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REDESCRIPTION OF *ANOMALOSAEPIA* (CEPHALOPODA: COLEOIDA): A SEPIOID WITH A BIMINERALIC CALCITE AND ARAGONITE SKELETON

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ABSTRACT—Redescription of the genus *Anomalosaepia* shows that the anomalous characters reported as defining the genus are partly preservational artifacts resulting from dissolution of aragonite from a skeleton composed of both calcite and aragonite. Thus, the presence of a slit-shaped opening and canal-like cavity in the skeleton is not supported. The skeleton of *Anomalosaepia* is composed of subequal amounts of aragonite and calcite, with an inner layer composed of radial-prismatic and fan-radial aragonite and an outer layer of elongate, non-prismatic calcite crystals secreted by the animal. The calcite microstructure has not been previously described. A new family, Anomalosaepiidae, is established and one new species, *A. parmula*, described. The species *A. mariettani* and *A. andreanae* are synonomized with *A. alleni*. The species *A. jeletzkyi* is valid and *A. vernei* is probably valid, but needs more documentation. Examination of North American and European specimens reveals that a bimineralic composition is a characteristic feature of species in the families Anomalosaepiidae and Belosaepiidae and implies that, in general, sepioids have a bimineralic skeleton with some calcite.

INTRODUCTION

ERECTION OF the belosaepiid genus *Anomalosaepia* by Weaver and Ciampaglio (2003), described as having skeletal characters much different from those present in other sepioids, presents a challenge to the understanding of ancient sepioids and sepioid relationships. The most unusual character described for the genus is the identification of a slit-like opening on the posterior end of the skeleton (Fig. 1.1) and interpretation that this is part of an elliptical cavity (the "canal" of Weaver and Ciampaglio) extending through the interior of the skeleton from posterior part of the alveolus to the posterior terminus. If present, this canal-like cavity would have contained a strand of living tissue extending posteriorly through the length of the skeleton. There is nothing comparable to this in other sepioid or coleoid skeletons so if verified the presence of this character would leave *Anomalosaepia* with uncertain relationship within the Order Sepioida.

In contrast, most other features of *Anomalosaepia* are comparable to characters present in members of the Family Belosaepiidae (Fig. 2). The heavily calcified posterior guard, thick callus dorsal to the protoconch, posteriorly directed solid prong, and ventral corona plate are recognizable in *Anomalosaepia* indicating that *Anomalosaepia* is related to the family Belosaepiidae. Several of the unusual features attributed to *Anomalosaepia* appear to be preservational artifacts resulting from loss of aragonite from the skeleton. *Anomalosaepia* was described using fossils from the Comfort Member of the Eocene Castle Hayne Formation, a carbonate unit where dissolution has removed aragonite from the sediments (Carter et al., 1988).

Another anomalous feature is that the partial skeletons used to describe *Anomalosaepia* are composed entirely of large calcite crystals (Fig. 1) that retain faint intracrystal markings corresponding to growth lines. This implies that the calcite is not a replacement of aragonite, but is an original component of the skeleton. The presence of large amounts of calcite is unusual for sepioids, a group that secretes a skeleton composed primarily of the mineral aragonite (Jeletzky, 1966; Dauphin, 1984). However, well preserved specimens of *Anomalosaepia* from Texas, Louisiana and Mississippi (Figs. 3, 4) also contain large amounts of calcite and have a shell microstructure with distinct layers of calcite and aragonite. We conclude that the calcite was secreted by the animal and that the genus has a bimineralic skeleton composed of approximately equal amounts of calcite and aragonite.

METHODS

Identification of calcite and aragonite in the skeleton is based on X-ray diffraction patterns of powdered sample. However, the two minerals can be visually recognized in sepioid skeletons because aragonite is microcrystalline and appears white whereas the coarsely crystalline calcite characteristic of anomalosaepiid skeletons appears dark or brown. Crystals of skeletal calcite are commonly much larger than the aragonite crystals.

SEM images illustrating microstructure were taken with a JEOL JSM-6400 scanning electron microscope with a secondary detector, set at 10 kv and 48 mm working distance, at the Texas A&M Microscopy and Imaging Center. Samples were cleaned for five seconds in 5% HCl and coated with gold-palladium for imaging.

SHELL MICROSTRUCTURE OF *ANOMALOSAEPIA*

The *Anomalosaepia* skeleton has two shell layers with contrasting microstructure in most areas (Figs. 5.1–5.4, 6.1, 6.2) and has a third type of microstructure in the posterior prong (Fig. 6.5, 6.6). Although the innermost conotheca layer and thin, weakly mineralized layer overlying the conotheca (Hewitt and Jagt, 1999; Dauphin et al., 2007; Yancey et al., 2010) are missing in these specimens, other shell layers are well preserved. The skeleton is different from other sepioid taxa in containing an outer layer of coarse, elongate but non-prismatic calcite. Another distinctive feature is the presence of shell wall formed of rows of arborescent plumes or plume-shaped elongate crystals of calcite (Fig. 5.5, 5.6).

The inner shell layer is composed of aragonite and consists of either 1) laminae formed of short radial-prismatic crystals or 2) laminae composed of complex-prismatic fans of crystals.

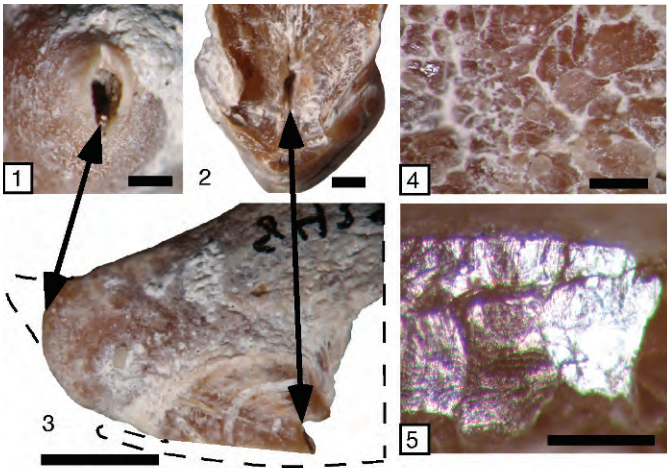

FIGURE *1*—Topotypes of *Anomalosaepia* sp. with calcite skeleton from Martin Marietta quarries, North Carolina. *1,* NCSM 5337a, feature described as a "slit-like" opening on posterior end of prong, view toward anterior; *2,* NCSM 8428, small cavity on the posterior end of alveolus suggested to be anterior end of a "canal" through the skeleton from alveolus to the posterior, view from alveolus toward posterior; *3,* NCSM 8428, lateral view of skeleton with dashed lines added to show missing portions of prong and corona, photo reversed to show standard orientation, posterior to left; *4,* NCSM 8482, coarse calcite crystals in dorsal shield of *Anomalosaepia*, view from alveolus, showing inner surface of calcite layer, posterior to left; *5,* NCSM 8419, broken surfaces of coarse calcite crystals showing cleavage faces on dorsal-ventral break perpendicular to growth axis, looking towards anterior. Scale bars indicate 1 mm for *1, 2, 4, 5* and 5 mm for *3*.

Microstructure of the central axis and the prong apex at the posterior end of the skeleton (Fig. 6.5, 6.6) is radial-prismatic, consisting of thin laminae of aragonite prisms that are 1 to 2 µm in diameter and elongated perpendicular to the growth surface. Prisms in these layers do not increase in diameter during growth, in contrast to aragonite in other parts of the skeleton. The prong growth axis is less mineralized than other areas of skeleton (lower part of Fig. 6.5), suggesting a high proportion of non-mineralized organic material that decayed after death. The prong's vertical median fissure (Fig. 3.7–3.9) is also a weak zone, apparently because of higher organic content along this surface.

