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Barremian rhyncholites (Lower Cretaceous Ammonoidea: calcified upper jaws) from the Serre de Bleyton (Département Drôme, SE France)

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(With 2 figures, 2 plates and 1 table)

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Abstract

Seven calcified upper jaw tips of *Rhynchoteuthis astieriana* d'Orbigny and *Palaeoteuthis infira* (Shimansky) from the Serre de Bleyton section (Dépt. Drôme, SE France) were redeposited from an outer shelf into an upper slope (upper bathyal) environment embedded in a highly fossiliferous Barremian bioclastic limestone. They represent a low diverse and poor preserved small Barremian pelagic rhyncholite fauna, also described from a few Tethyan and Alpine localities between Cuba, the Crimea, and the Caucasus. *Rhynchoteuthis* and *Palaeoteuthis* may most probably represent calcified tips of upper jaws of various taxa of Tethyan ammonites, e.g. of the Phylloceratina (*Phylloceras*, *Sowerbyceras*), Lytoceratina (Tetragonitidae), and/or some Ammonitina (*Arnioceras*, *Eleganticeras*, *Hildoceras*, *Aconeceras*). But due to their scarcity, poor preservation, and the allochthonous occurrence, the Serre de Bleyton rhynchoteuthids do not contribute further new knowledge to taxonomy, palaeoecology, stratigraphy or basinal history.

Kurzfassung

Sieben kalkige Oberkieferspitzen – *Rhynchoteuthis astieriana* d'Orbigny und *Palaeoteuthis infira* (Shimansky) aus einem Profil der Serre de Bleyton (Dépt. Drôme, SE-Frankreich) – gelangten vom Schelf durch Umlagerung in ein oberbathyales Milieu des oberen Kontinentalabhangs, in einen äußerst fossilreichen bioklastischen Kalkstein. Solche geringdiversen und mäßig erhaltenen pelagischen Rhyncholithenfaunen des Barremium sind auch von vereinzelten tethyalen und alpinen Fundorten zwischen Kuba, der Krim und dem Kaukasus beschrieben. *Rhynchoteuthis* und *Palaeoteuthis* sind höchstwahrscheinlich kalkige Oberkieferspitzen von verschiedenen Taxa tethyaler Ammoniten, so von Phylloceratina (*Phylloceras*, *Sowerbyceras*), Lytoceratina (Tetragonitidae) und/oder von bestimmten Ammonitina (*Arnioceras*, *Eleganticeras*, *Hildoceras*, *Aconeceras*).

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Darüberhinaus tragen die Rhynchoteuthen der Serre de Bleyton wegen ihrer Seltenheit, mäßigen Erhaltung und des allochthonen Vorkommens nichts Neues zur Taxonomie, Paläoökologie, Stratigraphie oder Beckenentwicklung bei.

Introduction

Fossil rhyncholites s. str. are known at least since 1799 and – as other cephalopod beaks – commonly refered to bird's bills ("becs de perroquet"; "Papageienschnäbel", "*Rhyncholites avirostris*", which means "bird's bill"), but since 1824/1825 also to coleoids as "becs de seiches". Commonly, they are comparatively small and rare which concerns both their abundance and the number of localities where they are to be found. Thus, they are not familiar enough to most invertebrate palaeontologists and fossil collectors. For this reason some of their most important characters have to be summarized or updated as follows below (for terminology see Fig. 1).

Rhyncholites are arrow-shaped strange Anisian to Recent macro- to microfossils (jaw tips) consisting of calcite and few organic tissue. Rare, usually larger specimens with a dorsal, undivided shaft are without doubts calcified tips of the upper jaw of fossil (Anisian) to Recent nautilids ("*Nautilus*-Typus" of Till 1906: 101; "Nautilusschnäbel" of Till 1907: 539). The more frequent and smaller specimens ("*Rhynchotheutis*-Typus" of Till 1906: 102; "Nicht-Nautilus-Schnäbel" of Till 1907: 560; rhynchoteuthids) occur from the Pliensbachian to Maastrichtian. In contrast to the nautilid upper jaws they show a broad longitudinal furrow on the dorsal side of the shaft and a longitudinal ridge on the ventral side of the hood. First figured by Guéttard (1799) from the Oxfordian of SE France, their ammonite-derived nature is defintively proven not later than in the monograph of Riegraf & Schmitt-Riegraf (1995) as being calcitic tips of the horny upper and lower beaks. All former speculations on their coleoid nature or an origin from "unknown cephalopods" have to be rejected for reason of being not justified by scientific observations. While this interpretation chiefly based on the type material figured by Till (1906), morphological researches on larger *Rhynchoteuthis*, and conclusions drawn by own stratigraphic field observations, these results were also underlined by observations of Septfontaine (1970: 124, text-fig. 12) and the compilation by Nixon (1998: 24-34).

The ammonite-derived rhyncholites (the so-called rhynchoteuthids) are lacking or rarely to be found outside the Alpine-Tethyan Jurassic and Cretaceous. More popular are the comparatively larger upper jaw tips and lower jaw remains of fossil nautilids since they were first discovered in the Germanic Muschelkalk (Lower and Upper Muschelkalk) of Lorraine, Southern and Northern Germany (Blumenbach 1803: 21, pl. 2, figs 5a-c; Gaillardot, 1824; d'Orbigny 1825). It is no problem to refer these calcitic jaw tips to their recent counterparts, the beaks of the living genera *Nautilus* v. Linné, 1758 and *Allonautilus* Ward & Saunders, 1997.

The present manuscript describes such Tethyan rhyncholites only which do not belong to nautilids, and which were identified as parts of ammonite jaws, the so-called rhyncho-

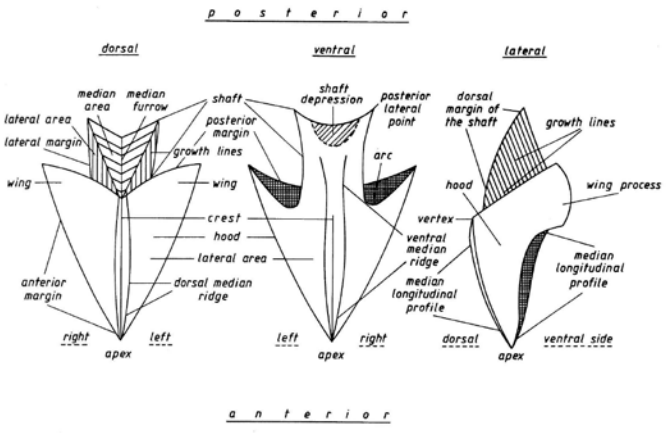

Fig. 1. Terminology of rhyncholites (according to RIEGRAF & SCHMITT-RIEGRAF 1995: Pl. 1).

teuthids. It is the result of a longer cooperation: GERO MOOSLEITNER collected successfully larger amounts (about 12,000 or more) of of Bajocian-Aptian rhyncholites on weathered and washed marlstone surfaces in the expanded and various badlands of the Jurassic and Cretaceous of the Alpine SE France over more than two decades. A small part of this collections of rhyncholites between 0.5 and 30 mm length is published (MOOSLEITNER 1990a, 1990b, 2004, Pliensbachian; 2008, 2009, Bajocian-Callovian; 2000, 2007a: Oxfordian; 1994a, 2004, Tithonian; 1999, 2006, Valanginian; 1990a, 1990b, 1994b, 2001: Aptian; 2002: pl. 25, fig. 1; pl. 27, figs 8-9, 11-12; pl. 31, fig. 1; pl. 32, fig. 8; pl. 39, fig. 6). The first preliminary description of the Barremian fauna of the Serre de Bleyton was presented two years ago in MOOSLEITNER (2007b). This Pliensbachian-Aptian rhyncholite material was largely granted to WOLFGANG RIEGRAF for further scientific research. It subsequently formed the base of the illustrated rhyncholite catalogue of RIEGRAF & SCHMITT-RIEGRAF (1995, supplement 1998). There all known references and taxa of fossil rhyncolites as well as new major aspects of their palaeobiology and stratigraphy are presented.

While GERO MOOSLEITNER collected rhyncholites in Austria and SE France chiefly on the mesofossil scale, WOLFGANG RIEGRAF as a micro- and macropalaeontologist collected and studied several thousands of rhyncholites from the epicontinental Jurassic and Cretaceous of England, Portugal, Switzerland, and Germany as well as in the famous Jurasssic-Cretaceous rhyncholite exposures of the neighbourhood of Castellane (Basses-Alpes, SE France). The material comes from

i) older museum and recent private collections,

ii) sections and exposures (on the mesofossil scale), and

iii) washed residues of microsamples up to several hundred of kilograms, often in larger numbers, from 0.2 to 10 mm in length.

