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Morphology, taxonomy and trophic interactions of rostrum-less coleoids from the Late Triassic Polzberg *Konservat-Lagerstätte* (Lower Austria)

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Abstract

Coleoid cephalopods are widespread from the Mesozoic till today. The extinct group of the Phragmoteuthida is thought to represent either stem-neocoleoids, stem-decabrachians, or stem-octobrachians. The well-known, almost complete specimens of *Phragmoteuthis bisinuata* from the Carnian Polzberg *Konservat-Lagerstätte* near Lunz am See (Lower Austria, Northern Calcareous Alps) and Cave del Predil (Northern Italy, Julian Alps) come from historical collections. These specimens do not reflect the entire coleoid assemblage within this environment. In order to obtain a more complete picture of the Carnian coleoid fauna, 430 coleoid specimens from the Polzberg locality and 60 specimens from contemporaneous localities around Cave del Predil were studied in detail. All available elements (phragmocones, proostraca, cartilages, hooks, beaks, ink sacs) attributed to the coleoid fauna were recorded, measured and evaluated taxonomically and taphonomically. Reviews of historical collection material permitted comparisons with recently collected material. The notation of co-occurrences of other faunal elements yielded insights into the palaeoecological context of this Upper Triassic environment within the Polzberg Basin. The new material from Polzberg does not support the previous assumption of a monospecific composition of the Polzberg coleoid fauna. Instead, we report the occurrence of the new phragmoteuthid *Phragmoteuthis polzbergensis* nov. sp. and a newly excavated specimen of *Phragmoteuthis* indicates the presence of ten arms within the group of the Phragmoteuthida for the first time. Phragmocones with small opening angles combined with cylindrical (roundly closed) body chambers, and arm hook types which are unusual for phragmoteuthids indicate the presence of the basal coleoid group comprising the rostrum-less genus *Mojsisovicsteuthis*.

Keywords Belemnoids, *Konservat-Lagerstätte*, *Mojsisovicsteuthis*, Octobrachia, Palaeobiology, *Phragmoteuthis*, Reingraben Shales, Taphonomy, Triassic

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Introduction

Coleoid cephalopods are well known for their important roles in recent marine ecosystems (e.g., Clarke, 1996; Villanueva et al., 2017). Bite marks and occurrences of material in bromalites (regurgitalites and coprolites) provide insight into past predator–prey-interactions (Brachaniec et al., 2015; Lukeneder et al., 2020; Mondini, 2023). So far, the Alpine Triassic system yielded—besides ectocochleate cephalopods—aulacoceratid, phragmoteuthid, and another group of rostrum-less belemnoids around the highly variable genus *Mojsisovicsteuthis* Jeletzky, 1966 (Košťák et al., 2023;

Pohle & Klug, 2024). Belemnitid belemnoids already existed during the Triassic, but are still unknown from the Alpine region. One Ladinian and one Norian gladius suggest that early octobranchians at least sporadically roamed the western Tethys (Schweigert & Fuchs, 2012).

Discovered 150-years ago, the Polzberg locality (Fig. 1) has yielded many belemnoid hard tissues including phragmocones, proostraca, cephalic cartilages and arm hooks (Doguzhaeva & Summesberger, 2012; Doguzhaeva et al., 2006, 2007b; Lukeneder & Lukeneder, 2022b; Mojsisovics von Mojsvar, 1882; Suess, 1865). Soft tissues from ammonoids and belemnoids have also

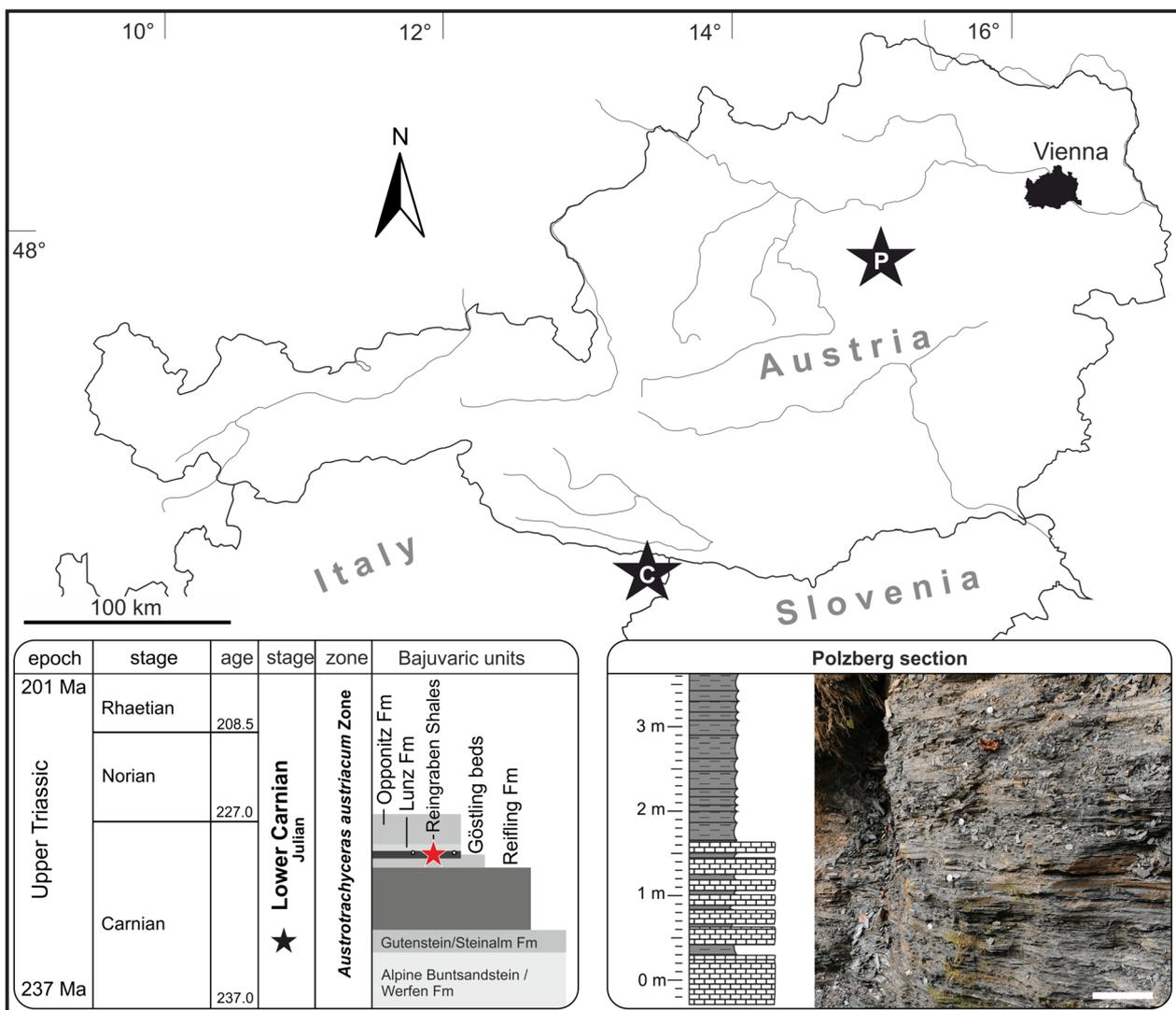


Fig. 1 Top: Austrian map with the Polzberg *Konservat-Lagerstätte* (= Schindelberggraben ravine, Polzberg locality) (star, P) and Cave del Predil (northern Italy; formerly: Raibl in Carinthia, Austria) (star, C) marked. Lower left: stratigraphic chart with Bajuvaric Formations and lithological overview log of Polzberg locality. Lower right: middle part of the vertical section with clays, marls and calcareous deposits of the Reingraben shales at Polzberg. Scale bar 20 cm

been reported (Doguzhaeva et al., 2007a; Lukeneder & Lukeneder, 2022a). However, much of the coleoid fauna is based on isolated, exceptionally preserved historical specimens, which do not reflect the entire faunal assemblage. Here, we apply taxonomic and taphonomic methods on specimens from this unique Carnian conservation deposit to capture the range of characteristics, which differ greatly from those of the few individual historical specimens previously described (Doguzhaeva & Summesberger, 2012; Doguzhaeva et al., 2006, 2007b). New examinations of nearly 500 individuals, some of which are nearly complete, allow us to provide a comprehensive systematic inventory, new taphonomic insights, and palaeoecological reassessments.

