

Late Cretaceous chimaeroids (Chondrichthyes: Holocephali) from Alabama, USA

DAVID J. CICIMURRI^{1*} and JUN A. EBERSOLE²

¹South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina 29201, USA; dave.cicimurri@scmuseum.org. ²McWane Science Center, 200 19th Street North, Birmingham, Alabama 35203, USA; jebersole@mcwane.org

Tooth plates of three extinct species of callorhynchid holocephalans, *Edaphodon mirificus*, *E. barberi*, and *Ischyodus bifurcatus* have been collected from Upper Cretaceous strata of Alabama. Of the two species of *Edaphodon*, *E. mirificus* is represented by isolated tooth plates as well as associated dentitions. *Edaphodon barberi* was based on a small left mandibular tooth plate, but additional mandibular tooth plates in museum collections show that the diagnostic features seen on the *E. barberi* holotype are consistently present and therefore useful for species differentiation. *Ischyodus bifurcatus* is reported for the first time in Alabama and is known from a partial associated dentition and several isolated tooth plates. Most of the fossils are from the upper Santonian to lower Campanian Mooreville Chalk, but two specimens of *Edaphodon* from a lower Campanian component of the Tombigbee Sand Member of the Eutaw Formation and one from the lower Maastrichtian Ripley Formation represent the first holocephalan records from these lithostratigraphic units in Alabama.

Keywords: Chondrichthyes, Holocephali, *Edaphodon*, *Ischyodus*, Alabama, Cretaceous

INTRODUCTION

The jaws of callorhynchids (Holocephali Bonaparte 1832) are composed of six separate elements. The upper jaw consists of two vomerine (anterior) and two palatine (posterior) tooth plates; the lower jaw has two mandibular tooth plates (Patterson 1992, Stahl 1999). Two fossil callorhynchids have been reported from the upper Santonian to lower Campanian Mooreville Chalk of Alabama, including *Edaphodon barberi* Applegate 1970 and *E. mirificus* Leidy 1856 (see Applegate 1970). Although *E. mirificus* is well represented by tooth plates from all positions, and even complete dentitions (i.e., Hussakof 1912, Stahl and Parris 2004), *E. barberi* is known only from the holotype, a small left mandibular tooth plate. Examination of additional mandibular tooth plates referable to *E. barberi* revealed subtle variations between the tooth plates, and that the morphological features originally used to diagnose the species are consistently present in all growth stages available.

Here we provide the results of a recent study on the Cretaceous record of holocephalan fish in Alabama, which includes the two species of *Edaphodon* Buckland 1838, as well as *Ischyodus bifurcatus* Case 1978, a taxon not previously described from the state. We discuss the morphological variation we observed within *E. barberi* mandibular tooth plates, and compare the elements to those of *E. mirificus*. In addition, three associated dentitions of *E. mirificus* and one of *I. bifurcatus* allow us to provide a

detailed account of how the tooth plates of these species occlude. Lastly, the specimens allow us to make some inferences about the paleobiology of these three species.

GEOLOGIC SETTING

Cretaceous strata in Alabama crop out in an arcuate belt extending between the western and southeastern parts of the state (Fig. 1). These strata range in age from the middle Cenomanian to the late Maastrichtian, but the fossils examined in this study were collected primarily from lowermost Santonian to uppermost Campanian deposits of the Mooreville Chalk (Fig. 2). A specimen from Greene County appears to have been derived from the Tombigbee Sand Member of the Eutaw Formation, but the tooth plate was collected from gravels occurring within a stream that also cuts into the overlying Mooreville Chalk (Ciampaglio et al. 2013), and the possibility that it was eroded from this lithostratigraphic unit cannot be discounted. Another specimen, from Sumter County, was found in an area where surface exposures consist of the Ripley Formation, but outcrops of overlying Prairie Bluff Chalk do occur nearby. Both units, however, are Maastrichtian in age.

Deposition of the Tombigbee Sand Member of the Eutaw Formation and the Mooreville Chalk spanned the Santonian/Campanian boundary (Mancini et al. 1995), and both are therefore time-transgressive units (Fig. 2). The Tombigbee Sand Member accumulated within inner

*author for correspondence

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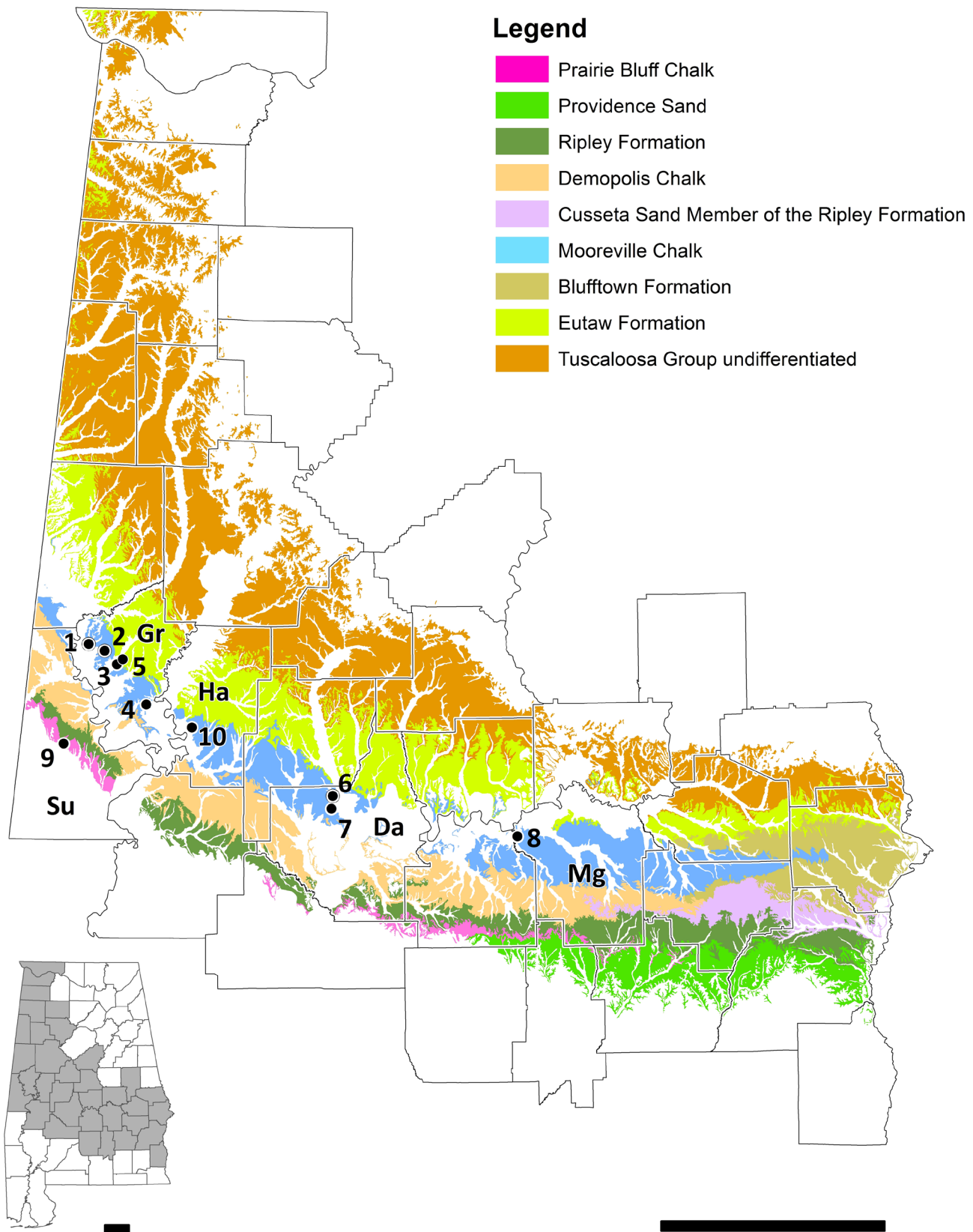


Figure 1. Geologic map of Alabama showing outcrop belt of Cretaceous strata. Fossil callorhynchid localities are indicated by numbered closed circles. **Da.** Dallas County. **Gr.** Greene County. **Ha.** Hale County. **Mg.** Montgomery County. **Su.** Sumter County. 1. Site AGr-8. 2. Site AGr-14. 3. Site AGr-43. 4. Site AGr-28. 5. Site AGr-16. 6. Site ADa-19. 7. Site ADa-3. 8. Site AMg-6. 9. Site AL.60.012 (Su). 10. Site AHL-1. Scale bars = 50 miles.

