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

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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it is, for instance, very helpful to revert to existing systematic compilations even though the information is outdated.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.

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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).

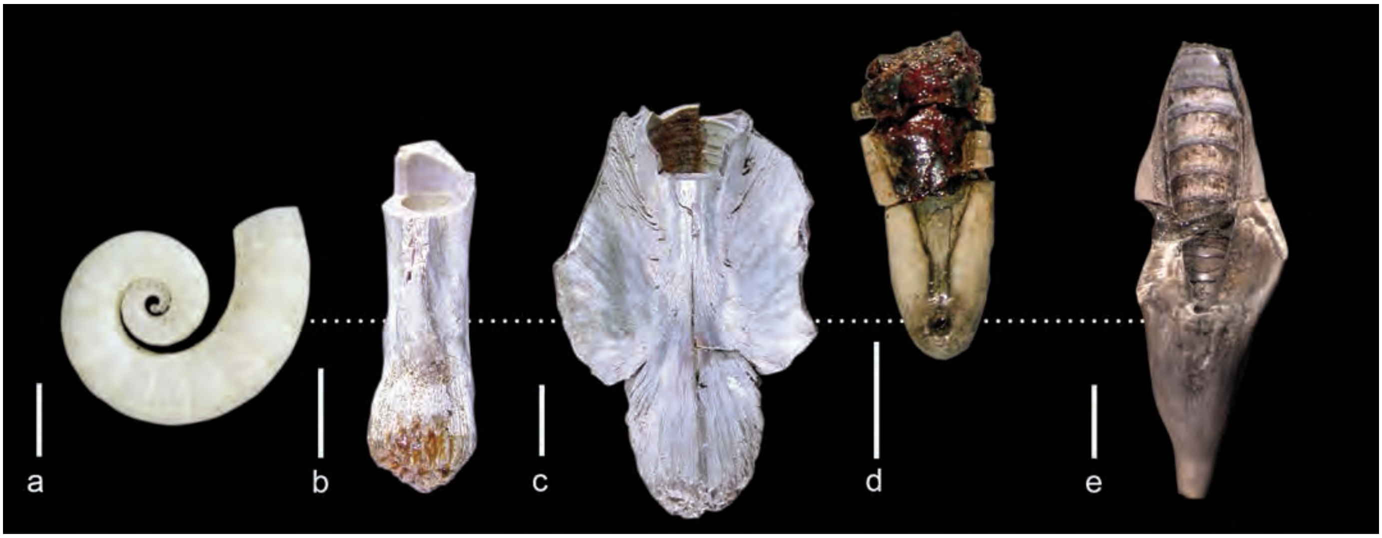


Fig. 1: Shells and shell remains of spirulid coleoids. **a**: *Spirula spirula*; lateral view of the complete phragmocone. **b**: *Belopterina levesquei* [original of Férussac & d'Orbigny (1839: pl. 20, figs. 10–12), MNHN R05666, Muséum National d'Histoire Naturelle], Eocene (Ypresian), Gilocourt (Dep. 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.

