



NEW MATERIAL OF *APOCOPODON SERICEUS* COPE,
1886 (MYLIOBATIFORMES, MYLIOBATIDAE) FROM THE
PARAÍBA BASIN (NORTHEASTERN BRAZIL), AND SOUTH
CAROLINA (USA) WITH A REANALYSIS OF THE SPECIES

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ABSTRACT

Myliobatiformes (Elasmobranchii: Batoidei) is circumglobally distributed and consists of 26 extant genera within ten families. The oldest records of the group occur in upper Cretaceous deposits, and one extinct species, *Apocopodon sericeus*, is found in the Danian (lower Paleocene) Maria Farinha Formation of the Paraíba Basin, Pernambuco state, northeastern Brazil. This taxon is known from isolated teeth and several partial dentitions in various states of completeness, and herein we describe a new, incomplete (lingual portion) Brazilian dental plate. Previously considered to be endemic to the Paraíba Basin, *Apocopodon* was recently identified from South Carolina, United States. The sample consists of a nearly complete upper(?) dentition and numerous isolated teeth, and the material is indistinguishable from *A. sericeus*. The precise stratigraphic position and age of the South Carolina fossils is unknown, but based on the other associated Paleocene vertebrate fossils, we believe that the fossils originated from the Danian Rhems Formation. The South Carolina occurrence of *Apocopodon* represents a significant geographic range extension of more than 7,000 km to the north of the type area, and the occurrence of this ray in such widely separated areas demonstrates the dispersion potential of fossil elasmobranch species. Analysis of the new specimens, along with reanalysis of all previously known *Apocopodon* dentitions maintained in Brazilian institutions, resulted in a revision of the morphological characteristics used to identify the taxon.

Introduction

Teeth, dermal denticles and caudal fin spines of Myliobatiformes are known from upper Cretaceous strata of Europe, Africa, North and South America, and Asia (Cappetta, 1987; Marmi *et al.*, 2010). In Brazil, remains of Myliobatiformes are found in the upper Cretaceous (Maastrichtian) Itapecuru Formation of the São Luís Basin (Eugênio, 1994), Maastrichtian Gramame (Silva, 2007) and lower Paleocene (Danian) Maria Farinha formations of the Paraíba Basin (Rebouças & Silva Santos, 1956; Silva, 1993; 1994), and Miocene Pirabas Formation of the Pará-Maranhão Basin (Silva Santos & Travassos, 1960; Silva Santos & Salgado, 1971).

Fossil Myliobatiformes have been known to occur within the Paraíba Basin since the 19th century and are represented by the extinct genera *Rhombodus* and *Apocopodon*, and extant genera *Rhinoptera* and *Myliobatis* (Silva Santos & Gomes, 1987; Silva, 1993; 1994; Silva, 2007). *Rhombodus binkhorsti* was reported by Rebouças & Silva Santos (1956) from the Gramame Formation, whereas the other three genera occur in the Maria Farinha Formation (*e.g.* Cope, 1886; Woodward, 1907; Silva *et al.*, 2001; Silva *et al.*, 2002). *Rhinoptera prisca* was erected by Woodward (1907) and the type material includes an incomplete dental plate. *Apocopodon sericeus* was based on an isolated tooth and three articulated teeth (Cope, 1886; later revised by Woodward, 1907; see also Silva Santos & Gomes, 1987). Until the 1980s, reference to *Apocopodon* has appeared sporadically in the literature and only in reference to the type material (*e.g.* Cappetta, 1987). However, thanks to extensive studies of the fossiliferous strata in Pernambuco over the past 25 years, new specimens of *A. sericeus* have come to light, including additional isolated teeth and several dentitions (*e.g.* Silva *et al.*, 1995; Silva, 2007; Santana *et al.*, 2009).

All of the Brazilian *Apocopodon* material, including a new specimen described in this work, was collected from coastal plain deposits that occur in the Paraíba Basin, Pernambuco State, predominantly in the Poty Quarry near Paulista city (around 30 km to north of Recife) but also in small limestone quarries around Paulista (figure 1). The Poty Quarry did not exist at the time Cope obtained his specimens, and the fossils he examined were probably collected from one of

the small quarries from which the local population extracted limestone blocks.

Apocopodon sericeus has been considered to be endemic to the Paraíba Basin (*e.g.* Silva *et al.*, 2001; Silva *et al.*, 2002), but some isolated teeth found in Texas, USA were tentatively attributed to the genus by Meyer (1974). However, our interpretation of the specimens he illustrated is that the Texas material can be assigned to other taxa. The Maastrichtian specimen that Meyer (1974) identified as *Apocopodon?* sp. 1 (p. 160, fig. 50) actually represents *Brachyrhizodus wichitaensis*, and his Cenomanian *Apocopodon?* sp. 2 (p. 162, fig. 51) appears to be an aberrant *Pseudohypolophus mcultyi*.

A nearly complete dentition collected from Williamsburg County, South Carolina (United States), is virtually indistinguishable from a specimen of *A. sericeus* discussed by Silva *et al.* (1995), and this specimen (in addition to isolated teeth) represents the first undeniable record of *Apocopodon* outside of the type area and extends the paleogeographic distribution of the genus more than 7,000 km to the north. Herein we present morphological descriptions of the new South Carolina and Brazilian fossils, and we provide the results of a morphological analysis of all known *Apocopodon* dentitions in museum collections. Additionally, we discuss geographic distribution, environmental preference, and other biological aspects of the genus.

Geological and Paleoenvironmental Settings

The coastal zone of the Paraíba Basin corresponds to that region of the platform margin between the Pernambuco Shear Zone (PESZ), near the city of Recife, and the Mamanguape Fault, an offshoot of the Patos Shear Zone (PASZ), located north of the city of João Pessoa, Paraíba state (figure 1C, D). The coastal basin is divided into three sub-basins, Olinda, Alhandra and Miriri (Mabesoone & Alheiros, 1993; Barbosa & Lima Filho, 2006; Barbosa, 2007), and the new Brazilian specimen described herein was collected from the Poty Quarry (Olinda sub-basin) in the southern region of the Paraíba Basin (figure 1C).

The sedimentary succession in the Paraíba Basin is divided into five formations, including the Coniacian(?) to Santonian Beberibe, upper Campanian to lower Maastrichtian Itamaracá,

