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.

Larisa A. Doguzhaeva [larisa.doguzhaeva@nrm.se], Department of Palaeozoology, Swedish Museum of Natural History, P. O. Box 50007, SE-104 05 Stockholm, Sweden;
Patricia G. Weaver [trish.weaver@gmail.com], North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601-1029, USA;
Charles N. Ciampaglio [chuck.ciampaglio@wright.edu], Department of Geology, Wright State University-Lake Campus, 7600 State Route 703, Celina, OH 45822, USA.

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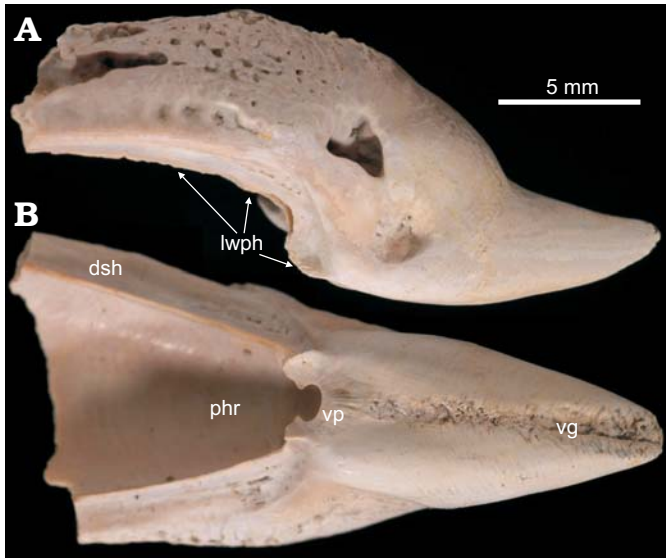
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Fig. 1. Cuttlebone of Late Eocene sepioid cephalopod *Mississaepia missississippiensis* Weaver, Dockery III, and Ciampaglio, 2010 from Mississippi, USA with a missing anterior-most part (MGS 1945), in left lateral (**A**) and ventral (**B**) views.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

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 β-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 (Danian), *Belocurta* Avnimelech, 1958 (Montian), *Belosaepia* Voltz, 1830 (Ypresian/Bartonian), *Anomalosaepia* Weaver and Ciampaglio, 2003 (Ypresian/Bartonian), *Mississaepia* Weaver, Dockery, and Ciampaglio, 2010 (Bartonian/Priabonian), *Hungarosepia* Doyle, Donovan, and Nixon, 1994 (Luteranian/Priabonian), and *Sepia* Blainville, 1927 (Oligocene?–Helvetian–Recent). Phragmocone structure and ultrastructure, and shell material composition in extinct sepiids is poorly known. Cuttlebone

morphology of early ontogenetic stages was illustrated from *Ceratisepia* (Meyer 1993) and *Belosaepia* (Yancey et al. 2010). A bimineralic, aragonite/calcite, composition of the cuttlebone was recently suggested for *Anomalosaepia* (Yancey and Garvie 2011). Preservation of organics consistent with β-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. mississipiensis* 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 mural 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-
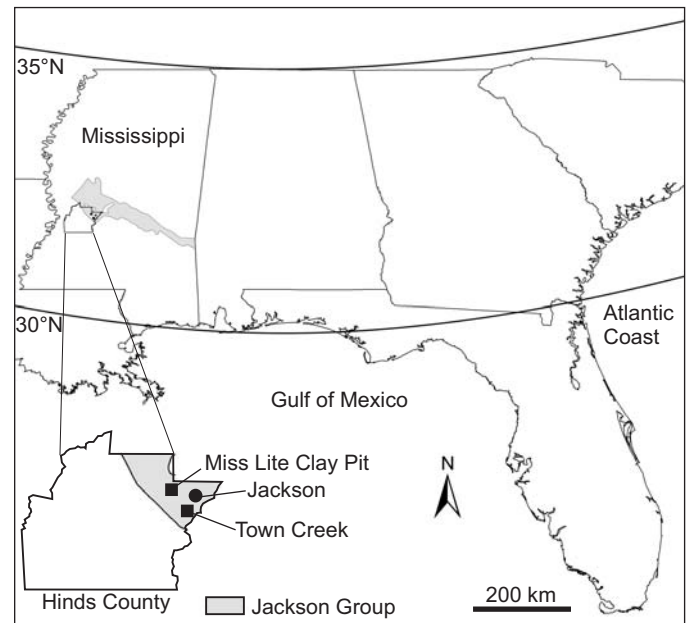

Fig. 2. Sketch map showing the location of the Yazoo Clay, the Miss Lite Clay Pit in the northwest corner of the town of Jackson and the Moodys Branch Formation, Town Creek locality south of Jackson in Hinds County, Mississippi, USA.

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 cerroauzulensis*, *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.
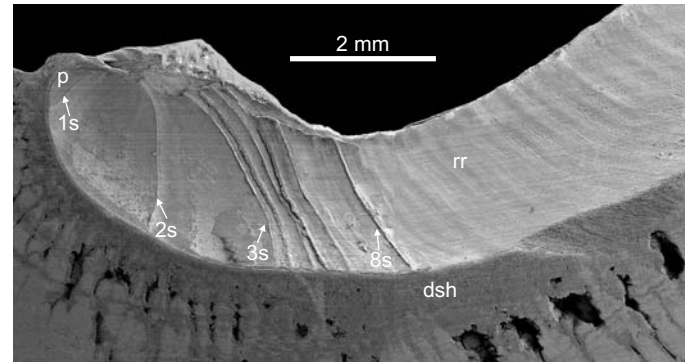

Fig. 3. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010 (MGS 1948); late Eocene, Mississippi, USA. Median cuttlebone section to show loosely mineralized dorsal shield (bottom), small cup-like protoconch covered by thin layer of the dorsal shield (on the left) and curved hollow phragmocone exhibiting two long chambers and next short chambers; to the right from the last preserved (eighth?) septum inner surface of phragmocone is transversely ribbed. Abbreviations: dsh dorsal shield; p, protoconch; rr, ribbed relief of the inner surface of the phragmocone; 1s, 2s, 3s, 8s, first, second, third, eighth septa.
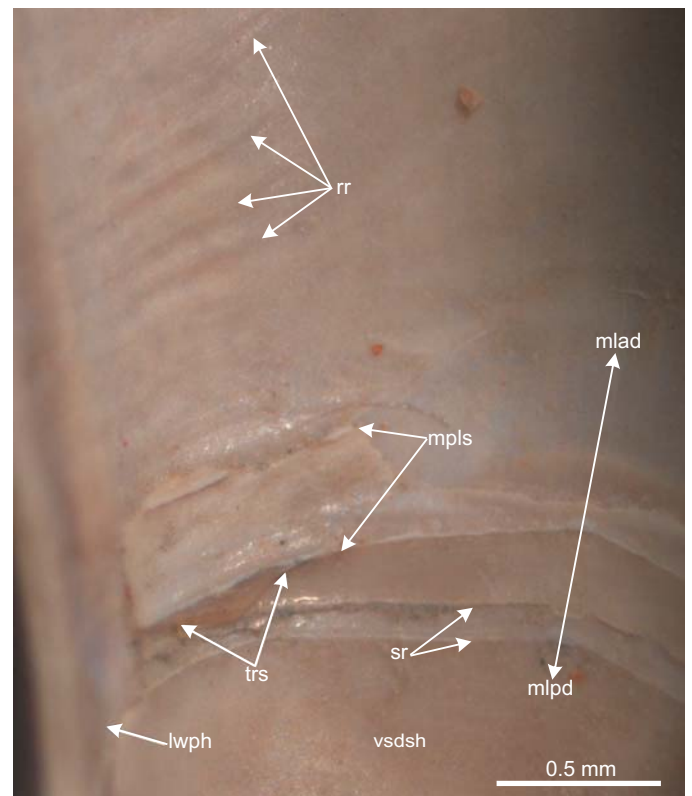

Fig. 4. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010 (MGS 1945); late Eocene, Mississippi, USA. Inner surface of the phragmocone exposing a small fragment of brownish transparent septum preserved. Abbreviatons: lwph, lateral wall of the phragmocone; mlad, median line indicating apertural direction; mlpd, median line indicating posterior direction; mpls, mural part of last septum; rr, ribby relief; sr, septal ridge; trs, transparent fragmentary septum; vsdsh, ventral side of dorsal shield.

