

FIRST OCCURRENCE OF A PARTIAL DENTITION OF *RHOMBODUS BINKHORSTI* (BATOMORPHI: RHOMBODONTIDAE) IN THE AMERICAS, WITH COMMENTS ON THE NORTH AMERICAN DISTRIBUTION OF THE SPECIES

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ABSTRACT

The first reasonably complete dentition from the Americas of a Late Cretaceous batoid, *Rhombodus binkhorsti*, was collected from the Maastrichtian Ripley Formation of Union County, Mississippi, USA. The specimen confirms that the diamond-shaped teeth characteristic of the genus are arranged into very tightly packed alternating files. *Rhombodus binkhorsti* was widely distributed during the Maastrichtian and has been reported from Asia, Africa, and North and South America. In North America, the species has been recovered from Maastrichtian strata of the Atlantic Coastal Plain and Cretaceous Mississippi Embayment, but not from time-equivalent deposits related to the Cretaceous Western Interior Seaway. North American occurrences of *Rhombodus binkhorsti* appear stratigraphically confined within calcareous nannoplankton Zones CC24–26, indicating it is an index fossil for the Maastrichtian stage.

INTRODUCTION

Rhombodus Dames, 1881 is an extinct genus of myliobatiform ray that is primarily known from the Maastrichtian Stage of the Cretaceous Period. Geographically widely distributed, the genus contains seven recognized species, all of which were originally based on isolated teeth. Although a single caudal spine has been attributed to *Rhombodus* (Hamelink, 1952), the specimen did not occur with any teeth and this association remains to be validated. All seven species of *Rhombodus* can be characterized by the combination of diamond-shaped crown (wider than long) and bilobed root (Noubhani and Cappetta, 1994; Cappetta, 2012), but individual species differ in various aspects, like the convexity of the crown, ornamentation on the occlusal surface and labial/lingual faces, and overall tooth size. As these species are known from isolated teeth, interpretations of tooth configuration within the dentition have been hypothetical.

Cappetta (1987) erected the family Rhombodontidae to account for the unique tooth shape of *Rhombodus* and the theoretical arrangement of teeth within the dentition. As there is no equivalent modern analogue to *Rhombodus*, assignment of the genus to the unique family Rhombodontidae (Cappetta, 1987) is appropriate. Various taxonomic rankings maintain the family within Myliobatiformes (Vullo, 2005; Kriwet et al., 2007; Cappetta, 2012). Enault et al. (2016) investigated the tooth histology of *Rhombodus*

binkhorsti Dames, 1881 and noted some potential taxonomically useful features that need further investigation (i.e., variation between *R. binkhorsti* and *Hypsobatis*). Based on the histological work of Enault et al. (2013; 2016), *Rhombodus* does appear to be more similar to Myliobatidae (eagle rays) by having a robust crushing dentition like *Myliobatis*, *Aetomylaeus* and *Rhinoptera*, rather than gymnurids (butterfly rays) and mobulids (devilrays).

Herein we report a partial dentition of *Rhombodus binkhorsti* that was collected from Maastrichtian strata of the Coon Creek Member of the Ripley Formation in Union County, Mississippi, USA. A second, much less complete dentition, was recovered from the lower Paleocene (Danian) Clayton Formation (reworked from the underlying Maastrichtian Arkadelphia Formation) of Hot Spring County, Arkansas, USA. These specimens confirm how isolated teeth are arranged into alternating files to form a rigid crushing structure (for durophagy). We also comment on the geographic, stratigraphic, and temporal distribution of the species within North America, with several new occurrences being presented.

METHODS

Two partial dentitions and isolated teeth of *Rhombodus binkhorsti* are described herein. The more complete dentition was collected as float from the exposed strata by an avocational collector, Mr.

Richard Keyes, who later donated the specimen to the paleontological collections at the Mississippi Museum of Natural Science (MMNS) in Jackson, U.S.A. The less complete specimen was also collected as float from the exposed strata and placed in the collections of the MMNS. As part of our study, we examined numerous other isolated teeth that were surface collected from several localities in Alabama and Mississippi, and that were recovered from *in situ* in South Carolina, U.S.A. These isolated teeth reside in the collections at the MMNS, South Carolina State Museum (SC) in Columbia, and Horry County Museum (HCM) in South Carolina. We reviewed the literature for published occurrences of *Rhombodus binkhorsti* in North America, but we only included in our dataset those references that provided illustrations of teeth from which we could verify the taxonomic identity. We also verified the reported geological units from which *R. binkhorsti* teeth have been collected and their ages, which are tabulated in Table 1. Dial calipers were used to measure the various morphological features discussed below, like the crown width and height. With respect to the terminology used to describe the teeth, we deviated from that utilized by Noubhani and Cappetta (1994) for *Rhombodus* and instead opted for a more descriptive and less ambiguous set of terms. However, we have provided their terminology in parentheses for comparative purposes. All of the specimens illustrated herein were photographed with a Nikon D80 or Nikon D300s digital SLR cameras with Tamron SP macro lenses. Photographs were rendered, and the accompanying figures designed, in Adobe Photoshop CC 2017. Higher taxonomic rankings follow Nelson et al. (2016).

SYSTEMATIC PALEONTOLOGY

- Class Chondrichthyes Huxley, 1880
- Subclass Elasmobranchii Bonaparte, 1838
- Infraclass Euselachii Hay, 1902
- Division Batomorphi Cappetta, 1980
- Order Myliobatiformes Compagno, 1973
- Suborder Myliobatoidei Compagno, 1973
- Family Rhombodontidae Cappetta, 1987
- Genus *Rhombodus* Dames, 1881
- Rhombodus binkhorsti* Dames, 1881
- Figures 1, 3 and 4

Material Examined—MMNS VP-5369, partial dentition (Figure 1).

Stratigraphic and Geographic Occurrence—Coon Creek Member of the Ripley Formation (Maastrichtian, Zone CC24), site MS.73.033a, Union County, Mississippi, USA (Figure 2; Table 1). More detailed locality information is on file at the MMNS and is available to qualified researchers upon request.

