

Cephalopod evolution: A new perspective – Implications from two Early Cretaceous ammonoid suborders (Northern Calcareous Alps, Upper Austria)

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Abstract: The status of two Early Cretaceous ammonoid groups from Upper Austria (Northern Calcareous Alps) is examined with respect to the evolution of their shape as well as to their morphology and environmental preference. The Valanginian *Olcostephanus guebhardi* (Verrucosum Zone, 137 mya) shows the evolutionary separation of sex in two different environments and has adapted its shape to the somewhat different environmental conditions. The heteromorph Barremian ammonoid *Karsteniceras ternbergense* (Coronites Zone, 124 mya) is shown to have evolved during times with intermittent oxygen-depleted conditions associated with stable, salinity-stratified water masses. Based on lithological and geochemical analysis combined with investigations of trace fossils, microfossils and macrofossils, an invasion of an opportunistic (r-strategist) *Karsteniceras* biocoenosis during unfavourable conditions is assumed. Both examples are chosen to demonstrate evolutionary trends in the Early Cretaceous which can be observed in the cephalopod group as a whole.

Key words: Evolution, ammonoids, palaeobiology, Northern Calcareous Alps, Early Cretaceous.

Introduction

ABEL (1916) was the first to show a strong correspondence and interaction between the environment and the newly evolving shapes, morphologies and structures of cephalopods. That seminal paper on the palaeobiology of cephalopods underlined that cephalopod evolution is typically closely related with changing environmental conditions in the sea. It is evident today that the different fields treated by cephalopod workers like evolution, biodiversity, ecology and palaeobiology are blending into one another. Evolution moulds the genetic programming of cephalopods and, in doing so, also moulds the potential for adaptation (YOUNG et al. 1998; YACOBUCCI 1999). Adaptation is the major motor for evolution, a situation recognized by ABEL (1916) when he erected the new field known as palaeobiology. Palaeobiology shows how important the animal-environment interaction is for promoting evolution.

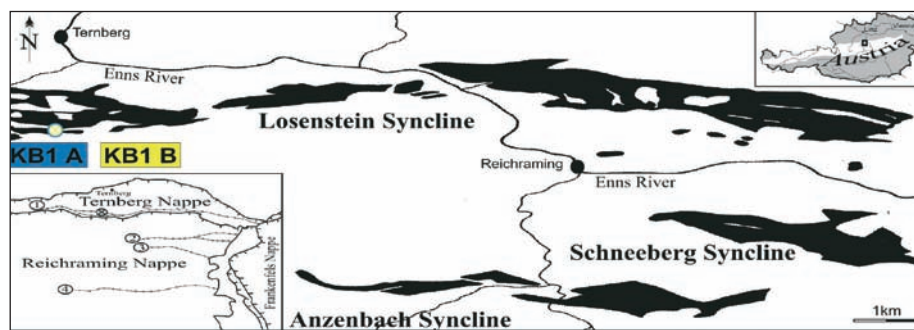
Do ammonoids speciate profusely because internal factors enhance variability and reproductive success? Or do ammonoids respond passively to environmental changes and therefore react after changes of the environment? These questions go beyond the scope of this paper, but the problems associated with these major issues in cephalopod research can be highlighted by diverse papers expressing different points of views. The adoption of new habits interacts with long-lasting mor-

phological change and therefore appears as a new evolutionary trend. Radial or linear evolutions are the main evolutionary directions and pathways, but are only descriptive mirrors for more important processes that more cephalopod workers should recognize (see HOUSE & SENIOR 1980). Spectacular evolutionary radiation and steps forward mostly took place when the environment changed drastically. The present paper examines the problem of ammonoid evolution from a palaeobiological point of view, using two cephalopod case studies from the Early Cretaceous of Upper Austria. These show striking evidence for the evolution of new forms due to environmental changes or due to adaption of habit to the preferred habitat. The adaptive strategy is clearly proven by the change of morphology in the fossil record and the embedding fauna.

Case study 1 shows the Early Cretaceous mass-occurrence (KB1 A = Klausrieglerbach 1, section A, Ternberg Nappe, of the Northern Calcareous Alps - NCA; Upper Austria) with dominating *Olcostephanus* (*Olcostephanus*) *guebhardi* KILIAN morph. *querolensis* BULOT, from the *Saynoceras verrucosum* Zone (Late Valanginian) (LUKENEDER 2004; LUKENEDER & HARZHAUSER 2003).

Case study 2 shows an Early Cretaceous mass-occurrence of ammonoids in the Ternberg Nappe of the NCA (Upper Austria), which is described for the first time. The mass-occurrence (section KB1 B = Klausrieglerbach

Fig. 1: 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. (1) Losenstein Syncline, (2) Schneeberg Syncline, (3) Anzenbach Syncline, (4) Ebenforst Syncline. The position of the KB1 A (blue) and KB1 B (yellow) section is marked by a cross (x).



1, section B) dominated by *Karsteniceras tembergense* LUKENEDER is of Early Barremian age (*Coronite darsi* Zone) (LUKENEDER 2003; LUKENEDER & TANABE 2002).

The main aim of this contribution is to show the significant effect of synecological stress, caused either by environmental changes of abiotic factors such as oxygen content, salinity and depth, or by autecological stress associated with biotic competitors occupying the same environment.