Anterior to the prong, the inner shell layer has complex-prismatic structure, with crystals arranged in fan-like sprays that grow outward (Fig. 7). Laminae in this layer grow with a nodular or bumpy surface (Fig. 5.5–5.8) and many of the nodes grow into elongate arborescent plumes that are the main structural unit over most of the shell wall. Microstructure composed of aragonite crystal growth in radiating sprays (often labeled spherulitic-prismatic: Carter, 1990; Doguzhaeva, 2000) occurs in skeletons of several groups, however it is highly variable, even within a single skeleton. In *Anomalosaepia*, radial structure occurs both as acicular-radial arrays of elongate 1 to 2 µm diameter crystals that grow out into arborescent high plumes (Fig. 5.1–5.4) and as fan-radial sprays of larger aragonite crystals (3–10 µm diameter and up to 100 µm in length; Fig. 7.1–7.3) that increase in diameter during outward growth, like the blades

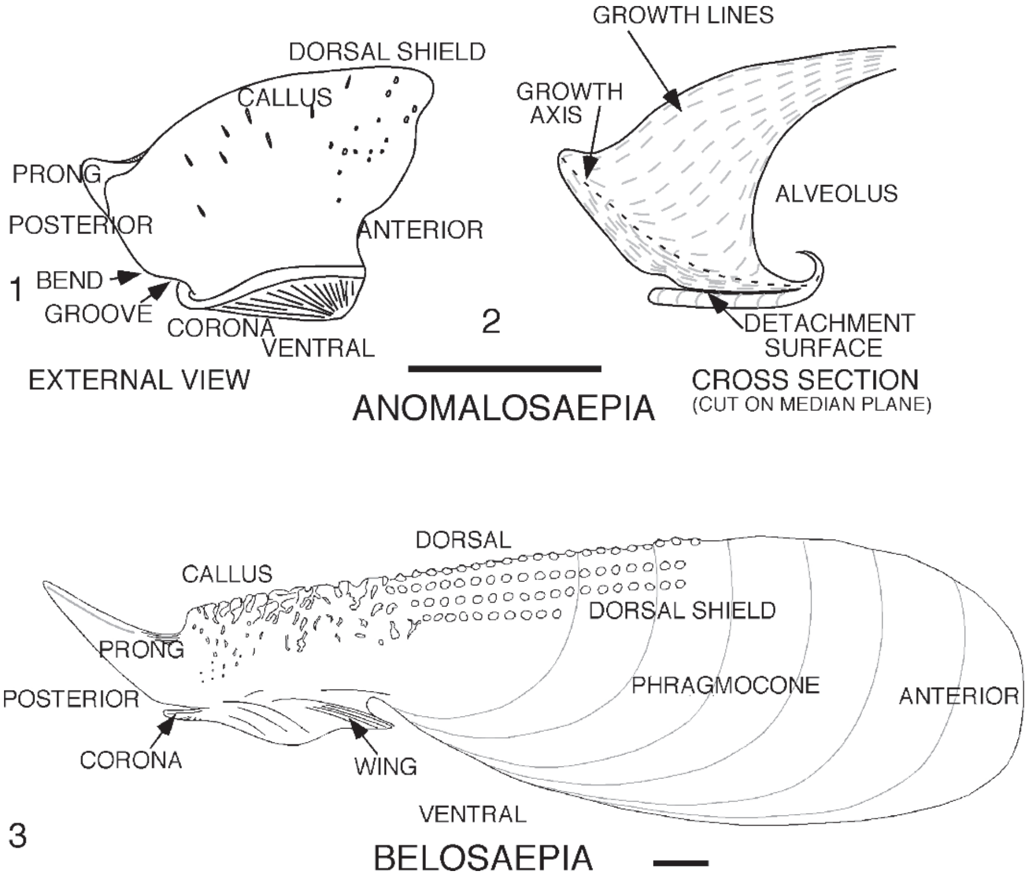

FIGURE *2*—General characters of the *Anomalosaepia* skeleton compared with *Belosaepia* skeleton. *1, 2, Anomalosaepia*, external view and cross section view along median plane of *Anomalosaepia* skeleton with size exaggerated relative to *Belosaepia* to better show characters of this smaller taxon, anterior portion of skeleton unknown; *3, Belosaepia,* general features belosaepiid skeleton based on nearly complete specimen of *Belosaepia ungula* Gabb, 1860. Scale bars indicate 10 mm.

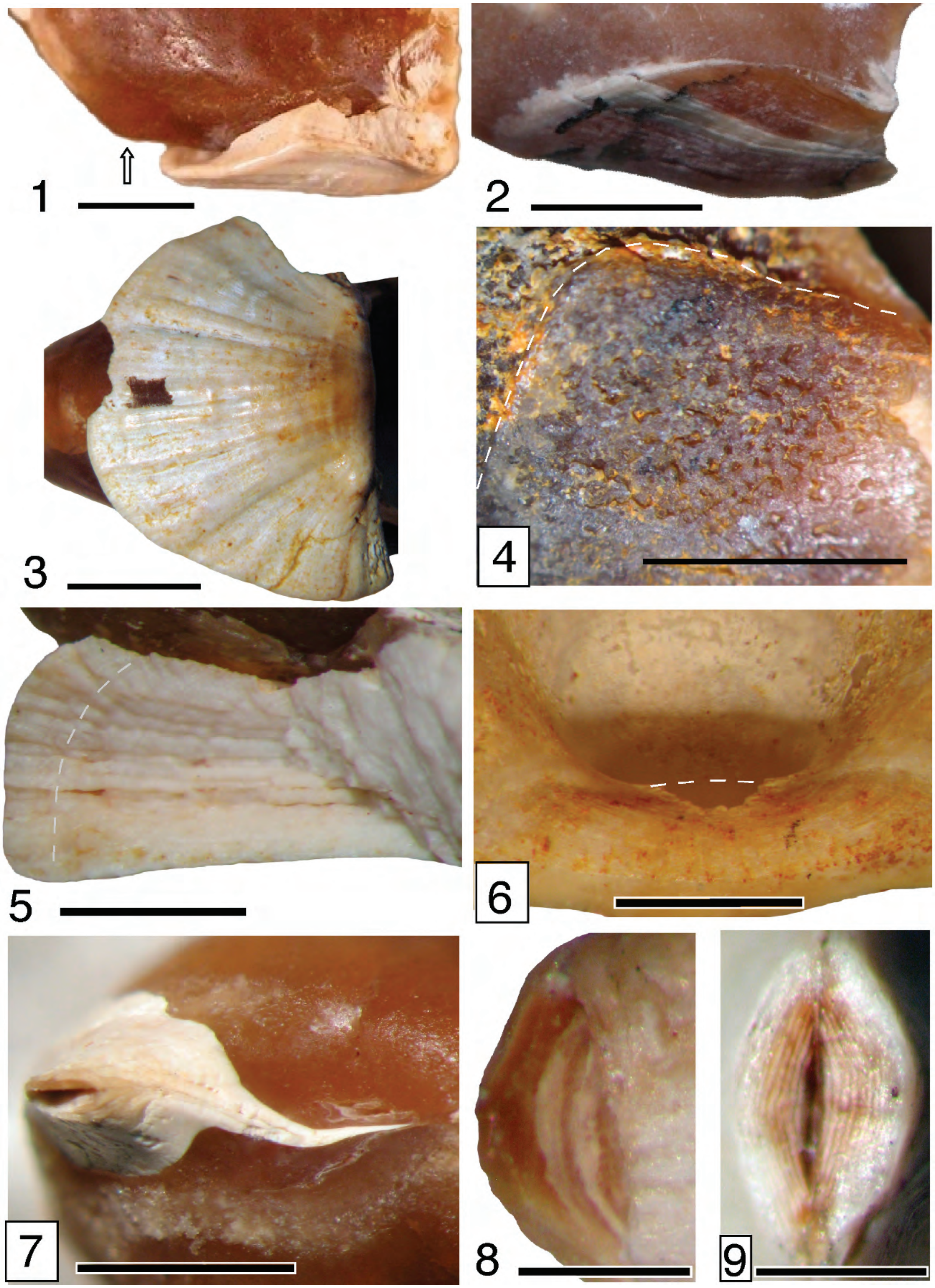

FIGURE 3—Ventral characters and posterior apex of *Anomalosaepia*. *1, 3, 5–8*, *A. parmula* n. sp., holotype, TMM NPL45252, Newton, Newton Co., Mississippi: *1*, well preserved corona on ventral surface, projecting beneath a shallow groove (arrow) on ventral surface, note sharp bend of ventral margin at posterior edge of groove, posterior to left; *3*, corona with nearly semi-circular outline and radial plumes, the small dark area near chipped posterior edge is where basal surface aragonite is broken off revealing the calcite shell layer, the anterior margin (right) of corona is curved inward to

