Olcostephanus guebhardi as cryptic habitat for an Early Cretaceous coelobite community (Valanginian, Northern Calcareous Alps, Austria)

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Abstract

Upper Valanginian (*Saynoceras verrucosum* Zone) deposits of Upper Austria (Ternberg Nappe, Calcareous Alps) yield large numbers of specimens of *Olcostephanus* (*O.*) *guebhardi* (Kilian) showing unique epifaunal encrustations by placopsilinid foraminifera, bryozoans, and serpulids. The pattern of infestation clearly documents a 100% preference of the adherent taxa for the inner shell surface of the ammonites, whereas the outer surface remained barren. Such a remarkable cavity-dwelling palaeocommunity is described for the first time. Furthermore, the restriction of epifauna to almost a single ammonite species within an overall fauna of more than 13 ammonite taxa proves a strong taphonomic bias. This is interpreted as out-of-habitat mixing of *Olcostephanus* (*O.*) *guebhardi*.

1. Introduction

Epibiosis is one of the few well-preserved biotic interactions in the fossil record dating back to the Early Palaeozoic (Palmer, 1982). Studying the spatial relationships among organisms that lived with each other provides insight not only into the autecology of these organisms but also into their palaeoenvironment and palaeocommunity structure.

A somewhat neglected part of the vast spectrum of epibioses is represented by so-called coelobites, which are defined by Ginsburg & Schroeder (1973) as cavity-dwelling organisms, often found in cryptic habitats. Studies on cryptic habitats in modern environments have focused mainly on coral reefs and reef-associated submarine caves (e.g. Jackson & Winston, 1982; Rasmussen & Brett, 1985; Meesters et al., 1991). Despite the smaller scale and limited spatial resource of the ammonite-shell biochore described herein, several parallels with modern cryptic habitats are obvious. As emphasized by Wunsch & Richter (1998) and Richter & Wunsch (1999), cavities and other cryptic habitats are 'spatially confined habitats' that provide living space for low-light-adapted organisms. Among these, cryptic suspension feeders especially predominate. Such cryptic habitats provide shelter for sessile and encrusting species from predation and physical disturbance (Gischler & Ginsburg, 1996). In modern cryptic habitats, the coelobite's mode of life is mainly developed by sponges, various algae, serpulids, tunicates, bryozoans, and foraminifera.

Coelobites found adhered to their original substrates are relatively scarce in the Austrian Early Cretaceous. During recent decades, however, a wealth of information on Cretaceous cryptic encrusting palaeocommunities in England and Oman has been provided by Wilson (1986a,b) and Wilson & Taylor (2001). Several taxa, such as placopsilinid foraminiferans and the bryozoan *Stomatopora*, turn out to be characteristic

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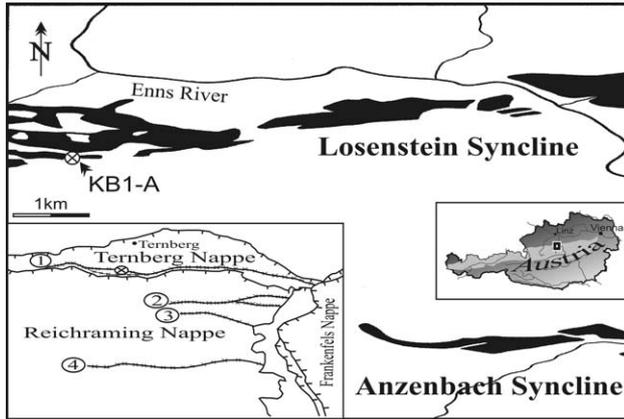*E-mail address:* alexander.lukeneder@univie.ac.at (A. Lukeneder).

Fig. 1. Position of the section investigated, KB1 (KB1-A), along a stream outcrop. Inset map shows the geological setting and geographic location of the study area. Cretaceous sediments are indicated in black. Numbers on geological map: 1, Losenstein Syncline; 2, Schneeberg Syncline; 3, Anzenbach Syncline; 4, Ebenforst Syncline.

constituents of all these palaeocommunities. These taxa are also recorded from the reported occurrence within ammonite shells herein, but the palaeoenvironmental background seems to differ fundamentally. In this case study we document the advantages for palaeoecological interpretations that can be derived from careful examination of sessile epibionts within a mass occurrence of ammonites.

2. Geological setting and dating

Setting. The ammonites with the attached epifauna derive from Valanginian beds exposed along a ravine near Ternberg (ÖK 1:50,000 sheet no. 69 Großraming) (KB1 in Fig. 1). This Upper Austrian Lower Cretaceous section is situated approximately 1 km southwest of the Enns River, in the Ternberg Nappe, which in this region forms the northernmost part of the Northern Calcareous Alps.

The section is positioned within the Losenstein Syncline and represents the basal part of the Early Cretaceous Schrambach Formation, which is overlain in the study area by the mid-Cretaceous Tannheim and Losenstein formations. The fossiliferous levels are located on the left, nearly vertical (dipping 040/85), step-like wall of the gorge, exposed along a length of 10 m and a height of 5 m. The exact position of the beds investigated was determined by GPS as N47°54′32″, E 14°21′10″.

