A unique late Eocene coleoid cephalopod Mississaepia from Mississippi, USA: New data on cuttlebone structure, and their phylogenetic implications

LARISA A. DOGUZHAEVA, PATRICIA G. WEAVER, and CHARLES N. CIAMPAGLIO


A new family, Mississaepiidae, from the Sepia–Spirula branch of decabrachian coleoids (Cephalopoda), is erected on the basis of the following, recently revealed, morphological, ultrastructural and chemical traits of the cuttlebone in the late Eocene Mississaepia, formerly referred to Belosaepiidae: (i) septa are semi-transparent, largely chitinous (as opposed to all other recorded cephalopods having non-transparent aragonitic septa); (ii) septa have a thin lamello-fibrillar nacreous covering (Sepia lacks nacre altogether, Spirula has fully lamello-fibrillar nacreous septa, ectochochleate cephalopods have columnar nacre in septa); (iii) a siphonal tube is present in early ontogeny (similar to siphonal tube development of the Danian Ceratisepia, and as opposed to complete lack of siphonal tube in Sepia and siphonal tube development through its entire ontogeny in Spirula); (iv) the lamello-fibrillar nacreous ultrastructure of septal necks (similar to septal necks in Spirula); (v) a sub-hemispherical protoconch (as opposed to the spherical protoconchs of the Danian Ceratisepia and Recent Spirula); (vi) conotheca has ventro-lateral extension in early ontogenetic stages (as opposed to Sepia that has no ventro-lateral extention of the conotheca and to Spirula that retains fully-developed phragmocone throughout its entire ontogeny). Chitinous composition of septa in Mississaepia is deduced from (i) their visual similarity to the chitinous semi-transparent flange of Sepia, (ii) angular and rounded outlines and straight compressive failures of the partial septa and mural parts of septa similar to mechanically-damaged dry rigid chitinous flange of Sepia or a gladius of squid, and (iii) organics consistent with β-chitin preserved in the shell. The family Mississaepiidae may represent a unknown lineage of the Sepia–Spirula branch of coleoids, a conotheca lacking a nacreous layer being a common trait of the shell of this branch. However, Mississaepiidae is placed with reservation in Sepiida because of similarities between their gross shell morphology (a cuttlebone type of shell) and inorganic-organic composition. In Mississaepia, as in Sepia, the shell contains up to 6% of nitrogen by weight; phosphatised sheets within the dorsal shield may have been originally organic, like similar structures in Sepia; accumulations of pyrite in peripheral zones of aragonitic spherulites and in-between the spherulites of the dorsal shield may also indicate additional locations of organics in the shell of living animal.

Key words: Cephalopoda, Coleoidea, cuttlebone, lamello-fibrillar nacre, chitin septa, fossilization, Eocene, Mississippi, USA.

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Introduction

A patchy fossil record of sepiids and inadequately known evolutionary development of the cuttlebone impede the understanding the phylogenetic relationships between the sepiids and the rest of decabranchian coleoids including spirulids, sepiolids, teuthids, and belemnoids (Voltz 1830; Naef 1922; Donovan 1977; Dauphin 1984, 1985; Young and Vecchione 1996; Haas 1997; Bonnaud et al. 1997; Sweeney and Roper 1998; Hewitt and Jagt 1999; Carlini and Graves 1999; Doguzhaeva et al. 1999; Lindgren et al. 2004; Warnke et al. 2011). Naef (1921) assumed, in spite of different shell morphology, that Sepia and Spirula arose from a common ancestor because they share similar phragmocone structure.
Extant sepiids, classified into three genera and more than 100 species (Lu 1998; Reid et al. 2005), have a markedly modified shell, a cuttlebone or sepion. The cuttlebone consists of a dorsal shield and a phragmocone built of extremely narrow chambers with strongly oblique septa. The phragmocone lacks ventral wall and siphonal tube, but retains a homologous structure of connecting rings named connecting strips because of their band-like shape (Doguzhaeva and Mutvei 2010, 2012). Because of its high organic component, the cuttlebone is considered an inorganic-organic structure: 10% of cuttlebone weight is $\sim$chitin linked with proteins (Florek et al. 2009), twice the amount found in other mollusc shells (Marin et al. 2010). About 90% of shell material is aragonite, with small amounts of calcite (Xiao et al. 2005) and hydroxyapatite (Jasso-Gastinel et al. 2009). The septa are richer in chitin, whereas pillars are richer in aragonite (Florek et al. 2009). Aragonite in septa shows fluctuations of Sr content: it is much higher in the growth increments that were secreted during the winter or the period of calcium deficiency (Hewitt 1973). Shell has no nacreous elements.

