Studies on Fossil and Recent Cephalopods

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Vorwort

Fossile wie rezente Kopffüßer nehmen seit Menschengedenken ihren Platz in unserer Kultur ein: so etwa der Oktopus und andere Tintenfische als Nahrungsmittel, Ammoniten als Kult- und Sammelobjekte in der Bevölkerung oder als Leitfossilien in der Wissenschaft, oder Kalmare als Modellorganismen in der neurologischen Grundlagenforschung. Natürlich taucht der Krake als Seeungeheuer auch in so manch einer schaurigen Seefahrer-Geschichte auf.

Im landumschlossenen Österreich würde man zunächst meinen, dass sich die Begegnung mit einem Kopffüßer auf die Fischtheke im Supermarkt beschränken würde. Allerdings wird jeder Fossiliensammler im Alpen- oder Voralpenraum eher früher als später auf Schalen der nächsten Verwandten der heutigen Tintenfische stoßen: den ausgestorbenen Ammoniten. Deren enorme Diversität, Häufigkeit und exzellente Erhaltung in den Nördlichen Kalkalpen hat es Wissenschaftlern bereits im frühen 19. Jahrhundert ermöglicht, eine zeitliche Abfolge im Auftreten der unterschiedlichen Arten zu etablieren. Mittels dieser Leitfossilien, die nur in einem bestimmten Abschnitt der Erdgeschichte existierten, ließ sich das relative Alter des sie umgebenden Gesteins auch in anderen Gegenden der Welt verlässlich ermitteln. Die Arbeit dieser frühen Forscher im und um das Salzkammergut herum hat, von Verfeinerungen abgesehen, bis heute Bestand und wird weltweit angewendet.

Des Öfteren hört man jedoch, dass Ammoniten als ‘Schnecken’ bezeichnet werden, was auch nicht sehr weit hergeholt ist, da die Gastropoden die nächsten Verwandten der Cephalopoden sind. Aber nicht in jedem aufgerollten Gehäuse steckt zwangsläufig eine Schnecke. Um die Unterschiede zwischen diesen schalentragenden Tieren deutlich zu machen, und insbesondere um die faszinierende Formen- und Verhaltensvielfalt, die Intelligenz sowie die erfolgreiche Evolution der Kopffüßer darzustellen, haben wir die Ausstellung ‘Tintenfisch und Ammonit’ konzipiert. Bei der Umsetzung waren wir auf die Leihgaben zahlreicher privater Sammler und wissenschaftlicher Institutionen angewiesen: bei allen bedanken wir uns herzlich für die bereitwillige Zusammenarbeit!

Der vorliegende Denisia-Band mit acht Beiträgen vermittelt einen Eindruck der Vielfalt und der Erfolgsgeschichte der Kopffüßer: von paläozoischen Nautiliden über mesozoische Ammoniten bis hin zu känozoischen und rezenten Tintenfischen wird thematisch und zeitlich ein äußerst breites Spektrum abgedeckt. Auch hier gilt unser Dank den Autoren für das erfolgreiche Zustandekommen!

Björn BERNING   Alexander LUKENEDER

Preface

Fossil and Recent cephalopods have always played a part in human culture: be it as readily available food such as the octopus, as ritual objects or collector's items and index fossils such as the ammonites, or as model organisms for fundamental research in neurology such as squids. And, of course, the infamous kraken is an important element in many a ghastful seafaring tale.

One would think that, in the landlocked country of Austria, an encounter with a cephalopod is usually restricted to the fish counter in a well-assorted supermarket. However, any fossil collector in the Alps or Alpine Foreland will, rather sooner than later, come across shells of the closest relatives of modern coleoids, the extinct ammonites. Their enormous diversity, abundance, and excellent preservation in the Northern Limestone Alps has allowed scientists of the early 19th century to establish a temporal sequence of appearance of different species. With the aid of these index fossils, which exist in only a very restricted period of earth's history, it was possible to precisely determine the relative age of the host rock, even in other parts of the world. The work of these early palaeontologists in and around the Salzkammergut region is, besides some minor changes, still valid today and in use worldwide.

Nevertheless, one can occasionally hear ammonites being addressed as 'snails', which is not extremely far-fetched as gastropods are the closest relatives of cephalopods. However, not every coiled shell hosts a snail. In order to detail the differences between these shelled animals and, even more important, to demonstrate the fascinating array of different forms and behaviour, the intelligence as well as the evolutionary success of cephalopods, we have produced the present exhibition on 'Coleoids and Ammonites'. A number of private collectors and research institutions have helped us stack the showcases with exhibits, and we are extremely grateful for their unhesitating support!

The present Denisia-volume comprises eight articles that represent the diversity and evolutionary success of cephalopods quite well: the topics cover a broad thematic and temporal range, from Paleozoic nautiloids via Mesozoic ammonites to Cenozoic and Recent coleoids. We would also like to express our gratitude to all authors for the successful collaboration!

Björn BERNING Alexander LUKENEDER

Nautiloid cephalopods – a review of their use and potential in biostratigraphy

D.H. EVANS, A.H. KING, K. HISTON & M. CICHOWOLSKI

Abstract: In terms of their use as biostratigraphical tools, nautiloid cephalopods are the poor relations of ammonoids. Nevertheless, in certain situations, they may provide useful biostratigraphical data, particularly where other biostratigraphically valuable taxa are not present; or in certain situations demonstrate a resolution as great as, or greater than ammonoids, trilobites, graptolites or conodonts. Nautiloid cephalopods are of especial value in palaeobiogeographical studies, but their use for this purpose may be hampered by the poor understanding of the stratigraphical ranges of individual taxa. The biostratigraphical value of nautiloid cephalopods is demonstrated here through a number of case studies of Ordovician taxa, combined with a review of their biostratigraphical use in Palaeozoic and Mesozoic successions. These both demonstrate the potential of this group and indicate great scope for further research.

Keywords: Nautiloids, cephalopods, biostratigraphy, Palaeozoic, Mesozoic

Introduction

The widespread stratigraphical and geographical occurrence of nautiloid cephalopods, particularly, but not exclusively during the Lower Palaeozoic is documented in many substantial monographic works (e.g. HALL 1847 [Ordovician and Silurian]; BARRANDE 1865-1877 [Ordovician to Devonian]; BLAKE 1882 [Ordovician and Silurian]; FOORD 1897-1903 [Carboniferous]; FOERSTE 1932, 1933 [Ordovician]; FLOWER 1946 [Ordovician]; KUMMEL 1953 [Triassic]; MILLER & YOUNGQUIST 1949 [Permian]; STURGEON et al. 1997 [Carboniferous]; ZHURAVLEVA 1974 [Devonian]). Unlike ammonoids, which have been utilised as stratigraphical tools since the early nineteenth century (e.g. SMITH 1816; OPPEL 1865; BUCKMAN 1898; HOUSE 1978; CALLOMAN et al. 1989; KORN 1996; KLUG 2002; BECKER 2000; PAGE 2009), and despite the great variation in conch morphology that 'nautiloids' display, examples of their use in the development of biostratigraphical schemes are relatively scarce. There are several possible reasons for this:

1. Biostratigraphical markers: There are a range of other rapidly evolving and widely occuring taxa such as graptolites, ammonoids, conodonts and foraminifera that are of proven value, and may occur in great abundance, facilitating correlations using samples extracted from cores.

2. Similarity of morphology: Many of the groups comprising these cephalopods cannot be determined taxonomically without investigation of the internal morphology of the phragmocone due to the similarities of the external features, thus entailing the preparation of polished or thin sections for study, requiring more effort, and possibly resulting in more equivocal data than might be gained from the preparation of (for example) a conodont sample.

3. Taphonomy: Amongst the many forms with orthoconic shells, there is great potential for post-mortem – pre-burial breakage and preferential removal of parts of the phragmocone to bring about the selective preservation of parts of the shell on which the diagnosis of a particular taxon may be based. Taphonomic studies of the post-mortem behaviour and deposition of nautiloid cephalopod shells (REYMENT 1958; BOSTON & MAPES 1991; HEWITT & WESTERMANN 1996; HISTON 2012a) deal with many aspects of their preservation. If there is more than one mode of preservation for a particular taxon, and particularly if these occur at different horizons, there is potential for mistakenly splitting that taxon and failing to recognise its full stratigraphical range. For example, *Polymeres demeterum* MURCHISON from the Floian of England and Wales occurs at several different horizons where the preserved remnants of conch represent either adoral, medial or apical portions, whilst their preservation may take the form of internal and external moulds, lacking original shell, or original shell may have been replaced by pyrite followed by further replacement with limonite. Without careful study of this material and an understanding of its taphonomy,

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it would be easy to determine these as separate taxa and set up spurious ranges for them.

4. Fidelity of palaeogeographical distribution: An important factor in this discussion is whether the nautiloid shell could float after death of the animal as then the original palaeoenvironmental setting and any hypothesis related to facies and assemblages would be prone to error. This has led to the use of nautiloids as reliable biostratigraphic markers and precise indicators of palaeoenvironment being treated with doubt or completely dismissed in holostratigraphical studies. HEWITT & WESTERMANN (1996) concluded that post-mortem buoyancy of nautiloid shells was limited as most individuals lived on or near the seafloor and would sink soon after death rather than float to the surface as the cameral chambers flooded. Therefore, it is considered that nautiloid shells were deposited on the seafloor shortly after the death of the organism and would have remained buoyant for only a short period, if at all (KRÖGER et al. 2009; KLUG et al. 2010; HISTON 2012b).

As a probable consequence, examples of the direct application of nautiloid cephalopods as biostratigraphical tools are relatively few. However, this is principally due to the fact that nautiloid biostratigraphical zones/schemes have never been attempted, not as a result of failure in their application. More often, biostratigraphical studies of these cephalopods are markedly descriptive, and may largely represent an extension of a monographic study (e.g. FREY 1995; STURGEON et al. 1997; KRÖGER 2008a; EVANS 2005, 2011), or the provision of known ranges for a particular region/locale (e.g. WILSON 1961; CATALANI in SLOANE 1987). Rousseau FLOWER was probably one of the main exponents of the use of these cephalopods as biostratigraphical tools, and used his knowledge of their distribution, particularly in North America, to review the biostratigraphy of various successions of Lower, Middle and Upper Ordovician age and also as a tool to better understand the evolution of this group of cephalopods (see FLOWER 1976; 1985 for summaries). In one instance, FLOWER (1964) used his knowledge of the stratigraphical distribution of Canadian (= Lower Ordovician) cephalopods of North America to date some of the larger clasts present in the Levis Conglomerate of Quebec, demonstrating that the boulders originated from carbonates ranging (in modern terminology) from Skullrockian to Blackhillsian in age, and indicating a source or sources further shoreward on the Laurentian platform. In this case the general lack of other macrofossils made these cephalopods a key to the age determination of this material, and although today, age would probably be determined by conodont sampling, the value of these cephalopods in assisting age determination in situations where other macrofossils are relatively rare, as in the Durness Group of Northwest Scotland (EVANS 2011) should not be underestimated.

The study of the distribution of nautiloid cephalopods for palaeobiogeography and as tools for palaeogeographical reconstruction was strongly proposed by CRICK in the 1980's and 1990's (CRICK 1980, 1988, 1990, 1993). He put forward valid arguments supported by a sound database of systematic works to support his hypotheses that these faunas are particularly sensitive to distance or water depth separating landmasses and to fluctuations in sea level. As CRICK pointed out faunas should be described using precise systematic criteria within a strictly controlled biostratigraphic framework in order to fully exploit their potential. When CRICK published his major contributions this was not always the case and many systematic studies were lacking a precise stratigraphic context even at series level, many taxa being referred to as "Upper Ordovician", "lower Silurian" etc. These seminal works by CRICK gave impetus to a broad array of studies over the last twenty years by other authors (e.g. CICHOWOLSKI, EVANS, FREY, HERWIG & POSENATO, HISTON, HOLLAND, KING, KLUG, KRÖGER, MAPES, and NIKO among others: see reference list for details) on these faunas from a variety of geographic locations ranging stratigraphically from the Ordovican to the Triassic that have shown without doubt that nautiloid cephalopods are indeed reliable palaeobiogeographical indicators. Nautiloid studies are now much more accurate in this respect when based on newly collected material, however, material being redescribed from historical collections is still a major problem and as CRICK suggested, is often only of use from a taxonomic point of view.

More recent studies of nautiloid cephalopods may recognise the difficulties that can arise when attempting to use these organisms as biostratigraphical tools and make use of new collections sampled within a well-constrained biostratigraphical frame-work. Studies of the Silurian cephalopods from Europe in particular (e.g. HISTON 2012a; HISTON et al. 2010; MANDA et al. 2009) make use of such a well-constrained biostratigraphical frame work to accurately constrain the range of taxa occurring within the succession, and contributes, in combination with previous studies of other European faunas (see sections below for references) to their use in biostratigraphical correlation as well as a palaeobiogeographical tool within the framework of Northern Gondwana. Such an approach, which recognises that the stratigraphical distribution of these cephalopods should be assessed within a background of other biostratigraphical constraints are more likely to yield useful results in terms of developing their biostratigraphical value.

Examples from recent studies

There are a number of situations where the real or potential biostratigraphical value of these cephalopods may be of significance. Where other biostratigraphically critical fossil biota may be relatively rare, as is the situation along parts of the Laurentian margin during the Early Ordovician (above), areas of the North Gondwana margin where Silurian cephalopod limestones dominate, or in parts of the Early Jurassic successions of the North Somerset coast (United Kingdom) described further below. Where these cephalopods are particularly abundant, as in parts of the Ordovician successions of Scandinavia and South China, some groups, such as the lituitids (see below), underwent a rapid evolution, and may be distinguished as a sequence of distinct taxa that in some cases can be recognised on both palaeoplates, and may potentially be used as correlative tools. Studies by Manda (2009) of the phragmocerids from the classic Silurian deposits of the Prague Basin also demonstrate this aspect. Use of Silurian nautiloid assemblages by Gnoli (1990) and Manda & Kriz (2006) highlight the potential for correlation. Significant, and/or relatively rapid evolutionary events during the history of these cephalopods may also have some degree of biostratigraphical value, and examples from the early history of the Orthoceratoidea and the Eothinoceratidae are described here. Finally, where the stratigraphical distribution of cephalopods are well constrained, whilst they may not provide the primary evidence on which to found a biostratigraphical scheme, may provide a significant contribution to more comprehensive, holostratigraphical schemes.

The examples provided below have a strong Ordovician and lower Palaeozoic bias, reflecting the research interests of the authors. As such, they provide an indication of the potential for the use of nautiloid cephalopods as biostratigraphical tools, and indicate, together with the Mesozoic examples that these cephalopods can be used in a biostratigraphical context.

Ordovician

1. Orthoceratoidea. Research carried out during the past decade has pushed back the origins of the Class Orthoceratoidea well into the late Tremadocian (Kröger 2008; Kröger & Evans 2011) whilst indicating that diversification of these cephalopods was already taking place in the Tremadocian (Kröger & Evans 2011) and increased in the early Floian (Evans 2005, 2011) as demonstrated by the extended ranges of several Laurentian taxa (Evans 2011, and Fig. 1 herein).

The proposed revision of the position of the Stairsian-Tulean boundary to approximately coincide with the Tremadoc-Floian boundary based on the stratigraphical and palaeogeographical distribution of pelagic trilobites (Adrain 2011) indicates that the delay between the appearance of the Orthoceratoidea in high latitude sites on the west Gondwana margin and at low latitudes (NW Scotland, Newfoundland, SW United States) is significantly less than previously thought. Such a rapid dispersion (if that is what we are observing) of this group of cephalopods would appear to be in accord with a move to a more pelagic habitat (Kröger et al. 2009) and would suggest that the adaptations noted by Kröger (2005); particularly the appearance of a small subspherical protoconch that may have facilitated the rapid dispersal of large numbers of offspring, took place very early in the history of the group and is likely to be present in all the taxa referred to in Fig. 1, despite the lack of any evidence of this morphology in most of these taxa as a consequence of the rarity of preservation of the apical portion of the phragmocone.

At present, with the exception of *Slemmestadoceras attavus* (Broegger), the earliest known members of the Orthoceratoidea are represented by taxa possessing marginal siphuncles. These may be assigned to *Bactroceras* Holm, or closely related genera, all of which so far have shown no evidence of the presence of cameral deposits, and only *Thoraloceras bactroceratoides* Kröger & Evans possesses endosiphuncular deposits that may be interpreted as a conical lining that is thicker at the septal necks than along the rest of the siphonal segment. Given that this taxon is known only from very fragmentary material and it is not known whether cameral deposits might have been present, some doubt will remain regarding its assignment to the Troedsonellidae (Dissidocerida).

Uncertainty regarding an appropriate assignment for *Thoraloceras*, together with the presence of *Bactroceras* in the same assemblage, combined with a possible *Cochlioceras* that is marginally younger means that it is not possible to resolve the relationships between these taxa without additional data. A cladistic analysis (Kröger 2008b) generated over one hundred similarly parsimonious trees, although it should be noted that characters including the presence/absence and nature of endosiphuncular and cameral deposits were not included in the analysis. Comparison of the two trees figured by Kröger (2008b, fig. 3) illustrates the problem. Nevertheless, if this group of taxa achieved their wide distribution through (at least in part) the innovation of the small spherical protoconch, then this could provide the character that unites the Orthoceratoidea. This implies that the late Tremadocian and the Floian was a period of rapid radiation for the Orthoceratoidea, much of the documentation of which remains to be discovered.

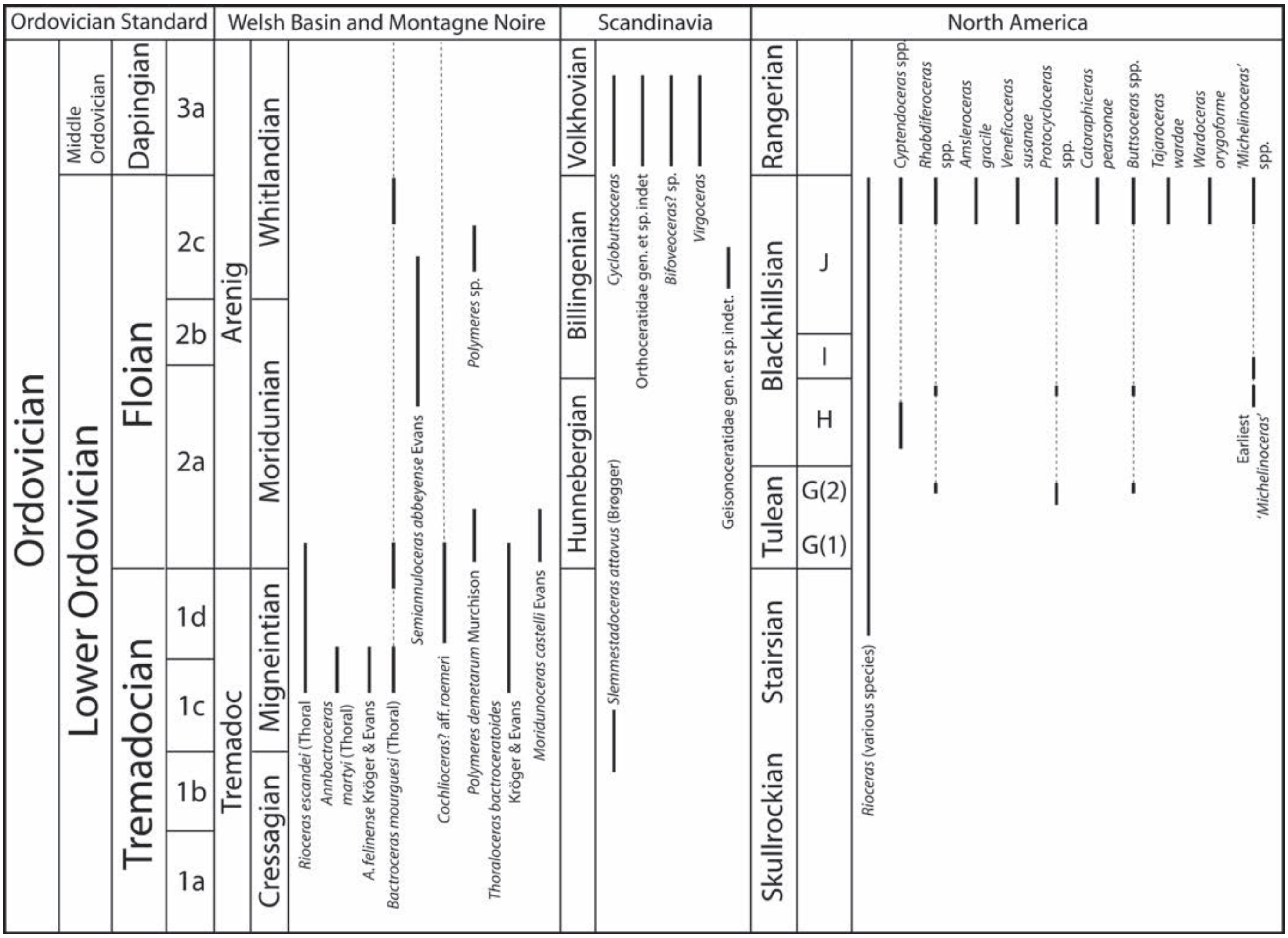

Fig. 1: Stratigraphical occurrences of members of the Orthoceratoidea in the areas forming the margins of the Iapetus Ocean during the Early Ordovician.

2. Eothinoceratidae and Bathmoceratidae. Although the families Eothinoceratidae and Bathmoceratidae achieved a distribution across several palaeocontinents during the Floian and Darriwilian, the oldest member of the Eothinoceratidae known is considered to belong to *Saloceras sericeum* (SALTER), represented by *S.* cf. *sericeum* from the Floresta Formation of the Cordillera Oriental of northwest Argentina (CICHOWOLSKI & VACCARI 2011), and by the lost type material of *Cyrtoceras praecox* SALTER, here considered likely to belong to *S. sericeum* (see discussion in EVANS 2005, p. 67) that originated from the Dol-cyn-afon Formation (*tennelus* graptolite biozone) of North Wales. As the material described by CICHOWOLSKI & VACCARI (2011) came from the *deltifer* conodont biozone, these two records are of broadly the same age, and appear to mark the first appearance of cephalopods in high latitudinal Gondwana.

Whilst *S. sericeum* appears to range up into the early Floian in the Welsh Basin, it is not known with certainty beyond this area. The genus occurs at various locations around Gondwana (EVANS 2007; CICHOWOLSKI & VACCARI 2011; KRÖGER & EVANS 2011) and certainly underwent diversification as indicated by the assemblages from the Montagne Noire (KRÖGER & EVANS 2011). *Proterocameroceras contrarium* TEICHERT & GLENISTER from the Emanuel Limestone of northwest Australia may belong to *Saloceras* (EVANS 2005, p. 11) or represent a new genus of eothinoceratid. *Saloceras* ranges into the mid and late Floian in the Welsh Basin (EVANS 2005) and the Central Andean Basin (CICHOWOLSKI unpublished data).

The earliest records of *Eothinoceras* are from the latest Tremadoc and earliest Floian of low latitude Gondwana (Western Australia [TEICHERT & GLENISTER 1954]) and Laurentia (ULRICH et al. 1944; KRÖGER & LANDING 2008). The occurrence of the genus in the Rochdale Formation of New York State suggests that it may be slightly older than *Protothinoceras* CHEN & TEICHERT from the early Floian Liangchiashan Formation of Hebei Province, North China and regarded as the ancestor of *Eothinoceras* by CHEN & TEICHERT (1987, text-

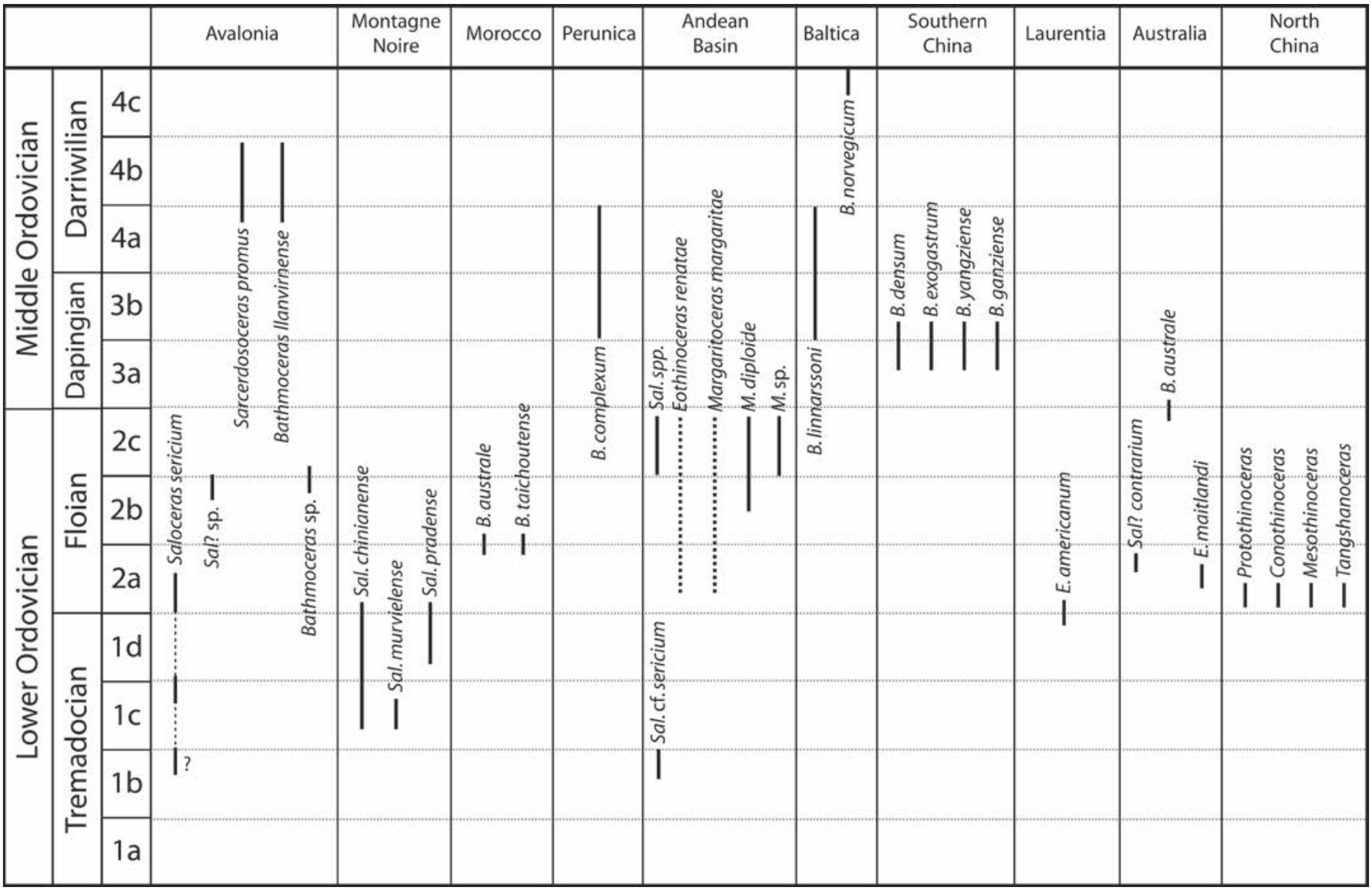

Fig. 2: Worldwide stratigraphical distribution of members of the Eothinoceratidae and Bathmoceratidae during the Early and Middle Ordovician.

fig. 3). Nevertheless, the fauna of the Liangchiashan Formation clearly records what may have been a short-lived proliferation of genera that could have arisen from *Eothinoceras* and probably gave rise to the Cyrtocerinidae through *Tangshanoceras* Chen (Chen & Teichert 1987). The appearance of *Eothinoceras* at distant locations during the latest Tremadoc and early Floian is difficult to explain unless it is accounted for by a longer history of the genus or a capacity for rapid dispersal. *Eothinoceras renatae* Cecioni & Flower from the Floian of Bolivia, and *E. marchaense* Balashov from the Floian of Siberia provide further evidence of this wide, if sporadic, distribution of this genus during the Floian.

The occurrence of *Eothinoceras* and *Saloceras? contrarium* (Teichert & Glenister) in the Canning Basin of Western Australia, combined with the occurrence of *Bathmoceras australe* (Teichert) from the late Floian-early Dapinginian Horn Valley Siltstone (Cooper 1981, fig. 5), as well as further occurrences of the latter species and *B. taichoutense* Kröger & Lefebvre, from horizons regarded as of early to mid-Floian age in Morocco (Kröger & Lefebvre 2012) make for difficulty in identifying the ancestor of *Bathmoceras*. Nevertheless, when all records are considered, with the exception of South America, *Bathmoceras* is present in western Gondwana from the mid-Floian to the Darriwilian and is also present in the Southern China and the Baltic during the Dapinginian and Darriwilian.

Margaritoceras Cecioni & Flower from the Floian of Bolivia and *Sarcerdosoceras* Evans from the Darriwilian of the Welsh Basin are similar, although the latter differs in its lower rate of conch expansion, narrower siphuncle, and compressed ovoid cross-section (Evans 2005). Although they are likely to be closely related, *Margaritoceras* is at present known only from the Central Andean Basin of Bolivia and northwest Argentina, where *M. diploide* is now known to be present in the mid Floian possibly late Floian (Cichowolski unpublished data) whilst a further species of *Margaritoceras* is known from the late Floian (Cichowolski unpublished data). Additional, undescribed taxa are known from the mid-Floian of the Central Andean Basin (Cichowolski unpublished data). As it stands, the evidence from South America suggests that the Eothinoceratidae underwent a radiation at least during the Floian that appears to be restricted to South America, although taxa such as *Sarcerdosoceras* may suggest that some of these lineages later extended into Avalonia.

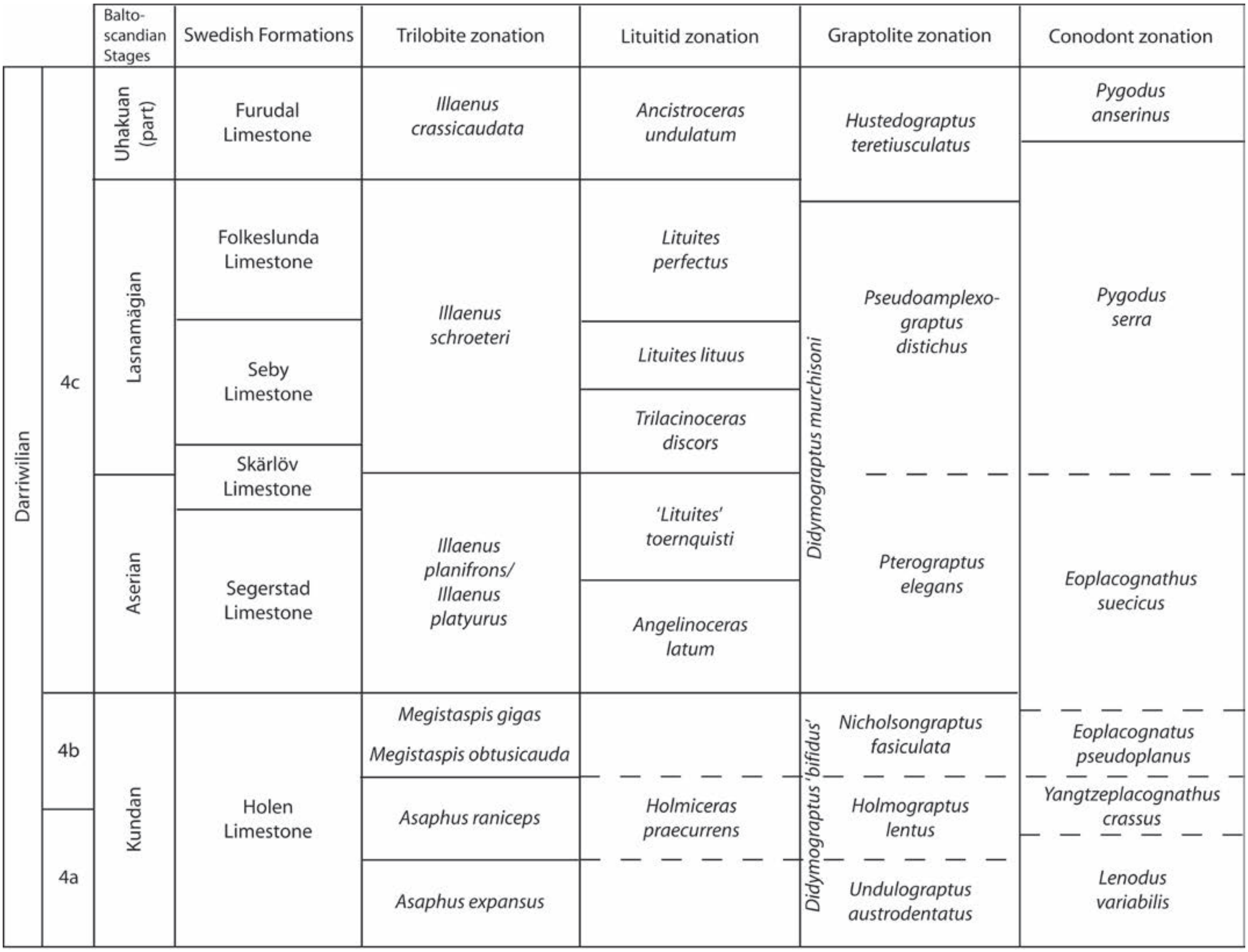

Fig. 3: Stratigraphical distribution of lituitid species in Baltica during the Darriwilian, demonstrating the high resolution provided by these taxa in comparison with trilobites, graptolites and conodonts.

The Eothinoceratidae and Bathmoceratidae were widely distributed around Gondwana during the Early and Middle Ordovician, and where the range of a species is known, may resolve to a stage or even a time-slice (Fig. 2). As some inshore assemblages of high latitude Gondwana (e.g. parts of the early Floian, Bolahaul Member of the Ogof Hên Formation of Wales) may be dominated by molluscs, whilst graptolites and trilobites are relatively rare (e.g. Fang & Cope 2004), these cephalopods may have the potential to constrain ages in some cases.

3. Lituitida. Lituitid nautiloids are common and distinctive components of Middle Ordovician cephalopod faunas in the 'Orthoceratite Limestone' facies of Baltoscandia (especially Sweden) and coeval carbonate sequences, such as the Dawan Formation in China. They are virtually cosmopolitan in occurrence, and are known from the USA and Newfoundland (Flower 1975), Wales (Evans 2005, and in prep.), China (e.g. Yu 1930; Lai 1982; Lai 1986; Qi 1980), Korea (Yun 1999, 2002), Estonia (Balashov 1953), Norway (Sweet 1958), Sweden (Angelin & Lindström 1880; Holm 1891; King 1999) and the 'Diluvium-Geschiebe' of northern Poland (Dzik 1984) and Germany (Boll 1857; Noetling 1884; Remelé 1880, 1881). A substantial number of lituitid genera have been described since the 19th century (e.g. Hyatt 1894; Teichert et al. 1964) and the taxa are firmly established within cephalopod literature.

The Swedish lituitid fauna extends mainly from the early Kundan to Uhakuan stages. This general succession of taxa closely corresponds with lituitid faunas described elsewhere, especially China (Chen & Liu 1976). In the Swedish 'Orthoceratite Limestone' sequence, biostratigraphical data from the latest Volkhovian and earliest Kundan stages of Öland and Östergötland indicate that the weakly cyrtoconic Sinoceratidae occur below the coiled Lituitidae. The former are represented by

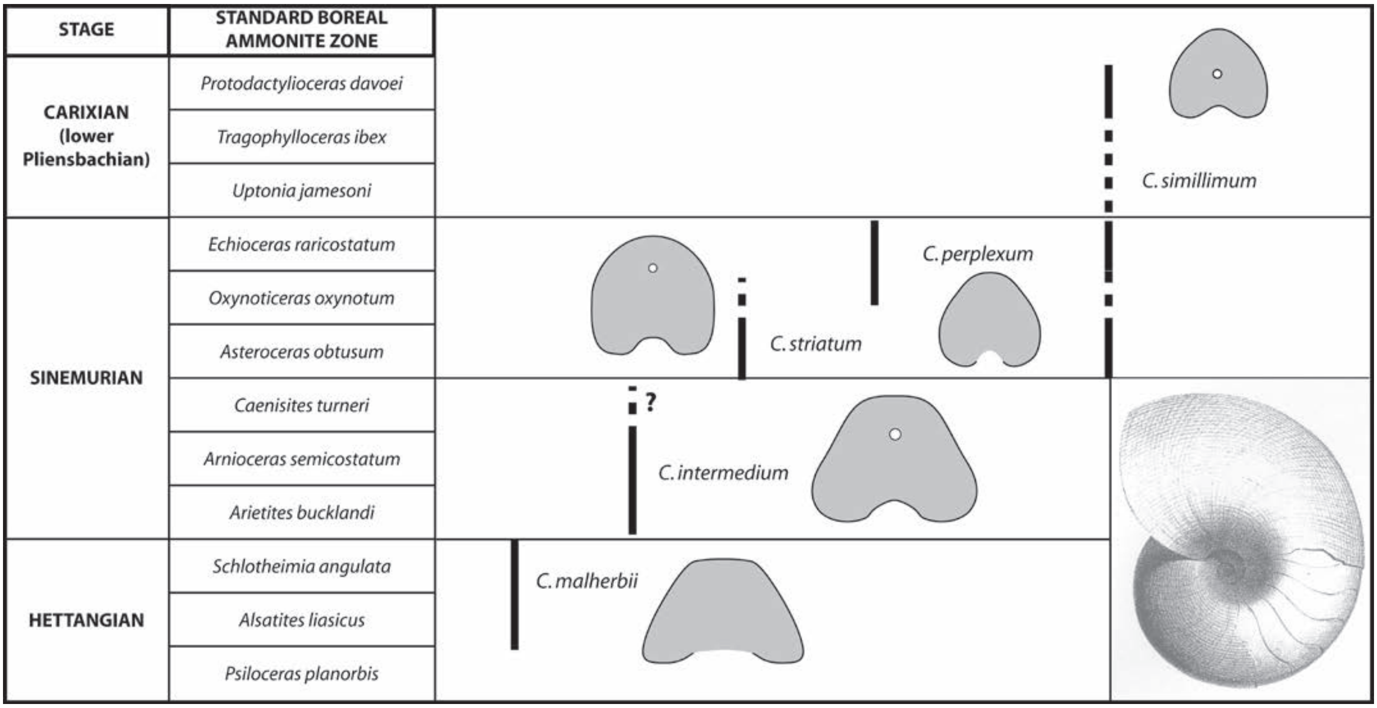

Fig. 4: Occurrence ranges of *Cenoceras* species in the Early Jurassic of southern England, compared with the standard ammonite zonation. Inset: *Cenoceras intermedium* (Sowerby, 1816), reproduced from d'Orbigny (1843: pl. 27, fig. 1).

Rhynchorthoceras and related genera that extend up into the Aserian and Lasnamägian stages. The earliest Lituitidae occur in the mid Kundan and are represented by forms such as *Holmiceras praecurrens* (Holm, 1891). *Ancistroceras*, with its very rapidly expanding conch is recorded from the late Kundan of Kinnekulle, Västergötland, and extends through the Aserian and Lasnamägian, but is more typical of and numerous in the late Lasnamägian and Uhakuan stages. *Angelinoceras latum* (Angelin & Lindström, 1880) is recorded only from the lower part of the Segerstad Limestone (Aserian) and the maximum development and diversity of Lituitidae is attained within the Lasnamägian-aged Seby and Folkeslunda limestones where various species of *Lituites*, *Trilacinoceras* and *Cyclolituites* are of common occurrence.

Apart from the possession of complex sutures, lituitids possess all the attributes typically associated with ammonoids (especially ammonites) which make them such valuable and reliable biozonal indicators and capable of biostratigraphic correlation with a high degree of resolution. Namely, lituitids possess distinctive, easily recognisable conchs whose form and ornament enables taxa to be readily distinguished; they evolved rapidly and have a wide geographical occurrence; and although they are more commonly found in shallow water, platform carbonate sequences, they also occur in mudstone facies, such as those of the Llanfawr Mudstone Formation of central Wales (Evans in prep).

Within Sweden, the use of some lituitid taxa as stratigraphical indicators has long been recognised (e.g. Jaanusson & Mutvei 1953; Jaannusson 1963) and their common occurrence in some beds has given rise to former names such as 'Ancistroceras Limestone' (now termed Furudal Limestone). Closer examination of the Darriwilian lituitid faunas (King 1990, unpublished and in prep.) demonstrates that these lituitids have considerable potential as zonal fossils, and achieve a resolution at least as good as, and for the Aserian and Lasnamägian portion of the succession, potentially finer than that currently recognised using established trilobite, graptolite or conodont zonal schemes (Fig. 3).

Silurian-Devonian

In recent years concentrated efforts have been made to improve the knowledge of the distribution and taxonomy of Silurian nautiloid cephalopod faunas and many existing collections have been revised using up to date taxonomic criteria as well as collection of new material from horizons with precise biostratigraphic data. Consequently systematic studies of Silurian nautiloid cephalopods from a variety of geographical settings and the observed temporal and spatial data from these faunas may now be considered a reliable tool for palaeobiogeographical reconstruction. In Europe the main work on Silurian faunas has been done in the British Isles (Evans 1994; Evans & Holland 1995; Holland 1998, 1999, 2000a–c, 2002, 2003, 2004, 2007, 2010; Hol-

LAND & STRIDSBERG 2004), Sweden (STRIDSBERG 1985), Prague Basin (DZIK 1984; GNOLI 1997; KOLEBABA 1975, 1977, 1999, 2002; MANDA 1996, 2008; MANDA & KŘÍŽ 2006, 2007; MANDA & TUREK 2009a,b; MAREK 1971; MAREK & TUREK 1986; STRIDSBERG & TUREK 1997; TUREK 1975, 2008), South West Sardinia (GNOLI 1990; GNOLI & SERPAGLI 1977, 1991; GNOLI & SERVENTI 2006, 2009 and references therein; SERPAGLI & GNOLI 1977), Spain (BOGOLEPOVA 1998a), France (RISTEDT 1968; SERVENTI & FEIST 2009) the Carnic Alps of Austria and Italy (BOGOLEPOVA 1998b; GNOLI & HISTON 1998; GNOLI & SERVENTI 2008; GNOLI et al. 2000; HISTON 1997, 1998, 1999a, b, 2002, 2012a, b; RISTEDT 1968, 1969, 1971; SERVENTI & GNOLI 2000; SERVENTI et al. 2006, 2010) and the Graz Palaeozoic of Austria (HISTON et al. 2010). Tentative correlations are now possible between Avalonia (British faunas), some areas positioned along the Northern Gondwana Margin (Carnic Alps, Sardinia, France and Spain) and Bohemia and Baltica, although problems do still exist in recognition of faunas at both generic and specific level due to poor preservation and lack of precise taxonomic diagnoses.

Detailed study of Silurian-Devonian nautiloid faunas from Morocco by (KRÖGER 2008) presented together with precise stratigraphic and lithofacies data for the collection localities has highlighted further exchange of faunas between Peri-Gondwana Terranes. Studies of particular taxa and nautiloid biodiversity, again within precise stratigraphic biozones and detailed facies studies, in the Silurian of the Prague Basin in relation to palaeobiogeographical distribution and oceanic states of the North Gondwana area and Perunica by MANDA et al. (2009, 2010) and others (see list above) are important contributions to these fields and confirms that nautiloid cephalopods are indeed reliable indicators for this interval. Studies of faunas at both a local and regional scale within single biozones are still preferable for building a consistent database for future reference.

Certain taxa show potential as biostratigraphical indicators for the Silurian-Devonian interval as has been shown by various studies (see list above): *Orthocycloceras*, *Hemicosmorthoceras*, *Plagiostomoceras*, *Pseudocycloceras*, *Columenoceras*, *Parakionoceras*, *Kionoceras*, *Dawsonoceras*, *Sphaerorthoceras*, *Temperoceras* as well as representatives of the Phragmocerids, Oncocerids and Tarphycerids such as *Ophioceras*. Nautiloid cephalopod assemblages were broadly defined by GNOLI & SERPAGLI (1991) and by MANDA & KŘÍŽ (2006) using a suite of taxa which dominated in certain Silurian series: *Pseudocycloceras transiens-Columenoceras grande* (Wenlock–early Ludlow), *Merocycloceras declive-Cryptocycloceras deludens* (early Ludlow), *Kopaninoceras thyrsus-Orthocycloceras fluminese* (late Ludlow–Pridoli/Early Devonian, *Pseudocycloceras duponti-Sphooceras truncatum* (Wenlock), *Pseudocycloceras duponti-Kionoceras doricum* (early Ludlow) and *Pseudocycloceras nereidum-Sphooceras truncatum* (Ludlow). Taxa such as *Deiroceras* and *Jovellania* have been seen to dominate in certain intervals of the Devonian in Morocco (KRÖGER 2008) and may prove useful for recognition of marker beds deposited within sequences.

There have been numerous studies of the well-known Silurian-Devonian in age 'Orthoceras limestones' or Cephalopod Limestone Biofacies both with regard to their depositional cycles and biotic content. The Carnic Alps of Austria is a key locality along the Northern Gondwana margin regarding Silurian biostratigraphical correlation where the Silurian Cephalopod Limestone Biofacies is well preserved. The Cellon section has been utilized as a geographic reference district (RD) for both conodont correlation studies (KLEFFNER 1989, 1995) and for evaluation of global eustatic changes (JOHNSON 2010) for the North Gondwana area. Recognition of environmental and water depth changes based on the fossil assemblages (mostly trilobites, brachiopods and bivalves) from the Silurian depositional sequences developed there (BRETT et al. 2009) places a tight control on small scale bioevents within well-defined conodont (WALLISER 1964), graptolite (JAEGER 1975) and chitinozoan (PRIEWALDER 1997) biozones. Particular emphasis has been placed in these studies on establishing the response of marine faunas to oscillations in sea-level and to the oceanic variations (chemistry, temperature, currents) recorded (WENZEL 1997; KŘÍŽ 1998, KŘÍŽ et al. 2003) during this time interval on a local scale for comparison with data from other North Gondwana terranes such as Sardinia and Bohemia and on a global scale with some sectors of Avalonia (the British Isles) and Laurentia (North America).

Correlation of the nautiloid faunal assemblages from the cephalopod limestone biofacies levels and their taphonomic signatures within the contexts outlined above with evidence for pronounced redox changes, surface currents, regression/transgression sequences within precise intervals from the Carnic Alps (Austria) successions may identify common controlling factors in the palaeogeographic distribution and migrational routes of these faunas (HISTON 2012b). Current studies, in line with those of MANDA (2009), MANDA & FRYDA (2010) and others, attempt to identify controlling factors on a local scale for nautiloid distribution within precise time slices that may then be recognized in other areas where these faunas occur along the North Gondwana Margin (HISTON 2012a). This is an on-going study done in parallel with revision of historical collections (GNOLI & HISTON 1998; HISTON 1999; GNOLI et al. 2000), systematic collection and description within precise biozones

(Histon 2002; Histon et al. 2010) and taphonomic studies (Histon 1999, 2002, 2012a and references therein;). This holostratigraphical approach may provide further evidence for the reconstruction of reliable nautiloid assemblages or identification of precise marker taxa.

Carboniferous

The monographic works by Hyatt, Miller and others in the USA, Shimansky in Russia, Foord and Turner in the British Isles, and de Koninck from Belgium constituted the foundations for the study on Carboniferous nautiloid cephalopods (see papers listed under references). In recent years some taxonomic revision of these nautiloids has been carried out (see studies listed by Histon, Mapes, Niko, Sturgeon and others), but the use of rapidly evolving goniatite lineages to establish a biostratigraphy, particularly for the Upper Carboniferous is predominant and consideration of the stratigraphical potential of nautiloid cephalopods has been neglected. However, several taxa are worthy of mention and are known to to be abundant at certain intervals in a diverse range of palaeogeographical settings. Large specimens of *Rayonnoceras* are known to be markers within Lower Carboniferous strata of Europe and the USA where they are common in the Brigantian /Mississippian. The annulated *Cycloceras* and taxa of the Oncocerida such as *Poterioceras* and *Welleroceras* are common in the Lower Carboniferous. Several Pseudorthocerataceae taxa are restricted to the Carboniferous such as *Mitorthoceras*. The distinctively ornamented *Brachycycloceras* is a common element in the Upper Carboniferous. A variety of coiled nautiloid taxa such as *Vestinautilus*, *Trigonoceras*, *Aphelaeceras*, *Epistroboceras*, *Maccoyoceras*, *Asymptoceras*, *Acanthonautilus* and *Bistrialites* are typical of the Lower Carboniferous of the British Isles, Belgium, Asia and the USA. More precise biostratigraphical data may be obtained through further study of the ranges of these taxa at species level. However, to date, such a zonal scheme has not been developed.

Permian

The papers by Miller et al. (1942, 1949) of the Permian nautiloids of the USA still stand as reference works for taxonomy of the group. However, there are few studies in relation to the development of the biostratigraphical potential of nautiloid cephalopods for this interval. An investigation of the Late Permian nautiloid faunas of the Bellerophon Formation from the Dolomites of Northern Italy (Posenato & Prinoth 2004, 2007; Posenato 2010) indicates that certain nautiloid taxa representing species of *Tainoceras*, *Tirolonautilus*, *Liroceras* and *Foordiceras* may indeed be used as markers for precise levels within the succession whilst some species may be assigned lineages and may be compared with assemblages described by Teichert & Kummel (1973) from the Late Permian of northwest Iran.

Triassic

Despite the relative paucity of works on Triassic nautiloid cephalopods, there is strong evidence of their potential value to some aspects of Triassic biostratigraphy. Kummel (1953) reviewed many Triassic nautiloid genera, indicating their stratigraphical ranges and a potential for their biostratigraphical use. This potential has been realised through the development of a detailed zonal scheme using nautiloids (Sobolev 1994) for the Boreal Triassic of Siberia. Such a scheme clearly demonstrates the value of the organisms as biostratigraphical tools.

Jurassic and Cretaceous

After the disappearance of seven families and approximately thirty genera during the Late Triassic extinctions (Kummel 1964, fig. 294), only the Nautilidae, represented by the single genus *Cenoceras* is conventionally regarded as having survived into the Jurassic where it underwent a radiation that led to all subsequent nautiloid genera including *Nautilus*. Analysis of the distribution of Middle Jurassic nautilids in western France by Branger (2004) indicates that the ranges of some taxa may be no more than one or two ammonite zones, indicating a potential utility as biostratigraphical tools. The same appears to be true for Lower Jurassic nautilids.

Historically the name *Cenoceras* has been broadly applied to a diverse range of Late Triassic to early Middle Jurassic nautilids that constitute a “plastic evolving complex” (Kummel 1956, p. 361). It is now recognised that this masks a number of distinct lineages within a rapidly evolving nexus of Lower Jurassic nautilid faunas (Tintant 1984, 1987; Rulleau 2008). Previous workers (Hyatt 1894; Spath 1927) recognised a number of different morphotypes within the ‘*Cenoceras* complex’ and provided names for several forms (including *Digonioceras*, *Ophionautilus* and *Sphaeronautilus*). The taxonomic status of these taxa requires revision.

More recently, Tintant (1984) described three subgenera within *Cenoceras*: *Cenoceras* (in a restricted sense) for forms with relatively stout, involute conchs possessing a spiral ornament on the ventral and lateral surfaces of the whorls; *Hemicenoceras* for compressed forms possessing spiral ornament that is mainly confined to the ventral area, and *Metacenoceras* for forms with a flattened venter and an ornament consisting only of weak transverse growth lines. The earliest *Metacenoceras* occur in the early Sinemurian (Shales-with-Beef

Member, Charmouth Mudstone Formation near Lyme Regis, Dorset, UK [King unpublished data]); *Hemicenoceras* is typically first encountered in the Carixian, where it is represented by *H. arare* (Dumortier, 1869) and *H. egregium* (Pia, 1914). In this paper, *Cenoceras* is used in the restricted sense employed by Tintant.

The Hettangian to Carixian sequence of *Cenoceras malherbii* (Terquem, 1855) – *C. intermedium* (Sowerby, 1816) – *C. striatum* (Sowerby, 1817) – *C. pertextum* (Dumortier, 1867) – *C. simillimum* (Foord & Crick, 1890) was recognised in French successions by Tintant (1984). In the United Kingdom, the same sequence of taxa is present (in part) in the Lower Jurassic of South Wales, and on the North Somerset and Dorset coasts (Fig. 4). Within this lineage there is a tendency for conchs to become more involute (from 20% in Hettangian forms to <10% in Carixian taxa); for the siphuncle to migrate from a ventrocentral to central position; for the whorl section to become more rounded and arched, and less quadrate; and for suture lines to become more sinuous, culminating with *C. jourdani* (Dumortier, 1874) in the Toarcian (King 2011).

Late Hettangian and early Sinemurian strata on the Somerset coast (particularly within the *angulata* and *bucklandi* zones) include several monotonous beds of dark grey to black shales and bituminous mudstones which are virtually devoid of ammonites. These units contain fossil nautilids that are embedded in the substrate at orientations that range from horizontal to vertical, and provided hard attachment surfaces for a range of organisms of which oysters and crinoids are the most abundant.

Wherever ammonites are present in the Lower Jurassic, by comparison, nautilids make relatively poor biostratigraphical indicators. However, when ammonites are absent, cenoceratid nautilids can be used for biostratigraphical purposes and provide a resolution of at least stage or even substage level. Unlike Middle Jurassic nautilids (Branger 2004), there are, at present, no known Lower Jurassic cenoceratid taxa that are characteristic indicators of an individual ammonite zone, although further research may change this picture.

Cretaceous nautilids from southern South America are relatively scarce and of low diversity. Most belong to one or two genera: *Cymatoceras* Hyatt, and *Eutrephoceras* Hyatt. Both genera possess a strongly involute, inflated and globose conch with an orthochoanitic, subcentral siphuncle, as well as simple sutures. Both genera are cosmopolitan in distribution, but at species level, cosmopolitan distributions are almost nonexistent (Cicholowski 2003) which may reflect the nektobenthic habit of these animals, as well as the lack of a planktonic larval stage. Furthermore, the skeletal morphology of nautilids in general, and of these genera in particular, is markedly homogeneous with respect to the characters used to diagnose different species.

All these considerations suggest that attempts to use Cretaceous nautilids for biostratigraphical purposes are likely to be disappointing. This is compounded when the long stratigraphical ranges of some of the species are taken into consideration. *Cymatoceras perstriatum* (Steuer) is a typical example of such a species. *C. perstriatum* (Steuer) occurs in strata of Tithonian-Hauterivian age in the Neuquén Basin (Cichowolski 2003); the late Tithonian-early Berriasian of the Chilean Aconcagua platform (Corvalán 1959; Biró-Bagóczky 1964), and the late Valanginian-early Albian of the Chañarcillo Basin (northern Chile: Hofstetter et al. 1957; Segerstrom 1960). The whorl cross-section, the sutural pattern, and overall shape of the conch all exhibit a marked ontogenetic and intraspecific variability (Cichowolski 2003). Such a range of variation implies that an extra effort may be required in order to positively identify individual members of this particular taxon.

However, there are some nautilid species possessing easily recognisable morphologies that present low variability within and between individuals. When such taxa have a relatively short stratigraphical range, and other biostratigraphic markers are lacking, they may provide valuable information with regard to the age of the strata in which they are found. One such example may be provided by *Eutrephoceras dorbygnianum* (Forbes in Darwin, 1846), known from the Antarctic Peninsula, Quiriquina Island in Chile, the Austral Basin of southern Argentina, and possibly from Angola (Steinman 1895; Spath 1953; Howarth 1965; Stinnesbeck 1986; Cichowolski et al. 2005; Nielsen & Salazar 2011). This species is characterized by an almost straight suture, combined with a small, acute, umbilical saddle, and a semilunate whorl cross-section (Cichowolski et al. 2005). Based on its occurrence, this species ranges through the Campanian and Maastrichtian, becoming particularly abundant during the Maastrichtian. Thus, like the Lower Jurassic *Cenoceras*, the stratigraphical range of some Late Cretaceous nautilids may resolve to one or two stages.

Concluding remarks

This survey of the use and potential use of nautiloid cephalopods in biostratigraphy is inevitably, incomplete. Nevertheless, examples provided by the lituitids (above) and the Triassic nautiloids of Siberia (Sobolev 1994) demonstrate that when diversification rates are high, these organisms may be used to define biostratigraphical schemes to resolutions that are at least equivalent to those generated through the use of other groups of organisms. In situations where other groups of organisms are rare or not present, nautiloid cephalopods may provide an alternative basis for a biostratigraphical scheme. Finally, and perhaps more significantly, nautiloid cephalopods are powerful palaeobiogeographical tools, especially, but not exclusively during the Ordovician and Silurian. In order to refine their value as palaeobiogeographical tools, it will be necessary also to further refine their biostratigraphy. This is a task that will continue through the study of well-documented collections as well as newly collected material that may help resolve questions related to older collections, and bring to light new material from poorly known areas.

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Cenozoic coleoids (Cephalopoda) from Austria – a review of SCHULTZ's Catalogus Fossilium Austriae

D. FUCHS & A. LUKENEDER

Abstract: The Cenozoic coleoids that were dealt with in SCHULTZ's 'Catalogus Fossilium Austriae' are reviewed: *Beloptera broilii* TRAUB, *Spirulirostridium obtusum* NAEF, *Spirulirostrum* sp., *Sepia vindobonensis* SCHLOENBACH, and *Argonauta joanneus* HILBER. Information on subsequently reported coleoids from Austria is also given, such as *Belopterina neumaieri* TRAUB, and several undetermined specimens.

Keywords: Cephalopods, Coleoidea, Octopoda, Oegopsida, Sepiida, Spirulida, systematics

Introduction

Scientists know well how time-consuming the collection of information from the literature can be. For taxonomists it is, for instance, very helpful to revert to existing systematic compilations even though the information is outdated. It is even more important to get such faunal lists for geographically restricted areas. SCHULTZ (1976a) did such a work when he compiled a list of Cenozoic cephalopods from Austria. Ortwin SCHULTZ was the Curator (1969-2007) for the Cenozoic collections of the Natural History Museum in Vienna. His main working field were Cenozoic fishes (SCHULTZ 1998a, b) and molluscs (SCHULTZ 1976a–c, 1998a, b, 2001, 2002, 2003, 2005, 2013).

In his 'Catalogus Fossilium Austriae', SCHULTZ (1976a) indexed (apart from ectocochleate nautiloids) five species of the endocochleate coleoids: *Beloptera broilii* TRAUB, 1938, *Spirulirostridium obtusum* NAEF, 1922, *Spirulirostrum* sp. (see STUR 1870), *Sepia vindobonensis* SCHLOENBACH, 1869, and *Argonauta joanneus* HILBER, 1915. Since these early works, TRAUB (1982), HIDEN (1995), and HARZHAUSER (1999) later provided new specimens and taxa (see Table 1), it is the purpose of the present paper to update the list of coleoid cephalopods from the Cenozoic of Austria, and to reconsider their systematic positions in the light of the current state-of-the-art.

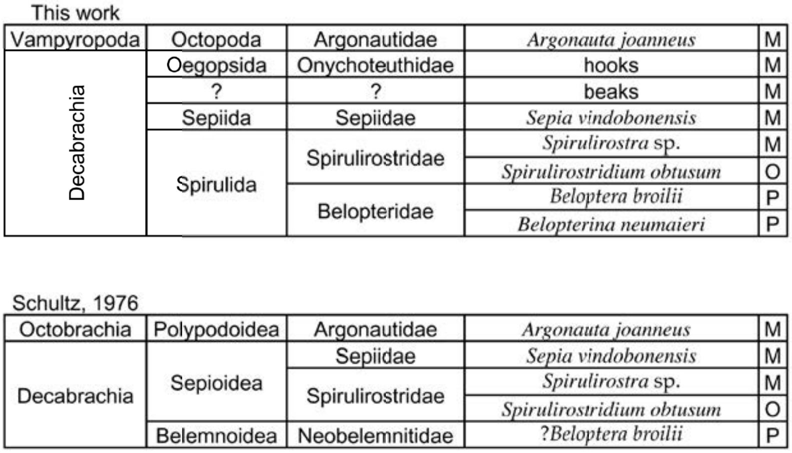
Systematic palaeontology

Class Cephalopoda CUVIER, 1797
Subclass Coleoidea BATHER, 1888
Superorder Decabrachia BOETTGER, 1952
Order Spirulida HAECKEL, 1896

The Spirulida is a group of small, ten-armed coleoids with a mineralized phragmocone whose shape ranges from straight (orthoconic), weakly curved (cyrtoconic) to distinctly enrolled. The order contains a single living species, *Spirula spirula* (Fig. 1a). This mesopelagic animal lives in waters throughout the world's tropical and subtropical oceans, generally above continental slopes. However, the fossil record of spirulids is rich, starting from the Late Cretaceous with the Groenlandibelidae; a family with straight (orthoconic) phragmocones (FUCHS et al. 2012, 2013). Different groups such as the Belopteridae (Fig. 1b, c), Belemnoseidae (Fig. 1d) or Spirulirostridae (Fig. 1e) diverged during the Cenozoic. The latter families are typified by different degrees of shell coiling and by guard-like sheaths that exhibit a complex and characteristic pattern of posterior, ventral and lateral swellings (calli). While earliest spirulids were presumably adapted to open waters, their Cenozoic descendants are thought to be associated with the sea floor.

Family Belopteridae OWEN, 1856
Beloptera broilii TRAUB, 1938 (Fig. 2a–c)

v.*1938 *Beloptera broilii* n. sp. TRAUB: 104, pl. 8, figs 20a–c.
v.1953 *Beloptera broilii* TRAUB: 10.
v.1976a *Beloptera broilii* TRAUB. SCHULTZ: 20.
v.1982 *Beloptera broilii* TRAUB: 35.
v.1999 *Beloptera broilii* TRAUB. RASSER & PILLER: 706.
Holotype: original of TRAUB (1938: pl. 8, figs 20a–c) by monotypy, BSP 1942 II 142, Bayerische Staatssammlung, Munich.



This work

Vampyropoda	Octopoda	Argonautidae	*Argonauta joanneus*	M
Decabrachia	Oegopsida	Onychoteuthidae	hooks	M
	?	?	beaks	M
	Sepiida	Sepiidae	*Sepia vindobonensis*	M
	Spirulida	Spirulirostridae	*Spirulirostra* sp.	M
			Spirulirostridium obtusum	O
		Belopteridae	*Beloptera broilii*	P
			Belopterina neumaieri	P

Schultz, 1976

Octobrachia	Polypodoidea	Argonautidae	*Argonauta joanneus*	M
Decabrachia	Sepioidea	Sepiidae	*Sepia vindobonensis*	M
		Spirulirostridae	*Spirulirostra* sp.	M
			Spirulirostridium obtusum	O
	Belemnoidea	Neobelemnitidae	*?Beloptera broilii*	P

Table 1: List of fossil coleoids recorded from Austria, and their systematic attributions. The present study and SCHULTZ (1976a) in comparison. M: Miocene; O: Oligocene; P: Paleocene.

Material: 1 specimen.
Type locality: Kroisbach (Haunsberg, north of Salzburg).
Type horizon: Oichinger Schichten, Paleocene (Thanetian).

Re-description: The holotype (which is to the authors knowledge still the single specimen) mainly consists of the internal (steinkern) and external mould of the phragmocone (dimensions are given by Traub). Most of the shell material adheres to the external mould. The steinkern of the weakly curved phragmocone (apical angle = 20–25°) therefore shows the mural parts of the septa. The chamber distance is comparatively low (ratio chamber height : chamber diameter = c. 0.25). The septa are not inclined and exhibit a wide dorsal saddle and a distinct ventral lobe. Owing to a fracture along the ventral midline, it must remain unclear whether the siphuncle was marginal or submarginal. Middorsally, the steinkern shows rectangular soft tissue attachment scars, which are nearly as long as the chamber height.

The external mould offers the internal surface of the conotheca. In some places, the investment-like sheath appears below the conotheca.

Systematic remarks: Unfortunately, the sheath is largely missing; hence there is no information about the postalveolar thickening of the sheath which is characteristic for the genus *Beloptera* and all Cenozoic spirulids. As TRAUB (1938) correctly stated, the generic attribution of the specimen is therefore problematic since the taxonomy of Cenozoic coleoids is mainly based on sheath characters.