The components were mixed for 20–30 min. in an ultrasonic heating machine at 40°C, then filtered. The specimens were
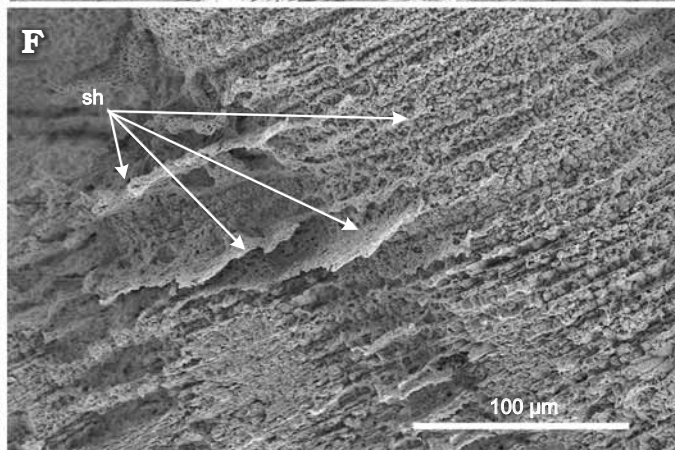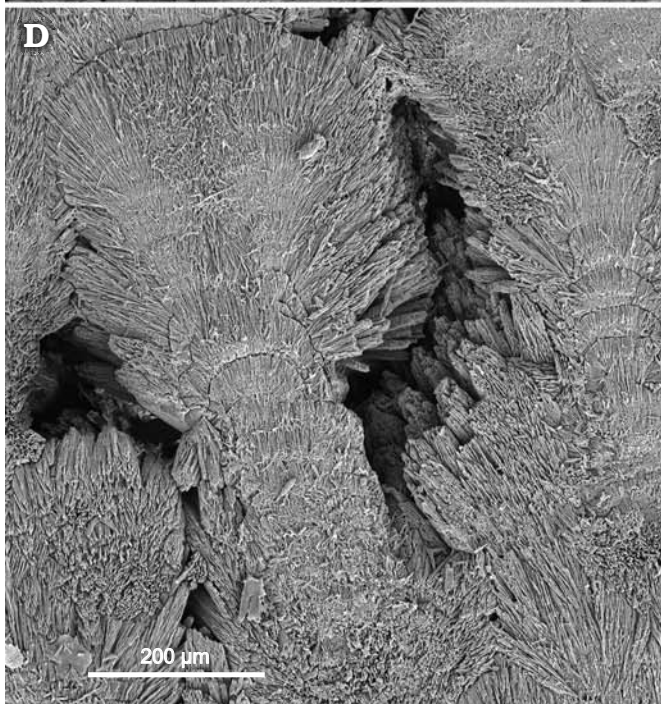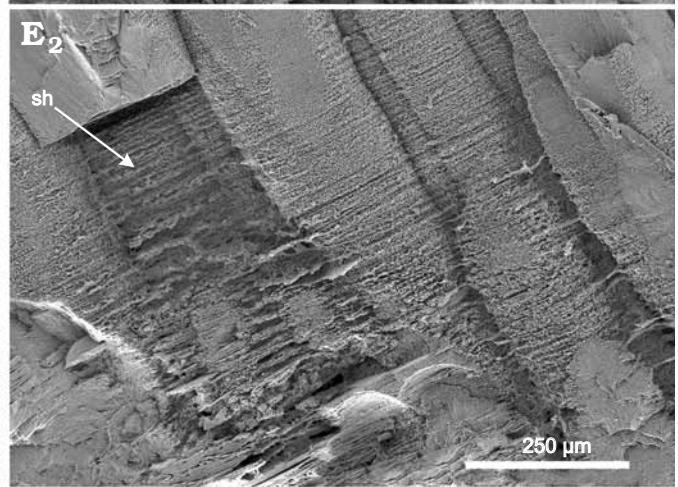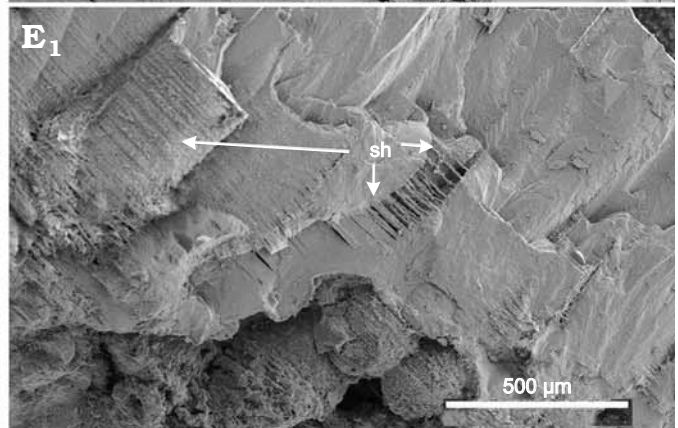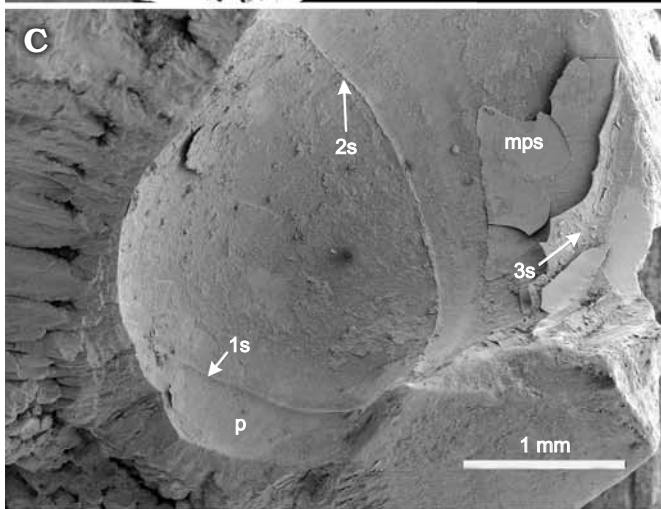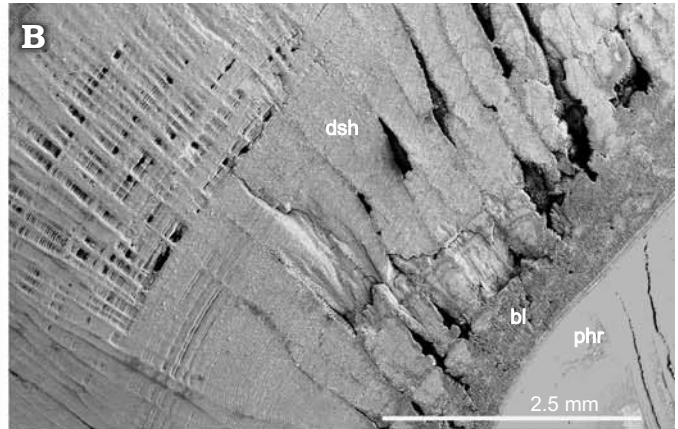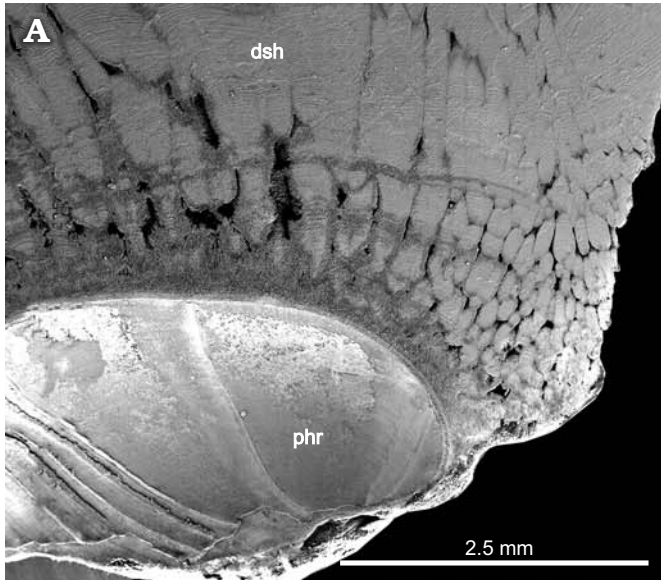
etched for 10–15 min. at 30–40°C, watered, dried, glued on stubs and coated with gold. The specimens were examined using a Hitachi S-4 300 Scanning Electron Microscope (SEM) with an attached Energy Dispersive Spectrometer (EDS) at the Swedish Museum of Natural History, Stockholm. Chemical analyses were 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 *Missi-ssaepia*.—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 ventro-lateral wall in several specimens show abrupt irregular terminations (Figs. 1, 9A$_2$, A$_3$; 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, E$_1$). 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 colour-less septa preserved closest to the mural parts of septa and mural ridges (Figs. 4, 6B, E$_1$, 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. 6E$_2$, 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. 7A$_1$, 8A$_1$, B, D). Siphuncle is ventro-marginal (Fig. 6C, E$_1$). Septal necks are flattened, about 2/3 chamber length, formed by lamello-fibrillar nacre (Figs. 6E, 7A$_2$–A$_4$). 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, 6A$_1$, C, E$_1$). 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. 6A$_1$, C, 7A$_1$, A$_2$). Spherulites consist of needle-like crystals arranged in growth rings separated by phosphatised sheets (Fig. 5D–F). The sheets continue between the spherulites (Fig. 5E$_2$). 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. 9A$_3$). 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 *Missi-ssaepia* 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 silicified tissue preserved along a contact between the cono-


