6. Actinopterygian Fish Remains from the Paleocene of South Carolina

Robert E. Weems
Mail Stop 926a, U.S. Geological Survey
Reston, VA 20192

Abstract

Remains of seven kinds of fishes of the subclass Actinopterygii were found at the St. Stephen hydroelectric turbine excavation site in Berkeley County, South Carolina. Only forms with exceptionally durable skeletal elements are represented. The most common finds were isolated crushing teeth and/or tooth batteries representing the presence of *Pycnodus* sp., *Albula oweni, Egertonia isodonta, Phyllodus toliapicus,* and *Progymnodon hilgendorfi.* Gars (Lepisosteidae) are documented by scales, and boxfishes are represented by dermal armor. Except for the gars, which mostly live in fresh water, all of these fish normally inhabit shallow, coastal marine waters.

Introduction

In contrast to the abundant shark teeth recovered at the Kingstree and St. Stephen localities (Purdy, 1998, this volume), teleost fish remains from Paleocene sediments in South Carolina are relatively rare. Only seven taxa of actinopterygians have been positively recognized. Limited *in situ* collections, taken directly

TABLE 1. Stratigraphic occurrence of actinopterygian fishes recognized from the St. Stephen site. Specimens of "uncertain origin" are from either the Lower Bridge or the Chicora Member of the Williamsburg Formation.

	WILLIAMSBURG FORMATION		
Taxon	Lower Bridge Member (NP 5)	Chicora Member (NP 8/9)	Uncertain origin (NP 5/9)
Lepisosteus sp.		X	
Pycnodus sp.			X
Albula oweni (Owen)			X
Egertonia isodonta Cocchi			X
Phyllodus toliapicus Agassiz	X	X	
Ostraciidae, gen. et sp. indet.			X
Progymnodon hilgendorfi Dames			X

from the St. Stephen hydroelectric pit wall, show that *Phyllodus* oral plates occur in both the Lower Bridge and the Chicora members of the Williamsburg Formations, while *Lepisosteus* scales and vertebrae occur in the Chicora Member of the Williamsburg Formation. In contrast, specimens of *Pycnodus, Egertonia, Albula,* Ostraciidae gen. et sp. indet., and *Progymnodon* all came from spoil heaps. Their precise horizon of origin within the South Carolina Paleocene stratigraphic column remains unknown.

Systematic Paleontology

Class Osteichthyes
Subclass Actinopterygii
Order Lepisosteiformes
Family Lepisosteidae
Lepisosteus sp.

Collectors and material: Dawn Hepler (ChM PV4249–4251) and Doris Holt (PV3305–3325, PV3419–3420, PV4145–4146).

Numerous gar scales (PV3305–3325, PV3419–3420, PV4249–4251) and two opisthocoelous gar vertebrae (PV4145–4146) (Figure 1) were found in the spoil heaps at the St. Stephen site. Additionally, a few gar scales were found *in situ* in the shelly sands of the Chicora Member of the Williamsburg Formation, associated with wood fragments and oysters that were presumably tolerant of brackish water (Weems and Bybell, 1998, this volume). Because modern gars mostly inhabit fresh water, and this horizon appears to have more freshwater influence than any other in the section exposed in the hydroelectric pit, it seems probable that all of the gar remains came from the Williamsburg. However, because gars range back to the Upper Cretaceous and can tolerate brackish or even marine conditions (Berra, 1981), it remains possible that some of the gar material came from the upper shelly sands of the Rhems Formation.

Tertiary and recent gars were split into two genera (*Atractosteus* and *Lepisosteus*) by Wiley (1976), but Grande (1980) more recently has considered *Atractosteus* to be inadequately defined and has recognized only *Lepisosteus.* The latter view is accepted here. Late Paleocene and early to middle Eocene gar remains from England and France, indistinguishable from those described here, have been assigned consistently to the taxon *Lepisosteus fimbriatus* (Wood, 1846), usually under the junior synonym *Lepisosteus suessionensis* (Leriche, 1900, 1902; White, 1931; Wiley, 1976; Kemp et al., 1990). Case (1986) also has applied the latter name to scales and teeth from lower Eocene horizons in Mississippi. Yet three species of *Lepisosteus* (*L. atrox, L. cuneatus,* and *L. simplex*) are known from the lower Eocene Green River Formation of Utah (Grande, 1980), and there is no compelling reason to believe that fragmentary remains of Atlantic or Gulf Coast gars would pertain to a European species any more than they would pertain to one or more of the described American species. Alternatively, the southeastern American gar material could pertain to a new taxon that cannot be diagnosed as yet. For all of these reasons, a specific assignment at our present state of knowledge is inadvisable.

Gars have been reported from the Late Quaternary of South Carolina (Leidy, 1860; Hay, 1902, 1923, 1929), but this is the first record of these fishes from the Tertiary beds of the state. Outside of South Carolina, lepisosteids have been reported from the Paleocene or lower Eocene of New Mexico (Lucas, 1984), Utah (Wiley, 1976; Grande, 1980), Montana (Estes, 1976), North and South Dakota (Cvancara and Hoganson, 1993), Mississippi (Case, 1986), England (White, 1931; Casier, 1966; Ward, 1978), France (Casier, 1966), Belgium (Casier, 1943), and central India (Gayet et al., 1984). *Lepisosteus* scales, not yet described in the literature, also occur in the upper Paleocene Aquia Formation of Maryland and Virginia and the lower Eocene Nanjemoy Formation of Virginia.

Order Pycnodontiformes
Family Pycnodontidae
Pycnodus sp.

