Sublethal injuries in Early Devonian cephalopod shells from Morocco

CHRISTIAN KLUG

Internal moulds of the relatively small- to moderate-size shells of Early Devonian ectocochleate cephalopods (typically <150 mm diameter) occasionally display traces of repaired shell damage. Presumably, these animals with their highly specialized buoyancy device, the phragmocone, lived in the water column. It is uncertain as to how the shells of these animals were damaged; one likely cause would be predatory attacks but the identity of the perpetrator remains uncertain. So far, no remains of arthropods capable of breaking or cutting shells have been found in the fossiliferous outcrops of this age in the Anti-Atlas (Morocco). The only macrovertebrate remains of this age are of acanthodian and placoderm fish which probably lived a more or less benthonic life style. Additionally, a fish attack on these cephalopods would probably have destroyed most of the thin-shelled conch and killed the animal. Most of the repaired shell breaks are triangular in shape which is characteristic for cephalopod bite marks. Additionally, the paired arrangement of the fractures in over 70 bactritoids supports the hypothesis that it was a cephalopod attacking another cephalopod. It cannot be excluded with certainty that occasional vertebrate attacks left traces on their shells. Fossil evidence indicates that the development of tightly coiled conchs was a rapid evolutionary event in the Ammonoidea in the Early Devonian; however, the evolution of coiling is probably not directly related to predation pressures because the ratio of injured to healthy specimens is roughly the same in Zlíchovian bactritoids with orthoconic and ammonoids with coiled shells.

Key words: Bactritoidea, Ammonoidea, Gnathostomata, injury, predation, mode of life, Devonian, Morocco.

Christian Klug [chklug@pim.uzh.ch], Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland.

Introduction

Because of their accretionary growth, mollusc shells carry information from their individual histories, including characteristic intraspecific growth changes (e.g., Bucher et al. 1996), growth changes as consequences of environmental fluctuations (especially caused by adverse conditions like low food supply etc.; e.g., Stridsberg 1985; Keupp and Riedel 1995), traces of healed shell damage (see Hengsbach 1996 for an overview; Palmer 1979; Vermeij 1977, 1982a, b; Keupp 1984, 1985, 2006; Korn and Klug 2002; Kröger 2002a, b, c; Kröger and Keupp 2004) and other deformities. Among ammonoids, damage and deformity may have been caused by predators (e.g., Crick 1898, 1918; DeLoriol 1900; Maubeuge 1949; Kolb 1955; Hölder 1956; Magraw 1956; Guex 1967; Bayer 1970; Ward 1981; Keupp 1984, 1985, 2006; Landman and Waage 1986; Bond and Saunders 1989; Kröger 2002a, b; Rein 2005), parasites or epizoans (Landman et al. 1987; Hengsbach 1996; Davis et al. 1999; Klug and Korn 2001; Checa et al. 2002). Speculatively, territorial disputes and mating contests may have produced damage. In many cases, repaired fractures were interpreted as having been caused by cephalopods (e.g., Mehl 1978; Keupp 2000), arthropods (e.g., Roll 1935; Vermeij 1977; Lehmann 1990; Radwański 1996; Keupp 2000; Kröger 2000) or vertebrates (e.g., Lehmann 1975;

Mapes and Hansen 1984; Hansen and Mapes 1990; Martill 1990; Mapes et al. 1995; Sato and Tanabe 1998; Keupp 2000) which tried to feed on these cephalopods but somehow did not succeed. Successful predation attempts often included a more or less complete destruction of the shell, leaving shell fragments behind which are often hard to interpret with respect to the taxonomic assignment of prey and predator (compare Keupp 2000, 2006).

Recent nautilids are again useful for an actualistic comparison: Their shells often display repaired shell fractures which occurred at various incidents. Comprehensive reviews of traces of predation attempts on Recent *Nautilus* have been compiled by Haven (1972), Saunders et al. (1987) and by Kröger (2000).

Palaeozoic nautiloids frequently display healed shell fractures but documentation and descriptions of such are rare. Impressive examples have been illustrated by Barrande (1877: pl. 511: 1, 2; pl. 514: 1, 6), Stridsberg (1985) and Kröger (2004). The latter two occurrences are of Ordovician and Silurian age, and the question of the perpetrator of the injuries arises. In these times, most fish lacked jaws and were probably not capable of damaging the shells of nautiloids. Besides cephalopods, only some arthropod groups, such as some chelicerates, are potential candidates who may have hunted cephalopods. Presuming a rather benthonic mode of
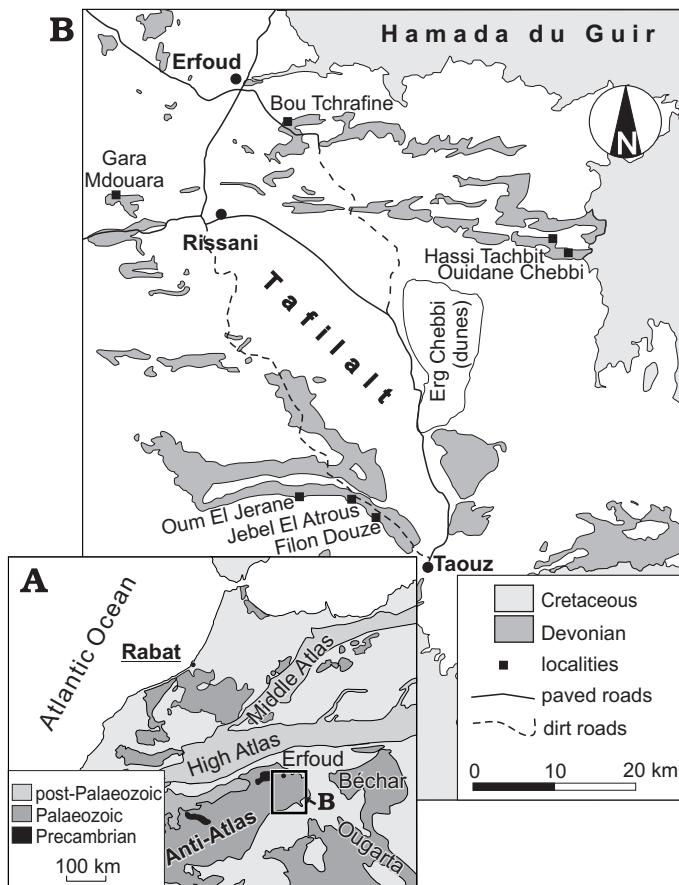
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Fig. 1. Geologic map of Morocco (**A**) and detail of the eastern Anti-Atlas (**B**).

