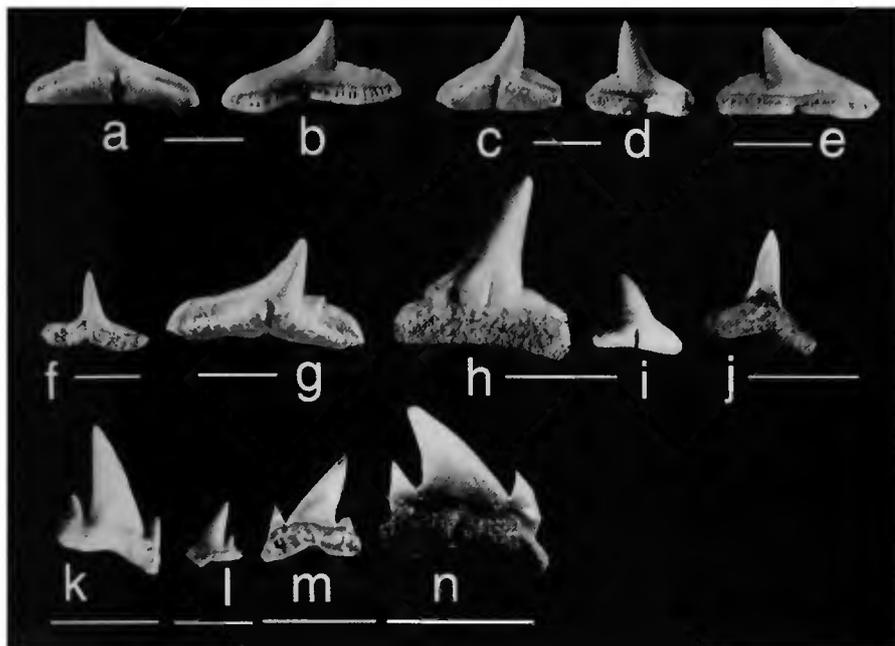


FIGURE 57.—*Rhizoprionodon?* sp.: a, USNM 207535, lower lateral tooth, lingual view; b, same specimen, labial view; c, USNM 207536, lower anterior tooth, lingual view; d, USNM 207537, lower anterior tooth, labial view; e, USNM 207538, lower anterior tooth, labial view; f, USNM 207539, male? lower anterior tooth, lingual view; g, USNM 207540, lower lateral tooth, lingual view. *Negaprion eurybathron*: h, USNM 207490, upper anterior tooth, labial view; i, USNM 207491, upper lateral tooth, lingual view; j, USNM 451338, lower lateral tooth, lingual view. *Triaenodon obesus*: k, USNM 312436, upper lateral tooth, labial view; l, USNM 312434, upper lateral tooth, lingual view; m, USNM 459824, upper anterolateral tooth, lingual view; n, USNM 459825, lower lateral tooth, lingual view. (Scale bars: a–g, l=0.5 cm; h–k, m=1.0 cm; n=1.25 cm.)

base of the crown there is a basal ledge. On the lingual face of the root, a transverse groove is usually present.

Philippi's holotype (1846, pl. 2: figs. 5–7) of *Otodus cattica* is identical to an upper lateral of *Triaenodon obesus*, with its extremely labiolingually compressed, distally inclined crown, large lateral cusplets, and shallow root. A transverse groove, which Philippi did not mention, is not evident in his fig. 6, but if this tooth was not functional or if the groove was not well defined by its tooth germ, the groove would be absent.

Antunes (1969–1970) used teeth from two genera to reconstruct a tooth set of *Lamna cattica totuserrata* from the Miocene of Angola. The anterior teeth illustrated by Antunes (1969–1970, pl. 1: fig. 1, pl. 2: figs. 17–19, pl. 3: figs. 20–24) are identical to the upper and lower anterior teeth of *Carcharias cuspidata*, and the lower lateral teeth (his pl. 3: figs. 25, 26) also are identical to those of *Carcharias cuspidata*. Those that Antunes (1969–1970) identified as upper symphyseal teeth, which are symphyseal (his pl. 1: fig. 2) and intermediate (his pl. 1: fig. 3) teeth, also belong to *C. cuspidata*. (Some of these teeth bear on their cutting edges what appear to be incipient serrations, which are not as well developed as those on the other teeth in his reconstruction that are assignable to *Triaenodon*. The cutting edges of the functional teeth of the extant *Carcharias taurus* are often nicked, giving them the appearance of bearing incipient serrations.) The specimens Antunes (1969–1970, pl. 2: figs. 10–16) identified as upper lateral teeth, except for their finely serrated cutting edges, are identical to those of *Triaenodon obesus*. Antunes's reconstructed tooth set, therefore, includes teeth from two different genera.

We do not think that serrations warrant separating the fossil teeth from *Triaenodon* because at least two genera in the Carcharhiniiformes, *Carcharhinus* and *Sphyrna*, contain species with smooth and serrated teeth. We believe, therefore, that serrations are not a valid criterion for assigning these teeth to a genus other than *Triaenodon*.

On the basis of Antunes's reconstruction, Cappetta (1987:95) assigned *Lamna cattica* and *L. totuserrata* to the genus *Carcharoides* Ameghino, 1901. In view of the above, we believe this assignment is unwarranted.

The referred teeth measure as follows (USNM 312434 is incomplete).

Catalog number	Height (mm)	Width (mm)
USNM 283497	10.2	10.1
USNM 312436	10.2	8.9
USNM 459824	13.4	13.2
USNM 459825	6.5	7.2

Compagno (1984:537) reported that the extant species is a bottom-oriented shark that inhabits tropical, shallow, clear water on or near coral reefs; it usually is found in waters of 8 to 40 m in depth, but it has been found occasionally as deep as 110 to 330 m.

Family SPHYRNIDAE (hammerhead sharks)

Genus *Sphyrna* Rafinesque, 1810

Compagno (1988:363) characterized these teeth as having weak ontogenetic heterodonty, with the heights of the cusps and crowns relative to root width lower in juveniles than in

adults. Under the subgenus *Sphyrna*, which includes all of the Lee Creek Mine hammerheads, Compagno (1988:366) described the teeth as follows: "Cusps of anterolateral teeth [lowers] slender and almost needlelike. Posterior teeth mostly cuspidate, not modified as molariform crushers. Basal ledges and grooves obsolete." Three species of hammerhead sharks occur at Lee Creek Mine, *Sphyrna lewini*, *S. cf. S. media*, and *S. zygaena*.

Sphyrna lewini (Griffith and Smith, 1834)

FIGURE 58a-c

HORIZON.—Yorktown Formation (unit 3).

REFERRED MATERIAL.—4 teeth, USNM 459728–459731.

REMARKS.—The teeth from Lee Creek Mine (Figure 58a-c) fit Compagno's (1984:545) description of teeth from the extant species: "Anterior teeth with moderately long, stout to slender cusps, smooth or weakly serrated, posterior teeth mostly cuspidate and not keeled and [not] molariform."

The anterior teeth of this shark range from 7.3 to 7.8 mm in height (mean=7.5 mm, $n=4$) and from 6.5 to 9.6 mm in width (mean=8.2 mm, $n=4$).

Compagno (1984:546) reported that this species is "probably the most abundant hammerhead, a coastal-pelagic, semioceanic warm-temperate and tropical species occurring over continental and insular shelves... [ranging] from the intertidal... to at least 275 m depth." He reported its principal prey as a wide variety of fish, including sea catfish, bluefish, jacks, porgies, and other sharks.

Sphyrna cf. S. media Springer, 1940

FIGURE 58d-g

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—111 teeth, USNM 207526–207529, 207533, 207534, 451341–451346.

REMARKS.—The upper teeth have triangular, distally inclined crowns with smooth cutting edges (Figure 58d,e). The crowns are deeply notched distally, setting off a distinct, vaguely serrated, convex enamel blade. They are similar to those teeth referred to *?Rhizoprionodon* sp. but may be distinguished by their wider-based crown, blunter point, and less concave mesial cutting edge. Of the sphyrnids, they resemble closely the teeth of *Sphyrna media* (Gilbert, 1967, fig. 14), but because dentitions of this species were not available to us for this study, we could not make direct comparisons between them and the fossil teeth. The teeth identified by Cappetta (1970:70–72, pl. 19: figs. 1–18) from the lower Miocene of France also closely resemble those of *S. media*.

In size, the anterior teeth range from 4.8 to 7.8 mm in height (mean=6.3 mm, $n=7$) and from 5.6 to 8.0 mm in width (mean=7.8 mm, $n=7$).

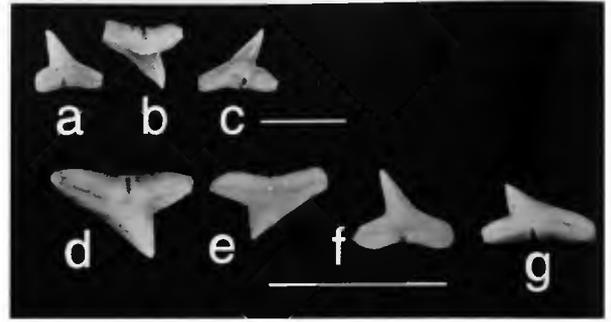


FIGURE 58.—*Sphyrna lewini*: a, USNM 459728, lower lateral tooth, lingual view; b, USNM 459729, upper lateral tooth, lingual view; c, USNM 459730, lower lateral tooth, lingual view. *Sphyrna cf. S. media*: d, USNM 207527, upper lateral tooth, lingual view; e, USNM 207534, upper lateral tooth, labial view; f, USNM 207529, lower anterior tooth, labial view; g, USNM 207533, lower lateral tooth, lingual view. (Scale bars: a-c=1.0 cm; d-g=0.33 cm.)

According to Compagno (1984:548), *Sphyrna media*, a little-known, inshore, tropical hammerhead, is found in the eastern Pacific Ocean, the southern Caribbean Sea, and the south Atlantic Ocean. The Lee Creek Mine occurrence, if it is *Sphyrna media*, indicates that this shark had a wider distribution during the Neogene.

Sphyrna zygaena (Linnaeus, 1758)

FIGURES 59, 60

Galeocerdo laevisimus Cope, 1867:141–142 [Calvert Formation, Maryland].
Carcharias laevisimus (Cope).—Eastman, 1904:84–85, pl. 32: fig. 2 [Calvert Formation, Maryland].

Carcharias (Scoliodon) kraussi Probst.—Leriche, 1927:83, pl. 14: fig. 16 [Miocene, Switzerland].

Sphyrna laevisima (Cope).—Leriche, 1942:84, pl. 7: figs. 23–27 [Calvert Formation, Maryland].—Casier, 1958:40, pl. 1: fig. 23 [Miocene, Trinidad].

HORIZON.—Pungo River Formation (units 1–5); Yorktown Formation (units 1–3).

REFERRED MATERIAL.—55 teeth, USNM 207520–207525, 459716–459719, 459721–459729.

REMARKS.—The Pungo River specimens (Figure 59a-e) are identical in size and form to teeth of juveniles and adults of the extant *Sphyrna zygaena*. In juveniles and young adults of the extant species, the teeth have smooth cutting edges, but in large individuals, they become weakly serrated (Gilbert, 1967:36). On the basal portions of their cutting edges, several teeth from the Pungo River Formation exhibit incipient serrations. These are similar in form to those found on the upper teeth from a 302 cm TL individual of the extant species (USNM 232633).

Cope's (1867) type suite for *S. laevisimus* consists of 19 teeth (ANSP 1195–1213) (Figure 60), two of which are not *Sphyrna*. The remaining teeth compare favorably with those of *S. zygaena*; therefore, we place *S. laevisimus* in synonymy

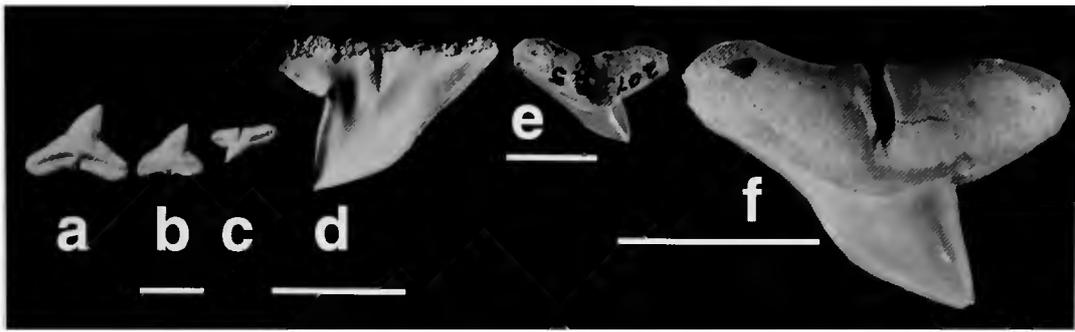


FIGURE 59.—*Sphyrna zygaena*: a, USNM 207522, Pungo River Formation, lower anterolateral tooth, labial view; b, USNM 207524, Pungo River Formation, lower anterolateral tooth, labial view; c, USNM 207520, Pungo River Formation, upper lateral tooth, lingual view; d, USNM 207523, Pungo River Formation, incomplete upper lateral tooth, labial view showing distinctive shape of mesial edge of larger teeth; e, USNM 207525, Pungo River Formation, upper lateral tooth, labial view; f, USNM 459716, Yorktown Formation, unit 3, upper lateral tooth, lingual view. (Scale bars: a-c,e=1.0 cm; d=0.5 cm; f=0.33 cm.)

with it. Although cataloged, the teeth were never numbered; in Figure 60 we give to each specimen a catalog number from the assigned series.

The few specimens from the Yorktown Formation (Figure

59f) (mean height=1.3 cm, range=1.2–1.4 cm, $n=4$), which are larger than the Pungo River Formation specimens (mean height=1.0 cm, range=0.8–1.1 cm, $n=10$), are more serrate than those from the latter formation.

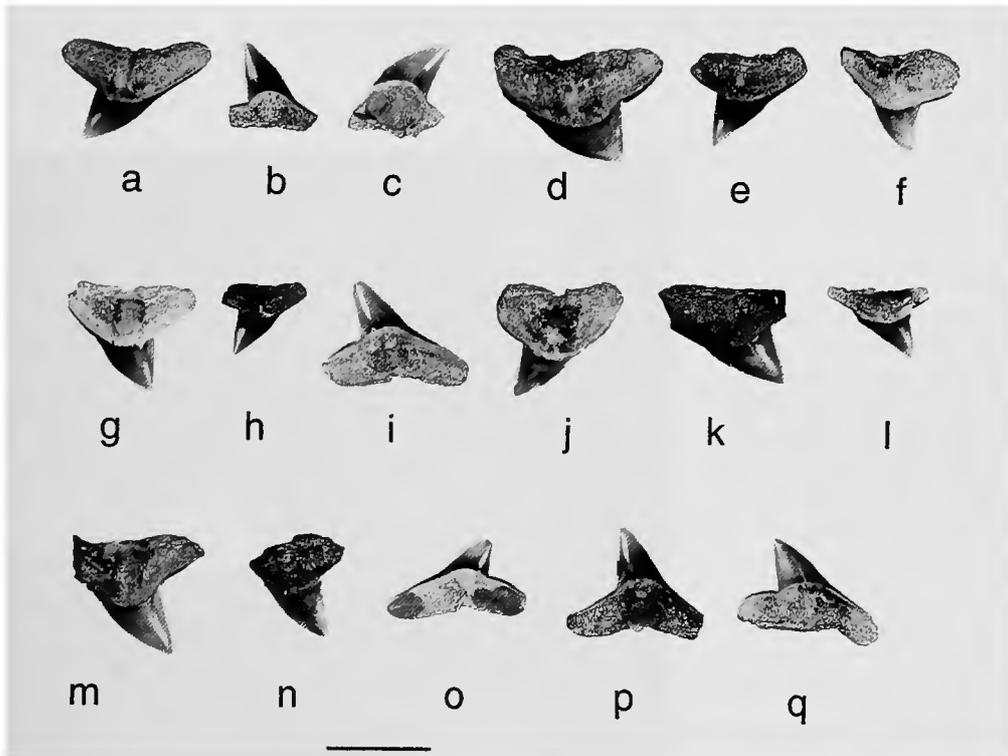


FIGURE 60.—Type suite of *Sphyrna laevisimus*: a, ANSP 1195, upper anterolateral tooth, lingual view; b, ANSP 1196, lower anterolateral tooth, lingual view; c, ANSP 1197, lower anterolateral tooth, lingual view; d, ANSP 1198, lectotype, upper anterolateral tooth, lingual view; e, ANSP 1200, upper anterolateral tooth, lingual view; f, ANSP 1201, upper anterolateral tooth, lingual view; g, ANSP 1202, upper anterolateral tooth, lingual view; h, ANSP 1203, upper anterolateral tooth, lingual view; i, ANSP 1204, lower anterolateral

tooth, lingual view; j, ANSP 1205, upper anterolateral tooth, lingual view; k, ANSP 1206, upper anterolateral tooth, lingual view; l, ANSP 1207, upper anterolateral tooth, lingual view; m, ANSP 1208, upper anterolateral tooth, lingual view; n, ANSP 1209, upper anterolateral tooth, lingual view; o, ANSP 1210, lower anterolateral tooth, lingual view; p, ANSP 1211, lower anterolateral tooth, lingual view; q, ANSP 1213, lower anterolateral tooth, lingual view. (Scale bar=1.0 cm.)

The extant species is a coastal-pelagic and semioceanic shark that inhabits temperate to tropical waters; it feeds on bony fishes, including sea catfishes, sea bass, and porgies, and on sting-rays (Compagno, 1984:554).

CARCHARHINIFORMES

FIGURE 61

HORIZON.—Yorktown Formation (units 1?, 2?).

REFERRED MATERIAL.—About 100 rostral nodes, USNM 476299–476302; about 20 postorbital and preorbital processes, USNM 476303–476306; 6 hypercalcified ?suprascapulae, USNM 476307, 476308.

REMARKS.—The Lee Creek Mine carcharhiniform rostral nodes occur in three forms: broad dish-shaped (USNM 476299, Figure 61*a*), T-shaped (USNM 476301, Figure 61*b*), and bar-shaped (USNM 476302, Figure 61*c,d*). In the first form, the two dorsal and one ventral rostral cartilages meet anteriorly to form a broad, unperforated, triangular dish. In the second form, in cranial or caudal view, the rostral cartilages form a “T,” which may be perforated at the point of juncture of the rostral cartilages. In the last form, the two dorsal rostral cartilages

meet anterior to the ventral one, forming a lateral bar in anterior view. Anterior to the juncture with the ventral rostral cartilage, the dorsal cartilages are perforated.

According to Compagno (1988:69), these types of rostral nodes occur in *Mustelus mosis*, *Rhizoprionodon acutus*, and *Carcharhinus macloiti*, but without comparative material, we could not identify the Lee Creek Mine specimens, which may be too large to belong to these species.

Hypercalcified postorbital (Figure 61*e*) and preorbital processes (Figure 61*f,g*) similar to those found in the extant *Rhizoprionodon* and *Mustelus* also occur at Lee Creek Mine; however, these specimens are from individuals larger than the largest extant form, and the Lee Creek Mine teeth for these genera fall within the size range for the extant forms. Because of this size discrepancy and the lack of comparative material at this time, we cannot identify the Lee Creek Mine specimens.

Finally, some bulbous specimens, which may represent suprascapulae, also were recovered from the mine (Figure 61*h*). The largest, USNM 476307, has a maximum diameter of 5.3 cm. Again, due to the lack of comparative material, we could not identify these.

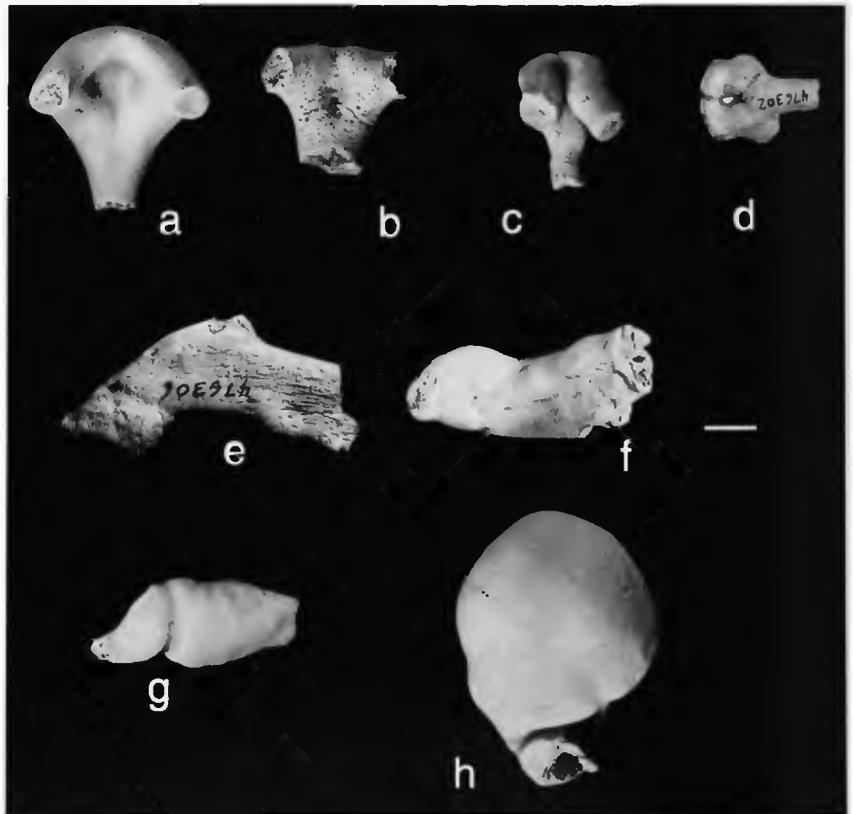


FIGURE 61.—Carcharhiniform: *a*, USNM 476299, rostral node, ventral view; *b*, USNM 476301, rostral node, ventral view; *c*, USNM 476302, rostral node, ventral view; *d*, same specimen, ventral view; *e*, USNM 476306, postorbital process, dorsal view; *f*, same specimen, ventral view; *g*, USNM 476303, preorbital process, dorsal view; *h*, USNM 476307, hypercalcified ?suprascapula, lateral view. (Scale bar=1.0 cm.)

Class HOLOCEPHALI

Order CHIMAERIFORMES, family indeterminate

FIGURE 62a-d

HORIZON.—Pungo River Formation?

REFERRED MATERIAL.—1 dentary fragment, USNM 282334; 1 tritor, USNM 476310; 1 partial dorsal spine, USNM 476309.

REMARKS.—Only three specimens of chimaeroid have been recovered from the Lee Creek Mine; none of these possess any characters that would allow their identification to genus. The dentary fragment (Figure 62a), which is the anterior portion and is badly abraded, lacks any evidence for the positions of the tritors. The tritor (Figure 62b) is 7.3 cm long and 1.7 cm wide.

In cross section the dorsal spine is triangular and has a double row of serrations caudally, which are separated by a groove; the cranial edge is smooth and sharp (Figure 62c,d). Its lateral surfaces are striated. This fragment is 3.9 cm in length and 1.5 cm in width.

Chimaeroids are deepwater fishes that feed on invertebrates and small fishes.

Class OSTEICHTHYES

Bone terminology herein follows Collette and Russo (1984) and Tyler (1980).

Order ACIPENSERIFORMES

Family ACIPENSERIDAE (sturgeons)

Acipenser cf. A. oxyrhynchus Mitchell, 1814

FIGURES 62e-h, 63

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—Several thousand fragments, including bony scutes, USNM 207602, 207603, 207607, 286998, 286999, 290533, 290645; pectoral spines, USNM 207604, 284823, 284908; neural spines, USNM 285375, 285384; skull bones, NCSM 9045, USNM 464059.

REMARKS.—The fossil sturgeon material from Lee Creek Mine consists of thick bony scutes or dermal plates with deeply ornamented outer surfaces (Figure 62e,f) and smooth inner surfaces. The pectoral spine (Figure 62g,h) is striated along its length and is ornamented at its proximal end. Among the skull bones we identified an intertemporal-supratemporal (Figure 63a) and a suborbital (Figure 63b).

From the Atlantic Coastal Plain of the United States, fossil sturgeon remains have been reported from the Miocene Calvert Formations of Virginia (Leidy, 1873) and Maryland (Kimmel and Purdy, 1984) and from the Pleistocene of Florida (Swift and Wing, 1968). Based on a lateral scute from the Virginia

Miocene, Leidy (1873) established a new species of fossil sturgeon, *Acipenser ornatus*. About this specimen, Leidy (1873:350) said, "Though exhibiting no positive distinctive character, it most probably pertained to a species now extinct." The type specimen was in a private collection and is now lost, but based on Leidy's description and illustration (Leidy, 1873, pl. 32: fig. 58), the scutes of *Acipenser ornatus* do not differ from those of *Acipenser oxyrhynchus*.

In morphology, the Lee Creek Mine scutes are very similar to USNM specimens from the Miocene sediments of Virginia, Maryland, and Delaware and to those of the extant Atlantic sturgeon, *Acipenser oxyrhynchus*. They closely resemble those from a 183 kg specimen of the extant species (USNM 260347) except that the Lee Creek Mine specimens are more massive. This difference in thickness between the fossil and modern dermal elements, however, may fall within the size range of *Acipenser oxyrhynchus*, which reaches a length of 4.2 m TL and a weight exceeding 370 kg (Manooch, 1984).

Acipenser oxyrhynchus is an anadromous species that occurs in the shallow waters of the Atlantic continental shelf from Labrador south to the northern coast of South America (Robins and Ray, 1986). Presently, it occurs off North Carolina in shallow (to 20 m), nearshore waters from the late fall to the early spring (Holland and Yelverton, 1973). Ross et al. (1988) stated that in North Carolina in the spring, the American Atlantic sturgeon is common in the ocean near the mouth of the Cape Fear River. The abundance of sturgeon fossils in the Lee Creek Mine fauna suggests that this fauna may have existed near the mouth of a large river.

The American Atlantic sturgeon is a bottom feeder, consuming worms, crabs, and small fishes (Manooch, 1984).

Order LEPISOSTEIFORMES

Family LEPISOSTEIDAE (gars)

Lepisosteus osseus (Linnaeus, 1758)

FIGURE 64a-d

HORIZON.—James City Formation.

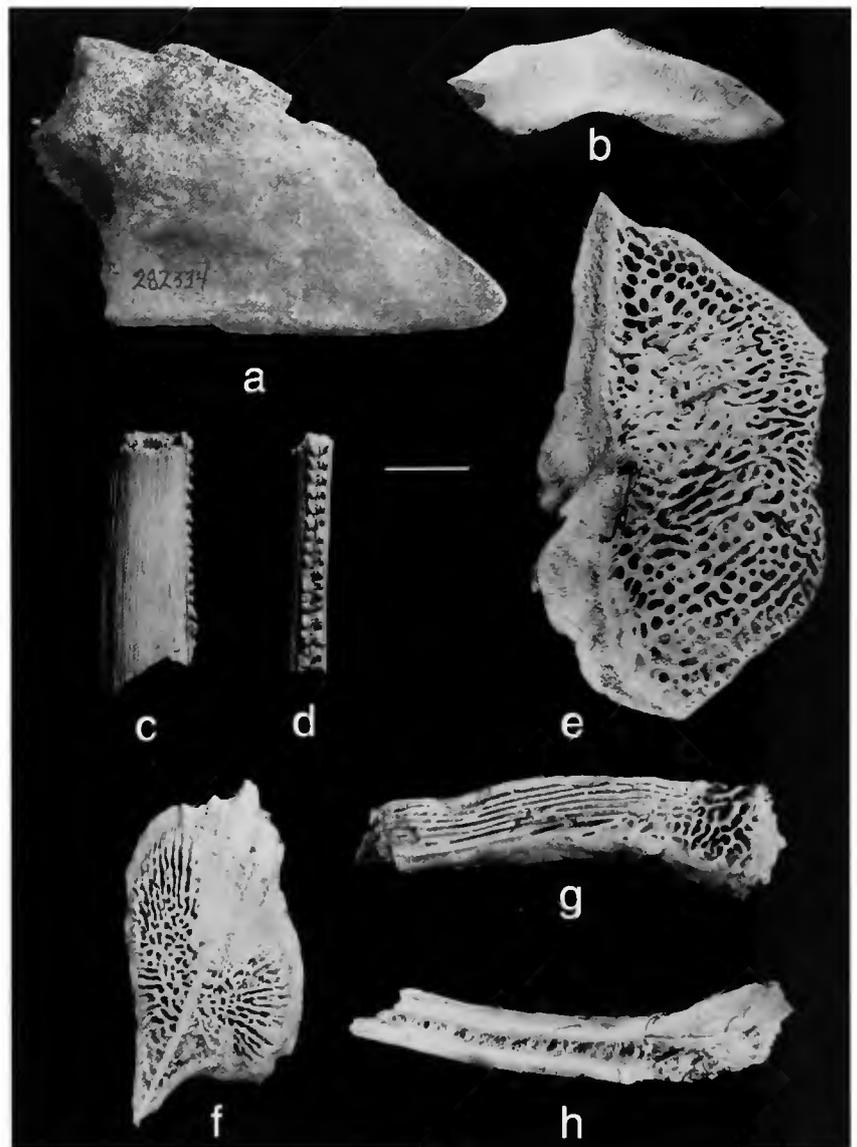
REFERRED MATERIAL.—1 partial skeleton, USNM 279492.

REMARKS.—A partial skeleton consisting of eight vertebrae, a rostral fragment, and numerous scales are referred to *Lepisosteus osseus*. The vertebrae are identical to those of the extant gar.

Lepisosteus osseus, a freshwater and estuarine species, occurs on the Atlantic slope of the United States from New Jersey to Florida; it is also found in the Mississippi, Great Lakes, and Rio Grande drainages (Page and Burr, 1991).

The gar feeds primarily on bony fishes, such as shiners, sunfish, shads, and catfish (Manooch, 1984).

FIGURE 62.—Chimaeroid: *a*, USNM 282334, fragment of dentary, lateral view; *b*, USNM 476310, tritor, lateral view; *c*, USNM 476309, fragment of dorsal spine, lateral view; *d*, same specimen, caudal view. *Acipenser* cf. *A. oxyrhynchus*: *e*, USNM 207603, lateral dermal scute, external view; *f*, USNM 207607, ventrolateral dermal scute, external view; *g*, USNM 207604, incomplete pectoral spine, dorsal view; *h*, same specimen, posterior view. (Scale bar=1.0 cm.)



Order ELOPIFORMES

Family ELOPIDAE (tarpons)

Megalops cf. *M. atlanticus* Valenciennes in Cuvier and Valenciennes, 1847

FIGURE 64*e,f*

HORIZON.—Pungo River Formation (units 5, 6).

REFERRED MATERIAL.—9 large, worn vertebrae, USNM 290630, 291256, 459863–459867, 476382, 476394.

REMARKS.—The Lee Creek Mine specimens, which range from 41.5 to 47.5 mm in length, closely resemble the vertebrae of the living tarpon, *Megalops atlanticus*. Like the extant species, the vertebral lateral surfaces are slightly concave (Figure 64*f*) and are striated. In axial view (Figure 64*e*) the vertebrae

are oval, with the lateral axis being slightly greater than the dorsoventral one.

Megalops atlanticus is a nearshore species that occurs from Virginia to Brazil (Robins and Ray, 1986). It feeds primarily on crabs and bony fishes, such as sardines, anchovies, mullets, silversides, hardhead catfish, and Atlantic Cutlassfish (Manooch, 1984).

Order ANGUILLIFORMES

Family CONGRIDAE (conger eels)

Conger cf. *C. oceanicus* (Mitchill, 1818)

FIGURE 65*a,b*

HORIZON.—Yorktown Formation (unit 1).

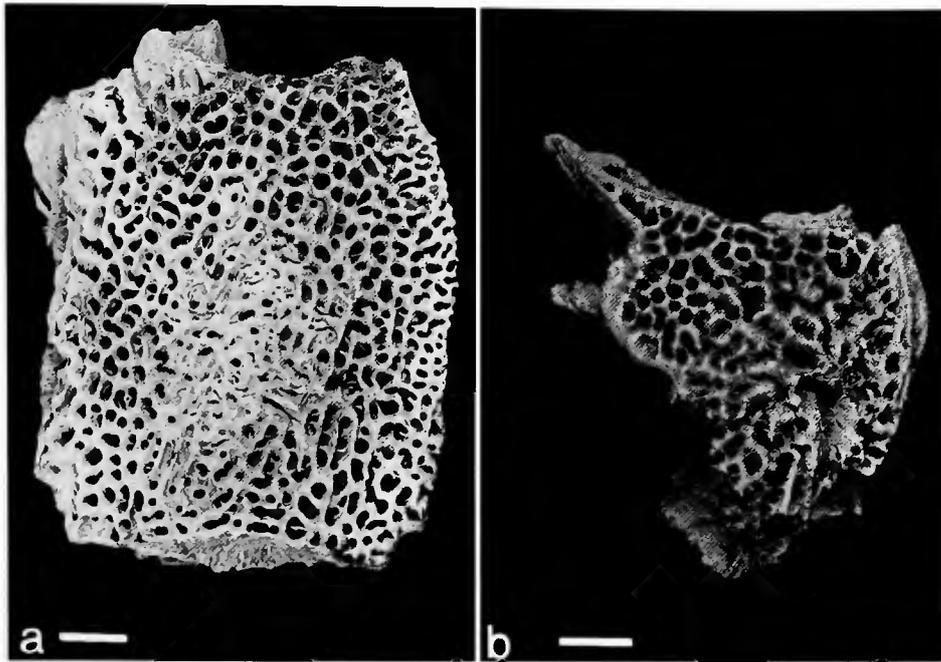


FIGURE 63.—*Acipenser* cf. *A. oxyrhynchus*: a, USNM 464059, partial left intertemporal-supratemporal, dorsal view; b, NCSM 9045, partial right suborbital, dorsal view. (Scale bars=1.0 cm.)

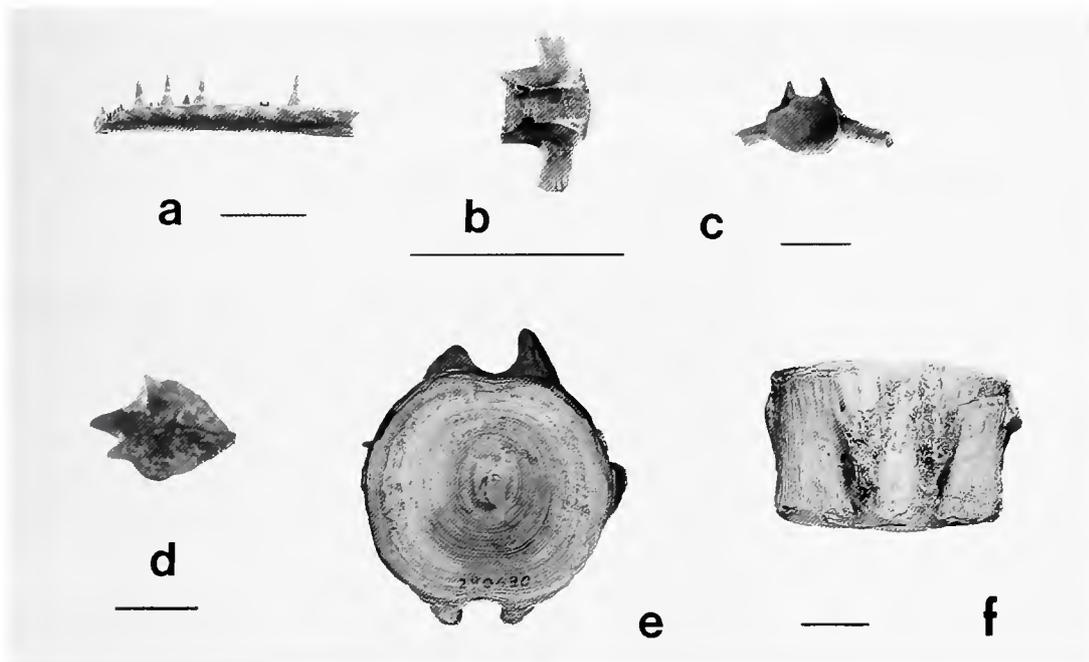


FIGURE 64.—*Lepisosteus osseus*, portions of partial associated skeleton, USNM 279492: a, partial premaxilla, labial view; b, vertebra, dorsal view; c, same specimen, articular view; d, scale. *Megalops* cf. *M. atlanticus*: e, USNM 290630, vertebra, articular view; f, same specimen, dorsal view. (Scale bars: a=0.9 cm; b-d=0.75 cm; e,f=0.9 cm.)

REFERRED MATERIAL.—1 partial left dentary without teeth, USNM 411948.

REMARKS.—This dentary compares favorably with that of the extant *Conger oceanicus*. Along its labial edge, the position

of the main tooth row is indicated by oval alveoli, and lingual to the alveoli there is a row of alveoli for villiform teeth (Figure 65a). At its anterior end, the dentary widens labially to form a small tooth patch with 12 small alveoli in two rows. In this area

of the dentary, several extant specimens of *Conger oceanicus* (USNM 30710, 265105, 265109) exhibited variable numbers of tooth rows (one to four). Kanazana (1958) stated that the number of teeth in the jaw of the genus *Conger* increases directly with age. The Lee Creek Mine specimen may be from a juvenile or a young adult.

Conger oceanicus is a benthic species that occurs from Cape Cod south to the Gulf of Mexico (Robins and Ray, 1986). This species has been recorded in depths from 1 to 520 m (Kanazana, 1958). It feeds primarily on bony fishes (Hildebrand and Schroeder, 1928) but also has been reported feeding on shrimp and mollusks (Thomson et al., 1978).

Order CLUPEIFORMES

Family CLUPEIDAE (shads and herrings)

Alosa cf. *A. sapidissima* (Wilson, 1811)

FIGURE 65c,d

HORIZON.—Yorktown Formation (unit 1?).

REFERRED MATERIAL.—Partial skull, USNM 411950.

REMARKS.—This partial skull has a posteriorly extending, enlarged epiotic as seen in the genus *Alosa*. The posterior extent of the epiotic is greater in the Lee Creek Mine specimen and in *A. sapidissima* than it is in the other species of *Alosa*. Also, the epiotics intersect at the midline of the skull to form a 90° V-shaped notch. In other species of *Alosa* (*A. aetivalis*, *A. pseudoharengus*, *A. mediocris*) these notches are greater than 90°. In this specimen, the preepiotic forms a depression at the

side of the cranium, bounded by the epiotic, squamosal, and parietal bones, which also is characteristic of clupeids (Ridgwood, 1904).

Alosa sapidissima is an anadromous species that occurs from Newfoundland and the Gulf of St. Lawrence south to northern Florida (Robins and Ray, 1986). They are found off North Carolina in nearshore waters (0–20 m), but they have been captured at depths of 160 to 250 m (Holland and Yelverton, 1973). It is a planktivore, feeding primarily on small crustaceans, insects, fish eggs, and algae (Manooch, 1984).

Order SILURIFORMES

Family ARIIDAE (sea catfish)

Bagre sp.

FIGURE 65e,i

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—30 pectoral-fin spines, USNM 256274, 284106, 284107, 284111–284113, 284151, 284152 (Pungo River Formation); 6 dorsal-fin spines, USNM 284098–284100, 476375 (Pungo River Formation, unit 4 or 5), USNM 284114 (Yorktown Formation); about 100 vertebrae, USNM 285646, 286142, 286147, 286161, 290517, 290947 (Yorktown Formation).

REMARKS.—The fossil pectoral-fin spines from Lee Creek Mine are similar to those of *Bagre marinus* (Mitchill), the gaff-

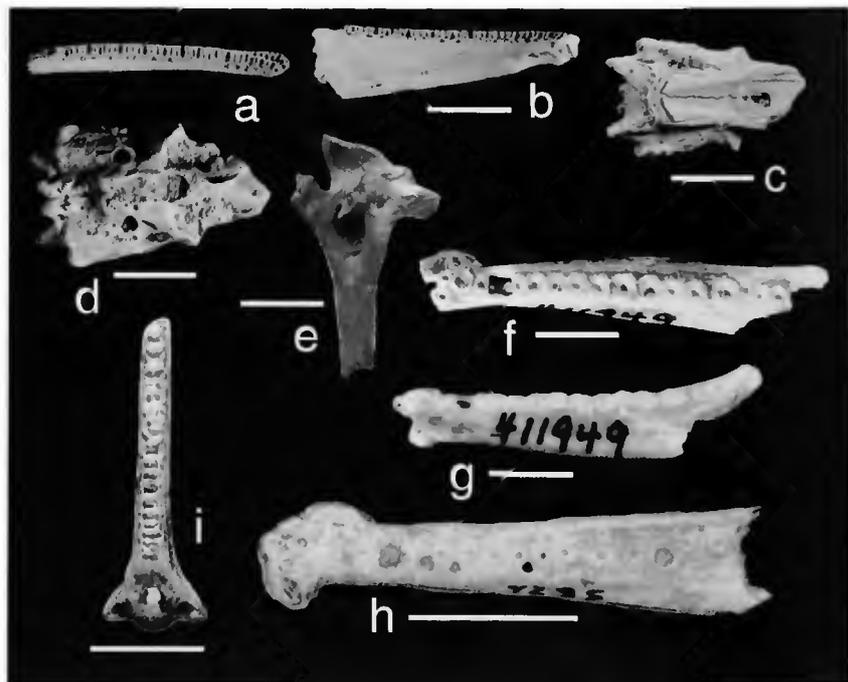


FIGURE 65.—*Conger* cf. *C. oceanicus*: a, USNM 411948, partial left dentary without teeth, occlusal view; b, same specimen, lingual view. *Alosa* cf. *A. sapidissima*: c, USNM 411950, skull, dorsal view; d, same specimen, ventral view. *Bagre* sp.: e, USNM 256274, partial pectoral-fin spine, posterior view. *Opsanus tau*: f, USNM 411949, partial right dentary, occlusal view; g, same specimen, labial view; h, NCSM 4285, partial right dentary, occlusal view. *Bagre* sp.: i, USNM 476375, dorsal-fin spine, anterior view. (Scale bars: a–g, i=1.0 cm; h=0.25 cm.)

topsail catfish, especially with regard to the shape of the proximal articulating surface. This surface, which articulates with the coracoid, is useful for identifying genera of catfishes. In *Bagre*, the central hinge process is flattened ventrally and laterally to form the outside part of the hinge, and medially it rises to form the hook-like hinge (Figure 65e). This differs from the pectoral attachment found in the genus *Arius*, which does not have its medial process ventrally flattened or hooked.

Several dorsal-fin spines from Lee Creek Mine, which are referable to *Bagre*, have an outer surface that is notched with rows of cross ridges, each ridge consisting of one or two peaks (Figure 65i). The serrae are very worn on both the dorsal- and pectoral-fin spines.

Among the numerous fossil fish vertebrae from Lee Creek Mine, we were able to identify those of *Bagre*. The precaudal vertebrae are easily recognizable by the smooth lateral surfaces of their centra, which are perforated by a large and a smaller foramen, and by the strong, caudally curving haemal arches on the ventral surfaces.

Other occurrences of sea catfish remains from sediments of the Chesapeake Group include a spine attributed to *Arius* (Leriche, 1942) and a skull with a left utricular otolith (Lynn and Melland, 1939), the holotype of *Bagre stauroforus* (Lynn and Melland), both from the Plum Point Member of the Calvert Formation. The spine assigned to *Arius* is incomplete and is too worn for generic identification. Because the skull and otolith of *Bagre stauroforus* were not associated with any pectoral-fin spines, comparison with the Lee Creek *Bagre* pectoral-fin spines is not possible.

Bagre marinus occurs from Cape Cod to Venezuela (Robins and Ray, 1986) in shallow coastal and bay areas and seasonally in estuaries (Boschung et al., 1983). It feeds primarily on crabs, supplemented by shrimp and fishes (Gudger, 1918).

Order BATRACHOIDIFORMES

Family BATRACHOIDIDAE (toadfishes)

Opsanus tau (Linnaeus, 1766)

FIGURE 65f-h

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—2 partial right dentaries, NCSM 4285, USNM 411949.

REMARKS.—Both of these partial right dentaries can be referred to the extant oyster toadfish, *Opsanus tau*. The first specimen, USNM 411949 (Figure 65f,g), which is 26 mm in length and broken at both ends, has a single row of alveoli stretching from the posterior end of the dentary to the anterior tooth patch, half of which is present. The second specimen, NCSM 4285 (Figure 65h), is 28 mm in length and is broken only at the distal end. Unlike the first specimen, several supernumerary teeth occur on either side of the single tooth row at two locations. Several of the teeth are displaced from the line

of this row. Other than these differences, the dentaries are identical to those of the extant species.

Ray et al. (1968) reported *Opsanus* sp. from the Pleistocene Kempsville Formation of Virginia; these specimens, the first fossil record for *Opsanus*, consist of a neurocranium and a right lower jaw and compare favorably with those from Lee Creek Mine. The Lee Creek specimens extend the fossil record for the genus *Opsanus* to the early Pliocene.

Opsanus tau is a benthic species that occurs from Cape Cod south to Florida (Robins and Ray, 1986). The primary habitats for this species are areas that are rocky or have some form of reef habitat. It has been recorded in depths of 1 to 50 m (Manooch, 1984). There is some evidence that this species migrates offshore during cold weather (Thomson et al., 1978). It feeds primarily on crabs, fishes, shrimp, amphipods, and worms (Manooch, 1984).

Order LOPHIIFORMES

Family LOPHIIDAE (goosefishes)

Lophius cf. *L. americanus* Valenciennes, 1837

FIGURE 66a-d

HORIZON.—Yorktown Formation (unit 1?).

REFERRED MATERIAL.—21 dentaries, USNM 290214, 290625, 291101, 476362; 50 premaxillaries, USNM 291116, 295340; 3 palatines, USNM 285259, 291188, 476361; 4 vertebrae, USNM 290493.

REMARKS.—In both size and shape of the various elements, the Lee Creek Mine specimens are very similar to those of *Lophius americanus*. On the lingual ventral surface at the symphyseal end, the fossil premaxillaries (Figure 66a) bear several rugose, caniniform teeth. These teeth point lingually, and they are followed distally by up to 12 smaller, caniniform teeth with triangular bases that decrease in size distally. The labial ventral surface has four to five large alveoli; after a short gap, these are followed distally by a row of smaller, triangular teeth. At the symphyseal end of the premaxillary, the articulating surface is square-shaped and slightly concave, whereas the articulating process is blade-like and nearly perpendicular to the ventral and articulating surfaces; this process is heavily striated on its lingual and labial surfaces.

The fossil dentary (Figure 66b) has a central tooth row of canine-like teeth with triangular bases. On the labial edge of the dorsal surface, a row of smaller teeth originates about one-quarter of the distance from the symphyseal end and extends to the distal end of the dentary. On the dorsal surface, the numerous alveoli give a pitted appearance to the bone. At the symphyseal margin of the dentary, there is a ventral, rectangular process, which is striated on its distal surface.

The fossil palatine (Figure 66c) has several rugose, caniniform teeth followed by a row of smaller caniniform teeth. The symphyseal surface is squarish, and the ethmoid process has two

tooth-like projections that point lingually. The fossil vertebrae (Figure 66*d*) that we assign to *Lophius* are the anteriormost vertebrae in the vertebral column; they are dorsoventrally compressed, with striations on the external surface of the centra.

The genus *Lophius* was recorded previously from the Pleistocene of Virginia (Ray et al., 1968) and the Oligocene of Belgium (Leriche, 1908, 1910). The Virginia specimens, a fragmentary left dentary and a right scapulocoracoid, were identified to family only. The Belgian specimens were identified as a new species of goosfish, *Lophius dolloi*, by Leriche (1908).

Lophius americanus, a benthic species, occurs from Quebec south to northern Florida (Robins and Ray, 1986). It inhabits areas with sand, mud, and broken-shell substrates in waters ranging in temperature from 0°C to 24°C (Manooch, 1984). The goosfish has been recorded at depths of 1 to 200 m (Bigelow and Schroeder, 1953). It feeds on small sharks, skates, eels, herring, weakfish, tautog, butterfish, puffers, cod, haddock, flounders, seabirds, lobsters, crabs, worms, shellfish, sand dollars, and starfish (Manooch, 1984).

Order GADIFORMES

Family MERLUCCIDAE

(hakes)

Merluccius bilinearis (Mitchill, 1814)

FIGURES 66*e-i*, 67

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—About 1000 dentaries, USNM 285254, 285273, 285291, 286875, 290546, 290553, 290561, 290584, 290603, 290613, 290617, 290635, 290640, 290660,

291102, 298293, 298302, 476311–476313; about 1000 premaxillae, USNM 290543, 290545, 290602, 290606, 290644, 290656, 291096, 291123, 291193, 291673, 476324–476326; 1 partial maxilla, USNM 476363; about 100 maxillae 476314–476320; 1 partial left angular, USNM 476321; 1 left angular, USNM 459851; 1 associated dentary, maxilla, and partial premaxilla, USNM 476322; 1 vomer, NCSM 10916; several hundred vertebrae, USNM 286131–286135, 286144, 286145, 286160, 286162, 290222–290229, 290231, 290238, 290240, 290242, 290243, 290251, 290253, 290255, 290256, 290259, 290264, 290272, 290275, 290326–290328, 290497, 290517, 290518, 290559, 291109, 291687, 291694, 476323; about 100 hyperostosed vertebrae, USNM 460120, 476351, 476352; 1 partial cleithrum, USNM 459849; about 100 hyperostosed cleithra, USNM 283825, 283869, 283905, 283960, 284012, 284043, 284045; 1 urohyal, USNM 476364; about 100 hyperostosed urohyals, USNM 421524, 421525.

REMARKS.—The Lee Creek Mine specimens are identical to those of *Merluccius bilinearis*. The presence of biserial teeth on both the dentary and premaxilla separates the genus *Merluccius* from all other gadiforms, which have single or multiple rows of teeth on the maxilla, dentary, or both. Although *Merluccius* differs from most gadoids in having a prognathous lower jaw (Rosen and Patterson, 1969), this feature is difficult to prove in unarticulated fossils.

In the Lee Creek dentaries, as in the extant *Merluccius*, the alveoli of the biserial tooth rows, which support medium-sized, triangular teeth, occupy approximately one-third of the depth of the dentary (Figure 66*e,f*). The tooth-row surface slants lingually so that the alveoli of the uppermost labial tooth row are higher than those of the lingual row. In the fossil specimens, the labial row of teeth is more securely attached to the dentary than is the lingual row of teeth, which is absent. On the ventral,

FIGURE 66.—*Lophius* cf. *L. americanus*: *a*, USNM 295340, premaxillary, labial view; *b*, USNM 476362, fragment of dentary, labial view; *c*, USNM 476361, fragment of palatine, ventral view; *d*, USNM 290493, vertebra, lateral view. *Merluccius bilinearis*: *e*, USNM 476313, left dentary, external view; *f*, same specimen, internal view; *g*, USNM 476326, right premaxilla, external view; *h*, same specimen, occlusal view; *i*, USNM 476363, partial maxilla, dorsal view. (Scale bar=1.0 cm.)

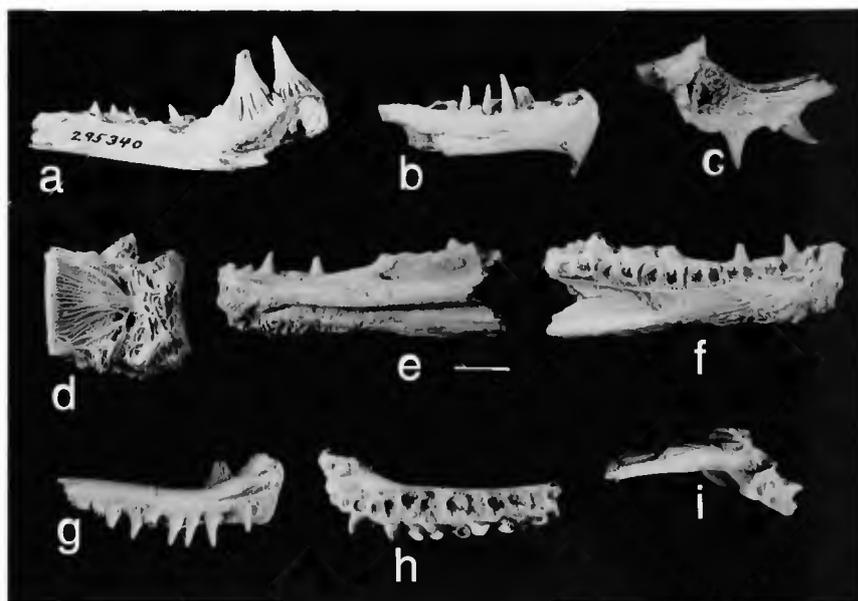




FIGURE 67.—*Merluccius bilinearis*: a, USNM 459851, left angular, external view; b, NCSM 10916, vomer, ventral view; c, USNM 459849, partial cleithrum, lateral view; d, USNM 290559, precaudal vertebra, articular view; e, USNM 291109, precaudal vertebra, articular view; f, USNM 460120, four hyperostosed caudal vertebrae, dorsal? view; g, same specimen, axial view; h, USNM 476351, five hyperostosed caudal vertebrae, dorsal? view; i, USNM 476364, urohyal, lateral view. (Scale bars: a,c-g,h=1.0 cm; b=0.33 cm; i=0.5 cm.)

lingual surface of the dentary, a ridge extends from a notch in the ventral edge of the symphyseal end down the entire length of the dentary. The ridge is thickest just posterior to the notch and then thins abruptly. On the ventral, labial surface of the dentary, a large groove extends from above the ventral notch to the posterior end of the dentary. The largest of these incomplete dentaries measures 5.8 cm in length and 1.5 cm in depth at the symphysis.

In the premaxillae (Figure 66g,h) the lingual row of teeth originates at a slightly more dorsal elevation than does the labial row. The much shallower dorsoventral depth of the premaxillae gives the teeth, which are in the same size range as those of the dentaries, a larger appearance. At the symphyseal end, the premaxilla flares out to form the slightly concave articular surface; on its lingual edge is a small process that articulates with the maxilla. The dorsal surface of the premaxilla is smooth and rounded, whereas the lingual and symphyseal surfaces are sculptured.

The maxilla is edentulous (Figure 66i). Its symphyseal end, which articulates with the symphyseal end of the premaxilla, has an elongated internal process dorsal to the shallow groove that accepts the articular process of the premaxilla. The shallowness of this groove is unlike the glove-shaped socket found

in the maxillae of other teleosts at Lee Creek Mine. Mesial to this shallow groove there is a process that extends toward the symphysis. The distal end of the maxilla is flattened on its ventral surface but with a slight concavity; the more mesial distal surface is smooth and rounded and has a half-oval cross section.

The vomer, angular, cleithrum, urohyal, and vertebrae are figured (Figure 67). With the exception of the urohyal and the precaudal vertebrae, these compare well with those of *Merluccius bilinearis*. The urohyal is hyperostosed (Figure 67i), giving it an inflated appearance, but its morphology is close to that of the extant species, which is not hyperostosed. Although the precaudal vertebrae (Figure 67d,e) are very similar to those of the extant species, they are more strongly ossified, which may be hyperostosis, and on their ventral surfaces a central groove rather than a central ridge is present.

Numerous hyperostosed vertebrae (Figure 67f-h) occurring in the basal Yorktown Formation are tentatively assigned to *Merluccius*. Although the hyperostoses give the vertebrae a large size, the centra they surround have a very small diameter (Figure 67g). In adults of the extant *Merluccius productus*, the precaudal vertebrae have diameters (9 mm) three times larger than that of the second caudal (3.0 mm), and the diameters of

the third (3.2 mm) and fourth (3.5 mm) caudal vertebrae are slightly greater than the diameter of the second caudal vertebra. Of the taxa we have identified at Lee Creek Mine, only *Meluccius* has caudal vertebrae with very small diameters (mean=5.0 mm, range=3.6–5.9 mm, $n=7$). The Lee Creek Mine specimens represent three to five caudal vertebrae fused by hyperostosis (Figure 67h); the greatest development (mean width=15.1 mm, range=11.6–25.5 mm, $n=8$) of this hyperostosis is along the lateral axis of the vertebrae, and as shown below, its development is independent of the diameter of the vertebral centra.

	Centrum diameter (mm)	Width of hyperostosis (mm)
USNM 460120	5.7	12.2
USNM 476351	4.8	18.6
USNM 476352	5.8	25.5

Because specimens of extant *Merluccius bilinearis* with hyperostosis were not available to us, we cannot ascertain the identity of these vertebrae.

The hake is a benthic species that occurs from the Gulf of St. Lawrence south to South Carolina (Robins and Ray, 1986). It has been recorded at depths of 1 to 400 m, with a preferred depth range of between 60 and 200 m (Almeida et al., 1984). The hake feeds on fishes and invertebrates (Thomson et al., 1978).

Order PERCIFORMES

Family TRIGLIDAE (searobins)

Prionotus cf. *P. evolans* (Linnaeus, 1766)

FIGURE 68

HORIZON.—Yorktown Formation (units 1–3).

REFERRED MATERIAL.—5 skulls, NCSM 2978, USNM 290627, 459826, 459828, 459862; about 100 partial skulls, USNM 289396, 289397, 290215, 290216, 290663, 291154,

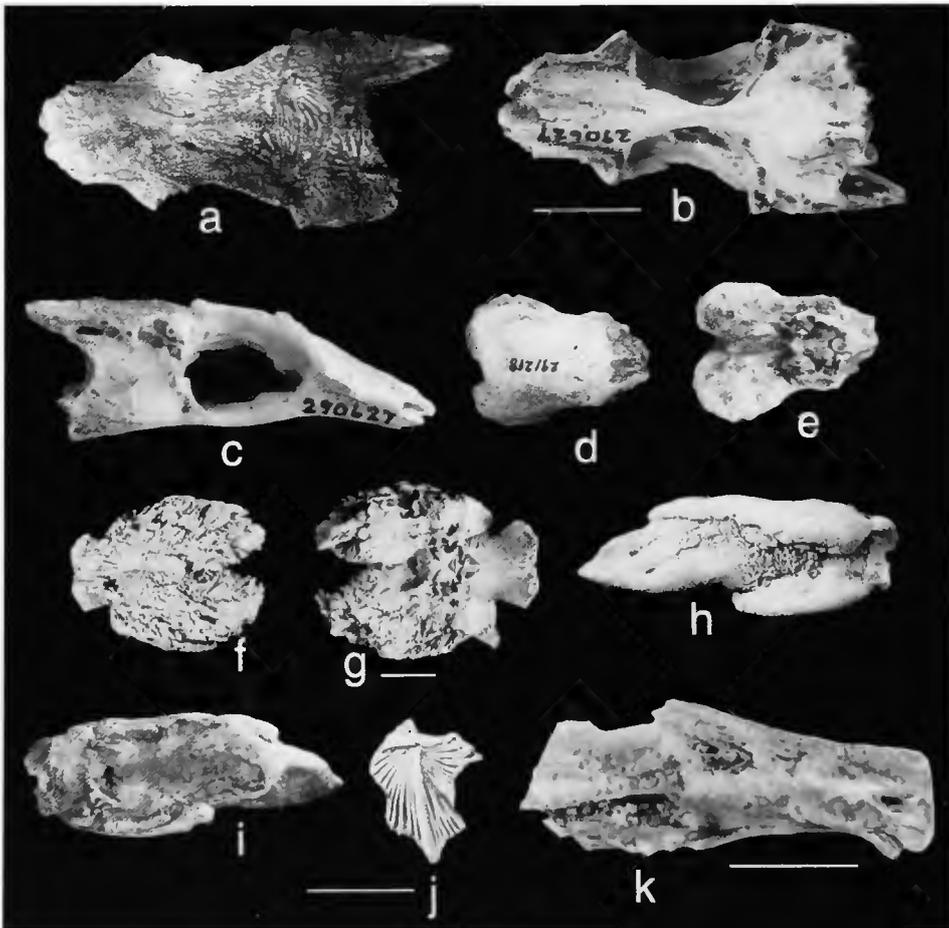


FIGURE 68.—*Prionotus* cf. *P. evolans*: a, USNM 290627, neurocranium, dorsal view of skull roof; b, same specimen, lateral view; c, same specimen, lateral view; d, USNM 291218, dorsal view of hyperostosed skull roof; e, same specimen, ventral view; f, USNM 459827, ?pathologic, hyperostosed skull roof, dorsal view; g, same specimen, ventral view; h, USNM 290663, dorsal view of hyperostosed skull roof; i, same specimen, ventral view; j, USNM 412167, lateral view of left operculum; k, NCSM 3106, lingual view of partial right dentary. (Scale bars: a–c,j=0.5 cm; d–i=1.0 cm; k=0.5 cm.)

291218, 291262, 459827; 4 preopercula, USNM 459830; 1 operculum, USNM 412167; 2 lacrimals, USNM 291192, 336359; 1 premaxilla, USNM 291156; 1 dentary, NCSM 3106.

REMARKS.—Numerous fossil skulls have been found at the Lee Creek Mine site that are very similar to the extant northern searobin, *Prionotus carolinus*, and the striped searobin, *Prionotus evolans*. They are easily recognized by the elaborate sculpturing of the external surfaces of the skull, which is characteristic of *Prionotus*. The posttemporals extend caudally well beyond the caudal margin of the supraoccipital. The skull roof is broad and somewhat flat and is slightly concave between the orbits, which penetrate the margin of the skull roof. The rostrum tapers from the orbits to the ethmoid, and its dorsal surface is slightly convex.

At Lee Creek Mine, three different skull types of *Prionotus* occur. In the first type (USNM 290627, Figure 68a–c), hyperostotic enlargement of the posttemporals is absent; only three skulls of this type are complete, and they measure 45.4 mm (USNM 290627), 35.8 mm (USNM 459862), and 45.6 mm (USNM 459826) in total length.

In the second type (USNM 291218, Figure 68d,e), the posttemporals are hyperostosed and fuse at the midline of the skull. None of these skulls are complete; the rostra are missing, and the largest, USNM 291218, measures 37.6 mm in total length. One specimen of this type, USNM 459827, may be pathologic (Figure 68f,g).

In the third type (USNM 290663), the hyperostosis is not a singular, bulbous mass as in the second type but develops in an elongate mass of a central and two lateral lobes, which are asymmetrical (Figure 68h,i). Although in all of these specimens ($n=43$) the rostral and orbital regions are missing, the outline of the braincase is identical to that in the other two types of *Prionotus* mentioned above. The largest specimen of this third type, USNM 290663, measures 64.9 mm in total length.

An isolated fossil operculum, USNM 412167 (Figure 68j), was found at Lee Creek Mine, and it exhibits a sculpture and structure similar to those of the extant species. A partial right dentary also was recovered (Figure 68k).

Fossil searobins from the eastern coastal plain of the United States have been reported from the Pleistocene of Virginia (Ray et al., 1968), New Jersey (Selden, 1986), Maryland (Blake, 1953), and Florida (Swift and Wing, 1968). All of these specimens are partial neurocraniums that were identified as *Prionotus* sp., but Blake (1953) and Selden (1986) suggested their specimens had a closer affinity to *P. evolans*.

Prionotus carolinus and *P. evolans* are benthic species that occur from Nova Scotia to Florida (Robins and Ray, 1986) at depths of 1 to 80 m (Thomson et al., 1978). Searobins feed on shrimp, amphipods, squids, and worms (Manooch, 1984).

Family SERRANIDAE (sea basses)

Epinephelus sp.

FIGURE 69a,b

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—13 incomplete premaxillae, USNM 256272, 285321, 286935, 290572, 290594, 290612, 290634, 291073, 291149, 291162, 291177, 291199, 291248; 5 incomplete dentaries, NCSM 4797, USNM 256273, 286907, 286925, 290539.

REMARKS.—The generic assignment is based on the great similarity of the fossil premaxillae to the premaxillae of *Epinephelus morio*. Because genera of groupers, not to mention species, are rather difficult to distinguish based on jaw elements alone, no attempt at specific identification is made.

The premaxilla (Figure 69a) has a labial row of large teeth that decrease in size posteriorly; the alveolus for the largest and anteriormost tooth is 4 mm in diameter. Lingual to this row of large teeth is a triangular area of numerous small alveoli supporting a cardiform tooth series. Alveoli in this area increase in size toward the lingual edge. Maximum height of the premaxilla (excluding teeth) is 20.5 mm, maximum width is 10.9 mm, and the width of the tooth-bearing area is 8.8 mm at the symphyseal end. At the symphyseal end, the ascending process is transversely compressed and is moderately low. The arrangement of the tooth series and the shape of the ascending branch of the premaxilla closely resemble that of *Epinephelus morio*.

The dentary contains teeth of three different sizes. On the labial side of the symphyseal end of the dentary is a tooth patch (Figure 69b) with large, conical teeth (usually two). Lingual to these teeth on this same tooth patch there are five to six rows of small teeth (about 1 mm in diameter at their bases), and lingual to these is a row of intermediate-sized teeth (about 1.5–2 mm in diameter at their bases); this row extends to the distal end of the dentary. On the main tooth surface of the dentary and labial to this row of intermediate-sized teeth there is a row of smaller teeth followed labially by a row of intermediate-sized teeth, three rows in all along most of the dentary. Dentary USNM 256273 is 8.9 mm wide and 16.9 mm deep (excluding teeth); the largest dentary, USNM 290539, which is incomplete, measures 13.7 mm in width, 56.0 mm in length, and 22.6 mm in depth (excluding teeth).

Groupers are offshore reef fishes that occur from Massachusetts to Brazil (Robins and Ray, 1986) at depths of 24 to 210 m (Manooch, 1984). They feed on a variety of bony fishes, including snappers, scuds, porgies, and searobins, and on a variety of invertebrates, including shrimp, crabs, squids, and worms (Manooch, 1984).

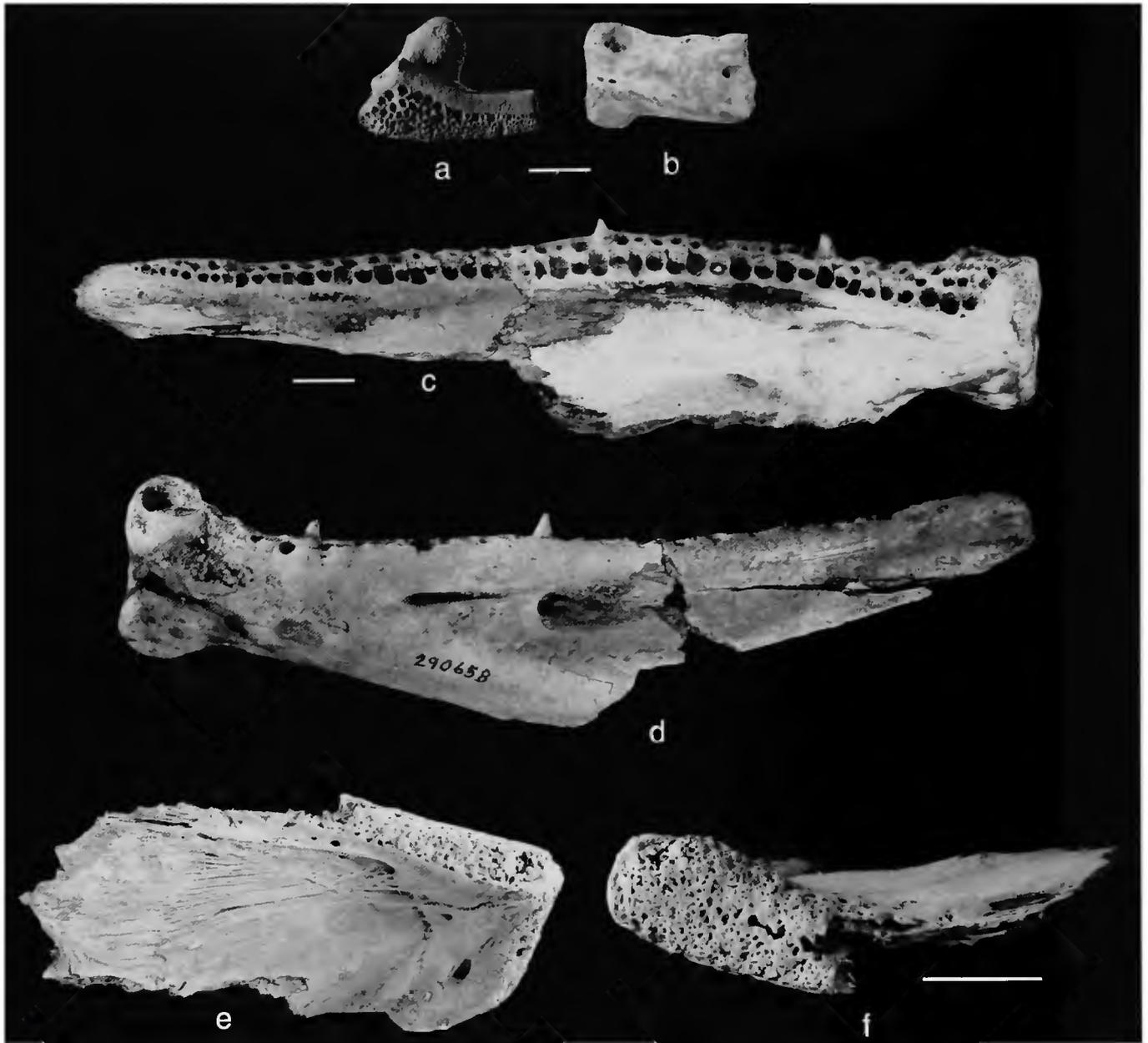


FIGURE 69.—*Epinephelus* sp.: *a*, USNM 256272, right premaxilla, ventrolingual view; *b*, USNM 256273, anterior fragment of left dentary, labial view. *Mycteroperca* sp., USNM 290658, left dentary: *c*, lingual view; *d*, labial view. *Seriola* sp., NCSM 1857, partial left dentary: *e*, labial view; *f*, occlusal view. (Scale bars=1.0 cm.)

Mycteroperca sp.

FIGURE 69*c,d*

HORIZON.—From spoil piles, probably lower Yorktown Formation (unit 1).

REFERRED MATERIAL.—1 left dentary, USNM 290658.

REMARKS.—A single dentary (Figure 69*c,d*) with the alveolar ridge complete and with several conical teeth resembles those of modern *Mycteroperca*. At the symphyseal end there

are two large alveoli for conical teeth, about 6 mm in diameter; these are followed lingually by a row of very small teeth that extends distally a short distance, about 20% of the length of the dentary. This row of small teeth is between two rows of intermediate-sized teeth, with alveoli of 2 to 4 mm in diameter; these intermediate-sized teeth extend distally to the end of the dentary. The total length of the dentary is 14.6 cm, and the depth at the symphysis is 2.9 cm.

Mycteroperca are offshore reef fishes that occur from Massachusetts to Brazil (Robins and Ray, 1986) at depths between 10 and 130 m (Manooch, 1984). They feed on shrimp, scuds, porgies, snappers, grunts, squids, and sardines (Manooch, 1984).

Family BRANCHIOSTEGIDAE
(tilefishes)

Two genera of branchiostegids, *Caulolatilus* and *Lopholatilus*, occur at Lee Creek Mine. This is the first occurrence in the fossil record for *Caulolatilus*. *Lopholatilus* was previously recorded from the Yorktown Formation as otoliths (Fitch and Lavenberg, 1983) and from the Calvert Formation of Maryland (Kimmel and Purdy, 1984).

Based on a specimen from Miocene sediments near Oran, Algeria, Arambourg (1927) described *Latilus mesogeus*, but Dooley (1978) found Arambourg's illustration and description too vague to ascertain the identity of this species. Except for this specimen, the specimens from Lee Creek Mine are the only definite fossil branchiostegids yet known.

***Caulolatilus* cf. *C. cyanops* Poey, 1866**

FIGURE 70a,b

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—Associated right and left ceratohyal, USNM 412151.

REMARKS.—A pair of associated ceratohyals (Figure 70a,b) compare well with those of the extant blackline tilefish, *Caulolatilus cyanops*. They are similar in having an anterior projection for articulation with the posteroventral notch of the hypohyal. The broad, flattened section of the ceratohyal is much shorter than in *Lopholatilus* and has only a short groove that extends from the upper one-third to about one-half of the length of the ceratohyal; in *Lopholatilus* this groove extends the entire length of the ceratohyal.

Robins and Ray (1986) reported that *Caulolatilus cyanops* ranges from North Carolina south to the Gulf of Mexico and to northern South America. This species has been recorded at depths between 45 and 495 m, with a preferred depth range of 150 to 250 m (Dooley, 1978).

***Lopholatilus rayus*, new species**

FIGURE 70c-f

HOLOTYPE.—Partial skull including associated partial left dentary (30 mm in length) missing distal end, partial left premaxilla lacking distal end, partial left operculum, epiotic, fragment of center portion of preoperculum, and fragments of maxilla, hyomandibular, and palatine, NCSM 2900.

TYPE LOCALITY.—Lee Creek Mine, Aurora, North Carolina.

HORIZON.—Yorktown Formation (unit 1).

PARATYPES.—1 partial left dentary, 22 mm long, NCSM 1572; 1 partial left dentary, 22 mm long, NCSM 3233; 1 partial left dentary, 26 mm long, NCSM 3160; 1 partial skull, USNM 437559, including symphyseal portions of both dentaries; 1 partial dentary, 37.3 mm long, USNM 336240; 1 vomer, 19.6 mm wide, USNM 437550.

ETYMOLOGY.—In recognition of Clayton E. Ray, whose determination has brought about the extensive study of the Lee Creek Mine fauna.

DIAGNOSIS.—A villiform tooth row extends from the anterior tooth posteriorly along the lingual margin of the coronoid process of the dentary. In all other branchiostegids, this villiform tooth row is absent.

REMARKS.—This is one of the most common species of the nonpelagic fishes found at the Lee Creek Mine site. It also is one of the few fish species for which numerous partial skeletons have been found. Although the otoliths from Lee Creek Mine have been described as *Lopholatilus chamaeleonticeps*, the extant species (Fitch and Lavenberg, 1983), we believe the difference between the dentaries of the fossil and extant species is sufficient to warrant the establishment of a new species.

Numerous skeletal elements have been identified as belonging to *L. rayus*. These include premaxillaries, dentaries, hyomandibulars, vomers, parasphenoids, lateral ethmoids, angulars, ceratohyals, epihyals, vertebra, exoccipitals, and more. Most of these elements, including the premaxillaries, angulars, hyomandibulars, ceratohyals, epihyals, vertebra, and exoccipitals, agree very well in structure with *L. chamaeleonticeps*.

The dentaries (Figure 70c,d) of *L. rayus* are very similar to those of *L. chamaeleonticeps* in having the same basic structure, including a broad anterior tooth patch and a well-defined ventral exterior groove. In *L. chamaeleonticeps* the villiform teeth are confined to the anterior tooth patch, with the remainder of the tooth row being made up of large, canine-like teeth.

The vomer (Figure 70e,f) of *L. rayus*, although similar to that of *L. chamaeleonticeps*, differs in being broader and in having a flatter ventral base. The lateral processes of the vomer are prominent, thinning out to a sharp edge, and the anterior surfaces of the lateral processes are slightly striated and are flat or very slightly concave rather than noticeably concave as in *L. chamaeleonticeps*.

Dooley (1978) reported that *Lopholatilus chamaeleonticeps* has a current range from Nova Scotia south to the Gulf of Mexico and to northern South America. This species has been recorded at depths of 81 to 540 m, but it occurs generally in a relatively narrow zone along the continental slope and along the upper reaches of canyons at depths of 120 to 200 m (Dooley, 1978). There are two critical habitat requirements for tilefish, a suitable temperature, 9° to 14°C, and shelter, which can be provided by rocks, boulders, or clay in which the tilefish can excavate vertical burrows (Grimes et al., 1986).

Lopholatilus feeds on various crustaceans, snails, worms, fish, sea urchins, anemones, and sea cucumbers (Manooch, 1984).

Family POMATOMIDAE
(bluefishes)

Pomatomus saltatrix (Linnaeus, 1766)

FIGURE 70g-o

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—Numerous premaxillae, USNM 286874, 290602, 290610, 290611, 290615, 290682, 291122, 291130; numerous dentaries, USNM 290600, 291063, 291088, 291100, 291131, 291172; 1 ethmoid, USNM 437564; 2 frontals, USNM 437562, 437563; 1 ceratohyal, NCSM 1442; 1 vertebra, USNM 437566; 2 angulars, USNM 437565, 476366; 1 hyomandibular, NCSM 8363; 3 quadrates, NCSM 2908, 6685, USNM 476365; 1 maxilla, NCSM 3648; 1 vomer, USNM 437564.

REMARKS.—Numerous skeletal elements of this fish have been found at Lee Creek Mine, including several associated partial skeletons. The premaxillae compare well with those of modern bluefish, *Pomatomus saltatrix*, in having a labial row of laterally compressed caniform teeth and a row of smaller but otherwise similar teeth along the lingual side of the jaw (Figure 70g,h). The two rows converge posteriorly until they are side by side just forward of the postmaxillary process. Anteriorly, the labial and lingual rows are separated by a toothless expanse. The arrangement of the tooth rows and the shape and angle of the ascending and articular processes match those of the modern species.

Other skeletal elements, including the dentary (Figure 70i), ceratohyal (Figure 70j), quadrate (Figure 70k), angular (Figure 70l), vertebrae (Figure 70m), frontal (Figure 70n), and vomer (Figure 70o), also agree well with *Pomatomus saltatrix*. This is

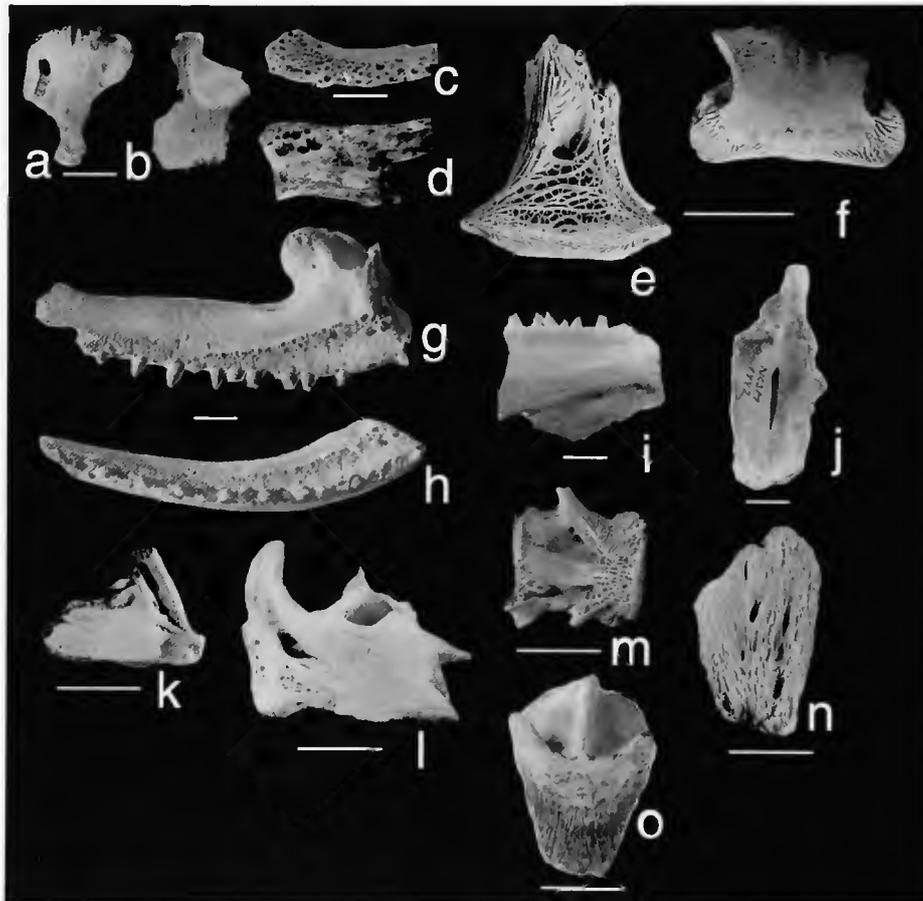


FIGURE 70.—*Caulolatilus* cf. *C. cyonops*, USNM 412151, left and right ceratohyal: a, medial view; b, lateral view. *Lopholatilus rayus*, new species: c, NCSM 2900 (holotype), left dentary, occlusal view; d, same specimen, labial view; e, USNM 437550 (paratype), vomer, ventral view; f, same specimen, labial view. *Pomatomus saltatrix*: g, USNM 290615, right premaxilla, ventrolingual view; h, same specimen, occlusal view; i, USNM 291100, right dentary, labial view; j, NCSM 1442, ceratohyal, lateral view; k, USNM 476365, left quadrate, lateral view; l, USNM 476366, right angular, labial view; m, USNM 437566, vertebra, lateral view; n, USNM 437562, right frontal, dorsal view; o, USNM 437564, vomer, dorsal view. (Scale bars: a-d,g-j=1.0 cm; e,f,k-m=0.5 cm; n=0.7 cm; o=1.0 cm.)

the first occurrence of the genus *Pomatomus* in the fossil record.

The extant bluefish is a pelagic species distributed worldwide except in the eastern Pacific Ocean (Robins and Ray, 1986). It feeds on various fishes, shrimps, lobsters, crabs, and worms (Manooch, 1984).

Family CARANGIDAE
(jacks)

Seriola sp.

FIGURE 69e,f

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—1 dentary, NCSM 1857.

REMARKS.—The dentary (Figure 69e,f) is similar to that of *Seriola dumerili* in having the same villiform teeth, numerous foramina on the outer surface, and the same anterior profile, a noticeable curvature, from dorsal or ventral view.

Seriola dumerili is an offshore reef fish with a world-wide distribution (Robins and Ray, 1986). It feeds on crabs, squid, round herring, round scad, filefish, little tunny, and other fishes (Manooch, 1984).

Family SPARIDAE
(porgies)

Archosargus cf. *A. probatocephalus* (Walbaum, 1792)

FIGURE 71a

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—Numerous frontals, USNM 287938, 476235–476243.

REMARKS.—Numerous frontals (Figure 71a), which compare well with those of the extant sheepshead porgy, *Archosargus probatocephalus*, have been found at Lee Creek Mine. They are very thick and robust, and at their anterior ends, they have a V-shaped groove for accepting the ethmoid. On the posterior half of the dorsal surface, along the midline, there is an elevated crest. Based on frontals alone, we hesitate to make a specific identification.

Archosargus probatocephalus is a benthic species that occurs from Nova Scotia south to Brazil, primarily in bays and estuaries (Robins and Ray, 1986). It feeds on shellfish and sea urchins (Manooch, 1984).

Lagodon cf. *L. rhomboides* (Linnaeus, 1766)

FIGURE 71b,c

HORIZON.—Pungo River Formation (units 2–6); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—Numerous isolated teeth, USNM 291137; 1 partial vomer-ethmoid, NCSM 9589.

REMARKS.—The isolated teeth (Figure 71b) from Lee Creek Mine compare well with those of the extant *Lagodon rhomboides*. In cross section, the teeth are round at the base and incisiform at the tip; a small notch divides the tip, and the resulting lobes of the tip are rounded or pointed.

The vomer-ethmoid fragment (Figure 71c) from the Yorktown Formation also compares well with that of the extant *L. rhomboides*; there are no characters in this specimen or in the isolated teeth that would warrant separating them from the extant species, but the remains are too fragmentary to determine that they are the same species.

We must remark on the abundance of these teeth at Lee Creek Mine. Because these teeth are small and phosphatic, they are found in the flotation concentrate produced by the mill. Along the base of the outdoor storage piles, the coarser grains of concentrate accumulate on the crests of wind ripples, and *Lagodon* teeth can be picked in great numbers from this coarse fraction. Because as many as two million tons of concentrate may be on the ground at a given time, the numbers of these fossil teeth are astronomical.

There are only two other reported fossil occurrences of *Lagodon*, one from the St. Marys Formation of Maryland (Berry, 1932) and one from a Pliocene deposit in Florida (Caldwell, 1957).

Lagodon rhomboides is a benthic species that occurs from Massachusetts to the Yucatan Peninsula (Robins and Ray, 1986) at depths from several centimeters to 67 m; it feeds on worms, crustaceans, and mollusks (Manooch, 1984).

Pagrus hyneus, new species

FIGURE 71d–i

HOLOTYPE.—One partial neurocranium from the frontals to the occipital area, NCSM 2916.

TYPE LOCALITY.—Lee Creek Mine, Aurora, North Carolina.

HORIZON.—Yorktown Formation (unit 1).

PARATYPES.—One partial neurocranium including the frontals and the occipital area and a nonswollen supraoccipital crest, USNM 479858; both frontals with supraoccipital crest, NCSM 10221.

ETYMOLOGY.—In recognition of Becky and Frank Hyne, whose collections at the Lee Creek Mine have increased our knowledge of the fossil fish faunas of North Carolina.

DIAGNOSIS.—This species differs from all other sparids by the narrow frontals, which thicken anteriorly; the articulation surface of the frontal with the ethmoid being, in profile, a deeply grooved “W”; the greatly hyperostosed supraoccipital, which in dorsal view is as wide as the frontals; and the apex of the supraoccipital crest being, in lateral view, above the posterior margin of the orbit.

REMARKS.—In the holotype (Figure 71d–f), the supraoccipital crest articulates along the midline ridge of the frontals, with its point of origin at the anterior end of the frontal. From the midline an oblique frontal ridge continues caudally onto the pterotic, where the ridge thickens and becomes grooved along

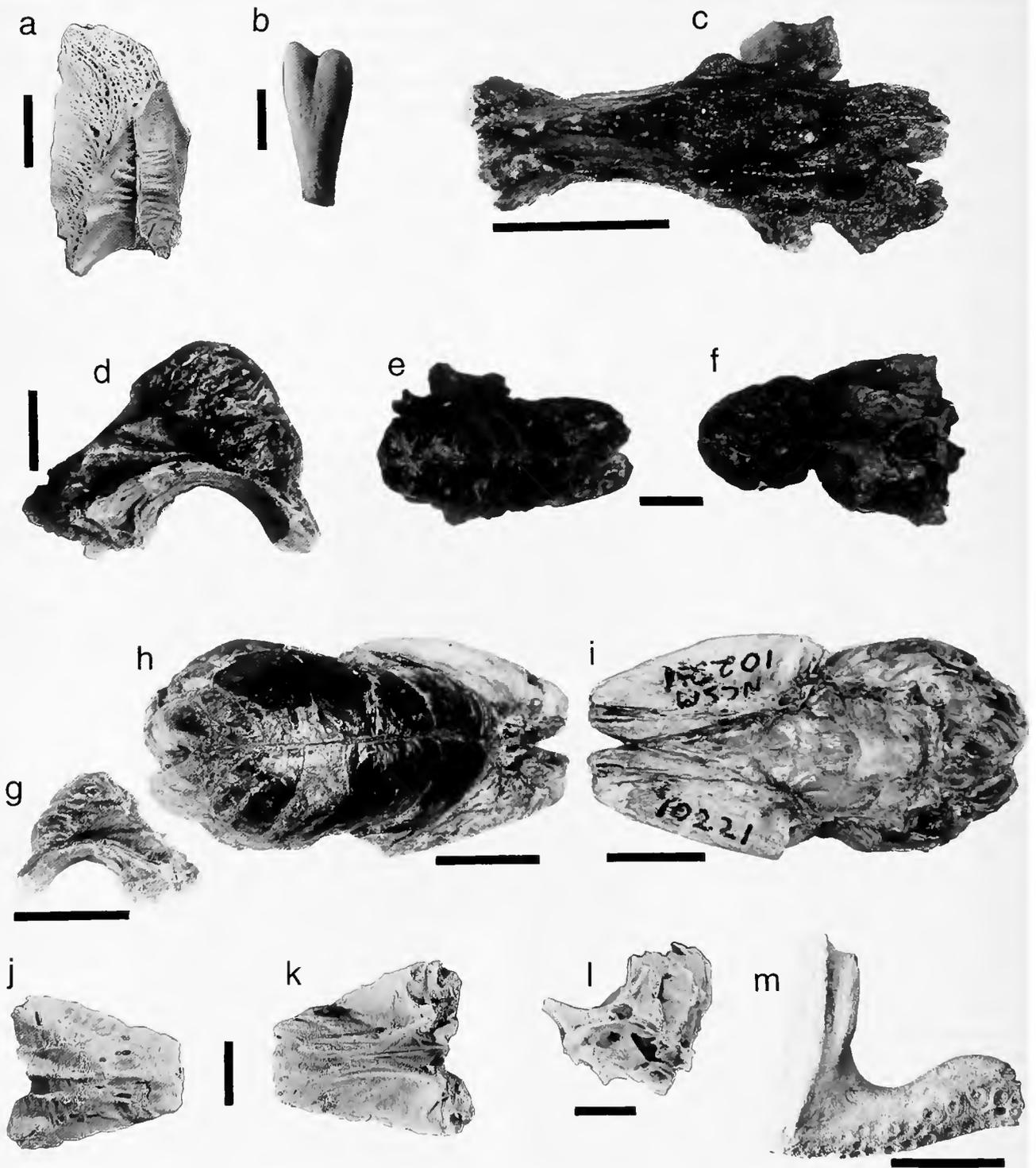


FIGURE 71.—*Archosargus* cf. *A. probatocephalus*: a, USNM 476240, left frontal, dorsal view. *Logodon* cf. *L. rhomboides*: b, USNM 291137, incisiform tooth; c, NCSM 9589, vomer-ethmoid, dorsal view. *Pagrus hyneus*, new species: d, NCSM 2916 (holotype), neurocranium, lateral view; e, same specimen, dorsal view; f, same specimen, ventral view; g, NCSM 10221 (paratype), both frontals with supraoccipital crest, lateral view; h, same specimen, dorsal view; i, same specimen, ventral view. *Pagrus* sp.: j, USNM 298296, paired frontals, dorsal view; k, same specimen, ventral view. *Stenotomus* cf. *S. chrysops*: l, USNM 412154, neurocranium, dorsal view; m, USNM 336236, right premaxilla, lingual view. (Scale bars: a, b, d-f, j-l=1.0 cm; c, g=0.5 cm; h, i, m=0.75 cm.)

its crest. Another ridge extending from the frontal-supraoccipital suture intersects this ridge on the pterotic. Lateral to the frontal and anterior to the pterotic, there is a triangular sphenotic. Caudal to the pterotic, on the dorsal surface of the epiotic, is the epiotic condyle, which articulates with the posttemporal.

Pagrus hyneus has characteristics that are similar to both *Pagrus pagrus*, the extant red porgy, and *Stenotomus*, the extant Atlantic scup. Like the fossil species, *P. pagrus* possesses the same frontal-supraoccipital articulation, the same frontal-pterotic ridge morphology, and the same shapes of the epiotic condyle and the sphenotic.

