Chapter 13

Jaws and Radula of *Baculites* from the Upper Cretaceous (Campanian) of North America

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1 Introduction

The seminal discovery by Meek and Hayden (1865) of an aptychus preserved inside the body chamber of a Late Cretaceous scaphite in close association with what is unmistakably an upper jaw demonstrated that the aptychus is part of the lower jaw. Lower jaws are known from many ammonites, but, surprisingly, these structures have rarely been reported in baculites from North America, even though these ammonites are extraordinarily abundant in Upper Cretaceous strata of this

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continent. In contrast, baculite lower jaws are relatively common in upper Campanian chalks of northern Europe where they are preserved as isolated elements, and much more rarely, inside the body chamber. This paradox has led to speculation about the taxonomic distribution of baculite lower jaws, the degree of variation in their morphology, and the extent to which the vagaries of preservation have altered their appearance.

We report the discovery of lower jaws inside the body chambers of *Baculites* sp. (smooth) and *Baculites* sp. (weak flank ribs) from the lower Campanian Pierre Shale of South Dakota, and the Cody Shale of Wyoming, respectively. We also describe aptychi of presumably one or both of these same species from the lower Campanian Mooreville Chalk of Alabama and the Smoky Hill Chalk Member of the Niobrara Formation of Kansas. Isolated lower jaws are also present in the upper Campanian Pierre Shale of South Dakota, where they are attributed to *Baculites compressus*, Say, 1821, and *Baculites cuneatus*, Cobban, 1962, and the upper Campanian Lewis Shale of Wyoming, where they are attributed to *Pseudobaculites natosini* (Robinson, 1945).

In addition to jaws, we describe a radula preserved inside the body chamber of a specimen of *Baculites* sp. (smooth). Radulae have been reported from fewer than a dozen ammonite species worldwide and the discovery of a new specimen substantially adds to our knowledge of these structures.

2 Previous Work

There are numerous reports of baculite aptychi from the Campanian Boreal Chalk facies of northern Europe (England, France, Germany, Belgium, and Sweden). Trauth (1927: 245) assigned these aptychi to the form genus *Rugaptychus*. The aptychi generally occur as isolated elements loose in the matrix (Hébert, 1856: 367, pl. 28, Fig. 6; Sharpe, 1857: 57, 58, pl. 24, Figs. 8a, b, 9, 10a, b; Binckhorst, 1861: 33 (said to be Maastrichtian); Lundgren, 1874: 70, pl. 3, Fig. 14; Schlüter, 1876: 144, 145, pl. 40, Fig. 8; Moberg, 1885: 41–43, pl. 1, Figs. 14–19; pl. 6, Figs. 25, 26; Blackmore, 1896: 532–533, pl. 16, Fig. 16; Ravn, 1902: 259; de Grossouvre, 1908: 39, pl. 10, Figs. 7–13; Diener, 1925: 40; Trauth, 1927: 245; Trauth, 1928: 122–130, pl. 2, Figs. 1–9; Picard, 1929: 436; Arkell, 1957: L440, Figs. 557.3, 558.5; Moore and Sylvester-Bradley, 1957: L469; Kennedy, 1986: 192, pl. 16, Figs. 1–22; Kennedy, 1993: 114, pl. 7, Fig. 25; Kennedy and Christensen, 1997: 112, 114, Fig. 31a–h; Klinger and Kennedy, 2001: 72–79, Fig. 55). Outside of Europe, isolated baculite aptychi have been reported from the Smoky Hill Chalk Member of the Niobrara Formation of Kansas (Miller, 1968: 48, 49, pl. 8, Fig. 14).

There are fewer reports of baculite jaws preserved inside the body chamber. Schlüter (1876: 147, pl. 39, Fig. 16) described and illustrated a lower jaw inside the body chamber of a large specimen of *Baculites knorrianus* Desmarest, 1817, from the upper Campanian Mukronatenkreide of Lüneburg, Germany. Nowak (1908: 339, pl. 14, Fig. 11) illustrated a lower jaw in the body chamber of

Baculites leopoliensis Nowak, 1908, from the same locality. Giers (1964: 256) described a jaw in a specimen of *Baculites vertebralis* Giers, 1964, Lamarck, 1801, from the lower Campanian of northwest Germany, but did not illustrate it. He also figured a structure in another body chamber of the same species but W. J. Kennedy (in Klinger and Kennedy, 2001: 79) concluded that the structure did not belong to the ammonite. Tanabe and Landman (2002: 161, pl. 1, Fig. 8; see also Matsumoto and Obata, 1963: 55) illustrated a lower jaw in the body chamber of *Baculites* cf. *princeps* Matsumoto and Obata, 1963, from the Campanian of western Japan.

Baculite jaws are not as common in older strata. Fritsch (1893: 80, Fig. 63c–e) described and illustrated a lower jaw inside the body chamber of what he called *Baculites faujassi* var. *bohemica* von Priesen, from the Coniacian of Bohemia, but the drawing is stylized and the description difficult to follow. Breitkreutz et al. (1991: 42, Figs. 6, 7; reillustrated in Klinger and Kennedy, 2001: 72, Fig. 56a, b) reported a lower jaw inside the body chamber of *Sciponoceras bohemicum anterius*? Wright and Kennedy, 1984, from the upper Cenomanian of Germany. Outside of Europe, Matsumoto and Obata (1963: 13, pl. 4; reillustrated in Tanabe and Landman, 2002: 161, pl. 1, Fig. 9) reported a lower jaw inside the body chamber of *Sciponoceras kossmati* (Nowak, 1908) from the lower Turonian of Hokkaido.

3 List of Localities

Numbers refer to Figs. 13.1 and 13.2.

1. AMNH loc. 3274: Upper Campanian *Baculites compressus–B. cuneatus* Zones, Pierre Shale, SE¼ sec. 6, T. 3N, R. 14E, Elk Creek, Meade County, South Dakota.
2. AMNH locs. 3280, 3281, 3294, and 3296: Lower Campanian *Baculites* sp. (smooth) Zone, Gammon Ferruginous Member, Pierre Shale, SW¼ sec. 21, east center sec. 27, SE¼ sec. 17, N½ sec. 27, T. 11N, R. 2E, respectively, Butte County, South Dakota.
3. Lower Campanian *Baculites* sp. (weak flank ribs) Zone, Cody Shale, sec. 6, T. 40N, R. 79W, Natrona County, Wyoming.
4. Upper Campanian *Baculites eliasi* Zone, Lewis Shale, sec. 30, T. 35N, R. 84W, Natrona County, Wyoming.
5. Lower Campanian *Baculites* sp. (smooth)-*Baculites* sp. (weak flank ribs) Zones, upper part of Mooreville Chalk, sec. 10, T. 22N, R. 1W, Greene County, Alabama.
6. Lower Campanian *Baculites* sp. (smooth)-*Baculites* sp. (weak flank ribs) Zones, upper part of Mooreville Chalk, sec. 26, T. 22N, R. 1W, Dallas County, Alabama.
7. Lower Campanian *Hesperornis* Zone, Smoky Hill Chalk Member of the Niobrara Formation, NW corner, Rooks County, Kansas.

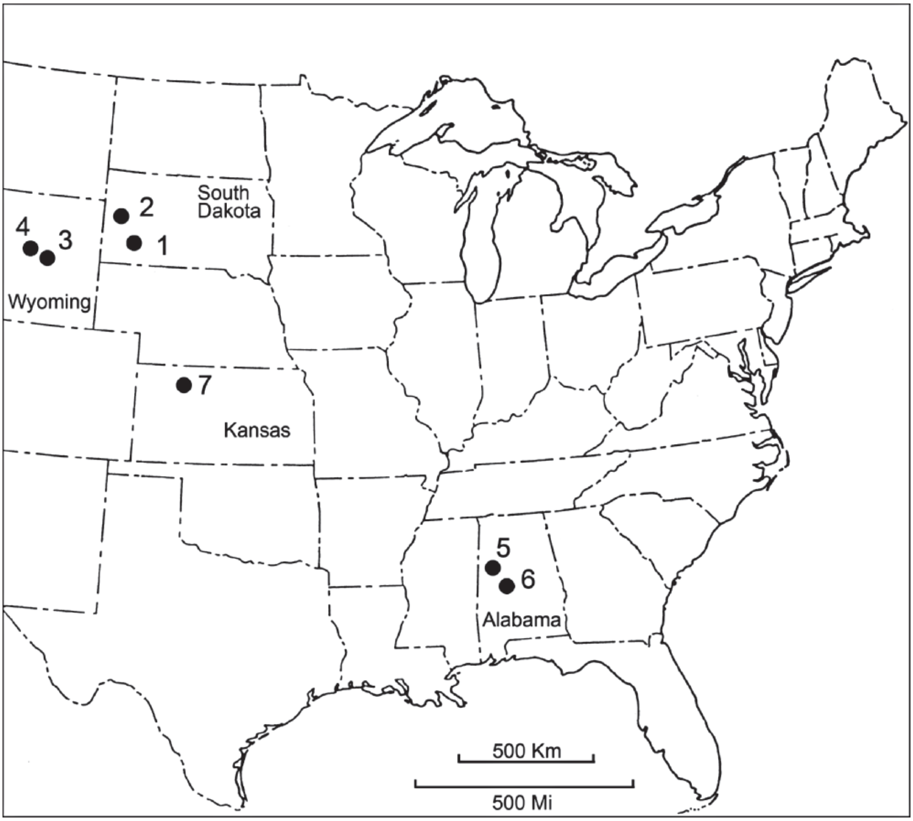


Fig. 13.1 *Map of part of the USA showing the localities mentioned in the text.*

4 Geologic Setting

A total of 12 specimens of *Baculites* sp. (smooth) with jaws preserved inside the body chamber were discovered in the upper part of the Gammon Ferruginous Member of the Pierre Shale, Butte County, South Dakota [lower Campanian Zone of *Baculites* sp. (smooth)] (Figs. 13.1, 2). Most of the specimens were collected by N.L.L. This locality was described by Gill and Cobban (1961), Robinson et al. (1964), and Bishop (1985). Baculites are extremely abundant, comprising thousands to tens of thousands of specimens. They occur loose and in concretions, in a silty shaly matrix, forming what Bishop (1985: 607) called a "Baculite Epibole." The baculites are preserved as steinkerns with pieces of aragonitic outer shell still attached (= composite internal molds) and bear traces of muscle scars and other imprints (Klinger and Kennedy, 2001; Henderson et al., 2002; Kennedy et al., 2002). Associated fossils include other ammonites, bivalves, gastropods, scaphopods, decapod crustaceans, bony fish, sharks, and mosasaurs. The sheer abundance of baculites, nearly all of which are large and consist of macroconchs and

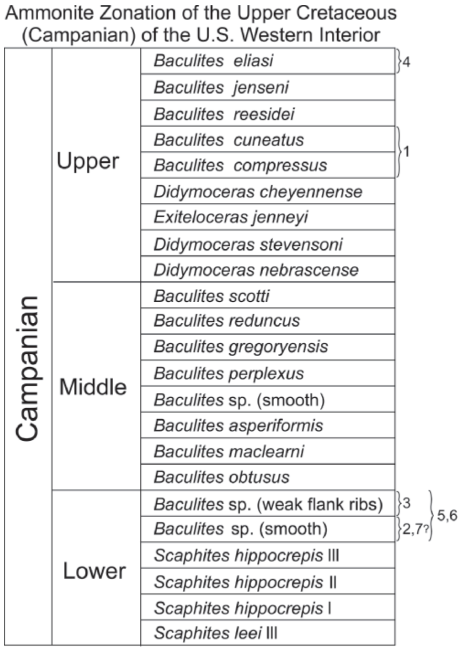


Fig. 13.2 *Ammonite zonation of the Campanian (Upper Cretaceous) of the US Western Interior (Cobban et al., 2006), with the biostratigraphic positions of the baculite localities indicated on the right.*

microconchs, suggests massive die-offs, perhaps following mating or spawning. Surprisingly, however, the incidence of jaws is very low. Based on our collecting, we estimate a recovery rate of 1 jaw for every 4,000 specimens.

A single specimen of *Baculites* sp. (weak flank ribs) with the jaw preserved inside the body chamber was discovered from a baculite-rich interval in the Cody Shale of Natrona County, Wyoming (Figs. 13.1, 2). This interval represents the lower Campanian Zone of *Baculites* sp. (weak flank ribs).

Isolated aptychi were recovered from near the top of the Mooreville Chalk below the Arcola Limestone Member in Dallas and Greene counties, Alabama (Figs. 13.1, 2). No aragonitic shells are preserved in this formation. The most common fossils are the originally calcitic bivalves *Exogyra* and *Cadeceramus*, and the worm tube *Hamulus*. The aptychi are relatively abundant; for example, N. Larson and T. Rust collected a total of 146 aptychi in a period of 7.5 h at five small (1–3 acre) outcrops.

The aptychi co-occur with baculite steinkerns, but these specimens are not well enough preserved for identification, thus precluding a definitive attribution of the aptychi. However, Kennedy et al. (1997) recorded *Scaphites hippocrepis* DeKay, 1827, form II Cobban, 1969, from the upper part of the Mooreville Chalk, which is below the aptychi-bearing interval. They also recorded *Menabites* (*Delawarella*) *danei* (Young, 1963), indicative of the Zone of *Baculites obtusus*, from strata above the aptychi-bearing interval. Therefore, the aptychi-bearing interval spans the zones of *Scaphites hippocrepis II* to *Baculites obtusus*, including the zones of *Baculites* sp. (smooth) and *Baculites* sp. (weak flank ribs), and is thus approximately equivalent to the baculite occurrences at localities 2 and 3 in South Dakota and Wyoming. Therefore, the aptychi in the Mooreville Chalk are tentatively attributed to *Baculites* sp. (smooth) and *Baculites* sp. (weak flank ribs).

Rugaptychi were previously reported from the Smoky Hill Chalk Member of the Niobrara Formation of Kansas (Miller, 1968). The rugaptychi occur as isolated elements in the upper part of this member, corresponding to the lower Campanian Zone of *Hesperornis* (see Stewart, 1990; Everhart, 2005: 36, Table 2.1). The associated baculites are preserved as smooth steinkerns and are referred to as *Baculites* sp. by Everhart (2005). It is possible that this species is synonymous with *Baculites* sp. (smooth) and, therefore, by implication, this site is equivalent in age to site 2.

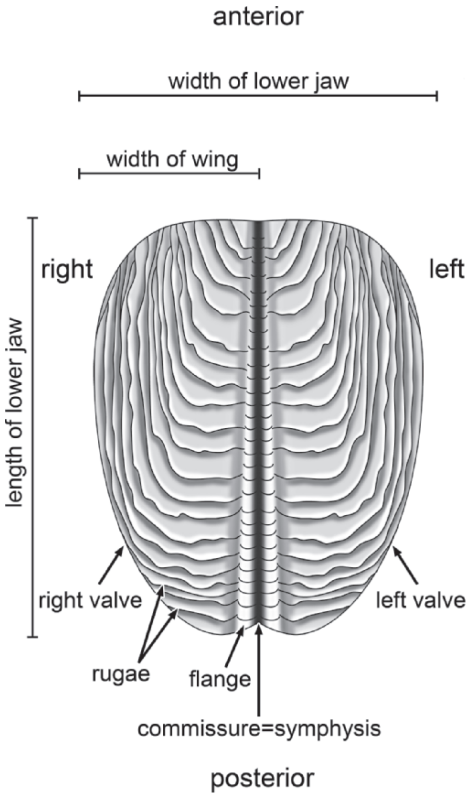
A baculite jaw was discovered in a concretion in the upper Campanian *Baculites compressus–B. cuneatus* Zones in the Pierre Shale of Meade County, South Dakota (Figs. 13.1, 2). The concretion contains benthic and nektic organisms, all of which are preserved with their original aragonitic shells. Associated ammonites include *Hoploscaphites landesi* (Riccardi, 1983), *Jeletzkytes nodosus* (Owen, 1852), *J. brevis* (Meek, 1876), *Placenticeras meeki* (Böhm, 1898), and *P. costatum* (Hyatt, 1903). The jaws of these other ammonites differ from those of *Baculites* and have been described elsewhere (for *Hoploscaphites* and *Jeletzkytes*, see Landman and Waage, 1993; for *Placenticeras*, see Landman et al., 2006). Although the baculite jaw is not preserved inside a body chamber, it is attributed to *B. compressus* or *B. cuneatus* because these are the only two species of *Baculites* at this site. Additional baculite jaws may be present in other concretions from this same horizon but require further study.

