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LATE MISSISSIPPIAN (CHESTERIAN) CHONDRICHTHYANS FROM THE MONTEAGLE LIMESTONE OF NORTHERN ALABAMA

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ABSTRACT

Twelve chondrichthyan genera (6 elasmobranchs and 6 holocephalians) were recovered from the Monteagle Limestone (Upper Mississippian, Chesterian) near Woodville, Jackson County, Alabama. Taxa include "*Cladodus*" *newmani*?, "*C.*" *magnificus*?, *Orodus micropterygius*, *Chomatodus* sp., *Fissodus bifidus*, *Lisgodus* cf. *L. serratus*, *Petalodus acuminatus*, *Helodus crenulatis*, *Cochliodus leidyi*, cf. *C. vanhorni*, *Deltodus* sp., cf. *Psephodus reticularis*, *Sandalodus minor*, *Sandalodus* sp., and *Synthetodus* cf. *S. trisulcatus*. The chondrichthyan fossils were found in rocks representing a shallow marine, pelmatozoan-rich carbonate facies, and they are associated with a diverse assemblage of invertebrates. Many of the Monteagle Limestone taxa are known from other Lower Carboniferous localities throughout the mid-continental United States, but the assemblage shows particularly strong similarities to those of Illinois and Indiana.

INTRODUCTION

In the fall of 2000 one of us (DJC) participated in a Clemson University-led field trip to examine an outcropping of the Monteagle Limestone along US 72 near Woodville, Jackson County, Alabama (Figure 1). Rock exposures along US 72 have been terraced by the ALDOT, and prospecting of one of these surfaces yielded several holocephalian and elasmobranch teeth. The outcrop was revisited in the fall of 2002 and 2003, and additional samples were collected. Associated invertebrate fossils include solitary rugose corals, brachiopods, bryozoans (especially *Archimedes*), and a variety of echinoderms (blastoids and crinoids).

The Mississippian rocks of northern Alabama (Figure 2) are well known for the abundance and diversity of echinoderm fossils, with 39 species of blastoids and crinoids having been reported in the literature (Bassler and Moodey, 1943; Horowitz and Waters, 1972; Maples and Waters, 1995). However, published records of chondrichthyan fossils from these rocks are scarce (Tuomey, 1858), and knowledge of occurrences seems limited to local collectors. The purpose of this paper is to provide the first detailed description of chondrichthyan fossils from the Monteagle Limestone and to speculate on the paleoecological implications of these remains.

METHODS

The fossiliferous rock is hard crinoidal limestone (Figure 3). At the outcrop, specimens exposed in situ were collected with hammer and chisel. Fossils were generally removed still embedded in matrix, but some specimens were extracted in several pieces. In the laboratory some specimens were freed completely from matrix with an air scribe. Fractured specimens were left embedded in matrix, and weak acetic acid was employed to expose additional details. Cyanoacrylate was used both to repair broken fossils and consolidate the fractured teeth.

We utilized the term "tooth base" when referring to the portion of a tooth that was attached to the jaw via connective tissue. This terminology follows Zangerl (1981), who pointed out that chondrichthyan teeth are not "rooted" in alveoli as in Mammalia. Refer to Table 1 for a listing of chondrichthyan taxa discussed in this report.

SYSTEMATIC PALEONTOLOGY

Subclass Elasmobranchii Bonaparte, 1838
Order Cladoselachida Dean, 1909
Family Cladoselachidae Dean, 1894
Genus "*Cladodus*" Agassiz, 1843
"*Cladodus*" *newmani*? Tuomey, 1858
Figure 4, A-C

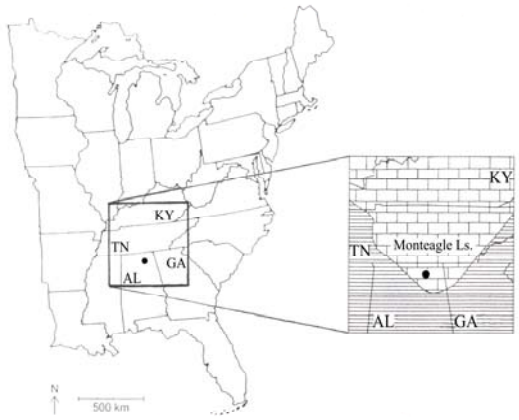

FIGURE 1--Map of the eastern United States showing the location of the outcrop discussed in this report (dark circle). Inset shows extent of the carbonate platform during the time of deposition of the Monteagle Limestone. The striped area represents contemporaneous deposition of the Floyd Shale. Modified from Driese et al. (1994).

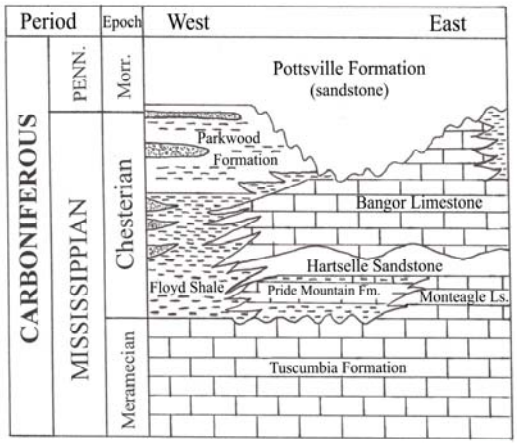

FIGURE 2--Interrelationships of Carboniferous rocks in northern Alabama. Modified from Kopaska-Merkel and Haywick (2001).

Material Examined--BCGM 1946, BCGM 4862, BCGM 4863, BCGM 6288, BCGM 6289, incomplete teeth

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 1946, BCGM 4862, BCGM 4863, BCGM 6288, and BCGM 6289 are incomplete teeth that are rather small and mesiodistally elongated. As preserved, the widths of the specimens measure 12 mm, 8.5 mm, 14.5 mm, 10.5 mm, and 11.5 mm respectively. The crown consists of a tall, narrow central cusp that curves lingually and, depending on tooth position, may be distally inclined (i.e., lateral teeth). The cross section of the central cusp may be circular or elliptical, due to the highly convex lingual face and moderately to highly convex labial face. The cutting edge is smooth and continuous along the central cusp, and appears to end just before the lateral cusplets. There are two pairs of lateral cusplets, the first pair being situated slightly in front of the central cusp. The second pair of cusplets is larger and highly divergent from the first pair. Crown ornamentation varies but generally consists of longitudinal ridges that bifurcate basally. The ridges extend to the apex of the lateral cusplets. There is a triangular medial labial sulcus located at the base of the central cusp. The tooth base is very thin apico-basally, forms a shelf-like projection extending lingually past the crown, and the basal attachment surface is weakly concave. There is a pair of dorsal protuberances near the lingual margin of the tooth base (one on each side of the central cusp), as well as a pair of basal protuberances located at the labial edge.

