Soft-tissue attachments in orthocerid and bactritid cephalopods from the Early and Middle Devonian of Germany and Morocco

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In the Early to Middle Devonian shale sequences of Germany and Morocco, pyritised and secondarily limonitised cephalopod remains are common. Details of the soft-tissue attachment structures are sometimes preserved on the internal moulds of the body chamber and phragmocone of these cephalopods. Some of the studied Orthocerida show a very faint annular elevation and a dorsal furrow. A few Bactritida show a distinctive annular elevation with two circular bands. The bands form a paired or threefold lobe at the dorsum of the shell. Morphological differences between Orthocerida and Bactritida suggest different soft part morphologies. A comparison of the attachment scars shows that the Bactritida are intermediate between the Orthocerida and ammonoids with regard to their muscle attachment scars. The shape of the muscle scars are interpreted as indication for a planktonic lifestyle in Orthocerida and a comparatively active, nektonic lifestyle in Bactritida and ammonoids. The new genus *Acanthomichelinoceras* is erected. *Acanthomichelinoceras commutatum*, *Cycloceras* sp., *Bactrites gracile, Bactrites* sp. A, *Bactrites* sp. B, and *Bactrites* sp. C are described.

Key words: Cephalopoda, Bactritida, Orthocerida, soft-tissue attachment, muscle scars, Emsian, Eifelian, Morocco, Germany.

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Introduction

With regard to the evolution of cephalopods, the Emsian and Eifelian stages (Early and Middle Devonian) are exceptional because this was the time when ammonoids appeared and when they underwent their early evolution (Erben 1966; Bogoslovsky 1969, 1972; Klug 2001; Klug and Korn 2004), a period of prosperity of Bactritida (Schindewolf 1933; Erben 1964 a, b), and of coiled nautiloids (Zhuravleva 1972, 1974). It was therefore a time of extraordinary cephalopod diversity that contrasted with the preceding orthocerid-dominated communities of the Silurian (Gnoli 2003).

The details of this Early Devonian radiation are still poorly known and many major questions remain unresolved seventy years after the influential work of Schindewolf. Ruzhencev (1960, 1962) and Erben (1964 a, b) illustrated the gradual transition in the early growth stages from Bactritida to the Ammonoidea, but the lack of a morphological distinction between these taxa has hampered the understanding of their evolutionary relationships. Some authors regard the Bactritida simply as straight ammonoids (House 1993; Sepkoski 2002) while others assert that latter should be recognized as a more distinct group (Korn and Klug 2002). Engeser (1996) stressed the para- or polyphyletic nature of the Bactritida. Therefore, the phylogenetic relationship of Devonian Bactritida to Silurian Orthocerida is still unclear (e.g., Ristedt 1981; Dzik 1984).

To address these ambiguities, new morphological data on the characters of these groups are desired. Such additional characters include attachment structures of the soft-tissues preserved on internal moulds of the body chamber. These structures also provide valuable information on the paleobiology of the groups.

Institutional abbreviations.—MB, Museum für Naturkunde, Berlin; BGR/S, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin-Spandau; NHW, Naturhistorisches Museum Wiesbaden; GZG, Institut und Museum für Geologie und Paläontologie, Universität Göttingen; PIMUZ, Paläontologische Institut und Museum der Universität Zürich.

Previous studies on soft-tissue attachment structures in cephalopods

Soft-tissue attachment structures were described in the 19th century for several groups of nautiloids (for a more detailed re-

view see Mutvei 1957; Kröger and Mutvei in press) and with the early 1960s for ammonoids (for reviews see Mutvei and Doguzhaeva 1997; Richter and Fischer 2002). Information on bactritoid soft-tissue attachment structures was given by Erben (1964b) for the Late Devonian *Bactrites ausaviensis* Steininger, 1853 these resemble some unpaired structures recognised in ammonoids (Richter and Fischer 2002: fig. 3E). Later, Clausen (1968) described more or less paired structures in Bactritida of Late Devonian age as muscle scars.

The micro-ornamentation known as "Runzelschicht" or wrinkle-layer is a shell-layer that is sometimes preserved on internal moulds of the body chamber in nautiloids, Bactritida, and ammonoids. In agreement with Kulicki (2001), we here consider the Runzelschicht as a soft-tissue attachment structure that roughened the inner surface, and therefore enhanced the control of soft body placement within the body chamber. For ammonoids and bactritids, this structure is fairly well known (see e.g., Walliser 1970; Mapes 1979; Kulicki et al. 2001). In nautiloids, however, it is rarely preserved (see Mapes 1979 for a review). Recent *Nautilus* represents the sole living example of an ectocochleate cephalopod displaying these structures. The soft body of *Nautilus* is attached to the inside of the conch by two strong cephalic retractor muscles and two sheet-like tendons ("aponeuroses"; Waagen 1870). The muscles form two characteristic imprints on the inner shell surface and a continuous band around the posterior end of the shell of the body chamber (see e.g., Wells 1988; Mutvei et al. 1993; Isaji et al. 2002). The entire structure, called the "annulus" (Keferstein 1862–1866) or "annular elevation", respectively (Mutvei 1957), represents an extra layer of shell that is deposited in this area. The septal aponeurosis attaches the body epithelium to the shell in front of the last septum. A small, unpaired middorsal scar ("septal furrow", Mutvei 1957 = "dorsal furrow", Chirat and Boletzky 2003) in front of the last septum and a narrow band at the posterior margin of the large scars of the cephalic retractors attaches the palliovisceral ligament. Chirat and Boletzky (2003) showed that a longitudinal structure, which commonly occurs on the ventral part of the shell, is not related to any attachment structure but represents simply a "fabricational noise".

Material

The material investigated in this study originates from two different outcrop areas of Devonian strata, and is located in repositories of several institutions in Germany and Switzerland. One part of the material was extracted from the Wissenbacher Schiefer, these comprising various Early to Middle Devonian black-shales of the German Rhenoherzynicum spanning the Emsian *Nowakia richteri* conodont Zone to the Givetian *Polygnathus varcus* conodont Zone. The "Wissenbacher Schiefer facies" that is famous for their pyritised mollusc faunas (Stürmer 1970) is exposed in various areas of the Rhenish Massif and the Harz Mountains. The shales were deposited in a dysaerobic environment in the Rhenoherzynian

Basin during a global transgressive episode (Schubert 1996) that is known as the transgressive Choteč Event-level (Chlupač and Kukal 1986; also *Pinacites jugleri* Event *sensu* Walliser 1985). Thus, black-shale sedimentation at the basal Eifelian is reported from e.g., Czech Moravia (Chlupač 1974), Morocco (Alberti 1981; Becker and House 1994; Klug 2002), and China (Vogel et al. 1989).

Extensive mining for shingle production in the 19th century led to a detailed description of the fauna of the Wissenbacher Schiefer. Important descriptions of the macrofauna are given by Sandberger and Sandberger (1850–1856) and by Maurer (1876, 1878, 1896). After mining activity had ceased, the possibilities of collecting macrofauna from the shales rapidly decreased. A modern taxonomic description of the fauna is still lacking. The material is in repositories of the Museum für Naturkunde, Berlin, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin-Spandau, at the Naturhistorische Museum Wiesbaden, and of the Institut und Museum für Geologie und Paläontologie, Universität Göttingen.

