Paleontology of the Cretaceous Coon Creek Formation

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The Paleontology of the Cretaceous Coon Creek Formation

Dana J. Ehret, T. Lynn Harrell, Jr. & Sandy Ebersole, Editors
The premier North American Maastrichtian bryozoan fauna: Coon Creek, Tennessee

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ABSTRACT—The Maastrichtian fauna from Coon Creek, Tennessee has particular importance in being the first Late Cretaceous bryozoan fauna described in North America. Canu and Bassler (1926) recognized 22 species, most of them new. Following revision of their material and study of subsequently collected samples, 23 species can now be distinguished, comprising six cyclostomes and 17 cheilostomes. Coon Creek is the type locality for three genera (Basslerinella, Dysnoetopora and Frurionella) and nineteen species of bryozoans.
of northern Europe, where individual assemblages can contain several hundred species (e.g. Voigt, 1987) and bryozoans are by far the most abundant macroscopic grains in some packstone and grainstone facies (e.g. Voigt, 1973, 1987; Håkansson et al., 1974; Thomsen, 1974; Jarvis et al., 1982; Quine and Bosence, 1991; Surlyk, 1997). By comparison, the only described tropical carbonate Cretaceous bryozoan fauna (Simsima Fm. of Arabia) contains 20 species (Di Martino and Taylor, 2013).

MAASTRICHTIAN BRYOZOANS AT COON CREEK

Canu and Bassler (1926) described 22 species of bryozoans from Coon Creek, only one of which was assigned to a previously named species (Table 1). They introduced two new cheilostome genera, Frurionella and Dysnoetopora.

Although Canu and Bassler (1926) described Dysnoetopora as a cyclostome, it is actually a cheilostome, as was recognized by Voigt (1971). This dendroid ascophoran is one of a minority of Mesozoic cheilostomes that have the branch axis composed of elongate zooids responsible for branch lengthening, which either bend through approximately 90° into the outer part of the branch where their continued growth results in branch thickening (e.g., Taylor and Badve, 1995), or are overgrown by multiple layers of box-like zooids to bring about branch thickening. The general aspect of such cheilostomes has a remarkable overall resemblance to cyclostome colonies. In the case of Dysnoetopora, however, there are many features that place it within the cheilostomes, notably the D-shaped autozooidal orifice, a conspicuous ascopore proximal to the orifice in each fully formed autozooid, and the presence of spatulate vicarious avicularia.

Canu and Bassler’s (1926) other new genus, Frurionella, was regarded by them as an anascan cheilostome but was transferred to the ascophoran family Lepraliellidae by Gordon (1993). The morphology of Frurionella is more typically cheilostome than Dysnoetopora, with narrow, slightly flattened branches that develop heavy surface calcification, obscuring the primary orifices of the zooids.

Collections made from Coon Creek since Canu and Bassler (1926) examined the specimens provided by Wade, plus re-evaluation of their Coon Creek species, results in a revised listing of bryozoans from Coon Creek (Table 1). At present 23 bryozoan species are known from Coon Creek, comprising six cyclostomes and 17 cheilostomes. The introduction by Taylor and McKinney (2006) of the new genus Basslerinella for a species described by Canu and Bassler (1926) as Conopeum prismaticum adds to the genera for which Coon Creek represents the type locality.

Figure 1. Malacostegan (A-C) and pseudomalacostegan (D-F) cheilostome bryozoans from Coon Creek. All images in this and subsequent figures are scanning electron micrographs of uncoated specimens described by Canu and Bassler (1926) and housed in the collections of the National Museum of Natural History, Smithsonian Institution, Washington (USNM), unless otherwise stated. A, Conopeum nelsoni (Canu and Bassler, 1926), USNM 69969, holotype; colony of monomorphic zooids (a few with closure plates) encrusting a free serpulid tube. B, Heteroconopeum ovatum (Canu and Bassler, 1926), USNM 528393, paralectotype; the rows of ovoidal autozooids separated by pointed avicularia are characteristic of this common species with erect dendroid colonies. C, Basslerinella prismaticum (Canu and Bassler, 1926), USNM 69967, lectotype; a rare species with denticulate zooids. D, Flustrellaria anatina (Canu and Bassler, 1926), USNM 69956, lectotype; early astogenetic stages of an encrusting species that may subsequently develop spatulate interzooidal avicularia. E, Akatopora sulcata (Canu and Bassler, 1926), USNM 69951, holotype; worn, encrusting colony. F, Marginaria stipata (Canu and Bassler, 1926), USNM 69955, lectotype; early astogenetic stages of encrusting colony showing autozooids and abundant small interzooidal avicularia. Scale bars: A–D, F = 200 µm; E = 500 µm.
Figure 2. Coilostegan (A-D) and cribrimorph (E-F) cheilostome bryozoans from Coon Creek. A, *Tylaporella cretacea* (Canu and Bassler, 1926), USNM 69952, lectotype; delicate encrusting colony preserved in the concave interior of a bivalve shell. B, *Amphiblestrum denticulatum* Canu and Bassler, 1926, USNM 69961; autozooids and a few spatulate avicularia are visible in this encrusting species. C, *Stichomicropora baccata* (Canu and Bassler, 1926), USNM 69954, lectotype; group of autozooids including one with an intact spinose ovicell (center) and one with a broken ovicell immediately above it. D, *Stictostega ovicincta* Taylor and McKinney, 2006, Natural History Museum, London (NHM) BZ 5949, holotype; autozooids with extensive cryptocrystal frontal shields. E, *Nannopora torquata* (Canu and Bassler, 1926), USNM 69962, holotype; the costate frontal shields of the visible autozooids are not preserved except for the proximal part of one zooid immediately right of center at the bottom of the picture. F, *Pelmatopora irregularis* (Canu and Bassler, 1926), USNM 69957, lectotype; corroded zooids of another encrusting cribrimorph. Scale bars: A, B = 500 µm; C–F = 200 µm.

Figure 3. Cribrimorph (A), ascophoran (B-D) and cyclostome (E) bryozoans from Coon Creek. A, *Tricephalopora lamellaria* (Canu and Bassler, 1926), USNM 69968, lectotype; autozooids, some ovicellate, with an avicularium proximolaterally of the orifice. B, *Frurionella parvipora* Canu and Bassler, 1926, USNM 528415, paralectotype; thick-walled autozooids and adventitious avicularia in this common erect species with slightly flattened branches. C-D, *Dysnoetopora celleporoides* Canu and Bassler, 1926, USNM 69960, lectotype; Figure C shows one of the robust branches and Figure D autozooids and a spatulate avicularium (upper right) of this erect dendroid species which is the most conspicuous bryozoan in the Coon Creek fauna. E, *Theonoa? radiobifurcata* (Canu and Bassler, 1926), USNM 69966, holotype; worn discoidal subcolonies with autozooidal apertures clustered in radiating fascicles. Scale bars: A, B = 200 µm; C, E = 2 mm; D = 500 µm.
Examples of Coon Creek bryozoans mostly from the Canu and Bassler Collection in the Smithsonian are shown in Fig. 1-4.

PALEOECOLOGY

Maastrichtian bryozoans in the Atlantic and Gulf coastal plains occur in both siliciclastic and carbonate facies. The most species-rich faunas that we know are in carbonate facies of the Ripley Formation and Prairie Bluff Chalk in Livingston County, Alabama, and calcareous siliciclastic sand facies of the PeeDee Formation in North Carolina (Taylor and McKinney, 2006; McKinney and Taylor, 2006). Most species in these bryozoan faunas encrust shells, especially pteriomorph bivalves. Erect bryozoan species tend to be few, delicate, and relatively uncommon, a notable exception being the fauna from the PeeDee Formation of the Neuse River, North Carolina described by McKinney and Taylor (2006).

The majority of bryozoan species in the Coon Creek fauna also have thin colonies that encrust shell substrates. However, at Coon Creek erect bryozoans constitute by far the greatest skeletal volume, especially the thick-branched colonies of *Dysnoetopora celleporoides*. On average, the known erect bryozoans of the Coon Creek Formation are substantially more robust than those of the northern European Chalk. Both *D. celleporoides* and *Tetroycycloecia tennesseensis* have robust radially symmetrical branches in the classification of McKinney (1986), and *Polysascosoeciella? tripora* is on the robust side of the size distribution of functionally unilaminate branches; most erect Maastrichtian species in northern European carbonates have delicate branches and smaller colonies (e.g., bryozoan mounds at Stevns Klint, Denmark, see Surlýk et al., 2006).

Numerous essentially complete, isolated *Dysnoetopora celleporoides* colonies have been collected from the Coon Creek Formation. This distributional pattern of *D. celleporoides* is reminiscent of the occurrence of large, complete, robust branched cyclostome colonies on isolated bivalves in the Lower *Gryphaea* Beds of the Lower Ferruginous Sands (Lower Cretaceous; Aptian), Lower Greensand Group (see Simpson, 1985), exposed near Whale Chine, on the south coast of the Isle of Wight, England. In both occurrences, the large erect bryozoans grew on shell substrate islands scattered across an otherwise slowly accumulating, offshore, glauconite-bearing quartz sand substratum (Wade, 1926; Cobban and Kennedy, 1994).

Occurrences of Maastrichtian bryozoans along the Atlantic and Gulf coastal plains seem to fall into two broad groupings. In carbonate-rich environments, encrusting bryozoans have both more species and greater skeletal mass than do erect bryozoans. However, where bryozoans occur in siliciclastic silts and sands, the greater species richness may or may not be found among the encrusting species, but most of the bryozoan skeletal mass is composed of robust erect colonies. The Coon Creek bryozoan fauna clearly epitomizes this latter group. With minimal diagenetic cementation, many of the Coon Creek encrusting bryozoans are very fragile and are apt to detach from their molluscan shell substrates. Careful sample processing is therefore required for an adequate appreciation of encruster abundance and diversity.

LITERATURE CITED
Cheetham, A. H., J., Sanner, P. D. Taylor, and A. N. Ostrovsky. 2006. Morphological differentiation of avicularia and the


Table 1. Cyclostome and cheilostome bryozoan species recorded from Coon Creek, Tennessee. The names used by Canu and Bassler (1926) are given in the second column.

<table>
<thead>
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<td><em>Idmidronea traceyi</em></td>
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<td><em>Annectocyma cirrata</em></td>
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<td><em>Theonoa radiobifurcata</em> (Canu and Bassler, 1926)</td>
<td><em>Berenea papillosa</em> (Reuss, 1846)</td>
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<td><em>Plagioecia maculata</em></td>
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<td><em>Tetrocycloecia tennesseensis</em> (Canu and Bassler, 1926)</td>
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<td><strong>Cheilostomata</strong></td>
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<td><em>Conopeum ovatum</em> Canu and Bassler, 1926</td>
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<td><em>Conopeum prismaticum</em> Canu and Bassler, 1926</td>
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<td><em>Mystriopora stipata</em> Canu and Bassler, 1926</td>
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<td><em>Micropora baccata</em> Canu and Bassler, 1926</td>
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<td><em>Gephyrotes lamellaria</em> Canu and Bassler, 1926</td>
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<td><em>Frurionella parviperata</em> Canu and Bassler, 1926</td>
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<td><em>Peedeesella guhai</em> Taylor and McKinney, 2006</td>
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<td><em>Dysnoetopora celleporoides</em> Canu and Bassler, 1926</td>
<td><em>Dysnoetopora celleporoides</em> Canu and Bassler, 1926</td>
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The Coon Creek decapod assemblages; Cretaceous marine paleocommunities of northern Mississippi and Tennessee

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ABSTRACT—Two decapod assemblages occur in the Upper Cretaceous Coon Creek Formation of the northern Mississippi Embayment. The *Avitelmessus* Assemblage may consist of the single decapod taxon, *Avitelmessus grapsoideus*, or of *A. grapsoideus* associated with a molluscan assemblage, and is preserved as repeated, discrete assemblages, a biocoenosis, in near shore shale-rich or clay-rich and muddy-sand lithosomes of the Coon Creek and Ripley Formations. The Blue Springs *Dakoticancer australis* Assemblage is similar to the South Dakota *Dakoticancer* Assemblages in faunal composition, mode of preservation and distribution, but differs significantly in taxonomic composition and taphonomic fabric. The Blue Springs *Dakoticancer australis* Assemblage, preserved in an off shore facies, consists of a complex of at least two preservational cycles over-printed on a molluscan thanatocoenosis. Both decapod assemblages represent discrete Cretaceous crab community fractions and occupy intermediate positions in Late Cretaceous marine food chains and food webs.

INTRODUCTION

Decapods have long been known to occur in the Upper Cretaceous sediments of the Mississippi Embayment (Wade, 1926; Rathbun, 1923, 1926, 1935; Stephenson and Monroe, 1940; Russell, 1965; Russell and Parks, 1975; Russell et al., 1982; Bishop, 1986a). Collecting done since 1976 by me, my students (Jacobs, 1983), and paraprofessionals has yielded impressive decapod collections from the Mississippi Embayment including those made in Tennessee (Rathbun in Wade, 1926; Kesling and Reimann, 1957), the Blue Springs *Dakoticancer australis* Collection at the South Dakota School of Mines and Technology in Rapid City, Locality GAB 37; 1,081 specimens (Bishop, 1983; Bishop 1991), and numerous occurrences of the *Avitelmessus grapsoideus* Assemblage in northern Mississippi and southern Alabama. The remarkable fossiliferous facies of the Coon Creek Formation preserve unparalleled record of Late Cretaceous marine taxa and provides the opportunity to contemplate the community structures of the communities represented by fossils in the Coon Creek faunas. Similar crab-rich communities are well known from the modern intertidal zone and crab communities have also been described from warm sea bottoms in the Sea of Japan (Thorson, 1957) and in the Western Interior Cretaceous (Bishop, 1981a). This chapter is intended to review current knowledge of the occurrences of these assemblages, establish probable paleoecological parameters and constraints of food chains and food webs of the ancient paleocommunities of the Coon Creek, making the hypotheses available for testing by geologists and paleontologists.

The Mississippi Embayment was a shallow epicontinental sea that extended as an arm of the Tethys Seaway northward from Mississippi and Louisiana to Cairo, Illinois (Fig. 1). Sediments deposited in the Mississippi Embayment are
time-transgressive lithosomes of clastic sediments to the north and carbonate sediments to the south. A composite lithologic sequence published by Russell, et al. (1982; fig. 4) allows the stratigraphic placement of the two distinct decapod assemblages, the Aristolemus Assemblage and the Blue Springs Dakoticancer australis Assemblage in northern Mississippi while other papers in this volume will allow placement of the Tennessee faunas into their geologic context.

Bishop, Feldmann, and Vega (1998) reviewed the family Dakoticancridae and made ecological inferences about the mode of life of these unusual crabs that until recently were only known only from the North American epicontinental shelves. The endemic Dakoticancer, from North America (Bishop, 1984) has been joined by the Ibericancer (and a new subfamily of Dakotacancroidea); the Ibericancridae described from Spain (Artal et al., 2008). The reason for the endemism and abundance of Dakoticancer, podotrematous crabs (crabs having genital openings in the coxae of the periopods or walking legs (Rathbun, 1917; Guinot and Tavares, 2001), has not yet been determined nor has the possible ancestral position of these crabs in the subsequent adaptive decapod radiation of the Paleogene. The systematic position of Dakoticancer has only recently been elucidated (Artal et al., 2008 with the description of a second genus, Ibericancer and the creation of a new Family Ibericancridae within the Superfamily Dakoticancroidea Rathbun, 1917).

On an even more fundamental level, these fossil assemblages, representing community fractions of the past (Bishop, 1986b), must have represented groups of interacting living animals during the past, animals that have not previously been placed into the context of ancient food chains and webs. A search of the internet (accessed 1/15/13) revealed that very few attempts have been made to set Cretaceous marine fossil assemblages into the context of trophic levels, food chains, or within food webs. Notable papers which have previously attempted to do so include Rhoads, Speden, and Waage (1972), Bishop (1981a), and Bishop, Feldmann and Vega, (1998). In parallel to the marine faunas, Mitchell, Roopnarine, and Angielczyk (2012) have very nicely modeled a terrestrial food web for the Cretaceous in which the terrestrial food web is used to test the implications of food web instability at the K/T extinction event. Many incidental papers allude to restricted aspects of the interactions of feeding organisms within marine Cretaceous habitats from which some information about ancient food webs may be extracted (Gallagher, 1990; Roopnarine, 2006; Sheehan and Hanson, 2008; Klompmaker and Fraaije, 2012; Chin et al., 2008; Hoganson, 2009). Chin et al. (2008) brought ichnology into the forefront reporting, “Abundant fossil faeces demonstrate that this planktonic bounty supported benthic invertebrates and large, possibly seasonal, vertebrates in short food chains.” This paper was foreshadowed by one by Bishop (1977) entitled “Pierre Feces that described coprolites and fecal pellets associated with the Dakoticancer Assemblages of the Western Interior.

Martin and Bjork (1987) described the last meal of a Cretaceous South Dakota mosasaur (SDSM 10439), Tylosaurus proriger, consisting of a fish, a bird, and a smaller mosasaur. Kear et al. (2003) reported on the discovery of hatchling-sized marine protostegid turtle, enantiornithine bird, actinopterygian fish and phosphatic nodules) within the body cavity of a gravid female ichthyosaur (Platypterygius longmani) from the Lower Cretaceous of Australia, giving evidence of trophic interactions within the Cretaceous. Similar data is
occasionally preserved within the invertebrates. In some of these papers singular specimens record the trophic interaction, Kaufman and Kesling (1960) described a large ammonite, a *Placenticeras*, that exhibited bite marks from a mosasaur, Bishop (1972) described a small raninid crab exhibiting bite marks attributed to a trophic interaction between a fish and the small crab, and Wahl presented a poster on an aborted bite attack on a *Placenticeral meeki*. Kruta et al. (2011) documented the jaw structures of baculitid cephalopods and a small isopod crustacean caught within the radular apparatus, indicating small crustaceans would constitute part of the diet of baculitids (this at the Tail Ranch Locality that was the source of so many lovely small decapod crustaceans forming the Heart Tail Ranch Decapod Assemblage (Bishop, 1985a)). These papers indicate a sparse and scattered literature on trophic interactions of Cretaceous marine organisms. The framework of trophic interactions in the decapod assemblages of the Coon Creek Formation is presented here to stimulate interest in new research. It should be possible to construct food webs for these community fractions based upon what is known in the Recent and elsewhere in the Cretaceous.

**PALEOECOLOGIC ANALYSIS OF COON CREEK FAUNAS**

One of the remarkable aspects of the extensive paleontological literature of the Cretaceous is the great number of publications describing the diversity and abundance of fossils from Cretaceous rocks; a robustness that contrasts strongly with the near lack of interpretations of these faunas in terms of ancient paleoecology, especially community structure.

Wade (1926) studied the faunas of the Ripley and Coon Creek Formations and remarked on the wonderful diversity of the faunas (350 species recognized at that time) and preservation of fossils in the northern Mississippi Embayment. He cited over 313 species collected from the Coon Creek in two weeks and listed eight genera of vertebrates, two echinoderms, two worms, two corals, one brachiopod, 114 species of pelecypods, four species of scaphopods, 174 species of gastropods, and five species of cephalopods (Wade, 1926; p. 12). Added to this diversity are 10 crustacean species (Rathbun, 1926) and 22 bryozoan species (Canu and Bassler, 1926). Sohl (1960) revised the Archeogastropoda and Mesogastropoda of the Ripley, Owl Creek, and Prairie Bluff Formations in the Mississippi Embayment. Bishop (1983) collected and described 1300 decapod specimens and added three new species to the decapod fauna from the Blues Springs Locality in northern Mississippi. The Coon Creek faunas were shown to occur at different levels in the Coon Creek Formation, which has been recognized as being time transgressive. Beautifully preserved marine faunas, bearing abundant decapod crustaceans, occur within these discrete lithosomes of the Coon Creek.

**The Avitelmessus Assemblages**

*Avitelmessus grapsoideus* Rathbun, 1923 is one of the most abundant fossil decapods from the Mississippi Embayment and Eastern Gulf Coastal Plain. Where found it often is abundant, and in a few instances, may represent the only common macrofossil preserved. Two types of occurrences have been documented: preservation in clayey sandstones as part of a molluscan biocoenosis and preservation as a discrete monotaxic fauna in claystones. Most occurrences of *Avitelmessus grapsoideus* preserve this crab as an element of diverse molluscan biocoenosis. Typical of those is a locality (GAB 49) in Union County, Mississippi where the crabs occur right side up in fissiliferous, glauconitic, micaceous, sands that have been preferentially cemented around crabs to form crab-bearing nodules. A similar locality in Union County, Mississippi was exploited about 1982 and approximately 33 crab concretions were collected and prepared in 1985 (James Honert, per. comm.). Many of these specimens now reside in museum exhibits around the country and world (Plate 1, Fig. 1), including the Museum of Geology and Paleontology at South Dakota School of Mines and Technology (SDSM 10183) and the Black Hills Museum of Geology (BHI 4451).

At other localities in laminated mudstones or claystones, *Avitelmessus grapsoideus* is abundant, but often occurs alone. Two of these sites in Mississippi (Bishop Decapod Collection; GAB Locality 40, GAB Locality 54) have been examined and numerous specimens collected (Plate 2). In each case, *Avitelmessus grapsoideus* occurs in great numbers in sandy shale or claystone. All specimens observed in situ were right side up and preserved encased in fragile, gypsum-rich nodules with very poor preservation.

A third mode of occurrence for the *Avitelmessus grapsoideus* Assemblage, exhibited at the Braggs locality in Alabama, has yielded thousands of specimens preserved within phosphatic nodules (Abston and Savrda, 1990) eroding from the Ripley Formation. The crabs at this locality are encased in dense phosphorite concretions (Plate 1), which assume the outline of the enclosed crab and form plate-like concretions. These concretions are virtually unpreparable except by destructive means such as serial sectioning. The concretions occur in situ in the Ripley Formation within entrenched valley walls of Dry Cedar Creek, eroding out and accumulating in point bars of Dry Cedar Creek, forming a modern, condensed lagerstätten. Preservation of these crabs in phosphorite concretions appears to be closely analogous to the formation of phosphorite-preserved decapod faunas of the Western Interior (Bishop, 1986a, 1986b). Bishop (2007) described the phosphatization process forming such concretions that preserve the abundant decapods
Among the abundant fossils in these rocks are numerous decapods (Plate 2). The decapods are preserved as relatively unaltered remains (Plate 2, Figs. 1-7, 9, 11-15) or as black or brown phosphatic nodules (Plate 2, Figs. 8, 16). The phosphatized crabs represent an early cycle of preservation followed by exhumation, as inferred from blackish crab-bearing nodules showing evidence of abrasion and overgrowth by epizoans, including the oyster *Exogyra* (Plate 2, Fig. 10). Bishop (1981b) described an *Exogyra* attachment scar from this locality, which preserved a xenomorphic impression of the carapace of the palinurid lobster *Linuparus*. In this outcrop, and others in the Ripley Formation, *Exogyra*, often shows rehealed breaks attributed to attacks by decapod crustaceans. Relatively few of the abundant, ablated, rounded phosphatic nodules, however, can be identified as to their specific organic origin.

Unphosphatized decapod remains are also found enclosed in the sediment amongst the dark phosphatic nodules. These crab specimens are rarely collected with their exoskeleton intact because it is extremely fragile and readily exfoliates, leaving behind a steinkern (Plate 2, Figs. 5, 12). The fossil decapods are found throughout the exposure, but seem to be concentrated in a 2 m thick interval marked by the abundant phosphatic nodules. The decapod portion of the assemblage (see Table 1;...
1,081 specimens) is dominated by the crab *Dakoticancer australis* Rathbun, (48.9%) with abundant mud shrimp, *Protocallianassa mortoni* (Pilsbry) (26.9%), and lobsters, *Hoploparia tennesseensis* Rathbun, (10.1%). Other decapod constituents are present in much smaller numbers (Table 1), reinforcing the importance of making large collections to adequately define paleocommunity fractions (Bishop, 1985b).

This unusual occurrence of decapods was interpreted (Bishop, 1983) to be an analog of the better-known *Dakoticancer* Assemblages of South Dakota (Bishop, 1981a). The Blue Springs Decapod Assemblage is similar to them in faunal diversity and perhaps similar in distribution, as they are now known to extend over about 18 km² (7 mi²) through a thin interval, approximately 4 m (13 ft) thick, from the Blue Springs locality to two nearby outcrops at the old Whitten Farm, a nearby reservoir to the northeast, and to a new Toyota Plant being built nearby to the west. The two modes of preservation of the Blue Springs Assemblage, indicate at least two episodes of opportunistic crab population growth and confound the taphonomic interpretation of the assemblage. It is known that fecal pellets are present in the Blue Springs phosphatic nodules just as they are in the South Dakota *Dakoticancer* Assemblages. It remains to be demonstrated, however, that the mode of preservation of the two *Dakoticancer* Assemblages is exactly the same. In any case, that the Blue Springs Assemblage is superimposed on a molluscan thanatocoenosis is quite apparent by the preservation of abundant molluscs. The accumulated data suggest that such crab assemblages represent opportunistic species capable of rapid population growth, perhaps to exploit burgeoning food resources, followed by a less rapid decline as a positive taphonomic short cycle becomes operative (Bishop, 1986b; Bishop and Williams, 1987). These repeated opportunistic crab communities seem in many cases to be overprinted on molluscan thanatocoenoses or biocoenoses (Bishop, 1986b).

**Paleoautecology of the Crabs**

The paleoautecology of fossil decapods can be approximated from comparison with modern analogs and by deduction from functional morphology (Schäfer, 1954). Schäfer (1954) described four groups of crabs based upon their functional morphology: 1) crabs that crawl and walk on the upper surface of sediment, 2) crabs that burrow and dig in the sediment, 3) crabs that climb within crevices in the substrate, and 4) crabs that actively swim in open waters. As with most fossil interpretations, the hypothesized modes of life remain open to question because the animals are extinct and evidence of their behavior usually is not preserved. Regardless, the assignment of fossil decapods to general life modes, including mode of transportation, relationship to the substrate, and feeding type, is attempted herein, as well as their assignment to food chains and food webs.

**Paleoautecology and Paleosynesecology of Dakoticancer overana**—Bishop, Feldmann and Vega (1998) summarized the paleoautecology of Dakoticancer overana, which is paraphrased here: Morphological characteristics of *Dakoticancer overana*, including equant, rectangular shape, long, slender equally-sized legs P2-P4, equant claws held free from the carapace margin, modest-sized, small-toothed downturned fingers, and functional-sized corneas on the eye stalks suggest that *Dakoticancer* was a generalized epifaunal crawler that lived on the soft substrates of the mud bottoms of the Western

### TABLE 1. The Coon Creek decapod assemblages.

<table>
<thead>
<tr>
<th>Fossil Pellets</th>
<th><em>Callianassa</em> (1.0)</th>
<th><em>Nuculana</em> (0.5)</th>
<th><em>Tetraloca</em> (0.5)</th>
<th><em>Nuculana</em> (0.1)</th>
<th><em>Nuculana</em> (0.1)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Callianassa</em> (1.0)</td>
<td><em>Nuculana</em> (0.5)</td>
<td><em>Tetraloca</em> (0.5)</td>
<td><em>Nuculana</em> (0.1)</td>
<td><em>Nuculana</em> (0.1)</td>
<td><em>Nuculana</em> (0.1)</td>
</tr>
<tr>
<td>n = 650</td>
<td>Inoceramus (2.1)</td>
<td><em>Dakoticancer</em> (0.7)</td>
<td><em>Dakoticancer</em> (0.7)</td>
<td><em>Dakoticancer</em> (0.7)</td>
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</tr>
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<td><em>Dakoticancer</em> (0.7)</td>
</tr>
</tbody>
</table>
Interior Cretaceous Seaway. Reduction of P5, hind-most legs, suggest a possible carrying and covering behavior exhibited by some modern crabs with reduced hind legs. Dactyli on P2-P4 are large, elongate and triangular, fully capable of folding over into “snow shoes” for walking across soft substrate. Of all the observable characteristics, none can be cited which unequivocally establish the mode of life of this primitive crab.

*Dakoticancer overana* in South Dakota occurrences is associated with a few concentrically layered straight burrows. Not only are they not abundant enough to have been *Dakoticancer* burrows, they are too small. The preservation of burrows (probably assignable to the thalassinoid *Protocallianassa cheyennensis*) in the *Dakoticancer* assemblages indicates that if *Dakoticancer overana* were a burrow dweller, its burrows would likely be preserved in abundance. Because they were not, Bishop (1981a) concluded that *Dakoticancer overana* was not an obligatory burrower.

The consistent association of *Dakoticancer overana* with segmented burrows and fecal-pellet packed burrow trails led Bishop (1987:325) to the conclusion that the presence and preservation of *Dakoticancer overana* was linked through a positive feedback cycle to population explosions of benthic worm populations. If this conclusion is valid, benthic worms may have been a preferred food item for *Dakoticancer overana*; a conclusion further supported by this decapod’s delicate, sharp, downturned fingers armed with small teeth that would be useful in capturing and pulling worms from the substrate. As with most crabs, *Dakoticancer overana* was probably not an obligatory feeder, but rather would have been a generalized omnivorous browser capable of rapidly responding to periodically burgeoning food resources, including the worms.

Lithologic evidence from the bentonitic claystone of the Pierre Shale in which *Dakoticancer overana* is preserved, usually enclosed within phosphatic concretions distributed through one to three meters of section and an associated fauna including inoceramid bivalves, bacularid cephalopods, often diverse foraminiferal suites (over 100 species at Mobridge, S.D.) and mosasaurs all indicate *Dakoticancer overana* lived in brackish to fully marine water of the Western Interior Cretaceous Seaway.

**Paleoautecology and Paleosyneiology of Dakoticancer australis**—Bishop et al. (1998) summarized the paleoautecology of *Dakoticancer australis* which is modified and presented for completeness here: *Dakoticancer australis* from the Mississippi Embayment is similar to *D. overana* in gross morphology, being significantly larger, more robust, with a higher, more strongly ridged carapace with a more granulated carapace and with a thicker cuticle. Pereiopods P2-P4 are equant and stout, longer than the carapace is wide. The last pair of legs P5 are reduced and possibly carried in a raised position to anchor carried items used for camouflage. Dactyli are triangular. The chelae are shorter through the propodus, more robust, and more granulated on their outer surface with fingers more downturned than those of *D. overanus* and probably were capable of considerable cutting pressure. Few epizoans have been observed except for one specimen carrying an oyster attached to its carapace. The lithology of the Coon Creek indicates a shallow near shore, muddy sand shelf habitat. Associated fossils of the Coon Creek facies include a very diverse and abundant marine fauna, attesting to the normal marine conditions of these sedimentary environments. The *Dakoticancer australis* Assemblage from the Coon Creek Formation of the Mississippi Embayment occurs in the muddy sandstone associated with abundant marine invertebrates including *Exogyra*, *Sphenodiscus*, *Turritella*, and many other invertebrates. Trace fossils indicate sparse *Thalassinoides*, leading to the conclusion that *D. australis* in the Coon Creek was not a burrow dwelling decapod.

*Dakoticancer australis* assemblages described from the Potrerrilos Formation in Nuevo Leon, Mexico, found by Vega and Feldmann (1991) occur in two types of lithofacies. At one locality, molds were found without any articulated appendages, with carapace material very weakly preserved and frequently lost. The lithology is represented by light-gray sandstone, with the layer containing the crabs situated one meter above a massive oestrid bank composed by *Pycnodonta mutabilis* and *Exogyra costata*. The second locality comprises a fine-grained lithology, with a great diversity of molluscan species preserved, mainly infaunal bivalves. Burrows filled with brown sandstone are conspicuous within the rather gray sandy-shales. Here, molds of *D. australis* were found inside galleries with diameters ranging from 7 to 12 cm. These crab remains, correctly inferred by Vega and Feldmann (1991) to be exuviae, are preserved within burrows and have preserved appendages that remain articulated, but show dislocation of the ventral side of carapace. To date, more than 20 specimens of *D. australis* have been collected at this locality, all within galleries and having dislocated plastrons. This suggests a molting behavior within burrows, a behavior uncommon for most brachyurans, as molting inside burrows has not been described frequently in extant crabs (Vega and Feldmann, 1991). However, *D. australis* specimens from the Cardenas Formation in San Luis Potosi, east-central Mexico, and those from the Coon Creek of the Mississippi Embayment, are not found associated with burrows, and most of them showed articulated appendages. It is possible that the difference in the molting behavior between assemblages of Nuevo Leon and San Luis Potosi reflect different taphonomic histories, rather than different molting behavior (Vega et al., 1995) or the molts found within burrows could be a case of opportunistic molting, taking advantage of nuances of different habitats, and the presence of burrows. It is also important to note that the mean size of the specimens from San Luis Potosi is
bigger than the mean size reported for the Poterillos and Coon Creek formations. However, the dakoticancerids of Maastrichtian deposits from Mexico are sparse, compared to some localities of the United States, such as the Coon Creek Formation, where Bishop (1986a,b) reported 637 specimens, compared to no more than 80 specimens of this species that had been collected in the Poterillos and Cardenas formations. We must consider differences in paleoenvironment, taphonomic histories, preservational histories, and collecting biases to explain such differences in size and number of individuals. Most samples, both from Poterillos and Cardenas formations are exuviae, evidenced by the displaced position of plastron and/or the altered height of the carapace. Bishop (1981a; 401, figs. 12-13) has observed similar squashing phenomena resulting in sternal displacement and rotational telescoping of the carapace and sternum, pointing out that these phenomena may be the result of cuticle weakening of the pleural suture during either exuviation or even during decomposition of a corpse. Most samples from Nuevo Leon (except those found preserved within burrows) show disarticulated appendages suggesting some transportation in a low-energy environment. It is possible that *D. australis* was a crawler in the intertidal zone, feeding on mollusks, breaking their shells with rather strong chelae. In fact, compared to other fossil crabs from the Maastrichtian of northeastern, southern, and east-central Mexico, *D. australis* seems to have the heaviest and strongest carapace, with robust legs that could have been useful in occasional incursions onto the supratidal zone.

**Paleoautecology and Paleosynecology of Avitelmessus grapsoideus**—*Avitelmessus grapsoideus* is one of the largest known crabs from the Late Cretaceous of North America (P1) often attaining a total width of 21 cm, a size so big that it is truly a giant compared to contemporaneous crabs. I. G. Reimann collected the best-preserved specimen of *Avitelmessus grapsoideus* described in the literature on November 9, 1955 at Dave Week’s farm at Coon Creek, Tennessee. This female specimen (UMM No. 33406) was carefully prepared and presented in various views in a well-illustrated paper (Kesling and Reimann, 1957) and is the primary data for these deductions on paleoautecology of *Avitelmessus*.

*Avitelmessus grapsoideus* had a robust, dorsoventrally flattened body with its carapace ornamented by shallow grooves and low ridges. The anterior margin was reflexed into the carapace and armed with a rostrum and anterolateral spines; the orbits were well formed and invaginated. Dorsal-lateral margins were tightly flexed, somewhat raised, and armored with numerous spine-like tubercles, the medial portion of the carapace was very tuberculate. Appendages included large, nearly symmetrical claws and four pairs of walking legs, the first three pairs are equal-sized and the fifth pair very much reduced in size and directed dorsally. The claws (P1) were curved along carapace line, tuberculate, with fingers that are slightly down turned and toothed with shearing denticles. The first three pairs of walking legs (P2–P4) were long, flattened dorsoventrally, corrugated longitudinally, and tuberculate. Color patterning is preserved on the beautiful Coon Creek Tennessee specimen described by Kesling and Reimann (1957) from the Dave Week’s place. The patterning is present as “a medium [umber] background, dark spots, and blotches, and light lines (Kesling and Reimann, 1957:9) exhibiting a counter shading on the chelae and periopods.

The morphology, size, color patterning, and variable modes of occurrence indicate that *Avitelmessus grapsoideus* was a surface dwelling, highly mobile vagrant crab that inhabited, or at least moved through, several habitats represented along the shores of the Mississippi Embayment. Its spiny, tuberculate ornamentation, strong corrugated walking legs, and appressed chelae indicate it was a bottom walker (“Laufcr” of Schäfer, 1954). Bishop et al. (1998) suggested that “The fifth legs are much smaller than the others and appear to have been held posteriorly or even above the carapace, suggesting the possibility for carrying behavior in these crabs. The last pair of legs in *Dakoticancer australis* are also slender and much reduced in length. They were probably carried in a subdorsal position, as well.”

The *Avitelmessus grapsoideus* Assemblage was a specialized paleocommunity dominated by this large crab that was able to exploit opportunistic food resources in the shallower waters of the Coon Creek shelf and Ripley nearshore habitats. This decapod assemblage is unique in that only one decapod constitutes the assemblage found repeatedly throughout the Coon Creek and Ripley formations and their equivalents in Tennessee, Mississippi, Alabama, and North Carolina. It is hypothesized that this giant crab (for the Cretaceous) was also able to utilize the shallower, lower salinity intertidal facies of the Coon Creek and equivalent formations which often carries a depauperate fauna, or a soft bodied fauna or flora not commonly preserved; perhaps a fauna dominated by abundant annelids or algae.

**The Dakoticancer australis Paleocommunity**

The *Dakoticancer australis* assemblage is similar to decapod assemblages described from the Western Interior Seaway (Bishop, 1986a, b), being similar in that mostly decapods constitute the assemblage. This assemblage has thus far been found to occur only once in the Coon Creek Formation near Blue Springs, Mississippi. The numerous decapod species of this assemblage can be characterized by their modes of life as inferred by analogy to Recent decapods and functional homeomorphs (Table 1). Infaunal decapod components of this assemblage consist of the deep burrowing thalassinoid ghost shrimp,
Protocallianassa mortoni, (Pl. 2, Figs. 2-3, 6) or the trace fossils of its burrow systems, **Ophiomorpha nodosa**. Most modern and ancient ghost shrimp exhibiting similar modes of life are active filter feeders, or may “farm” subterranean bacterial mats in their fecal-pellet lined burrows, which act as part of the integral skeletal support system of this lightly scleritized decapod (Bishop and Williams, 2005). Modern ghost shrimp spend their entire life as subterranean organisms, except for a short nektonic or planktonic larval interval. These ancestral forms are inferred to have had the same life cycle based on their similar morphology, lightly scleritized cuticle, and phylogenetic history. Burrows of the modern ghost shrimp, **Callichirus major** and **Callichirus islagrande**, are known to extend 2-5 meters beneath the surface (Bishop and Bishop, 1992; Felder and Griffis, 1994), are thought to house single animals for their entire life, and may be passed from generation to generation.

Semi-infaunal components of this decapod assemblage consist of three crabs and two lobsters. The two crab taxa each exhibit one of three characteristic body shapes attributable to a shallow burrowing mode of life (Schäfer, 1954); an elongate, arched, smooth carapace wide at the anterior and small, proximally-curved claws which can be held closely against the anterolateral margin of the carapace, and short, broad periopods. Both **Notopocorystes testacea** (Rathbun, 1926) (Pl. 2, Fig. 7) and **Raninella tridens** Roberts, 1962 (Pl. 2, Fig. 5) are inferred to be shallow burrowers similar to modern “frog crabs.” Two lobsters are described from the assemblage, the nephropid clawed lobster, **Hoploparia tennesseensis** Rathbun 1926 (Pl. 2, Fig. 8), and the palinurid, non-clawed lobster, **Linuparus canadensis** (Whiteaves) 1885 (Pl. 2, Figs. 9-10). **Hoploparia tennesseensis** was a nephropid lobster with a rounded cephalothorax, extended abdomen, heterochelous chelipeds, and periopods (P2-P5) adapted as walking legs. Recent nephropid lobsters function largely as scavengers in today’s seas, but will take live food when possible. Both of these animals have modern analogs and are inferred to have lived a wandering, benthic mode of life with nearly continuous sheltering beneath detritus, in shallow depressions, or simple burrows (Holthuis, 1974:751) as their modern analogs do today. **Linuparus canadensis** was a palinurid lobster with a flattened, spinose, three-keeled tuberculate cephalothorax, five pairs of periopods, long antennal peduncles and segmented antennae. The body shape, ornamentation, and appendages indicate this animal was a vagrant benthic organism, but might well have sheltered in shallow depressions or simple burrows on the sea bottom. The mandibles of linuparid lobsters were extremely massive and clearly adapted to eating molluscs. Bishop (1981b) described a linuparid cephalothorax impression preserved as an attachment scar of an **Exogyra**, confirming the vagrant nature of this animal (Pl. 1, Fig. 10). Modern linuparid lobsters, unlike their ancient ancestors that inhabited continental shelves around the world, now form relict faunas on the continental slopes of the Pacific and Indian Oceans.

Epifaunal crabs in this assemblage included the assemblage name bearer, **Dakoticancer australis**, two other dakoticancroid crabs, **Tetracarcinus subquadratus** Weller, 1905 and **Seorsus wadei** Bishop, 1988 a retroplumid crab, **Cristipluma mississippiensis**, Bishop 1983, and claws from the crabs “Ermyma” flecta Rathbun, 1935 and **Prehepatus harrisi** Bishop, 1985b. All were small, generalized, epifaunal, bottom walking crabs. **Dakoticancer australis** (Pl. 2, Figs. 1, 16) is a moderately sized dakoticancroid crab with a high body and a relatively unornamented carapace traversed only by shallow grooves, low ridges, and abundant small tubercles. The anterior margin is transverse and protected by a rostrum and small anterolateral projections; the orbits are well formed and invaginated. Dorsal-lateral margins are reflexed, and the dorsal portion of the carapace is slightly tuberculate. The appendages include symmetrical claws and four pairs of walking legs, the first three pairs equal-sized and the fifth pair very much reduced and directed dorsally. Claws (P1) **Protocallianassa mortoni**, (Pl. 2, Figs. 2-3, 6) or the trace fossils of its burrow systems, **Ophiomorpha nodosa**. Most modern and ancient ghost shrimp exhibiting similar modes of life are active filter feeders, or may “farm” subterranean bacterial mats in their fecal-pellet lined burrows, which act as part of the integral skeletal support system of this lightly scleritized decapod (Bishop and Williams, 2005). Modern ghost shrimp spend their entire life as subterranean organisms, except for a short nektonic or planktonic larval interval. These ancestral forms are inferred to have had the same life cycle based on their similar morphology, lightly scleritized cuticle, and phylogenetic history. Burrows of the modern ghost shrimp, **Callichirus major** and **Callichirus islagrande**, are known to extend 2-5 meters beneath the surface (Bishop and Bishop, 1992; Felder and Griffis, 1994), are thought to house single animals for their entire life, and may be passed from generation to generation.