← Fig. 5. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA. **A**. MGS 1948, medial section through the apical part of cuttlebone showing posterior portion of dorsal shield adjacent to the protoconch and first chambers of the phragmocone. **B**. MGS 1948, spherulitic-prismatic ultrastructure and lamination parallel to the outer surface of dorsal shield. **C**. MGS 1956, medial section through the apical part of cuttlebone showing posterior portion of dorsal shield adjacent to the protoconch (bottom) and first chambers of the phragmocone; fractured ventral plate is adjacent to the protoconch (bottom, right corner); the fractured forth septum with adjacent split mural part of the previous septum are preserved (to the right). **D**. MGS 1948, two spherulites of the dorsal shield showing growth increments and needle-like crystals. **E**. MGS 1956, thin parallel membranes within spherulitic-prismatic dorsal shield. **E$_2$**. Close-up of E$_1$ to show that membranes continue through the space between neighbouring spherulites. **F**. MGS 1956, a set of sheets in spherulitic-prismatic dorsal shield. Abbreviations: bl, basal layer; dsh, dorsal shield; mps, mural part of septum; p, protoconch; phr, phragmocone; sh, phosphatised sheet of dorsal shield; 1s, 2s, 3s, first, second, and third septa of the phragmocone.
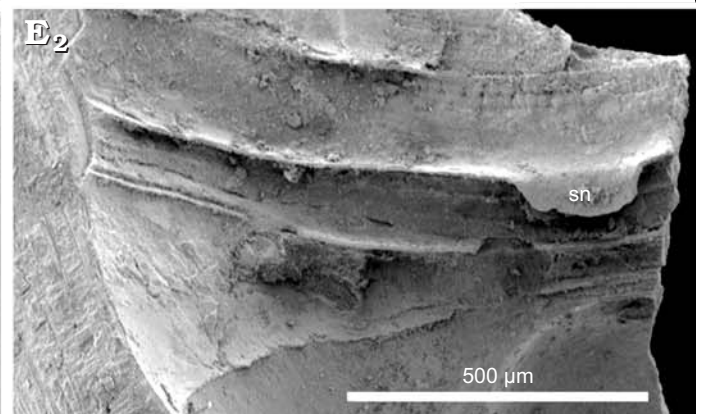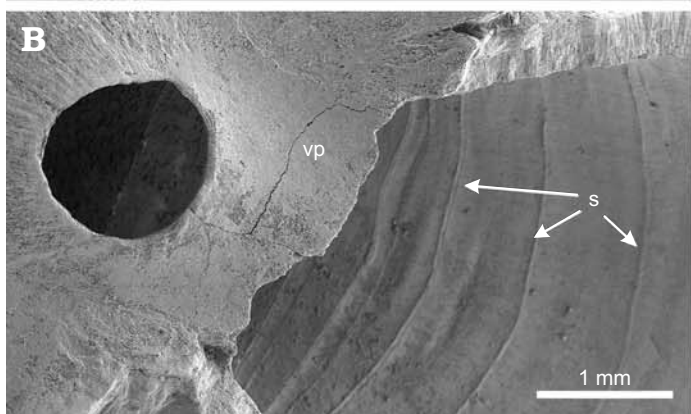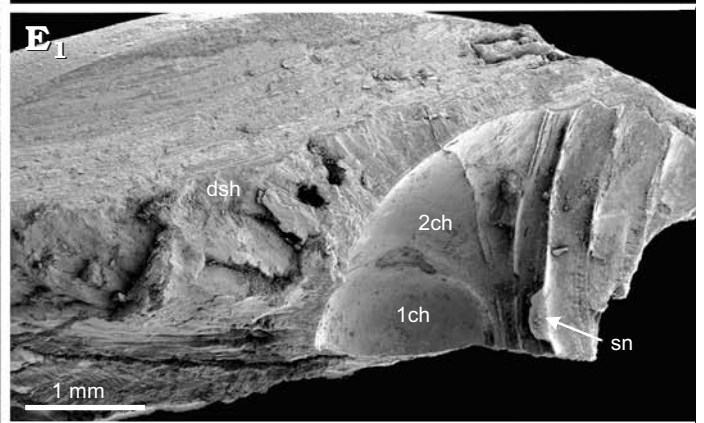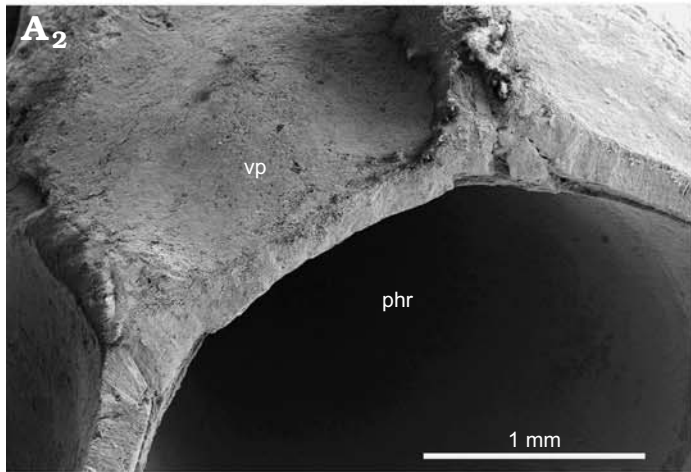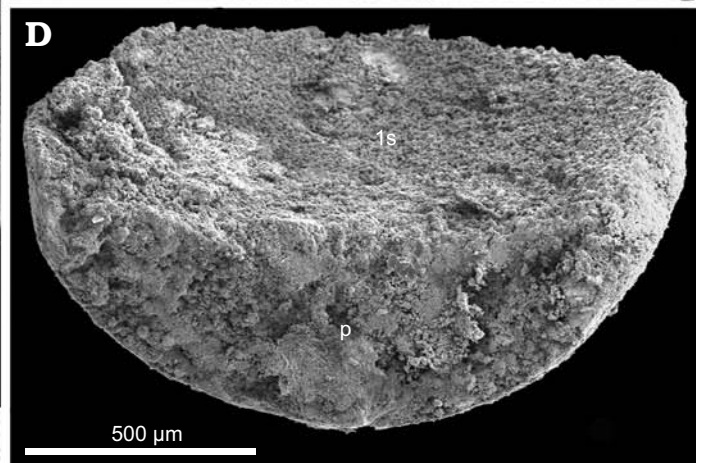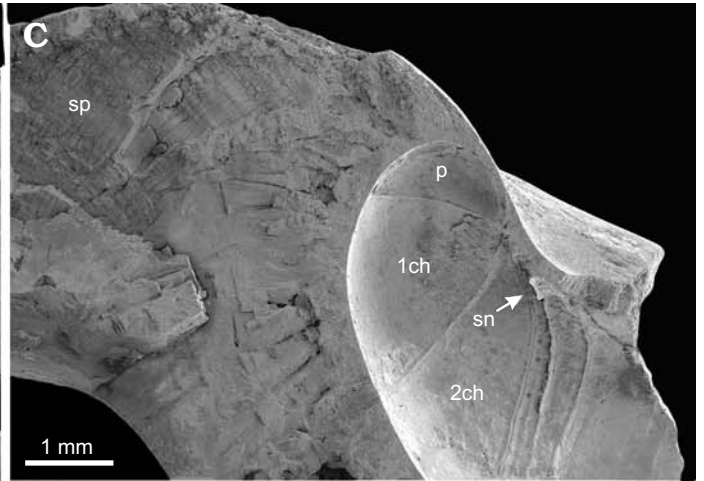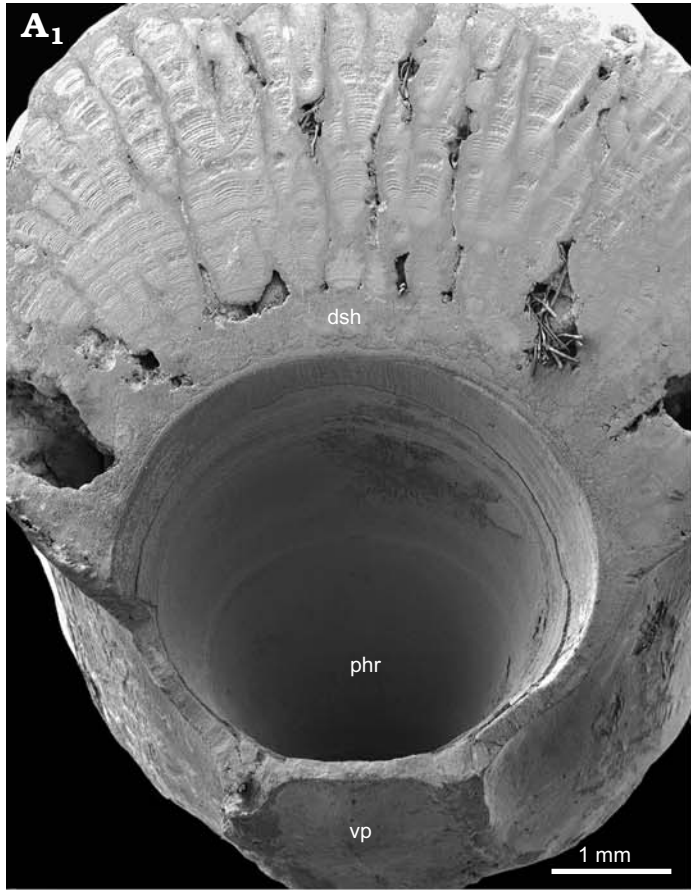
theca and septum (Fig. 11A), the whitish-pinkish conotheca, the whitish-grey material of septal ridges, the membranes between the growth increments of the dorsal shield (Fig. 11B), the whitish-grey material of dorsal shield (Fig. 11C), the peripheral zones of spherulites in the dorsal shield, the infilling 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.

