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Muscle Attachment and Mantle-Related Features in Upper Cretaceous *Baculites* from the United States Western Interior

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Cretaceous
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Anatomy

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Muskelbefestigung und Mantelstrukturen bei oberkretazischen Baculites aus den westlichen USA

Zusammenfassung

Außergewöhnlich gut erhaltene Exemplare von *Baculites* aus dem Santonium bis Maastrichtium des Western Interior der U.S.A. zeigen eine Reihe von Strukturen, die mit der Anheftung von Muskulatur und Mantel an der Schaleninnenseite in Zusammenhang stehen. Ältere Beobachtungen werden unter neuem Aspekt betrachtet. Folgende Strukturen werden beschrieben und abgebildet: eine zweigelappte Ansatzstelle des Dorsalmuskels, die am subadulten Phragmokon und in der adulten Wohnkammer erhalten bleiben kann, dorsale Grate sowohl im Phragmokon wie in der Wohnkammer; eine einzelne Ansatzstelle des ventralen Muskels, eine ringförmige Gratstruktur in der adulten Wohnkammer, die auf das letzte Septum folgt. Eine postseptale Gratstruktur (bei Steinkernen eine Rille) in der Wohnkammer und den Kammern des Phragmokons, die die Stelle einer postseptalen prismatischen Zone anzeigt, ein Siphonalband, das auf den Phragmokon beschränkt ist und eine komplexe Mikrostrukur aufweist, Verankerungsmarken und schlecht abgegrenzte Pseudosepten, ebenfalls auf den Phragmokon beschränkt, schillernde Linien, die die Stellen sekundärer Mantelansatzstellen vermuten lassen, am deutlichsten ringsum die adulte Apertur, Runzelstrukturen an der Innenseite der adulten Wohnkammer und ein mikroskopisches netzartiges Gratsystem unbekannter Herkunft und Funktion in der adulten Wohnkammer.

Bissverletzungen mit darauffolgender Schalenreparatur konnte beobachtet werden, in manchen Fällen waren schwere Schalen- mit Mantelverletzungen und Regeneration zu beobachten. Bei anderen Beispielen scheint der Mantel unverletzt geblieben zu sein. Dies deutet darauf hin, dass das angegriffene Tier seinen Weichkörper weit in die Wohnkammer zurückziehen konnte.

Abstract

Exceptionally well-preserved specimens of *Baculites* from the Santonian–Maastrichtian of the U.S. Western Interior show a range of structures associated with muscle and mantle attachment to the shell interior. Previous observations are reviewed, and the following structures are described and illustrated: a bilobed dorsal muscle scar, that may be preserved on the subadult phragmocone and in the adult body chamber; dorsal ridges in both phragmocone and body chamber; a single ventral muscle scar; an annular ridge in the adult body chamber that succeeds the final septum; a post-septal ridge (groove on moulds) in body chamber and camerae recording the site of a post-septal prismatic zone; a siphonal band that is restricted to the phragmocone, and has a complex micro-morphology; drag marks and ill-defined pseudosepta, again confined to the phragmocone; iridescent lines that may reflect sites of secondary mantle attachment, most conspicuous around the adult aperture; wrinkle structure on the interior of the adult body chamber, and a microscopic reticulate ridge system in the adult body chamber that is of unknown origin and function.

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Predation damage and subsequent shell repair are noted; in some cases massive shell damage was associated with mantle damage and regeneration. In other examples the mantle appears to have escaped damage, suggesting the animal may have been able to withdraw the tissues deep into the body chamber when under attack.

Introduction

The genus *Baculites* LAMARCK, 1799, has the simplest ammonoid morphology: a tiny coiled ammonitella is succeeded by a straight or only slightly curved shaft. As such, interpretation of tissue attachment and muscle function in the body chamber, which is essentially a straight tube with compressed oval or ovoid section is greatly simplified when compared with planispirally coiled or heteromorphic ammonites. In the present communication we outline some of the macroscopic features that appear to be related to muscle and mantle attachment in Upper Cretaceous (Santonian–Maastrichtian) *Baculites* from the United States Western Interior Seaway. In this region, notably in the mudrock facies of the Pierre Shale, early diagenetic concretions are commonly packed with *Baculites* in enormous numbers. Pristine aragonite preservation is common, and partially exfoliated specimens and internal moulds show features interpreted as muscle scars and mantle related structures in a small percentage of individuals. These individuals occur with others in the same concretion, in identical preservation, but without such structures, as though the record of these structures depended on atypical or unusual secretory processes. Muscle scars in particular are often conspicuous (or indeed present) in the adult body chamber only (Pl. 2, Figs. 6–11; Pl. 3; Pl. 4, Figs. 1–6), or in the last few camerae of adults (Pl. 2, Figs. 1–5): possibly the slowing of growth and longer interval of tissue attachment led to more substantial deposition of, or modification to, the associated inner shell layers than in more transient sites during the subadult phase, although subadult muscle scars also occur in the phragmocone (Pl. 5, Fig. 9).

As an indication of the low incidence of some at least of these features, we counted a total of 300 specimens of *Baculites* sp. from the Campanian Pierre Shale at USGS Mesozoic locality D2140 in Butte County, South Dakota. Of the structures described below, only two showed drag marks, two conspicuous dorsal muscle scars, and only one conspicuous dorsal and ventral muscle scars. In contrast, transverse lines were relatively common.

The general consensus on muscle scar and mantle attachment structures in ammonites was summarized by DOGUZHAEVA & MUTVEI (1996) as follows:

"The following terms are used to describe attachment scars in ammonoids:

1. *Paired dorsal scars. These scars are situated immediately in front of the last suture on dorsal or dorsolateral sides of the body chamber (= 'paarige Muskelansatz-Strukturen' [JORDAN, 1968]; 'Abdruck des Lateralmuskels' [SARIKADZE et al., 1990]). Most writers have interpreted these scars as attachment sites of the retractor muscles.*
2. *Unpaired mid-dorsal scar. This scar is situated in the internal (= dorsal, according to the Russian terminology) lobe of the suture (BANDEL, 1982; LANDMAN & BANDEL, 1985; WEITSCHAT, 1986; SARIKADZE et al., 1990; WEITSCHAT & BANDEL, 1991). As demonstrated by WEITSCHAT & BANDEL (1991), this scar is paired in the first chamber but becomes unpaired in subsequent chambers. It was probably the attachment site of the palliovisceral ligament.*
3. *Unpaired ventral scar. This scar is situated in front of the ventral lobe of the suture (VOGEL, 1959; JONES, 1961; DOGUZHAEVA & MUTVEI, 1991; 'Sipho-Struktur', 'dunkles Sipho-Band' [JORDAN, 1968]; 'Abdruck des Ventralmuskels' [SARIKADZE et al., 1990]). Its probable function was to support the circumsiphonal invagination in the posterior portion of the body.*
4. *Paired lateral scars. These scars are in the shape of an adorally directed lobe on each side of the body chamber (DOGUZHAEVA & KABANOV, 1988; DOGUZHAEVA & MUTVEI, 1991). This lobe extends from the last suture to about the midpoint of the body chamber.*
5. *Lateral sinus. A sinus with an adoral opening is situated on the side of the body chamber (= 'indentation', 'Einbuchtung' [JORDAN, 1968]; 'Abdruck des vorderen Lateralmuskels' [SARIKADZE et al., 1990]). It extends from the posterior portion of the body chamber to the shell aperture.*
6. *Annular elevation. This elevation forms a narrow zone in front of the last suture in some ammonoid genera ('Haftband-Struktur', 'Annulus-Struktur')".*

Other mantle-related structures are:

- Drag bands (VOGEL, 1959; JORDAN, 1968; SCHINDEWOLF, 1965; HEWITT et al., 1991; CHECA & GARCIA-RUIZ, 1996; TANABE et al., 1998), interpreted as impressions made by the rear part of the mantle during adapical movement.
- Pseudosutures (see references above), which are similarly interpreted.
- Transverse lines (LANDMAN et al., 1999) that may reflect narrow bands of mantle attachment, as may the longitudinal band of LANDMAN et al.

The following abbreviations are used to indicate the repositories of specimens mentioned in the text:

BHI-BHMNH: Black Hills Museum of Natural History, Hill City, South Dakota.
BMNH: The Natural History Museum, London.
USNM: U.S. National Museum of Natural History, Washington D.C.