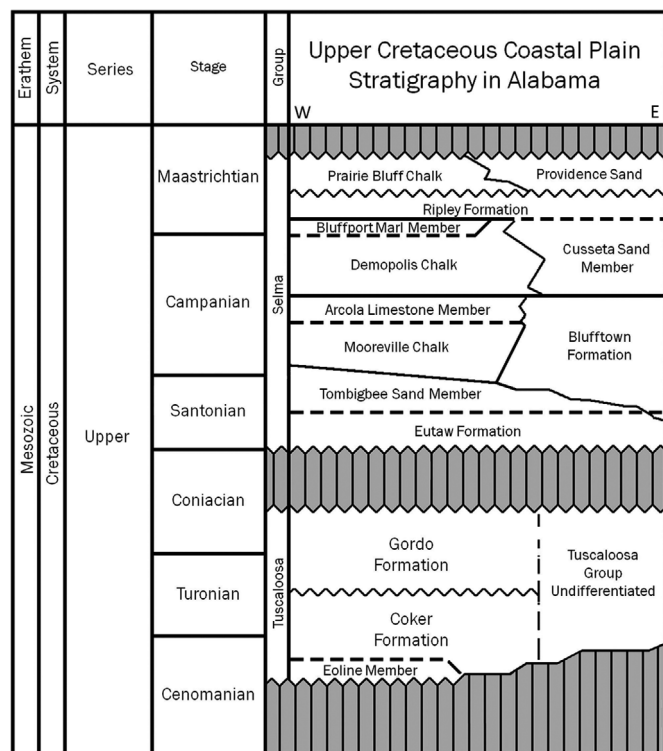


Figure 2. Correlation chart of Upper Cretaceous surface stratigraphy. Light gray areas represent unconformities.

to middle shelf environments under low to moderate energy conditions (Mancini and Soens 1994), but the Mooreville Chalk represents deposition in deeper, calmer water with dysoxic bottom conditions (Kiernan 2002). The deposition of the Ripley Formation reflects a storm-influenced shelf setting of lagoon-marsh, barrier island, and lower shoreface environments (Hall and Savrda 2008).

METHODS

The fossils we examined were measured using digital calipers to the nearest 100th of a millimeter along the greatest span between the mesial and distal tips of each tooth plate. Photographs were taken with a Nikon D80 digital camera, and Adobe Photoshop was used to enhance the contrast between the tritor pads and the surrounding dentine.

The general morphology of *Edaphodon* and *Ischyodus* tooth plates has been described in detail by several authors (i.e., Case 1978, Stahl 1999, Stahl and Parris 2004), and we largely focus on the diagnostic features for each species we report. However, some diagnostic features that distinguish *Edaphodon* from *Ischyodus* tooth plates are outlined below. Our descriptive terminology largely follows Stahl and Parris (2004). We note here that little to no tritor tissue is preserved due to taphonomic processes, but cancellous and lamellar-textured surfaces show where

these pads were located on the tooth plates.

Institutional abbreviations—ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MSC, McWane Science Center, Birmingham, Alabama; MMNS, Mississippi Museum of Natural Science, Jackson; NJSM, New Jersey State Museum, Trenton; RMM, Red Mountain Museum, Birmingham (collections now at MSC); ALMNH, University of Alabama Museum, Tuscaloosa. The acronym ALMNH supersedes older acronyms appearing in the literature, including ALAM PV and UAM PV.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley 1880

CHIMAERIFORMES Obruchev 1953

CALLORHYNCHIDAE Garman 1901

EDAPHODON Buckland 1838

Edaphodon mirificus Leidy 1856

(Figs. 3A–D, 4A–C)

Material examined—ALMNH 1990.17.1, associated right and left vomerine, palatine, and mandibular plates; ALMNH 2005.6.0123, associated right and left vomerine, palatine, and mandibular plates; ALMNH 1991.7.3, left mandibular; MSC 34209.1, left palatine; MSC 34335, right palatine; MSC 34363, left mandibular tooth plate; RMM 2605, right mandibular; NJSM 11362, associated right and left vomerine, palatine and mandibular plates; FMNH PF 209, left palatine tooth plate; FMNH PF 27529, left palatine tooth plate; FMNH 27536, right mandibular; FMNH 27537, right mandibular tooth plate.

Stratigraphic occurrence—All the Alabama specimens are from the Mooreville Chalk (Upper Cretaceous, uppermost Santonian to middle Campanian).

Remarks—The vomerine plates (Fig. 3B) of *E. mirificus* are rather high but labiolingually narrow, with the labial face being flat to convex and lingual face concave. There are a number of rod-like tritors exposed as circular or oblong pads on the oral surface, which is generally developed into an oblique shearing surface. The palatine plates are rather narrow mesially but distally expanded, resulting in a subtriangular outline in oral view (Fig. 3A). There are three tritors, including the anterior and posterior inner tritors, which are located near the symphyseal margin, and an outer tritor near the labial margin. A dorsally directed projection at the distal end of the vomerine articulates with a sloped mesial surface of the palatine tooth plate (Fig. 4A–C).

The mesial end of the mandibular tooth plate is narrow and rather elongated into a beak-like structure (Fig. 3C). The distal half to one third of the plate diverges labially, and this region is also dorsoventrally expanded (Fig. 3C, D). There