Early ammonoids of Zlíchovian age (early Emsian, Early Devonian) have been recorded almost worldwide. Only very few ammonoid specimens have been reported from most localities of this age. The area around Prague (Barrande 1865), the Rhenish Massif (Erben 1962, 1964, 1965, 1966; Göddertz 1989), Russia (Bogoslovsky 1969, 1972, 1980), South China (Ruan 1981) and North Africa (Termier and Termier 1950; Hollard 1963, 1974; Klug 2001) belong to the regions that provided fairly extensive collections of Early Devonian ammonoids and bactritoids. Among those, newly collected Moroccan localities bear the most abundant fossils and the most continuous and extensive outcrops containing comprehensive stratigraphic information. These new collections have yielded the first specimens of early ammonoids that display traces of healed injuries (younger Devonian ammonoids displaying healed shell fractures are illustrated in Korn and Klug 2002).

The aims of this study are (1) to document healed shell injuries that occur in several Early Devonian cephalopod groups, (2) to discuss the origin of the repaired fractures and (3) to reconsider some aspects of the evolution of the conch form, mode of life, and the resulting evolutionary success of these morphologic changes in the early evolution of bactritoids and ammonoids.

Institutional abbreviations.—MB.C., Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Switzerland.

Material

During the past decade of intense collecting, the Early Devonian sediments of the Ouidane Chebbi area and in the vicinity of the Jebel Ouaoufilal, Oum El Jerane and the Jebel El Atrous (eastern Anti-Atlas, Morocco; Fig. 1) have yielded hundreds of specimens of early ammonoids, bactritoids and nautiloids. Most of them are preserved as limonite (after pyrite) internal molds and a smaller number are preserved in limestone. A significant portion of the limonitic specimens weathered out of Zlíchovian claystones and marlstones (Unit B of Klug 2001; Faunules 1 and 2 of Klug et al. in press). They usually are preserved as incomplete shells, but otherwise show fine morphological details. Consequently, most irregularities that are described herein were found on limonitized fragments, except for some fragments of the shells of orthoconic nautiloids from the Pragian (Fig. 2). The fragmentation of the limonitic material was probably caused by incomplete pyrite infilling (later transformed into limonite) after burial, and when these fossils were eroded out of claystones, they were presumably fragmented during the modern weathering and erosion process. Some of the orthocones are kept in open nomenclature because these forms are currently being revised by Kröger (in press).
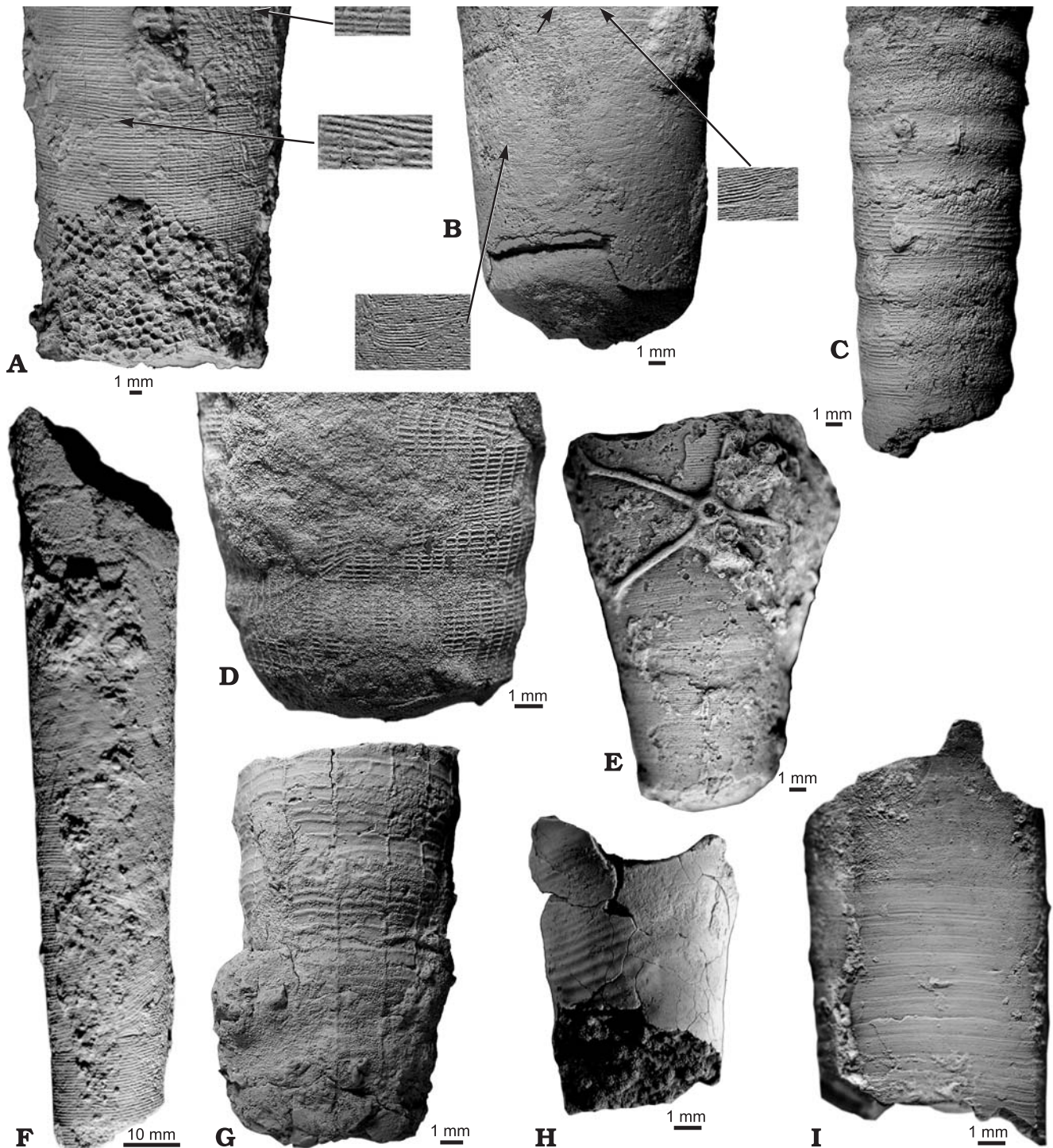
life for Palaeozoic marine chelicerates (for eurypterids see Strømer et al. 1955: 29; Bartels et al. 1998: 148) and a more or less planktonic mode of life of Palaeozoic nautiloids (Westermann 1977, 1996, 1999; Kröger 2002c, 2004), sublethal predator-prey interactions between chelicerates and nautiloids would probably have been exceedingly rare. A planktonic mode of life for most Palaeozoic nautiloids is corroborated by common occurrences of representatives of this group in sediments lacking benthonic fauna and the presence of the gas-filled phragmocone. Therefore, intra- or interspecific actions between cephalopods appear as the most likely origin of the sublethal injuries of the Ordovician and Silurian specimens (compare Kröger 2004).