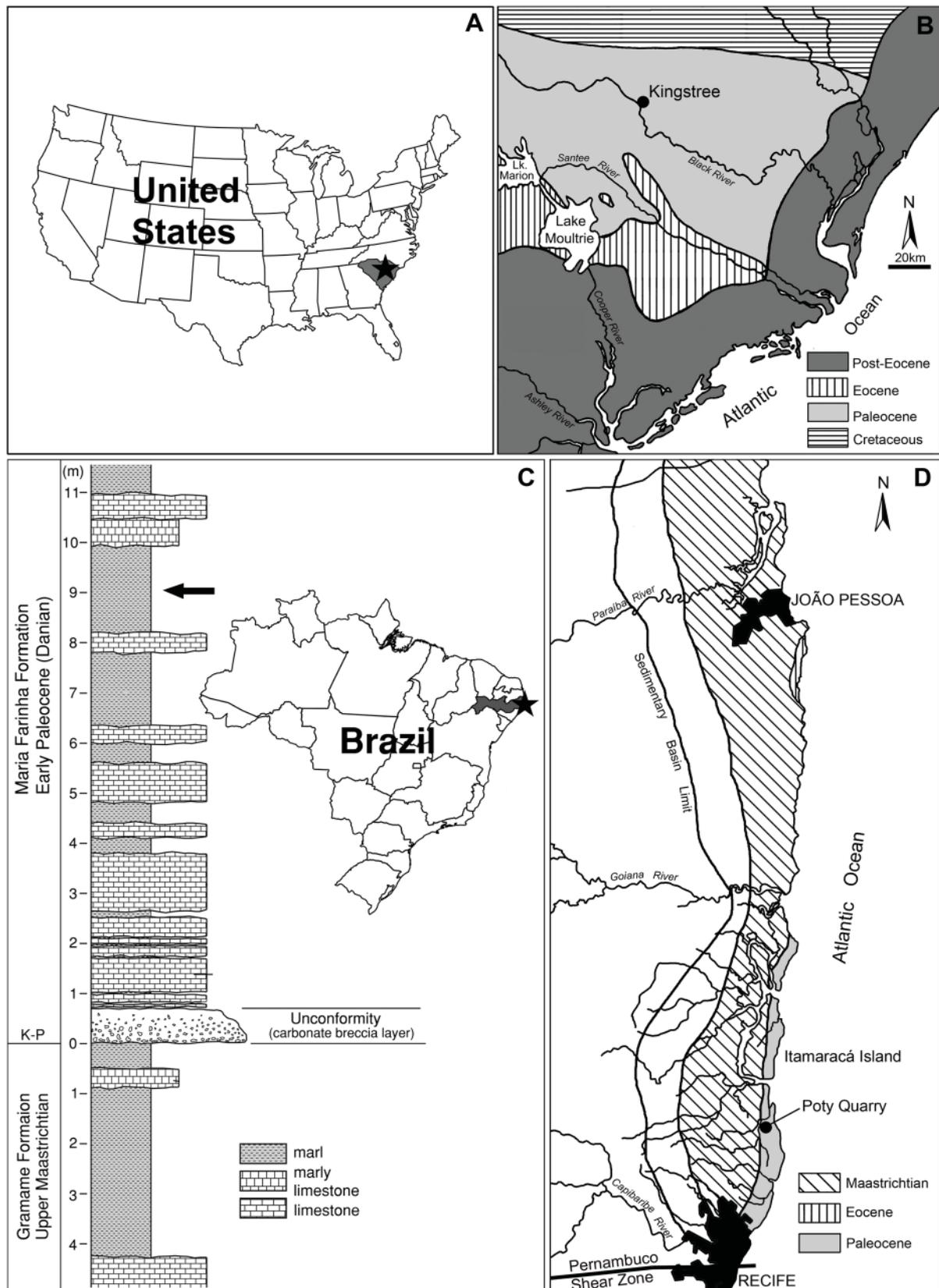


Figure 1. Geographic and stratigraphic occurrences of *Apocopodon* fossils. A) Map of contiguous United States showing location of South Carolina; B) Enlarged view of the fossil area (Kingstree) showing regional geology (modified from Weems & Bybell, 1998); C) Geographic map of Brazil and stratigraphic section of the Poty Mine (adapted from Barbosa, 2007); D) Enlarged view of Pernambuco State showing regional geology of the Paraíba Basin. Arrow in C indicates stratigraphic position of *Apocopodon sericeus*.

Maastrichtian Gramame, Danian Maria Farinha, and Plio-Pleistocene Barreiras formations (Souza, 1998; Barbosa, 2004; 2007). The Danian deposits that occur in the Olinda sub-basin are characterized by marl and marly limestone that was deposited in a shallow platform environment dominated by mud influx, probably in the proximity of estuaries (Barbosa *et al.*, 2006) (figure 1). These deposits represent lateral facies variations related to the regressive event that began at the end of the Maastrichtian, with regions near the paleo-coastline undergoing a change from a shallow platform environment to a sub-coastal environment, and increased energy and influx of terrigenous material (in the form of sand) in the shallowest regions (Barbosa *et al.*, 2006). Overall, the Poty Quarry deposits exhibit a coarsening upward sequence that reflects this increase of terrigenous material and possible growing influence of estuaries.

The Danian deposits in the Poty Quarry are rich in fossils of marine animals like mollusks, echinoids, fish, marine crocodiles, and sea turtles (Muniz, 1993; Silva *et al.*, 2001; Barbosa, 2004; Barbosa *et al.*, 2008). A large portion of the Danian invertebrate paleofauna is represented by colonizing species that occupied the basin after a major biotic reduction at the end of the Cretaceous (K/T event) (Stinnesbeck, 1989; Albertão *et al.*, 1994; Stinnesbeck & Keller, 1996; Barbosa, 2004; Neumann *et al.*, 2009). Most of the colonizing biota, mainly mollusks that inhabited the basin during the post-K/T recovery period, appears to have emigrated from the north in the Gulf of Mexico region and North America (Barbosa, 2004).

Unfortunately, less can be said about the South Carolina *Apocopodon* occurrence. The fossils were recovered from a lag deposit containing Cretaceous and Paleocene fossils that were probably mixed together during the Plio-Pleistocene, likely as the result of ancient coastal processes (based on the association of shark teeth like *Carcharodon carcharias* and *Galeocerdo cuvier* with terrestrial vertebrate remains like *Nanippus* sp.). The fossil site, located alongside a creek inside the city limits of Kingstree, Williamsburg County, is within the Maastrichtian Peedee Formation (or equivalent) outcrop belt, and the lower Paleocene Rhems Formation also occurs in the area (Weems & Bybell, 1998). Lithostratigraphic and biostratigraphic analyses of the Rhems Formation indicate that

deposition occurred in a nearshore marine, possibly deltaic environment (Weems & Bybell, 1998), and this interpretation is supported by vertebrate fossils attributed to the formation (Erickson, 1998; Hutchinson & Weems, 1998; Sawyer, 1998).

Age of *Apocopodon* Fossils

Cope (1886) thought that Brazilian strata yielding *Apocopodon* were of Maastrichtian age and correlative to the Fox Hills Formation of the United States Western Interior (also Branner, 1890). Upper Cretaceous elasmobranch taxa like *Rhombodus binkhorsti*, *Scapanorhynchus*, *Cretalamna biauriculata*, *Squalicorax kaupi* and *S. pristodontus* occur in the Paraíba Basin, but these fossils are derived from the Campanian-Maastrichtian Itamaracá and Gramame formations (Silva, 2007; Silva *et al.*, 2007). The Maria Farinha Formation, the source of *Apocopodon* fossils, is now known to have been deposited during the early Paleocene (Danian Stage; see Silva, 1994; Albertão *et al.*, 1994; Silva *et al.*, 1995; Stinnesbeck & Keller, 1996; Gallo *et al.*, 2001; Silva *et al.*, 2002; Silva, 2007; Barbosa *et al.*, 2008), and Cope may have examined a mixed assortment of fossils that lacked stratigraphic provenience. The temporal occurrence of *Apocopodon* was incorrectly reported as Thanetian (late Paleocene) by Cappetta (2006) and Cleason *et al.* (2010).

The source strata of the South Carolina *Apocopodon* sample are not known with certainty, as the fossils are part of a temporally mixed vertebrate assemblage that occurs in a lag deposit. Cretaceous taxa include dinosaurs and the elasmobranchs *Squalicorax kaupi*, *Cretalamna biauriculata*, *Serratolamna serrata*, *Schizorhiza stromeri*, and *Rhombodus binkhorsti*, an assemblage indicative of a Maastrichtian age (Case, 1979; Padian, 1984). The Paleocene fossils are believed to have been derived from the Rhems Formation (Erickson, 1998; Hutchinson & Weems, 1998), a lithostratigraphic unit that formed during the Danian Stage (calcareous nanofossil zone NP 1, possibly as young as NP 3; see Weems & Bybell, 1998). Considering the fact that *Apocopodon* is only known from the Danian of Brazil, it is parsimonious to consider the South Carolina material to be of equivalent age (not Cretaceous or Plio-Pleistocene). Supporting evidence for this hypothesis includes

occurrences of the elasmobranchs *Palaeocar-charodon* and *Hypolophites hutchinsi*, taxa reported from Danian strata elsewhere in the USA (see Case, 1989; 1993; 1996; Kent, 1994). Unfortunately, indurated matrix obtained from recesses within the aboral surface of the South Carolina dentition did not yield microfossils for relative age determination of the source deposit (J. Self-Trial personal communication, 2010).

Institutional Abbreviations

LAGESE - Laboratory of Sedimentary Geology, Federal University of Pernambuco, Brazil;
 DGEO-CTG-UFPE - Geology Department, Federal University of Pernambuco;
 UFRPE - Biology Department, Rural Federal University of Pernambuco;
 MN - Museu Nacional, Universidade Federal do Rio De Janeiro;
 ChM - Charleston Museum, Charleston, South Carolina, USA;
 NHM - Natural History Museum, London, England.

Materials and Methods

The new Brazilian specimen was mechanically prepared to free it from limestone matrix and then photographed. South Carolina *Apocopodon* specimens were recovered by screen-washing the fossiliferous lag deposit with sieves down to 0.25 mm. We have limited our analysis of *Apocopodon sericeus* to the articulated dentitions described herein because other material is often imperfectly preserved, and we have also found that *Apocopodon* teeth are very similar in gross morphology to lateral teeth of *Rhinoptera prisca*, a taxon also occurring in the Maria Farinha Formation. Cope's collection of ablated specimens was discussed by Silva (1994), and her descriptions of the fossils were taken into account in our diagnosis of *Apocopodon*. She listed as syntypes MN 2555/1-V (isolated tooth; pl. 1, figs. 2A-B) and MN 2555/2-V (three articulated teeth; pl. 1, figs. 1A-B), and an additional specimen consisting of four articulated teeth was included (MN 2555/3-V; pl. 1, figs. 3A-B).

