

# Paleoenvironmental analysis of a new occurrence of *Rhynchoteuthis gibber* (TILL, 1907) in the Alpine Lower Cretaceous (Cephalopoda, Valanginian, Northern Calcareous Alps, Upper Austria)

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**Abstract:** Upper Valanginian deposits of Upper Austria yield abundant *Rhynchoteuthis gibber* (TILL, 1907), a calcified tip of a supposed ammonoid upper jaw. A new occurrence was detected during paleological and sedimentological studies in the Ternberg Nappe in Upper Austria. The investigated stream section lies in the Losenstein Syncline (47°55' N and 44°21'E). The upper jaw elements together with fewer calcitic lower jaw remains (aptychi), are associated with a mass-occurrence of the genus *Olcostephanus*, which contributes 80% of the total ammonite fauna. Most of the investigated rhynchoteuthids display poor preservation, mainly due to diagenetic or biological dissolution.

Being characteristic Tethyan organisms, such rhynchoteuthids are valuable facies fossils and indicators for paleobiogeography, paleobathymetry and paleoclimate.

**Keywords:** Rhynchoteuthids, Ammonites, Upper Jaws, Valanginian, Preservation, Paleology

## 1. INTRODUCTION

Cephalopods develop highly complex jaw apparatuses, consisting of a radula, together with an upper and a lower element – the beaks or mandibles. These organic, horny hard structures are situated within the buccal mass in the proximal portion of the digestive system, reflecting various specialised modes of feeding (NIXON, 1988; TANABE & FUKUDA, 1999). The presence of a well-developed buccal mass in extant cephalopods is closely related to their predatory habits as active carnivores. Their diets include fish, crustaceans, molluscs and various other types of invertebrates (NIXON, 1988). The feeding and dietary habits of extinct cephalopods, however, are difficult to prove except under quite exceptional conditions of fossilisation. The prey identified in the crop or stomach of fossil cephalopods includes the remains of small fish (fish remains are known from fossil teuthids), small decapod crustaceans, ostracods, inoceramid bivalves, foraminifera, jaws of small ammonoids as well as fragmented arms and calices of stalkless crinoids.

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Additional to the horny beaks, the living *Nautilus* secretes two calcified deposits on the anterior tips of the upper and lower jaw, termed the rhyncholite (upper jaw) and the conchorhynch (lower jaw) (SAUNDERS et al., 1978; TANABE & FUKUDA, 1987; LOWENSTAM & al., 1984; DOGUZHAeva & MUTVEI, 1992). Both rhyncholites and conchorhynchs range from Middle Triassic to Recent (SAUNDERS et al., 1978). The stratigraphic range, in situ finds, morphological analogies between fossil rhyncholites and *Nautilus*-jaws and the different shape of ammonoid and coleoid mandibles indicate that rhyncholiths and conchorhynchs belong exclusively to the Nautilaceae (RIEGRAF & SCHMITT-RIEGRAF, 1995). The *Nautilus*-rhyncholite corresponds to arrow-shaped rhynchoteuthids in ammonites, which range from the Pliensbachian to the Maastrichtian.

In the present paper, the authors follow the terminology proposed by RIEGRAF & SCHMITT-RIEGRAF (1995), who called for a restriction in the usage of the term rhynchoteuthids to ammonite-jaws based on the clearly different origin and nature of rhyncholites and rhynchoteuthids. Hence the term rhyncholite should only be used for nautilid beaks.

Nevertheless, the sharp, thick rhynchoteuthids probably had an analogous function for biting and cutting up food, as does the rhyncholites in modern *Nautilus*. The ventral surface and the upper anterior surface are interpreted as emerging from the soft tissue of the rhynchoteuthid-bearing cephalopod, whilst the upper posterior surface was anchored within the soft tissue of the animal (see also GASIOROWSKI, 1969). As in Recent cephalopods, the upper jaw was probably overlapped by the rarely preserved, mainly horny lower jaw, termed anaptychus (cf. RIEGRAF & SCHMITT-RIEGRAF, 1995: pl. 20, fig. 4).

Since only a very few fossil beaks can be related to their specific ammonite producers, the use of parataxonomic form genera such as *Rhynchoteuthis* D'ORBIGNY, 1847 is both practical and necessary for classifying isolated cephalopod jaws.

Rhynchoteuthids are often overlooked because of their small size (range: 0.2 mm–50 mm), smooth surface with almost no ornamentation, and a colour hardly distinguishable from the rock matrix. In thin-sections they are rarely recognized due to the fact that their microstructure resembles that of oyster shells (SEPTFONTAINE, 1970).

Since the early 19<sup>th</sup> century, the cephalopod-nature of the calcitic and chitinous rhyncholites, rhynchoteuthids, anaptychi, aptychi, or conchorhynchi was accepted by most paleontologists. Nonetheless, the derivation of these remained from distinct groups of fossil or Recent cephalopods was hampered by misinterpretation, prejudice or simply by missing biological information. In situ findings of aptychi in ammonites on the one hand and the strong similarity of rhyncholites with calcified parts of nautilid beaks on the other hand led to an early understanding of these fossils. In contrast, the discussion on the origin of rhynchoteuthids remained controversial until the late 20<sup>th</sup> century. The amalgamation of rhyncholites (Triassic–Recent) with rhynchoteuthids (Jurassic–Cretaceous) caused misinterpretations of the stratigraphical range of the hardpart-producing cephalopods. This misunderstanding even resulted in the conclusion that the beaks derive from an unknown cephalopod family.

