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Cicimurri, David J.
Ebersole, Jun A.

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Paleocene chimaeroid fishes (Chondrichthyes: Holocephali) from the eastern United States, including two new species of *Callorhinchus*

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

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

Isolated tooth plates collected from Paleocene deposits of Alabama, Arkansas, Illinois, Maryland, Mississippi, New Jersey, South Carolina, Texas, and Virginia represent four genera of chimaeroid fishes. *Callorhinchus* is reported in the fossil record of North America for the first time and is represented by material from the Danian (early Paleocene) of Mississippi and the Thanetian (late Paleocene) of Maryland and Virginia. Specimens from both locations are identified as new species, the Danian *C. phillipsi* n. sp. and the Thanetian *C. alfordi* n. sp. New Paleocene *Elasmodus* records from North America include two partial mandibulars belonging to *E. hunteri* from the Thanetian of Maryland, and a nearly complete mandibular from the Danian of New Jersey, tentatively assigned to cf. *Elasmodus* sp. Two species of *Ischyodus* are recognized, *I. dolloi* (Danian and Thanetian) and *I. williamsae* (Danian), but the two species have not been found in the same lithostratigraphic deposits. *Edaphodon mirificus* is known from the Danian of New Jersey and Mississippi, and the genus also occurs in the Thanetian of Virginia.

Keywords: Paleocene, *Callorhinchus*, *Ischyodus*, *Edaphodon*, *Elasmodus*, n. sp.

INTRODUCTION

The genus *Callorhinchus* Lacépède, 1798 is represented by three extant species, all from the southern hemisphere (Sullivan 1977, Freer and Griffiths 1993, Di Giacomo and Perier 1996). The fossil record of the genus is also primarily from the southern hemisphere, with specimens collected from Late Cretaceous strata of New Zealand (Newton 1876) and Antarctica (Martin and Crame 2006, Otero et al. 2013b, Otero et al. 2014), the early Eocene of Antarctica (Kriwet and Gadżicki 2003), the Miocene of Australia (Woodward and White 1930); and the late Miocene and early Pliocene of Chile (Suárez et al. 2004, Carrillo-Briceño et al. 2013). Northern hemisphere records include the Jurassic and Cretaceous of Russia (Nessov and Averianov 1996, Popov and Shapovalov 2007), and the late Paleocene (Ward 1973) and early Eocene of England (Gurr 1962, Ward and Grande 1991).

Remains of *Edaphodon* Buckland, 1838 are commonly found in Cretaceous strata, and Stahl (1999) recognized eight species in the United States. The genus is known primarily from isolated tooth plates, but several associated dentitions of *E. mirificus* Leidy, 1856 have been described (Stahl and Parris 2004, Cicimurri and Ebersole 2014). *Edaphodon mirificus* spans the Cretaceous/Paleocene boundary (Parris and Hope 2002, Stahl and Parris 2004), but few other species have been reported from Paleogene sediments (Buckland 1838, Agassiz

1843, Cope 1869, 1875, Cicimurri and Ebersole 2014), and all of these occur within Eocene deposits. In the United States, species include *E. eoceanus* (Cope, 1875) from New Jersey and *Edaphodon* sp. from Georgia (Parmley and Cicimurri 2005). In England species include *E. bucklandi* Agassiz, 1843 and *E. leptognathus* Agassiz, 1843. An additional species, *E. minor* Ward, 1973, may represent a juvenile morphology of *E. bucklandi* (Kemp et al. 1990, Stahl 1999). A specimen that Case (1996) identified as *E. mantelli* (Buckland, 1835) is herein considered to be *E. mirificus*. *Edaphodon* is known to have survived into the Pliocene, as evidenced by isolated tooth plates reported from Italy (Carraroli 1897) and Australia (Chapman and Pritchard 1907, Chapman and Cudmore 1924).

Ischyodus Egerton, 1843 is known primarily from tooth plates, but associated dentitions and whole-body specimens have been found (Stahl 1999 provides a general overview of the genus; Cicimurri and Ebersole 2014). The geographic distribution of *Ischyodus* is expansive, having been documented from throughout the United States (e.g., Case 1991, Cvancara and Hoganson 1993), Europe (e.g., Egerton 1843, Pictet and Campeche 1858, Leriche 1902, 1908, Radwanski 1968, Ward 1973, Popov and Marchalski 2014), Australia and New Zealand (Long 1985, Fitzgerald 2005), South America (Otero et al. 2012, 2013a), and Antarctica (Ward and Grande 1991, Stahl and Chatterjee 2002). The temporal distribution of the genus is very long, with a record in the northern

*author for correspondence

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hemisphere extending from the Middle Jurassic to the late Eocene (e.g., Egerton 1843, Leriche 1902, Ward 1973), and the taxon apparently persisted into the Miocene (Ward and Grande 1991, Toscano et al. 2011) and Pliocene (Fitzgerald 2005) within the southern hemisphere.

The oldest records of *Elasmodus* Egerton, 1843 are from the Jurassic of England and Russia (Popov 2013), but the genus diversified during the Cretaceous and numerous species have been identified from rocks of this age, particularly in Russia (Agassiz 1843, Leriche 1929, Averianov 1999). Only three species occur in Paleogene strata, and the most widespread, *E. hunteri* Egerton, 1843, has been reported from Paleocene and Eocene strata of the United States, Europe, and Russia (Leriche 1902, 1909, 1951, Gurr 1962, Casier 1966, 1967, Herman 1972, Ward 1973, 1980, Cvancara and Hoganson 1993, Averianov 1999). The youngest record of the genus is arguably from the early Oligocene of Kazakhstan (Averianov 1999). Most of the published occurrences of *Elasmodus* are from the northern hemisphere, but Popov (2013) has indicated that the genus was present in the southern hemisphere, represented by specimens that had been previously misidentified (i.e., Consoli 2006).

Chimaeroid fossils are well represented in Cretaceous deposits of the eastern United States (e.g., Leidy 1873, Applegate 1970, Case 1978, Robb 1989, Case and Schwimmer 1992, Stahl and Parris 2004, Cicimurri 2010, Cicimurri and Ebersole 2014). The limited published Paleogene record includes *Edaphodon* from the Paleocene and Eocene of New Jersey (Cope 1875, Case 1996, Stahl and Parris 2004) and the Eocene of Georgia (Parmley and Cicimurri 2005), and *Ischyodus* from the Paleocene of Alabama (Denton et al. 1997), Illinois (Cope et al. 2005), Maryland (Case 1991), New Jersey (Case 1996), and South Carolina (Purdy 1998).

In this study, we examined Paleocene holocephalan material that is housed in museums in Alabama, Arkansas, Illinois, Maryland, Mississippi, New Jersey, South Carolina, Texas, and Virginia. As a result of our study, *Callorhynchus* (represented by two new species) is recognized for the first time in the North American fossil record, and new occurrences of *Elasmodus* are documented. In addition, the existence of two species of *Ischyodus* is validated, and the Paleocene geographic distribution of *Edaphodon* in North America is extended from New Jersey to Mississippi and Virginia.

LOCALITIES AND STRATIGRAPHIC OCCURRENCE

The Paleocene chimaeroid tooth plates examined in this study were collected from: Wilcox and Henry counties, Alabama; Hot Spring County, Arkansas; Pulaski County, Illinois; Charles County, Maryland; Oktibbeha County, Mississippi; Monmouth County, New Jersey; Berkeley County, South

Carolina; Hunt County, Texas; and King George County, Virginia (Fig. 1). Early Paleocene (Danian) specimens were collected from the Clayton Formation of Alabama, Arkansas, Mississippi, and Illinois, as well as the Hornerstown Formation of New Jersey. Two specimens from Texas were found as float along the banks of the South Sulphur River and therefore lack stratigraphic control. However, at the collecting site, the river cuts through a down-faulted block of the Danian Kincaid Formation. Late Paleocene (Thanetian) specimens were recovered from the “*Ostrea thirsae*” beds of the Nanafalia Formation in Alabama, and the Piscataway Member of the Aquia Formation of Maryland and Virginia. The South Carolina material was not collected *in situ*, but fossils were derived either from the lower Paleocene Rhems Formation or overlying upper Paleocene Williamsburg Formation. It must be noted here that the type horizon for *Ischyodus williamsae* Case, 1991 was misidentified as the Thanetian “lower Aquia Formation.” In reality, what is exposed at the cited locality are strata that belong to the Danian Brightseat Formation, a unit that is temporally equivalent to the Clayton and Kincaid formations (the type locality of *I. williamsae* is within 2 km of the type section for the Brightseat Formation). A correlation chart showing units listed above is presented in Fig. 2.

MATERIALS AND METHODS

This report originally began as a note discussing the significance of ALMNH 1994.9.19, a specimen mentioned by Denton et al. (1997) and identified as *Ischyodus williamsae*. The fossil was collected from the lower Danian Pine Barren Member of the Clayton Formation of Alabama, and the geologic provenance spurred a search for additional chimaeroid fossils from this formation. The sample size quickly grew to include material from the Clayton of Arkansas, Illinois (identified as *I. williamsae* by Cope et al. 2005), and Mississippi. Direct comparison of these fossils to the type specimens of *I. williamsae* was not possible because the type material is in France, but we examined other chimaeroid fossils that were collected from the Aquia Formation, the purported type formation of *I. williamsae* (Case 1991), with the hope of identifying additional tooth plates of this species. We also examined a specimen from the Hornerstown Formation of New Jersey that Case (1996) identified as *I. williamsae*, and to make additional comparisons we studied other chimaeroid material from this formation. The senior author (DJC) was aware of a Paleocene mandibular tooth plate in the collection of the Charleston Museum, South Carolina, but at the time of this study the specimen could not be located. However, while searching for this specimen, a palatine tooth plate was discovered and incorporated into this study. A request to examine Cretaceous chimaeroid fossils from Texas yielded two Paleocene specimens of *Ischyodus*. Towards the completion

of this study, 38 recently acquired specimens from the Aquia Formation were shipped to us by the Calvert Marine Museum in Maryland, nearly doubling our original sample size. We realize that we did not conduct an overly exhaustive search for Paleocene chimaeroid fossils in museum collections across the eastern United States, and some specimens mentioned in previous reports were not observed by us (i.e., Gallagher et al. 1986), but the 94 specimens we examined represents the most comprehensive review of such material thus far undertaken.

Larger specimens were photographed with Nikon D80 and Canon Eos Rebel T3i digital SLR cameras, but smaller specimens (< 15 mm in greatest dimension) were photographed through a Nikon Coolpix 995 digital camera attached via adapter to a microscope. Digital images were

enhanced with Adobe Photoshop CS4 software. Specimens were measured to the nearest tenth of a millimeter using digital calipers. Measurement and descriptive terminology largely follows Stahl and Parris (2004), and classification follows Stahl (1999).

Institutional abbreviations—ALMNH, Alabama Museum of Natural History, University of Alabama, Tuscaloosa; AMNH, American Museum of Natural History, New York, New York; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; ChM, Charleston Museum, Charleston, South Carolina; CMM, Calvert Marine Museum, Solomons, Maryland; ISGS, Illinois State Geological Survey, Champaign; MMNS, Mississippi Museum of Natural Science, Jackson; MSC, McWane Science Center, Birmingham, Alabama; NJSM, New Jersey State Museum,

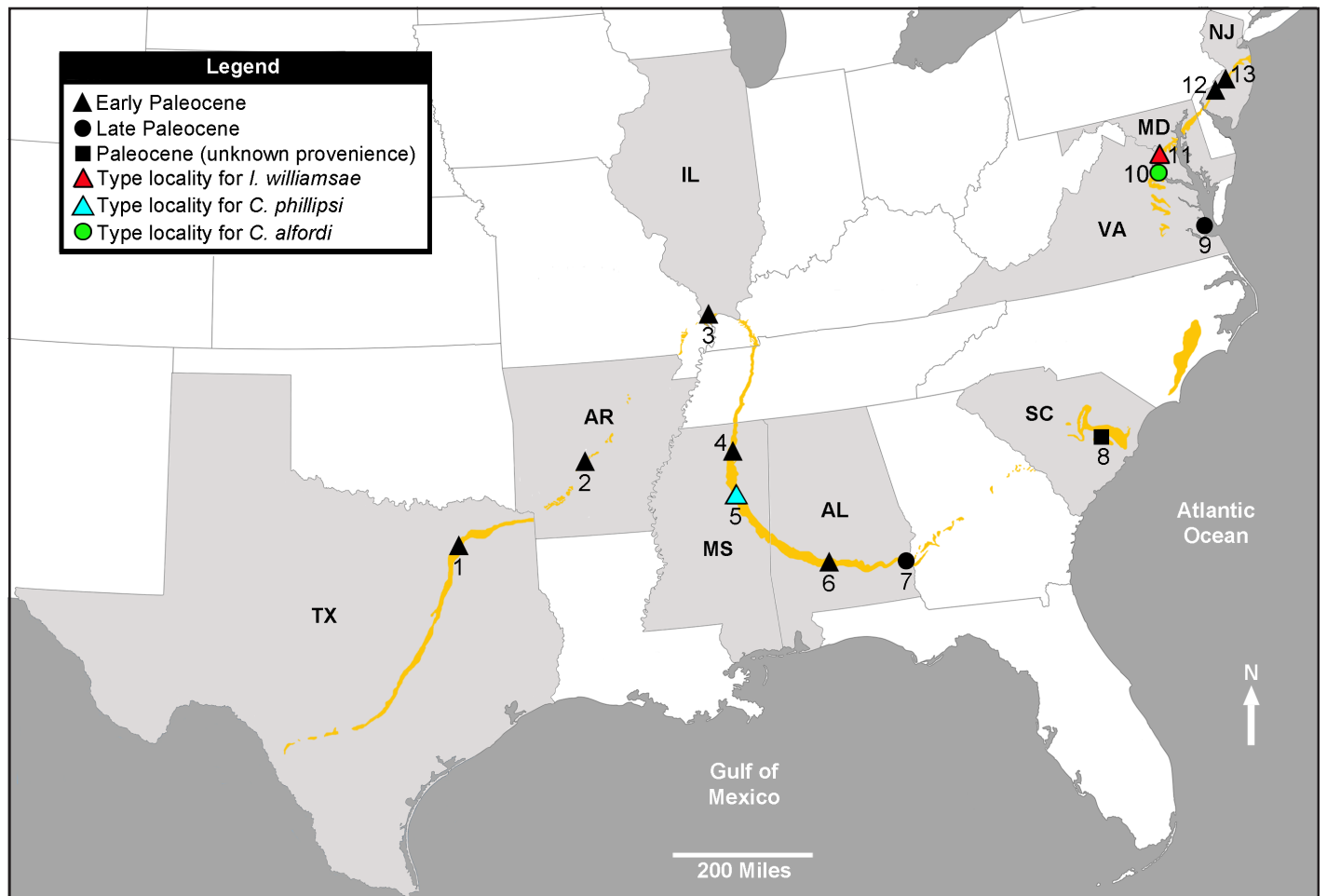


Figure 1. Geographic map of the United States showing contour of Paleocene marine strata (orange), with closed triangles, circles and squares representing localities that yielded chimaeroid fossils. Localities include: 1, Hunt County, Texas (TX); 2, Hot Spring County, Arkansas (AR); 3, Pulaski County, Illinois (IL); 4, Union County, Mississippi (MS); 5, Oktibbeha County, Mississippi; 6, Wilcox County, Alabama (AL); 7, Henry County, Alabama; 8, Berkeley County, South Carolina (SC); 9, King George County, Virginia (VA); 10, Charles County, Maryland (MD); 11, Prince Georges County, Maryland; 12, Gloucester County, New Jersey (NJ); 13, Monmouth County, New Jersey. Chimaeroid fossils collected from these localities include *Callorhinchus alfordi* n. sp. (10), *C. phillipsi* n. sp. (5); *Edaphodon mirificus* (4, 12, 13), *Edaphodon* sp. (9), *Elasmodus hunteri* (10), *Elasmodus* sp. (12), *Ischyodus dolloi* (1, 7, 10, 12), *I. williamsae* (2, 3, 5, 6, 11), and *Ischyodus* sp. (10).