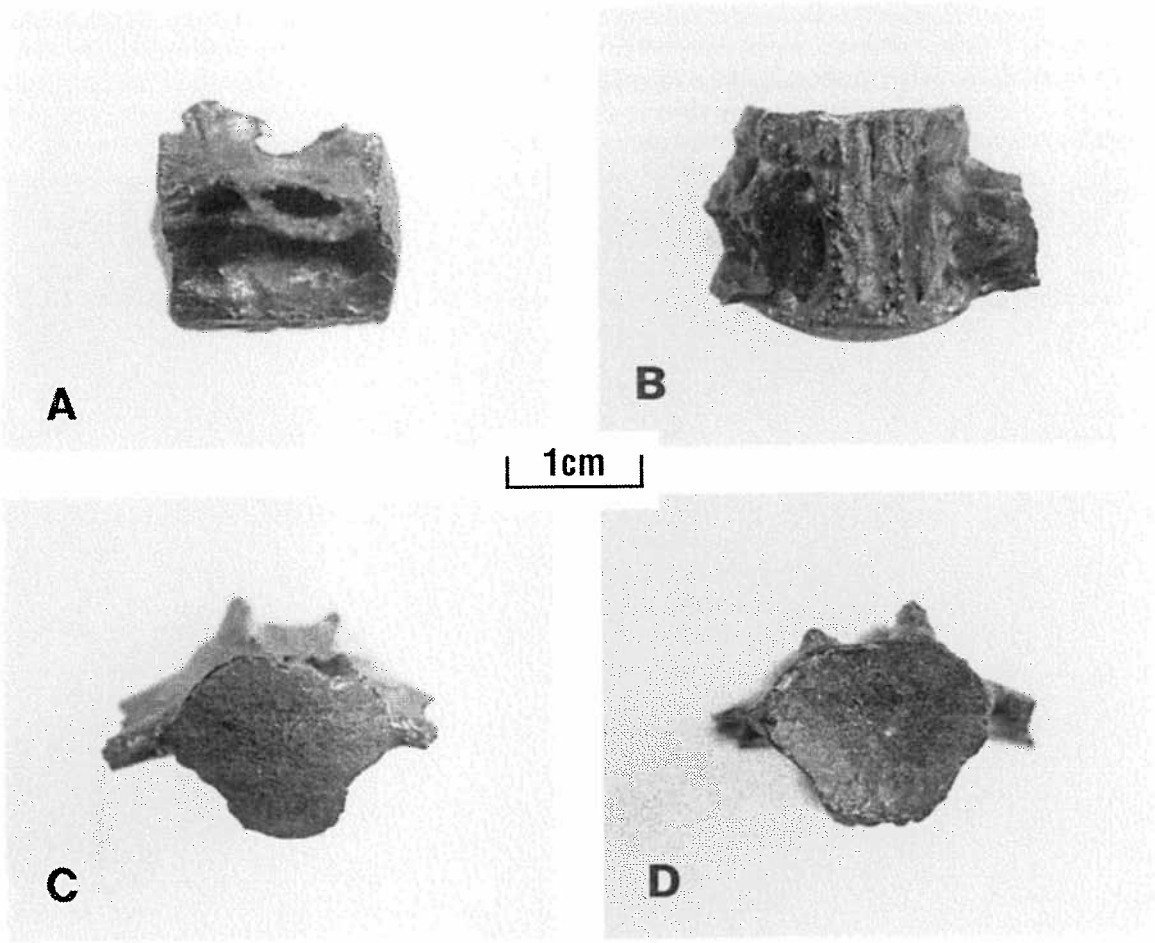
Collector and material: Vance McCollum (ChM PV4157).

A single crushing tooth (Figure 2), ovoid in oral view and containing a broadly convex pulp cavity in aboral view, is referred to this taxon. The shape of the tooth, slightly wider than long, is characteristic of the external marginal teeth of this genus. An isolated lateral tooth, lacking distinctive surface ornamentation, is insufficient for a specific identification. This genus is widespread throughout the Atlantic basin and Tethys Seaway, being known from Mississippi, England, Belgium, France, Italy, Tunisia, Algeria, Arabia, Mali, Togo, Nigeria, and Angola (Priem, 1902, 1903; Stromer, 1910; Savornin, 1915; White, 1935; Darteville and Casier, 1943–49; Arambourg, 1952; Casier, 1966; Madden, 1983; Longbottom, 1984; Case, 1986). *Pycnodus* also is known from the lower Eocene of northwestern India (Kumar and Loyal, 1987) and the earliest Paleocene of central India (Gayet et al., 1984). Undescribed specimens also have been found in the Aquia Formation of Maryland and the Nanjemoy Formation of Virginia.

Order Elopiformes
Family Albulidae
Albula oweni (Owen 1845)

Collector and material: Doris Holt (ChM PV5396.)

A single worn mollusk-crushing tooth (Figure 2) is somewhat smaller but otherwise identical in morphology to those assigned to this taxon and illustrated in Arambourg (1952, pl. 37) and Casier (1966, pl. 13). Although Casier (1966) illustrates associated teeth, they are not tightly bound together and are somewhat scattered within the sediment in which they are preserved. More typically, the teeth of this fish become entirely separated and scattered. The scarcity of this taxon in the St. Stephen collection is probably more a reflection of the small size of its teeth rather than its true abundance at that site. *Albula oweni* has been reported from England, Belgium, Tunisia, Morocco, and Mississippi (Casier, 1966; Case, 1986), and an undescribed Eocene species of *Albula* has been



figured from Nigeria (White, 1935; Darteville and Casier, 1943–49). Undescribed specimens also have been found in the lower Eocene Nanjemoy Formation of Virginia.

Family Phyllodontidae
Egertonia isodonta Cocchi 1866

Collector and material: Doris Holt (ChM PV4168–4169); Vance McCollum (ChM PV4156).

Two fragmentary pharyngeal plates and an isolated tooth referable to *Egertonia isodonta* were found in the spoil heaps of the St. Stephen site (Figure 3). Both contain flattened, rounded pavement teeth, of variable size but similar shape, that are densely clustered and fused together. In lateral view, the replacement teeth beneath the oral surface are stacked vertically. Aborally, the base of