Today, the ammonite-nature of rhynchoteuthids is accepted by modern workers nearly unequivocally. The state-of-the-art in cephalopod jaw knowledge, with special emphasis on rhynchoteuthids was critically summarised by RIEGRAF & SCHMITT-RIEGRAF (1995), whose considerations are adopted in the present study. Thus, the rhynchoteuthids s.s. can clearly be assigned the Neoammonoidea. Based on their stratigraphic

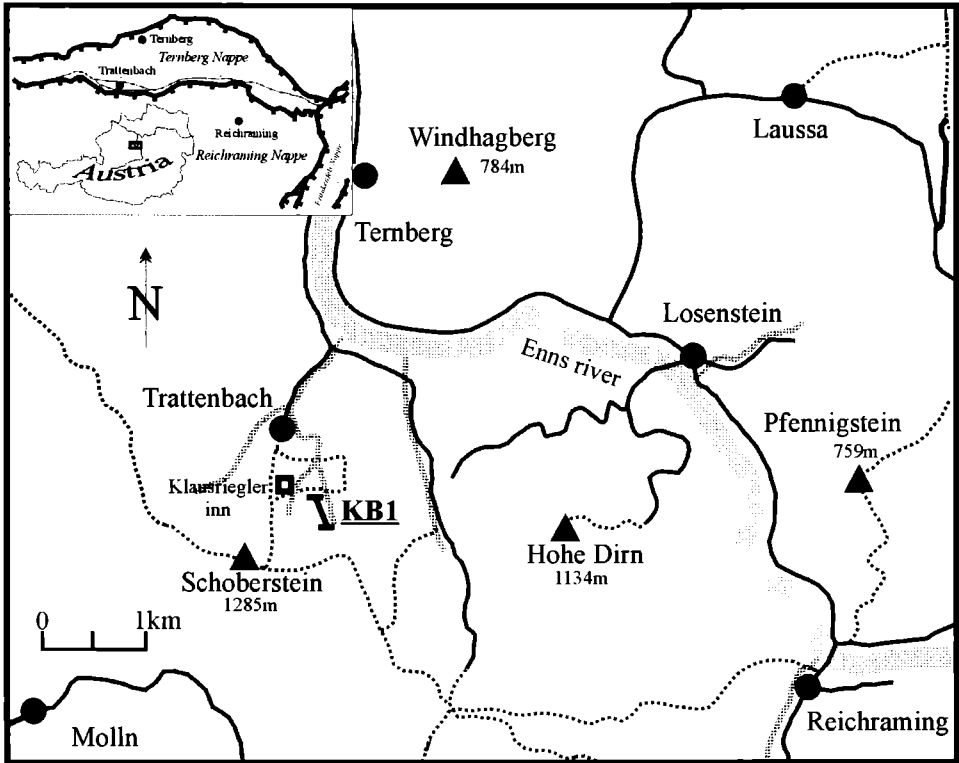


Fig. 1: Position of the investigated section KB1 along a stream outcrop. The map in the left upper corner shows the geological setting and the geographic position within this region (e.g. Ternberg Nappe, Reichraming Nappe).

and paleogeographic occurrence, most rhynchoteuthids derive apparently from lycoceratids or phylloceratids. Additionally, rhynchoteuthids are known from heteromorph ammonites (OOSTER, 1863). The remnants represent the calcified beaks of the chitinous upper jaws of these ammonites. The separation from the somewhat similar rhyncholiths of nautilids (and partly of ammonites) is based on the deep median furrow on their shaft. Corresponding to the jaws of modern coleoids, the rhynchoteuthids are separated into hood, wings and shaft. The species-level identification of the here-described *Rhynchoteuthis gibber* is based mainly on the prominent crest on the ventral side.

The rhynchoteuthids are almost completely restricted to the Tethyan Realm; they are distributed between paleolatitudes of 10°–25°N during the Jurassic, and between 10°–35°N and around 40°S during the Cretaceous (RIEGRAF & SCHMITT-RIEGRAF, 1987). The distribution patterns are similar to those of Tethyan ammonites, belemnites (STEVENS, 1973) and planktonic foraminifera (RIEGRAF & SCHMITT-RIEGRAF, 1987).

## 2. STUDY AREA

The rhynchoteuthids derive from Valanginian beds exposed along a ravine (KB1 A) near Ternberg (grid references referred to are from the topographic map of Austria, scale 1:50 000, sheet no. 69 Großraming). The investigated section lies 7 km west of Losenstein and 1 km south of Kienberg in the Ternberg Nappe (Upper Austria) (Fig. 1) – GPS data: N 47°54'33"; E 14°35'57". For detailed descriptions of the investigated outcrops see LUKENEDER (1997, 1998, 1999).

## 3. LITHOLOGY AND FOSSIL CONTENT

The section is positioned within the Losenstein Syncline and represents the basal part of the Lower Cretaceous Schrambach Formation (= "Schrambacher Kalk", LILL von LILIENBACH, 1830), which is overlain in the studied area by the mid-Cretaceous Tannheim and Losenstein Formations. Natural exposures of Lower Cretaceous strata are generally rare due to the steep topography. The local outcrops are therefore usually short-lived road-cuts or, as in our case, a steep ravine.

The Upper Valanginian beds of the Schrambach Formation at section KB1 consist of light-grey, bioturbated, marly limestones intercalating with dark grey marlstones. The investigated rhynchoteuthids are enriched in the marlstone layers between the limestone beds just a few cm to dm above the underlying Steinmühl Formation (Fig. 2).

The *Rhynchoteuthis*-bearing layers yielded an extraordinarily rich and diverse invertebrate fauna, consisting of radiolarians, foraminifera (*Lenticulina*, *Spirillina*, *Patellina*,

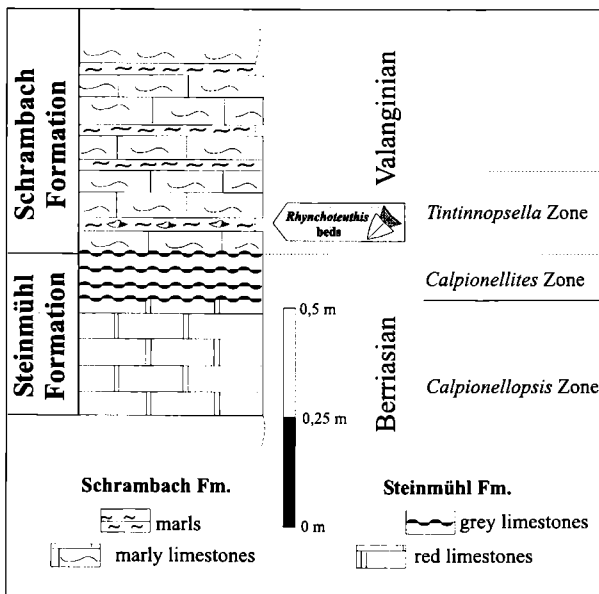


Fig. 2: Schematic biostratigraphical and lithological section KB1 A, exhibiting the *Rhynchoteuthis gibber*-bearing beds.