Epoch	Stage	Zone	Texas	Arkansas/ Illinois	Mississippi (southern down dip)	Alabama	South Carolina (St. Stephen area)	Virginia/ Maryland	New Jersey
			Paleocene	Thanetian	NP9a NP8 NP7 NP6	Rockdale Fm. Seguin Fm.	Wilcox Group (in part)	Tuscahoma Sand Grampian Hills Mbr. "O. thirsae beds" Gravel Creek Sand Mbr.	Tuscahoma Sand Grampian Hills Mbr. "O. thirsae beds" Gravel Creek Sand Mbr.
	Danian	NP5 NP4 NP3 NP2 NP1	Willis Fm. Porters Creek Fm. Clayton Fm. Kincaid Fm.	Midway Group Clayton Fm.	Naheola Fm. Matthews Lnd. Marl Mbr. Porters Creek Fm. Clayton Fm.	Naheola Fm. Matthews Lnd. Marl Mbr. Porters Creek Fm. McBryde Lms. Mbr. Pine Barren Mbr. Clayton Fm.	Black Mingo Group Williamsburg Fm. Lower Bridge Mbr. Rhems Fm.	Pamunkey Group Brightseat Fm.	Vincentown Fm. Vincentown Fm. Hornerstown Fm.

Figure 2. Correlation chart of Paleocene strata for localities within the nine states from which the examined chimaeroid fossils were collected. Modified from: Alabama and Mississippi (Cushing et al. 1964, Mancini and Tew 1991); Illinois (Cope et al. 2005); Maryland and Virginia (Nogan 1964); New Jersey (Olsen and Parris 1987), South Carolina (Colquhoun and Muthig 1991); and Texas (Baker 1995).

Trenton; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas. The acronym ALMNH takes precedence over previously published acronyms, including UAM PV and ALAM PV.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
 CHIMAERIFORMES Obruchev, 1953
 CALLORHYNCHIDAE Garman, 1901
 CALLORHINCHUS Lacépède, 1798

Callorhinchus phillipsi n. sp.
 (Fig. 3)

Holotype—MMNS 6210, right palatine.

Stratigraphic occurrence and age—lower Clayton Formation, approximately 4.5 m above the contact with the underlying Upper Cretaceous strata (2.5–3 m above the *Pycnodonte pulaskensis* beds), lower Paleocene (Danian Stage).

Geographic occurrence—Locality MS.53.035, Oktibbeha County, Mississippi. More precise locality information is on file at the MMNS.

Etymology—Species named for George Phillips (MMNS), who discovered the specimen, in honor of his contributions to Mississippi paleontology.

Diagnosis—This species is represented by a single adult palatine that measures 14.40 mm in length and is approximately one half the size of equivalent palatines of other known fossil *Callorhinchus* species. The palatine is further characterized by a smaller tritor compared to other Paleocene and Eocene species, and the tritor differs from all other fossil species in having an outer prong that is 50% of the length of the inner prong. This fossil species differs from extant species in having the tritor positioned further back on the tooth plate, with the posterior margin of the tritor located at the beginning of the post-oral margin.

Description—The palatine is essentially complete and measures 14.40 mm in length (measured along the labial margin from the mesial tip to the distal angle) and 7.97 mm in width (between the symphyseal margin and the distal corner of the postero-distal wing). The symphyseal surface is a straight, flat vertical surface measuring 3.02 mm in height (Fig. 3c, d). In aboral view the plate has a rounded mesial end, and the labial and symphyseal margins are roughly parallel for the anterior one half of the plate, but the distal half of the plate expands due to a latero-ventrally directed "wing" (Fig. 3b). There is a short sulcus at the aboral surface between the mesial tip and the descending lamina that forms the anterior margin of the basal surface. The descending lamina clearly delineates the basal surface labially and

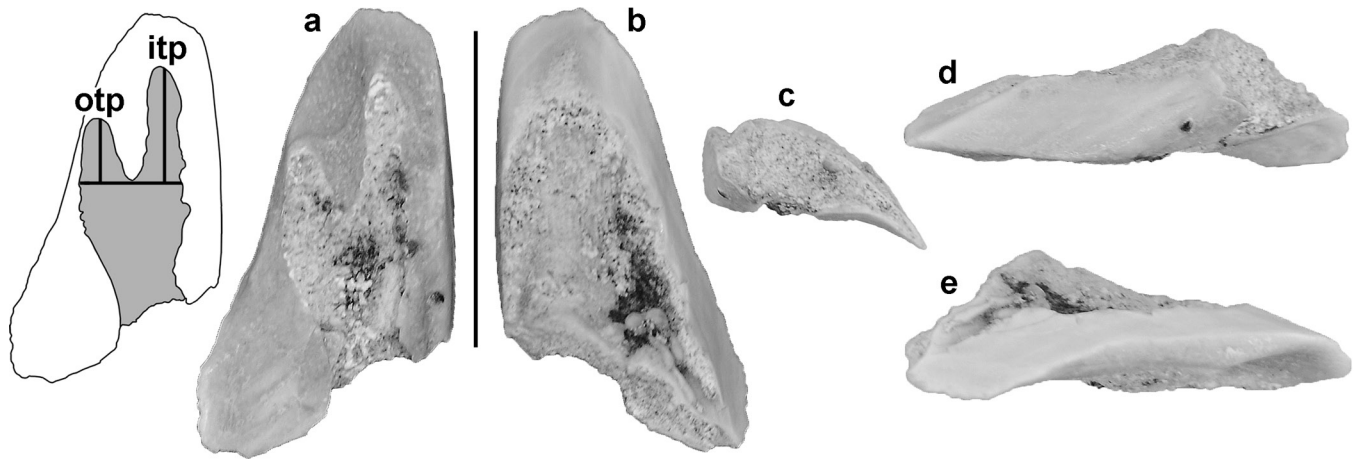


Figure 3. Images and line drawing of *Callorhinchus phillipsi* n. sp. right palatine, MMNS 6210, in oral (a), aboral (b), distal (c), symphyseal (d), and labial (e) views. **Abbreviations:** itp, inner tritor prong; otp, outer tritor prong. Scale bar = 1.0 cm.

symphyseally, but becomes less noticeable towards the distal margin of the plate. In oral view, the occlusal surface was largely occupied by a bifurcated tritor (Fig. 3a) measuring 9.51 mm in maximum length, but the exposed portion in life was 7.54 mm in length (the remainder of the post-oral portion would have been covered by dentine). Although the tritor tissue is not preserved, the surrounding dentine forms a clear and elevated rim that delineates its exact outline. The tritor bifurcates into prongs of unequal length, with the inner prong measuring 4.64 mm and the outer prong 2.41 mm in length, respectively. The surface between the two prongs is concave, and the post-occlusal portion of the oral surface diverges dorsally. In distal view it can be seen that the tritor tissue resided within a rather shallow depression within the dentine of the tooth plate (Fig. 3c).

Remarks—MMNS 6210 is identified as *Callorhinchus* because it possesses a single bifurcated tritor, a feature considered to be a synapomorphy of the genus (Didier et al. 1994, Kriwet and Gadżicki 2003). Morphological features of MMNS 6210 easily distinguish it from other fossil species within the genus. Late Cretaceous (Santonian) *C. hectori* Newton, 1876 from New Zealand differs from *C. phillipsi* in that the outer prong is 63.5% of the length of the inner prong, and the inner prong also extends nearly to the mesial tip of the tooth plate (Newton 1876). A palatine of *Callorhinchus* sp. from the late Campanian of Antarctica (Otero et al. 2014) has a bifid tritor on which the outer and inner prongs are of nearly equal length. A Late Cretaceous (Maastrichtian) *Callorhinchus* sp. palatine from Antarctica discussed by Martin and Crame (2006) exhibits an outer prong that is only 20% as long as the inner prong. *Callorhinchus torresi* Otero et al., 2013b has an unusual bifid tritor on which both prongs are very narrow and elongated, and they are widely separated by

a deep u-shaped embayment (Otero et al. 2013b). In sharp contrast, the outer prong of *C. phillipsi* is 50% of the length of the inner prong. The palatine of the Paleocene *C. newtoni* Ward, 1973 from England also has a more pointed mesial end than MMNS 6210, and it appears to lack the laterally expanded distal end, although this portion may not be preserved on the type specimen (Ward 1973). The palatine of the early Eocene *C. stahli* Kriwet and Gadżicki, 2003 has a bifid tritor bearing relatively short prongs of nearly equal length. The tritors of both *C. newtoni* and the Eocene *C. regulbiensis* Gurr, 1962 (also from England) differ from MMNS 6210 in having an outer prong that is much shorter than the inner prong, with the outer prong of *C. newtoni* being only 11% the length of the outer prong (Ward 1973), and on *C. regulbiensis* the inner prong is 23.5 to 30% of the length of the inner prong (Gurr 1962, Kriwet and Gadżicki 2003). Although the palatine tooth plates of *C. crassus* Woodward and White, 1930 from the Miocene of Argentina are unknown (Woodward and White 1930), a Miocene *Callorhinchus* sp. palatine from Chile appears more elongated than MMNS 6210, and its mesial end is more pointed, the labial margin is uniformly convex rather than sinuous, and there is a longer post-oral surface (Suárez et al. 2004). A Pliocene palatine from Chile assigned to *Callorhinchus* sp. (Carrillo-Briceño et al. 2013) is unusual in that it has two distinct, elongated tritors that are oblique to the labial margin. This specimen, measuring approximately 30.0 mm along its preserved labial margin, may represent a juvenile individual.

MMNS 6210 is notable for its small size, only 14.4 mm along the labial edge, being nearly half or less the size of the palatines of the fossil species noted above. The size is significant because MMNS 6210 is only two millimeters smaller than a juvenile specimen of *C. milii* Bory de Saint-Vincent,

1823 discussed by Didier et al. (1994: fig. 9), which had two distinct, parallel tritor pads instead of the characteristic bifurcated tritor. They also illustrate an adult palatine of *C. milii* that, at 30.0 mm in length, has a fully formed tritor like the one seen on MMNS 6210, indicating that the latter Paleocene specimen belonged to an adult individual. The palatine tooth plates of a recent adult *C. milii* that we examined, ANSP 177826, measure 29.0 mm along the labial margin and bear a single bifurcated tritor. These tooth plates belong to an adult fish that was 64.0 cm in total length, including the tail (32.2 cm excluding the tail). The palatine therefore represents approximately 4.5% of the total length (9% if measuring to the vent, excluding the tail). If the same method is applied to MMNS 6210, this specimen was a relatively small ratfish at approximately 12.6 cm to the vent. As the tail of extant chimaeroids essentially doubles the length of the fish, we surmise that the holotype of *C. phillipsi* represents a fish measuring around 25.3 cm in total length.

Callorhinchus alfordi n. sp.
(Fig. 4.1–4.11)

Hypodigm—CMM-V-5791, incomplete left mandibular (Holotype; Fig. 4.1); CMM-V-5787, incomplete right palatine (Paratype; Fig. 4.7); CMM-V-5792, incomplete right mandibular (Paratype; Fig. 4.2).

Referred specimens—CMM-V-5303, mesial end of left mandibular; CMM-V-5354, incomplete left palatine; CMM-V-5355, right palatine; CMM-V-5788, incomplete left palatine; CMM-V-5789, mesial end of right palatine; CMM-V-5790, mesial end of right palatine; CMM-V-5793, left mandibular fragment; CMM-V-5794, two tooth plate fragments.

Stratigraphic occurrence and age—Piscataway Member, Aquia Formation, upper Paleocene, Thanetian Stage.

Geographic occurrence—Charles County, Maryland and Prince Georges County, Virginia.

Etymology—Species named for Aaron Alford in recognition for his donation of a large proportion of the Aquia Formation *Callorhinchus* to the CMM.

Diagnosis—The palatine plate bears the following distinguishing features: a broad and elongated oral surface anterior to the inner prong of the tritor; the tritor occupies most of the oral surface, and although an inner prong is developed, there is little to no differentiation of an outer prong; the lateral edge of the tritor forms part of the labial margin of the tooth plate. The mesial end of the mandibular plate has a sub-rectangular to triangular shape, but it is not formed into a narrow beak as on some early Paleogene species. The middle tritor is a large ovate pad having a broadly rounded mesial margin that is not extended into a narrow prong. When articulated, the right and left mandibulars are in the horizontal plane, but the distal part of the labial margin curves dorsally.

Description—Due to the paucity of *Callorhinchus* material from North America, we describe in detail and illustrate the available Aquia Formation specimens in order to document tooth plate variations. Because all known specimens are isolated, we established a hypodigm that incorporates specimens that best show the described morphology, exhibit good preservation, and represent different elements within the dentition. The holotype, CMM-V-5791 (Fig. 4.1a–d) is a left mandibular missing an unknown portion of its distal end, but as preserved it measures 13.62 mm in length. The specimen has a triangular outline in oral/aboral view (Fig. 4.1a, b), with the mesial tip being pointed and the plate expanding distally to a width of 10.14 mm. The symphyseal surface is straight, flat, and has a maximum thickness of 4.16 mm (Fig. 4.1c). The labial margin is sharp and sinuous, with its most convex part lateral to the middle tritor, where the edge then continues distally to roughly parallel the outer margin of the middle tritor (Fig. 4.1a). In mesial view this section of the plate also curves dorsally (seen near the right side of Fig. 4.1d). The middle tritor is not preserved, but the remaining attachment surface shows that it was about half as wide as the entire tooth plate (5.36 mm) and its anterior end was broadly rounded. Tiny openings located between the middle tritor and the symphysis appear to represent the location for inner tritor tissue (line drawing of 4.1a), but this tritor does not appear to have been as well developed as the

Figure 4. Images and line drawings of *Callorhinchus alfordi* n. sp. tooth plates. **1.** CMM-V-5791 (holotype), incomplete left mandibular in oral (a), aboral (b), symphyseal (c), and labial (d) views. **2.** CMM-V-5792 (paratype), incomplete right mandibular in oral (a), aboral (b), and symphyseal (c) views. **3.** CMM-V-5303, partial left mandibular in oral view. **4.** CMM-V-5793, partial left mandibular in oral view. **5.** Oral view of hypothetical reconstruction of the lower dentition based on CMM-V-5792. A mirror image of the specimen was created as a substitute for the left mandibular. **6.** CMM-5354, incomplete left palatine in oral (a), symphyseal (b), labial (c), aboral (d), and distal (e) views. **7.** CMM-V-5787 (paratype), incomplete right palatine in oral (a), symphyseal (b), labial (c), and aboral (d) views. **8.** CMM-V-5355, incomplete right palatine in oral (a), aboral (b), and symphyseal (c) views. **9.** CMM-V-5789, partial right palatine in oral view. **10.** CMM-V-5790, partial right palatine in oral view. **11.** CMM-V-5788, partial left palatine in oral view. Gray areas of line drawings represent attachment surfaces for tritor tissues (e.g., 4.1a) or exposed tritor tissue (e.g., 4.4). **Abbreviations:** **it**, inner tritor; **mt**, middle tritor. Scale bars = 0.5 cm. ►

one seen on CMM-V-5792 (Fig. 4.2). There are no indications for an outer tritor, but if present it was likely on the part of the labial margin not preserved on CMM-V-5791.

A paratype, CMM-V-5792 (Fig. 4.2a–c), is an incomplete right mandibular tooth plate that is missing an unknown portion of its distal end, and its preserved length measures 20.34 mm. This specimen also has a roughly triangular outline in oral/aboral view (Fig. 4.2a, b), with the plate expanding distally to a maximum width of 13.62 mm. Although the beak is chipped, the mesial tip of the plate is similar to the beak of CMM-V-5791. The symphyseal surface of CMM-5792 is slightly curved but flat, and has a maximum thickness of 6.14 mm (Fig. 4.2c). The labial margin is chipped but thin and uniformly convex from the beak to the preserved distal end. In mesial view the labial margin is horizontal and perpendicular to the symphysis, but some dorsal curvature (similar to CMM-V-5791) is preserved at the distal end. The middle tritor is partially preserved and appears to have occupied the majority of the oral surface of the distal 2/3 of the plate (Fig. 4.2a). It measures 9.22 mm in width and its mesial end tapers to a rounded margin, with the main axis of the tritor being located closer to the labial margin of the tooth plate. The inner tritor is clearly visible and the tissue extends from the mesial end of the middle tritor to the broken distal end of the tooth plate (Fig. 4.2a). At least the anterior 4.76 mm of the tissue was exposed as a thin pad in life, but due to ablation of the overlying dentine, it cannot be determined if the pad was any larger or if more than one pad was exposed. The middle and inner tritors are separated by a thin wall (1.50 mm) of dentine. An outer tritor is not preserved. The descending lamina is not obvious but best seen at the symphyseal margin (Fig. 4.2b).