2. Previous Studies on *Baculites* Muscle and Mantle Attachment Features

CRICK (1898) described what he believed to be tissue attachment features in *Baculites* in his classic paper on ammonoid muscle attachment. He described and illustrated three specimens, reillustrated here in Pl. 1.

BMNH C5415 is the original of CRICK (1898, Pl. 17, Figs. 1–3). The original figures are reproduced here as Pl. 1, Figs. 1–3; photographs of the specimen are shown in Pl. 1, Figs. 4–7. The specimen was identified by CRICK as *Baculites ovatus* SAY; the horizon and locality given are "Upper Cretaceous, Fox Hills Group, Horsehead Creek, South Dakota, USA". CRICK figured a fragment of the internal mould of part of the penultimate camera, the final camera, and the adapical part of the body chamber of an individual with approximated sutures. There are a further four unfigured camerae 63.8 mm long, and most of the

body chamber. A total of 4 fragments comprise over 200 mm of a single individual. The figured fragment is 40 mm long, has a whorl breadth of 24.8 mm, and a whorl height of 37.5 mm. In all, the last four septa are approximated. CRICK described this specimen (1898, p. 77), and recognized traces of two successive positions of the dorsal muscle scar, the adapertural margin marked by adorally convex bilobed impressions at the adapical end of the body chamber, clearly indicated in his figure (Pl. 17, Figs. 1, 2; see Pl. 1, Figs. 1, 2). He also recognised adaperturally convex impressions that defined the adapertural margin of two successive single ventral muscle scars. On re-examination, the specimen (Pl. 1, Figs. 4–7) shows, when viewed dorsally with the phragmocone down, a trace of a line defining the right half of the bilobed dorsal muscle scar, particularly conspicuous in flank view (Pl. 1, Figs. 5, 7), where it extends adapically to intersect the line of the final septum. This corresponds to a part of the adapical of the two scars described by CRICK. Traces (if any) of the left half of the structure shown by CRICK, and the second, adapertural line are equivocal. Equally equivocal are the two traces of the unpaired ventral muscle described and illustrated by CRICK (compare Pl. 1, Figs. 3 and 6).

The second specimen from South Dakota described by CRICK is BMNH C73566 (formerly C5415b). The original figure is reproduced here as Pl. 1, Fig. 9; photographs of the specimen are shown in Pl. 1, Figs. 8, 10, 11. CRICK (1898, p. 78) stated that this specimen

" ... displays the muscular impression less distinctly, but clearly shows the anterior boundary of a portion of the annulus."

This leaves the muscular impression at the

" ... angle mentioned in the previous description, and, passing upward over the adjoining saddle at a distance of about 1.5 mm from the suture-line, crosses the next lobe in a shallow depression, and again rises over the next saddle at about the same distance from it as before. This depression, however, is seen only with difficulty by turning the specimen about in a fairly good light. There can, I think, be no doubt that the annulus was in the form of a simply-waved band, being elevated at the saddles and very feebly depressed in each lobe."

As with the previous specimen, the last two septa are approximated, showing the specimen to be an adult. There are no unequivocal traces of a depression marking muscle scars or CRICK's annulus (compare Pl. 1, Fig. 9 and Pl. 1, Figs. 8, 10, 11). The shell surface is smooth at the adapical end of the body chamber mottled in greys and blacks, with grey lines that suggest a curved line or lines that are within the sediment fill, and not a surface feature.

CRICK (1898, p. 78, Pl. 17, Fig. 5) described muscle scars in a further baculite, *Eubaculites vagina* (FORBES, 1846), from the Upper Maastrichtian of Pondicherry, South India. His original figure is reproduced here as Pl. 1, Fig. 13; his description (1898, 78–9) is as follows:

"It is merely the internal cast of the greater portion of the body-chamber, about 60 mm long, anteriorly incomplete, but fairly perfect posteriorly. Its transverse section is oval, the diameters of its anterior end being 24 and 14.5 mm; those of the posterior end being 19 and 12.5 mm. The antisiphonal surface is broad and slightly flattened, the siphonal being narrow, flattened, and with subangular borders. On the broad antisiphonal surface the feebly convex boundaries of the two muscular scars (indicated by a feebly-incised line on the internal cast) meet nearly in the middle line in an obtuse backwardly-directed point which is 3.25 mm in advance of the saddle on either side of the antisiphonal lobe, these two saddles occupying a large portion of the antisiphonal area. From this point each boundary passes forward and outward for a short distance, then turns backward and sweeps over on to the lateral area in a broad anteriorly-convex curve which gradually disappears before reaching the last septum; if continued to the septum it would meet the large lateral lobe on its antisiphonal side. It would seem therefore that, just as in the Baculites already described, the muscular scar on either side occupied the space between the central line of the antisiphonal area and the antisiphonal side of the large lateral saddle. There is no trace of the annulus in this example."

Photographs of the specimen are shown in Pl. 1, Figs. 12, 14; the structures described by CRICK are unclear to say the least.

Less equivocal muscle scars in *Baculites* were illustrated by KENNEDY & COBBAN (1976, Pl. 2, Figs. 1a, b); their specimen shows a well-developed bilobed dorsal muscle scar, the outline defined by a ridge of shell material.

HENDERSON (1984) described additional features in Cenomanian *Sciponoceras* HYATT, 1894, from northern Australia, most notably a post-septal prismatic zone, that appears as a narrow post-septal groove or gutter on internal moulds.

3. Dorsal Structures

The most conspicuous dorsal structure is the so-called dorsal muscle scar, generally described as paired in the literature, but in *Baculites* a bilobed structure, most conspicuous at the adapical end of the adult body chamber (Pl. 2, Figs. 2, 3, 5, 7, 8, 10; Pl. 3, Figs. 4, 5; Pl. 4, Figs. 3, 4, 6; Pl. 5, Figs. 5, 8). In its simplest form, it is defined on internal moulds by a groove or gutter, sharply indented on the mid-dorsal line, with two adaperturally convex, generally symmetrical elements. These are well-displayed in BHI-BHMNH 4953 (Pl. 4, Figs. 3, 4, 6) an adult *Baculites grandis* HALL & MEEK, 1854. The groove, which corresponded to a ridge of shell material on the shell interior, extends across the whole of the dorsum (Pl. 4, Figs. 3, 4) and has a steep adapical and lower angle adapertural face. The adapical edge is crenulate, and ridges within the groove suggest some internal structure. The groove declines on the dorsolateral margin (Pl. 4, Figs. 5, 6), but a faint depression extends across the flanks in a sinuous trace, corresponding to the annular ridge on the shell interior, adaperturally convex over the saddles and concave over the lobes (Pl. 4, Fig. 5). Within the area of the muscle scar enclosed by this groove, the surface of the internal mould can be differentiated into two zones, visible both uncoated (Pl. 4, Fig. 3) and coated (Pl. 4, Fig. 4). The adapertural area has a rougher surface. The adapical area is smoother, and is bounded adapically by a narrow post-septal groove, corresponding, presumably, to the site of HENDERSON's (1984) post-septal prismatic zone.

A similar bilobed dorsal groove is shown by USNM 507269 (Pl. 5, Fig. 5) an internal mould of a body chamber of *Baculites codyensis* REESIDE, 1927a. Here the groove extends across the dorsum of the specimen, passes adapically on the dorsolateral margin, and merges with the line of the (damaged) final suture. This specimen shows a faint, second bilobed dorsal line, adapically of main groove, recording the margin of an earlier muscle scar.

Other specimens retain shell material (or replaced shell material) in the groove, when the muscle scar is conspicuously defined (Pl. 2, Figs. 3, 7, 8, 10; Pl. 3, 4), but near invisible when coated, as the shell material breaks off flush with the surface, presumably because it was later overgrown on the main shell layer lining the body chamber (Pl. 3, Fig. 1).

Exceptionally, internal moulds of phragmocones show traces of successive dorsal muscle scars. This is best shown by USNM 507279 (Pl. 5, Fig. 9), a pyritic internal mould of a specimen of *Baculites gregoryensis* COBBAN, 1951. Here, the dorsal bilobed muscle scar is visible only when the specimen is viewed under high angle illumination. The adapertural margin of the scar is marked by a sharp boundary between the highly reflective surface of the adapertural part of the chamber fill, and the dull, matt surface of the muscle scar. The difference in reflectivity presumably reflects the different surface textures of the original shell interior, the smooth nacreous zone outside the muscle scar, and the textured surface of the superimposed muscle attachment area. These differences are not resolvable at optical level in this specimen.

