

# First nearly complete skeleton of the Cretaceous duvaliid belemnite *Conobelus*

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## ABSTRACT:

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The first Cretaceous belemnite preserved with the rostrum, slightly compressed phragmocone and part of the proostracum is described from the Early Cretaceous (Late Valanginian) Rossfeld Formation (Eibeck, Reichraming Nappe of the Northern Calcareous Alps). The rostrum has dorsal groove (alveolar furrow) typical of duvaliids, and its conical shape (round in transverse section outline), and the rounded apex allow its attribution to *Conobelus* STOLLEY, 1919. The new species *C. pseudoheres* sp. nov. is proposed based on the unique features of the specimen, i.e. persistently parallel lateral sides throughout the rostrum and the conical, blunt outline at the apex. The ration between rostrum and phragmocone is 0.78; the distances between the calcitic septa of the anterior end of the phragmocone range from 3 to 5 mm. The proostracum is 0.02 mm thick. The apical angle is 32° and the alveolar angle (posterior end of the phragmocone) is 24°. The alveolus is 40 mm long, yielding a ratio between rostrum and alveolus of 1.86. The depositional history with its fast sedimentation along with absent/limited post-mortem transportation led to extraordinarily good preservation of the examined specimen.

**Key words:** Belemnites, Rostrum, Phragmocone, Proostracum, Early Cretaceous, Valanginian, Northern Calcareous Alps.

## INTRODUCTION

The long early history of the various reconstructions of the belemnite animal was extensively reviewed by NAEF (1922). The main problem with reconstruction has always been the extremely rare preservation of entire phragmocones, proostraca and, of course, the soft-parts. Apart from the frequently calcitic rostra of belemnites, our knowledge of coleoids is based on rare soft-body findings in so-called preservational windows like the 'Solnhofen Plattenkalk' or the 'Posidonia Shales' (see SCHLEGELMILCH 1998). This stands in contrast to the enormous number of ectocochleate cephalopods comprising the ammonoids and nautiloids. Reconstructions of belemnite animals, based on entire findings, were

shown in OWEN (1844), MANTELL (1848), STEVENS (1965) and MONKS & al. (1996). Soft-part reconstructions have been boosted rather recently by the finds of unusually complete *Passaloteuthis bisulcata* (de BLAINVILLE, 1825), *Hibolithes semisulcatus* (von MÜNSTER, 1830) and *Cylindroteuthis puzosiana* (d'ORBIGNY, 1842). HEWITT & al. (1999) presented a combination of belemnite reconstructions and, from this, assumed that they were buoyant (see SPAETH 1975). As noted by RIEGRAF & REITNER (1979), caution is called for, because many of the so-called 'soft-part-belemnites' of the 'Posidonia Shales' (Lower Toarcian) have turned out to be forgeries.

The shell morphology of fossil coleoids (= Dibranchiata, Endocochlia) was studied by JELETZKY (1966, 1980) and critically restudied by HEWITT & al.

(1983) and compared with that of Recent Coleoidea, fossil Bacritida and Orthocerastida. KOBANOV (1967), BARSKOV (1972) and DAUPHIN (1985) drew conclusions about the microstructural differences of fossil and Recent coleoid cephalopods. They discussed in detail the morphological differences of phragmoteuthid, teuthid and belemnite proostraca. Special attention was devoted to the function of proostraca and nomenclature by VOLTZ (1830), PEARCE (1842), HUXLEY (1864), NAEF (1921, 1922), ROGER (1952), KRYMGOL'TS (1958), JELETZKY (1966) and HEWITT & PINCKNEY (1982).

In most coleoid cephalopods, however, the ventral and lateral (or only ventral) parts of the walls have been largely or completely lost, being replaced by the muscular mantle, which became attached to margins of the remaining dorsal part of the body chamber (proostracum) (Text-fig. 1). DOGUZHAEVA (2002), DOGUZHAEVA & *al.* (2002b, 2003a, b) assumed that the proostracum represented an innovation of coleoid evolution rather than a dorso-lateral remnant of the body chamber shell wall of their ectocochleate precursors, as had been suggested earlier (see JELETZKY 1966). Moreover, the latter authors suggested that the proostracum represented a structure not present in the shell of ectocochleate cephalopods (e.g. ammonoids and nautiloids).

The following list of important papers can give only a small insight into past and recent research on stratigraphy, taxonomic groups, different areas and taphonomy of Cretaceous belemnites (often combined with Jurassic belemnites): de BLAINVILLE (1827), CHALLINOR (1991), CLÉMENT (1999), COMBÉMOREL (1973, 1988), COMBÉMOREL & STOYANOVA-VERGILOVA (1991), DOGUZHAEVA & *al.* (2002a, b; 2003a, b) DOYLE (1987), DOYLE & MARIOTTI (1991), DUVAL-JOUVE (1841), JANSSEN (2003), JANSSEN & CLÉMENT (2002), JANSSEN & FÖZY (2003), JELETZKY (1966), LUKENEDER (1999, 2002), MUTTERLOSE (1979, 1988), MUTTERLOSE & *al.* (1983), NAEF (1916, 1921, 1922, 1923), RASPAIL (1829), RIEGRAF (1999), SCHLEGELMILCH (1998), SEIBERTZ &

SPAETH (2002), STEVENS (1965), STOLLEY (1919), STOYANOVA-VIRGILOVA (1965) and WEISS (1991, 1992).

Since JELETZKY (1966), new systematic ideas on coleoids were presented by DOYLE (1991), DOYLE & *al.* (1994), RIEGRAF (1995) and RIEGRAF & *al.* (1998).

## GEOGRAPHICAL POSITION, GEOLOGICAL SETTING AND STRATIGRAPHY

The outcrop is situated in the Reichraming Nappe in Upper Austria. The exact position is about 5 km south of Brunnbach (652 m, ÖK 1:50000, sheet 69 Grossraming, Text-fig. 2A). The stream outcrop is located near the middle of the Eibeckgraben in the south-easternmost part of the east-west striking Ebenforst Syncline, running between the Sulzkogel (840 m) to the west and the vicinity of the Eibeck (916 m) to the east (Text-fig. 2B). The grey to ochre succession, comprising the belemnite-bearing bed, is located on the north-eastern side of the Hochkogel (1157 m). The occurrence is badly exposed on the left side of the stream. The exact position of the ammonoid-occurrence is fixed by GPS data (Global Positioning System): N 47°47'14" and E 14°31'00" (Text-fig. 2B).

The Upper Valanginian succession of southeast Upper Austria was deposited in an unstable shelf setting characterized by thick stratigraphic units that reflect transgressive histories punctuated by tectonic events, as shown by the deposition of conglomerates and sandstones.