The Polzberg *Konservat-Lagerstätte*

The material derives from the Reingraben shales of the late Triassic (Julian II, Carnian) *Konservat-Lagerstätte* Polzberg (Fig. 1; GPS N 47° 53' 5.90" and E 15° 4' 27.70") (Lukeneder & Lukeneder, 2021, 2022a, 2022b; Lukeneder et al., 2020) at 712 m above sea level, which was first discovered by Stur (1874). The site is located about 4.5 km northeast of Lunz am See within the Polzberg Basin. It is part of the Bajuvaric Lunz Nappe System of the Northern Calcareous Alps (Piller et al., 2004). Historically, the Polzberg *Konservat-Lagerstätte* is synonymously known as Unter Polzberg, Pölzberg, Polzberg-Graben, Polzberg, Schindelberg and Schindelberggraben (Lukeneder & Lukeneder, 2021 and references therein). The site has yielded thousands of fossil specimens, many of which were found during targeted excavation campaigns in 1885 (GeoSphere, GBA; formerly Geological Survey of Austria) and in 1909 (Natural History Museum Vienna, NHMW) led by Bergwart Joseph Habermelner (Lukeneder & Lukeneder, 2021 and references therein).

First interpretations concerning the palaeoenvironmental conditions were published by Abel (1906), who proposed a shallow bay with temporary dessication (see also Krystyn, 1998). In contrast, Glaessner (1931) compared the Reingraben shales here with the German Posidonia shale, which represents a deeper, depositional environment, controlled by short- and long term oxygen-level fluctuations (Röhl et al., 2001). Krystyn (1998) proposed a basinal environment, cut-off from open marine conditions (see also Doguzhaeva et al., 2007b). More recent interpretations point to a deep marine environment with mainly nektic faunal elements (Lukeneder & Lukeneder, 2021, 2022a). Since this environment largely lacked infaunal elements and often even benthic fauna, the oxygen levels are proposed to have been dysoxic or even anoxic (Forchielli & Pervesler, 2013; Lukeneder & Lukeneder, 2021). The

exceptionally preserved fossils within these sediments support this hypothesis, which proposes a temporary extended oxygen minimum zone that prevented predators and scavengers from consuming the animal carcasses on the sea floor (see also Klug et al., 2024).

The significance of Polzberg coleoids

Fossils of Triassic coleoids are rare and thus insufficiently understood. Although a selection of well-preserved elements from the present coleoid fauna has been described (Doguzhaeva et al., 2007b; Mojsisovics von Mojsvar, 1882; Suess, 1865) a comprehensive report on its diversity and disparity is still missing.

Phragmoteuthida belong to a group of belemnoid coleoids that is commonly considered to include the last common ancestors of the two main lineages Decabrachia and Octobrachia (e.g., Fuchs & Donovan, 2018; Kröger et al., 2011; Stevens et al., 2023). Broadly speaking, phragmoteuthids are known to have a mineralized and chambered phragmocone with an anterior three-lobed (tripartite) proostracum and hook-bearing arms. The ventrally open proostracum makes Phragmoteuthida transitional between ancestral belemnoids (Hematitida, Donovaniconida, Aulacoceratida) with a tubular body chamber (final chamber) and Mesozoic neocoleoids that have a slender spatulate proostracum where the free and powerful muscular mantle inserted (Fuchs et al., 2016; Klug et al., 2016). This makes morphological knowledge of the Phragmoteuthida important for evolutionary character polarizations and reconstructions. As coleoid fossils often occur in black shales and thus are compacted, understanding their taphonomy is crucial to correctly interpret their morphology.

Several aspects of phragmoteuthid morphology are still unclear: (1) In belemnoid coleoids, hook morphologies can vary within the same specimen and even within a single arm (Hoffmann et al., 2017); the systemic value of belemnoid hooks is accordingly ambiguous. Hence, the perspective to find a hook morphotype unambiguously characterising phragmoteuthids is attenuated (Fuchs & Hoffmann, 2017; Fuchs et al., 2021). (2) The various cephalic cartilages described from the Alpine Triassic (Lukeneder & Lukeneder, 2022b, 2022c; Rieber, 1970) are mostly preserved without associated shell remains which makes it difficult to unambiguously identify a morphotype that belonged to phragmoteuthids. (3) Until now, rostrum-less specimens from the Alpine Triassic were tentatively assigned to the genus *Phragmoteuthis* Mojsisovics (1882). Given the morphological variation in specimens from Cave del Predil and Polzberg (Lukeneder & Lukeneder, 2022b, 2022c), it is likely that the diversity

is higher. More precisely, there are at least two genera with at least four species.

In addition to an incomplete knowledge, misleading information and doubtful identifications complicates the work with coleoids from Polzberg and Cave del Predil. The main goal of this study is to determine the taxonomic position of the coleoid remains from the Polzberg *Konservat-Lagerstätte*.

Material and methods

As the fossils from historical excavations or private collections are hardly assignable to particular stratigraphic horizons, a recent excavation campaign provided new bed-by-bed collected phragmoteuthid specimens. The lowermost fossiliferous layers (Po – 50 cm) at the Polzberg *Konservat-Lagerstätte* main outcrop were sampled directly in the stream.

Overall, 490 coleoid fossils were examined, 286 of which originate from in situ bed-by-bed collections and 204 specimens from historic collections. 60 historic specimens come from Cave del Predil, 144 from the Polzberg *Konservat-Lagerstätte*. All specimens were measured and taken into account within their group of fossil elements. 217 specimens from recent excavations include a phragmocone and/or a proostracum (shell material within coprolites was excluded as it would falsify the analysis). The numbers of examined specimens and their distribution in the institutional collections are provided in Table 1. Where possible, length and width of beaks were measured and noted. Their measurements and shapes need further research.

So far, 74 belemnoid cephalic cartilages from the two localities are known. 59 of them were previously described in Lukeneder & Lukeneder (2022b). The total number of preserved cephalic cartilages is

63 from the Polzberg *Konservat-Lagerstätte* (28 of which were collected bed-by-bed). Nine cartilages originate from historical excavations at Rinngraben (also Rinnengraben) near Cave del Predil, where they are much more poorly preserved and often appear distorted on the distal ends of the elements being bloated. Nevertheless, the particular elements can still be identified when comparing the structures to the cartilages from Polzberg.

The presence or absence of the main anatomical features of the phragmoteuthid body plan (phragmocone, proostracum, arm crown, hooks, cartilage, beaks, soft tissues) were noted and used to determine their degree of completeness. Where possible, the elements of the specimens were measured using a digital calliper (supplementary Figure S1; supplementary Table S2). Maximum lengths and widths of each phragmocone and/or proostracum were measured; phragmocone-lengths-to-proostracum-lengths-ratios were calculated. The lengths of the cephalic cartilages and hooks were measured. The hooks were assigned to one of the five basic hook types (Fig. 3), whereas type 2 hooks are supposed to represent so-called “megaonychites”.