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PLATE 3 The Pleasant Ridge **Dakoticancer australis** Collection Specimens of **Avilelmessus grapsoideus** collected in Union County, Mississippi and prepared by Mr. James Honert. Specimen at top was donated to the South Dakota Museum of Geology and Paleontology (SDSM IV 10183) (photograph courtesy of James Honert).
are stout, tuberculate, with short, down turned fingers that are toothed with shearing denticles. The three pairs of walking legs (P2-P4) are long, flattened dorsal-ventrally, and slightly tuberculate. *Tetracarcinus subquadratus* (Pl. 2, Fig. 11) is a small dakoticancroid crab with an arched carapace and a relatively unornamented carapace traversed by shallow grooves, and low ridges surmounted by abundant small tubercles. The anterior margin is transversely rounded and protected by a rostrum and anterolateral projections; the orbits are well formed, ridged dorsally, and invaginated. Dorsal-lateral margins are rounded and reflexed, and the dorsal portion of the carapace is very tuberculate on high areas. The appendages include symmetrical, globular claws and four pairs of walking legs, the first three pairs are equal-sized and the fourth pair very much reduced and directed dorsally. The claws (P1) are stout, globular, and smooth with thin, strongly down turned fingers that are toothed with small shearing denticles.

*Seorsus wadei* (Pl. 2, Fig. 12) is a medium sized, trapezohedral dakoticancroid crab with a flat carapace and an unornamented carapace traversed by shallow grooves, and low ridges. The anterior margin is rounded; the orbits are well formed, and invaginated. Dorsal-lateral margins are angular and reflexed, and the dorsal portion of the carapace is smooth. The appendages are poorly known, but decrease in size from P2 to P4, and the last pair of legs apparently is very small.

*Cristipluma mississippiensis* (Pl. 2, Fig. 13) is a medium sized, oval retroplumid crab with an oval, longitudinally arched carapace ornamented by prominent traverse ridges, shallow grooves, and low ridges. The anterior margin is unknown. Dorsal-lateral margins are angular and strongly reflexed. The dorsal portion of the carapace is smooth. The appendages are unknown.

*Eryma* "flecta*, (Pl. 2, Fig. 14) known only from claws, is ecologically undiagnosable except that is a crab and the strong longitudinal ridging indicates the chelipeds were functionally capable of absorbing considerable stress. This would suggest that this crab was an active predator. *Prehepatus harrisi* (Pl. 2, Fig. 15) is known only from a single claw and is ecologically undiagnosable, except that it is a crab.

That these were epifaunal crabs is substantiated by body shape, ornamentation, and the presence (at least on *D. australis* and *T. subquadratus*) of numerous setal pits (indicating the presence of numerous setae), as well as generalized claws and robust walking legs (P2-P4). The small, reduced, and dorsally directed last pair of appendages (P5) in these two species may indicate these crabs were capable of carrying camouflage on their carapace much like sponge crabs do today.

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### FIGURE 2. Hypothesized food chain for the Blue Springs *Dakoticancer australis* Community showing probable trophic relationships of various community members.

<table>
<thead>
<tr>
<th>Carnivores</th>
<th>Primary Producers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turtles</td>
<td>algae</td>
</tr>
<tr>
<td>Fish</td>
<td>bacteria</td>
</tr>
<tr>
<td>Cephalopods</td>
<td></td>
</tr>
<tr>
<td>Gastropods</td>
<td></td>
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<tr>
<td>Echinoids</td>
<td></td>
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<tr>
<td>Corals</td>
<td></td>
</tr>
<tr>
<td>Bivalves</td>
<td></td>
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<tr>
<td>Scaphopods</td>
<td></td>
</tr>
<tr>
<td>Bryozoans</td>
<td></td>
</tr>
</tbody>
</table>

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### TROPHIC ANALYSIS

This spectrum of crabs, inferred to be epifaunal generalists, would undoubtedly have partitioned food resources available within the habitat on the Cretaceous sea bottom. Rhoads et al. (1972) reconstructed trophic groups based on molluscan assemblages from the Fox Hills Formation of South Dakota. These trophic analyses produced a visual portrayal of benthic molluscan communities present in the Late Cretaceous of South Dakota, but because the analyses were limited to the molluscs, they are of limited value in the definition of ancient marine bottom communities, just as were the decapod community fractions of Bishop (1981a, 1986a, 1987), and Bishop and Williams (1986). In an attempt to enhance the understanding of these hypothesized paleocommunities, I have attempted a reconstruction of a hypothetical paleo-food chain (Fig. 2) and food webs (Fig. 3 and 4) for each of the Coon Creek decapod community fractions. In doing so, I have assumed that the decapods occupied an intermediate level in the web and were feeding opportunistically on prey items in their habitat as omnivores and, in turn, were being fed upon by contemporaneous predators, interacting with parasites, and, ultimately with decomposers. Without discrete biomass numbers, I have assumed the Eltonian pyramid of energy transference through the food chain was operable then, as now, transferring approximately 10% of the energy from one level to the next.

A hypothetical food web has been constructed for the Blue Springs Decapod (*Dakoticancer australis*) Assemblage (Fig. 3). Primary production would have been by phytoplankton in the water mass and possibly by benthic algal or bacterial mats or early water plants. These resources would have formed the base of the food chain as primary producers that were exploited by low-level...
herbivorous or omnivorous zooplankton, foraminifera (Alegret and Thomas, 2007; Alegret et al., 2012), worms, gastropods, and bivalves (including the epifaunal oysters), which would have in turn provided nutrition for corals, echinoderms, decapods, cephalopods, and sea turtles. These organisms would have, in turn, been fed upon by other carnivorous gastropods, cephalopods, asteroids, fish, birds, and possibly sea turtles. Small trophic subsystems would have existed in “compartamentalized environments” such as those occupied by the burrowing thalassinoid shrimp, Protocallianassa mortoni (Bishop and Williams, 2005) and microorganisms inhabiting the substrate (like Thiomargarita, one of the sulfur bacteria). Top predators would have included the mosasuars, large fish, sharks, pterosaurs, sea turtles, and birds.

Although this food web is somewhat speculative and is not quantitative, it is indeed, founded in real trophic relationships found documented throughout the literature and the tropic levels are summarized in Fig. 4.

On a final note, as paleontologists and paleobiologists we always have to speculate on what organisms are NOT preserved in ancient faunas and, in this case, how they would have fit in to the trophic schema. Were there shellless or lightly shelled cephalopods like squid and octopi, soft-bodied jellyfish, or other "cryptic organisms present in the Cretaceous Mississippi Embayment? The answer to this rhetorical question is almost certainly a resounding, YES! But lack of evidence does not allow us to say they had to be present, and modern analogy strongly suggests we ought to keep our minds open to their presence.

CONCLUSIONS

- The patterns of distribution of Avitelmessus grapsoideus suggest that this crab was opportunistic and capable of rapid fluctuations in population size in response to undetermined ecological parameters. Morphologically, Avitelmessus grapsoideus is very unusual because it is gigantic, so much larger than any other North American Cretaceous crab (Pl. 1, Fig. 1) and its cross-sectional profile is so flat, suggesting these animals inhabited a unique niche, perhaps sheltering by tightly pressing, or shallowly burrowing their flattened bodies against the muddy bottom on which they lived and possibly exhibiting a covering behavior.

- The occurrence of Avitelmessus grapsoideus and Dakoticancer australis preserved as elements of decapod assemblages indicates that each of these represents a preserved portion of a decapod paleocommunity. Only one specimen of Avitelmessus has been collected at the Blue Springs Dakoticancer locality; one possible specimen of Dakoticancer australis was collected at one of the three Avitelmessus localities examined by me. Both taxa occur at Union County Lake (Rathbun, 1926). This pattern of occurrence supports the conclusion that these assemblages represent discrete preserved community fractions of opportunistic decapod communities. As further data are accumulated on the occurrence of Avitelmessus and Dakoticancer, this hypothesis can be tested.

- The lobsters recognized from the Coon Creek are all vagrant benthic organisms likely to have sheltered on the sea bottom under debris, in depressions, or crude burrows.
• **Protocallianassa mortoni** is a ghost shrimp that inhabited burrows in the bottom of the Coon Creek sea floor.

• The record for North American Cretaceous hermit crabs is still very sparse and incomplete (Whetstone and Collins, 1982). This is partly due to the generally shallow habitats preferred by hermit crabs, habitats which tend to be high energy environments leading to the rapid destruction of remains of these decapods and the shells they inhabit. The preservation of isolated hermit crab claws (Stenzel, 1945) implies the sheltering of decapods, probably in large gastropod shells. Such shells are present in the Coon Creek faunas (Wade, 1926) but they remain to be examined for taphonomic evidence of habitation by hermit crabs (Walker, 1988).

• The organisms of the Coon Creek Formation can be assigned trophic and ecologic roles in the ancient community, can be ordered into a trophic chain, and can be arranged into food webs which can now be further tested by observational and quantitative data.

• The assignment of fossil taxa to extant taxa, always difficult and often misleading because characteristics utilized in biological classification and paleontological classification rest with soft and hard part morphologies, respectively, is paralleled by the difficulty in assigning fossil taxa to food chains and food webs.

• The probability of numerous functional convergences in morphology of the decapods, could, when articulated with the low preservation potential and fragmentary nature of the decapod record, lead to misinterpretation in assignment of taxa systematic and trophic units. This first attempt at establishing Coon Creek food webs should be quantitatively tested before being generally accepted.

**ACKNOWLEDGEMENTS**

Specimens from the Mississippi Embayment Cretaceous were collected by various groups consisting of Robert Mitchell, the late Richard M. Petkewich, Tony Hemphill, and Rob Priestley, who are thanked for their assistance. The help of the late Ralph Harris, colleague and friend, is especially acknowledged. Direct and indirect support for this study was provided by Georgia Southern University (through the Department of Geology and Geography, the School of Arts and Sciences, and the Faculty Research Committee), the National Science Foundation (Grant DEB 80 11570) and the National Geographic Society (Grants 1629 and 2867-84). Michael Gibson, Stan Dunagan, Katherine McCarville, Fred Rich, and Neal A. Larson reviewed the manuscript, strengthening it with their suggestions. Neal A. Larson helped process the images through PhotoShop®. The final manuscript was seen through the publication process by Terry (Lynn) Harrell for the paleontologists in this symposium and for the Alabama Museum of Natural History. Thank you, Lynn. All acts of omission and commission remain the responsibility of the author.

**LITERATURE CITED**


Bishop, G. A. 1986b. Taphonomy of the North American
Bishop, G. A. 1987. Positive taphonomic feedback in North
American Tethyan Cretaceous decapod-worm associations;
pp. 319–329 in K. McKenzie (ed.), Shallow Tethys 2:
Rotterdam, Balkema Press.
Late Cretaceous Coon Creek Formation, Union County,
Mississippi. Proceedings of the Biological Society of
Bishop, G. A. 1991. The Coon Creek decapod assemblages of
northern Mississippi. Mississippi Geology 12(1,2):8–17.
Bishop, G. A. 2003. Decapod Paleocommunity Structure of
Northern Mississippi and Tennessee, In A 21st Century
Look at the Cretaceous Coon Creek Formation; Geological
Society of America South-central and Southeastern Section
Meeting (52d).
Bishop, G. A. 2007. Mechanism for phosphatization of
Dakotican cucurbit Assemblages in the Late Cretaceous Western
Interior Seaway, USA. 3rd Symposium on Mesozoic and
Cenozoic Decapod Crustaceans - Museo di Storia Naturale
di Milano, May 23–25, 2007 Memorie della Societa Italiana
di Scienze Naturali e del Museo Civico di Storia Naturale di
Milano, Volume XXXV – Fascicolo II.
Shrimp; North Beach, St. Catherines Island, Georgia.
American Museum of Natural History Novitates No. 3042:1–
17.
*Linuparus canadensis*, Carlile Shale (Cretaceous, Turonian),
preservation of burrowing thalassinidean shrimps. Proceedings
Dakoticancranidae (Decapoda, Brachyura) from the Late
Cretaceous of North America and Mexico. Contributions
Blakey, R. 2016. Map of Cretaceous (Late) ca. 70 Ma. Deep Time
(ed.), The fauna of the Ripley Formation on Coon Creek,
Chin, K., J. Bloch, A. Sweet, J. Tweet, J. Eberle, S. Cumbaa, J.
Witkowski, and D. Harwood. 2008. Life in a temperate Polar
sea: a unique taphonomic window on the structure of a Late
Cretaceous Arctic marine ecosystem. Proceedings Royal
communities at risk in shoreline habitats: Burrowing
thalassinoid Crustacea. OCS Study #MMS 94-007. United
States Department of the Interior, Minerals management
Service, Gulf of Mexico OCS Regional Office, New Orleans,
La., 87 p.
Bishop. 1998. Early Cretaceous arthropods from the Tlayúa
Formation at Tepexi de Rodriguez, Puebla, Mexico. Journal
of Paleontology 72(1):79–90.
Gallagher, W. B. 1990. Biostratigraphy and paleoecology of
the Upper Cretaceous-Lower Tertiary sequence in the New
Jersey coastal plain (January 1, 1990) Ph.D. Dissertations
available from ProQuest. Paper AAI9026557.
crabes du Cretace, et la notion de Podotremata Guinot,
Scientifiques du Museum Nationale d'Histoire Naturelle,
Adventure An Epic Tale of Life in a Cretaceous Sea, 35(1)
Department of Mineral Resources, Newsletter.
Hothiuius, L. B. 1974. The lobsters of the Superfamily
Nephropoidea of the Atlantic Ocean (Crustacea, Decapoda).
Biological results of the University of Miami Deep-Sea
Jacobs, B. B. 1983. Genesis and stratigraphic significance of
phosphatic nodules in the Coon Creek Tongue, Ripley
Formation, Union County, Mississippi: Georgia Southern
University, Statesboro, Georgia: Unpublished Bachelor of
ammonite bitten by a mosasaur. University of Michigan
Kear, B. P. 2006. First gut contents in a Cretaceous sea turtle.
Biological Letters 2(1):113–115
gut contents in a Cretaceous ichthyosaur. Proceedings of
crab, *Avitelmessus grapsoideus* Rathbun. Contributions of the
frozen in time: Gregarious behavior of Early Jurassic lobsters
within ammonoid body chamber. PLOS One 7(3):1–9.
Kruta, I., N. Landman, I. Rouget, F. Cecca, and P. Tafforeau.
2011. The Role of Ammonites in the Mesozoic Marine Food
Martin, J. E., and P. R. Bjork. 1987. Gastric Residues Associated
within ammonite body chamber. University of Michigan
Department of Mineral Resources, Newsletter.
Formation on Coon Creek, Tennessee: U. S. Geological Survey
Professional Paper 137.
Rathbun, M. J. 1935. Fossil Crustacea of the Atlantic and Gulf
Coastal Plain. Geological Society of America Special Paper
21–60.


The Late Cretaceous (upper Campanian) cephalopod fauna from the Coon Creek Science Center, McNairy County, Tennessee

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Abstract: There is an unusually rich, Late Cretaceous (upper Campanian), molluscan fauna from the Coon Creek Formation at its type locality, 7 1/2 miles north of Adamsville, McNairy County, Tennessee. The cephalopod fauna is a typical, Late Campanian, Gulf Coast fauna consisting almost entirely of aberrant ammonites and only one tightly coiled, planispiral form. A few authors have published on the fauna from this locality, most notably Bruce Wade, who, in 1926, published on the entire known fauna; Norman Sohl, who later published on the gastropods; Cobban and Kennedy who published solely on the ammonites within the U.S. Geological Survey and Black Hills Institute of Geological Research collections; Brister and Young (2007), who published an overview on the fauna and history of Coon Creek at the type locality from the extensive collections made by the Pink Palace Museum; and Larson (2012) who published on the known cephalopod fauna from this site at the time. There are a couple of important new additions to report but to date no other author has yet addressed the cephalopod fauna and ages of the other localities within the Coon Creek Formation in Tennessee.

Except for *Discoscaphites* the ammonite fauna from the type locality compares both at a species level and stratigraphically with the fauna from the Nacatoch Sand in Kaufman and Navarro Counties of Texas (Stephenson, 1941). Except for *Discoscaphites*, nearly all of the ammonite fauna also correlates to the *Baculites cuneatus* through *Baculites jenseni* Zones of the Pierre and Bearpaw Shales in the Western Interior, most notably to that from the Middle Park and Fort Collins area of Colorado as reported by Kennedy et al. (2000). Because the aragonitic shell of this cephalopod fauna is so well preserved at this locality it makes it possible to give a more complete description of some of the heteromorph ammonite species than had been previously done, most importantly the rib indexes.

Prior to Larson (2003a) both invertebrate and vertebrate researchers published that the fauna from the Coon Creek Fm type locality constituted a lower Maastrichtian age. While one MPPM site in the Coon Creek Fm. from southern Tennessee contains *Sphenodiscus* (lower Maastrichtian?), based upon their fauna, all other known sites are upper Campanian in age. The presence of *Carixoceras comulis*, *Hoploscaphites reesidei*, *Solenoceras reesidei*, *S. texanum*, and *Nostoceras* (*Nostoceras*) *hyatti* places the age of the Coon Creek Tongue at the type locality at upper Late Campanian (72-71.5 MYA), the equivalent age of the *Baculites reesidei* through *B. jenseni* Zones of the Western Interior), at least three other sites are older. This is the first reported occurrence for *Hoploscaphites farinulim* from the Coon Creek Fm. at its type locality and a new species, *Hoploscaphites youngi*, is described.

**KEY WORDS:** Coon Creek Fm, cephalopods, heteromorphs, Gulf Coast, Upper Cretaceous

**INTRODUCTION**

The Coon Creek Fossil Site in southwestern Tennessee is world renowned for its well-preserved, invertebrate fossils. Several authors have published on this fauna, primarily the molluscan fauna that is preserved in almost pristine condition. The first collection of ammonites from the site appears to be by Bruce Wade of the United States Geological Survey (USGS) in the 1910s and 1920s, when the farm belonged to David Weeks. Bruce Wade (1917), made the first record of cephalopods from Coon Creek. Wade (1926) later published a nearly complete monograph...
on the entire known invertebrate fauna from this locality in The fauna of the Ripley Formation on Coon Creek, Tennessee. Norman Sohl and Glenn Scott collected at the site for the USGS in the 1950s and 1960s. Sohl (1960, 1964) described the gastropods that they collected while Cobban and Kennedy (1994a) described the ammonites. Brister and Young (2007) did an extensive report on the site regarding the history, collecting, geology, paleontology and the ongoing science investigations and research of the site. Larson (2012) did a detailed systematic description of all known cephalopods from the type locality.

The current Coon Creek Science Center was formerly known as the Coon Creek Fossil Farm. Mr. A. Z. Smith operated the Coon Creek Fossil Farm in the 1970s and 1980s as a ‘pay to collect’ fossil site. It was at this farm that A. Allen Graffham and Roger Van Cleef first took Black Hills Institute to collect fossils in 1978. From nearly 10 separate trips, Black Hills Institute staff collected more than 180 taxa from the site. The Coon Creek Fossil Farm was sold in 1988 to the Memphis Pink Palace Museum that had the foresight to purchase the site in order to preserve its fantastic paleontological treasure. The Memphis Pink Palace Museum has since assembled the most extensive and comprehensive collections of the fauna and flora from this site to date of more than 300 taxa of invertebrate, vertebrate and plant material. They have also developed unique collecting and preparation techniques to preserve large incredibly prepared blocks of the fauna. Along with the University of Tennessee, Martin, they continue to actively collect the site and have kept it open to researchers and the public ever since. The collections at the Pink Palace Museum are a treasure trove of information and ongoing science investigations and research of the site. The Memphis Pink Palace Museum are a treasure trove of information and include many new, undescribed bivalves, gastropods and other invertebrates that are still unknown from anywhere else in the Gulf Coast, Atlantic Coast or Western Interior Regions.

Along with its amazing gastropod and bivalve fauna, the type locality is renowned for its extensive heteromorph ammonite fauna. To date there have been 6 families, 11 genera and 18 species of cephalopods reported from this single locality and well more than 300 other taxa of mostly invertebrates (Wade, 1926; Sohl, 1960, 1964; Cobban and Kennedy, 1994a; Brewster and Young, 2007; Young, pers. comm., 2014). The cephalopod fauna consists of the ammonites Pachydiscus (Pachydiscus) arkansanus (Stephenson, 1941); Baculites claviformis Stephenson, 1941; B. undatus Stephenson, 1941; Leuconites ornensis (Levy, 1969), Parasolenoceras pulcher Cobban and Kennedy, 1991a; Solenoceras reesidei Stephenson, 1941; S. texanum (Shumard, 1861), Cirroceras conradi (Morton, 1841); Didymoceras cf. D. aurarium Kennedy et al., 2000a; Nostoceras (Nostoceras) approximans (Conrad, 1855); N. (N.) helicinum (Shumard, 1861); N. (N.) hyatti Stephenson, 1941; Hoploscaphites (Jeletzykes) reesidei (Wade, 1926); Hoploscaphites cf. H. brevis (Meek, 1876); Hoploscaphites pumilus (Stephenson, 1941); Hoploscaphites youngi n. sp.; Discoscaphites sp. and the nautiloid Eutrephoceras planoventer Stephenson, 1941.

This is the first reported occurrence for Hoploscaphites undatus from the type locality of the Coon Creek Fm and herein we describe Hoploscaphites youngii n. sp. Also of great importance is the discovery of Discoscaphites from the type locality, the earliest known occurrence from anywhere. The presence of Cirroceras conradi, Hoploscaphites (Jeletzykes) reesidei, Solenoceras reesidei, S. texanum, and Nostoceras (Nostoceras) hyatti places the age of the Coon Creek Tongue at the type locality in the equivalent age of the Baculites reesidei through B. jenseni Zones of the Western Interior, or upper, Late Campanian, 72-71.5 million years ago (Cobban et al., 2006). Discoscaphites is not known from the Campanian at any other site in the world. Cephalopods from other localities place the Coon Creek Formation’s age from the upper Campanian through the lower Cretaceous.

GEOLOGY AND AGE

The Coon Creek Fm. outcrops throughout western and central Tennessee from the north to the south. Throughout the region the Coon Creek Fm. outcrops along creeks and other drainages. Exposures are rare except where construction or weathering has eroded and removed the vegetation. Most deposits are sands and clays with some occasional shale. At the type locality the deposit contains glauconitic sands with occasional sandy, sideritic, calcium carbonate concretions.

The staff at the Memphis Pink Palace maintains collections of fossils from many different outcrops of the Coon Creek Fm. in Tennessee. Most contain cephalopods but not all. Only one site has abundant marine vertebrate fossils but all have a varied and diverse molluscan fauna. No other site in the formation compares with diversity from the type location at the Coon Creek Science Center in McNairy County.

The type locality for the Coon Creek Fm. is near the Coon Creek Science Center in McNairy County, Tennessee and is of upper, Late Campanian age, based on its cephalopod fauna. The Eastview Site in McNairy County is the same age equivalent as at the type locality, based on faunal comparisons. The Selmer Site in McNairy County is youngest and appears to be of lower Maastrichtian age; it contains abundant Baculites (or Eubaculites) sp., Nostoceras sp., Sphenodiscus sp., Eutrephoceras sp., and badly preserved scaphites whose genus cannot be determined. All mentioned sites are Memphis Pink Palace collecting sites and researchers may contact the Museum for more detailed locality information (Table 1).

The geologically oldest site in the Coon Creek Fm. appears to be at the Camden Landfill in Benton County; this site contains abundant Baculites sp., Eutrephoceras, and Placenticeras sp. and is possibly lower, upper or upper middle Campanian. The next youngest is
Table 1. Correlation of a portion of the Gulf Coast with a portion of the Western Interior

This correlative zonation is based on Cobban et al. 2006, A USGS Zonal Table for Upper Cretaceous Middle Cenomanian-Maastrichtian of the Western Interior of the US based on ammonites, inoceramids and radiometric ages. Correlation of the Gulf Coast ammonite zones is based on Bose, 1927; Stephenson, 1941; Cobban and Kennedy, 1991a, b & c, 1993a, b, & c; Kennedy et al., 1996, 2000a; Larson et al., 1997; Landman et al., 2004, Ciampaglio and Phillips (this volume); and Landman and Phillips, personal communication 2016.

<table>
<thead>
<tr>
<th>Age</th>
<th>Western Interior Ammonite zones</th>
<th>Gulf Coast Ammonite zones</th>
<th>Tennessee south central</th>
<th>Mississippi northeast</th>
<th>Texas east-central</th>
<th>Colorado north-central</th>
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</thead>
<tbody>
<tr>
<td>Upper Maastrichtian</td>
<td>Non-existent/ terrestrial</td>
<td>Discoscaphites iris/D. minardi</td>
<td>Owl Creek</td>
<td>Owl Creek/Prairie Bluff Formation</td>
<td>?</td>
<td>Laramie Formation (terrestrial)</td>
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<td></td>
<td>Hoploscaphites nebrascensis</td>
<td>Discoscaphites gulosus / D. conradi</td>
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<td></td>
<td>Hoploscaphites nicolletii</td>
<td>Sphenodiscus pleurosepta</td>
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<tr>
<td>Lower Maastrichtian</td>
<td>Hoploscaphites birkelundi</td>
<td>Baculites clinolobatus</td>
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<td>Upper Campanian</td>
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<td>Baculites jensi</td>
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<td>Baculites reesidei</td>
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<td>Baculites compressus</td>
<td>Didymoceras chevenense</td>
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<td>Exiteloceras jenneyi</td>
<td>Didymoceras stevensoni</td>
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<td>Didymoceras nebrascense</td>
<td>Didymoceras doneziunum</td>
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<td>Baculites scotti</td>
<td>Didymoceras tortum</td>
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<tr>
<td>Middle Campanian</td>
<td>Baculites reduncus</td>
<td>Baculites gregoryensis</td>
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<td>Baculites perplexus</td>
<td>Baculites sp. (smooth sp.)</td>
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<td>Baculites asperiformis</td>
<td>Baculites mclearni</td>
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<td>Baculites obtusus</td>
<td>Baculites scotti</td>
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known as both the Sawmill Site and Mangrum’s Pit in Decatur County; this site contains abundant *Baculites* sp., *Eutrephoceras*, *Placenticeras* sp., and *Didymoceras* sp. (or *Nostoceras*) sp. (lower, upper Campanian?).

At the type locality there seems to be no geological structures so the sediments are stratigraphically stacked with the oldest deposits downstream towards the north end of the Science Center property and the youngest upstream on the hills and on the east and south end of the property. There appears to be some biostratigraphic sorting that takes place as the fauna changes from higher to lower. The concretionary zones containing the fossils seem to be concentrated in the middle zones at this site.

**COLLECTIONS, MATERIAL AND METHODS**

Black Hills Institute of Geological Research (BHI), the Memphis Pink Palace Museum (MPPM), and the University of Tokyo collected all of the cephalopods utilized in the creation of this paper. BHI collections were made during several trips to the area in the 1970s through the 1990s. MPPM has acquired an extensive collection from the site since purchasing the property in the late 1980s. Most of the BHI ammonites were collected from the hard, sandy, limestone concretions that periodically erode out in the creek bottom and creek banks, though some were not associated with any concretions. There appears to be no single concretionary zone, rather, most of the concretions are scattered throughout the lower stratigraphic layers at the type locality. The cephalopods in the MPPM collections and a few in the BHI collection (most commonly *Baculites* and occasional *Nostoceras* and *Eutrephoceras*) were made from the isolated specimens found in poorly lithified sandstone, along with abundant gastropods and pelecypods in the creek bottom near the Coon Creek Science Center. Stephenson and Monroe (1940) classified the poorly consolidated sandstone at the type locality as ‘friable, very fine, micaceous, and light grey sand’.

Most specimens of cephalopods exhibit signs of breakage and/or predation. Very few specimens are complete and many are merely portions of phragmocones or partial body chambers. There were a host of predators (fish, reptiles, and other cephalopods) in the sea that would prey on the ammonites while they were alive, and a variety of scavengers (crabs, lobsters, and other cephalopods), along with the high energy of the sea, that would cause postmortem damage. It is for these reasons that it is rare for complete ammonite shells to be found. Healed pathologies, due to bites, are quite common in much of the ammonite fauna from the Western Interior (Larson, 1998, 2003b; Landman et al., 2010) yet at Coon Creek there is only a single ammonite specimen of *Nostoceras hyatti* (MPPM 1972.46.414) that exhibits healed pathologies in the shell. Why there is only one specimen when most ammonites show the ability to heal is unknown.

**SYSTEMATIC PALEONTOLOGY**

**Class Cephalopoda** Cuvier, 1797

**Order Ammonoidea** Zittel, 1884

**Suborder Ammonitina** Hyatt, 1889

**Superfamily Desmoceratoidea** Zittel, 1895

**Family Pachydiscidae** Spath, 1922

**Genus and Subgenus Pachydiscus (Pachydiscus)** Zittel, 1884

**Name Derivation:** *Pachydiscus* = (pachy = thick) + (discus = disc) = thick disc (Zittel, 1884).

**Type species:** The type species for the genus *Pachydiscus* is *Ammonites neubergicus*, as described by Hauer (1858; p. 12, plate 1, figs. 1-3; and plate 2, figs. 1-2), through subsequent designation by de Grossouvre (1894; p. 177).

**Diagnosis:** The genus is composed of broad, rounded, planispiral whors with a deep, moderately involute umbilicus. The flanks are rounded; they can be smooth, or ornamented with strong, widely spaced ribs. Microconchs are generally one-half to one-fourth the size of the macroconchs, and are typically ornamented with ventrolateral and umbilical tubercles. Macroconchs may also have umbilical tubercles. The suture pattern is very complex, and consists of auxiliary lobes, saddles, and foliars.

**Species Pachydiscus (Pachydiscus) arkansanus** (Stephenson, 1941)

Figure 1A-B as *Parapachydiscus arkansanus* Stephenson, 1941; p. 418-419, plate 84; plate 85, figs. 1-3; plate 86, figs. 1-5; plate 87, figs. 1-3

**Pachydiscus (Pachydiscus) arkansanus** (Stephenson). Cobban and Kennedy, 1991b; p. F2-F4, plate 1, fig. 4; plate 2-4; text fig. 2.

**Pachydiscus (Pachydiscus) arkansanus** (Stephenson). Emerson et al., 1994; p. 78, 358.

**Pachydiscus (Pachydiscus) arkansanus** (Stephenson). Larson et al., 1997; p. 61.

**Pachydiscus (Pachydiscus) arkansanus** (Stephenson). Larson 2012; p. 4-5, plate 1, figs. 1-2.

All Figures natural size unless otherwise noted (see scale with figures)
**Name Derivation:** *arkansanus* = named after the state of Arkansas (Stephenson, 1941), where the type specimen was collected.

**Type Specimen:** The holotype of *Pachydiscus* (*Pachydiscus*) *arkansanus*, as described by Stephenson (1941; p. 418-419, plate 84; plate 85, fig. 1; plate 86, fig. 1; and plate 87, figs. 1-2), is USNM 77286, from the Nacatoch Sand, near Washington, in Hempstead County, Arkansas. Paratypes, USNM 20962, and USNM 21094 (plate 85, figs. 2-3; plate 86, figs. 2-5; and plate 87, fig. 3) are from the Nacatoch Sand near Kaufman, Texas.

**Material:** There are two specimens in the collections of the Memphis Pink Palace Museum. One (MPPM 1972.46.431) is a portion of the body chamber (Fig. 1A), and the second (MPPM 1972.46.432) is a section of phragmocone (Fig. 1B). Both specimens depict the ribs typical of the species, as Stephenson (1941) described them. Based on similar specimens, the larger specimen (a small portion of the body chamber) would have measured perhaps as much as 25 cm across.

**Diagnosis:** *Pachydiscus (P) arkansanus* is a moderately large planispiral ammonite with an involute, broadly rounded venter, slightly rounded flanks, and a deep, moderately involute umbilicus. Umbilical shoulder is steep and rounded; the species has broad, moderately strong ribbing visible only when the shell is preserved. Ribs bend back toward the earlier whorls, then become fairly straight (rectiradiate) on the middle portion of the flanks, and bend towards the aperture (prorsiradiate) on the ventral shoulder. Sutures are typical of the genus.

**Occurrence:** *Pachydiscus (P) arkansanus* has been found at the Coon Creek Fm., McNairy County, Tennessee. The species has also been found in the Nacatoch Sand, near Washington, in Hempstead County, Arkansas; the Nacatoch Sand and Neylandville Marl near Kaufman, Texas; the *Exteteloceras jenneyi* Zone of the Pierre Shale in Larimer County, Colorado; the *Baculites compressus* Zone of the Bearpaw Shale in Rosebud County, Montana; and doubtfully from the DeGrey and Gregory Members of the Pierre Shale in Lyman County, South Dakota.

**Discussion:** This is the first recorded occurrence of *Pachydiscus (P) arkansanus* from the type locality of the Coon Creek Tongue of the Ripley Fm. It had previously been found from rocks of the same age with similar fauna, so it was only a matter of time before specimens were discovered from this site. Sutures are typical of the genus, and because they are not present, or at least visible, in any of the specimens found at Coon Creek, they will not be discussed any further.

**Suborder Ancyloceratina** Wiedmann, 1966

**Superfamily Turrilitoidea** Gill, 1871

**Family Baculitidae** Gill, 1871

**Genus Baculites** Lamarck, 1799

**Name Derivation:** *Baculites* = (baculum = staff) + (ites = stone) = stone staff (Lamarck, 1799).

**Type species:** The type for the genus of *Baculites* is *Baculites vertebralis* Lamarck (1799), by subsequent designation in Meek (1876; p. 391).

**Diagnosis:** The genus is composed of a mostly straight to slightly dorsally curved shell, except for the ammonitella which has a minute, planispiral coil. Cross section can be round, to ovate, to very compressed. Flanks can be smooth to coarsely ribbed. The venter may have large ribs or corrugations, or it can be smooth. Adults often have large, broad, concentric ribs, and a low degree of taper. Juveniles often have little ornamentation and more taper due to rapid growth. The dorsal lappet on the aperture is generally short (the length is nearly equal to the whorl height of the baculite from flank to flank); the ventral lappet is about twice the length of the dorsal lappet.

**Species Baculites claviformis** Stephenson, 1941

**Figure 2A-H**

*Baculites asper* Morton. Whitfield, 1892; p. 278, plate 46, figs. 10-11.

*Baculites asper* Morton?. Weller, 1907; p. 823, plate 109, figs. 6, 7.

*Baculites grandis* Hall and Meek. Wade, 1926; p. 182, plate 60, figs. 8, 12.

*Baculites claviformis* Stephenson, 1941; p. 403, plate 77, figs. 6-8; plate 78, figs. 1-6.

*Baculites sp*. Reeside; p. 117, plate 68, fig. 9.


*Baculites claviformis* Stephenson. Cobb and Kennedy, 1994a; plate 8, figs. 1-8; plate 10; plate 11, text fig. 3.

*Baculites claviformis* Stephenson. Emerson et al., 1994; p. 322, 394.


*Baculites claviformis* Stephenson. Larson, 2012; p. 6-7, plate 2, figs. 1-6.

**Name Derivation:** *claviformis* = (clava = club) + (formis = form) = club form (Stephenson, 1941), named as such because it is shaped like a club.

**Type Specimen:** The holotype of *Baculites claviformis*, USNM 77241, was designated by Stephenson (1941; p. 403, plate 77, figs. 1-3; plate 78, figs. 1-2). The paratypes consist of two figured (USNM 77242; plate 78, figs. 1-6)
Figure 2. A-H Baculites claviformis Stephenson, 1941. A. BHI 5298 [x 0.5], a large macroconch with partial body chamber and phragmocone, 7 cm x 39 cm. B. MPPM 1972.46.403 [x 0.5], large phragmocone of a macroconch, 7.5 cm x 28 cm. C. MPPM 1972.46.404 [x 0.5], large macroconch phragmocone, 7 cm x 26 cm. D. Cross section of MPPM 1972.46.404 [x 0.5]. E. Microconch, MPPM 1972.46.405, with partial body chamber and phragmocone. F. A partial body chamber and phragmocone, BHI 2022. G. Cross section of BHI 2022. H. Two juvenile specimens on matrix, both with partial body chambers and phragmocones, BHI 2028.
and five unfigured specimens (identified as USNM 77243 and USNM 77244). All types are from the Nacatoch Sand, near Kaufman, Texas.

**Material:** Three partial specimens were studied from the Memphis Pink Palace collection (MPPM 1972.46.403, MPPM 1972.46.404, MPPM 1972.46.405), and three specimens from the collection of Black Hills Institute of Geological Research (BHI 2022, BHI 2028, BHI 5298).

**Amended Diagnosis:** *Baculites claviformis* have broad concentric ribs or undulations on the flanks throughout the shell growth spaced about two per shell diameter. Mature forms taper slowly and have a compressed cross section. Venter is rounded, dorsum is rounded to flat and flanks are slightly rounded. Large adult body chambers have a highly ribbed shell with small fine ribs. Sutures are typical for Gulf Coast Campanian baculitids.

**Description:** Juvenile specimen (BHI 2028; Fig. 2H) has smooth flanks with indistinct ribs and an ovate to slightly compressed cross section. Adult forms have broad concentric swellings or undulations on the flanks (primarily on the body chamber), the shell tapers slowly, and has a compressed cross section. Venter is rounded, the dorsum is rounded to flat; the flanks are slightly rounded. Large adult body chambers also have a highly ribbed, outer layer shell. These ribs are thickened growth lines that parallel the shape of the aperture. The ribs, present on BHI 5298 (Fig. 2A), show that *Baculites claviformis* has a rib index of 8 (the number of ribs per whorl height, at the portion of the shell where the height is measured). Broad thickened undulations on the flanks of the body chambers of mature specimens occur about once for every two times the whorl height (or an index of 1/2 when the whorl height of the ammonite is measured at its thickest points, between the broad undulations on the flanks).

**Occurrence:** The species *Baculites claviformis* Stephenson is Late Campanian, Late Cretaceous in age. It has been reported from the Coon Creek Fm. in McNairy County, Tennessee; the Neylandville Marl in Delta, Rockwall, Kaufman, and Navarro Counties, Texas; Nacatoch Sand in Kaufman and Navarro Counties, Texas; and the Nacatoch Sand in Hempsted County, Arkansas. It has not yet been identified or found from the Western Interior, or from the Navesink Fm. in New Jersey so it may be restricted to only the Gulf Region.

**Discussion:** *Baculites claviformis* is quite common in the Coon Creek Tongue of the Ripley Fm. in the creek bed near the Coon Creek Science Center. It is easy to distinguish from the associated *Baculites undatus* by its compressed form versus the very ovate and almost noded form of *Baculites undatus*.

**Species Baculites undatus** Stephenson, 1941

**Figure 3A-L.**


**Name Derivation:** *undatus* = “wavy” for its wavy flanks (Stephenson, 1941).

**Type Specimen:** The holotype of *Baculites undatus*, USNM 77245 and two paratypes, USNM 77246 and 77247 were figured by Stephenson (1941; plate 79, figs. 5-10). All the types came from the Nacatoch Sand. The holotype and one paratype were found near Chatfield, Texas, the other paratype was collected near Corsicana, Texas.

**Material:** Six partial specimens were utilized from the Memphis Pink Palace collection (four are illustrated here: MPPM 1972.46.398, MPPM 1972.46.401, MPPM 1972.46.406, MPPM 1977.22.3), and eight specimens from the collection of the Black Hills Institute of Geological Research (five are illustrated herein, BHI 2017, BHI 2018, BHI 2023, BHI 2030, and BHI 5310).

**Diagnosis:** *Baculites undatus* have broad concentric ribs or undulations on the flanks throughout the shell growth spaced about one per shell diameter. Mature forms taper slowly, and have a very ovate cross section. Venter and the dorsum are rounded and flanks are moderately rounded. Large adult body chambers have a highly ribbed shell with small fine ribs. Sutures are typical for Gulf Coast Campanian baculitids.

**Amended Description:** Juvenile specimen (BHI 2017; Fig. 3F) has smooth to broadly ribbed flanks, and a round to ovate cross section. All forms have broad concentric ribs or undulations on the flanks throughout the shell growth spaced about one per shell diameter. Mature forms taper slowly, and have a very ovate cross section. Venter and the dorsum are rounded, and flanks are moderately rounded. Large adult body chambers have a highly ribbed shell with small fine ribs. Like *Baculites claviformis*, the ribs appear to be thickened growth lines that parallel the shape of...
the aperture. Fine ribs are visible on MPPM 1977.22.3 (Fig. 3A-B) and occur on and between the undulations, indicating that *B. undatus* has a rib index of 8.

**Occurrence:** *Baculites undatus* Stephenson is Late Campanian in age. From the Gulf Coast region, it is known from the Coon Creek Fm., McNairy County, Tennessee, the Saratoga Chalk in central Arkansas, and the Nacatoch Sand of Navarro County, Texas. From the Atlantic Coast, it is known from the Navesink Fm. in New Jersey, and the Mount Laurel Sand in Delaware. In the Western Interior, *Baculites undatus* is known from the *Didymoceras cheyennense* through the *Baculites reesidei* Range Zones in northern New Mexico and Colorado, and from the *Baculites compressus* and *Baculites cuneatus* Range Zones in Meade and Pennington Counties, South Dakota.

**Discussion:** *Baculites undatus* has strong affinities to *B. baculus* of the lower Maastrichtian from the Western Interior. *B. baculus* most likely descended from this Gulf Coast species. There is not a complete enough sequence of ammonites identified from the Gulf Coast region to fully understand their impact on the Late Cretaceous faunas of the Western Interior but it is understood that its impact was immense. Many forms of Campanian and Maastrichtian ammonites appear to have had their origins in the Gulf Coast region and migrated into the Western Interior. *Baculites undatus* was not successful in its colonization of the Western Interior during the Late Campanian, but after the demise of the endemic *B. eliasi*, its descendant, the Gulf Coast migrant *B. baculus*, became the dominant baculitid in the Western Interior.

**Family Diplomoceratidae** Spath, 1926

**Genus Lewyites** Matsumoto and Miyauchi, 1984

**Name Derivation:** *Lewyites* = named for the Oron phosphate field in Israel (Lewy, 1969).

**Type Species:** Holotype of *Lewyites oronensis* by designation is the same as for the genus, and is the original of Lewy, *Idiohamites (?) oronensis* HU 30021a (Lewy, 1969; p. 127, plate 3, figs. 10-11), in the collection of the Hebrew University, Jerusalem. It was described from the Mishash Fm. at the Oron phosphate field in Israel.

**Occurrence:** *Lewyites oronensis* is a Late Campanian, but after the demise of the endemic *B. eliasi*, its colonization of the Western Interior during the Late Campanian, but after the demise of the endemic *B. eliasi*, its descendant, the Gulf Coast migrant *B. baculus*, became the dominant baculitid in the Western Interior.

**Type Specimen:** Holotype of *Lewyites oronensis* by designation is the same as for the genus, and is the original of Lewy, *Idiohamites (?) oronensis* HU 30021a (Lewy, 1969; p. 127, plate 3, figs. 10-11), in the collection of the Hebrew University, Jerusalem. It was described from the Mishash Fm. at the Oron phosphate field in Israel.
parasolenoceras pulcher has a straight shaft followed by a partial coil. Whorl section is compressed, with the flank width about one and one-half times the ventral width. Ribs are weak on the dorsum, to strong and slightly curved (prorsiradiate) on the flanks. Dorsum and flanks are slightly rounded with a flat venter bordered by ventrolateral tubercles. Two to three flank ribs that join together on the ventrolateral shoulder form ventrolateral tubercles. The tubercles originally were probably bases of tall spines, but they are now represented as low nodes that project nearly straight out from the venter.