Diagnosis.—Dorsal shield posteriorly stout, convex, with ventral plate and thin lateral extensions. Spine with ventral groove. Protoconch sub-hemispherical. Phragmocone with ventral wall in apical portion, possibly extending anteriorly. Siphuncle ventro-marginal. Septa mainly organic, possibly chitinous, coated with a film of lamello-fibrillar nacre. Mural parts of septa as long as chamber length. Septal ridges pro-

Table 1. Chemical composition of septum, mural part of septum, septal neck, and septal ridge of *Mississaepia* (EDS data).

Element	Septum (Fig. 10B)	Mural part of the septum (Fig. 11A)	Septal neck	Septal ridge
Carbon	5.08–13.08	6.67–17.10	10.34–10.91	6.13–13.02
Nitrogen	0.61–4.53	2.48–4.57	no data	no data
Oxygen	19.06–52.43	28.78–50.61	47.81–52.41	32.09–55.56
Fluorine	0.19–4.53	2.69	0.19	no data
Sodium	0.22–0.65	0.06–0.23	no data	no data
Magnesium	0.05–0.42	0.03–0.93	0.05–0.23	0.12–0.66
Aluminium	0.17–1.80	0.05–4.35	0.36	2.28–4.11
Silicon	0.1–3.23	0.51–3.87	no data	5.27–10.21
Phosphorus	7.15–11.87	2.10–12.87	no data	no data
Potassium	0.37	0.65–0.92	no data	no data
Calcium	21.72–38.81	12.87–45.16	35.55–38.81	23.52–60.35
Iron	0.16–8.89	0.91–8.06	0.16–3.85	1.71–4.64
Zinc	0.07	no data	no data	no data
Strontium	0.15–1.20	0.8–3.17	0.54–1.20	0.36–3.45
Chlorine	no data	0.76–26.93	no data	no data

nounced. First septum perpendicular to protoconch axis. Second and third septa strongly inclined. Subsequent septa nearly perpendicular to phragmocone axis. Third chamber approximately ten times shorter than first two chambers. Septal necks flattened, broad about 2/3 chamber length.

Table 2. Chemical composition of dorsal shield of *Mississaepia* and *Sepia* (EDS data).

Element	*Mississaepia*: dorsal shield (Fig. 10C)	*Mississaepia*: membranes of dorsal shield (Fig. 11B)	*Mississaepia*: infillings between spherulites	*Sepia*: dorsal shield (Fig. 11D)
Carbon	5.11–12.76	5.00–18.97	5.31–22.35	38.88
Nitrogen	1.27–2.41	2.24	no data	1.47–4.91
Oxygen	42.25–54.18	26.07–49.84	29.65–41.85	27.49
Fluorine	no data	4.84–6.84	no data	no data
Magnesium	0.02–0.57	0.10–0.35	0.16–1.60	1.54
Phosphorus	no data	2.66–8.67	no data	no data
Chlorine	no data	0.38	no data	11.28
Silicon	1.75–22.46	no data	no data	no data
Sulphur	12.58–28.92	no data	11.45–13.02	no data
Aluminium	7.50	no data	no data	no data
Sodium	0.07–0.36	0.17–1.47	0.53	2.57
Potassium	0.16	no data	no data	no data
Calcium	7.38–53.05	22.56–57.35	6.13–14.11	10.15
Iron	0.38–30.87	0.36–7.85	32.85–38.80	no data
Strontium	0.36	0.32–3.57	3.03	3.18

← 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.
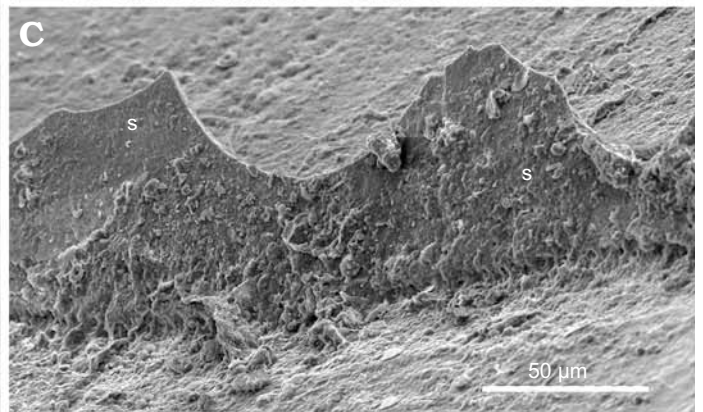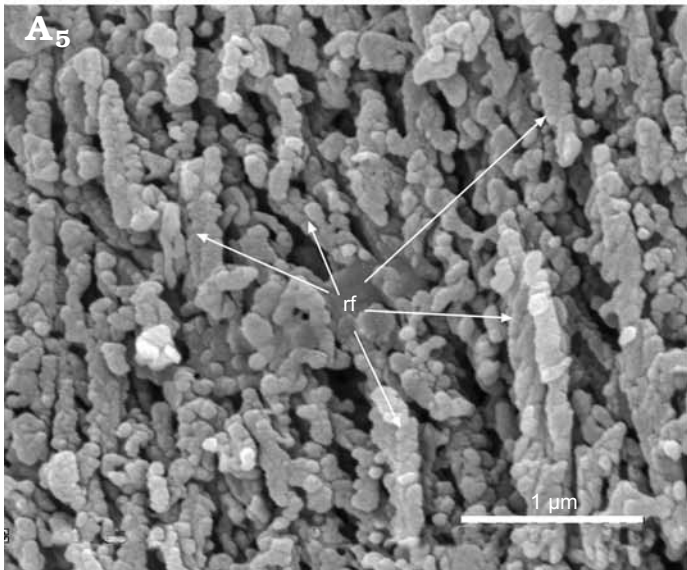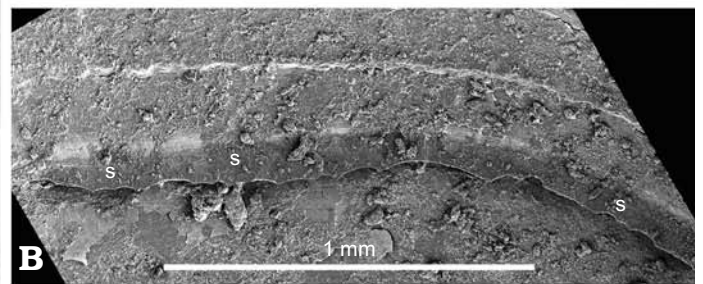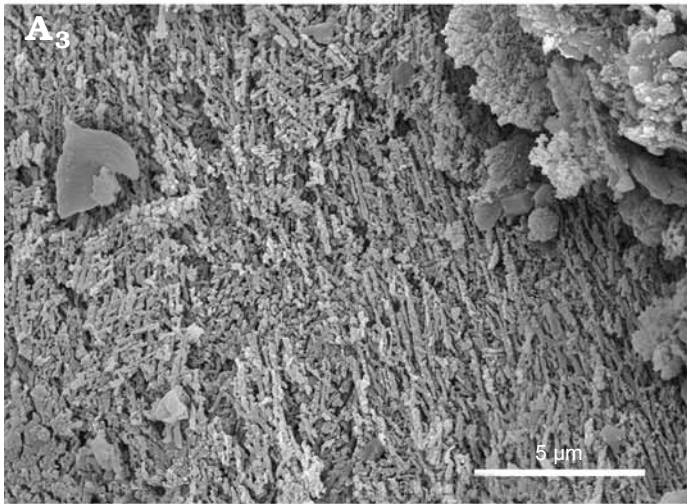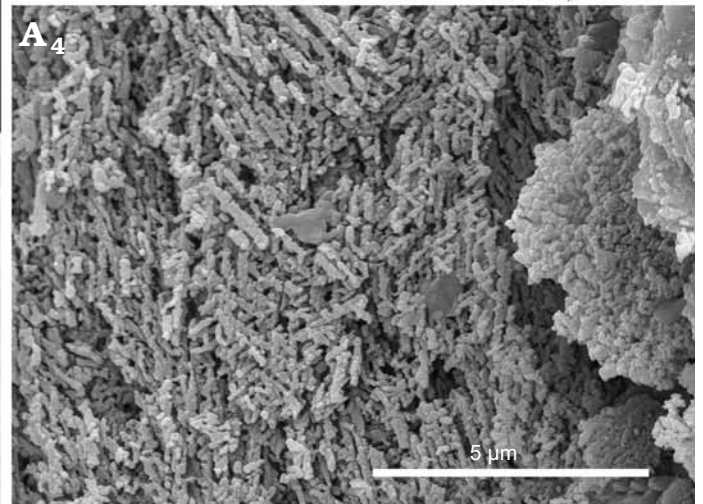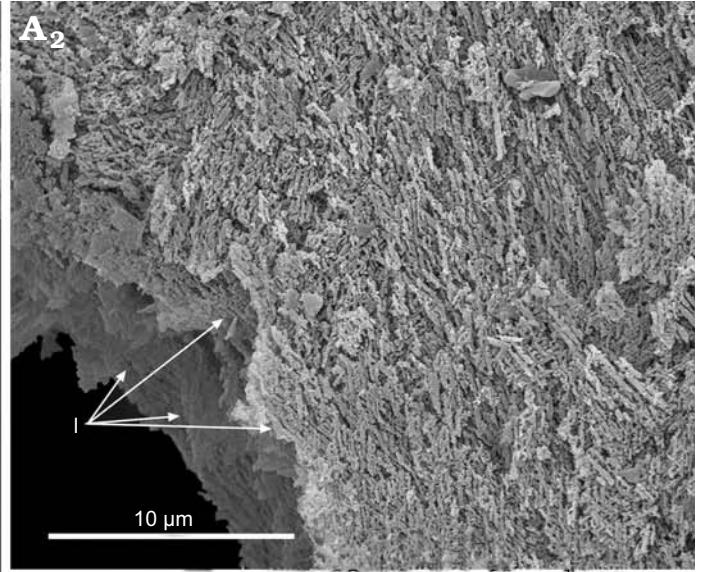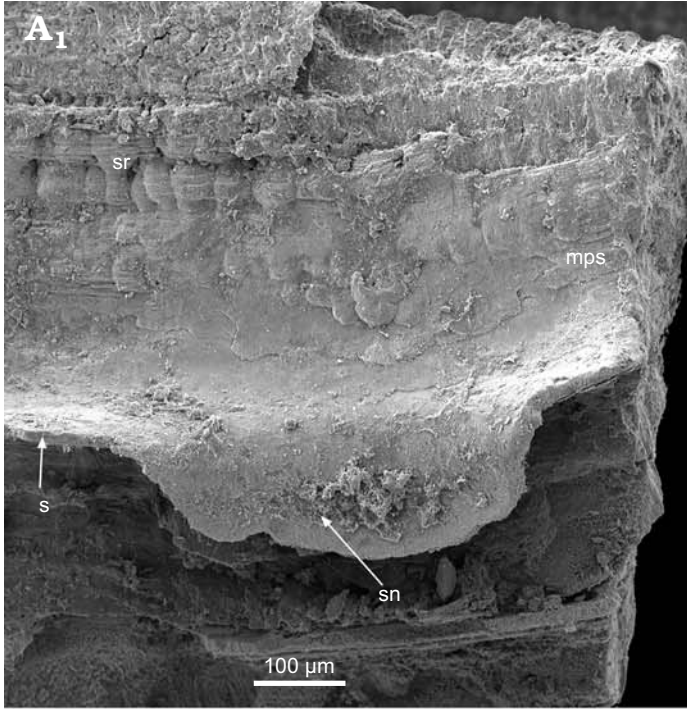
Table 3. Comparative data on extreme recorded values (% of total weight) of carbon, nitrogen, oxygen, sodium, magnesium, silica, sulphur, chlorine, potassium, phosphorus, calcium, iron, strontium of the dorsal shield of *Sepia* (1) and different parts of the cuttlebone of *Mississaepia mississippienses* (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.