Pagrus hyneus shows greater similarity to the genus *Pagrus* than to *Stenotomus* in the following characters: (1) the supraoccipitals articulate along two-thirds of the length of the frontals rather than along one-half of their length as in *Stenotomus*; (2) the structure of the ridge that runs from the frontal-supraoccipital articulation to the epiotic; and (3) the shape of the epiotic condyle. For these reasons we place the fossil species in the genus *Pagrus*. We also think that the differences in the shape and placement of the supraoccipital crest, the thickness of the frontals anteriorly, and the profile of the articular surface of the frontals with the ethmoid warrant the establishment of a new species.

Pagrus sp.

FIGURE 71j,k

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—About 100 frontals, USNM 287925, 287927, 287929, 289366, 290552, 290652, 298296.

REMARKS.—Numerous frontals (Figure 71j,k), which compare well with the extant red porgy, *Pagrus pagrus*, occur at Lee Creek Mine. Like *Archosargus*, these frontals are thickened by an elevated crest, which is worn down in most specimens, along the midline of the posterior half of their dorsal surfaces. Unlike *Archosargus* and *P. hyneus*, the anterior margins of the frontals are not grooved.

Pagrus pagrus is a benthic species that occurs from New York to Argentina in the deeper parts of the continental shelf (Robins and Ray, 1986) at depths of 27 to 110 m (Manooch, 1984). The extant species feeds on worms, snails, crabs, and sea urchins (Manooch, 1984).

Stenotomus cf. *S. chrysops* (Linnaeus, 1766)

FIGURE 71l,m

HORIZON.—Yorktown Formation (units 1, 2?, 3?).

REFERRED MATERIAL.—3 premaxillae, USNM 336236–336238; posterior portion of 1 neurocranium, USNM 412154.

REMARKS.—The Lee Creek Mine specimens agree well with those of *Stenotomus chrysops*, the extant Atlantic scup. The fossil neurocranium (Figure 71l,m) differs from *Stenotomus chrysops* in having a much broader and more massive anterior

section of the parasphenoid, but it is still not as great as that in *Pagrus*.

The premaxillae are similar to *S. chrysops* in having larger teeth distally, small villiform teeth toward the symphyseal end and on the labial edge at the symphyseal end, one row of large teeth, and a small descending process at the distal end of the premaxilla.

Stenotomus chrysops is a benthic species that occurs from Nova Scotia to South Carolina, inhabiting the near-shore region of the continental shelf; it feeds on shrimp, worms, clams, starfish, snails, crabs, and sea urchins and occasionally on small fishes (Manooch, 1984).

Family SCIAENIDAE

(drums)

Sciaenops sp.

FIGURE 72a–d

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—14 incomplete premaxillae, USNM 244482, 285336, 285348, 285366, 286857, 290621, 290623, 290653, 291067, 291117, 291144, 291166, 291203, 291668; 6 dentaries, USNM 244470, 284899, 285341, 286902, 291086, 291098; 2 vertebrae, USNM 244481.

REMARKS.—This is a large sciaenid that closely resembles *Sciaenops ocellatus*. The premaxillae (Figure 72a,b) differ from those of the latter species in that the alveoli within the cardiform tooth area, which is lingual to the row of enlarged teeth, are not uniform in size. The bases of the lingualmost tooth row enlarge toward the symphysis, which suggests the presence of teeth that were about one-half the size of those of the enlarged labial row. Among the other sciaenids, the presence of a labial row of large teeth distinguishes these premaxillae from those of *Micropogon* and *Leiostomus*. Lingual to this row, the presence of a cardiform tooth area distinguishes this form from *Cynoscion* and *Otolithus*. The closely spaced labial teeth are more like those of *Sciaenops* than like the widely spaced teeth of *Menticirrhus*.

The dentaries (Figure 72c) differ from those of *S. ocellatus* mainly in that the tooth-bearing area is convex dorsally rather than flattened.

Also illustrated (Figure 72d) is an associated pair of anteriormost vertebrae. These vertebrae match those of *S. ocellatus* and are about the right size to be associated with the above mouth parts, but all of the sciaenids have very similar vertebrae in this region, and they cannot be identified with certainty.

Sciaenops ocellatus (Linnaeus, 1766)

FIGURE 72e

HORIZON.—Yorktown Formation (?unit 3, possibly much higher).

REFERRED MATERIAL.—Fragmental skeletal parts from one individual, including pieces of both premaxillae, an opercular,

articular, quadrate, hyomandibular, atlas, and thoracic vertebrae lacking neural arches, USNM 475010.

REMARKS.—The stratigraphic position of this specimen is uncertain, but the preservation of the bone is similar to that of the material from unit 3 of the Yorktown Formation. The bones of this partial skeleton are so similar to the extant species that there is no question that the Lee Creek Mine specimen is this species. Consequently, the specimen may have come from a considerably higher position in the Lee Creek Mine section.

The extant *Sciaenops ocellatus* is a benthic species that occurs from Massachusetts to Tuxpan, Mexico, in coastal and estuarine waters (Simmons and Breuer, 1962). It feeds on shrimp, crabs, sand dollars, and bony fishes, such as menhaden, mullet, pinfish, pigfish, searobins, lizardfish, spot, croaker, and flounder (Manooch, 1984).

***Pogonias* cf. *P. cromis* Cope, 1869**

FIGURE 72f,g

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1, 2, 3?).

REFERRED MATERIAL.—6 complete upper pharyngeal plates, NCSM 3469, USNM 287978, 459832–459835; 1 complete lower pharyngeal plate, USNM 459836; numerous incomplete pharyngeal plates, USNM 256270, 256271, 290625, 290665, 290676, 291107, 291108, 291112, 291195, 291259, 291683; 2 premaxillae, questionably referred; isolated pharyngeal teeth (Pungo River Formation, units 4, 5); 2 worn pharyngeal plates (Yorktown Formation, unit 3).

REMARKS.—Compared to the extant black drum, *Pogonias cromis*, and the Miocene species, *P. multidentatus* Cope, the Lee Creek Mine pharyngeals are more similar to those of the extant species.

Based on a nearly complete, upper right pharyngeal dental battery from the Calvert Formation of Westmoreland County, Virginia, Cope (1869) described *P. multidentatus* as having

more crushing teeth in the same relative area than does the modern species, *P. cromis*. The number of teeth in the Lee Creek Mine specimens, all upper pharyngeals, falls within the range of the extant species (Table 4).

In contrast to *P. cromis*, the Lee Creek Mine pharyngeals (Figure 72f,g), are more elongate. Perhaps correlated with this elongation, a consistent difference appears in the articulation of the pharyngeal to the epibranchial. On the dorsal surface of the upper pharyngeal of *P. cromis*, a ridge originates near the anterior border, slightly toward the symphyseal side of the plate's midwidth. This ridge extends posteriorly and gives rise to a knob to which the second epibranchial attaches. This ridge originates relatively further back on the Lee Creek Mine specimens and is longer and narrower than that of the modern form. Therefore, we assign these specimens only tentatively to the extant species.

The extant *Pogonias cromis* is a benthic species that occurs from New England to Argentina in coastal and estuarine waters (Choa, 1978). It feeds on clams, mussels, oysters, crabs, worms, and some fishes (Manooch, 1984).

**Family LABRIDAE
(wrasses)**

***Tautoga* cf. *T. onitis* (Linnaeus, 1758)**

FIGURE 72h-j

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—4 incomplete premaxillae, USNM 207605, 459843–459845; 7 incomplete and 2 complete lower pharyngeals, USNM 290501, 297606, 281341, 459838–459841; 2 upper pharyngeals, 281341, 459842.

REMARKS.—Several premaxillaries (Figure 72h,i) collected at the Lee Creek Mine, except for size, compare favorably with those of the extant tautog, *Tautog onitis*. The fossil premaxillaries are nearly twice the size of those of the extant species available to us. The extant tautog premaxillaries were from individuals between 350 and 407 mm TL, which are less than half the maximum size (915 mm TL) for this species. This size difference, therefore, does seem not taxonomically significant.

In dorsal or ventral view the lower pharyngeals (Figure 72j) form an isosceles triangle, with the top pointing anteriorly. The dorsal surface of the pharyngeal is covered with cylindrical teeth of varying sizes, with the largest toward the midline, and with blunt, rounded crowns. In the one complete specimen with an associated upper left pharyngeal, the lower pharyngeal has an anteroposterior length of 16.7 mm and a width of 38.8 mm. In a nearly complete specimen, in which the anterior edge is missing, the anteroposterior length is about 21 mm, and it is 52.2 mm wide. These specimens, except for their sizes, are identical with those available of the extant species, *Tautoga onitis*.

Based on an incomplete premaxilla from the Miocene of Virginia, Leidy (1873) proposed the new genus and species *Prototautoga condens*. He distinguished it from *Tautoga onitis* by

TABLE 4.—Comparison of the upper pharyngeal in fossil and extant *Pogonias*. (VZ=vertebrate zoology collection.)

Specimen	Pharyngeal length (mm)	Number of teeth	Age
<i>Pogonias cromis</i>			
USNM VZ 26132	24.5	18	recent
USNM VZ 110700	51	33	recent
USNM VZ 110216	63	37	recent
<i>Pogonias multidentatus</i>			
Holotype	45	45	Miocene
<i>Pogonias</i> cf. <i>P. cromis</i>			
NCSM 3469	69	36	Pliocenc
USNM 287978	41	24	Pliocenc
USNM 459832	78	43	Pliocene
USNM 459833	67	41	Pliocene
USNM 459834	72	41	Pliocene
USNM 459835	68	35	Pliocenc

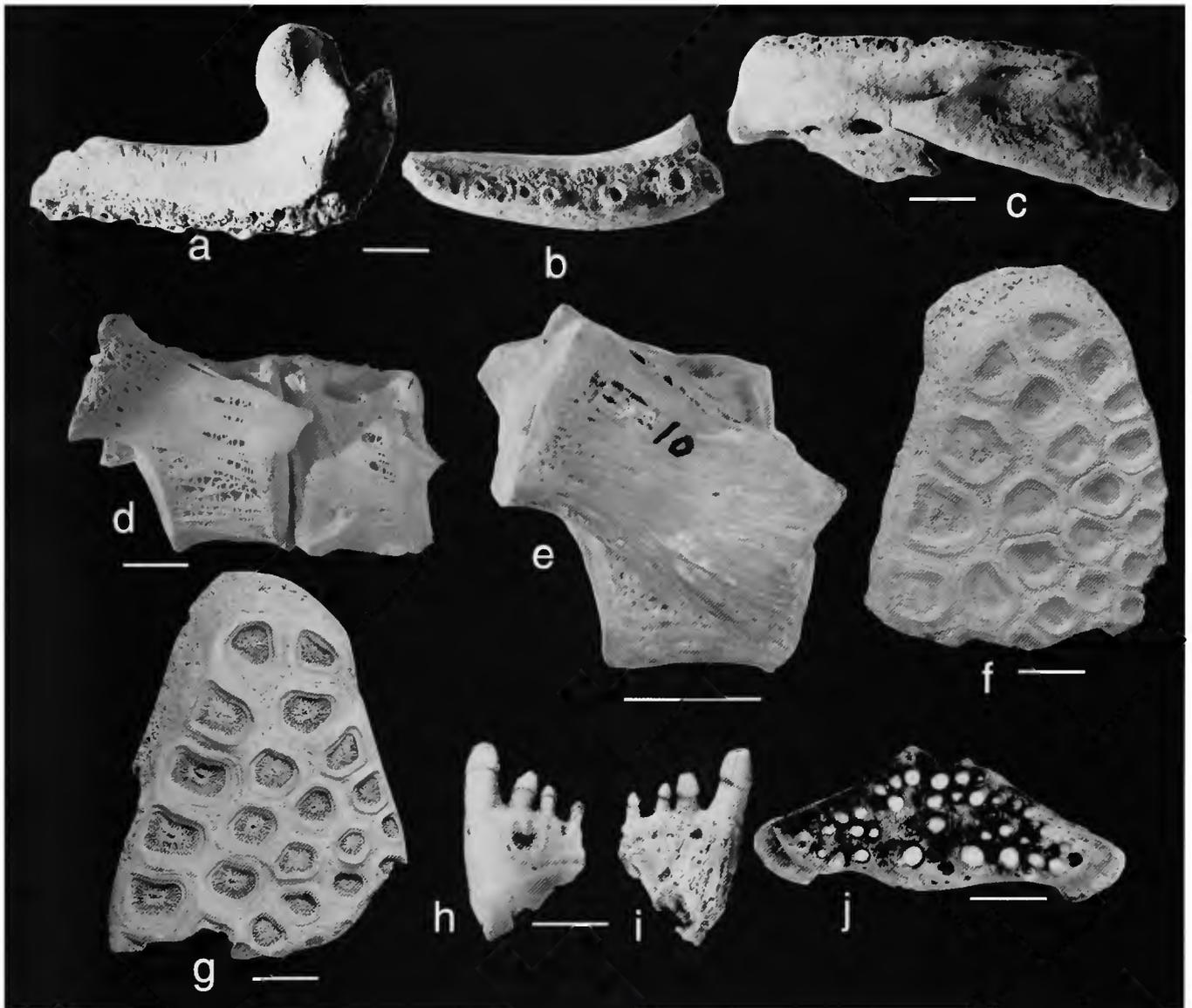


FIGURE 72.—*Sciaenops* sp.: a, USNM 244482, anterior portion of left premaxilla, lingual view; b, same specimen, occlusal view showing outer row of large alveoli and inner cardiform area; c, USNM 244470, anterior end of dentary, labial view; d, USNM 244481, associated atlas and second vertebrae. *Sciaenops ocellatus*: e, USNM 475010, lateral view of atlas. *Pogonias* cf. *P. cromis*, upper right pharyngeal plates, occlusal view: f, USNM 256270; g, USNM 256271. *Tautoga* cf. *T. onitis*: h, USNM 207605, incomplete right premaxilla, lacking delicate posterior and elongate ascending processes, labial view; i, same specimen, lingual view; j, USNM 459838, lower pharyngeal, occlusal view. (Scale bars: a–g=1.10 cm; h–j=1.0 cm.)

its large size, greater number of teeth, and the wider spacing of its teeth. As in the extant species, however, these characteristics reflect different stages of growth, and Leidy's species *Prototautoga condens* cannot be separated from the extant species, *Tautoga onitis*.

The extant tautog is a benthic species that occurs from Nova Scotia south to South Carolina (Robins and Ray, 1986) at depths of 1 to 30 m (Bigelow and Schroeder, 1953). It feeds on mussels, barnacles, crabs, shrimp, and worms (Manooch, 1984).

Family URANOSCOPIDAE (stargazers)

Astroscopus sp.

FIGURE 73a–c

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—5 opercula, USNM 412156, 412158–412160, 459837; 1 preoperculum, USNM 412157.

REMARKS.—The Lee Creek Mine opercula (Figure 73a,b) are very similar to those of *Astroscopus guttatus* in the shape of the articular fossa of the opercula, which articulates with the opercular process of the hyomandibular, in the ridge line extending from this facet posteriorly to approximately two-thirds of the mesial surface of the opercula, and in ornamentation.

The preoperculum is a somewhat crescent-shaped bone with three radially divergent processes along the caudal edge (Figure 73c). Like the extant species, the exterior surface of the bone is ornamented with circular depressions. The Lee Creek Mine specimens are insufficient for attempting a specific identification.

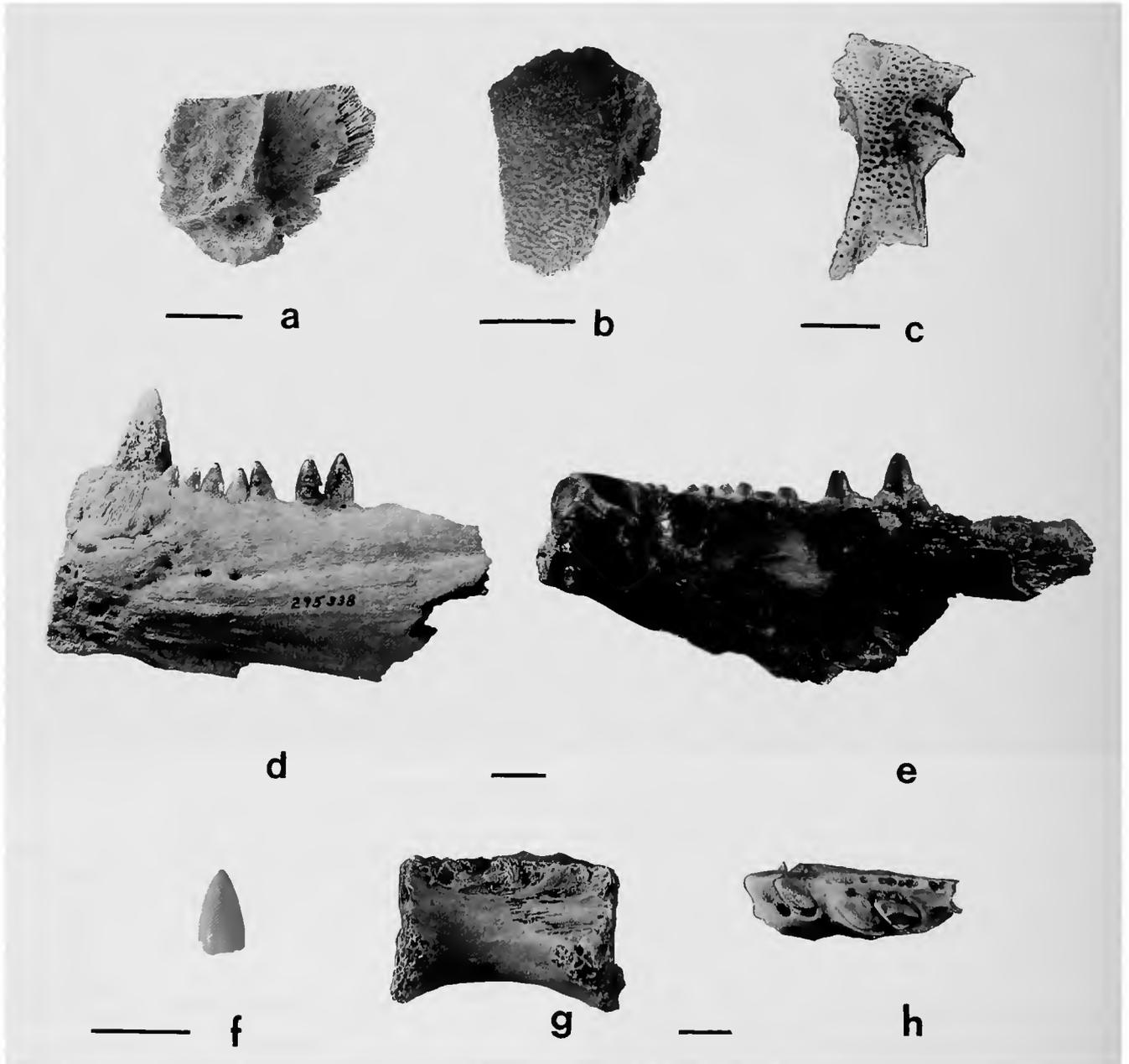


FIGURE 73.—*Astroscopus* sp.: a, USNM 412156, Yorktown Formation, operculum, medial view; b, same specimen, lateral view; c, USNM 412157, preoperculum, lateral view. *Sphyaena* cf. *S. barracuda*: d, USNM 295338, Yorktown Formation, anterior portion of left dentary, labial view; e, USNM 476367, Yorktown Formation, partial right dentary, lingual view; f, USNM 291168, Pungo River Formation, isolated tooth; g, USNM 291081, Yorktown Formation, vertebra, lateral view; h, USNM 476368, Yorktown Formation, premaxilla, occlusal view. (Scale bars=1.0 cm.)

Astroscopus has been previously reported from the Atlantic Coastal Plain. Ray et al. (1968) identified to this genus an otico-temporal portion of a neurocranium from the Pleistocene Kempsville Formation of Virginia, and Fitch and Lavenberg (1983) also identified otoliths from the Pliocene at Lee Creek Mine to this genus.

Of the two extant species along the Atlantic coast of the United States, *Astroscopus guttatus* is a benthic species that occurs from New York to North Carolina, and *A. y-graecum* occurs from North Carolina to Mexico (Robins and Ray, 1986).

Family SPHYRAENIDAE
(barracudas)

Sphyraena cf. *S. barracuda* (Walbaum, 1792)

FIGURE 73d-h

HORIZON.—Pungo River Formation (units 2–6); Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—9 vertebrae, USNM 291076, 291081; 1 dentary lacking teeth, USNM 291664; 4 partial dentaries with teeth, USNM 291236, 295338, 437561, 476367; 2 partial premaxillae, USNM 476368; about 40 uncataloged fragments of jaws; about 50 isolated teeth, USNM 291168.

REMARKS.—In both the Pungo River and Yorktown formations, lanceolate and compressed barracuda teeth (Figure 73f) are among the more common osteichthyan remains. The teeth offer no certain characteristics that distinguish them from the modern form, *Sphyraena barracuda*. Fossil sphyraenid species founded on isolated teeth, such as *S. major* Leidy or *S. speciosa* Leidy, probably cannot be distinguished from *S. barracuda*.

The Lee Creek Mine dentaries (Figure 73d,e) are within the size range of *S. barracuda*. On their symphyseal ends, they bear a large, lanceolate tooth that is followed by a single row of labiolingually compressed to flat, carinate teeth. Some of these dentaries came from individuals that attained a very great size; the largest, USNM 295338, which is lacking its posterior half (Figure 73d), has a depth at the symphysis of 37.5 mm.

In the symphyseal area of the premaxilla (Figure 73h), two large lanceolate teeth are followed by teeth similar to those in the dentary, but they are much smaller than those in the occluding dentary. Both the dentaries and the premaxillaries are indistinguishable from those of the extant *Sphyraena barracuda*.

Vertebrae, which we believe are sphyraenid (Figure 73g), also were collected at Lee Creek Mine. Although the neural arch is broken away in the available specimens, the long, smooth, medially constricted centra with deep sulci dorsal to the midheight duplicate recent specimens.

Sphyraena barracuda is an offshore reef species that occurs from Massachusetts to Brazil and also occurs worldwide in tropical and warm-temperate waters (Robins and Ray, 1986). It

feeds on many species of bony fishes, including jacks, silver-sides, parrotfish, and filefish (Manooch, 1984).

Family SCOMBRIDAE
(mackerels and tunas)

Sarda aff. *S. sarda* (Bloch, 1801)

FIGURE 74

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1–3).

REFERRED MATERIAL.—Numerous mesethmoids, USNM 290654, 291082, 291090, 291146, 291170, 291201; numerous portions of skulls, USNM 290544, 290595, 475012, 475013, 476225–476231; anterior end of 1 dentary, USNM 476250; numerous hypural elements, USNM 290681, 291092, 291095, 291104, 291140, 291152, 291158, 291160, 291167, 291169, 291197, 291233, 291252, 291677, 476396; numerous uncataloged vertebrae.

REMARKS.—The incomplete dentary (Figure 74f) from the Yorktown Formation belongs to the tribe Sardini, which includes the genera *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, *Allothunnus*, and *Sarda*. *Sarda sarda* is the only member of the group now occurring in the western Atlantic Ocean, and it is with this species that the fossil compares favorably.

A characteristic feature of Sardini dentaries, other than the large teeth, is the acute angle formed between the plane of the tooth row and the anterior margin of the dentary (see Collette and Chao, 1975). This angle is about 65° on the fossil, but it is usually less than 57° on dentaries of recent *Sarda*. In this aspect the fossil dentary resembles *Cybiosarda*.

In *Sarda*, Collette and Chao (1975) also noted the presence of a notch on the upper portion of the anterior margin of the dentary; in the Lee Creek Mine specimens, this notch is weakly developed or absent. The extant bonitos *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* lack this notch; however, unlike *Cybiosarda* and *Gymnosarda*, the Lee Creek Mine dentaries possess a notch in the anterior, ventral margin that is similar to the notch in the dentaries of *Orcynopsis* and *Sarda*.

Despite the noted differences between the fossil dentary and the dentaries of *Sarda*, the fossil dentary compares more favorably with those of this genus than with any of the others in the Sardini. It may prove to be a distinct species, but available fossil material is inadequate to establish its identity.

Mesethmoids (Figure 74a,b) and incomplete skulls (Figure 74c,d) are common fossils in the lower Yorktown Formation. On the center of the ventral surface of the mesethmoid, the anterior end of the vomer (or prevomer) is often present. Like most other bonitos except *Orcynopsis*, the anterior edge of the ethmoid is “concave... with an anteromedian projection and an anterolateral horn on each side” (Collette and Chao, 1975:539). These characters are found in the Lee Creek Mine mesethmoids, which are identical to those of the extant species.

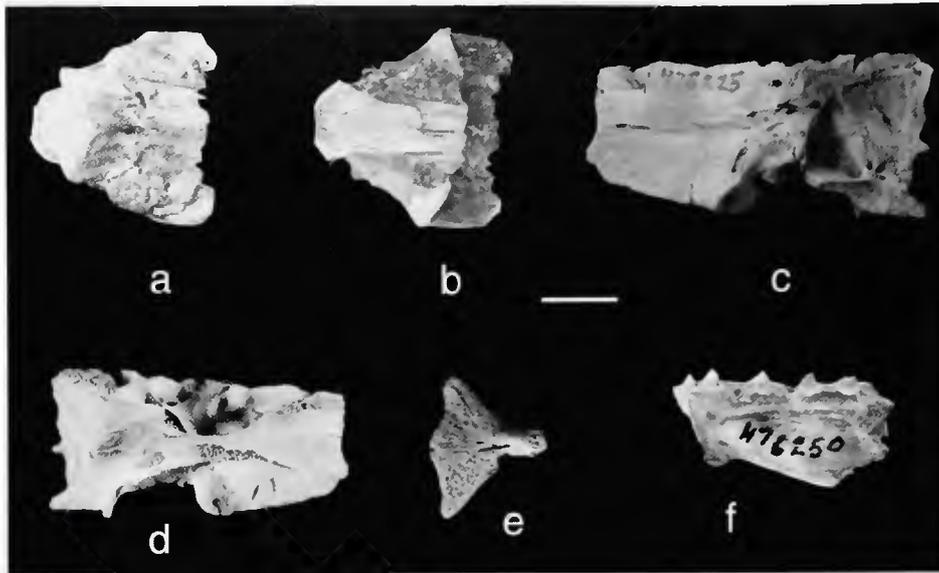


FIGURE 74.—*Sarda* aff. *S. sarda*: a, USNM 290654, mesethmoid, dorsal view; b, same specimen, ventral view, with anterior end of prevomer; c, USNM 476225, incomplete skull, dorsal view; d, same specimen, ventral view; e, USNM 476369, incomplete hypural, lateral view; f, USNM 476250, anterior portion of dentary, labial view. (Scale bar=1.0 cm.)

The incomplete skulls are principally left or right portions of the skull roof from the anterior tips of the frontals to the supraoccipital and epiotic. As in *Sarda*, the sphenotic is larger than it is in *Thunnus atlanticus* or *T. obesus*.

The triangular hypural plate is composed of five fused hypural bones (Potthoff, 1975). According to Collette and Chao (1975), the dorsalmost hypural bone, hypural 5, does not completely fuse with the hypural plate in the bonitos or in higher tunas, *Auxis* to *Thunnus*; they did not present characters for the hypural plates that could be used to separate *Sarda* from other bonitos or from tunas. A vestige of the primitive hypural notch is present only in the bonito genus *Gymnosarda*.

While examining the skeletons of the extant *Sarda sarda* and comparing them to the Lee Creek Mine specimens, we noticed that the majority of ethmoid fossils were equal to or smaller than those from the extant species (550 mm TL size range). A hypural from a 550 mm TL *Sarda sarda* had a cranio-caudal length of 13 mm and a dorsoventral height of 16 mm. The Lee Creek Mine hypurals (Figure 74e), which we have assigned to *Sarda sarda*, are very small, 13–14 mm in cranio-caudal length and 15 mm in dorsoventral width, and lack a hypural notch; therefore, based on size, these hypurals are assigned to *Sarda*.

Sarda sarda is a coastal pelagic species that occurs from the Gulf of St. Lawrence to Argentina (Robins and Ray, 1986); it feeds on squid, mackerels, anchovies, menhaden, silversides, and shrimp (Manooch, 1984).

Auxis sp.

FIGURE 75

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—1 nearly complete dentary, USNM 291139.

REMARKS.—This dentary (Figure 75) is a flat, thin bone with a single row of minute teeth. The dorsal surface bearing the tooth row rises toward the distal end; at the mesial end it is bent slightly toward the symphysis. The teeth are broken off, but the preserved tooth bases are circular in cross section, uniform in size (approximately 0.5 mm in diameter), and evenly spaced (13 teeth per cm). On the lingual face the intermandibularis fossa is short and broad. It is bounded above by a shelf-like anteroventrally directed ridge.

The dentary is 11.6 mm high and 5.2 mm wide at the symphysis. Height at the mesial termination of the notch dividing the dorsal and ventral rami is 14.8 mm. Width at the same place is 5 mm.

The combination of a distally rising tooth row, small teeth, and the peculiar intermandibularis fossa allies this dentary with *Auxis*. The fossil dentary differs only in minute detail from a dentary of *Auxis thazard* (Collette collection, USNM; uncataloged; 315 mm fork length). The fossil dentary is four times larger than that of the extant specimen; it has a shorter intermandibularis fossa, and at the distal end, the tooth row does not rise to as great an extent as it does in the extant species.

The genus *Auxis* is currently represented by two species, *Auxis rochei*, the bullet tuna, and *A. thazard*, the frigate tuna.



FIGURE 75.—*Auxis* sp., USNM 291139, nearly complete dentary: a, labial view; b, lingual view showing abbreviated intermandibular fossa. (Scale bar=1.0 cm.)

These are pelagic species that occur in the warm waters of the Indian, Pacific, and Atlantic oceans (Joseph et al., 1980).

Thunnus sp.

FIGURE 76

HORIZON.—Pungo River Formation (units 3, 4); Yorktown Formation (unit 1).

REFERRED MATERIAL.—Numerous isolated vertebrae, USNM 291070, 475232–475234, 494371; 36 hypural bones, including 1 nearly complete caudal complex, USNM 291069, 291092, 291140, 291152, 291160, 291167, 291169, 291197, 291252, 291677; about 100 incomplete dentaries, USNM 290162, 290163, 290575, 290622, 290672, 291093, 291094, 291119, 291242; about 50 incomplete premaxillae, USNM 290551, 475011; 1 articular, USNM 291147; 2 maxilla, USNM 291132, 291202; 5 quadrates, USNM 290648, 291111, 291129, 291237, 291247; 1 angular, USNM 319669.

REMARKS.—In the Yorktown Formation at Lee Creek Mine, the most abundant teleost remains are those belonging to *Thunnus*. This material agrees well with most of the available skeletons of the extant tunas. As Gibbs and Collette (1967) noted, the amount of variation that occurs in different skeletal elements of the genus *Thunnus* often overlaps between different species; although some skeletal characters for identifying species do exist, they are not preserved in the material available to us. Species determination will have to await the availability of articulated skeletons.

In the Lee Creek Mine collection, the numbers of tuna-like scombrid vertebrae (Figure 76a) exceed those of all other teleostean taxa combined. Many of these are exceptionally large and duplicate in size and form those of the extant *Thunnus thynnus*. The precaudal vertebrae are slightly wider than tall and bear deep upper and lower fossa. At the anterior border of the ridge that separates these fossae, there is a small triangular depression for ligament attachment.

In that the parhypural is not fused to the complex, the fused hypural plate does not bear a medial notch, and there is a deep fossa developed on the hypural just behind the terminal centrum. The hypural complex (Figure 76b) is typical of *Thunnus*. The large size of the complex suggests that it belongs to *Thunnus thynnus* rather to some other species in the genus.

The dentaries (Figure 76c) bear a single row of very small (1.5 mm in basal diameter), evenly spaced (4–6 per cm), conical

teeth. Due to a pronounced rounded crest on the lingual side situated above the intermandibularis fossa, the bone is unusually thick for scombrid dentaries. The head for the attachment of the geniohyoideus muscle is at the head of the fossa below this ridge and is unusually prominent.

Two incomplete dentaries from the Pungo River Formation, USNM 290162 and 290163, differ from those of *T. thynnus* in that the intermandibularis fossa does not reach up to the symphysis and the mesial edge of the bone is only faintly notched rather than prominently notched (Figure 76d). The available fragmental material is not sufficient to establish the specific identity of the Pungo River *Thunnus*, but it may be closely related to *T. thynnus*.

A small premaxilla (34 mm long; approximately 38 mm restored), USNM 290551 (Figure 76e), from unit 3 of the Yorktown Formation, has large, well-spaced teeth with labiolingually compressed bases and conical, lingually curved tips. Tooth shape and spacing and the overall shape of the bone are very similar to a premaxilla of *T. obesus*. The only apparent difference is the much thinner dorsal process of the fossil premaxilla. Premaxillae, however, appear to be conservative elements in *Thunnus* skeletons so identifications based on them are necessarily tenuous.

Tunas are pelagic species that have a world-wide distribution in tropical and temperate waters (Robins and Ray, 1986). They feed on larval crustaceans, squid, paper nautilus, filefish, triggerfish, jacks, mackerel, and many other bony-fish species (Manooch, 1984).

Acanthocybium solandri (Cuvier in Cuvier and Valenciennes, 1831)

FIGURE 77

Sphyraenodus bottii Capellini, 1878:250, pl. 3: figs. 1–6 [middle Miocene, Italy].

Scomberomorus botti (Cappellini).—Caria, 1973:19, pl. 6: figs. 1, 2, pl. 7: figs. 1, 2, pl. 8: figs. 1–3 [Miocene, Sardinia].

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—1 dentary, USNM 319668; 1 incomplete dentary, USNM 291077; 3 incomplete premaxillae, USNM 25782; 4 hypurals, USNM 291084; 1 precaudal vertebra, USNM 476370.

REMARKS.—In the fossil dentaries and premaxillae, each ridge, sulcus, and foramen as well as the shape and relative size of these jaw elements, and the replacement pattern of the teeth

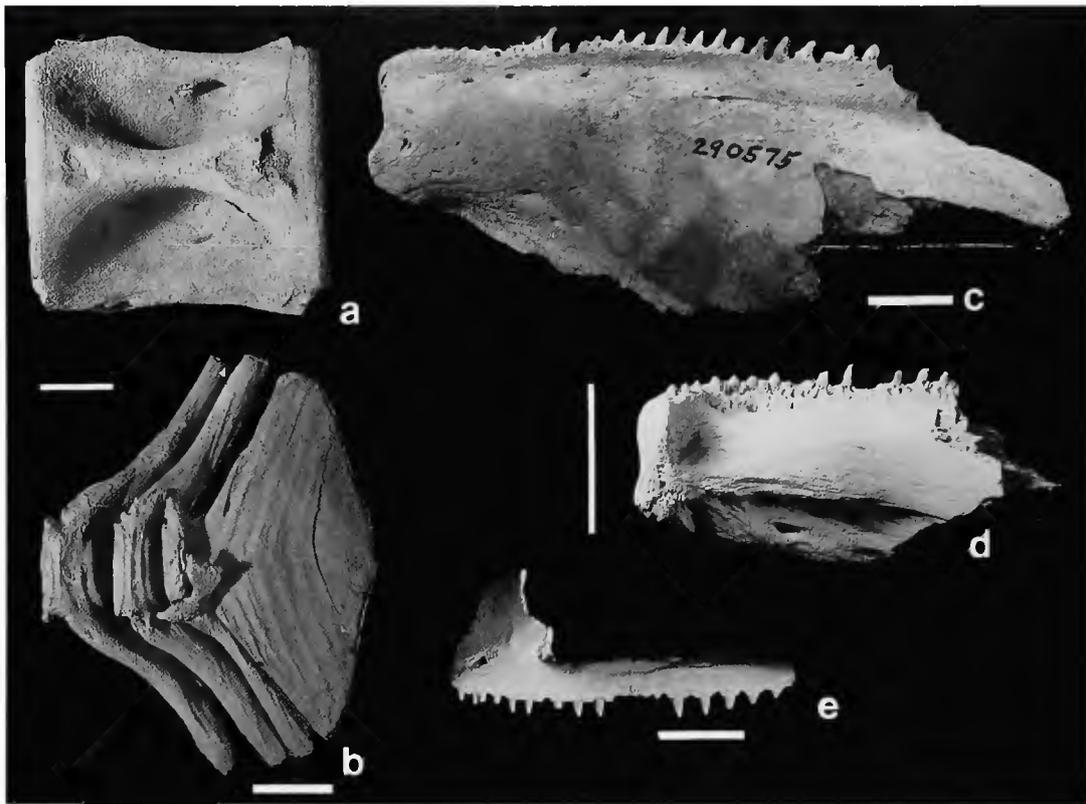


FIGURE 76.—*Thunnus* sp.: a, USNM 494371, Yorktown Formation, incomplete caudal vertebra, lateral view; b, USNM 291069, Yorktown Formation, associated hypural complex, lateral view; c, USNM 290575, Yorktown Formation, partial left dentary, labial view; d, USNM 290163, Pungo River Formation, partial right dentary, lingual view; e, USNM 290551, Yorktown Formation, left premaxilla with teeth, labial view. (Scale bars=1.0 cm.)

are duplicated in three western Atlantic specimens of *Acanthocybium solandri*. The fossils are from larger individuals than the largest recent individual available to us (1780 mm TL; 36.8 kg), and they exceed the known size range of the species (maximum observed size ~83 kg).

In the fossil form, the premaxillae (Figure 77a) have a greater transverse diameter compared with jaw depth, particularly at the dorsal edge below the tooth row. The ratio of the transverse diameter (width) to depth at the tenth alveoli from the symphysis of the fossil premaxilla averages 0.54, whereas this ratio in the modern specimens averages 0.44. This difference is minor compared to the much more marked differences in proportions and tooth shape encountered when comparing corresponding bones from two allopatric species of *Thunnus*, for example. Furthermore, this is the sort of change one would expect from a normal allometric growth pattern.

The most nearly complete and largest dentary (Figure 77b) of this species from Lee Creek Mine, USNM 319668, exhibits the characters identified by Collette and Russo (1984:575, 578–579) as diagnostic of dentaries of *Acanthocybium*: the teeth are more tightly packed, the notch on the anteroventral

margin is absent, and a prominent notch is present on the anterior margin of the dentary.

The fossil hypural (Figure 77c) is typical of *Acanthocybium solandri* in that the parhypural, which carries the laterally extending parhypurapophysis, is fused to the complex, and the posterior border of the plate carries a well-defined medial notch. The condition in *Gymnosarda* is similar (Collette and Chao, 1975) but differs in that hypural five and the parhypural are incompletely fused to the complex. *Scomberomorus*, the most closely related extant genus, also has a similar caudal construction, but the parhypural is not always completely fused. The only striking quality of the fossil caudal complex when compared to *A. solandri* is its large size. Dorsoventral diameters of the fossils range from 49 to 88 mm, but modern specimens that have been examined do not exceed 50 mm.

Precaudal *Acanthocybium* vertebrae (Figure 77d) are easily recognized by the development of three lateral sulci rather than the usual two.

Capellini (1878) established *Sphyraenodus bottii* on the basis of an associated dentary and premaxilla, which also compares favorably with *Acanthocybium solandri*.

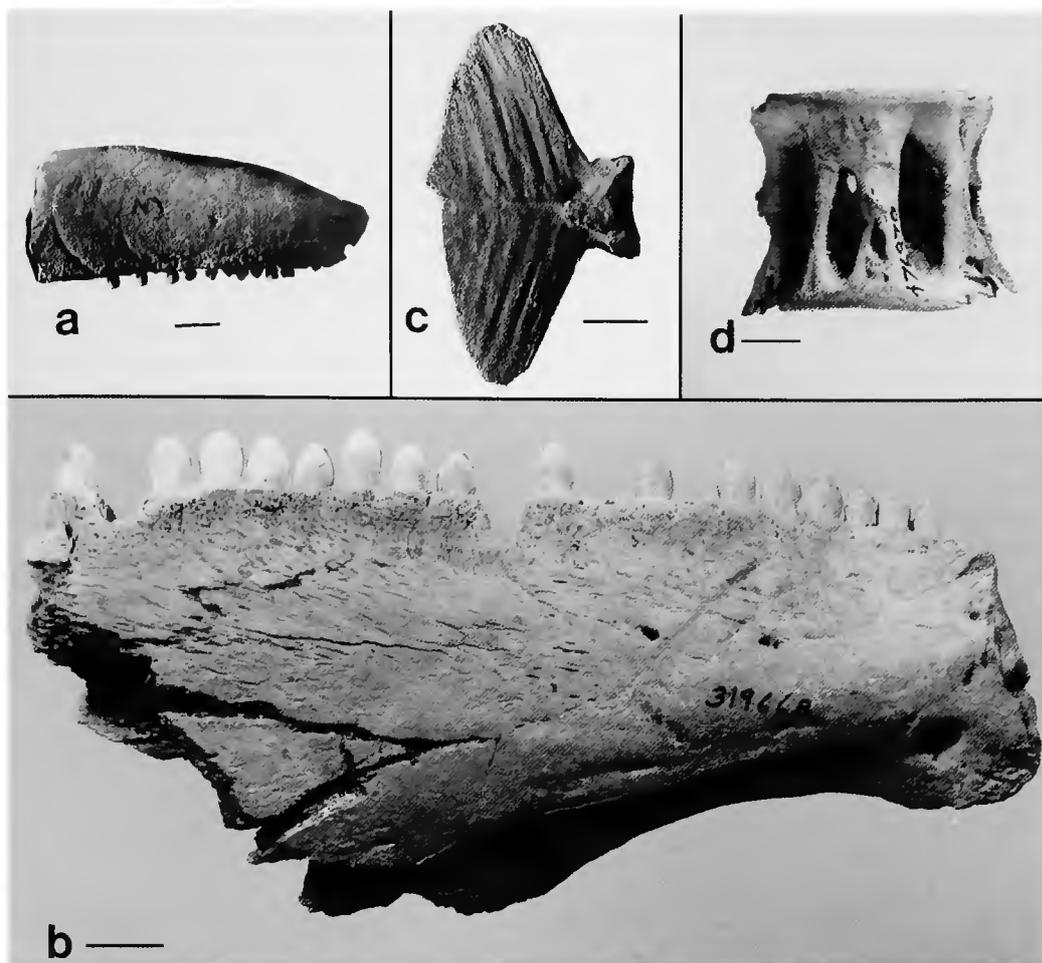


FIGURE 77.—*Acanthocybium solandri*: a, USNM 25782, posterior end of premaxilla, labial view; b, USNM 319668, anterior end of dentary, labial view; c, USNM 291084, hypural, lateral view; d, USNM 476370, vertebra, lateral view. (Scale bars: a=2.0 cm; b=1.0 cm; c=1.25 cm; d=0.9 cm.)

Acanthocybium solandri is a pelagic species that occurs from New Jersey to South America and is distributed worldwide in tropical and warm-temperate waters (Robins and Ray, 1986). It feeds on a variety of bony fishes, including frigate mackerel, butterfish, porcupinefish, and round herring (Manooch, 1984).

Family XIPHIIDAE
(swordfishes)

Xiphias gladius Linnaeus, 1758

FIGURE 78

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—1 rostrum fragment, USNM 476396.

REMARKS.—In the course of studying the Lee Creek Mine marlins, Harry Fierstine (pers. comm., Nov 1993) discovered a

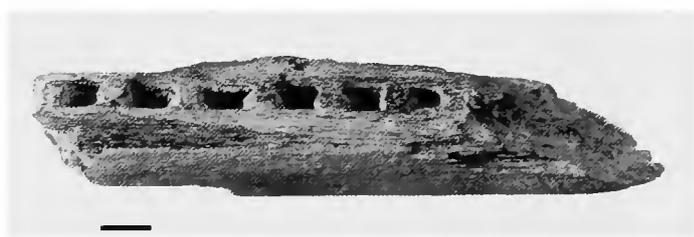


FIGURE 78.—*Xiphias gladius*, USNM 476396, lateral view of rostral fragment showing rectangular chambers. (Scale bar=1.0 cm.)

fragment of a swordfish rostrum (USNM 476396). He stated that the central chambers of the rostrum (Figure 78), which are rectangular in this specimen, are distinctive characters of *Xiphias* rostra (Poplin, 1975; Poplin et al., 1976).

According to Manooch (1984:306), the extant swordfish is a warm-water species; in the summer, it ranges from Newfoundland to Argentina. It feeds on squid and bony fishes, including hake, mackerel, and barracuda.

Family ISTIOPHORIDAE
(marlins)

For the genera *Makaira*, *Istiophorus*, and *Tetrapturus*, see Fierstine (this volume).

Hemirhabdorhynchus sp.

FIGURE 79

HORIZON.—Pungo River Formation (units 2–5).

REFERRED MATERIAL.—7 broken rostra, USNM 24745, 421907–421909.

REMARKS.—Leidy (1856a:12) gave the name *Cylindracanthus ornatus* to a fluted fish spine that was said to be from the Upper Cretaceous beds near Pemberton, Burlington County, New Jersey, but the type specimen was not illustrated. Later that year, in the same journal, Leidy (1856b:302) noted that Agassiz had previously described two species, *Coelorhynchus rectus* and *C. sinuatus*, based on the same type of spine, which Agassiz (1833–1843:92) said were from the London Clay (Ypresian) at Sheppey, England. In 1905 Leriche noted that *Coelorhynchus* Agassiz is a junior homonym of *Coelorhynchus* Giorna, and unaware of Leidy's genus *Cylindracanthus*, he erected the genus *Glyptorhynchus*. Four years later Leriche (1909:381–383) discovered the priority of Leidy's genus; at the same time he restricted the name *Glyptorhynchus* to fluted rostra with flat oral surfaces bearing two parallel bands of crowded alveoli for very small acicular teeth. He did not, however, know of these rostra until after he erected *Glyptorhynchus*; this last genus, therefore, is a junior synonym of *Cylindracanthus*, and it is not available for Leriche's rostra with flat oral surfaces bearing two bands of tooth alveoli.

Based on Leriche's holotype of *G. costatus* but excluding other species of *Glyptorhynchus*, Casier (1946:155) erected the genus *Hemirhabdorhynchus*, which he characterized as having "a more or less depressed cylindro-conical form, with longitudinal costae, limited to the dorsal half or nearly on this half, and by the existence of two ventral wide alveolar bands." These characters also may be applied to the species Casier excluded. If Leriche's and Casier's separation of these rostra from *Cylindracanthus* is correct, then *Hemirhabdorhynchus* is the senior name for these rostra.

The familial identity of these specimens is uncertain. On the basis of the two bands of small acicular teeth, Leriche (1910,

1936a, 1942) placed this genus in the Xiphiidae. As confirming evidence of this taxonomic assignment, Leriche (1910) mentioned a rostrum associated with vertebrae and a hypural from the Oligocene of Belgium. Concerning the hypural of Leriche's specimen, as in the Istiophoridae but not the Xiphiidae, the parhypural is fused to the ventral hypural plate; unlike the available hypurals of the extant Xiphiidae and Istiophoridae, the hypural notch is extremely shallow. In other scombroids, however, both of these characters may vary within a family. Because the shape of the rostra and tooth bands are characteristic of the Istiophoridae rather than the Xiphiidae, we assign *Hemirhabdorhynchus* to the Istiophoridae.

The rostra (Figure 79) are known only as detached elements, and they are very seldom found complete. They are long, straight, slender rods of dense bone that taper to a point, which may be rounded by wear. Except for the flattened tooth-bearing surface, they are covered completely by fine longitudinal grooves, which may be obscured by wear. The flattened surfaces bear two parallel bands of tooth alveoli, which are similar to those found on istiophorid rostra (Figure 79b); between these parallel rows the surface of the spine is smooth to very finely grooved.

Order PLEURONECTIFORMES

Family BOTHIDAE
(lefteye flounders)

Paralichthys sp.

FIGURE 80a–c

HORIZON.—Yorktown Formation (units 1, 2).

REFERRED MATERIAL.—2 anterior portions of dentaries with teeth, USNM 412162, 412163; 1 left maxilla, USNM 412164; 1 partial right articular, USNM 412165.

REMARKS.—The maxilla (Figure 80a), which consists of the articular end, is identical to that of the extant *Paralichthys dentatus*. The dentary (Figure 80b) has long, stout, rugose teeth, which, as in *P. dentatus*, are almost one-half the height of the dentary. The lower one-third of the dentary is striated distally and has a sculptured texture. The partial right angular (Figure 80c) is lacking most of the anterior process, the coronoid process, and part of the postarticular process. Because the fossil

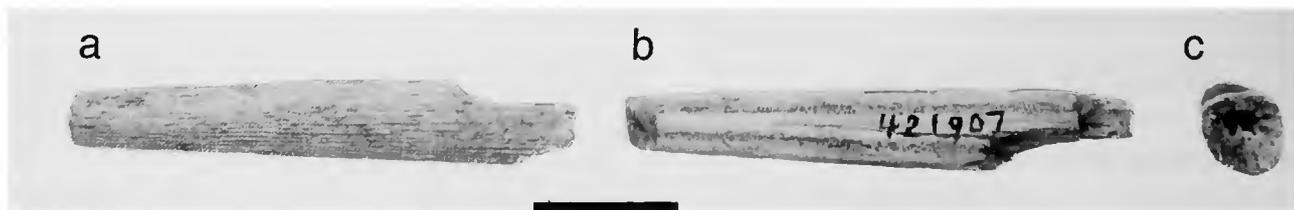


FIGURE 79.—*Hemirhabdorhynchus* sp.: a, USNM 421907, rostral fragment, dorsal view; b, same specimen, ventral view; c, same specimen, cross-sectional view. (Scale bar = 1.0 cm.)

material consists of isolated bone fragments, species determination is not possible at this time.

Paralichthys dentatus is a benthic species that occurs from Maine to northern Florida (Robins and Ray, 1986). It feeds primarily on menhaden, silversides, sand lances, herrings, anchovies, weakfish, squids, shrimp, and crabs (Manooch, 1984).

Order TETRAODONTIFORMES (Plectognathi)

Family MONACANTHIDAE (filefishes)

Aluterus sp.

FIGURE 80*d-f*

HORIZON.—Pungo River Formation (units 4–6); Yorktown Formation (units 1–3).

REFERRED MATERIAL.—About 200 hyperostosed vertebrae, USNM 286157, 286158, 286164, 290288, 290302, 290528, 291690, 291693, 291707–291729, 291731–291779, 291801, 291803–291805, 291807–291823, 291825–291827, 291831, 291834, 291840–291845, 291847–291849, 291851–291856, 291858–291862, 476354.

REMARKS.—The most common hyperostosed bones found in the lower Yorktown Formation are vertebrae, which are identical in their morphology and hyperostosis to those of the extant *Aluterus shoepfi*. Like the extant species, they are dorsoventrally compressed, with prominent dorsal and ventral grooves on the centra (Figure 80*d,e*). In articular view, the second precaudal vertebra is hexagonal in outline. Two or three precaudal vertebrae are often found as a fused unit (Figure 80*f*). The precaudal vertebrae from Lee Creek Mine have a more pronounced lateral ridge than do those of the extant species, and



FIGURE 80.—*Paralichthys* sp.: *a*, USNM 412164, proximal portion of left maxilla, labial view; *b*, USNM 412162, symphyseal portions of left dentary, labial view; *c*, USNM 412165, partial right articular, labial view. *Aluterus* sp.: *d*, USNM 290302 (left) and 290288 (right), vertebrae, dorsal view; *e*, same specimens, axial view; *f*, USNM 476354, three fused caudal vertebrae, dorsal view. (Scale bars: *a*=0.5 cm; *b*=1.25 cm; *c*=1.5 cm; *d,e*=1.0 cm; *f*=1.25 cm.)

the centra in the more cranial vertebrae are more elongate than those of *A. shoepfi*.

The average craniocaudal length is 2.1 cm (range=1.74–2.28 cm, $n=11$); the average dorsoventral height is 1.4 cm (range=1.15–1.63 cm, $n=11$), and the average lateral width is 1.8 cm (range=1.43–2.24 cm, $n=11$).

The extant *Aluterus shoepfi* ranges from Nova Scotia to Brazil and also is found worldwide in temperate and tropical waters (Robins and Ray, 1986). It prefers coral reefs and rocky bottoms. This species feeds on a variety of invertebrates, including crabs and shrimp (Thomson et al., 1978).

Family TETRAODONTIDAE
(puffers)

Spherooides hyperostosus Tyler, Purdy, and Oliver, 1992

FIGURES 81, 82e

HORIZON.—Yorktown Formation (units 1–3).

REFERRED MATERIAL.—Skull and first 4 vertebrae, USNM 437601 (holotype); incomplete cranium, USNM 290643; skull roof and first 3 vertebrae, NCSM 11179; 8 dentaries, USNM 364354, 364356, 437601; 7 premaxillae, USNM 364349, 364350, 364351; about 3000 opercula, USNM 364328–

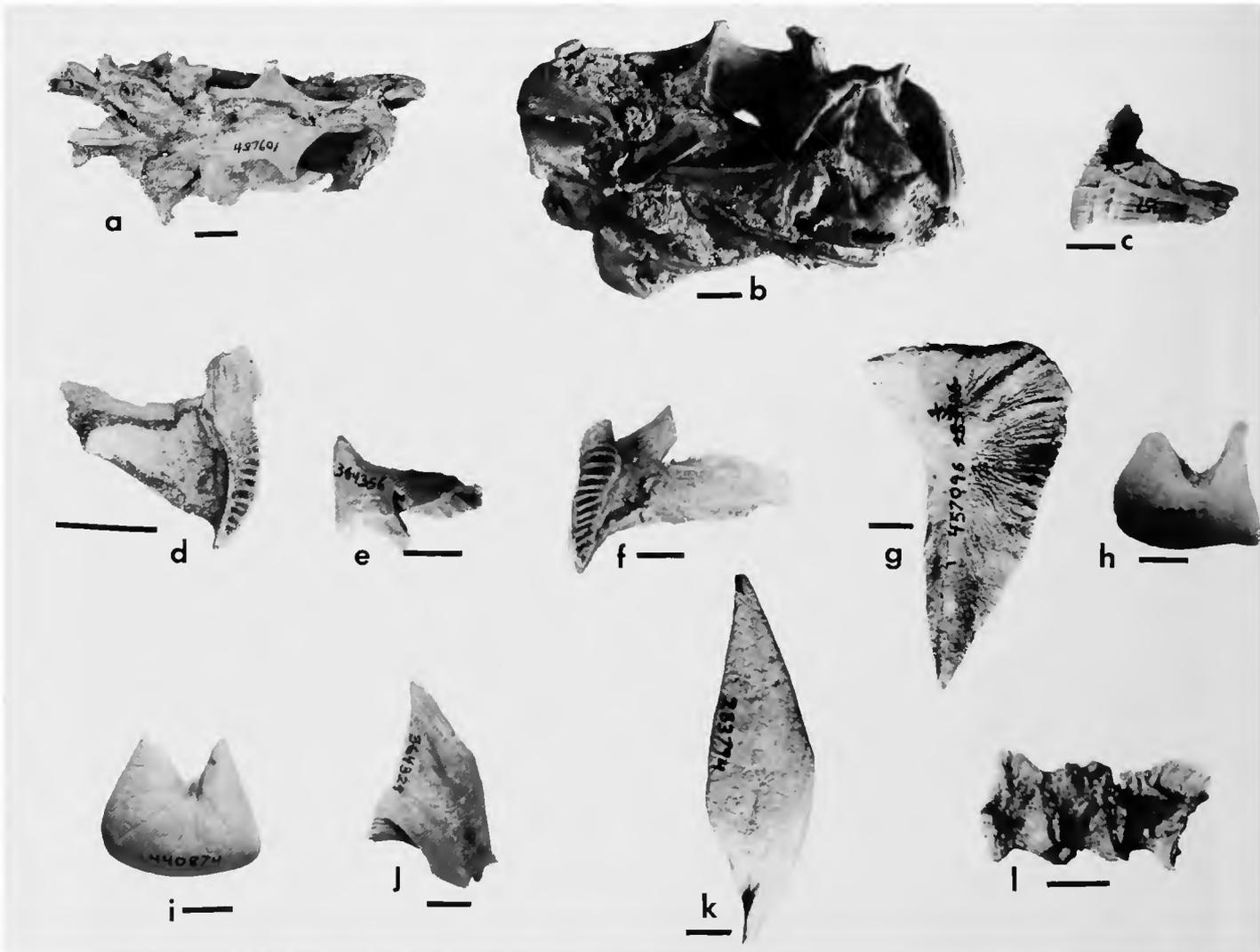


FIGURE 81.—*Spherooides hyperostosus*: a, USNM 437601, holotype, dorsal view of skull; b, same specimen, lateral view of left side; c, USNM 364351, left premaxilla, labial view; d, same specimen, lingual view; e, USNM 364356, left dentary, labial view; f, same specimen, lingual view; g, USNM 457096, preoperculum, lateral view; h, USNM 364322, slightly hyperostosed suboperculum, lateral view; i, USNM 440874, extremely hyperostosed suboperculum, lateral view; j, USNM 364329, operculum, lateral view; k, USNM 283794, ventral postcleithrum, lateral view; l, USNM 437601, second to fourth abdominal vertebrae removed from holotype, lateral view. (Scale bars=1.0 cm.)

364339; about 500 preopercula, USNM 364340–364346, 457096; about 500 subopercula, USNM 364321–364327, 440814, 440859, 440864, 440867, 440874, 440885, 440893; about 500 ventral postsupracleithra, USNM 283794, 283839, 283891, 284070, 364361–364363; about 100 uncataloged vertebrae.

REMARKS.—The remains of this fish are among the most abundant present in the lower units of the Yorktown Formation. Tyler et al. (1992) identified these remains as a new species of pufferfish, *Sphoeroides hyperostosus*. The reader is referred to this paper for a description of the Lee Creek Mine type material. Prior to Tyler et al., Weiler (1973:469–477) identified the suboperculum, preoperculum, and ventral postsupracleithra as hyperostosed parts of the fin skeleton of an indeterminate fish.

Subsequent to the publication of Tyler et al. (1992), one of us (V.P.S.) collected a third skull roof of this species, including the right operculum, cleithrum, dorsal postcleithrum, hyperostosed ventral postcleithrum, and three associated vertebrae from the Yorktown spoil piles (Figure 82e). From ethmoid to pterotics, the skull roof is nearly complete. On the left side, the frontal portion of the flange formed by the frontal and the sphenotic is missing; on the right side it is incomplete. Like the holotype, the lateral ethmoid is broad, with a flat, unornamented

upper surface, and the posterior dorsal surfaces of the frontals have thick, curved crests that extend posteriorly as short processes over the epiotics. The cleithrum and matrix adhering to the ventral portion of the skull roof obscure the morphological details of this area.

The closest living relative of *Sphoeroides hyperostosus*, *S. maculatus*, does not possess any hyperostosed bones (see Tyler et al., 1992).

Sphoeroides maculatus is a benthic species that occurs from Newfoundland to northern Florida (Robins and Ray, 1986). It is found in sandy-bottom habitats in waters ranging from 1 to 54 m deep (Manooch, 1984). It feeds primarily on clams, mussels, shrimp, worms, sea urchins, sponges, sea anemones, sea squirts, and crabs (Manooch, 1984).

Family DIODONTIDAE
(porcupinefishes)

Chilomycterus schoepfi (Walbaum, 1792)

FIGURE 82a–d

HORIZON.—Pungo River Formation (units 4, 5); Yorktown Formation (units 1–3); James City Formation.

REFERRED MATERIAL.—Partial skull, NCSM 8364; about 2000 mouthplates, USNM 291200, 291219 (Yorktown Forma-

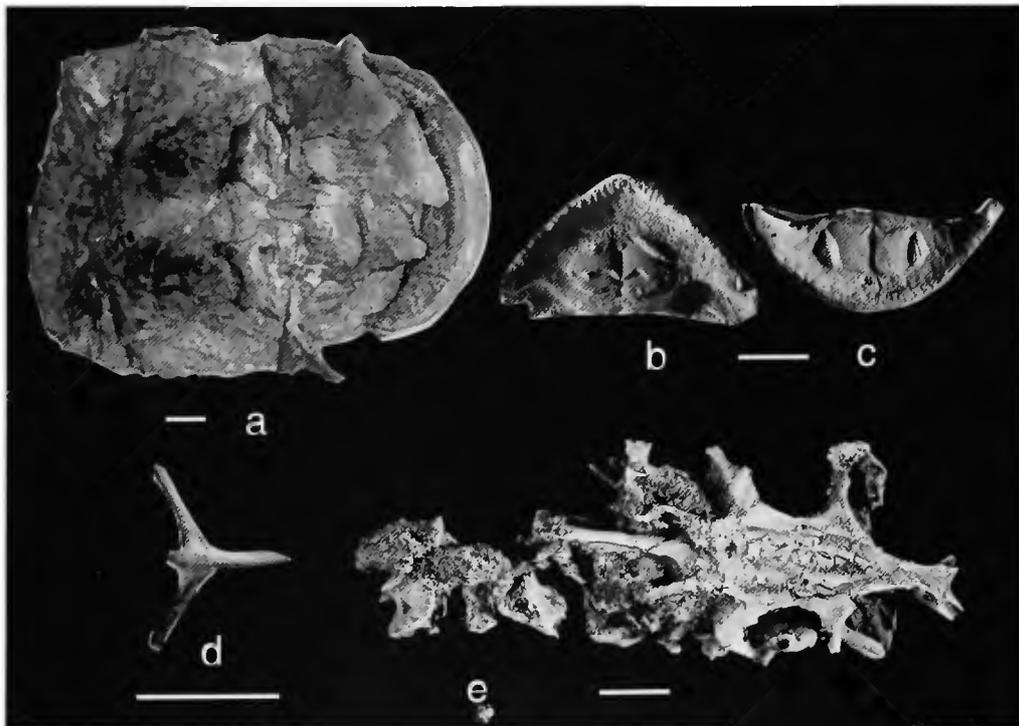


FIGURE 82.—*Chilomycterus schoepfi*: a, NCSM 8364, skull, dorsal view; b, USNM 291200, occlusal view of upper jaws showing trituration tooth plates; c, USNM 291219, occlusal view of lower jaws; d, USNM 476374, dermal spine, dorsal view. *Sphoeroides hyperostosus*: e, NCSM 11179, dorsal view of skull roof. (Scale bars: a=2.0 cm; b,c,e=1.0 cm; d=0.5 cm.)

tion), 476400, 476401 (James City Formation); numerous dermal spines, USNM 476374.

REMARKS.—Although many jaws (Figure 82*b,c*) and a partial skull were available for study, these bones are identical in *Diodon* and *Chilomycterus*; the skeletons can be separated only on the basis of dermal spines (Tyler, 1980). The dermal spines of *Diodon* are two-rooted and erectile, whereas those of *Chilomycterus* are three-rooted, short, and triangular. The spines found at Lee Creek Mine (Figure 82*d*) clearly resemble those of *Chilomycterus*. Because specimens of *Diodon* have not yet been found at the mine, we believe the other skeletal elements found at Lee Creek Mine also should be referred to *Chilomycterus*.

The partial skull, NCSM 8364 (Figure 82*a*), includes well-preserved fused dentaries, ethmoids, and frontals. The fused premaxillae are badly crushed as is the posterior portion of the skull. The skull is 65 mm wide and 106 mm long.

The most common remains of this fish at Lee Creek Mine are incomplete, fused dentaries and fused premaxillae that consist of the beak and tooth plate area; these are alike in both jaws and thus are difficult to distinguish from each other. In complete dentaries, on each side of the tooth plate area, there is a rounded, ventrally directed process that articulates with the angular. Remnants of these processes are often preserved in the fossils. A portion of the ventral surface of the dentary is often worn away, exposing a small area of the tooth-forming surface. On the dorsal surface of the premaxilla, the fragile processes that articulate with the vomer-ethmoid complex are missing, exposing a large area of the tooth-forming surface. In occlusal view, the beaks of the dentaries tend to be rounded; those of the upper jaw are usually pointed.

Chilomycterus schoepfi is a benthic species that occurs primarily from North Carolina to Brazil. It is common in seagrass beds in bays and coastal lagoons (Robins and Ray, 1986). Porcupinefishes feed primarily on shrimp and crabs (Manooch, 1984).

Family MOLIDAE (ocean sunfishes)

Mola chelonopsis (Van Beneden, 1883)

FIGURE 83*a,b*

HORIZON.—Yorktown Formation (unit 1).

REFERRED MATERIAL.—5 premaxillae, USNM 265650, 291211, 457143, 476341, 476395.

REMARKS.—Weems (1985:431–432) identified the Lee Creek Mine specimens to this species, and he characterized it as follows: “Premaxillary beak toothless, and lacking palatal tooth brace, toothless shelf anterior to location of the former tooth position much longer than in *M. mola*, such that the antero-posterior beak length is greater than the lateral beak width at the level of the back shelf. Dentary beak comparable to *M. mola*.” Due to the lack of comparative material of the extant species and the unavailability of Van Beneden’s type specimen, we cannot confirm or refute Weems’s identification.

The Lee Creek premaxillae have attached to them portions of the edentulous palate (Figure 83*a,b*). In all five specimens the articular ends of the premaxillae are missing.

Molas are pelagic fish that have a worldwide distribution in warm waters. In the Atlantic they range from Newfoundland to South America. They feed on jellyfishes, Portuguese man-of-war, ctenophores, and other soft-bodied pelagic invertebrates and on larval fishes (Robins and Ray, 1986).

Teleost incertae sedis

Emmons’s “fish tooth”

FIGURE 83*c–e*

HORIZON.—Yorktown Formation (unit 3).

REFERRED MATERIAL.—About 12 specimens, mostly broken, USNM 421518.

REMARKS.—Emmons (1858:244, figs. 99, 100) reported on a small fossil from the marl beds (probably the Yorktown Formation) in Edgecombe County, North Carolina, which he considered to be a “fish tooth,” attached by ligaments in the throat. Emmons’s fish tooth is not a tooth but a hyperostosed bone, the identity of which has eluded paleontologists and ichthyologists for over 140 years.

At Lee Creek Mine only a few of these enigmatic forms have been found in the thin unit 3 of the Yorktown Formation. Unit 3 was described by Gibson (1967:646) as “2 feet of blue clayey fine sand,” and the irregular contact and color contrast with the underlying unit 2 are shown very well in his pl. 1. Small, isolated patches of unit 3 sediments can readily be spotted on the weathered spoil piles by their darker color and finer grain texture. Close inspection of these patches has yielded distinctive small fossils (otoliths, porcupinefish spines, crab chelae, etc.), including the examples of Emmons’s “tooth.”

Emmons’s tooth is bilaterally symmetrical, consists of dense, brittle bone, and has a maximum height of 13 mm. It is bean-shaped but more attenuated at one end than the other, with a sulcus down the midline of the convex side, and some specimens split along this plane. On the concave side of the “bean,” there is a longitudinal, deep groove at the midline. It is also on the concave side that the attenuated end curls inward, forming a “beak.” In well-preserved specimens, the groove forms the back wall of a bifurcating tubular process that allowed the passage of nerves and blood vessels.

Paleoecology

The 104 species of Lee Creek Mine fossil fishes represent the first fossil record of a marine vertebrate, high-use feeding area and the largest and most diverse fossil fish fauna known from the Atlantic Coastal Plain. Of these taxa, 55 are found in the Pungo River Formation, and 77 are found in the Yorktown Formation. Because we were unable to bulk-sample the Yorktown fauna, it may be even more diverse than available evidence indicates.

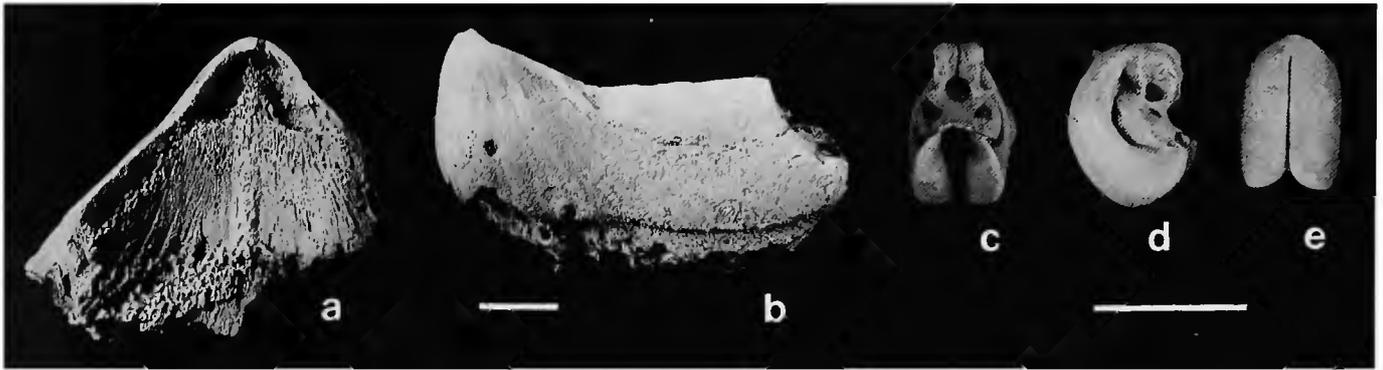


FIGURE 83.—*Mola chelonopsis*, USNM 265650, fused premaxillae: a, occlusal view; b, lateral view of right side. Emmons's "fish tooth," USNM 421518, anatomical orientation unknown: c, front view; d, lateral view; e, rear view. (Scale bars=1.0 cm.)

These faunas, and their associated sedimentological and invertebrate paleontological data, permit us to interpret the paleoecology of the Pungo River and Yorktown seas.

TEMPERATURE

Lee Creek Mine is at the southwestern extremity of the Aurora embayment, a deep Tertiary embayment (Figure 84) of the western Atlantic continental shelf (Popenoe, 1985). During the Miocene and early Pliocene, the 100 m depth contour was near the present mouth of the Pamlico River. During Pungo River and basal Yorktown time (Riggs, 1984; Snyder, 1988), this embayment allowed upwelling, colder waters to intrude over 100 km westward onto the continental shelf, an area covered by warm-temperate to subtropical surface waters. The Lee Creek fauna reflects this contrast in temperatures.

Gibson (1967) concluded from his study of benthic foraminifera that the bottom temperatures during Pungo River and lower Yorktown deposition were cool-temperate. In addition, Gibson's (1987) study of the pectens demonstrated a greater similarity to those of the Calvert Formation to the north than to those of similar ages in Florida. In contrast, approximately two-thirds of the modern representatives of the fossil fish fauna of both formations now have tropical and/or warm-temperate distributions, whereas only one-third of the fauna suggests a cool-temperate influence.

PUNGO RIVER FORMATION.—Taxa that can be broadly grouped as eurythermic tropical and warm-temperate dominate (70%) the Pungo River fauna. These are species that migrate to avoid temperature extremes ($>25^{\circ}$ – 28° C, $<15^{\circ}$ C), coming north during the spring and summer and returning south during the winter. This fauna has a distinctly warm but not a tropical character. The following examples support this warm character and suggest temperatures no colder than 20° C during the warm season.

Stingrays (*Dasyatis*, the dominant batoid) and other rays (*Rhinoptera*, *Mobula*) occur in the Carolinian province (North Florida to Cape Hatteras) only during the summer, when sur-

face temperatures are between 20° C and 27° C (Bigelow and Schroeder, 1953:11). Except *Rhinoptera*, which seems to tolerate cooler temperatures, they are not usually found north of the 21° C isotherm.

The most common shark taxa at Lee Creek Mine are warm-water carcharhiniforms: twenty of the species (30%) and 11 of

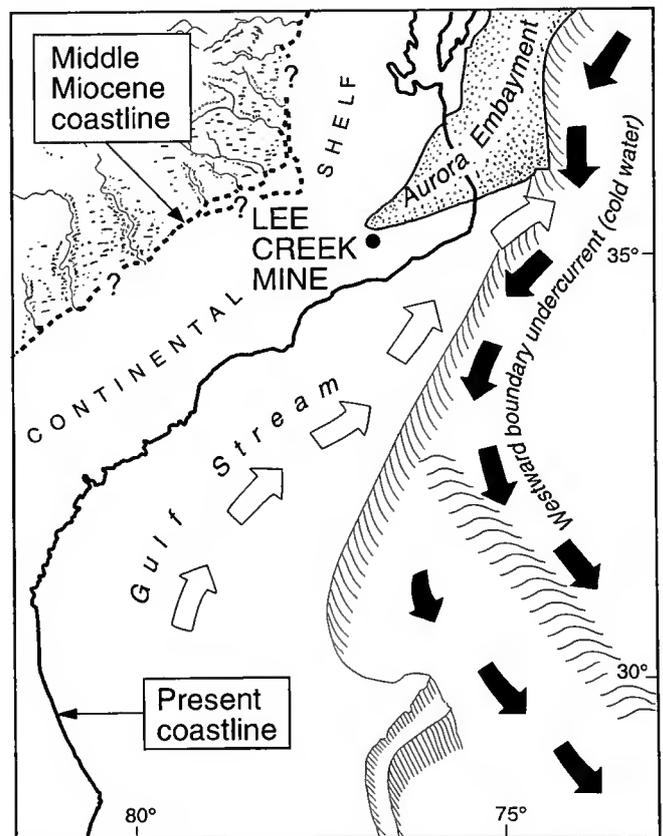


FIGURE 84.—Map showing location of Lee Creek Mine in relation to the Aurora Embayment (after Popenoe, 1985, published with permission of Kluwer Academic Publishers).

the genera (22%). This dominance also applies to the relative abundance of carcharhiniform remains. In samples obtained by screening substantial quantities of the phosphate ore, teeth of *Carcharhinus macloti* are as numerous as those of the other shark taxa combined. Following *Carcharhinus macloti* in these screen residues are (in decreasing order of abundance) *Carcharhinus brachyurus*, *Galeocerdo*, *Hemipristis*, and *Sphyrna* cf. *S. media*. The abundance of carcharhiniforms compared with other galeoid sharks parallels modern warm-temperate and tropical faunas. Also, the diversity of carcharhinid genera exceeds that now present on the middle Atlantic Seaboard and is similar to the diversity encountered in tropical seas.

Temperature range during the Pungo River deposition was probably at least as great as that of the Carolina province today (15°–25°C). Warm-water taxa such as *Sphyrna*, *Negaprion*, *Sphyrna* cf. *S. media*, and *Hemipristis* suggest maximum temperatures as great as 27°C. None of the Pungo River taxa are found only in cool waters; therefore, we believe that warm-temperate to subtropical temperatures persisted year round.

The warmth of the Pungo River sea may account for the lack of abundance of tuna and other pelagic fishes that are common in the Yorktown Formation. Horwood and Cushing (1978) observed that the largest stocks of pelagic fish are associated with thermal boundaries where the waters are high in nutrients. In his study on the phosphate-phosphorus and zooplankton volumes of the Pacific Ocean, Reid (1962:302) noted two conditions, which may also have affected the productivity of the Pungo River sea: (1) if the depth of the boundary between the warm surface water and the denser, cooler upwelling water is deeper than 75 m, the concentrations of phosphate-phosphorus, which are utilized by plankton, are low; and (2) "high temperatures are usually accompanied by lower plankton volumes." Popenoe (1985) noted also that in Pungo River time the Aurora embayment was isolated from both northward- and southward-flowing currents; the embayment was an area of quiet deposition. These conditions may have reduced the productivity of the Pungo River sea, which would account for the scarcity of oceanic fish, such as tunas, and sperm whales (see below), which are common in the Yorktown Formation.

YORKTOWN FORMATION.—Unlike the Pungo River fauna, the Yorktown fauna has a distinctly modern aspect, particularly among the teleosts, so paleoecologic inferences are more definite. The dominant taxa are sturgeon (*Acipenser*), scombrids (*Thunnus*, *Sarda*, *Acanthocybium*), billfish (*Makaira*), filefish (*Aluterus*), hakes (*Merluccius*), bluefish (*Pomatomus*), tilefish (*Lopholatilus*), pufferfish (*Sphoeroides*), porcupinefish (*Chilomycterus*), and the sharks—*Isurus*, *Hemipristis*, and *Galeocerdo*. Except *Hemipristis*, this is a mix of tropical, warm-temperate, and cool-temperate forms with ranges that overlap near Cape Hatteras today, but their abundance suggests that a thermocline existed in the Lee Creek area of the Yorktown sea.

The cool-temperate components of the assemblage (seven taxa, 15% of the fauna) include the genera *Merluccius* and *Lopholatilus*, which are common at Lee Creek Mine, and the rarer

Squalus, although its rarity may be due to collection bias. These taxa suggest temperatures in the 4°–18°C range (Grosslein and Azarovitz, 1982) (10°C is the optimum temperature for *Squalus acanthias*, according to the distributional data of Edwards et al., 1962). The abundance of *Merluccius* and *Lopholatilus* at Lee Creek Mine suggests that cool water was an important component of the Yorktown sea.

The warm component of the fauna (14 taxa, 30% of the fauna) includes the genera *Sphyrna*, *Makaira*, *Acanthocybium*, *Epinephelus*, *Hemipristis*, *Isistius*, *Negaprion*, and *Pristis*. Because they occur exclusively in tropical areas, the temperature regime suggested by these fishes is 27°C (the temperature boundary between warm-temperate and tropical in the western Atlantic Ocean) or warmer.

Abundant tuna, marlin, sea birds, sea turtles, and cetaceans suggest that the area was an important feeding ground. Off the west coast of Central America today, in waters underlain by a sharp thermocline, a similar abundance of marine vertebrates occurs: feeding tuna force schools of prey fish to the surface where cetaceans, sea turtles, and sea birds feed on them (Au and Perryman, 1985). Au (1991:346) elaborated on the make-up of these polyspecific associations with tuna schools, noting that "sharks clearly stood out among the fishes found associated with tuna." The most common species was *Carcharhinus falciformis*; less common sharks were *C. longimanus*, *C. leucas*, and *Rhincodon typus*. The rays observed were mostly "medium- to large-sized manta rays (Mobulidae)" (Au, 1991:346). Among the bony fishes present, he reported billfishes, including *Makaira*, dolphinfish (*Coryphaena*), amberjack (*Seriola* sp.), wahoo (*Acanthocybium solandri*), and triggerfish (Balistidae). Cushing (1971), in his study of upwelling and the production of fish, mentioned that hake (*Merluccius*) also are abundant in upwelling areas. Au (1991) could identify only three of the sea turtles he observed: *Lepidochelys olivacea*, *Dermochelys coriacea*, and *Chelonia mydas*. Boobies (*Sula* spp.), shearwaters (*Puffinus* spp.), and frigatebirds (*Fregata* spp.) were the most common birds in the area, and the porpoises included *Stenella* spp. and *Delphinus delphis* (Au, 1991). With the exceptions of *Carcharhinus longimanus* and *Dermochelys coriacea*, all of these genera occur in the Yorktown fauna. Their abundance at Lee Creek Mine suggests the presence of nutrient-rich, cold, upwelling waters meeting warm water from the Gulf Stream to provide an important feeding zone for both warm- and cold-water fishes and other marine vertebrates.

The abundance of tuna and sperm whale remains in the Yorktown Formation suggests a divergence of the Gulf Stream into the Aurora embayment. Cushing (1971:315) noted, "The coastal upwellings are less important to the tuna than offshore divergences. ... Although tuna may be caught in the area of coastal upwelling, it is likely that they pass 100 km or more offshore." Concerning sperm whale catches, Cushing (1971:320) stated, "This suggests that the sperm whales do not in fact aggregate in the coastal upwellings themselves but in offshore divergences. ... Thus the sperm whale must be a truly

oceanic animal like the tuna and may be excluded to some extent from the coastal upwelling themselves." At Lee Creek Mine, 100 km west of the edge of the continental shelf, these two oceanic vertebrates occur abundantly.

DEPTH

Three general bathytrophic groups of fishes occur at Lee Creek Mine (percentage constituted by the Pungo River assemblage and the Yorktown assemblage, respectively, follows): predominantly coastal fishes of the inner shelf (0–100 m) (33%, 49%), outer-shelf benthic or mesopelagic fishes (100–1000 m) (12%, 9%), and epipelagic fishes (45%, 21%). About 9% of the Pungo River assemblage and 11% of the Yorktown assemblage are benthic groups that may occur over either the inner or outer shelf; these are excluded in the figures given above.

In the Pungo River assemblage, the relative rarity of coastal fishes and the abundance of epipelagic, outer shelf, benthic, and mesopelagic fishes suggest a deeper depositional environment than that prevailing during the Yorktown deposition. The abundance of "blue water" fishes (open-ocean epipelagic species, such as *Thunnus thynnus* and *Acanthocybium solandri*) and the rarity of strictly near-shore species suggest deposition of the Yorktown Formation at the Lee Creek locality occurred in the deeper part of the inner shelf but not as deep as that of the Pungo River Formation.

In both formations, the same groups of coastal benthic fishes limit the maximum depth. Stingrays (*Dasyatis*), which are common in both formations, occur mostly in water shallower than 37 m and are unknown in water deeper than 110 m (Bigelow and Schroeder, 1953). *Lagodon* ranges from the shore down to 74 m. The largest individuals of *L. rhomboides* occur in the deepest part of the range (Caldwell, 1957); specimens from the Pungo River Formation are near the maximum reported size of the extant species.

In the Yorktown assemblage, the only taxa present that provide some indication of minimum depth are *Hexanchus*, *Isistius*, *Scyliorhinus*, a tilefish (*Lopholatilus*), and a hake (*Merluccius*). Both species of *Hexanchus* are mesopelagic or deep epipelagic in warm-temperate and tropical areas; they are usually found at depths of 90 m and greater (Compagno, 1984). Similarly, the species of *Isistius* inhabit epipelagic to bathypelagic waters (Compagno, 1984:93–96). The genus *Scyliorhinus* inhabits the outer shelf and continental slope, but there are exceptions. The fossil scyliorhinid *S.?* *distans*, which occurs in the Yorktown Formation, cannot now be satisfactorily related to any extant member of the genus, so any inference as to its depth tolerance would be suspect.

Merluccius and *Lopholatilus* are more limited in occurrence. If the habitats of *Merluccius* sp. and *M. bilinearis* are alike, fairly deep water is indicated. *Merluccius bilinearis* ranges from the shoreline to a depth of about 550 m off the New England coast (Grosslein and Azarovitz, 1982:72). It is not known

from the Carolinian coast, but it has been taken sporadically off the Virginia coast in waters between 160 and 350 m deep (Hildebrand and Schroeder, 1928). Winter ranges are somewhat shallower along the middle Atlantic Coast. Edwards et al. (1962) recorded occurrences of *M. bilinearis* as shallow as 31 m and in relative abundance between 131 and 316 m off the mouth of Chesapeake Bay. According to Grosslein and Azarovitz (1982:83), *Lopholatilus* "ranges in depth from about 75 to 460 m," and in the Middle Atlantic Bight, "it is concentrated in depths of approximately 110 to 240 m." In view of the latitude of the deposit and the inferred temperature, it is unlikely that depths were much shallower than 50 to 60 m.

In the Pungo River Formation, no species were found that would suggest a minimum depth. Based on foraminiferal assemblages, Gibson (1983:63–64) reported that the lower Belhaven Member "formed on the middle to outer shelf (approximately 100- to 200-m water depth)" and the upper Bonneron Member "formed on the middle to inner shelf (150 m to less than 70 m in the uppermost bed)."

PALEOECOLOGICAL COMPARISONS

PUNGO RIVER FAUNA.—When we compared this fauna to other fossil fish faunas in the Atlantic Coastal Plain and Europe, we discovered some important differences. The taxonomic composition of the two formations is very similar to that of the Calvert Formation of Maryland and Virginia, with three significant exceptions: the absence or scarcity of the mako shark *Isurus xiphodon*, the absence of tilefish, *Lopholatilus*, and the absence of sturgeon, *Acipenser*, in the Pungo River fauna. The absence of the mako shark may be due to the absence or rarity of pinnipeds in the Pungo River Formation, which were present in the Calvert sea. Tilefish are burrowers (Grosslein and Azarovitz, 1982) that inhabit areas with clay and boulder substrates; the abundance of sand, which is unsuitable for tilefish burrows, in the Pungo River Formation may explain their absence here. We found no clues to explain the absence of sturgeon.

In the Calvert Formation near Smyrna, Delaware, which was deposited in shallow coastal or estuarine waters (Purdy, in prep.), the fish fauna differs from that of the Calvert Formation of Maryland and Virginia and the Pungo River Formation. Except for sea catfish at Smyrna, teleost remains are less common. Unlike the Pungo River fauna, the teeth of *Carcharodon megalodon*, which represent very small individuals, and *Isurus* are uncommon. In contrast to the rarity of these species, the teeth of adult *Negaprion*, which are rare in the Calvert and Pungo River faunas, are very common. The shallower depths of the Delaware portion of the Calvert sea probably account for these faunal differences.

A slightly older (Aquitanian) fauna from the Belgrade Formation (Case, 1980), 47 km (30 mi) south of Lee Creek Mine at New Bern, is at the northern limit of the Atlantic Coastal Plain Miocene limestone beds and contains a subtropical fauna.

It differs from the Pungo River shark fauna in the presence of *Heterodontus* and *Carcharhinus isodon* (identified by Case (1980) as *Aprionodon acuarias*). In the extant shark fauna, both taxa prefer water temperatures above 20°C (Compagno, 1984; Castro, 1983). The Lee Creek Pungo River sea may have been slightly cooler than these sharks preferred.

Gillette (1984) noted a similarity between the Miocene faunas of Panama, Ecuador, and the Caribbean region and the Pungo River Formation, but some important differences exist. Odontaspids and species of *Isurus* are absent from the first three faunas and in them the number of carcharhiniform sharks (Panama, 8; Caribbean, 4; Ecuador, 7) is much less than the number present (19) in the Pungo River Formation. Although the taxa present in these faunas are similar to those in the Pungo River Formation, they are cosmopolitan, warm-water taxa, and their presence sheds little light on the similarity of the environments for these faunas.

In comparison to the European Miocene, the Pungo River Formation has a greater abundance of carcharhiniform sharks (19 species) than either the Belgian Miocene (4 species) (Leriche, 1927; Nolf, 1988) or the Swiss Molasse (8 species) (Leriche, 1926). The Belgian Miocene sea appears to have been cooler than that of the Swiss Molasse or the Pungo River Formation; *Hemipristis*, a subtropical shark common to the last two, was absent in the Belgian Miocene sea. Absent from both the Belgian and Swiss faunas is the subtropical lemon shark, *Negaprion*, which suggests that the Pungo River sea was warmer than those of Belgium or Switzerland.

The differences between these faunas reflect the important influence of ecological factors on the distribution of fish taxa, particularly sharks, an influence that must be considered in stratigraphic interpretations even in geographically close areas.

YORKTOWN FAUNA.—Unlike the Yorktown Formation, fish remains are uncommon in the Raysor Formation of South Carolina and the Duplin Formation of North and South Carolina, both of which were deposited in shallow, warm water during the early Pliocene (Ward et al., 1991). We know of no reports of fish remains from the Raysor Formation. From Duplin localities (south of the Neuse River), Leriche (1942) reported the presence of *Carcharodon carcharias* and *Chilomyxus vetus*, and from the Martin Marietta quarry at New Bern, amateur collectors Peter J. Harmatuk and Bob Johnson (pers. comm., 1991) reported the occurrence of *Carcharodon megalodon*. These shallow, warm-water deposits were evidently not high-use areas for fishes and other vertebrates.

The European Pliocene fish faunas offer some interesting contrast to the Yorktown fauna. They have fewer taxa, and they represent cooler environments. In the Belgian Pliocene fish fauna (Leriche, 1926), warm-water forms, such as *Hemipristis*, *Negaprion*, and *Galeocerdo*, are absent, and cold-water taxa, such as *Gadus*, *Merluccius*, *Carcharodon carcharias*, and *Cetorhinus*, are present. In the Pliocene of Italy (Landini, 1976) more taxa are present than in Belgium, including warm-water species, but at least two of the shark taxa, *Parotodus benedenii*

and *Galeocerdo* cf. *G. cuvier*, have smaller teeth than do those of the Yorktown Formation, and two subtropical taxa, *Hemipristis* and *Negaprion*, are rare or absent.

In comparison with other Pliocene faunas of the Atlantic Coastal Plain and Europe, the Yorktown fauna at Lee Creek Mine has the greatest abundance and diversity of fossil fish and other marine vertebrates. This suggests to us that at Lee Creek in Yorktown time, the physiography of the environment of deposition, the presence at shallow depths of upwelling waters, and the presence of an eddy of the Gulf Stream were significant factors contributing to the congregation of many marine vertebrates in this area.

Taxonomic Discussion

The abundant remains at Lee Creek Mine allowed us to reconstruct composite dentitions and to resolve some important problems in the taxonomy of fossil sharks, problems that cannot be resolved with a few isolated teeth. For example, by comparing the anterior teeth of *Carcharodon* and *Carcharocles*, we were able to reassign the teeth of the latter genus to the genus *Carcharodon*. The absence of ontogenetic heterodonty between juvenile and adult dentitions allowed us to separate *Isurus xiphodon* from *I. hastalis*. This fauna also provided sufficient specimens of *Parotodus benedenii* for us to reconstruct its dentition, and based on the mako-like nature of characters of the roots and the size relationships between the upper and lower teeth we assigned this species to the Lamnidae.

Composite dentitions, however, have their pitfalls. Shark teeth vary greatly within a species, even in the anterior teeth. Before we knew of the variation in mako teeth, we reconstructed a composite dentition of the invalid species *Isurus retroflexus*. The Miocene species of *Galeocerdo* are another example. Applegate (1978) believed that the teeth of *Galeocerdo contortus* were the lower teeth of *G. aduncus* Agassiz. Although his reconstruction seems very logical, we were able to identify characters that distinguish upper and lower teeth in the dentitions of the extant *Galeocerdo*. When we applied these characters to the teeth of fossil species, we were able to separate *Galeocerdo contortus* from *G. aduncus* (= *G. sp.* herein). Our experience with composite dentitions suggests that an extensive knowledge of tooth characters and variation in related extant species is a prerequisite to reconstructing fossil shark dentitions accurately.

Associated fossil dentitions are the most important tools of shark paleontology. At Lee Creek Mine, two associated dentitions of *Carcharodon subauriculatus*, two of *C. megalodon*, and one of *Parotodus benedenii* have been found, and these are more common than previously thought. The current commercial market for shark teeth, however, and the apathy of many amateur collectors toward preserving these scientifically important specimens in museums will make these specimens harder to obtain for scientific research, and thus retard progress in understanding the systematics and evolution of fossil sharks.