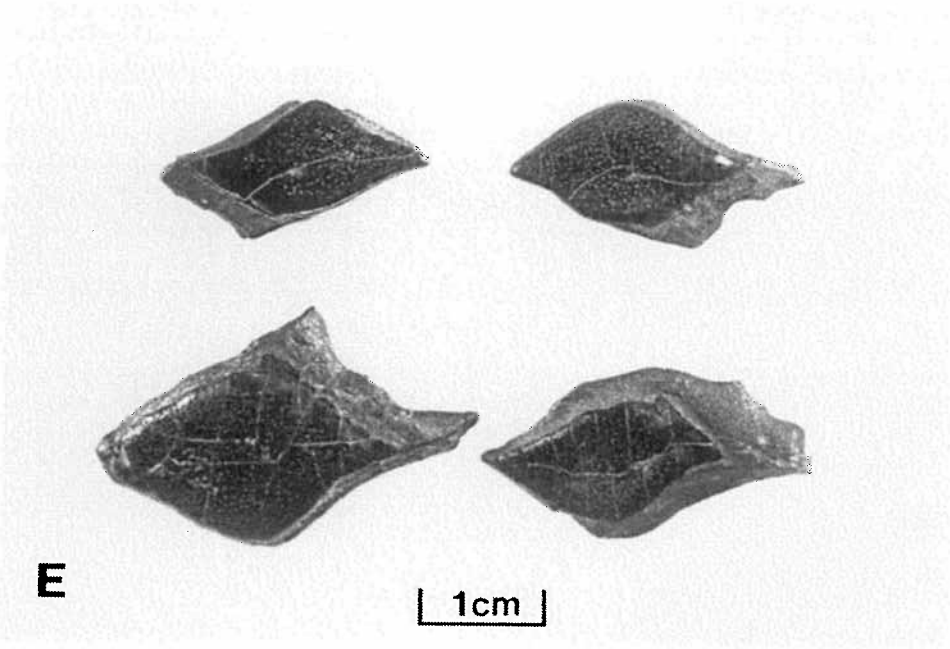


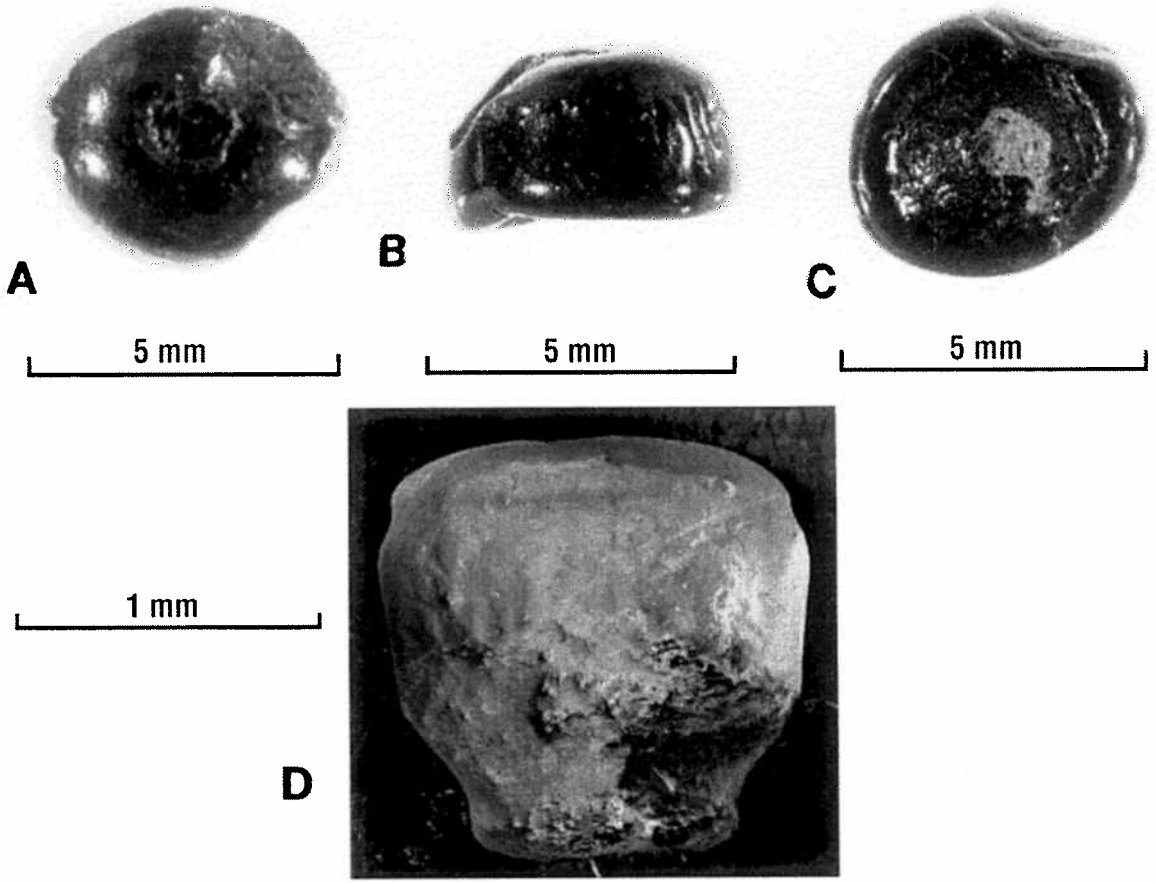
Figure 1. *Lepisosteus* sp.; vertebra (ChM PV4145) in (A) lateral, (B) dorsal, (C) anterior, and (D) posterior views; scales (E), ChM PV4249, PV3312, PV3419, PV 3420.

the teeth are broadly concave, with no hint of a discrete pulp cavity as is found in *Paralbula* (Blake, 1940). Collectively, these characteristics are diagnostic of *Egertonia* (Estes, 1969). The phyllodontid fishes are extinct, and thus their diets are unknown; but their tough batteries of pharyngeal teeth probably were used for mollusk-crushing, as in the living drumfish *Pogonias*. *Egertonia* has been reported from England and Belgium (Casier, 1966), North Dakota (Cvancara and Hoganson, 1993), and Mississippi (Case, 1986).

Phyllodus toliapicus Agassiz 1844

Collector and material: Doris Holt (ChM PV3400–3403, PV3415, PV4120–4121, PV4149).

Eight specimens were found that represent fused tooth batteries in which the teeth are of variable size and shape. The best preserved of these contain large, laterally elongated teeth in the center of the battery and much smaller rounded to elongated teeth along the lateral margins (Figure 4). Replacement teeth are stacked vertically in lateral view and lack a discrete pulp cavity in aboral view. Such tooth batteries are referable to *Phyllodus* (Estes, 1969). Although a number of nominal species of *Phyllodus* have been described over the years, current practice is to include them all in a single, variable species (Estes, 1969). That practice is followed here. *Phyllodus* was recovered *in situ* from both the Lower Bridge and Chicora Members of the Williamsburg Formations, so it appears to


A
5 mm
B
5 mm
C
5 mm
1 mm
D

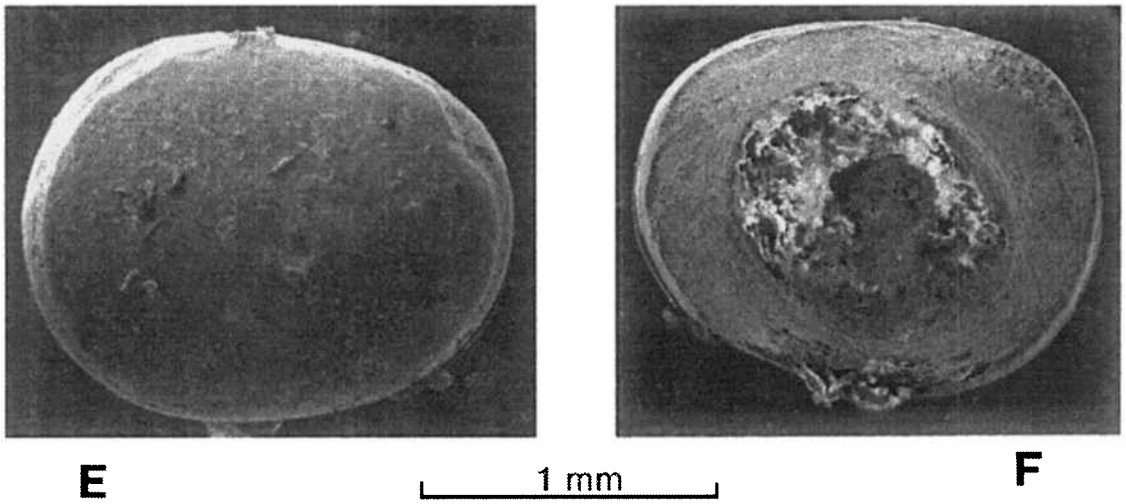


Figure 2. *Pycnodus* sp. (ChM PV4157), marginal tooth in (A) oral, (B) lateral, and (C) aboral view. *Albula oweni* (ChM PV5396), tooth in (D) lateral, (E) oral, and (F) aboral view.