The second part of the material was collected in the northern Tafilalt (Morocco). All limonitic specimens were collected from scree. Based on the outcrop topography, however, it is very likely, that all collected specimens were washed out of the claystones and marls of Zlíchovian age (Early Emsian). During this time interval, two claystone to marlstone units were deposited in the Tafilalt region ("Calcaires inférieurs" of the Seheb El Rhassel Group; Hollard 1967, 1974, 1981). These two are separated by 0.5 metres of bluish dacryoconarid packstones ("*Jovellania* limestone"). Each of the more clayey intervals yielded a disctinctive faunule; only the younger of the two contains early ammonoids. Both assemblages contain Bactritida as well as orthoconic nautiloids. Details of the stratigraphy of this interval were published by Massa (1965), Hollard (1967, 1974, 1981), and Alberti (1980, 1981). More recently, Becker and House (1994, 2002), Bultynck and Walliser (2000) as well as Klug (2001, 2002) contributed new facts on both bio- and lithostratigraphy of the Zlíchovian strata in the Tafilalt. The material is in the repository of the Paläontologisches Institut und Museum der Universität Zürich.

Fine-grained limonitic material in the steinkern (primarily pyrite) accounts for the preserves subtle details of the soft-tissue attachment structures in orthoconic cephalopods as well as in other fossils (e.g., various bivalves). Some of the specimens show a variety of colours in the posterior part of the body chamber. One specimen displays a slightly irregular black band about two millimetres anterior of the last septum that fades out posteriorly. As no chemical analyses have been made of this band, it is uncertain whether it is composed of carbon, goethite, fine-grained pyrite or some other mineral, but gold-coloured spots associated with the band are probably composed of pyrite. The majority of the fossil mass, however, consists of limonite/goethite, as indicated by the distinctive mixture of greyish, yellowish, and dark red colours. None of the specimens preserves traces of the original aragonitic shell.

Description of soft-tissue attachment structures

***Acanthomichelinoceras commutatum* (Giebel, 1852)**.— Specimens MB.C.5366.1–5 from the Scheibelsbach pit, Rupbachtal, specimens NHW 56.9.05/402 and NHW 56.9.05/404 from Wissenbach in the Rhenish Massif.

Specimen NHW 56.9.05/402 (Figs. 1E, 2A) preserves two chambers of the phragmocone, both with a chamber length of 18.0 mm and a diameter of 13.0 mm. The dorsal furrow is 0.4 mm wide and ca. 11.0 mm long, fading out adorally. The mural part extends over approximately 1.8 mm with numerous small irregular pits. A lirate band 8 mm long is visible in the adoral part of the mural area (annular elevation). The dorsal furrow starts 1.4 mm adoral of the mural area in the lirate band.

Specimen NHW 56.9.05/404 (Figs. 1D, 2B) is a body chamber fragment measuring 25 mm in length and 9 mm in width. Its dorsal furrow is 6.2 mm long and 0.5 mm wide, showing distinct lateral grooves. Its adapical part has a slightly irregular surface and does not span the entire mural part, which is 1.4 mm long with numerous small irregular pits. A band with several longitudinal lirae lies adoral of the suture line: it is 3.0 mm long (annular elevation) and parallel to the suture.

Specimen MB.C.5366.1 (Fig. 2D) is preserved with six chambers of pyritised phragmocone that are 24.0 mm long and 3.4 to 4.3 mm wide. The dorsal furrow can be seen on all chambers, beginning at the adapical rim of the mural part of each septum, fading out toward the following septum. The dorsal furrow is about 0.1 mm wide with two distinct lateral grooves at 4.3 mm shell diameter. The mural part of the septum is about 0.35 mm long and the adoral rim of each mural part forms shallow acute lobes towards the dorsal furrow. The middle part of each dorsal furrow is covered by ovate patches, of which the last is 0.75 mm wide. Adoral of the mural lobe, it is 0.85 mm long and forms a positive relief on the mould (i.e. negative relief in the shell) these ovate patches span the entire length of the dorsal furrow onto the successive suture line.

The specimen MB.C.5366.4 (Fig. 2C) preserves only one chamber of the phragmocone that is 19.0 mm long and 13.0 mm wide; the dorsal furrow is 10.0 mm long and 0.7–0.9 mm wide with distinct and irregular, lateral grooves. It thins out at the adoral part of the chamber. The mural part of the septum is ca. 2.6 mm long. The adoral rim forms an acute and shallow lobe towards the dorsal furrow that is irregular and rough at its adapical end. It does not span the entire mural band in length. An 8.0 mm long distinct band with thin irregular lirae can be seen at the adapical part of the chamber (annular elevation) with its adoral rim running parallel to the suture.

***Cycloceras* sp.**—Specimens PIMUZ 7260 to 7268 from Ouidane Chebbi (northern Tafilalt, Morocco); except for the fragments PIMUZ 7261, 7262 and 7268 (six specimens) which have been collected from late Zlíchovian sediments, all specimens were collected from the sediments of early Zlíchovian age.

Specimens PIMUZ 7261 and 7262 display elongate tearshaped ventral cavities (Figs. 4D–F, 5C). In the figured specimen (PIMUZ 7261), these cavities are about 1.5 mm long and 1.1 mm long. They are composed of an approximately 1 mm wide subcircular structure with concentric microribs. More or less in its centre, an elongate rib with well-defined parallel lateral margins and rounded ends emerges.

Specimen PIMUZ 7262 displays a dorsal furrow, sometimes accompanied by parallel striae. The dorsal furrow and cavities occur only between two septa and on the most apical part of the body chamber. Within the body chamber, the furrow is very faint and shallow, beginning with a tiny elongate depression in the terminal septum. Six specimens are preserved with remains of moulds of the wrinkle layer; the wrinkles are arranged in rows, more or less parallel to the sutures, consisting of ripples made of small bulges. In specimen PIMUZ 7263, 9 such ripples cover 400 μm in width. Specimen PIMUZ 7260 has a body chamber length of 12.6 mm; its last septum is 2.7 mm wide and 2.8 mm high; there is a well-defined straight furrow 2.0 mm in front of the last suture.

***Bactrites gracile* Blumenbach, 1803**.—Specimen NHW 62.11/W-23/64 from Wissenbach, Wissenbacher Schiefer (Fig. 1A). The only specimen wit soft-tissue attachment structures displays eight chambers and the body chamber; at the last chamber, it is 7.0 mm wide and the body chamber is 42.0 mm long. The body chamber is preserved only fragmentarily. The last suture is nearly straight and has a small and flat dorsal saddle and a distinct 0.3 mm wide dorsal node. The annular elevation displays two separate bands around the base of the living chamber; the posterior band begins at the suture; it is 0.5 mm high at the venter and 1.6 mm at the dorsum. It has a smooth surface with a distinct adoral groove, forming a dorsal saddle. The second band lies directly in front of this groove; its distance from the suture measures 1.2 mm at the venter and 5.3 mm at the dorsum with a faint longitudinal lirate surface. Its adoral limit was formed by a weak and irregularly undulated groove.

***Bactrites* sp. A**.—Specimen NHW 402 from Wissenbach, Wissenbacher Schiefer (Fig. 1B), with one chamber and a fragment of the body chamber; the specimen is a pyritised internal mould. Its conch cross section is nearly circular and 6 mm wide at the last chamber. The almost cylindrical body chamber is faintly undulated, resulting in the formation of ventral and dorsal saddles as well as lateral lobes in the ribs. The suture consists of a flat ventral lobe and a small dorsal saddle; the septa are shallow spherical. The last chamber is 1.6 mm high.