The rediscovery of some of Agassiz's fossil-fish type specimens allowed us to evaluate some of his species. Although Agassiz's syntypes of *Isurus desori* had not been lost, in over 150 years they were never examined and compared to the dentitions of extant makos. When we made these comparisons, besides designating a lectotype, we determined that one tooth of Agassiz's type series was definitely from a mako and that it is a junior synonym of *I. oxyrinchus*. In contrast, the unknown whereabouts of the holotype of Probst's *Oxyrhina exigua* (= *Alopias exigua*) leaves unresolved the generic identity of his species.

Many of the Lee Creek Mine taxa cannot be separated from the living forms, for example, the Lee Creek specimens identified as *Notorynchus cepedianus*, *Isurus oxyrinchus*, *Carcharhinus brachyurus*, *C. falciformis*, *C. leucas*, *C. macloti*, *C. obscurus*, *C. perezii*, *C. plumbeus*, *Negaprion brevirostris*, *Triacodon obesus*, *Sphyrna lewini*, and *S. zygaena*, which attests to the relative longevity of many shark species. Further study of the variability in the teeth of extant species may result in the synonymy of fossil species, such as *Hexanchus gigas*, with the extant species and extant species, such as *Echinorhinus cookei* and *Isurus paucus*, with the fossil species.

Conclusions

The Lee Creek fossil fish faunas are important because of their diversity and their abundance and because of the paleoecological information they yield about the Pungo River and Yorktown seas. Based on the taxa present and other geological data, we offer the following conclusions.

First, the fish faunas suggest that the Pungo River sea was warm temperate to subtropical and that the Yorktown sea was warm temperate with the presence of upwelling cold water.

Second, in Yorktown time this upwelling water supported a large vertebrate fauna of fish, sea turtles, sea birds, cetaceans, and pinnipeds. In Pungo River time, upwelling did not reach shallow depths and the fauna was not as diverse as in Yorktown time.

Third, the Pungo River fish fauna suggests that it was deposited in an epipelagic, outer-shelf, benthic environment, whereas the Yorktown fish fauna suggests that it was deposited in an inner-shelf environment.

Fourth, in comparing both Lee Creek faunas to those of the Atlantic Coastal Plain and Europe, the Pungo River fauna has the largest number of warm-water fishes but lacks the subtropical forms found in the Belgrade Formation that outcrops 47 km to the south. In comparison to these other Atlantic Pliocene fish faunas, the Yorktown fauna has the greatest abundance and diversity, and it has more warm-water forms than do the European faunas.

Fifth, the Lee Creek sediments yielded new records of occurrence for the Atlantic Coastal Plain for four fossil shark taxa: *Rhincodon* sp. from the Pungo River Formation, *Megascyliorhinus miocaenicus* from the basal Pungo River Formation,

Isistius sp. from the basal Yorktown Formation, and *Megachasma* sp. from the Pungo River and the Yorktown formations.

Sixth, the Yorktown Formation yielded two new species of bony fishes: *Lopholatilus rayus* and *Pagrus hyneus*.

Seventh, the Lee Creek shark taxa suggest that shark species or tooth morphologies existed for several million years or more.

Eighth, in the extant sharks, tooth form is highly variable; understanding this variation and knowing the tooth characters for each dental position is essential to reconstructing fossil shark dentitions accurately.

Future Study

As we stated earlier, our study is a beginning. Much work needs to be done in the study of the extant and fossil species. Recently, ichthyologists have made significant discoveries about the effects of segregation by size, water temperature, and ocean-floor topography upon the distribution of fishes (Muñoz-Chápuli, 1984; Klimley, 1985; Galvan-Magana et al., 1989; Stevens, 1990; Smale, 1991; Klimley et al., 1992; Simpfendorfer and Milward, 1993). Considering this information, the fossil record of Tertiary fishes needs to be reexamined in light of the ecology of modern fishes.

In extant sharks, age/size differences can exist between two or more populations of a species (see *Galeocerdo*), and these differences may occur in other extant species of sharks and also in the fossil species. Shark vertebrae can be aged by ring counts, a technique that can be applied to fossil vertebrae, which are common at Lee Creek Mine. By applying this technique to fossil faunas, the age and the mean tooth size of a fossil species could be compared with those from other areas. If, as seems possible (Applegate, 1967; Kozuch and Fitzgerald, 1989), shark vertebrae can be identified to species, the abundant shark vertebrae at Lee Creek Mine will be most useful for such a study, and by excavating the basal Yorktown Formation, some of these may be found associated with dentitions.

A new area of investigation for paleontologists is the effect of segregation by size on the distribution of fossil sharks and rays. In the extant species, some sharks and rays segregate by size and/or sex. Females pup in areas that are safe from predators, and as the pups increase in size, they migrate toward adult feeding areas. In many shark species, males and females—females are usually larger than males—live and feed in different areas except during mating season. This segregation by size and by sex raises some questions about the fossil record of sharks: Do size increases in shark teeth reflect evolutionary or environmental changes? What types of paleoenvironments are fossil shark teeth found in, and in comparison to the extant species, would these paleoenvironments favor sharks of one size or sex? Do the fossil teeth contribute to the interpretation of segregation by size or sex? The answers to these questions require careful stratigraphic sampling of shark-tooth-bearing

strata, the analysis of paleoecological data, and the comparison of the fossil species with, if they exist, extant species of the same genus.

Water temperature and ocean-floor topography affect the distribution of extant fishes, but their effects upon the distribution of fossil fishes have not been studied. In the Yorktown sea, large sharks (*Carcharodon megalodon*, *Isurus xiphodon*, *Hemipristis serra*, *Galeocerdo* cf. *G. cuvier*) and schooling fishes (*Merluccius*, *Pomatomus*, *Thunnus*) are more abundant in the area of the Aurora embayment than they are at other Yorktown localities in North Carolina and Virginia. The presence of a submarine canyon or embayment and upwelling affected the distribution of these fishes. We can ask, What effects may water temperature and ocean floor topography have had on other fossil fish faunas? At Lee Creek Mine, do the differences in the abundance and the diversity of taxa between units 1 and 3 reflect changes in water temperature? How great is the taxonomic difference between these two units?

The fossil beds at Lee Creek Mine offer the potential for answering some of these questions and for increasing our knowledge about the taxa that lived there, their environment, and their relationships with other fossil organisms that lived with them. A careful excavation of the fossil beds in units 1 to 3 of the Yorktown Formation would greatly increase our knowledge of the fauna. It would allow us to observe any faunal changes that occur in these units that cannot be observed adequately by spoil-pile collecting. It would allow us to gather additional information about predator-prey relationships. It would allow us to obtain large samples of the fauna, including many articulated skeletons, which are so important to the studies of taxonomy and functional anatomy. Such an excavation would allow us to create a more detailed and accurate picture of life in the Yorktown sea.

Lee Creek Mine is a hint of the fossil beds that may lie buried deep beneath the sea. In comparison to the limited and geochronologically incomplete outcrops of Tertiary sediments, the paleontological record of the outer continental shelf, where today marine vertebrates are abundant, is potentially much more extensive, and it may provide a more continuous record of the evolution of marine environments and marine vertebrates. The Yorktown fauna at Lee Creek Mine may be an indication of the species diversity of marine vertebrate faunas that existed during the Neogene along the edge of the continental shelf of eastern North America. Today, Lee Creek Mine is the only exposure of this part of the fossil record available to us, a part of the fossil record that we have only begun to understand.

NOTE ADDED IN PROOF

After our paper was submitted for publication, we received three publications, one by Bourdon (1999) and two by Arnold Müller (1992, 1999), on the fossil fishes of the Atlantic Coastal Plain Tertiary sediments. Bourdon, on the basis of teeth, described a new species of manta ray, *Manta hynei*. Because little is known about dental variation in recent manta rays, we cannot assess the validity of this species, but we think the naming of it is premature.

Müller's publications are all but unavailable in the United States, and we were unable to comment on his findings in the present paper. His 1999 work is the publication of his thesis (1992), which is based on about 12,000 otoliths and some 1000 elasmobranch teeth collected in the Eocene-Pliocene sediments of the Atlantic Coastal Plain, including Lee Creek Mine. None of his new species has priority over the two described herein.

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Turtles of the Lee Creek Mine (Pliocene: North Carolina)

George R. Zug

ABSTRACT

Eleven taxa of turtles have been recovered from the Lee Creek Mine: a sideneck turtle (*Bothremys*); six sea turtles (*Caretta*, ?*Chelonia*, *Lepidochelys*, *Procolpochelys*, *Sylloinus*, and *Psephophorus*); two pond turtles (probably *Pseudemys* and *Trachemys*); a softshell turtle (trionychid); and a giant tortoise (*Geochelone*). The fossils are largely disassociated skeletal elements and fragments derived from spoil piles created by drag-line mining of phosphate. The mining removes and discards the Yorktown Formation (Pliocene) and processes much of the Pungo River Formation (middle Miocene), hence the Lee Creek Mine turtles are mainly from the lower Pliocene. The turtle fauna appears to be a natural assemblage of extant and extinct taxa. *Caretta* and *Sylloinus* are the most abundant fossils; a few specimens of each had some adherent Yorktown matrix. *Geochelone* fossils are next in abundance, although an order of magnitude less than *Caretta* and *Sylloinus*. The other genera are each represented by fewer than 10 fragments or elements. Cranial and carapacial differences indicate that the Lee Creek *Caretta* represents a new species, *C. patriciae*. The *Geochelone* also differs from its eastern North American Pliocene contemporaries by its larger size and unique plastral morphology. The fossils of the other taxa are too few and fragmentary to identify reliably to species or genus.

Introduction

The middle Miocene to early Pliocene faunas of the central Atlantic coast and coastal plain of North America included a variety of marine, freshwater, and terrestrial turtles. Marine species dominated the turtle fauna, and at least one species each of the sideneck turtle *Bothremys*; the three hard-shelled sea turtles *Chelonia*, *Procolpochelys*, and *Sylloinus*; and the leatherback sea turtle *Psephophorus* have been reported. Other Miocene turtles from this region included a terrestrial tortoise, *Geochelone*, and a softshell turtle (freshwater trionychid). Additional hard-shelled sea turtles (Table 1) have been described

from the central Atlantic and adjacent regions, but close examination (Weems, 1974) of these fossils has shown these taxa to be synonyms of *Sylloinus aegyptiacus* (Lydekker). Representatives of these seven genera of turtle occur in the Miocene marine deposits of New Jersey, Maryland, and Virginia (Table 3). These turtles and the extant taxa of southeastern North America provided the comparative base for the identification and analysis of the temporally and geographically close fossil turtles of the Lee Creek Mine.

The Lee Creek Mine turtles appear to derive primarily from the Yorktown Formation and, thus, are a more recent fauna than the turtles from the Calvert Formation of Virginia and Maryland. The mining operation, however, penetrates and discards the top of the Pungo River Formation (temporally equivalent to the Calvert Formation), so there is a possibility that a few Calvert-aged (middle Miocene) turtles are mixed in with this predominantly (early to middle Pliocene) Yorktown fauna (see Gibson, 1983, for age and stratigraphy of mid-Atlantic coastal deposits). The mining operation scatters the fossils from the numerous beds of the Yorktown Formation, resulting in fewer associations of skeletal elements with one another or with their stratum of origin in the Lee Creek Mine fauna as compared to the Calvert fauna. This lack of positive association is unfortunate because the Lee Creek sea turtle fauna is diverse and straddles a faunal transition between a middle Tertiary and the Holocene fauna.

My primary objective has been to identify the Lee Creek Mine turtles and briefly describe their fossil remains. This task has forced me to make taxonomic decisions on isolated bony elements, and in some instances the amount of comparative material has been limited. These necessarily tenuous decisions must be and can be confirmed only with less fragmented and better associated fossils from Yorktown deposits.

ACKNOWLEDGMENTS.—All fossil specimens described herein are in the vertebrate paleontological collection of the National Museum of Natural History (NMNH, which houses collections of the former United States National Museum (USNM)). Some of the USNM catalog numbers cited herein represent lots rather than individuals due to the quantity of disassociated ele-

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TABLE 1.—Miocene turtles described as new species from the central Atlantic coast of North America.

Taxon	Citation	Type locality	Current name
Suborder PLEURODIRA			
Family PELOMEDUSIDAE			
<i>Taphrosphys miocenica</i>	Collins and Lynn, 1936:155	Calvert County, Maryland	(= <i>Bothremys miocenica</i>)
Suborder CRYPTODIRA			
Family CHELONIIDAE			
<i>Chelonia grandaeva</i>	Leidy, 1851:329	Salem County, New Jersey	(= <i>Procolpochelys grandaeva</i>)
<i>Chelonia marylandica</i>	Collins and Lynn, 1936:162	Calvert County, Maryland	(= <i>Syllomus aegyptiacus</i>)
<i>Peritresius virginianus</i>	Berry and Lynn, 1936:176	Westmoreland County, Virginia	(= <i>Syllomus aegyptiacus</i>)
<i>Syllomus crispatus</i>	Cope, 1896:139	Pamunky River, Virginia	(= <i>Syllomus aegyptiacus</i>)
Family DERMOCHELYIDAE			
<i>Psephophorus calvertensis</i>	Palmer, 1909:370	Calvert County, Maryland	
Family TESTUDINIDAE			
<i>Testudo ducateli</i>	Collins and Lynn, 1936:166	Calvert County, Maryland	(= <i>Geochelone ducateli</i>)
Family TRIONYCHIDAE			
<i>Trionyx cellulosus</i>	Cope, 1868:142	Charles County, Maryland	

ments received from the mine. My use of this collection was aided by Robert Purdy and Clayton Ray (both NMNH). Gladwyn Sullivan (NMNH) prepared and assembled the better-associated fragments. Victor E. Krantz (NMNH) photographed all of the specimens.

A number of individuals assisted in this study: Robert Weems (U.S. Geological Survey), Eugene Gaffney (American Museum of Natural History), and Rainer Zangerl (Rockville, Indiana) broadened my narrow outlook on this fossil assemblage, and I hope improved my interpretation of it, and they reviewed early drafts of the manuscript; more recent versions benefitted from the comments of D. Bohaska (NMNH), C. Crumly (Academic Press), K. Dodd (U.S. Geological Survey), C. Ernst (George Mason University), R. Estes (deceased), W.R. Heyer (NMNH), A. Holman (Michigan State University), and R. Weems. I thank all of the above for their assistance.

Seaturtle Identification

The Lee Creek Mine turtle fossils are predominantly hard-shelled seaturtle fragments, and many of these cannot be identified to species or even to genus. Having worked with these fossils intensely in the early 1970s and then only episodically until the final preparation of this manuscript in 1988, I discovered that my ability to assign taxonomic names with confidence was directly proportional to my current immersion in seaturtle osteology. To assist my memory, I developed diagnoses for the main fossil skeletal elements and include them herein to assist others in the identification of seaturtle elements and fragments. These diagnoses also document my criteria for the assignment of taxonomic names to the Lee Creek Mine fossils. The diagnoses are not complete; they emphasize the type and nature of the Lee Creek Mine fossils. For example, I describe only the tip of the dentary because only that part of the lower jaw has been recovered, and in *Psephophorus*, only osteoderms are known. The diagnoses also tend to state differences as absolutes when some of the differences are more subtle and subjective.

The major features for distinguishing the various genera of extant cheloniid seaturtles are summarized in Table 2. A partial skull of *Caretta* (USNM 186731; Figures 3, 4) was reassembled from fragments. The two critical features for identifying this skull as *Caretta* are the exclusion of the frontal from the orbit and the absence of vomerine-premaxillary contact on the secondary palate. The frontal also enters the orbit in *Procolpochelys* and *Syllomus*.

Dentaries can be differentiated by the nature of the ridges on the triturating surface. *Syllomus* has a complex pseudodont surface (Figure 7A) with a high, denticulate symphyseal ridge extending across the entire width of the dentary; a high, sharp-edged denticulate ridge on the lingual edge; and cone-shaped denticles along the labial border (Weems, 1980, fig. 2c). The dentary surface is nearly as complex in *Chelonia*; a high symphyseal ridge extends across the entire width of the dentary; a high, sharp-edged ridge is slightly inset along the entire lingual border; and the labial border is sharp-edged and occasionally faintly denticulate. In *Eretmochelys* a low symphyseal ridge occurs on the posterior half of the dentary's triturating surface and enlarges near the labial border to form a large, pyramidal protuberance; a lingual ridge is often evident, although weakly developed. The triturating surface in *Caretta* and *Lepidochelys* is a smoothly concave surface curving gently to a sharp labial edge. The labial and lingual borders are sharp-edged but low. Some *Caretta* have a low, sharp-edged symphyseal ridge across the entire width of the dentary. Juvenile *Lepidochelys kempii* (Garman) have a low pyramidal protuberance (Figure 7B) at the posterior end of the symphysis and occasionally have a faint lingual ridge; the protuberance and lingual ridge are not evident in adult *L. olivacea* (Eschscholtz). The dentary of *Procolpochelys* is unknown.

Of the many carapacial fragments, it is possible to distinguish the linked osteoderm (=epithecical ossicle) shell of dermochelyids from the typical testudine shell of cheloniids. The osteoderms of *Psephophorus* are large, thick, irregular polygons (Figure 7C), in contrast to the small, thin, irregular polygons of *Dermochelys*. The osteoderms forming the dorsal ridges of the

TABLE 2.—Comparison of cranial characteristics of Holocene cheloniid sea turtles and the Lee Creek Mine sea turtle skull. Abbreviations: Cc, *Caretta caretta* (Linnaeus); Cm, *Chelonia mydas* (Linnaeus); Ei, *Eretmochelys imbricata* (Linnaeus); Lk, *Lepidochelys kempii*; Lo, *Lepidochelys olivacea*; LCs, Lee Creek skull; +, structure present or as described; −, absent or not as described; ±, present or absent.

Cranial characteristics	Cc	Cm	Ei	Lk	Lo	LCs
Frontal in orbit	−	+	+	+	+	−
Strong temporal emargination	+	−	−	+	+	+
Supraoccipital ridge blade-like dorsally	+	−	−	±	−	−
Premaxillary-vomer contact on secondary palate	−	+	+	+	+	−
Trochlear process of pterygoid elongate and thin	+	−	−	−	−	+?
Articular surface of quadrate broad	+	−	−	−	−	+
Triturating surface of dentary strongly ridged	−	+	+	−	±	−

carapace in *Dermochelys* are as large in circumference as those of *Psephophorus* but are thinner. The reticulated external surface of the *Syllomus* carapace is unlike the surface texture of any other cheloniid, although the surface texture might be confused with that of trionychids. The shell elements are distinctly thinner (absolutely and relatively) in *Syllomus* than they are in any of the other Lee Creek Mine cheloniids.

Neurals are found frequently. In most cheloniids, the neurals are elongate hexagons with the posterior segment two to three times longer than the anterior segment (i.e., cassette-shaped). Only in *Procolpochelys* are the neurals regular hexagons; the neurals also are proportionately thicker in *Procolpochelys* than they are in any of the other sea turtles except *Psephophorus*. The neural series in *Caretta* and *Lepidochelys* appears to be evolutionarily undergoing fragmentation and size reduction. Regular polygonal neurals lie between elongate ones in these two taxa. In addition to their unique surface texture, *Syllomus* neurals often bear a longitudinal ridge along the entire length of each neural; the ridge ranges from a faint indication to a distinctly elevated (~5 mm), sharp-edged keel. Young *Caretta* and *Lepidochelys* (of extant species) also have keeled neurals; in the small juveniles, the middorsal ridge is continuous only in the youngest individuals. The ridge has five spines or knobs extending well above the keel. These spines are most evident in small (carapace length (CL) <25 cm) *Lepidochelys*; in larger juveniles (CL >40 cm) only the second spine may persist, and none remains in adults. In *L. kempii* the spines occur at the posterior edge of each vertebral scute, hence on neurals 1, 4, 7, and 10 (neural number may differ slightly because of tendency for neural fragmentation in caretine sea turtles) and on the posterior suprapygal. The reduction or loss of spines appears to occur from posterior to anterior, with the second spine being the last to disappear, and the external surface of all neurals flattens with increasing carapace length. This external surface is planar in all size classes of *Chelonia* and *Eretmochelys*.

Costal fragments are unidentifiable for most genera, although the surface texture of the *Syllomus* carapace is unique and readily identifies even small fragments. Peripherals also are difficult to assign to genus, other than those of *Syllomus*. In general, the larger ninth, tenth, and eleventh peripherals with distinct, serrate borders were identified as *Caretta* peripherals.

The pygals of caretine turtles characteristically show a wide, deep, medial V-shaped notch posteriorly (this notch is small or absent in *Procolpochelys*) and have medially slanted peripheral-pygale articular surfaces. The cheloniine pygal has a narrow, shallow notch posteriorly and nearly parallel peripheral-pygale articular surfaces. These differences emphasize the extremes, and pygal morphology in cheloniids forms a continuum.

The most numerous limb bones are humeri, and their morphology appears generically diagnostic in most cases. The *Syllomus* humerus (Figure 1C,E; Weems, 1974, pl. 3: figs. 1–3) is the most distinctive; however, rather than describe the entire humerus of each genus sequentially, a comparative description of each part of the humerus is offered. Humeral morphology terminology follows that proposed by Zug et al. (1986); the major difference from previous use is the recognition that the cheloniid humerus possesses both a radial (lateral) process and a deltopectoral ridge.

The ulnar (medial) process of sea turtles is elongate and extends proximally. This process is greatly elongated and pointed in *Syllomus* (Figure 1C,E) and extends proximally well beyond the humeral head (roughly the width of the head beyond); this elongation produces an attenuated appearance, although the *Syllomus* humerus is proportionately of the same width as that of the other genera. In *Caretta*, *Lepidochelys*, and *Procolpochelys* the ulnar process is rounded and extends only slightly beyond the head proximally. This process is intermediate in length and is somewhat acute in *Chelonia* and *Eretmochelys*.

The radial (lateral) process is low and lies distal to the level of the humeral head (Figure 1). In *Chelonia*, *Eretmochelys*, and *Syllomus* the process forms a narrow ridge extending nearly two-thirds across the ventral surface of the shaft. This ridge is broader in *Caretta*, *Lepidochelys*, and *Procolpochelys* and extends across no more than one-half of the shaft.

The articular (cartilage-supporting) surface of the humeral head is ellipsoidal in all cheloniids (Figure 1). This surface in *Syllomus* is narrower and more elongate than in the other five genera and is moderately pointed at its pre- and postaxial ends. This surface is usually continuous with the radial process in *Caretta*, *Lepidochelys*, and *Procolpochelys*, continuous or separate in *Eretmochelys*, usually separate in *Chelonia*, and always separate in *Syllomus*. The head appears to extend farther off the diaphysis in *Chelonia* and *Syllomus*.

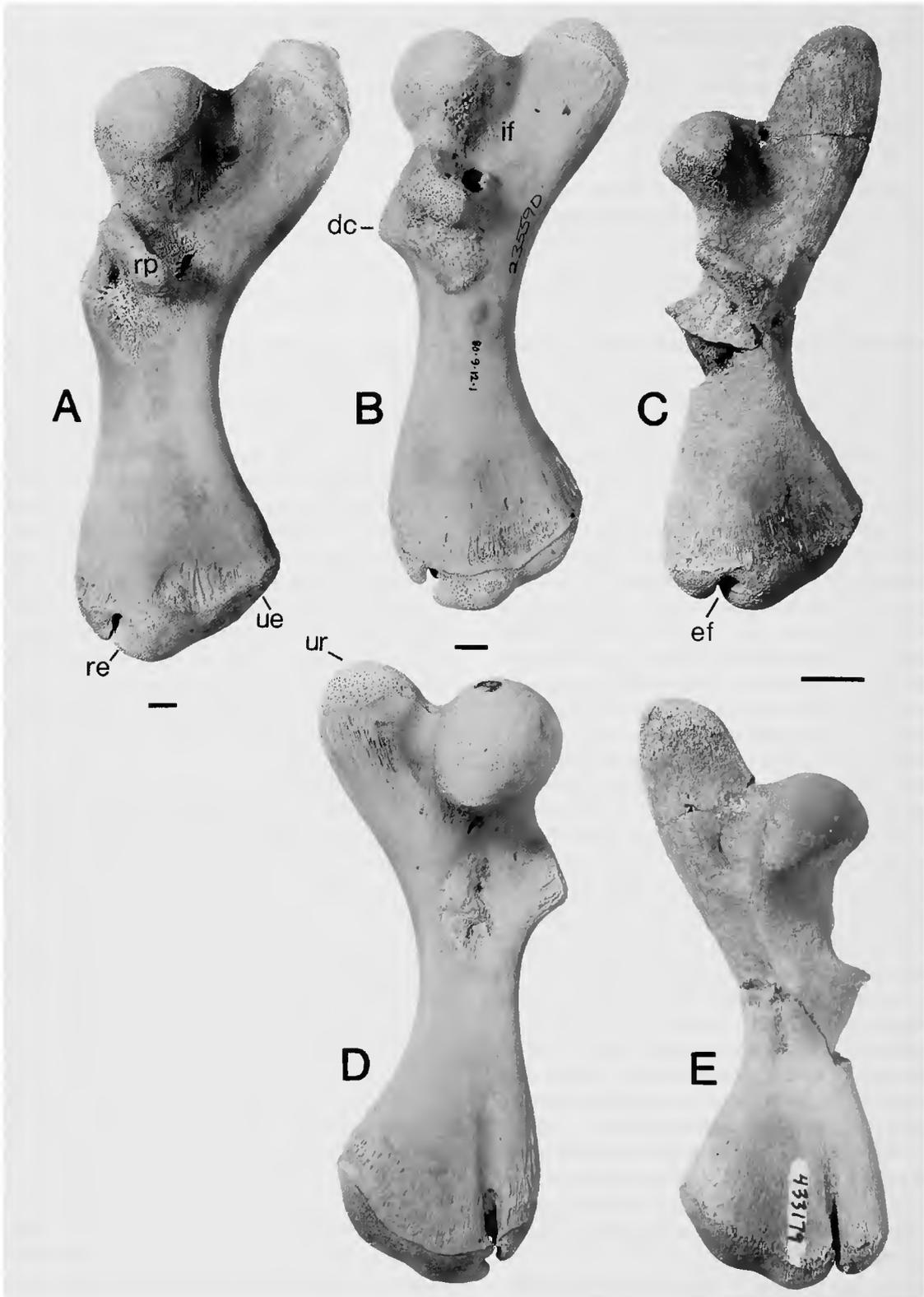


FIGURE 1.—Morphology of cheloniid right humeri. A, ventral view of a Holocene *Chelonia mydas* humerus (USNM, uncataloged); B,D, ventral and dorsal views, respectively, of a Holocene *Caretta caretta* humerus (USNM 235590); C,E, ventral and dorsal views, respectively, of a *Syllomus aegyptiacus* humerus (USNM 433179). Abbreviations: dc, deltopectoral crest or ridge; ef, ectepicondylar foramen; if, intertubercular fossa; re, radial epicondyle; rp, radial process; ue, ulnar condyle; ur, ulnar process. (Scale bar=1 cm.)

In *Syllomus* the deltopectoral crest is a cone-like tubercle projecting strongly beyond the preaxial surface. In the other genera the crest extends longitudinally along the preaxial surface, and it is continuous (or nearly so) with the lesser trochanter in all cheloniids except *Syllomus*, where it is separated from the radial process by a deep, U-shaped groove. In *Caretta* and *Lepidochelys* the crest is truncate and moderately projecting, and it is flattened and slightly projecting in *Chelonia* and *Eretmochelys*.

The *Syllomus* humerus differs strikingly from that of the other genera (Figure 1). Using the deltopectoral crest to divide the humerus into proximal and distal segments, these segments are subequal in length in *Syllomus*, and the proximal segment is one-third to three-eighths the length of the distal segment in the other five genera. The condylar surface has distinct trochlear and capitellar ridges in *Syllomus*; these articular ridges are low and rounded or are absent in the other genera.

Ulnae are fairly abundant. The ulna of *Syllomus* differs from the ulnae of other cheloniids by its robustness and shape. It is proportionately shorter; has a deep, concave, proximal articular surface facing postaxially; a raised, sharp-edged postaxial crest; and a broad, radial articular surface.

The cheloniid femur is similar in all of the Lee Creek Mine genera, with subtle differences that allow some differentiation of the taxa. The head is round (nearly circular in outline) in *Chelonia*, *Eretmochelys*, and *Syllomus* and is ellipsoidal in *Caretta*, *Lepidochelys*, and *Procolpochelys*. The greater (posterior) trochanter is large and angular, forming a broad surface anterior to the head in *Chelonia*, *Eretmochelys*, *Caretta*, and *Lepidochelys*. In *Syllomus* this trochanter is equally large, but the anterior border is curved and extends proximally beyond the head; it also is hook-shaped above the intertrochanteric fossa (Weems, 1980, pl. 1: figs. 7, 8). The greater trochanter of *Procolpochelys* is narrow and straight-edged relative to the diaphysis. The lesser (anterior) trochanter is large and protruding in *Chelonia*, *Eretmochelys*, *Caretta*, and *Lepidochelys*. It is about the same size in *Syllomus*, but the preaxial border is enlarged and rugose. It is only moderately protruding in *Procolpochelys*. The condylar surface bears distinct articular ridges only in *Syllomus*.

Turtle Fauna

Family PELOMEDUSIDAE (sideneck turtles)

Bothremys

FIGURE 2

Collins and Lynn (1936) described the sideneck turtle *Taphrosphys miocenica* from an anterior lobe of a plastron. Later, Gaffney and Zangerl (1968) reassigned this fossil to *Bothremys*; however, they were reluctant to confirm its specific identification owing to the incompleteness of the fossil. They did emphasize that this piece of plastron represented the only un-

questionable sideneck turtle from the Tertiary of North America. Later, Gaffney (1975) noted that the type material of *T. miocenica* was too incomplete to provide a reliable diagnosis, hence this species is a nomen dubium.

Several pieces of carapace and plastron match the *Bothremys* material. A single hexagonal nuchal (USNM 186773; Figure 2A,B) is 59 mm long at its midline, 47 mm wide anteriorly, and 84 mm wide posteriorly. The nuchal is thin (11 mm at thickest region) and possesses smooth dorsal and ventral surfaces. The scute sutures are lightly etched on the surface. A cervical scute is absent. Sutures of the left and right first marginals, left and right first pleurals, and first vertebral scutes are present dorsally on the nuchal. No scute sutures are visible ventrally. The ventral scute surface occupies the anterior third of the nuchal. The nuchal's shape and the absence of a cervical scute identify it as a pelomedusid element.

Four fragments are from the plastron. Three of these (USNM 358462A (Figure 2C), 358747, 358784) are xiphial fragments with pubic or ischial articular scars (fusion of pelvic girdle to plastron is characteristic of pleurodires), and the remaining fragment (USNM 358462B) is unidentifiable to plastron location. A small fragment of a costal (USNM 425594) has the texture of the other Lee Creek pleurodiran fragments.

A complete left humerus (USNM 358316; Figure 2D,E) is assigned to *Bothremys*. It is a short, robust humerus with a widely flaring greater trochanter, a squat, rugose lesser trochanter, and an ectepicondylar canal on the anterodorsal edge of the diaphysis (canal does not intersect the condylar articular surface). It shares some of the features of the humerus of *Taphrosphys sulcatus* (Leidy) (Gaffney, 1975, fig. 12C,D).

Family CHELONIIDAE (hard-shelled seaturtles)

I recognize five species of cheloniid and one species of dermochelyid seaturtles in the Lee Creek Mine fauna. *Caretta* and *Syllomus* are represented by hundreds of elements, the other seaturtles are represented by many fewer elements.

A partial skull and mandibular fragments match the morphology of these elements in *Caretta*. Numerous carapacial fragments (particularly posterior peripherals) and humeri possess the caretine morphology and also are assigned to *Caretta*. These fossil elements show sufficient differences to indicate that they represent a species distinct from extant *Caretta caretta*.

Caretta patriciae, new species

FIGURES 3-6

HOLOTYPE.—USNM 186731, a partial skull lacking basioccipital, basisphenoid, and left quadrate-squamosal complex through and including left jugal. Collected by J.H. McLellan, 17-20 Jul 1972.

TYPE LOCALITY.—North Carolina, Beaufort County, Lee Creek Mine (35°23'N, 76°47'30"W; United States Geological

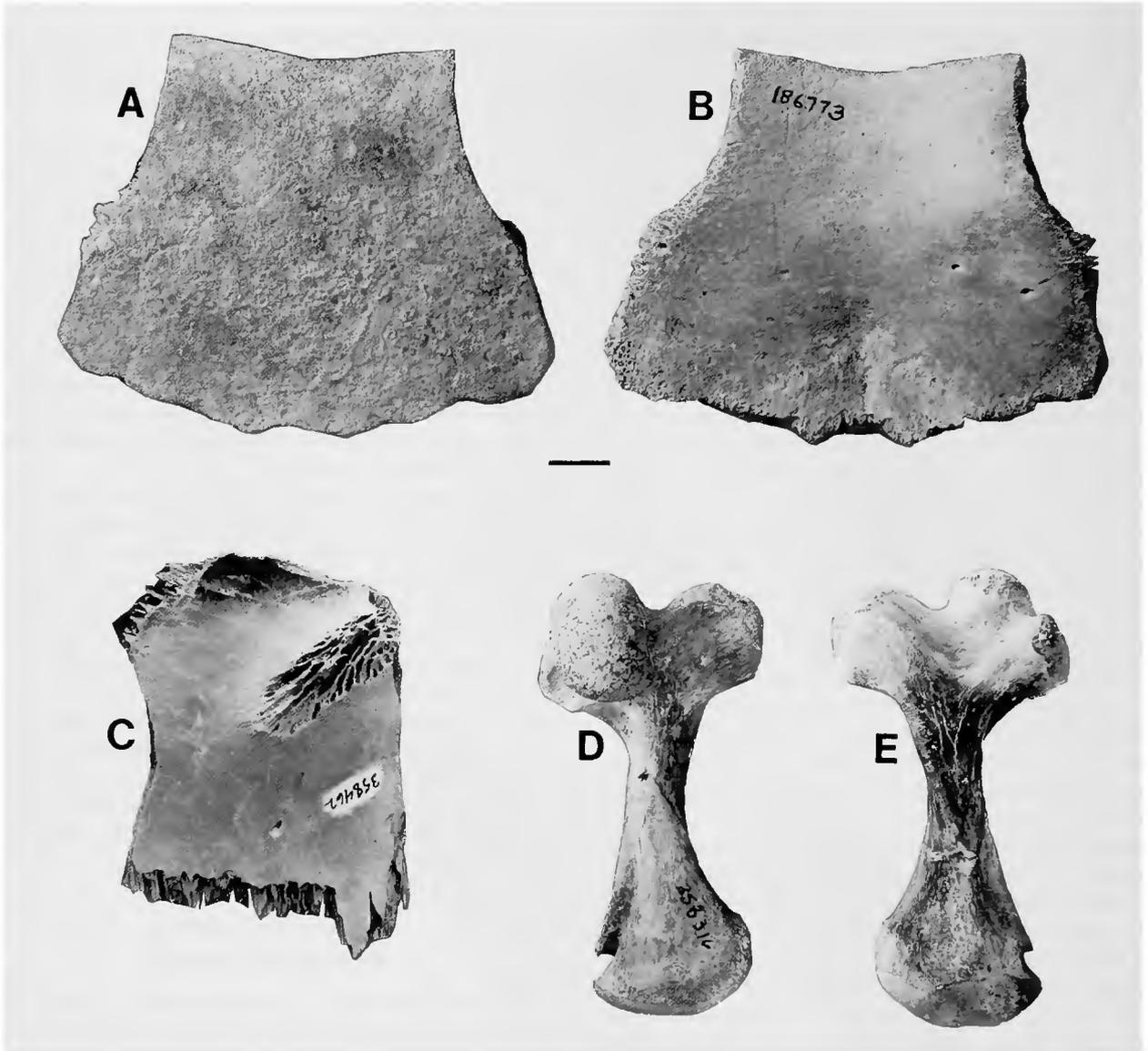


FIGURE 2.—Fossil remains of the sideneck turtle *Bothremys* from Lee Creek Mine. A,B, dorsal and ventral views, respectively, of a nuchal (USNM 186773); C, dorsal view of a fragmented xiphiplastron (USNM 358462A), showing a pelvic girdle attachment scar. D,E, dorsal and ventral views, respectively, of a humerus (USNM 358316). (Scale bar=1 cm.)

Survey quadrangle map, 7.5-minute series, Bath, North Carolina, quadrangle), south side of Pamlico River, near Aurora; from a spoil pile.

HORIZON AND AGE.—Presumably from the Yorktown Formation, lower Pliocene.

ETYMOLOGY.—The specific epithet is a patronym in honor of my wife, Patricia, for her years of support and love. It is proposed as a noun in the genitive case.

DEFINITION.—A cheloniid sea turtle with frontals excluded from orbits by prefrontal-postorbital contact, maxillary contact on secondary palate separating premaxillae from vomer, slight

temporal emargination, and deep pterygoid grooves. Triturating surface of dentary smoothly concave, with or without a low symphyseal ridge. Carapace morphology caretine, with strongly serrate posterior border, pygal widely and deeply notched posteriorly; neural series in adults bearing large, projecting spines or knobs on neurals 1, 4, 7, 10, and posterior suprapygal; suprapygal spine very large.

DESCRIPTION OF HOLOTYPE.—Most of the dorsal surface of the skull is present (Figures 3, 4A). The skull roof has a slight transverse arch and an equally slight longitudinal arch. Together, the parietals are trapezoidal and are 91 mm long, 50 mm

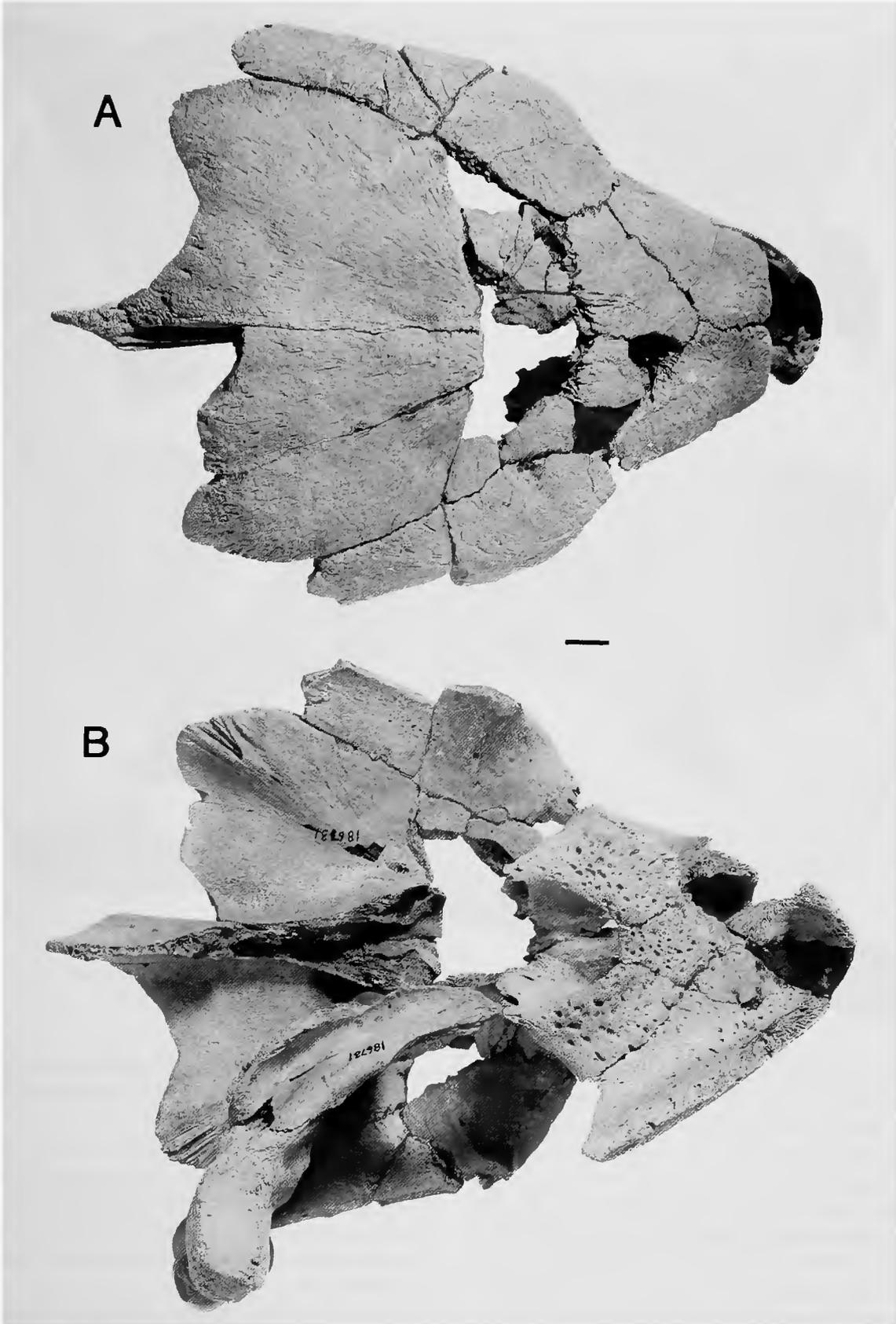


FIGURE 3.—Cranial skeleton of *Caretta patriciae*, new species. A,B, dorsal and ventral views, respectively, of a skull (USNM 186731, holotype). (Scale bar=1 cm.)

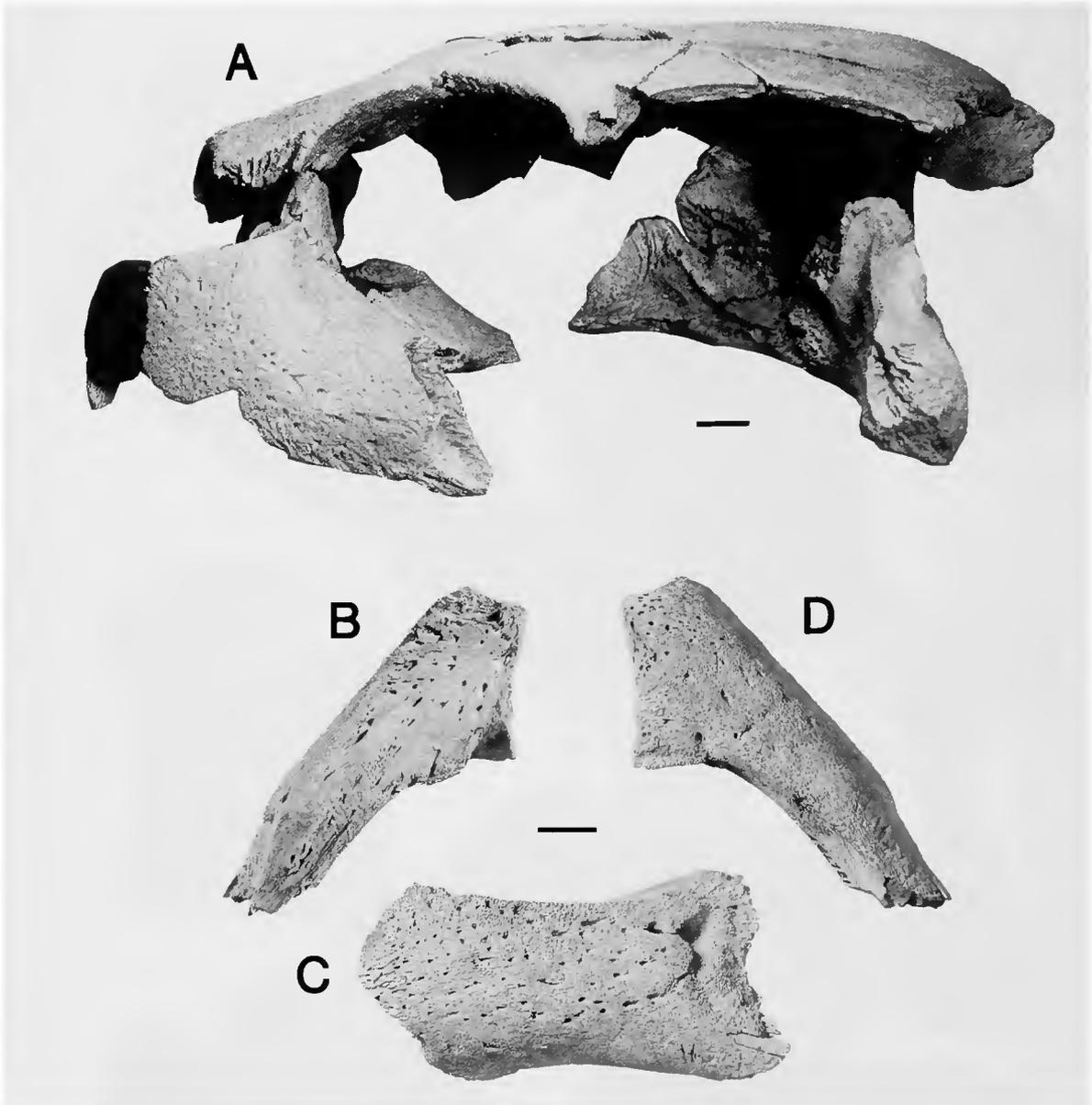


FIGURE 4.—Cranial skeleton of *Caretta patriciae*, new species. A, lateral view of a skull (USNM 186731, holotype); B–D, dorsal, lateral, and ventral views, respectively, of a dentary (USNM 186730). (Scale bars=1 cm.)

wide anteriorly, and 98 mm wide posteriorly. The frontals have a pentagonal outline, are 29 mm long medially, and are excluded from the orbits by the prefrontals and the postorbitals. The nasals are truncated anteriorly and are 20 mm long medially and 42 mm long laterally.

The anterior palatal region of the skull lacks only the right maxilla and left premaxilla. The triturating surface and adjacent secondary palatal surface are flat and smooth. There is a slight depression in the premaxilla for the tip of the mandible. Posteriorly, the left side of the skull is represented by the articular process of the quadrate and the adjacent part of the pterygoid. The articular surface is ellipsoidal with no distinct medial

constrictions, and the surface is inclined only slightly anteriorly. The pterygoid groove is deep and is bordered laterally and medially by well-developed ridges.

ADDITIONAL SPECIMENS.—Numerous fossil elements possess characteristics of *Caretta* or caretine seaturtles and are referred to *C. patriciae*. The morphology of the carapace is based entirely on these isolated elements (Figures 5, 6), even though their association with the skull is uncertain. A few elements are described below.

Parts of a supraoccipital and right opisthotic are present. In addition to unidentified skull fragments, pieces of a right jugal and right quadratojugal are recognizable. The skull fragments

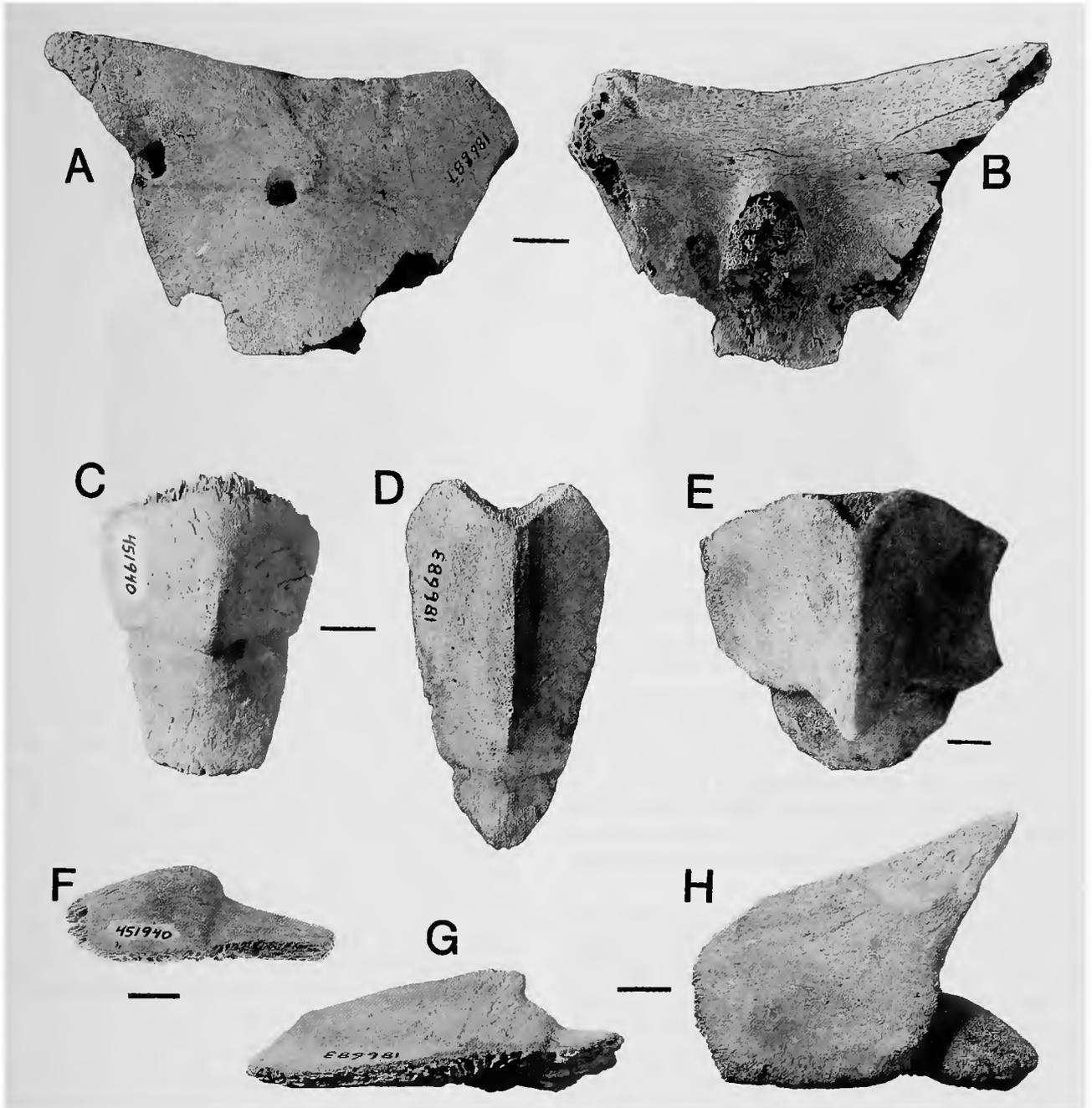


FIGURE 5.—Carapacial elements of *Caretta patriciae*, new species. A,B, dorsal and ventral views, respectively, of a nuchal (USNM 186687); C,D,E, dorsal views of a first neural (USNM 451940), a third or fourth neural (USNM 186683), and a suprapygal (USNM 358420), respectively, of adults; F,G,H, same specimens, lateral views. (Scale bar=1 cm.)

are derived from two individuals; the pieces represent two right jugals and two left pterygoids. Five dentaries are recognizable. The largest piece of dentary (USNM 186730; Figure 4B–D) comprises nearly the entire left half, with only the anterior tip and coronoid extension missing. The triturating surface is broad and smooth. There are no raised labial or tomial ridges. The sulcus cartilaginis meckelii is deep, and anteriorly the dorsal wall overhangs the ventral one. Two fragments are anterior

dentary tips (USNM 187101, 358792); each possesses a mucronate outline and a smooth, concave triturating surface with a low symphyseal ridge; anteroposterior widths are 21 and 26 mm, respectively.

Eighteen left and 32 right *Caretta* humeri have been identified from entire specimens or proximal ends. They were differentiated from those of other sea turtles by the diagnostic features listed earlier. Because I found no feature to differentiate

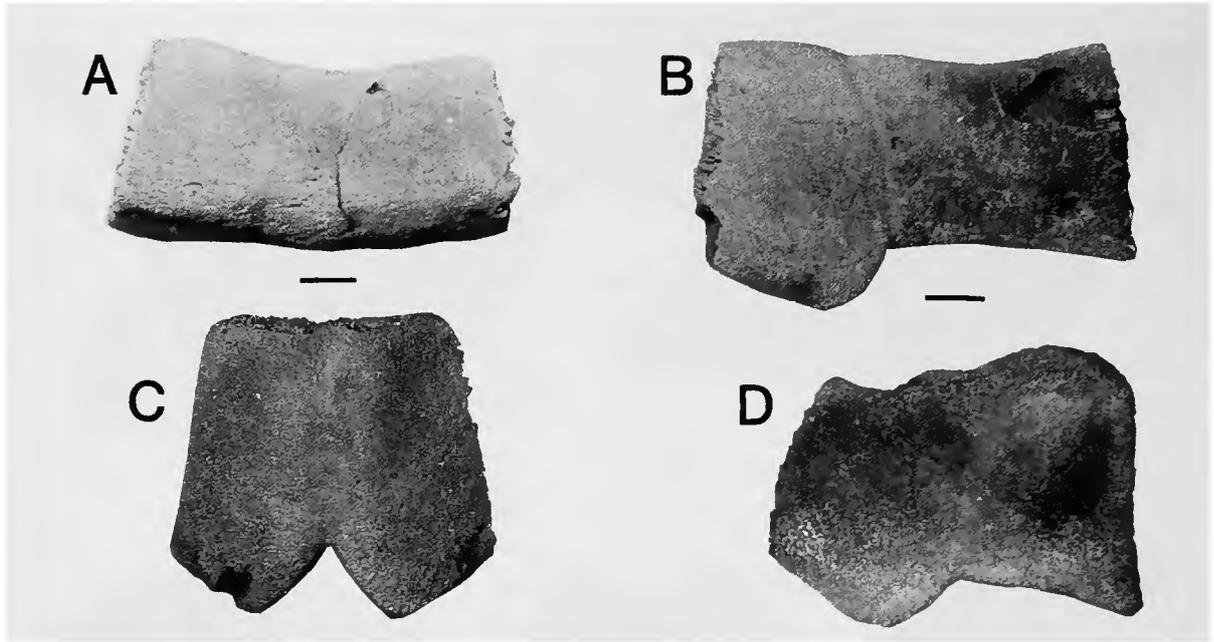


FIGURE 6.—Carapacial elements of *Caretta patriciae*, new species. A,B,D, dorsal views of a right eighth peripheral (USNM 186708), a left eleventh peripheral (USNM 186714), and a left twelfth peripheral (USNM 186703), respectively; C, dorsal view of a pygal (USNM 186688). (Scale bars=1 cm.)

unquestionably the humeri of *Caretta* and *Lepidochelys*, the latter taxon may be represented in this collection of humeri; however, the preponderance of *Caretta* cranial skeletal elements suggests a similar preponderance of postcranial elements. I also identified 15 femora as *Caretta*. Cheloniid ulnae (with the exception of the *Syllomus* ulna) and other appendicular skeleton elements in the Lee Creek Mine collection cannot be identified to genus.

Carettine carapace fragments are the most numerous turtle fossils from Lee Creek Mine. There are hundreds of carapace pieces. Many of the peripherals and neurals are complete or nearly so; costals are invariably highly fragmented; nuchals are rare and incomplete. The similarity of *C. patriciae* and *C. caretta* peripherals suggests that shell shape and size of both species are similar and that the posterior margin of the carapace in both was distinctly serrate. Pygals are numerous; 54 were identified as *Caretta*, and all show a strong notch on the posterior margin. The difference in carapace morphology is the smooth middorsal surface of *C. caretta* and the presence of a middorsal series of spines or knobs in *C. patriciae*. The spine-bearing neurals are 1, 4, 7, and 10 based on a comparison of neural outlines and vertebral scute-suture positions in juvenile and adult *C. caretta* and juvenile *Lepidochelys kempii*. The spines are variably developed on the neurals but clearly persisted in adult *C. patriciae* and could be quite large (Figure 5C,D,F,G); the suprapygal (Figure 5E,H) bears proportionately the largest spine, which remains sharply pointed even in the large adults. The largest nuchal fragment (Figure 5A,B) is the anteromedial part of the bone, which bears the an-

terior lip of the carapace and, ventrally, the bony process for the attachment of the eighth cervical vertebra. This bony process lies less than its longitudinal length from the anterior edge of the nuchal. This position is common in *Caretta*, whereas in the other extant cheloniids the process tends to be posterior.

?*Chelonia*

A single right humerus (USNM 186749, proximal end) appears to represent this genus. There are numerous other fossils that might also derive from *Chelonia*, but distinguishing characteristics are lacking for reliable identifications.

Lepidochelys

FIGURE 7B

A nearly complete left dentary (USNM 425612; Figure 7B), broken to the right of the symphysis, resembles closely the dentaries of juvenile *Lepidochelys kempii*. The fossil dentary is 17 mm wide at the symphysis, and a large symphyseal pyramid rises from the posterior edge of the triturating surface. This surface is deeply concave in the symphyseal area, gradually becoming more planar toward the articular end. The dentary is slightly deformed by a constriction extending diagonally from the middle of the ventral surface upward and posteriad to the coronoid process.

A small left humerus (USNM 508056) matches closely the humeral morphology of extant juvenile *Lepidochelys*.

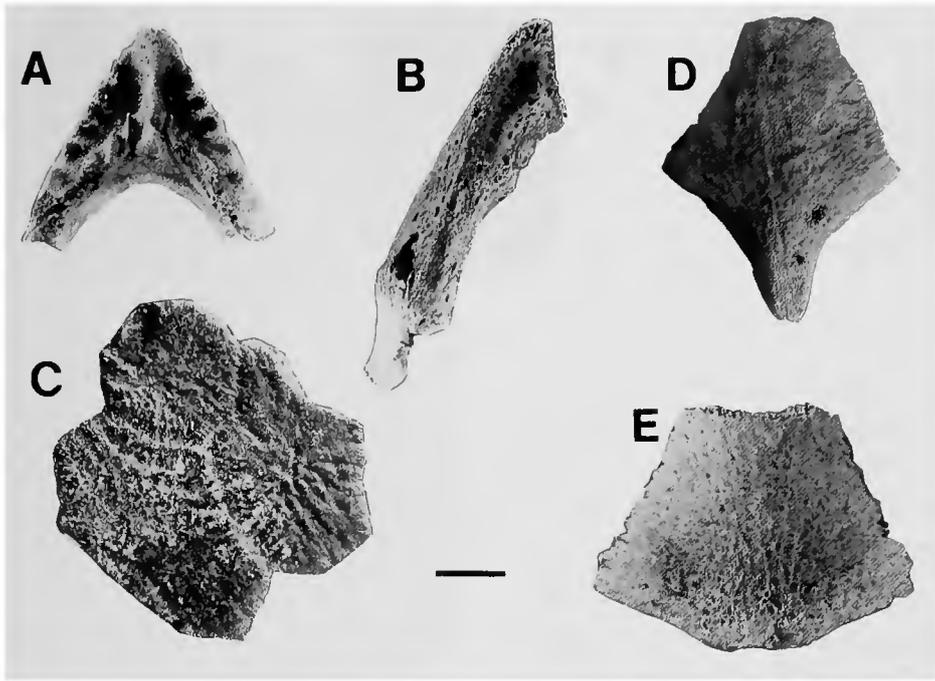


FIGURE 7.—Fossil remains of Lee Creek Mine seaturtles. A,B, dorsal views of *Syllomus aegyptiacus* (USNM 427790) and *Lepidochelys* (USNM 425612) dentaries, respectively; C, dorsal view of three osteoderms (USNM 214649) from the carapace of a *Psephophorus*; D,E, pygals (USNM 358461, 358457, respectively) of *Syllomus aegyptiacus*. (Scale bar=1 cm.)

Procolpochelys

A piece of a left hyoplastron (USNM 214648; principally the medial and posterior portion) possesses a strong xiphiplastral notch, which is covered ventrally by a bony shelf and projects from the midline at about a 30° angle. The shape and depth of this notch matches well plastral fragments of juvenile *Procolpochelys* from the Calvert fauna. Several neurals match Calvert *Procolpochelys* neurals in shape and thickness.

Syllomus aegyptiacus

FIGURE 7A,D,E

Syllomus is represented by numerous fragments. The distinctive surface texture of its carapace allows even the most fragmentary carapacial elements to be recognized. Neurals are numerous; most have distinct longitudinal keels. Eight pygals (two figured; Figure 7D,E) have been found, and all but the largest one bear an attenuate tip with a distal bifurcation. Humeri are extremely abundant, with 44 left and 56 right humeri recognized from either entire elements or proximal halves. One humerus (USNM 187122) contained a small amount of matrix, and sedimentological analysis of this matrix indicates that the humerus was derived from the Yorktown Formation. Thus, *Syllomus* survived into the Pliocene and probably was a contemporary of *Caretta patriciae*. Only six femora have been found.

Family DERMOCHELYIDAE (leatherback seaturtles)

Psephophorus

FIGURE 7C

Three articulated carapacial osteoderms (USNM 214649; Figure 7C) represent this genus. They are 10 mm thick, and the largest plate has a maximum length of 39 mm. Each of the three plates is of a different size and shape. There are eight other isolated osteoderms, and most of these are derived from a keeled area of the carapace. The three articulated osteoderms are darker and more mineralized than are most Lee Creek Mine fossils and may derive from the Pungo River Formation.

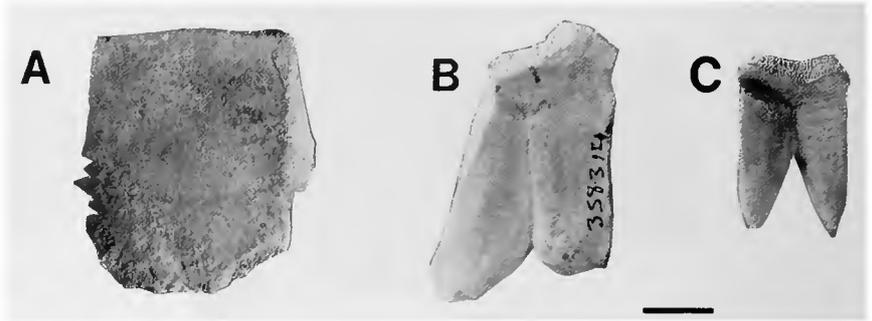
Family EMYDIDAE (pond turtles)

Chrysemys complex

FIGURE 8

A few emydid shell fragments represent the *Chrysemys* complex. Over the past three decades, the contents of this complex have been variously considered to be members of one genus or of two or three genera; the number of species has remained essentially static. Herein, I follow the three-genera concept

FIGURE 8.—Carapacial and plastral elements from turtles of the *Chrysemys* complex. A, ventral view of a *Pseudemys* left hyoplastron (USNM 187104); B,C, dorsal views of a *Trachemys* posterior peripheral (USNM 358314) and pygal (USNM 186774), respectively. (Scale bar=1 cm.)



(Ward, 1984; Seidel and Smith, 1986): *Chrysemys*, monotypic with *picta*; *Pseudemys*, containing the *floridana* and *rubriventris* species groups; and *Trachemys*, containing the *scripta* species group.

The Lee Creek Mine emydine fragments appear to derive from both *Pseudemys* and *Trachemys*. An emydine plastron is represented by a left hyoplastron (USNM 187104; Figure 8A). This hyoplastron lacks most of the bridge buttress, but the hypoplastral and hypoxiphiplastral sutures and the position of the abdominofemoral sulcus are distinct. The element is 39 mm long and 33 mm wide, approximately the size of a hyoplastron of an adult *Chrysemys picta*; however, its morphology is more similar to that of a juvenile *Pseudemys*. A piece of left hyoplastron (USNM 358315A) and a smooth-edged ninth or tenth right peripheral (USNM 358315B) also appear to be derived from a *Pseudemys*. Two pygals (USNM 186774 (Figure 8C), 359009) and a tenth or eleventh left peripheral (USNM 358314; Figure 8B) bear deep notches that have the serrated border of a *Trachemys* carapace.

Family TESTUDINIDAE (tortoises)

Geochelone

A giant tortoise is represented by a complete shell (USNM 336458; Figure 9) and miscellaneous shell fragments, principally peripherals. The complete shell has an estimated carapace length (CL) of 88 cm and an estimated plastron length (PL) of 70 cm. The costals and neurals have collapsed into the body cavity but retain their alignment. The shell was high-domed, with a smooth surface and distinct but lightly incised scute borders. In outline, the shell is slightly obovate, wider posteriorly than anteriorly; the peripherals possess a slight lateral flare. The plastron is smaller than the shell opening and bears a well-developed epiplastral lip, which extends beyond the anterior margin of the carapace. The plastral surface is very lightly etched with scute outlines.

Three lineages of tortoises are known from the late Tertiary of eastern North America: *Geochelone* (*Caudochelys*), *Geochelone* (*Hesperotestudo*), and *Gopherus*. The Lee Creek Mine tortoise is large, has a narrow nuchal scute, parallel-sided costals, and a plastron smaller than the carapace opening, traits that ally it to *Geochelone*. Two species of *Geochelone*, *G. ducатели* (Collins and Lynn) (Calvert Formation, Maryland) and *G. tedwhitei* (Williams) (Hawthorne Formation, Florida), occur in Miocene faunas (Auffenberg, 1974). Both of these species are moderate-sized tortoises of less than 40 cm PL and are considered to be members of the subgenus *Caudochelys*. Larger tortoises of the subgenus *Hesperotestudo* have members in midcontinental Miocene faunas but do not appear in Atlantic coast faunas until the Pliocene and then only in the Southeast. The Lee Creek Mine tortoise fossils do not closely match either of these two species groups. Although some of the isolated peripherals fall within the size range of *G. ducатели*, the Lee Creek Mine peripherals are proportionately thinner. The epiplastral lip of the shell also is more angular and projecting than that of *G. ducатели*. As in many *Hesperotestudo*, the fossil's humeropectoral scute border lies on the hyoplastron immediately posteriorad to the entoplastron; however, the pectoroabdominal border is widely separated from the humeropectoral border (pectoral/abdominal midline lengths, 0.30%). This feature distinguishes the Lee Creek Mine tortoise from the *Hesperotestudo* lineage, and this separation also is greater than in *Caudochelys*.

Of the eastern Pliocene *Geochelone*, only *G. (Caudochelys) hayi* (Sellards) is a large species, encompassing the size of the Lee Creek Mine tortoise. Both *G. (Hesperotestudo) alleni* Auffenberg and *G. (H.) turgida* (Cope) have plastron lengths of less than 25 cm and large plastra filling their shell openings. The Lee Creek Mine tortoise may be *G. hayi*; however, without additional comparative material, such an identification is tentative. The type of *G. hayi* (USNM 8815) has a carapace of equivalent size but has a proportionately larger plastron with broader epiplastra and a deeper xiphiplastral notch. The type

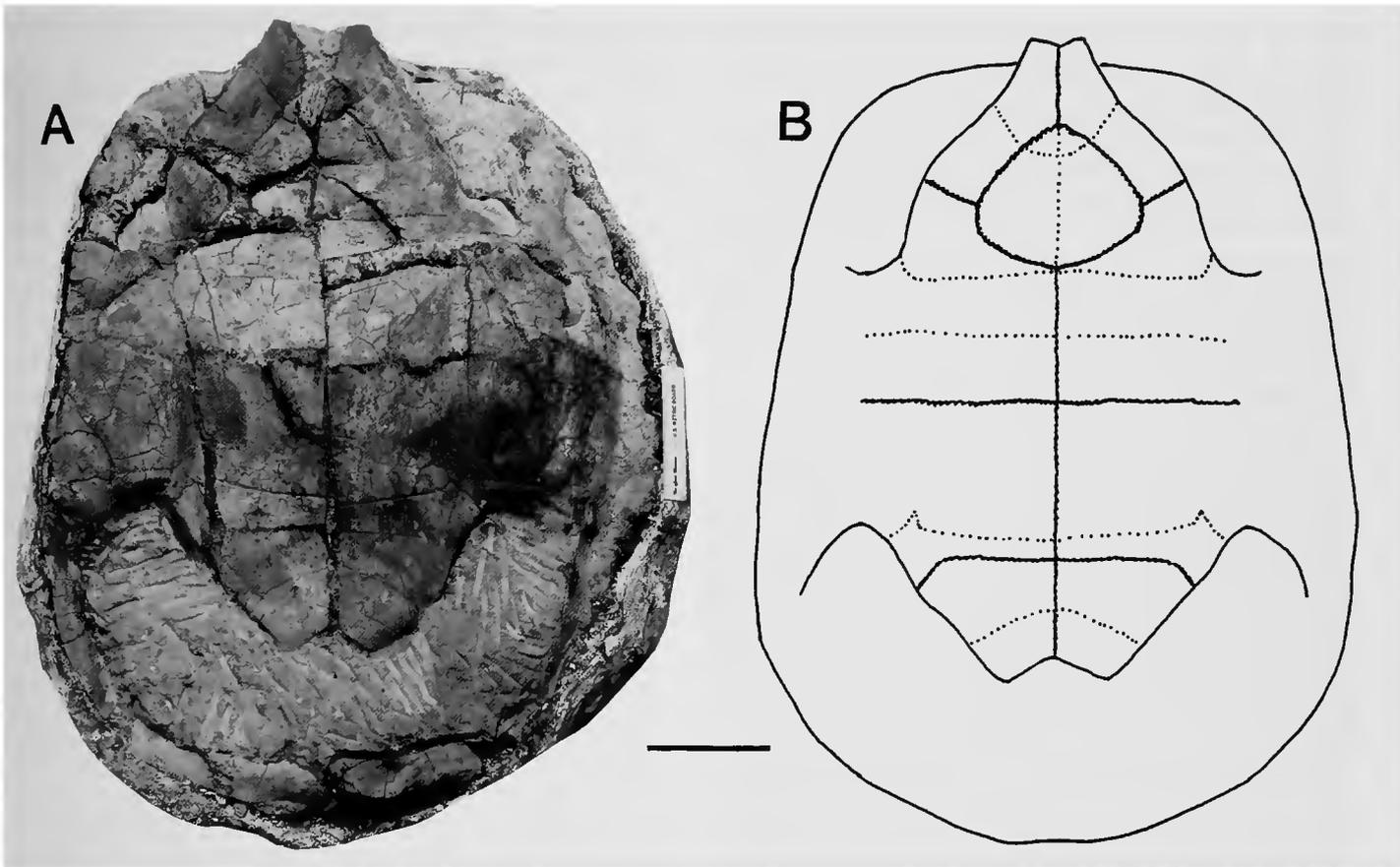


FIGURE 9.—Ventral view of the complete shell (USNM 336458) of the Lee Creek Mine *Geochelone*. A, shell resting in a plaster jacket (ruler on right=15 cm); B, reconstruction of the plastron proportionately matching the lengths and widths of the fossil elements. (Scale bar=15 cm.)

also has strongly flaring posterior peripherals, which flared only slightly in the Lee Creek Mine specimen.

Family TRIONYCHIDAE (softshell turtles)

Genus undetermined

Three carapacial fragments are referable to trionychid turtles. All possess the strongly pitted and ridged surface texture of the trionychid shell. A proximal end of a costal (USNM 186677) is extremely thick, with the thickness about 25% of the width. A neural (USNM 508057) is of equal thickness. These elements are darker and more mineralized than are most other Lee Creek Mine fossils and perhaps are derived from the Pungo River Formation.

The extant North American softshell turtles represent a monophyletic group (*Apalone*; Meylan, 1987) of three species. Although the Lee Creek Mine fragments likely represent *Apalone*, shell fragments, indeed entire carapaces or plastrons, are insufficient for the differentiation of *Apalone* from its Asian relatives.

Family incertae sedis

A nearly complete right ilium, USNM 187103, lacking the distal sacral border, is indeterminate. It is a small (~40 mm long), stout element with a straight anterior edge and a fan-shaped posterior edge. It possesses the stoutness of a *Cheylidra* ilium and the shape of an *Emydoidea* one.

A heavily mineralized right parietal (USNM 187100), ~45 mm long and unquestionably turtle, cannot be reliably assigned to genus. Its manner of fossilization suggests that it came from the Pungo River Formation.

Discussion

The Lee Creek Mine fauna has 11 recognizable turtles: a sideneck turtle, six seaturtles, two pond turtles, a softshell turtle, and a giant tortoise. This fauna derives principally from the Yorktown Formation, although the mining operation may have introduced some elements from the Pungo River Formation. Both of these formations are marine, yet the fauna has representatives of marine, freshwater, and terrestrial turtles. Nonetheless, it seems likely that both faunal components derive

from the waters and land immediately adjacent to the depositional site. None, in my opinion, requires a long-distance transportation hypothesis.

The turtles occurring in the two Miocene and one Pliocene marine deposits of the mid-Atlantic coast are summarized in Table 3. Only three species have been recovered from the New Jersey Miocene, and the "*Chelonia*" is almost certainly from an Eocene deposit. This small number probably reflects a lack of good collecting localities rather than a depauperate fauna. The Calvert and the Lee Creek faunas are similar in size and content, sharing six taxa: *Bothremys*, *Procolpochelys*, *Syllomus*, *Psephophorus*, *Geochelone*, and a trionychid.

The freshwater and terrestrial taxa are all extant taxa, although only the pond turtles occur in the Lee Creek Mine area today. The fragmentary nature of the fossil pond turtles allows only a statement of their presence in the fauna, not their specific identity or ecological significance. Their presence is not unusual because both are known from other late Tertiary and Quaternary faunas. *Trachemys* is both common and widespread in Cenozoic faunas east of the Rocky Mountains and has a temporal distribution from the early Miocene (Williams, 1953, pl. 4; Jackson, 1988) to the present in eastern North America. Williams (1953) also pictured a *Pseudemys floridana*-like turtle from an early Miocene deposit in Florida. Specific identification of the Lee Creek *Pseudemys* and *Trachemys* will require more complete specimens from Lee Creek Mine and a more comprehensive examination of the fossil history of the *Chrysemys* complex. The Lee Creek Mine specimens extend the geographic occurrence of these taxa in the Pliocene into the mid-Atlantic region.

Trionychids occurred at the Lee Creek site. Today, they are not present in that area or adjacent to the other two mid-Atlantic fossil sites, yet fragmentary fossils of the trionychids dem-

onstrate their Pliocene or Miocene occurrence (Table 3) in the rivers of the mid-Atlantic coastal plain.

Geochelone also is a common member of late Tertiary and Quaternary faunas of North America. Four of the previously known species (*G. ducatei*, *G. tedwhitei*, *G. alleni*, *G. turgida*) from eastern Miocene–Pliocene faunas are much smaller tortoises. Some Lee Creek tortoise fossils match the size of these species, but they are too fragmentary to discern whether they represent a second, smaller species in the Lee Creek Mine fauna or represent juveniles of the giant tortoise. The complete shell and many fragments show the Lee Creek *Geochelone* to be a giant tortoise, the first from the mid-Atlantic Tertiary. It may be *G. hayi*, but comparative material is inadequate for confirmation.

The pelomedusid *Bothremys* is considered to be a marine sideneck turtle. The presence of the xiphiplastra with girdle scars confirms its presence in the Lee Creek Mine fauna. Its occurrence is important because it may extend the temporal range of this genus from the Calvert Formation through the Yorktown Formation. Without precise stratigraphic data, however, the Lee Creek sideneck turtle must be assigned questionably to the Pliocene. Whether Miocene or Pliocene, the Lee Creek Mine occurrence confirms the presence of sidenecks in the North American Tertiary.

Procolpochelys and *Psephophorus* are very rare in the Lee Creek Mine assemblage, perhaps because they are from the Pungo River Formation; however, *Psephophorus* was recently discovered (Dodd and Morgan, 1992) in a Pliocene deposit in central Florida. They are assumed to be highly pelagic species. Although this pelagic behavior may account for their relative rarity, *Dermochelys*, the modern day counterpart of *Psephophorus*, seasonally migrates along the Atlantic coast (Shoop,

TABLE 3.—Occurrence of Miocene and Pliocene turtles in marine deposits of the central Atlantic coastal plains of North America. Symbols: +, species occurs in fauna; –, species absent from fauna; ?, occurrence doubtful.

Taxon	Miocene fauna of New Jersey	Calvert fauna of Maryland and Virginia	Lee Creek Mine fauna of North Carolina
Family PELOMEDUSIDAE			
<i>Bothremys</i>	–	+	+
Family CHELONIIDAE			
<i>Caretta</i>	–	–	+
<i>Chelonia</i>	?	? ¹	+
<i>Lepidochelys</i>	–	–	+
<i>Procolpochelys</i>	+	+	+
<i>Syllomus</i>	–	+	+
Family DERMOCHELYIDAE			
<i>Psephophorus</i>	–	+	+
Family EMYDIDAE			
<i>Chrysemys</i> complex	–	–	+
Family TESTUDINIDAE			
<i>Geochelone</i>	–	+	+
Family TRIONYCHIDAE			
cf. <i>Apalone</i>	+	+	+

¹Cope (1868) considered two fragments to represent *Chelonia*; Weems (1974) believed them to be from *Syllomus* and *Procolpochelys*, respectively.

1987), regularly enters the larger estuaries (e.g., Chesapeake Bay; Musick, 1988), although briefly and in small numbers, and strands regularly on Atlantic beaches (Prescott, 1988). I suspect that the rarity of *Psephophorus* is not because they are pelagic and their carcasses were lost at sea, but because the Lee Creek depositional environment was estuarine, equivalent to today's Albemarle and Pamlico Sounds. Stranding on high energy ocean-front beaches destroys carcasses and provides little opportunity for fossilization. This destruction occurs to all sea-turtles, whether they are near-shore or pelagic species.

Extant *Caretta caretta* and *Lepidochelys kempii* use the estuaries, bays, and sounds of North America (south of Cape Cod) as summer feeding grounds for juveniles and often occur in high densities in these areas. The abundance of *Syllomus* and *Caretta patriciae* suggests that the Lee Creek area was similarly used by these extinct species. This suggestion is further strengthened by the numerous limb bones of juvenile *Caretta* and *Syllomus*. To extend this suggestion into speculation, I note that juvenile *Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata*, and *Lepidochelys kempii* are year-around residents in some Florida bays and sounds (Ehrhart, 1983). During the winter, they burrow into the bottom of these bays and possibly hibernate (Ogren and McVea, 1982). It seems likely that the Lee Creek *Caretta* and *Syllomus* also were year-around residents of the Pliocene Lee Creek estuary. The abundant fossils of the latter two sea-turtles might be attributed to cold-stunning (K. Dodd, pers. comm., 1991), a regular event in some estuaries (Meylan, 1986; Witherington and Ehrhart, 1989) that kills many resident sea-turtles.

Without stratigraphic control, suggestions on the origin of the Lee Creek vertebrate fauna are speculative. The commonness of tortoises and juvenile sea-turtles and the types of sea-turtles present argue for a shallower, near-shore deposition. The teleost fish data is less precise, indicating a "deposition at 60 to 100 m, but could in fact have been much shallower or a great deal deeper" (Fitch and Lavenberg, 1983:527).

The similarity of the *Caretta patriciae* skull to that of *C. caretta* indicates a similar diet, dominated by mollusks and crustaceans (Mortimer, 1982; Plotkin, 1989). The skull of *Syllomus* is more elongate (Weems, 1980) and generally resembles that of *Eretmochelys*, so it may have shared a preference for sponges (Meylan, 1988) as well. One of the more striking features of *Syllomus*, however, is its humeral morphology, which is unlike that of any modern sea-turtle. *Syllomus* undoubtedly swam with the aquatic flight locomotor pattern, but the proportional and shape differences of the humerus suggest a modification of the typical pattern, perhaps a more rapid or powerful stroke. Rather than eating sponges, was it capable of chasing and capturing fish or squid? Another peculiarity of *Syllomus* is the surface texture of the carapace, suggesting a different type of epidermal covering. Scutes were present, but they may have been softer, less keratinized, perhaps similar to the scutes of *Natator depressa* (Garman). The relationships of these two taxa require closer examination.

The abundance of *Caretta* fossils in the Lee Creek Yorktown deposits and their absence from the Calvert Formation indicate a Pliocene arrival to the mid-Atlantic coast. *Caretta* has been reported from faunas as early as the Eocene and questionably the late Cretaceous (Mlynarski, 1976). These early fossils (Cretaceous and Eocene) are suspect, and their identities must be confirmed.

Zangerl and Turnbull (1955) placed the Miocene *Procolpochelys grandaeva* Leidy in the cheloniid tribe Caretini. They considered *Procolpochelys* to be a pelagic divergent and not ancestral to the extant caretines, *Caretta* and *Lepidochelys*. The presence of *Caretta* in the Lee Creek Mine assemblage is additional evidence against *Procolpochelys* as an ancestor of extant caretines. Carapace structure of these two is similar in two characteristics. Both lack surface sculpturing and possess costoperipheral fontanelles; however, the extent of fontanelle development can not be determined from the present Lee Creek Mine fragments. The fontanelles probably never closed in *Procolpochelys*. In extant *Caretta*, closure does occur but apparently only after sexual maturity. The extent of closure, its timing, and intra- and interpopulational variation remain undocumented. Some of the peripherals from Lee Creek *Caretta* are equivalent in size to those of extant, reproductively active *Caretta*, and these peripherals lack costoperipheral sutures. Further, the shape of the largest (and clearly adult) posterior suprapygial indicates the presence of large costoperipheral fontanelles in the posterior aspect of the carapace.

Conclusions

Examination of the turtle fossils from the Lee Creek Mine reveals the following: (1) The Pliocene turtle fauna of the mid-Atlantic coast and coastal plain contained extinct and modern genera. The marine or estuarine taxa were *Bothremys*, *Caretta patriciae*, ?*Chelonia*, *Lepidochelys*, *Procolpochelys*, *Syllomus*, and *Psephophorus*. The freshwater taxa were two pond turtles (probably *Pseudemys* and *Trachemys*) and a trionychid, and there was a single terrestrial taxon, *Geochelone*. (2) The estuarine/near-shore nature of the Lee Creek Mine deposit and the abundance of *Caretta* and *Syllomus* indicate that these two taxa were regular residents of the estuaries and coast of the Albemarle Embayment. Juveniles and adults are represented, so the area likely included both feeding grounds and nesting beaches, just as it does for *Caretta caretta* today. (3) The Pliocene *Caretta* is morphologically distinct from the modern species and is recognized as a new species, *C. patriciae*. (4) The Lee Creek *Geochelone* is the earliest Cenozoic record of a giant tortoise from the mid-Atlantic coast of North America. This tortoise also appears to be morphologically distinct from previously known Miocene–Pliocene *Geochelone*. (5) The presence of xiphialastral fragments with pelvic girdle articular scars confirms the presence and likely extends the temporal range of pleurodiran turtles in North America.

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Thecachampsa antiqua (Leidy, 1852) (Crocodylidae: Thoracosaurinae) from Fossil Marine Deposits at Lee Creek Mine, Aurora, North Carolina, USA

Albert C. Myrick, Jr.

ABSTRACT

Fossil remains of crocodylians at Lee Creek Mine have been few and fragmentary. Nevertheless, isolated teeth and dermal plates from the spoil piles are identifiable as *Thecachampsa antiqua* (Leidy). This species was established by Leidy on characters of teeth presumably from the Calvert Formation of Virginia (late early to early middle Miocene), but the species is now validated by skulls and numerous elements from the middle Miocene formations of the Chesapeake Group. The same form is common in the Florida early Pliocene, where it is represented by several fairly complete skeletons known as *Gavialosuchus americanus* (Sellards). It also is known from numerous skulls from early and middle Miocene formations near Lisbon, Portugal, as *Tomistoma lusitanica* (Vianna and Moraes). Teeth and a dermal scute indicating the same species have been collected from late early Miocene deposits. The resemblance among teeth, scutes, and skulls from the Chesapeake Group, Florida, and from Portugal indicates that these forms are conspecific. The earliest available name, *Thecachampsa antiqua*, has priority.

Introduction

A small collection of isolated and fragmentary remains of fossil crocodylians from Lee Creek Mine has accumulated in the collections of the National Museum of Natural History (which includes collections of the former United States National Museum (USNM)), Smithsonian Institution, over the past 25 years. The sample is a result of collecting from mixed tailings from the Pungo River Formation (late early to early middle Miocene; Gibson, 1983) and the overlying Yorktown

Formation (early Pliocene; Gibson, 1983; Hazel, 1983). It provides a first opportunity to study the Lee Creek crocodylian materials in relation to other similar forms of comparable geologic age. The purpose of this paper is to describe the Lee Creek Mine crocodylian specimens and to comment on the taxonomic status and paleozoogeographic implications related to the Lee Creek Mine occurrence and to occurrences of closely related forms elsewhere.

ACKNOWLEDGMENTS.—The Lee Creek Mine specimens cited in this report were collected and donated by P.J. Harmatuk, F. Hyne, and B. Hyne. I thank L.G. Barnes (Los Angeles County Museum of Natural History) for providing refresher information on the California specimens. S.D. Webb's (University of Florida) age estimations of the Florida localities were of great help. C. Repenning (United States Geological Survey) loaned crocodylian teeth from California. A. Sanders (The Charleston Museum) and B. Erickson (Science Museum of Minnesota) gave helpful advice. I am especially grateful to T. Deméré, at the San Diego Museum of Natural History, who permitted me to study the Museum's holdings of recent vertebrate paleontology literature.

MATERIALS AND PROVENIENCE

The fossil crocodylian remains from Lee Creek Mine consist of approximately 24 isolated teeth, 15 unassociated vertebrae, two incomplete dermal scutes, three skull fragments, a mandibular fragment, a right maxilla fragment, and several bones and bone fragments from appendicular skeletons (Figures 1–5). These have been assigned USNM catalog numbers. Field data indicate that none of the specimens were collected in association or in situ. Adherent matrix indicates at least one specimen (fragment of right maxilla, USNM 307548) came from the Pungo River Formation, but, because the spoil piles

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consist of disturbed mixtures of sediments from the Pungo River Formation and the Yorktown Formation, others could equally well have come from the Yorktown Formation. The most that can be said at present is that the Lee Creek Mine crocodilian fossils are of late early Miocene and possibly early Pliocene age.

Morphological Description

The appendicular elements, vertebrae, and skull fragments in hand are of little immediate diagnostic use below the family level. If, however, one may judge from the several robust vertebrae (USNM 412243, 412254) and the large size of the posterior fragment of a right maxilla (USNM 307548; Figure 2), which contains complete teeth, some of these animals probably attained greater sizes than most modern crocodilians.

Most of the crocodilian teeth collected at Lee Creek Mine, including those in the maxillary (USNM 307548) and mandibular (USNM 437930) fragments, are in a state of excellent preservation and are of diagnostic importance (Figures 1–3). They are heavily built simple cones, elliptical to subcircular in cross section, with bluntly pointed apices. A carina of variable prominence occurs on anterior and posterior surfaces of the crowns. It typically extends basally from near the apex to about one-half the length of the crown, although carinal distance also is highly variable. The carinae divide the tooth subequally, such that the greater half of the crown lies toward the labial side. The longer teeth are slightly recurved, the shorter, stouter ones are barely so. Labiolingual compression is exhibited especially in the shorter, presumably more posterior, teeth. The enamel is thin, variably transparent, and finely rugose, with a silky fibrous surface texture. Within the enamel can be seen various light and dark colored bands encircling the crowns horizontally at irregular intervals.

The two specimens of dermal plates or scutes (USNM 244391, 412252) also have diagnostically important characters (Figure 4). They are rectangular with one corner more or less rounded and with two edges more strongly beveled than the others. The external surface of the scute contains very large, irregularly rounded pits with no discernable pattern. In addition, the scutes have no keels (i.e., plate-like ridges that project at right angles from the pitted external surface), which commonly are found in the dermal scutes of most modern crocodilians.

COMPARISON WITH OTHER MATERIALS

I confine my remarks to the North American Miocene and Pliocene and the Portuguese Miocene forms.

In their diagnostic characters, the crocodilian teeth and scutes are identical to numerous isolated teeth and scutes from the Miocene formations of the Chesapeake Group of Maryland and Virginia. They also closely resemble elements asso-

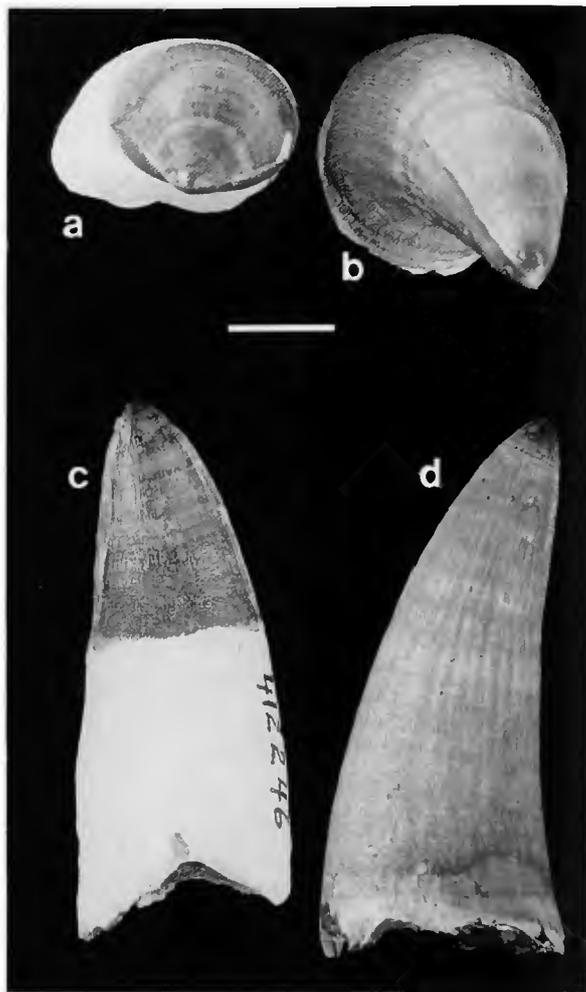


FIGURE 1.—Teeth of *Thecachampa antiqua* from Lee Creek Mine, North Carolina (a,c, USNM 412246; b,d, USNM 299794): a,b, apical view; c,d, lingual view. (Scale bar=1 cm.)

ciated with one well-preserved skull (USNM 25243; Figure 5b) from the Calvert Formation in northern Virginia (late early Miocene) and with at least several skulls from the Bone Valley Gravel and the Alachua formations (early Pliocene; S.D. Webb, pers. comm., 1967) of Florida. In addition, they do not differ in any consistent feature from teeth and dermal scutes associated with skulls from Miocene deposits near Lisbon, Portugal. Finally, the only crocodilian material known from late Tertiary marine deposits in southwestern California and in Baja California, one partial scute and more than a dozen teeth, compares favorably in detail with the Lee Creek Mine materials.