*Favusella*, etc.), ophiurids, echinoids, phyllocrinids, bryozoans, brachiopods (*Pygope catulloi* PICTET), ostracods, serpulids, bivalves (inoceramids), belemnites, ammonites and aptychi. The very abundant but generally poorly preserved cephalopods are:

*Olcostephanus (Olcostephanus) guebhardi* (KILIAN)  
*Neocomites (Neocomites) neocomiensis* (D'ORBIGNY)  
*Neocomites (Teschinites) neocomiensiformis* (UHLIG)  
*Bochianites neocomiensis* (D'ORBIGNY)  
*Bochianites oosteri* (SARASIN & SCHÖNDLMAYR)  
*Neohoploceras* sp.  
*Rodighieroites* sp.  
*Phylloceras* sp.  
*Phylloceras thetys* (D'ORBIGNY)  
*Lytoceras subfimbriatum* (D'ORBIGNY)  
*Lytoceras* sp.  
*Leptotetragonites honnoratianus* (D'ORBIGNY)  
*Protetragonites quadrisulcatus* (D'ORBIGNY)  
*Pseudobelus bipartitus* (DE BLAINVILLE)  
*Lamellaptychus* cf. *retroflexus* (TRAUTH)  
*Lamellaptychus* cf. *symphysocostatus* (TRAUTH)

Moreover, rare vertebrate remains such as indeterminable fish debris, scales, teeth and one tooth of the shark *Sphenodus* sp. are recorded. Amongst the trace fossils, *Zoophycos* and *Chondrites* are the most abundant. No size sorting by turbidity currents or transportation was observed within the benthic fauna, indicating a more or less autochthonous occurrence of most of the fauna.

#### 4. MATERIAL AND METHODS

About 26 calcified upper jaw elements of *Rhynchoteuthis gibber* (TILL) were found in residues from a microfossil sample of the Upper Valanginian of Upper Austria (Fig 3). About 300 g of marls from a single sample of 0.25 m<sup>2</sup> within a layer of dark-grey calcareous marls (Fig. 4), were alloyed with H<sub>2</sub>O<sub>2</sub> and washed through 500 µm, 250 µm, 125 µm and 63 µm mesh sieves. The rhynchoteuthids were found in medium and coarse fractions and range in size from 0.38 mm up to a maximum of 3.035 mm.

This rather small sample yielded 26 rhynchoteuthids, along with numerous radiolarians, ostracods, foraminiferans, and echinoderm fragments. The rhynchoteuthids were found in quite different stages of preservation; in some cases the shaft is partly dissolved (diagenetical dissolution), the hood is broken off and some have been crushed through sedimentary compaction. The horny portions of the upper and lower jaws have been completely lost in the examined material.

The material examined is deposited in the paleontological collection of the Natural History Museum, Vienna, Austria.

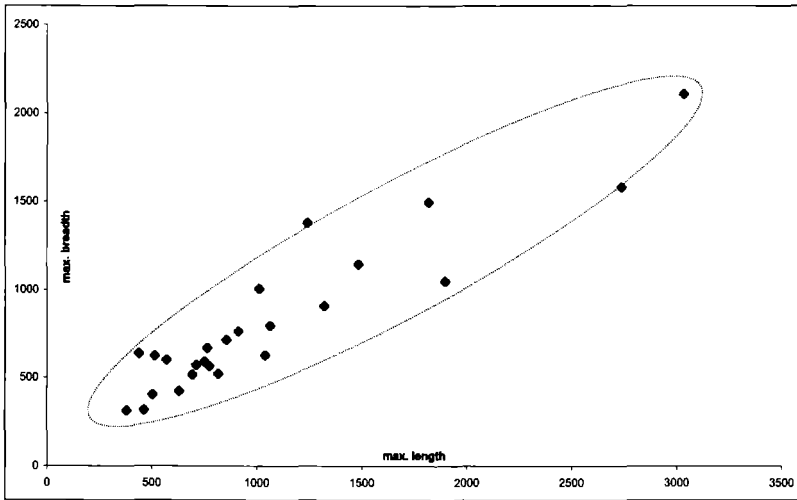
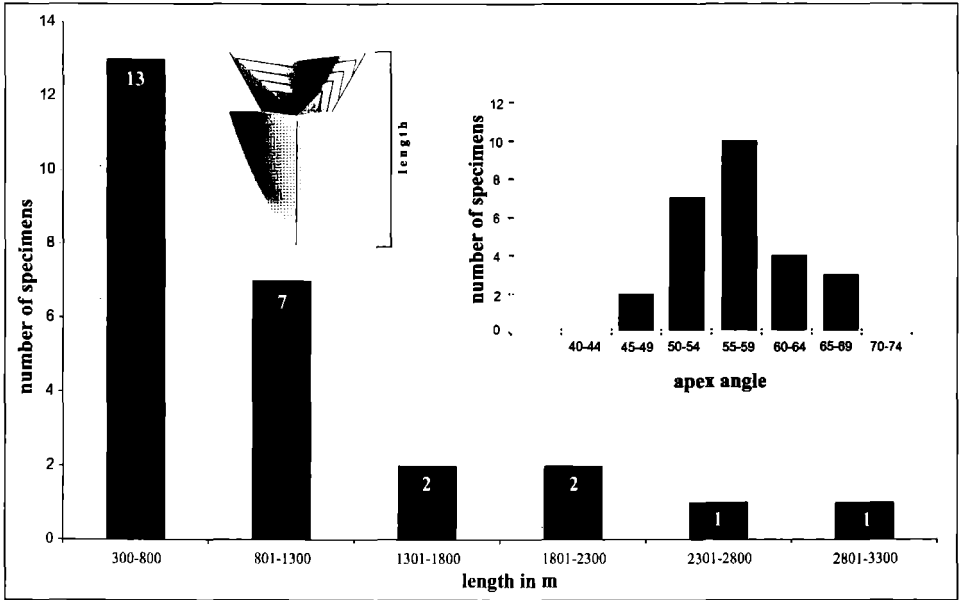


Fig. 3: Size distribution of 26 selected upper jaws of *Rhynchoteuthis gibber* TILL from the Upper Valanginian of Upper Austria (all specimens from section KB1).