The mural area is 0.3 mm long and the posterior band originates at the suture line. Its ventral and lateral height amounts to 0.3 mm and its adoral rim forms a distinct dorsal lobe being maximally 1.6 mm high (Fig. 1B$_1$, B$_2$, B$_4$). The
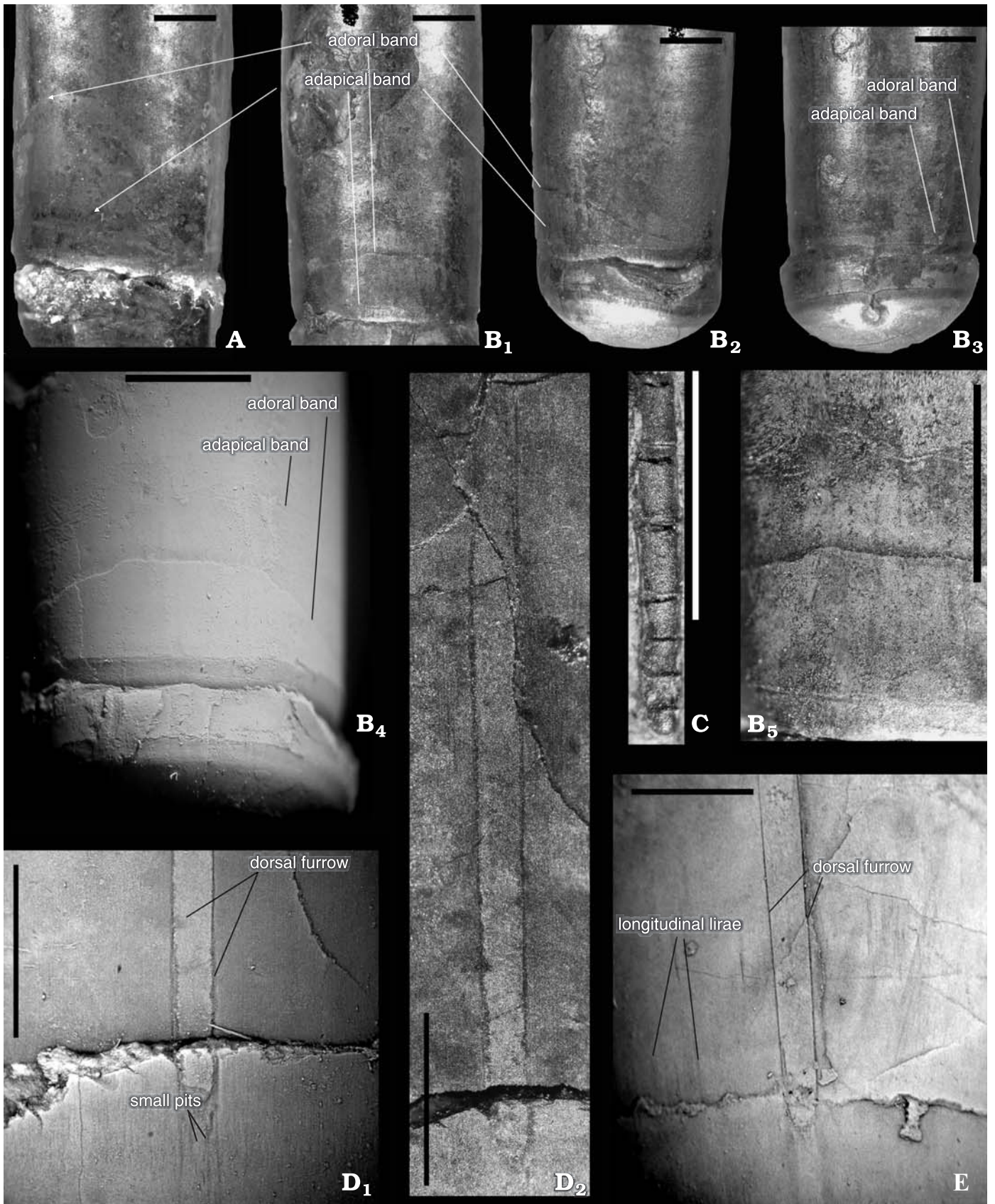
Fig. 1. Soft-tissue attachment structures in cephalopods from the Wissenbach Schiefer (early Eifelian). **A**. *Bactrites gracile* (Blumenbach, 1803), NHW 62.11/W-23/64, dorsal view, note the two different grayish bands (arrows) forming a lobe. **B**. *Bactrites* sp. A, NHW 402, dorsal view (B_1), note two successive, slightly undulated grooves. Same specimen, lateral view (B_2). Same specimen, ventral view (B_3), note the small lobe in suture line. Same specimen, →
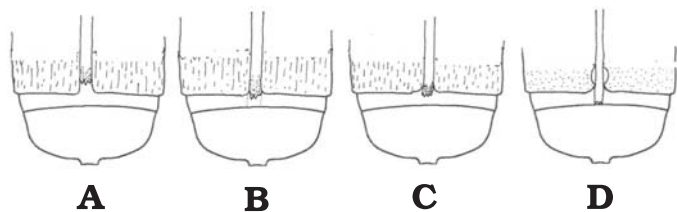
Fig. 2. Schematic outlines of the variability of the dorsal furrow in *Acantho-michelinoceras commutatum* (Giebel, 1852), showing the base of a chamber mould, with annular elevation dotted. Note the differences of the starting point of the dorsal furrow, sometimes within the mural area, sometimes within the annular elevation. **A**. NHW 56.9.05/402. **B**. NHW 56.9.05/404. **C**. MB.C.5366.4. **D**. MB.C.5366.1. Not to scale.

surface is slightly roughened and the anterior band has a faintly wrinkled surface, limited by a fine adapical groove and two fine adoral grooves. The latter undulate irregularly, with a distinctly paired dorsal lobe (Fig. 1B$_4$, B$_5$). The distance from the last formed suture measures 2.5 mm at venter and flanks, and approximately 6.0 mm at the dorsum. Additionally, the single specimen shows two faint grooves at the dorsum fading out after 6 mm in growth direction.

***Bactrites* sp. B**.—Specimen PIMUZ 7271, from Ouidane Chebbi (northern Tafilalt, Morocco), Early Zlíchovian, Early Emsian (Fig. 4C). The specimen is 5 mm long, 1.9–2.0 mm high, and 1.8–2.0 mm wide. Its middle part is slightly wider and higher than the anterior and posterior ends.

The incomplete specimen displays ten septa; some of the corresponding sutures display very shallow and broadly rounded ventral lobes. The broadly rounded dorsal lobes are of strongly varying depth, spanning more than half of the specimens perimeter. Septal spacing varies extremely; distances between each suture at the venter amount to 0.6, 0.5, 0.45, 0.4, 0.35, 0.2, 0.6, 0.7 and 0.7 mm, beginning from the last formed septum. The inclination of the septa is similarly variable. Some are perpendicular to the conch walls but the narrowly spaced septa are clearly oblique. Towards the dorsum, they are apically inclined.

Fine regular ribs or lirae (30 on 5 mm), with shallow and slightly pointed ventral projections and equally shallow dorsal sinuses can be seen. Two faint longitudinal bands are preserved on the venter.

***Bactrites* sp. C**.—Specimens PIMUZ 7272 to 7283 and 7285 were collected at Ouidane Chebbi (northern Tafilalt, Morocco) and the two specimens PIMUZ 7284 (one number) were found at Achguig; PIMUZ 7272 to 7280, 7282, 7283, as well as 7285 derive from the early Zlíchovian, PIMUZ 7281 and 7284 were collected from the late Zlíchovian, Early Emsian (Figs. 4A, B, 5A, D).

Table 1. Dimensions (in mm) and ratios of the body chambers of five specimens of *Bactrites* sp. C from the Emsian of Morocco.

specimen	length l	width w	height h	w/l	h/l	w/h
PIMUZ 7283	17.7	? 4.5	?6.2	?0.25	?0.35	?0.73
PIMUZ 7281	13.7	4.8	4.9	0.35	0.36	0.98
PIMUZ 7282a	13	4.2	4.7	0.32	0.36	0.89
PIMUZ 7278	11.9	4.8	5.1	0.40	0.43	0.94
PIMUZ 7282b	13	?3.6	?5.4	?0.28	?0.42	?0.67

All specimens are less than 19 mm long with an apical angle of approximately 5°. The mean value of the width (w, at widest part of the body chamber) to length (l, between last septum and youngest part of body chamber) ratios amounts to approximately 0.32, that of the height to length ratio is 0.38 and that of the width to height (h, at highest part of body chamber) ratio is over 0.9 (Table 1). None of the specimens preserves its aperture. The very faint ornament consists of dorsally projecting ribs or lirae that are oblique on the flanks.