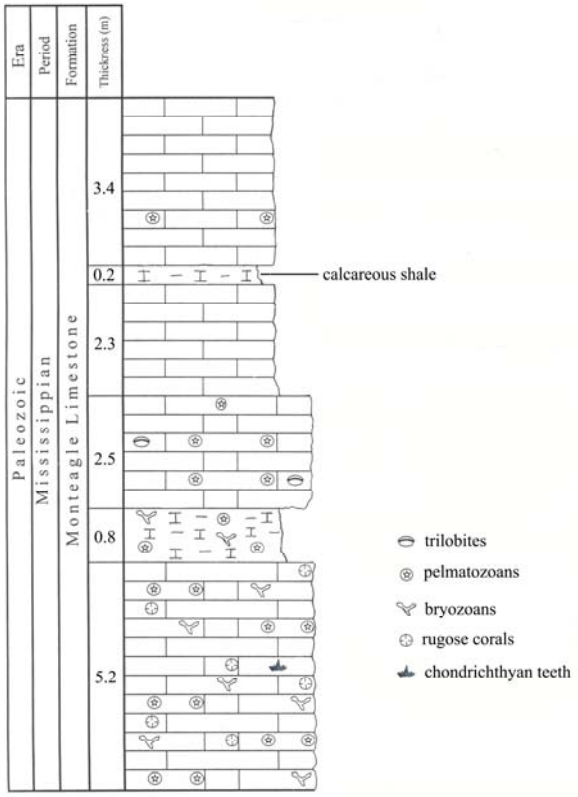

FIGURE 3--Generalized stratigraphic section of the Monteagle Limestone exposed along US 72 near Woodville, Jackson County, Alabama.

Discussion--The material described above is somewhat similar to a specimen of *Cladodus newmani* that was first described by Tuomey (1858). His original illustration (p. 39, fig. B) is of a tooth with

virtually no trace of lateral cusplets, but the specimen may have been badly abraded; Newberry (1889; p. 216) suggested that the tooth was too poorly preserved for specific identification. The original specimen is presumably of Mississippian age because it was collected from the Huntsville area, but unfortunately the current whereabouts of the tooth are unknown (Rindsberg, personal communication 2003). The Monteagle Limestone specimens are also similar to a tooth assigned to *Cladodus* that was reported by Miller (1981) from Upper Mississippian rocks of Utah.

According to Ginter (2002), Paleozoic shark teeth having a basal labial sulcus and dorsal/ventral "root" protuberances have been assigned to a number of taxa, including *Cladoselache*, *Heslerodus*, *Symmorium*, and *Cladodus*. However, *Cladodus* may not be a valid taxon because various species previously ascribed to the genus have been reassigned to a variety of Paleozoic sharks (Zangerl, 1981). It is possible that "*C.*" *newmani* represents a species of *Symmorium* and could be referred to as *S. newmani*, but it is equally plausible that the remains belonged to some other form of cladodont shark such as *Cladoselache*.

TABLE 1--Chondrichthyan taxa recovered from the Monteagle Limestone exposed along US 72 near Woodville, Jackson County, Alabama.

Taxon	# of specimens
"*Cladodus*" *newmani*?	5
"*Cladodus*" *magnificus*?	1
Orodus micropterygius	2
Chomatodus sp.	4
Fissodus bifidus	1
Lisgodus cf. *L serratus*	1
Petalodus acuminatus	4
Helodus crenulatis	4
Cochliodus leidyi	2
cf. *C. vanhorni*	1
Deltodus sp.	2
cf. *Psephodus reticularis*	1
Sandalodus minor	1
Sandalodus sp.	3
Synthetodus cf. *S. trisulcatus*	1
Total = 14 (not including *Sandalodus* sp.)	Total = 33

"*Cladodus*" *magnificus*? Tuomey, 1858
Figure 4, D

Material Examined--BCGM 4864, large incomplete tooth.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 4864 is a very large cladodont shark tooth measuring 37 mm wide x 31.5 mm high. The central cusp is tall and narrow, with a highly convex lingual face. The apex is pointed, and smooth cutting edges extend to the base of the cusp. The cusp was broken and slightly displaced labially sometime after deposition (most obvious in lingual and lateral views), however its original condition appears to have been rather vertical. There is only a very shallow labial basal sulcus. Ornamentation consists of fine longitudinal ridges extending from the crown foot nearly to the apex. Mesial and distal shoulders are long and nearly perpendicular with the central cusp. A diverging cusplet is located at the outer end of each shoulder. Between this cusplet and the central cusp, there are 13 to17 tiny peg-like cusplets. All cusplets bear longitudinal ridges. Overall the basal attachment surface is concave, and there is a pair of indistinct protuberances on the labial edge of the tooth base. The lingual projection of the tooth base is missing, but it appears that this portion was thickened.

Discussion--BCGM 4864 is similar in size and overall morphology to *Cladodus magnificus* reported by Tuomey (1858; collected from the same area as his *Cladodus newmani*). Although his original account lacks an informative description and the illustrations are rather poor (see figs. C, Ca, Cb, p. 39-40), it appears that the tooth also had multiple pairs of lateral cusplets (fig. C). The lingual view (fig. Ca) does not show indications of lateral cusplets, but the profile view (fig. Cb) shows that the crown was very tall and erect as in BCGM 4864. Newberry (1889; p. 216) mentioned observing specimens he believed referable to *C. magnificus* in Lower Carboniferous rocks of Illinois and Indiana. Newberry and Worthen (1866; p. 29-30) commented on the poor quality of Tuomey's presentation but questionably referred a large cladodont tooth to *C. magnificus*. However, although the specimen they illustrated (plate 2, fig. 6) is of the same dimensions, it apparently has fewer lateral cusplets, larger longitudinal ridges, and the transverse cross section of the central cusp is circular. BCGM 4864 very closely resembles a specimen of *C. grandis* illustrated by Newberry and Worthen (1866; plate 2, fig. 15), and those authors noted the similarity between *C. magnificus* and *C. grandis*. Without the aid of the original specimen described by Tuomey (1858), it is impossible to know for certain if Newberry and Worthen (1866) were correct in their identification of *C. magnificus*, and perhaps the species is conspecific with *C. grandis*. If so, *C. magnificus* has priority over *C. grandis*.

