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THE OLDEST GONDWANAN CEPHALOPOD MANDIBLES (HANGENBERG BLACK SHALE, LATE DEVONIAN) AND THE MID-PALAEOZOIC RISE OF JAWS

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Abstract: It is widely accepted that the effects of global sea-level changes at the transition from the Devonian to the Carboniferous are recorded in deposits on the shelf of northern Gondwana. These latest Devonian strata had been thought to be poor in fossils due to the Hangenberg mass extinction. In the Ma'der (eastern Anti-Atlas), however, the Hangenberg Black Shale claystones (latest Famennian) are rich in exceptionally preserved fossils displaying the remains of non-mineralized structures. The diversity in animal species of these strata is, however, low. Remarkably, the organic-rich claystones have yielded abundant remains of Ammonoidea preserved with their jaws, both *in situ* and isolated. This is important because previously, the jaws of only one of the main Devonian ammonoid clades had been found (Frasnian Gephuroceratina). Here, we describe four types of jaws of which two could be assigned confidently to the Order Clymeniida and to the Suborder Tornoceratina. These findings imply that chitinous normal-type jaws were likely to have already been present at the origin of the whole clade Ammonoidea, i.e. in the early Emsian (or earlier). Vertebrate jaws evolved prior to the Early Devonian origin of ammonoids. The temporal succession of evolutionary events suggests that it could have been the indirect positive selection pressure towards strong (and thus preservable) jaws since defensive structures of potential prey animals would otherwise have made them inaccessible to jawless predators in the course of the mid-Palaeozoic marine revolution. In this respect, our findings reflect the macroecological changes that occurred in the Devonian. [Correction added on 28 July 2016 after first online publication: In the Abstract, the sentence "Vertebrate jaws probably . . . in the Early Devonian" was amended]

Key words: Cephalopoda, Ammonoidea, mass extinctions, macroecology, Devonian, Morocco.

TWO of the ten most severe mass extinctions occurred during the Devonian, as far as reduction of biodiversity is concerned (Sepkoski 1984; Korn 1993, 2000; Bambach *et al.* 2004; Alroy 2010; McGhee *et al.* 2013; McGhee 2014), namely the late Frasnian Kellwasser Event and the latest Famennian Hangenberg Event. Both events are characterized by widespread deposition of sediments under oxygen-poor conditions (Buggisch 1991; Wendt & Belka 1991; Algeo *et al.* 2001; House 2002). Such oxygen-depleted conditions have been documented for the Hangenberg Event in many localities in North America (Exshaw Formation), Europe (Hangenberg Black Shale) and North Africa, while in sections in Siberia, India and the Antarctic, oxic conditions have been recognized (e.g. Becker 1993; House 2002; Kumpan *et al.* 2015; Becker *et al.* 2016).

As always when it comes to large-scale mass extinctions, nearly all possible explanations for the responsible physical or chemical triggers have been proposed. For example, Sandberg *et al.* (2002) suggested that rapid sea-level changes (see also Miller *et al.* 2005) linked to a glaciation near the palaeo-south pole caused the extinctions. Recently, Long *et al.* (in press) documented a depletion in selenium near the end of the Devonian and suggested that this could have contributed to the extinctions. Algeo *et al.* (1995, 2001) as well as Algeo &

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Scheckler (1998) hypothesized that the rise of land plants (Decombeix *et al.* 2011; Gibling & Davies 2012; McGhee 2014) caused the perturbations in the carbon cycle that were widely documented for the Late Devonian global events (e.g. Xu *et al.* 1986; Buggisch 1991; Buggisch & Joachimski 2006; Kaiser *et al.* 2006, 2008, 2009, 2011, 2015; Berner 2009; Qie *et al.* 2015).

In southern Morocco, the Devonian–Carboniferous boundary strata comprising the equivalents of the Hangenberg Event are excellently exposed over a wide area (e.g. Korn 1999; Kaiser *et al.* 2011, 2015). In the eastern Anti-Atlas (Fig. 1), the latest Devonian stratigraphic interval is usually dominated by clastic deposits including clayey and sandy intervals. The supposed equivalent of the Hangenberg Black Shale is normally deeply weathered, giving particularly the black shale intervals a whitish, light greyish to pinkish appearance (Fig. 2). However, these shales show their dark original colour in depths of more than half a metre, with greater amounts of the original organic matter preserved. Both the biostratigraphic and the lithostratigraphic context suggest a correlation of this horizon with the Hangenberg Black Shale (Korn 1999; Becker *et al.* 2002; Kaiser *et al.* 2011, 2015).

Assemblages with ammonoid specimens from the Hangenberg Black Shale are known from the Rhenish Mountains (e.g. Schmidt 1924; Schindewolf 1937; Korn 1991), but so far, only three species have been identified, *Postclymenia evoluta* Schmidt, 1924, *Cymaclymenia nigra* Korn, 1991 and *Acutimitoceras* sp. These species occur either as completely flattened impressions in the black shale or as three-dimensionally preserved specimens in black nodules embedded in the Hangenberg Black Shale. For the first time, such fossils are now described from North Africa.

While sampling the late Famennian strata of the southern Ma'der for alpha diversity, we trenched in the Hangenberg Black Shale equivalent. In contrast to earlier opinions, this claystone horizon is rich in bivalves, but it also contains abundant ammonoid specimens, subordinate orthoconic cephalopod conchs, bryozoans, occasional plant remains and rare vertebrate remains (ongoing research). Even more surprisingly, the supposedly unfossiliferous interval yielded what some black shales are famous for:

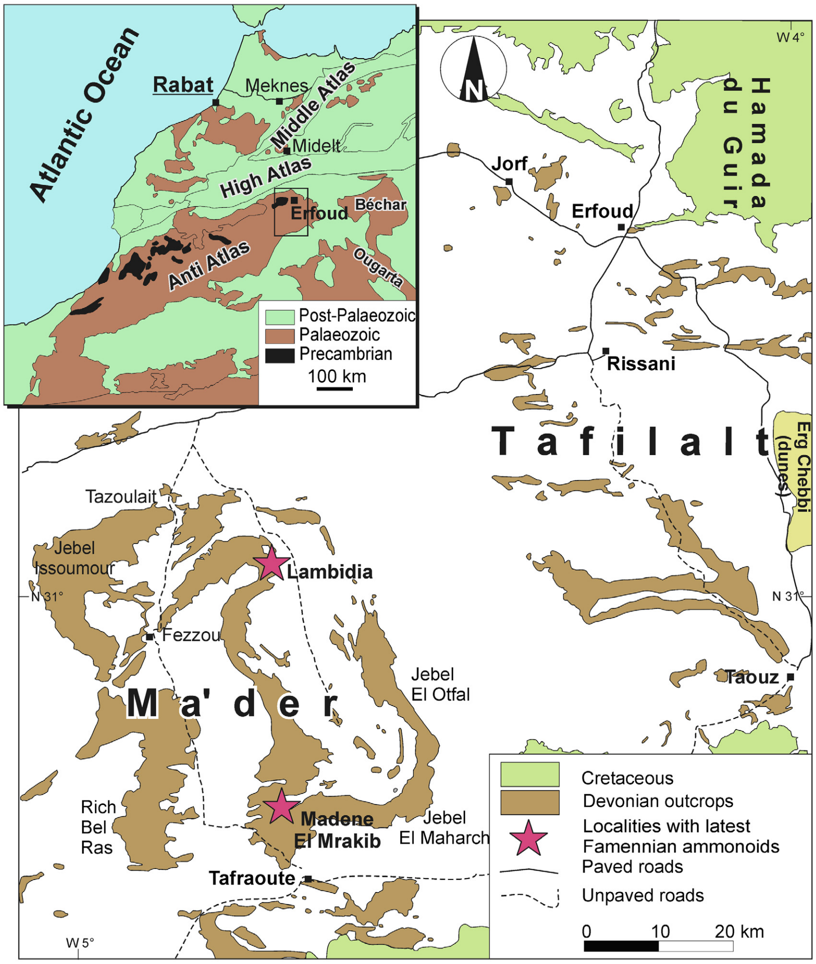


FIG. 1. Geological map of the eastern Anti-Atlas showing the localities mentioned in the text. Modified after Klug (2002). Colour online.