Systematic Paleontology

Elasmobranchii Bonaparte, 1838
 Neoselachii Compagno, 1977
 Batomorphii Cappetta, 1980
 Myliobatiformes Compagno, 1973
 Myliobatidae Bonaparte, 1838
Apocopodon Cope, 1886

Type and only known species – *Apocopodon sericeus* Cope (1886: 2). See also Woodward (1888: 297; 1889: 132; 1907: 194-195, pl. VII, figs. 4-5; 1912: 229, text fig. 73); Zittel (1887: 101), Branner (1890: 429), Pelacký (1895: 2), Jordan (1907: 215), Fossa-Mancini (1921: 210), Casier (1953: 34-36), Cappetta (1987: 171, fig. 144 D-H), Silva Santos & Gomes (1987: 38-47; pl. 1, figs. 1-5), Silva (1994: 317-319, pl. 1, figs. 1-3), Silva *et al.* (1995), Gallo *et al.* (2001: 269, fig. 8; 271), Silva *et al.* (2002: 7), Cappetta (2006: 277), Silva (2007: 43-44, 71-74, text fig. VI.17, pl. II, fig. 4; pl. VII, figs. 2-3), Silva *et al.* (2007: 88), Santana *et al.* (2009: 10), Cleason *et al.* (2010: 660, 666, 668, fig. 8C).

Type locality and stratigraphic horizon – Near Paulista city, Paraíba Basin, Pernambuco, Brazil; Maria Farinha Formation; Paleocene Series, Danian Stage.

General remarks – Cope named *A. sericeus* in an address to the American Philosophical Society on 17 April, 1885, but the description of the type material did not appear in print until the January, 1886 Transactions of the American Philosophical Society (vol. 23, no. 121). As such, the year attributed to the naming of the genus and type species is variously listed as 1885 (*e.g.* Cappetta, 1987; 2006) or 1886 (Silva, 2007). The correct date should appear as 1886 according to Article 8.4 of the International Code of Zoological Nomenclature. Depictions of the type material did not appear until 1907, when Woodward illustrated the fossils (pl. VI, figs. 4-5) as part of a discussion on Cretaceous fossils from Brazil. Cope's specimens do not actually reside at MN, but at the NHM where Woodward (*e.g.* 1907) examined them, and specimens have two catalog numbers associated with them; MN 2555/2-V is the same as NHM P24670.

Material examined – LAGESE V-00014, lingual portion of dentition; DGEO-CTG-UFPE 5680, partial dentition; DGEO-CTG-UFPE SN (not curated), partial dentition; UFRPE 3223, nearly complete dentition; ChM VP7709, partial dentition.

Diagnosis – Teeth of *Apocopodon sericeus* form a pavement-type dentition that consists of longitudinal rows of teeth. The first row of teeth is herein called the medial row, and this row was presumably located on the jaw symphysis. A line drawn labio-lingually along the middle of this row will divide the dentition into more or less symmetrical right and left halves (depending on the number of lateral tooth rows actually preserved). The second tooth row, herein called the paramedial row, directly adjoins the medial row and is therefore the first lateral tooth row within the dentition. The remaining lateral rows were numbered in ascending order towards the lateral margins of the dentition in a similar way that Leriche (1913) labeled his *Hypholophites mayombensis* dentition. The second lateral row, L2, articulates with the paramedial row mesially and L3, the third lateral row, distally. LAGESE V-00014 and DGEO-CTG-UFPE SN preserve a single tooth in L4 (= fourth lateral row; see figure 2A, D and 4A, D), and the mesial sides of these teeth articulate with L3, but the distal end appears to mark the lateral-most edge of the dentition. On all remaining dentitions, the distal ends of the teeth in L3 have well developed angles, indicating they articulated with at least one additional row of teeth that is not preserved.

The teeth in medial and paramedial rows are six-sided and generally the largest within the dentition, being approximately 1.5 times wider than long. The paramedial teeth are asymmetrical with a more rhomboidal outline (when compared to teeth in the medial row), and within the dentition it is apparent that their distal end is situated closer to the labial margin of the plate (e.g. figure 2F, 3A). Tooth size decreases distally, with teeth in L2 being roughly as wide as long. Although six-sided, teeth within the remaining L3 and L4 are asymmetrical in being longer than wide and having a more rectangular outline. The teeth of each row articulate with those of adjacent rows via lateral angles, and the angles of medial and paramedial teeth are approximately 90 degrees (and located near the transverse midline on medial teeth).

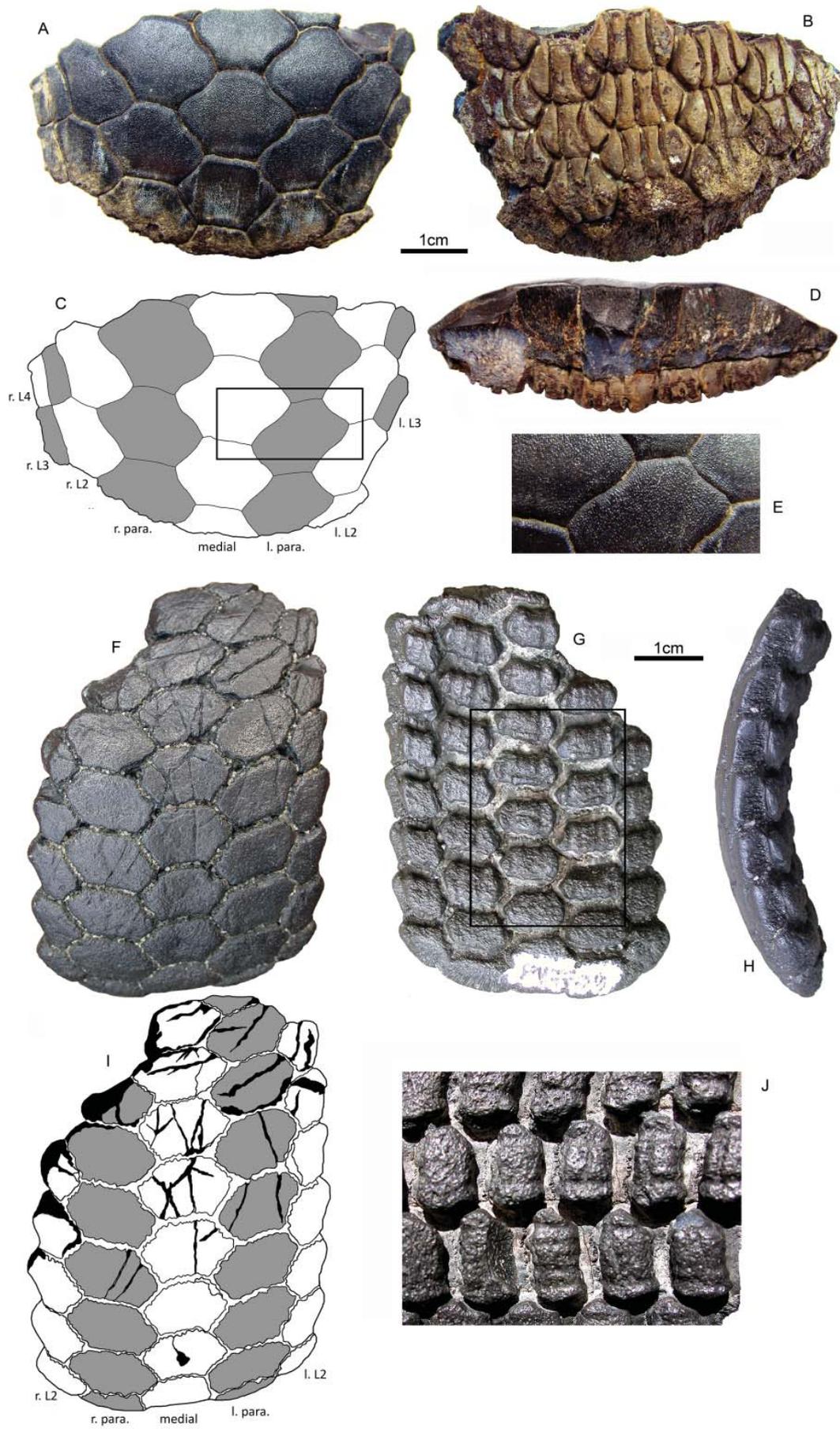
Individual teeth are robust, with crowns of unworn teeth in medial and paramedial rows reaching nearly 2 cm in thickness. The labial and lingual crown faces are lingually inclined and very coarsely wrinkled parallel to crown height (figure 4E-H), the net effect of these features being that the lingual face of the crown of one tooth overlaps the labial face of the succeeding tooth, and the teeth are very strongly interconnected. The wrinkles on the crown faces merge with fine ridges along the occlusal margins, and the entire occlusal surface of unworn teeth bears fine ornamentation of bifurcating and anastomosing longitudinal ridges (six ridges per millimeter), overall having a vermicular or even reticulated pattern. The occlusal crown margin of unworn teeth is somewhat rounded, and the contacts between teeth within the unworn portion of the dentition are seen as straight to slightly sinuous furrows. However, tooth contacts within the worn portion of the dentition have an interfingering, sutured appearance.