The Valanginian belemnite described was collected from a little outcrop containing marls, which is located at the southern-eastern margin of the Ebenforst Syncline. The Ebenforst Syncline is situated in the southernmost part of the Reichraming Nappe of the Northern Calcareous Alps (Text-fig. 2A and 2B). This region is a part of the Bajuvaric Unit, which is bordered and overlain in the south by the Tyrolian Nappes (Staufen-Höllengebirgs Nappe). At the Eibeck section,

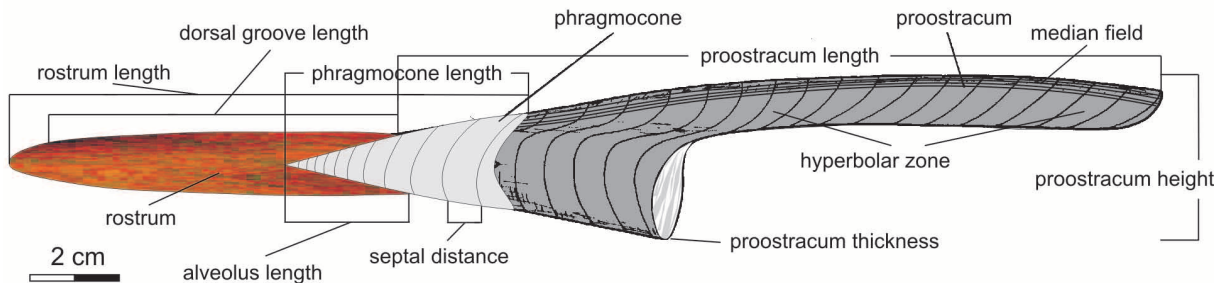


Fig. 1. Scheme of longitudinal section through hard parts of the belemnite *Conobelus* with estimated correct proportions and abbreviations used in the text;  $\times 0.4$

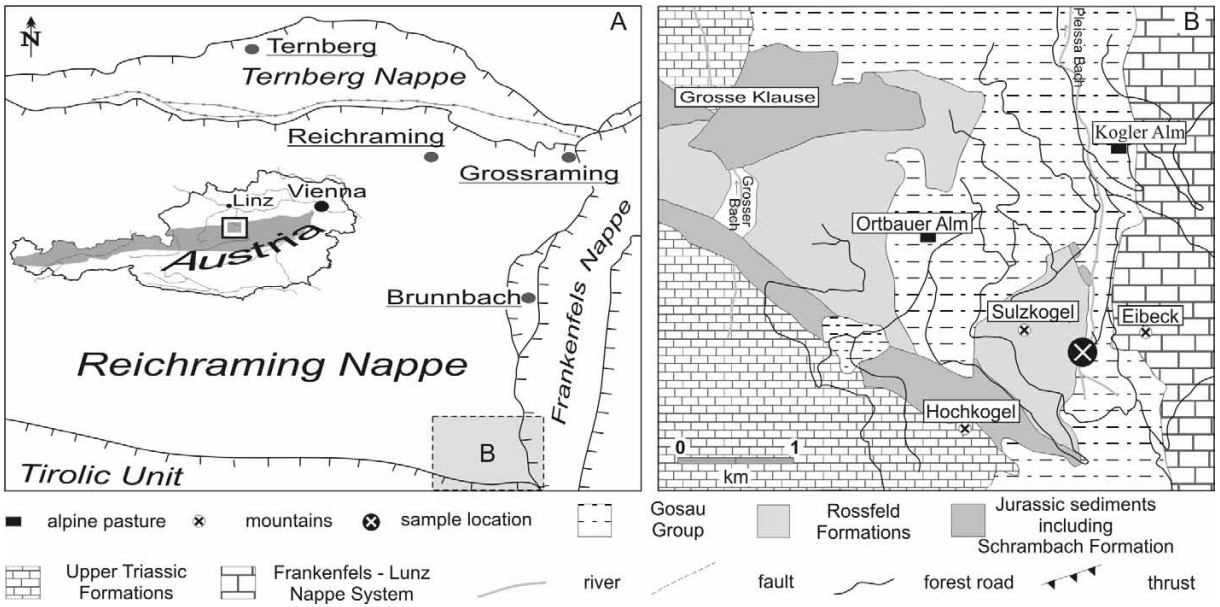


Fig. 2. A, Locality map of Upper Austria showing the outcrop of Lower Cretaceous sediments (black) around the section investigated within the Northern Calcareous Alps. Positions of the synclines are given in the tectonic map on the left. B, The outcrop is situated in the Rossfeld Formation

the Lower Cretaceous is represented by two formations, from bottom to top the Schrambach Formation (approx. 50 m, Berriasian), and the Rossfeld Formation (approx. 150 m, Late Valanginian) (Text-fig. 3). The terrigenous, proximal, deep-water, turbiditic Rossfeld Formation of the Reichraming Nappe represents a synorogenic development (FAUPL 1979). The Rossfeld Formation at the Eibeck section consists of essentially ochre calcareous marls and grey silty marlstones, accompanied by conglomerates and sandstones, and it is generally exposed in stream outcrops and on forest roads. The CaCO<sub>3</sub> (calcium carbonate contents, equivalents calculated from total inorganic carbon) attains values of about 31.3 %. The weight % TOC values (Total Organic Carbon) are about 2.94 within the marls of the outcrop. The maximum total sulphur content (S)

is about 1.76 mg/g. The belemnite described herein was found in beds with abundant olcostephanids, which are concentrated in the marlstone layers. This part of the section is fairly fossiliferous, yielding mainly ammonoids, aptychi and bivalves.

The association of the cephalopod-bearing beds indicates that the Rossfeld Formation belongs to the *Saynoceras verrucosum* ammonoid Zone of the early Late Valanginian (according to the results of the meeting of the Lower Cretaceous Ammonite Working Group of the IUGS in Lyon; HOEDEMAEKER & al. 2003).

The following ammonoids were observed: *Ptychophylloceras semisulcatum*, *Lytoceras* cf. *subfimbriatum*, *Leptotetragonites* cf. *honnoratianus*, *Haploceras grasiatum*, *Olcostephanus guebhardi*, *Neocomites neocomiensis*, *Neocomites teschenensis*, *Prodichotomites* sp., *Oosterella gaudryi*, *Eleniceras* sp., *Bochianites neocomiensis* and aptychi. Although *Saynoceras verrucosum* is missing, the typical association hints at the *Saynoceras verrucosum* Zone (*Saynoceras verrucosum* Subzone and/or *Karakaschiceras pronecostatum* Subzone) (Text-fig. 3) (LUKENEDER 2004).

VALANGINIAN	Upper	<i>C. furcillata</i>	<i>T. callidiscus</i>
			<i>C. furcillata</i>
		<i>N. peregrinus</i>	<i>O. (O.) nicklesi</i>
			<i>N. peregrinus</i>
		<i>S. verrucosum</i>	<i>K. pronecostatum</i>
			<i>S. verrucosum</i>
Lower	<i>B. campylotoxus</i>	<i>K. biassalense</i>	
		<i>B. campylotoxus</i>	
	<i>T. pertransiens</i>		

Fig. 3. Stratigraphical index (modified after HOEDEMAEKER & al. 2003) of the range within the Rossfeld Formation at the Eibeck section (in grey)

MATERIAL, PRESERVATION AND METHODS

The abundant and generally well-preserved cephalopods (except for fragmentation) are dominated by ammonoids (*Olcostephanus*). Several localities in Upper Austria have yielded numerous belemnite speci-

mens, all of which are preserved as rostra only. No phragmocones or proostraca have yet been observed.

During the course of this study a single belemnite specimen (Text-fig. 5; 2004z0046/0001) of *Conobelus* STOLLEY, 1919 was examined. The specimen was collected by Heinz KOLLMANN (Natural History Museum, Vienna) in the early 1970s and has been prepared by the author. The specimen was discovered due to its conspicuously large size. Based on similarities to *Conobelus heres* WEISS, 1991 (Text-fig. 4), the specimen was assigned to *Conobelus* STOLLEY, 1919.

In general the material is moderately well preserved. Although the specimen is asymmetrically distorted and compressed, it is sufficiently complete to provide measurements that enable a generalized biometric estimate of shape and size. The rostrum is visible on each side. The attached and extremely crushed phragmocone (by sediment compaction) is visible on one side only. The partly preserved proostracum is well-preserved; its anterior end is only minimally flattened because of its sediment filling. The fragmentation is due to sediment compaction and considerable tectonic deformation, which influences the precise determination of most cephalopods with chambered hard parts (e.g. ammonoids).