A selection of the preserved fossils was drawn digitally with the Software Corel Draw X5 and photographed with a Nikon D 5200 SLR, lens Micro SX SWM MICRO 1:1 Ø52 Nikon AF-S, Digital Camera, combined with the graphic tool (freeware) digiCamControl Version V.2.1.2.0 at the Natural History Museum Vienna (Macrophotography). For high-resolution digital microphotography a Discovery.V20 Stereo Zeiss microscope, processed with the software AxioVision SE64 Rel. 4.9 imaging system, was used at the NHMW.

EDX-Scanning Electron Microscopy (EDX-SEM) (supplementary Data S3): SEM surface images but also the present internal structures of the specimens NHMW 2021/0123/0080 (black substance, Polzberg), NHMW 2021/0123/0015a, b (hooks, Polzberg), NHMW 2005z0005/0010 (ink sac from Polzberg) and NHMW 2021/0016/0396 (ink sac from Cave del Predil) were examined at the Central Research Laboratories of the Natural History Museum Vienna. Belemnoid hooks and black substance associated with belemnoid proostraca were examined at the Institute of Physics and Materials Science (IPM) at the University of Natural Resources and Life Sciences (BOKU). Both gold-sputtered (BOKU) and un-sputtered (NHMW) specimens were measured in low-vacuum settings with an accelerating voltage of 15 kV. The microscope was equipped with an Everhardt Thornley SED-Detector. The JEOL “Hyperprobe” JXA 8530-F field-emission electron microprobe (FE-EPMA) in combination with an online JEOL quantitative ZAF-correction program was used for overview photos.

Table 1 Numbers of examined coleoid specimens in the various Austrian and Italian collections

	Polzberg (Lower Austria)	Cave del Predil (Italy)
IPUW	–	1
GBA	–	28
NHMW	430	25
MFSN	–	1
MUL	–	2
GEOW	–	3
Total sample size	430	60

GBA GeoSphere Austria (former Geological Survey of Austria), IPUW Department of Palaeontology, University of Vienna (Austria), NHMW Natural History Museum Vienna (Austria), MFSN Museo Friulano di Storia Naturale Udine (Italy), MUL Montanuniversität Leoben (Austria), PIMUZ Palaeontological Museum of the University of Zürich (Switzerland), GEOW University of Heidelberg (Germany)

A fully focused electron beam was combined with an accelerating voltage of 5 and 15 keV and a beam current of 5 nA. The beam diameter was approximately 70–80 nm for these analyses, while the count rate was 1055.00 CPS.

A reliable differentiation between *P. bisinuata* from Cave del Predil and the studied Polzberg specimens required restudying the type material of Bronn (1859), Suess (1865), and Mojsisovics von Mojsvar (1882). Therefore, the type material was examined and measured (see also supplementary Table S2). The adopted systematics and terminologies follow Fuchs and Hoffmann (2017), Fuchs and Donovan (2018), and Klug et al. (2023).

Institutional abbreviations

GBA GeoSphere Austria (former Geological Survey of Austria)

IPUW Department of Palaeontology, University of Vienna (Austria)

NHMW Natural History Museum Vienna (Austria)

MFSN Museo Friulano di Storia Naturale Udine (Italy)

MUL Montanuniversität Leoben (Austria)

PIMUZ Palaeontological Museum of the University of Zürich (Switzerland)

GEOW-HD University of Heidelberg (Germany)

Results

The fossil coleoids from the Polzberg locality

The exceptional preservation of coleoid remains in *Konservat-Lagerstätten* is linked to the palaeoecological factors in this stagnant, oxygen-poor environment. All remains are embedded parallel to bedding. No signs for transport such as current-aligned shell accumulations or size sorting are found in the Polzberg deposits.

Although most coleoid shells from the most recent excavation campaigns are preserved only as fragments, some specimens preserve aragonitic phragmocones and phosphatised proostraca, carbonised ink sacs (supplementary Data S3) and beaks, mineralized cephalic cartilages (see Lukeneder & Lukeneder, 2022b), and carbonized arm hooks (supplementary Data S3) of various shapes. Evidence of non-belemnoid coleoids, e.g. octobranchian gladius remains, is still absent in Polzberg.

Interestingly, the phragmocones and the proostraca (some of them with carbonized organic matter inside; see also supplementary Data S3) show different preservation states throughout the section. The proostraca of the lower, calcareous part of the section (layer Po –50 cm to Po 8) are usually whitish, while those from the middle (layers Po 9 to Po 12) and upper (layers Po 13 to Po 18) parts appear yellowish. A few remains are associated with Thylacocephalans (*Atropicaris striata*).

The mean phragmocone length from recently excavated material at the Polzberg main outcrop was 12.0 mm (n=47), the average proostracum length 13.9 mm (n=166). Among the entire material, five phragmoteuthids were found with a nearly complete phragmocone and proostracum (NHMW 2005z0005/0021; NHMW 2005z0005/0023; NHMW 2005z0005/0032; NHMW 2012/0228/0495). Four specimens (NHMW 2005z/0005/0023; NHMW 2021/0001/0003; NHMW 2021/0016/0400; NHMW 2021/0123/0090) include in situ preserved elements of the arm crown showing double rows of hooks. Specimen NHMW 2005z0005/0021 is particularly informative, because it portrays an in situ association of phragmocone with proostracum, cephalic cartilage, and scattered arm hooks (type 3, 5), as well as the large and rare type 2 hooks, interpreted as probable megaonychites. Overall, 77 specimens contain arm hooks, whereas 30 coprolithic samples contain belemnoid body parts (hooks, shell material, cartilage).

Although seven specimens were found with double-rowed hooks as parts of in situ preserved belemnoid arms, only one specimen with a complete arm crown was recorded (NHMW 2021/0123/0090). Additional historical specimens exhibit partly preserved arms.

Unless otherwise stated, the following measurements refer to the material from recent excavations. The phragmocone fragments range from widths of 1.49 mm to 49.56 mm, whereas the proostraca and corresponding fragments range from 1.00 to 73.86 mm. The fragment sizes decrease throughout the section from the older to the younger layers.

Beaks (jaws) measuring up to 7.10 mm were identified in five recently collected specimens and four historic collection specimens. These beaks are usually preserved close to the remaining carcass. Three specimens from recent collections at Polzberg include arm hooks and at least one beak element (upper or lower beak). 35 non-coprolite specimens contain associated hooks.

