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THE MIDDLE EOCENE *BELOSAEPIA UNGULA* (CEPHALOPODA: COLEOIDA) FROM TEXAS: STRUCTURE, ONTOGENY AND FUNCTION

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ABSTRACT—The ontogeny of *Belosaepia unguia* Gabb, 1860 from the Crockett Formation (Bartonian stage, Eocene) of Texas is documented for growth from embryo to old age. During the last stage of life, much skeletal resorption occurred, resulting in a major change in form of the skeleton. The animal produced a large skeleton (to 180 mm in length and 50 mm in diameter) with endogastric coiling, oblique septa and a very large siphuncle. The skeleton has a guard with a solid posterior prong, a posteroventral corona plate and a noded dorsal shield. The ventral margin of the skeleton consists of a thin flattened deck containing strongly recurved septa, conotheca and a secondary prismatic shell layer. New terms are defined for features of the skeleton not previously described. The microstructure of the ventral deck and the presence of a rod structure between the prong and callus are described for the first time. Chamberlets similar to those in living *Sepia* cuttlebones are present between closely spaced septa and they vary from walled units on lateral margins to pillar form in mid-venter. The siphuncle is secondarily thickened within the dorsal interior, producing a siphuncle band. The skeleton was produced by a deep-bodied animal of demersal life habits. The species *B. uncinata*, *B. harrisi* and *B. alabamensis voltzi* proposed by Palmer (1937) are synonymised with *B. unguia*. The species *B. veatchii* and *B. saccaria* of Palmer (1937) are considered to be valid species, but *B. alabamensis* proposed by Palmer (1937) is synonymised with *B. veatchii*. Descriptions of belosaepiid species must be based only on specimens of adult size that have not been affected by resorption.

INTRODUCTION

BELOSAEPIID FOSSILS, an uncommon component of Eocene marine biotas in North America, have attracted attention and interest because of their unusual appearance. The fossils have a large curved projection that is shaped approximately like a blunt tooth or beak (Fig. 1) but is composed of calcium carbonate and is unlike the skeleton produced by any modern marine animal. Although the presence of a phragmocone on the fossil indicates a cephalopod origin, the tooth-like projection is posterior and has no obvious function. Previous study has shown that belosaepiid fossils are not mouthparts (Cossmann, 1907; Curry, 1955; Naef, 1921) but are endoskeletons of an animal related to sepiids. Although the typical belosaepiid fossil is more deep-bodied than modern sepiid skeletons, they share enough skeletal features to show the two groups are directly related. Characteristic belosaepiid features of the heavily calcified secondary skeleton can be recognized in diminished form on the vertically flattened sepiid cuttlebone and the characteristic sepiid feature of chamberlets and pillar structure between closely spaced septal walls is present in belosaepiids.

Most belosaepiid fossils are incomplete when collected, consisting only of the solid prong and adjacent strongly calcified posterior portion of the skeleton. Typically this comprises only 20–25% of the entire length of the skeleton (Fig. 2.1). Because of this limitation, there is little knowledge of variation, ontogeny or function of the skeletal features. The recovery in Eocene deposits of east-central Texas of some nearly complete specimens and large numbers of well-preserved specimens of *B. unguia* Gabb, 1860, the largest and most common belosaepiid in Middle Eocene deposits of the northern Gulf of Mexico, provides an opportunity to greatly increase knowledge of *Belosaepia*. Study based on extensive examination of external form and determination of ontogenetic change, combined with description of microstructure,

provides comprehensive documentation of *Belosaepia* characters, expanding the character set available for reconstructing sepioid phylogeny. Microscopic examination has revealed microstructures not previously known or incompletely described. These observations are used to evaluate previously described North American species of *Belosaepia*. In addition to documenting the ontogeny and amount of variation within a species, this study presents a functional analysis of skeletal characters applicable for the genus.

MATERIALS AND METHODS

This study is based on a collection of 160 individuals of *Belosaepia unguia* from the late Middle Eocene (Bartonian Stage) Crockett Formation of east-central Texas. Specimens from Bartonian age deposits in Mississippi and Alabama and the Lutetian age Weches Formation of Texas were also examined for comparison. Nearly all specimens have well preserved surface features and unaltered shell microstructure that is well displayed on natural fractures. Determination of skeletal features is by microscopic observation of the specimens and photographs obtained with a Zeiss SR stereomicroscope. Calcite/aragonite mineral determination of skeletal components was confirmed with X-ray diffraction of powdered samples. To replicate the effects of wear on the skeleton surface due to mechanical abrasion on the sea floor, some specimens were placed in a rotary tumbler with abrasive grit and water and tumbled for several days. Christopher Garvie collected the majority of the specimens studied for this report. Specimens from the Texas Natural Science Center and the Paleontological Research Institution were also examined. Locality codes are those of the Texas Natural Science Center of the University of Texas, Austin.

THE BELOSAEPIID SKELETON

The belosaepiid skeleton has three contrasting components, often found separate from each other. These are the heavily

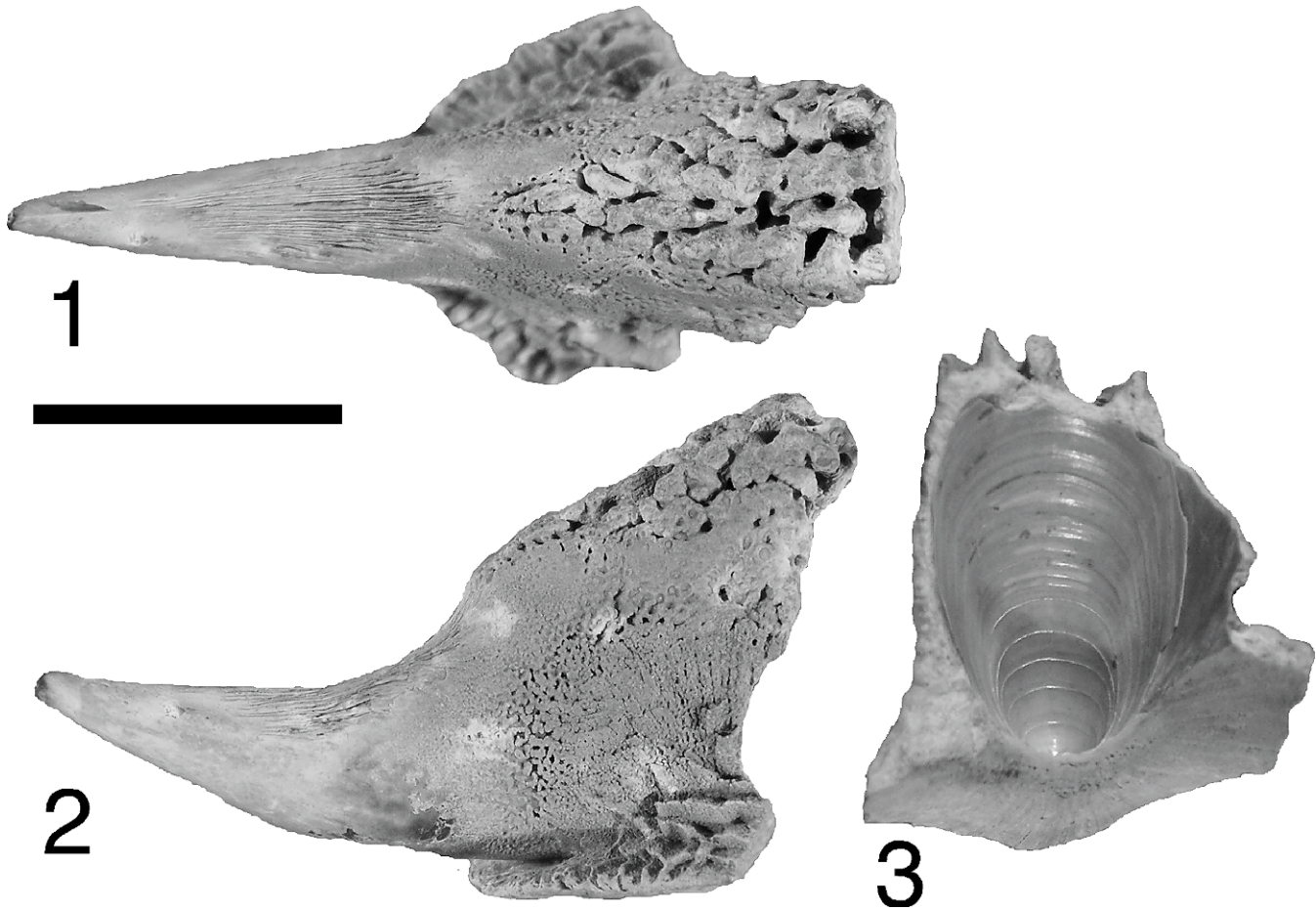


FIGURE 1—TMM NPL38040, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Dorsal, lateral and anterior views of the posterior portion of the guard of *Belosaepia unguia* Gabb, 1860. Although incomplete, this specimen is a typical example of belosaepiid fossils and is typical of specimens used to illustrate the genus. Scale bar is 10 mm.

calcified posterior guard (Fig. 1), the rugose anterior dorsal shield (Figs. 3.1, 3.2, 4.1–4.5) and the phragmocone with conotheca, septa and siphuncle (Fig. 3.3–3.5). A nearly complete specimen of the endoskeleton of *Belosaepia unguia* is illustrated in Fig. 2.1, showing the surface features of both the anterior and posterior regions. This specimen is similar in form and skeletal characters to the nearly complete specimens of *B. sepioidea* de Blainville, 1825, illustrated by Edwards and Wood (1877) and Newton and Harris (1894). The skeleton of *B. unguia* illustrated in Fig. 2 is 50 mm wide and 180 mm long, compared to dimensions of 30 mm by 100 mm (Edwards and Wood, 1877) and 30 mm by 70 mm (Newton and Harris, 1894) for *B. sepioidea*. Assuming an additional head and arm length of about 50%, the *B. unguia* animal reached a length of about 250 mm at maturity. The anterior part of the belosaepiid skeleton is easily broken (Fig. 1) and is missing in most fossils due to the fragile nature of its thin wall, composed of mixed mineral and organic materials. The phragmocone is structurally weak, containing septa that are very thin and weakly attached to the conotheca, so the chambers and siphuncle of the phragmocone are rarely preserved. A reconstruction of this skeleton and the belosaepiid animal is shown Fig. 2.2.

The phragmocone is coiled with a low angle of coiling that decreases during life. Chambers of increasing size were added until late maturity, when a few terminal chambers were added of smaller size, giving the skeleton a kummerform morphology

(Fig. 2.1) with a downturned margin on the anterior end. Although evidence is lacking, it is probable that this terminal constriction was not reflected in the body wall of the animal. This type of terminal growth constriction was documented (Edwards and Wood, 1877) in *B. sepioidea* and in the genus *Ceratisepia* (Meyer, 1993, pl. 1, fig. 4) and is an indication of the last stage of skeleton growth in these sepioids.

Belosaepia has many distinctive skeletal features, including some that have not been described previously or were inadequately described and were often given different names by different authors. This inconsistency for highly distinctive belosaepiid characters leads us to propose a comprehensive terminology for components of the belosaepiid skeleton (Fig. 2.3; Table 1). Although Jeletzky (1966) did not describe good belosaepiid fossils, he adopted some terms and established a convention for naming parts of the coleoid dorsal skeleton that fits portions of the belosaepiid guard very well. Where available, his terminology is used in this report.

The name *guard* is adopted here for parts of the belosaepiid skeleton composed of secondary material. In previous reports, Newton and Harris (1894), Palmer (1937) and Allen (1968) used *belosepion*, Jeletzky (1966) and Weaver and Ciampaglio (2003) used *guard-like sheath*, and Edwards and Wood (1877), Naef (1921) and Haas (2003) used *rostrum*. The term *rostrum* is rejected for use, despite common use of the term for comparable belemnoid secondary deposits, because the word has an established definition in language as a feature that is

