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REGULAR RESEARCH ARTICLE

Caught in the act? Distraction sinking in ammonoid cephalopods

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Abstract

Two specimens of the Late Mississippian ammonoid cephalopod *Metadimorphoceras* sp. were recovered from the Bear Gulch Limestone in Montana. This unit was deposited in the lowest part of the Big Snowy Basin, where the bottom waters are thought to have been strongly oxygen deficient. The two nearly equally sized specimens are impressions with soft tissues preserved as brown carbonaceous smears. Diagenetic processes destroyed their aragonitic shells. The preserved soft tissues are interpreted as mandibles, remains of food in the crop, and, possibly, ovaries and eyes. The specimens are on their sides, aperture-to-aperture, and probably the male is on the left and the female is on the right. The specimens are thought to have been in the process of copulation when they died. Copulation by most (all?) externally shelled cephalopods (extinct ammonoids and fossil and extant nautiloids) was probably in a head-to-head, aperture-to-aperture position. This was probably governed in part by restricted accessibility to the female reproductive organs due to the presence of the shell and the ability of both animals to partly withdraw into their shells during copulation. The shell protected them from predators during copulation. In coleoids, which lack an external shell, copulation is a more rapid affair due to the greater vulnerability from predators including other coleoids. We suggest that the fossils from the Bear Gulch Limestone and similar finds of paired ammonoids preserved together with interlocking apertures, and including soft parts in the body chamber, represent examples of ammonoid behavior frozen in time. The two ammonoids were probably too pre-occupied with copulation to notice that they were sinking into the hypoxic bottom waters of the basin and facing suffocation (distraction sinking).

Keywords Ammonoidea · Carboniferous · Bear Gulch · Exceptional preservation · Taphonomy · Reproduction

Introduction

The paleobiology of ammonoid cephalopods has been intensively studied for many decades. Recently, a two-volume summary was published (Klug et al. 2015a, b) that updated the "Red Book" on the Ammonoidea edited by Landman et al. (1996), which amplified, in part, the paleobiology sections in the 1962 Russian Treatise ammonoid volume (Ruzhencev 1962; translated, Ruzhencev 1974) and the American Treatise ammonoid volumes published in 1957 (Arkell 1957) and 2009 (Furnish et al. 2009). The recent summary by Klug et al. (2015a, b) covered many aspects of ammonoid paleobiology including embryonic development, isotopic composition, muscle scars, hydrodynamics, and mode of life. However, very little has been written on ammonoid copulation. The discovery of a pair of specimens from the Upper Mississippian Bear Gulch Beds in Montana provides some insights into this biological process.

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Copulating strategies in modern cephalopods

The two main groups of extant cephalopods are the Nautiloidea and the Coleoidea. The Coleoidea, including the octopods and the teuthoids, comprise approximately 700 species and occur in all oceans with the exception of the

Baltic and Black Sea. This cephalopod group has either an internal shell or gladius (for example, *Spirula, Sepia*, and *Loligo*) or a vestigial shell (for example, *Octopus*). In contrast, the Nautiloidea, with their large external shell, comprise only two genera (*Nautilus* and *Allonautilus*) with perhaps eight species and only occur in the Indo-Pacific.

Copulation has been observed in only two species of *Nautilu*s (*N. pompilius* and *N. macromphalus*). In all instances, the animals were studied in aquaria (Mikami and Okutani 1977; Arnold 1987, reprinted, Arnold 2010; R. Mapes, pers. observation). The actual transfer of genetic material from the male to the female requires the male to grasp the female and maneuver her shell so that the apertures are facing each other and in close proximity. Copulation can last for several minutes to several hours. During copulation, males have been observed biting the shell and mantle of the female, leaving "V"-shaped breaks on the apertural edge of the shell (Arnold 1985). In contrast, copulation in the Coleoidea is a much more rapid affair and sometimes ends in post-coital cannibalism (Hanlon and Messenger 1996).

Geologic setting

The precise collecting locality for the pair of ammonoid specimens is unknown. They were recovered from the Bear Gulch Limestone in Fergus County, central Montana, as a byproduct of fossil fish collecting by commercial collectors and vertebrate paleontologists (Fig. 1a). The beds are composed of fine-grained limestone and the cephalopods are preserved as impressions with traces of soft parts. The Bear Gulch Limestone is a world famous *Konservat-lagerstätte* (Seilacher 1970) that contains exceptionally well-preserved specimens of fish, soft-bodied invertebrates, and cephalopods including ammonoids, nautiloids, and coleoids (Hagadorn 2002). Some of the cephalopods from these strata have already been described (Mapes 1987; Mapes et al. 2010; Landman and Davis 1988; Lindholm et al. 2007; Landman et al. 2010).