Several isolated jaws were discovered in the upper Campanian *Baculites eliasi* Zone of the Lewis Shale of Natrona County, Wyoming (Figs. 13.1, 2). The jaws occur in a sandstone concretion associated with pieces of *Pseudobaculites natosini* (Robinson, 1945). This species is the largest baculite known from the Upper Cretaceous of the Western Interior of North America (Cobban and Kennedy, 1994). Other ammonites in these strata include *Jeletzkytes plenus* (Meek, 1876) and *Baculites eliasi* (Cobban, 1958). The large size of the jaws matches the large size of *P. natosini* and, therefore, the jaws are attributed to this species.

5 Conventions

The terminology used to describe the lower jaws of ammonites is that of Kanie (1982), Tanabe (1983), and Tanabe and Fukuda (1987), and illustrated in Fig. 13.3. We employ the terms anterior, posterior, ventral, dorsal, left, and right, to refer to the jaws as they were oriented in life. The jaws are illustrated with the anterior end on top. The most recently formed portion of the jaw is at the posterior end. The two symmetric halves of the lower jaw are called the wings, with the hinge line (symphysis = commissure) along the midline.

Fig. 13.3 *Terminology and measurements of the lower jaw of baculites, showing the ventral surface covered with an aptychus.*



Most of the jaws we describe are incomplete. We measured the width and length of each wing of the jaw, irrespective of curvature, following the approach of Kanie (1982) and Tanabe and Fukuda (1987). These measurements represent the maximum dimensions of the wing perpendicular and parallel to the symphysis, respectively. Width is a more reliable indicator of size than length, because the long end of the jaw is commonly broken, especially in isolated elements. The width of the jaw equals twice the width of the wings. The ratio of jaw width to length provides an approximation of jaw shape.

Landman et al. (2006) and Landman and Grebneff (2006) discussed the terminology surrounding aptychi. They defined an aptychus type lower jaw as a lower jaw bearing an aptychus. An aptychus is the entire calcareous layer covering the ventral surface of the lower jaw. It consists of a pair of left and right valves. (For additional discussions about the terminology used to describe aptychi, see Trauth, 1927–1936, 1938; Arkell, 1957; Moore and Slyvester-Bradley, 1957; and Farinacci et al., 1976).

Trauth (1927) assigned the coarsely ornamented aptychi of *Baculites* to the form genus *Rugaptychus*, and erected parataxa with binomial names written in italics, to describe variation within this morphotype. Moore and Sylvester-Bradley (1957:

L469) characterized *Rugaptychus* as follows: "Elongate diaptychi [pair of valves] with strong sharp ridges on outer surface, ridges characteristically arranged with angulated bend; inner surface with growth lines, nearly smooth." We follow the practice of Engeser and Keupp (2002) in employing the term rugaptychus as a common name without italics to refer to this kind of aptychus.

Specimens are reposited in the American Museum of Natural History (AMNH), New York; the Black Hills Museum of Natural History (BHMNH), Hill City, South Dakota; and the Sternberg Museum of Natural History (FHSM), Hays, Kansas; and the US National Museum (USNM), Washington, DC.

6 Description of Jaws

6.1 *Baculites* sp. (smooth), Pierre Shale, South Dakota

The body chambers containing lower jaws are fragmentary and range from 43.2 mm to 120.9 mm in length (Figs. 13.4–14, Table 13.1). All of the body chambers are steinkerns but several retain pieces of the aragonitic outer shell (= composite internal molds). The body chambers consist of four stout and eight slender individuals, presumably representing mature macroconchs and microconchs, respectively.

In specimens that preserve the ultimate septum or in which the shell expands enough to detect the adoral direction, the jaw is located in the adoral part of the body chamber. In most specimens, the long axis of the jaw lies at an angle of 45°–90° to the long axis of the body chamber, with the anterior end of the jaw on the dorsal side of the shell, and the posterior end of the jaw on the ventral side of the shell (Figs. 13.5–7, 8D–F, 9, 10, 11, 12A–C, 13). The jaws are nearly perpendicular to the whorl section except in BHMNH 5494a, in which the jaw is displaced to the left hand side of the shell (Fig. 13.7). In BHMNH 5147 and 5497 (Figs. 13.8A–C, 12D–F), in contrast, the long axis of the jaw is approximately parallel to the long axis of the body chamber, with the jaw lodged in the dorsal and ventral half of the shell, respectively.

The jaw consists of two wings with the symphysis along the midline. Both wings are preserved in AMNH 47109, BHMNH 5494a, 5147, 5143, 5491, and 5496

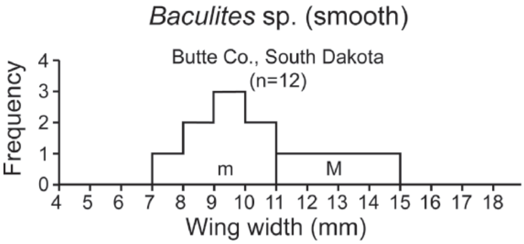


Fig. 13.4 *Size–frequency histogram of the wing width of the lower jaw of* Baculites *sp. (smooth) from the Gammon Ferruginous Member of the Pierre Shale, South Dakota. M = macroconch; m = microconch.*

Fig. 13.5 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), macroconch, AMNH 47109, Pierre Shale, South Dakota, with lower jaw inside. A. Right lateral view. X1. B. Ventral view. X1. C. Lower jaw with parts of the aptychus preserved, dorsal side of the shell on top, coated. X1.5.*

(Figs. 13.5, 7, 8A–C, 9, 11, 12A–C). The wings are folded in a U-shape in BHMNH 5147, 5143, and 5491 (Figs. 13.8A–C, 9, 11). In contrast, they are nearly flattened out in AMNH 47109 and BHMNH 5494a (Figs. 13.5, 7) and folded slightly outward in BHMNH 5496 (Fig. 13.12A–C). In the other six specimens, only one wing or one wing and part of the other wing is preserved. In BHMNH 5148 and 5495 (Figs. 13.8D–F, 13D–F), the partially preserved wing is oriented nearly perpendicular to the plane of the other wing.

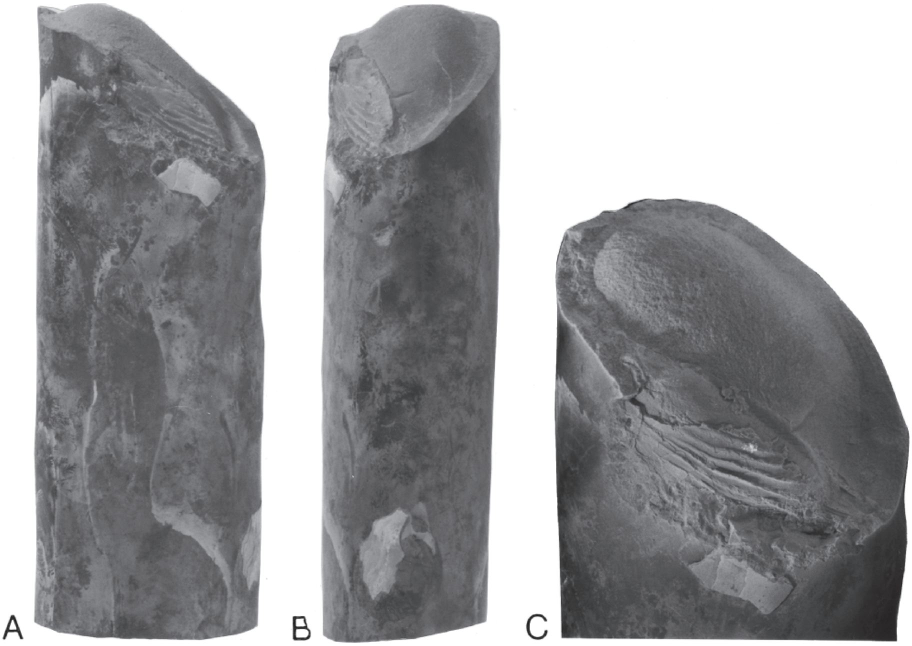


Fig. 13.6 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), microconch, AMNH 51329, Pierre Shale, South Dakota, with the lower jaw inside. A. Right lateral view. X1. B. Ventral view. X1. C. Lower jaw with part of the right side of the aptychus preserved, coated. X1.5.*

The jaw measurements are reported in Table 13.1. Jaw length ranges from 20.8 mm to 37.2 mm. Wing width ranges from 7.8 mm to 14.4 mm. Jaw width, which equals twice the wing width, ranges from 15.6 mm to 28.8 mm. The ratio of jaw width to jaw length ranges from 0.68 to 0.87 and averages 0.77, indicating an elongate shape.

A comparison of the shape of the jaws with that of the whorl cross section reveals that the jaws fit snugly into the body chamber (Table 13.1). The ratio of jaw length to whorl height ranges from 0.72 to 1.03, and averages 0.85. The ratio of jaw width to whorl width ranges from 0.81 to 1.04, and averages 0.94. The ratio of jaw width to jaw length is the same or slightly higher than the ratio of whorl width to whorl height. When one or both wings are splayed out across the whorl section, the sides of the jaw touch the sides of the shell, e.g., AMNH 47109, BHMNH 5148, 5144, and 5496 (Figs. 13.5, 8D–F, 10, 12A–C).

The variation in jaw size with respect to sexual dimorphism is illustrated in Fig. 13.4. The baculites were divided into macroconchs and microconchs based on the size and robustness of the shell. Wing width (= 1/2 aptychus width) was used as a measure of jaw size. The histogram of wing width shows no overlap between dimorphs.

The jaw is covered with a pair of calcareous plates or valves (= the aptychus). Each valve has a broadly rounded lateral margin, a straight symphysal margin, and

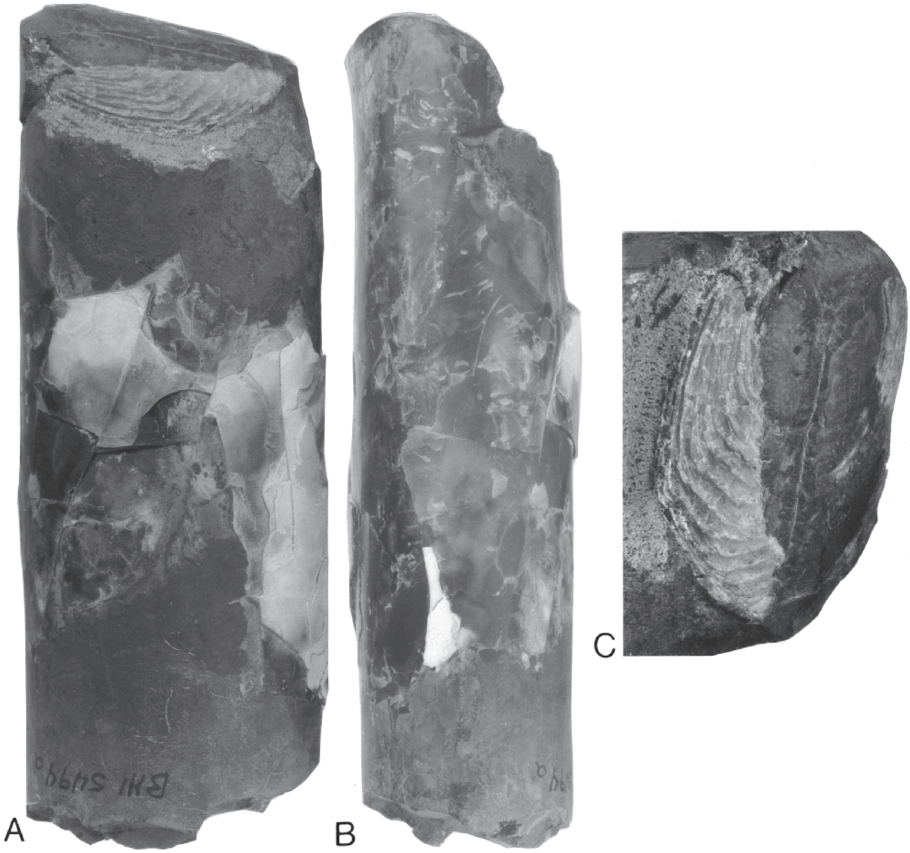


Fig. 13.7 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), macroconch, BHMNH 5494a, Pierre Shale, South Dakota, with lower jaw inside. A. Lateral view. X1. B. Dorsal view. X1. C. Lower jaw with part of the right side of the aptychus preserved, dorsal side of the shell on top. X1.5.*

a narrowly rounded posterior margin. The anterior margin is missing or obscured in all specimens. The symphysis is bordered by a flange with a sharp crest, as shown in BHMNH 5144 and 5491 (Figs. 13.10, 11).

The aptychi are composed of calcite, as indicated by X-ray diffraction analysis of a sample from BHMNH 5491. The calcite in this specimen is 0.50 mm thick at a ridge and 0.17 mm thick near the symphysis. The aptychi are covered with coarse, irregular rugae characteristic of rugaptychi. The rugae parallel the lateral and posterior margins and approach the symphysis at nearly a right angle. In BHMNH 5144 (Fig. 13.10), with the best preserved aptychus, there are 13 rugae, although additional ones are undoubtedly obscured in the anterior region. The rugae are more broadly spaced in the middle of the aptychus than near the posterior margin.

In some specimens, parts of the aptychus are broken off exposing large portions of the underlying chitinous layer. The chitinous layer bears a midline groove

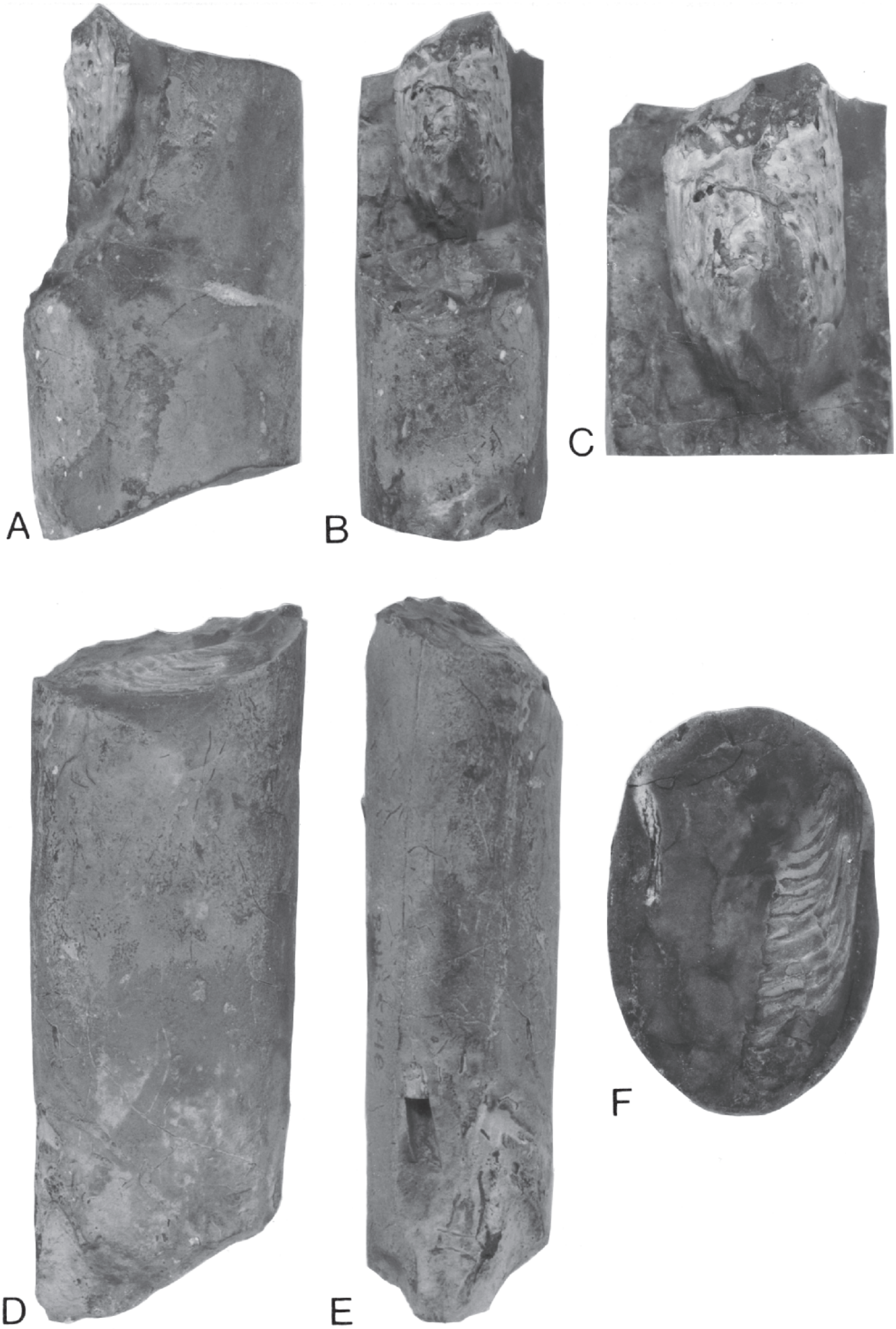


Fig. 13.8 *Steinkerns of parts of the body chambers of* Baculites *sp. (smooth), Pierre Shale, South Dakota, with lower jaws inside. A–C. BHMNH 5147, microconch. A. Right lateral view. X1. B. Dorsal view. X1. C. Close-up of the lower jaw folded in a U-shape. X1.5. D-F. BHMNH 5148, microconch. D. Left lateral view. X1. E. Ventral view. X1. F. Lower jaw with part of the left side of the aptychus preserved, dorsal side of the shell on top. X1.5.*

Fig. 13.9 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), BHMNH 5143, macroconch, Pierre Shale, South Dakota, with the lower jaw inside. A. Right lateral view. X1. B. Ventral view. X1. C. Lower jaw, dorsal side of the shell on top. X1.5.*

bordered by flanges. In BHMNH 5494a (Fig. 13.7), this layer is smooth with subdued undulations. The two wings in this specimen diverge at the anterior end and the symphysis disappears, so that there is a triangular gap between the wings.