Additional Material Examined—MMNS VP-394, two teeth; MMNS VP-4319, tooth; MMNS VP-4743, tooth (Figure 4J); MMNS VP-5022, two teeth; MMNS VP-5171, tooth; MMNS VP-5184, tooth; MMNS VP-5224, tooth; MMNS VP-5308, tooth; MMNS VP-5537, two teeth; MMNS VP-5715, tooth; MMNS VP-5722, tooth; MMNS VP-5766, tooth; MMNS VP-5782, two teeth; MMNS VP-5899, two teeth; MMNS VP-6015, four teeth (Figure 3E-I); MMNS VP-6017, tooth; MMNS VP-6027, tooth (Figure 4O); MMNS VP-6056, tooth; MMNS VP-6138, two teeth; MMNS VP-6155, five teeth; MMNS VP-6228, tooth (Figure 4P); MMNS VP-6531, tooth; MMNS VP-6671, two teeth; MMNS VP-7060, tooth; MMNS VP-7160, tooth; MMNS VP-7801, five teeth; MMNS VP-7963, tooth; MMNS VP-8087, partial dentition (Figure 3A-D); MMNS VP-8107, tooth; MMNS VP-8115, three teeth; MMNS VP-8282, two teeth; MMNS VP-8417, four teeth (Figure 4K); MMNS VP-8473, tooth (Figure 4L); MMNS VP-8474, tooth (Figure 4M); MMNS VP-8902, tooth; MMNS VP-9090, tooth; SC87.158.82, tooth (Figure 4D); SC87.158.83–SC87.158.86, isolated teeth; SC87.158.87, lateral tooth (Figure 4N); SC87.158.88–SC87.158.90, isolated teeth; SC87.158.91, tooth (Figure 4B); SC87.158.92, tooth; SC87.158.93, tooth; SC87.158.94, tooth (Figure 4C); SC87.158.95–SC158.99, isolated teeth; SC87.158.100, tooth (Figure 4F); SC87.158.101, tooth (Figure 4E); SC89.158.102, tooth; SC87.158.104–SC87.158.133, isolated teeth; SC87.158.134, five teeth; SC87.158.135, 28 small teeth; SC87.158.136, 18 tiny teeth; SC87.158.137, 187 teeth; SC2013.13.16, 121 teeth; SC2013.13.17, tooth (Figure 4I); SC2013.13.18, tooth; SC2013.13.19, tooth (Figure 4G); SC2013.13.28, six teeth; SC2013.13.100, tooth (Figure 4H); HCM uncatalogued (Figure 4Q). See Table 1 and Figure 4 for details on stratigraphic provenience.

Description—MMNS VP-5369 is a partial dentition measuring 3.6 cm wide (mesio-distal) and 3.5 cm long (labio-lingual). It consists of 47 articulated diamond-shaped teeth arranged into 12 parallel, alternating files (Figure 1A, B). An additional disarticulated tooth is embedded in matrix on the basal surface (Figure 1C, D). Individual teeth are slightly wider than long (6 mm vs. 5.5 mm, respectively). We could not accurately measure the crown height of unworn teeth located at the center of the dentition due to the curvature of the plate and the presence of indurated matrix on the basal surface. However, teeth from the medial region of the preserved plate and located labially (Figure 1E) or lingually (Figure 1F) measure up to 4.5 mm in crown height, and 6.5 mm in total height. In occlusal view, the labial and lingual angles (medio-labial and medio-lingual angles *sensu* Noubhani and Cappetta 1994) are sharp, whereas the

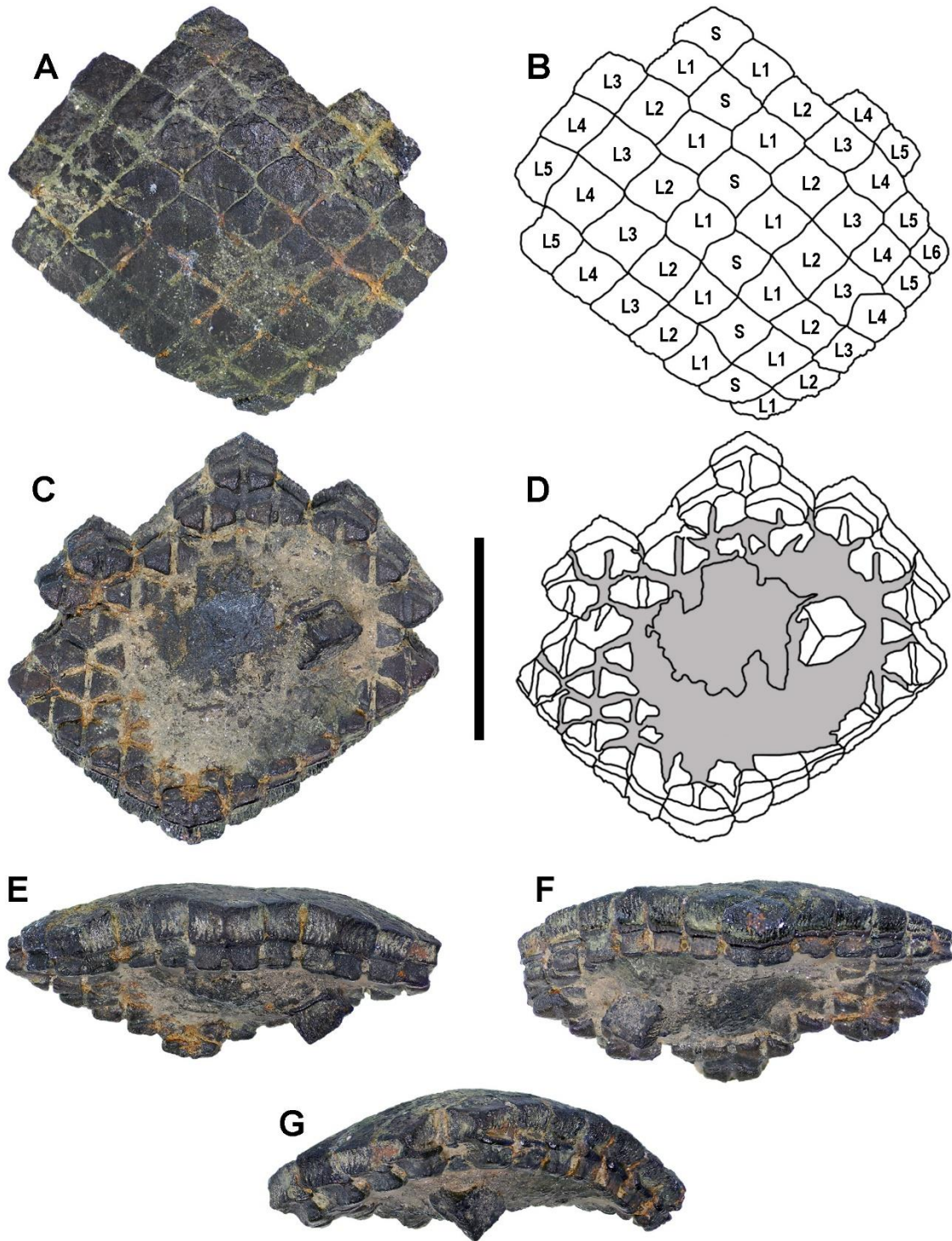


FIGURE 1. Partial dentition of *Rhombodus binkhorsti*, MMNS VP-5369. A–B, photograph (A) and line drawing (B) in occlusal view. C–D, photograph (C) and line drawing (D) in basal view. E–G, photographs of the specimen in labial (E), lingual (F), and profile (G) views. Labial at top in A–D, right in G. Scale bar = 2 cm. Abbreviations: s, symphyseal file; L1, first lateral file; L2, second lateral file; L3, third lateral file; L4, fourth lateral file; L5, fifth lateral file; L6, sixth lateral file.