The Bear Gulch Beds are part of the relatively fossiliferous Heath Formation (Fig. 1b). They are part of a transgressive sequence and were probably deposited 12° north of the paleoequator in the Big Snowy Trough, which connected the Big Snowy Basin to a north–south trending Cordilleran Miogeosyncline to the west (Harris 1972; Mallory 1972; Williams 1983; Witzke 1990; Hagadorn 2002). Biostratigraphic data from the ammonoids, nautiloids, palynomorphs, bryozoans, conodonts, and fish indicate that the age of the Bear Gulch Beds is Early Carboniferous (Late Mississippian: late Chesterian) (Scott 1973; Horner 1985; Cox 1986; Landman and Davis 1988; Feldman et al. 1994). Because of the exceptional preservation of the vertebrates and invertebrates, it is likely that the bottom waters and sediment along the axis of the basin (i.e., in its center) were oxygen deficient, and this environment prevented scavenging, thus promoting exceptional preservation.

Methods

The specimens were photographed using standard photographic techniques, with the specimens immersed in ethyl alcohol to enhance the contrast. In addition, the specimens were examined using Reflectance Transformation Imaging (RTI) at Yale University, New Haven, Connecticut (with the assistance of Jessica Utrop) and at the Soleil

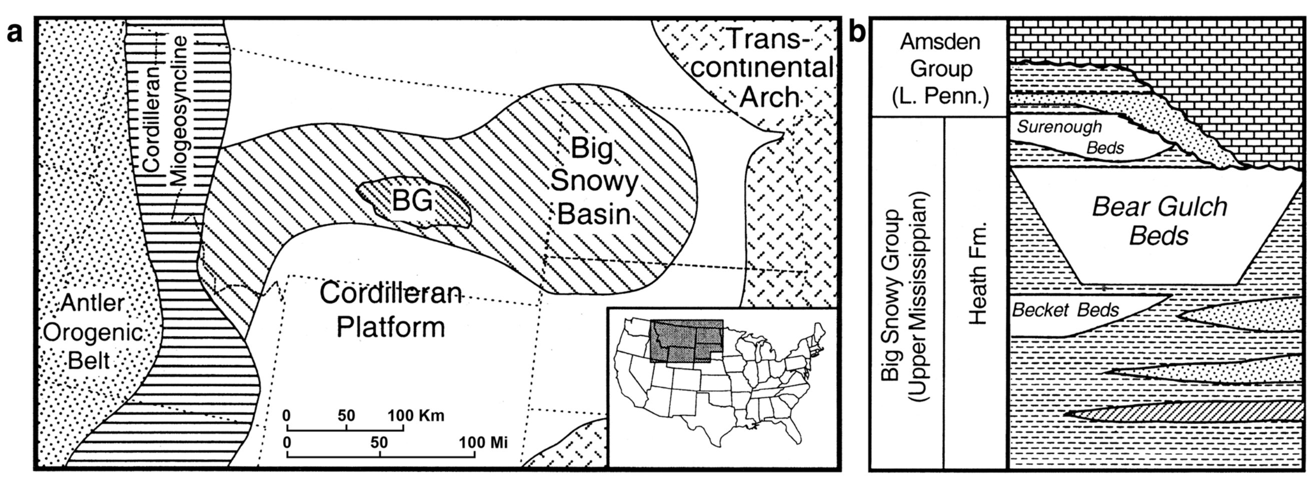

Fig. 1 **a** Paleogeographic map of the Bear Gulch Beds (BG) in the Big Snowy Basin. **b** Stratigraphic section of the Bear Gulch Beds in the Heath Formation Modified from Hagadorn (2002)