## 5. SYSTEMATIC DESCRIPTION

Subclass Ammonoidea von ZITTEL, 1884

Order Ammonitida

Suborder incertae sedis

Genus: *Rhynchoteuthis* D'ORBIGNY, 1847

### *Rhynchoteuthis gibber* (TILL, 1907)

(Pls. 1–3)

- 1907 *Hadrocheilus gibber* n. sp. – TILL, p. 590, pl. 12, fig. 14a–c.  
1907 *Hadrocheilus gibberoides* n.sp. – TILL, p. 599, pl.12, fig. 19a–c.  
1910 *Hadrocheilus* cf. *gibberiformis* – TILL, p. 588, pl. 19, fig. 8a–c.  
1969 *Hadrocheilus gibber* TILL – GASIOROWSKI, p. 711, pl.116, figs. 1–3.  
1971 *Hadrocheilus* (*Dentatobecus*) cf. *gibber* TILL – HUCKRIEDE, p. 140, pl. 1, figs. 26–27.  
1972 *Hadrocheilus* (*Dentatobecus*) cf. *gibberoides* TILL – GEYSSANT & GEYER, text-fig.3a–b; pl. 23, fig. 1a–c, 2a–c.  
1975 *Rhynchoteuthis* (*Rhynchoteuthis*) *gibber* (TILL) – DIENI, p. 52, pl. 63, figs. 10–13.  
1976 *Hadrocheilus* (*Dentatobecus*) *gibber* TILL – MANDOV, p. 25, pl. 1, figs. 1a–b.  
1989 *Rhynchoteuthis gibber* (TILL) – RIEGRAF & LUTERBACHER, p. 1154, figs. 36–40 and figs. 40–42.  
1995 *Rhynchoteuthis gibber* (TILL) – RIEGRAF & SCHMITT-RIEGRAF, p. 85, pl. 27, figs. 1–9, pl. 28, figs. 1–6, pl. 29, figs. 1–5, 7–9, (cum syn.).  
1998 *Rhynchoteuthis gibber* (TILL) – RIEGRAF & SCHMITT-RIEGRAF, p. 516 (cum syn.).

**Overall morphology:** The terminology of the calcified upper jaw element is shown in Figure 5. Its length varies between 0.38 mm and 3.035 mm. The specimens are bilaterally symmetrical, the plane of symmetry being antero-posterior and dorso-ventral. On the dorsal side, the smooth hood and the wings enclose an angle of 50°–73°. The relatively wide range is due to both different stages of preservation and natural variation. The wings cover the largest part of the shaft and the median furrow. All well-preserved specimens can be identified as *Rhynchoteuthis gibber* (TILL), a species with broad, stout hood and shaft, a deep and wide median furrow of the shaft, and a prominent crest on the anterior ventral part. Some of the corroded specimens cannot be definitively assigned to any distinct species. However, the beaks fully correspond in size and shape to those of *Rhynchoteuthis gibber* and are therefore interpreted as belonging to a monospecific rhynchoteuthid assemblage. All the remaining characters agree best with *Rhynchoteuthis gibber*.

**Ventral surface:** Elevated above the edges, forming a prominent ridge-like dome, except near the posterior edge, where it is almost flat and hardly emerges above the level of the edges. The elongate and distinct median ridge reaches from the apex to the end of the shaft. The arcs cut very deeply into the ventral side.

**Hood surface:** This strongly convex anterior part of the jaw is usually poorly preserved. Originally smooth, the surface of corroded specimens displays strong growth lines parallel to the anterior margins.

**Shaft surface:** Distinct yet rounded lateral ridges, the shallow median area is concave. In some cases, a median furrow appears to divide the shaft into two symmetrical pieces. The posterior edge seems to be straight when not dissolved.

**Geological and geographical distribution:** Bajocian (?Aalenian) to Aptian from Spain

(Mallorca), Great Britain (Farren, England), Switzerland (Ct. Bern; Fribourg), France (Provence, Ardèche), Italy (Piemont, Sicily), Austria (Achtal, northern Tyrol, Salzburg), Poland (Lower Silesia, Carpathians), Albania, former USSR (Azerbaijan, Caucasus), North Atlantic Ocean (Deep Sea Drilling Project).

## 6. BIOSTRATIGRAPHY

In the area around Ternberg, the *Rhynchoteuthis*-bearing bed was dated by LUKENEDER (1999) as Late Valanginian (stratigraphy according to RAWSON et al., 1999 and HOEDE-MAEKER & RAWSON, 2000). New data allow an even higher biostratigraphic resolution. The biostratigraphically indicative cephalopods clearly indicate the *verrucosum* Zone of the lower Upper Valanginian. These are: *Olcostephanus (Olcostephanus) guebhardi* morph. type *querolensis* (BULOT), *Neocomites (Neocomites) teschenensis* (UHLIG), *Neocomites (Neocomites) neocomiensis* (D'ORBIGNY), *Neocomites (Teschenites) neocomiensiformis* (UHLIG), *Bochianites neocomiensis* (D'ORBIGNY), *Neohoplloceras* sp., *Rodighierites* sp., *Lamellaptychus* cf. *retroflexus* (TRAUTH), *Lamellaptychus* cf. *symphysocostatus* (TRAUTH).

