

Size distribution of the Late Devonian ammonoid *Prolobites*: indication for possible mass spawning events

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Abstract Worldwide, the ammonoid genus *Prolobites* is only known from a few localities, and from these fossil beds almost all of the specimens are adults as shown by the presence of a terminal growth stage. This is in marked contrast to the co-occurring ammonoid genera such as *Sporadoceras*, *Prionoceras*, and *Platyclymenia*. Size distribution of specimens of *Prolobites* from three studied localities show that, unlike in the co-occurring ammonoid species, most of the material belongs to adult individuals. The morphometric analysis of *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851) demonstrates the intra-specific variability including variants with elliptical coiling and that dimorphism is not detectable. The *Prolobites* material shows close resemblance to spawning populations of Recent coleoids such as the squid *Todarodes filippovae* ADAM 1975. Possible mass spawning events are discussed in the context of the size distribution and limited geographic range of *Prolobites*. Finally, the potential fecundity and brooding behaviour of *Prolobites* is hypothesized using the examples of post spawning egg care in Recent coleoids.

Keywords Ammonoidea · Coleoidea · Morphometry · Late Devonian · Famennian · Spawning

Abbreviations

SMF Senckenberg Museum, Frankfurt a. M., Germany
MB.C. Cephalopod collection of the Museum für Naturkunde Berlin (the collections of Franz Ademmer, Werner Bottke, and Harald Simon are incorporated here)

Introduction

The mid-Famennian (Late Devonian) ammonoid genus *Prolobites* is only known from a few localities worldwide, mainly in the Rhenish Mountains and the South Urals. Where it does occur, the majority of the specimens show a terminal growth stage suggesting that these are adults. For all assemblages, the size range is generally in a relatively narrow growth distribution band, and in this paper, we discuss possible biological reasons for this conspicuous limited size variance.

Only a few Palaeozoic ammonoids show mature modifications of the shell; it can be assumed that they have kept growing throughout their lives producing new chambers as they grew or, having been r-strategists, true adults were just rather rare. A number of species show evidence for a terminal growth stage, sometimes visible in prominent terminal constrictions, more or less significant widening or narrowing of the aperture, occasionally bizarre extensions of the adult aperture, etc. (e.g., Davis 1972; Zhao and Zheng 1977; Seilacher and Gunji 1993; Korn and Klug 2002; Klug 2004). The presence of these terminal stages suggests the end of the somatic growth for the individual because when the shell cannot be further enlarged the body will also not grow anymore. *Prolobites* is such a genus with rather extreme terminal changes in growth patterns,

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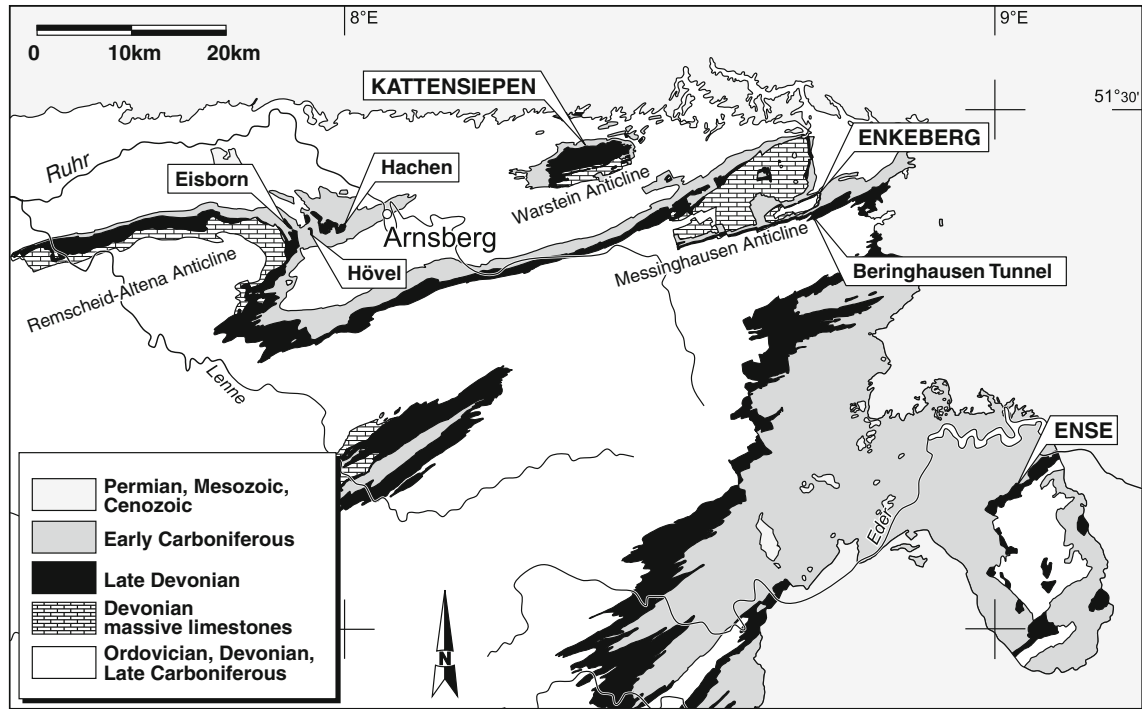


Fig. 3 Geographic and geological setting of the studied localities in the Rhenish Mountains (Germany). The three main localities Enkeberg, Kattensiepen, and Ense are *capitalized*

Methods

We obtained measurements of the conch diameters from all well-preserved specimens of the various horizons from three species of *Prolobites* (*P. delphinus*, *P. aktubensis*, *P. inops*) and the most important co-occurring genera. The data of the conch diameters were used in their logarithmic form to compile histograms of size distribution, using defined log size classes (Table 1), for each species. For the three investigated species of *Prolobites*, we measured two conch diameters, a first one (dm_1) at the terminal constriction of the conch, and a second one (dm_2) at 90° prior to the terminal constriction (Fig. 4). The ratio between dm_1 and dm_2 gives the whorl expansion rate of a quarter of the terminal volution, and the eccentricity rate can be calculated by adding the correction factor of 1.11 (per quarter of a whorl), taking into account the whorl expansion rate (per complete whorl) of approximately 1.50 for all species of *Prolobites*.

For a systematic excavation, a trench was opened on the Enkeberg, which allowed for an excavation of a surface area of ¼ square metre. As the amount of material was limited in this trench, all ammonoid specimens were collected regardless of their size and state of preservation. This enabled us to do a quantitative analysis of the material.

Results of measurements from *Todarodes filippovae* (a species of extant squid) published in a paper by Jackson et al. (2007) have also been included for comparisons. The

original data set from the paper has been converted into a logarithmic form to match the results from the ammonoid data sets.

Table 1 Size classes of conch diameters as used in the text and in the Figs. 6–8

Size class	Max. diameter	Log diameter
1	1.3	0.1
2	1.6	0.2
3	2.0	0.3
4	2.5	0.4
5	3.1	0.5
6	3.9	0.6
7	5.0	0.7
8	6.3	0.8
9	7.8	0.9
10	10.0	1.0
11	12.5	1.1
12	15.6	1.2
13	20.0	1.3
14	25.0	1.4
15	31.3	1.5
16	40.0	1.6
17	50.0	1.7
18	62.5	1.8
19	80.0	1.9
20	100.0	2.0

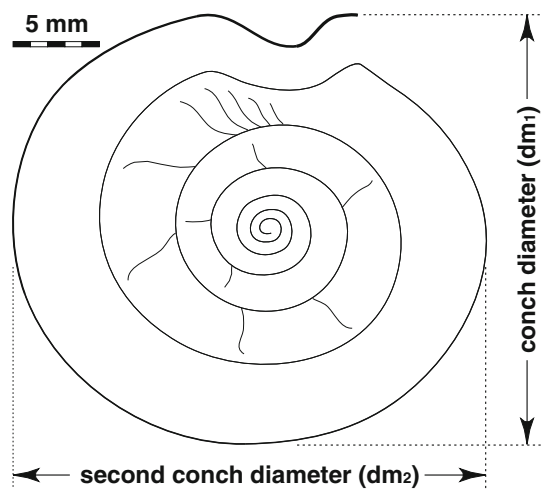


Fig. 4 Schematic, axial section of *Prolobites delphinus* (modified after Bogoslovsky 1969) and the conch measurements used for the calculation of the eccentricity rate

Investigated occurrences of *Prolobites* in the Rhenish Mountains

Three localities in the Rhenish Mountains of Germany (Enkeberg, Kattensiepen, and Ense, Fig. 3) with three different species of *Prolobites* (*P. delphinus*, *P. aktubensis*, *P. inops*) were investigated in greater detail. Assemblages from these localities contain specimens of the genus *Prolobites* in fair numbers (i.e. 24 or more specimens), together with accompanying species of the two major Famennian ammonoid orders Goniatitida and Clymeniida (Korn and Ziegler 2002; Korn and Klug 2002).

Enkeberg locality

The Enkeberg (or Enkenberg) is a locality on the Mes-singhausen Anticline, 2 km northwest of Beringhausen. It is the first known occurrence of *Prolobites delphinus* in the Rhenish Mountains and yielded most of the studied specimens. The Famennian section on the northern summit of the mountain has been sampled for more than 150 years

(Sandberger and Sandberger 1850–1856) and was the subject of a number of artificial trenches (described by Wedekind 1918; Lange 1929; Paeckelmann and Kühne 1936; Becker 1993; Korn and Ziegler 2002). In these trenches, a condensed and highly fossiliferous early and middle Famennian section was exposed.

