

On the dentition of *Meridiana convexa* Case (Myliobatoidea), an extinct Early Eocene ray from the United States

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Received 6 October 2008; revised version accepted 15 December 2009

A highly fossiliferous Ypresian (lower Eocene) deposit located in Berkeley County, South Carolina, yielded a very diverse elasmobranch assemblage that includes *Meridiana convexa* Case, 1994. More than 1,800 complete and partial teeth have been recovered, and this sample allows for a more complete understanding of tooth morphology and organization of the dentition. The dentition of *Meridiana* consisted of a closely packed (but not rigid) arrangement of teeth, with a single row of very wide medial teeth and multiple rows of progressively more symmetrical lateral teeth. Tooth bases are polyaulocorhizous in medial and mesially located lateral teeth, but those of distal lateral teeth are most often holaulocorhizous. Previous assignment of *Meridiana* to Dasyatidae is rejected in favor of Myliobatidae. Ontogenetic heterodonty is indicated by a change in crown morphology with increased tooth size, with small teeth (juveniles) having a distinct transverse ridge, and large teeth (adults) having more uniformly convex crowns. Extreme wear through in vivo usage suggests that teeth were retained for a long period of time, and the diet of *Meridiana* consisted of hard-shelled invertebrates. All known occurrences of *Meridiana* are from coastal plain strata of Ypresian age, and the paleogeographic distribution extends from eastern Texas into northeastern Virginia, USA.

KEY WORDS: elasmobranch, dentition, heterodonty, *Meridiana*, Myliobatidae, Ypresian

Introduction

Previously published reports of *Meridiana convexa* are limited to Mississippi and Virginia, USA. In his original description, Case (1994) reported "several dozen" specimens from the lower Eocene Bashi Formation of Lauderdale County, Mississippi. A slightly younger occurrence was later documented by Kent (1999a) from the lower Eocene Nanjemoy Formation of Stafford County, Virginia, but no new morphological or taxonomic interpretations were presented. Both authors described small teeth (up to 7 mm in width) having highly convex, six-sided crowns, and they divided the dentition into anterior and lateral tooth rows. Case (1994) placed *Meridiana* within Dasyatidae (Myliobatiformes), and this assignment was tentatively followed by Kent (1999a).

Material recently collected from lower Eocene coastal plain strata of South Carolina includes over 1,800 teeth referable to *M. convexa*, and the new sample is important because previously unknown tooth morphologies are represented. The purpose of this report is to provide descriptions and illustrations of the new material, offer hypotheses for tooth placement within the jaws, revise the systematic classification of the genus, and discuss the paleobiology and paleobiogeography of this extinct batoid.

Methods

The fossils described herein were collected from an active limestone quarry (Martin Marietta Aggregates) located near Jamestown, Berkeley County, South Carolina (Fig. 1). The deposit that yielded the *Meridiana* sample is overlain by a thick section of Middle Eocene Santee Limestone and is unavailable for observation. However, some material is brought to the surface from a water-filled portion of the quarry as the limestone is extracted, and I recovered macrofossils from spoil piles adjacent to their excavation site. Pieces of Santee Limestone were found associated with these spoil piles, and irregular bedding surfaces contain vertebrate fossils like those within the fossiliferous deposit. I therefore believe that the deposit directly underlies the Santee Limestone, the contact between the two units is disconformable, and material from the older deposit was reworked into the overlying deposit. I collected 80 kg of matrix for processing in the laboratory, and the sediment was disaggregated in water and washed through U.S.A. Standard Testing Sieves down to 0.25 mm (# 60 screen). Sediment that passed through this screen was saved. The remaining concentrates were dried and sorted under a binocular microscope. Broken specimens were repaired using thin butvar (B-76 in acetone).