At present, Palaeogene–Neogene sepiid genera outnumber the genera of extant sepiids. The cuttlebone gross morphology in these forms is illustrated in Ceratisepia (Meyer 1993) and Belosaepia (Yancey et al. 2010). A bimineralic, aragonite/calcite, composition of the cuttlebone was recently suggested for Anomalosaepia (Yancey and Garvin 2011). Preservation of organisms consistent with $\beta$-chitin within the cuttlebone of Mississaepia has recently been reported by Weaver et al. (2011).

The present paper reports new data on the phragmocone morphology, ultrastructure, and inorganic-organic nature of the cuttlebone in Mississaepia (Fig. 1). These data may be evidence of a previously unknown lineage of Sepia–Spirula branch of decabrachian coleoids. The systematic position of Mississaepia, which was previously tentatively referred to Belosaepiidae Dixon, 1850 by Weaver et al. (2010), is revised. A new family Mississaepiidae is proposed. Burial and fossilization of the inorganic-organic cuttlebone of M. mississippiensis are discussed.

**Institutional abbreviations.**—MGS, Mississippi Department of Environmental Quality, Geological Survey in Jackson, Mississippi, USA; NRM-PZ Mo., Swedish Museum of Natural History, Department of Palaeozoology, Collections of molluscs, Stockholm, Sweden; PRI, Paleontological Research Institute, Ithaca, New York, USA.

**Other abbreviations.**—bl, basal layer; c, conotheca; de, dendritic elements of lamello-dendritic ultrastructure of ventral plate; dsh, dorsal shield; g, gap between septal ridge and m marginal part of septum; l, lamella of lamello-fibrous nacre of septum; la, lamella of lamello-dendritic ultrastructure of ventral plate; lwph, lateral wall of the phragmocone; mlad, median line indicating apertural direction; mlpd, median line indicat-

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**Fig. 1.** Cuttlebone of Late Eocene sepioid cephalopod Mississaepia mississippiensis Weaver, Dockery III, and Ciampaglio, 2010 from Mississippi, USA with a missing anterior-most part (MGS 1945), in left lateral (A) and ventral (B) views. Abbreviations: dsh, dorsal shield; lwph, lateral wall of the phragmocone; phr, phragmocone; vg, ventral groove of spine; vp, ventral plate.

**Fig. 2.** Sketch map showing the location of the Yazoo Clay, the Miss Lite Clay Pit in the northwest corner of the town of Jackson and the Moodys Branch Formation, Town Creek locality south of Jackson in Hinds County, Mississippi, USA.
ing posterior direction; mpls, mural part of last septum; mps, mural part of septum; p, protoconch; phr, phragmocone; rf, rod-like fibre of lamello-fibrillar nacre; rr, ribby relief; s, partial septum; sh, phosphatised sheet of dorsal shield; sn, septal neck; sp, spine of dorsal shield; sr, septal ridge; trs, transparent fragmentary septum; vg, ventral groove of spine; vp, ventral plate; vsdsh, ventral side of dorsal shield; 1ch, 2ch, first, second chambers; 1s, 2s, 3s, first, second, and third septa of the phragmocone.

Geological setting

The cuttlebones of Mississaepia mississippiensis examined in this study come from the Yazoo Clay, Miss Lite Clay Pit, at Cynthia in northwestern Hinds County and two specimens come from the Moodys Branch Formation, Town Creek locality at Jackson, Mississippi, USA (Fig. 2). These deposits overlie the Middle Eocene Claiborne Group. The Bartonian–Priabonian age of the beds containing the coleoids under consideration was determined by the following foraminifera: Globorotalia cerroazulensis, Porticulasphaera semiinvoluta, and Truncorotoides rohri (Tew 1992). Fluegeman et al. (2009) give a radiometric age of 34.36 mya for the Yazoo Clay. The Yazoo Clay section exposed in the Cynthia pit is equivalent to the Shubuta Clay Member in eastern Mississippi. The Shubuta Clay, as well as its equivalents, is typically a greyish-olive-green blocky to massive, fossiliferous, calcareous clay (Tew 1992; Tew and Mancini 1995). The entire Yazoo sequence consists largely of middle shelf marine clay deposited in a suboxic environment. The Moodys Branch Formation underlies the Yazoo Clay and is slightly older.