Lithology. The Schrambach Formation at section KB1-A consists of light grey, bioturbated, marly limestones intercalating with dark grey marlstones. The olcostephanids investigated are concentrated in the marlstone layers between the limestone beds (beds 4, 10 and 16) just a few cm to dm above the underlying Steinmühl Formation (Fig. 2). This part of the section is
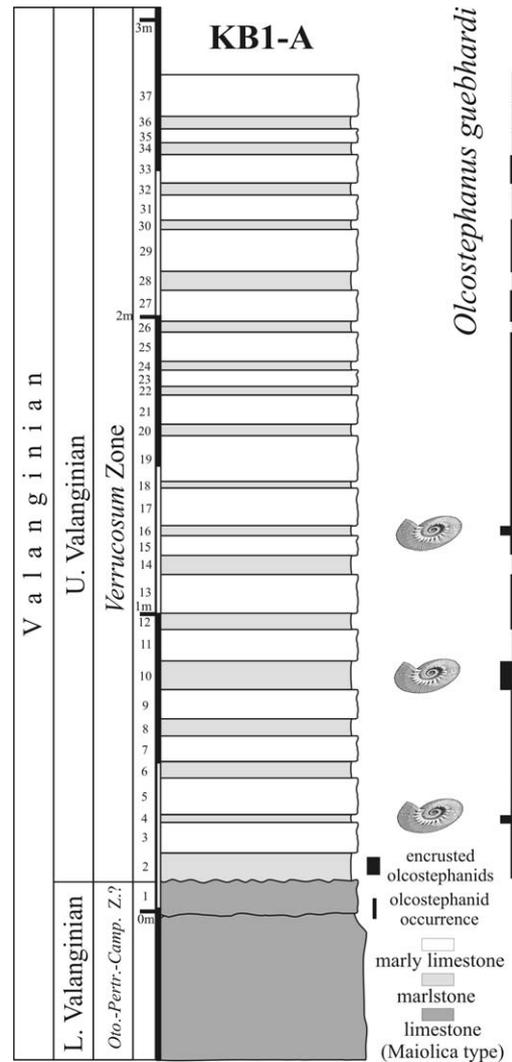

Fig. 2. Stratigraphic log of the *Olcostephanus*-abundance zone within the section studied (KB1-A), showing the position of encrusted olcostephanids. Abbreviations: Oto., *Otopeta*; Pertr., *Pertransiens*; Camp., *Campylotoxus*.

fairly fossiliferous, yielding mainly ammonites, aptychi, belemnites, brachiopods, ophiurids, benthic and planktonic foraminifera, and radiolarians. For detailed descriptions of the area investigated, see Lukeneder (2000, 2001).

Biostratigraphy. The *Olcostephanus*-bearing beds in the Schrambach Formation belong to the *Saynoceras verrucosum* ammonite Zone of the early Late Valanginian (Hoedemaeker & Rawson, 2000; Lukeneder, 2001).

The biostratigraphically significant cephalopods are: *Bochianites neocomiensis* (d'Orbigny), *Neocomites* (*Neocomites*) cf. *neocomiensis* (d'Orbigny), *N.* (*Teschenites*) cf. *neocomiensiformis* (Uhlig), *N.* (*Teschenites*) *teschenensis* (Uhlig), *Neohoploceras* sp., *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian) morphotype *querolensis* Bulot, *Rodighieroites* sp., *Lamellaptychus* cf. *retroflexus* (Trauth), and *L.* cf. *symphysocostatus* (Trauth).

The association indicates the *Karakaschiceras prone-costatum* Subzone and/or the *Neocomites peregrinus* Subzone (according to the results of the Vienna meeting of the Lower Cretaceous Ammonite Working Group of the IUGS; see Hoedemaeker & Rawson 2000).

3. Material and mode of fossil preservation

More than 13 ammonite taxa were recorded from the section KB1-A by Lukeneder (2001) and Lukeneder & Harzhauser (2002). Altogether about 300 ammonoid specimens derive from this locality. Despite this considerable number of species and specimens, it is almost exclusively *Olcostephanus* (*O.*) *guebhardi* that displays infestation by *Placopsilina* and/or other epibionts.

About 200 specimens of *Olcostephanus* (*O.*) *guebhardi* Kilian have been collected from section KB1-A (Fig. 2). Nearly every preservational stage has been observed. Most of the specimens have been crushed by sediment compaction. This effect is much greater within the marly layers than in the more calcareous layers of the limestones. Owing to the large number of specimens, however, even extraordinarily well-preserved individuals (e.g. microconchs with lappets) could be collected.

Fifty-two specimens show encrustation (Appendix A; Inv. NHMW 2003z0004/0001–2003z0004/0052). They were collected from beds 4, 10 and 16. Most of these could be assigned to the agglutinating foraminifera *Placopsilina cenomana* d'Orbigny. Bryozoans and serpulids are also present but subordinate in number. A total of 336 individuals of *Placopsilina cenomana* were counted on the 52 *Olcostephanus* specimens. Additionally, 40 individuals of *Placopsilina* were found on smooth shells of a single *Bochianites* specimen and on four unidentifiable ammonoids. On five of the ammonoids, encrustations by bryozoans and serpulids were also detected (see Appendix A).

4. Systematic palaeontology

The material examined has been deposited in the palaeontological collection of the Natural History Museum, Vienna, Austria (NHMW).

Conventions. The standard dimensions for normally coiled ammonites are given in millimetres. The following abbreviations have been used (text and Appendix): M, macroconch; m, microconch; D, shell diameter; WH, whorl height; U, umbilical width. We follow the classification of the Cretaceous Ammonoidea by Wright et al. (1996).

4.1. The 'host'

Olcostephanus (*O.*) *guebhardi* Kilian 1902
morph. type *querolensis* Bulot 1992 (pl. 1, fig. 1)
Fig. 3

1992 *Olcostephanus* (*Olcostephanus*) *guebhardi* Kilian: Bulot, pp. 151–152, pl. 1, figs 2a–2b (with synonymy).

Description. The shape ranges from discocone to sphaerocone (involute with ovate whorls). The shell is meso- to longidome. The secondary ribbing is fairly dense. The short bullate primary ribs are slightly rursiradiate to rectiradiate. The primaries (strong from beginning) start at the inner umbilical seam and cross the umbilical shoulder, from which they begin to form thick bullae. Twenty-four to 28 bullae give rise to 4–6 secondary ribs, which are slightly prorsiradiate and show no bifurcations. The secondaries diverge in fasciculate bundles to pass uninterrupted across the venter. The microconchs (m, up to 42 mm in diameter) show spatulate lateral lappets at the apertures, whereas the macroconchs (M, up to 102 mm in diameter) show simple collared apertures (peristomes). No suture lines are observable.