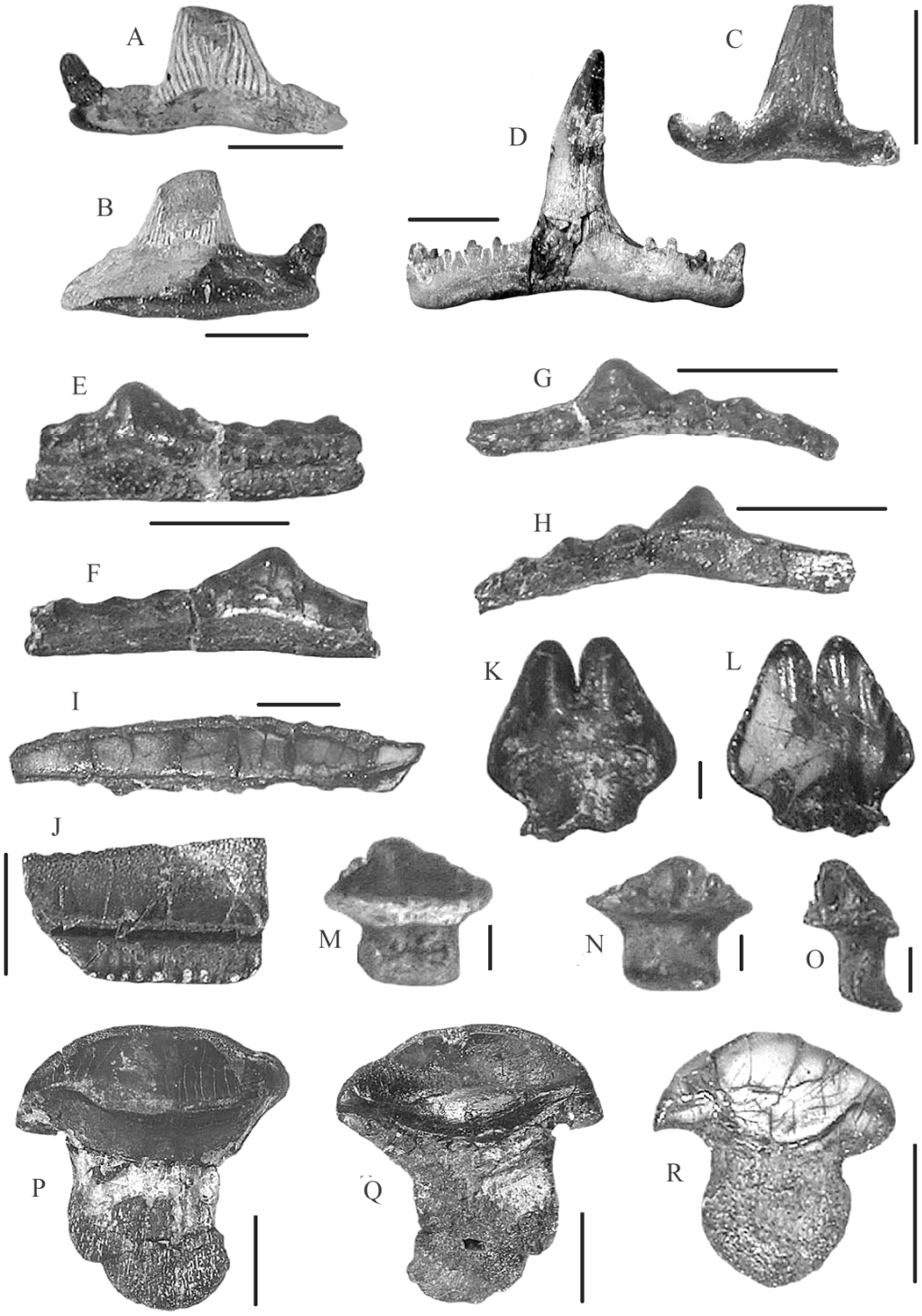

FIGURE 4--Monteagle Limestone elasmobranchs: A-C, "*Cladodus*" *newmani*?, A, labial view, B, lingual view of BCGM 1946; C, labial view of BCGM 4862. D, "*Cladodus*" *magnificus*? labial view of BCGM 4864. E-H, *Orodus micropterygius*, E, labial view, F, lingual view of BCGM 4868; G, labial view, H, lingual view of BCGM 6287. I-J, *Chomatodus* sp., I, labial view of BCGM 4866; J, lingual view of BCGM 6285. K-L, *Fissodus bifidus*, K, labial view, L, lingual view of BCGM 6290. M-O, *Lisgodus* cf. *L. serratus*, M, labial view, N, lingual view, O, distal view of BCGM 4867. P-R, *Petalodus acuminatus*, P, labial view, Q, lingual view of BCGM 4865; R, labial view of BCGM 1943. Scale bars = 1mm in K-O; 5mm in A-C, E-J, R; 10mm in D, P-Q.

Order Orodontida Zangerl, 1981
Family Orodontidae DeKoninck, 1878
Genus *Orodus* Agassiz, 1838
Orodus micropterygius Zangerl, 1981
Figure 4, E-H

Material Examined--BCGM 4868, incomplete tooth; BCGM 6287, complete tooth.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--Both specimens are mesiodistally elongated and have a very low crown. BCGM 4868 is missing part of the mesial end, and as preserved measures 11 mm wide x 4 mm in height. BCGM 6287 measures 12 mm wide x 3 mm in height. The crown possesses a low, conical cusp that is directed mesially. Teeth are asymmetrical, with the distal side being longer than the mesial side. Four very low, bulbous cusplets are located on the distal side of the central cusp, whereas there are only two on the mesial side (two are preserved on BCGM 4868). There is no cutting edge. The labial face of the crown overhangs the tooth base and the lingual crown foot is very convex, with inconspicuous nodes seen on BCGM 4868. The tooth base is very low and as wide as the crown, with a weakly convex basal attachment surface. In labial/lingual view BCGM 6287 is arched.

Discussion--Teeth of *Orodus* consist primarily of vascularized trabecular dentine, with the outer surface of the crown formed by hypermineralized tissue (Zangerl et al., 1993, p. 7). Trabecular dentine is visible in both BCGM 4868 and BCGM 6287, and pulp canals are also exposed on parts of the crown of BCGM 4868. The teeth we examined differ from other species of *Orodus*, such as *O. greggi* and *O. ramosus*, in their small size, asymmetrical crown, and lack of cutting edges and crown ornamentation (Zangerl, 1981). *Orodus micropterygius* was a relatively small-bodied shark (measuring just over one meter in length; see Zangerl, 1981) having teeth better designed for crunching rather than clutching.

