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Jaws of Late Cretaceous Placenticeratid Ammonites: How Preservation Affects the Interpretation of Morphology

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ABSTRACT

We describe upper and lower jaws of *Placenticeras* Meek, 1876, from the Upper Cretaceous (upper Campanian) Bearpaw Shale and Pierre Shale of the Western Interior of North America and lower jaws of the related ammonite *Metaplacenticeras* Spath, 1926, from the Campanian Yasukawa Formation of Hokkaido, Japan. One lower jaw is preserved inside the body chamber of *Placenticeras costatum* Hyatt, 1903. The other jaws are isolated but are generally associated with fragments of placenticeratid shells. The jaws from North America are attributed to *Placenticeras meeki* Böhm, 1898, and *P. costatum*, while those from Japan are attributed to *Metaplacenticeras subtilistriatum* (Jimbo, 1894). All of the jaws are presumed to be from adults.

The jaws of *Placenticeras* attain lengths of up to 95 mm. They are preserved as steinkerns with a thin film of black material, representing diagenetically altered chitin. X-ray diffraction analysis of samples of this material indicates that it consists of magnesium-rich calcite, pyrite, and amorphous material (organic compounds). The upper jaw is approximately the same length as the lower jaw and is U-shaped, with narrow wings that converge anteriorly to a dome-shaped hood. The lower jaw is composed of two lamellae. The outer lamella is broad and consists of two wings terminating in a bilobate posterior margin. The inner lamella is one-

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half the length of the outer lamella. The two lamellae are separated except in the apical region and along the sides. The junction between the lamellae appears as a U or V-shaped outline on the anterior portion on the ventral surface of the jaw. This junction is especially conspicuous in specimens in which part of the inner lamella has eroded away.

In crushed specimens, the lower jaw is subquadrate in shape. In specimens that retain some or all of their original curvature, the central portion is gently convex and the sides bend steeply dorsally. The rostrum projects slightly anteriorly and dorsally and there is a thickened rim of chitin along the anterior margin where the two lamellae are doubled over. A small indentation appears at the apical end and, in most specimens, develops into a midline slit that extends posteriorly 10–15 mm. However, as shown in well-preserved specimens and based on comparisons with the jaws of closely related ammonites, this slit represents the remnants of a narrow ridge on the ventral side of the inner lamella. This ridge is surrounded by an elongate boss of thickened chitin, which corresponds to a depression on the dorsal side. The ventral surface of the outer lamella bears a midline ridge with a central groove, which essentially forms a continuation of the ridge on the inner lamella. The ventral surface of the outer lamella is ornamented with thin, radial striations and irregular broad undulations paralleling the posterior margin. The posterior end is generally incomplete, probably as a result of predation or postmortem degradation, and the lateral margins are commonly creased, indicating postmortem plastic deformation.

The lower jaws of *Metaplacenticeras subtilistriatum* are much smaller than those of *Placenticeras* but are otherwise similar in morphology. However, they retain pieces of a very thin, fibrous outer layer comprising two plates. X-ray diffraction analysis of samples of this layer indicates that it consists of calcite enriched in magnesium. Each plate covers the ventral surface of one of the wings and terminates at the midline ridge. Based on the close affinity of *Metaplacenticeras* and *Placenticeras*, and in comparison with published descriptions of placenticeratid jaws from elsewhere, we hypothesize that similar plates covered the lower jaws of all placenticeratids, although these plates have not been found in any *Placenticeras* material from North America. The thin nature and fibrous microstructure of this layer would have made it susceptible to mechanical breakage and chemical dissolution. Furthermore, jaws are internal structures embedded in the buccal bulb. The micro-environment within this bulb may have promoted dissolution of the outer calcitic layer of the lower jaw.

The presence of a pair of calcitic plates (aptychi) and a midline ridge with a central groove on the outer lamella of the lower jaw are unique features of the lower jaws of the Aptychophora Engeser and Keupp, 2002. Although differences in preservation obscure this similarity, the lower jaws of placenticeratids conform to the description of aptychus-type jaws. However, unlike the thick calcitic aptychi of other Ammonitina, the thin calcitic aptychi of placenticeratids probably did not function as opercula and would have served simply to strengthen the lower jaw. The jaws of placenticeratids were probably designed for biting and cutting food rather than for passively collecting and straining plankton. Other data about the habitat and mode of life of placenticeratids are consistent with this interpretation. These ammonites probably inhabited surface waters and were capable of pursuing and attacking sluggish prey. An ecological analog of placenticeratids may be the modern ocean sunfish *Mola mola* (Linnaeus, 1758), which inhabits surface waters and feeds on gelatinous zooplankton.

INTRODUCTION

Jaws of Late Cretaceous placenticeratid ammonites have been reported from Slovenia (Summesberger et al., 1996, 1999) and India (Gangopadhyay and Bardhan, 1998). However, no placenticeratid jaws have been reported from the North American Western Interior. This is somewhat surprising given the abundance of large, well-preserved specimens of placenticeratids in this region. At some localities, placenticeratids are the most common ammonites. One might expect that the jaws of these ammonites, the shells of which sometimes attain diameters of approximately 1 m, would have been sufficiently robust to be preserved.

We describe several jaws of *Placenticeras* Meek, 1876, from the Upper Cretaceous (Campanian) Bearpaw Shale of Alberta (commonly referred to as the Bearpaw Formation by most Canadian workers) and the Pierre Shale of Colorado and South Dakota (fig. 1). One specimen occurs inside the body

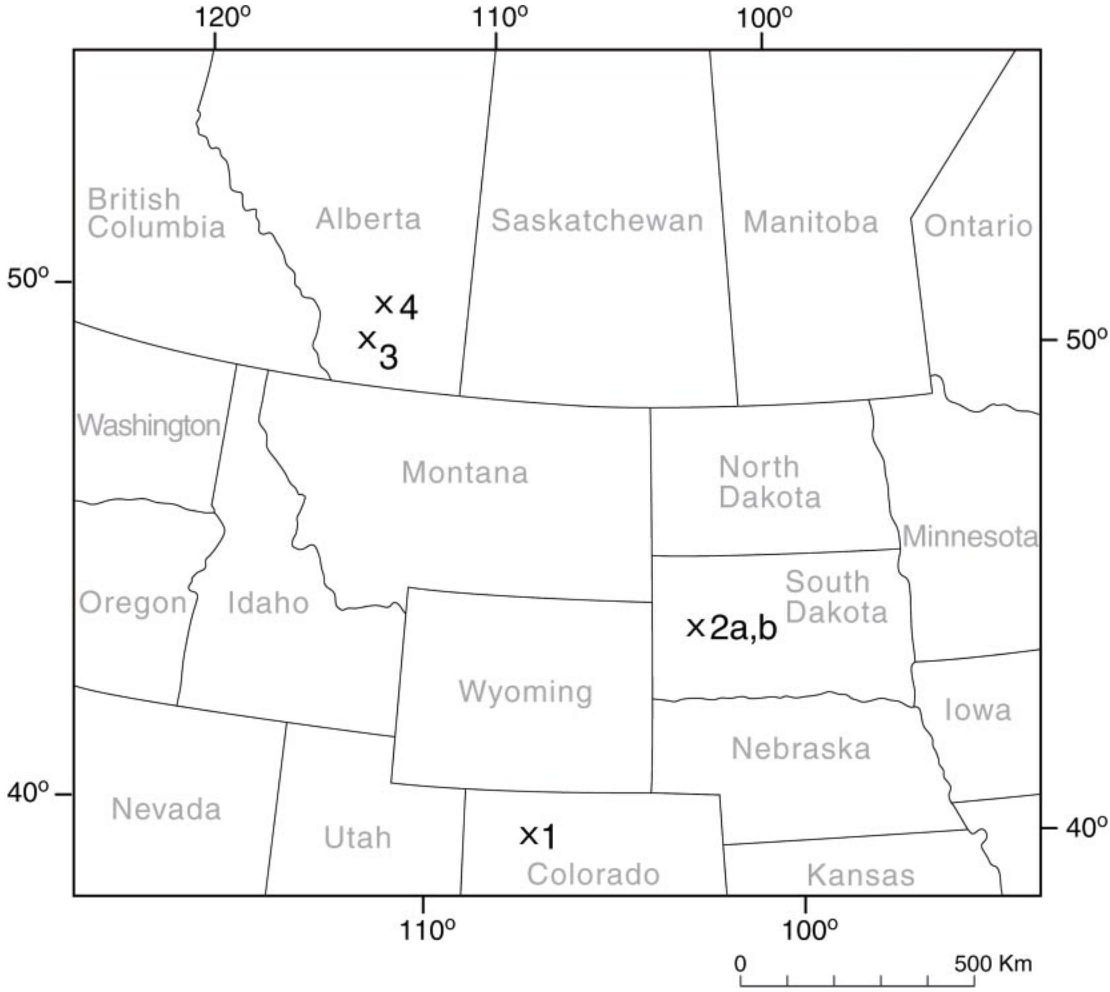


Fig. 1. Map of parts of the United States and Canada showing the localities of the jaws described in the text.

chamber of *Placenticeras costatum* Hyatt, 1903. The other specimens are isolated but are generally associated with shards of placenticeratid shell. They belong to either *Placenticeras meeki* Böhm, 1898, or *P. costatum* because these are the only two species of *Placenticeras* that occur in these strata. We also describe lower jaws of the closely related ammonite *Metaplacenticeras* Spath, 1926, from the Campanian Yasukawa Formation of Hokkaido, Japan. These jaws occur as isolated elements but are closely associated with specimens of *Metaplacenticeras subtilistriatum* (Jimbo, 1894), to which they are attributed. All of the jaws are presumed to be from adults.

In describing, comparing, and interpreting ammonite jaws, much depends on the state of preservation of the specimens. Sometimes a calcitic layer is preserved; sometimes just the impression of it; or sometimes none of it at all. However, the absence of a calcitic layer does not necessarily imply that it did not exist originally. In some specimens, the entire chitinous part of the jaw, now altered, is preserved. In other specimens, part of the chitinous layer has broken off. It is important to examine as many specimens as possible, because each specimen offers different information depending on its unique state of preservation, and all of this information contributes to an overall picture. Analysis of a single specimen, if poorly preserved, can lead to erroneous conclusions.

MATERIAL

The lower jaw of *Placenticeras costatum* from the Pierre Shale of Colorado is preserved inside the body chamber. The rest of the North American material consists of isolated jaws generally associated with fragments of placenticeratid shells in calcite- or siderite-cemented concretions. It is possible that some of these jaws occur inside the body chamber, but this is impossible to demonstrate.

The Pierre Shale of South Dakota also yields jaws of scaphites, baculites, and coleoids in addition to those of *Placenticeras*. However, the lower jaws of these other cephalopods differ from those of *Placenticeras* in either size, shape, or ornament. The lower jaws of scaphites are usually smaller (15–40 mm long in adults) and nearly triangular in shape (Meek, 1876; Landman and Waage, 1993). The outer lamella bears a prominent flange with a central groove and a pair of thick aptychi ornamented with lirae paralleling the posterior margin. The lower jaws of baculites vary in size, but are usually less than 40 mm long in adults (Klinger and Kennedy, 2001; Larson et al., in press). They are elongate in shape with a pair of thick aptychi ornamented with prominent rugae. The lower jaws of coleoids are sharply folded without a median ridge, and the apical end is strongly projected forward. In contrast, the lower jaws of *Placenticeras*, as reported in this paper, are massive, up to 95 mm in length, and subquadrate in shape. The outer lamella is characterized by a midline ridge with a central groove and a pair of very thin aptychi.

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; the Royal Tyrrell Museum of Palaeontology (TMP), Drumheller, Alberta, Canada; the University Museum of the University of Tokyo (UMUT), Tokyo; the U.S. National Museum (USNM), Washington, DC; and the University of Western Ontario (UWO), London, Ontario, Canada.

LIST OF LOCALITIES

Numbers refer to figure 1.

1. U.S. Geological Survey loc. D1353. Upper Campanian, *Baculites cuneatus* Zone, Pierre Shale, NW ¼ SW ¼ sec. 17, T. 3N, R. 80W, Grand County, Colorado, USA.

2a. Upper Campanian, *Baculites compressus* Zone, Pierre Shale, sec. 6, T. 3 N, R. 14E, Elk Creek, Meade County, South Dakota, USA.

2b. Upper Campanian, *Baculites cuneatus* Zone, Pierre Shale, approximately 11 km northwest of loc. 2a, Cheyenne River Drainage, Meade County, South Dakota, USA.

3. Upper Campanian, *Baculites cuneatus* Zone, Bearpaw Shale, Korite Mine, adjacent to St. Mary River, Welling, Alberta, Canada.

4. Upper Campanian, *Baculites reesidei* Zone, Bearpaw Shale, immediately below the lowest sandy transitional beds of the Horseshoe Canyon Formation, Travers Dam, Alberta, Canada.

5. Upper Campanian, Yasukawa Formation, Rubeshube Creek, Enbetsu Town, north Hokkaido, Japan.

CONVENTIONS

The terminology used to describe ammonite jaws is modified from Kanie (1982), Tanabe (1983), Clarke, (1986), and Tanabe and Fukuda (1987) and illustrated in figure 2. Upper and lower jaws are described with respect to the anterior, posterior, ventral, and dorsal directions. (The ventral and dorsal surfaces of the lower jaw are equivalent to the outer and inner surfaces, respectively; conversely, the ventral and dorsal surfaces of the upper jaw are equivalent to the inner and outer surfaces, respectively.) The left and right sides of the jaw refer to the jaw as it was oriented in life. However, because all of the lower jaws are preserved with the ventral side up, contrary to their position in life, the left and right sides of the jaws are opposite to what we observe. The terms ‘‘inner and outer lamellae’’ (Tanabe and Fukuda, l987) are used instead of ‘‘inner and outer plates’’ (Dagys et al., l989) to conform with the ter-

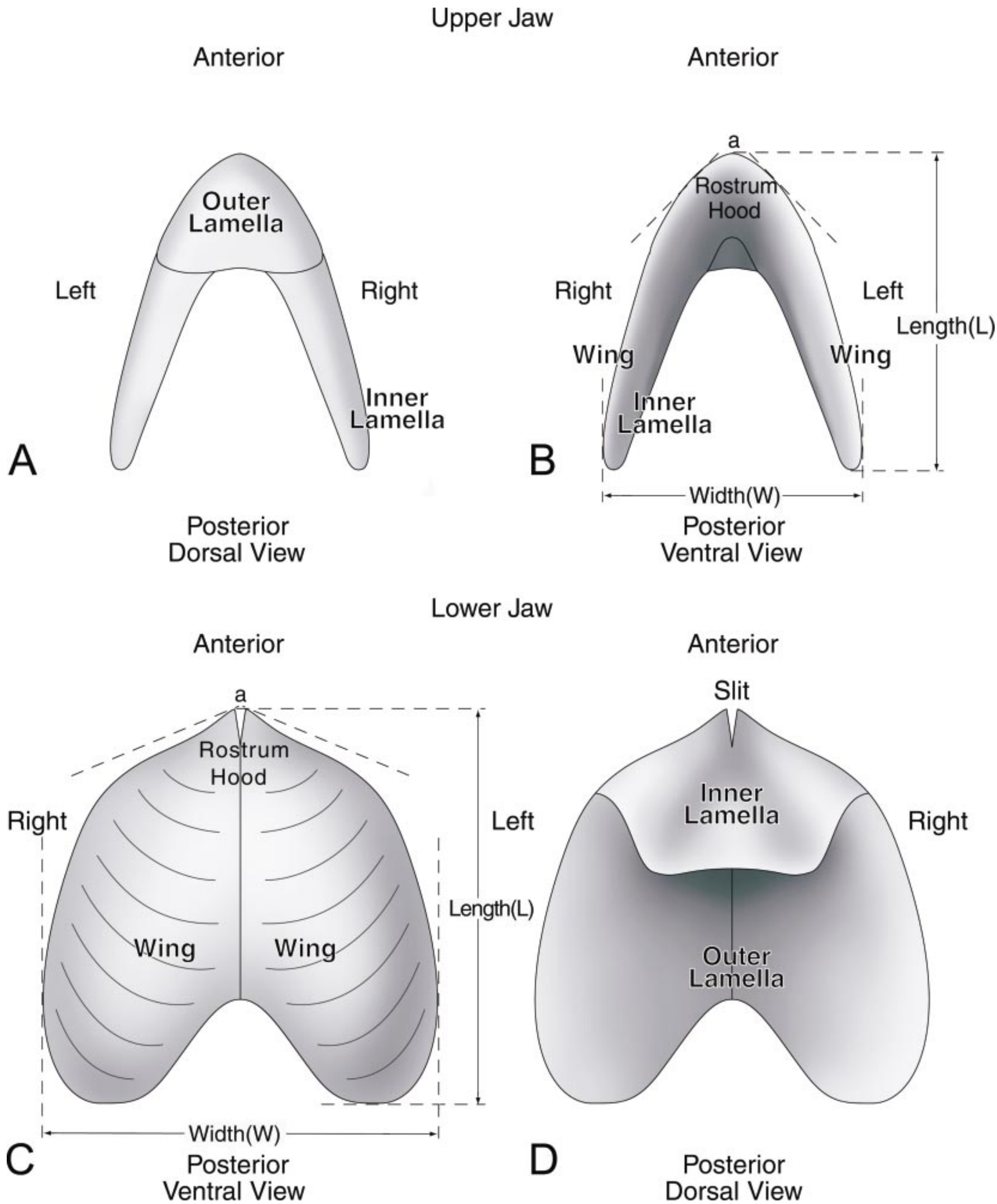


Fig. 2. Diagram of upper and lower jaws illustrating terminology and measurements. **A.** Dorsal view of upper jaw. **B.** Ventral view of upper jaw. **C.** Ventral view of lower jaw. **D.** Dorsal view of lower jaw. Abbreviation: a = apical angle.

minology of modern cephalopod jaws. The two symmetric halves of the lower jaw are referred to as wings, but this does not imply that they are separate structures. The apical tip of the jaw is called the rostrum. The hood of the jaw is the median portion just posterior of the rostrum.

The terms ''anaptychus'' and ''aptychus'' are commonly used to describe ammonite jaws (Lehmann, 1981; Engeser and Keupp, 2002), but often in different ways. For example, the term ''aptychus'' sometimes refers to the entire lower jaw; other times, it only refers to the calcareous plates covering the ventral surface of the lower jaw. In the interests of consistency, we define an anaptychus-type jaw as a lower jaw in which the outer lamella lacks a median fold, with or without a calcareous deposit. An aptychus-type jaw is defined as a lower jaw in which the outer lamella bears a median fold, as well as a calcareous layer in the form of two plates—the aptychi.

In measuring jaws, it is important to remember that most of our specimens are incomplete. The length (L) and width (W) of the jaws were measured following Kanie (1982) and Tanabe and Fukuda (l987). The measurement of width depends on whether the jaw is flattened (ironed out) or retains its original shape. The ratio of width to length of a single wing is a more reliable estimate of shape than the ratio of width to length of the entire jaw because both wings are seldom preserved intact. The measurement of the apical angle (also called the rostral angle) is also dependent on the state of preservation of the jaw.

Specimens are photographed with and without coating (magnesium oxide). The photographs are accompanied by camera lucida drawings highlighting certain features. We also illustrate hypothetical cross sections through various parts of the jaws, based on observations of whole specimens.

METHODOLOGY

To determine the mineralogical composition of the jaws, we analyzed samples from six specimens (one sample each from UMUT MM28896, UMUT MM28897, UWO.KMC. 100126, and BHMNH 5454b, two samples from AMNH 47275, and three samples from BHMNH 5456). At the AMNH, we used a Rigaku DMAX/RAPID Micro X-ray diffraction system employing a 100 μm monocapillary collimator and monochromatized Cu-Kα radiation to produce diffractions on an image plate. Samples were oscillated about a vertical axis (ω) and rotated around a ϕ-axis inclined at 45° (fixed) from ω to obtain sufficient diffractions on the cylindrial image plate. Images were integrated into diffractograms of two-theta (2θ) versus intensity. They were interpreted with Jade 7.0 (MDI) software, with phase identification based on the ICDD PDF-2 diffraction database and/or synthetic diffraction patterns derived from the Mineralogical Society of America (MSA) Crystal Structure Database (http: www.minsocam.org/MSA/Crystal_Database.html).

At the University of Western Ontario, the mineralogical composition of the jaws was determined using a Bruker D8 Discover diffractometer. The diffractometer was operated with Cu-Kα radiation generated at 40 kV and 40 mA. A Gobel mirror parallel optics system was employed to remove Kβ radiation and minimize the effect of sample displacement. A beam collimator snout was used to reduce the Kα beam diameter to 500 μm. Grains were mounted on double sided tape on an XYZ stage, which was moved via remote control to analyze selected points. An optical microscope/video camera and laser system permitted precise positioning of each sample. The θ-θ geometry of the diffractometer allowed the sample to remain stationary (flat), while the source and the detector moved independently. The angle between the sample and the source was θ_1 while the angle between the sample and the detector was θ_2, where $\theta_1 + \theta_2 = 2\theta$.