More remarkable still is USNM 507263 (Pl. 2, Figs. 1–5), a specimen of *Baculites haresi* REESIDE, 1927b. Here, the internal mould of the last five camerae and adapical part of the body chamber of an adult specimen (the last few septa are approximated) retains thin films of innermost shell layers in places. Traces of the bilobed adapertural ridges defining four successive muscle scars are visible, one overlain by the penultimate septum, one overlain by the final septum, and two at the adapical end of the body chamber. The final trace is bounded by a relatively wide ridge of shell material (Pl. 2, Fig. 5) that tapers on the dorsolateral margin, where it is initially convex, and follows a slightly sinuous course around the umbilical lobe. At high optical magnifications, the surface of the internal mould of the body chamber both within and outside the boundary ridge of the muscle scar show minute fingerprint-like ridges corresponding to wrinkle structure (see DOGUZHAEVA & MUTVEI [1986] for review of previous literature).

Dorsal ridges are a distinctive feature of internal moulds of many *Baculites* species; examples are shown in Pl. 3, Fig. 1; Pl. 5, Figs. 1, 2, 5, 7. These are delicate structures, conspicuous only when specimens are coated with ammonium chloride, and viewed/photographed under oblique light (compare Pl. 3, Figs. 1 and 4; Pl. 5, Figs. 6, 7). There is generally a conspicuous mid-dorsal ridge, that intersects the mid-point of the indentation in the adapertural groove/ridge of the bilobed dorsal muscle scar; it may show some internal structure defining a median element, so that the corresponding ridge on the shell interior will have been subdivided by a median groove (Pl. 5, Fig. 5). There are also prominent lateral grooves on the dorsum (Pl. 5, Figs. 1, 2, 5), and traces of much more delicate grooves between on some moulds (Pl. 5, Fig. 1). Taken together, these features of internal moulds indicate the development of three prominent dorsal ridges on the shell interior, the one mid-ventral, the other two flanking symmetrically, with delicate parallel ridges between. It is important to note that these ridges occur throughout the body chamber (Pl. 5, Figs. 2, 5, 7) and phragmocone (Pl. 5, Fig. 1). They interrupt ribbing in ornamented individuals (Pl. 5, Fig. 2), but do not interrupt the adapertural ridge defining the dorsal muscle scar, which appears to overlie, and thus post-date longitudinal ridge secretion (Pl. 5, Fig. 5).

More problematic structures of the dorsal region of the shell are iridescent lines and sheets that may be related to the transverse lines of LANDMAN et al. (1999). Some of these lines define more-or-less symmetrical zones on the surface of the body chamber in rare individuals, while others lack such symmetry. A strikingly symmetrical example that begs interpretation as a mantle-related feature is illustrated. USNM 508944 (Pl. 5, Fig. 8) is the body chamber of a smooth *Baculites* sp. The bilobed dorsal muscle scar is well-defined by traces of shell material, as is the mid-dorsal ridge. Some distance adapertural of the final septum, iridescent lines and sheets define a symmetrical pair of narrow, elongate U-shaped areas that appear to close adapically.

A final dorsal feature shown by some specimens are drag-marks (Pl. 7, Fig. 1), to be discussed further below.

4. Ventral Structures

The most conspicuous ventral feature is a single muscle scar, generally defined by an adapertural convex groove on internal moulds, or a ridge of shell material infilling that groove after the remainder of the shell material has been worn away or detached (Pl. 2, Figs. 1, 4, 6; Pl. 3, Fig. 6; Pl. 4, Figs. 1, 2; Pl. 5, Fig. 6).

The scar is strikingly defined in BHI-BHMNH 4153 (Pl. 4, Figs. 1, 2), where a deep gutter or groove defines the adapertural convex margin over the mid-ventral region. Traced laterally, the groove sweeps adapically and declines, merging into the annular band, marked by a much weaker groove adapertural of the final septum that undulates across the flanks and links to the dorsal bilobed muscle scar.

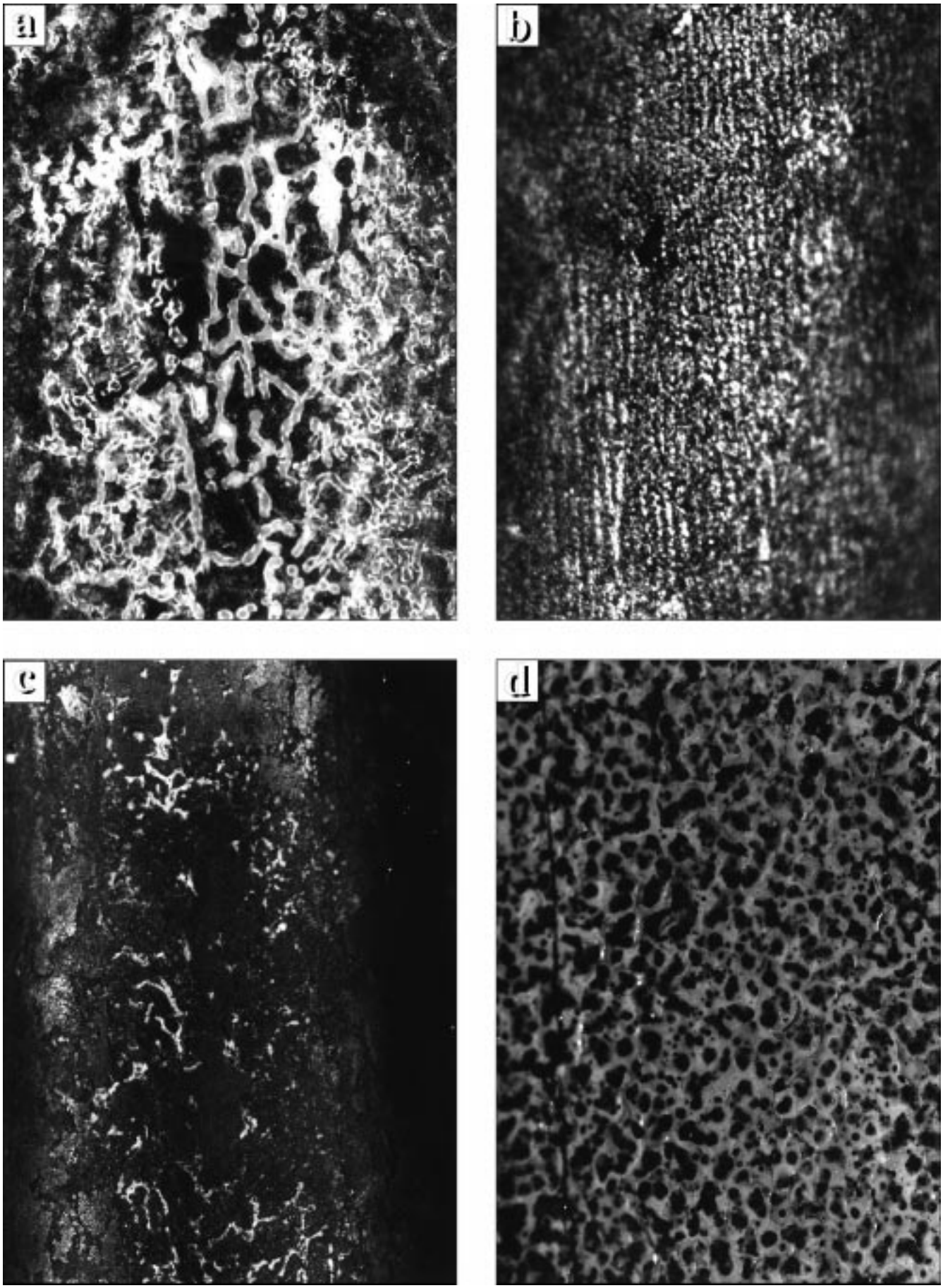
None of the *Baculites* studied to date shows serial repetition of the dorsal muscle scar in the subadult phragmocone, but USNM 507263 (Pl. 2, Figs. 1, 4) shows traces of four successive muscle scars, the adapical two overlain by the last two septa, the adapertural two within the adapical end of the adult body chamber, as with the dorsal muscle scars of the same specimen.