FIG. 2. The equivalent of the Hangenberg Black Shale at the two localities at Madene El Mrakib East (A) and West (B–D). A, latest Famennian exposed in a small canyon (HBS, Hangenberg Sandstone); note the whitish to pinkish weathered claystone of the Hangenberg Black Shale. B, one of the excavation sites (Madene El Mrakib West). C, the black shale is often covered by fallen blocks of the overlying sandstones; this site yielded the best organic preservation. D, detail of the black shale interval; note the colour changes and the decreasing weathering; the yellowish layer above the Swiss army knife is a sandstone devoid of macrofossils.

exceptionally preserved fossils. For instance, we discovered ammonoid jaws in organic preservation *in situ* as well as further undifferentiated organic remains of the animals (probably soft body remains; Figs 3–5). This is surprising because such preservation was previously unknown from the African Devonian occurrences and Palaeozoic cephalopod jaws have, to our knowledge, never been reported from Gondwana before. We are not aware of older occurrences of unequivocal cephalopod jaws, but it should be mentioned that a circular structure named *Aptychopsis* has been recorded from Silurian strata (Holland *et al.* 1978; Turek 1978; Dzik 1981). This fossil has been reported in association with orthocones and it is not entirely clear if this structure is homologous with other cephalopod jaws.

The new material is important because Devonian ammonoid mouth parts have been described previously mainly from the Frasnian gephuroceratids (Woodward 1885; Trauth 1927–1936; Matern 1931; Clausen 1969; Tanabe *et al.* 2015), only rarely from Famennian ammonoids (Frye & Feldmann 1991; Korn 2004) and more often from the Carboniferous (Closs 1960, 1967; Mapes 1987; Bandel 1988; Tanabe & Mapes 1995; Doguzhaeva *et al.* 1997; Doguzhaeva 1999; Landman *et al.* 2010). Remarkably, the above mentioned Frasnian occurrences still are the oldest records of cephalopod jaws worldwide although cephalopod conchs are reasonably to very common in strata dating from the latest Cambrian to the present day.

The new material comprises flattened, but otherwise well-preserved secondarily carbonaceous jaws, displaying several delicate morphological details. Such discoveries yield valuable morphological information helping us to establish and test phylogenetic and potentially also trophic relationships (e.g. Tanabe & Fukuda 1999; Kruta *et al.* 2011, 2015; Tanabe *et al.* 2015).

Herein, we: (1) portray the occurrence of the oldest Gondwanan cephalopod jaws; (2) describe the various forms of ammonoid jaws; (3) illustrate the accompanying fauna; (4) discuss their taphonomy; and (5) the ecological as well as (6) evolutionary implications.

MATERIAL AND METHOD

Geological setting and localities

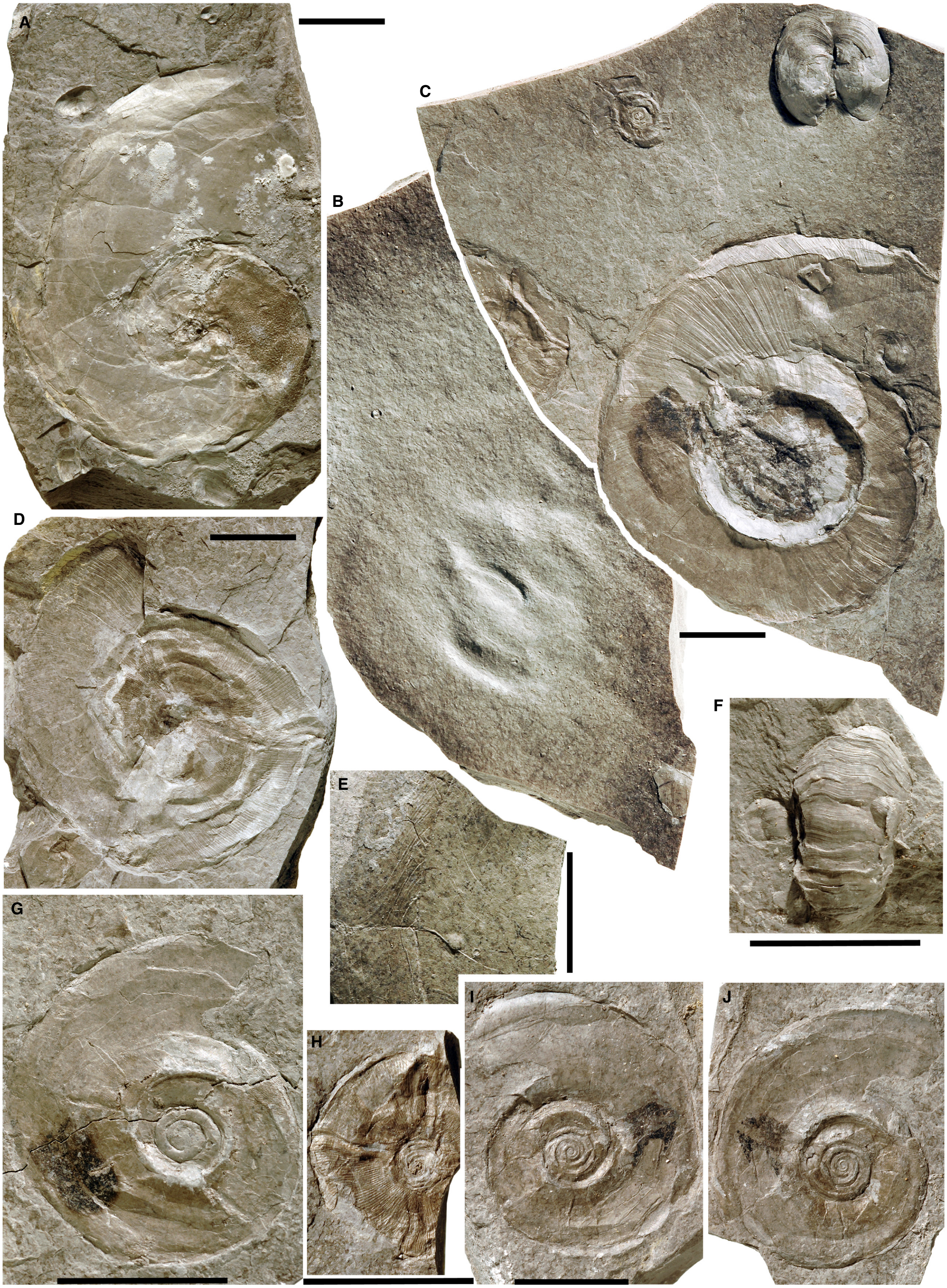
Devonian marine deposits crop out over a distance of about 1000 km in Morocco. These outcrops find their continuation to the east in Algeria and Libya, amounting to a total longitudinal extent of over 2500 km (e.g. Conrad 1985; Wendt *et al.* 2006). In the eastern Anti-Atlas (Morocco), the marine Devonian sediments were accumulated in two small basins, namely the Ma'der and the Tafilalt basins (Fig. 1), separated by a moderately shallow marine ridge and surrounded by exposed areas to the south, west and north (Wendt 1985, 1988; Kaiser *et al.* 2011). All specimens described herein derive from the outcrops in the Ma'der Basin, which extends over <100 km in width.