Material and methods

Section KB1 A. The olcostephanid-dominated material originates from section KB1 A in the Losenstein Syncline. Ammonoids represent almost the totality of the macrofauna (98 per cent). The very abundant but generally poorly preserved Late Valanginian assemblages consist of 9 genera. About 200 specimens of *Olcostephanus guebhardi* (BULOT) between 10 and 102 mm in maximum diameter were investigated. Many of the specimens are fragmented. Two groups of varying maximum size and different apertures are distinguishable. The smaller group represents the microconchs (up to 42 mm), whereas the larger specimens are macroconchs (up to 102 mm). Due to the large number of specimens, extraordinarily well-preserved specimens (e.g. lappets of microconchs) could be collected. Their casts (sculpture moulds), with perfectly preserved sculpture, are usually compressed. No suture lines are visible on the steinkerns.

Section KB1 B. About 300 specimens of *Karsteniceras tembergense* LUKENEDER between 5 and 37 mm in diameter were investigated from the KB1 B section. Most of the specimens are observable on one side only; most are entire and show no fragmentation. Juvenile stages and the ventral area are visible in just a few specimens. Two groups showing thick main ribs but different maximum size are distinguishable. The very abundant small heteromorphs are generally poorly preserved. Their casts (sculpture moulds), with perfectly preserved sculpture, are usually pyritized.

Bed-by-bed collecting and a systematic-taxonomic study provide the basic data for statistical analysis of the ammonite faunas from KB1 A and KB1 B. Palaeonto-

logical, palaeoecological and sedimentological investigations, combined with studies of lithofacies in thin sections, peels from polished rock surfaces and geochemical investigations (CaCO_3 , TOC, S), yielded information about the environmental conditions in the area of deposition. In particular, 'parameters' such as oxygen-level (deduced not measured), total organic carbon (TOC) content and sulphide contents help to solve the question of autochthonous versus allochthonous deposition of the ammonite shells. Sulphur analyses confirm the results of many other methods used to test for anoxic or oxic conditions (e.g. TOC, HI). Thus, the sulphur analysis methods developed by KOMA (1978) and others appear to be applicable for the study of anoxic-dysoxic event beds elsewhere.

The total sulphur content (weight per cent) of samples from the KB1 section was analysed using X-ray fluorescence and wet methods. All the chemical analyses were carried out in the Laboratory of the Institute of Forest Ecology at the University of Vienna. Calcium carbonate content was determined using the carbonate bomb technique. Total carbon content was determined using a LECO WR-12 analyser. Total organic carbon (TOC) content was calculated as the difference between total carbon and carbonate carbon, assuming that all carbonate is pure calcite.

Geographical setting

Both occurrences are located within the same log KB1. The section is situated in the Ternberg Nappe in Upper Austria. The exact position is about 7 km west of Losenstein, 1 km south of Kienberg and 500 m southwest of the Klausriegler inn (652 m, ÖK 1:50000, sheet 69 Großbraming, Fig. 1). The stream outcrop fixed by GPS data (global positioning system: N 47°54'32", E 14°21'10") crosses the western part of the east-west striking Losenstein Syncline at a line between the Kreuzmauer (853 m) to the north and the Pfaffenmauer (1218 m) to the south. For detailed descriptions of the investigation area see LUKENEDER (1997, 1998, 1999). This section was the starting point for a lateral analysis of the distribution of the reported ammonite mass-occurrence.

The *Olcostephanus* occurrence (KB1 A) is situated in the uppermost part of the KB1 ravine (800 m). The fossiliferous limestone, comprising the *Olcostephanus*-bearing interval, is located on the left wall of the gorge (dipping 080/70). The *Karsteniceras* occurrence (KB1 B) is situated in the middle of the KB1 ravine (717 m, dipping 080/70).

Geological setting

The Losenstein Syncline is situated in the southernmost part of the Ternberg Nappe of the Northern Calcareous Alps. This is followed directly to the south by the Schneeberg Syncline, the Anzenbach Syncline and then the Ebenforst Syncline of the Reichraming Nappe (Northern Calcareous Alps), all of which are constituted by Lower Cretaceous sediments. At the section investigated, the Early Cretaceous is represented by four formations, from bottom to top the Steinmühl Formation (c. 20 m, Early Berriasian to late Early Valanginian), the Schrambach Formation (c. 160-200 m, Late Valanginian to Late Barremian), and the Tannheim Formation (c. 40 m, Early Aptian to Late Aptian) and the Losenstein Formation (c. 20 m, Albian (Fig. 2).

The investigated ammonite ‘mass-occurrences’, representing the *Olcostephanus* Level and the *Karsteniceras* Level, are situated in the lowermost part (KB1 A, *Olcostephanus*, Late Valanginian) and the upper part (KB1 B, *Karsteniceras*, Early Barremian) of the Schrambach Formation (LUKENEDER 1997, 1998) (Fig. 3).

Case study 1: KB1 A

Facies-related evolution and sexual dimorphic pairs

The mass-occurrence of *Olcostephanus* (*Olcostephanus* *guebhardi* morph. *querolensis* (Fig. 4) over an interval of almost 3 metres (KB1 A) is interpreted to be the result of a combination of a long-term accumulation from the water column (autochthonous parts) during a favourable time interval and redepositional phases (allochthonous parts) of the Late Valanginian (*S. verrucosum* Zone, LUKENEDER 2004). The abundant olcostephanids reflect less offshore influences and nearness of shallow environments. Parts of the *Olcostephanus* mass-occurrence (accumulation beds) show some similarities to a ‘Kondensat-Lagerstätte’. An enrichment by redeposition, currents or turbidites is proposed for only a few marly layers with accumulated fragmented olcostephanids. The olcostephanids were deposited within a phyllocrinid-ophiurid association. Irregular echinoids proved soft bottom conditions of the secondary allochthonous depositional environment (LUKENEDER 2004). The abundance of *Olcostephanus* at the KB1 A section seems to be related to