Remarks. The specimens are very close to the described morphotype *querolensis* Bulot, 1992. This morphotype from La Querola outcrops (Cocentaina, Alicante province, Spain) was well illustrated by Company (1987) (as *O. densicostatus*, pl. 15, figs. 16–17). It differs markedly from *O.* (*O.*) *guebhardi* s.s. in its larger size and more dense ribbing, formed by 4–6 ribs per bundle as opposed to 3–4 in *guebhardi* s.s. For a detailed discussion of the genus *Olcostephanus* and its species attributes, see Bulot (1990, 1992); further remarks are noted in Lukeneder (2001).

4.2. The coelobites

Placopsilina cenomana d'Orbigny, 1850
Fig. 4

Description. An initially coiled, later rectilinear, multichambered agglutinated test up to 4 mm in length. Test attached along its entire length; attached surface flat, non-attached side convex, chambers arranged in a linear manner and increasing in size. Small initial coil (probably planispiral). Wall composed of calcitic microgranules cemented together.

Remarks. As pointed out by Hodgkinson (1992), the status of *Placopsilina cenomana* d'Orbigny is still in need of revision. Therefore, we are aware that we are using the name in a rather broad sense.

Mode of occurrence. The adherent foraminifera cautiously assigned to *Placopsilina cenomana* are the most abundant encrusters in the fauna. All specimens are found exclusively inside ammonite shells and are virtually restricted to the species *Olcostephanus guebhardi*. They are restricted to the body chambers of the 'host' ammonite. In every single ammonoid specimen the agglutinated epibionts are attached to one side of the
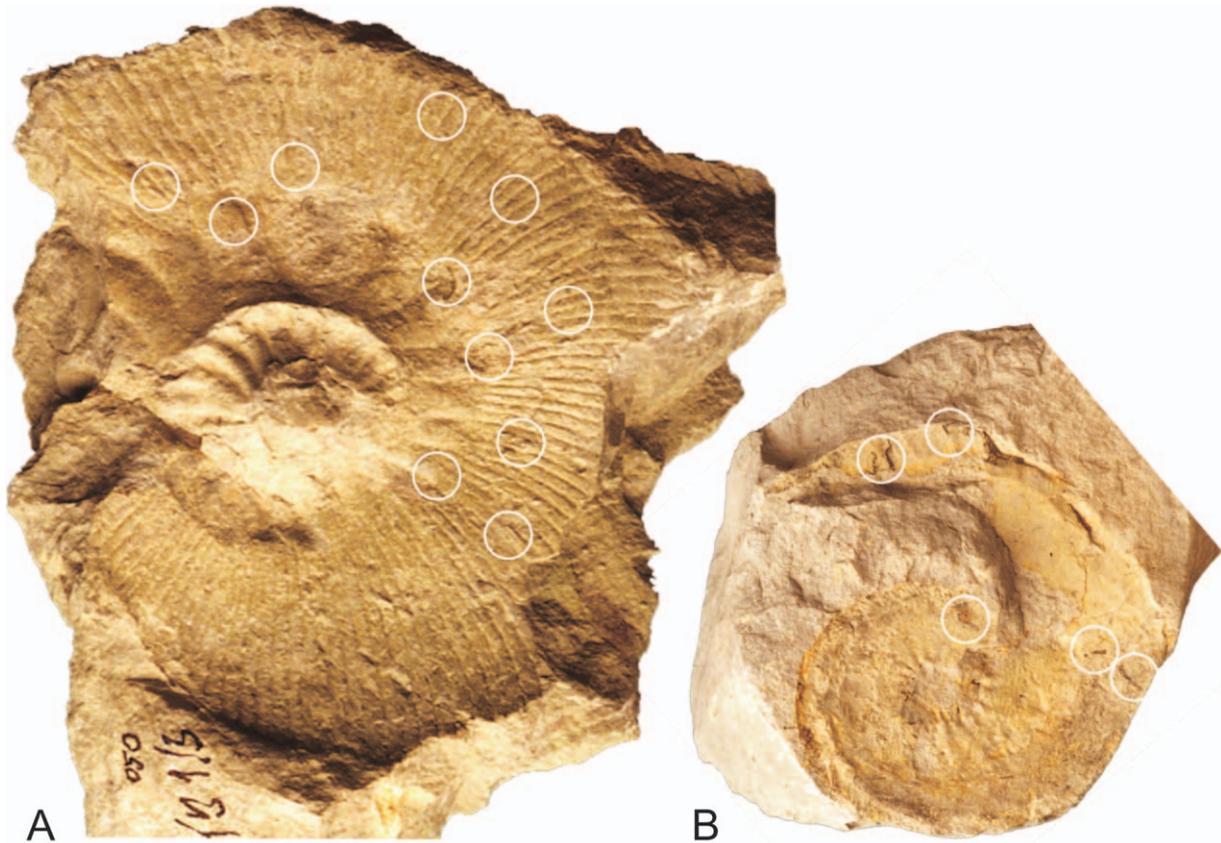
Fig. 3. Encrustation and its position on the ammonites (indicated by circles). A, *Olcostephanus guebhardi*; KB1-A; bed 4; 2003z0004/0001; ×1. B, *Neocomites* sp.; 2003z0004/0053; La Charce; ×1.

body chamber only. Within the body chamber the tests are attached strictly along the inner concavities of the ammonite ribs. Towards the umbilicus and also towards the external side, the arrangement is less strict. The foraminifera are strongly curved, especially in the cavities formed by the nodes close to the umbilicus of *Olcostephanus*, where they fill the depression. The foraminiferans clearly inhabited the empty body chambers of deceased ammonites. Owing to the diagenetic solution of the aragonitic shells of the ammonites, the attached surface of the foraminiferan tests is visible on the steinkerns of *Olcostephanus*. Additionally, *Placopsilina cenomana* was observed on a single *Bochianites* specimen and attached to four unidentifiable ammonoids from KB1-A.

