Jaws and Radulae in *Rhaeboceras*,
a Late Cretaceous Ammonite

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1 Text-Figure and 7 Plates

United States
Cretaceous
Ammonoidea
Scaphites
Jaws
Radulae

Contents

Kiefer und Radulae bei *Rhaeboceras*,
einem oberkretazischen Ammoniten

Zusammenfassung

Eine Anzahl von Exemplaren des wiederaufgerollten Scaphiten *Rhaeboceras halli* (MEEK & HAYDEN, 1856) aus dem Bearpaw Shale (Campanium, Oberkreide) von Montana beinhaltet wohlerhaltene Ober- und Unterkiefer zusammen mit von uns als Radulazähnchen interpretierten Strukturen. Die Elemente der Radula sind hohl und bis zu 21,8 mm lang. Das entspricht 50 % der Länge des Oberkiefers, während die Länge der Radulamasse bis zu 50 % des Schalendurchmessers ausmachen kann. Diese Form der Radula ist äußerst ungewöhnlich und relativ gesehen erheblich größer als früher beschriebene Radulae von Ammoniten und rezenten Coleoiden und wird als Filtrierorgan zur Trennung von Wasser und Beute interpretiert, das koordiniert war mit dem schwach mineralisierten Unterkiefer, der mit dem Symphysenrand verbunden war. Die hohlen, hakenförmigen Strukturen, die früher in *Hoploscaphites* und *Jeletzkytes* der Fox Hill Formation des U.S. Western Interior beschrieben worden waren, werden ebenfalls als riesige Radulazähne neu interpretiert.

Abstract

A series of specimens of the Late Cretaceous (Campanian) recoiled scaphite *Rhaeboceras halli* (MEEK & HAYDEN, 1856), from the Bearpaw Shale of Montana include well-preserved upper and lower jaws, associated with what are interpreted as radular teeth. The radular elements are hollow, and up to 21.8 mm long, equivalent to 50 % of the length of the upper jaw, while the length of the radular mass is equivalent to up to half the diameter of the shell. This radula is very unusual. It is substantially larger in relative terms than previously described radulae of ammonoids and extant coleoids. A function for transport of food as in recent cephalopods is favoured by Larson; the other authors interpret the *Rhaeboceras* radula as having served as a filtration device to separate water and prey, working in coordination with a slightly mineralised lower jaw hinged along the symphysial margins. The hollow, hook-like structures previously described in *Hoploscaphites* and *Jeletzkytes* from the Maastrichtian Fox Hills Formation of the U.S. Western Interior are reinterpreted as similarly giant radular teeth.

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1. Introduction

It is now well established that the single organic structures termed anaptychi, and the calcitic paired structures termed aptychi are the lower jaws of ammonoid cephalopods, having been described in association with elements that are clearly identifiable with the upper jaws of Recent cephalopods (see LEHMANN, 1970, 1971a,b, 1978, 1981a,b; NIXON, 1996; TANABE & FUKADA, 1999; TANABE & LANDMAN, this volume for reviews). The mandibular interpretation can be traced back to the account by MEEK & HAYDEN (1864) of what are clearly associated upper and lower jaws in the body chamber of a microconch *Jeletzkytes nebrascensis* (OWEN, 1852) (the specimen, U.S. National Museum of Natural History Collections no 386, has been re-illustrated by KENNEDY & COBBAN [1976, p. 13, Pl. 4, Fig. 1] and LANDMAN & WAAGE [1993, p. 57, Fig. 37]; see Text-Fig. 1). Most subsequent authors, unaware of this early account, interpreted anaptychi and aptychi as having an opercular function; even with the general acceptance of a mandibular origin, there have been arguments that although this may have been their origin, the function was opercular as well, as proposed by LEHMANN & KULICKI (1990), and SEILACHER (1993). The description of both jaws and an operculum in a Carboniferous *Eoasianites* (BANDEL, 1988) has been rejected by subsequent workers (DAGYS et al., 1989; LEHMANN & KULICKI, 1990; SEILACHER, 1993).

The recognition of radulae in ammonoids dates to the work of CLOSS & GORDON (1966) and CLOSS (1967) on *Eoasianites* from the Upper Carboniferous of Uruguay, and radular elements have been recognised subsequently in Lower Carboniferous *Cravenoceras* (TANABE & MAPES, 1995); Triassic *Nordophiceras* (ZAKHAROV, 1974, 1979); Lower Jurassic (Sinemurian) *Arnioceras* (LEHMANN, 1971a); Lower Jurassic (Pliensbachian) *Dactylioceras* (LEHMANN, 1979), Lower Jurassic (Toarcian) *Harpoceras* (LEHMANN, 1967, 1971a); and Lower Cretaceous (Albian) *Aconeceras* (DOGUZHAEVA & MUTVEI, 1992). It is to these records that we add the description of jaws and associated radulae in the Upper Cretaceous (Campanian) ammonite *Rhaeboceras* MEEK, 1876.

We have now recognized jaws and what we interpret as radulae in 11 specimens of *Rhaeboceras halli* (MEEK & HAYDEN, 1856) from the Late Campanian *Baculites jenseni* zone of the Bearpaw Shale at USGS Mesozoic locality D783, about 23 km north-northeast of Melrose, in the NW¼, sec. 24, T. 12 N., R. 31 E., Rosebud County,

Montana, and USGS Mesozoic locality D781, from the same horizon in the SE¼ SE¼ SE¼ sec. 6, T. 11 N., R.32 E., Rosebud County, Montana.

One specimen (BHMNH 2156) is preserved in the collection of the Black Hills Museum of Natural History, Hill City, South Dakota, and 10 in the collections of the U.S. National Museum of Natural History (USNM 508611 to 508620) in Washington D.C.; the Washington specimens formed part of a collection of more than 100 specimens, of which the remainder are held in the U.S. Geological Survey Collections in Denver.

Rhaeboceras halli (see revision in COBBAN [1987, p. 6, Pls. 1–5; Pl. 6, Figs. 1–15; Pl. 7, Fig. 2; Pl. 8, Figs. 1, 2; Pl. 11, Figs. 5, 6; Pl. 12, Figs. 1–3; Pl. 13]) is a recoiled member of the heteromorph family Scaphitidae, which reaches an adult diameter of 175–205 mm in complete specimens.

Complete specimens generally have body chambers that extend for 240° or more of the outer whorl (Fig. 1). Radulae are generally preserved in the adapical part of the body chamber (USNM 508611, Pl. 1, Figs. 1, 2; USNM 408618, Pl. 2, Figs. 1–3) lying against the inner surface of what was topographically the lower flank at the time of burial. The axis of the radulae may lie perpendicular to the direction of coiling (Pl. 1), or parallel to it (Pl. 2). Other specimens (Pl. 3, Figs. 5, 6) show radular elements disaggregated to varying degrees. In one specimen (USNM 508613), disaggregated elements lie adaperturally of the upper jaw, in USNM 408615 (Pl. 7, Fig. 4) the radular mass lies at the adapical end of the body chamber. In only one specimen, BHI 2156 (Pls. 4–6), does the radula lie between the upper and lower jaws, providing unequivocal evidence for the interpretation of these structures.