Order Petalodontida Zangerl, 1981
Family Petalodontidae Newberry and Worthen, 1866
Genus *Chomatodus* Agassiz, 1838
Chomatodus sp.
Figure 4, I-J

Material Examined--BCGM 4866, tooth crown; BCGM 6284, BCGM 6285, BCGM 6286, incomplete teeth.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 4866 is the most complete specimen, consisting of a mesiodistally elongated, rather low crown. The specimen measures 23 mm wide x 4 mm in height. The crown is labiolingually thin and it is sinuous in occlusal view. The labial face may be flat or weakly convex, whereas the lingual face is flat to weakly concave. The labial and lingual crown foot of each specimen is damaged, but a small section of BCGM 4866 shows several imbricated basal ridges. A distinct transverse ridge is also located at the crown foot of BCGM 6285. The tooth base is labiolingually thin and very low, not as wide as the crown. The labial face of the tooth base of BCGM 6285 is crenulated.

Discussion--In our opinion, the genus *Chomatodus* is in need of systematic revision, as we find it unlikely that all of the 35 species noted by Zangerl (1981) are valid. For example, BCGM 4866 resembles *C. cultellus*, whereas the cross section of BCGM 6285 resembles that of *C. multiplicatus*, and BCGM 6286 is close to *C. loriformis* (see Newberry and Worthen, 1866). However, we believe these specimens represent heterodonty within a single taxon, but we hesitate to make a specific distinction due to the incompleteness of our material.

In their study of tooth histology in Petalodontida, Zangerl et al. (1993) noted that teeth of *Chomatodus* consisted primarily of orthodentine and trabecular dentine that was covered by a rather thin outer layer of vitrodentine. In some species, the orthodentine forms a covering over the trabecular dentine on the labial and lingual sides of the teeth, whereas other species have an orthodentine wedge that penetrates downward into the trabecular dentine. In the specimens we examined, the former arrangement was observed, and vascular canals within the orthodentine are visible where the vitrodentine is missing.

Genus *Fissodus* St. John and Worthen, 1875
Fissodus bifidus St. John and Worthen, 1875
Figure 4, K-L

Material Examined--BCGM 6290, tooth lacking base.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 6290 consists of a complete crown measuring 6 mm wide x 6 mm high. The crown has a somewhat diamond-shaped outline in labial/lingual view, and the apex is bifurcated, forming two distinct rounded cusps. Cutting edges are continuous and serrated. The labial face of the crown is convex with a shallow medial basal sulcus, whereas the lingual face is concave but thickened medially to form the tooth base. The crown/tooth base interface indicates that the tooth was sigmoidal in lateral view.

Discussion--Teeth of *Fissodus* consist of highly vascularized trabecular dentine and, in the specimens examined by Zangerl et al. (1993), orthodentine only on the lingual side. This condition could have resulted if, rather than being shed, old teeth were retained to form a supporting structure for new functioning teeth (Zangerl, 1981, p. 16 and 97; Zangerl et al., 1993, p. 34). This interpretation is supported by BCGM 6290, where the lower half of the labial face is heavily worn. Vascularized trabecular dentine is also exposed where the base of the crown is broken. Lund (1989) noted that *Fissodus* is common in rocks of Mississippian age, and that specimens with a bifid crown may represent lower anterior teeth.

Genus *Lisgodus* St. John and Worthen, 1875
Lisgodus cf. *L. serratus* St. John and Worthen, 1875
Figure 4, M-O

Material Examined--BCGM 4867, isolated lateral tooth.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 4876 is a complete lateral tooth measuring 4.5 mm wide x 4 mm in total height (crown alone measures 2 mm in height). The crown is low, broadly triangular, and inclined lingually. The lingual face is small, vertical, and weakly convex. The labial face is longer, nearly flat, and sloping. Although much of the labial crown foot is broken, portions of four imbricated transverse ridges are preserved at the anterior and distal ends. There are two distinct imbricated ridges at the lingual crown foot. The apex is blunt and offset distally, making the crown asymmetrical in labial/lingual view. The distal cutting edge is short and bears two distinct cusplets, whereas the mesial edge (though abraded) is longer and bears at least one cusplet. The tooth base is rather short and constricted below the crown foot, flaring to form a larger, nearly flat basal attachment surface that is oblique to the vertical axis of the tooth. The surface of the tooth base is perforated by several large foramina.

Discussion-- BCGM 4876 is nearly identical to a specimen of *Lisgodus* sp. illustrated by Zangerl (1981; fig. 110) and later Hansen (1985; plate 1, fig. 1-3), and both of these specimens compare favorably to *L. serratus* illustrated by St. John and Worthen (1875; plate 10a, fig. 17-19). *Lisgodus* is usually placed within Petalodontiformes (Zangerl, 1981; Hansen, 1985; Zangerl et al., 1993), but Lund (1989) has argued, on the basis of tooth morphology and body form, that the taxon should be removed from this family.

Zangerl et al. (1993) reported that the upper half to two-thirds of the crown of a specimen of *L. selluliformis* consists of orthodentine, whereas the lower part of the crown and tooth base consist of trabecular dentine. In BCGM 4876, the crown is worn so that pulp canals are exposed.

Genus *Petalodus* Owen, 1845
Petalodus acuminatus Agassiz, 1838
Figure 4, P-R

Material Examined--BCGM 1941, lateral tooth, BCGM 1942 and BCGM 1943, anterior teeth; BCGM 4865, lateral tooth.

Occurrence--BCGM 1942, BCGM 1943, and BCGM 4865, Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama; BCGM 1941, Mississippian Hartselle Sandstone (Chesterian) exposed along AL 157 near Wolf Springs, Lawrence County, Alabama.

Description--BCGM 1941 is a large lateral tooth embedded in matrix with the lingual side exposed. The crown is mesiodistally wide and rather high, measuring 36 mm x 17 mm respectively. Total tooth height measures 32 mm. The lingual face is weakly convex and, although damaged, exhibits several imbricated ridges at the base of the crown. There is a transverse wear facet located just above the ridges. The cutting edge is continuous along the entire crown, and it is irregular in lingual view. The tooth base is massive, linguiform, perforated by several large foramina.

BCGM 1942 and BCGM 1943 (Figure 4.18) are embedded in matrix with their labial side exposed. The crown is mesiodistally wide and moderately high (each specimen measures 8 mm wide x 4 mm high; total tooth height measuring 9 mm), with a crescent-shaped cutting edge. Each tooth appears to be symmetrical, indicating they were medial teeth. The labial face is weakly convex with a distinct sigmoidal ridge located at the base of the crown. The tooth base is linguiform and not as wide as the crown. It is constricted below the crown but becomes globular basally.

BCGM 4865 (Figure 4.16, 4.17) appears to be a lateral tooth. It is free of matrix but damaged due to Recent weathering. The crown measures 30 mm wide x 15 mm high, with total tooth height measuring 32.5 mm. The labial face is very convex with a conspicuous medial transverse wear facet. The lingual face is very concave, and an inconspicuous sigmoidal ridge is located near the crown foot. There is also a lateral wear facet near the cutting edge. The cutting edge is convex and sinuous in occlusal and labial/lingual views. There is a distinct labial wear facet running the length of the cutting edge. The tooth base is linguiform.