Nevertheless, a systematic approach on higher-levels is possible thanks to the phragmocone characteristics described above. SCHULTZ (1976a) placed '*?Beloptera*' *broilii* in the belemnoid family Neobelemnitidae PAVLOV, 1913. This view is nowadays no more tenable. The 'Neobelemnitidae' were established for Cenozoic forms with a belemnite-like rostrum (*Bayanoteuthis*, *Styracoteuthis*). Since the presence of a long and solid rostrum in '*?B.*' *broilii* is considered as unlikely, affinities with the latter forms are unlikely. The presence of a weakly curved phragmocone with horizontal septa rather suggests placement with the Spirulida (see also NAEF 1922). The occurrence of rectangular dorsal attachment scars support this classification (FUCHS et al. 2013). Belemnoids are typified by long stripe-like scars.

Affinities with the Spirulirostridae (Eocene-Miocene) are unlikely, because this spirulid subgroup is known to have longer chambers and a distinctly enrolled phragmocone (FUCHS 2012). In terms of a weakly curved phragmocone with comparatively low chambers, the present specimen is hence more similar to Palaeocene–Eocene Belopteridae. The Belopteridae is known to possess a complex sheath with postalveolar club-like swellings as well as ventral and lateral extensions. With respect to their stratigraphical and geographical distribution, it is possible that the club-like post-alveolar sheath of co-occurring *Belopterina neumaieri* (see below) belongs to the present phragmocone. However, the phragmocone of the genus *Belopterina* is characterized by widely spaced chambers. The preliminary attribution of this species to the genus *Beloptera* by TRAUB (1938) was therefore correct.

Belopterina neumaieri TRAUB, 1982 (Fig. 2d–f)

*1982 *Belopterina neumaieri* TRAUB: 36, pl. 2, figs 1–6, text-fig. 1.
Holotype: original of TRAUB (1982: pl. 2, figs 1–6) by monotypy, BSP 1943 II 480, coll. TRAUB, Bayerische Staatssammlung München.
Material: only 1 specimen.
Type locality: Kroisbach (Kch11a), Haunsberg, north of Salzburg, Austria.
Type horizon: Oichinger Schichten, Paleocene (Thanetian).

Remarks: TRAUB (1982) provided an appropriate description and his taxonomic-systematic position is well-justified. *Belopterina neumaieri* has been compared only with *Belopterina levesquei* FERRUSAC & D'ORBIGNY, 1835 from the Eocene of Europe. It is here worthwhile to note, that TRAUB'S specimen appears to be closer to contemporary *Belopterina deshayesi* VINCENT, 1901 or Eocene *Beleopterina fabrezanensis* DONCIEUX, 1908 in having a sheath with only a weakly developed ventral ridge. The sheath of *B. levesquei* is, in contrast to the latter taxa, characterized by a pronounced ventral ridge and a shorter club-like apex (compare Fig. 1b).

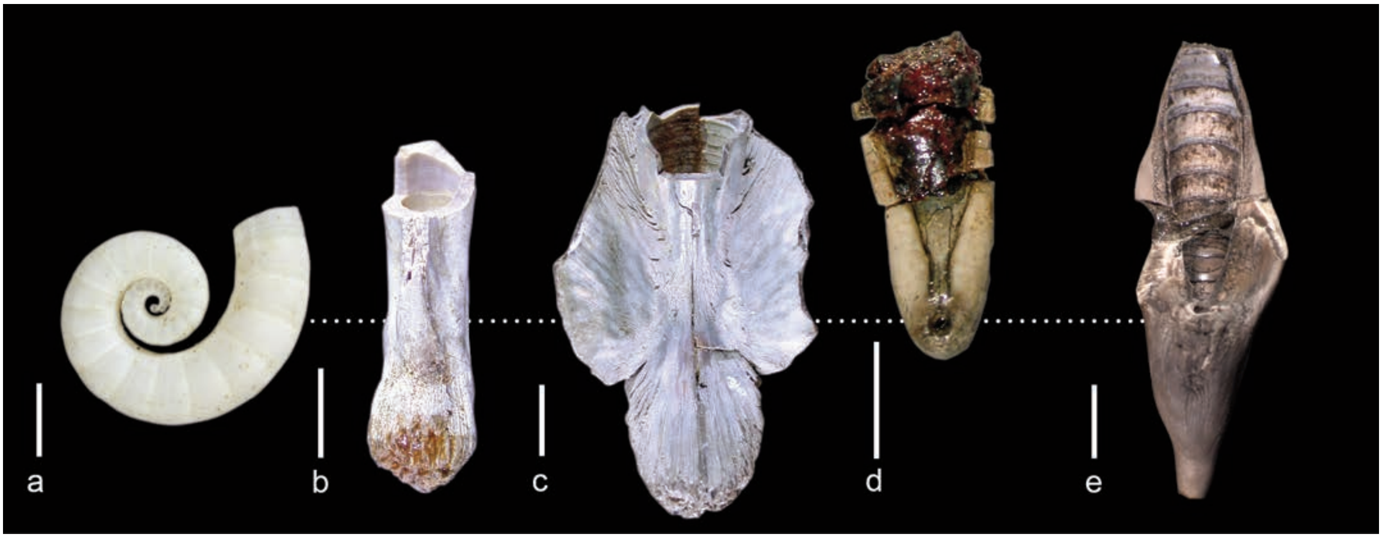


Fig. 1: Shells and shell remains of spirulid coleoids. **a**: *Spirula spirula*; lateral view of the complete phragmocone. **b**: *Belopterina levesquei* [original of Férussac & d’Orbigny (1839: pl. 20, figs. 10–12), MNHN R05666, Muséum National d’Histoire Naturelle], Eocene (Ypresian), Gilocourt (Dep. Oise, France), ventral view of the phragmocone enveloping guard-like sheath. **c**: *Beloptera belemnoidea* (MNHN J03303); Eocene (Bartonian), Bois-Gouët (Dep. Loire-Atlantique, France), ventral view of the phragmocone enveloping guard-like sheath. **d**: *Belemnosis anomala* [original of Sowerby (1826–29: pl. 591, fig. 3), BMNH C.4382, British Museum of Natural History London], Eocene (Ypresian), Highgate (UK), ventral view of the phragmocone enveloping guard-like sheath. **e**: *Spirulirostra hoernesi* (MC-183-3, palaeontological collection, FU Berlin), Miocene (Langhian), Twistringen (Germany), ventral view of the phragmocone enveloping guard-like sheath. Dotted line indicates the morphological position of the protoconch. Scale bars = 5 mm.

Fig. 2: **a–c**: Fragmentary phragmocone of *Beloptera broilii*; holotype [original of Traub (1938: pl. 8, figs 20a–c), BSP 1942 II 142, Bayerische Staatssammlung Munich], Paleocene (Thanetian), Haunsberg (north of Salzburg). **a**: Ventral. **b**: Lateral. **c**: Dorsal. **d–f**: Fragmentary sheath of *Belopterina neumaieri*, holotype [original of Traub (1982: pl. 2, figs 1–6), BSP 1943 II 480, Bayerische Staatssammlung München], Kroisbach (Kch11a), Haunsberg, north of Salzburg, Paleocene (Thanetian); photo courtesy Alexander Nützel. **d**: Ventral. **e**: Lateral. **f**: Reconstruction of the phragmocone enveloping sheath. Scale bars = 5 mm.

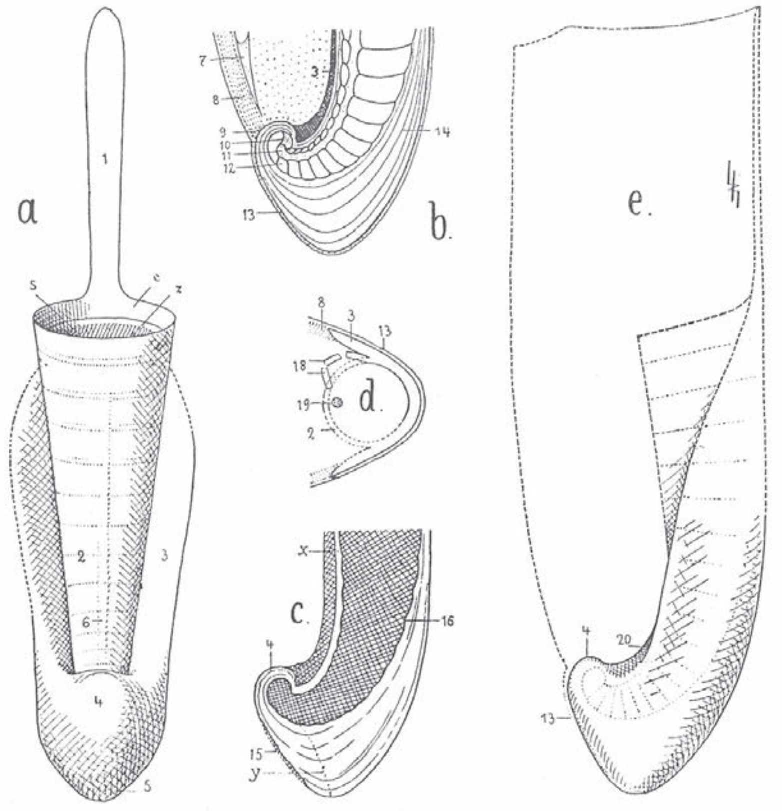


Fig. 3: *Spirulirostridium obtusum*, lost holotype (original of NAEF 1922: 61, fig. 21), Lower Oligocene (Rupelian), Häring, near Kufstein. Reproduced after NAEF (1922: fig. 21). Note that the anteriorly projected proostracum as indicated in reconstructions a) and e) is erroneous.

Family Spirulirostridae NAEF, 1921

Spirulirostridium obtusum NAEF, 1922 (Fig. 3)

*1922 *Spirulirostridium obtusum* nov. spec. NAEF: 61/2, figs 21a–e.
1933 *Spirulirostra obtusa* NAEF. SCHLOSSER: 277.
1939 *Spirulirostra obtusa* SCHLOSSER. SCHACHL: 289.
1976a *Spirulirostridium obtusum* NAEF. SCHULTZ: 20.
Holotype: original of NAEF (1922: fig. 21); lost probably during World War II (pers. comm. A. NÜTZEL, Bayerische Staatssammlung München).
Type material: three originals of NAEF (1922); lost probably during World War II (pers. comm. A. NÜTZEL, Bayerische Staatssammlung München).
Type locality: Häring, near Kufstein.
Type horizon: Zementmergel, lower Oligocene (Rupelian).

Remarks: *Spirulirostridium obtusum* is the type species of the genus. Since NAEF's type specimens are no more available for examinations, our knowledge is restricted to the short characterization given by NAEF (1922). Accordingly, *Spirulirostridium* can be distinguished from *Spirulirostra* by the absence of a spine-like posterior extension of the guard-like sheath (compare Figs 1e–f).

Spirulirostridium obtusum seems to be very similar to *'Belemnosis' rzehaki* OPPENHEIM, 1922 from the Eocene (Niemtschitzer Schichten) of Pausram (Morovia, Czech Republic) and still undescribed specimens from the Miocene of Malta (own observation).

Spirulirostra sp. STUR, 1870

1870 *Spirulirostra Hörnesi* n. sp. STUR: 308.
1874 *Spirulirostra Hoernesi* STUR. Anonymous: 249.
1976a *Spirulirostra* spec. SCHULTZ: 20.
Material: 1 specimen.
Type locality: Soos near Baden, Vienna.
Type horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).

Remarks: As already pointed out by SCHULTZ (1976a), no conclusions can be drawn, because no drawings have been provided by STUR (1870). An examination is impossible, because the deposition of the specimen is still unknown. Finally, it is still unclear why STUR (1870) indicated a new species even though *Sp. hoernesi* was already erected in 1865 by VON KOENEN.

Order Sepiida ZITTEL, 1895

Family Sepiidae LEACH, 1817

The Sepiidae is a diverse group of benthic or benthopelagic coleoids with a strongly modified phragmocone, commonly called cuttlebone (or sepion; = German: Schulp; Fig. 4d). Unlike the majority of cephalopod phragmocones, where septa are usually oriented perpendicular to the shell axis, the cuttlebone s septa are almost parallel to the shell axis. Although absent in some Recent species, Cenozoic cuttlebones are typified by the presence of a posterior spine.

Sepia vindobonensis SCHLOENBACH, 1869 (Fig. 4a–c)

v.*1869 *Sepia vindobonensis* sp. nov. SCHLOENBACH: 289ff., pl. 7, figs 1, 2.
1899 *Sepia vindobonensis* SCHLOENB. LÖRENTHEY: 269.
1920 *Sepia vindobonensis* SCHLÖNB. BÜLOW-TRUMMER: 248.
1922 *Sepia Vindobenesis* [sic] SCHLOENBACH. NAEF: 92.
v.1947 *Sepia* cf. *vindobonensis* SCHLOENBACH. ROGER: 225, 230, 231, text-figs 1, 2.
1952 *Sepia vindobonensis*. KÜHN: 121.
1952 *Sepia vindobonensis* SCHLOENBACH. ROGER: 734.
1958 *Sepia vindobonensis* SCHLB. SCHAFFER: 142–146, figs a–d.
1959 *Sepia vindobonensis* v. SCHLÖNB. SIEBER: 276.
1975 *Sepia vindobonensis* SCHLOENBACH. STOJASPAL: A191.
1976a *Sepia vindobonensis* SCHLOENBACH. SCHULTZ: 21
1977 *Sepia vindobonensis*. BAŁUK: 171, 174.
1987 *Sepia (Sepia) vindobonensis* SCHLOENBACH. KHROMOV: 1168.
1990 *Sepia vindobonensis*. IN UROVÁ: 3.
1995 *Sepia vindobonensis* SCHLOENBACH. HIDEN: 116, fig. 4.
2010 *Sepia vindobonensis* SCHLOENBACH. JAMRICH & HALASOVA: 123.
Holotype: original of SCHLOENBACH (1869: pl. 7, figs 1, 2.) by monotypy, Sammlung der Geologischen Bundesanstalt Wien, no. 8106.

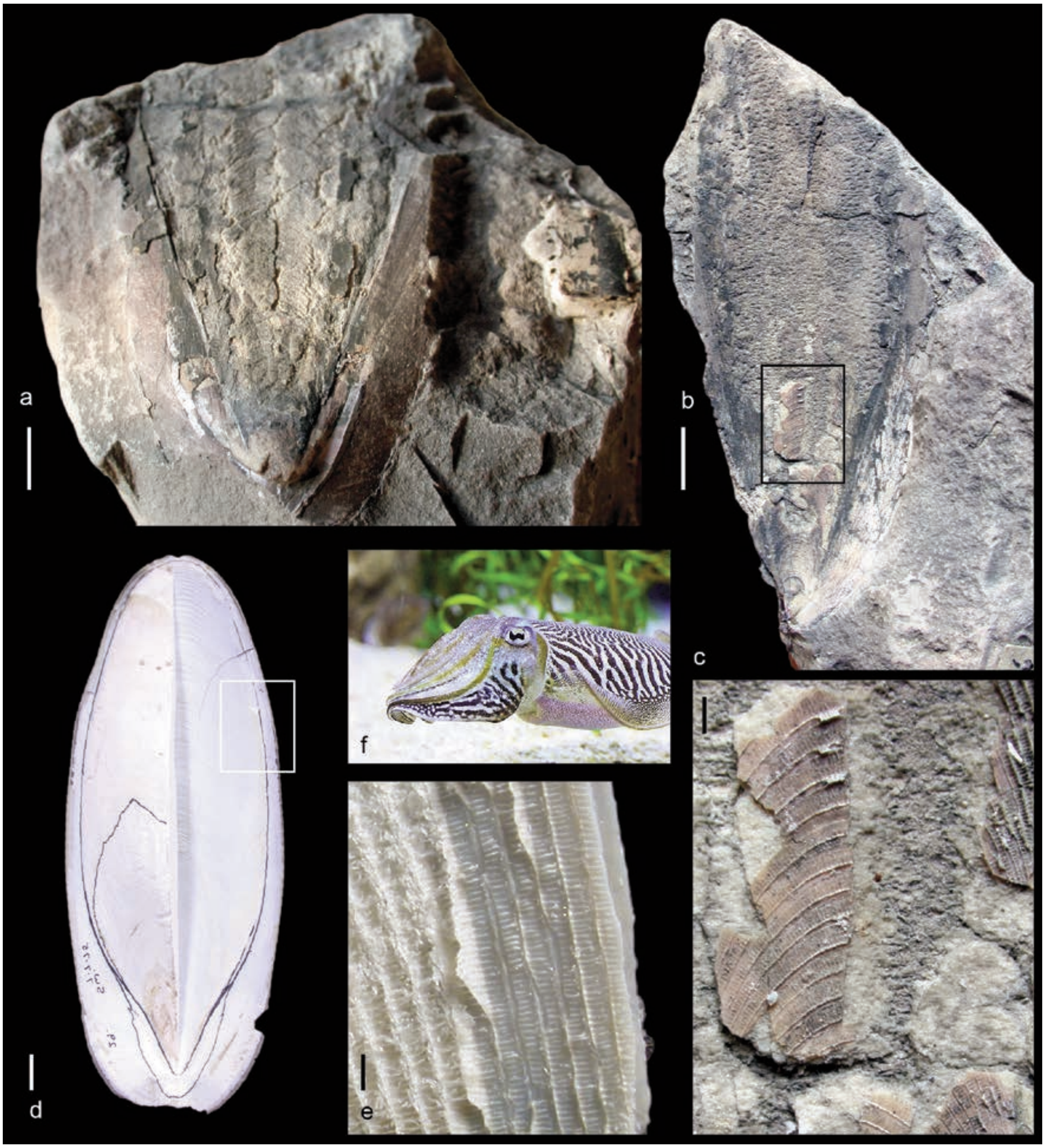


Fig. 4: Fossil (**a–c**) and Recent (**d–f**) cuttlebones. **a**: *Sepia vindobonensis*, holotype [original of SCHLOENBACH (1869: pl. 7, figs 1, 2), no. 8106, Sammlung der Geologischen Bundesanstalt Wien], Middle Miocene, Langhian, Baden near Vienna; positive in posterodorsal view. **b**: same specimen, negative in ventral view. **c**: Close-up of **b** to show the stubs of the septa as well as the pillars. **d**: partly sectioned cuttlebone of Recent *Sepia officinalis* in ventral view. The left half of the chambered part has been removed. **e**: close-up of **d** to show the inner surface of the dorsal shield and its stubs of the septa and pillars. **f**: Living *Sepia* in its natural habitat. Scale bars = 5 mm (**a**, **b**, **d**); = 1 mm (**c**, **e**).

Type locality: Baden near Vienna.

Type horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).

Other contemporary occurrences in Austria: Grund [Hollabrunn, Lower Austria, SCHAFFER (1958): 3 specimens, deposition unknown], Retznei [Steiermark, HIDEN (1995): 2 specimens, coll. WANZENBÖCK, Bad Vöslau].

Other occurrences outside Austria: Middle Miocene of Bratislava, Slovakia (ČINČUROVÁ 1990); Upper Miocene of Saubrigues, France (ROGER 1947).

Remarks: The material comprises different parts of the cuttlebones. SCHLOENBACH's holotype, which consists of the positive (Fig. 4a) and negative (Fig. 4b), shows the unflattened posterior half of the cuttlebone. The clasp-like structure visible in the positive corresponds to the outer cone of the cuttlebone. Arcuated striae in the centre of the outer cone indicate the siphuncular zone and therefore the shape of the septa. The white powder associated with the striae represents the smashed chambers. The negative mainly preserves imprints of the dorsal surface of the dorsal shield. However, the posterior part also exhibits shell material. Since the chambered part was attached to the positive, one can look at the inner surface of the dorsal shield (Fig. 4c), where stubs of the septa and their pillars are still extraordinarily well-preserved. Additionally, the spine is still present in the counterpart.

While the specimen of ROGER (1947) shows the ventral imprints of a complete cuttlebone, the SCHAFFER specimens yielded fragments of the posteriormost part of the cuttlebone (inner + outer cone, spine).

Sepia vindobonensis is without any doubts a sepiid and SCHLOENBACH (1869) correctly recognized its simi-

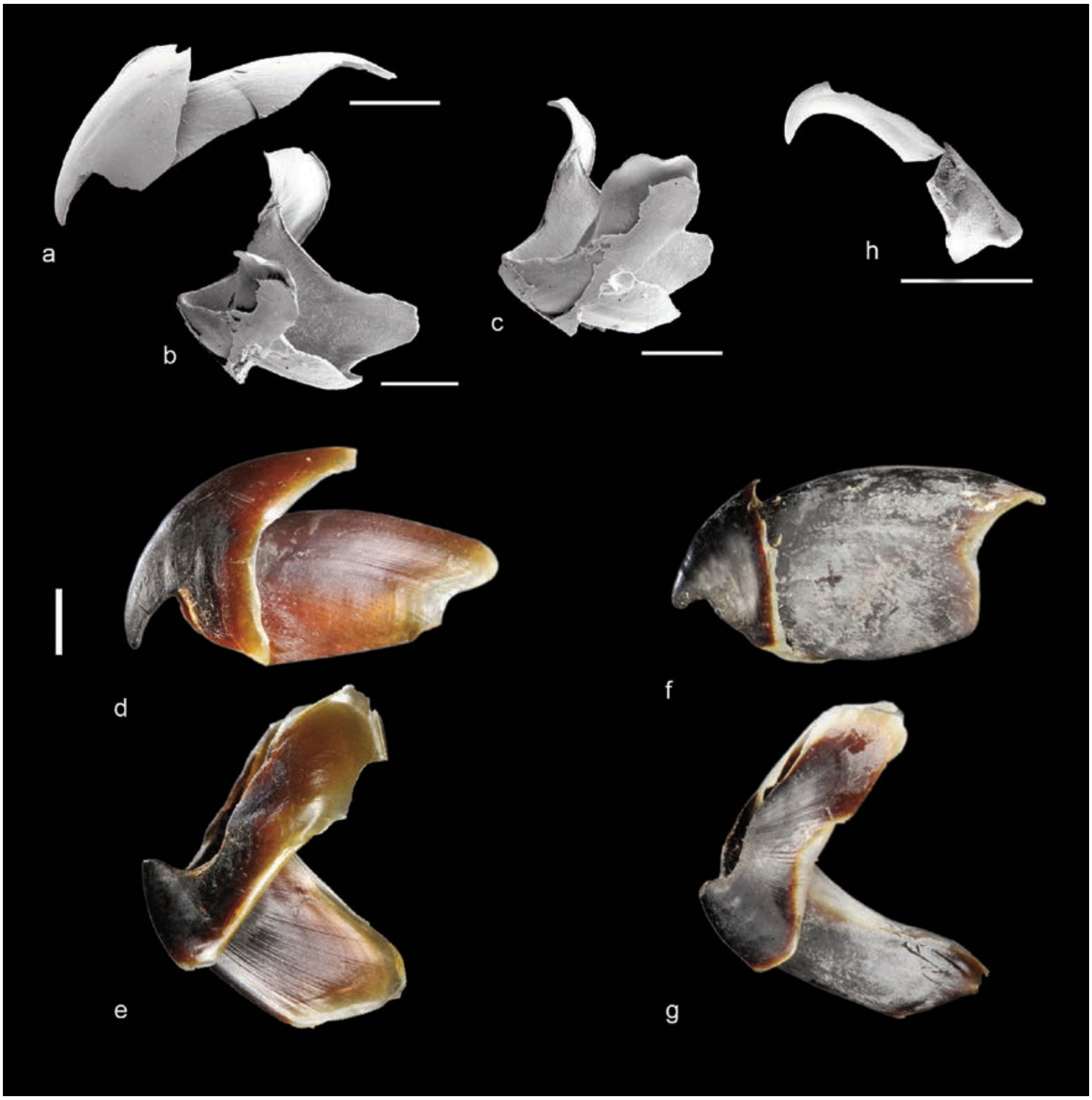


Fig. 5: Beaks of fossil and Recent Coleoidea [originals of Harzhauser (1999) from the Langhian of Vöslau (**a–c**) and Möllersdorf (**h**)]. **a**: NHMW1999z0050/0001, upper beak in lateral view. **b**: NHMW1999z0050/0002, lower beak in oblique ventrolateral view. **c**: Same specimen in oblique anterolateral view. **d**: Upper beak of *Sepia* sp. **e**: Lower beak of *Sepia* sp. **f**: Upper beak of *Octopus* sp. **e**: Lower beak of *Octopus* sp. (**d, e** in lateral views). **h**: Hook of a onychoteuthid oegopsid (?), NHMW1999z0050/0003, lateral view. Fossil specimens coated with gold before SEM and stored in the collections of the Natural History Museum Vienna. Scale bars = 1 mm.

larities with the living descendants of this genus. The Eocene sepiid *Belosepia* possess less inclined septa and a well-developed prong-like spine.

Order and family uncertain (Fig. 5e–g)

Material: 3 lower beaks + 1 upper beak; Museum of Natural History Vienna (NHMW 1999z0050/0001, NHMW 1999z0050/0002).

Locality: Vöslau, Lower Austria.

Horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).

Remarks: Since Harzhauser (1999) introduced these first Cenozoic beaks, no further specimens have been published. Harzhauser (1999) correctly identified the nicely preserved beaks as belonging to a ten-armed coleoid (Fig. 5a, b). The upper beaks of octopods do have a much shorter and less pointed rostrum (compare Figs 5d-f).

Order Oegopsida d'Orbigny, 1845

The Oegopsida, together with the Loliginida, are commonly referred to as the 'Teuthida' (German: Kalmare). Thanks to a torpedo-shaped body and the loss of a buoyant, mineralized shell, both groups belong to the fasted swimmers among invertebrate animals. The Oegopsida, in contrast to the Loliginida, prefer offshore waters. Many oegopsid squids such as the giant squids *Architeuthis* and *Mesonychoteuthis* are adapted to the deep sea.

Family Onychoteuthidae Gray, 1847 (Fig. 5h)

Material: 2 chitinous hooks; Museum of Natural History Vienna (NHMW 1999z0050/0003).

Locality: Möllersdorf, Lower Austria.

Horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).

Remarks: Similar to Cenozoic beaks, no further examples of Cenozoic hooks have been recovered since

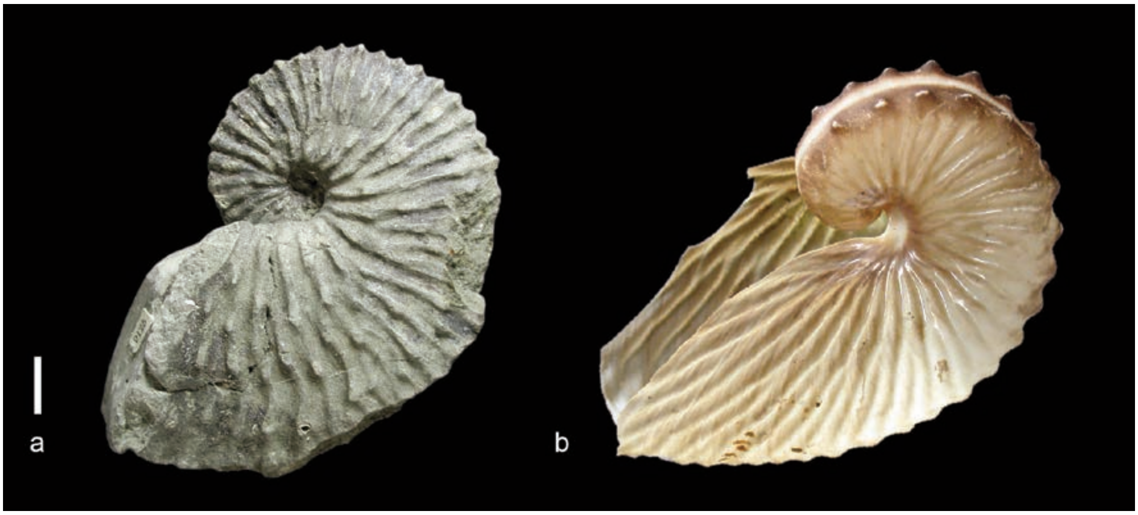


Fig. 6: 'Brood shells' of argonautids in lateral views. **a**: *Argonauta joanneus,* holotype [original of HILBER (1915: pl. 1), geological collection of the Universalmuseum Johanneum], Wenzelsdorf near Preding (Steiermark), Middle Miocene (Langhian); photo courtesy Martin GROSS. **b**: *Argonauta hians,* Recent. Scale bar = 10 mm.

HARZHAUSER (1999). It is here worthwhile to point out that the present arm hooks are not equivalents to the likewise-hook-shaped onychites of Mesozoic belemnoids (FUCHS et al. 2013). In belemnoids, chitinous onychites occur in pairs. One hook pair forms a functional unit together with one sucker. In Recent Decabrachia, the hooks ontogenetically derive from sucker rings, a phenomenon that is unknown in belemnoids.

Superorder Vampyropoda BOLETZKY, 1992 (= Octopodiformes)

The Vampyropoda include the eight-armed octopods (German: Kraken) and the pseudo-eight-armed vampire squid *Vampyroteuthis*. Whereas octopods largely reduced their shell, *Vampyroteuthis* retained a non-mineralized (chitinous) relict of the phragmocone, the gladius. Gladius-bearing ancestors are well-known from the fossil record. They appear in the Middle Triassic and disappear before the K/Pg-boundary (e.g. FUCHS 2006; FUCHS & LARSON 2011a, b; SCHWEIGERT et al. 2012). The first unambiguous octopods are known from the Late Cretaceous Plattenkalks of Lebanon (FUCHS et al. 2009).

Order Octopoda LEACH, 1817

Family Argonautidae CANTRAINE, 1841

The Argonautidae is an enigmatic group of octopods, not only because of its pelagic life style but also because argonaut females developed a thin 'shell' ('paper nautilus'). This likewise calcareous shell is secreted by flag-like membranes of the dorsal arm pair (in contrast to the actual molluscan shell gland). The male argonaut is 'shell-less' and dwarfed.

Argonauta joanneus HILBER, 1915 (Fig. 6a)

*1915 *Argonauta joanneus*, nova species. HILBER: 107, pl. 1.
1920 *Argonauta joanneus* HILBER. BÜLOW-TRUMMER: 270.
1922 *Argonauta johanneus* HILBER. NAEF: 294.
1976a *Argonauta joanneus* HILBER. SCHULTZ: 21.
2005 *Argonauta joanneus* HILBER. SAUL & STADUM: tab. 1.
2006 *Argonauta joanneus* HILBER. MARTILL & BARKER: 1037, tab. 1.

Holotype: original of HILBER (1915: pl. 1) by monotypy; geological collection of the Universalmuseum Johanneum.
Material: 1 specimen.
Type locality: Wenzelsdorf near Preding, Steiermark.
Type horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).

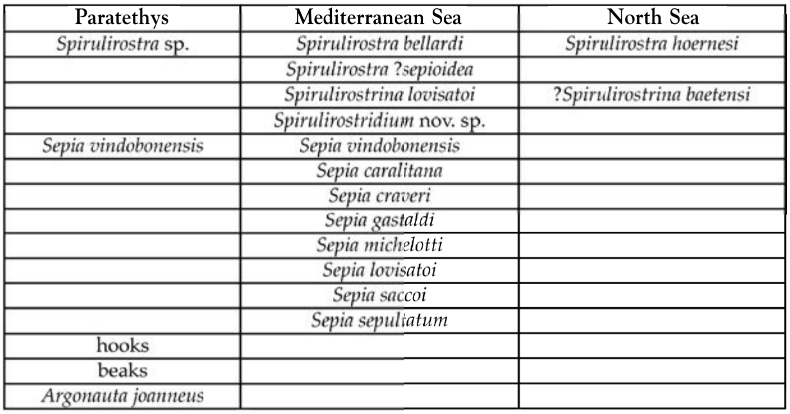
Remarks: *Argonauta joanneus* was long-time the oldest record of fossil argonauts, but in the second part of the 20th century older discoveries (Oligocene) indicate an early Cenozoic origin of this enigmatic group of pelagic octopods.

Discussion

The present 'Austrian' coleoids come from three different time periods: Paleocene (Thanetian: c. 58–55my), Oligocene (Rupelian: c. 33–28 my), and Miocene (Langhian: c. 15–13 my). During the Paleocene (*B. broilii*, *B. neumaieri*) and the Oligocene (*S. obtusum*), the coleoid diversity was apparently very low, while they appear to be more diverse during the Middle Miocene Langhian (5 taxa). The different diversities are likely to be explained by the limited availability of outcrops.

The Late Paleocene records of *B. neumaieri* and *B. broilii* were found in inner shelf deposits indicating waters depths of 50–150 m, as could be reconstructed from foraminiferal faunal compositions (RASSER & PILLER 1999; RÖGL & EGGER 2012).

The closure of the Tethyan Sea at the Eocene/Oligocene boundary induced the onset of the Eurasian Paratethys Sea. The Lower Oligocene 'Zementmergel' of Bad Häring were deposited in the western part of the Paratethys. On the basis of a mollusc fauna, LÖFFLER (1999) reconstructed a suptropical shelf areal for the life habitat of *Sp. obtusum*.



Paratethys	Mediterranean Sea	North Sea
Spirulirostra sp.	*Spirulirostra bellardi*	*Spirulirostra hoernesi*
	Spirulirostra ?sepioidea	
	Spirulirostrina lovisatoi	*?Spirulirostrina baetensi*
	Spirulirostridium nov. sp.	
Sepia vindobonensis	*Sepia vindobonensis*	
	Sepia caralitana	
	Sepia craveri	
	Sepia gastaldi	
	Sepia michelotti	
	Sepia lovisatoi	
	Sepia saccoi	
	Sepia sepuliatum	
hooks		
beaks		
Argonauta joanneus		

Table 2: A faunal comparison of Langhian coleoids from the Paratethys, the Mediterranean Sea and the North Sea.

The Middle Miocene (Langhian) coleoid fauna described above also roamed the Paratethys Sea and, more precisely, the Vienna Basin (i.e. a pull-apart basin, Hölzel et al. 2008), which covered large parts of eastern Austria and smaller areas in the southwestern Czech Republic and western Slovak Republic (Ková et al. 2004). The formation of the Vienna Basin and the Styrian Basin was initialized in the Early Miocene by the Eggenburgian (= lower Burdigalian) transgression (Harzhauser et al. 2008). Basal sedimentation is characterized by fluvial clays, sands and conglomerates passing into initial marine deposits. Sedimentation of more than 5000 m (Wessely 2006) of Cenozoic deposits lasted from the Early Miocene (Egerian) to the Late Miocene (Pannonian; Piller et al. 1996; Strauss et al. 2006; Wessely 2006).

The marine deposits of the Vienna Basin started to vanish from the Late Miocene onwards (i.e. Tortonian; Strauss et al. 2006). Hence the Austrian part of the Paratethys was fully marine only during a short time slice from the Early to Middle Miocene. The immigration of coleoids was probably triggered by a transgressive highstand during the Langhian (water depth c. 50–200 m; Piller & Harzhauser 2000). It seems that coleoids also benefited from the early-Badenian-build-up-event (EBBE), the ‘Badenian bloom’ of gastropods and foraminifera (Harzhauser et al. 2007). The Central Paratethyan fauna was part of the Proto-Mediterranean–Atlantic Region and was called the Danubian Province.

The total absence of further coleoids from the Langhian Paratethys might suggest that their occurrence was possibly concentrated in its western parts.

A faunal comparison with the Langhian Proto-Mediterranean Sea and the North Sea shows that the coleoid diversity in the Paratethys was moderate (Table 2). It was lower than in the Proto-Mediterranean Sea (12 species), but distinctly higher than in the North Sea (only 2 species; *?Spirulirostrina baetensi* & *Spirulirostra hoernesi*).

The limited availability of data on Cenozoic beaks and hooks deriving from coleoids can be explained by the mineralogy of those hard parts (Harzhauser 1999). The latter author noted the importance of the sediment/hard part mineralogy relation for preservation potential. The chitinous composition of such coleoid beaks and hooks excludes an adequate preservation. Only pelitic sediments with high clay contents (Harzhauser 1999), as observed by the ‘Baden Tegel’ from the Middle Miocene of the Vienna Basin, provide special conditions favouring the fossilisation of those fragile elements.

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Spirula – das unbekannte Wesen aus der Tiefsee

R. Hoffmann & K. Warnke

Wir widmen diesen Beitrag Prof. Dr. Malcolm Clarke,
einem der letzten ganz großen Meeresbiologen.

Zusammenfassung: *Spirula* ist eine der ungewöhnlichsten rezenten Tintenfischarten, da es eine gut ausgebildete, innere, gekammerte Schale besitzt. Aufgrund der Form dieser Schale wird *Spirula* umgangssprachlich auch Posthörnchen genannt. Die Schalen von *Spirula* können in großer Zahl an einigen subtropischen und tropischen Stränden gefunden werden, das eigentliche Tier ist aber schwer zu fangen, da es diurnale Wanderungen in Wassertiefen von etwa 100 m bis ca. 800 m durchführt. In der vorliegenden Arbeit wurde der aktuelle Kenntnistand über *Spirula* zusammengetragen.

Schlüsselwörter: Cephalopoda, Coleoidea, Lebensraum, Lebensweise, *Spirula spirula*

Abstract: ***Spirula* – the unknown deep sea creature.** *Spirula* is one of the most curious of the Recent cephalopod taxa owing to its well-developed, interior, chambered shell. Its common name ram's horn squid or little post horn squid derives from its peculiar, open spired shell. These shells may be found washed upon certain subtropical and tropical beaches in great numbers, whereas the living animal itself is difficult to catch because of its diurnal migration between approximately 100 m to 800 m water depth. The present work is a compilation of our present knowledge on *Spirula*.

Keywords: Cephalopoda, Coleoidea, habitat, mode of life, *Spirula spirula*

Einleitung

Die Gattung *Spirula* mit dem Trivialnamen Posthörnchen gehört neben *Sepia*, *Loligo*, *Octopus* und *Architeuthis* zur Gruppe der coleoiden Tintenfische. *Spirula* zeichnet sich durch ein nach innen verlagertes, spiralig aufgerolltes Gehäuse aus. Wie alle coleoiden Tintenfische besitzt *Spirula* zwei Kiemen zur Atmung. Bisher ist nur wenig über die Ernährungsweise, Fortpflanzung und den Lebensraum bekannt. Im Gegensatz zu den häufig an den Strand gespülten leeren Gehäusen sind Beobachtungen lebender Tiere äußerst selten. Erste Berichte über lebend gefangene und kurze Zeit am Leben gehaltene Tiere gibt Gray (1845). Dieser vertrat entgegen der vorherrschenden Meinungen seiner Zeit (vor allem Owen) die Ansicht, dass mit *Spirula* und nicht *Nautilus* der engste lebende Verwandte der ausgestorbenen Ammoniten vorliegt. Für einen detaillierten historischen Abriss der Erforschung von *Spirula* sei auf die Arbeit von Chun (1915) verwiesen. Innerhalb der Coleoideen, zu denen auch die ausgestorbenen Belemniten gehören, kam es wahrscheinlich mehrmals zu einer evolutiven, sukzessiven Rückbildung des Innenskeletts. So findet man als Relikte dieses bei den Octopoda am weitesten reduzierten Skelettes zum Teil nur noch zwei kurze hornige Stäbe im Weichkörper (Bizikov 2008). Nur *Spirula* besitzt als einziger Coleoideen-Vertreter ein lose, nahezu planspiral aufgewundenes Innengehäuse (Abb. 2, 4, 5). Innerhalb der rezenten Cephalopoden weist nur noch *Nautilus* (Perlboot) ein vollständig gekammertes Gehäuse auf. Das *Nautilus*-Gehäuse liegt jedoch nicht im Weichkörper sondern ist ein Außenskelett und seine Gehäusewindungen berühren sich. Zudem ist es andersherum aufgerollt als das *Spirula*-Gehäuse. Aufgrund des vollständig ausgebildeten Skelettes dienen beide Vertreter als Modellorganismen zur Rekonstruktion der Lebensweise ausgestorbener Cephalopodengruppen wie den Ammonoideen und unter anderem zur Beantwortung der Frage, ob Ammonoideen schwimmen konnten oder nicht. Aufgrund der leichteren Zugänglichkeit liegen umfangreiche Beobachtungen bisher nur für *Nautilus* vor (Dunstan et al. 2011a, b und die Zitate darin). So verwundert es nicht, dass vorrangig diese Beobachtungen auf Ammoniten übertragen wurden (Mutvei & Reyment 1973; Reyment 1980; Jacobs & Landman 1993, 1994; Lukeneder et al. 2010). Eine solche Herangehensweise steht jedoch im Gegensatz zur Erkenntnis, dass die Ammoniten aufgrund der Ausbildung des Juvenilgehäuses und

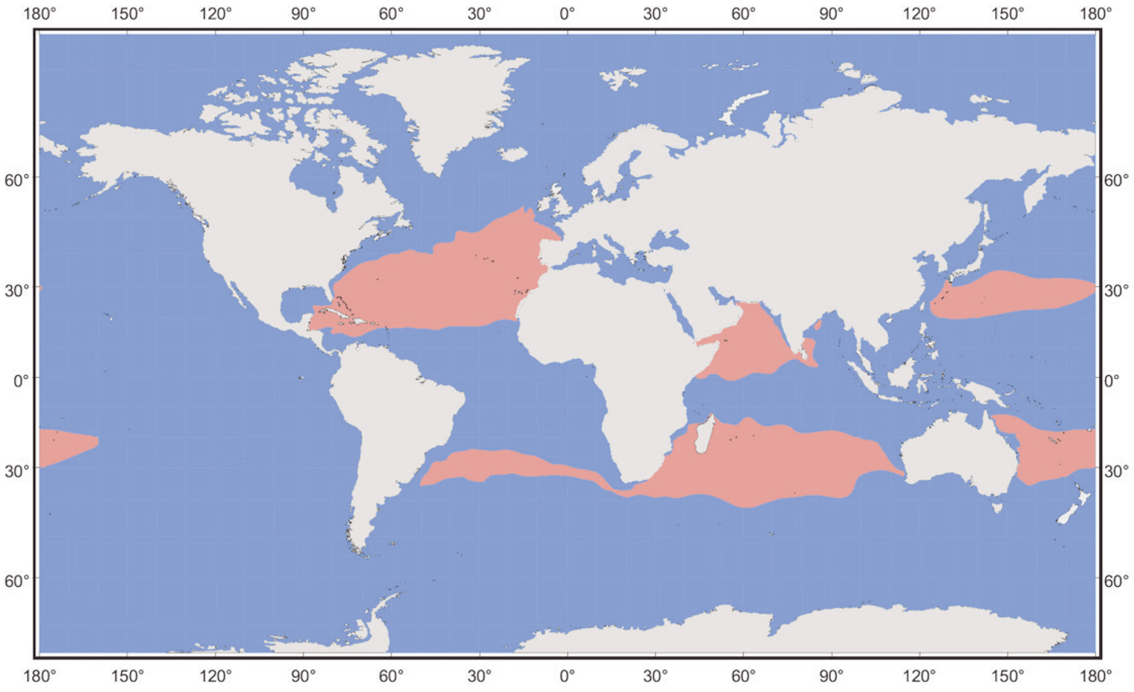

Abb. 1: Geographische Verbreitung von *Spirula spirula* (rot) (verändert nach Reid in Jereb & Roper 2005).

der Radula (Raspelzunge) neben anderen Merkmalen näher mit den Coleoideen verwandt sind als mit den Nautiloideen (Lehmann 1967; Engeser 1990; Keupp 2000). Sowohl Ammonoideen als auch Coleoideen besitzen eine, im Vergleich zu den Nautiloideen mit 13 Elementen pro Querreihe, schmale Radula mit 9 Elementen je Querreihe (Lehmann 1967; Kruta 2011). Auch die Schlupfgehäuse der Ammonoideen, die Ammonitellae, sowie die Ammoniten-Eier (Etches et al. 2009) entsprechen mit ca. 2 mm Durchmesser den Eigrößen vieler pelagischer Coleoideen (Boletzky 2003) und der Eigröße von *Spirula* (1.7–2 mm) im Speziellen (Chun 1910; Warnke & Keupp 2005; Lukeneder et al. 2010). Neuere Untersuchungen zeigen, dass die Eigröße in der Frühphase der Ammoniten einhergehend mit der zunehmenden Krümmung der Ammonitella und bei gleichzeitiger Vergrößerung der Wohnkammer rapide abnahm (De Baets et al. 2013). Nach De Baets et al. (2013) erhöhte sich die Anzahl der Eier (bis zu 25.000), die theoretisch in der Wohnkammer des Weibchens Platz gehabt hätten. Im Gegensatz dazu sind die Eier des rezenten *Nautilus* zwischen 2–3 cm groß (Martin et al. 1978). Bereits Jacobs & Landman (1993, 1994) und Saunders & Ward (1994) zweifelten an der Nutzbarkeit von *Nautilus* als Modelorganismus für Ammoniten. In der Folge steht nun *Spirula* verstärkt im Fokus für vergleichende Analysen zur Rekonstruktion der möglichen Lebensweise (Paläobiologie und Paläoökologie) der Ammonoideen (Warnke & Keupp 2005). Dafür spricht auch die nahezu identische Ausbildung der Anfangskammer (Protoconch) von *Spirula* und Ammoniten (Bandel & Boletzky 1979; Tanabe et al. 1980).

Spirula gehört, unter der Annahme dass die Verlagerung des Gehäuses nur einmal erfolgte, mit seinem innen liegenden Gehäuse zur Gruppe der Coleoidea. Die rezenten Vertreter werden unter anderem nach der Anzahl der Arme unterteilt. So haben z.B. *Octopus* und *Argonauta* acht Arme und gehören zur Gruppe der Octobrachia. *Spirula* hingegen hat wie *Sepia* zehn Arme und gehört somit folgerichtig zur Gruppe der Decabrachia Boettger, 1952. Der stammesgeschichtliche Ursprung der Ordnung Spirulida ist bisher nicht hinreichend geklärt. Zum Teil stützen sich die konkurrierenden Hypothesen auf schalenultrastrukturelle Untersuchungen, Untersuchungen der Embryonalgehäuse, Weichteilmerkmale und molekulare Daten (Haas 2003; Lindgren et al. 2004; Strugnell et al. 2005; Warnke et al. 2011; Keupp 2012). Erste echte Vertreter der Spiruliden tauchten demnach entweder bereits im Jungpaläozoikum (Doguzhaeva et al. 1999) oder aber wahrscheinlicher erst in der Oberkreide (Warnke et al. 2011; Fuchs et al. 2012) auf. Nur sehr selten wird über Fossilfunde von *Spirula* berichtet: So ein Fund aus dem unteren Miozän von Neuseeland durch Hayward (1976) und ?*Spirula mizunamiensis* aus dem Miozän von Japan (Tomida & Itoigawa 1981). Nach Engeser (1990) ist die Gattung *Spirula* erst ab dem Miozän (ca. 3,5 Millionen Jahre) belegt. Von etwas jüngeren Funden zwischen 800.000 und 131.000 Jahren berichten Kröchert et al. (2008) von fossilen Stränden auf Teneriffa und Semeniuk & Johnson (1982) von pleistozänen Stränden von West-Australien.

Frühere Autoren (Owen 1879; Huxley & Pelseneer 1885; Lönnberg 1896) erwähnten bis zu fünf Arten, die zur Gattung *Spirula* Lamarck, 1799 gestellt wurden. Eine Auflistung dieser „Arten“, von denen nur *Spirula spirula* (Linné, 1758) als valide Art durch Chun (1915), Naef (1923) und Bruun (1943) anerkannt wurde, findet sich in Young & Sweeney (2002). Nesis (1998) zieht allerdings in Zweifel, dass bei einer so weit verbreiten Art wie *Spirula spirula*, deren Verbreitung zudem auch noch unterbrochen ist, es sich um nur eine einzige *Spirula*-Art handelt. *Spirula* wurde bisher vor Indonesien, Melanesien, Australien, Süd- und Südost-Afrika, Nordwest-Afrika, zwischen den Kanarischen Inseln, in der Karibik, im Golf von Mexiko und vor Südbrasilien gefunden (Bruun 1943; Clarke 1969; Nesis 1987; Haimovici et al. 2007, Abb. 1). Neuere Fangdaten belegen, dass *Spirula spirula* auch in der Tasmanischen See (Haring et al. 2012) vorkommt.

Neuere morphometrische (Neige & Warnke 2010) und molekulargenetische Studien (Warnke 2007) kamen zu keinem eindeutigen Ergebnis, ob die Gattung *Spirula* mehr als eine Art enthält. Dies ist im Wesentlichen dem Mangel an für DNA-Analysen geeignetem Gewebe des ohnehin seltenen *Spirula*-Materials geschuldet. Haring et al. (2012) fügen den vorhandenen Tieren aus dem Atlantik Untersuchungen an einem Tier aus dem Pazifik hinzu. Aufgrund der geringen genetischen Distanzen der DNA-Sequenzen der drei analysierten mitochondrialen Gene kommen sie zu dem Schluss, dass die *Spirula spirula*-Populationen nicht genetisch voneinander isoliert sind und es sich um eine einzige Art handelt. Warnke (2012) führte auf der Basis von 13 Tieren aus den ostatlantischen Gewässern zwischen den Kanaren und Marokko sowie einem Individuum aus den Gewässern vor Südafrika eine AFLP (**a**mplified **f**ragment-**l**ength **p**olymorphism)-Analyse durch. Die Ergebnisse dieser Technik liefern ebenfalls keine Hinweise auf unterschiedliche Populationen oder gar unterschiedliche Arten. Da sich die molekularen Untersuchungen auf wenige Tiere stützen, wären zusätzliche molekulare Untersuchungen an weiteren Tieren sinnvoll.

Der wichtige Holotyp ist bis heute nicht auffindbar.

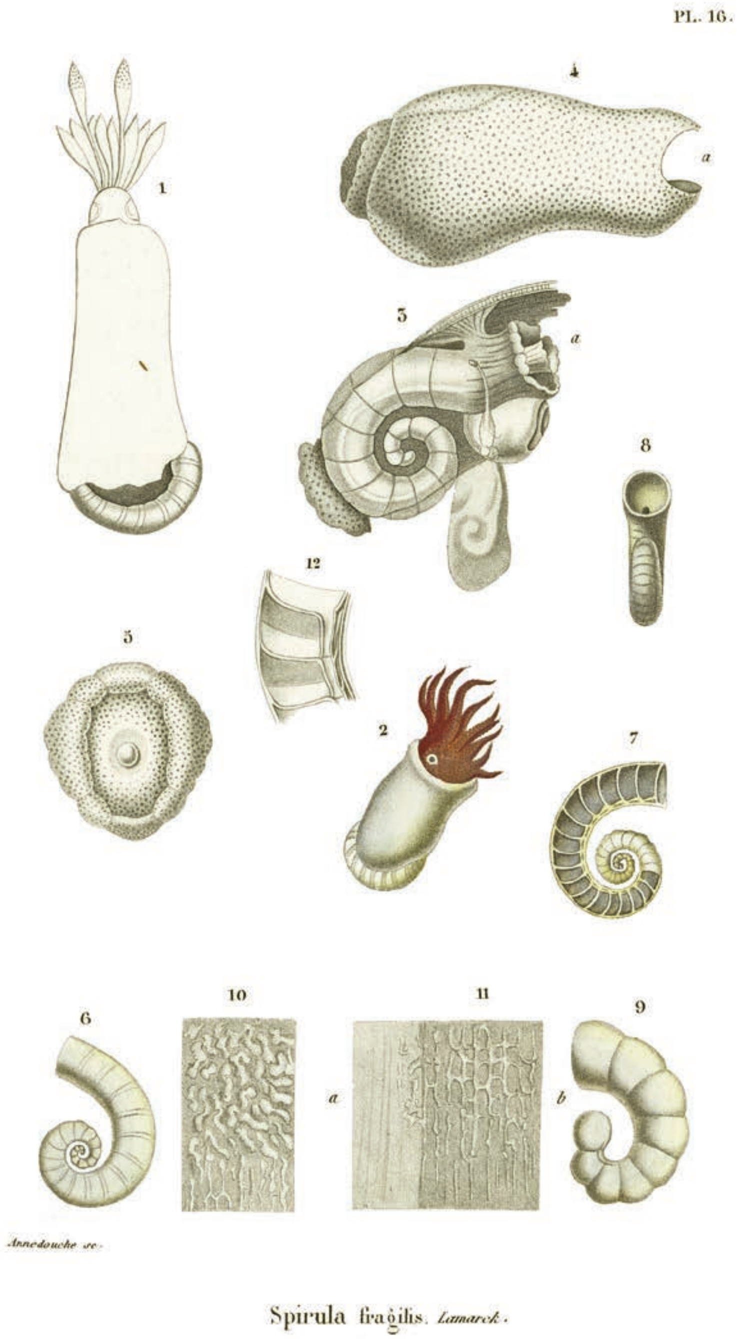

Abb. 2: Reproduktion aus d’Orbigny’s (1843) „Mollusques Vivants et fossiles“ mit einer ersten detaillierten morphologischen Studie zu *Spirula*.

Weichteile

Eine erste umfangreichere Studie der Morphologie von Hart- und Weichteilen liefert bereits d‘Orbigny (1843: Taf. 16; hier Abb. 2). Sehr detailliert beschreibt Chun (1915) die äußere Morphologie und den Aufbau innerer Organe und Organsysteme (Chun 1910) wie den Darmtrakt, das Gefäßsystem, den Harnsack und die weiblichen Geschlechtsorgane. Weitere Reviews und Ergänzungen finden sich bei Naef (1921–1923) und Nesis (1987). Das Nervensystem wurde in großen Teilen von Nixon & Young (2003) beschrieben. Da also insgesamt die Morphologie der Weichteile schwerpunktmäßig bereits im letzten Jahrhundert bearbeitet wurde, wird im vorliegenden Beitrag nur grob auf die allgemeine Morphologie der Weichteile eingegangen, ergänzt durch seltene Fotos von frischgefangenen Tieren. Einen guten Überblick über die Lage der wichtigsten Weichteile gibt Chun (1915).

Spirula erreicht eine Mantellänge von ca. 5 cm. Der Körper weist eine dunkelrot-braune z.T. silbrige Färbung

Abb. 3: (**A**) Lebende *Spirula* [Männchen, adult, Mantellänge (ML) ca. 4 cm, bei dem deutlich breiteren und längeren Arm handelt es sich um den Hectocotylus (Pfeil)] mit verletzter Mantelhautschicht. (**B**) Frischtote *Spirula* (Weibchen, ML ca. 3 cm, dorsale Ansicht) gefangen im Atlantik zwischen der Küste von Marokko und Fuerteventura mit Hilfe eines pelagischen Schleppnetzes auf der Meteorexkursion 65-3 (2005). Da das Tier tot ist, sind die Fangtentakel sichtbar (Pfeil). Zudem ist die innere Schale gut zu erkennen.

auf. Der zentrale Bereich des Mantels ist eher hellrosa bis hellbraun gefärbt und der Randbereich des Mantels erscheint weiß mit braunen Spitzen (Abb. 3b).

Am Kopf befindet sich die Armkrone mit insgesamt 10 Armen, von denen zwei als Tentakel ausgebildet sind (Abb. 3B, Pfeil). Die Saugnäpfe sind auf den Armen in Vierer-Reihen angeordnet (CHUN 1915). Beim Männchen sind zwei Arme zu Hectocotyles modifiziert. Die Hauptaufgabe des Hectocotylus ist es, ein Spermienpaket (Spermatophora) beim Weibchen in die Nähe des Mundes in die Bursa copulatrix zu platzieren. Die Hectocotyles sind länger und dicker als die restlichen Arme (Abb. 3A, Pfeil). Zwei weitere Arme sind bei Männchen und Weibchen zu Fangtentakeln mit speziellen Fangkeulen umgewandelt (Abb. 3A, Pfeil). Die Fangtentakeln sind wesentlich länger als die anderen acht Arme und besitzen an ihren Enden je eine etwas verbreiterte Tentakelkeule mit einer Vielzahl an Saugnäpfen, die in ca. 16 Reihen angeordnet sind und dem Fang von Beuteorganismen dienen. Seitlich am Kopf liegen die großen, hervorstehenden Linsenaugen oegopsiden Typs mit offener vorderer Augenkammer. Die Bedeutung der Augen wird auch durch den sehr großen Anteil der optischen Loben am zentralen Nervensystem deutlich (NIXON & YOUNG 2003). Das zentrale Nervensystem ist nach dem generellen Bauplan der Decabrachia aufgebaut (NIXON & YOUNG 2003).

Am posterioren Körperende befinden sich die horizontal orientierten, kleinen, nierenförmigen Flossen. Die Flossen werden als Stabilisatoren genutzt, um die Position bei Seitwärtsbewegungen zu halten oder wenn *Spirula* mit dem Kopf nach oben schwimmt (BRUUN 1943). Die eigentliche Schwimmbewegung wird, wie bei vielen anderen Coleoiden auch, mit Hilfe des muskulösen Mantels im Zusammenspiel mit dem Trichter ausgeführt.

Etwa mittig zwischen den Flossen befindet sich ein 1–3 mm großes Leuchtorgan (Photophore), welches als Terminalorgan bezeichnet wird. Bereits CHUN (1910) beschrieb aber die für ihn offensichtliche Ähnlichkeit des Terminalorgans mit den Leuchtorganen der Oegopsiden. Eine Studie von HERRING et al. (1981) ergab, dass – anders als bei vielen anderen zur Biolumineszenz befähigten Cephalopoden – bei *Spirula* keine Bakterien für das Leuchten verantwortlich sind. *Spirula* kann mehrere Stunden durch Eigen-Biolumineszenz ein schwach grünlich leuchtendes Licht mit schwankender Intensität erzeugen (SCHMIDT 1922; HERRING et al. 1981). Bisher gibt es keine hinreichend plausible Hypothese, die die Funktionsweise des Leuchtorgans erklären kann (NIXON & YOUNG 2003). Der Tintenbeutel, wie er auch von *Sepia* und *Octopus* bekannt ist, wurde zum ersten Mal von CARPENTER (1861) beschrieben und ist bei *Spirula* relativ klein (CHUN 1915).

Das bei reifen Weibchen stark entwickelte Ovar enthält viele, bis zu 2 mm große, gelbliche Eier verschiedener Entwicklungsstadien (Abb. 4A). Nur der linke Eileiter ist bei *Spirula* entwickelt (CHUN 1910). Beim Männchen ist ebenfalls nur ein Samenleiter entwickelt (Abb. 4B). HEALY (1990) untersuchte den Aufbau der Spermien sowie deren Entwicklung elektronenmikroskopisch. Aufgrund des ähnlichen Spermienaufbau vermutet HEALY (1990) eine nahe Verwandtschaft von *Spirula* zu den Sepiolida.

Hartteile

Die Schale von *Spirula* wurde bereits frühzeitig durch APPELLÖF (1893), MUTVEI (1964), BANDEL & BOLETZKY (1979) und BANDEL (1990) detailliert untersucht. Die kalkige Schale besteht aus prismatischen Aragonitkristallen. Die Schalenröhre weist keine Perlmuttlage auf. Perlmutt ist nur von den Septen des Phragmokons bekannt, weist jedoch eine veränderte Struktur im Vergleich zum Perlmutt bei *Nautilus* oder Ammoniten auf (MUTVEI 1964, 1970). Für Informationen zum ultrastrukturellen Aufbau der Schale sei auf die Übersicht in KEUPP (2000) und BANDEL & STINNESBECK (2006) verwiesen. Morphologisch ähnelt die Schale von *Spirula* stark der der Ammoniten, beginnend mit einer kugeligen bis schwach ovalen Anfangskammer, dem Protoconch. Dieser ist bei *Spirula* etwa 0,7 mm hoch und zwischen 0,5–0,7 mm weit. Die Schale des Protoconchs ist ca. 10 µm dick und durch eine markante Einschnürung deutlich vom restlichen Gehäuse abgesetzt (Abb. 5A). Die Öffnung der ersten Kammer ist ca. 0,4 mm groß und wird fast vollständig durch die Röhre des Siphos ausgefüllt (BANDEL & BOLETZKY 1979).

Daran schließt sich der Phragmokon, ein gekammerter Gehäuseabschnitt, der aus 30–35 [maximal 39 Kammern wurden für ein adultes Männchen berichtet (NIXON & YOUNG 2003)] Einzelkammern bestehen kann, an. Die gyrokon aufgewundene Schale erreicht ca. 2½ Windungen und wird maximal 45 mm im Durchmesser groß (SCHMIDT 1922). Der Vergleich aus maximaler Schalengröße und ungefährer Lebensdauer sowie Vergleiche zwischen Mantellänge und Anzahl der Schalenkammern lassen ein isometrisches Wachstum der Schale vermuten. Demnach wird im Abstand von 13–16 Tagen eine neue Kammer gebildet (PRICE et al. 2009). Die Gehäuseröhre ist im Querschnitt kreisrund (Abb. 5D). Vermutlich bilden sich der Protoconch und die erste Kammer bereits im Ei, wobei der Schlüpfling mit zwei Kammern insgesamt ca. 4 mm groß ist (NAEF 1923, 1928; BRUUN 1943: 73; SWEENEY et al. 1992). BANDEL & BOLETZKY (1979) berichten von einem Tier mit 2,7 mm Mantellänge mit bereits drei vollständigen Kammern und CLARKE (1970) von einem Tier mit 2 mm Mantellänge, jedoch ohne Angabe über die Anzahl der gebildeten Kammern. Eine Kammer wird jeweils durch eine Kammerscheidewand, auch Septum genannt, nach vorn und hinten begrenzt. Die Kammerscheidewände sind bei *Spirula* konkav und einfach uhrglasförmig ausgebildet (Abb. 5B). Alle Kammern sind durch einen organischen Schlauch (Sipho), der vom Mantelgewebe gebildet wird, durchzogen (Abb. 5B). Der Sipho ist auf der gesamten Länge von Blutgefäßen durchzogen und reicht bis in den kugeligen Protoconch hinein (DAUPHIN 1976; BANDEL & BOLETZKY 1979; BANDEL 1982; BANDEL & STINNESBECK 2006: Taf. 3, Abb. 2). Dort ist der Sipho an der Innenseite der Protoconchwand über ein deutlich dünneres organisches Band (Prosipho/Fixator) etwa gegenüber der Protoconch-Öffnung befestigt (MUNIER-CHALMAS 1873; HUXLEY & PELSENEER 1895; CHUN 1915; CRICKMAY 1925). An der Stelle, wo der Sipho alle anderen Kammerscheidewände passiert, wird das Septum nach hinten, von der Mündung weg, umgebogen. Diese den Sipho unterstützenden Strukturen werden Siphonalduten genannt und sind bei *Spirula* be-

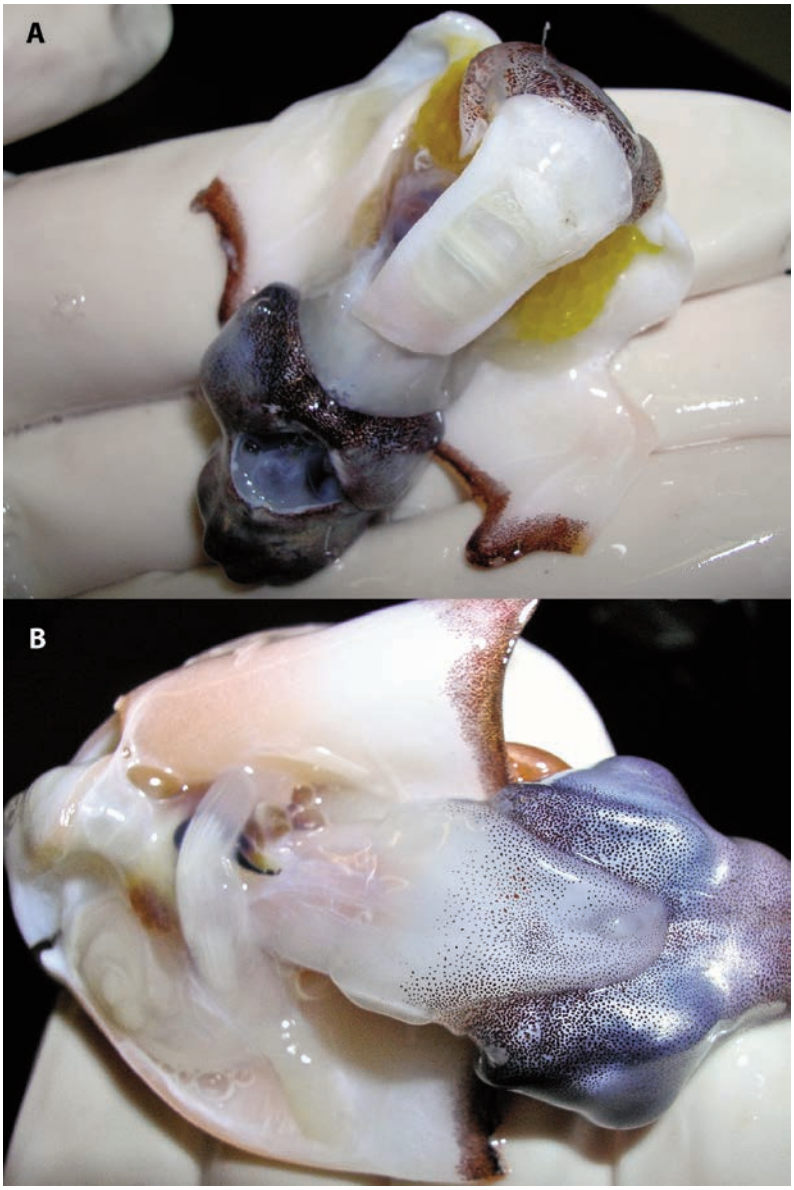

Abb. 4: (**A**) Frischtotes Weibchen (ML ca. 3,5 cm, Mantel von dorsal aufgeschnitten). Die unterschiedlich reifen Eier im Ovar sind gut an ihrer gelben Farbe zu erkennen. (**B**) Frischtotes Männchen (ML ca. 4 cm, Mantel von ventral aufgeschnitten). Bei der schneckenförmigen Struktur (links unten im Foto) handelt es sich um die Spermatophorendrüse. Die quer über den Tintenbeutel liegende Tasche ist der (nach oben im Bild) blind endende Needhamsche Tasche, in dem die fertigen Spermatophoren in Reserve aufgereiht liegen; der Penis ist die im Bild abwärts ragende, nicht sehr deutlich erkennbare Struktur.