For bactritoids, published reports of healed injuries are also scarce (although such injuries are not necessarily rare). Some excellent examples of severely fractured and repaired Late Palaeozoic bactritoid shells are described and figured in Mapes (1979). He did not give an interpretation of what circumstances and what kind of animals may have produced the initial fracturing. Additionally, Mapes (1979) described irregularly spaced, abnormal septa and interpreted these malformations by parasitism. He also illustrated asymmetrically inserted septa in Late Palaeozoic bactritoids; however, some of these deformations happened probably *post mortem*.

Fig. 2. Remains of orthoconic nautiloids with minor healed fractures ("forma substructa" of Hölder, 1973; a slightly more extensive fracture in D, F), Tafilalt, Morocco. **A**. *Spyroceras patronus* (Barrande, 1866), limestone, with shell, MB.C.9652, bed KMO-I, Pragian, Filon Douce near Taouz, length 38 mm. **B**. Pseudorthoceratidae indet., limestone, with shell, MB.C.9675, bed KMO-II, Pragian, Filon Douce near Taouz, length 27 mm. **C**. *Orthocycloceras* sp., MB.C.9655, bed KMO-II, Pragian, Filon Douce near Taouz, length 33 mm. **D**. *Spyroceras* aff. *patronus* (Barrande, 1866), limestone, with shell, MB.C.9653, bed KMO-I, Pragian, Filon Douce near Taouz, height of displayed detail 11 mm; this specimen and the one in F display two fractures, easily detectable by the course of the ribs after the fracture which gradually changes to the "normal" course, compensating for the shell loss. **E**. Pseudorthoceratidae indet., limestone, with shell, MB.C.9595, bed KMO-II, Pragian, Filon Douce near Taouz, length 22.9 mm. **F**. Pseudorthoceratidae indet., PIMUZ 27030, limestone, with shell, latest Pragian or earliest Emsian, Gara Mdouara, length 175 mm. **G**. *Anaspyroceras* sp. aff. *pseudocalamiteum* (Barrande, 1868), limestone, with shell, MB.C.9680, bed KMO-III, Pragian, Filon Douce near Taouz, length 18.25 mm. **H**. *Plagiostomoceras* sp., limonitic internal mould, PIMUZ 27031, earliest Emsian, El Atrous, length 14.3 mm. **I**. Arionoceratidae indet., limestone, with shell, PIMUZ 27032, latest Pragian or earliest Emsian, Gara Mdouara, length 175 mm. The specimens of figures A–C and D–G were collected and photographed by Björn Kröger (Berlin). All specimens were coated with NH$_4$Cl.

Description of specimens

In many cases, the excellent preservation of the fossils from the eastern Anti-Atlas (Morocco) allowed for the study of shell details such as the traces of sublethal injuries. This is especially true for specimens of orthoconic nautiloids with fine ornamentation of longitudinal lirae and more or less transverse growth lines that are preserved on the surface of the test. These specimens show the traces of minor fractures ("typus parvus" of Kröger 2000) that occurred at the aperture and that were subsequently repaired. Apparently, virtually all specimens preserved in this manner display shell damage even though such damage is often minute on the well preserved test. Some of these repaired fractures would be barely visible on internal moulds. Examples of this can be seen on fragments of *Anaspyroceras*, *Orthocycloceras*, *Spyroceras*, and some pseudorthoceratids (MB.C.9652, 9595, 9675, 9655, 9680; Fig. 2). In all these cases, the healed injuries can be detected by the discontinuity of growth lines, i.e., the angle between subsequent growth lines as well as between growth lines and shell wall changes (Fig. 2). In most specimens, minute pieces of shell broke off, apparently without significantly damaging the mantle (thus leaving no injury trace in the subsequently formed part of the shell). These injuries, as well as the ones described below (except for PIMUZ 7482), can be referred to as "forma abrupta" Hölder, 1956 or, more precisely, the "forma substructa" of Hölder, 1973 (compare also Keupp 2006: 114). In the case of some *Devonobactrites* (MB.C.9545, PIMUZ 7273, PIMUZ 27034, PIMUZ 27040, PIMUZ 27041, PIMUZ 27038; Fig. 3B, F, G, K, L) and one *Spyroceras* (MB.C.9653; Fig. 2F), larger shell fragments were chipped away and most likely, the mantle was also injured (visible in the discontinuous ornamentation immediately orad of the injured area; compare Fig. 3F, G, K and, e.g., Keupp 2000).