The suture has a very shallow, pointed ventral lobe and often displays a false, deep ventral lobe if the limonitic infill of the interspace between siphuncle and outer shell wall is broken off. Some late, more or less mature septa display a very shallow dorsal lobe. The septum is simply dome-shaped, slightly tilted dorsally with a very faint constriction at the mural band. The siphuncle is very close to the venter, leaving very little space between the connecting ring and the inside of the ventral shell wall.

Four specimens preserve the body chambers with faint remains of soft-tissue attachment structures (e.g., PIMUZ 7272, 7280, 7282, 7283). These consist of two roughly parallel lines at the posterior end of the body chamber. In specimen PIMUZ 7272 (Figs. 3D, 4A), the posterior line is more distinct and very close (0.15 mm) to the last suture, sweeping dorsally towards the aperture and forming three almost symmetrical saddles. The two lateral saddles are ca. 1.0 mm high (measured from last suture) and the middle saddle is 1.2 mm high; the anterior line is much fainter, it is marked by the anterior end of the tracking bands (traces of the translocation of soft-tissue attachment sites). Additionally, SEM pictures of specimen PIMUZ 7272 revealed the rough surface typical for a 0.4 mm wide muscle attachment scar between the anterior bands. The tracking bands terminate approximately 0.3–0.5 mm adapically of the last suture on the septum. They extend longitudinally and end at the anterior line; we counted approximately 65 tracking bands within the three lobes. There is a faint longitudinal line at the venter, crossing the

whitened, dorsal view (B$_4$). Same specimen, dorsal view (B$_5$), note two successive, slightly undulated grooves. **C**. Apical part of *Acanthomichelinoceras commutatum* (Giebel, 1852), GZG 1250, note the very small, short first chamber, and lack of any constriction between first chamber and successive chambers. **D**. *Acanthomichelinoceras commutatum* (Giebel, 1852), NHW 56.9.05/404. Detail of the mural area (at base of figure) (D$_1$) shows several small pits, dorsal furrow starts adoral of mural area. Same specimen, showing the entire length of a segment of the dorsal furrow (D$_2$), note minute longitudinal lirae on both side of the dorsal furrow, marking the area of the annular elevation **E**. *Acanthomichelinoceras commutatum* (Giebel, 1852), NHW 56.9.05/402, whitened, dorsal furrow, adoral limit of mural area at base of figure, note numerous longitudinal lirae. Scale bars 2.5 mm.

entire body chamber; specimen PIMUZ 7278 displays an irregular black band approximately 2.5 mm adoral of the last formed septum, fading out posteriorly.

Summary of soft-tissue attachment structures

Orthocerida.—The soft-tissue attachment structures of the described Orthocerida comprise three features. (1) Most Orthocerida of the Wissenbacher Schiefer and some of the Moroccan Emsian show a flat furrow with two distinct lateral ridges in the shell wall and mural part of the septum at the dorsum. This dorsal furrow fades out adorally in the body chamber. The length of the dorsal furrow is usually shorter than the distance between two successive chambers. Consequently, the dorsal furrow is not a continuous line but consists of several segments (e.g., Teichert 1964). The surface of that furrow is rough, especially at its origin in the mural surface. The individual differences between the shape and arrangement of this structure especially in the mural part are large in *Acanthomichelinoceras commutatum* (Fig. 2). (2) A simple, rough, and sometimes longitudinally striated band occurs at the base of the body chamber of some Orthocerida from the Wissenbacher Schiefer. This feature is here interpreted as a diagenetic artefact; the inner shell surface was probably irregular ($1D_1$, E). This band runs parallel to the suture line. (3) Several specimens of *Cycloceras* sp. from the Early Emsian of the Tafilalt display clear remains of the wrinkle layer.

Bactritida.—At the body chamber base of the Bactritida from the Wissenbacher Schiefer, two distinct bands are visible at the inner shell wall. The bands show a rough surface and are adorally delineated by faint ridges. The posterior ridge (next to the suture) is straight with a simple dorsal lobe (Fig. 1B). The anterior ridge forms two symmetric lobes at the dorsum and is irregularly undulated (Fig. $1B_4$, B_5). In contrast to the posterior band, the surface of the outer band is slightly wrinkled and its appearance is generally weaker. Additionally, the Bactritida in our material show a faint dorsal furrow and sometimes a small dorsal node just adoral of the suture line at the dorsum. It is noteworthy that one of the characteristics of Carboniferous Bactritida is a wrinkle layer on the inner shell wall of the body chamber (Mapes 1979). In
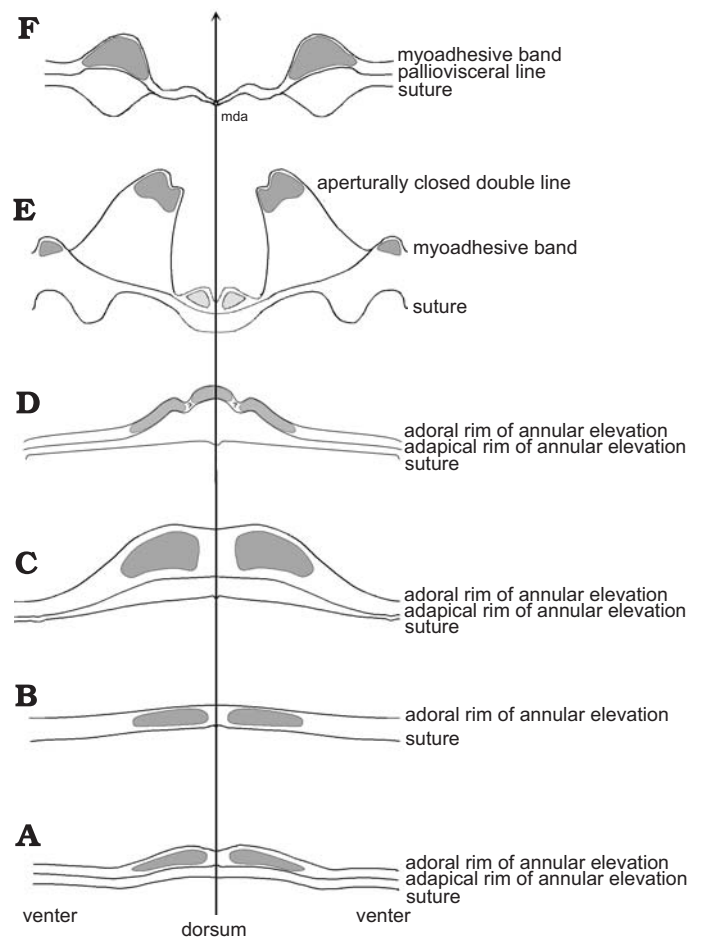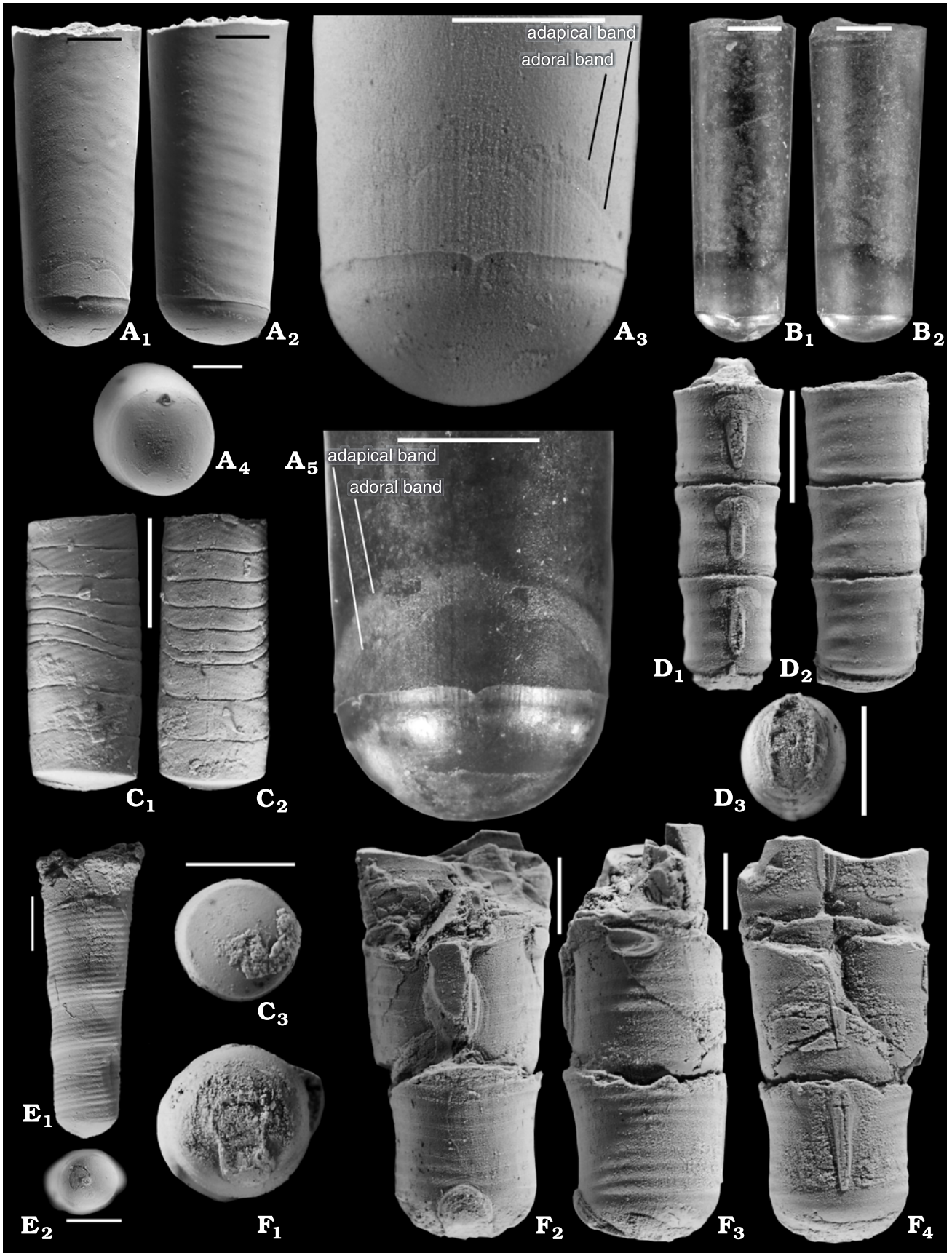