BHI 2016 (Fig. 1C) is a fragment of a body chamber with part of the aperture. It has broad, flexuous ribs that all have ventrolateral tubercles. The whorl section measures approximately 56 mm high x 34 mm wide. One row of ventrolateral tubercles is missing, so the width of the specimen is conjecture. Flanks and venter are slightly rounded. Flexuous, prorsiradiate ribs extend across the flanks, each one culminating in an elongated tubercle at either side of the venter. Rectiradiate rib stretches between the tubercles across the slightly rounded venter. Rib crests are steeply rounded, and rib valleys are broad. Each rib on the flank of the body chamber near the aperture is about 5 mm across, but these vary with the crowding near the aperture, with wider ribs farther up on the flank. The specimen exhibits some holes on the shell and at the aperture. Because it is so incomplete and the holes are quite distinct, it is probably all that is left from some fish’s lunch.

Occurrence: Besides being found at the type locality of the Coon Creek Fm., Lewyites oronensis (Lewy) has been found in the Mishash Fm. in Israel; the Nacatoch Sand in Texas; the Saratoga Chalk in Arkansas; the Navesink Fm. in New Jersey; the Bacinutes cuneatus Zone of the Pierre Shale in Middle Park, Colorado; and the B. resedeli Zone, Larimer Sandstone Member of the Pierre Shale near Fort Collins, Colorado.

Discussion: BHI 2009, USNM 449406, and USNM 449407 (Cobban and Kennedy, 1994a) are identical in ribbing and form as those specimens figured and assigned to Lewyites oronensis by Kennedy and Cobban (1993), and Kennedy et al. (2000c). The author believes that the North American Lewyites is a unique species and is not synonymous with that from Israel.

BHI 2016 (Fig. 1C) is not complete enough to definitively assign it to the species Lewyites oronensis. The specimen also resembles the apertural portion of Didymoceras nebrascense from the Western Interior. It may be possible that it could be the aperture of Didymoceras, a genus that is found at this locality. The specimen does not compare with Nostoceras or Cirrroceras from the site, and thus is obviously not from either of those genera. Cobban and Kennedy (1994a) assigned this fragment to the genus Lewyites, because of its comparison with a specimen from the Navesink Fm. of New Jersey. Cobban (1974b) assigned it to Exiteloceras oronensis, which was later identified as Lewyites oronensis. Exiteloceras rude Kennedy et al. (2000b), was recently described from the Navesink Fm. in New Jersey, and the Coon Creek fragment may be that species. However, unless some other specimens are found to dispute Cobban and Kennedy’s 1994 decision, this aperture fragment is assigned to the species Lewyites oronensis.

Genus Parasolenoceras Collignon, 1969

Name Derivation: Parasolenoceras = (para = alongside or resembles) + (solen = pipe) + (ceras = horn) = alongside, or resembling a pipe horn (Collignon, 1969). Named for the two shafts that bend or fold alongside of each other, or for the two shafts that resemble each other.

Type Species: Collignon (1969; p. 44, plate 530, figs. 2087-2088) described the type of Parasolenoceras splendens from the upper Campanian of Madagascar.

Diagnosis: Two widely separated, non-touching, small, nearly parallel (or oblique) shafts connected by an elbow or curved section of shell. The elbow and larger shaft comprise the body chamber in adult forms, the initial shaft consists of the phragmocone.

Discussion: Wright et al. (1996) thought that Parasolenoceras should be a subgenus of Pseudoxybeloceras. Neither Kennedy nor Cobban have ever ascribed to that interpretation, and the author also sees no reason to follow Wright’s classification for this genus. Parasolenoceras somewhat resembles a small or early form of Lewyites and also looks remarkably like a juvenile Didymoceras nebrascense (see figs. 8B, 8D in Kennedy et al. 2000c; p. 13) but whether the two are synonymous remains to be proven.

Species Parasolenoceras pulcher Cobban and Kennedy, 1991a

Figures 1F-J; 4M Parasolenoceras pulcher Cobban and Kennedy, 1991a; p. C4, plate 1, figs. 7-9.


Parasolenoceras pulcher Cobban and Kennedy. Larson et al., 1997; p. 48, unnumbered fig.

Parasolenoceras pulcher Cobban and Kennedy. Larson 2012; p. 12-13, plate 1, figs. 5-9; plate 4, figs. 12-13.

Name Derivation: pulcher = beautiful (Cobban and Kennedy, 1991a).

Type Specimen: The holotype of Parasolenoceras pulcher, as described by Cobban and Kennedy (1985; p. C4, plate 1, figs. 7-9), is USNM 442107, and the four paratypes (all designated by the number USNM 442108), are all from the Nacatoch Sand, near the town of Washington, Hempstead County, Arkansas.
Material: Two specimens from the Memphis Pink Palace Museum collection (MPPM 1972.46.429, MPPM 1972.46.430), and four specimens from the Black Hills Institute of Geological Research collections (BHI 1986, BHI 2032, BHI 5295). BHI 5295 is a multiple specimen, with two Parasolenoceras pulcher, four Solenoceras texanum, and one Cirroceras conradi.

Amended Diagnosis: The description of Parasolenoceras pulcher follows the genus. Widely separated, small, nearly parallel, compressed initial shaft and an ovate body chamber shaft, connected by a slightly curved elbow. Flanks are slightly rounded to moderately rounded, venter is flat. MPPM 1972.46.430 (Fig. 1F) has a length of 32.5 mm. It consists of two incomplete shafts with a rib index of 6 on the larger shaft. Cross section is ovate. Ventrolateral tubercles consist of tiny spines on every rib. The dorsal and flank are somewhat rounded, venter is flat. MPPM 1972.46.429 (Fig. 1I) and BHI 1986 (Fig. 1J) are both ovate to slightly compressed in cross section. The rib index on these specimens is 6 on MPPM 1972.46.429 and 8 on BHI 1986. The two most complete Parasolenoceras (with phragmocone, body chamber, and aperture) occur on BHI 5295 (Fig. 4M), with the most complete specimen lying underneath the Cirroceras.

Occurrence: Parasolenoceras pulcher is known from the Coon Creek Fm. in Tennessee, the Nacatoch Sand in Arkansas, and the B. reesidei Zone, Pierre Shale, northern Colorado.

Discussion: Parasolenoceras seems to be closely related to Solenoceras, specimens of juvenile Solenoceras greatly resemble juvenile Parasolenoceras. It is difficult to determine the genus when only the phragmocone is present. The main determining factors are the cross section, the shafts in contact with each other, constrictions in Solenoceras, and the rib index.

Genus Solenoceras Conrad, 1860

Name Derivation: Solenoceras = (solen = pipe) + (ceras = horn) = pipe horn (Conrad, 1860).

Type Species: Conrad (1960, p. 284) designated Hamites annulifer Morton (1842, p. 213), as the type for the genus Solenoceras.

Diagnosis: Two parallel shafts in contact with each other connected by a tight elbow leaving a small opening at the inside of the elbow. Ribs are distinct, generally straight to prorsiradiate. Whorl section is ovate to circular. Small ventrolateral tubercles or spines are present on either side of the generally flat venter. In mature specimens the two parallel shafts are of nearly equal length. The ammonitella and initial whorls is yet unknown.

Species Solenoceras reesidei Stephenson, 1941

Figure 4A-G; M

Solenoceras reesidei Stephenson, 1941; p. 401, plate 77, figs. 1-3.
Solenoceras cf. S. reesidei Stephenson. Lewy, 1969; p. 126, plate 3, figs. 7a-7b.
Solenoceras reesidei Stephenson. Emerson et al., 1994; p. 311, 392.
Solenoceras reesidei Stephenson. Larson et al., 1997; p. 47.

Name Derivation: reesidei = named in honor of John B. Reeside, Jr. (Stephenson, 1941). John B. Reeside, Jr. was a mid 1900s USGS geologist and paleontologist. He was one of the first to subordinate the marine Cretaceous strata of the Western Interior into ammonite Range Zones.

Type Specimen: The holotype of Solenoceras reesidei (USNM 77238), as designated by Stephenson (1941; p. 401, plate 77, figs. 1-3), and four unfigured paratypes (USNM 77239) are from the Neylandville Marl near the town of Corbett, Navarro County, Texas.


Amended Diagnosis: Two parallel, circular, slightly expanding shafts in contact with each other folded at an elbow. In mature individuals, the initial shaft forms a sharp elbow and the straight body chamber shaft bends back against the initial phragmocone shaft and both shafts are of nearly equal length. The shafts are finely
ribbed, with nearly straight inclined ribs that dip from the
dorsum to the venter (prorsiradiate on the initial shaft, 
rrursiradiate on the body chamber shaft). Rib index on 
the flanks is 6 ribs per whorl height. On the initial shaft, 
the ribs occasionally bear minute spines on either side of 
the venter. On the body chamber shaft, the ribs all bear 
minute ventrolateral spines that are connected by fine ribs 
across the venter. There are widely spaced constrictions 
present throughout both shafts.

BHI 1988 (Fig. 4F), BHI 1989 (Fig. 4B), and MPPM 
1972.46.424 (Fig. 4C), are microconchs; BHI 1987 (Fig. 
4A) and BHI 1993 (Fig. 4G) are juvenile macroconchs; 
and BHI 1990 (Fig. 4E) and BHI 1991 (Fig. 4D) are 
macroconchs. The diameter of both whorls just above the 
eflob is 6.2-6.3 mm on the microconchs, and 8.5 to 9.8 
mm on the macroconchs.

**Occurrence:** From the type locality of the Coon Creek 
Fm., McNairy County, Tennessee; the Nacatoch Sand and 
Neylandville Marl of Kaufman and Navarro Counties, 
Texas; and from the *B. compressus* and *B. reesidei* Zones of 
northern Colorado.

**Discussion:** *Solenoceras reesidei* differs from *Solenoceras 
texanum* by its finer ribbing and smaller size, particularly 
in the microconch.

**Species Solenoceras texanum** (Shumard, 1861)

*Psychoceras texanum* Shumard, 1861; p. 189.

*Psychoceras texanum* Shumard, Hyatt, 1894; p. 580.

*Oxybeloceras texanum* (Shumard). Adkins, 1928; p. 213.

*Solenoceras texanum* (Shumard). Stephenson, 1941; p. 399, 
plate 77, figs. 4-5; plate 79, figs. 1-4.

*Solenoceras cf. S. texanum* (Shumard). Lewy, 1969; p. 127, 
plate 3, fig. 8.

*Solenoceras texanum* (Shumard). Cobban and Kennedy, 
1991a; p. C3, plate 1, figs. 1, 6.

*Solenoceras cf. S. texanum* (Shumard). Kennedy and 
Cobban, 1995c; p. 424.

*Solenoceras texanum* (Shumard). Emerson et al., 1994; p. 
311, 392.

*Solenoceras texanum* (Shumard). Cobban and Kennedy, 

*Solenoceras texanum* (Shumard). Kennedy et al., 2000a; p. 
14-15, plate 1, figs. 10-16; plate 4, figs. 1-7; text fig. 11.

*Solenoceras texanum* (Shumard). Larson, 2012; p. 14-16, 
plate 1 fig. 9; plate 4, figs. 8-12.

**Name Derivation:** *texanum* = named for the state of 
Texas (Shumard, 1861).

**Type Specimen:** The type of *Solenoceras texanum*, 
described by Shumard from the Nacatoch Sand, near 
Chatfield Point and Corsicana in Navarro County, Texas, 
is lost. This prompted Stephenson (1941) to designate 
a lectotype (p. 399, plate 79, figs. 1-2) from specimens 
that were collected from the same area as the type. The 
lectotype, designated as USNM 21092a, is also from the 
Nacatoch Sand, near Chatfield, Navarro County, Texas.

**Material:** Five partial specimens in the Memphis Pink 
Palace collection with one illustrated (MPPM 1972.46.423), 
and nine specimens from the collection of Black Hills 
Institute of Geological Research with five illustrated (BHI 
1986 [Fig. 1J with *Parasolenoceras*], BHI 1992, BHI 1994, 

**Amended Diagnosis:** The description follows as for the 
genus with two parallel, slightly compressed, expanding 
shafts in contact with each other. The initial, smaller shaft 
(phragmocone) forms a sharp elbow and bends back 
against itself with a second, larger shaft (body chamber). 
Shafts are heavily ribbed, with nearly straight ribs that 
are inclined from the dorsum to the venter (prorsiradiate 
on the initial shaft, rursiradiate on the body chamber 
shaft). The rib index on the flanks is 4 to 5 ribs per whorl 
height. All ribs bear ventrolateral spines on either side 
of the venter and are connected by strong ribs across the 
venter. There are irregular vertical constrictions present 
throughout the shafts.

**Description:** BHI 1996 (Fig. 4H) is the most complete 
of all of the *Solenoceras* collected from the site to date. 
Both shafts measure 67 mm, and the rib index is 5.
Small ventrolateral spines are present on the entire body 
chamber. The body chamber shaft, and the diameter of 
the elbow, has a much smaller diameter than other 
specimens of *S. texanum*; it is believed to be a microconch. 
BHI 1994 (Fig. 4L), BHI 1995 (Fig. 4I), and BHI 1992 (Fig. 
4K) all have much larger body chamber diameters than 
BHI 1996. Diameter of the shafts just above the elbow on 
BHI 1996 is 7.6 mm and 7.8 mm on MPPM 1972.46.423 
(Fig. 4J) indicating that both are most likely microconchs. 
The diameter of the two shafts just above the elbow on 
BHI 1994, BHI 1995, and BHI 1992 is 10.5 mm, indicating 
that they are probably macroconchs. The rib index on all 
specimens of *Solenoceras texanum* from Coon Creek seems 
to be 5; that also follows the description of the species.

**Occurrence:** From the Gulf Coast region, *Solenoceras 
texanum* is known from the Coon Creek Fm., McNairy 
County, Tennessee; the Saratoga Chalk in central 
Arkansas; and the Nacatoch Sand, and Neylandville Marl 
in Navarro County, Texas. From the Atlantic Coast, it is 
known from the Navesink Fm. in New Jersey. From the 
Western Interior, it is known from the *Baculites cuneatus 
and B. reesidei* Zones in Colorado. Outside the US, it has 
been reported from the Mishash Fm. in Israel.

**Discussion:** *Solenoceras texanum* differs from *Solenoceras 
reesidei* by its larger size and its fewer number of ribs per 
whorl width (rib indices). In *Solenoceras texanum*, ribs are 
widder, shafts are larger, whorl section is more compressed, 
and the ventrolateral spines are larger. Macroconchs 
are much wider at the elbow than microconchs in both 
species.
Family Nostoceratidae Hyatt, 1894

Genus Cirroceras Conrad, 1868

**Name Derivation:** Cirroceras = (circros = curl) + (ceras = horn) = curl horn (Hyatt, 1894).  

**Type Species:** The genus *Cirroceras* was named by Conrad (1868; p. 730), for the specimen of *Ammonceratites conradi* described by Morton (1841; p. 109). The type specimen was collected near Arneytown, New Jersey from the Navesink Fm., and is in the collections of the Philadelphia Academy of Sciences.

**Diagnosis:** Helical whorls, often widely separated from each other, with a body chamber that curves like the other whors but turns up at the aperture. Whorl section is somewhat rounded with a flat, flattened venter. Large ventrolateral tubercles, or spines, border the venter and are joined together by broad ribs. Tubercles on the lower portion of the whors are larger and often fewer than those on the upper side. Two or three broad rounded ribs join together on the flanks to form the ventrolateral tubercles. Ribs on the dorsum are usually weak.

**Discussion:** *Cirroceras* probably had its origin from *Didymoceras*. On some specimens, the initial whors are similar, but other specimens show a great difference in cross section, ribbing, and tubercles. The body chamber on *Cirroceras* does not extend as far below the initial whors as that of *Didymoceras*. There are two distinct forms of large, loosely coiled whors found at Coon Creek. The form with the flat venter, and fewer ribs is assigned to *Cirroceras*, the form with the round venter and higher rib index is assigned to *Didymoceras*. Species within the genus *Cirroceras* coil both left handed (sinistral) and right handed (dextral).

**Species Cirroceras conradi** (Morton, 1841)  

*Ammonceratites conradi* Morton. Morton, 1841; p. 212, plate 10, fig. 1.  
*Heteroceras navarroensis* Shumard, 1861; p. 190.  
*Heteroceras conradi* (Morton). Whitfield, 1892; p. 269, plate 45, figs. 9-11, 14.  
*Helicoceras navarroensis* Shumard. Boyle, 1893; p. 146  
*Heteroceras conradi* (Morton). Johnson, 1905; p. 27.  
*Turritites (Heteroceras) conradi* (Morton). Diener, 1925; p. 90.  
*Helicoceras navarroense* Shumard. Wade, 1926; p. 184, plate 61, figs. 8-11; plate 62, figs. 1-2.  
*Helicoceras navarroense* Shumard. Shimer and Shrock, 1944; plate 246, fig. 10.  
*Didymoceras* sp. ind. Sornay, 1959; p. 222, plate 7, figs. 3a-b.  

*Didymoceras cf. navarroense* (Shumard). Lewy, 1969; p. 115, plate 1, fig. 1.  
*Didymoceras navarroensis* (Shumard). Cobban, 1974a; p. 16, plate 11, figs. 1-4; text fig. 13.  
*Didymoceras navarroense* (Shumard). Cobban and Kennedy, 1994a; p. B4-B5, plate 3, fig. 6; plate 4, figs. 1-8.; plate 5, figs. 1-5, 13-23; plate 6, figs. 4-6; text fig. 1.  
*Didymoceras navarroense* (Shumard). Emerson et al., 1994; p. 312-313, 4 unnumbered figs., p. 392.  
*Nostoceras (Didymoceras) conradi* (Morton). Wright et al., 1996; p. 247.  
*Cirroceras conradi* (Morton). Larson et al., 1997; p. 51, unnumbered fig.  
*Cirroceras conradi* (Morton). Kennedy et al., 2000a; p. 11-13, plate 1, figs. 29-37; plate 5, figs. 1-6; text fig. 9.  
*Cirroceras conradi* (Morton). Larson 2012; p. 16-18, plate 4, fig. 13; plate 5, figs. 1-8b; plate 6, fig. 4; plate 13, figs. 1a-b.

**Name Derivation:** conradi = named for T. A. Conrad (Morton, 1841), an 1800s invertebrate paleontologist and a colleague of Morton at the Philadelphia Academy of Sciences.

**Type Specimen:** The holotype of the species *Cirroceras conradi*, is the same as that for the genus, and was designated by Morton (1841; p. 109), for the specimen of *Ammonceratites conradi* collected in the Navesink Fm. near Arneytown, New Jersey.

**Material:** One specimen from the University of Tokyo (UMUT MM 28422), five specimens from the Memphis Pink Palace Museum (four illustrated: MPPM 1972.46.409, MPPM 1972.46.410, MPPM 1972.46.411, MPPM 1972.46.412), and thirteen specimens from the collection of the Black Hills Institute of Geological Research (five illustrated: BHI 2010, BHI 2012, BHI 2013, BHI 5293, BHI 5294).

**Amended Diagnosis:** Early whors are typically rounded, low spired, open helical whors that are not in contact with each other. Dorsum is rounded, flanks are slightly rounded, and the venter is slightly rounded to flat. Flanks are ornamented with broad ribs. The venter exhibits ribs between the ventrolateral tubercles or spines. Every other wide rib on the flanks forms ventrolateral tubercles, ventral ribbing is prorsiradiate and widely spaced, located between offset tubercles. Larger whors have 20 to 23 tubercles per whorl; smaller widely open whors have many more ribs per whorl. The rib index is 4 per whorl height throughout the growth on nearly all specimens, not matter what the size of the shaft. There are four ribs and two ventrolateral tubercles per whorl height. The small rib index on *Cirroceras* distinguishes it from the other heteromorph ammonites found at Coon Creek.

**Description:** BHI 2010 (Fig. 5E) and BHI 5293 (Fig. 6F) are two nearly complete specimens, missing primarily the early whors. BHI 2013 (Fig. 5H,I) and BHI 2012 (Fig. 5G) show the early whors, but are missing the body...
chambers. Whorls are nearly equal in size on the flanks, venter, and dorsum. UMMT MM 28423 (Fig. 14A-B) is the most complete, consisting of two full whorls (partial phragmocone and nearly complete body chamber). BHI 5294 (Fig. 4M) is important because it is the only known specimen that shows the initial whorls of *Cirroceras* (minus the ammoniella and first partial coil).

**Occurrence:** From the Gulf Coast region, *Cirroceras* is known from the Coon Creek Fm., McNairy County, Tennessee; the Saratoga Chalk in central Arkansas; and the Nacatoch Sand, and Neylandville Marl of Kaufman and Navarro Counties in Texas. From the Atlantic Coast, it is known from the Navesink Fm. in New Jersey. From the Western Interior, it is known from the Baculites cuneatus and *B. reesidei* Zones in Colorado. From outside the US, it has been reported only from the Mishash Fm. in Israel.

**Discussion:** *Cirroceras conradi* differs greatly from *Didymoceras* of the Western Interior. The whorl section of *Didymoceras* is typically round, versus almost square for *Cirroceras*. *Didymoceras* ribs are not as wide or broad, the tubercles are usually not as massive, and the venter is not flat. Also, *Didymoceras* is typified with a long, distended, hook-like body chamber, *Cirroceras* has a body chamber that does not separate from the other coils very much and bends up at the aperture. The different specimens of *Cirroceras* and *Didymoceras* from this site exhibit large differences in their shape, cross section, and ribbing on the earlier whors.

BHI 5293 (Fig. 6F) is a multiple, the ribbing on one of the heteromorphs becomes much more fine on the first coil of the phragmocone. This is the only specimen that exhibits this feature, and it cannot be explained unless it is a different species or a coil of *Didymoceras*.

**Genus Didymoceras** Hyatt, 1894

**Name Derivation:** *Didymoceras* = (didymos = double) + (ceras = horn) = double horn (Hyatt, 1894).

**Type Species:** The type for the genus *Didymoceras* is the specimen of *Ancyloceras nebrascensis* Meek and Hayden (1856; p. 71), from designation by Hyatt (1894; p. 574).

**Diagnosis:** Helical whorls in close contact, or separated. The whorl section of *Didymoceras* is typically round, the ribbing is fine to coarse, ventrolateral tubercles are common in all stages of growth, ribs are generally broad and distinct, and the venter is slightly rounded. *Didymoceras* is typified with a long, distended, hook-like or U-shaped body chamber. Species within the genus *Didymoceras* coil both left handed (sinistral) and right handed (dextral).

**Species Didymoceras cf. D. aurarium** Kennedy et al., 2000

![Figure 6A-H](image)


**Material:** Five specimens, BHI 2014, one-half of a whorl; just before the body chamber makes its downward U-shape; BHI 5289, one-third of whorl and pathological; BHI 5290 is a small section of phragmocone; MPPM 1972.46.412 and MPPM 1972.46.413 are early whors of *Didymoceras*.

**Description:** BHI 2014 (Figs. 6A-B) has sub-circular whorls, with narrow ribs and ventrolateral tubercles. The ribs follow the description of the genus but are very prorsiradiate on the upper portion of the whorl, slightly rursiradiate to rectiradiate across the venter, and rursiradiate on the underside of the whorl. Tubercles on this specimen occur on the upper ventrolateral shoulder as paired ribs join together to form bullae. Ribs (sometimes pairs of ribs) across the venter join again to form tubercles on the lower ventrolateral shoulder. Whorls are rounded on the dorsum and slightly rounded on the flanks and almost flat on the venter. Rib index is 7 per whorl height on the early whors, averaging 40 to 50 ribs per whorl. The whorl sections were apparently widely separated in early whors and close together to almost touching in latter and larger whors (Figs. 6C-D). The *Didymoceras* fragments exhibit a few possible constrictions that are present sometimes from the dorsum sometimes from the venter.

**Occurrence:** Until more complete specimens are discovered this species is only known from the Coon Creek Fm. at its type locality.

**Discussion:** Cobban and Kennedy (1994a) assigned a single specimen of *Didymoceras* to the species of *D. hornbyense* (a Pacific Coast Cretaceous ammonite) because there were no other *Didymoceras* found in any of the ammonite zones from the same approximate age as the sediments of Coon Creek. These specimens differ greatly from *D. hornbyense* in the width of the venter, the shape of the ribs, and the ribs across the venter, and the placement of tubercles.

This specimen differs from *Didymoceras draconis* Stephenson (1941), found in rocks of equivalent age in Texas, Colorado, and New Jersey, further described and illustrated by Kennedy et al. (2000a); and Kennedy et al. (2000b). It differs by the extreme curvature in the ribbing, the placement of tubercles on the ventral shoulders, expanding widely helical whors, and the shape of the venter.

The cephalopod fauna from the *Baculites reesidei* Zone in Larimer County, Colorado compares very favorably with the fauna of Coon Creek. *Didymoceras aurarium* (Kennedy et al., 2000a) has three to four very deep constrictions per whorl bordered by high ribs, but this feature is variable; early whors have five or more constrictions, latter whors three, and the constrictions are shallower. Predictably there may be only a few to no constrictions on the body chamber. In as much as there are no deep constrictions anywhere on any of these specimens, they cannot be
positively assigned to this species.

Of the specimens collected to date, none can be assigned to a named species of Didymoceras. There are almost enough specimens from different parts of the shell to describe a species, but without the presence of a body chamber, or a nearly complete specimen, further collecting of more specimens would be advised before giving it a formalized name.

**Genus** and **Subgenus Nostoceras (Nostoceras)** Hyatt, 1894

**Name Derivation:** Nostoceras = (nostos = return) + (ceras = horn) = return horn (Hyatt, 1894). Named as such because it bends back on itself.

**Type Species:** The type for the genus Nostoceras is the specimen of Nostoceras stantoni Hyatt (1894; p. 569); which is the same as Ancyloceras? approximans Conrad (1855; p. 266).

**Diagnosis:** Nostoceras is typified by a tightly coiled helical spire on a large U-shaped body chamber with the aperture, in mature individuals, nearly touching and lying underneath the spire. There are fine ribs on the initial whorls, and coarser ribbing on the body chamber, and periodic constrictions primarily on the phragmocone. Small spines may exist on the initial whorls, and large tubercles are present on the body chamber. Species within the genus Nostoceras coil both left handed (sinistral) and right handed (dextral).

**Species Nostoceras (Nostoceras) approximans** (Conrad, 1855)

Figure 7A-1

Ancyloceras? approximans Conrad, 1855; p. 266.
Nostoceras stantoni Hyatt, 1894; p. 570.
Nostoceras stantoni var. aberrans Hyatt, 1894; p. 572.
Nostoceras stantoni var. prematurum Hyatt, 1894; p. 572.
Nostoceras stantoni var. retrorsus Hyatt, 1894; p. 579.
Nostoceras stantoni (Hyatt). Stephenson, 1941; p. 407, plate 80, figs. 1-5.
Nostoceras stantoni prematurum Hyatt. Stephenson, 1941; p. 409, plate 80, figs. 6-8.
Nostoceras stantoni aberrans Hyatt. Stephenson, 1941; p. 409, plate 80, figs. 9-10.
Nostoceras (Nostoceras) approximans (Conrad). Conrad. Cobban and Kennedy, 1994a; p. B2-B3, plate 1, figs. 4-9, 18, 19, 22-24; plate 2, figs. 1-6, 11; plate 3, figs. 1-3.
Nostoceras (Nostoceras) approximans (Conrad). Emerson et al., 1994; p. 304, 391.
Nostoceras (Nostoceras) approximans (Conrad). Kennedy et al., 1995; plate 6, figs. 9-12.
Nostoceras (Nostoceras) approximans (Conrad). Wright et al., 1996; p. 247, fig. 191(6).
Nostoceras (Nostoceras) approximans (Conrad). Kennedy et al., 2000a; p. 6-7, plate 1, figs. 1-4.
Nostoceras (Nostoceras) approximans (Conrad). Kennedy et al., 2000b; p. 10-12, figs. 4S-4T, 5A-5E, 5K-5O.

**Name Derivation:** approximans = approximate = close together (Conrad, 1855). Named as such for the initial whorls, which are connected and close together.

**Type Specimen:** The holotype of Nostoceras (Nostoceras) approximans is the original specimen described by Conrad (1855; p. 266); and illustrated by Conrad (1860; plate 47), from the Nacatoch Sand, White River, Arkansas, currently in the collection at the Philadelphia Academy of Sciences.

**Material:** Two partial specimens from the Memphis Pink Palace collection (MPPM 1972.46.417, MPPM 1972.46.419), and five specimens from the collection of Black Hills Institute of Geological Research (BHI 2003, BHI 2008, BHI 5301a, BHI 5311, BHI 5312).

**Amended Diagnosis:** Adult specimens of N. (N) approximans have four to five whorls of increasing size on top of a thick U- or J-shaped body chamber. Whorl section is round, thick or fat, with round flanks and a round dorsum, and a slightly rounded venter. Diameter of the whorls remains small, giving the species a tall, high spire. Ventrolateral tubercles are small prominent on the last whorl before the body chamber, and weak on the body chamber itself. Initial whorls have a high spire angle of 53 to 92 degrees, 45 to 55 ribs per whorl, up to four constrictions per whorl (Cobban and Kennedy, 1994a). The rib index (number of ribs per whorl diameter) is normally 6.

**Occurrence:** From the Gulf Coast region, Nostoceras (Nostoceras) approximans is known from the Coon Creek Fm., McNairy County, Tennessee, the Saratoga Chalk in central Arkansas, and the Nacatoch Sand of Navarro County, Texas. From the Atlantic Coast, it is known from the Navesink Fm., in New Jersey. In the Western Interior, it has been found in the B. reesidei Zone, Larimer Sandstone Member of the Pierre Shale, near Fort Collins, Colorado.

**Discussion:** N. (N) hyatti is a larger species with much coarser distinct ribs with widely separated ventrolateral spines or tubercles N. (N) helicinum is also much larger, with the most abundant and finer ribs on the initial whorls. Neither of the other two species have the high spire typical of N. (N) approximans. Along with the high spire, N. (N) approximans has the thickest whorls in proportion to any of the species of Nostoceras, and is much smaller, making it fairly easy to distinguish from the other species.
Figure 8. A-G Nostoceras helicinum (Shumard, 1861). A. The backside of the macroconch on BHI 2141. B. BHI 2141, a double with a macroconch (left), and a microconch (right). C. Whorls on hypotype, BHI 2002 (Cobban and Kennedy, 1994). D. A double specimen, BHI 5314. E. MPPM 1972.46.418 showing the long spines on the early whorls. F. Partial low spired whors of BHI 1999. G. BHI 5301b, two and a partial Nostoceras helicinum, found with BHI 5301a.
Species *Nostoceras (Nostoceras) helicinum* (Shumard, 1861)

Figures 7K; 8A-G

*Turrilites helicinus* Shumard, 1861; p. 191.

*Turrilites helicinus* Shumard. Boyle, 1893; p. 293.

*Nostoceras helicinum* (Shumard). Hyatt, 1894; p. 573.

*Nostoceras helicinum* (Shumard). Stephenson, 1941; p. 410, plate 80, figs. 11-12.

*Nostoceras helicinum crassum* Stephenson, 1941; p. 412, plate 81, figs. 7-8.

*Nostoceras helicinum humile*. Stephenson, 1941; p. 412, plate 81, figs. 4-6.

*Nostoceras helicinum* (Shumard). Haas, 1943; p. 2, figs. 1a, 6-7.

*Nostoceras helicinum var. crassum* Stephenson. Easton, 1960; fig. 11.1-26.

?*Nostoceras helicinum* (Shumard). Howarth, 1965; p. 383, plate 8, figs. 3a-b, 5a-c.


?*Nostoceras helicinum* (Shumard). Lewy, 1969; p. 120, plate 4, figs. 1-21; text fig. 6.

*Nostoceras (Nostoceras) helicinum* (Shumard). Cobban, 1974b; p. 8, plate 81, figs. 9-12. The lectotype (USNM 21103a) is also from the Nacatoch Sand, near Chatfield, Navarro County, Texas.

*Nostoceras (Nostoceras) helicinum* (Shumard). Kennedy and Cobban, 1993c; p. 414, 417, figs. 8.6-8.12, 9.1, 10.1-10.23.

*Nostoceras (Nostoceras) helicinum* (Shumard). Stephenson, 1941; p. 412, plate 81, figs. 1-3.

*Nostoceras (Nostoceras) helicinum* (Shumard). Emerson et al., 1994a; p. 304, 391.

*Nostoceras (Nostoceras) helicinum* (Shumard). Kennedy et al., 1995; plate 6, figs. 1-3.

*Nostoceras (Nostoceras) helicinum* (Shumard). Larson, 2012; p. 22-23, plate 7, fig. 10; plate 8, figs. 1-6.

**Name Derivation:** helicinum = helical = named for its whorls which ascend, or descend in a helical manner (Shumard, 1861).

**Type Specimen:** The type specimen of *Nostoceras (Nostoceras) helicinum* described by Shumard from the Nacatoch Sand, near Chatfield, Navarro County Texas, is lost, prompting Stephenson (1941) to designate a new type (p. 410, plate 80, figs. 11-12). The lectotype (USNM 21103a) is also from the Nacatoch Sand, near Chatfield, Navarro County, Texas.

**Material:** Three partial specimens in the Memphis Pink Palace collection (two figured: MPPM 1972.46.418, MPPM 1958.37.21), and eight from the collection of Black Hills Institute of Geological Research (five figured: BHI 1999, BHI 2002, BHI 2141, BHI 5301b, BHI 5314). BHI 2141 is the only complete *N. (N.) helicinum* identified from the site, a microconch and a macroconch (Figs. 8A-B).

**Amended Diagnosis:** *N. (N.) helicinum* consists of about four whorls located on top of a larger U-shaped body chamber. *N. (N.) helicinum* has a low spire angle of 92 to 115 degrees, 68 ribs per whorl, up to four constrictions per whorl, and every third rib has a sharp tubercle (Cobban and Kennedy, 1994a). Rib index is 7 to 9 on the phragmocone whorls, and 6 to 7 on the body chamber. The phragmocone whorl diameter on this species is smaller and more slender than on either of the other species. There are occasional and somewhat indistinct umbilical bullae on *N. (N.) helicinum*, and this is the only species of *Nostoceras* that has them. Ribs on the body chamber are slightly prorsiradiate to rectiradiate and somewhat widely spaced. Ventrolateral tubercles are quite large and distinct.

**Occurrence:** From the Gulf Coast region, *Nostoceras (Nostoceras) helicinum* is known from the Coon Creek Fm., McNairy County, Tennessee, the Saratoga Chalk in central Arkansas, and the Nacatoch Sand of Navarro County, Texas. From the Atlantic Coast, it is known from the Navesink Fm. in New Jersey. From outside the US, it has been reported from the Mishash Fm. in Israel and from Angola, France, and Spain.

**Discussion:** *Nostoceras (Nostoceras) helicinum* has the lowest spire, narrowest, or most slender whors, is finer ribbed, and has more non-tuberculate ribs than either *N. (N.) hyatti* or *N. (N.) approximans*. *N. (N.) helicinum* also has umbilical bullae on the body chamber the other species do not. Cobban and Kennedy (1994a) described *N. (N.) helicinum* as the least common species of *Nostoceras* at Coon Creek but this author does not agree; it appears to be as common as *N. (N.) hyatti*. Cobban and Kennedy (1994a) described both *N. (N.) hyatti* and *N. (N.) helicinum* as being much larger than *N. (N.) approximans*. With all of these differences, it is believed that the best diagnosis for characters in species identification is that *N. (N.) helicinum* has the most-narrow whors of any described species.

Howarth (1965) illustrated two specimens as *Nostoceras helicinum* (Shumard). The major differences seem to be a different rib index, and the more rectiradiate ribbing, and bifurcated ribs emanating from the tubercles on the Coon Creek specimens but not on the Angola specimens. Lewy (1969) noted that *N. helicinum* from Israel are too few and incomplete and may only represent a subspecies of *N. helicinum*, or a different species. The best way to determine if these specimens are indeed the same as the North American species would be to compare the sutures. There do not seem to be any suture drawings published, except for Howarth (1965) and the Angola specimens. None of the specimens from Coon Creek are suitable for determining their sutures.

Species *Nostoceras (Nostoceras) hyatti* Stephenson, 1941

Figures 7J; 9A-J


*Nostoceras hyatti* Stephenson, 1941; p. 410, p. 81, figs. 9-12.

? *Nostoceras hyatti* Stephenson. Howarth, 1965; p. 378-381, plate 9, figs. 1-2; plate 10, fig. 1; text fig. 16.
Nostoceras cf. N. hyatti Stephenson. Lewy, 1969; p. 118, plate 1, figs. 4a-b.

Nostoceras hyatti Stephenson. Cobban, 1974b; p. 10, plate 5, figs. 1-21; plate 6, figs. 1-12; plate 7, figs. 1-10; plate 8, figs. 1-30; text fig. 7, p. 10.

Nostoceras pozaryskii Blaszkiewicz, 1980; p. 26, plate 10, figs. 1-5, 8-9, 11-15.

Nostoceras (Nostoceras) hyatti Stephenson. Kennedy, 1986; p. 90, plate 20, figs. 7-9.

Nostoceras (Nostoceras) pozaryskii Blaszkiewicz. Kennedy, 1986a; p. 92, text fig. 31A.


Nostoceras (Nostoceras) hyatti Stephenson. Kennedy et al., 1995; plate 6, figs. 7-8; plate 7, figs. 9-10.

Nostoceras (Nostoceras) hyatti Stephenson. Cobban and Kennedy, 1994a; plate 1, figs. 10-12, 16-17, 20-21, 25-27; plate 2, figs. 7-10, 12-15; plate 3, figs. 4-5, 9-11.


Nostoceras (Nostoceras) hyatti Stephenson. Kennedy et al., 2000b; p. 12, figs. 6, 7G-I.

Nostoceras (Nostoceras) hyatti Stephenson. Larson 2012; p. 23-25, plate 7, figs. 8-9; plate 9, figs. 1-7.

Name Derivation: hyatti = After Alpheus Hyatt (Stephenson, 1941), a late 1800s ammonite paleontologist, who is responsible for many of our modern views regarding the phylogeny and development of ammonites. He also published much regarding the different ammonites from the Late Cretaceous of North America.

Type Specimen: The holotype of Nostoceras (Nostoceras) hyatti was designated by Stephenson (1941; plate 81, fig. 9), and is at the Smithsonian Institution (USNM 77258). It is from the Nacatooch Sand on Postoak Creek, near Corsicana, Navarro County, Texas. Two paratypes (USNM 77259) are illustrated in the same publication and on the same plate, figs. 10-12.


Amended Diagnosis: Nostoceras (N.) hyatti has a moderate spire angle of 65 to 80 degrees, 43 to 60 ribs per whorl, 20 to 25 of the ribs per whorl have tubercles (Cobban and Kennedy, 1994a). The rib index is 6 on the early whorls, and 3 to 4 on the body chamber per whorl section. There are four to five initial whorls of increasing size, on top of a large U-shaped body chamber. Ribs are widely spaced on the body chamber, and become narrower towards the early stages. There appear to be irregular, periodic, weak constrictions that are somewhat disguised because of its very high ribs. Constrictions on N. (N.) hyatti are much weaker and less distinct than on Nostoceras helicinum.

Five complete specimens utilized for this paper: BHI 2114a, BHI 2000, BHI 5300, MPPM 1972.46.414 and MPPM 1972.46.420. The species show a host of varieties, some specimens are three-fifths the size of others, probably a result of sexual dimorphism.

Occurrence: From the Gulf Coast region, Nostoceras (Nostoceras) hyatti is known from the Coon Creek Fm., McNairy County, Tennessee, the Saratoga Chalk in central Arkansas, and the Nacatoch Sand of Navarro County, Texas. From the Atlantic Coast, it is known from the Navesink Fm. in New Jersey. From the Western Interior, it is only known from the Baculites jenseni Zone of the Pierre Shale in southern Colorado. Elsewhere, it has been reported from Poland, France, Spain, Israel, and Angola.

Discussion: N. (N.) hyatti has coarser ribs (especially on the body chamber), lack of lateral bullae, weak constrictions instead of prominent constrictions, high prominent ribs on the whorls, and lack of delicate or fine ribs on the hook to differentiate it from N. (N.) helicinum and N. (N.) approximans. Both N. (N.) hyatti and N. (N.) helicinum are much larger than N. (N.) approximans, and N. (N.) hyatti is the largest. Whorl diameter of N. (N.) helicinum is more slender than N. (N.) hyatti or N. (N.) approximans.

Howarth (1965) collected ten specimens of Nostoceras hyatti from Barra do Dande, Angola. The sculpturing of these shells compares favorably with those from the Atlantic and Gulf coast regions of North America. There are, however, a number of minor differences in the sculpturing of the ribs, the rib index, and the shape and placement of the tubercles, which could be interpreted as a different species. Except for N. (N.) helicinum, other species of ammonites from the North American upper Campanian among the fauna from Barra do Dande, Angola, are absent. Kennedy (1986a) considered that there were enough similarities between N. (N.) pozaryskii and N. (N.) hyatti to be considered as synonyms; the author has not examined these, or the specimens from Angola or Israel. The best way to tell if the Nostoceras from the other countries are indeed N. (N.) hyatti would be a comparison of the sutures and the rib index. Since the specimens of Nostoceras from Coon Creek are not suitable to take a suture sample from, there cannot be any further postulation as to whether or not they are the same.

The N. (N.) hyatti fauna from the Navesink Fm. of the Atlantic Highlands, New Jersey was directly correlated with the uppermost Campanian fauna from Europe (Kennedy et al., 2000). This correlation would put the Coon Creek fauna at the top of the Campanian. The correlation of the Coon Creek fauna with the Western Interior fauna also places it at the top of the Campanian in the Baculites jenseni Zone. The Baculites jenseni Zone (the ammonite Zone directly above B. reesidei) has been designated, and
is accepted by researchers worldwide, as the uppermost Campanian (Gill and Cobban, 1966).

**Family Scaphitidae** Gill, 1871

**Genus Discoscaphites** Meek, 1870

**Name Derivation:** Discoscaphites = (disco = flat) + (scaph = boat) + (ites = stone) = a flat stone boat (Gill, 1871).

**Type Species:** The type for the genus Discoscaphites as designated by Meek (1870; p. 429), is Ammonites conradi Morton (1834; p. 39, plate 16, fig. 3), from the Prairie Bluff Chalk of Alabama. The type was also figured by Jeletzky and Waage (1978; plate 1, figs. 1-4.), and Wright et al. (1996; p. 264, figs. 3a-b).

**Amended Diagnosis:** Discoscaphites is a multinodose scaphitid form, usually with four to five rows of tubercles on the flanks, all nearly equally spaced starting from above the umbilical margin and extending to the edge of the venter. Venter is typically narrow, bordered on either side by a row of ventrolateral tubercles. There is a second row of nearly equivalent sized tubercles set in on the flank from the ventrolateral tubercles about the same distance as the width of the venter. A third row of tubercles is located between the second row of tubercles and the umbilical margin, and a fourth row of tubercles is located on the umbilical shoulder. Robust macroconchs are usually one and one-half to two times as large as the smaller more gracile microconchs. Ribs are fine to coarse, but not as distinct as on the other scaphitid forms. Body chambers are short with recurved hooks.