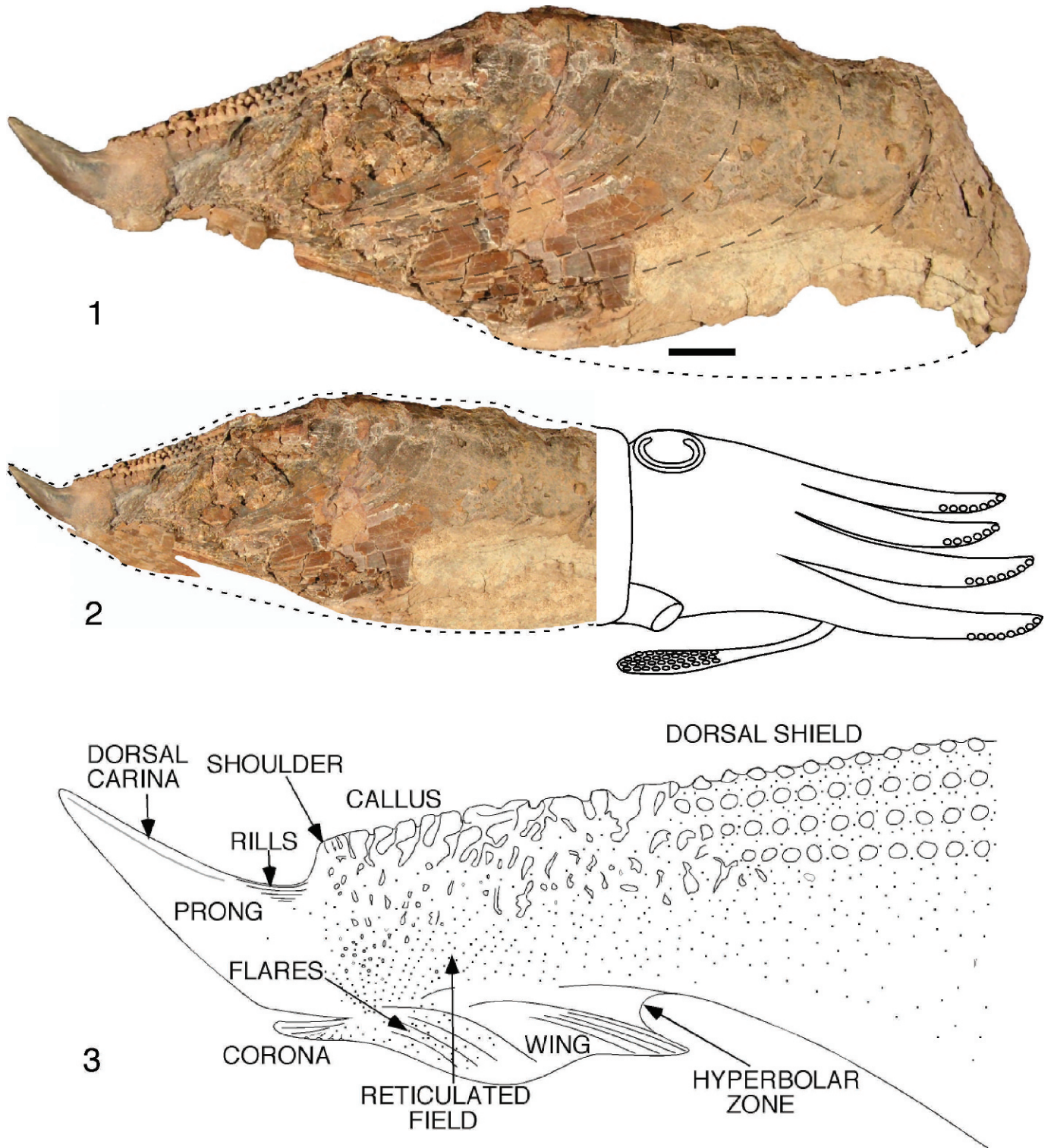


FIGURE 2—Nearly complete skeleton of a mature *Belosaepia unguia* Gabb. 1, 2, TMM NPL38029, TMM 21-T-100, Little Brazos River, Brazos Co., Texas. 1, the node-covered dorsal shield is preserved only on the posterior part of this specimen. The anterior and ventral areas show the smooth inner shell layer (conotheca) with oblique sutures (marked with light gray dashed lines). Note the abrupt change in growth curvature and downturned dorsal margin associated with addition of the terminal chambers to the phragmocone. Photo reversed to show standard orientation; 2, reconstruction of *Belosaepia unguia* Gabb, 1860, with anterior body tissue inferred. Parts of the ventral margin of the skeleton are reconstructed, based on comparison with other specimens of the species. Soft tissue covers the skeleton but is shown only as a dashed line marking inferred extent of tissue covering; 3, reconstruction drawing of the posterior portion of the skeleton. The drawing shows names and location of morphological features of the species. Scale bar is 10 mm.

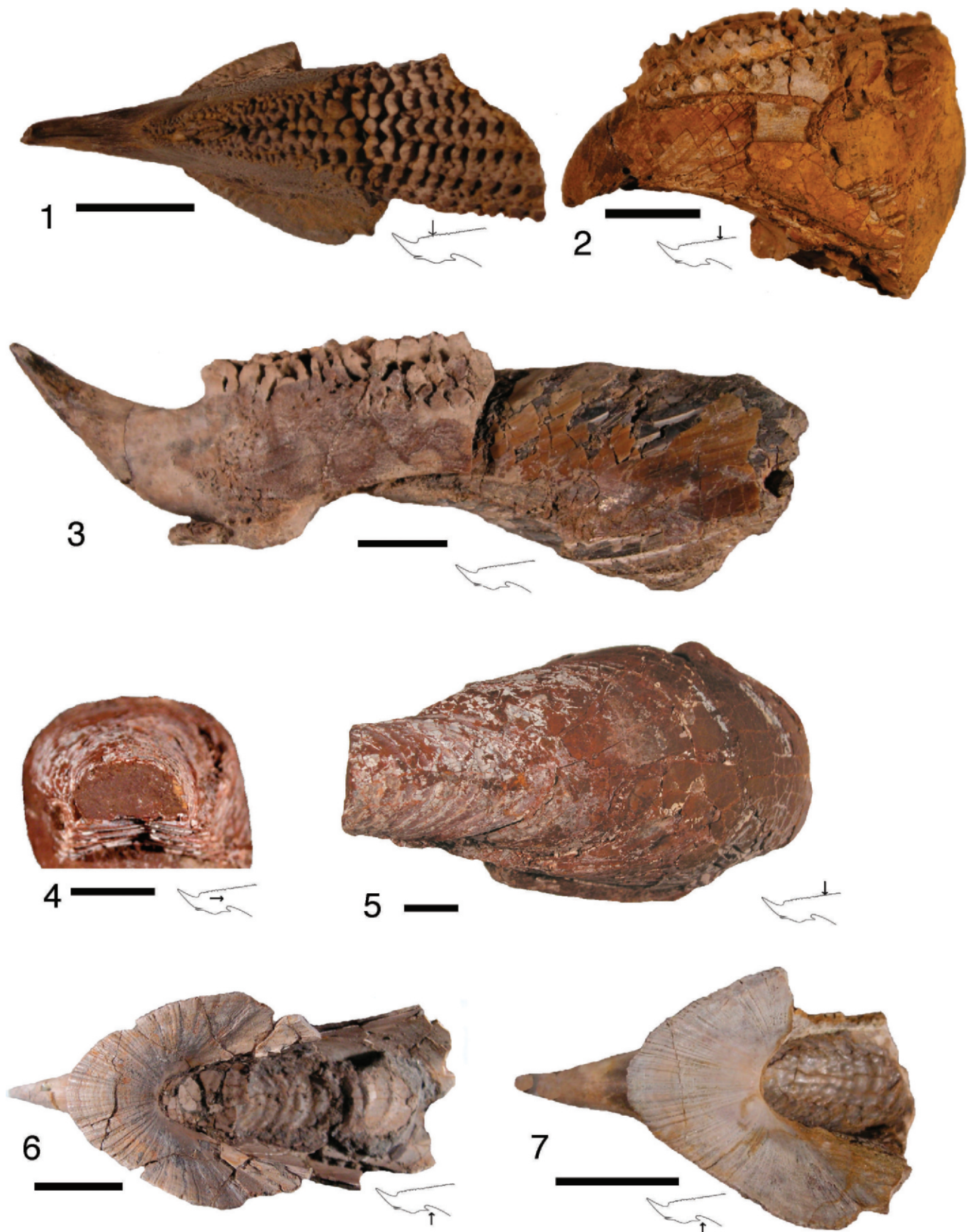


FIGURE 3—Posterior skeleton of *Belosaepia unguia* Gabb, 1860. 1, TMM NPL38051, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Dorsal surface of the posterior guard showing prong, callus and posterior portion of the rugose dorsal shield. Note the lengthwise rows of nodes on the dorsal shield that characterize this species; 2, TMM NPL8428, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Lateral view of posterior

TABLE 1—Definition of named characters of the belosaepiid skeleton.

Alveolus: curved conical space within guard occupied by phragmocone
 Callus: dorsal outgrowth formed of solid arborescent plumes, located over protoconch and early-formed portion of phragmocone
 Chamberlets: thin walled subdivisions or dense arrays of very small pillars within chambers of the phragmocone, present where septal walls of a chamber are very closely spaced
 Conotheca: thin wall to which septa are attached; separate from the guard
 Corona (new term): rounded V-shaped ventral plate formed of radiating rods, attached to the base of prong and extending anteriorly into the wings of the skeleton
 Deck (new term): flattened portion of ventral part of phragmocone where septa grow into tight curves and bend into posterior direction, growing parallel to siphuncle surface and producing a corrugated structure with tightly packed septa
 Dorsal carina (new term): sharp dorsal ridge on the middle and posterior portion of the prong on mature individuals
 Dorsal shield: dorsal region of skeleton above phragmocone, consisting of conotheca, periostracum and calcified guard layer and usually ornamented with thick nodes
 Fissure (new term): median dorsal-ventral surface within prong; is a plane where lateral halves of the prong are weakly joined
 Flares (new term): sharp ridges at base of lateral slope, below callus and at junction with corona
 Growth axis: Center of radial growth in prong, corresponding to position of tip of prong, and composed of less dense microgranular skeleton
 Hyperbolar zone: thin zone of proostracum located between median field and wings; in *Belosaepia* this feature is formed of guard tissue
 Knob (new term): small solid mass of siphuncle deposit that projects anteriorly in mature specimens, filling siphuncle in first few chambers; usually seen as dimple on siphuncle steinkerns
 Phragmocone: chambered part of skeleton with septa, deck, siphuncle, siphuncle band and siphuncle knob; in belosaepiids chambers are inclined relative to anterior-posterior axis
 Pillar structure: area of dense occurrence of minute rods and pillars joining closely spaced septa
 Prong (new term): solid tooth-like secretion at posterior end of guard, having dorsal curvature
 Proostracum: broad dorsal surface of guard above phragmocone, containing median field, hyperbolar zones and wings; in belosaepiids the hyperbolar zones and wings are limited to area below callus
 Reticulated field (new term): mass of small ridges and pits on side of guard below callus
 Rill field (new term): grooved area with fine ridges and grooves at anterior end of dorsal margin of prong, between dorsal carina and shoulder of callus
 Rod structure (new term): a dominantly radial array of fine rods weakly linked together, located in transition zone between prong structure and callus structure
 Shoulder (new term): angular posterior end of callus, where it narrows to an end
 Siphuncle: opening passing through the septa, extending to the protoconch
 Siphuncle band (new term): thickened band of siphuncle on dorsal side of phragmocone having wavy margins; margin thins abruptly to normal siphuncle wall thickness
 Wall structure: area of closely spaced minute walls that form chamberlets between closely spaced septa, usually along lateral margins of phragmocone
 Wing: portion of proostracum separated from median field by thin hyperbolar zones; in *Belosaepia* this feature is formed of guard tissue

anterior in position. Belosaepiid secondary deposits are posterior. Use of the term rostrum for these secondary deposits is misleading, suggesting an orientation of the skeleton opposite to the life orientation of the animal. Jeletzky (1966) was reluctant to adopt the belemnoid term guard for belosaepiid skeleton because of differences between belemnoids and belosaepiids. (Belosaepiids differ from belemnoids in having an endogastric coiled phragmocone and dorsally curved prong in contrast to the orthoconic growth of belemnoids; also, belosaepiids have a skeleton composed mostly of small microscopic aragonite prisms and plumes, in contrast to the large macroscopic radial calcite prisms, visible without magnification, on belemnoid guards.) Jeletzky (1966) preferred the equivocal term guard-like sheath, but the belosaepiid skeleton is produced in the same manner as the belemnoid guard, and it is most reasonable to use the term guard for the secondary deposits of belosaepiids. In reports on the functionally similar skeleton of spirulirostrids, Berry (1922) and Monks and Wells (2000) used the term guard without reservation, and we consider it appropriate to use the term guard for belosaepiids.

SKELETAL MICROSTRUCTURE

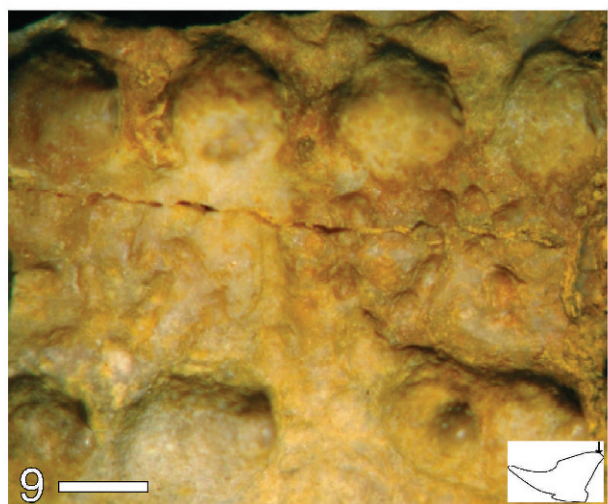
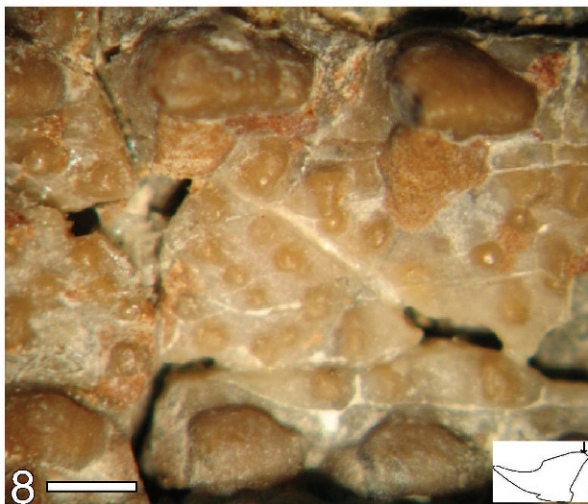
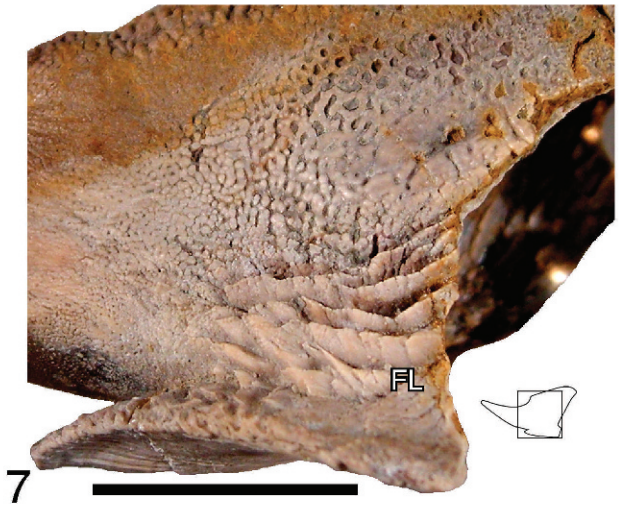
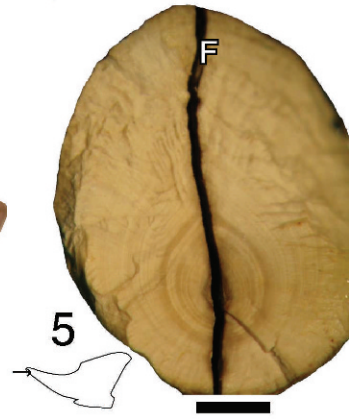
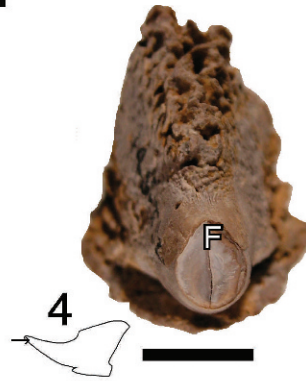
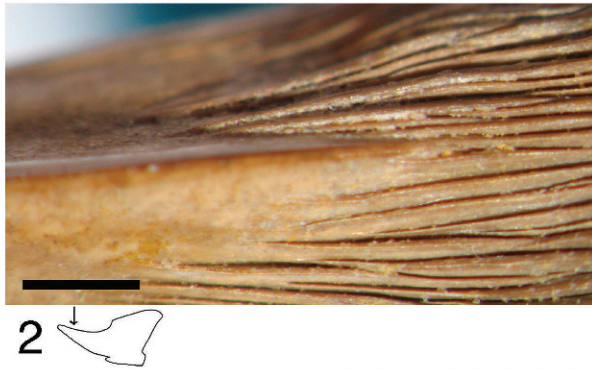
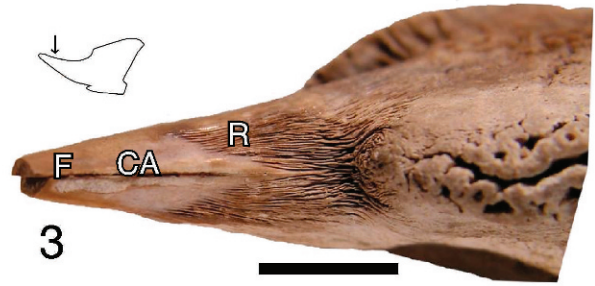
The wall structure of *Belosaepia* is three-layered, consisting of conotheca, mixed chitinous-mineralized layer (=periostracum) and outer guard (Hewitt and Jagt, 1999). The outer