Aside from *Olcostephanus*, hitherto only a single specimen of *Neocomites* sp. from the Valanginian of La Charce in southeast France (Vocontian Trough), collected by one of us (AL) in 2000, displays some similarities in placopsilinid encrustation (Fig. 3B). A slight difference, however, is indicated by the encrustation pattern: the foraminifera are located on the lateral and external side of the ammonite without any recognizable preference.

4.2.1. Serpulids

Scarce tubes of serpulid worms up to 8 mm in length and 0.15 mm in diameter occur attached to the inner surface of *Olcostephanus* shells. Only the relics of the cemented part of the tubes are preserved, which are reminiscent of *Glomerula*. A secure generic identification, however, is difficult owing to the poor preservation.

4.2.2. Stomatopora sp.

Remarks. Colonies of this encrusting cyclostome bryozoan, characterised by a uniserial, ribbon-like arrangement of the zooids, are found rarely on internal moulds of *Olcostephanus*. They are hardly developed and barely exceed 10 mm in length.

In contrast to the foraminifera, the bryozoans do not show a strict preference for settlement and may also be found on the convex intervals between the ribs. As with *Placopsilina*, they seem to have avoided settling on the outer shell of the ammonites. Generally, *Stomatopora* colonized all kinds of surfaces, but zooids survived only on shells where they were protected from overgrowth (McKinney & Jackson, 1989).
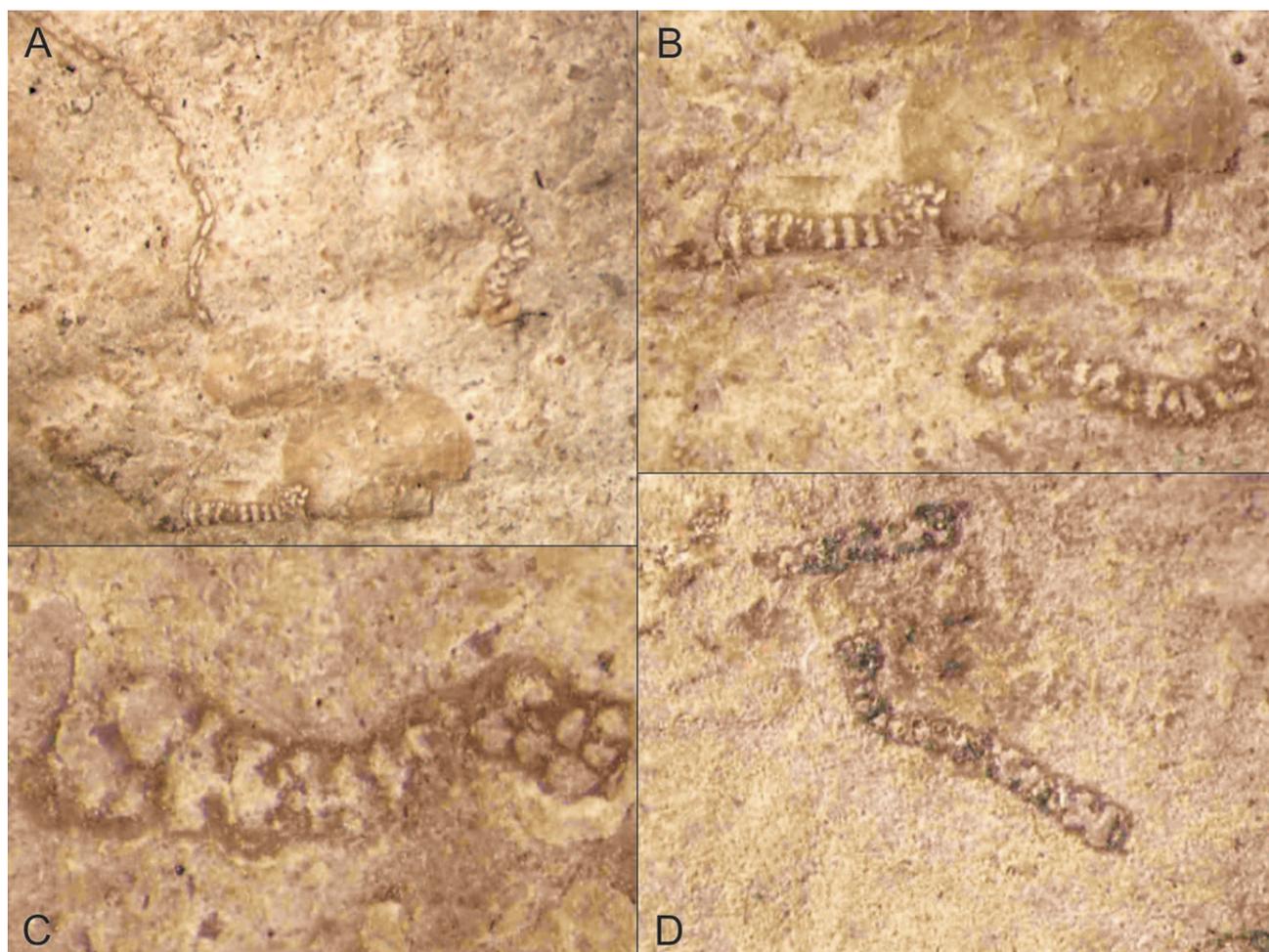
Fig. 4. A, *Placopsilina cenomana* and *Stomatopora* sp. (left upper corner) on *Olcostephanus*, bed 4, 2003z0004/0003; ×10. B, enlargement of A, bed 4, 2003z0004/0003; ×15. C, *Placopsilina cenomana*, bed 4, 2003z0004/0003; ×20. D, *Neocomites* sp., La Charce, 2002z0004/0053; ×1.

5. Discussion

The assemblage of encrusters is characterised by its low diversity and the strong predominance of placopsilinid foraminiferans. The infestation pattern of the encrusting organisms reveals them to be cavity dwellers utilizing solely empty ammonite shells as a cryptic habitat. By contrast, the outer shell surfaces of the ammonites were unsuitable for settling by epifauna, as proved by the total lack of any traces of infestation.

