

Filling a Gap - Beaks and Hooks of Cenozoic Coleoids (Cephalopoda)

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(With 2 text-figures and 1 plate)

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Summary

For the first time fossil beaks and hooks of coleoids are described from the Badenian (Middle Miocene) of the Paratethys. Comparisons with Recent coleoids proved the cephalopod-nature of the remains, which are therefore indisputable evidence for post-Cretaceous coleoid beaks and hooks in the fossil record. The fossil beaks display good resemblance with the jaw-apparatus of sepiolids; similarities with beaks of loliginids and cranchiids are also discussed. The hooks derive from oegopsids and might represent an Onychoteuthidae.

Keywords : Coleoidea, cephalopod beaks, oegopsid hooks, Badenian, Middle Miocene, Paratethys

Zusammenfassung

Erstmals werden Kiefer und Haken känozoischer Coleoiden aus dem Mittelmiozän der Paratethys beschrieben. Vergleichstudien an rezenten Coleoiden bestätigten die Identifikation der Überreste, die somit den ersten, fossilen, post-kretazischen Nachweis dieser Coleoidenorgane ermöglichen. Die Kieferreste weisen gute Übereinstimmung mit denen rezenter Sepioliden auf; zusätzlich werden Ähnlichkeiten mit Kiefern von Loliginiden und Cranchiiden diskutiert. Die Haken stammen von Oegopsiden und dürften Onychoteuthiden zuzuordnen sein.

Schlüsselwörter : Coleoidea, Cephalopodenkiefer, Oegopsidenhaken, Badenium, Mittelmiozän, Paratethys

Introduction

Aragonitic shells and cuttlebones of cephalopods are well documented in the fossil record during the Cenozoic era (BÜLOW-TRUMMER 1920; HILBER 1915; LÖRENTHEY 1898; SCHULTZ 1976; SIEBER 1959). Moreover, cephalopods produce aragonitic statoliths, chitinous beaks, and hooks as hard parts with some, yet minor fossilisation potential. The latter two structures are common in Mesozoic deposits, but are completely missing in Paleogene and Neogene sediments. An exception are the calcareous coverings of some Cenozoic nautilid beaks, which were correctly recognised as early as the 19th century by BELLARDI 1872 or PARONA 1898. Another rare remainder of Cenozoic cephalopods is the calcareous, tiny statoliths first described by CLARKE & FITCH 1979.

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Nevertheless, no published data is available on beaks and hooks deriving from post-Cretaceous, fossil coleoids. This can be explained easily by the mineralogy of those hard parts, which typically excludes an adequate preservation. Only pelitic deposits such as the "Baden Tegel" from the Middle Miocene of the Vienna Basin provide conditions which may favour the fossilisation of those fragile elements.

The Beaks

Terminology (text fig. 1)

The present paper follows the terminology proposed by CLARKE 1962b & 1986, who developed a terminology for beaks which is generally accepted by most Anglo-American workers, whilst German authors follow the corresponding terminology of KAISER & LEHMANN 1971. A slightly deviating French variation is given by MANGOLD & FIORONI 1966. Thus the jaw apparatus is divided into an upper and a lower beak. The smaller upper beak terminates anteriorly in the curved, pointed, and usually darkened rostrum. In posterior direction the rostrum passes into the expanding hood and the wings. From the inner side of the rostrum a folded sheet expands also in posterior direction, consisting of the lateral walls which unite in the crest. The lateral walls are much longer than the hood and thus extend beyond this structure. The same terms are used for the description of the lower beak. This part of the jaw is broader and larger than the upper one. The hood is shorter; in contrast its wings expand strongly. A more detailed description of the beaks and their main differences is given in the above-mentioned papers.

Taphonomy and Preservation

Exposed to the air, the beaks of Recent squids and cuttlefishes, either washed ashore together with the dead animal or caught by fishery, are soon disconnected from the soft-parts and dry.