FIGURE 4—*1–5, Anomalosaepia parmula* n. sp., holotype, TMM NPL45252, Newton, Newton Co., Mississippi in lateral, ventral, dorsal, anterior and posterior views; *6–9,* paratype, TMM NPL8427, TMM145-T-52, Two Mile Creek, Leon Co., Texas; *10–13,* Paratype, PRI 11018, west of Enterprise, Jasper Co., Mississippi; *14–17,* paratype, TMM NPL7916, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas. Note the outgrowth of calcite layer onto the dorsoanterior margin of the prong on holotype (*1–5*) and the rough surface of the unmodified paratype (*14–17*); areas of skeleton with white color are composed of aragonite; areas of brown color are composed of calcite; posterior to left. Scale bars indicate 10 mm.

of a fan. Microstructure composed of fan-radial sprays of larger aragonite crystals has not previously been described in coleoids, but radial-prismatic and acicular-prismatic shell microstructures occur in varied sepiid and spirulid genera (Doguzhaeva, 2000) and are major components of the *Belosaepia* skeleton (Dauphin, 1984, Figs. 2–6; Meyer, 1993; Yancey et al., 2010).

The outer surface of the complex-prismatic layer has numerous small pits (Fig. 7.3, 7.5), similar to the pores or tubes in *Kostromateuthis* noted by Doguzhaeva (2000) and inferred to contain organic matter. In *Anomalosaepia* the pits do not extend deep into the shell layer (Fig. 7.5) and do not produce a porous condition.

The outer shell layer is composed of large diameter elongate crystals of calcite (Figs. 1, 5.1–5.4, 6.1). This accretionary shell layer is thickest on the dorsal surface and extends down over the lateral sides as a thinner layer, but does not extend to the posterior apex of the prong and is not present on the flat ventral surface of the corona. Within the callus and anterior portion of the prong, single calcite crystals range in diameter from 0.2 to

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alveolar cavity and is continuous with a very small deck structure, posterior to left; *5,* broken vertical surface through corona, showing rod-like structural units and growth lines (dashed line shows shape of growth lines) indicating accretionary growth limited to posterior and dorsal surfaces, posterior to left; *6,* view of posterior end of phragmocone and anterior end of corona, showing remnants of deck structure, dashed line indicates restored extent of deck, anterior to top, posterior to bottom: *7,* view of dorsal surface of prong, showing depression (dimple) and irregular boundary between callus and prong, dorsal view, posterior to left; *8,* lateral view of apex of prong, showing growth lines exposed on median plane of prong, posterior to left; *2, A.* sp., NCSM 8419, Martin Marietta quarries, North Carolina, area of laterally upturned "ventral plate" of *Anomalosaepia*, a detachment surface produced by separation and loss of the corona, photo reversed to show standard orientation, posterior to left; *4, A. parmula* n. sp., TMM NPL7916, TMM 113-T-2, Hurricane Bayou, Houston Co, Texas, lateral view of detachment surface showing many unfilled pits on smoothed surface, indicating incomplete adhesion of corona to ventral guard, area to the right and below dashed line is detachment surface, area to upper left is normal bumpy surface of unmodified skeleton, posterior to left; *9, A. parmula* n. sp., TMM NPL8427, TMM 145-T-52, Two Mile Creek, Leon Co., Texas, view of posterior apex of prong, showing growth lines and poorly mineralized median fissure, median line is solid, not a void, view towards anterior, dorsal up. Scale bars indicate 5 mm on *1–4, 6*; 1 mm on *5, 9, 2* mm on 7; and 0.5 mm on *8*.