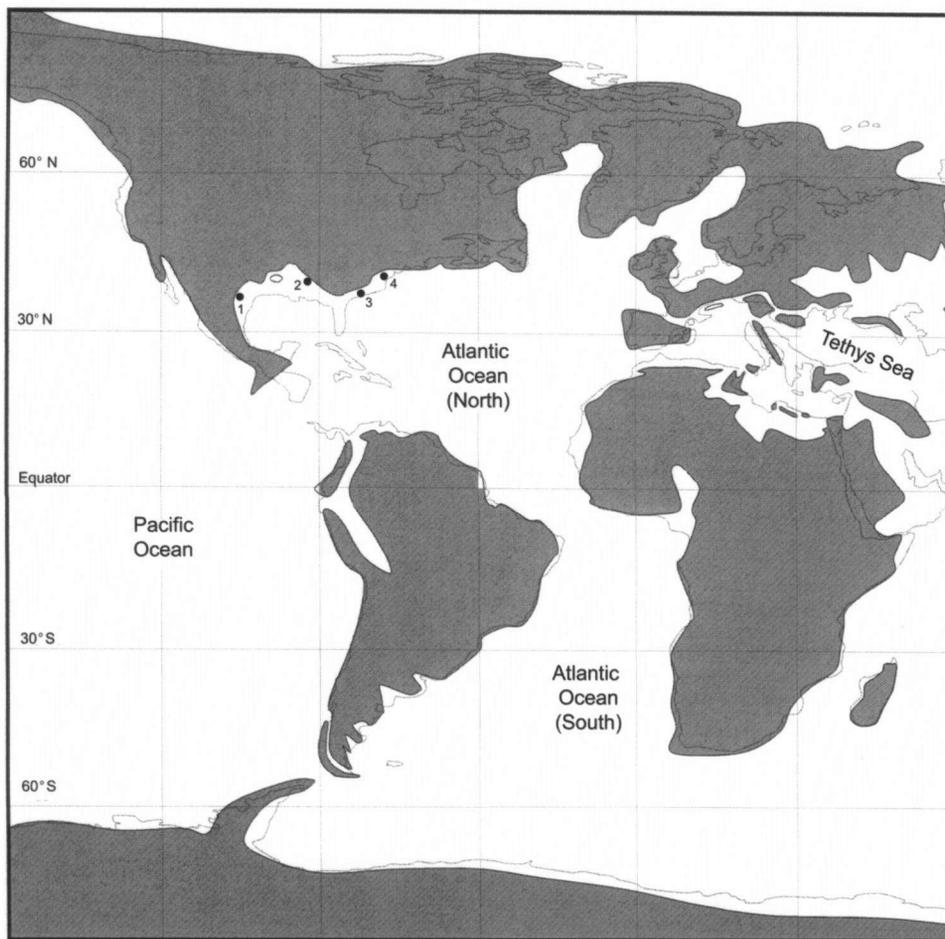


Figure 1. Paleogeographic map showing the locations of the continents during the lower Eocene, with shaded areas representing exposed landmass. Bullets denote occurrences of *Meridania convexa*: 1 – Bastrop County, Texas; 2 - Lauderdale County, Mississippi; 3 - Berkeley County, South Carolina; 4 - Stafford County, Virginia. Map adapted and modified from Weems and Grimsley (1999).

Crown dimensions were measured to the nearest tenth of a millimeter using digital calipers.

Systematic paleontology

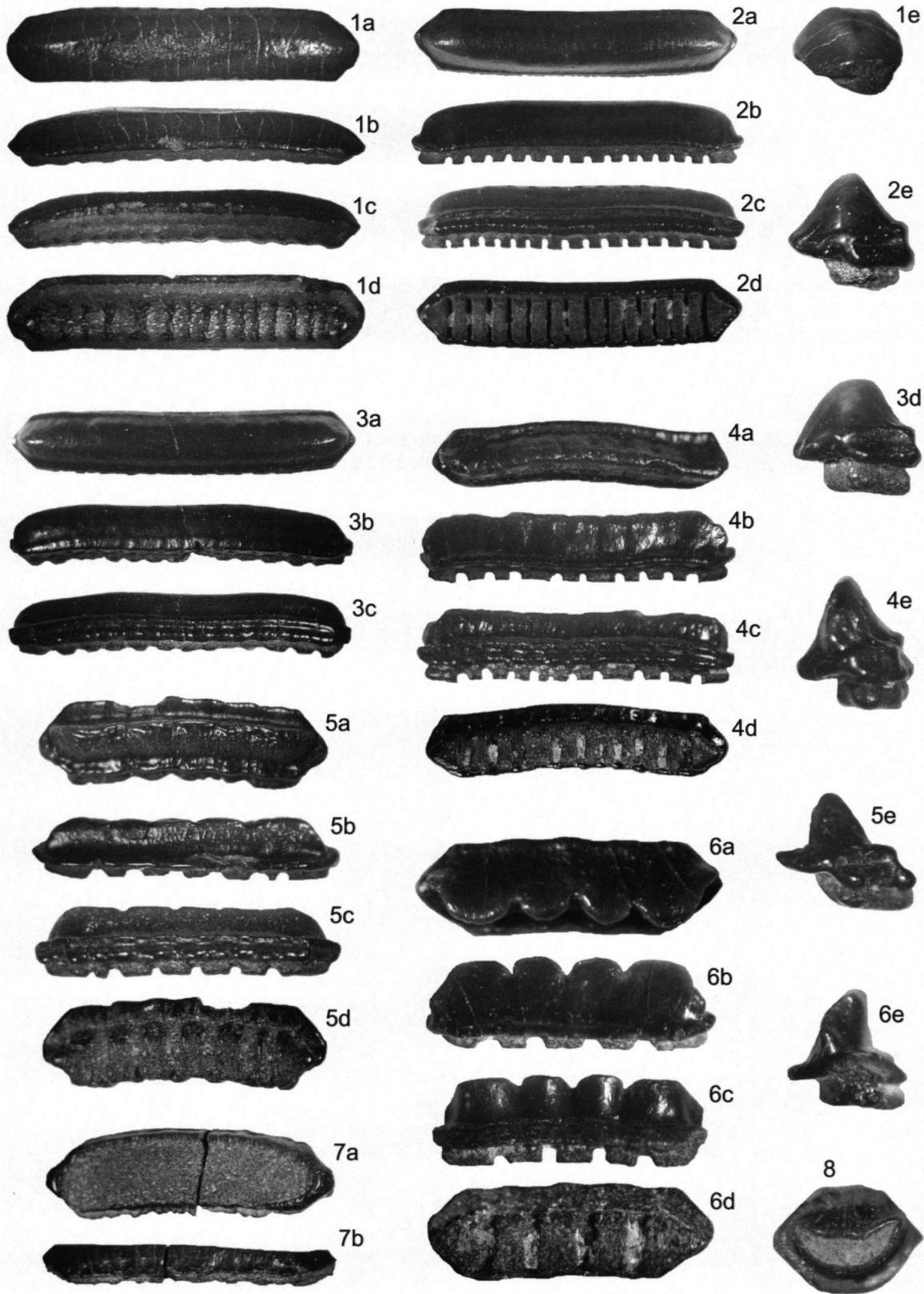
- Elasmobranchii* Bonaparte, 1838
- Batomorphii* Cappetta, 1980
- Myliobatiformes* Compagno, 1973
- Myliobatidae* Bonaparte, 1838
- Meridania* Case, 1994