## 7. DISCUSSION

### 7.1. Paleoenvironment

The macrofauna of the rhynchoteuthid-bearing beds is predominated by composite-moulds of ammonites, rare belemnites and scattered echinoderms. The latter are represented by regular and irregular echinids and by numerous calices of the crinoid *Phyllocrinus*. The first impression of a rather low-diversity benthic fauna changes radically upon examination of the microfauna. The rhynchoteuthid-sample yielded an unexpected well-preserved and rich microfauna, consisting of numerous elements of ophiurids. A large number of ostracods further contributes to the autochthonous fauna, whilst radiolarians and planktonic foraminifera points to open marine conditions. Ammonites with encrusting foraminifera and bryozoans on their inner shell surface indicate rather quiet conditions and low sedimentation rates, which allowed epifauna to settle secondary hardgrounds. These encrustations, as well as an echinoid test with attached spines, indicate an environment that suffered little disturbance by currents or wave action.

Thus, regional paleobiogeography and the analysis of the fauna support the interpretation of a soft to level bottom paleoenvironment with an ophiurid-dominated benthic fauna of the upper slope or deeper shelf. Based on the paleobiogeographic position of the studied section an influence by turbidity currents can be definitely excluded. Further remarks: 1) The Valanginian is always *Rhynchoteuthis*-dominated, in contrast to the Oxfordian. Maybe the *Rhynchoteuthis*-bearing ammonite inhabited cooler waters than the ammonites which bear *Leptocheilus* and *Palaeoteuthis*. 2) It is noteworthy that most well-known Valanginian rhynchoteuthid occurrences often show soft-part preservation (SE-France; W-Switzerland, OOSTER 1863; Upper Silesia, TILL, 1906). This points to oxygen-poor conditions due a highstand of the sea-level, producing a better rhynchoteuthid preservation than other stages. These exceptional features could not be recog-



nized at the investigated site, although there was a world-wide transgressive phase during the Upper Valanginian.

### 7.2. Hypothetical assignment of *Rhynchoteuthis gibber* (TILL)

Jaw apparatuses of ammonites are documented at the section not only by *Rhynchoteuthis gibber*, but also by numerous aptychi assigned to *Lamellaptychus* cf. *retroflexus* and *Lamellaptychus* cf. *symphysocostatus*. Additionally, the bed revealed a single, well-preserved anaptychus of 15 mm maximum diameter. Anaptychi are considered by many modern authors to represent lower jaws of some ammonitina such as desmoceratids (TANABE, 1983; TANABE & LANDMAN, in press) or phylloceratids. Actually, the lower jaws of Cretaceous lycoceratids and phylloceratids possess a calcified element, thus they are not anaptychi but rhynchaptychi. Whilst the discussed rhynchoteuthids are too small to fit to

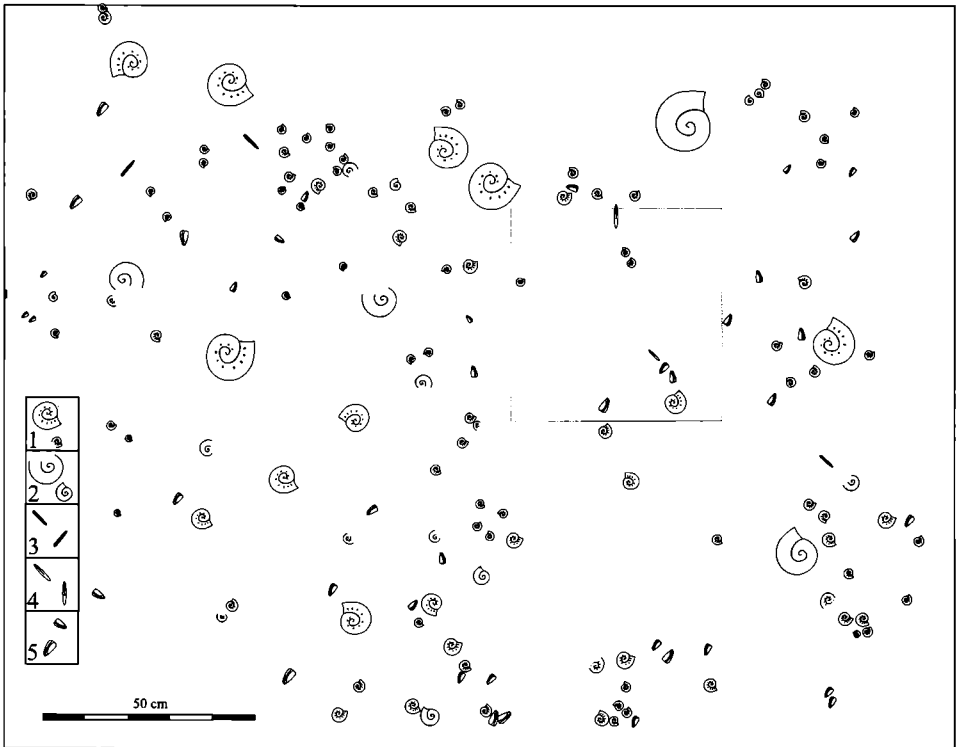


Fig. 4: Excavation area of 4.6 m<sup>2</sup> (steeply dipping 050/75°) within the rhynchoteuthid-bearing bed at section KB1. The small square indicates the position of the rhynchoteuthid-sample area (0.25 m<sup>2</sup>). Drawings show size and position of complete and fragmented specimens of *Olcostephanus* (O.) *guebhardi* (1), *Leptotetragonites honnoratianus* (2), *Bochianites neocomiensis* (3), *Pseudobelus bipartitus* (4) and lamellaptychi (5). All described rhynchoteuthids originate from this area.

any of the (documented!) co-occurring cephalopods, the anptychus would fit fairly well to the common lytoceratid *Leptotetragonites honnoratianus*.

The problem of isolated jaw elements and the corresponding cephalopod shells has been solved for several cephalopods such as the Upper Cretaceous ammonites *Tetragonites glabrus*, *Gaudryceras tenuiliratum*, *Gaudryceras denseplicatum* and *Neophylloceras subramosum* (TANABE et al., 1980; KANIE, 1982). The parataxon *Rhynchoteuthis*, however, is usually related to lytoceratids or phylloceratids (RIEGRAF & SCHMITT-RIEGRAF, 1995). In addition, OOSTER (1863) described an in situ *Rhynchoteuthis* in the heteromorph ammonite *Crioceras*.