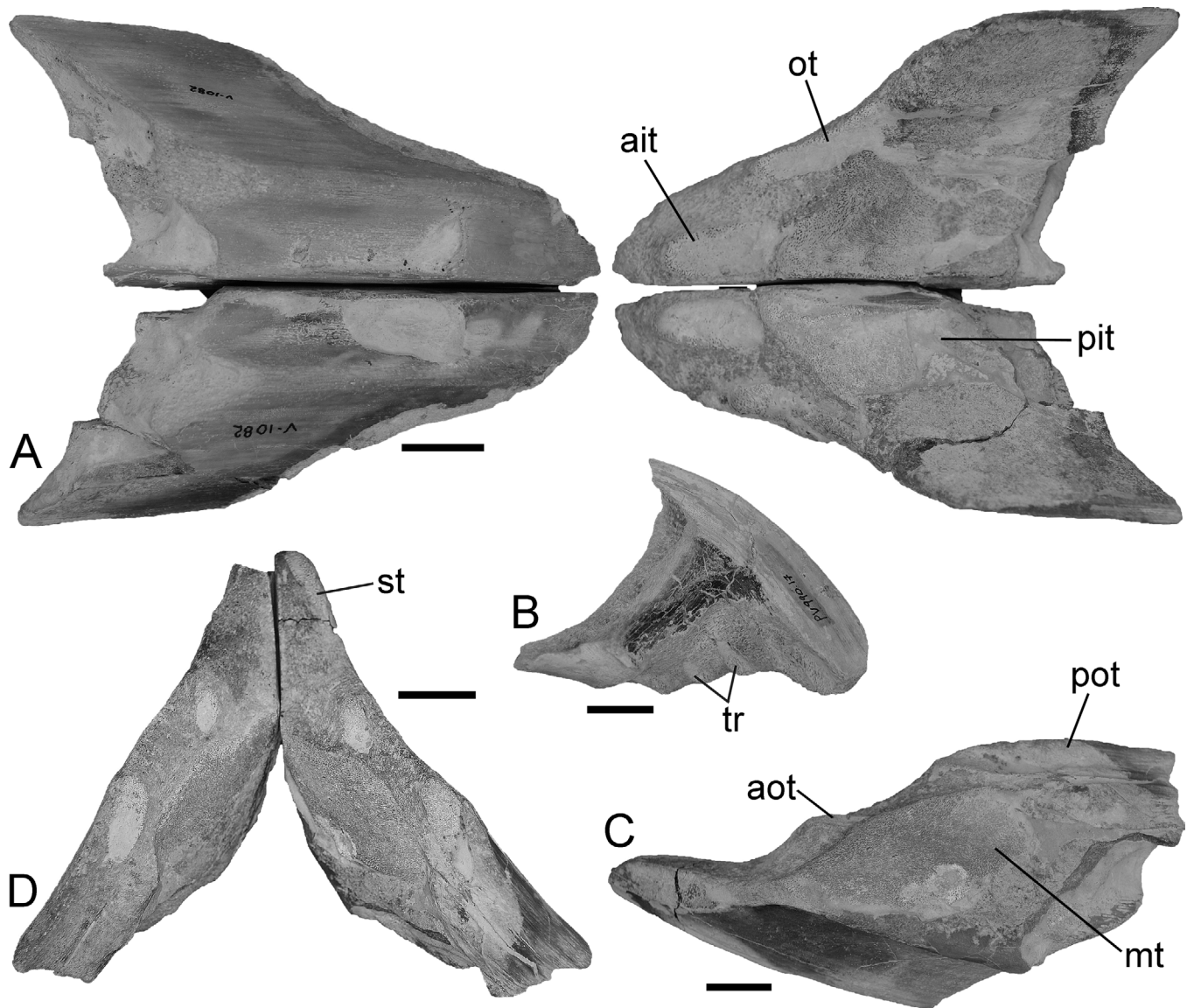


Figure 3. *Edaphodon mirificus* tooth plates. **A.** Articulated palatine tooth plates in aboral (left) and oral (right) views, ALMNH 2005.6.123. **B.** Left vomerine tooth plate in lingual view, ALMNH 1990.17.1. **C.** Right mandibular tooth plate in lingual view, ALMNH 2005.6.123. **D.** Articulated mandibular tooth plates in oral view, ALMNH 2005.6.123. Abbreviations: **ait**, anterior inner tritor; **aot**, anterior outer tritor; **mt**, middle tritor; **ot**, outer tritor; **pit**, posterior inner tritor; **pot**, posterior outer tritor; **st**, symphyseal tritor; **tr**, tritor rod. Scale bars = 2.0 cm.

are four tritors, including a symphyseal tritor that extends along the labial edge of the beak. Anterior and posterior outer tritors are both located on prominences at or near the labial margin, which creates a slight “stepped” appearance in profile view (Figs. 3C, 4A, B). The middle tritor is the largest crushing pad, and depending on wear, occupies much of the dorsal half of the distal oral surface (Fig. 3C).

Edaphodon sp.
cf. *Edaphodon mirificus*
(Fig. 5A–C)

Material examined—ALMNH 2013.4.70, left palatine tooth plate; MSC 34420, right vomerine tooth plate (Fig. 5A); MMNS VP-4959, left palatine tooth plate.

Stratigraphic occurrence—ALMNH 2013.4.70 and MSC 34420, lower Campanian Tombigbee Sand Member of the Eutaw Formation, Greene County; MMNS VP-4959, lower Maastrichtian Ripley Formation, Sumter County.

Description—Both palatines, ALMNH 2013.4.70 (Fig. 5B) and MMNS VP-4959 (Fig. 5C), have a sub-rectangular outline in oral view (as preserved) and bear three tritors. The anterior inner tritor is rather short and somewhat

ovate, whereas the posterior portion of the posterior inner tritor expands labially towards the outer tritor. The outer tritor is elongated and narrow.

Remarks—The palatine tooth plates of *Ischyodus bifurcatus* and *Eumylodus laqueatus* Leidy 1873, two species that have been reported from the Tombigbee Sand Member of the Eutaw Formation in Mississippi (see Case 1978, Case and Schwimmer 1992, Cicimurri et

al. 2008), are easily distinguished from *Edaphodon*. The palatines of *Ischyodus* are characterized by the presence of four large tritor pads. Similarly, the palatine tooth plate of *E. laqueatus* has four tritors (diminutive) and it lacks an aboral channel (Cicimurri et al. 2008). In contrast, ALMNH 2013.4.70 only has three tritor pads like *Edaphodon*. MMNS VP-4959 is quite similar to ALMNH 2013.4.70, and we believe that these tooth plates fall