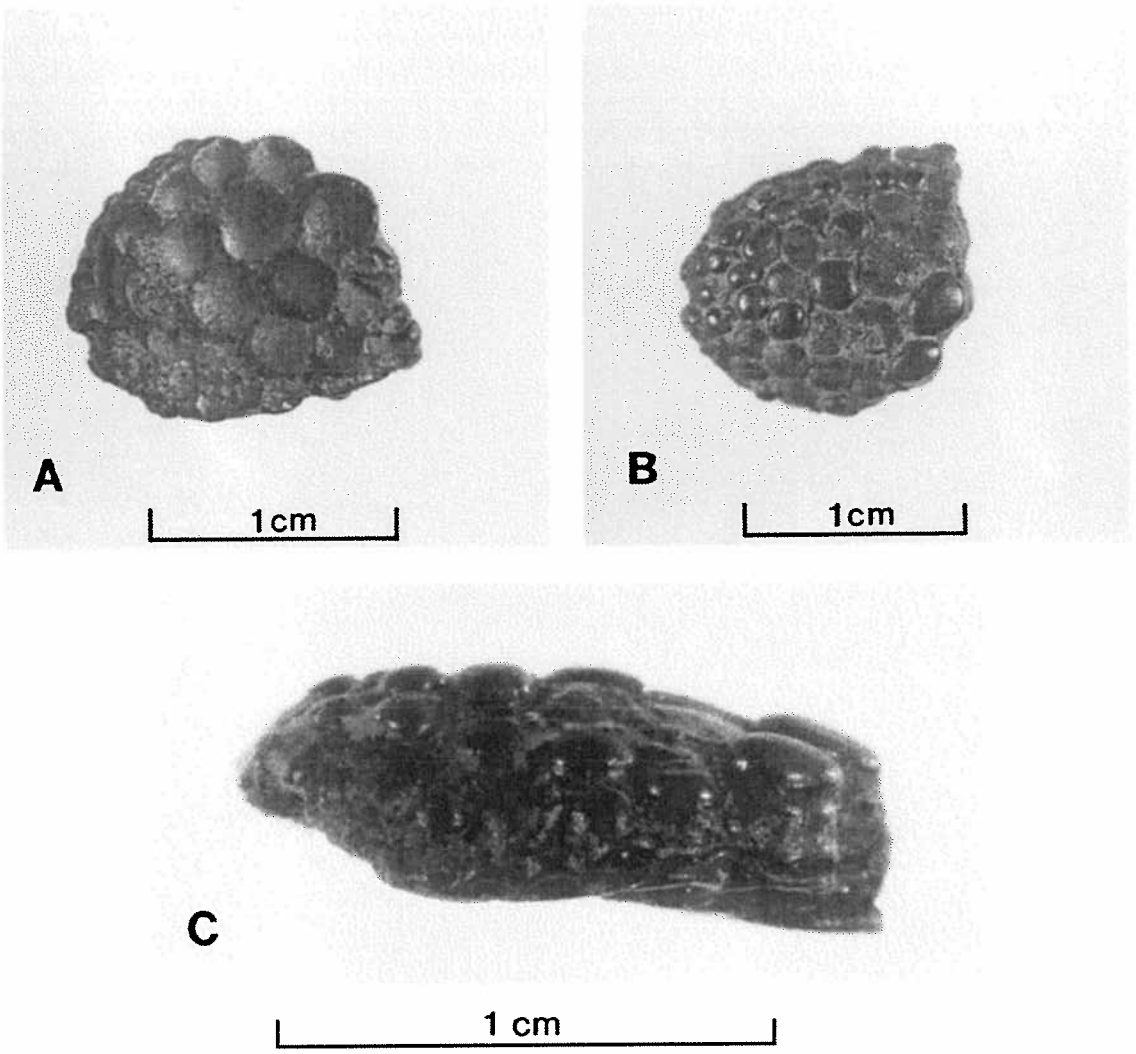


Figure 3. *Egertonia isodonta* Cocchi; fragmentary pharyngeal plate (ChM PV4169) in (A) aboral, (B) oral, and (C) lateral views.

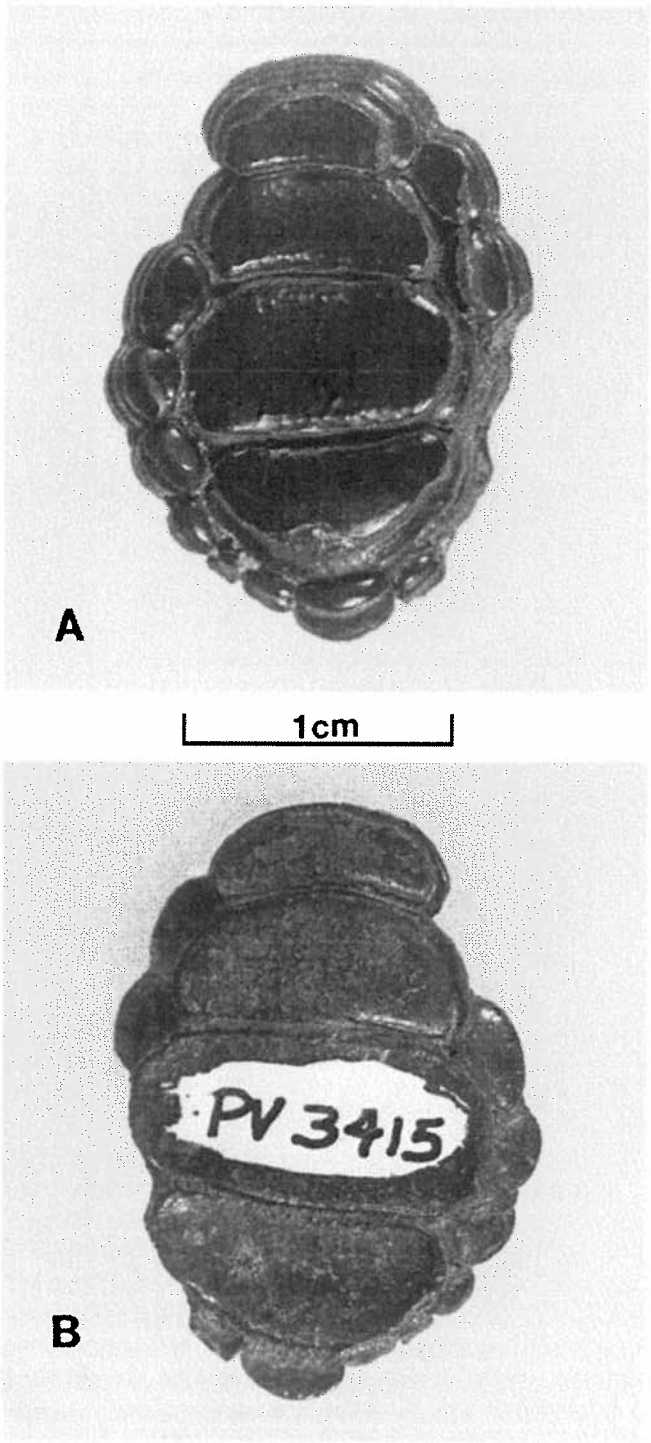


Figure 4. *Phyllodus toliapicus* Agassiz, dental plate (ChM PV 3415) in (A) oral view and (B) aboral view.