The last of these systematic excavations (done in 1992 by Dieter Korn, Christian Klug, and Rainer Schoch) yielded in total more than 2,100 ammonoid specimens, of which nearly 750 came from seven successive beds (in ascending order bed 101 to bed 95) constituting the *Prolobites delphinus* Zone (Korn and Ziegler 2002); the nominate species *Prolobites delphinus* itself is represented by 212 specimens (28% of the specimens from this zone) (Table 2). This zone is represented by only 72 cm of red nodular, so-called cephalopod limestone (Korn and Ziegler 2002). The lithology of the seven beds is uniform, characterised by micritic matrix, in which the cephalopod conchs are usually completely preserved with their body chambers indicating a low energy regime. It is important to note that any sorting by size can not be seen in any of the limestone beds. These cephalopod limestones are interpreted as deep shelf sedimentary rocks, formed in a depth of about 100 m (see e.g. Wendt et al. 1984 as well as Wendt and Aigner 1985 for the sedimentological study of similar limestones in the Anti-Atlas of Morocco). The cephalopod limestones of the Enkeberg are very fossiliferous; some beds are even packed with ammonoid specimens and are “ammonoid packstones”.

In addition to the material excavated in 1992, 120 specimens of *Prolobites delphinus* from the trench opened by Paeckelmann in 1925 and 75 specimens collected by various researchers (Denckmann, Lotz, etc.), all stored in the Museum für Naturkunde Berlin, are also included in this study.

At Enkeberg, an abundant species regularly accompanying *Prolobites delphinus* (Fig. 3a, c) is, among others, the very common *Sporadoceras bidens* (SANDBERGER & SANDBERGER 1851) (Fig. 1d), which makes up approximately 35% of the ammonoid assemblage. This species

Table 2 The ten most common ammonoid species from the *Prolobites delphinus* Zone at Enkeberg (numbers of specimens collected during the excavation in 1992)

<i>Sporadoceras bidens</i> (SANDBERGER & SANDBERGER 1851)	259 specimens	34.7%
<i>Prolobites delphinus</i> (SANDBERGER & SANDBERGER 1851)	212 specimens	28.3%
<i>Prolobites nanus</i> (PERNA 1914)	12 specimens	1.6%
<i>Cyrtoclymenia frechi</i> (TOKARENKO 1903)	65 specimens	8.7%
<i>Genuclymenia discoidalis</i> WEDEKIND 1908	32 specimens	4.3%
<i>Genuclymenia karpinskii</i> (PERNA 1914)	19 specimens	2.5%
<i>Genuclymenia frechi</i> WEDEKIND 1908	16 specimens	2.1%
<i>Pleuroclymenia brevicosta</i> (MÜNSTER 1842)	10 specimens	1.3%
<i>Protactoclymenia pulcherrima</i> WEDEKIND 1908	9 specimens	1.2%
<i>Protactoclymenia enkebergensis</i> (WEDEKIND 1908)	9 specimens	1.2%

Table 3 The five most common ammonoid species from the *Platyclymenia annulata* Zone at Kattensiepen

<i>Prionoceras divisum</i> (MÜNSTER 1832)	122 specimens	23.9%
<i>Prolobites aktubensis</i> BOGOSLOVSKY 1969	24 specimens	4.7%
<i>Platyclymenia annulata</i> (MÜNSTER 1832)	81 specimens	15.9%
<i>Platyclymenia subnautilina</i> (SANDBERGER 1855)	152 specimens	29.8%
<i>Pleuroclymenia costata</i> (LANGE 1929)	32 specimens	6.3%

does not show adult modifications like *Prolobites delphinus*.

Kattensiepen locality

A nearly complete Famennian section is exposed in the large productive Kattensiepen quarry 2 km north of Sutrop. Most of the section is composed of nodular limestone with scarce fossils, but one distinct two-fold black shale horizon (*Annulata* Black Shale) is remarkable for its content of well-preserved ammonoids (Korn et al. 1984; Korn 2002). Black limestone nodules occur occasionally in one distinct horizon within the upper of the two black shale horizons; these nodules yielded a very well preserved ammonoid fauna of the *Platyclymenia annulata* Zone containing *Prolobites aktubensis* Bogoslovsky 1969 (Fig. 1b). More than 500 specimens are available for study (Table 3); they were collected by Werner Bottke (Münster), Franz Ademmer (Warstein), Harald Simon (Wiek/Rügen), and D. K. and are stored in the Museum für Naturkunde, Berlin.

Ense locality

The Ense locality near Bad Wildungen (eastern margin of the Rhenish Mountains) belongs to the classic localities for Devonian ammonoid faunas. It was first intensely studied by Denckmann (1894), and later, several excavations were made to investigate distinctive topics of this Devonian section. An excavation by Schindewolf (1934) yielded a rich assemblage of the *Platyclymenia annulata* Zone, consisting of more than 600 ammonoid specimens (Table 4).

Another excavation in 1992 by Manfred Horn (Wiesbaden), studied by D. K. and C. K., yielded another sample from only one large limestone nodule within the same horizon with more than 200 specimens. The fauna consists mainly of small specimens of *Platyclymenia*, which are difficult to attribute to distinct species.

Table 4 The most common ammonoid taxa from the *Platyclymenia annulata* Zone at Ense

<i>Prionoceras divisum</i> (MÜNSTER 1832)	122 specimens	15.1%
<i>Prolobites inops</i> KORN 2002	72 specimens	8.9%
<i>Platyclymenia annulata</i> (MÜNSTER 1832)	19 specimens	2.3%
<i>Platyclymenia subnautilina</i> (SANDBERGER 1855)	12 specimens	1.5%
<i>Platyclymenia</i> div. sp.	260 specimens	32.0%
<i>Trigonoclymenia</i> div. sp.	52 specimens	6.3%

Other localities

Further ammonoids from the *Prolobites delphinus* Zone were studied from another ten additional localities on the Remscheid Altena Anticline (Table 5). This comprises material stored in the Museum für Naturkunde Berlin and collected at the northern margin of the Rhenish Mountains by the geologists of the Prussian Geological Survey, and by Dieter Korn in the Beringhausen Tunnel.

Morphology and distribution of *Prolobites*

Morphology

The subfamily Prolobitinae consists of three or four genera (*Prolobites* KARPINSKY 1885, *Renites* BOGOSLOVSKY 1969, *Aurilobites* KORN 2002, and *Afrolobites* BECKER & BOCKWINKEL 2002, the latter is possibly a synonym of *Prolobites*). All share several characters, which makes it possible to attribute specimens to the subfamily Prolobitinae:

- Two very conspicuous constrictions are present during ontogeny, of which the last one occurs near the end of the adult aperture. The first constriction has a position exactly 360° earlier so that both constrictions together cause a significant narrowing of the body chamber.
- The spiral growth of the conch is, after the last constriction, replaced by a short phase of slight uncoiling, where the whorl outline deviates from the spiral coiling.

The genus *Prolobites* is characterised by the following characters:

- The conch varies from thickly discoidal to globular; the umbilicus is moderately wide in juveniles and is being closed by an umbilical plug in the terminal growth stage (Bogoslovsky 1969; Korn et al. 1984; Klug and Korn 2002).
- The last volution has an elliptical coiling; eccentricity can vary within rather wide limits.

Table 5 Distribution of *Sporadoceras bidens* and *Prolobites delphinus* in the *Prolobites delphinus* Zone from 10 additional localities in the Rhenish Mountains

Locality	Total specimens	<i>Sp. bidens</i>	<i>P. delphinus</i>
Beul near Eisborn	41	34 specimens	3 specimens
Ebberg near Eisborn	19	16 specimens	Absent
Ballberg near Hövel	48	42 specimens	Absent
Roland near Hövel	4	3 specimens	1 specimen
Wettmarsen	164	118 specimens	1 specimen
Ainkhausen	23	20 specimens	Absent
Grasberg near Hachen	44	31 specimens	9 specimens
Mittelberg near Hachen	7	3 specimens	1 specimen
Rülsterberg near Hachen	10	7 specimens	2 specimens
Engelberg near Hachen	21	15 specimens	2 specimens
Beringhausen Tunnel	160	39 specimens	53 specimens

- The steinkern of some species shows a short longitudinal constriction, caused by an internal shell thickening, on the last volution.
- The growth lines extend with a convex arch across the flanks and form a low to deep ventral sinus; after the terminal constriction, they occasionally have a slightly biconvex course.
- The suture line is simple; it can vary within populations, but possesses a rather distinct rounded or acute lobe on the flank and a deep external lobe (Perna 1914; Bogoslovsky 1969; Korn and Klug 2002).

Due to the rather poor state of knowledge of some of the species, it is not clear how many true species can currently be separated within the genus *Prolobites*. At least the following are documented adequately:

- *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851)—with a pachyconic or globular conch of 20–35 mm diameter in the adult stage; with coarse growth lines. “*Prolobites ellipticus* WEDEKIND 1908” is regarded as a junior synonym, see below.
- *Prolobites aktubensis* BOGOSLOVSKY 1969—with a pachyconic conch of about 20 mm diameter in the adult stage; with very fine growth lines and faint spiral lines.
- *Prolobites inops* KORN 2002—with a discoidal or pachyconic conch of about 8–12 mm diameter in the adult stage; with coarse growth lines, which suddenly become weaker on the last volution.
- The following four species were, because of their rare occurrence, not included in our study.
- *Prolobites mirus* WEDEKIND 1908—with a discoidal conch of about 20–30 mm diameter in the adult stage; with coarse growth lines.
- *Prolobites striatus* LANGE 1929—with a pachyconic conch of about 20 mm diameter in the adult stage; with coarse growth lines.