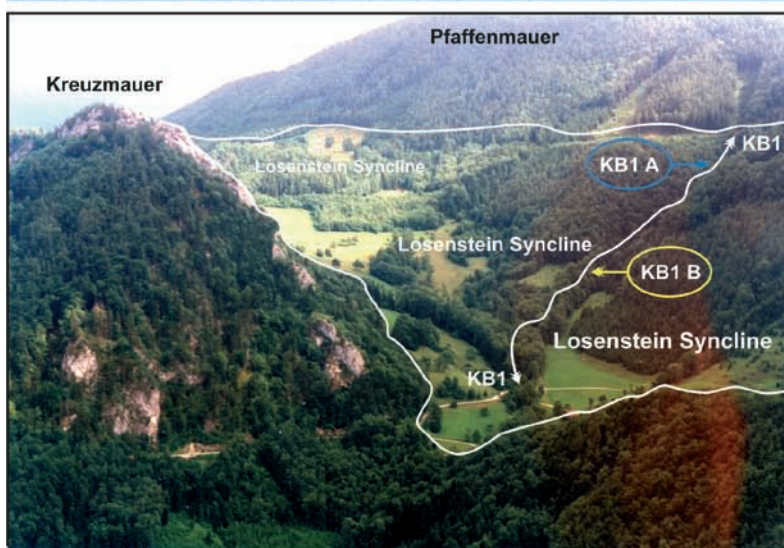


Fig. 2: Position of the outcrop at the KB1 section (centre), situated in the Schrambach Formation, with indicated exposure of the investigated detailed logs KB1 A (top photo) and KB1 B (bottom photo).

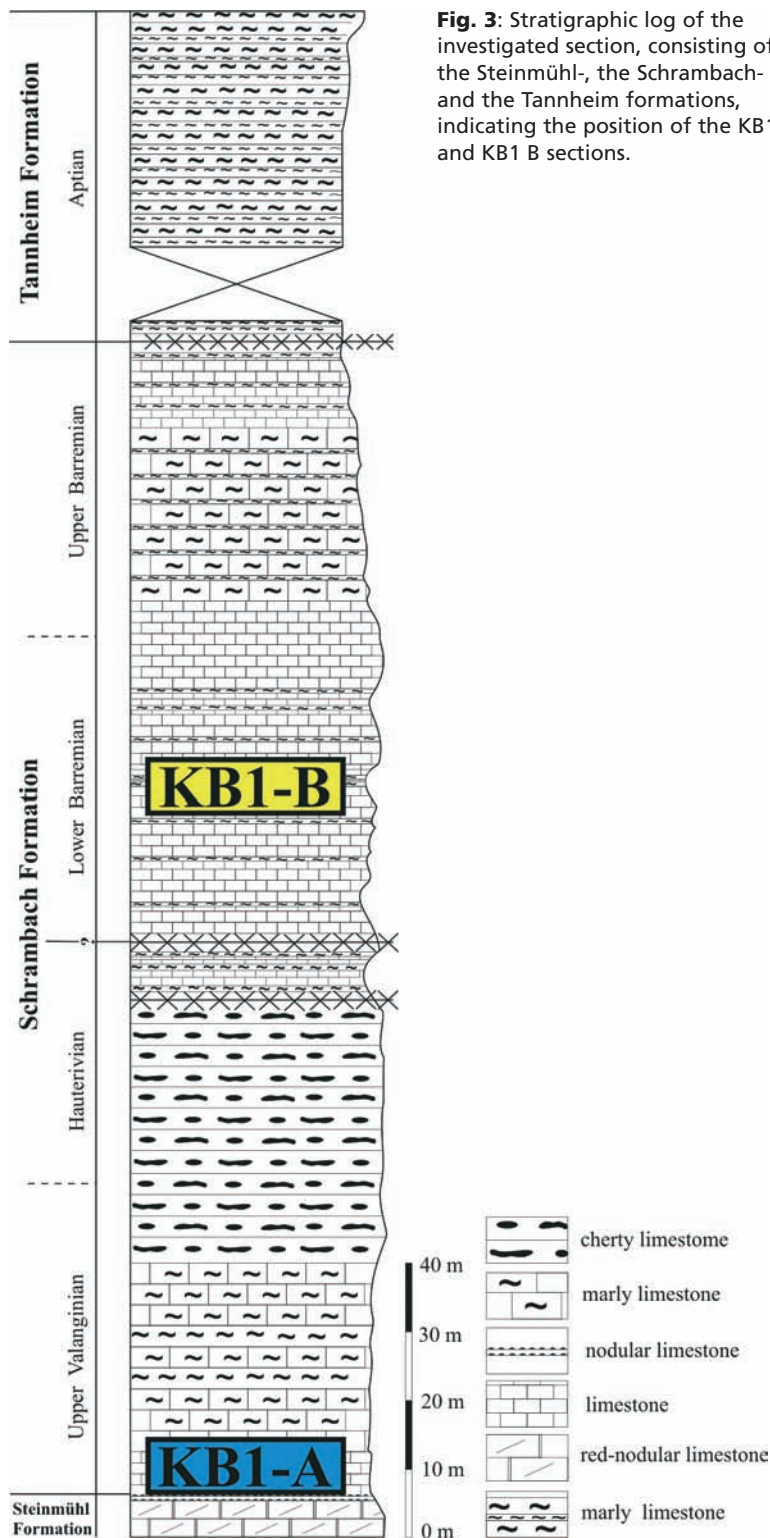


Fig. 3: Stratigraphic log of the investigated section, consisting of the Steinmühl-, the Schrambach- and the Tannheim formations, indicating the position of the KB1 A and KB1 B sections.