Tooth bases are low, only one third the height of the crowns of medial and paramedial teeth. The labial crown face extends forward of the base, and in lingual view the crown is separated from the base by a thick, rounded and irregular transverse ridge. In addition, bases are polyau-locorhize, with up to seven nutritive grooves occurring on medial and paramedial teeth, but generally only two nutritive grooves in more lateral rows (figure 2B, 3B, 4B). Some tooth bases exhibit nutritive grooves that are open at one end but closed at the other (figure 5), and this condition could be described as either vestigial or even “secondarily roofed over”, a condition also reported on *Igdabatis* (Cappetta, 1972) and *Meridiana* (Cicimurri, 2010).

Description

LAGESE V-00014 is the well preserved lingual portion of an upper(?) dental plate that consists of 22 articulated complete and fragmentary teeth. The teeth are arranged into eight longitudinal rows, but a ninth row appears to be missing from one side (figure 2A, C). Four

► Figure 2. Dental plates of *Apocopodon sericeus*. A-E, LAGESE V-00014. A) Occlusal; B) Basal; C) Schematic drawing of occlusal view; D) Labial; E) Enlargement of area within rectangle of D showing crown ornamentation. F-J, ChM VP7709; F) Occlusal; G) Basal; H) Profile; I) Schematic drawing in occlusal view; J) Enlargement of area within rectangle of G showing serrated contacts between teeth. Labial is at top except in D and J (right). Abbreviations: l. para., left paramedial row; l. L2, left second lateral row; l. L3, left third lateral row; l. L4, left fourth lateral row; r. para., right paramedial row; r. L2, right second lateral row; r. L3, right third lateral row; r. L4, right fourth lateral row.



teeth (two complete and two partials) are preserved in the medial row, whereas three complete teeth and fragments of a fourth are preserved in both paramedial (first lateral) rows. Two complete teeth and two partials make up the left L2, whereas two complete teeth are preserved in the equivalent row on the right side. Two teeth are preserved in L3 of both sides. Only one tooth is preserved in a right L4, and this appears to mark the distal margin of the dentition (figure 2A, C).

In occlusal view, the crown surfaces bear fine longitudinal vermicular ornamentation, and the contacts between teeth appear to be smooth (figure 2A, E). From the broken labial end, the occlusal surface is convex but the basal surface is less so. The crowns of medial teeth are three times the height of the root, with height diminishing towards the commissure, where crown height approximately equals root height (figure 2D). In basal view, three deep (approximately half of the thickness of the base) nutritive grooves divide the bases of medial and paramedial teeth into four lobes, whereas there are only two grooves (three lobes) on the bases of teeth within the remaining lateral rows (figure 2B). The nutritive grooves represent the locations where blood vessels entered the tooth.

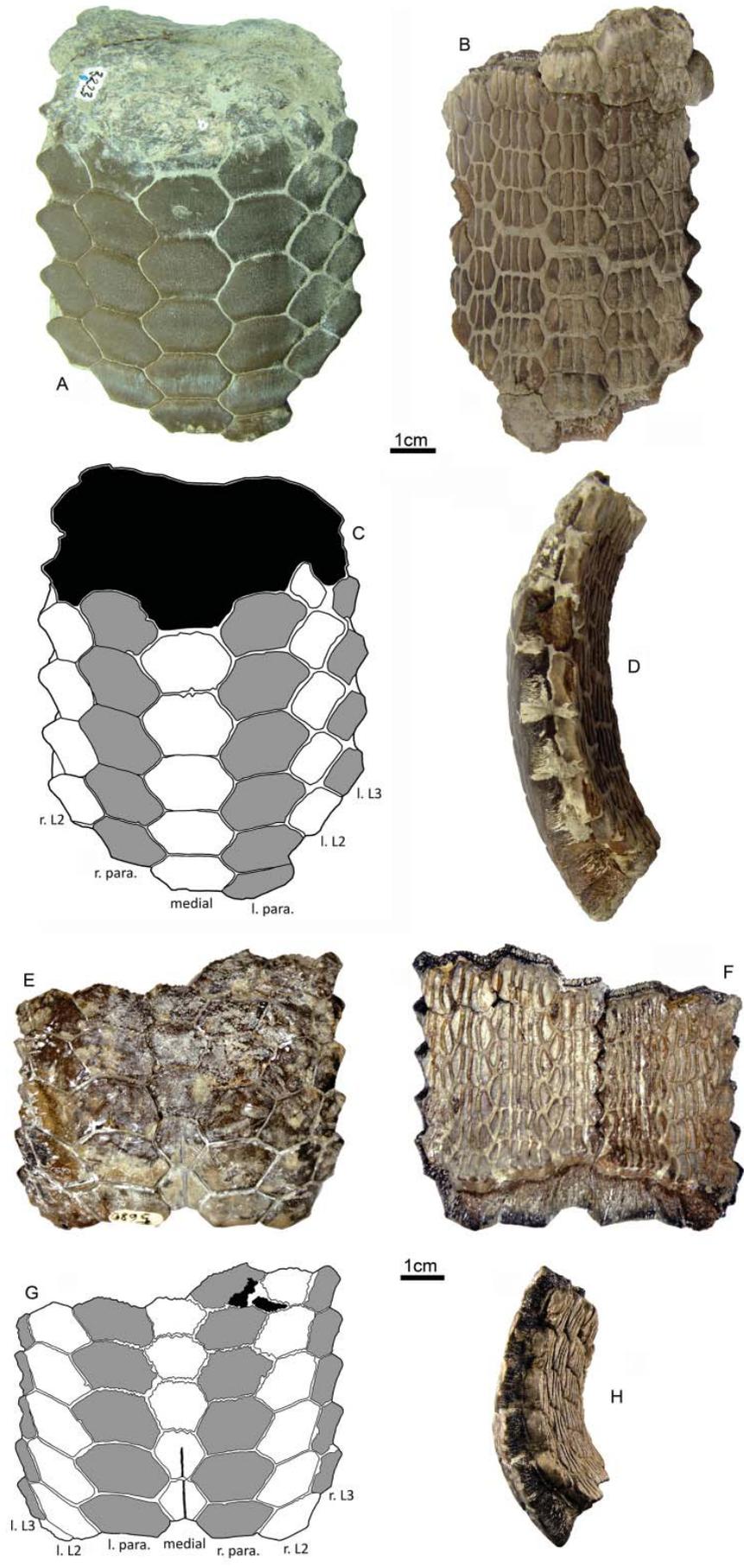
ChM VP7709 appears to represent an upper dentition that, although abraded, is remarkably complete, consisting of 36 articulated teeth (figure 2F, G, I). Only five tooth rows are preserved, and eight teeth comprise the medial row. Nine teeth (seven complete and two partials) are preserved in the left paramedial row, whereas seven teeth (five complete and two partials) make up the right paramedial row. Within L2, seven teeth are preserved on the left side and five on the right. The teeth are tightly packed together and form a rigid battery. Overall the dentition is convex in profile, but the labial half is rather flat to weakly concave (figure 2H, F, respectively). The crowns of medial teeth are six-sided, wider than long (1.2 cm x 0.72 cm; 1.7:1 ratio), with sharp lateral angles that are near perfect 90 degrees (figure 2F). The labial crown margin is weakly convex, whereas the lingual margin is weakly concave. Teeth in the paramedial row are six-sided and very nearly equal in

dimensions to the medial teeth, but they have an obvious rhomboidal appearance in occlusal view due to the mesio-labial and disto-lingual margins being longer than the mesio-lingual and disto-labial margins. The lateral angles are sharp on both sides of the crown. Teeth in L2 are six-sided but have a nearly trapezoidal occlusal outline (figure 2F, I). Tooth crowns measure up to 0.5 cm in thickness. In basal view, the tooth roots are very worn (a result of post-mortem abrasion) but obviously polyaulocorhize, with medial teeth bearing at least three nutritive grooves, at least four grooves on paramedial teeth, and at least two grooves on teeth in L2 (figure 2G, J). The root is 2-3 mm in height and located closer to the lingual crown margin (the labial crown face overhangs the root). ChM PV7709 (see figure 2F) is morphologically indistinguishable from UFRPE 3223 (see figure 3A), aside from the additional rows of lateral teeth preserved on the latter specimen.