	C	N	O	Na	Mg	Si	S	Cl	K	P	Ca	Fe	Sr
1	38.9	4.9	27.5	2.6	1.5	0	0	11.3	0	0	10.1	0	3.2
2	13.1	4.5	52.4	0.6	0.4	3.2	0	0	0.4	11.9	38.8	8.9	1.2
3	17.1	5.6	50.6	0.2	0.9	16.9	0	26.9	0.9	12.9	45.1	8.1	3.2
4	10.1	0	52.4	0	0.2	0	0	0	0	0	38.8	3.9	1.2
5	13.0	0	55.6	0	0.7	0	0	0	0	0	60.4	4.6	3.5
6	9.7	2.3	53.1	0.2	0	0	0	0	0	0	41.2	2.7	0.7
7	12.8	2.4	54.2	0	0.6	22.5	28.9	0	0.2	0	53.1	30.8	4.6
8	18.8	2.2	49.8	1.5	0.4	0	0	0.4	0	8.7	57.4	7.9	3.6
9	22.4	0	41.6	0.5	1.6	0	13.0	0	0	0	14.1	38.8	3.0

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 *Ceratisepia* and in *Spirula*. Conotheca with ventrolateral extension in early ontogenetic stages as opposed to *Sepia* that has no ventro-lateral extention 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, E_1); siphuncle ventro-marginal and septal necks about 2/3 chamber length (Figs. 6C, E, $7A_1$). 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 *Mississaepia* 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 mississaepid 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 *Mississaepia* 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 *Mississaepia*. 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 *Mississaepia*. Nitrogen signals in the approximately 35 mya cuttlebones likely indicate levels of organics approaching—or even surpassing—that of extant