***Meridania convexa* Case, 1994**
 Figures 2-3

Material examined – 1,112 complete teeth, 334 partial teeth (1,446 total specimens) in the Campbell Geology Museum collection (BCGM); additional 415 specimens in the South Carolina State Museum collection.

Locality – Martin Marietta Aggregates quarry near Jamestown, Berkeley County, South Carolina, 33° 15' 45" N latitude, 79° 39' 17" W longitude (Text Fig. 1).

Figure 2.1-8. *Meridania convexa* Case, 1994. All from the lower Eocene of Berkeley County, South Carolina. Fig. 1a-e, medial tooth, BCGM 8964. a) occlusal view x 3.2; b) labial view x 3.2; c) lingual view x 3.2; d) basal view x 3.2; e) lateral view x 3.7. Fig. 2a-e, medial tooth, BCGM 8968. a) occlusal view x 4.3; b) labial view x 4.3; c) lingual view x 4.3; d) basal view x 4.3; e) lateral view x 7.2. Fig. 3a-d, medial tooth, BCGM 8967. a) occlusal view x 3.7; b) labial view x 3.7; c) lingual view x 3.7; d) lateral view x 7.5. Fig. 4a-e, medial tooth, BCGM 8965. a) occlusal view x 7.6; b) labial view x 7.6; c) lingual view x 7.6; d) basal view x 7.6; e) lateral view x 7.5. Fig. 5a-e, medial tooth, BCGM 8969. a) occlusal view x 7.9; b) labial view x 7.9; c) lingual view x 7.9; d) basal view x 7.9; e) lateral view x 9.6. Fig. 6a-e, BCGM 8966. a) occlusal view x 10.8; b) labial view x 10.1; c) lingual view x 10.1; d) basal view x 10.1; e) lateral view x 8. Fig. 7a-b, medial tooth, BCGM 8970. a) occlusal view x 4.4; b) labial view x 4.5. Fig. 8, lateral tooth, BCGM 8975, occlusal view x 13.2. Labial is at top in occlusal and basal views, left in lateral views.



Description – Evaluation of tooth morphology was somewhat hampered by the preservation of the material which, in addition to wear through in vivo usage, was subjected to

abrasion and breakage prior to fossilization. In general, the teeth have highly convex, six-sided crowns that are covered with a thick layer of enameloid. Crown ornamenta-

tion may consist of fine crenulation and/or rugosity. The labial crown base is formed into a narrow, rounded edge, whereas a thin, shallow transverse groove is located at the base of the lingual faces.

Many teeth in the sample are much wider than long, with one specimen measuring 18.4 mm in width and 4 mm in length (Fig. 2.1). Three other teeth measure 12 to 15 mm in width (*i.e.*, Figs. 2.2, 2.3), and the width-to-length ratio of these teeth averages 7.5:1. Another specimen is 10 mm wide and 1 mm long. In occlusal view, the crowns of these teeth are straight or slightly sinuous. Viewed labially or lingually, the distal ends of the crown often curve basally (*i.e.*, Figs. 2.1c, 2.2c, 2.3c).