2. Jaw Morphology

The morphology of the *Rhaeboceras* jaws is basically similar to that of other scaphitid ammonites (*Scaphites*: KENNEDY, 1986, Text-Fig. 40H; *Hoploscaphites*: SCHLÜTER, 1876, Pl. 42, Figs. 4, 5; TRAUTH, 1927, p. 156, Pl. 4, Fig. 14; KENNEDY & KAPLAN, 1997, Pl. 78, Figs. 5, 6; *Trachyscaphites*: SCHLÜTER, 1876, Pl. 25, Figs. 5–7; TRAUTH,

Text-Fig. 1.
In-situ jaw apparatus in a microconch *Jeletzkytes nebrascensis* (OWEN, 1852). USNM 386, the original of MEEK & HAYDEN, 1864, Pl. 35, Fig. 3, "Cretaceous no. 5, Moreau River, Dakota"; in fact from the Maastrichtian Fox Hills Formation of South Dakota. Natural size.

114
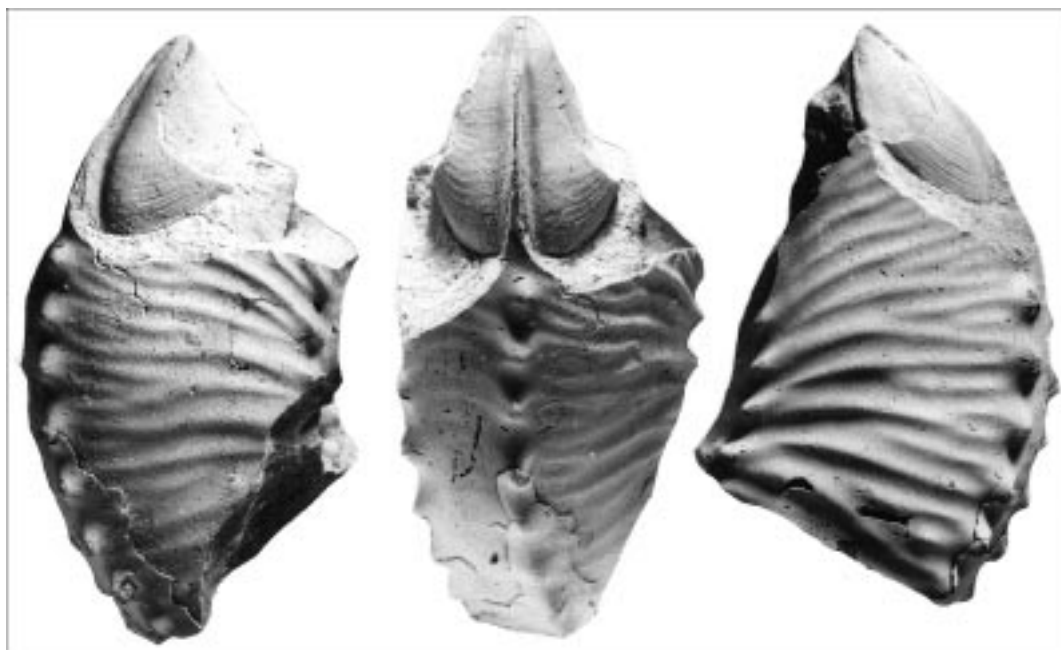
1927, p. 158, Pl. 4, Fig. 15; KENNEDY, 1986, Text-Fig. 42C, F; KENNEDY & KAPLAN, 1997, Pl. 69, Figs. 3, 5; *Jeletzkytes*: MEEK & HAYDEN, 1864, p. 118–121; MEEK, 1876, p. 438–441; KENNEDY & COBBAN, 1976, p. 13, Pl. 4, Fig. 1; LANDMAN & WAAGE, 1993, Figs. 37–42; *Yezoites*: TANABE & LANDMAN, in press, Pl. 1, Fig. 4).

Lower jaws (Pl. 3, Figs. 1–4; Pl. 4, Figs. 2–6; Pl. 5, Figs. 1, 2; Pl. 6, Fig. 1) are up to an estimated 50 mm in length, as measured along the symphysial margins (terminology after TRAUTH [1927]; see LEHMANN, 1981a, Fig. 82), and formed of two mirror image elements. These consist of a thin outer calcitic layer, the outer surface ornamented by concentric growth lines, ridges and striae (Pl. 3, Figs. 1–4; Pl. 4, Fig. 2; Pl. 5, Fig. 1). Where the outer calcitic layer is absent, the surface of the lower jaw bears a black coating, recording the former presence of an organic lining. This too preserves growth lines, and internal moulds (Pl. 4, Fig. 2; Pl. 5, Fig. 1) bear pronounced longitudinal striae.

The individual halves of the lower jaw are elongated, with an estimated length to breadth ratio of around 1.6. The outer margin is broadly rounded; the inner margin is not preserved. The two halves of the lower jaw are markedly convex, and appear to have been linked along their symphysial margins; by analogy with other lower jaws this would have been by the inner, organic layer (LEHMANN, 1972). The lower jaw is preserved in a variety of modes; at one extreme the lateral margins of the two halves are widely separated (Pl. 4, Fig. 3; Pl. 5, Fig. 2; 8B), forming a wide, shallow "U" in cross section, at the other extreme, the lateral margins are closer together (Pl. 3, Figs. 1, 2), forming a narrower deeper structure, the cross section having the form of a "U" with the upper parts of the limbs converging. This variation suggests that the two halves of the lower jaw could flex in life along the symphysial margin, from "open" to "closed".

We have observed this range of preservation modes in even more extreme form in scaphite jaws from the Maastrichtian Fox Hills Formation of the U.S. Western Interior, in which some specimens even occur with the two halves almost in contact.

The upper jaw is best preserved in BHMNH 2156 (Pls. 4–6). It is 44 mm long, and consists of two lateral, diverging elements that expand posteriorly to terminate in a broadly rounded posterior margin. The dorsal margin of these structures is folded inwards at 90° to the outer face, to form a concave flange that expands anteriorly into a dorsal platform that links the two lateral flanges. This dorsal platform tapers anteriorly, and curves ventrally (Pl. 4, Figs. 1, 3, 4; Pl. 5, Figs. 1, 2).

The sides of the jaw also taper anteriorly, to form a terminal beak-like structure. Viewed ventrally, the lower, ventral surface of the upper jaw is damaged, but, traced anteriorly, the lateral areas are folded inwards at 90° to the outer surface to form a concave flange that links the lateral elements of the jaw for at least 30 % of the total length of the structure. The anterior part of the jaw thus forms an enclosed asymmetric pyramidal structure.