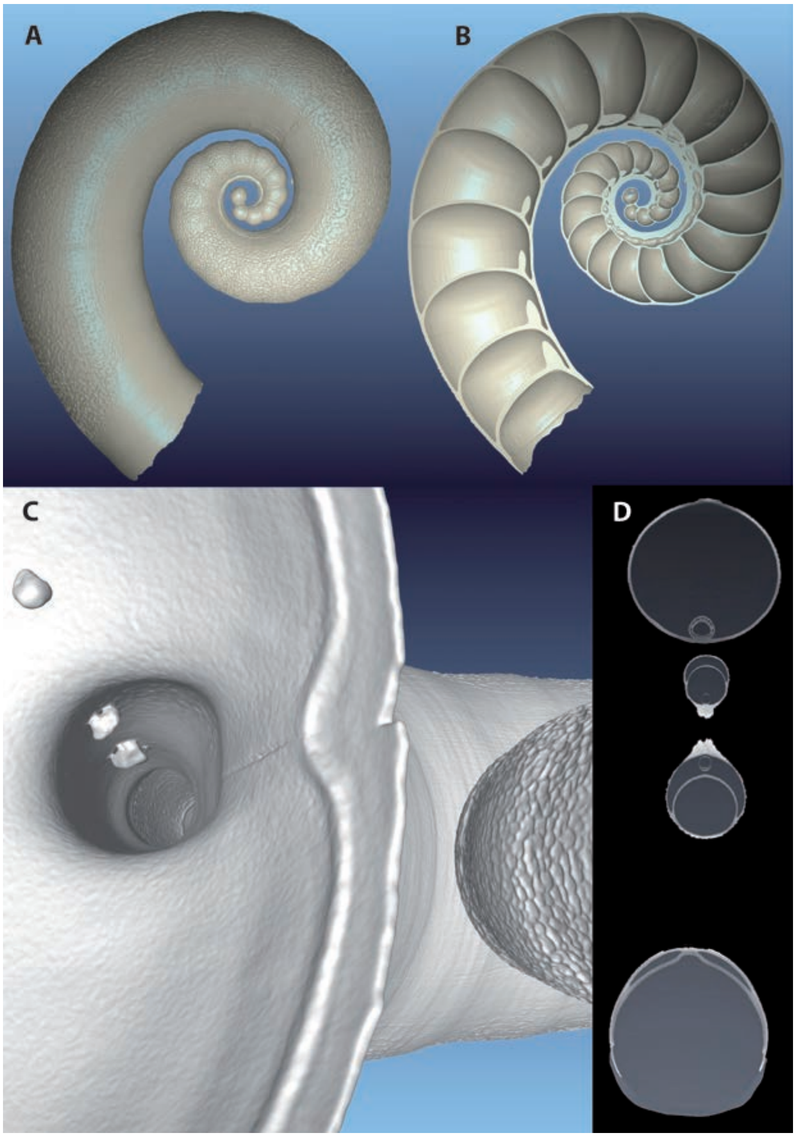

Abb. 5: Schale einer adulten *Spirula spirula*, ca. 17 mm im Durchmesser. (**A**) Schalenoberfläche mit retikulatem Muster, dem kugeligen Sipho und der verjüngten Gehäusemündung. (**B**) Längsschnitt durch die Schale mit sichtbarem Verlauf des Sipho und den einfach uhrglasförmigen Kammerscheidewänden. (**C**) Durchtritt des Siphos durch das zuletzt gebildete Septum auf der Röhreninnenseite. (**D**) Schale im Querschnitt mit erkennbarem Pendeln der Windungen um die Symmetrieebene.

sonders lang eistütenförmig ausgebildet, so dass die Siphonalduten der einzelnen Kammern beinahe ineinander stecken (Blainville 1839; Denton et al. 1967; Mutvei & Donovan 2006; Abb. 5B, C). Zwischen der organischen Hülle des Siphos und den kalkigen Siphonalduten des Septums befindet sich die Pillar-Zone die durch einen großen Porenraum charakterisiert ist, wodurch die Flüssigkeit abfließen kann (Mutvei 1964, Denton et al. 1967; Abb. 6A). Bei *Spirula* liegt der Sipho im Gegensatz zu den Ammoniten auf der Innenseite der Gehäuseröhre (Abb. 5B, C). Verantwortlich für diesen Unterschied ist eine anders geartete Aufrollung des Gehäuses. Ausgehend vom gradgestreckten Gehäuse der unmittelbaren Vorfahren der Ammonoideen, den Bactriten, erfolgte eine exogastrische Aufrollung des Gehäuses. Dies hatte zur Folge, dass der Sipho bei den Ammonoideen mehrheitlich auf der Außen- bzw. Ventralseite liegt (Kröger & Mapes 2007). Bei *Spirula* erfolgte, ausgehend von gradgestreckten Spiruliden-Vorfahren, eine endogastrische Gehäuseaufwicklung, wodurch der Sipho und damit auch die Ventralseite innen zu liegen kam und die Dorsalseite die Außenseite bildet (Keupp 2012).

Vor dem Phragmokon befindet sich bei Cephalopoden mit gekammerter Außenschale (ektocochleat) die Wohnkammer, in der der Weichkörper sitzt und mit Hilfe kräftiger Muskeln an der Innenseite der Wohnkammerschale befestigt ist. Durch die Verlagerung der Schale in den Weichkörper (endokochleat) ist die Wohnkammer bei *Spirula* reduziert (Abb. 5B). Die *Spirula*-Schale erreicht im Durchmesser etwa eine Größe von 2–3,5 cm. Ob es sich bei den häufigen Strandfunden um die Schalen ausgewachsener Tiere handelt, erkennt man zum Einen an der schwachen Verjüngung des Schalenendes sowie an den dichter stehenden Kammerscheidewänden (Abb. 5A, B). Im Querschnitt betrachtet, ist die lose aufgewundene Schale nicht perfekt symmetrisch angelegt und pendelt daher immer leicht um die Symmetrieachse (Abb. 5D). Die lose Aufwicklung und der schwach trochospirale Verlauf brachte dem Tier im Englischen den Namen ram's horn squid (deutsch: Widderhorn) ein. Die Schale von *Spirula* hält Drücken stand, die einer Tiefe von 1300–2300 m entsprechen (Denton & Gilpin-Brown 1971). Morphologisch ähnelt das Innengehäuse von *Spirula* dem Außengehäuse früher devonischer Ammoniten, die noch nicht planspiral aufgerollt waren, und dem Gehäuse der während der Kreidezeit dominierenden, heteromorphen Ammoniten z.B. *Aegocrioceras*, *Crioceratites*, die sekundär ihre Schale wieder entrollt hatten (Carpenter 1861).

Im letzten Abschnitt der zum Weichkörper hin offenen Röhre befindet sich die Leber, die von einem sackförmigen Mantelepithel umschlossen wird. Auf der dorsalen Innenseite der Gehäuseröhre befindet sich in jeder Kammer eine quadratisch bis rechteckige, ca. 1 mm breite und 2 mm lange Ansatznarbe (Bandel 1982; Bandel & Stinnesbeck 2006). Diese Narbe stellt eine feste Verbindung zwischen dem Mantel und der Schale dar und verankert somit den Weichkörper im jeweils letzten Schalenabschnitt. Durch den episodischen Einbau neuer Kammern muss diese Verbindung jedoch immer wieder gelöst bzw. neu hergestellt werden (Abb. 6B). Eine zweite Verbindung zwischen Weichkörper und Schale besteht fast auf der gesamten äußeren Schalenoberfläche und wird durch das retikulate, fein gekräuselte Oberflächenmuster der Schale angezeigt. Hier liegt der Schalensack fest an der Schale an (Chun 1915). Lediglich auf der Schaleninnenseite (ca. unteres Drittel) und dem vorderen Schalenrand fehlt diese feine Oberflächenstruktur und lässt daher vermuten, dass der Weichkörper dort nur lose auf der Schale aufliegt (Abb. 5A). Ähnliche Strukturen sind auf der Schalenoberfläche junger Gastropoden, z.B. dem Primärgehäuse von *Diodora italica*, zu finden und können zur Unterscheidung verschiedener Taxa herangezogen werden (Bandel 1982). Entlang des Schalenrandes kommt es zu einer dritten Verknüpfung, namentlich mit der Schale und dem Kopfretraktor (Naef 1923; Bizikov 2008), der dafür sorgt, dass *Spirula* sich bei Gefahr vollständig in den Mantel zurückziehen kann, so dass vom Kopf inklusive der Tentakel nichts mehr zu sehen ist (Chun 1910; pers. Beobachtung). Dadurch kann *Spirula* verhindern, dass bestimmte leicht erreichbare Teile des Weichkörpers (Arme) von Räubern abgebissen werden. Angreifer, die kleiner oder gleich groß sind wie *Spirula*, können die Beute kaum festhalten, da der Mantel fest ist und eine schmierige Oberfläche besitzt. So ist das Zurückziehen des gesamten Weichkörpers in den Mantel eine perfekte Strategie, um zu verhindern, von kleineren Räubern verschluckt zu werden (Bruun 1943).

Sehr selten lässt sich zwischen den Innenwindungen der Schale, beginnend am Protoconch, ein wenige Mikrometer dickes, unverkalktes Häutchen beobachten, das mittig zwischen den Windungen aufgespannt ist (Branco 1880; Warnke & Boletzky 2009). Die Funktion dieser Struktur ist nur unzureichend geklärt, könnte aber während der Bildung der ersten Kammern eine stabilisierende Wirkung gehabt haben und evolutiv mit einem Rostrum zusammenhängen (Warnke & Boletzky 2009). Möglicherweise handelt es sich bei der organischen Membran um eine zum Belemnitenrostrum homologe, stark reduzierte Struktur.

Mit Hilfe neuer bildgebender, nicht-invasiver Untersuchungsmethoden [Computer-Tomographie (CT), Magnetresonant-Tomographie (MRT)] ergeben sich neue Ansätze, um diesen selten lebend beobachteten Tiefsee-Tintenfisch weiter zu erforschen. So können die dreidimensionalen CT-Daten für detaillierte morphologische Analysen externer und interner Merkmale genutzt werden. Mit Hilfe der zusätzlichen Internmerkmale (z.B. Septenabstand, -dicke, Siphodicke, -lage, Schalendicke) wird es so vielleicht möglich herauszufinden, ob die Gattung *Spirula* aus einer oder mehreren Arten besteht, die sich klar morphologisch voneinander abgrenzen. Diese morphologische Studie kann und sollte auch durch weitere molekular-genetische Untersuchungen gestützt werden. Da in einem MRT-Datensatz hauptsächlich die Verteilung von Wassermolekülen wiedergeben wird, ist diese Methode hervorragend geeignet, das äußerst seltene Material vollständiger *Spirula*-Tiere zerstörungsfrei zu untersuchen. Dieses hochauflösende Verfahren kann zur Visualisierung der dreidimensionalen Anordnung der Weichteile innerhalb der Körpers genutzt werden und somit unser anatomisches Verständnis verbessern.

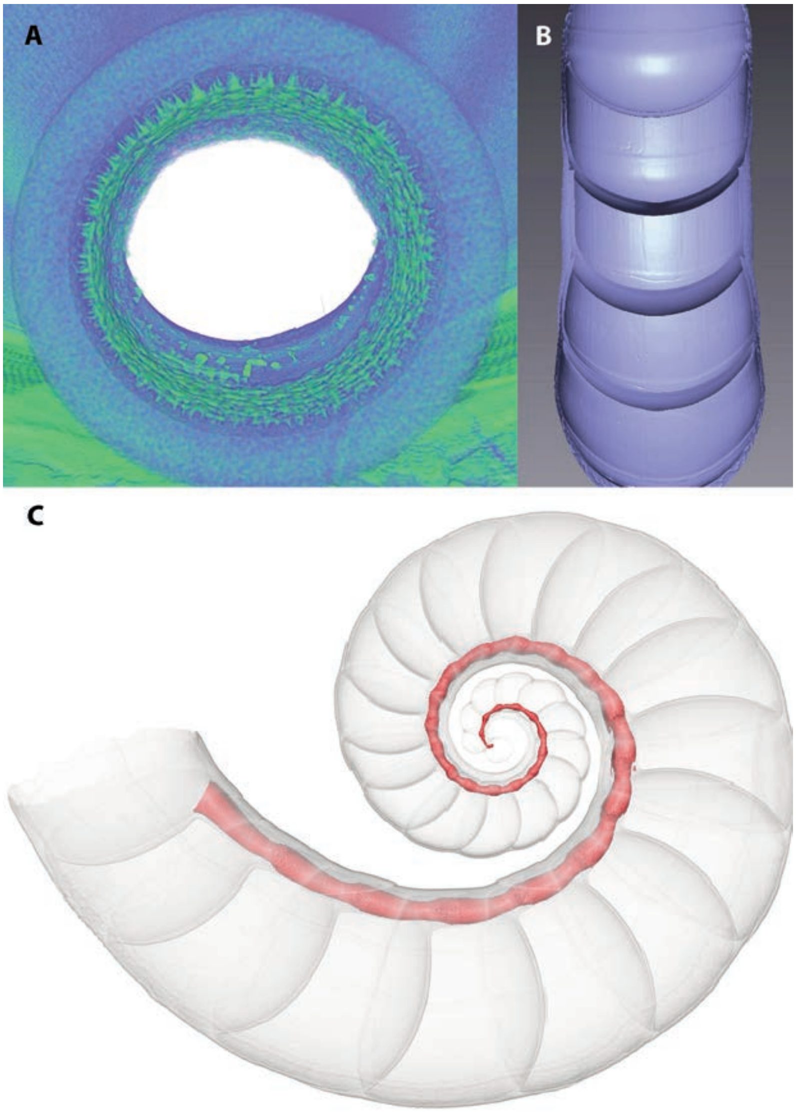

Abb. 6: (**A**) Pillarzone (Pfeilerzone, hier grünlicher Bereich der Röhreninnenseite, Röhrendurchmesser knapp 1 mm) des Siphos, durch die die Kammerflüssigkeit in Verbindung mit dem Siphogewebe steht. (**B**) Rechteckig ausgebildete Ansatznarbe (Pfeile) schwach in mehreren Kammern einer *Spirula*-Schale zu erkennen, Ansatznarbe ca. 2 mm lang und 1 mm breit. (**C**) Verlauf des Siphos von der ersten (Protoconch) bis zur letzten Gehäusekammer, man beachte das regelmäßige An- und Abschwellen des Siphodurchmessers, Gehäusedurchmesser ca. 17 mm.

Die kalkigen Statolithen liegen in einer mit Flüssigkeit (Endolymphe) gefüllten Kapsel – der Statozyste. Bei *Spirula* liegen zwei 12–13 mm^3 großen Statozysten in unmittelbarer Gehirnnähe. Darin befinden sich die aragonitischen Statolithen, die ca. 0.5–1 mm groß sind

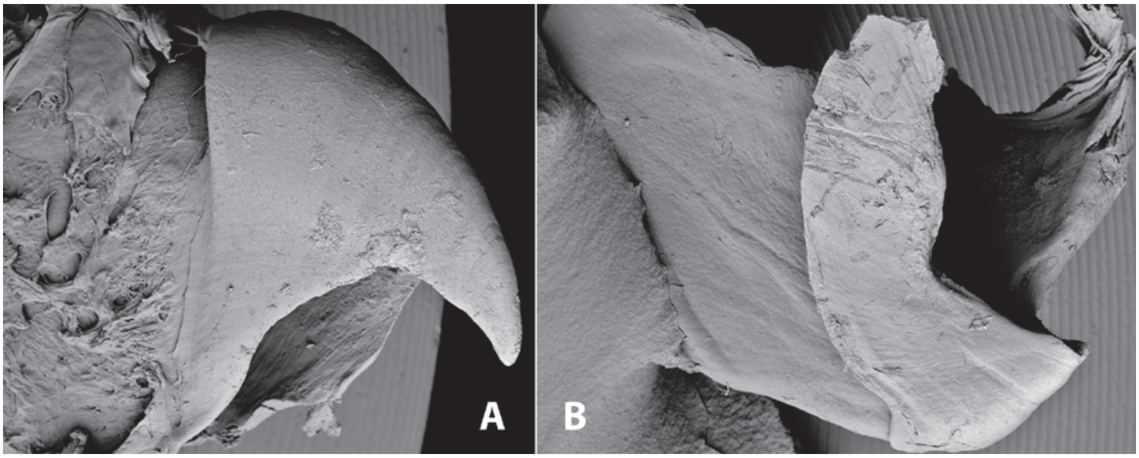

Abb. 7: Kieferapparat von *Spirula*. (**A**) Oberkiefer. (**B**) Unterkiefer im Rasterelektronenmikroskop-Bild, die Kieferelemente sind ca. 3 mm lang.

(NIXON & YOUNG 2003). Ihre komplexe Oberflächen-Morphologie ist nutzbar, um verschiedene Cephalopoden-Familien zu unterscheiden. Da sich ihre Form und Größe während des Wachstums ändern, werden meist nur die Statolithen ausgewachsener Tiere zur Bestimmung auf Artniveau herangezogen (CLARKE 1978, 2003). So unterscheiden sich die Statolithen von *Spirula* in ihrer Form deutlich von deren nahen Verwandten *Sepia*, Sepioliden und Teuthoiden (YOUNG 1989). Innerhalb der Statozyste, die ein Vielfaches des Volumens eines Statolithen hat, liegt der Statolith im vorderen, mit Sinneshärchen besetzten Feld, der Macula. Dabei ist der Statolith so orientiert, dass er mit seiner Längsachse in etwa in der Dorso-Ventralebene des Tieres liegt. Eine erste detaillierte Beschreibung der Cephalopoden-Statolithen gibt CLARKE (1978), der auch zum ersten Mal die Statolithen von *Spirula* abbildet. Die Statolithen sind flach scheibenförmig, in der Mitte am dicksten und zum Rand hin dünner-werdend, mit nahezu gleicher Ausdehnung in alle Richtungen (YOUNG 1989). Durch die Schwerkraft sinkt der Statolith durch die Flüssigkeit auf die Sinneshärchen. Der dadurch ausgelöste Reiz wird über Nervenbahnen direkt ins Gehirn geleitet. Zusätzlich gibt es in Streifen angeordnete Sinneshärchen (Crista). Sie verlaufen innerhalb der Statozyste vertikal, horizontal und diagonal – und sind in ihrer Funktion vergleichbar mit den Innenohren der Wirbeltiere. Mit den Statolithen kann sich das Tier in der Wassersäule orientieren. Somit sind die Cephalopoden-Statolithen in ihrer Funktion vergleichbar mit den Otolithen der Fische.

Der Buccal-Komplex bzw. die Buccalmasse ist eine kugelige Struktur, die als Hartteile neben dem Ober- und Unterkiefer in der Regel auch die Radula enthält und von Gewebe umhüllt wird (KERR 1931). Beide Hartteilstrukturen dienen dem Zerkleinern von Nahrung.

Die Kiefer, deren Spitzen aus der Buccalmasse hervorstehen können, sind dunkelbraun gefärbt (NIXON & YOUNG 2003) und *Spirula* kann damit kräftig zubeißen (SCHMIDT 1922; BRUUN 1943). Er ähnelt allen anderen Decabrachia-Kiefern (CHUN 1915). Das Rostrum des kürzeren Oberkiefers bildet eine nach vorn gerichtete zahnartige Spitze. Das Rostrum des längeren Unterkiefers ist eher kurz und geht in mäßig weite Flügel über (Abb. 7).

Die Raspelzunge (Radula) ist bei *Spirula* weitestgehend reduziert und fast nicht mehr nachweisbar. Lange Zeit galt die Radula bei *Spirula* als gut ausgebildet (CHUN 1915; NAEF 1923), bis erkannt wurde, dass die Zähnchen, die man gefunden hatte, nicht zur Radula, sondern zu den beidseits der Radula sich befindenden Buccal-Palpen gehörten (KERR 1931). Offensichtlich hatten diese eine ähnliche Funktion übernommen. Danach galt die Radula als vollständig reduziert (KERR 1931; NESIS 1987), bis NIXON & YOUNG (2003) die Radula in einer ca. 300 µm tiefen Tasche sitzend, mit kleinen, einheitlich stumpfartig-zugespitzten, verkümmerten Radulazähnen dokumentierten.

Lebensweise und Lebensraum

Über die Lebensdauer und -weise ist bisher am wenigsten bekannt, da *Spirula* – im Gegensatz zu *Architeuthis* – bis heute noch immer nicht lebend in ihrem natürlichen Habitat beobachtet werden konnte. Wahrscheinlich ist, dass *Spirula* nach Beobachtungen der Größenverteilung von Individuen einer Population zwischen 18–20 (CLARKE 1970) und 12–18 Monate alt werden kann (NESIS 1987). Die frisch geschlüpften Jungtiere ähneln im Aussehen wahrscheinlich im Wesentlichen den Adulten (NESIS 1987).

Abgesehen von den bekannten vertikalen Tag-/Nachtwanderungen (engl. diurnal migration) von juvenilen und adulten Tieren ist über den Lebensraum und mögliche Lebensraumwechsel während der Ontogenie von *Spirula* wenig bekannt. Dabei halten sich die Tiere tagsüber in größeren Tiefen (600–700 m) auf und wandern mit der Abenddämmerung in die oberen Wasserbereiche zwischen 100–300 m, um dann mit einsetzender Morgendämmerung wieder abzutauchen (CLARKE 1969).

Erst vor kurzem wurden durch geochemische Analysen stabiler Isotope (Sauerstoff, Kohlenstoff) genauere Erkenntnisse erlangt. Seitdem bekannt ist, dass Weichtiere, zu denen neben Muscheln und Schnecken auch die Cephalopoden gehören, Sauerstoffisotope im Gleichgewicht mit dem umgebenden Meerwasser in das Karbonat ihrer Schalen einbauen (WEFER & BERGER 1991), kann diese Methode erfolgreich genutzt werden, um die Wassertemperaturen zu rekonstruieren, bei denen die Schale gebildet wurde. Ist zusätzlich noch ein Temperaturprofil der in Frage kommenden Region vorhanden, kann somit die Wassertiefe ermittelt werden, in der die Schale gebildet wurde. Zur Beantwortung der Frage, in welcher Tiefe *Spirula* lebt, wurden deshalb unter anderem die Schalen lebend gefangener Tiere in den atlantischen Gewässern zwischen Fuerteventura und dem marokkanischen Festland analysiert (WARNKE et al. 2010). Die Ergebnisse der Sauerstoff-Isotope zeigten, dass die Tiere direkt nach dem Schlupf (Septum 1–9) bei Wassertemperaturen von etwa 8°C lebten. Danach wanderten die Jungtiere in wärmere Wasserbereiche von etwa 10–12°C ab (Septum 10-30). Die Isotopendaten der adulten Schalenabschnitte zeigten dann wieder abnehmende Temperaturen von etwa 8–10°C (Septum 30–31). Verknüpft man nun die bekannten Temperaturen mit einem Temperaturprofil der Wassersäule vor den Kanarischen Inseln, ergibt sich, dass die Jungtiere in ca. 800 m Wassertiefe geschlüpft sind. Dort verbleiben die frisch Geschlüpften für ca. 10–14 Wochen, unter der Annahme, dass alle 14 Tage ein neues Septum gebildet wird (WARNKE et al. 2010: Abb. 4). Danach erfolgt eine kontinuierliche Wanderung in wärmere Abschnitte bei etwa 350–400 m Wassertiefe. Dort verbringen die Tiere den längsten Lebensabschnitt bevor sie, vermutlich zum Ablegen von Eiern, wieder in tiefere Bereiche zwischen 550–600 m abwandern. Diese Daten gleichen in etwa den Isotopenanalysen, die an Strandfunden gemacht wurden (LUKENEDER et al. 2008; PRICE et al. 2009; WARNKE et al. 2010).

Mit den gewonnenen Erkenntnissen zur möglichen Wassertiefe, in der die Jungtiere schlüpfen, wird eine Ablage einzelner Eier oder großer Eimassen an der Wasseroberfläche nach dem Vorbild einiger Gastropoden unwahrscheinlich. Eine bodennahe Eiablage passt zu den Vorstellungen von BRUUN (1943) und NESIS (1987), die vermuteten, dass die Eier am Boden abgelaicht werden. Die Annahme, dass *Spirula* ihre Eier in tieferen Gefilden bodennah ablegt, wird auch durch die Beobachtung von CLARKE (1970) gestützt, der eine Konzentration sehr kleiner *Spirula*-Individuen (0,5 cm) in Wassertiefen von 1000–1750 m und etwas größere Tiere zwischen 600–700 m beobachtete.

Vergleichbar mit der Funktionsweise der *Nautilus*-Schale und sehr wahrscheinlich auch dem Ammoniten-Gehäuse dient die gekammerte *Spirula*-Schale, analog zur Schwimmblase der Fische, zum Ausgleich des Eigengewichts von Schale und Weichkörper. Die Aragonit-Schale hat einen Volumenanteil von ca. 8%, aber mit ihrer spezifischen Dichte (Aragonit = 2,6 g/cm^3) einen wesentlichen Anteil am Gesamtgewicht. Der Weichkörper hat nur eine unwesentlich höhere Dichte als das Meerwasser, weshalb dieser im Meerwasser nur ca. 3,6% des unter atmosphärischen Bedingungen gemessenen Gewichts anzeigt (DENTON & GILPIN-BROWN 1971). Im Gegensatz zu den *Nautilus*-Kammern mit bis zu 20 ml Volumen erreicht die größte *Spirula*-Kammer lediglich 2 ml Volumen (DENTON 1971). Der Kammerbau bei *Spirula* erfolgt nach DENTON et al. (1967) wie folgt: Zunächst wird die Schalenwand vorgebaut und anschließend ein neues Septum abgeschieden und verkalkt. Erst danach beginnt der Abpumpprozess der Flüssigkeit. Zu diesem Zeitpunkt ist die zuvor gebildete Kammer bereits vollständig geleert. Nur über den Sipho kann die zunächst in den Kammern enthaltene Flüssigkeit, die isosmotisch zum Meerwasser ist, abgepumpt werden. Das Abpumpen gelingt durch ein künstlich erzeugtes Konzentrationsgefälle der Salzionen zwischen Kammerflüssigkeit und Siphoblut. Die Kammerflüssigkeit enthält etwa 1/5 der Salzionenkonzentration verglichen mit der Konzentration des Siphoblutes. Das hat zur Folge, dass zunächst die Salzionen, dann die Flüssigkeit abtransportiert werden (DENTON 1973). Der durch das Abpumpen der Flüssigkeit erzeugte Unterdruck in der Kammer (0,8 atm und weniger) führt dazu, dass aus dem Siphonalblut Gas ausperlt (DENTON & GILPIN-BROWN 1971). Dieses Gas gibt dem Tier dann den erforderlichen ausgleichenden Auftrieb. Das Wachstum des Tieres (Gewichtszunahme) und der Vorbau des Gehäuses (Auftrieb) sind offensichtlich streng synchronisiert. Mit diesem einfachen osmotischen Prinzip ist ein Abpumpen jedoch nur in Tiefen oberhalb von 200 m möglich. *Spirula* hält sich aber die meiste Zeit in Tiefen >200 m auf. Erklärbar wird die Differenz zwischen tatsächlichem Lebensraum und theoretischer, maximaler Abpumptiefe durch einfache Osmose durch Annahme eines speziellen „Abpump-Gewebes“, in dem es zu deutlich höheren Salzkonzentrationen kommt und somit der osmotische Druck um ein Mehrfaches erhöht werden kann. Solch ein Gewebe wurde durch GREENWALD et al. (1982) für *Nautilus* beschrieben. Hierdurch wird es vermutlich auch *Spirula* möglich, ohne weitere Energie aufzuwenden, stabil in einer bestimmten Position innerhalb der Wassersäule schwebend zu verharren.

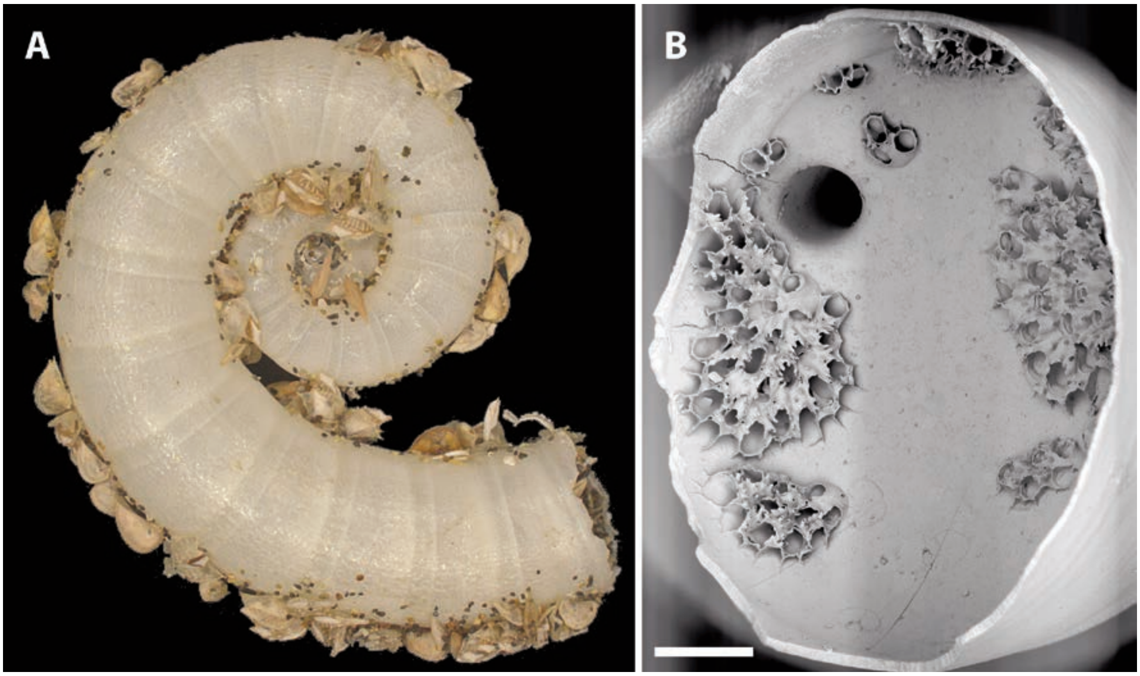

Abb. 8: (**A**) *Spirula*-Schale von ca. 16,5 mm Durchmesser mit beidseitig auftretendem postmortalen Bewuchs durch Entenmuscheln (Cirripedia), der erfolgt sein muss, während die leere Schale an der Meerwasser-Oberfläche trieb (leg. J. Schultz, Bonn). (**B**) Mehrere Kolonien der membraniporiden Bryozoe *Jellyella eburnea* (Hincks) inkrustieren das Innere der Wohnkammer (Kammerdurchmesser ca. 5,4 mm) (leg. und REM-Aufnahme J. Hartmann, Hamburg, Maßstab = 1mm).

Je mehr Kammern gebildet werden, desto stärker füllen sich die kleinsten Kammern wieder mit Flüssigkeit. So zeigten Denton & Gilpin-Brown (1971), dass bei 30 Kammern die letztgebildeten drei Kammern kaum Flüssigkeit enthielten, die darauffolgenden 18 Kammern keine, und die kleinsten Kammern wieder zunehmende Mengen an Flüssigkeit enthielten – die ersten bzw. kleinsten fünf Kammern sogar komplett gefüllt waren. Berücksichtigt man, dass die Schale lediglich 8% des Gesamtvolumens ausmacht und trotzdem die Gewichts- bzw. Auftriebsregulierung gelingt, dann ist dieses hydrostatische System sehr effizient. Da nur sehr geringe Mengen von Flüssigkeiten reguliert werden müssen, um ein positives oder negatives Schwimmgleichgewicht zu erreichen, liegt es nahe, dass *Spirula* die täglichen vertikalen Migrationsbewegungen mit Unterstützung dieses Auftriebsorgans bewerkstelligt bzw. unterstützend zum Rückstoßprinzip einsetzt. Bandel & Stinnesbeck (2006) beschreiben ferner, dass die permeable Zone des Siphos genau so lang wie die Kammer selbst und daher die Kammerflüssigkeit über die volle Länge in Kontakt mit dem Sipho steht. Die Flüssigkeit kann daher aktiv ab- und zurückgepumpt werden. Vermutlich wird die Vertikalbewegung aber auch einfach durch Gewichtsveränderungen des Tieres stark beeinflusst. Nach dem Fressen ist das Tier schwer und nach vollendeter Verdauung wieder leicht (Bandel & Stinnesbeck 2006).

Allerdings ist bis heute ungeklärt, wie lange es dauert, bis eine neugebildete Kammer vollständig leergepumpt ist und in welchem Maße *Spirula* auch in der Lage ist, Flüssigkeit in die Kammern zurückzufluten. Die vertikale Differenz zwischen der Tag- und Nachtposition von 300–600 m wird in mehreren Stunden zurückgelegt (Clarke 1969; Nixon & Young 2003).

Bei der Fortbewegung nach dem Rückstoß-Prinzip wird Wasser in die höhlenartige Erweiterung des Mantels eingeströmt und durch Zusammenpressen der kräftigen Mantelmuskulatur durch einen frei beweglichen Trichter wieder herausgepresst. Wird der Trichter beim Herauspressen nach unten gerichtet, bewegt sich das Tier aufwärts und umgekehrt. Da das Innengehäuse mit seinen gasgefüllten Kammern als Auftriebsorgan am adoralen/posterioren Körperende liegt, lebt *Spirula* vermutlich die meiste Zeit kopfüber schwebend in der Wassersäule. Aber auch kurzfristige Wechsel dieser Position (bis zu 1h) wurden an Lebendfängen beobachtet (pers. Beob. KW; mdl. Mitt. Clarke *in* Denton et al. 1967).

Spirula ernährt sich wahrscheinlich zum Großteil von pelagischen Crustaceen (Copepoden, Ostracoden und anderen), da Kerr (1931), Nixon & Dilly (1977) und Young (1977) bei Untersuchungen der Mageninhalte hauptsächlich Reste, zum Teil aber auch ganze Individuen davon gefunden haben. Nixon & Young (2003) berichten vom Mageninhalt eines präparierten Tieres, der Copepoden und Ostracoden als Nahrungsreste enthält. Dieses wurde durch den Nachweis bestimmter Sterole, die charakteristisch für pelagische Crustaceen sind, bei *Spirula* bestätigt (Ballantine et al. 1981). Nach Ballantine et al. (1981) kommen auch andere Crustaceen als Nahrung in Frage (Euphausiden, kleine Decapoden und Mysiden). Die Größe von *Spirula* spricht dafür, dass größere Nahrung nicht in Frage kommt und die diurnalen Wanderungen fallen in den Bereich der meist pelagischen Crustaceen. Da Hinweise auf Phytoplankton oder Nicht-Crustaceen als Nahrung fehlen, ist *Spirula* bei der Nahrungsaufnahme auf oben genannte Crustaceen spezialisiert (BALLANTINE et al. 1981). Daher erscheint die Angabe von LUKENEDER et al. (2008), dass auch andere Mollusken von *Spirula* gefressen werden, als unwahrscheinlich. Mit Hilfe der Analyse von Stickstoffisotopen kamen OHKOUCHI et al. (2012) zu dem Ergebnis, dass sich *Spirula* von Detritus und Zooplankton, zu dem auch die Larvenstadien sämtlicher Crustaceen zählen, ernährt.

Pathologien

Da von *Spirula* selbst kaum fossile Funde vorliegen, sind pathologische Veränderungen des Innengehäuses bisher nur von rezenten Vertretern bekannt. Bisher sind auch nur solche pathologischen Veränderungen bekannt geworden, die eine endogene Ursache haben, nicht jedoch solche durch Räuberattacken hervorgerufene anomale Veränderungen der Gehäuse. Zu diesen endogen verursachten Veränderungen gehören missgebildete Protoconche, die statt kugelig mützenförmig erscheinen. Inwiefern stark asymmetrische Gehäuse pathologisch bedingt sind, ist zurzeit unklar. Lokale Auflagerungen von sekundärem Aragonitmaterial im Bereich der letzten Kammern führen zu wulstigen Phänomenen und wurden von KEUPP (2012) als „Kallusbildung“ beschrieben. KEUPP (2012) führt diese auf besondere Belastungen des Kopfretraktormuskels zurück. Die Ursache für Schalenkonkretionen zwischen der äußeren und inneren Schalenschicht sieht KEUPP (2012) in einem möglichen Parasitenbefall und vergleicht sie mit ähnlichen Phänomenen, den Schalenperlen, bei Ammoniten (KEUPP 1987). Eine weitere pathologische Erscheinung betrifft die Ausbildung der oben beschriebenen Ansatznarbe auf der dem Sipho gegenüberliegenden Dorsalseite. Die sonst rechteckig bis quadratisch ausgebildet Ansatznarbe war in einem Fall pentagonal im Umriss und um ca. 20° gedreht (KEUPP 2012). *Spirula* ist aber auch ganz klar Beute anderer Organismen z.B. Seeschwalben (LONGLEY 1930) und anderen Seevögeln wie dem Petrel (Langflügel-Sturmvogel) und dem Albatross (IMBER 1973) sowie dem Gelbflossen-Thunfisch (OKUTANI & SUZUKI 1975; LANSDELL & YOUNG 2007) und Cephalopoden, z.B. *Illex argentinus* (SANTOS & HAIMOVICI 2002).

Postmortale Prozesse

Die Besiedelung von an der Wasseroberfläche flottierenden, leeren *Spirula*-Gehäusen durch Epöken erfolgte erst nach dem Tod. Epöken sind Organismen, die auf anderen hartteiltragenden Organismen sowie unbelebtem Hartgrund siedeln. Wie oben beschrieben, erzeugt die gekammerte Innenschale von *Spirula* einen positiven Auftrieb und nivelliert so das Eigengewicht von Schale und Weichkörper. Stirbt das Tier ab, wird nach und nach der Weichkörper zersetzt, und die Schale löst sich aus der sich zersetzenden toten Weichkörperhülle. Das Herauslösen der Schale geht einher mit dem Gewichtsverlust des Weichkörpers, womit die Auftriebskraft der Schale überwiegt und diese an die Wasseroberfläche auftreibt. Solange sich die Schale in der Körperhülle befindet, füllen sich deren Kammern auch bei höherem Druck nicht mit Flüssigkeit, dies kann erst geschehen wenn sich der Körper von der Schale gelöst hat (DENTON & GILPIN-BROWN 1971). Mit dem Lösen der Schale aus dem Weichkörper stellt die Schale ein potentiell zu besiedelndes Hartsubstrat für Epöken dar (Abb. 8). Fälle, in denen ein *Spirula*-Gehäuse durch Rankenfußkrebse (Cirripedia: Thoracia) der Art *Lepas anatifera* besiedelt wurden, berichten MCGINTY (1955), DAUPHIN (1979a) und DONOVAN (1989), Bewuchs mit Algen und Bryozoen berichtet DAUPHIN (1979b) von Strandfunden auf Mauritius. Genauere Untersuchungen des Bryozoenbewuchses unter anderem von *Spirula*-Schalen ergab, dass es sich um eine neue Gattung (*Jellyella*) aus der Gruppe der Membraniporiden handelt, die sich auf die Besiedelung pseudoplanktonischer Molluskenschalen und Algen spezialisiert hat (TAYLOR & MONKS 1997). Von der Außenschale des rezenten *Nautilus* sind Fälle bekannt, bei denen die Schale bereits zu Lebzeiten durch eine Vielzahl unterschiedlicher Epöken, z.B. Bryozoen, Foraminiferen, Korallen, Polychaeten, Cirripedia, Muscheln und Schwämme, besiedelt wurde (LANDMAN et al. 1987). Die Verbreitung leer aufgefundener *Spirula*-Gehäuse kann für eine naturgetreue Abbildung des Lebensraumes nicht herangezogen werden, da die leeren Schalen mit positivem Auftrieb ähnlich wie leere *Nautilus*-Gehäuse mehrere Monate im Meerwasser treiben und dabei mehrere 100 km durch Meeresströmungen verdriftet werden können (LUKENEDER et al. 2008; PRICE et al. 2009). So berichtet GIRARD (1892) über *Spirula*-Schalen von mediterranen Küstenabschnitten bei Tunis, Spanien und den Balearen, die mit der Strömung durch die Meerenge von Gibraltar transportiert worden sein müssen, da aus dem Mittelmeer bisher keine lebende *Spirula* gesichtet wurde (NAEF 1923).

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Taxonomic review of early Darriwilian estonioceratids (Tarphycerida, Nautiloidea) from Sweden, Estonia, and the 'Diluvium-Geschiebe' of northern Germany and Poland

A.H. KING

Abstract: Estonioceratid nautiloids are a common and attractive component of mid-Ordovician (early Darriwilian) cephalopod faunas in Baltoscandia. Their distinctive conchs are typically loosely coiled, and vary from forms which possess an apically coiled portion with divergent final whorl, to open gyrocones and even torticones. This paper briefly reviews the taxonomy of several mainly Swedish and Estonian estonioceratid genera which were formerly poorly known at the time of the publication of the Tarphycerida section of the 'Nautiloid Treatise Part K' (FURNISH & GLENISTER 1964) or have been described since.

Keywords: Systematics, Estonioceratidae, Kundan, Aserian

Introduction

Fossil tarphycerid nautiloids are widespread and commonly encountered within the Mid Ordovician 'Orthoceratite Limestone' facies of Baltoscandia, especially Sweden and Estonia, and coeval glacial erratic boulders ('Diluvium-Geschiebe') of northern Germany and Poland. The majority of forms that occur within the Kundan and Aserian Stages (early Darriwilian) belong to the family Estonioceratidae. Their loosely coiled gyroconic shells are very distinctive and in Sweden these nautiloids are referred to as 'böjda Cephalopoda' meaning literally 'bent Cephalopoda'.

In common with other groups of cephalopods, the preservation of tarphycerids within the 'Orthoceratite Limestone' facies is generally very good. Although many of the sequences are highly condensed, the fine-grained limestones often enable detail of external shell ornament to be discerned and many conchs are relatively uncrushed facilitating examination of whorl cross-sections and early apical stages. Occasionally limestone beds are phosphatised, which permits extremely fine detail of the siphuncle wall and structure of connecting rings to be observed (MUTVEI & DUNCA, 2011).

This paper briefly reviews the status and taxonomy of estonioceratid nautiloids from the early Darriwilian Stage of Baltoscandia. The taxa covered include *Estonioceras* HYATT *in* ZITTEL, 1900 along with five previously little known or obscure genera, namely *Falcilituites* REMELÉ, 1886, *Tragoceras* REMELÉ, 1890, *Eichwaldoceras* BALASHOV, 1955, *Bentoceras* STUMBUR, 1962 and *Aserioceras* STUMBUR, 1962. The torticonic genus *Pakrioceras* was extensively described by STUMBUR & MUTVEI, 1983, and is only briefly summarised here for reasons of completeness.

Revision of a number of these genera is long overdue. Within the Tarphycerida section of the 'Nautiloid Treatise Part K' (FURNISH & GLENISTER, 1964, pp. K357-K359) *Falcilituites* was regarded as synonymous with *Estonioceras*; *Eichwaldoceras* was "Poorly known. Apparently like *Tragoceras*" and *Tragoceras* was considered "similar to *Aphetoceras* and possibly synonymous". Although *Bentoceras* and *Aserioceras* were erected before publication of the Treatise Part K, they were omitted from the volume. The re-examination of type material along with study of additional specimens from Sweden and Estonia now enables the status of all these genera to be re-assessed, and provisional lists of their constituent species to be presented here. A more thorough revision of the Baltoscandian estonioceratids, including assessment of the range of intraspecific variation and the description of new taxa, is currently in preparation by the author.

Stratigraphy

Within Baltoscandia, the estonioceratid nautiloids are mainly found within limestones assigned to the ear-

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Table 1: Biostratigraphical correlation of the Baltoscandian Stages/Substages with trilobite, graptolite and conodont zonation schemes.

		Baltoscandian Stages / Substages		Trilobite zonation	Graptolite zonation	Conodont Zonation
DARRIWILIAN	4c	UHAKUAN		*Illaenus crassicaudata*	*Hustedograptus teretiusculatus*	*Pygodus anserinus*
		LASNAMÄGIAN		*Illaenus schroeteri*	*Pseudoamplexograptus distichus*	*Pygodus serra*
		ASERIAN		*Illaenus planifrons /* *Illaenus platyurus*	*Pterograptus elegans*	*Eoplacognathus suecicus*
	4b	KUNDAN	Aluojan	*Megistaspis gigas* *Megistaspis obtusicauda*	*Nicholsongraptus fasciculata*	*Eoplacognathus pseudoplanus*
	4a		Valastean	*Asaphus raniceps*	*Holmograptus lentus*	*Yangtzeplacognathus crassus*
			Hunderumian	*Asaphus expanses*	*Undulograptus austrodentatus*	*Lenodus variabilis*

GENUS ➡ **▼ CHARACTER**	*Estonioceras* Noetling, 1883	*Falcilituites* Remelé, 1886	*Tragoceras* Remelé, 1890	*Eichwaldoceras* Balashov, 1955	*Aserioceras* Stumbur, 1962	*Bentoceras* Stumbur, 1962	*Pakrioceras* Stumbur & Mutvei, 1983
Shell form	Stout, moderately expanding. Early whorls in contact, final whorl divergent	Slender, early whorls in contact, final whorl divergent	Very slender. Final whorl divergent, early whorls unknown but likely in contact	Moderately expanding, gyroconic. Final whorl divergent, inner whorl(s) unknown	Moderately expanding, likely gyrononic. Final whorl divergent, inner whorl(s) unknown	Slender, gyroconic, no whorls in contact. Final whorl divergent.	Moderately expanding, loose torticonic spiral
Whorl section	Early whorls depressed to fusiform, final whorl slightly depressed to circular	Slightly depressed to weakly compressed	Compressed	Circular	Weakly compressed	Subcircular to weakly compressed	Subcircular to weakly depressed
Siphuncle position	Subventral	Subventral - subcentral	Ventral	Ventral	Ventral	Subcentral to subventral	Ventral
Ornament	Indistinct, fine growth lines	Distinct raised growth lines and lirae	Moderately coarse, faint irregular lirae and growth lines	Coarse lirae	Coarse lirae	Smooth, with feeble growth lines	Distinct narrow annuli with growth lines
Sutures	Transverse	Transverse or with very shallow lateral saddle	Curved with distinct lateral saddle	Transverse	Broad shallow lateral and dorsal saddles	Transverse	Transverse laterally with shallow ventral lobe
Stage (Substage) occurrence	Kundan	Kundan	Kundan (Aluojan)	Kundan (Hunderumian – Valastean)	Aserian	Kundan	Aserian and possibly early Lasnamägian

Table 2: Character matrix table and stratigraphic occurrence of Baltoscandian estonioceratid genera.

ly Darriwilian Kundan or Aserian stages. The correlation of these stages (and their substages) with standard international graptolite and conodont zonation schemes is provided in Table 1. The Kundan and Aserian stages (represented in Sweden by the Holen Limestone and Segerstad Limestone formations respectively) equate approximately to the *Didymograptus* '*bifidus*' (*Undulograptus austrodentatus* to *Nicholsongraptus fasiculata*) and lower *Didymograptus murchisoni* (*Pterograptus elegans*) graptolite zones; and the upper part of the *Lenodus variabilis* to near top of the *Eoplacognathus suecicus* conodont zones. Megistaspid, asaphid and illaenid trilobites are also useful locally within the condensed Swedish and Estonian 'Orthoceratite Limestone' sequences to facilitate correlation.

Taxonomy

In this section and figure captions, the following abbreviations are used when referring to material or museum collections:

GIT – Institute of Geology, University of Tallinn, Estonia
RM – Museum of Natural History, (Naturhistoriska Riksmuseet), Stockholm, Sweden
MNH – Museum of Natural History, London, UK
MfN – Museum für Naturkunde, Berlin, Germany

Order Tarphycerida
FLOWER *in* FLOWER & KUMMEL, 1950

Family Estonioceratidae HYATT in ZITTEL, 1900

Diagnosis: Smooth or ribbed gyroconic to loosely coiled, rarely torticonic tarphyceracones, typically with divergent last whorl. Whorl section depressed to compressed, dorsal impression absent or only weakly developed. Siphuncle ventral to subventral. Septal necks orthochoanitic, connecting rings thick. Growth lines and raised lirae form conspicuous broad, shallow to deep hyponomic sinus (adapted from FURNISH & GLENISTER 1964: K357).

Discussion: Following FURNISH & GLENISTER (1964), the Estonioceratidae is retained here as a separate family and distinguished from the similar Tarphyceratidae (HYATT, 1894) on the general basis of conch form (more tarphyceraconic in the Tarphyceratidae) and for tarphyceratids to possess an impressed area in the dorsal region of the whorl, related to tightness of coiling. The Trocholitidae SCHRÖDER, 1891 differs from both the Tarphyceratidae and Estonioceratidae in possessing a dorsal siphuncle.

Estonioceratid faunas in Sweden, Estonia and Russia, and from coeval glacial erratic boulders in northern Germany and Poland have much in common. All taxa possess similar siphuncular features (orthochoanitic septal necks and thickened connecting rings) and distinction at generic and specific levels tends to reply upon overall conch form and expansion rate, whorl section, position of the siphuncle, shape of the suture and type of external shell ornament (KING 1999: 150). A summary of the main morphological features that distinguish each of the Baltoscandian estonioceratid genera and their stratigraphical occurrence is provided in Table 2.

Constituent genera: *Estonioceras* NOETLING, 1883; *Aethoceras* TEICHERT & GLENISTER, 1954; *Alaskoceras* MILLER & KUMMEL, 1945; *Aphetoceras* HYATT, 1894; *Aserioceras* STUMBUR, 1962; *Bentoceras* STUMBUR, 1962; *Clytoceras* ULRICH, FOERSTE, MILLER & FURNISH, 1942; *Eichwaldoceras* BALASHOV, 1955; *Falcilituites* REMELÉ, 1886; *Pakrioceras* STUMBUR & MUTVEI, 1982; *Pycnoceras* HYATT, 1894; *Shumardoceras* ULRICH & FOERSTE, 1936 and *Tragoceras* REMELÉ, 1890.

Occurrence: The Estonioceratidae, as defined above, occurs within the Floian to Darriwilian stages and has an extremely widespread distribution extending from Canada, Newfoundland, Alaska and North America through Baltoscandia (especially Sweden and Estonia) to Russia, Northwest China and Australia. The family is also recorded from glacial erratic boulders ('Diluvium-Geschiebe' derived from Baltoscandia) in northern Germany and Poland.

Genus *Estonioceras* NOETLING, 1883 (Fig. 1A–D)

Remeleceras HYATT, 1894

Type species: *Lituites lamellosus* HISINGER, 1837 [by original designation; NOETLING 1883: 275]

Diagnosis: Moderately expanding, relatively stout conch, early whorls in contact, with depressed or fusiform section and typically with umbilical perforation; last whorl divergent, slightly depressed to circular in section. Conch narrowly to widely camerate, sutures straight, transverse. Siphuncle subventral, septal necks short, orthochoanitic; connecting rings very thick and layered. External ornament indistinct, consisting of fine growth lines which form an inconspicuous, very broad ventral sinus.

Discussion: *Estonioceras* is a common tarphycerid in the Kundan Stage of Baltoscandia; its conch form and expansion rate readily distinguish it from other estonioceratid genera. The differences with *Falcilituites* are noted under that genus below.

HYATT (1894: 525) erected *Remeleceras* for forms closely allied to *Estonioceras* but differing in possessing a depressed, elliptical whorl section with deeper dorsal impressions and an "extraordinary form of annular muscle". Examination by the present author of material belonging to the type species of *Remeleceras*, *Estonioceras impressum* (HYATT, 1894, also figured by MUTVEI 1957: pl. 2) failed to provide sufficient evidence for distinguishing the two genera. Some species of *Estonioceras*, notably *E. perforatum* SCHRÖDER, 1891, also exhibit a very shallow, weak but conspicuous impressed area. The other characteristic features mentioned in the description of *Remeleceras* are also considered here to fall within the morphological range exhibited by *Estonioceras*.

Numerous Baltic cephalopod species have been assigned to *Estonioceras*. Many of these were described during the 19th century (e.g. HISINGER 1831, 1837; QUENSTEDT 1846; REMELÉ 1880, 1886, 1890; SCHRÖDER 1891) and were based primarily on the form of coiling. The diagnostic value of that criterion is regarded warily here, especially in view of the coiling variation exhibited by *Bentoceras proteus* (HOLM, 1891) and the variation in size of the apical coiled portion in *Falcilituites decheni* (REMELÉ, 1880) / *Falcilituites subcostatum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880). Consequently features such as expansion rate, whorl section and whorl width:whorl height ratios are considered as more reliable indicators on which to base taxonomic study. Ongoing research tends to corroborate many, although not all, the species of *Estonioceras* erected by earlier workers and it is considered likely that 'approximately half-a-dozen' species are genuinely distinct. Whilst recognising the amount of intraspecific variation in some species of *Estonioceras*, the

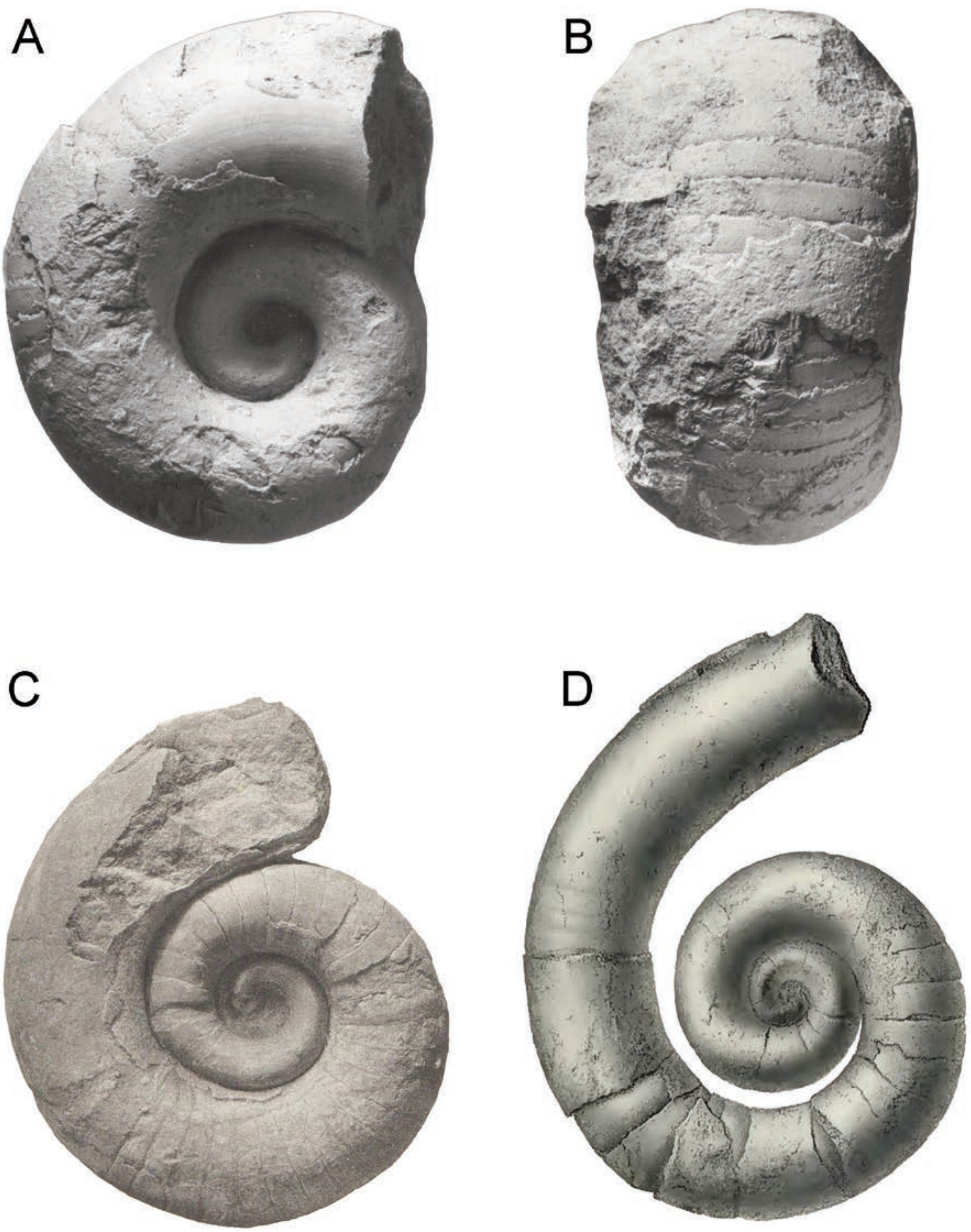


Fig. 1: (**A-B**) *Estonioceras lamellosum* (Hisinger, 1837), RM Mo152356, early Kundan stage, Dalarna, Sweden; lateral and ventral views, diameter 70 mm [original of Angelin & Lindström 1880: pl. 10, fig. 4]. (**C**) *Estonioceras imperfectum* (Quenstedt, 1846), RM Mo149982, late Kundan Stage, Tallin, Estonia; lateral view, diameter 90 mm [original of Mutvei 1957: pl. 3, fig. 4]. (**D**) *Estonioceras ariense* (Schmidt, 1858), late Kundan Stage, Kunda, Estonia; lateral view, maximum diameter 209 mm [Holotype, original of Schröder (1891: pl. 2, figs 5a-e) and Balashov (1953: pl. 1, fig. 1)].

claim expressed by Dzik (1984: 39) that “there is only a single described species of *Estonioceras* in the Baltic area” seems to be an over-simplification of the position.

Constituent species: The following list is provisional and represents ‘research in progress’ by the present author:

Estonioceras lamellosum (Hisinger, 1837)
Estonioceras convolvans (Hisinger, 1831). [*Estonioceras heros* (Remelé, 1880) and *Estonioceras kundense* Balashov, 1953 are probably synonymous with *E. convolvans* (Hisinger, 1831)]
Estonioceras imperfectum (Quenstedt, 1846)
Estonioceras ariense (Schmidt, 1858)
Estonioceras muellaueri (Dewitz, 1880) [Status uncertain]
Estonioceras peforatum Schröder, 1891
Estonioceras impressum (Hyatt, 1894) [Type of *Remeleceras*]

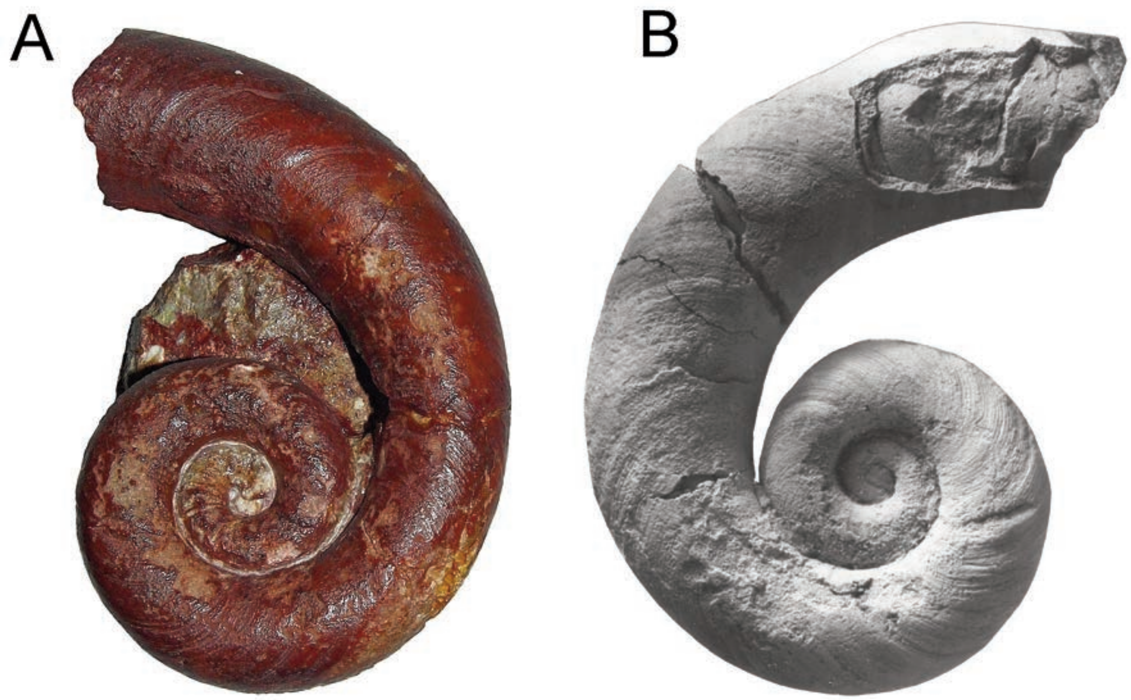


Fig. 2: (**A**) *Falcilituites decheni* (Remelé, 1880), Kundan Stage, glacial erratic boulder, northern Germany; lateral view, maximum diameter 66 mm [Holotype, original of Remelé (1880: pl. 2, figs 1a-c) and Neben & Krueger (1971: pl. 18, figs 2-3)]. (**B**) *Falcilituites subcostatum* (Angelin *in* Angelin & Lindström, 1880), RM Mo150566, late Kundan Stage, Alsarbyn, Dalarna, Sweden; lateral view, maximum diameter 80 mm [Syntype, original of Angelin & Lindström (1880: pl. 11, figs 5-8)].

Occurrence: *Estonioceras* is common and widespread in the Kundan Stage of Sweden, and is recorded from Öland, Dalarna, Östergötland and Västergötland. The genus is also known from the Kundan Stage of Estonia (Tallinn, Kunda, Aseri, Paldicki), Russia (St Petersburg district) and coeval erratic boulders in northern Germany. Chang (1964) recorded the genus from the middle Ordovician of Qilianshan, Northwest China, but records of *Estonioceras* sp. from the Emanuel Limestone of Western Australia (Teichert & Glenister 1954) may be based on a species of *Aethoceras*.

Genus *Falcilituites* Remelé, 1886 (Fig. 2A, B)

Type species: *Lituites Decheni* Remelé, 1880 [by original designation; Remelé 1886: 467]

Diagnosis: Slowly expanding, relatively slender conch with early loosely coiled inner whorls, often with small umbilical perforation; last whorl becoming divergent. Whorl section slightly depressed to weakly compressed or subquadrate. Conch narrowly camerate, sutures straight to weakly sinuous with broad ventral saddle. Siphuncle subventral to subcentral, septal necks short, orthochoanitic; connecting rings thick and layered. External ornament of distinct raised growth lines and lirae which form a conspicuous, deep ventral sinus.