The majority of samples were analyzed in Coupled Scan Mode, where $\theta_1 = \theta_2$ and $\theta_1 + \theta_2 = 2\theta$. This is a stationary mode, where the sample, the beam, and the detector remain stationary. This is useful for polycrystalline samples (or nearly so). The sample from BHMNH 5456 was analyzed in Omega Scan Mode, where the sample remains stationary but the X-ray optics (source = θ_1; detector = θ_2) are rotated through an omega angle of 30°. At the start of the omega scan, the source and detector were positioned at 6° and 30° θ, respectively. Both the source and detector were rotated clockwise, by an omega angle of 30°, stopping at 36° and 3° θ, respectively. At all points during rotation, 2θ remained constant at $\theta_1 + \theta_2 = 36°$. The second frame was collected with $\theta_{1(start)} = 27°$ and $\theta_{2(start)} = 45°$, rotated through 23° to $\theta_{1(stop)} = 50°$ and $\theta_{2(stop)} = 22°$, yielding a constant $2\theta = 72°$. Omega scans were performed for time intervals of 30 minutes per frame (at 500 μm beam diameter).

Diffracted X-rays were detected using a General Area Diffraction Detection System (GADDS) 2D detector positioned at a distance of ~15 cm from the sample and intersecting a 35° segment of diffraction space, centered at 28.5° 2θ. Powder lines and/or diffraction spots resulting from each lattice plane produced an arc of radius $2\theta_{hkl}$. The GADDS software integrated the intensity along each arc, and corrected for the effect of flat screen detection (unwarping) to create a one-dimensional plot of intensity versus 2θ, similar to a conventional powder diffraction pattern. The resulting diffraction pattern was imported into the evaluation software EVA, where phases were identified, after baseline subtraction, using the ICDD database.

DESCRIPTION OF JAWS

Placenticeras meeki/Placenticeras costatum

Lower Jaw

Bearpaw Shale, Alberta

AMNH 47275 is preserved as a flattened steinkern with a film of black material (figs. 3, 4). It is embedded in a chunk of maroon-colored concretion of calcite- and siderite-cemented silty mudstone. No placenticeratid shell material is preserved in the concretion.

The jaw is subquadrate in overall view, measuring approximately 95 mm in length and 65 mm in width (W/L = 0.68). The left side of the anterior margin is missing, and the jaw is compressed due to sediment compaction. However, the jaw is weakly convex in cross section, its lateral edges turning obliquely dorsally for a few millimeters.

The anterior margin is narrowly rounded, forming an apical angle of approximately 105°, increasing to a broader angle of 145° on the lateral margins. There is a narrow slit on the midline approximately 1.5 mm wide at the apex. This slit extends posteriorly 9 mm, narrowing down completely, although the point of the slit is covered. The edges of the slit are sharply defined. At the posterior end of the slit, the wings appear to be joined together, forming a ridge. The slit is bordered on each side by narrow radial ridges, the outer margins of which form radial depressions. These flexures are covered in places by patches of coarsely crystalline black material, eliminating most of the relief. The black material consists of finely fractured square and rectangular pieces, resembling a honeycomb, with tiny clear to yellowish crystals embedded in the fractures. The black material in this region represents the thickened portion of the inner lamella.

An elongate patch of golden, finely crystalline material approximately 8 mm long covers the midline starting at the end of the slit. (This material also occurs in patches on adjacent parts of the jaw where it overlies the black material.) This elongate patch is surrounded by coarsely crystalline black material that ends in a lobate outline, representing the border of the outer lamella. The rest of the jaw is partly covered by a thin film of fine-grained black material. There is a low median ridge between the wings but no gap. Starting at the midpoint of the jaw, the two wings are torn apart and become progressively more widely separated. The margins are ragged, probably resulting from postmortem degradation coupled with sediment compaction.

Where the black material is missing exposing the steinkern on the anterior end of the jaw, fine, nearly straight lirae are spaced at intervals of approximately 0.75 mm. The lirae are oriented perpendicular to the midline and slant backward at a slight angle to the anterior margin. The posterior end of the jaw on the right side is covered by thin, irregular ridges that are concave toward the posterior margin. There are also irregular longitudinal creases along the left lateral edge. The surface of the jaw shows bumps and wrinkles suggesting postmortem plastic deformation.

AMNH 47276 is preserved in a fragment of a concretion composed of siderite-ce-

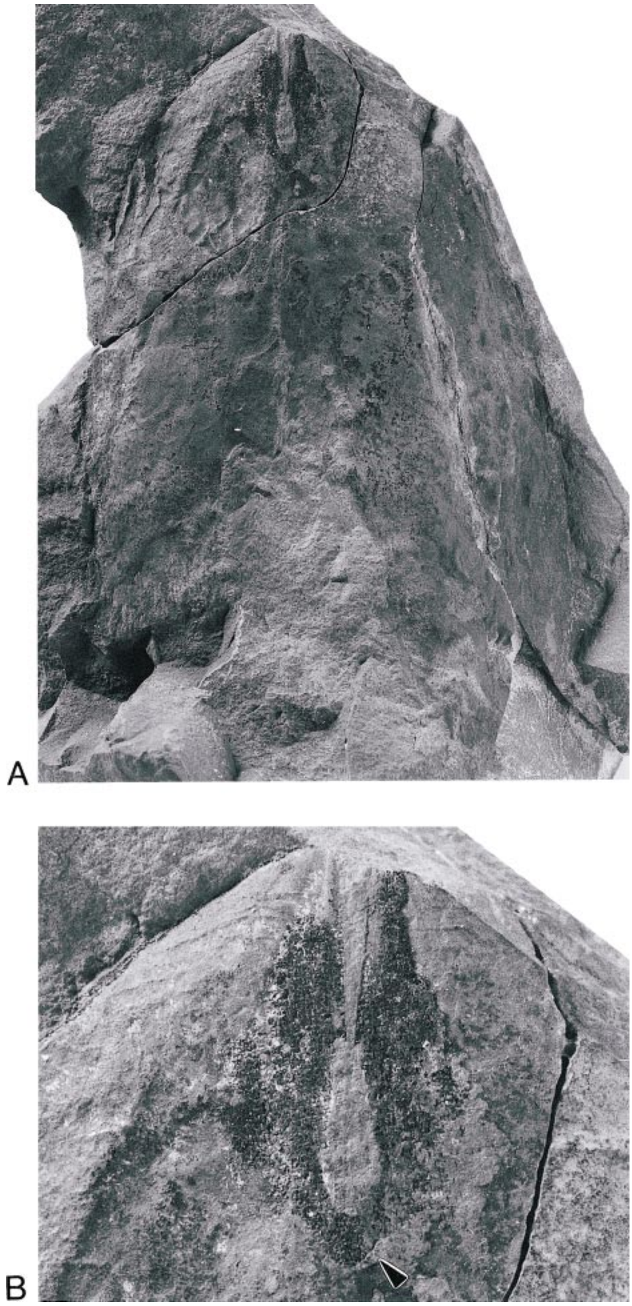


Fig. 3. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, AMNH 47275, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior on top. **A.** Overview showing the ragged posterior margin, ×1. **B.** Close-up of the anterior end showing the apical slit and U-shaped outline of the junction between the inner and outer lamellae (arrow), ×3.

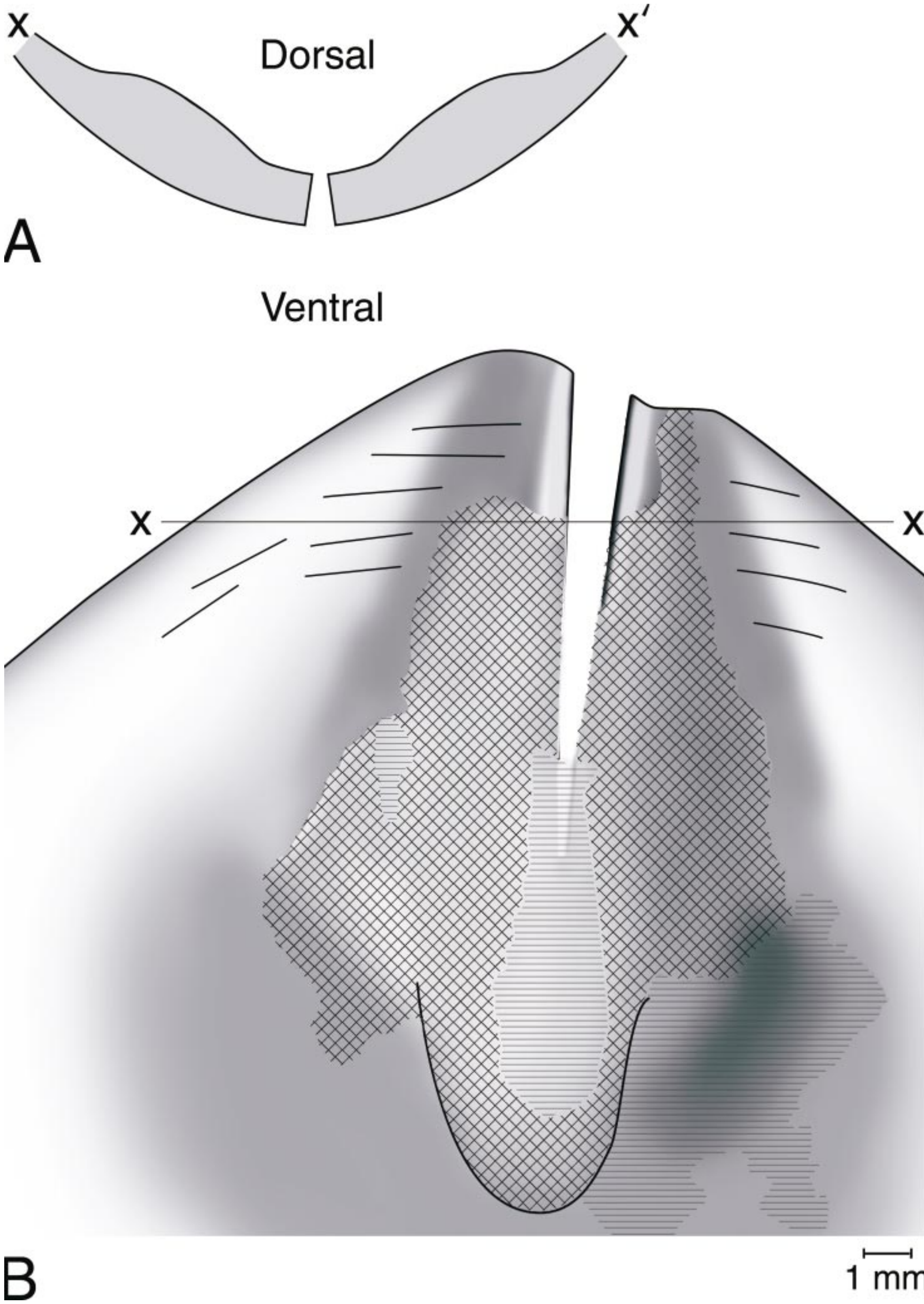


Fig. 4. Drawings of AMNH 47275 (see fig. 3). **A.** Hypothetical cross section near the apical tip. **B.** Close-up of the anterior end. The cross hatched area indicates coarsely crystalline black material; the lined area indicates finely crystalline yellowish material.

Fig. 5. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, AMNH 47276, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior end on top, showing the curved anterior margin, ×1.

mented sandstone (fig. 5). It is associated with an angular shard of iridescent shell that is probably a fragment of *Placenticeras*.

The jaw is preserved as a steinkern with patches of black material. It is approximately 85 mm long and 95 mm wide, but it is incomplete (W/L = 1.12). The right and left wings are each approximately 50 mm wide at their widest points (W/L of each wing = 0.59). The jaw is convex in cross section, with a gently arched median area and more steeply sloping sides. A small piece of the right anterior portion of the jaw is missing, and part of the posterior region is torn and crushed against a gastropod shell.

The jaw is parabolic in outline. The anterior margin is rounded, with an apical angle of 145°. The apex is slightly projected, with a shallow indentation on each side. A slit is not present at the apex, although the specimen is broken in this area. A groove occurs along the midline in the anterior region, but it is indistinct. It is bordered by two ridges that diverge posteriorly. The ridges develop into broad, raised areas, posterior of which the middle portion of the jaw is not preserved. The jaw ends in a ragged edge.

The material of the jaw consists of three layers. A patch of golden crystalline material makes up the outermost layer and occurs on part of the anterior one-third of the jaw. This material is underlain by a layer of shiny, crackled black material, which in turn is underlain by a layer of more finely textured black material—that is, the dorsal surface of the inner or outer lamella, depending on the position.

Distinct, longitudinal striations parallel the midline and occur at intervals of approximately 0.6 mm on the right wing, especially at its anterior end. They are visible on the layer below the crackled material—that is, on

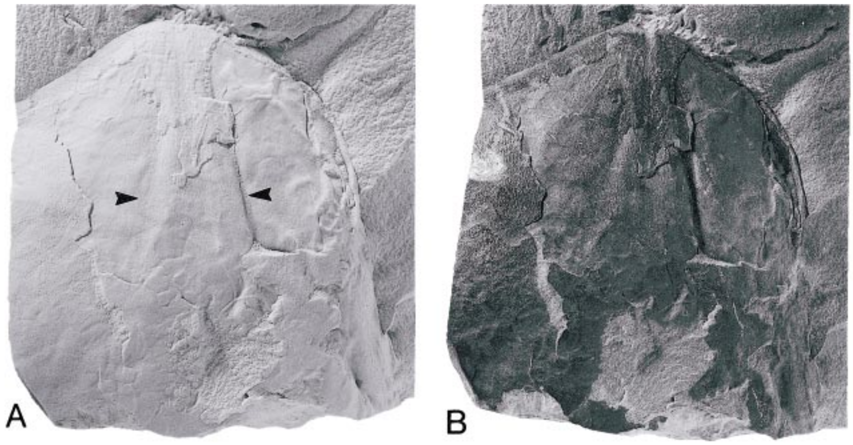


Fig. 6. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, AMNH 47277, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior end on top. **A.** Coated. **B.** Uncoated. Part of the coarsely crystalline black material is missing exposing two radial ridges flanked by grooves (arrows), which are expressed as grooves and ridges, respectively, on the dorsal side, ×1.

the steinkern—and thus reflect the texture on the dorsal surface of the inner lamella. The posterior end of the right wing also shows regularly spaced longitudinal flexures on the steinkern, but they are broader and more widely spaced than those on the anterior end. In addition, longitudinal creases are present on the lateral margins of the jaw, especially on the right side.

As with the other jaw specimens, the surface of the jaw bears irregularities—for example, a protuberance on the left anterior region—that suggest plastic deformation. The surface is also traversed by raised, meandering, root-like structures, especially on the right posterior region, which may represent postmortem epizoan traces.

AMNH 47277 is an incomplete lower jaw preserved in a fragment of a sideritic, silty mudstone concretion (figs. 6–8). It is not associated with any *Placenticeras* shell. The specimen is subrectangular in outline and includes most of the anterior and left lateral margins. It is approximately 55 mm long and 50 mm wide (W/L = 0.91). It is slightly convex in cross section. The posterior portion of the jaw is missing and ends in a ragged edge. Most of the specimen is a steinkern covered in parts with a black layer consisting of shiny granules.

The anterior margin is narrowly rounded with weak indentations on each side of the apex. The apical angle is approximately 120°. The angle expands to approximately 145° at the transition to the flanks. There is a shallow median depression at the rostral tip that widens to a maximum of approximately 8 mm at a distance of 30 mm from the tip. This depression is bordered by rounded ridges originating 7 mm from the apex. The ridges broaden and diverge posteriorly and are themselves bordered by depressions. Parts of the ridges and depressions are covered with coarsely crystalline black material eliminating some of the relief.

The wings are separated at the apex by a narrow slit 0.5 mm wide. The slit extends 8 mm posteriorly and narrows down completely. However, the edges of the slit are not nearly as distinct as those in AMNH 47275. Posterior of the end of the slit, the jaw is continuous across the midline and consists of a thick layer of coarsely crystalline black material representing part of the inner lamella. At approximately 19 mm adapical of the tip, there is a sharply defined V-shaped outline demarcated by finely crystalline golden material that overlies the black material. This margin represents the junction between the two lamellae and develops into a short median ridge. The outline of the V on the left side extends anteriorly forming a slight

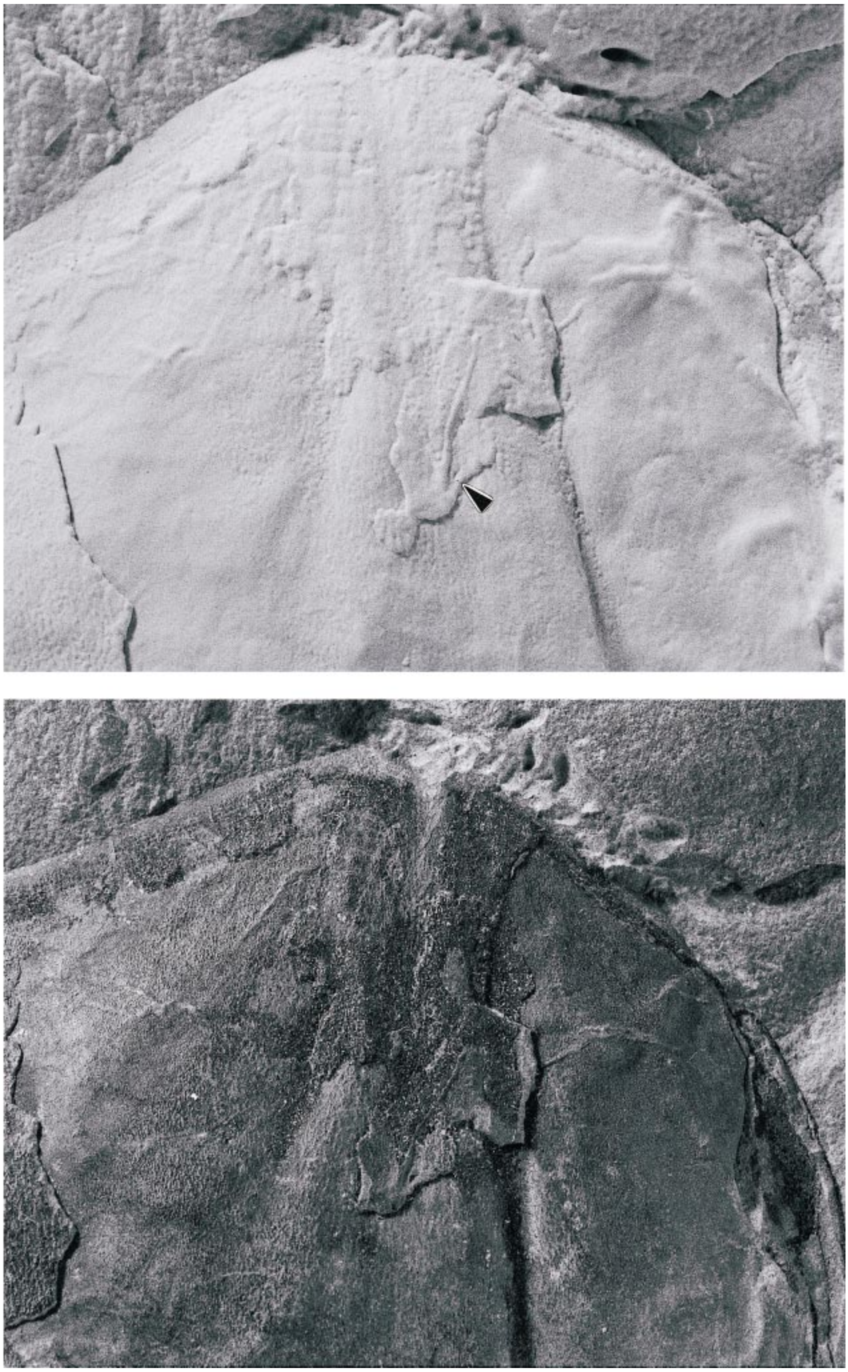


Fig. 7. Close-up of the anterior end of AMNH 47277 (see fig. 6). **A.** Coated. **B.** Uncoated. The arrow indicates the edge of the outer lamella, ×3.