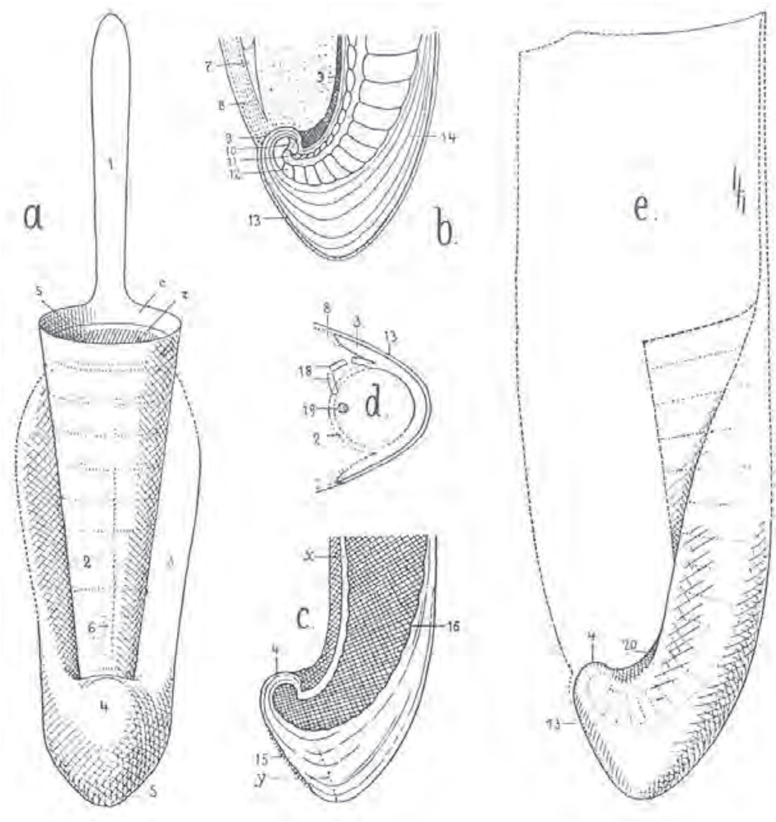


Fig. 3: *Spirulirostridium obtusum*, lost holotype (original of Naef 1922: 61, fig. 21), Lower Oligocene (Rupelian), Häring, near Kufstein. Reproduced after Naef (1922: fig. 21). Note that the anteriorly projected proostracum as indicated in reconstructions a) and e) is erroneous.

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.

