6. **Actinopterygian Fish Remains from the Paleocene of South Carolina**

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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>
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<tr>
<th>Taxon</th>
<th>Lower Bridge Member (NP 5)</th>
<th>Chicora Member (NP 8/9)</th>
<th>Uncertain origin (NP 5/9)</th>
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<tr>
<td><em>Lepisosteus</em> sp.</td>
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<td><em>Pycnodus</em> sp.</td>
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<td><em>Albula oweni</em> (Owen)</td>
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<td><em>Egertonia isodonta</em> Cocchi</td>
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<td><em>Phyllodus toliapicus</em> Agassiz</td>
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<td>Ostraciidae, gen. et sp. indet.</td>
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<td><em>Progymnodon hilgendorfi</em> Dames</td>
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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.

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from the St. Stephen hydroelectric pit wall, show that Phyllopus 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, Ostracidae gen. et sp. indet., and Progynodon 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), devoid 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
Egeronia 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 Egeronia 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
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).

*Phyllopus toliacicus* 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 ablial view. Such tooth batteries are referable to *Phyllopus* (Estes, 1969). Although a number of nominal species of *Phyllopus* 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. *Phyllopus* was recovered in situ from both the Lower Bridge and Chicora Members of the Williamsburg Formations, so it appears to
Figure 3. *Egertonia isodontia* Cocchi; fragmentary pharyngeal plate (ChM PV4169) in (A) aboral, (B) oral, and (C) lateral views.
Figure 4. Phyllopus 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.
have been a common species in the coastal marine waters of South Carolina throughout the late early and late Paleocene. As with *Egertonia*, *Phylloodus* 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, *Phylloodus* has been reported from England, Belgium, France, Virginia, New Jersey, and Mississippi (Gildersleeve, 1933; Estes, 1969; Case 1986).

**Order Tetraodontiformes**

**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 McCallum (PV4111–4112).

Ostracoid 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 triturative 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 triturative 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 triturative 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
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 Brockton's 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.

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REFERENCES