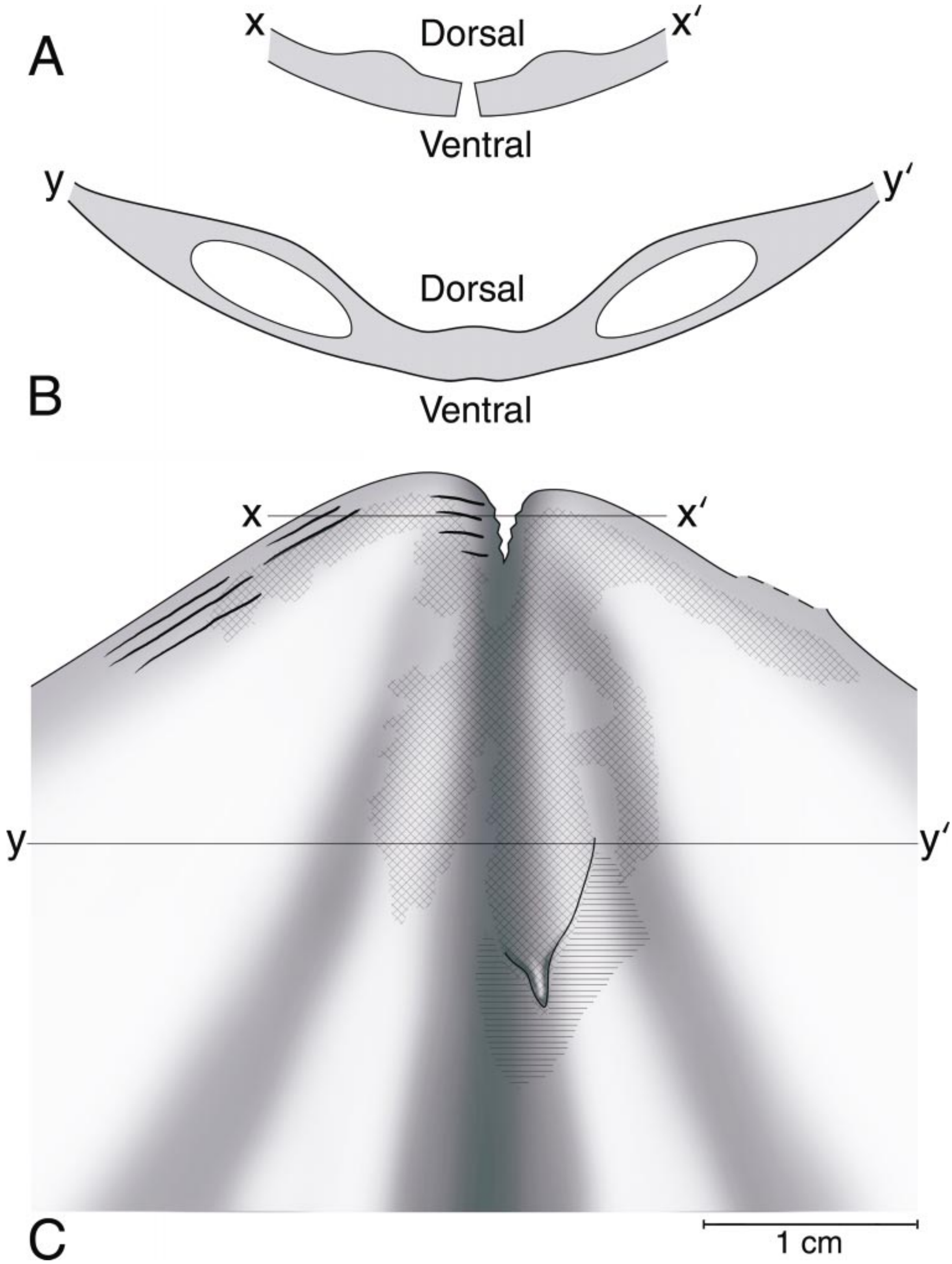


Fig. 8. Drawings of AMNH 47277 (see figs. 6, 7). **A.** Hypothetical cross section near the apex. **B.** Hypothetical cross section approximately 20 mm from the apex. The two lamellae are separated on each side of the midline but fused together along the lateral margins. **C.** Anterior end showing the V-shaped edge of the outer lamella. Texture as defined in figure 4.

curve. The inner and outer lamellae are separated from one another on the sides by an intervening layer of matrix. Posterior of this area, the jaw appears to be continuous across the middle, exposing the ventral surface of the inner lamella (the outer lamella is eroded away). The posterior edge of the jaw is ragged.

The anterior margin of the right wing shows a step-like change in slope 3 mm from the margin and running parallel to it. If the black material were evenly preserved everywhere, this step would not be apparent. The anterior edge of the left wing bends dorsally but is not recurved.

The jaw material is multilayered. The outermost layer consists of scattered patches of golden, finely crystalline material. It overlies a layer of shiny, black, fractured material, with a maximum thickness of approximately 0.3 mm. The black material has a grossly cellular to finely cellular appearance, with colorless to yellowish crystals embedded in it. This layer overlies another layer characterized by irregular small craters and dividing walls, which may represent the impression of beccublast cells (see below).

The tip of the right wing is covered with striations oriented perpendicular to the midline. These striations occur on the steinkern and are spaced at intervals of approximately 0.5 mm. In addition, there is a series of very thin lineations along the anterior margin of the right wing starting approximately 1 mm from the edge and persisting for approximately 2 mm. They occur on the steinkern and parallel the anterior margin. The left edge of the jaw is torn and folded into longitudinal creases. The rest of the jaw shows irregular bumps and wrinkles, indicating plastic deformation.

TMP 87.119.19 (figs. 9, 10) is a flattened steinkern in a chunk of grayish brown calcareous concretion, retaining a thin film of the same black material observed in the other jaw specimens. Most of the anterior and left lateral portions of the jaw are preserved. As in the other specimens, the middle part of the posterior end is missing.

The jaw is approximately 90 mm long and 70 mm wide but is incomplete (W/L = 0.78). It is nearly flat in cross section. The left margin of the jaw curves dorsally and bears longitudinal creases. The apical angle is 140° and the anterior margin shows a slight indentation on each side of the apex.

The apical tip is bisected by a small slit that extends 8 mm posteriorly and then closes up. It is surrounded by an oval area of coarsely crystalline black material, representing part of the inner lamella. Starting 19 mm from the apex, a central depression appears and widens posteriorly; it is bordered by two rounded ridges, which are themselves flanked by divergent grooves. The surface of the jaw is continuous across the middle, possibly representing the ventral surface of the inner lamella.

A thick band of black material 3 mm wide borders the anterior margin. This material is part of the inner lamella and merges into the patch of thickened material at the midline. It is ornamented on the right side with parallel ridges oriented perpendicular to the anterior margin and spaced at intervals of approximately 0.5 mm. These ridges connect up with similar features at the apex that extend at an oblique angle from the midline.

TMP 92.42.21 is a more or less intact left wing and part of the right wing of a lower jaw (fig. 11). It is a steinkern covered with a film of black material and occurs in a fragment of gray calcareous concretion that also contains an elongate piece of *Placenticeras* shell. The jaw is approximately 85 mm long and 70 mm wide but is incomplete (W/L of the left wing = 0.78). The anterior margin is nearly straight, and the apical angle is approximately 160°. The anterior edge bends slightly dorsally. The posterior end of the specimen is torn. Three broad flexures on the middle of the left wing parallel the posterior margin and are spaced at intervals of approximately 12 mm.

A small bit of material is missing from the left anterior tip; the right wing tip is more or less intact. The two wings are separated at the apex, but are joined together along the midline by a thin layer of black material starting 3 mm from the apex and extending another 4 mm. The black material reaches a maximum thickness of approximately 0.3 mm on each side of the midline and displays a honeycomb-like texture with elongate white crystals embedded in the spaces between black crystals. The two wings are sep-

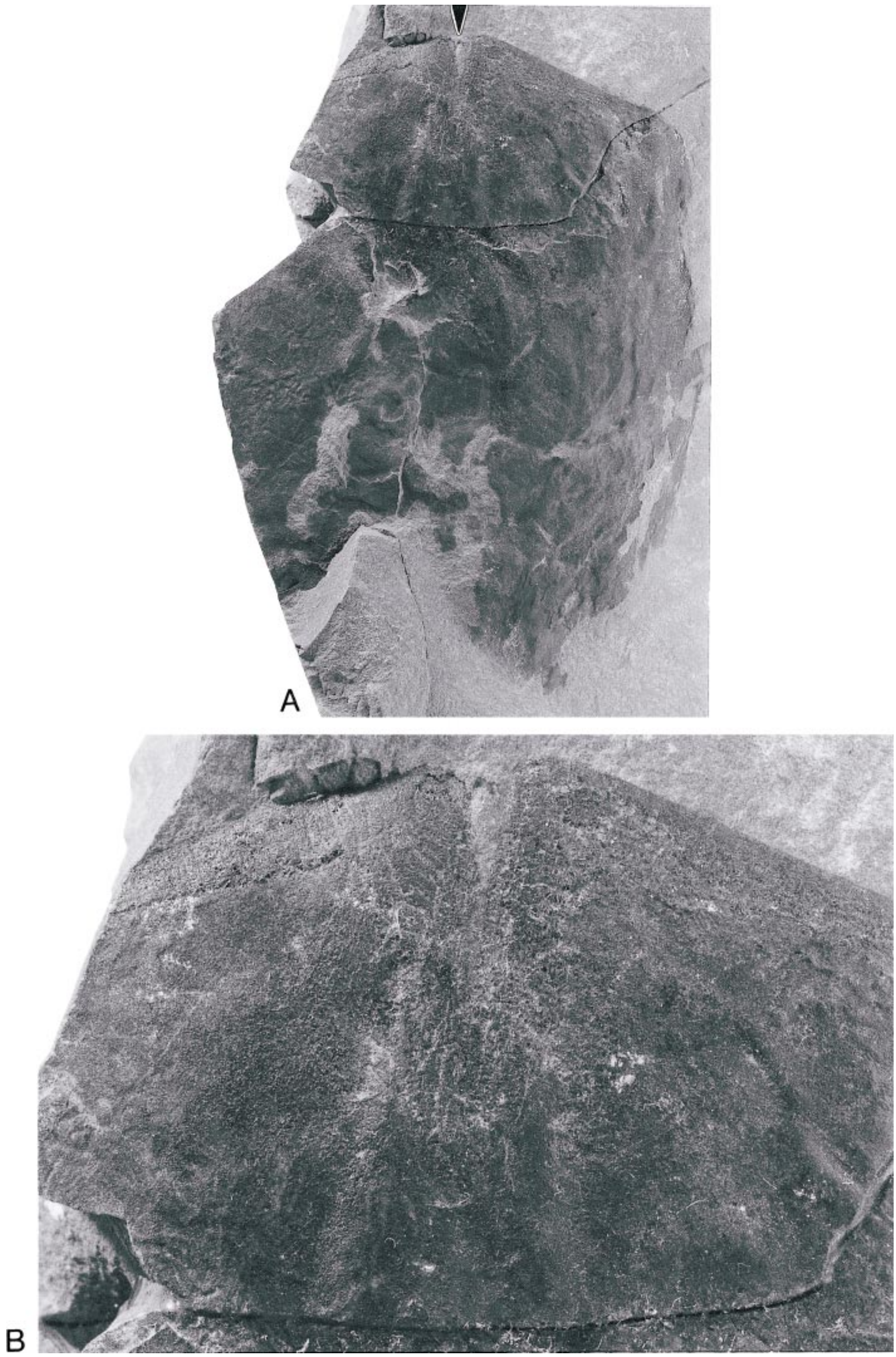


Fig. 9. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, TMP 87.119.19, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior end on top. **A.** Overview showing diverging ridges on the anterior end. The arrow indicates the position of the apex, ×1. **B.** Close-up of the anterior end with a median slit at the apex, ×2.9.

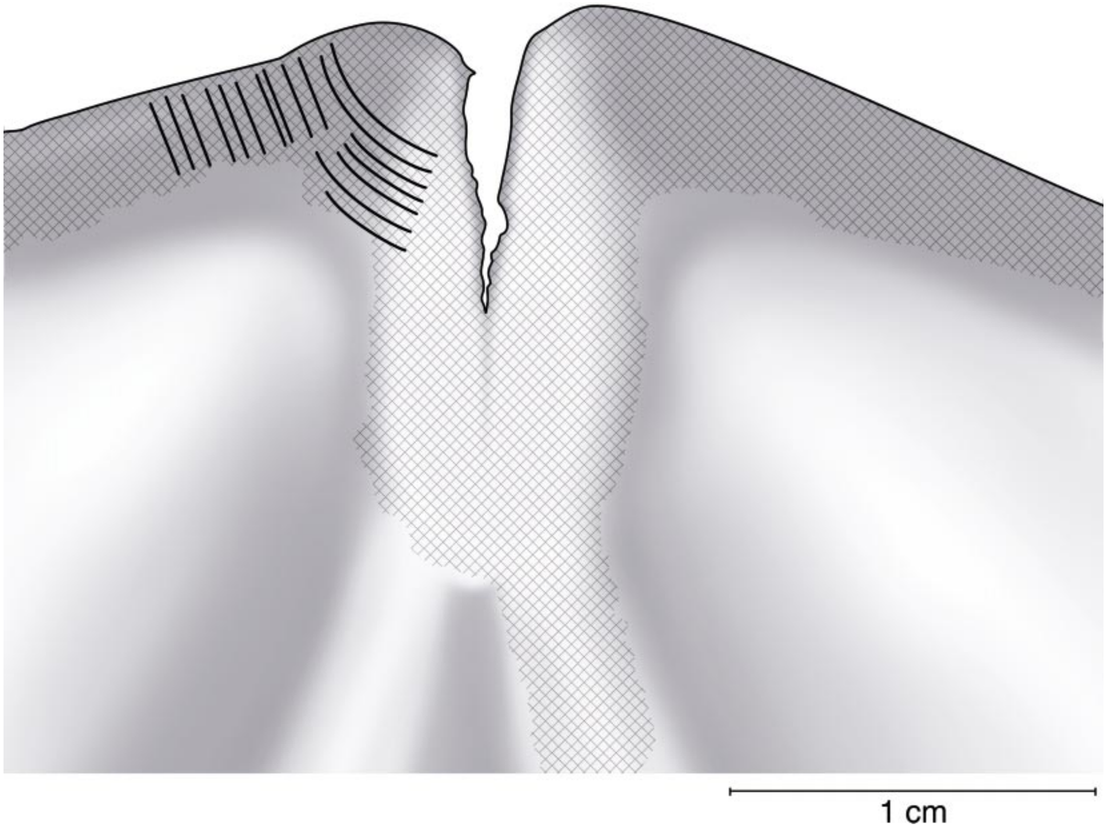


Fig. 10. Drawing of the anterior end of TMP 87.119.19 (see fig. 9) showing the thickened area of black material along the margin, with narrow ridges oriented perpendicular to the edge. Texture as defined in figure 4.

arated by a narrow, ragged separation, 1–2 mm wide, for the rest of the jaw. This separation is presumably postmortem.

Striations are present on the anterior margin of the jaw where the black material is worn away. They are spaced at intervals of approximately 1 mm and are oriented parallel to the edge, representing features on the dorsal surface of the jaw. In contrast, where the black material is still intact, thin ridges are spaced at intervals of approximately 0.8 mm and are oriented perpendicular to the anterior edge; these features are on the ventral surface of the jaw.

TMP 99.84.2 is a small specimen preserved as a steinkern with a film of black material (figs. 12, 13). It occurs in a fragment of gray calcareous concretion containing several pieces of iridescent *Placenticeras* shell. The lateral part of the jaw is missing on the right side and is partially covered on the left. The exposed portion is approximately 60 mm long and 40 mm wide, but it is incomplete (W/L = 0.67). The jaw is gently convex in cross section and bends strongly dorsally on the lateral margins, where it is covered with longitudinal creases.

The jaw is lozenge-shaped, its anterior margin forming a moderately well-rounded, parabolic outline with an apical angle of 105°. The anterior margin is bent dorsally and bears thin ridges paralleling the edge. The two wing tips are separated along the midline by a slit 1.25 mm wide that narrows down completely 12 mm from the apex. The slit rests on an oval platform of coarsely crystalline black material bordered by radial depressions that broaden posteriorly and extend another 30 mm. The slit ends in a patch

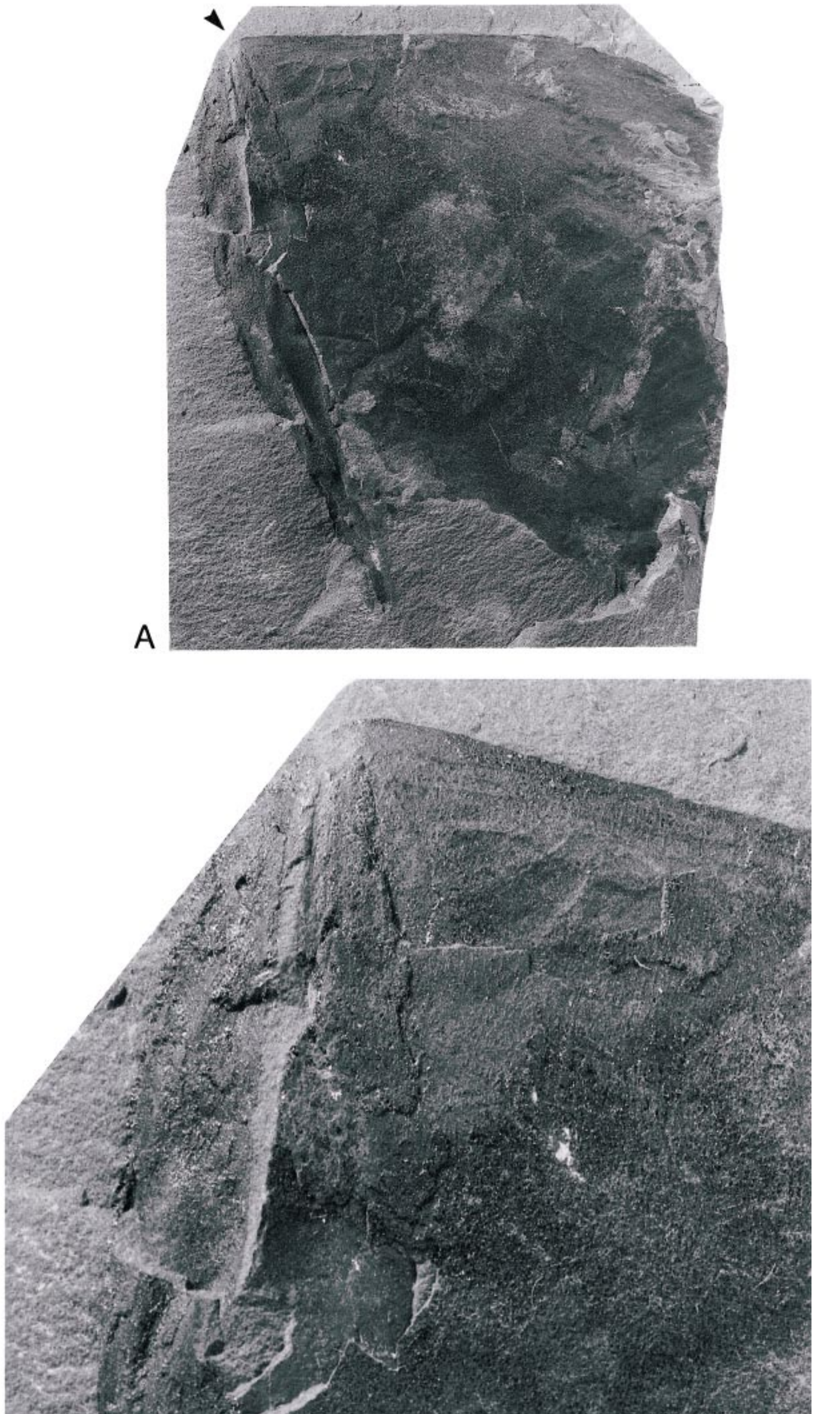


Fig. 11. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, TMP 92.42.21, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior end on top. **A.** Overview showing most of the right wing. The arrow indicates the position of the apex, ×1. **B.** Close-up of the anterior end, ×3.

Fig. 12. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, TMP 99.84.2, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada, ventral view, anterior end on top, ×1.

of golden-yellowish, finely crystalline material overlying the black material.

Posterior of the slit, the jaw is continuous across the middle and reflects the ventral surface of the inner lamella; the outer lamella is broken away in this area. Part of the outer lamella is preserved approximately 28 mm from the apex. It is separated by a thin layer of matrix from the inner lamella. The outer lamella is continuous across the jaw, but there is an irregular ridge along the midline that persists to the posterior end and is covered with finely crystalline golden material.

UWO.KMC.100125 is preserved in a fragment of grayish-brown, siderite cemented concretion containing numerous shell fragments of *Placenticeras* (fig. 14). The jaw is approximately 80 mm long and 80 mm wide but somewhat deformed (W/L = 1.0). The right wing, which is better preserved than the left wing, is approximately 50 mm wide (W/L of the right wing = 0.62).

The jaw is parabolic in outline, with a curved anterior margin. The middle of the jaw is nearly flat, and the lateral margins are folded dorsally, with the left margin more strongly folded than the right. Both margins show longitudinal creases.