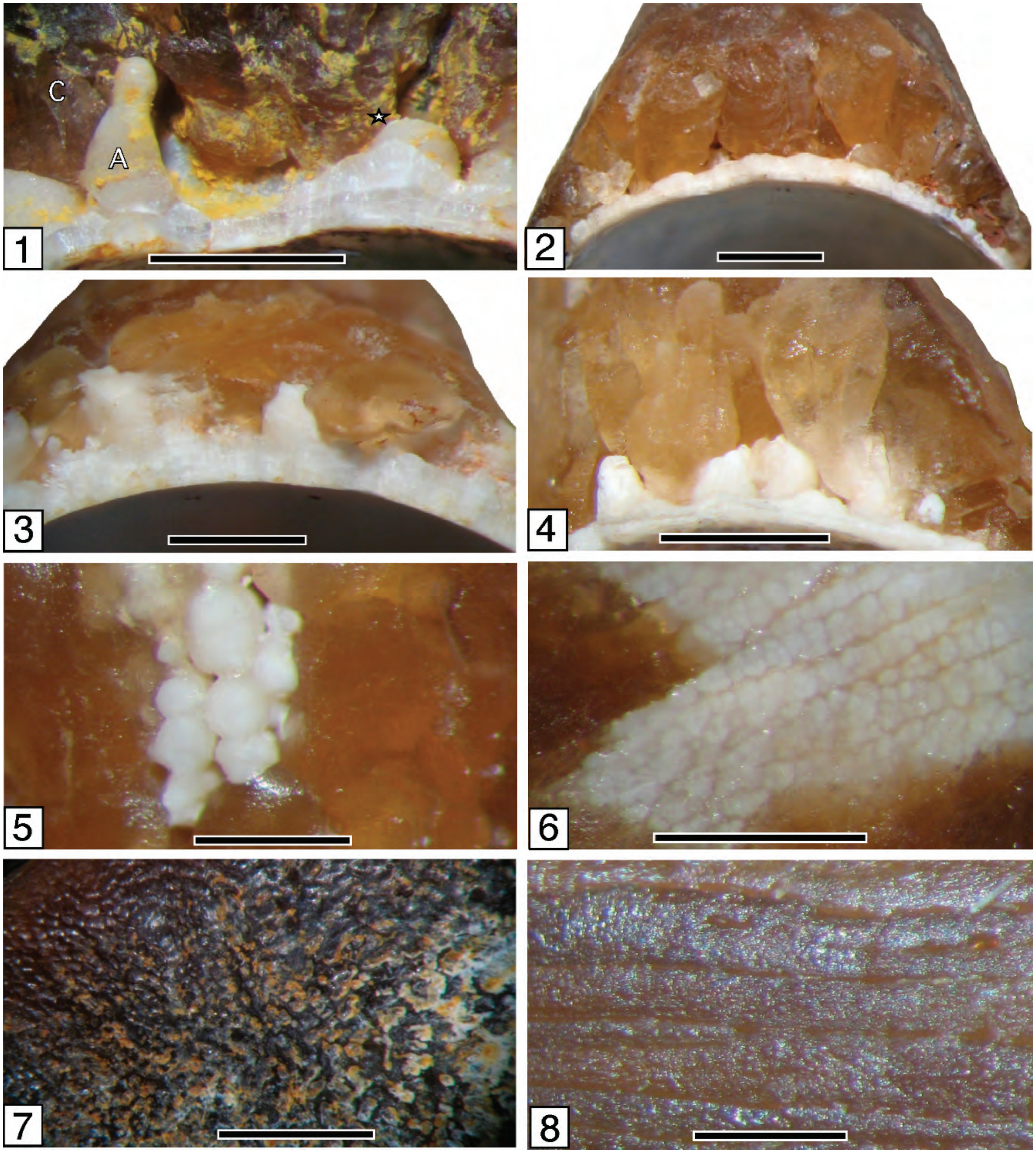

FIGURE 5—*1–8, Anomalosaepia parmula* n. sp., dorsal guard shell layers and surface features: *1, 7,* paratype, TMM NPL7916, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas; *1,* inner layer plumes (A) of complex-prismatic aragonite (white) overlain by coarse, elongate crystals (C) of calcite (brown), each calcite unit is a single crystal, star symbol indicates location where calcite grew onto unmodified surface of an aragonite plume, view towards posterior; *7,* unmodified surface of skeleton, lateral view; *2,* paratype, TMM NPL7384-2, TMM 201-T-24, Sabine River, Sabine Co., Texas, inner aragonite (white) shell layers and coarse calcite (brown) outer shell layer, each calcite unit is a single crystal, view towards posterior; *3,* holotype, TMM NPL45252, Newton, Newton Co., Mississippi, inner aragonite (white) shell layers and coarse calcite (brown) outer shell layer, view towards posterior; *4, 8,* paratype, TMM NPL7384-1, TMM 201-T-24, Sabine River, Sabine Co., Texas; *4,* inner aragonite (white) shell layers and coarse calcite (brown) outer shell layer, view towards posterior; *8,* anterior-posterior alignment of grooves in calcite layer on callus near base of prong, view of dorsal surface; *5, 6,* paratype, TMM NPL8427, TMM 145-T-52, Two Mile Creek, Leon Co., Texas; linear arrays of plumes on dorsal and lateral surface of skeleton with resorbed surface, each calcite unit (brown) consists of a single elongate crystal, lateral view. Scale bars indicate 1 mm on *1–4, 6*; 0.5 mm on *5, 8;* and 2 mm on *7*.

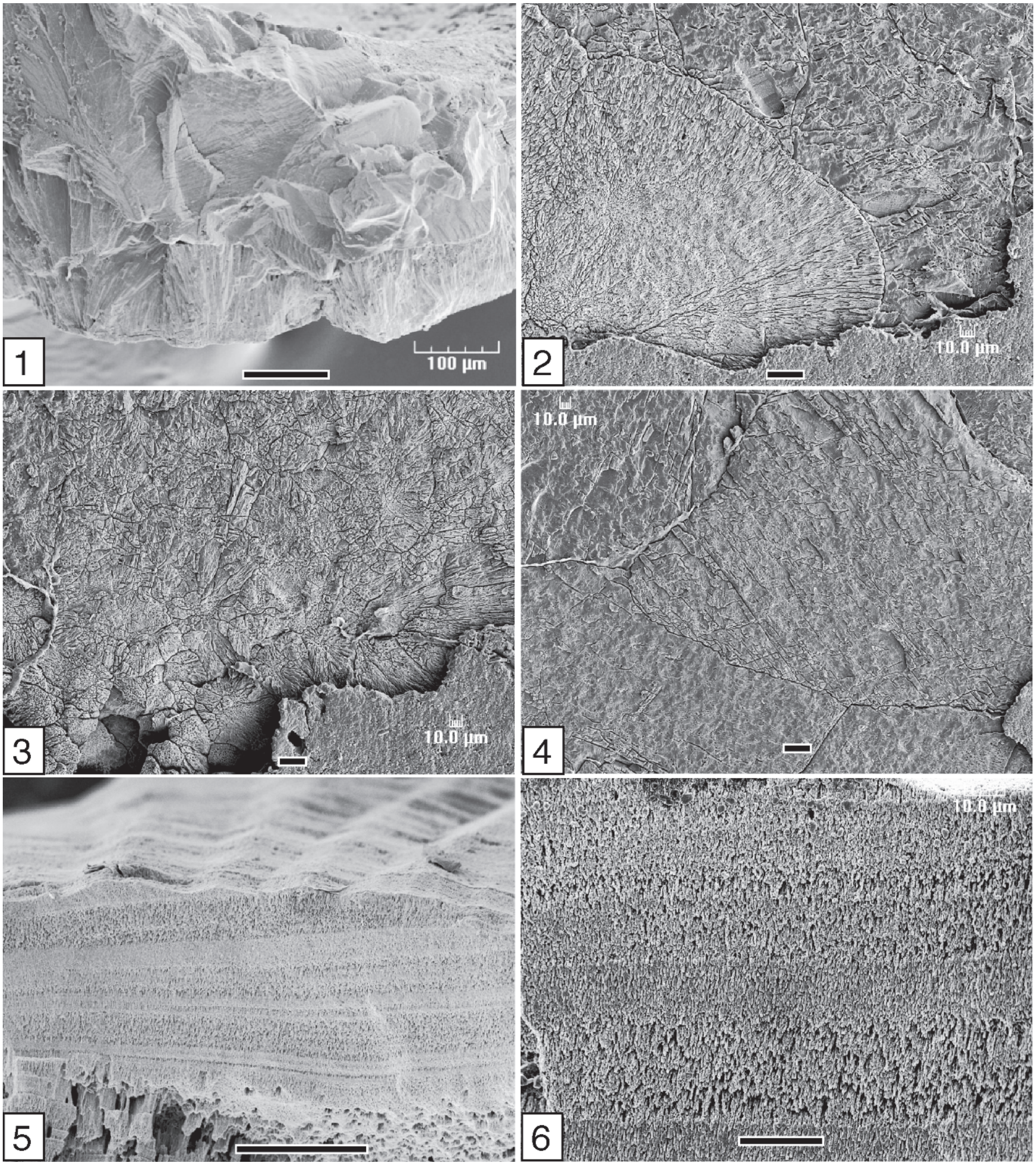

FIGURE 6—*1–6, Anomalosaepia parmula* n. sp., skeletal microstructure: *1,* holotype, TMM NPL45252, Newton, Newton Co., Mississippi, inner aragonite shell layer overlain by coarsely crystalline outer shell layer; *2–4,* paratype, TMM NPL7916, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas: *2,* rounded, unmodified surface of inner shell layer plume composed of radiating aragonite prisms (left) overlain by single crystal of calcite (right) in outer shell layer, lines in calcite are cracks along fractures and cleavage, raised area along bottom of image is epoxy cement; *3,* section through several radiating aragonite plumes of inner shell layer, raised area along bottom of image is epoxy cement; *4,* section through large crystals of calcite in outer shell layer; *5, 6,* paratype, TMM NPL7384-4, TMM 201-T-24, Sabine River, Sabine Co., Texas, broken section of radial-prismatic aragonite in prong showing variations in mineral density between growth bands, area at bottom of image is part of the growth axis in prong and is less mineralized than outer levels, wavy surface at top is mineral boundary between aragonite (shown) and the calcite outer layer with each long groove the impression of a long calcite crystal. Scale bars indicate 100 µm on *1* and *5*; 20 µm on *2–4* and *6*.