Many teeth have width-to-length ratios of about 3:1 and 2:1 (Figs. 3.1-3.2), but the majority of the sample has a ratio of nearly 1:1 (Figs. 3.3-3.7). These latter teeth are more symmetrically hexagonal, although some teeth are slightly wider than long and others longer than wide. Other unusual teeth are distinguished from the rest in that the margin of one side of the crown is angular, whereas the other is rounded and often basally curling (Figs. 3.9, 3.10a).

Whereas crowns of the largest teeth have a simple domed appearance and sub-triangular to hemispherical longitudinal cross section, smaller teeth bear a high ridge that does not reach the lateral edges of the crown. In occlusal view, the trend of the ridge on wide teeth follows that of the crown, but the ends of the ridge often curve labially. Additionally, the apex appears irregular when viewed labially. The labial face of the ridge is often nearly vertical and may be flat, weakly convex, or weakly concave. The lingual face is always convex and forms an acute angle with the basal plane of the crown. On more symmetrical teeth, the shape of the ridge is also highly variable, being crescent-shaped or straight (in occlusal view), with a labial face that is vertical (overall high ridge) to highly lingually inclined (overall low ridge), and concave or flat (Figs. 3.5-3.8). The lingual face is always convex. On some lateral teeth, it is apparent that one side of the crown is more heavily worn than the other. Teeth having one angular margin and the other rounded are generally very low-crowned with a short, very low, centrally located transverse ridge; a few of these teeth are completely flat, but others bear a large ridge.

The tooth bases are very low and polyaulocorhizous, with between three and 16 lobes that are separated by nutritive grooves (Figs. 2.1d, 2.2d, 2.4d, 3.2d). Nearly hexagonal teeth predominantly have holaulocorhizous (one nutritive groove) bases. Lobe width may vary, but the mesial- and distal-most lobes are always triangular. Basal attachment surfaces are flat. The lobes of holaulocorhizous bases may be equidimensional, but the nutritive groove of many specimens divides the base into a large mesial lobe and much smaller distal lobe (Fig. 3.10c). One or two small foramina are found within a nutritive groove, but no foramina were observed at the crown/base junction. Several specimens show that nutritive grooves can be secondarily roofed over, a condition also observed in *Igdabatis* Cap-

petta, 1972. In basal view, the labial edge of the crown extends past the base, but the root comes very close to the lingual edge of the crown (Figs. 2.2d and 2.4d).

Discussion

Tooth arrangement— In attempting to reconstruct the dentition of an extinct ray based on isolated teeth (see Shimada, 1997), the possibility of tooth heterodonty (changes in tooth shape within the dentition) must be taken into consideration. Heterodonty can be expressed in a number of ways, including monognathic, dignathic, gynandric, and ontogenetic (Compagno, 1970; Ward, 1983; Cappetta, 1987; Welton and Farish, 1993; Shimada, 2001). Based on the South Carolina material, it is apparent that several forms of dental heterodonty existed within *Meridania*.

Although I concur with Case (1994) and Kent (1999a) that the *Meridania* dentition exhibited monognathic heterodonty, their proposed differentiation into anterior, lateral and posterior rows is incorrect. I consider the very wide specimens (*i.e.*, Figs. 2.1-2.3) in the South Carolina sample to be homologous to medial teeth of *Myliobatis* and *Rhinoptera* Cuvier, 1829. Furthermore, I believe that the upper and lower dentitions consisted of a single row of wide medial teeth, one or two rows of lateral teeth having width to length ratios between 3:1 and 2:1, and multiple rows of nearly symmetrical lateral teeth having a 1:1 ratio. The height of the crown appears to have changed meso-distally (especially evident in ridged teeth), becoming lower towards the commissure. The margins of the upper and lower dentitions were formed from teeth seen in Figures 3.9 and 3.10, with only the angular mesial margin articulating with the rest of the dentition. Unfortunately, the exact number of lateral rows remains unclear, and this is variable in extant species of Myliobatidae (Bigelow and Schroeder, 1953). In fact, variation occurs within individuals, as a specimen of *Rhinoptera bonasus* (Mitchill, 1815) I examined (SC 88.120.1) has four rows of lateral teeth on the right side but only three on the left (upper and lower batteries).

Ward (1983: 109) pointed out that dignathic heterodonty occurs in only a few rays. In the South Carolina *Meridania* sample, some of the medial teeth are weakly arched but others are straight, and this variation could be interpreted as weak dignathic heterodonty, with the arched teeth belonging to the upper dentition and the straight teeth to the lower dentition. This condition is found in Myliobatidae, with the upper teeth combining to form a convex crushing surface, whereas the lower dentition is flat. An alternative hypothesis for dignathic heterodonty in *Meridania* is that medial teeth having a 7.5:1 (or greater) width-to-length ratio formed part of one battery, and teeth having a ratio of around 3:1 represent medial teeth in the opposing battery. This is observable in SC 88.120.1 (*R. bonasus*), but the upper medial teeth are wider than the lower medial teeth (see also Bigelow and Schroeder, 1953).