The carbonised hooks can be arranged in five general shapes (Fig. 3; supplementary Data S3). Two types of curved hooks (type 1 and type 5) can be distinguished by the length of their bases and by the curvature. The most frequently occurring hook type is characterised by a stylet shape (type 3). A single specimen (NHMW 2006z0235/0001) stands out by the presence of curved type 4 hooks (Fig. 3d) with a strongly knobbed inner process. These basic hook types were present in both the historical and in the new material. Arm hooks are frequently found in association with cephalic cartilages at Polzberg. Type A cephalic cartilages from recent and historical collections at both Polzberg are mainly found in association with type 3 (Figs. 3c, 6, 8, 9) and type 5

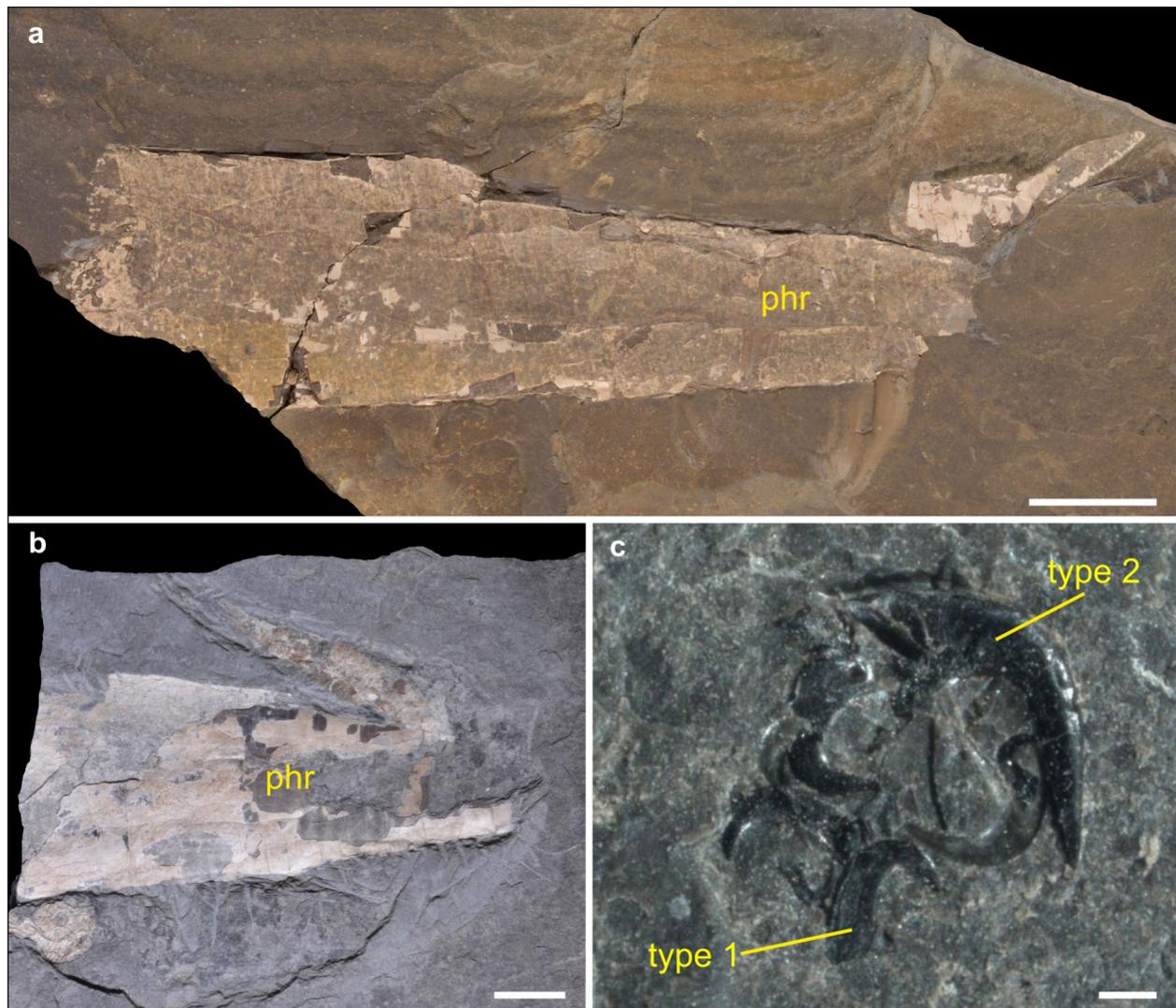


Fig. 2 Evidence for the presence of the *Mojsisovicteuthis* sp. from the Polzberg *Konservat-Lagerstätte*. **a** Phragmocone with low opening angle in clayey sediment shows a slight yellowish preservation. Note broken or even bitten apex of the phragmocone (NHMW 2021/0124/0047). **b** Phragmocone with low opening angle, assigned to *Mojsisovicteuthis* sp. (NHMW 2005z0005/0039). **c** Coprolithic specimen NHMW 2021/0123/0197 exhibiting arm hook type 1 and probable megaonychites (type 2). phr phragmocone. Scale bars **a, b** 1 cm; **c** 1 mm

(Figs. 3e, 9). In contrast, the more primitive hook-types 1 (Figs. 2c, 3a; curved uncinus, short base) and 2 (Figs. 2c, 3b) are mainly found within coprolites (Figs. 2c, 3f).

First evidence of aulacoceratid-like coleoids in Polzberg

Besides Phragmoteuthida, we found remains that display an unusual mosaic of characters suggesting the presence of another group of belemnoids.

1. Phragmocone opening angle: an opening angle of 25–30° is common for Phragmoteuthida. In several specimens of the other type, the measured mean

opening angle is 15–20° (see also supplementary Figure S1) and thus much lower (Fig. 2a, b). The flattened state of the phragmocones from Polzberg and Cave del Predil complicates their determination. Still, a much lower original opening angle can be inferred in most cases.

2. Absence of tripartite proostraca. In specimens with a lower opening angle, a tripartite “proostracum”—typical for phragmoteuthids—as a rule—absent. Instead, the body chambers are always long and tubular (Fig. 2a, b).

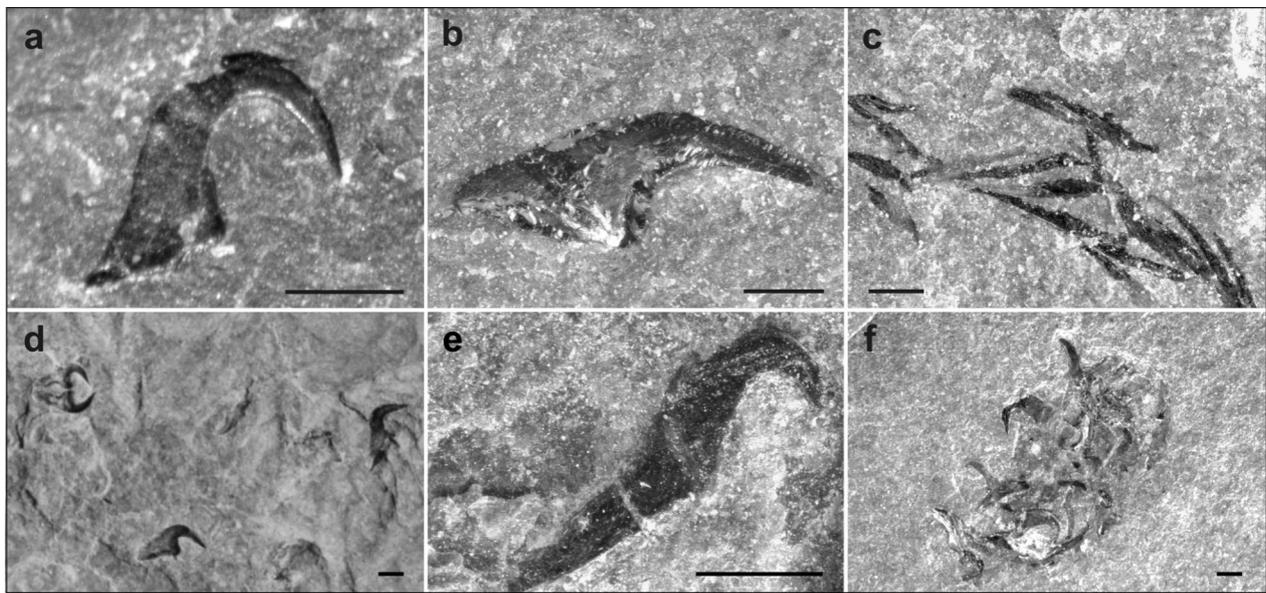


Fig. 3 General coleoid hook types from the Polzberg *Konservat-Lagerstätte* and Cave del Predil. **a** Curved hook type 1 (NHMW 2021/0123/0216). **b** Hook type 2 (“megaonychites”) which is commonly only found isolated or within coprolites (NHMW 2021/0123/0213). **c** Stylet shaped hook type 3 (GBA 2006/011/0001), as it is found in *Phragmoteuthis bisinuata*. **d** Curved hook type 4 (NHMW 2006z0235/0001) with curved, splitted base, found in association with specimen of *Mojsisovicsteuthis* sp. **e** A curved hook type with a long base (type 5; NHMW 2012/0117/0011). **f** Abundant coprolites include hook type 1 (NHMW 2021/0123/0227). All scale bars 250 μ m