Adherent placopsilinids have been detected frequently in Cretaceous hardground-dwelling palaeocommunities in England (Wilson, 1986a,b), Bohemia (Zitt et al., 1998) and Oman (Wilson & Taylor, 2001). In all of these occurrences the encrusting *Placopsilina* colonised bioclasts and cobbles. Furthermore, *Placopsilina cenomana* was described by Hofker (1965) from Cretaceous shallow-water deposits in the Netherlands, where it was found attached to the walls of presumed crustacean borrows. Although some of these occurrences point to a preference of the foraminifera to settle cryptic habitats such as erosional hollows, borings and burrows, many occurrences are also documented from exposed surfaces (Zitt et al., 1998).

One of the main differences between these occurrences and those described herein is the much lower diversity of encrusters in the ammonite shells. This clearly suggests quite different environments during settling of the epifauna. The English, Bohemian and Omanian coelobite and cobble-dwelling faunas formed in littoral to shallow sublittoral settings largely above the wave-base. In these cases the abandoned bivalve borings and erosional cavities were the most effective protection for encrusters to avoid abrasion.

Physical abrasion by wave-energy can be excluded for the calm setting of the *Olcostephanus*-bed described. The depositional setting of the Austrian section has been interpreted by Lukeneder & Harzhauser (2002) as upper slope or deep shelf. Open marine and rather calm conditions are inferred for the KB1-A section from abundant radiolarians, planktonic foraminifera and echinoid tests with attached spines. Thus, the analysis of
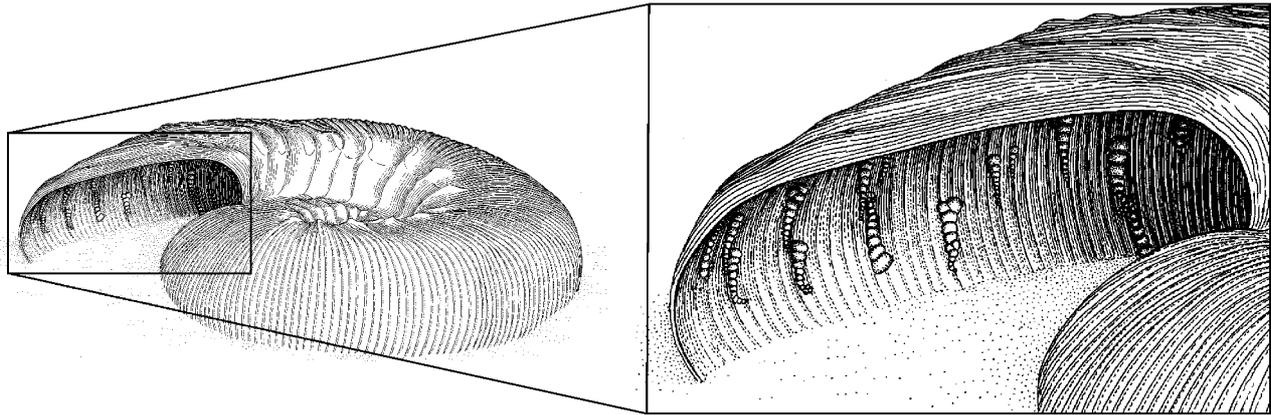
Fig. 5. Position of placopsilinid specimens in the 'sediment free' upper parts of an inhabited body chamber of *Olcostephanus* on the sea-floor.

the microfauna and new data on the cephalopod assemblage supports the interpretation of a soft, level-bottom habitat with an ophiurid-dominated benthic fauna in an offshore environment.

By contrast, *Olcostephanus guebhardi* is suggested to have preferred shallower areas and is interpreted to have been most abundant in water depths of 40–100 m (Bulot, pers. comm., 2002). Thus, the multitude of the olcostephanid specimens seems to have been redeposited from shallower shelf regions into a deeper shelf environment. Only a few well-preserved, non-fragmented specimens lacking any encrustation collected from the limestone layers seem to have been deposited directly in the final depositional environment.

The interpretation of an allochthonous origin of the encrusted and fragmented *Olcostephanus* specimens is strongly supported by the suggested palaeogeographic position of the section studied. The poorly preserved, fragmented specimens within the marly layers seem to have been transported from a nearby, shallow, platform-like area situated to the north, where they had been deposited originally. This is strengthened by the fact that olcostephanids with encrustations on their upper side and specimens with epibionts on their lower side are mixed within single layers. The shells sunk to the sea floor after the death of the cephalopod and became partly filled with sediment on the bottom, near-side of the shell. Thus, epibionts could not settle on these areas of the body chamber (Fig. 5). Only the 'sediment free' upper parts of the shells could be inhabited by epibionts (e.g. *Placopsilina*, bryozoans, serpulids). This mode of infestation indicates that encrustation during post-mortem drift can be excluded from consideration.

The fauna of the KB1-A section is, therefore, interpreted as a mixed assemblage, comprising transported elements from the shallower shelf and autochthonous benthic and parautochthonous pelagic elements from the open sea.

5.1. Why 'only' Olcostephanus?

The enigmatic affinity of the various coelobites to almost a single species is unusual in a moderately diverse fauna of 13 ammonite species. Even if disturbance by browsing and scraping organisms hampered a settling of unprotected surfaces, there is little reason why the shells of ten other ammonite species should not have acted as shelters.

Therefore, we suggest that the *Olcostephanus guebhardi* shells had settled elsewhere prior to their final deposition (Fig. 6). The fragmentary preservation of the five additional ammonoid specimens also points to some transportation, as discussed for the olcostephanids. Indeed, data on modern placopsilinids do not contradict a fairly shallow habitat as the source for the adherent foraminiferans.

Schnitker (1971) found *Placopsilina confusa* at water depths of between 15 and 70 m along the North Carolina shelf, where it was found to account for up to 20% of thanatocoenoses on the central shelf (20–60 m). According to Murray (1991), the species is a common constituent of the Eastern Atlantic *Cibicides lobatulus* Association and occurs in the English Channel from the mid-shelf region at depths of between 48 and 95 m. Thus, the preference of the coelobites for *Olcostephanus* could be explained by transportation of the ammonite shells from shallower environments, whereas most other ammonite taxa found represent the more or less autochthonous fauna, deposited in a habitat that was shunned by placopsilinids.