There is a slit 2 mm wide at the apex of the jaw, which narrows down completely 10 mm from the apex. The slit is not nearly as well defined as in other specimens. It is bor-

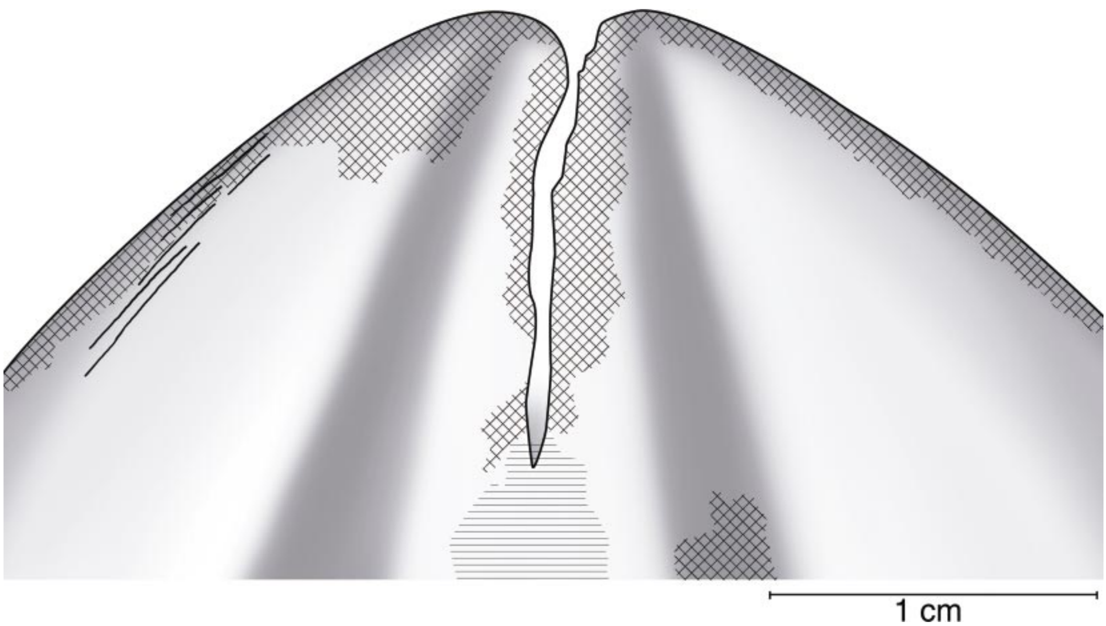


Fig. 13. Drawing of TMP 99.84.2 (see fig. 12) showing the anterior area. Texture as defined in figure 4.

Fig. 14. Lower and upper (?) jaws of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, UWO.KMC.100125, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada. The lower jaw shows a bilobate posterior margin (toward bottom of photo). The left arrow indicates the position of the apex of the lower jaw. The right arrow indicates a fragment of the upper jaw (?), ×1.

dered by narrow radial ridges, partly covered with thick, coarsely crystalline black material, forming an elongate V-shaped area. The ridges are themselves flanked by weakly defined radial depressions that diverge posteriorly. Patches of finely crystalline yellowish material overlie portions of the black material.

Immediately posterior of the V-shaped area, the jaw, which is preserved in this region as a steinkern, is continuous across the midline, reflecting the ventral surface of the inner lamella. However, approximately 13 mm posterior of this point, where the material of the outer lamella is preserved, there is a midline ridge 1 mm high and 1 mm wide, with a central groove. It extends 17 mm posteriorly at which point the two wings diverge and gently curve outward at an angle of approximately 40° from the midline. The ends of the wings are ragged with tears up to 5 mm deep, but if the ends were restored, they would be rounded in outline. An incomplete specimen of what appears to be an upper jaw is preserved in the same concretion, but there is no evidence of a radula.

Pierre Shale, South Dakota

BHMNH 5041 occurs in a carbonate cemented, shaly concretion with specimens of *Baculites compressus* Say, 1820 (figs. 15, 16). It is covered with a film of black material and is incomplete but preserves a strong convexity that presumably approaches the original cross section. The jaw is approximately 70 mm long and 60 mm wide (W/L = 0.86). The maximum width of the right wing, which is more complete than the left wing, is approximately 45 mm wide at its widest point (W/L of the right wing = 0.64).

The jaw consists of two symmetrical wings that are joined together along the midline but are progressively more torn apart toward the posterior end. The posterior margins of the two wings show irregular edges. Small fragments are also missing from the sides of the wings. In contrast, the anterior margin of the jaw is nearly complete.

The apex is broadly rounded with an angle of approximately 145°. The anterior margin shows a slight indentation on each side of the apex. There is a dramatic increase in the thickness of the black material, manifested as a step-like feature demarcating the boundary of the outer lamella. This feature does not parallel the anterior margin but runs at a slight angle to it so that this feature occurs at approximately 5 mm from the anterior margin near the midline and merges with it on the lateral edges.

A narrow slit 2 mm wide appears at the apex and extends 15 mm before closing up completely. This slit rests on a platform of coarsely crystalline black material, forming an elongate disc. The platform is bordered by two grooves that are nearly parallel, demarcating the boundary of the outer lamella. Immediately posterior of the disc, the jaw seems continuous across the middle, but in a few millimeters a midline ridge of yellowish material appears with the two sides of the wings raised up against it.

The black material of the jaw is similar to that of the other jaws examined and is characterized by a shiny, honeycomb-like texture. Thin, subvertical, curved walls create cells that sometimes contain yellowish colored crystals.

BHMNH 5454a and 5454b occur together in a single gray limestone concretion (figs. 17–19). They are associated with many specimens of *Baculites compressus* but no obvious pieces of *Placenticeras*. BHMNH 5454a (figs. 17A, 18, 19B) is well preserved and composed of black material. It retains its original convex shape and is approximately 35 mm long and 35 mm wide (W/L = 1.0). The left wing, which is more complete than the right wing, is 25 mm wide at its widest point (W/L of the left wing = 0.71).

The apex of the jaw forms a slightly pointed projection with an angle of approximately 160°. The anterior margin is weakly concave on each side of the apex. A narrow slit initially 1.5 mm wide extends approximately 10 mm along the midline, and develops into a solid ridge at its posterior end. This slit rests on a raised area composed of coarsely crystalline black material. This area is demarcated by narrow grooves, indicating the margin of the outer lamella, creating a V-shaped island. The outer lamella extends to the anterior edge, where it merges with the inner lamella.

BHMNH 5454b is part of a lower jaw in the same concretion as BHMNH 5454a (figs.

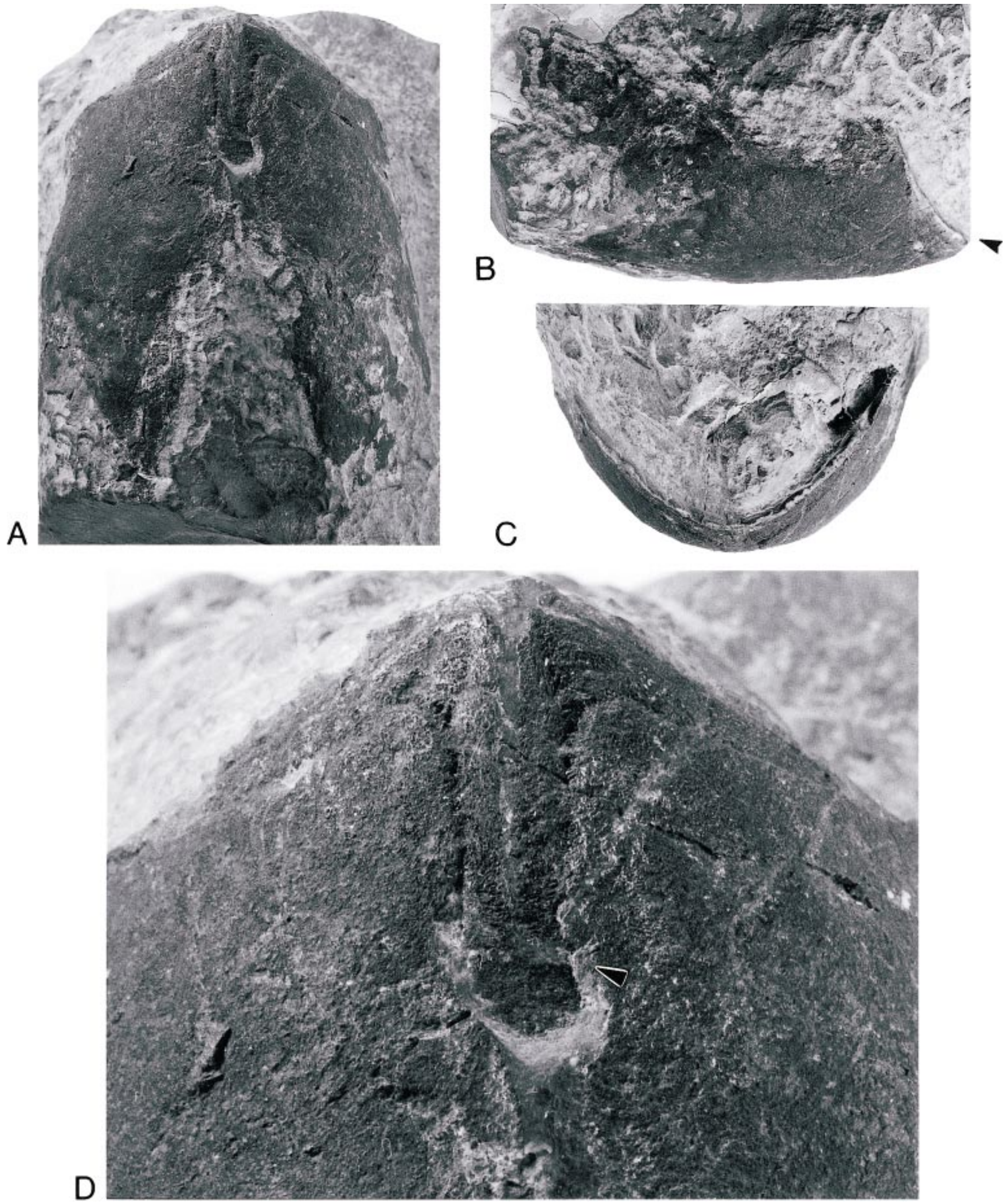


Fig. 15. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, BHMNH 5041, *Baculites cuneatus* Zone, Pierre Shale, Meade County, South Dakota. **A.** Ventral view, anterior end on top, showing bilobate posterior margin. The specimen retains a strong convex curvature, presumably similar to that in life, ×1. **B.** Right lateral view with the anterior end (arrow) to the right. The anterior margin is weakly indented and the apex is slightly projected, ×1. **C.** Anterior view, ×1. **D.** Close-up of the anterior end showing the outline of the outer lamella (arrow), ×3.1.

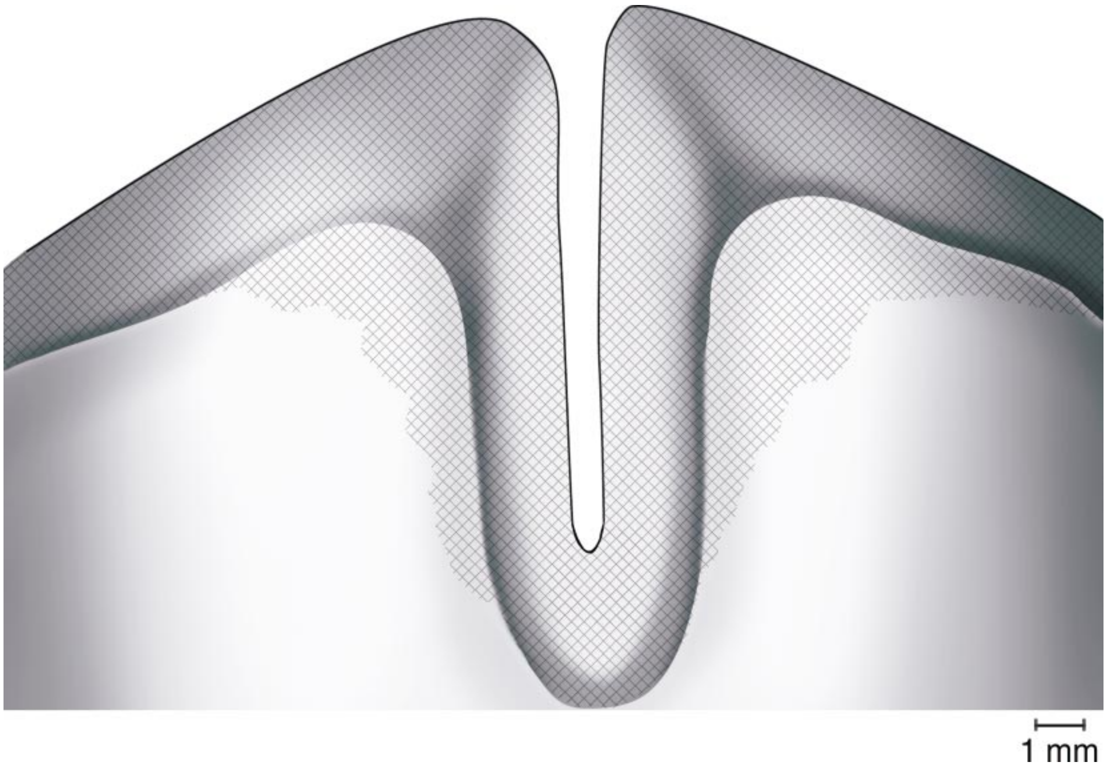


Fig. 16. Drawing of BHMNH 5041 (see fig. 15) showing the thickened area of black material on each side of the midline slit. Texture as defined in figure 4.

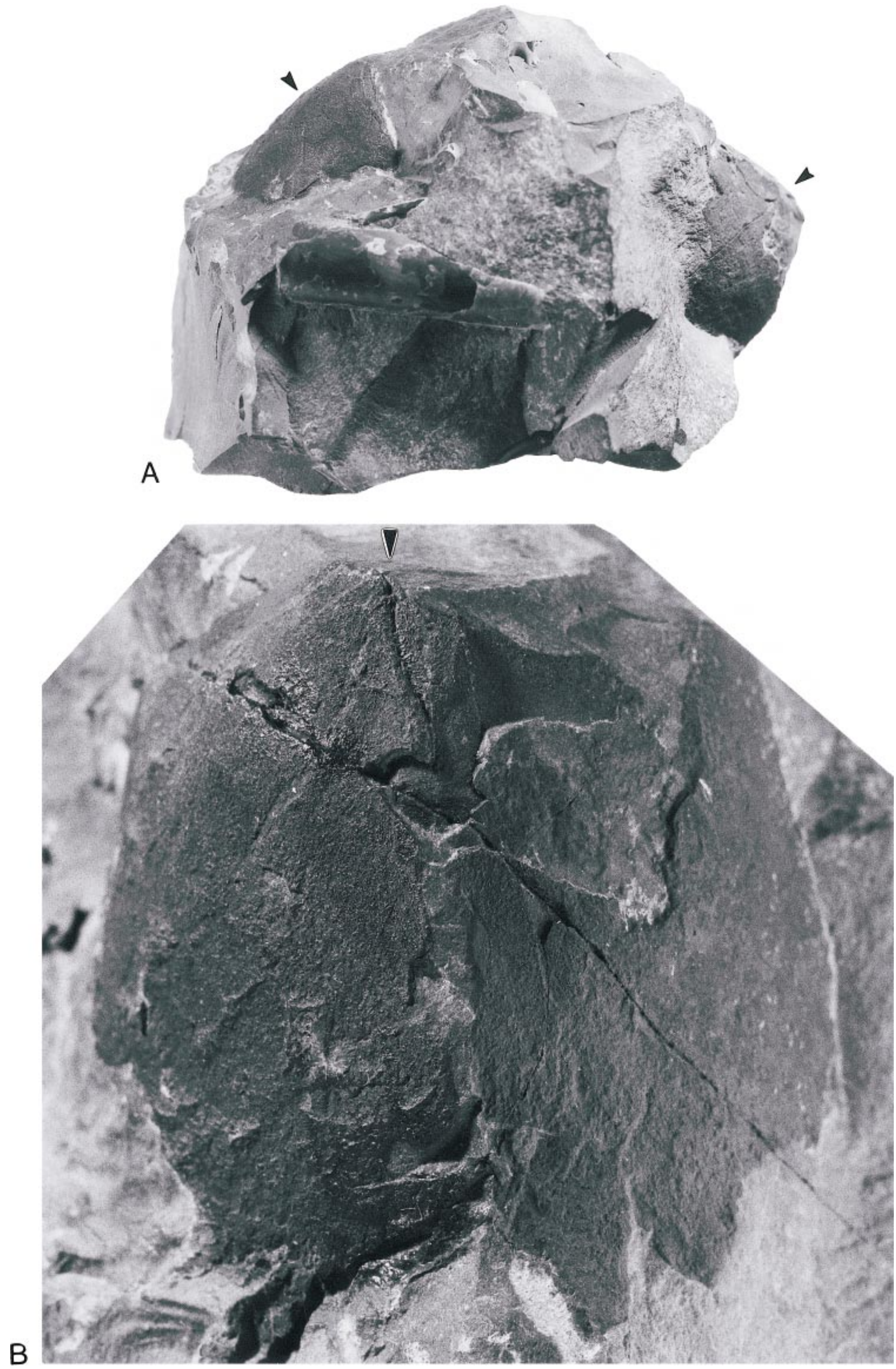
17B, 19A). It is a steinkern covered with a film of black material. It is convex and approximately 40 mm wide and 40 mm long (W/L = 1.00). The right wing, which is more complete than the left wing, is approximately 30 mm wide at its widest point (W/L of the right wing = 0.75). The jaw is subquadrate in overall shape. The anterior margin is well preserved, with a slight indentation on each side of the apex. A step-like feature is present near the anterior margin and forms a slight concavity with it.

Although the apex is broken off, enough of it remains to reveal a narrow median slit, which extends approximately 6 mm. This slit is surrounded by a raised platform of coarsely crystalline black material with a honeycomb-like texture. This material represents the inner lamella and is bordered on the right side by a thick ridge representing the margin of the outer lamella. The outer lamella forms the step-like feature on the anterior margin. On the left side, the outer lamella has broken off revealing a radial depression next to the central platform of black material. An intervening layer of matrix separates the two lamellae.

BHMNH 5456 is part of a lower jaw, with the posterior one-half broken away (figs. 20, 21). It is in a concretion full of mollusks,

→

Fig. 17. Lower jaws of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, BHNMH 5454a, b, *Baculites compressus* Zone, Pierre Shale, Meade County, South Dakota. **A.** Overview of a chunk of the concretion containing BHMNH 5454a (left arrow) and BHMNH 5454b (right arrow), ×1. **B.** BHMNH 5454b, ventral view, anterior end on top. The arrow indicates the position of the apex, ×3.


A
B

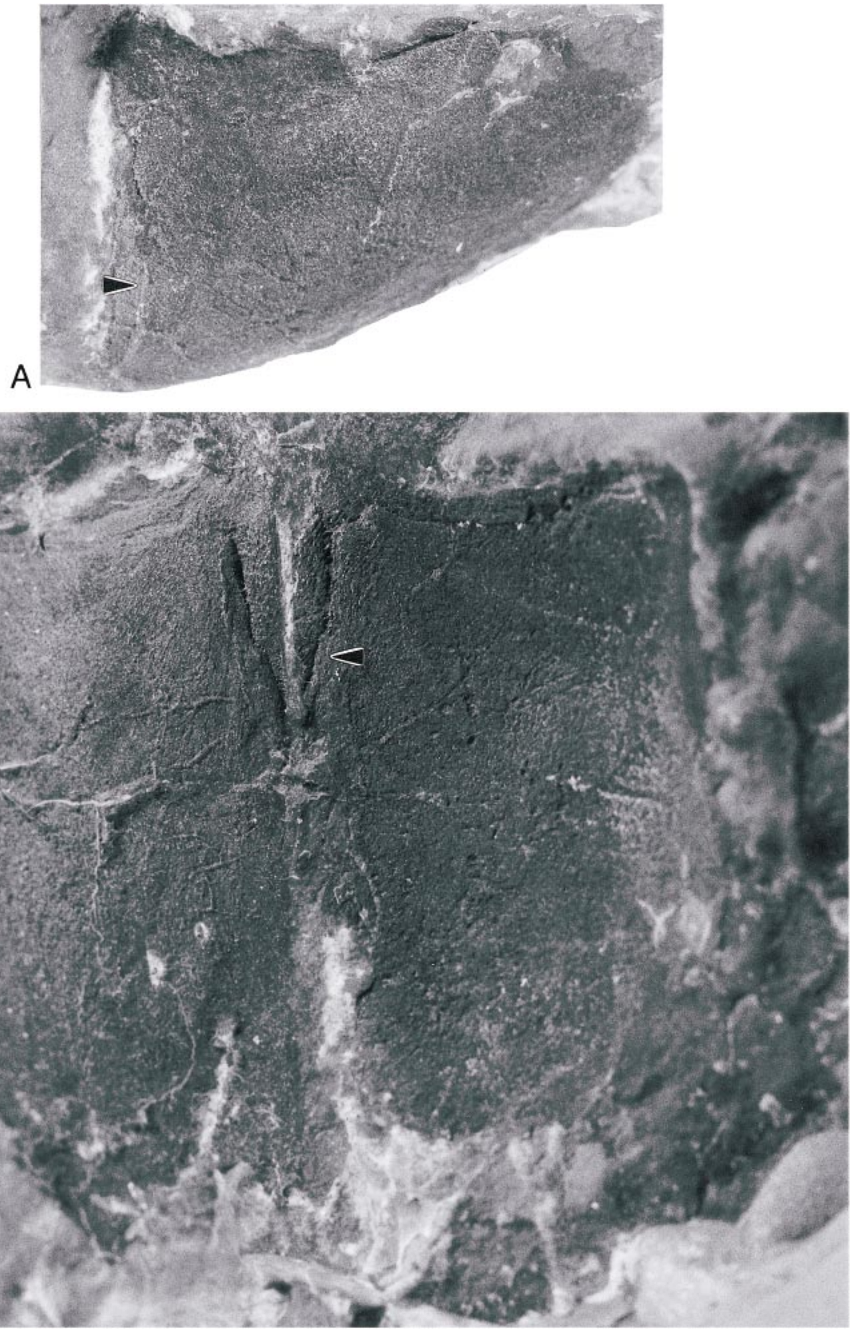


Fig. 18. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, BHMNH 5454a (see fig. 17). **A.** Left lateral view with anterior end to the left. The arrow indicates the step-like feature near the anterior edge, ×3. **B.** Overview showing the V-shaped outline (arrow) representing the margin of the outer lamella, ×3.