**Species Discoscaphites sp.**

Figure 10A-B

Discoscaphites sp. Larson, 2012; p. 26-27, Plate 10, Figs. 1a-b.

**Material:** The material consists of only one incomplete anterior portion of the body chamber (MPPM 1972.46.433). It is only a fragment of body chamber, from the last septa to just before the hook, with umbilical swelling on the mid portion of the shaft.

**Description:** The overall specimen is 32.6 mm in height, 20 mm across the widest part of the flank, and 19 mm thick at the widest part. There are four rows of tubercles (and bullae) present on either flank. The outer, or ventrolateral tubercles are short and thick, between 5 to 6 mm apart. The next set of tubercles are the same size as the ventrolateral tubercles, and are offset between the ventrolateral tubercles about 4 mm down on the flank. A third row of tubercles (slightly smaller) is located between the second row of tubercles and the umbilical tubercles. There are large umbilical bullae located above the umbilical margin, on the umbilical shoulder; they number one for every two of the second and third row of midflank tubercles. Ribbing is fairly indistinct, seemingly located between tubercles, and extending from the umbilical bullae to pairs of midflank tubercles. It looks much like one of the specimens of Discoscaphites gulosus from the Prairie Bluff Chalk of Alabama, as described by Morton (1834), and figured by Jeletzky and Waage (1978; plate 2, figs. 8-10).

**Occurrence:** This Discoscaphites sp. (Late Campanian) is only known from the Coon Creek Fm., at its type locality, McNairy County, Tennessee. However, Discoscaphites of Late Maastrichtian age are known from the Prairie Bluff Chalk of Alabama and Mississippi, the Owl Creek Fm. in Mississippi, the Kemp Clay and Corsicana Marl of Texas, the Monmouth and Severn formations of Maryland, the Navesink Fm. in New Jersey, and the Fox Hills Fm. of North and South Dakota. Discoscaphites was also reported and illustrated by Stephenson (1941 p. 428-431; plate 90, figs. 1-6, plate 91, fig. 6) but they were discovered in the top 15-20 feet of the Kemp Clay at the top of the Navarro Fm. (well above the Nacatoch Sand) and much higher than the geological strata at the type locality of the Coon Creek Fm.

**Discussion:** The specimen was collected from the creek bed at the Coon Creek Science Center. Roy Young (and other members of the MPPM staff) were present when it was found and they verify that it was found in place from the same zone where most of the ammonite fauna is collected (in the creek bed from the middle of the property below the Science Center). Because the specimen was found in situ, and there are no formations of a Maastrichtian age present anywhere near the site, and the matrix in the body chamber and the preservation of the shell matches other ammonites from the type locality, it does not appear possible that this was washed in or brought in from anywhere else.

Discoscaphites differs from Trachyscaphites with its shortened and abbreviated body chamber length. Even though there is not a complete body chamber preserved, there is enough to classify this specimen as Discoscaphites. Because of its position in the geological record, this particular specimen would constitute the closest missing link between Discoscaphites and Trachyscaphites.

This is the earliest known, recorded occurrence for Discoscaphites, by almost 3 million years. It should constitute a new species of Discoscaphites, but it would be better if more specimens, and preferably a more complete specimen were found. More extensive collectig should result in the discovery of additional specimens from this site, and with more specimens, the description of a new species can then take place.

**Genus Hoploscaphites** Nowak, 1911

**Name Derivation:** Hoploscaphites = (hoplo = tool, shield, or armor) + (skaphe = boat) + (ites = stone) = an armored stone boat (Nowak, 1911).

**Type Species:** The type is, by original designation,
Ammonites constrictus described by Sowerby (1818; p. 189, plate 184A, fig. 1).

**Amended Diagnosis:** *Hoploscaphites* is defined as small to large scaphitid form with a broad range of compression in cross section ranging from robust (fat, round) to almost flattened with a tightly coiled phragmocone. *Hoploscaphites* has a nearly straight shaft on microconchs, and a more robust, shorter shaft on the macroconchs; the shafts can be long or short. *Hoploscaphites* generally has abundant fine to coarse ribs on the phragmocone, wider ribs on the body chamber shaft, and finer ribs on the hook-like body chamber. Ventrolateral tubercles (from small to generous in size) are generally present on the last part of the phragmocone and on most of the body chamber. Small umbilical bullae may occur above the umbilical shoulder on the body chamber shaft but not in all forms.

As for the family, macroconchs are robust, with broad ribs, prominent tubercles on either side of the venter and around the umbilicus on the umbilical shoulder, and a slight swelling near the umbilicus in the middle portion of the body chamber. Microconchs are smaller, more compressed, and have a body chamber with a much straighter shaft. Ribs may be fine to coarse. Tubercles occur mid flank, and on either side of the venter and are commonly small on the later portion of the phragmocone, larger on middle portion of the body chamber, and smaller again near the aperture.

**Discussion:** The genus *Hoploscaphites* has undergone many name changes throughout its history. Owen (1852) named the type *Scaphites nodosus* after a specimen collected in the Baculites compressus Zone of the Pierre Shale from Sage Creek, in present day South Dakota. Nowak (1911) included the “nodosus” taxon under the junior synonym name for *Scaphites* that he called *Hoploscaphites*. Later, Nowak (1916) placed the “nodosus” group under the name of *Acanthoscaphites*. Both the genus *Acanthoscaphites* and *Scaphites* were used interchangeably until Gill and Cobban (1966) placed the “nodosus” group back under the genus name *Hoploscaphites*.

Depending on the author, the names of *Hoploscaphites*, *Acanthoscaphites*, and *Scaphites* were all used indiscriminately until 1983. It was at this time that Riccardi (1983) created the genus *Jeletzkytes* for the robust Campanian and Maastrichtian North American scaphitid forms and reserved the name *Hoploscaphites* for the compressed Campanian and Maastrichtian scaphitid forms. The width of the flank (whorl width) of *Jeletzkytes* was described as generally one to one and one-half times that of the width of the venter (whorl height), versus the width of the flank of *Hoploscaphites* that was described as generally two to three times the width of the venter.

Wright et al. (1996), made *Jeletzkytes* synonymous with *Hoploscaphites*. Landman et al. (2010) also agreed with that determination and placed those robust Late Campanian scaphitid forms from North America under the genus *Hoploscaphites*. This author agrees that there are good reasons to eliminate *Jeletzkytes* as a distinct genus but believes that *Jeletzkytes* should be preserved as a subgenus to further describe and separate the fat, robust forms of *Hoploscaphites*. Both *Acanthoscaphites* and *Hoploscaphites* are currently still used for the Campanian and Maastrichtian scaphitid forms in Europe although a revision may be in progress (personal communication Landman, 2014).

**Species* Hoploscaphites pumilus** (Stephenson, 1941)

Figure 10E-H; 11A-E

*Scaphites pumilus* Stephenson, 1941; p. 425-426, plate 90, figs. 10-12.

*Hoploscaphites pumilus* (Stephenson, 1941) Cobban, 1974b; p. 16, plate 11, figs. 9-12; text fig. 13.

*Hoploscaphites pumilus* (Stephenson, 1941) Kennedy, 1986b; p. 1018, plate 5, figs. 18-20.


*Hoploscaphites pumilus* (Stephenson, 1941) Kennedy et al., 1995; plate 6, figs. 1-2.

*Hoploscaphites pumilus* (Stephenson, 1941) Kennedy et al., 2000b; p. 18-20, figs. 9A-F.

**Name Derivation:** *pumilus* = dwarfish, diminutive; little; a dwarf pygmy.

**Type Specimen:** As designated by Stephenson (1941), the type is USNM 21041 from the Nacatoch Sand, Navarro Group, near Chatfield, Texas.

**Material:** The material consists of several specimens, a nearly complete macroconch (MPPM 1996.39.11) and a microconch (MPPM 1996.39.15) and two partial phragmocones BHI 1984 and MPPM 1972.46.408.

**Diagnosis:** Stephenson (1941; p. 46) described the species as such: “Shell small, closely coiled, and plumply rounded in early stages, straightening out and becoming strongly flattened on the sides and on the venter in the living chamber; the sides diverge a little inwardly....”

**Discussion:** *Scaphites pumilus* was described by Stephenson (1941) and redescribed as *Hoploscaphites pumilus* by Kennedy and Cobban (1993) and Kennedy et al. (2000). The ribs of *H. pumilus*, although somewhat variable, give rise to ventrolateral tubercles, umbilical margin tubercles, and occasionally inner ventrolateral tubercles. It is quite small for any contemporary scaphitids, making the name appropriate.

**Species* Hoploscaphites youngi* n. sp.

Figures 10C-D; 11F-I

*Scaphites brevis*, Stephenson, 1941; p. 425-426, plate 90, figs. 7-8.

*Hoploscaphites cf. H. brevis*, Larson, 2012; p. 28-29, plate 10, figs. 2a-b
**Name Derivation:** youngi = after the discoverer, Roy Young, conservator, preparator, and collector with the Memphis Pink Palace Museum from 1974 to the present.

**Type Specimen:** The holotype, MPPM 1996.39.18, was found in the Coon Creek Fm. at its type locality, 7 1/2 miles north of Adamsville, McNairy County, Tennessee.

**Material:** The material consists of one complete macroconch MPPM 1996.39.18, a nearly complete microconch MPPM 25 found in 2014, an incomplete phragmococone BHI 1982, and several incomplete specimens within the MPPM collection (for example see Fig. 10C-D).

**Diagnosis:** Compressed scaphitid form of small to medium size, with strong, thick, widely spaced, arcuate ribs on the phragmocone that originate from umbilicus where they form bullae at mid-flank and then become fasciculate and rectiradiate. Ribs fine to nearly absent on the body chamber, bifurcating at bullae. Ribs on the phragmocone are rursiradiate and fork 2/3 up the flank from the umbilicus. Bullae begin ½ to 2/3 mid-flank on the phragmocone. Tubercles number 4 to 5 and are widely spaced with one at the hook, and three on the shaft above the umbilical shoulder on the body chamber. Ventrolateral tubercles begin near the end of the phragmocone and continue on the body chamber where they become clavate to the aperture. They are separated by two secondary ribs and two additional ribs that originate at tubercles and cross over the venter. Flanks are mostly flat to slightly convex, venter is rounded to compressed. Flank width (whorl width) is two to three times that of the ventral width (whorl height) at its largest point.

**Description of type:** The holotype MPPM 1996.39.18 (Fig. 11G-I) measures 51.7 mm high by 40 mm across by 20 mm thick at the widest point. It is nearly complete, lacking only the final outer portion of the aperture. Compressed, small to medium size with strong, rectiradiate ribs. On the phragmocone, strong, thick, widely spaced, arcuate ribs originate from umbilicus where they form bullae at mid-flank and then become fasciculate in groups with some bifurcating, some trifurcating and some intercalatory and all rectiradiate. The few, widely spaced primary ribs originate from the umbilical region, while the secondary ribs originate as intercalatory from bullae mid flank. Ribs on the body chamber are all fine and bifurcate at bullae. Ribs become thicker after they bifurcate, nearly all of them remain rectiradiate. Widely spaced bullae exist on the mid-flank on the phragmocone and above the umbilical shoulder on the body chamber; the type only has 5 umbilical bullae. The umbilical shoulder on the body chamber is low and wide with bullae lying behind the umbilical swelling on the flank. Ribs emanating from the umbilicus are fine and rectiradiate. Ventrolateral tubercles are abundant and begin near the end of the phragmocone becoming clavate and continue on the body chamber to the aperture. Flanks are flat to slightly rounded with very fine ribs. Ventrolateral tubercles are generally separated by two secondary ribs and two additional ribs that originate at the umbilicus. Ventrolateral tubercles are abundant and are all nearly evenly spaced, crossing over the venter between the secondary ribs. The venter is rounded.

The paratype is MPPM 25 (Fig. 11F), it measures 38.8 mm by 34.5 mm and is 15.3 mm wide at the aperture. Like the macroconch it has strong, rectiradiate ribs that bunch together on the body chamber to form bullae above the umbilicus (between 5 or 6) and strong ventrolateral tubercles (8-10) only on the body chamber. Ribs on the phragmocone are also rectiradiate but do not appear to give rise to any tubercles or bullae. The venter is rounded with widely spaced rectiradiate ribs. There is no umbilical swelling as found with the holotype MPPM 1996.39.18 thus leading to the determination of a microconch (see Landman and Waage, 1993; p. 46-55).

**Occurrence:** This species is currently known only from the Coon Creek Fm. at its type locality and from the Nacatoch Sand near Chatfield, Texas (see Stephenson, 1941; plate 90, figs. 7-8). Both specimens were found near the same spot downstream near the northern end of the property in the creek wall. Because of their geologic location they are slightly older than the other scaphite fauna found at the site.

**Discussion:** Specimens resemble Hoploscaphites criptonodosus (Riccardi, 1983), but differ in having a more compressed form and well-pronounced umbilical swelling. Specimens resemble Hoploscaphites brevis (Meek, 1876) but differ in the ribbing, tubercle and bullae placement, large umbilical swelling, and small macroconch size. It compares favorably at first appearance with AMNH 56864 of Hoploscaphites brevis as described by Landman et al. (2010; p. 188, figs. 98M-P) but differs as AMNH 56864 has extremely fine, more abundant, flexuous, prorsiradiate ribs on the body chamber, wider spaced ventrolateral tubercles, tighter spaced umbilical bullae, does not have midflank tubercles on the phragmocone and bullae, and tubercles do not extend to the aperture. On H. youngi n. sp., the nodes on the venter become clavate once they begin on the body chamber where they are all tuberculate on H. brevis (see Landman et al., 2010; p. 201 for further discussion).

Specimens also distantly resemble Hoploscaphites sargeklofak Landman et al. (2015) but differ with a more rounded venter, ventrolateral tubercles are lower on the flanks and the ribbing is closer and more rursiradiate. This species also does not fit the description of Hoploscaphites pumilus (Stephenson, 1941) because of the naturally compressed whorl section of the ammonite, rounded venter and lack of ventrolateral tubercles on the phragmocone. Also macroconchs of H. pumilus have a very pronounced swelling with a large umbilical tubercle (see Fig. 11) above the umbilicus that is so different from H. youngi n. sp. along with a flattened venter. And finally H. youngi n. sp. differs from Hoploscaphites (Jeletzyktes)
Jeletzkytes (Wade, 1926) with a very compressed whorl section versus a thick and robust one on H. (J) reesidei, fewer and less pronounced (much, much smaller) tubercles, finer ribbing and overall shape (see Figs. 10-11 for comparison).

Subgenus Jeletzkytes Riccardi, 1983

Name Derivation: Jeletzkytes = After Von J. (Jeorgi) A. Jeletzky, a 20th century Canadian geologist and cephalopod paleontologist who published on much of Canada’s Jurassic and Cretaceous ammonites, belemnites and stratigraphy (Riccardi, 1983; p. 14).

Type Species: Riccardi (1983) named Jeletzkytes as a new genus designating the type as the specimen of Scaphites nodosus described by Owen (1852; p. 581, plate 8, fig. 4a). Landman et al. (2010) made Jeletzkytes synonymous with Hoploscaphites, but the basic differences between the compressed Hoploscaphites and the more robust Jeletzkytes are noteworthy.

Diagnosis: Riccardi (1983; p. 14) described Jeletzkytes as such: “Relatively large scaphitids, with involute phragmocone; body chamber with short shaft extending slightly beyond the phragmocone and weakly recurved hook; whorl section remaining depressed throughout the phragmocone and body chamber, or varying from depressed to slightly compressed during the ontogeny; ribs almost straight to weakly projected and flexuous; earlier representatives with stronger and sparser ribbing and bearing prominent lateral and ventrolateral tubercles on the body chamber; younger representatives with relatively finer and denser ribbing, and 2-3 rows of lateral nodes in the phragmocone, which tend to fade away on the flanks of the body chamber. Suture fairly indented, becoming more complex from older to younger species.”

Amended Diagnosis: Jeletzkytes is defined as a larger and more robust form within the genus Hoploscaphites. The width of the flank (whorl width) of Jeletzkytes is generally one to one and one-half times that of the width of the venter (whorl height), versus the width of the flank of the compressed form (Hoploscaphites (Hoploscaphites)) that is generally two to three times the width of the venter. Macroconchs are robust, with broad ribs, and prominent tubercles on either side of the venter and around the umbilicus on the umbilical shoulder, and a slight swelling near the umbilicus in the middle portion of the body chamber. Microconchs are smaller, more compressed, and have a body chamber with a much straighter shaft. Ribs may be fine to coarse. Tubercles occur mid flank and on either side of the venter. They are commonly small on the later portion of the phragmocone larger on middle portion of the body chamber, and smaller again near the aperture.

Discussion: As previously stated, Riccardi (1983) created the genus Jeletzkytes for the robust Campanian and Maastrichtian North American scaphitid forms and reserved the genus Hoploscaphites for the compressed Campanian and Maastrichtian scaphitid forms. Based on measurements and observations made by Landman et al. (2010) this author believes that Jeletzkytes should be preserved as a subgenus to further describe the robust forms of the genus Hoploscaphites and also use Hoploscaphites as a subgenus (i.e. Hoploscaphites (Hoploscaphites)) to describe the more compressed scaphitid forms.

Species Hoploscaphites (Jeletzkytes) reesidei (Wade, 1926)

Figure 10I-O

Scaphites reesidei Wade, 1926; p. 183-184, plate 61, figs. 3-7
Scaphites rugosus Stephenson, 1941; p. 425-426, plate 89, figs. 15-18.
Jeletzkytes cf. nodosus (Owen). Riccardi, 1983; p. 18, plate 3, fig. 1.
Jeletzkytes aff. nodosus (Owen). Riccardi, 1983; p. 18, plate 3, figs. 2-6; plate 4, figs. 1-2.
Jeletzkytes nodosus (Owen, 1852). Cobban and Kennedy, 1994a; p. B8-10, plate 9, figs. 7-11.
Jeletzkytes nodosus (Owen). Emerson et al., 1994; p. 334, 396.
Jeletzkytes cf. J. nodosus (Owen). Kennedy et al., 2000b; p. 20-24, figs. 9J-P, 10-11, 12C-F.
Jeletzkytes reesidei Larson, 2009; p. 209, fig. B.
Hoploscaphites aff. H. nodosus (Owen). Landman et al., 2010; p. 133, 162 fig. 81A-D.
Hoploscaphites aff. H. nodosus (Owen). Larson, 2012; p. 29-31, plate 10, figs. 3a-8b.

Name Derivation: reesidei = after John B. Reeside Jr. (Wade, 1926). Dr. Reeside was an early to mid 1900s USGS geologist and invertebrate paleontologist who was one of the first to recognize differences in the successive species of bacularites within the marine Cretaceous strata of the Western Interior. His work with W. A. Cobban led to the recognition and creation of the many ammonite Range Zones in the Western Interior.

Type Specimen: As designated by Wade (1926), the type is USNM 73112 from the Coon Creek Fm., at the type locality of Coon Creek, McNairy County, Tennessee.

Material: The material consists of six specimens. Two large, nearly complete macroconchs (BHI 1981 and MPPM 1972.46.407), a phragmocone of a microconch (MPPM 1972.46.408), plus three other partials (BHI 5291, BHI 1983, and BHI 1984). All of the specimens exhibit signs of predation, or breakage to the aperture of the body chamber. None of the specimens found at this site have been found with a complete body chamber. Wade (1926) illustrated the phragmocone of a macroconch (plate 61, figs. 3-5) and what appears to be an incomplete microconch phragmocone (plate 61, fig. 7).

Diagnosis: Wade (1926; p. 183-184) described the species as such: “…sharp, narrow ribs with relatively wide, flat interspaces, the position of the inner row of nodes, the compressed form of the septate whorl, the high arched venter, and the abrupt swelling of the living chamber. It is closest among American species to some forms of Scaphites
nodosus Owen var. quadrangularis Meek and in fact might be included under nodosus in the extremely wide sense in which that name has been applied… From Scaphites quadrangularis our species may easily be separated by the arched venter, the position of the inner nodes, which lie farther out on the flank, and the compressed form”.

**Description:** BHI 1981 (Figs. 10N-O) is a nearly complete macroconch missing its aperture, and a portion of the anterior portion of its body chamber. The initial whorls of the phragmocone are crushed, but the posterior phragmocone and the body chamber are not deformed. Broad ribs on the phragmocone and the early portion of the body chamber originate from the umbilical area and extend over the slightly rounded and broad umbilical shoulder until they form bullae at about midflank. On the remaining two thirds of the body chamber, only one in two of the ribs form bullae midflank. Ribs branch (bifurcate) or become intercalary midflank and flex a little between the bullae and the ventrolateral tubercles. The ribs then continue over the venter with a slight curvature towards the aperture midventer. Two midflank bullae near the middle portion of the body chamber are twice as large as any of the other midflank bullae. Ventrolateral tubercles, although large on the entire body chamber, are much larger in the same portion and emanate from the same ribs as the largest umbilical bullae.

MPPM 1972.46.407 (Figs. 10K-L) is also nearly a complete macroconch but is missing the entire hook portion of the body chamber. It follows the description of BHI 1981 closely, but the ribs are much wider and the overall width and size is larger. MPPM 1972.46.407 measures 42.4 mm across the widest portion of its body, BHI 1981 measures about 34 mm in the same place. On the body chamber of both specimens, the venter is quite wide with the whorl height is nearly equal to the whorl width. With careful preparation, MPPM 1972.46.407 could have an excellent suture pattern exposed across the flanks and venter.

MPPM 1972.46.408 (Figs. 10G-H) is possibly a microconch, and might be a juvenile. The phragmocone is well inflated, the body chamber is mostly gone probably a result of predation. Whorl height is about twice the whorl width. The specimen only has a few ribs in the umbilical area, and they arise just before the body chamber. Most of the ribs originate midflank, several are intercalary and are not necessarily associated with any midflank bullae. Ribs are very flexuous, except across the venter where they are quite straight. Ventrolateral tubercles are small and occur in no particular pattern (some on every other rib, some on every third, fourth, or fifth).

BHI 5291 and BHI 1983 both exhibit additional features that add to the description of the species. BHI 5291 is a broad, phragmocone ventral fragment from a macroconch. With careful preparation it could have an excellent suture pattern. BHI 1983 is a macroconch phragmocone that shows the broad coarse ribs and ventrolateral and midflank tubercles typical of H. reesidei. Both rows of tubercles originated early in the growth of this ammonite.

**Occurrence:** In the Western Interior, Hoploscaphites reesidei is found in uppermost Baculites cuneatus and throughout the B. reesidei Range Zones, Late Campanian (72 MYA). It is found within those Zones in the Pierre Shale from Colorado and South Dakota and the Bearpaw Shale of Montana. H. reesidei is also known to occur in the Navesink Fm. of New Jersey, the Nacatoch Sand in Texas, and the Coon Creek Fm. in Tennessee. It probably also exists in the Saratoga Chalk and the Nacatoch Sand in Arkansas.

**Discussion:** Cobban and Kennedy (1994a) made Hoploscaphites reesidei synonymous with H. nodosus. Landman, Kennedy, Cobban, and Larson (2010) conducted exhaustive research on the Campanian and Maastrichtian scaphitids of the Western Interior of North America, and their association with the scaphitids from the Gulf Coast and Atlantic Coast regions. Landman and Larson have determined that there are enough morphological and stratigraphical differences, to justify their separation. A more complete synopsis with descriptions on most Campanian and Maastrichtian scaphitids of North America is forthcoming from these researchers.

**Order Nautilidea** Agassiz, 1847

**Superfamily Nautiloidea** de Blainville, 1825

**Family Nautilidae** de Blainville, 1825

**Genus Eutrephoceras** Hyatt, 1894

**Name Derivation:** Eutrephoceras = (eu = begin or good) + (trepho = nourish or eat) + (ceras = horn) = a good nourishing horn (Hyatt, 1894).

**Type Species:** The type species for the genus was assigned by Hyatt (1894; p. 555-558) to Morton’s original Nautilus dekayi (1834; plate 8, fig. 4); the type was also figured by Whitfield (1892; plate 37, figs. 2-3; plate 38, fig. 1).

**Diagnosis:** The shell of Eutrephoceras is smooth and very subglobose in shape, whorl section is kidney shaped and broadly rounded on the flanks and venter. The umbilicus is very involute, aperture is sinuous shaped, suture is slightly flexuous.

**Discussion:** Stephenson (1941; p. 397) noted that Hyatt (1894) had described the genus based on specimens collected from the “Pierre group” of the Western Interior, and not from the Navesink Fm., where Morton had originally described the type species. Stephenson knew that the type came from the Lower Green Marl (Navesink Fm.) of New Jersey, Hyatt apparently did not. Stephenson further stated that nothing in Hyatt’s text indicated that Hyatt ever saw any of the material from New Jersey. Hyatt (1894) assumed that Morton’s type came from the
Cretaceous of Dakota, when in fact it came from the middle part of the Navesink Fm. of New Jersey. Hyatt thus described the genus *Eutrephoceras* from specimens collected from the Late Campanian of the Pierre Shale of South Dakota, yet he assigned the type species of the genus (*E. dekayi*) to a specimen that he never saw that came from nearly two thousand miles away (New Jersey), from a different formation (Navesink Fm.), from a different biostratigraphic age (Lower Maastrichtian), and from a different Cretaceous sea (Atlantic).

Stephenson (1941; p. 398) noted that the specimens from the Western Interior and the Atlantic Coast are very similar and must be congeneric, but that the “well preserved shells from the Pierre group of the Western Interior, ... should be treated as specifically distinct”. Larson et al. (1997) attempted to differentiate the species of *Eutrephoceras* from the Western Interior Campanian, but stopped short of elevating varieties (subspecies) to species status. According to Neil Landman (pers. comm.), *Eutrephoceras dekayi* is more ovate and obtuse, when compared with its nearly equivalent aged counterpart, *E. dekayi montanaensis*, from the *Baculites baculus* Zone of the Western Interior.

The rediscovery of the type locality of *E. dekayi* necessitates the revision of the Late Cretaceous nautiloids from the Western Interior, as well as those from the Gulf and Atlantic Coast regions. For over one hundred and seventy-five years, *Eutrephoceras dekayi* has seemingly been the ‘garbage can’ name for all North American Cretaceous nautiloids. Describing and differentiating the different species of *Eutrephoceras* is difficult. It is safe to assume that an individual cephalopod species would not last for millions of years, but yet all of the *Eutrephoceras* species look very similar. The siphuncle placement and height of whorl verses the whorl width seems to be the most diagnostic features for species determination within the genus *Eutrephoceras*. This redescription of taxa within *Eutrephoceras* is deferred to another paper.

**Species Eutrephoceras planoventer** Stephenson, 1941

Figures 12A-K; 13A-B; 14C


*Eutrephoceras planoventer* Stephenson, 1941; p. 397-398, plate 75, figs. 1-6; plate 76, figs. 9-11.


*Eutrephoceras planoventer* Stephenson. Emerson et al., 1994; p. 45, 354.

*Eutrephoceras planoventer* Stephenson. Larson, 2012; p. 32-34, plate 11, figs. 1-8b; plate 12, figs. 1-2; plate 13, fig. 2.

**Name Derivation:** planoventer = (plano = planus = flat) + (venter = belly) = flat belly (Stephenson, 1941).

**Type Specimens:** The holotype of *Eutrephoceras planoventer* is from the Nacatoch Sand near Chatfield, Texas. The type was designated as USNM 77223 by Stephenson 1941 (p. 397-398, plate 75, figs. 1-3). Paratypes assigned were USNM 77224 (plate 75, figs. 4-6) and USNM 77225 (plate 76, figs. 9-11), also from the Nacatoch Sand near Chatfield and Kaufman, Texas.

**Material:** The specimens consist of eight *Eutrephoceras* from MPPM (MPPM 1972.46.434, MPPM 1972.46.435, MPPM 1972.46.436, MPPM 1972.46.437, MPPM 1972.46.438, MPPM 1972.46.439, MPPM 1972.46.440,
the sides and noticeably flattened on the venter, closely coiled, umbilicus imperforate. Aperture much broader than high, reniform. Siphuncle a little dorsal of the center of the septum. Sutures rather widely spaced and gently sinusous with a gentle lateral lobe at the edge of the umbilicus with a broad lateral lobe, ventrolateral saddle and ventral lobe.”

**Description:** The specimens of *Eutrephoceras* from the Coon Creek Tongue at its type locality all follow the description of the species *E. planoventer* as described by Stephenson (1941). All specimens exhibit the typical subglobose shell, and nearly all of them have a rounded to somewhat flattened venter, although in juveniles the venter is broadly rounded. The siphuncle is located on the dorsal side of the center of the septum in MPPM 1972.46.436 (Fig. 12B-C), which follows for the species. Overall width of the venter is much wider than its height, which is also described for the species (72 mm W x 52 mm H, MPPM 1972.46.441; and 68 mm W x 47 mm H, MPPM 1972.46.436). The aperture is characterized by a hyponomic (recessed) sinus in the middle portion of the venter and is visible in several of the specimens (Fig. 12D, F, K) that have their aperture preserved. Ribbing is fine and quite distinct, depicted by growth lines following the shape of the aperture. Ribs form a sinusoidal curve from the umbilicus towards the aperture and back around the recessed sinus. Septal walls have a slight curve to them, giving the suture a slightly sinusous pattern, typical for the genus.

**Occurrence:** Late Campanian, from the Coon Creek Fm. in Tennessee; the Nacatoch Sand in Navarro and Kaufman Counties of Texas, and Hempstead County, Arkansas; probably from the Saratoga Chalk in Arkansas, and it is possibly also present in the *Baculites ruesidei* and *B. jenseni* Zones of the Western Interior.

**Discussion:** *Eutrephoceras dekayi* comes from the lower Maastrichtian part of the Navesink Fm. As mentioned earlier, nearly all occurrences of Late Cretaceous *Eutrephoceras* from North America have been called *Eutrephoceras dekayi*. Because of the difference in age between the two outcrops, and since the description of *Eutrephoceras planoventer* does not match with that of *Eutrephoceras dekayi* or any of the described species from the Western Interior (Larson et al., 1997), *Eutrephoceras planoventer* is determined to be a unique species. The type of *Eutrephoceras planoventer* was found alongside a similar fauna as at Coon Creek, and the description of the *Eutrephoceras* from Texas and Coon Creek is identical.

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**Figure 14.** A-B *Cirroceras conradi* (Morton, 1841). A. View of the whorls looking down at the top of UMUT MM 28423 [x 0.75], the most complete known from the Coon Creek Science Center. B. Side view of UMUT MM 28423 [x 0.75]. C. *Eutrephoceras planoventer* Stephenson, 1941. UMUT MM 28422 [x 0.5], a large body chamber, measuring 17 cm long x 16 cm wide.

MPPM 1972.46.441), one from the University of Tokyo (UMUT MM 28422), and four from BHI (two figured: BHI 5292 and BHI 5299). These specimens represent all sizes, ages, and most likely both sexes of *Eutrephoceras*. None of the specimens is complete, yet eight of them are preserved with most of their body chambers intact and some of these even have considerable portions of their apertures. All of the specimens of *Eutrephoceras* exhibit shell damage and breakage, probably the result of predation. The large portion of the body chamber (UMUT MM 28422; Fig. 14C) examined from the University of Tokyo, measures an incredible 16 by 17 cm. Another large, sutured *Eutrephoceras* portion (MPPM 1972.46.453; Fig. 13b) indicates evidence of limpets or some other parasite that was originally attached to the shell.

**Diagnosis:** According to Stephenson (1941; p. 397-398) “the adult shell is large, subglobose, broadly rounded on
uncovered from the site, new discoveries will undoubtedly take place. Equivalent aged fauna from Gulf Coast deposits also include Anaklniceras reflexum Stephenson (1941), Belemnilla americana Stephenson (1941), Gaudryceras sp., Pseudokossmaticeras galicianum (Favre 1869, see also Kennedy and Cobban, 1993c), among others; these species and several others could and should eventually be found at this site.

The discovery of Discoscaphites presents some interesting problems. Is this the earliest known Discoscaphites, that predates all other known species by about 3 million years, or is this the latest known Trachyscaphites a similarly ornamented genus described by Cobban and Scott 1964, or could this specimen possibly be the transitional form between the two genera? Stephenson (1841) illustrated a couple of specimens from this genus from the Navarro but he also illustrated several specimens of Sphenodiscus that come from higher in the formation than what is found at Coon Creek. MPPM also has other specimens of Sphenodiscus and Discoscaphites from other later outcrops in the Coon Creek Fm. This specimen represents the only known cephalopod genus from Coon Creek that has not been found in any other equivalent aged fauna in either the Gulf Coast or the Western Interior.

Larson (2003b) determined that the type locality along Coon Creek, near the Coon Creek Science Center, McNairy County, Tennessee is equivalent of the lower Baculites reesidei Range Zones from the Western Interior. That determination was based on correlating the Coon Creek ammonite fauna (primarily the species Cirroceras conradi, Hoploscaphites reesidei, Solenoceras reesidei, and S. texanum) with the ammonite fauna from the Western Interior (see Table 1). Thus the age of the Coon Creek fauna at the type locality should be classified as Late Campanian, approximately 72 million years ago (derived from Argon/Argon dating, based on currently accepted dates by Obradovich (1993) and Cobban et al. (2006)). However, the occurrence of Nostoceras (Nostoceras) hyatti makes this age less precise. The presence of N. (N.) hyatti from the Atlantic Highlands, New Jersey directly correlates with the N. (N.) hyatti Zone from the highest Campanian fauna of Europe; and because N. (N.) hyatti is also found only in the Baculites jenseni Zone from the highest Campanian fauna of Europe; and because N. (N.) hyatti is also found only in the Baculites jenseni Zone of the Western Interior, this too would place it in the latest Campanian. The use of N. (N.) hyatti as an indicator would thus position the age of the Coon Creek fauna in the uppermost Late Campanian, or approximately 71.5 million years ago. Thus the age for the Coon Creek fauna at its type locality should then be recorded between 72-71.5 million years ago or the equivalent of the upper Baculites reesidei through B. jenseni zones of the Western Interior.

The author observed that the gastropod Turritella and the bivalve Pterotrigonia are extremely abundant lower and less so in the upper portions. Further investigations into the biostratigraphy should be done with someone like Roy Young who best knows the site. Both specimens were of Hoploscaphites youngi n. sp. were found downstream near the southern end of the property indicating that this species is older than H. reesidei and H. pumilus that were found further upstream.

There is other cephalopod fauna from other numerous sites in the Coon Creek Formation throughout Tennessee and Mississippi that have never been published. These specimens show a wide and various fauna from the middle Campanian through the lower Maastrichtian. Though most of the specimens in the collections at both the Memphis Pink Palace Museum and those from the Ripley Fm at the Mississippi Museum of Natural History in Jacksonvile have been photographed and measured a paper illustrating and describing the other cephalopods is forthcoming.

ACKNOWLEDGEMENTS

I thank the late A. Allen Graffham of Geological Enterprises for initially taking me to the Coon Creek Fossil Farm in the late 1970s. Special thanks also to the late Roger Van Cleef, former Curator of Education with the Pink Palace Museum, who accompanied me to Coon Creek several times, and gave freely of his time and enthusiasm. Thanks especially to Roy Young, Tom Miller, Tamara Braithwaite, and Ron Brister of the Memphis Pink Palace Museum for loan of specimens, arranging permission to collect, and assisting in the collection and curation of the fossils. Kazu Tanabe, of the University of Tokyo, kindly shared specimens from their university collections for the manuscript. Black Hills Institute is currently housing their important invertebrate collection and displaying some of these magnificent pieces. And thanks to my son Luke, father Neal C., brothers Mark and Peter, and friends Leon Theisen and Roy Young for their help in collecting. Luke Larson discovered the paratype, a microconch of Hoploscaphites youngi, during a collecting trip to the site in May 2014 with a primary purpose of finding additional specimens of this new species. That particular specimen was found within a few feet of where Roy Young found the holotype 18 years earlier (Roy Young, personal communication).

The late W.A. (Bill) Cobban, Neil H. Landman, Steve Jorgensen and Earl Manning graciously reviewed, and edited an earlier version of this manuscript. Bill Cobban did much of the previous work on the ammonite fauna from Coon Creek: his help and comments were invaluable in the creation of this and a previous publication. Thanks to Michael Gibson, Stan Dunagan and David Dockery for the opportunity to present the information I had on this wonderful cephalopod fauna at the Southeastern GSA Convention on Coon Creek in 2002. From that symposium it was decided that a monograph would be published on the geology and fauna of Coon Creek through the Tennessee Division of Geology. That didn't happen, but thanks to the Alabama Museum of Natural History for
making the long-promised Coon Creek volume a reality.

Thank you to my sons Neal Andrew and Luke as well as Tamara Braithwaite for aiding me with photographs to use for the many Figures. Neal Andrew executed all of the photo editing and Figure compositions. A very special thanks to the Association of Applied Paleontological Sciences and Ken Carpenter for reviewing, editing and publishing an earlier version of this paper in their on-line journal, The Journal of Paleontological Sciences.

REFERENCES


Irregular echinoids of the Upper Cretaceous Coon Creek beds in Tennessee

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ABSTRACT—The Coon Creek type locality in McNairy County, Tennessee, USA, is world-renowned for its excellent preservation of Late Cretaceous mollusks. Lesser known, due to poor preservation, is its echinoid content. Echinoids are preserved typically as distorted internal molds occasionally accompanied by small remnants of delicate shell and/or corresponding external molds. Previously published identifications of Coon Creek echinoids were hindered by poor test preservation as well as plastic distortion of the moldic sandy clay matrix, resulting in several misidentifications. However, a much larger sample of both Coon Creek and comparative specimens, aided by a considerably greater understanding of echinoid diversity during the Late Cretaceous, permits a more informed examination of the taxa actually present at the Campanian-Maastrichtian boundary on the eastern side of the Mississippi Embayment.

INTRODUCTION

The Coon Creek locality lies along the eastern edge of the Mississippi Embayment in the central Gulf Coastal Plain, northwestern McNairy County, Tennessee (Fig. 1). Much has been written on the geology and fossil composition of this site, the type locality of the Coon Creek Formation. The site contains one of the most diverse and best preserved Upper Cretaceous marine mollusk assemblages ever reported (e.g. Wade, 1926; Sohl, 1960). Known also as the “Dave Weeks’ place” (Wade, 1926), USGS Meso. loc. 10198 (Wade, 1926), and USGS Meso. loc. 25406 (Sohl, 1960), this famous locality is more commonly known by its namesake stream (Brister and Young, 2007). The Coon Creek site has been sampled for mollusks by many researchers and collectors worldwide. Wade (1917, 1926) introduced the fossiliferous beds along Coon Creek as a member of the Ripley Formation. However, Russell (1975) elevated the Coon Creek beds to formational rank, at least in Tennessee.

Although the Coon Creek locality has achieved little notoriety for its echinoderms, moldic echinoids and fragmentary asteroids are among the varied fauna. The only major published work including a treatment of the echinoderms was that of Wade (1926). Wade’s Coon Creek samples amounted to a mere fortnight of field work, and echinoids were not commonly encountered. Based on his modest sample, Wade reported several species of spatangoid echinoids and described a new species of goniasterid asteroid (Metopaster tennesseensis Wade) from a handful of isolated marginal ossicles.

Wade’s original Coon Creek echinoid assemblage included the spatangoids Hemiaster ungula (Morton), Hemiaster stella (Morton), Hemiaster lacunosus Slocom (a


December 1, 2016
junior synonym of *H. wetherbyi* de Loriol—see Cooke, 1953), and an unassigned species of *Hemiaster* that Wade affiliated with *Pliotoxaster comanchei* (Clark) from the Lower Cretaceous of Texas. Given the greater understanding of the fossil record that always exists in the present, specifically as regards Upper Cretaceous echinoid populations in the Gulf of Mexico, these earlier assignments require considerable revision. In Wade’s defense, however, echinoid preservation at Coon Creek tends to be poor and incomplete, distortion being particularly common. This has complicated the identification of the Coon Creek material, both then and now. Test calcite is seldom preserved at all thus anatomical details are absent, and many specimens have undergone plastic deformation substantially altering general body form.

The improved identifications herein were possible because of the many specimens and information unavailable to Wade. Systematic collecting in the last few decades by the Pink Palace Museum in Memphis, Tennessee, has produced many more specimens (Table 1), providing a much clearer understanding of the taxa actually represented at Coon Creek. A second exposure of the same fossil layer(s) within the Coon Creek beds has also provided specimens for the current study. Known as Thompson Farm, it lies only a few miles distance to the northwest. Dunagan and Gibson (1993) introduced this locality in a study of its stratigraphy and paleoecology, including information on excellently preserved putative echinoid burrows. Unfortunately, echinoid preservation is no better than that at Coon Creek. Nevertheless, access to a considerably more comprehensive comparative
TABLE 1. Inventory of irregular echinoids recovered from the Coon Creek beds of Tennessee. An asterisk (*) marks those specimens that consist of two separate pieces—an internal mold and at least a portion of the test remaining in matrix, permitting a view of the internal surface of the test. All specimens are from the Coon Creek type locality except the UTM material, which is from Thompson Farm. Four of the specimens occur in the same matrix block—MPPM CC-60.

<table>
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<td>Family Faujasiidae: Subfamily Faujasiinae</td>
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collection than that available 85 years ago has permitted a major revision of Wade’s echinoid identifications.

STRATIGRAPHY & AGE

The fossil-bearing beds at the Coon Creek type locality lie within the Upper Cretaceous (Gulfian) depositional system in the eastern half of the Mississippi Embayment. The Coon Creek beds were originally erected as a member unit of the Ripley Formation by Wade (1917, 1926). Russell (1975) elevated the Coon Creek beds to formational rank in Tennessee and characterized the unit as approximately 140 feet of dark gray, micaceous, glauconitic, bedded and burrowed marine sands and clays weathering to a reddish brown upon exposure. Russell (1975) referred to two predominant facies in the Coon Creek beds—a ‘lower’ calcareous, burrowed, more massive bedded, more fossiliferous sand and clay containing a transitional basal clay that grades downward into the fine-grained Demopolis marl, and an ‘upper’ more distinctly bedded sand and clay with large, flattened concretions, which grades upward into the McNairy Sand. In Tennessee, the Coon Creek beds are bounded below by the “transitional clay” and above by the McNairy Sand (Fig. 2), both units also considered a part of the Ripley Formation by some workers (e.g. Conant, 1941). The Coon Creek beds extend northward approximately 80 miles where they pinch out just north of Paris Landing State Park. Southward from the type locality, near Pontotoc, Mississippi, the Coon Creek beds eventually grade into the more calcareous down-dip equivalent “Troy beds” of Swann and Dew (2008, 2009).