REHÁKOVÁ 2004). 'Faunal turnover', 'mass-occurrence', and 'migrations' have always been considered to be controlled by transgressive and regressive cycles in various Early Cretaceous ammonite groups (RAWSON 1981, HOEDEMAEKER 1990).

A huge rise in sea level took place in the Late Valanginian (*Verrucosum* Zone) succession (HOEDEMAEKER 1990) of the lowermost Schrambach Formation (KB1), containing the *Olcostephanus* Level, which is dominated by the migrated genus *Olcostephanus*. The presence of *Olcostephanus* in the Losenstein Syncline and especially at the KB1-A section is apparently related to transgressive facies, presumably associated with sea-level rises.

This was probably within the Late Valanginian transgression phase, which also led to a world-wide (e.g. Argentina, Mexico, Colombia, Spain, France, Italy, Switzerland, N. Germany, Austria, Czech Republic, Romania, Bulgaria, Russia, Tunisia, Algeria, South Africa, Madagascar, Pakistan) spreading or even explosion and occupation of new regions (e.g. Boreal Realm) by the *Olcostephanus* group. This mostly reflects the creation or renewal of sea-ways. Comparing field evidence and published data from the Vocontian Trough (e.g. BULOT 1993) supports the proposal of a facies dependence (e.g. depth, outer-inner shelf) of *Olcostephanus* (*Olcostephanus*) *guebhardi* morph. *querolensis* also for the Austrian KB1-A occurrence (Fig. 5). The descendants are most probably inhabitants of the outer shelf and related areas. It is also suggested that *Olcostephanus* (*Olcostephanus*) *guebhardi* morph. *querolensis* has its acme within the *S. verrucosum* Zone, whereas the ancient *Olcostephanus* (*Olcostephanus*) *guebhardi* s. str. is most abundant in the latest Early Valanginian (*Inostranzewi* Zone) (BULOT 1992; LUKENEDER 2004).

Among ammonoid genera of Tethyan origin, *Olcostephanus* (which apparently originated in the western Mediterranean area during the Early Valanginian) was dispersed over many parts of the world by the mid-Valanginian sea-level rise, when the 'guebhardi chronocline' extended to Mexico, Argentina, the Antarctic Peninsula, South Africa, Madagascar, and into the Boreal Realm (especially the West European Province) (BULOT 1990), although it never penetrated into truly boreal areas (RAWSON 1993).

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Lithological differences observed around the *Olcostephanus*-Level are clearly consequences of an altered palaeoceanography and therefore reflect sea-level fluctuations during the Early Cretaceous, especially within the Berriasian and Valanginian stages (LUKENEDER &

On the northern margin of the Tethys the ammonite assemblages of the outer platform areas in southern Spain and Provence (southern France) are dominated by *Olcostephanus* and by Neocomitidae (COMPANY 1987; BULOT 1993; REBOULET 1996). BULOT (1993) has shown distinct geographic distributions in some species of the *Olcostephanidae* in platform or basin environments.

Studies carried out in south-east France provided good evidence of ammonite distribution linked to facies. Among the Ammonitina, the Olcostephaninae and the Neocomitidae yielded the best examples of faunal assemblage variations between the basin and outer shelf (BULOT 1993; REBOULET 1996; REBOULET & ATROPS 1997). During most of the Valanginian, *Olcostephanus* was split into two different 'lineages': *Olcostephanus* (*Olcostephanus*) *guebhardi* (KILIAN) and related species are restricted to the outer shelf facies, while *Olcostephanus* (*Olcostephanus*) *tenuituberculatus* (BULOT) and its descendants correspond to the basin facies (BULOT 1993).

The splitting into two facies-linked olcostephanid lineages during the Valanginian clearly shows the evolution within the olcostephanids. Starting from the Berriasian uni-facial, deeper-water genus *Spiticeras* (e.g. *S. multiforme* DJANÉLIDZÉ), followed by the still uni-facial olcostephanid ancestor *Olcostephanus* (*O.*) *drumensis* KILIAN in the earliest Valanginian, the key evolutionary point follows in the middle Early Valanginian. The evolutionarily important split into a deep-water lineage and a more shallow-water lineage within the olcostephanids markedly changes the picture of olcostephanid distribution and systematics.

One lineage evolved the shelf forms from Early Valanginian *Olcostephanus guebhardi* s. str., over the Late Valanginian *Olcostephanus guebhardi* morph. type *querolensis* up to Hauterivian species like *Olcostephanus densicostatus* (WEGNER).

The second lineage inhabited the basins and evolved from *Olcostephanus drumensis*, continuing over the Early Valanginian *Olcostephanus stephanophorus* (MATHERON) into the Late Valanginian species of *Olcostephanus tenuituberculatus* (BULOT), *Olcostephanus balestrai* (RODIGHERO) and *Olcostephanus nicklesi* WIEDMANN & DIENI. This lineage ends with the end of the Valanginian.

This differentiation in *Olcostephanus* ended in the Early Hauterivian with evolving species linked to both basin and shelf facies. These are *Olcostephanus densicostatus* and its descendants *Olcostephanus astierianus* (ORBIGNY), *Olcostephanus sayni* KILIAN and *Jeannoticeas jeannoti* (ORBIGNY) for the Early Hauterivian. Other data from various places of the western Tethys confirm this facies-linked distribution of *Olcostephanus* (Northern Caucasus, KVANTALIANI & SAKHAROV 1986; Spain, COMPANY 1987; Switzerland, BULOT 1989, 1992) and therefore underline a general trend for the entire Tethys Realm (BULOT & COMPANY 1990).