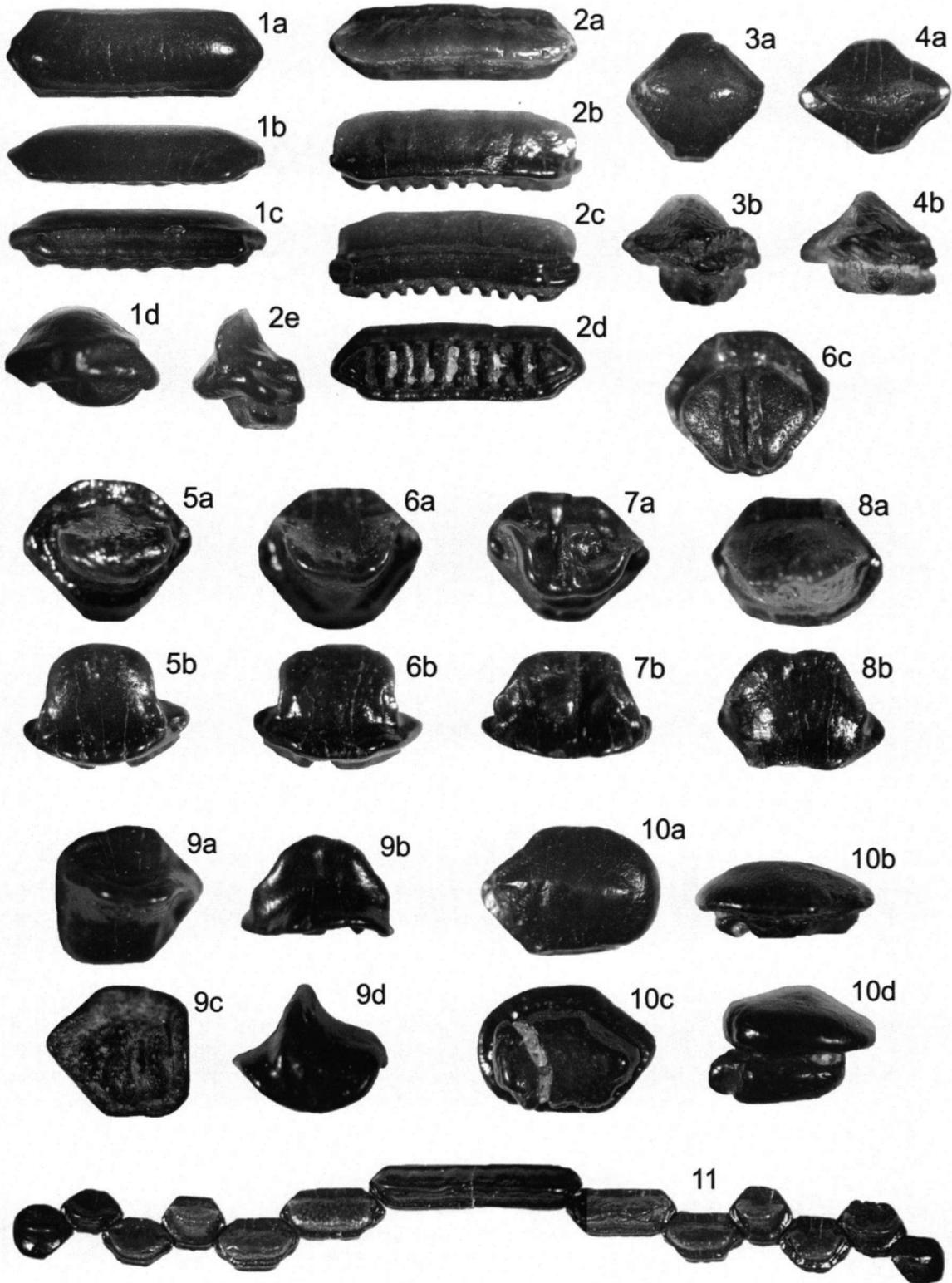


Figure 3.1-9. *Meridiania convexa* Case, 1994. All from the lower Eocene of Berkeley County, South Carolina. Fig. 1a-d, lateral tooth, BCGM 8972. a) occlusal view x 3.9; b) labial view x 3.9; c) lingual view x 3.9; d) lateral view x 6.5. Fig. 2a-e, lateral tooth, BCGM 9871. a) occlusal view x 8.4; b) labial view x 8.4; c) lingual view x 8.4; d) basal view x 8.4; e) lateral view x 11.9. Fig. 3a-b, lateral tooth, BCGM 8973. a) occlusal view x 5.5; b) lateral view x 5.9. Fig. 4a-b, lateral tooth, BCGM 8974. a) occlusal view x 4.8; b) lateral view x 7. Figs. 5a-b, lateral tooth, BCGM 8976. a) occlusal view x 11.2; b) labial view x 11. Fig. 6a-c, BCGM 8977. a) occlusal view x 11.7; b) labial view x 12.2; c) basal view x 12. Fig. 7a-b, lateral tooth, BCGM 8978. a) occlusal view x 11.7; b) labial view x 12.2. Fig. 8a-b, lateral tooth, BCGM 8979. a) occlusal view x 11.9; b) labial view x 11.7. Fig. 9a-d, distal-most lateral tooth, BCGM 8981. a) occlusal view x 12.9; b) labial view x 13.4; c) basal view x 12.4; d) distal view x 13.2. Fig. 10a-d, distal-most lateral tooth, BCGM 8980. a) occlusal view x 6; b) labial view x 6; c) basal view x 6; d) distal view x 7.8. Fig. 11, hypothetical reconstruction of tooth series, occlusal view x 4.9. Labial is at top in occlusal and basal views, left in lateral views (except 10d, which is at right).

Teeth of males and females are presumably present, but their morphologies are not readily differentiable. One unlikely hypothesis for gynandric heterodonty in *Meridiana* is that, if teeth having ratios of 3:1 also represent medial teeth, one sex had wider medial teeth than the other. A more plausible hypothesis is that teeth having a distinct transverse ridge belonged to males, whereas the domed specimens represent female teeth. However, well-developed ridges are only found on smaller examples for each tooth position (largest ridged medial tooth measures only 6 mm in width), and this then might imply that male individuals were smaller than females. Gynandric heterodonty is observable in rays like *Dasyatis* Gray, 1851 and “*Raja*”, where male teeth can be much higher crowned than female teeth (Feduccia and Slaughter, 1974; Kajiura and Tricas, 1996). However, this morphological variation is not necessarily related to dietary differences between the sexes. In *Dasyatis*, for example, cuspidate male teeth are used to grasp the pectoral fins of females during copulation (Kajiura *et al.