Discussion--The tooth crown of *Petalodus* consists of dense, vascularized trabecular dentine that is covered on the labial and lingual sides by a layer of

orthodentine, in turn covered by a very thin layer of vitrodentine (Zangerl et al., 1993, p. 23). As in some species of *Chomatodus*, an orthodentine wedge penetrates downward into the trabecular dentine of *Petalodus* teeth, which maintained a hard, sharp cutting edge throughout the functional life of the tooth (Zangerl et al., 1993, p. 21).

Tooth succession in *Petalodus* may have been similar to the neoselachian pattern, with labiolingual replacement of teeth (Zangerl, 1981). Lingual wear facets are preserved on BCGM 1941 and BCGM 4865, and a labial wear facet is located along the apex of the labial face of BCGM 4865. The wear patterns of BCGM 4865 could have resulted if, as illustrated by Zangerl et al. (1993, p. 18, fig. 14), an opposing tooth occluded both before (labial wear facet) and after (lingual facets) the tooth was fully functional.

Subclass Subterbranchialia Zangerl, 1979
Superorder Holocephali Bonaparte, 1838
Order Helodontiformes Patterson, 1965
Family Helodontidae Patterson, 1965
Genus *Helodus* Agassiz, 1838
Helodus crenulatis Newberry and Worthen 1866
Figure 5, A-E

Material Examined--BCGM 4869, BCGM 6291, BCGM 6680, BCGM 6681, isolated teeth.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--All of the specimens are similar in size - BCGM 4869 measures 10 mm wide x 4 mm high, BCGM 6291 is 11 mm x 6 mm, BCGM 6680 is 14 mm x 5 mm, and BCGM 6681 is 10 mm x 6 mm. BCGM 4869 and BCGM 6291 have been abraded post-mortem, whereas BCGM 6680 and BCGM 6681 are nearly pristine. The occlusal surfaces of BCGM 4869, BCGM 6291, and BCGM 6680 also show signs of *in vivo* usage.

The tooth plates are bar-shaped in general form, with long labial and lingual margins marked at the base by their contact with the lingual and labial sides of the adjacent plates. On the oral surface, the plates show punctae that are well separated from each other rather than crowded together. The central part of the crown is raised into a high, flat-topped boss that slopes slightly labially and mesially (except in BCGM 6680, which is rather low and convex along nearly its entire length), and juts beyond the base of the plate. The labial edge of BCGM 4869 is very slightly bifurcated.

In aboral view, the base of the plate of BCGM 6291, BCGM 6680, and BCGM 6681 are concave mesiodistally. Whereas BCGM 6291 exhibits a surface that is equally divided between the contact area for the adjacent tooth and the base of the plate (which rested on the jaw), the base of the plate of BCGM 6680 and BCGM 6681 is twice as wide. In BCGM 4869, the two areas are less distinct from one another, and both show the canals of the trabecular dentine forming the central part of the tooth plate beneath the hypermineralized crown. The base that rested on the jaw in BCGM 6291, BCGM 6680, and BCGM 6681 has an even black surface that may cover the lamellar tissue underlying the trabecular dentine.

The base of BCGM 4869, BCGM 6291, and BCGM 6681 extends the full length of the plate and is deeper than the mesial and distal ends of the crown (emphasizing the bar-shape of the tooth plate). Whereas the bases of these specimens are recessed under the edges of the crown (especially evident in labial view), the base of BCGM 6680 extends lingually past the crown and its dorsal surface is crenulated. The lingual face of the base of BCGM 6681 exhibits a series of short longitudinal ridges, each directly above a large foramen (Ridges are not preserved on BCGM 6291, but foramina are present).

Discussion--BCGM 4869, BCGM 6291, and BCGM 6681 differ from other species of *Helodus*, like *H. appendiculatus*, *H. simplex*, and *H. turgidus*, in that the central boss is more sharply separated from the flanks of the plate (Stahl, 1999). Although the Monteagle Limestone specimens are similar to material referred to *H. didymus* and *H. laevissimus* (see Stahl, fig. 57, D-E), these species lack the slight bifurcation of the medial boss seen in *H. crenulatis*.

Order Cochliodontiformes Obruchev, 1953
Family Psephodontidae Zangerl, 1981
Genus *Psephodus* Morris and Roberts, 1862
?*Psephodus reticularis* St. John and Worthen, 1883
Figure 5, F

Material Examined--BCGM 6182, incomplete plate

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--In oral view, the crown is quadrilateral, measuring 4.5 mm wide and 4 mm in mesiodistal length. Distally, the thick base projects behind the crown. The surface of the crown is covered with minute interconnecting striae. The mesial margin is sinuous; a central projection is flanked by a similar prominence to one side and a somewhat lower one on the other.

On the aboral side, the sinuous mesial margin of the crown overhangs the recessed base. The underside of the base is quadrilateral and deeply concave mesiodistally. The surface in the concavity is banded by a series of parallel ridges oriented mesiodistally. Viewed lingually, the base lacks a finished surface but

may bear marks of contacts with an overlapping adjacent tooth plate.

Discussion--BCGM 6182 resembles a specimen collected from the Lower Carboniferous Burlington Limestone of Iowa and referred to ?*Psephodus reticularis* by St. John and Worthen (1883). The uncertainty of the identification stems from the lack of crenulations on the margins of the tooth plates that are characteristic of other species of *Psephodus* (see Stahl, 1999, p. 61-65).

Family Cochliodontidae Owen, 1867
Genus *Cochliodus* Agassiz, 1838
Cochliodus leidyi St. John and Worthen, 1883
Figure 5, G-H

Material Examined--BCGM 1944, tooth plate; BCGM 6295, tooth plate.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 1944 is a lower left posterior tooth plate embedded in matrix (exposed in oral view). This specimen measures 2.2 cm from the mesial margin to the distal lingual angle. BCGM 6295, a lower right posterior tooth plate, measures only 1.7 cm in the same dimension. The breadth of the plates along the raised ridge from the lingual to the labial edge is 16 mm in BCGM 1944 and 12 mm in BCGM 6295. The oral surface of the plates is coarsely punctate.

The oral surface of BCGM 1944 is distinguished by a prominent teardrop-shaped boss that arches diagonally from the lingual to the labial margin of the plate. The broad end projects from the lingual margin and the narrow end, directed mesially, overlaps the labial edge. The central boss is separated from the mesial margin by a trough. The mesial part of the plate rises slightly from the trough and then falls steeply at the margin, making a flat or slightly convex surface for contact with the adjacent tooth plate. Distally, the boss descends sharply to the flatter part of the oral surface. From the boss, the distal part of the plate narrows but then flares slightly at the lingual angle. The distal surface of the plate, similar to the mesial, is almost flat. However, it is not parallel to the mesial edge because the lingual side of the tooth plate is longer than the labial, causing the distal edge to slant mesially.