- *Prolobites nanus* PERNA 1914—with a discoidal or pachyconic conch of about 12–15 mm diameter in the adult stage; with coarse growth lines.
- *Prolobites mrakibensis* KORN & KLUG 2002—with a pachyconic conch of about 12–15 mm diameter in the adult stage; with very fine growth lines and a rather weak terminal constriction.

However, only the first three of the above listed species (i.e., *P. delphinus*, *P. aktubensis*, *P. inops*) are available in a sufficient number (i.e. more than 20 specimens per sample) to allow a quantitative analysis.

Temporal and spatial distribution

The genus *Prolobites* occurs in a limited stratigraphic interval within the mid-Famennian (*Prolobites delphinus* Zone and *Platyclymenia annulata* Zone). A few reports of *Prolobites* in the preceding *Pseudoclymenia pseudogonia-tites* Zone (Lange 1929) require confirmation.

Specimens of *Prolobites* have been collected from a number of localities, but they are common in only two regions, the Rhenish Mountains of Germany (Sandberger and Sandberger 1850–1856; Kayser 1873; Wedekind 1908, 1918; Lange 1929; Korn et al. 1984; Korn 2002; Korn and Klug 2002) and the South Ural in Russia and Kazakhstan (Tokarenko 1903; Perna 1914; Kind 1944; Nalivkina 1953; Bogoslovsky 1969). From some regions, e.g. the Harz Mountains of Germany (Born 1912), the Carnic Alps of Austria (Flügel and Kropfisch-Flügel 1965), and the Anti-Atlas of Morocco (Becker et al. 2002; Korn and Klug 2002), specimens of *Prolobites* have occasionally been reported, but they are rarities within ammonoid assemblages. Other regions, such as Franconia and Thuringia in Germany, have not yet yielded any specimens of *Prolobites*, although time-equivalent sedimentary rocks with

ammonoid faunas from these regions have been intensely investigated (e.g., Schindewolf 1923).

The patchy pattern of occurrence on the large scale is also present in the regional scale. We investigated semi-quantitatively the ammonoid faunas from the cephalopod limestones of the *Prolobites delphinus* Zone from 12 localities at the northern margin of the Rhenish Mountains (Table 5).

The proportion of specimens of *Prolobites delphinus* within the various samples is variable. Both sections on the Messinghausen Anticline (Enkeberg and Beringhausen Tunnel) show *Prolobites delphinus* in the same numbers as *Sporadoceras bidens* and the remaining entire accompanying fauna (Figs. 5a, b). By contrast, the localities situated on the Remscheid-Altena Anticline contain *Prolobites delphinus* at a much lower frequency, with two sub-regions (Hövel and Eisborn) from which only one specimen from each was recorded.

Results

Size distribution patterns

The size distribution for the material of *Prolobites* shows closely resembling patterns in all of the histograms compiled from the log results (Figs. 6, 7, 8). Size distribution is similar for all of the studied horizons at the Enkeberg and for the other two localities (Kattensiepen, Ense) where large samples (i.e. with more than 20 specimens) were collected. Based on the histograms, the majority of the specimens fall within a narrow range in the log size classes. The bulk of the distinct assemblages stay within the confines of two or three of the defined size classes (Table 1)

and there is a rapid fall in numbers of individuals after the peak log size.

Enkeberg

The size distribution of all ammonoids from the *Prolobites delphinus* Zone at Enkeberg shows that juvenile conchs are extremely rare; specimens below 10 mm conch diameter are almost completely missing. Rigorous bed-by-bed sampling in the lithologically uniform succession offers the opportunity to observe the size distribution through time.

Prolobites delphinus was recorded from the seven successive beds 101–95 (in ascending order); a total of 212 specimens have been measured. The histograms for each bed (Fig. 6) show similar patterns—the vast majority of the specimens are assembled in a narrow range at the right margin. During the studied time interval, the size of *Prolobites delphinus* increases (Fig. 9a); the mean diameter increases, from bed 101 to bed 95, as follows: 22.1–21.2–24.2–22.3–23.8–26.5–26.6 mm.

Size distribution of the accompanying *Sporadoceras bidens* shows a different pattern in comparison with that of *P. delphinus*. Distribution of conch sizes in the histograms is almost symmetric with skewing to both sides (Fig. 6). Although juvenile specimens are also extremely under-represented in *S. bidens*, the variation in size is much larger. This means that the *S. bidens* assemblage probably does not represent a population, which includes all growth stages corresponding to any kind of survivorship curve. The size peak for *S. bidens* (mean value of the conch diameter ranging between 30 and 37 mm) is always above that for *P. delphinus*. As with *P. delphinus* there are a few individuals in the smaller size classes and then there is a

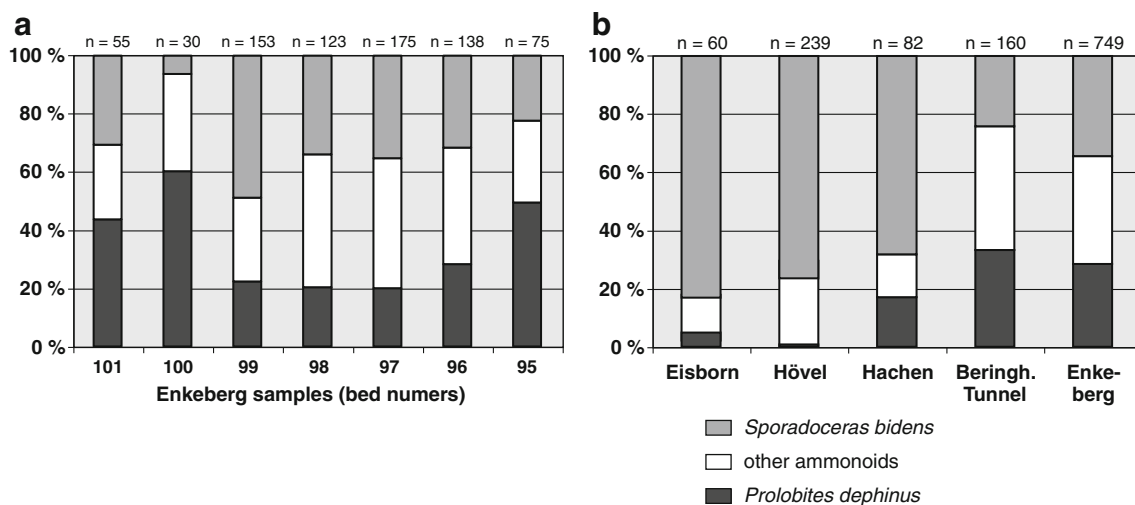
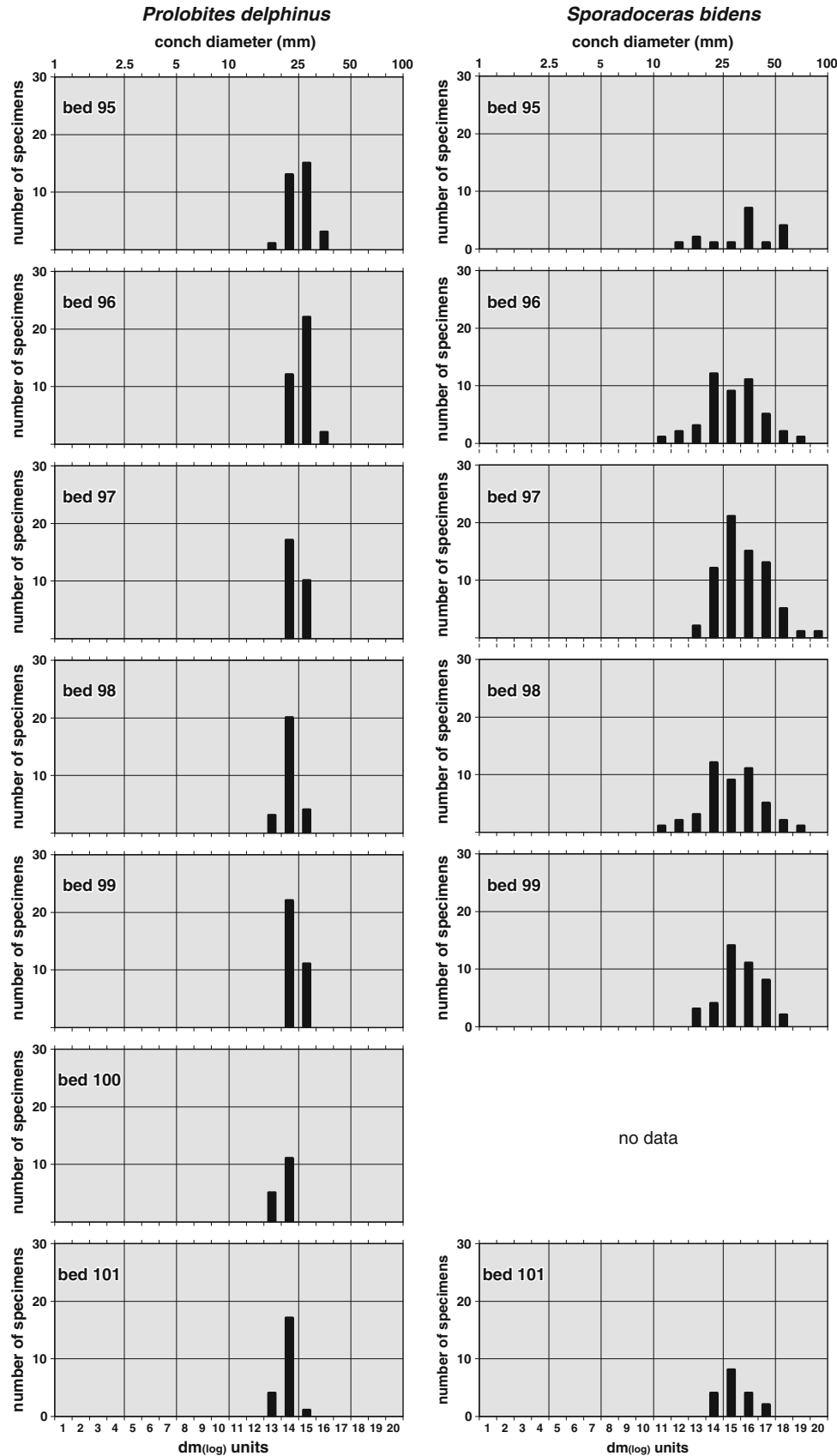