UFRPE 3223 also appears to represent an upper dentition, and it is formed of 45 teeth preserved in six longitudinal rows. There are nine teeth in the medial and both paramedial rows, whereas there are eight teeth in the left L2 but only seven remaining on the right side (figure 3A, C). A L3 is preserved on the left side that contains six teeth (figure 3B). Overall, the oral surface is convex and the basal surface correspondingly concave (figure 3D), but the anterior one third of the dentition is concave where the teeth have been worn down through in vivo usage (figure 3A). Although occlusal surfaces are abraded, crowns within the (unworn) lingual portion of the dentition are much thicker than those within the worn labial portion (figure 3D).

Tooth bases of medial teeth bear three nutritive grooves (four lobes), but nutritive groove formation on paramedial teeth is asymmetrical, with three grooves developed on teeth on one side and four grooves (five lobes) developed on the opposite side (figure 3B). Nutritive groove development within adjoining L2 is also asymmetrical, with three grooves (four lobes) found on one side and two grooves (three lobes) on the opposite side (in the opposite order as in the paramedial teeth). Two nutritive grooves are found on the bases of teeth within L3.

► Figure 3. Dental plates of *Apocopodon sericeus*. A-D, UFRPE 3223. A) Occlusal; B) Basal; C) Schematic drawing in occlusal view; D) Profile. E-G, DGEO-CTG-UFPE 5680; E) Occlusal; F) Basal; G) Schematic drawing in occlusal view; H) Profile. Labial is at top in all views. Abbreviations as in figure 2.



DGEO-CTG-UFPE 5680 consists of the labial half of what may be a lower dentition. This specimen is composed of seven longitudinal rows of teeth (figure 3E-G). Five teeth are preserved within the medial row, whereas the paramedial rows contain six teeth on the right side and five on the left (figure 3G). Within L2, six teeth are preserved on the right side and five teeth on the left side. Five teeth are preserved within L3 on of both sides (figure 3E-G). In profile the oral surface is convex and the basal surface is concave (figure 3H). The medial teeth are nearly perfectly hexagonal, whereas the paramedial teeth, although also six-sided, are approximately twice as wide and oriented with their distal ends located closer to the labial margin of the dentition (figure 3E, G). Teeth in L2 are slightly smaller but even more asymmetrical, having a roughly rhomboidal outline, and teeth within L3 are six-sided but very asymmetrical (figure 3F). The anterior half of the preserved dentition is highly worn (in vivo usage), whereas the remaining half is unworn (figure 3E).

There are three nutritive grooves (four lobes) on bases of medial teeth (figure 3F). Nutritive groove formation is asymmetrical on paramedial teeth, with five grooves (six lobes) on the bases of the right row, but seven grooves (eight lobes) on the left row. Within L2, there are three nutritive grooves (four lobes) on the right row, but four (five lobes) on the left row. Tooth bases in L3 have two to three grooves (three to four lobes).

DGEO-CTG-UFPE SN is presumed to be an upper dentition, and the teeth are distributed in eight longitudinal rows. There are five complete and two incomplete teeth remaining within the medial row, whereas six teeth are preserved in the left paramedial row and eight teeth on the right. In L2, there are five teeth on the left side and at least seven on the right side. Within L3, there are three teeth on the left side and six on the right. Only one tooth is preserved in a left L4 (figure 4A-C). The oral surface of the plate is convex and the basal surface is concave (figure 4D). The medial teeth and most of the paramedial teeth are six-sided, roughly equidimensional, with their labial margins being convex as opposed to straight (figure 4A, B). Within L2, all crowns are six-sided, but one row of teeth is approximately twice as wide as the opposite row (figure 4C). The anterior one third of the plate is worn (in vivo usage), whereas the remaining two thirds is unworn (figure 4A).

The number of nutritive grooves on tooth bases varies within the medial row, ranging from three grooves (four lobes) labially to five grooves (six lobes) lingually (figure 4B). This trend of increasing numbers of nutritive grooves is also seen on the left paramedial row, but in the right paramedial row the opposite is true – nutritive grooves decrease from six to four labio-lingually. Within the remaining lateral rows, the number of grooves decreases distally from three to two (figure 4B). The increase in the number of nutritive grooves within the medial row and left paramedial row also coincides with an increase in crown and tooth base width.

As mentioned previously, lateral teeth of *Rhinoptera prisca* are very similar to *Apocopodon* teeth, and DGEO-CTG-UFPE 6158 and 6177 are noted here in order to help differentiate the two species. DGEO-CTG-UFPE 6117 was identified as *A. sericeus* by Silva (2007), but we believe that it actually represents *R. prisca*. This specimen (figure 4E-H), although reminiscent of *A. sericeus*, is identical to paramedial teeth in a very well preserved, nearly complete upper dentition of *R. prisca* (LAGESE V-00013; currently under study). We consider DGEO-CTG-UFPE 6158 (figure 4I-4L) to belong to *A. sericeus*, and distinguishing features may be: 1) it has a more rhomboidal occlusal outline, whereas *R. prisca* is more trapezoidal (figure 4G vs. figure 4K); 2) the lingual tongue of the tongue-and-groove interlocking mechanism (sensu Cleason *et al.*, 2010) on *Rhinoptera* teeth is a straight, rounded a ridge, whereas in *Apocopodon* it is highly irregular (figure 4F vs. figure 4J); 3) tooth bases of *Apocopodon* have fewer nutritive grooves and wider laminae (see Cleason *et al.*, 2010) than equivalent teeth of *R. prisca* (figure 4H vs. figure 4L), and this is particularly true in medial teeth; 4) the occlusal ornamentation of *R. prisca* is less robust than on *Apocopodon*.

Discussion

Dentition

Previous descriptions of *Apocopodon sericeus* dentitions suggested that the contacts between the teeth would be serrated (*e.g.*, Silva Santos & Gomes, 1987; Silva 1993; 1994; Santana *et al.*, 2009). Our analysis of *Apocopodon* dentitions shows that, in occlusal view, the teeth of the unworn lingual portion of the dentition appear to