In cases where skulls and other skeletal elements have been closely compared and described (i.e., from the Virginia Calvert Formation, Maryland St. Marys Formation, Florida Pliocene formations, and Miocene formations near Lisbon,

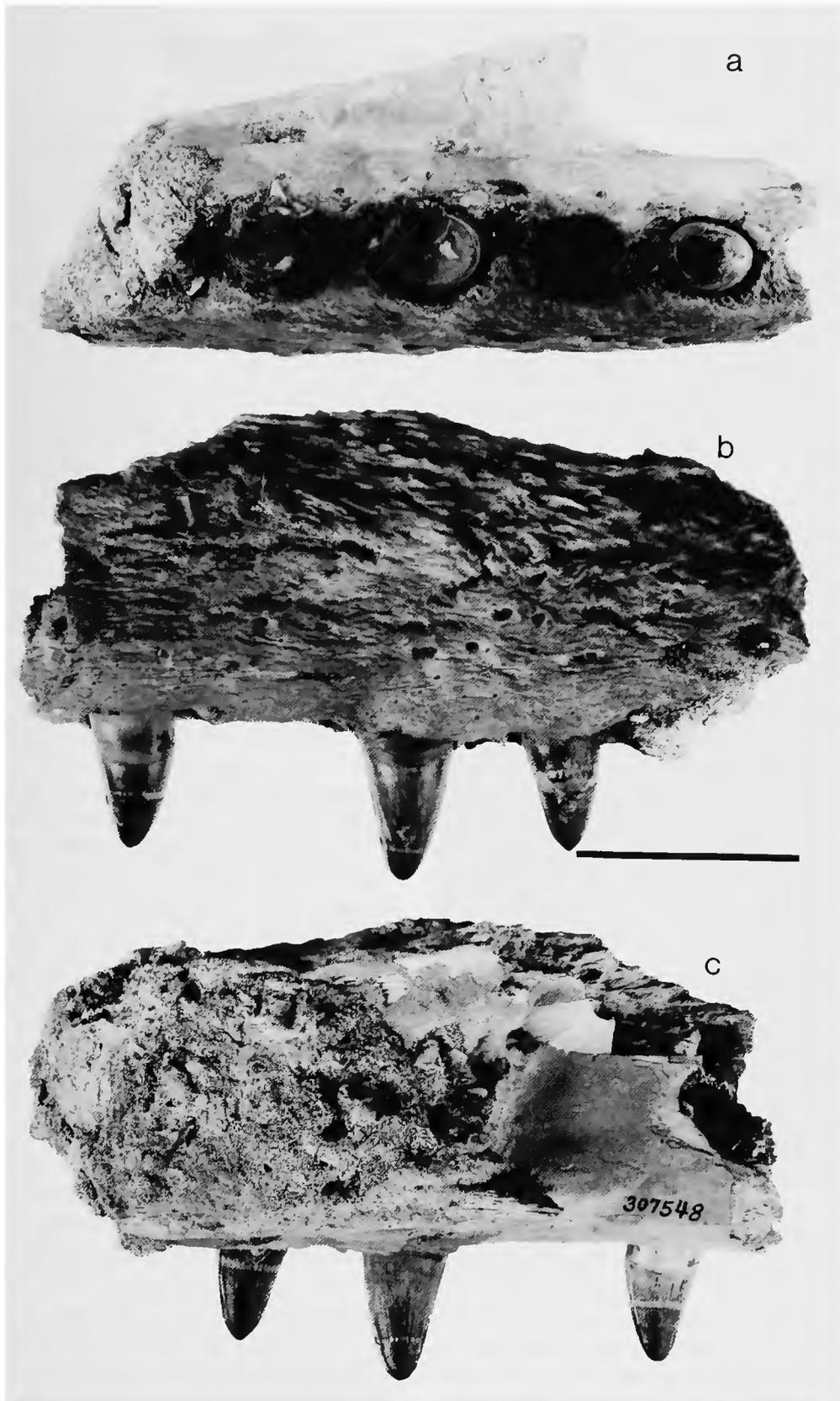


FIGURE 2.—Posterior fragment of right maxilla containing teeth of *Thecachampsia antiqua* from Lee Creek Mine, North Carolina, USNM 307548: *a*, dorsal view; *b*, lateral view; *c*, medial view. (Scale bar=5 cm.)

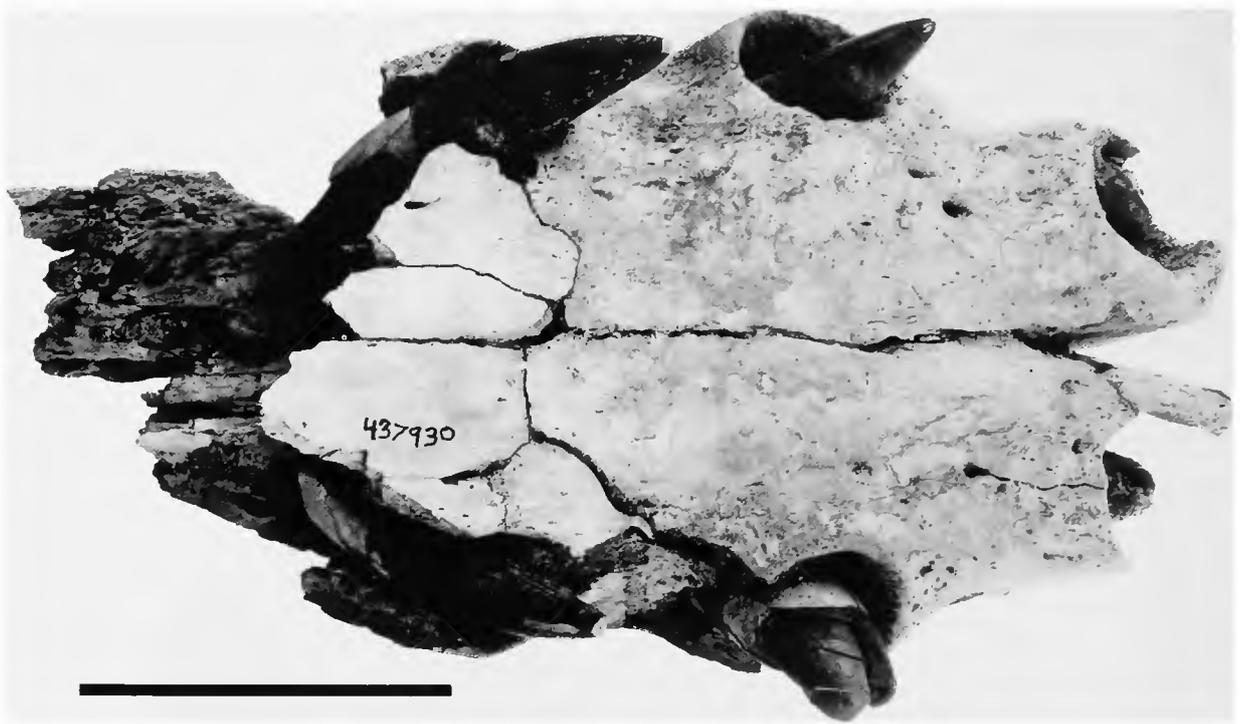


FIGURE 3.—Distal ends of mandibles of *Thecachampsia antiqua* from Lee Creek Mine, North Carolina, USNM 437930, dorsal view. (Scale bar = 5 cm.)

Portugal), I have not been able to identify consistent morphological differences. They all have long robust snouts that are gradually tapered from strongly built skulls (Figure 5b). Among other unifying features, they share the same or similar sutural patterns, bone proportions, tooth counts, and serial tooth diameter differentiation patterns.

Taxonomy

Although this is not the place for a revision of the European and North American thoracosaurine crocodiles, the fossil skulls are distinctly different in generic features from the modern false gavial, *Tomistoma schlegelii* Müller, of south-east Asia. Several studies (Toula and Kail, 1885; Mook, 1921, 1924; Vianna and Moraes, 1945; Auffenberg, 1954) have carefully pointed out that the European and North American “tomistomines” of Miocene–Pliocene age represent a genus separate from *Tomistoma*. Modern workers who have accepted evidence for a separate genus have used the name *Gavialosuchus* to designate the more robust Miocene and Pliocene forms. The name *Gavialosuchus* dates from Toula and Kail (1885). Mook (1921) referred the Florida fossils to *Gavialosuchus*, but Antunes (1994) continues to use the more conservative name *Tomistoma lusitanica* (Vianna and Moraes) for the Portuguese fossils.

Until a partial skeleton with skull, teeth, and dermal scutes (USNM 25243; Figure 5) was collected from the Calvert Formation in Virginia, in the late 1960s, it was not possible to show that *Gavialosuchus americanus* and *Tomistoma lusitanica* were junior synonyms of Leidy’s species, based on the tooth characteristics, and that *Gavialosuchus* was a junior synonym of Cope’s genus *Thecachampsia*, in which taxon Cope included Leidy’s species *antiqua* in 1869.

From my own study of USNM 25243 and other Chesapeake Group specimens, however, it now seems apparent that the four species of *Thecachampsia* (*antiqua*, *sericodon*, *sicaria*, and *contusor*) recognized by Cope on the basis of differences in tooth shape should be naturally combined under one name by virtue of the variation in teeth exhibited along the tooth rows of *Thecachampsia antiqua* skulls. In addition, considering that there seem to be no important morphological differences between skulls of different nominal species, in my opinion there is no useful purpose in maintaining taxonomic distinctions between specimens from the Chesapeake Group, Florida, and Lisbon, Portugal (and presumably now from Lee Creek Mine and possibly from southern and Baja California). I therefore consider these taxa to be conspecific and propose the following taxonomic scheme, which follows Steel (1973) in part.

CROCODYLIDAE

THORACOSAURINAE

Thecachamps Cope, 1867*Thecachamps* *antiqua* (Leidy, 1852)*Crocodylus antiquus* Leidy, 1852*Thecachamps* *sericodon* Cope, 1867*Thecachamps* *contusor* Cope, 1867*Thecachamps* *antiqua* (Leidy).—Cope, 1869*Thecachamps* *sicaria* Cope, 1869*Tomistoma americana* Sellards, 1915*Gavialosuchus americana* (Sellards).—Mook, 1921*Gavialosuchus americanus* (Sellards).—Auffenberg, 1954*Gavialosuchus americanus* (Sellards) var. *lusitanica* Vianna and Moraes, 1945*Tomistoma lusitanica* (Vianna and Moraes).—Antunes, 1961**Paleozoogeography of *Thecachamps* *antiqua***

The earliest known occurrences of this species in North America are from the Kirkwood Formation of New Jersey and the Calvert Formation of Maryland and Virginia (both late early to early middle Miocene, Gibson, 1983). This is probably a little later than the early Burdigalian appearance of the species in Portugal (Antunes, 1961; Benson, 1998).

A fragment of a right maxilla (USNM 307548) from the Pungo River Formation at Lee Creek Mine establishes a new southern record for eastern North America for *Thecachamps* *antiqua* in the middle Miocene. Further, if some of the other specimens are from the Yorktown Formation at Lee Creek Mine, then these would establish the most northern extension in the early Pliocene. *Thecachamps* *antiqua* remains have been collected from the St. Marys Formation (Chesapeake Group), but none have yet been reported in the Yorktown Formation (early Pliocene) in Virginia.

Although the species is well represented in the Bone Valley Gravel and Alachua formations in Florida (early Pliocene), it is surprising that there is no record of the species from the Hawthorn Formation (middle Miocene, Webb, pers. comm., 1967). These results may indicate that the *T. antiqua* populations were vacating Maryland-Virginia waters by the beginning of Yorktown deposition and may not have come to inhabit coastal areas of Florida in force until late in the Miocene.

The sparse remains that seem to place this or a related species on the southwestern coast of North America have been collected from Barstovian Age (Calvert equivalent?) marine deposits in California and deposits in Baja California of possible early Pliocene age (Barnes, pers. comm., 1988). The lack of crocodylians in otherwise abundantly rich fossiliferous marine and coastal deposits of late Miocene age is enigmatic. The problem is still under investigation.



FIGURE 4.—Partial dorsal dermal scute of *Thecachamps* *antiqua* from Lee Creek Mine, North Carolina, USNM 412252: a, dorsal view; b, ventral view. (Scale bar=1 cm.)

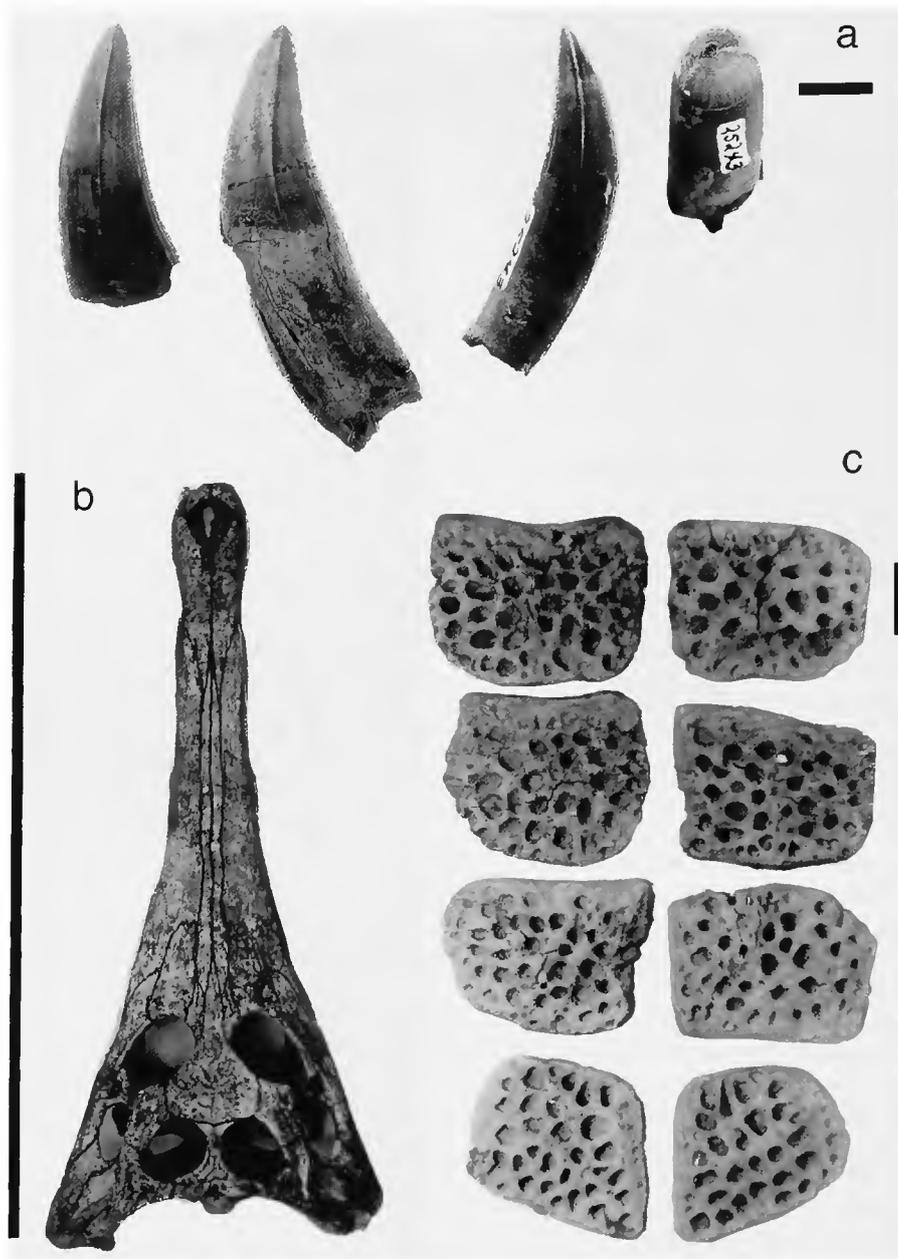


FIGURE 5.—Partial skeleton of *Thecachampsia antiqua* from the Calvert Formation of Virginia, USNM 25243: *a*, teeth (4) (scale bar=1 cm); *b*, skull, dorsal view (scale bar=1 m); *c*, dorsal dermal scutes (8), dorsal view (scale bar=3 cm).

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A New Pliocene Grebe from the Lee Creek Deposits

Robert W. Storer

ABSTRACT

A new species of *Podiceps* (Aves: Podicipedidae) is described from the early Pliocene Lee Creek marine deposits in North Carolina. The holotype is a femur. Referred material includes entire or partial femora (7), tarsometatarsi (5), coracoid (1), humeri (7), and ulna (1).

Introduction

Among the thousands of bird bones found in the Neogene marine deposits at Lee Creek Mine, near Aurora, Beaufort County, North Carolina, are 22 bones or parts of bones belonging to a small species of grebe. Different bones representing the same element of the skeleton vary considerably in overall size and in the positions of the muscle scars on them; however, comparable differences may be found within series of a single recent species (e.g., in a series of skeletons of the Horned Grebe, *Podiceps auritus* (Linnaeus)), and there is no reason to believe that they represent more than a single species. According to the characteristics listed by Murray (1967:278) for the appropriate elements, the Lee Creek Mine grebe is referable to the recent genus *Podiceps*. Comparisons with skeletons of living grebes in the University of Michigan Museum of Zoology (UMMZ) confirm this placement. The fossil form is about the size of *P. auritus* but differs in several respects that warrant describing it as a new species.

ACKNOWLEDGMENTS.—I am grateful to the curators of the National Museum of Natural History (which includes collections of the former United States National Museum (USNM)), Smithsonian Institution, and the University of Kansas Museum of Natural History (KUVF) for permission to borrow the fossils described herein, to L. Delle Cave (Museo Geologia e Paleontologia, Università di Firenze) for providing a cast of the holotype of *Podiceps pisanus* (Portis), and to the curators of the University of Michigan Museum of Paleontology (UMMP) for

permission to study comparative material. Clayton E. Ray, Storrs L. Olson, and T.J. Cohn offered valuable comments on the manuscript; Karna Steelquist and Jennifer Emry prepared the figure. Tom and Pat Burns, Raymond Douglas, Frank and Becky Hyne, Peter J. Harmatuk, and Clyde Swindell collected many of the Lee Creek Mine specimens used in this study.

Podiceps howardae, new species

FIGURE 1

HOLOTYPE.—Complete right femur, vertebrate paleontological collections of the National Museum of Natural History, Smithsonian Institution, USNM 252314.

PARATYPES.—Seven other femora (KUVF 21240, USNM 177918, 178151, 206413, 215453, 215649, 460785) probably represent this species. Their measurements are shown in Table 1.

TYPE LOCALITY.—Lee Creek Mine, near Aurora, Beaufort County, North Carolina (35°18'N, 76°48'W), collected in 1977 by Peter J. Harmatuk.

HORIZON AND AGE.—Yorktown Formation, early Pliocene.

ETYMOLOGY.—Named in honor of Hildegard Howard in recognition of her many important contributions to the study of fossil birds.

DIAGNOSIS.—*Podiceps howardae* was a small grebe, approximately the size of the recent *P. auritus*, and had similar leg proportions. It differed from the recent species in conformation of the known skeletal elements as noted below. It was smaller than the fossil species *Podiceps oligoceanus* (Shufeldt), *P. subparvus* (L. Miller and Bowman), *P. parvus* (Shufeldt), and *P. dixi* Brodkorb and was larger than *P. pisanus*, *P. discors* Murray, and *Pliolymbus baryosteus* Murray.

MEASUREMENTS OF HOLOTYPE.—Overall length 32.5 mm, width at head 8.6 mm, width at distal end 8.7 mm, least width of shaft 3.6 mm.

DESCRIPTION OF HOLOTYPE.—The specimen is similar in size to femora of *Podiceps auritus*, but it is considerably narrower across the distal end and has a much narrower external condyle. The latter is difficult to measure, but the differences are readily seen when the bones are viewed from the anterior or distal aspects.

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FIGURE 1.—Specimens of *Podiceps howardae*: a, holotype femur USNM 252314; b, paratype femur USNM 177918; c, tarsometatarsus KUVVP 21239; d, coracoid USNM 177927; e, humerus USNM 243764; f, distal portion of humerus USNM 215034. (Scale bar=17.5 mm.)

ADDITIONAL SPECIMENS.—A nearly complete tarsometatarsus (KUVVP 21239) is approximately the length of that of the largest available male of *Podiceps auritus* and, in general, it is similarly shaped. The foramen between the trochleae for digits three and four is longer in the fossil, and the trochlea for digit four is less offset and does not extend distally as far as that of digit three (in 27 out of 31 *P. auritus*, the trochlea for digit four is the longer). The proximal half of a tarsometatarsus (USNM 250773) is as wide as that of a large example of *P. auritus*, whereas the distal portion of another (USNM 210531) is noticeably more slender, differing to the same degree as tarsometatarsi of males and females of recent *P. auritus*. Two other fragmentary tarsometatarsi, a proximal portion (USNM 193175) and a distal portion (USNM 206326), are more similar in size to the smaller one. Unfortunately, the trochlea for digit four has been lost in each of the distal pieces.

The nearly complete tarsometatarsus measures 48.8 mm (if it were complete, it would measure approximately 50 mm.) Assuming that this bone and the largest femur (USNM 177918, paratype) belong to the same sex of the same species, the ratio of femoral length to tarsometatarsal length would be about 0.72. The comparable ratios of four specimens each of *P. auritus* and *P. griseigena* (Boddaert) are 0.73 and 0.76, respectively, whereas those of *Aechmophorus occidentalis* (Lawrence) and *Podilymbus podiceps* (Linnaeus) are 0.60 and 1.02, respective-

ly. Thus, the new bird presumably had similar hind-limb proportions to those of *P. auritus*.

The proximal two-thirds of a tarsometatarsus (USNM 250773) has a nearly complete articular portion and resembles that of a large male *P. auritus* in size and in width of the proximal end. This is in contrast with the relatively narrow distal end of the femur.

A nearly complete coracoid (USNM 177927) resembles coracoids of *P. auritus* in size and form but has a relatively deeper sternal facet. The bone is 30.5 mm long, 12.4 mm wide at the base, 3.0 mm in least width of shaft, and 4.0 mm in maximum depth of the external facet. In the shape of the head it differs markedly from that illustrated for the holotype of *Pliodytes lanquisti* Brodkorb (1953:954) of the Bone Valley Formation.

A nearly complete humerus (USNM 243764) measures 75.4 mm in length and thus is within the range of measurements of females of *P. auritus*.

Five partial humeri, consisting of a proximal portion (USNM 183430) and four distal portions (USNM 193242, 215034, 368557, 430524), also fall within the range of *P. auritus*. A fifth distal portion (USNM 407798) is somewhat larger and heavier (Table 2) than the extreme of *P. auritus* and probably is from a large male of *P. howardae*. The shaft of the humerus is somewhat wider and flatter in the fossil than it is in the living

form, but not enough to suggest an adaptation for using the wings under water.

The distal portion of an ulna (KUV 21292) is slightly heavier than it is in males of *P. auritus* and measures 5.8 mm in maximum width at the distal end, which is near the maximum for males of *P. auritus*.

COMPARISONS.—According to Brodkorb (1963b:227), the earliest fossil species of *Podiceps*, and the earliest record of the Podicipedidae, is *P. oligoceanus* from the early Miocene of Oregon. The holotype femur, as figured by Wetmore (1937:197), is considerably heavier and somewhat longer than that of *P. howardae*. Storrs Olson (in litt., 1986) reported that according to Jane Gray (in litt.) the provenance, and likewise the age, of the type of *P. oligoceanus* are in doubt. He added that "it is a typical modern grebe and could as well be Pleistocene as early Miocene."

Podiceps pisanus, from the middle Pliocene of Italy, is known from the distal portion of a humerus. According to Regalia (1902:233–234, pl. 27[1]: figs. 21, 22), *P. pisanus* was somewhat larger than *P. auritus*, and the holotype is characterized by the shape of the scar for the attachment of *M. brachialis anticus* near the distal end of the bone. A cast of the holotype was compared with four humeri of *P. howardae* (USNM 193242, 215034, 368557, 407798) and with a series of skeletons of recent *P. auritus* in the UMMZ (Table 2). In size it is at

or near the lower limits of females of *P. auritus* (from this, it appears that Regalia's comparisons were made with the smaller species, *P. nigricollis* Brehm, which for many years was called "auritus"). In its shorter, wider, more transverse scar for the attachment of *M. brachialis anticus*, *P. pisanus* differs from *P. auritus* (and also from *P. howardae*) as described by Regalia.

Podiceps subparvus, described by Miller and Bowman (1958:6–7) from the middle Pliocene of San Diego, California, was somewhat larger than *P. howardae* and was wider across the distal end of the femur.

Podiceps discors, described by Murray (1967:279–282) from the late Pliocene Rexroad Formation of Kansas, appears to have been a slightly smaller species than *P. howardae*. The type, a well-preserved tarsometatarsus (UMMP 52465), is smaller and more slender than the tarsometatarsi referred to *P. howardae*. The latter specimens also differ from *P. discors* and resemble *P. auritus* and *P. nigricollis* in having the support of the internal condyle more flared internally.

Murray (1967:281–282) referred several specimens from the Hagerman local fauna of Idaho to *P. discors*. One of these, a femur (UMMP 52423), is within the range of *P. howardae* and is proportionally too narrow at the distal end for *P. auritus*. It differs from the holotype of *P. howardae* in having facets for the insertion of *M. obturator internus* and *M. ischiofemoralis*

TABLE 1.—Measurements (in mm) of femora of *Podiceps howardae* and *P. auritus*. Data for *P. auritus* are the ranges of 12 individuals, six of each sex, in the collection of the UMMZ.

Specimen	Total length	Width at head	Least width of shaft	Width at distal end	Width at distal end/total length
<i>Podiceps howardae</i>					
Holotype					
USNM 252314	32.5	8.6	3.6	8.7	0.27
Paratypes					
USNM 177918	35.8	9.5±	3.5	9.5±	0.27±
USNM 178151	—	9.9	3.8	—	—
USNM 206413	—	10.0	4.0	—	—
USNM 215453	32.5	8.7±	3.6	—	—
USNM 215649	35.0	9.0	3.3	9.0±	0.26±
USNM 460785	32.4	9.9	3.8	9.3	0.29
KUV 21240	—	—	3.7	—	—
<i>Podiceps auritus</i>	31.3–35.7	8.7–10.3	3.4–3.9	9.3–10.9	0.27–0.31

TABLE 2.—Measurements (in mm) of the distal portions of humeri of *Podiceps auritus* (UMMZ), *P. howardae*, and *P. pisanus* (UMMP). Data for *P. auritus* are range and mean standard deviation for 10 individuals of each sex.

Specimen	Width at distal end	Least width of shaft	Height of shaft
<i>Podiceps auritus</i>	7.2–8.1 7.69±0.26	3.3–3.95 3.62±0.19	2.75–3.5 3.08±0.16
<i>Podiceps howardae</i>			
USNM 193242	7.5	4.0	3.4
USNM 215034	7.5	3.8	3.15
USNM 368557	7.9	4.1	3.35
USNM 407798	8.3	4.4	3.75
USNM 243764	7.3	4.0	3.25
USNM 430524	8.0	—	—
<i>Podiceps pisanus</i> (cast of holotype)	7.2	3.75	2.95

lying more on the lateral plane of the bone than in *P. howardae*, *P. auritus*, or *P. nigricollis*, and in having a larger, deeper depression for the insertion of *M. obturator externus*. Two of the three coracoids assigned to *P. discors* by Murray (UMMP 52277, 49590) have considerably shallower external sternal facets than in *P. howardae*.

Pliolymbus baryosteus, also described by Murray (1967:278–279) from late Pliocene deposits in Kansas, was placed in a new genus on the basis of characters in the sternum, an element that so far is unknown in *Podiceps howardae*. The other skeletal elements of *Pliolymbus* are much smaller than the corresponding ones of *P. howardae*.

The holotype of *Podiceps parvus* has been discussed and figured by Wetmore (1937:195–197, 200–201) and reviewed by Miller and Bowman (1958:4–5). This was a larger species than *P. howardae* and has been stated to range from the early middle Pliocene to the middle Pleistocene.

Podiceps dixi, from middle Pleistocene beds in Florida, is known from the proximal part of the carpometacarpus, an element as yet unknown for *P. howardae*. Measurements given in the original description (Brodkorb, 1963a:54) indicate that it was a larger bird than *P. auritus*, and hence, than *P. howardae*. Steadman (1984:49), after reviewing the literature on fossil grebes, pointed out the “unsatisfactory nature” of this species and preferred to regard it “as a synonym of *P. auritus*.”

Podiceps gadowi, described from Quaternary deposits on Mauritius (Hachisuka, 1953:124–125), is known from a single right ulna (205k) in the Cambridge University Museum of Zoology. This was examined by S.L. Olson (pers. comm.) in August 1985, who found that it had been annotated by Graham Cowles of the British Museum (Natural History) (now The Natural History Museum, London) as being from a whimbrel (*Numenius phaeopus*, Scolopacidae). According to Olson, the specimen measures 81.8 mm in length and is definitely not a grebe.

The fossil *Thiornis sociata* Navás from the middle Miocene of Spain has been recognized as a grebe and was redescribed by Olson (1995:131–140), who placed it tentatively in the genus *Podiceps*, although “in its general morphology, particularly the pelvis and hind limb, *Thiornis sociata* is decidedly more similar to *Tachybaptus* than to modern species of *Podiceps*.” Because comparisons with skeletons of recent grebes show that *P. howardae* clearly belongs in the genus *Podiceps*, comparison with *Thiornis* was not attempted.

REMARKS.—*Podiceps howardae* was a small grebe; it averaged slightly larger in size than the recent Horned Grebe, *Podiceps auritus*, but it was similar in proportions. The known specimens all come from offshore marine deposits; however, because the floating nests of all living grebes are subject to damage or loss by wave action and fluctuations in water level,

these birds do not nest near large expanses of open water or in tidal situations. Assuming that *P. howardae* had similar nesting requirements, it probably nested inland on fresh water and wintered on salt water. Thus, specimens of this Pliocene species may well be expected in inland localities. Such a pattern of distribution is already known for the fossil species *Podiceps parvus* (Miller and Bowman, 1958:5).

In spite of the similarities in size and proportions between *P. howardae* and *P. auritus*, whether the former was ancestral to the latter is unclear. Fjeldså (1983) has provided convincing evidence for character displacement in the bill length of grebes, and character displacement also is evident in the overall size of the Red-necked Grebe (*Podiceps grisegena*), which is considerably smaller in Europe, where it is sympatric with the larger Great Crested Grebe (*P. cristatus* (Linnaeus)), than it is in North America, where no larger congener occurs (Palmer, 1962:63–87). Even greater geographic variation in size is found in the White-tufted Grebe (*Rollandia rolland* (Quoy and Gaimard)), in which tarsometatarsal length of study skins varies from 51.7 mm in a male of the race on the Falkland Islands (Islas Malvinas) to 31.0 mm in a small female from northern Argentina (Storer, unpublished data). Smaller, but significant, differences in size in this species occur between lakes Junín and Titicaca, where *R. rolland* is found with different assemblages of grebes. There is no reason to doubt that geographic variation occurred in the past as it does today, and this should be taken into consideration in any analysis of fossils (Storer, 1992:419–422).

It is thus evident that size in grebes is not necessarily an indication of close relationships. It is therefore to be expected that as faunas change with the disappearance of some forms and the appearance of others, shifts in the size of at least some of the species can be expected. This being the case, other characteristics, especially the conformation of bones, should be more useful in assessing relationships among closely related species of grebes.

Differences in proportions can arise from more than one source. In birds using similar types of locomotion, wings must increase more rapidly than overall size in order for a bird to maintain the ability to fly. This explains most, if not all, of the differences in the ratios of humeral length to tarsometatarsal length mentioned above. Other proportional differences, such as those in the toes, are more likely to reflect differences in the way the foot is used and are presumably more significant in phylogenetic studies.

Compared with other pre-Pleistocene grebes, *Podiceps howardae* is represented by a fair number of specimens. Until other species become known from more adequate material, little can be shown about the relationships among them and recent species.

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Miocene and Pliocene Birds from the Lee Creek Mine, North Carolina

Storrs L. Olson and Pamela C. Rasmussen

ABSTRACT

An account is given of a collection of over 10,000 fossils representing at least 112 species of birds from middle Miocene (Pungo River Formation) and early Pliocene (Yorktown Formation) deposits exposed during phosphate mining in the Lee Creek Mine, near Aurora, Beaufort County, North Carolina.

Relatively few of these species are derived from the Pungo River Formation, as determined partly by similarity to contemporaneous species from the Calvert Formation of Maryland and Virginia. The tremendous avifauna now known from the Yorktown Formation consists of nearly 100 species, including three species of loons, two grebes, five albatrosses, at least 16 shearwaters and petrels, one pelican, two pseudodontorns (horizon less certain), three gannets, two cormorants, at least nine auks and puffins (probably 11 or more), one skua, three jaegers, five gulls, two terns, and 20 species of ducks, geese, and swans. Incidental land and shore birds, a few of which likely originated in the Pungo River Formation, are represented by 29 species, including three cranes, one rail, two oystercatchers, one plover, four scolopacids, one flamingo, one ibis, one heron, three storks, one condor, five accipitrids, one osprey, one chachalaca, one phasianid, one turkey, one pigeon, and one crow. Three new species are described, one in each of the genera *Gavia*, *Phoebastria*, and *Calonectris*. In numbers of individuals, the avifauna is dominated by a radiation of auks of the genus *Alca*. The avifauna of the Yorktown Formation indicates conditions of much greater marine productivity, with accompanying greater diversity of marine birds, than existed in the middle Miocene. Loss of diversity since the early Pliocene involved extinction of most of the radiation of *Alca*, two species of albatrosses, two species of gannets (*Morus*), a pelican, and possibly a cormorant. Diversity in the western North Atlantic Ocean also was reduced by the withdrawal of three species of albatrosses, numerous petrels, and a puffin (*Fratercula*) to the Pacific Ocean. Other species, mostly of land and shore birds, appear to have withdrawn from North America but have persisted in Europe and Asia. Apart from the relatively few extinctions and several range retractions, the avifauna in the early Pliocene of North Carolina was very modern in aspect, and many modern species lineages of birds may already have been in existence at least five million years ago.

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Introduction

This paper originated as a survey of an extensive fossil avifauna from Miocene and Pliocene marine deposits obtained in the late 1960s and early 1970s at what was then called the Texasgulf Lee Creek Phosphate Mine in North Carolina (now owned by the Potash Corporation of Saskatchewan). Bird fossils from this site were originally turned over to Alexander Wetmore for study, and he was to have prepared a paper on these specimens for inclusion in a projected volume on the geology and paleontology of the mine. Because of Wetmore's commitment to his magnum opus on the birds of Panama, Olson later volunteered to take on the bulk of the work associated with preparing a manuscript on the Lee Creek Mine birds. Olson and Wetmore (Figure 1) produced a manuscript entitled "Preliminary Survey of an Extensive Miocene and Pliocene Marine Avifauna from Lee Creek, North Carolina," which was submitted to the volume editor on 28 September 1973 and subsequently was optimistically cited as "in press" (Olson, 1975, 1977; Alvarez and Olson, 1978).

Years went by and the single volume that was originally envisioned was expanded to two, then three, and ultimately four volumes. The first of these appeared a decade after the original manuscript on birds had been submitted (Ray, 1983) and was followed by a second volume four years later (Ray, 1987). Meanwhile, the quantity of avian fossils from Lee Creek Mine increased. At the same time, Wetmore's health declined, and he was no longer able to participate in the several attempts Olson made to keep the Lee Creek manuscript up to date. By the time Wetmore died on 7 December 1978, the manuscript bore little resemblance to the first draft to which he had contributed. Some of the ideas first developed by Olson in the early drafts appeared subsequently in an overall summary of the fossil record of birds (Olson, 1985d).

Because so many new fossils were acquired after Olson's last lone revision of the manuscript, Jonathan Becker was enlisted to identify new specimens and worked to produce an updated version of the manuscript. This, too, eventually became almost completely obsolete, both apart from, and because of,



FIGURE 1.—Olson (left) and Alexander Wetmore (right) in the early 1970s, examining the available fossil bird bones from Lee Creek Mine. Since then, the number of specimens has increased by probably more than an order of magnitude.

acquisition of new material. By this time Becker had changed careers. Olson and Rasmussen began collaboration on a revision of the Lee Creek Mine avifaunas in 1991, greatly expanding the material included and gaining entirely new insights into systematics, biogeography, and evolution. The present manuscript thus bears little resemblance to its predecessors. We must therefore acknowledge with gratitude the contributions of our previous collaborators, Wetmore and Becker, to the early stages of study of this massive avifauna, while relieving them of any responsibility for our conclusions.

To our knowledge, the Lee Creek Mine collection constitutes what is probably the largest Tertiary marine avifauna now known, with at least 112 species of birds, most being pelagic forms, represented by over 10,000 specimens, not all of which,

however, have been included in the present study. The fossils from Lee Creek Mine are from two distinct faunas, one of middle Miocene age (~14 Ma) derived from the Pungo River Formation, and a much larger early Pliocene (3.7–4.8 Ma) avifauna derived from the Yorktown Formation. Because of the nature of the mining operations, it is often uncertain which horizon produced a given fossil, and this mixing contributes to the complexity of analyzing certain groups.

The Pungo River Formation is in part equivalent to the Calvert Formation of the Chesapeake Group of Maryland and Virginia. The avifauna of the Calvert Formation is now reasonably well known from fossils, many still undescribed, found in precise stratigraphic contexts. Thus, the horizon of certain Lee Creek Mine fossils may be inferred from their identity with

species known from the Calvert deposits. We also have a few additional undescribed specimens of fossil birds from the Choptank, St. Marys, and Eastover formations in Maryland and Virginia that we propose to study by systematic groups in conjunction with fossils from the Calvert Formation before attempting to synthesize the East Coast marine avifaunas that preceded those of the Pliocene.

For this reason, we have not dwelt at length on the avifauna of the Pungo River Formation in the present report, the species of which will be treated in more detail later in conjunction with those of the Calvert Formation. Instead, we emphasize herein the much more extensive and diverse avifauna of the Yorktown Formation, fossils of which are extremely rare in surface exposures. This very important marine avifauna would be all but unknown were it not for mining operations.

The present study is preliminary, and no one is more aware of its shortcomings than the authors. We have intended this mainly as a faunal survey, but of necessity we must deal with many issues of systematics as well. Needless to say, a great deal of revisionary work is still urgently needed, particularly among such difficult groups as the shearwaters (Procellariidae). By making these avifaunas better known, we hope to stimulate taxonomists to undertake revisions of various taxa, and we invite them to include the Lee Creek Mine material, especially that from the Yorktown Formation, in their studies.

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We owe our greatest debt to the many collectors whose sharp eyes spied thousands of small bird bones on the mine spoil piles and whose generosity in donating the specimens to the Smithsonian has permitted this study. In this connection the massive contributions of Peter J. Harmatuk and Frank and Becky Hyne must be singled out. The following additional collectors also donated specimens: Calvin Allison, David R. Amos, Elizabeth and Wallace L. Ashby, Donnie Bailey, Aura L. and J. Wayne Baker, Peter Ballmann, William C. Bean, N. Bikan, David and Paula Bohaska, Captain and Mrs. Michael Boroff, John Boyd, Eldon Branch, Pat and Tom Burns, Kerry Button, Ken Carpenter, John H. Carson, Richard Carter, Gerard R. Case, Ralph Chamness, Richard Chandler, Mike Cohen, Phillip Cox, Larry Decina, Daryl Domning, Raymond C. Douglass, Duke University Marine Lab (through Dan Rittschof), Ralph Eshelman, John Everette, Alan Feduccia, James Firebaugh, Mark Florence, George C. Fonger, Frank Garcia, Steve Gotte, Michael D. Gottfried, Fred Grady, Richard W. Grier, Jr., Robert W. Grier, Todd Grimsley, Leslie Hale, Christopher J. Harmatuk, Eugene F. Hartstein, Barbara Harvey, Bill Heim, Anne Henderson, Wayne Henschel, Linda Heritage, Carolynne and Scott Hertenstein, Pam Hester, Mr. and Mrs. L. Hodges, Candace Holiday, Sid Hostetter, Jane

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SYNOPSIS OF THE GEOLOGY OF THE LEE CREEK MINE

The Lee Creek fossil locality is an open-pit mining operation for obtaining commercial quantities of phosphate from the middle Miocene marine sediments of the Pungo River Formation. The mine is located on the south bank of the Pamlico River, north of the town of Aurora, Beaufort County, in central eastern North Carolina (35°23'22"N, 76°47'06"W). Mining was started at what was then the debouchment of Lee Creek into the Pamlico River (McLellan, 1983), the lower reaches of the lesser stream having since been obliterated by the mine to which it gave its name (see Ward and Blackwelder, 1987, figs. 1, 2).

This sacrifice of a bit of coastal topography has been more than compensated by the tremendous increase in knowledge of geology and paleontology that was made possible by the mining operations at Lee Creek. There are no naturally occurring outcrops of the Pungo River Formation anywhere, so the only fossil birds known from it have come from Lee Creek Mine. Practically the same may be said of the overlying Yorktown Formation, surface outcrops of which are very limited and which have yielded at most a handful of bird bones. This is in marked contrast with the thousands upon thousands of bird fossils of Yorktown age from Lee Creek Mine, an assemblage that constitutes the most extensive marine paleoavifauna in the world in terms of both species and numbers of specimens. Without these fossils we would scarcely have an inkling of the dramatic turnover that took place in the pelagic avifaunas of the North Atlantic Ocean between the moderately well-known

avifauna of the Calvert Formation, some 14 million years ago, and the present.

Mainly for the benefit of those who do not have access to the other volumes in this series, we have included herein a very brief synopsis of the geology of Lee Creek Mine, which, unless otherwise indicated, has been extracted from the lucid and informative papers of Gibson (1983a, 1983b).

Neogene sediments at Lee Creek Mine accumulated in a negative feature, the Albemarle embayment, flanked by two east-west trending positive geological structures, the Norfolk arch, running across southern Virginia, and the New Bern arch, running across central eastern North Carolina, just south of Pamlico Sound. Although the sediment column at the mine is capped unconformably by late Pliocene and Pleistocene sediments (see also Ward and Blackwelder, 1987), we are unaware of any fossil birds from these strata. If these deposits ever were exposed on the surface of spoil piles at the mine, they likely would not attract much attention from the amateur collectors responsible for collecting the majority of the fossil birds at the mine, who search mainly in sediments in which large sharks' teeth are likely to be found.

Thus, attention is focused herein on the other strata exposed at the mine—those of the Pungo River Formation and the overlying Yorktown Formation. The Pungo River Formation was laid down during an extensive marine transgression responsible for the mainly contemporaneous Calvert Formation to the north, around Chesapeake Bay, and the Kirkwood Formation in New Jersey (Figure 2). Commercially profitable phosphate deposits occur in the Pungo River Formation, so the mine, of course, does not extend below this level, although it is known from well cores that the formation rests unconformably on Paleogene sediments, as does the Calvert Formation. The Pungo River Formation is more than 122 m thick at its maximum, but at Aurora, near Lee Creek Mine, it is about 28 m thick. Sediments at the mine are characterized by the absence of terrigenous clastics and include diatomaceous clay, carbonates, and phosphatic sands. The lower part of the Pungo River Formation (Belhaven Member) formed on the middle to outer shelf in water depths of 100 to 200 m, whereas the upper part (Bonnerton Member) formed on the inner to middle shelf in water depths of 150 m to less than 70 m. The top of the formation is an erosional surface.

In the middle to late Miocene, three lesser marine transgressions resulted in the Choptank, St. Marys, and Eastover formations, but these all lie to the north and are not represented at Lee Creek Mine. The next great transgression gave rise to the Yorktown Formation and its lateral equivalents (the Cohansy Sand and the Duplin Formation), extending from New Jersey to South Carolina (Figure 3). The depth and composition of the sediments varies greatly geographically due to environmental differences. At Lee Creek, the 15 m thick Yorktown Formation rests unconformably on the Pungo River Formation. Its basal unit consists of muddy, gravelly phosphatic sand containing reworked phosphate nodules from the underlying Pungo River.

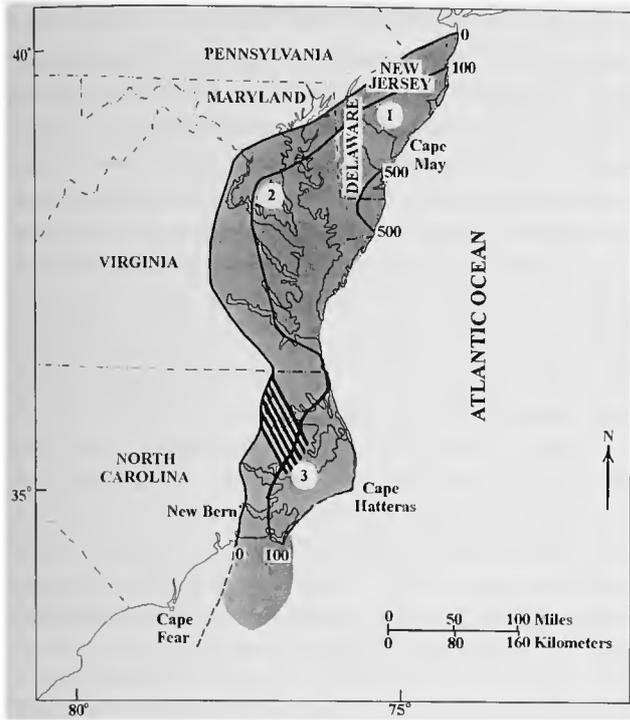


FIGURE 2.—Isopachous map of middle Miocene strata showing the extent of the Calvert/Pungo River embayment (shaded). 1=Kirkwood Formation, 2=Calvert Formation, 3=Pungo River Formation; contours in feet. Based on Gibson (1983a:39, fig. 3).

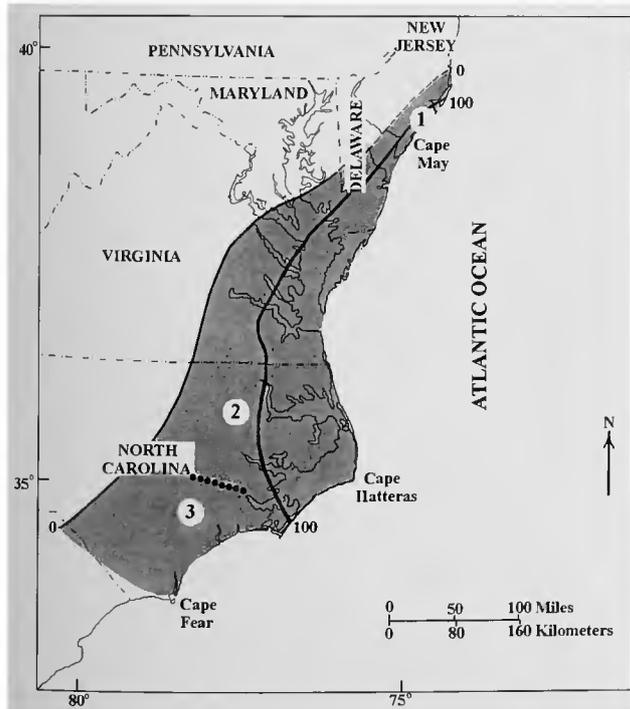


FIGURE 3.—Isopachous map of early Pliocene strata showing the extent of the embayment (shaded) of the Yorktown Formation and equivalent deposits. 1=Cohansey Sand, 2=Yorktown Formation, 3=Duplin Formation; contours in feet. Based on Gibson (1983a:70, fig. 32).

This is succeeded by several fossiliferous units of muddy sand and sandy mud (see section in Snyder et al., 1983, fig. 2). The top of the formation is an erosional unconformity.

There are lithic and faunal changes within the Yorktown Formation, as well as scour surfaces, although it is not known whether these formed below water or subaerially. The Yorktown Formation in the Albemarle embayment, which contains Lee Creek Mine, contains older strata deposited in deeper water than was in the Salisbury embayment to the north. The basal unit at Lee Creek Mine is thought to have formed under 80 to 100 m of water. The majority of vertebrate fossils from the mine are considered to have been derived from this basal part of the Yorktown Formation. This accords very well with the highly pelagic nature of almost the entire avifauna and the great scarcity of shore and land birds in the collections, indicating deposition on the high seas in relatively deep water.

Foraminifera could be obtained only from the upper 3.7 m of the Pungo River Formation. These correlated with foraminiferal zones N8 and N9, indicating a late early and early middle Miocene age, equivalent to the European Langhian stage, the middle of which is about 14 Ma, the same age as the upper part of the Calvert Formation. Foraminifera from the basal part of the Yorktown Formation indicate an age of N19/20, which is early Pliocene, falling within the European Zancian stage. The Yorktown Formation at Lee Creek Mine is considered to range in age from 3.7 to 4.8 Ma (Hazel, 1983:97). The majority of bird fossils from Lee Creek Mine come from the basal part of the Yorktown Formation, hence their age would be closer to 4.8 Ma.

PALEOENVIRONMENT

Marine conditions at Lee Creek during the period of deposition of the Pungo River and Yorktown formations have been ably summarized by Purdy et al. (this volume), and the avifauna strongly supports their reconstructions. Fossils were deposited well offshore in water of about 100 m depth at the southwestern end of the Aurora Embayment, a deep depression that allowed cold waters to upwell 100 km west of the margin of the continental shelf (Popenoe, 1985). Bottom temperatures in both time periods were cool temperate (Gibson, 1967).

The ichthyofauna of the Pungo River Formation indicates a warm but not tropical environment with few pelagic elements, suggesting an absence of cold upwelling. Fishes of the Yorktown Formation, on the other hand, are a mixture of tropical, warm-temperate, and cool-temperate taxa, with abundant tuna and other pelagic fishes, indicating a sharp temperature gradient in the region with nutrient-rich cold upwelling. In the vicinity of Lee Creek Mine, this created what Purdy et al. (p. 188, this volume) call, rather understatedly, a "marine vertebrate, high-use feeding area," in which tuna drove prey fish to the surface where they were fed upon by abundant cetaceans, sea-birds, and sea turtles in company with an extremely abundant and diverse shark fauna.

This must have been one of the most spectacular feeding assemblages of marine vertebrates the world has ever known. To put it in perspective, the total number of species of birds known from Lee Creek Mine is greater than the total number of species of fishes collected there. The figure is perhaps somewhat inflated for bird species by the relatively high proportion of very rare incidental shore and land birds, but nevertheless it is an extremely diverse avifauna that in terms of numbers of individuals is overwhelmingly dominated by pelagic, piscivorous species, particularly auks, along with abundant shearwaters, albatrosses, gannets, and loons.

TAPHONOMY

Although we have not attempted a taphonomic analysis, we discuss herein some impressions that may help to explain why there were so many fossils of birds in the area of Yorktown-age deposits that have been excavated at Lee Creek Mine. When the size of the mine is taken into consideration, however, the concentration of bird bones seems less impressive than that conveyed by the numbers of museum drawers filled with fossils. As of January 1998, the area excavated at Lee Creek Mine was 2408 hectares (5949 acres), or 24.1 km² (9.3 mi²). Using a conservative figure of 10,000 avian fossils collected so far from the mine, this averages out to only 0.7 bird specimens per hectare.

Very few fossil birds have been found in the Yorktown Formation as associated partial skeletons. These have been found in nodules that apparently come from higher levels in the stratum, as opposed to the basal part of the formation, from which most of the bird bones are believed to have been derived. In the basal part of the Yorktown Formation, we suspect that much of the accumulation of bird bone ultimately came from regurgita of predators.

The Yorktown seas off present-day North Carolina must have supported one of the greatest levels of marine productivity in the history of the earth. As a consequence, these waters seethed with a diversity of sharks, seals, and carnivorous cetaceans that has no parallel on the planet today. One may envision vast schools of fish, among which a multitude of auks, loons, and diving shearwaters swam in pursuit of their prey. These invaders of a piscine world, despite being well adapted to their environment, would have been highly susceptible to predation by larger carnivores. A large shark wreaking havoc on a school of hake would doubtless much prefer a large, fat auk, with a beakful of fish, to any smaller prey. Not only diving birds but any others that may occasionally venture below the surface, such as albatrosses and gulls, also would have been susceptible. Sharks, particularly tiger sharks (*Galeocerdo*), which were abundant at Lee Creek, will at times even take birds from the surface (e.g., Moseley, 1892:49; Gudger, 1949; Dodrill and Gilmore, 1978).

Most bird fossils from Lee Creek Mine are found singly and are typically broken. For example, at one point in our study

we had examined over 2700 alcid humeri, of which only 83 specimens (3%) were complete or nearly so. The most abundant bird fossils at Lee Creek Mine are the humeri, coracoids, and ulnae of the larger auks, particularly *Alca antiqua* (Marsh). These are among the densest and heaviest bones of any of the birds in the fauna and thus would have been the least subject to complete digestion. Furthermore, many appear etched as well as being broken. Obvious tooth marks of either predators or smaller scavengers are preserved on some (Figure 4). Sharks cannot pass solid objects such as these through their spiral intestines, so "indigestible bodies must come out where they went in—through the mouth" (Gudger, 1949:46). Thus, much of the accumulation of bird bones at Lee Creek Mine may be the result of shark regurgita, which would introduce considerable bias into the fossil record, not only in the relative abundance of species represented, but in the proportion of different elements of the body as well, with bones of the wing and pectoral girdle predominating over hindlimb elements, and the latter over cranial elements.



FIGURE 4.—Parallel scratches on a tarsometatarsus of an albatross (*Phoebastria anglica*, USNM 430533), presumably made by the teeth of a predator or scavenger. (Magnification \times 4.3.)

THE SPECIES QUESTION

In dealing with an avifauna such as that of the Yorktown Formation, we have been forced to deal with difficult questions, both practical and philosophical, regarding the limits of species, particularly through time, that are inescapable in a work of this nature. As might be expected, our own views evolved during the course of our investigations, and so some discussion of the approach used herein is warranted.

During the third quarter of the twentieth century, avian paleontology in North America developed under the influence of Pierce Brodkorb, who presumed that most species of birds did not cross epoch boundaries (Brodkorb, 1960). On the face of it, there is little reason why this should be so, and it is counterintuitive to presume that speciation occurred simultaneously in all lineages at the transition from the Pliocene to the Pleistocene, for example. Such may have been the wish of alpha-level systematists for whom the description of new species was an end in itself, but this is not helpful in documenting and comprehending evolution. There are also workers, whose research is more faunally oriented, who subscribe to nomenclatural recognition of any morphological variation that is temporally removed from modern taxa, advocating that "in the case of a smallest constant morphological difference a new systematic name is reasonable" (Jánossy, 1987:190).

Another matter that compounds the difficulties of referring to species in a fauna such as that at Lee Creek Mine is the cladistic viewpoint that ancestors cannot or should not be identified in the fossil record (e.g., Englemann and Wiley, 1977; Eldredge and Cracraft, 1980; Norell, 1996), although this has been vigorously contested by others (e.g., Wagner, 1995, 1996; Foote, 1996). The proposition that, within a relatively small and circumscribed basin such as the North Atlantic, none of the multitude of species that existed four to five million years ago in Yorktown times was ancestral to any extant species is hardly tenable. The main problem arises when a given lineage may have split into two species. How, then, does one recognize (and deal nomenclaturally with) the common ancestor of the two? The Pliocene loons at Lee Creek Mine may reflect just such a problem, with *Gavia concinna* Wetmore possibly being ancestral to the living Pacific Loon, *G. pacifica* (Lawrence), and the Arctic Loon, *G. arctica* (Linnaeus), and with a new large species (described below) conceivably being ancestral to the modern Common Loon, *G. immer* (Brünnich), and the Yellow-billed Loon, *G. adamsii* (Gray).

This is rather a different matter from saying that the harlequin duck (*Histrionicus*) at Lee Creek Mine, although differing somewhat from the single living species, is still probably on a direct line with that species and need not be named as a distinct taxon. Compounding the difficulties of communication are the semantic problems that arise from the fact that the same terminology—species—is applied to two completely different phenomena. As Haffer (1995) has discussed at length, extant species, regardless of which concept one employs to de-

fine them, are geographical entities that occupy areas with more or less defined borders that may or may not overlap with congeneric species. In contrast, temporal "species" are arbitrary, morphologically defined units of a continuous lineage through time. Haffer rightly concluded that Linnean species nomenclature should not be used for temporal entities, but no consensus on a useful alternative terminology has yet emerged.

Mammalian paleontologists have had much longer to contend with such issues, whereas the fossil record in birds has only recently become sufficiently extensive, particularly among seabirds, to provide investigators with any meaningful possibility of detecting changes within a lineage. Differentiating between extant lineages and those that are extinct, with no modern descendants, should be one of the most important activities of paleontologists dealing with late Cenozoic faunas. We can hardly have any sensible discussion of faunal changes and "turnover" without having at least some grasp of whether the "disappearance" of individual units is due to extinction or to the evolution of new morphologies.

In the present analysis, when the material from the Yorktown Formation is reasonably extensive and we can still find little or no differences from existing species, we have simply referred the fossils directly to living taxa, as, for example, among some of the albatrosses.

We attempted to identify extinct versus extant lineages, but there are various sources of potential error in this undertaking. Not the least of these is that different groups of birds have changed morphologically (but not necessarily speciated) at very different rates. Shearwaters and albatrosses (Procellariiformes), for example, have evolved very slowly. Some procellariiform lineages appear to date back at least to the late Oligocene with little change in morphology. *Puffinus conradi* Marsh from the Calvert Formation was very similar to the living Greater Shearwater, *P. gravis* (O'Reilly), so it would be very difficult to separate the Yorktown-age representative of this lineage from earlier and later manifestations.

On the other hand, loons (Gaviidae) evolved very rapidly in the Neogene. Since the middle Miocene, they have increased greatly not only in size but also in degree of specialization of both the leg and wing elements for underwater propulsion. Because there are three species of loons in the Yorktown Formation, it is tempting to suggest that these are the Pliocene representatives of the three major extant lineages, which may well be the case. Two of the three modern lineages of loons now consist of pairs of sibling species, of unknown times of divergence. Two of the early Pliocene forms therefore may represent the common ancestors of the sibling-species pairs rather than direct ancestors of any of the sibling species. Through the collection of more fossils from different time intervals and geographic areas, we can hope to resolve this problem satisfactorily.

Sometimes the problem is too many fossils. We can easily recognize a flightless early Pliocene relative of the modern

Great Auk, *Pinguinus impennis* (Linnaeus), lineage in the Yorktown deposits. In addition to the rare but unmistakable *Pinguinus* bones, however, the fauna contains a vast array of fragmentary and usually unassociated fossils of closely related species of the genus *Alca* that constitutes a continuum varying so much in size that we calculate it to have encompassed four species at minimum. Nevertheless, there is only one modern descendent of this assemblage, the Razorbill (*Alca torda* Linnaeus). Although the ancestor of *Alca torda* clearly is represented among all these broken bones, assigning individual fragmentary limb bones to this lineage is not always possible.

The other side of the coin, too few fossils, is the situation most frequently encountered. Many late Neogene species of birds have been founded on material too inadequate even to distinguish extant from truly extinct lineages.

We have designated lineages that are apparently ancestral to modern species with the prefix "aff." (Latin *affinis*, related to, neighboring), even if minor differences in structure can be discerned (for example, in *Histrionicus*). We have listed as synonyms previously named fossil taxa that evidently are continuous with modern lineages. We have used the designation "cf." (Latin *confer*, compare) to denote only a general morphological similarity, not necessarily a close relationship.

Even the ambiguous designation "aff." may be too precise when confronted with taxa such as the dabbling ducks of the genus *Anas*. Among modern species of this genus it is very difficult or impossible to identify fragmentary material to species because many species do not differ postcranially other than in size, and among species there may be considerable variation and overlap. In such osteologically difficult groups, we used the designation "magn." (from Latin, *magnitudo*) to indicate the approximate size range of the fossils in comparison with modern species, without implying possible relationship.

The waterfowl, i.e., ducks and geese (Anatidae), provide particularly illustrative examples of some of the problems we have attempted to address. The most abundantly represented duck at Lee Creek Mine turns out, unexpectedly, to be a harlequin duck, *Histrionicus*, the material of which is sufficient to show that the Yorktown bird was very similar to the extant species, although the wing was slightly less specialized. By previous standards, this would have been a nameable species, yet only the quality and abundance of the material would allow it to be distinguished from the modern species, and then only in some of the elements. Although it is interesting to find that the wing has changed slightly in this lineage in the past few million years, does this mean the Pliocene bird is a new species? When we found that this apparently new species was bracketed by names given to extremely scanty, generically misidentified fossils that were both older and younger than the Yorktown Formation, it reinforced our opinion that the use of Linnean nomenclature for such fossils that appear to belong to existing lineages is untenable. If we have been overly enthusiastic in our species attributions, we hope nevertheless to have fostered a healthy new trend in viewing late Cenozoic avifaunas.

METHODS

In a few instances, bird fossils were found on spoil piles of known stratigraphic position. In most cases, however, specimens were brought in as mixed lots gleaned from the spoil piles with no stratigraphic information. Some differences in preservation are apparent; bones from the Pungo River Formation are usually better preserved, black in color, less water-worn, and have a more polished appearance than do those from the Yorktown Formation, but such criteria cannot always be relied on. The stratigraphic position of a particular fossil can often be determined by examination of the adherent matrix and its contained microfauna. Thomas G. Gibson examined the microfossils in matrix samples from 43 fossil bird bones selected at random from the early collections from Lee Creek Mine. His determinations indicate that all of these probably came from the basal part of the Yorktown Formation.

The great quantity of fossil material, in particular that representing the Alcidae, and the unresolved systematics of some taxa make it impractical to list all specimens thus far identified. We have, however, listed by catalog number referred material for all but the most common species; for the latter we list specimens that are unusually complete or diagnostic or that belong to uncommonly represented skeletal elements. Unless designated by some other museum acronym (see "Acknowledgments"), all listed material is in the Vertebrate Paleontology collections of the National Museum of Natural History (NMNH, which includes collections of the former United States National Museum (USNM)), Smithsonian Institution.

To attempt to determine whether specimens from Lee Creek Mine were from the Pungo River Formation or the Yorktown Formation, we made comparisons with fossil birds from the Calvert Formation in Maryland and from the Upper Bone Valley Formation in Florida. Most of the Maryland specimens also are housed in the Vertebrate Paleontology collections of the National Museum of Natural History; most of those from Bone Valley are housed in the Florida Museum of Natural History (UF), which now includes the collection of Pierce Brodkorb (UF PB). Modern comparative material was mostly from the collections of the Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, and also have the USNM acronym, although these collections have a separate numbering system.

Measurements of bones were taken according to the illustrations in von den Driesch (1976), unless otherwise stated, and are given in millimeters. Osteological nomenclature is modified from Howard (1929). Literature citations are given for authorities of scientific names of fossil taxa only. Authorities for extant North American taxa are generally those cited in the seventh edition of the A.O.U. Check-list (American Ornithologists' Union, 1998); those for taxa extralimital to that work are from Sibley and Monroe (1990).

Elements are listed in the following order: skull, vertebrae (except synsacral vertebrae), sternum, furcula, coracoid, scapula, humerus, ulna, radius, carpometacarpus, alar phalanges in

numerical order, pelvis, femur, tibiotarsus, tarsometatarsus, and pedal phalanges in numerical order. Right elements are listed before left elements, and complete elements are listed before partial elements, with proximal portions listed before distal portions (scapular portions before sternal portions in the case of coracoids).

Systematic Paleontology

PELAGIC BIRDS

The species account are divided into two sections. The second section deals with shore and land birds that are incidental to the fauna, usually being known by a single bone or fragment or by at most a few specimens. The present section deals with the pelagic avifauna, which for the most part consists of species that lived and fed in the vicinity of deposition. Some of the species of waterfowl and gulls would probably not have met this criterion, although most are more commonly represented than the incidental shore and land birds. On the other hand, most of the species represented at Lee Creek Mine in these families would certainly have been members of the pelagic avifauna, and we did not consider it practical to split the accounts of these families along speculative ecological lines.

Order GAVIIFORMES

(loons)

Family GAVIIDAE

(loons)

Genus *Colymboides* Milne-Edwards, 1867

Colymboides? sp.

MATERIAL.—Distal end of right humerus, USNM 302286. Left carpometacarpus missing distal end, minor metacarpal, and proximal parts of carpal trochlea, KU 21251.

HORIZON.—Pungo River Formation inferred from known temporal distribution of genus.

MEASUREMENTS (mm).—*Humerus*: Distal width, 8.8.

Carpometacarpus: Length of alular metacarpal, 9.0.

REMARKS.—These specimens appear to be referable to *Colymboides* rather than to *Gavia* based on the following characters. In the humerus, the attachment of the anterior articular ligament extends proximally only to the level of the ectepicondyle, and the surface is nearly plane, rather than sloping medially; in distal view it is much flatter, and the condyles are much less bulbous; the olecranal fossa does not extend proximo-internally between the internal condyle and the entepicondylar process; and the ridge on the internal border of the impression of the brachialis anticus is more diagonally oriented with respect to the shaft. In the carpometacarpus, the alular metacarpal is very short; the shaft is relatively unflattened; the proximal symphysis between major and minor metacarpals is very short; and the lig-

amental attachment of the pisiform process is not flattened or produced anteriorly.

These specimens are from a species smaller than any of the other loons from Lee Creek Mine or the Chesapeake Group. Their size suggests that they pertain to an undescribed species, the humerus being smaller than that of *Colymboides anglicus* Lydekker but larger than that of *C. minutus* Milne-Edwards. If correctly referred to genus, they would provide the first record of the genus *Colymboides* outside of Europe. The latest occurrence of *Colymboides* in Europe is in the early Miocene of the Cheb Basin of the Czech Republic, where the tiny species *C. minutus*, otherwise known only from the early Miocene of France, has been found (Svec, 1980, 1982; Mlíkovský, 1996). This species is known only from freshwater deposits, so it is quite possible that the genus *Colymboides* may have persisted somewhat later in marine environments (see discussion of *Gavia egeriana*, below).

Genus *Gavia* Forster

Gavia egeriana Svec, 1982

MATERIAL.—Right coracoid, USNM 430523. Proximal two-thirds of right ulna, USNM 241423.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

MEASUREMENTS (mm).—*Coracoid*: Length with sternal facet flat on calipers, ~35; width and depth of shaft at midpoint, 4.3 × 3.8.

Ulna: Proximal width and depth, 7.3 × 8.3.

REMARKS.—*Gavia egeriana* is a very small species of loon described from two distal ends of humeri from early Miocene deposits at Dolnice, in the Cheb Basin in the Czech Republic (Svec, 1982). The micromammal zone of these deposits is MN 4b (Mlíkovský, 1996); thus, these deposits are probably slightly older than the Calvert or Pungo River formations, and fossils of this species form the earliest occurrence of the genus *Gavia*.

Several specimens of *Gavia* have been recovered from the Calvert Formation in Maryland, Virginia, and Delaware (Rasmussen, 1998) and appear to be referable to two species, differing in size. We were able to compare the holotype of *Gavia egeriana* directly with these specimens, and we assign the larger of the two Calvert loons to that species. The smaller Calvert loon is undescribed and is not known from Lee Creek Mine.

The coracoid from Lee Creek Mine listed above is black and phosphatized. It compares well with a coracoid from the Calvert Formation that is associated with a sternum, scapula, and furcula (USNM 23717) that we refer to *G. egeriana* based on size. Likewise, the ulna from Lee Creek Mine is close to one from the Calvert Formation that is associated with a radius and the proximal end of a humerus of *G. egeriana* (USNM 237204). We therefore assume that the specimens from Lee Creek Mine are from the Pungo River Formation, which is further supported by the preservation of the coracoid. The Calvert material will be described in detail elsewhere.

Gavia howardae Brodkorb, 1953c

PLATE 1a,c,d,f,h,j,l,m,o,g

MATERIAL.—Right coracoids, USNM 244209, 321271; complete left coracoids, USNM 192845, 366413; right coracoid lacking part of both ends, USNM 446482; left coracoid lacking part of both ends, USNM 430515; scapular end of right coracoid, USNM 257461; medial portion of left coracoid, USNM 302363. Anterior end of right scapula, USNM 430472. Left humerus, USNM 206448; proximal end of left humerus, USNM 446473; distal ends of right humeri, USNM 206347, 242363, 257480, 430508, 430510–430512, 446474, 446475; distal ends of left humeri, USNM 215850, 257465, 366664, 446478. Proximal end of right ulna, USNM 215436; proximal ends of left ulnae, USNM 252348, 446471; distal ends of right ulnae, USNM 215473, 215629, 430500; distal ends of left ulnae, USNM 193204, 430494. Distal end of right radius, USNM 177820. Right carpometacarpus missing alular and minor metacarpals, USNM 460766; proximal portions of left carpometacarpi, USNM 177783, 366702, 460767; distal end of left carpometacarpus, USNM 192449. Right femora, USNM 215426, 367161, 446480; right femur lacking distal end, USNM 248590; distal end of left femur, USNM 250681. Distal end of right tibiotarsus, USNM 192676. Left tarsometatarsus lacking most of both ends, USNM 430520; proximal end of right tarsometatarsus, USNM 446481; proximal ends of left tarsometatarsi, USNM 193274, 430522; distal ends of right tarsometatarsi, USNM 183423, 183431, 366565, 460768; distal ends of left tarsometatarsi, USNM 177879, 193059.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*San Diego Formation, California:* Right humerus, SDSNH 42762; right humerus lacking most of proximal end, SDSNH 42776; left humerus, SDSNH 42763; fragmented left humerus, SDSNH 42781. Distal half of right ulna, SDSNH 35252. Left radius, SDSNH 42778. Left carpometacarpus, SDSNH 42774; proximal end of right carpometacarpus, SDSNH 42768. Right femora, SDSNH 42764, 42775; left femur, SDSNH 42779. Right tibiotarsus, SDSNH 42765; left tibiotarsus, SDSNH 42772; distal end of left tibiotarsus, SDSNH 42773. Proximal half of right tarsometatarsus, SDSNH 35251.

MEASUREMENTS.—See Table 1.

REMARKS.—*Gavia howardae* was first described from the late Pliocene (Blancan) San Diego Formation of California (Brodkorb, 1953c). Chandler (1990a) referred a subsequent specimen from the same deposits to this species, and numerous additional specimens, which we examined (see list above), have since been found there. As in the Red-throated Loon, *G. stellata* (Pontoppidan), the bones of *G. howardae* are slim relative to those of the Arctic Loon, *G. arctica*, or the Pacific Loon, *G. pacifica*, and many of them are shorter than those of *G. stellata* (Table 1). Characters given for *G. howardae* by Chandler (1990a) were used to identify the Lee Creek Mine specimens,

and other elements were referred to this species mainly on their small size and gracile proportions. The small size of *G. howardae* suggests a relationship to *G. stellata*, the smallest modern loon, and this also is supported by small fossil coracoids from Lee Creek Mine. These agree with *G. stellata* in having only an incisura on the medial edge of the coracoid, whereas in most individuals of all other modern and fossil loons (in which the coracoid is known), there is a distinct, closed procoracoid foramen.

Gavia moldavica Kessler (1984) was described from portions of all the major wing elements from the early late Miocene (Middle Sarmatian) of Kishinev (Chisinau), Moldavia. The measurement given for the distal end of one of the paratypical humeri is 12.0 mm, which is within the range of *G. howardae* (Table 1). The length of a paratypical radius of *G. moldavica* was 87.6 mm, compared with 86.5 mm for a radius of *G. howardae* (SDSNH 42778). There is, however, a considerable period of time between the probable age of *G. moldavica* (MN ?9 (= planktonic foraminifera zone N15) according to Mlikovsky, 1996), the Yorktown Formation at Lee Creek Mine (N19), and the even younger San Diego Formation (N21). Given that loons appear to have been increasing rapidly in size during the last half of the Neogene, it is possible that *G. moldavica* could have been ancestral to the larger Pliocene species *G. concinna*.

Gavia schultzi Mlikovsky (1998), from the middle Miocene (upper Badenian) of Austria, is somewhat younger than the Calvert/Pungo River formations and apparently falls within the lower size range of *G. howardae*, being considerably larger than any middle Miocene loon yet known from North America.

Gavia brodkorbi Howard (1978) is known from a complete ulna from the early late Miocene (Clarendonian; N14–16) at Laguna Niguel, California. This is shorter and more robust than in *G. howardae*. The holotype of *Gavia paradoxa* Umanskaja (1981) is the proximal portion of an ulna from the late Miocene (MN 11–13 = –N16–17) of the Ukraine. The published dimensions of *G. paradoxa* suggest that it is very similar in size to *G. brodkorbi*, from which it appears to differ in its long attachment for the anterior articular ligament.

The relationship of these late Miocene loons to the tiny species of the middle Miocene and the larger ones of the Pliocene can only be determined with more and better material and direct comparisons with the types.

Gavia howardae is very similar to the modern Red-throated Loon, *Gavia stellata*, and is probably on a direct line with that species. Although there is overlap in size (Table 1), the fossil form on average is smaller, and some individuals were smaller than any of the individuals in the modern sample. The main qualitative difference noted was that the pectoral crest of the humerus in *G. howardae* is not as long and low as it is in the modern form.

Gavia concinna Wetmore, 1940

PLATE 2a,c,d,f,g,i,k-n,p,r-t,v,x,y

Gavia concinna Wetmore, 1940:25.*Gavia palaeodytes* Wetmore, 1943a:64.*Gavia* sp., Howard, 1982:3.

MATERIAL.—Because of the abundance of material of this species from Lee Creek Mine, only the best-preserved specimens and rarer elements are listed.

Right coracoid, USNM 430477; left coracoids, USNM 366592, 430476; scapular ends of left coracoids, USNM 192029, 192033, 192772. Anterior end of left scapula, USNM 192083. Proximal end of left humerus, USNM 430501; distal ends of right humeri, USNM 367020, 430470, 446489, 460771; distal ends of left humeri, USNM 181037, 252360, 366642, 366894, 430460, 430503. Proximal ends of right ulnae, USNM 430457, 430458, 446470, 446485, 446491, 460770; proximal ends of left ulnae, USNM 430453, 446472; distal ends of right ulnae, USNM 252340, 252377; distal ends of left ulnae, USNM 430443, 430456, 446488, 460769. Proximal end of left radius, USNM 446484. Right carpometacarpus missing minor metacarpal, USNM 430451; proximal ends of right carpometacarpi, USNM 215873, 446483; proximal ends of left carpometacarpi, USNM 367132, 430441. Proximal half of fused synsacral vertebrae, USNM 460774. Right femora lacking part of distal ends, USNM 183477, 430518, 446479; left femora lacking part of distal ends, USNM 366000, 460783. Proximal end of left tibiotarsus, USNM 430519; distal ends of right tibiotarsi, USNM 241388, 446490; distal ends of left tibiotarsi, USNM 215646, 430481, 430482. Right tarsometatarsi, USNM 366714, 430485, 430486; left tarsometatarsus, USNM 193359; proximal end of left tarsometatarsus, USNM 430446; distal ends of right tarsometatarsi, USNM 430490, 460773; distal end of left tarsometatarsus, USNM 460772. Pedal phalanx, USNM 192543.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*San Diego Formation, California:* Left humeri, SDSNH 42761, 42763; distal half of left humerus, SDSNH 42767. Right carpometacarpus missing minor metacarpal, SDSNH 42769. Right major alar digit phalanx 2, SDSNH 42771. Left femur, SDSNH 42777. Right tarsometatarsi, SDSNH 22916, 42766; left tarsometatarsi, SDSNH 42770, 42780.

Bone Valley Formation, Florida: Right coracoids, UF PB 132, USNM 256375. Proximal half of right humerus, UF PB 306; distal thirds of right humeri, UF PB 88, 524, USNM 256376; distal halves of left humeri, UF PB 297, USNM 256395. Distal third of right ulna, UF PB 89. Right femora, UF PB 133, USNM 256378; left femur, UF PB 298. Proximal half of right tarsometatarsus, USNM 256374.

Horizon Uncertain: Distal end of left radius, USNM 460775, from Renny Creek, New Bern, Craven County, North Carolina. Yorktown or equivalent deposits are exposed there, but the specimen might be Pleistocene and is included herein for purposes of illustration (Plate 2i).

MEASUREMENTS.—See Table 1.

REMARKS.—*Gavia concinna* Wetmore (1940) was described from the proximal end of an ulna from the Etchegoin Formation of Monterey County, California, which is late Hemphillian in age (Becker, 1987) and thus is approximately contemporaneous with the Yorktown and Bone Valley formations. This species was said to be intermediate in size between the modern species *G. stellata* and the Common Loon, *G. immer*. It was not stated how the fossil species could be discriminated from modern *G. arctica* or *G. pacifica*, however, which are in this intermediate size range. Wetmore (1943a) then described *Gavia palaeodytes* from an imperfect coracoid from the Bone Valley Formation of Florida. He considered the coracoid to be smaller than that of any then-known species of loon, living or fossil; however, it is stout and has a heavily rimmed procoracoid foramen, unlike *G. stellata* or the Lee Creek material referred to *G. howardae*. Brodkorb (1953c) referred additional material from California to *G. concinna*, which he regarded as being most similar to *G. pacifica*, although approaching *G. immer* in size. He also referred material from Bone Valley to *G. concinna*, which he considered to be a larger species than *G. palaeodytes*, which in turn was said to be the size of *G. stellata*. Delle Cave et al. (1984) described the skull of a loon from the Pliocene of Italy and identified it as *Gavia* cf. *concinna*.

Chandler (1990a) dismissed all published records of the occurrence of *Gavia concinna* in the San Diego Formation as misidentifications. At least seven specimens collected there in 1989 and 1990 (listed above), however, are best referred to this species, being far too large to be *G. howardae*; none is so large as definitely to pertain to the new species of *Gavia* described herein (see below).

A worn tarsometatarsus from the San Mateo Formation (early Hemphillian), in San Diego County, California, was referred to by Howard (1982) only as "*Gavia* sp.," but its size and age are compatible with *G. concinna* as defined herein, to which we tentatively refer the specimen.

The material from Bone Valley, including part of that referred by Brodkorb (1953c) to *G. concinna*, appears to be a composite, as it contains at least two specimens (proximal end of humerus UF PB 593; distal end of humerus UF PB 90) that are too large for that species and that we refer to the new species of *Gavia* described below. We regard all of Brodkorb's (1953c) material of *G. palaeodytes* as belonging to *G. concinna*. Although there is considerable size variation shown in this series, with some specimens being quite small, none of the material we have yet seen from Bone Valley can convincingly be referred to *G. howardae*. Therefore, we regard the great majority of specimens of loons from Bone Valley, including the holotype of *G. palaeodytes* Wetmore (1943a), to be referable to *G. concinna* Wetmore (1940).

Emslie (1998) referred to *G. concinna* the distal end of a tarsometatarsus from the earliest Pleistocene of Florida, where it was contemporaneous with *G. pacifica*. Otherwise, *G. concinna* would presumably be part of the lineage that includes *G. arctica* and *G. pacifica*, which have often in the past been con-

sidered conspecific. The fossils differ very little from the modern forms. A much more detailed analysis would be required to determine whether the split between *G. arctica* and *G. pacifica* took place before or after the early Pliocene, if indeed such a determination can be made osteologically.

Gavia fortis, new species

FIGURES 5, 6; PLATES 3*a,c,e,g-i,k,l,n*, 4*a-c,e,f,h,j,l,n,p,q,s,u,v,x,z*

HOLOTYPE.—Associated partial skeleton consisting of a portion of shaft of right humerus, distal end of left humerus, proximal ends of right and left radii and ulnae, proximal end of right carpometacarpus, synsacrum, fragment of left innominate with most of the acetabulum, distal end of right tibiotarsus, complete right tarsometatarsus, pedal phalanx, and various small fragments of bone, USNM 252432.

TYPE LOCALITY.—Texasgulf Inc. Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23'22"N, 76°47'06"W).

HORIZON AND AGE.—As determined from foraminifera and sedimentary characters of matrix, the holotype is from the lower to middle part of the Yorktown Formation, lower Pliocene. Paratype USNM 179222 is from the basal Yorktown, and paratype USNM 178148 is from the lower to middle part of the Yorktown Formation. Other paratypes are assumed to be of the same age.

DISTRIBUTION.—Known from the type locality and from the Bone Valley Formation in central Florida.

MEASUREMENTS OF HOLOTYPE (mm).—*Humerus*: Distal width, 17.5.

Ulna: Proximal width, 13.0; proximal diagonal, 13.1.

Radius: Proximal width, 7.4

Carpometacarpus: Proximal depth, 16.0.

Tibiotarsus: Distal width, 13.9; distal diagonal, 13.1.

Tarsometatarsus: Length, 77.5; proximal width, 14.1; distal width, 11.0.

TOPOTYPICAL PARATYPES.—*Associated Specimen*: Partial skeleton consisting of vertebral fragments, proximal end of left radius and ulna, left femur, proximal and distal ends of left tibiotarsus, left tarsometatarsus, and pedal phalanx, USNM 302392.

Individual Elements: Cervical vertebra, USNM 460782. Left coracoid, USNM 215562; scapular ends of right coracoids, USNM 215463, 215502; scapular ends of left coracoids, USNM 206368, 206432, 210452. Anterior end of right scapula, USNM 206587. Left humerus lacking most of proximal end, USNM 206625; proximal ends of right humeri, USNM 244212, 460778, 460779; proximal ends of left humeri, USNM 215840, 366588; distal ends of right humeri, USNM 178149, 192848, 192981, 193009, 252370, 252372, 460780; distal ends of left humeri, USNM 177742, 192450, 192771, 193230, 242173, 252353. Right ulna, USNM 250778; proximal end of right ulna, USNM 367044; proximal ends of left ulnae, USNM 206450, 215753; distal end of right ulna, USNM 366414; distal

ends of left ulnae, USNM 178148, 460777. Left radius, USNM 192060/192065 (two pieces fitting together); proximal end of right radius, USNM 460795; distal end of right radius, USNM 215749; distal end of left radius, USNM 430444. Right carpometacarpus lacking proximal end, USNM 460776; proximal end of right carpometacarpus, USNM 430442; proximal ends of left carpometacarpi, USNM 244210, 430440. Right femora, USNM 183459, 206348, 275779, 367062, 482593; left femora, USNM 177912, 179222, 250713, 257491, 275842, 460781; right femur lacking proximal end, USNM 308212; left femur lacking distal end, USNM 366681. Proximal end of right tibiotarsus, USNM 256254; distal ends of right tibiotarsi, USNM 178057, 430483; distal end of left tibiotarsus, USNM 206593. Right tarsometatarsus, USNM 206629; proximal ends of right tarsometatarsi, USNM 183492, 206533, 308193; proximal ends of left tarsometatarsi, USNM 215570, 242340, 308204, 366559, 446492, 482592; distal ends of right tarsometatarsi, USNM 206302, 257501, 430449, 430450; distal ends of left tarsometatarsi, USNM 192880, 215772, 250753, 430447, 430448, 446493. Pedal phalanx, USNM 236812.

ADDITIONAL PARATYPES.—*Bone Valley Formation, Florida*: Proximal third of right humerus, UF PB 593; distal third of left humerus, UF PB 90.

MEASUREMENTS OF PARATYPES.—See Table 1.

ETYMOLOGY.—Latin *fortis*, strong, powerful; from the robustness of the bones in comparison to the Common Loon, *Gavia immer*.

DIAGNOSIS.—Larger than any living or fossil species of *Gavia* except *G. immer* and the Yellow-billed Loon, *G. adamsii*. Smaller than all but the smallest individuals of *G. immer*, but all skeletal elements markedly more robust. Differs from *G. immer* in having the sacrum in lateral view more curved ventrally.

REMARKS.—This common species at Lee Creek Mine is larger than any of the known fossil forms of *Gavia* but is similar in overall size to the modern *G. immer*-*G. adamsii* superspecies. *Gavia fortis* is similar to *G. immer* and differs from *G. concinna* and *G. arctica* in that the ectepicondylar prominence of the humerus is more laterally produced, and the attachment for the anterior articular ligament is longer; the distal end of the ulna is much expanded, especially the palmar edge of the shaft immediately proximal to the articular surface, the base of the internal cotyla is rounded and heavy, the internal-palmar edge of the shaft is less ridge-like, and the internal cotyla and internal condyle are more produced palmarly; the distal end of the radius is more expanded; there is a larger spur on the posterior edges of the external and internal condyles of the tibiotarsus, the distal intercondylar sulcus is wider, and the entire distal end is more expanded; and the distal foramen of the tarsometatarsus is proportionately larger in posterior view, and the intertrochlear notch between trochleae III and IV is narrower.

Regalia (1902) described a large species of loon, *Gavia portisi*, based on a broken tenth or eleventh cervical vertebra from the Pliocene of Italy (middle Pliocene at Orciano Pisano near

TABLE 1.—Measurements (mm) of modern species of *Gavia* compared with fossil loons from Lee Creek Mine. Measurements are in list form when $n < 7$ for fossil species. (n =number of specimens, s =standard deviation.)

Element	<i>G. howardae</i>			<i>G. stellata</i> ($n=26$)			<i>G. concinna</i>			<i>G. pacifica</i> ($n=10$)			<i>G. fortis</i> , new species			<i>G. immer</i> ($n=24$)		
	n	Range	Mean s	Range	Mean s	n	Range	Mean s	Range	Mean s	n	Range	Mean s	Range	Mean s	Range	Mean s	
Coracoid																		
Medial length	4	40.8, 42.2, 43.7, 47.2	—	41.6–50.2	44.9 2.17 2	48.4, 50.6	—	45.6–53.5	48.5 2.32 1	57.3	—	—	—	54.1–73.5	64.1 5.32	—	—	—
Scapular facet depth	8	7.3–9.0	8.1 0.62	8.3–10.3	8.9 0.55 8	9.2–10.0	9.6 0.32	8.9–10.3	9.4 0.46 5	10.5(2), 11.1, 11.5, 11.8	—	—	—	10.2–15.4	12.5 1.36	—	—	—
Scapula																		
Anterior diagonal	1	8.9	—	7.0–10.2	8.5 0.77 1	11.1	—	7.9–11.4	9.5 1.16 1	11.8	—	—	11.3–16.0	13.2 1.37	—	—	—	—
Humerus																		
Length	1	120.4	—	123.8–150.0	134.8 5.90 —	—	—	137.2–159.5	144.4 7.08 1*	163.8*	—	—	163.2–211.1	186.2 13.85	—	—	—	—
Proximal width	1	19.1	—	18.3–21.6	19.9 0.91 1	19.0	—	20.2–22.2	21.5 1.00 —	—	—	—	24.8–31.8	27.8 2.22	—	—	—	—
Distal width	12	11.3–13.4	12.3 0.68	12.6–15.2	13.9 0.65 29	12.7–16.2	14.6 1.08	14.3–16.1	15.1 0.61 15	15.8–18.6	17.4 0.86	—	17.7–22.8	19.9 1.58	—	—	—	—
Ulna																		
Length	—	—	—	103.8–120.2	109.8 4.16 —	—	—	110.5–129.5	116.8 5.73 1	122.3	—	—	131.1–168.2	150.0 10.59	—	—	—	—
Proximal width	2	9.1, 9.2	—	9.5–11.5	10.3 0.51 15	9.9–13.3	11.4 0.99	10.3–12.1	11.2 0.59 5	12.9(2), 13.0, 13.2, 13.4	—	—	12.7–17.3	14.8 1.25	—	—	—	—
Distal diagonal	4	11.1, 11.2, 11.6, 11.7	—	10.8–13.5	12.0 0.67 8	13.7–16.7	15.4 0.94	12.2–16.2	14.3 1.32 4	16.6, 17.1, 17.6, 18.5	—	—	17.3–23.6	20.1 1.76	—	—	—	—
Radius																		
Length	—	—	—	102.0–118.0	107.9 4.25 —	—	—	110.0–127.5	116.0 5.65 1	126.9	—	—	134.2–167.3	147.8 10.51	—	—	—	—
Proximal width	—	—	—	5.2–6.5	5.8 0.33 1	6.3	—	5.5–6.9	6.3 0.42 3	6.9, 7.3, 7.4	—	—	6.9–9.3	8.0 0.67	—	—	—	—
Distal width	1	7.8	—	6.9–8.7	7.8 0.42 1	9.0	—	7.9–9.8	9.0 0.67 3	7.3, 7.5(2)	—	—	10.9–14.1	12.2 0.96	—	—	—	—
Carpometacarpus																		
Length	—	—	—	67.0–82.5	73.2 3.93 —	—	—	73.2–87.3	77.8 4.80 —	—	—	—	86.0–109.2	98.1 6.93	—	—	—	—
Proximal depth	1	12.3	—	10.2–13.3	11.5 0.72 5	13.7, 14.2, 14.4, 14.5, 14.8	—	12.3–15.2	13.4 0.95 4	15.9, 16.0, 16.1, 17.4	—	—	15.0–19.9	17.3 1.41	—	—	—	—
Distal diagonal	1	7.6	—	6.4–8.0	7.1 0.40 1	8.0	—	7.2–8.8	8.1 0.53 1	9.4	—	—	8.1–11.6	9.8 0.94	—	—	—	—
Pelvis																		
Acetabular diameter	—	—	—	5.9–7.9	6.8 0.52 —	—	—	6.2–7.5	7.0 0.39 1	8.1	—	—	7.6–10.9	9.4 0.79	—	—	—	—
Femur																		
Greatest length	1	34.6	—	35.1–42.7	38.2 1.88 3	37.9, 39.7, 45.8	—	39.6–45.8	42.3 1.93 10	47.0–52.7	49.6 1.63	—	48.8–64.2	56.4 4.55	—	—	—	—
Proximal width	2	13.0, 13.8	—	12.5–15.5	13.7 0.65 5	13.0, 13.4, 13.6, 14.1, 14.2	—	12.7–15.4	14.3 0.97 8	15.1–17.1	15.6 0.74	—	15.6–21.0	18.2 1.54	—	—	—	—
Distal width	—	—	—	13.1–16.5	14.6 0.72 —	—	—	13.3–17.1	15.1 1.06 11	15.8–18.2	16.7 0.63	—	17.1–21.8	19.0 1.52	—	—	—	—
Distal depth	—	—	—	8.3–9.8	9.1 0.39 —	—	—	8.9–10.4	9.8 0.52 10	10.4–12.1	11.2 0.62	—	10.8–14.3	12.7 1.06	—	—	—	—
Tibiotarsus																		
Proximal diagonal	—	—	—	13.0–15.5	14.2 0.69 —	—	—	13.6–16.2	15.1 0.82 2	14.8, 16.0	—	—	14.8–21.3	18.5 1.78	—	—	—	—
Distal width	—	—	—	10.5–12.1	11.4 0.39 5	11.0, 11.5, 13.0(2), 13.1	—	11.0–12.3	11.6 0.52 4	13.1, 13.9, 14.0, 14.5	—	—	13.1–17.2	14.9 1.23	—	—	—	—
Distal depth	—	—	—	10.7–12.8	11.6 0.56 4	11.2, 11.9, 12.0, 12.3	—	11.3–13.1	12.1 0.65 5	11.8, 12.4, 12.9, 13.4, 13.9	—	—	13.3–17.6	15.6 1.21	—	—	—	—
Tarsometatarsus																		
Length	—	—	—	68.3–79.1	72.0 3.19 4	61.4, 65.9, 67.6, 70.3	—	68.8–82.5	73.7 4.44 3	72.4, 77.5, 78.1	—	—	80.3–99.1	89.8 5.41	—	—	—	—
Proximal width	—	—	—	11.2–13.0	12.0 0.53 10	10.7–12.5	11.4 0.56	11.4–13.2	12.5 0.55 7	12.8–14.3	13.7 0.61	—	13.8–18.0	16.0 1.16	—	—	—	—
Distal width	5	7.8, 7.9, 8.1, 8.4, 8.6	—	7.5–9.1	8.3 0.49 7	7.6–8.9	8.1 0.50	8.4–9.5	9.2 0.60 8	9.7–11.2	10.5 0.65	—	9.5–14.7	12.0 1.20	—	—	—	—
Pes digit I1 phalanx 1																		
Length	—	—	—	30.6–37.5	33.4 1.68 —	—	—	33.7–39.6	36.1 1.82 2	41.7, 41.8	—	—	40.9–51.5	45.8 10.10	—	—	—	—
Proximal width	—	—	—	4.8–6.2	5.6 0.42 —	—	—	5.1–6.3	6.0 0.26 2	7.1, 7.9	—	—	6.3–8.7	7.4 0.71	—	—	—	—
Distal width	—	—	—	3.1–3.8	3.5 0.20 —	—	—	3.7–4.2	3.8 0.17 2	4.4, 4.5	—	—	4.1–5.5	4.8 0.42	—	—	—	—

*Estimate based on regression (r) using length to distal margin of pectoral crest ($n=27$ *G. immer*, $r=0.47$, $P<0.05$).