Text-Fig. 1 (opposite page). ►▷►

a) *Baculites haresi* REESIDE, 1927b.
USNM 507263, from the Gammon Shale Member of the Pierre Shale, Campanian, USGS Mesozoic locality D1587, sec. 3, T. 10 N., R. 4 E., Butte County, South Dakota. Detail of the ventral band on an internal mould of the fifth from last chamber of the specimen shown in Pl. 2, Figs. 1–5, showing the reticulate ridge system on the inner surface of the shell, projecting down into the sediment infill.
Magnification: ×23.

b) *Baculites* sp.
USNSM 508943, Pierre Shale, Campanian, USGS Mesozoic locality D2140, 12-2–21.3 m (40–70 ft) above the Groat Sandstone, 25.6 km (15.5 miles) north of Belle Fourche in the SW¼ SE¼ sec. 22, T. 11 N., R. 2 E., Butte County, South Dakota.
Detail of wrinkle structure on venter of specimen shown in Pl. 5, Figs. 6, 7.
Magnification: ×60.

c) *Baculites gregoryensis* COBBAN, 1957.
USNM 507279, from the Pierre Shale, Campanian, *B. gregoryensis* Zone near Fort Thompson, South Dakota. Detail of the ventral band of the specimen shown in Pl. 5, Fig. 9, Pl, 6, Fig. 5, showing the reticulate ridge system on the interior of the shell preserved in part as an external mould in pyrite, in part with original shell material preserved.
Magnification ×30.



d) BHI-BHMNH 4950, Pierre Shale, Campanian, near Scenic, Pennington County, South Dakota. Surface of polished internal mould of body chamber showing reticulate pattern of ridges on shell interior, projecting into sediment fill.
See also Pl. 6, Figs. 1–4. Magnification ×30.

A more commonly preserved feature of internal moulds of phragmocones that also occurs associated with ventral muscle scars in the body chamber of some individuals is the well-known linear trace, the siphonal band or siphuncular structure of authors.

USNM 507279 is a pyritic internal mould of the subadult phragmocone of a *Baculites gregoryensis* COBBAN, 1951. The venter (Pl. 6, Fig. 5) shows the siphuncular band largely in the form of an internal mould, but with traces of what is presumed to be aragonite shell material surviving (white in Pl. 6, Fig. 5). The band appears as a roughened area on the surface of the mould, approximately the same width as the median element of the ventral saddle. The "roughness" is due to pits and minute anastomosing grooves on the mould, that corresponded to bosses and anastomosing ridges of shell material on the interior of the shell (Text-Fig. 1c). In this specimen, the ridges give the impression of paralleling the elements of the ventral saddle, forming ill-defined, incomplete pseudosepta, as though they were deposited from tissue with the same folded morphology as the septal margin.

This anastomosing ridge system is perfectly preserved in USNM 507263 (Pl. 2, Figs. 1–5; Text-Fig. 1a), an internal mould of *Baculites haresi* REESIDE, 1927b. The highly polished surface of the mould corresponds to the inner surface of the nacreous layer, which has split off, leaving the ridge system perfectly preserved in the surrounding matrix. In places, the ridges appear continuous; elsewhere, they are seen to be chains of irregularly oval to subcircular, apparently hollow elements. A further example, associated with what appears to be a more continuous ribbon of adjacent, non-nacreous shell material, is shown by USNM 507265 (Pl. 7, Fig. 5) a specimen of *Baculites* sp.

5. Structures Associated with the General Surface of the Shell Interior

A striking feature of some internal moulds of phragmocones is the development of prominent drag marks (= drag bands of authors), interpreted as a record of the periodic forward translocation of the mantle between phases of septal secretion (Pl. 7, Figs. 1–4). These take the form of light and dark longitudinal parallel bands on the surface of internal moulds. When inspected in detail (Pl. 7, Fig. 4), these are seen to be less continuous or regular than superficial examination suggests. Furthermore, they are not associated with obvious ridges or grooves on the surface, rather, they reflect a variably porous surface to the internal mould (Pl. 7, Figs. 1, 2), or variation in the ratio of cement to matrix in the sediment infill of the mould (Pl. 7, Figs. 3, 4). This may possibly reflect the former presence of some long vanished coating of organic material.

The presence of wrinkle structure has been noted above. It seems to be only rarely preserved (or perhaps only rarely observed), and appears to extend over much of the interior of the adult body chamber of some individuals (Text-Fig. 1b).

Linear iridescent lines and bands that are interpreted as analogous to the transverse lines of LANDMAN et al. (1999), and similarly interpreted as being in part at least the sites of narrow bands of mantle attachment are conspicuous in *Baculites*.

Pl. 5, Fig. 3 shows these iridescent traces on the venter and ventrolateral area of USNM 508945, a specimen of *Baculites* sp. The lines define a series of narrow, adaperturally directed v-shaped chevrons on the venter, flanked by undulating linear traces. Pl. 5, Fig. 4 shows the flank of USNM 508946, a specimen of *Baculites eliasi* COBBAN, 1958, where this feature takes the form of parallel, adaperturally pointing chevrons.

The most remarkable example of these features is shown by BHI-BHMNH 4950, a specimen of *Baculites cuneatus* COBBAN, 1962. Here, the iridescent bands form a series of parallel, adaperturally directed chevrons on either side of the mid-dorsal line (Pl. 6, Figs. 1, 2). Traced onto the flank, these pass into a rounded, adapically closed lobe, the ventral side of which projects forwards into a broad convexity that runs into the adult aperture.

This specimen shows a further remarkable feature that extends over the whole of the surface of the body chamber (Pl. 6, Figs. 1, 3; Text-Fig. 1d): a reticulum of white lines on the mould that reflect the presence of an anastomosing network of ridges on the inner surface of the shell. The origin of these structures, and their significance is unknown.

6. Mantle Damage and Repair

Signs of mantle damage due to predation, and subsequent repair are frequent and often conspicuous in *Baculites* from the U.S. Western Interior. Such healed shell damage gives insights into the properties of the mantle.

Pl. 8, Figs. 1, 5, shows a partially exfoliated internal mould of a phragmocone of *Baculites gregoryensis* COBBAN, 1951 (BHI-BHMNH Collections), retaining extensive traces of the nacreous shell layers. The individual suffered extensive damage during life, probably as the result of unsuccessful predation by a pycnodont fish. The bite appears to have removed all of the end of the body chamber. The animal survived the damage and repaired the shell, but the distortion of the regrown shell into a large swollen portion suggests that the mantle tissues were badly damaged, the bulge recording the shape of the distorted, regenerated mantle tissue. In contrast, Pl. 8, Fig. 9 shows an internal mould, part phragmocone, part body chamber, with partially exfoliated shell preserved, of *Baculites reesidei* ELIAS, 1933 (BHI-BHMNH Collections). All of the end of the shell has been bitten off, again probably by a pycnodont fish, to a minimum length of 50 mm. The damage has been restored, with minimum distortion to shell shape: here, it would appear that the mantle was not severely damaged, if at all, having presumably been withdrawn at least 50 mm into the body chamber prior to attack.

A further distinctive form of predation damage in *Baculites* takes the form of deep, asymmetric v-shaped bites that occur on both flanks of the shell; typical examples are shown in Pl. 8, Figs. 2–4, 6–8. In both these examples, the deep embayment cut into the shell has been repaired with only minimum distortion, again suggesting that mantle tissue was not damaged. These observations also suggest that the animals may have been able to retract the mantle deep into the shell when under attack, and that massive shell damage does not always equate with damage to the mantle.

Recovery from parasitism/disease also indicates the regenerative power of affected mantle. A distinctive example of what is interpreted as parasitism/disease and full recovery is shown by a specimen of *Baculites eliasi* COBBAN, 1958, BHI-BHMNH 4362, shown in Pl. 8, Figs. 10–13. A partially exfoliated fragment from the adapical end of the body chamber bears a large, asymmetric blister-like swelling on the venter. A possible interpretation of this specimen is that the mantle at the aperture of the shell

was either parasitized or infected, producing a tumor-like growth, but not affecting normal secretory processes, as a result of which the shell was secreted around the growth, beyond which the mantle returned to its normal shape, and a simple tubular shell, without growth irregularities, was secreted. KEUPP (1984, Fig. 4; 1994, Fig. 2) illustrated and described a similar blister-like growth anomaly in a Jurassic (Kimmeridgian) *Orthosphinctes*.