Based on macrofaunal zonation, the Campanian-Maastrichtian boundary lies within the Coon Creek beds, its position is variable along the outcrop belt and dependent on the biozonation used (Fig. 2). Among macrofossils, oysters (e.g. *Exogyra*), ammonites, and other mollusks are frequently employed in the relative dating of Cretaceous beds in the eastern U.S. Stephenson (1914) introduced and later refined (1933) the *Exogyra cancellata* biozone as a potentially useful correlative tool across the southeastern United States. The mollusk-rich beds at the Coon Creek type locality lie within this zone based on the presence of *E. cancellata* Stephenson and the jingle shell *Anomia tellinoides* Morton. Based on nannofossil composition, Self-Trail and Gohn (1997) consider the *E. cancellata* biozone to be Late Campanian. In addition, Burnett et al. (1992) identified a Late Campanian subzone CC22c nannofossil suite from the mollusk-rich beds at Coon Creek, and Cobban and Kennedy (1994) established the same age in their discussion of the Coon Creek ammonites, which belong to the Late Campanian.
TABLE 2. Measurements of Coon Creek echinoids compared to dimensions of types and other comparative material (shaded). Not all dimensions were available (na), and many were estimated (italics) due to either distortion or fragmentation.
Nostoceras hyatti ammonite zone. More recently, Larson (2012) revisited the ammonite composition in greater detail, further strengthening a Late Campanian age for the main mollusk-rich beds at Coon Creek. To the south in Mississippi, the Late Campanian E. cancellata biozone occurs stratigraphically lower in the section (Sohl, 1960), and the ammonite assemblage is replaced in the Coon Creek beds by the Early Maastrichtian Nostoceras alternatum ammonite fauna (Cobban, 1974).

Based on planktonic foraminiferal distribution in the north-central Gulf Coastal Plain section (Mancini et al., 1996; Puckett, 2005), the Maastrichtian/Campanian and Early/Late Maastrichtian boundaries are younger than that indicated by other proxies. The current project relies on the ammonite zonal correlation for age relationships.

**OCCURRENCE & PRESERVATION**

Echinoids from the Coon Creek beds in Tennessee are incompletely preserved. Nearly all specimens are internal molds composed of typical Coon Creek matrix—micaceous, glauconitic clayey quartz sand and sandy clay. Although vestiges of original test material are occasionally preserved, it is very unstable, thus detailed anatomy is commonly indiscernible. Incomplete preservation coupled with a need for a systematic review of diversity contained within two of the genera present (Lefortia and Cardiaster) preclude specific assignment of some of the material. The remaining Coon Creek echinoid taxa—both spatangoids—are assigned to species, but not necessarily due to the identification of all, or even essential, indisputably species-diagnostic characters. Diplodetus and Paraster have been determined to be monospecific throughout the Campanian-Maastrichtian beds in the Gulf Coastal Plain (Cooke, 1953; Smith and Jeffery, 2000), and, as discussed below, the species of Hemaster described from this region are separated with relative ease on gross anatomy.

According to Pink Palace Museum curator Roy Young, who spent many field seasons collecting at Coon Creek, the most distorted echinoids are found in the lower dark bluish-green and gray clayey sand layer. Here, most echinoid specimens are represented as poorly preserved internal molds, although occasionally specimens can be found with intact albeit fragile tests. The upper yellow-brown semi-consolidated fine-grained sand contains echinoid casts that are better preserved. Here, identification of the echinoid fauna is facilitated by the preservation of test plating, but tests also tend to be less crushed and contorted.

Echinoid internal molds identical in preservation to those at the type locality were collected low in the Coon Creek section exposed at Thompson Farm (Dunagan and Gibson, 1993). The echinoids were recovered from a generally shelly zone, the top of which was 1.0 m subjacent to a zone the authors described and figured as containing common laminated burrow-fill structures attributable to echinoids.

**SYSTEMATIC PALEONTOLOGY**

Diagnostic characters and criteria used herein largely follow those compiled by Kier (1962), Néraudeau (1994), Smith and Jeffery (2000), Smith (2004), and Smith and Kroh (2011). Diagnoses are generally limited to features preserved in the material described herein. Synonymies are largely limited to original descriptions and relevant information and/or material additional to the type, primarily that overlooked in earlier synonymies; with only a few exceptions, catalogues and lists are not included. In the interest of brevity and eliminating redundancy, repetition of previous synonymies, namely those of Cooke (1953) and Smith and Jeffery (2000), is kept at a minimum. Nearly all references used in this study seemed faithful to the material being described and illustrated, at least in the context of the existing knowledge of the day. However, considering even the nascent understanding of the subject and the great scope of his foundational monograph, Clark (1915) and his artists used some liberties with drawings that cannot always be taken at face value. Several indexed and well-referenced inventories of described species were vital in preparing this section, namely Kier and Lawson (1978), Néraudeau (1994), and Kroh (2010). All referred material is listed in Table 1, and comparative measurements are provided in Table 2.


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**Order Cassiduloida** Claus, 1880 (sensu Kier, 1962)

**Family Faujasiiidae** Lambert, in Doncieux, 1905

**Subfamily Faujasinae** Smith and Wright, 2000 (sensu Smith and Kroh, 2011)

**Type Genus—Faujasia** d’Orbigny, 1856 (sensu Smith and Kroh, 2011)

**Included Genera—Pygurostoma** Cotteau and Gauthier, 1895; Lefortia Cossman, 1901; Clarkiella Lambert, 1916; Zuffardia Checchia-Rispoli, 1917 (sensu Smith, 1995); Pygidiolampas Clark, 1923; Euryptelatum Kier, 1962; Domechinus Kier, 1962 (sensu Smith and Kroh, 2011); and Himalayechinus Mu and Wu, 1976.

**Discussion—**Smith and Wright (2000) distinguished faujasines solely on the surficial development of the periproct. The Faujasinae have an anal opening (periproct) flush with the surface of the test as opposed to
lying in a depression, as with the Stigmatopyginae. Smith and Wright (2000) originally included Pygurus Agassiz, 1839, and Pseudopygurus Lambert, 1911, within the Faujasiinae, but these taxa were later removed by Smith and Kroh (2011), who added Pygurostoma, Clarkeiella, and Zuffardia. The faujasiine periproct is directed posteriorly to posterovertrally.

Outside of the Arabian Peninsula (e.g. Smith, 1995), most faujasiine species available for comparison are rare, inaccessible, distorted, and/or poorly preserved. Rarity and inaccessibility handicap the measurement of variability within and among populations, regionally and globally. Distortion and poor preservation in the available material have stymied identification and thus taxonomic evaluation.

Genus Lefortia Cossman, 1901

Type Species—Pomelia delgadoi De Loriol, 1900.

Included Species—Cassidulus hemisphericus Slocom, 1909 (placed in this genus by Smith and Kroh, 2011); Cassidulus conocidus Clark, 1915 (recognized by Cooke, 1953, as a synonym of C. hemisphericus Slocom); Lefortia barnabei Besairie, 1930; and Lefortia trojana Cooke, 1953.

Emended Diagnosis—Small to medium, hemispherical to subconical cassidulid with an ovate or subpentagonal ambulacral outline; a flat adoral surface; equant, lanceolate, petaloid dorsal ambulacra; a tetrabal apical system bearing four gonopores, one each in reduced genitals 1-4; short, arcuate, equant, petaloid phyllodes formed by two single-pored pore series, the outer forming a distally open parenthetoid arch; half amb of phyllodes 1 and 5 formed by an inner pore series with 2-3 pores and outer with 5-8; spineless interamb 5 ventrally; pointed, tooth-like bourrelets around a subcentral peristome; and a small, round or short, narrowly ovate periproct flush with the test surface, positioned on or immediately above the ambitus, and directed posteriorly.

Discussion—Until very recently, Lefortia trojana Cooke has been available for research only in the form of the bottomless holotype. Kier (1962) also recognized Cooke’s (1953) new cassidulid from Mississippi as a species of Lefortia. However, recent efforts have produced additional and more complete material of Lefortia trojana from the type and additional localities in North Carolina and Arkansas, confirming the placement of this species within Lefortia Cossman.

Among the emendations to the correct diagnosis of L. trojana is the shape of the periproct. The shape and position of this organ has been important to echinoid workers in distinguishing among the faujasiine genera. With only the incomplete holotype at hand, Cooke (1953) stated that the longitudinally elongated periproct was distinctive for the species. However, all of the new material exhibits a clearly circular anus. Obvious sagittal displacement in the posterior plating of the holotype strongly suggests that deformation produced a less than circular periproct.

Lefortia trojana Cooke, 1953

(Figure 3)

Cassidulus Conrad, 1860 (non Desor), shape of Faujasia apicalis (Desor, in Agassiz and Desor, 1847). Hilgard, 1860, p. 94.

Lefortia trojana Cooke, 1953, p. 17, pl. 4, figs. 8-10.

Holotype—USNM 108376, incomplete (bottomless) test from the Early Maastrichtian Ripley Formation of Troy, Mississippi.

Emended Diagnosis—Small to medium subconical faujasiine with a subrounded dorsoventral outline; aboral surface more gradually sloping posteriorly than anteriorly; petaloid, lanceolate dorsal ambulacra narrow and open distally; highest point on aboral surface (apex) anterior to peristome; four genital pores in a tetrabal apical system; marginal, circular periproct; gently rounded ambitus; tooth-like bourrelets; phyllodes short, consisting of two outer pore series of 7-8 pores each, forming a parenthetoid arch; and an inner pore series with 2-3 pores in each of two columns.

Referred Material—MPPM CC-22, CC-21/29, and more incomplete material listed in Tables 1 and 2.

Description and Discussion—The five Coon Creek cassiduloid specimens currently available represent a single species. All are incomplete, and the most intact specimen (MPPM CC-22) is distorted. Nevertheless, the discernible true form consists of a subconical test dome with the apex (apical system) anterior to the peristome; a subpentagonal ambulacral outline; equant, lanceolate, distally open petaloid dorsal ambulacra; tetrabal apical system; flattened ventral margin, marginal periproct at the end of a spineless interamb 5; short, petaloid, equant phyllodes with amb 1 and 5 each containing 2-3 inner pores and 8 outer pores in each column, the two outer pore columns forming an open, parenthetoid arch; and sharp, tooth-like bourrelets about a subcentral peristome. The most complete specimen—MPPM CC-22—has approximately 44.0 mm long by 33.5 mm wide; height could not be approximated. The remaining fragmentary material represents individuals of comparable dimensions.

The Coon Creek cassiduloid (Fig. 3) is a faujasiid because of its characteristic dorsal and ventral ambulacral anatomy, reduced genital plates 1, 3, and 4, tooth-like bourrelets, and smooth, keeled interamb 5 ventrally. It belongs within the Faujasiiinae because its periproct is flush with the surface of the test and in a marginal to inframarginal position, not recessed and supramarginal as in the Stigmatopyginae.

The Coon Creek internal molds share similarities with
several faujasiines, namely *Lefortia* Cossman, *Domchinus* Kier, *Faujasia apicalis* (Desor, in Agassiz and Desor, 1847), and Cooke’s (1955, 1958) hypodigm of “*Faujasia* geometrica” (Morton). Although the apical system and phyllode morphology distinguishes *Lefortia trojana* Cooke from *F. apicalis*, the gross morphology, particularly the lateral test profile, is essentially identical. The Coon Creek internal molds have this same body form, although the phyllode pores and the apical system, or what little is represented in MPPM CC-21/29, are like those of *L. trojana*. *Domchinus* has a monobasal apical system (Kier, 1962), whereas that of *Lefortia* is tetrabasal. A tetrabasal apical system is best observed in CC-21/29, where gonopores are discernible in fragmented genital plates (1, 3, and 4) closely abutting the madreporite (Fig. 3C). Although Cooke (1958) described the apical system of “*F.* geometrica” as “probably monobasal,” additional material examined from the type locality has genital plates (3 + madreporite) and is thus tetrabasal. However, “*F.* geometrica” (Morton), *Domchinus chelonium* (Cooke), and *D. teixeirai* Gonçalves, in Roman and (Gonçalves 1965) differ from *L. trojana* and the Coon Creek cassiduloid in the position of the apical system directly opposite (over) the peristome and their relatively broad, distally closed petals.

The currently definitive distinction among the faujasine genera is the position of the periproct with respect to the margin. The periproct position (and associated posterior test morphology) is most similar among *Lefortia*, *Euryptetalum*, and *Domchinus*. Kier (1962) and Smith and Kroh (2011) described *Euryptetalum* as having an inframarginal periproct, but this is not a fair comparison as the much lower test dome in this genus leaves little ambital room for a marginal periproct. Kier (1962) described the periproct of the type of *Domchinus* as marginal to inframarginal; Smith and Kroh (2011) as inframarginal. In the type of *Domchinus chelonium* (Cooke) and MPPM CC-22, the periproct has been turned to a more inframarginal direction due to compressive deformation of the test, which has resulted in pinching of the ambitus and ventral rotation of the periproct. Still, the Coon Creek cassiduloid does not have the sharp (angular) ambitus, central apex (directly above the peristome), and hemispherical test as exhibited by *Domchinus chelonium* (Cooke) and *D. vialovi* Moskvin, but instead a more rounded (robust) ambitus, more anteriorly placed apex (anterior to peristome), and subconical form associated with *Lefortia trojana*.

The current content of *Lefortia* is *L. delgadoi* (De Loriol), *L. hemispherica* (Slocom), *L. barrabei* Besaire, and *L. trojana* Cooke. Based on all the available material of unquestionable *L. trojana* (12 tests), the Coon Creek cassiduloid agrees most closely with this species. In the Coon Creek cassiduloid, the apex is positioned anterior to the central peristome, thus ruling out *L. delgadoi*, in which the apex lies directly over the peristome. The central peristome eliminates *L. hemispherica*, where the mouth is anterior to a central apex. The small, round periproct of *L. trojana* contrasts with the large, vertically elongate periproct of *L. barrabei*.

The closest geographic and stratigraphic occurrence of a published faujasine is in the roughly age-equivalent “Troy beds” to the south in Mississippi, which produced the holotype (and two additional specimens) of *Lefortia trojana* Cooke. Accounting for distortion, the most
complete MPPM specimen (CC-22) differs little from *L. trojana*, except in its larger size, which is \( \approx 1.7x \) that of the type (Table 2).

**Order Holasteroida** Durham and Melville, 1957

**Family Cardiasteridae** Lambert, 1917

**Genus Cardiaster** Forbes, 1850

**Type Species**—*Spatangus granulosus* Goldfuss, 1829.

**Included Species**—Several species worldwide (see Smith and Kroh, 2011), including a half dozen from the Upper Cretaceous of North America (Cooke, 1953, 1958).

**Diagnosis**—Cordate outline, planoconvex cross section; truncate dome posteriorly with third ambulacrum lying in a sulcus from apex to mouth and flanked by enlarged tubercles; elongate apical disk with four gonopores, posterior ocular plates touching; anterior columns of paired ambulacra having narrower columns of pore-pairs than posterior columns; peristome anterior, mouth directed anteroventrally; metasternous plastron, most posterior plastral plates alternately cuneate; peristome round; and inframarginal fasciole posteriorly.

*Cardiaster* sp.

(Figure 4)

**Referred Material**—UTM CC-E10 and several MPPM specimens listed in Tables 1 and 2.

**Description and Discussion**—At least a dozen of the available Coon Creek echinoids are holasteroids, most likely a single species. These specimens represent a holasteroid form that is planoconvex ventrodorsally, cordate in dorsoventral outline, with paired dorsal ambulacra that are flush with the dome of the test. The third petal is located in a deep oral-apical sulcus flanked by sharp margins (carinae) and well-developed tubercles. The petals are formed by distally diverging pore pairs, the anterior column always narrower (and pores smaller) than the posterior column.

The distorted and largely fragmentary Coon Creek holasteroid specimens likely belong to a single species. The Coon Creek form is generally similar to *Holaster* Agassiz, *Giralister* Foster and Philip, *Protocardiaster* Smith and Wright, *Pseudoholaster* Pomel, and *Cardiaster* Forbes. *Holaster* lacks the deep anterior sulcus with angular margins exhibited in the amb 3 of *Cardiaster*. The peristome of *Holaster* is also directed downwards; more anteriorly in *Cardiaster*, *Cardiaster* differs from *Giralister* in that the latter has a subanal fasciole; *Cardiaster* has a marginal fasciole only, which is absent in *Giralister* and *Pseudoholaster*. Unfortunately, none of the Coon Creek specimens exhibit sufficient preserved plating to determine the presence or distribution of fascioles, but, in all the other aforementioned characters, it is in agreement with *Cardiaster*.

Only three specimens were preserved sufficiently to observe the postoral plastral plating (e.g. Fig. 4H), which in the Coon Creek specimens is dominated by the unierial arrangement of wedge-shaped plates characteristic of *Cardiaster*. Based on this and the lack of contact between the labral plate and sternal plate 2a, the Coon Creek holasteroid has a primitive metasternous condition (Smith, 2004). The similar genera *Holaster*, *Giralister*, *Protocardiaster*, and *Pseudoholaster* all have biserial plastral plating—that of *Holaster* specifically meridosternous and the others protosternous.

In the current understanding of the taxonomy of the aforementioned holasteroidal genera, only species of *Holaster* and *Cardiaster* have been previously reported from North America, and the youngest occurrence of *Protocardiaster* is Turonian. North America has five described species of *Cardiaster* of Late Cretaceous age (Cooke, 1953) and one of Paleocene age (Cooke, 1959). *Cardiaster curtus* Clark, 1915, the content of which consists of two imperfect calcite pseudomorphs, occurs in the latest Campanian of Montana. *Cardiaster smocki* Clark, 1907, from the Early Campanian of New Jersey, and *C. marylandicus* Clark, 1916, from the Late Maastrichtian of Maryland each consist of only a couple of internal molds. These three species are too imperfect and too few to make a comparison to the equally imperfect Coon Creek material. The Coon Creek *Cardiaster* has a deeper amb III sulcus than the Campanian *Cardiaster hilli* Cooke, 1958, and Maastrichtian *Cardiaster leonensis* Stephenson, 1941, both from the western Gulf Coastal Plain. In addition, the Coon Creek *Cardiaster* and most other described species of *Cardiaster* from the Cretaceous (and Paleocene) of North America have a centrally located apical system. The two exceptions are *C. hilli* Cooke of Texas and *C. palmeri* Sánchez (Roig 1949) of Cuba, in which the apex lies noticeably anterior of center.

Geographically closest, *Cardiaster granulosus* (Goldfuss, 1829) (= *C. deciper* Cooke, 1953) occurs in the latest Campanian Saratoga Chalk on the western side of the Mississippi Embayment in Arkansas. There is also an unpublished species of *Cardiaster* occurring in the Maastrichtian of Mississippi. Although the Mississippi populations preserve test, specimens are rare and typically distorted, so a useful comparison is not possible. The youngest North American *Cardiaster* is *C. cinctus* (Morton, 1830), which occurs in the Late Paleocene of New Jersey. The latest Campanian *C. granulosus*, the undescribed Mississippi Maastrichtian form(s), and the Thanetian *C. cinctus* all bear gross similarities to the Coon Creek *Cardiaster*, but poor preservation and/or scarcity of the Coon Creek material and North American populations in general preclude a specific assignment.

The moldic Coon Creek material is the first *Cardiaster* to be reported from the southeastern United States, of
FIGURE 4. Cardiaster sp. (A, D-G, I) and Schizaster cf. S. variabilis (Slocom) (B, C) from the Coon Creek beds at the type locality. A. MPPM CC-02, Cardiaster sp., dorsal and ventral views; B, MPPM CC-57.1, S. cf. variabilis (Slocom), dorsal view, treated with magnesium oxide; C. MPPM CC-57.2, S. cf. variabilis (Slocom), ventral view; D. MPPM CC-08, Cardiaster sp., dorsal view; E. MPPM CC-60.3, Cardiaster sp. (removed from matrix block CC-60), dorsal view; F. same view, in matrix block; G. MPPM CC-60.2, Cardiaster sp., anterodorsal view, in matrix block; H. BMNH E41284, Cardiaster granulosus (Goldfuss), Late Campanian of Norfolk, England, ventral view, showing numbered plastral plates (Smith and Jeffery, 2000: text-fig. 123B); I. UTM CC-E10, ventral view, showing partially preserved plastral plating.
any age. The implications of this are discussed in the overall discussion section further below.

Order Spatangoidea Agassiz, 1840

Diagnosis—Cordate irregular echinoids with broadly rounded margins, depressed dorsal ambulacra (especially amb III), compact apical disk, anterior mouth, and interamb 5 modified adorally to form labrum.

Description and Discussion—Three spatangooid taxa have been identified in the available sample of Coon Creek echinoids (Table 1). Although moldic and thus lacking in important details of the test surface, they nonetheless exhibit certain diagnostic gross morphologies. The largest is an elongate, ovate form with a slightly recessed amb III. The few intact plates observed have tubercles interspersed among a groundmass of miliary granules. This echinoid is identified below as Diplodetus Schlüter. There is a notably smaller spatangooid with a less elongate body producing a more rounded dorsoventral outline and subospheroidal body. It has considerably shorter and diverging posterior amb, and the few associated plates recovered have closely set tubercles with deep areoles. This commonest form is Bolbaster Pomel. The third spatangooid, equivalent in size to the Coon Creek Bolbaster, is the rarest. This taxon, Schizaster, has a subhexagonal outline with a deeply recessed amb III and posterior petals intermediate in relative length between those of Diplodetus and Bolbaster.

Infraorder Micrasterina Fischer, 1966
(sensu Smith and Kroh, 2011)

Family Micrasteridae Lambert, 1920

Genus Diplodetus Schlüter, 1900

Type Species—Diplodetus brevistella Schlüter, 1900.

Included Species—Spatangus bucardium Goldfuss, 1829; Cyclaster coloniae Cotteau, 1877; Epiaster nutrix Lambert, in Boule, 1899; Plesiaster (?) parvistella Schlüter, 1899; Diplodetus gauthieri Cotteau, 1908; Micraster duponti Lambert, 1911; Diplodetus americanus (Stephenson, 1941).

Diagnosis—Robust, ovate test, posteriorly truncate, with 3rd amb in a shallow sulcus; generally depressed, cuneate profile, highest point between posterior ambulacra; central, ethmophact apical system with four gonopores; relatively short paired dorsal ambulacra, anterior longer than posterior; tubercles small and uniform adaptically, intervened by fine granules; D-shaped peristome facing anteriorly; projecting labrum producing a crescentic oral cavity in ventral view; periproct high on posterior; and subanal fasciole oval.

Discussion—Diplodetus is most similar to Plesiaster Pomel and Micraster Agassiz. Diplodetus has a ventrally visible oral opening, short petals, and ovate test in dorsoventral view. Plesiaster and Micraster have cordate tests. The labrum of Micraster is prognathic, hiding the mouth from ventral view. The petals of Plesiaster are longer.

Diplodetus americanus (Stephenson, 1941)
(Figure 5)

Spatangus sp. 2 Morton, 1830a, p. 286.*
Spatangus ungula Morton, 1833b, p. 131, pl. 10, fig. 6.*
Spatangus ungula Morton. Morton, 1834, p. 78, pl. 10, fig. 6.*
Hemiaster parastatus (Morton). Slocom, 1909, p. 9-10. (Prairie Bluff Formation, Mississippi)
Micraster sp. L. W. Stephenson in Dane, 1929, p. 109. (Saratoga Chalk, Arkansas)
Micraster (Plesiaster) americanus Stephenson, 1941, p. 69, pl. 7, figs. 1-4. (Corsicana Marl, Texas)
Hemiaster ungula (Morton). Cooke, 1953, p. 34-35, pl. 14, figs. 10-14.*
Hemiaster ungula (Morton). Cooke, 1958, p. 52, pl. 8, figs. 8-12.*
Diplodetus americanus (Stephenson). Smith and Jeffery, 2000, p. 306, fig. 129d-e.

* References to S. G. Morton's original material, namely ANSP 1503, from an unknown unit in the Campanian-Maastrichtian sequence at the Chesapeake and Delaware Canal, New Castle County, Delaware.

Note: Cooke (1953, 1958) excluded several references to Spatangus ungula Morton from synonymy (“Not Hemiaster ungula”), including Clark (1891, 1893, 1915).

Holotype—USNM 76285, complete test from the Maastrichtian Corsicana Marl of Castroville, Texas.

Referred material—ANSP 1503 [type of Spatangus ungula Morton], USNM 32707 [Hemiaster ungula (Morton) of Wade (1926: pl.1, figs.20, 21)], 32708 [Hemiaster sp. of Wade (1926: pl. 2, fig.1)]; and several MPPM specimens listed in Tables 1 and 2.

Description and Discussion—The large Coon Creek spatangoid is an ovate (vs. cordate), relatively elongate microsterid. Like the large Coon Creek echinoid, Diplodetus has a slightly greater length:width ratio than other Micraster-like taxa, having almost a subrectangular outline (on undeformed tests). Both D. americanus and the Coon Creek form have recessed dorsal ambulacra, the 3rd amb also recessed anteroventrally to the peristome (Fig. 5C,H). Amb III is not (or very imperceptibly) recessed in Diplodetus parvistella Schlüter, D. coloniae Cotteau, and D. gauthieri Cotteau. In the Coon Creek echinoid, the peristome is situated about one quarter test length from the anterior margin (Fig. 5C,H), which is consistent with D. americanus (Stephenson) and not D. nutrix (Lambert),
where the peristome is situated at a third the test length. The angle of anterior paired petal divergence is 100-105° (n=6), more consistent with *D. americanus* than the larger values for *D. duponti* (Lambert), 125-130°, and *D. coloniae*, 140-150°. The anterior petals are longer than the posterior (Fig. 5), as in *D. americanus*; in *D. gauthieri*, the anterior and posterior petals are of subequal length.

Morton (1834) described and illustrated *Spatangus unguла* as being compressed, but this is a response to the compressive distortion of sedimentary compaction. Wade’s (1926) use of the name *Hemiaster unguла* (Morton) for USNM 32707 is perhaps not without merit. Agassiz and Desor (1847) recognized the micrasterid affinities of *H. unguла* (Morton), or at least the type, but it is clear from reading subsequent assignments that the name has had a history of misuse in North America (Cooke, 1953). The type, a distorted internal mold, is from an unnamed stratum in the Upper Cretaceous beds exposed at the Chesapeake & Delaware Canal locality and was not adequately figured until Cooke (1953). The confusion began with Clark (1891), who began applying the name to a Paleocene echinoid from the Vincentown locality in New Jersey, eventually providing a composite drawing (Clark, 1893). This error was perpetuated in the literature until Cooke (1953). The type of *H. unguла* (Morton, 1833)—ANSP 1503—bears such a marked similarity to *Diplodetus americanus* (Stephenson, 1941), at least with respect to gross morphology (see *Diplodetus* description above), that the latter should almost certainly be considered a junior synonym of the former. However, the material of true *H. unguла* (Morton), which is unique (no paratypes or topotypes), precludes the perpetuation of the name, at least outside of the type locality, thus it should perhaps be considered a nomen dubium.

USNM 32708 was figured by Wade (1926: pl. 2, fig. 1) and identified as “*Hemiaster* sp.” Although he mentioned that “a few imperfect specimens” were recovered, the author only figured this one. Like many of the Coon Creek echinoids, this internal mold exhibits post-depositional stresses that resulted in considerable compressive distortion. The general body form, but especially the recessed amb III, is ostensibly similar to that of both *Proraster atavus* (Arnaud), reported regionally only from the Maastrichtian of Texas (Cooke, 1953), and the more locally known *Schizaster variabilis* (Slocom), from adjoining Mississippi (Slocom, 1909; Cooke 1953). However, in spite of the appearance of Wade’s (1926) image (pl. 2, fig. 1), amb III of USNM 32708 is recessed due to lateral compression. The posterior ambs are also proportionally longer in USNM 32708 than in *Proraster atavus* or *Schizaster variabilis*. This specimen most likely represents a deformed internal mold of *Diplodetus americanus*.

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**FIGURE 5.** *Diplodetus americanus* (Stephenson) from the Coon Creek beds at the type locality. A. MPPM CC-40, ventral (internal) view of adapical test; B. MPPM CC-42, dorsal view; C. MPPM CC-03, dorsal and ventral views; D. MPPM CC-20, dorsal view; E. MPPM CC-28, ventral (internal) view of adapical test; F. MPPM CC-60.1, anterodorsal view; G. USNM 32707 [*Hemiaster unguła* (Morton) of Wade (1926: pl.1, figs. 20, 21)], dorsal view; H. ventral view of same.
The only species of *Diplodetus* adequately described from North America is *D. americanus* (Stephenson), which is known from several Upper Cretaceous units in the Gulf Coastal Plain (Cooke, 1953).

**Suborder Hemiasterina** Fischer, 1966 (sensu Smith and Kroh, 2011)

**Family Hemiasteridae** Clark, 1917

**Included Genera**—In the North America Cretaceous, the Hemiasteridae consists of five genera (as defined by Smith and Kroh, 2011): *Hemiaster* Desor, in Agassiz and Desor, 1847; *Palhemiaster* Lambert, 1916; *Mecaster* Pomel, 1883; *Promaster* Lambert, 1895; and *Bolbaster* Pomel, 1869. Fischer (1966) and Néraudeau (1994) included *Bolbaster* and *Leymeriaster* within *Hemiaster*, although Fischer (1966) thought *Hemiaster* should also include *Mecaster*. In their respective reviews of hemiasterid echinoids, McNamara (1987) and Néraudeau (1994) distinguished *Hemiaster* (sensu lato) based on its subspherical test and very subtle to imperceptible anterior notch in the third ambulacrum. Smith and Kroh (2011) treat *Bolbaster* as a discrete genus for these same reasons but add to this its more symmetrical sternal plates compared to that of *Hemiaster*.

**Diagnosis**—Spatangoids possessing only a peripetalous fasciole. In common with other spatangoids, the hemiasterids also possess “petaloid paired ambulacra and differentiated anterior ambulacrum with enlarged pore-pairs adapically” as well as a regularly amphisternous plastron (Smith and Jeffery, 2000). Other family-defining characters defined by (namely) Smith and Kroh (2011) have no immediate bearing on the features preserved in the Coon Creek material.

**Description and Discussion**—Both *Mecaster* and *Palhemiaster* have more developed (i.e. longer) petals than *Hemiaster* and *Bolbaster*, the posterior pair is also significantly longer than the other species in the latter two. Like *Hemiaster* and *Bolbaster*, the smallest (also the most common) Coon Creek spatangoid has posterior petals less than half the length of the anterior petals. Like *Hemiaster* and *Bolbaster*, most of the smaller Coon Creek spatangoids are relatively short in length and gently rounded, unlike the subhexagonal *Mecaster* and more elongate *Palhemiaster*. Although none of the small Coon Creek spatangoids examined have many articulated plates, certain fine anatomical features of the test are visible as delicate impressions. At least two specimens exhibit a very shallow furrow in the shape of a hemiasterid peripetalous fasciole. No such depressions were observed at other locations (e.g. subanally or laterally) on the best preserved specimens that would suggest the presence of other fascioles.

#### Genus Bolbaster Pomel, 1869

**Type species**—*Spatangus prunella* Lamarck, 1816.

**Included species**—Speciose genus, the composition of which is too numerous to list here (see Néraudeau, 1994, for a comprehensive list). At least eight species of *Hemiaster* (sensu lato) have been described from the Upper Cretaceous of North America, but only two of these are attributable to the increasingly refined definition (e.g. Smith and Kroh, 2011) of *Bolbaster*—*H. wetherbyi* De Loriol, 1887, and *H. arcolensis* Cooke, 1953. Néraudeau (1994) placed both in the subgenus *Hemiaster* (*Bolbaster*), which he differentiated from the other Senonian subgenus *Hemiaster* (*Leymeriaster*) by the more globular test and shallower petals (particularly the third) of the former.

**Diagnosis**—Small, ovate, slightly longer than wide with a cuneate profile and subdual amb III sulcus; distally closed paired dorsal ambulacra, anterior pair approximately twice length of posterior pair; mostly central apical disk ethmophract with four gonopores; peripetalous fasciole; D-shaped peristome; symmetrical sternal plates; and small periproct lying high on truncate posterior.

**Discussion**—All described North American Upper Cretaceous *Hemiaster* (sensu lato) species are either junior synonyms of *B. wetherbyi* (De Loriol) (see Cooke, 1953; Smith and Jeffery, 2000), belong to *Mecaster* Pomel (or some other hemiasterine genus), or represent insufficient material not warranting continued perpetuation of the species name (see synonymies of Cooke, 1953 and Smith and Jeffery, 2000).

Kew (1920) described five species of *Hemiaster* (sensu lato) from two Upper Cretaceous units in California. Four species are described from the Chico Formation, which ranges in age from Santonian to Campanian (Haggart, 1984), and one from the Hornbrook Formation, which contains Albian through Maastrichtian beds (Nilsen, 1993). Although Kew’s (1920) California material is largely skeletal (i.e. not restricted to internal molds), the type and figured specimens upon which Kew (1920) based his new species, like the Coon Creek specimens, exhibit some degree of distortion. Regrettably, time constraints did not permit the examination of Kew’s (1920) California material.

*Bolbaster wetherbyi* (De Loriol, 1887)

Figure 6

*Spatangus parastatus* Morton, 1833a. Morton, 1834, p. 21, 77-78. (Prairie Bluff Formation, Alabama)

*Hemiaster wetherbyi* de Loriol, 1887, p. 391, pl. 17, figs. 5, 6. (Prairie Bluff Formation, Mississippi)

*Hemiaster* sp. Dane, 1929, p. 109, 132. (Saratoga Chalk, Arkansas)

*Hemiaster wetherbyi* de Loriol. Cooke, 1953, p. 31-31, pl. 12, figs. 17, 18.

Holotype—Unknown, although originating from Wahalak, Kemper County, Mississippi, most likely the Late Maastrichtian Prairie Bluff Formation (Cooke, 1953). Several North American species were placed in junior synonymy with H. wetherbyi de Loriol by Cooke (1953) and Smith and Jeffery (2000).

Diagnosis—Small, short, ovate/subrounded hemiasterid with a cuneate profile, evenly rounded margins, and gently truncate posterior; paired dorsal ambulacra extending well short of margins, posterior pair less than half the length of anterior pair; amb III sulcus of moderate depth dorsally, becoming very shallow to flush anteriorly; apical system posterior of center; conspicuous peripetalous fasciole with gentle indentations between petals; peristome one third test length from anterior margin; periproct ovate, pointing dorsally and high on the posterior; large, scrobiculate tubercles are recessed adorally and tightly packed together.

Referred Material—USNM 32709 [Hemiaster lacunosus Slocom of Wade (1926: pl. 2, figs. 2,3)], USNM 467974 [Hemiaster stella (Morton) of Wade (1926)], and the specimens listed in Table 1. Smith and Jeffery (2000) provide the most recent published synonymy list for this species.

Description and Discussion—The more common small Coon Creek spatangoid is bluntly ovate in dorsal outline, broader anteriorly, with a shallow anterior sulcus connecting dorsal amb III with the peristome. The test is wedge-shaped in profile, taller and truncate posteriorly. The dorsal amb are recessed, and the anterior pair is at least twice the length of the posterior pair. The peristome is positioned from the anterior margin at a distance of about one third of the test length. The angle of divergence of the anterior petals (81-100°, =90°, n=5) is slightly greater than that of the posterior petals (76-86°, =81°, n=4). Several intact plates indicate that the Coon Creek hemiasterid possessed tightly packed, deeply recessed tubercles, especially on the adoral surface.

The Coon Creek echinoid is similar to several species of Upper Cretaceous Bolbaster. As mentioned above, there are two other valid North American Senonian Bolbaster species—B. parastatus (Morton) and B. arcolensis Cooke. Bolbaster parastatus has a posterior apical system, more diverging posterior petals, slightly sigmoidal and proportionally longer anterior petals, and a deeper amb III sulcus than B. wetherbyi and the Coon Creek material. Cooke (1953) reported internal molds of B. parastatus (= B. humphreysanus Meek and Hayden, 1856) from the Coon Creek beds (lower Ripley Formation) of Mississippi, but none of the type locality echinoids resemble this species in the least. Bolbaster arcolensis is distinguished from B.
wetherbyi by its more central apical system, proportionally broader posterior, and the lack of sunken tubercles. The better preserved Coon Creek hemiasterids are in agreement with B. wetherbyi in their slightly posterior apical system, relatively narrow posterior, and sunken tubercles evident on what few plates were preserved.

In addition to the aforementioned North American Upper Cretaceous species, the Coon Creek hemiasterid is grossly similar to several European Senonian species of Bolbaster. However, among other differences, Bolbaster prunella (Lamarck, 1816) is nearly spheroidal and B. koninckanus (d'Orbigny, 1854) has longer posterior petals. Bolbaster stella (Morton, 1830) has the same 90°/80° (ant./post.) paired petal divergence as the Coon Creek echinoid; however, it’s paired petals are even shorter than those of B. wetherbyi, producing a greater distance between the petal tips and the ambitus in B. stella. Wade (1926) referred certain distorted small spatangoids from Coon Creek to B. stella (Morton, 1830) but did not provide catalog numbers nor figure examples. A group of specimens assigned USNM 467974 and collected by Wade (1926) fit this description, but this material is easily consistent with the variation observed within B. wetherbyi.

Wade (1926) assigned one Coon Creek specimen—USNM 32709—to Hemiaster lacunosus Slocom, 1909, which Cooke (1953) later placed in synonymy with H. wetherbyi De Loriol. Wade’s (1926) use of the name H. lacunosus Slocom, 1909, instead of H. wetherbyi De Loriol, 1887, is not surprising as Clark’s (1915) monograph of North American Mesozoic echinoderms, the principal reference for the region in the early 20th century, promoted the use of the former. Lambert (in Lambert and Thiery, 1924) renamed H. lacunosus Slocom for the author—H. slocomi—because the former name was preoccupied (see review of Cooke, 1953). The use of the name H. slocomi Lambert by Brister and Young (2007) follows this reasoning.

The oldest example of definitive Bolbaster in North America is Hemiaster cranium Cooke, 1946, from the Late Albian of Texas. It is subspheroideal with a barely perceptible anterior notch and possesses a peripetalous fasciole only. This species has proportionally shorter petals, more central apical system, and less steep posterior truncation than H. wetherbyi and the Coon Creek hemiasterid.

Although none of the Coon Creek specimens possess plating that would reveal the full extent of fascioles (or certain other skeletal features), they nevertheless agree in all other detectable respects with B. wetherbyi (De Loriol).

Suborder Paleopneustina Markov and Solovjev, 2001 (sensu Smith and Kroh, 2011)
Family Schizasteridae Lambert, 1905
Genus Schizaster Agassiz, 1836
Type species—Schizaster studeri Agassiz, 1836.
Included Species—Speciose, but only one—Schizaster variabilis (Slocom)—has ever been reported from the Upper Cretaceous of North America.

Diagnosis—Test with ovate to cordate outline and truncate posterior; petals deeply recessed, amb III lying in an even deeper sulcus; paired anterior petals longer and more flexed than posterior pair; posterior petaloid pair intervened by a keeled interamb 5 dorsally; reiform peristome, facing forwards; periproct positioned high on vertical or gently sloping posterior truncation; peripetalous and lateral fascioles present.

Among other closely related schizasterid genera, Linthia Desor, 1853, is the most similar. However, Schizaster has anterior ambulacra that are bent anteriorly (and sometimes distally), producing a notably more acute angle (e.g. Cooke, 1959). In addition to this distinctive flexure, the posterior petals of Schizaster are less than 80 per cent the length of the anterior pair (Smith and Jeffery, 2000). The anterior petals of Linthia are unflexed and obtuse (°115°-145°), and the posterior pair is equal to or slightly less than the length of the anterior pair. In Schizaster, the angle produced by the anterior petals may be obtuse (up to °140°) near the apical system, but the proximal flexure ultimately produces a distinctively acute effect.

Species Schizaster variabilis (Slocom, 1909)


Holotype—USNM 6852, complete test from the Late Maastrichtian Prairie Bluff Formation of Pontotoc, Mississippi.

Diagnosis—As for genus, but flatter ventrally; interamb 5 keel sharp dorsally, forming highest part of test; apical system central; anterior petal pair approximately twice the length of posterior pair.

Species Schizaster cf variabilis (slocom, 1909)

Figure 4

Description and Discussion—There are few features in the rare moldic Coon Creek schizasterids that would allow definitive assignment to a species. The characters used in the reviews of Cooke (1953, 1959) and Smith and Jeffery (2000) are not particularly useful in distinguishing Schizaster variabilis (Slocom) from Paleogene species of similar size and shape. Schizaster alabamensis (Clark, 1915), from the immediately superjacent Early Paleocene in the Gulf Coastal Plain, is similar in size to S. variabilis and the two are very similar in many morphologic details. The available comparative material of each species seems to suggest S. alabamensis has less recessed petals with a concomitantly reduced keel in interamb 5 dorsally. The
depth of the petals in the Coon Creek schizasterid is more in line with that observed in *S. variabilis*; however, a better sample of *S. alabamensis* is required to test this character as species diagnostic. The outline of the adoral ambulacra is preserved on one of the molds (Fig. 4B); however, this pattern is characteristic of several species of Late Cretaceous and Paleogene *Schizaster*, including *S. alabamensis* (Clark, 1915) from the Early Paleocene of the Southeast. Nevertheless, definitive *S. variabilis* has been collected by the writers in the adjoining Coon Creek and equivalent beds of Mississippi. In addition, *S. variabilis* (Slocum) is the only schizasterid species previously recognized from the Upper Cretaceous of the Gulf Coastal Plain (Clark, 1915; Cooke 1953, 1959; Smith and Jeffery, 2000).

**DISCUSSION**

In its early stages (Ciampaglio, 2003), the current project was only beginning to understand the scope of problems involved in accurate identification of the poorly preserved Coon Creek echinoids. Over the last several years, the project has advanced to its current form via a more comprehensive understanding of both echinoid diversity and types of preservation encountered in Late Campanian and Maastrichtian sites in the Southeast. Identifications were much improved upon by access to a considerably greater number of specimens for comparison (namely, the growing MMNS reference collection), a greater knowledge of variation within and diversity among North American Upper Cretaceous echinoid populations, as well as new insights into the degree and types of distortion exhibited by moldic echinoids in general. These factors resulted in the abandonment of several preliminary taxonomic assignments made by Ciampaglio (2003).

Five species populate the echinoid assemblage in the Coon Creek beds of McNairy County, Tennessee—a faujasid cassiduloid, a cardiasterid holasteroid, and three spatangoids of different familialities. *Lefortia trojana* Cooke is the first cassiduloid to be reported from the Upper Cretaceous of Tennessee. Although cassiduloids had not been previously reported from the Coon Creek beds, they are well-known from other Maastrichtian facies in the northeastern Gulf of Mexico (NGOM) (Veatch and Stephenson, 1911; Cooke, 1953, 1955; Phillips and Ciampaglio, 2008). For much of the Maastrichtian, *Hardouinia mortonis* (Michelin) was the ubiquitous large cassiduloid occurring in a variety of sandy facies in the NGOM and Northwest Atlantic. Based on its abundance in near-shore coarse sand facies, this stigmatopygine faujasid likely filled the “sand dollar” niche in high subtidal and intertidal zones. In the NGOM, this taxon is confined to and occurs throughout the UZAGC-5.0 transgressive sequence (Mancini et al., 1995), which began in the Early Maastrichtian, based on the stage boundaries as defined in this paper (Fig. 2). In the Gulf Coastal Plain (GCP), *Lefortia trojana* is known only from the lower Ripley Formation—the Coon Creek beds in Tennessee (this report) and the laterally equivalent but more calcareous “Troy beds” (sensu Swann and Dew, 2008) in north Mississippi (see Cooke, 1953). These lower Ripley facies constitute the highstand systems tract of the UZAGC-4.0 transgressive sequence. Cooke (1953) reported *Hardouinia micrococcus* (Gabb, sensu stricto) from this same sequence depositional interval in the lower Ripley (Ripley Sand equivalent) in east-central Georgia.