*, 2000). It has been shown that male teeth of *D. sabina* (Lesueur, 1824) are replaced in as little as seven days, and within a few short months (in preparation for the mating season) tooth morphology gradually changes from a low-crowned form identical to females, to a high-crowned form (Kajiura and Tricas, 1996; Kajiura *et al.*, 2000). However, this scenario seems unlikely in *Meridiana* because highly worn tooth crowns indicate long-term use in crushing hard-shelled invertebrates, rather than short-term use biting fleshy fins during copulation. In *Aetobatus narinari* (Euphrasen, 1790) and *Rhinoptera javanica* Müller and Henle, 1841, flat-crowned teeth within crushing dentitions are more than sufficient to grasp, and cause serious injuries to, a mate (Tricas, 1980; Kajiura *et al.*, 2000).

Ward (1983) noted that batoids exhibit ontogenetic heterodonty, and this phenomenon was developed in *Meridiana* at least in as much as the overall dimensions of teeth within each position changed as individuals grew larger. The South Carolina sample also shows that teeth in all positions can have a distinct transverse ridge, but this ridge is more often found on smaller examples within each position (*i.e.*, Figs. 2.5, 3.2, 3.6). In contrast, the largest medial and lateral teeth are more uniformly convex with a rounded apex (*i.e.*, Figs. 2.1-2.3, 3.1, 3.3). Many teeth appear to show a transition from a crown having a distinct transverse ridge to one being uniformly convex (*i.e.*, having a convex crown with a simple angular apex; see Fig. 3.4). This leads me to the interpretation that crown convexity represents ontogenetic heterodonty, with a transverse ridge being very well developed on teeth of juvenile individuals, but tooth size increases and ridge formation is gradually reduced as an animal ages.

One particularly interesting feature of the ridge on some medial and lateral teeth can be interpreted as further evidence for ontogenetic heterodonty. The ridge has the appearance of being formed from multiple small ridges (of the type seen on more distally located lateral teeth) that have coalesced into one continuous structure (Fig. 2.6a-c). These specimens suggest that teeth having a width-to-

length ratio of 2:1 or greater formed from the fusion of multiple small teeth early in ontogeny, perhaps even in utero. In utero tooth replacement is known to occur in myliobatids (Bigelow and Schroeder, 1953; Smith and Merriner, 1984), and the ontogenetic range from embryonic to adult tooth morphologies of sharks can be quite drastic (*i.e.*, Purdy and Francis, 2007).