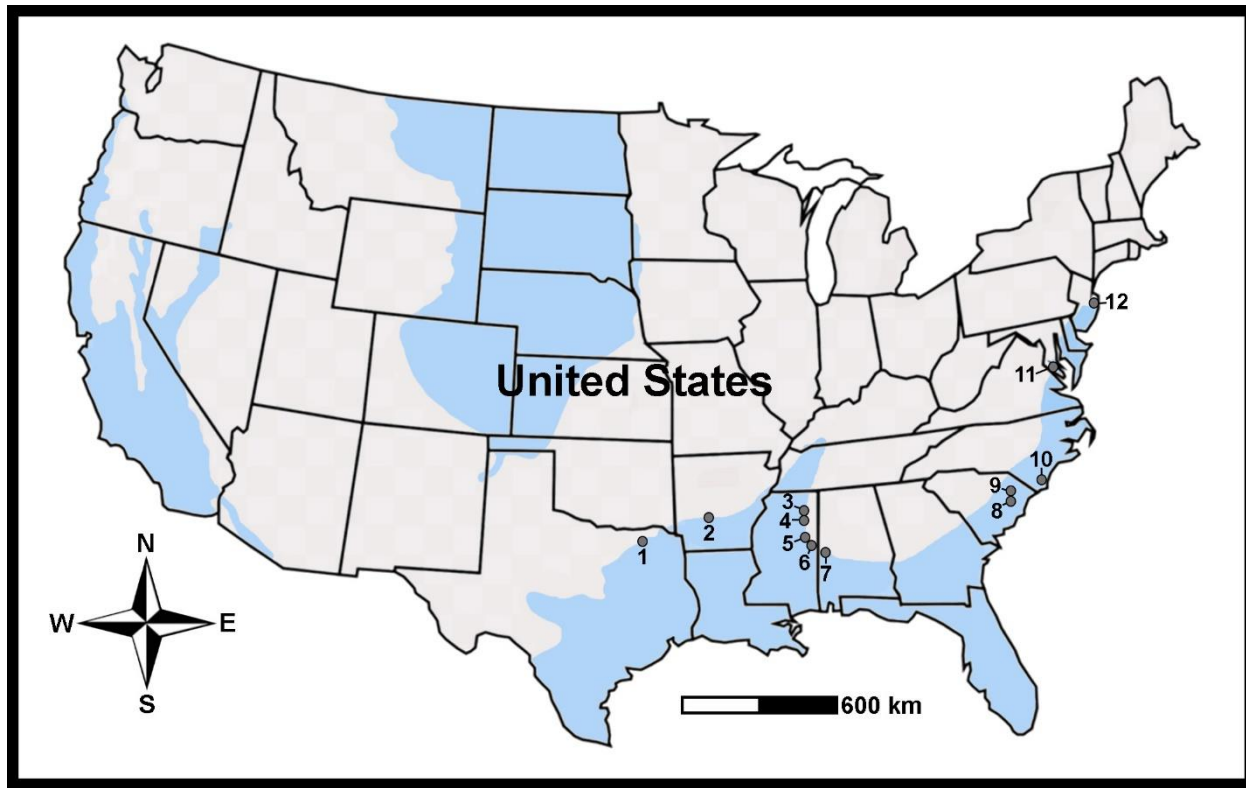


FIGURE 2. Paleogeographic distribution of *Rhombodus binkhorsti* in the USA. Blue regions represent water. Gray circles and numbers indicate known occurrences of *R. binkhorsti*, including: 1 Hunt County, Texas (Cappetta and Case, 1997); 2 Hot Spring County, Arkansas (Becker et al., 2006; this report); 3 Union County, Mississippi (this report); 4 Pontotoc County, Mississippi (this report); 5 Oktibbeha County, Mississippi (this report); 6 Noxubee County, Mississippi (this report); 7 Sumter County, Alabama (this report); 8 Williamsburg County, South Carolina (Cicimurri, 2010; this report); 9 Florence County, South Carolina (this report); 10 New Hanover County, North Carolina (Case et al., 2019; this report); 11 Prince George's County, Maryland (Hartstein et al., 1999); 12 Monmouth County, New Jersey (Case et al., 2001). The numbers also reflect the sample locations outlined in Table 1.

lateral angles (marginal angle *sensu* Noubhani and Cappetta 1994) may be slightly rounded. Teeth near the midline of the dentition have their labial and lingual angle vertices centrally located, whereas those near the lateral margins of the dentition are displaced mesially (labial angle) and distally (distal angle). In these lateral teeth, the mesio-labial face is smaller in area than the disto-labial face, and the disto-lingual face has a smaller area than the mesio-lingual face. Although Noubhani and Cappetta (1994) used the terms “margino-labial” and “margino-lingual” to identify the vertical crown faces, we prefer to use “mesio/disto-labial” and “mesio/disto-lingual” when possible, as with lateral teeth it is evident which side of the crown is mesial versus distal based on the crown thickness (see below). In occlusal view, the labial and lingual crown margins are slightly sinuous (Figure 1A). The occlusal surface of unworn teeth is weakly convex and exhibits a thin enameloid covering that is ornamented with a complex network of anastomosing and interconnected ridges and tubercles. In profile, the

labial crown faces of teeth appear concave and bear coarse vertical ridges (strongest basally but fading apically) that are overprinted with fine reticulation (Figure 1D, F, Figure 3E, F). The labial face extends beyond the root, with a conspicuously protruding crown foot (transverse labial basal crest *sensu* Noubhani and Cappetta 1994), and its basal surface bears a weak transverse furrow (lower border of the labial visor *sensu* Noubhani and Cappetta 1994) that may be smooth or coarsely crenulated. In labial view, the crown foot has a scalloped appearance, and a short ridge or tubercle is located at the juncture of the labial crown foot projection and basal furrow, seen at the base of a sharp ridge (medio-labial crest *sensu* Noubhani and Cappetta 1994) formed by the intersection of the mesio-labial and mesio-lingual faces. In profile view, the lingual crown faces are weakly convex with similar ornamentation as seen on the labial faces (Figure 1G, Figures 3F, G). The lingual crown foot bears a thick and rounded, shelf-like transverse ridge (lingual bourrelet *sensu* Noubhani and