Two layers are visible below the calcitic aptychus in BHMNH 5491: a black crystalline layer (80 μm thick near the symphysis) and an underlying tan layer (60 μm thick near the symphysis). X-ray diffraction analysis of these two layers indicates that they consist of an amorphous material and magnesium enriched calcite, respectively.

A radula is present in BHMNH 5496 (Figs. 13.12A–C, 14). It occurs in the middle of the jaw at the anterior end. The aptychus is missing in this area and the surface is eroded away. The radula is approximately 4.1 mm long and 2.0 mm wide. The teeth

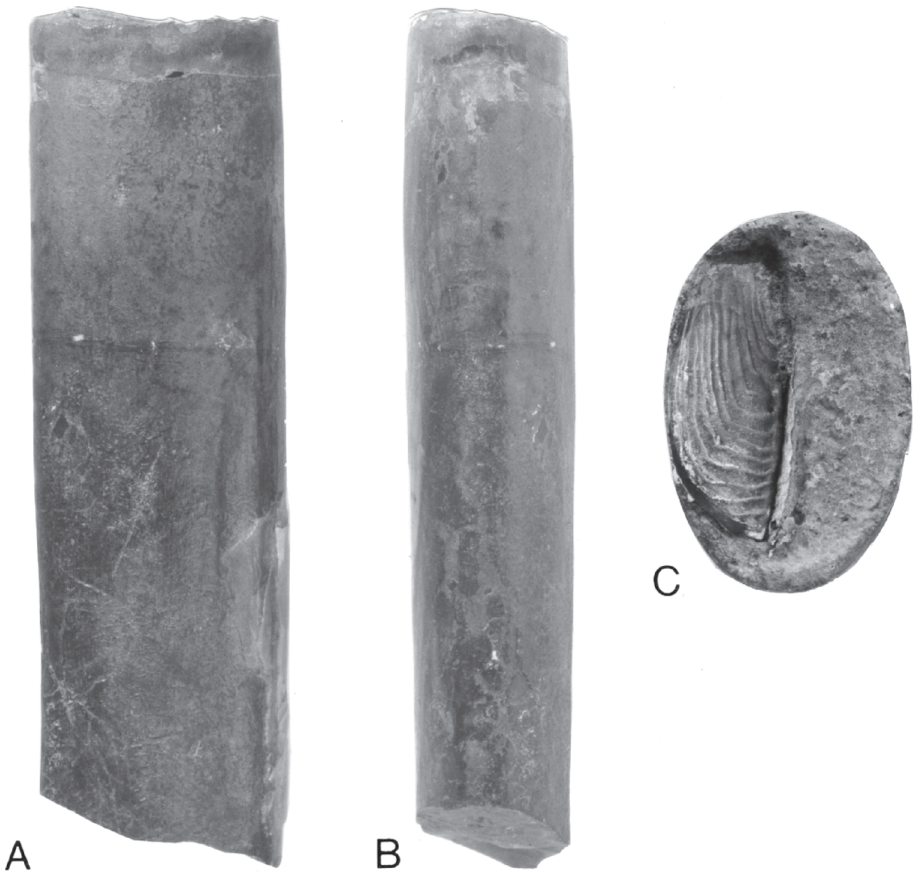


Fig. 13.10 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), BHMNH 5144, microconch, Pierre Shale, South Dakota, with the lower jaw inside. A. Left lateral view. X1. B. Ventral view. X1. C. Close-up of the lower jaw with the right side of the aptychus preserved, dorsal side of the shell on top. X1.5.*

are dark brown with reddish overgrowths. Three elongate, slightly curved elements are visible in the upper right side of the radula and represent the marginal teeth (Fig. 13.14B). Each tooth is approximately 990 µm long and lies on a curved sheet. The teeth point forward and inward. They are ornamented with ridges spaced at equal intervals of approximately 70 µm (Fig. 13.14C).

Three blunter, rectangular elements are visible just to the right of the marginal teeth, and represent the marginal plates. They are aligned almost perpendicular to the marginal teeth and are spaced between them.

Additional teeth are present on the lower right side of the radular complex but are indistinct (Fig. 13.14A). The middle of the radula is recrystallized. A small triangular tooth is visible at the lower end flanked by longer teeth on either side, which point inward. The left side of the complex also contains elongate teeth like those in the upper right side, but they are broken and embedded in the matrix.

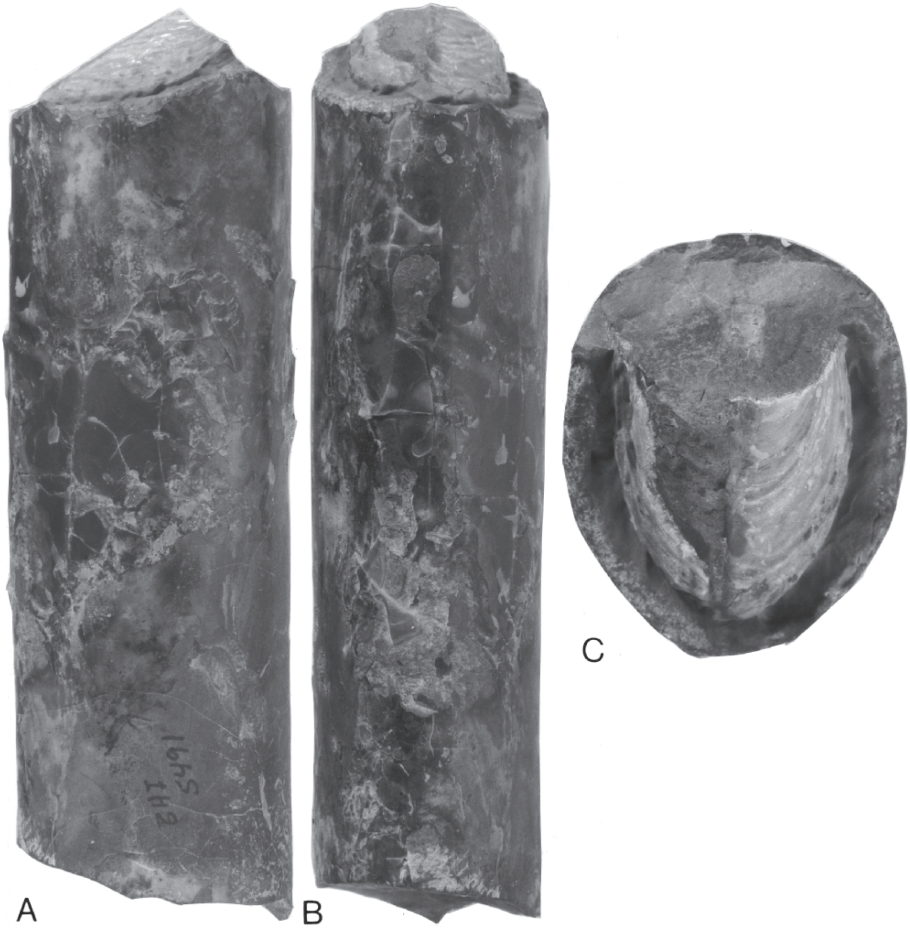


Fig. 13.11 *Steinkern of part of the body chamber of* Baculites *sp. (smooth), BHMNH 5491, macroconch, Pierre Shale, South Dakota, with the lower jaw inside. A. Left lateral view. X1. B. Ventral view. X1. C. Close-up of the lower jaw, dorsal side of the shell on top. X1.5.*

6.2 *Baculites* sp. (weak flank ribs), Cody Shale, Wyoming

A lower jaw (BHMNH 5331) occurs inside the adoral end of a weathered fragment of a body chamber of *Baculites* sp. (weak flank ribs) (Fig. 13.15, Table 13.1). The body chamber fragment is 111.0 mm long with a maximum whorl height of 33.8 mm. The long axis of the jaw is oriented at an angle of 70° with the long axis of the body chamber. The anterior end of the jaw points slightly backward against the ventral (?) side of the shell. The jaw is folded along the symphysis so that the two wings are perpendicular to each other, with the right wing splayed out across the opening.

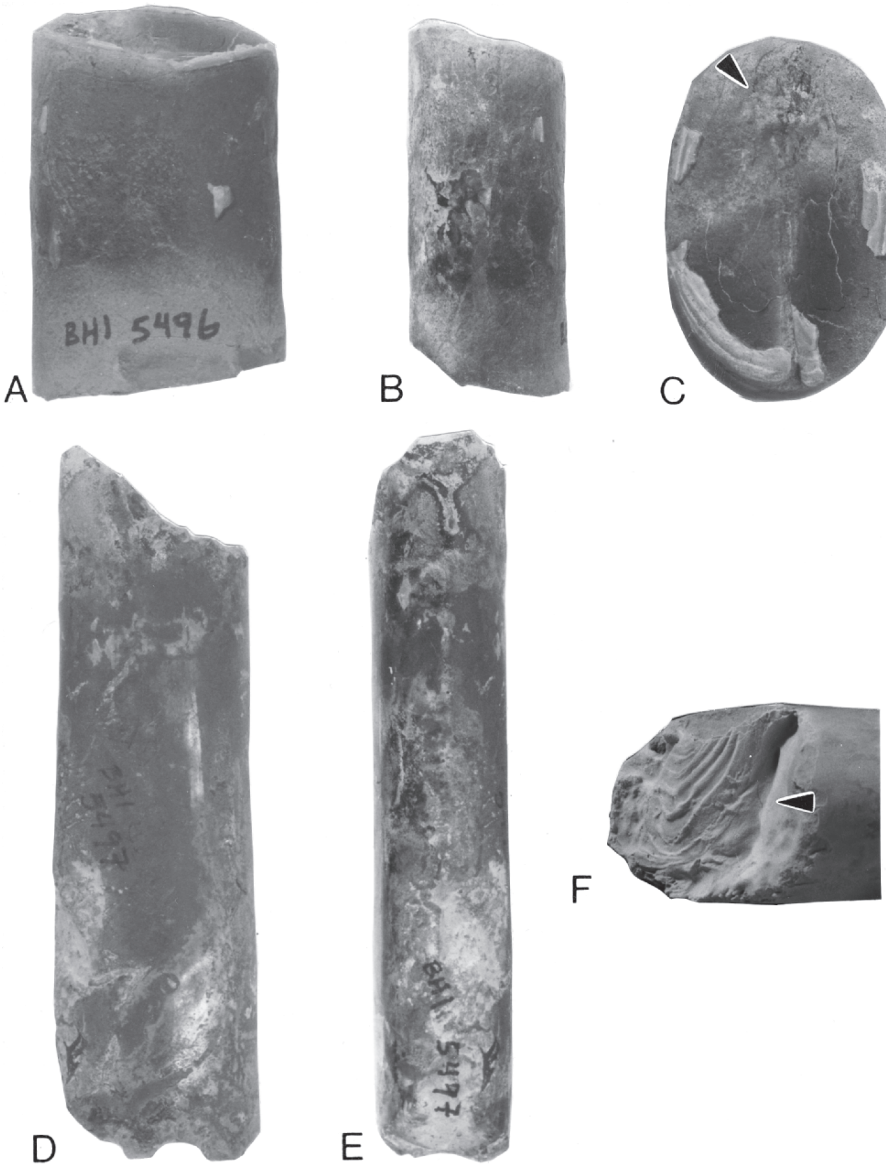


Fig. 13.12 *Steinkerns of parts of the body chambers of* Baculites *sp. (smooth), Pierre Shale, South Dakota, with lower jaws inside. A-C. BHMNH 5496, microconch. A. Right lateral view. X1. B. Dorsal view. X1. C. Close-up of the lower jaw, dorsal side of the shell on top. The radula (arrow) occurs at the anterior end of the jaw between the two wing tips. X1.5. D-F. BHMNH 5497, microconch. D. Left lateral view. X1. E. Ventral view. X1. F. Close-up of the lower jaw (arrow), with the left side of the aptychus preserved in the ventral half of the shell, coated. X1.5.*

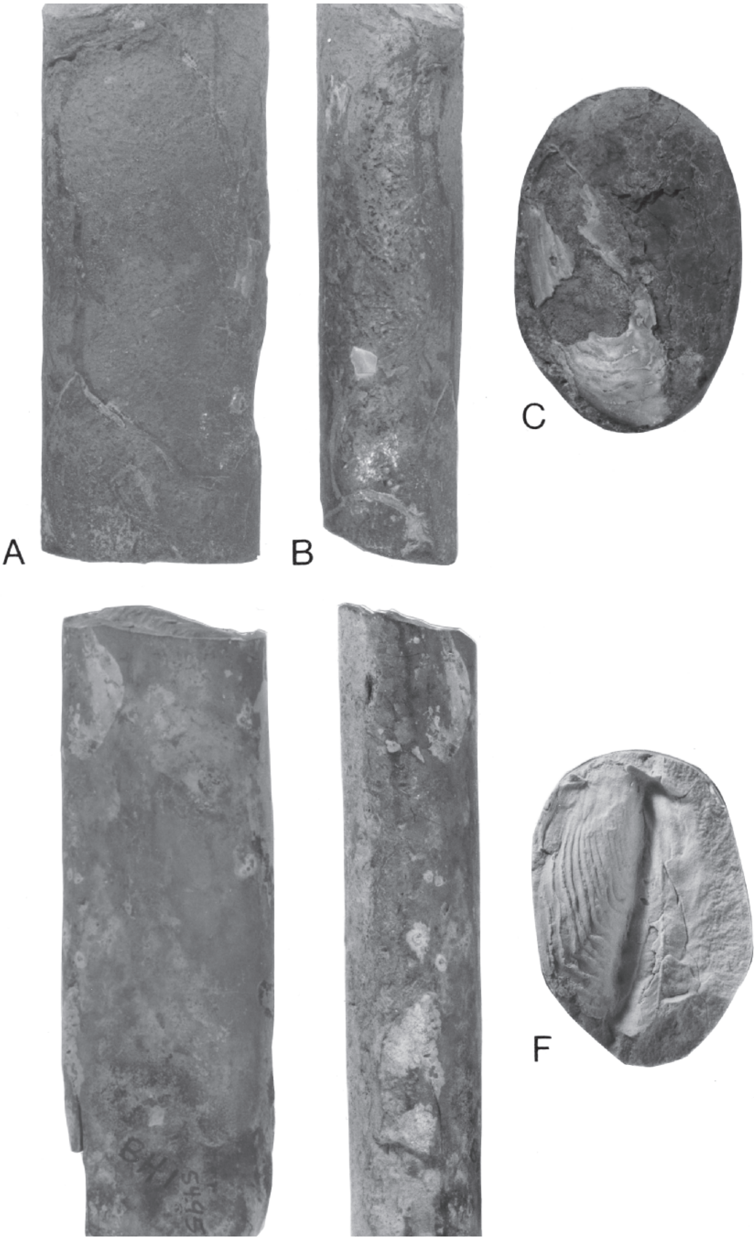


Fig. 13.13 *Steinkerns of parts of the body chambers of* Baculites *sp. (smooth), Pierre Shale, South Dakota, with lower jaws inside. A–C. BHMNH 5146, microconch. A. Right lateral view. X1. B. Dorsal view. X1. C. Close-up of the lower jaw with the right side of the aptychus preserved, dorsal side of the shell on top. X1.5. D-F. BHMNH 5495, microconch. D. Left lateral view. X1. E. Ventral view. X1. F. Close-up of the lower jaw with the right side of the aptychus preserved, dorsal side of the shell on top, coated. X1.5.*