Fortunately, the first author was encouraged by HANSPETER LUTERBACHER (Tübingen University, now Barcelona) in 1987 to revise the late Jurassic rhyncholites from the Deep

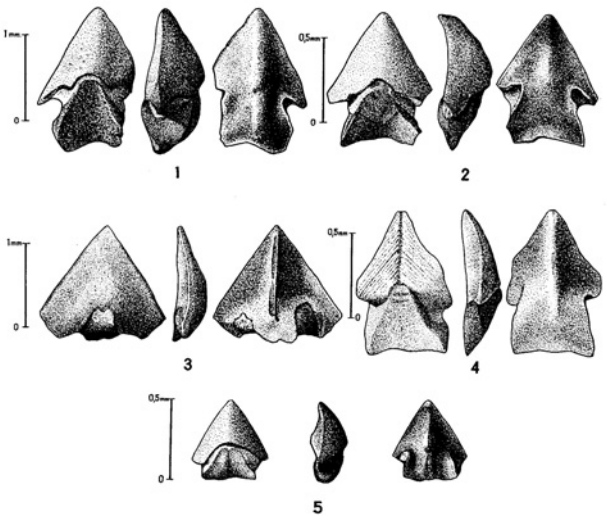

Fig. 2. Barremian rhynchoteuthids from the stratotype at Barrême, SE France (drawings according to SIGAL 1963, but taxonomy is revised herein). 1: *Hadrocheilus* cf. *H. costatus* TILL (= *Rhynchoteuthis astieriana* D'ORBIGNY); 2: *H.* aff. *gibber* TILL (= *Rhynchoteuthis gibber* TILL); 3: *Akidocheilus* cf. *ambiguus* TILL (= *Palaeoteuthis infira* (SHIMANSKY)); 4: *A.*? *sulcatus* TILL; *Leptocheilus* probable aff. *uhligi* TILL (= corroded *Rhynchoteuthis gibber* TILL); 5: *Hadrocheilus* aff. *H. gibber* TILL (= *Rhynchoteuthis gibber* TILL).

Sea Drilling Project (DSDP) Leg 11 boreholes (RIEGRAF & LUTERBACHER 1989) showing their westernmost occurrence offshore the southeastern coast of the USA.

As one of the major results, the first and and last occurrences of *Rhynchoteuthis* were detected, and also the supposed assignment to fossil cephalopods, e.g. the Neoammonoidea. Regarding morphology, chemistry, geographical and stratigraphical occurrences, and palaeobiological observations of the outer shelf to upper bathyal rhynchoteuthids they must be upper jaw remains of Tethyan ammonites of the suborders Phylloceratina, Lytoceratina, Ancyloceratina, and Ammonitina. To underline this, so far no rhyncholites referable to ammonites were found in Triassic deposits (e.g. the Germanic Muschelkalk Formation or the Alpine-Tethyan Anisian-Ladinian).

Episodical and scattered epicontinental occurrences are confined to periods of transgressions (sea-level highstands) which enabled Tethyan immigrants among ammonites to invade shelf areas in the neighbourhood of the western Tethys.

For complete historical background, terminology, stratigraphy, occurrences, publications, and taxonomy, as well as taphonomic and preservational aspects of rhycholites up to 1995 we largely refer to the compilation of RIEGRAF & SCHMITT-RIEGRAF (1995, 1998). Some taxonomical errors, mostly caused by the lack of extremely rare, very old papers

not available before 1995 (Guéttard 1799; Faure-Biguet, 1819), are corrected here. Since then no new results were published on the field of rhyncholite research beneath some scattered descriptions of "new" and well-known rhyncholite species in a handful of short papers (e.g. Komarov 1997, 1998, 1999, 2001a, 2001b, 2001c, 2002, 2003a, 2003b, 2003c, 2004a, 2004b, 2005; Laub 1994; Lukeneder & Harzhauser 2000, 2002). Neither there was a renewed effort to confirm the ammonite-nature of the rhyncholites (except by Nixon 1998), nor scientists were successful to find new rhyncholite fossils which would shed a new light on rhyncholite research.

Rhynchoteuthid material, stratigraphy, and geographical setting

The present paper based on seven small rhyncholite (rhynchoteuthid) specimens only, the result of more than 10 years of collecting and processing larger microsamples from the Serre de Bleyton sections by Gero Moosleitner. Two small *Rhynchoteuthis astieriana* specimens are also present from the Barremian of Tonils (SE France). Nautilid upper or lower jaw tips were not found – due to their scarcity in epicontinental and namely pelagic deposits. The rarity of Barremian rhyncholites contrasts to their frequent occurrences in other Jurassic-Cretaceous stages. Special SE France localities often enable to collect several thousands of rhyncholites within a short time. But Barremian occurrences of rhyncolites are chiefly low diverse, poor in individuals (not as frequent as in the Callovian-Oxfordian and the Valanginian/Hauterivian), and rarely investigated. The number of rhynchoteuthid papers and the number of individuals described therein do not represent their true abundance and geographical distribution at all. This is best exemplified by the monograph of Riegraf & Schmitt-Riegraf (1995) who quoted unexpected large numbers of *Rhynchoteuthis* (up to 70 specimens in a 3 kg sample of a Lower Pliensbachian marlstone of SW Germany and more than 700 specimens in 20 kg Campanian marlstone of NW Germany). They did nothing else than to process larger (1-20 kg) microsamples from hemipelagic to pelagic cephalopod clay- and marlstones.

We, therefore, present the first Barremian rhyncholite fauna from SE France which comes not of an old museum collection and which was collected *in situ* by Gero Moosleitner. The only exception is a preliminary paper of Sigal (1963) who described four rhynchoteuthids from the Barremian stage stratotype, specimens which have exclusively been described outside SE France to date (see below and Fig. 2).

The locality Serre de Bleyton (Commune d'Arnayon) is situated in a height of approx. 1,000 m above sea level in the Barronies (north of the Vocontian Trough of the Dauphiné) between Villepetrix and Remouzat, near the highway D94 between Serres and Nyons, Département Drôme, SE France. From the highly fossiliferous exposure, thus far known not described by geologists, section 1 is not more than 0.5 m long and 0.15 cm high, but contain a highly fossiliferous bioclastic limestone. Its basal turbiditic breccia is formed by size-sorted micro- to mesofossils, and the limestone is embedded in (calcareous) marlstones. It contains huge numbers of larger foraminifers, sponges, corals, gastropods,

bivalves, brachiopods, bryozoans, echinod remains, asterid, ophiuroid, and crinoid ossicles, serpulids, belemnite guards, rhyncholites, as well as remains of crabs and fishes (Moosleitner 2007b), often with species undescribed to date, set free by weathering, and giving reason for the present volume.

The Barremian age is unspecified and exclusively derived from the geological map (Moosleitner, 2007b: 290). The few small, pyritized ammonites found might be redeposited from the Valanginian, as Moosleitner (2007b: 293) quoted, and have been revised by Lukeneder (2010).

The rhyncholites described in the present paper are housed in the collection of the Naturhistorisches Museum Wien (Vienna, Austria) with collection nos. NHMW 2009z0035/0001 to 2009z0035/0007.

Updated research history

Guéttard (1799, pl. 9, fig. 8-11) was the first who figured a rhyncholite without name which might be *Palaeotheutis oxfordiensis* (Till, 1906) from the Oxfordian of SE France. It was later published as *Rhyncolites hirundo* by Faure-Biguet (1819), type species both of *Rhyncolites* Faure-Biguet, 1819 and *Rhombocheilus* Shimansky, 1947. d'Orbigny (1825), following Gaillardot (1824), erroneously named nautilid upper beaks of the Muschelkalk Formation (Ladinian) of Lorraine as *Rhyncholithes hirundo* – and since then the confusion about the rhyncholite taxonomy and the correct spelling of the name (Riegraf & Schmitt-Riegraf 1995: 36-38) arose and continues up to now.

Following a series of 19th century descriptions of scattered ammonoid and nautilid rhyncholites the subsequent papers of Till (1906, 1907, 1909, 1910, 1911) are of major scientific palaeobiological-taxonomic importance, and Till has to be regarded as the founder of scientific rhyncholite taxonomy. Till described and figured a huge crowd of Mesozoic and Tertiary rhyncholites showing a synopsis as base for further research. But unfortunately, most of his rhyncholites came from old European museum collections, often labelled with erroneous or doubtful stratigraphical and geographical data. His problematical heritage are further many unnecessary new names (synonyms) for genera and species, the latter often more a description of individual specimens and their preservational state, than true formal "species". But he (Till 1906) clearly showed the striking difference of "Nautilusschnäbel" (nautilid beaks, *Scaptorhynchus*) and "Nicht-Nautilidenschnäbel" (ammonoid beaks, rhynchoteuthids).