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Plate 1

Figs. 1–9,10,11: ***Baculites* sp.**
Figs. 1–7: BMNH C5415.
Figs. 1–3: Copies of CRICK (1898, Pl. 17, Figs. 1–3 [as *Baculites ovatus* SAY]).
Figs. 4–7: The same views of the specimen.
Fig. 7: × 2.
Figs. 8–11: BMNH C73566 (formerly C5415b).
Figs. 8,10: Lateral views.
Fig. 9: Corresponding view in CRICK (1898, Pl. 17, Fig. 4).
Fig. 11: Ventral view.
Figs. 10,11: × 2.
"Upper Cretaceous, Fox Hills Group, Horsehead Creek, South Dakota, U.S.A".

Figs. 12–14: ***Eubaculites vagina* (FORBES, 1846).**
Figs. 12,14: Original specimen.
Figs. 13: Copy of CRICK (1898, Pl. 17, Fig. 5, BMNH C73570 [formerly 83624]).
Upper Maastrichtian, Valudavur Formation, Pondicherry, South India.

All specimens are internal moulds.
Figs. 1–6,8,9,12,13: × 1.
Figs. 7,10,11,14: × 2.
Figs. 4–8,10,11,12: The originals were photographed uncoated.

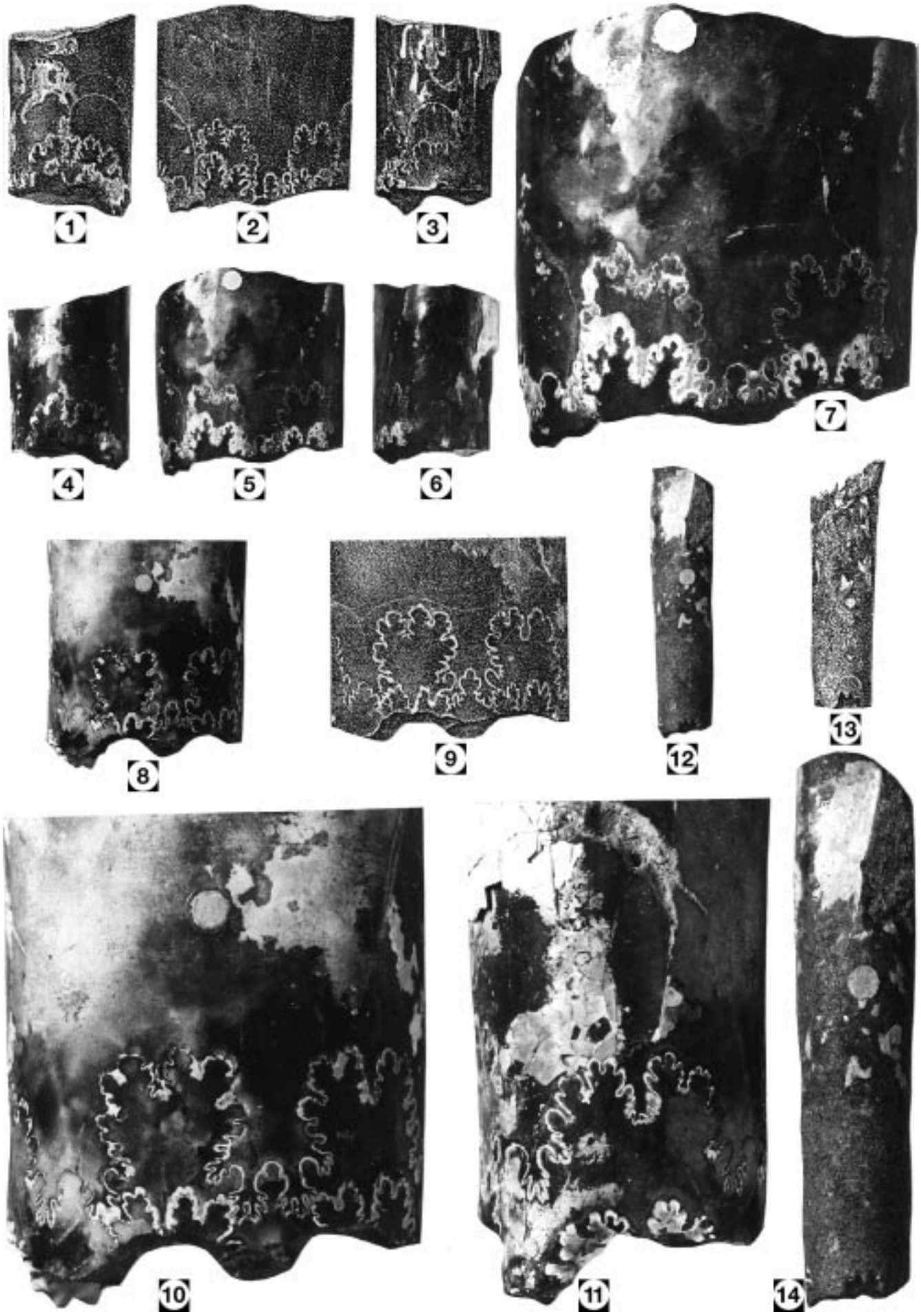

Plate 2

Figs. 1–5,8–11: ***Baculites haresi* REESIDE, 1927b.**
Figs. 1– 5: USNM 507263.
Figs. 1,4: Venter, showing traces of four successive ventral muscle scars.
Fig. 2: Flank, showing final dorsal muscle scar.
Figs. 3,5: Dorsum, showing four successive bilobed dorsal muscle scars; two are overlain by the penultimate and final septum; two are preserved within the adapical end of the adult body chamber.
Figs. 8–11: USNM 507260.
Figs. 8,10: Dorsum, showing well-defined bilobed dorsal muscle scar.
Figs. 9,11: Flanks, showing dorsal muscle scar.
From the Gammon Member of the Pierre Shale, Campanian, USGS Mesozoic locality D1587, sec. 3, T. 10 N., R. 4 E., Butte County, South Dakota.

Figs. 6,7: ***Baculites* sp.**
USNM 508947, Pierre Shale, Campanian, USGS Mesozoic locality 2141, 12.2–21.3 m (40–70 ft) above the Groat Sandstone, Belle Fourche – Albion road, in centre of E½ SW¼ sec. 17, T. 11 N., R. 2 E. Butte County, South Dakota.
Fig. 6: Venter, showing muscle scar.
Fig. 7: Dorsum, showing bilobed muscle scar.

All specimens are internal moulds.
All specimens were photographed without coating.
Figs. 1–3, 9–11: × 1.
Figs. 4–8: × 2.