Paleobiology and Paleobiogeography – I believe that teeth of *Meridiana* were arranged in a pavement-type dentition consisting of a single row of very wide medial teeth and multiple rows of progressively more symmetrical lateral teeth, and each series ended in a tooth having a rounded distal margin (Fig. 3.11). Tooth packing was not rigid because only the crown bases of articulating teeth were in contact with each other via a tongue-and-groove system. In contrast, dentitions of *Myliobatis* and *Rhinoptera* are inflexible, with articulating teeth being tightly packed and connected (sometimes sutured) via high vertical surfaces. Although the rate of tooth replacement of *Meridiana* is unknown, tooth wear indicates that it was rather slow. In the initial stages of wear, the apical surfaces of the crown are worn smooth. Basins eventually form on the crown as the enameloid is worn away (Fig. 2.8). Lateral teeth that are unevenly worn (*i.e.*, one side of crown is higher than the other) indicate that the occlusal surface was not perfectly centered over the opposing tooth. In the most extreme cases of wear, the crowns have become very low and the occlusal surfaces are flat and formed of the dentine core, with only a thin rim of enameloid remaining (Fig. 2.7). A series of fine closely spaced, parallel longitudinal striations are preserved on some teeth, suggesting labio-lingual motion during food processing. My interpretation of the organization of the dentition suggests that the symphyses of the palatoquadrates and Meckel’s cartilages were labio-lingually broad and fused. Additionally, tooth morphology indicates that *Meridiana* was a duraphagous predator, and potential prey species in the Jamestown deposit include *Cubitostrea multicosata* (Deshayes, 1832) (the most abundant macroinvertebrate), pectinids and other bivalves, gastropods, brachiopods, cidaroid echinoids, and decapod crustaceans. The proposed ontogenetic variation within the taxon may indicate a shift in diet from immaturity into adulthood. Polygonal tuberculated plates recovered from the Jamestown site are identical to those identified by Case (1994: pl. 14, figs. 295-297) as *Meridiana* dermal denticles, but these appear to be more similar to ostraciid dermal plates (see also Weems, 1998, fig. 5; Weems, 1999, pl. 4.7, figs. E-F).

Current knowledge of the paleobiogeography of *Meridiana* shows that the taxon was endemic to coastal south-central and southeastern USA, as no comparable material has been reported from temporally equivalent marine strata elsewhere in the USA, Europe (*i.e.*, Casier, 1946), or Africa (*i.e.*, Arambourg, 1952; Case and Cappetta, 1990; Noubhani and Cappetta, 1997). With the recent discovery of *M. convexa* in the Calvert Bluff Formation of Bastrop County, (identified as *Myliobatis* n. sp. by Claeson and Stidham (2007)), the geographic distribution of the taxon

extends from eastern Texas to northeastern Virginia (Fig. 1).

The horizon within the Calvert Bluff Formation that yielded the *Meridania* remains has been reported as being near the Paleocene-Eocene boundary and approximately time-equivalent to the Bashi Formation of Mississippi (Alexander and Stidham, 2007; Claeson and Stidham, 2007). In Mississippi, *Meridania* occurs in strata of the Bashi Formation that are within calcareous nannofossil zone NP 10 (Case, 1994; Harrington, 2003), and the sediments were deposited between 55.0 to 53.6 Ma (Berggren *et al.*, 1995; Danehy *et al.*, 2007). In Virginia, *Meridania* occurs in deposits of the basal part of Bed B of the Potapaco Member, Nanjemoy Formation (Kent, 1999a; Weems and Grimsley, 1999), which has been assigned to zone NP 11 (Gibson and Bybell, 1991). This zone represents an interval of time of only 800,000 years, from 53.6 to 52.8 Ma (Berggren *et al.*, 1995). Although a precise age for the South Carolina material is unknown, associated ostracodes (F. Swain, personal communication, 2006) and teleost otoliths (G. Stringer, personal communication, 2007) indicate the deposit formed during the lower Eocene, possibly as late as zone NP 12 (50.8 to 52.8 Ma). The fossiliferous deposit would therefore be roughly time-equivalent to the only formally recognized lower Eocene deposit in South Carolina, the Fishburne Formation (NP 11). The temporal duration of *Meridania* therefore appears then to have been less than 5 million years within the Ypresian Stage. At its type locality, Case (1994) did not recover *Meridania* or teeth of a similar design from the Paleocene portion of the Tusahoma Formation, nor have specimens been recovered from other Paleocene marine deposits in the USA (i.e., Cvacara and Hoganson, 1993; Case, 1996; Purdy, 1998). In addition, no such material has been reported from younger Eocene deposits within the US Atlantic or Gulf Coastal plains (i.e., Westgate, 1984; Manning and Standhardt, 1986; Case and Borodin, 2000).

As in the Bashi (Mississippi) and Nanjemoy (Virginia) formations, the Jamestown elasmobranch assemblage contains a variety of pelagic shark taxa, as well as a diverse benthic component consisting of orectolobiform, squatini-form, and heterodontiform sharks, and batoids. The depositional settings of the units producing these assemblages appear to have been similar, with the vertebrate taxa inhabiting tropical to subtropical neritic marine environments (Dockery, 1986; Ingram, 1991; Kent, 1999a, 1999b; Weems, 1999; Weems and Grimsley, 1999). There are indications that the Bashi Formation (and likely the Calvert Bluff Formation) was deposited within the Paleocene-Eocene Thermal Maximum (Danahy *et al.*, 2007).