← Fig. 7. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA. **A**. MGS 1944, close-up of Fig. 6C to show retrochoanitic septal neck and adjacent mural part of septum. A_2–A_4. Close-up of A_1, lamello-fibrillar nacre of septal neck and mural part of septum distinguished by criss-cross pattern of overlapped lamellas. A_5. Close-up of A_4 to show short bundles of fibres; the rods show grains of calcium phosphate that is a result of diagenetic phosphatization (see Fig. 10A, B). **B**. MGS 1963, band-like preserved portion of broken septum. **C**. MGS 1963, enlarged fragment of preserved portion of septum to show angular and rounded breakage that is characteristic of rigid, possibly chitinous, material of septum. Abbreviations: mps, mural part of septum; rf , rod-like fibre of lamello-fibrillar nacre; s, partial septum; sn, septal neck; sr, septal ridge.
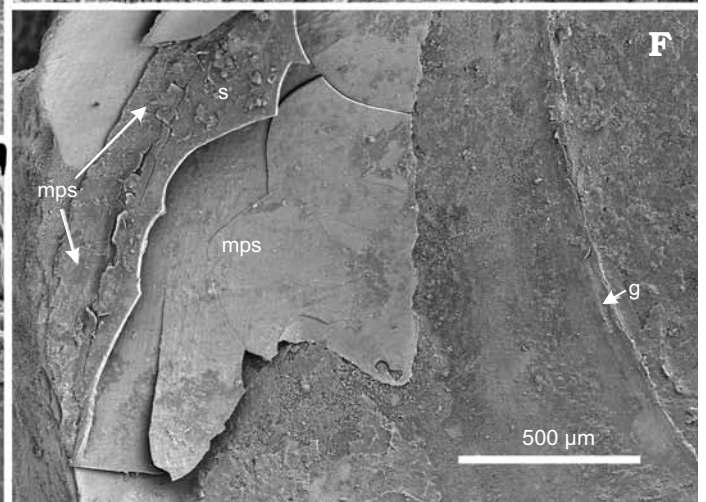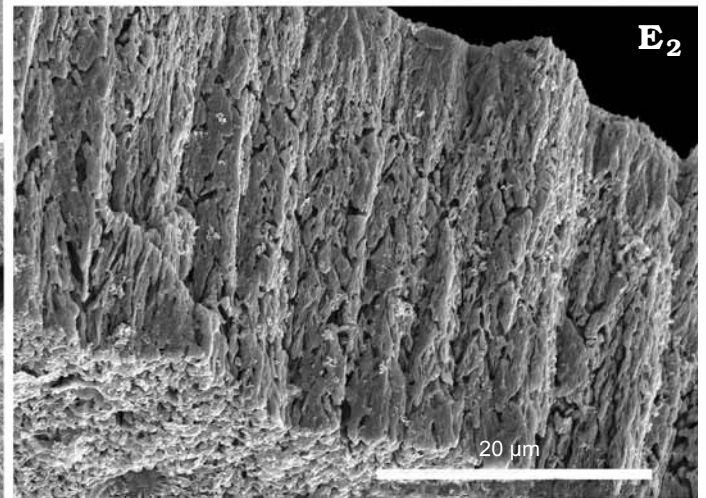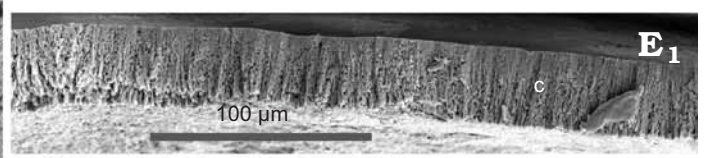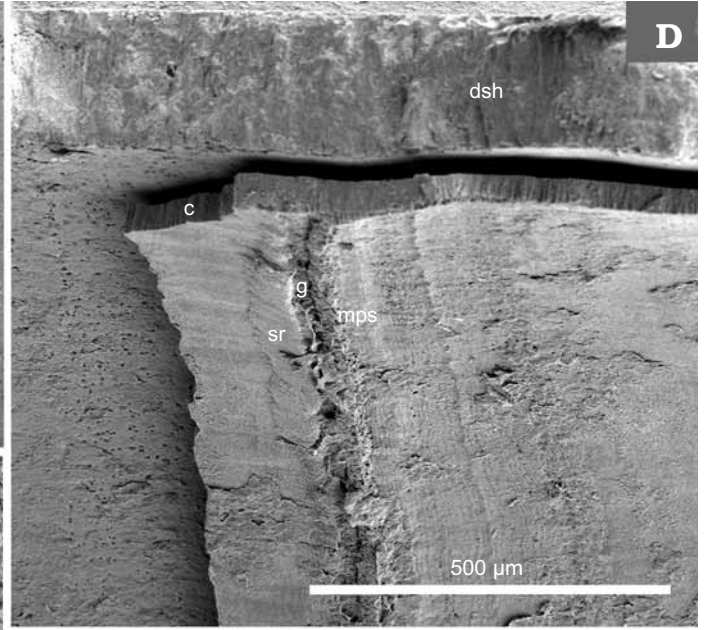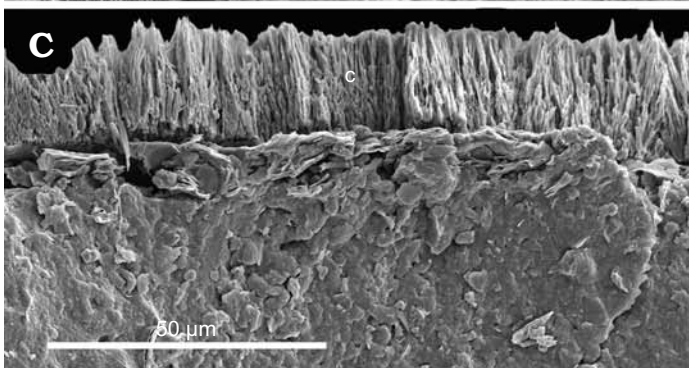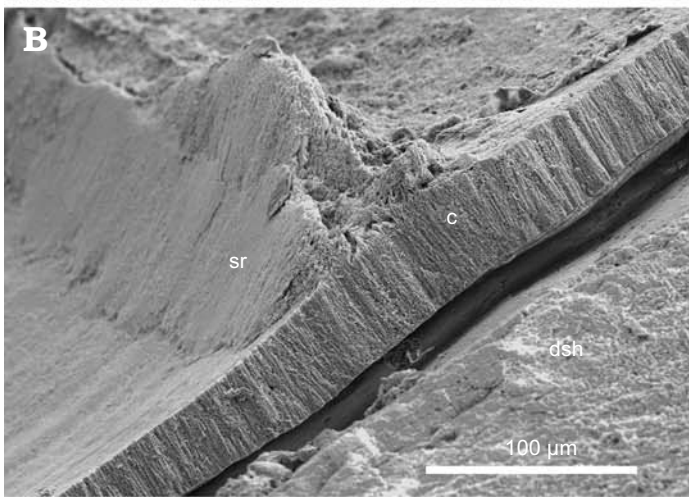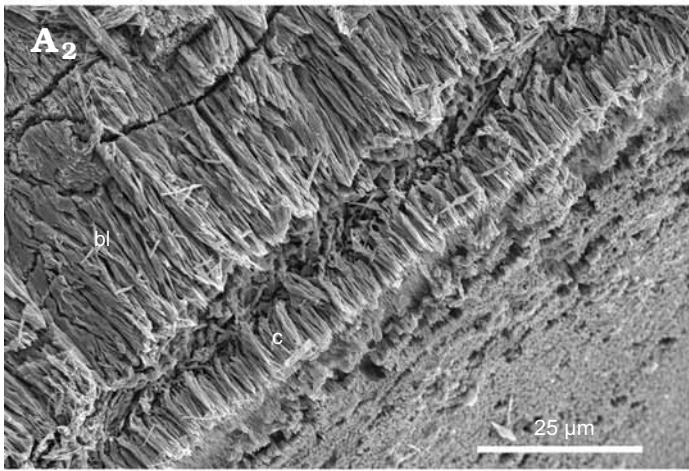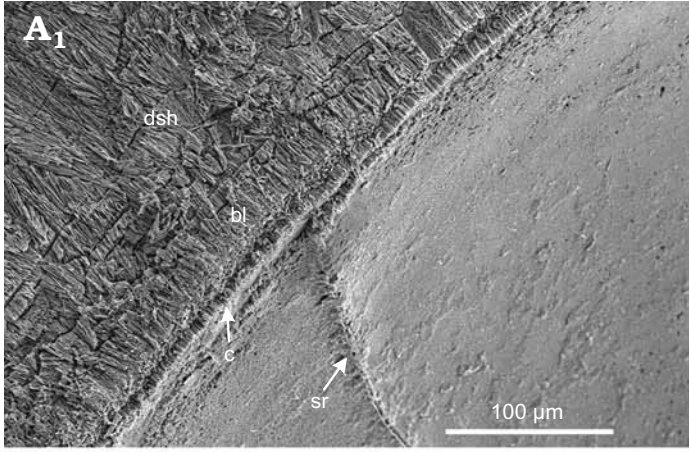
Sepia cuttlebones. In *Sepia* the organic laminas formed by β-chitin-protein complex are inter-layered with the aragonite and constitute about 10% of cuttlebone weight. In the organic laminas the average contents of the elements are: C, 15.36%; O, 0.68%; Na, 1.0%; Mg, 0.133%; N, 1.42%; K, 0.26%; Fe, 0.03%; and Sr, 0.28% (Florek et al. 2009).