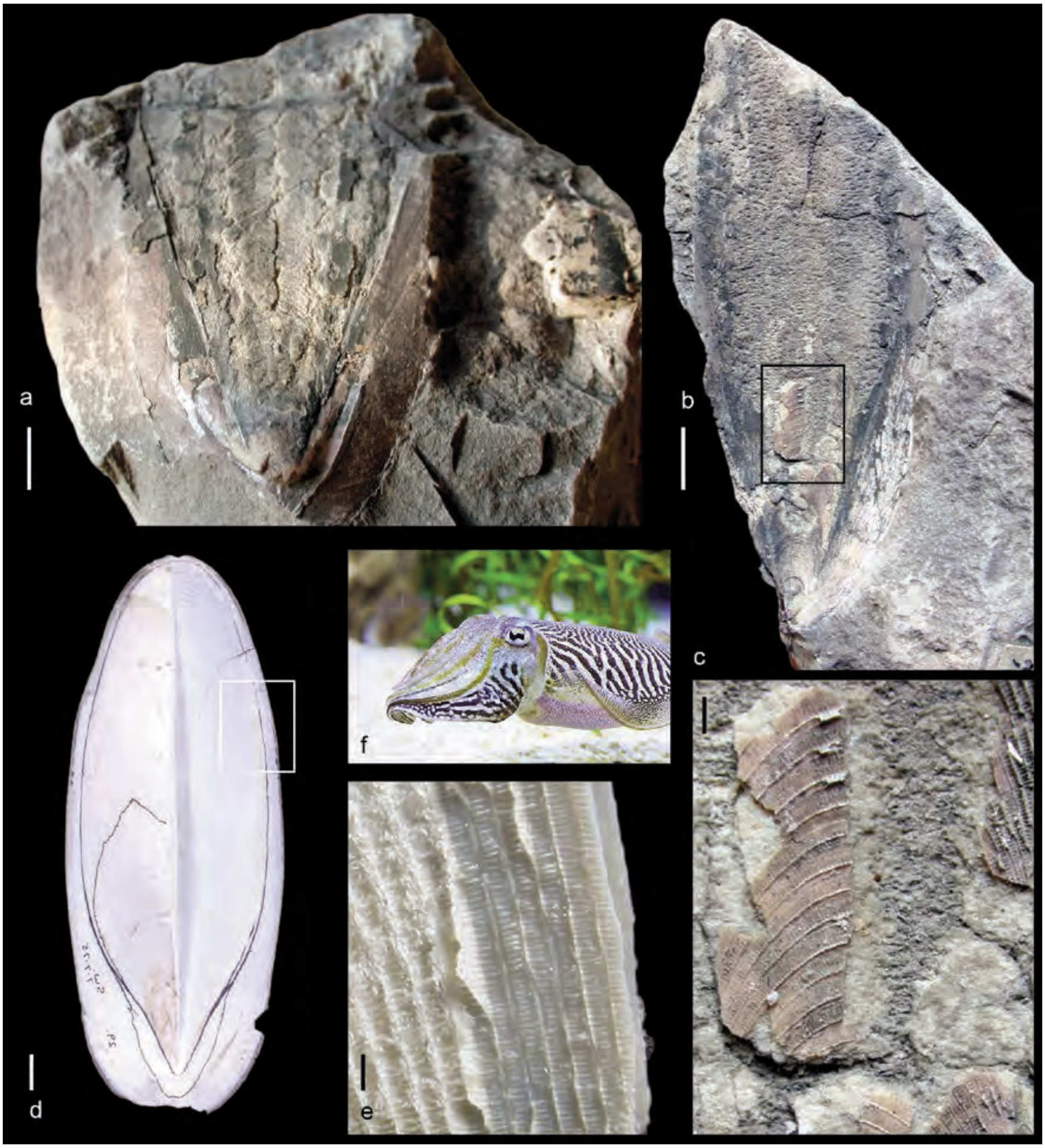


Fig. 4: Fossil (**a–c**) and Recent (**d–f**) cuttlebones. **a**: *Sepia vindobonensis*, holotype [original of SCHLOENBACH (1869: pl. 7, figs 1, 2), no. 8106, Sammlung der Geologischen Bundesanstalt Wien], Middle Miocene, Langhian, Baden near Vienna; positive in posterodorsal view. **b**: same specimen, 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**).

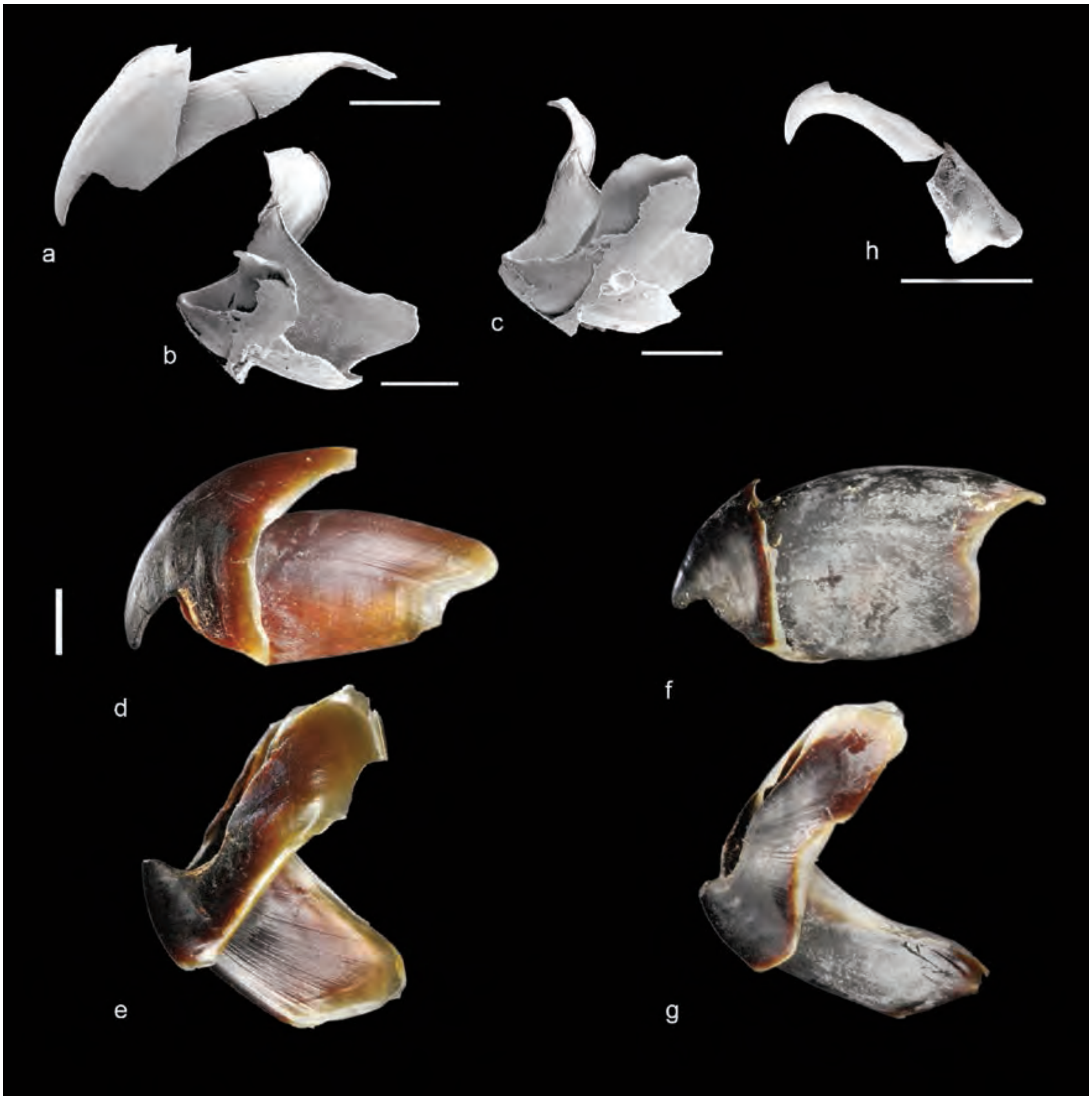
Type locality: Baden near Vienna.
Type horizon: Middle Miocene, Langhian (lower Badenian, Upper Lagenid Zone).
Other contemporary occurrences in Austria: Grund [Hollabrunn, Lower Austria, SCHAFFER (1958): 3 specimens, deposition unknown], Retznei [Steiermark, HIDEN (1995): 2 specimens, coll. WANZENBÖCK, 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