This is the first report of *Cardiaster* of any age from the NGOM. If the most fragmentary specimens were included (the current analysis includes only specimens representing at least a third to a half of an internal mold), *Cardiaster* would probably have had a higher relative abundance than the current Coon Creek samples suggest (Table 1). Regularly and widely occurring preservational bias against *Cardiaster* is suspected in many units in the GCP, particularly in the eastern portion. This suspicion is based on observations made of differential echinoid preservation along the same or related Upper Cretaceous lithofacies in Texas, Arkansas, and Mississippi, particularly among holasteroids (namely *Cardiaster* and *Echinocorys*). Differences in (1) burial environment, (2) postdepositional history (hydrology, depth of weathering, vegetation cover, exposure time, etc.), and (3) the abundance and availability/solubility of mobile ambient calcite, coupled with inter-taxonomic differences in local calcite mineralogy, produces taxon-specific effects on echinoid preservation. In the eastern GCP, holasteroids are most often encountered in one of three ways—(1) as mud steinkerns where test is not preserved, (2) in association with concretions (covering part or all of the test), or (3) encrusted by epifauna with calcitic skeletons. The Coon Creek beds from the type locality south to northern Union County, Mississippi, contain examples of the first type of preservation. The second and third types are characteristic of more calcareous facies to the south (*i.e.* downdip) in Mississippi and Alabama. Based on unpublished samples from and observations of more calcareous units to the south and far west of the Coon Creek beds, *Cardiaster* (and *Echinocorys* in Late Campanian sediments) may have gone undetected until recently due to these diagenetic effects, not because of unsuitable benthic environments. A more comprehensive analysis of native echinoid calcite, diagenetic calcite, benthic watersediment chemistry, and the postdepositional mineralogy of the ambient sediment may reveal the extent of the apparent preservational bias against holasteroids.

The spatangoids *Diplodetus americanus* and *Bolbaster wetherbyi* were previously encountered by Wade (1926), albeit both under different names. The two seem to occur in roughly equal abundance at Coon Creek (Fig. 1). *Bolbaster wetherbyi* is the ubiquitous small burrowing spatangoid within the Mississippi Embayment, from the
Late Campanian through the Maastrichtian (Cooke, 1953). We have found D. americanus to have a similar spatiotemporal distribution although in generally lesser relative abundance than that at Coon Creek. Given the low relative abundance of Schizaster variabilis in the MPPM Coon Creek sample (e.g. Table 1), it is not surprising that it went undetected by Wade (1926). We have encountered this species with greater frequency at several Early and Late Maastrichtian sites within the Mississippi Embayment; it is often locally abundant in the Nixon beds and Owl Creek Formation but has also been observed with regularity in the Troy beds and Chiwapa Sandstone (Fig 2).

Dunagan and Gibson (1993) reported common spatangoid-type burrow traces in a zone (their “Echinocardium zone”) immediately superjacent to an echinoid-rich interval in the Coon Creek beds at the Thompson Farm locality. The authors’ illustrated description of abundant meniscate (segmented) backfill burrows suggests the ichnogenus Laminites Ghent and Henderson, 1966. Dunagan and Gibson (1993) implied an association with the burrow Bichordites Plaziat and Mahmoudi, 1988, which is the single drain, Echinocardium-type Laminites trace; however, a formal ichnosystematic analysis was not performed. Nevertheless, the presence of such burrows is not surprising given the abundance of Coon Creek spatangoids, which are deep infaunal detrivores. In spite of an abundance of body fossils of Coon Creek spatangoids, which are deep infaunal detritivores. In spite of an abundance of body fossils of burrowing echinoids, their traces are seldom preserved and thus rarely reported from deposits as old as the

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REFERENCES


Cooke, C. W. 1958. Cretaceous Echinoida of New Jersey


Puckett, T. M. 2005. Santonian-Maastrichtian planktonic
foraminiferal and ostracode biostratigraphy of the northern Gulf Coastal Plain, USA. Stratigraphy 2(2):117-146.


Stephenson, L. W. 1941. The larger invertebrate fossils of the Navarro Group of Texas (exclusive of corals and crustaceans and exclusive of the fauna of the Escondido Formation). University of Texas, Austin, 641 pp.


Late Cretaceous actinopterygians represented by otoliths from
the Coon Creek Site
in southwest Tennessee

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ABSTRACT—The study and analysis of otoliths (ear stones) of actinopterygians from the Late Cretaceous Coon Creek Formation type section (approximately 71.5 - 72.0 Ma) provide pertinent information not available solely on the basis of skeletal fish remains. Although otolith studies from the site have been limited in number and scope, otoliths indicate ten bony fishes representing at least eight families. The otoliths point to a bony fish assemblage that includes an albulid and pterothrissid (bonefishes), a congrid (conger eels), an ariid (sea catfishes), a paralopid (cucumber fishes), a trachichthyid (roughies), two berycoids (alfonsinos), a pempherid (sweepers), and an unknown perciform. Several of the forms represented by otoliths (the pempherid and perciform) provide further evidence for the evolution of the Perciformes in the Cretaceous rather than later in the early Paleogene. By the time of the well-documented early Cenozoic radiation and speciation of the teleosts, the Perciformes had undergone tens of millions of years of evolution and development. The presence of perciform otoliths is in agreement with recent comprehensive molecular phylogeny studies (DNA sequence of mitochondrial and nuclear genes with fossil constraints). The bony fishes represented by otoliths indicate a shallow, marine environment probably inner to middle shelf with tropical to subtropical conditions. Several of the forms, such as the albulid and pterothrissid, suggest inner neritic, and other taxa suggest a soft substratum. Some factors seem to indicate that detailed, systematic bulk sampling and periodic, well-organized surface collecting would result in a greater diversity of bony fishes represented by otoliths at the Coon Creek type section.

INTRODUCTION

The Coon Creek Formation type section at the Coon Creek Science Center (also referred to as the Coon Creek site in this paper) in McNairy County in southwestern Tennessee is one of the most famous Late Cretaceous fossil localities in North America. The Coon Creek Formation represents shallow marine sediments deposited in a mixing zone between the deeper shelf Demopolis Formation below and the nearshore, shoreline, and fluvial McNairy Sand above (Russell and Parks, 1975). The formation is composed of well-sorted, fine-grained, glauconitic, marine sands and clays that are characteristic dark gray and ranges in thickness from 36 to 54 m. In Tennessee, the Coon Creek Formation can be differentiated into distinctive lower and upper lithofacies (Russell et al., 1982). The age of the Coon Creek type section is probably around 71.5 - 72.0 Ma according to recent research based on ammonites by Larson (2012) and other studies (this volume). According to the International Commission on Stratigraphy (Cohen et al., 2013), the Maastrichtian begins at approximately 72.1 ± 0.2 million years. Therefore based on these findings as well as previous studies (Brouwers and Hazel, 1978; Russell et al., 1982; Bishop, 1983), the Coon Creek type section would be in the earliest part of the early Maastrichtian.


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The uniqueness of the Coon Creek site is related to the large number of marine fossils found there, the tremendous diversity of the invertebrate and vertebrate faunas, and the excellent preservation of the fossil specimens. The site has produced over 600 species of invertebrate and vertebrate fossils (Wade, 1926; Adams, 1994; Noble, 1996; Brister and Young, 2007). However, research on the bony fishes represented by otoliths from the site has been very limited. This is unfortunate since otoliths or ear stones commonly provide valuable information on the fish assemblage that may not be discernible based exclusively on skeletal remains. The value of otoliths in paleontological sites has been clearly demonstrated in numerous studies. For example, Breard and Stringer (1995) in a study of the Late Eocene Yazoo Clay in Louisiana reported 12 bony fish based on skeletal remains (primarily teeth). This is in stark contrast to the 43 taxa of bony fish identified from the same locality using otoliths (Nolf and Stringer, 2003). Clearly, the diversity of the fishes would be grossly underestimated in the Yazoo Clay if only skeletal elements were considered. The value of otoliths for identifying and interpreting the actinopterygians for the Coon Creek site is clearly demonstrated by the number of bony fishes identified on skeletal remains. The author is aware of only four bony fishes from the Coon Creek site identified on the basis of otoliths. Anomoeodus robustus, Enchodus gladiolus, Enchodus ferox, and Cylindracanthus cretaceous. There are other skeletal remains such as fragments of bone, vertebrae, and scales that have been recovered, but these are not identifiable. The otoliths provided additional actinopterygians present at the Coon Creek site that would have otherwise gone unrecognized.

The use of fish otoliths provides a more detailed and accurate representation of the ichthyological fauna than skeletal components such as teeth, vertebrae, spines, and scales alone. Skeletal components of bony fish can also be misleading in the interpretation of the thanatocoenosis. The relationship of skeletal elements such as fish teeth to the actual abundance of a taxon is often difficult to ascertain. Theoretically, 20 fish teeth (such as those of the Enchodus) could easily originat with one individual or could represent teeth from 20 different individuals. However, since an individual fish has only two sagittal otoliths (sagittae), the presence of otoliths is a more accurate representation of abundance (Nolf, 1985; Nolf and Stringer, 1992; Breard and Stringer, 1995). Although otoliths may provide a more accurate record of bony fish diversity and abundance in some formations, the best scenario is to study both the skeletal material and otoliths.

Previous studies of actinopterygian otoliths from the Coon Creek site, although quite limited, are summarized below. The objective of this study is to provide an overview of the fishes identified on the basis of otoliths from the site from previous studies as well as from new material, which includes a brief systematic paleontology for each of the taxa represented by otoliths. In addition, the evolutionary and paleoecological significance indicated by the otoliths from the site are discussed. Finally, recommendations for future studies of the Cretaceous fishes represented by otoliths from the Coon Creek site are suggested.

### PREVIOUS STUDIES

Nolf (1985) reported less than 20 valid species represented by otoliths for the Cretaceous worldwide. This paucity of investigations of Cretaceous otoliths, especially in North America, increases the importance of this study of the Coon Creek site. Koken completed the first scientific description of Cretaceous otoliths in 1891 on otoliths from Europe, but studies of North American Cretaceous otoliths were not to occur until much later. Most Cretaceous otoliths from North America have been obtained primarily from Campanian and Maastrichtian strata although there are isolated reports from other ages such as Huddleston (1981), who described a single otolith from the Cenomanian of Oregon. One of the earliest reports on the occurrence of otoliths from the Cretaceous of North America was from the Coon Creek site in southwest Tennessee by Wade (1926), who figured a single otolith from the Cretaceous Formation. The otolith was mentioned in a section entitled “Class Pisces” (p. 192) that was actually written by J. Gidley of the United States National Museum. The otolith was figured on Plate LXXI (figs. 9 and 10) and was labeled as simply “otolith” in the plate description. The figured otolith specimen appears to be a lapillus (utriculith) from a marine arid (sea catfish), which are known from several other Cretaceous formations in North America (Huddleston and Savoie, 1983; Stringer, 1991; Nolf and Stringer, 1996). Although only one otolith is discussed in the section on fishes by J. Gidley and figured in the plates, Wade used the term “otoliths” in his table entitled “The Coon Creek fauna and its range” (pp. 22–26). Otoliths are listed, but they are not discussed. It is unclear if the “otoliths” in the table represent one taxon and how many otoliths were actually recovered by Wade from Coon Creek.

The first description of otoliths from the Coon Creek site was not completed until 70 years later. Dr. J. Zidek sent a small sample of screen washed residue (approximately 0.5 kg) from the Coon Creek site to Dr. D. Nolf in Belgium. Nolf and Stringer (1996) examined this material as part of a study of North American Cretaceous fish otoliths. Six taxa of bony fishes were represented by otoliths in the residue from the Coon Creek site (Table 1). The number of fish taxa at the Coon Creek site was much smaller than a stratigraphically and lithologically similar site in nearby northeastern Mississippi [the Blue Springs locality of Stringer (1991) and Nolf and Stringer (1996)]. Considering the diversity and preservation of other fossil groups within the Coon Creek Formation, a greater number of otolith specimens and a larger number...
of taxa were expected. Therefore, additional surface and bulk sampling (about 50 kg) were conducted at the Coon Creek site in summer of 1998 by the author with the assistance of R. Brister from the Pink Palace Museum in Memphis, Tennessee. Limited surface collecting at the site yielded no otoliths. Analysis of the bulk samples produced very sparse vertebrate material including otoliths. However, three additional otolith-based taxa were found and included *Kokenichthys ensis*, *Pterothrissidae* indeterminate, and “*Pempherida* huddlestoni” (Stringer, 1999). Four taxa were originally thought to have been found, but one of the otoliths was later determined to be the same as a form previously described (*Paraulopidae* indeterminate; originally reported as *Chlorophthalmidae* indeterminate; originally reported as *Chlorophthalmidae* indeterminate) by Nolf and Stringer (1996). A summary of the actinopterygians represented by otoliths from the Coon Creek site is shown in Table 2.

**MATERIALS AND METHODOLOGY**

The present study includes material that was collected by various researchers who utilized different techniques. It is not known with any certainty the procedure employed by Wade (1926) when he collected the illustrated otolith. Most likely, the otolith was collected along with other fossils on the surface at the Coon Creek site. Likewise, the author is not sure of the exact procedure employed by Zidek in the collecting of his samples that produced the approximately 0.5 kg of screen washed residue that produced the approximately 0.5 kg of screen washed residue that was examined as part of the study by Nolf and Stringer (1996).

The author conducted limited surface collecting and bulk sampling at the Coon Creek site in the summer of 1998. Surface collecting yielded no otoliths, but abundant aragonitic invertebrate fossils were found on the surface. The presence of aragonitic fossils is a strong indication for the potential for otoliths in sediments (Nolf, 1985; Stringer and Miller, 2001). Approximately 50 kg of fresh, unweathered sediment was collected from the site. The collected samples were air-dried for several weeks. The air drying assists in the disaggregation and processing of the samples. The samples were wet sieved using tap water through an U.S. Standard No. 20 sieve (opening 0.84 mm) and a No. 40 sieve (opening 0.42 mm). No detergents or cleaning solutions were used since they could adversely affect the aragonitic otoliths. Following the wet sieving, the residue was air-dried. Otoliths were extracted from the residue using a stereoscopic binocular microscope (10x-40x). All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique.

**DESCRIPTION AND SYSTEMATIC PALEONTOLOGY OF OTOLITHS**

A brief discussion and the systematic paleontology of each of the bony fishes represented by otoliths from the Coon Creek site are presented. The number of specimens examined for each taxon is given and includes specimens from two Late Cretaceous sites near Blue Springs, Mississippi. Otoliths from each of the bony fishes recovered from the Coon Creek site are illustrated in Fig. 1. The illustrations are modified from a study of North American Cretaceous fish otoliths by Nolf and Stringer (1996). A fairly extensive discussion of the terminology utilized in the description of otoliths is found in Nolf (1985; p. 7). A shorter, more concise glossary of morphological features of the inner face of the sagitta (saccular otolith) and the otolith margin is presented in Nolf and Stringer (2003; p. 3). Illustrations of the morphological features of otoliths used in this paper are in Nolf and Stringer (1992; text fig. 3, p. 49). An excellent figure of the morphological nomenclature of a sagitta is also illustrated in Nolf et al. (2009; p. 5).

From approximately the mid-1980s, many otolith researchers worldwide utilized a taxonomy proposed by Nolf (1985) specifically for otoliths. The taxonomy was extensively applied, but there were several major concerns and objections to the classification. The classification, which utilized genitive plural names, produced very long, awkward scientific names. More importantly, many taxonomists felt that it violated several articles of the Code of Zoological Nomenclature, namely articles 10.3, 11.4.1, 11.7, 11.8.1, and 42.2.1. Therefore, Nolf (2013) modified his classification to follow the Code. Genitative plural names are no longer used, and collective group names are employed as a genus group name. The collective group names are italicized and placed in quotation marks to clearly indicate their special status. The reader is referred to *The Diversity of Fish Otoliths, Past and Present* (Nolf, 2013; pp. 18–19) for a full and complete explanation of the nomenclature used in otolith taxonomy.

**Kingdom Animalia**

**Phylum Chordata**

**Class Actinopterygii Klein, 1885**

**Order Albuliformes Greenwood et al., 1966**

**Suborder Albuloidi** Jordan, 1923

**Family Albulidae** Bleeker, 1849

**Species Kokenichthys ensis** Nolf and Dockery, 1990

Nolf and Dockery first described this taxon (as “*Abulida* ensis”) from the Campanian Coffee Sand in Mississippi in 1990. It is also reported from the Blue Springs locality (Late Cretaceous Ripley Formation) in northeastern Mississippi (Stringer, 1991). Stringer (1999) first reported this species from the Coon Creek site. This taxon was designated as *Kokenichthys ensis* by Schwarzhens
The otoliths are quite distinct with a very large sulcus that covers well over one-half of the inner face of the otolith. The sulcus is undivided with no distinct ostium and cauda. The posterior end of the sulcus is deeply incised, which is a typical feature in many albulids. Otoliths of *Kokenichthys ensis* are thin and elongate with an elliptical outline (Fig. 1A). Additional material of this species has been recently obtained from a site in Union County, Mississippi (MS 73.033). This site is north of the locality of Stringer (1991) and has extensive exposures of the Coon Creek Member of the Ripley Formation (over 300 m long and 250 m wide). Specimens of the Coon Creek Member of the Ripley Formation (over locality of Stringer (1991) and has extensive exposures of the Coon Creek site. The otolith has an oval outline with a distinct, divided sulcus. The cauda is gently and evenly flexed and is about twice as long as the ostium (Fig. 1B). The otoliths may represent a new species of pterothrissid, but the lack of a complete growth series and the poor preservation of the specimens have prevented specific identification. It should be noted that in older classifications, the albulids and pterothrissids were placed in separate families, the Albulidae and the Pterothrissidae respectively (Nolf, 1995). However, both are now placed in the family Albulidae in separate subfamilies (Nelson, 1994, 2006). The posterior end of the sulcus is about twice as long as the ostium (Fig. 1C). This form was originally described as “Congrida diagonalis” by Wade (1926) from the Coon Creek site is similar to arid otoliths known from several Campanian and Maastrichtian localities in North America (Huddleston and Savoie, 1983; Nolf and Stringer, 1996). The rounded and flattened lapilli are also known from many Paleocene associations in North America and Europe (Nolf and Dockery, 1993; Nolf and Stringer, 1996; Nolf, 2003a).

These specimens represent lapilli or utricular otoliths rather than sagittae or saccular otoliths, which occur most commonly as fossils, and are believed to be related to the Recent sea catfishes or aruids. The arid otolith figured by Wade (1926) from the Coon Creek site is similar to arid otoliths known from several Campanian and Maastrichtian localities in North America (Huddleston and Savoie, 1983; Nolf and Stringer, 1996). The rounded and flattened lapilli are also known from many Paleocene associations in North America and Europe (Nolf and Dockery, 1993; Nolf and Stringer, 1996; Nolf, 2003a). Unfortunately, the lapillus is not highly diagnostic and is only identified to the family level (Fig. 1D). The number of specimens of Ariidae indeterminate examined was 21.

**PTEROTHRISSIDAE INDETERMINATE**

Otoliths of this form have been reported from the Campanian Coffee Sand in Mississippi (Nolf and Dockery, 1990) and from the Maastrichtian Ripley Formation in northeastern Mississippi (Stringer, 1991). Stringer (1999) noted the presence of this species at the Coon Creek site. The otolith has an oval outline with a distinct, divided sulcus. The cauda is gently and evenly flexed and is about twice as long as the ostium (Fig. 1B). The otoliths may represent a new species of pterothrissid, but the lack of a complete growth series and the poor preservation of the specimens have prevented specific identification. It should be noted that in older classifications, the albulids and pterothrissids were placed in separate families, the Albulidae and the Pterothrissidae respectively (Nolf, 1985). However, both are now placed in the family Albulidae in separate subfamilies (Nelson, 1994, 2006). Furthermore, *Pterothrissus* has been shown to be a synonym of *Istieus* (Nelson, 2006), but Pterothrissidae and Pterothrissus are still widely used in the palaeontological literature. The number of specimens of Pterothrissidae indeterminate examined was 19.

**Order Anguilliformes** Regan, 1909

**Suborder Congroidei** Nelson, 1984

**Family Congridae** Kaup, 1856

**Species “Congrida” aff. Thevenini** (priem, 1906)

This congrid otolith or one very similar to it is also known from the Late Cretaceous Blue Springs locality in northeastern Mississippi (Nolf and Stringer, 1996) and from the Maastrichtian Severn Formation in Maryland (Huddleston and Savoie, 1983). The otolith has a very generalized morphology and considerable variation. The sulcus is typical of many congrid genera and is undivided (Fig. 1C). This form was originally described as “Congrida diagonalis”, but it has been placed in synonymy with “Congrida aff. thevenini” (Nolf, 2013). Although “Congrida diagonalis” was first described from the Eocene (Lede Sands of Belgium), the Cretaceous otoliths from the Coon Creek site seem to be very closely related. However due to the wide stratigraphic and geographic range of the species as well as the variability within the form, the Coon Creek otoliths are designated as “Congrida” aff. thevenini. The number of specimens of “Congrida” aff. thevenini examined was 21.

**Order Siluriformes** Cuvier, 1817

**Family Ariidae** Gunther, 1864

**ARIIDAE INDETERMINATE**

These specimens represent lapilli or utricular otoliths rather than sagittae or saccular otoliths, which occur most commonly as fossils, and are believed to be related to the Recent sea catfishes or aruids. The arid otolith figured by Wade (1926) from the Coon Creek site is similar to arid otoliths known from several Campanian and Maastrichtian localities in North America (Huddleston and Savoie, 1983; Nolf and Stringer, 1996). The rounded and flattened lapilli are also known from many Paleocene associations in North America and Europe (Nolf and Dockery, 1993; Nolf and Stringer, 1996; Nolf, 2003a). Unfortunately, the lapillus is not highly diagnostic and is only identified to the family level (Fig. 1D). The number of specimens of Ariidae indeterminate examined was 21.

**Order Aulopiformes** Rosen, 1973

**Suborder Synodontoidae** Gill, 1872

**Family Paraulopidae** Sato & Nakabo, 2002

**PARAULOPIDAE INDETERMINATE**

Several otoliths from the Coon Creek site appear to be very similar to specimens first identified as “genus Synodontidarum” *pseudooperca* from the Late Cretaceous Ripley Formation at the Blue Springs locality of Stringer (1991) in northeast Mississippi (specimens are now believed to be more closely related to the Paraulopidae). The otolith is elongate with the length about twice the width. The sulcus is distinct and divided with the cauda at least twice the length of the ostium. One of the most distinct features is the pronounced posterodorsal angle (Fig. 1E). Specimens of the Coon Creek paraulopid otoliths are closely related to *Paraulopus pseudooperca* from the Campanian Coffee Sand of northeast Mississippi (Nolf and Dockery, 1990) and “Paraulopida” *postangulatus* from the Paleocene Porters Creek Formation of Alabama (Nolf and Dockery, 1993). Both of these forms were initially
thought to be in the family Chlorophthalmidae but are now classified in the family Paraulopidae (Sato and Nakabo, 2002; Nolf, 2013). Since the number of specimens from Coon Creek is limited with no growth series available, the Coon Creek paraulopids are identified only to the family level (Fig. 1E). The number of specimens of Paraulopidae indeterminate examined was 153, which includes otoliths from several other Late Cretaceous sites.

Order Berycoidei

Species “Trachichthyida” oscitans Nolf and Stringer, 1996

This species represents the largest otolith from the Coon Creek site. The otoliths tend to be fairly thick with a subpentagonal shape. The sulcus is quite distinct, and there is a pronounced anteroventral angle (Fig. 1F). The distinct ostium and cauda are approximately equal in length. The ostium is wide and dorsally expanded. There is considerable elongation along the anteroventral-posterodorsal axis, and the ostial portion of the crista superior shows a pronounced dorsal expansion (Nolf and Stringer, 1996). These two features distinguish this species from a similar form from the Campanian Coffee Sand, “Trachichthyida” coffeasandensis. The Coon Creek species appears to be the same as those from the Coon Creek bed of the Ripley Formation (Late Cretaceous) from the Blue Springs locality of Stringer (1991) in northeastern Mississippi. The number of specimens of “Trachichthyida” oscitans examined was 1511.

Suborder Berycoidei

Species Beryx? Maastrichtiensis Nolf and Stringer, 1996

This is one of two berycoids or alfonsinos known from the otoliths at the Coon Creek site. This species is characterized by nearly circular otoliths with a wide, continuously curved, distinct sulcus (Fig. 1G). The ostium and the cauda are approximately equal in length. The holotype of this species was described from the Ripley Formation at the Blue Springs locality of Stringer (1991) in northeastern Mississippi, and one paratype was described from the Coon Creek site (Nolf and Stringer, 1996). Although the Coon Creek otolith cannot be related to any Recent berycoid genus, it certainly has the salient characteristics of the berycoids. The number of specimens of Beryx? maastrichtiensis examined was 36. This form was originally thought to be an apogonid (Nolf and Stringer, 1996) but is now believed to be a berycoid.

Beryx? Zideki Nolf and Stringer, 1996

This is the second species of alfonsino known from the Coon Creek site. Like Beryx? maastrichtiensis, the otolith possesses generalized berycoid features. However, Beryx? zideki is characterized by elongate otoliths with a somewhat angular outline. The sulcus is distinct and divided. The ostial crista superior is almost straight with almost no dorsal extension. The surfaces of the otolith are quite smooth even in small specimens (Fig. 1H). The holotype of this berycoid species was also described from the Coon Creek bed of the Ripley Formation at the Blue Springs locality of Stringer (1991) in northeastern Mississippi. The species appears to be the same as the one found by Huddleston and Savoie (1983) in the Maastrichtian Severn Formation in Maryland but was identified only to the family level (Nolf and Stringer, 1996). The number of specimens of Beryx? zideki examined was 26. Like Beryx? maastrichtiensis, Beryx? zideki was originally identified as an apogonid (Nolf and Stringer, 1996).

Order Perciformes

Species “Pempherida” huddlestoni Nolf and Stringer, 1996

Otoliths attributed to pempherids or sweepers have been identified from the Coon Creek site. The otoliths of “Pempherida” huddlestoni are nearly round in outline except for the angular rostrum and a slightly pointed posterior end. The sulcus extends nearly across the inner face and is divided into a distinct ostium and cauda. The cauda is narrow with its posterior end flexed slightly downward. The ostium is almost twice as wide as the cauda. There is a slight depression above the sulcus (Fig. 1I). Stringer (1999) first noted this species at the Coon Creek site. The Coon Creek specimen of “Pempherida” huddlestoni appears to be the same as those from the Ripley Formation in northeast Mississippi (Blue Springs locality of Stringer, 1991, and locality for the holotype) and the Maastrichtian Severn Formation in Maryland (Huddleston and Savoie, 1983). The number of specimens of “Pempherida” huddlestoni examined was 19.

Perciformes incertae sedis

Species “Perciformis” cepoloides nolf and dockery, 1990

This otolith from the Coon Creek site compares favorably with “Perciformis” cepoloides known from the Late Campanian Coffee Sand at the Griffin sandpit (Nolf and Stringer, 1996). Nolf and Stringer (1996) first reported the taxon from the Coon Creek site. The otolith shows perciform characteristics, but it cannot be placed into a definite suborder or family (Fig. 1J). The number of specimens of “Perciformis” cepoloides examined was four.
Figure 1

FIGURE 1. Otoliths of the bony fishes from the Coon Creek site. A. *Kokenichthys ensis*, left sagitta, ventral view and inner face view; B. Pterothrissidae indeterminate, left sagitta, ventral view and inner face view; C. “Congrida” aff. “C.” thevenini, right sagitta, inner face view; D. Ariidae indeterminate, right lapillus, inner face view; E. Paraulopidae indeterminate, right sagitta, inner face view; F. *Trachichthyida* oscitans, right sagitta, inner face view; G. *Beryx? mastrichtiensis*, left sagitta, inner face view; H. *Beryx? zideki*, left sagitta, inner face view; I. “Pempherida” huddlestoni, left sagitta, ventral view and inner face view; J. “Perciformis” cepoloides, right sagitta, inner face view. Scale bar equals 1 mm.
EVOLUTIONARY AND PALEOECOLOGICAL IMPLICATIONS OF OTOLITHS

Evolutionary Implications

The fish fauna of the Coon Creek site as indicated by otoliths provides important information regarding the evolutionary development of the teleosts. In 1985, Nolf cited less than 20 valid species of bony fish as indicated by otoliths for the entire Cretaceous worldwide. Even more than a decade later, Schwarzhans noted less than 100 species worldwide (Schwarzhans, 1996). However, investigations of Late Cretaceous unconsolidated glauconitic sands, clays, and marls in the U.S. Gulf Coast in the 1990s have provided otoliths that have shown the presence of additional species (Nolf and Dockery, 1990; Stringer, 1991, 1999; Nolf and Stringer, 1996). Nolf and Stringer (1996) reported 43 teleost taxa in the Late Cretaceous of North America alone. Thus, the ten forms present at the Coon Creek site are important in understanding Late Cretaceous fish assemblages and their evolutionary development. Furthermore, the site has the potential to yield more otoliths and additional taxa of actinopterygians (see “Recommendations for Future Studies on Otoliths at the Coon Creek Site”).

Since fossil otoliths are found in a wide range of environments and habitats in various paleogeographic regions, they can provide a wealth of information for tracing the origin of Recent fish families (Nolf, 1995). Furthermore, Friedman and Sallon (2012:707) verified the significance and usefulness of fish analysis in the paleontological record in a large-scale diversity patterns study and stated, “No other vertebrate assemblage encompasses as much taxonomic richness and morphological disparity distributed over such a long geological interval and represented by such a diverse range of preservational styles as fishes.” Of course, the evolutionary and speciation rates of teleosts are going to be impacted by a combination of abiotic and biotic factors as shown in the evolutionary hypotheses testing of marine fishes by Tavera et al. (2012).

Nolf (2013) specifically stated that the most important data that fossil otolith studies provide regarding the evolutionary history of teleostan fishes is the geological extension of records compared to osteological remains. Basically, the fossil record for many teleostean families is extended considerably by otoliths, and otoliths play a primary role in tracing the history of modern teleost taxa. Patterson (1993) indicated that 244 extant families of teleostean fish have a fossil record and 58 of those families (24%) are represented exclusively by otoliths. However, in the last two decades, the number of teleostean fossil families represented by otoliths has only increased to 78 (Nolf, 2013). In a study of the North Atlantic Late Cretaceous teleost families, Nolf (2003a) found that the otolith records predated the osteological remains in 28 of the 37 cases and that 8 of the families were represented solely by otoliths. The Coon Creek otoliths and otoliths from other Late Cretaceous investigations verify their importance in ascertaining the geological range of fishes.

Several of the forms present in the Coon Creek Formation are classified as Perciformes and provide further evidence for the development of modern lineages of bony fishes in the Late Cretaceous rather than in the Early Paleogene as indicated by osteological remains. The Perciformes represents not only the most diverse and largest of all fish orders (over 10,000 species) but the largest vertebrate order in terms of the number of species (Nelson, 2006), and have long been considered as modern in their affinities by the Eocene (Carroll, 1988; Alfaro et al., 2009; Wiley and Johnson, 2010; Near et al., 2013). Perciformes from the Coon Creek site include extant families such as the Pempheridae (“Pempherida” huddlestoni) and an extinct perciform family (“Perciformis” cephaloides).

These Coon Creek taxa clearly indicate the presence of the Perciformes in the Cretaceous in North America. For many decades the paradigm for the presence of perciforms in the Cretaceous was summarized best by Romer (1966: p. 68): “Except for a few doubtful cases, not a single advanced spiny-finned form is known from any Cretaceous deposit. But, starting from the beryciform stock, an immense radiation of progressive actinopterygians began at the dawn of the Tertiary.” This pattern for the evolution of the Perciformes was reinforced by numerous other studies such as Carroll (1988), Patterson (1993), Johnson and Patterson (1993), Long (1995), Nelson (2006), Alfaro et al. (2009), and Wiley and Johnson (2010). In addition, Monsch (2005) in his revision of the perciform scombroid fishes from the Cenozoic of England based on skeletal remains emphasized that most of the radiation of the scombroid fossil record starts in the early Eocene. Likewise, Friedman (2010) described the explosive morphological diversification of the spiny-finned teleostans following the end of the Cretaceous mass extinction (i.e., in the Paleogene). Friedman and Sallon (2012) reported on this same observation noting the marked increase in the richness of teleosts in the Paleogene and attributed much of this phenomenon to a precipitous increase in the number of acanthomorphs, especially percomorphs. Until recently, osteological and molecular fish studies have continued to emphasize the development and radiation of groups such as the Perciformes in the Paleogene with little reference to their early evolution in the Late Cretaceous as indicated by the Coon Creek otoliths and otoliths from numerous other Late Cretaceous sites in the United States Gulf Coast and Europe (Nolf and Stringer, 1996; Schwarzhans, 1996; Nolf, 2003a, 2013; Woodward, 2003).

Osteological-based investigations of Late Cretaceous fish assemblages persist in reporting a lack of perciforms. A recent investigation of the skeletal remains of ray-finned fishes from the type Maastrichtian revealed only one group
of perciforms, namely the Tetradontiformes (Friedman, 2012). However, even this group is tenuous since there is evidence that indicates that the Tetradontiformes are pre-perciforms (Springer and Johnson, 2004; Nelson, 2006). In a phylogenetic examination of Late Cretaceous and Early Paleogene actinopterygians, Friedman and Sallan (2012) discussed the “pruning” of radiations from the teleost stem during this time interval. However, they noted that this decrease in the teleost stem radiations was complemented by the morphological and taxonomic proliferation of some crown-group radiations in the Paleocene and Eocene. They further noted that the most prominent of these crown-group radiations were the acanthomorphs or spiny-finned fishes.

Alfaro and Santini (2010) presented a “morphospace analysis” of Cretaceous and Paleogene fishes. They deduced that spiny-finned fish diversification resulted from ecological radiation. Furthermore, they proposed that modern fish owe their stunning diversity in part to an ecological clearing of the slate by the Cretaceous extinction. Wiley and Johnson (2010) systematically collected morphological synanomorphies from the published references for all currently recognized fish groups. This endeavor resulted in the first teleost classification based on monophyletic groups. Unfortunately, the undertaking did not produce a global phylogenetic hypothesis (Betancur-R, et al., 2013).

In their extensive review of Late Cretaceous vertebrates from Alabama, which entailed over 8,000 skeletal specimens from 12 institutions, Ikejiri et al. (2013) indicated the presence of no perciform fishes. This is in stark contrast to a Paleogene fish assemblage from Alabama in which well over half of the lower to middle Eocene skeletal remains of osteichthians represented perciforms (Clayton et al., 2013). An almost identical trend based on skeletal remains of perciforms can also be noted in Europe (Nolf, 2013). It is very revealing and significant that the perciforms are already well represented by otoliths in the middle Paleocene (Selandian) of the Ukraine where almost 25% of the fauna is Perciformes (Schwarzhans and Bratishko, 2011).

Until very recently, even molecular evolution studies have not really indicated the presence of perciforms in the Late Cretaceous (Near et al., 2012). This is unexpected since Cantatore et al. (1994) determined that the common ancestor of the Perciformes dated back to around 150 ma based on mitochondrial DNA from Recent perciforms. Wiley et al. (2000) utilized a total evidence approach (DNA sequence and morphological data) to analyze 25 acanthomorph fishes and stated that their research was basically in agreement with the hypothesis of Johnson and Patterson (1993) on percomorph phylogeny. However, Hurley et al. (2007) emphasized the discrepancies between mitochondrial and nuclear genetic data. Near et al. (2012) noted that using whole mtDNA genomes produced ages that were much older than the known fossils. Furthermore, Santini et al. (2009) postulated that the apparent large gap between DNA-based ages and the fossil record was produced by the limited number of taxa utilized in molecular timescale development for ray-finned fishes and the relatively few fossil calibrations used. Marshall (2008) had also noted the importance of multiple fossil calibration points. The investigations of Santini et al. (2009), which employed 225 bony fish species and 45 fossil calibrations and represented 80% of total teleost species diversity, pointed to the lineage diversification of the Percomorpha, which includes the Perciformes, at approximately 100 Ma (Fig. 4). This date would be consistent with the presence of several perciforms in the Coon Creek otolith assemblage at approximately 72 Ma.

Near et al. (2012) employed multiple nuclear gene sequences in conjunction with 36 fossil age constraints, which yielded ages much closer to the fossil record. Their research indicated molecular age estimates of just over 100 Ma for the percomorphs (Fig. 2A; Near et al. 2012). This would certainly be in agreement with the perciforms represented by otoliths in the Coon Creek site. However, Near et al. (2012) showed the oldest known fossil percomorphs, which includes the order Perciformes, at approximately 60 Ma. Again, this data must reflect osteological remains and does not take into account otoliths.

By far the most extensive molecular investigations involving acanthomorphs was conducted by Near et al. (2013). They investigated the pattern of lineage diversification of the acanthomorphs by utilizing a well-resolved, time-calibrated phylogeny that was inferred from a nuclear gene supermatrix. This supermatrix used 10 nuclear genes from 520 Recent acanthomorphs species and 37 fossil age constraints. The research indicated that lineage diversification rates through time exhibited no shifts across the K/Pg extinction. However, this exhaustive and detailed study indicated the perciforms as developing primarily in the Cenozoic (Figs. 1-2). Upon closer examination of Fig. 2A, which is a time-calibrated phylogenetic tree of the Acanthomorpha, the primary diversification of the Perciformes is clearly shown to occur at approximately 50 ma in the Paleogene or approximately early Eocene (Cohen et al., 2013).

Parham et al. (2012) indicated the increasingly sophisticated divergence dating methods that have been and continue to be developed and emphasized the significance of correct phylogenetic positions and accurate ages of the fossils used in divergence dating analysis. Betancur-R, and twenty-five other researchers (2013) presented a comprehensive molecular phylogeny for bony fishes that included all major lineages. This research has some of the most significant findings to date on the evolutionary history of the Percomorpha. Previous attempts using molecular phylogenetic methods to estimate divergence dates among crown-group
lineages has frequently produced conflicting views with paleontological research and findings. Studies based on several nuclear genes and larger sets of fossil calibration points have produced more agreement with the fossil record.

The protocol utilized by Betancur-R. et al. (2013) was extensive and extremely thorough with DNA sequences for 21 molecular marks (1 mitochondrial and 20 nuclear genes) for 1410 bony fishes. Their research provided unprecedented resolution and a high bootstrap support for most backbone nodes. The molecular phylogeny was calibrated using 60 fossil constraints to develop a comprehensive time tree. The number of fossil constraints was almost double that of other investigations such as Near et al. (2013). One of the primary research objectives of Betancur-R. et al. (2013) was to classify the uncertain relationships among the percomorphs, whose classifications have certainly perplexed ichthyologists for decades. This issue was resolved and the Percomorpha were separated into nine well-supported groups. Additionally, and of great importance for Late Cretaceous otolith research, the Perciformes was defined as a monophyletic group in the global phylogeny. Several significant figures are noted: fig. 9 illustrated the detailed relationships of the Percomorpharia or the “new bush at the top;” fig. 10 detailed relationships among the Perciformes families; and fig. 12 provided mean divergence dates (Betancur-R. et al. 2013).

The large-scale, exhaustive research of Betancur-R. et al. (2013) produced several highly significant results related to the evolution of the Perciformes and fossil otolith studies. The date estimates presented confirmed the “notion” that divergences of major ray-finned lineages are considerably older than the oldest known fossils for their respective groups. They noted that the fossil record patterns reveal an explosive morphological diversification of percomorphs in the aftermath of the end of the Cretaceous extinction (one should bear in mind that the pattern to which they refer is based on skeletal remains). However, according to the date estimates deduced by Betancur-R. et al. (2013), the major lineages within the Percomorphaceae, which includes the order Perciformes, originated between 132 Ma and 82 Ma, well before the end of the Cretaceous. Of course, otolith research on fossil fish faunas has indicated the presence of perciforms in the Late Cretaceous for many years (Huddleston and Savoe, 1983; Nolf and Dockery, 1990; Stringer, 1991; Nolf and Stringer, 1996; Schwarzhans, 1996; Nolf, 2003a; Woodward, 2003). Quental and Marshall (2010) asserted that while molecular phylogeny research can provide details and statistics on changes in diversification rates, it is still essential to access paleontological remains (“embrace the fossil record”) to fully understand the evolution and diversity of Recent species. This seems applicable to the Late Cretaceous evolution of the Perciformes as indicated by molecular studies and the otoliths at the Coon Creek site and other Late Cretaceous sites, especially in the Gulf Coast.

Several recent studies have noted the rapid evolution of the Perciformes after the Cretaceous extinction (Alfaro and Santini, 2010; Friedman, 2010; Friedman and Sallan, 2012; Near et al. 2012). Patterson (1993) indicated a marked gap of at least 20 million years in the fossil record of the actinopterygians between the Late Campanian (Late Cretaceous) and the Late Paleocene (Early Paleogene), both for otolith and osteological material. This would mean that the percoid fish must have undergone a period of extremely rapid anatomical evolution in the Late Cretaceous or Early Paleogene because most of the groups had achieved an essentially modern appearance by the Eocene. Only about 20 million years would have been available for the evolution of the essentially modern and enormously diverse percomorph fauna from the beryciforms of the Late Cretaceous.

However, the presence of perciforms at the Coon Creek site and other Cretaceous sites verifies that the differentiation of the modern percomorph lineages commenced as early as the beginning of the Late Cretaceous. This would provide perhaps 30 million years for the modern genera to evolve from the primitive, spiny-finned fishes. The 50 million year span seems to represent a more plausible interval of time for the evolutionary development of the Perciformes. Rather than developing in the Early Cenozoic and leading to the establishment of the modern families by the Eocene, the evolutionary development of the Perciformes probably began 30 million years earlier in the Late Cretaceous. The Coon Creek site otoliths as well as those from other localities such as the Kemp Clay (Maastrichtian from Hunt County, Texas) support the development of the perciforms in the Late Cretaceous (Schwarzhans, 1996; Stringer, 1998a, 1998b; Nolf, 1995; Woodward, 2003) and are in agreement with the findings of Betancur-R. et al. (2013). Furthermore, this research agrees with the proposal of Schwarzhans and Bratishko (2011) that a basal perciform radiation (as supported by monophyly) was likely of late Pre-Tertiary origin.