An additional paratype, CMM-V-5787 (right palatine; Fig. 4.7a–d), is complete but missing an unknown portion of the distal end, and as preserved it measures 18.26 mm in length. Overall this specimen is very similar to CMM-V-5354 (Fig. 4.6), but differs in having a broader, more expansive oral surface anterior to the tritor. In addition, the tritor of CMM-V-5787 has a wider, shorter outer prong, and an inner prong that is difficult to distinguish from the main body of the tritor (Fig. 4.7a). The symphyseal surface of CMM-V-5787 measures 5.04 mm in height (Fig. 4.7b), and the broken distal end of the specimen also shows that the tooth plate in this region mostly consists of tritor tissue. In aboral view the basal surface is clearly delineated on the labial and symphyseal sides by the descending lamina (Fig. 4.7d).

CMM-V-5354 (left palatine; Fig. 4.6a–e) lacks the mesial tip and an unknown amount of the distal end of the plate, but as preserved it measures 14.28 mm in length. In aboral view the plate has a roughly rectangular outline (Fig. 4.6d),

and the descending lamina is not conspicuous. The distal end of the plate has a slightly greater width (10.88 mm) than the widest part of the mesial end (8.88 mm). However, the mesial end appears to have been formed into a narrow projection, based on the sharp labial margin that follows the general contour of the tritor. The symphyseal margin is straight, flat, and measures 4.34 mm in height (Fig. 4.6b). In oral view, a single tritor occupies nearly the entire oral surface (Fig. 4.6a). The symphyseal margin of the tritor is virtually at the symphyseal margin of the tooth plate along its entire preserved length, and the labial margin of the tooth plate is actually partially formed by the tritor (Fig. 4.6a, c). The mesial end of the tritor is not bifurcated, but instead bears a single short (3.0 mm), triangular inner projection. Most of the broken distal end of the tooth plate is composed of the tritor tissue (Fig. 4.6e).

CMM-V-5355 (right palatine; Fig. 4.8a–c) is abraded and also lacks an unknown portion of the distal end of the plate, but the remaining portion measures 17.64 mm from the mesial-most tip to the distal-most tip. In aboral view the basal surface is framed by the descending lamina on the labial and symphyseal sides of the plate (Fig. 4.8b). The symphyseal and labial margins of the plate are nearly parallel, and the anterior end is broadly rounded and ends in a weak mesial point. The symphyseal surface is straight, flat, and measures up to 4.28 mm in height (Fig. 4.8c). In oral view the anterior 1/3 of the plate is thin, rather smooth and flat, but distal to this the remaining oral surface was occupied by the tritor (Fig. 4.8a). Although the tritor tissue is not preserved, the attachment surface shows that the mesial end was bifurcated into two broadly triangular prongs of nearly equal dimensions. As on CMM-V-5354 (Fig. 4.6) and CMM-V-5787 (4.7c), the inner tritor prong diverges from the symphyseal margin, and the labial margin of the tritor formed part of the labial margin of the tooth plate.

CMM-V-5788 (left palatine; Fig. 4.11) is incomplete, but as preserved measures 15.44 mm from the mesial-most tip to the broken distal end. Unfortunately, the labial side of the oral surface anterior to the tritor is damaged, but this region appears to have been as expansive as the equivalent region of CMM-V-5355 (Fig. 4.8). As is the case with CMM-V-5355, CMM-V-5788 lacks tritor tissue, but the preserved attachment surface shows that the tritor was also weakly bifid and had short inner and outer prongs of nearly equal length. The symphyseal surface reaches a maximum of 4.0 mm at the distal end of the tooth plate. The descending lamina is inconspicuous at the symphyseal side of the plate.

CMM-V-5789 and CMM-V-5790 are the mesial ends of two right palatines. CMM-V-5789 (Fig. 4.9) measures 9.02 mm in length (along the symphysis) and is unusual in that

the preserved portion has a triangular outline in aboral/oral view because the sharp-edged labial margin follows the contour of the leading edge of the tritor (a similar morphology is seen on CMM-V-5354). There is very little oral surface anterior to the tritor, and the preserved inner prong of the tritor is broadly triangular, with its sharply pointed mesial tip angled away from the tooth plate symphysis. In contrast, the preserved portion (preserved length along the labial margin measures 9.10 mm) of CMM-V-5790 (Fig. 4.10) has a square outline, with the mesial angle canted away slightly from the symphyseal margin (similar to the condition seen on CMM-V-5787; see Fig. 4.8). The tritor tissue is not preserved on this specimen, but the remaining attachment surface shows that the mesial edge of the tritor was very weakly bifid (apparently rounded prongs of nearly equal length), and that the tritor occupied nearly the entire width of the tooth plate. As is the case with the other palatines, the mesial tip of the inner tritor prong is directed away from the symphysis. The descending lamina on both CMM-V-5789 and CMM-V-5790 is difficult to discern.

CMM-V-5303 (Fig. 4.3) represents only the anterior end of the left mandibular, and the specimen measures 11.78 mm in length. The preserved symphyseal surface is straight, flat, and measures up to 3.64 mm in thickness. The labial margin is sharp along its length; it begins nearly perpendicular to the symphyseal margin, but turns sharply distally at the level of the middle tritor. The middle tritor was a large pad with an abruptly tapered and rounded mesial margin. The attachment surface for the smaller inner tritor is between the middle tritor and the symphysis, and its mesial end is nearly equal with the mesial end of the middle tritor. CMM-V-5303 is identified as a portion of a mandibular tooth plate because the mesial-most tip of the plate is at the symphysis, whereas the mesial tip of palatines is angled away from the symphysis and located at the labial margin. Additionally, the inner tritor does not diverge away from the symphyseal margin as does the inner prong of the palatine tritor (compare to Fig. 4.6a, 4.8a).

CMM-V-5793 is a fragment of left mandibular (10.90 mm total length) with parts of the symphyseal and labial margins preserved, and the attachment surface for the middle tritor is visible (Fig. 4.4). A thin cylinder of tritor tissue (0.72 mm in diameter), measuring 9.16 mm in preserved length, is located between the middle tritor and the symphyseal margin. This tritor tissue is exposed at several places where the symphyseal margin is damaged, but may only have been exposed as a tiny circular pad near the middle of the preserved attachment surface for the middle tritor. In aboral view the descending lamina is seen at the symphyseal surface.

Remarks—The Aquia Formation palatines differ

significantly from the holotype of *Callorhynchus phillipsi* n. sp. (Fig. 3.1) in that the tritors occupied a larger portion of the oral surface. In addition, the tritor of *C. phillipsi* is noticeably more bifurcated, with the inner prong being approximately 50% longer than the outer prong. Furthermore, the symphyseal and labial tritor margins of the Aquia specimens are very close to the symphyseal and labial margins of the plate, respectively, whereas the tritor margins of *C. phillipsi* are well separated from the margins of the tooth plate. Finally, the Aquia Formation palatines, CMM-V-5787 (Fig. 4.7) and CMM-V-5355 (Fig. 4.8) lack the sinuous mesial edge as seen on the *C. phillipsi* palatine.

The amount of intraspecific variation in the other early Paleogene species of *Callorhynchus*, *C. newtoni*, *C. regulbiensis*, and *C. stahli*, is poorly known, and the palatine tooth plates of each of the species are roughly similar to each other. The holotype (right palatine) of *C. regulbiensis* appears to be quadrilateral and bears a disto-lateral wing, and the tritor of the broken paratype (right palatine) is comparable to that on the holotype (Gurr 1962). Kriwet and Gadżicki (2003) reported some variation on the palatines of *C. regulbiensis*, with the outer and inner tritor prongs of one specimen being of equal length, a condition seen on some of the Aquia palatines (CMM-V-5355 and CMM-V-5788). However, none of the Aquia Formation palatines are as broad as *C. regulbiensis*, and there is no evidence of a distal wing. The holotype of *C. newtoni* has a roughly triangular outline and the internal tritor prong is elongated and extends nearly to the mesial tip of the tooth plate (Ward 1973). In contrast, the Aquia palatines have a more rectangular outline; the inner tritor prong is short and well separated from the mesial tip of the tooth plate, and the labial side of the tritor forms the labial edge of the plate. The palatines of *C. stahli* are known only from incomplete specimens, but they all have a bifid tritor similar in morphology to those of *C. regulbiensis* and *C. newtoni* (Kriwet and Gadżicki 2003). All three of the aforementioned Paleogene species have a bifid palatine tritor that occupies much of the oral surface, but of the four best preserved Aquia Formation palatines, two, CMM-V-5354 (Fig. 4.6) and CMM-V-5787 (Fig. 4.7), exhibit little to no differentiation of an outer prong. However, the short palatine tritor prongs of CMM-V-5355 and CMM-V-5788 are of roughly equal length and separated by a “v-shaped” interprong embayment, the latter morphology being a feature of *C. stahli* (Kriwet and Gadżicki 2003). The Aquia Formation palatines are different enough to warrant their description as a new species and there is no reason to believe at this time that the morphological variation within the Aquia sample represents anything other than normal variation within a single species. The variation does not appear to be attributable to

ontogeny, as most of the specimens are of approximately the same size. Furthermore, assuming the tooth plates of this Paleocene species grew in a manner similar to extant *Callorhinchus*, specimens like CMM-V-5354 and CMM-V-5787 belonged to adult fish based on tritor prongs that are clearly projections of a large exposed pad rather than one (or two) small, individual and clearly separated pads (Didier et al. 1994; also discussion above regarding *C. phillipsi*).

Unfortunately, the mandibular tooth plates of *C. newtoni* are unknown, but those of *C. regulbiensis* and *C. stahli* have been described. The mandibular of *C. regulbiensis*, originally identified as *Chimaera eophantasma* Ward, 1973, has its mesial end extended into a thin and pointed beak, two inner tritor pads are located near the symphyseal margin, and the middle tritor has a relatively narrow mesial end that impinges on the labial margin (Ward 1973, Stahl 1999, Kriwet and Gadzicki 2003). Ward (1973) noted some variation in tritor development, with the two inner tritors sometimes being exposed as one continuous pad, and/or the middle tritor fusing with the inner tritor(s). If more than one inner tritor was exposed on the Aquia Formation mandibulars, they were part of the same elongate, cylindrical mass of tritor tissue, as there is no evidence of multiple isolated masses of tritor tissue. There is also no indication within the Aquia Formation sample that the middle tritor fuses with the inner tritor, the tritors are well separated in all cases. Additionally, the beaks of CMM-V-5791 and CMM-V-5792 are broadly triangular and not developed into a thin and narrow structure as on *C. regulbiensis*, and CMM-V-5303 lacks a mesial projection entirely. The mesial end of the *C. stahli* mandibular is formed into a beak similar to *C. regulbiensis*, and the anterior end of the middle tritor of both of these species quickly tapers to a pointed projection (Ward 1973; Stahl 1999; Kriwet and Gadzicki 2003) that is distinct from the main body of the pad. In contrast, the middle tritor of the Aquia Formation mandibulars is broadly rounded and does not bear a distinctive anterior projection. Because the Aquia Formation mandibulars appear to differ from the aforementioned Paleogene taxa beyond what can be explained by intraspecific or ontogenetic variation, we believe assigning them to a new

Callorhinchus species is warranted. We presume that the mandibulars and palatines described are conspecific because the tooth plates were derived from the same stratigraphic interval (Piscataway Member).

ISCHYODUS Egerton, 1843

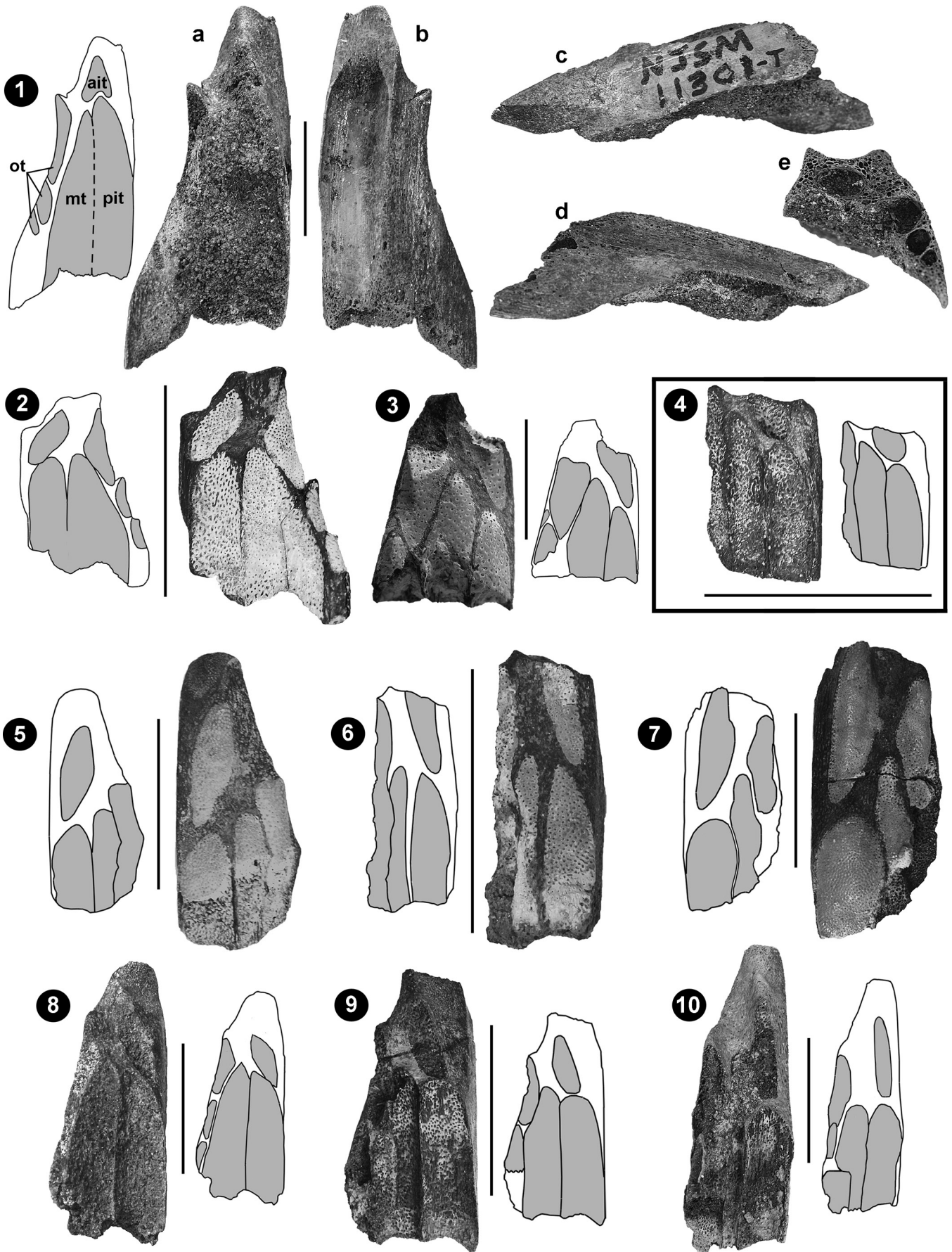
Ischyodus dolloi Leriche, 1902

(Figs. 5–7, 11.1)

Material—AMNH 14594, right mandibular tooth plate; CMM-V-1609, left palatine; CMM-V-2666, incomplete left palatine; CMM-V-2669, incomplete right mandibular; CMM-V-2812, partial right mandibular; CMM-V-4587, right palatine; CMM-V-4800, right mandibular; CMM-5255, left mandibular; CMM-V-5357, right mandibular; CMM-V-5358, right mandibular; CMM-V-5359, right mandibular; CMM-V-5360, left mandibular; CMM-V-5361, left mandibular; CMM-V-5765, right mandibular; CMM-V-5766, right mandibular; CMM-V-5767, right mandibular; CMM-V-5768, partial left mandibular; CMM-V-5769, partial right mandibular; CMM-V-5770, partial right mandibular; CMM-V-5771, partial right mandibular; CMM-V-5772, partial right mandibular; CMM-V-5773, partial left mandibular; CMM-V-5774, partial left mandibular; CMM-V-5775, partial left mandibular; CMM-V-5776, incomplete right palatine; CMM-V-5777, incomplete right palatine; CMM-V-5778, incomplete right palatine; CMM-V-5779, incomplete left palatine; CMM-V-5780, incomplete left palatine; CMM-V-5781, partial left palatine; CMM-V-5782, partial left palatine; MSC 34903, partial right mandibular tooth plate; NJSM 11301-AB, right palatine; NJSM 11301-AF, left mandibular; NJSM 11301-AG, right mandibular; NJSM 11301-AH, right mandibular; NJSM 11301-K, incomplete right palatine tooth plate; NJSM 11301-M, left mandibular; NJSM 11301-N, right palatine; NJSM 11301-T, right palatine; SMU 76939, incomplete right mandibular; SMU 76940, left palatine tooth plate.