In the Ma'der Basin, Eifelian and early Givetian deposits are mainly composed of carbonates and fine-grained clastics (Kaufmann 1998). These are overlain by a predominantly clayey succession of laterally strongly varying thickness (Wendt 1985, 1988). In the middle Famennian, some sideritic and calcareous layers are intercalated. At the top of the Devonian succession, a supposed regional equivalent of the Hangenberg Sandstone, several metres thick, forms a distinct index horizon, capping the fine-clastic succession (Fig. 2A–C). The sandstone body is overlain by a thick succession of shale and siltstone of the Tournaisian (Korn *et al.* 2007). Estimates of palaeobathymetry (ongoing research) suggest a maximum basin depth of 300–400 m in the Middle Devonian (based on the presence of a 200–300 m high reef-mound on the slope of the Ma'der Basin; Kaufmann 1998), a slight deepening during the Frasnian and rather high sea-levels during much of the Famennian, followed by a shallowing in the latest Famennian (e.g. Wendt & Belka 1991; Kaiser *et al.* 2011).

We excavated the Hangenberg Black Shale equivalent (Fig. 2) at three localities in the Ma'der Basin (Fig. 1). In all three localities, this stratigraphic interval turned out to be fossiliferous and the fossil content appears to be very similar. According to the presence of *Postclymenia calceola* Klein & Korn, 2014, the fossiliferous interval can be confidently correlated with the Postclymenia genozone and the Middle praesulcata conodont zone (Becker *et al.* 2002, 2016). The association found in this stratigraphic interval is dominated by small bivalves, occasional plant remains, moderately common ammonoid specimens and slightly less common orthoconic cephalopods, as well as bryozoans. Two chondrichthyan teeth have also been discovered.

The best preserved material was found around Madene El Mrakib in the southern Ma'der, north-east of the village of Tafraoute (Fig. 1). This region became famous for giant trilobites (Struve 1990), Famennian ammonoids (Petter 1959; Korn 1999; Becker *et al.* 2000, 2002; Klein & Korn 2014; Korn *et al.* 2014*a*, 2015*a*, *b*) and also placoderms (Lehman 1956, 1964; Rücklin 2010, 2011; Rücklin & Clément in press). One of the localities (30.733572°N, 4.718793°W) is near the summit of a hill, which is covered by the thick supposed Hangenberg Sandstone equivalent. This hill lies in a small, roughly east–west striking graben structure. The excavation site is called Madene El Mrakib West herein.

FIG. 3. Flattened ammonoids with beaks from the Hangenberg Black Shale of Madene El Mrakib West. A, E, Tornoceratoidea sp., adult specimens, note the growth lines and the strongly developed wrinkle layer (brownish); A, PIMUZ 31550; E, PIMUZ 31553. B–D, *Mimimitoceras* sp.; B, C, PIMUZ 31551, specimen with jaw remains and an organic coating between the jaw and the last septum; B, imprint of the specimen formed by compaction (cf. Seilacher *et al.* 1976); C, actual specimen; note the characteristic growth lines and the large lower jaw; D, PIMUZ 31552, note the constrictions and growth lines. F, H, *Acutimitoceras* sp.; F, PIMUZ 31555, vertically embedded juvenile specimen (note the coarse growth lines and constrictions); H, PIMUZ 31556, juvenile specimen (note the coarse growth lines and constrictions). G, I, J, *Postclymenia calceola* Klein & Korn, 2014 with lower jaws *in situ* and preserved sutures; G, PIMUZ 31554, semi-3D preserved inner whorls; I, J, slab and counterslab of PIMUZ 31557; lower jaw, wrinkle layer, ammonitella with initial chamber visible. All scale bars represent 10 mm. Colour online.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Similarly preserved material was excavated 1.3 km further north (30.756185°N, 4.714377°W). This locality is here dubbed Madene El Mrakib East.

The third locality did not reveal the same kind of carbonized fossil preservation, but essentially the same taxa (PIMUZ 31558, 31578, 31579). It is located west of the village of Lambidia (31.035181°N, 4.725605°W).

At all three places, it was necessary to remove some tens of centimetres of the deeply weathered claystone. The fossils are distributed unevenly in the horizon; some bedding planes are devoid of macrofossils while others are covered by deformed bivalves, ammonoids and other macrofauna.

Specimens

The material is stored in two places. All specimens with the abbreviation PIMUZ are kept at the Paläontologisches Institut und Museum of the University of Zurich (Switzerland). In most cases, we have additional specimens of the same quality as the illustrated one; in such cases, we returned the material to the Ministère de l'Energie, des Mines, de l'Eau et de l'Environnement (Rabat, Morocco).

Method

The fine-grained claystone is not metamorphosed and is extremely soft. Once the deeply weathered claystone was removed, we started splitting packages of clay by hand, sometimes with a hammer. In most cases, the fossils were more or less completely exposed immediately, in a few cases, details were prepared with needles. The photographs were taken without coating in order to show the subtle details in colouration of the fine carbon films.

Some details were imaged using the SEM (JEOL JSM-6010PLUS/LV) of the Paläontologisches Institut und Museum of the University of Zurich (Switzerland). The specimens were uncoated both for photography and for SEM-examination.

RESULTS

Ammonoid preservation and taxonomy

Ammonoids are quite common in the stratigraphic interval under consideration. The shell material of the specimens is completely dissolved and the conchs are largely flattened, most likely corresponding to the amount of clay compaction. Minute juveniles (early post hatching stages) are common. In some cases, dark organic coatings (carbon film) are preserved, sometimes limited to the body chamber between the last septum and the jaws (Fig. 3B, C). Although shell material is not preserved, all of the preadult and adult specimens preserve the wrinkle layer (e.g. Keyserling 1846; Walliser 1970; Korn *et al.* 2014*b*, and references therein). The wrinkle layer is so well preserved that it aids taxonomic assignment of the flattened specimens.

In spite of their strong deformation, most of the larger specimens display impressions of growth lines, constrictions and often even suture lines because of deposition in the fine-grained sediment. In combination with the knowledge of the fauna in three-dimensional preservation from other localities, this morphological information enabled us to assign most of the larger ammonoid conchs at least to generic level.