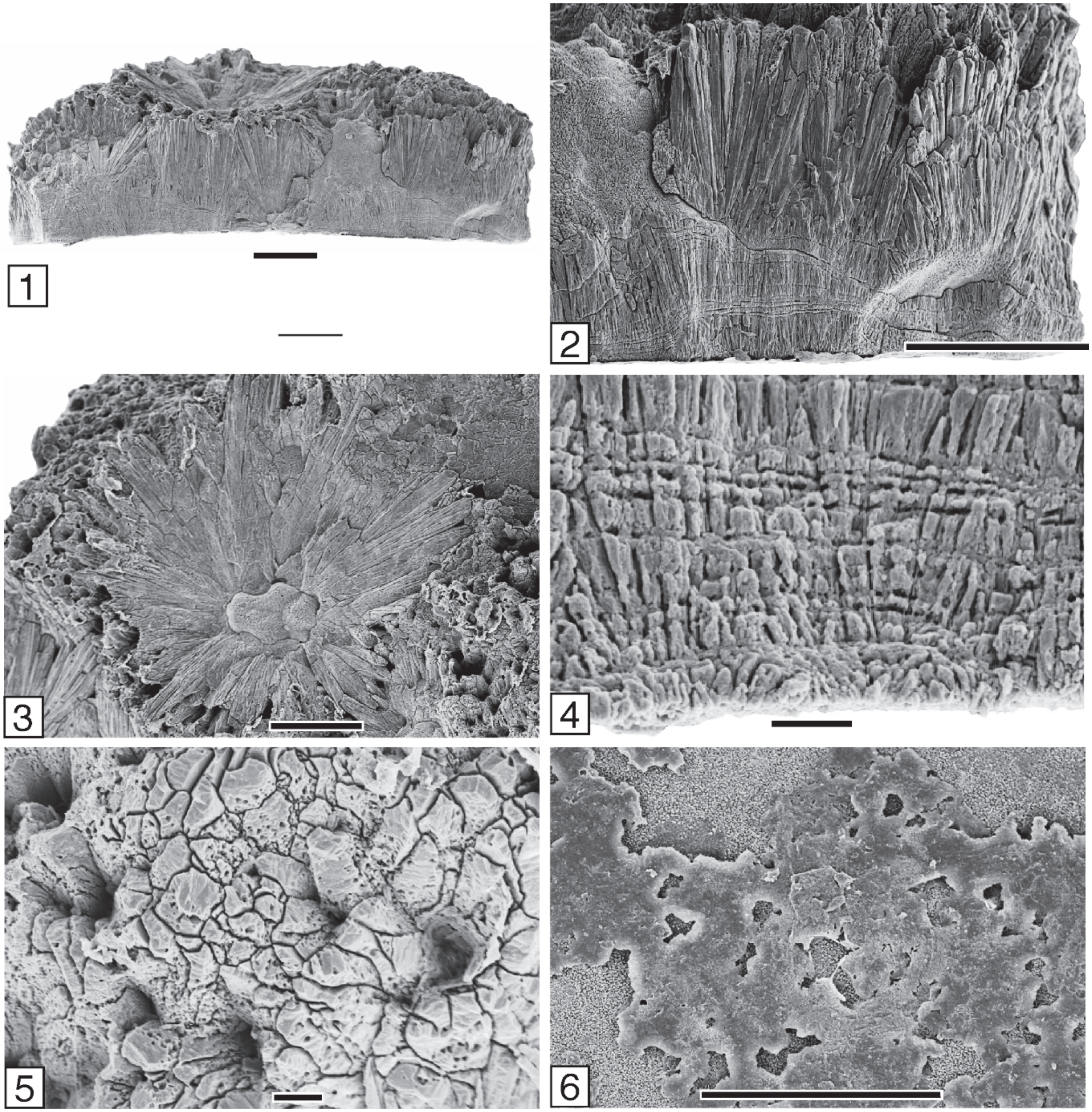

FIGURE 7—Skeletal microstructure. *1–6, Anomalosaepia parmula* n. sp., TMM NPL8427, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. *1, 2,* radial-prismatic and fan-radial aragonite microstructure of inner shell layers, the upper level is entirely fan-radial, with large and small pits on outer surface; *3,* top of plume of basal shell layer exposed by loss of fan-radial shell layer over top of plume, note presence of small pits in upper surface; *4,* basal laminae of lower radial-prismatic and fan-radial aragonite layer; *5,* detail of top surface of fan-radial aragonite layer, showing large and small pits that are closed at base; *6,* basal surface of aragonite shell layer, showing ends of aragonite prisms and presence of a thin homogenous shell layer that may be secondary in origin. Scale bars indicate 100 μm on *1–3, 6*; 10 μm on *4, 5.*

1.0 mm (Fig. 1.4, 1.5) and extend up to 6 mm in length (Fig. 8.1). These calcite crystals are many times larger than the needle-like aragonite prisms of the inner shell layers and have a diameter similar to that of multicrystal plumes of aragonite (Fig. 5.5).

The outer calcite layer has a sharp basal contact with underlying aragonite layers, although the boundary is not a smooth planar surface. On the dorsal shield, growth of calcite starts at numerous points on and between the tops of aragonite plumes (Figs. 5.1–5.4, 8.1) and does not fill all available space. The large calcite crystals merge a short distance above the top of aragonite plumes to form a continuous solid outer layer. Small voids are present between aragonite and calcite layers and are common on all specimens examined. These have the appearance of original non-mineralized spaces within the skeleton and may have been filled with a matrix of organic material, now decayed. They are not dissolution pits; the plumes are preserved with their original growth surface (Figs. 5.1, 6.2). In places where calcite and aragonite have a common boundary, growth lines can be traced from aragonite into calcite (Fig. 8.2).