All of the remaining specimens of this study are preserved as limonitic internal moulds. There are relatively few internal molds that show repaired injuries. This is not surprising because most of the minor repaired damage can only be detected by irregularities in the ornamentation expressed on the finely ornamented surface of the test, and these irregularities do not extend to the mantle. When mantle damage is present, then the possibility of detecting the repaired damage is greatly increased. When the test is missing, minor injuries are often not visible on the internal molds. This preservational phenomenon probably explains the relative scarcity of sublethally injured specimens preserved as internal molds. This conclusion is warranted by the fact that virtually all specimens of orthocones with finely ornamented shells from the Early Devonian of Morocco display repaired shell fractures. By contrast, almost 2000 limonite steinkerns of bactritoids and ammonoids from the Early Emsian (Zlíchovian) have been examined and less than 5% of the specimens preserve imprints of healed shell fractures. The percentage of shell fractures among Zlíchovian bactritoids and ammonoids

increases from the lowermost units (without ammonoids) to the late Zlíchovian units (with ammonoids) from 3.7 to 4.8%. This is, however, not considered a statistically significant difference.

Four different patterns of damage were detected among the 57 specimens of *Devonobactrites obliquiseptatus* (Sandberger and Sandberger, 1852) that show traces of repaired shell damage: (i) Irregular rib development or growth line spacing with no clearly defined fracture (possible preservational bias; PIMUZ 7273; Fig. 3B); (ii) Sharply delimited, more or less triangular fractures ("typus acutus" of Kröger 2000); these are actually the most common type of repaired damage. Remarkably, this type of fracture occurs twice (or more often) in the same individual in 34 specimens forming various patterns. In some specimens, the fractures are linked in some way with one smaller and one larger triangle (e.g., MB.C.9545, PIMUZ 27038; Fig. 3E, L), in some cases, they are longitudinally separated (PIMUZ 27033, PIMUZ 27041; Fig. 3D, K) in some cases laterally; (iii) More or less rectangular fractures ("typus stupidus" of Kröger 2000, PIMUZ 27035; Fig. 3H); (iv) Fractures which leave a linear trace in growth direction across younger portions of the shell since the mantle margin was damaged (this corresponds to a pattern known from many ammonoids which have a distinct ornamentation; for these taxa this phenomenon was termed "Rippenscheitelung"; compare Hengsbach 1996; PIMUZ 27034, PIMUZ 27038; Fig. 3F, L).

Distinct sculptural asymmetry or irregularities in the course of the ribs was found in seven specimens of the ammonoids *Erbenoceras advolvens* (Erben, 1960) and *Chebbites reisdorfi* Klug, 2001. In some cases, the ribs are slightly oblique on one flank and can be traced to the venter, where they form a broad parabolic sinus (PIMUZ 7485, 7479; Fig. 4). On the other flank, the same rib either fades out gradually or disappears completely. Since these specimens do not display clearly delimited fractures, the origin of these asymmetries is unclear. In one ammonoid, one rib forms a little hook immediately next to the ventral midline (PIMUZ 7482; Fig. 4C_2, D_1). The injury of the latter specimen can be assigned to the "forma verticata" of Hölder, 1956 (see also Hengsbach 1996 and Keupp 2006), since the spot-like fracture caused parting of the subsequent ribs on the venter. In another specimen, the ribs seem to split from the venter towards the dorsum and also in the other direction (PIMUZ 7481; Fig. 4A). Two of the three resulting branches merge with the preceding and the following rib and the middle branch are more or less continuous. This injury might also be a "forma substructa" of Hölder, 1973. In three bactritoids, faint ridges form a little triangular hook on one flank (PIMUZ 7273, 7275, MB.C.9545; Fig. 3). In specimen MB.C.9545 (Fig. 3B), the fracture was rather deep and extended over approximately one quarter of the body chamber length (perhaps a "forma substructa" of Hölder, 1973?).