Worth to mention is a paper of Nagao (1931) who established the new term "*Neoanptychus*" for anaptychi which also show a calcareous outer layer. Dagys *et al*. (1989: 45) referred to this (section through an anaptychus type jaw apparatus: 50, text-fig. 7), and also showed the morphology of the *Neoanaptychus* (*Rhynchaptychus*) type of jaw apparatus, but doubted the *in situ* position of such ammonoid beaks in late Cretaceous nod-

ules from Japan (Hokkaido), published, e. g., by KANIE (1982), KANIE *et al.* (1978), and TANABE *et al*. (1980).

SHIMANSKY (1949: 200) presents in its stratigraphical scheme four hypotheses what rhyncholites could be: upper jaws of

i) nautilids,

ii) nautilids and ammonites

iii) nautilids and coleoids, and

iv) nautilids and unknown cephalopods without shells (not Coleoidea).

In disregard of all knowledge on recent and fossil cephalopod jaws, he did not make up his mind to make a definite decision. And that is the present situation one will meet even in the most recent rhyncholite papers which appeared since 1995.

GASIOROWSKI's (1973) useful and nearly complete stratigraphical revision chiefly based on TILL's work. But GASIOROWSKI do not revise the taxonomy of rhyncholites. This was also not the fact in TEICHERT et al. (1964), a compilation which shows thus many individual errors so that the reader cannot rely on details in it.

When RIEGRAF & SCHMITT-RIEGRAF (1995, 1998) published their rhyncholite monograph, the paper of FAURE-BIGUET (1819) was not available to them, and consequently they did not know the true type species of *Rhyncolites*, *Rh. hirundo* FAURE-BIGUET, 1819. The latter was always referred to a Muschelkalk nautilid upper jaw, as noted above, by all authors up to date. At the present state of knowledge *Rhyncolites* is a valid senior synonym of *Palaeotheutis* TILL, 1906 and *Rhombocheilus* SHIMANSKY, 1947, and could not be refered to nautilid jaws. For upper beaks of nautilids no other valid names remained than *Scaptorrhynchus* BELLARDI, 1873, the latter a somewhat corroded Miocene nautilid upper jaw, but in spite recognizeable as such. The Muschelkalk nautilid upper jaws called *Rhyncholites hirundo* auct., not FAURE-BIGUET, 1819 should be renamed as *Scaptorrhynchus orbignyanus* (v. MÜNSTER, 1836). And for the Oxfordian rhynchoteuthid *Rhyncolites hirundo* FAURE-BIGUET, 1819 from SE France a neotype is urgently needed (kindly communicated by I. DIENI, Padua).

Although the type species of *Rhynchoteuthis* D'ORBIGNY and *Hadrocheilus* TILL, 1907 are the same, and both consequently objective synonyms, SHIMANSKY (1947), TEICHERT et al. (1964: K479), GASIOROWSKI (1973), and several Russian workers (ALIEV, 1961, 1965; KHALILOV, 1961, 1988; KOMAROV (1997, 1998, 1999, 2001a, 2001b, 2001c, 2002, 2003a, 2003b, 2003c, 2004a, 2004b) ignored or overlooked this fact.

DIENI (1975) was the first who presented an acceptable taxonomic concept and an accurate synonymy with excellent and numerous photographs important for further study of the individual and preservational variation.

What concerns now the nature of the not-nautilid jaws? Are they from coleoids, from nautilids, ammonites, or naked unknown cephalopods? It was lately detected by RIEGRAF

& Schmitt-Riegraf (1995) as being ammonite upper jaws, based on own observations on the types of Till (1906, pls 4-5), which are largely housed at the Bayerische Staatssammlung für Paläontologie und Geologie at Munich (Bavaria), on the morphology of larger *Rhynchoteuthis* specimens, on observations on Japanese ammonites with jaw apparatuses in upper Cretaceous nucleus concretions of Tanabe et al. 1980 (summarized in Nixon 1998: 24-34), and also by the study of Septfontaine (1970).

But up to date there are a few "hard-liners", apparently not familiar enough with Tethyan rhynchoteuthids which continously ignore their ammonite-nature and favour the ancient hypothesis of Gaillardot (1824) that they would belong to coleoids, not to ammonites, being unaware of Till (1906), the syntheses of Riegraf & Schmitt-Riegraf (1995) and Nixon (1998: 24-34). One cannot understand why they exclusively argue with the "conservative morphology of the anaptychus in epicontinental phylloceratids".

Modern rhyncholite terminology

Rhyncholites s. l. are a special development of calcified upper jaw tips on the horny beaks of

a) nautilids (the former "rhyncholites") and

b) ammonoids (rhyncholites s. str. = rhynchoteuthids).

As Faure-Biguet (1819) formally introduced the term "*Rhyncolites*" one should correctly use "rhyncolites", but "rhyncholites" is commonly accepted and in a wider usage.

For rhyncholite terminology (hood, shaft, crest etc.) we adopted those of Riegraf & Schmitt-Riegraf (1995: pl. 1), and refigure their scheme in Fig. 1.

Barremian rhyncholite occurrences

Barremian (?Hauterivian) rhynchoteuthids known to date are presented in Table 1. Barremian nautilid upper jaws are always great scarcities, e.g. *Rhyncolites curvatus* (Till, 1907) from Lower Saxony, *R. grayensis* (Till, 1907) from SE France, *R. besnossowi* (Shimansky, 1947), *R. belbekensis* Shimansky, 1960, and *R. karakaschi* Komarov, 2005 from the Crimea.

During the Barremian, rhyncholites, e.g. rhynchoteuthids, experienced a continued decrease in diversity and individual abundance. Barremian rhynchoteuthids (Table 1) are exclusively described from Cuba (Housa 1969), deep sea boreholes in the western Atlantic Ocean (Teichert & Spinosa 1971; Windisch et al. 1968), the Capverde Islands (Stahlecker 1935), the Baleares (Colom 1966), SE France (Guillaume 1957: 101; Sigal 1963; present paper), Albania (Patzelt 1971: 82), the Caucasus (Aliev 1961, 1965;

Khalilov, 1961; 1988), and the Crimea (Gasiorowski, 1973: 178, 181; Komarov 1998, 2001a, 2001b, 2004a, 2004b; Shimansky 1986).

In many rhyncholite papers, e.g. Till (1906, 1907, 1909, 1910, 1911) the stratigraphical age is unfortunately given as "Neocomian" only, an old-fashioned, poorly defined term

Table 1. The worldwide known Barremian rhyncholithe occurrences with their species published up to date.

Publication	Locality	Species described
Housa (1969)	Cuba	*Planecapula albeari* Housa
		Mesocheilus? *pinarensis* Housa
Teichert & Spinosa (1971); Windisch et al. (1968)	NE San Salvador	*Hadrocheilus* (*Arcuatobeccus*) *atlanticus* Teichert & Spinosa
Stahlecker (1935)	Maio, Capverde Islands	*Akidocheilus* sp.
Guillaume (1957)	Montsalvens, Ct. Fribourg	*Rhynchoteuthis* sp. indet.
Colom (1966)	Mallorca	*Rhynchoteuthis* cf. *lorioli* (Till)
		R. brunneri (Ooster)
		Akidocheilus sulcatus Till in Sigal 1963
Sigal (1963)	Barrême, SE France	*Hadrocheilus* cf. *H. costatus* Till
		H. aff. *gibber* Till
		Akidocheilus cf. *ambiguus* Till
		A.? *sulcatus* Till
		Leptocheilus probable aff. *uhligi* Till
Gasiorowski (1958: 196, 200)	Polish Carpathians	"rhyncholites"
Gasiorowski (1968, 1971)	W Tethys	"rhyncholites"
Gasiorowski (1973)	Crimea	*Rhynchoteuthis astieriana*
		Akidocheilus (*Planecapula*) *infirus* Shimansky
Patzelt (1971)	Albania	*Hadrocheilus* cf. *gibber* Till
		Tillicheilus obtusus Till
Aliev (1961)	Dibrar, SE Caucasus	*Hadrocheilus dibrarensis* Aliev
		Leptocheilus gilgilensis Aliev
Aliev (1965)	SE Caucasus	*Hadrocheilus transcaucasicus* Aliev
		H. tschikiltchaensis Aliev
Khalilov (1961, 1988)	Azerbaijan, Caucasus	*Hadrocheilus kiliani* Till
		Akidocheilus fortis Khalilov
Shimansky (1960)	Crimea	*Rhynchoteuthis astieriana* d'Orbigny
		Erlangericheilus insigne Shimansky
		Akidocheilus infirmum [= *infirus*] Shimansky
Shimansky (1986)	Crimea	*Hadrocheilus* (*Arcuatobeccus*) *menneri* Shiman.
		H. (*A.*) *nerodenkoi* Shimansky
Komarov (1998)	Mountainous Crimea	*Hadrocheilus* (*Hadrocheilus*) *mirus* Komarov
		Akidocheilus (*Shimanskia*) *dichotomus* Komarov
Komarov (1999)	SW Crimea	paper not available (not seen)
Komarov (2001b, 2001c)	SW Crimea	*Hadrocheilus* (*Hadrocheilus*) *optivus* Shimansky
		H. (*H.*) *fissum* Shimansky
		H. (*Arcuatobeccus*) *shymanskyi* (Zakharov)
Komarov (2004)	SW Crimea	*H.* (*Convexiterbeccus*) *kachensis* Komarov
		H. (*C.*) *geniatus* Komarov
		H. (*C.*) *inexpectatus* Komarov

which often comprise the Berriasian-Barremian, and in some cases the Aptian, too, and which should, therefore, be avoided. It is almost impossible to revise the stratigraphic age of single rhyncholites subsequently without having the associated cephalopod fauna.