Material and methods

The study material comprises 32 available specimens including holotype PRI 10258 and paratypes PRI 10259, MGS 1941–MGS 1969 of the late Eocene (Bartonian/Priabonian) cuttlefish Mississaepia mississippiensis from Mississippi, USA (Weaver et al. 2010) collected over the course of several years by David Dockery III. The studied fossil material is housed at the Mississippi Geological Survey (MGS). The cuttlebone of Recent Sepia used for comparison is housed at the Department of Palaeozoology, Museum of Natural History, Stockholm.

Visual similarity between transparent material of broken septa in Mississaepia and chitin flanges in cuttlebones of extant Sepia was observed under light photomicroscope (Wild M 400). Four specimens were split longitudinally to access the site of partially preserved septa (Figs. 3, 4). Pieces of two fractured shells were etched with glutaraldehyde-acetic acid-alcian blue solution. The solution contains 1:1 of glutaraldehyde and acetic acid with additive of alcian blue powder.
etched for 10–15 min. at 30–40°C, watered, dried, glued on stubs and coated with gold. The specimens were examined using a Hitachi S-4 300 Scanning Electron Microscope (SEM) with an attached Energy Dispersive Spectrometer (EDS) at the Swedish Museum of Natural History, Stockholm. Chemical analyses were performed at accelerating voltage 15 kV and energy calibration was measured on standard minerals. All elements were analyzed and no peaks were omitted. Data obtained for septa, conotheca, and dorsal shield were compared.

Results

Morphology and ultrastructure of cuttlebone in Mississaepia.—Protoconch was observed in three specimens (Figs. 3, 5A, C, 6C, D). It is sub-hemispherical, 0.5 mm long and 1.5 mm broad. Shell wall is prismatic. First septum is perpendicular or slightly inclined to axis of protoconch (Fig. 6D). The apical portion of phragmocone is strongly curved dorsally but flattened ventrally. Its inner surface is smooth in the first five to seven chambers and rippled in later chambers where the conotheca is not preserved (Figs. 3, 4). Ventral wall of the phragmocone is preserved a short distance from the protoconch (Fig. 6A, B). Preserved fragments of ventrolateral wall in several specimens show abrupt irregular terminations (Figs. 1, 9A2, A3; Weaver et al. 2010: pl. 1: C, I, L) indicating that it must have continued anteriorly; it is uncertain how far it extended. On the dorsal side the conotheca, or phragmocone wall, is formed by a thin prismatic layer and lacks a nacreous layer (Fig. 8A–E). First and second chambers occupy the short, strongly curved initial portion of phragmocone (Figs. 3, 5A, C, 6C, E1). They are markedly longer on dorsal side than on ventral side. This indicates that first two septa were strongly inclined dorsally. The third and subsequent chambers are shorter than the first two. Six specimens expose band-like remains of transparent or semi-transparent brownish, yellowish or colourless septa preserved closest to the mural parts of septa and mural ridges (Figs. 4, 6B, E1, 7B, C, 8F). Partially preserved septa regularly show mechanical breakage with straight and rounded outlines (Figs. 7B, C, 8F). Completely broken septa left a slit-like space between the mural parts of septa and mural ridges (Figs. 6E2, 8D). Remains of broken septa differ from the white or white-pinkish prismatic conotheca and whitish or gray spherulito-prismatic dorsal shield. Near the conotheca, fragments of preserved septa show whitish thin film-like covering of lamello-fibrillar nacre (Fig. 7A–C). Mural parts of septa extend the length of the chamber (Figs. 5C, 8F). Septal ridges are posterior to the mural parts of septa and have a complex structure, the details of which are not yet wholly understood (Figs. 7A1, 8A1, B, D). Siphuncle is ventro-marginal (Fig. 6C, E1). Septal necks are flattened, about 2/3 chamber length, formed by lamello-fibrillar nacre (Figs. 6E, 7A2–A3). Mural parts of septa are possibly organic, with a lamello-fibrillar nacreous covering (Figs. 5C, 8F). Connecting rings are not preserved. Rugose dorsal shield thins anteriorly but is re-enforced by a large posterior spine (Figs. 1, 3, 4A–G, 6A1, C, E1). Preserved cuttlebone length range is 24–65 mm. The full length of the cuttlebones is not known because the furthest anterior portions are typically missing. The dorsal shield has thin basal prismatic layer (Fig. 8A). Bulk of the dorsal shield is spherulitic-prismatic (Figs. 6A1, C, 7A1, A2). Spherulites consist of needle-like crystals arranged in growth rings separated by phosphatised sheets (Fig. 5D–F). The sheets continue between the spherulites (Fig. 5E2). The dorsal shield has thin ventral extension and forms a ventral plate below the curved apical part of the phragmocone (Figs. 6A, 9A, B).