Irregular rib spacing is very common among early ammonoids and was probably caused by minor environmental changes or by minute injuries (forma substructa Hölder,
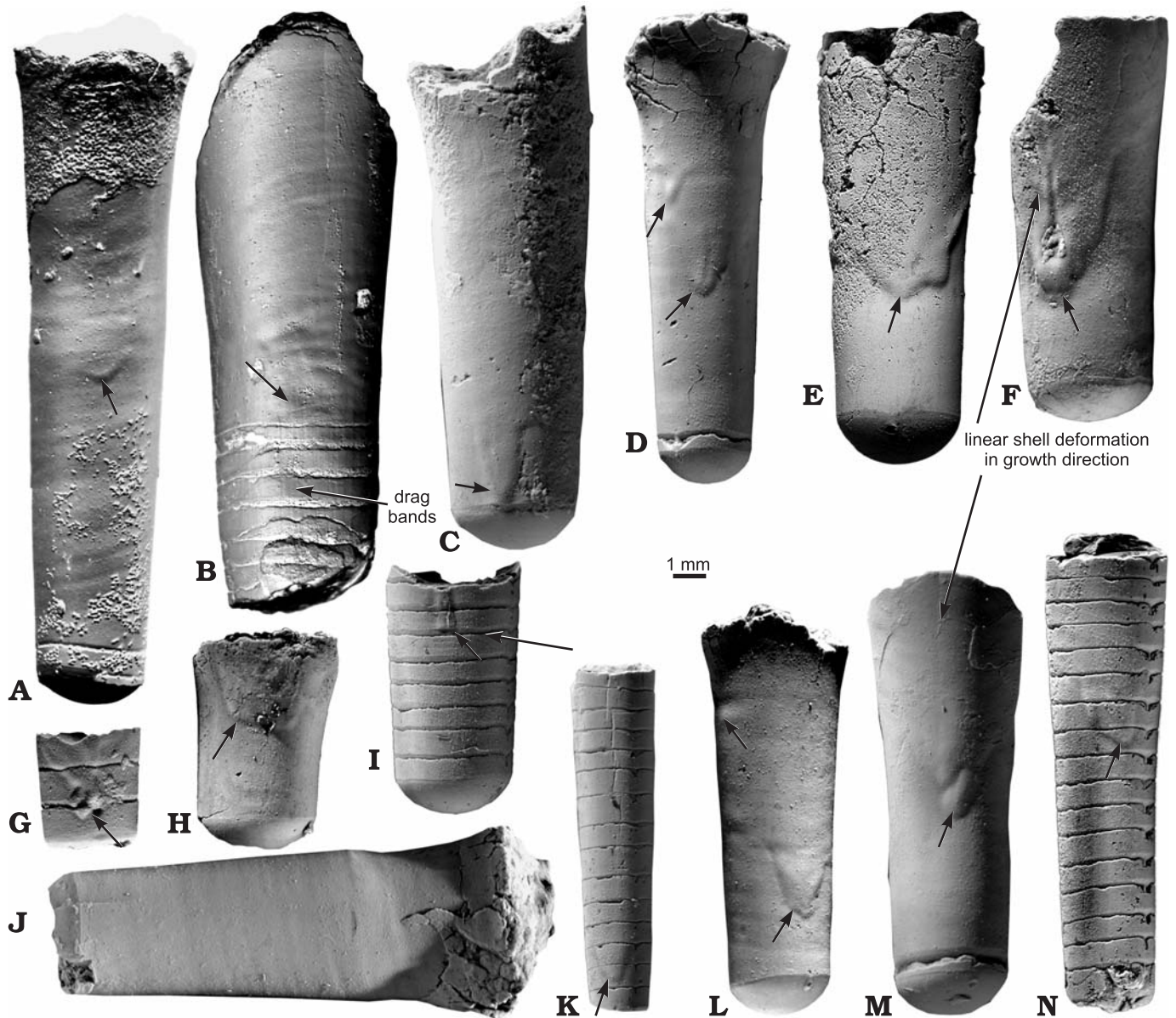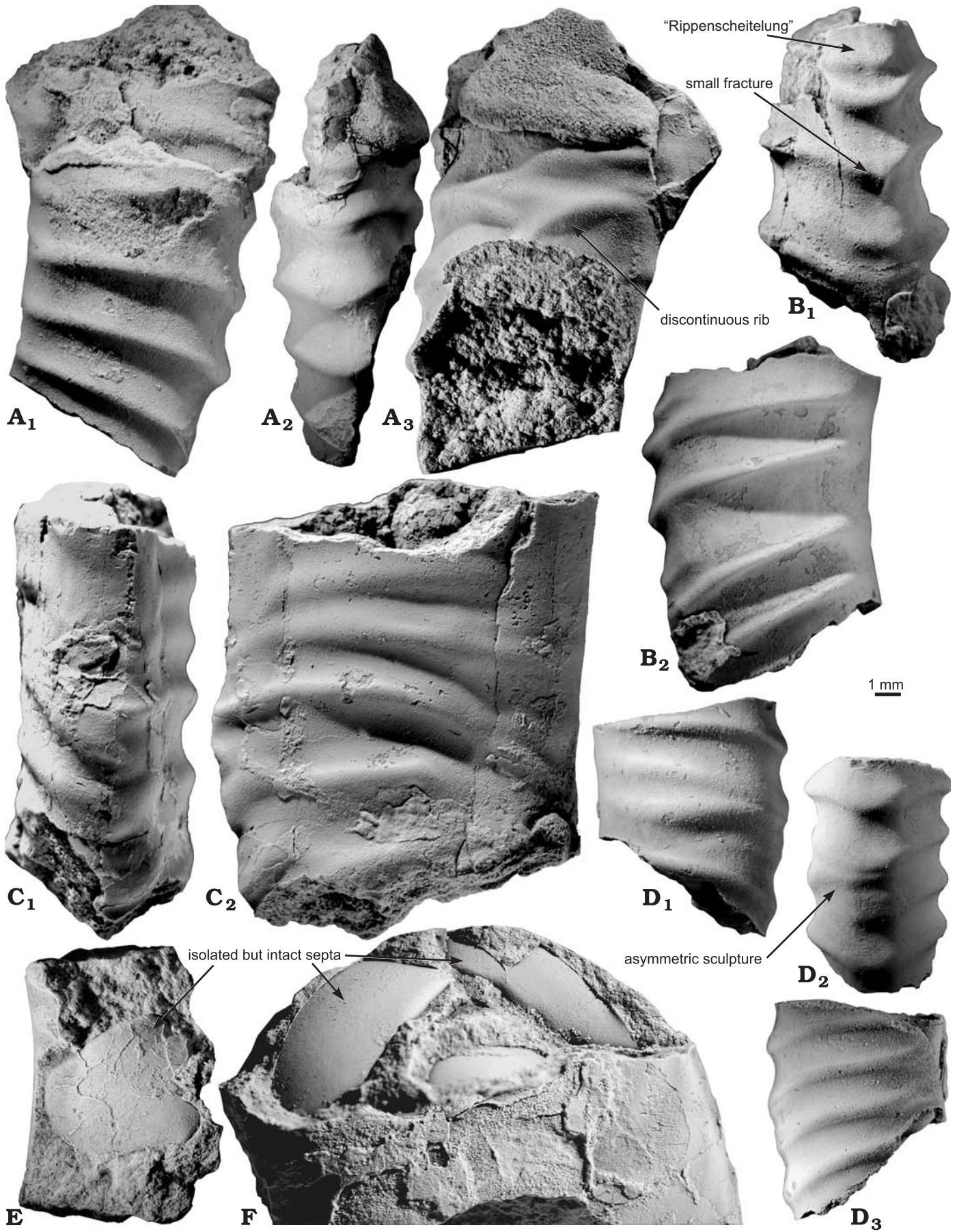
Fig. 3. Limonitic internal moulds of *Devonobactrites obliquiseptatum* (Sandberger and Sandberger, 1852) with minor healed injuries ("forma substructa" of Hölder, 1973) from the early Zlíchovian (early Emsian, Early Devonian) of the Tafilalt (Morocco). **A**. PIMUZ 7275, Ouidane Chebbi, note the small triangular fracture. **B**. PIMUZ 7273, Ouidane Chebbi, irregular insertion of ridges after injury. **C**. PIMUZ 27032, Oum El Jerane. **D**. PIMUZ 27033, Oum El Jerane; two injuries. **E**. MB.C.9545, bed EF, Filon Douze; note the deep fracture which extended over approximately one fourth of the body chamber length; at the posterior end of the fracture, two triangles can be seen as in C, reminding of other cephalopod bite-marks. **F**. PIMUZ 27034, Oum El Jerane; in this case, the mantle was most likely affected, causing the formation of a linear deformation in growth direction. **G**. PIMUZ 27040, south of Hassi Tachbit, near Ouidane Chebbi. **H**. PIMUZ 27035, Oum El Jerane; in contrast to most healed injuries, the apical end of the fracture is broad. **I**. PIMUZ 27036, Oum El Jerane. **J**. PIMUZ 27042, El Atrous, note the questionable terminal constriction, possibly indicating adulthood and not a malformation. **K**. PIMUZ 27037, Oum El Jerane. **L**. PIMUZ 27041, El Atrous; two injuries. **M**. PIMUZ 27038, Oum El Jerane. **N**. PIMUZ 27039, Oum El Jerane; like in F, the mantle was also affected, causing the formation of a linear deformation in growth direction. All specimens were coated with NH$_4$Cl. The arrows indicate healed injuries unless otherwise stated.