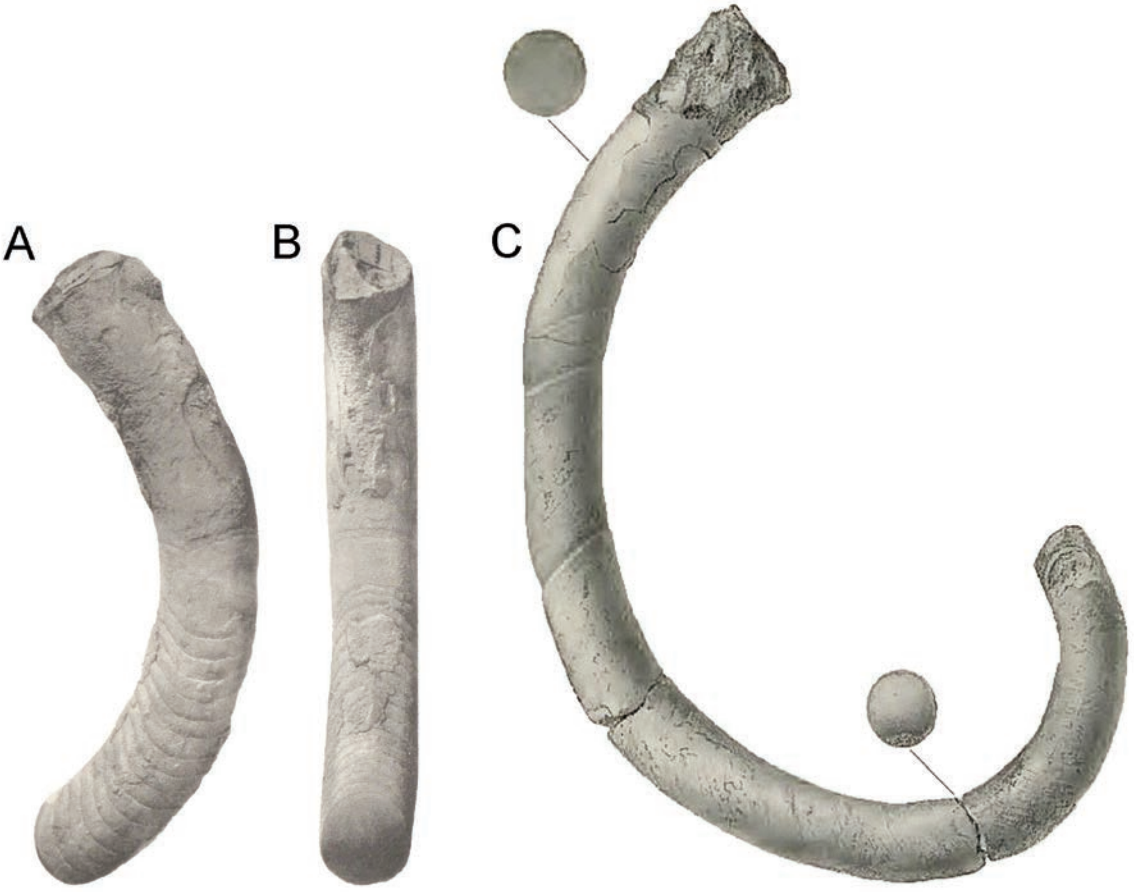
Discussion: *Falcilituites* was placed in synonymy with *Estonioceras* by Furnish & Glenister (1964: K357) although Flower (1976: 544) listed the genera separately. Despite both taxa possessing shells with an apical coiled portion and divergent last whorl, beyond this any external similarity ceases and comparison of the type species readily confirms they are distinct; *Estonioceras* is a much stouter and often larger shell than *Falcilituites*, typically with a greater expansion rate and a fusiform section to the inner whorls. In contrast, the shell form of *Falcilituites* is much more slender than *Estonioceras*, the whorls are slightly depressed to compressed in section and the external ornament is much more distinct and regular.

Ongoing research on Swedish specimens of *Falcilituites* indicates that the apical coiled portion may vary from 1.5 to 2 whorls being in contact before the final whorl becomes divergent. Consequently the diameter of the coiled portion may also vary slightly within a species. Therefore more reliable morphological features of the shell (such as expansion rate, whorl section, detailed form of the ornament and sutures) are currently being used by the author to elucidate the taxonomy of new species of *Falcilituites* present in the Kundan Stage of Sweden.

Constituent species: *Falcilituites decheni* (Remelé, 1880) and *Falcilituites subcostatum* (Angelin *in* Angelin & Lindström, 1880) are currently assigned to the genus, although these species are similar and further study may demonstrate they are conspecific.

Occurrence: From the Kundan Stage (Valastean and Aluojan Substages) of Sweden (Öland, Dalarna, Västergötland), Estonia (Tallinn, Kunda, Aseri, Iru), Russia (St Petersburg district) and coeval erratic boulders in Poland (Mochty) and northern Germany.

Fig. 3: *Tragoceras falcatum* (SCHLOTHEIM, 1820), late Kundan Stage, Tallin, Estonia. (**A**-**B**) RM Mo149984, lateral and dorsal views, length 114 mm [original of MUTVEI (1957: pl. 5, figs 4-6)]. (**C**) Lateral view, length 218 mm [original illustration of SCHRÖDER (1891: pl. VI, figs 1a-c)].



Genus *Tragoceras* REMELÉ, 1890 (Fig. 3A–C)

Planctoceras SCHRÖDER, 1891

Type species: *Orthoceratites falcatus* SCHLOTHEIM, 1820 [by monotypy; REMELÉ 1890: 35]

Diagnosis: Slender, very slowly expanding gyroconic conch with laterally compressed section, and outer divergent whorl; inner whorls unknown but probably in contact. External ornament of moderately coarse, irregular, relatively faint growth lines and lirae which form a broad, ventral sinus. Sutures sinuous with wide lateral lobes and corresponding ventral saddle. Siphuncle narrow, situated near ventral margin; septal necks orthochoanitic, connecting rings thickened.

Discussion: SCHRÖDER (1891: 41) rejected *Tragoceras* REMELÉ, 1890 as a valid genus and proposed *Planctoceras* in its place on the grounds of similarity of name with *Tragoceros* or *Tragocerus* which had previously been used for a Pleistocene antelope. However under ICZN rules, *Tragoceras* was available and is a valid taxon. FURNISH & GLENISTER (1964: K359) maintained *Tragoceras* REMELÉ, 1890 with *Planctoceras* SCHRÖDER, 1891 regarded as an objective junior synonym. That course is followed here.

The inner whorls of *Tragoceras* are unknown, but on the basis of coiling geometry are likely to be similar to *Falcilituites* REMELÉ, 1886; DZIK (1984: 38, fig. 8) provides a very plausible reconstruction of the complete shell. Study of Swedish material indicates that *Tragoceras* and *Falcilituites* are closely related: A new species of *Falcilituites* from northern Öland exhibits undulatory sutures of a style normally associated with *Tragoceras falcatum* (SCHLOTHEIM, 1820), and a specimen of *Tragoceras falcatum* (from Fjäcka, Dalarna) has a laterally compressed whorl section which when traced apicad becomes more circular in section, approaching the condition found in *Falcilituites decheni* REMELÉ, 1880. However, both genera are retained here on the basis that in all known specimens *Tragoceras* consistently exhibits a very slowly expanding, slender conch with near- ventral siphuncle and the shell ornament is coarser and more irregular than in *Falcilituites*. However, discovery and study of more complete specimens showing variation with shell size and maturity may necessitate a rethink of this position.

DZIK (1984: 37) suggested that *Aserioceras purtsensis* STUMBUR, 1962 may represent the youngest record of *Tragoceras*. However, the different expansion rates, posi-

Fig. 4: (**A**) *Eichwaldoceras crispulum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880), RM Mo15047, early Kundan Stage, Gerse, Dalarna, Sweden; lateral view, length 53mm [Holotype, original of ANGELIN & LINDSTRÖM (1880: pl. 16, figs 6, 12)]. (**B**) *Eichwaldoceras volchovense* BALASHOV, 1955, RM Mo158400, early Kundan Stage, Hälludden, Öland, Sweden; lateral view, maximum length 184 mm.

tion of siphuncle and types of ornament readily distinguish the two taxa, and makes this relationship unlikely.

Constituent species: Two species have previously been assigned to *Tragoceras*, *T. falcatum* (SCHLOTHEIM, 1820) and *T. arciforme* BALASHOV, 1953. However, there are taxonomic problems in recognising the latter species (which BALASHOV [1953] may have mistakenly based on true *T. falcatum*), and consequently the genus may be regarded as monotypic.

Occurrence: From the Late Kundan Stage (Aluojan Substage) of Estonia (Tallinn, Kunda, Aseri, Iru), Russia (St Petersburg district), Sweden (Fjäcka, Dalarna) and coeval 'Diluvium-Geschiebe' in Poland (Mochty) and northern Germany.

Genus *Eichwaldoceras* BALASHOV, 1955 (Fig. 4A, B)

Type species: *Eichwaldoceras volchovense* BALASHOV, 1955 [by original designation; BALASHOV 1955: 45]

Diagnosis: Conch gyroconic with moderate expansion rate adorally, inner whorls not known; whorl section circular. External ornament of distinct, coarse growth lirae which form a broad, shallow ventral sinus; sutures straight. Siphuncle narrow, situated at the ventral margin; septal necks orthochoanitic, connecting rings very thick.

Discussion: BALASHOV (1955) based *Eichwaldoceras* on four incomplete but well preserved specimens from the Kundan Stage of Estonia and the Saint Petersburg (Leningrad) area. FURNISH & GLENISTER (1964: K359) regarded the genus as poorly known, but revision here using Swedish material confirms *Eichwaldoceras* is a valid taxon which can be readily distinguished from all other estonioceratids in its combination of conch form, circular section, ventral siphuncle and coarse ornament (comments regarding the similar genus *Aserioceras* STUMBUR, 1962 are dealt with under that taxon below).

The apical parts of *Eichwaldoceras* remain unknown, although evidence from the coiling geometry of Swedish specimens indicates that the conch may have been gyroconic with a relatively large protoconch, and comprise approximately two volutions. Reconstructions based on specimens of *E. volchovense* in the RM suggest that complete conchs could easily have reached 20-25cm in diameter.

Constituent species: Two species are currently recognised within the genus: *E. volchovense* BALASHOV, 1955 and *E. crispulum* ANGELIN *in* ANGELIN & LINDSTRÖM, 1880.

Occurrence: Early Kundan Stage (Hunderumian-Valastean Substages) of Russia (St Petersburg district), Estonia (Kunda) and Sweden (Öland, Östergötland and Dalarna). The genus has not yet been recorded from the 'Diluvium-Geschiebe'.

Genus *Bentoceras* STUMBUR, 1962 (Fig. 5A–C)

Type species: *Bentoceras rubeli* STUMBUR, 1962 [by original designation; STUMBUR 1962: 141]

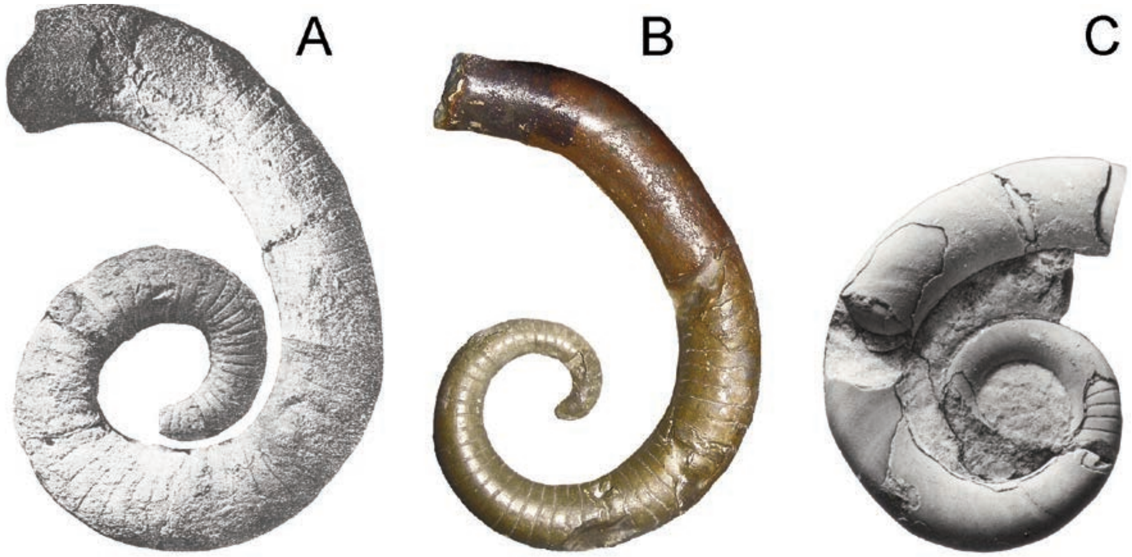


Fig. 5: (**A**) *Bentoceras rubeli* Stumbur, 1962, GIT C1341, late Kundan Stage, Hiimäe, northern Estonia; lateral view, maximum diameter 96 mm [Holotype, original of Stumbur (1962: pl. 1, fig. 1)]. (**B**) *Bentoceras proteus* (Holm, 1898), Kundan Stage, glacial erratic boulder, northern Germany; lateral view, maximum diameter 62 mm [original of Neben & Krueger (1971: pl. 18, fig. 6), assigned in error to *Tragoceras falcatum* (Schlotheim, 1820)]. (**C**) *Bentoceras proteus* (Holm, 1898), RM Mo158393, early Kundan Stage, Hälludden, Öland, Sweden; lateral view, maximum diameter 66 mm.

Diagnosis: Conch gyroconic and slender, consisting of two to two and a quarter whorls which are not in contact; the last volution becomes divergent at maturity. Whorl section subcircular to weakly depressed, expansion rate low. Body-chamber relatively short, approximately one quarter of a whorl long. External ornament of indistinct, feeble growth lines which trace out a broad ventral sinus; sutures transverse to very slightly sinuous. Siphuncle subventral; septal necks orthochoanitic, connecting rings thick.

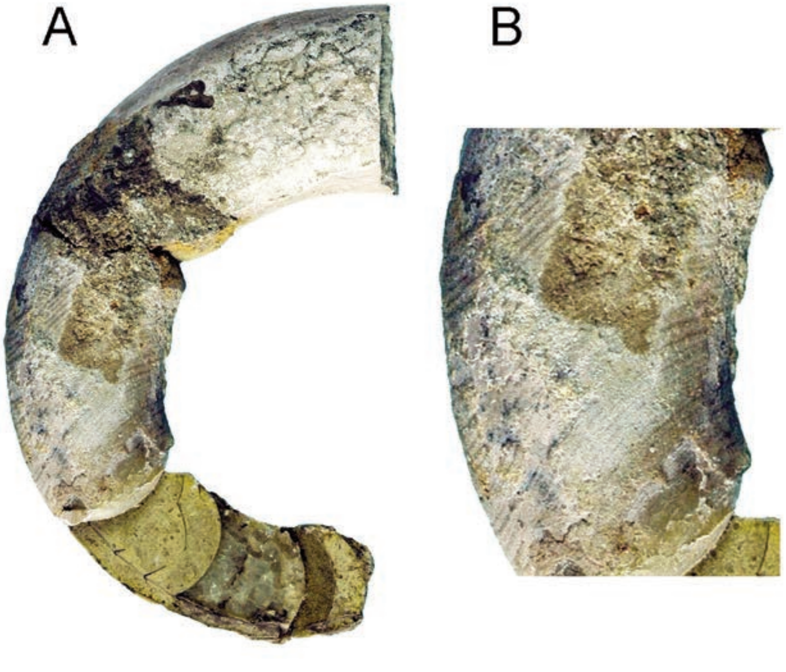


Fig. 6: (**A**) *Aserioceras purtsensis* Stumbur, 1962, GIT C1331, Aserian Stage, Lüganuse, northern Estonia; lateral view, maximum diameter 85 mm [Holotype, original of Stumbur (1962: pl. 1, fig. 2)]. (**B**) Same, detail of ornament.

Discussion: The distinctive gyroconic conch form with weak external ornament readily identifies *Bentoceras* from all other tarphycerids; *Eichwaldoceras* and *Aserioceras* are typically larger, more rapidly-expanding shells with strong lirate ornament; *Tragoceras* has marked undulatory sutures, a ventral siphuncle and coarser external ornament. Dzik (1984: 37, fig. 12) linked *Aphetoceras* Hyatt, 1894 (from the Floian of North America, Newfoundland and Western Australia) with *Bentoceras* and indicated the former may have been ancestral to the Kundan forms. *Aphetoceras* (based on the type species *A. americanum* Hyatt, 1894) is distinguished here from *Bentoceras* by its larger conch consisting of three or more whorls, weak ribbing, more laterally compressed section and smaller protoconch.

Bentoceras proteus (Holm, 1898) shows considerable variation in the degree of coiling, varying from an open, circular gyrocone to forms with a more tightly coiled conch (see Figs 5B, C). The volutions may not lie exactly in one plane and the conch is very slightly torticonic. Holm (1898: 363) regarded the more tightly coiled form as sufficiently distinct to merit the variety name *demissa*. However, examination of more than 20 specimens in collections held at the RM, SGU and MNH indicates that a whole range of variously coiled ‘morphological intermediates’ occur.

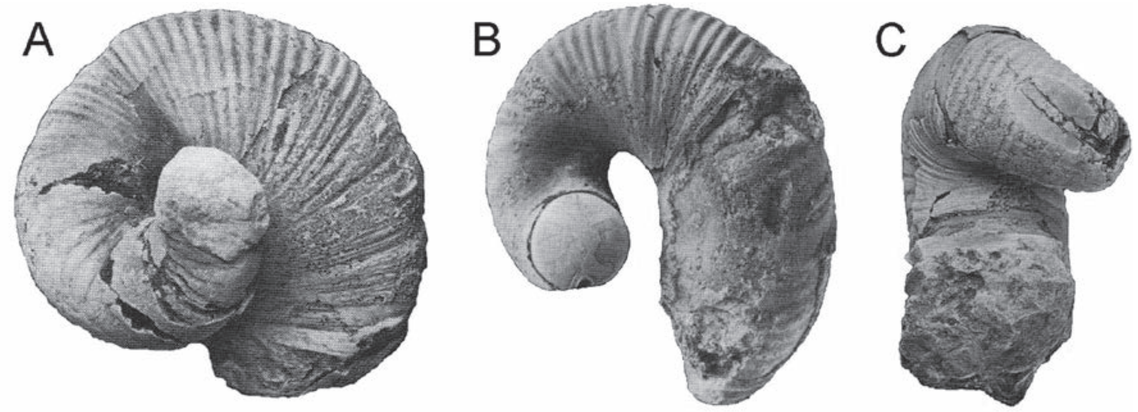


Fig. 7: *Pakrioceras holmi* Stumbur & Mutvei, 1983, Aserian Stage, Estonia. (**A**) RM Mo5690, lateral view, maximum diameter 42 mm. (**B**) GIT C1710, lateral view, maximum diameter 43 mm. (**C**) RM Mo5689, ventral view, maximum length 49 mm [GIT C1710, RM Mo5690 and RM Mo5689 are Holotype and two Paratypes respectively, originals of Stumbur & Mutvei (1983: figs 1D, G and B respectively)].

Constituent species: *Bentoceras proteus* (Holm, 1898), *B. rubeli* Stumbur, 1962 and *B.* sp. Stumbur, 1962 are currently assigned to the genus.

Occurrence: *Bentoceras proteus* is known from the early Kundan Stage (Hunderumian-Valastean substages) of northern Öland and Kinnekulle, Västergötland. Neben & Krueger (1971: pl. 18, fig. 6) figured a specimen of *B. proteus* (mistakenly identified under *Tragoceras falcatum* (Schlotheim, 1820)) from an erratic boulder of early Kundan age from northern Germany. Stumbur (1962) recorded the slightly younger *B. rubeli* and *B.* sp. from the late Kundan Stage (Aluojan Substage) of northern Estonia (Hiimäe, Ida-Viru County).

Genus *Aserioceras* Stumbur, 1962 (Fig. 6A, B)

Type species: *Aserioceras purtsensis* Stumbur, 1962 [by original designation; Stumbur 1962: 143]

Diagnosis: Shell likely gyroconic with moderate expansion rate, but inner whorls unknown. Conch section compressed, slightly flattened laterally. Siphuncle narrow, positioned near the ventral margin, siphuncle wall orthochoanitic, connecting rings slightly thickened. Sutures with broad, shallow lateral and dorsal saddles, camerae relatively deep. Shell ornament consists of relatively coarse lirae which run obliquely across the lateral areas and trace out a broad ventral sinus.

Discussion: Stumbur (1962) originally assigned *Aserioceras* to the Barrandeoceratidae, although its gyroconic form and slightly thickened connecting rings supports placement within the Estonioceratidae. *Aserioceras purtsensis* is the only species definitely assigned to the genus, although Stumbur (1962: 143) also briefly refers to two other fragments from the Lasnamägian Stage of Estonia which may belong to a different species. *Aserioceras* is similar to *Eichwaldoceras*, and the two taxa are likely related. A distinction is maintained here on differences in conch section (circular in *Eichwaldoceras*, compressed in *Aserioceras*), and stratigraphical occurrence (Kundan Stage for *Eichwaldoceras*, Aserian stage for *Aserioceras*). However, further material may prove these genera to be synonymous.

Constituent species: *Aserioceras purtsensis* Stumbur, 1962 is the only species currently assigned to the genus.

Occurrence: Aserian Stage at Lüganuse, northern Estonia (Stumbur 1962).

Genus *Pakrioceras* Stumbur & Mutvei, 1983 (Fig. 7A–C)

Type species: *Pakrioceras holmi* Stumbur & Mutvei, 1983 [by original designation; Stumbur & Mutvei 1983: 43]

Diagnosis: Medium-sized shell, comprising approximately two whorls which coil dextrally in a loose torticonic spiral. Shell diameter increasing moderately except in the body chamber where it remains constant. Conch section subcircular to weakly depressed. Siphuncle narrow, in contact with the ventral margin of the shell. Septal necks orthochoanitic, connecting rings considerably thickened. Sutures straight laterally, forming an adorad-pointing lobe across the venter. The shell ornament consists of distinct narrow annuli with growth lines (adapted from Stumbur & Mutvei 1983).

Discussion: *Pakrioceras* is readily distinguished from all other estonioceratids by its combination of torticonic form and conch ornament. The poorly known Floian (Upper Canadian) genus *Aethoceras* Teichert & Glenister, 1954 from Western Australia, is also a loosely-coiled dextral torticone with slightly depressed section, but it differs from *Pakrioceras* in possessing a submarginal siphuncle, and an ornament of ribs which attenuate as delicate flanges.

Constituent species: The only species currently assigned to the genus is *Pakrioceras holmi* STUMBUR & MUTVEI, 1983.

Occurrence: Aserian Stage of northern Estonia (Väike Pakri Island and Viimsi, near Tallinn). STUMBUR & MUTVEI (1983: 47) also mention a fragmentary specimen which may belong to *Pakrioceras* from the Vikarby or Seby Limestone (late Aserian or early Lasnamägian age) at Nedre Gärdsjö, Dalecarlia (Dalarna), Sweden.

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Cretaceous ammonites from Upper Austria

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Abstract: Lower Cretaceous ammonite faunas from Upper Austria are presented. Lithological, sedimentological and palaeoecological studies over the last decade of the Lower Cretaceous (Northern Calcareous Alps, Upper Austria) uncovered rich spectra of Valanginian-Barremian ammonites. Distinct ammonite faunas derive from limestones, marls and sandstones of well know tectonical nappes from Upper Austria (e.g. Ternberg Nappe, Reichraming Nappe, Staufen-Höllengebirgs Nappe, Langbath Unit). The main sections are, from north to south, the KB1-A Klausrieglerbach 1 section (Schrambach Formation), the KB1-B Klausrieglerbach 2 section (Schrambach Formation), the Hirner section (Schrambach Formation), the Eibeck Section (Rossfeld Formation), the Hochkogel section (Rossfeld Formation), the Traunkirchen section (Tannheim Formation) and the Kolowratshöhe section (Rossfeld Formation).
Thousands of ammonite specimens were collected, prepared and described. The ammonite assemblages clearly indicate a Mediterranean character with intermittent short pulses of Boreal immigrants. The composition of the ammonite assemblages is clearly linked to environmental changes during Lower Cretaceous stages. Sea level changes and variations in climate triggered the evolution of ammonite species. The palaeontological studies on the Lower Cretaceous ammonite material increased the knowledge on palaeoceanographic and palaeoenvironmental conditions at the time of formation of the Northern Calcareous Alps in Upper Austria. The intermittent palaeogeographic situation of the Northern Calcareous Alps during the Lower Cretaceous serves as a key for understanding the ammonite distribution in the Mediterranean Realm.

Keywords: Ammonites, palaeontology, geology, Lower Cretaceous, Northern Calcareous Alps, Upper Austria

Introduction

Lower Cretaceous pelagic sediments are well known to form a major element of the northernmost tectonic units of the Northern Calcareous Alps (e.g. Ternberg-, Reichraming-, Frankenfels-, Lunz-, Staufen- and Höllengebirgs nappes). As noted by numerous authors (VAŠÍČEK & MICHALÍK 1999; STAMPFLI & MOSAR 1999; SCOTESE 2001; WAGREICH et al. 2008), the area investigated (Northern Calcareous Alps) was situated at the eastern border of the Alpine-Carpathian Block during the Early Cretaceous. This was located between the Penninic Ocean in the North and the Vardar Ocean (= Meliata Ocean) in the South-East.

In the Northern Calcareous Alps, Valanginian to Barremian cephalopod-bearing deposits are mainly recorded in two different facies, the Schrambach and the Rossfeld Formation (PILLER et al. 2004; WAGREICH et al. 2008). Additionally the Aptian-Albian Tannheim Formation and the Albian Losenstein Formation in can occur in the lower Bajuvaric units (PILLER et al. 2004). Lower Cretaceous sediments of the Valanginian-Barremian Rossfeld Formation comprise turbiditic marls and sandstones, whereas the Valanginian-Aptian Schrambach Formation consist limestones and marly limestones, with in its lower parts frequent turbiditic sandstone intercalations (VAŠÍČEK & FAUPL 1996). The Schrambach Formation occurs in both, the lower and the upper Bajuvaric units. Contrastingly the siliciclastic Rossfeld Formation is characteristic for the higher Bajuvaric units to the south. The limestones and marly limestones of the Schrambach Formation are typical sediments of pelagic to hemiopalagic enviroments based on the sedimentation of calcareous muds and oozes in deeper waters of the Penninic Ocean at that time. The source area for the Rossfeld Formation and the sandstone intercalations of the Schrambach Formation was situated to the south of the basin (FAUPL 1979; FAUPL & WAGREICH 1992; VAŠÍČEK & FAUPL 1996, 1998; EGGER et al. 2011). The Rossfeld Formation is restricted to southern parts of the nappes. It is interpreted as a synorogenic succession deposited at the beginning of the compressional deformation within the Austroalpine unit (FAUPL 1979; DECKER et al. 1987). The palaeogeographical reconstruction of the investigated area through the Lower Cretaceous shows that the sedimentation of these turbiditic sediments, in the internal and eastern parts of the Northern Calcareous Alps (southern parts of the 'Bajuvarikum') is apparently connected with an uplift of the southernmost parts. The thickness of Lower Cretaceous sediments occurring in the northern tectonic units of the NCA decreases to-

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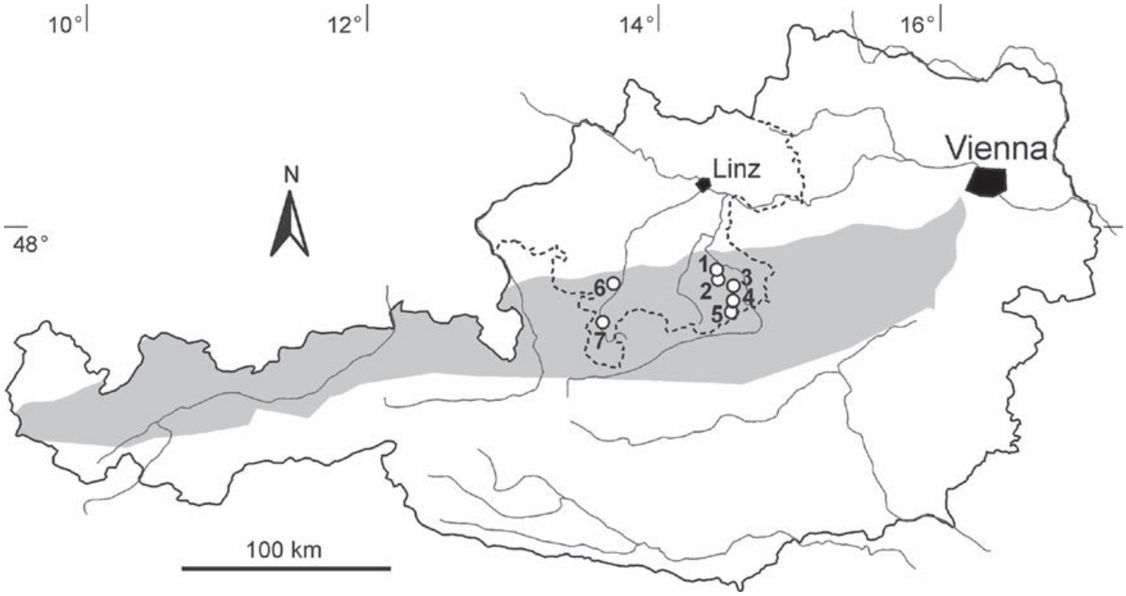

Fig. 1: Locality map of Austria showing the Lower Cretaceous outcrops (white circles) within the Northern Calcareous Alps (grey). 1. KB1-A Klausrieglerbach 1 section (Schrambach Formation), 2. KB1-B Klausrieglerbach 2 section (Schrambach Formation), 3. Hirner section (Schrambach Formation), 4. Eibeck Section (Rossfeld Formation), 5. Hochkogel section (Rossfeld Formation), 6. Traunkirchen section (Tannheim Formation), 7. Kolowratshöhe section (Rossfeld Formation).

wards the north. Geodynamical processes occurring within the basins involved were reviewed by Faupl & Wagreich (2000). The dominating sandstone deposits within the Tyrolic Unit (e.g. Rossfeld Formation) become less prominent within northern nappes (e.g. Bajuvaric units; Piller et al. 2004). This reflects either beginning subduction of the Penninic Ocean in the North or the obduction of oceanic crust of the former Vardar Ocean at the boundary Austroalpine/Southern Alps (Schlagintweit 1991). The Eastern Alps originated within the northwestern Tethys palaeogeographic belt due to repeated convergence between the European and the African plate and intervening microplates. A Jurassic-Cretaceous, 'Eoalpine' orogeny was followed by Meso- and Neoalpine deformational events (Faupl & Wagreich 2000).

The Austro-Alpine units are a characteristic unit of the Eastern Alps. Based on palaeomagnetic data the Austro-Alpine domain is considered to be a partly independent microplate situated along the northern margin of the Adriatic (Apulian) plate, and represents the northern tip of continental fragments of African affinity during the Cretaceous (Stampfli & Mosar 1999; Stampfli & Borel 2002). Eoalpine deformation strongly influenced Cretaceous sedimentation and the formation of sedimentary basins within of the Austro-Alpine domain (Wagreich et al. 2008). Thus, a complex history of synorogenic basins with strongly varying geometries and short-lived subsidence and uplift events characterizes the Austro-Alpine realm, especially during mid- and Late Cretaceous times. The best documented Cretaceous successions of the Austro-Alpine domain are preserved within the Northern Calcareous Alps (NCA, Fig. 1). Cretaceous deformation resulted in thrusting and faulting within the NCA (Wagreich et al. 2008).

Within the Northern Calcareous Alps deep-water carbonate and marls predominate in the Lower Cretaceous. Synorogenic clastic successions and marl facies of the Lower Cretaceous comprises Maiolica-type limestones at their base grading into a shale-limestone cyclic facies. Resedimented clasts of shallow-water Urgonian-type carbonates (Schlagintweit 1991) give evidence that small carbonate platforms were present in northern parts of the NCA during the Early Cretaceous, but were later completely eroded. The deposits are interpreted as pelagic sediments of the deep-water shelf to slope of the passive margin of the Austroalpine microplate. The onset of siliciclastic synorogenic strata marked the change to a tectonically active margin due to compression at the Austroalpine-Penninic margin (Wagreich 2003; Wagreich et al. 2008).

The Kimmeridgian - Early Berrasian Oberalm Formation represents a pelagic deep-water limestone with grey, cherty, bedded micrites including carbonate turbidites of varying thicknesses. The microfauna is dominated by radiolarians, calpionellids and foraminifera (Weidich 1990; Reháková et al. 1996; Boorová et al. 1999). Turbiditic Barmstein Limestone beds within the Oberalm Formation contain a diverse fauna of calcareous algae and foraminifera indicating an early Berriasian age. The Upper Jurassic to Berriasian carbonate platforms of the Plassen Formation (Schlagintweit & Ebli 1999; Gawlick et al. 2006) can be regarded as the source for the resedimented shallow-water material.

The Oberalm Formation grades into grey micritic limestones and limestone-marl rhythmites of the Schrambach Formation (Vašíček & Faupl 1999; Rasser et al. 2003; Lukeneder 1997, 1998, 2000; Aptychus limestone and Ammergau Formation p.p. of some authors) during the Berriasian. Sandy turbidites are largely absent in the Schrambach Formation, and the amount of marl intercalations increases upwards. Considering different tectonic units of the NCA both the base and especially the top of the Schrambach Formation are diachronous.

In more internal nappe complexes of the NCA (Tirolic units west and south of Salzburg; Reichraming and Lunz nappes further to the east), deep-water limestones graded into synorogenic terrigenous facies of the Rossfeld Formation during Valanginian to Aptian time (Decker et al. 1987; Vašíček & Faupl 1998). The Rossfeld basin is interpreted as a deep-water foreland to piggyback trough in front of overthrusting higher NCA-nappes (Decker et al. 1987). The Rossfeld Formation comprises a coarsening upward succession of marls and sandstones, grading into deep-water conglomerates/breccias as well as slump deposits sedimented on an active north-facing slope. The sandstones contain considerable amounts of siliciclastic and ophiolitic detritus from southern source terrains, including chrome spinels from ophiolites of the Tethys-Vardar-Hallstatt suture (Pober & Faupl 1988; von Eynatten & Gaupp 1999).

The stratigraphy of the Lower Cretaceous sediments within the Northern Calcareous Alps around the investigated areas is based on ammonoids. During the last two decades, a rich cephalopod fauna was collected from Lower Cretaceous sediments (Immel 1987; Vašíček & Faupl 1996, 1998, 1999; Vašíček et al. 1994; Faupl et al. 2003).

The present contribution provides a detailed study of the rich and extraordinarily well-preserved Lower Cretaceous ammonoid faunas from various sections of Upper Austria, which yields new and important biostratigraphical data, and presents a compilation of ammonite faunas and facies within the Northern Calcareous Alps. Lower Cretaceous cephalopod faunas (i.e. ammonites, aptychi and belemnites) and facies described herein are given in detail within numerous papers of Lukeneder (1997, 1998, 1999, 2000, 2001a, b, c, d, 2002a, b, c, d, 2003a, b, c, 2004a, b, c, d, 2005a, b, c, d, e), Lukeneder & Harzhauser (2002, 2003), Lukeneder & Tanabe (2002), and Lukeneder & Reháková (2004, 2007).

The main goal of this paper is to present results of the Lower Cretaceous ammonite studies over the last two decades for a broader readership. Case studies on Lower Cretaceous ammonites from Upper Austria were basically performed within two 3-year projects of the Austrian Science Fund (FWF P13641 and P16100).

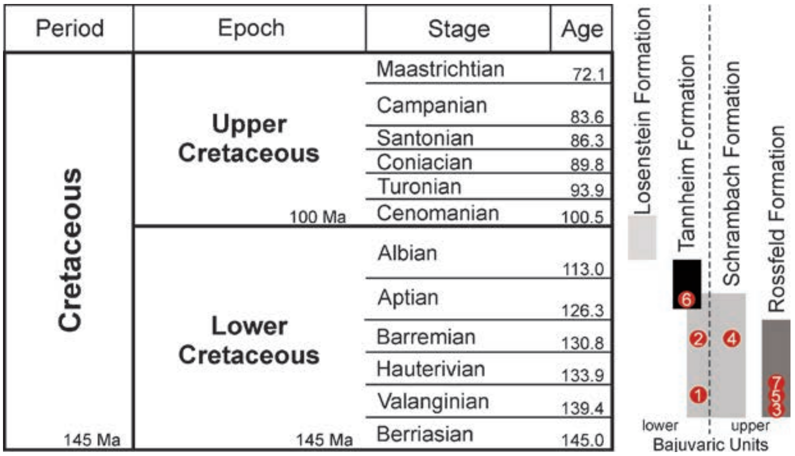

Fig. 2: Stratigraphical index and lithology (modified after Gradstein et al. 2012; Piller et al. 2004) with the indicated range of the Schrambach Formation, the Rossfeld Formation, the Tannheim Formation and the Losenstein Formation. Numbers are according to localities given in Fig. 1.

Geography and geological setting

The geography and geological situation is summarised for each distinct locality and outcrop. The exact position of the ammonite occurrences is fixed by GPS data (global positioning system). All localities presented are located in Northern Calcareous Alps of Upper Austria. Due to the 'soft' marly lithology of the composing sediments the outcrops are mostly located in morphological synclines. The Losenstein Syncline of the Ternberg Nappe, the Schneeberg Syncline, the Anzenbach Syncline, and the Ebenforst Syncline in the the Reichraming Nappe (from north to south). The Traunkirchen section is located in the Langbath Unit ('Langbath Scholle') with the Hohenau Syncline and the Fahrnau Syncline to the south. The material examined is deposited in the palaeontological collections of the Natural History Museum Vienna.

KB1-A Klausrieglerbach 1 section

The investigated Lower Cretaceous section KB1-A (Klausriegler-Bach 1, Fig. 1) is situated near the Enns River, approximately 1 km southwest, in the Ternberg Nappe (N47°54'32", E14°21'10"). This region is part of the northernmost Northern Calcareous Alps. The Losenstein Syncline is situated in the southernmost part of the Ternberg Nappe (lower Bajuvaric Unit). This syncline is the last syncline to the north filled by Lower Cretaceous sediments. The investigated fossiliferous section is located on the left, nearly vertical (dipping 040/85), step-like wall of the gorge, exposed on a length of 10 m and a height of 5 m.

At the area around Ternberg, the Lower Cretaceous sequence is presented by two different formations from the Steinmühl Formation to the Schrambach Formation (Fig. 2). Steinmühl Formation (approx. 15 m): early Berriasian to late early Valanginian in age (Lukeneder 2000; Lukeneder & Reháková 2004), its lower part consisting of red ('Ammonitico rosso' type) and its upper part of grey ('Maiolica' type) condensed pelagic limestones with a few ammonoids, but abundant calpionellids and calcareous dinoflagellates enabling precise biostratigraphic correlations. The brachiopod *Pygope cattuloi* is abundant in the topmost bed (Lukeneder 2002a). Schrambach Formation (approx. 150 m): late Valanginian to late Barremian in age, consisting of pale grey, even bedded limestones intercalated with grey to black calcareous marlstones (laminated 'black shales'), and marls. The beds are intensively bioturbated, and the trace fossils *Zoophycos*, *Chondrites* and *Planolites* occur throughout (Lukeneder 2001b, 2004a).The wavy boundary between the Steinmühl and the Schrambach Formation is marked by a primary hardground characterized by fragmented, encrusted, and partly eroded ammonoids and several bored cephalopods (e.g. belemnites; Lukeneder 1999).

KB1-B Klausrieglerbach 2 section

The outcrop is situated in the Ternberg Nappe in Upper Austria approximately 100 m below KB1-A in the same ravine. The exact position is about 7 km west of Losenstein, 1 km south of Kienberg and 500 m southwest of the Klausriegler inn (N47°54'32", E14°21'10", 652 m, ÖK 1:50,000, sheet 69 Großraming, Fig. 1). The stream outcrop crosses the western part of the east-west striking Losenstein Syncline along a line running between the Kreuzmauer (853 m) to the north and the Pfaffenmauer (1218 m) to the south (Lukeneder 2001b; Lukeneder & Tanabe 2002). The general geological and tectonical features are equal to the described for KB1-A. This section was the starting point for a lateral analysis of the distribution of the reported ammonite mass-occurrence. For detailed descriptions of the investigation area see Lukeneder (1997, 1998, 1999). The outcrop comprises an ammonite 'mass-occurrence', representing the *Karsteniceras*-Level, is situated in the upper part of the Schrambach Formation (lower Barremian, *Moutoniceras moutonianum* Zone) within the intercalated black calcareous marls (Lukeneder 2001a, 2003b; Lukeneder & Tanabe 2002 (Fig. 2).

Hochkogel section

The outcrop is situated in the Reichraming Nappe in Upper Austria (Lukeneder 2005a; Lukeneder & Reháková 2007). The exact position is about 5 km south of Brunnbach (N47°47'15", E14°30'00", 652 m, ÖK 1:50,000, sheet 69 Großraming, Fig. 1). The outcrop is located in the southernmost part of the east-west striking Ebenforst Syncline along a forest road, running between the Sulzkogel (840 m) to the north and the Hochkogel (1157 m) to the south at the topmost part of the Reixengraben at 885 m. The grey sandstone succession comprising the marly ammonoid-bearing beds (dipping 225/60) is located on the northern side of the Hochkogel, on a nearly vertical wall of the outcrop, which was exposed by road-cutting. The occurrence is exposed in 3 distinct beds of 10–40 cm thickness.

The lower to upper Valanginian cephalopods described here were collected from a little outcrop containing sandstones and marly limestones, located at the southern margin of the Ebenforst Syncline. The Ebenforst Syncline is situated in the southernmost part of the Reichraming Nappe of the Northern Calcareous Alps. This region is part of the higher Bajuvaric Unit, which is neighboured and overlain in the south by the Tyrolian Nappes (Staufen-Höllengebirgs Nappe). The Ebenforst Syncline is followed directly to the north by three additional synclines – the Anzenbach Syncline, the Schneeberg Syncline of the Reichraming Nappe and the Losenstein Syncline of the Ternberg Nappe – all of which are constituted by Lower Cretaceous sediments. The locality is situated 500 m north of the border to the southern Tyrolian Units and is tectonically shifted into the Weyer Arc Structure (Lukeneder 2005a). The Ebenforst Syncline is formed of a Jurassic sequence (Oberalm Formation, Scheiblberg-Kirchstein Formation, Hierlatzkalk). The core of the Ebenforst Syncline consists of the Lower Cretaceous Rossfeld Formation. The investigated ammonoid 'mass-occurrence' is situated in marly limestones of the Rossfeld Formation (lower to upper Valanginian; Lukeneder 2005; Lukeneder & Reháková 2007; Fig. 2).

The terrigenous, proximal, deep-water turbiditic Rossfeld Formation of the Reichraming Nappe represents a synorogenic development. The Rossfeld Formation is mainly composed of grey silty marls accompanied by conglomerates and sandstones. The sandstones are fine, grey calcareous with slump structures. The intercalated marly bioturbated limestones are light-coloured and are associated with a relatively monotonous benthic macrofauna (brachiopods and bivalves). The fabric is burrow-mottled to completely homogenised due to bioturbation and indicates rich benthic colonization. The sedimentological situation at the Hochkogel outcrop differs somewhat from that of other 'Rossfeld Formation' localities. In most cases we find marls or marlstones with intercalated sandstone layers. In contrast to the latter situation, the Rossfeld Formation at the Hochkogel section shows approx. 30 m of fine, grey calcareous sandstones (5–50 cm beds) with mass-plant debris on their upper side (Lukeneder 2005a). Three intercalated limestone beds of 10 to 40 cm thickness (rich in ammonoids) can be distinguished. These limestone beds are in turn marked by 'small' rhythmically intercalated turbiditic sandstone layers of about 2–3 cm. A short-term sedimentation is proposed for the sandstone layers, whereas the limestones and marl-beds reflect 'normal' sedimentation rates.

Hirner section

The outcrop is situated in the northeastern part of the Reichraming Nappe (Upper Austria), about 3 km southwest of Großraming (446 m, ÖK 1:50,000, sheet 69 Großraming, Fig. 1). The outcrop (640 m) is located in the southeastern-most part of the east-west striking Schneeberg Syncline along a forest road, between the farmhouse Hirner (560 m) to the south and the farmhouse Scharnreitner (580 m) to the north, both situated at the west side of the Lumplgraben (LUKENEDER 2004d).

The limestone succession on the western side at a forest road comprises the ammonoid-bearing beds (dipping 225/80). The material derives from a little outcrop of marly limestones and is located at the southeastern margin of the Schneeberg Syncline (N47°51'47", E14°31'29"; Fig. 2). The Schneeberg Syncline is one of the northernmost parts of the Reichraming Nappe (higher Bajuvaric Unit, Northern Calcareous Alps). It is situated between three more Lower Cretaceous synclines, directly to the north by the Losenstein Syncline of the Ternberg Nappe and to the south the Anzenbach Syncline and the Ebenforst Syncline (Fig. 1). The locality is affiliated with the Upper Cretaceous Gosau Group (20 m to the north and 250 m to the west), which in this area forms of the border of the Weyer Arc Structure. The ammonoid occurrence in the Schrambach Formation (lower Barremian, *Moutoniceras moutonianum* Zone) is composed of marls and marly limestones (about 40 m; LUKENEDER 2004d; Fig. 2). The succession is intercalated by fossiliferous ammonoid-bearing beds. Light-coloured, grey, fine, marly limestones and limestones are associated with a relatively monotonous benthic macrofauna. The pelagic sediments reflect once more 'normal' sedimentation rates.

Eibeckgraben section

The outcrop is situated in the Reichraming Nappe in Upper Austria, about 5 km south of Brunnbach (652 m, ÖK 1:50,000, sheet 69 Großraming; Fig. 1). The stream outcrop is located near the middle of the Eibeckgraben in the south-easternmost part of the eastwest striking Ebenforst Syncline, running between the Sulzkogel (840 m) to the west and the vicinity of the Eibeck (916 m) to the east (LUKENEDER 2004c, 2005b). The succession, comprising the ammonoid-bearing beds, is located on the southern side of the Hochkogel (1157 m). The occurrence is badly exposed on the left side of the stream (N47°47'14", E14°31'00"). Steep terrain and the 'soft nature' of the marly rocks made sampling very difficult.

The upper Valanginian succession of southeastern Upper Austria was deposited in an unstable shelf setting characterized by thick limestone units that reflect transgressive histories punctuated by tectonic events, as shown by the deposition of conglomerates and sandstones (see FAUPL 1979). The terrigenous, proximal, deep-water turbiditic Rossfeld Formation of the Reichraming Nappe represents a synorogenic development (VAŠÍČEK & FAUPL 1998). The Ebenforst Syncline is situated in the southernmost part of the Reichraming Nappe. Three more synclines are present to the north: the Anzenbach Syncline, the Schneeberg Syncline of the Reichraming Nappe, and the Losenstein Syncline of the Ternberg Nappe, all of which consist of Lower Cretaceous sediments in their cores. Lower Cretaceous sediments are represented at the Eibeck section by two formations, the Schrambach Formation (approx. 50 m, Berriasian) and the overlying Rossfeld Formation (approx. 150 m, upper Valanginian, Fig. 2).

Traunkirchen section

During the construction of the Traunkirchen tunnel in Upper Austria, a traffic bypass of Traunkirchen at the Traunsee (Lake Traunsee at the Seestraße, B51; Geological map 1:50,000, sheet 66 Gmunden; see Egger 1996; Fig. 1), an important ammonite could be detected (LUKENEDER 2005c). On a rock blasted wall at 2 meters height (N47°50'35", E13°47'00") several parts of a fossil cephalopod were visible that were not even recognised as belonging to an ammonite at the time of excavation. The ammonite from the Traunkirchen tunnel originates from the lower Aptian beds of the Tannheim Formation (Fig. 2). The Tannheim Formation consists mainly of dark grey and black marly limestones and marls from the Lower Cretaceous. The Lower Cretaceous in this area belongs to the Bajuvaric Zone with the Langbath Unit, a local part of the northern nappes of the Northern Calcareous Alps. The Siegesbachgraben (VAŠÍČEK & SUMMESBERGER 2004) near Traunkirchen and the closely neighboured but tectonically and stratigraphically distant Gschliefgraben are well known.

Kolowratshöhe section

The outcrop is situated in the Staufen-Höllengebirgs Nappe in the southernmost part of Upper Austria, about 3 km southeast of Bad Ischl and 1.5 km east of Perneck (588 m, ÖK 1:50,000, sheet 96 Bad Ischl; see SCHÄFFER 1982; Fig. 1). The succession comprising the

Fig. 3: Ammonites from the upper Valanginian KB1-A Klausrieglerbach 1 section (Schrambach Formation). The dominant species at KB1-A *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian) morph. type *querolensis* Bulot. **1**: M, bed 10, 2002z0070/0001. **2**: M and m, bed 4, 2002z0070/0005. **3**: M, bed 4, 2002z0070/ 0004. **4**: m, bed 4, 2002z0070/0002. **5**: M, bed 10, 2002z0070/ 0006. **6**: M+m, m with lappet, bed 29, 2002z0070/0003. All specimens are in natural size and coated with ammonium chloride before photographing. M: macroconch, m: microconch.

ammonoid-bearing beds is located at the end of an old, overgrown forest road on the western side of the Kolowratshöhe (1109 m). The sandstone succession of the Rossfeld Formation is running between the Rettenbach (557 m) to the north and the vicinity of the Salzberg (827 m) to the south (Lukeneder 2005e; Fig. 2). The poor exposure is situated on the left side of the small road (N47°41'24", E13°39'24"). The site can only be accessed with permission from the forest agency, over a steep forest road (approx. 10 km) which has its initial point on the main road from Bad Ischl to Bad Goisern.

The locality is situated in the southernmost part of the Tyrolic Unit, which in this region lies under and/or adjoins the small 'Hallstätter Scholle'. The Tyrolic Unit forms part of the 'Traunalpen Scholle', which in this region represents the westernmost part of the Staufen-Höllengebirgs Nappe (Tollmann 1976).

Lower Cretaceous sediments are represented in the area around the Kolowratshöhe section by two formations, the Rossfeld Formation (approx. 120 m, upper Valanginian) and the Schrambach Formation (approx. 40 m, Hauterivian; LUKENEDER 2005e). The allochthonous slope-trench sediments of the Rossfeld Formation have been divided at the type locality (DECKER et al. 1987) into three different depositional settings: lithofacies A, which is characterized by silty grey marls (approx. 175 m), lithofacies B, characterized by thin to thick bedded sandstones (approx. 120 m) and lithofacies C, characterized by coarse clastics (approx. 50 m).

Lower Cretaceous ammonite assemblages from Upper Austria

KB1-A Klausrieglerbach 1 section

The Lower Cretaceous mass-occurrence of *Olcostephanus* (*Olcostephanus*) *guebhardi* morph. *querolensis* BULOT, 1992 from the upper Valanginian *Saynoceras verrucosum* Zone of the KB1-A section, Ternberg Nappe, the Northern Calcareous Alps (Upper Austria) is described (LUKENEDER 2004a; Fig. 3). This horizon, spanning an interval of almost 3 metres, is interpreted as a longterm accumulation from the water column combined with temporary redeposition from local submarine highs. The fauna of the *Olcostephanus* horizon is composed of 9 genera and 10 species. The *Olcostephanus* mass-occurrence represents a widespread phenomenon. It appears most commonly at oceanographic elevations where olcostephanid shells accumulated on the seafloor during sea-level highs.

No sorting or packing due to sedimentological or biological effects can be observed, whereas concentrations due to subsequent transport or bottom currents can be seen in several beds. An enrichment by redeposition, currents or turbidites is proposed for a few marly layers (e.g. layers 4, 10 and 16) with accumulated fragmented olcostephanids (LUKENEDER 2004a). The olcostephanids were deposited within a phyllocrinid-ophiuroid association. Irregular echinoids proved soft bottom conditions of the secondary allochthonous depositional environment. The mass-occurrence of *Olcostephanus* (O.) *guebhardi* morph. *querolensis* (Fig. 3) over an interval of almost 3 metres 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 of redepositional phases (allochthonous parts) of the upper Valanginian. The abundant olcostephanids reflect less offshore influences and the proximity of shallow environments (LUKENEDER 2004a). Parts of the *Olcostephanus* horizon show some similarities to a 'Kondensat-Lagerstätte'.

The *Olcostephanus* horizon in the KB1-A section occurs in the transgressive facies, marking a distinct upper Valanginian sea-level rise. This was probably within the upper Valanginian transgression, 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, mostly due to the creation or renewal of seaways. By comparing field evidence and published data from the Vocontian Trough (e.g. BULOT 1993), it seems valid to propose a facies dependence (e.g. depth, outer-inner shelf) of *Olcostephanus* (O.) *guebhardi* morph. *querolensis* also for the Austrian KB1-A occurrence (Fig. 3). The descendants are most probably inhabitants of the outer shelf and related areas. It is also suggested that *Olcostephanus* (O.) *guebhardi* morph. *querolensis* has its acme within the *verrucosum* Zone, whereas the ancient *Olcostephanus* (O.) *guebhardi sensu stricto* is most abundant in the uppermost lower Valanginian (*Busnardoites campylotoxus* Zone) (see BULOT 1992; REBOULET et al. 2009). Comparable occurrences have been recognized by VAŠÍČEK et al. (1994), who (briefly) reported an upper Valanginian 'lumachelle-like' occurrence of *Olcostephanus* and *Haploceras* sp. from the Rossfeld Formation in the Ebenforst Syncline (Upper Austria). The olcostephanid shown in their paper lacks bifurcation of the secondary ribbing and is therefore herein suggested to be an *Olcostephanus* (O.) *guebhardi sensu stricto*. Thus, the association described by VAŠÍČEK et al. (1994) is probably older (e.g. ?uppermost lower Valanginian) than the olcostaphanid accumulation of the KB1 section. The extraordinary KB1-A occurrence was most probably formed on an elevation near a sloping ramp that dipped to the south (LUKENEDER 2004a). The redeposited specimens were transported from a nearby deep-water swell.

KB1-B Klausrieglerbach 2 section

A Lower Cretaceous mass-occurrence of ammonites in the Ternberg Nappe of the Northern Calcareous Alps (Upper Austria) is described (LUKENEDER 2001b, 2003b). The mass-occurrence (section KB1-B = Klausrieglerbach 1, section B) dominated by *Karsteniceras ternbergense* LUKENEDER, 2002 is of early Barremian age (*Moutoniceras moutonianum* Zone). The *Karsteniceras* mass-occurrence comprises eight different genera, each apparently represented by a single species, of which four are identified to species level. About 300 specimens of *K. ternbergense* between 5 and 37 mm in diameter were investigated (Fig. 4). Two groups showing thick main ribs but different maximum size are distinguishable. The latter parameters are suggested to reflect sexual dimor-

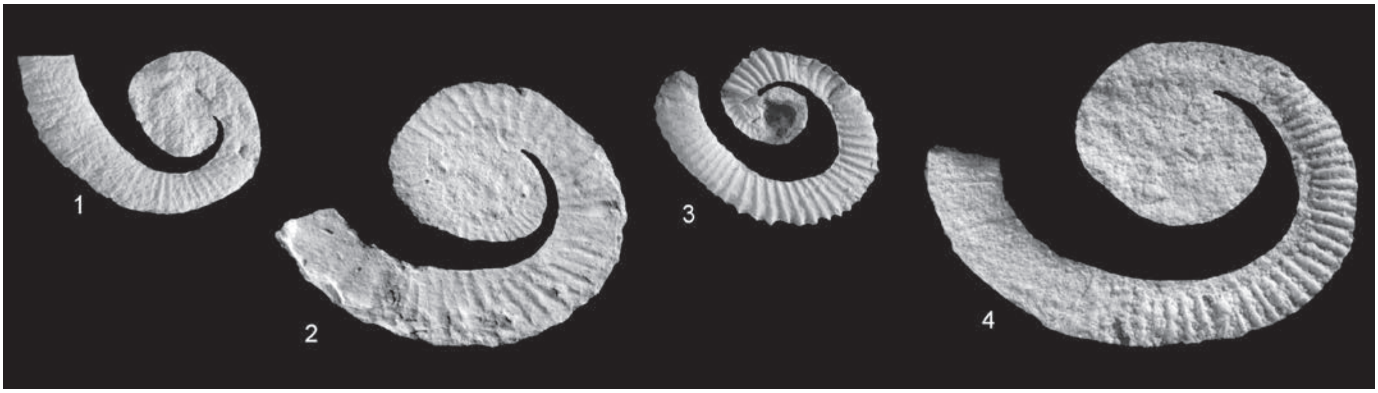

Fig. 4: Ammonites from the lower Barremian KB1-B Klausrieglerbach 2 section (Schrambach Formation). The dominant species at KB1-B *Karsteniceras ternbergense* (LUKENEDER). 1: Holotype of the species *Karsteniceras ternbergense*, bed 22, 2001z0170/0001. 2: *Karsteniceras ternbergense*, bed 18, 2001z0170/0004. 3: *Karsteniceras ternbergense*, thick main ribs on the body chambers, bed 22, 2001z0170/0002. 4: *Karsteniceras ternbergense*, thick main ribs on the body chamber, bed 22, NHMW 2001z0170/0007. All specimens twice their natural size.

phism within *K. ternbergense*, a condition that is most probably applicable to the whole leptoceratoid group. The geochemical results indicate that the *Karsteniceras* mass-occurrence within the described Lower Cretaceous succession was deposited under intermittent oxygen-depleted conditions associated with stable, salinity-stratified water masses. The rhythmicity of laminated black-marly limestone layers and light-grey bioturbated, organic-poor limestones suggests that the oxic and dysoxic conditions underwent highly dynamic changes (LUKENEDER 2003b). The deposition of the limestones in this interval occurred in an unstable environment and was controlled by short- and long-term fluctuations in oxygen levels. *Karsteniceras* (Fig. 4) inhabited areas of stagnant water with low dissolved oxygen; it showed peak abundance during times of oxygen depletion, which partially hindered other invertebrates from settling in such environments. The autochthonous *Karsteniceras* mass-occurrence can be assigned to the deposition-type of 'Konservat-Lagerstätte', which is indicated by the preservation of phosphatic siphuncle structures and proved by the *in situ* preservation of aptychi within *K. ternbergense*. Based on lithological and geochemical analysis combined with investigations of trace fossils, micro fossils and macrofossils, an invasion of an opportunistic (r-strategist) *Karsteniceras* biocoenosis during non favourable conditions over the sea bed during the lower Barremian is proposed for the KB1-B section.

A unique feature in fossil cephalopods was detected from the *Karsteniceras* beds by LUKENEDER & TANABE (2002). Lower Barremian deposits (KB1-B) of Upper Austria yield some extraordinarily preserved ammonoids with *Lamellaptychus* type lower jaws in their body chambers. The ammonoids with *in situ* lower jaws are assignable to *K. ternbergense* (see LUKENEDER & TANABE 2002). This new occurrence was detected during palaeoecological and sedimentological studies at an outcrop in the Ternberg Nappe in Upper Austria. The jaw apparatuses are found in situ or in an isolated condition but are associated with a mass-occurrence of the genus *Karsteniceras*, which contributes 91% of the total ammonite fauna (LUKENEDER 2003b). Most of the lower jaws are flattened, but their characteristic mode of occurrence with conchs of the Tethyan ammonoid *Karsteniceras* allows their use as indicators of palaeobiogeography, palaeobathymetry and palaeoecology.

About five calcified lower jaws (plus horny parts) of *Lamellaptychus*-type appearance were found in split samples of the lower Barremian black to dark grey, laminated limestones of Upper Austria. The morphotype described fits well with morphogroup 5 of TANABE & LANDMAN (2002). These aptychus-type jaws show long commissures and gently arched anterior margins. They are attributed to Cretaceous heteromorphs. All of the specimens derive from two separate beds of *Karsteniceras* level KB1-B, horizons 18 and 22. The rather large sample yielded five aptychi associated with the ammonite *K. ternbergense* along with numerous other ammonites and inoceramids. The lower jaws were found in quite different stages of preservation. In some cases the wings are fragmented and/or isolated. The *in situ* specimens show a significant double-wing preservation (LUKENEDER & TANABE 2002). Some have been crushed through sediment compaction. The problem of the correct correlation of isolated jaw elements and shells has been solved for several ammonite species within the Cretaceous (mostly Upper Cretaceous) genera *Aconeceras*, *Baculites*, *Damesites*, *Discoscaphites*, *Gaudryceras*, *Hoploscaphites*, *Jeletzkytes*, *Karsteniceras* (Fig. 4), *Menuites*, *Placenticeras*, *Phyllopachyceras*, *Polyptychoceras*, *Reesidites*, *Rhaebdoceas*, *Scalarites*, *Scaphites*, *Sciponoceras*, *Supptychoceras*, *Tetragonites*, *Tragodesmoceratoides* and *Yezoites* (KANIE et al. 1978; LEHMANN 1978; TANABE et al. 1980; KANIE 1982; SUMMESBERGER et al. 1996; TANABE & FUKUDA 1999; LUKENEDER & TANABE 2002; TANABE & LANDMAN 2002).

Low energy on the sea floor (absence of bottom currents) and dysaerobic conditions, which prevented predators from isolating the shells from the jaw apparatuses, led to the extraordinary preservation of the ammonite conch-jaw association. These exceptional preservational features are typical for 'Konservat-Lagerstätten' or 'Stagnate' (SEILACHER et al. 1976), which always show exceptional preservation, either of articulated hard parts or soft body preservation.

According to the interpretations of the authors cited above, the aptychi described herein are ammonite lower jaws. The positions of the lower jaw in the body chamber of the ammonite *Karsteniceras* clearly indicate that the dead ammonite bodies were not subjected to long post-mortem drift but rapidly became waterlogged and sank to the sea floor. This interpretation is consistent with geochemical, sedimentological and faunal data on the *Karsteniceras* horizons.

A similar isochronous *Karsteniceras* mass-occurrence was detected by LUKENEDER (2005d) approximately 150 km to the east at the Sparbach section in the Nappe (Lower Austria, Northern Calcareous Alps). It is located in the Frankenfels-Lunz Nappe System (Höllenstein Unit) within the Flössel Syncline. The distinct *Karsteniceras* occurrence appears to be the lateral continuation of the lower Barremian KB1-A *Karsteniceras* level.

Hochkogel section

Lower Cretaceous ammonoids were collected at the Hochkogel locality in the southernmost part of the Reichraming Nappe (Ebenforst Syncline, Northern Calcareous Alps; see LUKENEDER 2005a; Fig. 5). The cephalopod fauna sampled from marly parts of the Rossfeld Formation indicates upper lower Valanginian age. The ammonoid fauna comprises 7 different genera, each apparently represented by 1 or 2 species. The occurrence at the Hochkogel section is dominated by *Bochianites* (49%), *Ptychophylloceras* (18%) and *Haploceras* (18%). Ancyloceratids (represented only by bochianitids) are the most frequent component. Ammonitids and phylloceratids are roughly balanced (each about 20%). Lytoceratids are represented with below average values (7 %). A single deepwater nautiloid and 2 belemnite guards complete the cephalopod fauna. Brachiopods, bivalves and gastropods make up the main components of the benthic macrofauna (Fig. 5).

The deposition of the limestones in this area occurred in an unstable environment. Gravitational transport of different sediments and fragmented cephalopod specimens is assumed for the accumulated layers from the source area (situated to the south). The cephalopod fauna consists solely of Mediterranean elements.

The tectonically strongly deformed Lower Cretaceous sediments of the Ebenforst Syncline do not necessarily create the perfect conditions for excellent preservation of ammonoids (LUKENEDER 2005a). The macrofauna, as already stated, is represented especially by ammonoids. The whole section yielded about 800 ammonoids (includes fragments). The ammonoid moulds are restricted to the limestone beds. No ammonoids were found within the encompassing sandstone layers. The latter were formed by turbidity currents, show gradation and, on their top, plant debris. Some specimens (e.g. *Ptychophylloceras*) described from the Hochkogel show exceptional shell preservation (Fig. 5). The accompanying invertebrate fauna (LUKENEDER 2005a) consists of nautiloids, lamellaptychi, echinoderms (*Phyllocrinus*), brachiopods (*Triangope*) and bivalves (e.g. inoceramids and others; Fig. 5).

The stratigraphic investigation of the ammonoid fauna revealed that the Hochkogel section comprises upper lower Valanginian sediments of the *Busnardoites campylotoxus* and *Tirnovella pertransiens* zones and belongs exclusively to the Mediterranean Province. No descendants of the Boreal Province are observed at the Hochkogel section.