Systematic palaeontology

Till (1906, 1907, 1909, 1910, 1911) and more recent Aliev (1961, 1965), Khalilov (1961, 1988), and Komarov (1997, 1998, 1999, 2001a, 2001b, 2001c, 2002, 2003a, 2003b, 2003c, 2003d, 2004a, 2004b) made almost for each individual rhyncholite a new species, even when they are misshaped or show preservational abnormities. Today this rhyncholite species concept is impracticable and largely rejected here: namely in regard of the zoological systematics and "true" biological species, and much more due to the poor morphology of rhyncholites, their various preservational and ontogenetic states, and the huge variation species they show when a larger number of specimens are available, e.g. in *Rhynchoteuthis bucklandi* (Ooster, 1857). This intraspecific variation was exemplified by Riegraf & Schmitt-Riegraf (1995, pls 22-26). Many authors establish new species based on individual, ontogenetical or preservational pecularities only. We, therefore, prefer collective names as are given in Riegraf & Schmitt-Riegraf (1995, 1998) due to the fact that rhyncholite "species" are no true biological species and that such collective taxa could represent several species or even genera in the corresponding ammonites.

Phylum Mollusca Cuvier, 1795

Subphylum Conchifera Agassiz, 1847

Class Cephalopoda Cuvier, 1795

Subclass Ammonoidea v. Zittel, 1884

Order, superfamily, and family *incertae sedis*

Rhynchoteuthis d'Orbigny, 1845

(1845a: 593; = *Hadrocheilus* Till, 1907, obj.; *Arcuatobeccus*, *Globosobeccus*, *Convexiterbeccus*, *Dentatobeccus* Shimansky, 1947; *Erlangericheilus* Shimansky, 1947 (biologically corroded specimen; ICZN invalid); *Eurycheilus* Septfontaine, 1970; *Microbeccus* Shimansky & Nerodenko, 1983 (biologically corroded specimens; ICZN invalid); *Nerodenkoina* Komarov, 2003 (biologically corroded specimens; ICZN invalid); *Parakidocheilus* Strausz, 1941 (nom. nud.); not *Rhynchoteuthis* Chun, 1903 (= living coleoid larva)

Type species: *Rhynchoteuthis Astierianus* d'Orbigny, 1845: 598, by subsequent designation in Shimansky 1947: 1476 (not by Teichert et al., 1964: p. K478).

First appearance: *Rhynchoteuthis bucklandi* (Ooster, 1857), Lower Pliensbachian, Ibex and Davoei Zones, Numismalismergel Formation, Schömberg in the Zollernalbkreis, SW Germany (Riegraf & Schmitt-Riegraf 1995: 84-85, pl. 21-26).

Last appearance: *Rhynchoteuthis* sp., late Lower Maastrichtian, Hachau, Bavarian Alps, S Germany (Riegraf & Schmitt-Riegraf 1995: 218, pl. 42, fig. 13-14; pl. 43, fig. 1a-c, 2a-c).

Stratigraphical and geographical distribution: Lower Pliensbachian-Cenomanian, Tethyan-Alpine Belt between Cuba and the Caribic Sea, Portugal, Bavarian Alps, Austrian Alps, Romania, Hungary, Poland (Carpathians), Ukraine (Crimea), Azerbaijan (Caucasus), India (Trichinopoly District) in the east, Northern Africa (Algeria, offshore Morocco) in the south, and Maastrichtian, Bavarian Alps; also epicontinental occurrences in the Pliensbachian of England (Dorset), France (Lorraine), SW Germany, and in the Campanian of NW Germany (Westphalia). It is the most long-ranging and most-widely distributed "genus" among rhyncholites.

Remarks: Quantitatively *Rhynchoteuthis* has a first acme with *R. bucklandi* Ooster in the Lower and basal Upper Pliensbachian (Tethyan and epicontinental), is absent during the Toarcian, with "*Eurycheilus*" *fallbachensis* Septfontaine (a corroded *Rhynchoteuthis*?) rare in the Aalenian (Septfontaine 1970) to get more frequent during the Bajocian (Cañigueral Cid 1952; Till 1907, 1909) and Bathonian. During Bajocian/Bathonian *Leptocheilus* Till, 1907 evolved from *Rhynchoteuthis* via the transitional *Mesocheilus* Till, 1909. From Callovian to Berriasian *Rhynchoteuthis* is continuously an uncommon to rare element in rhyncholite faunas, but is always dominant in Valanginian/Hauterivian assemblages. During the Barremian *Rhynchoteuthis* is always present, sometimes associated with *Palaeotheutis* or even in monospecific assemblages. In Aptian deposits *Rhynchoteuthis* occurs exclusively, often in large individuals, but always quite scarce, in SE France and the Crimea (Till 1910: 412, 416, 418, 419, 420; 1911: 361; Shimansky & Nerodenko 1983: 36). Rare Albian finds are confined to Hungary (Fülöp 1966: 20, 23, 67, 69) and Madagascar (Besairie & Collignon (1959: 141). A Cambridge Greensand (basal Cenomanian) *Rhynchoteuthis* is – quite unexpectedly – known from Cambridge, England (Foord 1891: 370, text-fig. 81a). Cenomanian discoveries are confined to the Tiruchirapalli and Trichopoly districts (Utatur Stage) of Southern India (Chiplonkar & Badve 1979; Lakshmirarayana & Saha 1979; Sahni & Jain 1962; Sastry, Mamgain & Rao 1965; Till 1910: 425) and the Crimea (Shimansky 1973: 133). Gasiorowski (1973: 492, tf. 5) emphasized that *Rhynchoteuthis* (his "crushing type") were exclusively represented in "Middle Cretaceous" time. Even abundant occurrences of *Rhynchoteuthis minima*, associated with the corresponding lower jaw tip named *Tillicheilus* are known from the Campanian of central Westphalia, namely from several formations in the country around Coesfeld, Münster and Beckum, the so-called Münsterland, from glauconitic, spiculitic, and turbiditic deepwater marlstones, often secondarily enriched in basal

breccias of turbidites (Riegraf & Schmitt-Riegraf 1987; 1995). From the stratigraphic youngest *Rhynchoteuthis* sp., three always poor preserved, rare and small specimens, were found in a 4 kg microsample from the Lower Maastrichtian (Zementmergel Series) of the Bavarian Alps.

Another deep water mass occurrence with flattened, small, horny ammonite upper jaws (up to 20 specimens per 400 cm^2) associated with both rare *Naefia* phragmocones and ammonites in soft-part preservation, is currently under description by Klug, Lehmann & Riegraf, in prep.) from the late Cenomanian "Rotpläner" or "Schwarzbunte Wechselfolge" member of the Galgenknapp quarry of Lengerich and Rheine (Westphalia). Due to the flattened preservation in a 2 cm thick, bituminous black shale it is not to decide whether this upper jaws are remains of former calcitic rhynchoteuthids, or original horny upper jaws. In rare cases they were associated with the flattened radula. Those bed is to correlate over a longer distance from Lengerich to Halle in Westphalia, but is no subject of description here.

Teichert et al. (1964: K479) erroneously quoted a "Permian" occurrence of *Rhynchoteuthis*, but it does not occur earlier than Pliensbachian, because the Permian *Rhynchoteuthis kaibabensis* revealed to be indeed fish remains (Yochelson 1971).

Remarks: The date of apparition of d'Orbigny's "Mollusques vivants", pl. 1, livr. 1, is 1845, not 1847. The latter date is sometimes stated, e.g. by Teichert et al. (1964: K478). The complicated structure of d'Orbigny's monographs "Mollusques vivants" (1845-1847), "Paléontologie universelle" (1846), "Terrain Jurassique" (1842-1849), and "Terrain Crétacé" (1840-1842), caused always some confusion in correct citation of the type references. d'Orbigny sometimes presented one and the same plate for three monographs contemporaneously!