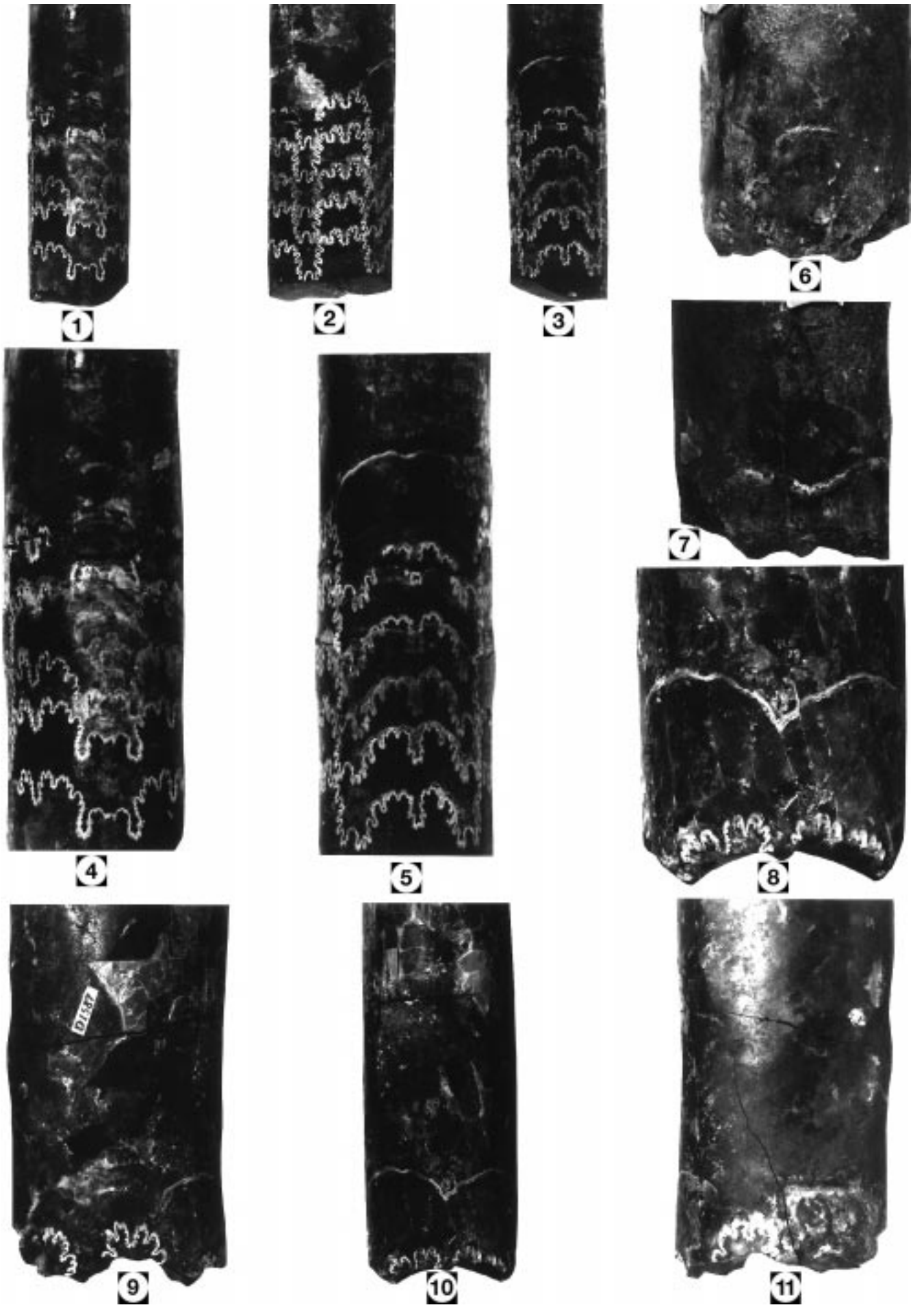

Plate 3

Figs. 1–6: ***Baculites codyensis* REESIDE, 1927a.**
U.S. Geological Survey Collections, Denver, from the Marias River Shale, Santonian, USGS Mesozoic locality 21425, east bank of Marias River, 18.15 km (11 miles) south-west of Shelby in W½ NE¼ SE¼ sec. 14, T. 31 N., R. 4 W., Toole County, Montana.
Fig. 1: Dorsum, with prominent longitudinal grooves, corresponding to ridges or the shell interior.
Fig. 4: Dorsum, with prominent bilobed muscle scar, barely visible in 1.
Figs. 2,5: Flank; traces of dorsal muscle scar and post-septal prismatic zone are clearly visible in 5.
Figs. 3,6: Venter; adapertural edge of ventral muscle scar is visible in both figures.

Figs. 1–3: Coated with ammonium chloride.
Figs. 4–6: Uncoated.
All figures: × 2.

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Plate 4

Figs. 1–6: ***Baculites grandis* HALL & MEEK, 1854.**
BHI-BHMNH 4953, Pierre Shale, Campanian, *B. grandis* Zone, Wright Ranch, Weston County, Wyoming.
Figs. 1,2: Venter with well-defined gutter marking edge of ventral muscle scar.
Figs. 3,4: Dorsum showing well-defined gutter marking edge of bilobed dorsal muscle scar. Note adapertural rough, and adapical smooth zones of scar surface, and indication of postseptal prismatic zone.
Fig. 5: Flank, showing gutter linking to delicate groove defining annular elevation on shell interior.
Fig. 6: Oblique view of dorsum. Note internal detail of gutter defining bilobed dorsal muscle scar; groove marking post-septal prismatic zone is conspicuous in 4 and 6.
Specimen is an internal mould.

Figs. 1, 2: Uncoated.
Figs. 2–6: Coated with ammonium chloride.
All figures: × 1.

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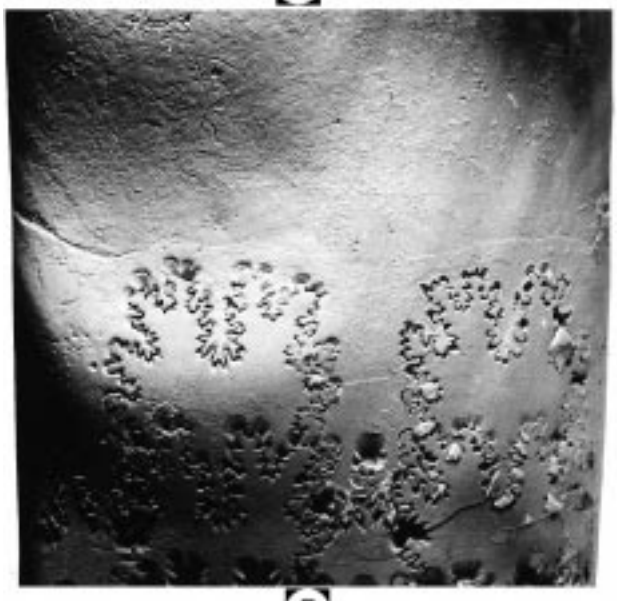

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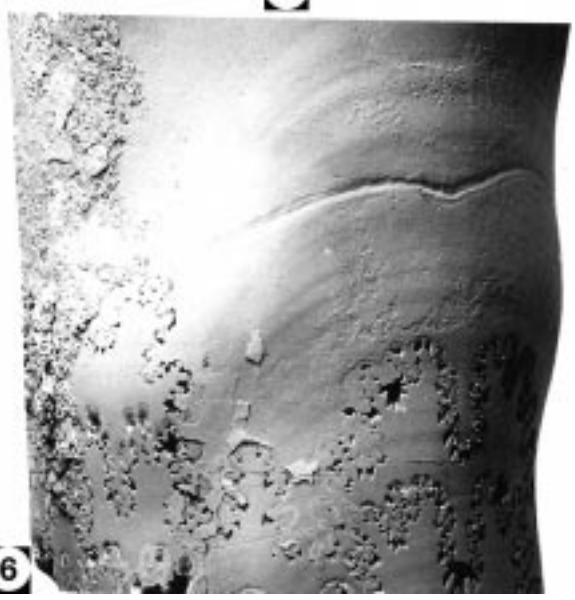

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Plate 5

Figs. 1,2,5: ***Baculites codyensis* REESIDE, 1927a.**

Fig. 1: USNM 507262, phragmocone, showing prominent dorsal grooves, one median, the others lateral, with traces of additional delicate grooves, all corresponding to ridges on the inner shell surface.

Fig. 2: USNM 507261, body chamber of ribbed variant with prominent median, and weaker lateral grooves on dorsum.

Fig. 5: USNM 507269, body chamber of smooth variant showing two grooves at adapical end defining successive positions of bilobed dorsal muscle scar, and three prominent longitudinal grooves, corresponding to ridges on the interior of the shell.

All specimens are from the Marias River Shale, Santonian, USGS Mesozoic locality 21425, east bank of Marias River, 18.15 km (11 miles) south-west of Shelby in W¼ NE¼ SE¼ sec. 14, T. 31 N., R. 4 W., Toole County, Montana.

Figs. 3,6–8: ***Baculites* sp.**

Fig. 3: USNM 508945, ventral view of a body chamber showing near-symmetrical iridescent bands that may reflect sites of mantle attachment.

Figs. 6,7: USNM 508943, ventral views of a body chamber.

Fig. 6: Shows muscle scar and symmetrical iridescent lines (possible sites of mantle attachment).

Fig. 7: Shows faint longitudinal mid-ventral groove, corresponding to ridge on inner surface of shell. This specimen has well-preserved wrinkle layer.

Both specimens are from the Pierre Shale, Campanian, at USGS Mesozoic locality D2140, 12.2–21.3 m (40–70 ft) above the Groat Sandstone, 25.6 km (15.5 miles) north of Belle Fourche in the SW¼ SE¼ sec. 22, T. 11. N., R. 2 E., Butte County, South Dakota.

Fig. 8: USNM 508944, from the Pierre Shale, Campanian, at USGS Mesozoic locality D2141, 12.2–21.3 m (40–70 ft) above the Groat Sandstone, Belle Fourche – Albion road in centre E½ SW¼ sec. 17, T. 11 N., R. 2 E., Butte County, South Dakota.

Dorsum, showing bilobed dorsal muscle scar, traces of mid-dorsal groove corresponding to ridge on inner shell surface, and symmetrical iridescent bands that may be sites of mantle attachment.