Table 13.1 *Measurements of the whorl cross section and lower jaws of* Baculites/Pseudobaculites *from the Pierre Shale, Cody Shale, Lewis Shale, Mooreville Chalk, and Niobrara Formation. Abbreviations: M/m = macroconch/microconch; WW = whorl width; WH = whorl height; W = width of wing as measured perpendicular to the symphysis, irrespective of convexity; L = length of wing measured parallel to the symphysis; 2W/L = ratio of jaw width to jaw length; 2W/WW = ratio of jaw width to whorl width; L/WH = ratio of jaw length to whorl height; *=estimate due to poor or incomplete preservation. All measurements in millimeters.*

Specimen M/m	WW	WH	WW/WH	W	L	2W/L	2W/WW	L/WH
Baculites sp. (smooth), Pierre Shale, South Dakota								
BHMNH 5143 M	25.8*	33.2	0.78*	11.3	26.0*	0.87*	0.88	0.78*
5144 m	17.8	27.0	0.66	8.4	20.8	0.81	0.94	0.72
5146 m	18.8	28.4	0.66	9.8	25.0*	0.78*	1.04	0.88*
5147 m	22.6	32.4	0.70	10.2	25.2*	0.81*	0.90	0.75*
5148 m	21.9	31.4	0.70	10.2	26.3	0.78	0.93	0.86
5491 M	30.1	37.8	0.80	14.4	–	–	0.96	–
5494a M	28.1	41.1	0.68	13.2	34.5	0.76	0.94	0.87
5496 m	19.1	27.4	0.70	9.2	27.0*	0.68*	0.96	0.98
5497 m	16.0	22.2	0.72	7.8	–	–	0.98	–
5495 m	17.2	25.3	0.68	8.5	21.2	0.80	0.99	0.81
AMNH 47109 M	26.9	36.2	0.74	12.9	37.2	0.69	0.96	1.03
51329 m	22.8	30.4	0.75	9.2*	25.1*	0.73*	0.81*	0.82*
Baculites sp. (weak flanks ribs), Cody Shale, Wyoming								
BHMNH 5331	26.6	33.8	0.79	12.5	33.2	0.75	0.94	0.98
Baculites sp. (smooth and weak flank ribs), Mooreville Chalk, Alabama (selected specimens)								
BHMNH 5406				15.8	38.6	0.82		
5407				11.7	27.5*	0.85*		
5408				9.9	21.5*	0.92*		
5409				13.3	31.5*	0.84*		
5410				12.1	27.2*	0.89*		
5484				11.8	30.6	0.77		
5450				6.4	15.2*	0.84*		
5150				17.2	–	–		
AMNH 51293				13.3	30.6*	0.87*		
51316				13.8	–	–		
Baculites sp., Niobrara Formation, Kansas								
FHSM 968:1				10.2	20.1*	0.51*		
Baculites compressus or *B. cuneatus*, Pierre Shale, South Dakota								
BHMNH 5498				7.9	19.5	0.81		
Baculites compressus, Pierre Shale, South Dakota								
AMNH 51885	17.2	31.0	0.55					
51880	13.9	24.9	0.56					
51865	15.5	27.1	0.57					
51879	19.6	40.4	0.48					
51871	15.7	26.9	0.58					
51872	16.3	30.0	0.54					
51886	19.3	36.1	0.53					
51887	16.1	30.3	0.53					

Specimen M/m	WW	WH	WW/WH	W	L	2W/L	2W/WW	L/WH
Baculites cuneatus, Pierre Shale, South Dakota								
AMNH 51866	24.6	50.2	0.49					
51873	16.8	32.4	0.52					
50422	15.2	26.2	0.58					
BHMNH 5498	25.2	40.6	0.62					
Pseudobaculites natosini, Lewis Shale, Wyoming								
BHMNH 5501				25.8	50.1*	1.03*		
AMNH 51328				26.3	59.0	0.89		
BHMNH 5502				23.6	52.8	0.89		
BHMNH 5500				28.1	–	–		
USNM 458243	31.9	87.3	0.36					
458241	60.0	141.0	0.43					
458239	72.0	152.0	0.48					

Some of the rugose ornament of the aptychus is preserved on the left wing. The calcite is approximately 0.4 mm thick. Most of the aptychus is missing on the right wing and there is a dark brown surface comprising the underlying chitinous layer. This layer is broadly convex and is covered with fine ridges spaced at intervals of 300 µm and very fine lines spaced at intervals of 80 µm, both of which parallel the lateral and posterior margins.

6.3 *Baculites* sp. (smooth and weak flank ribs), Mooreville Chalk, Alabama

There are approximately 150 isolated aptychi. They are attributed to *Baculites* sp. (smooth) and *Baculites* sp. (weak flank ribs) by comparison with the jaws inside the body chambers of these species and the fact that these two species occur in age-equivalent strata elsewhere. In terms of measurable specimens, the collection contains 8 pairs of valves found in close association, 19 left valves, and 11 right valves. The valves range from 15.2 mm to 38.6 mm in length and 6.4 mm to 17.2 mm in width, although nearly all of the valves are slightly broken (Table 13.1). The ratio of jaw width (=twice the width of the valve) to jaw length (=length of the valve) ranges from 0.77 to 0.92.

The size distribution of 38 valves in our collection is illustrated in Fig. 13.16, using valve width rather than length as an indicator of size, because the specimens are more commonly broken in length than width. Only one valve of each pair was counted. As a cautionary note, the widths of valves in a pair do not always match, presumably due to breakage of one of the valves, but the difference is usually trivial. In case of a discrepancy, the larger value was used. The resultant histogram shows a bimodal distribution of valve width with modes at 9–10 mm and 13–14 mm.

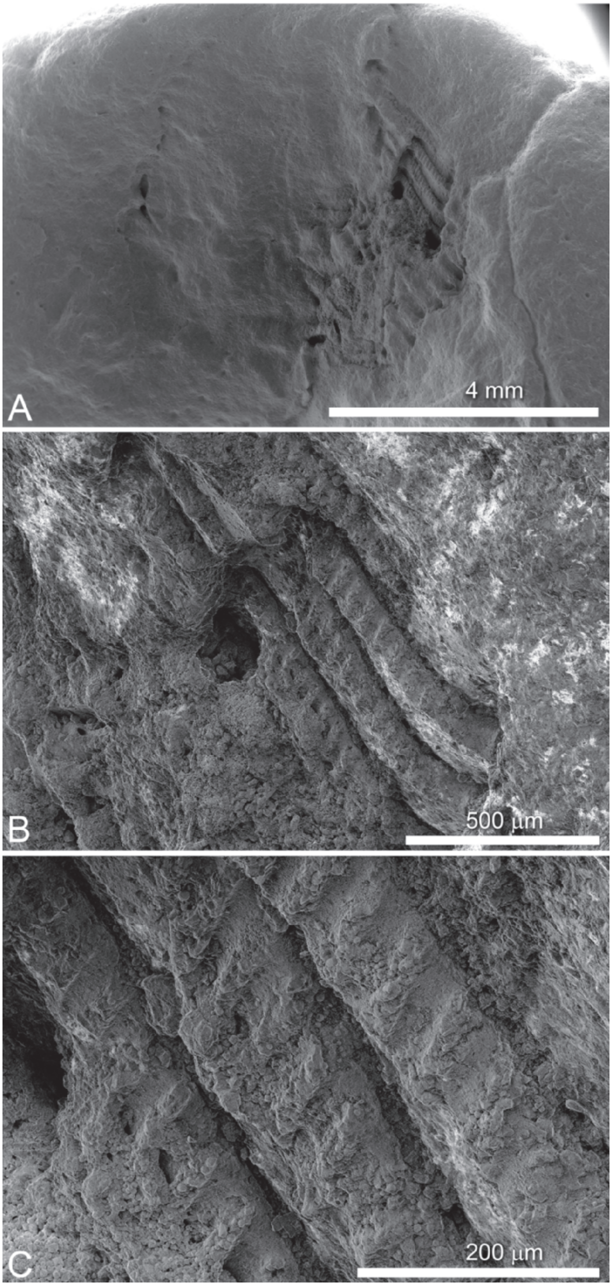


Fig. 13.14 *Radula in* Baculites *sp. (smooth), BHMNH 5496, microconch, Pierre Shale, South Dakota. A. Overall view of the radula with the marginal teeth exposed on the right; dorsal side of the shell on top. B. The marginal teeth are long and ornamented with ridges. C. Close-up of the marginal teeth.*

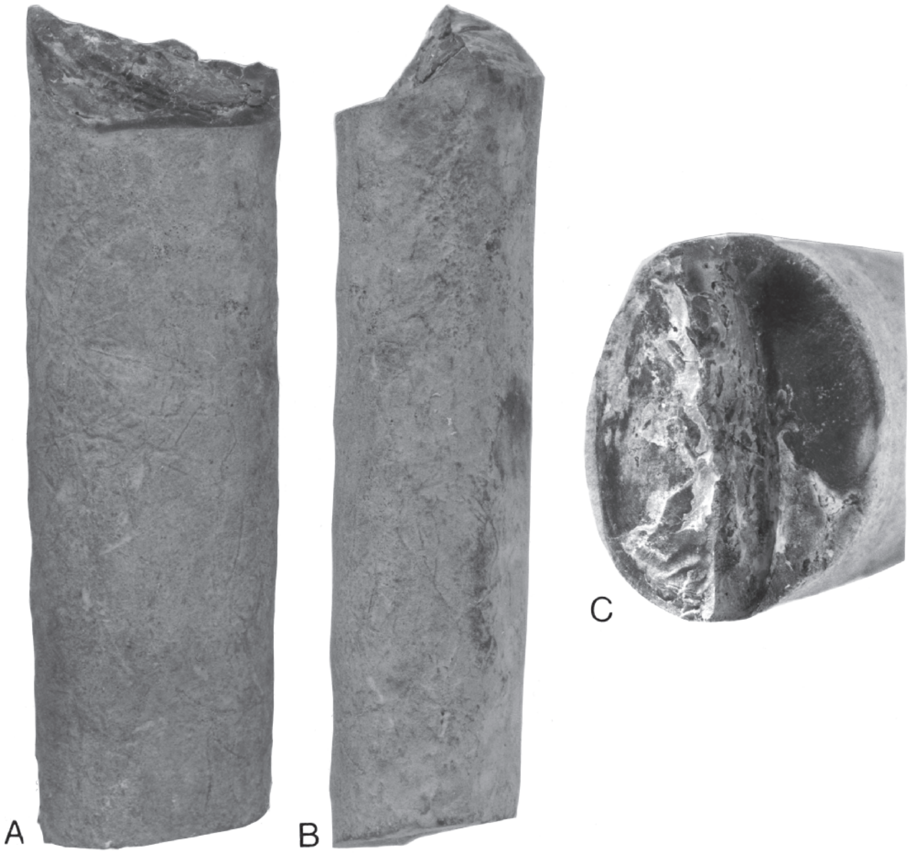


Fig. 13.15 *Steinkern of part of the body chamber of* Baculites *sp. (weak flank ribs), BHMNH 5331, macroconch, Cody Shale, Wyoming, with the lower jaw inside. A. Right lateral (?) view. X1. B. Ventral (?) view. X1. C. Close-up of the lower jaw with part of the aptychus and underlying chitinous layer preserved, ventral (?) side of the shell on top. X1.5.*

Because some of the isolated valves may belong to the same jaw and are thus counted twice, we reevaluated the data by constructing histograms using only left valves (including the left valve of each pair), and histograms using only right valves (including the right valve of each pair). The histogram of left valves retains the mode at 13–14 mm but the other mode disappears. The histogram of right valves yields the original two modes at 9–10 mm and 13–14 mm.

This bimodal distribution may reflect sexual dimorphism. However, it is difficult to demonstrate that all of the aptychi were derived from adults. One indication of ontogenetic stage is the degree of convexity of the aptychus, with flatter aptychi characteristic of later ontogenetic stages (see below). According to this criterion, most of these aptychi are mature, with the exception of the two smallest specimens.

The shape of each valve is semilunate (Figs. 13.17–20). The lateral margin is broadly rounded and the posterior margin is more sharply rounded. The anterior

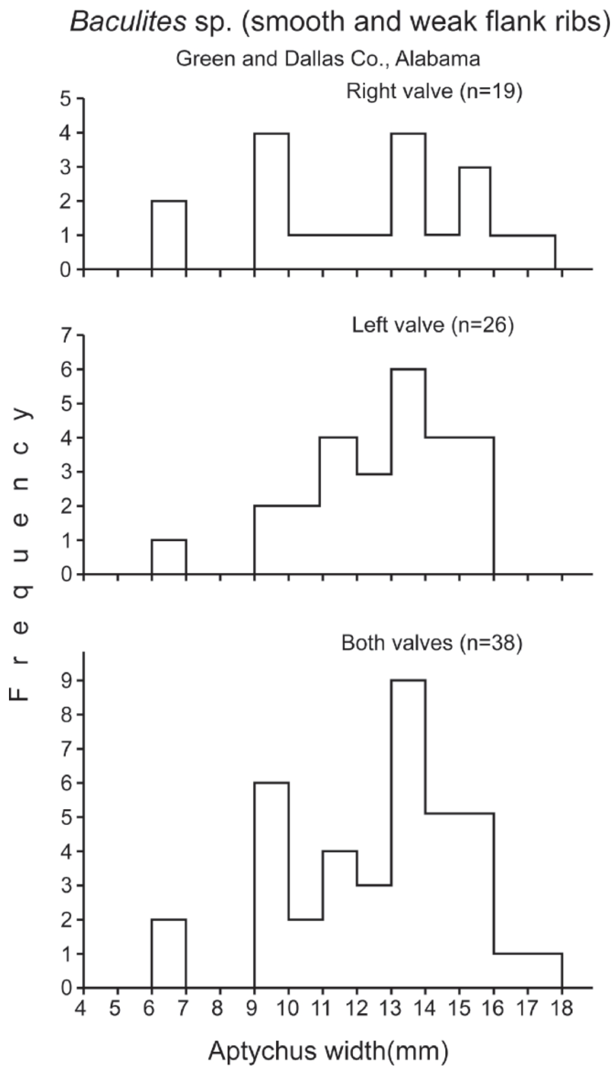


Fig. 13.16 *Size–frequency histograms of aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Greene and Dallas counties, Alabama. The bimodal distribution with peaks at 9–10 mm and 13–14 mm may reflect sexual dimorphism, provided that the specimens are all mature.*

margin usually ends in a notch that parallels the rugae and is probably the result of breakage. The symphysal edge is bordered by a flange, reflecting the morphology of the underlying chitinous layer.