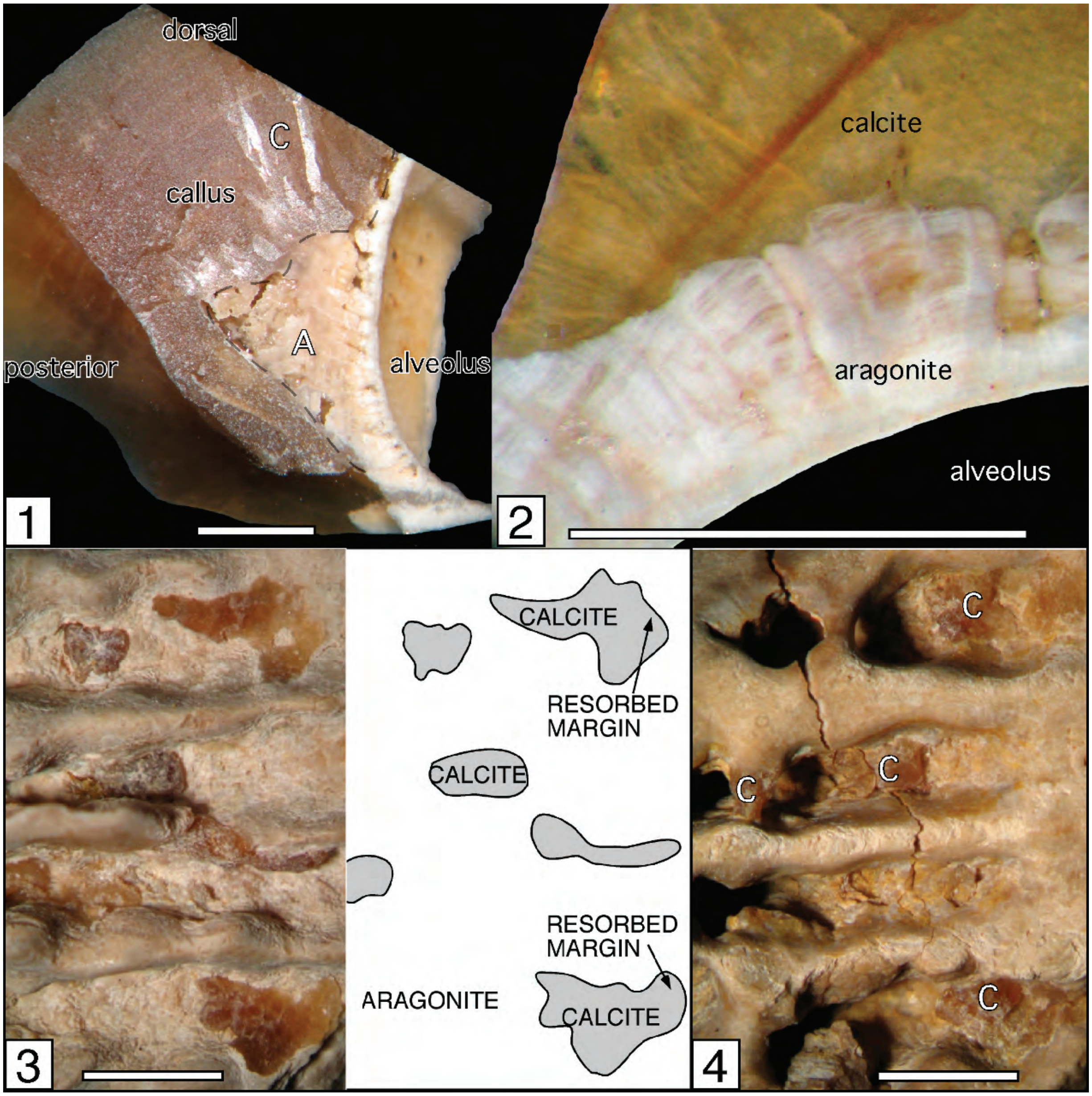

FIGURE 8—Examples of skeleton resorption during life on *Anomalosaepia* and *Belosaepia*. *1, 2,* paratype, *Anomalosaepia parmula* n. sp., TMM NPL7384-3, TMM 201-T-24, Sabine River, Sabine Co., Texas: *1,* section cut near median plane of skeleton, showing areas of inner aragonite and outer calcite (boundary shown by dashed line), aragonite area composed of plumes with scattered voids between them, elongate white streaks in calcite area are reflections off cleavage surfaces, posterior to left; *2,* section cut across part of callus, showing closely spaced growth lines in aragonite plumes and widely spaced growth lines in calcite, dark growth band in middle of calcite field extends into aragonite field, showing concurrent growth of both minerals, view towards posterior; *3, Belosaepia ungula*, TMM NPL45253, TMM26-T-100, Rocky Branch, Burleson Co., Texas, patches of large calcite crystals on anterior part of callus showing thinned, resorbed edges on right side of photo, calcite patches are grown mostly on the sides of aragonite plume ridges and are composed of a single or a few crystals, dorsal view, posterior to left; *4, Belosaepia ungula*, TMM NPL4871–3, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas, patches of large calcite crystals on anterior part of callus, dorsal view, posterior to left. Scale bars indicate 1 mm on *1, 2*; 5 mm on *3, 4*.

SYSTEMATIC PALEONTOLOGY

Repository.—Figured specimens are housed in the nonvertebrate paleontology collections of the Texas Natural Science Center of the University of Texas, Austin (TMM NPL), the Paleontological Research Institution at Trumansburg, New York (PRI) and the North Carolina Museum of Natural Sciences (NCSM).

Material examined.—Holotype of *Anomalosaepia jeletzkyi* Allen, 1968 from Saline Bayou, St. Maurice, Louisiana (PRI 27553), paratypes of *Anomalosaepia alleni* Weaver and Ciampaglio, 2003 (PRI 49666), *A. mariettani* Weaver and Ciampaglio, 2003 (PRI 49668), *A. vernei* Weaver and Ciampaglio, 2003 (PRI 49670) and *A. andreani* Weaver and Ciampaglio, 2003 (PRI 49672), and eight undesignated paratypes (NCSM 5337a, 5337b, 8419, 8421, 8428, 8434, 8453 and 8482) from the North Carolina collection used by Weaver and Ciampaglio (2003) in describing the genus, 11 topotypes of *Anomalosaepia* spp. from Ideal Cement quarry, Wilmington, North Carolina (PRI 40021), holotype and three paratypes of *A. parmula* new species from Newton, Newton Co., Mississippi (TMM NPL45252), Two Mile Creek, Leon Co., Texas (TMM NPL8427), Hurricane Bayou, Houston Co., Texas (TMM NPL7916) and Enterprise, Mississippi (PRI11018) and seven specimens of *A. parmula* from Sabine River, Sabine Co., Texas (TMM NPL7384.1–7384.7).

Family ANOMALOSAEPIIDAE new family

Diagnosis.—Skeleton with small, blunt prong; large wide corona attached at anterior end and weakly adhering to ventral surface of skeleton; thick outer shell layer of elongate large calcite crystals; skeleton composed of both calcite and aragonite.

Type genus.—*Anomalosaepia* WEAVER AND CIAMPAGLIO, 2003, emended.

Discussion.—This family is characterized by having a thick outer shell layer composed of coarsely crystalline calcite, a shell microstructure unknown in other sepioids. The inner aragonite shell layers contain a fan-radial shell structure not described in other sepioids. The Anomalosaepiidae is related to the Belosaepiidae but differs from it and other coleoid families in having a skeleton composed of about equal amounts of calcite and aragonite. The extent of calcite outer layer varies among individuals.

Genus ANOMALOSAEPIA Weaver and Ciampaglio, 2003, emended

Figures 1, 2.1, 2.2, 3–7, 8.1, 8.2

Anomalosaepia WEAVER AND CIAMPAGLIO, 2003, p. 1103, fig. 1.

Diagnosis.—Bimineralic sepioids with inner shell layers composed of prismatic aragonite and outer shell layer of large elongate blocky calcite crystals; prong small, with blunt apex and laterally compressed cross section; callus with narrow, rounded dorsal crest containing few elongate grooves; surface of skeleton with small low bumps, but smooth on specimens with resorbed surfaces.

Description.—Small, heavily calcified sepioids with outer shell layer composed of large elongate calcite crystals; guard with high narrow callus; prong small and triangular in outline with blunt rounded apex; well developed fissure plane in prong; corona weakly attached to guard and often missing, leaving curved detachment surface; dorsal surface of callus rounded; lateral sides covered with small low bumps; alveolar cavity of phragmocone coiled, containing oblique septa; small, short deck present; corona wider than long and composed of small radial rods.

Discussion.—Well-preserved specimens of *Anomalosaepia* have a solid skeleton (Fig. 4), without a posterior slit-shaped opening or a canal-like cavity extending into the prong of a type mentioned in the original description. Those features are produced by post-burial dissolution of weakly calcified or aragonite components of the skeleton. The "alveolar cavity lacks[ing] sutures" reported by Weaver and Ciampaglio (2003) is a consequence of substantial dissolution of the alveolar cavity, where inner aragonite shell layers are missing and the base of the outer calcite shell layer is exposed. Sutures are present only on the innermost shell layer. Belosaepiid fossils do not often preserve sutures or septa because the phragmocone is weak and the conotheca is weakly attached to the outer guard. The conotheca to which septa are attached is underlain by a thin organic-rich shell layer (Hewitt and Jagt, 1999) that degrades to a weak zone in the shell, allowing the conotheca to separate and flake away from the solid guard.

The laterally upturned surface referred to as the ventral plate by Weaver and Ciampaglio (2003) is a posteroventral detachment surface (Figs. 1.3, 2.2, 3.2) where the corona (a weakly supported fan-like sheet of the ventral guard, called ventral process in some reports) separates from the skeleton after death. Accretionary growth of supplementary younger guard tissue occurred only on the posterodorsal surface of the corona (Fig. 3.5), filling in most space between it and the main part of the skeleton, but adhesion was incomplete. Cementation occurred on only half of the joined surfaces, so few specimens (including well-preserved ones) retain the corona. Limited adhesion is shown by the presence of unfilled pits remaining between bumps on the main skeleton (Fig. 3.4). Detachment surfaces reveal xenomorphic impressions of radiating plumes (Fig. 3.2) and growth lines (Weaver and Ciampaglio, 2003, fig. 1.5, 1.8). Well-preserved specimens (Fig. 4.1–4.4) show that the corona of *A. parmula* n. sp. is about 20% larger than its detachment surface.