The ventral plate regularly shows broken anterior edge (Fig. 9A3). Because of this, it is not known how far the ventral plate extended adorally. The ventral plate has a small dome-like structure surrounding the protoconch. Five specimens show a circular hole in the cuttlebone above the protoconch (Fig. 6B). This hole is the same size as the protoconch. The protoconch seemed to push out a thin part of the cuttlebone and this formed a circular hole during post-mortem compaction. This circular hole was erroneously interpreted as a siphuncle related structure (Weaver et al. 2010: 59, text-fig. 5, pl. 1: B, E). The ventral plate has a lamello-dendritic ultrastructure formed by parallel aragonitic laminas with irregular lengths between transverse dendrite-like fibres (Fig. 9C). Dorsal shield and conotheca differ from the mural parts of septa as they are whitish, carbonate and lack a nacreous lustre whereas, mural parts of septa are iridescent and have a nacreous lustre.

EDS data on chemical composition of cuttlebone in Mississaepia and Sepia.—In Mississaepia the following shell structures and post-mortem infillings between the spherulites of the dorsal shield were analysed: the lamella-fibrillar nacreous film of septa (Fig. 10B) and mural parts of septum (Fig. 10A), the lamella-fibrillar nacreous septal neck, the spherulitic tissue preserved along a contact between the cono-
theca and septum (Fig. 11A), the whitish-pinkish conotheca, the whitish-grey material of septal ridges, the membranes between the growth increments of the dorsal shield (Fig. 11B), the whitish-grey material of dorsal shield (Fig. 11C), the peripheral zones of spherulites in the dorsal shield, the infilling in between the spherulites of the dorsal shield (Fig. 11B). In *Sepia* the dorsal shield was analysed (Fig. 11D). The chemical composition of these structures is shown in Tables 1–3.

**Systematic palaeontology**

*Cephalopoda* Cuvier, 1797

*Coleoidea* Bather, 1888

*?Sepiida* Gray, 1849

*Family Mississaepiidae* nov.

*Type genus: Mississaepia* Weaver, Dockery, and Ciampaglio, 2010; monogeneric.


![Fig. 6. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA. A. MGS 1943, cross section through the apical part of cuttlebone showing thick, loosely mineralized dorsal shield above the alveolus. A2. Close-ups of A1 to show a smooth surface of ventral plate. B. MGS 1946, ventral plate showing rounded hole corresponding to a place above the protoconch. C. MGS 1944, shows loosely mineralized apical part of dorsal shield and basal part of spine (on the left), a cup-like protoconch and a hollow phragmocone showing a retrochoanitic septal neck preserved in fourth septum that indicates a ventral position of siphuncle. D. MGS 1947, mould of sub-hemispherical protoconch. E. MGS 1944, longitudinal section of the posterior portion of the dorsal shield (on the left) and a hollow phragmocone to show the mural parts of second through sixth septa and a single preserved retrochoanitic septal neck in fifth septum. E2. Close-up of retrochoanitic septal neck on E1. Abbreviations: dsh, dorsal shield; p, protoconch; phr, phragmocone; s, partial septum; sh, phosphatised sheet of dorsal shield; sn, septal neck; sp, spine of dorsal shield; vp, ventral plate; 1ch, 2ch, first, second chambers; 1s, first septum of the phragmocone.

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Table 3. Comparative data on extreme recorded values (% of total weight) of carbon, nitrogen, oxygen, sodium, magnesium, silica, sulphur, chlorine, potassium, phosphorus, calcium, iron, strontium of the dorsal shield of Sepia (1) and different parts of the cuttlebone of Mississaepia mississippiensis (2–9): 2, lamello-fibrillar nacreous covering of septum; 3, lamello-fibrillar nacreous covering of mural parts of septum; 4, lamello-fibrillar nacreous septal neck; 5, whitish-grey material of septal ridge; 6, whitish-grey material of dorsal shield; 7, a peripheral zone of spherulites in the dorsal shield; 8, sheet-like structures in between the growth increments of spherulites in the dorsal shield; 9, the infillings in between spherulites of the dorsal shield.