Various evidence points to the fact that the evolution of the Early Cretaceous olcostephanids was closely linked to the evolution and concurrent appearance of the neocomitids. Olcostephanids had their widest distri-

bution when neocomitids (e.g. *Neocomites* appears in the Early Valanginian) were rare or absent in the same area, which leads to the well-known "bottle neck" effects in the evolution of the olcostephanid group. The olcostephanids may have inhabited more shallow seas than the neocomitids. In contrast, the neocomitids were able to live in deeper areas. The living realm of both ammonoid groups were therefore shifted against each other. Due to the ecological stress caused by the other ammonoid genus, the different ammonoids evolved into free niches of the shallower or deeper sea. The latter fact most probably explains why we can observe only one genus (*Olcostephanus*) in the shallowest facies, although this situation requires further investigation.

Sexual dimorphism in ammonoid cephalopods is discussed in detail for example by DAVIS et al. (1996) and COOPER (1981). The latter author precisely described sexual dimorphism in *Olcostephanus*. In *Olcostephanus*, as in other ammonoids, the ontogenetic development of the shell is similar in both antidimorphs (sensu DAVIS 1972) until the onset of maturity.

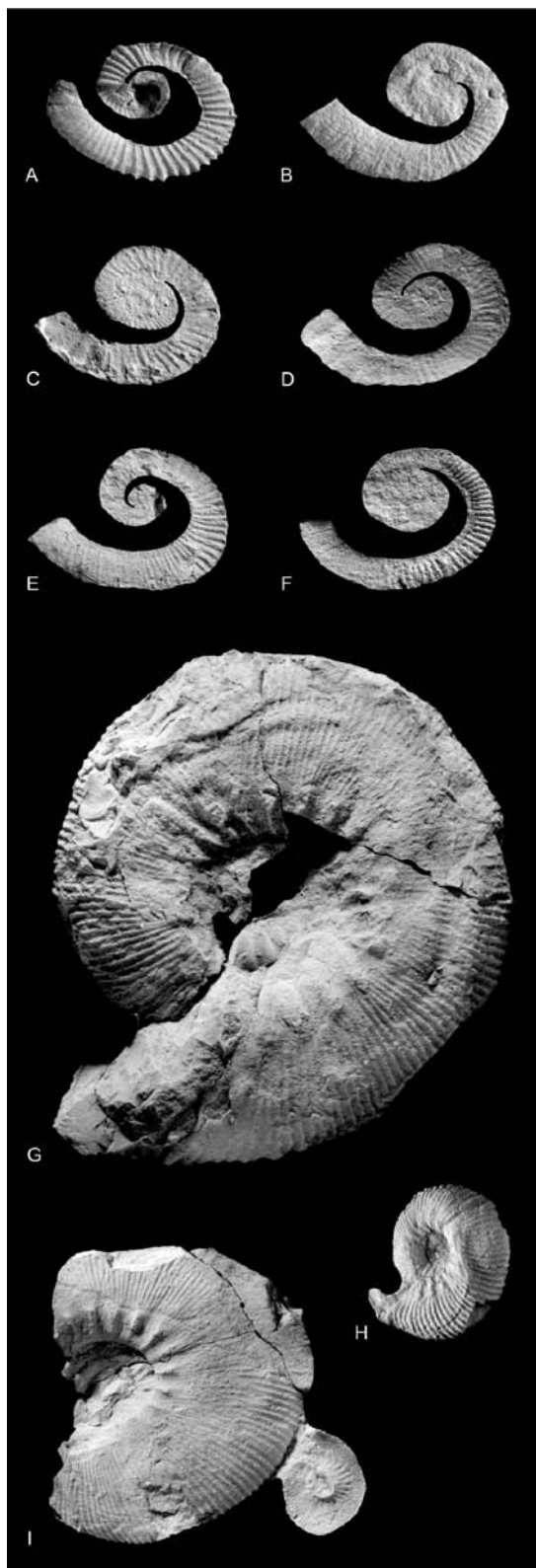
Within the KB1-A olcostephanid fauna, sexual dimorphism is very apparent due to the unusually large size attained by the macroconch forms (M; measured specimens = adult size), some of which exceed 102 mm in diameter. In contrast, the largest confirmed microconch (m) so far recorded from these beds measures only slightly more than 42 mm in diameter, with the average being far less (LUKENEDER 2004). The macroconchs range in size from 82 to 100 mm and the microconchs 20 to 42 mm, indicating a size overlap between antidimorphs of approximately 20 % of the total combined size range of the two antidimorphs. The microconchs show at the aperture a final constriction coupled with lateral lappets, whereas the macroconchs have only a final constriction. In *Olcostephanus guebhardi*, sexual dimorphism is expressed by differences not only in adult shape, size and ornament but also in the form of the apertural margin (Fig. 4).