In our search for a hypothetical rhynchoteuthid-bearer, we studied the accompanying ammonites of the Upper Valanginian beds in detail. The key question was whether the rhynchoteuthids correspond with one of the co-occurring cephalopods in size and number. Despite the poor exposure conditions, an area of 4.6 m<sup>2</sup> within the rhynchoteuthid-bearing layer was excavated. The macrofauna of this area was analysed and all cephalopod taxa were counted. Among the cephalopod-dominated macrofauna *Olcostephanus (Olcostephanus) guebhardi* is represented by 102 specimens, whereas *Leptotetragonites honnoratianus* (16 specimens), *Bochianites neocomiensis* (3 specimens) and *Pseudobelus bipartitus* (2 specimens) are distinctly less abundant. The assemblage also bears 40 specimens of lamellaptychi (e.g. *Lamellaptychus cf. retroflexus* and *Lamellaptychus cf. symphysocostatus*).

These numbers strongly contrast to the 26 specimens of *Rhynchoteuthis gibber* within only 0.25 m<sup>2</sup>, allowing a cautious projection of at least 470 rhynchoteuthids within the total 4.6 m<sup>2</sup>. Obviously, none of the counted cephalopods corresponds in number to this enormous amount of beaks. *Olcostephanus guebhardi* appears in higher numbers, but the large shells can hardly be correlated with the tiny jaw elements. Even if the diameter-range of the olcostephanids is taken into account (between 0.6 mm and 14 cm), this variation is not reflected in the size-distribution of the rhynchoteuthids.

Unfortunately, nothing is known about the ratio between jaw-size and shell-size of *Rhynchoteuthis*. Only RIEGRAF (1995) and RIEGRAF & SCHMITT-RIEGRAF (1995) assumed *Rhynchoteuthis minima* to belong to the lytoceratid *Gaudryceras obscurum* due to the paleogeographic and stratigraphic co-occurrence of both endemic taxa. This would mean a correlation of a 6–10 mm long *Rhynchoteuthis* with a *Gaudryceras* of a maximum diameter of about 80 mm. A very rough estimation would thus indicate rather small ammonites of 2–4 cm size for the jaws described in the present paper. As nothing is known about *Rhynchoteuthis* in situ-finds, almost nothing is known about the *Rhynchoteuthis*-size to ammonite-shell ratio.

The stratigraphic range of *Rhynchoteuthis gibber* spans an interval from the Aalenian up to the Aptian. It has to be noted that *Rhynchoteuthis gibber* is a collective name belonging at least to several ammonite genera, and could therefore belong to any of the following mentioned genera. The genus *Olcostephanus* ranges from the Lower Valanginian to the Lower Hauterivian. Correspondingly, the ranges of *Leptotetragonites* (?Lower Berriasian – ?Upper Hauterivian), *Bochianites* (Lower Tithonian – Barremian) do not correspond with the occurrence of *Rhynchoteuthis gibber*. It is therefore impossible to correlate the described *Rhynchoteuthis gibber* directly with any of the documented cephalopods without severe reservation.

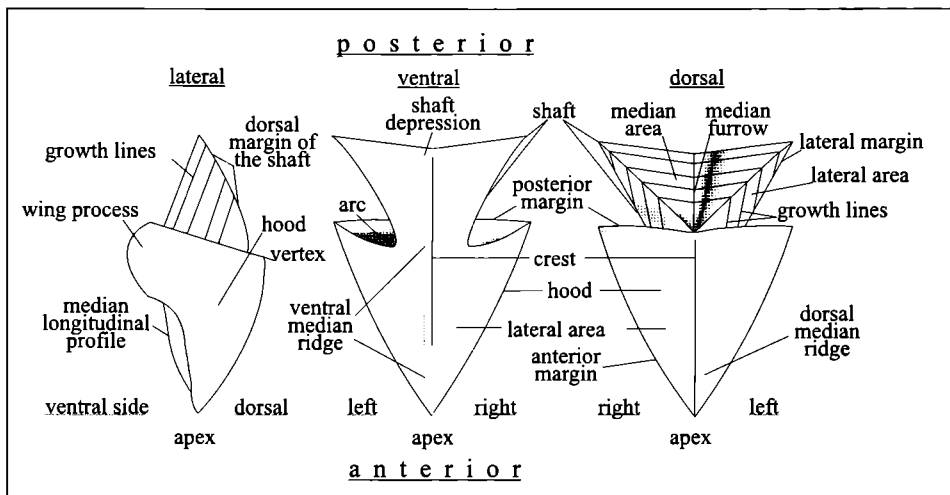


Fig. 5: Terminology of a rhynchoteuthid upper jaw (modified after DIENI, 1975 and RIEGRAF & SCHMITT-RIEGRAF, 1987).

### 7.3. Origin of rhynchoteuthid accumulations

Several comparable accumulations of rhynchoteuthids are quoted in the literature. These are usually interpreted as resulting from gravitational sorting, typically related to turbidity currents. RIEGRAF (1995), for example, describes large numbers of rhynchoteuthids concentrated in pelagic turbiditic beds of the Campanian of Westphalia (NW Germany).

Additionally, condensation has been stressed as a cause for the unusual concentration of rhynchoteuthids in sediments. On the other hand, biological/environmental causes have also been mentioned. Accordingly, the accumulations are interpreted to have been derived from faeces of cephalopod-feeding vertebrates, as indicating anoxic conditions, or as cephalopod breeding-sites.

As discussed above, significant transport by turbidity currents, or by wave action can be excluded, based on sedimentological and paleontological data. Similarly, black-shale conditions can be excluded. An accumulation by predation cannot be based on any morphological data, since the typical dissolution patterns and partially soft part preservation described by RIEGRAF & SCHMITT-RIEGRAF (1995) for rhynchoteuthids which probably passed through the digestive tract of vertebrates are completely missing. The "breeding-station-theory" (GASIOROWSKI, 1973a) should be rejected, because this theory does not explain the absence of shells in beds where shelly preservation would be possible.