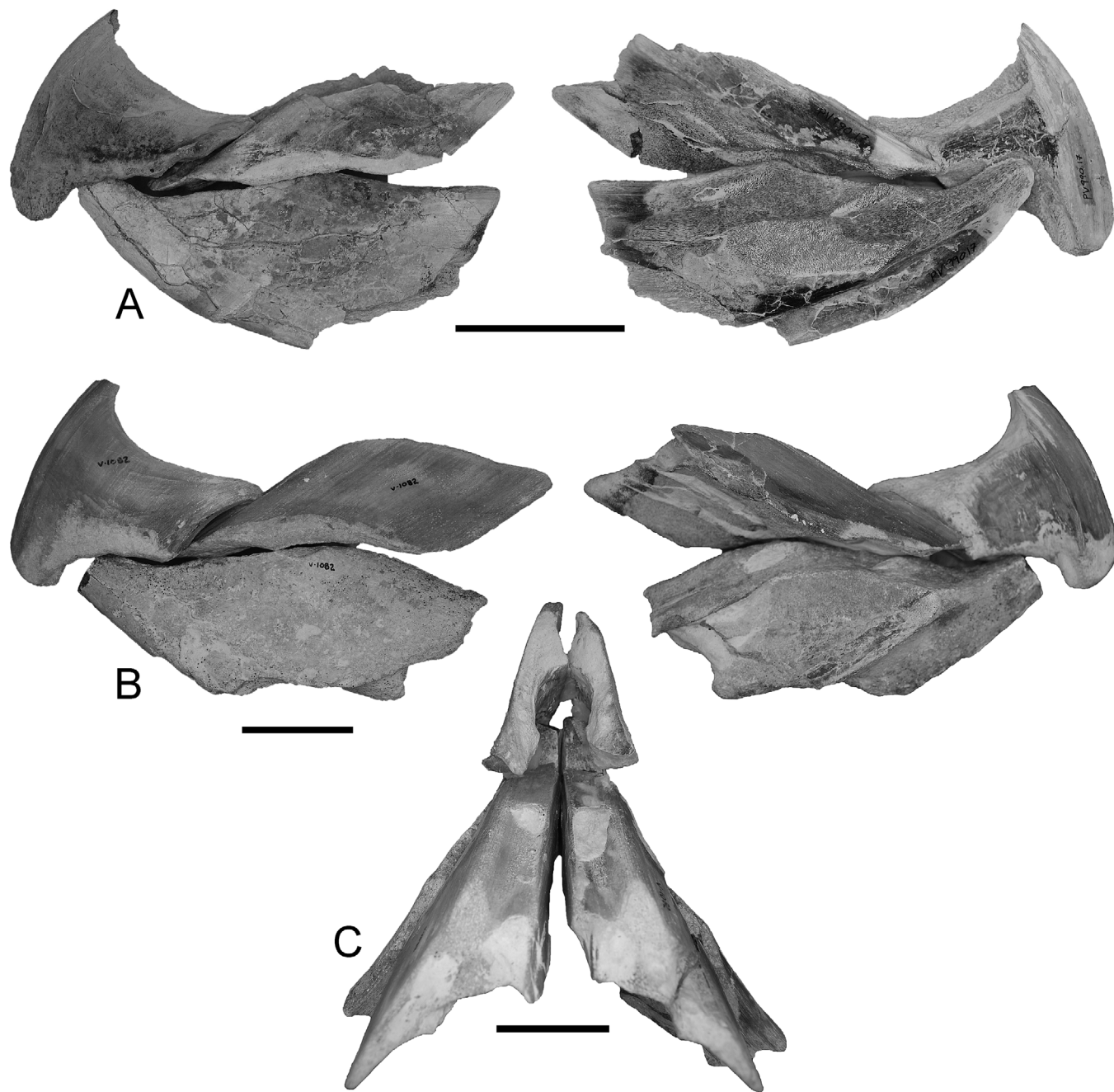


Figure 4. Associated dentitions of *Edaphodon mirificus* in approximate life position. **A, B.** Left tooth plates in labial (left) and lingual (right) views; ALMNH 1990.17 (**A**), ALMNH 2005.6.123 (**B**). **C.** ALMNH 2005.6.123 in dorsal view showing right and left tooth plates in approximate life position. Scale bars = 4.0 cm.

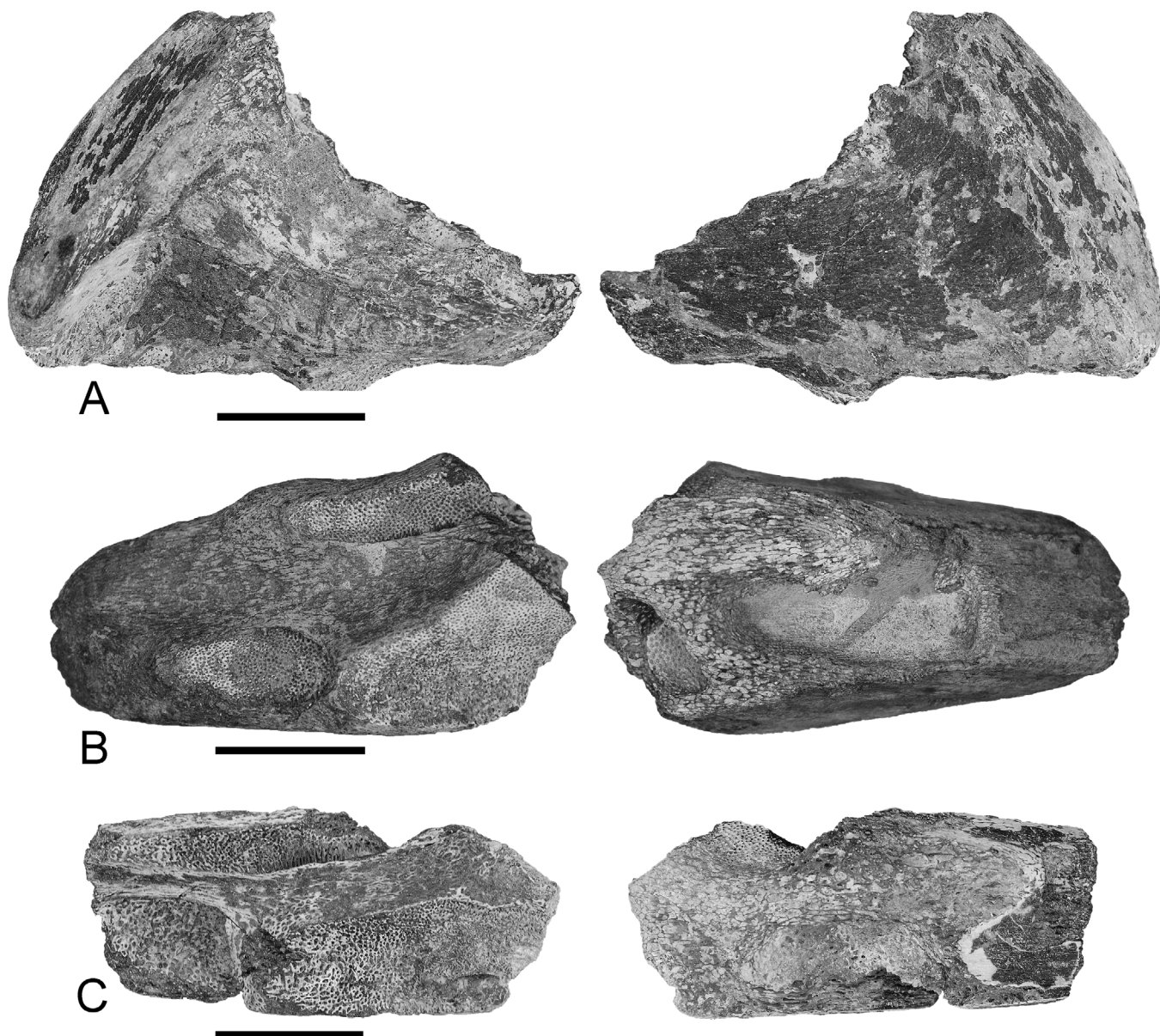


Figure 5. *Edaphodon* sp. cf. *E. mirificus* tooth plates. A. Right vomerine tooth plate in lingual (left) and labial (right) views, MSC 34420. B, C. Left palatine tooth plate in oral (left) and aboral (right) views; ALMNH 2013.4.70 (B), MMNS VP 4959 (C). Scale bars = 4.0 cm.

within the range of variation that we have observed for *E. mirificus*. All specimens represent first Alabama records of *Edaphodon* for the lithostratigraphic units from which they were collected.

Edaphodon barberi [Applegate 1970](#)
(Figs. 6A–C, 7A–C)

Material examined—FMNH PF 290, holotype, left mandibular; FMNH PF 3501(?), right mandibular; RMM 3603, associated right and left mandibulars; RMM 5809, left mandibular tooth plate; RMM 6134, associated right

and left mandibulars; RMM 6134.2, right mandibular tooth plate; ALMNH 1988.20.156.3, right mandibular tooth plate; ALMNH 1994.1.23, left mandibular tooth plate.

Stratigraphic occurrence—The species is known only from the Mooreville Chalk (Upper Cretaceous, uppermost Santonian to middle Campanian) of Alabama.

Remarks—*Edaphodon barberi* is represented only by mandibular tooth plates, and they are comparable to those of *E. mirificus* in terms of general morphology. Unfortunately, the specimens are not preserved in entirety, but the maximum length of the tooth plates from the mesial