Case study 2: KB1 B

Oxygen as impulse for evolution in heteromorph r-strategists

About 300 specimens of *Karsteniceras ternbergense* between 5 mm and 37 mm in diameter were investigated. Juveniles, adults, including micro- and macroconchs, could be separated. A sexual dimorphism in *Karsteniceras* can be observed. An enrichment by redeposition through currents or turbidites can be clearly ruled out based on the autochthonous character of the nearly monospecific benthic macrofauna (e.g. *Inoceramus*, *Propeamussium*), the preservation of fragile parts and the extraordinary

Fig. 4: *Karsteniceras ternbergense* specimens from case study 2 (KB1 B): (A) NHMW 2001z0170/0002, x 1; (B) holotype, NHMW 2001z0170/0001, x 1; (C) NHMW 2001z0170/0004, x 1; (D) NHMW 2001z0170/0003, x 1; (E) NHMW 2001z0170/0005, x 1; (F) NHMW 2001z0170/0007, x 1. *Olcostephanus (Olcostephanus) guebhardi* morph. type *querolensis* specimens from case study 1 (KB1 A): (G) macroconch, 2002z0070/0001, x 1; (H) microconch, 2002z0070/0002, x 1, (I) macro- and microconch 2002z0070/0003, x 1.



preservation of in situ aptychi within the body chambers of *Karsteniceras ternbergense* (Fig. 4).

The geochemical results indicate that the assemblage was deposited under conditions of intermittent oxygen-depletion associated with stable water masses. The rhythmicity of laminated black shale layers and

light-grey bioturbated, organic-depleted limestones suggests that the oxic and dysoxic conditions episodically changed. A highly dynamic environment, controlled by short- and long-term fluctuations in oxygen levels, and poor circulation of bottom-water currents within an isolated, basin-like region, led to the accumulation of the *Karsteniceras* Level. The lamination generally indicates a very quiet depositional environment, which was not disturbed by currents (LUKENEDER 2003).

Within the Schrambach Formation, dysaerobic (not anaerobic) conditions prevailed, allowing endobenthic colonization of the incompletely bioturbated sediment by *Chondrites* (accompanied by *Planolites* in some beds). Increasing levels of dissolved oxygen in bottom waters over time are suggested by well-bioturbated, pale grey limestone beds, whereas dysaerobic conditions are expressed through thin, black, laminated limestones ('black shales'). The *Karsteniceras* mass-occurrence is situated in the laminated horizons. The following features are observable: (1) high TOC, (2) high sulphur content, (3) concentrations of pyrite, (4) phosphatic siphuncle structures, (5) indistinct lamination, (6) almost monospecific trace fossil community (e.g. *Chondrites*), (7) fish remains, (8) extremely rare benthos (e.g. inoceramids, 'paper pectens'), (9) rare microfauna, (10) 'mass-mortality' of *Karsteniceras*, very abundant and small in size, (11) nearly 'monospecific' faunal spectrum and (12) in situ aptychi.

It is assumed that, based on the described features from KB1 B and literature data, *Karsteniceras* most probably had an opportunistic (r-strategist) mode of life and was adapted to dysaerobic sea-water. These ancyloceratids most likely inhabited regions reaching from the sea floor to at least a few tens of meters into the overlying water-column, based on the in situ aptychi and the nearly monospecific faunal assemblage of small heteromorphs. Most of the associated other ammonoids (e.g. *Barremites* cf. *difficilis*) show different overgrowth stages (serpulids). These can be explained as a reflection of life in the upper, oxygenated water-column, with subsequent sinking to the sea floor or drifting after death. *Karsteniceras* probably inhabited areas of water stagnation with low dissolved oxygen, showing abundance peaks during times of oxygen depletion, which hindered other invertebrates from colonising such environments. The described autochthonous *Karsteniceras* mass-occurrence features fit well into the scheme of a 'Konservat Lagerstätte' (LUKENEDER 2003).

Interbedding of sediments alternately rich and poor in organic matter can be the result of either differential preservation of organic matter, differential rates of supply of organic matter, different sources of primary production, and/or differential sedimentation rates. Differ-

ent preservation can result if bottom waters at the accumulation site are alternately oxic and dysoxic (or near-anoxic). Cyclic variation in the amount of organic matter accumulating at a continental margin site may be explained by cyclic fluctuations in the thickness and intensity of a midwater oxygen-minimum layer. Both depositional models (basin deoxygenation as well as expansion and establishment of an oxygen-minimum layer) have been proposed to explain the accumulation of organic carbon-rich strata.

Oxygen is a bio-limiting element for metazoans and is among the key factors influencing species diversity and abundance in the marine realm. Reduced concentrations of dissolved oxygen can have disastrous consequences for marine life, reducing diversity and ultimately leading to mass-mortality.

Factors associated with low diversity include high stress and ecological immaturity. Most opportunists (r-strategists) are characterized by small size and a short life span. The latter facts also hint at positive mutations. The small-sized leptoceratids seem to be resistant against oxygen depletion in the sea water. The robust small-sized forms evolved morphologies and evolutionary adaptations which allowed them to inhabit such hostile environments. They became accustomed to such conditions, occurring in masses and becoming geographically widespread (LUKENEDER 2003). The body size of the leptoceratids was therefore reduced to give rise to other features important for living in oxygen-depleted waters, and the opportunistic (r-strategist) mode of life was perfectly adapted to dysaerobic sea-water. This was the sense in which the word “Paläobiologie“ was originally meant by its founder O. ABEL (1916). He noticed almost 100 years ago for the cephalopods in general the same relation shown for the special cases presented herein. The change in body size and morphology in *Karsteniceras* is accompanied causally by the specialisation of the animal during environmental changes.

This phenomenon can be detected through the whole Early Cretaceous. The phylogenetically totally separated Berriasian *Leptoceratoides* (THIEULOY 1966) show the same facies-linked distribution as that of the much younger Barremian *Veveysiceras* descendants. The favoured sediments are clayey, dark to laminated marls with increasing content of organic matter and pyrite.