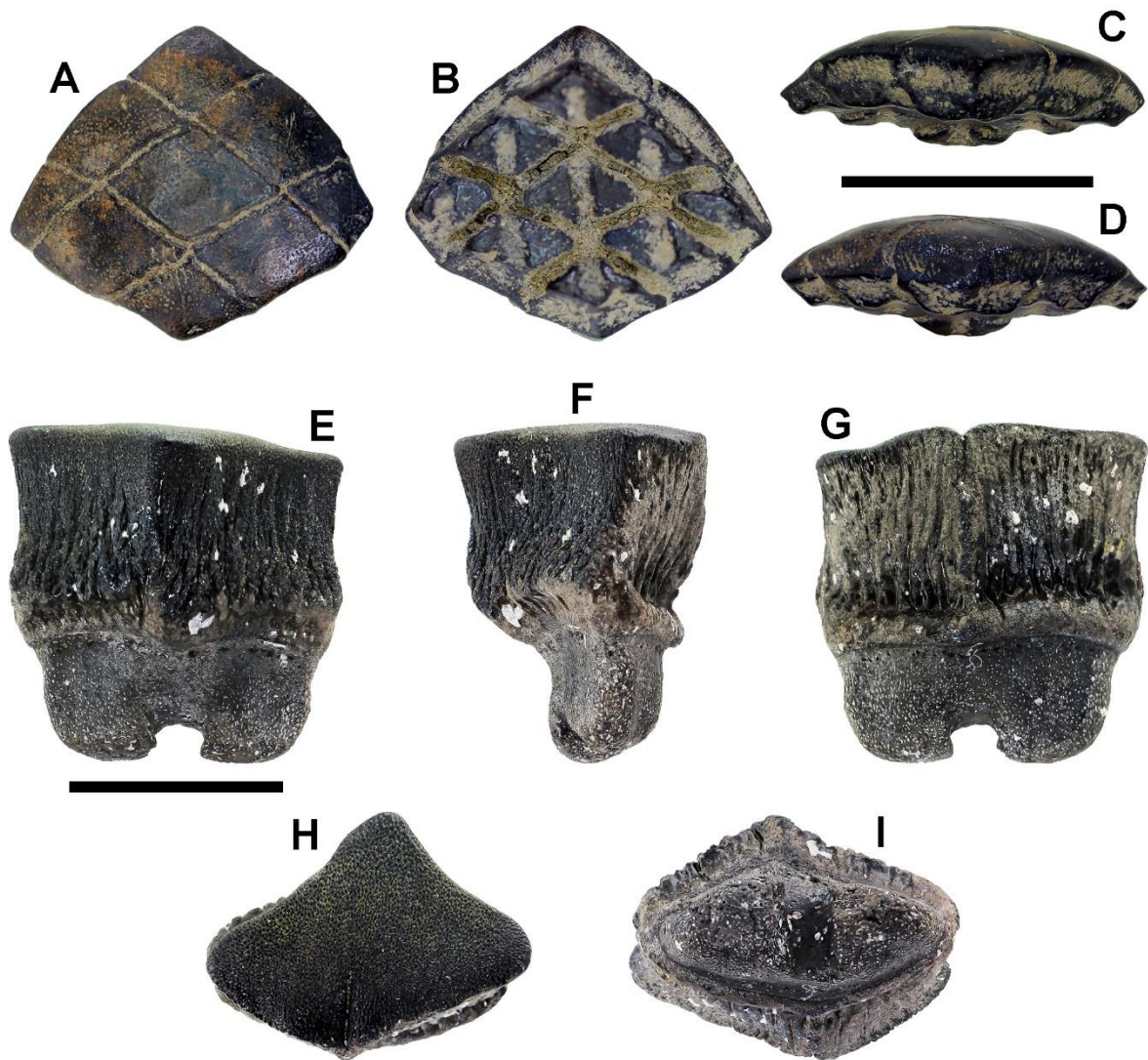


FIGURE 3. *Rhombodus binkhorsti* partial dentition and isolated tooth. A–D, MMNS VP-8087, partial dentition from the Clayton Formation (reworked from underlying Arkadelphia Formation), Mississippi, in occlusal (A), basal (B), labial (C), and lingual (D) views. E–I, MMNS VP-6015.1, tooth from Prairie Bluff Chalk, Mississippi, in labial (E), profile (F), lingual (G), occlusal (H), and basal (I) views. Scale bars = 1 cm. Labial at top in A and B, H and I.

Cappetta 1994), often with a deep sulcus (transverse lingual depression *sensu* Noubhani and Cappetta 1994) located immediately above. In basal view, the root is bilobate, being subdivided into triangular lobes by a shallow nutritive groove, and the lobes do not extend beyond the lateral angles or the lingual basal transverse ridge (Figures 1C, D, Figure 3I). The root is rather high (approximately one third total tooth height), and numerous small foramina are located immediately below the crown.

In labial and lingual views, teeth in the medial files of the preserved plate are uniform in crown thickness (Figures 1E, F), and in basal view the

nutritive groove of these teeth is centrally located and divides the root into equidimensional lobes (Figure 1C, D). In contrast, tooth crowns at the lateral margins of the plate are obviously thicker mesially than distally, and the nutritive groove is offset laterally so that the distal lobe is smaller than the mesial lobe (Figure 1C–F).

Remarks—In addition to MMNS VP-5369, we examined a much less complete dentition, represented by MMNS VP-8087 (Figure 3A–D). This specimen measures approximately 15 mm in width and length and consists of nine teeth comprising portions of six parallel files (Figure 3A, B). In occlusal view, it is

interesting to note that the teeth are obviously wider than long, and crown margins are straight. In contrast, the teeth of MMNS VP-5369 are only slightly wider than long and crown margins are sinuous.

Specimens MMNS VP-5369 and MMNS VP-8087 clearly show that the dentition of *Rhombodus binkhorsti* consists of multiple labio-lingually oriented, tightly packed, alternating parallel files of diamond-shaped teeth, which form a robust crushing plate. In labial view, MMNS VP-5369 exhibits a weak medially located, labio-lingually oriented sulcus (Figure 1E) along the entire length of the plate. This sulcus potentially indicates the middle of the original plate and therefore the location of the jaw symphysis. If so, the symphyseal tooth file (directly on the symphysis) is flanked by five lateral files on one side and 6 lateral files on the other, for a total of 12 files (Figure 1B). In occlusal view, teeth in the medial file of MMNS VP-8087 are rather symmetrical, particularly the tooth at the very center of the preserved specimen (Figure 3A), which could indicate the jaw symphysis. The crowns of the teeth in the immediately adjacent files are asymmetrical (Figure 3A), and the nutritive grooves are slightly offset distally (Figure 3B). The lateral-most file on both sides of the preserved plate is represented by a single tooth, which has a highly asymmetrical crown and conspicuously distally offset nutritive groove. These features suggest that the medial file represents the symphyseal file, which would therefore be flanked by two lateral files on each side. However, the exposed teeth at the mesial and distal edges of both dentitions clearly show that additional lateral files were once present (Figures 1F, G, Figures 3C, D).

In occlusal view, both dentitions show that individual teeth within each file are situated so that the labial vertex of a tooth is in contact with the lingual vertex (medio-lingual crest *sensu* Noubhani and Cappetta 1994) of the preceding tooth. Additionally, the lateral angles of the teeth within a file are positioned in between the lateral angles of the adjacent row(s), with the labial and lingual crown faces in tight contact with each other (Figure 1A, Figure 3A). Individual teeth are very strongly articulated with each other via the coarse longitudinal ridges of the labial and lingual faces, which essentially form interlocking tongue-and-groove joints. The labial crown foot also overlaps the transverse ridge at the lingual crown foot, such that 1) the lingual ridge rests within the transverse furrow on the basal surface of the labial crown foot of the succeeding teeth, and 2) the labial crown foot sits within the transverse sulcus above the lingual ridge of the preceding teeth (Figure 1G).

Overall, MMNS VP-5369 is labio-lingually convex (Figure 1G), which we presume to reflect how the dentition was affixed to the jaws. In labial (Figure

3C) and lingual (Figure 3D) views of MMNS VP-8087, the base of the dentition is mesio-distally straight, whereas the occlusal surface is very convex. The convexity is in part due to the labio-lingual curvature of the plate, but more so to the lateral taper of the dentition, which is the result of articulation of the evenly thick-crowned symphyseal teeth and the two rows of lateral teeth that are higher mesially than distally. The occlusal surfaces of these teeth are also slightly convex.