Preservation of the specimen is such that we cannot say if part or all of the upper jaw was mineralised; it is now preserved as an internal mould with a brownish surface coating that we presume to be a diagenetic replacement of the original organic material. Concentric growth lines, ridges and striae are prominent at the anterior end, less so when traced posteriorly. Longitudinal striae, prominent on the lower jaw, are absent.

3. The Radula

All known ammonite radulae have the same number of solid teeth in each row as are found in living coleoids, with a symmetrical central rhachidian tooth, two rows of lateral teeth, a single row of marginal teeth, and, in the case of living coleoids and *Aconeceras* (MUTVEI & DOGUZHEVA, 1992), a marginal plate. A pair of marginal plates in each row are also present in *Eosianites* (CLOSS, 1967), and *Cravenoceras* (TANABE & MAPES, 1995; see also TANABE & FUKADA [1999, Fig. 19.6]) The elements form left and right mirror image sets on either side of the rhachidian tooth (NIXON, 1995, 1998). Pls. 1, 2; Pl. 3, Figs. 5, 6; Pls. 4–6 show the associations of radular teeth found in *Rhaeboceras halli*. Individual teeth are hollow, and preserved to lengths of 16 mm in BHMNH 2156, and are incomplete; the length of the upper jaw is 44 mm. We have failed to recognize a symmetrical rhachidian tooth or marginal plates, even though parts of at least 30 teeth are present in this specimen. Instead, all of the elements are made up of a hollow tubular body, seemingly elliptical in cross section, terminating in a pair of elongate cusps, one much longer than the other. There is a suggestion that the inner of the two cusps is the longer in this specimen, and that successive teeth in at least one row imbricate, the anterior tooth of successive rows lying in a dorsal position with relation to the preceding (posterior) tooth. There is a range in tooth body length of 6.3–10.5 mm in the specimen; the longest cusp is 11.3 mm long, suggesting that the largest teeth, when complete, may have been as much as 21.8 mm long, equivalent to 50 % of the total length of the upper jaw.

There is no clear arrangement of the teeth into what could be described as a radular ribbon, but there is a clear indication of larger teeth in the median area of the mass of teeth (a in Pl. 6, Fig. 2), with smaller teeth (b in Pl. 6, Fig. 2) to either side. There are at least two apparently near-symmetrical narrowly tapering elements present (c in Pl. 6, Fig. 2), up to 17.8 mm long. They are only partially clear of matrix, and they may well be bicuspid elements viewed edge on, rather than a different type of tooth.

Considered overall, the impression is of a partially disaggregated structure, the radular teeth filling the whole of the inner surface of the lower jaw, and extending into the hollow, asymmetrically pyramidal anterior apex of the upper jaw.

USNM 508611 (Pl. 1, Figs. 1, 2) shows radular teeth forming an elongated mass 33 mm long and up to 19.4 mm wide, lying against what was the topographically inner lower surface of the shell as it lay on the sea floor, the long axis of the mass aligned normal to the direction of coiling, and subparallel to the ribs, approximately 120° adapertural of the final septum. More than 30 teeth are present, the largest preserved having a maximum incomplete length of 11.6 mm. Bicuspid teeth, like those that dominate the assemblage in BHMNH 2158 form the majority of those elements that have their apices visible. What may be a second tooth type is represented by a single example (a in Pl. 1, Figs. 2,3) that has a third cusp. Other elements present appear to be single cusped, but we cannot be certain that this is not an artefact of orientation, or their being merely fragmentary cusps from larger bicuspid teeth.

The most striking feature of the assemblage in USNM 508611 is the very clear bilateral symmetry of the mass. The teeth diverge from the axis of the structure in a series of imbricating chevrons, successive chevron-forming pairs overlapping to a degree, their bases tightly packed,

and in some cases seemingly articulated. Close inspection shows the most completely exposed teeth to be in the plane of the broken surface of the specimen, whereas other teeth, of which only the base survives, are directed both outward and away from the major axis of the structure, suggesting that the overall arrangement may have had a semicircular cross-section. It is difficult to dismiss this arrangement as a chance juxtaposition of regular rows of teeth, as described in other well-preserved ammonoid radulae (CLOSS, 1967, Pl. 1, Fig. 4; DOGUZHAEVA & MUTVEI, 1992, Pl. 3C, Pl. 5, Pl. 9; TANABE & MAPES, 1995, Fig. 2), and in those of other cephalopods (e.g. NIXON, 1995, 1998).

USNM 508613 (Pl. 3, Fig. 5) and USNM 508614 (Pl. 3, Fig. 6) are typical of the remaining specimens, in having radular teeth disaggregated and patchily distributed in part of the adult body chamber. All those that are completely exposed are of the bicuspid type. USNM 508614 (Pl. 3, Fig. 6) gives an indication of the original composition of the radular teeth. Some of the teeth show a polygonal network of mineral-filled sheets, rather like the walls of mortar between crazy paving when the slabs are removed. This suggests an original material that has crazed, contracted and brecciated during diagenesis. Elsewhere on the specimen, traces of black material survives, which we presume to represent the carbonised remains of originally organic material.

4. Discussion

The observations above provide an account of the radular structures in *Rhaeboceras halli*. When compared to the radulae known from other ammonoids, the present material is distinctive in several respects. Obvious is the absence, among several hundred teeth examined, of unequivocal rhachidian teeth or marginal plates. A second difference is that the teeth appear to have been hollow, rather than solid. A third difference is the seeming semicircular cross-section of the radular mass, rather than flat and ribbon-like. But the most striking difference is the enormous size of the individual teeth in relation to the jaw – an estimated 50 % of the length of the upper jaw in BHMNH 2156 – where the mass of teeth fill the floor of the buccal apparatus formed by the lower jaw. The great size of the radular apparatus is demonstrated even more strikingly by USNM 508618 (Pl. 2). This specimen is a nearly-complete adult, preserved to a diameter of 135 mm, the original diameter of which cannot have exceeded 150 mm; the radula is preserved in the ventrolateral region of one flank, and extends to a length of just over 70 mm, just under half the diameter of the shell, and occupies a substantial volume of the body chamber. By contrast, the longest radula tooth in a specimen of *Dactylioceras* described by LEHMANN (1979) was 1.2 mm long, 15 % of the length of the upper jaw (versus 50 % in *Rhaeboceras*). In a specimen of *Arnioceras* (see LEHMANN, 1971b), the radula was 2.4 mm long in a specimen 13.6 mm in diameter, thus representing 17.6 % of the diameter (versus an estimated 50 % in *Rhaeboceras*). In a specimen of *Eleganticeras* (LEHMANN, 1967), the radula length : shell diameter ratio expressed as a percentage is 21–22 % (2 individuals). LEHMANN (1967) provided figures for *Nautilus* that gave a percentage ratio of 12.2 %, while the ratio of radula length to body length in coleoids is (after LEHMANN) 13.8 % in *Sepia* sp., and 13–15.7 % in *Octopus* (2 individuals).