The aboral surface of BCGM 6295 is generally concave. There is a deep trough arcing under the mesial, labial, and distal margins, outlining the central surface that lies beneath the broad end of the oral boss. The floor of this trough is not smooth but is marked by a series of large, circular, shallow depressions (filled in this specimen by matrix). Similarly, the central area under the boss outlined by the trough, though raised, shows two large depressions, one lingual to the other (both filled with matrix).

Cochliodus cf. *C. vanhorni* St. John and Worthen, 1883
Figure 5, I.

Material Examined--BCGM 6181, isolated plate

Occurrence—Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--The specimen is partially embedded in matrix on the aboral side. The exposed crown is marked by large punctae that are widely spaced. The crown lacks the mesiolabial corner and, more distally, the original surface of the labial edge. From the intact part of the mesial margin to the distal border, the plate measures 6 mm. In oral view, the lingual and labial margins are straight, parallel, and joined by a short distal border, giving the crown a U-shaped appearance. The occlusal surface of the crown shows two arched prominences, each rising from the lingual margin and curving mesially to the labial side of the plate. The distal one is the broader and more complete, whereas the mesial one is slightly narrower and truncated by the boss of the corner of the plate toward which it was directed. These raised regions are separated by a deep trough, and each descends on the opposite side to the depressed border adjacent to it. In this view, the distance from the lingual to the labial edge is 4 mm.

In aboral view, the labiolingual thinning of the plate along the distal edge is visible. The underside of the crown shows the bases of the denteons that rise in parallel through the crown and open as punctae on the surface. The thin basal layers that underlie this tissue have been lost.

Discussion--BCGM 6181 has the curled appearance of tooth plates referred to "*Streblodus*", which is a form that has been discovered in the intact palate of *Cochliodus*. Our specimen closely matches a tooth plate collected from the Lower Carboniferous St. Louis Limestone of Illinois that St. John and Worthen (1883) referred to as a maxillary tooth of *C. vanhorni*. In *C. vanhorni*, the groove that divides the central part of the plate just to one side of the center is deeper than it appears to be in BCGM 6181, although this may be an artifact of wear.

Genus *Deltodus* Morris and Roberts, 1862
Deltodus sp.
Figure 5, J-K

Material Examined--BCGM 6292 and BCGM 6294, incomplete tooth plates

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

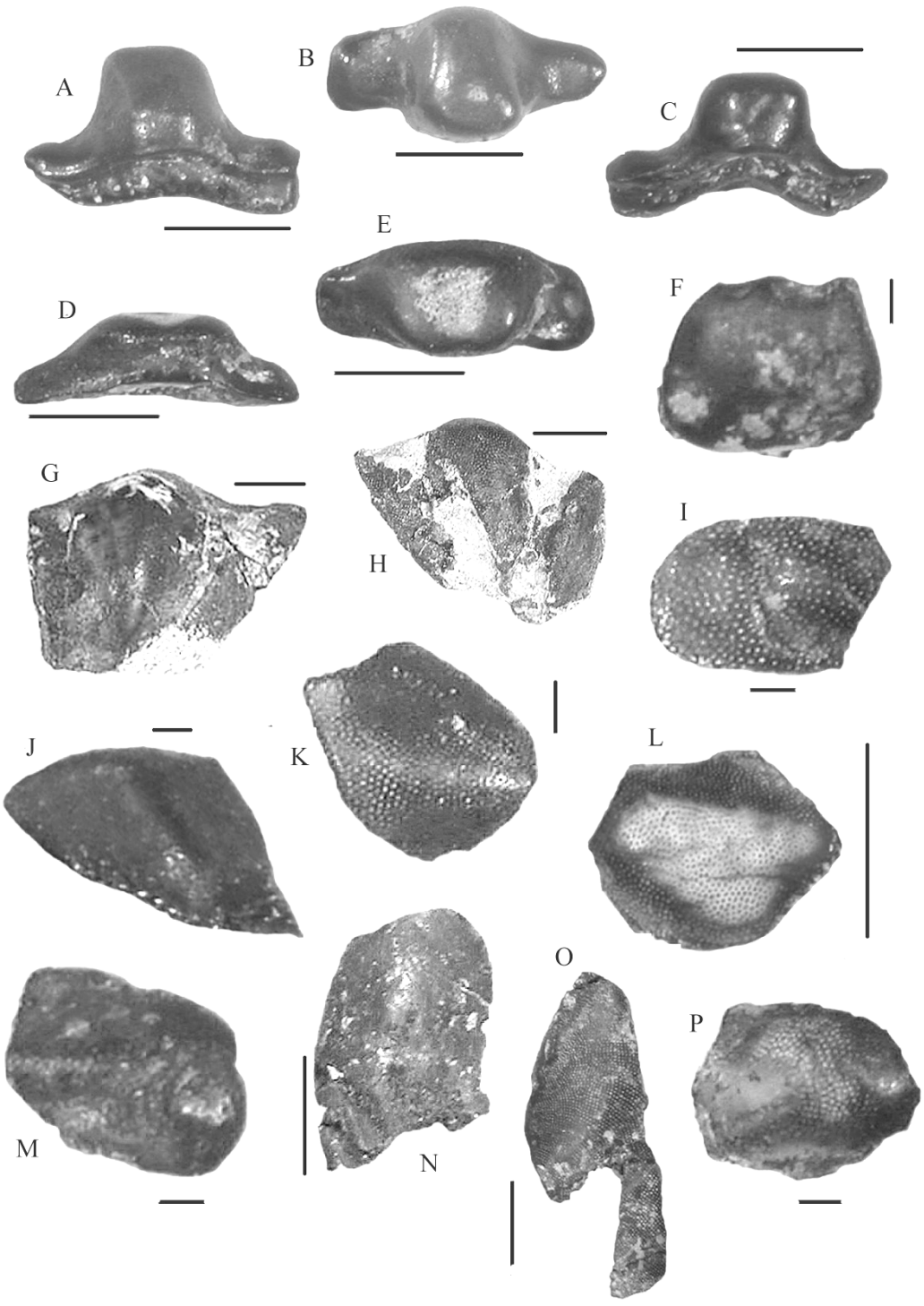

FIGURE 5--Monteagle Limestone holocephalians: *A-E*, *Helodus crenulatis*, A, lingual view, B, occlusal view, C, labial view of BCGM 6291; D, labial view, E, occlusal view of BCGM 4869. F, ?*Psephodus reticularis*, occlusal view of BCGM 6182. G-H, *Cochliodus leidyi*, G, occlusal view of BCGM 1944; H, occlusal view of BCGM 6295. I, cf. *C. vanhorni*, occlusal view of BCGM 6181. J-K, *Deltodus* sp., J, occlusal view of BCGM 6292; K, occlusal view of BCGM 6294. L, *Sandalodus minor*, occlusal view of BCGM 1945. M-O, *Sandalodus* sp., M, occlusal view of BCGM 4871; N, occlusal view of BCGM 6180; O, occlusal view of BCGM 6293. P, *Synthetodus* cf. *S. trisulcatus*, occlusal view of BCGM 4870. Scale bars = 1mm in F, I-K, M, P; 5mm in A-E, G-H, L, N-O.