The aptychi are weakly convex on the ventral side and weakly concave on the dorsal side. Smaller specimens are more strongly curved than larger specimens, which probably reflects a change in shape during ontogenetic development (compare

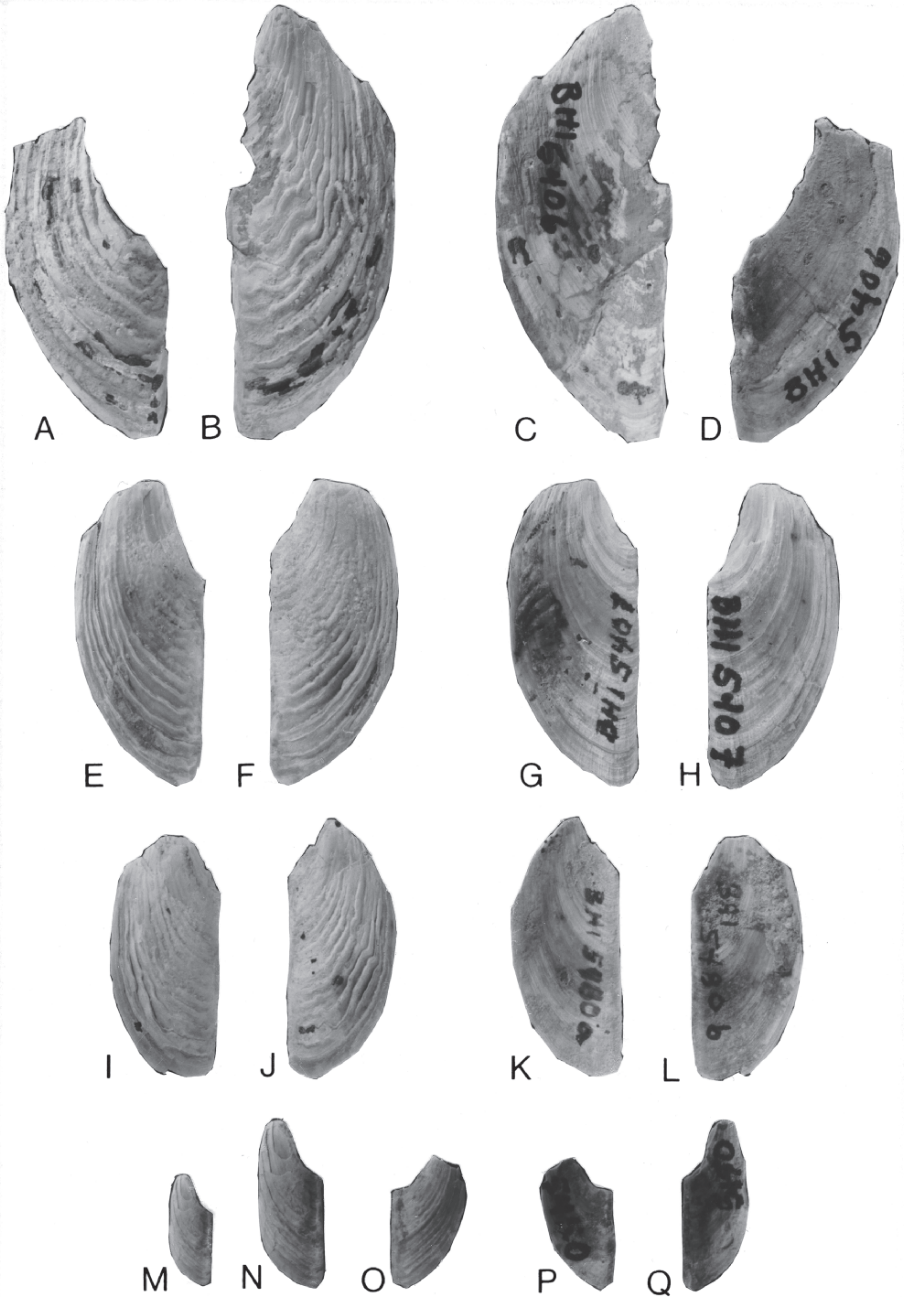


Fig. 13.17 *Aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Greene and Dallas counties, Alabama. A–D. Aptychus, BHMNH 5406. A. Right valve, ventral view. B. Left valve, ventral view. C. Left valve, dorsal view. D. Right valve, dorsal view. E-H. Aptychus, BHMNH 5407. E. Right valve, ventral view. F. Left valve, ventral view. G. Left valve, dorsal view. H. Right valve, dorsal view. I-L. Aptychus, BHMNH 5480. I. Right valve, ventral view. J. Left valve, ventral view. K. Left valve, dorsal view. L. Right valve, dorsal view. M–Q. Aptychus, BHMNH 5450. M, N. Right valve, ventral view. O. Left valve, ventral view. P. Left valve, dorsal view. Q. Right valve, dorsal view. M is X1; all other figures X1.5.*

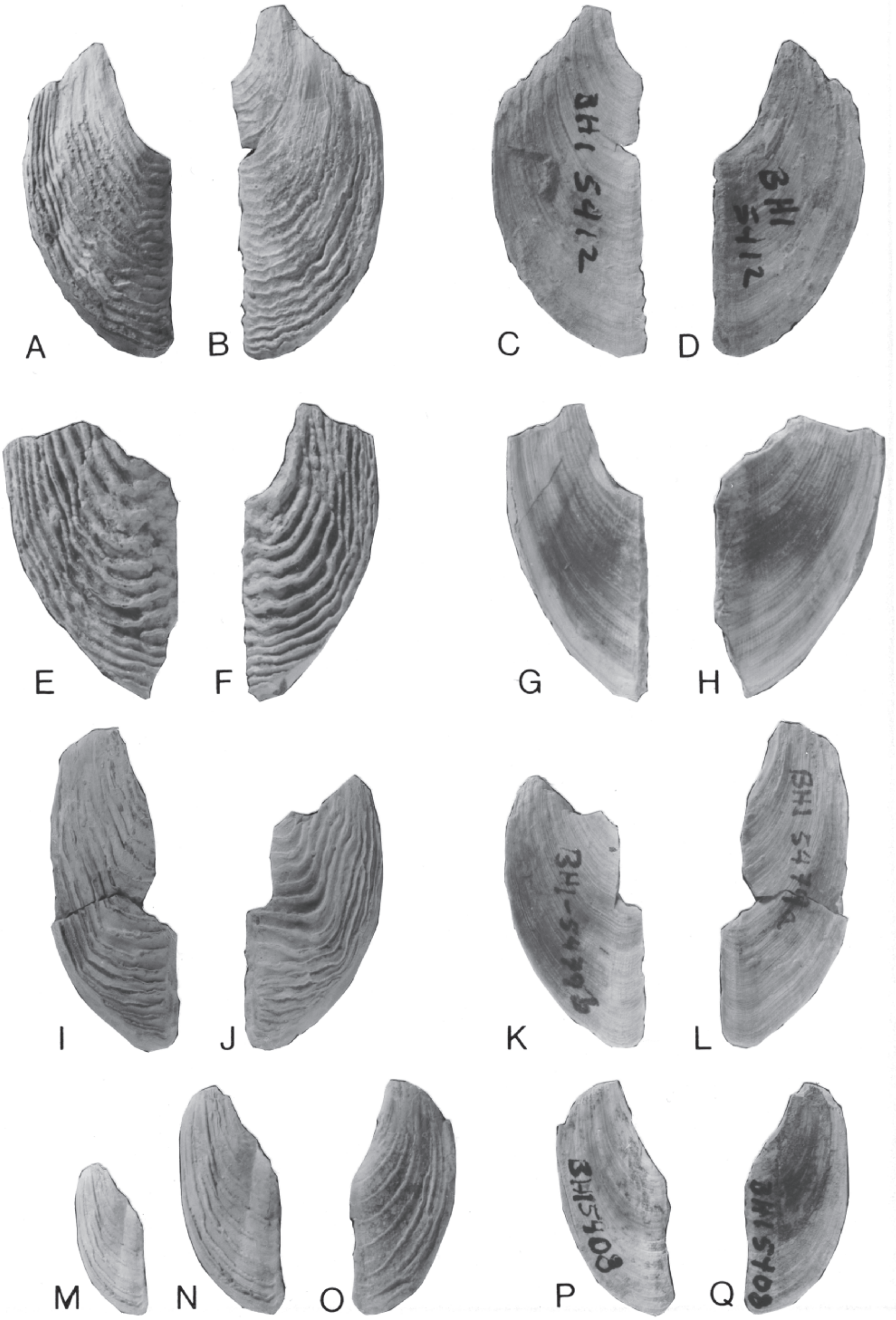


Fig. 13.18 *Aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Greene and Dallas counties, Alabama. A–D. Aptychus, BHMNH 5412. A. Right valve, ventral view. B. Left valve, ventral view. C. Left valve, dorsal view. D. Right valve, dorsal view. E–H. Aptychus, BHMNH 5149. E. Right valve, ventral view. F. Left valve, ventral view. G. Left valve, dorsal view. H. Right valve, dorsal view. I–L. Aptychus, BHMNH 5479. I. Right valve, ventral view. J. Left valve, ventral view. K. Left valve, dorsal view. L. Right valve, dorsal view. M–Q. Aptychus, BHMNH 5408. M, N. Right valve, ventral view. O. Left valve, ventral view. P. Left valve, dorsal view. Q. Right valve, dorsal view. M is X1; all other figures X1.5.*

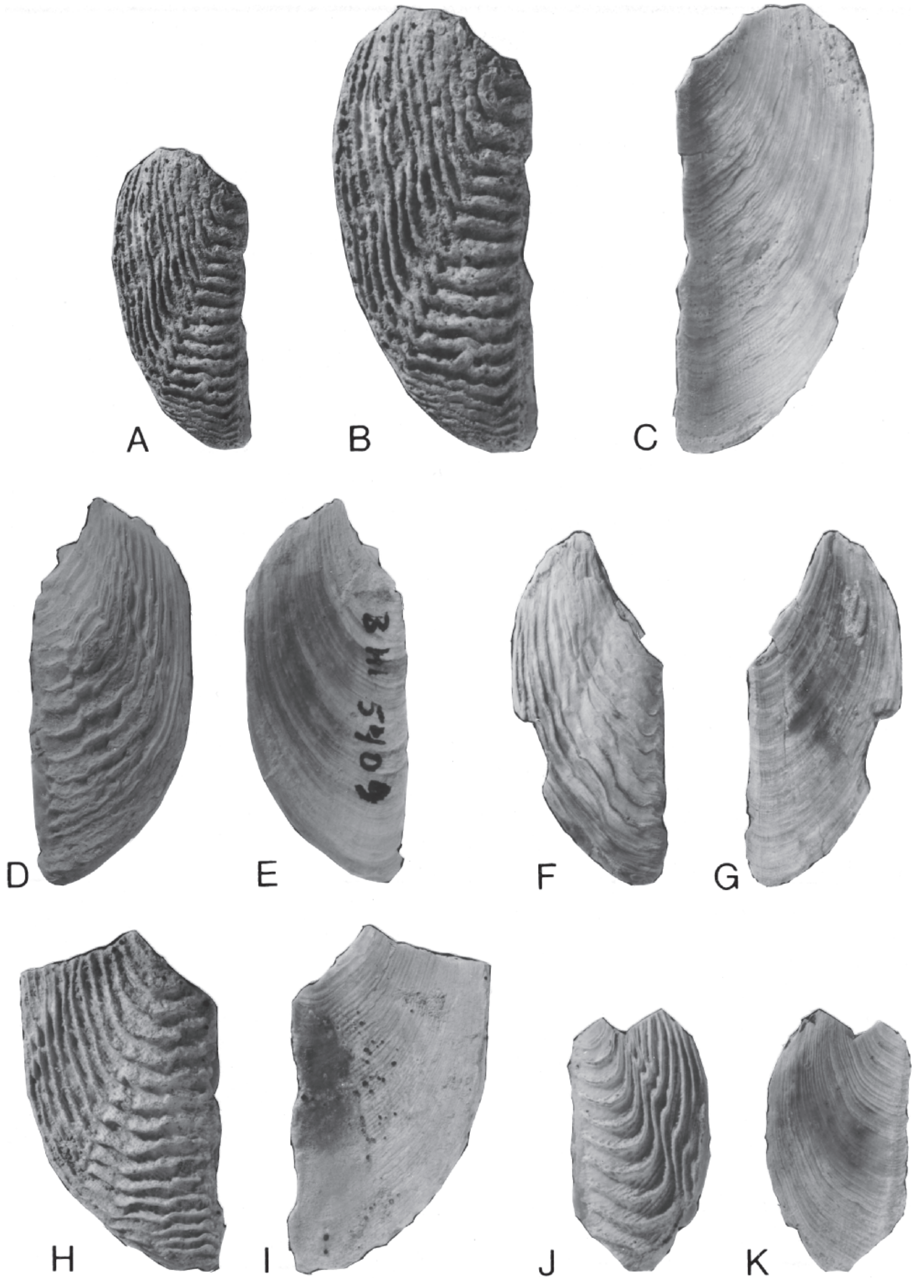


Fig. 13.19 *Aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Greene and Dallas counties, Alabama. A–C. Right valve, BHMNH 5156. A, B. Ventral view. C. Dorsal view. D, E. Left valve, BHMNH 5409. D. Ventral view. E. Dorsal view. F, G. Right valve, BHMNH 5152. F. Ventral view. G. Dorsal view. H, I. Right valve, BHMNH 5157. H. Ventral view. I. Dorsal view. J, K. Left valve, AMNH 51342. J. Ventral view. K. Dorsal view. A is X1; all other figures X1.5.*

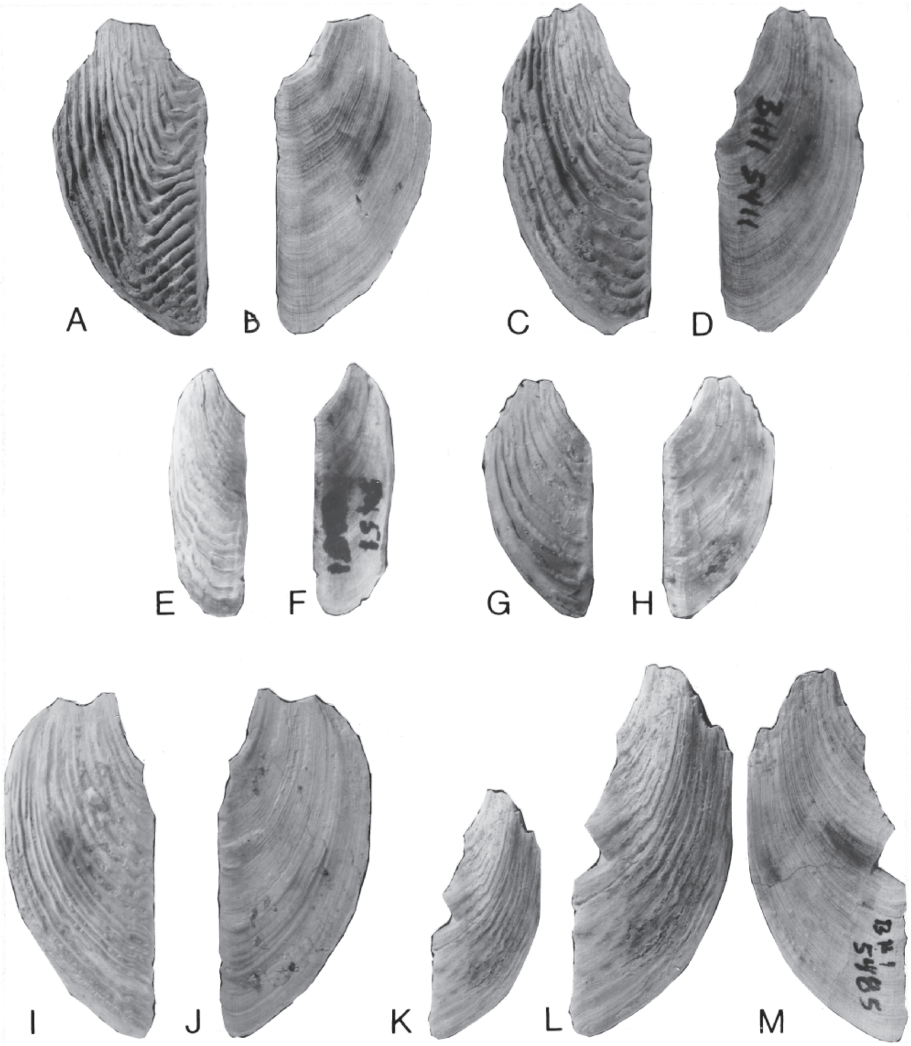


Fig. 13.20 *Aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Greene and Dallas counties, Alabama. A, B. Right valve, AMNH 51316. A. Ventral view. B. Dorsal view. C, D. Right valve, BHMNH 5411. C. Ventral view. D. Dorsal view. E, F. Right valve, BHMNH 5451. E. Ventral view. F. Dorsal view. G, H. Right valve, BHMNH 5151. G. Ventral view. H. Dorsal view. I, J. Right valve, AMNH 51293. I. Ventral view. J. Dorsal view. K–M. Left valve, BHMNH 5485. K, L. Ventral view. M. Dorsal view. K is X1; all other figures X1.5.*

Figs. 13.17M–Q and 20K–M). Some valves, such as BHMNH 5152, also show longitudinal flexures, associated with fractures on the dorsal side (Fig. 13.19F, G).