Stratigraphic and geographic occurrences—MSC 34903 was recovered from the base of the “*Ostrea thirsae* beds” within the Nanafalia Formation, middle Thanetian Stage (calcareous nannofossil zone NP 7) at locality AHe-1 in Henry County, Alabama. AMNH 14594 was collected from the basal

Figure 5. Images and line drawings of *Ischyodus* palatine tooth plates. **1.** *I. dolloi*, NJSM 11301-T, right palatine in oral (a), aboral (b), symphyseal (c), labial (d), and distal (e) views. **2.** *I. dolloi*, SMU 76940, left palatine in oral view. **3.** *I. dolloi*, CMM-V-5776, incomplete right palatine in oral view. **4.** *Ischyodus* sp., ChM PV4152, incomplete right palatine in oral view. **5.** *I. dolloi*, CMM-V-1609, incomplete left palatine in oral view. **6.** *I. dolloi*, CMM-V-4587, incomplete right palatine in oral view. **7.** *I. dolloi*, CMM-V-2666, incomplete left palatine in oral view. **8.** *I. dolloi*, NJSM 11301-N, incomplete right palatine in oral view. **9.** *I. dolloi*, NJSM 11301-AB, incomplete right palatine in oral view. **10.** *I. dolloi*, NJSM 11301-K, incomplete right palatine in oral view. Gray areas of line drawings represent attachment surfaces for tritor tissues (e.g., 5.1a) or exposed tritor tissue (e.g., 5.3). **Abbreviations:** ait, anterior inner tritor; mt, middle tritor; ot, outer tritor; pit, posterior inner tritor. Scale bars = 2.0 cm. ►



Hornerstown Formation within 1.0 m above the contact with the Upper Cretaceous Red Bank Formation, Danian Stage near Hornerstown, Monmouth County, New Jersey (Case 1996). The NJSM specimens were recovered from the “main fossiliferous layer” of the Hornerstown Formation (Danian Stage) at the Inversand Marl Company pit in Sewell, Gloucester County, New Jersey (see Olsen and Parris 1987). The SMU specimens were found as float along the South Sulphur River in Hunt County, Texas, and were likely eroded from Danian strata of the Kincaid Formation. The CMM fossils are from two closely spaced localities in Charles County, Maryland, and all were derived from the Thanetian Piscataway Member of the Aquia Formation.

Description—We assigned 14 palatine tooth plates to *Ischyodus dolloi*, and NJSM 11301-T, a right palatine, is the most complete (Fig. 5.1a–e). This specimen lacks the tritor tissues and the remaining attachment surfaces are partly obscured by adhering glauconite matrix, but four main tritors are evident. Overall, NJSM 11301-T has a triangular outline in oral/aboral view, with the mesial end being narrowest and pointed. The posterior half of the plate expands into a disto-ventrally directed process (“wing” of Ward 1973, Fig. 5.1b, d). The symphyseal surface is vertical and measures 9.9 mm in height, and is concave along its entire length (Fig. 5.1c). In aboral view, a deep longitudinal sulcus begins 7.42 mm from the mesial tip and continues to the distal end of the plate, and is flanked by sharp medial and lateral ridges (Fig. 5.1b). In oral view, the exact outlines for the anterior and posterior outer, middle, and outer tritors are difficult to determine as they are obscured by the presence of glauconite (Fig. 5.1a). However, the anterior inner tritor was small and roughly triangular in shape. The posterior inner and middle tritors were separated by a thin wall of dentine. The outer tritor forms the straight part of the labial margin that is parallel to the aboral medial ridge, and its mesial end is located on a prominence that is separated from the anterior inner tritor by a deep sulcus. Posteriorly, the outer tritor is subdivided into two additional small tritors that are located at the leading edge of the “wing.” These are best seen at the distal end of the tooth plate, where the tubes once bearing the tritor tissues are visible (Fig. 5.1e).

Of the 26 mandibular tooth plates available, NJSM 11301-AG is the best preserved and exhibits all of the diagnostic features of the species (Fig. 6.1a–c). The external surface of the plate is weakly convex dorso-ventrally, but more strongly concave meso-distally. The mesial end of the plate is drawn out into a short and pointed beak, and the laminated symphyseal tritor has been exposed along the ventral margin of the external surface (Fig. 6.1a). From the beak, the labial margin curves dorsally to a prominence bearing the anterior

outer tritor. At the distal end of the anterior outer tritor, the labial margin again curves dorsally to a higher prominence bearing the posterior outer tritor, and from here the margin curves sharply towards the distal tip of the tooth plate. The middle tritor occupied much of the oral surface distal to the beak, and it tapered anteriorly to a blunt mesial margin (Fig. 6.1b, c). There is a miniscule depression at the distal end of the plate, located between the posterior outer and middle tritors, which we interpret to be the attachment surface for a median accessory tritor. There is a very small, ovate anterior inner tritor on the symphyseal crest that is entirely mesial to the leading margin of the middle tritor. There is an apparent posterior inner tritor at the distal end of the symphyseal crest, but this appears to be a posterior presentation of the anterior inner tritor, rather than a distinct, separate structure (Fig. 6.1c).

Remarks—Variation was observed in the 14 palatine tooth plates that we examined, primarily with respect to the shape of the mesial end of the plate and the exact size, shape, and orientation of the tritors. These variations do not appear to be dependent on the size of the tooth plate (ontogeny), as many of the specimens are comparable in size. The mesial end of the plates may appear to be elongated and rectangular (Fig. 5.10), short and quadrilateral (Fig. 5.2, 5.9), pointed (Fig. 5.1), or broadly rounded (Fig. 5.5, 5.8). The anterior outer tritors among the plates vary from a rather short, triangular structure (Fig. 5.1a), elongated teardrop shape (Fig. 5.9, 5.10), to an elongated ovate pad (Fig. 5.2, 5.5–5.7). The mesial end of this tritor is angled towards the labial margin to varying degrees. The mesial end of the posterior inner tritor may be uniformly rounded (Fig. 5.2, 5.7, 5.10) or more pointed towards the labial margin (Fig. 5.5, 5.8). This tritor is usually wholly distal to the posterior end of the anterior inner tritor, but specimens like Fig. 5.8 show that the posterior part of the anterior inner tritor extends distally past the anterior end of the posterior outer tritor. The middle tritor is usually half as wide as the posterior outer tritor, but it may be equally wide, although this is difficult to tell with certainty on the specimens due to lack of preservation of the tritor tissue or the incompleteness of the tooth plate. Regardless, the anterior end of the middle tritor extends mesially past the anterior margin of the middle tritor to varying degrees (compare Fig. 5.7 to 5.8), but there is one exception (Fig. 5.10) where it is slightly posterior. The outer tritor is along the labial margin of the plate, is never wider than the middle tritor, and its anterior end is well forward of the mesial margin of the middle tritor, extending halfway or fully up to the anterior margin of the anterior inner tritor. The labial margin of the Texas and New Jersey palatines are well enough preserved to see that the outer tritor is divided distally into one or two smaller

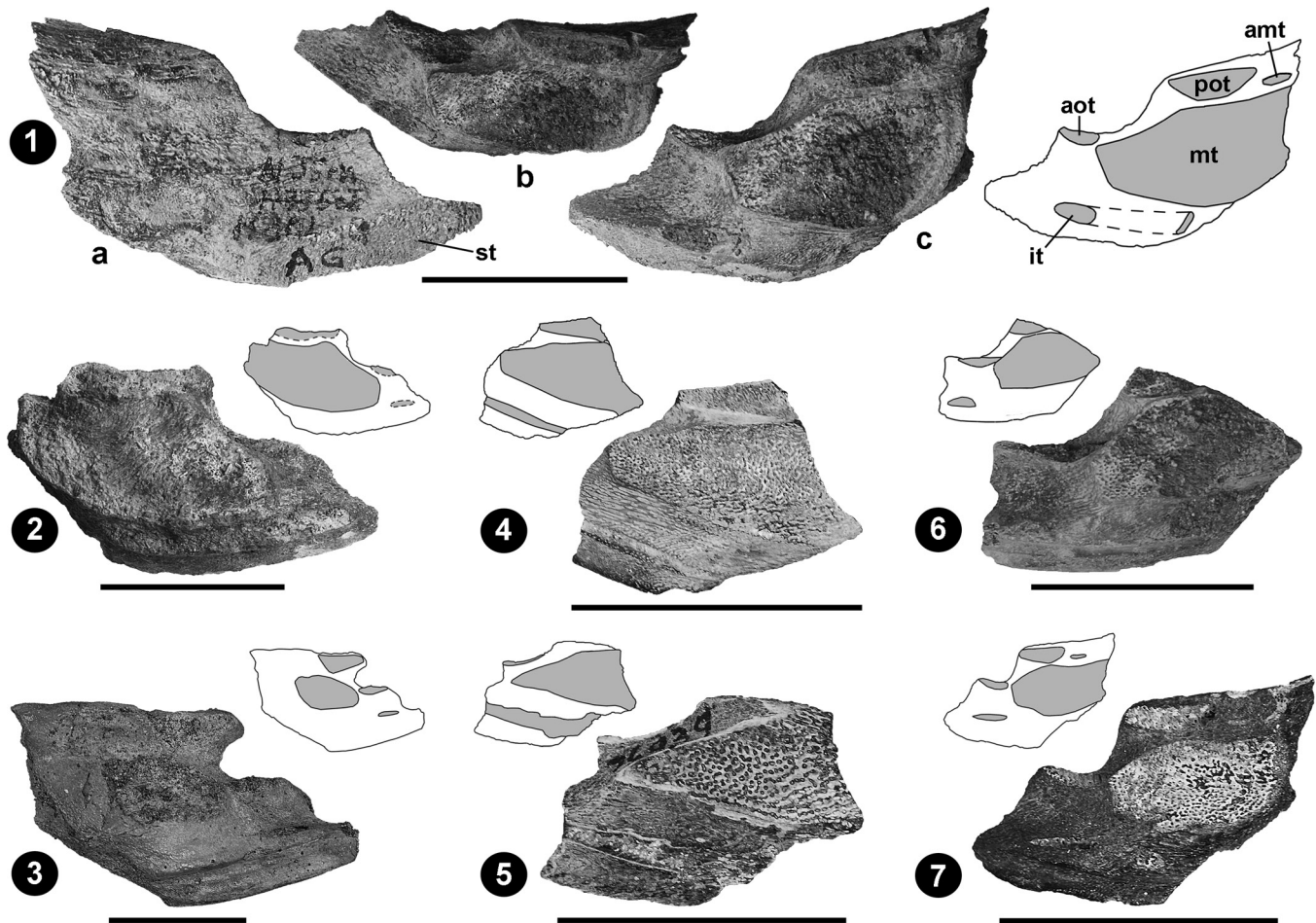


Figure 6. Images and line drawings of *Ischyodus dolloi* mandibular tooth plates. 1. NJSM 11301-AG, left mandibular in aboral (a), oral-oblique (b), and oral (c) views. 2. NJSM 11301-AE, left mandibular in oral view. 3. NJSM 11301-M, left mandibular in oral view. 4. MSC 34903, right mandibular in oral view. 5. SMU 76939, right mandibular in oral view. 6. NJSM 11301-AH, right mandibular in oral view. 7. AMNH 14594, right mandibular in oral view. Gray areas of line drawings represent attachment surfaces for tritor tissues (e.g., 6.2) or exposed tritor tissue (e.g., 6.1c). **Abbreviations:** amt, accessory median tritor; aot, anterior outer tritor; it, inner tritor; mt, middle tritor; pot, posterior outer tritor; st, symphyseal tritor. Scale bars = 2.0 cm.

pads that are on the leading edge of the wing. Figure 5.1a and 5.2 shows that these tritors are distinct from the main body of the outer tritor, and they are easily seen at the distal end of the tooth plates (Fig. 5.1e). Although the tritor tissues of several of the Maryland specimens are well preserved (Fig. 5.3, 5.5–5.7), only one is complete enough to show that the outer tritor is divided distally into at least two smaller pads (Fig. 5.3). We cannot ascertain the morphology of the outer tritor on the remainder of the Maryland palatines because the tritor tissues are not preserved and the labial margins are damaged.

NJSM 11301-AG, described above, serves as a model for the gross morphology of the remaining 25 mandibular tooth plates, which are remarkably consistent within the growth series represented, from the smallest specimen (Fig. 6.7) to the largest (Fig. 7.5). NJSM 11301-M (Fig. 6.3) differs slightly

in that the prominence for the posterior outer tritor is formed into an anteriorly-directed projection on the labial margin. The anterior outer tritor is generally teardrop-shaped and varies in length, and usually ends slightly distal to the mesial end of the middle tritor (sometimes it is completely anterior to the middle tritor, as seen in Fig. 6.3 and 6.7). In most cases the posterior outer tritor begins distal to the front of the middle tritor, but it is at the same plane as the middle tritor on some specimens (i.e., Figs. 6.7, 7.10), and well mesial on another (Fig. 6.3). The middle tritor generally has a tapered mesial end, with this margin being either gently rounded (i.e., Figs. 6.3, 7.9, 7.11, 7.12) or pointed (i.e. Figs. 6.5, 7.1–7.4, 7.6–7.7). On other specimens the mesial margin is blunt (i.e., Figs. 6.1–6.2, 6.6, 7.5). Of all of the specimens on which is it clearly preserved (Figs. 6.1c, 6.3, 6.6, 6.7, 7.5), the inner tritor is a small pad that is far anterior and ventral to the mesial

margin of the middle tritor. The remaining specimens also show that the inner tritor tissue began well forward of the middle tritor, but we cannot determine the size of the tritors because the overlying dentine has been broken away through taphonomic processes. This, however, has allowed us to observe that the reserve tissue of the inner tritor was expanded posteriorly and approached the symphyseal margin of the middle tritor (Fig. 7.7, 7.8). CMM-V-4800 is unique in that two smaller accessory tritors fill the gap between the middle and inner tritor, and there are two smaller tritors ventral to the inner tritor (Fig. 7.5). Each of these pads are clearly distinct from each other, in contrast to NJSM 1130-AG (Fig.

6.1c), where there is a posterior exposure of the same tissue that forms the anterior inner tritor.