guard layer is much thicker than the conotheca layer, similar to the structure of modern sepiid cuttlebones (Naef, 1921; Hewitt and Jagt, 1999). Many *Belosaepia* specimens retain only small portions of the thin conotheca on the inside of the guard (Fig. 5.1), due to the presence of the mixed chitinous-mineralized layer between the conotheca and the guard. A thin three-fold layering is present on the dorsal shield, but posterior and posterolateral areas have thickened guard secretions, and the posterior prong, callus and corona are formed entirely of guard skeleton. Hewitt and Jagt (1999) determined that the outer shell layer of the anterior guard of sepioids is spherulitic in nature and tends to form a reticulate (noded) ornament by calcification of protein-chitin sheets, a shell microstructure condition also suggested by Bandel and Boletzky (1979).

The posterior guard is composed of minute aragonite prisms aligned perpendicular to the surface of the guard and added in thin accretionary growth layers (Dauphin, 1984). This growth pattern is most visible on the prong. Growth increments on the prong are thinnest on the ventral margin and thicker on other surfaces, producing a shallow upward (dorsal) curvature to the prong during growth (Fig. 6.5). Dauphin (1984, fig. 2D, 2E) illustrated the same pattern of accretionary growth in the prong of *Belosaepia*. On cut sections of the prong, distinct dark bands or surfaces are visible (Figs. 4.5, 6.9) that are probably the boundaries of annual growth bands.

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portion of the dorsal shield, showing part of the rugose shield at top and steinkern of phragmocone below. The callus is missing; 3, TMM NPL38032, TMM 21-T-101, Little Brazos River, Brazos Co., Texas. Posterior guard (with callus) and phragmocone; the anterior dorsal shield is missing; 4, 5, TMM NPL38033, TMM 145-T-200, Two Mile Creek, Leon Co., Texas. Steinkern of phragmocone of a mature specimen, showing shape of the skeleton; 6, TMM NPL38030, TMM 145-T-83, Two Mile Creek, Leon Co., Texas. Rounded V-shaped margin of corona. The corona has two small chips broken from its margin and merges anteriorly with the wings (tips of wings are broken off); 7, TMM NPL38040, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Rounded V-shaped margin of corona. Corona of older individual with smoother margin and smoother ventral surface. Scale bars are 10 mm.



POSTERIOR SKELETON (WITH PRONG)

The heavily calcified posterior portion contains the solid prong, a thin fan-like corona attached to the ventral base of the prong, and a rough dorsal callus located above the protoconch and juvenile portion of the phragmocone (Fig. 2.3). In *B. ungula* the prong projects dorsally at an angle of 30° from the horizontal.

The callus consists of a complex set of arborescent skeletal plumes that grow to a similar height and occur in linear arrays joined together to form irregular ridges separated by equally irregular grooves. The callus usually develops three ridges separated by two grooves that converge posteriorly and expands anteriorly by intercalation of rows (Fig. 3.1) to seven or more rows of large nodes (Fig. 3.2) on the dorsal shield. The plumes grow together irregularly and have more contact with adjacent plumes at their tops, leaving small to large unfilled cavities between plumes (Figs. 7.1, 7.2). The callus has a sharp posterior termination (Fig. 3.3) that rises abruptly above the dorsal end of the prong on full-grown specimens, forming a shoulder. On some specimens the end of the callus projects posteriorly beyond the junction with the prong, creating an overhanging shoulder.

The microstructure of plumes in the callus consists of thin layers of prismatic aragonite that grow primarily in plumose arrays rather than in regular lamellae (Fig. 7.2), and the prisms are of variable rather than uniform length (Dauphin, 1984). This is an exaggeration of the semi-plumose or feathery type of aragonite crystal growth seen in sepiids and spirulids (Dauphin, 1984; Doguzhaeva, 1996). On some specimens of *Belosaepia*, masses of coarsely crystalline calcite grow on and between the aragonite plumes in highly variable overgrowths. The areas of calcite are distinct and recognized by their dark brown color and large crystal size (to 0.5 mm diameter) that contrasts with the light colored, finely crystalline aragonite.

The sides of mature belosaepiid skeletons ventral to the callus are usually coated with irregular sheets of late stage overgrowths of guard skeleton (Fig. 4.6). These start as an initial growth of small bumps and nodes scattered over the sides and develop into an extensive covering. They develop into a nearly continuous covering or as a pitted, laterally continuous covering. On the sides near the corona there are flares (sharp-edged ridges) present with an anterior-posterior or oblique orientation (Fig. 4.7). Flares occur on the wings and may occur in groups of subparallel irregular ridges. They differ from the ridges present in the rill field on the prong in being sharp-edged in contrast to the rounded edges of the sheets.

The corona is a thin, fan-like solid sheet composed of rod-like plumes that radiate out posteriorly and laterally from the base of the prong (Figs. 2.3, 3.3, 4.7). It extends in a nearly

horizontal direction (relative to the anterior-posterior growth axis) and is attached to the main part of the guard anteriorly but is mostly separated from the prong. The central part of the corona wraps around the base of the prong, producing a low amplitude fold. The outer margin of the corona has a rounded V shape with the base of the V pointed posteriorly (Figs. 3.6, 3.7). Because the corona is thin and has a limited area of attachment, portions often break away and are lost. The corona is one of the most distinctive components of the belosaepiid skeleton.

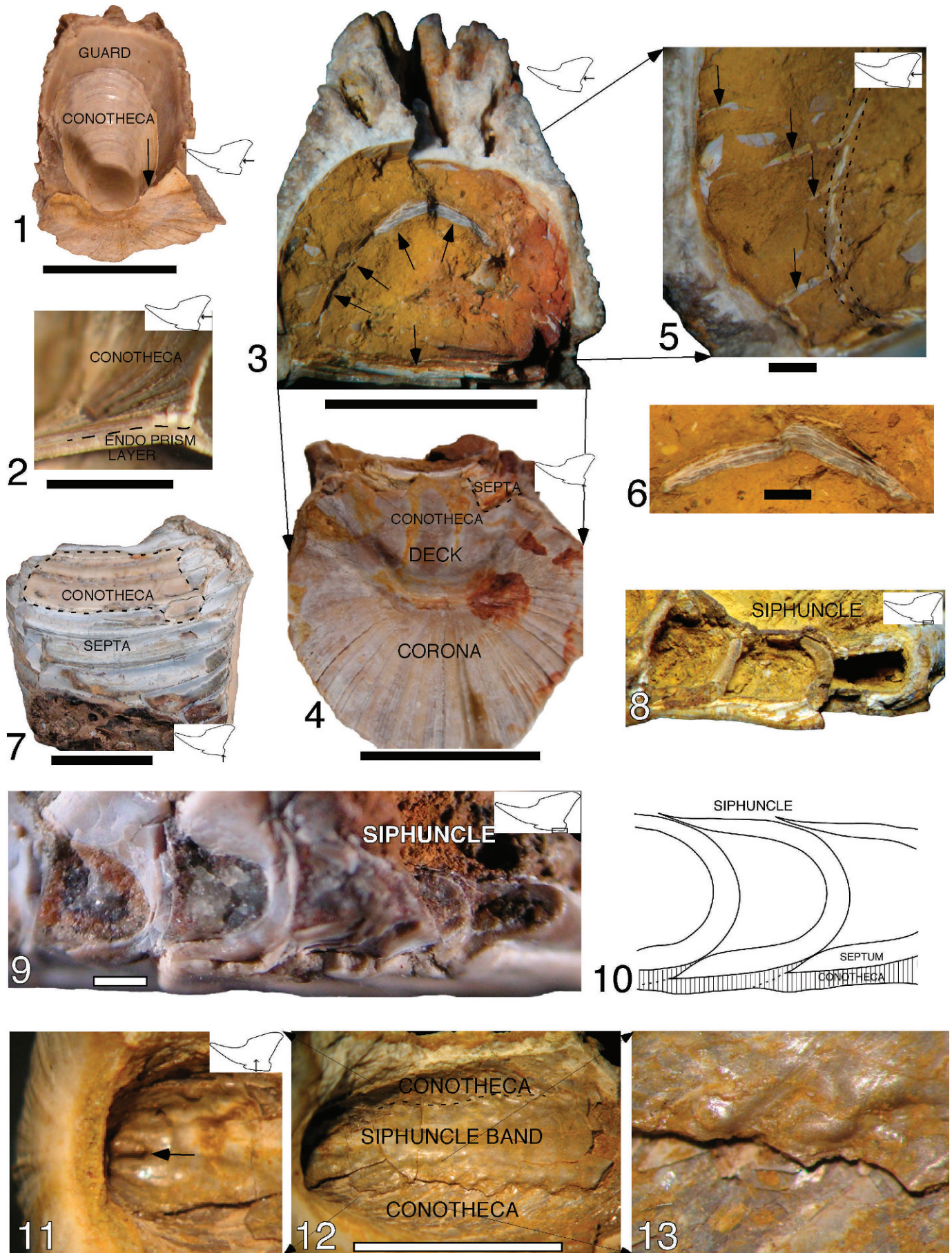
The radiating plumes of the corona are arranged side-by-side in a planar array and increase in diameter at a low rate. The plumes are outlined by grooves on the ventral surface of the corona. They are sometimes rolled into tube-like structures (Figs. 3.6, 3.7, 8.1–8.3) and there may be small void spaces between adjacent plumes. The radiating plumes tend to terminate as small bumps along the edge of the corona. The dorsal surface of the corona is covered with a thick layer of accretionary guard skeleton. Most of the ventral surface is covered with a very thin (<0.1 mm) solid layer of endoventral prismatic layer (term used by Meyer, 1993) that thickens anteriorly as it extends onto the deck. On very well preserved specimens of the corona, the ventral surface has numerous tiny nodes on the surface of plumes (Fig. 8.1).

The prong is a solid posterior projection that tapers to a pointed end, giving it a tooth-like appearance. It has a shallow dorsal curvature and a ventral margin that is nearly straight. The prong is approximately ovoid in cross-section, higher than wide, with the ventral margin more evenly rounded than the dorsal margin. The prong has a small, sharp carina along the posterior dorsal edge, whereas the anterior dorsal edge develops a set of rills adjacent to the callus (Figs. 4.1; 4.2). The prong has a well-defined median dorsal-ventral fissure surface that is a plane of weakness in many belosaepiid fossils (Figs. 4.3–4.5), the only part of the prong that is structurally weak. Consequently, the prong of fossil specimens often breaks into halves along this fissure and parts of the prong break off in semi-circular segments. The prong is formed of regular additions of aragonite over the entire surface and arranged in many thin concentric growth lamellae. The prong corresponds to the spine of *Sepia* cuttlebones, but the strong dorsal curvature, complex microstructure, prominent surface features and size of the prong are sufficiently different from the sepiid spine to justify adopting a different term for this feature in belosaepiids.

The central and posterior parts of the prong are composed of regular concentric lamellae, but the anterior lateral and dorsal portions of the prong contain both lamellae and radial structures that grow outward and cross the growth increments (Figs. 6.7, 6.8). These radial sheets are aligned parallel with

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FIGURE 4—Characters of *Belosaepia ungula* Gabb, 1860. 1, TMM NPL38039, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Dorsal surface of the prong with dorsal carina (CA) developed on posterior end, merging with an anterior rill field (R) adjacent to the posterior end of the callus; 2, TMM NPL38040, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Closeup showing junction of sharp dorsal carina and rill field; 3, TMM NPL4871.1, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Dorsal surface of a prong with dorsal carina (CA) and anterior rill field (R). The prong has split along fissure plane (F) and crest of carina, but only the tip has broken off; 4, TMM NPL8435.2, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Prong broken off near base, showing fissure plane (F). This specimen illustrates how breaks in the prong are consistently perpendicular to the fissure plane and aligned in a dorsal-ventral direction; 5, TMM NPL38047, TMM 145-T-200, Two Mile Creek, Leon Co., Texas. Cross-section showing concentric growth lines and fissure plane (F) and location of the growth axis near ventral margin. The halves of the prong are split and separated along the fissure; 6, TMM NPL38035, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Secondary overgrowths on the side of the posterior guard below callus. Nodes expand laterally and merge to form a uniform surface with remnant pits; 7, TMM NPL38040, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Sharp-edged flare ridges (FL) on ventral area above the anterior end of the corona and below secondary overgrowth. Callus at top, corona at base. 8, TMM NPL38029, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Detail of noded ornament on dorsum of anterior guard; 9, TMM NPL8428, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Detail of noded ornament on dorsum of anterior guard. Scale bars 1, 2, 5, 8, 9 are 1 mm; scale bars 3, 4, 6, 7 are 10 mm.



the axis of the prong, extending outward as curved sheets bent up in a dorsal direction rather than with true radial growth. They originate as wrinkles of the accretionary lamellae (Dauphin, 1984, fig. 4F) and as they extend upward, accretionary lamellae are confined to an arch across the crest of the narrow sheet (Dauphin, 1984, fig. 5A). Most of the sheets grow together with a tight bond and do not separate easily, but in some areas there are small pore spaces (or areas that were filled with non-mineralized organics) between sheets, and the sheets may split apart along these surfaces. Dauphin (1984) determined that there is an abundance of non-mineral organics in the *Belosaepia* skeleton, an observation made for sepiids and spirulids by Doguzhaeva (1996) and Haas (2003).