The series of alternating files of the *R. binkhorsti* dentition is reminiscent of *Dasyatis* (i.e., Underwood et al., 2015), but the method in which the individual *Rhombodus* teeth interlock into a solid tooth plate differs from the arrangement seen in *Dasyatidae*. This interlocking tooth system is analogous to *Aetomylaeus*, *Myliobatis*, and *Rhinoptera* (i.e., Ebersole et al., 2019; Hovestadt and Hovestadt-Euler, 2013), although the *Rhombodus* dentition lacks a symphyseal file of very wide teeth as occurs in those other taxa. Instead, the symphyseal teeth in the *Rhombodus* dentition are comparable in size and shape to those in immediately adjacent lateral files. Thus, ontogenetic variation is not evident in the *Rhombodus* dentition, as teeth in the medial/symphyseal file remain relatively constant in size over the life of the animal, as far as is represented by MMNS VP-5369. In contrast, embryonic and neonatal specimens of *Myliobatis* show that the medial teeth quickly develop into a very wide symphyseal file (i.e., Underwood et al., 2015).

DISCUSSION

Review of *Rhombodus* Species—Seven *Rhombodus* species are currently recognized, including *R. andriesi* Noubhani and Cappetta, 1994, *R. binkhorsti*, *R. carentonensis* Vullo, 2005, *R. ibericus* Kriwet et al., 2007, *R. levis* Cappetta and Case, 1975, *R. meridionalis* Arambourg, 1952 and *R. microdon* Arambourg, 1952. Of these, only *R. levis* and *R. binkhorsti* have been reported from the USA, with the remaining species occurring in Africa and Europe (Cappetta, 2012). The genus is generally known from the Maastrichtian, but *R. carentonensis* is only known from the Campanian (Vullo, 2005) and records of *R. levis* are predominantly from the late Santonian to late Campanian (Cappetta and Case, 1975; Case and Schwimmer, 1988; Cicimurri, 2007; Cicimurri et al., 2014).

There is some doubt as to the correct taxonomic assignment of *R. levis*, as Vullo (2005) has suggested that the morphology compares more closely to *Hypsobatis* (i.e., *Hypsobatis*, *Angolobatis*). Alternatively, Cicimurri et al. (2014) indicated that the morphology could represent heterodonty within

Brachyrhizodus, a taxon that is consistently coeval with *R. levis* in Santonian to Campanian strata within the Gulf and Atlantic coastal plains (Cappetta and Case, 1975; Case and Schwimmer, 1988; Cicimurri, 2007; Cicimurri et al., 2014). Future comparison of *R. levis* tooth histology to that of *R. binkhorsti* (Enault et al., 2016) and *Brachyrhizodus wichitaensis* (Enault et al., 2013) could resolve this issue. Regardless of its taxonomic status, the *R. levis* morphology is easily distinguished from *R. binkhorsti* by its squared (as opposed to diamond-shaped) occlusal outline, smooth labial and lingual crown faces, and smaller overall size.

Rhombodus microdon is known from the late Maastrichtian, and Noubhani and Cappetta (1994) presented various dimensions that indicate that the largest teeth of this species measure less than 4 mm in width. Additionally, the species differs from *R. binkhorsti* in having less wrinkled labial and lingual faces, and the lingual angle can sometimes occur as an elongated projection (Arambourg, 1952; Noubhani and Cappetta, 1994). Darteville and Casier (1959) suggested that *R. microdon* represented ontogenetic variation within *R. binkhorsti* (and was therefore a junior synonym), but Noubhani and Cappetta (1994) argued that the two morphologies each represented a distinct species because teeth of an intermediate size were unknown. Nearly all of the specimens we directly examined are larger than the maximum size reported for *R. microdon*, and the vertical crown faces are very heavily wrinkled (particularly at the crown foot), features consistent with *R. binkhorsti*.

The late Maastrichtian species *R. andriesi* also has small teeth (less than 6 mm in greatest width), but the lingual basal crown sulcus seems to be more conspicuous and the base of the crown wider with respect to the occlusal surface, when compared to *R. binkhorsti* (Noubhani and Cappetta, 1994). *Rhombodus meridionalis* appears to differ from *R. binkhorsti* in its smaller size, more convex but weakly ornamented labial and lingual faces, and more convex occlusal margin (Arambourg, 1952; Noubhani and Cappetta, 1994). In addition to having finer ornamentation than *R. binkhorsti*, the teeth of *R. carentonensis* are unusually tall and labio-lingually thin which, according to Vullo (2005), falls outside of the range of variation for *R. binkhorsti* as determined by Noubhani and Cappetta (1994). *Rhombodus ibericus* is similar to *R. meridionalis*, and clearly different from *R. binkhorsti* based on its overall smaller size, rounded corners, smooth lingual surfaces, and convex labio-occlusal surface that is highly ornamented with a reticulated network of ridges (resulting in a pitted texture).

North American Distribution of *R. binkhorsti*—*Rhombodus binkhorsti* was widely distributed during the Maastrichtian, having been identified in Asia (Lewy and Cappetta, 1989; Noubhani and Cappetta, 1994), Africa (Darteville and Casier, 1943; Arambourg, 1952; Jacobs et al., 2016; Cuny et al., 2012), Europe (Dames, 1881; Herman, 1977; Corral et al., 2016), the Atlantic and Pacific coasts of South America (Schneider, 1936; Rebouças and Silva Santos, 1956; da Silva, 2007; da Silva et al., 2007), and North America. The Chilean record noted by Schneider (1936) remains to be verified, as he cited an earlier work and no specimens were available to him for analysis. In North America, the species has been reported from Maastrichtian strata of Arkansas (Becker et al., 2006), Maryland (Hartstein et al., 1999), New Jersey (Case et al., 2001), North Carolina (Case, 1979; Case et al., 2017), and Texas (Welton and Farish, 1993; Case and Cappetta, 1997; Figure 2). Examination of 479 isolated *R. binkhorsti* teeth from various units within the Gulf and Atlantic coastal plains (housed at HCM, MMNS, SC) and from Morocco (housed at SC) allowed us to corroborate previous identifications and document new records of this taxon in North America.

Although the specimen from the Arkadelphia Formation reported by Becker et al. (2006) is small, identification as *R. binkhorsti* is appropriate because it is larger than teeth reported for *R. microdon* and the vertical faces are heavily wrinkled. We were able to examine additional *Rhombodus* material from the same site and confirmed they represent *R. binkhorsti*. In addition to the partial dentition described above (MMNS VP-5369, Figure 3A–D), we also confirmed isolated *R. binkhorsti* teeth from other Maastrichtian Mississippi Embayment deposits of Alabama and Mississippi, which represent first paleobiogeographic occurrences for these states, as well as from Maastrichtian strata of South Carolina (Figure 2, Table 1). Direct comparisons of the Alabama, Mississippi, and South Carolina *Rhombodus* teeth to those of *R. binkhorsti* from Morocco showed that the remains are conspecific (Figure 4G–I). These specimens also compare to Dames' (1881) type description (p.1–3) and illustration (i.e., Figure a) of *R. binkhorsti*. One sample of *R. binkhorsti* teeth (SC87.158 n=284) from a site in South Carolina includes specimens from 4 mm to 12.5 mm in maximum width (Figures 4B and F, respectively). Although the smaller specimens are worn, through *in vivo* usage and postmortem ablation, the crown foot of each of these is heavily crenulated like those of the larger (8 mm to 12.5 mm width) teeth. An additional specimen 2.5 mm in width (Figure 4A) is too ablated to provide comment beyond that its diamond-shaped occlusal outline indicates that it is *Rhombodus*. Although these smaller specimens are