Postclymenia calceola Klein & Korn, 2014 belongs to the most common species. It was described by Korn *et al.* (2004) under the name *Postclymenia evoluta* Schmidt, 1924, from the northern Ma'der, from more or less coeval strata and later described under a new species name (Klein & Korn 2014). Its assignment is corroborated by the characteristic lateral lobe, which is preserved in several specimens (e.g. PIMUZ 31561; Fig. 4G, H). Additionally, it is the only species in this fauna, which has a moderately wide umbilicus (umbilical width/diameter *c.* 0.40 according to Korn *in* Klein & Korn 2014).

The ammonoid wrinkle layer (Korn *et al.* 2014*b*, and references therein) usually extends over one-third to about half a whorl; it consists of narrow transverse ridges (Fig. 5B). One whorl fragment (PIMUZ 31563) of a body chamber of a probably adult specimen is covered by several bryozoan colonies and also shows a finely pitted surface (Fig. 5A), reminiscent of Ritzstreifen (Sandberger &

FIG. 4. Orthocones and morphological details of ammonoids from the Hangenberg Black Shale of Madene El Mrakib. A, B, undetermined bactritids; A, PIMUZ 31558, fragmentary phragmocone; B, PIMUZ 31559, nearly complete specimen with body chamber revealing the curved growth lines and the peristome. C, PIMUZ 31551, detail of Fig. 3C showing the lower jaw in the body chamber. D–H, complete specimens of *Postclymenia calceola* Klein & Korn, 2014 with lower jaws *in situ* and sutures; D, E, PIMUZ 31560, with well-preserved normal-type lower jaw; D, detail showing the jaw with growth lines on the wings; E, overview; F–H, PIMUZ 31561, with lower jaw and wrinkle layer; F, detail showing the jaw with fractured organic remains and the wrinkle layer; G, overview; H, detail of the characteristic suture lines and the overprinted wrinkle layer. I, J, Tornoceratoidea sp.; I, PIMUZ 31562, juvenile specimen with ventrolateral furrow and organic structures in the body chamber; J, PIMUZ 31550, probably adult specimen with strongly developed wrinkle layer (brownish). Scale bars represent 10 mm (A–C, E, G, I, J) 1 mm (D, F, H). Colour online.

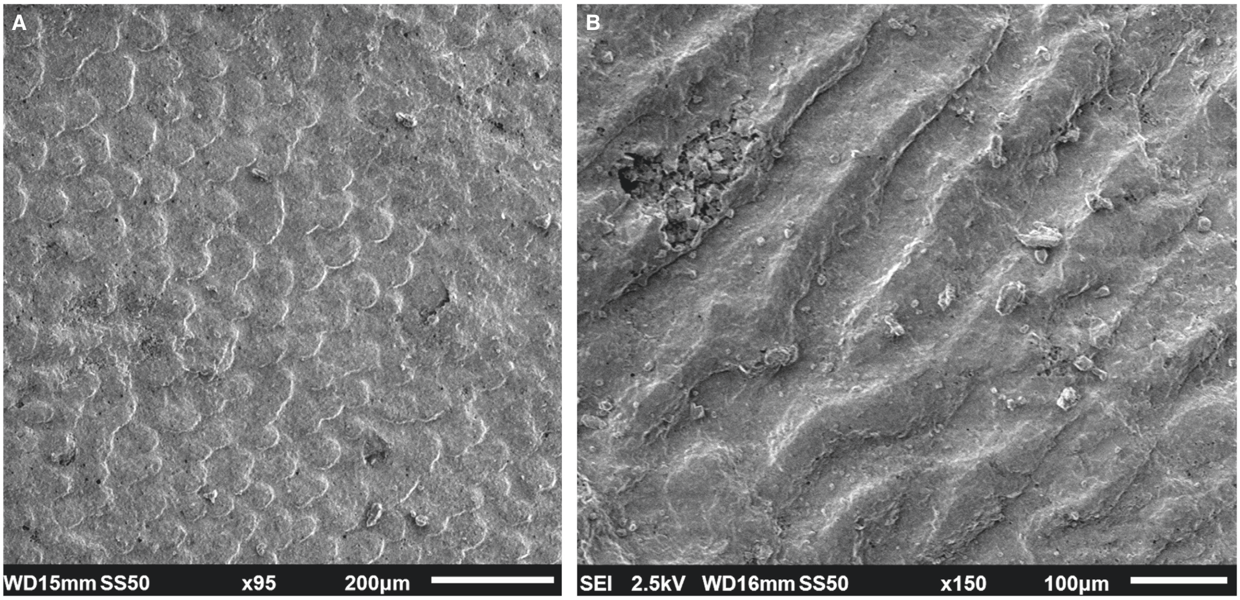

FIG. 5. SEM-images of fine structures on conchs of *Postclymenia calceola* Klein & Korn, 2014 from the Hangenberg Black Shale of Madene El Mrakib. A, shell surface structure on the body chamber, PIMUZ 31563. B, wrinkle layer, PIMUZ 31557.

Sandberger 1850–1856; House 1971; Korn 1985; Klug 2001), although here, the pits are not arranged in lines; they are crescent-shaped, *c.* 50 µm wide, slightly asymmetric, with a slightly inclined and a steeper side, and distributed over the ventral and lateral parts of the shell. Presumably, it is also the casts of small elevations that are preserved, probably from the inside of the conch.

Mimimitoceras sp. is the second most common taxon. It can be recognized by the strongly developed, broadly rounded rursiradiate growth lines and the practically closed umbilicus in the adult stage (PIMUZ 31551; Fig. 3C, D). Remarkably, this species either did not develop a wrinkle layer or it is not preserved. The largest available specimen PIMUZ 31551 (diameter 46 mm; Fig. 3B, C) is preserved with the lower jaw *in situ*. The jaw is 12.5 mm long and quite dark due to a comparatively thick carbon film. Interestingly, the part of the body chamber behind the jaw is rather dark, probably also due to a fine carbon layer. This points to the potential for soft-tissue preservation in ammonoids at Madene El Mrakib.

Acutimitoceras sp. is represented by two small impressions with strong constrictions of the juvenile shells (Fig. 3F, H). The constrictions with biconvex course allow genus determination even in vertically embedded specimens (PIMUZ 31551; Fig. 3F).

We discovered several specimens (Tornoceratoidea indet.) with a conch that is rather smooth except for a distinct wrinkle layer. Since the conch has a closed umbilicus, the area covered by the wrinkle layer is rather wide and is easily recognized because it is somewhat darker and brownish (PIMUZ 31550; Figs 3A, 4J). In this case, the wrinkle layer consists of a rather regular rugosity without distinct ridges. Even small specimens (diameter *c.* 10 mm) show this wrinkle layer. The growth lines are much finer than in *Mimimitoceras* sp. They have a broad lateral sinus, a high ventrolateral projection and a ventral hyponome sinus (PIMUZ 31553; Fig. 3E). We have not found jaws in the conchs of this species yet.