Fig. 3. Schematic reconstruction of the outlines of the annular elevation in some cephalopods. **A**. *Orthoceras scabridum* Angelin, 1880, middle Ordovician, after Mutvei (1957: text-fig. 15). **B**. *Acanthomichelinoceras commutatum* (Giebel, 1853), middle Devonian. **C**. *Bactrites gracile* (Blumenbach, 1803), middle Devonian. **D**. *Bactrites* sp. C, Emsian. **E**. Goniatite, late Devonian, after Richter and Fischer (2002: text-figs. 3d, 6). **F**. *Nautilus*, Recent, after Mutvei and Doguzhaeva (1996). Note the dorsal position of muscle scars in straight, and the ventrolateral position in coiled cephalopods. Arrow in direction of growth, gray areas, hypothetical muscle attachment sites, stippled lines hypothetical reconstruction of attachment sites, For discussion see text.

Devonian Bactritida, the wrinkled structures are either absent or not as distinctive as in Carboniferous forms (see Clausen 1968; Ristedt 1971). Since all other structures of the inner shell wall are exceptionally well preserved in the py-

Fig. 4. *Bactrites* and *Cycloceras* of early Emsian age (Early Devonian) from Ouidane Chebbi (Tafilalt, Morocco). The specimens except in A_5, B_1, and B_2 were coated with ammonium chloride. **A**. *Bactrites* sp. C; PIMUZ 7272. dorsal view of the entire specimen (A_1), note the outline of the annular elevation, the spherical septum, the imprint of the lirae, and the tiny dorsal lobe, maybe a trace of the middorsal area. Same specimen, lateral view (A_2). Same specimen detail of A_2, note the tracking bands, the three-lobed annular elevation, and the adapical and adoral rims of the annular elevation (A_3). Same specimen, septal view (last formed septum) (A_4). Same specimen as in A_4, for this picture, the specimen was not coated with ammonium chloride in order to show the changes in colour and surface structure in the various parts of the annular elevation, the body chamber, and the septum (A_5). **B**. *Bactrites* sp. C; PIMUZ 7278., dorsal view; note the black line; the origin of this colour pattern is unclear (B_1). Same specimen lateral view (B_2). **C**. *Bactrites* sp. B; PIMUZ 7271., lateral view; note the variation of the curvature and the spacing of the sutures (C_1). Same specimen dorsal view; note the increase in width towards the apex and the conchal furrow (C_2). Same specimen septal view (C_3). **D**. *Cycloceras* sp.; PIMUZ 7261., dorsal view; note the conchal furrow (D_1). Same specimen lateral view (D_2). Same specimen septal view (D_3). **E**. *Cycloceras* sp.; PIMUZ 7260., lateral view; note the constrictions and (?) lirae, as well as the fine straight line 1 mm adoral of the last septum; it is unclear whether this represents the adoral rim of the annular elevation (E_1). Same specimen, septal view (E_2) **F**. *Cycloceras* sp.; →