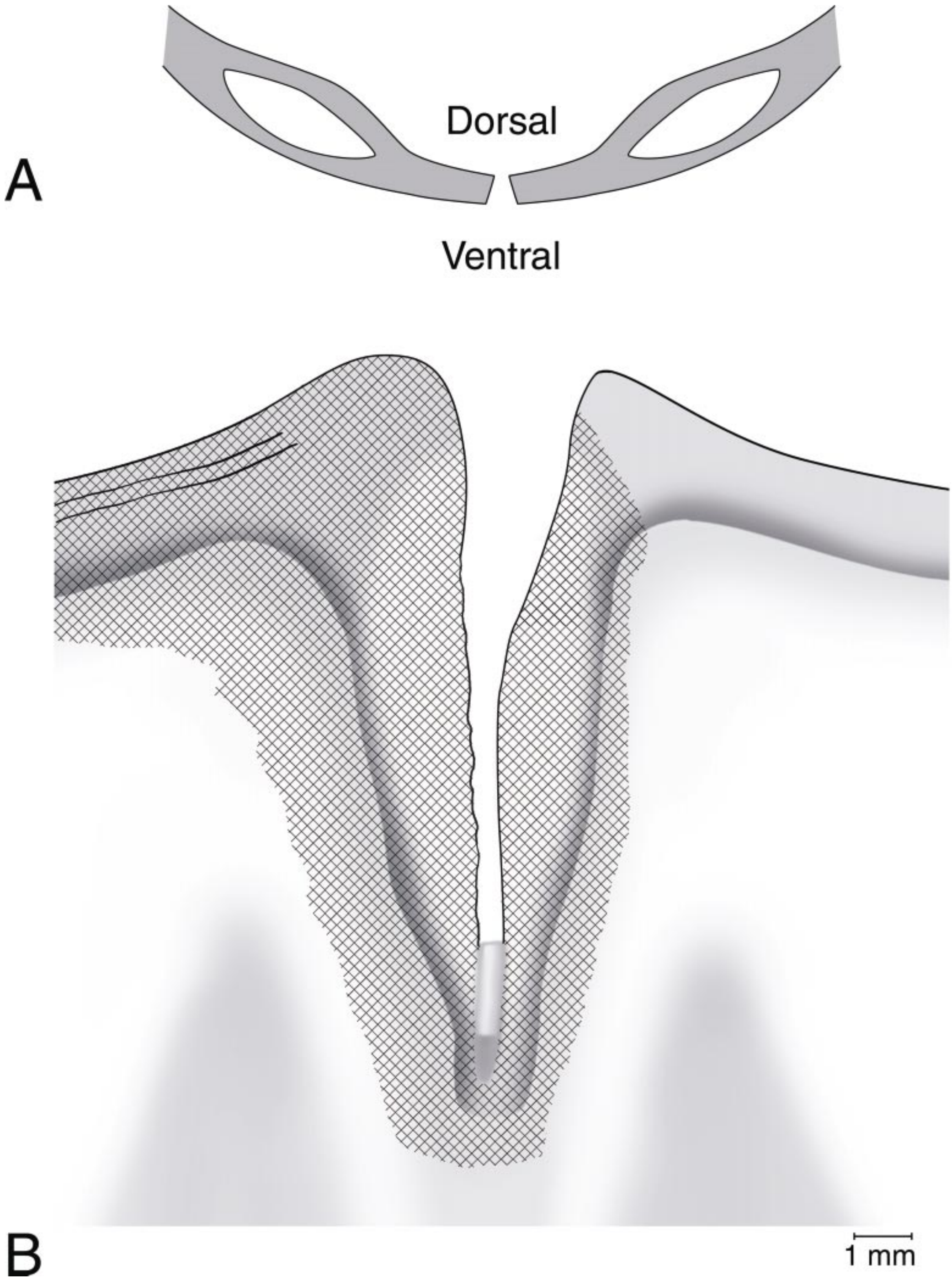


Fig. 19. Drawings of BHMNH 5454a and 5454b (see figs. 17, 18). **A.** Hypothetical cross section through BHMNH 5454b approximately 10 mm from the apex. The two lamellae are separated on each side of the midline. **B.** Close-up of the anterior end of BHMNH 5454a showing the junction of the inner and outer lamellae, which is visible due to weathering away of part of the inner lamella. Texture as defined in figure 4.

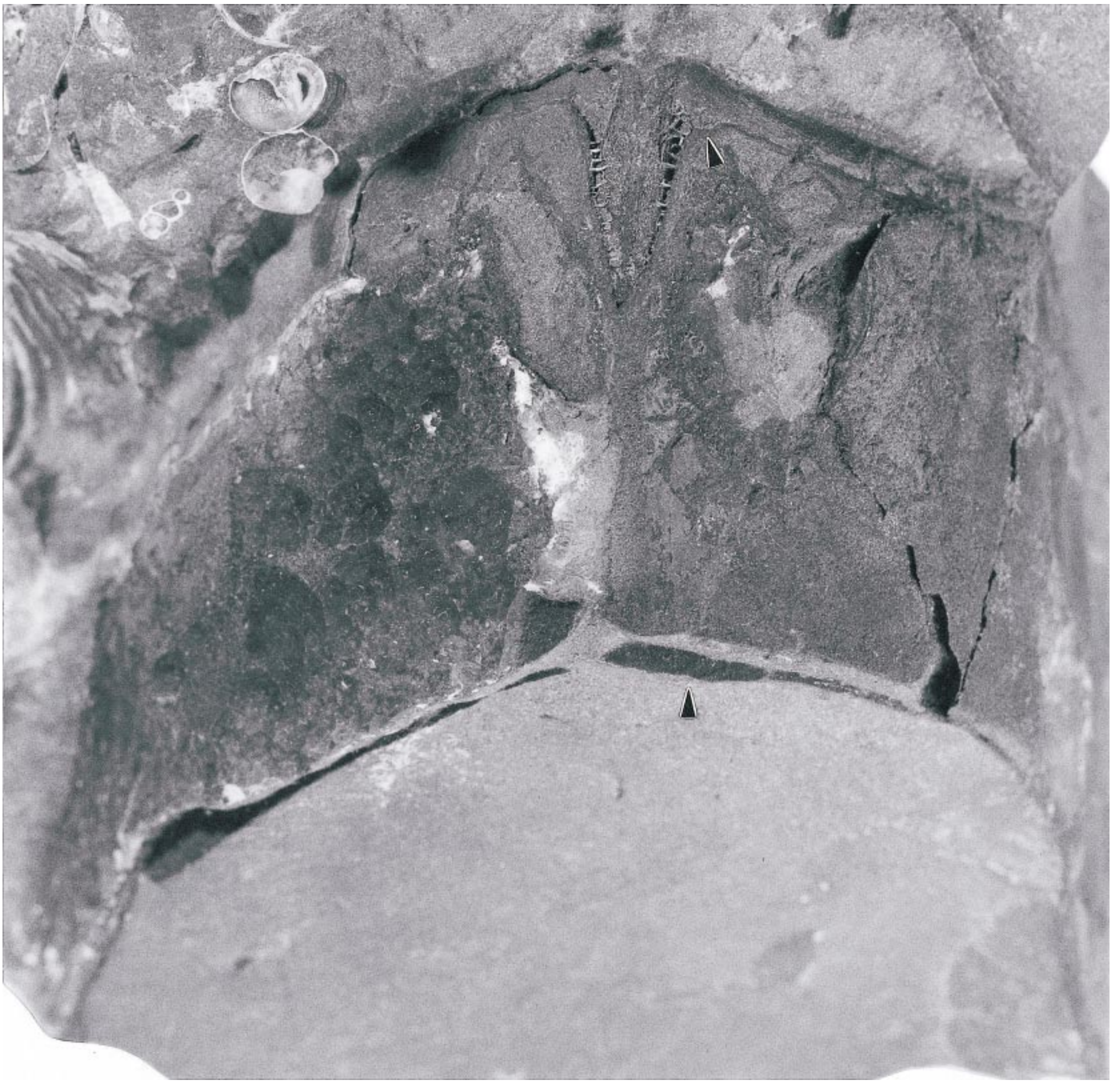


Fig. 20. Lower jaw of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, BHMNH 5456, *Baculites cuneatus* Zone, Pierre Shale, Meade County, South Dakota, ventral view, anterior end on top. The upper arrow indicates the edge of the outer lamella. The lower arrow indicates the separation between the two lamellae, fortuitously exposed at a break in the jaw, ×2.7.

including cephalopods that retain aragonitic shells. The jaw is convex and is approximately 55 mm wide at its widest point.

The anterior margin is rounded with an apical angle of approximately 140°. The margin is slightly indented on each side of the apex. There is a step-like feature that forms a slight concavity with respect to the anterior edge. The apex displays a narrow slit 7 mm long, which is replaced by a narrow ridge that extends another 4 mm before disappearing altogether. The slit/ridge is surrounded by an elongate boss of coarsely crystalline black material with clear to yellowish crystals embedded between the black crystals. This central elevation is bordered by grooves that demarcate the margin of the outer lamella. The grooves are filled with bits of black material, but the most striking aspect is the presence of clear to yellowish crystalline struts that

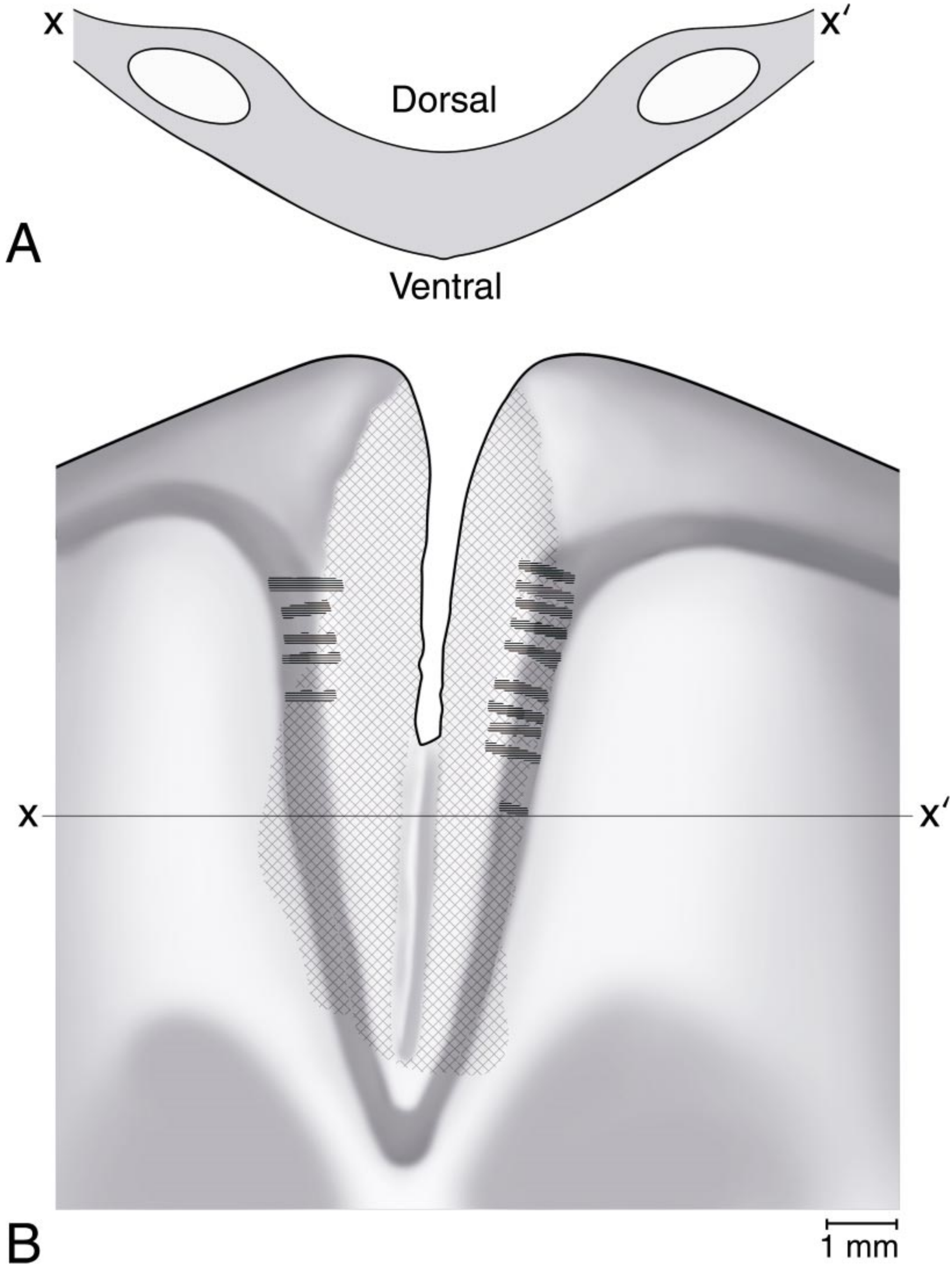


Fig. 21. Drawing of BHMNH 5456 (see fig. 20). **A.** Hypothetical cross section (restored) near the apex. **B.** Close-up of anterior end showing an elongate boss and narrow ridge along the midline. The horizontal lines indicate the crystalline struts that cross the grooves. Texture as defined in figure 4.

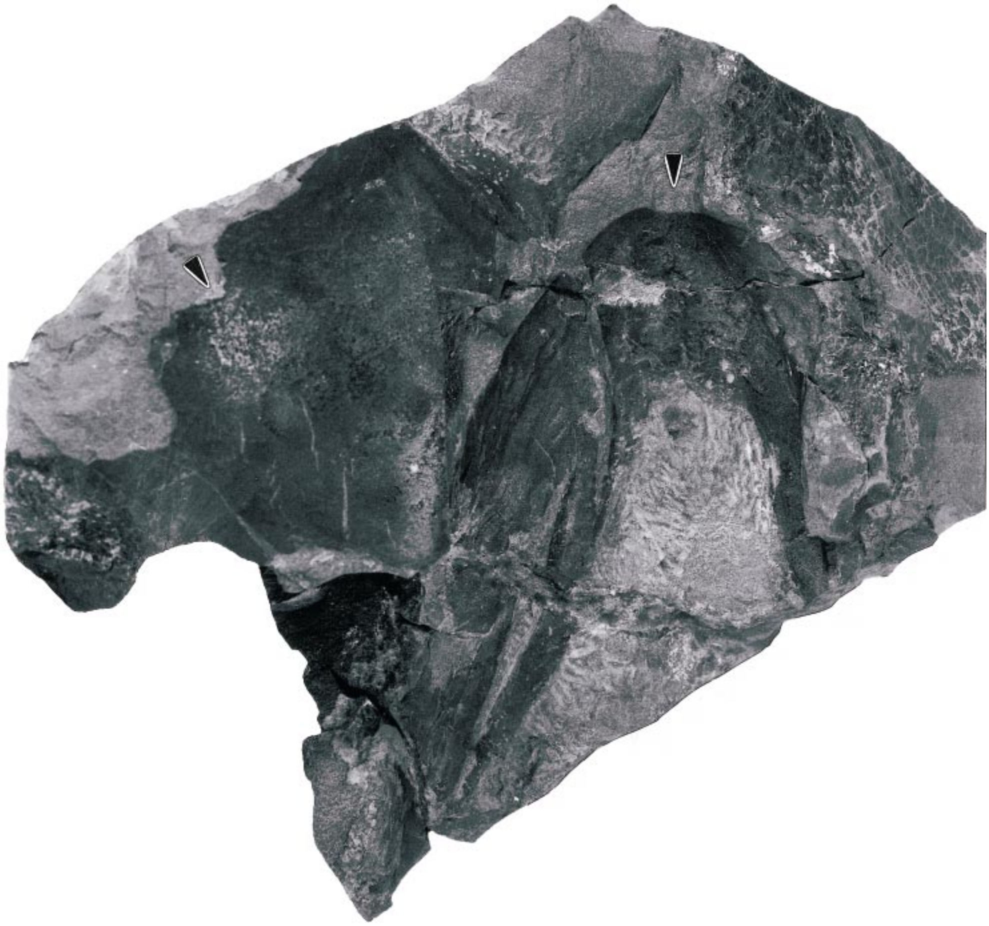


Fig. 22. Upper jaw (right arrow) and lower jaw (?)(left arrow) of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, UWO.KMC.100126, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada. The ventral surface of the upper jaw is exposed with the anterior end on top. Most of the right wing is preserved. Part of the lower jaw (?) is visible on the left side, ×1.

cross the grooves at nearly right angles to the midline.

The outer lamella forms the characteristic V-shaped outline around the central boss and the step-like feature on the anterior margin. The outer lamella bears a midline ridge posterior of the V-shaped area. On part of the right side of the specimen, there is a tan crystalline layer that is weathered and pockmarked. It is approximately 1.2 mm thick and lies on the surface of the outer lamella. It is probably diagenetic in origin.

The jaw is broken 27 mm from the apex and reveals a layer of matrix between the outer and inner lamellae (fig. 20). This suggests that the two lamellae are distinct at this point but are fused together on the lateral margins.

Upper Jaw

Bearpaw Shale, Alberta

UWO.KMC.100126 is an incomplete upper jaw preserved in a fragment of reddish brown, siderite cemented concretion (fig. 22). The specimen is approximately 95 mm long and 50 mm wide, with the left wing sharply folded, and most of the posterior part missing. The jaw is U-shaped, with the anterior margin parabolic in outline. As in the lower jaws, the upper jaw consists of coarsely crystalline black material.

The hood area is approximately 25 mm long and shows some thickening in the apical region, although the tip is broken. In dorsal view, the hood is strongly convex, both longitudinally and transversely, nearly forming a dome. Two well-defined radial flexures originate at the apex and diverge posteriorly at an angle of 70°, each eventually fading into the longitudinal axis of one of the wings.

Posterior of the thickened apex, the hood is preserved as a black film forming a relatively flat surface that joins together both wings of the jaw. As indicated by the more or less complete right wing, the wings reach a maximum width of approximately 25 mm. Both wings preserve longitudinal wrinkles and cracks.

Part of what is presumably the lower jaw is preserved in the same concretion (fig. 22). It appears as a layer of coarsely crystalline black material. The fragment is approximately 50 mm long and 80 mm wide but is not well enough preserved for description. There is no evidence of a radula.

AMNH 47278 and 47279 are fragments of what appear to be parts of upper jaws (fig. 23). AMNH 47279 (fig. 23A) is better preserved and is approximately 90 mm long and 25 mm wide and occurs in a maroon-colored calcareous concretion. Several large pieces of *Placenticeras* shell are preserved in the same concretion, although it is impossible to demonstrate that the jaw occurs inside a body chamber. The specimen is probably one of the two long wings that make up the upper jaw. Both ends of it are broken off, but it most likely represents the right wing. It is fairly flat with gently sloping sides and consists of coarsely crystalline black material. Longitudinal striae cover one-half of the specimen along its entire length, and are spaced at intervals of approximately 1.5 mm.

Placenticeras costatum

Pierre Shale, Colorado

A lower jaw occurs inside the body chamber of an incomplete adult (USNM 529075), missing part of the outer whorl (figs. 24, 25). Based on the rate of whorl expansion, the shell would have attained a diameter of approximately 195 mm. The jaw lies in the back of the body chamber on the right side. It is convex and approximately 25 mm long; the left wing is approximately 15 mm wide (W/L of the left wing = 0.6). The ratio of shell diameter (restored) to jaw length is 7.75. The jaw is folded along the midline, and more of the left wing is exposed than the right wing. Part of the jaw is covered with a black film but the jaw appears to extend beyond the edge of the black color.

The apex is slightly projected, and the rest of the anterior margin is fairly straight. The apical angle is approximately 140°. A slit appears on the midline and is filled with matrix. It is flanked by ridges, which broaden posteriorly, and which are themselves bordered by radial depressions. Starting approximately 10 mm from the tip, the two wings of the jaw are faulted with the right wing thrown upward. Part of the outer surface of the jaw bears an orange crystalline layer.