The aptychi vary in thickness. For example, the thickness at the posterior margin ranges from 2.8 mm in BHMNH 5149 to 0.8 mm in BHMNH 5485. In any one specimen, the valve is thickest in the center and thinnest at the symphysis, which

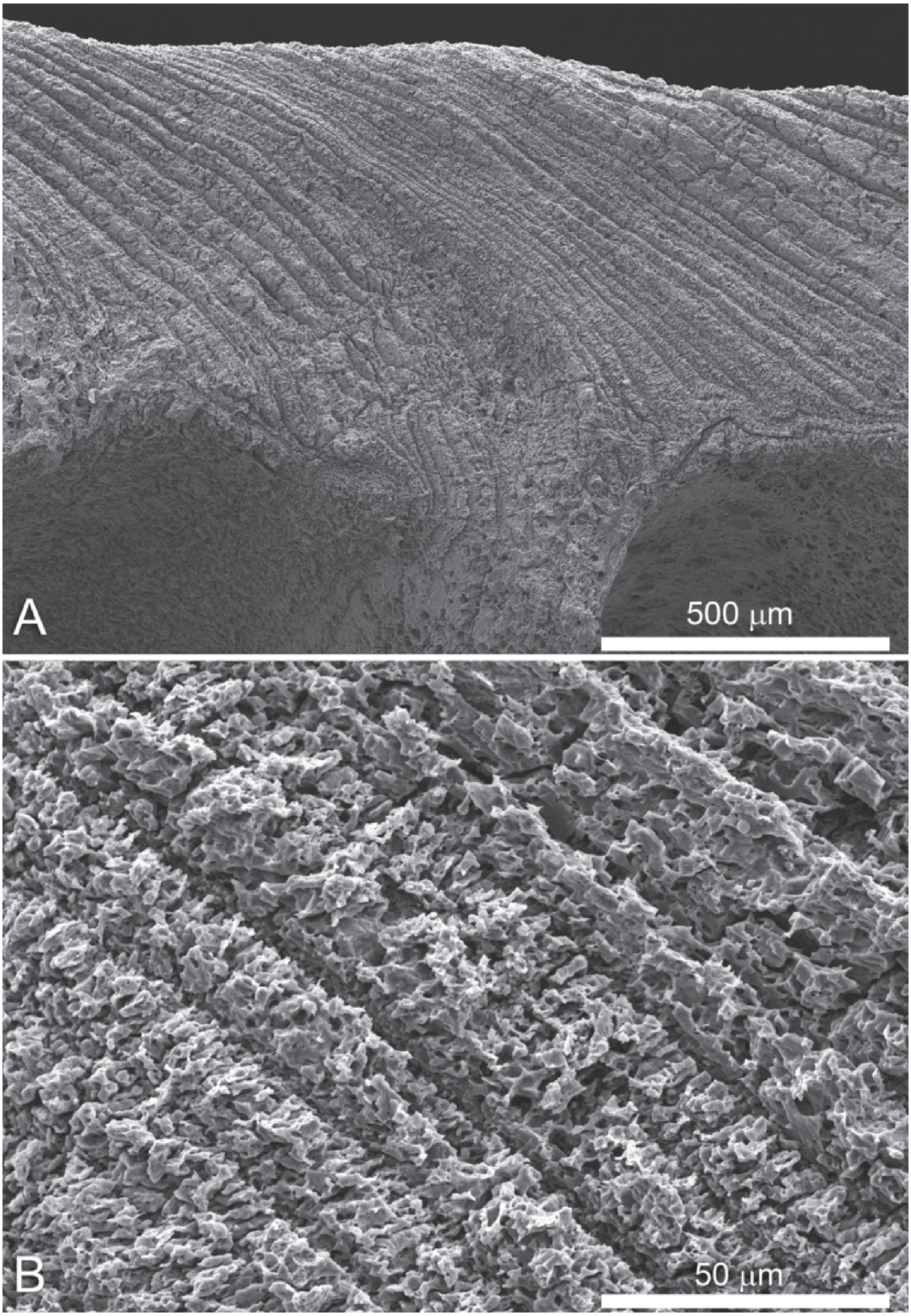


Fig. 13.21 *Cross section through the long axis of an aptychus of* Baculites *sp. (smooth or weak flank ribs), AMNH 54277, Mooreville Chalk, Alabama. A. The aptychus is composed of thin calcitic increments secreted at the posterior end. Dorsal surface is on the top, ventral surface on the bottom. B. Each increment is approximately 20 um thick.*

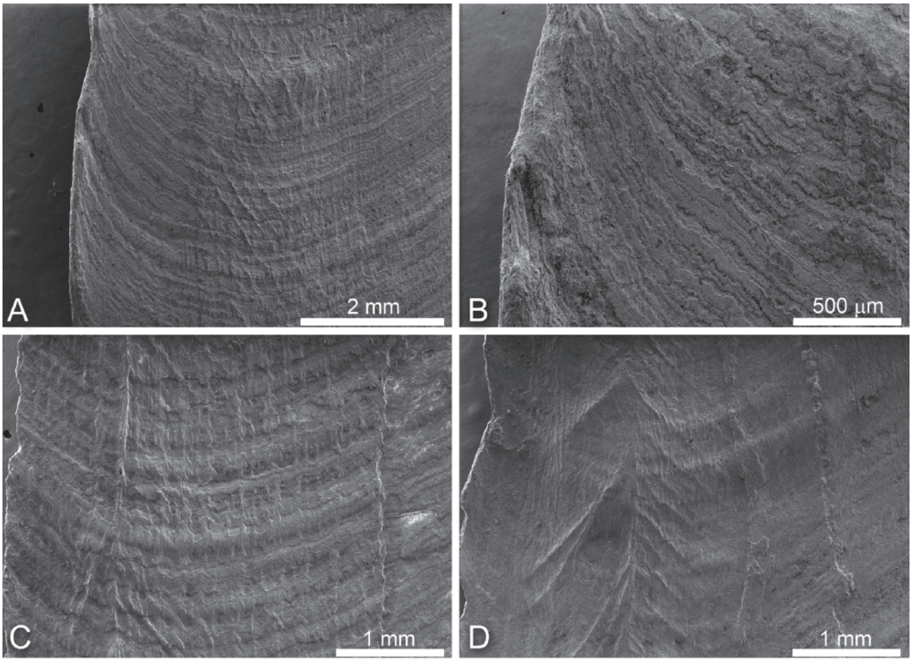


Fig. 13.22 *Dorsal surface of aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Alabama. The symphysal edge is on the left side of each photo and the anterior direction is toward the top. A. BHMNH 5479. View of the symphysal edge showing delicate diagonal striations. B. BHMNH 5479. The increments composing the aptychus bend forward as they approach the symphysis. C. BHMNH 5152. Thin longitudinal striations are common near the symphysis. D. BHMNH 5151. The area near the symphysis is covered with chevrons in this specimen, which may be the result of an injury or growth pathology.*

ends in a flat, beveled edge (e.g., 2.8 mm versus 0.6 mm, respectively, in BHMNH 5154). Variations in thickness are also associated with injuries and pathologies. The thick ridge and accompanying fold at the posterior margin in BHMNH 5406 is such an example (Fig. 13.17A–D).

X-ray diffraction analysis indicates that the aptychi are composed of calcite. A cross section through the long axis of a valve reveals a series of thin increments, each approximately 20 µm thick (Fig. 13.21). The increments are stacked shingle-style with more recent increments lying underneath older increments, forming an angle of 30° with the dorsal edge. The increments seem to be bundled into clusters, but this requires further research.

The dorsal surface of the aptychus is relatively smooth. There are broad undulations covered with fine lines that parallel the lateral and posterior margins. The lines bend forward at the symphysis, which they approach at an angle of 45° (Fig. 13.22B). It is unclear if the fine lines become more closely spaced toward the posterior end. Many specimens also show delicate longitudinal or diagonal striations, especially near the symphysis (Fig. 13.22A, C). In BHMNH 5151 (Fig. 13.22D), this area is covered with chevrons, which may be the result of a repaired injury.

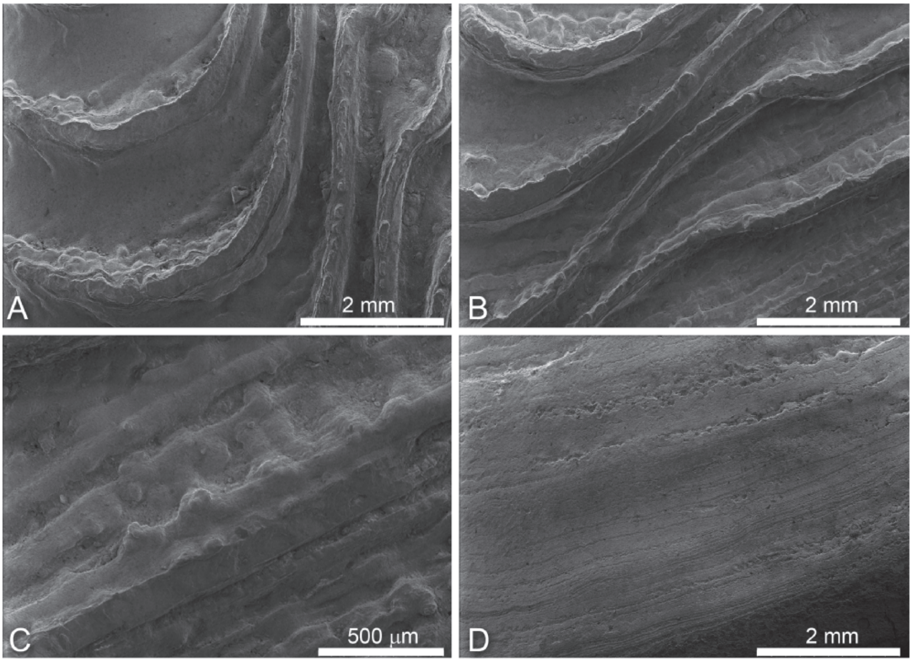


Fig. 13.23 *Ventral surface of aptychi of* Baculites *sp. (smooth and weak flank ribs), Mooreville Chalk, Alabama. The symphysal edge is toward the left of each photo and the anterior direction is toward the top. A–C. AMNH 51342. A. The rugae turn almost perpendicularly (left) toward the symphysis, forming a geniculation. B. The rugae, especially on the lateral margin, are twisted over, resembling flexible sheets of metal. C. Rugae with botryoidal excrescences. D. BHMNH 5485. The increments composing the aptychus are visible where the rugae have eroded away.*

The ventral surface of the aptychus is ornamented with coarse ridges or rugae that parallel the lateral and posterior margins. The rugae usually attain their widest spacing at midlength (Figs. 13.18E, F, I, J, M–O, 19B, D, J), and sometimes bunch up at the posterior end (compare Figs. 13.18E, F, 20C). In general, the rugae are closely spaced along the lateral margins (Fig. 13.17A, B, E, F). They turn almost perpendicularly toward the symphysis, forming a geniculation (Figs. 13.18I, J, 20A, 23A), but do not continue onto the symphysal fold, which is covered instead with fine ridges that are convex toward the posterior end.

In addition to the geniculation, the rugae sometimes develop a series of kinks (zigzags) that are aligned longitudinally (Fig. 13.19A, B, H). These kinks may or may not correspond to fractures on the dorsal side. Conversely, fractures on the dorsal side may or may not correspond to kinks on the ventral side.

The rugae vary in their degree of coarseness and waviness, which may reflect ontogenetic development. For example, the rugae in BHMNH 5450 (Fig. 13.17M–O), the smallest specimen in our collection, and presumably from a juvenile, are fine and relatively straight, whereas those in BHMNH 5149 (Fig. 13.18E, F), one of the larger specimens in our collection, and presumably from an adult, are coarse and wavy. However, specimens of nearly the same size also show wide variation in coarseness and sinuosity (compare Fig. 13.20A, I), which may be related to different states of preservation.

The rugae are asymmetric in profile, with one side more steeply sloping than the other. Commonly, the crests of the rugae bend backward (anteriorly) at an acute angle, e.g., AMNH 51316 (Fig. 13.20A). In AMNH 51342, the rugae on the lateral margin are twisted over, resembling flexible sheets of metal (Fig. 13.23B). In some specimens, the edges of the rugae are very sharp, whereas in others, they are worn down. In general, the rugae are sharper on the posterior end, suggesting erosion of earlier formed rugae during ontogeny, but this pattern requires further documentation.

Close examination of the ventral side of the aptychi reveals several additional features: a thin, chalky outer layer covering the surface; botryoidal excrescences (Fig. 13.23C), which may be accentuated by weathering; fine ridges that cross the sides of the rugae diagonally and disappear in the troughs (e.g., AMNH 51316); and thin increments in areas where the rugae are worn down (Fig. 13.23D).

6.4 *Baculites* sp., Niobrara Formation, Kansas

FHSM 968:1 was previously described and illustrated by Miller (1968: 87, pl. 8, Fig. 14) and consists of an aptychus with part of the anterior portion of the left valve missing (Fig. 13.24G). According to Miller (1968: 87), the specimen was closely associated with the mold of a smooth baculite. The aptychus is 10.2 mm wide and 20.1 mm long, with a ratio of aptychus width to aptychus length of 0.51, which is probably an underestimate. The ventral surface of the aptychus is ornamented with coarse rugae that parallel the lateral and posterior margins.

6.5 *Baculites compressus/B. cuneatus*, Pierre Shale, South Dakota

BHMNH 5498 is a right wing of a lower jaw (Fig. 13.24F, Table 13.1). It is 7.9 mm wide and 19.5 mm long. The estimated ratio of jaw width to jaw length is 0.81. The wing is convex with a prominent flange along the symphysal edge. The anterior margin of the wing is broadly rounded and the posterior margin is more sharply rounded; the lateral margin is obscured.

The jaw consists of a dark brown to black crystalline layer approximately 200 μm thick. X-ray diffraction analysis indicates that it consists of magnesium enriched calcite. This layer shows broad folds that parallel the posterior margin. In areas where the black layer is broken away, it exposes a smooth brown layer bearing finer ridges, spaced at approximately equal distances of 0.5 mm.

An analysis of the relationship between the shape of the jaw and the whorl cross section is complicated because the jaw is not preserved inside the body chamber,

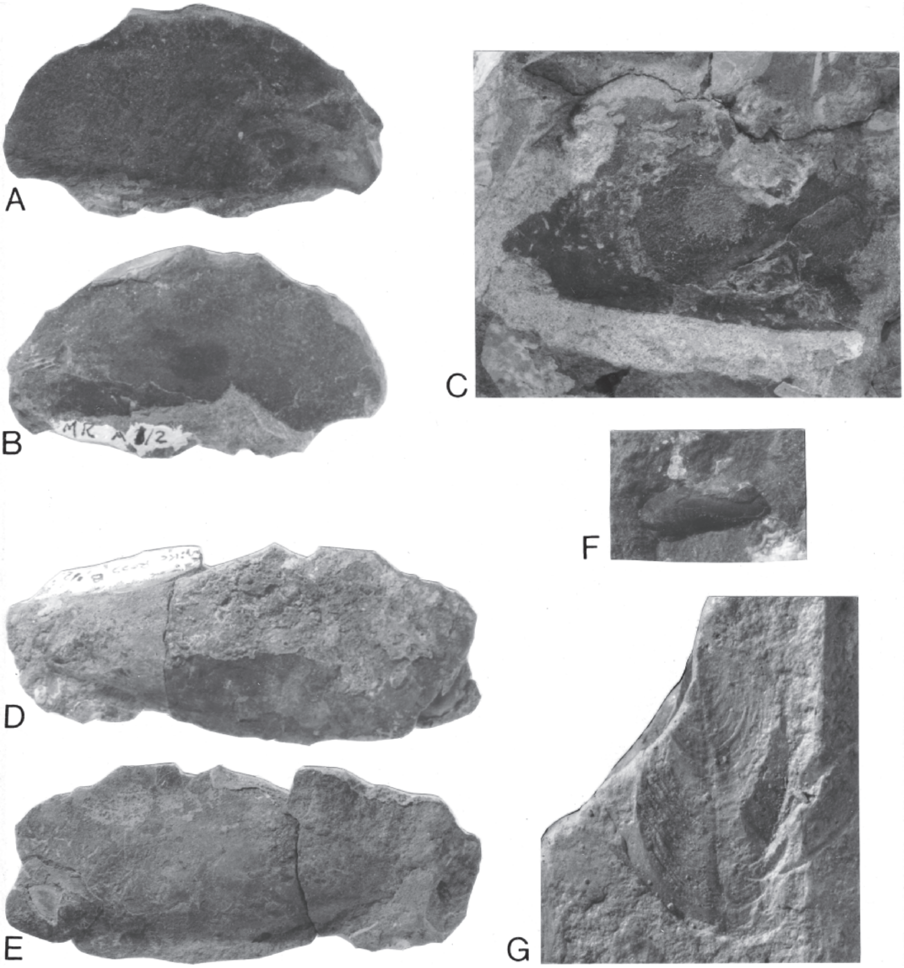


Fig. 13.24 *A–E. Lower jaws of* Pseudobaculites natosini *(Robinson, l945), Lewis Shale, Natrona County, Wyoming. A, B. BHMNH 5501. A. Right wing, anterior direction toward the right. B. Left wing, anterior direction toward the left. C. Right wing, BHMNH 5500, anterior direction toward the right. D, E. AMNH 51328. D. Left wing, anterior direction toward the left. E. Right wing, anterior direction toward the right. F. Right wing of a lower jaw attributed to* Baculites compressus *Say, 1820, or* Baculites cuneatus *Cobban, l962, BHMNH 5498, Pierre Shale, Meade County, South Dakota. Anterior direction toward the right. G. Aptychus attributed to* Baculites *sp., FHSM 968:1, Smoky Hill Chalk Member, Niobrara Formation, Rooks Co., Kansas. G is X2; all other figures are X1.*

and, therefore, no measurements are available for the corresponding whorl cross section. Instead, we measured specimens of *Baculites compressus/B. cuneatus* from the same concretion as the jaws, as well as specimens from other concretions in the same stratigraphic interval. Our calculations indicate that the shape of the jaw is much broader than the whorl cross section (Table 13.1).