There is a narrow but well-defined transition zone between prong structure and callus structure in the center of the posterior guard skeleton. This occurs where the planar sheet units of the rill portion of the prong give way to the arborescent plumes of the callus. In this transition zone, planar radial sheets of the anterior prong change to poorly defined plates composed of a radial array of fine rods weakly linked together (Figs. 6.10, 6.11). There is a sharp boundary where this structure changes to typical arborescent plumes in the callus. The transition zone between prong structure and callus structure widens dorsally from 0.5 to 2 mm and extends outward about 10 mm before becoming indistinct in later growth lamellae. It is structurally weak, with less dense skeletal tissue between the rods. The small size of the structural units and less dense areas between rods provides conditions for enhanced internal corrosion and leaching after deposition of the skeleton in sediments.

The median fissure surface is a plane of weakness (Figs. 4.3, 6.6) in the prong, because crystal units in the fissure zone are microgranular and less densely packed. The median fissure contains the growing tip of the prong, where growth increments are more widely spaced (Figs. 6.5, 7.3; also illustrated in Dauphin, 1984, fig. 2E). This narrow zone also contains a sparse array of small, dense sheets that fan out from the growth axis (Fig. 7.3). The porous skeleton along the growth axis is structurally weak and more susceptible to alteration or leaching after death. Erosion of this zone can produce a cavity on the tip of the prong, a feature that Weaver and Ciampaglio (2003) identified as a canal terminating in a slit-like aperture at the tip of the prong in the *belosaepiid*

genus *Anomalosaepia*. However, in *Belosaepia* this feature can be shown to be a product of dissolution after burial and the resultant gap is not original. This conclusion was also noted by Newton and Harris (1894, p.122) for *Belosaepia* with the comment: "The slit at the extremity of the rostrum (sic) alluded to by some authors appears to be due to erosion, which has removed the outer surface and revealed part of the internal structure."

ANTERIOR SKELETON (DORSAL SHIELD)

The dorsal shield (term used by Naef, 1921) is large (50 mm wide, 150 mm long) but thin (1–3 mm), with a low curvature on adult portions of the phragmocone and ornamented with many rounded nodes (Figs. 4.8, 4.9). The dorsal shield is generally similar in outline to the sepiid cuttlebone, although more curved in lateral section. The nodes of the dorsal shield are larger (to 2 mm high) than nodes present on the sides of the callus or lateral slopes near the protoconch, and they are aligned in rows. Scattered among the large nodes on the flanks of the anterior guard are much smaller nodes that decrease in density down the slopes of the guard. There is no distinct proostracum on the dorsal shield of *Belosaepia*.

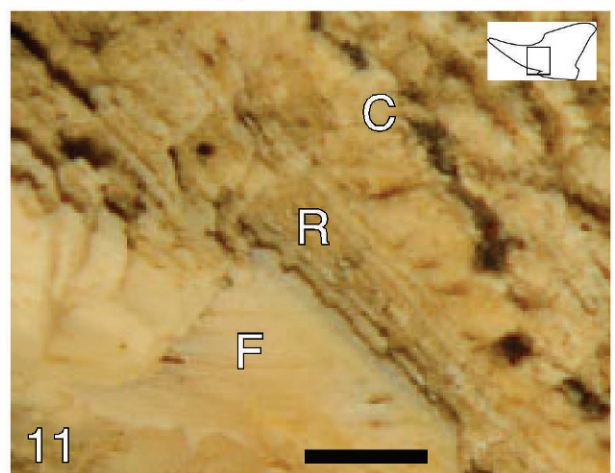
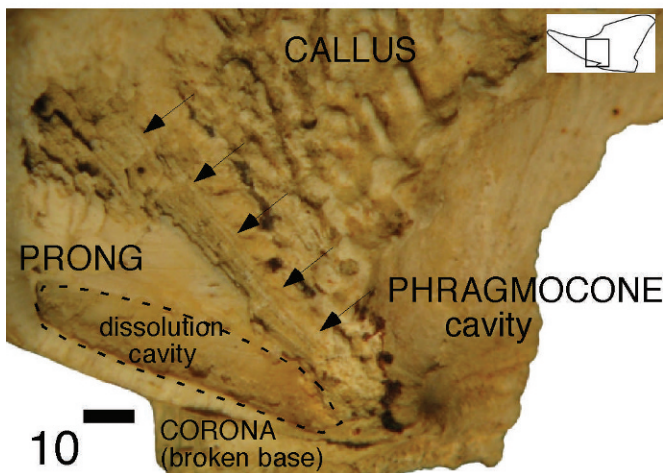
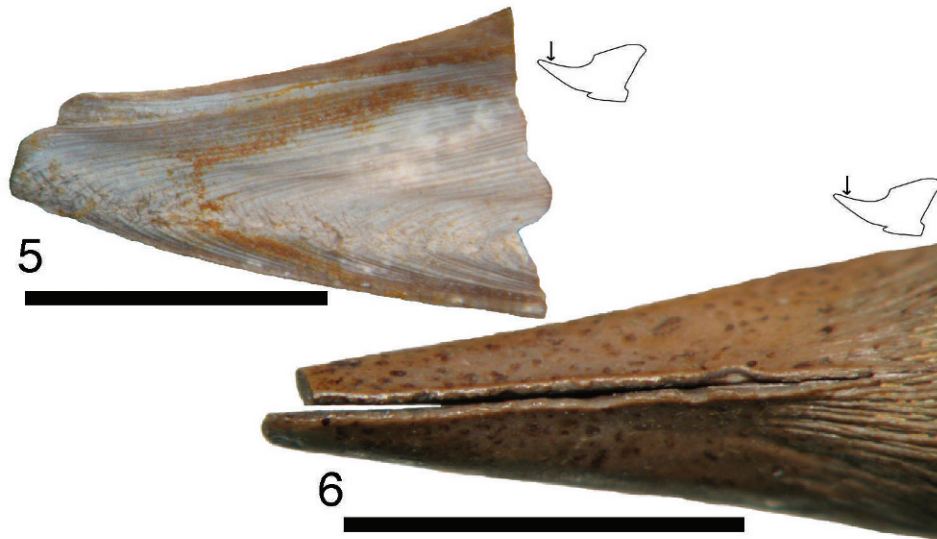
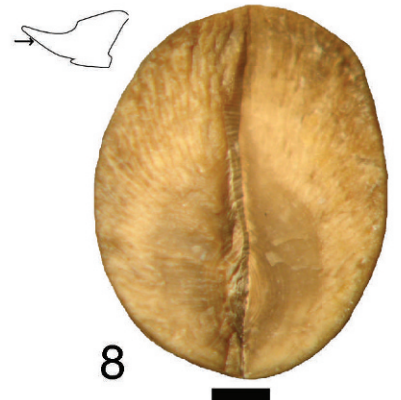
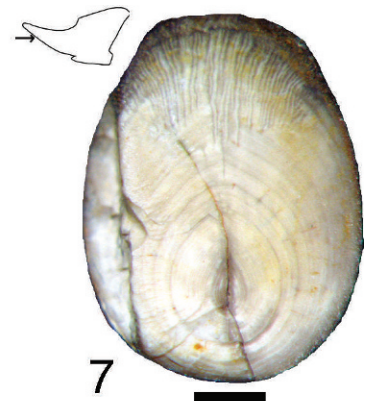
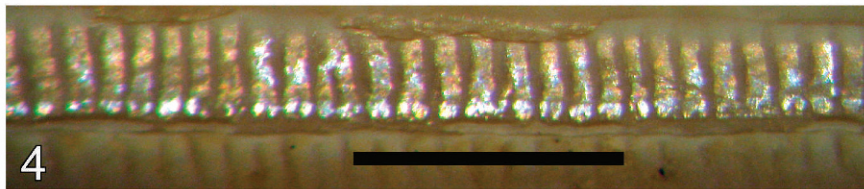
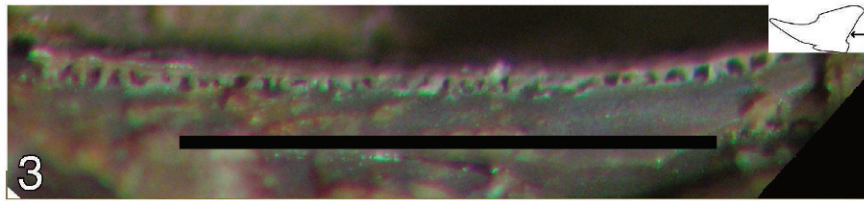
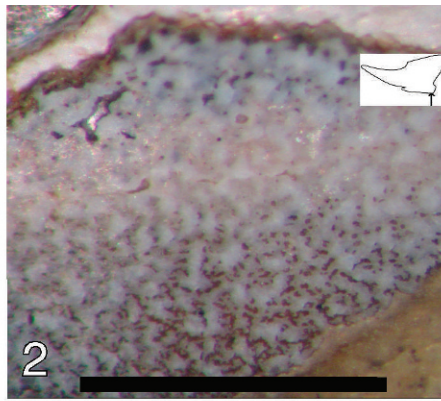
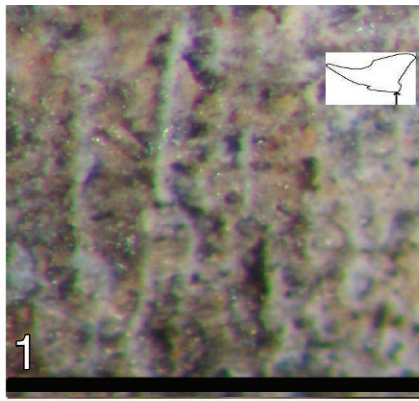
The *belosaepiid* skeleton has a shape and lateral outline similar to the three-fold lateral subdivision of the coleoid dorsal skeleton described by Jeletzky (1966, p. 33) for phragmoteuthids and teuthids and described by Haas (2003) for rossiids. This design consists of a large median field bordered by lateral wings that are set off from the median field by a hyperbolic zones (Fig. 2.3). On the *belosaepiid* skeleton, the wings are small and limited to the posterior part of the guard. They terminate in sharp points and usually are broken off during fossilization. The hyperbolic zone consists of thin shell and is a zone of weakness in the skeleton.

PHRAGMOCONE (WITH SIPHUNCLE)

Belosaepiids have a very asymmetric phragmocone, with a much longer dorsal margin than ventral margin, a distinctive D-shaped cross section, and a very large siphuncle (Fig. 5.3). Starting in the embryonic portion of the phragmocone, the growth rate along the dorsal margin is much greater than along the ventral margin, resulting in the formation of strongly oblique septa. Even the embryonic portion of the phragmocone contains oblique septa. In the portion of the

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FIGURE 5—Phragmocone characters of *Belosaepia unguia* Gabb, 1860. 1, TMM NPL38042, TMM 21-T-102, Little Brazos River, Brazos Co., Texas. Conotheca layer attached to the guard on the dorsal surface of the phragmocone. The conotheca is thin and loosely attached, falling off in many areas. The curved lines on conotheca are sutures of septa, but septa are broken away. Arrow points to the position of close-up photo; 2, TMM NPL38043, TMM 26-T-100, Rocky Branch, Burleson Co., Texas. Closeup view of the conotheca layer and endoventral prismatic layer on deck portion of phragmocone. The dashed line marks the boundary between layers. Orientation of specimen is similar to A, but oriented to look along the deck wall. Small remnants of septa are present on the conotheca in lower right corner; 3–6, TMM NPL8434, TMM 145-T-52, Two Mile Creek, Leon Co., Texas: 3, cross-section of phragmocone near posterior end (looking toward posterior, dorsal callus at top), showing large siphuncle (inner surface indicated by arrows) with a heavy dorsal thickening that forms the siphuncle band (indicated by top two arrows). Thin areas of siphuncle wall are mostly fragmented and are missing on the right side; 4, ventral view of corona and deck of phragmocone. The deck has a small area of conotheca and endoventral prismatic layer removed, showing the curved septa within the deck; 5, enlargement of chambers on left side of siphuncle, with position of the thin siphuncle wall shown by double dashed lines and arrows pointing to septa and fragmented septa enclosed in matrix; 6, enlargement of siphuncle band in cross section, showing accretionary growth bands; 7, TMM NPL38031, TMM 21-T-102, Little Brazos River, Brazos Co., Texas. Ventral view of the deck of a partial phragmocone missing most of the conotheca. Area where conotheca is preserved is indicated by dashed line; 8, TMM NPL8428, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Curved septa of the deck, exposed along oblique fracture surface; posterior to left, anterior to right; ventral down; matrix fill of the siphuncle at upper right. Note the shingled arrangement of the septa and conotheca. 9, 10, TMM NPL38031, TMM 21-T-102, Little Brazos River, Brazos Co., Texas. Curved septa of the deck, exposed along oblique fracture surface; posterior to left, anterior to right; ventral down; matrix fill of the siphuncle at upper right. Note the shingled arrangement of septa and conotheca, with boundary between septa and conotheca shown at line between white (conotheca) and light gray (septum). The diagram shows structural units, with dashed line showing orientation of growth surface at time of beginning of new septum formation: 11–13, TMM NPL38040, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas; 11, knob of siphuncle deposits (indicated by arrow) at posterior end of phragmocone; 12, ventral view of siphuncle band, displaced and collapsed onto dorsal conotheca. Upper broken margin of siphuncle band marked by thin dashed line. Corona at left; deck broken away; 13, enlargement of noded edge of siphuncle band, showing broken margin where thinner parts of siphuncle wall have broken away (lower part of photo). Scale bars 1, 3, 4, 7, 12 are 10 mm; scale bars 2, 5, 6, 9 are 1 mm.



phragmocone bounded with a ventral deck, the siphuncle occupies 50% or more of the cross-sectional area.