A typical group of such opportunistic small-sized heteromorph ammonoids is the monophyletic subfamily Leptoceratoidinae THIEULOY. The latter subfamily is assigned to the family Ancyloceratidae GILL. Within the latter, three evolutionary lines are recognized; the herein-described *Karsteniceras tembergense* is a member of one of these lines. These lineages are separated through

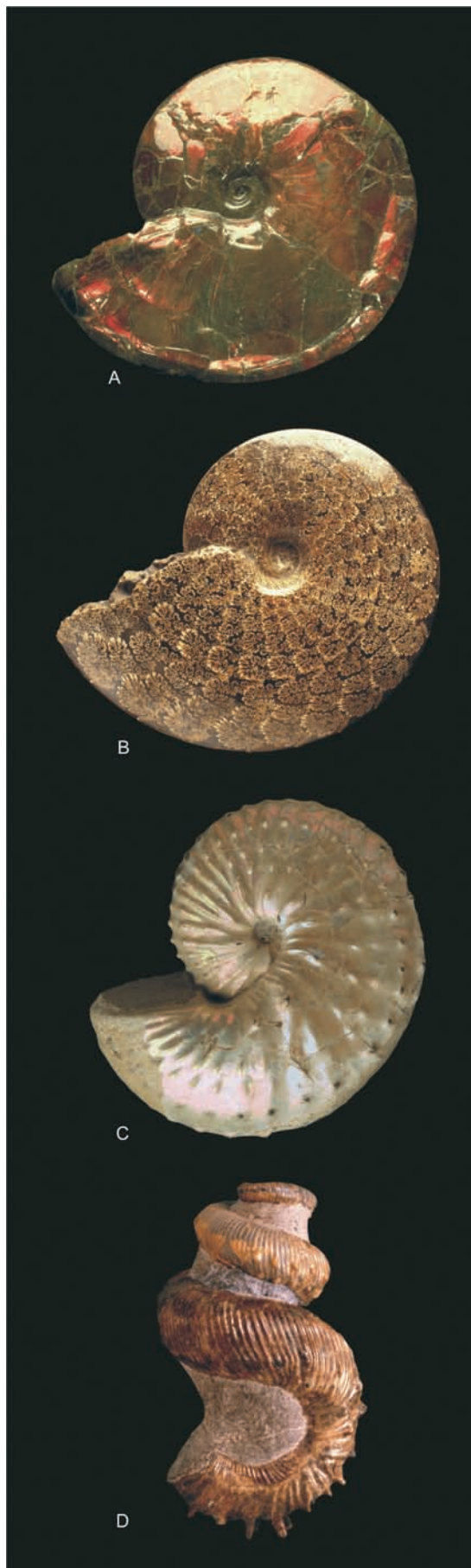
Stages		Zones	Subzones		
BARREMIAN	Upper	<i>P. waagenoides</i>			
		<i>C. sarasini</i>			
		<i>I. giraudi</i>			
		<i>H. feraudianus</i>			
		<i>G. sartousiana</i>	<i>C. provincialis</i>		
	Lower	<i>A. vandenheckii</i>	<i>C. sartousiana</i>		◀ KB1 B
		<i>C. darsi</i>			
		<i>K. compressissima</i>			
		<i>N. pulchella</i>			
		<i>K. nicklesi</i>			
HAUTERIVIAN	Upper	<i>P. angulicostata auctorum</i>	<i>P. catulloi</i>		
			<i>P. angulicostata auct.</i>		
		<i>B. balearis</i>			
		<i>P. ligatus</i>			
	Lower	<i>S. sayni</i>			
		<i>L. nodosoplicatum</i>			
		<i>C. loryi</i>	<i>O. (J.) jeannoti</i>		
		<i>A. radius</i>	<i>C. loryi</i>		
	VALANGINIAN	Upper	<i>T. callidiscus</i>		
			<i>H. trinodosum</i>	<i>C. furcillata</i>	
			<i>O. (O.) nicklesi</i>		
<i>S. verrucosum</i>			<i>V. peregrinus</i>		
Lower			<i>K. pronecostatum</i>		◀ KB1 A
		<i>B. campylotoxus</i>	<i>S. verrucosum</i>		
		<i>T. pertransiens</i>			
	<i>T. otopeta</i>				

Fig. 5: The stratigraphic position of the case studies KB1 A (blue) and KB1 B (yellow) within the Early Cretaceous (Valanginian – Barremian) of the KB1 1 fauna in the Losenstein Syncline. Table after HOEDEMAEKER et al. (2003, with modifications).

different morphologies and sizes. They all originate from the Late Hauterivian genus *Veveysiceras* VAŠÍČEK & WIEDMANN (VAŠÍČEK & WIEDMANN 1994). The three important lineages are: 1) *Karsteniceras* (criocone), 2) *Hamulinites* (ancylocne) and 3) *Eoheteroceras* (ancylocne) together with *Manoloviceras* (slightly curved). All of these arose in the Early Barremian. *Eoheteroceras* most probably was the ancestor of the Late Barremian *Heteroceras*. *Karsteniceras* forms the central stock, with most descendants up into the early Late Barremian.

The phylogenetically and stratigraphically separated group around UHLIG'S (1883) type species *Leptoceras brunneri* belongs to an unrelated earlier group from the Berriasian to Valanginian (THIEULOY 1966). No leptoceratid transitional forms are known from the Hauterivian.

Fig. 6: Cretaceous shape examples for "normal" coiled ammonoids: **(A)** phosphatized *Placenticeras meeki* (BOEHM) with shell preservation, Campanian, Alberta, Canada, NHMW-2006z0260/0001 and **(B)** *Placenticeras placenta* (DEKAY) showing suture line, South Dakota, USA, NHMW-2002z0066/0001. Heteromorph ammonoids are: **(C)** *Discoscaphites gulosus* (MORTON) with shell preservation, Maastrichtian, South Dakota, USA, NHMW-2006z0260/0002, and **(D)** *Didymoceras nebrascense* (MEEK & HAYDEN) with shell preservation, Campanian, South Dakota, USA, NHMW 1980/0023/0000.