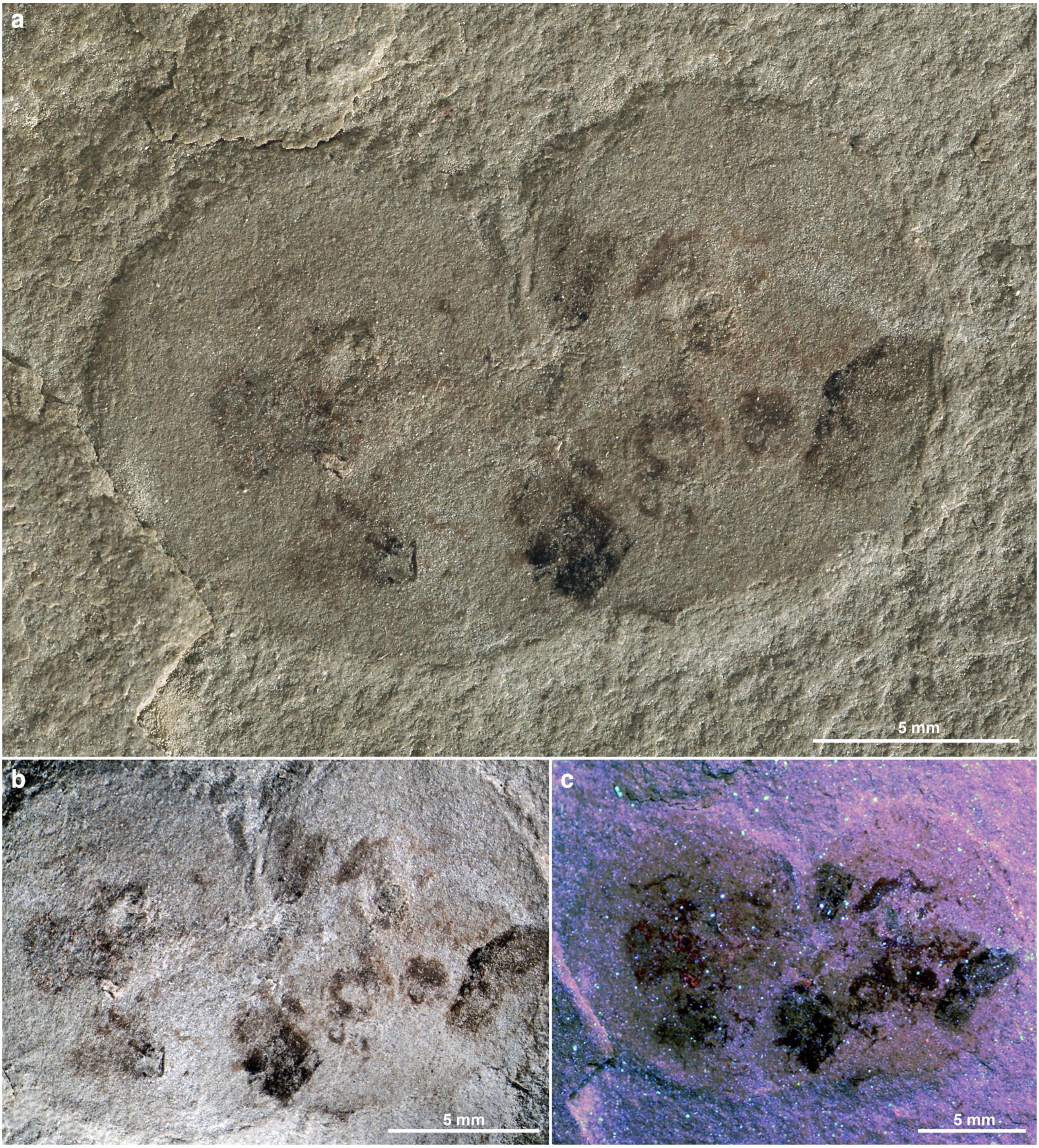

Fig. 2 Overview of the two specimens of *Metadimorphoceras* sp. (AMNH 108497) from the Bear Gulch Limestone, Montana. **a** Photo under white light, at a low angle. **b** Photo using Reflectance Transformation Imaging (RTI) at Yale University, New Haven, Connecticut. **c** Photo under blue and red light at the Soleil Synchrotron, Gif-sur-Yvette, France (color figure online)

Synchrotron in Gif-sur-Yvette, France, using various light sources (with the assistance of Pierre Guériau). The specimens from the Bear Gulch Limestone are reposited at the American Museum of Natural History (AMNH 108497) in New York, NY, USA. The specimens of *Lingulaticeras solenoides* from the Tithonian (Upper Jurassic) of Eichstätt are on display at the Museum Bergér at Blumenberg near Eichstätt, Germany.