Fig. 4: ***Baculites eliasi* COBBAN, 1958.**

USNM 508946, Kara Bentonitic Member of the Pierre Shale, Lower Maastrichtian, SE¼, SE¼ sec. 6, T. 51 N., R. 67 W., Crook County, Wyoming.

Flank view, with well-defined iridescent bands, interpreted as possible sites of mantle attachment.

Fig. 9: ***Baculites gregoryensis* COBBAN, 1951.**

USNM 507279, from the Pierre Shale, Campanian, *B. gregoryensis* zone near Fort Thompson, South Dakota.

Dorsal view of specimen, which is a pyritic internal mould. Photographed under high angle illumination, the specimen shows the median incision in the bilobed muscle scars in five chambers; the surface of the muscle scar is dull, that of the remainder of the mould of each chamber is highly reflective.

All specimens are internal moulds; 4 retain much original shell material.
Figs. 1,2,5,7: Originals coated with ammonium chloride.
Figs. 3,4,6,8,9: Uncoated.
Figs. 1,2,5–9: × 2.
Figs. 3,4: × 1.

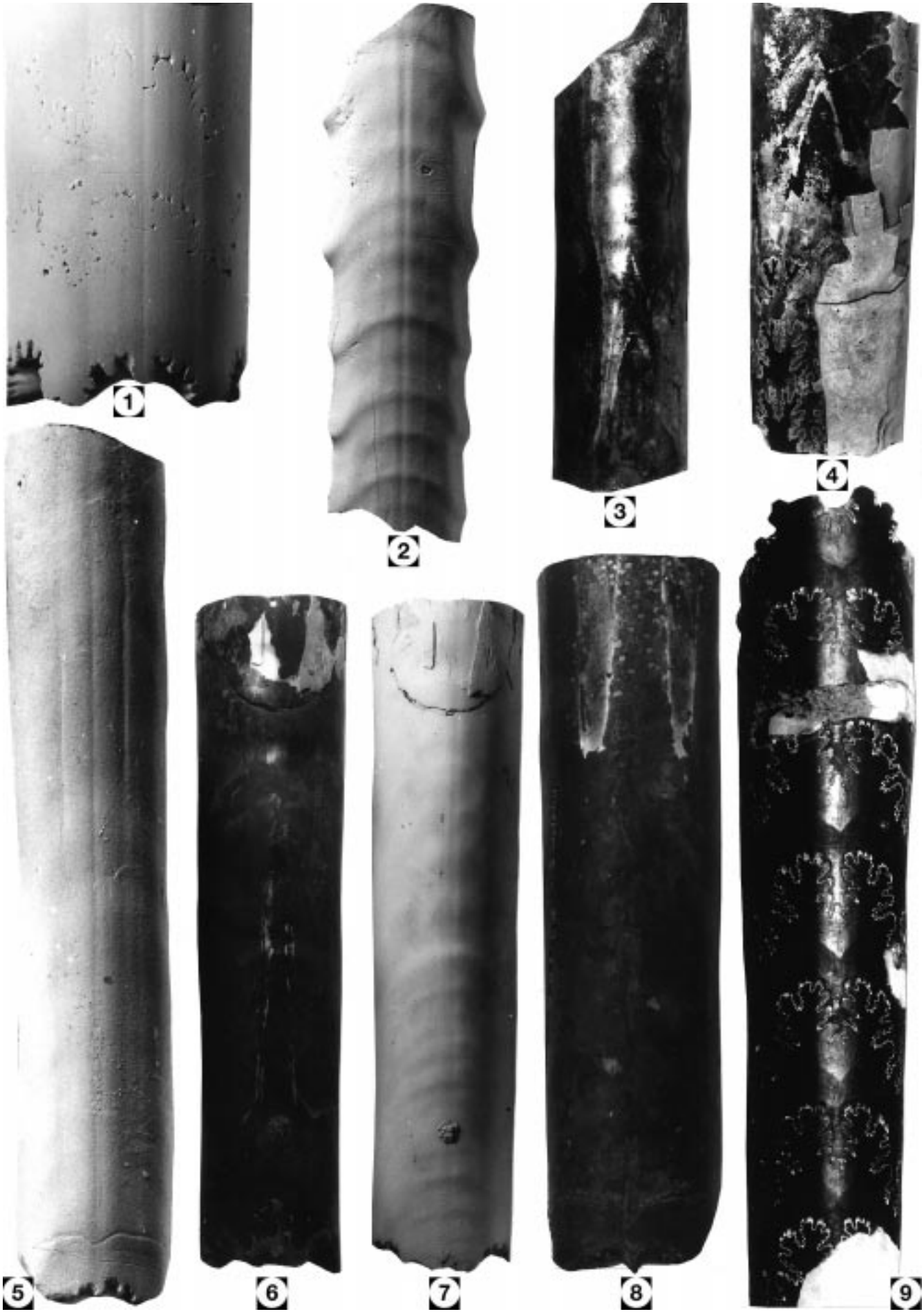

Plate 6

Figs. 1–4: ***Baculites cuneatus* COBBAN, 1962.**
BHI-BHMNH 4950, Pierre Shale, Campanian, near Scenic, Pennington County, South Dakota.
The specimen shows a complex pattern of symmetrical iridescent lines and bands towards the apertural end in Figs. 1,2,4, and traces of dorsal ridges in Figs. 1 and 2.
Fig. 3 shows the complex reticulum of ridges that covered much of the original inner surface of the body chamber (see also Text-Fig. 1d).

Fig. 5: ***Baculites gregoryensis* COBBAN, 1951.**
USNM 507279, from the Pierre Shale, Campanian, *B. gregoryensis* zone, near Fort Thompson, South Dakota.
Ventral view of a pyritic internal mould showing the complex reticulum of ridges of shell material on the inner surface of the shell that define the siphonal band. Note the local arrangement into what appear to be pseudosutures that reproduce, in part, the form of the external saddle (see also Text-Fig. 1c).

All figures are of uncoated specimens.
Figs. 1,4: × 1.
Fig. 2: × 2.
Fig. 3: × 2.2.
Fig. 5: × 3.