Val di Fine). From the illustrations it appears that the specimen was correctly identified as a loon. Although Brodkorb (1953c) stated that this came from a species the size of modern *G. immer*, the measurements seem to indicate a smaller species (Delle Cave et al., 1984), but the holotype can no longer be found (Delle Cave et al., 1984; Delle Cave, 1996). Although *Colymbus portisi* Regàlia is the earliest name applied to any Pliocene loon and almost certainly pertains to one of the younger epithets we have used in this paper, the application of the name can seemingly no longer be determined. Thus, we regard *Colymbus portisi* Regàlia as a nomen dubium and we have not used it. There appear to be no records of *Gavia immer* earlier than the late Pleistocene (Emslie, 1998).

Differences in proportions between the modern and fossil loons were confirmed by a bootstrapped principal components (PC) analysis of 12 variables (listed in Table 2) for *Gavia immer* ($n=13$), *G. pacifica* ($n=10$), and *G. fortis* ($n=2$ associated partial skeletons) using a covariance matrix of \log_{10} -transformed data (Figure 5). By far the greatest amount of variation (89%) was explained by PC-I, on which all variables loaded highly and positively, as is typical for a general-size axis (Table 2). All T statistics (resampled eigenvectors divided by

their standard errors) for PC-I were greater than T value ($|T|=5$), which can be considered the level above which T statistics are significant (Marcus, 1990), although tarsometatarsus-shaft width had a much smaller $|T|$ than did any other variable (Table 2). *Gavia fortis* is similar on factor I, and thus in overall size, to small *G. immer* and large *G. pacifica*. The only length measure available for both of the associated skeletons of *G. fortis*, however, was tarsometatarsus length, which was shorter than that of *G. immer*; elements from other specimens of *G. fortis* are shorter than similarly stout elements of *G. immer* (Table 1). On PC-II, tarsometatarsus-shaft width was by far the most important variable (Figure 6), with a $|T|>2$ (Table 2), contrasted with the less important ulna-shaft width. On PC-III, which remained the third axis after 500 bootstrap iterations, tibiotarsus distal depth and tarsometatarsus length (Figure 6) were the most important variables, based on their T values (Table 2). On factors II and III, *G. immer* and *G. pacifica* overlap widely (Figure 5), whereas *G. fortis* differs from both extant species in having a combination of a relatively short, heavy tarsometatarsus (scores low on PC-III and high on PC-II), and a relatively thin ulnar shaft immediately distal to the external condyle (scores high on PC-II). In proportions, the

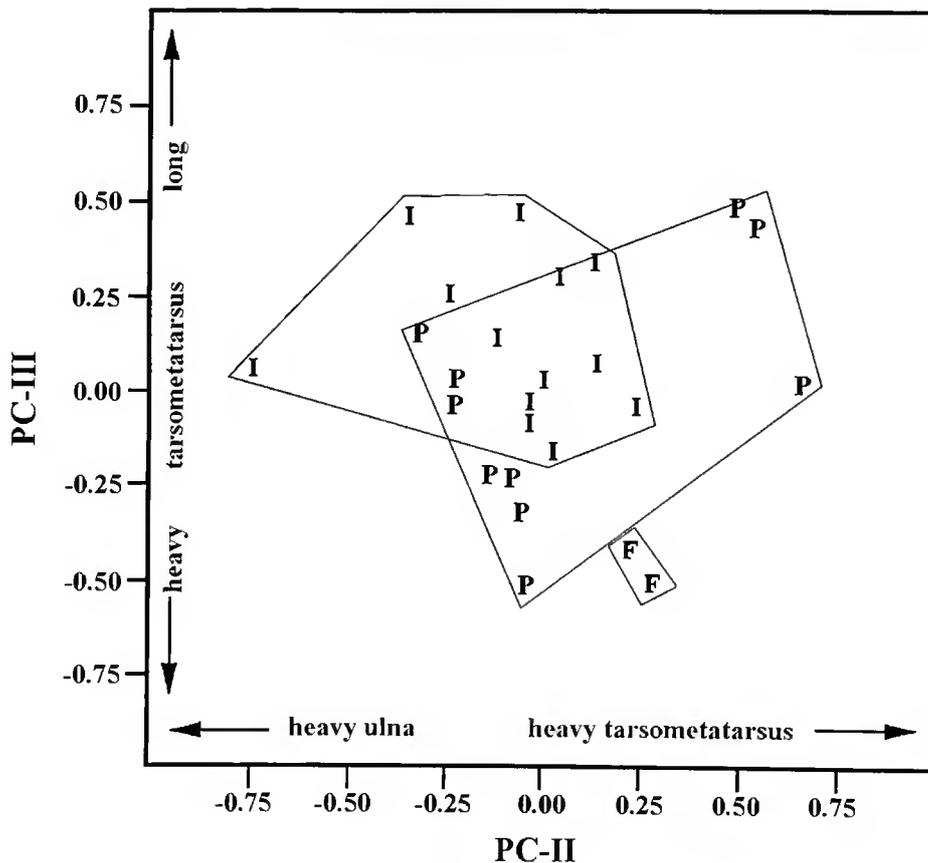


FIGURE 5.—Scatter plot of individual factor scores from principal components analysis of loons *Gavia immer* (I), *G. pacifica* (P), and associated specimens of *G. fortis*, new species (F).

two associated specimens available of *G. fortis* differ more from these two recent species than they differ from one another. In fact, the principal components analysis underrepresents the distinctness of *G. fortis* because of the scarcity of usable length measures for this species.

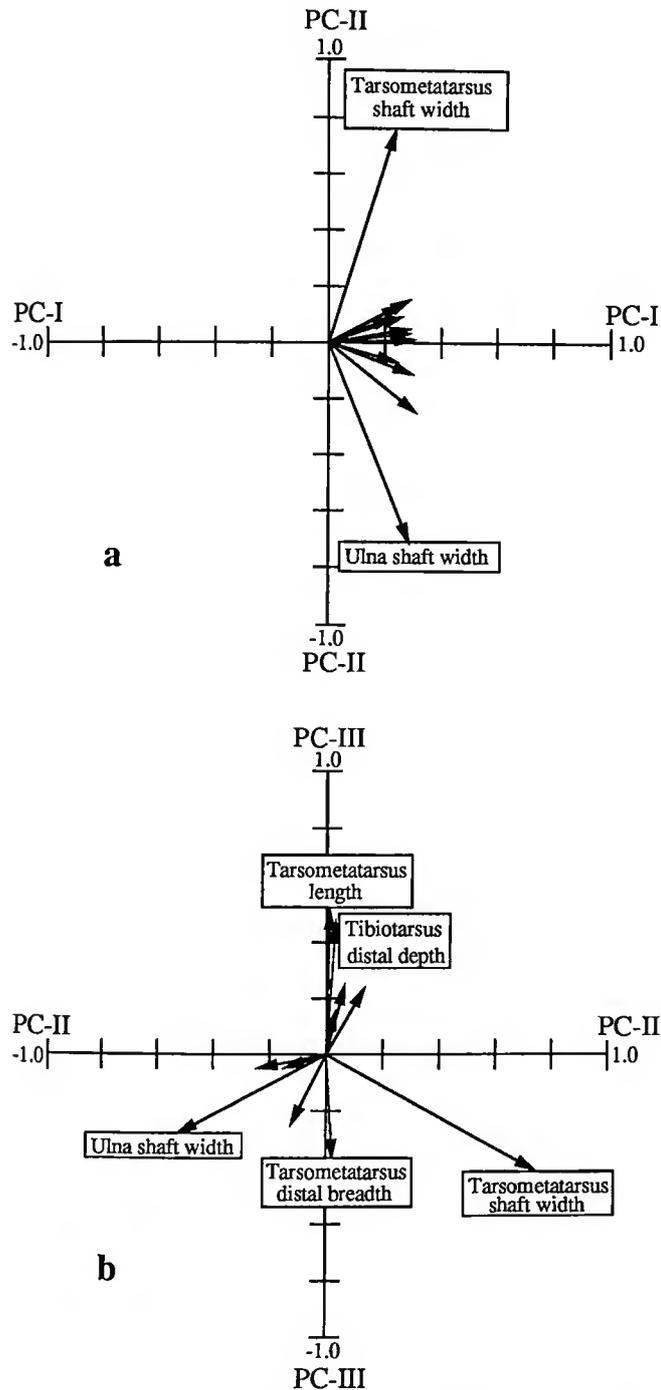


FIGURE 6.—Component loadings for principal components analyses of loons *Gavia immer*, *G. pacifica*, and *G. fortis*, new species: a, factors I and II; b, factors II and III.

TABLE 2.—Summary of results (T statistics, eigenvalues, and percent of variance explained) for factors I–III of a bootstrapped principal components analysis of 12 skeletal variables for loons *Gavia immer*, *G. pacifica*, and *G. fortis*, new species.

Variable	T statistics		
	PC-I	PC-II	PC-III
Ulna proximal width	19.76	-1.34	-0.15
Ulna shaft width (immediately distal to base of external condyle)	10.41	-1.60	-0.51
Ulna proximal diagonal	21.87	-0.79	-0.19
Tibiotarsus distal width	19.68	0.71	0.95
Tibiotarsus distal depth	19.37	0.06	1.76
Tibiotarsus condyle height	14.28	-0.33	-0.36
Radius proximal width	24.90	0.16	0.52
Tarsometatarsus length	14.90	0.03	1.46
Tarsometatarsus proximal width	21.84	0.41	0.89
Tarsometatarsus distal width	13.80	0.25	-0.67
Tarsometatarsus distal depth	20.74	0.85	-0.27
Tarsometatarsus shaft width	7.82	2.04	-0.58
Eigenvalues	0.0296	0.0009	0.0007
Percent of variance explained	89.26	2.9	2.2

Discussion of Gaviidae

Although modern loons breed in the boreal zone and are entirely confined to the Northern Hemisphere, even in winter, the fossil record shows that the family once occurred, and perhaps even originated, in the Southern Hemisphere. Once thought to belong to the Mesozoic toothed divers of the order Hesperornithiformes, *Neogaeornis wetzeli* Lambrecht (1929), from the Late Cretaceous of Chile, has been shown to belong to the Gaviidae (Olson, 1992). Another Late Cretaceous fossil, from Seymour Island, Antarctica, also is referable to the Gaviidae (Chatterjee, 1989) and possibly to *Neogaeornis*.

The published fossil record of loons resumes with *Colymboides anglicus* Lydekker (1891a), from the late Eocene of England (Lydekker, 1891a; Harrison and Walker, 1976). The genus *Colymboides* comprises two species that differ considerably from *Gavia* in many aspects of their osteology (Storer, 1956; Cheneval, 1984), and they are believed to represent a separate lineage (Storer, 1956). The type of the genus is *C. minutus* Milne-Edwards (1867), a tiny species described from the rich early Miocene (Aquitainian) deposits at St.-Gérand-le-Puy, France. *Colymboides minutus* also has been identified from the early Miocene of the Dolnice basin in the Czech Republic, where it occurs together with a small species of *Gavia* (Svec, 1980, 1982), and from the early Miocene Faluns de Saucats in France (Cheneval, 1984). The two specimens from Lee Creek Mine referred to *Colymboides* sp. and presumed to be from the Pungo River Formation thus probably represent the latest occurrence of the genus.

The genus *Gavia*, as represented by *G. egeriana* Svec (1982), was first known from the early Miocene of the Czech Republic. This was a very small species, which we also have identified from the Calvert and Pungo River formations. The Calvert material differs considerably, in characters that are

doubtless primitive, from modern species of *Gavia*. Contemporaneous with *G. egeriana* in the Calvert Formation is a second, somewhat smaller, undescribed species. Both of these middle Miocene species are much smaller than any known later species of *Gavia*.

Loons intermediate in age between the early middle Miocene and the early Pliocene are known from several localities in Europe and are briefly discussed above. Abundant material of *Gavia* from the early Pliocene Yorktown Formation clearly encompasses at least three species, which differ in size. These are all much larger than any loons of the Calvert Formation or deposits of equivalent or earlier age, and they may represent the three modern lineages, consisting of *G. stellata*, *G. arctica/pacifica*, and *G. immer/adamsii*.

The three extant species-groups of loons are essentially Holarctic in distribution, breeding on fresh water at much higher latitudes than North Carolina but wintering almost entirely at sea. All forms except *G. stellata* have such high wing loadings that their flight would presumably be impaired by any loss of remiges during molt. Because of the necessity of leaving their breeding grounds before the waters freeze, adults do not molt until they reach their wintering grounds at sea, where they molt the remiges simultaneously and undergo a flightless period (Woolfenden, 1967).

Gavia fortis, certainly, and *G. concinna*, probably, were already sufficiently large by the early Pliocene as to have necessitated this pattern of molt of the flight feathers, and it seems reasonable to assume that all loons from the Yorktown Formation at Lee Creek Mine were individuals on their wintering grounds. Thus, the basic pattern of loons wintering at sea had evidently already evolved by the early Pliocene.

If the three species identified at Lee Creek Mine are really the predecessors of the three modern species groups, then there have been some interesting changes in the wintering distributions of the lineages. *Gavia stellata* is "a common migrant and regular winter resident" off North Carolina (Lee, 1995:119), although it is much scarcer farther south in Georgia and Florida. *Gavia immer* is the common wintering loon in eastern North America today, being abundant in Florida, yet what we have identified as *G. fortis* is very rare in the Bone Valley deposits. *Gavia concinna* is by far the most common loon in the Bone Valley deposits and is at least as abundantly represented at Lee Creek Mine as is either of the other two species. If this represents the *G. arctica/pacifica* lineage, then its status has changed dramatically since the Pliocene because *G. pacifica* is only a casual visitor to the western North Atlantic, where it does not regularly winter. For North Carolina there are only a few sight reports and one specimen found just north of the North Carolina/Virginia border (Lee, 1995:119).

Order PODICIPEDIFORMES (grebes)

Family PODICIPEDIDAE (grebes)

Genus *Podiceps* Latham

Pliodytes Brodkorb, 1953d:953.

Podiceps aff. *auritus* (Linnaeus)

PLATE 5a-g

"*Fulica* sp. (*Pisana* Nob.)" Portis, 1888:195.

"*Fulica* sp. (*pisana* Portis)" Portis, 1891:13.

Podiceps pisanus (Portis).—Regalia, 1902:233.

Podiceps pisanus (Portis).—Lambrecht, 1933:262.

Pliodytes lanquisti Brodkorb, 1953d:953.

Podiceps howardae Storer, p. 227, this volume.

MATERIAL.—Right coracoid, USNM 177927. Right humerus, USNM 243764; proximal three-fourths of right humerus, USNM 183430; distal ends of right humeri, USNM 193242, 215034, 407798; distal ends of left humeri, USNM 368557, 430524. Right femora, USNM 215453, 215649, 252314, 460785; left femur, USNM 177918; proximal ends of left femora, USNM 178151, 206413. Proximal ends of right tarsometatarsi, USNM 193175, 250773; distal end of right tarsometatarsus, USNM 206326, distal end of left tarsometatarsus, USNM 210531.

HORIZON.—Yorktown Formation inferred from identity with specimens in Bone Valley Formation and similarity to modern species.

ADDITIONAL MATERIAL EXAMINED.—*Bone Valley Formation, Florida*: Proximal half of right humerus, USNM 447059.

MEASUREMENTS.—See Storer (p. 227, this volume).

REMARKS.—Grebes are uncommon among the Lee Creek Mine fossils, almost all of the few specimens appearing to be from a single species that was very similar in size and other characters to the modern Horned Grebe, *Podiceps auritus*, which is the common species of grebe wintering at sea in North Carolina today.

We compared the appropriate specimens from Lee Creek Mine with a cast of the holotype of *Podiceps pisanus* (Portis, 1888, original in the Museo di Geologia e Paleontologia dell'Università di Firenze, Italy), which was described from the distal end of a humerus from the Pliocene of Italy, and we could detect no meaningful differences. The species originally was described by Portis (1888) as a coot (*Fulica*, Rallidae) and at that point was almost a nomen nudum. It was well described and figured by Portis, still as a coot, in a subsequent publication (Portis, 1891). Brodkorb (1963:227) cited the latter as the original description, with the date 1889, but the *Zoological Record* (1892, volume 28:21) lists the publication for 1891.

The supposed extinct genus and species *Pliodytes lanquisti* Brodkorb (1953d), based on a coracoid from the Bone Valley

Formation in Florida, is in this size range. The length of a coracoid from Lee Creek Mine (USNM 177927) is exactly the same as that given for the holotype of *Pliodytes lanquisti* and falls within the range of *Podiceps auritus*, from which it shows no significant differences. The proximal end of a humerus from Bone Valley (USNM 447059), which presumably is from the same species of grebe as represented by the holotype of *Pliodytes lanquisti*, is indistinguishable from comparable elements from Lee Creek Mine, and these in turn are identical to *Podiceps auritus*. Storer (this volume), although recognizing the affinities of the Lee Creek grebe with *P. auritus*, according to long-accepted practice has emphasized slight differences and has named it as a new species, *Podiceps howardae*. In accordance with the philosophy outlined in our introduction, we emphasize its similarities to *P. auritus*.

Podiceps sociatus (Navás, 1922), a fossil species of grebe also the size of *P. auritus*, is known from as far back as the middle Miocene of Spain, although it was more primitive in some respects than the modern species (Olson, 1995).

The Horned Grebe is circumpolar in distribution and is one of the commoner grebes in the Northern Hemisphere, especially in marine environments, so it would not be surprising if its antecedents occurred in the same situations in the Pliocene.

PODICIPEDIDAE, genus and species indeterminate

MATERIAL.—Left tarsometatarsus lacking distal end and with proximal end badly damaged, USNM 501509.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Estimated length, 36.8.

REMARKS.—This poorly preserved specimen comes from a grebe considerably smaller than *Podiceps* aff. *auritus* (above). The tarsometatarsus is relatively shorter and more robust than it is in the Eared Grebe, *Podiceps nigricollis* Brehm, and perhaps comes from a grebe with less specialized tarsal morphology, such as the species of *Tachybaptus* Reichenbach (see Olson, 1995).

Order PROCELLARIIFORMES (tubenoses)

Two of the four families of this order, Diomedidae and Procellariidae, are abundantly represented at Lee Creek Mine. The diving-petrels (Pelecanoididae) are known only from the Southern Hemisphere and would not be expected, whereas the absence of storm-petrels (Oceanitidae=Hydrobatidae auct.) is almost certainly an artifact of collection and taphonomy. Although storm-petrels are common in the same area today and would doubtless have been so in the Pliocene, they are the smallest members of the order and feed entirely from the surface of the water; thus, they would be less likely to fall prey to submarine predators. This is probably the main factor contributing to their absence at Lee Creek Mine, although the small size of their bones also would make them less likely to be spotted by collectors. The only Tertiary locality where fossils of

storm-petrels have been found in numbers is a coastal site in South Africa thought to be in the immediate vicinity of insular breeding colonies (Olson, 1985b), whereas in nearby pelagic deposits storm-petrels were all but absent (Olson, 1985c).

Family DIOMEDEIDAE (albatrosses)

Albatrosses now occur largely in the southern oceans, with only three modern species found in the North Pacific and none found in the North Atlantic, except as very rare vagrants. Thus, it is of considerable interest that over 500 specimens representing five species of albatross have been recovered from Lee Creek Mine. The only albatross known from the Calvert Formation is a rare, very small species, even smaller than the smallest one known from Lee Creek Mine. Because of this and the similarity of the Lee Creek birds to modern species, and as indicated by microfossil analysis of the matrix associated with some of the fossils, all of the Lee Creek albatross material is regarded as being from the Yorktown Formation.

In attempting to identify the Lee Creek fossils and in making comparisons with modern taxa, we found that all the North Pacific albatrosses (Short-tailed Albatross, *Phoebastria albatrus* (Pallas); Black-footed Albatross, *P. nigripes* (Audubon); Laysan Albatross, *P. immutabilis* (Rothschild)) differ from all the smaller Southern Hemisphere albatrosses (mollymawks, *Thalassarche* Reichenbach; sooty albatrosses, *Phoebastria* Reichenbach) in having the tarsometatarsus proportionately longer and more slender (Plate 8). In this respect the North Pacific albatrosses were more similar to the "great" albatross group, which consists of the Wandering Albatross, *Diomedea exulans* Linnaeus; Amsterdam Albatross, *D. amsterdamensis* Roux et al.; and Royal Albatross, *D. epomophora* Lesson, than to the mollymawks or the sooty albatrosses.

These osteological observations have been corroborated by DNA sequences in which four major groups of albatrosses were recognized (Nunn et al., 1996): the North Pacific species just mentioned (plus the Waved Albatross, *D. leptorhyncha* Coues (= *D. irrorata* Salvin auct.)), which take the name *Phoebastria*; the great albatrosses, genus *Diomedea* Linnaeus, which forms the sister group of *Phoebastria*; the mollymawks, genus *Thalassarche*; and the sister-group of the latter genus, *Phoebastria*. We have followed this classification herein.

Genus *Phoebastria* Reichenbach

Phoebastria anglica (Lydekker, 1891a), new combination

PLATES 6a, 7e, g, i, l

Diomedea anglica Lydekker, 1891a:189.

?*Diomedea californica* L. Miller, 1962:471.

Diomedea sp. A, Chandler, 1990a:100.

MATERIAL.—Fragment of ramus of furcula, USNM 206434. Proximal ends of right scapulae, USNM 192688, 430529,

464253. Proximal end of right humerus, USNM 242324; distal end of right humerus, USNM 366454; distal end of left humerus, USNM 183511. Proximal end of left ulna, USNM 430602; distal ends of right ulnae, USNM 193160, 252321; distal end of left ulna, USNM 430528. Associated(?) distal ends of left ulna and radius, USNM 215748, 215751. Proximal ends of right carpometacarpus, USNM 193170, 321242, 366628; proximal end of left carpometacarpus, USNM 430590; distal ends of right carpometacarpus, USNM 302354, 366922, 464254. Major alar digit phalanx 1, USNM 430526. Left femur, USNM 210458; proximal end of right femur, USNM 368546; distal ends of right femora, USNM 181085, 308201, 366689, 366906, 430530; distal ends of left femora, USNM 464255, 464256. Distal ends of right tibiotarsi, USNM 206486, 206638, 241429, 248495, 464257; distal ends of left tibiotarsi, USNM 181045, 248533, 321230, 430531, 430532, 464258. Right tarsometatarsi, USNM 250732, 430538; left tarsometatarsi, USNM 250777, 430533; proximal ends of left tarsometatarsi USNM 250739, 366627, 368543, 430622, 464259, 464260; shafts of right tarsometatarsi, USNM 192809, 215478, 241431; shaft of left tarsometatarsus, USNM 256257; distal ends of right tarsometatarsi, USNM 193142, 257457, 366716, 430539, 464261–464263; distal ends of left tarsometatarsi, USNM 215884, 250743, 250758, 252303, 256250, 275850, 321236, 430534, 430535, 430537, 430619, 464264, 464265. Pedal phalanges, USNM 192469, 257482, 366380, 464266–464274.

HORIZON.—Yorktown Formation (USNM 181085 from basal Yorktown as determined from foraminifera in matrix).

ADDITIONAL MATERIAL EXAMINED.—*Red Crag Formation, England:* Right tarsometatarsus, USNM 215038 (cast of holotype).

Coralline Crag Formation, England: Proximal two-thirds of right ulna, USNM 215040 (cast of paratype).

Bone Valley Formation, Florida: Distal end of left ulna, UF 123829. Right carpometacarpus, UF 65765. Distal end of right tibiotarsus (cast), USNM 16751. Left tarsometatarsus, UF 53942; distal end of left tarsometatarsus, UF 57309.

San Diego Formation, California: Right tarsometatarsus, SDSNH 27872.

MEASUREMENTS.—See Table 3.

REMARKS.—*Diomedea anglica* was originally described by Lydekker (1891a) from an associated tarsometatarsus and phalanx 1, supposedly of pedal digit IV, from the late Pliocene Red Crag at Foxhall, Suffolk, England. The phalanx, however, is actually that of digit II, the phalanx for digit IV in albatrosses being proportionately much longer and more slender. The proximal end of an ulna from the underlying Coralline Crag in the same vicinity (Lydekker, 1891b:395) was soon after considered to belong to the same species. Both these records are now considered to be late Pliocene (MN 16–17) in age (Mlikovsky, 1996:766). Later, Wetmore (1943a) referred the distal end of a tibiotarsus from Bone Valley, Florida, to *D. anglica*.

Lydekker (1891a) characterized the tarsometatarsus of *Diomedea anglica* as being somewhat smaller and proportionate-

ly more slender than that of *D. exulans*. Harrison and Walker (1978) concluded that *D. anglica* was a valid species that seemed most similar to *D. albatrus* but was larger. An albatross the size of *D. anglica* is one of the two most common albatross species at Lee Creek Mine. We examined additional material from the Bone Valley Formation in Florida that falls in the same size class, as well as a specimen from the San Diego Formation in California first reported by Chandler (1990a:100) as an unidentified species of *Diomedea*. We refer all of this material to Lydekker's species *Diomedea anglica*, but under the genus *Phoebastria*, as explained below.

The species known as *Diomedea californica* L. Miller, 1962, may be the Miocene representative of this same lineage. It was originally described from the distal end of a tarsometatarsus from the middle Miocene of Sharktooth Hill (Miller, 1962), with the distal end of a humerus and another tarsometatarsus from the same locality being referred later (Howard, 1966, 1978). A tibiotarsus from the late Miocene at Laguna Niguel, Orange County, also was referred, with a query, to *D. californica* (Howard, 1978). The distal width of the holotypical tarsometatarsus was 20.6 mm, and that of the referred specimen was about 21.5 mm (as extrapolated from the percentages given by Howard, 1978), which is within or very near the range for the series of tarsometatarsi from Lee Creek Mine assigned to *Phoebastria anglica* (18.7–21.2 mm, $n=21$). The humerus referred to *D. californica* had a distal width of 27.5 mm, which compares very well with three assigned to *P. anglica* from Lee Creek Mine (27.3, 28.5, 30.2 mm).

There are few living albatrosses the size of *Phoebastria anglica*, which was larger than all known species except the great albatrosses. The largest living species are the Wandering and Royal albatrosses (*Diomedea exulans* and *D. epomophora*). Based on specimens available to us, these have larger and much more robust tarsometatarsi than does *P. anglica* (Table 3). Our series of both modern species, however, was quite inadequate because there are several recognized subspecies in this complex, some of which differ in size, so there may be more overlap than was apparent in our comparisons.

Another enigmatic member of the great albatross group is the Amsterdam Albatross, *Diomedea amsterdamensis* (Plates 6b, 7f,h,m), known from a small remnant population on Amsterdam Island in the southern Indian Ocean. This was named as recently as 1983 (Roux et al., 1983), and although photographs of living specimens were published with the original "description," the so-called "holotype" was evidently a composite assortment of subfossil bones, perhaps belonging to several different individuals. It was not stated what elements of the skeleton were included in the "holotype," nor were any measurements or comparisons made of these bones, the characterization of the species thus being utterly inadequate. The taxon is sometimes considered to be a subspecies of *D. exulans* (e.g., Warham, 1990:424).

We were able to examine a small composite assortment of bones of *Diomedea amsterdamensis* (USNM 560597), which

shows this species to be smaller than any of the available specimens of *D. exulans*, although it is about the size of the fossils we have referred to *Phoebastria anglica* (Table 3). Although *P. anglica* possibly falls within the lower size ranges of the great albatrosses of the restricted genus *Diomedea*, there is no other indication of now-exclusively Southern Hemisphere albatrosses in the Northern Hemisphere. Thus, it appears much more likely that *anglica* is a very large member of the Northern Hemisphere albatrosses of the genus *Phoebastria*, to which we refer it. As such, it may be regarded as an extinct lineage with no living descendants.

Phoebastria aff. *albatrus* (Pallas)

PLATES 6f,k, 7a,j, 8a

Diomedea howardae Chandler, 1990a:96.

MATERIAL.—Portion of ramus of furcula, USNM 430609. Fragment of shaft of right coracoid, USNM 206548. Anterior end of right scapula, USNM 193298. Proximal end of left humerus, USNM 460858; distal ends of right humeri, USNM 242347, 256249, 430607; distal end of left humerus, USNM 430606. Proximal ends of left ulnae, USNM 179230, 181039; distal ends of right ulnae, USNM 430598, 430599, 430601; distal ends of left ulnae, USNM 206623, 430603, 430605. Proximal ends of left radii, USNM 181068, 250825; distal ends of right radii, USNM 193149, 241368; distal ends of left radii, USNM 215563, 244300, 464290. Left carpometacarpus lacking minor metacarpal, USNM 430588; proximal ends of right carpometacarpi, USNM 192023, 206499, 256211, 275854, 430593; proximal end of left carpometacarpus, USNM 430589; distal end of right carpometacarpus, USNM 193319; distal end of left carpometacarpus, USNM 430591. Major alar digit phalanx 1, USNM 193378. Left femur, USNM 192945; distal ends of left femora, USNM 177921, 366925, 430610. Proximal end of right tibiotarsus, USNM 308215; distal ends of right tibiotarsi, USNM 241361, 308249; distal ends of left tibiotarsi, USNM 275849, 430614, 430616. Right tarsometatarsi, USNM 193223, 275847, 430629; left tarsometatarsi, USNM 181095, 430618; proximal end of right tarsometatarsus, USNM 368545; proximal end of left tarsometatarsus, USNM 178191; distal end of right tarsometatarsus, USNM 464245; distal ends of left tarsometatarsi, USNM 192858, 192876, 430626. Pedal phalanges, USNM 464275–464280.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*Bone Valley Formation, Florida:* Distal end of right ulna, UF 53915. Left tarsometatarsus, UF 94549.

San Diego Formation, California: Distal half of left carpometacarpus, SDSNH 25244. Right major alar digit phalanx 1, SDSNH 25243. Right tarsometatarsus, SDSNH 25245 (holotype of *Diomedea howardae*).

MEASUREMENTS.—See Table 3.

REMARKS.—The Short-tailed Albatross, *Phoebastria albatrus* (Plates 6l–o, 7b), was probably the common inshore al-

TABLE 3.—Length (mm) of the tarsometatarsus in large living and fossil albatrosses *Diomedea* and *Phoebastria*. (*n*=number of specimens.)

Species	<i>n</i>	Range	Mean
<i>D. epomophora</i>	2	125.0–128.1	126.5
<i>D. exulans</i> subsp.	5	113.2–125.8	121.3
<i>D. amsterdamensis</i>	2	106.9–111.6	109.2
<i>P. anglica</i> (holotype)	1	—	110.9
<i>P. anglica</i> , Lee Creek Mine	4	110.3–117 ⁺	113.5
<i>P. anglica</i> , Bone Valley	1	—	118.5
<i>P. anglica</i> , San Diego Formation	1	—	112.8
<i>P. albatrus</i>	25	89.5–104.0	98.4
<i>P. aff. albatrus</i> , Lee Creek Mine	5	97.7–103 ⁺	100.9
<i>P. aff. albatrus</i> , Bone Valley	1	—	105.2
<i>P. albatrus</i> , San Diego formation (holotype of <i>D. howardae</i>)	1	—	101.7

batross in the North Pacific in pre-human times. Hunting and fishing cultures around the northern Pacific rim took a heavy toll on the species, at least on the wintering grounds. In the nineteenth and twentieth centuries the combination of Japanese feather hunters and volcanic eruptions nearly exterminated the species from its remaining breeding grounds in the Volcano Islands, south of Japan, and the population of this species is still perilously low but has been increasing.

The commonest albatross at Lee Creek Mine is similar to *P. albatrus* in size, being larger than any of the Northern Hemisphere species except *P. anglica*. We have identified specimens from Bone Valley, Florida, as belonging to the same species. Further evidence of the presence of this lineage in the North Atlantic comes from a mid-Pleistocene deposit on Bermuda, where there was clearly a breeding colony of *P. albatrus*, as numerous bones were found of non-volant juveniles, and in some cases even of embryos (Olson, unpublished data). A rapid and very high sea-level stand about 450,000 years ago (Hearty et al., 1999) probably caused the extinction of this species on Bermuda and in the entire North Atlantic.

The Lee Creek Mine material shows some differences from *P. albatrus*, such as in the shape and orientation of the internal tuberosity of the humerus and the less proximally oriented head of the femur. These may be only temporal differences in the same species lineage.

The species described as *Diomedea howardae* from a tarsometatarsus from the late Pliocene San Diego Formation in California (Chandler, 1990a) is the size of *Phoebastria albatrus* (Table 3), but it was not compared with that species in the original description. It was diagnosed on supposed differences in the shape of the distal foramen that do not hold up in a series of modern *P. albatrus*. We consider *Diomedea howardae* Chandler, 1990a, to be synonymous with *Phoebastria albatrus* (Pallas, 1769).

That albatrosses of this size have occurred in the Pacific well before the early Pliocene is shown by a tarsometatarsus from the middle Miocene Astoria Formation in Oregon (USNM 424081, Plate 6g) that has a decidedly modern aspect.

Phoebastria aff. nigripes (Audubon)

PLATE 8d

MATERIAL.—Distal ends of right humeri, USNM 430608, 464243; distal end of left humerus, USNM 366898. Distal ends of right tibiotarsi, USNM 183457, 248572, 275798; distal ends of left tibiotarsi, USNM 177900, 192950, 430613, 430615.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Tables 4, 5.

REMARKS.—The Black-footed Albatross, *Phoebastria nigripes* (Plates 7k, 8b,f), and the Laysan Albatross, *P. immutabilis* (Plates 6d, 8c,g), are medium-sized species confined today to the North Pacific, where their main breeding grounds are in the northwestern Hawaiian Islands. Despite their considerable differences in plumage, the two species hybridize with some regularity.

Although *P. nigripes* is definitely the larger species, there is overlap in the measurements of some of the elements (e.g., see Table 4) so that many of the fossils in this general size range from Lee Creek Mine probably cannot be identified except as belonging to one or the other of these two species. We have not undertaken a comprehensive analysis of this material but have attempted only sufficient comparisons to establish that both species are indeed present in the fauna.

Among eight distal ends of humeri in this size class recovered at Lee Creek Mine (Table 4) are three that are larger than the largest available specimen of *P. immutabilis* and hence are assigned to *P. aff. nigripes*. Three others are in the area of overlap between the two species and could belong to either.

The situation with distal ends of tibiotarsi was more complex. In our comparative series, there was essentially no overlap in this measurement between the two species, *P. nigripes* being larger (Table 5). All of the fossil specimens that had originally been assigned to this size class, however, fell within the range of *P. immutabilis*. We then found that some of the specimens that had been assigned to the *P. albatrus* size class were too small for that species. The smallest of six modern specimens of *P. albatrus*, a juvenile, had the distal width of the tibiotarsus 16.9 mm, which is barely larger than the largest *P. nigripes*, but the shaft in this specimen is markedly more robust. Based on measurements of distal width and visual comparison of the robustness of the shaft, we assign the tibiotarsi listed above to *P. aff. nigripes*.

Although more material than we have identified doubtless belongs to this species, *P. aff. nigripes* is apparently less common in the Lee Creek Mine deposits than is *P. aff. immutabilis*. We also examined the distal end of a left ulna from the Bone Valley Formation in Florida (UF 95654) that belongs in the *P. nigripes/P. immutabilis* size range and which appears to be the first record of an albatross other than *P. anglica* in those deposits.

Phoebastria aff. immutabilis (Rothschild)

PLATES 6c, 7c

MATERIAL.—Distal end of right humerus, USNM 367115; distal end of left humerus, USNM 430677. Right carpometacarpus lacking minor metacarpal, USNM 460841. Distal ends of right tibiotarsi, USNM 193387, 302293, 321274, 366669, 430686–430688, 460864, 460865; distal ends of left tibiotarsi, USNM 183440, 430680, 430681, 430683, 430684, 460847, 464247, 464248. Right tarsometatarsus, USNM 464250; left tarsometatarsus, USNM 430689.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Carpometacarpus*: Length, 96.9 (within range of *Phoebastria immutabilis* and smaller than any of four females of *P. nigripes* (100.0–103.6); see also Tables 4, 5).

REMARKS.—As discussed under the preceding species, several distal ends of tibiotarsi and two distal ends of humeri from Lee Creek Mine are too small to belong to *Phoebastria nigripes* and fall within the range of variation of *P. immutabilis*. In addition, there are two complete tarsometatarsi with lengths of 87.5 and 87.8 mm, values well within the range of females of *P. immutabilis* (Table 6), from which they are inseparable.

Phoebastria aff. nigripes or *P. aff. immutabilis*

The following specimens from Lee Creek belong to one or the other of these two species but have not been further identified.

Proximal, shaft, and distal fragments of left humerus, USNM 193231; distal ends of right humeri, USNM 193250, 430679; distal ends of left humeri, USNM 430678. Proximal ends of right ulnae, USNM 366663, 366717; proximal ends of left ulnae, USNM 210448, 242315, 430656, 430657; distal ends of right ulnae, USNM 181057, 192487, 206350, 215743, 366417, 366648, 430658–430663, 430666, 460840, 460859; distal ends of left ulnae, USNM 181075, 193388, 206475, 366803, 366939, 367000, 368466, 368542, 430664, 430665, 430667–430669, 430671, 430672. Proximal end of left radius, USNM 366435; distal ends of left radii, USNM 464288, 464289. Proximal portions of right carpometacarpi, USNM 430654, 460854; proximal halves of left carpometacarpi, USNM 430647–430649, 460855, 460856; distal ends of right carpometacarpi, USNM 206566, 275799, 368554, 430592, 460857; distal ends of left carpometacarpi, USNM 178090, 256237, 430655. First phalanges of major alar digit USNM 206557, 460846, 460862, 460863, 464282, 464283. Right femur, USNM 460860; proximal ends of right femora, USNM 321302, 430674; proximal end of left femur, USNM 215479; distal ends of right femora, USNM 308223, 430675, 430676, 460861; distal ends of left femora, USNM 321312, 430673. Proximal end of right tibiotarsus, USNM 430685. Proximal and distal ends of right tarsometatarsus, USNM 464251; proximal and distal ends of left tarsometatarsus, USNM 430691; proximal ends of right tarsometatarsi, USNM 275816, 366346,

430694, 430695, 430707; proximal ends of left tarsometatarsi, USNM 192654, 241372, 252306, 366347, 430690, 464252; distal ends of right tarsometatarsi, USNM 181110, 192705, 275823, 302317, 430696, 430697, 460851, 460852, 464249; distal ends of left tarsometatarsi, USNM 248542, 257500, 302292, 430693. Pedal phalanges, USNM 177819, 248577, 321229, 464284–464287.

Phoebastria rexsularum, new species

PLATES 6*h,i*, 8*e*

HOLOTYPE.—Right tarsometatarsus, USNM 302313.

TYPE LOCALITY.—Texasgulf Inc. Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23'22"N, 76°47'06"W).

HORIZON.—Yorktown Formation, lower Pliocene.

DISTRIBUTION.—Known so far only from the type locality and from the Rappahannock River in Middlesex County, Virginia.

MEASUREMENTS OF HOLOTYPE (mm).—Length, 73.9; proximal width, 13.7; width and depth of shaft at midpoint, 5.5 × 6.0; distal width, 13.8; depth of middle trochlea, 8.4; width through outer and middle trochleae, 9.7.

TOPOYTICAL PARATYPES.—Distal end of left humerus, USNM 302414. Distal ends of right tibiotarsi, USNM 250848, 275795, 308185; distal ends of left tibiotarsi, USNM 178050, 430682, 430701, 430702, 464291. Right tarsometatarsi, USNM 430704, 430705; proximal ends of right tarsometatarsi, USNM 242334, 366607, 430708, 460848, 460849; proximal end of left tarsometatarsus, USNM 460850; distal ends of right tarsometatarsi, USNM 366611, 460838; distal ends of left tarsometatarsi, USNM 430703, 460853. Pedal phalanx, USNM 464281.

The following specimens are tentatively referred to this species, most being very fragmentary or undiagnostic, although they appear to be too small for *Phoebastria* aff. *immutabilis*.

Shaft of right coracoid, USNM 430700. Three fragments of proximal end of left humerus, USNM 430699. Distal end of right ulna, USNM 430670; distal end of left ulna, USNM 460839. Proximal ends of right carpometacarpi, USNM 178066, 430653; proximal ends of left carpometacarpi, USNM 460842, 460843; distal ends of right carpometacarpi, USNM 250702, 460844, 460845; distal end of left carpometacarpus, USNM 257494.

ADDITIONAL PARATYPE.—Left tarsometatarsus lacking proximal end, USNM 256620, south side of Rappahannock River, 3 mi (5 km) upstream from Stingray Point, near Deltaville, Middlesex County, Virginia; collected by Eldon Branch, received in 1979.

The specimen was found as a "float" and is presumed to be from the Yorktown Formation, which crops out there.

MEASUREMENTS OF PARATYPES (mm).—*Tarsometatarsus* (USNM 256620): Distal width, 14.1.

For measurements of other paratypes see Table 6.

ETYMOLOGY.—"King of the gannets," from Latin *rex*, king, and the genitive plural of *Sula*, now used as the generic name

TABLE 4.—Comparison of distal width (mm) of humerus of modern and fossil medium-sized albatrosses, *Phoebastria*. Measurements are in list form for fossil species. (*n*=number of specimens.)

Species	<i>n</i>	Range	Mean
<i>P. immutabilis</i> females	9	20.9–22.2	21.5
<i>P. immutabilis</i> males	9	21.9–23.5	22.9
<i>P. aff. immutabilis</i> , Lee Creek Mine	2	21.6, 21.8	—
<i>P. aff. immutabilis/nigripes</i> , Lee Creek Mine	3	22.6, 22.9, 23.0	—
<i>P. aff. nigripes</i> , Lee Creek Mine	3	23.7, 23.8, 24.0	—
<i>P. nigripes</i> females	4	22.6–24.0	23.4
<i>P. nigripes</i> males	5	23.1–24.3	23.8

TABLE 5.—Comparison of distal width (mm) of tibiotarsus of modern and fossil medium-sized albatrosses, *Phoebastria*. (*n*=number of specimens.)

Species	<i>n</i>	Range	Mean
<i>P. immutabilis</i> females	6	12.1–13.2	12.6
<i>P. immutabilis</i> males	8	14.4–15.0	14.7
<i>P. aff. immutabilis</i> , Lee Creek Mine	17	13.0–14.8	14.0
<i>P. aff. nigripes</i> , Lee Creek Mine	5	14.9+–16.5	15.8
<i>P. nigripes</i> females	4	14.9–15.4	15.2
<i>P. nigripes</i> males	5	15.1–16.7	15.6

TABLE 6.—Measurements (mm) of hindlimb elements of *Phoebastria rexsularum*, new species, compared with females (the smaller sex) of modern *P. immutabilis*.

Element	<i>P. rexsularum</i> , n. sp.			<i>P. immutabilis</i> , females		
	<i>n</i>	Range	Mean	<i>n</i>	Range	Mean
Tibiotarsus						
Distal width	6	12.1–13.2	12.6	9	13.3–14.1	13.9
Tarsometatarsus						
Length	3	73.8–82+	78.5	9	83.7–88.5	86.1
Proximal width	9	12.5–14.2	13.5	9	14.8–15.8	15.4
Distal width	6	12.9–14.2	13.6	9	14.4–15.8	15.0

of boobies but derived from the Scandinavian name applied to the Northern Gannet, *Morus bassanus*. The name comes from the extraordinary example of a single female of the Southern Hemisphere Black-browed Albatross, *Thalassarche melanophris* (Temminck), that appeared in a gannetry on Myggenaes Holm in the Faeroe Islands in 1860 and returned each summer for 34 years until shot in 1894 (Andersen, 1894, 1895; Murphy, 1936:511). During this time it was known among the Faeroese who visited the gannetry as "Sulekongen," or "Gannet King," as the gannets would make way for the albatross when it moved about the colony.

DIAGNOSIS.—This species is referable to *Phoebastria* by the slender configuration of the tarsometatarsus; it is without expanded articular surfaces seen in *Thalassarche*, but it is smaller than any other member of the genus and is probably smaller than any existing species of albatross.

REMARKS.—In sorting the albatross material from Lee Creek Mine, it became evident that some of the specimens at the small end of the observed size variation were too small to be encompassed by the range of variation seen in the size class including *P. nigripes* and *P. immutabilis*. Although in life there may have been overlap in size between this smallest species

and *P. aff. immutabilis*, we have assigned fossil leg elements to the new species only when they are smaller than observed in a series of females of modern *P. immutabilis*. The holotype of *P. rexsularum* is from a particularly small individual, being a full centimeter shorter than the shortest available tarsometatarsus of *P. immutabilis*.

The distal width of the humerus assigned to *P. rexsularum* is 20.7 mm, which is smaller than that in any available specimen of *P. immutabilis* or *P. nigripes* (Table 4). The pedal phalanx referred to *P. rexsularum* is the diagnostic long, slender proximal phalanx of the fourth toe, which measures 43.9 mm in length. The same element in a small female of *P. immutabilis* was 51.8 mm long, again illustrating how small some individuals of *P. rexsularum* must have been.

Howard (1966) described a new species of rather small albatross, *Diomedea milleri*, from the middle Miocene deposits of Sharktooth Hill, California. The holotype is the most proximal portion of a left ulna and was compared only with a single modern specimen of *D. (=Phoebastria) nigripes*. The proximal end of a tarsometatarsus from the same locality was referred to *D. milleri* in the same publication. Howard and Barnes (1987) later tentatively referred another proximal end of an ulna with associated fragments of radii from middle Miocene deposits at Oso Creek, Orange County, California, to *D. milleri*. The proximal widths of the holotype and of the Oso Creek specimen were 14.4 and 15.8 mm, respectively, whereas in a small female of *Phoebastria immutabilis* (USNM 488178) the same measurement is 12.7 mm. No measurements were given for the referred tarsometatarsus, but if the illustration (Howard, 1966, fig. 1e) is at natural size, as stated, the proximal width would be about 18 mm, which is considerably larger than it is in any female of *P. immutabilis* measured (Table 6). The material of *D. milleri* is probably inadequate for characterization of a new species of albatross, but the available evidence suggests that it was not smaller than *P. immutabilis*. Therefore there is no reason to identify it with *P. rexsularum*.

Chandler (1990a:100) mentioned the distal end of a tibiotarsus from the San Diego Formation as belonging to a small albatross ("*Diomedea* sp. B") that he said was "86 percent that of *D. nigripes* in distal width." Because no measurements were given for either species, there is no way to assess the actual size of the specimen from his publication.

Phoebastria rexsularum represents the least-common size class of albatross at Lee Creek Mine. Curiously, this smallest of the Northern Hemisphere albatrosses, and *D. anglica*, the largest, were the ones that became extinct, whereas the three species of intermediate size have persisted elsewhere up to the present.

Family PROCELLARIIDAE (shearwaters and petrels)

By far the majority of fossils of this family from Lee Creek Mine are referable to the genus *Puffinus* Brisson and the close-

ly related genus *Calonectris* Mathews and Iredale. The identification of these fossils was extremely difficult for reasons given below. To begin with, many fossil species of *Puffinus* have been described and named from deposits of various ages on both sides of the Atlantic and from the eastern Pacific. A proper treatment of the Lee Creek fossils would have to take these fossil taxa into account, necessitating a great deal of revisionary work.

Another problem with the Lee Creek Mine material in particular is that species lineages in the Procellariidae appear to have changed very slowly, if at all, through time. Species of *Puffinus* in the Calvert Formation, for example, may be extremely similar to living species. Thus, when precise stratigraphic information is absent it is impossible to determine whether a given form of *Puffinus* from Lee Creek Mine is middle Miocene or early Pliocene in age.

Shearwaters of the genera *Puffinus* and *Calonectris* were treated in an admirable monograph by Kuroda (1954), who examined osteology in addition to external characters. He was careful to attempt to distinguish between primitive and specialized characters well before the advent of cladistics.

In summary, the species of shearwaters are marked by a progression from a primitive, aerially adapted condition (*Calonectris*) to increasing use of both the wings and feet for underwater propulsion—what Kuroda referred to as "aquatic" adaptations—in which the humerus becomes flattened, the forewing shortened, the pelvis laterally compressed and lengthened, the femur stouter and more curved, the cnemial crest of the tibiotarsus lengthened, and the tarsometatarsus more laterally compressed—all of these being typical diving adaptations also found in other groups of birds. The groups consisting of the Wedge-tailed Shearwater (*Puffinus pacificus* (Gmelin)) and Buller's Shearwater (*P. bulleri* Salvin, subgenus *Thyellodroma* Stejneger), and the Pink-footed Shearwater (*P. creatopus* Coues) and Flesh-footed Shearwater (*P. carneipes* Gould, subgenus *Hemipuffinus* Iredale), are only slightly more specialized along these lines than is *Calonectris* and are hardly separable from one another except on size. The Greater Shearwater, *Puffinus gravis* (O'Reilly) (subgenus *Ardenna* Reichenbach), occupies an intermediate position between those species and the most specialized members of the family, which are of the subgenus *Puffinus*. Among the last, the Short-tailed Shearwater, *P. tenuirostris* (Temminck), appears to be the least derived.

Despite the distinct osteological differences between *Calonectris* and the different subgroups of *Puffinus*, the nature of the fossils from Lee Creek Mine still renders them difficult to identify. There is practically no associated material. Bones of the wing are much more frequently represented than are elements of the hindlimb, and these are almost always broken. Whereas complete humeri of *Puffinus* would be relatively easy to assign to one subgroup or another, the differences become greatly blurred when hundreds of fragmentary distal ends with varying degrees of wear are compared. Therefore, we have not attempted to identify many of the specimens of Procellariidae

to species. Instead we have selected only a few specimens of some of the more diagnostic elements in order to attempt to assess the minimum number of species that are present in the faunas. Further refinements will have to await much patient revisionary analysis. The great majority of the procellariid fauna at Lee Creek Mine is apparently made up of the five medium-large species *Calonectris* aff. *diomedea*, *C.* aff. *borealis*, *Puffinus* aff. *gravis*, *Puffinus* (*Ardenna*) sp., and *P.* aff. *pacificoides*.

Below, we identify 16 species of Procellariidae from the Lee Creek deposits. This is undoubtedly a minimum and others will almost certainly be distinguished among the specimens already at hand.

Genus *Pterodromoides* Seguí et al. (in press)

Pterodromoides minoricensis Seguí et al. (in press)

PLATE 9o

MATERIAL.—Distal end of left humerus lacking ectepicondylar spur, USNM 464315.

HORIZON.—Yorktown Formation (see below).

MEASUREMENTS (mm).—Distal width, 8.9; distal depth through ulnar condyle, 5.8; width and depth of shaft 20 mm above distal extremity, 4.4 × 3.1.

REMARKS.—This bone seemingly cannot be assigned to any living genus in the family. There is practically no expansion of shaft above the entepicondyle, even to the rather limited extent seen in *Pterodroma* Bonaparte and quite unlike *Puffinus*, and the brachial depression is large and deep. The specimen appears to be closest to that of the so-called "fulmarine" petrels, exemplified by *Fulmarus* Stephens, but it is smaller than any of those birds. It is of a rather unusual size class for the family, being intermediate in size between the largest of the smaller species of *Pterodroma* and the smallest of the larger species of that genus.

We had originally listed this specimen only as "Procellariidae, genus and species indeterminate," the preceding paragraph having been written before we thought to compare the specimen with *Pterodromoides minoricensis* Seguí et al. (in press). This is a new genus and species described from Mio/Pliocene deposits on Menorca in the Balearic Islands of the Mediterranean, which was shown to have similarities to the Fulmarinae. Olson examined and compared some of the type material and agreed that it could not be referred to any known genus of Procellariidae. The distal width of the humerus of *P. minoricensis* was given as 9.2, 9.3, and 9.6 mm, and the slightly smaller size of the Lee Creek fossil (8.9 mm) would probably fall within the range of a larger sample. The fact that, as remarked above, this is an unusual size class within the Procellariidae makes the assignment of the Lee Creek fossil all the more likely.

The deposits on Menorca from which *P. minoricensis* was obtained could not be dated directly but were reasoned from faunal evidence to be Mio/Pliocene, but younger than Langhian

(middle Miocene), and they were inferred to be late Miocene. The shared presence of this species in Menorca and North Carolina suggests that the Lee Creek Mine specimen came from the Yorktown Formation. The temporal range of such a seabird could surely encompass both the late Miocene and the early Pliocene.

This trans-Atlantic correlation suggests that the wintering grounds of *P. minoricensis* included the western North Atlantic. That it is so rare at Lee Creek Mine may be due to taphonomic processes discussed above relating to its having been a surface feeder.

Genus *Procellaria* Linnaeus

This genus, including *Adamastor* Bonaparte, is now used for the four largest species of the family, apart from the albatross-sized giant petrels *Macronectes* Richmond. One of the species of petrels at Lee Creek Mine is of this size class, but it appears to be more closely related to *Calonectris* and is listed under that genus. The living species of *Procellaria* are practically confined to southern oceans, only two of them being found in the South Atlantic. For our comparisons we had only a single skeleton of each of the species except the White-chinned Petrel, *P. aequinoctialis*, of which we had 13.

Procellaria cf. *aequinoctialis* Linnaeus

PLATE 9y

MATERIAL.—Distal end of right tibiotarsus, USNM 464312.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 9.7; depth through inner condyle, 9.7; width of shaft 30 mm above distal extremity, 5.7.

REMARKS.—This bone is from a very large procellariid the size of males of *Procellaria aequinoctialis*, there apparently being no other species of the family that falls in this size range or any other procellariid fossils from Lee Creek Mine of such great size. At present, the breeding stations of *P. aequinoctialis* in the Atlantic are at Inaccessible Island in the Tristan da Cunha group, the Falklands, South Georgia, and possibly Gough Island. The normal modern range at sea does not extend north much beyond 15°S, so the Lee Creek bird may have been only a vagrant.

Procellaria cf. *parkinsoni* Gray

PLATE 9q,r

MATERIAL.—Proximal half of right humerus lacking most of pectoral crest and internal tuberosity, USNM 430845; distal third of right humerus, USNM 430726.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Greatest depth through head, 5.8; width and depth of shaft below pectoral crest, 7.6 × 6.1; distal width, 14.4; depth through radial condyle, 8.2 mm.

REMARKS.—The proximal portion of the humerus appears to be nearly identical with that of Parkinson's Petrel, *Procellaria parkinsoni*, not only in size and details of attachments, but also in the shape of the shaft, which is noticeably flattened on the anconal surface. The distal portion is an equally good match. The smallest species in its genus, *P. parkinsoni* breeds only in New Zealand but crosses the Pacific to winter off western America as far north as the latitude of Guatemala. Evidently it or a related form occurred in the Atlantic in the early Pliocene, possibly having been a vagrant entering through the Panamanian seaway.

Genus *Pterodroma* Bonaparte

Gadfly petrels of the genus *Pterodroma* are all but absent in the fossil record except at their nesting islands. Their rarity in marine deposits may be due to their feeding entirely from the surface, thus making them much less susceptible to predation by aquatic carnivores.

Pterodroma magn. lessonii (Garnot)

PLATE 9ff

MATERIAL.—Left tarsometatarsus lacking only the inner trochlea, USNM 430854.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Length, 45.0; proximal width, 7.9; width through outer and middle trochleae, 6.0; width and depth of shaft at midpoint, 3.9×3.7 .

REMARKS.—The lack of either lateral compression or asymmetry of the shaft distinguishes this bone from any of the species of *Puffinus*. It is too small for any of the species of *Procellaria* or *Fulmarus*, and it is compatible with the morphology in *Pterodroma*, within which, however, it is very large, being the size of the White-headed Petrel, *P. lessonii*. We did not have appropriate comparative skeletal material for this species, but the fossil matched very well in size with the tarsus as visible in skin specimens. *Pterodroma lessonii* is very much a southern species today, being found circumpolarly from Antarctica to about 33°S latitude. Gadfly petrels the size of those resident in the western North Atlantic, the Black-capped Petrel (*P. hasitata* (Kuhl)) and the Cahow (*P. cahow* Nichols and Mowbray), have not been found at Lee Creek Mine.

Genus *Bulweria* Bonaparte

Bulweria? sp.

MATERIAL.—Most of shaft of left humerus with distalmost portion of pectoral crest, USNM 464298; proximal two-thirds of shaft of left humerus with portions of pectoral and bicipital crests, USNM 501505.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Width and depth of shaft at approximate midpoint, 3.7×3.0 , 3.9×3.2 .

REMARKS.—The relatively terete shafts of these fragmentary specimens remove them from association with species of *Puffinus*. They indicate a species larger than Bulwer's Petrel, *Bulweria bulwerii* (Jardine and Selby), and about the size of the smallest of the forms of *Pterodroma* or of Jouanin's Petrel, *Bulweria fallax* Jouanin. The only species in this size range reported from the Atlantic Ocean is *B. bifax* Olson (1975), known only from Quaternary deposits on St. Helena Island (Olson, 1975), although the Indian Ocean species *B. fallax* has been recorded as a vagrant in Italy (Olson, 1985a).

Genus *Pachyptila* Illiger

The prions of the genus *Pachyptila* are small, filter-feeding petrels that are now entirely confined to the southern oceans. Thus, the following record was quite unexpected.

Pachyptila sp.

PLATE 9a,c,e

MATERIAL.—Distal end of right humerus, USNM 464313. Distal end of left tarsometatarsus, USNM 496162.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 7.6; distal depth through ulnar condyle, 6.0.

Tarsometatarsus: Distal width, 4.7; depth of middle trochlea, 2.7; width and depth of shaft 10 mm above distal extremity, 2.3×1.8 .

REMARKS.—These specimens are indistinguishable from medium-sized modern species of *Pachyptila*, the systematics of which is complex. The only previously known fossils of the genus are those reported from deposits contemporaneous with the Yorktown Formation in South Africa, where fossils in the size range of modern species occurred with those of a much larger extinct species, *P. salax* Olson (1985b).

Genus *Calonectris* Mathews and Iredale

Calonectris krantzi, new species

PLATE 9m,u

HOLOTYPE.—Distal end of left humerus, USNM 430724.

TYPE LOCALITY.—Texasgulf Inc. Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina ($35^{\circ}23'22''N$, $76^{\circ}47'06''W$).

HORIZON AND AGE.—Yorktown Formation, early Pliocene, inferred from preservation and lack of any known species of Procellariidae of such large size in deposits of middle Miocene age.

DISTRIBUTION.—Known so far only from the type locality.

MEASUREMENTS OF HOLOTYPE (mm).—Distal width, 15.8; depth through radial condyle, 9.5; shaft width and depth at proximal margin of brachial depression, 9.9×5.5 .

PARATYPES.—Right coracoid lacking part of head and external distal angle, USNM 250805. Proximal end of left humerus, USNM 464308; distal third of right humerus lacking ectepicondylar spur, USNM 430728; distal fourth of left humerus lacking ectepicondylar spur, USNM 464307. Distal two-thirds of right carpometacarpus, USNM 430718.

MEASUREMENTS OF PARATYPES (mm).—*Coracoid*: Head to tip of internal distal angle, 37.4.

Humerus: Proximal width, 21.2; distance from head to distal extent of pectoralis scar, 28.6; distal width, 15.9, 15.0.

ETYMOLOGY.—To Smithsonian photographer Victor E. Krantz, who, for nearly 30 years, has photographed thousands of fossil bird bones to illustrate dozens of publications, including this one, in recognition of his long service to avian paleontology.

DIAGNOSIS.—Referable to *Calonectris* by the following combination of characters: ectepicondylar spur relatively short and somewhat triangular (unlike the more elongate process in *Procellaria*); attachment of anterior articular ligament relatively short and wide (longer and narrow in *Procellaria*); brachial depression large and deep, extending proximally well past proximal margin of ectepicondylar spur, and shaft showing no signs of flattening or expansion of entepicondylar area (in the last two respects differing from *Puffinus*). Larger than any known species of *Calonectris*, falling within the size range of smaller species of *Procellaria*.

REMARKS.—The coracoid and carpometacarpus are referred to this species almost entirely on size and could belong with one of the other large species, although the coracoid differs in shape from that of *Procellaria*.

The largest form of *Calonectris* is Cory's Shearwater, *C. borealis* Cory, in which the distal width of the humerus ranges from 13.0 to 14.6 mm ($n=12$, all unsexed, average 13.9 mm). These figures do not adequately convey the more massive nature of the bones of the new species.

Calonectris aff. borealis (Cory)

PLATE 9i

MATERIAL.—Distal two-thirds of right humerus lacking most of ectepicondylar spur, USNM 501506.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 14.2.

REMARKS.—This specimen is clearly within the size range of Cory's Shearwater, *Calonectris borealis*, which is the largest of the living taxa of the genus. The Atlantic forms of *Calonectris*, all often considered to be subspecies of the Mediterranean Shearwater, *C. diomedea* (Scopoli), differ considerably in size. The material from Lee Creek Mine suggests that at least two of these lineages have been separate for some 5 Ma, for which reason subspecific rank seems inappropriate. The

Cape Verde Shearwater, *C. edwardsi* (Oustalet), of the Cape Verde Islands, is the smallest form and is supposed to winter in the vicinity of its natal islands, although this appears to be little more than an assumption. The largest species, *C. borealis*, nests on islands in the North Atlantic (Azores, Canaries, Madeira, Desertas, Porto Santo, Salvages, and the Berlengas off Portugal). *Calonectris diomedea* is of intermediate size and nests on islands of the Mediterranean. The nonbreeding ranges of *C. diomedea* and *C. borealis* have been confounded because both taxa have usually been considered together. Both, however, certainly occur in the North Atlantic Ocean off North Carolina today and evidently did so in the past as well (see following species). We depart from any of the modern lists we have cited in recognizing these taxa at the specific level.

Calonectris aff. diomedea (Scopoli)

PLATE 9s

MATERIAL.—Distal ends of right humeri, USNM 215433, 366013; distal end of left humerus, USNM 430745. Left femur lacking internal distal condyle, USNM 430950.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 12.5, 12.0, 12.7.

Femur: Length, 38.1; proximal width, 8.7.

REMARKS.—These specimens agree in size and general morphology with *Calonectris diomedea*, the Mediterranean member of the genus. These birds leave the Mediterranean in winter, and large numbers occur in the western North Atlantic Ocean off North Carolina (Lee, 1995:126). This also is the most abundant bird in a beach deposit on Bermuda dating to about 450,000 BP (Olson, unpublished data), which, with the Lee Creek Mine specimens, suggests that this pattern of winter distribution has been established for a very long time.

Genus *Puffinus* Brisson

Puffinus aff. pacificoides Olson, 1975

PLATE 9v,ee

MATERIAL.—*Associated Specimen*: Partial skeleton consisting of right and left coracoids, right humerus lacking head, proximal two-thirds of shaft of left humerus, and left carpometacarpus lacking minor metacarpal, USNM 464335.

Individual Elements: Left humerus lacking portions of pectoral crest, USNM 193130; right humeri lacking most of proximal end, USNM 430751, 430840. Left femora, USNM 242227, 501507; left femur lacking proximal end, USNM 501508. Right tarsometatarsus, USNM 430852; left tarsometatarsus, USNM 464297.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Coracoid*: Length with sternal facet flat on calipers, 25.8.

Humerus: Length, 99.4; length from distal extent of pectoral crest to ectepicondyle, 76.9, 74.5, 77.2, 77.7; distal width, 11.9, 11.8, 11.7, 12.4.

Femur: Length, 35.2, 37.8; proximal width, 8.2, 8.7; distal width, 8.1, 8.4, 7.9.

Tarsometatarsus: Length, 47.6, 47.3; proximal width, 7.6, 8.0; distal width, 7.7, 6.9.

REMARKS.—These specimens indicate a shearwater referable to the subgenus *Thyellodroma*, the existing members of which are *Puffinus pacificus*, of wide distribution in the Indian and Pacific oceans, and *P. bulleri* of New Zealand, wintering to the eastern Pacific. That this group formerly extended outside the Indo-Pacific was established by Olson (1975), who described a new species, *P. pacificoides*, from Pleistocene deposits on St. Helena Island in the South Atlantic Ocean. Most of the Lee Creek Mine fossils are from a species more robust than either *P. pacificus* or *P. bulleri* but quite similar to *P. pacificoides*. One femur (USNM 242227) is slightly smaller and decidedly more gracile than the other Lee Creek femora or those of *P. pacificoides* and closely resembles that of *P. bulleri*, possibly indicating a third species in the *Thyellodroma* group (see following species). Regardless, this group of shearwaters had a long history in the Atlantic, from which it vanished at some time in the Pleistocene.

Puffinus (Thyellodroma) sp.

PLATE 9gg

MATERIAL.—Distal end of right humerus, USNM 464303; distal end of left humerus, USNM 464301. Complete left tarsometatarsus, USNM 250810.

HORIZON.—Uncertain, but Pungo River Formation inferred from similarity to fossils of an unnamed species from Calvert Formation and differences from any modern species lineage.

MEASUREMENTS (mm).—*Humerus*: Distal width, 9.7, 9.0.

Tarsometatarsus: Length, 42.1; proximal width, 6.0+; distal width, 6.3.

REMARKS.—The humerus and tarsometatarsus in this species have a morphology consistent with that in the *Thyellodroma* group of shearwaters but come from a species much smaller than any modern taxon.

Puffinus (Ardena) sp.

PLATE 9bb,cc

MATERIAL.—Distal end of right humerus, USNM 179269; distal ends of left humeri, USNM 177786, 179249, 242329, 366613. Left tarsometatarsus lacking inner and outer trochleae, USNM 366625; proximal ends of left tarsometatarsi, USNM 177806, 366977; distal ends of left tarsometatarsi, USNM 181072, 215620.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 14.3, 14.6, 15.2, 14.3, 14.0.

Tarsometatarsus: Length, 65.1; proximal width, 9.5+, 9.7, 9.2; distal width, 8.3.

REMARKS.—This shearwater is a fairly common species in the Lee Creek Mine fauna. The humerus and tarsometatarsus are similar in morphology to those of *Puffinus gravis* (subgenus *Ardena* Reichenbach) but are larger.

Puffinus aff. gravis (O'Reilly)

PLATE 9p

MATERIAL.—Distal ends of right humeri, USNM 177890, 178187; distal end of left humerus, USNM 430709.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 13.7, 12.8, 12.4.

REMARKS.—The modern Greater Shearwater breeds at Tristan da Cunha and Gough islands and breeds in limited numbers in the Falklands, spending the boreal summer in the North Atlantic, a pattern of distribution that the fossils suggest may have been in effect for millions of years. *Puffinus conradi* Marsh (1870), from the Calvert Formation, is quite similar to the modern *P. gravis* and would be expected in the Pungo River Formation, as would the Pliocene representative of this subgenus.

Puffinus aff. tenuirostris (Temminck)

PLATE 9k,z

MATERIAL.—Distal portions of right humeri, USNM 430760, 430761; distal two-thirds of left humerus, USNM 464333. Complete left ulna, USNM 366014.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 10.8+, 11.9, 11.7.

Ulna: Length, 88.0.

REMARKS.—These remains indicate a shearwater with a very compressed shaft of the humerus. This species is smaller than the Sooty Shearwater, *Puffinus griseus* (Gmelin), but is larger than the Christmas Island Shearwater, *P. nativitatis* Streets, or any of the Manx Shearwater, *P. puffinus* (Brünnich), assemblage. No existing shearwater with these qualities is found in the Atlantic today, the only other one being *P. tenuirostris*, which breeds on islands around Australia and ranges widely over most of the Pacific. The well-preserved left humerus listed above (Plate 9k) is virtually identical to that of *P. tenuirostris* except for the shorter scar for the anterior articular ligament. The ulna is at the low end of the size range for *P. tenuirostris* or perhaps is smaller, but it has no closer match among other modern species of *Puffinus*. The species described as *P. holei* (Walker et al., 1990; emended to *P. holeae* by Mischeaux et al., 1991:806, note 11), from the Pleistocene of the Canary Islands, may bear scrutiny in connection with this material.

***Puffinus cf. puffinus* (Brünnich) sensu lato**PLATE 9*i*

MATERIAL.—Right humerus lacking head, internal tuberosity, and ectepicondylar spur, USNM 430765.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Length from distal extent of pectoralis scar to entepicondyle, 64.5; distal width, 10.8.

REMARKS.—Among the Lee Creek Mine collections are several specimens of humeri with compressed shafts that fall in the general size range of the various taxa often grouped as subspecies of the Manx Shearwater, *Puffinus puffinus*. The best preserved of these, listed above, has the size and proportions of the Levantine Shearwater, *P. mauretanicus* Lowe, a Mediterranean breeder that winters in the eastern North Atlantic. Nominate *P. puffinus* breeds on both sides of the North Atlantic and is highly migratory. The fossil taxa *P. nestori* (Alcover, 1989) and *P. olsoni* (McMinn et al., 1990), from the late Pliocene of Eivissa (Ibiza) and the Holocene of the Canary Islands, respectively, also belong in this group of small shearwaters.

***Puffinus magn. lherminieri* Lesson**PLATE 9*g, hh, ii*

MATERIAL.—Proximal end of right humerus, USNM 464332. Proximal end of left tarsometatarsus, USNM 464311; distal end of right tarsometatarsus, USNM 178074.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Proximal width, 11.3.

Tarsometatarsus: Distal width, 5.8.

REMARKS.—Remains of *Puffinus* in this smallest size class of the genus (which also includes the Little Shearwater, *P. assimilis* Gould) are extremely rare at Lee Creek Mine, despite the fact that Audubon's Shearwater, *P. lherminieri*, now occurs abundantly off North Carolina. The distal end of a tarsometatarsus listed above is only tentatively included because, although it is of an appropriate size, it is not referable with certainty to *Puffinus*.

Order PELECANIFORMES
(pelicans, cormorants, and allies)

Family PELECANIDAE
(pelicans)

Genus *Pelecanus* Linnaeus***Pelecanus schreiberi* Olson (1999)**PLATE 10*a-d*

MATERIAL.—Distal end of right femur, USNM 192077 (holotype); distal end of left femur, USNM 263567 (paratype). Pedal phalanx 1 of digit III, USNM 446506 (paratype); pedal phalanx 2 of digit III, USNM 421948 (paratype).

HORIZON.—Basal Yorktown Formation from matrix analysis of paratypical femur (Olson, 1999); also tentatively identified from early Pliocene Bone Valley Formation in Florida.

ADDITIONAL MATERIAL EXAMINED (paratypes).—*Bone Valley Formation, Florida*: Right quadrate lacking orbital process, UF 125031. Axis vertebra lacking dorsal spine, UF 65677.

MEASUREMENTS.—See Olson (1999).

REMARKS.—This large species exceeds in size either of the living North American pelicans (American White Pelican, *Pelecanus erythrorhynchos* Gmelin; Brown Pelican, *P. occidentalis* Linnaeus) and would have equalled the two largest modern pelicans in size (Dalmatian Pelican, *P. crispus* Bruch; Great White Pelican, *P. onocrotalus* Linnaeus). The fossil femora differ from all modern pelicans in having the rotular groove markedly deeper and narrower, the internal condyle more elevated anteriorly, and the intercondylar fossa narrower and deeper. The pedal phalanges are much more robust than are the comparable elements of modern pelicans.

The shaft of the femur of the holotype is filled with dense medullary bone. This serves as a calcium reserve in females, forming 10 to 14 days prior to egg-laying and being quickly resorbed afterwards (see references cited in Ballmann, 1979, and Mourer-Chauviré et al., 1999). Thus, this species must have been breeding in the vicinity of deposition.

Family PELAGORNITHIDAE
(pseudodontorns, false-toothed birds)

These gigantic, soaring, pseudotoothed birds are rather well represented in the Lee Creek Mine collections, but, as is usual in this group, only by scraps because the extremely thin walls of the bones are easily broken. Olson (1985d) reviewed some aspects of the systematics of these birds, concluding that all those known are referable to a single family, Pelagornithidae, which has several synonyms. The first species to be named was *Pelagornis miocaenus* Lartet (1857), from the Miocene of France. So far, all of the considerable material of these birds found in late Oligocene and Neogene deposits around the North Atlantic appear to be referable to a single genus—*Pelagornis*—although this includes a variety of species. Evidence from other localities suggests that as many as three species of pseudodontorns may have coexisted. We have not attempted to describe the Lee Creek Mine material in detail, pending planned revisionary studies of the group by K.I. Warheit and Olson.

Adding to the problems of identifying the Lee Creek pseudodontorns is the fact that we do not yet know from which horizon any of the material comes. The preservation of much of the material resembles that of Yorktown-age specimens. The most frequently represented species of pseudodontorn in the Calvert Formation, including the Pollack Farm site in Delaware (Rasmussen, 1998), is smaller than either of the two species known so far from Lee Creek Mine, which also is indirectly suggestive of their derivation from the Yorktown Formation. This line of reasoning has its limitations, however, because there was an

extremely large pseudodontorn in the late Oligocene of South Carolina (Warheit and Olson, unpublished data) and presumably there would have been large species in the middle Miocene as well.

Although mainly fragmentary, the material from Lee Creek Mine is important, as certain elements represented are otherwise unknown, or nearly so, for the entire family. At least two species can be distinguished, mainly on the very different sizes of comparable elements: in this case, the heads of humeri, fragments of coracoid, and distal ends of femora.

Genus *Pelagornis* Lartet, 1857

Pelagornis sp. 1

PLATE 11*p,q,t,u*

MATERIAL.—Fragment of left coracoid with glenoid and scapular facets, USNM 464329. Heads of right humeri, USNM 215442, 308155. Proximal ends of left femora, USNM 321289, 446499; distal end of right femur, USNM 242202; distal ends of left femora, USNM 205473, 242327, 446498. Inner and middle trochleae of left tarsometatarsus, USNM 446500.

HORIZON.—The stratigraphy is uncertain; preservation and abundance suggest that most specimens are probably from the Yorktown Formation, but the Pungo River Formation cannot be ruled out because pseudodontorns were already diverse in the late Oligocene and early Miocene in the North Atlantic.

MEASUREMENTS (mm).—*Femur*: Proximal width, 29, 30; distal width, 29.6, 30.9, 32.7, 30.6.

Tarsometatarsus: Width and depth of middle trochlea, 11.7 × 17.1.

REMARKS.—The very long but light humeri of these birds did not preserve well at Lee Creek Mine, and they are represented only by the heavy, rounded heads. These and the scapulae articulate well with the single fragment of coracoid and associate these elements with the smaller species present in the deposits. There are two size classes of femora, the larger species (see below) being represented only by a very worn distal end. All of the remaining femoral fragments are referred to the smaller species, along with the fragment of tarsometatarsus. The shafts of all of the femora are filled with medullary bone, as are those of a specimen from the Calvert Formation, so either all of these were from laying females or the presence of medullary bone in these birds has some other significance.

Pelagornis sp. 2

PLATE 11*l,n*

MATERIAL.—Fragment of sternal articulation of right coracoid, USNM 425109; fragment of left coracoid with glenoid and scapular facets, USNM 446501. Heads of right humeri, USNM 425111, 446497; head of left humerus, USNM 464331. Distal end of left femur, USNM 252307.

HORIZON.—The stratigraphy is uncertain; preservation and abundance suggest that most specimens are probably from the Yorktown Formation, but the Pungo River Formation cannot be ruled out because pseudodontorns were already diverse in the early Miocene and late Oligocene in the North Atlantic.

MEASUREMENTS (mm).—*Femur*: Distal width, >33.

REMARKS.—The coracoidal fragment is much larger than that referred to the preceding species, and the humeral heads articulate well with it, except for USNM 446497, which appears almost intermediate in size. The sternal portion of the coracoid is so large and massive as to suggest its placement here rather than with the smaller species.

Pelagornis sp. 1 or *Pelagornis* sp. 2

PLATE 11*a-d,f,h,j*

MATERIAL.—The following material cannot at this point be identified certainly with one or the other of the above species and is referred only to the genus *Pelagornis*.

Rostral "tooth" (pseudotooth), USNM 464325; fragment of mandible with "tooth," USNM 182106; distal end of right mandible, USNM 425108; associated distal ends of right and left mandibles, USNM 446494; right quadrate, USNM 446495 (height 45.6 mm); right pterygoid, USNM 425110 (length 40.1 mm, greatest anterior width 17.2 mm). Cervical vertebrae: axes, USNM 275777, 446502, 464326; vertebral centra, USNM 250715, 425102, 425103; basal cervical vertebra, USNM 425101. Anterior portion of carina of sternum, USNM 464328 (depth of furcular facet 44.0 mm). Proximal end of left radius, USNM 183512 (greatest diameter 22.4 mm). Left radiale, USNM 446496 (greatest diameter 27.0 mm). Distal end of right tibiotarsus lacking external condyle, USNM 446507; distal end of left tibiotarsus lacking internal and part of external condyle, USNM 448913. Pedal phalanx, USNM 183506.

Also of questionable placement are the following scapulae: anterior end of right scapula lacking much of acromion, USNM 464330 (greatest width 35+ mm), anterior end of left scapula lacking much of acromion, USNM 425104 (greatest width 38.7 mm), and anterior portion of shaft of left scapula with part of glenoid facet, USNM 425105. These are all of roughly the same size, which is approximately the size of the largest Oligocene pseudodontorn known from South Carolina (K.I. Warheit, pers. comm., 1998). This suggests that they should be referred to the larger species at Lee Creek Mine, but the two scapulae that preserve the coracoidal heads do not articulate well with the largest coracoidal fragment having a scapular facet (USNM 446501, *Pelagornis* sp. 2), yet they fit nearly perfectly with the smaller one (USNM 464329, *Pelagornis* sp. 1).

Family SULIDAE (boobies and gannets)

The phylogeny and paleontology of the Sulidae have been studied extensively by K.I. Warheit, who included fossils from

Lee Creek Mine in his investigations. Some discussion of fossils may be found in his dissertation and elsewhere (Warheit, 1990, 1992), but most of his paleontological studies remain to be published. Pending his revisionary study of this material, we have set forth herein only a skeletal outline (with measurements omitted) concerning the sulid faunas from Lee Creek Mine based partly on Warheit's unpublished data and partly on our own observations. Specimens listed follow Warheit's identifications.

Genus *Morus* Vieillot

The modern Sulidae consists of the tropical boobies (*Sula* Brisson and *Papasula* Olson and Warheit) and the temperate gannets (*Morus*). The three living species of gannets, often considered to form a superspecies, occur in the North Atlantic, in southern Africa, and in New Zealand and along the southern coast of Australia. Fossil taxa also are known from the North Pacific. Although neontologists have frequently included *Morus* in the genus *Sula*, the two are quite distinct osteologically, with *Morus* being the more derived genus (Warheit, 1990). The distinguishing characters of *Morus* are evident at least as far back as the late early Miocene, which is argument enough for recognizing the genus.

All fossil Sulidae from Lee Creek Mine and the Calvert Formation are referable to the genus *Morus*, which was much more diverse in the North Atlantic in the past, with at least three contemporaneous species occurring sympatrically in both the middle Miocene and the early Pliocene.

Gannets are the most abundant fossil birds in the Calvert Formation. For some time it has been known that at least three species are represented in the fauna, and that despite their having been originally referred to *Sula*, all are more closely related to gannets (Olson, 1984). Thus, the three named taxa are herein referred to *Morus*. All are smaller than any modern species of *Morus*, and one, *M. avitus* (Wetmore), is smaller than any living member of the family. These same three species also occur at Lee Creek Mine, where they are known or assumed to come from the Pungo River Formation. All are generally less pneumatic than the larger Pliocene species.

Of the three species of gannets from the early Pliocene, the smallest, which is about the size of or slightly smaller than the living Northern Gannet, *Morus bassanus* Linnaeus, is referred to the species *Morus peninsularis* Brodkorb (1955), previously known from the Bone Valley Formation in Florida. The other two are new, as yet undescribed species, both larger than living gannets. It is not known whether the three Pliocene species are larger descendants of the three Miocene lineages or which of the Pliocene species, if any, gave rise to modern gannets. The Pliocene species all have pneumaticity well developed, in contrast to those from the Miocene.

Morus avitus (Wetmore), new combination

Sula (subgenus *Microsula*) *avita* Wetmore, 1938:22.

MATERIAL.—Left coracoid, USNM 177798; left coracoid lacking sternal end, USNM 501510. Distal half of right humerus, USNM 178033. Proximal end of right ulna, USNM 501511. Distal end of radius, USNM 210530. Left carpometacarpus missing minor metacarpal, USNM 215722; proximal ends of right carpometacarpi, USNM 183481, 215638; distal end of right carpometacarpus, USNM 178186. Left femur, USNM 215761. Left tarsometatarsi, USNM 181029, 426057; distal end of left tarsometatarsus, USNM 426063.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

REMARKS.—A small amount of material exists that is inseparable from the type of *Sula* (*Microsula*) *avita*, from the Calvert Formation of Maryland. Several elements (ulna, coracoid) were collected by J.H. McLellan from spoil derived from units 4 and 5 of the Pungo River Formation. This was a tiny gannet, much smaller than the smallest living member of the family.

Morus atlanticus (Shufeldt, 1915), new combination

Sula atlantica Shufeldt, 1915:62.

MATERIAL.—Distal end of left humerus, USNM 411963. Proximal end of right ulna, USNM 426031; proximal ends of left ulnae, USNM 302327, 368551, 412039; distal ends of right ulnae, USNM 192574, 206512, 275806, 367103; distal ends of left ulnae, USNM 177943, 215686, 241374. Left carpometacarpus missing minor metacarpal, USNM 193364; proximal end of left carpometacarpus, USNM 257493; distal ends of left carpometacarpi, USNM 210439, 412056. Left femur, USNM 252310. Distal end of right tibiotarsus, USNM 368562; distal end of left tibiotarsus, USNM 426068.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

REMARKS.—The holotype of this species came from the Kirkwood Formation in New Jersey, which is temporally equivalent to the Calvert Formation, whence specimens inseparable from the holotype have been collected. This species was intermediate in size between *M. avitus* and *M. loxostylus* (Cope), but there is probably some overlap in size with the latter (K.I. Warheit in litt., 1997).

Morus loxostylus (Cope, 1870)

Sula loxostyla Cope, 1870:236.

Morus loxostyla [sic].—Brodkorb, 1963:259.

MATERIAL.—Right coracoid lacking sternal end, USNM 241426; right coracoid lacking most of both ends, USNM 367004. Distal ends of right humeri, USNM 366796, 411973; distal ends of left humeri, USNM 181116, 215456. Proximal end of right ulna, USNM 177935; proximal end of left ulna, USNM 366936; distal end of right ulna, USNM 236836; distal

end of left ulna, USNM 367088. Proximal ends of radii, USNM 412008, 426089; distal ends of radii, USNM 178055, 192075. Right tarsometatarsus, USNM 215476; left tarsometatarsus, USNM 412010; distal end of right tarsometatarsus, USNM 366715; distal ends of left tarsometatarsi, USNM 193002, 412089, 412094.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

REMARKS.—This fairly common form is about the size of the modern Blue-footed Booby, *Sula nebouxii* Milne-Edwards. The fossil material compares well with material from the Calvert Formation of Maryland assigned by Wetmore (1926) to *Morus loxostylus*, the holotype of which has been lost. Study of the original illustration and description (K.I. Warheit, pers. comm., 1997) indicates that it is reasonable to assign the largest Calvert gannet to this species, as has been done for material from the Calvert Formation of Delaware (Rasmussen, 1998).

Morus peninsularis Brodkorb, 1955

PLATES 12*h,l*, 13*a,e,g,i,m,n*

MATERIAL.—Right coracoids, USNM 412054, 426052; left coracoids, USNM 367093, 412016, 412021, 426053, 501512, 501514; right coracoid lacking part of sternal end, USNM 308220, left coracoid lacking much of both ends, USNM 412042; sternal end of left coracoid, USNM 426054. Proximal portions of left humeri, USNM 464323, 501514; distal end of right humerus, USNM 215691; distal ends of left humeri, USNM 215716, 411971, 411981. Proximal two-thirds of right ulna, USNM 412017; proximal end of left ulna, USNM 412023; distal half of right ulna, USNM 412006. Left carpometacarpus missing minor metacarpals, USNM 412066, 426023; proximal end of left carpometacarpus, USNM 366806. Left femora, USNM 177910, 412048. Right tarsometatarsus, USNM 426061; left tarsometatarsus lacking much of proximal end, USNM 275838; distal ends of left tarsometatarsi, USNM 179261, 248510.

HORIZON.—Yorktown Formation (USNM 179261 probably from the middle Yorktown as determined from foraminifera and sedimentary characteristics of matrix).

REMARKS.—The most abundant sulid at Lee Creek Mine is a large gannet that appears to be identical to material from the Bone Valley Formation described by Brodkorb (1955) as *Morus peninsularis*, which was characterized as being somewhat smaller than the modern Northern Gannet, *M. bassanus*, similar in size to or slightly smaller than either the Australian Gannet, *M. serrator* (Gray) or the Cape Gannet, *M. capensis* (Lichtenstein), but slightly larger than the Masked Booby, *Sula dactylatra* Lesson.

Morus, undescribed species 1

PLATES 12*a–g,i,n*, 13*b,k,o*

MATERIAL.—*Associated Specimen:* Partial skeleton consisting of mandible (lacking symphysis), 3 cervical vertebrae, proximal portions of right and left humeri, distal ends of left ulna and radius, left ulnare, and proximal end of left carpometacarpus, USNM 181052.

Individual Elements: Left coracoid, USNM 464322; right coracoid lacking much of sternal end, USNM 193086, 412053. Proximal half of right humerus, USNM 368548; distal ends of left humeri, USNM 411966, 411982, 426011. Proximal ends of right ulnae, USNM 321227, 412077, 426030; proximal ends of left ulnae, USNM 366880, 412087, 426029; distal end of right ulna, USNM 366883; distal end of left ulna, 412078. Proximal end of radius, USNM 193019; distal ends of radii, USNM 411983, 412083. Proximal ends of right carpometacarpus, USNM 412065, 412067; proximal ends of left carpometacarpus, USNM 308197, 321241. Distal two-thirds of right tibiotarsus, USNM 426069. Left tarsometatarsus, USNM 366904.

HORIZON.—Yorktown Formation.

REMARKS.—This is a large gannet, being intermediate in size between *Morus peninsularis* and the following extremely large species; it is larger than *M. bassanus* by roughly the same amount as the latter is larger than *M. capensis*.

Morus, undescribed species 2

PLATES 12*j,m*, 13*c*

MATERIAL.—Scapular ends of left coracoids, USNM 183499, 321253; sternal ends of left coracoids, USNM 366666, 412047. Proximal end of left humerus, USNM 426009; distal end of right humerus, USNM 242374; distal ends of left humeri, USNM 411951, 411987. Proximal end of left ulna, USNM 215558; distal end of left ulna, USNM 183508. Distal end of radius, USNM 177881. Right carpometacarpus missing minor metacarpal and most of distal end, USNM 206346; proximal end of right carpometacarpus, USNM 412062; distal end of right carpometacarpus, USNM 256212.

HORIZON.—Yorktown Formation.

REMARKS.—This is a huge species, at least half again larger than the largest living gannets (*Morus*).

Family PHALACROCORACIDAE (cormorants)

Genus *Phalacrocorax* Brisson

Because cormorants have never been found in the Calvert Formation, we assume that it is unlikely that any of the cormorant fossils from Lee Creek Mine come from the Pungo River Formation. Furthermore, the morphology of the Lee Creek cormorants does not differ greatly from that of modern species, which would not be expected of taxa as old as middle Miocene.

***Phalacrocorax wetmorei* Brodkorb, 1955**FIGURE 7; PLATE 14*a,b,d,e,g,h,j,n,o,q,s,t*

MATERIAL.—*Associated Specimen*: Distal end of left ulna, carpometacarpus, and radiale, USNM 179307.