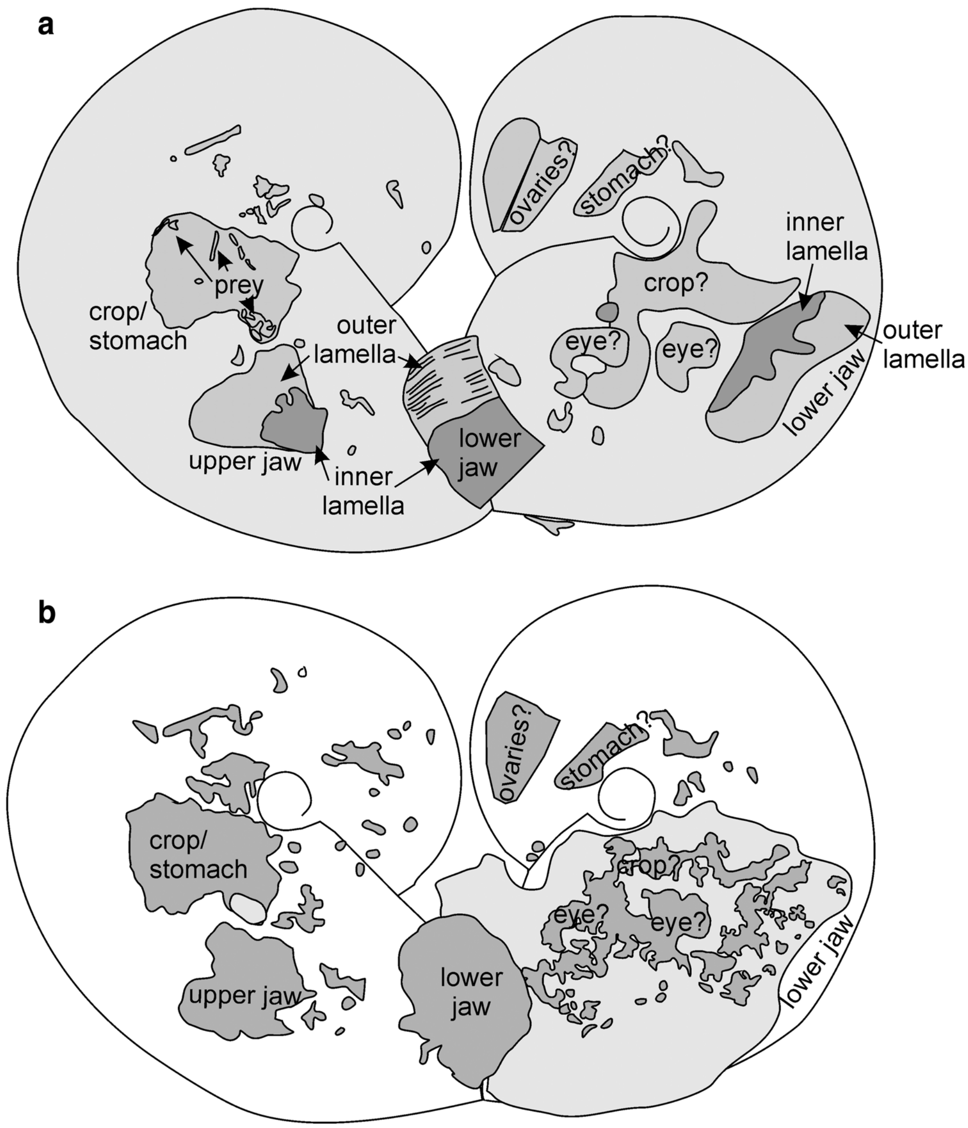

Fig. 3 Sketches with labels of our interpretations of the soft parts. **a** Drawing based on Fig. 2a. **b** Drawing based on Fig. 2c. The male is interpreted as the specimen on the left and the female is interpreted as the specimen on the right

Previous studies

Ammonoids are relatively common in the Bear Gulch Limestone and although specimens are flattened and missing the aragonitic shell, they contain traces of soft parts (Mapes 1987; Mapes et al. 2010). Landman et al. (2010: Figs. 2, 3) described several specimens with jaws that occur 30°–90° adapical of the aperture. These authors also reported black smudges at the backs of the body chambers, which they interpreted as stomach contents. They also observed two other features: a spiral red band extending from midway in the body chamber to the adapical end of the jaw, which may represent the cephalic retractor muscle, and a dark spiral band on the dorsum of the body chamber extending approximately 200° along the dorsum, which may represent the trace of the dorsal muscle.