Rhynchoteuthis astieriana d'Orbigny, 1845

(Plate 1, Figs 1a-4c)

*	1845	*Rhynchoteuthis Astierianus* d'Orb. – d'Orbigny: 598 (1845a)
	1846	*Rhynchoteuthis Astierianus* d'Orb. – d'Orbigny, pl. 80, figs 5-7
	1957	?*Rhynchoteuthis* sp. indet. – Guillaume: 101 (lower Barremian, Préalpes Fribourgeoises, Switzerland)
	1963	*Hadrocheilus* cf. *H. costatus* Till. – Sigal: 192-193, tf. 1 (Barremian, Barrême, SE France)
?	1971	*Hadrocheilus* cf. *gibber* Till. – Patzelt: 82, pl. 10, fig. 7 (Barremian, Albania)
	1983	*Hadrocheilus* (*Microbeccus*) *jucundus* sp. nov. – Shimansky & Nerodenko: 36, pl. 4, figs 7a-c (Lower Aptian, Crimea)
	1983	*Hadrocheilus* (*Hadrocheilus*) *theodosiae* Till. – Shimansky & Nerodenko, pl. 4, figs 2a-c (Barremian-Lower Aptian, Crimea)
	1983	*Erlangericheilus insigne* Shimansky. – Shimansky & Nerodenko, pl. 4, figs 3a-c (Barremian-Lower Aptian, Crimea)

not	1994	*Rhynchoteuthis* (*Rhynchoteuthis*) *astieriana* D'ORBIGNY. – LAUB: 131-132, pl. 5, figs 3-4, table 2 (pl. 5, figs 3-4 = *Rh. gibber* TILL (Tithonian); p. 132 (Pliensbachian) = *Rh. bucklandi* OOSTER)
v	1995	*Rhynchoteuthis astieriana* d'ORBIGNY. – RIEGRAF & SCHMITT-RIEGRAF: 78-84, pl. 20, figs 4a-d (full synonymy before 1995)
v	1995	*Palaoteuthis larus* (FAURE-BIGUET). – RIEGRAF & SCHMITT-RIEGRAF: 202, pl. 35, figs 1a-c, 2a-c (Valanginian-Hauterivian, Upper Silesia, Poland)
	1998	*Hadrocheilus* (*Hadrocheilus*) *mirus* sp. nov. – KOMAROV: 30-31, text-figs 2a-c (upper Barremian-Aptian, Crimea)
	2001a	*Hadrocheilus* (*Hadrocheilus*) *optivus* SHIMANSKY. – KOMAROV: 36, 38, text-figs 2-3 (upper Barremian, SW Crimea)
	2001a	*Hadrocheilus* (*Hadrocheilus*) *fissum* SHIMANSKY. – KOMAROV: 39, 40, text-figs 4-5 (upper Barremian-Aptian, SW Crimea)
	2001b	*Hadrocheilus* (*Hadrocheilus*) *optivus* SHIMANSKY. – KOMAROV: 485-487, text-figs 2-3 (upper Barremian, SW Crimea)
	2001b	*Hadrocheilus* (*Hadrocheilus*) *fissum* SHIMANSKY. – KOMAROV: 485, 488-489, text-figs 4-5 (upper Barremian-Aptian, SW Crimea)
	2003c	*Hadrocheilus* (*Nerodenkoina*) *aenigmatosus* sp. nov. – KOMAROV: 40, text-figs 1a-c (crushed and misshaped specimen; ICZN invalid; Aptian, SW Crimea)
	2003d	*Hadrocheilus* (*Nerodenkoina*) *aenigmatosus* sp. nov. – KOMAROV: 261-262, text-figs 1a-c (crushed and misshaped specimen; Aptian, SW Crimea)
	2004a	*Hadrocheilus* (*Convexiterbeccus*) *expressus* sp. nov. – KOMAROV: 35-36, pl. 3, figs 1-3 (corroded specimen; upper Barremian, SW Crimea)
	2004a	*Hadrocheilus* (*Convexiterbeccus*) *kachensis* sp. nov. – KOMAROV: 37, pl. 3, figs 7-9 (corroded specimen; upper Barremian-Aptian, SW Crimea)
	2004a	*Hadrocheilus* (*Convexiterbeccus*) *geniatus* sp. nov. – KOMAROV: 37-38, pl. 3, figs 10-12 (corroded specimen; upper Barremian, SW Crimea)
	2004a	*Hadrocheilus* (*Convexiterbeccus*) *inexpectatus* sp. nov. – KOMAROV: 38-39, pl. 3, figs 13-15 (corroded specimen; upper Barremian, SW Crimea)
v	2007b	*Palaeoteuthis bruneri* [sic] (OOSTER). – MOOSLEITNER: 294, 297, pl. 11, figs 16-17 (Barremian, Serre de Bleyton, SE France)

Description: The morphology is sufficently described by the figures (pl. a). The lateral view is – as in most rhyncholites – of major importance. The species is one of the largest in the "genus", but present four specimens are comparatively small. Striking differences to *R. bucklandi* are the more straight hood, the shorter shaft, to *R. gibber* the lacking protrution on the ventral longitudinal crest. *R. minima* is more slender, has an elongated hood, is more acute, and the latter three show another profile. *R. teschenensis* is more *Palaeotheutis*-like incurved in profile (see RIEGRAF & SCHMITT-RIEGRAF 1995: pl. 35, figs 1a-c, 2a-c; erroneously called "*Palaeotheutis larus*"). Two of present specimens (pl. a, fig. 1 and 3) are comparatively thick in lateral view – a character which could mean that they belonged to adult individuals when compared with "adult" specimens of *R. bucklandi* (RIEGRAF & SCHMITT-RIEGRAF 1995: pl. 25, figs 1a-c, 2a-c). The accessory longitudinal wrinkles (pl. 25, fig. 1) on the ventral side of the shaft have been found in both adult

rhynchoteuthid and nautilid rhyncholites exclusively (Riegraf & Schmitt-Riegraf 1995: pl. 25, figs 1a-c, 2a-d; pl. 6, fig. b; pl. 11, figs 1a-c; pl. 12, figs 1a-c; pl. 14, figs 3a-c). The wings of the hood in present specimens are less or more damaged, do not show soft-parts, and their surface is somewhat corroded and weathered. Dorsal and ventral views do not exhibit aspects which have not been observed in other descriptions of the taxon. Some slightly ?pathological individuals of *R. minima* as figured in Riegraf & Schmitt-Riegraf (1995: pl. 39, figs 4-6) could fall into the variation of *R. astieriana*.

Remarks: For date of apparition of d'Orbigny's "Moll. vivants" see remarks above under *Rhynchoteuthis*. Few *Rhynchoteuthis* "species" (e.g. *Rhynchoteuthis gibber* Till, 1907 or *Rhynchoteuthis bucklandi* Ooster, 1857) show such a marked morphology that they distinctly may be separated from the numerous other *Rhynchoteuthis* "species" described in literature. A species closely related to *Rh. astieriana*, and at maximum a little bit slender due to its elongated shaft, is *Rhynchoteuthis hoheneggeri* (Till, 1906), syn.: *Rh. teschenensis* (Till, 1906), from the Hauterivian of Upper Silesia (Polish Carpathians).

Palaeoteuthis d'Orbigny, 1849

(Prodrôme, p. 327; = *Akidocheilus* Till, 1907, not: *Palaeotheutis* Till, 1906; *Gonatocheilus* Till, 1907, obj.; *Planecapula* Shimansky, 1947; *Shimanskia* Komarov 1998; *Romanovichella* Komarov, 2003a)

Type species: *Rhynchoteuthis honoratiana* d'Orbigny, 1847: 594, by monotypy.

First appearance: *Akidocheilus* sp. 1 in Septfontaine (1970: 107-108, text-figs 9.3a-c, 9.4a-c) from the Upper Aalenian and Lower Bajocian) and *Leptocheilus duplofractus* (Till) in Septfontaine (1970: 108-109, text-figs 3.1a-c, 3.2a-c, 3.3a-c) from the "Préalpes médianes romandes" in Switzerland. *Akidocheilus* sp. in Sigal & Colom (1971: 145-146, pl. 3, figs 1-3) from the "Toarcian/Aalenian" of Mallorca, Spain, is a *Rhynchoteuthis*, no *Palaeoteuthis* species.

Last appearance: *Akidocheilus* (*Romanovichella*) *plenus* Komarov, 2003, *A.* (*Planecapula*) *explicatus* Komarov, 2003, middle Cenomanian, SE Crimea.

Distribution: Exclusively Tethyan, Aalenian to Cenomanian, from Cuba to the Crimea and the Caucasus (see also under *P. infira* (Shimansky).