Although AMNH 14594 has been previously assigned by Case (1996) to *I. williamsae*, here we refer this specimen to *I. dolloi*. Curiously, Case (1996) did not directly compare AMNH 14594 to any referred specimens of *I. dolloi*, but he confidently stated that it differed from the type of *I. williamsae* only in that there was no fusion between the “internal posterior” and “anterior” tritors (middle tritor and anterior inner tritor, respectively, as identified herein). Based on the morphological criteria outlined above, it is our opinion that AMNH 14594 represents *I. dolloi*. One feature that Case

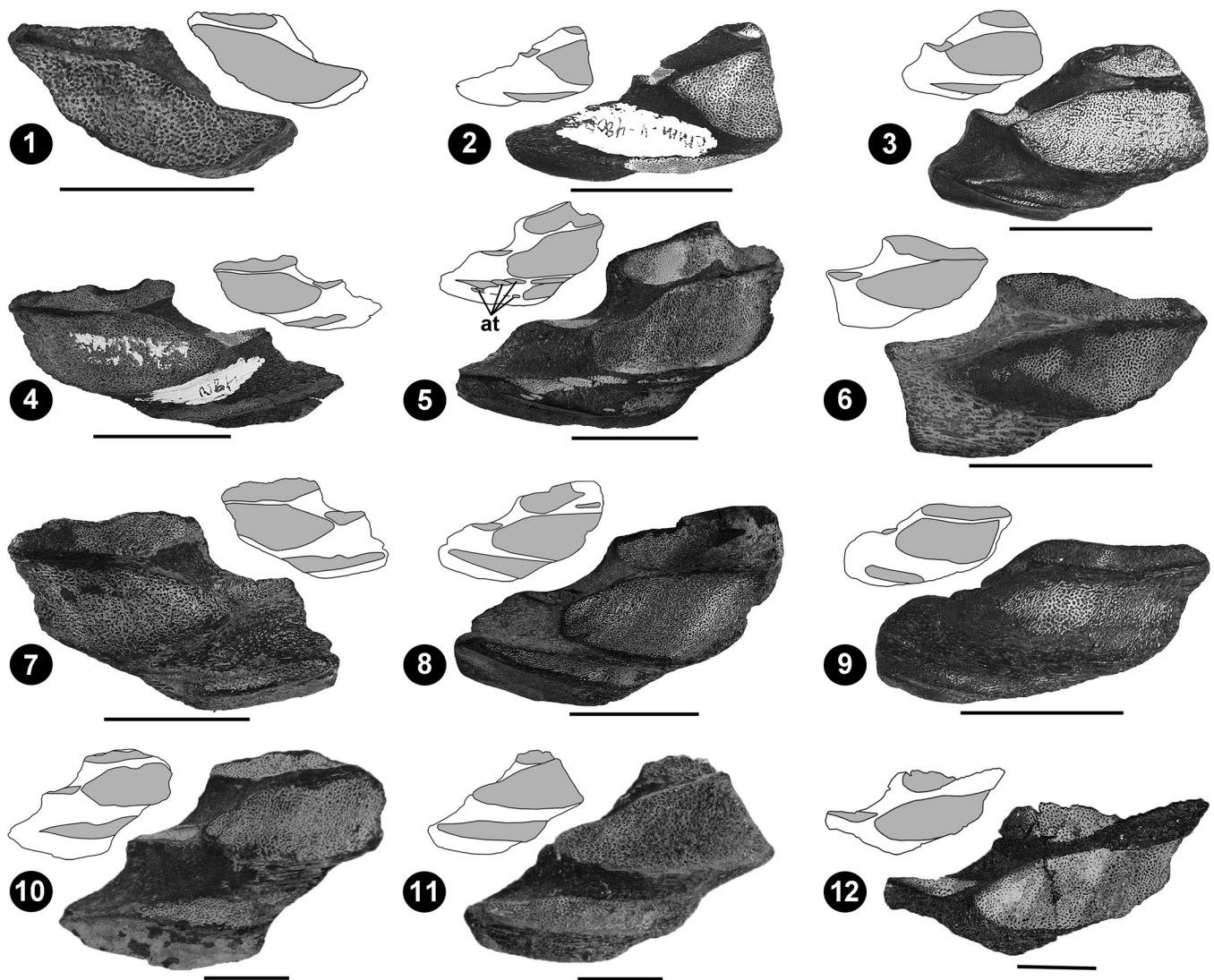


Figure 7. Images and line drawings of *Ischyodus dolloi* mandibular tooth plates in oral view. **1.** CMM-V-5255, left mandibular. **2.** CMM-V-5359, right mandibular. **3.** CMM-V-5358, right mandibular. **4.** CMM-V-5361, left mandibular. **5.** CMM-V-4800, right mandibular. **6.** CMM-V-2812, right mandibular. **7.** CMM-V-5360, left mandibular. **8.** CMM-V-5357, right mandibular. **9.** CMM-V-2669, right mandibular. **10.** CMM-V-5766, right mandibular. **11.** CMM-V-5767, right mandibular. **12.** CMM-V-5765, right mandibular. Gray areas of line drawings represent attachment surfaces for tritor tissues (e.g., 7.3) and/or exposed tritor tissue (e.g., 7.12). **Abbreviations:** at, accessory tritor. Scale bars = 2.0 cm.

(1996) may not have observed is that there is, in fact, a tiny accessory median tritor, located distal to the posterior outer tritor. The pad itself is not preserved, but it is represented by a small elongated furrow on the surface of the dentine, distinct from the posterior outer tritor tissue. Such a tiny median accessory tritor is also seen on CMM-V-4800 and NJSM 11301-AG. The absence of an accessory median tritor is a character that Case (1991) himself originally used to distinguish *I. williamsae* from *I. dolloi*.

Ischyodus williamsae Case, 1991
(Fig. 8.1 – 8.11)

Referred specimens—ALMNH 1994.9.19, left mandibular tooth plate, a specimen mentioned by Denton et al. 1997 but identified by the obsolete catalog number ALAM PV1994.3.1; ISGS 90P107, left mandibular; ISGS 90P108, right mandibular; ISGS 90P109, left mandibular; ISGS 90P110, right vomerine; ISGS 90P111, right vomerine; ISGS 90P112, incomplete right mandibular; ISGS 90P113, left palatine; ISGS 90P116, mesial fragment of left palatine preserving attachment surfaces for posterior inner tritor and adjacent middle tritor, as well as anterior inner tritor; ISGS 90P117, mesial fragment of left palatine (preserving part of posterior inner tritor, with tubular cavity for anterior inner tritor visible in cross section); ISGS 90P118, fragment of left mandibular preserving part of symphyseal crest, anterior inner tritor and symphyseal tritor; MMNS 5231.1, partial right mandibular; MMNS 6812, partial left mandibular; MMNS 6877; left mandibular tooth plate.

Stratigraphic and geographic occurrences—ALMNH 1994.9.19 was collected from the Pine Barren Member of the Clayton Formation, Danian Stage at locality AWi-40 in Wilcox County, Alabama. The ISGS material was collected from the basal Clayton Formation at the Golden Cat Company clay pit, 1.0 km northeast of Olmstead, Pulaski County, Illinois. MMNS 5231.1 and MMNS 6812 were derived from the lower part of the Clayton Formation from locality MS.53.035 in Oktibbeha County, Mississippi, whereas MMNS 6877 was recovered from the Clayton Formation at a site near a Walmart in Hot Spring County, Arkansas.

Description—Two right vomerines, ISGS 90P110 and ISGS 90P111, are essentially complete, although the mesial angles of both specimens are damaged and much of the external surface of ISGS 90P111 is broken away. The external and internal surfaces of ISGS 90P110 are largely obscured by indurated matrix (Fig. 8.11a, b). ISGS 90P111 is larger and less labially convex than ISGS 90P110, but otherwise the elements are comparable. The elements are thin, with ISGS 90P111 measuring only 5.25 mm in thickness. A symphyseal projection that extends dorsally beyond the main body of the

plate is well preserved on ISGS 90P110 (Fig. 8.11a, b), but less so on ISGS 90P111 (Fig. 8.10a, b). The symphyseal margin of ISGS 90P110 curves from the damaged mesial angle to the dorsal projection, and this margin measures approximately 15.80 mm. This margin is straighter on ISGS 90P111 and measures 14.71 mm as preserved. The symphyseal surfaces of both specimens are rather flat, indicating the right and left elements were touching or nearly so, and the transition from the symphyseal surface to the postoral area is marked by a roughly 90 degree angle (Fig. 8.10c). The distance from the mesial angle to the distal tip of the labial side of ISGS 90P110 measures 19.42 mm, and 15.58 mm on ISGS 90P111. From the mesial angle, the labial margin trends dorsally, forming something of a pointed beak with the symphyseal margin. The occlusal portion the labial margin then extends approximately 8.82 mm on ISGS 90P110 and 11.79 mm on ISGS 90P111, after which the margin turns sharply dorsally again to parallel the symphyseal margin. The oral surfaces of both plates are oblique to the external surface, and they bear a series of rod-like tritors, exposed as circular pads arranged in a row, closer to the labial margin (Fig. 8.10b, c, 8.11c). There are six such tritors visible on ISGS 90P110, but only five on ISGS 90P111 (Fig. 8.10c). These tritors are evenly spaced, with the last one located near where the labial margin makes a sharp turn dorsally. The postoral area of both specimens is dorso-ventrally high and concave (more so on ISGS 90P110). A distinct ridge is visible on ISGS 90P110 that marks the junction between the postoral surface and a nearly flat portion of the plate that ascends to the distal part of the labial margin (not preserved on ISGS 90P111). This is the region that overlapped the mesial end of the palatine plate (Fig. 8.11b). The lingual margins of the vomerines are concave between the dorsal symphyseal projection and the distal corner of the plate, and this marks the area of growth of the plate and connection to the chondrocranium.

ISGS 90P113 (Fig. 8.9) is a broken and ablated left palatine missing an unknown portion of its mesial and distal ends, and the presence of a distal projection (“wing” of Ward 1973) cannot be determined. As preserved the specimen measures 22.1 mm in length, and 9.50 mm in maximum width. The symphyseal surface is straight, flat, and vertical, measuring 5.20 mm in height. In aboral view, a sulcus extends the preserved length of the plate, and this structure is flanked by parallel medial and lateral ridges. The attachment surfaces for five tritors are visible in oral view, including anterior and posterior inner, middle, and outer (Fig. 8.9b). The fifth tritor is expressed as a tiny circular depression located anterior to the outer tritor, and it is also visible on the labial surface near the distal end (Fig. 8.9a). The exposed portion of the anterior outer tritor was triangular, with the symphyseal

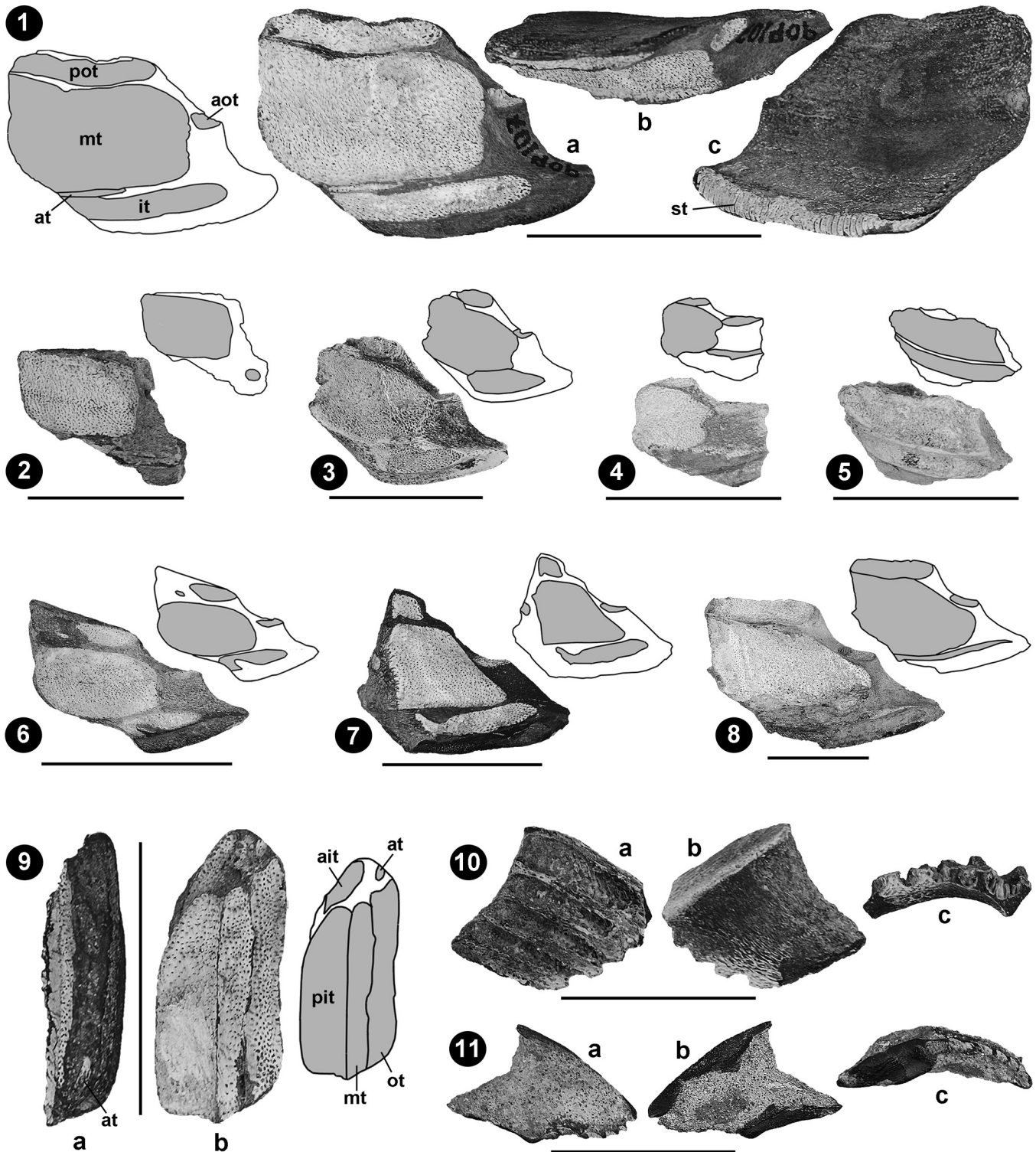


Figure 8. Images and line drawings of *Ischyodus williamsae* tooth plates. **1.** ISGS 90P107, left mandibular in oral (a), oral-oblique (b), and aboral (c) views. **2.** ISGS 90P112, partial right mandibular in oral view (flipped horizontally 180°). **3.** MMNS 6877, left mandibular in oral view. **4.** MMNS 6812, partial left mandibular in oral view. **5.** MMNS 5231, partial right mandibular in oral view (flipped horizontally 180°). **6.** ISGS 90P109, left mandibular in oral view. **7.** ISGS 90P108, right mandibular in oral view (flipped horizontally 180°). **8.** ALMNH 1994.9.19, left mandibular in oral view. **9.** ISGS 90P113, right palatine in labial (a) and oral (b, line drawing) views. **10.** ISGS 90P111, right vomerine in lateral (a), medial (b), and oral (c) views. **11.** ISGS 90P110, right vomerine in lateral (a), medial (b), and oral (c) views. Gray areas of line drawings represent attachment surfaces for tritor tissues. Abbreviations for mandibular tritors as in Figure 6, those for palatine tritors as in Figure 5. Scale bars = 2.0 cm.

margin being its longest side (7.45 mm). The posterior inner tritor appears to have been the widest pad at 4.50 mm. Its mesial end was rounded, and the remaining attachment surface extends to the distal end of the plate a distance of 17.17 mm. The medial and lateral margins of this surface are parallel, and the width measures 4.50 mm. The middle tritor was narrower at 2.54 mm, and its tapered mesial end began slightly anterior to the posterior outer tritor. As a result, the length of this surface measures 17.88 mm to the broken distal end. The attachment surface for the outer tritor measures 3.16 mm, and the mesial end of the crushing pad was well anterior to those of the posterior outer and middle tritors. The total length of this surface to the broken distal end measures 18.40 mm. In distal view the posterior inner, middle, and outer tritors are directly adjacent to each other and separated by very thin walls of dentine, but are arranged in a slightly stacked pattern so that the posterior inner tritor was the ventral-most tritor, and the outer tritor the dorsal-most pad, which was at approximately the same level as the anterior inner tritor. Unfortunately, we cannot know to what degree, if any, a disto-lateral projection was developed on this specimen, or if accessory tritors distal to the outer tritor were present (see descriptions of *I. dolloi* palatines above).