The exposures of most Lower Cretaceous lithological units (e.g. Schrambach Formation and Rossfeld Formation) in the Northern Calcareous Alps yield numerous belemnites. However, without close scrutiny, the locality described would be regarded as being barren of belemnites.

The fauna is characterized by ammonoids that were discovered in sediments of the Eibeck section by Heinz Kollmann and the author; they are published elsewhere (LUKENEDER 2004). About 70 ammonoid specimens have been collected at the Eibeck section. Nearly every preservational stage was observed. Most of the specimens have been crushed by sediment compaction, but there are also some extraordinarily well-preserved individuals (e.g. lapets of microconchs). Their composite moulds show perfectly preserved sculpture on the rarely preserved shell.

Calcium carbonate contents ( $\text{CaCO}_3$ ) were determined using the carbonate bomb technique. Total carbon content was determined using a LECO WR-12 analyser. TOC contents were calculated as the difference between total carbon and carbonate carbon, assuming that all carbonate is pure calcite. The chemical analyses were carried out in the laboratory of the Department of Geology at the University of Vienna.

#### SYSTEMATIC PALAEOONTOLOGY

The type and figured material is deposited in the Macropalaeontology collections of the Department of Geology and Palaeontology, Natural History Museum, Wien (NHMW), with prefixed catalogue number.

The following abbreviations are employed: a, alveolus length; aa, apical angle; dgl, dorsal groove length; dgd, dorsal groove depth; pha, phragmocone angle; phl, phragmocone length; prol, proostracum length; proh,

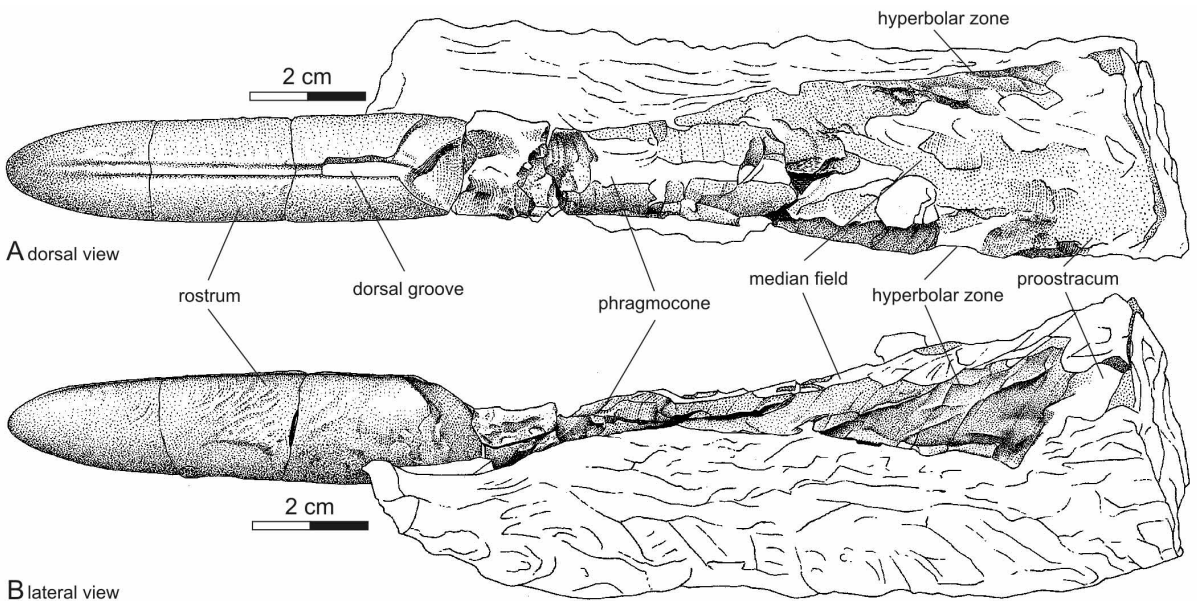


Fig. 4. A, drawing of dorsal view of holotype of *Conobelus pseudoheres* sp. nov. (NHMW 2004z0046/0001);  $\times 0.8$  (mirrored to have rostra below each other).

B, drawing of lateral view of the specimen figured in A;  $\times 0.8$

prostracum height, prot, prostracum thickness; rl, rostrum length; rh, rostrum height; rb, rostrum breadth; s, septal distance (see measurements). The standard dimensions for normally coiled ammonites are given in mm. We follow the coleoid classification of DOYLE & *al.* (1994), RIEGRAF (1995, 1999) and RIEGRAF & *al.* (1998). WEISS (1992) and JANSSEN (2003) extensively reviewed the genera *Conobelus* and *Berriasibelus*.

Phylum Mollusca CUVIER, 1795  
 Class Cephalopoda CUVIER, 1795  
 Subclass Coleoidea BATHER, 1888  
 Superorder Belemnoida HYATT, 1884  
 Order Belemnitida GRAY, 1849  
 Suborder Pachybelemnopseina RIEGRAF, 1998

Family Duvaliidae PAVLOV, 1914

REMARKS ON THE FAMILY: The dorsal groove of this specimen clearly indicates the affinity with members of the Duvaliidae.

Genus *Conobelus* STOLLEY, 1919

REMARKS ON THE GENUS: *Conobelus* shows a conical, club-shaped rostrum with a rounded or pointed apex. The rostrum is not or only slightly laterally compressed, with a round to rounded-trapezoidal transverse section. The dorsal side is somewhat flat, containing a wide and deep groove. The deep alveolus (approx. halfway) is positioned eccentrically, closer to the ventral side (Text-fig. 5).

The genus *Conobelus* differs from the genus *Duvalia* BAYLE, 1878 in the absence of a flattening of the lateral sides and in the apical area. It is distinguished from *Pseudoduvalia* NAEF, 1922 by different transverse sections (rhomboidal in *Pseudoduvalia*) and a lanceolate, subconical outline in the latter genus. It differs from *Berriasibelus* DELATTRE, 1952 in its conobeloid to rhopaloteuthoid rostrum and the somewhat smaller alveolar groove, the single-plane compression of the whole rostrum, and the different apical margin. *Produvalia* RIEGRAF, 1981 can be differentiated from *Conobelus* by the shape of the rostrum (short, clavate), a wider dorsal furrow, the presence of lateral lines and the straight central apical line.

TYPE SPECIES: *Belemnites conophorus* OPPEL, 1865, from the Upper Jurassic, Czech Republic.

ORIGINAL DIAGNOSIS: STOLLEY, 1919 created the

genus *Conobelus* based on “the club shaped, not or only slightly lateral compressed and deformed specimen (*Conophori*). I [STOLLEY] propose the new genus *Conobelus* Stolley with *C. conophorus* as type.....”.

SPECIES ORIGINALLY INCLUDED: Only the nominal species, *Belemnites conophorus* OPPEL, 1856, was specifically mentioned. However, one might conclude that STOLLEY also included other species mentioned by OPPEL, such as *Belemnites strangulatus* (personal communication N. JANSSEN).

STRATIGRAPHICAL REMARKS: Latest Malm and Neocomian according to STOLLEY (1919).

OTHER SPECIES OF THE GENUS: *Conobelus strangulata* (OPPEL, 1865); *Conobelus gemmelaroi* (ZITTEL, 1870) (= *Conobelus siciliensis*, COMBÉMOREL & MARIOTTI, 1986, according to JANSSEN personal communication); *Conobelus propinquus* WEISS, 1991; *Conobelus kabanovi* WEISS, 1991; *Conobelus triguetrus* WEISS, 1991; *Conobelus heres* WEISS, 1991. *Conobelus conicus* (de BLAINVILLE, 1872); *Conobelus conophora* (OPPEL, 1865); *Conobelus barskovi* (WEISS, 1991); *Conobelus incertus* WEISS, 1991; *Conobelus beneckeii* (NEUMAYR, 1873) (= *Conobelus jouvei* TOUCAS, 1890, according to N. JANSSEN personal communication).