The following Mediterranean genera are observed with *Phylloceras*, *Ptychophylloceras*, *Ptychophylloceras*, *Lytoceras*, *Leptotetragonites*, *Haploceras* and *Bochianites* (Fig. 5). The ammonoid assemblage, the abundance of *Bochianites neocomiensis*, and the occurrence of *Haploceras extracornutum* hint at the lower Valanginian *Busnardoites campylotoxus* and *Tirnovella pertransiens* ammonite zones. Sorting, packing due to sedimentological or biological effects, and alignments or concentration due to transport or bottom currents can be observed. Thus, the analysis of the macrofauna and the sedimentological data support the interpretation of a highly dynamic palaeoenvironment on the slope to basin.

The suggested palaeogeographic position of the studied section indicates an influence of turbiditic redeposition ('debris flow') and an allochthonous origin of the fragmented ammonoids collected. The shell transport took place via 'mudflows' after the embedding in the sediment, as is reflected in the different alignments of the ammonoid shells and fragments within the sediment. The badly preserved, fragmented specimens within the marly limestone layers were apparently transported from a nearby, more shallow area such as that situated to the south, where they had been deposited primarily. The fragmentation and the diverse orientations of the ammonoid specimens within the sediment furnish evidence for a post-mortem turbidity-flow transport of the shells (LUKENEDER 2005a).

Fig. 5: Ammonites from the lower Valanginian Hochkogel section (Rossfeld Formation). **1**: *Ptychophylloceras ptychoicum* (Quenstedt), 2004z0116/ 0001. **2**: *Ptychophylloceras ptychoicum* (Quenstedt), 2004z0116/ 0002. **3**: *Leptotetragonites* cf. *honnoratianus* (d'Orbigny), 2004z0116/0009. **4**: *Haploceras grasianum* (d'Orbigny), 2004z0116/0010. **5**: Microconch lappet of *Neocomites* sp. (d'Orbigny), 2004z0116/0017. **6**: Fragment of a body chamber of an indet neocomitid ammonite, 2004z0116/0019. **7**: Nautiloid, 2004 z0116/0021. **8**: *Lamellaptychus* sp., 2004z0116/0025. **9**: Belemnite rostrum, 2004 z0116/0026. **10**: Bivalve, 2004z0116/0027. **11**: The brachiopod *Triangope* sp., 2004z0116/0028. All specimens are in natural size and coated with ammonium chloride before photographing.

The ammonoid beds are accompanied by layers showing orientated 'autochthonous' straight ammonoid shells (e.g. *Bochianites*) on bedding planes. Thus, for the specimens concentrated in such thin layers, a reorientation due to bottom currents is probable. Note that caution should be exercised when applying the terms autochthonous and allochthonous in cephalopods.

The Hochkogel was additionally analyses on the chronostratigraphical significance of its lower Valanginian calpionellid association (Lukeneder & Reháková 2007). Early Cretaceous calpionellid samples were collected at the ammonoid-bearing Hochkogel locality in the southern most part of the Reichraming Nappe (Ebenforst Syncline, Northern Calcareous Alps). The microfossil fauna sampled from limestone parts of the Rossfeld Formation indicates an early Valanginian age. The standard *Calpionellites* Zone (with *Calpionellites darderi* and *Calpionellites major* subzones) coincides with

Fig. 6: Ammonites from the lower Barremian Hirner section (Schrambach Formation). **1**: *Phylloceras* (*Hypophylloceras*) *serum* (Oppel), 2003z0045/0001. **2**: *Lytoceras subfimbriatum* (d'Orbigny), 2003z0045/0004. **3**: *Protetragonites* aff. *crebrisulcatus* (Uhlig), 2003z0045/0005. **4**: *Karsteniceras* cf. *ternbergense* (Lukeneder), 2003z0045/0008. **5**: *Hamulina lorioli* (Uhlig), 2003z0045/0007. **6**: Accumulation of *Barremites* (*Barremites*) cf. *difficilis* (d'Orbigny), 2003z0045/0006. **7**: Belemnite, 2003z0045/0009. All specimens are in natural size and coated with ammonium chloride before photographing.

the lower Valanginian ammonoid zones of *Busnardoites campylotoxus* and *Tirnovella pertransiens*. The deposition of the limestones in this area occurred in an unstable environment disturbed by gravitational transport which accounts for the different sedimentary components and accompanying fossils in the accumulated layers, transported from a source area situated to the south.

The stratigraphic investigation of the microfauna revealed that the Hochkogel section comprises lower Valanginian deposits of the *Calpionellites* Zone (*C. darderi* and *C. major* Subzones), which corresponds to the *Busnardoites campylotoxus* and/or *Thurmannia pertransiens* ammonoid zones. The importance of this small microfossil fauna is that it enables dating of the sandstones of the Rossfeld Formation, which are normally barren of macro- and microfossils. Only thin limestone layers, intercalated in a sandstone interval of the Rossfeld Formation, yielded microfossil faunas. Based on the microfossil investigation, a better defined age could be detected, leading to a change from early late Valanginian (LUKENEDER 2005a) to a late early Valanginian (LUKENEDER & REHÁKOVÁ 2007).

Thirty two thin sections were examined from beds 1 and 3, which are formed of several different layers (A, B, C). Each of these could be further subdivided by the microfossil content with *Praecalpionellites*, *Calpionellites*, *Calpionella*, *Calpionellopsis*, *Tintinnopsella*, *Lorenziella*, *Remaniella*. The calpionellid fauna is accompanied by the following calcareous dinoflagellate genera *Cadosina* and *Colomisphaera*. The macrofauna is represented especially by ammonites.

The entire section yielded about 800 ammonites (including fragments; LUKENEDER 2005a). The ammonite moulds are restricted to the limestone beds. No ammonoids were found within the enclosing sandstone layers. The latter were deposited by turbidity currents, show gradation and, on their top, plant debris. Sorting or packing of fossil components due to sedimentological or biological effects, and alignments or concentration due to transport or bottom currents were observed. The macrofauna and the sedimentological data support the interpretation of a highly dynamic palaeoenvironment on the slope. The suggested palaeogeographic position of the section studied indicates an influence of turbiditic redeposition ('debris flow') and an allochthonous origin of the fragmented ammonoids collected.

Hirner section

An early Barremian ammonoid fauna from the Lower Cretaceous Schrambach Formation of the Schneeberg Syncline (Reichraming Nappe, Northern Calcareous Alps) yielded 8 genera, each represented by 1 or 2 species (LUKENEDER 2004d; Fig. 6). The exclusively Mediterranean ammonoids are dominated by Barremites (54.2%) of the Ammonitina, followed by the Lytoceratina (22.9%), Phylloceratina (12.5%) and *Karsteniceras* (10.4%) from the Ancyloceratina.

The macrofauna is represented especially by ammonoids. The whole section yielded about 48 ammonoids. Due to the preservation (moulds) of the cephalopods and the lithologic character of the Schrambach Formation, collecting and preparing ammonoids is difficult. The stratigraphic investigation of the ammonoid fauna revealed that the Hirner section comprises uppermost lower Barremian sediments of the *Moutoniceras moutonianum* Zone, and belongs exclusively to the Mediterranean Province. The association indicates that the cephalopod-bearing beds in the Formation belong to the latest early Barremian (*Moutoniceras moutonianum* ammonoid Zone; according to the Lower Cretaceous Ammonite Working Group; REBOULET et al. 2009).

The occurring cephalopods are: *Lytoceras subfimbriatum*, *Protetragonites* aff. *crebrisulcatus*, *Phylloceras serum*, *Phyllopachyceras infundibulum*, *Sowerbyceras ernesti*, *Barremits* (*Barremites*) cf. *difficilis*, *Hamulina lorioli* and *Karsteniceras* cf. *ternbergense* (Fig. 6). Although *Moutoniceras moutonianum* is missing, the typical association hints to a latest early Barremian age (LUKENEDER 2004d).

Sorting and packing due to sedimentological or biological effects, and alignments or concentration due to transport or bottom currents, cannot be observed. The analysis of the macrofauna and the sedimentological data support the interpretation of a palaeoenvironment on the outer shelf to slope.

The presented paper is a further step toward correlating rare Barremian faunas (e.g. layers of ammonoid occurrences) in Lower Cretaceous sediments within the Northern Calcareous Alps. Most of the ammonoids found at the Hirner section were apparently abundant or accumulated in few beds over the whole section (e.g. *Barremites*-abundance Zone, see LUKENEDER 2004d). Such beds show extraordinary abundance of more or less a single species (LUKENEDER 2003a). This was investigated on bedding planes from the Hirner section. The main future investigation topics concerning these ammonoid abundance zones and biohorizons within the above-described framework will be the palaeoecological, palaeobiogeographic and biostratigraphic development of Lower Cretaceous ammonoid beds within the Northern Calcareous Alps.

Eibeckgraben section

Ammonoids of Early Cretaceous age were collected at the Northern Calcareous Alps in the southernmost

Fig. 7: Ammonites from the upper Valanginian Eibeck Section (Rossfeld Formation). **1**: *Lytoceras subfimbriatum* (d'Orbigny), 2004z0080/0021. **2**: *Leptotetragonites* cf. *honnoratianus* (d'Orbigny), 2004z0080/0019. **3**: *Ptychophylloceras ptychoicum* (Quenstedt), 2004z0080/ 0022. **4**: *Olcostephanus guebhardi* (Kilian), 2004z0080/0005. **5**: *Olcostephanus guebhardi* (Kilian), 2004z0080/0006. **6**: Olcostephanus guebhardi (Kilian), 2004z0080/0007. **7**: *Neocomites teschenensis* (Uhlig), 2004z0080/0008. **8**: *Neocomites teschenensis* (Uhlig), 2004z0080/0009. **9**: *Neocomites teschenensis* (Uhlig), 2004z0080/0010. **10**: *Neocomites teschenensis* (Uhlig), 2004z0080/0011. **11**: *Neocomites neocomiensis* (d'Orbigny), 2004z0080/0015. **12**: The boreal ammonite *Prodichotomites* sp., adult specimen, 2004z0080/0016. **13**: *Bochianites neocomiensis* (d'Orbigny), 2004z0080/0026. All specimens are in natural size and coated with ammonium chloride before photographing.

Fig. 8: The belemnite *Conobelus pseudoheres* (LUKENEDER) from the upper Valanginian Eibeck Section (Rossfeld Formation). **1**: Holotype, lateral view, 2004z0046/0001. **2**: Dorsal view of the same specimen. **3**: Lateral view of the same specimen. Specimens in natural size.

part of the Reichraming Nappe (Ebenforst Syncline; LUKENEDER 2004c). The cephalopods (Fig. 7), which derive from the Rossfeld Formation indicate an earliest late Valanginian age (*Saynoceras verrucosum* Zone; *Karakaschiceras pronecostatum* Subzone).

The deposition of the marly limestones and marls in this interval occurred during unstable environmental conditions which led to a mixed autochthonous/allochthonous ammonoid fauna. During the course of this study, 129 ammonoids and 4 lamellaptychi were examined. The ammonoid fauna comprises 10 different genera, each apparently represented by 1–2 species. Ammonitina are the most frequent components (89%, represented by *Haploceras*, *Neocomites*, *Oosterella*, *Eleniceras*, *Olcostephanus*, *Prodichotomites*; Fig. 7), followed by the lytoceratids (5%, *Lytoceras*, *Leptotetragonites*), the phylloceratids (5%, P*tychophylloceras*) and the ancyloceratids (1%, *Bochianites*). The cephalopod fauna consists of numerous Mediterranean elements (dominated by *Olcostephanus*) and scarce Boreal ammonoids (the latter represented by *Prodichotomites*). The described Prodichotomites provides the first evidence of Boreal ammonoids within the Northern Calcareous Alps during the Valanginian and moreover the southernmost occurrence of this genus so far.

The macrofauna of the Eibeck section is represented especially by ammonoids, belemnoids, aptychi and bivalves. The whole section has yielded 129 ammonoids. The poor preservation (mostly internal moulds, limonitic steinkerns) of the ammonoids and the lithologic character of the Rossfeld Formation makes the sampling difficult. The fauna can be assigned to the *Saynoceras verrucosum* Zone (*Karakaschiceras pronecostatum* Subzone) sensu REBOULET et al. (2009). It contains descendants of the Mediterranean Province and a single Boreal genus. According to the stratigraphic investigations the boreal ammonoid corresponds to the genus *Prodichotomites*. The described Boreal descendant *Prodichotomites* (Fig. 7) provides the first evidence of Boreal ammonoids within the Alpine region (Northern Calcareous Alps) during the Valanginian, and marks the southernmost limit of migration of the genus (LUKENEDER 2004c).

The deposition of the marls took place during conditions of relatively stable water masses and high sedimentation rates but under unstable sedimentological

Fig. 9: Ammonites from the lower Aptian Traunkirchen section (Tannheim Formation). **1**: Left side view of *Procheloniceras* aff. *albrechtiaustriae* (HOHENEGGER). **2**: External view of the specimen. **3**: Right side view of the specimen. The specimen was coated with ammonium chloride before photographing. The natural size is 30 cm. No inventory number can be given since the original specimen is in property of Helmut KREISEDER (Department of the Upper Austrian Government). A cast of the specimen is stored at the Natural History Museum Vienna.

(e.g. turbidites, bottom morphology) conditions. The shells were transported within 'mudflows' following embedment in the sediment. The abundant olcostephanid specimens seem to have been redeposited from shallower shelf regions into a deeper shelf environment. The fauna of the Eibeck 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. Different life habitats are assumed for males (microconchs) and females (macroconchs) of the genus *Olcostephanus*. Microconchs probably lived in the open sea, whereas the macroconchs dwelt in the shallower water of the lower shelf (LUKENEDER 2004c).

The first Cretaceous belemnite preserved with the rostrum, slightly compressed phragmocone and part of the proostracum was described from the Lower Cretaceous (upper Valanginian) Rossfeld Formation (Eibeck, Reichraming Nappe of the Northern Calcareous Alps (LUKENEDER 2005b). 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 species *Conobelus pseudoheres* LUKENEDER, 2005b (Fig. 8) was introduced 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.

The Early Cretaceous coleoid *C. pseudoheres* is preserved with almost its entire shell (LUKENEDER 2005b; Fig. 8). The rostrum with its dorsal groove, the partly but three-dimensionally preserved pharagmocone and parts of the extremely rarely 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 seafloor) of the shell.

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 deposition 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 are given in Lukeneder (2005b). The stratigraphic investigation of the cephalopod fauna revealed that the Eibeck section comprises lower upper Valanginian sediments of the *Saynoceras verrucosum* Zone.

Traunkirchen section

The only ammonite specimen (Fig. 9) from the Traunkirchen locality was found by Helmut Kreiseder (Department of the Upper Austrian Government) during the construction of the Traunkirchen tunnel in Upper Austria. The outcrop, in which the ammonite *Procheloniceras* was detected (Fig. 9), is no longer accessible. The characteristic ribbing, tuberculation and conch morphology enabled a systematic determination as *Procheloniceras* aff. *albrechtiaustriae* from the lower Aptian (Lukeneder 2005c) The important and unique (for Upper Austria) ammonite from the Tannheim Formation is approximately 125 million years in age.

Kolowratshöhe section

Ammonoids of Early Cretaceous age were collected in the Kolowratshöhe section, which is located in the easternmost part of the Staufen-Höllengebirgs Nappe (Tyrolic Unit, Northern Calcareous Alps; Lukeneder 2005e). The cephalopods, which occur in turbidite sandstones of the Rossfeld Formation, indicate a latest late Valanginian age (*Criosarasinella furcillata* Zone). The ammonoid fauna (483 specimens) comprises 13 different genera, each represented by one or two species. Ammonitina are the most frequent components (65%, represented by *Haploceras*, *Neocomites*, *Criosarasinella*, *Rodighieroites*, *Olcostephanus*, *Jeanthieuloyites*, Fig. 10), followed by the lytoceratids (17%, *Lytoceras*, *Leptotetragonites*, *Protetragonites*), the phylloceratids (7%, *Phylloceras*, *Phyllopachyceras*) and the ancyloceratids (11%, *Bochianites*, *Crioceratites*, *Himantoceras*). The ammonite genera and species were identified as *Phylloceras serum*, *Phyllopachyceras winkleri*, *Lytoceras subfimbriatum*, *Lytoceras sutile*, *Protetragonites* sp., *Haploceras* (*Neolissoceras*) *grasianum*, *Haploceras* (*Neolissoceras*) *desmoceratoides*, *Olcostephanus densicostatus*, *Neocomites praediscus*, *Neocomites subpachydicranus*, ?*Rodighieroites* sp., *Jeanthieuloyites* cf. *quinquestriatus*, *Criosarasinella furcillata*, *Crioceratites* sp., *Himantoceras* sp. and *Bochianites oosteri* (see Lukeneder 2005e; Fig. 10).

Fig. 10: Ammonites from the upper Valanginian Kolowratshöhe section (Rossfeld Formation), with the dominant species *Olcostephanus densicostatus* (Wegner). **1**: *Phylloceras serum* (Oppel), 2005z0233/0002. **2**: *Lytoceras subfimbriatum* (d'Orbigny), 2005z0233/0003. **3**: *Lytoceras sutile* (Oppel), 2005z0233/0004. **4**: *Phyllopachyceras winkleri* (Uhlig), 2005z0233/0006. **5**: *Protetragonites* cf. *quadrisulcatus* (d'Orbigny), 2005z0233/0007. **6**: *Phyllopachyceras* cf. *rogersi* (Kitchin), 2005z0233/0009. **7**: *Haploceras desmoceratoides* (Wiedmann), 2005z0233/0012. **8**: *Haploceras grasianum* (d'Orbigny), 2005z0233/0014. **9**: *Olcostephanus densicostatus* (Wegner), M, 2005z0233/0015. **10**: *Olcostephanus densicostatus* (Wegner), M, 2005z0233/0016. **11**: Accumulation of *Olcostephanus densicostatus* (Wegner), M and m, 2005z0233/0022. **12**: *Jeanthieuolyites cf. quinquestriatus* (Besairie), 2005z0233/0024. **13**: *Criosarasinella furcillata* (Thieuloy), 2005z0233/0027. **14**: *Criosarasinella furcillata* Thieuloy, body chamber, 2005z0233/0030. **15**: *Neocomites subpachydicranus* (Reboulet), 2005z0233/0032. **16**: *Neocomites praediscus* (Reboulet), 2005z0233/0034. **17**: *Crioceratites* sp., 2005z0233/0039. **18**: *Bochianites oosteri* (d'Orbigny), 2005z0233/0041. **19**: *Lamellaptychus* sp., 2005z0233/0043. **20**: *Triangope* sp., 2005z0233/0045. **21**: *Sphenodus* sp., shark tooth, 2005z0233/0046. **22**: *Brachyphyllum* sp., Coniferales, 2005z0233/0047. All specimens x0.5 and coated with ammonium chloride before photographing. M: macroconch, m: microconch.

The cephalopod fauna consists only of Mediterranean elements (dominated by *Olcostephanus*, microconchs and macroconchs, 231 specimens). The term '*Olcostephanus densicostatus* abundance Zone' was established for these abundance beds (Lukeneder 2005e). The ammonoid specimens of the Kolowratshöhe are accumulated into 3 different layers within an interval of 30 centimetres of sandstone. The fauna of the Kolowratshöhe section is interpreted as a mixed assemblage, comprising allochthonous elements transported from the shallower shelf and parautochthonous pelagic elements from the open sea. The presence of abundant glauconite indicates low sedimentation rates in the source area, whereas the final deposition of the sandstones of the Rossfeld Formation took place during conditions of relatively high sedimentation rates but under the influence of turbidites and varying bottom morphol-


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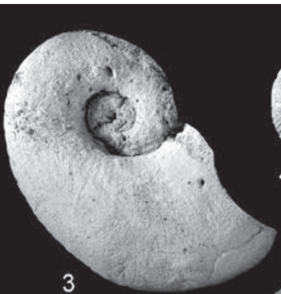
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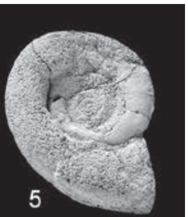
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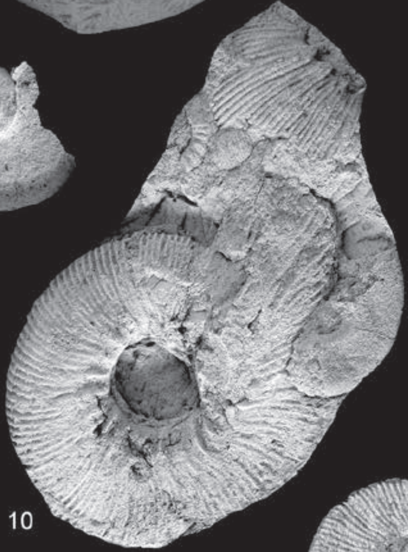
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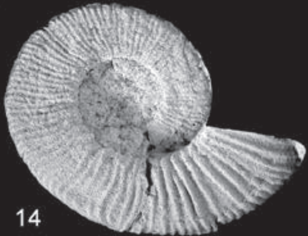
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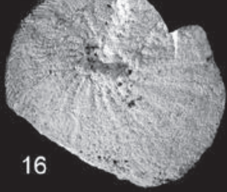
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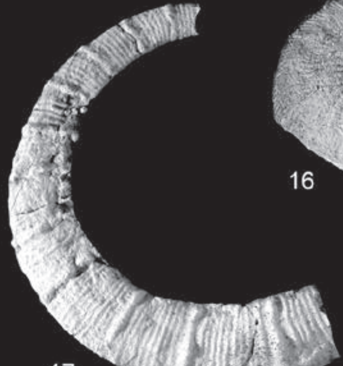
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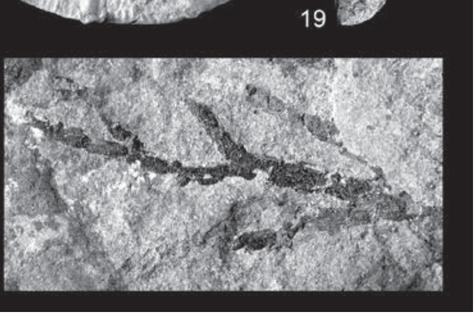
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ogy. The allochthonous glauconite points to a shallow shelf environment as the primary source for the sandstones. This source area was interpreted as a land high and a shelf from which the sediments were delivered into basins of the Northern Calcareous Alps (e.g. Tyrolic Unit) to the north of the swell. The basin palaeogeography is interpreted as a submarine, northward-directed proximal/distal slope belonging to an uplifted area situated to the south of the basin.

The final deposition of the sandstones from the Kolowratshöhe took place during conditions of relatively high sedimentation rates. The sandstones of the Rossfeld Formation in this area consist mainly of turbidites. The source area was a subaerial high and a shelf from which the sediments were delivered into northern basins of the Northern Calcareous Alps. The high has been shown to extend above the sea-level as confirmed by findings of the land plant *Brachyphyllum* (Fig. 10). On the whole, the presence of glauconite indicates a low deposition rate in the source area (LUKENEDER 2005e). The lithological and mineralogical diagnostic findings point to an amalgamation of single turbidite beds after a decline or cessation of sedimentation. A cessation is strongly supported by the accumulation of glauconitic grains in single layers that separate single beds of glauconitic sandstones. The macrofauna of the Kolowratshöhe section is represented especially by ammonoids. The whole section yielded 483 ammonoids. Based on the presence of the index fossil *Criosarasinella furcillata*, the fauna can be assigned to the *C. furcillata* ammonoid Zone (*C. furcillata* Subzone). The ammonoid fauna contains only descendants of the Mediterranean Province.

The invertebrate fauna (e.g. ammonites and brachiopods) are accumulated in isolated single layers. The shells are aligned concentrated in particular levels and some show current-induced orientation. This applies both to straight shells (e.g. *Bochianites*) as well as coiled shells (e.g. *Lytoceras*, *Haploceras*, *Olcostephanus*). This points to orientation by currents (LUKENEDER 2005e). Additionally, accumulated small ammonoids and shell fragments in the body chambers of somewhat larger ammonoids supports the assumed effect of agglomeration and scavenging by currents. The accumulation of ammonoid layers (Fig. 10) indicates either deposition on site at short, favourable 'time-intervals', or to reworked accumulation-layers after turbiditic transport.

At least some of the abundant ammonoid specimens seem to have been redeposited from shallower shelf regions into a slope environment. The encrustation of larger smooth shell fragments by serpulids indicates a somewhat longer depositional history for such shells. This is interpreted as a sign for overgrowth of such secondary 'hardgrounds' uncovered by sediments, by the benthic organisms during lengthier exposure.

Most probably the encrustation took place already at the primary depositional area on the shelf. The very small number (14) of aptychi contrasts the very high (483) number of ammonoid specimens. Isolation took place either through transport (and therefore different behaviour in the water column) or through current-induced grain differentiation during accumulation. The latter scenario leads to different places of deposition for these two cephalopod elements of the same animal (LUKENEDER 2005e). Based on all these data, the fauna of the Kolowratshöhe section is interpreted as a mixed assemblage, comprising transported elements from the shallower shelf (allochthonous) along with more parautochthonous pelagic elements (olcostephanids) from the open sea.

Conclusions

Distinct ammonite faunas derive from limestones, marls and sandstones of well known tectonical nappes from the Northern Calcareous Alps of Upper Austria. The specimens were collected during the last two decades in the Ternberg Nappe, Reichraming Nappe, Staufen-Höllengebirgs Nappe, and the Langbath Unit. The main sections are from north to south the KB1-A Klausrieglerbach 1 section (Schrambach Formation), the KB1-B Klausrieglerbach 2 section (Schrambach Formation), the Hirner section (Schrambach Formation), the Eibeck Section (Rossfeld Formation), the Hochkogel section (Rossfeld Formation), the Traunkirchen section (Tannheim Formation) and the Kolowratshöhe section (Rossfeld Formation).

During the study, thousands of ammonite specimens were collected, prepared and described. More than 100 species of Valanginian to Barremian cephalopods (ammonites and belemnites) were detected and several new species introduced, such as the ammonite *Karsteniceras ternbergense* (named after the village Ternberg in Upper Austria) and the belemnite *Conobelus pseudoheres*. Palaeontological studies on the Lower Cretaceous ammonite material increased the knowledge on palaeoceanography and palaeoenvironments prevailing during Cretaceous times in the Upper Austrian Northern Calcareous Alps. The Lower Cretaceous ammonite fauna is dominated by Mediterranean faunal elements accompanied by a single Boreal member, *Prodichotomites*. Additional ammonite collections will be carried out in the future to determine the exact position of stage-, zone-, and subzone-boundaries. These studies will include palaeomagnetic, isotope and geochemical analyses along with a detailed biostratigraphy based on micro- and nannofossils.

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Computed tomography and laser scanning of fossil cephalopods (Triassic and Cretaceous)

A. LUKENEDER, S. LUKENEDER & C. GUSENBAUER

Abstract: We here present a computed tomography and 3D visualisation of Mesozoic cephalopods from the Southern Alps and the Taurus Mountains. Study objects were ammonoids and ammonoid mass-occurrences that were deposited during the Upper Triassic (approx. 234 mya) of SW Turkey and during the Lower Cretaceous of N Italy (approx. 129 mya). Computed tomography, a non-destructive and non-invasive method, facilitates the view inside rocks and fossils. The combination of computed tomography and palaeontological data enable us to produce 3D reconstructions of the extinct organisms. Detailed reconstructions of the fossil cephalopods and the ammonite animals are based on shell morphologies, adapted from CT data. Object-based combined analyses from computed tomography and various computed 3D facility programmes aid in understanding morphological details as well as their ontogenetic changes in fossil material. The presented CT and laser scan data demonstrate the wide range of applications and analytical techniques, and furthermore outline possible limitations of computed tomography in earth sciences and palaeontology.

Keywords: Computed tomography, laser scan, palaeontology, ammonoids, Triassic, Cretaceous

Introduction

X-ray computed tomography and laser scanning is known in palaeontology as providing data for 3D visualisation and geometrical modelling techniques. Computed tomography and laser scans down to a few microns (or even below) of spatial resolution are increasingly employed for geoscientific investigations, using an equally variable range of processing techniques and software packages. Additionally, internal structures are visualised without the destruction of fossils, as computed tomography is a non-destructive method.

The creation of 3D models from fossils (e.g. cephalopods) based on CT and laser scan imaging aids in visualisation and interpretation, and may serve for the reconstruction of mechanical models. 3D models of fossil specimens have become increasingly popular, providing more or less accurate information about volume, spatial distribution, orientation and size of fossils in a sample as well as insights into biostratinomic and diagenetic processes. Numerous complementary techniques have been advanced in recent years. These provide 3D datasets of palaeontological objects and involve both surface and volume scanning methods (e.g. microtomography), as well as laser scanning (airborne, terrestrial or desktop scanners) of surface morphology. These methods can be combined with point cloud data generated from digital images. Numerous authors (e.g. MARSCHALLINGER 2001; MALOOF et al. 2010; MAYRHOFER & LUKENEDER 2010; KRUTA et al. 2011; MARSCHALLINGER et al. 2011; LUKENEDER S. & A. LUKENEDER 2011; SAUPE et al. 2012) show the multitude of applications of 3D geometrical models in palaeontological studies. The great variability, the wide range of applications, and the analytical techniques in the fossil record are demonstrated for dinosaurs (RAYFIELD et al. 2001, 2007; BALANOFF et al. 2008; WITMER and RIDGELY 2009; FORTUNY et al. 2011; TSUIHIJI et al. 2011; KNOLL et al. 2012), lizards (POLCYN et al. 2002), birds (ROWE et al. 2001; DEGRANGE et al. 2010; ZELENITSKY et al. 2011), fishes (GAI et al. 2011), mammals (LUO et al. 2002), molluscs (HOFFMANN & ZACHOW 2011; LUKENEDER A. 2012; LUKENEDER A. et al. 2012, 2014), brachiopods (GASPARD et al. 2011), insects (GARWOOD 2010, 2011; GARWOOD et al. 2009), plants (FRIIS et al. 2007; SCOTT et al. 2009; LUKENEDER A. et al. 2012), algal or acritarch fossils (CUNNINGHAM et al. 2012), and protists (DONOGHUE et al. 2006, DONG et al. 2010; HULDTGREN et al. 2011). The latter papers additionally outline possible limitations of 3D models in earth sciences and in palaeontology.

The main goal of this paper is to present methods and possibilities for visualisation of palaeontological material based on computed tomography, laser scanning and palaeontological features (e.g. morphology; Fig. 1). Case studies on computed tomography within two 3-year projects of the Austrian Science Fund (FWF

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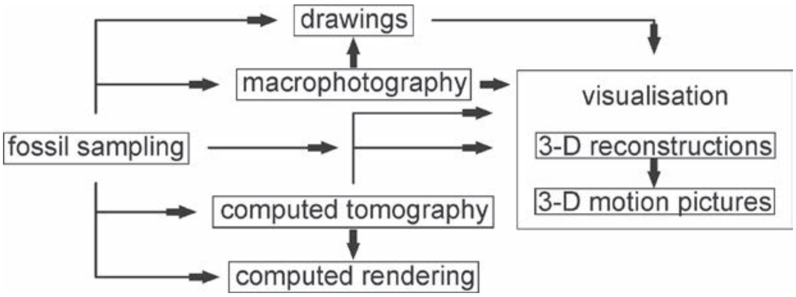

Fig. 1: Principal steps in 3D visualisation of palaeontological material such as ammonoids.

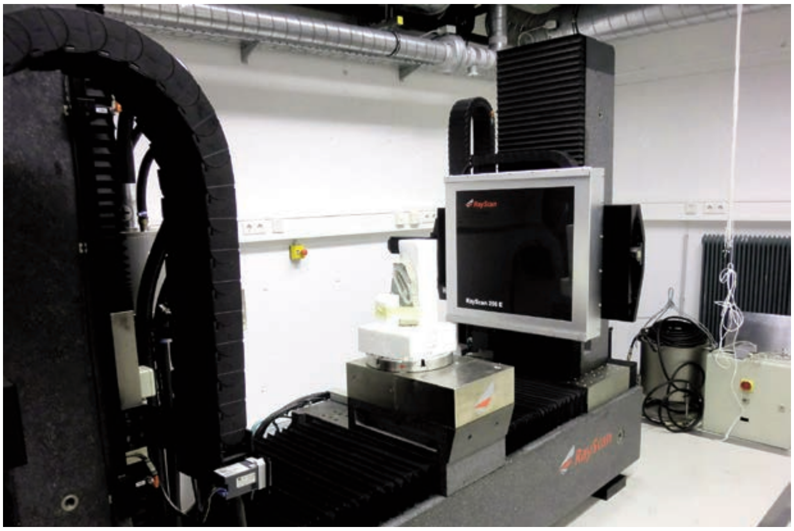

Fig. 2: The CT RayScan 250 E device, with a 225 kV micro-focus and with a 450 kV mini-focus X-ray tube and a 2048 × 2048 pixel flat panel detector (cone beam reconstruction) located at the University of Applied Sciences Upper Austria, Wels Campus. Note the fixed limestone sample with the Lower Cretaceous ammonite *Dissimilites* in the centre.

P22109-B17 and P20018-N10) on Triassic and Cretaceous ammonoids can demonstrate the increasing importance of CT and laser scanning methods in palaeontology.

Experimental design of computed tomography and laser scanning

Computed tomography

Non-invasive techniques, e.g. computed tomography, allow to process great volumes of information without causing any alteration of fossil material (Lukeneder A. 2012; Lukeneder A. et al. 2014). The tomography scans used within this study were made at the Upper Austria University of Applied Sciences in Wels. The 3D computed tomography (CT) device RayScan 250 E is a 3D CT system equipped with two X-ray sources (a 225 kV micro-focus and a 450 kV mini-focus X-ray tube) for the inspection of a wide variety of parts, ranging from micro-objects (high resolution) to macroscopic ones (large penetration length). The system is additionally equipped with a 2048 x 2048 pixels flat-panel detector; it absorbs energy of the X-rays and re-emits the absorbed energy in the form of light, which can be detected (Fig. 2). In the case of an industrial CT-system, the specimen is rotated by 360° and at each predefined angle step a 2D-projection image is captured. The complete set of projection images is then reconstructed to 3D volume data using a mathematical algorithm. The data consists of volumetric pixels (voxels), whose size limits the spatial resolution (down to 5 µm) and the detail-detectability. For each fossil part, the optimal voxel size and tube voltage were set according to the specimen's dimensions. A more detailed introduction to computed tomography is beyond the scope of this article. For the details of X-ray computed tomography as a technique of imaging and quantification of internal features of sediments and fossils see Mees et al. (2003). The non-destructive CT provides the basal information on morphological features of the respective fossil cephalopods.

Laser scanning

Laser scanning of surface morphology is increasingly employed for geoscientific investigations, using an equally variable range of processing techniques and software packages. By using laser surface scans, individual statistical information (e.g. length, breadth, diameter) can be measured very fast and accurately without destruction of the fossil material. Statistical analyses can be performed much quicker and occasionally even more precise in digital systems (Lukeneder S. & A. Lukeneder 2011). For instance, surface scans of single ammonoids of the genus *Kasimlarceltites* (with 99.9% the dominant species of the Triassic ammonoid mass-occurrence) can be used for reconstructing *Kasimlarceltites* as close as possible to nature (Fig. 10a, b). Therefore 3D surface laser scan data were produced down to a resolution of 0.25 mm by using a FARO® Laser Scanner Photon 120/20 and visualised with a new software-version FARO Scene 4.6. The software package 3D-Tool V8 was used for creating digital-slices of single ammonoids (Fig. 10e) and processing size, orientation and distribution of the ammonoids within the mass occurrence (Fig. 10f–h). 3D laser scans and their visualisation were made in cooperation with the Department of Geodynamic and Industrial Geometry Group (3D technology at the University of Technology Vienna) and the Lower Austrian government agency for Hydrogeoloy and Geoinformation.

The new FARO® Laser Scanner Photon 120/20, with the new software-version FARO Scene 4.6, possesses the fastest Phase Shift Laser Scanner (976.000 points/seconds) with the biggest range that is currently

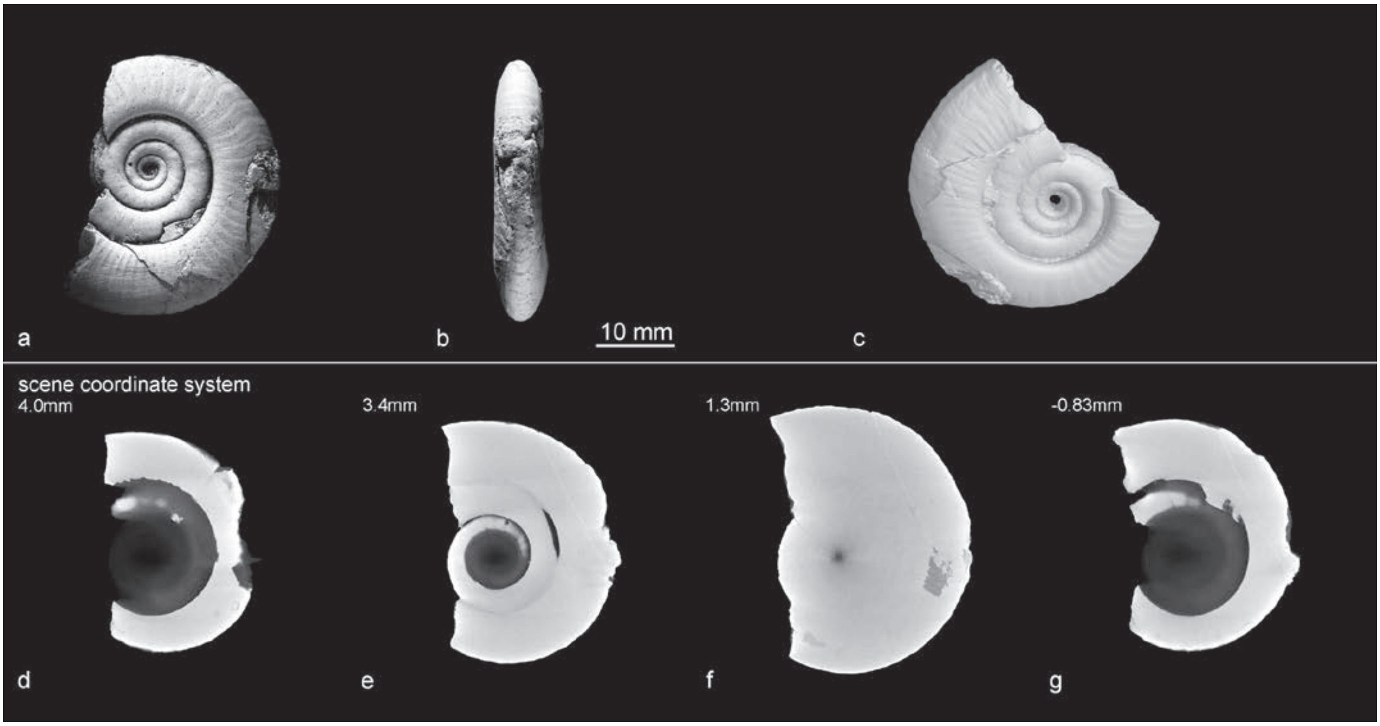

Fig. 3: *Kasimlarceltites krystyni*. (a) Lateral view; (b) ventral view of the holotype, NHMW-2012z0133/0014, both coated with ammonium chloride; (c) rendered CT surface of the same specimen. CT frontal view slices: (d) CT slice 048; (e) CT slice 076; (f) CT slice 168; (g) CT slice 260. Embedding and infilling sediment is limestone.

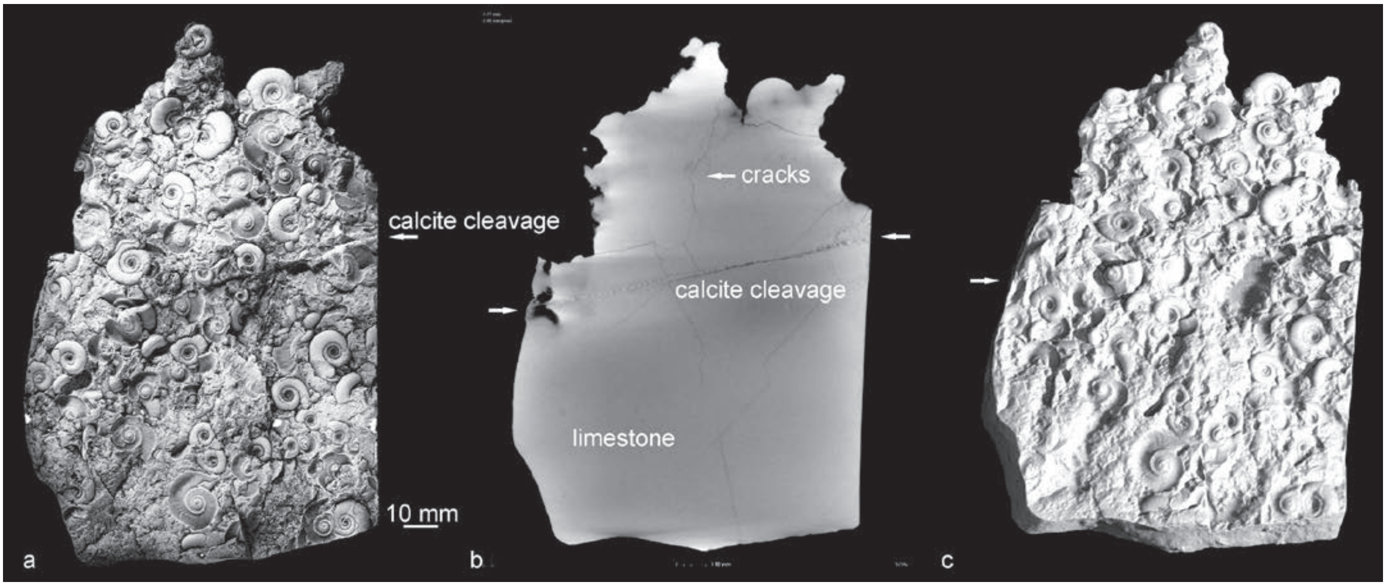

Fig. 4: Rock sample with the mass-occurrence of *Kasimlarceltites krystyni*. (a) Lateral view, NHMW-2013/0568/0003, coated with ammonium chloride; (b) CT frontal view slice 733; (c) rendered CT surface of the same sample. Embedding and infilling sediment is limestone. Note the visible cleavage and cracks.

available on the free market. New technical features of the Photon 120/20 make the scanner a useful system for performing high-speed 3D scans with reduced random-noise obtained by efficient hyper-modulation. Surfaces of ammonoids can therefore be reconstructed digitally without loss of information.

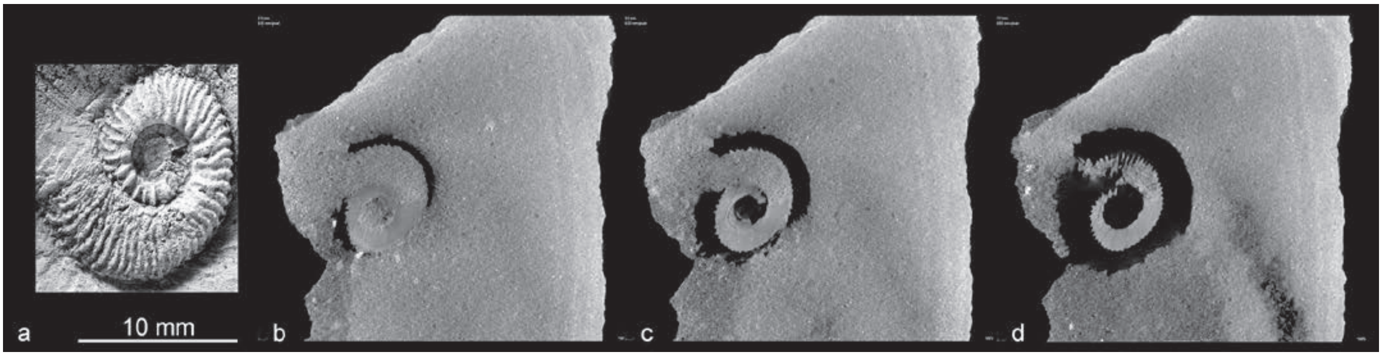

Fig. 5: *Sandlingites* cf. *pilari*. (a) Lateral view, NHMW-2012/0133/0475, coated with ammonium chloride. CT frontal view slices: (b) CT slice 185; (c) CT slice 199; (d) CT slice 215. Spotty grey, embedding sediment and infilling of body chamber is sandstone. Smooth grey, internal parts filled by secondary calcite in the phragmocone.

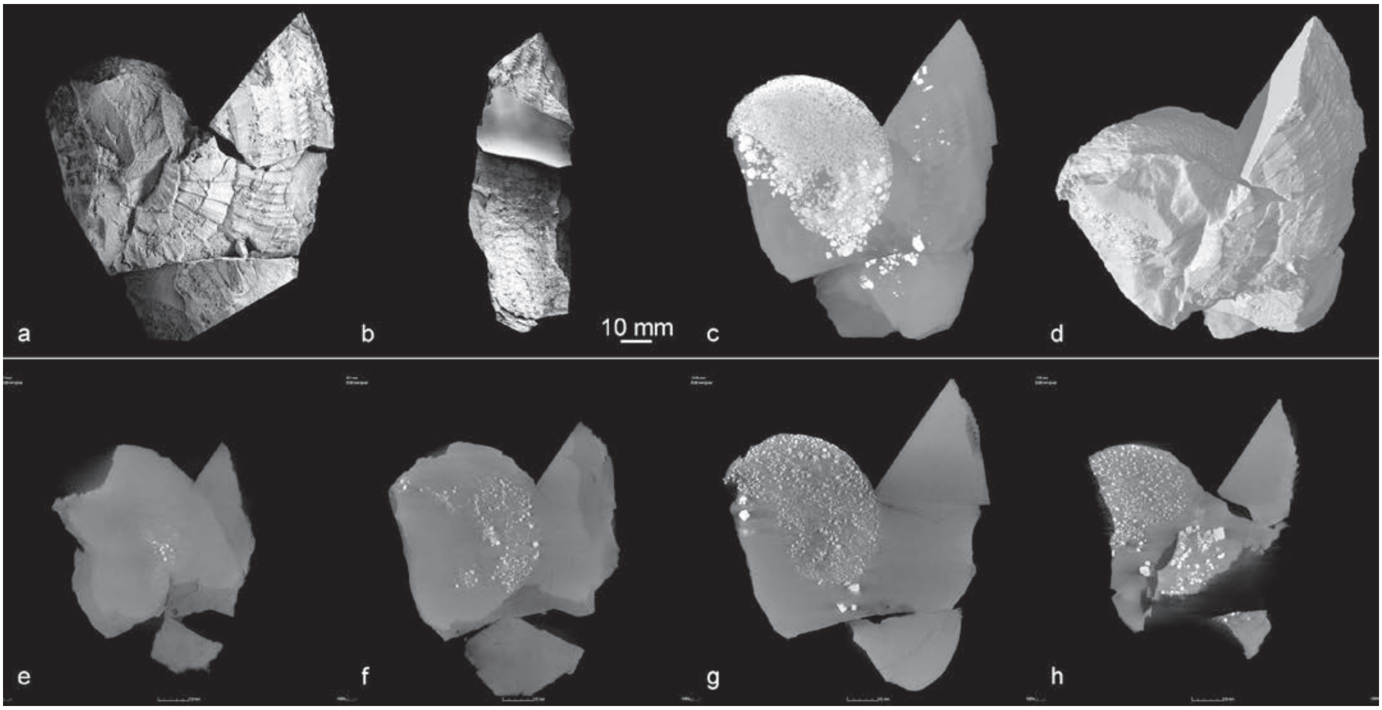

Fig. 6: *Trachysagenites* cf. *beckei*. (a) Lateral view, NHMW-2012/0133/0350; (b) ventral view, coated with ammonium chloride; (c) maximum intensity projection; (d) rendered CT surface of the same specimen. CT frontal view slices: (e) CT slice 095; (f) CT slice 144; (g) CT slice 295; (h) CT slice 418. Embedding and infilling sediment is limestone. Note the numerous whitish pyrite cubes in the phargmocone.

Palaeontological material

Triassic ammonoids from the Taurus Mountains in Turkey

Computed tomography was tested on the Triassic ammonoid genera *Kasimlarceltites* (and its mass-occurrence), *Sandlingites* and *Trachysagenites*. These fossil cephalopods originate from the Upper Triassic (Carnian, approx. 234 mya) Aşağiyaylabel locality (Taurus Mountains, southwest Turkey). The material was collected within the FWF project P22109-B17 and is stored at the Natural History Museum in Vienna (NHMW). Inventory numbers are given for the investigated specimens of *Kasimlarceltites* (holotype NHMW-2012/0133/0014), *Sandlingites* (NHMW-2012/0133/0475) and *Trachysagenites* (NHMW-2012/0133/0350). The ammonoids were collected by Alexander and Susanne LUKENEDER, Andreas GINDL, Mathias HARZHAUSER, Leopold KRYSTYN, Philipp STRAUSS, and Franz TOPKA.

The outcrop at Aşağiyaylabel is situated at steep limestone walls (dipping 50 degrees NE) within the Taurus Mountains of southern Turkey (Anatolia), about 90 km NNE of Antalya, between the lakes Egirdir and Beyshehir (GPS coordinates N37°33 05 E31°18 14 ; LUKENEDER S. & A. LUKENEDER 2014). The fossil cephalopods reported within this work derive from the

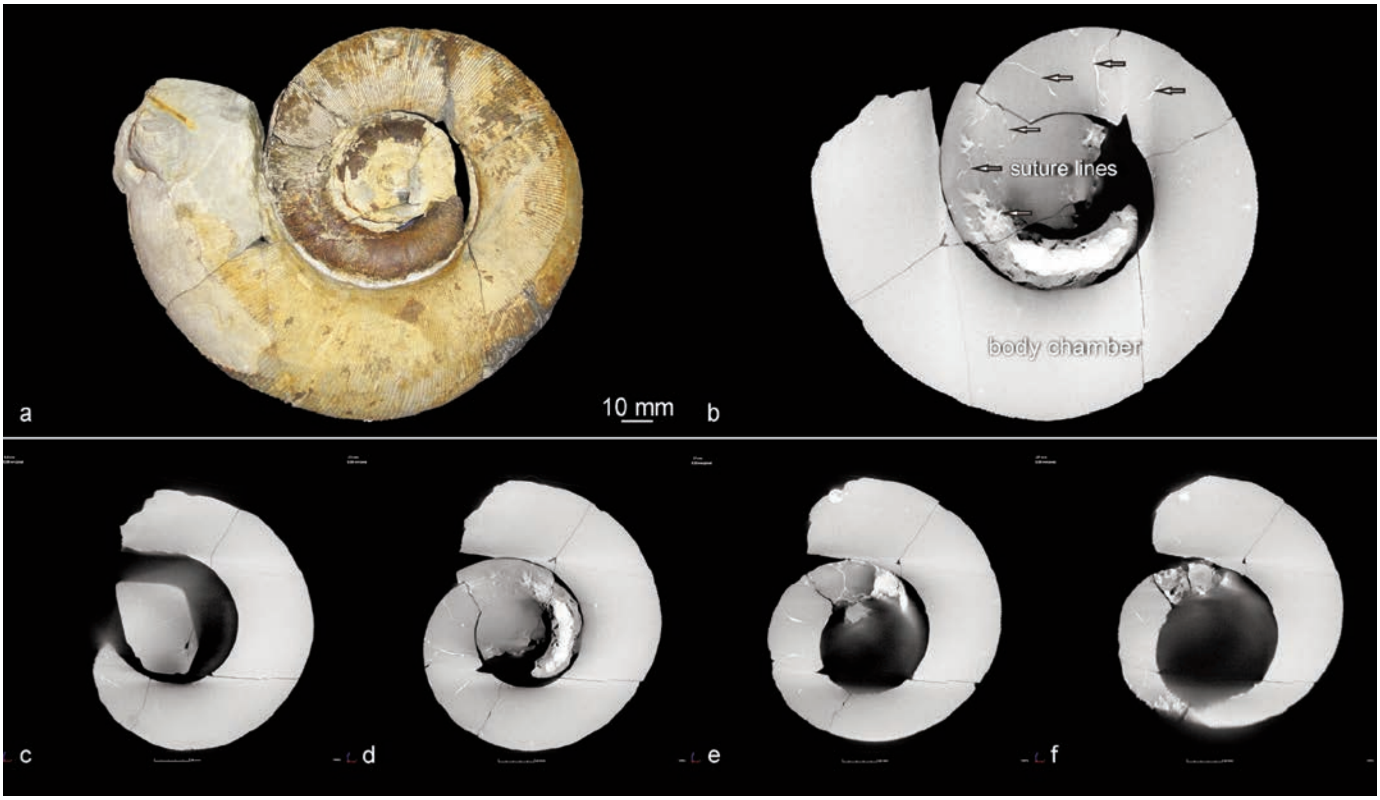

Fig. 7: *Lytoceras subfimbriatum*. (a) Lateral view, uncoated with yellow limonitic crust, NHMW- 2013/0569/0001; (b) maximum intensity projection. CT frontal view slices: (c) CT slice 186; (d) CT slice 252; (e) CT slice 317; (f) CT slice 351. Note the visible, whitish suture lines and an additional ammonite [in (e)] at the apertural end of the body chamber due to the limonitic preservation and the embedding limestone in grey. Cracks through the ammonite are dark grey. The surrounding air is black.

Lower to Upper Carnian Kasimlar Formation (Julian 2–Tuvalian1, *Austrotrachyceras austriacum* Zone–*Tropites dilleri* Zone). A detailed description of the geology and lithostratigraphy is given in LUKENEDER S. et al. (2012) and LUKENEDER S. & A. LUKENEDER (2014).

The investigated Upper Triassic ammonoids are *Kasimlarceltites krystyni* LUKENEDER S. & A. LUKENEDER (family Celtitidae MOJSISOVICS; Fig. 3, 4), *Sandlingites* cf. *pilari* DIENER (family Sandlingitidae TOZER; Fig. 5) and *Trachysagenites* cf. *beckei* DIENER (family Haloritidae MOJSISOVICS; Fig. 6). All ammonoids are members of the order Ceratitida HYATT.

Cretaceous ammonoids from the Dolomites in Italy

This case differs in lithology and taphonomical features from the Triassic case study above. The same methods and equipment were used as for the Triassic samples.

This fossil cephalopod originates from the Puez locality (Dolomites, northern Italy). The material was collected within the FWF project P20018-N10 and is stored at the NHMW. Inventory numbers are given for the investigated specimens from *Lytoceras* (NHMW-2013/0569/0001) and *Dissimilites* (holotype NHMW-2012/0002/0001). The lytoceratid ammonite *Lytoceras* was collected by Martin MASLO and the heteromorph ammonite *Dissimilites* by S. LUKENEDER from Lower Barremian beds (approx. 129 million years old) at the Puez section. The outcrop is situated on the Puez-Geisler-Gardenaccia Plateau in the Dolomites (maps Trentino – Alto Adige; South Tyrol; LUKENEDER A. 2010). The position is about 30 km northeast of Bozen (E011°49 15 N46°35 30 ; LUKENEDER A. 2010, 2012). The fossil cephalopods derive from the Puez Formation (Puez Limestone Member; LUKENEDER A. 2010). The ammonoids reported within this work derive from the middle part of the Puez Limestone Member with Lower Barremian sediments (*Moutoniceras moutonianum* Zone; LUKENEDER A. & S. LUKENEDER 2014). A detailed description of the geology and lithostratigraphy is given in LUKENEDER A. (2010).

The investigated Lower Cretaceous ammonoids were *Lytoceras subfimbriatum* (D'ORBIGNY) (family Lytoceratidae NEUMAYR) and *Dissimilites intermedius* LUKENEDER A. & S. LUKENEDER (family Acrioceratidae VERMEULEN; Fig. 7). The ammonoids are members of the order Ammonoidea ZITTEL, and the subsequent suborders Lytoceratina HYATT and Ancyloceratina WIEDMANN.

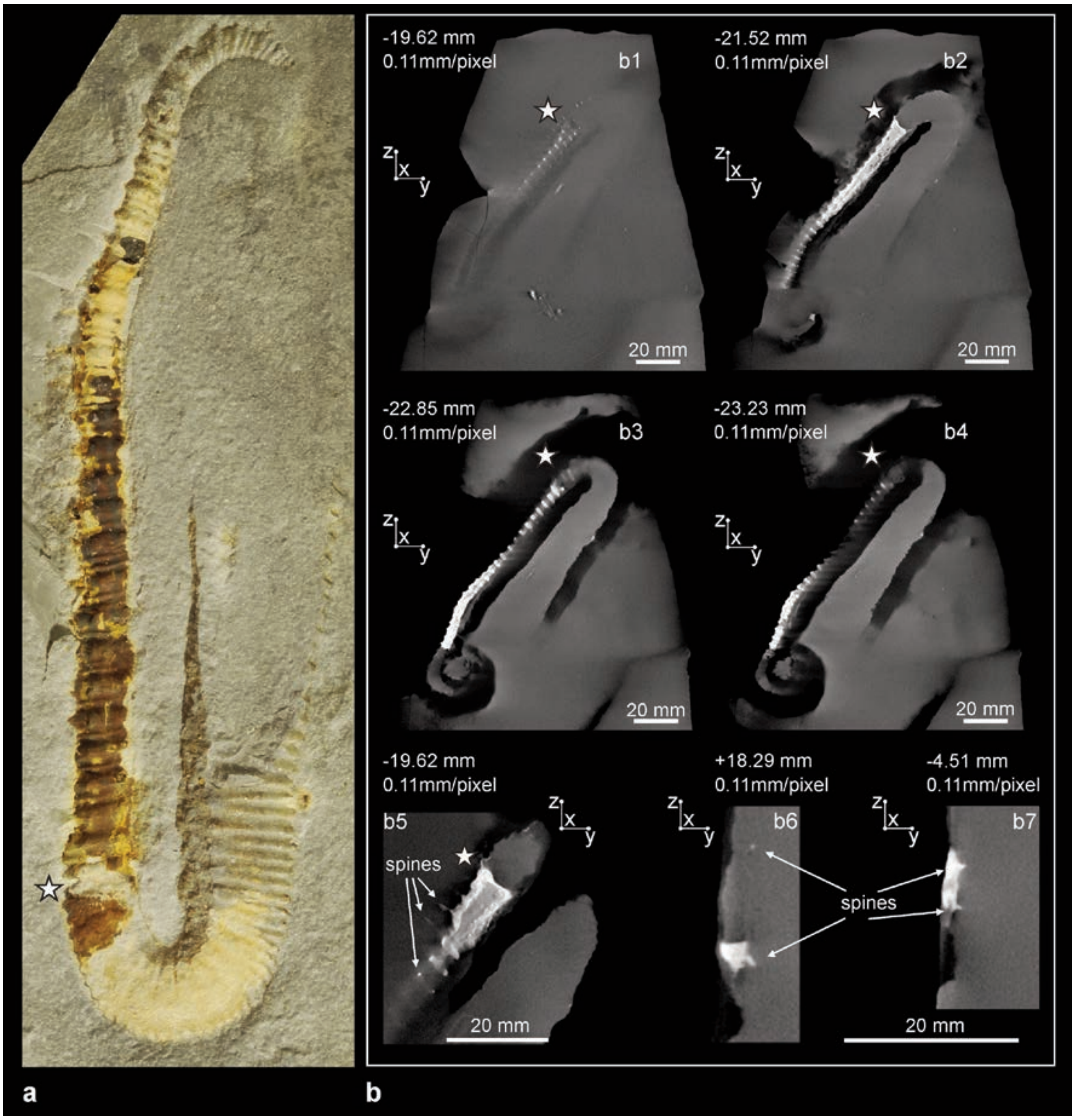

Fig. 8: *Dissimilites intermedius.* (a) Lateral view, uncoated with limonitic preservation, yellow to orange, holotype NHMW-2012/0002/0001. (b) CT frontal (b1-b5) and axial (b6-b7) view slices: (b1) CT slice 421; (b2) CT slice 441; (b3) CT slice 455; (b4) CT slice 460; (b5) detail of CT slice 797; (b6) detail of CT slice 862; (b7) detail of CT slice 622. Computed tomography slices from the specimen with limonitic preservation in white and the embedding limestone in grey. Asterisks mark the beginning of body chamber. Note the delicate spines in CT slices (b5), (b6) and (b7).

Methods, results and visualisation

Macrophotography

Detailed images of the specimens were taken with a Kodak Professional DCS Pro combined with the photo device Stereo Discovery V20 with AxioCam MR5 Zeiss. All images have the same file structure with 600 dpi resolution. Black-and-white images are combined with full colour images for high visibility of edges and details of the fossil.

Computed tomography

3D computed tomography was performed with a 225 kV microfocus and a 450 kV minifocus X-ray tube. The specimen and the embedding fossiliferous marly limestone were tomographed frontally and axially (angle of 90°; Figs 2, 3). Frontal and axial slice-images were animated to videos as motion pictures.

From the Triassic *Kasimlarceltites* (holotype, NHMW-2012/0133/0014), 320 frontal slices (0000.jpg–319.jpg; 146 MB) with 0.11 mm/pixel space were produced. The rock sample with the *Kasimlarceltites* mass-occurrence (NHMW-2013/0568/0003) appears with

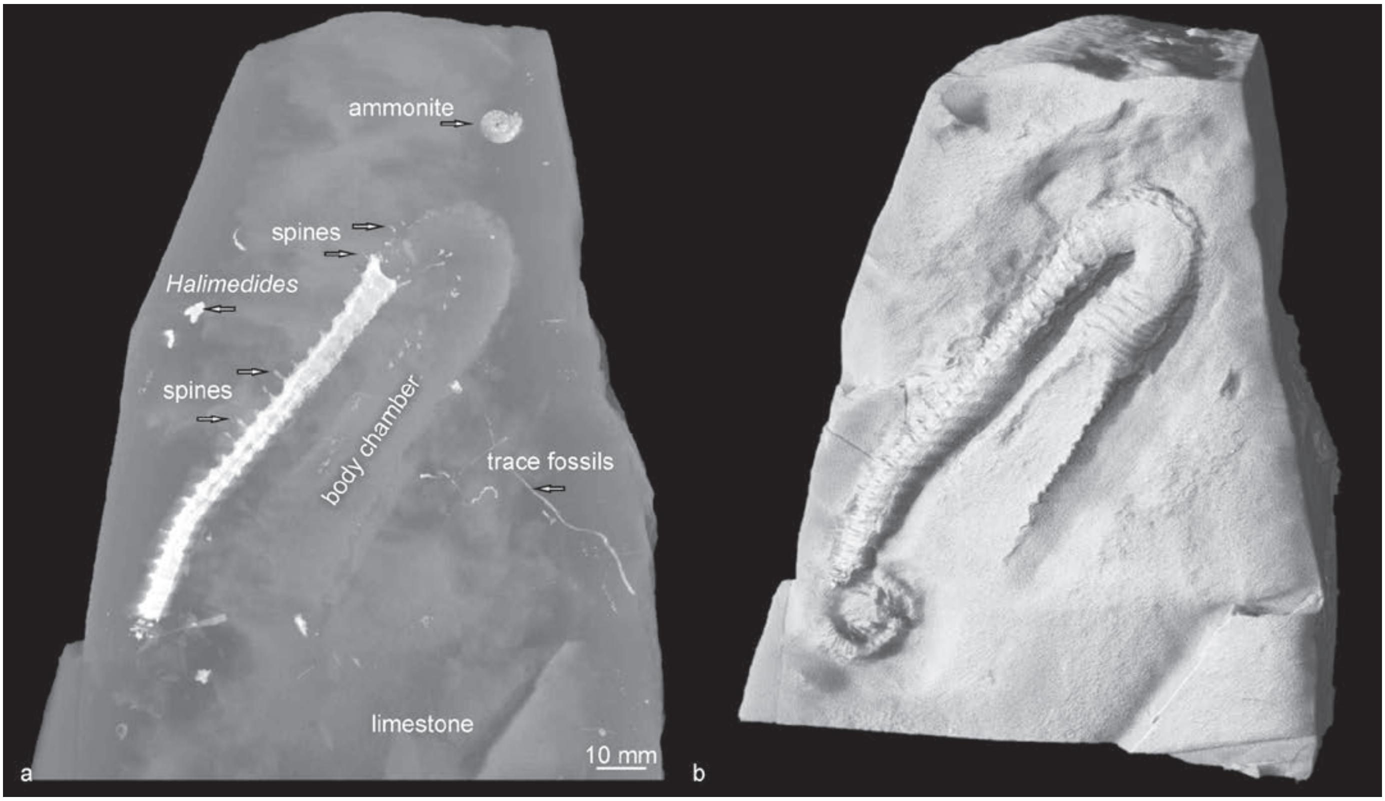

Fig. 9: Limestone rock with the holotype of *Dissimilites intermedius*, lateral view, NHMW-2012/0002/0001. (a) Maximum intensity projection with visible ammonoids and trace fossils with *Halimedides*; (b) rendered CT surface of the same specimen. Whitish suture lines and trace fossils due to the limonitic preservation and the embedding limestone in grey.