3. Body chamber with well-preserved dorsal crests. The body chambers of specimens NHMW 2005z0005/0028 (Fig. 4a), NHMW 2012/0228/0515 (Fig. 4c) and NHMW 2005z0005/0010 (Fig. 4d) unambiguously portray short dorsal projections. Forward projecting growth increments visible on fragmentary specimens support such a dorsal crest, which is known from aulacoceratid body chambers (Fig. 4).
4. Septal spacing: although septa are poorly visible in our material, phragmocones with a narrow angle and a tubular body chamber suggest that the chambers are shorter than the corresponding phragmocone diameter.
5. Hook types: isolated hooks or hooks in coprolites are dominated by forms with a short base and distinctly curved uncinus typical of the *Arites* shape complex (Type 1; Figs. 2c, 3a, compare Zawidzka, 1974) (see also supplementary Table S2). The stylet-shaped hooks exclusively associated with phragmoteuthid remains are not included in coprolites.

The tubular body chamber with a dorsal crest and a comparatively low opening angle of the phragmocone could point to the presence of aulacoceratid coleoids in Polzberg. However, the short chambers, and most importantly, absence of aulacoceratid rostra, do not support aulacoceratid affinities. Instead, such a

character combination matches that of the poorly known genus *Mojsisovicsteuthis* (Anisian-Carnian). So far, *Mojsisovicsteuthis* is a heterogenous genus including forms with longiconic as well as breviconic phragmocones (Košťák et al., 2023; Pohle & Klug, 2024). Opposite to earlier works, Mariotti and Pignatti (1992, 1994) and Mariotti et al. (2021) indicated that the genus is not an aulacoceratid. Mutvei (1971) mentions *Mojsisovicsteuthis?* sp., but its identification is doubtful. Since it is beyond the scope of the present contribution to resolve the taxonomy and the systematic affinities of *Mojsisovicsteuthis*, we preliminarily follow Pohle & Klug (2024) and Košťák et al. (2023) who regarded this catch-all genus as being of uncertain ordinal and family status.

Systematic palaeontology

Subclass Coleoidea Bather, 1888

Stem Neocoleoidea Haas, 1997

Order UNCERTAIN

“*MOJSISOVICSTEUTHIS* Group”

Family UNCERTAIN

Genus *MOJSISOVICSTEUTHIS* sp.

(Figs. 2a, b, 3d, 4).

Remarks: The genus *Mojsisovicsteuthis* is here regarded as a waste-basket taxon for endococheate cephalopods that exhibit a long and tubular body chamber, a phragmocone opening angle of 15° to 20°, and that lack a massive rostrum covering the apex of the phragmocone.

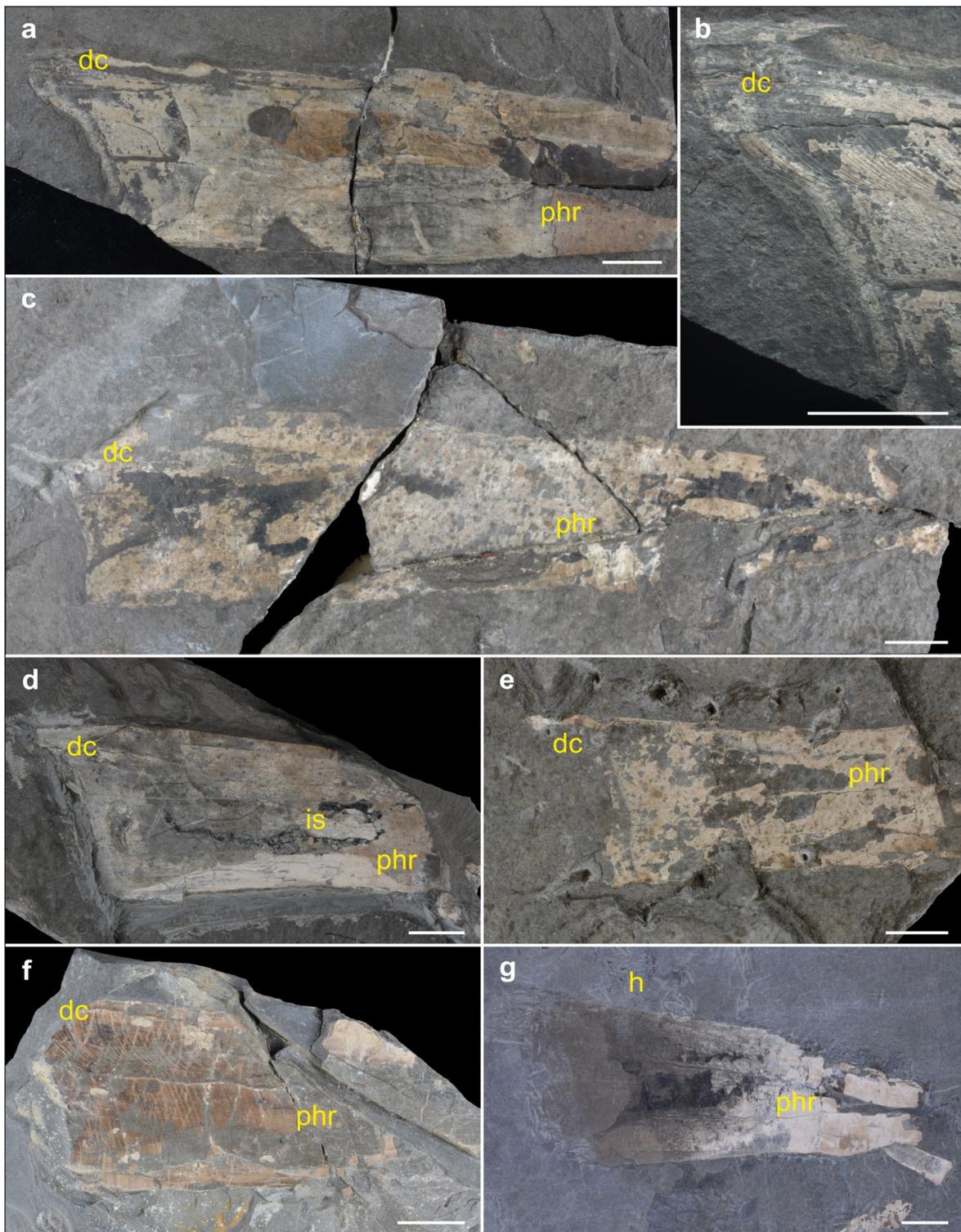


Fig. 4 *Mojsisovicsteuthis* sp. **a** NHMW 2005z0005/0028 with low opening angle and characteristic dorsal crest preserved. **b** Magnification of **a**, with well-preserved dorsal crest. **c** NHMW 2012/0228/0515 with dorsal crest preserved and low opening angle of 14.4°. **d** Phragmocone with dorsal crest and probable remains of ink sac (NHMW 2005z0005/0010). **e** Poorly preserved dorsal crest of living chamber (NHMW 2012/0228/0561). **f** Well-preserved dorsal crest in specimen NHMW 2021/0124/0057. **g** Specimen with non-mineralised last chamber, low opening angle of phragmocone and hooks with a curved base (hook type 4) (NHMW 2005z0005/0027). dc dorsal crest; h arm hooks; is ink sac; phr phragmocone. All scale bars 1 cm

It appears to be transitional between rostrum-bearing Aulacoceratida typified by a comparatively wide septal spacing, and proostracum-bearing Phragmoteuthida with a comparatively dense septal spacing (compare Fuchs & Donovan, 2018; Mariotti et al., 2021).