Description

The two ammonoids are impressions on medium brownish-gray limestone (Fig. 2). In their flattened state, the diameter of the specimen on the right is 12.0 mm and the diameter of the specimen on the left is 13.0 mm. The specimen on the left is circular in shape whereas the specimen on the right is slightly ovoid, probably representing deformation due to compaction. The specimens are facing each other, with the apertures overlapping. Both specimens have a pin point umbilical opening. No sutural patterns or ornament are preserved on the flattened specimens. The aragonitic shell has been destroyed by diagenetic processes leaving only the shell impressions.

Both specimens exhibit traces of mandibles and soft parts preserved as brown carbonaceous films with black phosphatic outlines (Figs. 2, 3). The most readily

Fig. 4 Copulation in *Nautilus macromphalus,* photographed at the Aquarium in Nouméa, New Caledonia (Photo: R. H. Mapes). Note that the specimens are facing each other but their apertures are not perfectly lined up, so that the resultant arrangement is slightly asymmetrical

identifiable features are the mandibles. In the specimen on the right, they are retracted part way inside the body chamber. In the specimen on the left, what we interpret to be the lower jaw appears as a prominent brownish rectangular patch in the space between the apertures. A faint striation is visible in the lighter part of this area (Fig. 3), which is reminiscent of the growth lines on the outer lamella of the lower jaw (for a comparison, see Klug et al. 2012, 2016). The darker part of this area probably represents the more strongly tanned inner lamella of the lower jaw (for a comparison, see Klug and Jerjen 2012; Klug et al. 2012). In both specimens, possible traces of food contents occur in the position where the crop or stomach would be expected, based on a comparison with nautilus. The dark spot in the posterior part of the body chamber in the specimen on the right may represent the reproductive organs, possibly the ovaries, again, in comparison with nautilus. In addition, two structures appear in the anterior part of the body chamber of this specimen, which may represent the eyes.

Discussion

Based on the small umbilicus and age-equivalent material from the Imo Formation of northern Arkansas, as described by Gordon (1964) and Saunders (1973), the most likely candidates for the Bear Gulch ammonoids are the homoceratid goniatite *Rhadinites* Saunders, 1973, the anthracoceratid goniatite *Anthracoceras* Frech, 1899, and the dimorphoceratid goniatite *Metadimorphoceras* Moore, 1958. However, the much larger diameter at sexual maturity in *Rhadinites* (56.5 mm, as reported in Saunders 1973) and *Anthracoceras* (80.0 mm, as reported in Saunders 1973) eliminates them as possibilities (unless they are juveniles). The largest specimens of *Metadimorphoceras* in North America are approximately equivalent in diameter to the specimens from the Bear Gulch, although European specimens are known to attain larger diameters. This genus has not previously been identified from the Bear Gulch Beds, but it is present in age-equivalent strata (the Imo Formation) in Arkansas (Manger and Quinn 1972; Manger and Pareyn 1979). Our specimens cannot be identified to species level because they lack ornament and sutural patterns, which have been destroyed by dissolution. The two ammonoids are nearly equal in diameter and, on this basis, cannot be sorted into dimorphs. In addition, they lack mature morphological features such as apertural modifications, revolving *Runzelschicht* (wrinkle layer), or changes in the coiling of the body chamber. Indeed, sexual dimorphism is generally rare in Paleozoic ammonoids (see review in Klug et al. 2015).

The two ammonoids are locked together as in an embrace (Figs. 2, 3). Although ammonoids are relatively common in the Bear Gulch Limestone, this is the first instance of two specimens recovered side by side. As in other ammonoids from the Bear Gulch Beds, these specimens contain traces of jaws and soft parts. For example, the lower jaw is present in both specimens; in the left specimen, it occurs near the aperture and in the right specimen, it occurs farther back inside the body chamber.