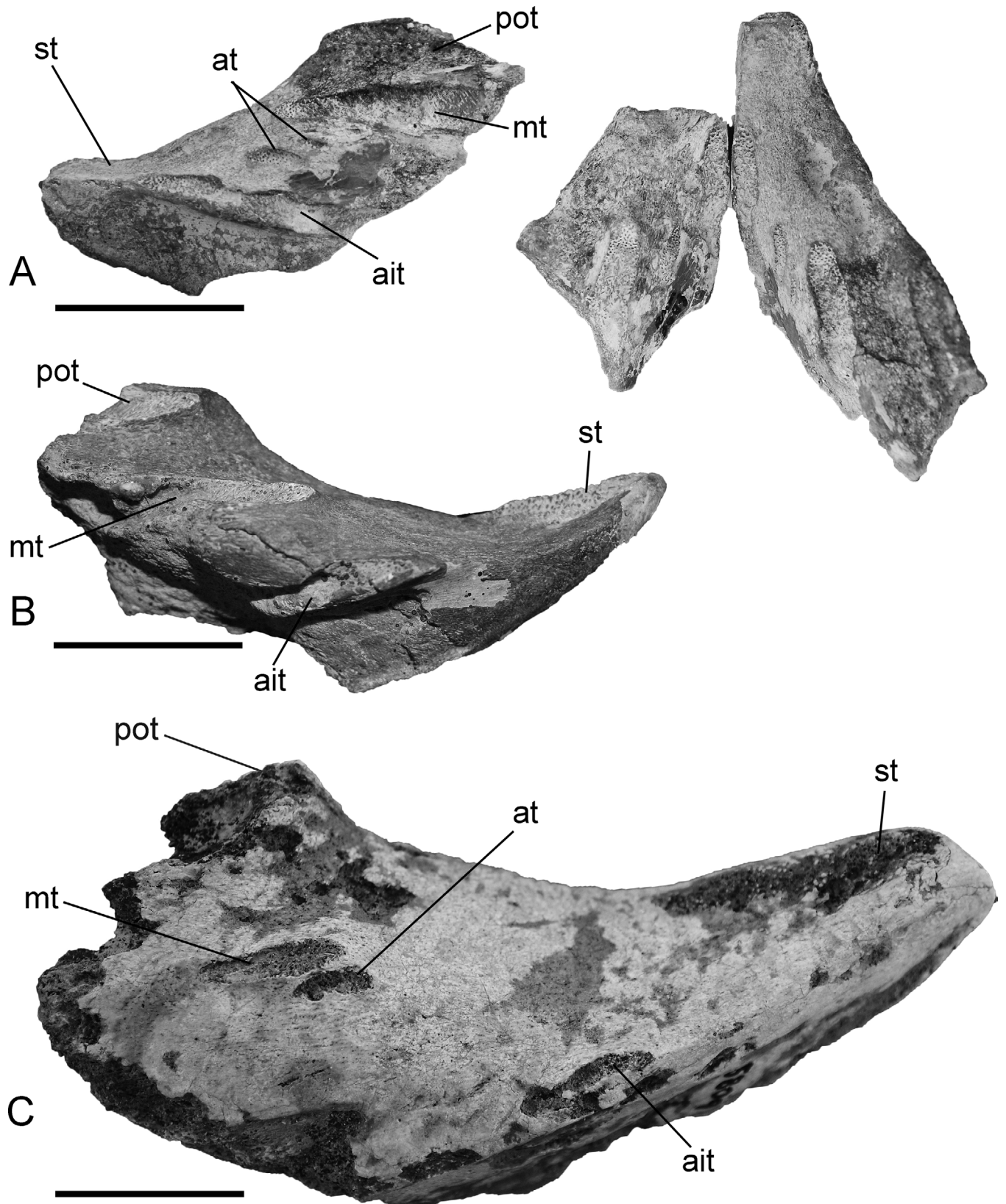


Figure 6. *Edaphodon barberi* mandibular tooth plates showing variations in overall size and development of tritors. **A.** Right tooth plate in lingual view (left), associated left and right tooth plates in oral view (right), RMM 3603.1. **B.** Left tooth plate in lingual view, FMNH PF 290. **C.** Left tooth plate in lingual view, RMM 5809. Abbreviations: ait, anterior inner tritor; at, accessory tritor; mt, middle tritor; pot, posterior outer tritor; st, symphyseal tritor. Scale bars = 2.0 cm.

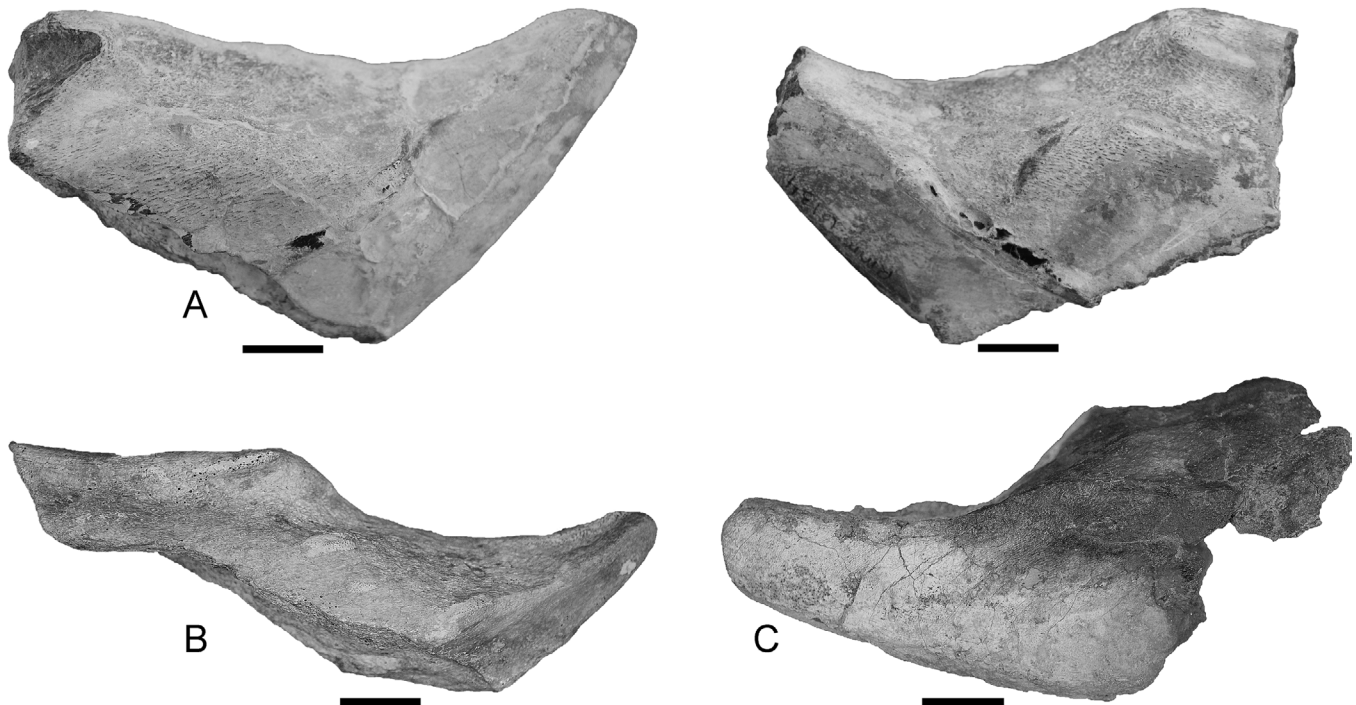


Figure 7. *Edaphodon barberi* mandibular tooth plates showing minor variations in morphology. **A.** Associated left (left side) and right (right side) tooth plates in lingual view, RMM 6134. **B.** Left tooth plate in lingual view, RMM 5809. **C.** Right tooth plate in lingual view, ALMNH 1988.20.156.3. Scale bars equal 2.0 cm.

end to the distalmost tip ranges from 61.36 mm to 126.34 mm, with FMNH PF 290 (holotype; Fig. 6B) measuring 64.66 mm in this dimension.

Four tritors are consistently present on the oral surface, and one or two smaller accessory tritors may also be visible (Fig. 6A–C). The symphyseal tritor, which Applegate (1970) called the apical tritor, is exposed at the mesial tip of the beak and extends distally various distances along the labial oral margin. There is no anterior outer tritor as seen on *E. mirificus* mandibular tooth plates, but the posterior outer tritor (called the postero-dorsal tritor by Applegate (1970) is narrow, elongated, and located on a prominence that forms the highest part of the labial margin. The posterior outer tritor is adjacent to and parallels the middle tritor (= Applegate's (1970) postero-intermediate tritor), which is elongated and occupies a rather small portion of the distal oral surface. The fourth large tritor, which Applegate (1970) called the antero-intermediate tritor, is narrow and located at the lower one third of the lingual face, immediately distal to the symphyseal margin of the beak. This tritor appears to be equivalent to the inner tritor as identified on *Ischyodus* mandibular tooth plates (i.e., Case 1978, Stahl and Chatterjee 2002, Hoganson and Erickson 2005).