A small specimen (PIMUZ 31573, diameter *c.* 10 mm) is broken and the last half whorl is slightly dislocated. Like the conchs described before, this one also has a rather high whorl expansion rate, clearly higher than in *Mimimitoceras* sp., and fine growth lines with high ventrolateral projections (Fig. 4I). The specimen has a distinct ventrolateral ridge paralleled by a furrow. It is likely that this is a juvenile of the specimen described above. The finds are the first records of non-prionoceratid tornoceratids in the Hangenberg Black Shale and its equivalents.

Jaw morphology

We found four morphologically different jaw types. According to their shape, we think that most of them are lower jaws.

Type 1. This is the most common jaw type. It can be recognized easily by the strong concentric growth lines of the wings of the outer lamella (Fig. 6A–C, E, F). The inner lamella appears to be very narrow. It is visible in the specimen in Figure 6E, on the right. The overall morphology of this ammonoid jaw is unique among ammonoids. The central part of the outer lamella is drop-shaped and carries a thick carbon coating. This carbonaceous layer shows parallel fractures, which probably formed during diagenesis. The dark central part is peculiar because we are not aware of other ammonoid jaws where the thickness of the carbonaceous layer (and thus the visibility of growth lines) varies so strongly between the elongate middle part of the outer lamella and the rounded subtriangular wings of the outer lamella.

Type 2. This type is also quite common and reaches reasonably large sizes. The largest specimen (PIMUZ 31572, Fig. 6I, J) is 23 mm wide and 21 mm long in its flattened state. It has a large outer lamella with long and rounded wings. In some specimens, the inner lamella seems to be very short, most likely due to compaction. Before deformation, it was probably oriented quite steeply relative to the bedding plane and thus became telescoped. We think that it is also due to this compaction effect that the inner lamella appears wider in the posterior part of the wings than anteriorly in specimen PIMUZ 31570 (Fig. 6G, H). In specimen PIMUZ 31572, the more or less original width of the inner lamella is visible (Fig. 6I, J). The posteromedian indentation of the outer lamella is deep, which is one of the main differences to jaw Type 1. Additionally, the growth lines on the wings are much weaker, but still discernible in large specimens.

Type 3. Only two specimens are available (PIMUZ 31569 to 31577). In this type (Fig. 6D), the wings are also elongate, but the median indentation on the posterior edge is much shallower than in Type 2. The inner lamella seems very narrow; probably, it was broader originally and only appears narrow due to the compaction. The largest specimen (PIMUZ 31569) is 8 mm long.

Type 4. One specimen could be assigned to this type; it is associated with PIMUZ 31567. It is slightly smaller (12 mm long right wing) than the associated lower jaw of Type 1 and, in contrast to the other types, it displays a deep U-shaped posterior indentation. The outer lamella seems rather narrow but it is arguable to what extent this is due to deformation by compaction. The wings of the inner lamella seem asymmetrical because the specimen was embedded obliquely. The supposed right wing is fully exposed and displays some concentric growth lines (Fig. 6E, left). The overall morphology is reminiscent of an upper jaw of the normal type *sensu* Tanabe *et al.* (2015).

Composition of the fauna

Compared to some older Famennian assemblages from Madene El Mrakib, species richness appears to be low in the Hangenberg Black Shale (ongoing research). Bivalves such as *Guerichia elliptica*, ?*Ptychopteria* sp., and ?*Streblopteria* sp. (Fig. 7) are quite common and often cover bedding planes in great numbers. However, the determination of the bivalves was difficult as they were often heavily compressed. Two ammonoid genera could be identified confidently in spite of the almost two-dimensional preservation (*Postclymenia* and *Mimimitoceras*); specimens of these genera are very common, which is quite characteristic for the latest Famennian (e.g. Korn 1991; Korn *et al.* 2004). In our samples, conchs of juvenile ammonoids smaller than 5 mm are especially abundant, but usually these are nearly impossible to determine. Occasionally, small orthoconic conchs of bactritids and orthocerids occur (Fig. 4A, B); their determination is hampered by the lack of morphological detail, but further collections might shed more light on their systematic positions. Many of the ammonoid conchs carry bryozoan colonies (Fig. 7B, E). The zooids show hardly any morphological details, which is probably due to the fact that the shell material is not preserved.

In addition to these animal remains, undeterminable carbonized plant remains are not rare (Fig. 7C, D); further collecting might also reveal determinable specimens. Many of the bedding planes show fine burrows, which are *c.* 0.1 mm wide and up to 1 mm long Fig. 7A). Sometimes they branch and resemble the ichnogenera *Chondrites* (R. Hofmann, Berlin, pers. comm. December 2015) and *Multina* (L. H. Vallon, Tylstrup, pers. comm. December 2015). The alpha diversity of the Madene El Mrakib section will be published elsewhere (ongoing research).

DISCUSSION

Systematic assignment of jaw types

All specimens of Type 1 are almost completely flattened, thus prohibiting a direct three-dimensional reconstruction. However, this jaw type was also found in several specimens of *Postclymenia calceola* (PIMUZ 31554, Fig. 3G; PIMUZ 31557, Fig. 3I, J; PIMUZ 31560, Fig. 4D, E; PIMUZ 31561, Fig. 4F, H). Since the characteristic coarse growth lines of the wings are partially preserved in these specimens, we can confidently assign Type 1 to *Postclymenia*. To our knowledge, this is the first record of *in-situ* clymeniid jaws. The whorl cross section of *P. calceola* is well known (Klein & Korn 2014). Accordingly, we assume that the part of the outer lamella with the thick carbon coating was originally slightly vaulted similar to the rounded venter of that species (Fig. 8H, K). By contrast, the wings were probably positioned subparallel to the ventrally slightly converging flanks (Fig. 8I, J), giving the lower jaws a rounded V-shaped cross section.

Type 2 is slightly more difficult to assign to a species because of the lack of fine morphological characters. The largest specimen of *Mimimitoceras* sp. (PIMUZ 31551; Fig. 3B, C) is preserved with the lower jaw in the body chamber. We assign Type 2 to this species because of its size and the deep posterior indentation separating the wings (Fig. 6A, D). This might be owed to the fact that *Mimimitoceras* has a deep imprint zone; therefore, this indentation increases the manoeuvrability of the lower jaw within the body chamber.

Accordingly, Type 3 is likely to belong to a tornoceratid. We did not find jaws in the body chambers of tornoceratids but this is the only other group of ammonoid conchs and, like the Type 3 jaws, their conchs are rather rare. This is not a proof of their assignment, but we consider it plausible that Type 3 represents a tornoceratid lower jaw.

Type 4 has not been found in an ammonoid conch yet. It is associated with a lower jaw of *Postclymenia calceola*. Both jaws are rather big, although the supposed lower jaw is shorter, pointing at the possibility that Type 4 represents the upper jaw of this clymeniid. This finds some support in the fact that the upper jaw also displays some concentric growth lines.

Preservation and taphonomy

All the Devonian ammonoid jaws reported herein are made wholly of a black material like those of the known Palaeozoic and Triassic ammonoids (Tanabe *et al.* 2015 and references therein) and modern and fossil coleoids (Tanabe 2012). They apparently lack the calcified jaw elements, either calcitic or aragonitic or both, that are present in modern and fossil nautilids (Saunders *et al.* 1978; Klug 2001), in Jurassic and Cretaceous ammonoids belonging to the Phylloceratina and Lytoceratina (Tanabe *et al.* 1979, Tanabe *et al.* 2013), and in the Aptychopora including most Ammonitina and Ancyloceratina (Engeser & Keupp 2002; Tanabe *et al.* 2012, 2015).