We think that it is unlikely that the juxtaposition of these two specimens is due to random settling on the sea floor. Instead, we interpret this association as the result of ammonoid behavior, possibly copulation, combat (rivalry), or cannibalism. We consider cannibalism as the least likely scenario because, if it were true, one of the animals would have left after it ate its meal. Instead, the animals must have died at the same time because both of them are locked together in a fatal embrace and both of them show the same mode of preservation.

We favor the copulation hypothesis. Because of the difference between the ectocochliate versus endocochliate condition in cephalopods, different copulation strategies

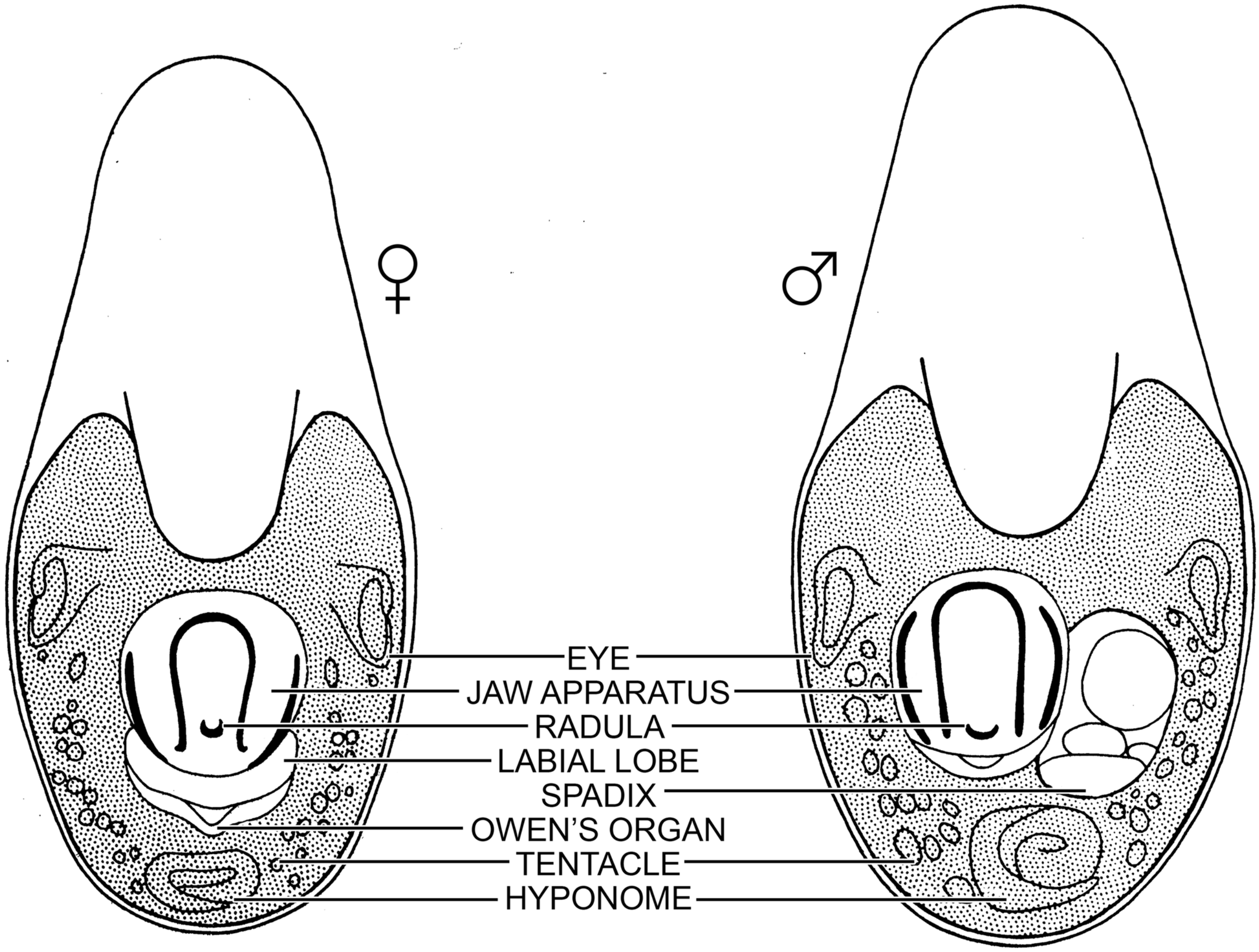

Fig. 5 Cross sections of mature female (left) and male (right) specimens of *Nautilus belauensis*. In the male, the spadix is located on the left side of the animal causing the jaw to be displaced to the right side Modified from Saunders and Ward (1987)

are required in the two groups to reduce the vulnerability from predators during copulation. Ammonoids probably followed the behavioral pattern observed in modern nautilus. In nautilus, the two shells face each other, but are slightly asymmetrical because the spadix containing the sperm is located on the left side of the male (Figs. 4, 5).