The ancestral stock of the second and totally separated later micromorph Barremian group the Leptoceratoidinae (before *Veveysiceras*), is still obscure. No transitional forms can be observed and the ancestor is unknown. *Veveysiceras* occurred first with *Pseudothurmannia* in the latest Hauterivian. The evolutionary centre expands in a longitudinal east-west region from central/southeastern Europe to Japan (VAŠÍČEK & WIEDMANN 1994).

In the field, researchers should therefore look for thin, relatively widespread (but isochronous) horizons dominated by one species of body or trace fossil. The thin, black laminated layers with mass-occurrences of *Karsteniceras* are a case in point. The 'normal-accumulation' of *Karsteniceras* within such black, laminated sediments is interpreted to be the result of special palaeoenvironmental conditions (e.g. poor oxygen, low to no currents). Here, *Karsteniceras*, as a member of an opportunistic (r-strategist) ammonite group, sought the unfavourable, oxygen-limited environmental conditions that other ammonite groups were unable to tolerate.

Taking into account the speculations on ammonoid life-habitats, the demersal forms, feeding on the sea floor, should be very rare or even absent in the anoxic levels (BATT 1993). VAŠÍČEK & WIEDMANN (1994) already noted the possibility that the biotope of the Leptoceratoidinae was close to stagnant, poorly oxygenated environments, where they usually occurred concentrated in 'nests' dominating the faunal spectrum. This has been recently interpreted to reflect opportunistic behaviour of some taxa (Bochianitidae and leptoceratoids) in unfavourable environments (CECCA 1998). Leptoceratoid and spiroceratid ecology, palaeobiology and life-habitats were discussed by UHLIG (1883), NIKOLOV (1960), THIEULOY (1966), DIETL (1973, 1978), RIEBER (1977), VAŠÍČEK (1977), WESTERMANN (1990), VAŠÍČEK & WIEDMANN (1994), CECCA (1997) and AVRAM (1999). Summarizing the various opinions on leptoceratoid ecology, clear differences are evident between those of THIEULOY (1966; autochthonous life assemblage), RIEBER (1977; nektonic above anoxic bottom) and LUKENEDER (2003, nektonic in dysoxic water column), WESTERMANN (1990, 1996; distal shelf), and VAŠÍČEK & WIEDMANN (1994; autochthonous between turbidites).

Concluding remarks

This contribution shows the significant effect that synecological stress – caused either by environmental changes of abiotic factors as oxygen content, salinity and depth or by autecological stress from biotic competitors occupying the same environment – has on the shape and morphology of Cretaceous ammonoids. Examples for different Cretaceous ammonoid shapes are given in Figure 6.

Two contrary examples (*Olcostephanus* and *Karsteniceras*) were selected to show evolutionary trends in ammonoids. The older case study (Valanginian) deals with “normal” coiled *Olcostephanus*. A number of facts show that the evolution of the Early Cretaceous olcostephanids was closely linked to the evolution and concurrent appearance of the neocomitids. Due to the ecological stress generated by the neocomitids, the olcostephanids evolved into free niches of the shallower or deeper sea. The split into two facies-linked olcostephanid lineages during the Valanginian clearly shows the evolution within this group. The olcostephanids reacted to the stress created for them by other antagonists (e.g. neocomitids).

The younger case study (Barremian) deals with the heteromorph ammonoid group around *Karsteniceras*. Reduced concentrations of dissolved oxygen have obvious consequences for marine life, reducing diversity but giving rise to new forms which are resistant to oxygen-depleted waters. Most opportunists (r-strategists) such as *Karsteniceras* are characterized by small size and a short life span. The robust small-sized forms evolved morphologies and evolutionary adaptations which allowed them to inhabit such hostile environments. They became accustomed to such conditions, occurred in masses and were geographically widespread. The change in body size and morphology in *Karsteniceras* is accompanied causally with the specialisation of the animal over the course of environmental changes.

Zusammenfassung

Der Status zweier Unterkreide Ammoniten Gruppen aus Oberösterreich (Nördliche Kalkalpen) wird, mit besonderer Rücksicht auf die Evolution ihrer Form, der Morphologie und deren Umwelt-Präferenzen, aufgezeigt. *Olcostephanus guebhardi* aus dem Valanginium (*Verrucosum* Zone, 137 Mio.) zeigt die evolutionäre Trennung der beiden Geschlechter in zwei unterschiedliche Umweltbereiche und deren Anpassung der Form an die verschiedenen Umweltbedingungen. Es wird gezeigt, dass sich der heteromorphe Ammonit *Karsteniceras tembergense* aus dem Barremium (*Coronites* Zone, 124 Mio.) in Perioden zeitweiligen Sauerstoffmangels gekoppelt mit stabilen, geschichteten Wassermassen, entwickelte. Basierend auf lithologischen und geochemischen Analysen, welche mit Untersuchungen von Spurenfossilien, Mikro- und Makrofossilien gekoppelt wurden, wird eine Invasion einer opportunistischen (r-Strategen) *Karsteniceras* Biozönose während ungünstiger Bedingungen angenommen. Beide Beispiele wurden ausgewählt um evolutionäre Trends in der Unterkreide aufzuzeigen, welche in der gesamten Gruppe der Cephalopoden beobachtet werden können.

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