Individual Elements: Mandibular articulation, USNM 215700. Anterior fragment of sternum, USNM 446468. Right coracoids, USNM 242346, 446444–446450; scapular ends of right coracoids, USNM 192013, 192922, 192944, 206303, 206482, 206586, 248565, 302344, 366352, 366411, 446451, 446452; scapular ends of left coracoids, USNM 177761, 192868, 193279, 193306, 215467, 215752, 215842, 241407, 308186, 446454–446464; sternal ends of right coracoids, USNM 256244, 446453; sternal ends of left coracoids, USNM 178179, 250762. Anterior end of right scapula, USNM 242361. Proximal end of right humerus, USNM 501515; proximal ends of left humeri, USNM 446409, 446410, 446469; distal ends of right humeri, USNM 177745, 215818, 366340, 366446, 446407, 446408; distal ends of left humeri, USNM 446411–446413. Proximal ends of right ulnae, USNM 215745, 252320, 256265, 302380, 446397–446399; proximal ends of left ulnae, USNM 177846, 181088, 250701, 367019; distal ends of right ulnae, USNM 177859, 192491, 206436, 210482, 236825, 250776, 250821, 252428, 321250, 446400–446404; distal ends of left ulnae, USNM 177856, 177863, 178099, 192982, 206613, 215636, 215672, 241428, 242352, 308194, 366919, 446405, 446406. Proximal end of radius, USNM 446467. Right carpometacarpus, USNM 446391; left carpometacarpus, USNM 446394; proximal ends of right carpometacarpi, USNM 306343, 366445, 367139, 446392; proximal ends of left carpometacarpi, USNM 192942, 206472, 215650, 242336, 242370, 446395, 446396; distal ends of right carpometacarpi, USNM 178204, 446393; distal end of left carpometacarpus, USNM 206534. Alar phalanges, USNM 193068, 206542. Synsacral fragments, USNM 210440, 308191, 446465. Right femora, USNM 242205, 302304, 446414, 446415; left femora, USNM 179250, 367159, 446419, 446420; proximal ends of right femora, USNM 366692, 446416; proximal ends of left femora, USNM 179291, 446421, 446422; distal ends of right femora, USNM 215542, 248562, 368478, 446417, 446418; distal ends of left femora, USNM 177938, 192935, 248571, 250748, 366950, 446423, 446424. Right tibiotarsus, USNM 446425; distal ends of right tibiotarsi, USNM 177882, 181115, 446426, 446427; distal end of left tibiotarsus, USNM 446428. Right tarsometatarsi, USNM 193098, 275785, 366903, 446429; left tarsometatarsi, USNM 210425, 215429, 446435–446437; proximal ends of right tarsometatarsi, USNM 193129, 215815, 252302, 257499, 367030, 368556, 446430–446432; proximal ends of left tarsometatarsi, USNM 242364, 446438–446443; distal ends of right tarsometatarsi, USNM 181065, 446433, 446434; distal ends of left tarsometatarsi, USNM 178184, 179229, 179262, 206354, 215765, 248504. Pedal phalanges, USNM 192458.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*Bone Valley, Florida*: Right coracoid, UF 95488. Right femur, UF 101946. Distal end of right tibiotarsus, UF 65772. Right tarsometatarsus, UF 94550.

MEASUREMENTS.—See Table 7. The common species of cormorant at Lee Creek Mine overlaps broadly in size with *Phalacrocorax wetmorei* Brodkorb (1955) from the upper Bone Valley Formation but tends to average smaller. When skeletal measurements of the two modern subspecies of Double-crested Cormorant (*P. auritus auritus* Lesson, *P. a. floridanus* Audubon) from the Atlantic coast of North America are plotted with those of the fossil cormorants from Lee Creek Mine and Bone Valley, all populations show broad overlap in most measurements. Two measurements of the humerus (width of the proximal end and depth of the head), however, separate the fossil populations from the modern ones (Figure 7).

REMARKS.—*Phalacrocorax wetmorei* was described by Brodkorb (1955) from the Bone Valley Formation as a new species of cormorant similar in size to *P. auritus*. Comparisons of humeri and tarsometatarsi of cormorants of this size class from Lee Creek Mine with those of Bone Valley revealed no osteological differences.

Detailed comparisons were made between the Pliocene fossils and the European Shag, *P. aristotelis* Linnaeus, a species of somewhat similar size that occurs along the coasts of the eastern Atlantic and Mediterranean. Both fossil populations, however, are decidedly more similar to *P. auritus* than to *P. aristotelis* in most qualitative characters, as well as in size. Most Lee Creek and Bone Valley specimens of *P. wetmorei* differ from *P. auritus* in having the posterior rim of the medial condyle of the tarsometatarsus forming an angle with the shaft, rather than being confluent with it; the accessory distal foramen of the tarsometatarsus positioned nearer the primary distal foramen; the bicipital crest of the humerus less laterally expanded (in some *P. wetmorei*); and the ventral tubercle of the humerus less laterally produced. In these four characters the fossils seem more like *P. aristotelis*, whereas in all other respects they are more similar to *P. auritus*. Although it seems likely that *P. wetmorei* is only a temporal manifestation of *P. auritus*, which latter may date back at least to the earliest Pleistocene of Florida (Emslie, 1998), we have used the former name for the Lee Creek Mine fossils pending future revisionary work.

***Phalacrocorax*, large species**PLATE 14*c,f,i,k-m,p,r,u,v*

MATERIAL.—Nearly complete right coracoid, USNM 177880; scapular end of right coracoid, USNM 242335. Distal end of right humerus, USNM 215774. Proximal end of right radius, USNM 179256. Right femur, USNM 177791. Proximal ends of left tibiotarsi, USNM 177901, 215597; distal end of left tibiotarsus, USNM 177787. Distal end of left tarsometatarsus, USNM 430872.

ADDITIONAL MATERIAL EXAMINED.—*Bone Valley, Florida*: Right tibiotarsus, UF 67935.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 7.

REMARKS.—These bones are from one or more species of cormorant considerably larger than the preceding. The only large cormorant in the North Atlantic today is the Great Cormorant, *Phalacrocorax carbo* Linnaeus. Compared with a large male of that species from the Netherlands (USNM 555669), the fossil femur is larger, but the shaft is slightly less robust and curved. One of the tibiotarsi proximal ends is not quite as large as that of *P. carbo*, but the fibular crest is longer, extending farther proximally. The other is poorly preserved and is considerably smaller. The distal ends of the tibiotarsi and tarsometatarsi are larger and have much heavier shafts than they do in the modern species. The fossil pectoral elements are all either slightly or much smaller than in *P. carbo*.

The fossil cormorants of North America are much in need of revision, and many of the described taxa, which have been summarized by Emslie (1995b), are known from inadequate material. On the other hand, Emslie (1995b) described a new species, *Phalacrocorax filyawi*, from abundant material from a

late Pliocene death assemblage in central Florida. This was related to the large Pacific cormorants (Brandt's Cormorant, *P. penicillatus* (Brandt); the extinct Pallas's Cormorant, *P. perspicillatus* Pallas; and the Flightless Cormorant, *P. harrisi* Rothschild) and represents a lineage that must have invaded the Atlantic prior to the closing of the Panamanian seaway. It would have existed in a region of cold upwelling that was disrupted after the emergence of the Panamanian isthmus, causing the extinction of the cormorant.

Another large cormorant, *Phalacrocorax idahensis* (Marsh, 1870), has been reported from late Pliocene and Pleistocene deposits in Idaho and Florida, although there is some doubt that all the material ascribed to it belongs to the same species (Emslie, 1995b, 1998). Emslie (pers. comm., 1997) made comparisons of the large cormorant bones from Lee Creek Mine, noting that the femur compared well with *P. idahensis*, the coracoids with *P. filyawi*, and the remaining bones with neither of those species. Given the amount of intraspecific variation in some modern cormorants, however, it is highly unlikely that the large cormorant material from Lee Creek Mine would be referable to more than two species.

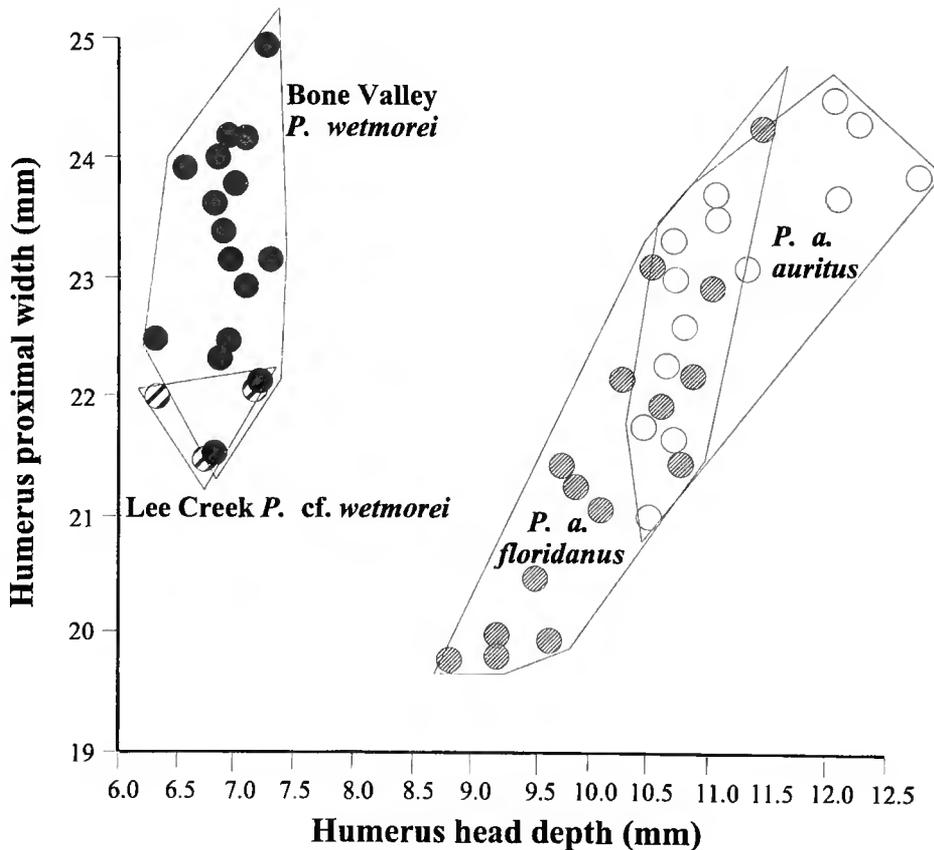


FIGURE 7.—Bivariate scatter plot of depth versus width of humerus head for cormorants: Lee Creek Mine *Phalacrocorax wetmorei*, Bone Valley *P. wetmorei*, and two Atlantic coast subspecies of Double-crested Cormorant (*P. auritus auritus* and *P. a. floridanus*).

TABLE 7.—Measurements (mm) for recent and fossil cormorants (*Phalacrocorax*): *P. wetmorei* and *P. large* species from the Lee Creek Mine (LC); *P. wetmorei* from the upper Bone Valley Formation (BV), and modern specimens of *P. auritus auritus* (7 males, 7 females). Measurements are in list form when number of specimens (n) < 3 for fossil species. (s = standard deviation.)

Element	<i>P. wetmorei</i> (LC)				<i>P. large</i> sp. (LC)	<i>P. wetmorei</i> (BV)				<i>P. a. auritus</i> ($n=14$)		
	n	Range	Mean	s		n	Range	Mean	s	Range	Mean	s
Coracoid												
Length	—	61.3, 63.5	—	—	—	4	59.3–67.9	64.4	2.6	—	64.3	2.8
Glenoid facet												
Length	—	11.3, 11.7	—	—	13.0	4	12.0–12.6	12.4	0.3	11.5–13.3	12.4	0.5
Carpometacarpus												
Length	3	67.8–73.5	69.9	3.1	—	—	—	69.6	—	63.8–73.3	69.0	2.5
Proximal depth	10	13.4–15.3	13.9	0.7	—	24	13.1–14.2	13.7	0.4	12.7–14.1	13.3	0.4
Distal depth	5	4.4–4.8	4.7	0.2	—	8	4.4–5.4	4.9	0.3	4.6–5.4	5.0	0.2
Distal width	5	7.1–7.5	7.3	0.2	—	9	7.2–7.8	7.4	0.2	7.1–7.7	7.4	0.2
Humerus												
Proximal width	—	22.0	—	—	—	16	21.5–24.8	23.2	0.9	21.0–24.6	22.9	1.0
Head depth	—	6.3, 6.7	—	—	—	16	6.3–7.3	7.0	0.3	10.5–12.3	11.1	0.5
Shaft depth	—	6.0	—	—	—	18	5.4–7.0	6.2	0.3	6.0–7.7	6.8	0.4
Distal width	7	13.2–15.0	14.2	0.7	—	35	14.9–16.8	15.6	0.4	15.4–16.9	15.9	0.5
Distal depth	8	9.8–11.0	10.4	0.4	—	34	9.4–11.1	10.3	0.4	10.0–11.9	10.9	0.6
Ulna												
Proximal width	6	10.8–12.4	11.4	0.7	—	26	10.6–12.8	11.5	0.4	11.4–12.7	11.9	0.4
Proximal depth	6	10.0–11.2	10.7	0.5	—	26	10.5–12.3	11.6	0.4	11.5–13.5	12.5	0.6
Femur												
Length	4	50.0–56.6	53.9	3.2	62.0	9	53.3–59.2	55.5	1.6	49.5–58.7	54.9	2.4
Head depth	7	5.9–7.0	6.6	0.4	8.0	16	6.3–7.2	6.8	0.3	6.4–7.6	7.0	0.3
Proximal width	6	14.2–17.5	15.3	1.4	17.9	19	14.5–16.7	15.4	0.6	15.4–17.4	16.3	0.6
Shaft width	12	5.7–7.0	6.2	0.3	7.9	17	5.9–7.0	6.5	0.3	5.6–7.1	6.5	0.4
Distal width	10	13.2–16.4	15.0	1.1	—	17	14.4–16.0	15.1	0.5	14.9–16.6	15.7	0.6
Tibiotarsus												
Shaft width	—	6.0	—	—	—	5	6.6–7.2	7.0	0.3	6.6–7.4	6.9	0.2
Shaft depth	—	4.8	—	—	—	5	5.0–5.2	5.1	0.1	4.8–6.5	5.4	0.5
Tarsometatarsus												
Length	5	59.8–66.8	63.3	2.9	—	5	60.3–69.2	64.6	3.7	55.2–65.0	62.0	2.4
Proximal width	10	11.5–13.4	12.6	0.6	—	22	12.1–14.1	13.0	0.5	12.0–13.6	12.8	0.4

Order CHARADRIIFORMES
(shorebirds, gulls, and auks)

Family STERCORARIIDAE
(skuas and jaegers)

The skuas and jaegers constitute a small group of predaceous relatives of gulls, the humerus of which appears to be primitive (Olson, 1985d) within the suborder Lari (as is also that of the noddies (*Anous*) and skimmers (*Rynchops*)). The jaegers, *Stercorarius*, comprise three species that breed entirely in the Arctic, and the skuas, *Catharacta*, consist of a complex of taxa that breed at high latitudes in the Southern Hemisphere, with the exception of the Great Skua, *C. skua* Brünnich, which breeds on islands in the eastern North Atlantic, having recently expanded into the Barents Sea (Cohen et al., 1997:188). We have retained the two genera mainly to promote comprehension as we can find no osteological differences between the two groups, *Catharacta* merely being an enlarged version of *Stercorarius* as far as the skeleton is concerned. Various authors, with the perspectives offered by both morphology and behav-

ior, have previously suggested merging these two genera (see references cited in Braun and Brumfield, 1998:998).

Recent molecular and other evidence has made the traditional view of relationships within this family the object of considerable contention (Cohen et al, 1997; Braun and Brumfield, 1998). The most unexpected result was the apparent closer relationship of the Pomarine Jaeger (*Stercorarius pomarinus* (Temminck)) to *Catharacta* in general, and to the Great Skua (*C. skua*) in particular (Cohen et al., 1997). This, combined with the proposed very recent origin of *C. skua* in the North Atlantic (Andersson, 1973), led Cohen et al. (1997) to suggest three different possible hypotheses of origin of *S. pomarinus*, including hybridization between *Catharacta* and one of the other species of *Stercorarius*.

We do not intend to dwell on the specifics of these recent studies but wish instead to elucidate what bearing the fossil record may have on the issues. At Lee Creek Mine there are scarce fossils assignable to all three size classes of modern jaegers, including *S. pomarinus*. Although there are some slight differences from modern species in some of the bones, the similarities are greater, and all of the fossils are assumed to have come from the Yorktown Formation. There also are a

few bones, including a diagnostic distal end of a tarsometatarsus, that clearly belong to a much larger species the size of *Catharacta*.

The last is not necessarily an indication of a breeding population of skuas in the North Atlantic at that time. Given the propensity of the modern Southern Hemisphere forms of *Catharacta* to wander across the equator and the presence at Lee Creek Mine of other Southern Hemisphere vagrants, especially among the Procellariidae, it is just as likely that bones of *Catharacta* at Lee Creek Mine represent strays from the south, particularly as skuas and jaegers commonly follow flocking shearwaters.

Nevertheless, the fossil record indicates that the diversity of Stercorariidae in the North Atlantic was just as great nearly five million years ago as it is today. The size range of *Stercorarius* that existed then appears to encompass three species, and we assume that these are the same three lineages represented by the modern species. Although it is still quite possible that the North Atlantic Great Skua (*Catharacta skua* sensu stricto) may be of much more recent origin, the fossil record suggests that a much greater period of time may need to be allowed for the point of origination of *S. pomarinus*.

Genus *Catharacta* Brünnich

Catharacta sp.

PLATE 15a,c,d

MATERIAL.—Distal end of left ulna, USNM 366602. Proximal end and shaft of left carpometacarpus, USNM 430889. Left tarsometatarsus lacking most of both ends, USNM 430892; distal end of left tarsometatarsus, USNM 183482.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS.—See Table 8.

REMARKS.—The above elements are from a large stercorariid the size of the Great Skua, *Catharacta s. skua* Brünnich, or the South Polar Skua, *C. maccormicki* (Saunders).

The distal portion of the tarsometatarsus from Lee Creek Mine differs from that of *Catharacta skua* and *C. maccormicki* in having a smaller, rounder distal foramen, especially notable in posterior view. The metatarsal facet is more deeply excavated in the fossil and extends farther distally. In posterior view, the external edge of trochlea III extends farther proximally in the fossil. In anterior view, there is no distinct furrow proximal to the internal intertrochlear notch. The carpometacarpus is as large and heavy as that in large female specimens of *C. maccormicki*, and the preserved portion is similar to modern species examined. The ulna is from a very large skua, larger than *C. maccormicki*, with an especially heavy shaft, but the specimen is poorly preserved.

These cold-water birds occur mainly in the Southern Hemisphere, with the isolated Great Skua being the only form to breed in the Northern Hemisphere. Its breeding is restricted to the subarctic of the eastern North Atlantic, but it winters regu-

larly in the western North Atlantic, virtually never being found close to land. The South Polar Skua (*C. maccormicki*) occurs rarely but regularly in the western North Atlantic in the warmer months only.

The material from Lee Creek Mine provides the first fossil record of *Catharacta* from the North Atlantic, but its scarcity makes it equivocal as to whether this constitutes evidence for birds of this group having established breeding colonies north of the equator by that time. As discussed above, the possibility of the fossils having originated in vagrants from the south is perhaps just as likely.

Genus *Stercorarius* Brisson

Stercorarius aff. *pomarinus* (Temminck)

PLATE 15f,h,j,k,m,o

MATERIAL.—Left coracoid lacking sterno-coracoidal process, USNM 430891. Partial distal end of right humerus, USNM 192818; distal end of left humerus, USNM 366015. Distal third of left ulna, USNM 430890.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS.—See Table 8.

REMARKS.—The shaft of the coracoid is longer than it is in the Pomarine Jaeger, *Stercorarius pomarinus*. In other respects the fossil material agrees with the modern species. Emslie (1995b:324) reported a coracoid of "*Stercorarius* sp." from the late Pliocene of Florida that was considered likely to be an undescribed species larger than *S. pomarinus* but smaller than any species of *Catharacta*. He also noted differences between that specimen and USNM 430891.

Stercorarius aff. *parasiticus* (Linnaeus)

PLATE 15q,r,t,u,z

MATERIAL.—Distal ends of right humeri, USNM 178064, 460819. Proximal end of right carpometacarpus, USNM 193269.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS.—See Table 8.

REMARKS.—The distal end of the humerus has the shaft much more flattened in medial view and has a deeper pit in the brachial depression than in 15 Parasitic Jaegers (*Stercorarius parasiticus*) examined. Larine ulnae (USNM 237149, 237176) that resemble *Stercorarius* and are the size of *S. parasiticus* (Plate 15w,x) also have been recovered in the Calvert Formation.

Stercorarius aff. *longicaudus* Vieillot

PLATE 15bb,cc,ee,ff,hh

MATERIAL.—Distal ends of left humeri, USNM 430893, 448914. Proximal three-fourths of left carpometacarpus, USNM 460818.

TABLE 8.—Measurements (mm) for recent and fossil skuas (*Catharacta*) and jaegers (*Stercorarius*) from Lee Creek Mine. Measurements are in list form when number of specimens (n) < 5 and for fossil samples. (s = standard deviation.)

Element	<i>C. skua</i> ($n=4$)	C. sp.	<i>C. maccormicki</i> ($n=17$)			<i>S. pomarinus</i> ($n=7$)			<i>S. aff.</i> <i>pomarinus</i>	<i>S. parasiticus</i> ($n=16$)			<i>S. aff. parasiticus</i> ($n=2$)	<i>S. longicaudus</i> ($n=9$)			<i>S. aff.</i> <i>longicaudus</i>
			Range	Mean	s	Range	Mean	s		Range	Mean	s		Range	Mean	s	
Coracoid																	
Median length	51.0, 53.4, 56.5, 57.2	—	47.7–53.5	51.2	1.7	38.7–43.0	40.8	1.5	44.7	32.8–36.5	34.4	1.2	—	28.8–32.3	30.2	1.0	—
Humerus																	
Distal width	18.2, 19.3, 19.7, 20.5	—	17.0–19.7	18.2	0.6	13.6–15.3	14.5	0.6	15.3	12.4–13.6	13.0	0.4	12.4, 13.0	10.4–11.8	11.0	0.4	11.4
Ulna																	
Distal diagonal	11.6, 12.9, 12.9, 14.0	—	11.3–13.3	12.4	0.6	9.3–10.6	10.0	0.5	10.7	8.4–9.2	8.9	0.3	—	7.1–8.2	7.8	0.3	—
Carpometacarpus																	
Proximal width	15.6, 16.8, 16.9, 17.3	16.0	14.5–16.8	15.6	0.6	12.1–13.6	13.0	0.6	—	11.1–12.2	11.5	0.3	11.7	9.5–10.9	10.1	0.4	—
Tarsometatarsus																	
Distal width	12.3, 12.9, 12.9, 14.9	11.2+	11.3–13.0	12.2	0.5	8.2–9.0	8.7	0.3	—	6.7–7.8	7.2	0.3	—	6.1–6.8	6.5	0.2	—

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS.—See Table 8.

REMARKS.—These humeri are indistinguishable from the modern Long-tailed Jaeger, *Stercorarius longicaudus*, a regular migrant in the western Atlantic.

Family LARIDAE
(gulls and terns)

Genus *Larus* Linnaeus

***Larus aff. argentatus* Pontoppidan**

PLATE 16a,c,d,f,h

MATERIAL.—Portion of right mandibular ramus, USNM 430931. Proximal end of left humerus, USNM 366923; distal half of left humerus, USNM 366896. Proximal ends of right ulnae, USNM 430896, 430897, 430903; distal end of right ulna, USNM 430905. Proximal end of right carpometacarpus, USNM 430895.

MEASUREMENTS (mm).—*Humerus*: Proximal width, 20.3; distal width, 16.1.

Ulna: Proximal width, 12.7, 13.7, 14.9+; distal width, 10.5.

Carpometacarpus: Proximal width, 15.0, 15.7.

HORIZON.—Yorktown Formation.

REMARKS.—The above material represents a gull the size of the modern Herring Gull, *Larus argentatus*. Emslie (1995b:324) referred the two humeral fragments listed above to his new species *Larus perpetuus*, from the late Pliocene of Florida. The holotype of that species is a complete humerus with a length of 107.0 mm and a distal width of 14.2 mm, whereas the material from Lee Creek Mine indicates a larger species, within the lower size range of *Larus argentatus*, and from which we can detect no significant differences.

***Larus aff. delawarensis* Ord**

PLATE 17a,c,e,h,j,m,p,q

Larus elmoresi Brodtkorb, 1953b:94.

MATERIAL.—Associated left coracoid lacking sternal end and fragment of shaft of left humerus, USNM 215592. Scapular halves of right coracoids, USNM 430914, 460820; shaft of right coracoid, USNM 430915. Right humerus lacking most of both ends, USNM 181025; proximal portions of right humeri lacking much of proximal ends, USNM 430911, 460821; partial proximal end of left humerus, USNM 460822; distal ends of right humeri, USNM 192869, 242326, 250678, 321294, 366791, 367136, 430912, 430913, 460826, 460827; distal ends of left humeri, USNM 206408, 242184, 275819, 366791, 430907–430910, 460823–460825. Proximal third of right ulna, USNM 430918; proximal ends of left ulnae, USNM 430900, 430917; distal ends of right ulnae, USNM 308228, 430904, 430906, 460830, 460831; distal ends of left ulnae, USNM 366295, 366651, 430901, 430902, 460832. Right carpometacarpus lacking minor metacarpal, USNM 460833; proximal half of right carpometacarpus, USNM 256349. Distal end of right tibiotarsus, USNM 464293; distal end of left tibiotarsus, USNM 430848. Distal end of right tarsometatarsus lacking trochleae II and IV, USNM 178070; distal end of left tarsometatarsus, USNM 236892.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*Cobham Wharf, James River, Surrey County, Virginia*: Distal third of left humerus, USNM 237211. Lower Yorktown Formation, 25 ft (7.6 m) above beach. Collected by Warren Blow, received 1965.

Bone Valley Formation, Florida: Distal ends of right humeri, USNM 447048, 447049. Proximal half of left ulna, UF 61951. Proximal half of left carpometacarpus, USNM 447047.

MEASUREMENTS (mm).—*Humerus*: Distal width, mean=13.6, standard deviation (s)=0.63, range=12.9–14.8, n =9.

Ulna: Proximal width, 10.5, 11.2, 11.9; distal width, mean=9.1, s =0.48, range=8.4–9.7, n =8.

Carpometacarpus: Length, 57.4; proximal width, 12.0; distal diagonal, 7.4.

Tibiotarsus: Distal width, 7.5, 8.2.

REMARKS.—These elements are from a gull of the same size and general morphology as *Larus elmorei* Brodkorb (1953b) from Bone Valley (Plate 17*f,g,k,o*), thus approximating the modern Ring-billed Gull, *L. delawarensis*.

Larus aff. atricilla Linnaeus

PLATE 16*j,l,n*

MATERIAL.—Shaft of left coracoid, USNM 192102. Distal ends of right humeri, USNM 430921, 430922, 464292, 464299; distal ends of left humeri, USNM 215622, 367112, 430920. Distal two-thirds of right ulna, USNM 366451. Right carpometacarpus missing minor metacarpal, USNM 460828.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 10.4, 11.0, 11.0, 11.3, 11.5, 11.6, 11.7.

Ulna: Distal width, 7.8.

Carpometacarpus: Length, 54.1; proximal width, 11.0.

REMARKS.—These specimens, indistinguishable from the Laughing Gull, *Larus atricilla*, indicate a species larger than the Franklin's Gull, *L. pipixcan* Wagler; Black-headed Gull, *L. ridibundus* Linnaeus; or Sabine's Gull, *L. (Xema) sabini* Sabine, and smaller than *L. delawarensis* or the Royal Tern, *Sterna maxima* Boddaert. The carpometacarpus is similar in size to that of *S. maxima* but differs from it in having the alular metacarpal with the extensor attachment more rugose and less slanted.

Larus magn. ridibundus Linnaeus

PLATE 16*p*

MATERIAL.—Proximal half of left humerus lacking internal tuberosity, USNM 210461.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—No standard measurements possible.

REMARKS.—The lack of extension to the median crest distalward along the shaft shows this specimen to be a gull rather than a tern. It differs from the slightly smaller *Larus sabini* in having a less rounded bicapital crest. This specimen is similar in size to both *L. ridibundus* and *L. pipixcan*; we cannot distinguish between these species on the basis of the proximal end of the humerus. The ulna and radius of a gull of about this size was reported from the late Miocene Big Sandy Formation of Arizona (Bickart, 1990).

Larus aff. minutus Pallas

PLATE 16*v,w,y,z,bb*

MATERIAL.—Left humerus lacking most of proximal end, USNM 430916; partial distal end of right humerus, USNM 430924; distal ends of left humeri, USNM 430923, 464337. Right ulna, USNM 460817; distal end of left ulna, USNM 464338.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 7.7, 8.2, 8.6.

Ulna: Length, 61.8+; proximal width, 6.9; distal diagonal, 5.4.

REMARKS.—The virtually complete ulna is almost indistinguishable from that of the Little Gull, *Larus minutus*. The fossil has the distal end less rotated internally than it is in modern *L. minutus*. The Lee Creek ulna and those of modern *L. minutus* differ from North American species of *Sterna* of similar size as follows: in the former, the prominence for the anterior articular ligament juts farther internally; the distal edge of the external cotyla is smoothly continuous with the shaft, not squared; the shaft is not swollen just proximal to the distal end so that the carpal tuberosity is more distinct from the shaft; the anconal edge of the external tuberosity is less flared; and there is no distinct pit proximal to the internal condyle, but instead a ridge extends from this area to the carpal tuberosity. The fossil ulna and that of *L. minutus* differ from the Black Noddy, *Anous minutus* Boie, in having a straighter shaft from internal view; having the external cotyla more flared externally; and lacking a strongly shelf-like internal edge of the proximal radial depression.

The Little Gull is essentially an Old World species, although it has recently begun nesting in North America. As a result of this recent colonization, the species now regularly occurs during the nonbreeding season in North Carolina, where the first record was in 1971 (Lee, 1995:147), and elsewhere in eastern North America.

Larus sp.

PLATE 16*r,t*

MATERIAL.—Scapular half of right coracoid, USNM 430834.

HORIZON.—Pungo River Formation. Collected from Pungo River spoil pile (fide R. Purdy, Smithsonian Institution).

MEASUREMENTS (mm).—Length from head to distal rim of scapular facet, 11.0; depth through head, 8.9; length and width of glenoid facet, 7.6 × 4.7.

REMARKS.—This specimen lacks the pneumaticity under the furcular facet found in other gulls and thus resembles the Ivory Gull, *Larus (Pagophila) eburnea* Phipps. Perhaps this is a primitive feature, retained among living gulls only in *L. eburnea*, that may have been characteristic of most or all gulls in the early middle Miocene.

Genus *Sterna* Linnaeus

Sterna aff. *maxima* Boddaert

PLATE 16dd

MATERIAL.—Proximal end of right carpometacarpus, USNM 215643; proximal end of left carpometacarpus, USNM 430898.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Proximal width, 10.8, 11.9.

REMARKS.—These specimens differ from *Larus atricilla* and are similar to the Royal Tern, *Sterna maxima*, in having the extensor attachment of the alular metacarpal strongly slanted and in lacking the pronounced rugosity of *L. atricilla*. The Royal Tern is a common species in coastal environments in eastern North America and breeds in North Carolina today.

Sterna aff. *nilotica* Gmelin

PLATE 16ff

MATERIAL.—Right carpometacarpus lacking minor metacarpal, USNM 495588.

HORIZON.—Uncertain, probably Yorktown Formation.

MEASUREMENTS (mm).—Length, 37.8.

REMARKS.—This specimen is recognizable as a tern by the longer and more slender alular metacarpal and by having the carpal trochlea more squared in outline than it is in *Larus*. It is too small for the Sandwich Tern, *Sterna sandvicensis* Latham, or for any of the tern species larger than that, and it is too large for any North Atlantic species except the Gull-billed Tern, *Sterna nilotica*, with which it agrees very closely. The fossil is slightly smaller than the comparative modern material available to us, but this series of three modern skeletons is insufficient to determine the amount of size variation in *S. nilotica*. The Gull-billed Tern is a nearly cosmopolitan species that occurs during the breeding season along most of the eastern coast of North America, including North Carolina.

Family ALCIDAE
(auks and puffins)

Auks are by far the most abundantly represented birds at Lee Creek Mine both in numbers of specimens and in individuals. Thousands of fossil bones, representing no fewer than 11 species, have been collected. Three skeletal elements are the most commonly found: the humerus, ulna, and coracoid. We have examined thousands of specimens just of these elements. By contrast, elements of the pelvic limb are scarce, and portions of the skull and mandible are decidedly rare. Greatly compounding the difficulties of sorting and identifying the alcid material is its fragmentary nature and the fact that most of the taxa present are the product of a radiation from a single basic stock, so that there are very few qualitative differences between species in the wing elements.

A further complication is the apparently great intraspecific variation in size. We know from the modern Common Murre, *Uria aalge* (Pontoppidan), and Thick-billed Murre, *U. lomvia* (Linnaeus), that morphological differences between sibling species may be very subtle (Spring, 1971), and if such pairs of sibling species occur in the fossil record, as seems probable, they would be very difficult to distinguish. At the same time, they would increase the amount of variation observed within a size class.

Intraspecific size variation in modern alcids may be correlated with latitude or with oceanic environment, with larger individuals occurring in colder regions, as in the Atlantic Puffin, *Fratercula arctica* (Linnaeus), and the Great Auk, *Pinguinus impennis* (Moen, 1991; Burness and Montevecchi, 1992). If the Lee Creek Mine sample consists in part of wintering birds from different parts of a species' range, this would increase the variability within species and contribute further to the difficulty of separating one species from another.

In spite of the difficulties, it has been possible to identify a minimum of 11 species of auks from Lee Creek Mine, nine of which are thought to be from the Yorktown Formation and presumably would have been contemporaneous. Our estimate of four species in the great radiation of *Alca* is almost certainly too low, and if there were sibling species of the same general size and if more taxa are included at the high and low ends of the size variation, as we suspect, then the number of species of *Alca* might well double. The fossil record of alcids at Lee Creek Mine is so extensive that the absence of certain taxa, such as *Uria* Brisson and *Cephus* Pallas, must be considered as reflecting reality rather than being a product of sampling bias.

The compatibility analysis of the family by Strauch (1985) and the phylogenetic analysis by Chandler (1990b) were consulted, but many of the conclusions in the latter unpublished work seem untenable, and we have not considered them further. Both the American Ornithologists' Union (1998) and Strauch (1985) divide the Alcidae into tribes while omitting any division at the subfamilial level. Because there are no criteria for determining whether characters are of subfamilial or tribal value, the next level for grouping genera below the family level is the subfamily, so we list the subdivisions of the Alcidae at that level.

Subfamily ALCINAE
(auks)

This subfamily has usually been considered an Atlantic radiation and includes the Dovekie (*Alle*), the murre (*Uria*), and the auks (*Alca*, *Pinguinus*, and fossil relatives). Rather unexpectedly, however, the genus *Uria*, at least in its modern aspect, appears to have originated in the Pacific, as it is entirely absent at Lee Creek Mine and in all other Atlantic deposits that have yielded alcids older than Pleistocene. The only fossil that is truly referable to *Uria* that has been discovered so far in the

Atlantic is the type of *U. affinis* (Marsh, 1870), which is only about 12,000 years old (see Ray and Spiess, 1981), whereas two species of *Uria* have been named from the late Miocene of California (Howard, 1981, 1982). Thus, despite its similarities in plumage to *Alca*, the genus *Uria* appears to have had a long, separate history in the Pacific and is probably only distantly related to *Alca*.

The genus *Miocepphus* Wetmore, 1940, known from the Chesapeake Group in Maryland and Virginia, as well as from Lee Creek Mine, has nothing to do with the genus *Cepphus* (see Howard, 1978; Olson, 1985d:184), but it is closely related to and possibly ancestral to the *Alca* radiation.

Genus *Miocepphus* Wetmore, 1940

Miocepphus mcclungi Wetmore, 1940

MATERIAL.—Right coracoids, USNM 460810, 495602. Left humeri, USNM 495597, 495599; proximal ends of right humeri, USNM 177884, 192467; proximal ends of left humeri, USNM 192775, 495598; distal ends of right humeri, USNM 210424, 210526; distal ends of left humeri, USNM 178052, 250674.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

MEASUREMENTS.—Omitted pending revision of genus.

REMARKS.—Wetmore (1940) described a new genus and species of alcid, *Miocepphus mcclungi*, from a right humerus collected in the Calvert Formation of Maryland. Another humerus from the same locality was later referred to this species (Wetmore, 1943b), and we now have on hand several additional specimens of various elements from the Calvert Formation in both Maryland and Virginia. The specimens listed above from Lee Creek Mine are the size of *Miocepphus* and compare very favorably with the specimens of *M. mcclungi* from the Calvert Formation, although the stratigraphic position of the Lee Creek specimens was not otherwise determined.

Miocepphus, undescribed species

MATERIAL.—Left humerus, USNM 302324; right humeri missing heads, USNM 430948, 495584, 495600; proximal end of right humerus, USNM 192879; proximal ends of left humeri, USNM 178015, 192691, 192698; distal ends of right humeri, USNM 215499, 242316; distal end of left humerus, USNM 242178. Distal end of radius, USNM 366359.

HORIZON.—Pungo River Formation inferred from similarity to fossils from Calvert Formation.

MEASUREMENTS.—Omitted pending revision of genus.

REMARKS.—We have recognized a second species of *Miocepphus* in the Calvert Formation, although it is as yet undescribed. This was somewhat larger than *M. mcclungi*, as are the above specimens from Lee Creek Mine.

Both species of *Miocepphus* were rather small alcids, about the size of small individuals of the Black Guillemot, *Cepphus grylle* (Linnaeus). *Miocepphus mcclungi* was likened by Wetmore (1940) both to *Cepphus* and to *Brachyramphus*. The broad, flattened humeral shaft in *Miocepphus*, however, is quite unlike the distinctively terete, and probably primitive, shaft of *Cepphus*. The less-expanded distal end, more distinct pectoralis scar, and higher, more pointed ectepicondylar process of *Miocepphus* are other points that set it apart from *Cepphus*. *Miocepphus* is actually very similar to the Atlantic *Alca* group of auks, although it is smaller, and it may well have been ancestral to some of the Pliocene forms of that assemblage. In any case, it now appears to be quite unrelated to *Cepphus*, the pre-Pleistocene history of the latter probably having taken place entirely in the Pacific.

Genus *Alca* Linnaeus

FIGURES 8, 9

Australca Brodkorb, 1955:25.

The great masses of alcid material from Lee Creek Mine come mainly from several species belonging to the same genus as the modern Razorbill, *Alca torda* Linnaeus, which is confined to the North Atlantic. The humeri of *Alca* are most easily distinguished from those of *Uria* by having the internal and external tricripital grooves of equal width, whereas in *Uria* the internal groove is noticeably wider. Also, the ectepicondylar prominence extends higher on the shaft and projects farther in a distinct point, whereas in *Uria* this prominence is lower and more rounded. The premaxilla is definitely known for only one of the extinct fossil species, but this is high and laterally compressed, as in *Alca*, and is unlike the terete, pointed bill of *Uria*.

To attempt to determine how many species might be encompassed by the range of size variation shown in bones identified as *Alca*, a principal components (PC) analysis was done using the following four measurements of the distal ends of 566 fossil humeri from Lee Creek Mine: greatest distal width (with calipers parallel to axis of shaft); width through the condyles; mediolateral width of shaft just proximal to ectepicondyle; and shaft thickness (palmar-anconal) at the same point. This sample included all specimens then available in which all four measurements were unaffected by wear or breakage. A correlation matrix was used, and axes were unrotated. PC-I scores were plotted as a polygon in a density graph, where proportion per standard unit is the number of cases in each interval divided by the standard deviation (*s*).

Factor I was a general-size axis and was the only factor with eigenvalues above 1.0; this factor explained 93% of the variation. Because the eigenvalues for factors II and III were far below 1.0, these axes were not interpreted, and instead, PC-I was taken as a measure of size and was plotted as a density polygon (Figure 8). This density graph of PC-I shows at least a trimodal pattern, with each peak (at PC-I = ~ -3.0, -1.5, 0, 2.5) possibly representing the mode of a different species of *Alca*.

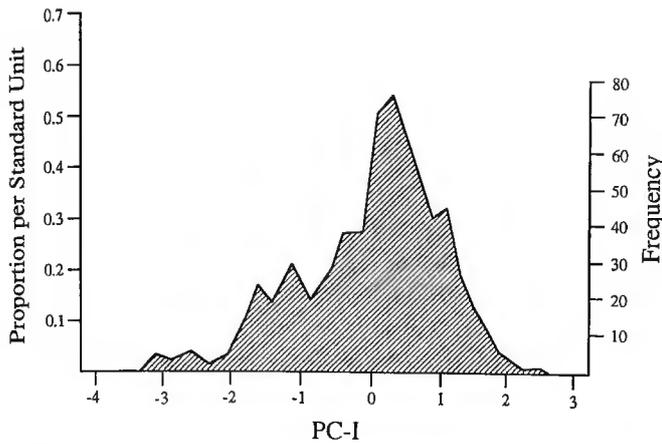


FIGURE 8.—Density polygon of factor 1 scores from a principal components analysis of four measures of the distal end of the humerus of auks, *Alca* spp., from Lee Creek Mine. Factor 1 is a general-size axis explaining 93% of the variation.

To determine the minimum number of species of *Alca* that must have been present at Lee Creek, we estimated the maximum expected variance (s^2) within species of Strauch's (1985) tribe Alcini, following the rationale developed by Warheit (1992). However, rather than using a parsimony procedure to determine an ancestor's expected variance where the variance of the two recent sister taxa differed (Warheit, 1992), to avoid oversplitting we simply used the maximum variance of species within the clade.

The Dovekie (*Alle alle* (Linnaeus)) was omitted from this analysis because its relationships with the subfamily Alcinae are equivocal. Greatest width of the distal end of the humerus was measured for 56 Common Murres, *Uria aalge*; 18 Thick-billed Murres, *U. lomvia*; 27 Razorbills, *Alca torda*; and 203 Great Auks, *Pinguinus impennis*. Sexes were pooled for each species because size dimorphism between the sexes of extant alcids is minimal (Storer, 1952; Livezey, 1988), and the sexes could not be determined for the specimens of *Pinguinus*.

For distal width of the humerus, variances of taxa thus determined in the subfamily Alcinae were $s^2=0.33$ (*Uria aalge*), $s^2=0.38$ (*U. lomvia*), $s^2=0.51$ (*Pinguinus impennis*), and $s^2=0.51$ (*Alca torda*). The maximum variance expected for any fossil species within that clade (assuming no evolution in that trait between ancestors and descendents; Warheit, 1992) is therefore 0.51, that shown by *Pinguinus impennis* and *Alca torda*; *Alca torda* also is the only living representative of the entire radiation of *Alca*.

To determine how best to assign individual specimens to each of four species, a K-means cluster analysis of the four measurements of the distal end of the humerus used in the previously mentioned principal components analysis was done, using K=4 clusters. In addition, K=3 and K=5 analyses were done to determine if these would provide better clustering. All analyses resulted in highly significant F-ratios. With K=3,

cluster 3 includes a group with the variance of $s^2=0.96$ for the distal width of the humerus, which is considerably larger than that for any extant species in the Alcinae, and the within-groups sum-of-squares (ss) is large (245.18). With K=5, on the other hand, cluster 5 has a very small variance ($s^2=0.11$), and clusters 1, 2, and 5 have largely coincident ranges and similar means, the range of one of the clusters falling entirely within that of another. With K=4, however, the standard deviations of the distal widths of the humeri for clusters 1 through 4 were 0.32, 0.20, 0.21, and 0.45, respectively, thus better fitting the predicted level of variation for any given species in this clade. In addition, there was less overlap between ranges of each group than if five clusters were used, and the within-groups sum-of-squares is not much larger than for K=5 ($ss_{K=4}=162.19$; $ss_{K=5}=112.6$). Also, four species each with a variance of 0.51 would account for most of the total variance shown by the distribution of distal humerus width. Therefore, based on the four measurements of the distal end of the humerus, fossils of *Alca* from Lee Creek Mine are statistically best considered as belonging to four species.

Species intervals as defined by the cluster analysis with K=4 are shown on a histogram of distal humerus width of 621 fossil specimens of *Alca* (Figure 9). For the entire distribution the mean=13.5, range=9.0–17.2, $s=1.46$, and the distribution is strongly skewed to the left (skewness=-0.58) but is not kurtotic (kurtosis=0.07). The skewness simply reflects the smaller number of specimens of the smallest species of *Alca* at Lee Creek Mine.

Alca aff. *torda* Linnaeus

FIGURE 10c,d

MATERIAL.—*Associated Specimens*: Left humerus and ulna, USNM 321314; proximal two-thirds of scapula, anterior end of left coracoid, left humerus lacking most of both ends, and alar digit, USNM 252414.

Individual Elements: Anterior portion of sterna, USNM 215778, 495678. Right coracoids, USNM 177758, 179258, 181070, 306263, 367014, 495625, 495626; left coracoids, USNM 308158, 321264, 495596, 495628, 495629. Right humeri, USNM 257519, 446653, 446657, 446658, 446686, 446691, 495589, 495668; right humeri lacking part of proximal ends, USNM 495591, 495592; proximal half of left humerus, USNM 193252; distal ends of right humeri, USNM 193259, 250772; distal half of left humerus, USNM 178032. Right ulnae, USNM 193184, 215809, 448898, 448904, 448908, 448909; left ulnae, USNM 368515, 446644; left ulna lacking part of proximal end, USNM 495594; proximal half of left ulna, USNM 495595. Right carpometacarpi, USNM 178072, 368532; left carpometacarpus, USNM 193292; right carpometacarpus missing minor metacarpal and part of distal end, USNM 495593; proximal ends of right carpometacarpi, USNM 183421, 215586, 215836; proximal ends of left carpometacarpi, USNM 192731, 367107. Right femur, USNM

460797; left femur 430949; proximal half of left femur, USNM 460798; distal end of right femur, USNM 460805; distal end of left femur, USNM 459393. Proximal ends of left tibiotarsi, USNM 179243, 495641; distal ends of right tibiotarsi, USNM 366660, 366712; distal ends of left tibiotarsi, USNM 215862, 495638–495640. Left tarsometatarsus, USNM 495633.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Figure 9.

REMARKS.—The smallest size-class of *Alca* at Lee Creek Mine is similar to and probably contains the ancestral form of the modern Razorbill, *Alca torda*. Some of the fossil specimens grouped here seem too small and gracile to be included in the same species, and further analysis may make it possible to discern a smallest species that could be described as new. This will need to be carefully distinguished from the much earlier species of *Miocepphus* that are mixed in among the Yorktown alcids, so we have postponed the attempt until undertaking a revision of the Miocene auks.

Alca ausonia (Portis, 1891), new combination

FIGURE 10e; PLATE 18a,i

Uria ausonia Portis, 1888:195 [nomen nudum]; 1891:15 [description and illustration].

MATERIAL.—Because of the abundance of this species at Lee Creek Mine, only the most important and best preserved elements are listed.

Associated Specimen: Left coracoid and distal end of left humerus, USNM 495623.

Individual Elements: Partial cranium, USNM 430925. Right mandibular articulation, USNM 206627; left mandibular articulations, USNM 177804, 460790. Anterior portion of sterna, USNM 178152, 496140–496146. Symphyseal portion of furcula, USNM 193317. Right coracoids, USNM 177759, 181077, 192718, 192841, 193075, 210498, 215779, 250666, 252300, 308159, 366741; left coracoids, USNM 177751, 179242, 192452, 193145, 206464, 215512, 215852, 242332, 248515, 248575, 366363, 367007, 367155. Proximal ends of scapulae, USNM 192608, 193353, 215480, 495674, 495675. Right humeri, USNM 181038, 215443, 366571, 366584, 446661, 446670; left humeri, USNM 179220, 183425, 275870, 368479, 368480, 446685, 446698, 495670–495672. Right ulnae, USNM 192706, 192983, 193411, 206353, 210459, 306258, 446545–446547, 446553, 446556, 446568, 446578, 446599, 448902, 448903; left ulnae, USNM 178173, 183432, 183433, 183490, 215723, 215905, 242223, 242300, 252331, 302357, 302364, 366567, 446622, 496160; pathological left ulna, USNM 446647. Right carpometacarpi, USNM 178109, 178182, 183463, 192866, 215673, 215855, 250720, 306313; left carpometacarpi, USNM 177784, 178053, 181102, 192679, 192948, 193399, 236873, 241379, 446536. Synsacra, USNM

275868, 496122–496128. Right femora, USNM 275789, 446702, 446703; left femora, USNM 446721–446723, 460799. Proximal ends of right tibiotarsi, USNM 366561, 495645, 495646; proximal ends of left tibiotarsi, USNM 206394, 206461, 495642–495644; distal ends of right tibiotarsi, USNM 178137, 206569, 366401, 368477; distal ends of left tibiotarsi, USNM 177902, 206440, 210496, 241396, 252311, 256251. Right tarsometatarsi, USNM 183468, 321272, 446728, 446729, 446731, 495635; left tarsometatarsi, USNM 177812, 179232, 183491; incompletely ossified right tarsometatarsus, USNM 206329; incompletely ossified left tarsometatarsus, USNM 206393.

HORIZON.—Yorktown Formation (USNM 178137, 179220, and 183425 from basal Yorktown Formation as determined from foraminifera in matrix).

MEASUREMENTS.—See Figure 9.

REMARKS.—This species was hitherto known only from the holotype, the distal two-thirds of a left humerus from the Pliocene at Orciano Pisano, about 25 km SSE of Pisa in the province of Pisa, Italy. Although Portis's 1888 publication is usually cited as the original description (e.g., Lambrecht, 1933; Brodkorb, 1967), the species is stated only to accord well in size and characters with *Uria rhingvia* (sic) Brünnich (= *U. aalge*), which does not diagnose it in any way. The holotype is discussed at great length and is excellently illustrated in Portis (1891), which should stand as the original description.

Ausonia, incidentally, refers to the country of the ancient Ausonians in lower Italy and has been used in poetical writing as an allusion to Italy. It also refers to a bay "on the south coast of Italy, between the Japygian Peninsula and the Sicilian Straits" (Andrews, 1856:180). We were able to study an excellent cast of the holotype of *Uria ausonia*, the original of which is in the Museo di Geologia e Paleontologia dell'Università di Firenze (IGF 14875). Although originally described in the genus *Uria*, in which subsequently it was always listed, the specimen is in fact referable to *Alca* on the basis of the characters of the humerus outlined under *Alca antiqua* (Marsh).

There are specimens of humeri from Lee Creek Mine that are identical with the holotype of *Alca ausonia*. This species was larger and more robust than the *Alca torda* lineage but was smaller than *Alca antiqua*, which is much more abundant at Lee Creek Mine. Unfortunately, no premaxillae of *A. ausonia* have as yet been recovered, and the species is thus far recognized only on quantitative characters. Most of the smaller and more common of the two alcids in the Bone Valley collection belong in this size range, whereas a few fit better in the *Alca* aff. *torda* range but may simply be small *A. ausonia*.

Two fossil tarsometatarsi determined to be from immatures (USNM 206329, 206393) were of a size appropriate for *A. ausonia* and indicate probable wintering at Lee Creek (see discussion under *A. antiqua*).

Alca antiqua (Marsh, 1870), new combination

FIGURES 10g–l, 11a–d, 12b, 13; PLATE 18c,e,g,k,m,o,q,r,t

Catarractes antiquus Marsh, 1870:213.*Lomvia antiqua* (Marsh).—Coues, 1884:825.*Uria antiqua* (Marsh).—American Ornithologists' Union, 1886:363.*Australca grandis* Brodkorb, 1955:27.

MATERIAL.—*Associated Specimens:* Rostrum, fragment of mandible, right ulna, and right tibiotarsus, USNM 336380; distal half of right femur, proximal half of right tibiotarsus, both fibulae, and proximal half of scapula, USNM 495617; basicranial fragment, pterygoid, quadrate, left mandibular articulation, and distal halves of right ulna and radius, USNM 367907; three vertebrae, right coracoid, and distal half of left ulna, USNM 495609; scapular two-thirds of right coracoid and proximal half of left humerus, USNM 495614; fragment of manubrium, distal end of right humerus, proximal two-thirds of left humerus, distal third of right ulna, distal three-fourths of left ulna, proximal ends of both radii, distal end of radius, distal two-thirds of right carpometacarpus, and fragment of synsacral vertebra, USNM 192101; cervical vertebra, nearly complete left humerus, proximal half of right humerus, proximal ends of right ulna and radius, distal two-thirds of left ulna, and right carpometacarpus lacking minor metacarpal, USNM 495612; left tibiotarsus lacking proximal end, left tarsometatarsus lacking digits 2 and 4, and pedal phalanx, USNM 495611; right and left humeri, USNM 236802; right coracoid and shaft and distal end of right humerus, USNM 215454; nearly complete left humerus and left ulna, USNM 495613; anterior portion of sternum, nearly complete furcula, left coracoid, left humerus, right humerus lacking proximal end, left ulna, and left radius, USNM 454590; left humerus, right ulna, and proximal two-thirds of right radius, USNM 495616; partial sternum missing manubrium, distal third of right humerus, right ulna missing part of distal end, distal half of right carpometacarpus, alar digits, partial pelvis, right femur, and proximal half of right tibiotarsus, USNM 336379; left humerus, USNM 446684, and left radius, USNM 446699; left coracoid and shaft of left humerus, USNM 495624.

Individual Elements: Rostra, USNM 299814, 321244, 430927–430929, 460794, 495615; nasal processes of premaxillary, USNM 193257, 210460; tips of premaxillaries, USNM 252286, 430930. Partial cranium, USNM 206383; right otic fragment, USNM 430934; left otic region, USNM 490932, 490933; right jugal bar, USNM 430926. Right mandibular articulations, USNM 192974, 460791–460793, KU 21215, 21217; left mandibular articulations, USNM 192532, KU 21216.

Anterior portion of sterna, USNM 496147–496157. Furcular rami, USNM 210516, 256225, 366383. Right coracoids, USNM 178122, 192852, 193349, 206492, 206515, 206521, 215824, 215854, 241350, 242320, 250790, 250814, 252288, 366366, 366367, 366999, 367008, 367109; left coracoids, USNM 177764, 181092, 183473, 192034, 206532, 241366, 248540, 250667, 368521, 368528, 448862. Anterior ends of

scapulae, USNM 192052, 192064, 192937, 193205, 206614, 252437, 306314, 366444, 366452, 366752, 367002, 496158. Right humeri, USNM 177981, 179285, 181086, 192840, 206301, 242288, 252381, 275787, 302358, 367013, 446649, 446652, 446654, 446662–446669; left humeri, USNM 192014, 215795, 275846, 302320, 321235, 366793, 446671–446677, 446680–446683, 446687, 446688, 446690, 446692, 446694–446697, 495669, 495673. Right ulnae, USNM 366294, 366944, 446555, 446558, 446561, 446562, 446566, 446567, 446571, 446580, 446582; left ulnae, USNM 446609, 446614, 446629, 446630, 446632, 446643, 446645, 495618. Right radii, USNM 495630, 495631; left radius, 496159. Right carpometacarpus, USNM 177782, 177785, 181097, 192020, 192448, 236803, 308157, 308219, 367106, 446534; left carpometacarpus, USNM 178091, 178106, 178172, 183447, 215858, 275872, 275875, 302371, 306277, 366428, 366622.

Synsacra, USNM 192627, 193004, 193316, 206389, 250687, 496129–496137. Right femora, USNM 179309, 206607, 215456, 250663, 306253, 306286, 368533, 446700, 446701, 446704–446712, 460800, 460801; left femora, USNM 183496, 193109, 275857, 367063, 446713–446720, 446724, 460802. Proximal ends of right tibiotarsi, USNM 495647, 495648, 496161; proximal ends of left tibiotarsi, USNM 192069, 242279, 495655, 495656; distal ends of right tibiotarsi, USNM 367060, 495649–495654; distal ends of left tibiotarsi, USNM 178104, 495657–495667. Right tarsometatarsi, USNM 446726, 446727, 446730, 446734, 495636, 495637; left tarsometatarsi, USNM 177809, 192441, 446737, 446738, 446740, 448816, 448820, 448821; incompletely ossified right tarsometatarsi, USNM 192090, 460814, 460816; incompletely ossified left tarsometatarsi, USNM 177928, 210524, 302396, 446739, 448815, 448817, 460815, 495632.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Figure 9.

Rostral Measurements (mm, taken at or from anterior edge of narial openings): Length to tip, 31.3, 31.4, 33.3, 30.1+; height, 12.8 (immature), 14.8 (immature), 16.3+, 13.3+, 16.4, 16.4, 14.5, 12.3; width 7.5, 8.4, 9.1, 8.5.

REMARKS.—By far the most abundant bird at Lee Creek Mine is a large species of *Alca* for which the earliest available name is *Catarractes* (= *Uria*) *antiquus* Marsh, 1870. This was established on a nearly complete left humerus from Tarboro, Edgecombe County, North Carolina. The age of the specimen was not known; Marsh (1870) assumed only that it was of Tertiary age. Shufeldt (1915) assigned it to the Miocene, and Brodkorb (1967:215) referred it to the "Middle Miocene (Chesapeake group)." The exposures at Tarboro, however, are Yorktown in age (Mansfield, 1943) and are thought to be slightly younger than the principal bone-bearing layer at Lee Creek Mine (T.G. Gibson, pers. comm., 1972; Olson and Gillette, 1978).

Shufeldt (1915) was incorrect in asserting that the holotype of *antiqua* agrees with *Uria* in all particulars except size. In the distal end, the internal and external tricipital grooves are equal-

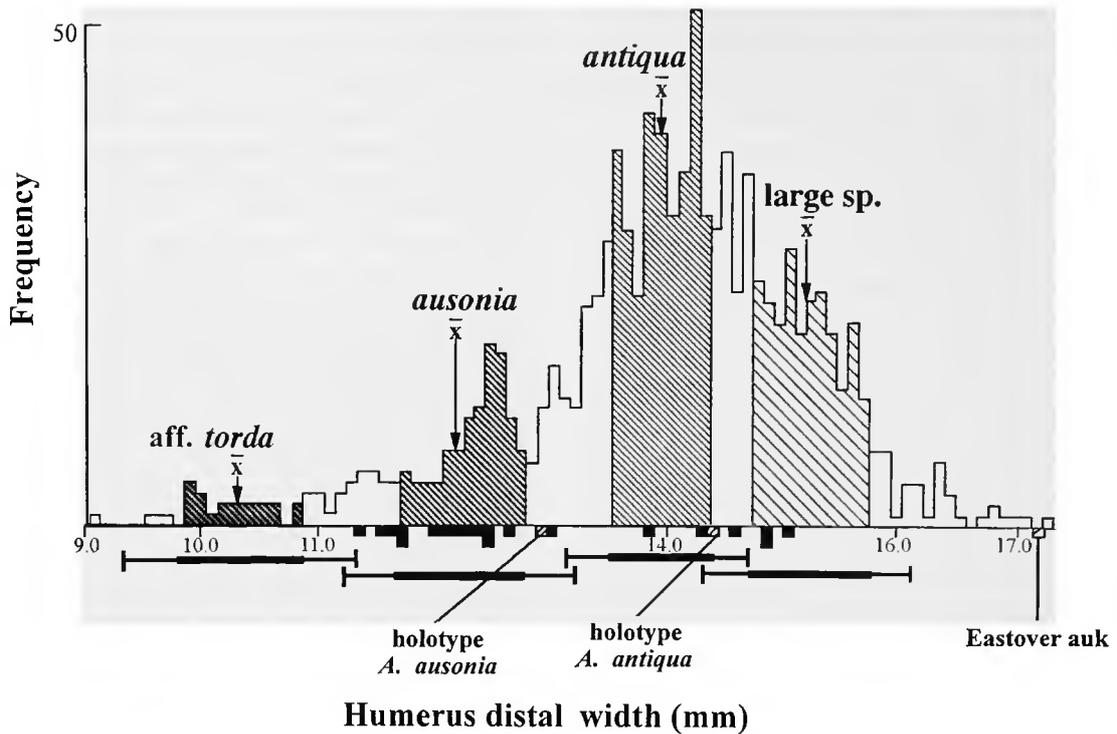


FIGURE 9.—Species intervals for *Alca* spp. from Lee Creek Mine as defined by cluster analysis with $K=4$ groups, shown on a histogram of humerus distal width. Means are shown as arrows; species intervals are defined by standard deviations from the mean (heavy bars, shaded polygons); specimens outside a single standard deviation from the predicted mean are unshaded and are considered identical; black squares below the x-axis are Bone Valley fossils. The positions of the holotypes of two of the named fossil taxa are indicated (squares below the x-axis with diagonal shading; both fall slightly outside the standard deviations of their species groups), as is that of a very large late Miocene specimen (USNM 242238) from the Eastover Formation of Virginia. Very large and very small specimens fall outside the predicted range of any species.



FIGURE 10.—Comparison of size variation in right humeri of *Alca* in palmar view: *a, b*, modern *Alca torda* showing a small and a large individual, respectively; *c-l*, fossils from Lee Creek Mine, which we estimate to include at least four species (*c, d*, *Alca* aff. *torda*; *e, f*, *Alca ausonia*; *g-l*, *Alca antiqua*); *m*, *Alca*, very large undescribed species from the late Miocene Eastover Formation of Virginia (USNM 242238); *n*, *Alca*, very large undescribed species from Lee Creek Mine (USNM 446650). All figures $\times 0.45$. (All USNM: *a*, 502377; *b*, 502389; *c*, 446657; *d*, 495589; *e*, 181038; *f*, 446654; *g*, 181086; *h*, 446664; *i*, 446663; *j*, 446666; *k*, 206301; *l*, 367013.)

ly wide, as was noted by Marsh (1870) in the original description, whereas in *Uria* the internal groove is noticeably wider. Also, in *antiqua* the ectepicondylar prominence extends higher on the shaft and projects farther in a distinct point than it does in *Uria*, in which this prominence is lower and more rounded. In all respects, the holotype of *antiqua* agrees with *Alca*, and we therefore propose that the species be removed to that genus as *Alca antiqua*. The holotype of *Alca antiqua* is matched very closely by specimens from Lee Creek Mine.

Brodkorb (1955) named a new genus and species of large auk, *Australca grandis*, from the upper Bone Valley Formation (latest Hemphillian) of Florida. The holotype is a nearly complete right coracoid. Sixteen wing and leg elements were referred to this species from Bone Valley in the original description, but all but one of these (ulna, UF PB 596) are from smaller species than the one indicated by the holotype of *A. grandis*. Many coracoids from Lee Creek Mine are indistinguishable from the holotype of *A. grandis*, and these fall in the same size class as the humeri referable to *Alca antiqua*; therefore, we consider the species *Australca grandis* Brodkorb, 1955, to be a junior subjective synonym of *Catarractes antiquus* Marsh, 1870.

The genus *Australca* was diagnosed on characters of the coracoid, with the following differences from *Alca* being given

by Brodkorb (1955:26): "somewhat shorter relative distance from head to scapular facet; more produced brachial tuberosity; greater depth of head; wider sternal end." There are now, however, hundreds of coracoids from Lee Creek Mine in the size range of *A. grandis*, and these show that the supposed characters of *Australca* are either not consistently different from *Alca* or are simply size related.

The phylogenetic position of *Australca* was thought by Brodkorb (1955) to be between *Pinguinus* on one hand and *Alca* and *Uria* on the other. Portions of 10 rostra from Lee Creek Mine of a size compatible with the holotype of *Australca grandis* (= *Alca antiqua*) show that the bill in this genus was high and compressed (Figure 11a-d) like that of *Pinguinus* and *Alca* (Figure 11e-h) and unlike the pointed bill of *Uria*. The characters of these fragments, and of the several lower-jaw articulations referable to the same species, are indeed intermediate between those of *Pinguinus* and *Alca* (Figure 12), but they are much longer than in *Alca*, making them closer to *Pinguinus*.

We find no characters of the bill and mandible of *antiqua* that could be considered of generic significance, this being simply a much larger form of *Alca*. Therefore, we consider *Australca* Brodkorb, 1955, to be a synonym of *Alca* Linnaeus,



FIGURE 11.—Comparison of rostra of *Alca* in lateral view: a-d, *Alca antiqua* from Lee Creek Mine; e-h, modern Razorbill, *Alca torda*. All figures $\times 1.15$. (All USNM: a, 430929; b, 336380; c, 430927; d, 430928; e, 502382; f, 502383; g, 502549; h, 502377.) (Apparent ages: a,b,e,f, adult; c,d, immature; g,h, juvenile.)

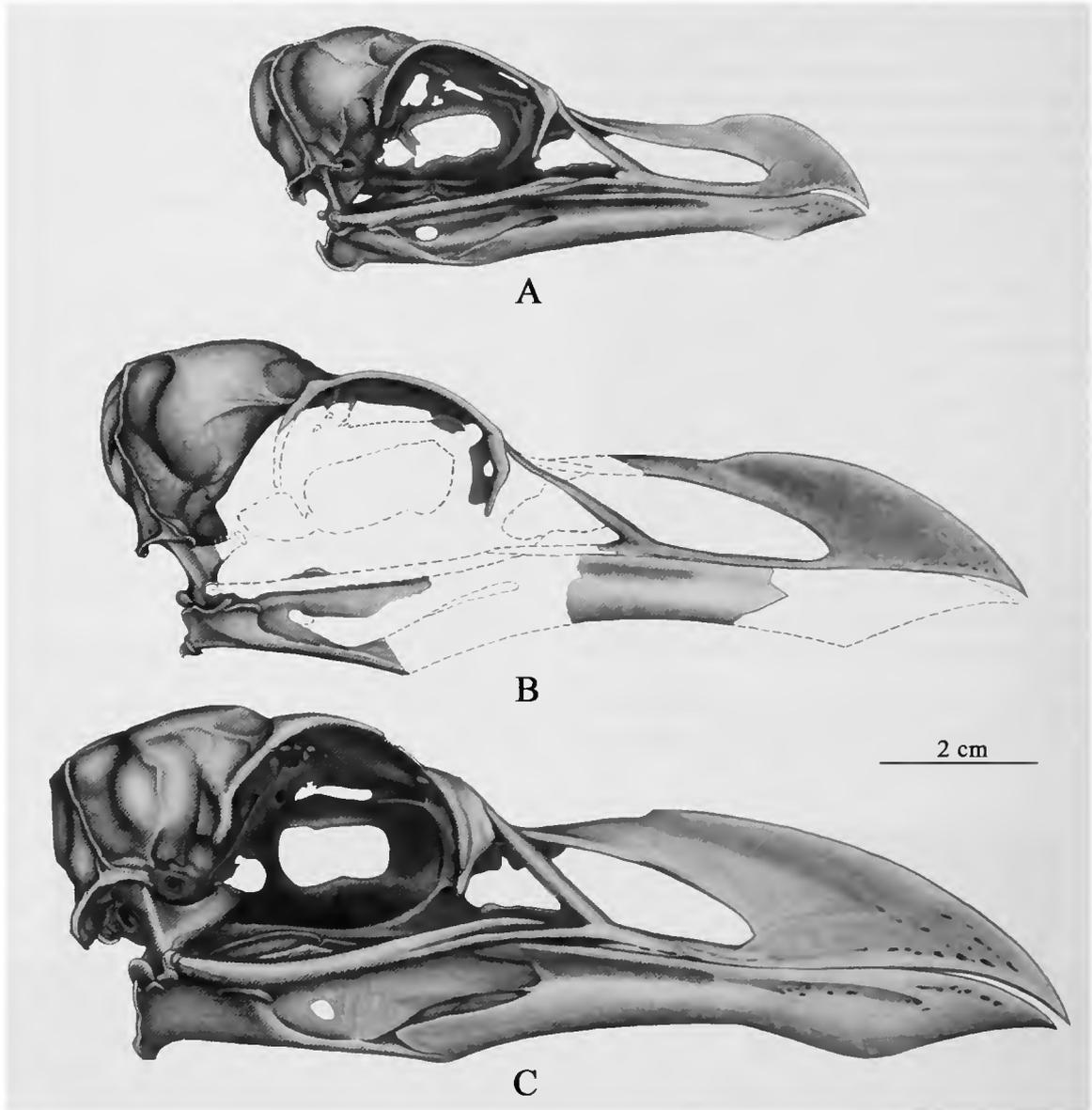


FIGURE 12.—Comparison of skulls of *Alca*: a, modern Razorbill, *A. torda*; b, composite reconstruction of the skull of *Alca antiqua*, based on fossils from Lee Creek Mine; c, Great Auk, *Pinguinus impennis*. Drawings by P.C. Rasmussen.

1758. The name *Australca grandis* Brodkorb thus disappears entirely in the synonymy of *Alca antiqua* (Marsh).

This species was not "on the road to flightlessness," as Brodkorb (1955:29) suggested, as that idea was based on the wing bones of a smaller species. Furthermore, *Alca antiqua* was not ancestral to *Pinguinus* because the latter genus existed contemporaneously in the early Pliocene at Lee Creek (see below).

There appears to be a great deal of what may be individual variation within *Alca antiqua*. For example, one of the associated specimens (USNM 336379) has an ulna that is proportionately very short. Yet statistical tests (principal components analyses and K means) on isolated ulnae failed to obtain any

consistent separation of the specimens in the *A. antiqua* size range into discrete groups.

A few tarsometatarsi of medium size (USNM 448815, 448817, 495632) have the distal and especially the proximal ends incompletely ossified. These are more ossified than two juvenile *Uria aalge* collected in October in California but are much less ossified than four juvenile *Alca torda* taken in January and February. Juvenile Razorbills begin to migrate south in August and early fall (Nettleship and Birkhead, 1985); thus, the presence of juvenile remains at Lee Creek Mine does not necessarily indicate that alcids bred nearby. Conversely, eight fossil tarsometatarsi (USNM 177928, 192090, 210524, 302396,

446739, 460814–460816) show degrees of ossification comparable to that of a specimen of *Alca torda* (USNM 610935) collected in January off North Carolina. These specimens are less completely ossified than are two other January specimens of *A. torda* (USNM 502377, 502549) and one February specimen (USNM 555668). Several other fossil tarsometatarsi also appear to be incompletely ossified. The stage of ossification of these specimens suggests that *Alca antiqua* probably wintered at Lee Creek.

We have direct evidence of food preferences in one individual of *Alca antiqua*, a partial associated skeleton (USNM 336379) preserved with remains of the stomach contents in place (Figure 13; Boucot, 1990). These small fish bones were identified by Camm C. Swift as being most similar to those of the silver hake, *Merluccius bilinearis* (Mitchill), probably be-

longing to a single individual about 100–120 mm standard length. The most common hake otoliths from Lee Creek Mine were those identified as *Merluccius* cf. *bilinearis* and were regarded as “unquestionably... from an extinct ancestor, if not from the extant *M. bilinearis*” (Fitch and Lavenberg, 1983:516). This fish is a predator that ranges widely in the water column at variable distances from shore from the Newfoundland Banks to South Carolina, but it is more abundant in the northern part of its range (Bigelow and Schroeder, 1953). As determined by otoliths, *Merluccius* was among the three most abundant genera of fish at Lee Creek (Fitch and Lavenberg, 1983:509), which corresponds well with the abundance of *Alca antiqua* in the deposits.

In connection with the present work on *Australca antiqua*, we examined the holotypical humerus of *Uria affinis* (Marsh,

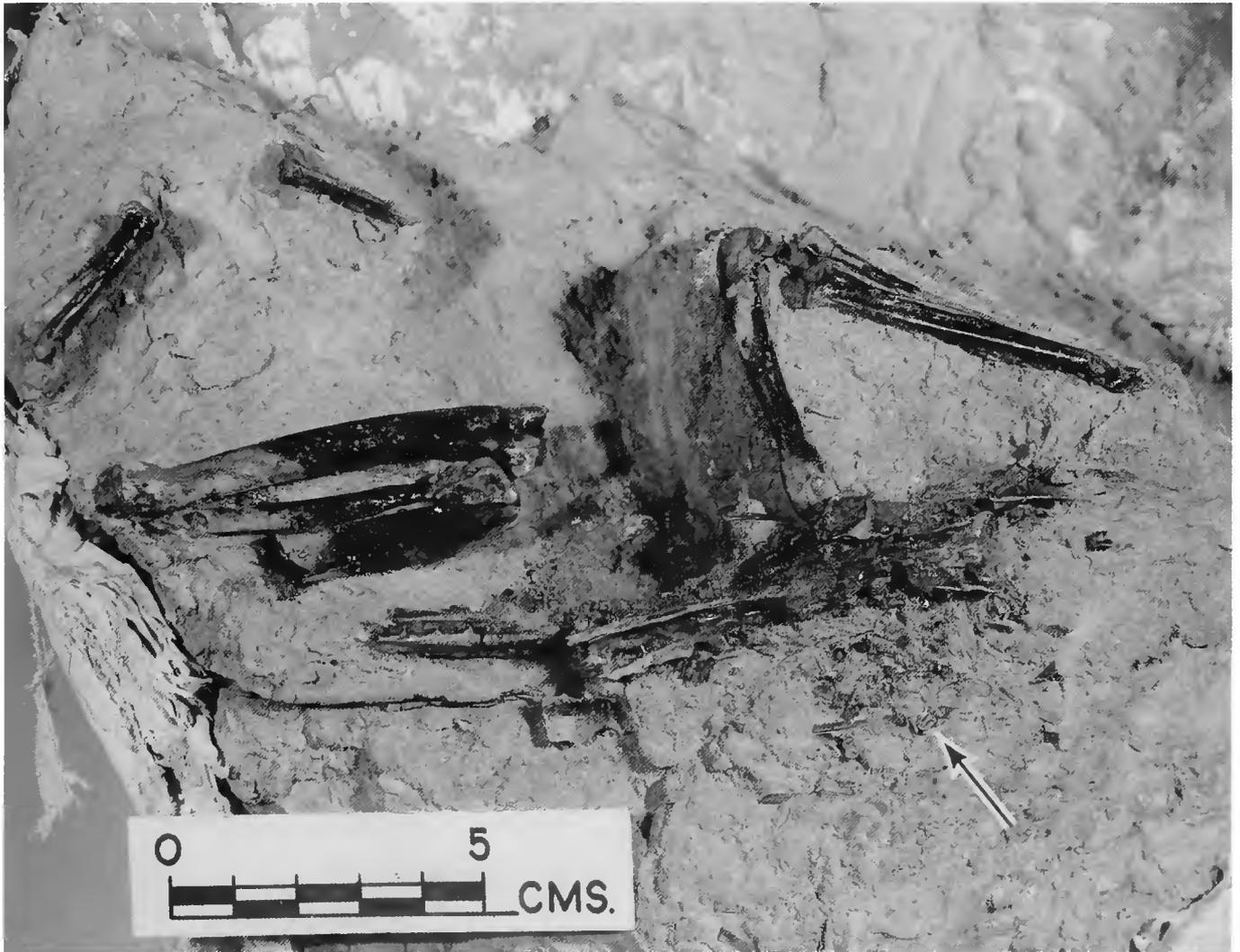


FIGURE 13.—Partial associated skeleton of *Alca antiqua* (USNM 336379) with stomach contents including bones of silver hake, *Merluccius bilinearis*, preserved in situ (arrow).

1872), from Pleistocene deposits at Bangor, Maine. This specimen, in contrast to "*Uria*" *antiqua*, is indeed referable to *Uria*. It is large, as noted both by Marsh (1872) and by Shufeldt (1915), but it falls within the size range of the large Pacific form of the Thick-billed Murre, *Uria lomvia arra* Pallas. It was probably a Pleistocene representative of one of the two modern species of the genus.

Alca, undescribed species

FIGURE 10*m,n*; PLATE 19*a,d,e,g,h*

MATERIAL.—Anterior portions of sterna, USNM 252417, 366785, 495679. Right coracoid, USNM 308221; left coracoids, USNM 308210, 308211, 495590, 495619, 495620. Right humerus, USNM 446650; proximal third of left humerus, USNM 299643; distal ends of right humeri, USNM 299637, 460811. Right ulna, USNM 306340; proximal end of right ulna, USNM 181090. Right carpometacarpus, USNM 446520; left carpometacarpi, USNM 446525, 446528. Distal half of right femur, USNM 460803. Right tarsometatarsi, USNM 193013, 446736, 495634; left tarsometatarsi, USNM 177865, 181026, 306342; proximal two-thirds of left tarsometatarsus, USNM 177804.

HORIZON.—Yorktown Formation (USNM 181090 from basal Yorktown as determined from foraminifera in matrix).

ADDITIONAL MATERIAL EXAMINED.—*Westmoreland County, Virginia*: Claremont Manor Member of the Eastover Formation, USNM 242238, partial associated skeleton consisting of anterior portion of sternum with most of carina, left coracoid, right humerus, right ulna, and proximal and distal halves of right radius.

MEASUREMENTS.—See Figure 9.

Coracoid: Length, 52.8, 52.8, 53.1, 54.2, 55.1, 57.4.

Humerus: Length, 111.6; proximal width, 24.9, 25.4; distal width, 16.5, 16.3, 16.8.

Ulna (USNM 181090 in parentheses): Length, 91.4; proximal depth, 15.9 (18.5); proximal width, 11.5 (12.1).

Femur: Distal width, 12.5+.

Carpometacarpus: Length, 57.5, 57.5, 57.6.

Tarsometatarsus: Length, 45.3, 46.6, 47.1, 47.5, 47.5, 47.6.

REMARKS.—From a partial associated wing and pectoral girdle (USNM 242238) from the late Miocene Eastover Formation of Virginia, we know of the existence of a species of *Alca* much larger than *A. antiqua*; it was nearly the size of *Pinguinus* but was volant. This can only be distinguished from other species of *Alca* by its larger size (Figure 10*m*; Plate 19*a,d,g*). We plan to describe it in a revision of the Miocene Alcidae of the Chesapeake Group.

There are several specimens of *Alca* from Lee Creek Mine that also are too large to be referred to *A. antiqua*. We are not certain, however, how many species may be present in this size class. Most of the elements that are comparable are about the same size as the associated specimen from the Eastover Formation and presumably would be referable to the same species.

That there are as many as seven tarsometatarsi that seem to belong here is odd, considering the relative scarcity of that element in the collections, and perhaps some of these may be from the upper size range of *A. antiqua*.

One proximal end of an ulna (USNM 181090) is so much larger than USNM 306340 or the ulna of the Eastover specimen that perhaps an additional extremely large species may be indicated. Apart from its large size, this ulna is inseparable from ulnae of *Alca* and is not at all modified as in *Pinguinus* (Plate 19*i*).

Genus *Pinguinus* Bonnaterre

Pinguinus alfrednewtoni Olson

PLATES 19*b,f*, 20*a,c,e,g,i,k,m,o,q,s*

Pinguinis [sic] *alfrednewtoni* Olson, 1977:690.

MATERIAL.—Right mandibular articulation, USNM 460786. Anterior portions of sterna, USNM 459391, 495603. Symphyseal portions of furculae, USNM 459389, 460787. Right coracoids, USNM 275780, 430942; left coracoids, USNM 367160, 430941, 459392; 495621; scapular two-thirds of right coracoid, USNM 250682; left coracoid lacking sternal end, USNM 495622. Anterior ends of right scapulae, USNM 460812, 460829, 495606. Right humerus, USNM 366630; proximal ends of right humeri, USNM 206636, 248570, 250731, 430940, 460788; proximal ends of left humeri, USNM 236818, 250664, 250834, 430938; distal ends of right humeri, USNM 192497 (paratype), 252396; distal ends of left humeri, USNM 179226 (paratype), 275863, 368472, 430939. Right ulnae, USNM 193334 (holotype), 430936, 430937; left ulnae, USNM 250813, 459390. Left radius, USNM 430935. Right femur, USNM 430943; left femora, USNM 206362 (paratype), 257541; distal ends of right femora, USNM 302314, 495604, 495605. Proximal end of right tibiotarsus, USNM 366727; distal ends of right tibiotarsi, USNM 193101 (paratype), 430946; distal ends of left tibiotarsi, USNM 430944, 430945, 495607. Right tarsometatarsus, USNM 179277 (paratype); left tarsometatarsus, USNM 430947; right tarsometatarsus lacking proximal and part of distal end, USNM 495608; proximal end of left tarsometatarsus, USNM 241395.

HORIZON.—Yorktown Formation (USNM 179226, 206636, from basal Yorktown as determined from foraminifera in matrix).

MEASUREMENTS (mm).—*Coracoid*: Length, 59.8, 60.2.

Furcula: Dorsoventral height at symphysis, 12.1+.

Humerus: Length, 101.9; proximal width, 23.9, 25.0, 24.8, 24.8, 26.9; distal width, 16.5, 16.6, 16.8, 17.0, 17.5, 17.7.

Ulna: Length, 54.8, 55.3, 56.5, 59.3; proximal width, 10.3, 11.1, 11.5, 11.7; distal depth, 10.9, 11.2, 11.4, 11.4. Radius: length, 54.5; distal width, 7.2.

Femur: Length, 69.3, 70.7; proximal width, 15.0, 15.1; distal width, 15.0, 15.3.

Tibiotarsus: Distal width, 12.5, 12.6.

Tarsometatarsus: Length, 56.1; proximal width, 13.4, 14.0.

REMARKS.—In addition to the characters given by Olson (1977) for the species *Pinguinus alfrednewtoni*, the fossil humeri differ from those of the Greak Auk, *P. impennis* (Plate 20 r,t), in being even heavier, tending to have thicker walls of the shaft, and by having the proximo-external edge of the bicipital surface forming a more pronounced knob edged by the ligamental and tricipital furrows, the scar for the pectoral attachment more strongly developed, and the internal-distal edge of the bicipital crest more elongated internally. The radius in the fossil is more mediolaterally expanded distally from the bicipital tubercle.

The fossil coracoids have a smaller coracoidal foramen than in *Pinguinus impennis* (Plates 19c, 20h,j), despite being heavier overall; the ventro-posterior edge of the coracoidal neck has a heavy lip, which is much less marked and more anteriorly situated in *P. impennis*. The furcula is more robust in the fossil form. In addition to the characters given in Olson (1977), the fossil femora have a heavier trochanteric ridge and usually have the anterior ridge of the internal condyle extending farther proximally than in *P. impennis*. The tibiotarsi show no differences other than those noted in the original description, although no complete fossil tibiotarsi are yet available. The fossil tarsometatarsi are slightly longer and more gracile than in the recent species.

These fossils show such substantial differences from the modern Great Auk that we are forced to consider that *P. alfrednewtoni* is not a temporal antecedent of the same lineage. Although the *Pinguinus* from Lee Creek was already highly specialized along the same lines as the Great Auk with regard to modification of the wing as a paddle, it is not only larger and more robust, but in other regards it is seemingly even more specialized than *P. impennis*. Thus, *Pinguinus* appears to have diverged into at least two lineages prior to the early Pliocene, perhaps as eastern Atlantic and western Atlantic vicariants. The *P. alfrednewtoni* lineage died out some time after the early Pliocene and was apparently replaced in the western Atlantic by the modern species *P. impennis*.

One fossil tarsometatarsus of *Pinguinus alfrednewtoni* (USNM 430947) is considerably less ossified in the region of the anterior proximal foramen than are any of 181 *P. impennis* tarsometatarsi examined from the breeding ground at Funk Island. Olson (1977) mentioned that another tarsometatarsus (USNM 179277, paratype) appeared to be from an immature. USNM 430947 is similar in degree of ossification to tarsometatarsi of first winter *Alca torda* (see "*Alca antiqua*," above), supporting the hypothesis that *Pinguinus* wintered at Lee Creek, as apparently did *Alca antiqua* and probably the other species of the genus as well.

Genus *Alle* Link

The fossils discussed below belong to a tiny species of alcid referable to the genus *Alle* by the following combination of characters.

In the coracoid, the procoracoidal process is triangular in shape, with only a posterior notch rather than a closed foramen, as opposed to *Synthliboramphus* Brandt and *Endomychura* Oberholser, in which there is a complete foramen, or *Ptychoramphus* Brandt, *Cyclorrhynchus* Kaup, and *Aethia* Merrem, in which the procoracoid is strap-like, with no foramen. The procoracoid in *Brachyramphus* Brandt varies from strap-like to triangular with no foramen. The internal distal angle of the coracoid is more elongated medially in *Brachyramphus* and is much more twisted dorsally in *Ptychoramphus* than it is in *Alle*. The sternal facet of the coracoid is much thicker dorsoventrally in *Brachyramphus*, *Ptychoramphus*, and *Synthliboramphus* than it is in *Alle*.

In the humerus, in *Synthliboramphus* the shaft is sigmoid (straight in the fossils), and the distal edge of the bicipital surface forms a wide obtuse angle to the shaft. In *Aethia* the shaft is flatter in the distal portion, the distal end is more rotated, and the distinct furrow on the external edge of the bicipital crest is lacking. The shaft in *Brachyramphus* is much more flattened, with ridges along both the internal and external edges. The pectoral crest extends farther proximally in *Ptychoramphus*, and the internal condyle is more expanded medially and distally.

In the carpometacarpus, compared to the fossil, the process of the alular metacarpal is larger, more anteriorly produced, and more proximally curved in *Brachyramphus*; it is much less extensive distally and is more curved proximally in *Ptychoramphus*, *Aethia*, and *Endomychura*; and it has a notch between it and the pollical facet in *Synthliboramphus*.

Alle aff. *alle* (Linnaeus)

PLATE 21a,c,e,g,i,k,m,o,q

MATERIAL.—Left coracoid, USNM 192856. Right humerus, USNM 448912; right humerus lacking proximal end, USNM 367158; left humerus lacking much of both ends, USNM 430954; proximal third of shaft of left humerus with distal half of proximal end, USNM 430955; distal ends of right humeri, USNM 367129, 430956; distal ends of left humeri, USNM 206572, 495585, 495601. Distal half of right ulna, USNM 430953. Right carpometacarpus lacking minor metacarpal, USNM 430952.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 9.

REMARKS.—The fossils differ from the modern Dovekie, *Alle alle*, in their slightly smaller size (Table 9); the smaller procoracoid process; the neck of the coracoid being shorter and in medial view thinner at the level of the glenoid facet; the more pointed coracohumeral surface; the proportionately short and stout humerus, with the proximal end of the shaft wide rather than constricted; the distal edge of the bicipital crest of the humerus being more nearly perpendicular to the axis of the shaft and slightly notched at the juncture with the shaft; the much better developed and more triangular pectoral crest of the humerus; the much shorter scar for pectoralis attachment; the

TABLE 9.—Measurements (mm) of modern *Alle alle* and fossil *Alle aff. alle* (measurements in list form) from Lee Creek Mine. (n =number of specimens, s =standard deviation.)

Element	<i>A. alle</i>				<i>A. aff. alle</i>
	n	Range	Mean	s	
Coracoid					
Medial length	15	21.1–23.4	22.3	0.74	20.0
Humerus					
Length	21	40.6–43.6	42.0	0.77	39.6
Proximal width	21	9.3–10.5	9.8	0.36	10.0
Distal width	21	6.0–6.9	6.6	0.24	6.4, 7.0
Ulna					
Distal diagonal	18	4.4–5.2	4.8	0.18	4.5
Carpometacarpus					
Length	15	21.5–24.0	22.5	0.62	21.6
Proximal width	15	5.7–6.5	6.2	0.25	6.0
Distal diagonal	15	3.4–4.2	3.8	0.21	3.5

much less flattened distal third of the humerus shaft, without a ridge on the internal margin; the distal end of the humerus being less rotated; the more rounded external condyle of the carpometacarpus; and the distal end of the major metacarpal being more produced as a distinct anterior projection. These differences probably reflect changes through time within a lineage and not a speciation event.

Storer (1945:453) regarded *Alle alle* as an “ancient species with no near relatives” but later (1952:190) felt that its plumage pattern and distribution suggested that “it may be closer to the auks (*Alca*) and murre (*Uria*) than is currently thought.” The specimens from Lee Creek Mine constitute the first fossil record for the genus *Alle*.

In contrast to the Pacific, where there has been a considerable radiation of small auklets and murrelets, the tiny modern Dovekie, *Alle alle*, is the only very small alcid now native to the Atlantic. It breeds in the high Arctic and usually winters no further south than the Gulf of St. Lawrence and Bay of Fundy, although it is subject to irruptive movements. It is considered to be an “uncommon sporadic winter visitor” in North Carolina today (Lee, 1995:154). *Alle aff. alle* is certainly rare at Lee Creek Mine, which may in part be attributable to its small size, but most likely it was not common in the early Pliocene of North Carolina.

AETHIINAE, genus and species indeterminate

PLATE 22s,v

MATERIAL.—*Associated Specimen:* Partial shaft of right humerus with ectepicondylar process and portion of a shaft of an ulna, USNM 495675.

Individual Elements: Right coracoid, USNM 495586. Shaft of left humerus with part of proximal end, USNM 192508; proximal two-thirds of shafts of right humeri with part of bicipital and pectoral crests, USNM 459396, 459397; distal two-thirds of left humerus lacking condyles, USNM 236881.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—*Humerus:* No standard measurements possible.

Coracoid: Length to medial angle of sternal articulation, 31.8.

REMARKS.—This enigmatic alcid is thus far represented only by very fragmentary and undiagnostic fossils. The shape of the procoracoid unambiguously indicates that it belongs to the Aethiinae. The humerus is flattened in the manner characteristic of most Alcidae but is less so than in *Synthliboramphus*, *Brachyramphus*, or *Endomychura*. Its size indicates a species too large for *Alle* but too small for *Miocepphus*. In the structure of the shaft, the ridge arising at the pectoralis attachment, and the hint of a more excavated head and pneumatic foramen, this humerus seems closest to *Cyclorrhynchus*, a genus now confined to the Pacific.

Subfamily FRATERCULINAE (puffins)

Certain alcid fossils from Lee Creek Mine are clearly referable to the Fraterculinae by characters that include some of those delineated by Strauch (1985), especially the strongly developed second tricipital fossa of the humerus and the shape of the extensor process of the carpometacarpus. Within this subfamily, only two genera are now generally recognized, *Cerorhinca* Bonaparte and *Fratercula* Brisson, although these are only weakly differentiated. Characters observable in the Lee Creek fossils that refer them to *Fratercula* as opposed to *Cerorhinca* are as follows: procoracoid process more expanded and triangular in shape; entepicondylar area of humerus flared outward, away from shaft, instead of curving inward toward midline; depression on distal surface of internal tuberosity deeper; and tarsometatarsal cotylae more expanded laterally and medially (the tarsometatarsus in *Cerorhinca* thus appearing proportionately longer and more slender). We refer all of the fossils from Lee Creek Mine to *Fratercula*, whereas all previously reported Tertiary taxa of Fraterculinae have been described in *Cerorhinca*.

Genus *Fratercula* Brisson

Howard (1971:8) found *Cerorhinca*, *Fratercula*, and *Lunda* Pallas to be extremely similar osteologically, with *Cerorhinca* being distinguishable on “small details,” the implication being that *Fratercula* and *Lunda* would not be separable. This also was the conclusion of Strauch (1985) and was the classification used by the American Ornithologists’ Union (1998), with which we strongly concur. Thus, the monotypic genus *Lunda* becomes a synonym of *Fratercula*, and the Tufted Puffin is known as *Fratercula cirrhata* (Pallas).

Two species of *Fratercula*, small and large, occur uncommonly at Lee Creek Mine. These appear to represent the lineages leading to the modern Atlantic Puffin, *F. arctica*, and Tufted Puffin, *F. cirrhata*. There apparently are no other Tertiary records of the genus *Fratercula*.