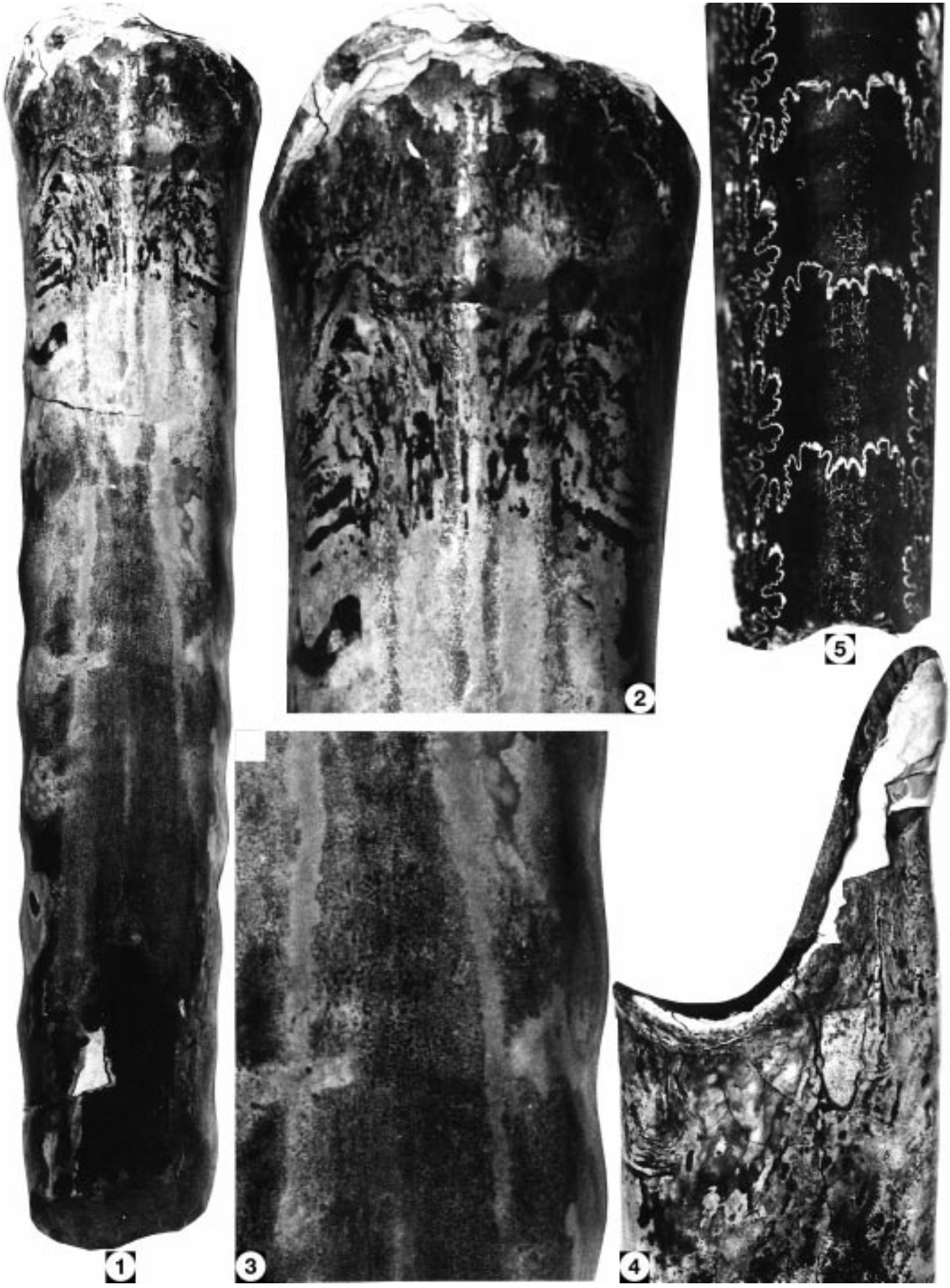

Plate 7

Figs. 1–5: ***Baculites* sp.**
Figs. 1,2: USNM 507264, showing prominent drag marks on the dorsum and dorsolateral margins.
Fig. 1: Dorsal view.
Fig. 2: Dorsolateral view.
Figs. 3,4: USNM 508948, showing general appearance, and drag marks on the flank.
Fig. 5: USNM 507265, ventral view, showing well-developed ventral band.
Note complex reticulum of shell material (white) projecting into the matrix, and longitudinal alignments.
All specimens are from the Pierre Shale, Campanian, at USGS Mesozoic locality D2140, 12.2–21.3 m (40–70 ft) above the Groat Sandstone, 25.6 km (15.5 miles) north of Belle Fourche in the SW¼ SE¼ sec. 22, T. 11 N., R. 2 E., Butte County, South Dakota.

All figures are of uncoated specimens.
Figs. 1–3: × 1.
Fig. 4: × 3.
Fig. 5: × 4.


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Plate 8

Figs. 1,5,6–8: ***Baculites gregoryensis* COBBAN, 1951.**

Figs. 1,5: BHI-BHNMH collections, the specimen is a partially exfoliated internal mould of phragmocone retaining extensive traces of the nacreous shell layers.
The individual suffered traumatic damage to the venter and one flank in life as a result of a bite, possibly by a pycnodont fish. The swollen portion records regeneration and shell repair by the severely damaged mantle tissues.

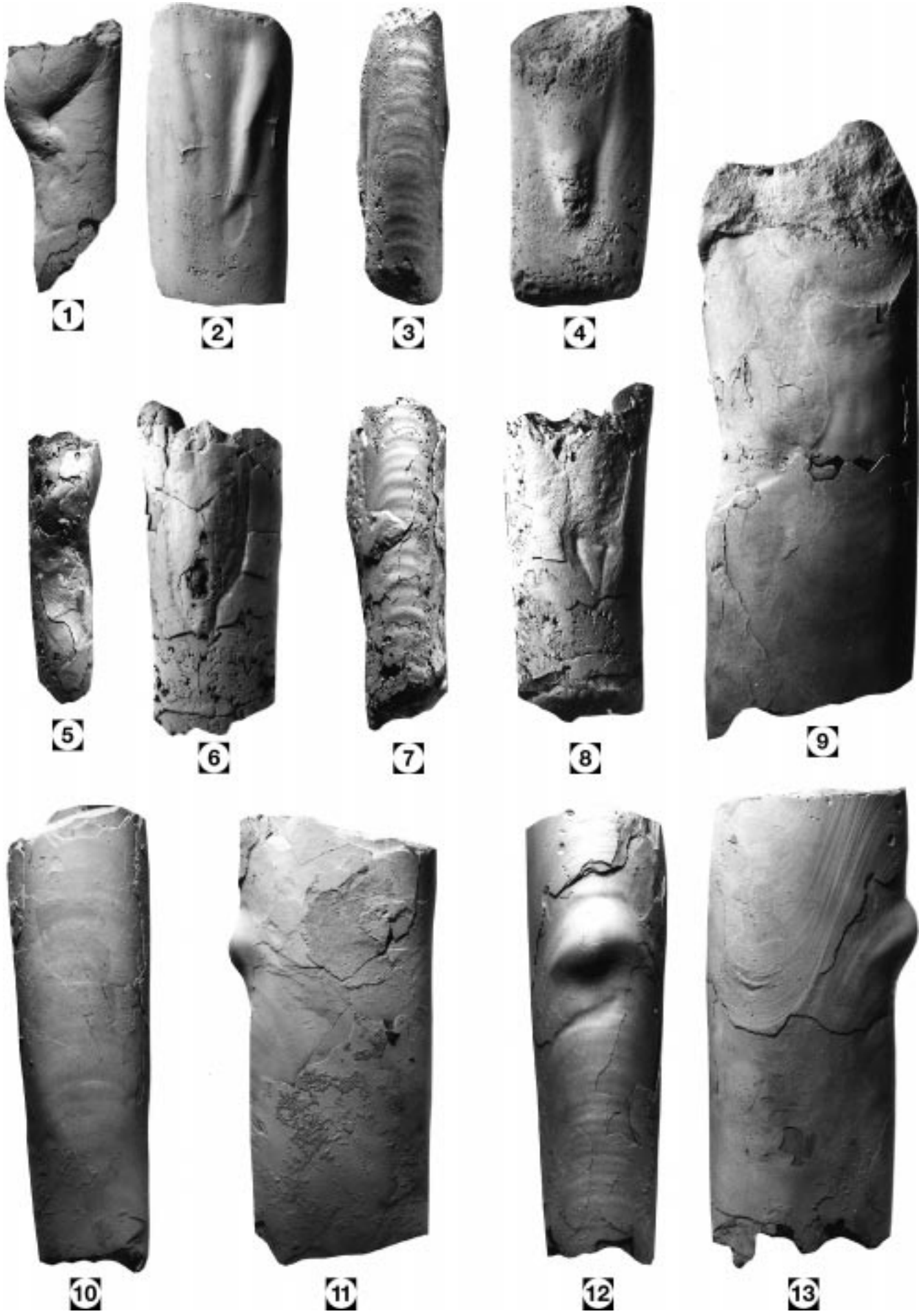
Figs. 6–8: BHI-BHMNH 4370, partially exfoliated internal mould of phragmocone showing asymmetric v-shaped bite mark and subsequent repair, possibly the result of coleoid cephalopod attack.
Both specimens are from the Campanian *B. gregoryensis* zone Pierre Shale of Lyman County, South Dakota.

Figs. 2–4: ***Baculites* sp.**
BHI-BHMNH 4358, Campanian *Baculites compressus* or *B. cuneatus* zone Pierre Shale, Campanian, Meade County, South Dakota.
Specimen is an internal mould of part of the body chamber and shows a healed and repaired v-shaped bite on both flanks, possibly the result of coleoid cephalopod attack.

Fig. 9: ***Baculites reesidei* ELIAS, 1933.**
BHI-BHMNH Collections, Campanian, *B. reesidei* zone Pierre Shale, Meade County, South Dakota.
Specimen is an internal mould, part body chamber, part phragmocone, with partially exfoliated aragonitic shell preserved. The individual suffered traumatic damage in life: all of the apertural end of the shell was bitten off to a minimum length of 50 mm, possibly as a result of attack by a pycnodont fish, and subsequently fully repaired.

Figs. 10–13: ***Baculites eliasi* COBBAN, 1958.**
BHI-BHMNH 4362, from the Maastrichtian *B. eliasi* zone Pierre Shale of Garfield County, Montana.
The specimen is a partially exfoliated internal mould of a body chamber retaining traces of the originally aragonitic shell. The blister-like protuberance on the venter is interpreted as the result of parasitism by some unknown organism, followed by full recovery and a return to normal shell secretion, corresponding to the "Volumensanomalie" of KEUPP (1984, 1994).

All figures of specimens coated with ammonium chloride.
All figures: × 1.



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