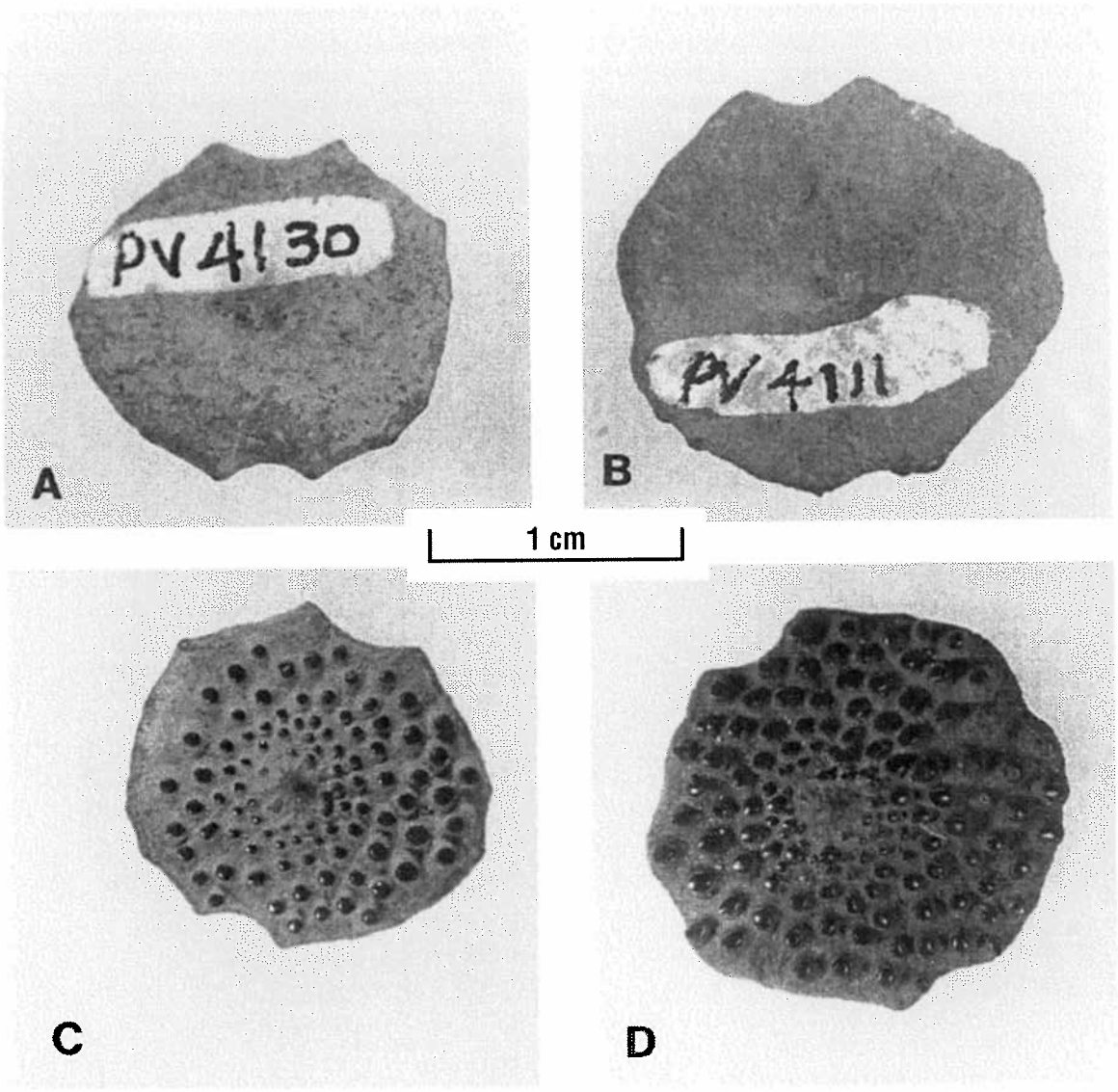


Figure 5. Ostraciidae, gen. et sp. indet., dermal plates; (A) inner surface and (C) outer surface of ChM PV4130; (B) inner surface and (D) outer surface of ChM PV4111.

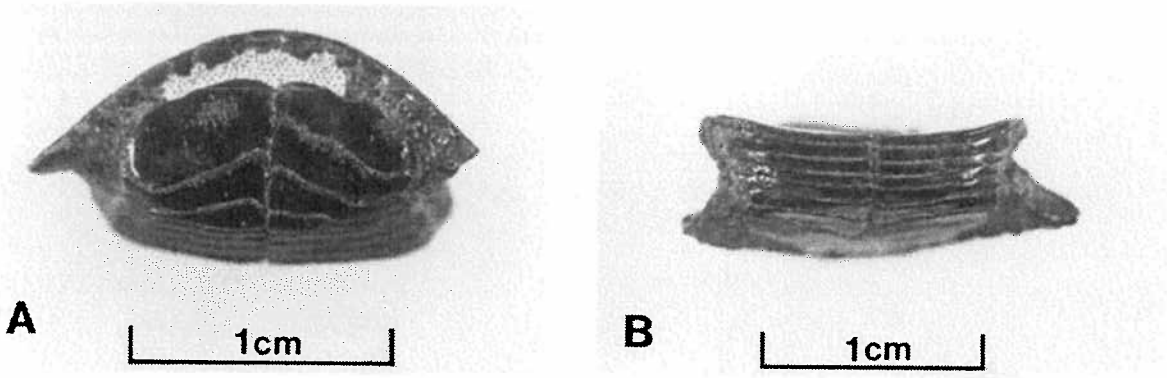


Figure 6. *Progymnodon hilgendorfi* Dames, tooth battery (ChM PV 3304) in (A) dorsal occlusal and (B) posterior view (ventral side up)

have been a common species in the coastal marine waters of South Carolina throughout the late early and late Paleocene. As with *Egertonia, Phyllodus* was probably a mollusk-crushing fish. Its presence in South Carolina was reported long ago (Wyman, 1850; Hay, 1902, 1929), but the St. Stephen specimens are the first South Carolina records with stratigraphic control. Elsewhere, *Phyllodus* has been reported from England, Belgium, France, Virginia, New Jersey, and Mississippi (Gildersleeve, 1933; Estes, 1969; Case 1986).

Order Tetraodontoformes
Family Ostraciidae
gen. et sp. indet.