The mandibular tooth plates are comparable in their gross morphology to those of *I. dolloi*, with the mesial end drawn out to a short pointed beak, anterior and posterior outer tritors on progressively higher prominences, a large middle tritor, an inner tritor, and laminated symphyseal tritor. With respect to the middle tritor, on most specimens it is a conspicuously rectangular structure (Fig. 8.1a, 8.2, 8.5, 8.6), and the anterior outer tritor is entirely anterior to the middle tritor. Fig. 8.5, 8.7 and 8.8 illustrate how the lower mesial corner of the middle tritor can extend further anteriorly than the upper corner, to be nearly at the same plane as the leading margin of the anterior outer tritor. The inner tritor is very closely associated with the middle tritor, and the tissues of the two structures are separated by a wall of dentine 1.0 mm or less in thickness. Of note, one specimen exhibits a small accessory median tritor distal to the posterior outer tritor, above the middle tritor (Fig. 8.6).

The mandibulars have a short but stout mesial beak, and the tooth plates widen distally. From the beak, the labial margin slopes backward and upward to a prominence bearing the anterior outer tritor. This slope may be straight (Fig. 8.7) or convex (Fig. 8.1a, c, 8.6). Distal to the anterior outer tritor, the labial margin again slopes backward and upward to a higher prominence that bears the posterior outer tritor. This slope can be straight (Fig. 8.1), sinuous (Fig. 8.7), or concave (Fig. 8.6, 8.8). From the mesial end of the posterior outer tritor, the labial margin turns sharply and roughly parallels the symphyseal margin. The anterior outer tritor was an

ovate pad that varies in length (3.69–5.49 mm) and thickness (1.53–2.43 mm) among the mandibulars, and this structure is completely anterior to the middle tritor on some specimens (Figs. 8.1, 8.6). On one specimen, only the mesial end of the anterior outer tritor is anterior to the middle tritor (Fig. 8.7). The posterior outer tritor is located on the medial side of the prominence and it extends along the entire length of the dorsal margin of the plate (up to 15.14 mm; Fig. 8.1). This tritor is separated from the middle tritor by 1.0 mm or less of dentine, and one specimen shows that only the anterior 8.09 mm of the tritor tissue was exposed as a crushing pad (Fig. 8.6). The middle tritor was by far the largest crushing pad, occupying most of the oral surface, but we cannot ascertain how much of this structure was exposed in life because dentine that would have surrounded at least some of the distal surface is broken away. The inner tritor, located along the symphyseal crest, was a large pad, and its mesial margin is roughly equal to the mesial margin of the anterior outer tritor. The inner tritor extended all the way to the distal end of the plate up to 17.68 mm (Fig. 8.1), and this tritor tissue is separated from the middle tritor by a wall of dentine only 1.0 mm in thickness. Figure 8.1 and 8.6 shows that the portion of the inner tritor exposed in life was up to 12.43 mm long and 7.93 mm long, respectively, and that these pads extended distally well past the leading margin of the middle tritor.

Remarks—MMNS 6877 (Fig. 8.3) is smaller than the type material of *I. williamsae*, but its overall morphology is not dissimilar and its inner tritor does appear to achieve fusion with the middle tritor as interpreted by Case (1991) for *I. williamsae*. One conspicuous difference is that the posterior outer tritor of MMNS 6877 begins approximately at the middle of the middle tritor, whereas it begins nearly at the mesial end of the middle tritor on the type specimen of *I. williamsae* (see Case 1991: pl. 1, b and c). Denton et al. (1997) confidently identified ALMNH 1994.9.19 as *I. williamsae* because it is “a mandibular element, precisely matching tritor tracts” for this species (p. 394). This nearly complete specimen is the same size as the type material of *I. williamsae* and it lacks an accessory median tritor. ALMNH 1994.9.19 (Fig. 8.8) differs from the type *I. williamsae* mandibulars in that the middle tritor has a more triangular appearance due to mesial tapering, the anterior outer tritor begins at nearly the same vertical plane as the middle tritor (as opposed to being situated completely anterior to the mesial edge of the middle tritor), the posterior outer tritor begins approximately at the middle of the middle tritor (not near the mesial edge), and the inner tritor is more clearly differentiated from the middle tritor. However, these specimens, along with MMNS 6812 (Fig. 8.4) and MMNS 5231 (Fig. 8.5), are morphologically consistent with the Illinois specimens described above and bear features that we attribute to *I. williamsae*.

Ischyodus sp.
(Fig. 5.4)

Referred specimens— ChM PV4152, partial right palatine tooth plate; CMM-V-5783, mandibular fragment; CMM-V-5784, partial left mandibular; CMM-V-5785, partial left mandibular; MMNS 5231.2, mandibular? fragment.

Stratigraphic and geographic occurrences— The ChM specimen was collected as float from a site near St. Stephen in Berkeley County, South Carolina. It lacks stratigraphic provenience but was derived from either the Danian Rhems Formation or Thanetian Williamsburg Formation. The CMM fossils are from Charles County, Maryland, and were derived from the Thanetian Aquia Formation. MMNS 5231.2 is from the lower (Danian) part of the Clayton Formation, Oktibbeha County, Mississippi.

Remarks—All of the specimens are well enough preserved to identify them as *Ischyodus*, but they lack enough diagnostic features for specific determination. MMNS 5231.2 and the CMM specimens were derived from deposits within which only *I. williamsae* or *I. dolloi* (respectively) occur. ChM PV4152 resembles the palatines of both *I. dolloi* (i.e., Fig. 5.6) and *I. williamsae* (Fig. 8.9), but re-discovery of a mandibular tooth plate from the same locality as ChM PV4152, its whereabouts presently unknown, could help make a more specific identification.

EDAPHODON Buckland, 1838
Edaphodon mirificus Leidy, 1856
(Fig. 9.1, 9.3–9.9)

Referred specimens—MMNS 7263, left palatine; NJSM 23772, vomerine tooth plate; NJSM 23773, distal portion of right vomerine; NJSM 23771, left palatine; NJSM 11301-V, left palatine; NJSM 11301-AE, mesial end of left palatine; NJSM 11301-AD, partial right palatine; NJSM 11301-AA + AC, incomplete right palatine (cataloged as two separate parts); NJSM 11301-Z, right mandibular.

Stratigraphic and geographic occurrences—MMNS 7263 was collected from the Danian part of the Clayton Formation at locality MS.73.024 in Union County, Mississippi. The NJSM specimens were recovered from the basal Hornerstown Formation (Danian Stage) exposed at the Inversand Company Marl Mine in Gloucester County, New Jersey.

Remarks—Stahl and Parris (2004) provided a detailed description of the tooth plates from an associated dentition found at the same locality as the NJSM specimens listed above. However, we found some morphological variations within the palatines examined, notably in the shape of the mesial end of the plate and the exact size, shape, and orientations of the tritor pads. The mesial end of the plate ranges from broadly (Fig. 9.4b) to narrowly (Fig. 9.5) rectangular, sharply pointed (Fig. 9.1, 9.6), and rounded (Fig. 9.3). Of the three tritors, the anterior inner tritor ranges from roughly circular (Figs. 9.1b), elongated and ovate (Fig. 9.3), and triangular to varying degrees (Fig. 9.4–9.7). It may be entirely anterior to the mesial end of the posterior inner tritor (Fig. 9.1, 9.3, 9.6), or its posterior end extends distally to varying degrees past the mesial end of the posterior inner tritor (Fig. 9.4b, 9.5, 9.7). In all cases, the posterior inner tritor is the largest crushing pad and it occupied much of the oral surface. The medial margin of the posterior inner tritor is straight along the symphysis, whereas the labial margin is roughly parallel to the labial margin of the tooth plate (see Fig. 9.3 for an exception). The outer tritor is not preserved in its entirety on most specimens, but its anterior end may be distal to the posterior end of the anterior inner tritor (Fig. 9.5) or extend anteriorly approximately to the middle of the anterior inner tritor (Fig. 9.7). Some of these variations may be related to ontogeny (compare Fig. 9.3 to 9.4), but intraspecific differences between individuals of equivalent size is also apparent (compare Fig. 9.1 to 9.7).

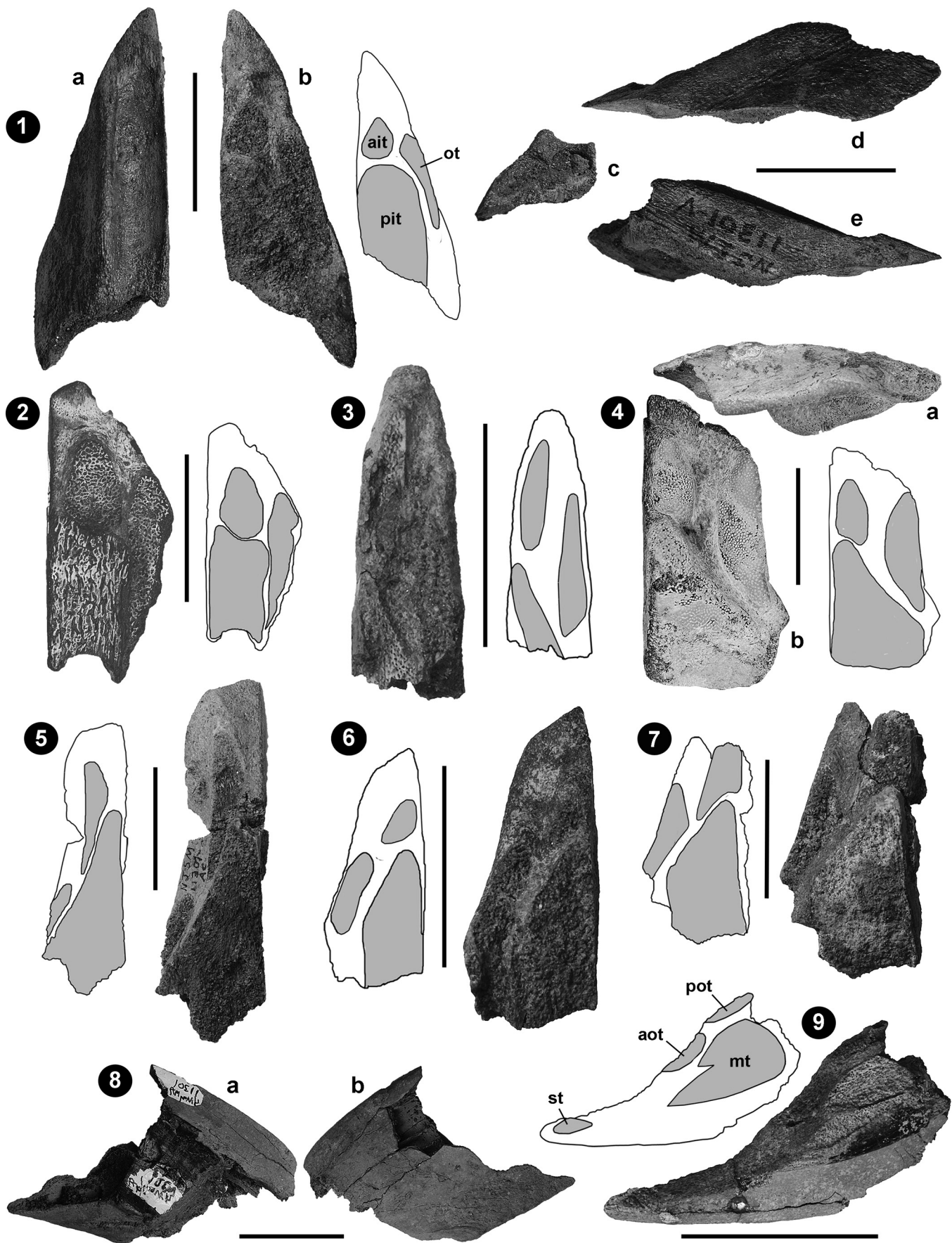
Edaphodon sp.
(Fig. 9.2)

Referred specimen—NJSM 13495, incomplete left palatine.

Stratigraphic and geographic occurrence—This specimen was derived from the Aquia Formation (Thanetian Stage) at Belvedere Beach in King George County, Virginia.

Description—NJSM 13495 measures 44.2 mm in preserved length, although when complete it was probably equivalent in size to the *I. dolloi* palatine (NJSM 11301-T) shown in Fig. 9.1. The mesial tip is bluntly pointed, an aboral sulcus is discernable, and the symphyseal surface is straight, flat, and vertical. Attachment surfaces for three

Figure 9. Images and line drawings of *Edaphodon* tooth plates. 1. *E. mirificus*, NJSM 11301-V, left palatine in aboral (a), oral (b), distal (c), labial (d), and symphyseal (e) views. 2. *Edaphodon* sp., NJSM 13495, partial left palatine in oral view. 3. *E. mirificus*, NJSM 11301-AE, mesial end of left palatine in oral view. 4. *E. mirificus*, MMNS 7263, left palatine in labial (a) and oral (b, line drawing) views. 5. *E. mirificus*, NJSM 11301-AA+AC, right palatine in oral view. 6. *E. mirificus*, NJSM 23771, left palatine in oral view. 7. *E. mirificus*, NJSM 11301-AD, partial right palatine in oral view. 8. *E. mirificus*, NJSM 23772, left vomerine in medial (a) and lateral (b) views. 9. *E. mirificus*, NJSM 11301-Z, juvenile right mandibular in oral view (rotated laterally to show the symphyseal surface). Gray areas of line drawings represent attachment surfaces for tritor tissues (e.g., 9.1b) or exposed tritor tissue (e.g., 9.4b). Abbreviations as in Figures 5 and 6. Scale bars = 2.0 cm. ►



tritators are visible, including the anterior and posterior inner, and outer. The anterior inner tritor was roughly triangular, with the narrower, rounded mesial end being located on a slight prominence. Due to damage to the mesial margin of the posterior outer tritor, the remaining attachment surface measures 13.47 mm in length and 8.42 mm in maximum width. As preserved, the attachment surface for the posterior inner tritor is rectangular and measures 11.17 mm in width and 22.36 mm in length. The outer tritor was the narrowest, measuring 6.36 mm in width. Maximum length of the attachment surface measures 29.89 mm, but only approximately 11.88 mm of the mesial end was exposed in life based on the preserved mesial margin of the posterior outer tritor.

Remarks—NJSM 13495 is broken and ablated, but the overall shape of the remaining portion is similar to palatines of *Ischyodus* and *Edaphodon* described above. The two genera can occur within the same deposits, but their palatine tooth plates can be distinguished by the number of tritators. Palatines of *Ischyodus*, like *I. dolloi*, have anterior and posterior inner, middle, and outer tritators (four large tritators), whereas palatines of *Edaphodon* typically lack a middle tritor (three tritators). NJSM 13495 is identified as *Edaphodon* sp. because only three tritators were developed. There is absolutely no indication of a middle tritor, either in the form of dentine walls on the oral surface or the remains of a tubular structure at the distal end. This is in stark contrast to ChM PV-4152 (Fig. 5.4) and ISGS 90P113 (Fig. 8.9), where these features are clearly visible even though the tooth plates are incomplete and abraded.

RHINOCHEMAERIDAE Garman, 1901

ELASMODUS Egerton, 1843

Elasmodus hunteri Egerton, 1843

(Fig. 10.1, 10.2)

Referred specimens—CMM-V-5356, partial right mandibular tooth plate; CMM-V-5786, partial right mandibular.

Stratigraphic and geographic occurrences—Both specimens were derived from Aquia Formation (Thanetian) exposures at Liverpool Point in Charles County, Maryland.

Description—CMM-V-5356 represents only the upper part of the tooth plate, posterior to the beak, and as preserved its length from the broken mesial to broken distal end measures 13.16 mm. The occlusal surface bears a large ovate middle tritor that is situated on a slight prominence, and it appears that the entire 8.72 mm of the preserved pad was exposed in life rather than a portion being overlain by dentine (Fig. 10.1a, b). A series of small outer tritators are seen along the sinuous labial margin, and their laminated tissues are visible on the external surface of the plate due to loss of the overlying dentine through taphonomic processes (Fig.