Palaeoteuthis infira (Shimansky, 1947)

(Plate 2, Figs 1a-3c)

?	1909	*Akidocheilus novosimilis* n. sp. – Till: 596, pl. 20, figs 7a-c (Aptian, Ardêche)
	1935	?*Akidocheilus* Till. – Stahlecker: 289 (Barremian, Maio, Capverde Islands)
*	1947	*Akidocheilus* (*Planecapula*) *infirus* [sic] sp. nov. – Shimansky: 1477, 1478, text-figs 1a-d (Aptian, Crimea)

1960 *Akidocheilus infirmum* Shimansky. – Shimansky: 246, pl. 6, figs 6a-c (nom. van.; erron. pro *infirus* Shimansky) (Aptian, Crimea)
1961 *Akidocheilus fortis* A. Khalilov sp. nov. – Khalilov: 54-55, text-figs 3-4 (Barremian, NE Caucasus)
1962 *Akidocheilus infirmum* Shimansky. – Shimansky, pl. 2, figs 6a-c (nom. van.; err. pro *infirus* Shimansky) (Aptian, Crimea)
1963 *Leptocheilus* probable aff. *L. uhligi* Till. – Sigal: 192, text-figs 2a-c (Barremian, Barrême, SE France)
1963 aff. *Akidocheilus*? *sulcatus* Till. – Sigal: 192, text-figs 4a-c (Barremian, Barrême, SE France)
1964 *Akidocheilus* (*Planecapula*) *infirus* Shimansky. – Teichert, Moore & Nodine Zeller: K481, text-figs 346,5a-c (Aptian, Crimea)
1969 *Planecapula albeari* n. sp. – Housa: 121-122, pl. 23, figs 1-6 (Hauterivian/Barremian, Cuba)
1969 *Mesocheilus*? *pinarensis* n. sp. – Housa: 121-122, pl. 23, figs 1-6 (Hauterivian/Barremian, Cuba)
1971 *Hadrocheilus* (*Arcuatobeccus*) *atlanticus* Teichert & Spinosa, n. sp. – Teichert & Spinosa: 6-7, pl. 3, figs 7-9; not: pl. 3, figs 1-6; pl. 4, figs 1-3, table 3 = *Rhynchoteuthis astieriana* d'Orbigny (Hauterivian/Barremian, NE San Salvador)
1973 *Akidocheilus* (*Planecapula*) *infirus* Shimansky/une forme de passage entre *Akidocheilus* et *Gonatocheilus*. – Gasiorowski: 178-179, text-figs 54.7; p. 181, text-fig. 55.4 (Barremian-Aptian, Crimea)
1988 *Akidocheilus fortis* A. Khalilov sp. nov. – Khalilov in Alizade: 333, pl. 1, figs 3a-c, 4a-c (Barremian, NE Caucasus)
1998 *Akidocheilus* (*Shimanskia*) *dichotomus* sp. nov. – Komarov: 30-31, text-figs 1a-c, d-f (upper Barremian, Crimea)
v 2004 *Palaeoteuthis brunneri* (Ooster). – Moosleitner: 154, pl. 69, figs 6-8 (Barremian, SE France)
2003 *Akidocheilus* (*Romanovichella*) *plenus* Komarov, sp. nov. – Komarov: 21-23, text-figs 1a-c (middle Cenomanian, SE Crimea) (2003a)
2003 *Akidocheilus* (*Planecapula*) *explicatus* Komarov, sp. nov. – Komarov: 23, text-figs 2a-c (middle Cenomanian, SE Crimea) (2003a)

Distribution: Lower Bajocian to middle Cenomanian, Tethyan-Alpine belt, exclusively in Cuba, Spain (Betic Chain, Baleares), France (Ardèche, Provençe), Swiss Alps (Cantons Fribourg, Bern, Vaud), Italy (Sicily), Austrian Alps (Tyrol, Salzburg), Poland (Carpathians), Hungary (Comitat Baranya), Ukraine (Crimea), and Azerbaijan (Caucasus).

Description: The specimens of the Serre de Bleyton do not show new pecularities which would contribute to the knowledge of the taxon. Their preservation is medium to poor, but allows sure species recognition. They show mechanical damaging and chemical weathering. But one specimen (pl. 2, figs 2a,c) has an almost complete right wing of the hood.

Remarks: The name has to be derived from the Latin *infirmus* (weak, not firm) or *inferus* (low, below); unfortunately SHIMANSKY did not give a *derivatio nominis* and, therefore, the name has to remain unchanged being apparently no *lapsus calami* sensu ICZN. The subsequent emendation in SHIMANSKY (1960: 245) and SHIMANSKY (1962: pl. 2, fig. 6) as "*infirmus"* contradicts the ICZN, and consequently *infirmus* is a nom. van.

TILL's (1909) taxon *Akidocheilus novosimilis* is a little bit more acute than *Akidocheilus infirus* (SHIMANSKY), poorly figured and preserved (GASIOROWSKI 1973 assigned it to, and draw it as, a *Leptocheilus*) and its holotype (Humboldt University Berlin) might be lost, but both may later reveal to be conspecific. We, therefore, refer to the better defined junior taxon. The subgenus *Romanovichella* KOMAROV differs in having a ventral crest with rounded edges which seems to be more accidental (or due to better preservation) than of true diagnostic value. Same is with some individual differences which led KOMAROV (2003a, 2003b) to make two new "species". The only difference between *Palaeoteuthis* D'ORBIGNY and *Planecapula* SHIMANSKY is the flatter shaft of the latter; the former has a slightly concave one, often due to preservation or individual variation. From the Serre de Bleyton specimens it is not clear wether they would be more related to the "subgenus" *Palaeoteuthis* D'ORBIGNY or *Planecapula* SHIMANSKY due to their medium to poor preservation.

Palaeobiology

Rhynchoteuthids are often excellently preserved with remains of the adjacent soft parts, but unfortunately sure *in situ* finds are lacking up to date (in contrast to some Triassic, Jurassic and Cretaceous nautilids). The reason might be that in the Tethyan realm, where such rhyncholites are common, suitable Fossillagerstätten (means fossil "bonanzas") are unknown to date.

Rhynchoteuthids, e.g. *Rhynchoteuthis gibber* (TILL, 1907), were found in association with *Phylloceras*, *Phyllopachyceras*, *Sowerbyceras*, *Lytoceras*, *Eulytoceras*, *Protetragonites*, and *Leptotetragonites* in the Schrambach Formation of Austria (LUKENEDER 2004: LUKENEDER & HARZHAUSER, 2000, 2002). In the Pliensbachian of Portugal, Lorraine, SW-Germany, and Dorset *Rhynchoteuthis bucklandi* occurred first when Tethyan immigrants like *Tragophylloceras* (and *Lytoceras*) invaded the epicontinental shelfs of Europe. In the Campanian of Westphalia *Rhynchoteuthis minima* (V. D. MARCK, 1858) geographical distribution and the long stratigraphical range agreed with the accompanying *Gaudryceras* (or *Tetragonites*) *obscurum* (SCHLÜTER, 1872) (shells most recently figured in RIEGRAF & SCHMITT-RIEGRAF, pl. 37, figs 1-4). In the latter case no other ammonite species would offer an alternative, and, therefore, *R. minima* and *G. obscurum* may belong to the same cephalopod species with a higher certainty than in other Mesozoic cases discussed here. This is emphasized by the fact that both species do not occur outside Westphalia in the surrounding Chalk seas of Great Britain, France, Lower Saxony and Schleswig-Holstein, Denmark, Poland, and the Ukraine, except a new discovered occurrence of

Gaudryceras obscurum in southern Poland (MACHALSKI et al. 2004). NIXON (1998: 29-34) summarized the known calcified upper jaw tips of the Cretaceous ammonite genera *Neophyllites*, *Tetragonites*, *Gaudryceras*, *Scalarites*, *Scaphites*, and *Aconeceras*, which means that such jaws occur in Phylloceratina, Lytoceratina, Ancyloceratina, and some Ammonitina.

MOOSLEITNER (2007b: 294) quoted small *Phylloceras*, *Sowerbyceras*, and ?"*Valanginites*" from the Serre de Bleyton section. In the rhynchoteuthid-rich Callovian Terre Noire Formation in SE France abundant *Palaeoteuthis* D'ORBIGNY, *Palaeotheutis* TILL, and *Leptocheilus* TILL are also associated with small *Phylloceras* and *Sowerbyceras* in the Castellane region (W. R., own observation) and in the Col de Peyruergue sections, as recently exemplified by MOOSLEITNER (2007a: 234).

If future ammonite researcher will pay more attention to the relationship of Jurassic/Cretaceous ammonites versus associated rhynchoteuthids in Tethyan shelf and pelagic localities, as did LUKENEDER (2004), there could be a good chance to assign even "species" of rhynchoteuthids to the corresponding ammonites and aptychi/anaptychi. But this fact was hampered by authors who doubted even up to date any relationship between certain Tethyan ammonite taxa and rhynchoteuthids.