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**Differential diagnosis.**—Septa semi-transparent, apparently chitinous as opposed to aragonitic septa in all other cephalopods, with only a thin lamello-fibrillar nacreous covering as opposed to total absence of nacre in Sepia, and fully lamello-fibrillar nacreous septa in Spirula. Siphonal tube present in only early ontogeny, as opposed to its lack in Sepia and to its development throughout the entire ontogeny in Spirula. Protoconch sub-hemispherical as opposed to spherical protoconchs in Danian Ceratitsepi and in Spirula. Conotheca with ventro-lateral extension in early ontogenetic stages as opposed to Sepia that has no ventro-lateral extension of conotheca and to Spirula that retains fully developed phragmocone throughout its entire ontogeny.

**Remarks.**—A new family, Mississaepiidae, is erected based on the following characteristics: semi-transparent apparently chitinous septa (Figs. 4, 7B, C); ventro-lateral wall over the apical portion of the phragmocone possibly extending adorally (Fig. 1; Weaver et al. 2010: pl. 1: C, I, L); sub-hemispherical protoconch with rounded first septum perpendicular to the protoconch axis (Fig. 6C, D); second and third septa strongly oblique and first and second chambers much longer dorsally than ventrally; short latter chambers with septa nearly perpendicular to the phragmocone axis (Figs. 5A, C, 6C, E1); siphuncle ventro-marginal and septal necks about 2/3 chamber length (Figs. 6C, 7A). Based on gross morphologic similarities such as a strongly curved phragmocone and large apical spine these specimens were tentatively placed in Belosaepiidae (Weaver et al. 2010). New data on protoconch and phragmocone structures of Mississaeaepia described herein show significant differences from belosaepiids. Contrary to mississaepiids, belosaepiids have calcified septa, spherical protoconch and steeply inclined septa adorally (Meyer 1993: pls. 3: 1, 5: 1, 2). The mississaepiid phragmocone structure at later ontogenetic stages is yet unknown.

**Geographic and stratigraphic range.**—Late Eocene (Bartonian/Priabonian) Yazoo Clay and Moodys Branch Formation, Jackson Group, Hinds County, Mississippi, USA.

**Discussion**

**Inorganic-organic structure of the cuttlebone of Mississaepia and the distribution of nitrogen, phosphorus, and iron.**—Nitrogen is known to be a reliable indicator of organic material (Oeheler et al. 2009). The presence of nitrogen was used to argue for preservation of chitin in Late Carboniferous scorpion cuticles (Gupta et al. 2007). In Mississaeaepia the signals of nitrogen were obtained from different parts of the cuttlebone: septa, mural parts of septa, silicified tissue preserved along contact between conotheca and septum, and dorsal shield (Figs. 10, 11, Tables 1, 2). The presence of nitrogen is herein used to argue for preservation of organic material in the cuttlebone of the late Eocene Mississaeaepia. The maximal recorded value of nitrogen—5.57% of total weight—was detected in the silicified tissue preserved along contact between conotheca and septum (Fig. 11A, Table 3). The limited data available do not allow for quantitative evaluation of the distribution of organics within the cuttlebone. Nevertheless they demonstrate consistent presence of organic material in all parts of the cuttlebone of Mississaeaepia. Nitrogen signals in the approximately 35 mya cuttlebones likely indicate levels of organics approaching—or even surpassing—that of extant...
Sepia cuttlebones. In Sepia the organic laminas formed by β-chitin-protein complex are inter-layered with the aragonite and constitute about 10% of cuttlebone weight. In the organic laminas the average contents of the elements are: C, 15.36%; O, 0.68%; Na, 1.0%; Mg, 0.133%; N, 1.42%; K, 0.26%; Fe, 0.03%; and Sr, 0.28% (Florek et al. 2009).

Phosphorus was recorded from the sheet-like structures in between the mural part of septum (left) and mural ridge of septum (right), the gap indicates position of septum where it is broken. In Mississaepia minerals of phosphorus were also recorded in lamello-fibrillar nacreous film on septa (Fig. 10B, Tables 1, 3) and mural parts of septa (Fig. 10A, Table 1, 3). The maximal values of the phosphorus in these structures are 8.7%, 1.9% and 12.9%, respectively (Table 3). In vivo all listed above phosphatised structures apparently were rich in organic material. In Sepia the organic laminas in the dorsal shield lack phosphorus (Table 3).