Several types of isolated beaks have been compared by the author, including octopods (*Octopus vulgaris* CUVIER, *Octopus dofleini* WULKER), cuttlefish (*Sepia officinalis* LINNÉ, *Sepioloa rondeleti* STEENSTRUP), and squids (*Loligo* sp., *Alloteuthis media* LINNÉ, Ommastrephidae). In the latter, upon drying, usually no relevant change in the shape of the rostrum and hood can be observed, but large parts of the lateral walls display a significant shrinking and tend to curl. It should be kept in mind that in the case of fossil beaks an exposure to air, e.g. in the supralittoral, can be excluded, since all findings derive from at least moderately deep sublittoral environments. Hence, drying effects as shown above could not have affected preservation. In reality, this observation merely emphasises the different structure and hardness of the pigmented crests and the light lateral walls of some beaks. Accordingly, the higher fossilisation potential of the crest in relation to the weak lateral walls - as documented by the upper jaw from Vöslau - is evident.

Material

The investigated material consists of 3 lower beaks; only one of them is more or less complete, with just slight damage at the inner side of the crest and lateral wings. The others consist of the rostrum, fragments of the hood without wings, and small parts of the crest. Additionally, 1 upper beak with rostrum and hood but broken wings is described.

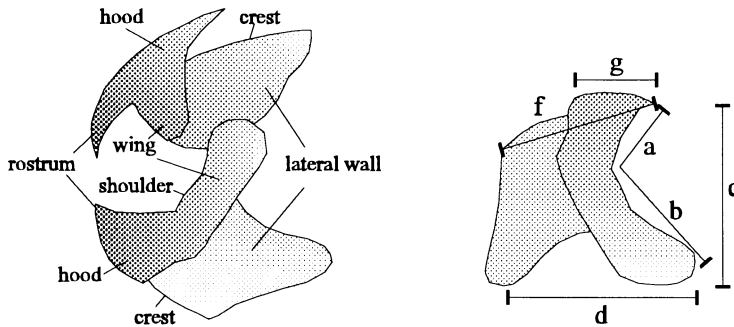


Fig. 1: Terminology of cephalopod beaks (for abbreviations see text).

The specimens were collected at the section of the brickyard Vöslau (Lower Austria) in the late 19th century and are stored in the collection of the Museum of Natural History in Vienna (Inv. Nr.: NHMW1999z0050/0001, NHMW1999z0050/0002). Although the section Vöslau is not exposed anymore, it is dated to Middle Miocene (Lower Badenian, Upper Lagenid Zone). The beaks derive from the Baden Tegel, bluish to greenish clays and marls with ancillary intercalations of sandy layers. The marls, actually representing the basinal facies in the Middle Miocene Vienna Basin, contain an extraordinarily diverse and well-preserved micro- and macrofauna as well as calcareous nannoplankton. The depositional depth of these marls is interpreted as ranging from 50-100 m by PAPP & STEININGER 1978 and 100-200 m by TOLLMANN 1985.

Description

1. Lower Beaks (pl. 1, figs. 3, 4, text fig. 2)

Two lower beaks consist only of the rostrum and fragments of the crests, but the third specimen is rather well preserved, representing the rostrum, the hood and almost complete wings; only the posterior edge of the hood-wing complex is damaged. Crest and lateral walls display some fractures, but one lateral wall is mainly complete; the very posterior termination of the crest might be broken.

From tip to the posterior termination the maximum length of the crest measures about 3.4 mm. The rostrum and a narrow area close to the jaw angle still display a concentration of dark colouring, whereas the wings and the crest are rather pale. The relations according to CLARKE 1986 are 2.2 for the edge-wing ratio (b/a), 0.9 for the height-base ratio (c/d), 1.8 for the hood-crest ratio (f/g), 1 for the crest-base ratio (d/f), 1 for the rostral-base ratio (h/a), and 1.9 for the hood-edge ratio (g/a); additionally d/e is 4.

The rostral edge is nearly straight, forming a very shallow, elongated S and terminates in a small, hardly hook-like rostral tip. In the same way the shoulder is slightly wavy, passing into the strongly wavy wing edges. On the inner surface the rostrum displays several scratches, probably caused by the feeding habits of the animal. The wing is narrow and elongated, broadening towards the inner end. Nonetheless the wings are slightly shorter than the crest, which is not very clear from the REM photos. The jaw angle is

obtuse rounded and barely hidden by a very weak wing fold; its wing angle is about 100°. None of the specimens displays a sharp, acute or even recessed angle. In lateral view the hood and the crest are both moderately curved. On the lateral walls an indistinct, hardly developed lateral wall fold is visible on the REM photos.