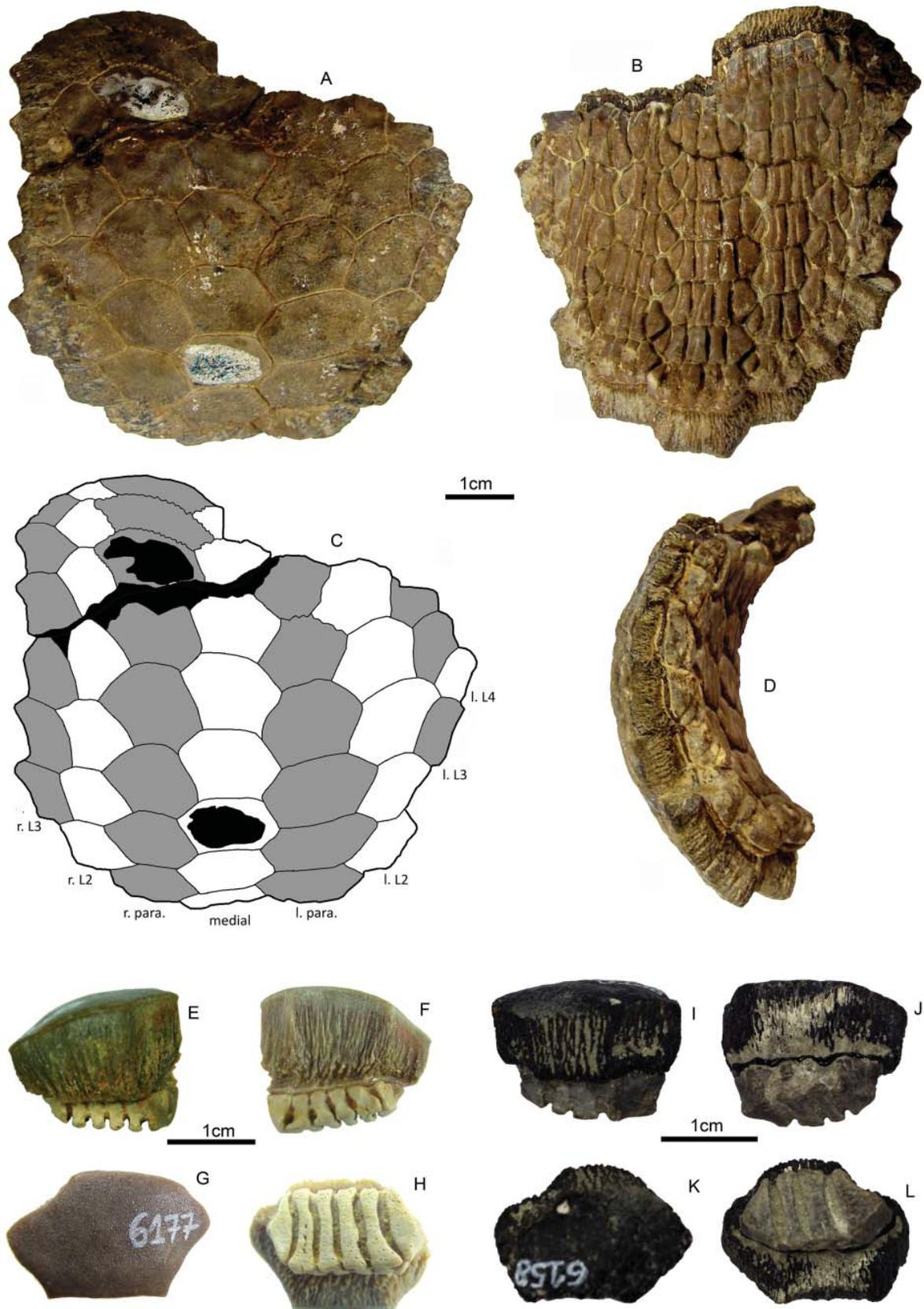


Figure 4. A-C, dental plate of *Apocopodon sericeus*, DGEO-CTG-FPE SN. A) Occlusal; B) Basal; C) Schematic drawing in occlusal view; D) Profile. E-H, isolated *Rhinoptera prisca* tooth, DGEO-CTG-FPE. E) Labial; F) Lingual; G) Occlusal; H) Basal views. I-L, isolated *A. sericeus* lateral tooth, DGEO-CTG-FPE 6177. I) Labial; J) Lingual; K) Occlusal; L) Basal views. Labial at top in A-D, G-H, K-L. Abbreviations as in Figure 2.

be united by smooth contacts (Santana *et al.*, 2009), whereas the worn labial portion exhibits serrated contacts (*e.g.* figure 2A, 3A, 3E, 4A). The basal surface of ChM VP7709 is free of matrix, and the specimen demonstrates that all of the teeth are in fact united by serrated contacts (figure 2G, J). The lingual portion of the occlusal surface appears to have smooth contacts between teeth because the unworn teeth have a beveled edge, which eventually wears down to reveal the highly interdigitating wrinkles on the crown faces (resulting in serrated contacts as seen in figure 4A). This same phenomenon is observable on the *Rhinoptera prisca* upper dentition (LAGESE V-00013) that we are studying. It is likely that the interdigitating crown faces increased the strength and rigidity of the dentition to resist the forces exerted during mastication (see below).

Previously unnoted in the labial part of *Apocopodon* dentitions, the tooth crowns may be approximately equal in thickness to the tooth base, whereas crowns within the lingual part are two and one half times the thickness of the base (LAGESE V-00014; figure 2D). This characteristic of decreasing crown height towards the labial margin is seen in DGEO-UFRPE 3223 (figure 3D), CTG-UFPE 5680 (figure 3H), and DGEO-CTG-UFPE SN (figure 4D), as well as the *R. prisca* upper dentition (LAGESE V-00013) previously mentioned. Crown height therefore is not of taxonomic importance, and in our opinion crown thickness is related to the presumed diet of *Apocopodon* (see below).

Other interesting phenomena we observed include the number of apparently incomplete nutritive grooves present on the tooth bases (*e.g.* figure 5), as well as the asymmetrical development of grooves between equivalent rows on the right and left sides of the dentition (*e.g.* figure 4B). At present we are unsure if the incomplete nutritive grooves represent a developmental abnormality, the initial formation of additional grooves to improve blood supply to the developing tooth, or if the groove is partially "secondarily roofed over" (blood vessel partially enclosed by dentine). As noted above, the lingual increase in the number of nutritive grooves on teeth within some rows of a dentition (*e.g.* DGEO-CTG-UFPE SN) also coincides with an increase in crown and tooth base width. Our interpretation is that this reflects ontogeny, with tooth size increasing as the animal grew (new,

larger teeth form at the lingual-most margin of the dentition). These features indicate that the number of nutritive grooves is an uninformative characteristic in diagnosing *Apocopodon* (*e.g.*, Silva Santos & Gomes, 1987; Silva, 1994).

Taxonomic Remarks

Woodward (1888; 1889; 1907; 1912) consistently speculated that *Apocopodon* represents a transitional species between Cretaceous *Ptychodus* (a taxon that became extinct by the early Campanian) and Cenozoic Myliobatidae. This hypothesis may have been influenced by the belief that *Apocopodon* was a Cretaceous taxon (see Cope, 1886; Jordan, 1907) and the fact that the crown faces of *Apocopodon* teeth are heavily wrinkled. However, the resemblance to *Ptychodus* is at best only superficial and a result of convergent evolution, and there is no close phylogenetic relationship between *Ptychodus* (Hybodontiformes?, Ptychodontidae) and *Apocopodon* (Myliobatiformes, Myliobatidae).

Cleason *et al.* (2010) recently conducted a phylogenetic analysis of Myliobatiformes, and the dental characters they utilized led them to conclude that *Apocopodon* is the sister taxon to "Crown-Myliobatidae" (which includes, among others, *Rhinoptera*, *Myliobatis*, *Weissobatis*, *Aetobatus*). Their analysis relied solely on three articulated teeth described by Cope (1886), and we are currently utilizing the five *Apocopodon* dentitions reported herein to test Cleason *et al.*'s (2010) conclusion. This will be presented as a companion to our study of the *Rhinoptera prisca* upper dentition (LAGESE V-000130) previously mentioned.

Based solely on our observations, *Apocopodon* is firmly grounded within Myliobatidae because: 1) the pavement-like dentition consists of six-sided teeth; 2) medial teeth are expanded (although only slightly); 3) teeth do exhibit tongue-and-groove articulation; 4) tooth bases are polyaulocorhize (*e.g.*, Cleason *et al.*, 2010; see also Silva Santos & Gomes, 1987; Silva, 1993; 1994). A close phylogenetic relationship between *Apocopodon* and *Rhinoptera* was suggested by Fossa-Mancini (1921), and Casier (1953) later indicated that *Apocopodon* could be an evolutionary intermediate between Cretaceous *Rhombodus* and Cenozoic *Rhinoptera*. Although there are similarities in tooth morphology between these three taxa, the ancestor-descendent hypothesis advocated by Fossa-