The D-shaped cross section is the result of a flattened ventral margin on the phragmocone. Early in ontogeny, the ventral margin forms a flattened, slightly curved surface (the deck) that has distinct and well-marked boundaries separating it from the remainder of the phragmocone. The deck consists of ventral conotheca thickened with an outer endoventral prismatic shell layer and tightly recurved septa (Fig. 5.4). Meyer (1993) reported the presence of a prismatic shell layer in the deck of *Belosaepia* (his “externe prismatique vacuolaire” of the “lame ventrale”). The deck is equivalent to the structure formed of non-mineralized remnants of ventral septa (the “fork” of Naef) of modern sepiids (Naef, 1921). Within the deck, between the siphuncle and conotheca, septa occur as strong arcuate curves, with the ventral edge of the septum turned towards the posterior end of the skeleton (Figs. 5.8–5.10). This produces a 180-degree fold of the septa and generates a nested set of folds arched towards the anterior, a curvature opposite to normal septal curvature. They adhere tightly to each other, producing a strong planar deck structure. The arcuate folds are more tightly compressed in the center of the deck where separation between the conotheca and siphuncle surface is only 1 mm. The septal folds widen into more open folds (2 mm wide) along the outer edges of the deck and open out abruptly at the margins of the deck to become widely spaced on dorsal portion of the phragmocone. The ventral surface of the deck has very low amplitude undulations produced by thickening at places where edges of septa meet and overlap part of the preceding septum.

Haas (2003, p. 121) stated that the structure forming the deck does not contain conotheca in *Belosaepia*; that the conotheca extends posteriorly to form the corona. This is not true for *B. ungula* and probably not correct for the genus. Fig. 5.2 shows the conotheca curving continuously from the sides of the phragmocone onto the ventral deck, with septa attached to the conotheca in both areas. The conotheca is very thin and is covered ventrally by the thicker endoventral prismatic layer (Fig. 7.4–7.6), a shell layer confined to ventral regions of the skeleton and extending from the deck posteriorly onto the corona and partway up the sides of the skeleton. In *B. ungula*, the endoventral prismatic shell layer extends continuously beyond the deck and covers some of the wings and anterior portions of the corona, providing an anchor for the layer and strengthening the deck. It thins posteriorly on the corona. The corona is part of the guard and composed entirely of secondary shell material. Prisms of the endoventral prismatic layer are 0.01–0.03 mm in diameter and

composed mostly of calcite (determination by X-ray diffraction).

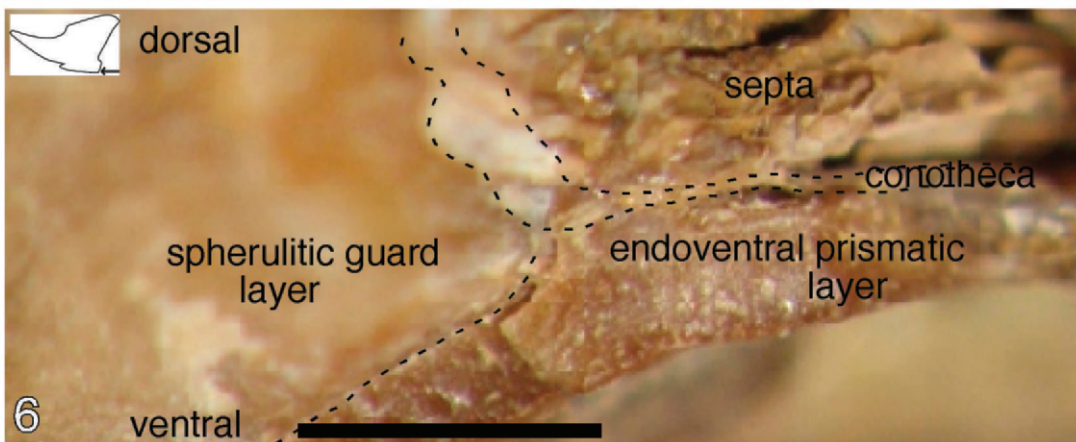
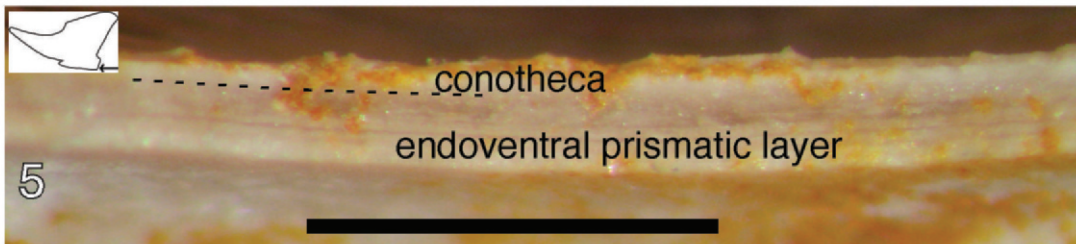
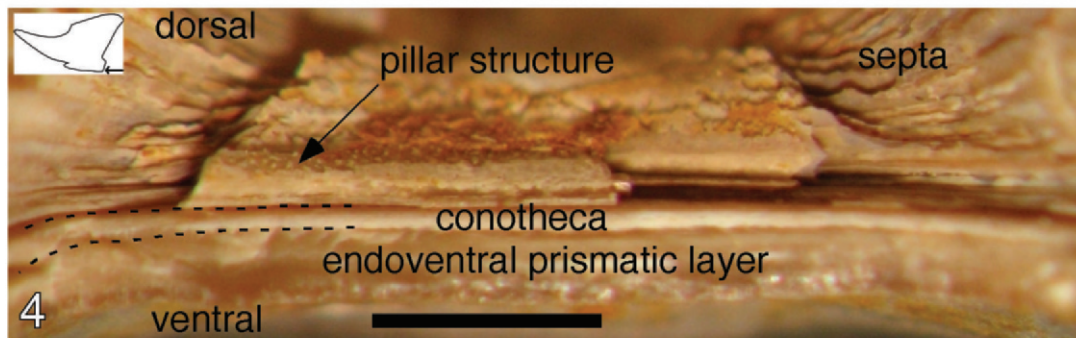
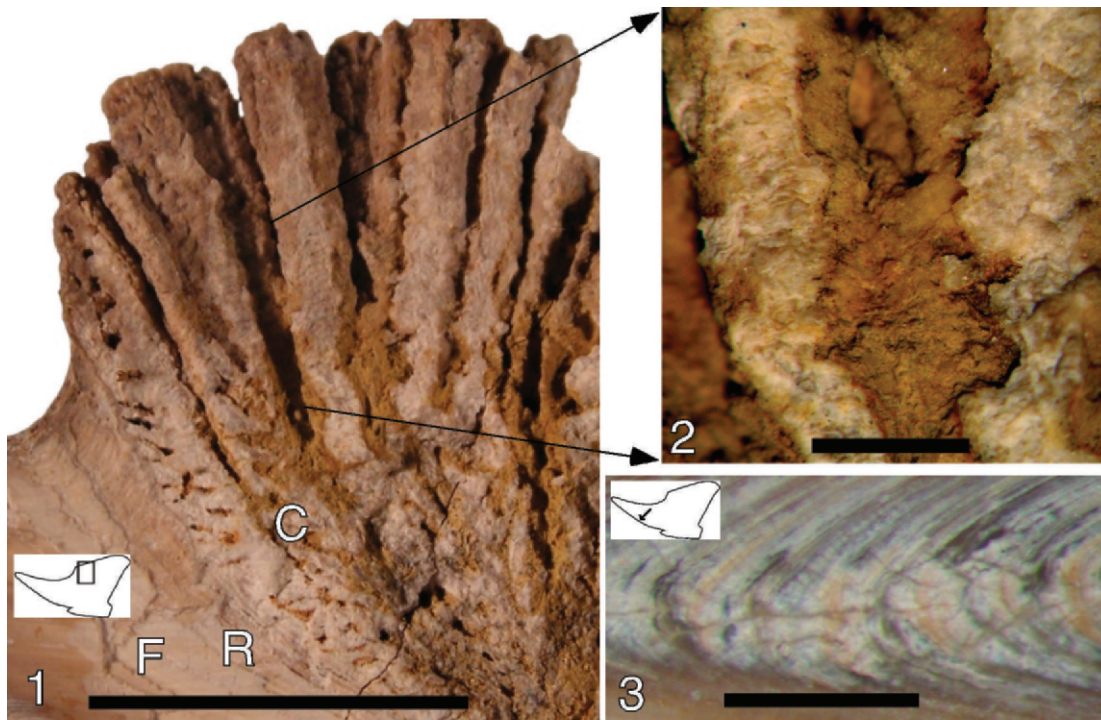
The septa are very thin (0.1 mm or less) in most areas of the phragmocone (Fig. 5.5), especially in the juvenile portion, but thicken to 0.3–0.4 mm thickness on the ventral deck areas of mature specimens (Figs. 5.5–5.10). They are structurally weak, so most skeletons lose their septa and siphuncle early after death and are preserved without chambers. Sutures along the sides of the phragmocone have a very shallow lobe deflection, but this is not apparent on siphuncle steinkerns. The inner portions of septa curve into wide septal necks that extend back to the preceding septum, forming the wall of the siphuncle. The inner surface of the conotheca commonly shows tracking bands, fine lineations aligned in the direction of growth that are formed by translocation of the cephalic retractor muscles as new chambers are formed (Kröger et al., 2005).

Meyer (1993) interpreted the attachment of septa to conotheca of the deck portion in *Belosaepia* to consist of septal margins that flare out and widen within the conotheca. This is structurally improbable in a skeleton produced by accretionary growth and is not consistent with the attachment of septa to conotheca in the deck of *B. ungula* (Figs. 5.8–5.10). In this species, the septa are recurved and attach to the conotheca at a low angle. Growth proceeds with a small posterior offset of the septum-conotheca boundary, producing a wedge-shaped edge on the septum and an overlap of conotheca on the septum margin. When the next septum is added, the conotheca abruptly expands outward and the process repeats, resulting in a shingled arrangement of septal edge and conotheca. This is unlike the structure portrayed by Meyer. The manner of deep septal insertion and thickening of septal margins within conotheca shown in drawings by Meyer (1993) for *B. tricarinata* (and *Ceratisepia*) needs to be re-evaluated.

In areas where septa are closely spaced, tiny chamberlets are present between the septa (Figs. 6.1–6.4), similar to the chamberlets that are present throughout the cuttlebone of *Sepia* (Bandel and Boletzky, 1979; Sherrard, 2000). In both *Sepia* and *Belosaepia* there is a gradient of change from chamberlets formed by linear walls in lateral areas to pillar structures formed of rods and pillars in mid-dorsal and mid-ventral positions. In *B. ungula*, chamberlets with planar walls are present on the edges of the deck (Fig. 6.1) and in some lateral areas (Fig. 6.3), but in dorsal areas chamberlets are produced by pillar structures (Figs. 6.2, 7.4). This same pattern of change in chamberlets from planar wall structure (Fig. 6.4) to pillar structure occurs in sepiid cuttlebones (Sherrard, 2000; personal observations). Chamberlets are also

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FIGURE 6—Characters of *Belosaepia ungula* Gabb, 1860. 1, 2, TMM NPL38031, TMM 21-T-102, Little Brazos River, Brazos Co., Texas: 1, ventral view of chamberlets present in the deck, exposed on an eroded surface beneath the conotheca. Note the planar form of chamberlet walls; 2, chamberlet pillars present between closely spaced septa on dorsal side of phragmocone in posterior region; 3, *Belosaepia* sp., TMM NPL38048, TMM 145-T-200, Two Mile Creek, Leon Co., Texas. Chamberlets in narrow edge of chamber where septum approaches conotheca on lateral wall of phragmocone. Chamberlets have spacing of 0.04–0.05 mm. View looking towards anterior along side of phragmocone; 4, *Sepia* sp., Ras al Khaimah, United Arab Emirates, Persian Gulf. Chamberlets along lateral margin of modern *Sepia* cuttlebone, where central chambers are pulled away from the dorsal guard; 5, TMM NPL8435.1, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Half of a prong tip, split open along fissure plane and broken off at mid-position along length, showing growth lines. This is a natural broken surface exposing the fissure plane, not a cut section; 6, TMM NPL38044, TMM 26-T-100, Rocky Branch, Burlison Co., Texas. Delamination along fissure plane in a prong; 7, TMM NPL38046, TMM 145-T-200, Two Mile Creek, Leon Co., Texas. Growth lines arranged in probable monthly clusters. Upper part of the prong shows radial plates that produce ridges and rills on the dorsal surface of the prong; 8, TMM NPL8435.1, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Cross-section of prong, showing growth lines and radial plates that form the dorsal and lateral portions of the prong; 9, TMM NPL4871.2, TMM 113-T-9, TMM 4871, Alabama Ferry, Trinity River, Houston Co., Texas. Accretionary growth lines in the posterior end of a prong; 10, 11, TMM NPL38054, Newton, Mississippi: 10, part of skeleton split along the median plane of the fissure surface and adjacent callus. Arrows indicate the rod structure in a transition zone between prong and callus. Areas where skeleton has been dissolved after burial are labeled and marked by a dashed line (see text for explanation). Photo is reversed to show orientation consistent with other specimens; 11, detail of rod structure (R). Note the sharp boundaries with the arborescent plumes (C) of the callus and plate units of the prong adjoining the fissure plane (F). Scale bars 1–4, 7–11 are 1 mm; scale bars 5, 6 are 5 mm.



reported to occur in the phragmocone of *B. dufourti* by Meyer (1993). In both *Belosaepia* species, chamberlets have a limited occurrence within the posterior region of the phragmocone and are present only where chamber walls are very closely spaced. The limited development and minute size of chamberlets makes them difficult to observe. Only a few specimens in our sample set show them clearly. The significance of pillar structure in determining relationships of coleoids is considered further in the Discussion section.

