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Growth and function of spines in Jurassic and Cretaceous ammonites

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ABSTRACT

Spinose ammonoids occur in Earth history from the origin to the extinction of the subclass. In many cases, entire groups were concerned. The growth of spines in Kimmeridgian (Jurassic) aspidoceratids are described, discussed, and their construction and possible functions are compared with those of euomphaloceratine ammonites from the lower Turonian (Cretaceous) of Mexico, Venezuela and Brazil, and with those of collignoniceratid ammonites from the lower Coniacian of Venezuela. The basic construction of spines is similar in all taxa, irrespective of their position, length or the geological age of the taxon. It is suggested that shell secretion for spine formation may have been rapid compared with that of the rest of the shell. Spines do not appear to have been suitable for protection against predators or for a demersal or epibenthic mode of life. Instead, a sensory function is probable, but only for the outermost one to three pairs of spines near the aperture. An increased weight of the body chamber and increased friction during rocking motions and thus a stabilization of the shell in the open-water column are additional plausible explanations for the function of spines sealed by a basal septum.

1. Introduction

Ammonites display a wide range of morphologies and ornamentation. The anatomy and function of long spines in ammonites were studied by Checa and Martin-Ramos (1989), on the basis of the Upper Jurassic genera *Aspidoceras* and *Orthaspidoceras*, and by Batt (1989) on the basis of morphotypes from the Cenomanian–Turonian of the Western Interior Seaway. Keupp (2000) summarized these and other interpretations and suggested that spines served as balancing aids, for water canalization used in filter-feeding nutrition, or that they had sensory and defensive functions. He favoured a demersal mode of life for spinose aspidoceratids. Here we describe and interpret the growth and function of spines in Jurassic aspidoceratids from the Kimmeridgian of Germany, and in euomphaloceratine and collignoniceratine ammonites from the Turonian of Mexico, Venezuela and Brazil.

2. Localities, material and preservation

2.1. Kimmeridgian (Upper Jurassic) Lithographic Limestone, Nusplingen, Germany

The ammonites from the Nusplingen Lithographic Limestone in south-western Germany were collected and described formally by Schweigert (1998). They are of late Kimmeridgian (Late Jurassic) age. The ammonites are preserved as flattened impressions, occasionally as flattened internal moulds in bioturbated beds. Sutures are only exceptionally preserved, but the presence of material with sipho and shell collapse structures allows us to estimate the size of the preserved body chambers. The ammonite shells were generally embedded laterally, and many were damaged by predators before burial (Schweigert, 1998). The calcitic aptychi are occasionally preserved as thick porous calcitic layers (Schweigert, 1998; Schweigert and Dietl, 1999; Schweigert, 2009).

A three-dimensionally preserved *Epaspidoceras rupellense* from Aalen was illustrated by Ziegler (1987, pl. 6, fig. 1); its precise age is unknown but an early Kimmeridgian age (late Planula or early Platynota Zone) is most likely. All specimens are housed in the Staatliches Museum für Naturkunde, Stuttgart (SMNS). The spines of these ammonites are preserved on internal whorls, irrespective of their mode of preservation.

2.2. Lower Turonian Platy Limestone, Vallecillo, Mexico

The spinose ammonites from Mexico studied here were collected from the Platy Limestone Member of the Agua Nueva Formation, at Vallecillo, north-eastern Mexico (Ifrim, 2006; Ifrim and Stinnesbeck, 2007). The specimens are housed in the Facultad de Ciencias de la Tierra (FCT) of the Universidad Autónoma de Nuevo León (UANL-FCT) in Linares, and in the Colección

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Paleontológica de Coahuila (CPC), Museo del Desierto de Coahuila (MuDe) in Saltillo, Mexico. The registration codes are UANL-FCT-VC (VC for Vallecillo) and CPC, respectively.

The ammonites are generally preserved as flattened impressions in the sediment. The body chamber is present in many specimens, in some cases as flattened internal moulds. Most ammonite shells from Vallecillo were laterally embedded, but some were deposited in a vertical or oblique position (see e.g., Ifrim, 2013, fig. 2, or Fig. 1 herein), indicating a soft sediment and a calm environment on the seafloor. Fine details of sculpture and growth lines are particularly well preserved in large ammonites. The outermost suture line is partially visible in some specimens. The phragmocones are less well preserved, because the empty shells collapsed under sediment overburden, and the septa are crushed irregularly. The fact that only one side of the aragonitic ammonite shells is preserved indicates a sensitive equilibrium between dissolution of aragonite and preservation before burial. Among hundreds of ammonites collected, only two specimens of less than 100 mm diameter were found. Specimens with less than 100 mm diameter usually preserve only the sipho, suggesting that their shells were dissolved either before being embedded or during early diagenesis.

The spines of the ammonites from Vallecillo are preserved in the same way as the shells, in many cases as imprints and rarely as black recrystallized calcite (Ifrim, 2013, fig. 10). They are usually preserved on the body chamber, with only a single phragmocone with spines on the outermost half whorl found. All spinose specimens are assigned to the lower Turonian *Pseudaspidoceras flexuosum* Powell, 1963. In this species, spines have never been observed on internal whorls, neither from Vallecillo nor from other localities, indicating that they were either resorbed or secondarily discarded (Ifrim, 2013). The only other spinose specimen is a *Kamerunoceras turoniense* (d'Orbigny, 1850), a species previously not recorded from this locality (Fig. 2).