Material: Overall 54 specimens were assigned to *Mojsisovicsteuthis* sp. These specimens encompass three that are of uncertain affinity and hence cf. *Mojsisovicsteuthis* sp., 28 from historical collections at the NHMW, and 26 from recent excavations, inventoried at the NHMW. Exceptional specimens are NHMW 2005z0005/0027 (Fig. 4g), NHMW 2005z0005/0028 (Fig. 4a), NHMW 2005z0005/0039, NHMW 2005z0005/0010 (Fig. 4d), NHMW 2006z0235/0001, NHMW 2012/0228/0515 (Fig. 4c), NHMW 2012/0228/0561 (Fig. 4e), NHMW 2021/0124/0057 (Fig. 4f) and NHMW 2021/0124/0092, as they preserved their long and tubular body chamber including its dorsal crest. Specimen NHMW 2005z0005/0028ab exhibits a nearly complete shell allowing to reliably reconstruct its relative length.

Description: The orthoconic phragmocone opens with angles ranging from 10° to 20° (mean: 15.25°). The almost fully preserved specimen (apex poorly visible) NHMW 2012/0228/0515 (Fig. 4c) is 143.37 mm long, and 35.62 mm wide (at its widest; corresponding to its maximum diameter). Statements about the phragmocones cross sections are impossible owing to the flattened state of preservation. Sutures are poorly visible, but NHMW 2006z0235/0004 suggests a ratio chamber length to chamber diameter of approximately 0.2. Phragmocones with preserved apex lack a rostrum proper. The body chamber is nearly tubular (opening angle < 5°) without evidence of a ventral opening. It is almost as long as the phragmocone (ratio body chamber length to total shell length c. 1) and furnished with a short dorsal projection. This projection (dorsal crest after Jeletzky, 1966) is evenly rounded and takes c. 15% of the body chamber length (or 8% of the total shell length).

A specimen with in situ arm crown and hooks was not available for examination, but scattered type 4 hooks are preserved next to specimen NHMW 2005z0005/0002 (=NHMW 2006z0235/0001) (Fig. 3d). These hooks are curved with a bimodal base and prominent knobbed inner process. Cephalic cartilages associated with shell remains belonging to *Mojsisovicsteuthis* sp. are still unknown.

Comparisons: Apart from the opening angle, which is larger in *P. bisinuata* than in *Mojsisovicsteuthis* sp., the long tubular body chamber is strikingly different from the three-lobed proostracum of *P. bisinuata*. The dorsal crest is similar to that described for aulacoceratids (Jeletzky & Zapfe, 1967) and cannot be confused with the anteriorly rounded median field of *P. bisinuata*. Moreover, the

specimens appear larger and more massive than those of *Phragmoteuthis* from Polzberg.

The strongly curved hooks of morphotype 4 associated with NHMW 2006z0235/0001 are not observed in the arm crowns attributed to *P. bisinuata*.

Three specimens described and figured as *P. bisinuata* in Doguzhaeva et al. (2007b: NHMW 2006z0235/0001, 0003, 0004) are here reinterpreted as *Mojsisovicsteuthis* sp. Comparisons of the specimens indicate that the presence of a three lobed proostracum is questionable, while a tubular body chamber is likely. The apical angle of the phragmocone ranges between 18.4° and 19.9°. The total lengths of these specimens are extrapolated as 135.00 mm (NHMW 2006z0235/0001), 150.00 mm (NHMW 2006z0235/0003) and 150.00 mm (NHMW 2006z0235/0004).

The here described specimens and the previously described materials of *Mojsisovicsteuthis* (e.g., Pohle & Klug, 2024) share a comparatively short septal spacing, and the lack a massive rostrum. These characters exclude a systematic affinity with the order Aulacoceratida. More specifically, the Polzberg specimens resemble forms with a longiconic phragmocone such as *Mojsisovicsteuthis boekhi* (Košťák et al., 2023), *M. convergens*, the type species of the genus (Jeletzky, 1966) and the recently described *Ticinoteuthis chuchichaeschli* Pohle & Klug, 2024. In the latter taxa, the phragmocone cross section is elliptical (laterally compressed in *M. boekhi* and *M. convergens*; dorsoventrally depressed in *T. chuchichaeschli*). Unfortunately, this character is difficult to determine in our flattened specimens. Similarly, we are currently unable to determine the suture line course, which usually exhibits lateral lobes in at least some species of *Mojsisovicsteuthis* (Košťák et al., 2023).

Until now, our knowledge of the genus *Mojsisovicsteuthis* was solely based on phragmocones and internal moulds of partially preserved body chambers (Rieber, 1973); complete body chambers were unknown until now.

The genus *Mojsisovicsteuthis* is known to be morphologically intermediate between Aulacoceratida and Phragmoteuthida (Jeletzky, 1966; Košťák et al., 2023; Pohle & Klug, 2024; Rieber, 1974). Its identification is supported by smaller phragmocone angles, presence of a tubular body chamber (rather than a tripartite proostracum) and various hook types, which apparently do not belong to phragmoteuthid belemnoids. Hence, there is strong evidence that the genus *Mojsisovicsteuthis* contemporaneously lived in the same area as *Phragmoteuthis*. Both taxa were believed to share their stratigraphic ranges but they have not been found in the same localities yet.

We reject systematic affinities with the Aulacoceratida for the following reasons. Unambiguous aulacoceratids (as well as orthoceratoids; see Pohle & Klug, 2024) are

known from different regions of the Alps (Bülow, 1916; Hauer, 1847; Mojsisovics von Mojsvar, 1871; Wöhrmann, 1893), but not from Polzberg. As aragonitic shell elements are preserved in Polzberg, it is unlikely that the aragonitic rostra of *Mojsisovicsteuthis* are diagenetically lost. Instead, it indicates that aulacoceratids were absent in this locality. Westermann (1973) states for aulacoceratids meso- to epipelagic habitats, while *Mojsisovicsteuthis* had implosion depths of around 250 m.

At least four taxa were described from the lower Carnian of Austria and neighbouring countries (“*Aulacoceras*” *convergens* Hauer, 1847, “*Aulacoceras*” *ellipticum* Mojsisovics, 1871, “*Aulacoceras*” *obeliscus* Mojsisovics, 1871, “*Orthoceras*” *boeckhi* Stürzenbaum, 1876). “*Orthoceras*” *styriacum* Mojsisovics von Mojsvar, 1873 (pl. 1, Figs. 6, 7) is potentially another member of this group, and seems to have a similar dorsal crest (see also Pohle & Klug, 2024). Further species, tentatively assigned to *Mojsisovicsteuthis* are “*Atractites*” *meneghini* and “*Atractites*” *subrotundus* Rieber (1973).

It is likely that their arms were equipped with hooks. Our results support the presence of primitive hook types such as type 1 and 4 (Fig. 3) and the probable megaonychites (type 2) within this belemnoid group.