Thus, the *Rhynchoteuthis*-bearing cephalopod probably did not live close to the calm seabottom as would be expected for benthic cephalopods. Otherwise its shells would be represented in the fauna in some abundance. It is also noteworthy that the dead ammonite animal could have drifted, after filling with gas during decomposition and decay, and then the rhyncholites could have sunk down to the sea ground. Since even very small ammonite shells are preserved, the obvious absence of the *Rhynchoteuthis*-

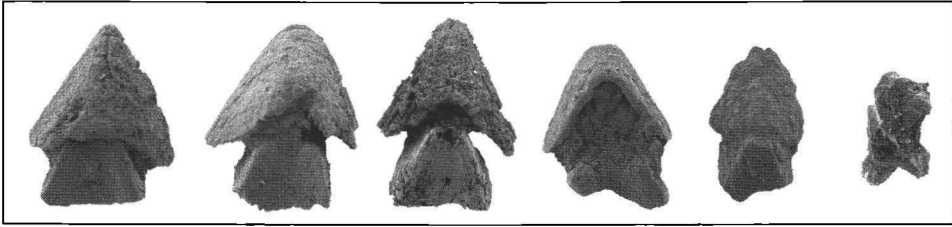


Fig. 6: Various preservational stages of *Rhynchoteuthis gibber* TILL caused by pre-sedimentary and diagenetic processes.

related shells cannot be explained by preservational effects. Therefore, the *Rhynchoteuthis gibber*-bearing ammonite probably inhabited upper, near-surface waters. The shells of the dead animal would then be exposed to surface drifts – being thus missing in the documented bottom thanatocoenosis – whilst the decaying soft-tissue and the beaks sank to the bottom, producing a major bias in the fossil record. The generally poor preservation of all specimens is probably not only related to postsedimentary diagenetic processes, but may also represent various stages of presedimentary corrosion (Fig. 6). As discussed above, abrasion during longer transport is unlikely. In contrast, as documented by encrustations on ammonites, the shells probably lay on the seabottom for a lengthier period without becoming covered by sediment. Therefore, the large number of *Rhynchoteuthis gibber* is interpreted by the authors to result from accumulation over a long time.

## 8. RESULTS

1. *Rhynchoteuthis gibber* (TILL, 1907), is documented for the first time from the Upper Valanginian of the Losenstein Syncline in Upper Austria.
2. The associated cephalopod fauna indicates an Upper Valanginian (*verrucosum* Zone) age of the *Rhynchoteuthis gibber*-bearing beds.
3. About 26 calcified upper jaw elements between 0.38 and 3.035 mm in length were investigated; no sorting due to sedimentological or biological effects can be observed.
4. A concentration by redeposition or turbidity currents can be clearly ruled out based on the autochthonous character of the benthic fauna.
5. The cephalopod mandibles were deposited within a phyllocrinid-ophiurid association, indicating offshore conditions in deeper water (deeper shelf).
6. The present state of knowledge does not allow to assign *Rhynchoteuthis gibber* to any known ammonite species or group.
7. The *Rhynchoteuthis gibber*-bearing ammonite probably inhabited upper, near-surface water masses. The mass-occurrence of the beaks is interpreted as a long-term accumulation out of the water column.
8. The separation of the shells from the beaks is interpreted – though highly speculative – as being related to drifts.

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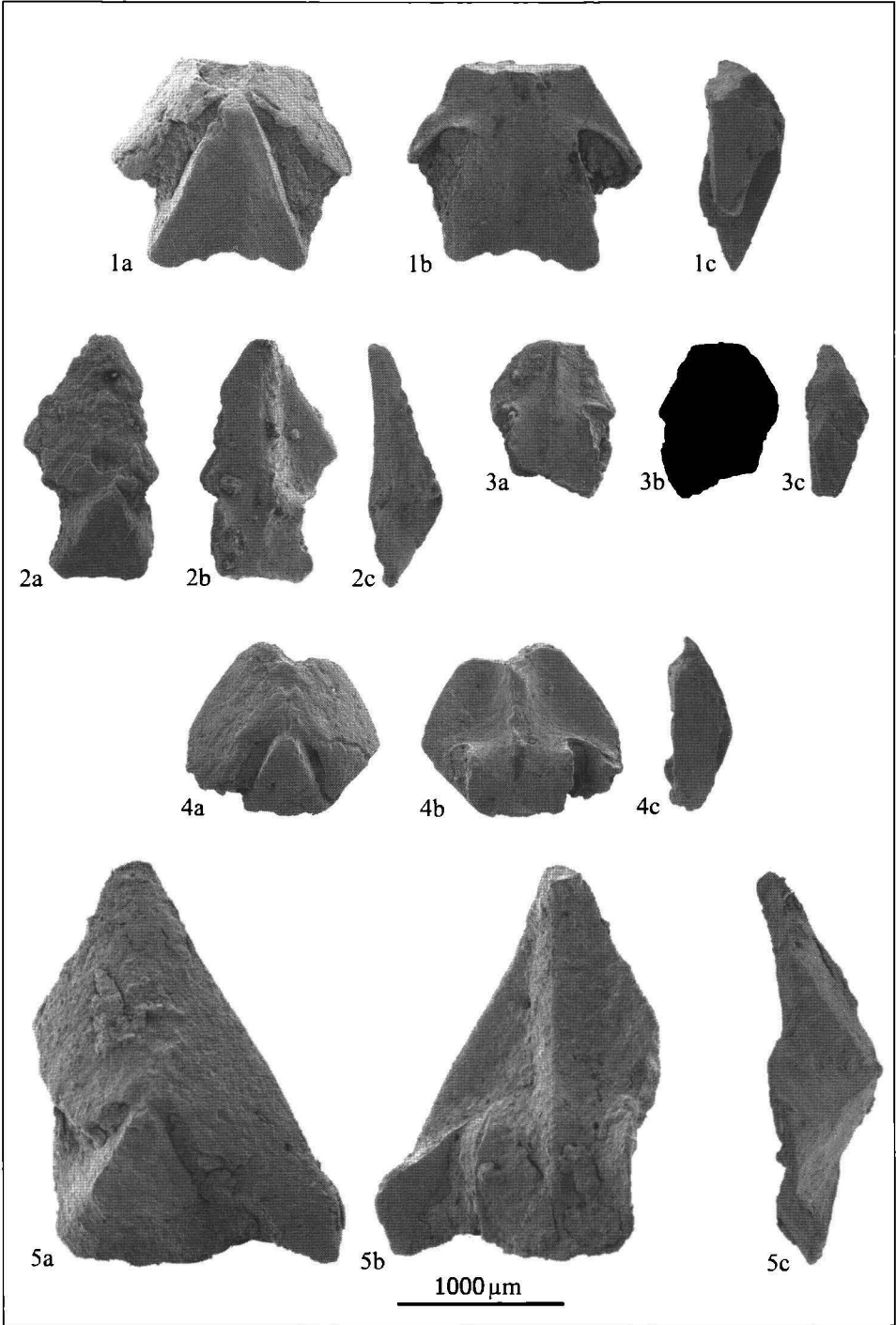
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## Plate 1