Metaplacenticeras subtilistriatum

Yasukawa Formation, Hokkaido

UMUT MM28896 is a lower jaw that occurs in a calcareous concretion with numerous plant fragments and shells (figs. 26E–H, 27). It is 25.4 mm long and the left wing is 13.4 mm wide (W/L of the left wing = 0.53). The jaw is folded along the midline with most of the right wing smashed in.

The anterior margin is slightly indented on each side of the apex. The apical angle is approximately 130°. There is a step-like feature near the anterior margin but most of the space between this feature and the anterior margin is filled in with coarsely crystalline black material eliminating any relief.

A narrow slit 0.15 mm wide is present at the apex and extends approximately 1.5 mm, after which it is covered in black material for a distance of 1 mm. It is subsequently replaced by a narrow groove 3 mm long, which is bordered by narrow ridges on each side, posterior of which, the jaw is torn apart.

The left wing consists of multiple layers. The basal layer is the steinkern, which is covered with coarsely crystalline black material. This layer is very thick in the median region and shows a honeycomb-like texture. It is overlain by a very thin sheath of brown-

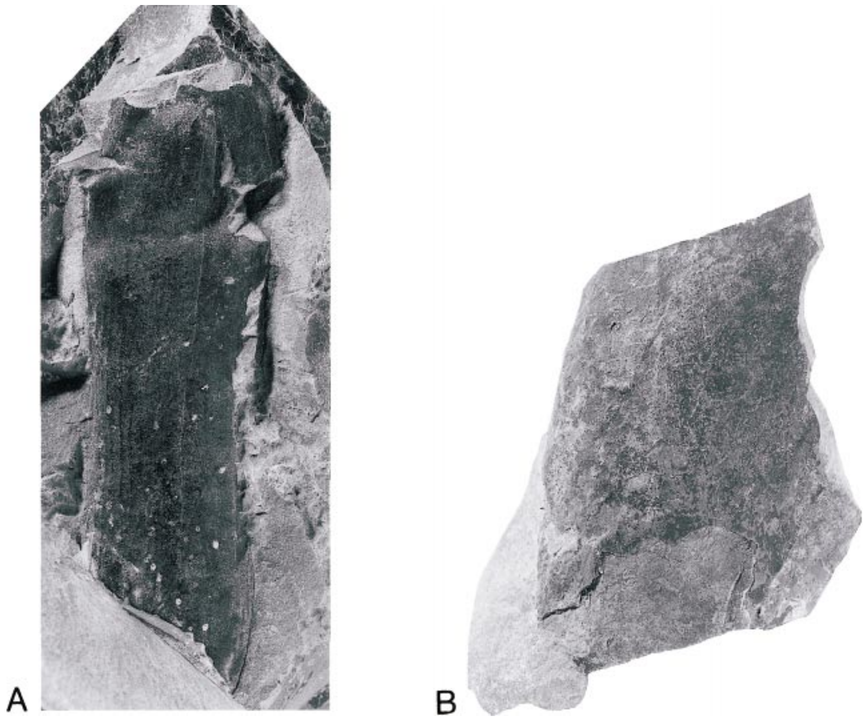


Fig. 23. Parts of upper jaws (?) of *Placenticeras meeki* Böhm, 1898, or *Placenticeras costatum* Hyatt, 1903, ×1. **A.** AMNH 47279, *Baculites reesidei* Zone, Bearpaw Shale, Travers Dam, Alberta, Canada. **B.** AMNH 47278, *Baculites cuneatus* Zone, Bearpaw Shale, Welling, Alberta, Canada.

ish, finely crystalline material. This is overlain, in turn, by patches of a white crystalline layer approximately 8 μm thick, which seems to be composed of elongate sections forming an angle of 45° with the midline (figs. 26F, 27). This layer may actually consist of two sublayers.

Ridges and grooves are visible on the black layer on most of the left wing, and parallel the posterior margin, becoming coarser and more widely spaced posteriorly. The posterior one-half of the wing also shows irregular bumps suggesting plastic deformation. The steinkern shows a fingerprint-like pattern, reflecting the texture of the overlying black material.

UMUT MM28897 is an isolated lower jaw preserved in a piece of calcareous concretion with plant and shell fragments (figs. 26A–D, 28). It is 17 mm long and the left wing is approximately 9 mm wide (W/L of the left wing = 0.53). Most of the jaw is intact, but the posterior portion is crumpled and ragged. The jaw is composed of three layers: the steinkern, an overlying layer of coarsely crystalline black material, and a top layer of finely crystalline yellowish material (calcite, see below) in the form of two plates (aptychi).

The apex is pointed, and the anterior margin is slightly indented on each side. The apical angle is approximately 120°. The usual step-like feature near the anterior margin is not present and is presumably covered over. The apex shows a slit that extends approximately 4 mm along the midline. This slit is filled in with matrix, but black material is visible underneath—at least, at the posterior end of the slit. A groove is present on the rest of the jaw and is partly lined with black material, indicating that the two wings are continuous across the groove. The two calcitic plates (aptychi) terminate at the midline in a well-defined beveled edge. Thus, the underlying black layer is continuous across the middle, whereas the overlying calcitic plates are separate.

The calcitic plates (aptychi) are ornament-

Fig. 24. *Placenticeras costatum* Hyatt, 1903, with lower jaw (right arrow) in body chamber, USNM 529075, U.S. Geological Survey loc. D1353, *Baculites cuneatus* Zone, Pierre Shale, Grand County, Colorado. The left arrow indicates the base of the body chamber, ×1.

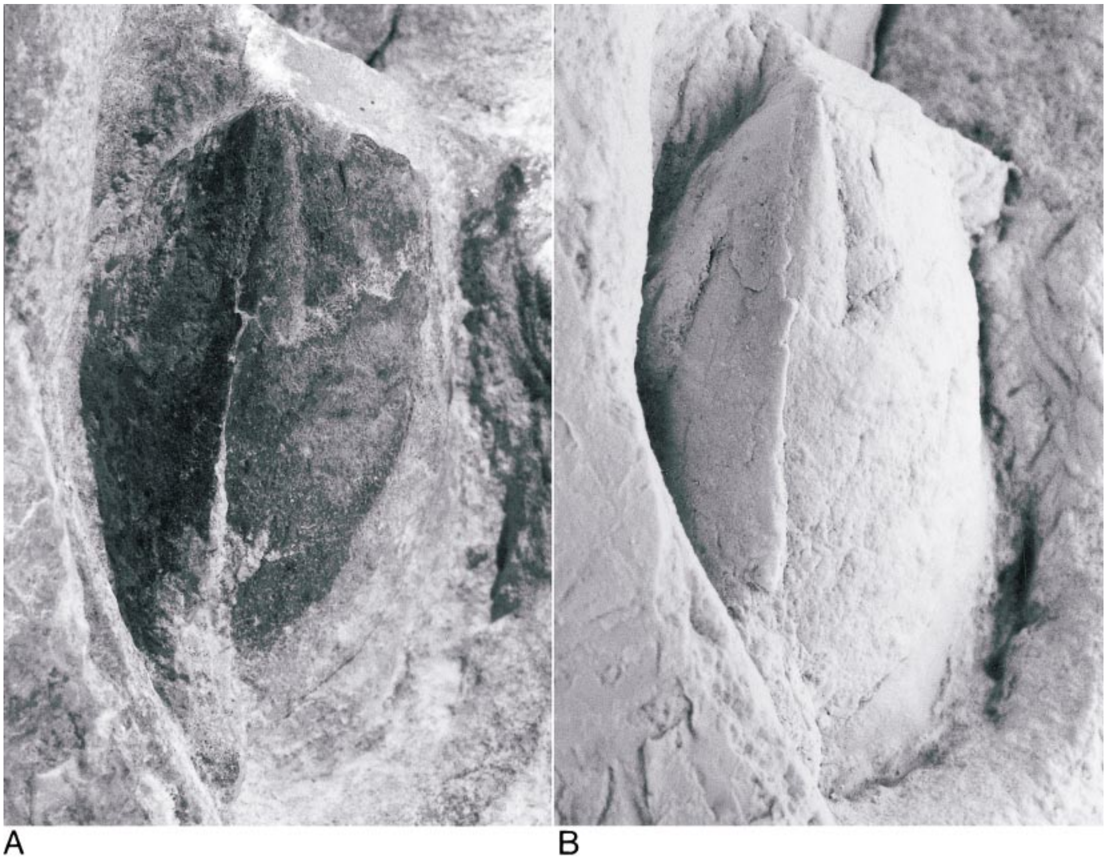


Fig. 25. Close-up of the lower jaw of *Placenticeras costatum*, Hyatt, 1903, USNM 529075 (see fig. 24), ventral view, anterior end on top, ×3. **A.** Uncoated. **B.** Coated.

ed with ridges and grooves that parallel the posterior margin. The ornament becomes coarser, more irregular, and more widely spaced toward the posterior end. Longitudinal striations are also present. The underlying black layer shows the same ornament as the aptychi, but the longitudinal striations are more prominent.

COMPOSITION AND MICROSTRUCTURE OF THE JAWS

The lower jaws of placenticeratids consist of several layers. The same layers are probably present in the upper jaws, but there are not enough data to confirm this.

The surface of the steinkerns of the lower jaws of AMNH 47275 and 47277 shows a network of small, irregular craters, each approximately 80 μm long (fig. 29C, D). Tanabe and Fukuda (1983) noted a similar pattern on the dorsal surface of the outer lamella of the lower jaw of the Late Cretaceous ammonite *Gaudryceras*. They interpreted this pattern as an impression of beccublast cells, which attach the jaws to the musculature (see Dilly and Nixon, 1976), as in the jaws of coleoids and modern *Nautilus*. If the pattern in *Placenticeras* also reflects the imprints of beccublast cells, it would imply that the dorsal surface of the outer lamella of the lower jaw was attached to the jaw muscles.

The principle component of the placenticeratid lower jaws is coarsely crystalline black material with a honeycomb-like texture. This material probably represents diagenetically altered chitin, which is very resistant to decay (Lehmann, l981; Kear et al., 1995). X-ray diffraction analysis of samples of this material from AMNH 47275, UWO.KMC.100126, BHMNH 5456, and BHMNH 5454b indicates that it consists of magnesium enriched calcite and amorphous material (organic compounds). In addition, the sample from AMNH 47275 contains pyrite, and the sample from UWO.KMC. 100126 contains siderite and illite, which probably reflect the composition of errant pieces of matrix.

The thickness of the coarsely crystalline black material varies on different parts of the lower jaw. It is thickest in the anterior region—for example, it is 0.3 mm thick at this point in AMNH 47277. However, no specimen is sufficiently well enough preserved to measure the thickness on the entire jaw. Compaction and exfoliation of the chitin after death have undoubtedly altered the original thickness of this layer. As a point of reference, the thickness of the lower jaw of *Nautilus belauensis* Saunders, 1981, is approximately 0.5 mm near the posterior end.

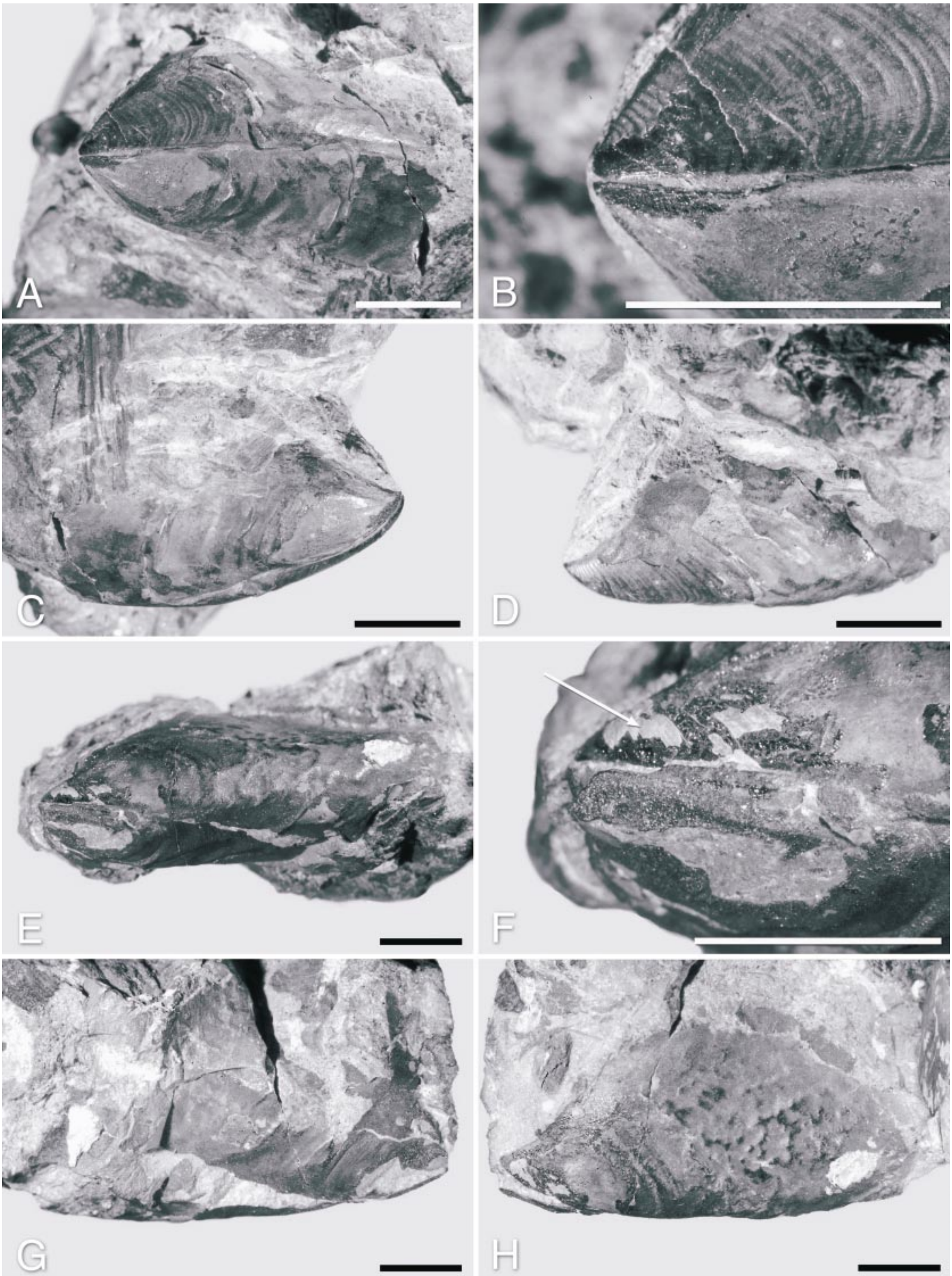
Clear to yellowish crystals are commonly embedded in the interstices in the black material. These crystals also occur as elongate struts on each side of the central boss at the junction of the inner and outer lamellae in BHMNH 5456 (fig. 20). Analysis of this material indicates that it consists of calcite enriched in magnesium. The calcitic crystals embedded in the black material are probably diagenetic in origin. However, it is conceivable that the struts represent an original calcitic thickening in the apical region of the jaw.

In many specimens, there is a finely crystalline yellowish to golden material overlying the black layer. X-ray diffraction analysis of a sample of this material from AMNH 47275 indicates the presence of calcite enriched in magnesium, organic compounds, and pyrite. This layer demarcates the junction between the inner and outer lamellae in AMNH 47277 (fig. 7), suggesting that although it may be diagenetically altered, this layer actually represents an original deposit.

A thin outer calcitic layer is present in the two specimens of *Metaplacenticeras subtilistriatum*. In UMUT MM28896, this layer is only 8 μm thick and shows a fibrous microstructure (fig. 29A,B). It is covered with fine ridges and grooves that parallel the posterior margin. X-ray diffraction analysis of samples of this material from both specimens indicates that it consists of magnesium enriched calcite. In addition, the sample from UMUT MM28897 contains quartz, which probably reflects the composition of errant pieces of matrix. A crystalline layer also covers part of the right wing in BHMNH 5456 (fig. 20). However, unlike the layer in *M. subtilistriatum*, the layer in BHMNH 5456 is very thick (1.2 mm), pockmarked due to weathering, and devoid of any morphological features. It probably represents a diagenetic deposit. X-ray diffraction analysis of this layer reveals the presence of calcite.

A calcitic layer comparable to that in *Metaplacenticeras* is absent in the *Placenticeras* jaws from North America. Interestingly, the North American jaws sometimes occur in association with ammonite shells retaining their original aragonitic composition. Based on the differential solubility of calcite versus aragonite, one would have supposed that the aragonite would have dissolved before the calcite, a fact that is commonly cited in studies of ammonite jaws (Morton and Nixon, 1987). Thus, the absence of a calcitic layer in these jaws would suggest that such a layer never existed at all.

We propose an alternative explanation, however. We suggest that a thin calcitic layer also covered the lower jaws of *Placenticeras* from North America, but that this layer was simply not preserved. This argument is based on the close affinity of *Metaplacenticeras* and *Placenticeras*, and homology with the lower jaws of closely related ammonites (see below). Judging from the jaws of *M. subtilistriatum*, the calcitic layer in *Placenticeras* would also have been very thin and fibrous, unlike the thick aragonitic layer of the outer shell. As a consequence, the calcitic layer of the lower jaw would have been very friable and easily broken. In addition, jaws, as internal structures embedded in the buccal bulb, experienced a different taphonomic history from that of the outer shell. The microenvironment created within the buccal bulb after death may have promoted local dissolution of the calcite compared with the conditions affecting the outer shell. Indeed, in their study of the lower jaws of scaphitid ammonites from the Upper Cretaceous Fox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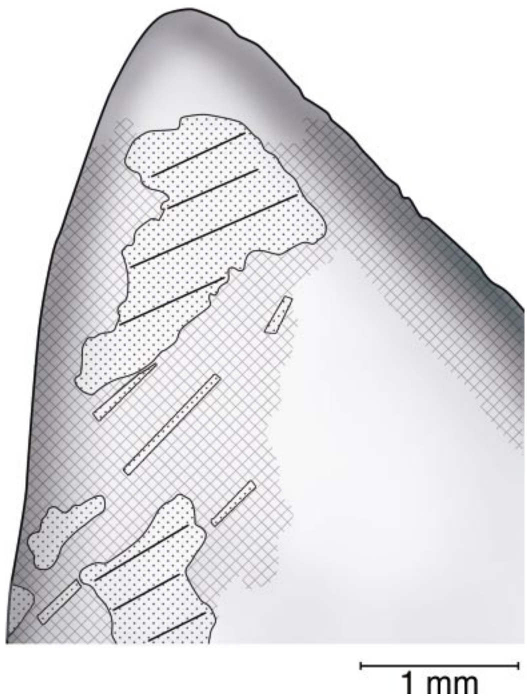

Fig. 27. Drawing of the left wing of the lower jaw of UMUT MM28896 (see fig. 26E–H), showing pieces of the outer calcitic layer (dotted area). Texture as defined in figure 4.

Hills Formation, Landman and Waage (1993: 60) noted that ''The calcitic layer is usually absent on even slightly weathered surfaces, and in freshly exposed specimens it may be partly or entirely absent as a result of removal prior to formation of the enclosing concretion.''

PRESERVATION OF THE JAWS

The rarity of placenticeratid jaws poses the more general question of what determines whether or not ammonite jaws are, in fact, preserved. The probability of jaw preservation depends on a number of factors including (1) how the animal died (quietly or by a violent predatory attack that smashed the shell to smithereens), (2) if and how long the shell floated after death, (3) how quickly the soft body disintegrated and detached from the shell, and (4) the environment of deposition (pH, redox, oxygen level, current activity, and rate of sedimentation). The length of the body chamber (e.g., brevidome, mesodome, or longidome) and the orientation of the aperture would have additionally affected the likelihood that the jaw remained in the body chamber after death. In general, ammonites with longer body chambers and upwardly facing apertures would have preferentially favored the preservation of jaws inside the body chamber (although the position of the jaws always would have been near the aperture during life). The fact that only one of our jaws is preserved inside the body chamber indicates how rare this phenomenon is.

Our sample contains only one clearly recognizable upper jaw and two possible fragments, whereas there are at least 14 lower jaws. The disproportionate number of lower jaws over upper jaws is common in other ammonites as well—for example, scaphites (Landman and Waage, 1993). This preservational bias may simply reflect the larger size and bulkier shape of lower jaws.

There is no evidence of a radula in any of our jaw specimens. The only ones in which a radula conceivably could have been present are UWO.KMC.100125 and 100126 and USNM 529075 in which both the upper and lower jaws are preserved, albeit not in life position.