According to JANSSEN (personal communication), additional species exist: *Conobelus suborbigny* (TOUCAS, 1890); ?*Conobelus zitteli* (GREGORIO, 1886); *Conobelus? piraddoensis* JANSSEN, 2003; *Conobelus* sp. cf. *sauvanausis* (d'ORBIGNY, 1842); *Conobelus* sp. A JANSSEN, 2003; and *Conobelus* sp. B JANSSEN, 2003. Due to their problematic and unclear taxonomic status, the latter species are not discussed in the diagnosis below.

*Conobelus pseudoheres* sp. nov.  
 (Text-figs 4 and 5)

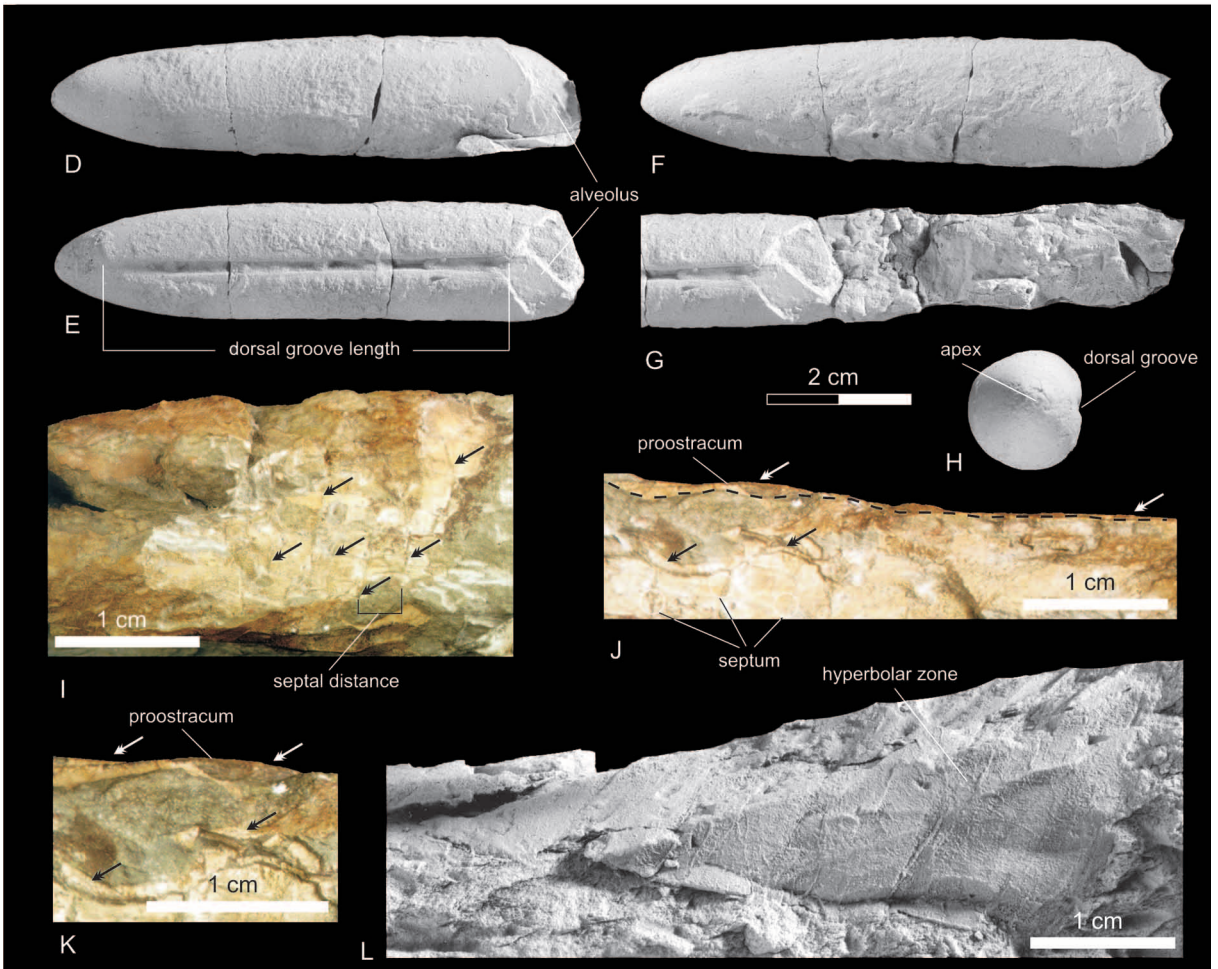
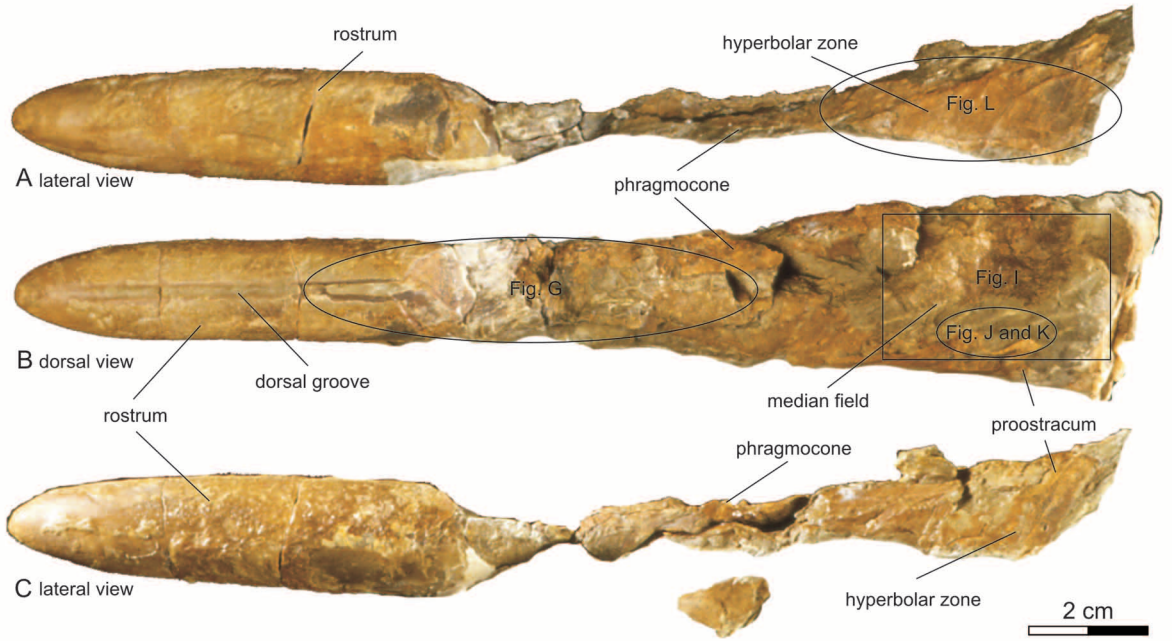
1999. *Hibolites* sp.; LUKENEDER, p. 138, pl. 1, figs 1-4.

DERIVATION OF NAME: Due to the close affinity and morphological similarities to the species *Conobelus heres* WEISS, 1991.

HOLOTYPE: Specimen illustrated in Text-figs 4 and 5 (NHMW 2004z0046/0001).

MATERIAL: Only the holotype is known.

LOCALITY: Stream outcrop near the middle of the Eibeckgraben in the south-easternmost part of the east-



west striking Ebenforst Syncline, running between the Sulzgoegel (840 m) to the west and the vicinity of the Eibeck (916 m). The outcrop is badly exposed on the left side of the stream. GPS data: N 47°47'14" and E 14°31'00" (Text-fig. 2).