The radula mass in *Rhaeboceras* thus appears to be two or three times larger in relation to shell diameter than in other ammonites in which this figure can be determined, and four times larger in relative terms than in *Nautilus*.

What was the function of this enlarged radula? Interpretation of radula function in ammonites is hindered by our relative ignorance of radula function in extant cephalopods (see recent reviews in YOUNG [1993], and MESSENGER & YOUNG [1999]). To quote NIXON (1996, p. 38):

"Little is known of the function of the radula in living cephalopods. The radula of Octopus vulgaris is concerned mainly with the passage of food toward the entrance of the esophagus (ALTMAN & NIXON, 1970). It is involved in the very early stages of drilling the shells of molluscs (NIXON, 1979) and the exoskeletons of crustaceans (NIXON & BOYLE, 1982); the later stages of drilling involve only the toothed regions of the posterior salivary gland papilla and duct (see NIXON, 1988a; NIXON & MACONNACHIE, 1988). The role of the radular teeth in the life of modern cephalopods is otherwise not known, and as yet none has been found to possess such tall and seemingly delicate marginal teeth as those found in some of the ammonites."

It should also be noted that *Spirula*, a plankton feeder, has lost its radula (KERR, 1931; NIXON, 1988b).

LARSON believes that the radula of *Rhaeboceras* functioned as in extant cephalopods. The other authors speculate here that the buccal apparatus in *Rhaeboceras* in part functioned to separate water from prey. The lightly mineralised lower jaw elements were joined by an unmineralised, flexible proteinaceous zone along their symphysial margins, which acted as a hinge. The bulky radula filled much of the space between the jaws. When the halves of the lower jaw "opened", the resultant cavity was filled by a substantial volume of water, containing the prey, which we suggest was an element of the plankton (see below). "Closure" of the halves of the lower jaw would lead to the expulsion of water through the three-dimensional meshwork of the radular teeth, filtering out prey, which could then be transferred by the radula towards the entrance of the oesophagus, as is known to be the case in *Octopus*.

This function is similar to that proposed by MORTON & NIXON (1987, p. 237):

"… the function of the large shovel-like lower jaw was the collection of large numbers of small prey. The bluntness of the beaks makes them unsuitable for biting (KAISER & LEHMANN, 1971, 29–30), and the apparent absence of distinctive areas of either lower or upper jaw for insertion of strong muscles indicates that a crushing or shearing action is unlikely. However, the broad rounded surfaces of the lower and upper jaws brought closer together by vertical and/or lateral movement to one another would, together with the actions of the buccal complex, provide an ideal mechanism for the expulsion of large volumes of water while retaining trapped prey."

SEILACHER (1993) argued (as did LEHMANN & KULICKI [1990]) that ammonite lower jaws evolved a secondary function as operculae, that the two halves of mineralised jaws were joined by an elastic element, while, speaking of anaptychi (p. 31), SEILACHER noted that

"… the anaptychus had already lost the jaw function. Its elastic deformability did not only allow accomodation of the oversized structure into the shell but enabled the former jaw to take over a new, distinctive role in the processes of food catching. Whether the antagonistic interaction of adducting muscles and anaptychus spring has been used as continuous pump or for spontaneous suction-feeding must

remain an open question, but the fact that flexibility was maintained also in the calcareous aptychus attests for the continued importance of this feeding apparatus, along with its emerging secondary function as an operculum.”

Note also the observation of WESTERMANN (1990), who suggested that the thinly calcified aptychus of the Stephanoceratidae had a secondary function whereby the movement of the two mineralised parts of the lower jaw would have produced water currents.

If our speculations are correct, what might *Rhaeboceras* have filtered from sea water? It is a feature of the Bearpaw Shale and correlative Pierre Shale that early diagenetic concretions that are crowded with ammonites often contain little else in the way of macrofossils, and, indeed, the typical association is of ammonites and inoceramid bivalves only. The sheer abundance of ammonites at these levels, and absence of obvious prey suggests to us that these animals fed on a group of abundant organisms with a very low fossilisation potential. We also note the work of HATTIN (1975) who documented the abundant occurrence of ellipsoidal coccolith-rich pellets in Turonian to Campanian sediments of Kansas and Saskatchewan. These were interpreted as the fecal pellets of either copepods or pelagic tunicates. From the abundance of their pellets, it is clear that these organisms were important elements in the trophic structure of the late Cretaceous Western Interior seaway, even though they are unknown as body fossils. Copepods occupy a major position in the trophic structure of the present oceans, and we suggest that these, or some other group of pelagic/planktonic arthropods may have been a major element of the diet of *Rhaeboceras*, and, indeed, other ammonites. Their absence from the fossil record in the Western Interior is not surprising; trace fossils attributable to larger arthropods are near-ubiquitous in Cretaceous shelf sediments, but the remains of the producers are generally rare. The chitinous, variably mineralised exoskeletons of these animals were destroyed by bacterial degradation under normal circumstances, as a result of the activities of chitinoclastic bacteria (see, for example, SEKI & TAGAN [1963]). The fecal remains survive; the exoskeletons do not.

Rhaeboceras was not alone in possessing giant, hollow radular teeth. The bicuspid "hook-like structures" described by LANDMAN & WAAGE (1993, p. 63, Figs. 43–46) from both *Hoploscaphites* and *Jeletzkytes* from the Maastrichtian Fox Hills Formation of the U.S. Western Interior are clearly analogous structures, here interpreted as disagregated radular elements.

Acknowledgements

Plate 1

Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: Side view; ✕1
        Arrow marks position of last septum.
Fig. 2: Detail of radula mass; ✕3.
Fig. 3: Sketch of tricuspid element at A in Figure 2.

USNM 508611, from the Late Campanian *Baculites jenseni* Zone.
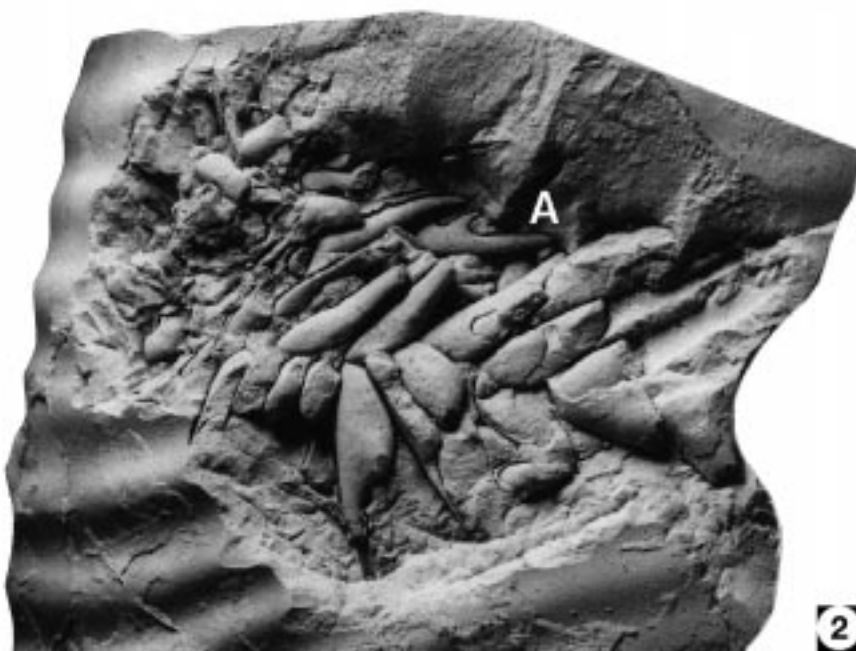Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.