Although the posterior terminations of the lateral walls are damaged, they seem to have been parallel rather than spread.

Identification

As emphasised by many authors working on isolated beaks, a distinct identification is often very difficult. Nonetheless the general shape of beaks is rather homogeneous within many cephalopod families. Thus it is possible to compare the discussed lower beaks from Vöslau with distinct families. Several groups can be excluded with certainty on the family level.

Nautilidae: The nautilids are represented in the Paratethys by shells of *Aturia*. The beaks of nautilids with their calcareous layers are very different from those of the coleoids (KAISER & LEHMANN 1971) and can thus be excluded as candidates for the fossil beaks.

Octopoda: *Octopus* as well as *Argonauta* are known from the Middle Miocene of the Paratethys by borings or shells. The beaks of the Octopoda described by CLARKE 1986 and MANGOLD & FIORONI 1966 distinguish this group clearly from the specimens described herein. Especially the usually worn and very short rostrum and the narrow lateral walls are typical of octopuses, whilst the fossil beak bears a larger rostrum.

Sepiidae: The Sepiidae are documented from the Badenian of the Paratethys by various cuttlebones. The lower beaks of *Sepia* lack any jaw angle but display a curved connection between rostrum and shoulder, therefore differing clearly from the fossil beak, which developed an obtuse jaw angle.

Oegopsida: Among the oegopsid squids the recessed and/or acute jaw angle of many beaks allow an exclusion of the following families: Ommastrephidae, Architeuthidae, Thysanoteuthidae, Enoploteuthidae, Neoteuthidae, and Grimalditeuthidae. A usually strong ridge or fold crossing the lateral walls - a feature absent in the fossil specimens - characterises the lower beaks of the Psychroteuthidae, Enoploteuthidae, Lycoteuthidae, Octopoteuthidae, Lepidoteuthidae, Histioteuthidae, Cycloteuthidae, Mastigoteuthidae, Chiroteuthidae, and Batoteuthidae. Others such as the Gonatidae, ranging in cold to temperate waters, or the Bathyteuthidae, preferring deeper water, may be excluded based on their ecological requirements from having lived in the tropical/subtropical, rather shallow Vienna Basin.

Most of the Onychoteuthidae differ by a strong ridge on the lateral wall, whilst other representatives of this widespread family develop a marked step below the jaw angle. Some resemblance may be stated for species of the Cranchiidae, which are very diverse concerning beak form and are hard to identify from single specimens (CLARKE 1986). Beaks of *Leachia* and related genera correspond in many aspects to the described beak; According to CLARKE (1999 pers. comm.) all cranchiids are oceanic and avoid the shelf, thus this group probably did not enter the shallow Vienna Basin.

Myopsida: Among the Recent Loligonidae, several genera produce lower beaks highly similar to the fossil ones. As CLARKE 1986 pointed out they also closely resemble certain

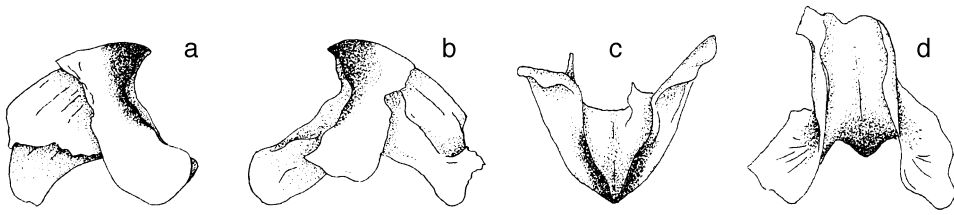


Fig. 2: Sketch-drawings of the lower beak from Vöslau: (a, b) lateral views, (c) front view, (d) inner view (all 8x).

sepiolids. Corresponding to the most complete lower beak from Vöslau the loliginid beaks display obtuse jaw angles, lack any distinct ridge or fold on the lateral walls, and show a similar extension of the colouring on the rostrum and the wings. A difference may be the rather short hood in relation to the crest ($f/g > 2$ after CLARKE 1986, $f/g = 1.8$ Viennese specimen), but due to the preservation the significance of this measurement is limited.