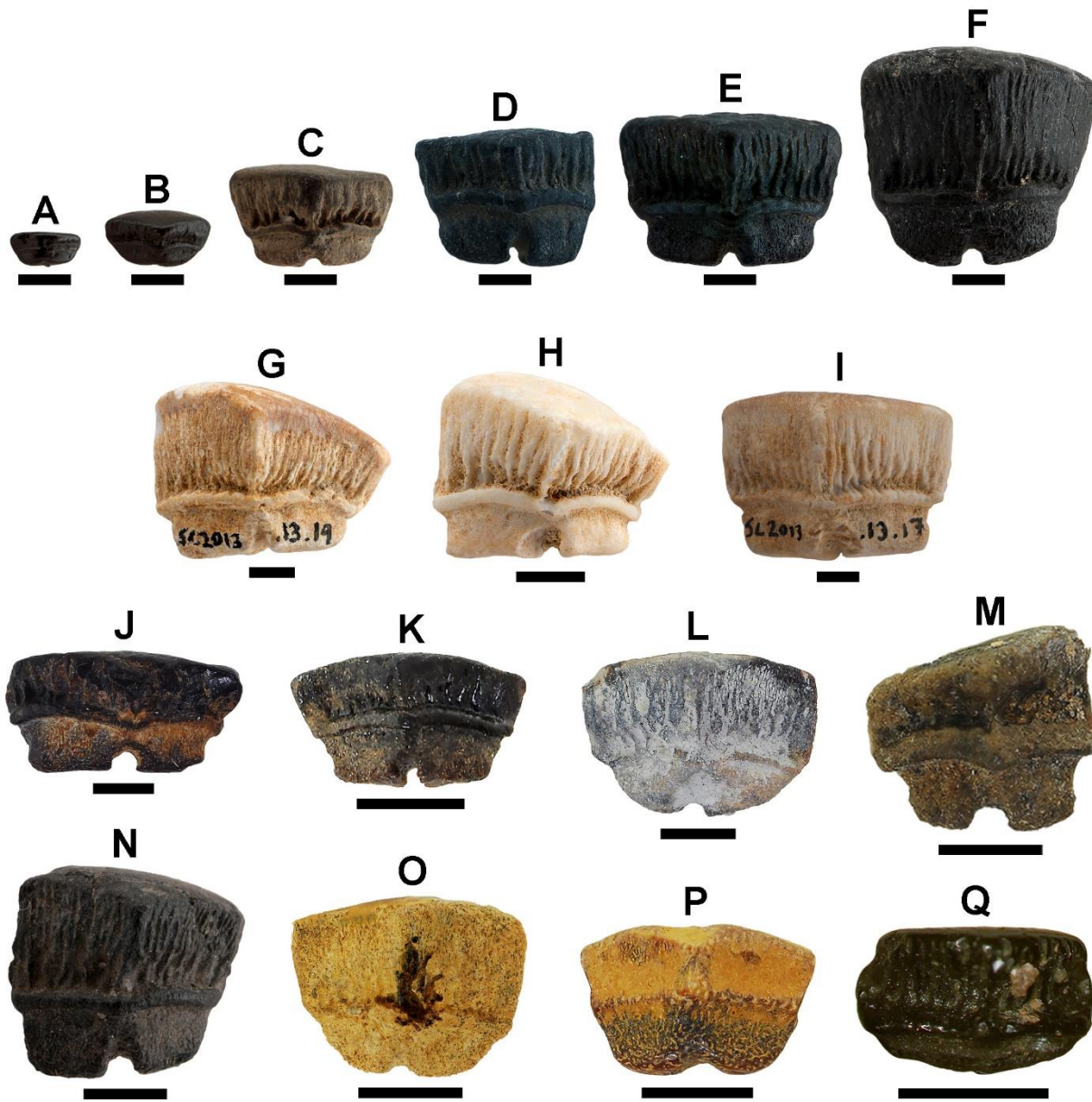


FIGURE 4. Lingual views of representative isolated teeth of *Rhombodus binkhorsti* from Alabama, Mississippi, North Carolina, South Carolina, U.S.A., and Morocco. **A–F**, hypothetical ontogenetic series, **A**, SC87.158.138, **B**, SC87.158.91, **C**, SC87.158.94, **D**, SC87.158.82, **E**, SC87.158.101, **F**, SC87.158.100, Steel Creek Formation(?), South Carolina. **G**, SC2013.13.19, lateral tooth, Morocco. **H**, SC2013.13.100, lateral tooth, Morocco. **I**, SC2013.13.17, medial tooth, Morocco. **J**, MMNS VP-8474, Prairie Bluff Chalk, Alabama. **K**, MMNS VP-8417.1, Peedee Formation, North Carolina. **L**, MMNS VP-8473, Ripley Formation, Mississippi. **M**, MMNS VP-8473, lateral tooth, Prairie Bluff Chalk, Mississippi. **N**, SC87.158.87, lateral tooth, Steel Creek Formation(?), South Carolina. **O**, MMNS VP-6027, Owl Creek Formation, Mississippi. **P**, MMNS VP-6228, Ripley Formation, Mississippi. **Q**, HCM uncurated, Peedee Formation, South Carolina. Scale bars = 3 mm.

within the *R. microdon* and *R. andriesi* size ranges (*sensu* Noubhani and Cappetta, 1994), we attribute the size variation in our sample to ontogenetic variation within *R. binkhorsti*, and our sample sizes from North America and Morocco (SC2013.13 n=131) are large enough to also account for monognathic/dignathic heterodonty. The teeth we examined as part of this

study do not exhibit differences that cannot be attributed to anything other than variation within a single species, and our conclusion is that they are conspecific and referable to *R. binkhorsti*.

Unfortunately, part of the South Carolina *Rhombodus binkhorsti* sample (i.e., Figures 4A–F, N) was derived from a lag deposit that also contains

TABLE 1. Geographic, stratigraphic, and temporal records of *Rhombodus binkhorsti* in the U.S.A., including paleoenvironmental interpretations for strata from which specimens have been recovered. Numbers in the far-left column represent the localities shown on Figure 2. Superscript numbers represent various sources from which the compiled data were obtained, including: ¹this report; ²Pitakpaivan and Hazel (1994); ³Renken (1996); ⁴Case and Cappetta (1997); ⁵Hartstein et al. (1999); ⁶Case et al. (2001); ⁷Kielan-Jaworowska et al. (2005); ⁸Harris and Self-Trail (2006); ⁹Ross and Fastovsky (2006); ¹⁰Callahan et al. (2009); ¹¹Becker et al. (2010); ¹²Christopher and Prowell (2010); ¹³Case et al. (2017); ¹⁴Dockery and Phillips (2017); ¹⁵Farke and Thompson (2016); ¹⁶Nyborg et al. (2017); ¹⁷Gifford et al. (2020); ¹⁸Stringer et al. (2020).