Systematic position – The South Carolina material allows for a new interpretation of the systematic placement of *Meridania*. Case (1994: 124) originally assigned *Meridania* to Dasyatidae “with confidence,” and Kent (1999a) tentatively followed this assignment. However, nearly symmetrical hexagonal teeth (lateral teeth as interpreted in this report) were incorrectly used to differentiate the dentition into anterior and lateral rows (based on the doming of

the crown or development of a transverse ridge). Case (1994) also erroneously considered *Dasyatis globidens* Arambourg, 1952 to be synonymous with *Meridania* (i.e., *M. globidens*). Noubhani and Cappetta (1995) have shown that the similarity of *D. globidens* (referred by them to a new taxon, *Ishaquia globidens*, but retained in Dasyatidae) to lateral teeth of *Meridania* is superficial.

The previous placement of *Meridania* in Dasyatidae is incorrect because the dentition was composed of a single row of very wide medial teeth and multiple rows of more symmetrical lateral teeth (Fig. 3.11). In addition, tooth bases of *Meridania* medial and mesially located lateral teeth are polyaulocorhizous (also noted by Case (1994)), whereas teeth of Dasyatidae are holaulocorhizous. Two extinct genera considered members of Dasyatidae, *Hypolophites* Strömer, 1910 and *Hypolophodon* Cappetta, 1980, had a dentition modified for crushing, but there are significant differences between these taxa and *Meridania*. Species within *Hypolophites* and *Hypolophodon* have teeth that are more or less equidimensional, and tooth bases are holaulocorhizous (Strömer, 1910; Leriche, 1913; Cappetta, 1972, 1980). *Meridania* cannot be considered a basal member of Dasyatidae because the group is known from older Upper Cretaceous and Paleocene strata (Arambourg, 1952; Noubhani and Cappetta, 1997; Cappetta and Case, 1999).

A recent phylogenetic analysis of Myliobatoidea showed that two monophyletic groups, Myliobatinae and Rhinopterinae, comprise the clade Myliobatidae (González-Isáís and Domínguez, 2004). My interpretations of tooth morphology and dental organization of *Meridania* indicates a close similarity to taxa within Myliobatidae. The tooth base morphology of *Meridania* is very similar to the Cretaceous taxa *Igdabatis* and *Brachyrhizodus* Romer, 1942, and these latter two taxa are considered members of Myliobatidae (Cappetta, 1972; Prasad and Cappetta, 1993; Welton and Farish, 1993). It is interesting to note that all three taxa appear to have exhibited the rhinopterid characteristic of decreasing tooth width away from the jaw symphyses (see Bigelow and Schroeder, 1953; Cappetta, 1987). Unique dental characteristics like the convexity and thick enameloid covering of the crown, the nature of tooth articulation, and the development of ontogenetic heterodonty, might justify the creation of a new family for *Meridania*, but I refrain from doing so because the taxon is currently monospecific.

Conclusions

Meridania convexa represents an extinct ray that appears to have been geographically limited to the south-central and southeastern United States. In addition, the taxon appears to be temporally restricted to the lower Eocene and may be a marine index fossil for the Ypresian Stage of the USA. Based solely on dental characteristics, it is more appropriate to assign *Meridania* to Myliobatidae as opposed to Dasyatidae. *Meridania* had a pavement-like dentition consisting of a row of very wide, six-sided medial teeth

and multiple rows of lateral teeth that became more symmetrical away from the jaw symphyses. The teeth articulated with each other via thin labial basal edges and narrow lingual basal grooves, and the overall triturating surface was rather knobby. Wear patterns on *Meridania* crowns indicate extensive use in crushing hard-shelled invertebrates. Ontogenetic heterodonty is expressed through the formation of a distinct transverse ridge on small examples (juveniles) of medial and lateral teeth, with a transition to a more uniformly domed crown in larger specimens (mature individuals).

Acknowledgements

I would like to thank Billy Palmer for bringing the Jamestown material to my attention. Palmer also organized a trip to the Martin Marietta quarry and donated a significant fossil collection to the BCGM. Vance McCollum provided insightful comments on Paleogene fossil occurrences in South Carolina. Jim Knight (South Carolina State Museum) permitted me to examine specimens in his care, and his editorial remarks improved an earlier version of this manuscript. Frederick Swain (retired, University of Minnesota) identified the Jamestown ostracodes and Gary Stringer (University of Louisiana, Monroe) identified the teleost otoliths, and their time and effort is greatly appreciated. Kerin Claeson (The University of Texas, Austin) graciously allowed me to use data she presented at the 2007 annual meeting of the Society of Vertebrate Paleontology in Austin, Texas.

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