Fig. 5 Proportion of the species *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851) and *Sporadoceras bidens* (SANDBERGER & SANDBERGER 1851) with regards to the total number of specimens. **a** Enkeberg section. **b** Various sections in the Rhenish Mountains.

The region of Eisborn contains the localities Beul and Ebberg; the region of Hövel contains the localities Ballberg, Roland, Ainkhausen, and Wettmarsen; the region of Hachen contains the localities Grasberg, Mittelberg, Rülsterberg, and Engelberg

Fig. 6 Histograms showing the size distribution of the two species *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851) and *Sporadoceras bidens* (SANDBERGER & SANDBERGER 1851) within the seven successive horizons of the *Prolobites delphinus* Zone at the Enkeberg locality (excavation in 1992)



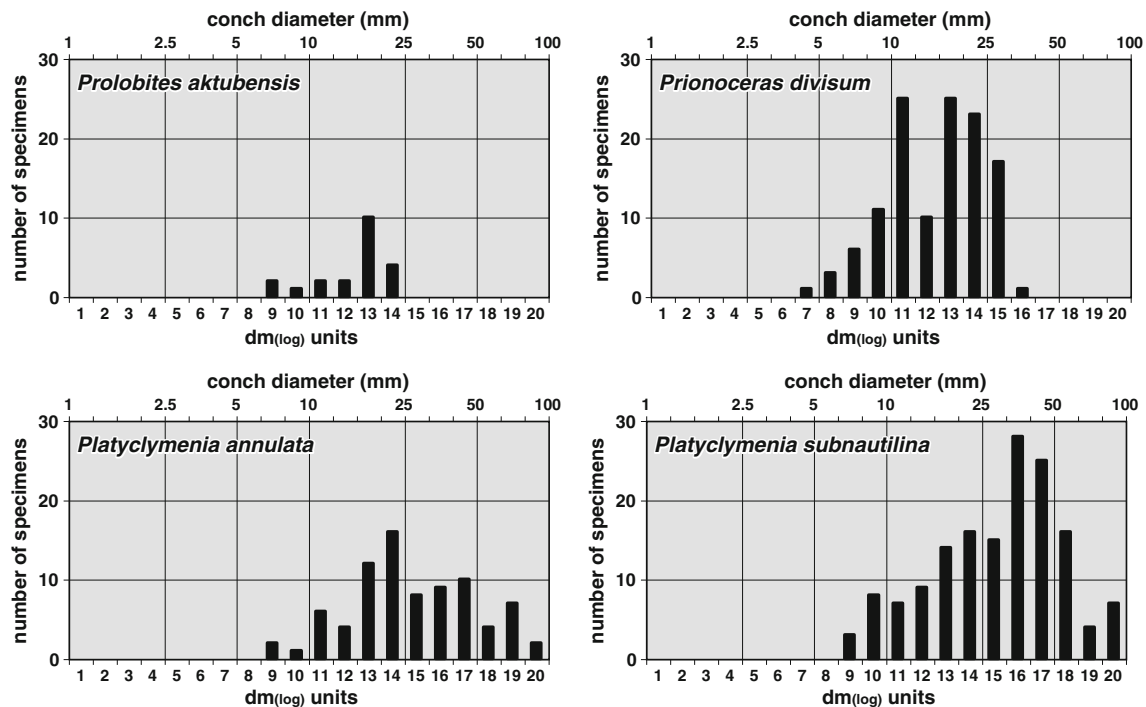


Fig. 7 Histograms showing the size distribution of the four species *Prolobites aktubensis* BOGOSLOVSKY 1969, *Prionoceras divisum* (MÜNSTER 1832), *Platyclymenia annulata* (MÜNSTER 1832), and

Platyclymenia subnautilina (SANDBERGER 1855) within the *Platyclymenia annulata* Zone of the Kattensiepen locality

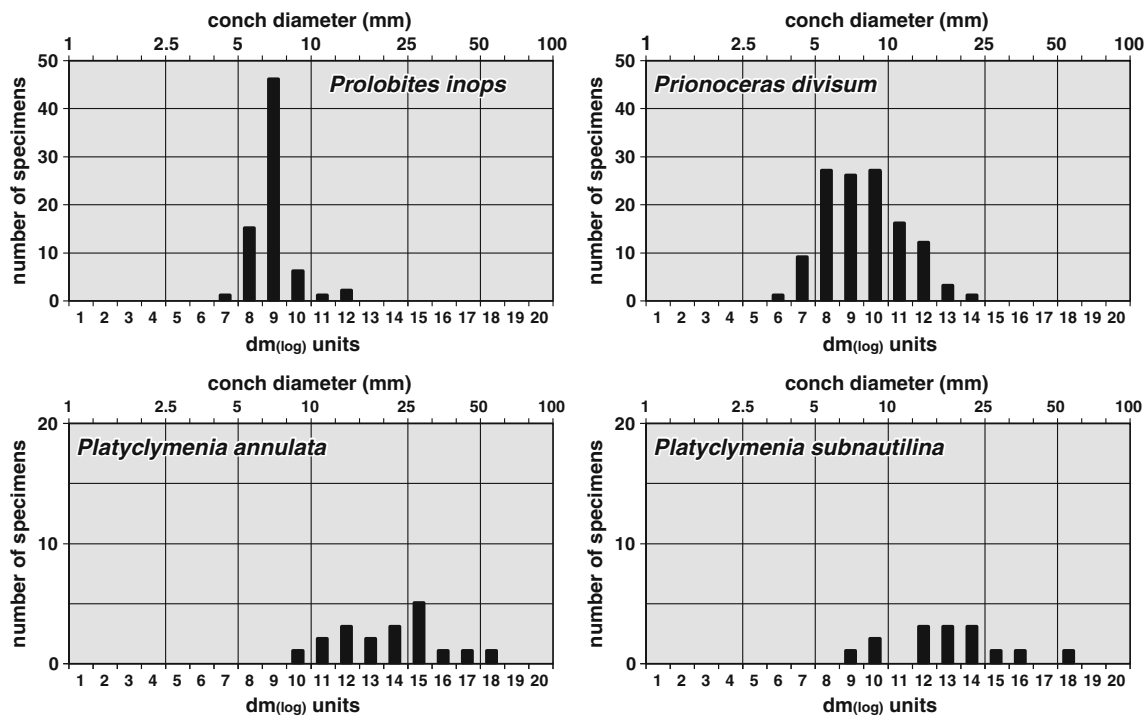


Fig. 8 Histograms showing the size distribution of the four species *Prolobites inops* KORN 2002, *Prionoceras divisum* (MÜNSTER 1832), *Platyclymenia annulata* (MÜNSTER 1832), and *Platyclymenia*

subnautilina (SANDBERGER 1855) within the two shale layers of the *Platyclymenia annulata* Zone of the Ense locality