1973?) that cannot be identified. This feature can be seen in specimens of *Erbenoceras advolvens* (Erben, 1960) (PIMUZ 7480, 7482) and *Chebbites reisdorfi* Klug, 2001 (PIMUZ 7479).

Isolated septa were found within the shell in one specimen (PIMUZ 7489) of *Erbenoceras advolvens* (Erben, 1960) and in one specimen of *Chebbites reisdorfi* Klug, 2001

(PIMUZ 7486). The former specimen (PIMUZ 7489; Fig. 4D$_2$) displays one complete septum which rests more or less in the plane of symmetry with the ventral part near the dorsal wall of the whorl and the convex (posterior) side facing the left flank. In this specimen, no other septa or suture lines are visible. Because of its whorl size, this specimen is either part of a body chamber of a juvenile specimen or a fragment of

"Rippenscheitelung"

small fracture

discontinuous rib

A_1 A_2 A_3 B_1

B_2

1 mm

C_1 C_2 D_1

asymmetric sculpture

D_2

isolated but intact septa

E F D_3

phragmocone that displays no suture lines. The latter specimen (PIMUZ 7486; Fig. 4D$_3$) actually has three, completely chaotically arranged septa lying in the phragmocone. Anterior to these dislocated septa, one septum is still more or less *in situ*. As a matter of course, this could have happened *syn vivo* (and would have caused the animal's death because it requires a severe damage of the phragmocone wall), or it could be a *post mortem* phenomenon. Logically, it can not be concluded with certainty what process caused this damage. It is remarkable, though, that the septa were separated from the shell wall as a whole.

Discussion

Which animals injured the early bactritoids and ammonoids?—Although it is usually difficult to impossible to show what animal produced a shell fracture that subsequently was repaired, such shell repairs still tell a story of the life history of the animal. So far, only very few cephalopod mandibles of orthoconic nautiloids of pre-Late Devonian age have been described, and these may be opercula rather than jaw elements (*Aptychopsis*; Turek 1978; Tanabe and Fukuda 1999). No bactritoid mandibles have been reported. The first undoubted ammonoid mandibles are of Frasnian age (Late Devonian) and belong to gephuroceratid ammonoids and are rather rare (Trauth 1935; Clausen 1969; Frye and Feldman 1991; for a survey of cephalopod mandibles in the Late Palaeozoic see Mapes 1987). Therefore, the question arises whether Early Devonian cephalopods possessed mandibles at all. Because of the absence of clear fossil evidence, other indications to answer this question are needed. For instance, Engeser (1996) considered a chitinous mandible as an autapomorphy of the Cephalopoda (see also Dzik 1981). Additionally, Stridsberg (1985) and Kröger (2004) reported healed injuries from Ordovician and Silurian orthoconic and breviconic nautiloids, which presumably were caused by either other cephalopods or eurypterids, and fossilized eurypterids are usually rare faunal elements in fully marine environments. A report of predation by cephalopods on Upper Carboniferous (Desmoinesian) brachiopods was published by Elliott and Brew (1988). It thus appears probable that some or all Early Devonian cephalopods possessed some kind of mandibles.