As noted in the description of AMNH 108497, the specimen on the left is circular in outline whereas the specimen on the right is slightly ovoid in outline, having been deformed during preservation. The specimen on the left also overlaps the specimen on the right. Based on the presumption that the reproductive organ of the male was asymmetrically displaced like that in nautilus, the male would have been slightly shifted to the side of the female, so that the male could insert its sperm into the female reproductive receptacle. This asymmetry may help explain the difference in deformation between the two specimens. If these two specimens were indeed copulating, we interpret the specimen on the right as the female and the specimen on the left as the male, which is supported by the possible presence of ovaries in the specimen on the right (Figs. 2, 3).

This example of two ammonoids preserved side by side is not unique. We illustrate two specimens of *Lingulaticeras solenoides* from the Upper Jurassic of Germany (Fig. 6). Both specimens are mature microconchs with lappets at the aperture (for a comparison, see Klug et al. 2015). The apertures are interlocked, but both specimens are preserved in the same plane of symmetry and their mandibles occur in situ at the anterior end of the body chamber. In addition, soft tissues, possibly comprising the stomach, crop, and oesophagus are preserved in the middle of the body chamber. Because both specimens are microconchs, they probably belonged to the same sex, presumably males, thus making reproductive behavior an unlikely explanation for their juxtaposition. An alternative, more likely explanation is rivalry for food or mating partners (Fig. 6).