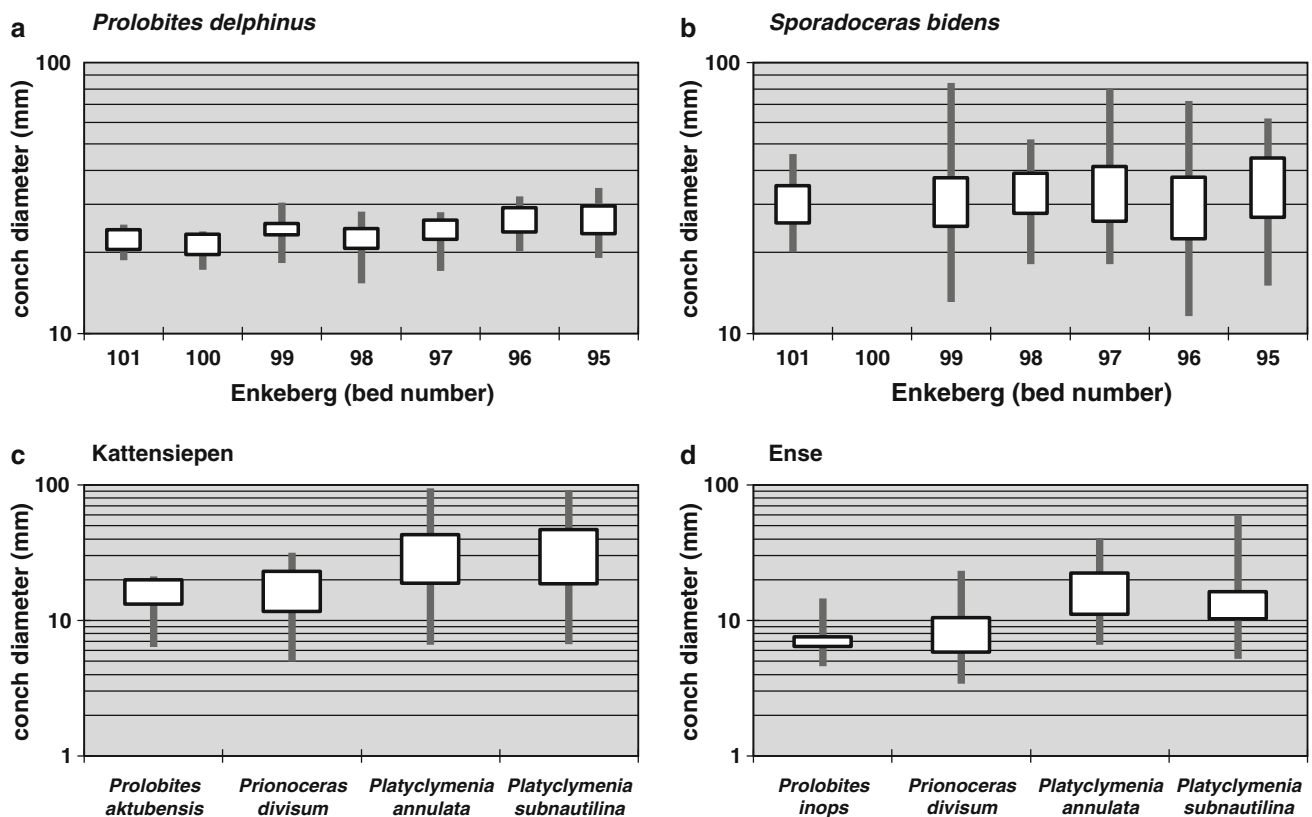


Fig. 9 Box-and-whiskers diagrams showing the size distribution of *Prolobites* and species of co-occurring ammonoid genera. **a–b** Size distribution of *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851) and *Sporadoceras bidens* (SANDBERGER & SANDBERGER 1851) within the seven successive horizons of the *Prolobites delphinus* Zone of the Enkeberg locality. **c** Size distribution of the four species *Prolobites aktubensis* BOGOSLOVSKY 1969, *Prionoceras divisum*

(MÜNSTER 1832), *Platyclymenia annulata* (MÜNSTER 1832), and *Platyclymenia subnautilina* (SANDBERGER 1855) within the *Platyclymenia annulata* Zone of the Kattensiepen locality. **d** Size distribution of the four species *Prolobites inops* KORN 2002, *Prionoceras divisum* (MÜNSTER 1832), *Platyclymenia annulata* (MÜNSTER 1832), and *Platyclymenia subnautilina* (SANDBERGER 1855) within the *Platyclymenia annulata* Zone of the Ense locality

sudden increase in the number of individuals found in the medium size classes, which accommodates the majority of the specimens. However, the drop off in specimen numbers in the larger size classes is not as severe as it is for *P. delphinus*, normally showing a more gradual decline over a number of larger size categories.

Kattensiepen

The size distribution of all ammonoids from the black limestone nodules is markedly different from those of Enkeberg. Almost all growth stages from the initial stage up to specimens of nearly 100 mm conch diameter are represented, but the very small specimens (i.e. smaller than 10 mm conch diameter) are extraordinarily rare (only 10% of the ammonoid fauna).

Prolobites aktubensis from this locality usually possesses the adult constriction at a conch diameter between 16 and 21 mm. Apart from a few immature specimens, which may have been damaged when extracted from the matrix, all fall within two size classes (Figs. 7, 9c).

Prionoceras divisum reaches, at many places, a maximum conch diameter of nearly 35 mm. The histograms of size distribution (Fig. 7) confirm this for Kattensiepen; it is asymmetric with a long tail on the left side and a rather abrupt truncation on the right side. This truncation is probably caused by the limitation of the maximum size in the species. Skewing to the left side demonstrates the prominent representation of juveniles and preadult *P. divisum* specimens at this locality.

Platyclymenia annulata is known, from the Kattensiepen locality, with specimens up to 100 mm conch diameter. The size distribution is almost normal with symmetric tails on both sides (Fig. 7) with the majority of the specimens between 20 and 50 mm conch diameter.

Platyclymenia subnautilina shows an asymmetric size distribution with a steeper right flank in the histogram (Fig. 7). The peak of size is in the size class between 32 and 40 mm dm; it is exceeded by a relatively large number of individuals.

The histograms for *Platyclymenia annulata* and *Pl. subnautilina* both show a more evenly distributed

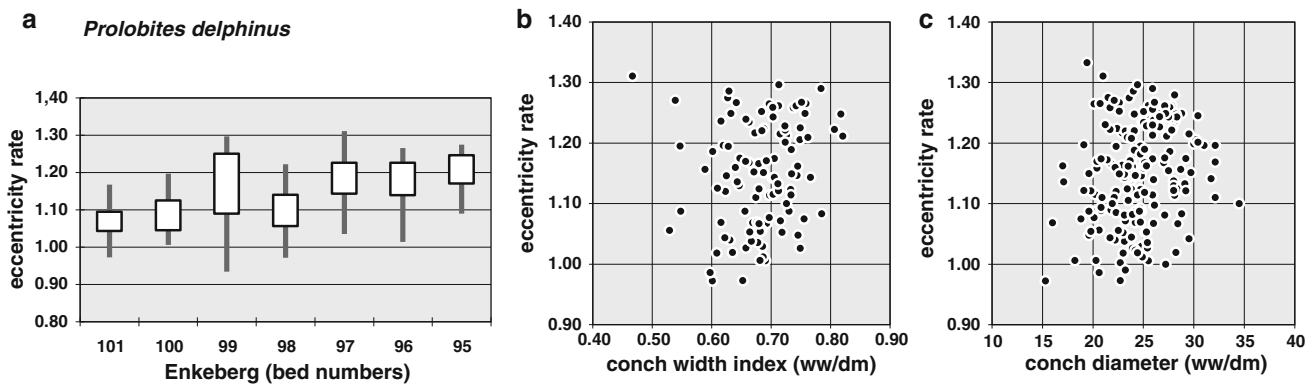


Fig. 10 Analysis of *Prolobites delphinus* (SANDBERGER & SANDBERGER 1851) within the seven successive horizons of the *Prolobites delphinus* Zone on the Enkeberg, **a** Box-and-whiskers diagram showing the eccentricity rate. **b** Scatter plot of 125 specimens with

respect to their conch width index (ww/dm) and their eccentricity rate. **c** Scatter plot of 189 specimens (stored in the collection of the Museum für Naturkunde, Berlin) from the Enkeberg section with respect to their conch diameter and their eccentricity rate

population over many more log classes than in the two goniatite species *Prolobites aktubensis* and *Prionoceras divisum*. Also, there is a more gradual increase in individuals with the progression of size classes until the peak and then again a gradual decline in numbers and not the rapid drop off seen in *P. aktubensis*.

Ense

In contrast to Kattensiepen and other localities at the northern margin of the Rhenish Mountains, the ammonoid fauna of the *Platyclymenia annulata* Zone from the Ense locality is mainly composed of rather small specimens (less than 40 mm; Figs. 8, 9d), a phenomenon that can at the moment not be explained with confidence. It is possible that there is a preservational bias that may involve size sorting or perhaps an ecological bias. The three species *Prionoceras divisum*, *Platyclymenia annulata*, and *Pl. subnautilina* occur in significantly smaller sizes.

The genus *Prolobites* is represented by *P. inops*, a species with an extremely small conch attaining diameters of only about 9 mm. All identified individuals display the adult morphology with a deep constriction; they fall into only three size classes and display the same size distribution as the occurrences at Enkeberg and Kattensiepen.

Size distribution of *Prionoceras divisum*, *Platyclymenia annulata*, and *Pl. subnautilina* is also consistent with the fauna from Kattensiepen, but the maximum and mean diameters are smaller.

Eccentricity of *Prolobites* conchs

Prolobites is well known for its eccentric coiling (Wedekind 1908, 1918; Bogoslovsky 1969; Korn et al. 1984; Korn and Klug 2002), and as a result of this, the species

“*P. ellipticus* WEDEKIND 1908” has been separated from *P. delphinus* to describe the eccentrically coiled forms (Wedekind 1908; Bogoslovsky 1969). However, a detailed statistical analysis of the material had not been achieved, and in the following, we will test if this separation is justified. The following questions ranged in the centre of interest to test a null hypothesis (i.e. that all patterns are random):

1. Can two (or even more) morphological groups be separated on the base of conch coiling?
2. Are temporal trends observable in the eccentricity rates of *Prolobites delphinus*?