Plate 2
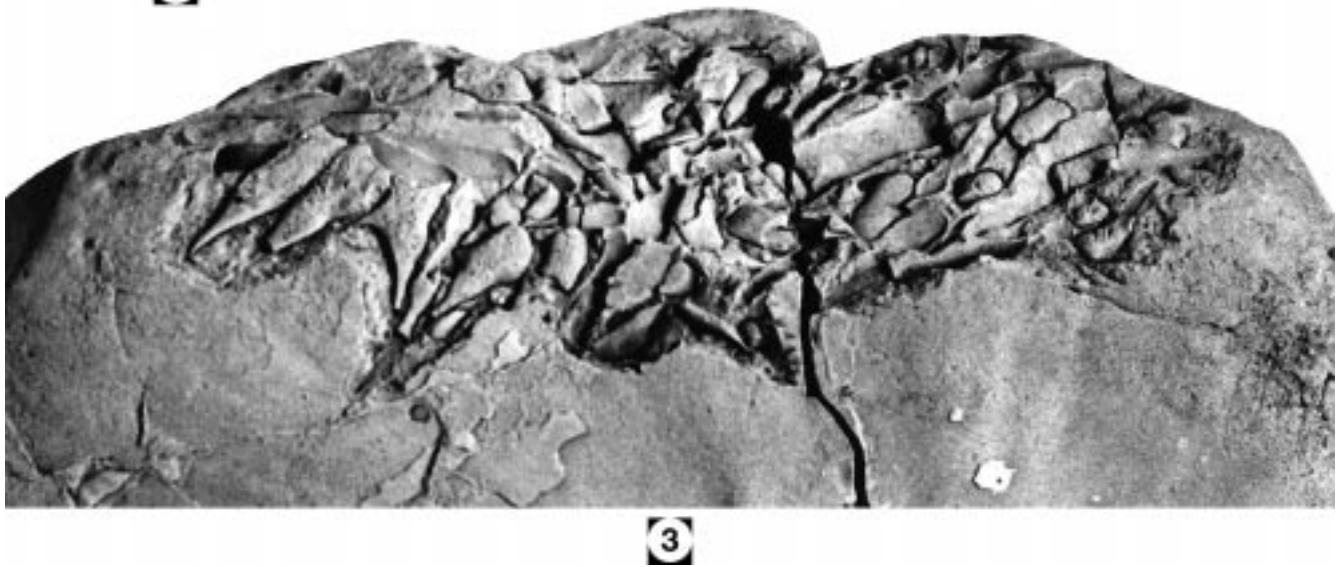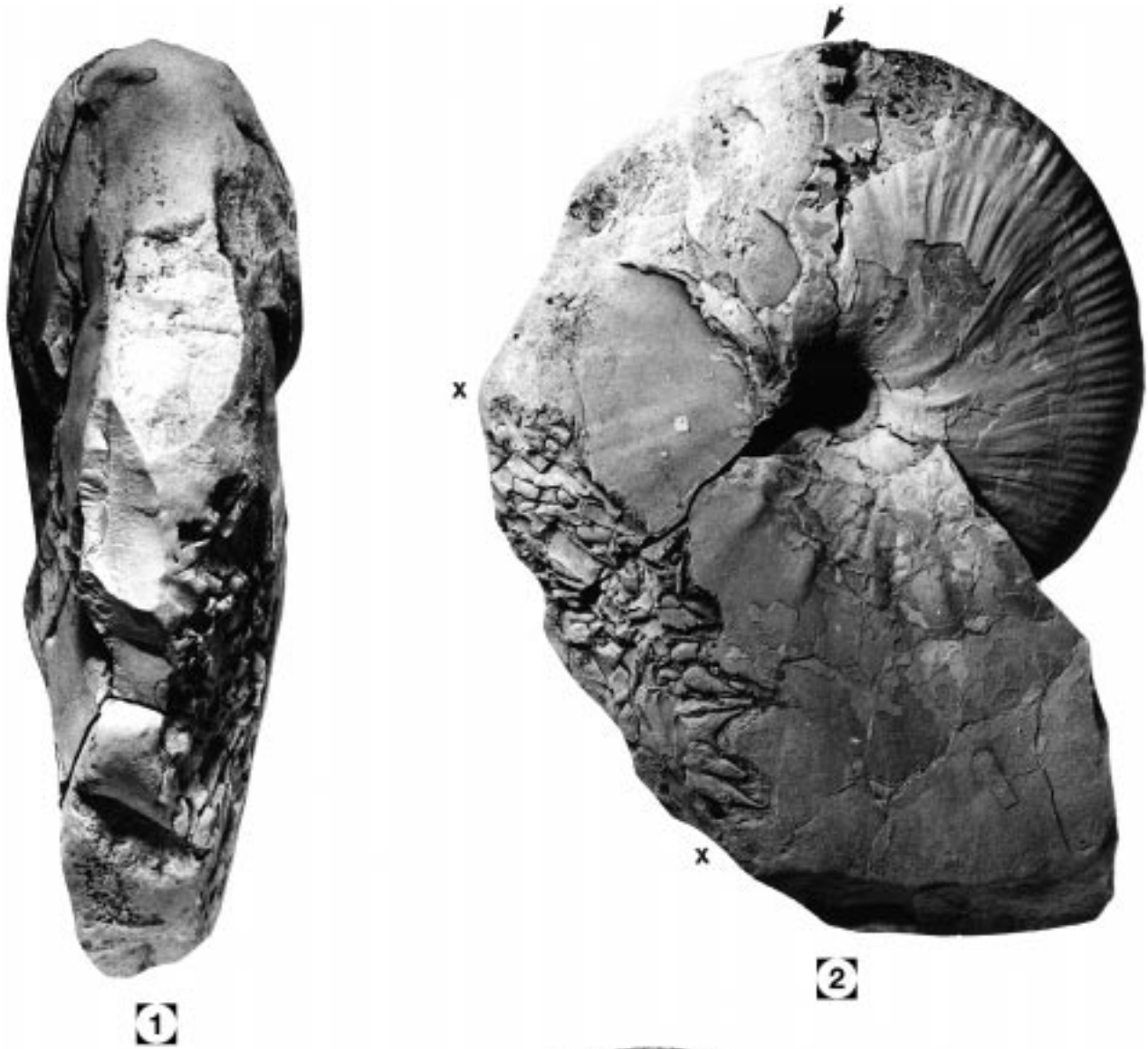
Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: Ventral view; ✕1.
Fig. 2: Side view; ✕1.
       Arrow marks position of last septum. X — X' marks extent of radula mass.
Fig. 3: Detail of radula mass; ✕2.