Sepiolidae: Agree in producing slightly S-shaped jaw edges and the obtuse jawangle. A narrow shoulder groove is usually developed and the lateral walls bear no folds or ridge. The measurements of the fossil beak range well within the data given by CLARKE, 1986 (bold letters represent fossil beak: $b/a = 1.7-4.3 / \mathbf{2.2}$, $g/a = 1.2-2.4 / \mathbf{1.9}$, $f/g = 1.8-2.6 / \mathbf{1.8}$). Similarly, the colouring of the fossil beak corresponds well to the pigmentation of several sepiolids.

Hence, the general features of the best-preserved lower beak from Vöslau allow a clear identification as a coleoid cephalopod. Among this group a relationship to the family Sepiolidae is indicated by the close resemblance of the lower beaks. Some similarities with representatives of loliginids and to a lesser extent with cranchiids can be stated but a classing within these groups seems less likely.

2. Upper beak (pl. 1, figs. 1, 2)

The 4.1 mm long beak is in a poor state of preservation, consisting of the rostrum, large parts of the hood and the crest. The lateral walls are completely missing and the wings are damaged. A detailed identification is hardly possible since many diagnostic features are lacking and exact measurements are hindered. Nonetheless some general observations can be made which reduce the number of possible producers of the beak. The following description concerns only the preserved hard parts; the derived relations between the single parts might thus not represent the relations of the beak before fossilisation and cannot be interpreted in the same manner as the data usually given for complete, Recent beaks.

The jaw angle is obscured by fractures, which actually only imitate a recessed type. The rostrum is pointed, terminating in a moderately curved tip; on its inner surface more or less concentric growth-lines are visible. The hood is well-rounded without an angulation or notch and fairly long in relation to the crest ($f/g = \text{ca. } 1.5$). Both rostrum and hood are largely pigmented; only the very posterior edges of the hood are yellowish clear. (Note that those edges do not correspond to the natural margins but are fractures). The crest also displays amber-like colouring but lacks dark pigmentations. Due to the lower fossilisation potential the lateral walls are broken and therefore only the ship-hull-like crest remained, terminating posteriorly in a narrow tip.

Identification

The poor preservation allows no distinct identification, and the beak may thus derive from a cuttlefish or from a squid; only nautilids and octopods can be ruled out. In correspondence to the lower beak, the typical shape and structure of these cephalopod groups exclude them clearly as producers of this upper beak. The beak can be distinguished from that of the octopuses by the hood length and the long rostrum; *Nautilus* develops a calcareous covering and displays a rather straight crest.

Since the upper beak corresponds well in size to the lower beak and because of the good fit in width, the author interprets both beaks deriving from the same species. The identification of the upper beak as a sepiolid is also supported by its size, width and the shallow water paleoenvironment.

The Hooks

(pl. 1, fig. 5)

Introduction

Fossil hooks of coleoid cephalopods are very rare; the stratigraphic range of the described cephalopod hooks covers a span from the late Carboniferous up to the late Cretaceous (ENGESER & CLARKE 1988), but no data on coleoid hooks from Tertiary sediments are published. The pre-Cenozoic remains are generally related to various belemnoid coleoids (ENGESER & CLARKE 1988). The ontogenetic formation of these fossil "belemnoid" hooks is primary (ENGESER 1990), thus displaying a markedly different development than hooks of Recent oegopsid coleoids, whose hooks derive from the chitinous rings in the suckers of the arms and/or tentacles (KRISTIANSEN 1977). The total lack of Cenozoic cephalopod hooks is explained by the very low fossilisation potential of the chitinous structure (ENGESER & CLARKE 1988).

Among Recent squids only few families produce hooks; the most important forms are represented by the Onychoteuthidae, Enoploteuthidae, Gonatidae, Octopoteuthidae, and Cranchiidae (ENGESER & CLARKE 1988). The hooks may appear both on the tentacular club and the arms or be carried only on one of them, a feature that differs from family to family. A detailed description of the hooks of some representatives of the families Onychoteuthidae, Enoploteuthidae, Gonatidae, Octopoteuthidae, and Cranchiidae is given by ENGESER & CLARKE 1988.

Terminology

KULICKI & SZANIAWSKI 1972 introduced a terminology for the description of Recent hooks and gave sketch drawings based on descriptions of the genera *Onychoteuthis* and *Ancistroteuthis* by NAEF 1922. This terminology was basically accepted by ENGESER & CLARKE 1988 and slightly modified; the latter terminology is adopted also in this paper. Accordingly, the hooks -both fossil and Recent - are generally divided into the uncinus, the shaft, and the base. For a detailed introduction to hook terminology and ontogenetic steps in hook formation see ENGESER & CLARKE 1988.