310 frontal slices (000.jpg–309.jpg; 157 MB) with 0.11 mm/pixel space and 338 axial slices (527.jpg–864.jpg, 93.3 MB) with 0.11 mm/pixel space. From *Sandlingites* 463 frontal slices (000.jpg–462.jpg; 450 MB) with 0.11 mm/pixel space were produced. From *Trachysagenites* 602 frontal slices (000.jpg–601.jpg; 388 MB) with 0.11 mm/pixel space were produced.

From the Cretaceous *Dissimilites*, 655 frontal slices (000.jpg–654.jpg; 342 MB) with 0.11 mm/pixel space and 1768 axial slices (0000.jpg–1767.jpg, 518 MB) with 0.11 mm/pixel space were produced. From *Lytoceras* 675 frontal slices (000.jpg–674.jpg; 528 MB) with 0.11 mm/pixel space were produced.

Measurements were performed with durations of 56, 68 and 92 minutes. Voxel sizes were 95 and 75.01 m. Tube voltage was adjusted to 220 and 400 kV with 425 and 1500 A. Exposure time was 600, 999, and 2000 ms. 1440 projections with a Cu pre-filter 1.0, 2.0 and 4.0 mm were made. Additionally, the surface (e.g. stone vs. air) was rendered to image the cephalopod's morphology.

3D visualisation and motion pictures of fossil cephalopods

Studies on computed tomography and laser scans are essential for palaeontologic and systematic investigations. Especially when extraction of fossils from embedding sediments is impossible, or the fossil and its delicate morphological parts (e.g. spines, ribs) would be destroyed by preparation.

Triassic ammonoid shells and filled phragmocones (both secondary calcite) from the *Kasimlarceltites* beds (Lukeneder S. & A. Lukeneder 2014) possess the same mass-density as the matrix (i.e. limestone) in which the ammonoid specimens are embedded. The almost identical mass-density of the various carbonates of the embedding matrix (about 2.8 g/cm^3), the ammonoid shell (secondary calcite, about 2.6–2.8 g/cm^3), and the infilled matrix (about 2.8 g/cm^3) avoids their visualisation, especially of morphological details, via computed tomography. It is therefore not possible to visualise inner parts of the ammonoids by computed tomography (Fig. 3–5). In few cases ammonoid shells, body chambers, and secondary formed calcite fissures can be observed in computed tomographic images and movies (Fig. 4). For instance, a secondarily precipitated sparry calcite (in cleavage and cracks) is visible in the Triassic sample of the *Kasimlarceltites* beds (Fig. 4b). In contrast, hundreds of ammonoid specimens within that mass-occurrence "vanish" on CT slices. Disseminated pyrite cubes within the chambered part of the ammonoid (i.e. the phragmocone) define exactly the internal dimension and

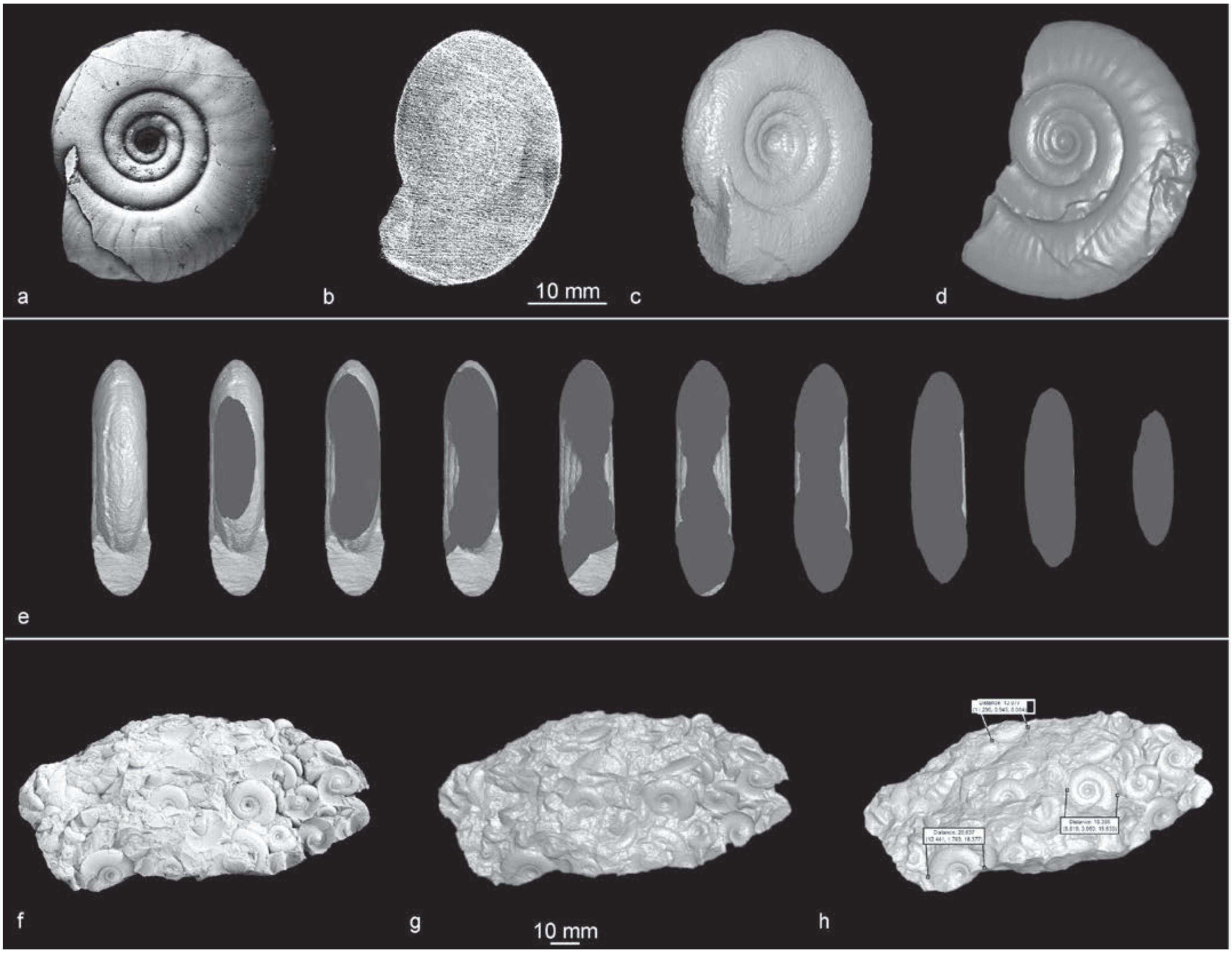

Fig. 10: *Kasimlarceltites krystyni*. (a) Lateral view, NHMW-2012/0568/0001, coated with ammonium chloride; (b) basic laser scan point cloud; (c) rendered laser scan surface; (d) rendered laser scan surface of the holotype, NHMW-20120133/0014; (e) digital slices through rendered laser scan surface; (f) rock sample of the mass-occurrence NHMW-2013/0568/0002, coated with ammonium chloride; (g) rendered laser scan surface; (h) rendered laser scan surface with dimensions of ammonoids.

shape of *Trachysagenites* (Fig. 6a–h). Future work will be done within a project on the possibilities of computed tomography in such dense Mesozoic limestones. GARWOOD et al. (2009, 2010) described two additional possibilities for using CT scans on material of similar density. These authors suggested scanning the material at low X-ray energy in order to reveal the different phases. By the use of a phase contrast holotomography at a synchrotron computed tomography device, crystal structures can rendered visible (GARWOOD et al. 2010).

In rare cases, the investigated Cretaceous ammonoids are secondarily coated by iron sulphides as pyrite and marcasite (both FeS_2), or by hydrated iron oxide-hydroxides as limonite ($FeO(OH) \times nH_2O$). Such steinkerns or limonitic fillings are detected by CT due to the increased density of these iron compounds (pyrite and marcasite: 4.8–5.0 g/cm^3; limonite: 2.7–4.3 g/cm^3). Hence, these dense structures, e.g. fine coatings on fossils or pyrite cubes, can be visualised by computed tomography without any destruction of the fossils, morphological features can be analysed in three-dimensional space, and, furthermore, internal structures can be visualised. The shape data derive from the recently described species *Dissimilites intermedius* LUKENEDER A. & S. LUKENEDER, 2014 (Fig. 8).

The main differences between the Triassic and the Cretaceous fossil material are the embedding sediments (i.e. the matrix) as well as the secondary material of ammonoid shells and penetrating trace fossils. The presence of iron sulphides and iron oxide-hydroxides within sediments or fossils increases the potential of useful computed tomography data. Surface laser scans are un-

Fig. 11: 3D reconstruction of successive ontogenetic stages in the fossil cephalopod *Dissimilites intermedius*, based on CT data (after LUKENEDER 2012). (a) cyrtocone juvenile animal; (b–d) mid-aged animal with straight shell stages; (e–h) different views of the adult, mature ammonite animal.

affected by the difference in sediments. Within marly limestones from the Lower Cretaceous numerous ammonoids from the Lower Barremian (e.g. *Lytoceras*, *Dissimilites*) and trace fossils (*Halimedides*) are preserved as secondary limonitic steinkerns or limonitic fillings. These dense structures can be visualised by computed tomography (Fig. 9). New morphological details such as spines and delicate parts on ammonite shells, the shape and position of suture lines, and the exact structure of trace fossils can be detected and visualised (Fig. 9).

The modelling procedure of the fossil cephalopods is based on a series of CT images, which turned out to be an essential source to understand the cephalopod morphology and shape. Invisible (e.g. when covered by sediment) delicate structures such as spines and suture lines appear within CT data. The digital CT images present a grey scale spectrum which was further refined by converting its height information, ranging from darker to lighter areas, to a so-called "Normal Map" image. This helped to refine the visual appearance and understand various delicate structures. The process involved projecting this Normal Map onto a surface inside a 3D Realtime Editor, and then introducing a virtual light source (LUKENEDER A. 2012), which was tilted in different directions to gain plasticity from highlights and shadows.

The 3D modelling procedure was carried out in different stages using different 3D modelling and animation software facilities and programmes (e.g. Nurbs Realtime Editor, Model Editor or 3d Studio Max® from

Autodesk®), each specialised for its defined task. The first step was to achieve a precise volume model of the fossil cephalopod, followed by refining its geometric shape by adjusting scale and patterns to place the discrete spines. Final textures can be created by colouration and image information directly on its surface in preparation for the final rendering and animation process (LUKENEDER A. 2012; Fig. 11).

The outline of *D. intermedius* was vectorised and imported into a CAD Application (Rhinoceros® 4.0), which is orientated to create 3D geometry from so-called NURBS (Non Unified Rational B-Splines), and hereafter used as a guideline to extrude the prepared cross-sections along its edges (LUKENEDER A. 2012). Various other techniques had been tested before, including the manual extrusion of the sections or their replication, but with unsatisfactory results.

The final geometries were then re-imported to 3D Studio Max© for the animation and rendering setup (LUKENEDER A. 2012). For the animation of the animal's body, virtual "elements" were created by the inverse kinematic bones system and linked to a hierarchy with inverse kinematic constraints. This allows the animator to move several bones by using only the last link of this hierarchy.

Although the presented animation is based on the best preserved and most complete specimen known, the embryonic stage is still unknown in *Dissimilites* (LUKENEDER A. 2012; LUKENEDER A. & S. LUKENEDER 2014).

The exact position of the suture lines in *Lytoceras subfimbriatum* appears clearly in the CT- as well as in the rendered images (Fig. 7)

Conclusions

The study presents results of an object-based combined analysis from computed tomography and various computed 3D facility programmes performed on the most complete shells of fossil cephalopods from Mesozoic sediments. Upper Triassic (Carnian) ammonoids from the Taurus Mountains in Turkey and Lower Cretaceous (Barremian) species from the Southern Alps of Italy have been investigated.

Upper Triassic ammonoids are *Kasimlarceltites krystyni* LUKENEDER S. & A. LUKENEDER, *Sandlingites* cf. *pilari* DIENER, and *Trachysagenites* cf. *beckei* DIENER. All of these are members of the order Ceratitida HYATT. Lower Cretaceous ammonoids were *Lytoceras subfimbriatum* (D'ORBIGNY) and *Dissimilites intermedius* LUKENEDER A. & S. LUKENEDER. The ammonoids are members of the order Ammonoidea ZITTEL.

The almost identical mass-density of the embedding limestone matrix (about 2.8 g/cm^3), the ammonoid shell with secondary calcite (about 2.6–2.8 g/cm^3), and the infilled limestone matrix (about 2.8 g/cm^3) prevents the visualisation of internal parts and structures in the palaeontological material of the Upper Triassic from Turkey. Only pyrite cubes, formed in the phragmocone of a few ammonoids, passively show the morphology of the ammonoids' internal dimensions and structures (e.g. body chamber versus phragmocone).

In rare cases, especially in the Lower Cretaceous, the ammonoids are coated by iron sulphides as pyrite and marcasite (both FeS_2) or by hydrated iron oxide-hydroxides as limonite ($FeO(OH) \times nH_2O$). Such steinkerns or limonitic fillings are detected by CT due to the increased density of these iron compounds (pyrite and marcasite: 4.8–5.0 g/cm^3; limonite: 2.7–4.3 g/cm^3). Dense structures as fine coatings on fossils or infillings of trace fossils can be visualised by computed tomography. Hence, pyritised or limonitic fossils bear the highest potential for high quality CT imaging and subsequent palaeontological reconstruction.

The use of computed tomography images and laser scans of fossil cephalopods from the Taurus Mountains of Turkey and the Southern Alps of Italy resulted in 3D visualisations. Moreover, computed tomography and palaeontological data were combined to produce 3D reconstructions, yielding animated clips running through CT data slices. The case studies demonstrate the non-destructive possibilities of 3D visualisation of palaeontological material. The resulting images are of high quality shots that are combined to short animated clips showing the morphology of fossils within CT slices in 3D. Another advantage is that the digital CT data, CT slices and CT clips can easily be shared amongst palaeontologists. This digital information can be discussed online and the resulting interpretation, based on the more detailed morphology, quickly be adapted.

The additional use of high-speed 3D scans with reduced random-noise obtained by efficient hyper-modulation increases the details in reconstructions and digitalisation of palaeontological material. Surfaces of ammonoids can therefore be reconstructed digitally without loss of information, and digital-slices can be created from rendered outlines without any destruction of the fossil.

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Die ‚Fossilien- und Mineralien-Sammlung Ferdinand ESTERMANN' aus dem Gschliefgraben-Rutschgebiet am Traunsee-Ostufer – Eine Dauerausstellung in den Kammerhof Museen Gmunden und ihre geologisch-tektonische Herkunft

J.T. WEIDINGER

Zusammenfassung: Ein Großteil der Fossilien- und Mineralien-Sammlung im Schausaal ‚Traunsee-Schätze' der Kammerhof Museen Gmunden (www.k-hof.at) geht auf die mehr als 35-jährige Sammeltätigkeit des Pinsdorfers Ferdinand ESTERMANN im Gschliefgraben-Rutschgebiet, am Nordfuß des Traunsteins (1691 m) zurück. Nach einer saisonalen Präsentation dieser einmaligen Kollektion im Jahre 2005 und ihrer Schenkung an die Stadtgemeinde Gmunden, konnte die Sammlung nach dem Museumsumbau und der Neugestaltung erst wieder im Jahre 2013 dem Besucher zugänglich gemacht werden. Die nunmehr vollständige Präsentation der wissenschaftlich interessantesten, schönsten und ausstellungswürdigsten Sammlerstücke bedingte auch einen für Besucher und Hobby-Paläontologen bzw. Hobby-Mineralogen brauchbaren und übersichtlichen Leitfaden, dem dieser Aufsatz (ansatzweise) gerecht werden möchte. Diese Unterlage sollte aber auch als brauchbarer Leitfaden fürs Gelände zum Auffinden spezieller Fundpunkte verstanden werden.

Schlüsselwörter: Ultrahelvetikum, Buntmergelserie, Kreide-Tertiär, Ammoniten, Seeigel, Mineralien, Septarien

Abstract: **The 'fossil- and mineral-collection Ferdinand ESTERMANN' from the Gschliefgraben-Earthflow-Area at the eastern shore of Lake Traunsee – The permanent exhibition in the Kammerhof Museums of Gmunden and its geologic-tectonic origin**. Most of the fossils and minerals presented in the exhibition hall 'Traunsee-Schätze' (= 'Treasures of Lake Traunsee') of the Kammerhof Museums of Gmunden (www.k-hof.at) were collected over a period of more than 35 years in the Gschliefgraben-Earthflow-Area at the foot of Mount Traunstein (1691 m) by Ferdinand ESTERMANN from Pinsdorf village near Gmunden. Following a seasonal presentation of this unique collection in 2005, its subsequent donation to the community of Gmunden town, and the renovation of the museum, the scientifically most interesting and beautiful specimens could again be presented to visitors in 2013. This paper gives a brief overview of these permanently displayed exhibits for visitors, hobby-paleontologists and -mineralogists. Furthermore, it provides a simple but helpful tool for an excursion to the Gschliefgraben field.

Keywords: Ultra-Helvetic, Buntmergelseries, Cretaceous-Tertiary, ammonites, echinoids, minerals, septaries

Einleitung: Geologisch-Tektonischer Überblick

Der Gschliefgraben, zwischen dem NW-Fuß des Traunsteins und dem Ostufer des Traunsees bei Gmunden gelegen, stellt tektonisch ein ultrahelvetisches Fenster dar, das im Norden vom Rhenodanubischen Flysch des Grünbergs und im Süden von den tiefsten Einheiten der Nördlichen Kalkalpen begrenzt wird (Abb. 1A, B). Letztere sind die Kalkalpine Randschuppe zuunterst (lokal auch Kalkofen-Klippenzug genannt) sowie das Bajuvarikum (lokal auch Zirlerberg-Scholle genannt).

Als großtektonisches Fenster entspricht der Gschliefgraben einer Antiklinal-Struktur, das heißt einer faltenartigen Aufwölbung in relativ weichen Mergeln und Tonsteinen, die von den etwas rigideren Widerlagern der Flysch-Sandsteine im Norden und des spröden Kalks im Süden begrenzt bzw. ‚wie in einem Schraubstock' eingeengt wurde. Kleintektonisch kommt es daher im Fenster auch zu weiteren Verfaltungen und Zerscherungen weicherer Materialien und (diversen) Einschuppungen von festeren Gesteinsschollen, die stratigraphisch deplatziert oft recht zusammenhangslos aus dem Gelände ragen können. Meist kann

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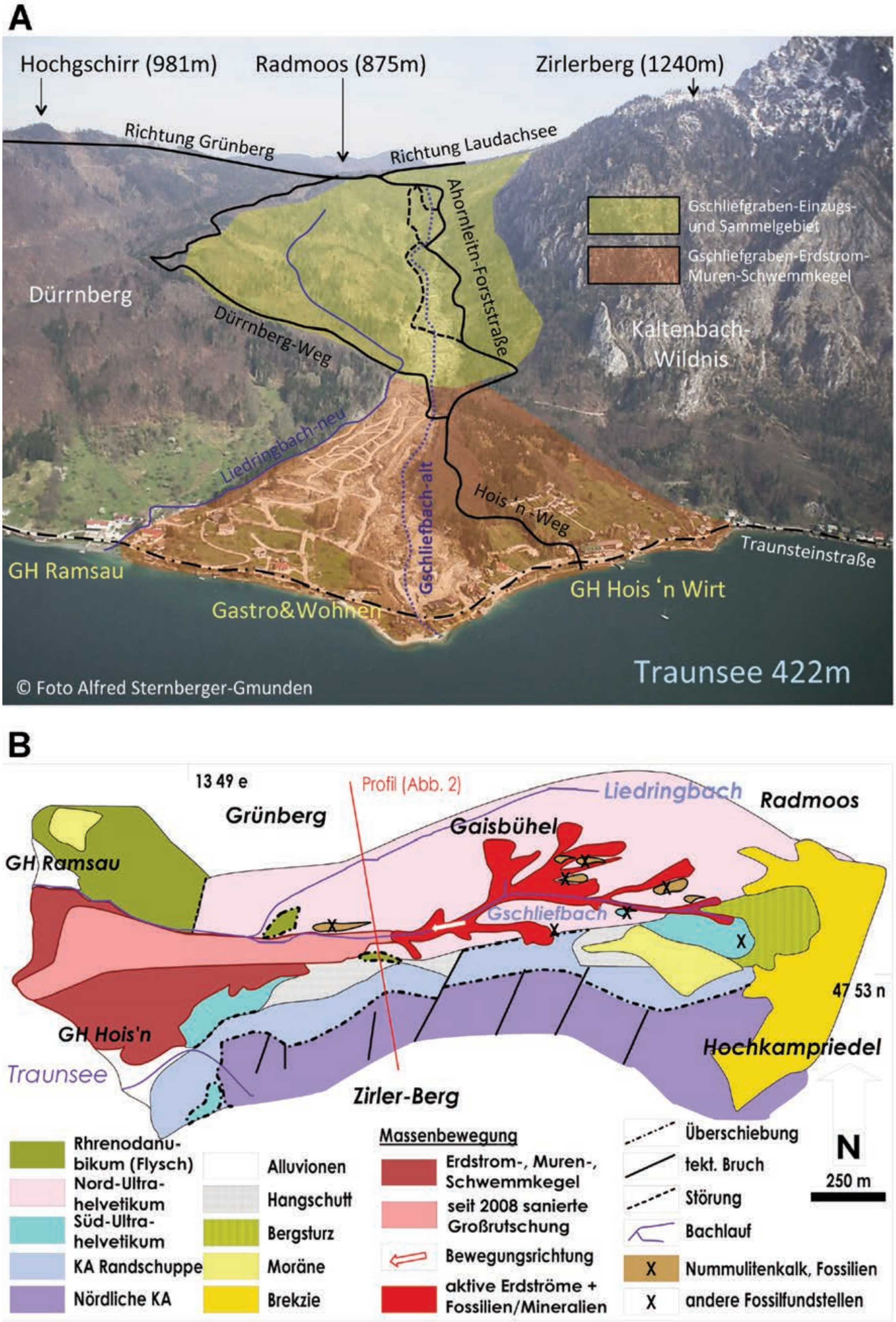


Abb. 1: Gschliefgraben. **A**: West-Ost-Blick aus der Vogelperspektive auf den Gschliefgraben und seine Umrahmung; mit den schwarzen Linien wird der Verlauf einer möglichen Sammelroute gezeigt, und zwar vom Gasthof Hois'n Wirt über den sogenannten Hois'n-Weg und die Ahornleitn-Forststraße zum Radmoos (Wegkreuzung in die Richtungen Grünberg, Flachberg, Laudachsee) und über den Dürrnberg-Weg zurück zum Ausgangspunkt. Gestrichelt eingezeichnet sind mögliche Sammelrouten im freien Gelände (Im Schadensfall kann für die Begehung einer solchen weder vom Autor noch vom Grundbesitzer ÖBF Haftung übernommen werden!). **B**: Geologisch-tektonische Übersichtsskizze des Gschliefgrabens und seiner Umrahmung, wie er sich seit der Großrutschung 2007–2008 und deren Sanierung darstellt; eingezeichnet sind auch mögliche Fossilfundpunkte (Anmerkung: die dieser Kompilation zugrunde liegende detaillierte Karte, die vom Verfasser im Maßstab 1:2000 aufgenommen wurde, findet man bei WEIDINGER & KÖCK (2010) unter http://epub.oeaw.ac.at/?arp=0x0025a627.

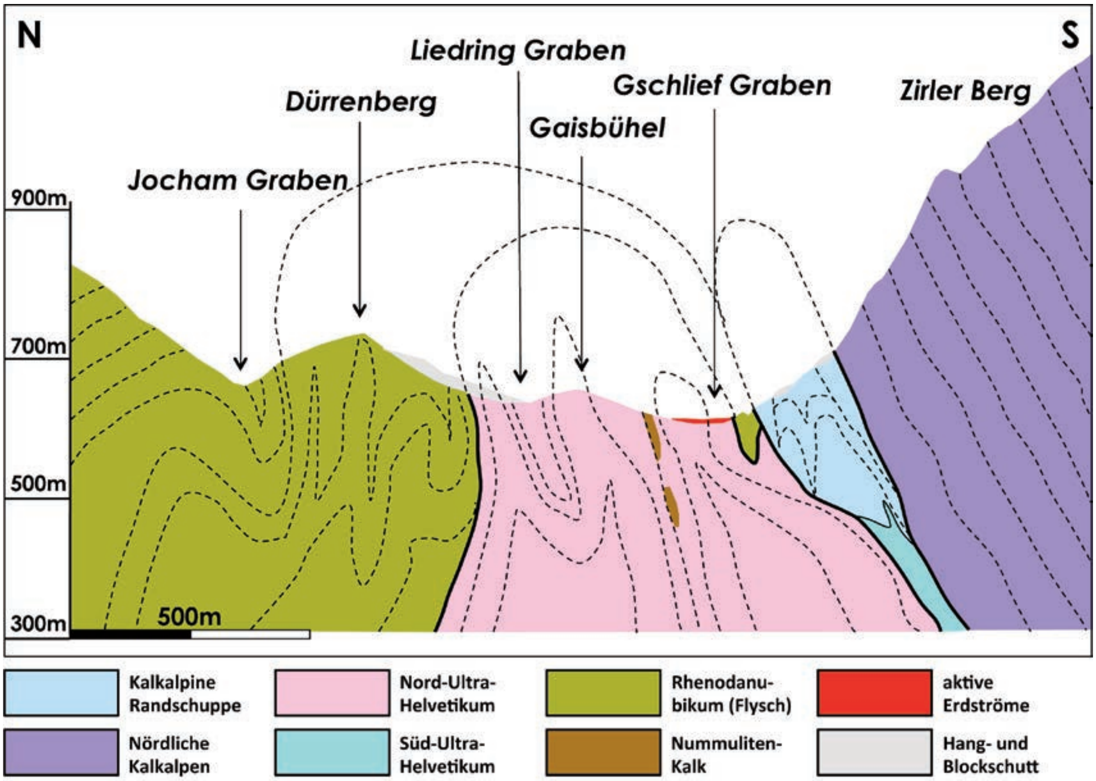


Abb. 2: Geologisch-tektonisches N-S-Profil durch den Gschliefgraben und seine Umrahmung; mit dem Verlauf der strichlierten Linien soll die antiklinale (aufgewölbte und durch Erosion freigelegte) Lagerung der weichen tonig-mergeligen Gesteine des Nord-Ultrahelvetikums und deren komplexe Verfaltung innerhalb des tektonischen Fensters, zwischen den Widerlagern des Rhenodanubikum (Flyschzone) im Norden und der Kalkalpinen Randschuppe samt Zirlerbergscholle im Süden, verdeutlicht werden. Zur Lage des Profils siehe Fig. 1B [überhöht, verändert und vereinfacht nach Prey (1983) sowie ergänzt nach eigenen Aufnahmen].

man jedoch davon ausgehen, dass die aufgeschlossenen Schichten (falls im vegetationsreichen Gelände überhaupt anzutreffen) von Osten nach Westen streichen und recht steil in den Untergrund einfallen (Abb. 2).

Das Gschliefgrabengebiet wurde vor der Großrutschung 2007–2008 (Weidinger et al. 2011) vom Gschliefbach sowie von dem aus Nordosten einmündenden Liedringbach entwässert. Mit der geotechnischen Sanierung der Rutschmassen in den nachfolgenden Jahren wurde der Gschliefbach allerdings trockengelegt und nur als Notgerinne für allfällige Starkniederschläge ausgebaut, während man den Liedringbach an den Nordrand der Rutschung umleitete und ihn heute kontrolliert in den Traunsee abfließen lassen kann (Weidinger & Köck 2010). Dieser eher wasserarme Zustand im Rutschgebiet wirkte sich ‚leider' negativ auf das Sammeln und Finden von Fossilien aus (Weidinger 2012), d.h. die Ferdinand-Estermann-Sammlung der Kammerhof Museen Gmunden (Weidinger 2003) ist somit zu einem echten Juwel geworden.

Gschliefgraben – stratigraphischer Überblick für den Sammler

Unterschiedlich alte und genetisch-faziell völlig verschieden entstandene Gesteine mit mehr oder weniger großem Makrofossilanteil können im Gschliefgrabengebiet durch die komplexe Tektonik oft räumlich sehr nahe nebeneinander liegen. Dazu kommt, dass es vor allem im oberen Einzugsbereich des Gschliefgrabens aufgrund der dort anstehenden tonigen Gesteine und der hohen Bodenfeuchte zur Ausbildung von Erdstrom-artigen Rutschmassen kommt (Weidinger 2009). So werden alle, durch die tektonischen Vorgänge bereits mechanisch zerscherten und zerstückelten Gesteinstypen, mit einem tonreichen Brei als Matrix vermengt, kriechend zu Tal befördert. Dort, im unteren Drittel des Gschliefgrabens herrscht morphologisch und lithologisch der stark durchmischte Erdstrom-, Muren- und Schwemmkegel des Rutschgebietes vor.

In fast allen Lithologien wird der Fossiliensammler fündig, kann aber häufig schwer beurteilen, aus welchem Anstehenden seine Funde stammen. Aus diesem Grunde soll nachfolgend ein grober Überblick gegeben werden, und zwar von Süden nach Norden fortschreitend (Abb. 3):

Marschiert man die Ahornleitn-Forststraße, nahe am Fuße der Zirlerberg-Nordwand bergwärts nach Osten, so kann man in den dunklen Kalken und Fleckenmergel der Kalkalpinen Randschuppe fallweise, aber immer seltener Fossilien, wie Ammoniten (des Jura) etc. finden. Die Nähe zu den steilen Rinnen und Schutthalden am Fuße der Traunstein-Nordwand bedingt einen Eintrag von Neokom-Gesteinen (graue Kalkmergel) der Zirlerberg-Scholle (Bajuvarikum), in denen Ammoniten der Unterkreide zu finden sind.

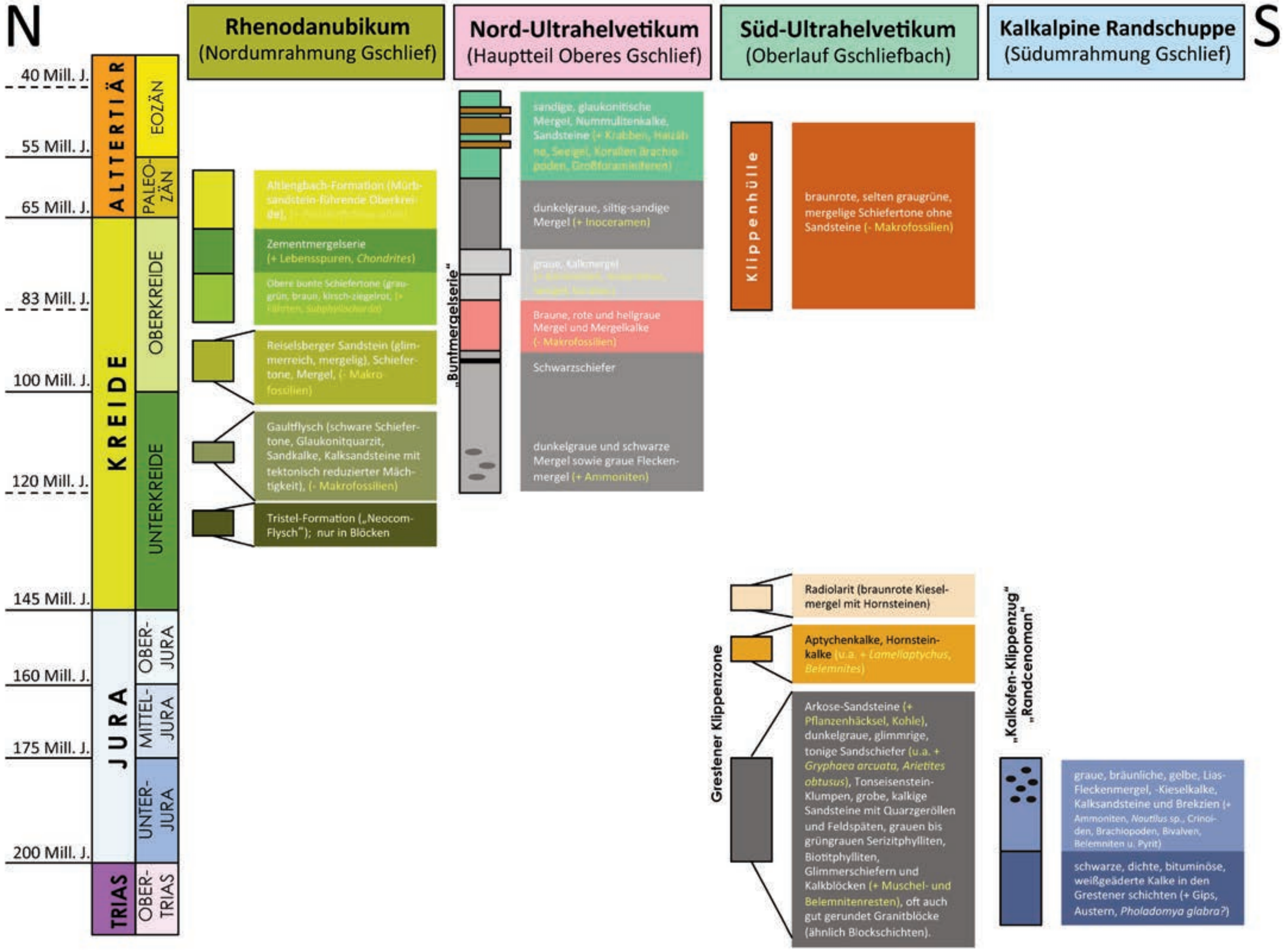


Abb. 3: Stark vereinfachte, stratigraphische Säulenprofile durch die lückenhaften (weil tektonisch stark gestörten) Schichtfolgen des Gschliefgrabens und seiner Umrahmung; der Zeitrahmen reicht über 200 Millionen Jahre. Die Nördlichen Kalkalpen, an deren Basis südlich des Gschliefgrabens das Haselgebirge (Oberperm, ca. 250 Mill. Jahre alt) mit seinen Gipsvorkommen ausbeißt, wurden nicht berücksichtigt (Kompilation aus Egger 2007; Prey 1983; Summesberger & Kennedy 2004; Wagreich & Neuhuber 2007; Weber 1958).

Nach dem Steilstück der genannten Forststraße gelangt man, links in den Wald abzweigend, allmählich in den Bereich des oberen Gschliefbaches und trifft entlang dessen auf einen schwarzschieferigen Gesteinskomplex, der von Sandsteinen, sandig-tonigen Schiefern und Konglomeraten sowie Kristallingeröllen überlagert wird und hier das Süd-Ultrahelvetikum repräsentiert (Prey 1983). Dies ist die Gresten-Formation des Unterjura (Lias–Dogger). Darin befindet sich auch die klassische Fundschichte der Austernverwandten *Gryphaea arcuata* (Abb. 38, 39), aber auch Belemniten und Kohle sind von dort bekannt. (Vom Oberlauf des Gschliefbaches zieht diese Fundschichte weiter bergwärts nach Osten bis hin zum Laudachsee.)

Wer von hier durch den Wald bergwärts steigt, der wird bald auf vorerst flach (‚Schwarze Kirche') später steil aufragende Klippen stoßen; letztere wird im Volksmund auch als ‚Rote Kirche' bezeichnet. Diese ist aus dem stratigraphisch Hangenden und damit aus den jüngsten Schichtgliedern des Nord-Ultrahelvetikums aufgebaut. In ihren tertiären (Paleozän–Untereozän) Glaukonit-sandigen Mergel und Nummulitenkalken findet man neben Großforaminiferen, die hier wirklich gesteinsbildend sein können, u.a. auch Brachiopoden, Seeigel, Wurmgänge etc. (Dulai et al. 2010).

Nur wer sich von dieser Lokalität weiter nach Norden und Nordwesten in die echten Erdströme des Oberen Gschliefgrabens vorwagt, trifft auf die Bunten Mergel und Tonsteine (Alb–Eozän). Besonders fossilreich sind hier die Schichten aus dem späten Campanium, worin man neben Crustaceen, Echinoideen und Inoceramen vor allem seltene Ammoniten (Fraaye et al. 1999; Kroh & Jagt 2004; Summesberger & Kennedy 2004) finden kann.

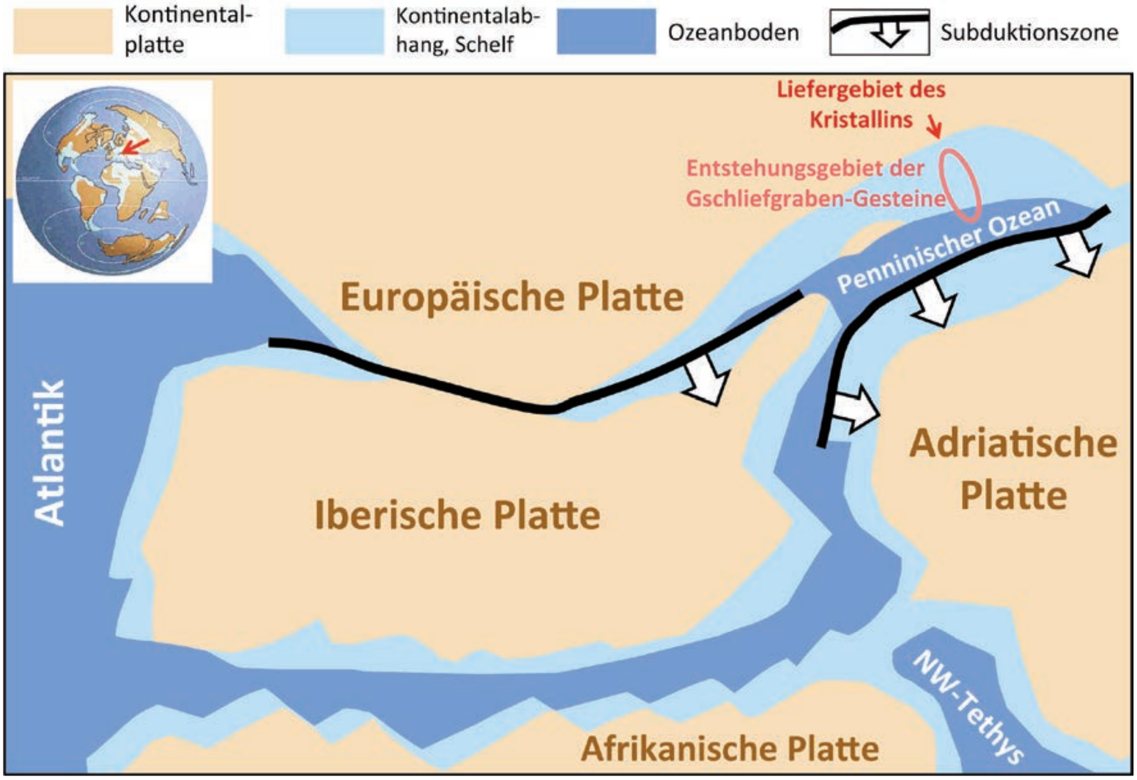


Abb. 4: Schematische paläogeographische Karte der nordwestlichen Tethys und ihrer angrenzenden Gebiete im beginnenden Alttertiär mit der Lage der Entstehung der Gesteine des Gschliefgrabens (verändert aus Egger et al. 2009).

Erst weiter Richtung Norden, über den Liedringgraben hinweg, trifft man auf Flyschgesteine. Entlang der Abstiegsroute über den Dürrnberg oder entlang der zahlreichen Wege und Forststraßen im Bereich des Grünbergs lassen sich an Schichtflächen immer wieder Spurenfossilien entdecken.

Paläogeographie der Gschliefgraben-Gesteine aus drei Zeitebenen: Unterjura – Oberkreide – Alttertiär

Die ältesten Ablagerungen im Fenster des Gschliefgrabens stammen aus dem Unterjura. Dies war jener erdgeschichtliche Zeitabschnitt der Alpenentstehung, als die Sedimentation in der Tethys ein Ende fand und sich durch plattentektonische Bewegungen nordwestlich davon der Penninische Ozean entwickelte. Dieser hatte auch Verbindung zum Atlantik und trennte die Europäische Kontinentalplatte im Norden von der Adriatischen Platte im Süden. Durch fortschreitende Plattenbewegungen wurde Meeresboden unter die Adriatische Platte subduziert (= hinuntergeführt). Dadurch erhielt der Penninische Ozean in seinem Profil eine asymmetrische Tiefenverteilung, d.h. er war im Süden ein mehrere Tausende Meter tiefer Trog, der mit vom Kontinentalhang lawinenartig abgleitenden Sedimenten gefüllt wurde – die heutigen Flyschgesteine, während er gegen Norden hin auf dem Kontinentalschelf ‚Ur-Europas' immer seichter wurde. Aus diesem Übergangsbereich vom tiefen zum seichten Meer stammen nun die Gesteine des Gschliefgrabens (Abb. 4).

Die Sedimente der Grestener Klippenzone des Süd-Ultrahelvetikums hatten ihren Ursprung in einem Grundgebirge aus Graniten und kristallinen Schiefern, vermutlich aus der Europäischen Kontinentalplatte. Die Fossilien der Grestener Schichten belegen ein Lias-Alter (Unterjura). Grobblockige, oft gut gerundete Einschaltungen, vor allem aus Graniten sowie z.T. flözartige Kohlevorkommen bzw. Pflanzenhäcksel sprechen weiters für eine marine Bildung im ufernahen, flachen Wasser mit fluviatilem Transport, wobei das Liefergebiet petrographisch jenem der östlichen Böhmischen Masse (Moravikum) nahe zu stehen scheint (Faupl 1975) – d.h. unser heutiges Mühl- und Waldviertel war damals bereits das Festland im Norden!

Bei den bunten Tonsteinen und Mergeln der Kreide-Tertiär-Zeit des Nord-Ultrahelvetikums, die im Gschliefgraben flächenmäßig den Hauptanteil einnehmen, handelt es sich um epikontinentale Ablagerungen eines nicht allzu tiefen Schelfmeeres, die etwa mit dem heutigen Globigerinenschlamm zu vergleichen sind (Prey 1983). Dort lagerte sich speziell in der späten Kreidezeit bis ins Alttertiär (Abb. 3, 4) ton- und kalkreicher Schlamm mit reichem Bodenleben ab, etwa unterschiedlichste Arten von Seeigeln, Muscheln, Krebsen und Meeresschwämmen. Im offenen Meer lebten mehrere Dutzend Arten von Kopffüßern mit Außengehäuse, die Ammoniten. Neben diesen Makrofossilien –

Abb. 5–8: Ferdinand Estermann, Fossilien- und Mineraliensammler im Gschliefgraben. **5**: Fund der Riesen-Septarie. **6**: Fund einer kleineren Septarie. **7**: Ammonitenfund. **8**: Fund eines Spurenfossils(?) in den Grestener Schichten.

begehrte Sammelobjekte – sind es aber vor allem Mikrofossilien, wie etwa Foraminiferen, mit Hilfe derer man das Alter der Schichten klären kann. Diese umfassen vor allem den Zeitabschnitt 90–50 Millionen Jahre vor heute.

Die süd-ultrahelvetische Klippenhülle (siehe Abb. 3) nimmt in ihrer Ablagerungstiefe eine vermittelnde Zwischenstellung zu den Tiefseeablagerungen des Flysches ein, in dem Trübeströme zu recht monotonen Schichtfolgen mit geringem Fossilgehalt führten.

Die aus dem Gschliefgraben beschriebenen Faunen, vor allem jene der Ammoniten, belegen eine nahe Verwandtschaft zu den Faunen von NW-Europa und Einzelfunde, wie der Ammonit *Menuites deccanensis* auch eine Meeresverbindung über die Tethys bis nach Indien, was bei dieser ‚vermittelnden' paläogeographischen Lage nicht verwunderlich ist; allerdings könnten Belemniten dafür sprechen, dass es auch eine Verbindung zum östlichen Gosau-Meer gab, welches in der späten Kreidezeit über bereits konsolidiertes Festland im Süden transgredierte (Summesberger & Kennedy 2004).

Die Fossilien- und Mineralien-Sammlung Ferdinand Estermann im Schauraum ‚Traunsee-Schätze' der Kammerhof Museen Gmunden

Viele der im Folgenden genannten Fundstücke aus der Sammlung des Pinsdorfers Ferdinand Estermann können im Schauraum ‚Traunsee-Schätze' der Kammerhof Museen Gmunden besichtigt werden (Weidinger 2003). Diese Sammlung, die mit Stücken aus der hauseigenen Sammlung dieses Gebietes ergänzt wurde, bietet gerade deshalb einen Querschnitt durch alle tektonischen Einheiten des Gschliefgrabens (Abb. 5–8). Besonders reichhaltig sind die Funde allerdings aus dem Campanium-Mergel des Nord-Ultrahelvetikums, die in neuerer Zeit in erster Linie von Paläontologen, und zwar aus Österreich, Holland, England, Dänemark und Deutschland untersucht wurden. Viele weitere paläontologische Einzelheiten wurden der Arbeit von Prey 1983 entnommen, während mineralogische Untersuchungen vom Arbeitskreis rund um das NHM-Wien bzw. von den OÖ Mineraliensammlern getätigt wurden.

Im Folgenden sollen die Fossilien nicht nach ihrer systematischen Stellung im Tierreich (Lehmann & Hillmer 1997), sondern nach ihrem stratigraphisch-tektonischen Vorkommen im Gschliefgraben beschrieben werden.

Fossilien des Gschliefgraben-Nord-Ultrahelvetikums

Die Kopffüßer (Cephalopoden-Fauna)

Aus dem Gschliefgraben sind bisher eine Belemnitenart, eine Nautiloidenart sowie 45 Ammonitenarten aus dem Campanium der Oberkreide beschrieben worden. Im Gegensatz zu den Belemniten, die nur ein Innenskelett besitzen, sind Ammoniten schalentragende Kopffüßer, die am Ende der Kreidezeit ausstarben. Die Nautiloiden leben bis heute mit einigen wenigen Arten, wie etwa dem ‚Perlboot', weiter.

Die Eier und Larven der Ammoniten wurden durch Meeresströmungen über alle Weltmeere verbreitet. Dazu kommt, dass die relativ kurze Lebensdauer einzelner Arten ideal ist, um sie als Leitfossilien für bestimmte Zeitperioden heranzuziehen.

Allgemein bekannt sind die in einer normalen Spirale aufgerollten Gehäuse, die am Ende der Kreidezeit mit *Parapuzosia seppenradensis* eine Riesenform mit über 2 m Durchmesser hervorbrachten. Wissenschaftlich in-

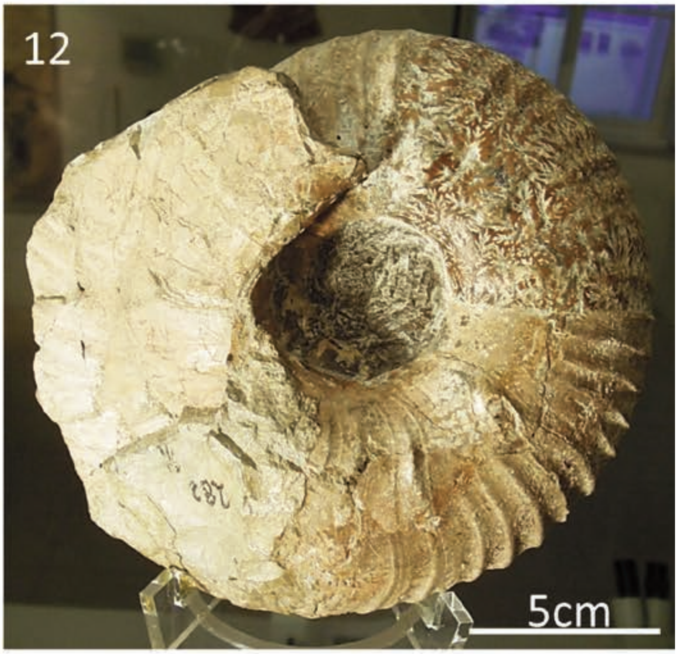


Abb. 9–14: Ammoniten. **9–11**: *Pachydiscus perfidus* (De Grossouvre). **12**: *Menuites deccanensis* (Stoliczka, 1865). **13, 14**: *Pachydiscus haldemsis* (Schlüter).

teressant sind aber vor allem jene Gehäuse aus dem Gschliefgraben, die nicht normal aufgerollt gebaut sind – man bezeichnet solche als ‚heteromorphe' Ammoniten und einige davon aus dem Gschliefgraben wurden weltweit erstmals beschrieben.

Hauericeras (*Hauericeras*) *pseudogardeni* (Schlüter)

Dieser Einzelfund ist zwar ein Fragment, zeigt aber eine vollständig erhaltene Wohnkammer. Diese Art wird in das untere Campanium gestellt, ist also älter als die meisten anderen Ammonitenarten des Gschliefgrabens. Es ist eine typische Form aus NW-Europa und ist auch aus Deutschland, Schweden und England bekannt. Da ein großes Exemplar auch aus der Gosau von Gams beschrieben wurde (Summesberger et al. 1999), ist sie ein Beweis für eine Verbindung beider Meere (Summesberger & Kennedy 2004).

Pachydiscus perfidus (De Grossouvre)

Dies ist eine der häufigsten Ammonitenarten im Gschliefgraben, die meist in Knollen (Konkretionen) vorkommt, die vom Sammler aufgeschlagen werden müssen (Abb. 9–11). Je nach Erhaltungszustand und Festigkeit des Materials, die vom Kalkgehalt abhängig ist, sind auch immer wieder die Lobenlinien (Linien der Verschneidung von Kammerscheidewänden und Außengehäuse) zu erkennen. Die Art kommt auch in gleichalten Ablagerungen von Polen und Frankreich vor (Summesberger & Kennedy 2004).

Pachydiscus haldemsis (Schlüter)

Diese Art weist einen sehr starken Sexual-Dimorphismus auf, d.h. die männlichen Individuen (Microconch) unterscheiden sich maßgeblich von den weiblichen (Macroconch). Die erstmals aus Haldem (Westfalen/BRD) beschriebene Art, die auch aus Polen, Schweden, der Ukraine (Donbas) und aus dem Kopet Dag Gebirge an der Grenze zwischen Turkmenistan und dem Iran bekannt ist, ist auch im Gschliefgraben sehr häufig zu finden (Abb. 13, 14) (Kennedy & Summesberger 1984).

Menuites deccanensis (Stoliczka)

Dieser seltene Verwandte der Pachydiscus-Arten wurde erstmals vom Austro-Tschechen Dr. Ferdinand Stoliczka aus der Arrialoor Gruppe von Karapaudy in Süd-Indien beschrieben. Bei der in Gmunden ausgestellten, bestens erhaltenen Schale mit gut sichtbaren Lobenlinien und teilweise erhaltener Wohnkammer (Abb. 12) handelt es sich um den europaweiten Erstfund durch Ferdinand Estermann, der damit einen zusammenhängenden Ozean zwischen Europa und Indien in der Oberen Kreidezeit belegt. Bisher ist diese Art von keinem weiteren Fundort bekannt (Summesberger & Kennedy 2004).

Placenticeras cf. *milleri* (Hauer)

Dieses bruchstückhafte Exemplar wurde offenbar in einer kleinen Konkretion konserviert, teilweise ist auch noch die Wohnkammer erhalten. Die Höhe der Windungen nimmt bei dieser Art rasch zu. Sie findet sich auch in Ablagerungen des Gosau-Meeres bei Kainach (Steiermark), allerdings mit etwas anderem Aussehen, was auf einen Sexualdimorphismus hinweisen könnte. Der bisherige Einzelfund dürfte älter sein als die Mehrzahl der Ammoniten aus dem Gschliefgraben (Summesberger & Kennedy 2004).

Hoplitoplacenticeras coesfeldiense (Schlüter)

Dieses Einzelstück aus dem Gschliefgraben auf einer Schichtfläche des Tonmergels ist mitsamt seiner Wohnkammer auch als Negativabdruck erhalten. Durch tektonische Vorgänge und/oder Konsolidierung des Sediments während der Diagenese (Gesteinsverfestigung) wurde das Gehäuse, das feine geschwungene Rippen zeigt, zusammengedrückt. Diese Art kommt von Frankreich bis Zentralasien vor (Kennedy & Summesberger 2001).

Parapuzosia? sp. indet.

Bei diesem Fragment, das von zwei Kammerscheidewänden begrenzt wird, handelt es sich um einen ca. 90° Sektor einer Windung eines großen Ammoniten-Gehäuses, das bisher nur aus dem Gschliefgraben bekannt ist. Die eigentliche Schale samt einer möglichen Ornamentierung wurde durch Korrosion zerstört. Außenseitig (ventral) befindet sich ein Grat, der einem Kiel sehr ähnlich sieht, Dieser könnte aber auch ein Teil des Siphos (Verbindungsgang durch die einzelnen Kammern des Gehäuses) sein. Der aus diesem Bruchstück rekonstruierte Durchmesser des Gehäuses samt der Wohnkammer dürfte ca. 90 cm betragen haben, womit es sich bei diesem Exemplar um den größten, je im Gschliefgraben gefundenen Ammoniten handeln würde. Die Größe spricht zwar für die Gattung *Parapuzosia*, die allerdings keinen Kiel besitzt (Kennedy & Summesberger 2001).

Heteromorphe Ammoniten

Nostoceras (*Euskadiceras*) *unituberculatum* (Blaszkiewicz)

Der Name dieser Art stammt von der einfachen Knotenreihe auf der Außenseite des Gehäuses, wodurch sie sich auch von anderen Arten unterscheidet, die größere Knoten oder auch zwei Reihen von Knoten besitzen. Bei dem nur bruchstückhaft erhaltenen Exemplar (Abb. 22) ist die typisch nach unten gebogene Wohnkammer gut zu sehen – auch in ihrem Bau besteht ein Unterschied zu anderen –, während sie bei dem wesentlich schöneren Exemplar (Abb. 15) nur ansatzweise zu

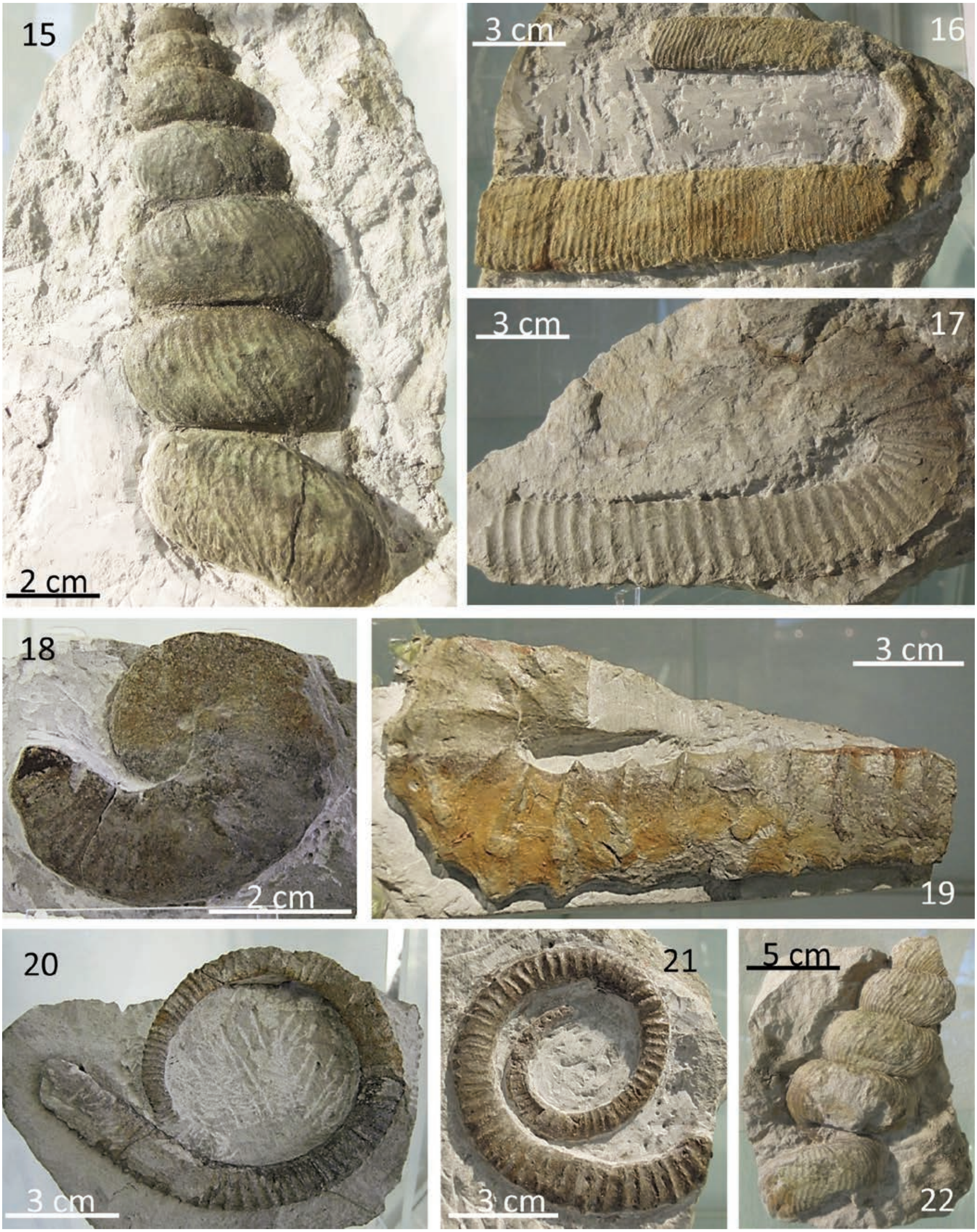


Abb. 15–22: Heteromorphe Ammoniten. **15**(?) und **22**: *Nostoceras (Euskadiceras) unituberculatum* (Blaszkiewicz). **16**: *Diplomoceras cylindraceum* (Defrance). **17**: *Pseudoxybeloceras wernickei* (Wollemann). **18**: *Trachyscaphites pulcherrimus* (Römer). **19**: *Pseudoxybeloceras kollmanni* (Summesberger & Kennedy). **20** und **21**(?): *Neancyloceras bipunctatum* (Schlüter).

erkennen ist. Diese Art ist neben dem Gschliefgraben auch aus Rumänien, Deutschland, Polen und Spanien bekannt (SUMMESBERGER & KENNEDY 2004).

Diplomoceras cylindraceum (DEFRANCE)

Dieses Einzelstück aus dem Gschliefgraben (Abb. 16) ist ein u-förmiges Fragment mit zwei unterschiedlich langen sowie verschieden dicken Schäften, die auf der Außenseite fein gerippt sind. Diese Art ist weltweit verbreitet und kommt sowohl in der obersten Kreide (Maastrichtium) als auch im späten Campanium von Polen und Frankreich vor. Auch dieses aus dem Gschliefgraben stammende Stück wurde mithilfe von Nannofossilien in der umgebenden Tonmatrix ins Campanium datiert (SUMMESBERGER & KENNEDY 2004).

Pseudoxybeloceras wernickei (WOLLEMANN)

Auch dieser Ammonit ist hakenförmig gebaut, wobei die Kurve im Gehäuse zwei annähernd parallele Schäfte miteinander verbindet. Diese können bei kleineren Individuen eng nebeneinander, bei größeren gut voneinander getrennt liegen. Die Ornamentierung auf dem Gehäuse besteht aus starken Rippen, die kantig und deutlich schmäler als die Zwischenräume sind; auf ihnen befinden sich ventral auch Knoten. Die Art ist aus dem oberen Campanium Norddeutschlands, aus der Ukraine, aus Zentral-Tunesien und Nordspanien sowie aus dem Zululand Südafrikas(?) bekannt. Mehrere Exemplare aus dem Gschliefgraben wurden von KENNEDY & SUMMESBERGER (1984) beschrieben, in der Sammlung der Kammerhof Museen Gmunden befindet sich nur eines (Abb. 17).

Pseudoxybeloceras kollmanni (SUMMESBERGER & KENNEDY)

Bei dem in den Kammerhof Museen Gmunden ausgestellten Exemplar handelt es sich um den Holotyp dieses weltweiten Erstfundes (Abb. 19), der zu Ehren von Dr. Heinz A. KOLLMANN (NHM-Wien) benannt wurde. Das große Fragment einer ausgewachsenen Wohnkammer endet mit einer u-förmigen Biegung in einem durch Bruch verursachten Fragment des dünneren Endschaftes, der vermutlich am Ende einen Haken hatte. Besonders auffällig ist bei dieser Schale aber die spektakuläre Ornamentierung mit breiten, leicht konkaven Rippen und noch breiteren Zwischenräumen, wobei jede Rippe drei reguläre Reihen von großen Knoten aufweist. Dieses grobstrukturierte Aussehen unterscheidet die Art von allen anderen, bisher beschriebenen heteromorphen Ammoniten des Campanium (SUMMESBERGER & KENNEDY 2004).

Neancyloceras bipunctatum (SCHLÜTER)

Eine zirkuläre Windung wird von einem langgestreckten Bereich des Gehäuses gefolgt, bei dem es sich um die Wohnkammer handeln könnte. Das vermutlich leicht flach gedrückte Gehäuse ist mit 75 Rippen ornamentiert, wobei die Zwischenräume etwas breiter als die Rippen sind; auf der Windungs-Außenseite ist jede Rippe zudem von zwei kleinen Knoten besetzt. Zwei Exemplare davon sind in den Kammerhof Museen Gmunden ausgestellt (Abb. 20 und 21?). Neben dem Gschliefgraben ist diese Art typisch für das obere Campanium von Deutschland, Polen, Russland und Frankreich (KENNEDY & SUMMESBERGER 2001).

Trachyscaphites pulcherrimus (RÖMER)

Diese Art hat fünf Knotenreihen, was ihr vermutlich den Beinamen ‚der Schönste' eingebracht hat. Interessant sind auch seine Rippen, die konkav auf der Innenseite, konvex auf der Seite und gerade weiterziehen. Diese Rippen verzweigen sich unregelmäßig. Durch zwischengeschaltete Rippen vermehrt sich deren Anzahl nach außen hin. Diese Art ist aus dem oberen Campanium der BRD, Frankreichs, Nord-Spaniens (Lleida), Polens der ehem. UdSSR sowie New Jersey und Texas in den USA bekannt. Mehrere Exemplare dieser Art wurden auch aus dem Gschliefgraben von KENNEDY & SUMMESBERGER 1984 beschrieben; in der Ausstellung in den Kammerhof Museen Gmunden sind ebenfalls mehrere Exemplare von unterschiedlich gutem Erhaltungszustand zu sehen (Abb. 18).

Seeigel (Echinoidea)

Die bisher beschriebenen Seeigel aus dem Gschliefgraben decken stratigraphisch einen Zeitraum von der Oberkreide bis ins Alttertiär, genauer vom Turonium (ca. 90 Mill. Jahre) bis ins Danium (ca. 63 Mill. Jahre) ab. Wie bei den Kopffüßern und den Muscheln sind auch hier manche Formen eher der nördlich gemäßigten Zone zuzuordnen, während andere dem Tethys-Ozean zugerechnet werden müssen. Sie dokumentieren damit eine biogeographische Verwandtschaft zu den französischen und spanischen Pyrenäen und dem Kaukasus, also zu einer Übergangszone von beiden Ozean-Regionen, was recht gut zur paläogeographischen Position des Gschliefgrabens, am Südrand des Europäischen Kontinents passt. Die Fossilien stammen aus dem äußeren Schelfbereich bzw. dem oberen Kontinentalhang des Europäischen Südrandes. Die Seeigelfauna umfasst sowohl Seichtwasser- als auch Tiefwasserformen. Dies wird damit erklärt, dass erstere durch untermeerische Lawinenabgänge (Trübeströme, turbidity currents) in tiefere Meeresbereiche verfrachtet wurden. Diese stratigraphische und paläobiogeographische Interpretation sowie die nachfolgenden Kurzinformationen zu den Schaustücken in den Kammerhof Museen wurden den Arbeiten von JAGT (1999) sowie KROH & JAGT (2004) entnommen.