Iron was recorded in different structures of the cuttlebone of Mississaepia (Figs. 10A, B, 11A, B, Table 1), however, the infillings in between and the periphery of aragonitic spherulites within the dorsal shield show highest recorded values—up to 38.8% and 30.8%, respectively (Table 3). Iron signals are irregular and maximal values are lower in sheet-like structures in between the growth increments of spherulites in the dorsal shield (7.9%) and in lamello-fibrillar nacre (3.9–8.9%) (Tables 2, 3). In Mississaepia, iron is either iron sulphide (pyrite) or iron-oxide. In Sepia the organic laminas inter-layered with aragonitic layers in the dorsal shield show 0.03% of iron (Tables 2, 3). The distribution of iron in the cuttlebone of Mississaepia shows its post-mortem distribution and likely indicates the original accumulations of organic material in between the aragonitic spherulites in the dorsal shield and presence of organic material in growth zones of spherulites.

In Mississaepia sulphur was recorded in the sites of maximum concentrations of iron, namely: in infillings between the aragonitic spherulites and in the peripheral zones of them. The maximal values are 13.0% and 28.9%, respectively (Table 3). Hence, sulphur is associated with iron, as pyrite, and is diagenetic. It is missing from a list of the elements detected in organic laminas of Sepia (Table 3).

Silica was recorded in the lamello-fibrillar nacreous covering of septa, mural parts of septa, and the peripheral zone of the spherulites in the dorsal shield of Mississaepia. Their maximal values are 3.2%, 16.9% and 22.5%, respectively (Figs. 10B, 11A, Table 3). Silica is missing from a list of the elements detected in organic laminas of Sepia (Table 3).

The signals of the carbon, oxygen, sodium, magnesium, potassium, and strontium reported from the organic laminas inter-layered with aragonitic layers in the dorsal shield of Sepia (see section Results and Florek et al. 2009) were recorded in Mississaepia as well (Table 3). The average content of these elements in Sepia differs from that in Mississaepia.

Inorganic-organic composition of the cuttlebone of Mississaepia, revealed here by light microscope, and SEM and EDS analyses was recently confirmed by discovery of the degraded organics consistent with β-chitin in the cuttlebones of this taxon by molecular techniques (Weaver et al. 2011). Chitin composition of septa of Mississaepia, revealed here by light microscopy was not analyzied by molecular techniques due to the limited number of preserved septa, there was not enough de-mineralized material for analysis.

Nevertheless, chitin composition of septa is generally supported by data on β-chitin consistent organics in Mississaepia (Weaver et al. 2011). Further search for more Eocene cuttlebones and their study with a focus on the phragmocone structure and septal composition will possibly reveal so far unknown taxa with chitinous septa.

Burial and fossilization of cuttlebones of Mississaepia in Mississippi.—The late Eocene cuttlebones of Mississaepia were buried in a partially suboxic environment of a middle shelf in a muddy bottomed basin with intensive precipitation of fine-grained clays (Tew 1992; Tew and Mancini 1995; Hansen et al. 2004) in the water depth of 25–50 m (Echols et al. 2003).

All studied specimens represent partial cuttlebones regularly showing mechanical breakage anteriorly (Fig. 1; Weaver et al. 2010; pl. 1: A–L). Phragmocones are partially preserved in the posterior portions of the cuttlebones (Fig. 3). Thin conotheca bearing attached mural ridges, long mural parts of septa lining the chambers and band-like remains of semi-transparent septa between the chambers is observed in the apical portion of the phragmocones. Remains of septa expose uneven margins with acute triangular and round elements in contour (Fig. 7B, C). Mural parts of septa show long straight longitudinal cracks and splitting. Regular mechanical breakage of the anterior portions of the cuttlebones and destruction of the apical parts of the phragmocone suggest that the anterior parts were removed prior to settling on the bottom. Predators may
have caused destruction of the cuttlebones in Mississaepia: co-occurring abundant remains of ray and bony fish, primitive whales, and sharks (Breard 1991) indicate potential predators of Mississaepia.