*Rhynchoteuthis gibber* TILL. Upper jaws in dorsal (a), ventral (b), and lateral (c) views. Upper Valanginian (*verrucosum*- Zone), Schrambach Formation, section KB1 (near Ternberg).

Figs. 1–10.

Scale 1000 µm

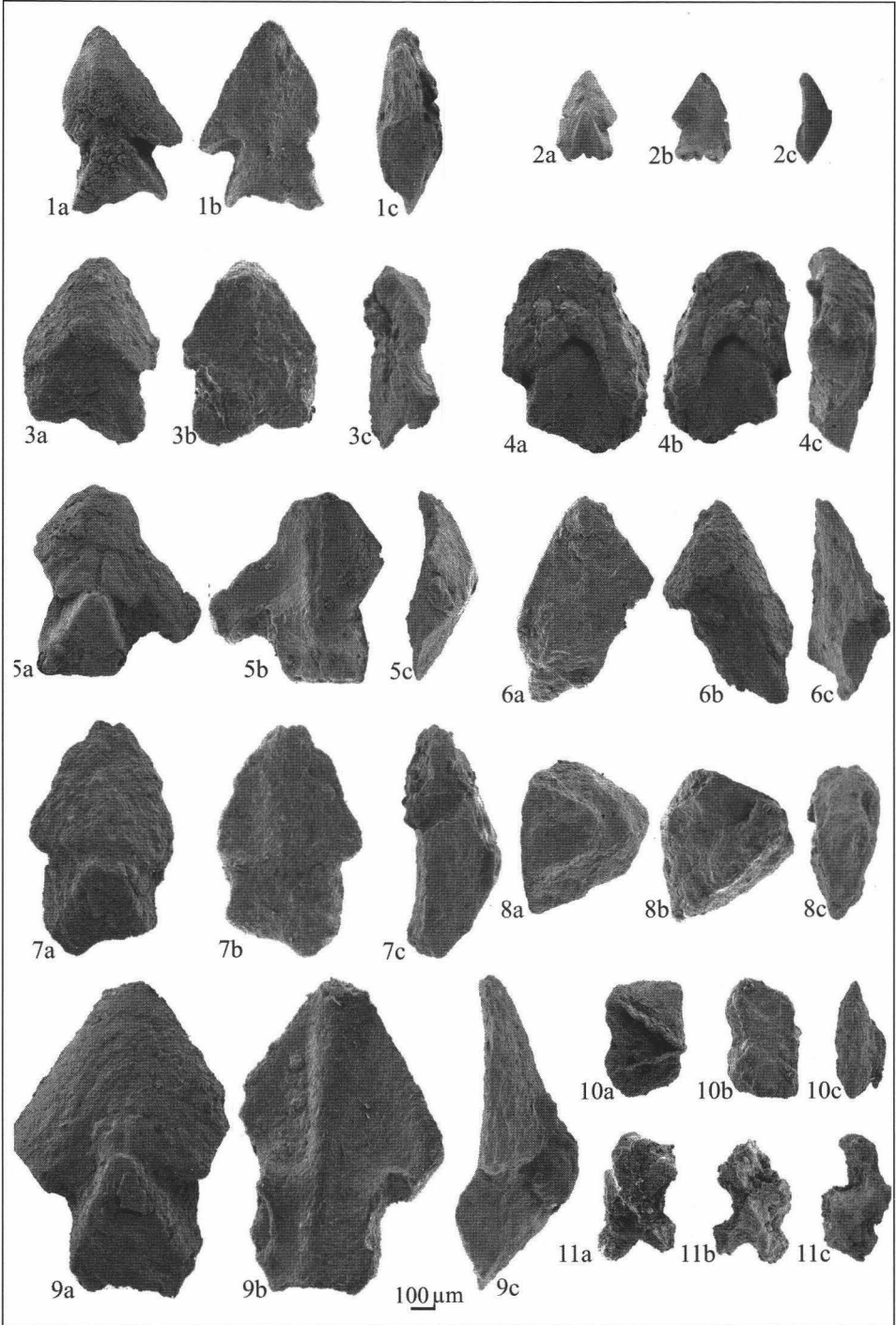


**Plate 2**

*Rhynchoteuthis gibber* TILL. Upper jaws in dorsal (a), ventral (b), and lateral (c) views. Upper Valanginian (*verrucosum*- Zone), Schrambach Formation, section KB1 (near Ternberg). Figs. 1–11.  
Scale 100  $\mu\text{m}$

200





### Plate 3

*Rhynchoteuthis gibber* TILL. Upper jaws in dorsal (a), ventral (b), and lateral (c) views. Upper Valanginian (*verrucosum*- Zone), Schrambach Formation, section KB1 (near Ternberg). Figs. 1–5.

Scale 100  $\mu\text{m}$

The scanning electron micrographs were taken out with a Cambridge stereoscan at the Institute of Paleontology, University of Vienna. The rhynchoteuthids were coated with gold. All material examined is deposited in the paleontological collections of the Natural History Museum, Vienna, Austria.