#	County and State	Unit	CC Zone	Depositional setting
1	Hunt County, TX ⁴	Kemp Clay ⁴	CC26 ⁷	Estuarine ⁷
2	Hot Spring County, AR ¹¹	Arkadelphia Formation ¹¹	CC26 ²	Shallow marine shelf ¹¹
2	Hot Spring County, AR ¹	Clayton Formation ¹	NA	Reworked from underlying Arkadelphia Fm.
3	Union County, MS ¹	Chiwapa Sandstone Member, Ripley Formation ¹	CC25/26 ¹⁵	Inner neritic marine ¹⁵
3	Union County, MS ¹	Coon Creek Member, Ripley Formation ¹	CC24 ¹⁸	Neritic ¹⁸
3	Union County, MS ¹	New Albany beds, Prairie Bluff equivalent ¹	CC25/26 ¹⁶	Shallow middle shelf ¹⁶
3	Union County, MS ¹	Owl Creek Formation ¹	CC25/26 ¹⁵	Inner neritic marine ¹⁵
4	Pontotoc County, MS ¹	Nixon beds, Prairie Bluff Chalk ¹	CC25/26 ¹⁶	Shallow middle shelf ¹⁶
5	Oktibbeha County, MS ¹	Prairie Bluff Chalk ¹	CC25/26 ¹⁶	Shallow middle shelf ¹⁶
6	Noxubee County, MS ¹	Prairie Bluff Chalk ¹	CC25/26 ¹⁶	Shallow middle shelf ¹⁶
6	Noxubee County, MS ¹	upper Ripley Formation ¹	CC24 ¹⁸	Transitional marine ³
7	Sumter County, AL ¹	Prairie Bluff Chalk ¹	CC25/26 ¹⁶	Shallow middle shelf ¹⁴
8	Williamsburg County, SC ¹	Steel Creek Formation? ¹	CC26 ¹²	Deltaic ¹²
9	Florence County, SC ¹	Peedee Formation ¹	CC25/26 ⁸	Neritic ⁸
10	New Hanover County, NC ¹³	Peedee Formation, Island Creek Member ¹³	CC26 ¹³	Inner neritic ¹³
11	Prince George's County, MD ⁵	Severn Formation ⁵	CC26 ⁹	Shallow to open marine ⁵
12	Monmouth County, NJ ⁶	New Egypt Formation ⁶	CC26 ⁶	Middle shelf environment ¹⁰

Paleocene and Pliocene material (Knight et al., 2007; Cicimurri, 2010; Schwimmer et al., 2015). Although Schwimmer et al. (2015) suggested that the source of the Cretaceous fossils was the Donoho Creek Formation, Cicimurri (2010) proposed that they were derived from a unit of Maastrichtian age based on the co-occurrence of *Schizorhiza stromeri* (see Knight et al., 2007), *Serratolamna serrata*, and *R. binkhorsti*. The upper Maastrichtian Steel Creek Formation, a lithostratigraphic unit representing deltaic deposition, has been mapped in the area (Schwimmer et al., 2015). The large number of dinosaur teeth that have been recovered from the same deposit also points to a Steel

Creek Formation origin, based on its deltaic depositional environment as opposed to outer-to-middle neritic environments represented by the Peedee Formation (see below). The Steel Creek Formation was deposited during the time represented by calcareous nannofossil Zone CC25 (Christopher and Prowell, 2002). Falls and Prowell (2001) showed the Steel Creek and Peedee formations to be laterally equivalent, and correlative with the Prairie Bluff and Ripley formations of the Gulf Coastal Plain.

The remainder of the South Carolina *R. binkhorsti* sample available to us was collected *in situ* from the Peedee Formation, which has been assigned

to zones CC25 and CC26 (Self-Trail and Bybell, 1997; Edwards et al., 2000). One sample, from Burches Ferry in Florence County, was collected from the basal-most 10 cm of the Peedee Formation. At this site, the Peedee Formation has been assigned to subzone CC25a (Self-Trail et al., 2002), and the unit disconformably overlies the late Campanian Donoho Creek Formation (Cicimurri, 2007). This section of the Peedee Formation is part of the Peedee I Sequence of Harris and Self-Trail (2006), and the unconformity between the Peedee and Donoho Creek formations represents up to 5 million years of missing time. Other *R. binkhorsti* specimens were collected from Allison's Ferry in Florence County (Figure 4Q), where strata higher within the Peedee Formation are exposed (Kirkpatrick and Cicimurri, 2019). Analyses of palynomorphs (i.e., Christopher and Prowell, 2002) and calcareous nannofossils have not yet been conducted, and it is currently unclear to which Peedee phase (zones CC25 and CC26) the Allison's Ferry material can be assigned. The deposits of the Peedee Formation phases in South Carolina reflect a transition from an outer neritic (Phase I) to middle neritic (Phase II) environment (Edwards et al., 2000; Harris and Self-Trail, 2006).

Rhombodus binkhorsti records in the Peedee Formation of North Carolina are from the Island Creek Member (Case et al. 2019), the uppermost Cretaceous unit in the state, occurring at the top of the formation. We were able to examine specimens (i.e., Figure 4K) from this lithostratigraphic unit and confirm that the species represented is *R. binkhorsti*. The Island Creek Member represents an inner neritic environment of normal salinity (Dockal et al., 1998), which contrasts to the outer-to-middle neritic environment of the Peedee Formation in South Carolina, and more significantly to the brackish-water, deltaic environment represented by the Steel Creek Formation. Harris and Self-Trail (2006) correlated the Peedee Formation of North and South Carolina with the Navesink Formation of New Jersey, but this is likely to the older, CC25 range of the unit (Phase I). Landman et al. (2004) showed the New Egypt Formation as having formed during CC26, which therefore correlates to the Phase II part of the Peedee Formation of Harris and Self-Trail (2006).

In New Jersey, Case et al. (2001) documented the occurrence of *R. binkhorsti* from the New Egypt Formation of southern Monmouth County. Although we did not directly examine specimens from this formation, the material discussed by Case et al. (2001) does appear to represent *R. binkhorsti*. The New Egypt Formation was applied by Olsson (1963) to strata occurring in southern Monmouth County that were slightly different from time-equivalent facies occurring elsewhere in the state. Numerous authors

have shown the New Egypt Formation to be laterally equivalent to the Navesink, Red Bank, and Tinton formations (in ascending stratigraphic order) (Sugarman et al., 1995; Sugarman and Owens, 1996), and Gallagher et al. (1986) suggested restricting the use of the term to the stratotype area. Landman et al. (2004) showed the New Egypt Formation as laterally equivalent to the Red Bank and Tinton formations, and reported that the New Egypt conformably overlies the Navesink Formation. Unfortunately, Case et al. (2001) confusingly indicated that their fossils were from the Red Bank Formation, but reference to this lithostratigraphic unit should be disregarded. Although invertebrates are known from the Red Bank and Tinton formations, and invertebrates and vertebrates have been documented from the Navesink Formation, *R. binkhorsti* has yet to be reported from any of these lithostratigraphic units (Gallagher et al., 1986; Sugarman et al., 1995; Landman et al., 2004).

Ross and Fastovsky (2006) correlated the Navesink Formation with the lower part and the New Egypt Formation with the upper part, respectively, of the Severn Formation of Maryland. They placed the New Egypt and upper part of the Severn within Zone CC26, whereas the Navesink and lower Severn within Zone CC25, consistent with the work of other authors (see above). Hartstein et al. (1999) documented *R. binkhorsti* from what was identified as a transgressive lag occurring at the base of the Severn Formation (therefore Zone CC25). Although the authors noted that the Severn Formation paleofauna contained a mixture of marine, fluvial and terrestrial taxa, they indicated the possibility that some of the fossils were reworked from the underlying Matawan Formation. As the Matawan Formation is a pre-Maastrichtian unit, we consider it highly unlikely that the *R. binkhorsti* fossils were reworked from this lithostratigraphic unit. Based on their ammonite biozonation, Kennedy et al. (1997) correlated the Severn Formation at least in part with the upper Maastrichtian Prairie Bluff Chalk of the Gulf Coastal Plain.