Description--BCGM 6292 is approximately two-thirds complete, and the preserved length of the specimen measures 7 mm. It is exposed both orally and aborally but held to matrix along the labial edge. The aboral surface is concave and smooth, marked with irregularly distributed punctae. There is a broad, shallow longitudinal channel that suggests an area of attachment to the jaw. Distally, the labial edge that remains visible flares as if it were the base of a thin *Deltodus*-like labiodistal wing; however, this area is not exposed in oral view. In that view, the fragment is sub-triangular with a sharp but smoothly rounded mesial tip at the apex. The crown rises from the distal end in low rounded steps and remains elevated along the straight lingual margin. It descends gradually toward the labial and mesial edges of the plate. A depression due to wear appears in the center of the crown, revealing widely spaced punctae.

Only the crown of BCGM 6294 is exposed in matrix. It appears sub-triangular, however the mesial end of the plate is broken off. The specimen lacks the alate projection characteristic of many *Deltodus* species, and is instead spatulate at the wide distal end. From that margin to the mesial break the plate measures 6 mm, and at its widest it is 5 mm. The crown is covered with large, well-separated punctae that are aligned in distinct, nearly straight rows. There is only a small depressed area at the mesiodistal corner of the crown, and the inner (or symphyseal) and distal margins rise sharply to form a high platform as an occlusal surface. This surface is not completely flat but slightly undulatory, with broad, shallowly depressed areas producing barely perceptible ridges between them running diagonally across the tooth plate.

Discussion--Teeth of *Deltodus* are highly variable between species and within the same dentition. However, BCGM 6292 and BCGM 6294 fall within the morphological range attributed to the genus (see Stahl, 1999, p. 70-74). Both specimens are rather small, and BCGM 6294 may represent a posterior tooth plate. As in *D. mercurei*, the crown of BCGM 6294 is smooth surfaced instead of being marked with undulations parallel to the lingual margin as seen in many *Deltodus* tooth plates (Branson, 1916; Stahl, 1999).

Genus *Sandalodus* Newberry and Worthen 1866
Sandalodus minor Davis 1884
Figure 5, L

Material Examined--BCGM 1945, isolated plate.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description and Discussion--The tooth plate is partially exposed in matrix in oral view. The mesial corner of the plate is missing, as is a small part of the thin distal edge that flared as a "wing" on the labial side. What remains visible is the broad triangular mass of the crown that is high and convex, with a coarsely punctate surface. A wear surface whitens the elevated area of the crown almost entirely, and beyond it the sides of the crown descend sharply to the thinner margins of the plate. The plate measures 4 mm from the lingual margin to the broken mesial edge, and the broadest exposed area of the tooth is 7 mm wide.

Davis (1884) reported *Sandalodus minor* from the Lower Carboniferous of England, and BCGM 1945 very closely resembles a specimen collected from the Upper Devonian of Colorado and referred to *S. minor* by Bryant and Johnson (1936).

Sandalodus sp.
Figure 5, M-O

Material Examined--BCGM 4871, tooth plate; BCGM 6180, incomplete plate; BCGM 6293, isolated plate.

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--BCGM 4781 (Figure 5, M) is complete except for the mesial end. The depth of the broken surface suggests that a quarter to a third of the anterior end of the plate is missing. From the lingual margin to the broken edge the length is 5 mm. At its widest, near the lingual margin, the plate measures 4 mm. In oral view, the lingual margin appears bulbous because the crown rises sharply from it. Although the margin is slightly bifurcated, giving it a sinuous outline, the bifurcation disappears as the surface of the crown rises to form a crest that slopes labially to the broken mesial edge. As it courses mesially, the crest is accentuated by slight concavities of the crown on either side of it as the surface descends to the flanking margins of the plate.

In aboral view, the distal region appears flat and bears the coarse punctae that cover the crown. More mesially the plate is concave. It is partly filled by matrix, but an exposed area is inconspicuously marked by linear lamellar tissue of the base.

BCGM 6180 (5, N) is embedded in matrix and exposed in oral view. The specimen is missing a large part of the distal end, and from the broken edge to the mesial tip its length measures 14 mm. The mesial tip is gently rounded and the surface of the crown, which is convex from the labial margin to the inner side, slopes downward to it. Mesial to the broken edge, covering one third of the remaining crown, the surface of the crown is thrown into parallel convolutions that, if

complete, would have made a band across the distal end of the tooth plate. The fine punctae on the surface of the crown are partially obscured by a thin film of matrix that covers much of the mesial end of the plate.

BCGM 6293 (Figure 5, O) is embedded in matrix, but the crown and a small portion of the aboral surface is exposed. No structural detail is discernable on the aboral surface. The crown is grossly punctate, and in some places on the highest part of the crown the punctae are aligned in parallel rows. The mesial part of the crown, perhaps three fifths the length of the tooth plate, measures 16 mm from the mesial tip to the distal broken edge. This part of the crown has a straight lingual margin, a sharply curved mesial tip, and a labial edge that is smoothly convex (widening the crown distally). Near the tip, the crown is 2 mm wide, and at the widest (distally) it measures 6 mm. The crown rises to its highest point along the lingual margin immediately anterior to the broken edge and then descends gradually towards the labial margin and the mesial tip. The surface of the crown descends into a shallow trough distally where the plate is broken. Behind the break, a part of the plate appears to be missing. However, there is a fragment (almost completely broken away) from the rest of the plate that almost certainly provided the lower distal end of the crown. Measuring 6 mm long, it is 3 mm from the lingual to the incomplete labial edge.