The only larger predators which produced abundant fossils in the early Emsian of Morocco were early gnathostome fish such as acanthodians and placoderms; remains of eurypterids

and other arthropods with potentially shell-breaking appendages have not been found in Devonian sediments in North Africa. The excellent *Fossillagerstätte* of the Bundenbach Shale provides a rare opportunity to obtain insight in an ecosystem that contains the earliest ammonoids (Bartels et al. 1998). Together with the early gnathostomes preserved in the Hunsrück Slate, remains of numerous arthropods were discovered. Among those, however, only some of the chelicerates like the xiphosuran *Weinbergina opitzi* Richter and Richter, 1929, the eurypterid *Rhenopterus diensti* Strømer, 1939 and the large pantopod *Palaeoisopus problematicus* Broili, 1928 possessed organs (the chelae) that had the potential to fracture and break ammonoid shells. Fossils of Early Devonian chelicerates appear to be exceedingly rare as elements of marine invertebrate faunas, and their mode of life is interpreted to be (except for *Palaeoisopus*) rather benthonic (Bartels et al. 1998). Remains of various early gnathostome fish are comparatively abundant in Morocco, but most Early Devonian representatives of the Gnathostomata had a benthonic to demersal life style (see Janvier 1996 and references therein); for some Devonian fish, this can be demonstrated by the traces of mechanical wear at the tips of pectoral fin spines (e.g., in *Machaeracanthus*; compare Janvier 1996). *Machaeracanthus* remains are especially abundant at the localities that yielded the Devonian cephalopod remains with the healed injuries at the following locations in North Africa: the Ouidane Chebbi (Belka et al. 1999; Klug et al. in press), Jebel Ouaoufilal, Jebel El Atrous and Oum El Jerane regions (Hollard 1974; Klug 2001; Klug et al. in press). At these sites, over 200 fin spines of the acanthodian *Machaeracanthus* and some remains of the dermal bones of placoderms (gen. et. sp. indet.) have been recovered. Thus, a few of the previously described healed injuries of cephalopod shells might have their origin in attacks from early gnathostome fish.

In many other cases, cephalopods probably interacted with each other in various physical ways. This is corroborated by the characteristically clearly delimited, triangular outline of the fractures (compare Keupp 2000) seen in the Emsian bactritoids (Fig. 3). As described above, these fractures usually do not occur alone. They are often close to each other and more rarely are longitudinally separated. These patterns are interpreted here as traces of two opposing parts of pointed mandibles or jaws which most likely belonged to cephalopods. The rectangular appearance of some fractures (e.g., Fig. 3H) can conveniently be interpreted as being caused by the upper and lower mandibles of cephalopods, which were inserted at a low angle causing the shell to break

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← Fig. 4. Sculptural asymmetry, irregular rib course and isolated septa in various early ammonoids (limonitic internal moulds) from the early Zlíchovian (early Emsian, Early Devonian) from the Ouidane Chebbi region (Tafilalt, Morocco). **A**, **B**, **D**, **E**. *Erbenoceras advolvens* (Erben, 1960). **A**. PIMUZ 7481, asymmetric sculpture and irregular rib course, in right lateral (A$_1$), ventral (A$_2$), and left lateral (A$_3$) views; note the interrupted rib. **B**. PIMUZ 7482, irregularly spaced ribs and triangular deformation of the mid-ventral part of a rib (cephalopod-bite-mark? "forma verticata" of Hölder, 1956), in ventral (B$_1$) and left lateral (B$_2$) views. **D**. PIMUZ 7485, sculptural asymmetry, in right lateral (D$_1$), ventral (D$_2$), and left lateral (D$_3$) views. **E**. PIMUZ 7489, with one complete, but loose septum. **C**. cf. *Erbenoceras advolvens* (Erben, 1960), PIMUZ 27031, irregularly spaced ribs, inflated venter, and a subsequent smooth venter; the actual fracture is not visible, just the deformed part of the shell which had formed after the injury, in ventral (C$_1$) and left lateral (C$_2$) views. **F**. *Chebbites reisdorfi* Klug, 2001, PIMUZ 7486, with three isolated septa. All specimens were coated with NH$_4$Cl.

more or less parallel to a growth line. Additionally, many fish attacks on the small bactritoids and the smaller and moderate sized ammonoids would have caused a more or less complete destruction of the shell.

Thus, the most likely explanation for the small, repaired injuries is that they were caused by cephalopods. Since the repaired fractures have a similar appearance, it appears reasonable to conclude that the perpetrator of these shell breaks was in most cases one or more of the cephalopod species that coexisted with the victims. However, in one of the localities (Oum El Jerane), *Devonobactrites* is by far the most abundant cephalopod (737 specimens out of 853 cephalopods, i.e. 85% of the cephalopods and 67% of the entire fauna). There it appears possible that the bactritoids themselves could have been the perpetrators. This also happens among Recent nautilids as demonstrated by Saunders et al. (1987) and by Kröger (2000). The V-shaped fractures closely resemble those produced by nautilids on other nautilids.

Relation between conch form, mode of life, and evolutionary success.—According to Kröger (2005), tight coiling of cephalopod shells must be explained by adaptive evolution. One important question about coiling is as follows: What made the difference between ammonoids and other cephalopods with respect to the predator-prey relationship among cephalopods as well as between cephalopods and gnathostome fish. As discussed by various authors (e.g., Klug and Korn 2004; Kröger 2005), shell curvature that ultimately evolved into tightly coiled shells probably played an important role with respect to the origin of sublethal injuries in several respects discussed below: (i) Coiling probably enabled even early ammonoids to increase their maximum swimming velocity compared to cephalopods with orthoconic shells (for explanations see e.g., Jacobs 1992; Jacobs and Chamberlain 1996; Westermann 1996; Korn and Klug 2002; Klug and Korn 2004); (ii) Increased coiling enhanced manoeuvrability because the distance between the centre of gravity and the aperture rises with increased coiling, and thus, the leverage effect from the hyponome action increases (see also Stridsberg 1985; Saunders and Shapiro 1986; Jacobs 1992; Jacobs and Chamberlain 1996; Westermann 1996, 1999; Seki et al. 2000; Klug and Korn 2004); (iii) Coiling produces an additional advantage in that the animal spans less space with the same volume, and thus, the animal is more difficult to be detected and captured by a predator. In this respect, the optimised morphology would be spherical with a more or less closed umbilicus. For the openly coiled Early Devonian ammonoids, the loose coiling probably represented a small selective advantage over those cephalopods with orthoconic conchs; (iv) The earliest, still loosely coiled ammonoids carry a strong sculpture consisting of strong ribs and coarse growth lines. Potentially, this can be explained as a by-product of the particular mode of coiling, i.e., as some kind of "fabricational noise" (Seilacher 1973). Alternatively, this sculpture might have enhanced the resistance of the shell towards breakage during predation attempts (see also Ward

1981). Tight coiling implies an increased resistance against breakage of entire whorls when compared to loosely coiled shells (see Nützel and Frýda 2003 and references therein).