USNM 508618, from the Late Campanian *Baculites jenseni* Zone.
Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.

Plate 3
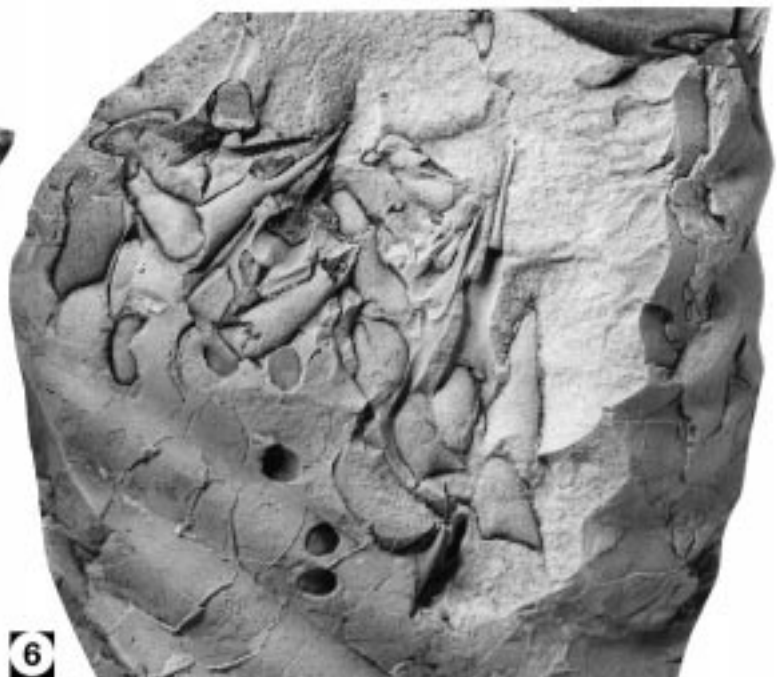
Rhaeboceras halli (Meek & Hayden, 1856).

Figs. 1,2: USNM 508612.
      Fig. 1: Lateral view, with lower jaw inclined away from the observer, ×1.
      Fig. 2: Ventral view showing symphysial margins of the two halves of the jaw; ×10.
Figs. 3,4: USNM 508613a.
      Fig. 3: Lateral view; ×1.
      Fig. 4: Ventrolateral view of half of a lower jaw; ×1.
Fig. 5: Disarticulate radular teeth in USNM 508614; ×2.
Fig. 6: Disarticulate radular teeth in USNM 508614; ×2.

All from the Late Campanian *Baculites jenseni* Zone.
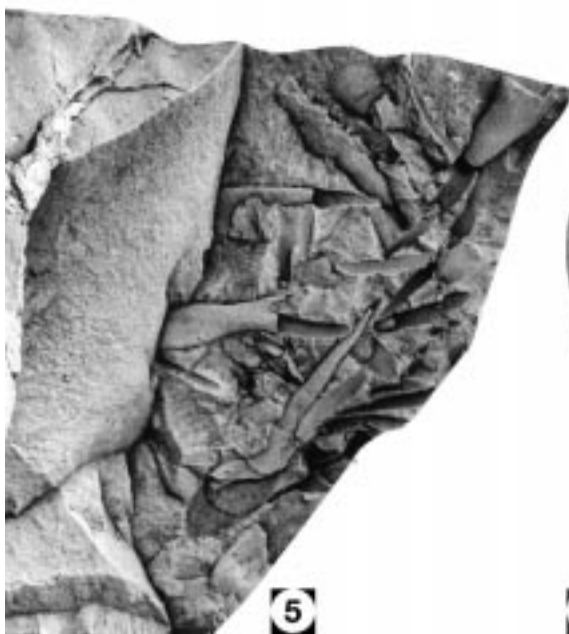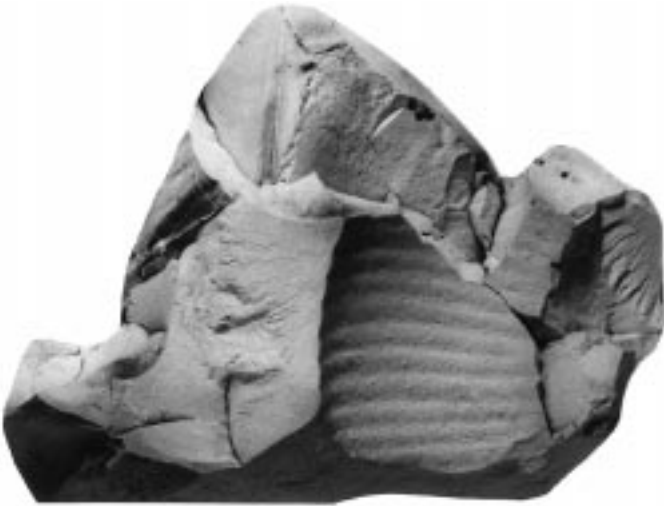Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.

123

Plate 4

Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: Dorsal view.
Figs. 2,4: Lateral views.
Fig. 3: Anterior view.
Fig. 5: Ventral view.
Fig. 6: Ventrolateral view of buccal apparatus.