PIMUZ 7262. septal view (F_1) same specimen ventral view (F_2). Same specimen, lateral view (F_3). Same specimen, dorsal view; note the tear-shaped outline of the conchal furrow (F_4). Scale bars 2.5 mm.
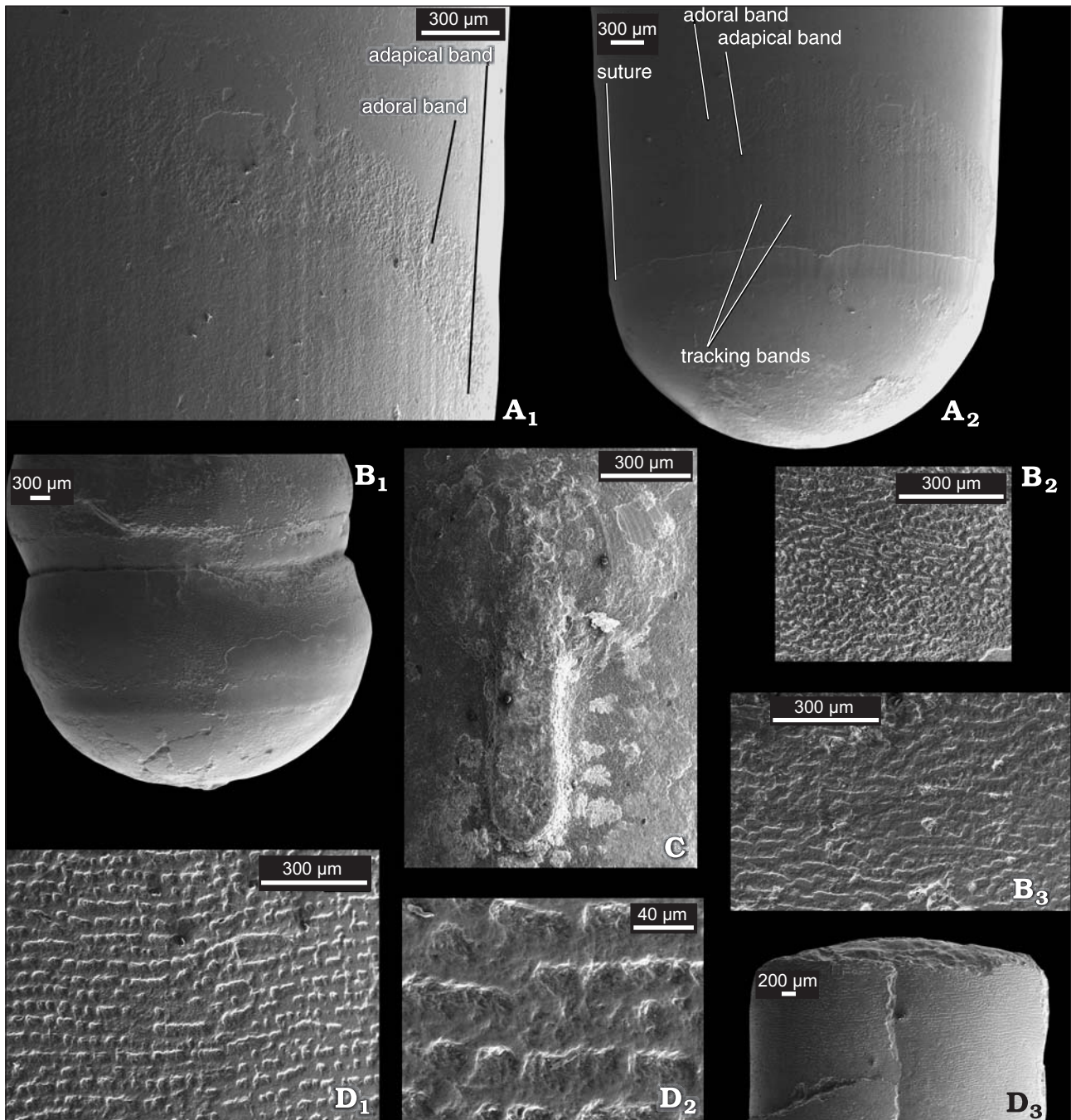
Fig. 5. SEM micrographs of *Bactrites*, and *Cycloceras* of early Emsian age (Early Devonian) from Ouidane Chebbi (Tafilalt, Morocco). The specimens coated with carbon. **A**. *Bactrites* sp. C; PIMUZ 7272; A_1, detail of the annular elevation; note the rugged surface of the adoral part as well as the right and the median lobe of the annular elevation; A_2, dorsal view of the same, showing last formed septum and posterior portion of body chamber; note the tracking bands, the mural band, and the annular elevation. **B**. *Cycloceras* sp.; PIMUZ 7263; B_1, lateral view of a part of the phragmocone; B_2, B_3, same specimen, details of the wrinkle layer; note that the wrinkles are asymmetric in cross section with the steeper slope pointing adapically. **C**. *Cycloceras* sp.; PIMUZ 7261; detail of the conchal furrow. **D**. ?*Bactrites* sp.; PIMUZ 7269; D_1, detail of the wrinkle layer; D_2, same specimen detail of the wrinkle layer in a smaller scale, note the asymmetry; D_3, same specimen, overview of the adoral part of the body chamber.

ritic internal moulds of the Wissenbacher Schiefer and in the limonitic internal moulds from the Zlíchovian of the eastern Anti-Atlas, the lack of a wrinkle layer in these specimens deserves further attention for future investigations.

The muscle attachment structures of *Bactrites* from the Emsian strata of Morocco are similar to those on the Wissenbacher Schiefer specimens that display two circular bands at the base of the body chamber. As observed in the Wissenbacher Schiefer specimens, the anterior band is faint and consists of two lines. A more distinct posterior line and a faint anterior line are preserved. The latter of which is defined by the anterior end of the tracking bands and by a

0.4 mm wide band with a rough surface. The tracking bands were probably formed in the course of the translocation of the cephalic retractor muscles. Nevertheless, *Bactrites* sp. C differs at least in one respect from other Bactritida; it shows three instead of two dorsal lobes. The only specimen of *Bactrites* sp. B displays a furrow which may be interpreted as the conchal furrow. It extends from the septum into the chambers but only through the posterior part of the body chamber.

Interpretation of the soft-tissue attachment structures

Distinct bands that are limited by faint adoral and adapical grooves at the base of the body chamber are interpreted here as imprints of the annular elevation. In Recent *Nautilus* (for review see Mutvei 1957; Mutvei and Doguzhaeva 1997), the annular elevation is a composite structure of multiple soft-tissue attachment sites. In *Nautilus*, two myoadhesive attachment zones are present, an adoral and an adapical site; these two zones provide a moderately strong attachment of the posterior part of the mantle to the shell (compare Isaji et al. 2002).

Additionally, the palliovisceral ligament attaches the body wall to the shell at a point at the dorsum (middorsal area) and encircles the shell wall in form of a narrow zone. The dorsal attachment site of the palliovisceral ligament is situated at the base of a small dorsal lobe of the suture. Finally two major retractor muscles, the cephalic retractors, form crescent-shaped attachment sites on the flanks of the shell interior.

The principal pattern of the annular elevation with its three subparallel, narrow grooves and a pair of distinct retractor muscle scars are found in Ordovician Orthocerida (Fig. 3A) and in Devonian Ammonoidea (Fig. 3E; see also Richter 2002 as well as Richter and Fischer 2002). The annular elevation in the studied Bactritida shows the same principle pattern including the appearance of a dorsal tubercle (Fig. 3C, D).

The annular elevation in the Orthocerida from the Wissenbacher Schiefer differs from other ectocochleate cephalopods in that it is generally very weakly developed. In contrast, the dorsal furrow is very distinctive. The shape of the dorsal furrow and its large variability match exactly the shape of the dorsal attachment site of the palliovisceral ligament in *Nautilus* as shown in Mutvei and Doguzhaeva (1997: text-fig. 11; see also Chirat and Boletzky 2003). We conclude therefore that the dorsal furrow in Orthocerida represents the most important part of the attachment site of the palliovisceral ligament, which is the primary attachment site of the soft body in *Nautilus* (Mutvei and Doguzhaeva 1997). Therefore the main attachment zone of the orthocerid soft body might have been the palliovisceral ligament, muscles and the myoadhesive band having played a subordinate role.

Fig. 4 shows regular patches of retractor muscle attachment sites in *Bactrites* from the Zlíchovian of Morocco. These patches are not visible in the orthocerid material used in our study. Reconstructed positions and shapes of the patches are based on comparisons with an presumably equivalent features in Recent *Nautilus*. There, the main retractor muscles are positioned between the anterior lobe of the myoadhesive band and the palliovisceral ligament. Evidence for the position and shape of the main attachment sites for the retractor muscles refers also to known attachment sites in Ordovician Orthocerida (Mutvei 1957). One specimen of *Bactrites*, however, shows a rough surface on the venter between the adoral and the adapical site (Figs. 4A, 5A). The structure of the surface strongly resembles muscle attachment scars in other molluscs, and thus, this is interpreted as the site of attachment of the cephalic retractor muscles. Consequently, the adoral and adapical sites may be homologous with the attachment scars of the palliovisceral ligament and the mantle myoadhesive band. The retractor muscles may have been paired or alternatively threefold at the dorsum (as it is the case in *Bactrites*; Figs. 3–5). In various Bactritida the wrinkle layer is distinctively preserved as a pattern which may reflect the paired patches of the dorsal retractor muscle attachment sites (Clausen 1968: fig. 27h, pl. 5: 15; Mapes 1979: pl. 17: 9; pl. 19: 4; pl. 26: 2, 7).