The *Rhombodus binkhorsti* specimens from Mississippi and Alabama were recovered from units that were deposited within the Maastrichtian Mississippi Embayment. These units include the Owl Creek Formation (i.e., Figure 4O), Prairie Bluff Chalk (i.e., Figure 3E–I, Figures 4J, M), and upper Ripley Formation (i.e., Figure 4L, P). These units accumulated during the time represented by Zones CC24–CC26 and are interpreted to represent shallow middle shelf or neritic deposits (Dockery and Thompson, 2016; Nyborg et al., 2017; Stringer et al., 2020).

Case and Cappetta (1997) reported *R. binkhorsti* teeth from the upper Maastrichtian Kemp Clay in Hunt County, Texas, and their figured specimens (pl. 15,

figs. 4, 5) fall within the morphological range that we observed for *R. binkhorsti*. The Kemp Clay was assigned to Zone CC26 and interpreted to represent an estuarine environment (Kielan-Jaworowska et al. 2005). In addition to the Hunt County occurrence, Welton and Farish (1993) also noted the presence of *R. binkhorsti* in the Maastrichtian Escondido and Littig formations in Fannin, Medina, and Travis counties, Texas. Although they did not figure any specimens from these latter units or counties (we therefore could not verify the occurrences), Welton and Farish (1993) stated that *R. binkhorsti* was not known from any Campanian deposits in the state.

Rhombodus binkhorsti teeth are conspicuously lacking from strata representing the Cretaceous Western Interior Seaway (Murray and Cook, 2016). In the Great Plains states (i.e., North and South Dakota, Montana, Wyoming), Maastrichtian marine units include the Fox Hills Formation and Breien Member of the Hell Creek Formation (Hoganson and Murphy, 2002; Hoganson et al., 2019). However, the Fox Hills and Brien paleoenvironments were separated from the southern arm of the Western Interior Seaway (see Hoganson et al., 2019) and, particularly, the Mississippi Embayment, where the species is known to occur (Becker et al., 2006; Case and Cappetta, 1997). Therefore, *R. binkhorsti* was not able to penetrate into those northern habitats. We note here that *R. levis* has been reported from the Fox Hills Formation (Becker et al., 2004; Hoganson et al., 2019), although it cannot be ruled out that these specimens actually represent morphological variation (ontogeny, monognathic/dignathic heterodonty) within one of the other species that have been reported, which include *Protoplatyrhina* and *Myledaphus*.

Overall, the fossil record from the U.S.A. demonstrates that *R. binkhorsti* existed in the Atlantic Coastal Plain at least during the time interval represented by zones CC25–CC26, but older CC24 records within the Gulf Coastal Plain are known (Table 1). These records support the work of Corral et al. (2016), who suggested that *R. binkhorsti* is an appropriate index fossil for the Maastrichtian Stage. We propose that *R. binkhorsti* is representative of the middle-to-late Maastrichtian.

Paleobiology of *R. binkhorsti*—Based on the known lithostratigraphic occurrences of *Rhombodus binkhorsti* in North America, the species occurred in a range of depositional settings, including various neritic environments with normal marine salinity, as well as brackish-water deltaic and estuarine environments (Table 1). *Rhombodus binkhorsti* has been identified as a durophagous taxon (Enault et al., 2016), and the dentition of the species supports this conclusion, as it is comparable to those of extant durophagous rays like *Myliobatis*, *Aetomylaeus*, and

Rhinoptera (Ebersole et al., 2019). Within the *R. binkhorsti* dentition, teeth are arranged into parallel files that alternate so that the lateral angles of one tooth fit into a V-shaped recess formed by the lateral angles of the preceding and succeeding teeth in the adjacent file(s). Individual teeth tightly articulate with each other via vertical ridges and grooves occurring on vertical faces, as well as the overlap of the labial crown foot of one tooth with the lingual transverse ridge of the preceding tooth in the adjacent file(s). This tooth arrangement forms a continuous, rather smooth surface, which in the case of MMNS VP-5369 and MMNS VP-8087 is convex both labio-lingually and mesio-distally, producing an overall domed surface. This convex surface likely increased the bite force into a smaller area when occluding with the opposing dentition, thereby creating a more effective surface to break shells. The thickened tooth crown of *R. binkhorsti* is a mechanism to offset *in vivo* wear until the replacement teeth became functional. Additionally, the internal structure of individual teeth was strengthened by dentine tubules, which are visible at the occlusal surface of worn teeth (punctate appearance) and in transverse section, where they appear to emanate from the base of the crown. The thin enameloid covering observed on unworn teeth may not be functional (*sensu* Enault et al., 2016), as it likely was quickly worn away through *in vivo* usage. Various types of mollusks, including oysters, clams, snails, and ammonites, occur within the lithostratigraphic units that contain *R. binkhorsti*, any of which may have been preyed upon by this ray.

In addition to monognathic and/or dignathic heterodonty, we also observed ontogenetic heterodonty in the *R. binkhorsti* dentitions and isolated teeth we examined. Within the sample of isolated teeth from South Carolina, symmetrical specimens (from the medial portion of a dentition) range in size from 4 mm to 12.5 mm in greatest width (Figure 4B–F). The ornamentation on vertical faces of teeth in the smaller size range typically consists of robust ridges restricted to the crown base, with ornament continuing towards the apex being very faint or absent altogether. This contrasts with the ornamentation occurring on teeth within the larger size range, which generally consists of more numerous robust ridges extending nearly or all the way to the apex, and are overprinted by even finer vertical ridges. As MMNS VP-5369 shows that tooth size does not significantly decrease across the dentition (mesio-distally), we consider the tooth size range to represent a range of dentition sizes (and therefore individual body size). MMNS VP-5369 contains teeth with a maximum width of 6 mm, but other North American specimens we examined are more than twice that width, and teeth from Morocco measure nearly 20 mm in width. These latter

specimens indicate a ray of rather large size possessing a dentition of approximately 120 mm in width (based on the ratio of tooth width to preserved dentition width of MMNS VP-5369).

CONCLUSIONS

Rhombodus binkhorsti had a nearly cosmopolitan distribution during the Late Cretaceous based on published occurrences from Asia, Africa, Europe, North America, and South America. In North America, *R. binkhorsti* occurs along both the Atlantic and Gulf coastal plains, having been reported from Arkansas, Maryland, New Jersey, North Carolina, and Texas. Herein we document new occurrences from Alabama and Mississippi and confirm previous mention of the species from South Carolina. *Rhombodus binkhorsti* is apparently absent from the Western Interior of North America, likely the result of the continuing regression of the seaway during the Maastrichtian. The partial tooth plate reported herein corroborates the notion of a durophagous diet for *R. binkhorsti* and helps us better understand the range of variation in tooth morphology. An analysis of North American records supports the use of *Rhombodus binkhorsti* as an index fossil for the middle to late Maastrichtian, as the species appears to be indicative of calcareous nannoplankton Zones CC24–CC26.

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