Firstly, the distribution patterns for each bed, in which *Prolobites delphinus* occurs in the Enkeberg section, precludes a strict separation of the non-eccentric from the eccentric forms. Most of the beds show a nearly normal distribution of the eccentricity rates, and Fig. 10a, does not indicate any clear separation between two forms. The possibility that two species or two sexual dimorphs can be distinguished based on the eccentricity values is thus unlikely.

Secondly, a distinct pattern can be observed in the eccentricity of *Prolobites delphinus* in the Enkeberg section (Fig. 10a). From base to top (i.e. bed 101–95 in ascending order), an almost continuous increase can be observed, which is correlated with the size increase during this interval. While the eccentricity of the conchs is very low in bed 101 (median value = 1.07), there occurs a rapid increase to a median value of 1.17 in bed 99, followed by a temporal decrease towards 1.10 in bed 98 and then an increase to 1.21 in bed 95.

The correlation of size increase and the increase of eccentricity could lead to the assumption that larger specimens of *Prolobites delphinus* are generally more elliptical

in their coiling. We tested this by plotting the conch diameter and eccentricity rates for each bed (Figs. 10b–c). The result is that there is no correlation between the conch diameter of individual specimens and their eccentricity. The hypothesis that a replacement of smaller, more regularly coiled conchs by larger, more eccentric conchs occurred could not be confirmed.

Since the comprehensive study of the fossil material from the Enkeberg by Wedekind (1908, 1918), most of the subsequent authors (e.g. Lange 1929; Matern 1931; Nalivkina 1953; Bogoslovsky 1969; Nikolaeva and Bogoslovsky 2005) separated the two species *Prolobites delphinus* and “*Prolobites ellipticus*”, whereas Korn (2002) synonymized them.

The material from the excavation in 1992 allows for an analysis of the one and only criterion for the subdivision of the material, i.e. the eccentricity of the last volution. For this purpose, 125 complete adult specimens from beds 101 to 95 as well as 60 loosely collected specimens were measured with respect to the diameter at the terminal constriction.

The patterns of the eccentricity do not show any indication of a bimodal distribution, and hence, a separation of two species is not reasonable. None of the beds show a gap between less eccentric or more eccentric specimens, and also, there is no correlation between the size of the specimens and their eccentricity. Most of the specimens are somewhat eccentric, and there is almost a continuous series with most of the specimens ranging in the centre of variability. Consequently, “*Prolobites ellipticus*” must be regarded as a subjective junior synonym of *Prolobites delphinus*.

For similar reasons as those discussed in the section on the synonymy of *Prolobites delphinus* and “*Prolobites ellipticus*”, sexual dimorphism in *Prolobites delphinus* appears unlikely. The study of the samples from each of the seven horizons on the Enkeberg containing *P. delphinus* reveals there is no defined group separation. The conch morphology is somewhat variable, but there appears to be only weak correlation between the major investigated conch parameters; maximum diameter, conch width index (ww/dm), and eccentricity rate. No grouping is apparent, and dimorphic pairs can be ruled out.

The conch width index/eccentricity rate scatter diagram shows an almost evenly occupied morphospace, in which the centre is densest (Fig. 10b). An indistinct pattern can be seen, in that more globular conchs tend to be slightly more eccentric.

Discussion

Specimens of *Prolobites* have only been recorded in high numbers from a few sites around the world. As can be seen

from the data sets from occurrences in the Rhenish Mountains, the assemblages found in these areas consist almost entirely of adults and these specimens fall within a narrow range of size classes. What could be the cause behind such a pattern? The following points may help to clarify what is unique about the genus *Prolobites* in the fossil record.

Size distribution patterns of *Prolobites* and the associated other ammonoid species

The investigated localities containing *Prolobites* show three different patterns of size distribution:

- *Platyclymenia annulata*, *Pl. subnautilina*, and *Sporadoceras bidens* show an almost normal (Gaussian) size distribution with symmetric tails on both sides when the diameter is used in the log scale (Figs. 6, 7, 8, 9). Juveniles and also adult specimens occur in decreasing frequency, and there is probably no strict upper limit. Nevertheless, hatchlings and small juveniles appear to be underrepresented, as in *Prolobites*.
- *Prionoceras divisum* has an asymmetric distribution with a long tail on the left side and a more abrupt truncation on the right side than any of the three aforementioned species (Fig. 7). This means that a variety of juvenile specimens are available, but that the species is probably limited in the maximum diameter.
- The size distribution of all species of *Prolobites* falls, in all the investigated occurrences, within a narrow range of size classes and tails are absent from the histograms. A Gaussian distribution is not the case with any of the investigated assemblages of *Prolobites*. There are neither left-biased nor right-biased tails present on the histograms.

Small size of *Prolobites* and presence of a terminal growth stage

The maximum diameter of the *Prolobites* species is in general quite small, not exceeding 30 mm, which represents the size of a large individual. This is related to the fact that further growth is retarded by the terminal growth stage, capping individuals at sizes of 30 mm or less.

But why did this taxon have a limited growth at all? Other ammonoid genera (such as the also investigated *Platyclymenia* and *Sporadoceras* as described herein) attain conch diameters greater than 100 mm. Therefore the habitat appears not to be responsible for the retardation of growth in *Prolobites* as the conditions allowed to accommodate larger ammonoid specimens. Of course, *Prolobites* may have occupied a different feeding niche to other ammonoids, and the adaptation or constraints applied to

Prolobites in this niche may have set an upper limit on the optimum size.

Most ammonoid species appear to have an upper size limit, but this is rarely as clearly determined as in *Prolobites*. The terminal growth stage is indicative of the cessation of somatic growth and as such would suggest that any individual within this stage is an adult, therefore the majority of the *Prolobites* so far found would appear to be adults. But why is the abundance of adult ammonoids of various species in ammonoid assemblages so extremely different? Some ammonoid species are hardly ever found as adults while in taxa such as *Prolobites*, juvenile specimens are exceedingly rare. And this phenomenon can certainly not be explained by significantly different survivorship patterns. Most ammonoids were, compared to many nautiloids (extant and extinct) and some coleoids, rather r-strategists (Korn and Klug 2007), as reflected in their small embryo-size (usually <2 mm; Landman et al. 1996).

Scarcity of *Prolobites* in other contemporary fossil ammonoid horizons

Occasionally *Prolobites* specimens have been found in other areas within Central Europe, but these are rare and only represent a few individuals. For some reason or reasons (feeding, security or breeding), *Prolobites* species seem to be preferentially found at the Kattensiepen, Enkeberg and Ense localities. The distribution of *Prolobites* suggests ecological preferences, which differed from other ammonoids such as many clymeniids, prionoceratids and sporadoceratids. Some of the discussed localities, where *Prolobites* commonly occurs, share a rather condensed sedimentation and have been suggested to represent pelagic highs or ridges with reduced water depth and reduced sediment accumulation rates. Such a situation has been suggested by (Korn 1995a, b) for Late Famennian cephalopod limestones, where ammonoid taxa with minute conchs occur.

This relation of abundance of certain taxa to a special facies supports ecological preferences for *Prolobites*, but it still does not explain the scarcity of juvenile specimens. This apparent geographic separation of juvenile and adult specimens suggests a link of this distributional pattern with a behaviour linked to reproduction. We will discuss this aspect in the following sections.

Possible spawning effects

If *Prolobites* congregated at the studied localities simply for feeding, that would not explain why there is such a narrow range of sizes and why all the specimens have terminal growth patterns. Surely, individuals covering a much wider

spectrum of ages could feed in the same area, as seen in the other co-occurring ammonoid species, which show a much wider spectrum of sizes including juvenile individuals. Perhaps, the terminal growth stage and the concurrent change in conch and corresponding soft-part morphology aided in a new feeding strategy, thereby excluding individuals without the necessary modifications irrespective of size. This possibility can not be ruled out, but why would an animal make such changes in its feeding apparatus if it then at the same time stops its somatic growth and enters the last stage of its life? Also, the changes in conch morphology appear to be more of a hindrance to feeding rather than a benefit, the aperture opening of the body chamber after the terminal growth stage is greatly reduced therefore also reducing the size of potential food items which could be handled within the body chamber (if this was their preferred feeding mechanism). Additionally, it is usually assumed (based on stomach contents), that ammonoids were microphagous, i.e. no larger prey items had to fit through the aperture and pass the constrictions.

If the studied localities represented a safe habitat for *Prolobites*, it is intriguing that the vast majority of the individuals found are adults. So why should not spawning be one of the possible reasons behind the observed distribution patterns of *Prolobites*? The relationship between the Ammonoidea and the Coleoidea could be potentially useful for using extant Coleoidea species to help in the interpretation of at least some ammonoid species.

Spawning in Recent coleoids

The Coleoidea are generally short-lived animals and individuals of most species have life spans ranging from 6 months to 3 years (Boyle 1987). They therefore grow very rapidly to attain their adult size; an example is the Recent jumbo squid *Dosidicus gigas* D'ORBIGNY 1835 which can grow up to 2 mm a day to reach a mantle length of 87.5 cm in 14–15 months (Markaida et al. 2004). There can be quite a large variation in size of the adults depending on water temperature, food availability (Yang et al. 1986; Boyle 1987), and how many months they have to mature, the latter case occurs in species with more than one cohort in a year (Argüelles et al. 2001).