All figures are ×1.
BHMNH 2156, from the Late Campanian *Baculites jenseni* Zone.
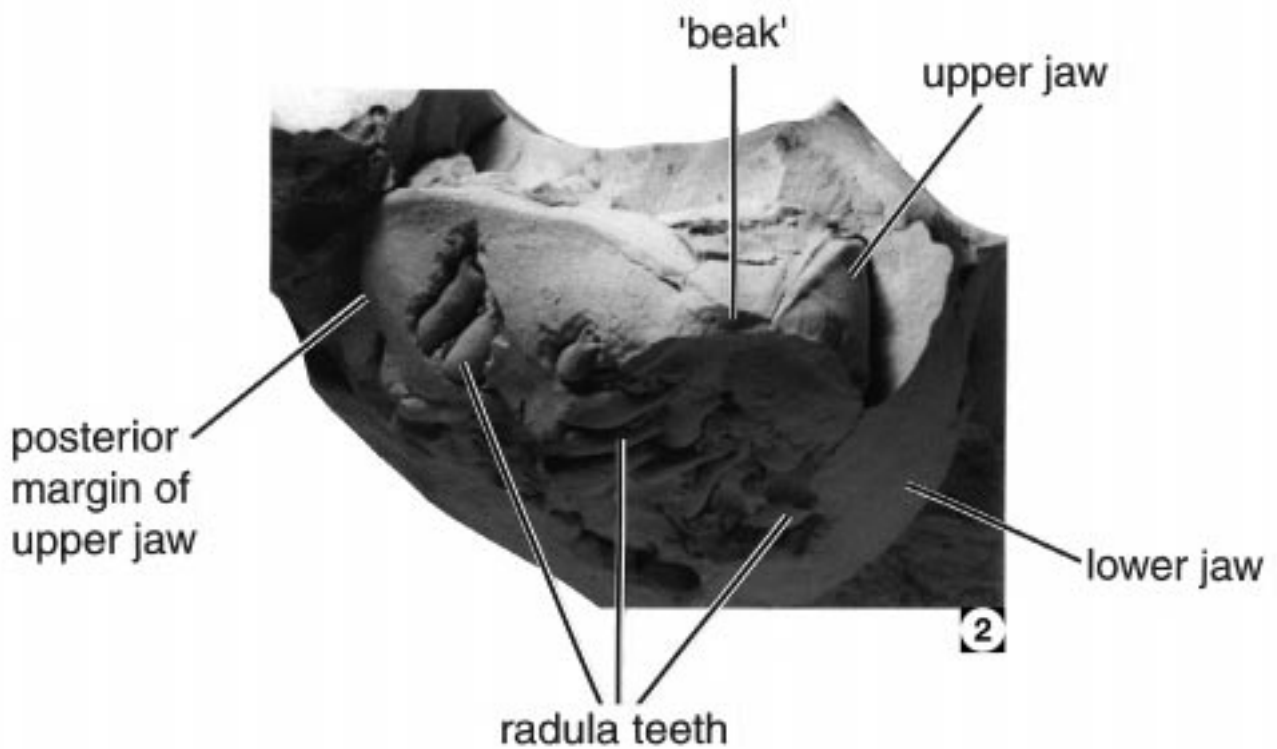Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.

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Plate 5

Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: Lateral view; ×1.5.
Fig. 2: Anterior view; ×1.5.

BHMNH 2156, from the Late Campanian *Baculites jenseni* Zone.
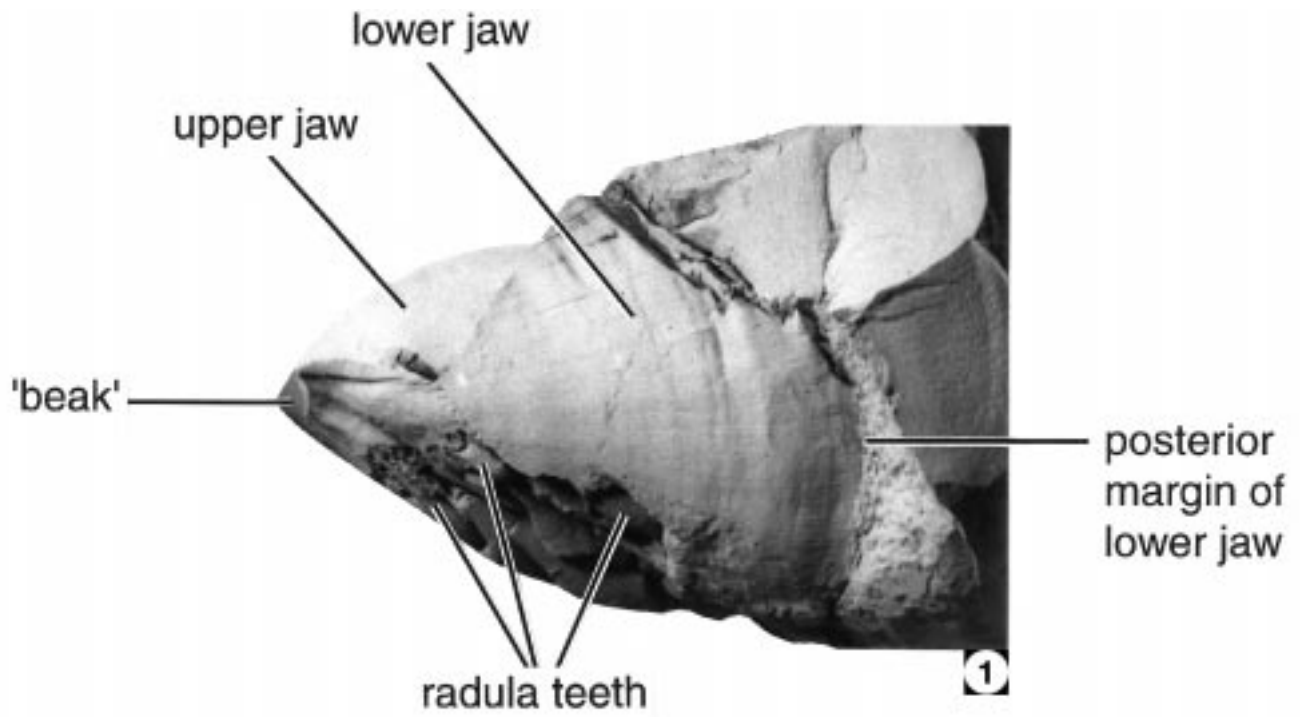Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.

lower jaw

upper jaw

'beak'

posterior margin of lower jaw

radula teeth

①

'beak'

upper jaw

posterior margin of upper jaw

lower jaw

radula teeth

②

Plate 6

Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: Ventral view of buccal apparatus; ×2.
Fig. 2: Sketch of anterior portion.
   a = area of imbricating bicuspid teeth; b = smaller bicuspid teeth; c = elongate cusps, either a second type of tooth, detached cusps, or bicuspid teeth in lateral view; d = broken margin of lower surface of anterior end of upper jaw (shown shaded), partially concealing radular teeth.