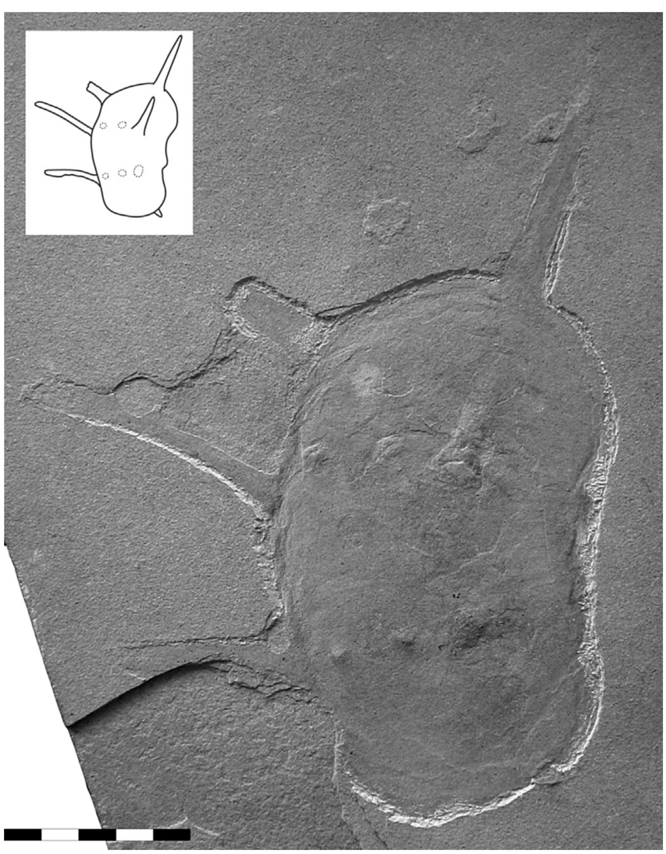

Fig. 1. Spinose specimen of *Pseudaspidoceras flexuosum*. Lower Turonian of Vallecillo, Mexico, UANL-FCT-VCII/95B. This is the only specimen that shows the full length of the spine. However, the most adapical spine is shortened as a result of compaction. The left outermost spine is broken, whereas the right spine is preserved in full length. The variation in bending is comparable to that in other spinose ammonoid species. Scale in cm.

2.3. Lower Turonian–lower Coniacian of the La Luna Formation, Venezuela

The spinose ammonites from Venezuela studied here were collected by Otto Renz from the La Luna Formation, interpreted as a pelagic limestone (1982). The specimens are housed in the Naturhistorisches Museum Basel (NHMB). Part of the material has been described (Renz, 1982), e.g. *Pseudaspidoceras armatum* Renz, 1982. These specimens were placed in synonymy with *K. turoniense* by Chancellor et al. (1994). Revision of the Renz material by CI led to the discovery of three unpublished specimens of *P. flexuosum*, a taxon previously unknown from Venezuela.

The ammonites from Venezuela are uncompressed and partly preserved with recrystallized shells, including fine details of the ornament such as striae and growth lines. Specimen NHMB Re6850 is preserved in several fragments, allowing to remove the shell with spines to study the striation. This specimen thus allows us to study the internal structure of spines and their impact on shell formation.

2.4. Lower Turonian of the Cotinguiba Formation, Sergipe Basin, north-eastern Brazil

The specimens of *Pseudaspidoceras flexuosum* from Brazil were collected by PB from the *Vascoceras harttii* Zone (Bengtson et al., 2018), exposed in quarries near the town of Laranjeiras, Sergipe. *P. flexuosum* was described from Sergipe by Gale et al. (2005, p. 180, fig. 7g-h). However, we regard the determination of their fragmentary specimen as doubtful and did not include it in our study. The specimen of *Kamerunoceras turoniense* derives from the *Mammites nodosoides* Zone (Bengtson et al., 2018), locality São Roque 2, Sergipe (Bengtson, 1983).

The ammonites are preserved as three-dimensional internal moulds, in places with striation, epizoic bivalves and bryozoans preserved on the body chambers. The conchs are slightly compressed. The body chambers are better preserved than the internal whorls. The Brazilian specimens are housed in the collections of the Natural History Museum in Stockholm, Sweden (collection prefix: NRM-PZ).

3. Construction of the spines

Growth of the spines is reconstructed mainly from microscopic observation of growth lines of three-dimensionally preserved specimens of *Kamerunoceras turoniense*, *K. andinum* and *Pseudaspidoceras flexuosum* from Venezuela. Observations were confirmed by well-preserved *P. flexuosum* from the Vallecillo Platy Limestone of Mexico. According to the 'Treatise on Invertebrate Paleontology' (Wright et al., 1996), both genera belong to the subfamily Euomphaloceratinae, as does the upper Cenomanian spinose *Euomphaloceras septemseriatum* (Cragin, 1893). Preservation and construction of spines can be compared to those of early Coniacian *Prionocycloceras* and Jurassic aspidoceratids, the latter preserved in different ways.

3.1. Upper Jurassic Aspidoceratidae

Checa and Martin-Ramos (1989) discussed the anatomy and function of spines in *Aspidoceras* and *Orthaspidoceras* from Spain. Aspidoceratid spines generally extend laterally (Fig. 3D–E) and