6.6 *Pseudobaculites natosini,* Lewis Shale, Wyoming

BHMNH 5501 is 50.1 mm long but is incomplete (Fig. 13.24A, B; Table 13.1). Each wing is approximately 25.8 mm wide. The specimen is folded in half along the symphysis. A flange is present on the middle one-third of the jaw. The posterior margin is broken but the lateral margin is intact and broadly curved. The apex is more strongly convex than the rest of the wing.

The jaw is preserved as a fine-grained, tan layer covered by a dark brown to black, coarsely crystalline layer 160 µm thick. This crystalline layer bears broad ridges that parallel the posterior margin. X-ray diffraction analysis indicates that it consists of calcite. This layer is covered near the symphysal margin of the left wing by patches of a thin (100 µm thick) translucent layer bearing very fine lirae spaced at approximately equal distances of 60 µm. X-ray diffraction analysis indicates that this layer consists of gypsum, which is undoubtedly diagenetic.

AMNH 51328 is 59.0 mm long with a wing width of 26.3 mm (Fig. 13.24D, E; Table 13.1). The estimated ratio of jaw width to jaw length is 0.89. The jaw is folded together along the midline and the flange is visible on the middle two-thirds of the jaw. The left apical tip is bluntly rounded and points away from the midline. The apex is more strongly convex than the rest of the wing. The specimen is preserved as a fine grained tan layer. The counterpart is covered with a dense, dark brown crystalline layer 220 µm thick, similar to that in BHMNH 5501. X-ray diffraction analysis of this layer indicates that it is composed of calcite. It bears low folds and very fine, evenly spaced lirae, which parallel the posterior margin.

BHMNH 5502 is a negative of the right wing of a lower jaw with a well-defined lateral margin (not illustrated). The width and length of the wing are 23.6 mm and 52.8 mm, respectively. The estimated ratio of jaw width to jaw length is 0.89. The anterior portion is composed of tan grainy material and the rest of the jaw is composed of dark brown to black crystalline material with a thickness of approximately 200 µm. X-ray diffraction analysis indicates that this crystalline material consists of calcite.

BHMNH 5500 is a partially preserved right wing (Fig. 13.24C). The width of the wing is 28.1 mm. The flange is visible on most of the specimen. The jaw is covered with a coarsely crystalline brown to black material overlain in parts with a platy yellowish material. The flange is ornamented with thin ridges that intersect the symphysis at an angle of 60°.

An analysis of the relationship between the shape of the jaw and the whorl cross section is again complicated by the fact that none of the jaws is preserved inside the body chamber and, therefore, no measurements are available for the corresponding whorl cross section. To circumvent this problem, we relied on measurements reported by Cobban and Kennedy (1994) for specimens of this species from the Lewis Shale of Wyoming (Table 13.1). Based on these measurements, the shape of the jaw is broader than the whorl cross section.

7 Discussion

7.1 Preservation

Differences in the preservation of jaws can obscure similarities in morphology (Landman et al., 2006). Therefore, in comparing jaws, it is important to take into account their state of preservation. In some instances, only the chitinous layer of the lower jaw, now altered, is preserved, whereas in other instances, only the calcitic layer (aptychus) is preserved. However, the absence of one or the other of these layers does not necessarily imply that it was absent during life.

We have documented three modes of occurrence of baculite jaws in North America:

(1) In the Gammon Ferruginous Member of the Pierre Shale and in the Cody Shale, the jaws occur inside the body chamber and retain both the chitinous layer, now altered, and the calcitic aptychus. The outer aragonitic shell of the body chamber is also usually present.
(2) In the Mooreville Chalk, only the aptychus is present, not the underlying chitinous layer. The aragonitic outer shells of the baculites are absent. Likewise, in the Smoky Hill Chalk Member of the Niobrara Formation, only the aptychi are present, not the outer shells of the baculites. This mode of occurrence is similar to that of baculite jaws in the Boreal chalks of northern Europe and has traditionally been interpreted as resulting from differential dissolution in which the aragonite of the outer shell dissolves away leaving the calcitic aptychi behind (Morton and Nixon, 1987; Barthel et al., 1990; Sanders, 2003).
(3) In the Lewis Shale and the upper part of the Pierre Shale, the jaws occur as isolated elements in concretions containing aragonite-preserved fossils. The chitinous layer of the lower jaw, now altered, is present, but the outer calcitic layer (aptychus) is absent, fragmentary, or recrystallized. The aptychi may have partially or completely disintegrated before or during the formation of the concretion. A similar loss of aptychi has been hypothesized in scaphites (Landman and Waage, 1993) and, possibly, placenticeratids (Landman et al., 2005).

In instances in which the chitinous layer of the lower jaw is still present, it consists of black crystalline material, similar to that reported in other ammonite jaws (Landman et al., 2006). X-ray diffraction analysis of samples of this material from five specimens (AMNH 5138, BHMNH 5496, 5498, 5501, and 5502) reveals the presence of calcite, calcite enriched in magnesium, and amorphous material. However, it is possible that part of this black crystalline material actually represents a recrystallized portion of the aptychus. In order to better understand these relationships, it is important to more thoroughly study the diagenetic history of the chitinous and calcitic parts of the ammonite jaw.

The rarity of baculite jaws inside the body chamber indicates the low preservation potential of these structures. After death, the soft body must have easily fallen out of the orthoconic body chamber and become separated from the shell. It required unusual circumstances for both the shell and soft body to fall to the sea bottom and be preserved together.

7.2 Comparative Jaw Morphology

The lower jaws of baculites from North America are elongate. The ratio of jaw width to jaw length in *Baculites* sp. (smooth) from South Dakota averages 0.77. The ratio in two specimens of *Pseudobaculites natosini* averages 0.89. These differences in proportions may be related to differences in the whorl cross section. However, it is notable that the proportions of the jaws of the early Campanian species more closely match those of the corresponding whorl cross section than in the late Campanian species (see below).

The outer lamella of the lower jaw consists of two wings with a midline groove bordered by flanges. The inner layer, which was originally composed of chitin, is ornamented with broad undulations and fine ridges, which parallel the posterior margin, as shown in BHMNH 5331 (Fig. 13.15). This layer is covered by a pair of calcitic valves, although these are poorly preserved, if present at all, in the two late Campanian species.

In the material from the lower Campanian Pierre Shale, Cody Shale, Mooreville Chalk, and Nobrara Formation, representing *Baculites* sp. (smooth and weak flank ribs), the aptychi conform to the description of rugaptychi. They are elongate with a flange at the symphysal edge, reflecting the morphology of the underlying chitinous layer. The aptychi from Alabama commonly show a notch at the anterior end, which was also noted in material from the Campanian of England by Sharpe (1857: 57), and which may be the result of breakage.

The aptychi are ornamented on the dorsal side with broad undulations covered with fine lines that parallel the lateral and posterior margins. The aptychi from the Campanian of Europe also show this same pattern (Sharpe, 1857: pl. 24, Figs. 8b, 10a; Moberg, 1885: pl. 1, Figs. 14, 15; reillustrated by Kennedy and Christensen, 1997: Fig. 31E, H).

The aptychi are ornamented on the ventral side with coarse rugae that parallel the lateral and posterior margins, and approach the symphysis almost perpendicularly. In many aptychi, the rugae show a well-developed geniculation as they turn toward the symphysis, forming a series of chevrons pointing posteriorly (Figs. 13.18I, J, 20A). This geniculation is characteristic of rugaptychi and has been widely documented in European material (Hébert, 1854: pl. 28, Fig. 6; Sharpe, 1857: pl. 26, Fig. 9; reillustrated by Blackmore, 1896: pl. 16, Fig. 16; Moore and Sylvester-Bradley, 1957).

The aptychi from the lower Campanian Pierre Shale, Cody Shale, Mooreville Chalk, and Niobrara Formation are nearly identical to those from the Campanian of northern Europe. For example, the North American specimens closely match those from

Belgium illustrated by de Grossouvre (1908: 39, pl. 10, Figs. 7–13; reillustrated with other specimens from the same locality by Kennedy, 1986: 192, pl. 16, Figs. 1–22). These similarities imply that rugaptychi are common features of many baculite species.

The aptychi in *Baculites compressus/B. cuneatus* and *Pseudobaculites natosini* are not well preserved, making comparisons with other species difficult. One specimen of *P. natosini* (BHMNH 5501) retains a thin layer of clear material with very fine lirae, which may represent part of the aptychus. If so, it is thinner and more finely ornamented than the aptychi of the early Campanian species, but this requires further study.

The radula in *Baculites* sp. (smooth) features long marginal teeth and blunt marginal plates. Although the other teeth of the radula are not well preserved, enough of the radula is present to suggest its similarity to those reported in other ammonites (Nixon, 1996). The radular teeth are distinct from the hooklike elements reported in scaphites (Landman and Waage, 1993; Kennedy et al., 2002; Landman and Klofak, 2004), and variously interpreted as radular teeth or tentacular hooks. The ridges on the marginal teeth of the baculite radula resemble those on the marginal teeth of the radula of *Vampyroteuthis infernalis* Chun, 1903, as illustrated by Solem and Roper (1975).

7.3 Function of the Aptychus Type Jaw

The aptychus type jaw has generally been interpreted as an adaptation for feeding on small prey (microphagy) (Morton and Nixon, 1987; Lehmann and Kulicki, 1990; Seilacher, 1993; Engeser and Keupp, 2002). Several morphological features of the jaw have been cited in support of this interpretation: (1) the presence of a blunt anterior margin with the two wing tips diverging at the apex, (2) the general absence of a thickened calcareous deposit at the apical end, (3) the presence of a groove, rather than a thickening, along the middle of the jaw, which creates a line of weakness incompatible with a crushing function (Seilacher, 1993), (4) the much larger size of the lower jaw relative to the upper jaw, with a concomitant loss of the gliding joint between the upper and lower jaws (Seilacher, 1993), and (5) the reduction in size of the inner lamella of the lower jaw, thus reducing the surface area required for muscular attachment to facilitate biting (Lehmann and Kulicki, 1990). A microphagous feeding habit is also consistent with rare finds of ammonite stomach contents (Lehmann, 1981; Jäger and Fraaye, 1997), although such finds have not yet been documented in baculites.

In contrast, the morphological features of lower jaws that are adapted for biting and crushing are very different. The apical end of the jaw is beaklike and usually reinforced with a mineralized deposit [e.g., *Nautilus*, *Gaudryceras*, and some species of Ammonitina with thin aptychi such as *Aconeceras* (see Kulicki et al., 1988; Doguzhaeva and Mutvei, 1992) and, possibly, *Placenticeras* (see Landman et al., 2006)]. In addition, the lower jaw is smaller or equal in size to the upper jaw (Lehmann, 1981; Morton and Nixon, 1987).

Although the morphology of the lower jaws of baculites is consistent with a microphagous feeding habit, the exact feeding mechanism is unknown. Several hypotheses have been proposed for other members of the Aptychophora, including scooping up soft-bodied organisms off the seafloor (Lehmann, 1981), straining out plankton from seawater (Morton and Nixon, 1987), and sucking in prey through a pump-like action of the lower jaw (Seilacher, 1993). Of these, the first scenario is the least likely to apply to baculites, because these animals probably lived several tens of meters above the bottom, based on their lithologic and faunal associations (Westermann, 1996), and oxygen isotopic analyses of their shells (Landman et al., in prep.).

In addition to its role in food capture, the aptychus type jaw has also been interpreted as an operculum (Trauth, 1927–1936; Schindewolf, 1958), largely because of the close correspondence between the shape and size of the jaw and the whorl cross section. Lehmann and Kulicki (1990) developed a model to accommodate a dual function – both as an operculum and as a feeding device. According to these authors, the aptychus type jaw was capable of rotating into a nearly vertical position to serve as an operculum. Seilacher (1993) also advocated a dual function, and detailed the evolutionary steps culminating in this innovation. This interpretation was also favored in the most recent treatment of the subject by Engeser and Keupp (2002).

With respect to baculites, the evidence for an opercular function of the lower jaw is based on the following criteria:

(1) The correspondence between the shape and size of the lower jaw and the whorl cross section. In *Baculites* sp. (smooth and weak flank ribs) from the lower Campanian Pierre Shale and Cody Shale, the correspondence between the shape and size of the lower jaw and the whorl cross section is excellent. When the jaw is splayed out, it touches the sides of the shell. However, the jaw may not have been splayed out during life. Indeed in some specimens where the jaw is preserved in the body chamber, it forms a U-shaped structure (Fig. 13.8A–C). In addition, in *Baculites compressus/B. cuneatus* and *Pseudobaculites natosini*, the fit is much poorer. The shape of the jaw in these species is much broader than the whorl cross section.

(2) The mode of occurrence of the lower jaw in the body chamber. In *Baculites* sp. (smooth and weak flank ribs) from the lower Campanian Pierre Shale and Cody Shale, most of the jaws are aligned at an angle of 45°–90° relative to the long axis of the shell, with the anterior end of the jaw near the dorsal side of the shell, and the posterior end near the ventral side of the shell, effectively occluding the opening (Figs. 13.5–7, 8D–F, 9, 10, 11, 12, 13; see also Nowak, 1908: pl. 14, Fig. 13.11). However, this position may simply represent an artifact of preservation related to how the jaw settled in the body chamber after death [see Morton (1975), Seilacher (1990), and Landman and Waage (1993) for a discussion of taphonomic biases affecting the preservation of ammonite jaws].

(3) The presence of healed injuries on the aptychus. Many of the aptychi from the Mooreville Chalk show fractures on the dorsal side, which may represent healed injuries. However, healed injuries are also present on the jaws of *Nautilus*, which are used for biting, not as opercula (Landman and Kruta, 2006). The injuries in *Nautilus* may have been inflicted during feeding, while subjugating prey.
(4) The composition and ornament of the aptychus. In *Baculites* sp. (smooth and weak flank ribs), the aptychi are composed of hard calcite and covered with coarse, rugose ornament. These features are usually interpreted as adaptations against predation. However, Seilacher (1993) has argued that the ornament on some aptychi may simply represent fabricational noise associated with biomineralization, with no functional value at all.

In conclusion, the evidence for an opercular function in baculites is ambiguous, with as many arguments as counterarguments. We suggest an alternative interpretation that is consistent with many of the morphological features described above. The jaws of baculites may have protruded out from the aperture to facilitate food capture. Even if the jaws were exposed to the outside temporarily, they would have been vulnerable to predation. The thick, coarsely ornamented aptychus could have served as protection. Indeed, in some modern coleoids, the jaws can extend out from the oral cavity during feeding (Kasugai, 2001; S. v. Boletzky, 2004, personal communication). Such flexibility may also have characterized baculites and other ammonites.

7.4 Rate of Growth

The jaws provide some insights into the rate of growth of baculites. Analysis of the microstructure of the aptychi from the Mooreville Chalk reveals that they are composed of thin increments, each approximately 20 um thick (Fig. 13.21). The rate of formation of these increments is unknown, but studies of aptychi from other ammonites suggest that such increments were deposited daily (Hewitt et al., 1993: 207).

If we assume a daily rate of deposition, we can calculate the approximate age of a baculite by dividing the length of its aptychus by the thickness of a single increment. The size–frequency histogram of valve width of aptychi from the Mooreville Chalk reveals two modes at 9–10 mm and 13–14 mm. These modes presumably represent the modal size classes of mature microconchs and macroconchs, respectively. The corresponding aptychus lengths are approximately 21 and 31 mm. Using these values and dividing by the thickness of a single increment yields an average age at maturity of approximately 3 and 4 years for microconchs and macroconchs, respectively. This estimate is consistent with estimates of the age at maturity of other shallow-water ammonites (Bucher et al., 1996). However, this result must be confirmed with oxygen isotopic analyses of the aptychi and examination of the variation in increment thickness through ontogeny.

8 Conclusions

The lower jaws of baculites are longer than wide and consist of two subquadrate wings. The inner chitinous layer of the outer lamella shows a groove along the midline bordered by flanges. This layer bears a pair of calcitic plates (=the aptychus), comparable to those in all other members of the Aptychophora.

In the early Campanian species in which the aptychi are well preserved, they conform to the rugaptychus morphotype. The dorsal side is characterized by fine lines and broad undulations that parallel the posterior margin. The ventral side is characterized by irregular rugae that parallel the lateral and posterior margins and approach the symphysis almost perpendicularly. In contrast, the aptychi of the late Campanian species seem thinner and less coarsely ornamented, but this difference may be due to preservation and requires further research.

Jaws are a fundamental feature of all cephalopods and were undoubtedly present in all members of the Baculitidae. This family ranges from the Albian to the Maastrichtian, but so far jaws have only been reported from the Cenomanian, Turonian, and Campanian. We suspect that it is only a matter of time before they are discovered in the rest of the Upper Cretaceous.