Comparisons

Two features are striking when comparing the soft-tissue attachment structures in Paleozoic ammonoids, *Nautilus*, *Bactrites*, *Orthoceras*, and *Acanthomichelinoceras*.

(1) In many coiled forms (e.g., Nautilida), the muscle attachment scars are positioned ventrolaterally whereas in straight cephalopods, they are in a dorsal position. This difference may be explained in terms of function of the retractor muscles in coiled and straight nautiloids, respectively. In coiled cephalopods the optimal position is ventrolateral, because this ensures a posterodorsally directed retraction of the soft body and allows for a maximal length of the retractor muscle strands in the body chamber. Additionally, fully dorsally positioned muscles would be pressed against the dorsum when contracted. This would increase friction and limit the space for the widening of the muscle strands. In straight cephalopods, the retractor muscles are only functional when they retract the head/hyponome in an upward direction. When considering horizontal, vertical and intermediate poises in straight cones the position of the attachment sites must have been at the dorsum.

(2) The presence of large muscle scars indicates strong retractor muscles in several ammonoids and *Nautilus,* slightly weaker retractor muscles in *Bactrites*, and much weaker cephalic retractor muscles in Devonian Orthocerida. This may reflect different modes of life of these taxa. Strong retractor muscles are required for increased rates of both respiration and locomotion (see Packard et al. 1980; Wells 1988; Shad-

wick 1994). In Recent cephalopods, both needs are functionally coupled with characteristic modes of life. It appears likely that Orthocerida (with their smaller retractor muscles) had a much more passive mode of life compared to Recent *Nautilus*. It appears questionable whether Orthocerida, and especially *Acanthomichelinoceras*, were capable of a nektonic mode of life by means of jet propulsion produced by the retractor muscles with respect to the comparatively small area of their attachment areas. Thus, based on soft-tissue attachment structures and shell morphology, many Orthocerida may be interpreted as rather passive planktonic drifters (see e.g., Westermann and Tsujita1999).

Bactrites shows an interesting intermediate pattern between early Ammonoidea and Orthocerida. Their annular elevation displays a clear dorsoventral asymmetry and the distinct dorsal lobe indicates the presence of moderately strong retractor muscles. In contrast to ammonoids, these bactritidan retractor muscles were dorsally attached. These fundamental differences in the morphology of the annular elevation indicate marked differences in soft-tissue organisation. Thus, Devonian Bactritida probably had a more active mode of life and foraging behaviour compared to Devonian Orthocerida. More importantly, the aperture of most Devonian Bactritida was oblique with the dorsal edge extending further than the ventral edge. Because of the ventral position of the siphuncle, a slightly inclined living position of many Bactritida appears likely (Klug and Korn 2004). Bearing in mind the probably tilted life orientation of bactritidan conchs (and therefore oblique apertural orientation) the localisation of dorsal soft-tissue attachment is not surprising.

Systematic palaeontology

Order Orthocerida Kuhn, 1940

Subfamily Michelinoceratinae Flower, 1945

Genus *Acanthomichelinoceras* nov.

Type species: *Acanthomichelinoceras commutatum* (Giebel, 1852).

Derivation of the name: From *acanthis* (Lat.) = thorny, spiny, referring to its acute apex.

Diagnosis.—Medium sized, slightly compressed Michelinoceratinae with central siphuncle, long chambers and well-developed dorsal furrow ("Normallinie"). Very small, smooth, cap-shaped apex (dimension ca. 0.3 mm); cicatrix and primary constriction are absent.

Stratigraphic range.—Late Eifelian–early Givetian.

Remarks.—The mature growth stages of the new genus display the same morphology as those of *Michelinoceras* (Barrande 1866). However, the new genus differs in the wider spacing of the septa, and the size and shape of the apex relative to other michelinoceratids. The apex of *Acanthomichelinoceras* measures only half of the diameter of *Michelinoceras*: it is blunt-ended, cup-shaped and significantly smaller

in diameter (compare Ristedt 1968; Kiselev 1971; Serpagli and Gnoli 1977).

Attributed species.—Type species only.

Acanthomichelinoceras commutatum (Giebel, 1852)
Figs. 1C–E, 2A–D, 3B.

non *Orthoceras gracile* sp. nov.; Blumenbach 1803: pl. 2: 6.
Orthoceras gracile Blumenbach; Hoeninghaus 1830: 96.
Orthoceras gracile Blumenbach; Beyrich 1837: 14.
Orthoceratites gracilis Blumenbach; Quenstedt 1840: 268.
Orthoceras regulare v. Schlotheim; d'Archiac and de Verneuil's 1842: 344, pl. 27: 2.
Orthoceras regulare v. Schlotheim; Sandberger and Sandberger 1850–56: 173, pl. 20: 2.
*Orthoceras commutatum sp. nov.; Giebel 1852: 233.
Orthoceras regulare v. Schlotheim; Roemer 1862: 2.
Orthoceratites gracilis Blumenbach; Quenstedt 1866: 407, pl. 34: 7.
Orthoceras gracilis Blumenbach; Roemer 1866: 225.
Orthoceras regulare v. Schlotheim; Maurer 1876: 830.
Orthoceras gracilis Blumenbach; Maurer 1876: 830.
Orthoceras commutatum Giebel; Kayser 1878: 69, pl. 10: 4, 8.
Orthoceras longicameratum sp. nov. (non *Orthoceras longicameratum* Hall, 1859) [nom. nud.]; Foord 1888: 80.
Orthoceras nassovensis sp. nov. [nom. nud.]; Foord 1888: 80.
Orthoceras commutatum Giebel; Maurer 1896: 671–673.
Orthoceras aff. *commutatum* Giebel; Paeckelmann 1913: 210–211.
Orthoceras commutatum Giebel; Dienst 1928: 108.

Syntypes: Sandberger and Sandberger (1850–1856) in repository of NHW, original collection Sandberger, Kayser (1878) in repository of BGR/S.

Type horizon and locality: Wissenbacher Schiefer, early Eifelian, Middle Devonian. Wissenbach near Dietz in the Rhenish Massif, Germany.

Material.—A total of five specimens, two of them, specimens BGR/S t833 from the borehole Silberborn near Blankenburg, Harz mountains, and specimen GZG 1250 from Steinberg near Goslar, with preserved apex. The specimens MB.C.5366.1–5 come from the Scheibelsbach pit, Rupbachtal. The specimens NHW 56.9.05/402 and NHW 56.9.05/404 from Wissenbach in the Rhenish Massif preserve fragments of the phragmocone with the dorsal furrow.

Diagnosis.—As for genus.

Description.—The nearly mature growth stages of this species were described in detail by d'Archiac and de Verneuil (1842), Sandberger and Sandberger (1850–1856), as well as Maurer (1896).

Apex.—Specimen GZG 1250 has a simple and blunt, cone- or cup-shaped apex (Fig. 1C); no ornamentation is preserved and a cicatrix is absent. The shell tip is not accentuated by different ornamentation or constriction from the rest of shell. The first chamber measures about 0.3 mm in diameter and is 0.25 mm long (Table 2) whereas, the second chamber measures 0.25 mm. Specimen BGR/S t833 preserves the ten most apical chambers. The entire phragmocone measures 5.3 mm and the body chamber is 8.7 mm long; the phragmocone grows is 0.25 to 0.5 mm wide. Its tip is very poorly preserved, showing the principle dimensions of apex with a diameter of 0.25 mm. An apical constriction is missing.

Table 2. Height (in mm) of the apicalmost chambers of *Acantho-michelinoceras commutatum* sp. nov. BGR/S t833.