BHMNH 2156, from the Late Campanian *Baculites jenseni* Zone.
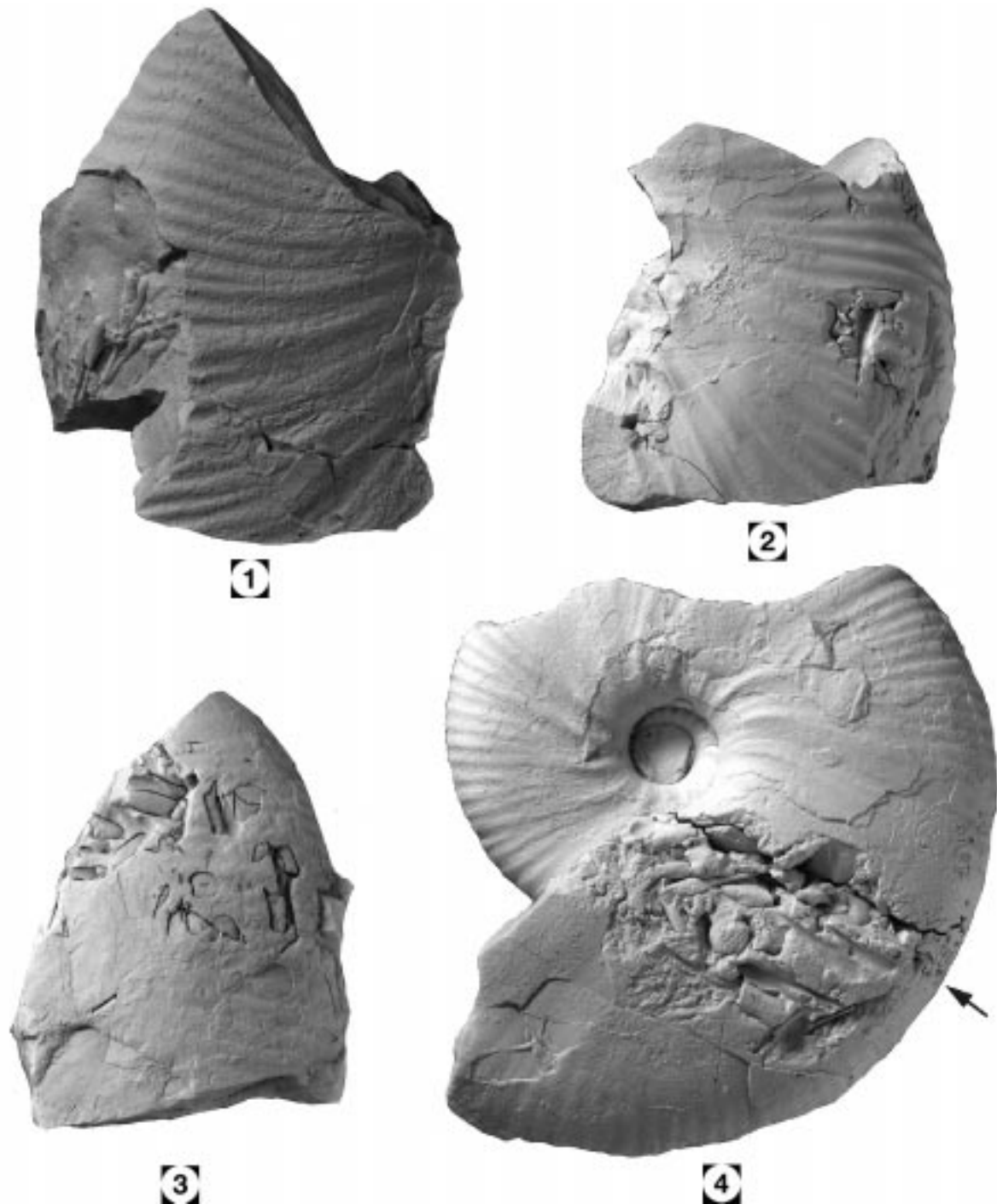Bearpaw Shale at USGS Mesozoic locality D783 in Rosebud County, Montana.
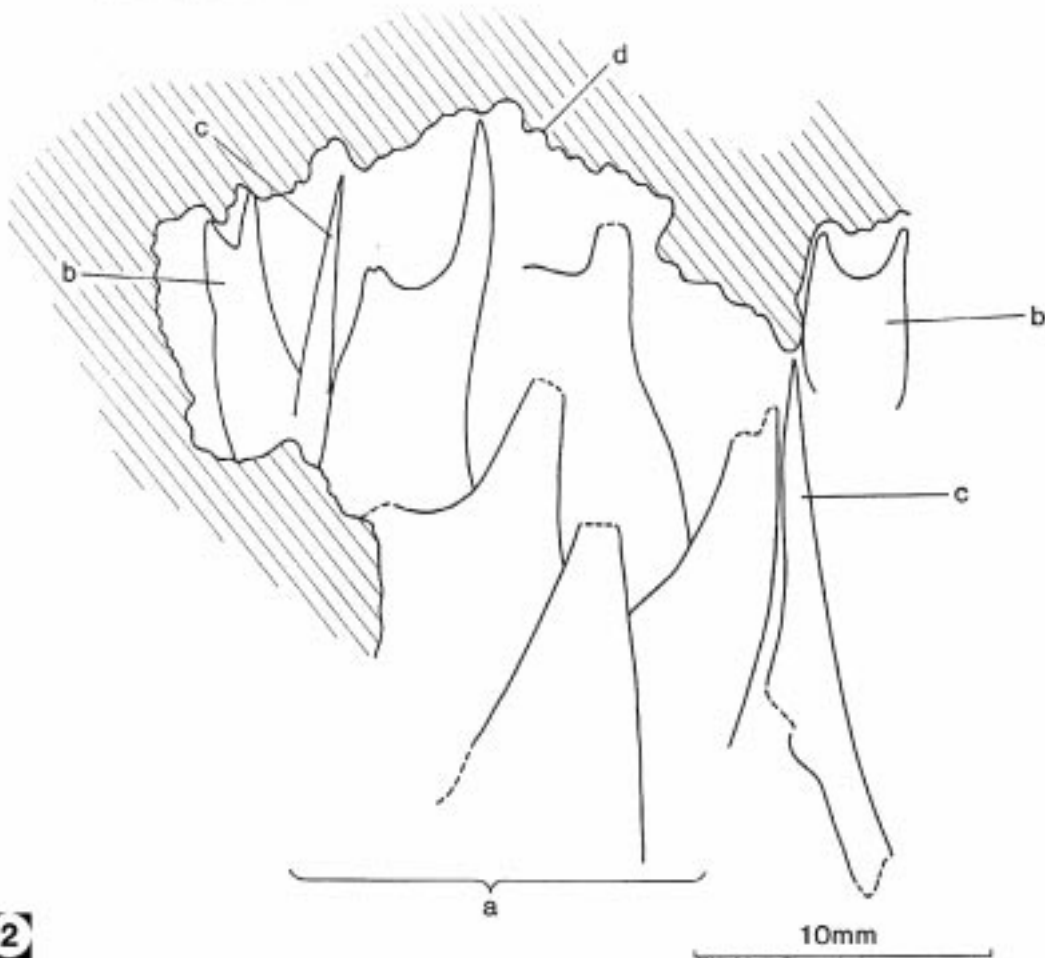
Plate 7

Rhaeboceras halli (MEEK & HAYDEN, 1856).

Fig. 1: USNM 508619.
Fragment of a body chamber from USGS Mesozoic locality D781, lateral view showing cluster of teeth.
Fig. 2: USNM 508617.
Fragment of a body chamber, probably from USGS Mesozoic locality D781 or D783, lateral view showing several teeth.
Fig. 3: USNM 508620.
Fragment of a body chamber, from USGS Mesozoic locality D781, lateral view showing cluster of teeth.
Fig. 4: USNM 508615.
From USGS Mesozoic locality D783, lateral view with cluster of teeth in the adapical part of the body chamber.

All figures are ×1.

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