Crown group node Neocoleoidea Haas, 1997

Order PHRAGMOTEUTHIDA Mojsisovics von Mojsvar, 1882

Family PHRAGMOTEUTHIDAE Mojsisovics von Mojsvar, 1882

Genus PHRAGMOTEUTHIS Mojsisovics von Mojsvar, 1882

Type species. *Phragmoteuthis bisinuata* (Bronn, 1859), designated by Mojsisovics von Mojsvar (1882) (pl. 305).

Diagnosis (modified from Fuchs & Donovan, 2018): Phragmocone medium sized, orthoconic, opening angle 25°–30°; chamber length short; sutures simple; septal necks orthochoanitic, connecting rings extremely long and superimposing 5–6 previous rings; siphuncle marginal; proostracum length equals phragmocone length, anterior median field weakly acute; lateral field slightly shorter than median field, relative length variable; hooks mainly, stylet shaped (sometimes with small, curved uncinus).

Regional distribution: Austria, Germany, Italy, UK, ?Vietnam.

Stratigraphic range. The genus *Phragmoteuthis* is reported from the Anisian (Middle Triassic) to the latest Sinemurian (Lower Jurassic).

Phragmoteuthis bisinuata Bronn, 1859
(Figures 5, 6)

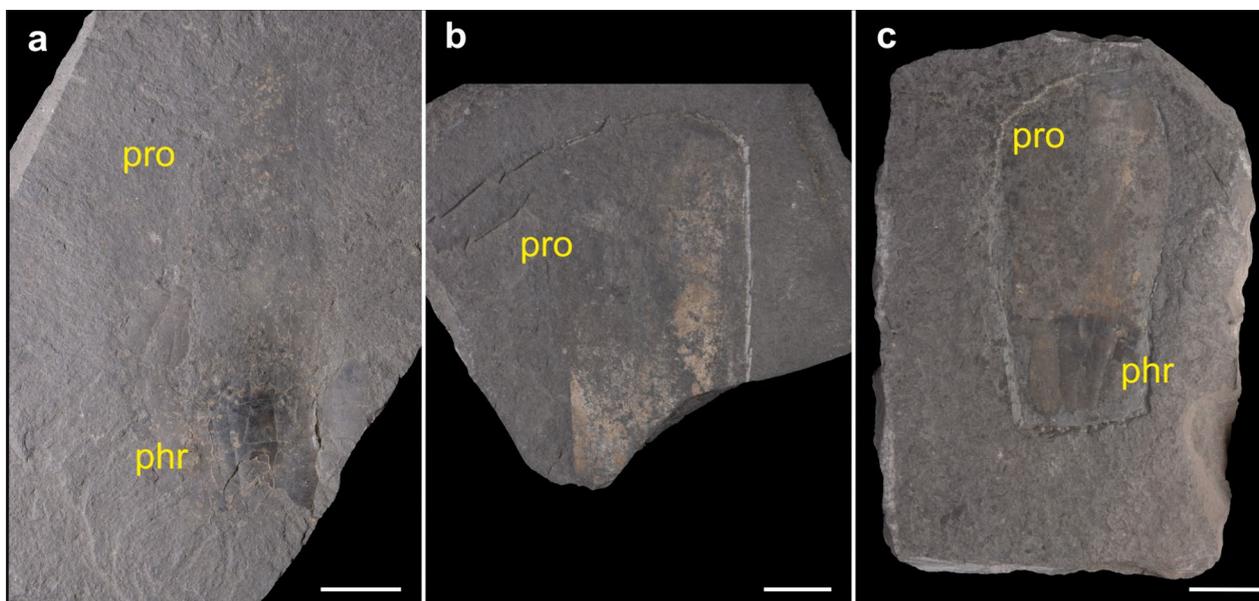


Fig. 5 Photographs of “*Belemnoteuthis bisinuata*” syntypes figured as illustrations in Bronn (1859). **a** The best preserved specimen from Bronn (1859) (Taf. 1, Fig. 1) exhibits a phragmocone and a proostracum (GEOW-HD_OS-BRO-00001). **b** The proostracum corresponding to Taf. 1 Fig. 2 in Bronn (1859) (GEOW-HD_OS-BRO-00002). **c** The best preserved specimen from Bronn’s lectotypes, showing a phragmocone with the entire proostracum, corresponding to Taf. 1 Fig. 3 in Bronn (1859) (GEOW-HD_OS-BRO-00003). All scale bars 1 cm