Fratercula aff. arctica (Linnaeus)

PLATE 22a,c,e,g,i,k,m,o,q

MATERIAL.—Left coracoid lacking sternal end and furcular facet, USNM 192994. Right humerus lacking most of bicapital crest, USNM 183471; proximal ends of right humeri, USNM 177800, 192901, 206640; proximal ends of left humeri, USNM 181103, 192894, 193070, 206517, 210475, 215617, 215677, 215720; distal ends of right humeri, USNM 181031, 206639; distal ends of left humeri, USNM 193243, 241402, 248555. Proximal ends of right ulnae, USNM 179264, 181073; proximal halves of left ulnae, USNM 177828, 193336; distal halves of left ulnae, USNM 193296, 215794. Right femur, USNM 430951. Distal half of right tibiotarsus lacking condyles, USNM 215783.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 10.

REMARKS.—These fossils indicate a species much smaller than either the Horned Puffin, *Fratercula corniculata* (Naumann), or *F. cirrhata*, and they also are smaller than any of the nine skeletons of *F. arctica* examined, all of which, however, are from the range of the nominate subspecies. The coracoid is extremely small, with a long, thin neck, and the femur is likewise small, with the head less proximally oriented. Because birds from the southern part of the Atlantic Puffin's range in Europe (subspecies *grabrae* (Brehm)) are on the small end of a size cline and intergrade with nominate *F. arctica arctica* to the north (Salomonsen, 1944; Bédard, 1985; Moen, 1991), it is

possible that there may be overlap in measurements between the modern species and the Lee Creek Mine fossils. For this reason, and because we cannot find any convincing qualitative characters by which to distinguish the fossils, we have referred to them under the modern species.

Fratercula aff. cirrhata (Pallas)

PLATE 23a,c,e,g,i,k,l,n,o,q

MATERIAL.—Right coracoid, USNM 242309; scapular half of right coracoid, USNM 460806. Right humerus, USNM 490887; left humerus, USNM 257520; left humerus lacking proximo-internal portion, USNM 368496; proximal ends of right humeri, USNM 193051, 206324, 256229, 275800, 459394, 459395, 460789; proximal ends of left humeri, USNM 193131, 215678, 250704, 430958; distal ends of right humeri, USNM 177996, 192813; distal ends of left humeri, USNM 178023, 192053, 192726. Right ulna, USNM 250676; left ulna, USNM 178086, 302373, 460807; proximal half of left ulna, USNM 460808. Right carpometacarpus lacking distal end and minor metacarpal, USNM 193340. Left femur lacking distal end, USNM 366781; distal end of right femur, USNM 193074; distal end of left femur, USNM 460809. Right tibiotarsus lacking distal end, USNM 256260; distal end of left tibiotarsus, USNM 215449. Right tarsometatarsus lacking intercotylar knob, USNM 430959.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 10.

TABLE 10.—Measurements (mm) of modern *Fratercula* and fossil *Fratercula* (measurements in list form) from Lee Creek Mine. (n =number of specimens, s =standard deviation.)

Element	<i>F. arctica</i> ($n=9$)				<i>F. corniculata</i> ($n=20$)			<i>F. aff. cirrhata</i>	<i>F. cirrhata</i> ($n=20$)		
	<i>F. aff. arctica</i>	Range	Mean	s	Range	Mean	s		Range	Mean	s
Coracoid											
Medial length	—	33.7–38.8	35.7	1.76	35.9–43.1	39.0	1.94	41.0	41.2–45.9	43.7	1.33
Scapular facet depth	3.5	4.2–4.9	4.5	0.21	4.4–5.6	4.9	0.30	4.7	4.6–5.2	4.8	0.22
Humerus											
Length	60.0	61.3–69.3	64.6	3.07	66.0–77.2	71.5	3.01	67.6	72.9–81.5	77.3	1.89
Proximal width	12.6, 12.7, 13.0	13.5–15.4	14.0	0.60	14.4–17.0	15.6	0.67	15.2, 15.7, 16.1, 16.2, 16.4, 16.9, 17.1	15.2–17.3	16.2	0.51
Distal width	8.2, 8.2, 8.7, 8.8	9.6–10.8	10.0	0.40	10.2–11.8	11.0	0.48	10.5, 10.7, 10.9(2), 11.6, 11.9	10.3–12.0	11.4	0.37
Ulna											
Length	—	48.8–54.6	51.4	2.4	53.4–62.8	57.9	2.46	59.5	57.2–65.2	61.6	1.85
Proximal width	6.0, 6.3, 6.8	6.7–7.8	7.0	0.36	6.7–8.2	7.4	0.43	7.0	7.3–9.0	7.9	0.42
Distal diagonal	6.6	7.6–8.6	7.9	0.31	7.7–8.8	8.2	0.37	7.1	8.4–9.3	8.8	0.30
Carpometacarpus											
Proximal width	—	8.6–9.5	9.0	0.33	8.7–10.2	9.3	0.48	9.6	9.3–10.6	9.9	0.36
Tibiotarsus											
Distal width	—	—	6.3	0.30	6.2–7.6	6.8	0.40	7.0	7.0–8.0	7.4	0.32
Distal depth	—	6.0–7.1	6.6	0.38	6.5–7.9	7.1	0.42	7.2	7.2–8.5	7.7	0.37
Tarsometatarsus											
Length	—	26.3–31.2	28.3	1.66	28.8–35.2	30.9	2.05	31.8	31.9–37.1	34.3	1.40
Proximal width	—	6.7–7.3	7.0	0.29	7.0–8.5	7.6	0.47	7.4	7.7–8.9	8.3	0.32
Distal width	—	6.9–7.7	7.3	0.24	7.3–8.6	7.8	0.42	7.4	8.1–9.6	8.7	0.35
Distal depth	—	5.5–6.8	6.1	0.46	5.8–8.5	6.8	0.65	6.1	7.0–8.4	7.8	0.43

REMARKS.—These fossils resemble *Fratercula cirrhata* and differ from *F. arctica* and *F. corniculata* as follows: ventral edge of coracohumeral surface of coracoid large and flared, usually with a distinct pit; articular surface of distal end of tibiotarsus in posterior view extending farther proximally; and distal foramen located farther proximally so that the distance between it and the intertrochlear foramen is greater. They differ from *F. cirrhata* only in the somewhat smaller size of most elements (Table 10), the lack of a ridge on the medial surface of the neck of the coracoid, and the more gracile tarsometatarsus, with the distal foramen situated more proximad.

There are definitely two species of puffins at Lee Creek Mine, the larger of which is evidently in the same lineage as the modern Tufted Puffin, *F. cirrhata*, now confined to the Pacific Ocean. *Fratercula arctica* and *F. corniculata* are considered to be Atlantic and Pacific vicariants, respectively, and would not be expected to occur sympatrically. *Fratercula corniculata* varies considerably in size and overlaps with *F. cirrhata* (Table 10).

There is no evidence of any species of puffin in the Atlantic prior to the fossils from the Yorktown Formation, the supposition being that the two species at Lee Creek were relatively recent invaders from the Pacific that probably entered the Atlantic during a late Tertiary breach of the Bering land bridge (see "Conclusions"). The larger of these two species was later extirpated locally, leaving *F. arctica* as the only representative of its subfamily in the Atlantic.

Order ANSERIFORMES
(screamers, swans, geese, and ducks)

Family ANATIDAE
(swans, geese, and ducks)

By Lee Creek standards, anseriform birds are decidedly uncommon, with fewer than 300 specimens having been recovered so far. Yet these belong to no fewer than 20 species, which probably makes this among the most diverse Neogene anseriform faunas yet found. In identifying this material we have relied heavily on the valuable osteological study of Woolfenden (1961).

Subfamily ANSERINAE
(whistling-ducks, swans, and geese)

Tribe CYGNININI
(swans)

Genus *Cygnus* Bechstein
Cygnus aff. columbianus (Ord)

PLATE 24a,c,e,g,i,k

MATERIAL.—Scapular end of left coracoid, USNM 366792. Anterior end of left scapula, USNM 193256. Distal end of right humerus, USNM 306312; distal end of left humerus, USNM

430876. Proximal ends of right ulnae, USNM 302310, 430875; proximal end of left ulna, USNM 242201; distal end of right ulna, USNM 446508. Left carpometacarpus, USNM 308156; distal end of right carpometacarpus, USNM 193338; distal half of left carpometacarpus, USNM 459410. Phalanx 1 of major alar digits, USNM 308182, 430874. Distal end of right tibiotarsus, USNM 510078; distal end of left tibiotarsus, USNM 210454. Left tarsometatarsus lacking trochlea IV, USNM 430877; distal end of left tarsometatarsus, USNM 430878.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Scapula*: Anterior diagonal, 26.1.

Humerus: Distal width, 32.2, 34.4.

Ulna: Distal width, 22.8.

Carpometacarpus: Distal diagonal, 13.8.

Phalanx 1 of Major Alar Digit: Length, 52.8.

Tibiotarsus: Distal depth, 21.3*.

Tarsometatarsus: Length, 117.3.

REMARKS.—These specimens are all within the size range of the Tundra (=Whistling) Swan, *Cygnus columbianus*, from which they do not differ in any significant way. The only Tertiary species of *Cygnus* based on diagnostic material is *C. mariae* Bickart (1990) from the nearly contemporaneous (latest Hemphillian) Big Sandy Formation in Arizona. Some of the Lee Creek Mine specimens fall within the size range given for *C. mariae*, whereas others are slightly smaller. Unfortunately, none of the characters used to diagnose that species are preserved in any of the Lee Creek Mine fossils. The most diagnostic specimen of swan from Lee Creek Mine is a nearly complete tarsometatarsus, an element as yet unknown in *C. mariae*. There is no basis for considering the Lee Creek swan to be closer to *C. mariae* than to *C. columbianus*.

The modern Tundra Swan, which now includes the Old World *Cygnus [cygnus] bewickii* Yarrell, is Holarctic in distribution and breeds only in Arctic regions. On the Atlantic coast of North America, it occurs regularly in winter as far south as North Carolina.

Tribe ANSERINI
(true geese)

Genus *Anser* Brisson

Anser cf. arizonae Bickart, 1990

PLATE 25a,b

MATERIAL.—Scapular end of right coracoid, USNM 193126. Right tarsometatarsus, USNM 257458; left tarsometatarsus, USNM 430881.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Tarsometatarsus*: Length, 71.1; distal width, 15.3, 16.3.

ADDITIONAL MATERIAL EXAMINED.—*Big Sandy Formation, Arizona*: Left tarsometatarsus referred to *Anser arizonae*, F:AM 19991.

REMARKS.—The two tarsometatarsi from Lee Creek Mine are markedly short and robust, especially the more complete one. Although there is great intraspecific variation in size and robustness of the tarsometatarsus in the forms of *Anser*, in all of more than 20 skeletons of the Snow Goose, *Anser caerulescens* (Linnaeus), that we examined, the tarsometatarsus was always longer and more gracile. The closest approach to the Lee Creek fossils was found in one individual of the Greater White-fronted Goose, *Anser albifrons* Scopoli. The coracoid listed above is small and may not be from the same species as the tarsometatarsi.

Fossil species of *Anser*, of which there are many, most based on inadequate specimens, were briefly reviewed by Bickart (1990) in the process of describing two new species based on excellent material from the Big Sandy Formation in Arizona. Unfortunately, only one tarsometatarsus of *Anser* was present among the extensive Big Sandy material. This was referred by Bickart (1990:23) to his new species *Anser arizonae*, but only tentatively because it was so unusually stout that he felt its generic assignment was uncertain. We found that it compares very well with the specimens from Lee Creek Mine (Plate 25a,b). *Anser thompsoni* Martin and Mengel, 1980, from the late Pliocene (Blancan) of Nebraska, was a much larger species than the Lee Creek bird, with the tarsometatarsus 20 mm longer. *Heterochen pratensis* (Short, 1970), of the Pliocene of Nebraska, has a much thinner tarsometatarsus than do the Lee Creek Mine fossils.

This Lee Creek goose is rather enigmatic, as it seems to have no close affinity with *A. caerulescens*, the species of *Anser* that winters abundantly along the Atlantic Coast of North America today. Presumably the fossil form only wintered in the Lee Creek area, as most modern species of *Anser* breed at much higher latitudes.

Genus *Branta* Scopoli

Branta aff. *bernicla* (Linnaeus)

PLATE 25c

MATERIAL.—Distal end of right humerus, USNM 457386. Proximal end of right ulna, USNM 206421. Left carpometacarpus, USNM 206366.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 16.1.

Ulna: Proximal width, 10.6; proximal diagonal, 13.0⁺.

Carpometacarpus: Length, 64.8.

REMARKS.—These specimens are indistinguishable from comparable elements of the modern Brant, *Branta bernicla* (Plate 25d), another Arctic breeder that winters regularly south to North Carolina. It is a maritime species on its wintering grounds, a favored food being the marine eelgrass *Zostera* (Palmer, 1976:269).

ANSERINI, genus and species indeterminate

MATERIAL.—Proximal end of left humerus, USNM 430880; proximal end of right humerus, USNM 430879. Proximal end of right ulna, USNM 248528; proximal end of left ulna, USNM 250799. Left phalanx 1 of major digit, KU 21220.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Ulna*: Proximal width, 14.4⁺, 16.4.

Phalanx: Greatest length, 33.7⁺; length between articular surfaces, 30.5.

REMARKS.—These fragmentary specimens indicate at least one species of goose larger than either of the two preceding species. The pectoral crest in both humeri is particularly broad, being similar to but even more expanded than it is in the Canada Goose, *Branta canadensis* (Linnaeus), some forms of which the fossils resemble in size. The humeri are considerably larger than are those of *B. woolfendeni* (Bickart, 1990). The major alar digit is larger than that of *B. bernicla* and is similar in size to medium-sized races of *B. canadensis* or *B. woolfendeni*. The elements are not, however, sufficiently diagnostic to refine the identification further.

Apart from *Branta bernicla*, there seems to be no evidence of the extant North American lineages of geese at Lee Creek Mine, in the Big Sandy Formation of Arizona, or, apparently, elsewhere in the Miocene and Pliocene of North America. Possibly, North America was inhabited in the Neogene by an endemic fauna of geese that has since become extinct and that was replaced by species that have evolved more recently following colonization from Europe or Asia.

Subfamily ANATINAE (ducks)

Ducks are notoriously difficult to work with as fossils due to their relative homogeneity in osteology, even between genera that differ radically in external morphology. Also, an extreme amount of individual variation, coupled with the diversity within genera of modern species that overlap in size, greatly complicates any analysis of fossil ducks. Unfortunately, many new species have been founded on undiagnostic single fragments of bone.

Most of the fossil ducks from Lee Creek Mine appear to belong to modern lineages. Except for the species of *Anas*, which would have been incidental, mainly fresh-water species, these are now all marine ducks that winter at sea or along seacoasts. Interestingly, the most abundant duck in the fauna is a form of *Histrionicus* Lesson. The modern Harlequin Duck, *H. histrionicus* (Linnaeus), is a maritime species in winter. Considering that most other genera of sea ducks are present at Lee Creek Mine, such as scoters, eiders, and goldeneyes (*Melanitta* Boie, *Somateria* Leach, and *Bucephala* Baird), the apparent absence of the osteologically distinctive genus *Clangula* is puzzling because the modern Oldsquaw, or Long-tailed Duck,

C. hyemalis (Linnaeus), is a common wintering bird in North Carolina today. A small tarsometatarsus of a juvenile duck (USNM 448823) is from a species somewhat larger than a teal. Although it cannot be identified to genus, its presence in the deposits shows that at least some ducks may have bred nearby. The more worn and undiagnostic anatic fossils remain unidentified (at least 76 specimens out of 173 referable to the Anatinae).

Tribe TADORNINI
(shelducks)

Genus *Anabernicula* Ross, 1935

***Anabernicula* cf. *minuscula* (Wetmore, 1924)**

PLATE 25e,h,j,l

MATERIAL.—Left femur, USNM 457388. Left tarsometatarsus, USNM 457387.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*Big Sandy Formation, Arizona:* Left tarsometatarsi of *Anabernicula* sp., F:AM 19998, 19999.

MEASUREMENTS (mm).—*Femur:* Length, 53.2; proximal width, 12.0.

Tarsometatarsus: Length, 60.3; proximal width, 11.7; distal width, 12.9.

REMARKS.—These two specimens are from an anatic that we identified as a tadorine that differs generically from the modern genus *Tadorna* Boie. Although the tarsometatarsus differs only subtly from that of *Tadorna*, the femur is very distinct in having the head relatively smaller and the neck much narrower, so that the head is more strongly demarcated. Also, the entire distal end of the bone is deflected medially in comparison to *Tadorna*. These characters of the femur are not specifically mentioned in any of the descriptions of the femora of *Anabernicula* but are well shown in Howard's illustration (1964a, pl. 7e,f) of bones of *A. gracilentia* Ross, 1935. Both of the Lee Creek Mine specimens fall well within the measurements of femora and tarsometatarsi of *A. gracilentia* given by Howard (1964b:11).

The earliest known species of *Anabernicula* was originally described by Wetmore (1924) as *Branta minuscula* based on the proximal end of a humerus from the Pliocene (early Blaccan) Benson fauna in Arizona. *Anabernicula gracilentia* was described by Ross (1935) as a new genus and species of "pigmy" Anserinae from Pleistocene (Rancholabrean) tarpit deposits at McKittrick, California. Howard (1936) almost immediately identified additional material of this taxon from the tarpits at Rancho La Brea, California, but synonymized *gracilentia* Ross with *minuscula* Wetmore, while recognizing the validity of the genus *Anabernicula*.

Later, Howard (1946:171) referred fossils from the Pleistocene of Fossil Lake, Oregon, to "*Anabernicula*, species." She considered this material to be separable from the California species but was uncertain as to which taxon the name *minuscula* applied. She also mentioned (1946:172) that the affinities of the genus merited further investigation, noting similarities to the "shelldrakes" (=Tadornini). Bones referable to *Anabernicula* also were identified from three Pleistocene cave deposits in Nevada and New Mexico (Howard, 1952, 1962). After further study, Howard (1964a:286) concluded that comparison with *Tadorna* "strongly indicates alliance [of *Anabernicula*] with the Tadornini." She restored the name *A. gracilentia* for the fossils from California and tentatively referred the Oregon material to *A. minuscula*, but in a footnote (1964a:287) she commented that these fossils indicated a distinct species. This she soon described as *Anabernicula oregonensis* (Howard, 1964b), and she further confirmed the placement of the genus in the Tadornini. On the basis of the associated avifauna at various localities, Howard (1964b) suggested that *Anabernicula* was aquatic in habits, presumably as opposed to the more terrestrial predilections of the true geese.

Short (1970) described an additional species, *Anabernicula robusta*, on a single humerus from the Pleistocene of Nebraska. Bickart (1990) referred a large number of specimens from the Big Sandy Formation (latest Hemphillian) of Arizona to *Anabernicula* (Plate 25f,g,i,k,m,n) but did not assign them to species. He expressed strong doubts that *robusta* Short was correctly referred to *Anabernicula*. Material assigned to *A. gracilentia* has been reported from two early Irvingtonian sites in central Florida (Emslie, 1995a). A tarsometatarsus and distal portion of tibiotarsus from an early Pliocene shell bed in central Florida were referred to *A. minuscula* by Emslie (1995b:323), who compared the former with USNM 457387 from Lee Creek Mine; the two specimens were considered similar except for the slightly longer and more robust shaft of the Lee Creek Mine specimen.

Discounting *A. robusta*, the forms of *Anabernicula* may represent a single species lineage. We have tentatively referred this material to *A. minuscula* because it is the earliest known taxon of the genus, as well as the earliest available specific name. It is possible that the proximal end of an ulna from the middle Miocene Calvert Formation in Maryland that was assigned only to the Tadornini (Alvarez and Olson, 1978) also may pertain to *Anabernicula*.

Anabernicula appears to have been a rather common component in aquatic avifaunas of southwestern North America from at least the early Pliocene until the end of the Pleistocene. The occurrence of *Anabernicula* at Lee Creek Mine and at three sites of two different ages in Florida shows that birds of this genus probably occurred continent-wide throughout the late Cenozoic.

Tribe ANATINI
(dabbling ducks)

Genus *Anas* Linnaeus

Dabbling ducks form a small minority of the anatid fossils from Lee Creek Mine. None of these specimens is particularly well preserved or diagnostic beyond the level of genus. As we have discussed above, even in modern skeletons of *Anas* it is frequently difficult or impossible to distinguish postcranial elements of the various species except on size. The dabbling ducks tend to inhabit freshwater ponds, streams, and marshes, but a number of species show varying degrees of preference for salt marshes, bays, and estuaries. That a few are represented in the Lee Creek deposits is not surprising, nor is the fact that they are far outnumbered by diving ducks.

***Anas magn. platyrhynchos* Linnaeus**

MATERIAL.—Scapular two-thirds of right coracoid, USNM 306260. Proximal third of right ulna, USNM 459398; proximal half of left ulna, USNM 459399.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Ulna*: Proximal depth, 9.3, 9.5; proximal diagonal, 11.6⁺, 12.0.

REMARKS.—These specimens are from a large duck, the size of the Mallard, *Anas platyrhynchos*, or the American Black Duck, *A. rubripes* Brewster.

***Anas magn. acuta* Linnaeus**

MATERIAL.—Scapular half of right coracoid, USNM 215737; scapular half of left coracoid, USNM 459405. Proximal end of right humerus, USNM 321248.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Proximal width, 18.4; proximal diagonal, 19.2.

REMARKS.—These bones are the size of those of the Northern Pintail, *Anas acuta* Linnaeus, or the Gadwall, *A. strepera* Linnaeus, and may overlap with other species as well.

***Anas magn. americana* Gmelin**

MATERIAL.—Left coracoid, USNM 459402. Proximal halves of right humeri, USNM 366409, 459403.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Coracoid*: Medial length, 41.7.

REMARKS.—These bones are the size of those of the American Wigeon, *Anas americana*.

***Anas magn. clypeata* Linnaeus**

MATERIAL.—Sternal three-fourths of left coracoid, USNM 459406. Proximal fourth of right ulna, USNM 367095.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Ulna*: Proximal width, 7.7; proximal diagonal, 9.6.

REMARKS.—These bones are from a rather small duck, about the size of the Northern Shoveler, *Anas clypeata*.

***Anas magn. discors* Linnaeus**

MATERIAL.—Right coracoid, USNM 510079. Distal end of right humerus, USNM 459408; distal end of left humerus, USNM 459407.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 9.5, 9.9.

REMARKS.—These fossils are from a small duck, approximately the size of the Blue-winged Teal, *Anas discors*.

***Anas* sp.**

MATERIAL.—Distal end of right humerus, USNM 459404.

HORIZON.—Pungo River Formation?

MEASUREMENTS (mm).—Distal width, 8.3.

REMARKS.—This heavily mineralized bone is black in color and appears to have originated in the phosphate-bearing beds of the Pungo River Formation. In morphology it is close to *Anas*, but it is much smaller than any living Northern Hemisphere species of that genus, being the size of the Hottentot Teal, *A. hottentota* Eyton, of Africa. Tiny forms of *Anas* also are known from the late Miocene (latest Clarendonian) Love Bone Bed in Florida and from other Neogene localities in North America (J. Becker, pers. comm., 1986), and a very small species, *Anas schneideri*, was described from a carpometacarpus from the late Pleistocene of Wyoming by Emslie (1985), who also reported an undescribed species of this size from the Love Bone Bed in Florida dated at 9 Ma, indicating "that a niche for a very small duck has existed in North America since the late Miocene" (Emslie, 1985:205, footnote). If the Lee Creek specimen is actually from the Pungo River Formation, such a niche would have existed for an even longer time.

Tribe AYTHYINI
(pochards)

Genus *Aythya* Boie

***Aythya* aff. *affinis* (Eyton)**

PLATE 26a

MATERIAL.—Left humerus, USNM 457389; left humerus lacking most of proximal end, USNM 178217; proximal ends of right humeri, USNM 178240, 183487, 215740, 215817, 302410, 366410, 366795; distal ends of right humeri, USNM 215628, 459409.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Length, 77.7; proximal width, 16.3, 16.6, 16.8 (3), 17.4; proximal diagonal, 17.4; distal width, 11.1, 11.2.

REMARKS.—These bones are indistinguishable from those of the Lesser Scaup, *Aythya affinis*, a species restricted to North America and an abundant wintering duck on the mid-Atlantic coast, where the greatest numbers are found in maritime habitats.

Tribe MERGINI

(eiders, scoters, mergansers, and allies)

Genus *Somateria* Leach

Eiders are boreal sea ducks that normally winter in more northern latitudes and occur only casually farther south than New York and New Jersey. We know of no previous Tertiary record of the group. The only presumptive paleospecies is *Somateria gravipes* Harrison (1979) from the middle Pleistocene Cromer Forest Bed Series in Norfolk, England. This species was based on a tarsometatarsus similar in size to that of the modern Common Eider, *S. mollissima* (Linnaeus), but with a thicker shaft, and a referred incomplete coracoid that was said not to differ from *S. mollissima*. Ericson (1987) documented a great deal of temporal and geographic variation in the osteology of *S. mollissima*, and Mlikovsky (1982) synonymized *S. gravipes* with *S. mollissima*.

Somateria aff. *mollissima* (Linnaeus)

PLATE 26g

MATERIAL.—Scapular portion of left coracoid, USNM 275860.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—No standard measurements possible.

REMARKS.—This fragmentary specimen comes from a large eider, the size of males of the Common Eider, *Somateria mollissima*, from which it cannot be differentiated.

Somateria sp.

PLATE 26c,e

MATERIAL.—Distal third of right humerus, USNM 183498; distal three-fourths of right humerus, USNM 275781. Left carpometacarpus missing minor metacarpal, USNM 206597.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 11.

REMARKS.—The carpometacarpus has the distinctive, gently sloping distal margin of the alular metacarpal process characteristic of eiders. The olecranal fossa of the humerus is shallower than it is in most specimens of *Somateria*, but in this respect it differs even more from the next most similar genus, *Melanitta*, in which this fossa is always very deep. The carpometacarpus and the right humerus are smaller than they are in the smallest female specimens of the King Eider, *S. spectabilis* Linnaeus, or in the Spectacled Eider, *S. fischeri* (Brandt), the smallest species of the genus.

The following osteological characters distinguish the fossil *Somateria* from *S. fischeri* ($n=6$). In the fossil humerus, the ectepicondyle in palmar view is more laterally produced, forming a broad, flat surface, and in lateral view the ectepicondyle is more flattened dorsoventrally, and there is a shallow depression on the anconal side of the ectepicondyle; the attachment of the pronator brevis is more proximally located in relation to the attachment of the anterior articular ligament, which is less proximally extended; the entepicondyle is less distolaterally and more anconally produced; the attachment for the anterior articular ligament faces more medially and less palmarly; the entepicondyle has a more concave proximo-anconal edge; the internal edge of the impression of the brachialis anticus tends more laterally and less proximally; and the more anconal pit on the entepicondyle is more distinctly rimmed.

In the fossil carpometacarpus, the external carpal trochlea is less pointed proximally; the length is much shorter than it is in any of nine female *S. fischeri* measured; the distal edge of the external carpal trochlea angles more sharply toward the shaft; the proximal and distal ends are relatively large despite the short shaft; the distal third of the shaft is straight, not bowed anteriorly; and the pit between the carpal trochleae just proximal to the minor metacarpal is deeper distally, more heavily rimmed with bone, and extends farther proximally, nearly to the groove that is just distal to the external carpal trochlea.

The Lee Creek Mine fossils may pertain to an extinct species of eider because they differ not only in size but in the above-mentioned characters. Because, however, only three incomplete, unassociated specimens were available, we deemed it inadvisable to describe a new species until more material becomes available.

TABLE 11.—Measurements (mm) of females of modern eiders (King Eider, *Somateria spectabilis*, and Spectacled Eider, *S. fischeri*) compared with a small fossil species (measurements in list form) from Lee Creek Mine. (n =number of specimens, s =standard deviation.)

Element	S. sp.	<i>S. spectabilis</i> ($n=14$)			<i>S. fischeri</i> ($n=9$)		
		Range	Mean	s	Range	Mean	s
Humerus							
Distal width	13.1, 13.9	14.3–15.7	15.1	0.4	13.3–15.0	14.2	0.6
Carpometacarpus							
Greatest length	52.4	55.3–63.6	60.5	2.1	57.4–60.8	59.0	1.1

Genus *Histrionicus* Lesson

Ocyplonessa Brodkorb, 1961:177.

The genus *Histrionicus* is monotypic, containing only the Harlequin Duck, *Histrionicus histrionicus* (Linnaeus), which has hitherto been recorded as a fossil only from the Pleistocene (Howard, 1964a). Harlequin Ducks are rare in winter in the Carolinas today; therefore, it was something of a surprise to discover that the best preserved and most abundant of the identifiable duck bones from Lee Creek Mine were referable to the genus *Histrionicus*, which otherwise was thought to have no Tertiary fossil record.

Among diving ducks, the following combination of characters was used to refer the fossils to the genus *Histrionicus*. In the coracoid, the ventromedial edge of the shaft is narrower than it is in *Melanitta* but is wider than it is in most species of *Bucephala* or mergansers, and the medial edge of the furcular facet has a medial interruption as in *Histrionicus*, *Bucephala*, and mergansers, and unlike other diving ducks. In the humerus, there is a tendency towards pneumaticity of the tricripital fossa (found in diving ducks only in *Histrionicus* and mergansers except *Mergellus*); the internal tuberosity is gracile (unlike *Melanitta*); the bicripital crest tapers gradually into the shaft and is not rounded and sharply set off as it is in *Bucephala* and mergansers; the pectoral crest is not markedly triangular as it is in *Lophodytes* Reichenbach; and the most proximal point of the head is not greatly elevated above the external tuberosity as it is in *Melanitta*. In the ulna, the internal cotyla is ventrally produced, similar to *Histrionicus* and mergansers. Characters of the tarsometatarsus of *Histrionicus* are outlined in Alvarez and Olson (1978).

NOTA BENE.—The new genus and species *Ocyplonessa shotwelli* was described by Brodkorb (1961:178) from the distal half of a left tarsometatarsus (the holotype) and a carpometacarpus from a locality in Oregon then thought to be lower Pliocene but now considered to be middle to late Miocene (Clarendonian; Becker, 1987:47). These were thought to represent a duck close to *Histrionicus*. We reexamined the holotype (Condon Museum of Geology, University of Oregon, F-10485, F-11291; see Plate 27*bb, ee, hh*) and believe that the differences that it shows from modern *Histrionicus* are not sufficient for separate generic status; thus, it should be known as *Histrionicus shotwelli*, new combination. The material is too scanty to determine the relationships of this species to succeeding populations of *Histrionicus*.

Histrionicus aff. *histrionicus* (Linnaeus)

PLATE 27*a, c, e-h, j, k, m-s, u, w, y, aa, dd, gg*

Melanitta ceruttii Chandler, 1990a:130.

MATERIAL.—Left coracoid, USNM 459431; right coracoid lacking sternocoracoidal process, USNM 457382; right coracoid lacking most of sternal end, USNM 459428; left coracoids lacking most of sternal ends, USNM 459430, 459432, 459433;

right coracoids lacking much of both ends, USNM 459425, 459426; scapular ends of right coracoids, USNM 459427, 460350; scapular end of left coracoid, USNM 459429. Right humeri, USNM 457378, 457379, 459414; left humeri, USNM 457380, 457381, 459412; right humerus lacking much of distal end, USNM 244231; right humerus lacking much of proximal end, USNM 459415; portion of right humerus, USNM 302336; proximal ends of right humeri, USNM 250697, 275845, 459413, 459417, 459418; proximal ends of left humeri, USNM 302378, 459420, 459421; proximal end of left humerus lacking internal portion, USNM 459411; distal ends of right humeri, USNM 192861, 275811, 459416, 459419; distal ends of left humeri, USNM 368558, 459422, 459423. Right ulna, USNM 366233; left ulna, USNM 459424. Left carpometacarpus lacking minor metacarpal, USNM 457383. Right tarsometatarsus, USNM 336132.

HORIZON.—Yorktown Formation.

ADDITIONAL MATERIAL EXAMINED.—*San Diego Formation, California*: Right humerus lacking most of proximal end, SDSNH 23584 (holotype of *Melanitta ceruttii*); right humeri, SDSNH 42782, 42783.

MEASUREMENTS.—See Table 12.

REMARKS.—This material comes from a harlequin duck the size of modern *Histrionicus histrionicus*, but it shows slight differences, the most pronounced being as follows: the tricripital (pneumatic) fossa of the humerus is larger in diameter and extends deeper into the shaft, usually with obvious bony trabeculae; the distal end of the humerus is not strongly rotated medially (in distal view, the distal end of the humerus in *H. histrionicus* is rotated counterclockwise in comparison with the Lee Creek Mine fossils); the furcular facet of the coracoid is more produced ventrally and medially; and the distal foramen of the tarsometatarsus is situated more proximally, with the bony bridge between the foramen and the intertrochlear notch noticeably wider.

Lesser differences between the fossil and modern material include the following. In the fossils, the procoracoid process of the coracoid is more produced and more flaring at the base, extending farther sternally, and the sternal facet in sternal view is usually thicker medially. In the humerus, the attachment of the anterior articular ligament is more rounded (it extends farther proximally in *H. histrionicus*); the pit for the attachment of *M. pronator brevis* is more anconally situated; and the proximomedial border of the impression of *M. brachialis anticus* is more diagonally oriented away from the medial edge of the shaft (it is nearly parallel in the modern species). In the ulna, the impression of *M. brachialis anticus* is more pointed distally (it is more squared in *H. histrionicus*). In the carpometacarpus, the process of the alular metacarpal is more produced internally, with the proximal edge curving more proximally; the distal end of the major metacarpal in internal view is more gracile; and the external ligamental attachment is not as pronounced. In medial view, in the tarsometatarsus of *H. histrionicus* there is a convex swelling just above the middle trochlea that contributes

TABLE 12.—Measurements (mm) of modern *Histrionicus* compared with fossil *Histrionicus* from Lee Creek Mine. Measurements of the fossil species are in list form when number of specimens (n) < 9. (s = standard deviation.)

Element	<i>H. histrionicus</i>				<i>H. aff. histrionicus</i>
	n	Range	Mean	s	
Coracoid					
Medial length	11	38.3–42.3	40.2	1.55	41.7
Humerus					
Length	11	62.9–67.8	66.1	13.73	67.0, 67.9, 69.6
Proximal width	12	15.4–16.4	15.9	0.33	14.8 (2), 15.4, 15.6, 16.0, 16.1, 16.2
Distal width	10	9.9–11.0	10.4	0.35	9.3–10.6 (mean=10.2, n =9)
Ulna					
Length	9	56.4–57.7	57.3	0.45	56.8 ⁺ , 57.2 ⁺
Proximal width	10	6.9–7.4	7.2	0.19	–
Carpometacarpus					
Length	11	39.6–42.5	41.4	0.93	41.7
Proximal width	11	9.0–9.8	9.4	0.30	9.9
Tarsometatarsus					
Length	10	34.2–38.8	37.2	1.47	37.2
Proximal width	12	7.5–8.4	8.1	0.27	7.6 ⁺
Distal width	12	7.8–8.8	8.1	0.35	7.8

to a much more pronounced transverse groove at the proximal border of the articulating surface of the middle trochlea, as in *Histrionicus shotwelli*, and a more distinct vertical groove or pit along the base of the inner trochlea. This condition is absent in the fossils from Lee Creek Mine.

Included among the material from Lee Creek Mine are several specimens (USNM 457379–457381) that are considerably larger than the other fossils or than any individual in our modern comparative series. These do not otherwise differ from the remainder, so we have referred them to the same species on the assumption that either these birds were occasionally larger in the Pliocene or our modern series does not encompass the full range of individual variation in *H. histrionicus*, which we found to be considerable, both in size and robustness of the elements.

The differences between the Lee Creek fossils and the living species are for the most part of a very minor nature and would probably not have been detectable were there not ample fossil material. There is no reason to assume that the *Histrionicus* from Lee Creek Mine is anything other than the Pliocene representative of *H. histrionicus*, in which modest evolutionary change has taken place since the early Pliocene. The strong rotation of the distal end of the humerus in the modern bird, for example, suggests a modification in wing function, perhaps for increased use of the wings in underwater propulsion. The changes in the coracoid may be associated with this.

It is possible that similar, minor morphological changes took place in other lineages of ducks at Lee Creek Mine, but these are not detectable because of the insufficiencies of the material. The naming of new species of Neogene ducks based on single fragments of bone contributes virtually nothing to our understanding of evolution in this group.

In connection with fossils of *Histrionicus*, we reevaluated the species described by Chandler (1990a) as *Melanitta ceruttii*,

from the late Pliocene San Diego Formation of California, which was based on a single humerus lacking the proximal end. Chandler (1990a) distinguished it from all species of *Melanitta* by its much smaller size, but no comparisons were made with *Histrionicus*. We examined the holotype and two additional complete humeri from the San Diego Formation discovered subsequent to the description of *M. ceruttii*. These are all clearly referable to *Histrionicus*, and, like some of the material from Lee Creek Mine, they are in the upper end of size variation of *H. histrionicus* and are no more deserving of separation from the modern form than is the Lee Creek material. If one were to recognize a Tertiary species in this lineage, it would probably have to take the name *Histrionicus ceruttii* (new combination), but we regard *Melanitta ceruttii* Chandler (1990a) as a synonym of *Anas histrionica* Linnaeus, 1758.

The modern Harlequin Duck breeds mainly along fast-flowing mountain streams in forested areas in western North America, eastern Asia, and in eastern Canada, Greenland, and Iceland. It winters on rocky seacoasts; in the western North Atlantic it does not occur regularly south of Long Island, New York. Because it is usually associated with rocky shorelines, the Harlequin Duck would not be expected to winter regularly in the mid-Atlantic region today. More suitable conditions, however, were probably present during the Pliocene: Pliocene marine sediments (Duplin Formation) have been found surrounding granite knobs near the fall line in southern Virginia and northern North Carolina, suggesting that there may have been areas of rocky coastline here similar to those now occurring in Maine (R. Weems, United States Geological Survey, pers. comm. to Olson, 22 Dec 1997). At this time the fall line was much closer to the coast, and suitable breeding habitat for Harlequin Ducks in mountain streams may have occurred much farther south than at present.

Although the birds at Lee Creek may have fed near shore and roosted farther out at sea, their abundance as fossils suggests that they may have been preyed on with some regularity. They may have regularly fed in the vicinity of deposition, as a bird swimming underwater is much more likely to be taken by a shark or marine mammal than is one resting at the surface.

Genus *Melanitta* Boie

The three species of scoters also are boreal sea ducks, but they occur more regularly in winter in the Carolinas today than do eiders. The White-winged Scoter, *Melanitta fusca* Linnaeus, is much the largest of the three, and no fossils of scoters of this size class have as yet been found at Lee Creek Mine. Temporal representatives of both of the other two species appear to be present, however.

The Tertiary record of scoters has thus far been very meager. Howard (1963) tentatively identified a fragmentary scapula from the late Pliocene (Blancan) Vallecito Creek Local Fauna from the Anza-Borrego Desert in southern California as "*Melanitta perspicillata?*," while acknowledging the undiagnostic nature of this element. There are no other characteristically marine elements in that avifauna, making the identification even more dubious. As discussed above, the putative diminutive "scoter" *Melanitta ceruttii* Chandler (1990a) is referable to *Histrionicus*.

Melanitta aff. *perspicillata* (Linnaeus)

PLATE 26k

MATERIAL.—Right coracoid lacking sternocoracoidal process, USNM 215780; scapular ends of right coracoids, USNM 215486, 215546; scapular end of left coracoid, USNM 192553. Proximal half of right humerus, USNM 250837; proximal two-thirds of left humerus, USNM 459438; distal ends of right humeri, USNM 181079, 459437. Left ulna, USNM 275827; distal half of right ulna, USNM 459436. Right carpometacarpus lacking minor metacarpal, USNM 459435.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Coracoid*: Medial length, 42.3.

Humerus: Proximal width, 17.5; distal width, 11.7, 11.0.

Ulna: Length, 71.9; proximal width, 9.2; distal width, 9.2, 9.4.

Carpometacarpus: Length, 46.5; proximal width, 11.5; distal diagonal, 6.7.

REMARKS.—The wing elements are all much smaller than they are in the White-winged Scoter, *Melanitta fusca* (Linnaeus), and are considerably more robust than the long, slender wing bones of the Black Scoter, *M. nigra* (Linnaeus). These fossils appear to come from the Pliocene representative of the modern Surf Scoter, *M. perspicillata*, from which they cannot be distinguished on the basis of the material at hand.

Melanitta aff. *nigra* (Linnaeus)

PLATE 26i

MATERIAL.—Distal half of left humerus, USNM 457384.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 12.2.

REMARKS.—This specimen preserves enough of the shaft to indicate the more slender humerus, with narrower distal end, of *Melanitta nigra*. It does not differ from modern specimens of *M. nigra* of comparable size.

The proportions of the wing bones of *M. nigra*, along with other osteological differences, are sufficient to suggest that retention of the name *Oidemia* Fleming for this species, at least at the subgeneric level, may be warranted.

Genus *Bucephala* Baird

This genus comprises the two modern species of goldeneyes, which are of similar size, and the much smaller Bufflehead, *Bucephala albeola* (Linnaeus). All are diving ducks that breed on bodies of fresh water, mainly in boreal forests, and winter along seacoasts. Two fossil species have been named, corresponding to the two modern size classes, but these are based on very unsatisfactory, fragmentary specimens.

Bucephala aff. *clangula* (Linnaeus)

PLATE 26m

MATERIAL.—Right coracoids, USNM 457385, 459400, 460351; scapular ends of right coracoids, USNM 179296, 366802, 459401. Distal end of left tibiotarsus, USNM 244207.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Coracoid*: Medial length, 45.2, 49.0.

Tibiotarsus: Distal width, 7.6.

REMARKS.—The coracoids closely resemble those in the modern Common Goldeneye, *Bucephala clangula*, a species that regularly winters as far south as the coast of the Gulf of Mexico. We have not attempted to ascertain whether postcranial elements of the Barrow's Goldeneye, *Bucephala islandica* (Gmelin), can be consistently distinguished from those of the Common Goldeneye; certainly they cannot be on size. That species is uncommon in the Atlantic, and its normal winter range extends south only to New York.

Brodkorb (1955) described a new species, *Bucephala ossivallis*, from the Bone Valley Formation in central Florida, based solely on a single scapular end of a coracoid. The chief distinguishing feature of this species was size, being smaller than *B. clangula* but larger than the Bufflehead (*B. albeola*). Although Howard (1963:12) stated that Brodkorb's measurements ranged "from 7 per cent smaller to within range of specimens of *B. clangula*," in none of the modern specimens we examined were the measurements as small as those given by Brodkorb for *B. ossivallis*. We were impressed, however, with

the individual differences in proportions of the coracoid. One of the measurements given by Brodkorb (1955:19) was "head to lower end of scapular facet." In some instances, however, this measurement could be small, yet the overall size of the entire bone might be larger than in other individuals. This presumably reflects differences in the relative development of the head. In any case, a given measurement within a bone may not be a reliable indicator of the overall size of the species from which it came. In summary, the single incomplete bone of *Bucephala ossivallis* simply does not contain enough information to be of any evolutionary significance.

We did note seemingly consistent differences between the Lee Creek Mine fossils and modern specimens of *B. clangula*. In the latter, the scapular facet in medial view is better developed and more rounded, and the head is more pointed than in the fossils; however, the nature of these differences does not suggest that the fossils are from anything other than the same lineage as the modern goldeneyes.

Bucephala aff. albeola (Linnaeus)

PLATE 26o

Bucephala fossilis Howard, 1963:11.

MATERIAL.—Scapular end of left coracoid, USNM 206518.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—No standard measurements possible.

REMARKS.—This well-preserved partial coracoid of a very small duck is inseparable from coracoids of the modern Bufflehead, *Bucephala albeola*, which winters commonly all along the western Atlantic seacoast today.

Howard (1963) described a new species, *Bucephala fossilis*, from late Pliocene (Blancan) deposits in the Anza Borrego desert of southern California. This was based on the proximal end of a carpometacarpus, a portion of the proximal end of a humerus, and a few other tentatively referred fragments that came from a small species the size of *B. albeola*. Wetmore (1944) identified a nearly complete tarsometatarsus from the Blancan Rexroad fauna of Kansas as *B. albeola*. This was listed by Feduccia (1975:68) as "*Bucephala albeola*, sp.?" and by Becker (1987:99) as "*Bucephala albeola* (?)." From the Blancan Hagerman beds of Idaho, Brodkorb (1958:239) reported as "*Bucephala* sp." the distal portion of a carpometacarpus that was said to be larger than that in *B. albeola*. Brodkorb (1964:230) later suggested that this specimen possibly belonged to *B. fossilis*. It was listed as "*Bucephala fossilis*?" by Feduccia (1975) and, without the query, by Becker (1987).

In view of the identity of the Lee Creek Mine specimen with *B. albeola*, and Wetmore's (1944) inability to distinguish the nearly complete tarsometatarsus from the Rexroad fauna from that species, we do not think that there is fossil evidence for any lineage of small *Bucephala* other than that leading to the modern species. *Bucephala fossilis* was likewise considered by Mlikovsky (1982) to be a probable synonym of *B. albeola*.

Genus *Mergus* Linnaeus

Mergus aff. serrator Linnaeus

PLATE 26q

MATERIAL.—Scapular ends of right coracoids, USNM 192703, 206317; scapular end of left coracoid, USNM 192481. Distal ends of right humeri, USNM 302405, 459434. Right ulnae, USNM 206615, 244230; left ulna, USNM 192018.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Humerus*: Distal width, 11.8, 12.4.

Ulna: Length, 67⁺, 65.4⁺, 71.9⁺; proximal width, 8.2⁺; distal width, 9.3, 9.4, 10.0.

REMARKS.—The Red-breasted Merganser, *Mergus serrator*, is the commonest merganser wintering at sea in North Carolina today.

ANATIDAE, genus and species indeterminate

MATERIAL.—Right humerus lacking much of both ends, USNM 460784.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS.—None possible.

REMARKS.—This specimen has an unusually stout, sigmoidally curved and flattened shaft, and although it cannot be identified further because of preservation, it certainly represents yet another species of anatid from Lee Creek Mine.

INCIDENTAL LAND AND SHORE BIRDS

Order GRUIFORMES (cranes, rails, and allies)

Family GRUIDAE (cranes)

Subfamily GRUINAE (typical cranes)

Genus *Grus* Pallas

Grus aff. americana (Linnaeus)

PLATE 28f

MATERIAL.—Distal end of right tarsometatarsus, USNM 210421.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width through trochleae, 21.6; width through middle and outer trochleae, 16.2; width and depth of middle trochlea, 8.5 × 10.5; width and depth of shaft above distal expansion, 10.2 × 6.2.

REMARKS.—This well-preserved distal end of a tarsometatarsus comes from a crane larger than the living Sandhill Crane, *Grus canadensis* (Linnaeus). It may fall within the lower size

range of the Whooping Crane, *G. americana*, but we had no certain female skeletons with tarsometatarsi with which to compare it. One unsexed skeleton that was probably female was only slightly larger than the fossil and otherwise differed remarkably little. Olson compared this specimen with the type of *Grus conferta* A. Miller and Sibley (1942), from the early Pliocene Siesta Formation of California. Not only is *G. conferta* a larger species than the Lee Creek fossil, but it differs so markedly that it may well be generically distinct.

***Grus* aff. *antigone* (Linnaeus, 1758)**

PLATE 28a,c-e

MATERIAL.—Distal end of right femur, USNM 368539. Proximal end of right tibiotarsus, USNM 446503; distal end of right tibiotarsus, 368540; distal end of left tibiotarsus, USNM 430886.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Femur*: Distal width, ~32.7; depth through external condyle, 28.7.

Tibiotarsus: Width through proximal articulating surface, 25.8; distal width, 25.7, 25.4; depth through external condyle, 25.4, 25.4; width and depth of shaft above distal expansion, 13.5 × 12.0.

REMARKS.—These four specimens are very similar in preservation and may well have come from a single individual of a huge bird the size of the modern Sarus Crane, *Grus antigone*. In fact, it would be difficult to find any meaningful differences between the fossils and that species. No crane of such immense size occurs in the New World today.

The Sarus Crane is known historically from Pakistan east through Southeast Asia; it formerly occurred on Luzon in the Philippines and colonized northern Australia during the 1960s (Johnsgard, 1983). A closely related form also is known from Pleistocene deposits in France, Germany, England, Mallorca, and Eivissa (Ibiza). Several of these records have been published as *Grus antigone* (e.g., Brodkorb, 1967:153), but more recently, Northcote and Mourer-Chauviré (1985, 1988) have maintained that this species is distinct from *G. antigone* and should be known as *G. primigenia* Milne-Edwards (1869), which was first described from the Pleistocene of France. Northcote (1992) also regarded the fossil species *G. melitensis* Lydekker (1890), from the Pleistocene of Malta, to be distinct from either *G. primigenia* or *G. antigone*, although all three are the same size. Alcover et al. (1992:281), however, considered it "improbable that an endemic, volant species of *Grus* lived only on Malta."

Although the differences between *Grus primigenia* and *G. antigone* are valid, they are nonetheless rather subtle and the two are identical in size. Based on the descriptions of these differences and the illustrations in Northcote and Mourer-Chau-

viré (1985, 1988), the fossils from Lee Creek Mine would seem to be as similar to *G. antigone* as to *G. primigenia*. Regardless, all constitute a very closely related lineage of immense cranes, one that has since vanished from North America and Europe.

In view of the considerable number of other Eurasian species of birds found at Lee Creek Mine, it is not unreasonable to assume that *Grus antigone*, or an extremely closely related species, was once present in North America. A crane the size of *G. antigone* also has been reported from the early Pleistocene of Florida (Emslie, 1995a:333). These occurrences may solve the problem of the derivation of *G. cubensis* (Fischer and Stephan, 1971), a giant crane with reduced wings known from the Pleistocene of Cuba. This crane seems far too large to have been derived from either *G. canadensis* or *G. americana*, but the species represented by the huge crane remains from Lee Creek Mine would have made a much more likely ancestor of the Cuban endemic.

**Subfamily BALEARICINAE
(crowned cranes)**

Genus *Balearica* Brisson

***Balearica?* sp.**

PLATE 28h

MATERIAL.—Distal end of right tarsometatarsus, USNM 242236.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

Balearica-like cranes are known in North America from the Oligocene through the Pliocene (Olson, 1985d).

MEASUREMENTS (mm).—Distal width, 17.8; width through outer and middle trochleae, 12.3; depth of middle trochlea, 9.0; width and depth of shaft above scar for hallux, 8.6 × 5.8.

REMARKS.—This specimen comes from a bird similar to the crowned cranes, *Balearica*, and is different from *Grus* in the more distal placement of the inner trochlea, which, however, is shaped very differently from either. A variety of fossils related to *Balearica* are known through much of the Tertiary of North America (Olson, 1985d), although there has never been a proper revision of them. Feduccia and Voorhies (1992) named a new species, *Balearica exigua*, based on excellent associated skeletons from the lower upper Miocene of Nebraska, although it is likely that the same taxon has been named previously from much more fragmentary material.

The fossil from Lee Creek Mine is smaller than modern forms of *Balearica* (Feduccia and Voorhies, 1992, table 1), but it is fairly close in size to *B. exigua*. The two measurements of the distal width of the tarsometatarsus of that species given by Feduccia and Voorhies (1992:241, 244) are 14.8 and 16.5 mm.

Family RALLIDAE
(rails)

RALLIDAE, genus and species indeterminate

PLATE 29e,f

MATERIAL.—Proximal end of right tarsometatarsus, USNM 215524.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Proximal width, 8.4.

REMARKS.—This specimen, which lacks the hypotarsus, is from a large rail similar in size to that of a King Rail, *Rallus elegans* Audubon. Unfortunately, the specimen is too fragmentary to allow further determination.

Order CHARADRIIFORMES
(shorebirds, gulls, and auks)

Family HAEMATOPODIDAE
(oystercatchers)

Genus *Haematopus* Linnaeus

Palostralegus Brodkorb, 1955:19.

The two *Haematopus* humeri from Lee Creek Mine are near the extremes in size for the entire genus (Figure 14), with most other species of oystercatcher falling between them in size. Thus, it is inescapable that there were two sympatric species of oystercatcher in eastern North America in the early Pliocene.

Haematopus aff. *palliatu*s Temminck

FIGURE 14; PLATE 29c

Palostralegus sulcatus Brodkorb, 1955:20.

MATERIAL.—Right humerus lacking proximal end, USNM 215799.

HORIZON.—Yorktown Formation (basal portion) based on microfossils from matrix sample from specimen.

MEASUREMENTS.—See Table 13.

REMARKS.—This well-preserved humerus was discussed and illustrated by Olson and Steadman (1979:977), who referred to

it only as "*Haematopus* sp." and thought it to be larger and more robust than the American Oystercatcher, *Haematopus palliatus*, the only species of the genus occurring in eastern North America today. Additional comparative material, however, indicates that it falls near the upper size limits of the species (Figure 14). The supposed new genus and species of oystercatcher from the Bone Valley Formation in Florida, *Palostralegus sulcatus* Brodkorb, 1955, was transferred to *Haematopus* by Olson and Steadman (1979). This was based on a single distal end of a tibiotarsus showing only minor differences from extant species. There does not seem to be any justification, however, for regarding either of these two bones as being anything other than the Pliocene representative of *H. palliatus*.

Haematopus aff. *ostralegus* Linnaeus

FIGURE 14; PLATE 29a

MATERIAL.—Right humerus lacking proximal end, USNM 460835.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 13.

REMARKS.—This humerus is clearly from a species of oystercatcher that was considerably smaller than nearly all *Haematopus palliatus*, but it is very close in size to the Eurasian Oystercatcher, *H. ostralegus*, from which the fossil is essentially indistinguishable (Figure 14).

Species of the genus *Haematopus* occur on all continents (except Antarctica) and in New Zealand. Their systematics is complex and controversial and has been reviewed most recently by Hockey (1996). The species are mainly coastal in distribution and exclusively so in winter, but *H. ostralegus* breeds widely in inland areas along rivers and in meadows in Europe and Asia and also on the South Island of New Zealand, provided that the South Island Oystercatcher, *H. finschi* Martens, is regarded as a subspecies of *H. ostralegus*. In southern South America, the Magellanic Oystercatcher, *H. leucopodus* Garnot, also breeds in inland localities. Only in Australia, New Zealand, and southern South America do more than one species now occur sympatrically, and in northern Patagonia there are three sympatric species.

TABLE 13.—Measurements (mm) of the humerus in modern oystercatchers (Eurasian Oystercatcher, *Haematopus ostralegus*, American Oystercatcher, *H. palliatus*, and Black Oystercatcher, *H. bachmani*) compared with *H. aff. palliatus* and *H. aff. ostralegus* from Lee Creek Mine. Length was measured from distal end to distal edge of pectoral scar. (*n*=number of specimens, *s*=standard deviation.)

Measurement	<i>H. ostralegus</i> (<i>n</i> =9)				<i>H. palliatus</i> (<i>n</i> =12)				<i>H. bachmani</i> (<i>n</i> =8)		
	<i>H. aff. ostralegus</i>	Range	Mean	<i>s</i>	<i>H. aff. palliatus</i>	Range	Mean	<i>s</i>	Range	Mean	<i>s</i>
Length	53.5	48.7–52.8	51.2	1.4	62.6	54.2–61.9	58.8	2.1	53.4–59.3	56.0	2.0
Distal width	12.8	11.7–13.0	12.3	0.4	14.9	12.8–13.9	13.3	0.3	12.7–14.8	13.4	0.7
Least width shaft	5.4	4.9–5.6	5.2	0.2	6.2	5.1–6.1	5.6	0.3	5.3–6.4	5.6	0.4
Least depth shaft	4.2	3.6–4.3	3.9	0.2	4.6	3.9–4.7	4.2	0.2	3.8–4.7	4.2	0.3

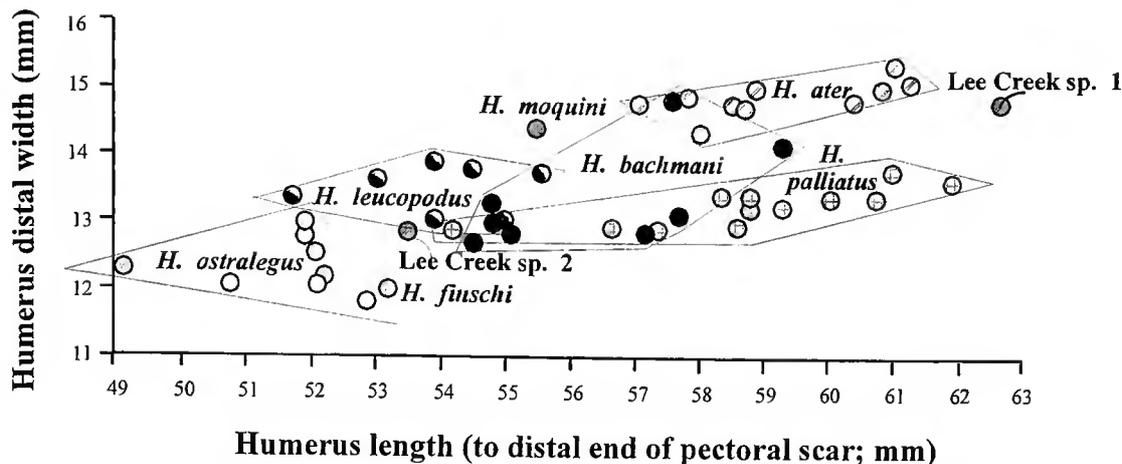


FIGURE 14.—Bivariate scatter plot of humeral measurements (length vs. distal breadth) for Lee Creek fossil and modern oystercatchers (*Haematopus*). Lee Creek Mine sp. 1=*H. aff. palliatus*; Lee Creek Mine sp. 2=*H. aff. ostralegus*.

Because of their allopatric distribution, *H. ostralegus* and *H. palliatus* have frequently been treated as conspecific, despite their great differences in size, plumage, and habits.

In an extremely conjectural history of speciation in oystercatchers, Larson (1957) proposed that the original stock of oystercatchers consisted of dark forms in Eurasia that spread to the Southern Hemisphere in the Pliocene. Most northern populations then mutated into pied forms and spread again to the Southern Hemisphere in the Pleistocene, becoming sympatric in places with the original colonizers. This hypothesis has been criticized as being “flawed on several grounds” (e.g., Hockey, 1996:255), and the Lee Creek material demonstrates that two modern species lineages, regardless of what color pattern they may have had, not only already existed by the early Pliocene, but were then sympatric in the Northern Hemisphere.

Family CHARADRIIDAE
(plovers)

Genus *Pluvialis* Brisson

***Pluvialis aff. squatarola* Linnaeus**

PLATE 30a,c

MATERIAL.—Left humerus lacking proximal end, USNM 430887.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 8.9.

REMARKS.—This specimen is very similar in size and morphology to the modern Black-bellied Plover, *Pluvialis squatarola*, now a common migrant along the Atlantic coast. This is the first valid Pliocene record for any plover this large. Bickart (1990) found a charadriid the size of the Piping Plover,

Charadrius melodus Ord, in the Big Sandy Formation in Arizona, and Chandler (1990a) recorded yet another plover the size of a Killdeer, *C. vociferus* Linnaeus, in the San Diego Formation in California.

Family SCOLOPACIDAE
(sandpipers)

Genus *Numenius* Brisson

***Numenius aff. borealis* Forster**

PLATE 30e

MATERIAL.—Right coracoid, USNM 250709.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Length, 24.6.

REMARKS.—The coracoid is the size of that of an unsexed specimen of the Eskimo Curlew, *Numenius borealis* (USNM 12595). It agrees with *Numenius* and differs from *Limosa* in having the head less lengthened ventromedially but more sharply twisted ventrally; having a marked depression anterior to the furcular facet on the dorsal surface; and having the internal edge of the distal half of the shaft sharply ridged, not smoothly rounded as in the Hudsonian Godwit, *Limosa haemastica* (Linnaeus). The fossil coracoid differs from other scolopacids and from the Upland Sandpiper, *Bartramia longicauda* (Bechstein), in its much more ventrally deflected head.

The Eskimo Curlew was once an abundant breeding bird in the Arctic tundra that migrated from northeastern North America in fall across the Atlantic to South America. Market gunning at the turn of the century has been blamed for the drastic decrease in the species, which is now nearly if not entirely extinct. The record from Lee Creek Mine is the first Tertiary indication of this lineage of shorebirds.

Genus *Capella* Frenzel***Capella* aff. *media* (Latham)**

PLATE 30g,h,j,k

MATERIAL.—Proximal half of right humerus, USNM 430888.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Proximal width, 10.0.

REMARKS.—This humerus resembles that of snipe and is different from other scolopacids in that the bicipital crest is sloping (as it also is in curlews), there is a well-marked ridge from the median crest to the head, the lateral extension of the ligamental furrow is poorly marked, and the degree of ridging on the proximal portion of the anconal shaft ridge is consistent with species of *Capella* (for use of *Capella* vs. *Gallinago* see Olson, 1987).

This specimen is clearly from a snipe larger than the Common Snipe, *Capella gallinago* (Linnaeus). Large Pleistocene snipe from the Bahamas and other parts of the West Indies (Olson and Hilgartner, 1982) are very similar in size and characters to the Lee Creek Mine fossil (Plate 30h,k). Newly available modern comparative material of the Great Snipe, *C. media* (Latham), shows that this Old World species was once present in the New World. The modern species breeds in northwestern Eurasia and winters mostly in Africa. A similar pattern of tropical wintering is indicated in the New World by the fossils from the Bahamas. The modern snipe fauna of North America is notably depauperate, consisting of only the Common Snipe, a subspecies of which occurs in Eurasia as well. That another currently Old World species of snipe once occurred in the New World is thus not too unexpected, but its disappearance is more difficult to explain.

Genus *Tringa* Linnaeus***Tringa* magn. *ochropus* Linnaeus**

PLATE 30m,o

MATERIAL.—Right humerus lacking most of proximal end, USNM 241412.

HORIZON.—Yorktown Formation (inferred).

MEASUREMENTS (mm).—Distal width, 5.7.

REMARKS.—This specimen differs from the Green Sandpiper, *Tringa ochropus*, of the Palearctic, only in that the ectepicondylar process is more expanded on its distal edge and forms a less acute angle with the shaft on its proximal edge. No North American shorebird is more similar in size and characters to the fossil than is the Old World *T. ochropus*. *Tringa antiqua* Feduccia (1970), from the Pliocene of Kansas, is considerably smaller than the Lee Creek fossil. Two species referred to *Tringa* by Bickart (1990) are larger than the Lee Creek fossil.

Genus *Calidris* Merrem***Calidris* aff. *melanotos* (Vieillot)**

PLATE 30q,s

MATERIAL.—Left humerus lacking proximal end, USNM 460836.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 6.0.

REMARKS.—This specimen does not differ materially from male Pectoral Sandpipers, *Calidris melanotos*, and differs from *Tringa* magn. *ochropus* in having a more deeply excavated brachial depression on the medial edge and a larger scar at the proximal-lateral tip of the ectepicondylar process.

**Order CICONIIFORMES
(storks, herons, and allies)****Family PHOENICOPTERIDAE
(flamingos)****Genus *Phoenicopterus* Linnaeus*****Phoenicopterus* cf. *floridanus* Brodkorb, 1953a**

PLATE 10n,o

MATERIAL.—Cervical vertebra, USNM 241381. Distal end of right tibiotarsus, USNM 242204.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Vertebra*: Dorsal length from openings of neural canal, 45.3; width and depth at midpoint, 7.4 × 9.6.

Tibiotarsus: Width of shaft, 9.7; see also Table 14.

REMARKS.—The distal end of the tibiotarsus was compared with eight specimens of *Phoenicopterus floridanus* Brodkorb (1953a) from the Bone Valley Formation and with 15 specimens of the Greater Flamingo, *P. ruber* Linnaeus, the largest living species of flamingo (Table 14). The Lee Creek Mine specimen is decidedly above average size for either species (as is the cervical vertebra), but it is slightly smaller than the largest specimen from Bone Valley (UF 117658). It differs from the Bone Valley specimens in the morphology of the supratendinal bridge and tendinal groove, but all of these fossils may be part of the same lineage leading to *P. ruber*.

**Family PLATALEIDAE
(ibises)****Genus *Eudocimus* Wagler*****Eudocimus* sp.**

PLATE 10g-j

MATERIAL.—Distal end of right tibiotarsus, USNM 181027.
HORIZON.—Basal Yorktown Formation as determined from foraminifera in matrix.

TABLE 14.—Measurements (mm) of the tibiotarsus of the modern flamingo, *Phoenicopterus ruber* (6 males, 7 females, 2 unsexed), compared with *P. floridanus* from the Bone Valley Formation and *P. cf. floridanus* (USNM 242204) from Lee Creek Mine. (n =number of specimens, s =standard deviation.)

Measurement	<i>P. cf. floridanus</i>	<i>P. floridanus</i>				<i>P. ruber</i>			
		n	Range	Mean	s	n	Range	Mean	s
Distal width	17.1	5	13.9–17.6	15.3	1.4	15	14.6–17.2	15.7	0.9
Depth lateral condyle	21.1	7	16.8–22.0	18.3	1.7	15	16.6–21.2	18.8	1.2

MEASUREMENTS (mm).—Width and depth of shaft, 4.8×4.8 ; distal width across anterior border, 9.0; distal width across posterior border, 6.4; depth of lateral condyle, 10.0; depth of medial condyle, 10.5.

ADDITIONAL MATERIAL EXAMINED.—*Bone Valley Formation, Florida*: Distal ends of left tibiotarsi, UF 60040, 91040 (Plate 10*h,i*).

REMARKS.—Olson (1981) previously reported on this specimen, which differs only in minor details from the modern White Ibis, *Eudocimus albus*. Two distal ends of tibiotarsi (UF 60040, 91040) of *Eudocimus* from the upper Bone Valley Formation correspond to the morphology of the Lee Creek Mine specimen. In all specimens, the proximal border of the posterior face of the articular surface extends further proximally on the external side, whereas in the modern forms the border is straight. *Eudocimus* also was reported from the Bone Valley Formation by Brodkorb (1972) and from the late Pliocene Rexroad local fauna in Kansas by Collins (1964). *Eudocimus leiseyi* Emslie (1995a), from the early Pleistocene of Florida, was a smaller species than that represented at Lee Creek Mine.

Family ARDEIDAE

(herons)

Genus *Ardea* Linnaeus

Ardea aff. *cinerea* Linnaeus

FIGURE 15; PLATE 10*p,s*

MATERIAL.—Proximal end of right tarsometatarsus and associated fragment of shaft, USNM 495587.

HORIZON.—Yorktown Formation.

MEASUREMENTS.—See Table 15.

REMARKS.—This interesting specimen differs from the

North American Great Blue Heron, *Ardea herodias* Linnaeus (Plate 10*q,t*), the species that would be expected at Lee Creek Mine, in its smaller size and in the much narrower, more vertically oriented (rather than laterally slanting) intercotylar knob. In both these respects it is in perfect agreement with the Old World Gray Heron, *A. cinerea* (Plate 10*r,u*). These two species are invariably regarded as vicariant forms that constitute part of a superspecies, or even as subspecies of a single species (e.g., Mayr and Short, 1970:31, and references cited therein). There is, however, relatively little overlap in size between *A. cinerea* and *A. herodias* (Table 15 and Figure 15). In a principal components analysis of the five measurements in Table 15, in which factor I (the only significant axis) was a strong general-size axis, the Lee Creek fossil fell well within the exclusive multivariate space of *A. cinerea*.

We have noted the distinctive difference in the intercotylar knob, and there may well be qualitative differences in other parts of the skeleton that we have not studied. The Lee Creek fossil suggests that *A. cinerea* may once have been in North America and that its supposed conspecificity with *A. herodias* is therefore unlikely, the situation being parallel with that of European and American oystercatchers (see *Haematopus*).

Family CICONIIDAE

(storks)

Genus *Ciconia* Brisson

Ciconia sp. 1

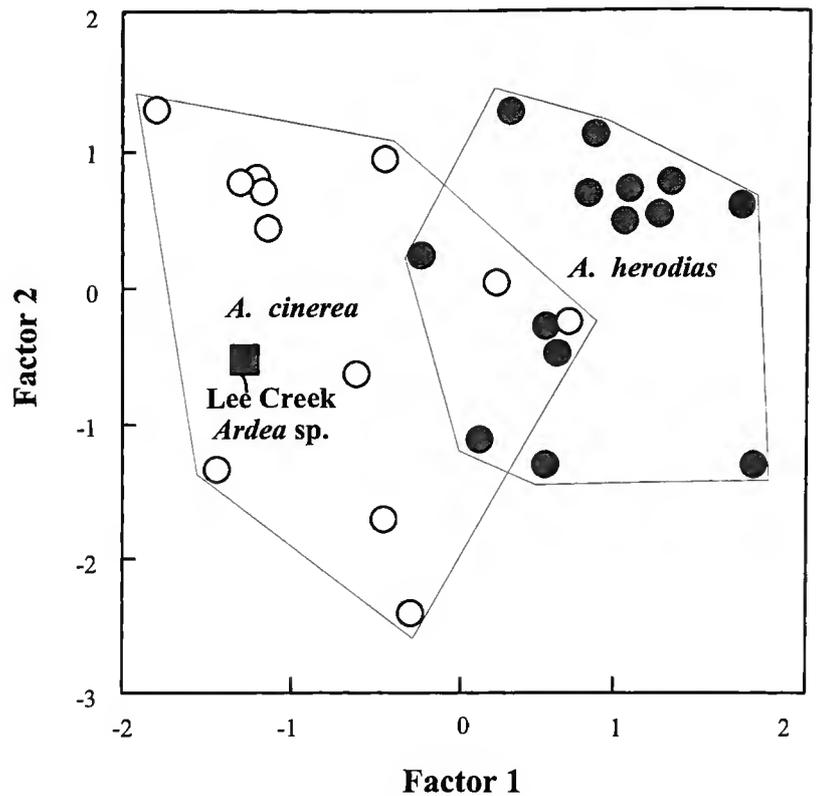
PLATE 10*e,f*

MATERIAL.—Right coracoid lacking head and sternal articulation, USNM 302372. Distal end of left tibiotarsus, USNM 193116.

TABLE 15.—Measurements (mm) of the tarsometatarsus of the modern Grey Heron, *Ardea cinerea* (3 males, 5 females, 5 unsexed), the Great Blue Heron, *A. herodias* (1 male, 8 females, 5 unsexed), and fossil *A. aff. cinerea* from Lee Creek Mine. PC-1=principal components analysis factor I scores for each variable (factor I: eigenvalue=3.8, 76.3% variation explained; factor II: eigenvalue=0.7, 13.4% variation explained). (n =number of specimens, s =standard deviation.)

Measurement	<i>A. cinerea</i> ($n=13$)			<i>A. aff. cinerea</i>	<i>A. herodias</i> ($n=14$)			PC-1 scores
	Range	Mean	s		Range	Mean	s	
Proximal width	13.1–15.4	14.2	0.7	13.7	14.8–17.5	16.2	0.8	0.90
Intercotylar knob height	2.3–3.8	2.9	0.5	3.0	2.9–4.2	3.4	0.3	0.67
Hypotarsus length	9.4–12.1	10.8	0.9	11.1	11.6–14.0	12.5	0.8	0.87
Proximal depth through hypotarsus	15.4–18.6	16.6	1.0	15.9	17.1–20.0	18.5	0.9	0.95
Depth of proximal articular surface	8.6–10.8	9.5	0.7	8.3	9.9–11.5	10.6	0.5	0.94

FIGURE 15.—Scores on factors I and II for herons *Ardea herodias* (solid circles), *A. cinerea* (open circles), and Lee Creek Mine *Ardea* sp. (= *A. aff. cinerea*) (solid square). Summary statistics for this principal components analysis are given in Table 15.



HORIZON.—Uncertain but probably Pungo River Formation from blackish, apparently phosphatized appearance (see also “Remarks”).

MEASUREMENTS (mm).—*Coracoid*: Width and depth of shaft at midpoint, 5.5×5.8 .

Tibiotarsus: Width of shaft, 5.9; depth of shaft, 5.7; distal width, 9.9; depth of lateral condyle, 13.4; depth of medial condyle, 14.1.

REMARKS.—These are from a very small species of stork in the approximate size range of the modern Abdim’s Stork, *Ciconia abdimii* Lichtenstein; the Woolly-necked Stork, *C. episcopus* Gray; and the Storm’s Stork, *C. stormi* (Blasius). The coracoid is especially small, being smaller than that in any available skeleton of the preceding species except a female of *C. stormi*; however, in that species the shaft is more robust. All known New World storks, both recent and fossil, are much larger. The smallest modern storks are found in Africa and southern Asia, with no representatives known in Europe. Thus, it seems unlikely that a small species would occur in the Yorktown Formation, the avifauna of which has a modern aspect, and it reinforces the impression, based on preservation, that at least the tibiotarsus is from the Pungo River Formation.

Ciconia sp. 2

PLATE 10*k-m*

MATERIAL.—Distal end of right tarsometatarsus, USNM 250706.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 23.4; width and depth of middle trochlea, 8.3×11.9 ; width through middle and inner trochleae, 16.7; width through middle and outer trochleae, 17.8; shaft width at level of distal foramen, 18.1.

REMARKS.—This specimen is comparable in size to the Maguari Stork, *Ciconia maguari* (Gmelin), of South America. It should be compared with the Pleistocene species *C. maltha* L. Miller (1910a), which was originally described from Rancho La Brea, California, and subsequently was identified from several other sites in North America.

CICONIIDAE, genus and species indeterminate

MATERIAL.—Distal end of left femur and fragments of shaft, USNM 430873.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 23.4; depth through outer condyle, 18.8.

REMARKS.—This appears to be from a stork somewhat larger than the Wood Stork, *Mycteria americana* Linnaeus, and thus is possibly from a species the size of the larger fossil species *M. wetmorei* Howard (1935), known from the Pleistocene of California and Florida (Olson, 1991). It is from a stork intermediate in size between the two species of *Ciconia* listed above, but it is not sufficiently diagnostic to be referred to genus.

Order FALCONIFORMES
(diurnal raptors)

Family VULTURIDAE
(New World vultures)

VULTURIDAE, genus and species indeterminate

PLATE 31*c,e,g,i,k*

MATERIAL.—Scapular end of right coracoid, USNM 430882. Distal end of right tibiotarsus, USNM 430883. Pedal phalanx 1, digit III, USNM 464324.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—*Coracoid*: Length from head to distal extent of gleno-scapular facet, 46.7; length of gleno-scapular facet, 31.9; width of glenoid facet, 14.2.

Tibiotarsus: Distal width, 20.8; depth of internal condyle, 19.3.

Pedal Phalanx: Length, 47.6; proximal width and depth, 13.8 × 14.5; distal width and depth, 8.9 × 9.7.

REMARKS.—The sizes of the above elements are similar to or slightly smaller than those of the California Condor, *Gymnogyps californianus* (Shaw), or *Breagyps clarki* (L. Miller, 1910b), except that the pedal phalanx is relatively longer and more slender than it is in the former. The species of *Pliogyps* Tordoff (1959), *Sarcoramphus* Duméril, *Cathartes* Illiger, and *Coragyps* Geoffroy Saint-Hilaire are all smaller, and the Andean Condor, *Vultur gryphus* Linnaeus, is larger. Howard (1974), in her review of the postcranial elements of *Breagyps* L. Miller and Howard (1938), found only one character on the distal end of the tibiotarsus that would distinguish *Breagyps* from *Gymnogyps*, this being the blunt external condyle in anterior view projecting laterally in *Breagyps*. The Lee Creek Mine material, however, is so abraded that the condition of this structure cannot be determined. Emslie (1988) did not find characters of the coracoid or tibiotarsus to be of use in his phylogenetic analysis of condors. Since then he has described another new genus and species of large condor, *Aizenogyps toomeyae*, from the latest Pliocene of Florida (Emslie, 1998).

Breagyps has not been recorded outside of California and Nevada, whereas the California Condor, *Gymnogyps californianus*, was probably once found throughout unglaciated portions of North America, having been found in Florida and more recently in western New York (Steadman and Miller, 1987), with the same or a closely related form in Cuba (Arredondo, 1976). Given the fragmentary and undiagnostic nature of the Lee Creek Mine fossils and the greater diversity of large vulturids in the Pliocene–Pleistocene, it does not seem prudent to refer the fossils to a particular genus.

Family ACCIPITRIDAE
(hawks and eagles)

With the exception of a fragment of coracoid from a bird the size of a large eagle, all of the remaining seven speci-

mens of Accipitridae from Lee Creek Mine consist of the distal ends of right tarsometatarsi. This amazing coincidence has greatly facilitated comparisons and has made it possible to determine that these specimens are probably referable to at least four different species, although in their fragmentary condition, generic determinations for some of them are difficult.

Genus *Buteo* Lacépède

Buteo magn. jamaicensis (Gmelin)

PLATE 32*m,r*

MATERIAL.—Distal half of right tarsometatarsus missing trochlea IV, USNM 464321.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width through middle and inner trochleae, 11.9; depth through middle trochlea, 5.5; width and depth of shaft at proximal border of scar for hallux, 7.6 × 5.4.

REMARKS.—This specimen is from a hawk that falls within the range of size variation of the modern Red-tailed Hawk, *Buteo jamaicensis*.

Buteo? sp.

PLATE 32*p,q,u,v*

MATERIAL.—Distal half of right tarsometatarsus, USNM 464319; abraded distal end of right tarsometatarsus, USNM 464320.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm, in the same sequence as listed above).—Distal width, 19.9, 17.6; depth through middle trochlea, –, 8.4; width and depth of shaft at proximal border of scar for hallux, 10.3 × –, 9.1 × 6.6.

REMARKS.—These bones are from a hawk larger and more robust than *Buteo jamaicensis*. They differ in size from one another but only to the degree found between sexes, such as within species of *Buteo*, and may represent a single species.

Genus *Neophrontops* L. Miller, 1916

Neophrontops? sp.

PLATE 32*c,d,f,g,w,x*

MATERIAL.—Partial distal end of right tarsometatarsus missing trochlea IV, USNM 430884; distal halves of right tarsometatarsi, USNM 464317, 464318.

HORIZON.—Probably Yorktown Formation.

MEASUREMENTS (mm, in the same sequence as listed above).—Distal width, –, 17.6, 16.4; depth through middle trochlea, –, 7.9+, 7.8; width and depth of shaft at proximal border of scar for hallux, 8.2 × 5.3, 9.9 × 5.1, 9.2 × 5.1.

REMARKS.—These specimens are distinctive in the rather poorly developed trochleae, especially that of digit II, that lie nearly in the same anteroposterior and proximodistal planes, conveying the impression of a foot that is only weakly grasping. This is characteristic of the New World fossil genus *Neophrontops*, which has often been referred to the Old World vultures (Aegyptiinae or Gypaetinae) (e.g., Howard, 1932). The genus *Neophrontops* was erected for the species *N. americanus* L. Miller (1916) from the late Pleistocene tarpits at Rancho La Brea, California, and since then an additional five species have been named from Neogene deposits extending as far back as late Hemingfordian (16 Ma) (Becker, 1987). We compared the Lee Creek Mine specimens with two tarsometatarsi of *N. americanus* (LACM D8439, E4233; Plate 32*e,h,y*) and found them to be generally similar but considerably larger, with a much less abruptly narrowed shaft.

ACCIPITRIDAE, genus and species indeterminate 1

PLATE 32*i,k,z*

MATERIAL.—Distal end of right tarsometatarsus, USNM 464316.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 20.2; depth through middle trochlea, 9.2.

REMARKS.—This is from an accipitrid that is larger and more robust than any of the above, with a very wide middle trochlea, but the inner trochlea is not as expanded as in the more typically raptorial species. Thus, it shows considerable similarity to the tarsometatarsus of the fossil genus and species *Neogyps errans* L. Miller (1916), of Rancho La Brea, but the trochleae are less splayed, the distal foramen is situated considerably more proximally, and the shaft is more robust (compared with *N. errans*, LACM D8346, D9456; Plate 32*j,l,aa*). Comparisons with other extinct taxa of the family are needed.

ACCIPITRIDAE, genus and species indeterminate 2

PLATE 32*a*

MATERIAL.—Sternal two-thirds of right coracoid, USNM 446504.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Width and depth of shaft above coracobrachialis impression, 15.1 × 10.2.

REMARKS.—This fragment is from a coracoid approximately the size of that of the Golden Eagle, *Aquila chrysaetos* Linnaeus. Material of comparable age from large eagles is known from the Bone Valley Formation, but none of this material is directly comparable to the Lee Creek Mine specimens.

Family PANDIONIDAE

(ospreys)

Genus *Pandion* Savigny

Pandion sp.

PLATE 31*a*

MATERIAL.—Ungual phalanx (claw), USNM 192913.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Width and depth of proximal end, 5.0 × 12.6.

REMARKS.—This single claw of an osprey differs from the modern Osprey, *Pandion haliaetus* (Linnaeus) (Plate 31*b*), in the shape of the articular end. A record of *Pandion* from Bone Valley also is based on a single claw (Brodkorb, 1972). These specimens were mentioned by Warter (1976) in his description of *P. homalopteron*, based on humeri and ulnae from the Miocene of California. Becker (1985) has described another species of osprey, *P. lovensis*, from Miocene deposits in Florida. The specific identity of the claw from Lee Creek Mine cannot be determined absent comparable fossils.

Order GALLIFORMES

(gamebirds)

Family, genus, and species indeterminate

PLATE 33*j,k*

MATERIAL.—Distal third of left tibiotarsus, USNM 256228.

HORIZON.—Uncertain, but possibly Pungo River Formation (see "Remarks").

MEASUREMENTS (mm).—Transverse width of shaft, 8.9; depth of shaft, 8.2; transverse width of distal end, measured across anterior border, 7.2; depth of lateral condyle, 7.3; depth of medial condyle, 8.0.

REMARKS.—This specimen is characterized by a very narrow, deep intercondylar sulcus, which led Olson (1985d:111) to report it as a large cuckoo of uncertain affinities. Extensive further comparisons indicate that it is not referable to the Cuculidae and may be closer to the Galliformes, although it differs from any of those compared in the shape of the condyles and especially in the much narrower tendinal bridge. It comes from a bird smaller than any extant species of Cracidae or Tetraoninae but would fall within the range of some of the larger New World quails, such as the Spot-winged Wood-Quail, *Odontophorus capueira* (Spix). This is a most puzzling bone, the ordinal affinities of which may still be questioned. The great extent of its differences from any living taxon and its excellent, unetched preservation suggest that it may have been derived from the Pungo River Formation rather than the younger Yorktown Formation.

Family CRACIDAE
(curassows and allies)

Genus *Ortalis* Merrem

***Ortalis?* sp.**

PLATE 33a,c

MATERIAL.—Distal end of left tibiotarsus, USNM 430885.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Distal width, 9.6; depth through external condyle, 10.0.

REMARKS.—This specimen is decidedly larger than the Plain Chachalaca, *Ortalis vetula* (Wagler), and is somewhat larger than a female of the Chestnut-winged Chachalaca, *O. garrula* (Humboldt). We had no male skeleton of the latter species nor did we have one of either sex of the Highland Guan, *Penelopina nigra* (Fraser), which may be of approximately similar size to the fossil. In all morphological details, however, it is very close to *Ortalis* and is certainly referable to the Cracidae. We also have examined fossils from the early middle Miocene Calvert Formation that are referable to the Cracidae. Emslie (1998:47) also referred several bones from the early Pleistocene of Florida to the Cracidae. These and other records cited by Emslie (1998) therefore negate the hypothesis that cracids are of Gondwanan origin and were not present in North America until after the closing of the Panamanian seaway in the late Tertiary (Crowe and Short, 1992).

Family PHASIANIDAE
(quails and pheasants)

Genus and species indeterminate

MATERIAL.—Proximal end of right tarsometatarsus lacking most of the hypotarsus, USNM 177936.

HORIZON.—Uncertain, either Pungo River Formation or Yorktown Formation.

MEASUREMENTS (mm).—Proximal width, 6.4.

REMARKS.—This very fragmentary fossil appears to be from a species about the size of the Mountain Quail, *Oreortyx picta* (Douglas), and thus is smaller than any other galliform in the Lee Creek Mine fauna.

Genus *Meleagris* Linnaeus

***Meleagris* sp.**

PLATE 33d,g

MATERIAL.—Left carpometacarpus, USNM 446505.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Protocol as in Steadman (1980). Length, 63.8; proximal depth, 18.3; length of alular metacarpal, 10.5; least width of major metacarpal, 7.5; least depth of major

metacarpal, 5.8; greatest depth of intermetacarpal space, 6.0; distal depth, 17.0; protrusion of minor metacarpal beyond knob of major metacarpal, 3.0.

REMARKS.—The specimen appears to be well mineralized, with a preservation typical of fossils from the Yorktown Formation, including gnaw marks presumably made by small scavenging fish. This carpometacarpus falls at the lower end of the size range for females of the Wild Turkey, *Meleagris gallopavo* Linnaeus. Turkey fossils of roughly similar size are known that bracket the presumptive Yorktown age of the Lee Creek bone—a tibiotarsus from the Eastover Formation of Virginia, and another from the upper Bone Valley Formation in Florida (Steadman, 1980).

The Lee Creek Mine fossil is generally similar to the carpometacarpus in *M. gallopavo*, although it has a narrower and more proximally directed alular metacarpal and a much more distinct ventral protuberance on the proximal third of the minor metacarpal. Also, the minor metacarpal does not project beyond the major metacarpal as far distally as it does in the modern specimens with which it was compared. The small size of the fossil accords with the tendency for turkey lineages to decrease in size with increasing geological age (Steadman, 1980).

Because early Pleistocene turkeys do not have a pneumatic foramen in the scapula, whereas all three Holocene species do, Steadman (1980) concluded that these three species arose from a common ancestor during the Pleistocene. Because pneumaticity of the scapula is definitely a size-related character, being found elsewhere in the Phasianidae only in peacocks (*Pavo* Linnaeus) (Steadman, 1980), the possibility that this character may have evolved independently more than once in *Meleagris* needs also to be considered. From its distribution alone, it would seem most likely that the Lee Creek turkey would have been part of the same lineage as *M. gallopavo*.

Order COLUMBIFORMES
(pigeons, doves, and sandgrouse)

Family COLUMBIDAE
(pigeons and doves)

Genus *Ectopistes* Swainson

***Ectopistes* aff. *migratorius* (Linnaeus)**

PLATE 33l,o

MATERIAL.—Left humerus, USNM 430960.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Length, 44.3; transverse width of shaft, 5.2; depth of shaft, 3.8; transverse width of distal end, 10.1; depth of distal end, 6.4.

REMARKS.—This specimen is from a pigeon-sized columbid, of which there are but two recent species in temperate North America: the Band-tailed Pigeon, *Columba fasciata* Say, a species of western mountains but which is known from a late Pleistocene site in Florida (Emslie, 1995a), and the now-extinct

Passenger Pigeon, *Ectopistes migratorius*, which once abounded in extraordinary numbers in the eastern deciduous forests to which it was highly adapted.

The fossil is too small to be *Columba fasciata* but falls within the lower size range of the domestic pigeon or Rock Dove, *Columba livia* Gmelin. It is only slightly larger than humeri in the available series of *Ectopistes migratorius* (two males, one female, four unsexed), in which the humerus ranges from 40.6 to 43.3 mm. Compared with *Columba*, the fossil has a more slender shaft, a less expanded distal end, a smaller ectepicondylar papilla situated more proximally on the shaft, and proportionately smaller condyles. In all of these respects it agrees with *Ectopistes*. Apart from the slightly larger size, which probably would have been encompassed by variation in the recent species, the fossil shows no distinguishing differences from *E. migratorius*. This specimen provides the earliest record of the Passenger Pigeon, or its immediate antecedent, which was previously unknown outside the Quaternary.

Order PASSERIFORMES
(perching birds)

Family CORVIDAE
(crows and jays)

Genus *Corvus* Linnaeus

***Corvus* aff. *ossifragus* Wilson**

PLATE 33r,1

MATERIAL.—Distal end of left tibiotarsus, USNM 407797.

HORIZON.—Yorktown Formation.

MEASUREMENTS (mm).—Width and depth of shaft, 3.7×3.4 ; distal width, 7.4.

REMARKS.—This bone comes from a crow smaller than the American Crow, *Corvus brachyrhynchos* Brehm, but equivalent in size to the Fish Crow, *C. ossifragus*, a smaller species whose distribution is coincident with the coastal plain of eastern North America (and the Mississippi Valley). Thus, at least some portion of the Fish Crow's modern distribution may have been established as long ago as the early Pliocene.

Conclusions

Given the preliminary state of our knowledge, any summary of such an immense avifauna as has been accumulated from Lee Creek Mine is destined to be sketchy. As always, the mixing of faunas of two different ages greatly increases the difficulty of maintaining the cohesiveness of any discussion. It would be circular to dwell on the similarity of the birds from the Pungo River Formation with those of the Calvert Formation because our determination of specimens as having originated in the Pungo River deposits is based in part on their similarity with taxa known to occur in the Calvert Formation. Birds from the middle Miocene Pungo River and Calvert formations as

well as those from the early Pliocene Yorktown Formation were deposited in offshore marine environments. The physical and ecological differences in the marine environments of the two different ages, however, require the summarization of data from many fields beyond that of paleornithology. We have thus postponed any discussion contrasting the Miocene and Pliocene avifaunas. Nor shall we further discuss the Pungo River avifauna herein, as we plan to take this up in future studies of the birds of the Calvert Formation.

Therefore, the following observations pertain to the avifauna of the Yorktown Formation and how it differs from that of the present. This could be expanded almost indefinitely. We recognize that numerous doctoral dissertations could be written about the birds of the Yorktown Formation, both at the revisionary and at the synthetic level, and we invite paleontologists to undertake these much-needed investigations. We only hope to point out in this paper what some of the possibilities may be.

The attempt to identify fossil species from the early Pliocene with their most likely modern descendents frees us from the necessity of trying to justify and describe species that are most likely only temporal variants and much more readily allows comparison of the Yorktown age avifauna with that of the present-day North Atlantic. The most noticeable difference is that the Pliocene avifauna was much more diverse. Loss of diversity in the modern coastal and marine avifauna of the western North Atlantic came about through two different means—extinction and retraction of range.