The siphuncle tube is formed by adjoining septal necks of the septa, not as a separate shell component. Septal necks form by a sharp curvature of the septum and turn adapically to touch but not fuse with the preceding septum. Because of the curvature of septum to form the septal neck and lack of connecting ring, the majority of siphuncle pinches and swells in diameter and has an undulose wavy surface (Fig. 2.1). This manner of siphuncle construction is also present in the genus *Ceratisepia* (Meyer, 1993, pl. 2, fig. 9). The siphuncle wall is of similar thickness except along the dorsal margin of early-formed parts of the phragmocone. In this area, the siphuncle is secondarily thickened to nearly 0.2 mm thickness in a narrow elongate strip described here as the siphuncle band (Figs. 5.6, 5.11–5.13). This unusual feature is distinct from other parts of the siphuncle wall because the siphuncle band has well-defined wavy margins where it thins abruptly to the much thinner lateral portions of the siphuncle. Prominent accretionary growth lines are visible in the cross section of a siphuncle band shown in Fig. 5.6, an illustration showing how the siphuncle band formed by infilling into the siphuncle interior. It is a secondary deposit produced during late stage growth.

On mature specimens, the first-formed portion of the siphuncle is entirely filled with secondary deposits. These secondary deposits produce knobby projections on the posterior end of the secondary deposits fill (Fig. 5.13) and the knobs can be recognized as dimples on siphuncle steinkerns.

ONTOGENY

Growth banding in the prong of *B. ungula* indicates that large individuals lived as long as three years. Thick dark bands visible in prong cross-sections near the base of the prong are probable annual increments (Figs. 4.5, 8.4, 8.5), similar to accretionary growth present in most molluscan shells and other phyla (Schöne et al., 2006). Commonly, two zones of darker growth bands can be seen in mature specimens. Bettencourt and Guerra (2001) showed that sepiids add thin daily growth layers and add septa at a rate of 3–8 days per septum (the rate of septal addition correlates with ambient temperature), a rate of growth comparable to interpretations of growth in *B. ungula*. The last set of growth bands in the prong of *B. ungula* is typically thin, suggesting that the animal stopped adding skeletal material at the time of sexual maturity. Subsequent life is associated with skeletal resorption instead of secretion. The dominance of skeletons of similar size (determined by measurements of diameter of base of the prong) in fossil collections is consistent with a life history of

post-spawning mortality, with death following a single episode of reproduction (Boyle, 1983).

The first growth stage is an embryonic skeleton with a protoconch having the shape of a shallow bowl. The initial chamber is produced by a 1 mm diameter septum secreted at the back of the bowl, and the protoconch is enclosed within a second 2 mm diameter septum emplaced along the rim of the bowl (Fig. 8.6). Asymmetric growth of the dorsal and ventral margins of the conotheca began during subsequent embryonic chamber formation, producing the slanted septa and chambers characteristic of belosaepiids. After the first few chambers were added, the phragmocone changed from a circular cross-section to a rounded rhomboid cross-section with a flattened ventral surface. Sutures marking the position of chamber walls on the dorsal margin are widely spaced for the first two or three chambers after the protoconch, then become closer, with the narrowest spacing present on the fifth or sixth chamber (counting initial chamber) before the spacing becomes greater with growth (Fig. 8.7). This is consistent with hatching from a large egg in a shallow water environment (Boyle, 1983), when it emerged from the egg as a fully functional individual. The chamber with narrowest septal spacing probably marks the time of hatching from the egg. The conotheca sometimes shows small irregularities for several chambers following this position, indicating variable conditions that fit with a new life as a hatchling exposed to ocean waters. At this growth stage there is a tiny anterior deflection on the dorsal margin of the septa (Figs. 8.6–8.7). Hewitt and Jagt (1999) concluded that *Belosaepia* hatched when chamber four had formed, comparable to the seven septa condition and 8 mm shell length for modern *Sepia* (Naef, 1922; Denton and Gilpin-Brown, 1961a), a pattern similar to the embryonic development and hatching of modern *Nautilus belauensis* (Landman et al., 1989; Mutvei et al., 1993). The shell diameter of *B. ungula* increases smoothly from the protoconch to the adult shell. There is no constriction in phragmocone diameter at the position of hatching or at the septal boundary of the protoconch. Thus, there is no indication of a caecum and prosiphon constriction indicating the development of a closing membrane on the protoconch.

During the rapid expansion of chambers in adolescence and early maturity, a heavy mineralized guard was secreted over the surface of the phragmocone. Late in maturity, skeletal secretion ceased and the entire skeleton was thinned by resorption (Fig. 9). Areas of the skeleton modified by resorption can be recognized by the appearance of truncated growth lines showing on the surface, often shown in unusual patterns. Growth lines are not visible on unmodified skeleton surfaces because growth occurs by accretion of thin layers over the entire surface of the skeleton. Therefore, any surface that shows distinct growth lines is either a dissolved or broken surface. As dissolution continued to an advanced state, many distinctive characters were greatly modified or lost. The skeleton became smaller and thinner and acquired a different appearance. The prong was thinned and surfaces show

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FIGURE 7—Microstructure characters of *Belosaepia ungula* Gabb, 1860. 1–3, TMM NPL38047, TMM 145-T-200, Two Mile Creek, Leon Co., Texas; 1, arborescent plume growth in callus, exposed along break propagated from fissure plane in prong (in lower left corner of the photo); 2, enlargement showing wavy lamellae capping the tops of plumes; 3, detail of growth axis in prong, showing less dense microgranular construction of the axial zone, with a sparse array of denser skeletal plates that fan out from the growth axis; 4, TMM NPL8429, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. View of cross section of the ventral layers of the deck and attached partial septa. The small stubs present on septa are the bases of pillars in the pillar structure zone; 5, TMM NPL7915.1, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas. Closeup of broken surface of the ventral layers of the deck, showing thin conotheca and thick endoventral prismatic layer; 6, TMM NPL38039, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. View of lateral edge of deck where the endoventral prismatic layer extends onto edge of corona. Scale bar 1 is 10 mm; scale bars 2–6 are 1 mm.

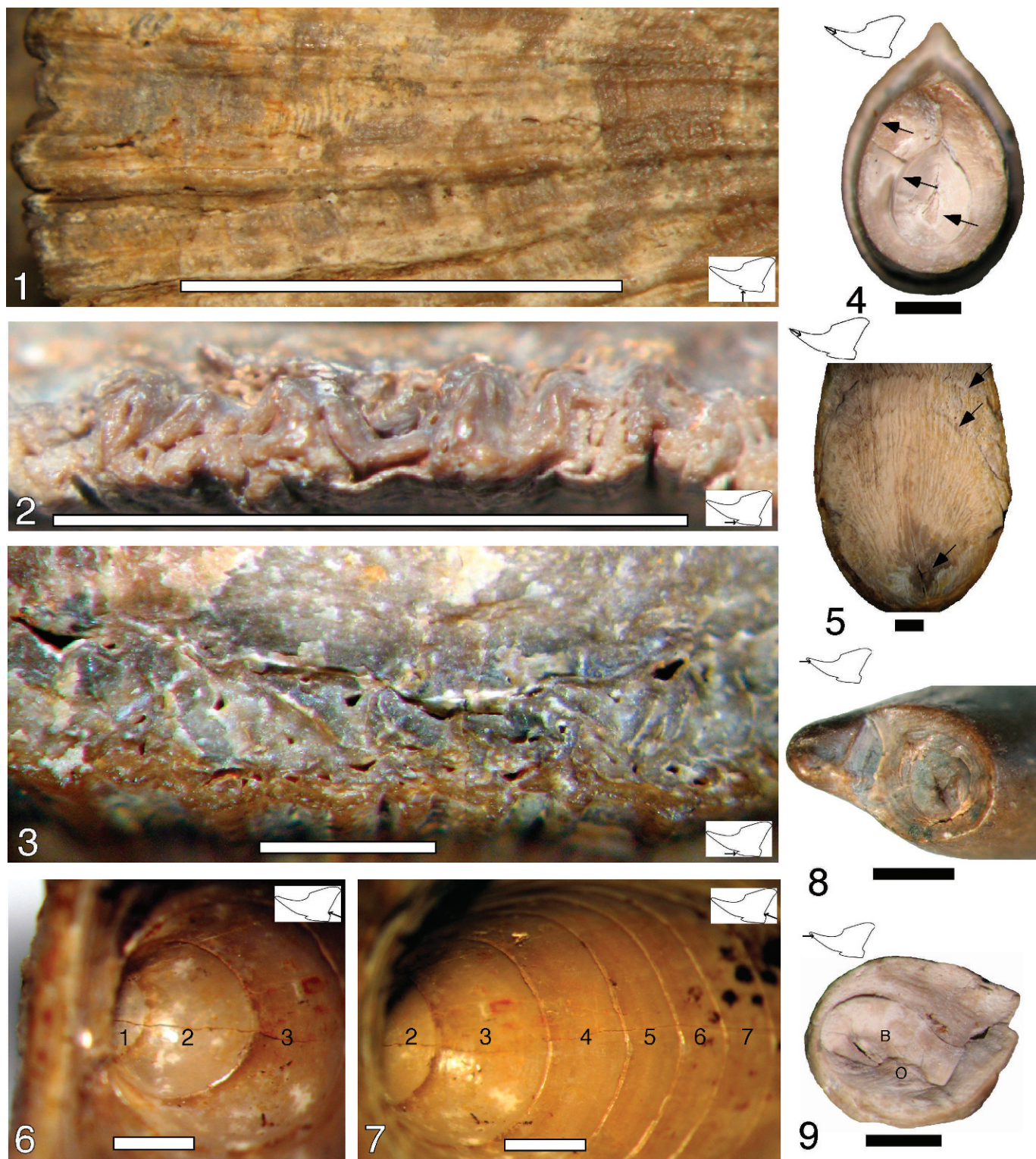


FIGURE 8—Characters of *Belosaepia unguia* Gabb, 1860. 1, 2, TMM NPL38041, TMM 21-T-102, Little Brazos River, Brazos Co., Texas; 1, ventral surface of posterior edge of corona beneath prong, showing radial growth elements, fine grooves between growth elements and concentric growth increments; 2, posterior edge of corona beneath prong, showing irregular form of growth elements; 3, TMM NPL38049, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Fracture surface across corona, showing irregular form of growth elements and void cavities. Upper half of photo shows more regular lamellae of secondary guard layer. At this posterior location, the corona lacks a distinct endoventral prismatic layer; 4, TMM NPL8432, TMM 145-T-52, Two Mile Creek, Leon Co., Texas. Cross-section of a prong, showing growth bands. Arrows points to prominent growth bands marking probable annual increments; 5, TMM NPL7913.3, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas. Cross-section of anterior portion of a prong, showing concentric growth bands and radial plate structure. Arrows points to prominent growth lines marking probable annual increments. The sawtooth surface of growth bands in upper part of prong show successive positions of dorsal rills on the prong; 6, 7, *Belosaepia* sp., TMM NPL38045, TMM 26-T-100, Rocky Branch, Burleson Co., Texas. Photos reversed to match orientation of other specimens; 6, embryonic dorsal conotheca showing the protoconch (part) and spacing of septal sutures. The protoconch chamber is at far left and subsequent chambers are numbered; 7, embryonic and nepionic conotheca showing a wider spacing of three septa anterior to the protoconch, followed by a closer spacing of septa. The change

truncated growth lines (Figs. 9.8–9.10), the corona was thinned or completely removed (Figs. 9.1–9.2), the callus was smoothed off (Figs. 9.2, 9.6) and nodes on the dorsal shield were smoothed (Figs. 9.3, 9.5–9.6). Associated with loss of the corona by dissolution, resorption proceeded to the point of removal of the ventral deck and some of the ventral wall surrounding the protoconch and early chambers. When the phragmocone was truncated in this manner, support was removed for the thin-walled septa and it is probable that most of the phragmocone was resorbed, reducing the skeleton to a rudimentary remnant of the formerly elaborate guard. The presence of truncated growth lines on a smooth surface is a characteristic feature of skeletal resorption. This old age modification of the shell appears to be a normal part of the life cycle of belosaepiids that may be due to a biochemical need for calcium during a phase of the life cycle. Late stage dissolution often produced a semi-circular groove over the truncated protoconch (Figs. 9.4, 9.7). The presence of this semi-circular groove was used as a defining character in the description of some proposed species of *Belosaepia* (especially *B. uncinata* Palmer, 1937), but the feature is indicative of a growth stage and is not species specific.

Ontogenetic changes produced a skeleton with very different appearance during early growth and late growth stages. While growing to maturity, the skeleton was large and had well developed distinctive morphological characters that are definitive for the species. In late maturity, dissolution removed many of these characters as the skeleton thinned. Because of resorption, the oldest specimens are smaller than mature adult specimens. As resorption increased, dissolution modified the skeleton so much it became indeterminate for species identification. Many skeletons in belosaepiid collections show evidence of dissolution, but only a few show extreme dissolution.

PRESERVATION

Most belosaepiid fossils consist of fragments of the heavily mineralized posterior part of the skeleton. Only specimens excavated from fine grained sediment matrix or preserved in concretions retain weak areas of skeleton. The skeletons recovered as fossils were subject to damage from predation on the animal, scavenging on the carcass, fragmentation in the sediment due to sediment compaction, dissolution and alteration by diagenesis in the sediment and degradation by weathering upon exposure by erosion. Skeletons were commonly tunneled by endolithic borers while on the seafloor and preserved in a weakened condition.

Examples of skeletons abraded during transport by currents show roughened outer surfaces on the skeleton and rounding of edges (Fig. 10.1), but interior recesses remain smooth and parts of the conotheca remain attached to the guard. A test to determine if abrasion would produce smooth surfaces showing truncated growth lines was performed by placing specimens with well-preserved ornamentation and conotheca, but lacking septa, in a rotary tumbler with abrasive grit (Fig. 10.2–10.4). After 120 hours of tumbling with a half sand and half water mixture, some wear of surface layers was produced on protruding areas and high points, including the spalling of parts of the outermost growth layer. There was no loss of shell

on protected areas of the skeleton, including no further loss of conotheca within the phragmocone. The result of sand abrasion is to roughen the surface, not smooth it.