We examined the mineralogy of the black material preserved in our jaw material by EDX. We measured a lower jaw (Type 3) at four points. At none of these points was P, Ca or F present (i.e. no apatite, no francolite, no calcite), while over 30 weight % of C was detected. Additional elements that were detected probably belong to the clay mineral of the matrix (K, Al, Si, O). In combination with the black colour, we interpret the results of the EDX-analysis as indicating that the jaws were preserved in carbonaceous material, unlike the jaws of Cretaceous ammonoids published by Tanabe *et al.* (2012).

All the ammonoid jaws studied herein are carbonaceous and lack the mineralized portions of other cephalopod jaws (Nautilida, Aptychophora; e.g. Saunders *et al.* 1978; Engeser & Keupp 2002; Tanabe *et al.* 2015). In all cases, where cephalopod jaws are partially or wholly carbonaceous, this coincides with the primarily chitinous portions. This is corroborated in the cases of Recent (Saunders *et al.* 1978) and fossil nautilid jaws (Klug 2001), but also for ammonoid jaws, which have strongly varying amounts of calcite in their jaws (Tanabe *et al.* 2015 and references therein). Most Palaeozoic ammonoid jaws have either very small or no carbonatic portions in their jaws, which we suggest also for the new Devonian jaws. Definitive evidence is lacking, because in the Hangenberg Black Shale, no carbonatic skeletal materials are preserved; only their casts. It is noteworthy that such carbonaceous preservation of chitinous fossils has, to our knowledge, never been reported from Devonian rocks of North Africa. We think that this preservation of jaws in combination with other carbonized parts (e.g. the coating of the body chamber in Fig. 3B, C and the carbonized aperture as well as other carbonized structures in the tornoceratid in Fig. 4I) points at the possibility that further soft parts of ammonoids and possibly other organisms might be preserved in this Konservat-Lagerstätte (Seilacher, 1970).

Evolutionary implications

Previously, predominantly jaws of only one clade of Devonian ammonoids (Suborder Gephuroceratina) were known (Woodward 1885; Trauth 1927–1936; Matern 1931; Clausen 1969; Tanabe *et al.* 2015); isolated Famennian ammonoid jaw material has also only rarely been described (Frye & Feldmann 1991; Korn 2004). We can

FIG. 6. Isolated jaws from the Hangenberg Black Shale of Madene El Mrakib West. A–C, E, F, isolated jaws of *Postclymenia calceola* Klein & Korn, 2014; A, PIMUZ 31564, obliquely embedded specimen; second smaller jaw above; B, PIMUZ 31565, obliquely embedded specimen; C, PIMUZ 31566, obliquely embedded specimen showing the indented anterior edge; E, PIMUZ 31567, with upper (left) and lower jaw as well as embryonic conchs of an undetermined ammonoid; F, PIMUZ 31568, fragment of a wing of the outer lamella. D, Tornoceratoidea sp., PIMUZ 31569, ventral view of lower jaw; the inner lamella is visible. G–J, large isolated lower jaws of adult *Mimimitoceras* sp.; G, H, PIMUZ 31570, part and counterpart; the shape of the inner lamella is altered by the strong compaction; I, J, PIMUZ 31572, moderately compacted specimen; part and counterpart with small bivalves and neanic ammonoid conchs; due to the breakage, the overall outline of the inner lamella is revealed. Scale bar represents 10 mm. Colour online.