Phosphorus was recorded from the sheet-like structures in between aragonite spherulites in the dorsal shield of *Mississaepia* (Fig. 11B, Table 3; Weaver et al. 2011: fig. 3A, B). Similarly located organic laminas are present in the dorsal shield of *Sepia* (Weaver et al. 2011: fig. 3C). Based on this similarity the phosphatised sheet-like structures are considered to be organic in vivo but phosphatised due to activity of P-accumulating bacteria post-mortem. In *Mississaepia* signals 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*.
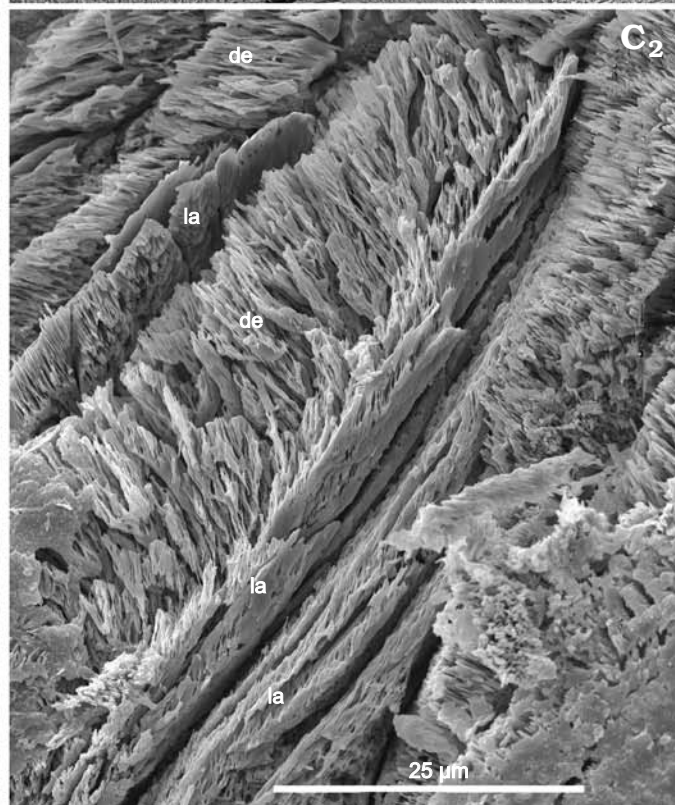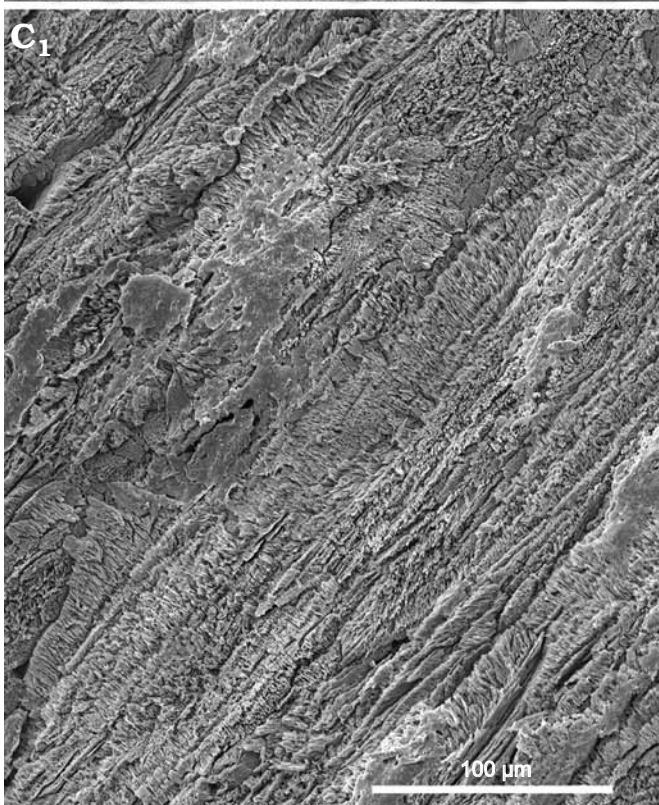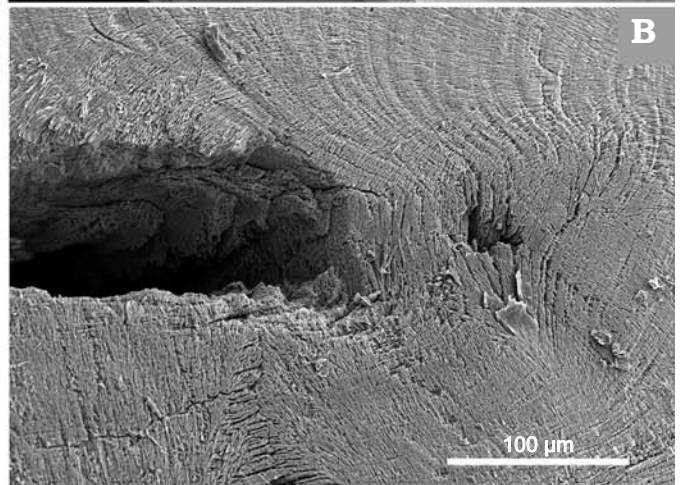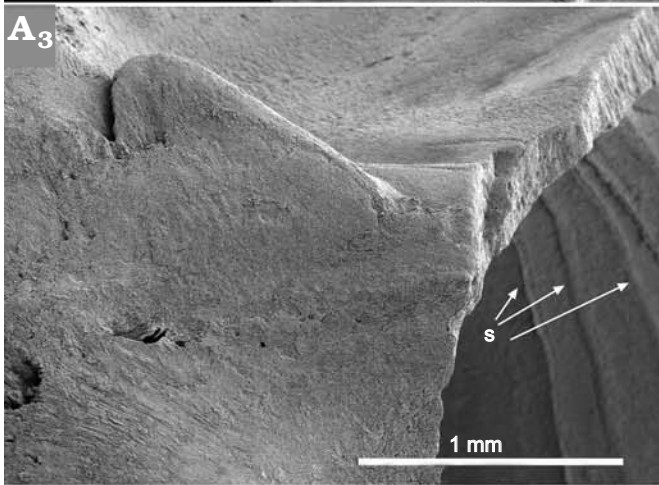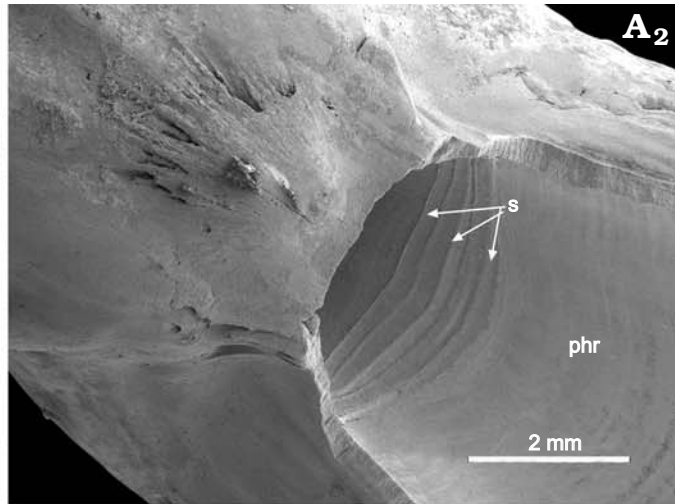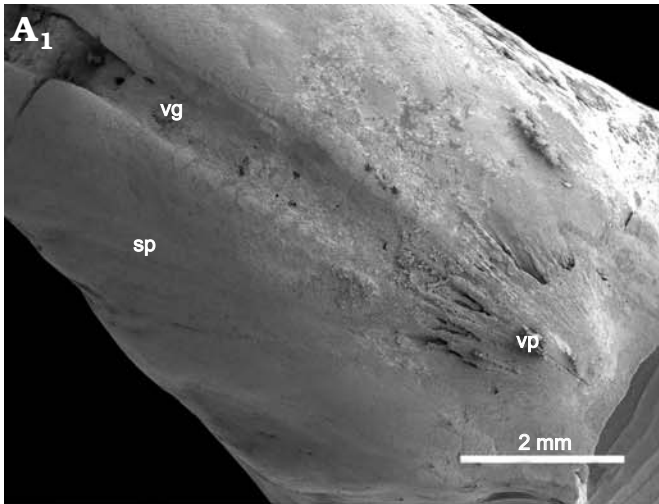
Inorganic-organic composition of the cuttlebone of *Mississaepia*, revealed here by light microscope, and SEM and EDS analyses was recently confirmed by discovery of the degraded organics consistent with β-chitin in the cuttlebones of this taxon by molecular techniques (Weaver et al. 2011). Chitin composition of septa of *Mississaepia*, revealed here by light microscope was not analyzed 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

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← Fig. 8. Sepioid cephalopod *Mississaepia mississippiensis* Weaver, Dockery III, and Ciampaglio, 2010; late Eocene, Mississippi, USA. **A**. MGS 1948. A_1. Longitudinal section to show thin prismatic conotheca, basal prismatic layer of dorsal shield and spherulitic-prismatic bulk of dorsal shield (left top corner). A_2. Close-up of A_1 to show distinctly separated prismatic conotheca and basal prismatic layer of dorsal shield. **B**. MGS 1944, uni-layered prismatic conotheca and mural parts of septum on its inner surface. **C**. MGS 1946, prismatic conotheca. **D**. MGS 1944, inner surface of phragmocone showing a gap between the mural part of septum (left) and mural ridge of septum (right), the gap indicates position of septum where it is broken. **E**. MGS 1944, loosely mineralized basal part of dorsal shield on ventral side of phragmocone. E_2. Close-up of E_1 to show that inner portion of the dorsal shield is loosely mineralized while its outer portion is more compact. **F**. MGS 1956, inner surface of phragmocone showing remains of broken septum (left) and split mural parts of next missing septum (right). Preserved parts of septum show sharp and rounded edges that are characteristic of rigid chitin material. Abbreviations: bl, basal layer; c, conothec; dsh, dorsal shield; g, gap between septal ridge and mural part of septum; mps, mural part of septum; p, protoconch; sr, septal ridge.

Element	Weight %
C K	7.67
N K	5.16
O K	28.78
Na K	0.15
Mg K	0.42
P K	12.87
Ca K	43.24
Fe L	0.91
Sr L	0.80
Totals	100.00