Lampadocorys? *estermanni* (KROH & JAGT)

Diese Art wurde nach dem Stifter der gesamten Gschliefgrabensammlung in den Kammerhof Museen Gmunden, Ferdinand ESTERMANN benannt, von dem alle drei bisher gefundenen Exemplare stammen. Holotyp (NHMW 2003z0067/0001) und Paratyp (NHMW 2003z0067/0002) dieses weltweiten Erstfundes befindet sich im NHM-Wien; das in den Kammerhof Museen Gmunden ausgestellte Exemplar (Abb. 29) stellt das Abbildungsoriginal in KROH & JAGT (2004: pl. 1, figs 3–4 und pl. 2, fig. 3) dar. Daneben sind weitere verwandte Arten ausgestellt.

Lampadocorys? sp.nov. (KROH & JAGT)

Es existieren mehrere voneinander abweichende Exemplare. Da es nur eine begrenzte Anzahl von Fundstücken des *Lampadocorys estermanni* gibt, ist es schwer zu sagen, ob es sich bei ähnlichen Formen um Variationen ein und derselben Art handelt oder ob tatsächlich eine oder mehrere Arten vorliegen.

Rispolia subtrigonata (CATULIO)

Das Vorkommen dieser Art im Gschliefgraben ist bisher nur mit einem Exemplar belegt.

Seunaster heberti (SEUNES)

Aus der ESTERMANN-Sammlung ist neben mehreren Einzelstücken dieser Art (Abb. 24). besonders jenes Mergelhandstück einzigartig, in und auf dem gleich vier Exemplare dieser Art gemeinsam konserviert wurden (Abb. 23). Eine frontale Rille ist nur in Ansätzen zu erkennen, die Gehäuse sind insgesamt recht flach.

Echinocorys subglobosa (GOLDFUSS)

Diese Art findet sich sehr häufig im Gschliefgraben (Abb. 27), wobei sich diese gut mit den verwandten Arten des frühen ober-Campanium von Belgien und Deutschland vergleichen lässt (JAGT 1999).

Echinocorys ancileformis (MOSKVIN & SHIMANSKAYA)

Die auffällige Größe (im Gschliefgraben bis zu ca. 14 cm Länge), die flache Unterseite, der scharfe Kiel an der Oberseite und die schwach ausgeprägten Knoten im Oralbereich sind für diese Art, die erstmals aus dem oberen Paleozän von Kasachstan (West-Ustyurt) beschrieben wurde, charakteristisch. Bisher sind weltweit nur diese beiden Fundorte und aus dem Gschliefgraben zwei Exemplare bekannt.

Echinocorys ex gr. *fonticula* (ARNAUD)

Ein Exemplar aus der ESTERMANN-Sammlung mit ca. 10 cm Größe wurde beschrieben [EST 135 (65)]; dieses ist auch aus Frankreich sowie aus dem steirischen Gams bekannt.

Micraster stolleyi (LAMBERT)

Ein Exemplar aus der ESTERMANN-Sammlung wurde beschrieben. Typisch für das obere Campanium von England, Deutschland, Belgien, Südpolen und den Pyrenäen(?) sowie aus dem steirischen Gams bekannt.

Micraster aturicus (HÉBERT)

Aus der ESTERMANN-Sammlung wurden 4 Exemplare beschrieben, die mit dem Material von SEUNES (1891) aus Frankreich übereinstimmen (Abb. 26).

Coraster beneharnicus (SEUNES)

Die Gehäuse dieser Seeigelart sind mit ca. 13–18 mm durchwegs sehr klein und oval, wobei sie nur geringfügig länger als breit sind. Diese Art ist bisher nur aus dem unteren Paleozän Frankreichs und Spaniens sowie aus dem Campanium(?) oder Paleozän(?) des Gschliefgraben bekannt. Aus der ESTERMANN-Sammlung wurden 11 Exemplare beschrieben; in der Ausstellung sind sie – so wie ein Crinoiden-Stielglied – durch eine Lupe zu betrachten (Abb. 28 und 30).

Epiaster? sp.

Siehe Abb. 25.

Infulaster excentricus (WOODWARD)

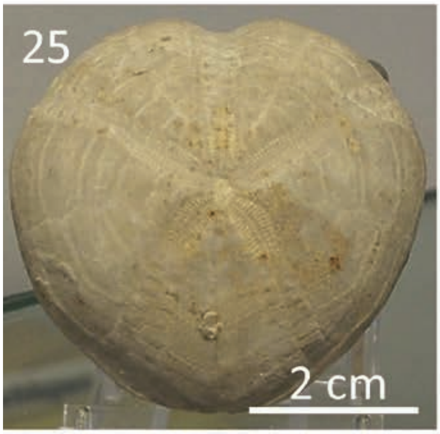
Dieses Leitfossil für das mittlere und obere Turonium ist als erstes Makrofossil aus diesem Zeitabschnitt und der Tethys aus der Oberkreide des Gschliefgraben von KROH & WAGREICH (2007) beschrieben worden. Typisch ist seine schmale, frontale Rille sowie ein kaum zu erkennender Kiel an seiner Oberseite.

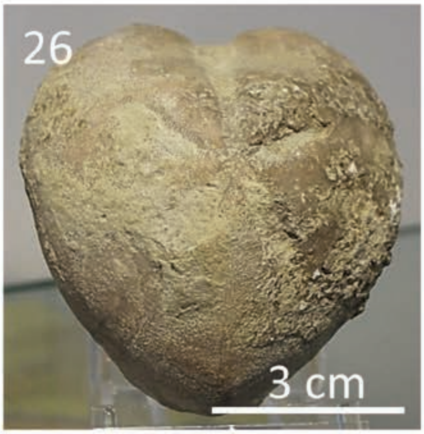
Krebstiere

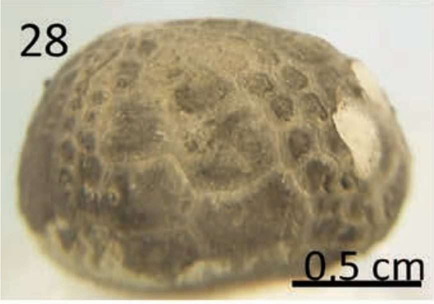
PREY (1983) beschreibt das Vorkommen zweier Krabbenarten in sandigen Tonmergel des Eozäns, knapp unterhalb der Nummulitenkalkbank der ‚Roten Kirche' – *Ranina marestiana* (KÖNIG) sowie den Langschwanzkrebs *Maexura* sp., andere Arten sind noch unbestimmt (Abb. 32).

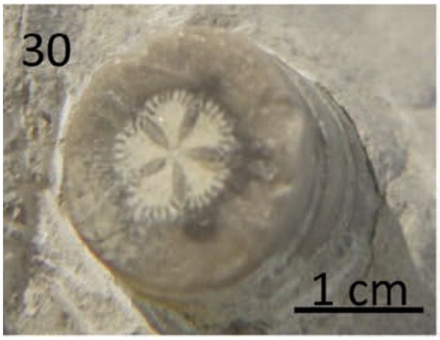
Palaega huetteri (FRAAYE & SUMMESBERGER)

Bei diesem Krebstier (*Crustacea*) handelt es sich um den ersten in Zentraleuropa gefundenen Isopoden aus der Kreidezeit (ober-Campanium, Polyplocum Zone). Typisch sind u.a. der 6-teilige Kopfschild, der Kiel im Hinterleibbereich sowie die dichte Punktierung auf dem









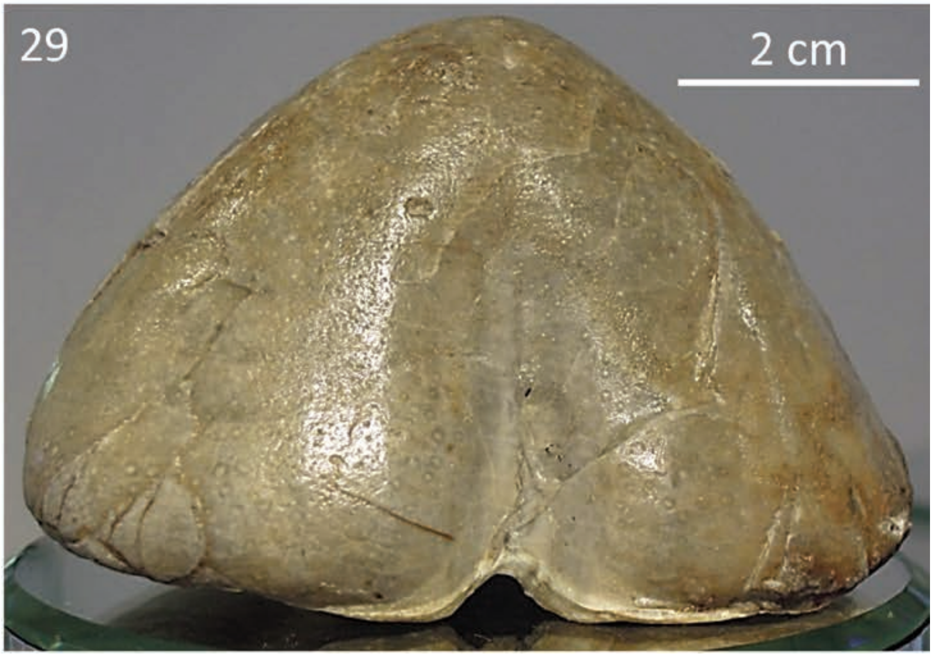


Abb. 23–30: Seeigel/Seelilien. **23** und **24**: *Seunaster heberti* (Seunes). **25**: *Epiaster*? sp. **26**: *Micraster aturicus* (Hébert *in* Seunes). **27**: *Echinocorys subglobosa* (Goldfuss). **28**: *Coraster beneharnicus* (Seunes). **29**: *Lampadocorys*? *estermanni* (Kroh & Jagt). **30**: Crinoiden-Stielglied (unbestimmt).

gesamten Panzer. Diese Art wurde nach dem aus Gmunden stammenden ehemaligen Direktor der HAK Bad Aussee, Mag. Herbert HÜTTER, benannt, von dem das erste Exemplar stammte. Der Holotyp dieses weltweiten Erstfundes befindet sich im NHM-Wien (1998z42/2), ist aber nicht so schön erhalten wie das in den Kammerhof Museen gezeigte Exemplar, das durch eine Lupe betrachtet werden kann (Abb. 36).

Muscheln (Bivalven)

Neben unzähligen Arten kleiner Individuen sind aus dem Gschliefgraben besonders 2 Gruppen von Muscheln bekannt geworden, die aus unterschiedlich alten Gesteinen stammen. Sie werden hier in der Reihenfolge ihres erdgeschichtlichen Erscheinens besprochen.

Inoceramidae

Die oft flach-ovalen, gleichklappigen bis nur mäßig ungleichklappigen Muscheln zeigen immer mehr oder weniger gut ausgeprägte konzentrische Rillen oder Wülste, die fein oder recht grob sein können. Sie sind typisch für die Jura- und Kreidezeit und kommen im Gschliefgraben recht häufig in den Mergel des Nord-Ultrahelvetikums (Campanium–Maastrichtium, oberste Kreide) vor. Während die Mehrzahl der Exemplare 10–15 cm Größe nicht überschreitet, wurden auch schon solche mit 4 dm Durchmesser gefunden. Die zwölf wichtigsten Arten der Gattungen *Cataceramus*, *Endocostea*, *Inoceramus*, *Cordiceramus* und *Cremnoceramus* wurden von TRÖGER et al. (1999) beschrieben (Abb. 40).

Spondylus

Diese Muscheln, die eine kräftige Radialskulptur zeigen, kommen seit dem Jura bis heute vor. Im Gschliefgraben findet man sie recht häufig – wenn auch oft nur bruchstückhaft – in den Nummulitenkalken (Abb. 34).

Einzeller, Brachiopoden, Krabben und Haizähne aus den Eozän-Rippen

Das Alter der Schichtfolge des Gschliefgrabengebietes wurde ursprünglich mithilfe von Mikrofaunen und Nannofloren bestimmt, die in ihren sandig-tonig-mergelig-kalkigen Gesteinen massenhaft, aber eben nur mikroskopisch klein vorkommen (PREY 1983). Besonders reizvoll für den Sammler sind aber die im Gschliefgraben vorkommenden Großforaminiferen, die im Eozän massenhaft auftreten und gesteinsbildend wurden. Neben einem ockergelb gefärbten, tonig-sandigen Bindemittel sind sie die Hauptsubstanz der Nummulitenkalke. Diese im Gschliefgraben stellenweise auftretenden Felsrippen (Abb. 31) stellen die jüngsten, noch in den Gebirgsbau miteinbezogenen Ablagerungen der Alpen dar und ragen aus den tonig-breiigen Erdströmen oft bis zu 10 m Höhe empor. Sie sind im Unterschied zu diesen relativ ortsfest und rutschen nicht mit, d.h. steuert man sie gezielt im Gelände an, kann man auf jeden Fall Fossilien finden, was in den Erdströmen eher selten der Fall ist.

Als Einzeller treten *Nummulites*, *Assilina*, *Discocyclina*, *Nemkovella*, *Asterocyclina* und *Orbitoclypeus* auf. Von letzteren wurde von DULAI et al. (2010) auch eine neue Großforaminiferen-Chronosubspecies beschrieben, die nach der Stadt Gmunden mit dem Namen *Orbitoclypeus multiplicatus gmundenensis* benannt wurde.

Als kleine Besonderheit finden sich in den Nummulitenkalken vor allem Brachiopoden (Armfüßer), die man neben Echinodermenresten (z.B. Seeigelstachel, Crinoidenstielglieder), Schnecken, Korallen, Krebsbeinen, Bryozoen, Fisch- und Haizähnen (Abb. 33) finden kann. DULAI et al. (2010) beschreiben 6 Taxa (*Gryphus*, *Meznericsia*, *Terebratula*, *Orthothyris*, *Megathiris* und *Argyrotheca*), die im Bodenleben des Eozän-Meeres normalerweise selten sind. Bekannt waren sie bisher aus dem Bereich der westlichen Tethys von England, der Ukraine, sowie entlang der Achse Belgien-Ägypten; die von diesen Autoren und von PREY (1983) beschriebenen Arten sind die ersten diesen Alters aus Österreich. Die Dominanz von *Gryphus* und *Terebratula* belegt eine Ablagerung im tiefen Wasser (Bathyal) des äußeren Schelfbereiches. Diese Transgression des Europäischen Schelfbereichs fand nach EGGER et al. (2009) im späten Ypresium, vor ca. 50 Millionen Jahren, statt.

Fossilien des Gschliefgraben-Süd-Ultrahelvetikums

Muscheln (Bivalven)

Eines der bekanntesten Fossilien aus dem Gschliefgraben ist die in den Gesteinen der Grestener Klippenzone (Abb. 37) gemeinsam mit fallweise Belemniten vorkommende:

Gryphaea arcuata LAMARCK

Die beiden Klappen dieser Muschel sind stark voneinander abweichend geformt (Abb. 38 und 39); oft findet man auch nur die linke Klappe, die durch konzentrische, teilweise schuppige Anwachsstreifen gekennzeichnet ist und im Volksmund auch als ‚Teufelsklaue' bezeichnet wird. Die rechte Klappe stellt eine Art Deckel dar. Die Muschel ist ein Leitfossil für den Unterjura (Lias alpha), und findet sich im Gschliefgraben fast ausschließlich entlang des Gschliefbach-Oberlaufes (ab ca. 780 m Sh), wo die recht verschiedenen Gesteine der Klippenzone zu Tage treten (Abb. 3). Wenn die Muscheln dort in schwarzen Tonschiefern vorkommen, sind sie recht

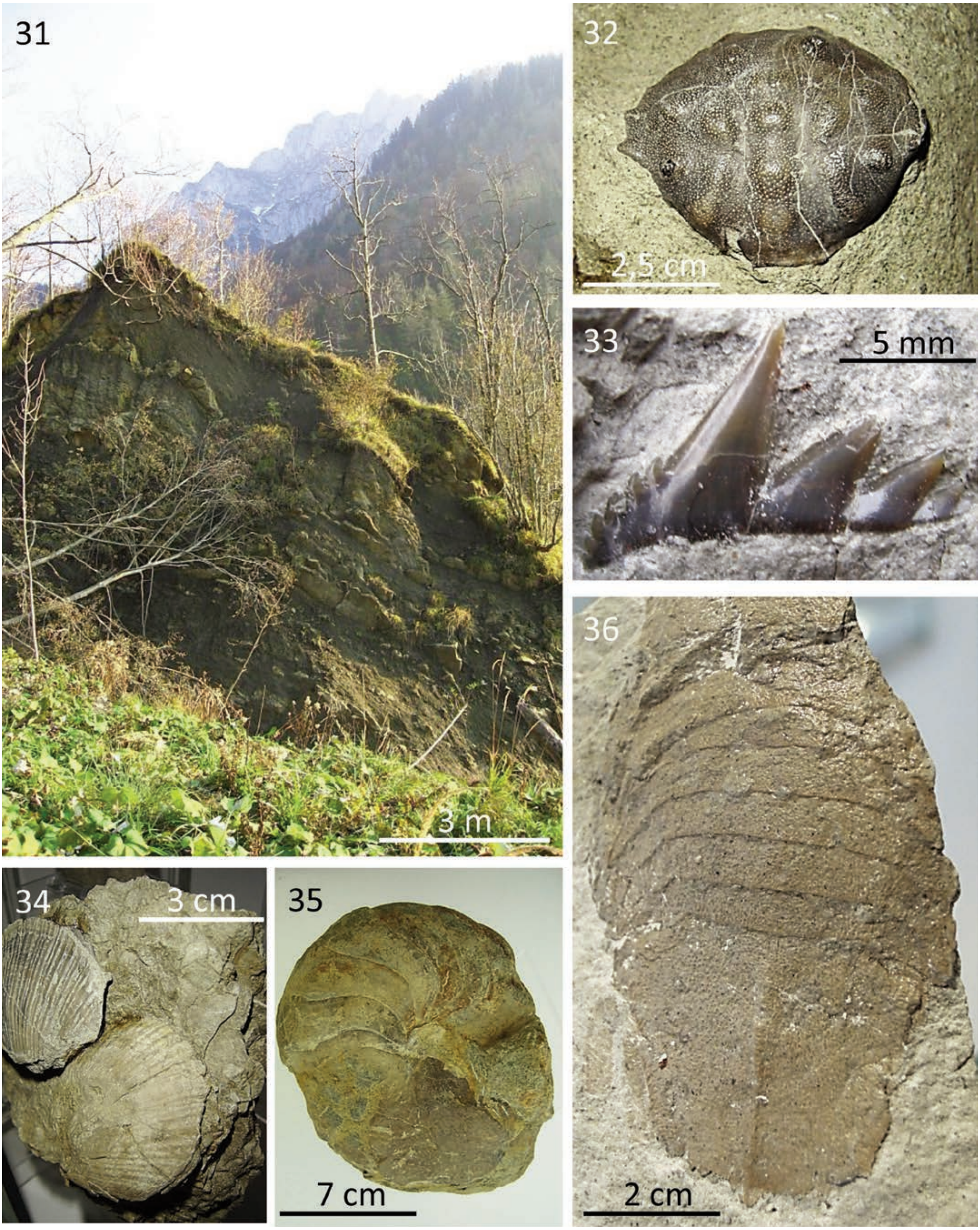


Abb. 31–36: Paleozän-Eozän-Fossilien. **31**: Paleozän-Eozän-Felsrippe. **32**: Krabben-Panzer von (?)*Ranina marestiana* (König). **33**: Zähne des Grauhais (?)*Notidanus primigenius* (Agassiz). **34**: Muschel (?)*Spondylus* sp. **35**: (?)*Nautilus* sp. **36**: *Palaega huetteri* (Fraaye & Summesberger).

leicht heraus zu präparieren, jedoch gibt es auch rostbraun anwitternde, kieselige Konkretionen (Knollen) aus denen sie unversehrt nur mit Mühe freizulegen sind.

Spurenfossilien des Gschliefgraben-Rhenodanubikums (Flyschzone)

Wie in allen sandig-mergeligen Flyschgesteinen findet man auch zwischen Gschliefgraben und Laudachsee immer wieder Spurenfossilien (siehe dazu auch LEHMANN & HILLMER 1997). Hier sind vor allem Freßbauten (Fodichnia) von halbsesshaften Sedimentfressern zu nennen, die das ehemals weiche Sediment nach Nahrung durchpflügten. Zu ihnen gehört *Chondrites*, das sind pflanzenähnlich aussehende, bäumchenförmig verästelte Fressbauten, die wie Bergwerke angelegt sind und deren Einzelröhren zwischen 0,5 und 5 mm Durchmesser erreichen können (Abb. 42 und 43).

Daneben findet man sehr häufig Weidespuren (Pascichnia). Diese wurden von aktiven Tieren verursacht, die das nahrungsreiche Sediment mäandrierend durchwühlten, da sie danach trachteten, bei geringer Wegstrecke möglichst viel Nahrung aufzunehmen. Dazu zählen die, in den Schichten der Zementmergelserie recht häufigen *Helminthoida* (Abb. 44).

Äußerst interessant können Kriech- bzw. Lokomotionsspuren (Repichnia) sein, die häufig von am Boden lebenden Würmern, Muscheln und Schnecken erzeugt werden. Zu ihnen zählt eines der interessantesten Fossilien aus dem Traunseegebiet, dass auch nahe dem Gschliefgraben gefunden wurde:

Pinsdorfichnus abeli (VIALOV)

Dabei handelt sich um ein recht spektakulär aussehendes Spurenfossil, das im Entfernten an eine Wirbelsäule erinnert. Von diesem wurden in der am Pinsdorfberg anstehenden Altlengbach-Formation im Jahre 1903 vom Steinmetzmeister L. NUSSBAUMER etliche Exemplare gefunden und im Zuge des fast gleichzeitig stattfindenden, Internationalen Geologenkongresses in Wien ausgiebig untersucht. Im Laufe des 20. Jahrhunderts kamen ähnliche Funde dazu. So etwa aus dem Flysch (Turonium–Santonium) der tschechischen Karpaten der Fund *Radhostium carpaticum* PLICKA & ŘÍHA, 1989 oder auch aus Italien, wodurch es zu einem Wirrwarr an wissenschaftlichen Namen kam. In der Arbeit von VIALOV (1989) taucht zum ersten Mal der oben genannte wissenschaftliche Name auf, der auf den Erstfundort dieses Spurenfossils auf dem Gemeindegebiet von Pinsdorf bei Gmunden und seine Erstbeschreibung durch Prof. O. ABEL zurückgeht. Auch wenn die Pinsdorfer Spurenfossilien viel größer sind, stellen UCHMAN (1999) wie zuvor auch SEILACHER & SEILACHER (1994) sie zu den *Protovirgularia*, die von Muscheln oder auch Scaphopoden mit ihrem Spaltfuß produziert werden. Das in den Kammerhof Museen Gmunden gezeigte Fundstück (Abb. 45) stammt aber nicht vom Pinsdorfberg sondern wurde im Flysch der Grünberg-Südhänge, nahe dem Gschliefgraben vom Apotheker ZELLER gefunden.

Mineralien und Septarien der Ferdinand-ESTERMANN-Sammlung

Sieht man von den exotischen Gesteinen der Klippenzone ab, in denen eine bunte Palette an Quarz und Silikaten sowie auch an Kohle anzutreffen ist, sind die im Gschliefgraben mengenmäßig am häufigsten auftretenden Gesteine mitsamt den darin vorkommenden Mineralien gemäß ihrer kalkig-tonigen Natur auf ein relativ enges geochemisches Spektrum begrenzt (REITER 1999, 2011).

Schon seit Jahrhunderten weiß man von mehr oder weniger ergiebigen Gipsvorkommen ($CaSO_4$ x $2H_2O$), die sich manchmal auch im Zuge von Großrutschungsereignissen aufschlossen und z.T. lokalwirtschaftlich genutzt wurden. Die vorkommenden Gipse sind oft weiß faserig, können aber auch blassrosa körnig ausgebildet sein und sind oft mit grauen Tonschiefern vergesellschaftet. Ob es sich dabei um das am Nordfuß des Traunsteins anstehende Haselgebirge oder auch um karnische Ablagerungen handelt, kann nicht immer zweifelsfrei geklärt werden (PREY 1983).

Relativ häufig trifft man im Gschliefgraben auch auf Kalzit ($CaCO_3$), der die kalkig-tonigen Gesteine weißädrig durchziehen kann und nach dessen selektiver Verwitterung als weiße Plättchen übrigbleibt. Kalzit findet sich aber auch in kleinen Klüften im eozänen Nummulitenkalk, wo er – wie etwa bei der ‚Roten Kirche' – bis zu 3 cm große, fast transparente Kristalle bilden kann (Abb. 47). Im Nummulitenkalk sind auch die rostigbraunen Kügelchen von Bohnerz aus Limonit, $FeO(OH)$ x nH_2O, anzutreffen.

Relativ häufig sind in tonreicheren Partien auch knollige oder unregelmäßig geformte Konkretionen sowie an Schichtflächen auch sogenannte Sonnen von Markasit (FeS_2) zu finden (Abb. 50). Auch ein völlig markasitisierter Ammonit findet sich in der ESTERMANN-Sammlung.

Eine echte Besonderheit aus dem Gschliefgraben sind aber im tonig-kalkigen Ablagerungsmilieu entstandene, knollenartige Konkretionen, die vor allem in den Erdströmen gefunden werden. Diese sogenannten Septarien, die bis zu mehrere Hundert Kilogramm schwer werden können (Abb. 52), entstanden durch Kalkaus-

Abb. 37–41: Fossilien der Klippenzone. **37**: Tonschiefer-Aufschluss an der Basis der Gresten Formation entlang des oberen Gschliefbaches. **38**: Mehrere Individuen von *Gryphaea arcuata*. **39**: *Gryphaea arcuata* mit beiden Klappen. **40**: (?)*Inoceramus* sp. **41**: Muschel (unbestimmt) in Kieselkalkknolle.

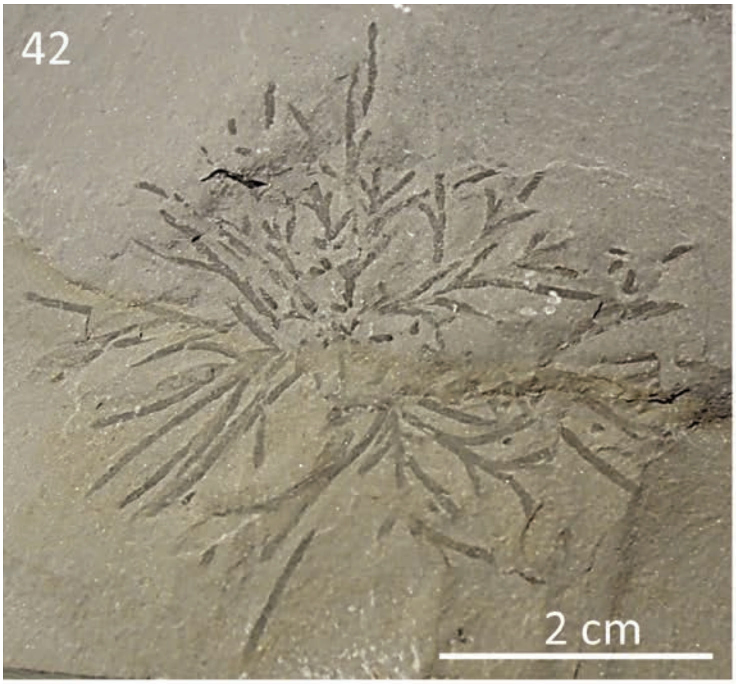
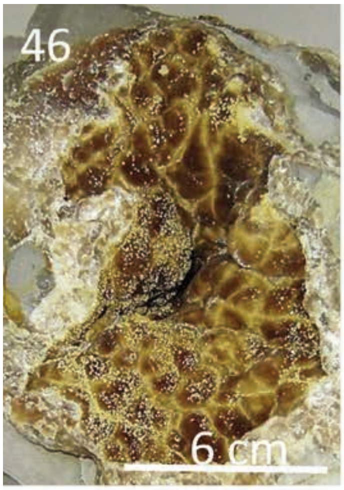
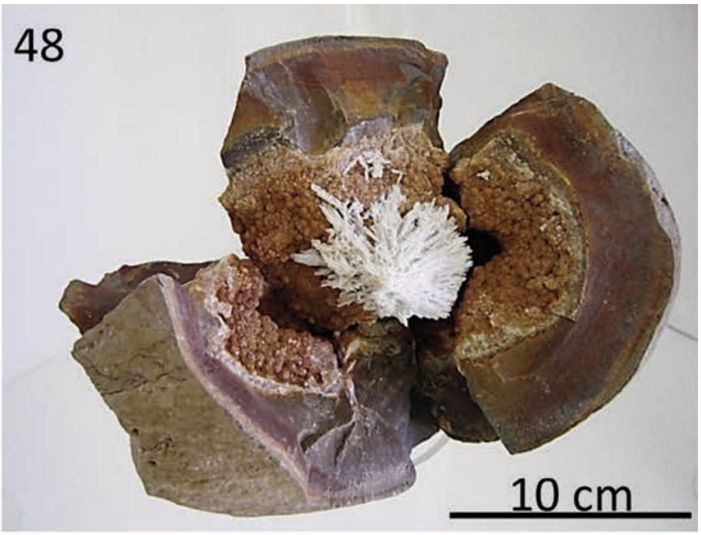
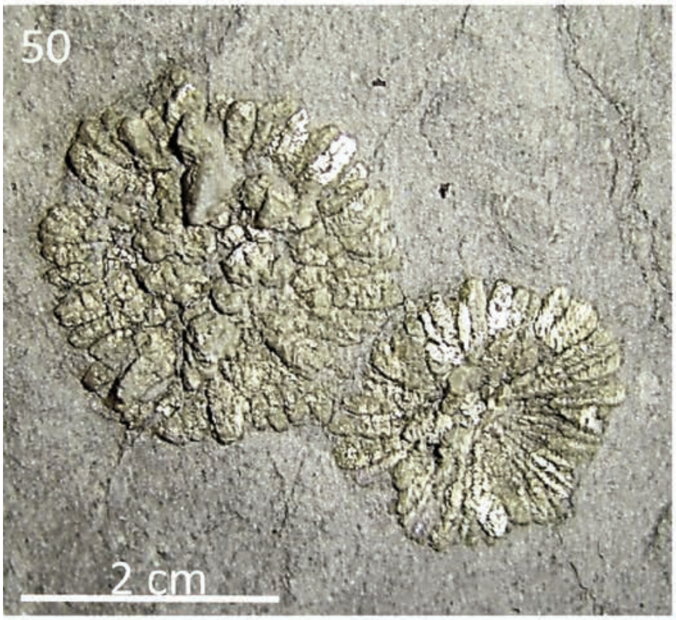


Abb. 42–45: Flysch-Spurenfossilien. **42** und **43**: *Chondrites*. **44**: *Helminthoida*. **45**: *Pinsdorfichnus abeli*.







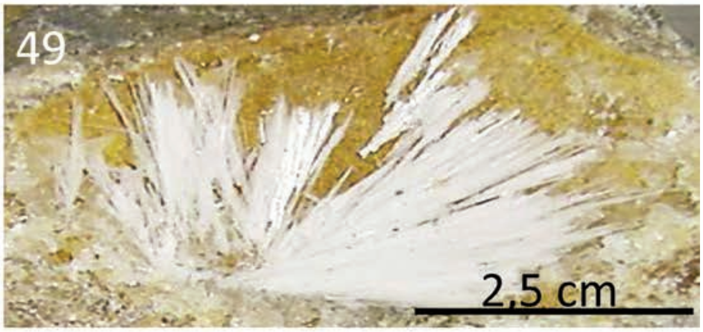


Abb. 46–52: Mineralien/Septarien. **46**: „Samtiger" Kalzit-Rasen im Septen-Hohlraum einer Septarie. **47**: Kalzit-Kristalle in Mergel. **48**: Hohlraum einer Septarie mit schneeweißem, faserigem Coelestin-Aggregat auf Kalzit. **49**: Coelestin-Aggregat auf Kalzit/Dolomit. **50**: Markasit-Sonnen auf Tonmergel. **51**: Baryt-Knolle. **52**: Riesen-Septarie.

fällung vermutlich rund um die Zersetzung von organischen Substanzen, die sie in Spuren fallweise noch im Kern beinhalten. Ihr Name leitet sich von darin enthaltenen Radialrissen, den Septen, ab. Diese Schrumpfungsrisse, die durch Austrocknung der noch wasserreicheren Ausfällungen entstanden, können wiederum mit Mineralausfällungen aus, das Sediment durchwandernden Lösungen gefüllt sein. Und darin liegt nun auch die Besonderheit der Gschliefgraben-Septarien, denn meist verrät bereits ihr Gewicht, dass sich darin neben Kalzit und Dolomit auch andere Mineralien, wie Markasit (FeS_2), Coelestin ($SrSO_4$) oder Baryt ($BaSO_4$), verbergen können (Götzendorfer 1990, Niedermayr et al. 1991).

Aufgeschlagene Septarien zeigen, dass Baryt sowohl in Form einer hellorangen, feinkörnigen Matrix, als auch in Form dunkelbrauner, transparenter und dicktafeliger Kristalle mit bis zu 8 mm Größe vorkommen kann (Niedermayr et al. 2000). Die in den Kammerhof Museen Gmunden ausgestellte, ca. 30 cm große grobkristalline Knolle zeigt oberflächlich eine polygonale Kristallstruktur und dürfte zur Gänze aus hellgrauem Baryt bestehen (Abb. 51).

Coelestin bildet einerseits grobkristalline, schlecht entwickelte Kristalle, die deutlich bläuliche Färbung erkennen lassen. Am schönsten sind aber bis zu mehrere Zentimeter lange, schneeweiße und fasrig-stengelige Aggregate (Abb. 48). Diese sind in den Schwundrissen häufig mit einem honigbraunen Kalzit (Abb. 46), der oberflächlich einen feinen, samtig anmutenden Kristallrasen bilden kann, vergesellschaftet. Bei einem weiteren Fundstück der Estermann-Sammlung dürfte es sich um eine Kluftfüllung aus rosarot gefärbtem Kalzit handeln, der ebenfalls mit weißen Coelestin-Stengeln paragenetisch verwachsen ist.

Während Baryt in Sedimenten des Kontinentalhanges gelegentlich angetroffen werden kann, ist die Anwesenheit von Coelestin vermutlich auf die diagenetische Umsetzung im Schalenmaterial der Fossilreste von Aragonit zu Kalzit zurückzuführen (siehe dazu auch Niedermayr et al. 2000).

Danksagung

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New data on microstructure and isotopic composition of some cephalopods from the Upper Cretaceous of North America and Europe: significance for oxygen isotope palaeotemperature measurements

Y.D. ZAKHAROV, K. TANABE, P.P. SAFRONOV & O.P. SMYSHLYAEVA

Abstract: Oxygen and carbon isotope ratios were measured on well-preserved molluscs collected from the Peedee, Fox Hills, and Coon Creek formations in South Carolina, South Dakota and Tennessee, respectively, to compare their relative depth habitats. Judging from calculated palaeotemperatures (13.1–22.4°C), all investigated late Campanian–early Maastrichtian bivalves and ammonoids from these areas inhabited warm waters of epipelagic depths in the Western Interior Seaway (WIS), being in agreement with already published data. Anomalously light $\delta^{18}O$ signatures preserved in an aragonitic ammonoid *Sphenodiscus lenticulata* shell from the Fox Hills Formation confirm the previous interpretation that some well-streamlined Late Cretaceous ammonoid shells were secreted in brachyhaline, shallow waters of the WIS. In contrast, measurements of $\delta^{18}O$ from high-resolution samples across growth bands of the early Maastrichtian *Belemnitella americana* from South Carolina indicate that its representatives were inhabitants of deeper, cooler waters of mesopelagic depths: palaeotemperatures varied mainly between 9.4°C to 12.0°C, occasionally to 17.8°C, on average to 12.3°C. Similar original results have been obtained from some late Maastrichtian and early Campanian belemnite rostra from Poland and Germany (10.6° and 12.9°C, respectively), whereas the late Maastrichtian bivalve *Dhondtichlamys* from Poland shows a palaeotemperature of 20.7°C. Oxygen isotopic data of *B. americana* are consistent with these findings, suggesting a considerable vertical range of migration of belemnites in the seawater column; therefore, the assessment of belemnite-derived palaeotemperatures for any reconstructions should be made with caution.

Keywords: Campanian, habitat, Maastrichtian, molluscs, palaeodepth.

Introduction

The oxygen isotope method for measuring temperatures of the oceans in the geologic past was offered by UREY, LOWENSTAM, EPSTEIN and others (UREY 1948; UREY et al. 1951; EPSTEIN et al. 1951), who firstly determined the relationship between temperature and O^{18} content relative to that for a belemnite *Belemnitella americana* (MORTON) from the Peedee Formation exposed along the Peedee River, South Carolina. The bulk geochemical signature contained within belemnite rostra from the Peedee Formation has long been used as global standard (PDB) (CRAIG 1957) against which other geochemical samples were measured, for both oxygen and carbon isotopes, and main oxygen isotope palaeotemperature data were reported relative to this standard. However, the supply of important PDB carbonate in 1976 became exhausted. The need for procuring additional stable isotope reference material was recognized (COPLEN et al. 1983). A Vienna-based laboratory has calibrated a new reference sample to the original *Belemnitella americana* fossil, giving rise to the widespread use of the term Vienna-Peedee Belemnite standard, abbreviated to V-PDB. A result of the work by COPLEN et al. (1983) was an improved equation for relating the PDB isotope scale to the V-SMOW (Vienna-Standard Mean Ocean Water) scale. In spite of these changes, isotopic data on original *B. americana* fossil from the Peedee Formation still deserve apt attention.

Since the early works (UREY 1948; UREY et al. 1951; EPSTEIN et al. 1951) nobody investigated the mentioned belemnite *B. americana* and associated fossils in detail. Besides, the palaeodepth habitat of belemnite species, as well as the nature of their rostra, is still debated (e.g. NAIDIN 1969; SPAETH 1971a, b, 1973; STEVENS & CLAYTON 1971; TEISS & NAIDIN 1973; WESTERMANN 1973; TAYS et al. 1978; BANDEL et al. 1984; DOYLE & MACDONALD 1993; ANDERSON et al. 1994; PRICE & SELLWOOD 1994; HUBER et al. 1995; HUBER & HODELL 1996; MONKS et al. 1996; PRICE et al. 1996; HEWITT et al. 1999; HEWITT 2000; VAN DE SCHOOTBRUGGE et al. 2000; PIRRIE et al. 2004;

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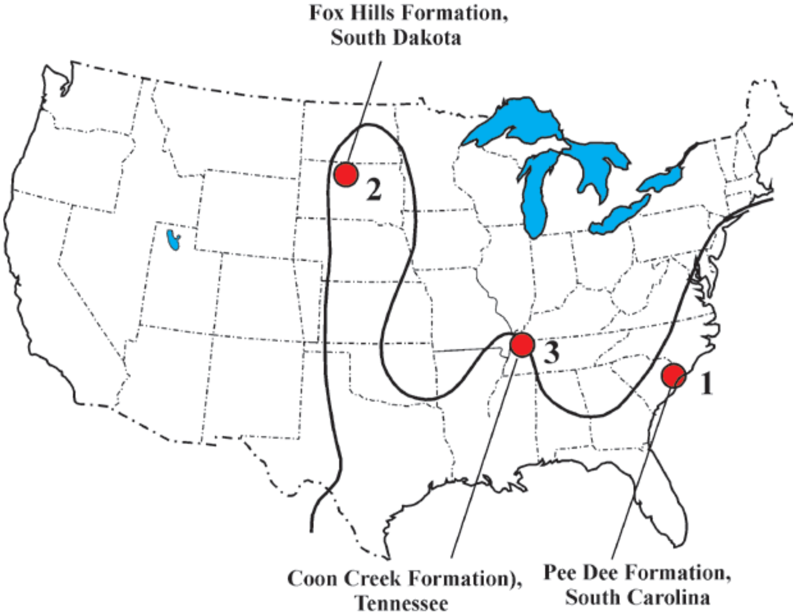


Fig. 1: Location map of the Maastrichtian sections sampled in the USA: 1 – Peedee River, South Carolina (early Maastrichtian belemnite rostra PD1, PD3, and PD4 and bivalve shell PD2 from the Peedee Formation); 2 – River Gravel in Morow River, South Dakota (ammonite shells Fox2, Fox3, Fox4, PM14787, PM14781-2, PM14784-1, and DK-3 and bivalve shells FH-2, PM14784-2, PM14787, and D1-5 from lower/upper Maastrichtian boundary beds, Fox Hills Formation, *Hoploscaphites nebrascensis* Zone); 3 – Coon Creek, Western Tennessee (late Campanian bivalve shells T2-1, T2-2, and T3-1). After USGU palaeogeographic map of the Maastrichtian coastline of the Western Interior Seaway.

Table 1: Trace and minor element composition of the *Belemnitella americana* (Morton) rostrum from the Peedee Formation of the Peedee River, South Carolina (PD3), and Recent *Nautilus pompilius* Linné from Bohol Island area, Philippines (N3).

Elements, weight %	Bulk sample from the Recent *Nautilus pompilius* shell N3 (wall area)	Bulk sample from the *Belemnitella americana* rostrum PD3
V	0.00041	0.00033
Cr	0.00055	0.00051
Co	0.00009	0.00012
Ni	0.00027	0.00026
Cu	0.00137	0.00048
Zn	0.00507	0.00034
Ga	0.00010	0.00060
Ba	0.00079	0.00017
Rb	0.00015	0.00010
Sr	0.16740	0.12560
Zr	0.00038	0.00157
Nb	0.00023	0.00018
Pb	0.00025	<0.0002

Wierzbowski 2004; Zakharov et al. 2006a, b, 2007a, b, 2010, 2013; Dutton et al. 2007; Dauphin et al. 2007; Wierzbowski & Joachimski 2007; Li 2011; Price & Passey 2013).

The main aims of this study are to reconstruct the original microstructure of the *B. americana* rostrum, and to recognize the palaeodepth habitat of *Belemnitella* species by comparing its stable isotope composition with those of other Late Cretaceous molluscs, including ammonoids and bivalves, from South Carolina, South Dakota, Tennessee, and some areas located outside of North America (Poland and Germany).

Material and methods

In this study oxygen and carbon isotope ratios were measured mainly on well-preserved cephalopod and bivalve molluscs collected by K. Tanabe from the Peedee, Fox Hills and Coon Creek formations in South Carolina, South Dakota and Tennessee, respectively (Fig. 1).

Most well-preserved material from the Peedee Formation used for isotopic analysis consists of: (1) Early Maastrichtian belemnite *Belemnitella americana* (Morton) rostra and (2) a cooccurred bivalve *Exogyra costata* (Say) shell.

Cephalopod shells from the Lower–Upper Maastrichtian boundary beds of the Fox Hills Formation (Trail City Member) with retaining original aragonitic mineralogy and shell structure were also examined. They are three ammonoid species – *Sphenodiscus lenticulatus* (Morton), *Discoscaphites gulusus* (Morton) and *Hoploscaphites nicolleti* (Morton). Well-preserved bivalve and ammonoid *Hoploscaphites spedeni* (Landman & Waage) and *Discoscaphites gulusus* (Morton) shells from the Trail City Member were investigated by us earlier (Zakharov et al. 2006a).

Among late Campanian fossils from the Coon Creek Formation in Tennessee only well preserved bivalves *Crassatellites robustus* (Morton) and *Inoceramus* (*Endocostea*) sp. were investigated on this occasion. Isotopic data on *Pterotrigonia eufaulensis* Gabb from the mentioned formation was obtained by us earlier (Zakharov et al. 2007b).

In addition, well-preserved late Maastrichtian molluscs [a shell of the bivalve *Dhondtichlamys acuteplicata* (Alth) from Poland, and a rostrum of the belemnite *Belemnitella*? sp. associated with it] as well as a rostrum from the late Campanian belemnite *Gonioteuthis granulataquadrata* (Stolley) from Germany (K. Tanabe's coll.) were analysed for comparison.

The following criteria were used in this study to determine diagenetic alteration: (1) visual signs; (2) percentage of aragonite in a skeleton, when the shells were originally represented by 100% aragonite, or presence of diagenetic admixture in both original aragonite or calcite (using X-ray analysis), 3) a degree of integrity of skeleton microstructure, determined under a scanning electron microscope) (SEM); (4) preliminary metallic-element measurements (using X-ray spectrometer coupled with a SEM to obtain geochemical spectra).

Table 2: Carbon and oxygen isotope analyses of the early Maastrichtian belemnite *Belemnitella americana* (Morton) rostrum PD4 from the Peedee Formation of the Peedee River, South Carolina (D: diameter).

Sample	Rostrum	Location (D, mm)	Diagenetic alteration			δ^{13}C (V-PDB)(‰)	δ^{18}O (V-PDB) (‰)	T°C
			Original calcite (%)	Admixture (α-SiO$_2$)	Colour			
PD4-1	PD4	11.50-11.75	100	No	Colourless	0.94	0.27	11.0
PD4-2	Same rostrum	11.25-11.50	100	No	Colourless	-0.21	0.72	9.3
PD4-3	Same rostrum	11.00-11.25	100	No	Colourless	0.65	0.46	10.3
PD4-4	Same rostrum	10.75-11.0	100	No	Colourless	0.59	0.42	10.4
PD4-5	Same rostrum	10.50-10.75	100	No	Colourless	0.02	0.68	9.4
PD4-6	Same rostrum	10.25-10.50	100	No	Colourless	-0.5	0.37	10.6
PD4-7	Same rostrum	10.00-10.25	100	No	Colourless	-0.64	0.08	11.7
PD4-8	Same rostrum	9.75-10.00	100	No	Colourless	0.34	0.19	11.3
PD4-9	Same rostrum	9.50-9.75	100	No	Colourless	-0.26	0.23	11.1
PD4-11	Same rostrum	9.00-9.25	100	No	Colourless	0.23	0.36	10.6
PD4-12	Same rostrum	8.75-9.00	100	No	Colourless	0.14	0.21	11.2
PD4-13	Same rostrum	8.50-8.75	100	No	Colourless	0.14	0.38	10.6
PD4-14	Same rostrum	8.22-8.50	100	No	Colourless	0.15	0.44	10.3
PD4-16	Same rostrum	7.75-8.00	100	No	Colourless	0.22	0.32	10.8
PD4-17	Same rostrum	7.50-7.75	100	No	Colourless	0.17	0.10	11.6
PD4-18	Same rostrum	7.25-7.50	100	No	Colourless	0.24	0.16	11.4
PD4-19	Same rostrum	7.00-7.25	100	No	Colourless	0.39	0.74	9.2
PD4-21	Same rostrum	6.50-6.75	100	No	Colourless	0.36	0.29	10.9
PD4-22	Same rostrum	6.25-6.50	100	No	Colourless	0.33	0.42	10.4
PD4-23	Same rostrum	6.00-6.25	100	No	Colourless	0.57	0.47	10.2
PD4-24	Same rostrum	5.75-6.00	100	No	Colourless	0.54	0.63	9.6
PD4-26	Same rostrum	5.25-5.50	100	No	Colourless	0.53	0.32	10.8
PD4-27	Same rostrum	5.00-5.25	100	No	Colourless	0.31	0.34	10.7
PD4-28	Same rostrum	4.75-5.00	100	No	Colourless	0.40	0.26	11.0
PD4-29	Same rostrum	4.50-4.75	100	No	Colourless	0.91	0.30	10.9
PD4-31	Same rostrum	4.00-4.25	100	No	Colourless	0.69	0.68	9.4
PD4-33	Same rostrum	3.50-3.75	100	No	Colourless	0.63	0.64	9.6
PD4-35	Same rostrum	3.00-3.25	100	No	Colourless	0.37	0.44	10.3
PD4-36	Same rostrum	2.75-3.00	100	No	Colourless	0.62	0.35	10.7
PD4-37	Same rostrum	2.50-2.75	100	No	Colourless	0.25	0.48	10.2
PD4-38	Same rostrum	2.25-2.50	100	No	Colourless	0.07	0.41	10.4
PD4-39	Same rostrum	2.00-2.25	100	No	Colourless	0.20	0.33	10.7
PD4-40	Same rostrum	1.50-2.00	100	No	Colourless	0.33	0.46	10.3
PD4-41	Same rostrum	0.00-1.50	100	No	Colourless	0.05	0.42	10.4

Selected shell samples from our collection were broken into pieces and examined with a scanning electron microscope (Zeiss EVO 40 and 50 XVP) at the Analytical Centers of the Institute of Marine Biology, and the Far Eastern Geological Institute (Vladivostok), respectively, in order to obtain textural information and to ascertain the degree of diagenetic alteration. Another variant is to examine the mentioned pieces, which were polished and etched for 5.5 minutes with 1.0% HCl, as recommended by Sælen (1989), Podlaha et al. (1998) and Voigt et al. (2003). Among 18 energy dispersion X-ray microanalytical (EDX) spectra, covering the entire surface of the *B. americana* rostrum PD4 in the transverse section, only a single has documented a minor diagenetic alteration immediately near the alveolus, indicated by Fe, Mn and Cu data [Figs 8 and 9 (spectrum 1), and Table 1]. A similar result has been obtained from the transverse section of the PD1 rostrum (Table 1). Rare samples of the mentioned zones, exhibiting elevated Fe, Mn or Cu concentrations, were excluded from further analysis.

As a result, the SEM photographs and EDX spectra of Late Cretaceous molluscs from South Carolina, South Dakota and Tennessee demonstrate that their skeletons fulfil diagenetic screening criteria and were therefore considered suitable in general for isotopic analysis. It was confirmed additionally by X-ray diffraction analysis that showed a lack of secondary admixtures, including α-SiO$_2$, in the investigated calcitic belemnite rostra, and in almost all aragonitic bivalve and ammonoid shells. Nevertheless, diagenetic alter-

Fig. 2: SEM photomicrographs of the belemnite *Belemnitella americana* rostrum PD4a-5 from the Peedee Formation of South Carolina, longitudinal section – polished and etched surface. **a**: Wedge-shaped structure, the arrow shows position of the investigated part. **b**: Crystallites (*cr*) of the same microstructure. **c**: Crystallites (*cr*) and their subchips (*su*) of the same microstructure, named in longitudinal section as microstructure "a". **d**: Subchips (*su*) of the same microstructure.

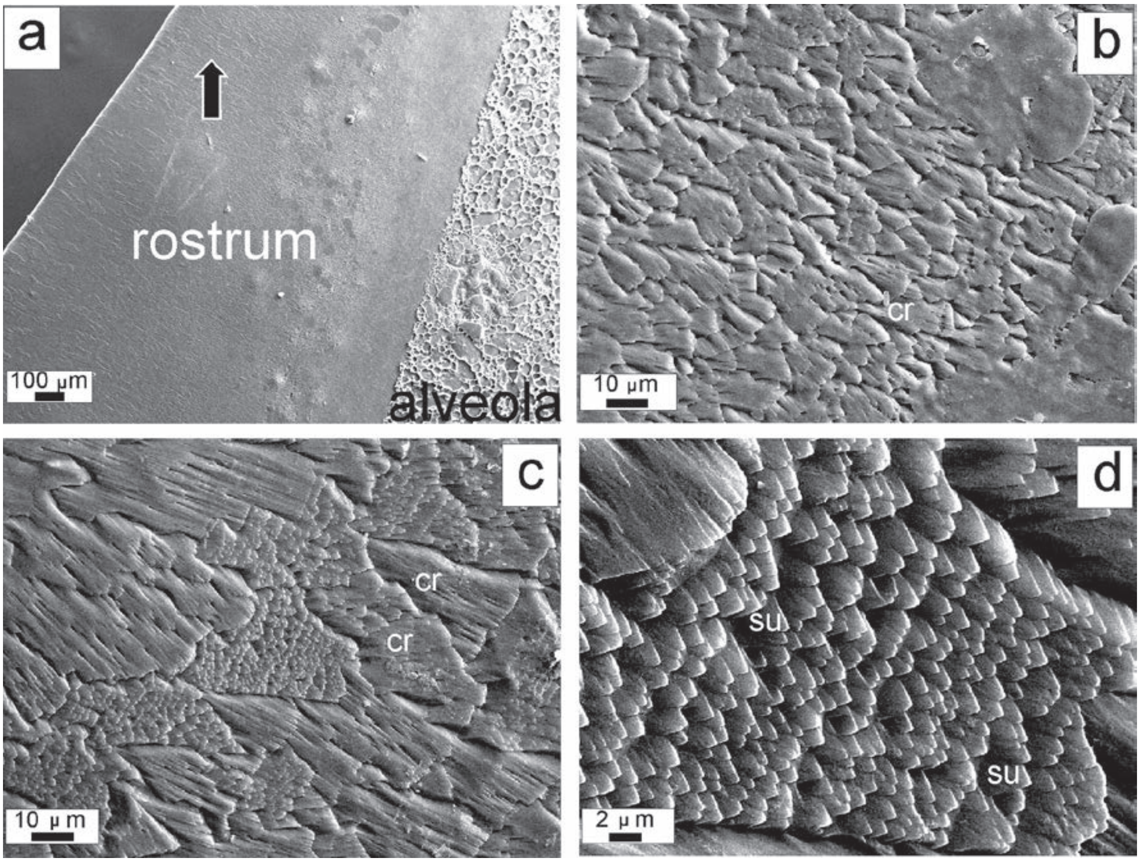


Fig. 3: SEM photomicrographs of the belemnite *Belemnitella americana* rostrum 7a-2 from the Peedee Formation of South Carolina, longitudinal break. **a**: Radial elements, the arrow shows position of the investigated part. **b**: Radial elements, the arrow shows position of discovered thin lamellar microstructure crossed coarse radial elements. **c, d**: Thin lamellar microstructure in longitudinal section, named here as microstructure "b".

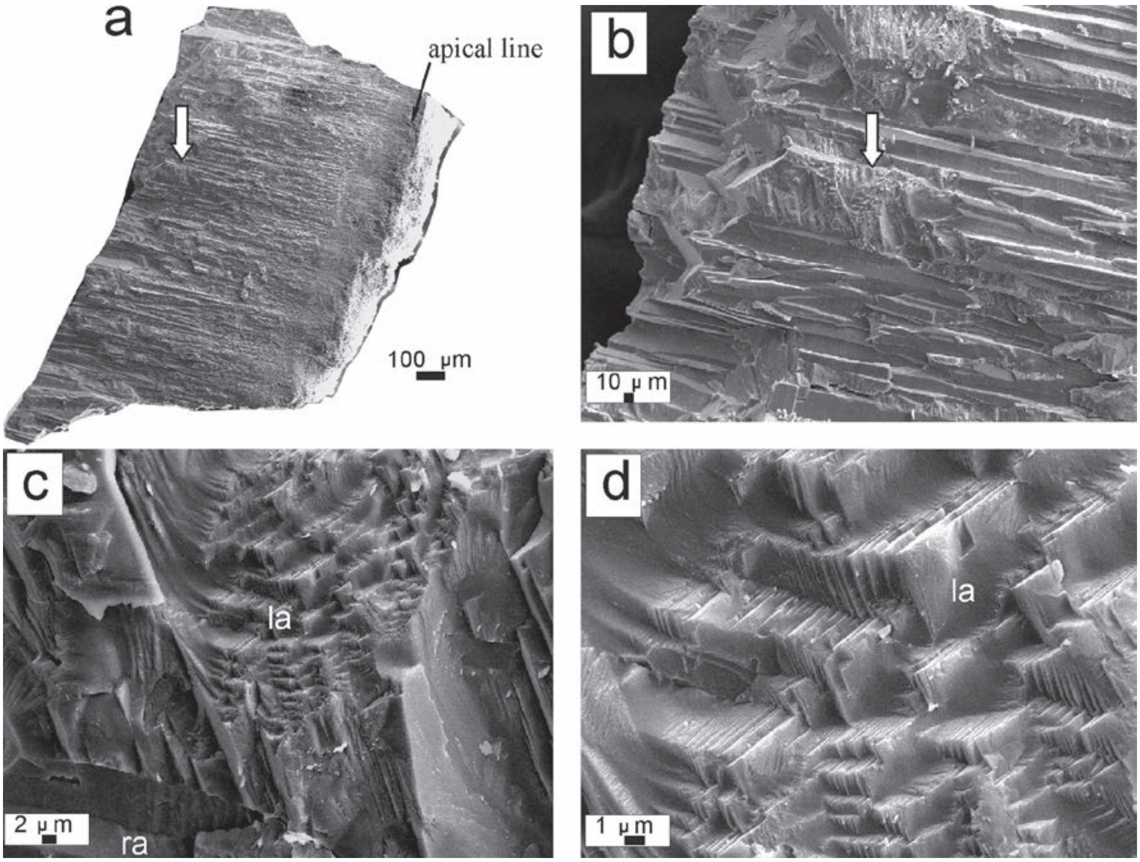


Table 3: Carbon and oxygen isotope analyses of the early Maastrichtian belemnite *Belemnitella americana* (Morton) rostrum PD1 and the bivalve *Exogyra costata* (Say) shell PD2 from the Peedee Formation of the Peedee River, South Carolina (D: diameter, H: height).

Sample	Species (rostrum or shell number)	Stage, formation (locality)	Location (D and H, in mm)	Diagenetic alteration			$\delta^{13}C$ (V-PDB)(‰)	$\delta^{18}O$ (V-PDB)(‰)	T°C
				Original calcite (%)	Admixture (α-SiO_2)	Colour			
PD1-1	*Belemnitella americana* (Morton) (PD1)	Lower Maastrichtian Pee Dee Formation (Pee Dee River, South Carolina)	13.50-14.00	100	No	Colourless	-0.2	0.1	11.7
PD1-4	Same rostrum	Same level	12.00-12.50	100	No	Colourless	0.3	-0.01	12.0
PD1-7	Same rostrum	Same level	10.50-11.00	100	No	Colourless	0.2	-0.01	12.0
PD1-11	Same rostrum	Same level	8.50-9.00	100	No	Colourless	0.2	-0.01	12.0
PD1-15	Same rostrum	Same level	7.25-7.50	100	No	Colourless	0.03	-0.01	12.0
PD1-19	Same rostrum	Same level	6.25-6.50	100	No	Colourless	0.10	0.10	11.7
PD1-23	Same rostrum	Same level	5.25-5.50	100	No	Colourless	0.20	0.20	11.3
PD1-27	Same rostrum	Same level	4.25-4.50	100	No	Colourless	0.30	0.4	10.6
PD1-31	Same rostrum	Same level	3.25-3.50	100	No	Colourless	-0.10	0.20	11.3
PD1-33	Same rostrum	Same level	2.75-3.00	100	No	Colourless	-0.10	0.20	11.3
PD1-35	Same rostrum	Same level	2.25-2.50	100	No	Colourless	-0.10	0.20	11.3
PD1-39	Same rostrum	Same level	1.25-1.50	100	No	Colourless	-0.10	0.40	10.6
PD1-43	Same rostrum	Same level	0.00-0.50	100	No	Colourless	-0.20	0.50	10.2
PD3-1	*Belemnitella americana* (Morton) (PD3)	Same level	11.00-11.20	100	No	Colourless	-0.87	-0.02	12.1
PD2-1	*Exogyra costata* (Say) (PD2)	Same level and locality	27.50 (inner surface)	100	No	Colourless	-0.40	-1.60	15.1
PD2-2	Same shell	Same level	6.00	100	No	Colourless	-0.17	-0.78	15.1
PD2-3	Same shell	Same level	11.00	100	No	Colourless	-0.93	-1.22	16.9
PD2-4	Same shell	Same level	14.00	100	No	Colourless	0.09	-0.79	15.1
PD2-5	Same shell	Same level	16.5	100	No	Colourless	-1.52	-1.43	17.8
PD2-6	Same shell	Same level	18.5	100	No	Colourless	-2.04	-1.89	19.8
PD2-7	Same shell	Same level	21.5	100	No	Colourless	-1.70	-0.34	13.3
PD2-8	Same shell	Same level	23.5	100	No	Colourless	-1.59	-2.01	20.3
PD2-9	Same shell	Same level	25.5	100	No	Colourless	-1.01	-1.77	19.3
PD2-10	Same shell	Same level	27.5	100	No	Colourless	-2.39	-1.79	19.4
PL1-3	*Dhondtichlamys acuteplicata* (Alth) (PL1)	Upper Maastrichtian (Bochotnica near Kazimierz Dolny, Poland)	H=11.0	100	No	White	0.96	-1.27	17.1
PL2-1	*Belemnitella*? sp. (PL2)	Same level and locality	D=6.9	100	No	Colourless	-0.56	0.36	10.6
H1-1	*Gonioteuthis granulate quadrata* (Stolley)	Lower Campanian (Hannover, Germany)	D=16.2	100	No	Colourless	1.30	-0.22	12.9

ations cannot be entirely excluded, especially in the apical line area of belemnite rostra, as suggested by the chemical tests.

Samples for our isotopic analyses were carefully removed from the shells and rostra using a special method (Zakharov et al. 2005, 2007b): material was taken by a scalpel mainly from narrow, small areas along growth striations on the external surface of bivalve and ammonoid shells, and from successive growth portions in the belemnite rostra, which enabled investigated shell (rostrum) material formed apparently during different seasons of the year to be identified. Individual ages of the investigated molluscs was determined using only data on ontogenetic fluctuation of $\delta^{18}O$ and $\delta^{13}C$ values in their skeleton, which seems to reflect some seasonal changes. The same method has been used earlier by some other workers (e.g. Stevens & Clayton 1971). There are no reliable criteria to determine the individual age of a fossil cephalopod using data on its external or internal morphology to date.

The palaeotemperature equations of Anderson & Arthur (1983) and Grossman & Ku (1986) were used

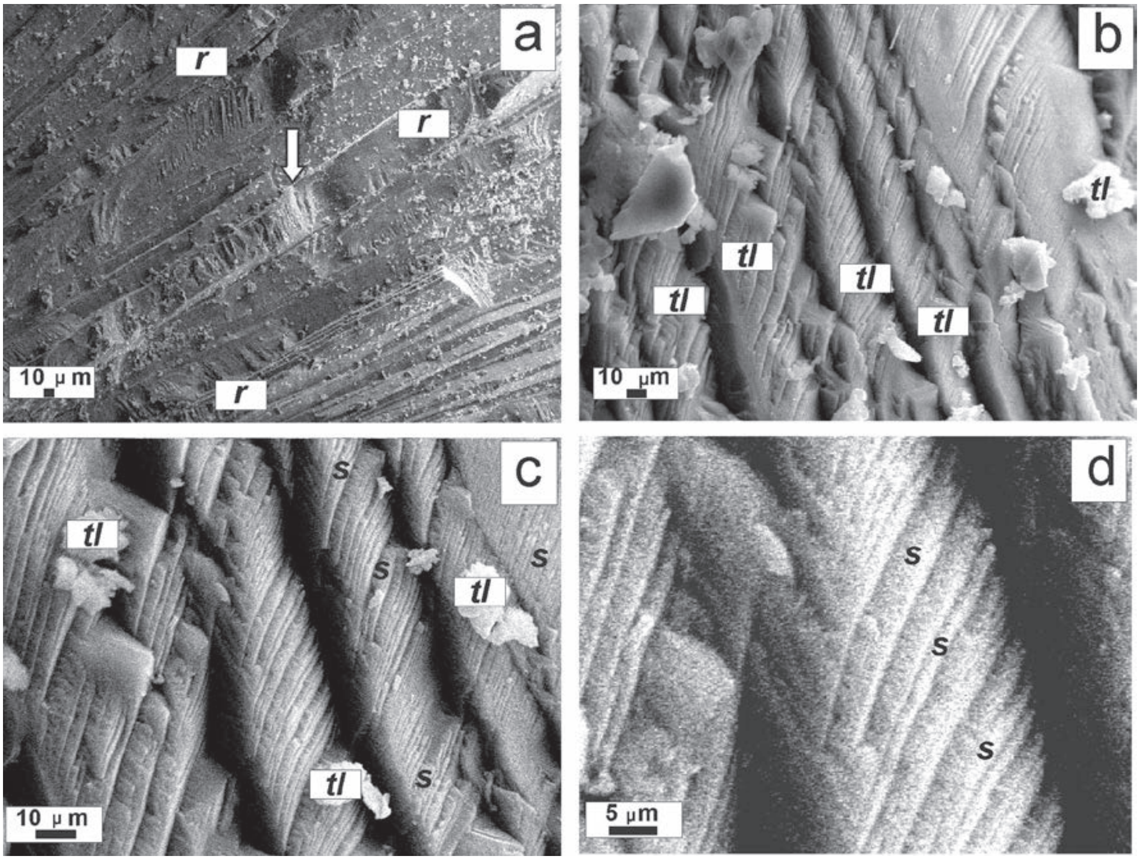


Fig. 4: SEM photomicrographs of the belemnite *Belemnitella americana* rostrum 7a-1 from the Peedee Formation of South Carolina, transverse break. **a**: Coarse radial elements, the arrow shows position of discovered microstructure in transverse section, named as microstructure “c”. **b–d**: Microstructure “c”, thick lamellar microstructure (*tl*), located transversely to coarse radial elements and crossed in its turn by thin sinuous elements (*s*).