Among seabirds, total extinction of lineages was most prevalent among the previously unrecognized great Atlantic radiation of the genus *Alca*. Only a single species, the Razorbill, *Alca torda*, survived into modern times, whereas in the early Pliocene there was a minimum of three additional species and quite possibly as many as six or more. The closely related genus *Pinguinus* is present at Lee Creek Mine, although the species was evidently a different lineage from that that survived into historic times. Of the five species of albatrosses in the Yorktown Formation, the largest and the smallest have become totally extinct. Gannets of the genus *Morus* were reduced from three species to the single remaining modern species, *M. bassanus*. The genus *Morus* also disappeared entirely from the Pacific Ocean since some time in the Pleistocene. It is as yet unclear whether the extinction of pseudodontorns (Pelagornithidae) took place before or after the early Pliocene in the North Atlantic, but in any case this was a global event because the entire family is now extinct. The pelican from Lee Creek Mine appears to represent another lineage with no modern descendents.

Among the Anatidae and land birds at Lee Creek Mine, complete extinction of lineages occurred in *Anabernicula* and *Neophrontops* and possibly in other lines of Accipitridae—groups whose extinction was documented decades ago based on the Pleistocene deposits at Rancho La Brea in California and elsewhere. There may have been turnover in North American species of geese, also suggested by other recent studies. One of the *Somateria* eiders from Lee Creek Mine may possibly be an extinct lineage.

Retraction in range has contributed greatly to the loss of diversity of pelagic birds in the North Atlantic. Most notable here is the complete retreat of albatrosses. Whereas there were five species present in the Yorktown Formation, not one remains in the Atlantic. Perhaps unexpectedly but not illogically, three of the species at Lee Creek Mine are now found only in the North Pacific. Certain lineages of shearwaters, such as the *Puffinus pacificus* group, also retreated from the Atlantic to the Indo-Pacific. The Tufted Puffin lineage, *Fratercula cirrhata*, also became extinct in the Atlantic but has persisted in the Pacific. The same may apply to the scarce and enigmatic auklet belonging to the Aethiinae.

Another line of retreat, more evident among land and shore birds than among pelagic ones, is from North America to Europe or elsewhere in the Old World, a pattern that we hope to expand upon more fully at a later time. Such species may include *Gavia arctica*, *Grus antigone*, *Ardea cinerea*, *Balaerica* sp., *Haematopus ostralegus*, *Capella media*, *Tringa ochropus*, *Larus minutus*, and others.

Some of the biogeographical implications of the Lee Creek Mine avifauna may have important ramifications. The presence of two species of puffins (*Fratercula*) and the unidentified auklet of the Aethiinae in the Yorktown Formation of North Carolina can seemingly be explained only if there were a northern connection between the Pacific and the Atlantic oceans during, or not long before, the early Pliocene. It is hardly likely that these three species made it from the Pacific Ocean to North Carolina via the Panamanian seaway and the Gulf of Mexico. This will have to be reconciled with data that would have the Bering land bridge in place "from the second half of the Miocene to the Early Pliocene" and that a strait existed in this area "in the 'middle' Pliocene, Early and Middle Pleistocene" (Petrov, 1984:30). The ornithological evidence suggests that this strait may have been in existence even earlier.

Were alcids prone to cross the land bridge from one ocean to another, we would expect to see much more interchange between the Atlantic and Pacific oceans than is the case. On the other hand, the fact that *Uria* and *Cepphus* evidently did not enter the Atlantic from the Pacific until the Pleistocene may mean only that they were unable to colonize until the extinction of most the great Atlantic radiation of *Alca* opened up niches that were previously unavailable.

What forces may account for the great loss of diversity among seabirds in the North Atlantic since the early Pliocene? Several factors, all probably interrelated, come to mind. For whatever reason, marine biological productivity in the eastern Gulf of Mexico, and probably the western North Atlantic, declined markedly in the Quaternary relative to that of the Pliocene, with the closing of the Panamanian seaway at the end of the Pliocene probably being a major factor in disrupting marine ecosystems (Emslie, 1995b; Allmon et al., 1996). Superimposed on this were the fluctuating glacial cycles of the Pleistocene, which had multiple effects. Great eustatic changes in sea level would have had more of an effect on nesting seabirds dependent on oceanic islands than has probably been acknowl-

edged. On a world-wide basis, many islands suitable as breeding sites would have been nearly or completely inundated during the high sea levels of interglacial episodes, particularly that of Stage 11 some 400,000 years ago, which were up to 21 m above present sea level (Hearty et al., 1999). This would have been far more serious in the Atlantic, where there are fewer islands than in the Pacific.

The fact that the North Atlantic is the smallest of the world's ocean basins made it more susceptible to the rigors of glacial periods (Briggs, 1970). Glacial periods not only brought about depressed temperatures and greater winds, but the glaciers themselves may have directly affected seabirds by covering coastal nesting sites with ice, particularly during the most extreme glacial episode of the Wisconsinan (Arbib, 1972). The fossil record since the early Pliocene is insufficient for determining exactly when many extinctions of seabirds took place in the North Atlantic, but in some cases we know that extinctions must have taken place well into the Pleistocene. For example, Short-tailed Albatrosses, *Phoebastria albatrus*, were breeding on Bermuda until about 400,000 years ago (Olson, unpublished data), and birds related to *Puffinus pacificus* bred on St. Helena (Olson, 1975) and possibly on Mona Island, Puerto Rico (Olson, unpublished data), in the Pleistocene.

In some cases, the loss of diversity of seabirds in the North Atlantic has been offset by subsequent colonizations from the Pacific. The devastation visited upon the Atlantic Alcidae in particular left so many empty niches that amelioration of climate following the Wisconsinan glaciation appears to have permitted two species of murre (*Uria*) and one species of guillemot (*Cepphus*) to enter the Atlantic and successfully establish themselves, as these genera are definitely not present at Lee Creek Mine.

If we look beyond the species that have become extinct, have retreated elsewhere, or have entered the Atlantic since the Pleistocene, we find that the early Pliocene avifauna at Lee Creek Mine otherwise has a remarkably modern aspect. Apart from the exceptions previously noted, the waterfowl are just about what one would expect to find in North Carolina today, except for the abundance of *Histrionicus* and the lack of *Clangula*. One sees what may likely be the progenitors or close relatives of the Horned Grebe, various shearwaters similar to modern species in the North Atlantic, the Northern Gannet, Double-crested Cormorant, Razorbill, Dovekie, Great Auk, Atlantic Puffin, the three jaegers, the three common gulls, Whooping Crane, American Oystercatcher, Eskimo Curlew, various other shorebirds quite similar to modern species, White Ibis, Red-tailed Hawk, Turkey, Passenger Pigeon, and Fish Crow. To these may be added all the species now found elsewhere but scarcely differing from their modern descendents, such as three of the albatrosses. Thus, we must accept that many modern species lineages of birds, however they may have differed slightly in morphology from those of today, were well established by the early Pliocene and have therefore been in existence for at least five million years.

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PLATE 1

Pectoral and pelvic elements of *Gavia howardae* from Lee Creek Mine compared with *G. howardae* from the San Diego Formation and with the modern Red-throated Loon, *G. stellata*. All figures $\times 1$.

Gavia howardae, Lee Creek Mine

- a.* Right coracoid (USNM 244209), ventral view.
- c, f.* Left humerus (USNM 206448): *c*, palmar view; *f*, anconal view.
- h.* Distal end of right ulna (USNM 430500), internal view.
- j.* Proximal portion of left carpometacarpus (USNM 460767), internal view.
- l.* Right femur (USNM 215426), anterior view.
- a, q.* Distal end of right tarsometatarsus (USNM 460768): *a*, medial view; *q*, anterior view.

Gavia howardae, San Diego Formation

- d.* Left humerus (SDSNH 42763), palmar view.
- m.* Right femur (SDSNH 42775), anterior view.

Gavia stellata (USNM 561471)

- b.* Right coracoid, ventral view.
- e, g.* Left humerus: *e*, palmar view; *g*, anconal view.
- i.* Distal end of right ulna, internal view.
- k.* Proximal portion of left carpometacarpus, internal view.
- n.* Right femur, anterior view.
- p, r.* Distal end of tarsometatarsi: *p*, left, medial view; *r*, right, anterior view.



PLATE 2

Pectoral and pelvic elements of *Gavia concinna* from Lee Creek Mine (except *i*) compared with *G. concinna* from the San Diego Formation and the Bone Valley Formation and with the modern Pacific Loon, *G. pacifica*. All figures $\times 1$.

Gavia concinna, Lee Creek Mine

- a. Right coracoid (USNM 430477), ventral view.
- c. Proximal end of left humerus (USNM 430501), palmar view.
- f. Distal end of left ulna (USNM 430443), internal view.
- i. Distal end of left radius from Renny Creek, North Carolina (USNM 460775), external view.
- k. Distal end of right humerus (USNM 430470), palmar view.
- n. Right carpometacarpus (USNM 430451), internal view.
- p. Distal end of left tibiotarsus (USNM 430481), anterior view.
- r. Right femur (USNM 430518), anterior view.
- v,y. Right tarsometatarsus (USNM 366714): v, medial view; y, anterior view.
- x. Left tarsometatarsus (USNM 193359), anterior view.

Gavia concinna, San Diego Formation

- d. Left humerus (SDSNH 42761), palmar view.
- l. Distal end of left humerus (SDSNH 42767), palmar view.

Gavia concinna, Bone Valley Formation

- g. Distal end of right ulna (UF PB 89), internal view.
- m. Distal end of right humerus (UF PB 88), palmar view.
- s. Left femur (UF PB 298), anterior view.
- t. Right femur (UF PB 133), anterior view.

Gavia pacifica (USNM 500337, female)

- b. Right coracoid, ventral view.
- e. Left humerus, palmar view.
- h. Distal end of right ulna, internal view.
- j. Distal end of left radius, external view.
- o. Right carpometacarpus, internal view.
- q. Distal end of left tibiotarsus, anterior view.
- u. Right femur, anterior view.
- w. Right tarsometatarsus, medial view.
- z. Left tarsometatarsus, anterior view.

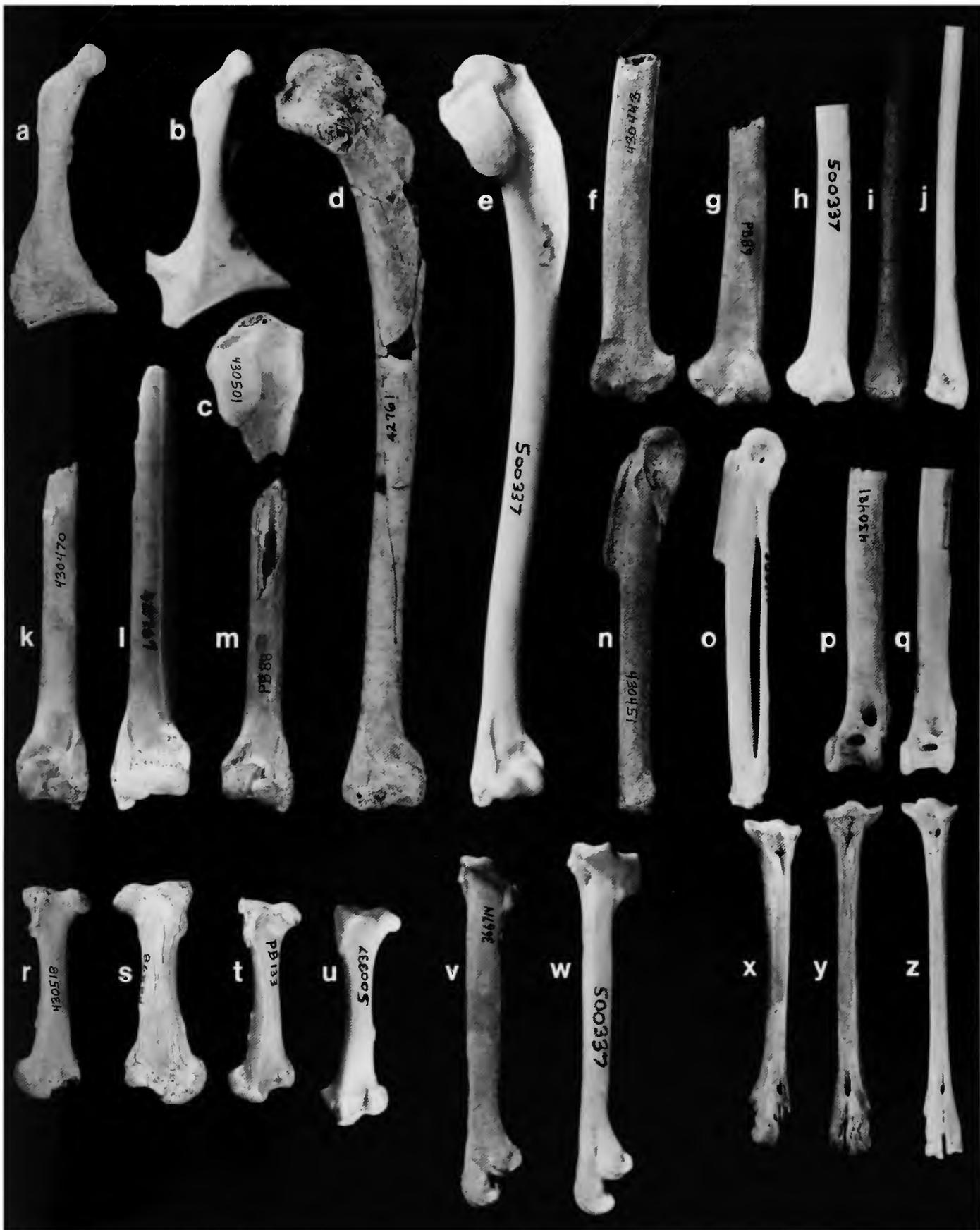


PLATE 3

Pectoral and pelvic elements of *Gavia fartis*, new species, from Lee Creek Mine and the Bone Valley Formation compared with the modern Common Loon, *G. immer*. All figures $\times 1$.

Gavia fartis, new species, Lee Creek Mine

- a. Left coracoid (paratype, USNM 215562), ventral view.
- c. Synsacrum (part of holotype, USNM 252432), lateral view.
- e. Anterior end of right scapula (paratype, USNM 206587), dorsal view.
- g. Proximal end of right humerus (paratype, USNM 460779), palmar view.
- i,k. Distal end of left humerus (part of holotype, USNM 252432): i, anconal view; k, palmar view.
- n. Left humerus lacking proximal end (paratype, USNM 206625), palmar view.

Gavia fartis, new species, Bone Valley Formation

- h. Proximal end of right humerus (UF PB 593), palmar view.
- l. Distal end of left humerus (UF PB 90), palmar view.

Gavia immer (USNM 500850, exceptionally small female)

- b. Left coracoid, ventral view.
- d. Synsacrum, lateral view.
- f. Anterior end of right scapula, dorsal view.
- j,m. Distal end of left humerus: j, anconal view; m, palmar view.



PLATE 4

Wing and hindlimb elements of *Gavia fortis*, new species, from Lee Creek Mine (associated partial skeleton USNM 252432, holotype; associated partial skeleton USNM 302392, topotypical paratype) compared with the modern Common Loon, *G. immer*. All figures $\times 1$.

Gavia fortis, new species, Lee Creek Mine

- a, b.* Proximal ends of left ulnae, internal view: *a*, USNM 252432; *b*, USNM 302392.
- c.* Right ulna (paratype, USNM 250778), internal view.
- e.* Proximal end of left radius (USNM 302392), external view.
- f.* Left radius (paratype, USNM 192060/192065), external view.
- h.* Proximal end of right carpometacarpus (USNM 252432), external view.
- j.* Pedal phalanx (USNM 302392), lateral view.
- l.* Left femur (USNM 302392), anterior view.
- n.* Proximal end of left tibiotarsus (USNM 302392), posterior view.
- p, q, s.* Distal ends of tibiotarsi: *p*, left (USNM 302392), anterior view; *q*, right (USNM 252432), anterior view; *s*, left (USNM 302392), posterior view.
- u, v, x, z.* Tarsometatarsi: *u*, left (USNM 302392), medial view; *v*, right (USNM 252432), medial view; *x*, same, posterior view; *z*, same, anterior view.

Gavia immer (USNM 500850, exceptionally small female)

- d.* Left ulna, external view.
- g.* Left radius, external view.
- i.* Proximal end of right carpometacarpus, external view.
- k.* Pedal phalanx, lateral view.
- m.* Left femur, anterior view.
- a.* Proximal end of left tibiotarsus, posterior view.
- r, t.* Distal ends of tibiotarsi: *r*, right, anterior view; *t*, left, posterior view.
- w, y, aa.* Right tarsometatarsus: *w*, medial view; *y*, posterior view; *aa*, anterior view.



PLATE 5

Fossil grebes (*Podiceps*) from Lee Creek Mine and the Bone Valley formations. All figures $\times 1$.

Podiceps aff. *auritus*, Lee Creek Mine

- a, b.* Right coracoid (USNM 177927): *a*, dorsal view; *b*, ventral view.
c, d. Right humerus (USNM 243764): *c*, palmar view; *d*, anconal view.
f, g. Right femur (USNM 252314): *f*, anterior view; *g*, posterior view.

Podiceps aff. *auritus*, Bone Valley Formation

- e.* Proximal end of right humerus (USNM 447059), anconal view.

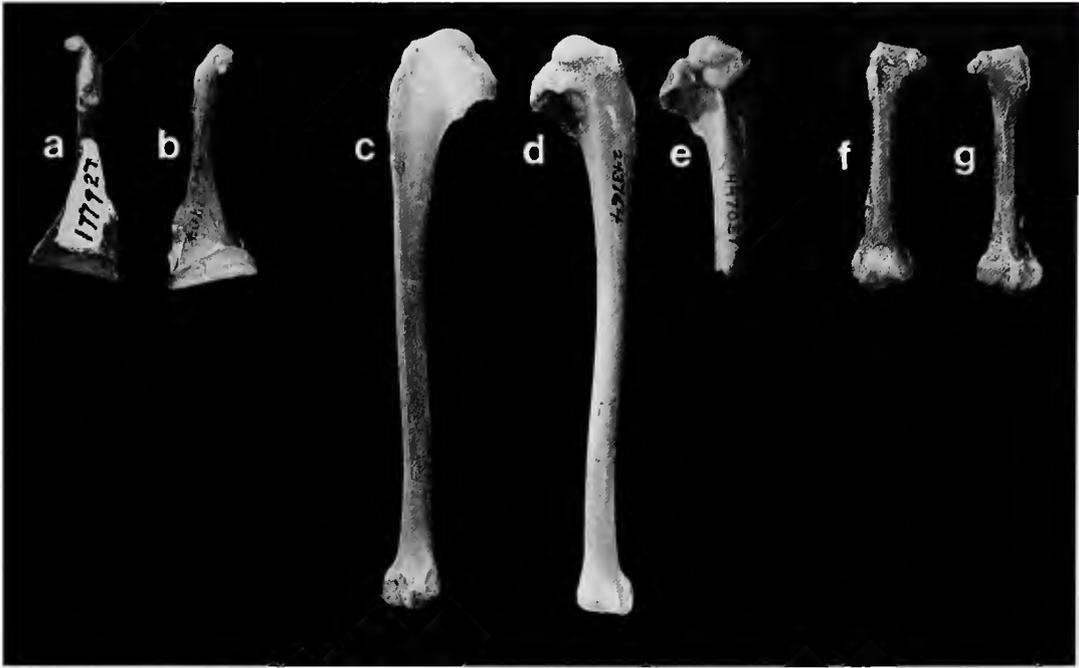


PLATE 6

Right tarsometatarsi (except *a, b, a*=left) of modern and fossil albatrosses (*Phaebastria*, *Diamedea*, *Thalassarche*) in anterior view. Note the much more robust shaft and expanded ends in *Thalassarche*. All figures $\times 1$.

- a.* *P. anglica*, Lee Creek Mine (USNM 430533).
- b.* Holocene Amsterdam Albatross, *D. amsterdamensis* (USNM 560597).
- c.* *P. aff. immutabilis*, Lee Creek Mine (USNM 464250).
- d.* Modern Laysan Albatross, *P. immutabilis* (USNM 488177).
- e.* Modern Black-browed Albatross, *T. melanophris* (USNM 553256).
- f.* *P. aff. albatrus*, Lee Creek Mine (USNM 193223).
- g.* Distal end, *P. sp.*, Miocene Astoria Formation of Oregon (USNM 424081).
- h, i.* *P. rexsularum*, new species, Lee Creek Mine: *h*, holotype (USNM 302313); *i*, paratype (USNM 430705).
- j.* Modern Yellow-nosed Albatross, *T. chlorarhynchus* (USNM 488384).
- k.* *P. aff. albatrus*, Lee Creek Mine (USNM 275847).
- l-o.* Short-tailed Albatross, *P. albatrus*, archeological specimens: *l*, USNM 343777; *m*, USNM 343777bis; *n*, USNM 343655; *o*, USNM 343654.

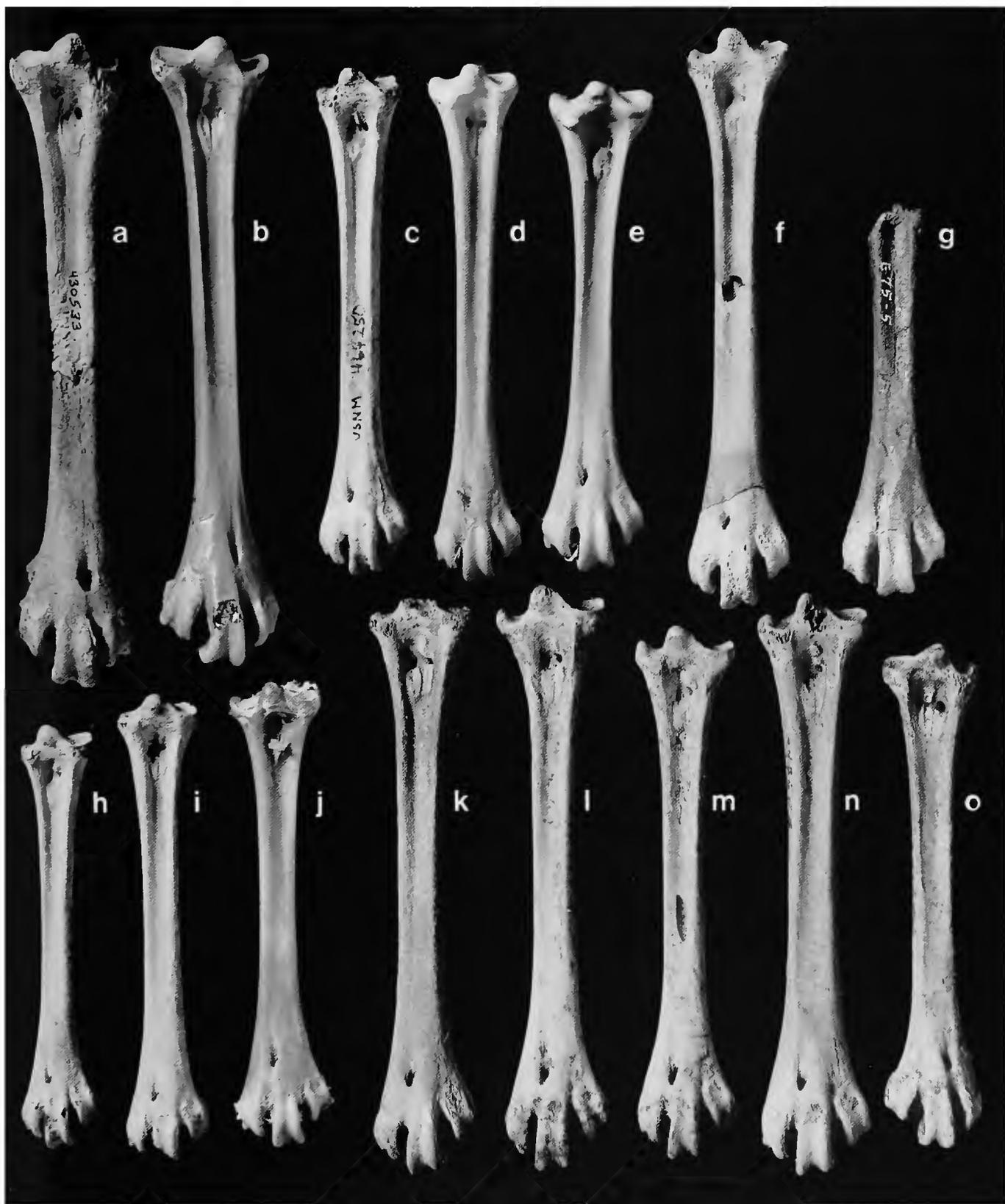


PLATE 7

Wing and hindlimb elements of fossil and modern albatrosses (*Phoebastria*, *Diomedea*, *Thalassarche*). All figures $\times 1$.

Phoebastria

- a, b.* Left carpometacarpus, internal view: *a*, *P.* aff. *albatrus*, Lee Creek Mine (USNM 430588); *b*, modern Short-tailed Albatross, *P. albatrus* (USNM 434654).
c, d. Right carpometacarpus, internal view: *c*, *P.* aff. *immutabilis*, Lee Creek Mine (USNM 460841); *d*, modern Yellow-nosed Albatross, *T. chlororhynchos* (USNM 488384).
e, f. Distal end of right ulna, internal view: *e*, *P. anglica*, Lee Creek Mine (USNM 252321); *f*, *D. amsterdamensis* (USNM 560597, Holocene).
g–i. Distal end of right tibiotarsus, anterior view: *g*, *P. anglica*, Lee Creek Mine (USNM 241429); *h*, *D. amsterdamensis* (USNM 560597, Holocene); *i*, *P. anglica*, Bone Valley Formation (cast, USNM 16751).
j–m. Left femur, anterior view: *j*, *P.* aff. *albatrus*, Lee Creek Mine (USNM 192945); *k*, modern Black-footed Albatross, *P. nigripes* (USNM 488172); *l*, *P. anglica*, Lee Creek Mine (USNM 210458); *m*, *D. amsterdamensis* (USNM 560597, Holocene).

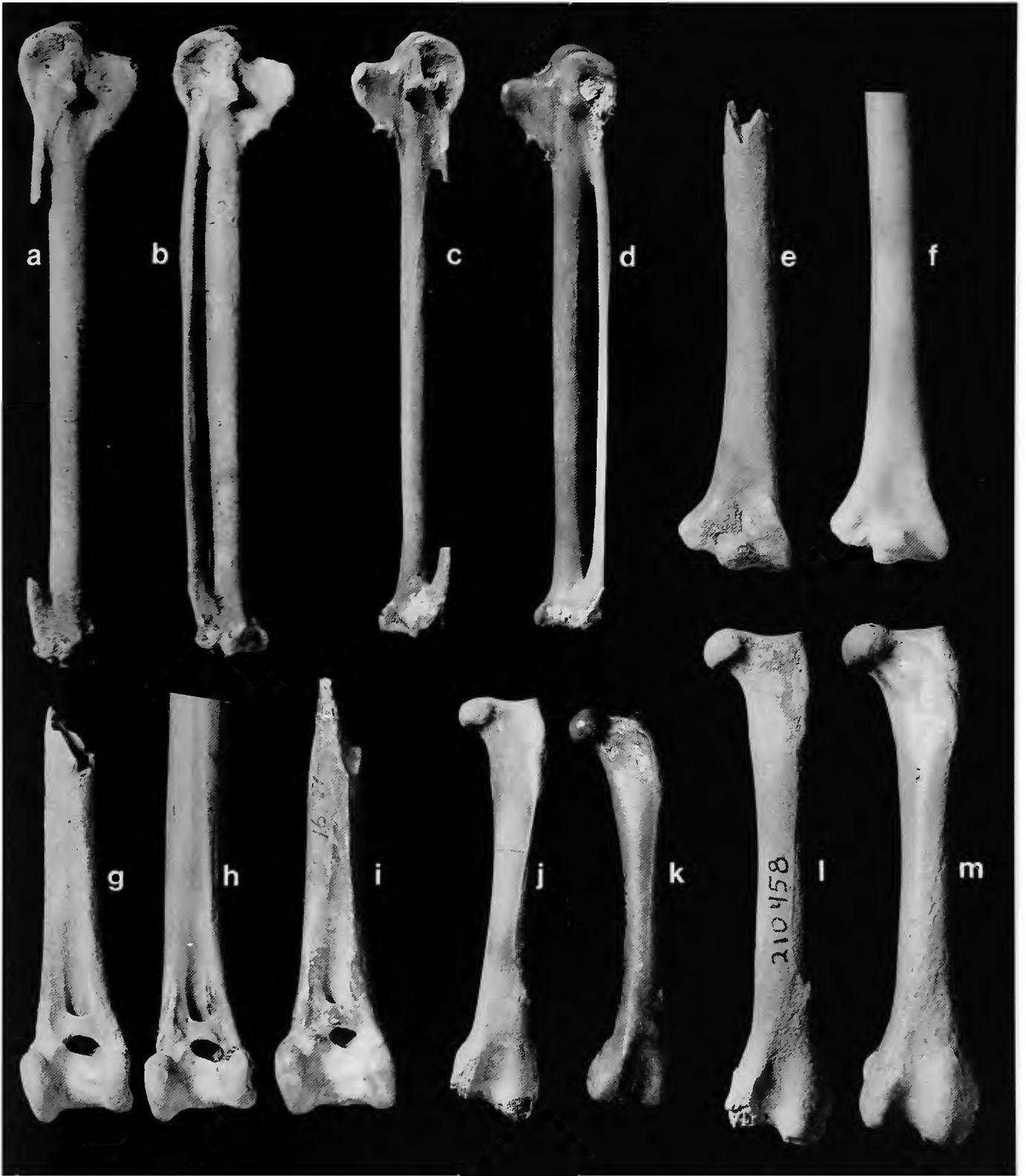


PLATE 8

Fossil albatrosses (*Phoebastria*) from Lee Creek Mine compared with modern counterparts. All figures $\times 1$.

Phoebastria

- a-c.* Proximal end of left humerus, palmar view: *a*, *P. aff. albatrus* (USNM 460858); *b*, modern Black-footed Albatross, *P. nigripes* (USNM 497964); *c*, modern Laysan Albatross, *P. immutabilis* (USNM 488177).
d-g. Distal end of left humerus, palmar view: *d*, *P. aff. nigripes* (USNM 366898); *e*, *P. rexularum*, new species, Lee Creek Mine (paratype, USNM 302414); *f*, *P. nigripes* (USNM 497964); *g*, *P. immutabilis* (USNM 488177).



PLATE 9

Pectoral, wing, and hindlimb elements of petrels and shearwaters (Procellariidae) from Lee Creek Mine compared with modern counterparts. All figures $\times 1$.

Pachyptila

a-f. Distal end of right humerus: *a*, *P.* sp. (USNM 464313), palmar view; *c*, same, anconal view; *e*, same, internal view; *b*, modern Medium-billed Prion, *P. salvini* (USNM 559767), palmar view; *d*, same, anconal view; *f*, same, internal view.

Puffinus

- g,h.* Right humerus, palmar view: *g*, *P. magn. lherminieri*, proximal end (USNM 464332); *h*, modern Audubon's Shearwater, *P. lherminieri* (USNM 498005).
i,j. Right humerus, palmar view: *i*, *P. cf. puffinus* (USNM 430765); *j*, modern Manx Shearwater, *P. puffinus* (USNM 491461).
k,l. Left humerus, palmar view: *k*, *P. aff. tenuirostris*, distal portion (USNM 464333); *l*, modern Short-tailed Shearwater, *Puffinus tenuirostris* (USNM 556481).
p. Distal end of right humerus, palmar view, *P. aff. gravis* (USNM 178187).
v,w. Left femur, posterior view: *v*, *P. aff. pacificoides* (USNM 242227); *w*, modern Buller's Shearwater, *P. bulleri* (USNM 620815).
z,aa. Left ulna, anconal view: *z*, *P. aff. tenuirostris* (USNM 366014); *aa*, modern *P. tenuirostris* (USNM 556481).
bb,cc,dd. Left tarsometatarsus, anterior view: *bb*, *P. (Ardenna)* sp. (USNM 366625); *cc*, *P. (Ardenna)* sp., distal end (USNM 215620); *dd*, modern Greater Shearwater, *P. gravis* (USNM 561134).
ee. Right tarsometatarsus, anterior view, *P. aff. pacificoides* (USNM 430852).
gg. Left tarsometatarsus, anterior view, *P. (Thyellodroma)* sp. (USNM 250810).
hh,ii,jj. Tarsometatarsus, anterior view: *hh*, left proximal end, *P. magn. lherminieri* (USNM 464311); *ii*, right distal end, *P. magn. lherminieri* (USNM 178074); *jj*, right, modern *P. lherminieri* (USNM 498005).

Calonectris

- m,n,u.* Left humerus, palmar view: *m*, *C. krantzi*, new species, proximal portion (paratype, USNM 464308); *u*, *C. krantzi*, new species, distal portion (holotype, USNM 430724); *n*, modern Cory's Shearwater, *C. borealis* (USNM 347825).
s,t. Distal portion of right humerus, palmar view: *s*, *C. aff. diomedea* (USNM 366013); *t*, *C. aff. borealis* (USNM 501506).

Pterodromoides minoricensis

- o.* Distal end of left humerus (USNM 464315), palmar view.

Pterodroma magn. lessonii

- ff.* Left tarsometatarsus (USNM 430854), anterior view.

Procellaria

- q,r.* Right humerus, palmar view: *q*, *P. cf. parkinsoni*, proximal portion (USNM 430845); *r*, same, distal portion (USNM 430726).
y. Distal end of right tibiotarsus, anterior view, *P. cf. oequinactialis* (USNM 464312).

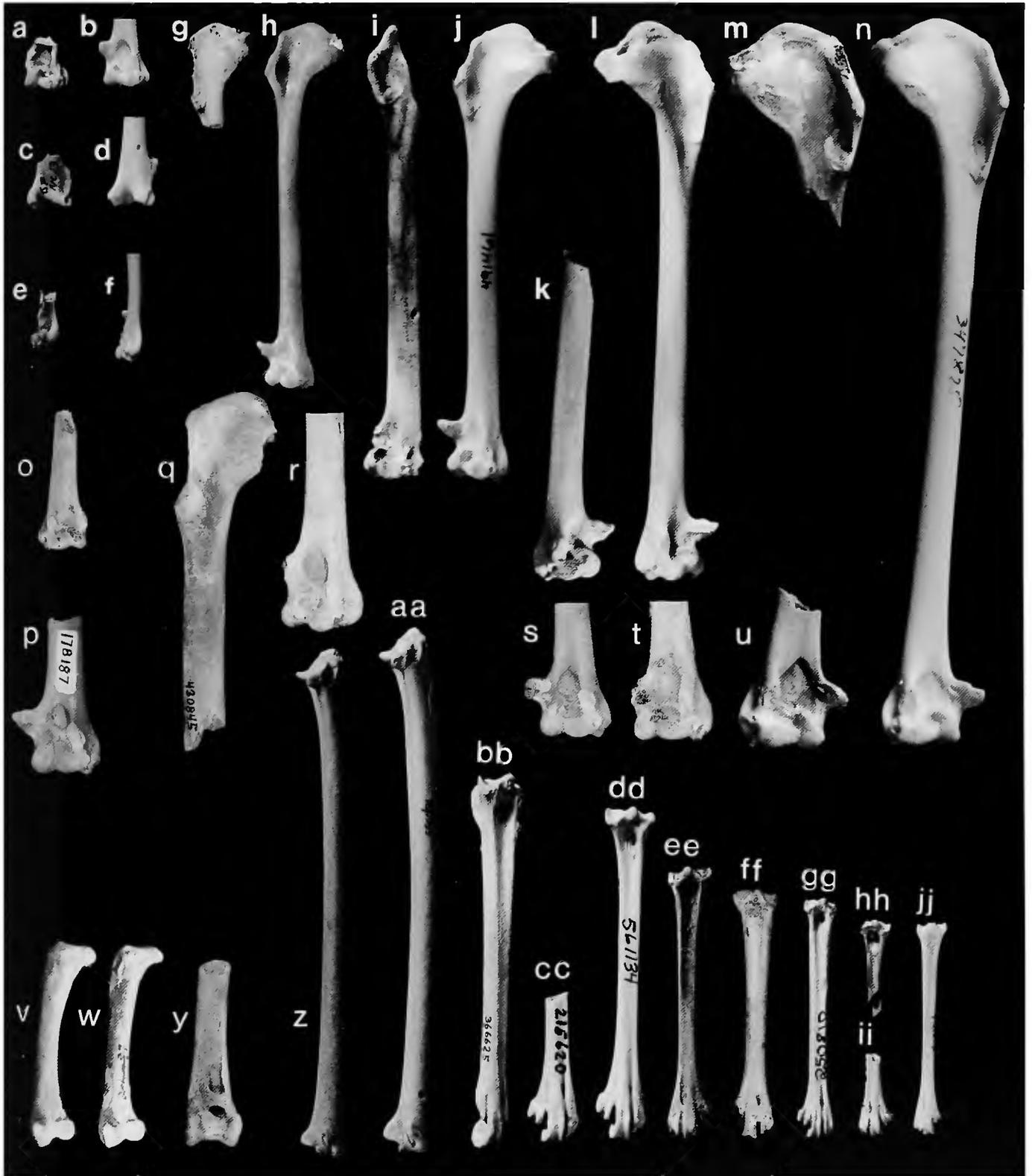


PLATE 10

Hindlimb elements of *Pelecanus* and various species of Ciconiiformes from Lee Creek Mine. All figures $\times 1$ except $j = \times 2$.

Pelecanus schreiberi

- a, c.* Distal end of left femur (paratype, USNM 263567): *a*, posterior view; *c*, anterior view.
b, d. Distal end of right femur (holotype, USNM 192077): *b*, posterior view; *d*, anterior view.

Ciconia

- e, f.* Distal end of left tibiotarsus, *Ciconia* sp. 1 (USNM 193116): *e*, anterior view; *f*, distal view.
k–m. Distal end of right tarsometatarsus, *Ciconia* sp. 2 (USNM 250706): *k*, anterior view; *l*, posterior view; *m*, distal view.

Eudocimus sp.

- g, j.* Distal end of right tibiotarsus (USNM 181027): *g*, anterior view; *j*, distal view.
h, i. Distal end of left tibiotarsus, anterior view, Bone Valley Formation: *h*, UF 91040; *i*, UF 60040.

Phoenicapterus cf. *floridanus* (USNM 242204)

- n, o.* Distal end of right tibiotarsus: *n*, anterior view; *o*, distal view.

Ardea

- p–u.* Proximal end of right tarsometatarsus: *p*, *A. aff. cinerea* (USNM 495587), posterior view; *s*, same, medial view; *q*, modern Great Blue Heron, *A. herodias* (USNM 610599), posterior view; *t*, same, medial view; *r*, modern Gray Heron, *A. cinerea* (USNM 553297), posterior view; *u*, same, medial view.

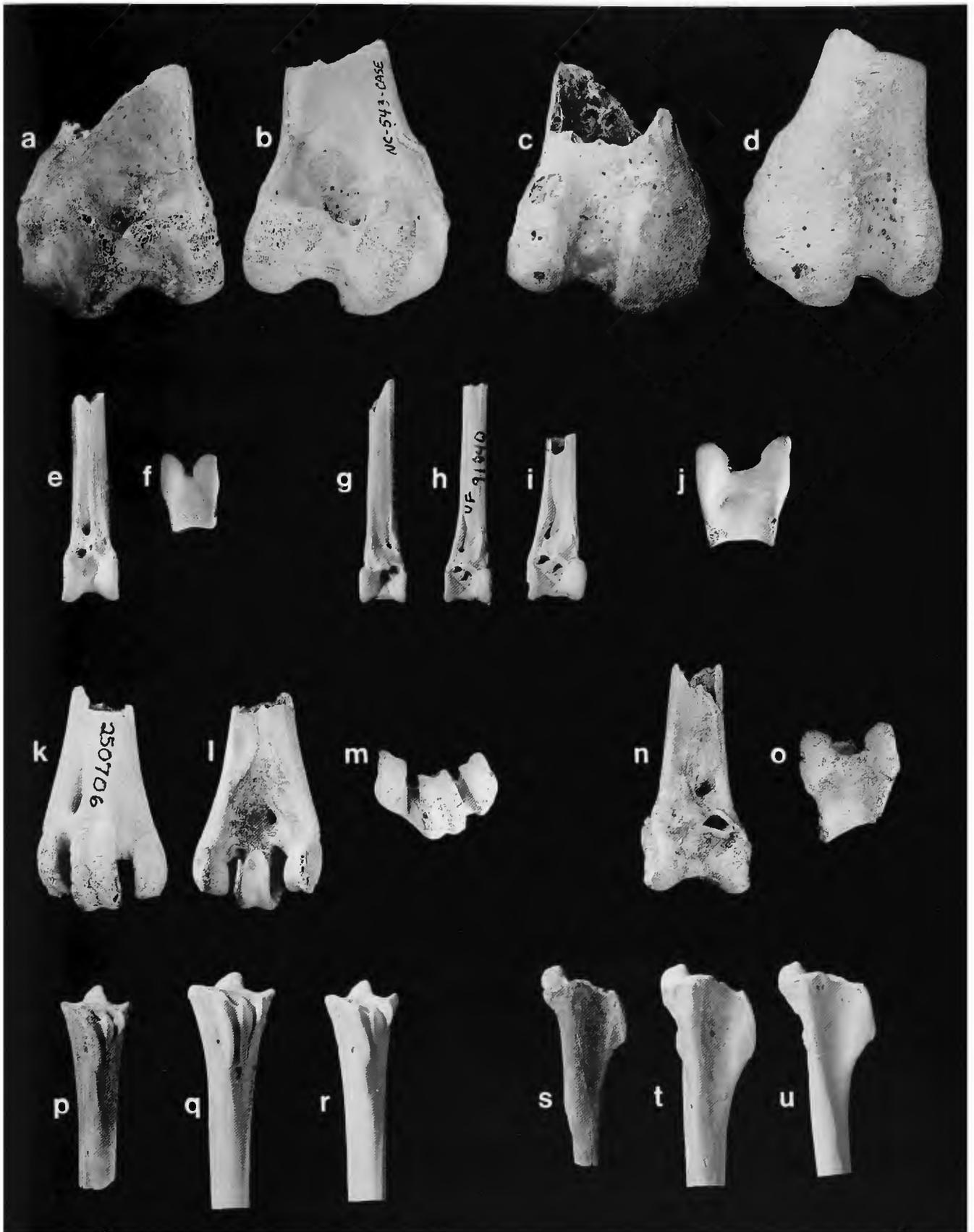


PLATE 11

Cranial, pectoral, and hindlimb elements of pseudodontorns (*Pelagornis* spp.) from Lee Creek Mine compared with the modern Northern Gannet, *Morus bassanus*. All figures $\times 1$.

Pelagornis spp.

- a, b.* *P.* sp., anterior portion of mandible (USNM 446494): *a*, labial view; *b*, lingual view.
- c.* *P.* sp., unassociated pseudotooth (USNM 464325).
- d.* *P.* sp., right pterygoid (USNM 425110), medial view.
- f.* *P.* sp., right quadrate (USNM 446495), medial view.
- h.* *P.* sp., axis vertebra (USNM 446502), ventral view.
- j.* *P.* sp., anterior portion of left scapula (USNM 425104), dorsal view.
- l, n.* *P.* sp. 2, proximal portion of right humerus (USNM 425111): *l*, palmar view; *n*, anconal view.
- p, t.* *P.* sp. 1, proximal end of left femur (USNM 321289): *p*, anterior view; *t*, posterior view.
- q, u.* *P.* sp. 1, distal end of left femur (USNM 205473): *q*, anterior view; *u*, posterior view.

Morus bassanus (USNM 16643)

- e.* Right pterygoid, medial view.
- g.* Right quadrate, medial view.
- i.* Axis vertebra, ventral view.
- k.* Anterior portion of left scapula, dorsal view.
- m, o.* Proximal portion of right humerus: *m*, palmar view; *o*, anconal view.
- r, s.* Left femur: *r*, anterior view; *s*, posterior view.



PLATE 12

Associated partial skeleton and humeri (palmar views) of fossil gannets (*Morus*) from Lee Creek Mine compared with the modern Northern Gannet, *Morus bassanus*. All figures $\times 1$.

Morus, Lee Creek Mine

- a-g*. Associated material of *Morus*, undescribed species 1 (USNM 181052): *a*, right mandible, lingual view; *b*, left mandible, lingual view; *c*, right humerus lacking distal end; *d*, proximal end of left carpometacarpus, internal view; *e*, distal end of left radius, internal view; *f*, distal end of left ulna, internal view; *g*, left ulnare.
- h*. Proximal half of left humerus, *M. peninsularis* (USNM 464323).
- i*. Proximal portion of right humerus, *M. undescribed species 1* (USNM 368548).
- j*. Proximal end of left humerus, *M. undescribed species 2* (USNM 426009).
- l*. Distal two-thirds of left humerus, *M. peninsularis* (USNM 411971).
- m,n*. Distal end of left humerus: *m*, *M. undescribed species 2* (USNM 411951); *n*, *M. undescribed species 1* (USNM 426011).

Morus bassanus (USNM 614826)

- k,o*. Left humerus: *k*, proximal end; *o*, distal end.



PLATE 13

Coracoid, distal wing, and hindlimb elements of fossil gannets (*Morus*) from Lee Creek Mine compared with the modern Northern Gannet, *Morus bassanus*. All figures $\times 1$.

Morus, Lee Creek Mine

- a–c. Left coracoid, ventral view: a, *M. peninsularis* (USNM 412021); b, *M. undescribed species 1* (USNM 464322); c, *M. undescribed species 2* (USNM 183499), scapular end.
- e. Proximal end of right ulna, internal view, *M. peninsularis* (USNM 412017).
- g. Left carpometacarpus, internal view, *M. peninsularis* (USNM 426023).
- i. Left femur, anterior view, *M. peninsularis* (USNM 177910).
- k. Incomplete right tibiotarsus, anterior view, *M. undescribed species 1* (USNM 426069).
- m. Distal end of right ulna, internal view, *M. peninsularis* (USNM 412006).
- n. Right tarsometatarsus, posterior view, *M. peninsularis* (USNM 426061).
- o. Left tarsometatarsus, anterior view, *M. undescribed species 1* (USNM 366904).

Morus bassanus (USNM 614826)

- d. Left coracoid, ventral view.
- f. Right ulna, internal view.
- h. Left carpometacarpus, internal view.
- j. Left femur, anterior view.
- l. Right tibiotarsus, anterior view.
- p. Left tarsometatarsus, anterior view.



PLATE 14

Coracoids and hindlimb elements of fossil cormorants (*Phalacrocorax*) from Lee Creek Mine and the Bone Valley Formation. All figures $\times 1$.

Phalacrocorax wetmorei, Lee Creek Mine

- a.* Right coracoid (USNM 242346), ventral view.
- d.g.* Right femur (USNM 242205): *d.* anterior view; *g.* posterior view.
- j.q.* Right tibiotarsus (USNM 446425): *j.* anterior view; *q.* posterior view.
- s.* Right tarsometatarsus (USNM 446429), anterior view.

Phalacrocorax wetmorei, Bone Valley Formation

- b.* Right coracoid (UF 95488), ventral view.
- e,h.* Right femur (UF 101946): *e.* anterior view; *h.* posterior view.
- n,o.* Distal end of right tibiotarsus, anterior view: *n.* UF, number not recorded; *o.* UF 65772.
- t.* Right tarsometatarsus (UF 94550), anterior view.

Phalacrocorax large species

(All Lee Creek Mine except UF 67935, Bone Valley Formation)

- c.* Right coracoid (USNM 177880), ventral view.
- f,i.* Right femur (USNM 177791): *f.* anterior view; *i.* posterior view.
- k,r.* Right tibiotarsus (UF 67935): *k.* anterior view; *r.* posterior view.
- l.* Proximal end of left tibiotarsus (USNM 215597), anterior view.
- m.* Proximal end of left tibiotarsus (USNM 177901), anterior view.
- p.* Distal end of left tibiotarsus (USNM 177787), anterior view.
- u,v.* Distal portion of left tarsometatarsus (USNM 430872): *u.* anterior view; *v.* posterior view.



PLATE 15

Pectoral and hindlimb elements of jaegers and skuas (Stercorariidae) from Lee Creek Mine (unless otherwise specified) compared with modern taxa. All figures $\times 1$.

Catharacta

- a, b.* Distal end of left ulna, external view: *a*, *C. sp.* (USNM 366602); *b*, modern South Polar Skua, *C. maccormicki* (USNM 576076).
c–e. Left tarsometatarsus, anterior view: *c*, distal end, *C. sp.* (USNM 183482); *d*, incomplete, *C. sp.*, (USNM 430892); *e*, modern South Polar Skua, *C. maccormicki* (USNM 576076).

Stercorarius aff. pomarinus

- f–i.* Left coracoid: *f*, *S. aff. pomarinus* (USNM 430891), ventral view; *h*, same, internal view; *g*, modern Pomarine Jaeger, *S. pomarinus* (USNM 17807), ventral view; *i*, same, internal view.
j. Distal end of right humerus, *S. aff. pomarinus* (USNM 192818), palmar view.
k–n. Distal end of left humerus: *k*, *S. aff. pomarinus* (USNM 366015), palmar view; *m*, same, internal view; *l*, modern *S. pomarinus* (USNM 17807), palmar view; *n*, same, internal view.
o, p. Distal end of left ulna, internal view: *o*, *S. aff. pomarinus* (USNM 430890); *p*, modern *S. pomarinus* (USNM 17807).

Stercorarius aff. parasiticus

- q–v.* Distal end of right humerus: *q*, *S. aff. parasiticus* (USNM 178064), palmar view; *t*, same, external view; *r*, *S. aff. parasiticus* (USNM 460819), palmar view; *u*, same, external view; *s*, modern Parasitic Jaeger, *S. parasiticus* (USNM 502329), palmar view; *v*, same, external view.
z, aa. Proximal end of right carpometacarpus, internal view: *z*, *S. aff. parasiticus* (USNM 193269); *aa*, modern *S. parasiticus* (USNM 502329).
w–y. Distal portions of right ulnae, internal view: *w*, specimen the size of *S. parasiticus* from the middle Miocene Calvert Formation (USNM 237149); *x*, same (USNM 237176); *y*, modern *S. parasiticus* (USNM 502328).

Stercorarius aff. longicaudus

- bb–gg.* Distal end of left humerus: *bb*, *S. aff. longicaudus* (USNM 430893), palmar view; *ee*, same, internal view; *cc*, same (USNM 448914), palmar view; *ff*, same, internal view; *dd*, modern Long-tailed Jaeger, *S. longicaudus* (USNM 428034), palmar view; *gg*, same, internal view.
hh, ii. Proximal end of left carpometacarpus, internal view: *hh*, *S. aff. longicaudus* (USNM 460818); *ii*, modern *S. longicaudus* (USNM 428034).



PLATE 16

Pectoral elements of gulls and terns (Laridae) from Lee Creek Mine compared with modern taxa. All figures $\times 1$.

Larus aff. argentatus

- a, b.* Distal end of left humerus, palmar view: *a, L. aff. argentatus* (USNM 366896); *b*, modern Herring Gull, *L. argentatus* (USNM 347081).
c–e. Proximal end of right ulna, internal view: *c, L. aff. argentatus* (USNM 430896); *d, L. aff. argentatus* (USNM 430903); *e*, modern *L. argentatus* (USNM 502297).
f, g. Proximal end of right carpometacarpus, internal view: *f, L. aff. argentatus* (USNM 430895); *g*, modern *L. argentatus* (USNM 502297).
h, i. Distal end of right ulna, internal view: *h, L. aff. argentatus* (USNM 430905); *i*, modern *L. argentatus* (USNM 502297).

Larus aff. atricilla

- j, k.* Distal end of right humerus, palmar view: *j, L. aff. atricilla* (USNM 430921); *k*, modern Laughing Gull, *L. atricilla* (USNM 560290).
l, m. Distal portion of right ulna, internal view: *l, L. aff. atricilla* (USNM 366451); *m*, modern *L. atricilla* (USNM 502178).
n, o. Right carpometacarpus, internal view: *n, L. aff. atricilla* (USNM 460828); *o*, modern *L. atricilla* (USNM 553707).

Larus magn. ridibundus

- p, q.* Proximal end of left humerus, palmar view: *p, L. magn. ridibundus* (USNM 210461); *q*, modern Black-headed Gull, *L. ridibundus* (USNM 610491).

Larus sp.

- r–u.* Scapular end of right coracoid: *r, L. sp.* (USNM 430834), ventral view; *t*, same, internal view; *s*, modern Ivory Gull, *L. albus* (USNM 491600), ventral view; *u*, same, internal view.

Larus aff. minutus

- v–aa.* Partial left humerus: *v, L. aff. minutus* (USNM 430923), palmar view; *y*, same, anconal view; *w*, same (USNM 430916), palmar view; *z*, same, anconal view; *x*, modern Little Gull, *L. minutus* (USNM 502550), palmar view; *aa*, same, anconal view.
bb, cc. Right ulna, internal view: *bb, L. aff. minutus* (USNM 460817); *cc*, modern *L. minutus* (USNM 553647).

Sterna aff. maxima

- dd, ee.* Proximal end of right carpometacarpus, internal view: *dd, S. aff. maxima* (USNM 215643); *ee*, modern Royal Tern, *S. maxima* (USNM 555482).

Sterna aff. nilotica

- ff, gg.* Right carpometacarpus, internal view: *ff, Sterna aff. nilotica* (USNM 495588); *gg*, modern Gull-billed Tern, *S. nilotica* (USNM 610912).



PLATE 17

Pectoral elements of *Larus* aff. *delawarensis* from Lee Creek Mine compared with *Larus elmorei* from the Bone Valley Formation, Florida, and the modern Ring-billed Gull, *L. delawarensis*. All figures $\times 1$.

Larus aff. *delawarensis*, Lee Creek Mine

- a, c.* Scapular portion of right coracoid (USNM 430914): *a*, ventral view; *c*, dorsal view.
- e.* Incomplete right humerus (USNM 181025), palmar view.
- h.* Distal end of left humerus (USNM 366791), palmar view.
- j.* Proximal end of right ulna (USNM 430918), internal view.
- m.* Distal end of right ulna (USNM 430904), internal view.
- p, q.* Right carpometacarpus, internal view: *p*, USNM 256349; *q*, USNM 460833.

Larus elmorei, Bone Valley Formation

- f, g.* Distal end of right humerus, palmar view: *f*, USNM 447048; *g*, USNM 447049.
- k.* Proximal end of left ulna, internal view (UF 61951).
- o.* Proximal end of left carpometacarpus, internal view (USNM 447047).

Larus delawarensis (USNM 556839)

- b, d.* Scapular portion of right coracoid: *b*, ventral view; *d*, dorsal view.
- i.* Left humerus, palmar view.
- l.* Proximal end of right ulna, internal view.
- n.* Distal end of right ulna, internal view.
- r.* Right carpometacarpus, internal view.



PLATE 18

Pectoral and hindlimb elements of fossil species of auks (*Alca*) from Lee Creek Mine compared with the modern Razorbill, *Alca torda*. All figures $\times 1$.

Alca ausonia, Lee Creek Mine

- a. Anterior portion of sternum (USNM 178152), anterior view.
- i. Left ulna (USNM 496160), internal view.

Alca antiqua, Lee Creek Mine

- c. Medial portion of furcula (USNM 256225), anterior view.
- e. Proximal portion of left scapula (USNM 496158), dorsal view.
- g. Left coracoid (USNM 448862), ventral view.
- k. Left radius (USNM 496159), internal view.
- m. Left carpometacarpus (USNM 183447), internal view.
- o. Left femur (USNM 275857), posterior view.
- q,r. Right tibiotarsus, anterior view: q, proximal end (USNM 496161); r, distal end (USNM 367060).
- t. Left tarsometatarsus (USNM 177809), anterior view.

Alca torda (USNM 610935)

- b. Anterior portion of sternum, anterior view.
- d. Furcula, anterior view.
- f. Left scapula, dorsal view.
- h. Left coracoid, ventral view.
- j. Left ulna, internal view.
- l. Left radius, internal view.
- n. Left carpometacarpus, internal view.
- p. Left femur, posterior view.
- s. Right tibiotarsus, anterior view.
- u. Left tarsometatarsus, anterior view.



PLATE 19

Pectoral elements of large species of auks (Alcidae). All figures $\times 1$.

Alca, undescribed species

- a, d, g.* USNM 242238, Miocene Eastover Formation of Virginia: *a*, left coracoid, dorsal view; *d*, right humerus, anconal view; *g*, right ulna, internal view.
e. Right humerus (USNM 446650), anconal view.
h. Proximal end of right ulna (USNM 181090), internal view.

Pinguinus alfrednewtoni, Lee Creek Mine

- b.* Left coracoid (USNM 459392), dorsal view.
f. Right humerus (USNM 366630), anconal view.

Pinguinus impennis

- c.* Left coracoid (USNM uncataloged), dorsal view.
i. Right ulna (USNM uncataloged), internal view.



PLATE 20

Fossil pectoral and hindlimb elements of *Pinguinus alfrednewtoni* from Lee Creek Mine compared with the modern Great Auk, *Pinguinus impennis*. All figures $\times 1$. Additional skeletal elements illustrated in Olson (1977).

Pinguinus alfrednewtoni, Lee Creek Mine

- a. Furcular symphysis (USNM 459389), anterior view.
- c. Anterior portion of sternum (USNM 459391), anterior view.
- e. Left radius (USNM 430935), anconal view.
- g,i. Left coracoid (USNM 459392): g, dorsal view; i, ventral view.
- k,m. Right tibiotarsus, anterior view: k, proximal end (USNM 366727); m, distal end (USNM 430946).
- o. Left tarsometatarsus (USNM 430947), anterior view.
- q,s. Right humerus (USNM 366630): q, anconal view; s, internal view.

Pinguinus impennis (USNM uncatalogued)

- b. Furcular symphysis, anterior view.
- d. Anterior portion of sternum, anterior view.
- f. Left radius, anconal view.
- h,j. Left coracoid: h, dorsal view; j, ventral view.
- l,n. Right tibiotarsus, anterior view: l, proximal end; n, distal end.
- p. Left tarsometatarsus, anterior view.
- r,t. Right humerus: r, anconal view; t, internal view.





PLATE 21.—Pectoral elements of *Alle* aff. *alle* from Lee Creek Mine compared with the modern Dovekie, *Alle alle*. *a, c, e, g, i, k, m, o, q*, *Alle* aff. *alle*: *a*, left coracoid (USNM 192856), dorsal view; *c*, same, internal view; *e*, right humerus (USNM 448912) palmar view; *g*, same, anconal view; *i*, same, external view; *k*, distal end of right ulna (USNM 430953), internal view; *m*, same, external view; *o*, right carpometacarpus (USNM 430952), internal view; *q*, same, external view. *b, d, f, h, j, l, n, p, r*, *Alle alle* (USNM 502391): *b*, left coracoid, dorsal view; *d*, same, external view; *f*, right humerus, palmar view; *h*, same, anconal view; *j*, same, internal view; *l*, distal end of right ulna, internal view; *n*, same, external view; *p*, right carpometacarpus, internal view; *r*, same, external view. (All figures $\times 2$.)

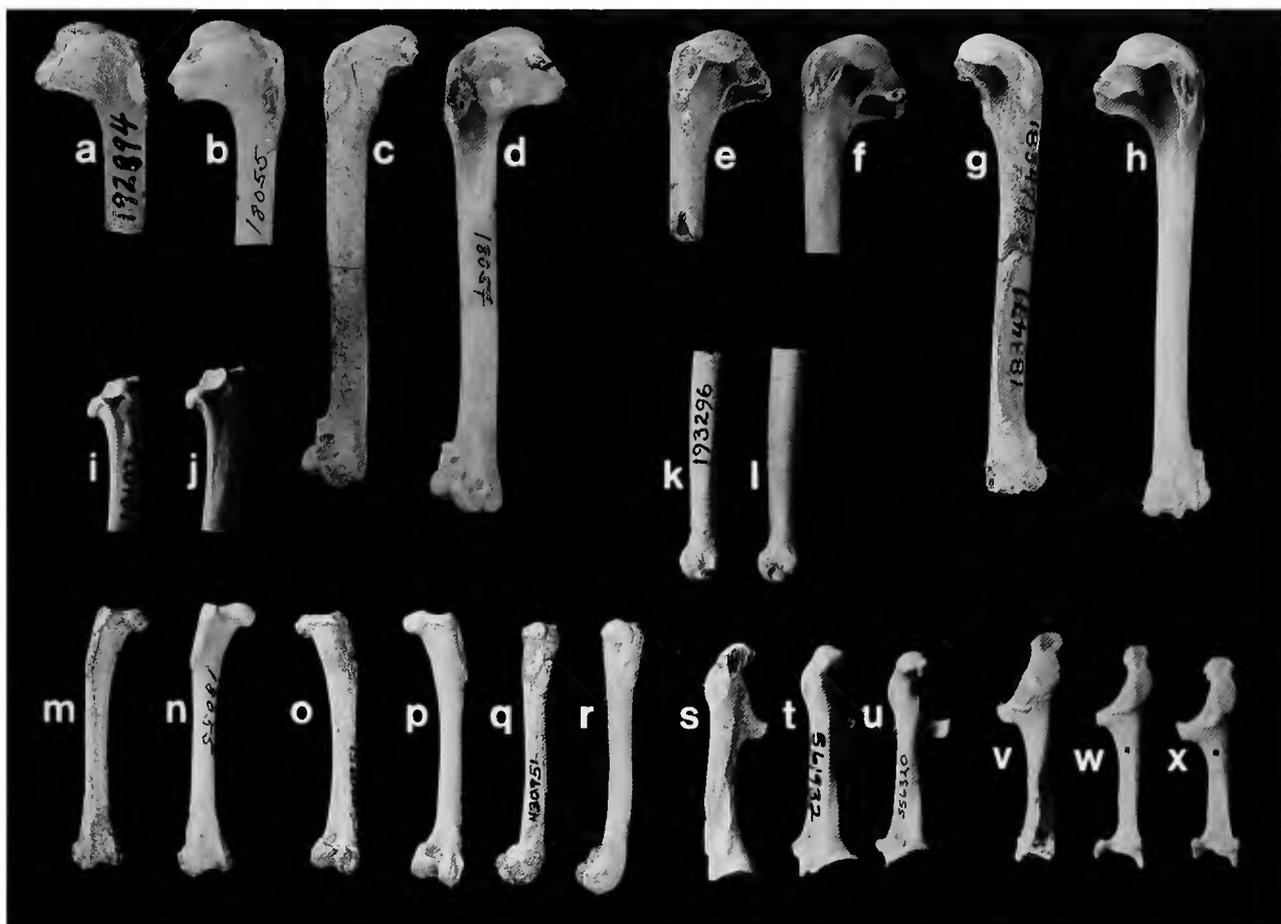


PLATE 22.—Pectoral and hindlimb elements of *Fratercula* aff. *arctica* compared with the modern Atlantic Puffin, *F. arctica*; undetermined auklet, Aethiinae genus and species indeterminate, compared with the modern Crested Auklet, *Aethia cristatella*, and Parakeet Auklet, *Cyclorhynchus psittacula*. *a,c,e,g,i,k,m,o,g*, *Fratercula* aff. *arctica*, Lee Creek Mine: *a*, proximal end of left humerus (USNM 192894), palmar view; *e*, same, anconal view; *c*, right humerus (USNM 183471), palmar view; *g*, same, anconal view; *i*, proximal end of right ulna (USNM 181073), internal view; *k*, distal end of left ulna (USNM 193296), internal view; *m*, right femur (USNM 430951), anterior view; *o*, same, posterior view; *q*, same, external view. *b,d,f,h,j,l,n,p,r*, *Fratercula arctica*: *b*, proximal end of left humerus (USNM 18055), palmar view; *f*, same, anconal view; *d*, right humerus (USNM 18054), palmar view; *h*, same, anconal view; *j*, proximal end of right ulna (USNM, number not recorded), internal view; *l*, distal end of left ulna (USNM, number not recorded), internal view; *n*, right femur (USNM 18055), anterior view; *p*, same, posterior view; *r*, same, external view. *s,v*, Aethiinae, genus and species indeterminate, Lee Creek Mine: *s*, right coracoid (USNM 495586) ventral view; *v*, same, external view. *t,w*, *Aethia cristatella* (USNM 561932): *t*, right coracoid, ventral view; *w*, same, external view. *u,x*, *Cyclorhynchus psittacula* (USNM 556320): *u*, right coracoid, ventral view; *x*, same, external view. (All figures $\times 1$.)

PLATE 23

Pectoral and hindlimb elements of *Fratercula* aff. *cirrhata* from Lee Creek Mine compared with the modern Tufted Puffin, *Fratercula cirrhata*. All figures $\times 1$.

Fratercula aff. *cirrhata*, Lee Creek Mine

- a,c,e.* Right coracoid (USNM 242309): *a*, ventral view; *c*, dorsal view; *e*, internal view.
g,i. Right tarsometatarsus (USNM 430959): *g*, anterior; *i*, posterior view.
k,n. Proximal end of left humerus (USNM 215678): *k*, palmar view; *n*, anconal view.
l,o. Left humerus (USNM 257520): *l*, palmar view; *o*, anconal view.
q. Right carpometacarpus lacking distal end (USNM 193340), external view.

Fratercula cirrhata (USNM 561951 except *d*=USNM 556444)

- b,d,f.* Right coracoid: *b*, ventral view; *d*, dorsal view; *f*, internal view.
h,j. Right tarsometatarsus: *h*, anterior; *j*, posterior view.
m,p. Left humerus: *m*, palmar view; *p*, anconal view.
r. Right carpometacarpus lacking distal end, external view.



PLATE 24

Wing and hindlimb elements of *Cygnus* aff. *columbianus* from Lee Creek Mine compared with the modern Tundra Swan, *C. columbianus*. All figures $\times 1$.

Cygnus aff. *columbianus*, Lee Creek Mine

- a. Distal end of right humerus (USNM 306312), palmar view.
- c. Proximal end of right ulna (USNM 430875), internal view.
- e. Distal end of right ulna (USNM 446508), internal view.
- g. Left tarsometatarsus (USNM 430877), anterior view.
- i. Left carpometacarpus (USNM 308156), internal view.
- k. Distal end of left tibiotarsus (USNM 210454), anterior view.

Cygnus columbianus

- b. Distal end of right humerus (USNM 502567), palmar view.
- d. Proximal end of right ulna (USNM 502567), internal view.
- f. Distal end of right ulna (USNM 502567), internal view.
- h. Left tarsometatarsus (USNM 610614), anterior view.
- j. Left carpometacarpus (USNM 610614), internal view.
- l. Distal end of left tibiotarsus (USNM 610614), anterior view.





PLATE 25.—Wing and hindlimb elements of geese and shelducks (Anserini and Tadomini). *a, b*, *Anser* cf. *arizonae*, left tarsometatarsus, anterior view: *a*, USNM 430881, Lee Creek Mine; *b*, F:AM 19991, Big Sandy Formation, Arizona. *c, d*, *Branta*, distal end of right humerus, palmar view: *c*, *Branta* aff. *bernicla*, Lee Creek Mine (USNM 457386); *d*, modern Brant, *B. bernicla* (USNM 561062). *e–g, l–n*, *Anabernicula*, left tarsometatarsus: *e*, *A. cf. minuscula*, Lee Creek Mine (USNM 457387), anterior view; *l*, same, posterior view; *f*, *A. sp.*, Big Sandy Formation, Arizona (F:AM 19998), anterior view; *m*, same, posterior view; *g*, *A. sp.*, Big Sandy Formation, Arizona (F:AM 19999), anterior view; *n*, same, posterior view. *h–k*, *Anabernicula*, left femur: *h*, *A. cf. minuscula*, Lee Creek Mine (USNM 457388), anterior view; *j*, same, posterior view; *i*, *A. sp.*, Big Sandy Formation, Arizona (F:AM 20005), anterior view; *k*, same, posterior view. (All figures $\times 1$.)

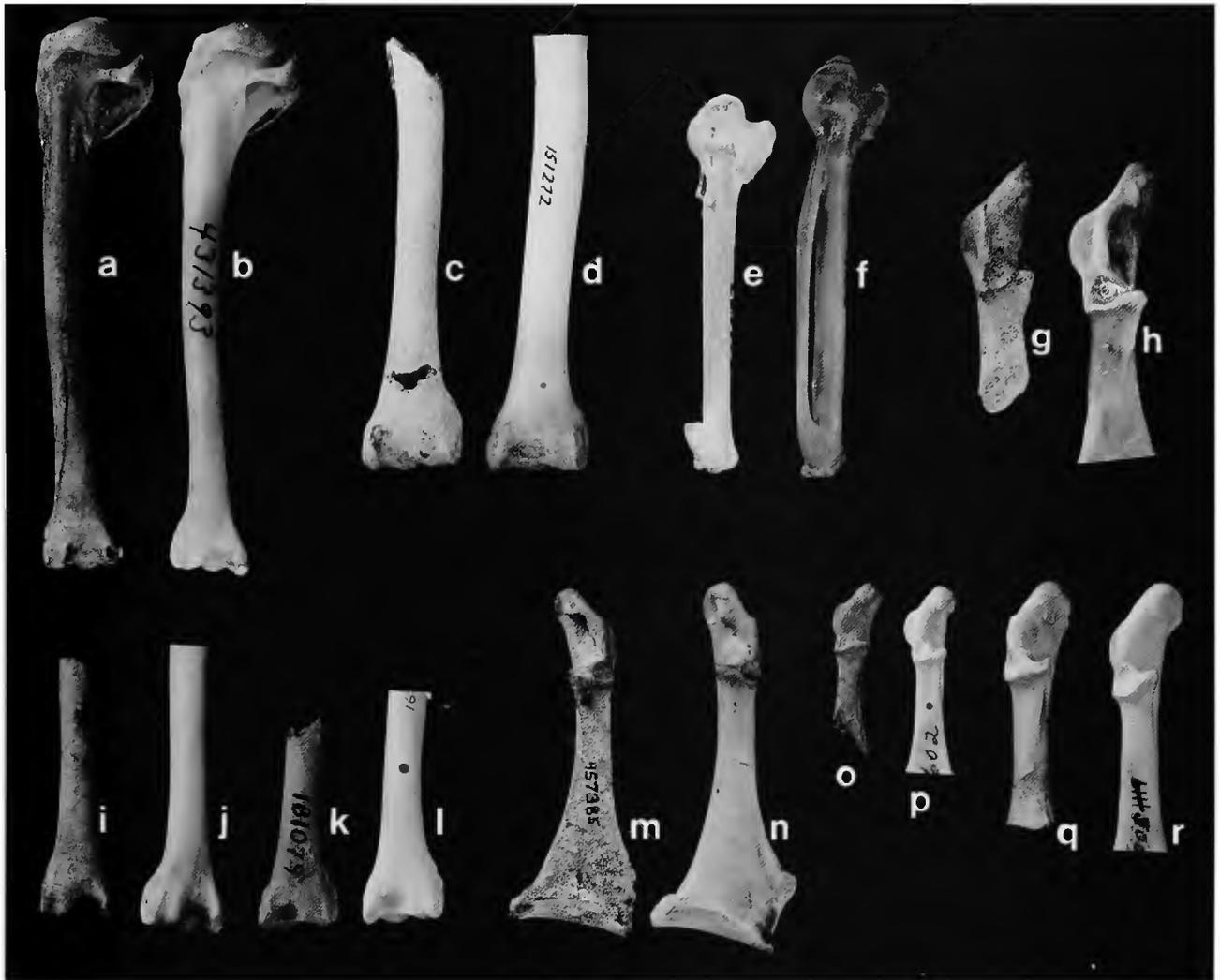


PLATE 26.—Pectoral elements of diving ducks (Aythyini and Mergini) from Lee Creek Mine compared with modern relatives. *a,b*, *Aythya*, left humerus, anconal view: *a*, *A. aff. affinis* (USNM 457389); *b*, modern Lesser Scaup, *A. affinis* (USNM 431393). *c,d*, *Somateria*, distal portion of right humerus, anconal view: *c*, *Somateria* sp. (USNM 275781); *d*, female modern Spectacled Eider, *S. fischeri* (UMMZ 151272). *e,f*, *Somateria*, left carpometacarpus, internal view: *e*, *S. sp.* (USNM 206597); *f*, female modern Spectacled Eider, *S. fischeri* (UMMZ 151272). *g,h*, *Somateria*, scapular portion of left coracoid, dorsal view: *g*, *S. aff. mallissima* (USNM 275860); *h*, female modern Common Eider, *S. mallissima v-nigrum* (USNM 431987). *i,j*, *Melanitta*, distal end of left humerus, anconal view: *i*, *M. aff. nigra* (USNM 457384); *j*, modern Black Scoter, *M. nigra* (USNM 499416). *k,l*, *Melanitta*, distal end of right humerus, anconal view: *k*, *M. aff. perspicillata* (USNM 181079); *l*, modern Surf Scoter, *M. perspicillata* (USNM 291291). *m,n*, *Bucephala*, right coracoid, dorsal view: *m*, *B. aff. clangula* (USNM 457385); *n*, modern Common Goldeneye, *B. clangula* (USNM 488606). *o,p*, *Bucephala*, scapular end of left coracoid, dorsal view: *o*, *B. aff. albeala* (USNM 206518); *p*, modern Bufflehead, *B. albeala* (USNM 610709, original no. 602). *q,r*, *Mergus*, scapular portion of left coracoid, dorsal view: *q*, *M. aff. serrator* (USNM 192481); *r*, modern Red-breasted Merganser, *M. serrator* (USNM 500967). (All figures $\times 1$.)

PLATE 27

Pectoral and hindlimb elements of fossil *Histrionicus* compared with the modern Harlequin Duck, *Histrionicus histrionicus*. All figures $\times 1$.

Histrionicus aff. *histrionicus*

- a,c.* Right coracoid (USNM 457382), Lee Creek Mine: *a*, ventral view; *c*, dorsal view.
e,j,m. Right humerus (USNM 457378), Lee Creek Mine: *e*, palmar view; *j*, distal view; *m*, anconal view.
f,q. Right humerus (holotype of *Melanitta ceruttii*, SDSNH 23584), San Diego Formation: *f*, palmar view; *q*, anconal view.
g,r. Right humerus (SDSNH 42783), San Diego Formation: *g*, palmar view; *r*, anconal view.
h,k,s. Right humerus (SDSNH 42782), San Diego Formation: *h*, palmar view; *k*, distal view; *s*, anconal view.
n,o,p. Humerus, anconal view, Lee Creek Mine: *n*, USNM 457379, right; *o*, USNM 457380, left; *p*, USNM 457381, left.
u. Right ulna, internal view (USNM 366233), Lee Creek Mine.
w,y. Left carpometacarpus (USNM 457383), Lee Creek Mine: *w*, internal view; *y*, external view.
aa,dd,gg. Right tarsometatarsus (USNM 336132), Lee Creek Mine: *aa*, anterior view; *dd*, posterior view; *gg*, internal view.

Histrionicus histrionicus (USNM 612970)

- b,d.* Right coracoid: *b*, ventral view; *d*, dorsal view.
i,l,t. Right humerus: *i*, palmar view; *l*, distal view; *t*, anconal view.
v. Right ulna, internal view.
x,z. Left carpometacarpus: *x*, internal view; *z*, external view.
cc,ff,ii. Right tarsometatarsus: *cc*, anterior view; *ff*, posterior view; *ii*, internal view.

Histrionicus shotwelli, new combination

- bb,ee,hh.* Distal portion of left tarsometatarsus from the late Miocene of Oregon (holotype of *Ocyplonessa shotwelli*, Condon Museum of Geology, University of Oregon F-10485 and F-11291): *bb*, anterior view; *ee*, posterior view; *hh*, internal view.



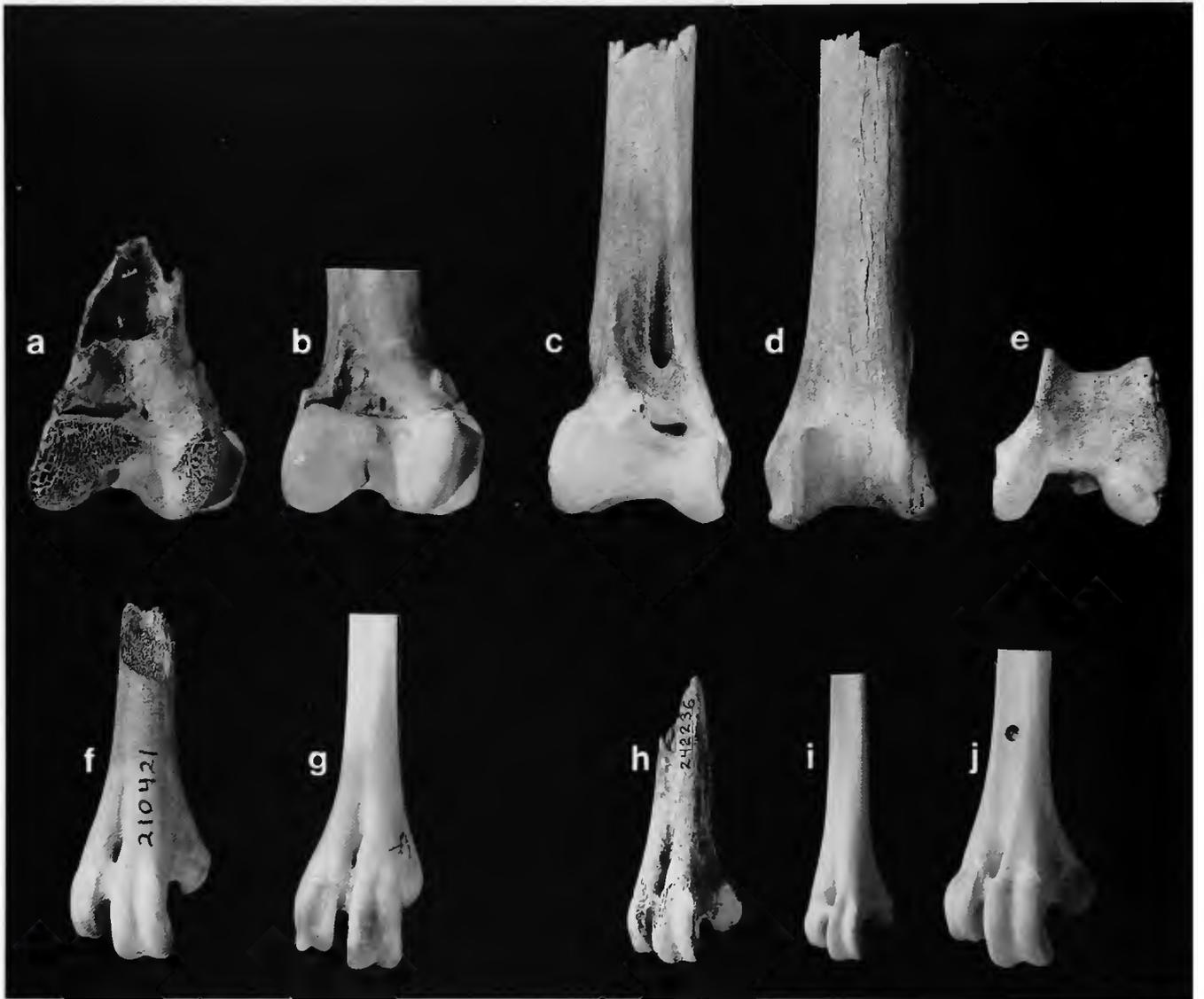


PLATE 28.—Hindlimb elements of fossil cranes (Gruidae) from Lee Creek Mine compared with modern species. *a, b*, *Grus*, distal end of right femur, posterior view: *a*, *G. aff. antigone* (USNM 368539); *b*, male modern Whooping Crane, *G. americana* (USNM 491260). *c–e*, *G. aff. antigone* (USNM 368540), distal end of right tibiotarsus: *c*, anterior view; *d*, posterior view; *e*, distal view. *f, g*, *Grus*, distal end of right tarsometatarsus, anterior view: *f*, *G. aff. americana* (USNM 210421); *g*, male modern Sandhill Crane, *G. canadensis tabida* (USNM 431924). *h–j*, *Baelearica*, distal end of right tarsometatarsus, anterior view: *h*, *Baelearica?* sp. (USNM 242236); *i*, modern Limpkin, *Aramus guarauna* (USNM 501021); *j*, female modern Crowned Crane, *B. pavonina* (USNM 431695). (All figures $\times 1$.)



PLATE 29.—Humeri of fossil oystercatchers (Haematopodidae) and tarsometatarsi of rails (Rallidae) from Lee Creek Mine compared with modern counterparts. *a-d*, *Haematopus*, right humerus, palmar view: *a*, *H. aff. ostralegus* (USNM 460835); *b*, modern Eurasian Oystercatcher, *H. ostralegus* (USNM 554123); *c*, *H. aff. palliatus* (USNM 215799); *d*, modern American Oystercatcher, *H. palliatus* (USNM 554769). *e-g*, Rallidae, proximal end of right tarsometatarsus: *e*, Rallidae, genus and species indeterminate (USNM 215524), posterior view; *f*, same, anterior view; *g*, modern King Rail, *Rallus elegans* (USNM number not recorded). (All figures $\times 1$.)



PLATE 30.—Pectoral elements of fossil plovers and sandpipers (Charadriidae and Scolopacidae) from Lee Creek Mine compared with modern counterparts. *a-d*, *Pluvialis*, left humerus: *a*, *P. aff. squatarola* (USNM 430887), palmar view; *c*, same, anconal view; *b*, modern Black-bellied Plover, *P. squatarola* (USNM 500229), palmar view; *d*, same, anconal view. *e, f*, *Numenius*: right coracoid, ventral view: *e*, *N. aff. borealis* (USNM 250709); *f*, modern Eskimo Curlew, *N. borealis* (USNM 12595). *g-l*, *Capella*, proximal portion of right humerus: *g*, *C. aff. media* (USNM 430888), palmar view; *j*, same, anconal view; *h*, *C. aff. media* (USNM 283266), palmar view, Quaternary of the Bahamas; *k*, same, anconal view; *i*, modern Paramo Snipe, *C. nobilis* (USNM 346753); *l*, same, anconal view. *m-p*, *Tringa*, right humerus: *m*, *T. magn. ochropus* (USNM 241412), palmar view; *o*, same, anconal view; *n*, modern Green Sandpiper, *T. ochropus* (USNM 322503), palmar view; *p*, same, anconal view. *q-t*, *Calidris*, left humerus: *q*, *C. aff. melanotos* (USNM 460836), palmar view; *s*, same, anconal view; *r*, modern Pectoral Sandpiper, *C. melanotos* (USNM 610840), palmar view; *t*, same, anconal view. (Images in *c, d, j-l, o-p, s*, and *t* have been photographically reversed; all figures $\times 1$.)

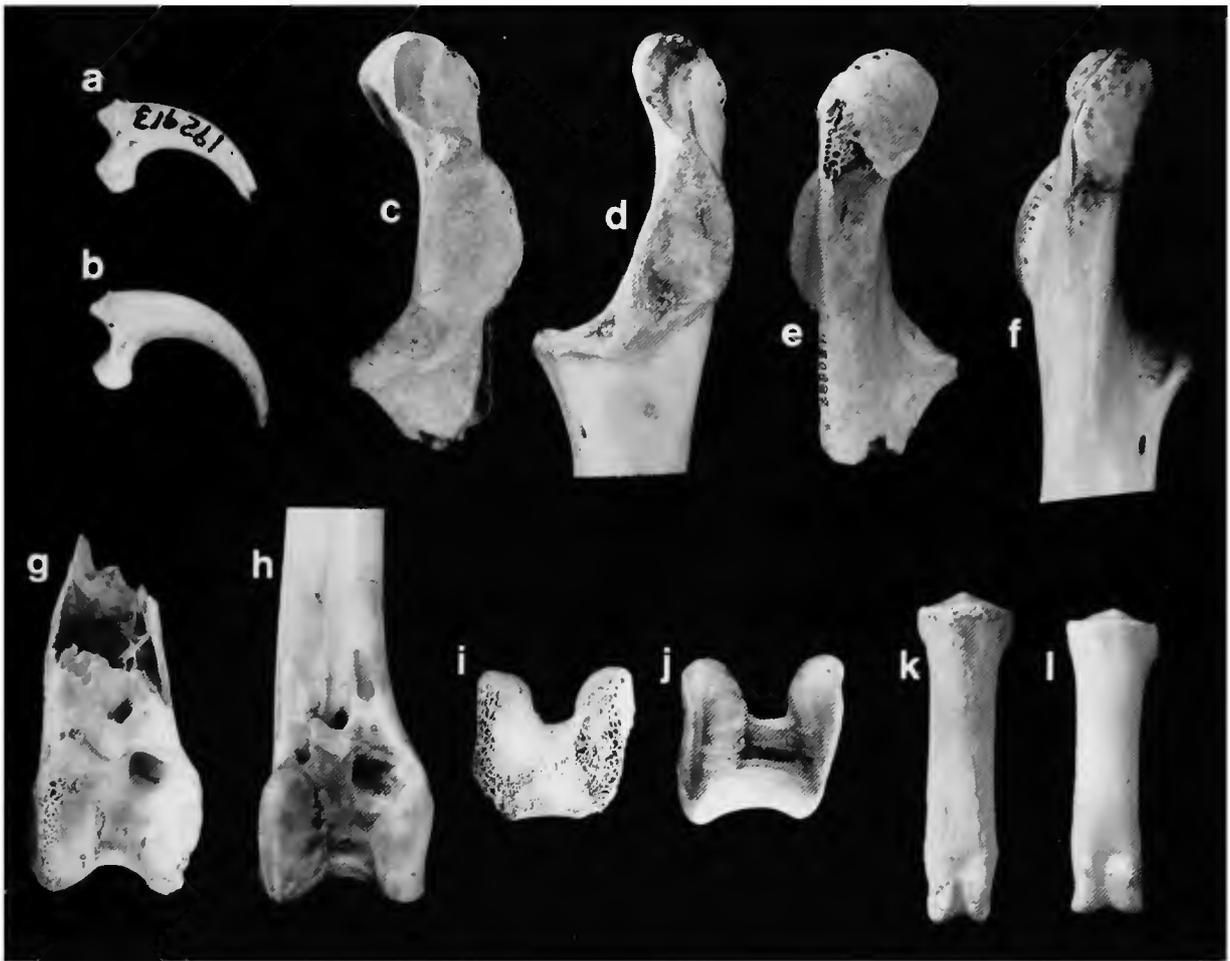


PLATE 31.—Pectoral and hindlimb elements of fossil ospreys and New World vultures (Pandionidae and Vulturidae) from Lee Creek Mine compared with modern counterparts. *a, b*, *Pandion*, ungual phalanx, lateral view: *a*, *P. sp.* (USNM 192913); *b*, modern Osprey, *P. haliaetus* (USNM 612546). *c–f*, Vulturidae, scapular end of right coracoid: *c*, Vulturidae, genus and species indeterminate (USNM 430882), dorsal view; *e*, same, ventral view; *d*, modern California Condor, *Gymnogyps californianus* (USNM 3369), dorsal view; *f*, same, ventral view. *g–j*, Vulturidae, distal end of right tibiotarsus: *g*, Vulturidae, genus and species indeterminate (USNM 430883), anterior view; *i*, same, distal view; *h*, modern *G. californianus* (USNM 3369), anterior view; *j*, same, distal view. *k, l*, Vulturidae, pedal phalanx 1, digit III, dorsal view: *k*, Vulturidae, genus and species indeterminate (USNM 464324); *l*, modern *G. californianus* (USNM 13823). (All figures $\times 1$.)

PLATE 32

Coracoid and tarsometatarsi of fossil eagles and hawks (Accipitridae) compared with modern counterparts. All figures $\times 1$.

Accipitridae, genus and species indeterminate

- a, b.* Sternal portion of right coracoid, ventral view: *a*, large "eagle," Accipitridae, genus and species indeterminate 2, Lee Creek Mine (USNM 446504); *b*, modern Golden Eagle, *Aquila chrysaetos* (USNM number not recorded).
- i-l, z, aa.* Distal end of right tarsometatarsus: *i*, Accipitridae, genus and species indeterminate 1 (USNM 464316), anterior view; *k*, same, posterior view; *z*, same, distal view; *j*, *Neogyps errans* (LACM D9456), Pleistocene of Rancho La Brea, California, anterior view; *l*, same, posterior view; *aa*, same, distal view.

Neophrontops?

- c-h, w-y.* Distal end of right tarsometatarsus: *c*, *Neophrontops?* sp. (USNM 464318), Lee Creek Mine, anterior view; *f*, same, posterior view; *w*, same, distal view; *d*, *Neophrontops?* sp. (USNM 464317), Lee Creek Mine, anterior view; *g*, same, posterior view; *x*, same, distal view; *e*, *Neophrontops americanus* (LACM D8439), Pleistocene of Rancho La Brea, California, anterior view; *h*, same, posterior view; *y*, same, distal view.

Buteo

- m-v.* Distal end of right tarsometatarsus: *m*, *B. magn. jamaicensis* (USNM 464321), Lee Creek Mine, anterior view; *r*, same, posterior view; *n*, modern Red-tailed Hawk, *B. jamaicensis* (USNM 17950), anterior view; *s*, same, posterior view; *o*, same (USNM 291369), anterior view; *t*, same (USNM 291369), posterior view; *p*, *Buteo?* sp. (USNM 464320), Lee Creek Mine, anterior view; *u*, same, posterior view; *q*, same (USNM 464319), Lee Creek Mine, anterior view; *v*, same (USNM 464319), posterior view.



PLATE 33

Wing and hindlimb elements of miscellaneous fossil land birds from Lee Creek Mine compared with modern counterparts. All figures $\times 1$ except $k, t = \times 2$.

Ortalis

a-c. Distal end of left tibiotarsus: *a*, *Ortalis?* sp. (USNM 430885), anterior view; *c*, same, distal view; *b*, modern Chestnut-winged Chachalaca, *O. gorrula* (USNM 430180), anterior view.

Meleagris

d-i. Left carpometacarpus: *d*, *M.* sp. (USNM 446505), external view; *g*, same, internal view; *e*, modern Wild Turkey, *M. gallopavo* (USNM 556335), external view; *h*, same, internal view; *f*, modern *M. gallopavo* (USNM 556307), external view; *i*, same, internal view.

Galliformes, family indeterminate

j, k. Distal end of left tibiotarsus (USNM 256228): *j*, anterior view; *k*, distal view.

Ectopistes

l-q. Left humerus: *l*, *Ectopistes* aff. *migratorius* (USNM 430960), palmar view; *o*, same, anconal view; *m*, modern Rock Dove, *Columba livia* (USNM 556281), palmar view; *p*, same, anconal view; *n*, modern Passenger Pigeon, *E. migratorius* (USNM 224322), palmar view; *q*, same, anconal view.

Corvus

r-t. Distal end of left tibiotarsus: *r*, *C.* aff. *ossifragus* (USNM 407797), anterior view; *t*, same, distal view; *s*, modern Fish Crow, *C. ossifragus* (USNM, number not recorded), anterior view.