There is a wide variety of breeding strategies that have been reported amongst the Recent Coleoidea, this paper uses spawning terminology from 'Cephalopods of the World' (FAO Species Catalogue for Fishery Purposes No. 4, Vol. 1, by Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione Jereb et al. 2005). Some general observations and specific examples are provided below (see, e.g., Boyle and Boletzky 1996; Rocha et al. 2001).

Many species of squid, for example *Todarodes pacificus* STEENSTRUP 1880 (see Ikeda et al. 1993) are single event

spawners (SES) breeding in large spawning masses and then dying off afterwards (semelparous), other squid such as *Loligo vulgaris* LAMARCK 1798 (see Rocha et al. 2001), *Photololigo* sp. (see Moltschaniwskyj 1995), and in *Stenoteuthis oualaniensis* LESSON 1830 (see Harman et al. 1989), are termed multiple event spawners (MES), which means that they can breed several times, over a period of a few months and then die off (iteroparous).

In a lot of the *Octopus* species, for example *Octopus cyanea* GRAY 1849 (see Rocha et al. 2001) and *Octopus vulgaris* CUVIER 1797, the females are SES but instead of dying immediately after spawning, they protect their eggs until hatching and then die shortly afterwards, due to degeneration of their bodies during the nursing period, as they are unable to actively hunt for sufficient quantities of food without abandoning their eggs to predators (Wodinsky 1978). The Recent Nautiloidea are classed as MES but unlike the Coleoidea, they do not die after their breeding season; they can live for many years (Saunders 1983; Cochran and Landman 1984; Westermann et al. 2004) and can breed repeatedly over a number of years (Saunders 1983). The extant species tend to lay a few large eggs (25–30 mm in diameter) singularly and then abandon them, thus leaving the eggs to develop and hatch without post spawning egg care (Ward 1987).

The common theme in the majority of the Recent Coleoidea species is a major reduction in the condition of the body after the breeding period, which is often the reason behind mass die offs. The mass of the mantle tissue is often greatly reduced as the proteins are metabolised for energy (Moltschaniwskyj 2004), the feeding tentacles can also be lost in some squid species (*Gonatus onyx* Young, 1972) to enable the egg mass to be held more securely in the arms of brooding females (Seibel et al. 2000), therefore affecting mobility and the ability to actively hunt or evade predators.

Knowing the breeding strategies and life histories of the modern Coleoidea can help to interpret aspects of the ammonoid fossil record. It is with this in mind that this paper examines the size of *Prolobites* specimens and suggests a possible reason behind the apparently strange skewed nature of its size distribution by comparing it with a living species of squid, *Todarodes filippovae* ADAM 1975.

Many species of squid and some cuttlefish come together at breeding times and congregate in spawning masses (Sauer et al. 1992; Naud et al. 2004). If these populations were to be fossilised, they would reveal distinctive size distributions. For example a lack of small juvenile individuals, as they have either all matured or they are spread out over a wider area foraging for food (Bjørke et al. 1997), results in a more sudden recruitment of larger specimens; this could be seen on a histogram by the lack of a left biased tail. In semelparous species like *Loligo opalescens*

(Berry 1911), which are single event spawners (Rocha et al. 2001), all the adults die after spawning (Fields 1965). Therefore, there is a cap as to how big an individual can be as it only has between 12 and 24 months to grow depending on temperature and food availability (Yang et al. 1986). So a species like *L. opalescens*, if fossilised after spawning, would be represented only by adult individuals in the fossil record, all of which would fall within a fairly narrow range of sizes due to the restricted growing time, the sudden die off after breeding being responsible for the lack of a right biased tail in a histogram.

In the histogram (Fig. 11) for the size distribution of the Recent squid species *Todarodes filippovae* ADAM 1975 (see Jackson et al. 2007), measurements of specimens, which were caught as by-catch (by a trawler) were used. When compared with the *Prolobites* histograms, there is a fairly good congruence between the two size distribution patterns.

Spawning sites in *Prolobites*?

From the fossil record we can find several examples of supporting evidence, which are suggestive of the possible type of spawning behaviour used by *Prolobites*. The terminal growth constrictions, the changes in shell geometry such as the closure of the umbilicus and the septal crowding are good evidence for adulthood of the specimens. Since most of the specimens were adult, this suggests that they may represent spawning populations. The above mentioned mature modifications in *Prolobites* indicate the end of the somatic growth, which, in the Recent Coleoidea, usually signals the onset of breeding and the gradual decline of the condition of the individual. This decline may be reflected in the changing growth-line spacing, their irregular appearance as well as their increased strength at the terminal aperture (compare Klug et al. 2007).

The almost complete representation of adult *Prolobites* specimens in the studied localities is not due to size sorting, as evident from the lithology of the cephalopod limestones and the presence of smaller and larger fossils of various groups. Irrespective of size it is the constrictions that declare the adult specimens, within the populations if sorting occurred, we would be able to find large immature individuals, greater in size than mature smaller individuals, but who are not quite mature enough to possess the terminal growth constrictions, however, almost every single specimen has a terminal growth constriction and, currents, wave actions or sedimentation could not differentiate between such slight changes in conch morphology or size. There is also the other concurrent ammonoid species, which possess a greater size distribution than *Prolobites*. So, if sorting had occurred for *Prolobites*, then it would have affected all other ammonoids in the same horizons to

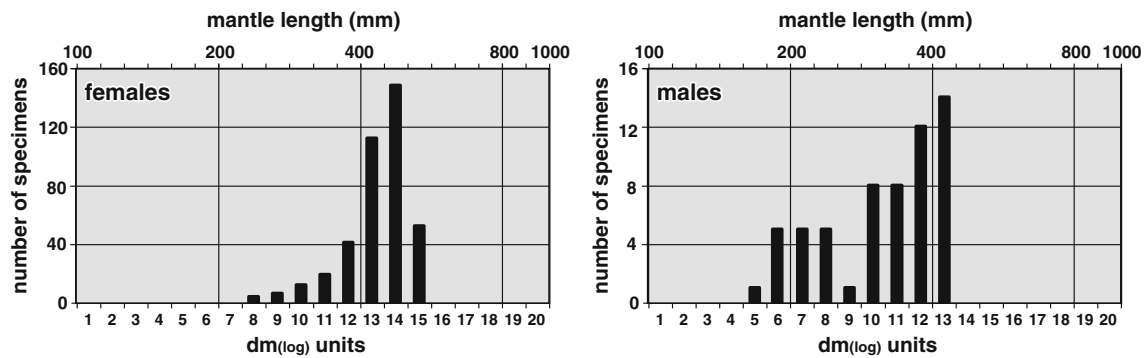


Fig. 11 Histograms of size distribution for captured adult female and male specimens of *Todarodes filippovae* ADAM 1975 based on data by Jackson et al. (2007)

the same extent. It appears more logical and sensible that a deliberate grouping of *Prolobites* occurred whilst they were still alive and that the reason behind this grouping was a biological consequence of possessing a terminal growth constriction rather than simply the size of the individual.

Of course, even though the material is indicative of mass spawning events for *Prolobites*, it is hard to say with certainty whether *Prolobites* were SES or MES. However, because of the terminal growth stage, it can be suggested that individuals had only one breeding cycle within their lifespan.

Patchy distribution of Prolobites

Mass spawning, as a hypothesis, helps to explain the strange patchy distribution of *Prolobites*.

It has been suggested recently, that Palaeozoic ammonoids produced floating egg-masses (Mapes and Nützel 2008) and the hatchlings became part of the free-swimming plankton (Korn and Klug 2007). This would have caused a rapid dispersal of eggs and juveniles, including transport away from the spawning grounds. The lower preservation potential of embryonic and early juvenile conchs (the low amounts of aragonite are quickly dissolved by sea-water after death) would have added to the poor record of *Prolobites*-juveniles.

The size distribution of *Prolobites* is unique when compared with other contemporary ammonoids; the distribution for individual sizes in a population of fully grown specimens should be expected to be Gaussian unless there is a bias within that population affecting recruitment, for example an area used for breeding. The restricted nature of the distribution of large numbers of specimens of *Prolobites* leads to the interpretation that there is an ecological driving factor behind certain popular sites.

The peak in growth at about 30 mm diameter with an abrupt cut off after that (documented by strongly crowded

growth lines and septa) would suggest similar lifespans and thus synchronous deaths of populations of the same age. Possible semelparous behaviour is reflected (although not proven) by this peculiar mature growth. By contrast, iteroparous species would be expected to either grow continuously or to display repeated growth modifications of the same type. Since ammonoid growth patterns are nearly as diverse as the group's morphologic disparity, it is very likely that ammonoids followed different reproductive strategies. In the case of *Prolobites*, the combination of extreme terminal growth in combination with the repeated findings of assemblages of exclusively mature individuals can be explained by mass spawning of a semelparous species, which only has one breeding cycle in its life span and then dies. Alternatively, it cannot be excluded that the representatives of this genus reproduced during more than one breeding season. Nevertheless, the empirical data of ammonoid growth stages and sizes supports a synchronized die-off, possibly linked with mass-spawning.

Possible spawning in Prolobites?