# chamber	1	2	3	4	5	6	7	8	9	10
height	0.25	0.25	0.35	0.35	0.63	0.55	0.72	0.75	0.66	0.78

Remarks.—This species is one of the most common molluscs in the Wissenbacher Schiefer. The former name of the slate, "Orthoceras-Schiefer" (Schubert 1996), refers to its abundance. Description of the Orthocerida began in the early 19th century (see above). Because of the scarcity of characters in general and a lack of knowledge of the early growth stages, however, a genus designation was formerly impossible. A comparison with known michelinoceratids shows that the apex characters of these species are unique: The Llandoverian "*Orthoceratites*" described by Zhuravleva (1959: pl. 1: 6) resembles *A. commutatum* but it is about five times as large. The Wenlockian *Michelinoceras michelini* (Barrande, 1866) differs in its accentuated, cup-shaped apex as well as in its dimension by being about two times as large (e.g. Ristedt 1968: pl. 1: 1, 2; Histon 1999: pl. 2: 660). Notably the first chamber of *Acanthomichelinoceras commutatum* measures only 1/4 of the protoconch of *Bactrites gracilis* (Blumenbach 1803; see Schindewolf 1933: pl. 3: 2–6).

Stratigraphic range and geographic occurrences.—Late Emsian–early Givetian, Harz mountains, Rhenish Massif, Bergisches Land (Germany).

Order Bactritida Shimansky, 1951
Family Bactritidae Hyatt, 1884
Genus *Bactrites* Sandberger, 1843
Bactrites gracile Blumenbach, 1803
Figs. 1A, 3C.

Orthoceras gracile sp. nov.; Blumenbach 1803: pl. 2: 6.
Orthoceratites gracilis Blumenbach; d'Archiac and de Verneuil 1842: 344–345, pl. 27: 4.
Bactrites gracilis sp. nov. [jun. homonym]; Sandberger 1843: pl. 8: 2.
Orthoceratites crebriseptatus sp. nov. [nom. nud]; Roemer 1844: 81.
Orthoceratites schlotheimii sp. nov. [nom. nud.]; Quenstedt 1845–1849: 44, pl. 1: 11.
Bactrites gracilis Sandberger; Sandberger and Sandberger 1850–56: 130–131, pl. 11: 9, pl. 12: 2, pl. 17: 5.
Orthoceratites schlotheimi Quenstedt; Giebel 1852: 279.
Orthoceratites schlotheimi Quenstedt; Steininger 1853: 40, pl. 1: 12, 12a.
Orthoceratites schlotheimii Steininger [lapsus calami] 1857; Eichwald: 201.
Bactrites gracilis Sandberger; Chénu 1859: 77, fig. 308.
Bactrites gracilis Sandberger; Eichwald 1860: 1261.
Orthoceratites schlotheimii Quenstedt; Quenstedt 1866: 407, pl. 34: 6.
Bactrites schlotheimi (Quenstedt); Maurer 1876: 827.
Bactrites Schlotheimi (Quenstedt); Koch 1881: 241
Bactrites gracilis Sandberger; Chelius 1881: 12.
Orthoceras schlotheimi, Steininger; Foord 1888: 97–98.
Bactrites gracilis Sandberger; Clarke 1894: 40–43, figs. 2–5.
Orthoceras schlotheimi Steininger; Crick 1898: 87.
Bactrites schlotheimi (Quenstedt); Maurer1896: 638.
Bactrites schlotheimii (Quenstedt); Schindewolf 1933: 73, pl. 3: 2–6.

Orthoceratites schlotheimii Steininger; Teichert 1940: 590.
Michelinoceras cf. *schlotheimi* (Steininger); Teichert and Glenister 1952: 737.
Bactrites schlotheimi (Quenstedt); Shimansky 1962: pl. 3: 6.
Bactrites schlotheimi (Quenstedt); Gordon 1964: 101.
Bactrites gracilis Sandberger; Gordon 1964: 102.
Bactrites schlotheimi (Quenstedt); Clausen 1968: 58–59, pl. 7.
Bactrites schlotheimi (Quenstedt); Shimansky 1974: 811–812, pl. 3: 6.
Bactrites schlotheimi Sandberger [sic]; Brinckmann 1977: 121, fig. 8.

Syntypes: Sandberger and Sandberger (1850–1856) in repository of NHW.

Type horizon and locality: Wissenbacher Schiefer, early Eifelian, Middle Devonian. Wissenbach near Dietz in the Rhenish Massif, Germany.

Material.—Specimen NHW 62.11/W-23/64, the original of Sandberger and Sandberger (1850–1856: pl. 11: 9) from Wissenbach, syntype, preserves seven chambers of the phragmocone and body chamber, pyritised mould.

Diagnosis.—The shell is slightly compressed, with a very low apical angle, faint undulation of the shell with ventral sinus and dorsal lobe, and a faint lateral undulation that is oblique towards the growth axis. The chamber height is variable. The suture is slightly oblique towards the growth axis with a small ventral lobe and subspherical septa. Its initial chamber is ovate, smooth, with a circular cross section, ca. 0.9 mm wide and 1.2 mm long and highly variable in cross section from compressed to circular.

Description.—The mature characters were described in detail by Sandberger and Sandberger (1850–1856) and numerous later authors (see above); the apex characteristics were described by Schindewolf (1933).

Remarks.—The extraordinarily long list of synonymy is given here in order to document a long established misinterpretation of putative "two" mid-Devonian bactritoid taxa. This misinterpretation resulted from the designation of the *nomen nudum* "*Orthoceratites schlotheimii*", by Quenstedt (1845–1849). Sandberger and Sandberger (1850–1856) showed that it is a subjective junior synonym of *B. gracile*. Unfortunately, few copies of the latter were printed while Quenstedt's monograph had wider circulation. Because of the difference in publicity, the name "*O. schlotheimii*" became more popular for this typical "Wissenbach"-bactritoid, while the original was (and still is) not known to the great majority of palaeontologists. *B. gracile* and *B. subconicus* Sandberger, 1843 are the most common Bactritida in the Wissenbacher Schiefer.

Stratigraphic range and geographic occurrences.—Late Emsian–Givetian, Germany, England, USA.

Conclusions

In orthocone cephalopods from the Silurian and Devonian, two main patterns of soft-tissue attachment sites are recognized. (1) Among the Orthocerida examined in this study, the adoral (aoa) and adapical (apa) sites are arranged almost parallel to each other and to the last formed septum. Cephalic re-

tractors were probably attached between these two sites. According to the dimensions of the surface area between these two sites, the musculature was evenly distributed and small compared to other ectocochleate cephalopods. This indicates a planktonic mode of life with a usually vertical position during life. (2) In contrast to the Orthocerida, the Bactritida show two or three distinct and prominent lobes in the adoral site, giving space for the attachment of larger cephalic retractors. In combination with the ventral siphuncle and the inclined aperture, a dorsal concentration of the retractor musculature appears in the Bactritida, giving evidence for an oblique orientation of the conch and a more active mode of life among the Bactritida.

Thus, among the Orthocerida, the muscle scars are small, poorly differentiated and distributed over a wide portion of the conch cross section. By contrast, the muscle scars of Palaeozoic and Mesozoic ammonoids are larger, differentiated in dorsal, lateral and ventral portions and highly localized. This differentiation is recognisable in the soft-tissue attachment pattern of the Bactritida.

For a more detailed phylogenetic interpretation of these soft-tissue attachment patterns, however, additional material of well-preserved internal moulds of Bactritida and early ammonoids is needed. In the future, the study of such soft-tissue attachment structures might help to further clarify the phylogeny of the Bactritida and might help to test whether this taxon is monophyletic.

Acknowledgements

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