Three specimens among the nine studied show small accessory tritors may develop. These seem to be discrete

superficial pads within the dentine tissue, rather than exposed portions of a larger middle tritor. RMM 5809, which measures nearly 103 mm in greatest dimension, bears a single accessory tritor just ventral and slightly mesial to the middle tritor (Fig. 6C). In contrast, the right mandibular of RMM 3603, a small specimen roughly 61 mm in greatest dimension, bears a tiny tritor just below the middle tritor, as well as a slightly larger tritor roughly between the middle and inner tritors (Fig. 6A). FMNH PF 290 (holotype; Fig. 6B) is only slightly larger than RMM 3603 but has no accessory tritors, nor are these structures present on the remaining specimens, which are larger than RMM 5809. This would seem to preclude attributing the formation of accessory tritors to ontogeny, and it is more likely that their development is an example of individual variation within the species.

If Hussakof's (1912) ontogenetic series for *E. mirificus* is correct, the number of mandibular tritors remained constant throughout life, and their relative positions did not vary appreciably. The growth series for *E. barberi*, with specimens measuring 60 to 70 mm ($n=2$) and 100 to 120 mm ($n=5$), shows that the four main tritors are present throughout life. More importantly, the presence of an inner tritor and lack of the anterior outer tritor are features that distinguish *E. barberi* mandibular plates from those of *E. mirificus*, regardless of growth stage.

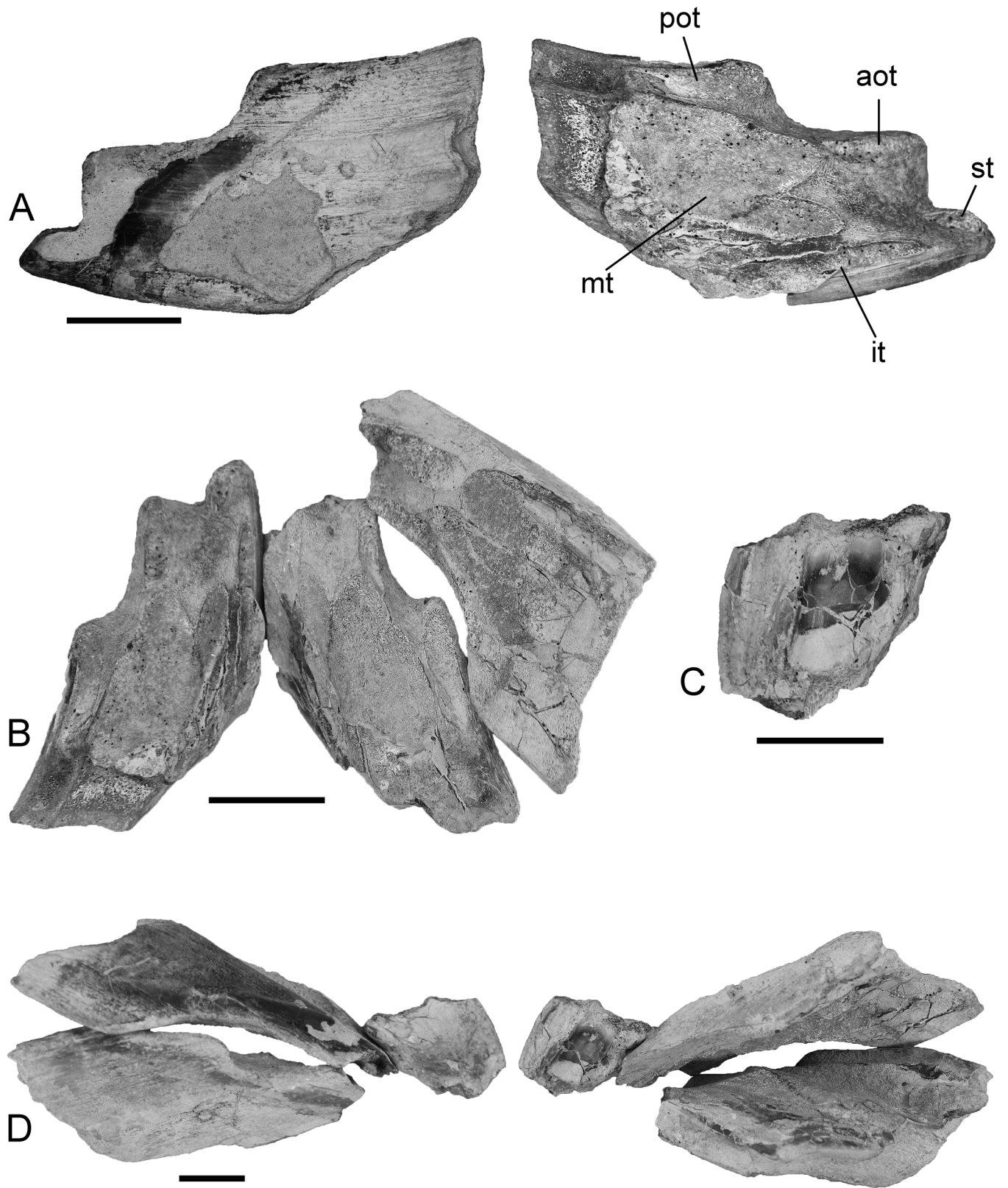


Figure 8. *Ischyodus bifurcatus* associated dentition, ALMNH 1994.1.22. **A.** Left mandibular tooth plate in labial (left) and lingual (right) views. **B.** Articulated mandibular tooth plates in oral view (mesial at top), with right palatine “opened up” and in oral view to reveal tritor occlusion. **C.** Right vomerine tooth plate in lingual view. **D.** Approximate life position of right tooth plates in labial (left) and lingual (right) views. Abbreviations: **aot**, anterior outer tritor; **it**, inner tritor; **mt**, middle tritor; **pot**, posterior outer tritor; **st**, symphyseal tritor. Scale bars = 2.0 cm.