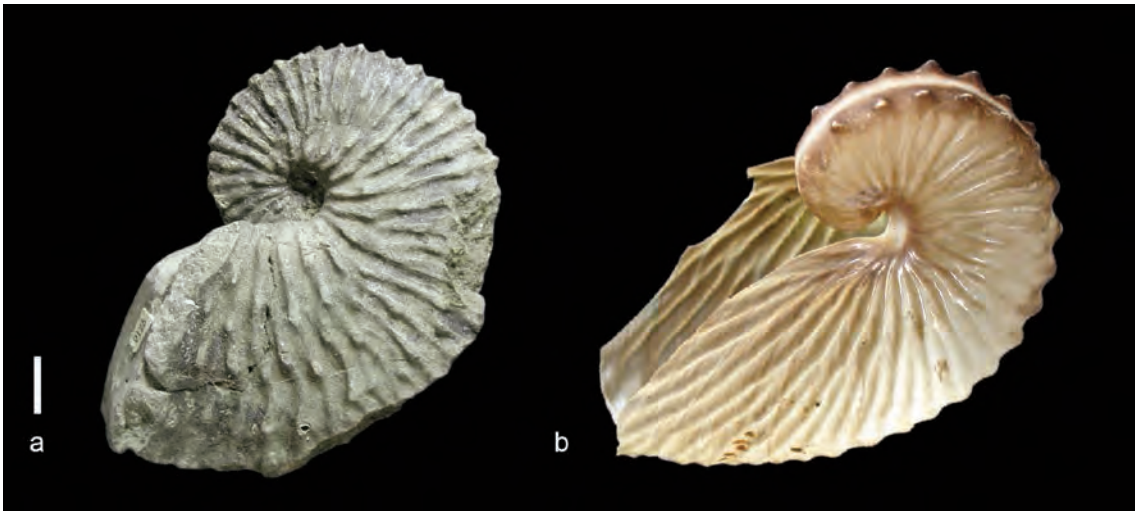


Fig. 6: 'Brood shells' of argonautids in lateral views. **a**: *Argonauta joanneus,* holotype [original of HILBER (1915: pl. 1), geological collection of the Universalmuseum Johanneum], Wenzelsdorf near Preding (Steiermark), Middle Miocene (Langhian); photo courtesy Martin GROSS. **b**: *Argonauta hians,*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