10.1c). The laminated symphyseal tritor is also visible on the ventral half of the outer surface (Fig. 10.1c). CMM-V-5786 (Fig. 10.2) is virtually identical to CMM-V-5356 in size, morphology, and preservational state, the only difference being that the tritor tissues are not preserved on the former specimen, but their attachment surfaces are clearly visible.

Remarks—The Aquia Formation specimens represent only the second occurrence of *Elasmodus hunteri* to be reported from North America, with the only other record (a palatine fragment) being from the Thanetian Cannonball Formation of North Dakota (Cvancara and Hoganson 1993). CMM-V-5356 and CMM-V-5786 are virtually identical to the neotype of *E. hunteri* as specified by Gurr (1962: pl. 25, 3), and consistent with what Ward (1977) considers to be a juvenile growth stage.

cf. *Elasmodus* sp.

(Fig. 10.3)

Referred specimen—NJSM 11301-W, left mandibular tooth plate.

Stratigraphic and geographic occurrence—This specimen was collected from the basal Hornerstown Formation (Danian Stage) exposed at the Inversand Company Marl Mine in Gloucester County, New Jersey.

Description—NJSM 11301-W measures 26.36 mm in total length, but the mesial tip of the plate is not preserved. However, it is still apparent that the mesial end of the plate was formed into a beak. The attachment surfaces for three tritators are clearly visible, including anterior and posterior outer, and middle (Fig. 10.3a–c). There is no evidence for a laminated symphyseal tritor at the labial side of the plate. The narrow anterior outer tritor is located on a distinctive prominence that forms an anteriorly pointed projection on the labial margin (Fig. 10.3a, b). This tritor has its mesial end on the labial margin, but posteriorly it diverges medially towards the middle tritor, from which it is separated by 2.24 mm of dentine (Fig. 10.3a). On the external surface of the plate, the dentine has broken away to reveal the internal tube within which the tissue for the anterior outer tritor extended the entire length of the plate (Fig. 10.3c). The posterior outer tritor is located on the highest part of the labial margin, separated from the middle tritor by approximately 2.0 mm of dentine (Fig. 10.3a, b). There is a thin and shallow longitudinal furrow visible on the external surface, immediately below the labial margin, that may represent the location of the tissue for an additional outer tritor (Fig. 10.3c). The middle tritor has a rounded mesial margin and was by far the largest crushing pad, measuring 6.80 mm in height and probably exposed along the entire 15.08 mm length of the visible attachment surface (Fig. 10.3a, b). There is evidence

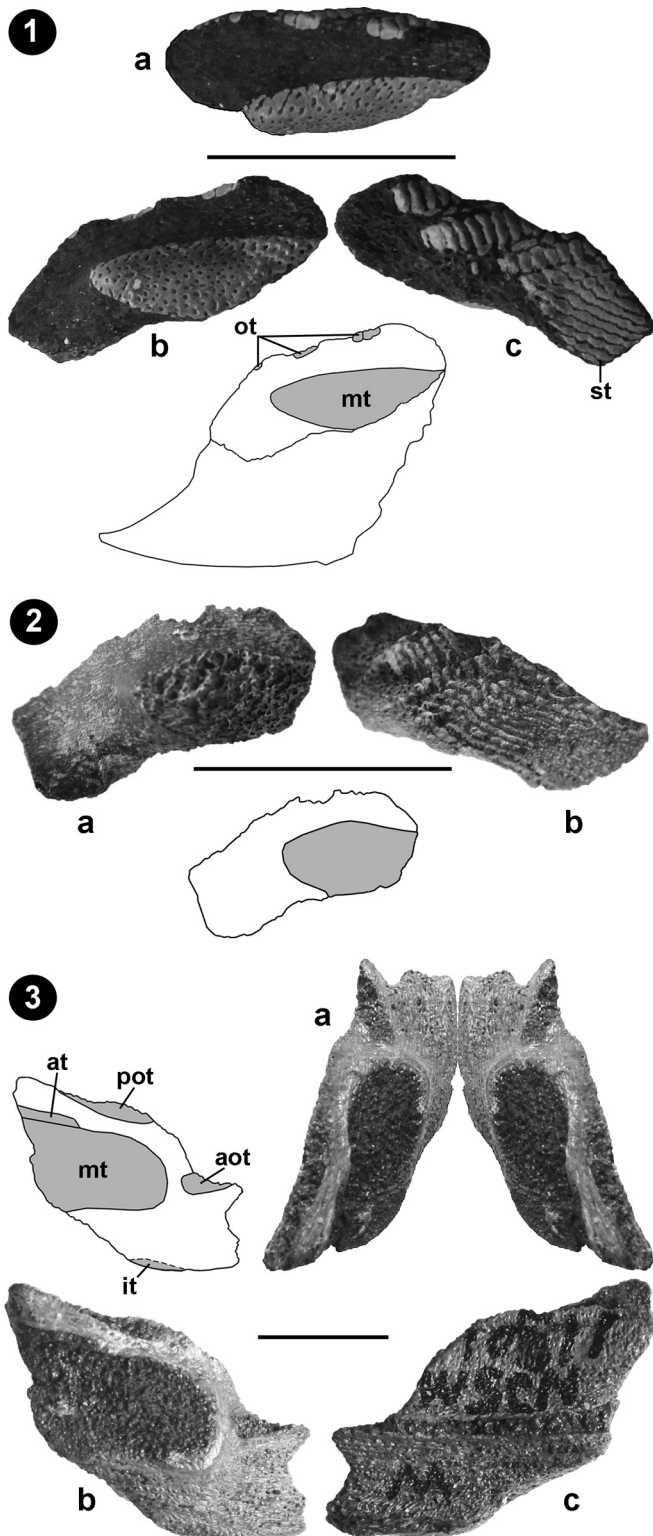


Figure 10. Images and line drawings of *Elasmodus* mandibular tooth plates. 1. *E. hunteri*, CMM-V-5356, partial right mandibular in oral (a), medial (b), and lateral (c) views. 2. *E. hunteri*, CMM-V-5786, partial right mandibular in medial (a) and lateral (b) views. 3. cf. *Elasmodus* sp., NJSM 11301-W, left mandibular in medial (b) and lateral (c) views. 3a shows hypothetical articulation of mandibular plates, with NJSM 11301-W mirror-imaged to represent the right side. Outline reconstruction associated with 1b based on Gurr (1962). Gray areas of line drawings represent exposed tritor tissue (e.g., 9.1a) or attachment surfaces for tritor tissues (e.g., 9.3b). Scale bars = 1.0 cm. Abbreviations as in Figures 6 and 7.

for an accessory tritor at the dorsal margin of the middle tritor, represented by a short furrow (Fig. 10.3b). A thin (1.5 mm) inner tritor (symphyseal tritor of Ward 1977, mesial tritor of Averianov 1999), measuring 6.22 mm in length, is located at the symphyseal margin, but it is difficult to distinguish without magnification (Fig. 10.3b). The area anterior to the middle tritor, between the anterior outer tritor and the symphyseal margin, is weakly concave.

Remarks—NJSM 11301-W resembles mandibular tooth plates of *Ischyodus* (see specimens shown in Figs. 6–8), but it differs significantly in lacking a symphyseal crest and having the inner tritor located at the symphyseal margin. This specimen is also superficially similar to the holotype left mandibular of *Elasmodus kemp* Ward, 1977 from the middle Eocene of England (also Kemp et al. 1990). Unfortunately, the distal part of the labial margin of NJSM 11301-W is damaged, and we cannot know if the outer tritor was one continuous element or subdivided into smaller parts, or even if the tritor was laminated. Based on the attachment surfaces for the middle, anterior outer and inner tritors, the tissues were composed of tubular dentine, as is the case with *E. kemp*. Unlike *E. kemp*, as well as other species of *Elasmodus*, NJSM 11301-W appears to lack a laminated symphyseal tritor (apical dentine of Gurr 1962, beak tritor of Ward 1977, anterior outer tritor of Averianov 1999).

DISCUSSION

Identifying isolated fossil chimaeroid tooth plates can be a daunting task, even in the case of complete specimens. Species have been erected based on the number, size, shape, and orientation of tritors, variations in beak length, height of prominences, morphology of the labial margin, etc. Many species are known from only a few, often incomplete specimens, and while the range of variation is unclear, tooth plates of one species have been found to be highly variable (Hussakof 1912, Stahl 1999, Cicimurri and Ebersole 2014). Additionally, morphological features identified by authors for species determination may be ambiguous due to inadequate descriptions or poor preservation of material. Questions therefore arise as to which features are taxonomically significant when identifying species, and whether the specimens in a given sample represent multiple species or variation within a single taxon. On the generic level, the palatine and/or mandibular tooth plates in the sample of 94 specimens that

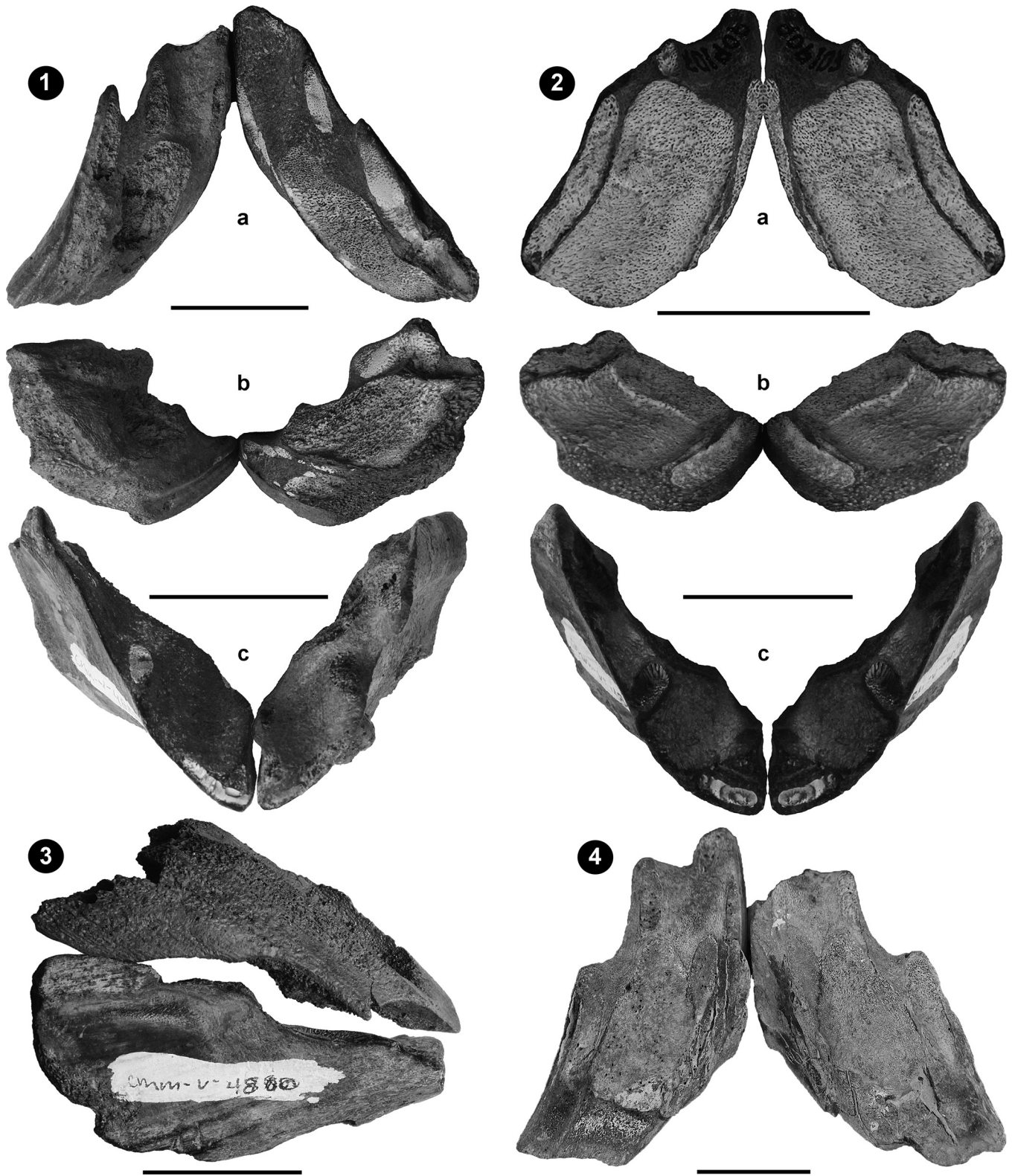


Figure 11. *Ischyodus* tooth plates in approximate life position. **1.** *I. dolloi* mandibulars in oral (a), distal (b), and mesial (c) views based on NJSM 11301-M (left) and CMM-V-4800 (right). **2.** *I. williamsae* mandibulars in oral (a), distal (b), and mesial (c) views based on ISGS 90P107 (mirror-imaged to represent the right side). **3.** *I. dolloi* palatine (NJSM 11301-T) and mandibular (CMM-V-5357) plates in labial view. **4.** Associated mandibulars of *I. bifurcatus*, ALMNH 1994.1.22 (Late Cretaceous Mooreville Chalk, Alabama), in oral view for comparison. Scale bars = 2.0 cm.

we examined differ significantly enough that we were able to identify four genera; *Callorhinchus*, *Ischyodus*, *Edaphodon*, and *Elasmodus*. *Callorhinchus*, *Ischyodus*, and *Edaphodon* are represented by palatine tooth plates, and although all are similar in their gross morphology, the number of tritors can be used to identify each genus. *Callorhinchus* palatines have a single tritor that bears one or two anterior prongs (Didier et al. 1994), whereas *Edaphodon* palatines exhibit three separate tritors (Stahl and Parris 2004). Four or more tritors are present on the palatines of *Ischyodus* (Stahl 1999, Hoganson and Erickson 2005). Species differentiation within these genera proved to be more challenging.

The Danian (early Paleocene) specimens described herein were collected from lithostratigraphic units that overlie Upper Cretaceous (Maastrichtian) strata, including the Clayton Formation within the region of the Mississippi Embayment (Alabama, Arkansas, Mississippi, Illinois, and Texas) and the Hornerstown Formation in the Atlantic Coastal Plain (New Jersey). Within the upper reaches of the Mississippi Embayment, in Missouri and Illinois, as well as the coastal plain of New Jersey, basal Paleocene strata contain Late Cretaceous fossils that were reworked during the Danian (Shourd and Winter 1980, Stahl and Parris 2004, Cope et al. 2005, Dastas et al. 2014). Considering this factor, as well as the possibility that species survived the K/Pg extinction, comparison of the Paleocene fossils to Cretaceous species is warranted. In the case of *Ischyodus*, two species are recognized from the Cretaceous of North America, *I. bifurcatus* Case, 1978 and *I. rayhaasi* Hoganson and Erickson, 2005, but neither taxon appears to have survived past the K/Pg boundary. It is worth noting that mandibular tooth plates of both of these Cretaceous species have a distinctively bifurcated middle tritor (i.e., the mesial end is split into elongated dorsal and ventral projections of varying lengths), a feature completely absent or only very weakly evident on the Paleocene mandibulars that we examined.

Several species of *Ischyodus* have been identified in North American Paleocene deposits, including *I. zinsmeisteri* Applegate, 1975, *I. dolloi* (Cvancara and Hoganson 1993) and *I. williamsae* (Case 1991, 1996). *Ischyodus thurmanni* Pictet and Campeche, 1858, a Cretaceous taxon, was reported from the main fossiliferous layer of the basal Hornerstown Formation (Gallagher et al. 1986), but we consider this specimen (NJSM 11301-M) to be *I. dolloi* (Fig. 6.3). *Ischyodus zinsmeisteri* is based on the mesial half of a small right mandibular tooth plate from the Danian of California (Applegate 1975). The specimen has an elongated beak, and symphyseal, anterior inner, anterior and posterior outer, and middle tritors are preserved. Ward and Grande (1991) concluded that the specimen represents a tooth plate from a young individual of *I. dolloi*.