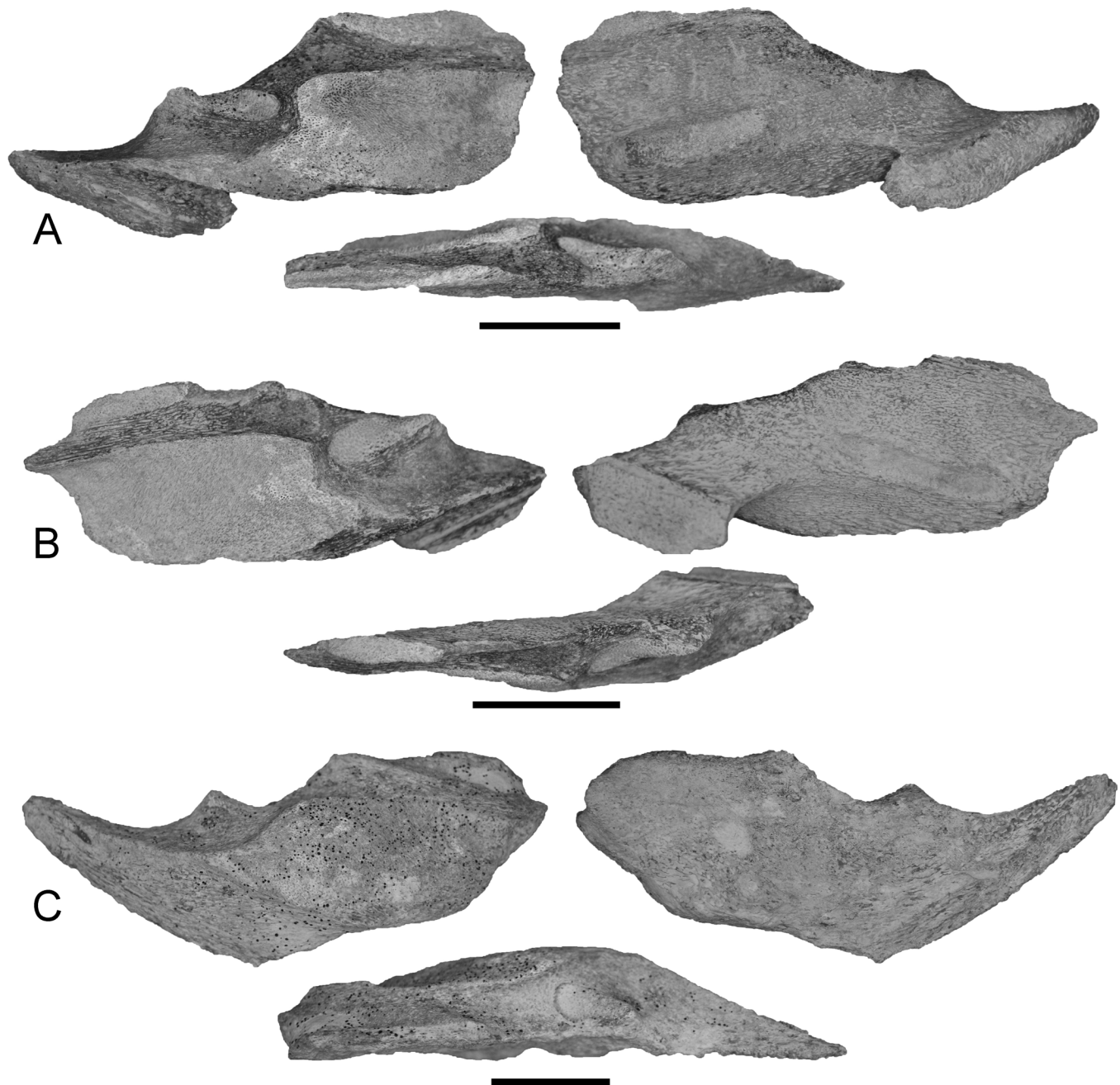


Figure 9. *Ischyodus bifurcatus* mandibular tooth plates showing variations in overall morphology. Lingual views for all specimens are at left, oral views center, and labial views at right. **A.** Right tooth plate, ALMNH 2004.18.9. **B.** Left tooth plate, ALMNH 2006.2.2. **C.** Right tooth plate, ALMNH 1994.24.23. Scale bars = 2.0 cm.

ISCHYODUS Egerton 1843
Ischyodus bifurcatus Case 1978
 Figs. 8A–D, 9A–C

Material examined—ALMNH 2004.18.9, right mandibular tooth plate; ALMNH 2006.2.2, left mandibular tooth plate; ALMNH 1994.24.23, right mandibular tooth plate; ALMNH 1993.0002.0134, right mandibular;

ALMNH 1994.1.22, associated right vomerine, right palatine tooth plate, distal tip of left palatine, and right and left mandibular tooth plates.

Stratigraphic occurrence in Alabama—All specimens are from the Mooreville Chalk (Upper Cretaceous, uppermost Santonian to middle Campanian).

Remarks—The palatine tooth plate within ALMNH 1994.1.22 (Fig. 8B) is morphologically similar to those of

E. mirificus, but it can easily be distinguished by the presence of four large tritors instead of three (see also Case 1978, Hoganson and Erickson 2005). The vomerine tooth plate of ALMNH 1994.1.22 is incomplete but morphologically comparable to *Edaphodon* and articulated with the palatine in the same manner (Fig. 8C, D). *Ischyodus bifurcatus* mandibular tooth plates are also generally similar to *Edaphodon*, but they are comparatively thinner labiolingually and the beak is usually shorter. The plates articulate near the ventral margin (Fig. 8B), as opposed to flat vertical surfaces along the entire beak as in *E. mirificus* and *E. barberi* (Figs. 3D and 6A, respectively). *Ischyodus bifurcatus* also has a similar tritor arrangement to *E. mirificus*, with symphyseal, anterior and posterior outer, and middle tritors being present. However, the symphyseal tritor is much shorter and the location of the anterior outer tritor on *I. bifurcatus* is entirely anterior to the mesial margin of the middle tritor (Figs. 8A, 9A–C), not more or less even with the middle tritor as on *E. mirificus* (Figs. 3C, 4A, B). Furthermore, the labial margin of *I. bifurcatus* mandibular tooth plates has a jagged, “stepped” appearance (Fig. 9A) rather than a sinuous labial margin as in *E. mirificus* (Fig. 3C) or the simple, concave margin of *E. barberi* (Fig. 6A–C). The middle tritor of *I. bifurcatus* mandibular tooth plates occupies nearly the entire oral surface beyond the anterior outer tritor, and its mesial margin is conspicuously bifurcated (Figs. 8A, 9A, B). In contrast, the middle tritor of *E. mirificus* is less expansive and generally has a rounded mesial margin (Figs. 3C, 4B). Interestingly, only one specimen, ALMNH 1994.1.22, clearly exhibits an anterior inner tritor, a structure apparently not observed on specimens previously reported, but only speculated as being “dormant” (Case 1978, Case and Schwimmer 1992). However, the specimens illustrated by Case (1978; pl. 1a) and Case and Schwimmer (1992; fig. 2.1) appear to show this structure in approximately the same position as ALMNH 1994.1.22 (Fig. 8A). ALMNH 1994.1.22 shows that the anterior inner tritor tissue extended all the way to the distal end of the tooth plate, but the majority was covered by a thin layer of dentine and only a relatively small portion was exposed at any one time. This morphology likely resulted in the tritor remaining in approximately the same position as the tooth plate was worn throughout life.

DISCUSSION

Three callorhynchid holocephalans, *Edaphodon barberi*, *E. mirificus*, and *Ischyodus bifurcatus*, are now known from the Mooreville Chalk of Alabama. Fossil callorhynchid tooth plates can be highly variable, even

within the mouth of a single individual (i.e., Hussakof 1912, Stahl and Parris 2004), but significant variations can be used to accurately identify their isolated tooth plates. For example, palatine tooth plates of *I. bifurcatus* and *E. mirificus* are similar to each other, but they can be easily distinguished by the number of tritor pads, with three on *E. mirificus* (Fig. 3A) and four on *I. bifurcatus* (Fig. 8B). Although the palatine tooth plates of *E. barberi* are unknown, the number and location of the tritors on the mandibular tooth plates leads us to believe that the tritors were relatively small, with the outer tritor being shorter and located in the area directly over the posterior outer tritor of the mandibular tooth plate.

Although *E. barberi* and *E. mirificus* mandibular tooth plates are similar to each other, key differences distinguish the two species, with the most obvious being the lack of an anterior outer tritor on *E. barberi* tooth plates (Fig. 3A–C). The anterior outer tritor on *E. mirificus* mandibulars is located on a small prominence roughly between the middle tritor and the labial margin, and this structure, along with the mesial beak and high position of the posterior outer tritor, contributes to a sinuous labial margin (i.e., Figs. 3A, 4A, B). In contrast, the labial margin of *E. barberi* mandibular tooth plates is rather arcuate (concave) due to the lack of an anterior outer tritor (Fig. 7A–C). Additionally, the middle tritor of *E. barberi* is smaller than the pad of similar-sized *E. mirificus*, which occupies much of the dorsal half of the oral surface distal to the beak (compare Fig. 6B with Fig. 3C). Also, the “antero-intermediate” tritor of *E. barberi* is a distinct structure that is well separated from the middle tritor by an expanse of dentine (see Fig. 6A–C). This particular tritor appears to be equivalent to the anterior inner tritor occurring on some *Ischyodus* species (i.e., Leriche 1902, Stahl and Chatterjee 2002, Hoganson and Erickson 2005).