The belosaepiid skeleton is heavy and probably sank to the seafloor upon death of the animal, in contrast to the sepiid cuttlebone that floats away from the carcass of the animal after death. Because of the heavy mineralization on the posterior end of belosaepiid skeletons, the skeleton tended to sink prong-downward, leaving the structurally weaker anterior areas exposed in the water, exposing the anterior body tissue to predation and scavenging. This is another factor contributing to the rarity of preservation of the anterior regions.

There are many examples of damage to the prong that occurred during the life of the animal, resulting in abnormal growth on the prong. Some specimens show loss of the tip of the prong, with skeletal tissue later secreted over the broken surface (Figs. 8.8, 8.9), and one specimen in our collection has the entire prong broken off at the base with a thin layer of regenerated skeletal tissue over the break. More common are examples of damage to a small area that is overgrown with irregular skeletal layers, producing weak areas on the prong. Other examples show a twisted fissure plane in the center of the prong or lateral areas with swellings and/or cavities. The areas presently seen as cavities were probably not original cavities but were repaired with skeletal tissue containing a large amount of organic tissue that has subsequently been lost by decay. Even so, these areas would have been structurally weaker than the fully mineralized portion of the prong.

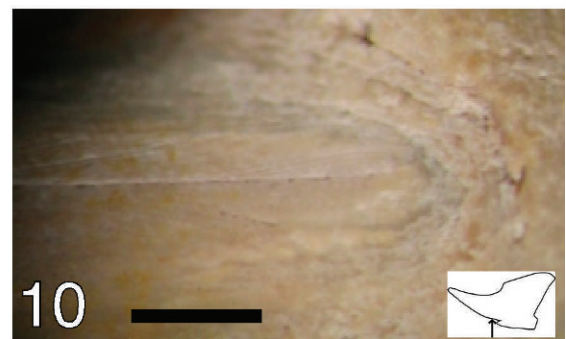
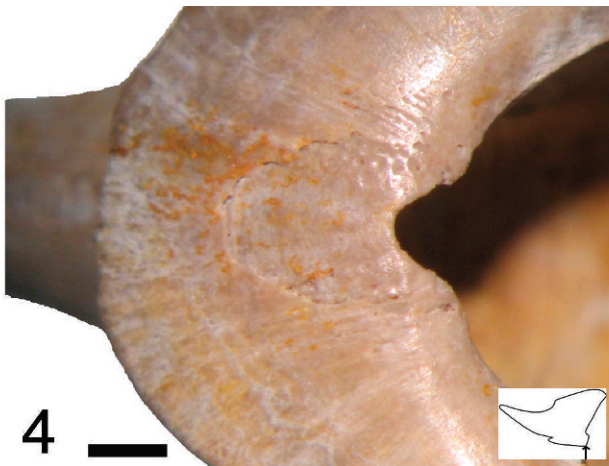
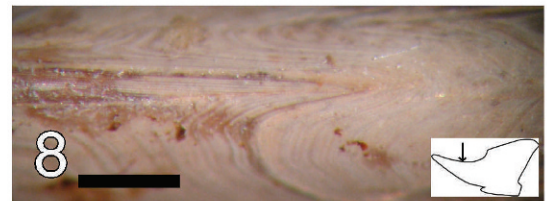
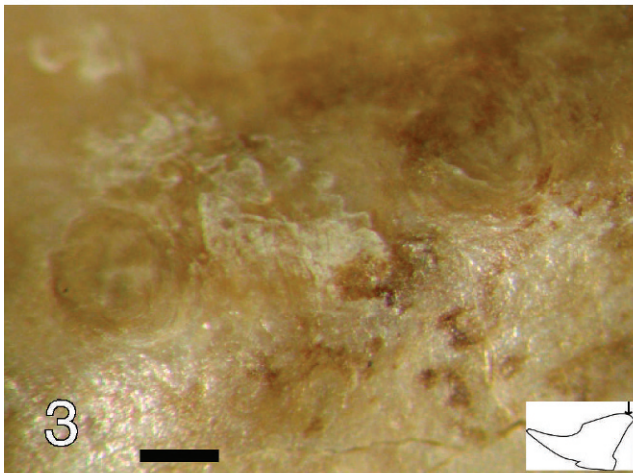
BELOSAEPIID TAXONOMY

The heavily calcified posterior portion of the skeleton has been used for describing and naming 16 North American belosaepiid species (Gabb, 1860; Palmer, 1937; Allen, 1968; Garvie, 1996; Weaver and Ciampaglio, 2003). These were named without knowledge of ontogenetic changes in the belosaepiid skeleton, so a re-assessment of these species is needed at this time. Appearance and size proportions change during ontogeny, especially when selective dissolution occurred in later growth stage. These changes reveal that some differences in skeleton used as a basis for species determination are the result of ontogenetic change, indicating the need for placing some previously described species names in synonymy.

Characters used to distinguish species are primarily characters present on the heavily calcified posterior guard portion of the skeleton. These include size and shape of the prong, angle and direction of curvature of the prong relative to anterior-posterior axis, size and shape of the ventral corona, arrangement of plumose elements in the callus, presence and shape of a shoulder at the posterior end of the callus, features of secondary solid overgrowths and the size, shape and arrangement of nodes on the dorsal shield. Genera are distinguished by major differences in development of the prong and callus and secondary overgrowths.

Various authors following Bronn (1838) have used the spelling *Belosepia*; however that is an unjustified emendation of *Belosaepia* (Voltz, 1830, p. 23).

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in septal spacing at chambers 4 to 6 marks a time of hatching from egg. Note the small deflection of suture on mid-dorsal line of conotheca. Fine lineations of retractor muscle tracking bands are present on the chamber walls between septa; 8, TMM NPL38050, TMM 113-T-9, Alabama Ferry, Trinity River, Houston Co., Texas. Breakage of the tip of a prong and repair with irregular growth layers. The small secondary tip was produced by damaged tissue; 9, TMM NPL38034, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Irregular growth and repair on a prong with previously broken tip (B). Area marked with (O) is zone of growth lamellae that overlap broken tip. Scale bars 1, 2 are 5 mm; scale bars 3–9 are 1 mm.



SYSTEMATIC PALEONTOLOGY

Repository.—Figured specimens are housed in the non-vertebrate paleontology collections of the Texas Natural Science Center of the University of Texas, Austin.

Family BELOSAEPIIDAE Dixon, 1850
Genus BELOSAEPIA Voltz, 1830

Belosaepia VOLTZ, 1830, p. 22–23; EDWARDS AND WOOD, 1877, p. 23–29, pl. 1, figs. 1–7; NEWTON AND HARRIS, 1894, p. 119–122, pl. 10; NAEF, 1922, p. 82–83, figs. 33–34; PALMER, 1937, p. 505–510, pls. 76–77; ALLEN, 1968, p. 34–37; MEYER, 1993, p. 292–300, pl. 3, figs. 1–39, pl. 5, figs. 1–3; GARVIE, 1996, p. 121; HEWITT AND JAGT, 1999, p. 311–314, figs. 1A,B, 5B.

BELOSAEPIA UNGULA Gabb, 1860
Figures 1–11

Sepia (*Belosepia*) *ungula* GABB, 1860, p. 376, pl. 67, figs. 1–4; PALMER, 1937, p. 505–506, pl. 77, figs. 2, 3, 5–7, 14.

Belosaepia uncinata PALMER, 1937, p. 507–508, pl. 77, figs. 8, 9, 18, 20, 21.

Belosaepia alabamensis voltzii PALMER, 1937, p. 509, pl. 77, figs. 10, 12.

Belosaepia harrisi PALMER, 1937, p. 510, pl. 77, figs. 11, 17, 19.

Description.—Large belosaepiid (to 50 mm wide, 180 mm length) skeleton with stout tooth-like posterior prong; prong curved dorsally and with sharp dorsal carina, rills and median fissure plane; dorsal callus composed of plumose skeletal elements partly fused and arranged in 3–5 rows; zone of rod structure present on median plane between callus and prong; arcuate ventral corona attached to base of prong; noded lateral surfaces on posterior region below callus; arched dorsal shield decorated with large and small nodes, with large nodes arranged in rows; small wings and hyperbolar zones on posterior part of dorsal shield near protoconch; phragmocone with oblique septa and thin ventral deck; deck covered with endoventral prismatic shell layer, that extends onto adjacent parts of corona and wings; siphuncle large and with D-shaped cross-section, formed by septal necks of the septa; extensive resorption of skeleton occurring on older specimens, changing shape and size of guard characters and loss of posterior ventral portion of phragmocone.

Discussion.—Resorption of the skeleton late in life produces major changes in appearance of *Belosaepia* specimens. Nearly all of the specimens described by Palmer (1937) show moderate to extensive resorption of the skeleton (Palmer's type specimens were examined June 2008). The feature of concavity in the ventral surface used to define the species *B. uncinata* Palmer, 1937, and also present in *B. harrisi* Palmer, 1937, is a late stage dissolution feature (see Fig. 9.4) without value in defining species. The smooth, flattened surfaces used to characterize *B. harrisi* are also the result of general

dissolution produced late in life. The names *B. uncinata*, *B. harrisi* and *B. alabamensis voltzi* Palmer, 1937 all are based on resorbed specimens that fit well within the growth series of *B. unguila*. The species *B. veatchii* Palmer, 1937 and *B. saccaria* Palmer, 1937 are based on specimens with little resorption and are valid species. However, *B. alabamensis* Palmer, 1937 is most similar to *B. veatchii* and is a synonym of that species.

FUNCTIONAL MORPHOLOGY

Interpretations of the function of parts of the belosaepiid skeleton are aided by comparison with the cuttlebone of living sepiids and reconstructions of ancient sepioids. Jeletzky (1966) stated that the heavy skeleton of Cenozoic sepioids was probably important for multiple purposes of buoyancy control, protection and digging into substrate, a conclusion that is supported by our study. The numerous chambers of belosaepiids indicate that the phragmocone was important in buoyancy control, but the distinctive form of the heavy prong and callus suggest that digging and protection were also important functions. The belosaepiid animal was more deep-bodied than the vertically compressed modern sepiids (Figs. 2, 5.3, 11).

Discussion of function for the belosaepiid skeleton must first consider the role that a chambered shell plays in buoyancy for the living animal. The belosaepiid body plan is similar to sepiids', indicating belosaepiids maintained a horizontal orientation. With a center of buoyancy (produced by phragmocone chambers) located in a posterior position and heavy body tissue (head, tentacles) at the anterior end of the body, dense tissue is needed at the posterior end to achieve a horizontal orientation without having to exert energy continually while in the water (Naef, 1921; Haas, 2003). Monks and Wells (2000), in a discussion of the orientation of the coleoid *Spirulirostra anomala*, also indicate that the placement of the relatively heavy guard would give the animal a horizontal orientation instead of the head-down vertical position of modern *Spirula*. The belosaepiid prong and vascular callus of the skeleton provide a dense tissue counterweight to the dense head region, on opposite sides of the center of buoyancy. In sepiids, lipids and gases in the chambers provide assistance in maintaining neutral buoyancy (Denton and Gilpin-Brown, 1961c; Denton, 1974) and this mechanism for fine-tuning balance was probably utilized by belosaepiids as well.

Belosaepiid skeletons grew with a definite ventral curvature. Naef (1921) argued that the ventral curvature of the chambered skeleton caused the position of the center of buoyancy to continually shift away from the central axis of the body during growth, if not compensated by changes in mass distribution. Jeletzky (1966) noted that there is a strong correlation between degree of coiling of the phragmocone and development of a heavy skeleton in Cenozoic sepioids. The tendency of skeleton growth to create complex changes in the

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FIGURE 9—Late stage dissolution features on the skeleton of *Belosaepia unguila* Gabb, 1860. 1–3, TMM NPL38036, TMM 21-T-1, Little Brazos River, Brazos Co., Texas: 1, 2, smoothed, resorbed surfaces on prong, flanks, callus and corona. Most of the corona has been dissolved. The callus has been smoothed and the pits between plumes enlarged; 3, enlargement of a dorsal shield, where node ornament is resorbed down to the underlying surface; 4, TMM NPL7913.1, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas. Ventral surface of a corona where dissolution has removed the outer shell layer and breached the protoconch portion of the phragmocone, producing a notch on the anterior edge of the corona, and removed the deck; 5–7, TMM NPL38038, TMM 21-T-1, Little Brazos River, Brazos Co., Texas; 5, skeleton with very late stage dissolution that has shortened the prong to a blunt stub and completely resorbed the callus and corona; 6, rounded callus and dorsal shield; 7, a large notch present over breached protoconch, on phragmocone with dorsal conotheca and septal remnants present; a demonstration that dissolution occurred during life and not on dead shells; 8, TMM NPL38037, TMM 21-T-1, Little Brazos River, Brazos Co., Texas. Closeup of dorsal surface of a prong, showing truncated growth lines; 9, 10, TMM NPL7913.2, TMM 113-T-2, Hurricane Bayou, Houston Co., Texas. Dissolution on side of a prong, showing truncated growth lines. Scale bars 1, 2, 5–7 are 10 mm; scale bars 3, 4, 8–10 are 1 mm.

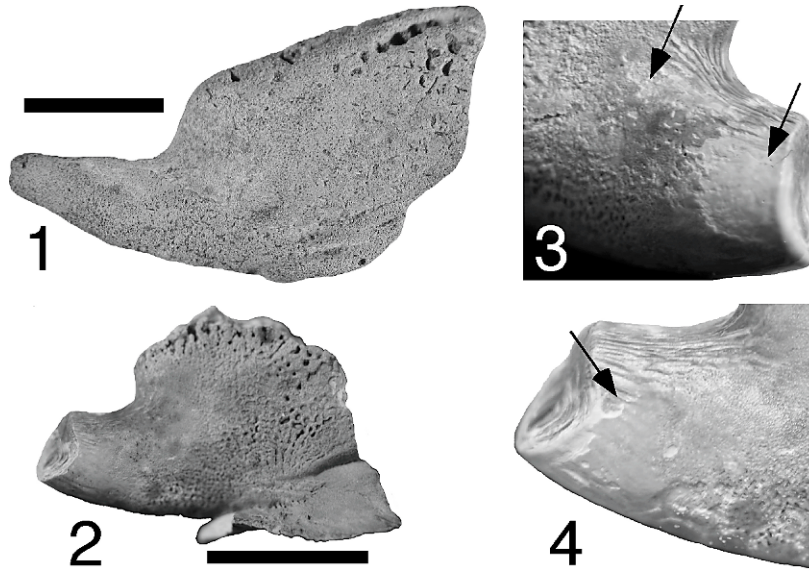


FIGURE 10—Natural and artificial abrasion on specimens of *Belosaepia unguia* Gabb, 1860. 1, TMM NPL38053, TMM 113-T-36, upstream of Alabama Ferry, Houston Co., Texas. Natural abrasion on specimen recovered from channel sand deposit, showing extensive pitting of surface and rounding of corners; 2–4, TMM NPL38052, TMM 21-T-1, Little Brazos River, Brazos Co., Texas: 2, unworn specimen before abrasion experiment; 3, 4, condition of same specimen after abrasion experiment, with arrows pointing to areas of wear and smoothing, showing that wear is confined to protruding corners of skeleton. Scale bar is 10 mm.

location of center of buoyancy suggests that belosaepiids were not pelagic swimmers. A benthic demersal life habit was much more practical, where minor changes in center of buoyancy would be less significant, especially if the animal rested on or in the sea bottom much of the time.