If the studied *Prolobites* localities do represent spawning or brooding grounds, then, how might the species have reproduced? In spite of the absence of evidence, it is still possible to get some idea of the reproduction of these ammonoids by taking the following information into account:

1. There is some indication that Carboniferous ammonoids and most likely also Devonian ammonoids produced floating egg-masses from which planktonic juveniles hatched (Mapes and Nützel 2008).
2. Egg-size is expected to be not so much larger than ammonitella-size, as suggested by Etches et al. (2009) who described structures which might be egg-sacs and eggs of Jurassic ammonoids (compare also Landman et al. 2010); however, none of the reports of supposed

ammonoid-eggs are completely free of doubt. The ammonitella-size of *Prolobites* measured probably around 1.5 mm in diameter (compare sections in Bogoslovsky 1969 and values for tornoceratid ammonitellae in Landman et al. 1996). Therefore, egg-size was at least this size and probably slightly larger. At this size, the eggs would have been able to pass through the narrow passage at the constriction, which was 3–5 mm high in some species of *Prolobites*. At the flanks, the whorl section was too low for egg-storage, so the ovaries most likely had a ventral to ventrolateral position in the soft-body. At a diameter of 30 mm, presuming (ad hoc) the posterior half of the adult body chamber was partially filled with eggs, the ovary volume might have amounted to the following volume: At an apertural height of 3.5 mm, a space filled with the ovary 10 mm wide (i.e. not the entire width) and, at a diameter of 20 mm, amounting to a whorl section length = $\pi \times dm/2$ (half a whorl, roughly circular), i.e. 31.4 mm, the ovary could have filled a volume of 1,099 mm³. With an egg-diameter of 1.5 mm (low estimate), one egg would have filled 3.375–3.5 mm³. Consequently, at a uniform egg-size and when densely packed, the body chamber of *Prolobites* could have housed about 200–300 eggs. With this number, this genus could still be considered as an r-strategist (type III survivorship curve). Presuming a larger egg-size ($dm_{\text{egg}} = 3$ mm, egg volume = 14–27 mm³) and smaller ovaries (reproductive organ volume = $10 \times 15 \times 3.5$ mm³ = 525 mm³), the number of eggs could be as low as 20–40 eggs per adult female. Naturally, empirical data to test either value are not available, but the evolutionary behaviour of ammonoids with their high evolutionary rates indicates that the former value might have been closer to reality, making an interpretation of *Prolobites* as an r-strategist (type III survivorship curve) more plausible.

Is there any evidence that can be found on the phragmocone, which may help us to test hypotheses concerning the breeding habits of *Prolobites*? As stated earlier, at least two very conspicuous constrictions are present during ontogeny, of which the last one occurs near the end of the adult aperture and the first one has a position 360° earlier so that both constrictions together cause a significant narrowing of the body chamber (a third, oval shell thickening can occur shortly behind the last constriction). In the following we present three possible hypotheses about the reason and function of the terminal constrictions in *Prolobites*:

1. The null hypothesis: The constrictions reflect simple growth halts without function, just as in many other mollusc shells.
2. The constrictions made it difficult for some predators to break the shell in order to get access to the soft-parts and the valuable reproductive organs (compare, e.g. Palmer 1979; Vermeij 1982; Keupp 2000). This was important especially for adult females, which stored numerous eggs in their body chamber. For our suggestion of external brooding, this interpretation would not hold, logically.
3. The adult modifications of *Prolobites* may have been adaptations towards a special kind of brooding behaviour: The narrowing of the body chamber, the last constriction and the small lateral constrictions directly posterior to that constriction could have acted as an anchoring point for the soft-parts of *Prolobites*. This anchoring point could have allowed the animals to extend their bodies far out of the apertural opening. In this position, the female animals could nurture an egg mass within their arms; brooding of eggs held in their arms has been reported for the squid species *Gonatus onyx* from deep-sea areas (Okutani et al. 1995; Seibel et al. 2000, 2005) and for *Gonatus fabricii* Lichtenstein, 1818 (Arkhipkin and Bjørke 1999; Bjørke et al. 1997). External brooding would have increased the potential amount of eggs significantly, and, speculatively, more than 1,000 eggs per adult female would be conjecturable. Presuming the egg-masses could float (cf. Mapes and Nützel 2008), this strategy would not have imposed a problem to maintain buoyancy in these ammonoids. Some support for this speculation comes from ammonoid specimens preserved with egg sacs figured by Etches et al. (2009): None of these egg-clusters lies within a body chamber, which, however, casts doubt on these findings since the eggs might as well belong to other organisms (compare Zaton et al. 2009). Nevertheless, egg and brood care is well known from coleoids (e.g. Recent *Octopus*) and if the eggs were neutrally buoyant, it would have been possible that ammonoids carried their eggs along for some time. But what of the dangers posed from predators if such brooding methods were used? The horizons that *Prolobites* species are found in consist of cephalopod limestones, which were originally formed at an estimated water depth of less than 200 m (Wendt et al. 1984; Wendt and Aigner 1985). If the brooding females held the eggs whilst floating, then they would be able to protect the eggs from benthic organisms, but attacks by pelagic predators were still possible. Nevertheless, both the *Prolobites*-bearing layers at Enkeberg and Ense are rather poor in remains of potential predators such as fish or larger arthropods. Only the Kattensiepen locality yielded phyllocarids that could be predators of the ammonoids (Koch et al. 2003).



Fig. 12 Life reconstruction of *Prolobites*. Since hardly anything is known about the anatomy of ammonoid soft parts, reconstructions are still largely speculative, two different reconstructions are proposed. On top, a mature female *Prolobites* carrying an egg sac externally like the Recent decabrachian squid *Gonatus*, and at the bottom, *Prolobites* as an active swimmer with the aperture oriented at roughly 40°–50°, due to its body chamber exceeding 360° in length (compare with Saunders and Shapiro 1986; Klug and Korn 2002). We show ten arms because this appears to be the plesiomorphic state in coleoids and perhaps also in nautilids, as indicated by the ten arm-buds displayed by *Nautilus*-embryos (compare Shigeno et al. 2007)

Speculatively, they could have used their hyponome to bathe the eggs in circulated water, the constriction at the hyponome aiding this behaviour in directing and controlling the current so as not to dislodge eggs from the egg mass (Fig. 12), as observed in *Gonatus* (Seibel et al. 2005). A loss of feeding ability due to the reduced size of the aperture would not necessarily pose a problem as coleoid females often do not eat whilst brooding.

The peculiar specialisations in the adult body chamber of *Prolobites* and their potential meanings are:

1. The long body chamber has a constriction at its beginning and close to the terminal aperture. The latter one is often associated with a smaller constriction, which never crosses the entire whorl cross section; this might putatively be a specialised soft-tissue attachment structure to which the structure, which held the egg-mass might have been attached or for special hyponome muscles to support its “ventilating” action.

2. Between the terminal aperture and the terminal constriction, the whorl is nearly straight. This might have been an adaptation to the downward orientation of parts of the soft-body including the hyponome.
3. The long body chamber (360°–400°) indicates a low orientation of the aperture (30°–50°; cf. Saunders and Shapiro 1986; Klug 2001), comparable to *Nautilus*. Such an orientation is rather unusual among adult ammonoid shells (Westermann 1996; Klug 2001; Korn and Klug 2003), which usually show a tendency towards rather horizontal apertures (ca. 90°) at maturity. The horizontal orientation is advantageous for horizontal swimming and thus, this altered orientation in *Prolobites* is striking. Again, this specialisation conforms to the hypothesis of external brooding of eggs.
4. The apparently successful reproduction of Late Devonian ammonoids with low apertures and strong constrictions (e.g. mass occurrences of cheiloceratids) might also support the external brooding of eggs hypothesis: These often small ammonoids could have produced a higher number of eggs at smaller adult shell-sizes and -again speculatively- after a rather short time-span between hatching and maturity.

Conclusions

Prolobites is a very special ammonoid genus in a number of respects:

- It is locally abundant but very rare at most other localities of the same age.
- Usually, almost exclusively adult specimens are found; the size-distributions are extremely limited and juveniles are strikingly under-represented.
- The body chamber is very long (>1 whorl), causing a rather low orientation of the aperture. According to Klug and Korn (2002) and Jacobs and Chamberlain (1996), this orientation may indicate poor swimming.
- The body chamber carries two aligned constrictions, giving the subterminal body chamber an unusual configuration not seen in almost all other Palaeozoic ammonoids.
- A third, small, and sometimes more or less bean-shaped shell thickening occurs behind the younger of these two constrictions, and could have served as an attachment point some specialised tissues.

The peculiar combination of extreme shell morphology (extraordinary terminal growth) and the “adult-only” *Prolobites* assemblages point to a peculiar mating (and

possibly spawning) behaviour such as the choice of joint mating and/or spawning sites.

The striking morphological features of *Prolobites* could eventually be related with external brooding of eggs. However, this hypothesis cannot be tested further, because recovery of soft-parts to prove this hypothesis is extremely unlikely.

Alternatively, the strange size-distribution might have some sedimentological or ecological reason, maybe the adults met at certain places for mating. The body chamber length and orientation might simply reflect a rather planktonic mode of life and active horizontal swimming was less important in this genus. Alternatively, the rather downward orientation of the aperture might indicate an orientation towards the sediment surface, i.e. a rather demersal habit of the adult specimens. This would then fit with the interpretation of the constrictions to make the body chamber more resistant towards attacks by predatory fish or arthropods. No matter what these ammonoids actually did with their eggs.

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