Consequently, a simple change in morphology had a major impact with respect to ecological fitness representing a partial explanation for the evolutionary success of ammonoids. This hypothesis is corroborated by their rapid dispersal and high initial diversity in the early Emsian, where some taxa (like *Erbenoceras* and *Ruanites*) rapidly reached an almost cosmopolitan distribution (apparently except for polar and subpolar latitudes).

With regard to cephalopod coiling and given the above information, the question arises why were early coiled nautiloids less "diverse" than the ammonoids after the Devonian? Possibly, the origin for this phenomenon can—at least partially—be sought in differing reproductive strategies and early ontogenies (compare Kröger 2005). Many fossil nautiloids probably produced a smaller number of much larger eggs than ammonoids (see dimensions listed in Landman et al. 1996; Chirat 2001). In order to obtain an estimate of the number of eggs laid by an adult female specimen of the early ammonoid *Erbenoceras*, the largest body chamber (conch diameter 156.2 mm) available from the Moroccan material (GPIT 1849–2002, Klug 2001: figs. 8, 6) was used to measure its approximate volume. Since this body chamber is only filled approximately to the plane of symmetry, the obtained volume (50 ml) was multiplied by 2. Consequently, the body chamber volume of *Erbenoceras* amounted to approximately 10 cm^3. Speculating that 25% of the body chamber (2.5 cm^3) was filled by eggs, and each egg had a volume of estimated 0.08 cm^3 (deduced from ammonitella sizes listed in Landman et al. 1996; the earliest ammonoids had an elongate ammonitella; see Korn and Klug 2002 and references therein). Based on these assumptions, a mature early ammonoid with a loosely coiled shell may have stored about 30 eggs in the body chamber (or perhaps as many as 50 presuming that they were not all in the same growth stage or that they continued to grow after egg deposition). Korn and Klug (2007) estimated 35,000 eggs for the more derived, larger diameter ammonoid *Manticoceras* (according to Clarke 1899, "*Manticoceras*" *oxy* reached 46 to 60 cm, based on large fragments; I have measured an adult *Manticoceras* sp. from Morocco which has a diameter of 40 cm) from the Late Devonian, whereas Recent *Nautilus* produces fewer than 10 eggs of a diameter of roughly 2 cm (compare Tanabe et al. 1993; Kröger 2005). The "average" and more derived ammonoid had a diameter of about 10 cm and may have produced several hundred small (1.0 to 2.0 mm diameter) eggs per female individual. It may be speculated that the often smaller ammonoid hatchling size as compared to the coiled nautiloids allowed a higher number of ammonoid offspring (which probably lived planktonically) a more rapid geographic dispersal than the more demersal nautiloids. Possible additional important information is obscured by the lack of knowledge of where ammonoids laid their eggs (compare Westermann 1996). Hypothetically, floating egg masses of ammonoids (Tanabe et al. 1993) would make a big difference

for the interpretation of their ecology, their fast geographic dispersal, and their evolutionary success.

A morphological adaptation of the ammonoid shell to escape predators in the early Devonian is, however, not supported by the repaired shell fractures. The percentage of injured ammonoids (13 out of 293, i.e., 4.4%) roughly equals that of the bactritoids (57 out of 1535, i.e., 3.7% in the early Zlíchovian versus 7 out of 293 specimens, i.e., 5.7% in the late Zlíchovian; 3.8% in the entire Zlíchovian). However, it is logically not possible at this time to determine if this Early Devonian coiling and predation relationship is maintained to the end of the Cretaceous when the ammonoids became extinct.

Conclusion

Repaired shell injuries of Zlíchovian (early Emsian, Early Devonian) cephalopod shells are tentatively interpreted as traces of interactions between cephalopods in the Early Devonian. This is corroborated by the fact that many of the injuries have a triangular outline and often occur in pairs. Because of the overwhelming abundance of *Devonobactrites* in some localities which is combined there with a scarcity in vertebrates as well as in other cephalopods, these sublethal injuries speculatively may have been caused by intraspecific attacks. However, it cannot be excluded that jawed fish may have caused some of the healed injuries. Arthropods appear rather unlikely as perpetrators of these fractures because fossils of arthropods that possessed appendages suitable for shell-breaking have not yet been documented from the Devonian of Morocco. Additionally, many of the larger, predatory arthropods probably had a benthonic life style, and the cephalopods probably lived in the water column as part of the active nekton or as semi-pelagic feeders.

Tightly coiled cephalopod shells potentially had survivorship advantages over loosely coiled and orthoconic shells. The tightly coiled cephalopod's advantages were a gain in maximum swimming velocity as well as manoeuvrability, the conch span (= diameter in coiled forms and length in orthoconic forms) was decreased in the relation to the volume of the entire animal with a concurrent decrease in the risk of being captured, and the shell was more resistant to breakage. There is no clear evidence from the new data on shell fractures in bactritoids and ammonoids from the early Emsian, however, that the changed shell morphology would have enabled the early ammonoids to more successfully escape from any kind of attack. Hence, the apparently almost explosive initial radiation of ammonoids requires a different explanation that may be related to changes in feeding strategies, the reproductive mode and the behaviour of the offspring.

Acknowledgements

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