The two associated *E. mirificus* dentitions from Alabama and a specimen from New Jersey (see Stahl and Parris 2004) allow us to understand how the tooth plates functioned together. The vomerine and palatine plates were fused to the cranium and worked as a single unit, with the distal process of the vomerine overlapping the mesial margin of the palatine. When the mouth was closed, the mesial tip of the mandibular beak rested within a small facet on the lingual side of the vomerine plate (Fig. 4A, B). The symphyseal tritor on the mandibular plate, located along the labial margin, moved across the lingual side of the vomerine plate’s tritoral rods and dentine in a shearing motion, resulting in the formation of a dull cutting edge on the vomerine.

Distal to the beak, the mesial end of the anterior inner

tritor of the palatine contacts the anterior part of the anterior outer tritor on the mandibular, but it appears that the majority of these two tritors do not actually touch each other (Fig. 4A, B). The outer tritor of the palatine, for the most part, contacts the posterior outer tritor on the mandibular, and also comes close to the softer dentine between the mandibular's anterior and posterior outer tritors. This differential wear of the dentine results in the formation of the prominences upon which the outer tritors of the mandibular are situated. Interestingly, no tritor comes in direct contact with the middle tritor of the mandibular tooth plate when the mouth is closed. Rather, the palatine's posterior inner tritor lies above the mandibular plate's middle tritor, and it appears that prey was crushed within the space (see Fig. 4; also fig. 3 of [Stahl and Parris 2004](#)) in much the same way a nut is cracked in between the arms of a nutcracker—the pivot point being the articulation between the mandibular tooth plate and skull. The amount of wear seen on the mandibular tooth plate's middle tritor, as in the amount of tritor pad exposed from surrounding dentine, is therefore dependent upon the amount of abrasion from prey hard parts moving across the surface, rather than direct contact by a tritor.

ALMNH 1994.1.22 (Fig. 8B, D) shows that the tooth plates of *Ischyodus bifurcatus* articulated and occluded in a manner similar to *E. mirificus*, but with significant differences. The mandibular tooth plates of *I. bifurcatus* articulated along their ventral margins (Fig. 8B), but in *E. mirificus* and *E. barberi* the tooth plates were united via a flat, vertical to nearly vertical surface along the entire beak (Figs. 3D, 6A). Although it is poorly preserved, the right vomerine tooth plate exhibits a roughly circular worn area where the tip of the mandibular tooth plate's beak rested when the mouth was closed (Fig. 8C). The mesial tip and the distal end of the outer tritor on the palatine tooth plate come in contact with the mesial tip of the anterior outer tritor and mesial end of the posterior outer tritor, respectively, of the mandibular tooth plate. Curiously, and in contrast to *E. mirificus* (Fig. 4A, B), this orientation produces a large gap between the labial margins of the palatine and mandibular tooth plates (Fig. 8D). The work of the palatine's outer tritor against the mandibular's posterior outer tritor was helped by the labial side of the palatine's middle tritor. The palatine's middle and posterior inner tritors formed a wide crushing surface that lies above and is comparable in size to the mandibular's middle tritor (Fig. 8B), and prey appears to have been largely processed within this region. Although the mesial end of the palatine's anterior inner tritor contacts the distal part of the mandibular's symphyseal tritor, this palatine

tritor largely overlies a tritor-less region of the mandibular plate between the symphyseal, anterior outer, and middle tritors. The anterior inner tritor on the mandibular tooth plates of ALMNH 1994.1.22 undoubtedly assisted with prey mastication, working in conjunction with the anterior inner tritor of the palatine plate, but this structure is not apparent on other Alabama specimens we examined and may not be ubiquitous. The vomerine tooth plate appears to have played a smaller role in prey manipulation, touching only a small portion of the mandibular beak compared to *E. mirificus* (Fig. 4A).

Edaphodon and *Ischyodus* are generally considered to have been durophagous predators, and the formation of numerous hard tritoral pads within broad tooth plates would seem to have facilitated crushing hard-shelled prey. The three chimaeroid species reported here, *E. barberi*, *E. mirificus* and *I. bifurcatus*, show progressively greater development of tritor pads within the dentition. *Edaphodon barberi* has the smallest tritors and lacks the anterior outer mandibular tritor as seen on *E. mirificus* and *I. bifurcatus* (compare Fig. 6A–C with Figs. 3C and 8A). However, it does have what can be considered an anterior inner mandibular tritor near the symphyseal region (Fig. 6A–C), indicating this was an area where prey was masticated. The reduced size and number of tritors is reminiscent of the condition seen on *Leptomylus densus* [Cope 1869](#) mandibular tooth plates. A right mandibular of *L. densus*, ANSP 9440, shows only a middle tritor, and the palatine tooth plate (ANSP 9441) bears only the outer and a single inner tritor. All of these tritors are narrow and elongated, those of the palatine appearing to flank the mandibular tritor, but making no contact when the mouth was closed.

Edaphodon mirificus and *I. bifurcatus* have comparably-sized tritors, but the middle tritor of *E. mirificus* mandibulars (Fig. 3C) is slightly less expansive than the bifurcated middle tritor of *I. bifurcatus* (Fig. 8A). The wide posterior inner tritor of *E. mirificus* palatine tooth plates (Fig. 3A) has a slightly smaller surface area than the combination of middle and posterior inner tritors of *I. bifurcatus* palatine tooth plates (Fig. 8B). Also, the anterior and posterior outer tritors of the mandibular tooth plate of *I. bifurcatus* appear to be more robust and larger relative to overall plate size compared to *E. mirificus*. These variations in tritor development may indicate that each species had a slightly varied diet, with *I. bifurcatus* eating the hardest/thickest shelled invertebrates and *E. barberi* the softest/thinnest shelled invertebrates. However, studies by [Huber et al. \(2008\)](#) suggest that the broader surfaces of extant chimaeroid tooth plates could effectively distribute bite

forces to crush prey without the need for highly mineralized tissues. It is possible that *E. mirificus* had a more diverse diet, as indicated by the sharper anterior portion of the upper dentition that could have been used to slice non-shelled invertebrates and even other vertebrates (see also Consoli 2006).

If tooth plates of extant holocephalan fishes can be used as a model, the body size of extinct species like *Edaphodon* and *Ischyodus* can be estimated. Study of some extant callorhynchid and rhinochimaerid specimens at the ANSP revealed that the palatine tooth plate represents 4% of the body length of the fish (posterior to the gill opening and excluding the elongated tail). With a right palatine tooth plate measuring 6.72 cm, the *E. mirificus* represented by ALMNH 2005.6.123 had a body length of approximately 1.7 m, the 9.90 cm long left palatine of ALMNH 1990.17.1 belonged to a fish measuring 2.47 m in length, and the 13.7 cm right palatine of NJSM 11362 was from a fish with a body length of 3.43 m. The 3.94 cm palatine of ALMNH 1994.1.22 represents an *I. bifurcatus* that measured approximately 0.99 m in length. Although *E. barberi* palatine tooth plates are currently unknown, larger mandibular plates (i.e., RMM 6134.1) indicate fish of comparable size to an *E. mirificus* like ALMNH 1990.17.1.

CONCLUSIONS

Three species of extinct callorhynchid holocephalan fishes are now known from upper Cretaceous strata of Alabama, including *Edaphodon barberi*, *E. mirificus* and *Ischyodus bifurcatus*. The fossils primarily occurred within the upper Santonian to lower Campanian Mooreville Chalk, but two tooth plates referred to *Edaphodon* sp. cf. *E. mirificus* were collected from the lowermost Campanian Tombigbee Sand Member of the Eutaw Formation. A palatine tooth plate of *Edaphodon* sp. cf. *E. mirificus* has also been collected from a region in which the lower Maastrichtian Ripley Formation is exposed.

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