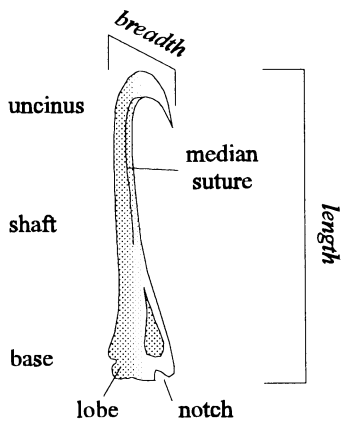


Fig. 3: terminology of coleoid chitinous hook.

Material

Two hooks were found at the locality Möllersdorf in Austria, about 4 km ENE from Baden near Vienna, and are stored in the systematic collection in the Museum of Natural History in Vienna (Inv. Nr. NHMW1999z0050/0003). The Coleoidea remains are historical samples labelled as „Krallen eines Cephalopoden,, („claw of a cephalopod,,) making them the first recognised, fossil Cenozoic hooks of a cephalopod.

The section Möllersdorf was intensively investigated by D. STUR 1870, F. KARRER 1877, and R. HOERNES 1875; the latter author additionally published a drawing of the section. During the early 20th century the outcrop fell into ruin and is no longer accessible. The described hooks derive from the “Baden Tegel”, which are dated to the Middle Miocene, Lower Badenian, Upper Lagenid Zone.

Only one hook is complete, but was broken during manipulation. The second hook consists of a fragment of the uncinus and the distal part of the shaft. No detailed information on the chemistry of the hooks can be given. Since the chitinous material has a low fossilisation potential, an - at least partial - replacement by calcium phosphate seems likely.

Description

The completely preserved hook was broken into two pieces during manipulation. The larger part consists of the uncinus and the main part of the shaft; its maximum length is 1.16 mm. The second piece comprises the base and the proximal part of the shaft, with a maximum length of 0.9 mm and a maximum diameter of 0.55 mm. Since a small part between the fragments crumbled, an exact measurement of total hook-length is impossible, but the approximate length was slightly more than 2 mm.

Generally the hook is asymmetrical, elongated, and slender with a rather short uncinus. In the area where the uncinus passes into the shaft a narrow, shallow depression appears and extends towards the base. In cross-section the shaft is blade-like on its inner side and gently rounded on the outer side. The very proximal part of the base bears a rounded

lobe which passes into a small ridge towards the shaft, being bordered by a narrow furrow. A broad notch on the basal side separates the lobe from a weaker lobe-like swelling, which develops a flattish ridge in distal direction. No external opening or pseudopulp cavity can be recognised, probably due to preservation.

Identification on family level

Following the hypothesis that the two tiny hooks from the Middle Miocene of the Vienna basin represent one of the Recent squid-families, instead of treating them as remnants of an extinct family, it is possible to approximate an identification on family level. On the one hand only a small number of squidfamilies develop hooks; in addition each of these families produces rather characteristic hooks, thus allowing a rough determination.

On the other hand some of the hook-bearing, Recent squids are highly adapted to geographically restricted habitats, for example the Gonatidae. These are chiefly cold water forms and among the most abundant squids in higher latitudes (ROPER, SWEENEY & NAUEN 1984), thus being rather unlikely candidates for the Viennese squid, which lived in the tropical/subtropical Paratethys Sea. In addition the hooks of the Gonatidae display a stronger curvature from uncinus to the shaft than the Viennese form does. The tentacular club hooks of *Gonatopsis borealis*, *Gonatus pyros*, *G. berryi*, and *G. californiensis* as illustrated in YOUNG 1972 are semicircular in side view and their shafts are short compared with the uncinus.

The hooks of the Octopoteuthidae are rather stout with a short shaft, therefore clearly differing from the slender, elongated hook of the Viennese species. The arm hook of *Octopoteuthis*, illustrated in YOUNG 1972, exhibits an extraordinarily broad base and a short shaft, while those of *Octopoteuthis deletron* differ also in their tendency to develop secondary hooks close to the base.