**DIAGNOSIS:** *C. pseudoheres* sp. nov. shares with all other members of the genus *Conobelus* a relatively long dorsal furrow and the general conical shape but shows notable differences, justifying the erection of a new species. As the specimen described is the first find of a duvaliid rostrum with attached phragmocone and part of the proostracum, comparisons can only be undertaken by comparing features of the different rostra.

The specimen described (phragmocone and proostracum) is coated by a thin limonitic (yellow) patina showing a conical, medium-sized rostrum with a hastate outline. The profile and outline are symmetrical to weakly asymmetrical with a transverse section almost circular and a broad dorsal furrow extending from the alveolar area to approximately 10 mm from the apex, which is minimally displaced to the dorsal side of the rostrum. The rostrum is slightly compressed, but not exceeding values of 1.06 (rh/rb, 1.8 /1.7) (Text-fig. 6).

**DESCRIPTION: Rostrum.** The perfectly preserved rostrum (guard) shows no compaction or fragmentation. It surrounds half of the preserved phragmocone. Because of its darker colour and its smooth surface, it can easily be distinguished from the phragmocone and the proostracum. From about 10 mm from the rounded apex, the guard remains more or less equally thick to the anterior end. The rostrum shows an up to 2 mm deep and 2 mm broad, dorsal groove (alveolar groove), which begins at the anterior end and extends almost up to the apex (60 mm) (Text-fig. 6). It possesses a rounded base throughout. The boundary to the phragmocone is sharp.

**Phragmocone.** The phragmocone is crushed and flattened. Its yellow colour is due to its limonitic preservation (partly aragonitic). The estimated length is about 140 mm, of which 40 mm are hidden in the rostrum (apical portion of the phragmocone is so far unknown). No outer-shell is preserved, except for septa. About three calcitic septa (in the middle part) and seven septa (at the anterior part) are

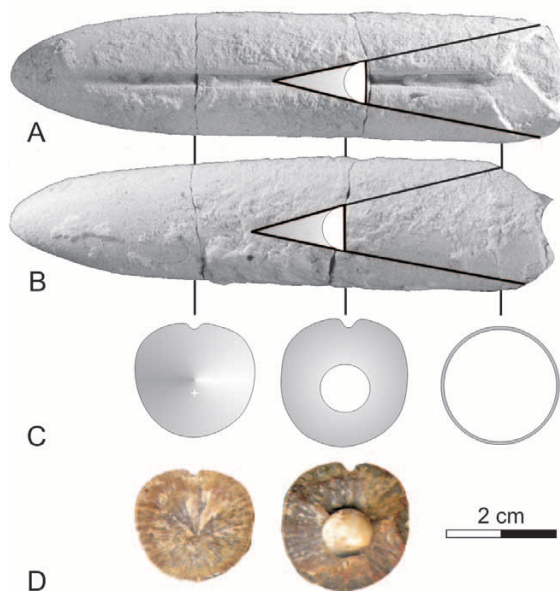


Fig. 6. A, (dorsal view) and B, (lateral view) of the rostrum of holotype of *Conobelus pseudoheres* sp. nov.; Angles of the phragmocone are plotted on the rostrum. C, Drawings of transverse-sections of the rostrum at different lengths. D, original fracture surfaces corresponding to transverse-sections in C. Note position and shape of the calcitic phragmocone; all  $\times 0.8$

visible near the dorsal beginning of the 'visible' proostracum and the area between the lateral 'wings' (hyperbolar zones). The proostracum is mostly preserved with netting structure (striate preservation). Distances between septa are from 1 mm to 4 mm. The transverse septa follow the shape of the apertural edge and end at the dorsal edges of the lateral fields, where they directly pass beneath the hyperbolar zones. The phragmocone has an angle of expansion ranging from 24° and 26°. The phragmocone is filled with calcite (part in rostrum) (Text-fig. 6). The calcitic conothecal layer which envelopes the phragmocone in the rostrum (0.5 mm thick at 46 mm of rostrum) is visible on the broken areas of the guard.

**Proostracum.** Limonitic (partly aragonitic) remnants of the proostracum can be observed 80 mm from the anterior end. The yellow colour is due to the limonitic preservation. The remnants of the organic proostracum show a netting structure (striate preservation) over the whole surface. The proostracum shows little deforma-

Fig. 5. Holotype (NHMW 2004z0046/0001) of Late Valanginian *Conobelus pseudoheres* sp. nov. from the Losenstein Syncline (Austria). Representative of the Eibeck assemblage. A, right lateral view  $\times 0.9$ . B, dorsal view;  $\times 0.9$ . C, left lateral view;  $\times 0.9$  (mirrored to have rostra below each other). D, right lateral view of rostrum. E, dorsal view. F, left lateral view. G, rostrum/phragmocone (crushed) boundary,  $\times 1$ . H, apical view; all  $\times 1$ . I, magnified view of the median field (anterior part) of the proostracum shown in Fig. 4B with positions (arrows) of calcitic septa indicated;  $\times 2$ . J, left side of the anterior phragmocone, note the boundary (dashed black line) of median field (indicated with black arrows) and hyperbolar zones (white arrows), calcitic septa at lower left (white circles);  $\times 2$ . K, magnified view of the hyperbolar layer (white arrows) and median field layer (black arrow). L, magnified view of left hyperbolar zone of proostracum shown in Fig. 4A to show growth lines;  $\times 2$ . All photographs in the black area of Fig. 9 were coated with ammonium chloride before photographing, except I, J and K

tion because it was filled with sediment at an early stage prior to burial. In almost all belemnoids the proostracum surrounds the entire phragmocone and protrudes as a large, comparatively broad, dorsal projection toward the anterior end of the shell. In the specimen under discussion, the proostracum originally covered the entire phragmocone. The preserved remnants of the proostracum now surround the dorso-lateral parts of the crushed phragmocone. The concentric growth lines on the anterior side of the hyperbolar zones are clearly visible. The median field is crushed and badly preserved throughout. It provides a view of the last 34 mm of the underlying phragmocone, with its septa. The median field is broad (max. 17 mm). The median field ('Mittelplatte' of NAEF 1922) is apparently less well preserved due to its different primary structure (horny) in contrast to the hyperbolar zones (VOLTZ 1830; 'Seitenplatte' of NAEF 1922), which are preserved because of their weakly calcified primary structure. Their lateral surfaces of the hyperbolar zones are ornamented by straight growth lines. Outlines are well defined throughout. The medial asymptotes (longitudinal ridges) are not visible. The proostracum is most probably broken at its anterior end.

MEASUREMENTS: a 40; aa 32°; dgl 55; dgd 2; pha 24°; phl 140; prol 80; proh 21; prot 0.02; rl 74.5; rh 18; rb 17; s 3-5.

DIFFERENCES FROM RELATED TAXA: *C. pseudoheres* sp. nov. differs from the smaller *C. heres* (WEISS, 1991) in showing a parallel, regular lateral outline, a deeper alveolar furrow, a deeper alveolus (half of rostrum) and a smaller alveolar angle (32° versus 36°). It differs from *C. propinquus* (WEISS, 1991) in the bigger rostrum (7.5 cm), in contrast to the smaller, laterally compressed rostra (max. 3 to 5 cm) of the latter species; the tiny 'thin' rostra of *C. propinquus* show a mid-apical line, a shorter (3/5) alveolar line and a shallower (1/3) alveolus combined with a longer apical area resulting from a smaller apical angle (24° versus 32°). It differs from *C. triquetrus* (WEISS, 1991) in the larger apical angle (32° versus 25°) and the resulting shorter apical area; the alveolus is considerably deeper in *C. pseudoheres* sp. nov. It differs from the smaller *C. kobanovi* (WEISS, 1991) in a longer alveolar groove, a shorter apical region, a larger apical angle (32° versus 26°) and the deeper alveolus (1/2 versus 1/3). It differs from the smaller *C. conicus* (de BLAINVILLE, 1827) in a shorter apical area, a larger apical angle (32° versus 29°), a longer alveolar groove and a blunt apex. It differs from the smaller *C. beneckeii* (NEUMAYR, 1873) by the shorter apical area and a bigger apical angle (32° versus 30°).