5.2. Why only inside?

The strict preference of the encrusters to attach only to the inner shell surface of the ammonites indicates that the exposed surface was unsuitable for infestation. The 'out-of-habitat' approach does not exclude the
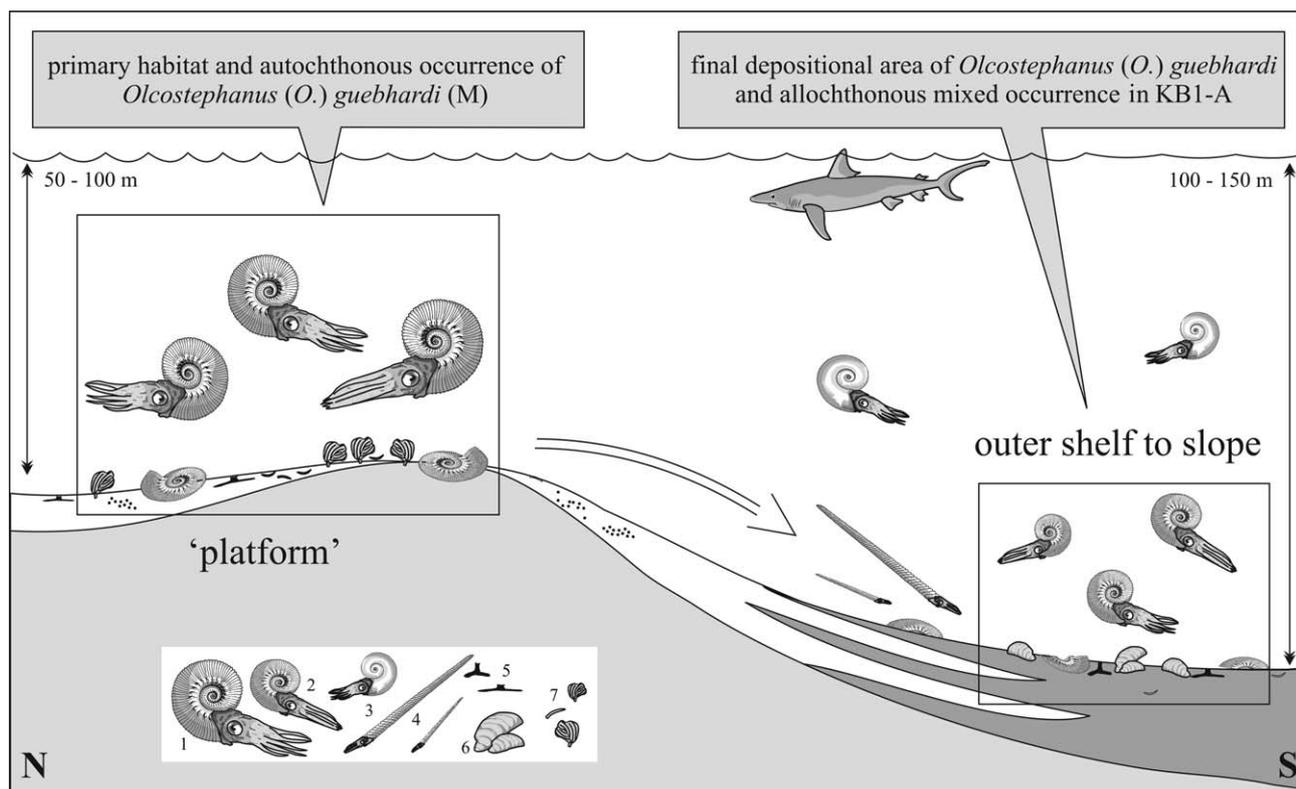
Fig. 6. Temporary sequence of the facies zones during the Late Valanginian related to water depth and bottom currents and indicated positions of living habitat and final depositional environment in the KB1-A section. 1, macroconchs of *Olcostephanus*; 2, microconchs *Olcostephanus*; 3, *Leptotetragonites*; 4, *Bochianites*; 5, trace fossils; 6, inoceramids; 7, pygopids and bivalves.

possibility that the coelobite palaeocommunity was derived from a less calm environment, which might have favoured settling of protected inner shells of ammonites. Abrasion by high-energy conditions, however, seems a rather unlikely trigger for such a settling pattern because of the well-preserved surfaces of even fragmented *Olcostephanus* shells, which must have been broken up during transport.

There is no evidence on which to base a satisfactory solution to this problem. One explanation might be that the surfaces were protected by non-skeletonized encrusters such as algae and sponges. This hypothesis is somewhat contradicted by the observation of Rasmussen & Brett (1985) that non-skeletonized encrusters such as demosponges usually follow solitary 'pioneer' organisms such as serpulids. Another solution might be that browsing organisms negatively affected overgrowth by encrusters.

5.3. Why only macroconchs?

In the KB1-A section, only macroconchs display encrustation by placopsilinids, bryozoans and serpulids; the microconchs are totally barren of any epibiont settling. A somewhat heretical approach to this problem is to suggest that the males (microconchs) of *Olcostepha-*

nus (*O.*) *guebhardi* lived in another habitat, e.g. the open sea, whereas the females (macroconchs) dwelt in the shallower water of platforms. A less sophisticated solution might be that the smaller size of the body chamber of *Olcostephanus* (*O.*) *guebhardi* microconchs became filled with sediment before epibionts had a chance to settle in them.

5.4. Zonations

A zonation of coelobites, as described by Jackson & Winston (1982) within coral reefs, cannot be expected in the spatially very-restricted environment of an *Olcostephanus* shell. Bryozoans and serpulids are only of subordinate importance in these palaeocommunities. The growth patterns of the predominant placopsilinids, however, indicate a slight differentiation within that microhabitat. In the less protected apertural part of the body chamber, the foraminiferans attached preferentially along the concave furrows and pits corresponding to the ribs and nodes of the outer shell surface. This position provided maximum stability and protection. In the deeper parts of the shells, this strict arrangement becomes looser; the placopsilinids, as well as rare bryozoans, also became attached to the convex areas between the ribs, and the foraminiferans formed less linear tests.