Similarly, the hooks of the Cranchiidae, as far as can be judged from the descriptions and illustrations in ENGESER & CLARKE 1988, are clearly differentiated from the discussed fossil hook by their short shaft, the tendency to produce ancillary teeth, and the different overall appearance of the curvature formed by uncinus and shaft.

Finally, among the living squid families the best correspondence with the fossil hook is exhibited by the families Onychoteuthidae and Enoploteuthidae.

The latter develop arm-hooks and larger tentacular-hooks. They are distributed mainly in tropical and subtropical seas but may extend also to temperate waters (ROPER, SWEENEY & NAUEN 1984). The hooks of the enoploteuthid and pyroteuthid genera *Pterygioteuthis* and *Pyroteuthis* (*Pterygioteuthis gemmata*, *Pyroteuthis addolux*, *P. margaritifera*), illustrated in YOUNG 1972, are typically short shafted with an acute angle between uncinus and shaft. Similarly the arm hooks of *Abraliopsis falco* and *A. felis* differ from the Viennese species by the short shaft, the extended uncinus, and the broad base. On the other hand the tentacular club hooks of these species are much more slender with elongated shaft, but differ also in their larger uncinus from the discussed form.

In contrast the Onychoteuthidae bear hooks only on the tentacular clubs; this is a cosmopolitan family ranging from the tropics to the Antarctic region. Some species attain maximum mantle lengths of more than 2 m, but the mean size is about 30 cm (ROPER, SWEENEY & NAUEN 1984).

The good resemblance between the fossil hooks and those of the central part of the tentacular clubs of the *Onychoteuthis borealijaponicus* - *banksii* group (illustrated in YOUNG 1972 and KULICKI & SZANIAWSKI 1972) furnishes evidence of a likely relationship between the new fossil species with representatives of the Onychoteuthidae.

Accordingly, at least the larger fossil hook can only be regarded as a tentacular club hook, since the Onychoteuthidae lack any hooks on their arms and the arm-hooks of the Enoploteuthidae differ markedly in their stout shape.

Other Cenozoic oegopsid squids

Until now no Neogene coleoid-hooks - a feature restricted to the oegopsids in Recent seas - have been reported (ENGESER & CLARKE 1988). Nonetheless, evidence for the Neogene is given by CLARKE & FITCH 1979. These fossil taxa from late Pliocene deposits in California are based only on aragonitic statoliths and are classified as remains of Gonatidae, Ommastrephinae, and Onychoteuthidae. The same authors published fossil, Cenozoic statoliths of the related myopsid squids of the genus *Loligo* (see also CLARKE & MADDOCK 1988).

Along with the squids, the shells and calcareous coverings of beaks of Nautilidae, cuttlebones of the Sepioidea, *Argonauta*-shells, and *Octopus* bore holes are often recorded. These remains are widespread but usually rather scattered in marine Cenozoic deposits all over the world.

Significance of the beaks and hooks for identification on species level

An identification of Recent coleoids on family or generic level based on isolated beaks is indeed possible as proved by several investigations on the stomach contents of whales (CLARKE 1986). An identification to species is apparently also reliable in many cases but is complicated by the various stages of preservation as well as by the high resemblance of beaks among some groups. From that, as pointed out by CLARKE 1986, a definition of a new species based only upon the beaks should be avoided. Therefore the almost complete lower beak from Vöslau cannot be used as the basis for a new species, and the fragmentary preservation of the other beaks clearly allows neither the distinction of a new species nor the identification of a distinct species. The same applies to the hooks from Möllersdorf.

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Plate 1

- Fig. 1: Coleoidea (Sepiolidae), upper beak oblique inner view – 29x
Vöslau, Inv. Nr. NHMW1999z0050/0001
- Fig. 2: Coleoidea (Sepiolidae), upper beak lateral view – 28x
Vöslau, Inv. Nr. NHMW1999z0050/0001
- Fig. 3: Sepiolidae, lower beak oblique lateral view – 22x
Vöslau, Inv. Nr. NHMW1999z0050/0002
- Fig. 4: Sepiolidae, lower beak oblique lateral view – 22x
Vöslau, Inv. Nr. NHMW1999z0050/0002
- Fig. 5: Coleoidea (Onychoteuthidae?), hook lateral view – 39x
Möllersdorf, Inv. Nr. NHMW1999z0050/0003