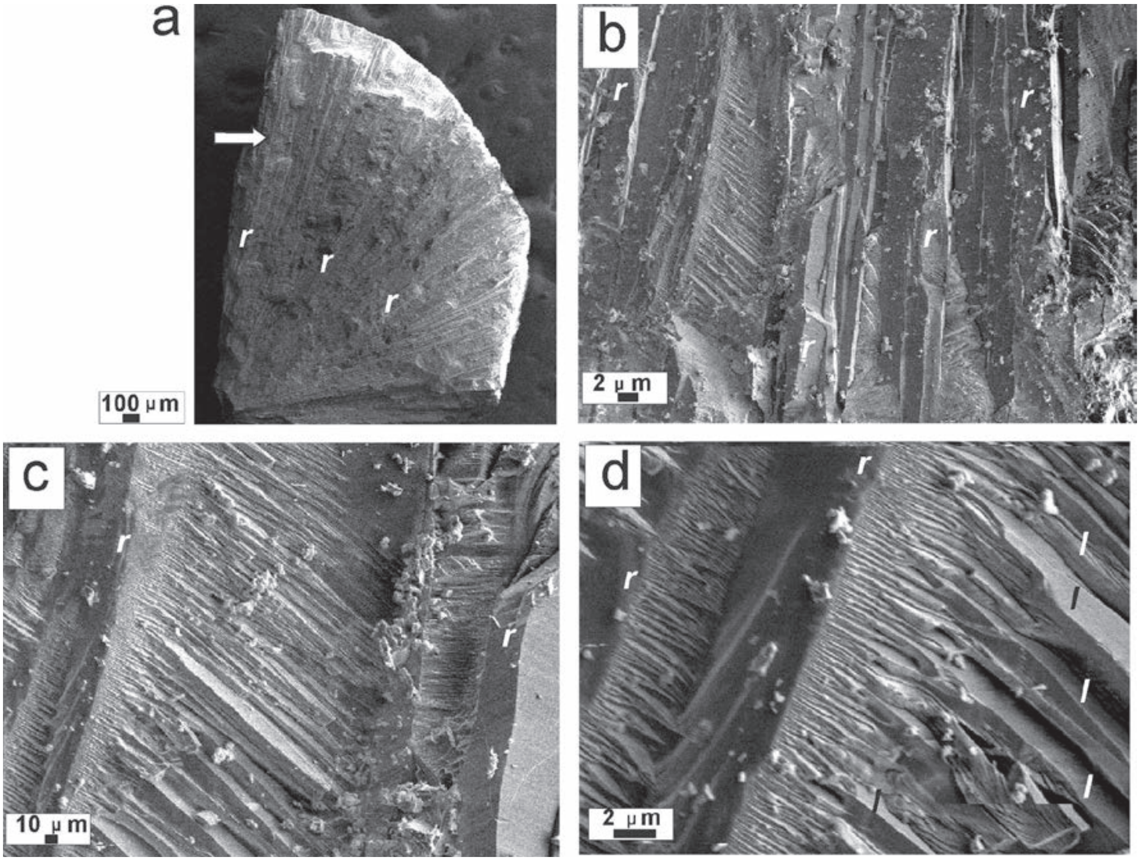


Fig. 5: SEM photomicrographs of the belemnite *Belemnitella americana* rostrum 7a-1 from the Peedee Formation of South Carolina, transverse break. **a**: Coarse radial elements (*r*), the arrow shows position of discovered microstructure, named as microstructure “d” (transverse section). **b–d**: Microstructure “d”, thin lamellar microstructure (*l*), crossed coarse radial elements.

for palaeotemperature calculation (for calcite and aragonite material, respectively). In calculating the temperatures from the isotopic composition of Cretaceous belemnite rostra, a $\delta^{18}O$ of the ambient water of –1.2‰ VPDB (equivalent to –1.0‰ VSMOW) was thought to be appropriate, since icecaps were not present during most of the Cretaceous Period. Oxygen and carbon isotope measurements were carried out using a Finnigan MAT-252 mass spectrometer at FEGI, Vladivostok. The laboratory gas standard used in the measurements was calibrated relative to NBS-19 standard $\delta^{13}C$ = 1.93‰ and $\delta^{18}O$ = –2.20‰ (COPLEN et al. 1963). Reproducibility of replicate standards was always better than 0.1‰. X-ray powder analyses were carried out using a DRON-3 diffractometer also at FEGI, following the method of DAVIS & HOOPER (1963). Elemental concentrations in belemnite rostra were determined by energy dispersion X-ray spectrometer INCA Energy 350 (Oxford) at the Analytical Center of FEGI, and EVO 40 XVP at the Center of the Electronic Microscopy of Institute of Marine Biology, Russian Academy of Sciences (Far Eastern Branch).

Microstructure, oxygen and carbon isotope results

South Carolina (lower Maastrichtian Peedee Formation)

The Peedee Formation in the Peedee River basin, South Carolina, comprises about 270 m of predominantly glauconitic and argillitic sands, many layers of which are calcareous, intercalated with dark marine clays; the depositional environment of this sequence has been interpreted as an open marine shelf (e.g. SOHL & OWENS 1991; EDWARDS et al. 1999; LANDMAN et al. 2004.).

High-resolution sampling was employed to characterise microstructure and chemical composition of *Belemnitella americana*, collected by K. TANABE and D.W. WILLIAMS from the Peedee Formation of the riverside cliff exposed along the Peedee River (Locs. 1 and 3). The longitude and latitude of Loc. 1 are: 79°31'14''W and 34°03'17''N, those of Loc. 3 are: 79°31'19''W and 34°03'10''N. The lithology at both investigated localities is intensely bioturbated grey silty sandstone or sandy siltstone.

SEM photographs of the *B. americana* rostrum show that in both the central longitudinal and transverse sections microstructures of the following two types can be recognized: (1) wedge-shaped crystallite structure with numerous subchips found at the polished and etched surface in longitudinal section – we here term it microstructure "a" (Fig. 2), (2) thin lamellar microstructure with crossed radial elements (microstructure "b", found in the longitudinal break) (Fig. 3), (3) thick lamellar microstructure located transversely to radial elements and crossed in its turn by thin sinuous elements (microstructure "c", found in the transverse break) (Fig. 4), (4) thin lamellar microstructure with crossed radial elements (microstructure "d", found in the transverse break) (Fig. 5). These microstructural features of the *B. americana* rostrum, as well as those observed in the shells of the ammonoids *Discoscaphites* and *Sphenodiscus* indicate indifferent stages of their ontogeny (Figs 6 and 7), and do not represent diagenetic alteration.

The three rostra – PD4 (35 samples), PD1 (13 samples) and PD3 (1 sample) – were isotopically analyzed in detail (Tables 2 and 3). All samples taken from the rostra are represented by original calcite without any α-SiO_2 admixture. $\delta^{18}O$ and $\delta^{13}C$ values for the first one vary between 0.10 and 0.74‰, and between –0.64 and 0.91‰, respectively (Table 2), and for the second and third ones between –0.02 and 0.50‰, and between –0.87 and 0.30‰, respectively (Table 3).

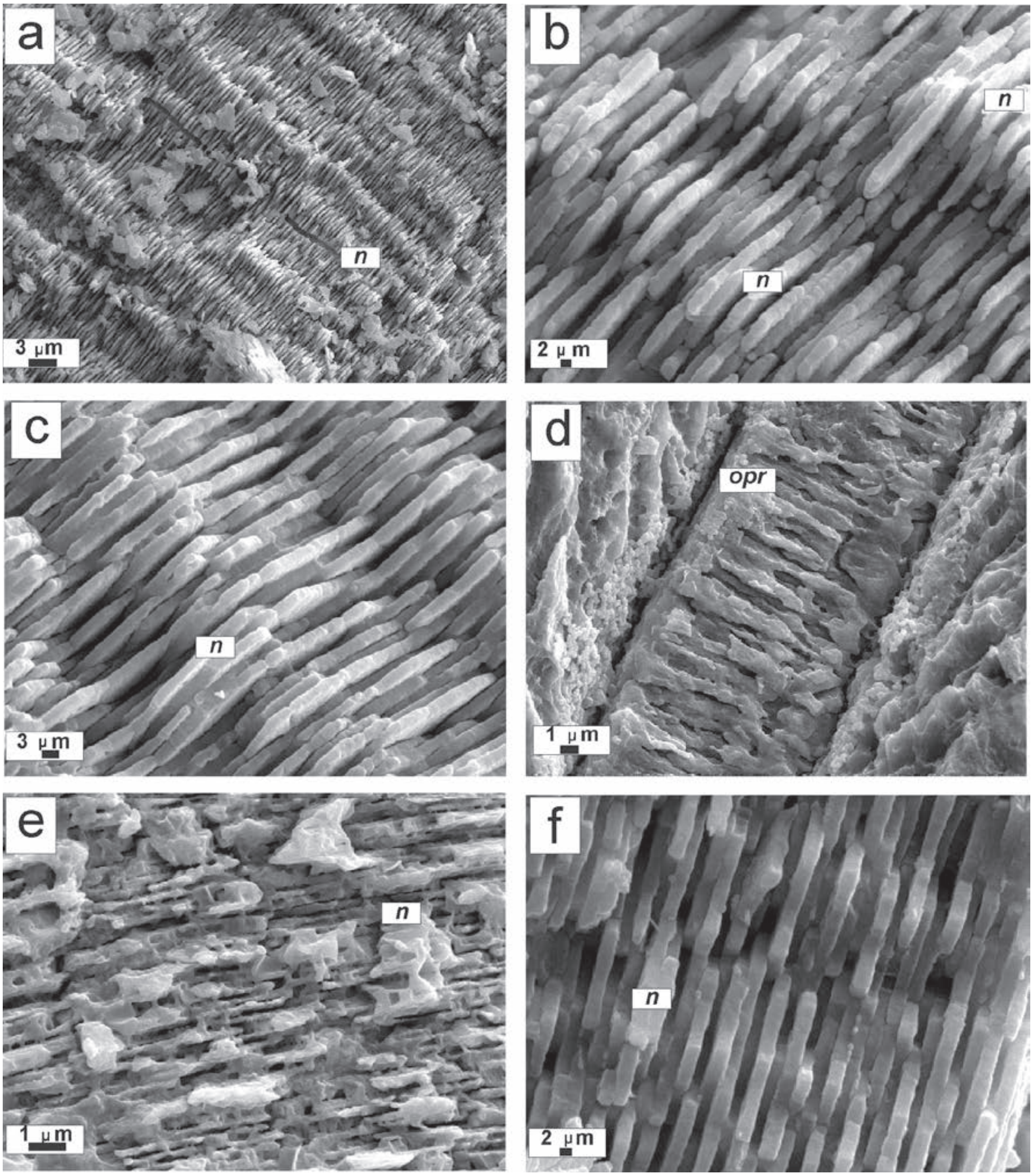
In contrast to isotopic compositions of the aforementioned *Belemnitella americana* rostra, a shell of the bivalve *Exogyra costata* that was found together with the belemnites, shows lighter $\delta^{18}O$ and $\delta^{13}C$ values fluctuating from –2.0 to –0.34‰ and from –2.39 to 0.09‰, respectively (observation from 10 samples) (Table 2).

These analyses demonstrate that average stable isotope composition of belemnite *Belemnitella americana* rostra from the Peedee Formation do not agree with those of oyster bivalves from the same formation and suggest different habitats for them. Alternatively, it may be caused, for instance, by 'vital effects' if the mollusc would be photosymbiotic, as is the case in some corals (e.g. ADKINS et al. 2003), foraminifera (HOUSTON & HUBER 1998; ZEEBE et al. 2008), or possibly in some inoceramid bivalves ('isotopic effect') (e.g. ZAKHAROV et al. 2007b).

South Dakota (upper lower Maastrichtian Fox Hills Formation)

The depositional environment of the Fox Hills Formation sequence in South Dakota has been interpreted as nearshore interior and brackish interior (WAAGE 1968; COBBAN & KENNEDY 1992; HAY et al. 1993; KAUFFMAN et al. 1993; LANDMAN et al. 1983; LANDMAN & WAAGE 1993; LANDMAN & COBBAN 2003; WHITTAKER & KYSER 1993; MCARTHUR et al. 1994; COCHRAN et al. 2003; LANDMAN & COBBAN 2003). This formation includes nearly 120 m of dominantly silty (Trail City Member) to sandy (Timber Lake Member) strata. Most of the marine fossils found in the lower part of the Fox Hills Formation occur in carbonate concretions (LANDMAN & WAAGE 1993).

Fig. 6: SEM photomicrographs of the ammonite shells from the Fox Hills Formation of South Dakota. **a**, **b**: Nacreous layer of the *Discoscaphites gulusus* shell 6-1 (adult stage, at H = 33 mm), found in medial break. **c**: Nacreous layer of the *Discoscaphites gulusus* shell 6-2 (adult stage, at H = 37 mm), found in medial break. **d**: Protoconch outer prismatic layer (*opr*) of the *Sphenodiscus lenticulatus* shell Fox3-4. **e**: Nacreous layer (*n)* of nepionic realm in the same shell in medial section – polished and etched surface. **f**: Nacreous layer (*n)* of the *Sphenodiscus lenticulatus* shell 5-1, adult stage at H = 14.3 mm, found in medial break.



All investigated shells of the ammonoids *Sphenodiscus lenticulatus*, *Discoscaphites gulusus* and *Hoploscaphites nicolleti* recovered from the early Maastrichtian of the Trail City Member of the Fox Hills Formation (45°16'07"N and 100°54'27"W) consist of mainly original aragonite (96–100%), and, judging from SEM photographs, have preserved their original structure. Original microstructures (well-preserved nacreous and prismatic layers) have been discovered in *Sphenodiscus lenticulatus* and *Discoscaphites gulusus* shells (Figs 6 and 7).

In spite of this, all three samples taken from different parts of a *Sphenodiscus lenticulatus* shell show unusually low δ^{18}O and δ^{13}C values, fluctuating from –4.04 to –3.47‰, and from –6.09 to –4.78‰, respectively (Table 4).

δ^{18}O and δ^{13}C values recorded by the belemnite *D. gulusus* are significantly higher, ranging between –1.77 and 1.00‰, and between –4.42 and –2.38‰, respectively (observation from 11 samples) (Table 4). A similar result was obtained from a single *Hoploscaphites nicolleti* shell (Table 4), which more or less agrees with data on this species obtained by us earlier (ZAKHAROV et al. 2006c).

Table 4: Carbon and oxygen isotope analyses of aragonitic ammonoid shells and inoceramid bivalve elements from the upper part of the lower Maastrichtian of the Fox Hills Formation in South Dakota, and the upper Campanian Coon Creek Formation in Tennessee.

Sample	Species (shell number)	Stage, formation (locality)	Location (H and D, in mm)	Diagenetic alterations				$\delta^{13}C$ (V-PDB)(‰)	$\delta^{18}O$ (V-PDB)(‰)	T°C
				Diagenetic stage	Aragonite, %	Admixture (α-SiO_2)	Colour			
Fox2	*Haploscaphites nicolleti* (Morton) (Fox2)	Upper lower Maastrichtian Fox Hills Formation (South Dakota)	H=25.0	1st	96±4	0	Silvery -cream	-1.28	-2.37	[25.7]*
Fox3-3	*Sphenodiscus lenticulatus* (Morton) (Fox3)	Upper lower Maastrichtian Fox Hills Formation (South Dakota)	H=18.0	-	-	-	Silvery -cream	-4.78	-4.04	[32.9]*
Fox3-4	Same shell	Same level	H=10.0	-	-	-	Silvery -cream	-6.09	-3.65	[31.2]*
Fox3-5	Same shell	Same level	H=12.0	-	-	-	Silvery -cream	-5.51	-3.69	[31.4]*
Fox3-13	Same shell	Same level	H=22.0	-	-	-	Silvery -cream	-5.36	-3.47	[30.5]*
Fox4-15	*Discoscaphites gulusus* (Morton) (Fox4)	Same level	H=27.0		100	0	Silvery -cream	-4.22	-1.17	20.5
Fox4-16	Same shell	Same level	H=29.0	1st	99±1	0	Silvery -crea	-4.19	-1.0	19.7
Fox4-17	Same shell	Same level	H=30.0	1st	100	0	Silvery -cream	-4.42	-1.04	19.9
Fox4-18	Same shell	Same level	H=31.8	1st	99±1	0	Silvery -cream	-4.42	-1.15	20.4
Fox4-19	Same shell	Same level	H=34.0	1st	99±1	0	Silvery -cream	-3.78	-1.09	20.1
Fox4-20	Same shell	Same level	H=34.5	1st	99±1	0	Silvery -cream	-3.49	-1.20	20.6
Fox4-21	Same shell	Same level	H=35.0	1st	99±1	0	Silvery -cream	-3.38	-1.77	23.1
Fox4-22	Same shell	Same level	H=35.5	1st	99±1	0	Silvery -cream	-3.38	-1.44	21.6
Fox4-23	Same shell	Same level	H=36.3	1st	99±1	0	Silvery -cream	-3.31	-1.38	21.4
Fox4-24	Same shell	Same level	H=38.0	1st	99±1	0	Silvery -cream	-3.10	-1.52	22.0
Fox4-25	Same shell	Same level	H=39.0	1st	99±1	0	Silvery -cream	-2.38	-1.24	20.8
T3-1	*Inoceramus* (*Endocostea)* sp. (T3-1)	Upper Campanian Coon Creek Member (Tennessee)	H=31.5	1st	99±1	Trace	Silvery -cream	3.89	-0.11	15.9
T2-1	*Crassatellites rodustus* (Morton)	Same level	H=41.6	1st	100	Trace	Yellowish white	0.75	-1.13	20.3
T2-2	Same shell	Same level	H=19.5	1st	100	Trace	Yellowish white	2.05	-0.38	17.0

* Unrealistic palaeotemperatures (because of diagenetic alteration) are placed in brackets.

Tennessee (upper Campanian Coon Creek Formation)

The Coon Creek Formation consists of approximately 43 m of micaceous sand, and sandy glauconitic clay at its base that may locally be fossiliferous.

Samples taken from the bivalves *Crassatellites rodustus* and *Inoceramus* (*Endocostea*) sp. from the late Campanian Coon Creek Formation of the Coon Creek, Mississippi River basin, are 100% aragonite. The highest $\delta^{18}O$ (–0.11‰) and $\delta^{13}C$ (3.89‰) values were recorded for *Inoceramus* (*Endocostea*) sp.; $\delta^{18}O$ and $\delta^{13}C$ values in samples taken from *Crassatellites rodustus* shells fluctuate from –1.13 to –0.38‰ and from 0.75 to 2.05‰ (Table 4). Oxygen-isotopic data obtained from C. *rodustus* and *Inoceramus* (*Endocostes*) sp. of the Coon

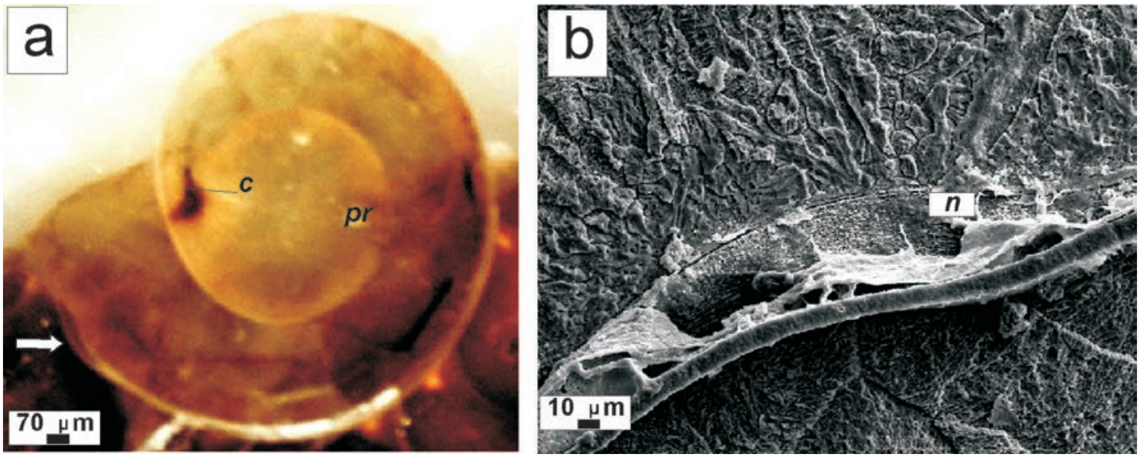


Fig. 7: *Sphenodiscus lenticulatus* shell 5-1 from the Fox Hills Formation of South Dakota. **a**: Ammonitella in the medial section – polished and etched surface, the arrow shows position of nepionic realm; *c* – caecum, *pr* – protoconch. **b**: SEM photomicrograph of nepionic realm of the shell.

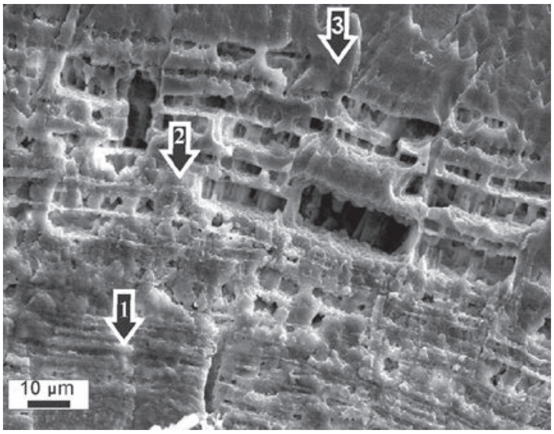


Fig. 8: SEM photomicrograph of the belemnite *Belemnitella americana* rostrum PD4 from the Peedee Formation of South Carolina, transverse break – polished and etched surface; the arrows 1–3 show position of some geochemical spectra.

Creek Formation agree with previous data obtained from shells of the bivalve *Pterotrigonia* (Zakharov et al. 2007b) and the nautiloid *Eutrephoceras* (Moriya et al. 2010), collected from the same formation.

However, co-occuring planktic foraminifera *Rugoglobigerina* shells, investigated by Moriya et al. (2010), show lighter $\delta^{18}O$ values. Oxygen-isotopic temperature offset of 14.1°, 14.0°, 9.7–13.0° and 8.8–13.3°C between foraminifera *Rugoglobigerina* from the late Campanian Coon Creek Formation in McNairy County and the molluscs *Inoceramus*, *Eutrephoceras*, *Crassatellites* and *Pterotrigonia* from the same formation, respectively, indicates that both bivalve and cephalopod mollusc (nautiloid) shells were secreted in near bottom conditions where the mentioned animals, as well as apparently other Late Cretaceous molluscs from this region, spent most of their life in shallow marine basins.

Poland, Bochotnica (upper Maastrichtian) and northern Germany (lower Campanian)

Interestingly, isotopic analyses demonstrate significant differences between such well-preserved fossils as a calcitic belemnite *Belemnitella*? sp. rostrum and a calcitic bivalve *Dhondtichlamys acuteplicata* shell found in the same association in Poland. The $\delta^{18}O$ value in the belemnite rostrum is 0.36‰, but in the bivalve shell only –1.27‰ (Table 4). A comparatively high $\delta^{18}O$ value (–0.22‰) was recorded also for a belemnite *Gonioteuthis granulataquadrata* (Stolley) rostrum from the lower Campanian of the Hannover area (Table 4). These differences in isotopic composition may have been caused by different environments inhabited during life and/or biological fractionation, and are in agreement with data on early Maastrichtian fossils from the Peedee Formation.

Discussion

Discussion on microstructure of belemnite rostra

Several detailed studies of diagenetic and morphological aspects of some Jurassic and Cretaceous belemnite rostra (e.g. Mutvei 1964; Sælen 1989; Pirrie & Marshall 1990; Anderson et al. 1994; Price & Sellwood 1994; Podlaha et al. 1998; van de Schootbrugge et al. 2000, 2005; McArthur et al. 2000, 2004; Longinelli et al. 2002a, b; Niebuhr & Joachimsky 2002; Price & Gröcke 2002; McArthur et al. 2000, 2004; Gröcke et al. 2003; Voigt et al. 2003; Florek et al. 2004; Rosales et al. 2004; Pirrie et al. 2004; Price & Mutterlose 2004; Wierzbowski 2004; Fürsich et al. 2005; Dunca et al. 2006) have been conducted. These studies, first of all Sælen's (1989) data, have shown that the original mineralogy of the majority of belemnite rostra was low-Mg calcite, and that the aragonite found e.g. in *Neohibolites minimus* (Miller) from the Albian of Europe (Spaeth 1971a, b, 1973) and *Goniocamax* sp. from the Turonian of Arctic Siberia (Tays et al. 1978) does not necessarily indicate that all belemnite rostra were originally composed of this mineral.

Siberian *Goniocamax* was recently investigated in detail by Dauphin et al. (2007). They confirmed the coexistence both aragonitic and calcitic components in the investigated rostrum and hypothesized that belemnite rostra in general seem to be composed of primary aragonite, rather than low-Mg calcite.

As was shown by us above, the two types of microstructure have been discovered in the longitudinal section of the *Belemnitella americana* rostrum (microstructures “a” and “b”), as well as in its transverse one (microstructures “c” and “d”). According to our reconstruction (Fig. 10), microstructures indicated by us as “a” and “b” in the longitudinal section correspond to microstructures “c” and “d” in the transverse section, respectively. These structures, investigated by SEM in detail (Figs 2–5), look as original ones, in particular because of the fact that the wedge-shaped structure (Fig. 2) seems to be characteristic only for belemnites [e.g. it was discovered by us in the belemnite rostrum from the Albian of South India (Zakharov et al. 2008)], and was never discovered in recrystallized (calcitic) ammonoid or other mollusc shells. Besides, diagenetically altered (calcitic) ammonoid shells as a rule show significantly lower δ^{18}O values as compared with those of aragonite-bearing ammonites (Zakharov et al. 1975). However, almost all belemnite rostra, collected in different palaeolatitudes of the world, in contrast to most other mollusc shells, have consistently higher δ^{18}O values (Zakharov et al. 2006c, 2010). All mentioned sharp distinctions are usually graded during a pronounced diagenetic process. These observations favour Sælen’s (1989) hypothesis that the original mineralogy of the majority of belemnite rostra was low-Mg calcite.

Isotopic evidence of a considerable range of vertical migration of Late Cretaceous belemnites

Urey et al. (1951) wrote that “Since the abundance of the O^{18} isotope in calcium carbonate varies with the temperature at which it is deposited from water, the variation in abundance can be used as thermometer” (p. 399). “Whether the photosynthetic process concentrates the carbon isotopes by some equilibrium or near-equilibrium process is not certain” (Urey et al. 1951: 400). Epstein et al. (1951) additionally noted that not all biogenetic minerals are deposited in equilibrium and that biological processes (‘physiological effect’), overriding the environmental signals, take place in certain groups of animals and plants. These equilibrium offsets were later (Weber & Woodhead 1972) referred to as a ‘vital effect’, a term first introduced by Urey et al. (1951) albeit in a different sense (p. 401). In Weiner & Dove’s (2003) opinion, the problem lies in the absence of a deep understanding of vital effects (kinetic and taxonomic ones).

According to Rexfort & Mutterlose (2006, 2009), oxygen isotope ratios of the cuttlefish *Sepia*, the modern analogue of belemnites (Price et al. 2009), show no signs of biofractionation when reared under con-

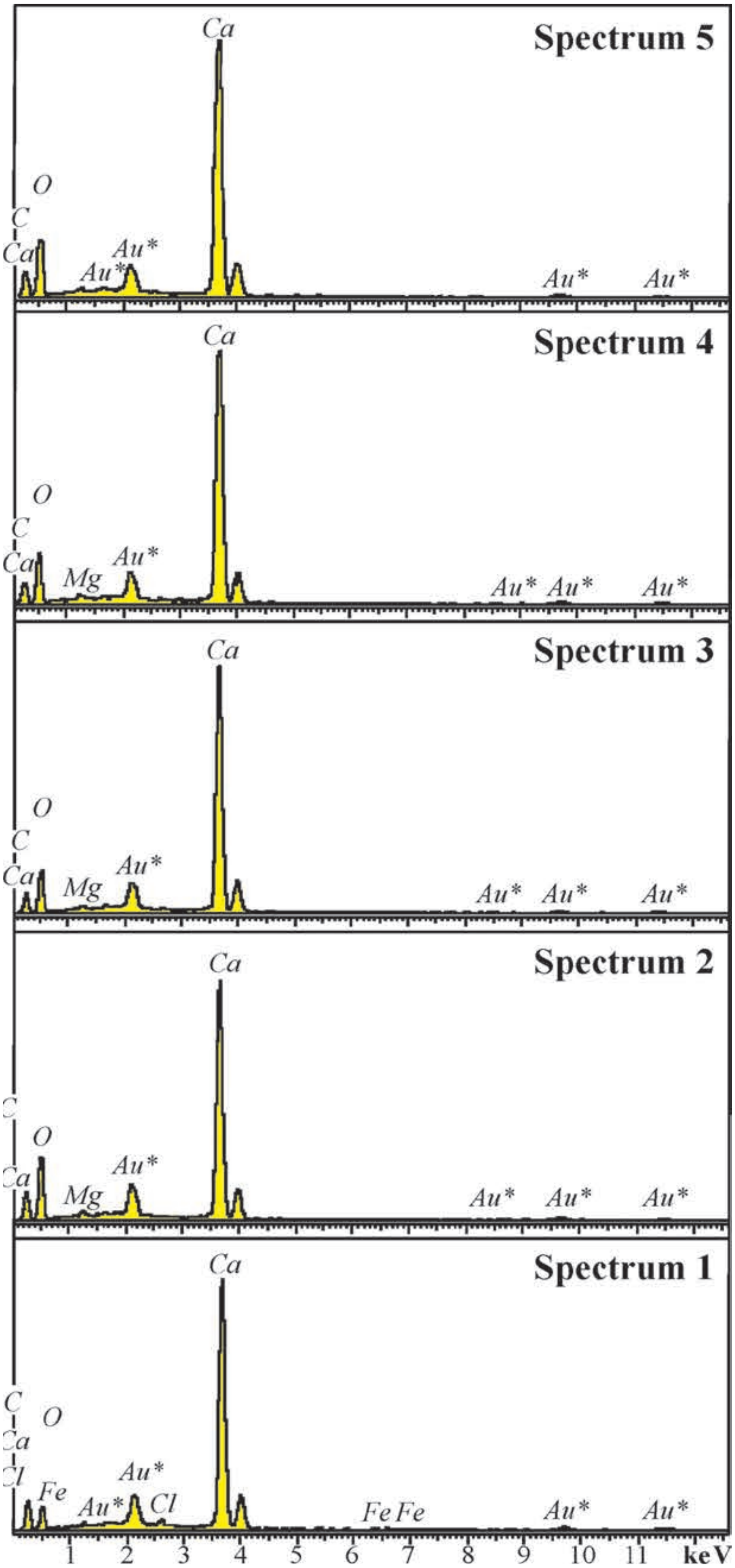


Fig. 9: Elemental composition of the belemnite *Belemnitella americana* rostrum PD4 in (EDX spectra 1–6 from the cross-section; position of the first three ones are shown in Fig. 8). *Au* indicated by the asterisk is not original because just before SEM-investigation its section was covered by gold.

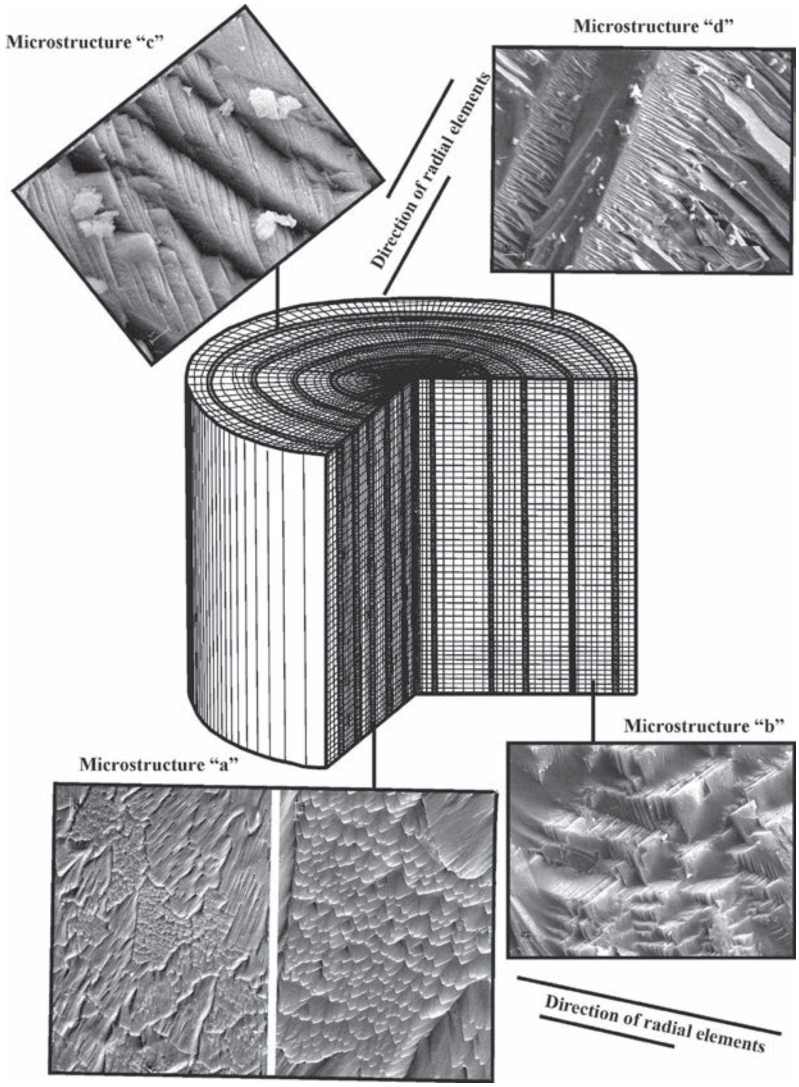


Fig. 10: Microstructure reconstruction of the belemnite *Belemnitella americana* rostrum from the Peedee Formation of South Carolina on the basis of data from longitudinal (microstructures "a" and "b") and transverse (microstructures "c" and "d") sections.

trolled temperature conditions, and therefore perfectly reflect the temperature-characteristics of their habitat. Accordingly, no effect of oxygen isotope biofractionation is to be expected in belemnites. At the same time the δ^{13}C values are thought, in their opinion, to be controlled by vital effects (Rexfort & Mutterlose 2009).

Comparisons between stable isotope compositions of co-occurring belemnites and bivalves from the Peedee Formation suggest that they were living in different environmental conditions (Figs 11 and 12). Measurements of δ^{18}O on high-resolution samples across growth bands of an early Maastrichtian *Belemnitella americana* (49 analyses) from the Peedee Formation indicate that this belemnite was mainly an inhabitant of deeper, cooler waters of the Mesopelagic Zone. Its stable isotope profile is sinusoidal in shape in general, which partly reflects apparently seasonal cycles of temperature. The belemnite rostrum PD4 seems to be secreted during two years in conditions of both the lower (9.4–10.2°C) and the upper (10.6–11.7°C) parts of the Mesopelagic Zone (Fig. 11). Other investigated belemnite rostra (e.g. PD1 and PD3) were secreted apparently mainly within the upper Mesopelagic Zone (10.6–12.1°C). Warmest (summer) early Maastrichtian palaeotemperatures of the lower and upper parts of the Mesopelagic Zone in the Peedee River area possibly fluctuated between 9.8–10.2° and 11.3–12.0°C, respectively.

Judging from previous analyses of Lowenstam & Epstein (1954) that were newly revised, most *B. americana* belemnites from the Peedee, Prairie Bluff and Navesink formations were inhabitants of the upper Mesopelagic Zone (12.1–14.9°C), rarely of the lower Epipelagic Zone (15.3–17.8°C). Similar isotopic results were obtained from *Belemnitella* cf. *bulbosa* Meek & Hayden of the Fox Hills Formation and the Pierre Shales of North America (Cochran et al. 2003), which allow calculating a temperature interval of 10.7–17.3°C. Some portions of the early Campanian *Gonioteuthis granulataquadrata* rostrum from northern Germany, and the late Maastrichtian belemnite from Poland (Table 4), were also secreted in cooler conditions (10.6–12.9°C).

New evidence and revised data are consistent with the hypothesis suggesting a considerable vertical range of migration of the belemnites in the water column [e.g. Huber & Hodell (1996) and our previous data (Zakharov et al. 2006a, b, 2010, 2012)]. For this reason, it is particularly difficult to determine the mean annual range of temperature for sea-surface waters on the basis of data from the aforementioned belemnites.

Possible correlation between *Belemnitella americana* δ^{13}C value changes and solar activity fluctuations

The first attempt to show a possible correlation between invertebrate δ^{13}C value changes and solar activity fluctuations was done by us using the Recent cephalopod *Nautilus pompilius* and dallinid brachiopods from the Philippines (Zakharov et al. 2006b). The most negative δ^{13}C excursion in the ninth septum of *Nautilus pompilius* (–2.5‰) seems to be connected with a weakening of phytoplankton bioproductivity provoked by the low solar activity at the end of 1996, which was documented by Gnezdilov (2004). However, the highest δ^{13}C values in both the investigated *Nautilus pompilius* and dallinid brachiopod shells were recognized in the portions of their shells secreted at the beginning of 1999, just before the peak of the solar activity of the 23rd cycle (Zakharov et al. 2006b).

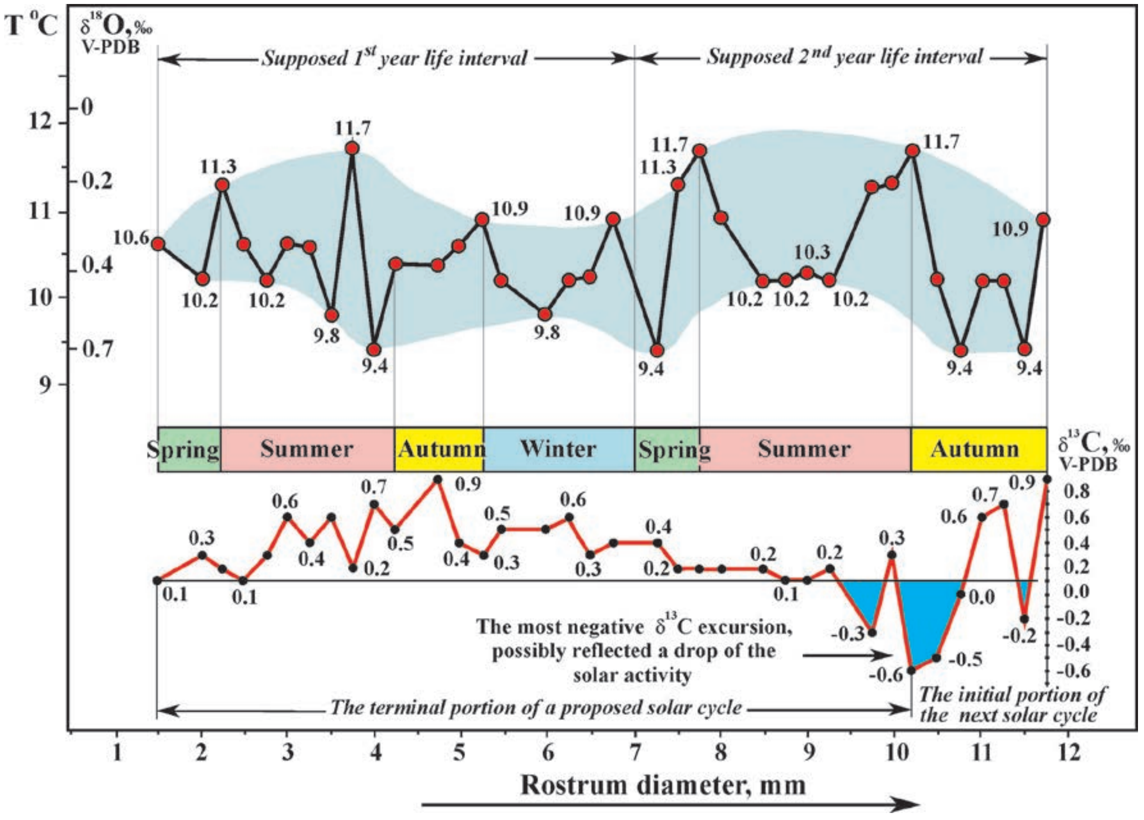


Fig. 11: Seasonal growth temperatures for the two-years-old belemnite from the lower Maastrichtian Peedee Formation; Peedee River, South Carolina.

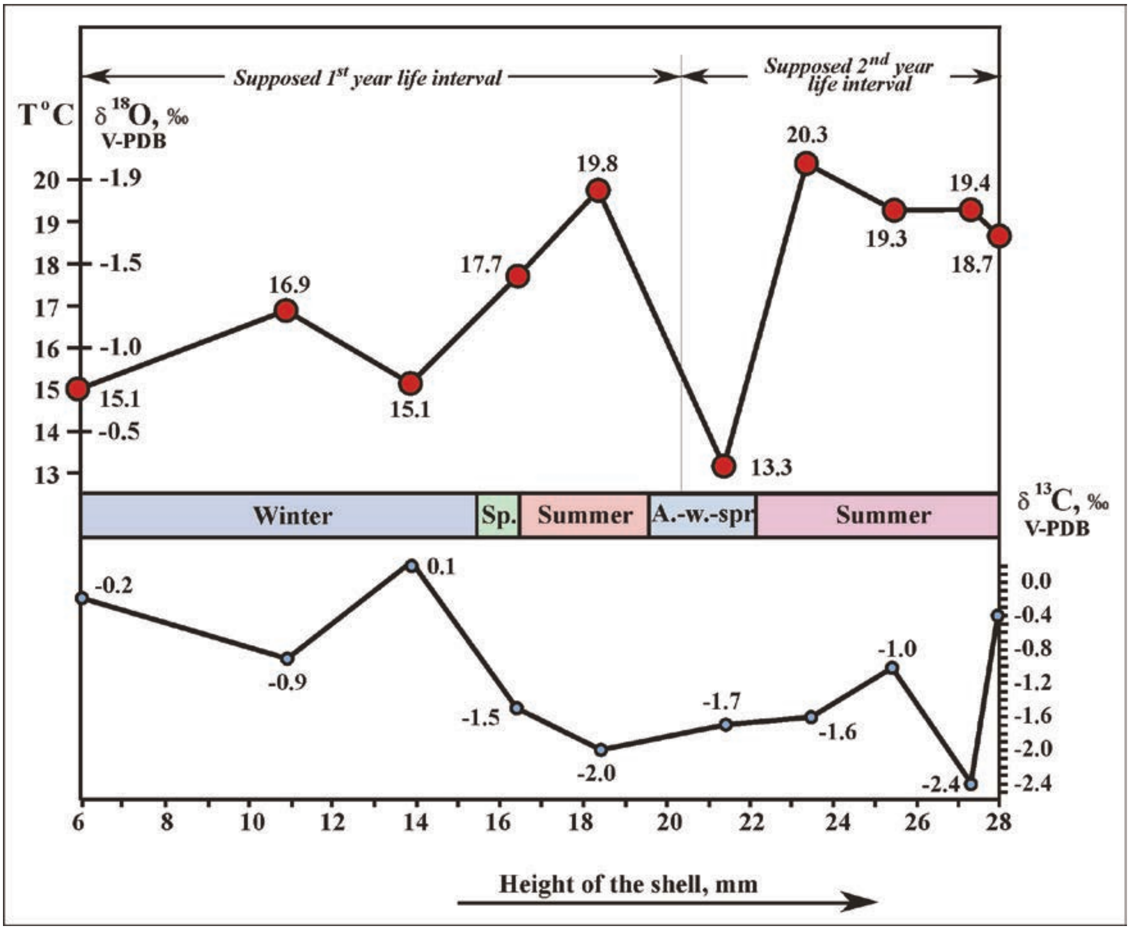


Fig. 12: Seasonal growth temperatures for two-years-old bivalve *Exogyra costata* from the lower Maastrichtian Peedee Formation, South Carolina.

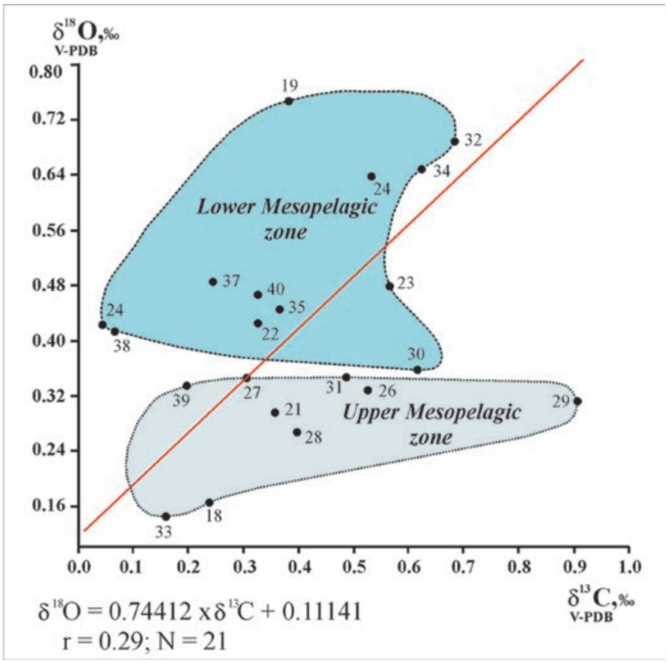


Fig. 13: δ^{18}O-δ^{13}C cross-plot for *Belemnitella americana* from the lower Maastrichtian Peedee Formation (early ontogenetic stage).

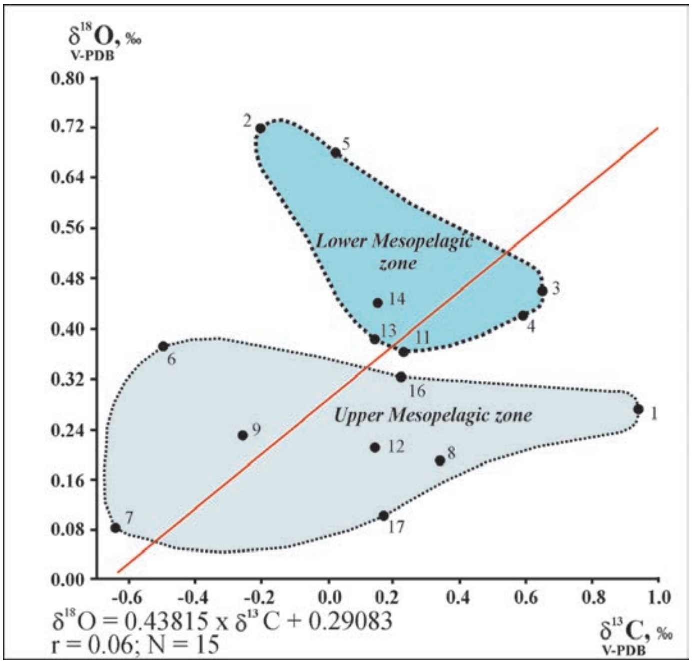


Fig. 14: δ^{18}O-δ^{13}C cross-plot for *Belemnitella americana* from the lower Maastrichtian Peedee Formation (last ontogenetic stage).

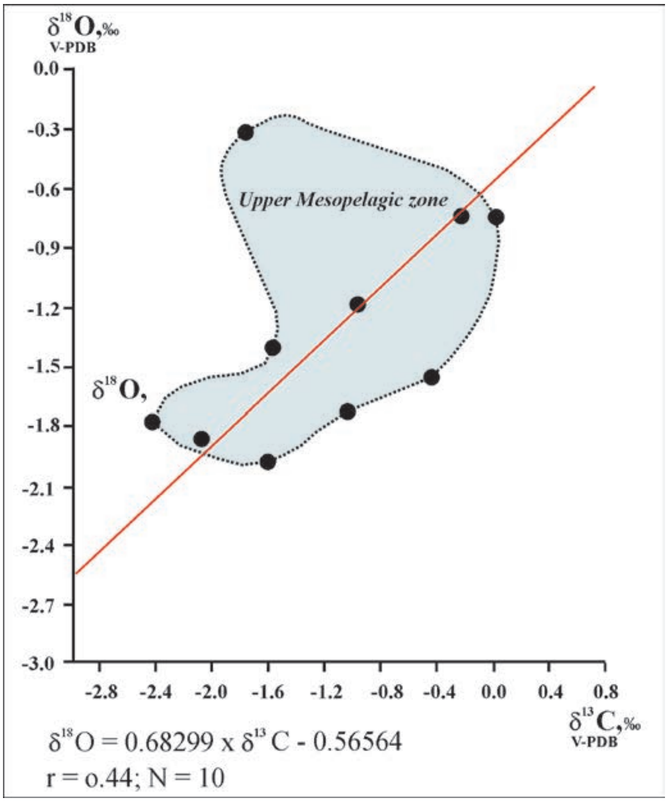


Fig. 15: δ^{18}O-δ^{13}C cross-plot for *Exogyra costata* from the lower Maastrichtian Peedee Formation.

The *Belemnitella americana* rostrum PD4 from the Peedee Formation records early–middle ontogenetic δ^{18}O and δ^{13}C patterns that are generally positively correlated: r = 0.29 (Fig. 12). However, there is a strong deviation from the direct relation between δ^{18}O and δ^{13}C in the last individual stage of the most thoroughly investigated *B. americana* [r = 0.06 (Fig. 14)] because it is followed by a pronounced negative δ^{13}C excursion. The mentioned negative excursion seems to be also generally connected with one of the cycles of low solar activity. However, higher correlation index (r = 0.44) was calculated for *Exogyra costata* from the same formation (Fig. 15). There is still considerable uncertainty in the interpretation of δ^{13}C values in fossils.

Palaeodepth habitat of Maastrichtian molluscs from the Peedee and Fox Hills formations

This paper is the recurrent attempt to reconstruct temperature and salinity conditions for an inhabitation of bivalve and cephalopod molluscs in Maastrichtian seas of North America. Because there is a significant contrast in oxygen isotopic composition of the bivalve *Exogyra costata* and the belemnite *Belemnitella americana* (Tables 2 and 3), found in a single association of the Peedee Formation, it is reasonably to consider that, following REXFORT & MUTTERLOSE (2006, 2009), corresponding portions of their skeletons were secreted in different temperature conditions (Figs 16 and 17). Shells of the bivalve *Exogyra costata* were apparently formed in conditions of normal

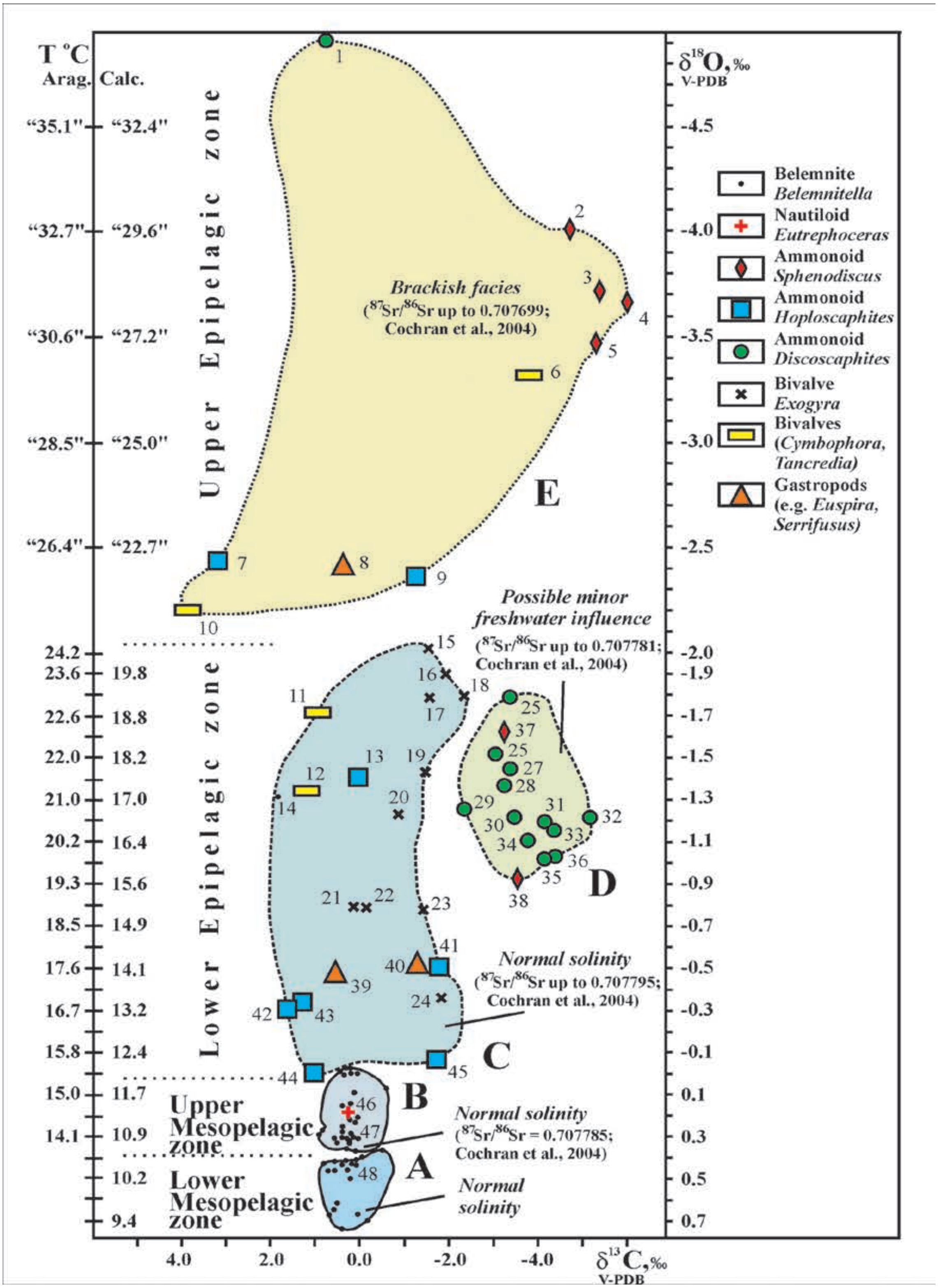


Fig. 16: Maastrichtian mollusc-bearing marine facies of South Carolina (Peedee Formation) and South Dacota (Fox Hills Formation). A–E – inhabitants of the lower Mesopelagic zone with normal salinity (A), upper Mesopelagic zone with normal salinity (B), lower Epipelagic zone with normal salinity (C), lower Epipelagic zone with possible minor influence of fresh waters (D), brackish facies of the upper Epipelagic zone (E). Samples: 1 – DK3 (Zakharov et al. 2006a); 2–5 – Fox3 (Table 3); 6 – D1-5 (Zakharov et al. 2006a); 7 – K18 (Cochran et al. 2003); 8 – K19 (Cochran et al. 2003); 9 – Fox2 (Table 4); 10 – FH2 (Table 2); 11 – PM14784-2; 12 – K7 (Cochran et al. 2003); 13 – PM14781-1 (Zakharov et al. 2006a); 14 – K33 (Cochran et al. 2003); 15–24 – PD2 (Table 2); 25–36 – Fox 4 (Table 4); 37 – K8 (Cochran et al. 2003); 38 – K5g (Cochran et al. 2003); 39 – K15 (Cochran et al. 2003); 40 – K10; 41 – PM14784-1 (Zakharov et al. 2006a); 42 – K20 (Cochran et al. 2003); 43 – K14 (Cochran et al. 2003); 44 – K1 (Cochran et al. 2003); 45 – K13; 46 – K11; 47 – PD4 and PD1 (Tables 3 and 2); and 48 – PD4 (Table 2).

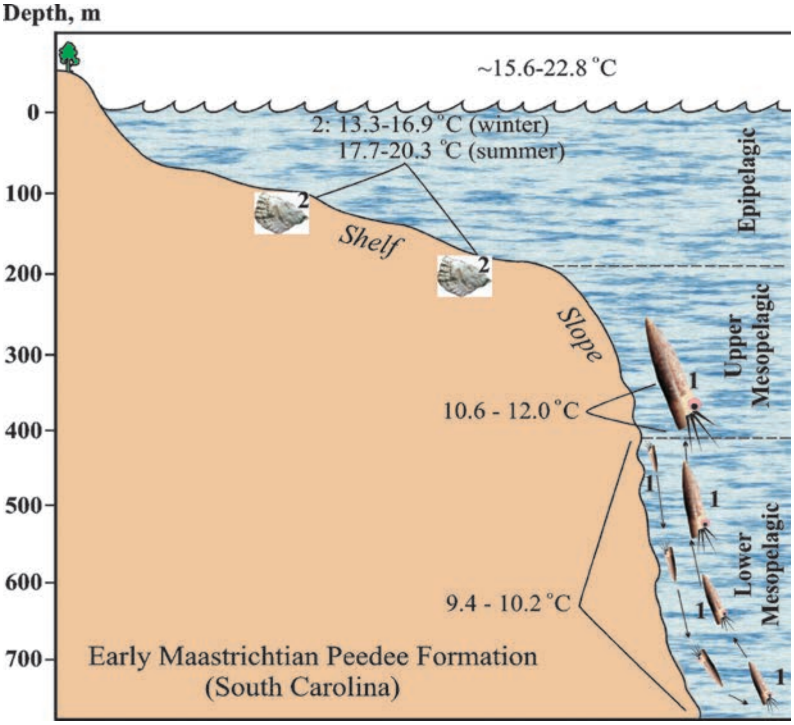


Fig. 17: Inhabitation of early Maastrichtian belemnite *Belemnitella americana* and bivalve *Exogyra costata* from the Peedee Formation of South Carolina.

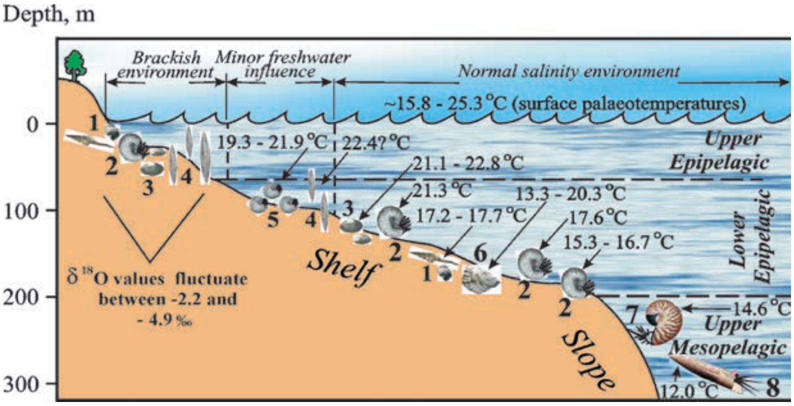


Fig. 18: Palaeotemperatures in a Maastrichtian shallow-shelf sea recorded by individuals of cephalopod, bivalve and gastropod molluscs from the Peedee (this study) and Fox Hills (COCHRAN et al. 2003; this study) formations.

salinity of the lower Epipelagic Zone, where temperatures of 13.3–20.3°C are quite reasonable. It is in consistence with LOWENSTAM & EPSTEIN's (1954) isotope data, newly revised (18.2–19.1°C).

As was shown above, most portions of *B. americana* rostra were secreted in cooler conditions of the Mesopelagic Zone (with summer palaeotemperatures of 9.8–14.9°C, and winter ones of 9.4–10.9°C) [Tables 2 and 3; and revised data of LOWENSTAM & EPSTEIN (1954)]. Judging from the isotopic data by COCHRAN et al. (2003), we expect that another Maastrichtian belemnite species (*B.* cf. *bulbosa*) and the nautiloid *Eutrephoceras dekayi* are characterised by a similar mode of life, which is reflected in the secretion of some elements of their skeletons also in cooler conditions (10.7° and 14.6°C, respectively) .

The investigated ammonoid *Hoploscaphites nicolleti* from the Maastrichtian Fox Hills Formation seems to be an inhabitant of the lower Epipelagic Zone with normal salinity and warm temperature conditions (about 17.6°C) (ZAKHAROV et al. 2006a), which is consistent with the data by COCHRAN et al. (2003) on another *Hoploscaphites* species (*H. nebrascensis*) from the same formation (15.3–25.8°C). Similar temperatures were obtained from the shells of bivalves (21.1–22.8°C) and gastropods (17.2–17.7°C) that co-occurred with ammonoids from the Fox Creek Formation (Figs 16 and 17) (COCHRAN et al. 2003).

The maximum seasonal variation in early Maastrichtian, *Exogyra*-derived temperatures is about 7.0°C (Table 3). A similar result (6.6°C) has been obtained using oxygen-isotope composition of ammonoid shells (Table 4).

Judging from the calculated palaeotemperatures, all investigated late Campanian–early Maastrichtian bivalves and ammonoids of the Peedee and Fox Hills formations (13.3–21.9°C), as well as late Campanian trigoniid (16.7–19.8°C; ZAKHAROV et al. 2007b) and inoceramid (15.8–20.1°C; Table 4) bivalves from the Coon Creek Member inhabited warm waters of epipelagic depths. This is in agreement with published data (LOWENSTAM & EPSTEIN 1954; COCHRAN et al. 2003) on Maastrichtian bivalves, gastropods, nautiloids and some belemnites and ammonoids from the Fox Hills (nearshore interior and brackish biofacies), Peedee and Severn (near open-ocean facies) formations.

The maximum seasonal variation in early Maastrichtian bivalve *Exogyra*-derived temperatures was about 7°C, in ammonoid-derived temperatures about 6.6°C.

Anomalously light $\delta^{18}O$ signatures preserved in an aragonitic shell of the ammonoid *Sphenodiscus lenticulata* from the Trail City Member of the Fox Hills Formation confirm the previous suggestions by TSUITA & WESTERMANN (1998) and COCHRAN et al. (2003) that some Late Cretaceous ammonoid shells, incidentally well-streamlined ones, were secreted in brachyhaline, shallow waters of the upper Epipelagic Zone. However, some of them, suggesting a palaeotemperature of 22.4°C and being associated with many *Discoscaphites* ammonoids showing similar palaeotemperatures (19.3–21.7°C), lived apparently in conditions of possible minor freshwater influence.

Except *Sphenodiscus*, brackish facies of the Western Interior Seaway were inhabited by the rare ammonoids *Hoploscaphites* and *Discoscaphites*, and bivalves ($\delta^{18}O$

values fluctuate between –2.2 and –4.9‰; ^{87}Sr/^{86}Sr is up to 0.707699; Figs 16 and 18) (Cochran et al. 2003; Zakharov et al. 2006c). Earlier, similar δ^{18}O results were obtained by Zakharov et al. (1975) from Early Triassic ammonoids with aragonitic shells from Arctic Siberia.

Conclusions

1. Microstructural and isotopic data obtained, and some previously published evidence, favour Sælen's (1989) hypothesis that the original mineralogy of the majority of belemnite rostra was calcitic, and that calcitic material of well-preserved belemnite rostra may be used for isotopic palaeotemperature calculation, as was originally postulated by Urey et al. (1951).

2. Oxygen isotopic data on the early Maastrichtian belemnite *Belemnitella americana* from the Peedee Formation in South Carolina are consistent with findings (e.g. Huber & Hodell 1996; Monks et al. 1996; Dutton et al. 2007; Zakharov et al. 2006a, b, 2010, 2012) that belemnites usually record cooler palaeotemperatures than shallow-water taxa, suggesting a considerable vertical range of their migration in the seawater column, including the Mesopelagic zone.

3. In view of new facts, δ^{18}O values in the samples taken from the *B. americana* rostra were found to be positively correlated with δ^{13}C through its successive growth portions, with the exception of the latest one. The most negative δ^{13}C excursion in the last portion of its development seems to be connected with a weakening of phytoplankton productivity in the ocean, possibly provoked by the lower solar activity during secretion of the mentioned portion.

4. Published and original data on isotopic composition and shell structure of ammonoids from the Maastrichtian of the Western Interior Seaway strongly support the idea by previous authors (Zakharov et al. 1975; Tsuita & Westermann 1998; Cochran et al. 2003) that anomalously light δ^{18}O signatures preserved in some well-preserved ammonoids seem to be evidence for their possibility to secrete some portions of their shells in hyposaline and brackish conditions, in contrast to the known reduced salinity tolerance of modern cephalopods.

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