Paleoecological Determinations

The basic taphonomic consideration in the use of otoliths for paleoecological interpretations is whether the otoliths accurately represent fishes that inhabited an area during a specific interval of geologic time. The fundamental question is whether the otoliths represent fish that are autochthonous in nature and represent part of the biocoenosis or life assemblage. The two major taphonomic processes by which otoliths become part of the sediment are: 1) death and decay of the fish as the otoliths are released from the neocranium or skull, and 2) excretion of piscivorous vertebrates by sharks, predatory fish, and whales (Fitch, 1967; Schafer, 1972; Stringer, 1992). Nolf (1985) believes that predation and
subsequent excretion are the most common method by which otoliths become part of the sediment. Analysis of otoliths obtained from bottom sediments from varying depths from the Atlantic Ocean off the United States coast (Wigley and Stinton, 1973) and the Gulf of Mexico (Stringer, 1992) indicate that the otoliths represent fishes that were actually living at those depths. There seems to be a strong correlation between otolith associations in modern bottom sediments and the expected fishes. Although various taphonomic processes may affect the otoliths, they appear to remain part of the biocoenosis and can be interpreted as such in the fossil record.

Further evidence of the reliability of otoliths in paleoenvironmental interpretation is illustrated in numerous studies, especially in the Cenozoic of the Gulf of Mexico and Caribbean (Nolf and Stringer, 1992; Stringer, 1992, 1998c; Breard and Stringer, 1995; Stringer and Breard, 1997; Nolf and Aguilara, 1998; and Aguilara and Aguilara, 1999). These studies utilized foraminifera and ostracodes to determine the paleobathymetry as well as other paleoenvironmental parameters for various sites. Fish otoliths were also used independently to derive the paleoenvironmental parameters for each of the sites. Results indicated close agreement between the paleoecology indicated by microfossils and otoliths. The foraminifera provided greater detail and reliability about paleoenvironmental conditions, but the otoliths appeared to be reliable indicators of general paleoecological parameters. Other studies, international in scope, have also demonstrated the value of fish otoliths for interpreting paleoenvironments including Schwarzhans (1984, 2008), Nolf and Brzobohaty (1992, 1994, 2009), Nolf (1995), Stringer (1998c), Reichenbacher and Cappetta (1999), and Girone (2003). Studies seem to indicate that an otolith association will reflect with reasonable certainty the teleostean fauna inhabiting an area during a certain interval of geological time (Stringer and Breard, 1997). However, the utilization of fish otoliths for paleoecological determinations in the Cretaceous becomes more difficult and tedious for several reasons.

Taxonomic identification of fossil otoliths is accomplished primarily by comparison to collections of Recent otoliths. The use of comparative Recent material and an application of the principle of uniformitarianism work very well for younger fossil material (especially Paleogene and Neogene). It was noted earlier that most of the modern families of fishes were established by the Eocene; thus increasing the validity of comparisons to modern comparative material. Unfortunately, this is not the case in the Cretaceous. There are fish represented by otoliths with unclear relationships to modern families and genera (Nolf and Stringer, 1996). The uncertainty of the relationship of Cretaceous otoliths to Recent taxa results in a more generalized paleoecological interpretation. However, the presence of more modern taxa such as various perciforms in the Cretaceous increases the reliability of otoliths for paleoecological determinations.

Even with the limitations explained above, it is still possible to determine general paleoecological conditions at the Coon Creek site by utilizing data on the preferred habitats of comparable modern fishes. Examination of the otolith assemblage from the Coon Creek site (Table 2) reveals the absence of representatives that are indicative of deep waters only (greater than outer shelf or 200 m). The otolith assemblage seems to indicate a neritic environment with little open ocean influence. All but one of the teleost taxa represented by otoliths from the Coon Creek site are presently found in onshore waters of the continental United States on or above the continental shelf (less than 200 m) according to Nelson et al. (2004). The pterothrissids are the only group reported from the Coon Creek site that is not listed in Nelson et al. (2004). However, the presence of pterothrissids in Cretaceous and Paleogene nearshore deposits of the United States has been well established by numerous studies including Huddleston and Savoie (1983), Nolf and Dockery (1990, 1993), Stringer (1991, 1998a, 1998b, 1999), Nolf and Stringer (1996, 2003), and Muller (1999). Therefore as a general interpretation, the bony fishes represented by otoliths indicate a marine environment no deeper than outer shelf and probably much shallower.

Specific analysis of the otolith assemblage can provide additional insight into the paleoenvironment at the Coon Creek site during the Late Cretaceous. If the Coon Creek bony fishes represented by otoliths are compared to the modern ichthyological fauna from the Gulf of Mexico (Hoese and Moore, 1998; McEachran and Fenchelmann, 1998, 2005; Nelson, 2006), the fossil otoliths represent fish that are mainly tropical, subtropical, and warm temperate in nature. Furthermore, most of the fossil otoliths represent fish expected in normal marine salinity although a few of the forms could tolerate reduced salinities. Unfortunately, many of the diagnostic forms that have been found to be very useful in the Paleogene and Neogene for paleoecological analysis are rarely present or have not evolved in the Cretaceous. This would include groups such as the sciaenids, myctophids, macrourids, and bregmacerotids (Nolf, 1985, 1995, 2003b; Nolf and Brzobohaty, 1992; Schwarzhans, 1993, 1996, 2007; Nolf and Stringer, 1996, 2003; Muller, 1999; Takeuchi and Huddleston, 2008). However, several forms from the Coon Creek site do provide additional paleoecological information.

The albulid and pterothrissid otoliths represent forms that are probably indicators of shallow marine conditions. The modern albulids are common in inner neritic waters and rarely in brackish or freshwater (Nelson, 2006). McEachran and Fenchelmann (1998) noted that the only species of albulid in the Recent Gulf of Mexico, Albulia vulpes, also occurs worldwide in tropical to warm temperate seas and is an inshore marine fish rarely found in brackish or freshwater. Recent congrids
generally prefer tropical and temperate seas with the juveniles being found mainly in shallow, marine, coastal waters (Hoese and Moore, 1998). Congrid otoliths are very common in Paleogene sediments of neritic environments with soft, muddy bottoms (Bread and Stringer, 1995). Modern marine catfish (ariids) are abundant in bays, passes, and the shallow marine waters of the present-day Gulf of Mexico. The two berycid taxa are indicators of marine conditions.

The majority of the Coon Creek fishes identified by otoliths indicate a shallow marine, neritic environment, but one family seems anomalous. The Trachichthyidae generally occurs in deep marine waters according to Nelson (2006). However, Schwarzhans (1984) found that representatives of this family are found in shallower environments in Paleogene sediments. Furthermore, Nelson et al. (2004) reported this family as occurring in the modern shelf waters off the United States. McEachran and Fechhelm (1998) noted that three species of trachichthyids occur in the modern Gulf of Mexico in waters as shallow as 100 m. Gallaway et al. (1972) also recorded a trachichthyid, Hoplostethus mediterraneus, from the marine waters in the modern Gulf of Mexico off Texas. The otoliths of the modern forms are very similar to the trachichthyid from the Coon Creek site. Therefore, the otoliths from the family Trachichthyidae do not disagree with the indications of a shallow marine environment.

The paleoenvironment suggested by the actinopterygians based on otoliths compares well with the paleogeography suggested by Smith et al. (1994) as well as the environment indicated by the various invertebrate fossil groups from the site (various authors this volume). Line drawings of modern representatives from Nelson (1994) closely related to the Coon Creek site bony fishes represented by otoliths are presented in Fig. 2. These drawings provide a possible, generalized appearance of the Late Cretaceous bony fishes from the Coon Creek site as indicated by the otoliths.

It should be pointed out that there appears to be no correlation between the bony fishes known from skeletal remains (primarily teeth) and the bony fishes represented by otoliths at the Coon Creek site. However, this is not unexpected, and is in fact, quite common in the fossil record. It is extremely rare to find the same fish taxa represented by osteological remains and otoliths in the marine environment (Nolf, 1985, 2013; Bread and Stringer, 1995; Stringer and Miller, 2001). There seems to be an inherent difference between the two in that isolated skeletal remains such as teeth and bones tend to represent larger and often predatory fish, whereas otoliths tend to represent smaller and most likely prey fish. It should be noted that predatory fish are present in otolith assemblages, but they are rarer, which is to be expected, as predatory fish are usually much less common than prey fish. Of the four fishes known from skeletal remains at the Coon Creek site by the author, three of them are larger, predatory fishes.

**RECOMMENDATIONS FOR FUTURE OTOLITH STUDIES AT THE COON CREEK SITE**

The potential for the discovery of additional species of Late Cretaceous fishes represented by otoliths at the Coon Creek site is considered high. Research on the otoliths and resulting fish assemblage from the site is limited to mainly two studies (Nolf and Stringer, 1996; Stringer, 1999). Neither of these studies involved large bulk samples, which are often required in the analysis of Cretaceous sediments for otoliths. For example, Nolf and Dockery (1990) processed approximately 3,000 kg of sediment from the Tupelo Tongue of the Coffee Sand (Campanian) in Lee County in northeastern Mississippi to obtain 117 otoliths. Although 20 taxa were identified, the abundance of otoliths was low with only 0.04 otoliths per kg of bulk sample. However, in contrast, Huddleston and Savoie (1983) recovered approximately 1,000 otoliths from a 100-kg bulk sample from the Severn Formation (Maastrichtian) of Maryland (10.0 otoliths per kg of bulk sample). The abundance of otoliths at the Coon Creek site is believed to lie between these two extremes (approximately 0.2 otoliths per kg of bulk sample) based on studies by Stringer (1999).

Studies on otoliths recovered from the Ripley Formation (Late Cretaceous) near Blue Springs, Union County, in northeastern Mississippi by Stringer (1991) and Nolf and Stringer (1996) recognized 23 taxa of bony fishes (Table 3). A 42-kg sample from the site yielded 257 otoliths (an average of 6.2 otoliths per kg of sample). The Ripley Formation at Blue Springs is stratigraphically equivalent in part and lithologically similar to the sediment at the Coon Creek site. An on-going investigation of another site in Union County, Mississippi (MS 73.033), which is north of the locality of Stringer (1991), has extensive exposures of the Coon Creek bed of the Ripley Formation (over 300 m long and 250 m wide). Bulk and surface collecting have already produced over 2,000 otoliths and more than 30 taxa (unpubl. data). The abundance of otoliths and the similarity of the sediments at these Late Cretaceous localities in northeast Mississippi suggest the potential for more otoliths resulting in additional species of bony fishes at the Coon Creek site.

It is recommended that detailed, systematic bulk sampling be conducted at the site with subsequent analysis to ascertain which horizons are most productive for otoliths. Once these horizons have been determined, then large volumes of sediment from the productive horizons can be collected, screen-washed, and examined for fish otoliths. This procedure should result in the identification of a larger number of bony fishes based on otoliths from the site. Periodic and systematic surface collecting for otoliths is also highly recommended for the site. Considering the limited knowledge of bony fishes represented by otoliths from the Cretaceous of North...
America, the identification of additional taxa from the Coon Creek site would be significant.

CONCLUSIONS

Study and analysis of the otoliths from the Coon Creek site have provided pertinent and important information regarding the Late Cretaceous bony fish assemblage. The otoliths have allowed for the identification of taxa that would not have been discerned based exclusively on the skeletal remains. The value of otoliths for identifying and interpreting the actinopterygians for the Coon Creek site is clearly demonstrated by a comparison to the number of bony fishes identified on skeletal remains. The author is aware of only four bony fishes from the Coon Creek site on the basis of skeletal remains: Anomoedus robustus, Enchodus gladiolus, Enchodus ferox, and Cylindrichthys cretaceus. Although otolith collection and studies from the site have been limited (Wade, 1926; Nolf and Stringer, 1996; and Stringer, 1999), the otoliths indicate ten bony fishes representing at least eight different families. The bony fish assemblage as shown by otoliths included an albulid and perirothrisiid (bonefishes), a congrid (conger eels), an ariid (sea catfishes), a paraluplid (cucumber fishes), a trachichthyid (roughies), two berycoids (alfonsinos), a pimpherid (sweepers), and an unknown perciform. The advantage of studying otoliths of the bony fishes as well as skeletal remains is clearly confirmed at the Coon Creek site.

The fishes identified on the basis of otoliths contribute additional information on the Cretaceous bony fish assemblages of North America especially the evolutionary development of the modern lineages of the fishes. At least four representatives from the order Perciformes are present in the Coon Creek assemblage. These taxa provide further evidence of the development of the Perciformes in the Cretaceous of North America rather than later in the Early Cenozoic. The fishes indicated by otoliths also provide paleoecological information regarding the Late Cretaceous environment in this area. The fishes represented by otoliths indicate a shallow, marine environment that was no deeper than outer shelf and probably much shallower. Several of the forms, such as the albulid and perirothrisiid, suggest inner neritic, while other taxa suggest a soft substratum. The otoliths represent taxa that are found in tropical to warm temperate conditions with primarily normal marine salinities.

Otoliths recovered from investigations of similar Late Cretaceous sediments from northeast Mississippi have resulted in a much more diverse bony fish assemblage than the one represented at the Coon Creek site. This, coupled with the limited surface and bulk collecting at Coon Creek, strongly suggests that additional species of bony fishes identified on the basis of otoliths may be possible at the Coon Creek site. Detailed, systematic bulk sampling in otolith-rich horizons is recommended, as is periodical and systematic surface collecting at the site.

ACKNOWLEDGMENTS

The author thanks R. Brister, Curator of Collections at the Pink Palace Museum, Memphis, Tennessee, who arranged for the author to collect at the site and provided invaluable assistance with the stratigraphy, paleontology, and fieldwork. Thanks to J. Zidek who supplied residue from the site that was the basis of the 1996 study by Nolf and Stringer and to B. Stringer who assisted with bulk sampling in 1998. As he has in many other studies, D. Nolf of the Institut Royal des Sciences Naturelles de Belgique in Brussels, Belgium provided important input, suggestions, and specimens. The late J. Nelson, University of Alberta in Canada, assisted the author in obtaining permission to use figures from his book Fishes of the World. The late S. Breard, Biostratigraphix Inc, Houston, Texas, provided input on an early draft of the manuscript, and M. Gibson and S. Dunagan, both of the University of Tennessee at Martin, supplied initial comments on the manuscript. Thanks also to M. Gibson for the invitation to speak at the Geological Society of America Southeastern Section symposium on the Coon Creek site. Special thanks to G. Takeuchi, Page Museum, Los Angeles, California, and B. Woodward, East Tennessee State University and General Shale Brick Natural History Museum, Johnson City, Tennessee for their preliminary reviews of the paper. An anonymous reviewer provided excellent suggestions. Dr. S. Ebersole’s editorial comments were especially appreciated. Special thanks to Dr. W. Bomar (Executive Director of the University of Alabama Museums) for publishing the monograph as a bulletin through the Alabama Museum of Natural History and to Dr. D. Ehret (Curator of Paleontology, the Alabama Museum of Natural History) and Lynn Harrell (Geological Survey of Alabama) for all of their work coordinating this endeavor and serving as editors of the bulletin.

LITERATURE CITED


Figure 2.


Gallaway, B. J., Parker, and D. Moore. 1972. Key to the estuarine and marine fishes of Texas. Texas A & M University, College Station, Texas, 177 pp.


Schwarzhan, W. 2007. The otoliths from the middle Eocene of


TABLE 1. Bony fish from the Coon Creek site on the basis of otoliths by Nolf and Stringer (1996).

<table>
<thead>
<tr>
<th>Family or suborder</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congridae</td>
<td>“Congrida” aff. thevenini</td>
</tr>
<tr>
<td>Paraulopidae (reported as Chlorophthalmidae)</td>
<td>Paraulopidae indeterminate</td>
</tr>
<tr>
<td>Trachichthyidae</td>
<td>“Trachichthyida” oscitans</td>
</tr>
<tr>
<td>Berycoidei (reported as Apogonidae)</td>
<td>Beryx? maastrichtiensis</td>
</tr>
<tr>
<td></td>
<td>Beryx? zideki</td>
</tr>
<tr>
<td>Perciformes incertae sedis</td>
<td>“Perciformis” cepoloides</td>
</tr>
</tbody>
</table>

TABLE 2. A summary of bony fishes from the Coon Creek site recognized on the basis of otoliths reported by Wade (1926), Nolf and Stringer (1996), and Stringer (1999).

<table>
<thead>
<tr>
<th>Family</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albulidae</td>
<td>Kokenichthys ensis$^3$</td>
</tr>
<tr>
<td></td>
<td>Pterothrissidae indeterminate$^3$</td>
</tr>
<tr>
<td>Congridae</td>
<td>“Congrida” aff. thevenini$^2$</td>
</tr>
<tr>
<td>Ariidae</td>
<td>Ariidae indeterminate$^1$</td>
</tr>
<tr>
<td>Paraulopidae</td>
<td>Paraulopidae indeterminate$^2$</td>
</tr>
<tr>
<td>Trachichthyida</td>
<td>“Trachichthyida” oscitans$^2$</td>
</tr>
<tr>
<td>Berycoidei</td>
<td>Beryx? maastrichtiensis$^2$</td>
</tr>
<tr>
<td></td>
<td>Beryx? zideki$^3$</td>
</tr>
<tr>
<td>Pempheridae</td>
<td>“Pempherida” huddleston$^3$</td>
</tr>
<tr>
<td>Perciformes incertae sedis</td>
<td>“Perciformis” cepoloides$^2$</td>
</tr>
</tbody>
</table>

Superscripts on the taxa refer to the reference in which the bony fish otolith was first noted: $^1$Wade (1926); $^2$Nolf and Stringer (1996); $^3$Stringer (1999).

<table>
<thead>
<tr>
<th>Family</th>
<th>Taxa</th>
</tr>
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<tr>
<td>Osteoglossidae</td>
<td>“Heterotidina” tavernei</td>
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<td>?Megalopidae</td>
<td>?Megalopidae indeterminate</td>
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<tr>
<td>Albulidae</td>
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<tr>
<td></td>
<td>“Albulida” ripleyensis</td>
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<td>“Congrida” aff. thevenini</td>
</tr>
<tr>
<td>Ariidae</td>
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<tr>
<td>Paraulopidae (reported as Chlorophthalmidae)</td>
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</tr>
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<td>Polymixiidae indeterminate</td>
</tr>
<tr>
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<td>“Trachichthyida” oscitans</td>
</tr>
<tr>
<td>Moronidae</td>
<td>Moronidae indeterminate</td>
</tr>
<tr>
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<tr>
<td>Caristiidae</td>
<td>“?Caristiida” dockeryi</td>
</tr>
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<td>Pempheridae</td>
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<td>Perciformes incertae sedis</td>
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</tr>
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<td>Percoidei sp. 2</td>
</tr>
<tr>
<td></td>
<td>Percoidei sp. 4</td>
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<tr>
<td></td>
<td>Percoidei sp. 6</td>
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<tr>
<td>Euteleostei incertae sedis</td>
<td>Euteleostei indeterminate</td>
</tr>
<tr>
<td>Not determinable</td>
<td>Utricular otoliths</td>
</tr>
</tbody>
</table>
A cervical vertebra of *Arambourgiania philadelphiae* (Pterosauria, Azhdarchidae) from the Late Campanian micaceous facies of the Coon Creek Formation in McNairy County, Tennessee, USA

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ABSTRACT– Late Cretaceous azhdarchid pterosaurs are known from fairly incomplete remains in North America. These remains have primarily been reported from continental and fluvial deposits of the western United States. Here we refer a fragmentary cervical vertebra from the Late Campanian micaceous facies of the Coon Creek Formation of Tennessee, a near-shore marine deposit, to the azhdarchid pterosaur taxon *Arambourgiania philadelphiae*. This specimen represents the first reported occurrence of *A. philadelphiae* from North America, expands the temporal range of *A. philadelphiae* from the Maastrichtian to the Late Campanian, is the first reported occurrence of Pterosauria from the state of Tennessee, and extends the known geographic range of the Azhdarchidae to the eastern Gulf Coastal Plain of the United States.

INTRODUCTION

Remains of the sometimes gigantic pterosaurs of the Azhdarchidae (Nessov, 1991) are known on all continents except Antarctica, and possibly Australia (Bennett and Long, 1991; Averianov et al., 2005). In North America, azhdarchid pterosaurs have been reported from Alberta, Canada (Currie and Russell, 1982), and in the United States, from Texas (Lawson, 1975), Wyoming (Estes, 1964), New Jersey (D. Baird, pers. comm. in Bennett, 1989), Montana (Padian and Smith, 1992; McGowen et al., 2002; Henderson and Peterson, 2006), and possibly New Mexico (Sullivan and Fowler, 2011). Here we note a new North American record of these long-necked pterosaurs from the state of Tennessee, which has no previous record of pterosaur fossils (Corgan, 1976; Corgan and Breitburg, 1997).
SYSTEMATIC PALEONTOLOGY
PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Pleninger, 1901
AZHDARCHOIDEA Nessov, 1984
AZHDARCHIDAE Nessov, 1984
ARAMBOURGIANIA PHILADELPHIAE (Arambourg, 1959)

Titanopteryx philadelphiae Arambourg, 1959
Arambourgiania philadelphiae (Arambourg, 1959): Nessov, 1984

The specimen is a fragmentary cervical vertebra (MPPM 2000.23.1) in the collections of the Memphis Pink Palace Museum. It was discovered in 1999 by Wendy Melton-Beeson of Memphis, Tennessee and collected by the first author (LH). The locality, known to local fossil enthusiasts as "The Selmer Crab Site", is in an exposed hillside along U.S. Highway 45 South, just south of the town of Selmer, McNairy County, in southwestern Tennessee. The source bed is in the lower Coon Creek Formation of Late Campanian (Late Cretaceous) age (Dunagan and Gibson, 1993; Gibson et al., 2003). When found, most of the vertebra had weathered out of a bank, with only the posterior end remaining in situ. No other bones were found in proximity.

Preservation of the bone is poor, and distinguishing between bone and matrix is difficult. In places the bone is friable and so soft that extensive preparation has not been feasible.

Institutional abbreviations used in this paper: MPPM, Memphis Pink Palace Museum, Memphis, Tennessee and TMM, Texas Memorial Museum, Austin, Texas.

Morphological abbreviations: cb, layered cortical bone, con, condyle, cot, cotyle, fel, fovea for elastic ligament, hyp, hypapophyseal ‘keel’, ns, neural spine, pc, postexapophysis, pf, pneumatic foramen, poz, postzygapophysis, prz, prezygapophysis, tb, base of tubercular elevation, vac, vertebrarterial sulcus, vnc, vestibule of the neural canal, x?, anomalous foramen in pedicel.

GEOLOGIC SETTING

The Coon Creek Formation, exposed in a north-south trending outcrop belt within the Mississippi Embayment in western Tennessee and eastern Mississippi, consists of fossiliferous gray to dark-green, micaceous, glauconitic quartz sand and fossiliferous shale, silty-shale, and silt (Wade, 1926; Moore, 1974; Russell and Parks, 1975; Dunagan and Gibson, 1993; Gibson et al., 2003; Ebersole, 2009). Moore (1974) interpreted the Coon Creek as representing deposition during a regressive sequence. The Coon Creek Formation grades laterally and vertically into the McNairy Sand, which consists of over 90 meters of non-glauconitic quartz sand, sandstone, and clay (Russell and Parks, 1975). The underlying Demopolis and Sardis Formations represent the transgressive open marine sequence and consist of glauconitic sand (Sardis) that...
grade upward and laterally into sandy- and silty-marl with localized argillaceous chalk (Demopolis).

Russell and Parks (1975) recognized two lithofacies within the Coon Creek Formation, the boundary between the two is marked by phosphatic concretions and platy ferruginous sandstone layers. The lower Coon Creek is a brown weathering, massively bedded, glauconitic clayey-sand and shale that is often very fossiliferous. The upper Coon Creek (originally called the “ferruginous clay member” by Wade, 1926) is more clay rich and contains red siderite concretion beds (Russell and Parks, 1975).

The pterosaur material described in this study was collected at Moore’s (1974) I.T.T. (International Telephone and Telegraph) measured section (Fig. 1). The exposure belongs to the upper Coon Creek lithofacies and is dominated by interbedded dark gray shale, silty-shale, and iron concretion layers (Fig. 2) and can be subdivided into 4 subunits based upon subtle variations in silt-clay content and distribution of iron concretion layers. The pterosaur remains were preserved in Subunit 3, consisting mainly of thinly laminated, micaceous silty clay. Subunit 3 is interpreted as a quiet water marine deposit, based upon lithology and fossil associations. The matrix surrounding the fossil is fine-grained dark argillaceous sand of glauconitic character, containing minute grains of muscovite, biotite, glauconite, quartz silt and about 80% organic clay typical of quiet-water marine shales. Gypsum is also present in the bone. Associated fossils include abundant articulated crab carapaces (Fig. 3), fish spines and teeth, occasional turritellid gastropod steinkerns, and unidentified horizontal burrow structures. The overlying ironstone concretions contain vertical burrows and rare crab impressions.

**DESCRIPTION**

The vertebra (MPPM 2000.23.1) consists of badly damaged and incomplete anterior and posterior ends, each approximately 50.0 mm long, and numerous shard-like fragments of compact bone believed to belong to the centrum. The estimated minimum length for the vertebra is 223.0 mm based on the preserved length of the articular ends and the length of the reassembled centrum fragments, whereas the anterior width is estimated at approximately 28.0 mm across the prezygapophyses. The long and narrow dimensions of MPPM 2000.23.1 are comparable to the mid-cervical series of other azhdarchid pterosaurs, of which C5 is typically the largest (Averianov, 2013). It is therefore hypothesized that MPPM 2000.23.1 represents a C4 or C5 vertebra.

The surficial texture of the cortical bone is essentially smooth in both the anterior and posterior portions of the vertebra. The surface of the fragments of the centrum is, however, densely sculptured by microscopic, irregular, sub parallel, anastomosing longitudinal striae. This unusual surface texture has been observed in long bones of immature *Pteranodon* specimens by Bennett (1993), who suggested that it is evidence of rapid growth of periosteal bone. The subperiosteal layer in MPPM 2000.23.1 is paper-thin. It exfoliates readily from the subjacent bone and is thus preserved only in isolated patches. The periosteal bone is further foliated into concentric (radial) laminae (Fig. 4A-C), which vary in thickness and hardness, and separate easily from one another.

The caudal end of the vertebra is better preserved than the cranial end. The sub-hemispherical condyle (Fig. 4A-D) is the dominating feature of the caudal
end. It has a diameter of 19.0 mm. Its convex surface is slightly irregular in that it possesses a posterodorsally directed bulge (Fig. 4A). A faint intermittent annular sulcus, seen dorsally and ventrally, defines the edge of the articular condyle. Owing to the rounded condyle, the small exapophyses (Fig. 4A-D) are not widely separated. They do not extend caudally beyond the condyle. A smooth, broad, saddle-shaped articular surface exists dorsolaterally on the left exapophysis and is continuous with the articular surface on the condyle. This saddle-
shaped facet, which is similar to those observed in other pterosaur taxa, oppose a corresponding ventromedial emargination of the succeeding vertebra, creating the anterior accessory articulation of Bennett (2001), or "preexapophysis" of Williston (1897) and other authors. The structure is less evident on the right side of the vertebra, which is taphonomically deformed and abraded. The postexapophyses grade anteriorly into strong, medially converging crests that project slightly from the ventrolateral edges of the centrum. Approximately 31.0 mm from the caudal end of the condyle, the crests contract more rapidly and merge into the ventrolateral edges of the centrum.

The opening to the neural canal, surrounded by the centrum, pedicels, zygapophyses and the roof of the neural arch, is round and slightly smaller than the condyle. Structure within the vestibule is obscured by matrix; however, the left lateral edge of the neural canal extends upward, suggesting that it was narrowly ovate vertically. Convincing evidence of any large pneumatic foramina in the caudal face of the neural arch is lacking, but a trace of a possible foramen occurs on the left side of the vestibule. It is possible, however, that this is an artifact resulting from the preparation of the specimen.

The posterior neural arch rises 20.0 mm above the top of the centrum, being almost half as high as the whole vertebra posteriorly. The sides of the arch are constricted transversely, the arch being wider above than at its base. The broken base of the posterior neural spine (Fig. 4A-C) is thickened posteriorly, suggesting a stouter structure than the anterior neural spine. How far the posterior spine extends anteriorly before presumably merging into the dorsal surface of the centrum is unknown. It is clear from what remains of the neural spine, however, that the spine was vestigial and lacked any connection between its anterior and posterior portions. The base of the spine is bounded on either side by a shallow caudolaterally and anteroventrally directed trough (best seen on the left side of the specimen). This trough is bounded laterally by the broken base of a longitudinally ovate tubercle of unknown height (Fig. 4A-C). A matching elevation was probably present on the right side of the arch, but has been destroyed. The broken, ventrolaterally directed base of the postzygapophysis (Fig. 4A-C) occurs lateral and ventral to the elevation. The pedicel of the neural arch is notched below the base of the zygapophysis, creating what appears to be the incomplete edge of a 1.5 mm wide foramen (Fig. 4A-B). This opening passes diagonally below the zygapophysis into the intervertebral space.

Where preserved, the sides of the centrum are shallowly excavated longitudinally, but most of the lateral concavity is missing. There is no evidence of a lateral pneumatic foramen. The ventral side of the posterior end of the vertebra is upwardly concave transversely between the exapophyses, but flattens out anteriorly suggesting that the bottom of the centrum was partially flat.

In anterior aspect, the vertebra (Fig. 4F) has a roughly rhomboidal cross-sectional shape, measuring 29.0 mm high and 26.5 mm wide. As in caudal view, the opening into the neural canal is obscured by matrix and is fractured. The edges of the cotyle are damaged so its dimensions and shape are unclear. A shallow sulcus passes posterodorsally along the neural canal, and along the medial side of the prezygapophysis.

The anterior neural spine (Fig. 4F) is a simple triangular elevation bounded laterally by downwardly diverging laminae, which house a shallow, triangular matrix-filled space that is the fovea for the elastic ligament. In lateral aspect, the top of the anterior spine (Fig. 4E, G) diminishes posteriorly and either formed a low sagittal crest or merged with the dorsal surface of the centrum, as is the case in other azhdarchid taxa.

The sides of the anterior face of the centrum are flat and smooth. They converge ventromedially, meeting sagittally below at an angle of 80 degrees, in a longitudinal hypapophyseal ridge (Fig. 4E, H). The preserved part of the carina is 19.0 mm long. The ridge diminishes posteriorly, and merges with the ventral surface of the centrum.

The right prezygapophysis is well preserved (Fig. 4E-H). Its dorsomedial-facing articular surface is about twice as long as it is wide, slightly arched longitudinally, and inclined 26 degrees medioventrally in its anterior half. The process rises laterally from a stout longitudinal crest or buttress on the dorsolateral edge of the vertebra. The lateral margin diminishes rapidly posteriorly, narrowing into an almost intelligible dorsolateral ridge. This ridge possibly disappeared shortly beyond the point where it is broken off on the specimen. The ventral edge of the prezygapophysis forms an acute, ventrally directed crest, which bounds the longitudinal vertebrarterial sulcus dorsally on the side of the centrum (Fig. 4E, F, H). The sulcus rises anteriorly, and curves broadly mesially around the edge of the pedicel, where it emerges onto the anterior surface of the centrum and then disappears. There is no evidence of a cervical rib. The prezygapophyses diverge anteriorly at an angle of about 80 degrees. Their anterior ends are 20.0 mm apart.

Among the presumed fragments of the centrum are five slender fragments, which when reunited, comprise a 130.0 mm long segment of transversely arcuate bone about 0.9 mm thick (Fig. 5). The position of this fragment within the vertebra is unknown. Other small fragments lined with matrix include two longitudinal parallel broken edges of a thin (0.1 mm thick), trough-like structure. This trough is thought to be a remnant of the ossified neural canal. It lies close to the internal surface of the outer wall of the centrum. There are no indications of supporting trabeculae, but such delicate structures may have easily been destroyed. The diameter of the intact canal exceeded 5.5 mm, whereas the diameter of the surrounding intact centrum was at least 22.0 mm. One small shard displays
Cretaceous pterosaurs, Bennett (2001) notes that the measurements [pers. obs. by W. L.]. Of other large Late taxa as determined from illustrations in lieu of recorded Quetzalcoatlus a sample of 19 of the condyle does not exceed 58% of its width (from than a high length/width ratio. The hemispherical condyle of and a centrum that is long and narrow with a comparatively compressed as is the case with most azhdarchid cervicals) laterally compressed (as opposed to being dorsoventrally between the two specimens include a centrum that is from the Maastrichtian phosphates of Jordan. Similarities (BSM 1978/1) by Frey and Martill (1996; figs. 4, 9A, C) Arambourgiania philadelphiae cervical vertebra referred to Arambourgiania philadelphiae (BSM 1978/1) by Frey and Martill (1996; figs. 4, 9A, C) from the Maastrichtian phosphates of Jordan. Similarities between the two specimens include a centrum that is laterally compressed (as opposed to being dorsoventrally compressed as is the case with most azhdarchid cervicals) and a centrum that is long and narrow with a comparatively high length/width ratio. The hemispherical condyle of the Tennessee specimen (height/width ratio of 0.95) is a notable departure from the transversely ovate condyle of most azhdarchids and other large pterodactyloids, other than Arambourgiania philadelphiae, in which the height of the condyle does not exceed 58% of its width (from a sample of 19 Quetzalcoatlus sp. cervicals and in other taxa as determined from illustrations in lieu of recorded measurements [pers. obs. by W. L.]). Of other large Late Cretaceous pterosaurs, Bennett (2001) notes that the width of the condyle in Pteranodon is 3.0 to 3.5 times its height. The height and notable narrowness of the posterior end of MPPM 2000.23.1 and its flat posterocentral surface, also compare well with an incomplete and taphonomically deformed putative fourth cervical of Quetzalcoatlus (smaller morph) from the Maastrichtian Javelina Formation of Texas (TMM 41544.8). However, the substantial deformation of TMM 41544.8 limits the credibility of this comparison. Furthermore, the Tennessee fossil is only about two-thirds as large as TMM 41544.8 (see Description for measurement estimates of MPPM 2000.23.1).

The large, rounded vestibule that leads to the neural canal is similar to that observed in Arambourgiania philadelphiae and unlike the relatively broad and low space observed in most azhdarchid cervicals. In other azhdarchid vertebrae (e.g. Nessov, 1984; pl 7:2a, 3b, 4a, 5a), Pteranodon, (Bennett, 2001; fig. 39) and Santanadactylus (de Buisonjé, 1980; fig. 5D-E, pl 2:D) the mid-cervicals typically exhibit three openings at each end of the neural arch: the neural canal, and on either side a large pneumatic foramen (Martill et al., 1998). The foramina in MPPM 2000.23.1 are relatively smaller than in the above mentioned taxa, as there appears to be insufficient space to accommodate a neural canal and large paired foramina at the ends of the neural arch. Although evidence of a small pneumatic foramen is present on the left side of the posterior vestibular opening (Fig. 4B), further preparation of the specimen will be necessary in order to confirm this hypothesis. Another opening present at the anterior end of the arch, above the neural canal, in some Azhdarcho cervicals was presumed by Nessov (1984) and confirmed by Averianov (2010) to be an additional pneumatic foramen. No such opening occurs in Quetzalcoatlus sp. or Arambourgiania. A median ‘foramen’ is present however in some Pteranodon cervicals (Bennett, 2001). The triangular excavation at the base of the neural spine in MPPM 2000.23.1 was likely occupied in by the elastic ligament. The absence of a transverse foramen and cervical rib in the Tennessee specimen differs from Quetzalcoatlus sp. and Arambourgiania philadelphiae (Martill et al., 1998) where these structures are present. However, the small size of MPPM 2000.23.1, and the presence of anastomosing longitudinal striae on the
periosteal surfaces (termed “immature grain” by Bennett, 1993; p. 95), suggests that this specimen was a juvenile and that the ribs likely were not fused to the centrum at the time of death.

The poorly-defined hypapophyseal keel of MPPM 2000.23.1 is unlike the hypapophyses of *Quetzalcoatlus* cervicals, which vary from a broad hump-like tumescence (Cervicals 3–4) to a wide and low longitudinal ridge, which terminates anteriorly with a forward directed process (Cervicals 5–7).

A small round passage, extending from the intervertebral space across the posterior pedicel and opening laterally below the postzygapophysis in MPPM 2000.23.1 is unique among available comparative material. It is perhaps an accessory vascular or neural passage, and is potentially anomalous. A morphologically similar feature visible anteriorly in the holotype of *Arambourgiania philadelphiae* is identified as the transverse foramen by Martill et al. (1998). However, the foramen present in MPPM 2000.23.1 appears at the opposite end of the vertebra from the transverse foramen. The interpretation of this feature is difficult due to the damage in the area and it is much more likely that this passage is part of the pneumatic foramen lateral to the neural canal.

The postexapophyses, highly visible in azhdarchid cervicals, are much less developed in MPPM 2000.23.1 and extend caudally beyond the condyle only slightly. However, this may be a result of damage from weathering. Their relationships to adjoining structures accord with those of azhdarchids.

A small elevation, marked by its broken base on the left postzygapophyseal buttress in MPPM 2000.23.1, has not been reported in azhdarchid vertebrae, where the corresponding space is occupied by a relatively broad and featureless surface. A longitudinal trough separates the elevation from the base of the neural spine. This elevation is possibly homologous with the torus dorsalis (= processus dorsalis of Boas, 1929), which is seen variably in birds where it provides attachment for the Mm. Ascendentes (Baumel and Witmer, 1993). Certain cervical postzygapophyses bear a torus or tubercle in *Anhanguera* (C2–C8) (Wellnhoffer, 1991), *Pteranodon* (C2–C9) (Bennett, 2001) and *Gnathosaurus macrurus* (one middle-series cervical) (Hosse, 1986, as “Doratorhynchus”), but there the process extends freely posteriorly beyond the articular facets. A similar tubercle is found in *Quetzalcoatlus* only in Cervical 7, with the zygapophyses on the other cervicals having thin, unadorned surfaces.

Excluding the rudimentary neural spine, the caudal end of MPPM 2000.23.1 is higher in relation to its width (~1.5) than in any known *Quetzalcoatlus* cervical - the estimated height to width ratio of TMM 41544.8 is 1.24. This highly elevated azhdarchid cervical (MPPM 2000.23.1) is similar to reconstructed material referred to *Arambourgiania philadelphiae* (Frey and Martill, 1996; fig. 9C) in which the height to width ratio is approximately 1.4.

An ossified neural canal has been detected in the holotype of *Arambourgiania philadelphiae* (Martill et al., 1998) and in a few cervical vertebrae of *Quetzalcoatlus*. In every instance the canal is seen in cross-section and appears to be displaced within the lumen of the tubular centrum. Possibly owing to varying locations at which it is visible in different specimens, the canal as described here, seems relatively larger in diameter and may lie artificially closer to the wall of the centrum than in other taxa. The crumby nature of the matrix, as well as the similarity of color between the matrix and bone, makes the internal canal difficult to discern in a photograph. The position of the canal as reconstructed by Martill et al. (1998; fig. 7b) seems likely, but the arrangement of the trabeculae supporting the tuba has not been confirmed in *Quetzalcoatlus*. It is reasonably inferred by Martill et al. (1998) that the bony canal extended through the length of the centrum in the more elongated azhdarchid cervicals. The authors are unaware of such architecture in any other vertebrates, but it is somewhat reminiscent of the tubular cervical centra in the Triassic protorosaurian *Tanystropheus* in which the chorda is believed to have passed “garland-like” through the lumen without bony support (Wild, 1973).

An approximate reconstruction of MPPM 2000.23.1 is depicted in Figure 5. Some uncertainties exist, particularly regarding the proportions of the centrum. The most reliable dimension available in MPPM 2000.23.1 is the transverse diameter of the condyle (26.0 mm). Ratios between condylar width and vertebral length (measured from the condyle to the ventral edge of the cotyle) in cervicals of *Quetzalcoatlus* sp. are: C3 (4.1), C4 (5.35), C5 (8.891), C6 (7.01), and C7 (5.85). Combining the preserved lengths of the reconstructed fragments of the centrum and the two articulating ends of MPPM 2000.23.1 (neither of which contact the preserved segment of the centrum) yields a minimum length for this vertebra of 223.0 mm and a (anterior) width to length ratio of 7.96. This ratio compares favorably with the estimated range (6.88 – 8.50) reported for a presumed C5 vertebra of *Arambourgiania philadelphiae* (Frey and Martill, 1996; p. 239).

In dorsal view, the elongate cervical vertebrae in azhdarchids show a ‘waisted’ plan wherein the lateral edges are “pinched into a narrow waist” (Hosse, 1986:316) about two-thirds the length of the centrum from the anterior end, where they diverge posteriorly. The authors have been unable to reconstruct this morphology with the available material. The resulting reconstruction produces a vertebra that is 14 times as long as its smallest estimated diameter, and in which the sides of the centrum are roughly parallel throughout. Similar proportions are found in *Arambourgiania philadelphiae*; however, in other azhdarchid cervicals the width toward the ends of vertebrae is often exaggerated by dorsoventral crushing. A badly crushed mid-series cervical vertebra of an azhdarchid pterosaur
from Montana was similarly reconstructed with a narrow centrum and parallel sides (Henderson and Peterson, 2006). However, the high degree of taphonomic distortion prevents their reconstruction from being conclusive.

**DISCUSSION**

The pterodactyloid clade Azhdarchidae is believed to contain the last of the pterosaurs (Unwin and Lü, 1997; McGowan et al., 2002; Andres et al., 2014), with the exception of Nyctosaurus lamengoi from the Maastrichtian of eastern Brazil (Price, 1953; Kellner, 1989; Bennett, 2003; Andres et al., 2014). All currently accepted azhdarchids are of Late Cretaceous age with the possible exception of a fossil wing from the Crato Formation (Aptian, Early Cretaceous) of Brazil (Martill and Frey, 1999), although this identification is suspect given the considerable taphonomic crushing evident in the specimen. A second, more plausible Early Cretaceous (Berriasian) occurrence of the Azhdarchidae is represented by a partial cervical vertebra from a bauxite mine in Romania (Dyke et al., 2011). However, because elongated cervical vertebrae are not exclusive to early azhdarchids (Dong, 1982; Unwin and Lü, 1997), the recovery of additional material at this site will be necessary to confirm this age range extension for the group. An even earlier reported occurrence of an azhdarchid from the Late Jurassic of Tanzania (Savão and Kellner, 2001) was subsequently referred to the Ctenochasmatidae by Andres and Qiang (2008), although the azhdarchid affinities of these specimens have also been suggested (Costa et al., 2013).