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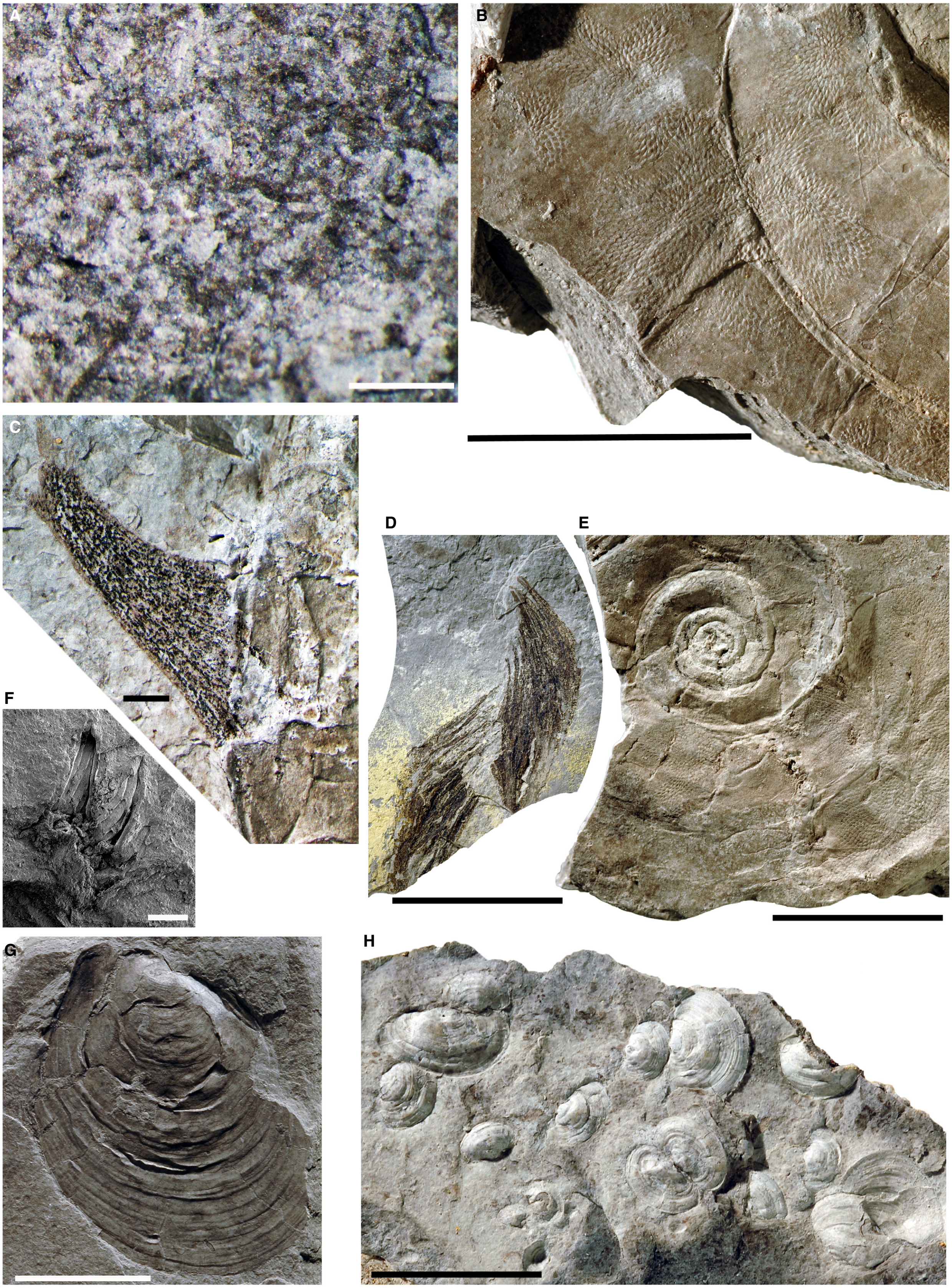
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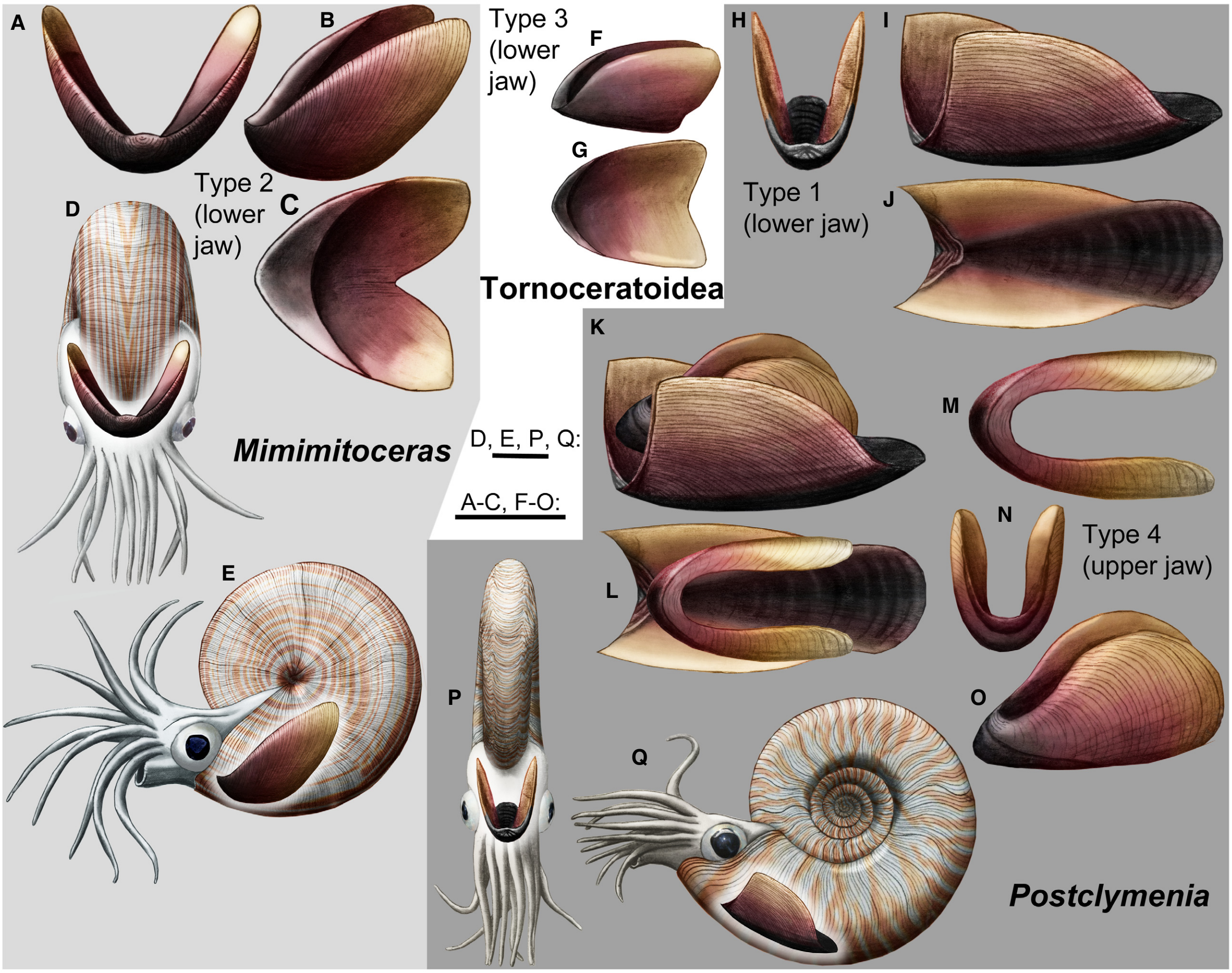

FIG. 8. Reconstructions of the four jaw types. Note the covariation of jaw shape with the whorl cross section. A–E, *Mimimitoceras* sp. A–C, reconstruction of the lower jaw; A, anterior; B, lateral; C, dorsal. D, E, reconstruction of the living animal with a possible position of the lower jaw; D, dorsal; jaw form reconstructed according to whorl cross section; E, lateral; note the low aperture due to the low whorl expansion rate. F, G, lower jaw of Tornoceratoidea gen. et sp. indet.; F, lateral; G, dorsal. H–Q, *Postclymenia calceola* Klein & Korn, 2014; H–J, reconstruction of the lower jaw; H, anterior; I, lateral; J, dorsal. K, L, upper and lower jaw in articulation; K, lateral; L, dorsal. M–O, reconstruction of the supposed upper jaw; M, dorsal; N, anterior; O, lateral. P, Q, reconstruction of the living animal with a possible position of the lower jaw; P, dorsal; jaw form reconstructed according to whorl cross section; Q, lateral; note the moderately high aperture due to the moderately high whorl expansion rate. Both scale bars represent 10 mm.

now add knowledge about the jaw morphology of members of the Order Clymeniida and of the Suborder Tornoceratina. Naturally, because of the low numbers of ammonoid taxa per order or suborder that are known, it is difficult to extrapolate the extent to which these known jaw morphologies are representative of the suborders.

It has long been known that commonly the lower jaws fit quite well into the aperture (e.g. Woodward 1885; Clausen 1969; Lehmann 1972, 1975; Morton 1981; Lehmann & Kulicki 1990; Seilacher 1993; Lehmann *et al.* 2015). In turn, this implies a strong covariation of lower jaw morphology with conch form throughout all ontogenetic changes in conch form (e.g. Klug 2001). Both

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FIG. 7. Accompanying fauna and flora from the Hangenberg Black Shale of the Ma'der Basin. A, PIMUZ 31559, minute *Chondrites* (?) burrows. B, PIMUZ 31563; detail of the encrusting bryozoan colonies. C, PIMUZ 31571, plant (?) attached to the conch of a *Postclymenia calceola* Klein & Korn, 2014. D, PIMUZ 31573, plant fragments. E, *P. calceola* Klein & Korn, 2014 with bryozoan colonies, PIMUZ 31574. G, ?*Streblopteria* sp., PIMUZ 31576. H, numerous specimens of *Guerichia elliptica* Phillips, 1841, note that in some cases, the valves are still attached to each other; PIMUZ 31575. Scale bars represent 1 mm (A, C); 10 mm (B, D, E, G, H); 0.2 mm (F). Colour online.