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References

Arkell, W. J. 1957. Aptychi. *In* R. C. Moore (editor), *Treatise on Invertebrate Paleontology, Part L. Mollusca* **4**: L437–L440. New York: Geological Society of America; Lawrence, KS: University of Kansas Press.

Barthel, K. W., N. H. M. Swinburne, and S. C. Morris. 1990. *Solnhofen: A Study in Mesozoic Palaeontology*. Cambridge: Cambridge University Press.

Binckhorst van den, J. T. 1861. *Monographie des Gastropodes et des Céphalopodes de la Craie Supérieure du Limbourg*. vi + 83pp. Brussels: Muquardt; Maastricht: Muller Frères.

Bishop, G. A. 1985. Fossil decapod crustaceans from the Gammon Ferruginous Member, Pierre Shale (Early Campanian), Black Hills, South Dakota. *Journal of Paleontology* **59**: 605–624.

Blackmore, H. P. 1896. Some notes on the aptychi from the Upper Chalk. *Geological Magazine* **3**: 529–533.

Böhm, J. 1898. Über *Ammonites pedernalis* v. Buch. *Zeitschrift der Deutschen Geologischen Gesellschaft* **50**: 183–201.

Breitkreutz, H., R. Diedrich, and R. Metzdorf. 1991. Fossilfunde aus der Schwartz-Bunten Wechselfolge (Ob. Cenoman bis Unter Turon) des Ostwestfalendammes bei Bielefeld. *Berichte des Naturwissenschaftlichen Vereins für Bielefeld und Umgegend* **32**: 37–48.

Bucher, H., N. H. Landman, S. M. Klofak, and J. Guex. 1996. Mode and rate of growth in ammonoids. *In* N. H. Landman, K. Tanabe, and R. A. Davis (editors), *Ammonoid Paleobiology*, pp. 407–461. New York: Plenum Press.

Chun, K. 1903. *Aus den tiefen des weltmeeres*. Jena: G. Fischer.

Cobban, W. A. 1958. Two new species of *Baculites* from the Western Interior region. *Journal of Paleontology* **32**(4): 660–665.

Cobban, W. A. 1962. New baculites from the Bearpaw Shale and equivalent rocks of the Western Interior. *Journal of Paleontology* **36**(1): 125–135.

Cobban, W. A. 1969. The Late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (DeKay) in the Western Interior of the United States. *U.S. Geological Survey Professional Paper* **619**: 1–29.

Cobban, W. A., and W. J. Kennedy. 1994. A giant baculite from the Upper Campanian and Lower Maastrichtian of the Western Interior. *U.S. Geological Survey Bulletin* **2073C**: C1–C4.

Cobban, W. A., I. Walaszczyk, J. D. Obradovich, and K. C. McKinney. 2006. A USGS zonal table for the Upper Cretaceous middle Cenomanian-Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. *U.S. Geological Survey Open – File Report* 2006–1250, 45p.

Desmarest, A. G. 1817. Mémoire sur deux genres coquilles fossiles cloisonnées et à siphon. *Journal de Physique, de Chimie, d'Histoire naturelle et des Arts* **85**: 42–51.

DeKay, J. E. 1827. Report on several multilocular shells from the State of Delaware; with observations of a second specimen of the new fossil genus *Eurypterus. Annals of the Lyceum of Natural History of New York* **2**: 273–279.

Diener, C. 1925. Ammonoidea neocretacea. *Fossilium Catalogus (1: Animalia)* **29**: 1–244.

Doguzhaeva, L. A., and H. Mutvei. 1992. Radula of the Early Cretaceous ammonite *Aconeceras* (Mollusca: Cephalopoda). *Palaeontographica Abteilung A* **223**: 167–177.

Engeser, T., and H. Keupp. 2002. Phylogeny of aptychi-possessing Neoammonoidea (Aptychophora nov., Cephalopoda). *Lethaia* **24**: 79–96.

Everhart, M. J. 2005. *Oceans of Kansas: A Natural History of the Western Interior Sea*. Bloomington, IN: Indiana University Press.

Farinacci, A., N. Mariotti, R. Matteucci, U. Nicosia, and G. Pallini. 1976. Structural features of some Jurassic and Early Cretaceous Aptychi. Bollettino della Società Paleontologica Italiana **15**: 111–143.

Fritsch, A. 1893. Studien im Gebiete der böhmischen Kreideformation, Palaeontologische Untersuchungen der einzelnen Schichten. V. Die Priesener Schichten. *Archiv für naturwissenschaftliche Landesdurchforschung von Böhmen* **9**: 1–135.

Giers, R. 1964. Die Grossfauna der Mukronatenkreide (unteres Obercampan) im östlichen Münsterland. *Fortschritte in der Geologie von Rhineland und Westfalen* **7**: 213–294.

Gill, J. R., and W. A. Cobban. 1961. Stratigraphy of lower and middle parts of the Pierre Shale, northern Great Plains. *U.S. Geological Survey Professional Paper* **424D**: D185–D191.

Grossouvre, A. de. 1908. Description des ammonitides du Crétacé supérieur du Limbourg belge et hollandais et du Hainaut. *Mémoires du Musée royal d'histoire naturelle de Belgique* **4**: 1–39.

Hébert, E. 1856. Tableau des fossiles de craie de Meudon et description de quelques espèces nouvelles. *Mémoires de la Société Géologique de France* **5**(2): 345–374.

Henderson, R. A., W. J. Kennedy, and W. A. Cobban. 2002. Perspectives of ammonite paleobiology from shell abnormalities in the genus *Baculites. Lethaia* **35**: 215–230.

Hewitt, R. A., G. E. G. Westermann, and A. Checa. 1993. Growth rates of ammonites estimated from aptychi. *Geobios Mémoire Spécial* **15**: 203–208.

Hyatt, A. 1903. Pseudoceratites of the Cretaceous. *Monograph. U.S. Geological Survey* **44**: 1–351.

Jäger, M. and R. Fraaye. 1997. The diet of the Early Toarcian ammonite *Harpoceras falciferum. Palaeontology* **40**(2): 557–574.

Kanie, Y. l982. Cretaceous tetragonitid ammonite jaws: a comparison with modern *Nautilus* jaws. *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series **125**: 239–258.

Kasugai, T. 2001. Feeding behavior of the Japanese pygmy cuttlefish *Idiosepius paradoxus* (Cephalopoda: Idiosepiidae) in captivity: evidence for external digestion? *Journal of the Marine Biological Association of the United Kingdom* **81**: 979–981.

Kennedy, W. J. 1986. The ammonite fauna of the type Maastrichtian with a revision of *Ammonites colligatus* Binkhorst, 1861. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* (*Sciences de la Terre*) **56**: 151–267.

Kennedy, W. J. 1993. Campanian and Maastrichtian ammonites from the Mons Basin and adjacent areas, Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* (*Sciences de la Terre*) **63**: 99–131.

Kennedy, W. J., and W. A. Christensen. l997. Santonian to Maastrictian ammonites from Scania, southern Sweden. *Fossils and Strata* **44**: 75–128.

Kennedy, W. J., W. A. Cobban, and N. H. Landman. 1997. Campanian ammonites from the Tombigbee Sand Member of the Eutaw Formation, the Mooreville Formation, and the basal part of the Demopolis Formation in Mississippi and Alabama. *American Museum Novitates* **3201**: 1–44.

Kennedy, W. J., W. A. Cobban, and H. C. Klinger. 2002. Muscle attachment and mantle-related features in Upper Cretaceous *Baculites* from the United States Western Interior. *In* H. Summesburger, K. Histon, and A. Daurer (editors.), *Cephalopods-Present and Past. Abhandlungen der Geologischen Bundesanstalt* **57**: 89–112.

Klinger, H. C., and W. J. Kennedy. 2001. Stratigraphic and geographic distribution, phylogenetic trends and general comments on the ammonite family Baculitidae Gill, 1871 (with an annotated list of species referred to the family). *Annals of the South African Museum* **107**(1): 1–290.

Kulicki, C., L. A. Doguzhaeva, and G. K. Kabanov. 1988. *Nautilus*-like jaw elements of a juvenile ammonite. *In* J. Wiedmann, and J. Kullmann (editors), *Cephalopods – Present and Past*, pp. 679–686. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

Lamarck, J. P. B. A. de M. de. 1801. *Système des Animaux sans vertebrès*. Deterville, Paris: The Author.

Landman, N. H., and A. Grebneff. 2006. Jaws of Triassic ammonoids from New Zealand. *New Zealand Journal of Geology and Geophysics* 49: 121–129.

Landman, N. H., and S. M. Klofak. 2004. Radulae and red herrings. *Sixth International Symposium, Cephalopods – Present and Past, Abstracts Volume*, p. 99.

Landman, N. H., and I. Kruta. 2006. Injuries on the jaws of modern *Nautilus* as clues to the function of ammonite aptychi. *A Symposium on the Paleontology, Geology, and Stratigraphy of the*

Late Cretaceous Western Interior Seaway. A Tribute to the Life of Willian Aubrey "Bill" Cobban, 26 & 27 August 2006, *Abstracts Volume*, p. 31.

Landman, N. H., C. J. Tsujita, W. A. Cobban, N. L. Larson, K. Tanabe, and R. L. Flemming. 2006. Jaws of Late Cretaceous placenticeratid ammonites: how preservation affects the interpretation of morphology. *American Museum Novitates* 3500: 1–48.

Landman, N. H., and K. M. Waage. 1993. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota and Wyoming. Bulletin of the American Museum of Natural History **215**: 1–257.

Lehmann, U. 1981. *The Ammonites: Their life and Their World*. Cambridge: Cambridge University Press.

Lehmann, U., and C. Kulicki. 1990. Double function of aptychi (Ammonoidea) as jaw elements and opercula. *Lethaia* **23**: 325–331.

Lundgren, B. 1874. Om en Comaster och en Aptychus frän Köpinge. *Öfversigt af Kongl. Vetenskaps- Akademiens Förhandlingar* **3**: 61–73.

Matsumoto, T., and I. Obata. 1963. A monograph of the Baculitidae from Japan. *Memoirs of the Faculty of Science, Kyushu University* (series D, Geology) **13**(1): 1–116.

Meek, F. B., and F. V. Hayden. 1865. Paleontology of the Upper Missouri: a report upon collections made principally by the expeditions under command of Lieut. G. K. Warren, US. Top. Engrs., in 1855 and 1856, Invertebrates. Part I. *Smithsonian Contributions to Knowledge* **14**(Art. 5): 1–136.

Meek, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country. *U.S. Geological Survey of the Territ*ories (Hayden) **9**: 1–629.

Miller, H. W. 1968. Invertebrate fauna and environment of deposition of the Niobrara Formation (Cretaceous) of Kansas. *Fort Hays Studies* series no. 8: 1–90.

Moberg, J. C. 1885. Cephalopoderna i Sveriges Kritsystem. II. Artbeskrifning. *Sveriges geologiska undersökning. Afhandlingar och uppsatser* (series C) **73**: 1–63.

Moore, R. C., and P. C. Sylvester-Bradley. 1957. Taxonomy and nomenclature of aptychi. *In* R. C. Moore (editor), *Treatise on Invertebrate Paleontology, Part L, Mollusca 4*: L464–L471. New York: Geological Society of America; Lawrence, KS: University of Kansas Press.

Morton, N. 1975. The position of the aptychus in some Jurassic ammonites. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **1975**(7): 409–411.

Morton, N., and M. Nixon. 1987. Size and function of ammonite aptychi in comparison with buccal masses of modern cephalopods. *Lethaia* **20**: 231–238.

Nixon, M. 1996. Morphology of the jaws and radula in ammonoids. *In* N. H. Landman, K. Tanabe, and R. A. Davis (editors), *Ammonoid Paleobiology*, pp. 23–42. New York: Plenum Press.

Nowak, J. 1908. Untersuchungen über die Cephalopoden der oberen Kreide in Polen, I. Teil, Genus *Baculites* Lamarck. *Bulletin international de l'Académie des Sciences de Cracovie (Classe des Sciences mathématiques et naturelles)* **1908**(4): 326–353.

Owen, D. D. 1852. Description of new and imperfectly known genera and species of organic remains, collected during the geological surveys of Wisconsin, Iowa, and Minnesota, by D. D. Owen. *Report of a Geological Survey of Wisconsin, Iowa, and Minnesota*, 638p.

Picard, L. 1929. On Upper Cretaceous (chiefly Maestrichtian) Ammonoidea from Palestine. *Annals and Magazine of Natural History* **3**(10): 433–456.

Ravn, J. P. J. 1902–1903. Molluskerne i Danmarks Kridtaflejringer. *Kongelige Danske Videnskabernes Selkskabs Skrifter* (raekke 6) **11**, 2, Scaphopoder, Gastropoder g Cephalopoder, 209(5)–269(65), pl. 1–5 (1902); 3, Stratigrafisker undersøgelser, 339(5)–443(99), 1 pl. (1903).

Riccardi, A. C. 1983. Scaphitids from the upper Campanian-lower Maastrichtian Bearpaw Formation of the Western Interior of Canada. *Bulletin Geological Survey of Canada* **354**: 1–103.

Robinson, C. S., W. J. Mapel, and M. H. Bergendahl. 1964. Stratigraphy and structure of the northern and western flanks of the Black Hills Uplift, Wyoming, Montana, and South Dakota. *U.S. Geological Survey Professional Paper* **404**: 1–134.

Robinson, H. R. 1945. New baculites from the Cretaceous Bearpaw Formation of southwestern Saskatchewan. *Transactions of the Royal Society of Canada*, 3rd series **39**(4): 51–54.

Sanders, D. 2003. Syndepositional dissolution of calcium carbonate in neritic carbonate environments: Geological recognition, processes, potential significance. *Journal of African Earth Sciences and the Middle East* **36**: 99–134.

Say, T. 1821. Art. IV. Observations on some species of zoophytes, shells, & tc., principally fossil. *American Journal of Science and Arts* **2**: 34–45.

Schindewolf, O. H. 1958. Über Aptychen (Ammonoidea). *Palaeontographica Abteilung A* **111**: 1–46.

Schlüter, C., 1871–1876, Cephalopoden der oberen deutschen Kreide. *Palaeontographica* **21**: 1–24, pl. 1–8 (1871); **21**: 25–120, pl. 9–35 (1872); **24**: 1–144, pl. 36–55 (1876).

Seilacher, A. 1993. Ammonite aptychi: how to transform a jaw into an operculum. *American Journal of Science* **293A**: 20–32.

Sharpe, D. 1853–1857. Description of the fossil remains of Mollusca found in the Chalk of England. 1. Cephalopoda. *Palaeontographical Society Monographs* 1–26(1853); 27–36(1855); 37–68(1857).

Solem, A., and C. F. E. Roper. 1975. Structures of Recent Cephalopod radulae. *The Veliger* **18**(2): 127–133.

Stewart, J. D. 1990. Niobrara Formation vertebrate stratigraphy. *In* S. C. Bennett (editor), *Niobrara Chalk Excursion Guidebook*, pp. 19–39. Lawrence, KS: University of Kansas Museum of Natural History and Kansas Geological Survey.

Tanabe, K. l983. The jaw apparatuses of Cretaceous desmoceratid ammonites. *Palaeontology* **26**(3): 677–686.

Tanabe, K., and Y. Fukuda. 1987. The jaw apparatus of the Cretaceous ammonite *Reesidites. Lethaia* **20**: 41–48.

Tanabe, K., and N. H. Landman. 2002. Morphological diversity of the jaws of Cretaceous Ammonoidea. *In*: H. Summesberger, K. Histon, and A. Daurer (editors), *Cephalopods – Present and Past, Abhandlungen der Geologischen Bundesanstalt* **57**: 157–165.

Trauth, F. 1927–l936. Aptychenstudien I–VIII. *Annalen des Naturhistorischen Museums in Wien* **41**: 171–259 (l927); **42**: 121–193 (l928); **44**: 329–411 (l930); **45**: 17–136 (l931); **47**: 127–145 (1936).

Trauth, F. 1938. Die Lamellaptychi des Oberjura und der Unterkreide. *Palaeontographica Abteilung A* **88**: 115–229.

Westermann, G. E. G. l996. Ammonoid life and habitat. *In* N. H. Landman, K. Tanabe, and R. A. Davis (editors), *Ammonoid Paleobiology*, pp. 607–707. New York: Plenum Press.

Wright, C. W., and W. J. Kennedy. 1984. The Ammonoidea of the Lower Chalk. I. *Palaeontographical Society Monographs (London)* **137**: 1–126.

Young, K. 1963. Upper Cretaceous ammonites from the Gulf Coast of the United States. *University of Texas Publications* **6304**: ix + 367pp.