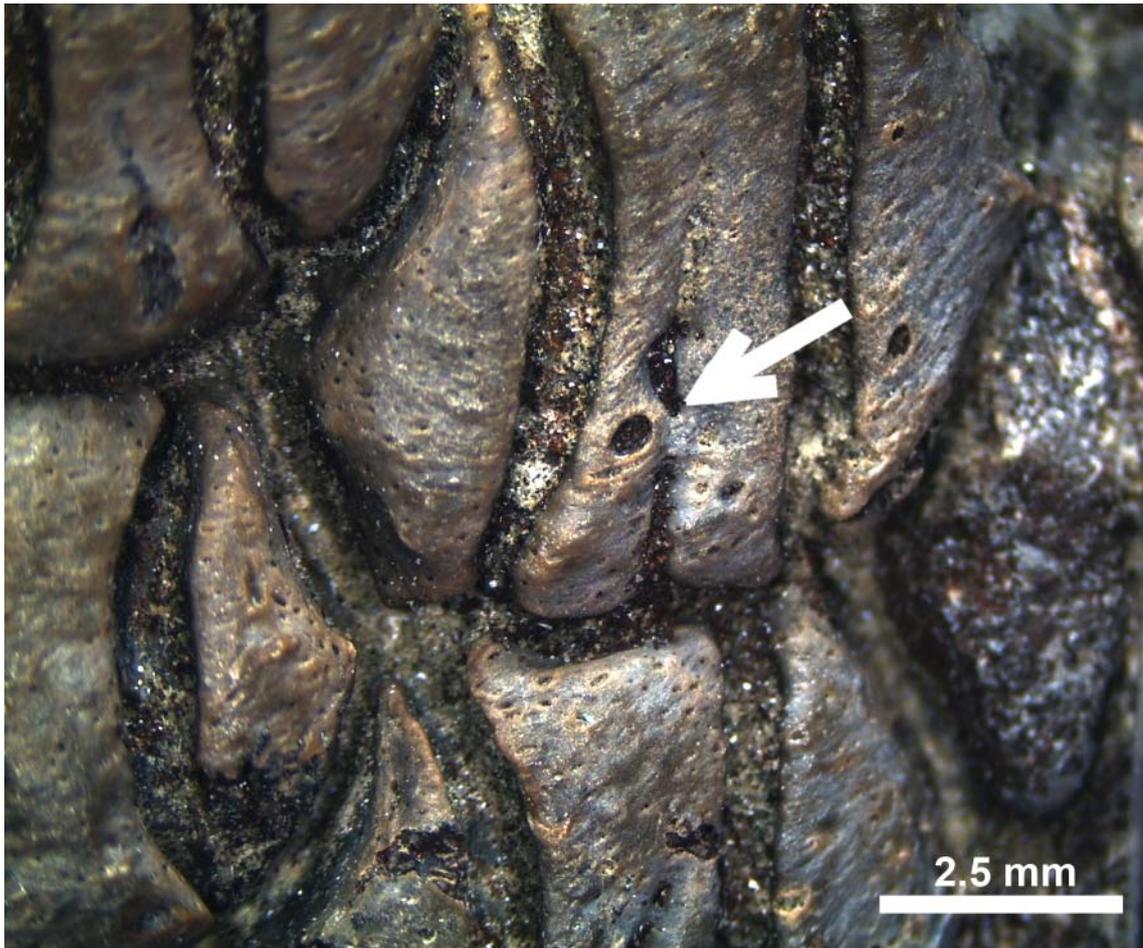


Figure 5. Detail of LAGESE V-00014 in basal view showing partially closed nutritive groove. Labial is at top.

Mancini (1921) and Casier (1953) may have relied more on the belief that *Apocopodon* was a Cretaceous taxon that occurred stratigraphically between *Rhombodus* and *Rhinoptera*. However, *Apocopodon* is an early Paleocene taxon that was coeval with *Rhinoptera* in both Brazil and South Carolina.

Morphological features that *Apocopodon* shares with *Rhinoptera* (Rhinopterinae) include lateral teeth that are thicker mesially than they are distally and, although the teeth in the medial and paramedial rows are generally nearly equal in size, the teeth in remaining lateral rows of the *Apocopodon* dentition decrease in width towards the commissure (observable in the *R. bonus* [SC 88.120.1] and *R. brasiliensis* [LAGESE uncurated] we examined; see also Bigelow & Schroeder, 1953; Cappetta, 1987; Purdy *et al.*, 2001). In contrast, tooth sizes within all lateral rows of a *Myliobatis californica* (BCGM uncurated specimen) dentition are rather consistent towards the commissure (see Bigelow & Schroeder, 1953 for other examples within *Myliobatis*).

The characteristics outlined above indicate that the *Apocopodon* dentition is more similar to *Rhinoptera* than to *Myliobatis* (all three genera occur in the Maria Farinha Formation). Preliminary examination of the upper *R. prisca* dentition (LAGESE V-00013) revealed that the lateral teeth are very similar in size, shape and crown thickness to those of *Apocopodon*, demonstrating the potential difficulty of accurately identifying isolated teeth to the generic level. When comparing the *R. prisca* dentition to *Apocopodon*, it is obvious that *R. prisca* medial teeth are wider (3.12 cm vs. 2 cm).

Histological analyses may prove to be useful in separating morphologically similar tooth types within Myliobatidae, and in their analysis of *Myliobatis* sp. cf. *M. dixonii* from the Maria Farinha Formation, Silva *et al.* (2002) found that the histology of *Myliobatis* differs from *Rhinoptera*. Silva Santos & Gomes (1987) discussed the tooth histology of *A. sericeus*, but their description is very similar to what Silva *et al.* (2002) reported in *Rhinoptera*. This leads to

the possible conclusions that *Apocopodon* is indeed very closely related to *Rhinoptera*, or Silva Santos & Gomes (1987) actually thin-sectioned specimens of *Rhinoptera* and not *Apocopodon*. Additional histological analysis of *Apocopodon* teeth appears to be warranted.

It is interesting to note here that the upper and/or lower dentitions known for *Hypolophites*, a genus recently placed as the sister taxon to Myliobatidae, have a comparable tooth morphology, dental arrangement and plate size to *Apocopodon* (see Stromer, 1910; Leriche, 1913; White, 1934; Cappetta, 1972). However, the two genera can be differentiated at least on the basis that all of the teeth within a *Hypolophites* dentition have holaulocorhize bases, whereas medial and paramedial teeth of *Apocopodon* are polyaulocorhize, and only the teeth in the more distal lateral rows are holaulocorhize (e.g. L3).

Paleobiology

Apocopodon sericeus was considered to be endemic to Brazil (Silva *et al.*, 2007) because the taxon was heretofore not known to occur outside of Pernambuco State, and within this region the ray only occurs within the Maria Farinha Formation. Discovery of *Apocopodon* in South Carolina was therefore a surprise and extends the paleogeographic distribution northwards by more than 7,000 km. The occurrences demonstrate the dispersion potential of elasmobranch species and show that faunal interchange between these widely separated areas occurred during the Paleocene. This appears to be a pattern continuing at least from the latest Cretaceous because the elasmobranch species *Rhombodus binkhorsti*, *Squalicorax pristodontus* and *Cretalamna biauriculata*, occur in these two regions. The discovery of three coeval batoids in the Maria Farinha Formation (and at least three early Paleocene taxa in the Kingstree lag deposit) also highlights the rapid diversification of the group shortly after the K/T extinction.

Barbosa *et al.* (2008) suggested that after the K/T extinction dyrosaurid (longirostrine) crocodylians could have reached North America by first crossing the Atlantic Ocean from western Africa to northeastern Brazil. *Apocopodon* is currently unknown from Africa, but the genus could have reached South Carolina via the northeastern coastline of Brazil (figure 6) into

the Caribbean, where warm water circulated to North America (see Haq, 1984; Pinet & Popenoe, 1985). Alternatively, mollusk species within the Maria Farinha Formation have affinities to the Gulf of Mexico and North America (Barbosa, 2004), and southward migration of *Apocopodon* is a possibility to consider. The timing and direction of migration of *Apocopodon* may be resolved when the source strata of *Apocopodon* fossils are identified in South Carolina and dated using biostratigraphic markers.

The *Apocopodon*-bearing strata within the Maria Farinha Formation were deposited in an inner littoral, probably deltaic environment (< 20 m depth) where water temperature was between 25° and 29° C (Silva & Silva, 2007; see also Silva, 2007; Silva *et al.*, 2007). If indeed derived from the Rhems Formation, the South Carolina *Apocopodon* also likely inhabited a nearshore marine, deltaic environment (Erickson, 1998; Sawyer, 1998; Hutchinson & Weems, 1998; Weems & Bybell, 1998).

Tooth articulation within the *Apocopodon* dentition is complex, with the lingual crown face overlapping the labial face of the succeeding tooth, and the extensive longitudinal wrinkling on crown faces allows for increased surface contact area between teeth through interdigitating of the wrinkles. This results in a serrated suture and is visible in basal view and within the worn labial region of the occlusal surface. Sutured contacts are not visible at the unworn lingual ends of the dentitions because the margins of the occlusal surface appear slightly beveled (e.g. LAGESE V-00014), resulting in a V-shaped furrow between teeth. The serrated contacts become visible as teeth are worn down through occlusion (see below). In addition, there is an irregular transverse lingual ridge located at the crown-root junction, and the labial crown base has a correspondingly irregular furrow. This furrow overlaps the lingual ridge of the preceding tooth. Overlapping and highly interdigitating contacts between teeth could explain the good sample of partial and nearly complete Brazilian plates, and survival of the nearly complete South Carolina plate through at least one episode of reworking.