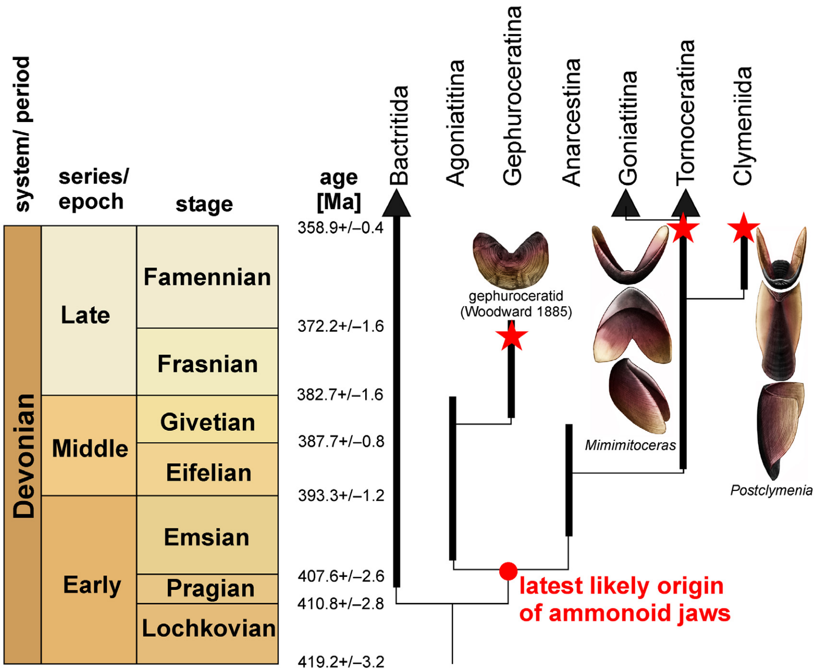

FIG. 9. Reconstructions of the jaw types and their position in Devonian ammonoid phylogeny. The asterisks show the position of the jaw findings. Absolute ages from Cohen *et al.* (2013).

gephuroceratid and tornoceratid jaws have a very simple shape and represent the classic normal-type of lower jaw. By contrast, the clymeniid lower jaw is quite different, which is in accordance with the other peculiarities of the clymeniids such as the thick dorsal siphuncle (Gottobrio & Saunders 2005).

Of course the number of Devonian ammonoid taxa for which the jaw morphology is known is exceedingly low, even when the new material is included. We need many more taxa, both of the same and of the remaining clades to evaluate to what degree jaw morphology can contribute to our understanding of the phylogeny of early ammonoids.

We illustrate the distribution of jaw fossils over the phylogeny of Devonian ammonoids in Figure 9. From their distribution over three of the main clades of early ammonoids, we can infer that it is highly likely that some kind of simple normal-type jaw was already present in the first ammonoids (cf. Kröger *et al.* 2011; Klug *et al.* 2015). The absence of preserved cephalopod jaws from strata older than the Frasnian raises the question of whether cephalopod jaws (or a thicker, resistant chitin layer) evolved after the origin of cephalopods, perhaps following selection pressure of the intensifying gnathostome radiation in the Late Silurian to Early Devonian (Signor & Brett 1984; Bambach 1993; Vermeij 1994; Klug *et al.* 2010), or if they are simply not preserved, for example due to a thin chitin layer (cf. Kröger *et al.* 2011). The presence of jaw-like structures in some gastropods (Luchtel *et al.* 1997; Boletzky 2007) perhaps suggests that at least some anlagen for reinforced oral structures were present even in early cephalopods, but these possibly had an exceedingly low preservation potential.

The preservation of radulae in Ordovician orthocones (Gabbott 1999), however, in the absence of the slightest jaw relics, supports the hypothesis that jaws were either completely absent or lacked a sufficiently thick chitin coating in pre-Devonian cephalopods. It is also striking that the Hunsrück Slate has not yielded cephalopod jaws, especially since truly soft structures such as pedicles of brachiopods and ambulacral feet of echinoderms have been found pyritized (Südkamp 1997; Glass & Blake 2004). Presuming that hardened jaws really are a character that evolved in earliest ammonoids or bactritids, it could have been the evolution of hard jaws in combination with the coiled conchs that lead to the great success of the Ammonoidea. In that case, the Devonian would have seen the mid-Palaeozoic victory of biting in addition to the ‘Nekton Revolution’ (Klug *et al.* 2010).

Ecological implications

The fine grain-size, the absence of ripple marks and other indicators for sediment transport indicate a water depth below the fair weather wave base. Benthic diversity is rather low, pointing to low oxygen conditions (ongoing research). The latter is supported by the presence of abundant *Chondrites*-like traces on bedding planes, being reminiscent of the Posidonia Shale in southern Germany. As in this Jurassic Fossillagerstätte, other trace fossils are absent. Finally, the carbonized preservation of chitin also corroborates low oxygen levels. All these facts suggest that this fossiliferous level indeed represents a classic black shale, which was probably deposited under quiet water conditions with prevailing low oxygen conditions. The stratigraphical position below massive sandstones and the ammonoid fossil content suggest a correlation with the Hangenberg Black Shale and the corresponding global transgression (e.g. Johnson *et al.* 1985; Haq & Schutter 2008).

There are quite strong differences in jaw morphology between the jaws of the three Devonian ammonoid groups for which jaws are known. Especially when combined with the knowledge of differences in conch morphology, the question arises of whether these morphological differences in lower jaws and conchs are merely an effect of covariation or reflect differences in habit and diet. Although evidence from stomach or crop contents are missing from these Devonian cephalopods, we tentatively suggest that the morphological peculiarities reflect differences in diet as well.

CONCLUSION

In the eastern Anti-Atlas of Morocco, the sedimentary succession around the Devonian–Carboniferous boundary is generally poorly exposed. Usually, this latest Famennian interval is characterized by a transition from carbonates via shale to sandstone. In the Ma'der Basin, a dark fine-grained shale horizon is locally exposed below a massive sandstone formation. The dark shale has been correlated with the Hangenberg Black Shale and the latter with the Hangenberg Sandstone.

In contrast to an earlier opinion, the correlate of the Hangenberg Black Shale is fossiliferous, although the fauna is somewhat impoverished compared to older strata of the Famennian. In the study area, this black shale contains exceptionally preserved ammonoids, which still show fine shell surface structures such as the wrinkle layer and, more remarkably, the lower jaws, sometimes even *in situ*, as well as other organic structures.

In total, we found four different jaw types. Due to the presence of jaws in the body chambers, we can even assign some of these types to distinct taxa. Notably, these represent the first records of jaws of the Order Clymeniida (*Postclymenia*) and of the Suborder Tornoceratina (*Mimimitoceras* and a tornoceratid). While the tornoceratid jaws display a classic normal-type morphology, the clymeniid jaw is quite peculiar, stressing the exotic character of the clade Clymeniida.

To test existing phylogenetic hypotheses, more Devonian ammonoid taxa preserved with jaws are needed. Our new findings demonstrate that there are good reasons to be optimistic of finding more such material in the future, filling the big gaps in our knowledge of these extinct cephalopods. Additionally, the distribution over three of the most important clades of Devonian ammonoids makes the presence of jaws in the earliest ammonoids highly likely (unless one assumes their convergent evolution in three lineages). These findings also point to the likelihood that the first ammonoid lower jaws were indeed of the normal-type. Missing cephalopod jaw fossils from deposits older than the Devonian lead to the speculation that cephalopods evolved hard jaws only with increasing selection pressure from the diversification of jawed fish, and the consequent evolution of defensive features in many other organism groups (e.g. Signor & Brett 1984; Bambach 1993; Vermeij 1994; Klug *et al.* 2010).

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