Ischyodus dolloi has been reported from Paleocene strata of North Dakota, USA (Cvancara and Hoganson 1993), the Paleocene and Eocene of Belgium and France (Leriche 1902, 1908), England (Gurr 1962) and Antarctica (Ward and Grande 1991), and it has been identified from the Late Cretaceous of Antarctica (Stahl and Chatterjee 2002) and the Pliocene of Australia (Fitzgerald 2005). Four tritors are consistently present on the palatine tooth plates attributed to *I. dolloi*, including the anterior and posterior inner, middle, and outer, although their exact shape and arrangement are variable (Stahl 1999, Otero et al. 2013b). Leriche (1902, 1908) and Gurr (1962) noted the presence of a small tritor distal to the outer tritor, and in fact the outer tritor can appear to be subdivided into three to five distinct smaller pads extending along the labial margin of the lateral wing of the tooth plate (Ward 1973, Ward and Grande 1991, Cvancara and Hoganson 1993, Stahl 1999). However, this feature is useless for species determination if the lateral wing is not preserved, as we cannot know if the outer tritor was subdivided or one continuous structure. Additionally, other species of *Ischyodus* are known to have subdivided outer tritors, like *I. gubkini* Nessov and Averianov, 1996, which has a much-reduced middle tritor, whereas *I. dolloi* palatines are characterized by having similar-sized posterior inner and middle tritors.

The mandibular tooth plates of *I. dolloi* are generally similar to those of other species within the genus, but a feature that is observed on tooth plates assigned to this species is a small tritor located distal to the posterior outer tritor, above the middle tritor (“accessory median tritor” of other authors, including Gurr 1962, Ward and Grande 1991, Stahl 1999). Based on our observations, this structure is a true pad distinct from the posterior outer and middle tritors, rather than a portion of either of those two pads that is exposed from the dentine. Unfortunately, this feature is also useless for species determination if the posterior half of a tooth plate is not preserved or the dentine overlying the posterior outer tritor has been broken away. We believe that the following combination of features can be used to identify mandibular plates of *I. dolloi*: 1) middle tritor with tapered mesial margin that is rounded, pointed, or blunt; 2) exposed portion of anterior inner tritor is well separated from the mesial margin of the middle tritor; 3) anterior inner tritor tissue separated from ventral margin of middle tritor by 3.0–5.0 mm of dentine; and 4) presence of accessory median tritor.

Ischyodus williamsae was erected by Case (1991) based on three mandibular tooth plates, and although Stahl (1999) mentioned that vomerine and palatine plates have been referred to this species, descriptions of these elements are lacking. The criteria that Case (1991) utilized to differentiate the mandibulars of *I. williamsae* from those of *I. dolloi* include being smaller, lacking an accessory median tritor,

and having an inner tritor fused to the middle tritor. The characteristic of “small size” has not been quantified, and it may be difficult to ascertain if a “small” tooth plate represents a diminutive taxon or a juvenile/immature growth stage of a truly larger species. We concur with Ward and Grande (1991) that the overall size of a tooth plate is not a taxonomically significant character when identifying a species. If a tooth plate is incomplete it may be impossible to determine if an accessory median tritor was present, and only three of the 26 mandibular tooth plates we identified as *I. dolloi* were preserved well enough that this structure could be observed. Additionally, this structure may not be unique to *I. dolloi*, as an accessory median tritor is clearly visible on ISGS 90P109, a tooth plate that we identify as *I. williamsae*. The remaining character, the inner tritor appearing to achieve fusion with the middle tritor, may be the singular feature to identify *I. williamsae* mandibular tooth plates.

It is important to note here that our tritor terminology differs from that of Case (1991, 1996), who followed Gurr (1962), and what we call the middle tritor has been referred to as the “internal posterior” tritor. The middle tritor has also been termed the median tritor (i.e., Ward and Grande 1991). Case (1991) stated that the inner tritor of *I. williamsae* is fused with the middle tritor, and the very close spacing of these two tritors on the holotype does give the appearance of fusion. However, photographs of the specimen (Case 1991: pl. 1a, Stahl 1999: fig. 139G) show a very thin wall of dentine separating the tissues of the middle and inner tritors. The paratypes, both right mandibulars, as well as the specimens in our sample that we identified as *I. williamsae*, also clearly show a thin (1.0 mm or less) dentine wall separating the inner and middle tritors. In contrast, the tissues of the middle and inner tritors of *I. dolloi* are separated by 3.0–5.0 mm of dentine.

Case (1996) identified AMNH 14594 as *I. williamsae*, even though the inner tritor is well separated from the middle tritor, stating simply that AMNH 14954 “has not quite developed that fusion” (p. 10) of the middle and inner tritors. It is not clear to us if Case (1996) was attributing this difference to the smaller size of AMNH 14954 when compared to the type *I. williamsae* (ontogeny), or the supposed older geologic age of the specimen (evolutionary stage). Wide separation of the middle and inner tritors was observed on all of the mandibulars that we identified as *I. dolloi*, regardless of tooth plate size (ontogeny) and geologic age. Identification of the tooth plate as *I. williamsae* could also have been based on the apparent lack of an accessory median tritor, but this structure is in fact present and could have originally been overlooked due to its tiny size. Although at least one *I. williamsae* specimen has an accessory median tritor (ISGS

90P109), the combination of a middle tritor with tapered and rounded mesial margin, wide separation of the middle and inner tritor pads, and wide separation of the middle and inner tritor tissues, leads us to conclude that AMNH 14594 is *I. dolloi*, not *I. williamsae*.

The vomerines of *I. williamsae*, ISGS 90P110 (Fig. 9.11) and ISGS 90P111 (Fig. 9.10), are comparable to the vomerine tooth plates of *I. dolloi* and to *Edaphodon* and are of little taxonomic value. We refer the specimens to *I. williamsae* because of their association with mandibulars that we assigned to this species. The identification of a palatine, ISGS 90P113 (Fig. 8.9), as *I. williamsae*, is similarly circumstantial. ISGS 90P113 is approximately the same size as a palatine of *I. dolloi* that we examined (CMM-V-4587, Fig. 5.6), and as preserved it cannot be readily distinguished from the suite of *I. dolloi* palatines in our sample. One feature of note on ISGS 90P113 that we did not observe on any of the *I. dolloi* palatines is the presence of a small tritor adjacent to the anterior inner tritor, mesial to the outer tritor (Fig. 8.9a, b). Unfortunately, we cannot say that this is a taxonomically useful character because of the sample size (n=1), and accessory tritors were observed on some *I. dolloi* mandibular tooth plates (CMM-V-4800, Fig. 7.5). Development of accessory tritors on *Edaphodon* mandibulars is also known to be variable (Cicimurri 2010, Cicimurri and Ebersole 2014).

If *I. williamsae* can be considered a valid species, we propose the following combination of features to separate mandibulars of this species from those of *I. dolloi*: 1) the middle tritor appears as a rectangular structure, with the mesial margin being nearly perpendicular to the upper and lower margins (we did observe some variability, with some being slightly bifurcated at their mesial margin and others more tapered, although these are asymmetrical when compared to *I. dolloi*); 2) the inner tritor pad is close to the mesial margin of the middle tritor (separated by 2.0–5.0+ mm of dentine on *I. dolloi*); 3) tissues of the inner and middle tritors are separated by a thin dentine wall measuring 1.0 mm or less in thickness (3.0–5.0 mm on *I. dolloi*); 4) and the inner tritor is dorso-ventrally wider (more than 3.0 mm, as opposed to slightly more than 1.0 mm on *I. dolloi*). In addition, a palatine of *I. williamsae* bears a small tritor adjacent to the anterior inner tritor, mesial to the outer tritor.

Although the tritor tissues are not preserved on most of the specimens, the attachment surfaces for these structures are visible. Unfortunately, the exact amount of tritor that was exposed at the time of the animal’s death often cannot be determined because the overlying dentine has been broken away. However, in some cases the original shape of the tritor is still visible, and this is true for the anterior and posterior outer, inner, and accessory median tritor of mandibular

tooth plates, and the anterior inner tritor of the palatine. NJSM 11301-M, a mandibular plate (Fig. 6.3), still preserves dentine over the unused portion of the middle tritor tissue, and it shows that only 64% of the total length of tritor was exposed as a crushing pad in life. This percentage could be variable within the species, as this specimen and others on which the length of the actual tritor pad can be discerned (Figs. 6.3, 6.7, 7.8) show that 36–70% of the posterior outer tritor tissue was exposed *in vivo*.

The mandibulars of *I. dolloi* and *I. williamsae* articulate with each other in a manner similar to Cretaceous *I. bifurcatus*, with contact or near-contact between the symphyseal crests and the symphyseal margins (Cicimurri and Ebersole 2014). However, mandibulars of *I. dolloi* and *I. williamsae* articulate in the relatively small region between the tip of the beak and the mesial end of the inner tritor (compare Fig. 11.1a and 11.2a to 11.4). One specimen of *I. dolloi*, CMM-V-4800, exhibits a small, flat vertical surface that indicates actual contact with the left mandibular. This symphysis is much less extensive than seen on *Edaphodon*, and the angle of divergence between the beak and the remainder of the tooth plate not nearly as pronounced (i.e. Stahl and Parriss 2004, Cicimurri and Ebersole 2014). With the mandibulars articulated in life position, it is easy to see the approximate way in which the tritors functioned to crush prey. It is interesting to note that the middle tritor of *I. dolloi* appears to have been more vertical than those of *I. williamsae*, and the middle tritor of *I. williamsae* is much more near the horizontal. These differing morphologies could be useful for species determination if an isolated mandibular can be oriented in life position.

The palatine and mandibular plates of *I. dolloi* articulate in a similar fashion to *I. bifurcatus*, except for slight variations in occlusion between the posterior inner and middle tritors of the palatine with respect to the middle tritor of the mandibular, as well as the outer and accessory tritors of the palatine and the posterior outer tritor of the mandibular. On *I. bifurcatus*, the posterior inner and middle palatine tritors work against a large bifurcated middle mandibular tritor (Cicimurri and Ebersole 2014), whereas on *I. dolloi* the two palatine tritors occlude with the singular mass of the mandibular's middle tritor. The outer tritor of *I. bifurcatus* (as well as *Edaphodon mirificus*) palatines is a single elongated structure that extends onto the distal wing (Cicimurri and Ebersole 2014). Functionally, the anterior portion of the outer tritor on the palatine occludes with the anterior outer tritor of the mandibular, and the mandibular's posterior outer tritor works against the posterior end of the palatine's outer tritor. In contrast, the outer tritor of *I. dolloi* is structurally subdivided into three or more smaller pads, and the net

effect is that the smaller accessory tritors work against the mandibular's posterior outer tritor.

The Aquia Formation *Callorhynchus* material allows us to recreate how the palatine and mandibular plates articulated, and how the tritor pads of these plates occluded with each other. The straight, high symphyseal surfaces of the palatines indicate that the right and left plates were very close to each other (probably separated by a thin wall of connective tissue) along their entire length. The symphysis is not perfectly vertical but directed ventro-laterally, resulting in the aboral surface of the tooth plates being pitched rather than horizontal. Interestingly, this orientation brings the tritulating surface of the tritor into the horizontal plane.

The high, flat, straight symphyseal surfaces of the Aquia Formation *Callorhynchus* mandibular plates indicates that the right and left elements were very close to each other along their length (Fig. 4.5). Articulation of the right and left plates along their vertical symphyseal surfaces results in the oral surface of each plate being oriented in the horizontal plane. This orientation would account for the wear pattern observed on the palatine tritors. Additionally, wear patterns observed on the labial edge of tooth plates indicates that the dorsally curving distal portion of the mandibular plate overlapped the palatine in this area. The wear pattern also suggests the presence of an outer tritor along the distal part of the mandibular plates' labial margin, and that this structure acted against the labial margin of the palatine tritor.

Studies of the feeding habits of *Callorhynchus* have shown that extant species are benthic predators of shelled invertebrates like clams and crustaceans (Ribbink 1971, Freer and Griffiths 1993, Di Giacomo and Perier 1996). Di Giacomo and Perier (1996) noted variations in prey preference between juvenile and adult *C. callorhynchus* Linnaeus, 1758, with juveniles consuming shelled invertebrates whole or choosing thin-shelled animals. This was attributed at least in part to the more delicate tooth plates (and presumably smaller tritor pads; Didier et al. 1994) and weaker jaw musculature of juveniles compared to adults. The palatine tooth plate of *C. phillipsi* is remarkably similar to those of extant species of *Callorhynchus*, and it stands to reason that the fossil species was also a benthic predator that consumed a diet of crustaceans and mollusks. In contrast to *C. phillipsi*, palatines of *C. newtoni*, *C. regulbiensis*, and the Aquia Formation taxon have much more robust tritors that occupy a much larger proportion of the oral surface, leading us to conclude that these latter taxa consumed harder shelled prey than *C. phillipsi*. Based on studies of modern chimaeroids, the type of prey consumed by *I. williamsae* and *I. dolloi* may have depended upon prey size and shape (rounded vs. flat), in addition to availability. When comparing the reconstructed mandibular

dentitions of *I. williamsae* to *I. dolloi*, it appears that a broader surface would have been available to *I. williamsae* for prey mastication, and this taxon may have consumed more flat-shelled prey (e.g., pectinids) than *I. dolloi* (rounder shelled snails and/or clams).

With respect to *Elasmodus*, [Averianov \(1999\)](#) concluded, based on geologic occurrence and geographic locations of specimens, that the genus occupied coastal habitats within epeiric seas. In North America, this was the case for *E. hunteri* living within the Cannonball Sea covering much of North and South Dakota during the Danian ([Cvancara and Hoganson 1993](#), [Boyd and Lillegraven 2011](#), [Weems 2014](#)). However, specimens from Danian strata of New Jersey and Thanetian deposits of Maryland and Virginia belong to individuals that inhabited coastal marine environments along the western margin of the Atlantic Ocean.

CONCLUSIONS

A total of 94 holocephalan tooth plates from Paleocene strata of Alabama, Arkansas, Illinois, Maryland, Mississippi, New Jersey, South Carolina, Texas, and Virginia were examined, and four genera are identified. The sample includes the first North American records of *Callorhinchus*, and a palatine from the Danian of Mississippi represents a new species, *C. phillipsi*. Ten additional *Callorhinchus* specimens were identified from Thanetian strata of Maryland and Virginia, and these also represent a new species, *C. alfordi*.

Two species of *Ischyodus* are recognized, *I. dolloi* and *I. williamsae*, and while vomerine and palatine tooth plates of the latter species were described for the first time, they were found to be of limited taxonomic value. Mandibular tooth plates of the two species may be differentiated based on morphology of the middle tritor and the location of the inner tritor with respect to the middle tritor. *Ischyodus dolloi* occurs in Danian and Thanetian strata and is widely distributed within the eastern United States, occurring in Alabama, Maryland, New Jersey, and Texas, with additional records from North Dakota ([Cvancara and Hoganson 1993](#)) and possibly California ([Applegate 1975](#), [Ward and Grande 1991](#)). The identification of *I. dolloi* in Alabama and Texas represents the first records of this species within the Paleocene Mississippi Embayment. Contrary to the original report ([Case 1991](#)), the type material of *I. williamsae* is not from the Thanetian Aquia Formation, but from the Danian Brightseat Formation, and in fact all other specimens that we identified as *I. williamsae* occurred in Danian strata. The geographic distribution of this species now includes Alabama ([Denton et al. 1997](#)), Arkansas, Illinois ([Cope et al. 2005](#)), Maryland ([Case 1991](#)), and Mississippi.

Edaphodon mirificus is known to have survived the K/Pg extinction ([Stahl and Parris 2004](#)), and additional Danian records now include specimens from the Clayton Formation of Mississippi. The genus also occurs in the Thanetian of Virginia. The second North American record of *Elasmodus hunteri* is represented by two partial mandibular tooth plates from Maryland, with the only other reported occurrence being from the Thanetian of North Dakota ([Cvancara and Hoganson 1993](#)). A Danian specimen from the Hornerstown Formation of New Jersey, similar to *E. kempi*, is the oldest Paleogene representative of *Elasmodus* in North America.

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