Except for LAGESE V-00014, the lingual part of a dentition, the specimens we examined all display an arched morphology (seen in profile). This arching reflects the way in which the dentition wrapped over the jaw cartilages and was

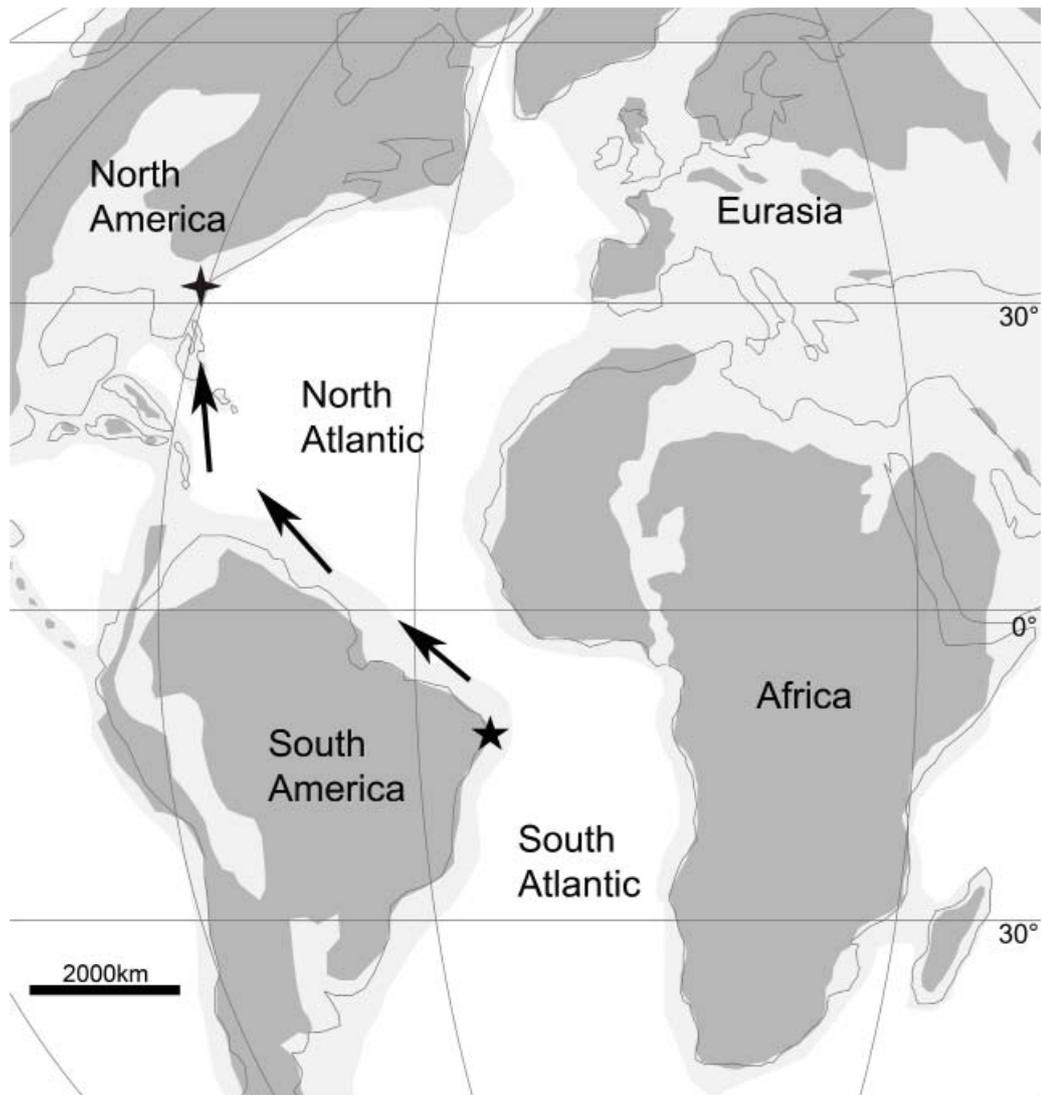


Figure 6. Paleogeographic map showing early Paleocene (Danian) continental distribution (dark gray) and sea level (light gray). Stars indicate *Apocopodon* occurrences in Brazil (five-pointed star) and South Carolina (four-pointed star), and arrows indicate possible dispersal route of marine vertebrates between these regions (modified from Barbosa *et al.*, 2008).

attached via connective tissue. Unfortunately, we are not sure if the preserved arching represents the original state or the effects of taphonomic processes (*e.g.* was the arching more pronounced or less?). In the jaws of *Rhinoptera bonasus* (SC 88.120.1), *R. brasiliensis* (LAGESE uncurated) and *Myliobatis californica* (BCGM uncurated) that we examined, the upper dentitions are more tightly arched than the lower dentitions, and the lower medial teeth are not as wide as the upper medial teeth. If this latter characteristic can be applied to *Apocopodon*, then the nearly symmetrical medial teeth of DGE0-CTG-UFPE 5680 indicate that Gallo *et al.* (2001) were correct in considering the plate to represent a lower dentition. The remaining specimens, which have medial and paramedial

teeth of nearly the same dimensions, would be upper dentitions.

The morphology of the *Apocopodon* dentition indicates that the symphyses of the palatoquadrate (upper jaws) and Meckel's cartilages (lower jaws) were labio-lingually broad and fused, a condition observed on the *M. californica*, *R. bonasus* and *R. brasiliensis* jaws we examined. Extensive ablation is evident on the labial portion of four *Apocopodon* dentitions (LAGESE V-00014 represents only the lingual portion of a dentition). The occlusal surfaces of the teeth in this area have a rough appearance because the enameloid is partly or completely worn away (see especially UFRPE 3223 and DGE0-CTG-UFPE 5680; figure 3A and D, respectively), and this region is also noticeably

concave. Extant members of Myliobatidae use their dentitions to crush and grind up various shelled invertebrate prey animals like crustaceans and mollusks, which results in a similar wear pattern (e.g. Randall, 1967; Cappetta, 1987; Summers *et al.*, 1998; Jardas *et al.*, 2004; Sasko *et al.*, 2006). We concur with previous interpretations that *Apocopodon* was a durophagous predator and the wear seen on dentitions is the result of occlusion between the upper and lower batteries during food processing (see Summers, 2000; Gallo *et al.*, 2001). We may also infer that, based on studies of extant Myliobatidae having comparable tooth plate morphologies, that the dentition-bearing sections of *Apocopodon* jaws were reinforced by multiple layers of calcified cartilage at the jaw surface, as well as internal struts (Summers *et al.*, 1998; Summers, 2000).

Conclusions

Apocopodon was once considered to be endemic to the Paraíba Basin of Pernambuco, Brazil, but the discovery of fossils in South Carolina, USA extends the paleogeographic distribution of this ray more than 7,000 km to the north. *Apocopodon* seems to have been a short-lived taxon because fossils have only been found in deposits of known or suspected early Paleocene (Danian) age (Maria Farinha and Rhems formations). It is possible that the apparently fast evolution of early Cenozoic Myliobatiformes and distribution of *Apocopodon* is related to the filling of ecological niches left vacant after the K/T extinction. Tooth shape and organization of the dentition indicates that *Apocopodon* can be placed within Myliobatidae and that the genus has a closer affinity to Rhinopterinae than to Myliobatinae or Mobulinae.

Apocopodon has a crushing/grinding dentition composed of at least eight longitudinal rows of six-sided (up to 1.5 times wider than long) and thick-crowned (over 1 cm high) teeth, and each row consisted of at least up to nine teeth. The teeth are very strongly articulated to each other via longitudinal wrinkles that interfinger with each other, forming a tightly packed and very rigid dentition (contacts between teeth actually appear serrated in basal view and in regions of the dentition that are highly worn). In addition, the lingual crown face is inclined such that it overlaps the labial

face of the succeeding tooth, and the labial edge of the crown base overlaps a lingual transverse ridge at the crown/root junction. The occlusal surface of unworn teeth is slightly convex and ornamented with longitudinal anastomosing and bifurcating ridges, resulting in a vermicular and/or reticulated texture. Tooth bases are polyaulocorhize, with up to five nutritive grooves on medial teeth, seven grooves on paramedial teeth, and two to three grooves in subsequent lateral rows. The anterior one third to one half of four of the dentitions we studied are heavily worn, with the occlusal surface being concave and with a rough texture. This wear indicates that *Apocopodon* was a durophagous predator and the dentition was used to crush/grind the shells of prey animals during feeding.

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