The placenticeratid jaws we studied bear evidence of having undergone a variety of postmortem processes including compaction, breakage, folding, dissolution, and exfoliation. The lower jaws of *Placenticeras* show

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Fig. 26. Lower jaws attributed to *Metaplacenticeras subtilistriatum* (Jimbo, 1894), Hokkaido, Japan. **A–D.** UMUT MM28897. **A.** Ventral view, anterior end on left, showing undulations paralleling the posterior margin. **B.** Close-up of the anterior end. **C.** Right lateral view. **D.** Left lateral view. E–H. UMUT MM28896. **E.** Ventral view, anterior end on left. The right wing is crumpled. **F.** Close-up of the anterior area showing fragments of the calcitic plate (arrow). **G.** Right lateral view. **H.** Left lateral view. Scale bar = 5 mm.

Fig. 28. Drawing of part of the anterior end of UMUT MM28897 (see fig. 26A–D) showing the ridges paralleling the posterior margin. Texture as defined in figures 4 and 27.

a range in degree of compaction. Most of the jaws are flattened out, as shown in TMP 87.119.19 (fig. 9), TMP 92.42.21 (fig. 11), and AMNH 47275 (fig. 3). Among the jaws from Canada, only UWO.KMC.100125 (fig. 14) and AMNH 47276 (fig. 5) retain some of their original curvature. In contrast, all of the jaws from South Dakota are strongly convex, with BHMNH 5041 (fig. 15), perhaps approaching the shape during life.

In addition to compaction, nearly all of the larger placenticeratid jaws are torn. The middle part of the posterior portion is commonly missing, as shown in TMP 87.119.19 (fig. 9), AMNH 47275 (fig. 3), AMNH 47277 (fig. 6), and BHMNH 5041 (fig. 15). The posterior margins of the wings are usually ragged, either with a finely scalloped edge, as in BHMNH 5454b (fig. 17B), or with larger chunks missing, as in BHMNH 5041 (fig. 15). This damage may have been caused by predation, perhaps by an attack of a mosasaur, evidence of which sometimes appears on placenticeratid shells from the Western Interior of North America (Kauffman, 1990; Tsujita and Westermann, 1998). Alternatively, it may be due to postmortem destruction. In experiments on the taphonomy of modern coleoid jaws, Kear et al. (1995) reported that the posterior margins of the jaws suffered fracturing and disintegration approximately 10 weeks after death.

The large lower jaws of *Placenticeras* also exhibit indications of postmortem plastic deformation. Creases occur along the lateral margins, as shown in AMNH 477275 (fig. 3) and TMP 87.119.19 (fig. 9). In addition, many specimens display folds, bumps, and wrinkles, as shown in AMNH 47276 (fig. 5) and AMNH 47277 (fig. 6). The presence of these features suggests that the jaws were flexible enough after death to be twisted and folded.

Postmortem changes in the jaws imply that care must be taken in the interpretation of their morphology. For example, the V-shaped junction of the two lamellae in the anterior portion of the lower jaw must have resulted from the inner lamella ‘‘punching’’ through the outer lamella on the ventral side. This junction is especially conspicuous when part of the inner lamella has worn away (fig. 20). In addition, the step-like feature on the anterior margin where the two lamellae are

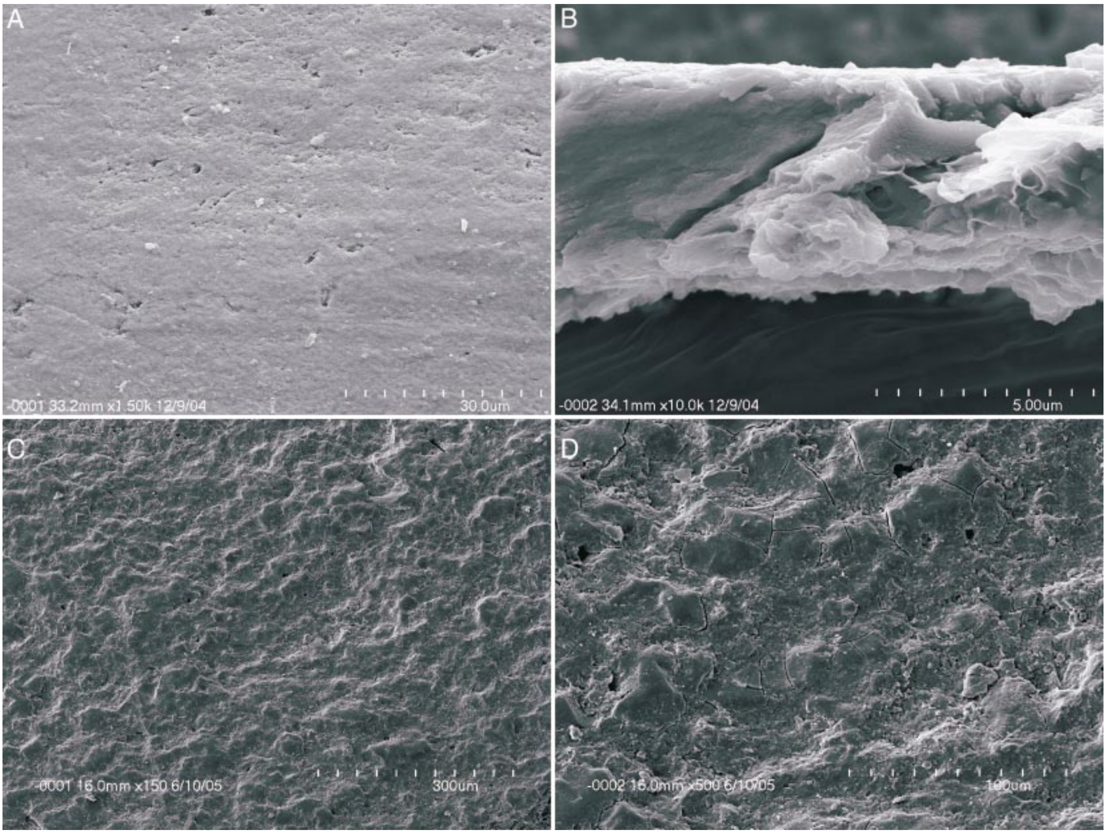

Fig. 29. A,B. Calcitic layer on the ventral side of the outer lamella of the lower jaw of UMUT MM28896 (see figs. 26E–H, 27). **A.** The surface is marked with growth lines. **B.** Cross section of the calcitic layer with fibrous microstructure. C, D. Dorsal surface of the outer lamella of the lower jaw of AMNH 47277 (see figs. 6, 7). **C.** The surface exhibits a network of small irregular craters, perhaps reflecting the impression of beccublast cells. **D.** Close-up of C.

doubled over is the result of breaking off of part of the inner lamella (fig. 17B). Finally, features on the ventral surface of some lower jaws actually reflect the morphology of the inner lamella because the outer lamella has broken off. For example, in UWO.KMC. 100125 (fig. 14), the ventral surface of the lower jaw immediately posterior of the V-shaped junction of the two lamellae lacks a median ridge. However, this area reflects the morphology of the inner lamella rather than that of the outer lamella.

MORPHOLOGY OF PLACENTICERATID JAWS

The jaws of placenticeratids are reconstructed in figure 30, including ventral and dorsal views. The ventral surface of the lower jaw is illustrated with and without calcareous plates (aptychi).

The jaws of *Placenticeras* attain lengths of up to 95 mm (AMNH 47275). The specimen inside the body chamber of *Placenticeras costatum* (USNM 529075) is smaller (25 mm long). The ratio of shell diameter (restored) to jaw length in this specimen is 7.75. Using this ratio, the size of the shell with the largest jaw (95 mm) would have been approximately 75 cm in diameter, which is not an unreasonable estimate. However, the relationship between shell diameter and jaw length is probably not strictly linear (Morton and Nixon, l987).

In flattened specimens, the shape of the lower jaw is subquadrate. In specimens that retain some or all of their original curvature,

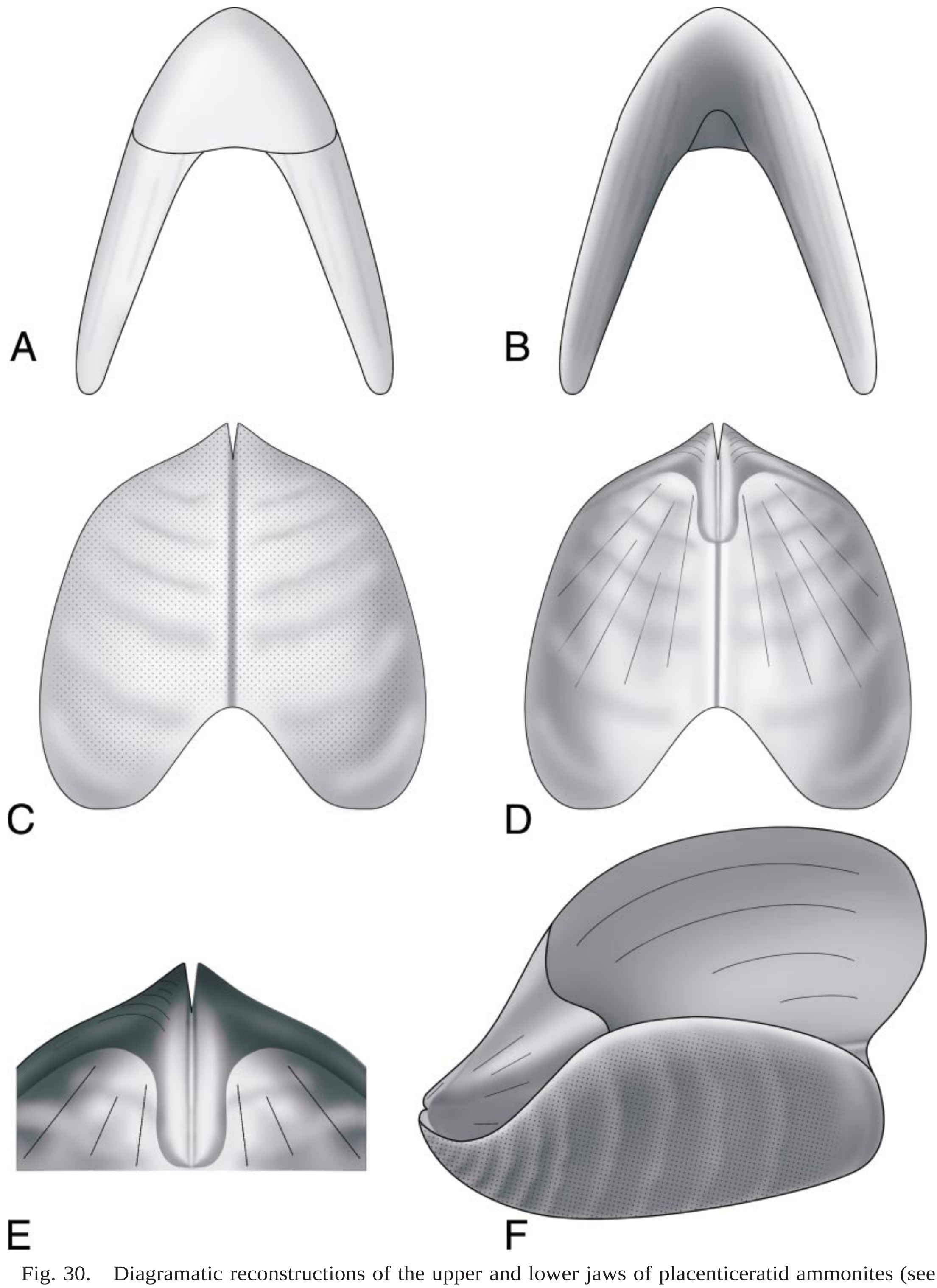

Fig. 30. Diagramatic reconstructions of the upper and lower jaws of placenticeratid ammonites (see fig. 2 for orientation and terminology). **A.** Dorsal view of the upper jaw. **B.** Ventral view of the upper jaw. **C.** Ventral view of the lower jaw with thin calcitic aptychi (dotted area). **D.** Ventral view of the

the middle portion is gently convex, and the sides bend steeply dorsally (fig. 30F). The apex is weakly projected, both anteriorly and dorsally, and the anterior margin is slightly indented on each side. The ratio of jaw width to jaw length is variable, reflecting different states of preservation and ranges from 0.75 to l.l in nearly complete specimens such as BHMNH 5041 (fig. 15) and 5454a (fig. 18). The ratio of width to length of individual wings ranges from 0.60 to 0.75. The value of the apical angle also depends on the degree of compaction, and in specimens that are still convex, it ranges from 140 to 160°.

A small indentation appears at the apex of the lower jaw (fig. 30C–F). In most specimens, this indentation develops into a midline slit that extends a distance of 10–15 mm before narrowing down completely. In AMNH 47275 (fig. 3B), the edges of the slit are razor sharp, whereas in AMNH 47277 (fig. 7), they are ragged. A narrow ridge develops at the posterior end of the slit in BHMNH 5454a (fig. 18) and 5456 (fig. 20). Based on comparisons with the jaws of closely related ammonites (see below), it is clear that the slit is what remains after part or all of this ridge has broken off. This explains why the edges of the slit are sometimes ragged and other times razor sharp.

The midline ridge rests on a thickened, elongate boss of coarsely crystalline black material flanked by grooves on each side (these features correspond on the dorsal side to a midline depression flanked by ridges). The midline ridge and the surrounding black material (chitin) are part of the inner lamella. In more complete specimens, the grooves are filled in with chitin, eliminating any relief and resulting in an even surface on the ventral side.

The outer lamella joins the inner lamella 5–10 mm posterior of the end of the ridge (fig. 30D,E). The junction between them forms a V- or U-shaped outline, with the point of the V or U centered on the midline. This junction is usually emphasized by grooves on each side of the central boss. For example, in BHMNH 5456 (fig. 20), in which some of the chitin of the inner lamella has eroded away, the outer lamella forms a raised edge above the inner lamella. In contrast, in AMNH 47277 (fig. 7), in which most of the chitin of the inner lamella is still intact, the V-shaped outline does not show much relief.

The outer lamella intersects the inner lamella at a slight angle to the anterior edge (fig. 30D). In BHMNH 5456 (fig. 20) and 5454b (fig. 17B), in which most of the chitin of the inner lamella has eroded away, there is a band approximately 3 mm wide that ends posteriorly in a step-like feature that represents the edge of the outer lamella. This band exposes the dorsal surface of the inner lamella and is ornamented with thin striations that approximately parallel the anterior margin (fig. 30F). In TMP 87.119.19 (fig. 9B) and UMUT MM28896 (fig. 26F), the thick chitin of the inner lamella is still present; as a result, the step-like feature is absent, so that the entire anterior margin is smoothly continuous. This corresponds to the area in which the two lamellae are doubled over.

The inner lamella extends approximately one-half the length of the outer lamella. A space develops between the two lamellae on each side of the midline, although they are fused together on the lateral margins. At the midlength of the jaw, the two lamellae are completely separated except on the sides.

The outer lamella of the lower jaw is continuous across the middle and forms a midline ridge, which is effectively a continuation of the ridge on the inner lamella. The midline ridge on the outer lamella is visible in BHMNH 5456 (fig. 20) in which the ventral surface of the outer lamella is well preserved just posterior of the junction of the inner and outer lamellae. As shown in UWO.KMC. 100125 (fig. 14) and, to a lesser extent, in TMP 99.84.2 (fig. 12), the ridge on the outer lamella bears a central groove and extends the entire length of the jaw. (These features

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lower jaw with the aptychi removed. Note the U-shaped junction between the inner and outer lamellae. **E.** Close-up of the anterior end of the lower jaw with the aptychi removed, showing the midline ridge. **F.** Dorsolateral view of the lower jaw, exposing the dorsal surface of the inner lamella.

presumably correspond on the dorsal side to a midline groove with a central ridge.) In *Metaplacenticeras subtilistriatum*, the jaws are preserved with both wings folded together due in part to the presence of this narrow crease, which created a natural line of weakness along which the wings folded after death (fig. 26).

Commonly, the two wings of the lower jaw are torn apart along the midline posterior of the hood, as shown in BHMNH 5041 (fig. 15). In addition, as noted, the posterior edge is generally ragged, with pieces missing. However, the margin was probably originally bilolate, with the two wings protruding beyond the middle (fig. 30C, D, F).

A thin outer calcitic layer is present on parts of the lower jaws of both specimens of *Metaplacenticeras subtilistriatum* and represents the aptychi (fig. 26). Although they are now incomplete, the aptychi would have almost entirely covered the whole ventral surface of the jaw, obscuring the junction of the inner and outer lamellae. However, the plates may not have extended to the posterior and lateral margins. In other ammonites, the calcitic plates only cover 66% (Dagys et al., 1989) to 75–80% (Lehmann and Kulicki, 1990) of the underlying chitinous layer. Each plate ends in a beveled edge at the midline.

As discussed earlier, we argue that calcitic plates were also characteristic of the lower jaws of the genus *Placenticeras*, although these plates have not been found in any specimens from North America. The calcitic crystals commonly embedded in the black material of the lower jaws are probably of secondary origin. If calcitic plates existed in *Placenticeras*, then by homology with *Metaplacenticeras*, they would have rested against the narrow midline ridge of the outer lamella and would have covered nearly the entire ventral surface. It is possible that the elongate calcitic crystals in the apical region of BHMNH 5456 (fig. 20) represent an additional mineralized deposit in this area.

In *Metaplacenticeras subtilistriatum*, both the calcareous and chitinous layers of the outer lamella of the lower jaw are ornamented with ridges and grooves that parallel the posterior margin (figs. 26–28). These features become progressively coarser and more irregular toward the posterior end. Longitudinal striations are also present on both the calcareous and chitinous layers. Ridges and striations are less conspicuous on the lower jaws of *Placenticeras* but are visible in TMP 92.42.21 (fig. 11) and AMNH 47276 (fig. 5).

The best-preserved upper jaw (UWO. KMC.100126) is 95 mm long and is as long as the longest lower jaw (fig. 22). It consists of two widely divergent wings forming the inner lamella and a short reduced outer lamella. The two wings are narrow and converge anteriorly to a dome-shaped hood (fig. 30A). The apex is broadly rounded and the chitinous material is thicker in this area.

COMPARISON WITH JAWS OF OTHER AMMONITES

Summesberger et al. (1996) described small lower jaws associated with steinkerns of placenticeratids from the Upper Cretaceous black limestone of the Lipica Formation, Slovenia. The ammonites cannot be identified to species level because of poor preservation. Most of the jaws are isolated, but one is preserved inside the body chamber, and another is preserved just outside the body chamber. All of these jaws are flattened to some degree by compaction and are nearly as broad as they are long, with a small slit at the apex and a bilobate posterior margin. The apical angle is 100° in a relatively uncrushed specimen and ranges from 106 to

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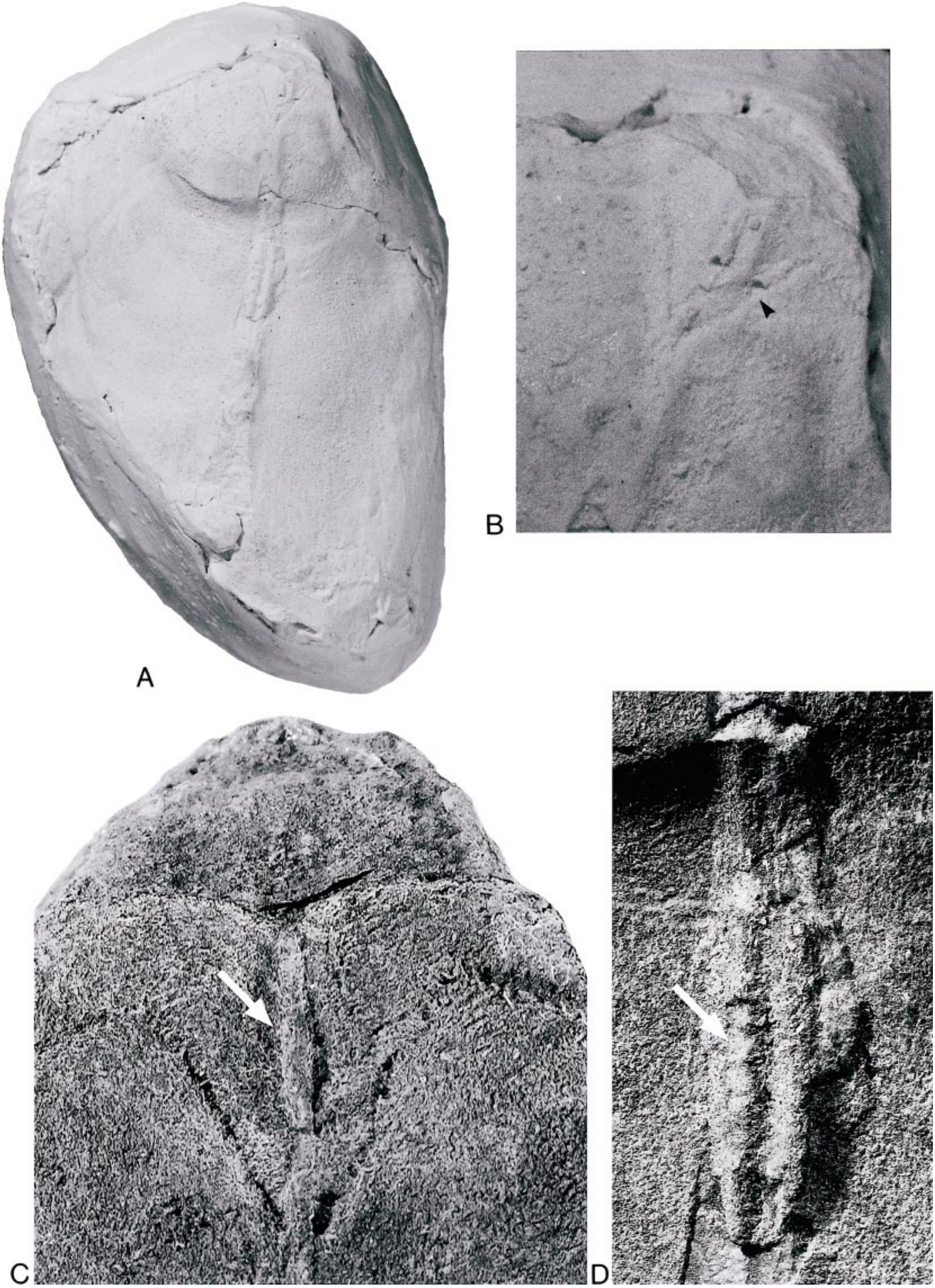
Fig. 31. Lower jaw attributed to *Neogastroplites cornutus* (Whiteaves, 1885) var. B Reeside and Cobban, 1960, USNM 129338, Mowry Shale, Park County, Wyoming. **A.** Ventral view of a plaster cast, anterior end on top, ×1. **B.** Close-up of the anterior area of the plaster cast showing the V-shaped junction between the inner and outer lamellae (arrow), ×3. **C.** Close-up of the anterior end of the actual specimen showing a narrow ridge along the midline (arrow), ×6.7. **D.** Close-up of the outer lamella of the actual specimen approximately 11 mm posterior of the junction between the inner and outer lamellae. The midline is marked by a midline ridge with a central groove (arrow), ×4.7.