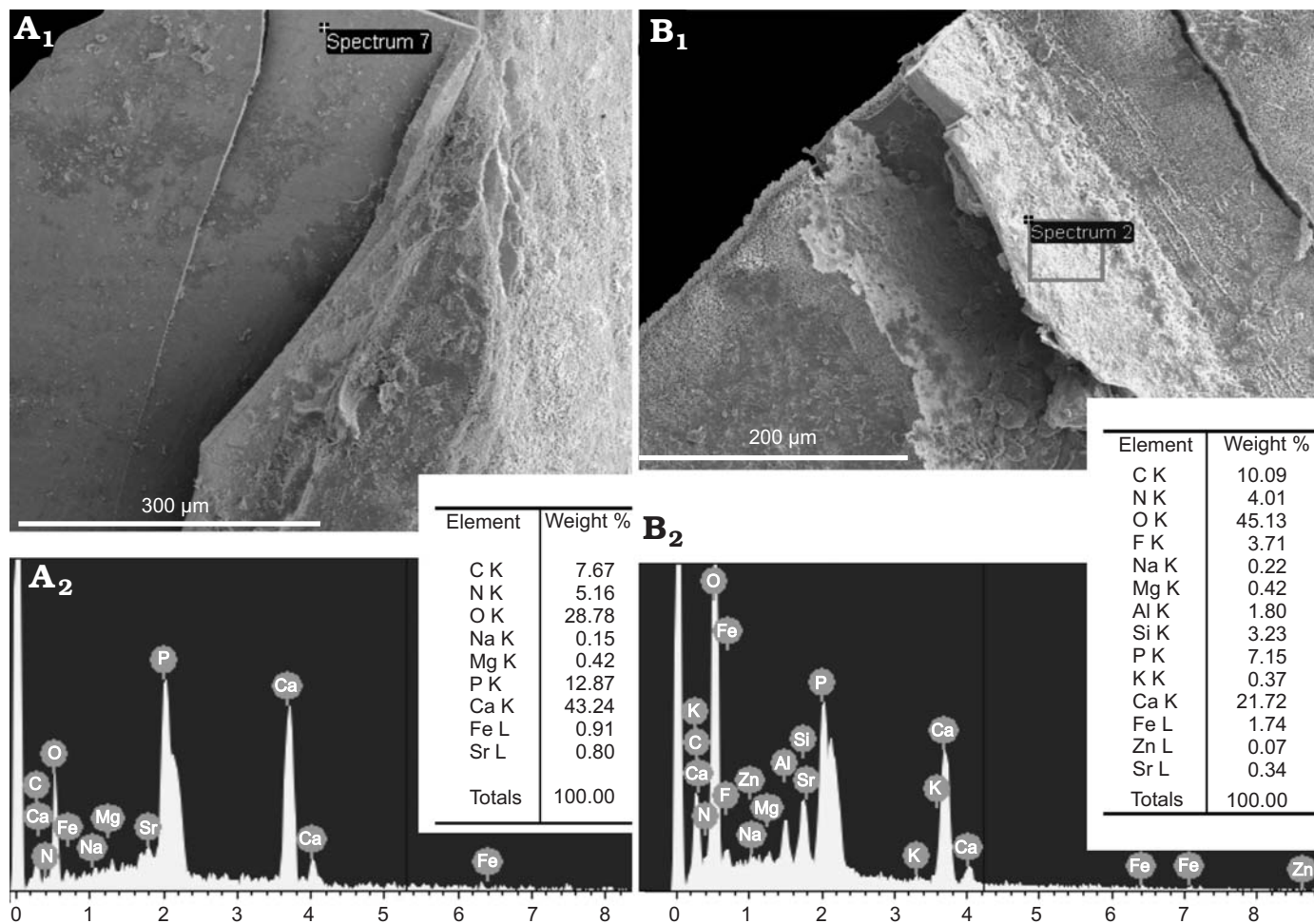| Element	Weight %
C K	10.09
N K	4.01
O K	45.13
F K	3.71
Na K	0.22
Mg K	0.42
Al K	1.80
Si K	3.23
P K	7.15
K K	0.37
Ca K	21.72
Fe L	1.74
Zn L	0.07
Sr L	0.34
Totals	100.00

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 (A_1, B_1); EDS data to show chemical composition (A_2, B_2); in both cases nitrogen indicates organic ingredient and phosphorus indicates diagenetic phosphatization of apparently originally organic material.

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 Mississaepiidae.—Mississaepiidae 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 *Mississaepia* the septa are largely chitinous, with only a film of lamello-fabrillar 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. A_2. Close-up of A_1; the hollow phragmocone and ventral plate above it. A_3. Enlarged detail of A_2; 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. C_2. Close-up of C_1; 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.
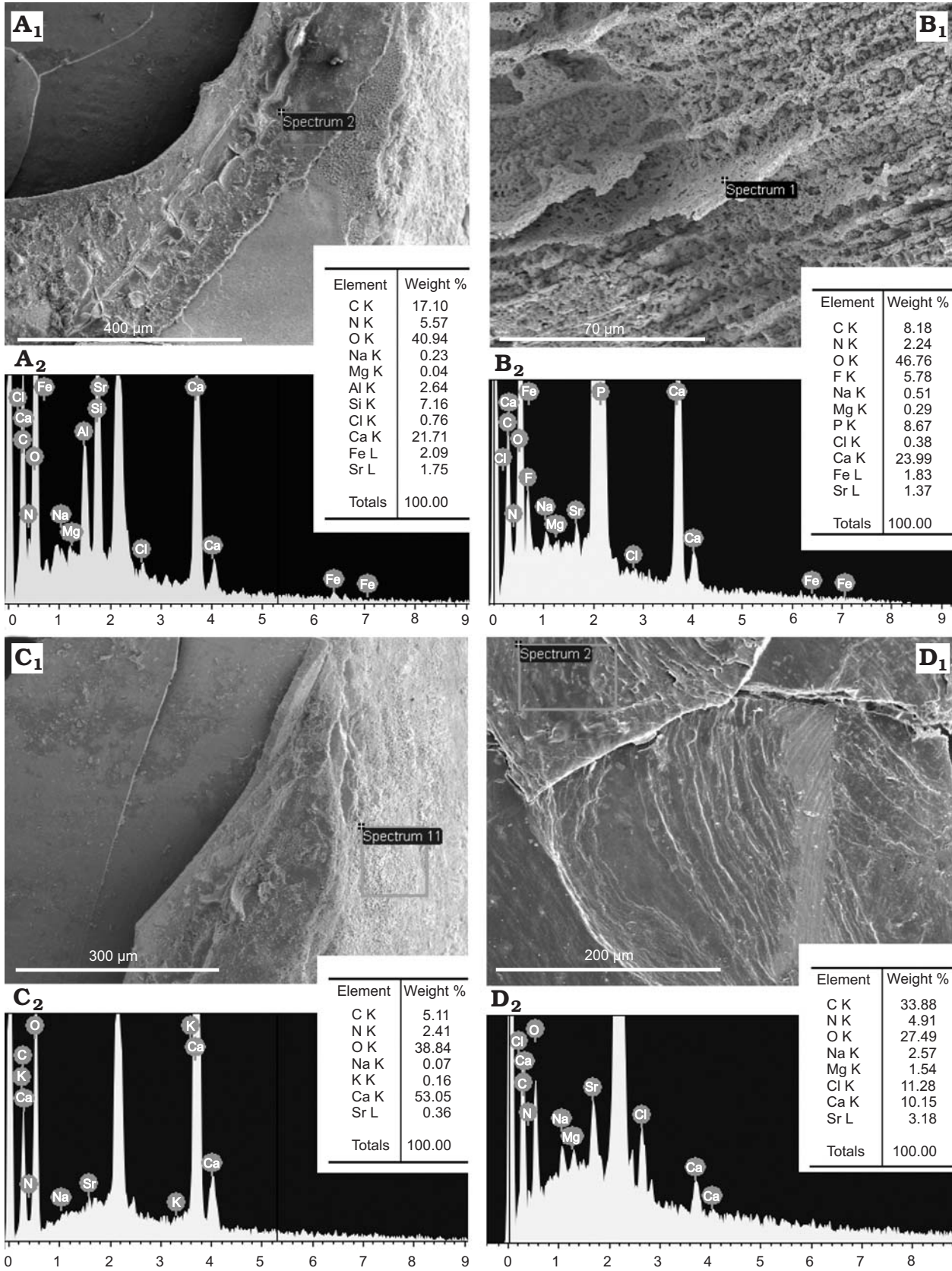
Element	Weight %
C K	17.10
N K	5.57
O K	40.94
Na K	0.23
Mg K	0.04
Al K	2.64
Si K	7.16
Cl K	0.76
Ca K	21.71
Fe L	2.09
Sr L	1.75
Totals	100.00

Element	Weight %
C K	8.18
N K	2.24
O K	46.76
F K	5.78
Na K	0.51
Mg K	0.29
P K	8.67
Cl K	0.38
Ca K	23.99
Fe L	1.83
Sr L	1.37
Totals	100.00

Element	Weight %
C K	5.11
N K	2.41
O K	38.84
Na K	0.07
K K	0.16
Ca K	53.05
Sr L	0.36
Totals	100.00

Element	Weight %
C K	33.88
N K	4.91
O K	27.49
Na K	2.57
Mg K	1.54
Cl K	11.28
Ca K	10.15
Sr L	3.18
Totals	100.00

Fig. 11. Cuttlebone of sepioid cephalopod *Mississaepia 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 (A_1-D_1); EDS data on chemical composition shows presence of: A_2, high content of nitrogen indicating organic ingredient in silicified tissue preserved along contact between conotheca and septum; B_2, nitrogen indicating organic ingredient of phosphatised sheet within the dorsal shield; C_2, D_2, 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 lamellofibrillar nacre is an ultrastructural characteristic of septa of *Spirula* rather than of *Sepia*. Therefore, we think that Mississaepiidae 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 *Mississaepia* provide additional support for Naef's (1921) view on common origin of *Sepia* and *Spirula* that was based on similar phragmocone morphology in these two taxa. *Mississaepia*, *Sepia*, and *Spirula* have a phragmocone 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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