The medium-sized *C. beneckeii* shows a dorso-laterally compressed, club-shaped rostrum. *C. beneckeii* shows its maximal rostrum expansion at the last third of the alveolar groove. It differs from the subfusiform to club-shaped *C. barskovi* (WEISS, 1991) in a different transverse section and a larger apical angle (32° versus 25°). *C. barskovi* has the apical line near the venter (1/2), an eccentric apex near the dorsal side and a pointed apex. It differs from the smaller *C. incertus* (WEISS, 1991) in a rounder transverse section, a shorter apical region and a blunt apex (pointed in *C. incertus*). It differs from the smaller *C. conophora* (OPPEL, 1865) in a longer dorsal furrow. *C. conophora* is only known from Jurassic sediments. It differs from the smaller *C. strangulatus* (OPPEL, 1865) in the longer apical area. It differs from the smaller *C. gemmellaroi* (ZITTEL, 1870) in the cylindrical rostrum, whereas in *C. gemmellaroi* club-shaped to lanceolate rostra occur. The transverse section in *C. gemmellaroi* is elongated to elliptical. *C. gemmellaroi* is only known from Jurassic sediments.

A more detailed comparison is given in the following paragraph in respect to the most similar species to *Conobelus pseudoheres* sp. nov. The described specimen (Text-fig. 8C) is very close to the morphotype of WEISS (1991) and shows close similarities to *Conobelus (Coctebelus) heres* WEISS, 1991. The latter was described and figured (WEISS, 1991; p. 33; pl. 2, fig. 7; aa 36°) in a revision of the genus *Conobelus* STOLLEY, 1919. The most noticeable contrast to the specimens of WEISS (1991) is that the present specimen has parallel lateral sides throughout the rostrum (Text-fig. 6), whereas *Conobelus (C.) heres* WEISS, 1991 shows a larger angle (aa 36°) of the rostrum and exhibits a deeper dorsal furrow (see Text-figs 7 and 8).

Based on morphological features, the author attributes the species described (*C. pseudoheres* sp. nov.), to the genus *Conobelus* STOLLEY, 1919, and not to the genus *Berriasibelus* Delattre, 1952, to which JANSSEN (2003), referred species like *Conobelus (Coctebelus) heres* WEISS, 1991. The rounded base of the alveolar groove shows that the studied specimen is close to the group of '*Belemnites conicus* de BLAINVILLE, 1827'. In the original description '*Conobelus heres* WEISS, 1991' also shows rounded, rather long, typically broad alveolar grooves (WEISS 1991; p. 25, fig. 2 f).

The related species *Berriasibelus extinctorius* (RASPAIL, 1829) is distinguished by its acute apical area (aa 40°) and its more angular dorsal groove. BLAINVILLE (1827) figured the original of *Belemnites conicus* (p. 118; pl. 5, fig. 4; aa 29°). That specimen shows a more acute apical area than the specimen described herein. As noted by MUTTERLOSE (1979), '*Conobelus conicus* de BLAINVILLE, 1827', with conical outline at its apex, is closely



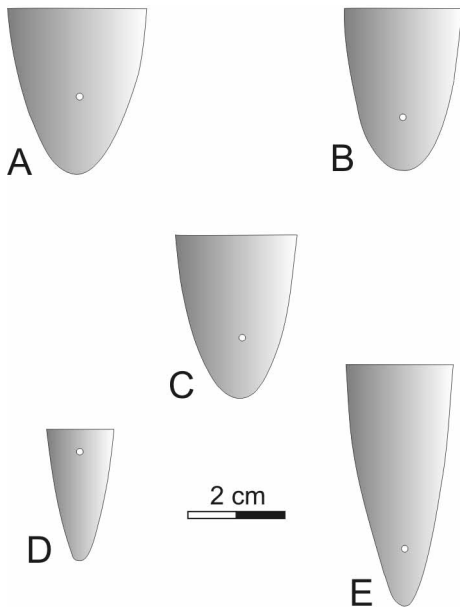


Fig. 7. Comparison of profiles (apical area) from species related to *Conobelus pseudoheres* nov. sp.. A, '*Hibolites*' sp. in LUKENEDER (1999; pl. 1, figs 2 and 4). B, *Conobelus (C.) heres* WEISS, 1991 (WEISS 1991, 1992; pl. 2, fig. 7a). C, *Conobelus pseudoheres* nov. sp. (this paper). D, *Belemnites conicus* in BLAINVILLE (1827; pl. 5, fig. 4a). E, *Duvalia conica* in COMBEMOREL (1973; pl. 2, fig. 8a). Note indicated position of the end of the dorsal furrow (white circle)

related to *Berriasibelus exsintorius* (RASPAIL, 1829), which shows a well-defined apical region (Text-fig. 7). '*Duvalia conica*' (de BLAINVILLE, 1827) (COMBÉMOREL 1979; p. 71; fig 18; aa 19°-22°, Text-fig. 7E), is often confused with '*Duvalia lata*' (de BLAINVILLE, 1827) (COMBÉMOREL 1979; p. 70, fig. 16; aa 35°). Juvenile stages of '*Duvalia lata*' (de BLAINVILLE, 1827) are more compressed than comparable ones of '*Duvalia conica*' (de BLAINVILLE, 1827). Based on the regularly conical form of its rostrum, '*Belemnites conicus* de BLAINVILLE, 1827' (Text-fig. 7D) is distin-

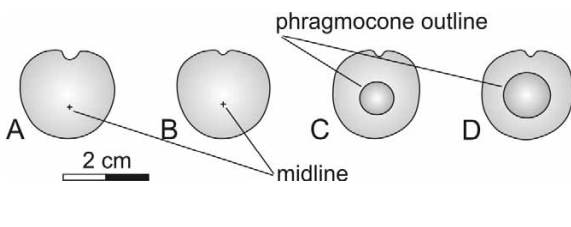


Fig. 8. Comparison of profiles. A, *Conobelus (C.) heres* WEISS, 1991 (WEISS 1991, 1992; p.25, fig. 2 f). B, profile at 25 mm and C, profile at 45 mm from apex of *Conobelus pseudoheres* sp. nov. (this paper). D, profile at 50 mm from apex of '*Hibolites*' sp. in LUKENEDER (1999; pl. 1, fig. 2 and 4). Note indicated midline (black crosses) of rostra and phragmocone outline (black circles)

guished from *Berriasibelus exsintorius* (RASPAIL, 1829), whose post-alveolar constriction is characteristic. The development of the alveolar area is most important, while the apical development is less important for taxonomy (personal communication Janssen).

A further specimen from the *S. verrucosum* Zone (Late Valanginian) published by Lukeneder (1999; pl. 1, figs 1-4; aa 38°; Text-fig. 7A) as '*Hibolites* sp.' most probably also belongs to *Conobelus pseudoheres* sp. nov. Additional remarks on the Duvaliidae are made in DOYLE & MARIOTTI (1991). Further discussions on the genera *Conobelus* STOLLEY and *Berriasibelus* are given by WEISS (1991, 1992) and JANSSEN (2003).