130° in crushed specimens. The outer lamella is covered in part with a thin calcareous layer, and consists of two symmetric wings joined at the midline, which appears as a thin groove on the ventral side. Broad, evenly spaced undulations parallel the posterior margin and become progressively coarser toward the posterior end.

These lower jaws are very similar to the two lower jaws of *Metaplacenticeras subtilistriatum*, which also retain parts of a calcitic layer (fig. 26). In addition, the ornament in the Japanese specimens becomes progressively coarser toward the posterior end. The jaws from Slovenia are also similar in size and shape to the small lower jaw of *Placenticeras costatum* (figs. 24, 25). Of the larger placenticeratid lower jaws, only TMP 92.42.21 (fig. 11) preserves a few undulations paralleling the posterior margin.

Summesberger et al. (1999) reported two upper jaws possibly belonging to placenticeratids from the same strata. Both specimens are isolated and crushed. The better-preserved one is U-shaped with a slightly protruding apical tip. This jaw is very similar to UWO.KMC.100126 (fig. 22) from Alberta, although the Canadian specimen is much larger.

Gangopadhyay and Bardhan (1998) described lower jaws attributed to *Placenticeras* sp. and *Placenticeras kaffrarium* Etheridge, 1904, from the Upper Cretaceous Nodular Limestone Formation of central India. Two of the jaws occur inside the body chamber, and a third occurs just outside the body chamber. The jaws are convex in cross section, with a slightly projected rostrum. Part of a calcitic covering is preserved in one of the specimens. The outer surface of the jaws shows fine, closely spaced undulations paralleling the posterior margin. However, it is puzzling that there is no evidence of a midline groove on either specimen.

Jaws have been reported from several species in the superfamily Hoplitaceae, to which the placenticeratids belong. Reeside and Cobban (1960) described jaws of *Neogastroplites*, which they referred to as aptychi, from the Upper Cretaceous Mowry Shale of the U.S. Western Interior. These jaws are very well preserved and are similar to those of *Placenticeras*, even though *Neogastroplites* predates *Placenticeras* by approximately 25 million years.

One specimen of *Neogastroplites* bears a striking resemblance to the large lower jaws of *Placenticeras* from the Western Interior. USNM 129338 (Reeside and Cobban, 1960, pl. 20, figs. 2–4; listed as USNM 129328 in their caption; refig. as fig. 31) is a lower jaw attributed to *Neogastroplites cornutus* (Whiteaves, 1885) var. B Reeside and Cobban, 1960. It is approximately 90 mm long and 65 mm wide (W/L = 0.68) and approaches the size of many of our larger placenticeratid jaws. The specimen is convex in cross section, with the lateral margins bending dorsally. The surface is covered with thin longitudinal striations and broad folds paralleling the posterior margin. The apical end shows a V-shaped outline, indicating the junction of the inner and outer lamellae.

There are two features on this specimen that help elucidate the morphology of the placenticeratid jaws. First, the ventral surface of the inner lamella bears a narrow ridge along the midline. This ridge runs the entire length of the exposed inner lamella and even extends onto the outer lamella. It rests on an elongate boss consisting of thickened black material (chitin) studded with yellowish crystals, presumably calcite. This implies that the slit observed on the inner lamella of placenticeratid jaws actually represents the broken outline of a ridge, as previously discussed. Second, the outer lamella shows a prominent midline ridge with a central groove. The material of the jaw is continuous across the groove. This feature is identical to that observed on UWO.KMC.100125 (fig. 14).

USNM 129548 (Reeside and Cobban, 1960: pl. 45, fig. 7; refig. as fig. 32) is also similar to our placenticeratid lower jaws. It is attributed to *Neogastroplites americanus* (Reeside and Weymouth, 1931) var. A Reeside and Cobban, 1960, and is approximately 35 mm long and 35 mm wide (W/L = 1.0). A slit 2 mm wide appears at the apex and extends approximately 9 mm. The edges of the slit are very sharp and are reminiscent of those in AMNH 47275 (fig. 3) and BHMNH 5041 (fig. 15). The jaw seems to be joined together immediately posterior of the slit, but thereafter the two halves of the jaw are fault-

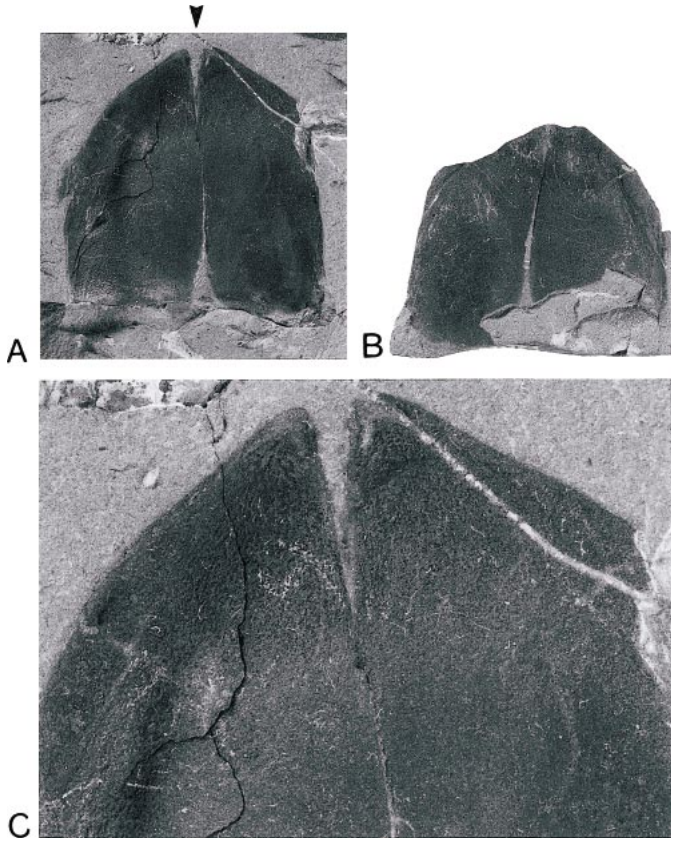


Fig. 32. Part and counterpart of a lower jaw attributed to *Neogastroplites americanus* (Reeside and Weymouth, 1931) var. A Reeside and Cobban, 1960, USNM 129548, Mowry Shale, Park County, Wyoming. **A.** Overall view of the negative half showing a slit at the apex (arrow), ×1. **B.** Overall view of the positive half. The sides are bent dorsally and display longitudinal creases, ×1. **C.** Close-up of the anterior area in A, ×2.9.

ed with respect to each other. The jaw is composed of a honeycomb-like material without a calcitic layer.

USNM 129546 (Reeside and Cobban, 1960, pl. 45, figs. 8, 9; refig. as fig. 33) is attributed to *Neogastroplites americanus* var. A. It is approximately 45 mm long and 25 mm wide (W/L = 0.56). A narrow median groove with a central ridge appears on the negative half of the jaw and corresponds to a median ridge with a central groove on the positive half. The lateral margins of the jaw preserve longitudinal creases.

USNM 129547 (Reeside and Cobban, 1960: pl. 45, fig. 6; refig. as fig. 34) is an upper jaw 22 mm long, with most of the right wing and hood preserved. It is attributed to *Neogastroplites americanus* var. A. Aside from its smaller size, it is nearly identical to the upper jaw of *Placenticeras* from Alberta (fig. 22). It is U-shaped, with a slightly projecting apex.

In a broader context, the jaws of placenticeratids are similar to those of other members of the aptychus-bearing ammonites known as the Aptychophora Engeser and Keupp, 2002. Although differences in preservation obscure this similarity, the ventral surface of the outer lamella of the lower jaws of placenticeratids bears a pair of calcitic plates (aptychi) and a midline ridge with a central groove, both of which are unique features of the Aptychophora.

There are many descriptions of aptychus-type jaws, most of which focus on the morphology of the aptychi themselves. In con-

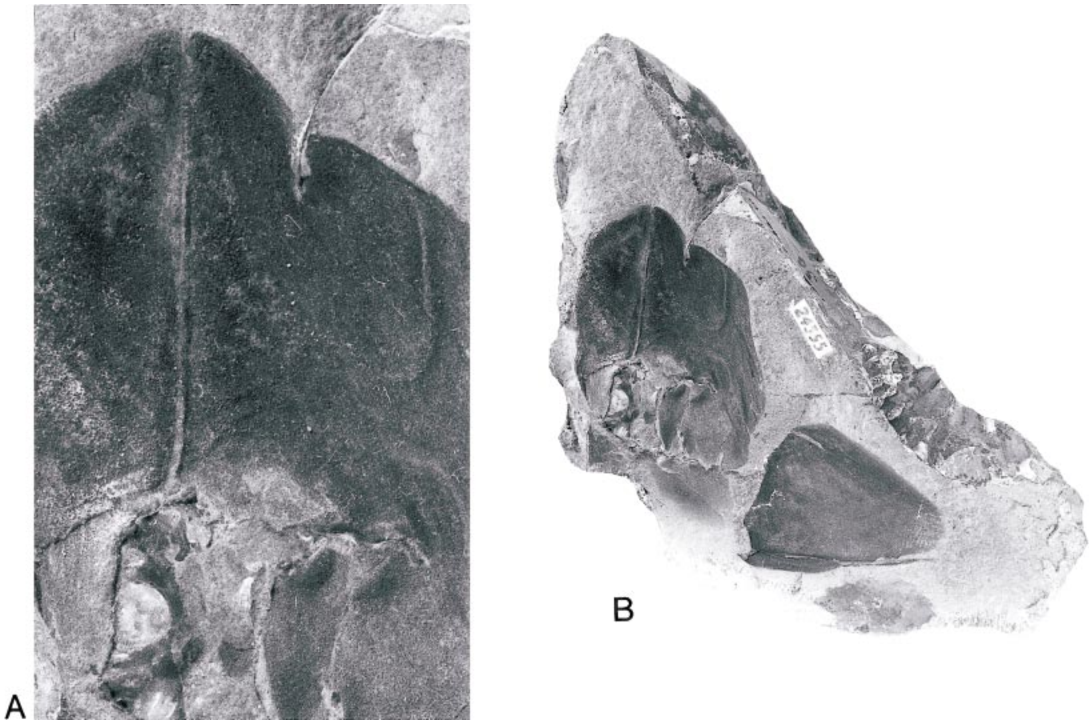


Fig. 33. Lower jaws attributed to *Neogastroplites americanus* (Reeside and Weymouth, 1931) var. A Reeside and Cobban, 1960, USNM 129546, Mowry Shale, Park County, Wyoming. **A.** Close-up of the anterior end (negative half of the specimen), ×3. **B.** Overall view of chunk with two lower jaws. The jaw on the left is illustrated in A, ×1.

trast, the chitinous parts of the jaws have not received as much attention (for exceptions, see Tanabe and Fukuda, 1987; Dagys et al., 1989; Doguzhaeva and Mikhailova, 2002). This is due to the fact that in jaws with thick aptychi, the only way to study the chitinous part is to section the jaw or to rely on fortuitous breaks. In jaws with thin aptychi, the chitinous layer may be partially exposed at the surface, but the preservation may be so

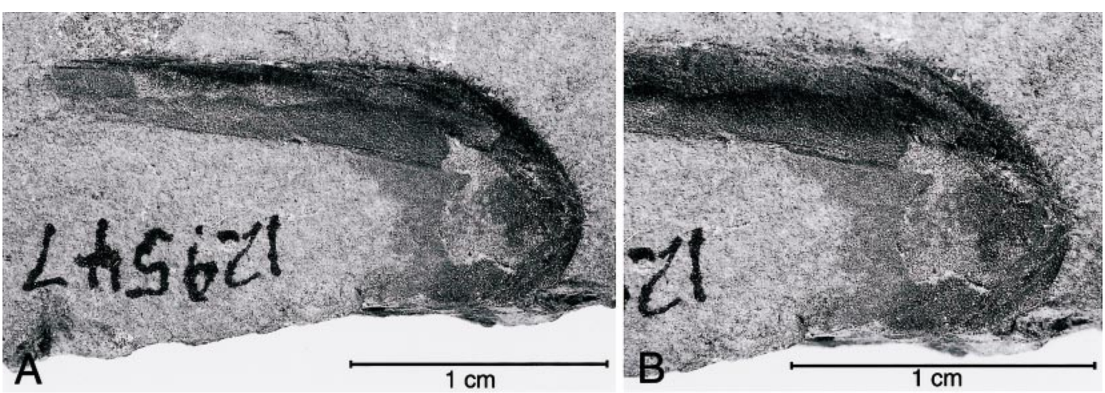


Fig. 34. Upper jaw attributed to *Neogastroplites americanus* (Reeside and Weymouth, 1931) var. A Reeside and Cobban, 1960, USNM 129547, Mowry Shale, Park County, Wyoming. **A.** Ventral view, anterior end on right, ×1. **B.** Close-up of anterior end, ×3.

poor that no details of the morphology are visible. Therefore, it is important to examine as many specimens as possible to obtain an overall picture.

One of the features of the chitinous parts of ammonite jaws that has not yet been well documented is the median ridge on the ventral surface of the inner lamella of the lower jaw. It appears at the posterior end of the midline slit in BHMNH 5454a (fig. 18) and 5456 (fig. 20) but is only well exposed in USNM 129338 (fig. 31). Interestingly, this ridge is not dissimilar to a structure described on the lower jaws of ceratites. Dagys and Dagys (1975) described an ''apical septum'' between the two lamellae of the lower jaw and Dagys and Weitschat (1988) later referred to this feature as a ''lateral ridge'', stating that it was only visible in casts. Further research is required to determine if this feature is homologous to that in placenticeratids.

Once differences due to preservation are eliminated, the actual variation among ammonite jaws can be better evaluated, providing insights into their evolution. Several different types of lower jaws have been identified, including the anaptychus-type, rhynchaptychus-type, and aptychus-type. In the anaptychus-type, the ventral surface of the outer lamella lacks a midline groove, although the ridges that parallel the posterior margin sometimes show a flexure at this point (Lehmann, 1970; Dagys and Dagys, 1975; Dagys et al., 1989). The ventral surface of the rhyncaptychus-type jaw is similar to that of the anaptychus-type jaw except for the presence of a thick calcareous covering on the anterior end (Tanabe et al., 1980; Tanabe and Landman, 2002). In contrast, the ventral surface of the outer lamella of the aptychus-type jaw has a midline ridge with a central groove and a pair of aptychi (Engeser and Keupp, 2002).

A ''transitional form'' between anaptychus and aptychus type-jaws has been identified in Late Cretaceous desmoceratid ammonites (Tanabe, 1983; Tanabe and Landman, 2002). The outer lamella of the lower jaw is characterized by a midline ridge with a central groove and a thin calcareous layer. This jaw resembles that of *Placenticeras* and is simply an aptychus-type jaw with thin calcitic plates. Similarly, Tanabe and Landman (2002) described an anaptychus-type jaw from the Late Cretaceous ammonite *Menuites*, another member of the Desmocerataceae. They noted the absence of a median ridge on the outer lamella of the lower jaw. However, this absence is probably due to poor preservation, suggesting again that the jaw is actually an aptychus-type with thin calcitic plates. These lower jaws, in addition to those of *Placenticeras*, highlight the variation within the traditional aptychus-type jaw.

FUNCTION OF THE JAW

The lower jaws of placenticeratids are basically similar to those in most other Ammonitina. They are broad and covered ventrally with thin calcitic plates, although these plates may not have extended to the lateral and posterior edges of the jaw. However, the placenticeratid jaws are distinguished by their sheer size. In *Placenticeras meeki* and *P. costatum*, the upper and lower jaws attain lengths of as much as 95 mm. In addition, the anterior portion of the lower jaw is characterized by a thickened layer of chitin. In some specimens, this region also contains calcitic crystals, which may have provided additional strength.

Although thick aptychi may have functioned as opercula in some ammonites, the thin plates in placenticeratid jaws seem unlikely to have served this purpose. It is worth noting that in modern *Nautilus*, the wings of the lower jaw are covered with a thin calcareous layer 50–75 μm thick (Fukuda, personal commun. in Kanie, 1982). The lower jaw of *Nautilus* does not, of course, function as an operculum, and the calcareous layer on it must simply help strengthen the jaw. Such a layer may have served a similar purpose on the lower jaws of placenticeratids.

There is no direct evidence about the feeding habits of placenticeratid ammonites. Several morphological features of the jaws suggest that these structures were designed for biting and cutting, a function similar to that proposed for the jaws of *Reesidites* by Tanabe and Fukuda (1987). These features include (1) a slightly projecting apex; (2) a thickened chitinous area on the anterior portion, possibly reinforced with a calcitic deposit at the apex of the lower jaw; (3) a thin calcitic layer covering the ventral surface of the lower jaw providing additional strength; and (4) the large surface area on the dorsal side of the outer lamella of the lower jaw, which would have provided ample space for muscular attachment (see Tanabe and Fukuda, 1983). As described in other ammonites, the upper jaw would have been enclosed within the lower jaw, with the beak of the upper jaw sliding smoothly against the edge of the inner lamella of the lower jaw.

In contrast, these jaw features are less consistent with a shovel-like function of the lower jaw for collecting and straining out plankton, as proposed by Lehmann (l981) and Morton and Nixon (l987) for other members of the Aptychophora. Interestingly, this interpretation has recently been challenged based on rare finds of stomach contents of ammonites from the Jurassic Solnhofen Limestone of southern Germany. Jäger and Fraaye (1997) noted that the stomach contents of *Harpoceras* consist only of certain parts of decapod crustaceans (pereiopods rather than cephalothorax). Such prey selectivity would have been unlikely if the jaws functioned as wholesale strainers.

A biting and cutting function of the jaws is consistent with inferences about the mode of life and habitat of placenticeratids. In their study of *Placenticeras* from the Bearpaw Shale in southern Alberta, Tsujita and Westermann (1998) observed that this ammonite commonly occurs in concretions in the absence of benthos and other ammonites and concluded that it lived in a pelagic habitat in the upper part of the water column. This hypothesis was also supported by analyses of septal and siphuncular strength, which suggested habitat depths of less than 40 m, and analyses of the oxygen isotopic composition of the shell, which indicated very light values of $\delta^{18}0$. On the basis of shell shape and length of the body chamber, as indicators of swimming ability, Tsujita and Westermann (1998) proposed that these ammonites were capable of pursuing and attacking sluggish prey. *Placenticeras* was preyed upon, in turn, by mosasaurs, which may also have inhabited shallow water (Tsujita and Westermann, 2001).

If these inferences are correct, a possible ecological analog of *Placenticeras* may be the modern ocean sunfish *Mola mola* (Linnaeus, 1758). These animals are discoidal and reach lengths of up to 3 m (Gudger, 1928), superficially resembling placenticeratids. Their mouth is relatively small, and their teeth are fused together to form a parrot-like beak. They are pelagic and occur worldwide in subtropical and temperate waters. They are active swimmers, making daily vertical migrations (Cartamil and Lowe, 2004), and mainly feed on gelatinous zooplankton (medusae, salps, and ctenophores), which they nibble and suck into their mouth (MacGinitie and MacGinitie, 1968). With a little bit of effort, one could easily imagine placenticeratids pursuing a similar mode of life, migrating vertically up and down in the water column tracking the diel movements of gelatinous zooplankton.

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