Collectors and material: Dawn Hepler (ChM PV4230–4232); Doris Holt (PV3298–3303, PV3433, PV4127–4131, PV4147–4148), and Vance McCollum (PV4111–4112).

Ostraciid dermal bone plates were the most abundantly found remains of bony fishes at the St. Stephen site. Two typical specimens are shown in Figure 5. Two families of boxfish are known, the Aracanidae and the Ostraciidae (Tyler, 1980). Well preserved fossil material is known only as far back as the early Eocene (Tyler, 1975), but at that time these two families already were quite distinct from each other. On the basis of dermal armor plates, the two families can be readily distinguished by the fact that, on each bony plate, the Aracanidae have a very large central hump or spine from which radiates six "spokes" composed of rows of moderately large papillae. Between these rows of large papillae are fields of much smaller papillae. In contrast, the Ostraciidae lack spines in the centers of their bony plates and the papillate patterns are not organized into discrete spokes as they are on the plates of the aracanids. The plates described here are clearly ostraciid in pattern. Within this family, however, there is considerable diversity of pattern among genera, from area to area of the body

of single individuals, and with age (Winterbottom and Tyler, 1983; Tyler and Gregorova, 1991). In the absence of any well preserved articulated specimens from the Paleocene or Eocene of the Atlantic Coastal Plain, it is impossible to assign these isolated plates to any particular genus or species in that family.

The materials discussed here represent the first fossil record of this family from South Carolina. Their occurrence might have been expected, however, because Leriche (1942) described very similar (and equally undiagnostic) bony plates from the upper Paleocene Aquia Formation of Virginia under the name *Ostracion meretrix*. Casier (1966) suggested that this taxon might represent dermal plates from a "hypolophid" (dasyatid) shark rather than from an ostraciid. However, Herman (1972) considered fossils assigned to *Ostracion* to be teleost in origin, and Cappetta (1987) does not include this species among remains he assigns to selachians or figures anything remotely similar to it. Therefore, *O. meretrix* generally still is accepted as a plectognath fish. Outside of South Carolina and Virginia, cf. *O. meretrix* has been reported from the mid-Danian of Morocco (Herman, 1972), and *Ostracion* sp. has been reported from the basal Paleocene of central India (Gayet and others, 1984). Also, Tyler and Gregorova (1991) have noted ostraciid plates from the lower Eocene London Clay, and Tyler (1975) has described the ostraciid *Eolactoria* from the lower Eocene Monte Bolca beds of Italy.

Family Diodontidae
Progymnodon hilgendorfi Dames 1883

Collectors and material: Doris Holt (ChM PV3304) and Vance McCollum (PV3852).

Two isolated tooth batteries are readily assigned to the Diodontidae. The better preserved of these (PV3304, Figure 6) has a trituration plate with fused teeth stacked with only a slight tilt. Because the tilt of the teeth is slight, all or part of only three teeth in the trituration plate were undergoing wear on the right side, and all or part of only four teeth were undergoing wear on the left side. Four pairs of teeth lie unerupted beneath those that were undergoing wear. The groove separating the teeth of the trituration plate from the marginal jaw teeth is narrow, and the marginal jaw teeth (eight preserved on the left side and seven on the right) are relatively large and stout. This suite of characters is typical of *Progymnodon*. The width/length ratio of the tooth battery (approximately 2:1) is quite comparable to the proportions of *Progymnodon hilgendorfi* (Dames, 1883) and contrasts with the approximately 1:1 width/length ratio of *Progymnodon batalleri* (Casier, 1952). The South Carolina specimen is strikingly similar, both in size and appearance, to the type of *P. hilgendorfi*. Its rounded anterior border, with only slightly raised jaw margin teeth, suggests that it is a lower tooth battery (Zittel, 1923; Tyler 1980).

It is surprising to find any diodontid at a horizon in the Tertiary as low as the Paleocene. No representative of this family is known from the Paleocene or Eocene parts of the Pamunkey Group farther north in Virginia and Maryland. The type of *P. hilgendorfi* is from the middle Eocene of Egypt (Priem, 1914), and

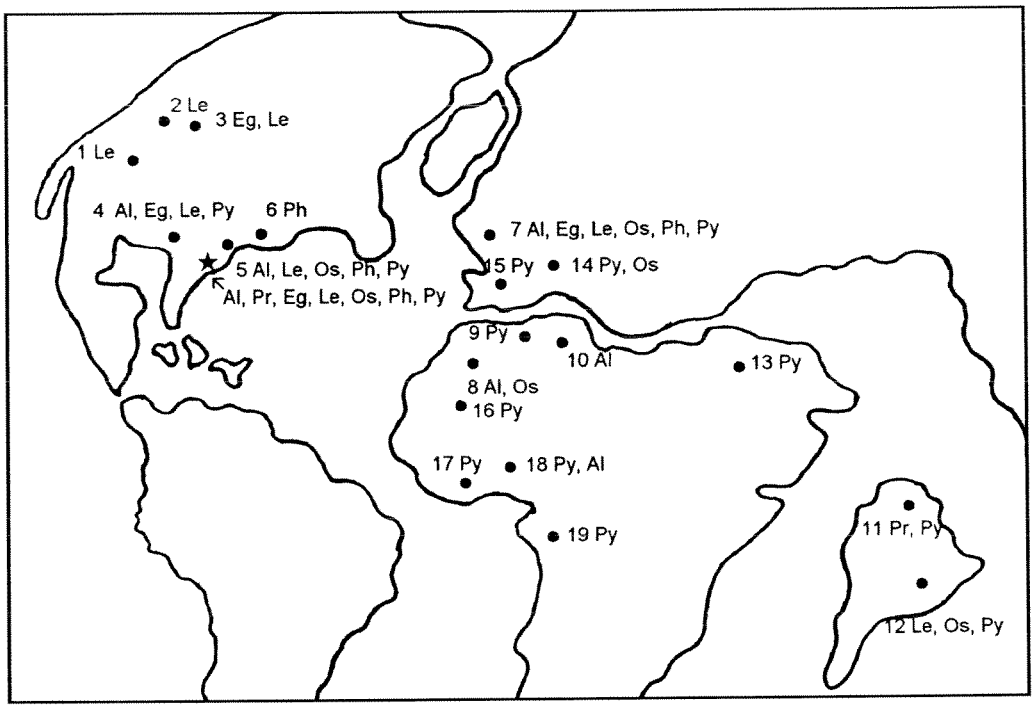


Figure 7. Reported occurrences of Paleocene and early Eocene teleosts similar to those found in South Carolina. South Carolina deposits are noted by star (★), solid circles mark other Paleocene/early Eocene localities. Map adapted from Smith et al. (1981). Al = *Albula*, Eg = *Egertonia*, Le = *Lepisosteus*, Os = Ostraciidae, Ph = *Phyllodus*, Pr = *Progymnodon*, Py = *Pycnodus*.
1. Utah (Wiley, 1976) 2. Montana (Estes, 1976) 3. North and South Dakota (Cvancara and Hoganson, 1993) 4. Mississippi (Case, 1986) 5. Maryland/Virginia (Leriche, 1942; Weems, 1984; Weems, this paper) 6. New Jersey (Leriche, 1942; Estes, 1969) 7. England/France/Belgium (Casier, 1966; Ward, 1978; Tyler and Gregorova, 1991) 8. Morocco (Casier, 1966; Herman, 1972) 9. Algeria (Savornin, 1915; Casier, 1966) 10. Tunisia (Priem, 1903; Casier, 1966) 11. Northwestern India (Kumar and Loyal, 1987) 12. Central India (Gayet et al., 1984) 13. Arabia (Madden, 1983) 14. Italy (Longbottom, 1984; Tyler, 1975) 15. Southern France (Priem, 1902) 16. Mali (Longbottom, 1984) 17. Togo (Stromer, 1910) 18. Nigeria (White, 1935) 19. Angola (Darteville and Casier, 1943–49)