Available free Fe$^{2+}$ ions in the partially suboxic environment of burial and an inorganic-organic lamination of the cuttlebone contributed to their exceptional preservation. These environmental and ultrastructural factors likely inhibited microbial or enzymatic degradation of chitin. Organic laminas within cuttlebones were protected by mineralized laminas, similar to collagen in bones. This mineral-organic interaction may have played a role in their preservation (Collins et al. 2002; Schmidt-Schultz and Schultz 2004). Signals of calcite were not recorded in these cuttlebones (Weaver et al. 2011). Hence, bimineral aragonite-calcite composition (Yancey and Garvie 2011) recently assumed for the Eocene cuttlebone of Anomalosaepia Weaver and Ciampaglio, 2003 is not evident in Mississaepia.

Taphonomic peculiarities listed above imply that cuttlebones of Mississaepia were buried in place of dwelling of this mollusc, namely, above the middle shelf with an estimated depth about 25–50 m.

Systematic position of Mississaeididae.—Mississaeididae is tentatively placed in the order Sepiida based on similar gross morphologic characters of the cuttlebone. However, Danian Ceratisepia and extant Sepia, as well as Spirula have mineralized septa in the phragmocone while in Mississaeid the septa are largely chitinous, with only a film of lamello-fibrillar nacre. It is reasonable to suggest that an Eocene

Fig. 9. Sepioid cephalopod Mississaepia mississippiensis Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA. A. MGS 1949, posterior portion of the cuttlebone, ventral view. A2. Close-up of A1; the hollow phragmocone and ventral plate above it. A3. Enlarged detail of A2; a fin-like structure of the ventral plate. B. MGS 1944, cross section through the cuttlebone to show that layers of the dorsal shield turn into the ventral plate. C. MGS 1949, lamello-dendritic ultrastructure of ventral plate. C2. Close-up of C1; dendrites “growing” on lamella surfaces. Abbreviations: de, dendritic elements of lamello-dendritic ultrastructure of ventral plate; la, lamella of lamello-dendritic ultrastructure of ventral plate; phr, phragmocone; s, partial septum; sp, spine of dorsal shield; vp, ventral plate.

Fig. 10. Sepioid cephalopod Mississaepia mississippiensis Weaver, Dockery III, and Ciampaglio, 2010 (MGS 1963); late Eocene, Mississippi, USA. Mural part of septum lining a chamber (A), adoral surface of peripheral portion of septum (B), photographs (A1, B1); EDS data to show chemical composition (A2, B2); in both cases nitrogen indicates organic ingredient and phosphorus indicates diagenetic phosphatization of apparently originally organic material.
Fig. 11. Cuttlebone of sepoid cephalopod *Mississaea mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA (A–C) and contemporary *Sepia* (D). A. MGS 1956. B. MGS 1956. C. MGS 1956. D. NRM–PZ Mo. 180818. Photographs (A1–D1); EDS data on chemical composition shows presence of: A2, high content of nitrogen indicating organic ingredient in silicified tissue preserved along contact between conotheca and septum; B2, nitrogen indicating organic ingredient of phosphatised sheet within the dorsal shield; C2, D2, nitrogen indicating organic ingredient of dorsal shield.
member of Sepiida and Spirulida should not have less mineralized septa than their extant relatives as there is an evolutionary trend in coleoids to develop new organic rich or chitinous shell structures, like a capsule of Late Cretaceous belemnites (Doguzhaeva and Bengtson 2011) or a gladius of fossil and Recent squids (Doguzhaeva and Mutvei 2006), and to decrease shell mineralization. Moreover, the lamellobibrillar nacre is an ultrastructural characteristic of septa of Spirula rather than of Sepia. Therefore, we think that Mississaeppidae belong to a third, likely dead-end lineage of the Sepia/Spirula branch of decabrachian coleoid cephalopods.

The exceptionally well-preserved cuttlebones of the late Eocene Mississaeapia provide additional support for Naef’s (1921) view on common origin of Sepia and Spirula that was based on similar phragmocoine morphology in these two taxa. Mississaeapia, Sepia, and Spirula have a phragmocoine wall, or a conotheca, with no nacreous layer. The conotheca without a nacreous layer is considered to be an ultrastructural characteristic of Sepia–Spirula branch of decabrachian coleoids. However, it should be noted that partial reduction of nacreous layer in the dorsal portion of conotheca took place in the Middle Jurassic Belemnotheutis (Fuchs et al. 2007) and occurred in some other belemnoids (LD, unpublished data). This seems to be an example of parallel development of the ultrastructural trait in different lineages of decabrachian coleoid cephalopods.

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