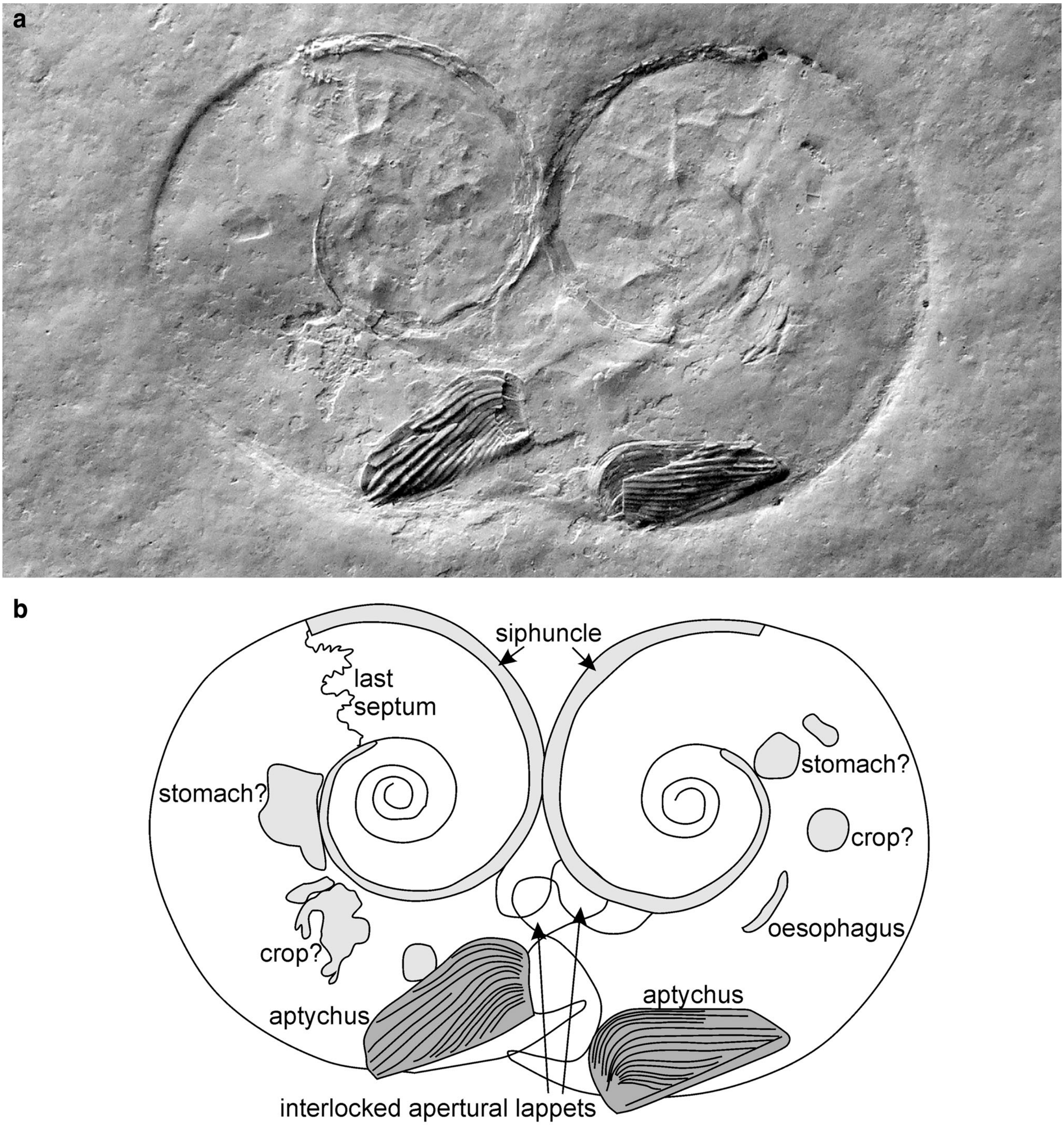

Fig. 6 Pair of *Lingulaticeras solenoides* from the Tithonian (Upper Jurassic) of Eichstätt, Germany, on display in the Museum Bergér, Eichstätt, Germany. **a** Photograph under white light, taken at the museum. **b** Interpretative sketch. In this example, reproduction is an unlikely explanation for the juxtaposition because both specimens are microconchs, presumably males. An alternative explanation is a struggle involving rivalry for food or mating partners. Specimens are approximately 35 mm in diameter

Examples of animal behavior frozen in time are rare (Boucot 1990). The reason that such fossils exist at all is that many animals lack the ability to track changes in their environment when they are engaged in an all-consuming activity such as feeding, fighting, or reproduction. For example, one of the best documented records of frozen behavior involves aquatic turtles from the Eocene Messel Pit between Darmstadt and Frankfurt, Germany (Joyce et al. 2012). The turtles occur as pairs of males and females, presumably reflecting mating behavior. Evidently, the turtles began mating near the surface of the water, but while copulating, they sank into the deeper poisonous portions of the lake where they died. This interpretation is consistent with our hypotheses presented above in which copulation or a fight for survival or mating partners may have distracted the ammonoids, so that they sank into the poorly oxygenated waters near the bottom and became asphyxiated. We coin the new term "distraction sinking" for this potentially lethal behavior resulting in the preservation of exceptional fossils.

Conclusions

Given the diameters of the specimens and the tightness of the umbilical opening, the Bear Gulch ammonoids are probably dimorphoceratid goniatites that belong to the genus *Metadimorphoceras*. Based on the position of the organs in modern nautilus, we identify the carbonized traces as jaws, stomach contents, and possible remains of the ovaries and eyes. If correct, this marks the first and oldest report of ovaries and eyes in ammonoids. No trace of arms or hood was detected, suggesting that these structures were either absent or too fragile to be preserved.

Ammonoids in the Bear Gulch Limestone are moderately common (Landman et al. 2010), but we are unaware of any other paired specimens preserved with their shells in contact with each other from this stratigraphic unit. Thus, we reject the hypothesis that this ammonoid occurrence represents a random taphonomic event. Instead, we interpret the position of the two nearly identically sized specimens as evidence of copulation, in line with the reproductive strategy of nautilus.

Geologic occurrences of paired ammonoids preserved face-to-face are rare in the fossil record. Such occurrences have usually been treated as taphonomic artifacts and have been considered as curiosities (Szives et al. 2007). Indeed, the majority of such occurrences are probably due to random settling on a single bedding plane. However, in the fossils described here (from the Bear Gulch Limestone of Montana and the Upper Jurassic of Germany), the combination of soft tissue preservation, similar orientation of the shells, and tightly interlocked apertures suggests that they represent instances of behavior frozen in time. Because these ammonoids were distracted by copulation or fighting, they did not realize that they were sinking into the oxygen depleted waters near the bottom, leading to asphyxiation.

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