Discussion--The difficulties in identifying isolated *Sandalodus*-type tooth plates has long been recognized (Branson, 1905), and there have been many taxonomic changes within the genus. BCGM 4871 and BCGM 6293 are tooth plates similar to forms that St. John and Worthen (1883) referred to *Vaticinodus similis* and *V. simplex*. Their identifications were based on incomplete material, but they attempted to restore the entire plate. Stahl (1999) later found these reconstructions unconvincing and syonymized *Vaticinodus* with *Sandalodus*, and she considered the species *V. similis* and *V. simplex* generically indeterminate. The morphology of BCGM 6180 is close to that of *Stenopterodus parvulus*, a taxon erected by St. John and Worthen (1883), but this form has also been placed in synonymy with *Sandalodus* (Stahl, 1999). It should be noted that at least some species of *Sandalodus* are synonymous with *Deltodus*, representing upper and lower tooth plates, respectively (Woodward, 1889; Stahl and Hansen, 2000). However, for the purposes of this report we have chosen to treat *Sandalodus* as a valid taxon because of the incompleteness of the material and the lack of associated dentitions.

Family Copodontidae Incertae cedis
Genus *Synthetodus* Eastman 1908
Synthetodus cf. *S. trisulcatus* Eastman 1896

Figure 5, P

Material Examined--BCGM 4870, incomplete plate

Occurrence--Mississippian Monteagle Limestone (Chesterian) exposed along US 72 near Woodville, Jackson County, Alabama.

Description--The crown is ovate, coarsely punctate, and gently rounded at the mesial end. Distal to the center of the high, smoothly convex occlusal surface is a depression (filled with matrix) that extends to the lingual margin of the plate. The lingual margin is straight except for a slight centrally located distal protrusion where the depression reaches it. From this point to the mesial tip the plate measures 6 mm, and at its widest it is 4.5 mm. On the aboral side, the base is incomplete and partially covered with matrix. The best-preserved area lies beneath the distal depression on the crown, and it is gently concave.

Discussion--*Synthetodus* has been reported from the Late Devonian of Iowa, but St. John and Worthen (1883) commented on the persistence of genera from the earliest Carboniferous up through the Chesterian. We believe it entirely possible that this applies to *Synthetodus* as well, and tentatively refer BCGM 4870 to *S. trisulcatus* because the crown is divided into three parts by sulci. Although BCGM 4870 is smaller than specimens referred to *S. trisulcatus*, the tooth could represent an immature growth stage.

PALEOECOLOGICAL IMPLICATIONS

Depositional Environment--Norman (1981) reported that deposition of the Monteagle Limestone took place on a carbonate ramp (rather than a steep-margin platform) because rocks indicated high-energy, subtidal facies. His interpretation seems to be supported by the diversity and preservation of fossils observed during this study. For example, the rocks yielding the fossils contain a high proportion of fragmented crinoids, with isolated brachiopod valves and abraded rugose corals. In addition, fronds were torn away from the helical axis of *Archimedes* bryozoans, and several of the chondrichthyan teeth were abraded and/or broken post-mortem. However, on bedding surfaces we observed chondrichthyan fossils that are pristine (although they exhibit *in vivo* wear), as well as several partially disarticulated crinoids, numerous complete blastoid calyces, and long sections of complete *Archimedes*. These fossils seem to indicate that quick burial occurred, but some time after the death of the animals. In general we envision a depositional environment similar to that seen in other Carboniferous rocks, where chondrichthyan remains are associated with well developed crinoid-rich carbonate facies that contain a diverse assemblage of

invertebrates (Lockley, 1984; McKenzie and Bamber, 1979). Currents were active over a significant amount of time to result in disarticulation and abrasion of the invertebrate and vertebrate remains, but quick burial events occurred that prevented further decay/abrasion.

The majority of the vertebrate fossils in our sample are less than 20 mm in greatest dimension, and we believe these represent animals of relatively small body size. Using data reported by Williams (1979), Mapes and Hansen (1984) calculated a body length of 2.5 m for a cladodont tooth measuring 21 mm in height. Lockley (1984) later suggested that a tooth measuring 35 mm in height represented a shark having a body length of 4 m. Comparing these specimens to the Monteagle Limestone cladodont teeth, the smaller specimens (BCGM 1946, BCGM 4862, BCGM 4863, BCGM 6288, and BCGM 6289) suggest body lengths less than 1.5 m, whereas BCGM 4864 indicates a body length of nearly 4 m. Although it is possible that the lack of large vertebrate fossils (> 20 mm) is a taphonomic artifact, our sample suggests small-bodied animals inhabited the shallow-water environment, possibly taking advantage of biological diversity and avoiding predation by larger piscivorous fish.

Species Diversity--We suspect that the chondrichthyan assemblage recovered from the Monteagle Limestone of northern Alabama is incomplete given the recovery methods employed. However, the assemblage described in this report is moderately diverse, with 12 genera being described (6 elasmobranchs and 6 holocephalians; see Table 1). Tuomey (1858, p. 39) noted that teeth of *Psammodus* were "conspicuous" in the rocks of the Huntsville area, but unfortunately he did not provide an illustration of such specimens, and it is impossible to know if they represent *Psammodus* or any of the other taxa described above. It is interesting to note that crunching/crushing-type teeth (i.e. petalodonts and holocephalians) dominate the assemblage.

Predation--Invertebrates doubtless formed much of the diet of the Monteagle Limestone taxa, and differences in tooth morphology between forms such as *Petalodus*, "*Cladodus*", and *Helodus* imply diversity in feeding strategies. In addition, the variation in tooth morphology between the petalodont sharks suggests minimal competition within this group. One can imagine *Petalodus* consuming polyps of rugose corals in a manner similar to modern puffer and triggerfish, whereas "*Cladodus*" might be expected to have consumed other fishes. Holocephalians have been implicated in predation of brachiopods (Alexander, 1981, Brunton, 1966), but Elliott and Bounds (1987) attributed unrepaired shell damage to other causes, such as compaction and lithification of sediment. However, Malzahn (1968) and Moy-Thomas and Miles (1971) have reported brachiopod shells in gastric residues of some Paleozoic chondrichthyans. Maples and Waters (1995) speculated that the Mississippian crinoid *Camptocrinus multicirrus* employed a defensive posture to protect against predation, a theory supported by the work of Malzahn (1968), who documented crinoid remains in the gastric mass of a petalodont shark. Zangerl and Richardson (1963) suggested that damaged crustacean carapaces and cephalopod phragmocones were the result of chondrichthyan predation, and this interpretation has been supported by Malzahn (1968) and Mapes and Hansen (1984).

Other vertebrates such as palaeonisciform fish, a group known to have formed part of the diet of cladodont sharks (Hyde, 1926), have not yet been recovered from the Monteagle Limestone. Although it is possible that the depositional environment was unsuitable for these fish, their apparent absence could be the result of a collection bias because these fossils are usually very small and would be difficult to detect from macroscopic examination of the rocks. As indicated by Zangerl and Richardson (1963) and Mapes and Hansen (1984), cladodont sharks appear to have been opportunistic and could have preyed upon local invertebrates and other chondrichthyan species.

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