The shape of the prong with a tooth-like morphology and a pointed termination suggests that this feature had function beyond simple balancing for buoyancy control. With a body shape similar to modern cuttlefish, the belosaepiid animal was probably demersal, moving rapidly only for short periods of time and resting on or in the sea floor and digging down into loose sediment to hide when not active. A benthic life habit is indicated by the large protoconch and hatching stage (Figs. 8.6, 8.7), similar to that of modern sepiids (Boyle, 1983). Behavioral studies of living sepiids and rossiids show that these animals dig backwards into sand or mud. Anderson et al. (2004) described burying behavior in *Rossia pacifica* (family Sepiolidae). Burial begins by using the funnel to create a depression, and the animal dives into the depression while the resulting sand cloud settles over it. The second pair of arms sweeps sand over the body until only the eyes remained exposed. Naef (1921) and Denton and Gilpin-Brown (1961b) noted similar behavior with sepiids that use the lateral fins to stir up sediment and then bury themselves, adjusting the

sediment until only the eyes are exposed. Naef (1921, p. 479–480) stated that extinct sepioids with a spine-like process on the posterior end of the skeleton (including *Spirulirostra*) were probably bottom dwellers like sepiids and inferred an important functional role for the belosaepiid prong in initiating digging for burial: “The large rostrum [=prong] has to be considered as an indispensable burrowing tool, because large fins like those of the Sepiidae and Sepiolidae probably were not yet present.” A large posterior prong would thus be useful for the belosaepiid as a digging tool.

It is noteworthy that purse crabs (*Myropsis quinquespinosa*), which also dig backward into sediments, possess a relatively large prong-like posterior spine on the carapace (Williams, 1984, fig. 222; M. Wicksten, personal observation). Belosaepiid fossils are found in deposits from shallow marine sandy or muddy bottoms, environments in which modern digging cephalopods live. The location and use of the funnel in these fossils remains unknown, but the heavy prong could have aided the animal in burying itself in the sediment and staying in place, leaving the respiratory opening and eyes exposed but camouflaged.

The corona is a distinctive feature attached to the base of the prong whose function is difficult to interpret. Because the corona is thin and structurally weak, it is unlikely to be an

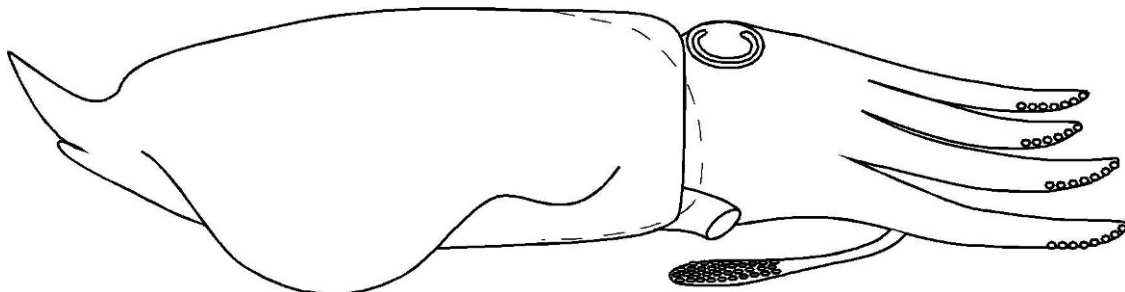


FIGURE 11—Interpretation of living *Belosaepia unguia* Gabb, 1860. The skeleton indicates that animal was probably more deep-bodied than living sepiids. Tissue of the head and tentacles modeled on living sepiid species. For orientation with fossils, anterior end of the skeleton (dashed line) is shown.

attachment site for fin muscles. It is located close to the posterior end of the body cavity where the body wall becomes thin over the prong and may have served as an attachment site for the more muscular mantle wall of the body cavity. The arched shape and flared sides of the corona would serve an excellent attachment point for the posterior end of the body cavity wall. For some individuals, late stage resorption removed all or nearly the entire corona, showing that this attachment area was not needed during late maturity.

The callus and adjacent areas of the dorsal surface of the skeleton are more vascular than the dorsal surface of the sepiid cuttlebone. An irregular surface on skeletal elements is often associated with attachment of major muscles. However, modern sepiids provide evidence against this interpretation. The sepiid cuttlebone is located beneath the tough body wall, but is loosely held within the body and has no major muscle attachments, even in areas of roughened dorsal surface (T. Yancey, personal observation). There is no obvious function for the callus and vascular areas, and the great variability in development of the callus is compatible with lack of direct function. However, a minor protective function for strengthening the skeleton above the phragmocone or as a storage device for storing excess calcium carbonate is possible. Large amount of skeleton were removed (at least one-half by volume) in late maturity. This may have been associated with spawning or general reproductive activity at maturity, when metabolic activity changes and skeletal mass is not needed.

DISCUSSION

The documentation of many distinctive macrostructure and microstructure characters in the skeleton of *B. unguis* provides a basis for comparing it with other belosaepiid taxa. Several very distinctive characters of *Belosaepia* are present in species of other belosaepiid genera, including *Ceratisepia* Meyer, 1993, and *Anomalosaepia* Weaver and Ciampaglio, 2003. The characters may be modified in these other taxa or may be suppressed, but there is a common plan of organization among species of the Belosaepiidae. Many of these characters also occur in the family Sepiidae and a similar plan of organization will probably be found in other Cenozoic coleoid families as well. These appear to be homologous structures that will be important in determining phyletic relationships of skeleton-producing coleoid taxa. Much work remains to be done to determine which characters can be used to identify homology among coleoid taxa.

The similarity of characters present in coleoid taxa is useful in testing the hypothesis of Bandel and Boletzky (1979, p. 348–349) that pillar structure is confined to septal necks in cephalopod skeletons and is a homologous structure in different genera. Based on a comparison of pillar structure in sepiids, spirulids and nautiloids, Bandel and Boletzky proposed that pillar structure is confined to septal necks adjacent to the siphuncle and extended the concept to infer that the chambered portion of sepiid skeletons is composed of exaggerated development of septal necks. Therefore, they concluded that the chambered portion of sepiids is not equivalent to regular chambers in other cephalopods. The presence of pillar structure and chamberlets adjacent to conotheca and in mid-portions of septal walls as well as on the septal necks in *Belosaepia* is evidence that the deduction of Bandel and Boletzky is not correct. A better explanation is that chamberlets and pillar structure occur where septa are very closely spaced and develop as a strengthening device. Therefore, the sepiid chambered skeleton is composed of dorsal septal walls strengthened by pillar structure. This

interpretation is further supported by the equivalence of the fork structure (of Naef) in sepiids to the deck structure in *Belosaepia*. Thus, the suggestion that the septa in *Sepia* are exaggerated septal necks is not justified and pillar structure should not be regarded as a homologous feature among major groups of coleoids.

The determination that a prismatic shell layer (the endoventral prismatic layer) covers the ventral surface of *B. unguis* and covers a very thin conotheca layer on the deck of this species contradicts the interpretation of Haas (2003) that the conotheca extends in a posterior direction in *Belosaepia*, instead of towards the anterior. Species of the genus *Belosaepia* contain a partly modified but fairly typical phragmocone, indicating that the degree of similarity of *Belosaepia* with other coleoid skeletons is greater than previously assumed. An implication of this determination is that the endoventral prismatic layer may be present on other belosaepiid genera. Meyer (1993) indicated that an endoventral prismatic shell layer is present on other species of *Belosaepia* and on other belosaepiid genera, which suggests this is a general character. This is a reasonable inference, but it needs to be verified with further observations.

The determination that *B. unguis* does not have a prosiphon and caecum is important if this feature is used to infer phyletic relationships among coleoid taxa. Jeletzky (1969, p. 27) and Meyer (1993) inferred the presence of a shallow constriction of the phragmocone at the position of the first septum in *Belosaepia*, a feature also reported to be present in the ancestral *Ceratisepia* (Meyer, 1993; Hewitt and Jagt, 1999). This constriction was interpreted to be indicative of a prosiphon and caecum condition; features that are associated with a pelagic life habit (Jeletzky, 1966). The presence of a prosiphon and caecum condition should not be expected in *Belosaepia*, an animal that had a benthic life habit. Illustrations of the embryonic chambers in *B. unguis* show no indication of a constriction in diameter. The interpretation that this feature is present in *Belosaepia* needs to be re-evaluated. Although used as a character for determining phylogeny (Engeser, 1990; Meyer, 1993), a prosiphon and caecum condition appears to be environmentally controlled and is important mostly at a low taxonomic level, as suggested by Hewitt and Jagt (1999).

The presence of a weak fissure surface within the prong is puzzling. The remainder of the prong is solid and strong. The fissure surface may correspond to a line formed by the junction of separate lobes of mantle tissue secreting the prong. The mechanism can be compared to the midline on modern cowrie gastropod shells (family Cypraeidae), in which folds of the mantle overlap the dorsal surface of the shell to secrete the overgrowths that cover the shell. In *Belosaepia*, the tendency of the prong to split easily into halves suggests that the fissure could have contained a much higher organic content than the other parts of the skeleton. If this interpretation of prong formation is correct, it suggests that tissue covering the prong was very thin or retractable, a deduction supported by the frequency of damage to the end of the prong (Fig. 8.8–8.9).

A specimen of *B. unguis* from Mississippi (Figs. 6.10, 6.11), collected in more carbonate-rich sediments than belosaepiid-producing sediments in Texas, shows cavities along the fissure surface in the prong and reveals them to be a result of selective dissolution. The prong on this specimen has a large cavity in the center of the posterior end, but the cavity does not extend to the anterior end. The anterior end of the prong can also be seen (Fig. 6.10) because this specimen has partly fractured along the median plane of the prong and callus, revealing the interior of the anterior end of the prong and adjacent callus.

There is a small amount of dissolution along the growth axis at the anterior end of the prong, but it also has a blind termination. Selective dissolution also provides an excellent view of the rod structure present between the plume structure of the callus and sheet structure of the proximal part of the prong. The presence of a slit-like opening on the posterior end of a belosaepiid prong is the result of post-depositional dissolution, not a primary character.

Belosaepiids referable to the genus *Belosaepia* occur only in Eocene (Ypresian - Bartonian) strata and have not been documented from Late Eocene (Priabonian) strata in North America or Europe. Younger coleoids documented in North America are species of the genera *Belosepiella* and *Belemnosella*, which are members of families other than the Belosaepiidae. In the Gulf Coast region, the youngest occurrence is in the Crockett Formation of Texas (*Cubitostrea sellaeformis* Zone) and the Gosport Formation of Alabama (Christopher Garvie and David Dockery, personal observations). The heavy posterior guard preserves easily, so it is unlikely that the belosaepiids had an earlier origin with a hidden fossil record. Their origin correlates with the episode of peak Cenozoic global temperatures in the early Eocene, followed by diversification during the Eocene warm climate optimum. Belosaepiids are not known in younger strata, an apparent casualty of the rapid cooling of climate at the end of the Eocene (Yancey et al., 2003). The probable descendent genus *Hungarosepia* (= *Archaeosepia*) is of late Eocene age.

CONCLUSIONS

A study of the common Middle Eocene belosaepiid species *B. ungula* provides documentation for a detailed description of skeleton characters of this species and a basis for interpretation of ontogeny and functional morphology. Names for skeletal characters are defined and several new terms are defined for features not previously recognized, including microstructural characters. Documentation is presented to show that the presence of a complex set of chamberlets similar to chamberlets of modern sepiids is present in *B. ungula* and that pillar structure is present over many areas of the septa. Pillar structure is considered to be a strengthening device that forms where septa are closely spaced and not confined to septal necks. The formation of siphuncle walls by enlarged septal necks is confirmed and evidence is presented to show that *B. ungula* lacks a prosiphon and caecum structure during the embryonic growth stage. The ventral margin of the siphuncle and phragmocone forms a flat surface (the deck) where septa are recurved in tight folds with curvature that project anteriorly, and it contains conotheca and is covered with an endoventral prismatic shell layer. The skeleton of *B. ungula* grew to nearly 200 mm length (with an animal length of reaching as much as 250 mm at maturity) and had a rhomboid cross section, indicating that it was a deep-bodied animal, probably demersal in life habits. The presence of a large and sturdy prong on the posterior end is interpreted to have a dual function as a counterbalance weight and as a digging tool for digging into loose sediment, enabling the animal to bury itself and hide in seafloor sediments.

This study suggests that the species lived a maximum of three years and at late maturity began to resorb large amounts of skeleton, greatly modifying the appearance of the skeleton. Dissolution at maturity tended to thin and shorten the prong, producing stubby, short-pronged specimens with an appearance very different from specimens with a fully developed guard. This agrees with the determination that the species lived a benthic demersal life. Because of this ontogenetic

change, specimens that are smoothed and have a short prong are likely to be gerontic individuals. Valid determination of species characters and species comparisons can be done only with individuals of adult size that have not had significant resorption of the skeleton. Several Gulf Coast *Belosaepia* names based on type specimens of this nature are synonymized here. A similar evaluation of European *Belosaepia* species names needs to be performed. Gulf Coast species placed in synonymy include: *B. uncinata*, *B. harrisi* and *B. alabamensis voltzi*, synonymized with *B. ungula*, and *B. alabamensis*, synonymized with *B. veatchii*.

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