**OCCURRENCE:** Upper Valanginian calcareous marls (*Saynoceras verrucosum* Zone) of the Eibeck section (Rossfeld Formation; Northern Calcareous Alps), Austria.

**DISTRIBUTION:** *Conobelus pseudoheres* sp. nov. has so far been found only in Lower Cretaceous sediments of Upper Austria. The closely related *Conobelus (C.) heres* WEISS, 1991 was considered to be a Valanginian to Lower Hauterivian species by WEISS (1991, 1992). The affiliated species '*Conobelus gr. conicus* (de BLAINVILLE, 1827)' has a rather long stratigraphical range. As noted by JANSSEN & CLÉMENT (2002), '*Belemnites gr. conicus*' (de BLAINVILLE, 1827) is commonest in the *Tirnovella pertransiens* Zone (personal communication N. JANSSEN), and commonly occurs in the *Busnardoites campylotoxus* and *Saynoceras verrucosum* Zone. '*Conobelus conicus*' (de BLAINVILLE, 1827) is common in Valanginian sediments of France and Morocco (personal communication J. MUTTERLOSE).

## DISCUSSION

The fragmentary knowledge of most fossil belemnites makes it difficult to assess the relative taxonomic value of their morphological features (JELETZKY 1980). Only the shells of coleoids are sufficiently common to be useful for classification; while the belemnite rostra (guards) are common, the phragmocones and especially the fragile proostraca are extremely rare (HEWITT & WESTERMANN 1996). As noted by SEILACHER (1983), coleoids without a chambered phragmocone seem to have sunk to the bottom immediately after death, therefore leading to the preservation of the non-calcified gladius and soft parts.

The detailed study of the well-preserved Late Valanginian belemnite specimen from the Eibeck section, described herein as *Conobelus pseudoheres* sp. nov., yields new data on Cretaceous belemnites. The tectonically

strongly deformed Lower Cretaceous sediments of the Ebenforst Syncline do not normally represent optimal conditions for the preservation of entire belemnites. Nonetheless, the specimen described from the Eibeck section shows exceptional preservation of its thinner parts (phragmocone and proostracum) (Text-fig. 5). This allows a precise reconstruction of the shell proportions of the entire living belemnite animal (Text-fig. 9). It has to be noted that the location and form of the soft-parts in the reconstruction are mostly conjecture, whereas the proportions of hard-parts can be confirmed by measurements.

*Conobelus pseudoheres* sp. nov. is characterized by its regularly cylindrical shape towards the apex, its persistently parallel lateral sides throughout the rostrum, and by its conical blunt outline at the apex, and differs in the latter respects from all other representatives of *Conobelus* STOLLEY, 1919. Due to the preservation of the whole phragmocone and the partly preserved proostracum, the characteristic dorsal position of the alveolar furrow can be proven for the genus *Conobelus*. The ratio between rostrum and phragmocone (0.78) can be given for the first time, as can the distances between the calcitic septa of the anterior end of the phragmocone (3 to 5 mm). The covering proostracum is 0.02 mm thick. The apical angle of the described species is 32° and the alveolar angle (posterior end of the phragmocone) is 24°. The alveolus is 40 mm long and the resulting ratio between rostrum and alveolus is 1.86.

Current knowledge of the detailed morphology and ratio of the rostrum versus phragmocone and proostracum in belemnites is based mainly on findings within quiet-water sediments such as the Oxford Clay, 'Solnhofen Plattenkalk', and 'Posidonia Shales', which show exceptional depositional histories. The sediment and coleoid taphonomy of the Oxford Clay have been recently studied by ALLISON (1988) and reviewed by HEWITT & *al.* (1999) with a focus on post-mortem drifting

and buoyancy. In contrast to the latter localities, the mainly 'aerobic' conditions during burial at the Eibeck section hindered the preservation of the soft-parts.

New approaches are needed to help clarify certain central questions of cephalopod palaeontology, for example to provide new morphological details on Cretaceous belemnites and their taphonomy. The clearest indication of the 'real' size in belemnites is to find them with the phragmocone and proostracum preserved: depending upon their morphologies, organic skeletons are variably subject to reorientation, disarticulation, fragmentation and corrosion (BRETT & BAIRD 1986). The buried rostra are soon subject to diagenetic effects. The extent of shell dissolution and the types of diagenetic fillings or coatings on shells are related to both sedimentation rates and seafloor geochemistry.

The investigation of the macrofossil assemblage and its taphonomy (LUKENEDER 2004) indicates a mixed autochthonous/allochthonous occurrence at the Eibeck section. The assemblage is composed of specimens derived from the local community and preserved in 'life-position' (or as an 'in place assemblage') as well as of drifted or moved specimens (broken specimens). The taphonomy of cephalopods that lived together provides insight not only into the autecology of these organisms, but also into their palaeoenvironment and palaeocommunity structure.

Entire coleoids (e.g. belemnites) found in the substrate above which the animal lived originally, are not known from the Early Cretaceous. The fragmentation of most belemnites furnishes evidence for post-mortem transport as well as for breakage on the sea floor through current effects and/or consequences of predation of the cephalopod shell (RIEGRAF & HAUFF 1983, SEIBERTZ & SPAETH 2002, SEILACHER 1983). The fragmentary preservation of such assemblages points to at least minimal transportation. Most of the fractures in transported coleoids do not appear to be of biogenic origin. They typi-

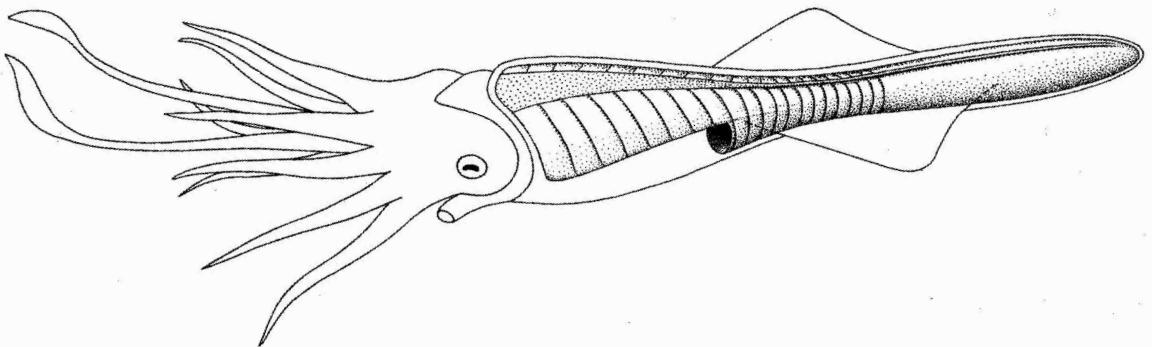


Fig. 9. Reconstruction of the Late Valanginian belemnite *Conobelus pseudoheres* sp. nov., lateral view, to show the correct proportions of rostrum, phragmocone, proostracum and soft body (modified after SPAETH 1975).

cally resulted from the impact of shells with other bioclasts during episodes of current transport prior to burial.

The specimen described here was deposited in a shelf habitat (Text-fig. 10). The shell was then buried relatively rapidly. The secondary calcite-filled phragmocone (within the rostrum) shows that it remained empty (of sediment) during burial. This reconstruction allows a tentative interpretation of the habitat: these belemnoids probably inhabited waters shallower than those in which they were ultimately deposited. This is also confirmed by the presence of acrothoracic cirripede borings on redeposited belemnite guards (see LUKENEDER 1999).