TABLE 1—Measurements of holotype and paratypes, *Anomalosaepia parmula* n. sp. All measurements in mm.

	NPL45252	NPL8427	NPL79	PRI11018
Length	15	15	18	16
Height	9	11	16	12
Width	10	8	9	9

The smooth outer surface present on many *Anomalosaepia* skeletons (Figs. 3.1, 3.2, 4.1, 4.6, 4.10) contrasts with the irregular rough and/or pitted surface of belosaepiids. This appears to be a consequence of skeleton resorption by the animal. A specimen with no resorption has a rough outer surface (Figs. 4.14, 5.7, 5.8). Evidence of resorption is visible on portions of the prong and callus of TMM NPL8427 (Fig. 4.6–4.9), indicating that the smooth surface attributed to *Anomalosaepia* was produced during late maturity by skeleton resorption in a manner similar to that documented for *Belosaepia ungula* (Gabb, 1860) (Yancey et al., 2010).

Four species of *Anomalosaepia* are recognized in this report. Specimens from Texas and Mississippi belong to *A. parmula* n. sp., described here. *A. jeletzkyi*, described by Allen (1968, p. 36, 37) on a single specimen from Louisiana is a distinct species characterized by elongate form and a wide, parallel-sided skeleton between the callus and prong. Most of the specimens from North Carolina belong to the species *A. alleni*, although some can be assigned to *A. vernei*.

Weaver and Ciampaglio (2003) separated their collections of North Carolina specimens into groups based on a combination of 1) presence or absence of S-shaped curvature on the dorsal margin and 2) width of the posterolateral margin. Statistical analyses of measurements made on the sample set identified four groups defined by the combined presence or absence of these two features and each group was described as a new species, using inflation of dorsal and posterolateral margins as major species-defining criteria. There is a considerable range of inflation on those margins, produced by the combined effects of tendency for variable growth of the calcite outer shell layer, late stage resorption during life and post-deposition dissolution of the skeleton. This makes the aforementioned shape characters of North Carolina specimens of uncertain value for species determination.

When North Carolina partial specimens are oriented by reference to the corona detachment surface as a guide to horizontal axial orientation, most have a moderately upturned prong and tend to be elongate with the dorsal crest sloping down to the posterior at a low angle, a form that fits *A. alleni*. A nearly straight dorsal margin was described as indicating the lack of a callus for *A. andreanae* and *A. vernei* but callus development can be reduced by dissolution and is not a reliable character for characterizing these two proposed species. The species names *A. mariettani* and *A. andreanae* are best placed in subjective synonymy with *A. alleni*. Some specimens with a laterally thickened posterior skeleton and a sharply upturned posterior margin are referred to *A. vernei* (Weaver and Ciampaglio, 2003, fig. 1.7). The prong apex of this species emerges from calcite guard far above the ventral margin, but hypertrophied outgrowth of the calcite shell layer on the posteroventral margin may distort the shape of the skeleton considerably, masking the real shape of the prong. A re-evaluation of this species is needed and better preserved specimens are needed to get a reliable guide to intra-species variation for all *Anomalosaepia* species.

ANOMALOSAEPIA PARMULA new species
Figures 3.1, 3.3–3.9, 4–7, 8.1, 8.2

Description.—Small, with heavily calcified skeleton up to 10 mm wide and 20 mm long; guard with high callus, small prong and small corona; prong up to 4 mm long, 4 mm high and 2 mm wide, triangular in lateral outline with sharp-edged dorsal and ventral margins diverging at ~60°; prong with blunt rounded apex inclined dorsally at 35–40° from horizontal; well developed vertical fissure plane in prong; dorsal margin of prong raised into narrow knife-like edge at junction with callus on mature specimens, usually with pair of deep dimples located on each side of prong at this boundary; corona wider than long (to 7 by 10 mm) with wide semi-circular posterior margin and anterior end upcurved towards phragmocone cavity; corona composed of small radial rods and covered on dorsal surface with secondary guard layers; posteroventral surface of main part of skeleton has flexure consisting of well-defined bend posterior to corona margin or corona detachment surface; callus arched and merging with thickenings on sides of skeleton; lateral sides nearly flattened and form arch with sides diverging at about 60°, with more rounded crest towards anterior; dorsal margin of callus inclined downwards towards posterior at low angle, but some specimens have distinct shoulder on posterior end of callus; dorsal surface of callus marked by few longitudinal fine grooves; most of callus and lateral sides covered with small bumps that produce rough surface, but this roughness often smoothed by resorption late in life; first-formed layers of guard composed of complex-prismatic microstructure (small aragonite prisms arranged in radial sprays) and outer layer composed of large elongate irregular calcite crystals; aragonite shell layer on dorsal margin contains elongate plumes separated by small voids; alveolar cavity round (6 to 7 mm wide) and curved, coiled in half circle; oblique septa; simple suture lines spaced about 1 mm apart on adult portion of skeleton; small, very short deck present.

Types.—Holotype TMM NPL45252, Newton, Newton Co., Mississippi; paratype TMM NPL8427, Two Mile Creek, Leon Co., Texas; paratype TMM NPL7916, Hurricane Bayou, Houston Co., Texas; paratype PRI11018, Enterprise, Mississippi. Dimensions of type specimens given in Table 1.

Other material examined.—Seven specimens from the Veatch collection, TMM NPL7384.1–7384.7, Sabine River, Sabine Co., Texas.

Etymology.—The name *parmula*, (Roman, small shield) refers to the relatively short posterior guard of this species.

Discussion.—The majority of specimens have a smooth outer surface, due to secondary resorption of the skeleton late in life of the animal (Fig. 4.1–4.13). The unmodified skeleton of adult animals has a moderately rough surface covered with bumps and pits (Fig. 4.14–4.17), with bumps corresponding to the tips of coarsely crystalline calcite of the outer shell layer. The surface roughness of *Anomalosaepia* is less than that of co-occurring *Belosaepia*.

Comparison with other species.—There is variability in the shape of the posterodorsal and posteroventral portions of the guard and in the projection of the prong beyond the margin of the calcite outer shell layer causing corresponding variability in standard dimensions of shell height, length and width. This is mostly the result of secondary resorption of the skeleton, making species determination and comparison difficult unless unmodified specimens are available for examination. With this qualification in mind, the following conclusions can be made: *Anomalosaepia parmula* is characterized by its relatively short posterior guard and small, short prong. It differs from *A. alleni* in being less elongate and having a different calcite:aragonite ratio. *A. alleni* and co-occurring species have skeletons composed of as much as 70% calcite, compared to 50% calcite for *A. parmula*. It differs from *A. vernei* in having a small but well-formed prong that extends out from near the ventral margin or the posterior center. It differs from *A. jeletzkyi* in having a short, small prong at the end of a tapered callus and guard, in contrast to the more elongate and parallel-sided callus and posterior guard that surrounds the base of the prong in *A. jeletzkyi*. The holotype of *A. jeletzkyi* (Allen, 1968, pl. 12, figs. 9, 11) is partly modified by dissolution, indicated by the loss of ventral wall of the phragmocone, exposing the protoconch, and small amounts of dissolution along the axis of the prong, but the skeleton is more elongate than *A. parmula*.

DISCUSSION

Anomalosaepia has a skeleton with similar form and characters to that of *Belosaepia* (see Fig. 2), including shell layers containing rows of aligned plumes (Fig. 5.6, 5.8). The major differences are in shell microstructure and mineral composition.