the only reported lower Eocene representative of this family (assigned to *Diodon* but more probably *Progymnodon*) is from India (Kumar and Loyal, 1987). Perhaps the lack of material farther north is the result of sporadic collecting, but it is also possible that the Diodontidae were climatically restricted to near-tropical and tropical latitudes during the Early Tertiary.

Although these specimens are the first evidence of the Diodontidae from the Paleocene, they are not the first record of the family from the Cenozoic of South Carolina. Tuomey (1848) long ago reported a diodontid from the Miocene or Pliocene at Brocktons Ford on the Salkehatchie River. Soon after, Leidy (1855, 1877) described *Chilomycterus vetus* from the "Ashley River phosphate beds". Because the known age of fossils mixed into this phosphate bed range from late Oligocene to late Pleistocene, the age of *C. vetus* is very uncertain.

Discussion

The limited actinopterygian fish fauna that has been recovered from the Paleocene strata of South Carolina includes taxa that occur widely in the fossil record throughout the North Atlantic basin and along the Tethys Seaway (Figure 7). In contrast, faunal similarities with central and southern Africa are much weaker, being limited to *Pycnodus* and an undescribed species of *Albula*. No genera from South Carolina have been reported from the Early Tertiary of the Pacific basin. It is tempting to conclude that this distribution represents a discrete North Atlantic-Tethys biogeographic province that existed in the early Tertiary, and this interpretation could be correct. However, it must be kept in mind that the early Tertiary marine fishes of the South Atlantic and the Indo-Pacific region remain poorly sampled. Therefore, this apparent provincialism could prove to represent only an artifact of our current state of knowledge of early Tertiary marine fish faunas. In either case, it is apparent that there was no marked provincialism within the area encompassing the Northern Atlantic basin and the adjacent Tethys Seaway, and that a variety of marine fishes dispersed readily throughout this region.

All of the actinopterygian fishes from the St. Stephen site, except for gars, today normally inhabit marine to marginal marine waters. Therefore, remains of these fishes probably were entombed in marginal marine to shallow marine environments of deposition. Sporadic influxes of fresh water, possibly due to flooding of a nearby river, easily could have carried carcasses of gars into these environments. Alternatively, the Paleocene gars represented in this fauna may have been more tolerant of brackish to marine water than modern species and may have ventured into coastal marine waters on a regular basis. The absence of other freshwater fish remains from this site tends to support the second hypothesis.

All of the preserved fragments of actinopterygian fish are pieces of the hardest and most durable parts of their respective skeletons. This implies that local scavengers and/or current abrasion selectively destroyed the less durable skeletal remains. It is likely that many other actinopterygians were present during the Paleocene in South Carolina, but their lack of exceptionally durable skeletal elements probably precluded their representation in this particular sample.

Acknowledgments

The author wishes to thank Dawn Hepler, Doris Holt, and Vance McCollum for the extended amount of time and effort they each spent searching the spoil piles at the Santee Rediversion Canal hydroelectric pit site for the fish remains described herein. Thanks also go to Lance Grande, Albert Sanders, and others for critically reading the manuscript of this paper and making suggestions for improvements.

References

Arambourg, C. 1952. Les Vertébrés fossiles des gisements de Phosphate (Maroc-Algerie-Tunisie). *Notes et Mémoires du Service des Mines et de la Carte Géologique du Maroc,* 92:1–372.

Berra, T. M. 1981. *An atlas of distribution of the freshwater fish families of the world.* University of Nebraska Press, Lincoln. 197 pp.

Blake, S. F. 1940. *Paralbula,* a new fossil fish based on dental plates from the Eocene and Miocene of Maryland. *Journal of the Washington Academy of Science,* 30:205–209.

Cappetta, H. 1987. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii. *Handbook of Paleoichthyology,* vol. 3B. Gustav Fischer Verlag, New York. 193 pp.

Case, G. R. 1986. The bony fishes (teleosts) of the Tuscahoma and Bashi formations, early Eocene, Meridian, Lauderdale County, Mississippi. *Mississippi Geology,* 6(4):6–8.

Casier, E. 1943. Contributions à l'étude des poissons fossiles de la Belgique; II, Restes du genre *Lepidosteus* du landénien continental de la Hesbaye. *Bulletin de l'Institut Royal Sciences Naturelles de Belgique,* 19(1):1–12.

——— 1952. Deux Diodontides Éocènes nouveaux: *Progymnodon batalleri* nov. sp., du Bartonien de Catalogne, et *Eodiodon bauzai* nov. gen., nov. sp., du Bartonien de Belgique. *Bulletin de l'Institit royal Sciences naturelles de Belgique,* 28(4):1–14.

——— 1966. *Faune ichthyologique du London Clay.* British Museum (Natural History), London. 496 pp.

Cvancara, A. M., and J. W. Hoganson. 1993. Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakota. *Journal of Vertebrate Paleontology,* 13(1):1–23.

Dames, W. Von. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel des Birket-el-Qurun im Fajum (Aegypten). *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin,* 6:1–25.

Darteville, E., and E. Casier. 1943–49. Les poissons fossiles du Bas-Congo et des regions voisines. *Annales de Muséum du Congo Belge, Tervuren,* (A, ser. 3), 2(1):1–200 and 2(2):201–256.

Estes, R. 1969. Studies on fossil phyllodont fishes: Interrelationships and evolution in the Phyllodontidae (Albuloidei). *Copeia,* 1969(2):317–331.

——— 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. *Journal of Paleontology,* 50(3):500–520.

Gayet, M., J.-C. Rage, and R. S. Rana. 1984. Nouvelle ichthyofaune et herpetofaune de Gitti Khada, le plus ancien gisement connu du Deccan (Cretace/Paléocène) à microvertébrés. Implications paléogéographiques. *Société Géologique de France,* N.S., 147: 55–65.

Gildersleeve, B. 1933. Pharyngeal plates of *Phyllodus* from the Virginia Eocene. *Journal of the Washington Academy of Science,* 23:380–389.