None of the numerous specimens of *Olcostephanus* displays any infestation on the outer shell surface. As the outer shell surfaces of the ammonites are devoid of encrustations, the exposed shell was obviously not suited for settlement and growth of hardground-dwelling species. Strong predation by browsing and scraping organisms, such as echinoids and gastropods, on the rather rare 'islands' of secondary hardground may have hampered the settling of epifauna. Therefore, the hardground-dwelling community may have gained a refuge from predation by settling the cryptic habitat of empty ammonite shells.

6. Conclusion

A Cretaceous coelobite palaeocommunity that was associated mainly with the ammonite *Olcostephanus* (*O.*) *guebhardi* is described for the first time. The encrustation in the body chamber furnishes evidence for a post-mortem settlement of the ammonite shells.

Within this palaeocommunity the adherent, agglutinated foraminiferan *Placopsilina cenomana* is the predominant encrusting organism. The fact that it is almost exclusively *Olcostephanus* that is infested by coelobites, whereas nearly all other ammonites are devoid of encrustings, hints at faunal mixing. The *Olcostephanus* shells were deposited in comparatively shallow habitats, where the placopsilinids along with the subordinate bryozoans and serpulids used the empty shells as a cryptic habitat. Later, the shells were transported to their final resting place on the deeper shelf or upper slope. This reconstruction allows a tentative interpretation of the habitat of *Olcostephanus guebhardi*, which, accordingly, might have dwelt in shallow waters instead of offshore, open-marine areas. Furthermore, the restriction of the coelobites to macroconchs of *Olcostephanus* might even point to a temporary habitat separation of the two sexes of this ammonite, leading to the accumulation of macroconchs in a shallower environment of a nearby platform-like structure prior to final deposition on the shelf.

The striking restriction of the epibionts to the inner shell surfaces of macroconchs remains enigmatic. This pattern may reflect encrustations on the outer shell by non-skeletonized, and thus unpreserved, organisms such as sponges, which prevented other taxa from settling, and/or stress as a result of browsing activity.

Appendix A. Measurements of *Olcostephanus* (*O.*) *guebhardi* specimens that display encrustations. Numbers correspond to individuals, except for the bryozoans, which represents a small colony. Additionally, four unidentified ammonoids and a single *Bochianites* from KB1–A and a neocomitid from La Charce are documented. Abbreviations: p., preservation; f., fragment; P., *Placopsilina*; B., bryozoans; S. serpulid.

Specimen	sex	p.	D	WH	U	P.	B.	S.
Olcostephanus								
2003z0004/0001	M	−	80	36	27	24	−	−
2003z0004/0002	M	±	73	31	23	30	−	−
2003z0004/0003	M	+	f.	−	−	39	1	−
2003z0004/0004	M	+	f.	−	−	12	−	1
2003z0004/0005	M	+	90	38	23	5	−	−
2003z0004/0006	M	+	f.	−	−	5	−	−
2003z0004/0007	M	+	f.	−	−	1	−	−
2003z0004/0008	M	+	f.	−	−	1	−	1
2003z0004/0009	M	+	f.	−	−	1	−	−
2003z0004/0010	M	+	f.	−	−	1	−	−
2003z0004/0011	M	+	f.	−	−	5	−	−
2003z0004/0012	M	−	f.	−	−	7	−	−
2003z0004/0013	M	±	f.	−	−	7	−	−
2003z0004/0014	M	−	f.	−	−	2	−	−
2003z0004/0015	M	−	f.	−	−	32	−	−
2003z0004/0016	M	+	f.	−	−	6	−	−
2003z0004/0017	M	+	f.	−	−	5	−	−
2003z0004/0018	M	+	f.	−	−	3	−	−
2003z0004/0019	M	−	f.	−	−	3	−	−
2003z0004/0020	M	+	f.	−	−	1	−	−
2003z0004/0021	M	−	f.	−	−	2	−	−
2003z0004/0022	M	−	f.	−	−	5	−	−
2003z0004/0023	M	+	f.	−	−	1	−	−
2003z0004/0024	M	+	f.	−	−	1	−	−
2003z0004/0025	M	+	f.	−	−	3	−	−
2003z0004/0026	M	+	f.	−	−	1	−	−
2003z0004/0027	M	+	f.	−	−	13	−	−
2003z0004/0028	M	±	f.	−	−	5	−	−
2003z0004/0029	M	−	f.	−	−	1	−	−
2003z0004/0030	M	−	f.	−	−	8	−	−
2003z0004/0031	M	−	f.	−	−	3	−	−
2003z0004/0032	M	−	f.	−	−	2	−	−
2003z0004/0033	M	−	f.	−	−	4	−	−
2003z0004/0034	M	−	f.	−	−	5	−	−
2003z0004/0035	M	+	f.	−	−	1	−	−
2003z0004/0036	M	+	f.	−	−	1	−	−
2003z0004/0037	M	−	f.	−	−	3	−	−
2003z0004/0038	M	−	f.	−	−	2	−	1
2003z0004/0039	M	+	f.	−	−	8	−	−

Specimen	sex	p.	D	WH	U	P.	B.	S.
Olcostephanus								
2003z0004/0040	M	+	f.	–	–	2	–	–
2003z0004/0041	M	±	f.	–	–	4	–	–
2003z0004/0042	M	–	f.	–	–	4	–	–
2003z0004/0043	M	–	f.	–	–	16	–	–
2003z0004/0044	M	–	f.	–	–	8	–	–
2003z0004/0045	M	+	f.	–	–	4	–	–
2003z0004/0046	M	+	f.	–	–	2	–	–
2003z0004/0047	M	+	f.	–	–	7	–	–
2003z0004/0048	M	+	f.	–	–	19	–	–
2003z0004/0049	M	–	f.	–	–	2	–	–
2003z0004/0050	M	–	f.	–	–	2	–	–
2003z0004/0051	M	+	f.	–	–	4	–	–
2003z0004/0052	M	+	f.	–	–	6	–	–
Neocomites								
2003z0004/0053	–	–	60	33	7	6	–	–
Bochianites								
2003z0004/0055	–	+	f.	–	–	1	–	–
unident.								
2003z0004/0054	–	+	f.	–	–	7	–	–
2003z0004/0054	–	–	f.	–	–	1	–	–
2003z0004/0054	–	+	f.	–	–	29	3	–
2003z0004/0054	–	+	f.	–	–	2	–	–