Anomalosaepia is noteworthy for containing large amounts of calcite in its skeleton. The occurrence of a sepioid skeleton with nearly equal amounts of calcite and aragonite is a major departure from the generally accepted belief that sepioid skeletons are composed of aragonite (Jeletzky, 1966; Bandel and Boletzky, 1979). In modern sepiids, only very small amounts of calcite are reported in the cuttlebone of *Sepia pharaonis* Ehrenberg, 1831 (Bandel and Boletzky, 1979, p. 320; Adam and Rees, 1966, pl. 8, figs. 39, 41, 43). In ancient sepioids, Yancey et al. (2010, p. 277) report minor amounts of calcite present in the callus and presence of calcite (determined by X-ray diffraction) forming the endoventral prismatic layer on the ventral surface of the skeleton of *Belosaepia ungula* (Gabb). Mature specimens of Texas *Belosaepia* commonly have a few percent of semi-equant or irregular large diameter calcite crystals grown in spaces between plumes or on the side of plumes in the callus (Fig. 8.3, 8.4).

Evidence that calcite present in fossil sepioids was secreted by the animal and is not a product of diagenetic replacement can be seen on specimens (Fig. 8.3) where both calcite and aragonite show thinning by resorption in late maturity, before death of the animal. Several species from the Gulf of Mexico region (including *B. saccaria* Palmer, 1937, and *B. pennae* Garvie, 1996) have a dominantly aragonite skeleton with small amounts of calcite present (personal examination) and a similar bimineralic composition occurs in several European belosaepiid taxa (personal examination by C. L. Garvie, 2009, in collections of the Natural History Museum, London). These observations show that sepioids typically have a bimineralic composition with small amount of calcite present on mature individuals of the species. It suggests that original bimineralic aragonite-calcite composition is a normal condition among sepioids and thus descriptions stating that sepioids have an aragonite-only skeleton need to be modified.

Similar observations of bimineralic composition in belemnoid skeletons were presented by Bandel and Spaeth (1988). They documented the occurrence of belemnoids with a conotheca, phragmocone and posterior growth axis composed of aragonite and other parts of the skeleton composed of coarsely crystalline calcite. This suggests that mixed calcite-aragonite composition is a more general condition in coleoids and can be expected to occur more commonly when the mineral composition of more species is documented.

Coarsely crystalline calcite is characteristic of coleoid skeletons containing large amounts of calcite. On cut surfaces of *Anomalosaepia* (Fig. 8.1, 8.2), growth lines are visible that show concurrent growth of calcite and aragonite and an overlap of aragonite by calcite. This can also be seen at the boundary between the callus and prong (Fig. 4.1, 4.10), where calcite often grew out laterally (Fig. 4.1, 4.3, 4.10–4.12) and posteriorly to engulf the aragonite surface of the prong (Fig. 4.1, 4.3).

An opposing view stating that calcite present in coleoid skeletons is of diagenetic origin was presented by Dauphin et al. (2007), based on observations of co-occurring calcite and aragonite in the skeletons of the belemnite *Goniocamax* (Dauphin et al., 2007) and sepioid *Belopterina* (Dauphin, 1986). However, shell microstructure in *Anomalosaepia* and *Belosaepia* indicate that sepioids commonly secrete calcite and that the presence of irregular calcite crystals is not necessarily evidence of diagenetic mineral change. Bandel and Hemleben (1975) give evidence that for molluscs, calcite crystal growth occurs in places not in direct contact with mantle epithelium. Aragonite crystal growth forms only under direct contact with mantle epithelium or on previous shell surface, while calcite grows from solutions in closed off cavities or areas not influenced by epithelium, the amount of fluid present determining the size of calcite crystals. For *Belosaepia* and *Anomalosaepia* this implies the change from aragonite to calcite deposition occurred when mantle epithelium lost contact with the shell surface and mineral precipitation continued from fluids produced by non-epithelial tissue. The termination of mantle epithelium contact would likely correspond with end of growth of the animal; the extent of calcite growth might now be dependent on the amount of interstitial fluid remaining and time necessary to form calcite crystals. Other factors being equal, this could imply a longer adult period before mating (and death for many cephalopods) for *Anomalosaepia* than for *Belosaepia*.

Anomalosaepia is distinguished from other genera by its outer shell layer of large diameter calcite crystals and by common aragonite fan-radial microstructure. It has little similarity with *Sepia*, despite common occurrence of complex-prismatic shell microstructure in the dorsal guard (Bandel and Boletzky, 1979; Doguzhaeva, 2000, p. 397) and radial-prismatic shell in the spine (=prong). Only *Sepia pharaonis* Ehrenberg possesses some calcite in the skeleton and the skeleton also has a well-developed posterior spine, a character homologous to the belosaepiid and anomalosaepiid prong and regarded as primitive by Adam and Rees (1966, pl. 135). The very short ventral wall of the *Anomalosaepia* phragmocone is not comparable to the open ventral phragmocone of *Sepia*. *Anomalosaepia* has a curved phragmocone coiled into a half circle in contrast to the nearly straight phragmocone of *Sepia*. These differences suggest that *Anomalosaepia* is not directly ancestral to *Sepia* and that it is a separate lineage derived from *Belosaepia* or a similar form such as *Belosaepia pennae* Garvie, 1996.

Little can be inferred about the life habits of *Anomalosaepia*. The formation of a small, high-density skeleton with a small alveolus suggests that the animal did not use the phragmocone as a flotation aid. That implies that the animal was either a persistent bottom dweller or that the skeleton was small compared to the body size of the animal, making it incidental to life functions. It is possible that *Anomalosaepia* was restricted to the western Atlantic region. The genus is relatively common in the Eocene Castle Hayne Formation of North Carolina and occurs in deposits along the northern Gulf of Mexico but has not been reported from the well-studied Eocene deposits of Europe.

CONCLUSIONS

An emended description of the genus *Anomalosaepia* is given and a new family is established for the genus. Well-preserved specimens of the genus show that it possesses skeletal characters similar to those of belosaepiids and that the anomalies described when the genus was erected are mostly the result of partial loss of the skeleton after death and deposition in sediments. Species of the genus are distinctive in secreting large amounts of coarsely crystalline calcite in the skeleton in addition to aragonite. The presence of a slit-like opening on the posterior end of the prong and cavities near the protoconch portion of the phragmocone are the result of post-depositional dissolution of the growth axis within the prong. Therefore, the suggestion that *Anomalosaepia* possesses an internal "canal" is not supported.

The calcite shell layer of *Anomalosaepia* distinguishes it from other sepioids, both in the quantity of calcite present and in the size and shape of the calcite crystals. A shell layer composed of elongate large semi-irregular crystals has not previously been recorded in molluscan shell. Another distinctive feature of *Anomalosaepia* is the size and expanding diameter of aragonite prisms in the fan-like sprays of the complex-prismatic aragonite shell layer. These distinctive shell microstructures of *Anomalosaepia* and the high proportion of calcite to aragonite (50–70%) justify placing *Anomalosaepia* in a family separate from the Belosaepiidae.

Most specimens of *Anomalosaepia* have lost the ventral corona. This was weakly attached to the main part of the skeleton but left a detachment scar on the ventral surface near the protoconch and below the callus. The skeleton of most specimens has a smooth surface which is the product of skeleton resorption by the animal during life. *Anomalosaepia* and belosaepiids commonly resorbed parts of the skeleton during late maturity before death and *Anomalosaepia* shows evidence of truncation of growth layers on the prong and on the callus and sides of the skeleton, indicating resorption. Resorption may be a widespread feature among heavily calcified mature sepioid skeletons.

As much as 70% of the *Anomalosaepia* skeleton consists of coarse elongate crystals of calcite that forms by accretionary growth. Examination of other species of American and European belosaepiids reveals that a minor to substantial amount of calcite occurs in the skeletons of many belosaepiids. A bimineralic composition appears to be typical of anomalosaepiid and belosaepiid species.

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