Grande, L. 1980. Paleontology of the Green River Formation, with a review of the fish fauna. *Wyoming Geological Survey Bulletin* 63:1–333.

HAY, O. P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *U.S. Geological Survey Bulletin* 79:1–868.

——— 1923. *The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian provinces east of longitude 95°*. Carnegie Institution of Washington Publication 322. 499 pp.

——— 1929. *Second bibliography and catalogue of the fossil vertebrata of North America*. Carnegie Institution of Washington Publication 390. 2 vol.

HERMAN, J. 1972. Contribution à la connaissance de la faune ichthyologique de phosphates du Maroc. *Annales de Société Géologique de Belgique*, 95(2):271–283.

KEMP, D., L. KEMP, AND D. WARD. 1990. *An illustrated guide to the British middle Eocene vertebrates*. London, David Ward. 59 pp.

KUMAR, K., AND R. S. LOYAL. 1987. Eocene ichthyofauna from the Subathu Formation, northwestern Himalaya, India. *Journal of the Palaeontological Society of India*, 3260–84.

LEIDY, J. 1855. Indications of twelve species of fossil fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7:395–397.

———. 1860. Description of fossil vertebrates; pp. 99–122 in F. S. Holmes, *Post-Pleiocene fossils of South Carolina*. Charleston.

———. 1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. *Journal of the Academy of Natural Sciences of Philadelphia*, ser. 2, 8:209–262.

LERICHE, M. 1900, Sur la faune ichthyologique des Sables à Unios et Teredines des Environs d'Epernay (Marne). *Annales de Société Géologique du Nord*, 29:173–196.

———. 1902. Les poissons paléocènes de la Belgique. *Mémoires de Muséum Royal de Histoire Naturelle de Belgique*, 2:1–48.

———. 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la plaine côtière Atlantique et du centre des États-Unis. *Mémoires de Société Géologique de France*, n.s., 20(2–4):1–111.

LONGBOTTOM, A. E. 1984. New Tertiary pycnodonts from the Tilemsi Valley, Republic of Mali. *British Museum (Natural History), Bulletin, Geological Series*, 38(1):1–26.

LUCAS, S. G. 1984. Early Paleocene vertebrates, stratigraphy and biostratigraphy, West Fork of Gallegos Canyon, San Juan Basin, New Mexico. *New Mexico Geology*, 6(3):56–60.

MADDEN, C. T. 1983. Paleocene Pycnodont fishes from Jabal Umm Himar, Harrat Hadan area, Kingdom of Saudi Arabia. *U.S. Geological Survey Open-File Report* 83–453: 1–25.

PRIEM, F. 1902. Sur des pycnodontes tertiaires du departement de l'Aude. *Bulletin de Société Géologique de France*, (ser. 4) 2:44–49.

———. 1903. Sur les poissons fossiles des phosphates d'Algerie et de Tunisie. *Bulletin de Société Géologique de France*, (ser. 4), 3:393–406.

———. 1914. Sur des vertébrés du Crétace et de l'Éocène d'Egypte. *Bulletin de Société Géologique de France*, (ser. 4), 14:366–382.

PURDY, ROBERT W. 1998. Chondrichthyan fishes from the Paleocene of South Carolina; pp. 122–146 in A. E. Sanders [ed.], Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A. *Transactions of the American Philosophical Society* 88(4).

SAVORNIN, M. J. 1915. Les pycnodontes éocènes de l'Algerie. *Comptes Rendus, Association Française pour l'Avancement de Science,* 1914 (Sess. 43):368–377.

SMITH, A. G., A. M. HURLEY, AND J. C. BRIDEN. 1981. *Phanerozoic palaeocontinental world maps* Cambridge University Press, Cambridge. 102 pp.

STROMER, E. 1910. Reptilien-und fischreste aus dem marinen Alttertiar von Sudtogo (Westafrika). *Zeitschrift, DeutschesGeologischen Gesellschaft,* 62(7):478–507.

TUOMEY, M. 1848. *Report on the geology of South Carolina.* A. S. Johnson, Columbia. 293 pp.

TYLER, J. C. 1975. A new species of boxfish from the Eocene of Monte Bolca, Italy, the first unquestionable fossil record of the Ostraciontidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca. II. Miscellanea Paleontologica,* pp. 103–126. Museo Civica. di Storia Naturale, Verona.

———. 1980. *Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes).* Department of Commerce, NOAA Tech. Rept. NMFS Circular 434. pp. 422

———, AND R. GREGOROVA. 1991. A new genus and species of boxfish (Tetraodontiformes: Ostraciidae) from the Oligocene of Moravia, the second fossil representative of the family. *Smithsonian Contributions to Paleobiology,* 71:1–20.

WARD, D. J. 1978. The lower London Tertiary (Palaeocene) succession of Herne Bay, Kent. *Institute of Geological Sciences (Natural Environment Research Council) Report 78/10.* London, Her Majesty's Stationery Office. 12 pp.

WEEMS, R. E. 1984. Vertebrate biozones of the Pamunkey Group (Paleocene and Eocene, Maryland and Virginia); pp. 198–204 *in* L. W. Ward and K. Krafft.(eds.), *Stratigraphy and paleontology of the outcropping Tertiary beds in the Pamunkey River Region, central Virginia Coastal Plain—Guidebook for Atlantic Coastal Plain Geological Association 1984 field trip:* Atlantic Coastal Plain Geological Association.

WEEMS, R. E., AND L. M. BYBELL 1998. Geology of the Black Mingo Group (Paleocene) in the Kingstree and St. Stephen areas of South Carolina; pp. 9–27 in A. E. Sanders [ed.], Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A. *Transactions of the American Philosophical Society* 88(4).

WHITE, E. I. 1931. The vertebrate faunas of the English Eocene. Vol. 1, From the Thanet Sands to the Basement Bed of the London Clay. British Museum (Natural History). 123 pp.

———. 1935. Fossil fishes of Sokoto province. *Bulletin of the Geological Survey of Nigeria,* 14:1–78.

WILEY, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *University of Kansas Museum of Natural History, Miscellaneous Publications,* 64:1–111.

WINTERBOTTOM, R., AND J. C. TYLER. 1983. Phylogenetic relationships of Aracanin genera of boxfishes (Ostraciidae: Tetraodontiformes). *Copeia,* 1983(4):902–917.

WOOD, S. V. 1846. On the discovery of an alligator and of several new Mammalia in the Hordwell Cliff, with observations upon the geological phenomena of that locality. *London Geological Journal,* 1:1–7, 117–122.

WYMAN, J. 1850. Notice of remains of vertebrated animals found at Richmond, Virginia. *American Journal of Science,* ser. 2, 10:228–235.

ZITTEL, K. A. 1923. *Grundzüge der Paläontologie (Paläozoologie), II. Abteilung: Vertebrata.* Druck und Verlag von R. Oldenbourg, Munich. 706 pp.