References

Bulot, L.G., 1990. Révision des types et figures de la collection Matheron. 2. *Olcostephanus* (*Olcostephanus*) *perinflatus* (Matheron, 1878) et *Olcostephanus* (*Olcostephanus*)?*mittreanus* (Matheron non d'Orbigny, 1850). Mésogée 5, 3–8.

Bulot, L., 1992. Les Olcostephaninae Valanginiens et Hauteriviens (Ammonitina, Cephalopoda) du Jura Franco-Suisse: systématique et intérêt biostratigraphique. Rev. Paléobiol. 11, 149–166.

Ginsburg, R.N., Schroeder, J.H., 1973. Growth and submarine fossilization of algal cup reefs, Bermuda. Sedimentology 20, 575–614.

Gischler, E., Ginsburg, R.N., 1996. Cavity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs. Bull. Mar. Sci. 58, 570–589.

Hodgkinson, R.L., 1992. *Placopsilina' cenomana* d'Orbigny from France and England and the type species of *Placopsilina* d'Orbigny, 1850 (Foraminiferida). Bulletin of the British Museum (Natural History). Geol. Ser. 48, 1–8.

Hoedemaeker, P.J., Rawson, P.F. Report on the 5th International Workshop of the Lower Cretaceous Cephalopod Team (Vienna, 5 September 2000). Cretaceous Research 21, 857–860.

Hofker, J., 1965. Foraminifera from the Cretaceous of South-Limburg, Netherlands. Arenaceous Foraminifera attached on the walls of the holes in the hard grounds of the lower Md in the quarry Curfs: *Coscinophragma cribrosum* (Reuss); *Placopsilina cenomana* d'Orbigny; *Bdellodina vincentownensis* Hofker. Natuurhist. Maandblad 54, 29–32.

Jackson, J.B.C., Winston, J.E., 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. J. Exper. Mar. Biol. Ecol. 57, 135–147.

Lukeneder, A., 2000. Bericht 1998 über stratigraphische Untersuchungen eines Faziesüberganges zwischen Steinmühl-Formation und Schrambach-Formation auf Blatt 69 Großraming. Jahrb. Geol. Bundes. 142, 393–394.

Lukeneder, A. 2001. Palaeoecological and palaeooceanographical significance of two ammonite mass-occurrences in the Alpine Lower Cretaceous. Unpublished PhD thesis, University of Vienna, Vienna, 316 pp.

Lukeneder, A. & Harzhauser M. 2002. Paleoenvironmental analysis of a new occurrence of *Rhynchoteuthis gibber* (Till, 1907) in the Alpine Lower Cretaceous (Cephalopoda, Valanginian, Northern Calcareous Alps, Upper Austria). In Aspects of Cretaceous stratigraphy and palaeobiogeograph, Schriftenreihe der Erdwissenschaftlichen Komissionen, Proceedings of the 6th International Cretaceous Symposium, 2000 (ed. Wagreich, M.), 15, 185–203, Vienna.

McKinney, F.K. & Jackson, J.B.C. 1989. Bryozoan Evolution. 238 pp. (Unwin Hyman, Winchester).

Meesters, E., Knijn, R., Pennarts, R., et al., 1991. Sub-rubble communities of Curacao and Bonaire coral reefs. Coral Reefs 10, 189–197.

Murray, J. W. 1991. Ecology and Palaeoecology of Benthic Foraminifera. 397 pp. (Longman Scientific & Technical, Essex).

Palmer, T.J., 1982. Cambrian to Cretaceous changes in hardground communities. Lethaia 15, 309–323.

Rasmussen, K., Brett, C., 1985. Taphonomy of Holocene cryptic biotas from St. Croix, Virgin Islands: information loss and preservational biases. Geology 13, 551–553.

Richter, C., Wunsch, M., 1999. Cavity-dwelling suspension feeders in coral reefs-a new link in reef trophodynamics. Mar. Ecol. Prog. Ser. 188, 105–116.

Schnitker, D., 1971. Distribution of foraminifera on the North Carolina continental shelf. Tulane Stud. Geol. and Paleontol. 8, 169–215.

Wilson, M.A., 1986a. Coelobites and spatial refuges in a Lower Cretaceous cobble-dwelling hardground fauna. Palaeontology 29, 691–703.

Wilson, M.A., 1986b. New adherent foraminiferans from the Lower Cretaceous (Aptian) of south-central England. J. Micropalaeontol. 5, 1–8.

Wilson, M.A., Taylor, P.D., 2001. Paleoecology of hard substrate faunas from the Cretaceous Qahlah Formation of the Oman Mountains. Palaeontology 44, 21–41.

Wright, C.W., Calloman, J.H. & Howarth, M.K. 1996. Treatise on invertebrate paleontology, Part L, Mollusca 4, Revised (Cretaceous Ammonoidea), 362 pp. (Geological Society of America, Boulder and University of Kansas Press, Lawrence).

Wunsch, M., Richter, C., 1998. Note-The Cave Cam-an endoscopic underwater videosystem for the exploration of cryptic habitats. Mar. Ecol. Prog. Ser. 169, 277–282.

Zitt, J., Nekvasilová, O., Hradecká, L., et al., 1998. Rocky coast facies of the Unhost-Tursko High (Late Cenomanian–Early Turonian, Bohemian Cretaceous Basin). Acta Musei Nationalis Pragac, Series B. Hist. Nat. 54, 79–116.