While fossil nautilid beaks are to be found in neritic environments (middle to outer shelf), but apparently nowhere quite abundantly, are rhyncholites (which do not belong to nautilids) characteristic fossils of pelagial and deep sea environments (outer shelf to upper bathyal). In those environments Mesozoic Neommonoidea are highly diverse and most frequent.

Since the Deep Sea Drilling Project (DSDP/ODP) started, smaller not-nautilid rhyncholites were sometimes recovered from Pliensbachian, Oxfordian-Tithonian and Lower Cretaceous boreholes (RIEGRAF, LUTERBACHER & LECKIE, 1984: 695, pl. 3, figs 108-109; RIEGRAF & LUTERBACHER 1989) ín the Northern Atlantic Ocean offshore the east coast of North America and Morocco. Their occurrences revealed that i) those North Atlantic deep water environments are also part of the Western Tethys and ii) yielded ammonites, but their shells are not preserved due to increasing aragonite dissolution with increasing depth (ACD).

Not found in the Serre de Bleyton were the calcified tips of the lower jaws (anaptychus) of Lytoceratida and Phylloceratida introduced as *Rhyncholithes obtusus* TILL (1906: 121-123, pl. 4, figs 25-28, text-fig. 16.II, as "eigener Typus"), which is subsequently assigned to *Tillicheilus* SHIMANSKY (1947: 1477). This lower jaw tip was also found in the late Lower and early Upper Campanian deep water marlstones in the country around Münster and Beckum in Westphalia (RIEGRAF & SCHMITT-RIEGRAF 1987: 8-12, 28-29, pl. 4, figs 1-12, 21, and refigured in RIEGRAF & SCHMITT-RIEGRAF (1995: 216, pl. 42, figs 1-12) as *Tillicheilus minimus* (V. D. MARCK, 1858), at a rate upper/lower jaw tips of 10:1 due to the low fossilisation potential of the latter.

Taxonomy and discussion

Rhyncholites as such would theoretically have an excellent fossilisation potential due to their calcitic lamellae (Komarov 2001b, 2001c), separated by thin chitinous (β-chitin) layers, precipitated around the tip of a horny upper jaw. In fossil state the chitin maybe altered to Francolite – $Ca_5[F,O|(SiO_4,SO_4,PO_4,)_3]$ –, as in most fossil coleoids, or to Wilkeite – Fluorellestadite, $Ca_5[F|(PO_4,CO_3)_3]$, as quoted by Nixon (1998: 29). But the scarcity of Jurassic nautilid upper jaws stood in sharp contrast to the number of shells found, to their seize of up to several centimeters, and their calcitic character. One must assume that a part of them has largely or completely been destroyed before being embedded in the sediment, dissolved by biological digestion in stomachs or by mechanical and/or diagenetical damaging (Riegraf & Schmitt-Riegraf 1995: pl. 3, figs 3a-c; pl. 4, figs 3a-c; pl. 5, figs 1a-c, 2a-c; pl. 7, figs 4a-b; pl. 9, figs 2a-c; pl. 10, figs 1a-c; pl. 11, figs 2a-c; pl. 12, figs 1a-c; pl. 13; 14, figs 3a-c; pl. 31; pl. 38, figs 2a-o). This might be the fate of an unknown number of rhynchoteuthids, too.

On the other hand, in most epicontinental Mesozoic "Fossillagerstätten" (Lower Toarcian Posidonienschiefer Formation, Oxford Clay Formation, Solnhofen Formation, Baumberge Formation, Sendenhorst Member of the Ahlen Formation) *in situ* rhyncholite-bearing ammonites are lacking. In rare cases (Till 1906) upper and lower jaw (anaptychus) tips have been preserved in articulation. Rhyncholites which have been redeposited or transported by currents often show sedimentary corrosion. This is best demonstrated by specimens with a surface lacking the hood and exhibiting growth lamellae, to specimens with a final flat state where the corroded rhyncholite is hardly to recognize (Riegraf & Schmitt-Riegraf 1995: 16, 88, 208, pl. 38, figs 2a-g; see also preservational stages in Lukeneder & Harzhauser 2002). In contrast, biological corrosion even caused hollow rhyncholites which underwent various ways of strange deformation (Riegraf & Schmitt-Riegraf 1995: 16, 208, pl. 38, figs 2h-o) without crushing. When the shaft is protected by the soft-parts digestion leads to dissolution of the hood alone leaving behind a relic which led Shimansky (1947) erroneously establish his new genus *Erlangericheilus*. *Erlangericheilus*-like rhyncholites can rarely be found in larger collections of the massive *Rhynchoteuthis* forms and clearly belong to this genus.

Erlangericheilus-like preservation is also known in fossil nautilid upper jaws (Riegraf & Schmitt-Riegraf 1995: 46, 140, pl. 4, figs 3a-c). Shimansky & Nerodenko (1983: 35, pl. 4, figs 4a-c, 5a-c) established such corroded specimens as *Hadrocheilus* (*Microbeccus*) *arendti*. Riegraf & Luterbacher (1989: 1153, text-figs 30-35; p. 1155, text-figs 36-44); p. 1157, text-figs 50-55) also show heavily corroded specimens due to sedimentation below the CCD, sedimentary transportation, and early diagenetic dissolution. In upper Cretaceous chalk environments of England, the Netherlands, Belgium or Northern Germany nautilid upper jaws are heavily damaged up to the loss of the shaft and dissolution by early diagenesis (Riegraf & Schmitt-Riegraf: 158, pl. 13, figs 1-6; Riegraf, Werner & Lörcher, 1984: 83, figs 26b, 26d).

The Barremian bioclastic limestone, which yielded the rhynchoteuthids described herein, and other Cretaceous deposits, could be derived by slumping from the nearby Montagne d'Angèle (Tithonian) into the bathyal (kindly communicated by HUBERT ARNAUD, Grénoble).

Unfortunately, none of the preservational states quoted here are observed in the specimens from Serre de Bleyton. They only show minor corrosion by sedimentary transportation (redeposition). One shows some silica growth rings, others weak traces of sedimentary transportations, but no remains of soft-parts, and also nothing what could reveal additional taphonomic or palaeobiological information. The bioclastic limestone, object of the studies in present volume, is the result of facies components and organisms which were redeposited from the shallow-water and shelf environment into the upper bathyal (upper slope enviroment, trivially called "trough" or "basin"). The same case is in the turbiditic fossil (rhyncholite, aptychi, fish remains etc.) breccia of the Callovian of SE France earlier described by MOOSLEITNER (2007a).

Conclusions

i) A poor and low-diverse rhyncholite fauna of *Rhynchoteuthis astieriana* D'ORBIGNY, 1845 and *Palaeoteuthis infira* (SHIMANSKY, 1947) from an allochthonous bioclastic limestone in the Serre de Bleyton complete the knowledge which resulted from the few Barremian rhynchoteuthid localities of the western Tethys between the Carribean realm in the west and the Crimea and Caucasus in the east.

ii) The Barremian stratotype at Barrême yield additionally *Rhynchoteuthis gibber* TILL and *Leptocheilus* aff. *uhligi* TILL.

iii) Occurrences of Barremian deposits outside the Tethys do not contain rhynchoteuthids at all.

iv) In Barremian rhynchoteuthid faunas *Rhynchoteuthis* dominate over *Palaeoteuthis*, *Palaeotheutis*, and *Leptocheilus* (rare). Due to the scarcity of rhynchoteuthids in Barremian strata at all and their poor descriptions and figures, there are no representative statistics at the moment.

v) There is a widespread decrease of rhynchoteuthids in abundance and frequency of localities from the Barremian onwards to the Cenomanian. Isolated Campanian and Maastrichtian rhynchoteuthid (*Rhynchoteuthis*) occurrences are exclusively known from northern, respective southwest Germany. From the Lower Pliensbachian to Aalenian *Rhynchoteuthis* occurr exclusively, and dominates also during the Valanginian-Hauterivian. The acme of rhynchoteuthids spans between the Bajocian-Hauterivian.

vi) Rhynchoteuthids are often to be found not only in pelagic cephalopod marlstones and claystones (e.g. aptychi beds) of the outer shelf and upper bathyal, but also secondarily

enriched in turbiditic breccias, black shales, and/or washed or slumped into deeper (outer shelf, upper bathyal) environments, as it is observed in the Serre de Bleyton.

vii) Regarding morphology, chemistry, geographical and stratigraphical occurrences, and palaeobiological observations of the outer shelf to upper bathyal rhynchoteuthids they must be upper jaw remains of Tethyan ammonites of the suborders Phylloceratina, Lytoceratina, Ancyloceratina, and Ammonitina. Episodical and scattered epicontinental occurrences are confined to periods of transgressions (sea-level highstands) which enabled Tethyan immigrants among ammonites to invade shelf areas in the neighbourhood of the western Tethys.