The most complete azhdarchid material is comprised of some near complete skeletons of the Early Campanian Zhejiangopterus linhaiensis from China (Cai and Wei, 1994; Unwin and Lü, 1997), and a large assemblage of partly associated skeletal elements of a small morph of Quetzalcoatlus from Maastrichtian deposits in Texas (Langston, 1981). Additionally, a collection of small bones of Azhdarcho lanciaillii, from the Upper Turonian to Coniacian in Uzbekistan, has been described briefly by Nessov (1984, 1991) and in more detail by Averianov (2010). Less complete examples of azhdarchids include the giant holotype wing of Quetzalcoatlus northropi (TMM 41450-3) from west Texas (Lawson, 1975; Langston, 1981) and the intriguing partial skeleton of Montanaazhdarcho minor (Campanian) from Montana (McGowan et al., 2002). Isolated azhdarchid remains from widely separated localities around the globe include; some large cervical vertebrae of Arambourgiania from the Maastrichtian of Jordan (Frey and Martill, 1996; Martill et al., 1998) and an enigmatic fragmentary skull and humerus of possibly the largest of all flying creatures, Hatzegopteryx thambema Buffetaut et al. 2002, from Romania.

Previous researchers (Lawson, 1975; Padian, 1984, 1986; Howse, 1986; Nessov, 1991; Bennett, 1994) emphasized the hyper-elongation of the mid-series cervical vertebrae as a defining feature of the Azhdarchidae. Elongated cervicals are, however, now known to occur in at least one other pterodactyloid group, the Late Jurassic Ctenochasmatidae (Dong, 1982; Unwin and Lü, 1997; Andres and Qiang, 2008). Extreme vertebral length is therefore not an autapomorphy in the Azhdarchidae. Other features of azhdarchid mid-cervical vertebrae noted by authors including, a reduced neural spine, lack of lateral pneumatic foramina on the centrum, and presence of large pneumatic foramina at opposite ends of the neural arch, no longer appear diagnostic of the Azhdarchidae either.

**CONCLUSIONS**

The vertebra described here (MPPM 2000.23.1) is the first record of an azhdarchid pterosaur, or pterosaur of any type, from Tennessee. This specimen is also the first record of azhdarchid pterosaur from the eastern Gulf Coastal Plain of the United States, although azhdarchids have previously been reported from the western Gulf Coastal Plain region in Texas (Lawson, 1975; Langston, 1981). Although the specimen is poorly preserved, its distinctive features allow MPPM 2000.23.1 to be referred to Arambourgiania philadelphiae (Nessov, 1984). These features include: a posterior height to width ratio of approximately 1.5, a rounded, unflattened condyle, and an elongated and unconstricted centrum with subparallel margins. The relatively small size, presence of “immature grain” (Bennett, 1993:95) on the periosteum of the centrum, and unfused cervical ribs suggest that MPPM 2000.23.1 represents a juvenile individual. This is the first record of Arambourgiania philadelphiae from North America and confirms the presence of this taxon in the late Campanian, as suggested by Andres et al. (2014).

Although most azhdarchid remains have been found in non-marine sediments (Witton and Naish, 2008; Andres et al., 2014; Averianov, 2014), Arambourgiania philadelphiae, including MPPM 2000.23.1, is presently known only from marine deposits (Frey and Martill, 1996; Andres et al., 2014). The discovery of this isolated specimen in the quiet, near-shore marine depositional environment of the Coon Creek Formation further suggests that this taxon likely lived along the coast or obtained its prey in a littoral habitat.

The occurrence of Arambourgiania philadelphiae (MPPM 2000.23.1) in the late Campanian Coon Creek Formation adds another taxonomic group to a growing list of vertebrate taxa from this geologic unit.

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REFERENCES CITED


Howse, S. C. B. 1986. On the cervical vertebrae of the


Palynological analysis of a sample from the Coon Creek Member, Union County, Mississippi

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ABSTRACT—Exposures of the Upper Cretaceous Coon Creek Member of the Ripley Formation occur in Alcorn, Tippah, and Union counties in Mississippi. Its lithology consists of dark-gray to black, fossiliferous clays and silty, micaceous sands. The Coon Creek Member is known for its well-preserved and diverse assortment of marine gastropods, bivalves, ammonites, crabs, and trace fossils. The depositional environment is interpreted to have been located in an intertidal to inner-shelf area. In this study, one palynomorph sample was collected along the Little Tallahatchie River, Union County, Mississippi. The microfossils in this sample include well-preserved dinoflagellate cysts, a diverse assemblage of monolete and trilete spores, bisaccates and other gymnosperms, and tricolpate, triporate, and tricolporate angiosperms. The climate was probably semi-tropical and humid, based on the abundance of pteridophyte spores, and the diversity of gymnosperm and angiosperm pollen. Dinoflagellates identified as Areoligera senonensis Lejeune-Carpentier, Cordosphaeridium spp., and Exochosphaeridium bifidum (Clarke and Verdier) Clarke et al. (1968) imply an open marine environment but the abundance of terrestrial palynomorphs suggest that the inner shelf was not far removed from a coastal mainland or barrier island system. Palynomorphs identified in this study support a Late Cretaceous, likely an Early Maastrichtian, age.

INTRODUCTION

Reported here is a preliminary palynological investigation of a sample from the Upper Cretaceous Coon Creek Member of the Ripley Formation in northeastern Mississippi. The objectives of this study are to generate a list of palynomorphs and infer a biostratigraphic age. The palynomorphs can be used collectively to infer the paleoenvironmental setting for the bed from which they were extracted. There are few published accounts of
Upper Cretaceous palynomorphs from the Gulf Coastal Plain. Most of these accounts were compiled by Tschudy (1965a, 1965b, 1967, 1970, 1973b) in the form of open-file reports that provide only tables of unpublished taxa. Tschudy (1973a, 1975), Wolfe (1976), and Frederiksen et al. (1982) utilized specific angiosperm palynomorphs from the Coon Creek to erect palynozonations (Ebersole, 2009) but did not document other marine and freshwater cysts, pollen, and spores. Numerous and diverse types of palynomorphs were found in the sample, including dinoflagellates, trilette and monolette spores, gymnosperm pollen, and tricolporate and tricolpate angiosperm pollen. These can be used to better understand depositional environment and biostratigraphy.

Geologic Setting

The sample analyzed for this study was obtained during a lithostatigraphic analysis of the 7-½ minute Keownville Quadrangle in Union County, northeastern Mississippi (Fig. 1) that was conducted by Kelly (2002). Exposures of the Ripley Formation represent the oldest sediments exposed in the Keownville Quadrangle. In this quadrangle the Ripley consists of four distinct members (Sohl, 1960): an unnamed basal transitional unit, the Coon Creek Tongue, McNairy Sand, and Chiwapa Sandstone. The transitional clay is not exposed on the surface in this area but occurs in stratigraphic test cores, and the McNairy Sand and Chiwapa Sandstone are locally interbedded and are mapped in the Keownville Quadrangle as the upper Ripley. The lower Ripley is represented by the Coon Creek Tongue (Kelly, 2002). The palynomorph sample was collected from the base of an 18 m (60 ft) exposure of the Coon Creek in the channel of the Little Tallahatchie River (Fig. 2). It is associated with fossil hash of gastropods, bivalves, and Exogyra costata Say, an index fossil for latest Campanian and Maastrichtian units of the Atlantic and Gulf Coastal Plain provinces (Couper, 1971; McBride et al., 1974; Russell et al., 1982; Vega and Feldmann, 1991).

In Mississippi, the Coon Creek Member occurs in Alcorn, Tippah, and Union Counties, but becomes indistinguishable from other Ripley sediments that are located to the south in Pontotoc County (Sohl, 1960). Its lithology throughout consists of dark-gray, fossiliferous clays and massive, micaceous, glauconitic, fossiliferous, silty sands (Sohl, 1960; Kelley, 2002). Clay mineral assemblages analyzed by Pryor and Glass (1961) and invertebrate fossils including Ophiomorpha sp. burrows, the oyster Exogyra costata, the gastropod Trochus ripleyanus Wade, and others suggest that the Coon Creek was deposited in an inner-neritic to inner-shelf environment (Wade 1917, 1926; Kelley 2002) and lies within the Campanian/Maastrichtian boundary (see stratigraphic section by Ciampaglio and Phillips in this volume).

In Tennessee, however, the Coon Creek is elevated to formation status and is divided into two predominant lithofacies. The lower lithofacies is characterized by a dark to greenish gray calcareous burrowed, massive bedded, micaceous, glauconitic clay, silts, and fine sands that possess well-preserved macrofossils (Russell, 1975; Dunagan and Gibson, 1993; Ebersole, 2009; Ciampaglio and Phillips, this volume) including cephalopods, mollusks, shrimp, and crabs (Dockery, 2003; Brister and Young, 2007). The upper lithofacies contains more distinctly bedded dark gray to greenish-gray calcareous, glauconitic, micaceous, fine-to-medium-grained, clayey silts and sands. The fossil preservation is poor (Ebersole, 2009), consisting mainly of steinkerns (internal molds), and vertebrate material is more abundant than invertebrates. The type section, a lagerstätte deposit, occurs in northern McNairy County, Tennessee, and is up to 58 m (190 ft) thick (Keroher, 1966; Russell and Parks, 1975). Most of the Coon Creek outcrops that occur in Mississippi resemble the upper lithofacies of the type section (Sohl, 1960; Russell and Parks, 1975; Ebersole, 2009).

MATERIALS AND METHODS

This study was performed on a dark, gray-to-black, organic rich, clay sample collected at the base of an 18 m (60 ft) Coon Creek interval along the bottom of the Little Tallahatchie River, adjacent to County Road 150 in Keownville Quadrangle (NW1/4, NE1/4, Sec. 17, T6S, R4E), Union County, Mississippi (Figs. 1, 2). A 25-gram sample was treated utilizing the following palynological preparation techniques. Chemicals used in processing include 49% hydrofluoric acid (HF), 40% hydrochloric acid (HCl) and hot water mixture, zinc chloride (ZnCl₂, 2.0 specific gravity) used for heavy liquid separation, dilute nitric acid (HNO₃), and 2.5% potassium hydroxide (KOH). The residue was sieved and separated into greater than 90 µm, 25 to 90 µm, and 10 to 25 µm fractions before being placed into vials or mounted onto slides using Elvacite (a plastic polymer) as the mounting medium. Scanning electron photomicrographs were taken using a JEOL Scanning Electron Microscope (JSM840) equipped with a digital imaging system at the USDA in Stoneville, Mississippi. Prior to 2006, light microscope photomicrographs were taken using an Olympus BH-2 microscope mounted with an Olympus C-35 camera. Some dinoflagellate cysts were photographed with an Olympus Vanox microscope at the U.S. Geological Survey, Reston, Virginia. From 2012-2013 transmitted light photomicrographs were taken with an Olympus System Microscope CX-41 with an Olympus Q-Color 3 digital camera at Delta State University. During this time palynomorphs were also photographed at the Smithsonian National Museum of Natural History using a 60x plan apo VC DIC lens on a Nikon *ci Eclipse compound microscope with a Nikon Dxm 1200F digital camera. England Finder references are provided for illustrated specimens. Identifications of palynomorphs were made using published accounts (Stanley, 1965;
FIGURE 1. Geologic map of the Keownville Mississippi, 7.5 minute quadrangle. The palynological sample location is designated by the white dot (Kelley, 2002).
RESULTS

A preliminary analysis of the sampled material yielded 40 genera including five dinoflagellate taxa, a probable marine algal spore (Tasmanites), undifferentiated acritarchs and dinoflagellate cysts, Schizosporis (a probable freshwater algal cyst), one monolete spore, 12 trilete spores, nine gymnosperm pollen, and 10 angiosperm pollen (see Figs. 3-6; Appendix 1). The most common specimens include chorate dinoflagellate cysts of Areoligera senonensis Lejeune-Carpentier, Spiniferites spp. and Exechosphaeridium bifidum (Clarke and Verdier) Clarke et al. (1968); and trilete spores of Stereisporites psilatus (Ross) Pfug (Sphagnaceae), species of Hamulatisporis and Retitriletes (Lycopodiaceae), Cicatricosisporites (Schizaceae), Cyathidites (Dicksoniaceae/Cyatheaceae), and Gleicheniidites (Gleicheniaceae). Bisaccate pollen are the most abundant gymnosperm components and include Podocarpaceae (Phyllocladidites and Podocarpidites), and Pinaceae (Alisporites grandis, Piceapollenites, Pinuspollenites, and Rugubivesiculites). Diverse and abundant genera of angiosperms include Liliacidites (Liliales), Nyssapollenites (Nyssaceae), Momipites (Juglandaceae), Rhoipites (Rhamnaceae or Anacardiaceae), Triporopollenites, and Tricolporopollenites among other tricolporates and triporates (Appendix 1). Most of the angiosperms were less than 30 µm. Subordinate genera include Callialasporites (Araucariaceae), Classopollis (the extinct conifer family Cheirolepidiaceae), Cycadopites (?Ginkgo or Cycadales), Holkopollenites chemardensis Fairchild (tricolporate eudicot), and the palm Spinizonocolpites baculatus Muller. Coincidentally, Nypa mangrove palm fruit was reported by Berry (1925) from the Coon Creek Formation. Specimens

FIGURE 2. Description of the Little Tallahatchie measured section from the Keownville 7½ minute Quadrangle, Mississippi (Kelley, 2002).

FIGURE 3. Coon Creek 300-point palynological count showing various taxonomic categories.
FIGURE 4. Trilete and monolet spores from the Coon Creek Member, Ripley Formation from Union County, Mississippi. All figures are at 1,000x. All photographs were taken in plain transmitted light. Specimens are denoted by a slide number (e.g., 2003 CC04), and England Finder location (e.g., N30-3). Scale bars are at 10 μm.

A. *Klukisporites variegatus* Couper 1958, sample 2003, slide CC06, R16-3  
B. *cf. Todisporites* sp. sample 2003, slide CC04, O45-1  
C. *Laevigatosporites ? ovatus* Wilson and Webster 1946, sample 2003, slide CC04, J47-1  
D. *Matonisporites excavatus* Brenner 1963, sample 2003, slide CC05 L35-1  
E. *Cicatricosisporites* sp., sample 2003, slide CC04, G12  
F. unknown spore, sample 2003, slide CC04, X46  
G. *Stereisporites psilatus* (Ross 1943) Pflug in Thomson & Pflug 1953, sample 2003, slide CC06, P16  
H. *Hamulatisporites* sp., sample 2003, slide CC03, H46-4  
I. *Biretisporites* sp., sample 2003, slide CC04, E16-2/4  
J. unknown spore, sample 2003, slide CC03, L43-4  
K. *Cingulatisporites* sp., sample 2003, slide CC03, L43  
L. *Gleicheniidites* sp., sample 2003, slide CC03, K42-1  
M. *Cyathidites minor* Couper 1953, sample 2003, slide CC04, S14
FIGURE 5. Gymnosperm and angiosperm pollen from the Coon Creek Member, Ripley Formation from Union County, Mississippi. All photographs, except for Fig. 5I were taken in plain transmitted light at 1,000x magnification. Specimens are denoted by a slide number (e.g. 2003 CC04), and England Finder location (e.g. N30-3). Fig. 5I was taken using a JOEL SEM microscope. A. Nyssapollenites anther, sample 2003, slide CC04, F9  B. Podocarpidites sp, sample 2003, slide CC03, W43-1  C. ? Callialasporites sp., sample 2003, slide CC04, K19-4  D. ? 'Vitis' affluens Stanley 1965, sample 2003, slide CC03, J37-3  E-F. Rugubivesiculites rugulatus Pierce 1961, sample 2003, slide CC04, N19-2  G. Pinuspollenites sp., sample 2003, slide CC04, M52  H. Spinizonocolpites baculatus Muller 1968, sample 2003, slide CC04, V19-1  I. Rugubivesiculites reductus Pierce 1961, SEM image.  J. Pinuspollenites sp. sample 2003, slide CC03, T38-4  K. Momipites triradiatus Nichols 1973, sample 2003, slide CC04, U50  L. Nyssapollenites bindae Sirvastava 1969, sample 2003, slide CC03, Q41-2  M. Holkopollenites chemardensis Fairchild, sample 2003, slide CC06, R15-4  N. pollen of Betulaceae, sample 2003, slide CC05, S49-4  O. Rhoipites crassus Stanley, sample 2003, slide CC04, H16-4
FIGURE 6. Marine and freshwater palynomorphs from the Coon Creek Member, Ripley Formation from Union County, Mississippi. All photographs, except for Fig. 6D were taken in plain transmitted light at 1,000x magnification. Specimens are denoted by a slide number (e.g. 2003 CC04), and England Finder location (e.g. N30-3). Fig. 6D was taken using a JOEL SEM microscope. A. *Cordosphaeridium* sp. sample 2003 slide CC04, O20-3  B. *Schizosporis* sp. sample 2003, slide CC04, S25  C. *Exochosphaeridium bifidum* (Clarke and Verdier) Clarke et al., sample 2003, slide CC02, O35-2  D. *Aerogilera senonensis* Lejeune-Carpentier 1938, SEM image, sample 2003  E. *peridiniacean* dinoflagellate, sample 2003, slide CC03, M46-1  F. *? Tasmanites* spore (Prasinophyceae), sample 2003, slide CC04, R4-1  G. *Chatangiella ? robusta* Benson 1976 Stover & Evitt 1978, sample 2003, slide CC04  H. pale peridinoid, high focus, sample 2003, slide CC01, P38  I. inner lining of a foraminifera, sample 2003, slide CC02, H40  J. *Spiniferites* sp., sample 2003, slide CC03, L36-3  K-L. Cladopyxiaceae, orientation uncertain, sample 2003, slide CC04, V19-3
of non-marine algae, acritarchs, trilete spores, and angiosperms, which were not identified to the genus level, were categorized as undifferentiated. Fungal spores were neither morphologically differentiated nor counted in the sieved slides. Additionally, internal linings of foraminifera (Fig. 61) and an anther containing numerous specimens of Nyssapollenites were noted. Palynodebris include leaf cuticles of conifers and angiosperms, red-to-yellow-orange fragments of resinite, angular-to-somewhat-rounded pieces of inertinite, fragments of conifer wood with bordered pits, and amorphous organic matter.

Palynomorph preservation is either excellent or poor, implying two populations with differing taphonomic histories. Some of the unidentified trilete spores appear to be brittle, oxidized, and generally abraded. Amorphous clay floccules in the 10–25 μm mesh screen fraction also concealed small tricolporates and triporates, making identification difficult. Another population comprises pristine and unaltered bryophyte, lycopod and pteridophyte spores, angiosperm and gymnosperm pollen, and dinoflagellate cysts that possess exceptional detail (Figs. 4-6).

Marine elements (dinoflagellate cysts and thecae, acritarchs, and marine algae) comprise 36% of the total palynomorph count, with terrestrial elements making up the rest. Of the terrestrial component, 29% are trilete spores, 2% are monolete spores, 16% are gymnosperms, and 16% are angiosperms. Bryophyte, lycopod, and pteridophyte spores were categorized as trilete spores (Fig. 3).

**DISCUSSION**

**Environmental Setting**

Dinoflagellates, acritarchs, and foraminifera are important constituents of marine food chains and they probably supported the diverse fauna that have been reported from the Coon Creek Formation: brachiopods (Wade, 1926), bryozoans (Ebersole, 2009), crabs (Wade, 1926), crayfish (Brister and Young, 2007), fish (Brister and Young, 2007), molluscs (Dockery, 2003), mosasaur (Gibson and Dunagan, 2003), sea turtles (Collins, 1951), shrimp (Brister and Young, 2007), sharks (Gibson and Dunagan, 2003), a plesiosaur (Whetstone, 1977) and trace fossils of sponges (Griffin and Gibson, 1998). The high yield of cysts of mostly marine dinoflagellates indicates an open-marine, inner-shelf, depositional environment for the sampled horizon (Fig. 6). Well-preserved marine fauna associated with this sample and previous regional studies of molluscan fauna from the Cook Creek Formation (Sohl, 1960; Larson et al. 1997; Dockery, 2003; Ebersole, 2009) are indicative of open-marine environments. Reineck and Singh (1975; p. 308) point out that “wood, freshwater diatoms, pollen, and spores can be present in minor amounts” in shelf sediments.

May (1980) and Hubert (1963), however, noted that modern phytoplankton populations, dominated by a few species, are reflective of nearshore guild environments. Additionally, the large quantity of terrestrial palynomorphs observed in this palynological sample indicates that the inner shelf environment was not far removed from a coastal mainland or barrier island system (Fig. 3). Well-preserved specimens of, Spinizonocolpites spinatus (a Nypa-like mangrove palm; Fig. 5H), an intact, anther-like structure assigned to Nyssapollenites (Fig. 5A), and the relative abundance of pteridophyte and bryophyte spores (Fig. 4) further support the close proximity to land. This sample, collected at the base of the Little Tallahatchie section (Fig. 2), may indicate a pulse of terrestrial material from an unusual flooding event or of a freshwater channel carrying pollen and spores for some distance. Furthermore, the component of the pollen and spores that are particularly well preserved may have been transported by wind from coastal environments. The majority of the palynoflora was transported by water into the marine environment. Accumulation rate, chemical properties of the water, proximity of terrestrial vegetation, dispersal rates of pollen/spores, and sea-level changes also affect organic-matter distribution (Oboh-Ikuenobe et al., 2012). Dysaerobic conditions in bottom waters that resulted in excellent preservation of the marine fauna also likely preserved the palynomorphs.

Warm temperate to subtropical conditions prevailed in the ancestral Gulf Coastal plain during the Late Cretaceous (Srivastava, 1994; Benton, 2004). The Normapolles phyto-geoprovince in eastern North America was well established and persisted through the lower Paleogene (Graham, 1993; Srivastava, 1994). By the end of the Maastrichtian, the estimated mean annual temperature was above 25°C throughout southeastern North American (30 - 45° N) and was dominated by evergreen woodlands (Upchurch and Wolfe, 1987; Graham, 1993). The physiognomy of fossil wood from low-middle latitudes implies that little seasonality occurred because of the lack of distinct growth rings (Upchurch and Wolfe, 1987; Behrensmeier et al., 1992). Palynofloral elements associated with this palynological sample indicate nearby coastal forest vegetation consisting of mosses, ferns, lycopods, conifers, cycads, mangroves, eudicots, and other angiosperms. The presence of abundant (> 20%) and diverse ferns including Cicutricosisporites spp. (Fig. 4E) Gleichenioidites spp. (Fig. 4L) Klukisporites sp., (Fig. 4A) and Matonistipites excavatus (Fig. 4D), Classopolis sp. and Cycadopites sp., Nyssapollenites bindae (Fig. 5L) and Spinizonocolpites baculatus (Fig. 5H) suggest a relatively humid and moist, sub-tropical to temperate paleoenvironment (Srivastava, 1994; Ding and Zhang, 2004). Bisaccates, the most abundant gymnosperms, along with cycads represent the evergreen components. Conifers, including podocarpous, araucarianeous, and pineaceous forms, probably were the dominant large trees whereas angiosperms dominated early successional forests.
and were abundant in brackish habitats (Behrensmeyer et al., 1992).

**Age**

Macroinvertebrates in the type Coon Creek Formation in Tennessee suggest a Late Campanian age. However, the formation is time transgressive and further south the Coon Creek member in Mississippi is dated as Early Maastrichtian based on the ammonite *Nostoceras alternatum* assemblage (Stephenson, 1941; Cobban and Kennedy, 1974; Giaiaglio and Phillips, this volume). As mentioned previously, *Exogyra costata*, associated with this palynological sample site, is regarded as a latest Campanian to Maastrichtian index fossil. Tschudy (1975) and Wolfe (1976) placed the Coon Creek palynostratigraphic sections across the Northern Mississippi Embayment in the informal, palynomorph assemblage zone CA-5B of Wolfe. They based their placement on angiosperm pollen types, which they considered to be Late Campanian (Frederiksen et al., 1982; Ebersole, 2009). These taxa included *Osculapollis aequalis* Tschudy, *Pseudoplicapolis serena* Tschudy, and *Chaonopollenites* cf. *C. conspicous* Tschudy. Their samples were drawn from sections in western Alabama, Tennessee, and northeastern Mississippi, which spanned the Campanian/Maastrichtian boundary.

Species identified in this study cannot be used to determine whether the Coon Creek Member is Late Campanian or Early Maastrichtian. Many are long ranging, such as *Cyathidites minor* Couper (Fig. 4M), *Stereisporites psilatus* (Ross 1943) Pflug in Thomson & Pflug (Fig. 4G), *Klukisporites variegatus* Couper (Fig. 4A), *Gleicheniids* *senonis* Ross (Fig. 4L), *Rugubivesiculoites rugulatus* Pierce (Fig. 5E-F), and *Rugubivesiculoites reductus* Pierce (Fig. 5I). Typical *Normapolles* pollen markers such as *Plicapollis retrusus* Tschudy, *Plicapollis usitatus* Tschudy, *Pseudovacuopollis inovatus* Tschudy, *Trudopollis variabilis* Tschudy, and *Vacuopollis munitus* Tschudy were not observed in this sample. *Holkopollenites chevandensis* is used as a biozone indicator for the Maastrichtian of South Carolina (Christopher and Prowell, 2002), but this species is also reported from the Tar Heel Formation in North Carolina (Mitra, 2002), which is Early Campanian, based on ostracode assemblages of *Fissocarinocythere pittensis*, *Fissocarinocythere gappensis*, and *Halocytheridea plumeria* (Owens and Sohl, 1989; Sohl and Owens, 1991) and the presence of *Exogyra ponderosa* (Sohl and Owens, 1991). *Rhoiptes crassus* Stanley (Fig. 5O) and "Vitis" *affluens* Stanley (Fig. 5D) observed in this study were originally reported from the Late Maastrichtian Hell Creek Formation in South Dakota; however, some pollen taxa may have different stratigraphic ranges in the southeastern United States compared to the Western Interior. *Cardosphaeridium* (Fig. 6A), *Exosphaeridia bidenta* (Fig. 6C), *Spinifertes*, small peridiniacean, and areoligeracean forms found in this sample are known from the Campanian Black Creek Group in Screven and Burke counties in eastern Georgia (Frederiksen et al., 2001), but also from the Early Maastrichtian sediments of the Navesink Formation and Sandy Hook Member of Red Sand (May, 1980).

The McNairy Sand Formation is generally considered to be a facies equivalent of the more marine Coon Creek Formation (Dockery, 1996; Russell and Parks, 1975). It would therefore be logical to assume that the two facies are, at least in part, time equivalent as well. This time equivalency could account for the large overlap between the Coon Creek sample and the McNairy from northern Mississippi (Baghai-Riding and Swann, 2003, 2006). *Cordosphaeridium*, *Matonisporites excavatus* Brenner, *Toroisporis major* Stanley, *Callialasporites sp.*, and *Spinizonocolpites baculatus* Muller are the only taxa found in the Coon Creek but not the McNairy Member. Spinizonocolpites baculatus defines Middle and Late Maastrichtian units in South America and West Africa such as the Arimogija-Okeluse Shale from Southwestern Nigera (Ola-Buraimo et al., 2012). This species may be a stratigraphic outlier in North America. Further palynological collection and research of the Coon Creek Formation/member could clarify age and environmental setting.

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**LITERATURE CITED**


Ann Arbor, Michigan, 368 pp.


Stephenson, L. W. 1941. The larger invertebrate fossils of the Navarro Group of Texas. The University of Texas Publication 4101:1-625.


Appendix 1. Palynomorph taxa from the Coon Creek Member sample, Union County, Mississippi.

**Bryophytes**
- Cingulatisporites sp.
- Stereisporites psilatus (Ross, 1943) Pflug in Thomson & Pflug, 1953

**Lycopsods**
- Hamulatisporis spp.
- Retitriletes spp.

**Ferns**
- Biretisporites sp.
- Cicatricosisporites spp.
- Cyathidites minor Couper, 1953
- Gleicheniidiates spp.
- Gleicheniidiates senonicus Ross, 1949
- Laevigatosporites ?ovatus
- Klukisporites sp.
- Klukisporites variegatus Couper, 1958
- Matonisporites excavatus Brenner, 1963
- Todisporites sp.
- Toroisporis major Stanley, 1965

**Gymnosperms**
- Alisporites grandis (Cookson) Dettmann, 1963
- Callialastorites sp.
- Classopollis sp.
- Cycadophites sp.
- Piceapollenites sp.
- Pinuspollenites sp.
- Podocarpidites sp.
- Phylycostalidites sp.
- Rugubivesiculites reductus Pierce, 1961
- Rugubivesiculites rugulatus Pierce, 1961

**Dicotyledons**
- Betulaceae
  - Holkobollenites chemardensis Fairchild in Stover, Elsik & Fairchild, 1966
  - Momipites spp.
  - Momipites triradiatus Nichols, 1973
  - Nyssapollenites bindae Srivastava, 1970
  - Quercoidites sp.
  - Rhoipites sp. cf. R. cryptoporus Srivastava, 1972
  - Rhoipites crassus Stanley, 1965
  - Triporopollenites sp. (Juglandaceae type)
  - Tricolporopollenites sp.
  - “Vitis” affluens Stanley, 1965

**Monocots**
- Liliacidites sp.
- Spinizonocolpites baculatus Muller 1968

**Freshwater algal cysts**
- Schizopora sp.
- Sigmopollis sp.

**Marine palynomorphs**
- Arioroligera senonensis Lejeune-Carpentier, 1939
- Cordosphaeridium spp.
- Exochosphaeridium bifidum (Clarke and Verdier) Clarke,
  Davey, Sarjeant, and Verdier, 1968
- Spiniferites sp.
- Tasmanites sp. (Prasinophyceae)
- Undifferentiated acritarchs
- Undifferentiated dinoflagellate cysts
Abstract—This is a report of the plant megafossils collected from the shell beds of the Coon Creek Formation. While numerous fragments of plants occur, only 8 were intact sufficiently to warrant inclusion here. Conifer cones, angiosperm leaves including 2 dicot leaf types and seagrass leaves are described here. A rhizome of seagrass was preserved encrusted with bryozoa and penetrated by a small Teredo clam. This is the first report of seagrass from the Cretaceous of the Americas at the western extension of the Tethys seaway.

Fossil plants are rarely found in the shell-rich sediments of the Coon Creek Formation in Tennessee; however, they do occur. After several years of collecting only a handful of plant remains have been found and made available for careful analysis. The total number of plant remains is about twelve, many of which are very fragmentary. Only 8 of the more complete plant specimens are reported here. The abundance of plant megafossils is low, while microfossils are more abundant and diverse, thus providing a more complete record of plants growing in the region. Numerous spores, pollen and dinoflagulates are preserved in the Coon Creek sediment and are associated with the preserved megafossil plant remains (slides of these microfossils have been prepared, but it is beyond the scope of this report to present that data here). This paper focuses on the megafossil plant record within the Coon Creek Formation of Tennessee, with most of the plants having been collected from the type locality.

The fossil plants are of particular interest for several reasons. Such questions as, what kinds of plants are found there, how did the plants become incorporated in the shell beds, and can the plants add any information about the environment and the plant-animal associations so important in shallow marine areas today? None of the fossils recovered are complete nor are they as nice to look at as the shells for which this locality is famous. But they represent large enough fragments that it is possible to use them to characterize the plants. The fragmentary nature of the leaves suggests that there was some transport with some abrasion that broke up the leaves during transport. This abrasion is more obvious in the two axes of cones that are preserved. In both cones the apex and the base are missing and the cone scales are abraded and incomplete. The orientation of the fossils in the shell bed indicates that there was turbulence or a current that was present when the plant material was deposited. Alternatively, the plants may have been reoriented by bioturbation from the indigenous fauna. The plant material does not follow any bedding plane but is bent between the shells, rolled and oriented at various angles within the sandy, gray, calcareous, silt stone that cements the shell bed together.

There are two cone axes that represent a conifer, perhaps something such as pine or an extinct type of conifer. There is a rhizome that has very small Teredo borings in it and bryozoa encrusting it. There are three types of angiosperm leaves preserved.

This paper was originally prepared and submitted in 2003 to be part of Coon Creek Special Volume. This Coon Creek Volume was delayed in its publication and now this paper has been updated to include more recent relevant literature.
Figure 1. Angiosperm leaf fragments. A, C, G, Linear dicot leaves. A, C, 1x. G, 3x. B, D-F, H, I, Sea grass leaves. B, D, 1x. E. Leaf division, 7.5x, 1 mm bar. F. Leaf venation, 1 x, 1 mm bar. H, I, 3x. Scale bars 5 mm unless otherwise noted.

SYSTEMATICS

Conifer cones (Fig. 3D-G). The main cone axes are fragmentary with neither the apex nor the base intact. The axes are 0.5 cm in diameter and both were broken when collected so the lengths are 3.5 cm and 5.0 cm. These lengths are shorter than what actually was preserved in Fig. 1E-F, but the total cone was just not collected. The cone axes bear woody growths that extend at about 45 to 55 degree angles, which appear to resemble eroded cone scales. These scales are seen only in sectional view and they broaden to a thickened base at their attachment. There is no evidence of seeds, seed attachments or a thickened terminal umbo at the end of the scales. It is impossible to assign them to a distinct modern genus.

Angiosperm leaves (Fig. 1A, C, G, Fig. 2A, C-D). There are three different types of angiosperm leaves preserved:

Dicot leaf: This leaf is illustrated in Fig. 2C-D. The leaf is at least once lobed (with the poorly preserved lobe folded under the leaf), otherwise has an entire margin, and a thick, conspicuous mid vein and the leaf blade extends along the incompletely preserved petiole. Broadly divergent, thin secondary veins extend nearly to the leaf margin. Leaf more than 8.0 cm long by 4.5 cm wide. Berry (1925) did not figure any leaf that is similar to this specimen in his Flora of the Ripley Formation.

Linear Dicot leaf: Fig. 1A, C, G, and Fig. 2A. Leaf fragments missing both the leaf apex and leaf base. Thick and conspicuous mid vein, entire margins. Leaves linear, one fragment is 3.2 cm long by 1.3 cm wide, Fig. 1C, G, and the other specimen (Fig. 1A, 2A) is 3.8 cm long by 1.2 cm wide. Secondary veins fine, branch at broad angles of about 70 degrees and extend to near the leaf margin. Fine reticulate mesh vein network preserved in the leaf blade. These leaves are similar to *Myrophyllum angustum* (Velenovksy) Berry and *Apocynophyllum ripleyensis* Berry (Berry, 1925).

Seagrass leaves: Fig. 1B, D-F, H-I. There are two leaf specimens that are incompletely preserved, missing both the apex and base. However, they have several features similar to modern and fossil leaves of seagrass. The leaves are linear, margin entire, mid vein obvious with about 7-10 parallel veins (Fig. 1E-F). Leaves are ligulate (Fig. 1H-I). Leaves are more than 5.5 cm long and 0.7 to 0.9 cm wide. These leaves are similar to some described as *Cymodocea floridana* as presented and discussed in Ivany et al. (1990).

Rhizome: Fig. 2B and Fig. 3A. This appears to be a
rhizome of seagrass. It is segmented into sections that are uniformly 2.5 cm long. It is flattened, suggesting that it was not strongly woody however it does have a small Teredo clam that has started to bore into the preserved tissue. It is encrusted with a bryozoan, which suggests that this rhizome had a long residence time in a marine environment.

DISCUSSION

The plant megafossils illustrated and briefly described here are the result of several years of collecting and demonstrate how rare fossil plant material is in the Coon Creek locality. These plant fossils represent an interesting mixture of terrestrial plant life and marine plant life deposited in this shell bed. The conifer cones probably came from coastal pine forests. Cones are shed in abundance and are quite resistant to decay and have been subjected to degradation and transport. The linear dicot leaves are similar to material described by Berry (1925) for the Upper Cretaceous Coon Creek and Ripley formations with many of the specimens coming from the western Tennessee clay deposits. The leaves are similar to *Myriophyllum angustum* (Velenovsky) Berry and *Apocynophyllum ripleyensis* Berry, which both come from the Cooper Clay Pit in Carroll County 75 kilometers NNE of the Coon Creek locality in McNairy County. The Cooper Clay Pit is dominated by an angiosperm flora (mostly leaves) that is representative of the terrestrial plants living at the time and was deposited in a fresh water environment. The lobed dicot leaf is not similar to any of the leaf material described or illustrated by Berry (1925) for the Coon Creek (Ripley) Formation. It seems to have a single lobe and may be similar to some of the lobed leaves that have single lobbing such as seen today in the mitten shaped leaves of Sassafras however the venation pattern is not similar. The lobe is folded under in the fossil but can be seen with careful observation.

Water transport is the most effective method to carry the cones, leaves and stems that are found mixed in with the shell bed. However, the presence of seagrass argues against an inflow of fresh water as a transport mechanism for these terrestrial plants. Seagrass is generally not tolerant of fresh water sources and the marine organisms, such as the bryozoans living upon the rhizome, would argue against a fresh water source as a transport mechanism. Therefore, I suggest that wind is the most likely method to carry the dicot leaves and cones into the marine environment where they were then carried to the region of the shell bed by marine currents and deposited.

Wind transport into a marine environment, ocean currents carrying the plant material and its final deposition also explains other aspects of these fossils. The presence of encrustation by bryozoans and the presence of Teredo boring clams in the seagrass rhizome suggest that it lived in the marine environment longer than the other plant organs before final burial. This certainly is to be expected of the rhizome of seagrass. Also the abrasion of the cones, the fragmentary nature of the linear leaves, the lobed leaf abrasion, and several small leaf fragments too small to describe here, all suggest that some energy, such as wave action may have acted upon this plant material. These fossils may have been resident in marine water for some time before their final burial. If the terrestrial plant material had been flushed out onto the shell bed by a near by fresh water stream there should be much more diversity of leaf types. Also, large woody logs and fruits and seeds, such as the material known from the Red Hot Truck Stop locality (Call et al., 1993; Danehy et al., 2007) would be present.

It is interesting to note that this report seems to be the first record of seagrass growing in the Gulf of Mexico during the Upper Cretaceous. This is also the first report of seagrass from the Mississippi Embayment. While this paper was in press an extensive and excellent report was published of seagrass foliage from Maastrichtian deposits in northeastern Belgium and southeastern Netherlands (Van der Ham et al., 2007). The extensive shallow water

![Figure 3. Rhizomes and conifer cones. A-C, Sea grass rhizome. A. 2x, 5 mm bar. B. Teredo bivalve in rhizome, 7x, 2 mm bar. C. Bryozoan alongside rhizome, 3.3x, 2 mm bar. D-G, Conifer cones. D. 1x, 5 mm bar. G. 2x, 5 mm bar. E. 1x, 5 mm bar. F. 3x, 5 mm bar.](image)
environments of the Embayment should have been an excellent place for the growth of large beds of seagrass. Brasier (1975) considered that seagrasses did not reach the Caribbean Basin until Miocene times. Eva (1980), using the occurrence of foraminifera in the Caribbean Basin revised Brasier’s (1975) interpretation. Eva (1980) suggested that seagrass distribution followed the shallow areas of the Tethyan seaway and used the presence of foraminifera, such as Ayalaína rutteni and species of Chubbina, in the Late Cretaceous Neotropics as evidence that seagrasses could have been present in the Caribbean by that time. Furthermore, the work of Ivany et al. (1990) confirms the presence of the seagrasses Thalassodendron and Cymodocea during the middle Eocene in the Avon Park Formation in peninsular Florida.

This report is the earliest direct evidence of the presence of seagrasses in the Upper Cretaceous in the Gulf of Mexico. It is appropriate that these seagrass fossils occur in the shallow waters of the Mississippi Embayment, suggesting that there was a broad distribution of Tethyan plant and animal associations extending across the shallow marine continental shelves halfway around the world. There have been numerous examples of regional extinctions of terrestrial plants that dispersed in these shallow seas and along the coastal margins of these seas (McCoy and Heck, 1976; Gee, 1990; Westgate and Gee, 1990; Dilcher, 2000). Therefore the relationships between similar species and families of land plants that still persist in southeastern North America, many elements of the forests of Mexico and Central America and the floras of southeastern Asia have their origin in this broad dispersal that followed the Tethyan Seaway (Dilcher, 2000).

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REFERENCES CITED

1. Systematics of the Percid Fishes of the Subgenus *Ammocrypta*, Genus *Ammocrypta*, with Descriptions of Two New Species. James D. Williams. 56 pp., illus., June, 1975. $5.00

2. Endangered and Threatened Plants and Animals of Alabama. Herbert Boschung, Editor. 95 pp., illus., October, 1976. $7.50


4. Systematics of the Percid Fishes of the Subgenus *Microperca*, Genus *Etheostoma*. Brooks M. Burr. 53 pp., illus., July 1978. $5.00

5. Containing: *Notropis candidus*, a New Cyprinid Fish from the Mobile Bay Basin, and a Review of the Nomenclatural History of *Notropis shumardi* (Girard). Royal D. Suttkus. *Notropis stanauli*, a New Madtom Catfish (Ictaluridae) from the Clinch and Duck Rivers, Tennessee. David A. Etnier and Robert E. Jenkins. 23 pp., illus., May, 1980. $5.00

6. Containing: A New Species of Cyprinodontid Fish, Genus *Fundulus* (*Zygonectes*), from Lake Pontchartrain Tributaries in Louisiana and Mississippi. Royal D. Suttkus and Robert C. Cashner. Karyotypes in Populations of the Cyprinodontid Fishes of the *Fundulus notatus* species-complex: A Geographic Analysis. W. Mike Howell and Ann Black. An Isozymic Analysis of Several Southeastern Populations of the Cyprinodontid Fishes of the *Fundulus notatus* Species-Complex. Fred Tatum, Ronald Lindahl and Herbert Boschung. 35 pp., illus., April, 1981. $5.00


9. Systematics of *Notropis cahabae*, a New Cyprinid Fish Endemic to the Cahaba River of the Mobile Basin. Richard L. Mayden and Bernard R. Kuhajda. 16 pp., illus., November, 1989. $3.50


18. pH and Temperature in Ectothermic Vertebrates. Gordon R. Ultsch and Donald C. Jackson. Life Histories of Notus baileyi and *N. flavipinnis* (Pisces: Ictaluridae), Two Rare Madtom Catfishes in Citico Creek, Monroe County, Tennessee. Gerald R. Dunkins and Peggy W. Shute. 69 pp., illus., December, 1996. $10.00


21. Unionid Mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia. Jayne Brim Box and James D. Williams. 143 pp., illus., April, 2000. $20.00


Jack W. Feminella. The Osteology of the Stone Cat, *Noturus flavus* (Siluriformes: Ictaluridae), with Comparisons to other Siluriforms. Jacob J. Egge. 89 pp., illus., August, 2007. $20.00


SPECIAL PUBLICATIONS

2. Ten Thousand Years of Alabama History, A Pictorial Resume. W. Phillip Krebs. 130 pp., illus., January, 1986. $10.00
3. The Mounds Awaken: Mound State Monument and the Civilian Conservation Corps. Joy Baklanoff and Arthur Howington. 36 pp., illus. October, 1989. $3.00

MUSEUM PAPERS (1910-1960, TERMINATED)

4. Annotated List of the Avery Bird Collection. Ernest G. Holt. 142 pp., 1 plate, 1921. $3.00
6. The Anculosea of the Alabama River Drainage. Calvin Goodrich. 57 pp., 3 plates, 1922 Out of Print
7. The Genus Gyrotema. Calvin Goodrich. 32 pp., 2 plates, 1924. Out of Print
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