Compression and breakage through sediment pressure is assumed for the *Conobelus* specimen (phragmocone). Fragments are found in contact or compounded to other fragments of the same shell. The fragmented specimen lacks any encrustation, pointing to rapid sinking with minimal transport at the sea-surface or to lying for only a short time on the sea-floor. The place of original deposition and final position are therefore not far apart.

Numerous papers on belemnite preservation and taphonomic history deal with the sinking of belemnites to the sea-floor immediately after the death of the animal. DOYLE & MACDONALD (1993), RIEGRAF (1973), REITNER & ULRICH (1983), Riegraf (in KELLER 1977), RIEGRAF & HAUFF (1983), SCHLEGELMILCH (1998), SEIBERTZ (2002) and SEILACHER (1983) followed the theory forwarded by HÖLDER (1955) that the front part of the rostrum (and therefore in most cases the conothec) was bitten by a predator, allowing water to infiltrate the phragmocone

and leading to rapid sinking after death. DOYLE & MACDONALD (1993), POLLARD (1968) and SEILACHER (1983) suggested that only the heads of these cephalopods were consumed, the rest discarded. For a divergent interpretation, see BROWN (1900) and POLLARD (1990). The latter authors show that belemnites were also eaten entirely (guard plus soft parts) by marine invertebrates.

Another potential explanation for almost entire preservation is that the belemnite animal lived at greater depths that did not allow its dead body to float up to the sea surface due to the water pressure. Accordingly, such animals became negatively buoyant after water entered the chambers, causing them to sink (see WESTERMANN 1985). All of the latter scenarios do not adequately explain the present case.

The interpretation of an autochthonous origin is strongly supported by the preservational history suggested above (e.g. almost entire, little fragmentation, no encrustation). Note, however, that caution must be used when applying the term 'autochthonous' to cephalopods.

## CONCLUSIONS

The Early Cretaceous coleoid *Conobelus pseudoheres* sp. nov. (NHMW 2004z0046/0001) – preserved with its almost entire shell – is described. The rostrum with its dorsal groove, the partly but three-dimensionally preserved phragmocone and parts of the extremely rarely

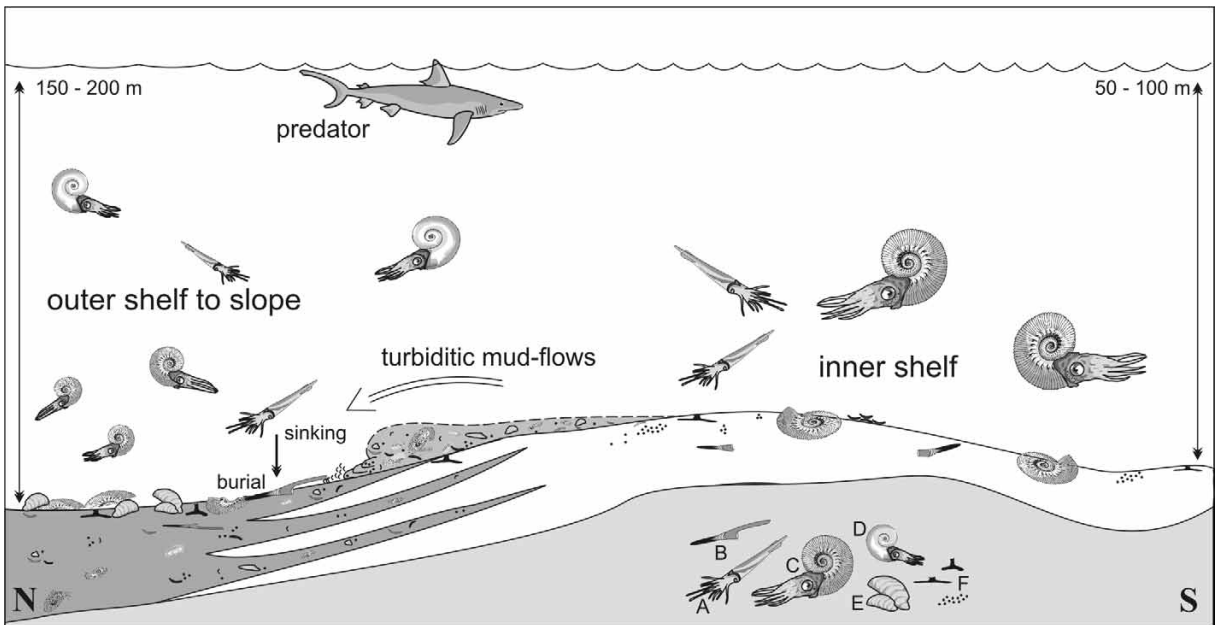


Fig. 10. Temporal sequence of the facies zones during the Late Valanginian related to water depth and bottom currents. Indicated positions of living habitat and final depositional environment at the Eibeck section. A, belemnite animal. B, dead animal (shell). C, *Olcostephanus guebhardi*. D, *Leptotetragonites honnoratianus*. E, *Inoceramus neocomiensis*. F, trace fossils (*Chondrites*, *Planolites*)

observed proostracum of the family Duvaliidae are preserved. This specimen represents the first published finding of an almost entire belemnite within Cretaceous sediments. The preservation of the belemnite furnishes evidence of fast burial and minimal or no post-mortem transport (on the sea-floor) of the shell.

*Conobelus pseudoheres* sp. nov. is erected as a new species due to the morphological differences from all other representatives of the genus *Conobelus* STOLLEY, 1919. The species is characterized by cylindrical shape, persistent parallel rostral outline and the conical blunt apical area, and differs in this respect from all the other related species. In 'normal' preservation, the phragmocones and proostraca are missing, and specific assignments are therefore based on comparisons of rostra. A detailed scheme of the hard parts based on the new morphological observations is presented, demonstrating the most important morphological differences from all other representatives of the genus *Conobelus*. The preservation of the whole phragmocone and its position relative to the rostrum provides proof of the characteristic dorsal position of the alveolar furrow in the genus *Conobelus*. The calculated ratio between rostrum and phragmocone is about 0.78. Distances between the calcitic septa of the anterior end of the phragmocone are between 3 and 5 mm. The outer layer of the partly preserved proostracum is 0.02 mm thick. The apical angle of the described species is 32° and the alveolar angle (posterior end of the phragmocone) is 24°. The alveolus is 40 mm long, yielding a ratio of 1.86 between rostrum and alveolus. In most Jurassic and Cretaceous belemnites with short-conical rostra, the ratio between the rostrum and the phragmocone is about 1 (personal communication W. RIEGRAF). *Conobelus pseudoheres* sp. nov. shows a somewhat smaller ratio (0.78), due to its longer phragmocone. The alveolar angle of about 24° exceeds that of most Duvaliidae, which typically exhibit values of approximately 12° to 18° (personal communication W. RIEGRAF).

No sorting, no packing due to sedimentological or biological effects, and no alignments or concentration due to transport or bottom currents were observed. The investigation of the macrofossil assemblage and its taphonomy indicated a mixed autochthonous/allochthonous occurrence at the Eibeck section. The assemblage is composed of specimens derived from the local community and preserved in 'life-position' (or as an 'in-place-assemblage') as well as of drifted or moved specimens (broken specimens). Re-deposition of the presented belemnite specimen through currents or turbidites can be ruled out based on the extraordinary preservation of fragile parts (e.g. phragmocone, proostracum). Compression and breakage of this *Conobelus* individual (phragmocone) through sediment pressure is assumed. The deposi-

tion took place under conditions of relatively stable water masses and a high sedimentation rate. New aspects of the morphology of Cretaceous belemnites are shown, taxonomic problems discussed, and additional nomenclature perspectives given. The stratigraphic investigation of the cephalopod fauna revealed that the Eibeck section comprises lower Upper Valanginian sediments of the *Saynoceras verrucosum* Zone.

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