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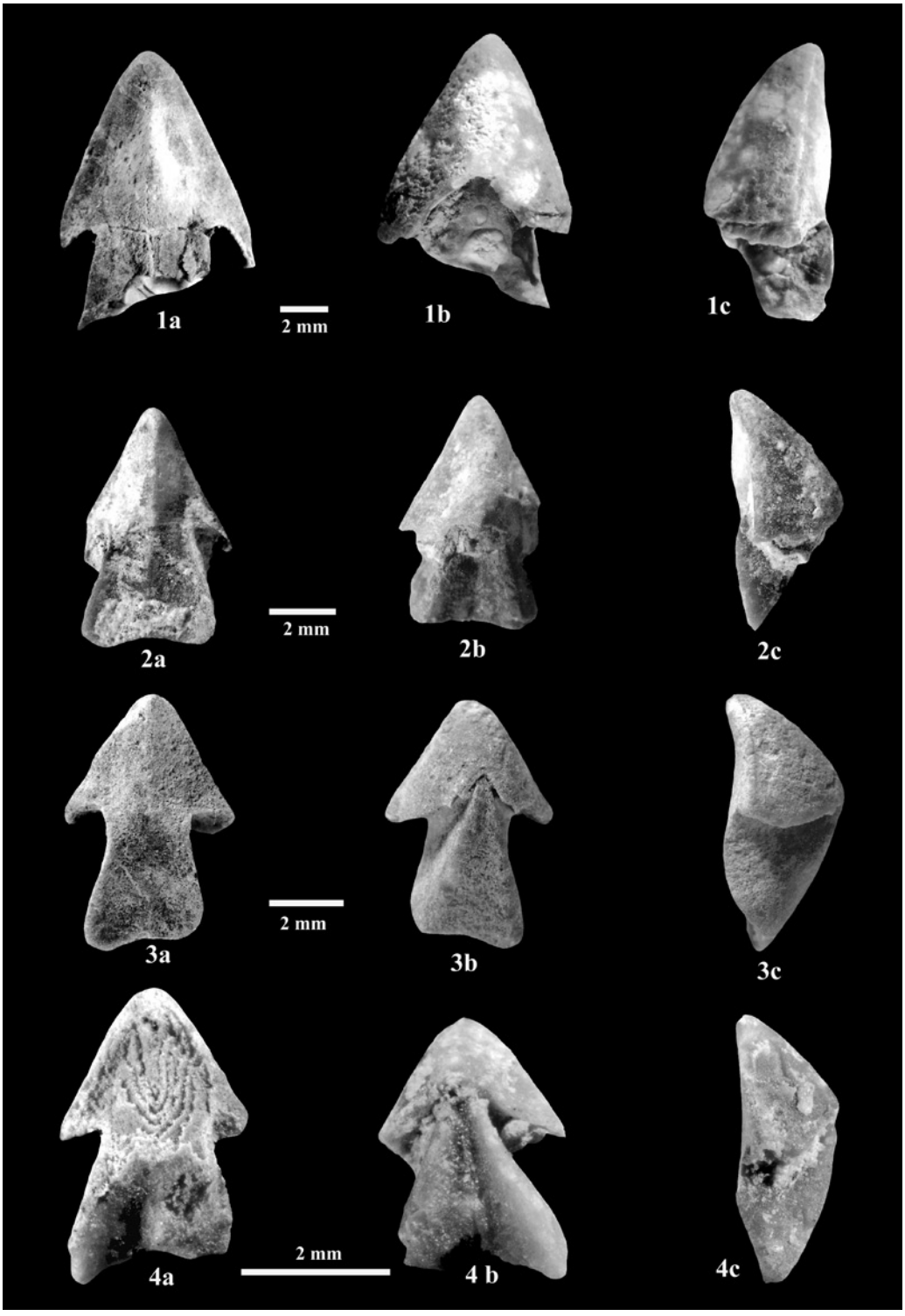
Plate 1

Figs 1-4. *Rhynchoteuthis astieriana* D'Orbigny, 1845. Barremian. Serre de Bleyton. NHMW 2009z0035/0001, 2009z0035/0002, 2009z0035/0003, 2009z0035/0004.

Scale: 2 mm. – a ventral, b dorsal, c lateral, respectively.

The rhyncholites described in present paper are housed in the collection of the Naturhistorisches Museum Wien (Vienna, Austria) with collection nos. NHMW 2009z0035/0001 to …/0004.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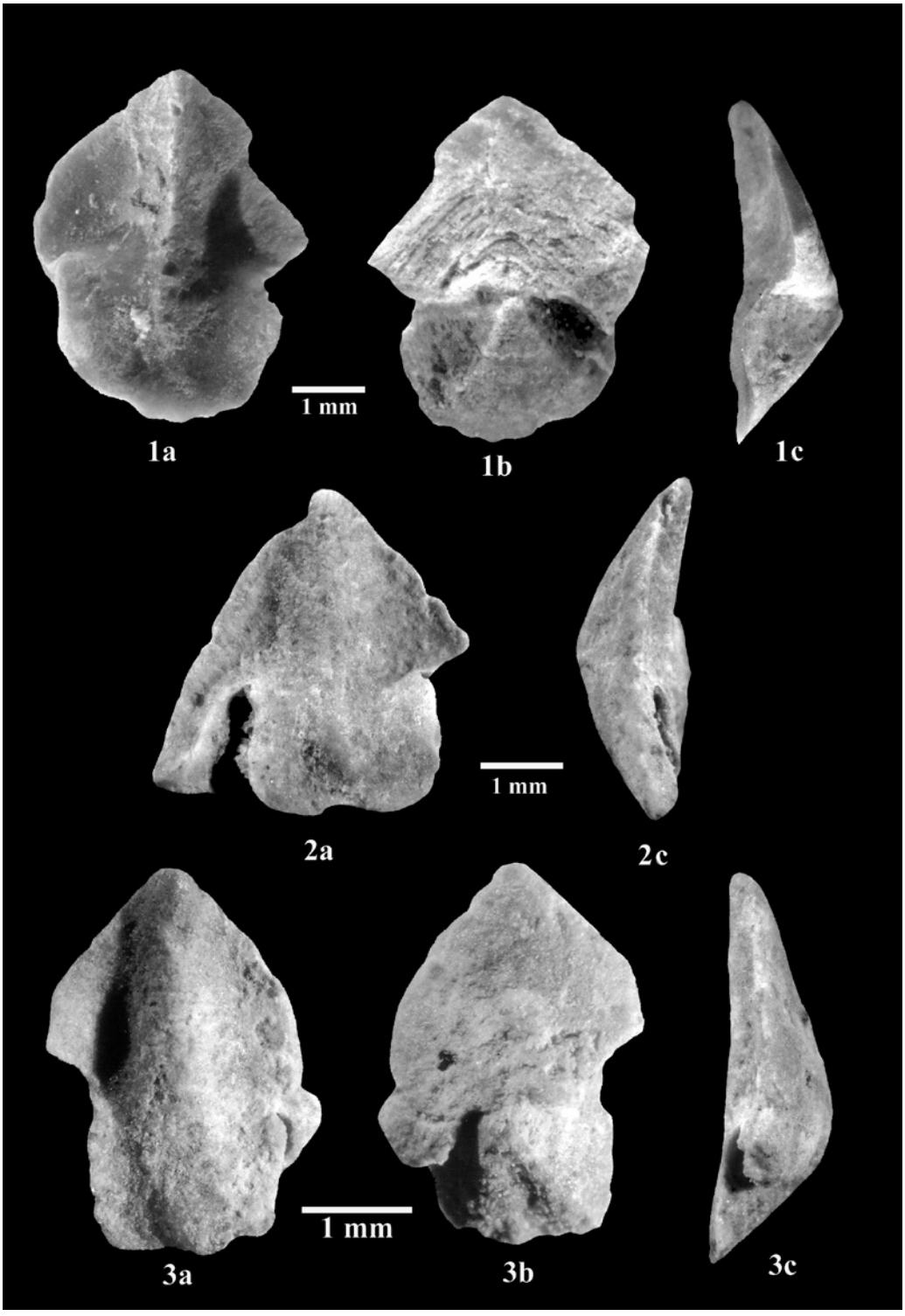
2 mm
4 b
4c

Plate 2

Figs 1-3. *Palaeoteuthis infira* (Shimansky, 1947). Barremian, Serre de Bleyton. NHMW 2009z0035/0005, 2009z0035/0006, 2009z0035/0007.

Scale: 1 mm. – a ventral, b dorsal, c lateral, respectively.

The rhyncholites described in present paper are housed in the collection of the Naturhistorisches Museum Wien (Vienna, Austria) with collection nos. NHMW 2009z0035/0005 to …/0007.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