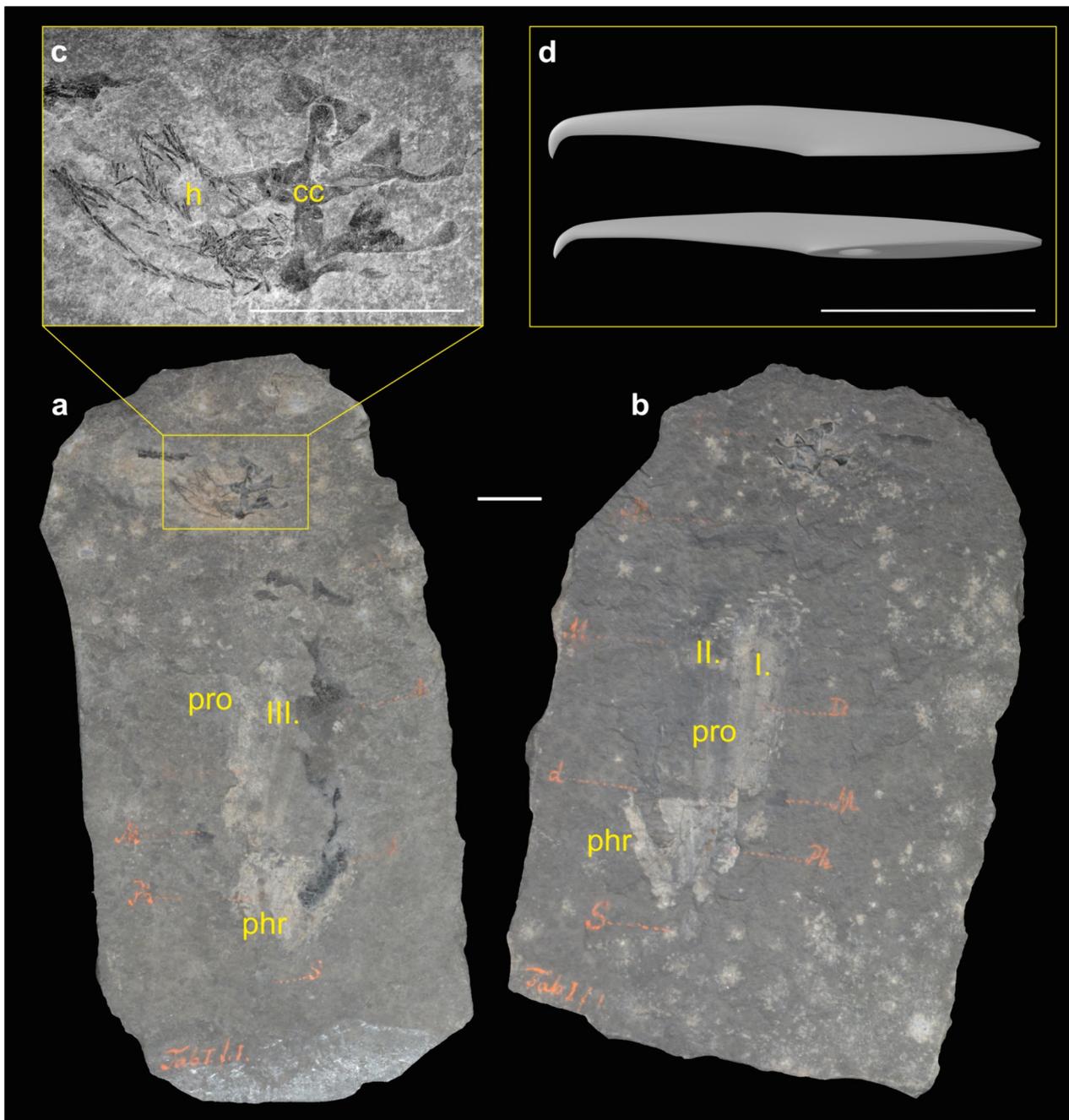


Fig. 6 Most complete specimen of *Phragmoteuthis bisinuata*. **a** Specimen GBA 2006/011/0001 exhibiting a phragmocone with tripartite proostracum (marked with lateral fields I. and III., median field II. (lateral field III. only visible on counterprint), cephalic cartilage with associated stylet shaped arm hooks. **b** Counterpart shows two rows of abundant arm hooks (type 3 and 5). **c** Magnification showing the furcate cartilage area and part of the arm crown with stylet shaped hooks. **d** Reconstruction of stylet-like hooks with basal opening (top: lateral view, base ventro-lateral view). h arm hooks; cc cephalic cartilage, phr phragmocone; pro proostracum. All scale bars 1 cm, except d 250 µm

*V. 1859 *Belemnoteuthis bisinuata* Bronn (1859), p. 43, Pl. 1, Figs. 1–3. (Cave del Predil)

1863 *Acanthoteuthis bisinuata* Bronn & Keferstein (1863), Pl. 131, Fig. 5, 6.

1865 *Acanthoteuthis bisinuata* Suess (1865), p. 229–244, Pl. 1–4.

1882 *Phragmoteuthis bisinuata* (Bronn). Mojsisovics von Mojsvar (1882), p. 304, Pl. 94, Figs. 1–8.

1885 *Phragmoteuthis bisinuata* (Bronn). Zittel (1885), p. 510–511 Fig. 702ab.

1966 *Phragmoteuthis bisinuata* (Bronn). Jeletzky (1966), p. 31, Fig. 4A.

1978 *Phragmoteuthis bisinuata* (Bronn). Reitner (1978), p. 211, Fig. 5. (Cave del Predil)

1979 *Phragmoteuthis bisinuata* (Bronn). Riegraf and Reitner (1979), p. 297–301, Figs. 9, 14.

non 2007b *Phragmoteuthis bisinuata* (Bronn). Doguzhaeva et al. (2007b), p. 273; Figs. 2A, 3B–D.

2007b *Phragmoteuthis bisinuata* (Bronn). Doguzhaeva et al. (2007b) p. 274, Fig. 3A, F.

2018 *Phragmoteuthis bisinuata*. Fuchs & Donovan (2018), p. 4, Fig. 1A, B.

2021 *Phragmoteuthis bisinuata* (Bronn). Lukeneder & Lukeneder (2021), p. 5; Fig. 3B.

2022 *Phragmoteuthis bisinuata* (Bronn). Doguzhaeva et al. (2022) p. 655; Figs. 2–4.

2022b *Phragmoteuthis bisinuata* (Bronn). Lukeneder & Lukeneder (2022b), p. 4; Fig. 2C.

Type specimens: A holotype was not designated by Bronn (1859, pl. 1, Figs. 1–3.). The repository of Bronn's specimens was unknown for a long time. One of the authors (DF) unsuccessfully searched for them during 2001 and 2010 in the collections of the NMHW and Geosphere Austria. Doguzhaeva et al. (2007a, 2007b) remarked that the whereabouts of the syntypes remain unknown. Herbert Summesberger later found them in the collection of the University of Heidelberg (Germany). For this study these syntypes (GEOW-HD_OS-BRO-00001; GEOW-HD_OS-BRO-00002; GEOW-HD_OS-BRO-00003) were photographed (Fig. 5a–c) and measured.

Type locality: Cave de Predil (northern Italy).

Type horizon: black claystones.

Re-description

The syntypes of Bronn (1859) from Cave del Predil are poorly preserved compared to those described later by Suess (1865) and Mojsisovics von Mojsvar (1882). Bronn's phragmocones are crushed, proostraca are incomplete and hardly visible; the phragmocone-to-proostracum ratios were therefore not determinable. Neither hooks nor cephalic cartilages are preserved.

Fortunately, the specimens described by Suess (1865) and Mojsisovics von Mojsvar (1882) are more informative for comparative studies, in particular the best preserved specimen GBA 2006/011/0001 (Taf. 1, Fig. 1ab in Suess, 1865; Taf. 94, Fig. 1 in Mojsisovics von Mojsvar, 1882). This specimen consists of part and counterpart;

it exhibits the phragmocone with the proostracum, the cephalic cartilage and in situ arm hooks.

The complete shell, which is compacted in dorsolateral direction, measures 54.6 mm in length. The flattened phragmocone is 24.24 mm long and 18.66 mm wide. Septal spacing is poorly visible. The proostracum length is 30.36 mm, the proostracum width 23.95 mm. It is accordingly longer than the phragmocone length (ratio phragmocone length to proostracum length 0.7). Specimens NHMW 1864/0052/0047 (also: NHMW 2006z0235/0054) (Pl. 2, Fig. 2ab in Suess, 1865; Pl. 94, Fig. 3 in Mojsisovics von Mojsvar, 1882) and in NHMW 2005z0005/0033 (counterpart to Pl. 2, Fig. 1; Pl. 3 Fig. 1 in Suess, 1865; Pl. 94, Fig. 4a, b in Mojsisovics von Mojsvar, 1882) suggest a ratio of 0.6. Growth increments redraw a rounded median field. The left lateral field is poorly preserved in GBA 2006/011/0001, but complete proostraca in other specimens (Fig. supplementary S1 Figure) indicate a dorsolateral, deep and evenly arcuated hyperbolar zone that is intercalated between median and lateral fields. The hyperbolar zone length occupies c. 83% of the total shell length, while the likewise evenly rounded lateral fields take c. 88% of the total shell length.

The carbonised, bilateral, furcate cephalic cartilage (type A) is positioned anteriorly, 18.01 mm in front of the anterior margin of the proostracum. The cartilage of the specimen consists of two connected elements, of which each of them is characterised by an angular central part and a distal extension (processus). The processus is much thinner and less curved than in *P. polzbergensis* nov. sp. A clear “c-structure” cannot be delimited.

Biserially arranged hooks, situated anterior to the proostracum and next to the cephalic cartilage, probably reflect 6–7 arms (Fig. 6c). The hooks are stylet-like, which is exemplified by a very low hook height (0.12–0.14) relative to total hook length. Accordingly, the shaft angle is strongly inclined (12–16°) and the uncinus angle is very high (130–150°). The ratio base length to uncinus length is moderate. Importantly, there is no evidence of a strongly curved hook type (supplementary Figure S1).

Remarks: The only known specimen of *Lunzoteuthis schindelbergensis* Doguzhaeva et al., (2006) (NHMW 2005z0005/0001) from Polzberg was obtained from an unknown specimen from the historical collections of the Natural History Museum Vienna (NHMW). Due to treatment for SEM imaging, the remains are damaged and thus questionable. The taxonomic status of *L. schindelbergensis* is problematic; it was introduced by Doguzhaeva et al. (2006) based on a tiny fragment of a proostracum (3 mm wide). In our opinion, the faint growth lines indicating a three lobed proostracum are sufficient to postulate phragmoteuthid affinities, but –as the present study

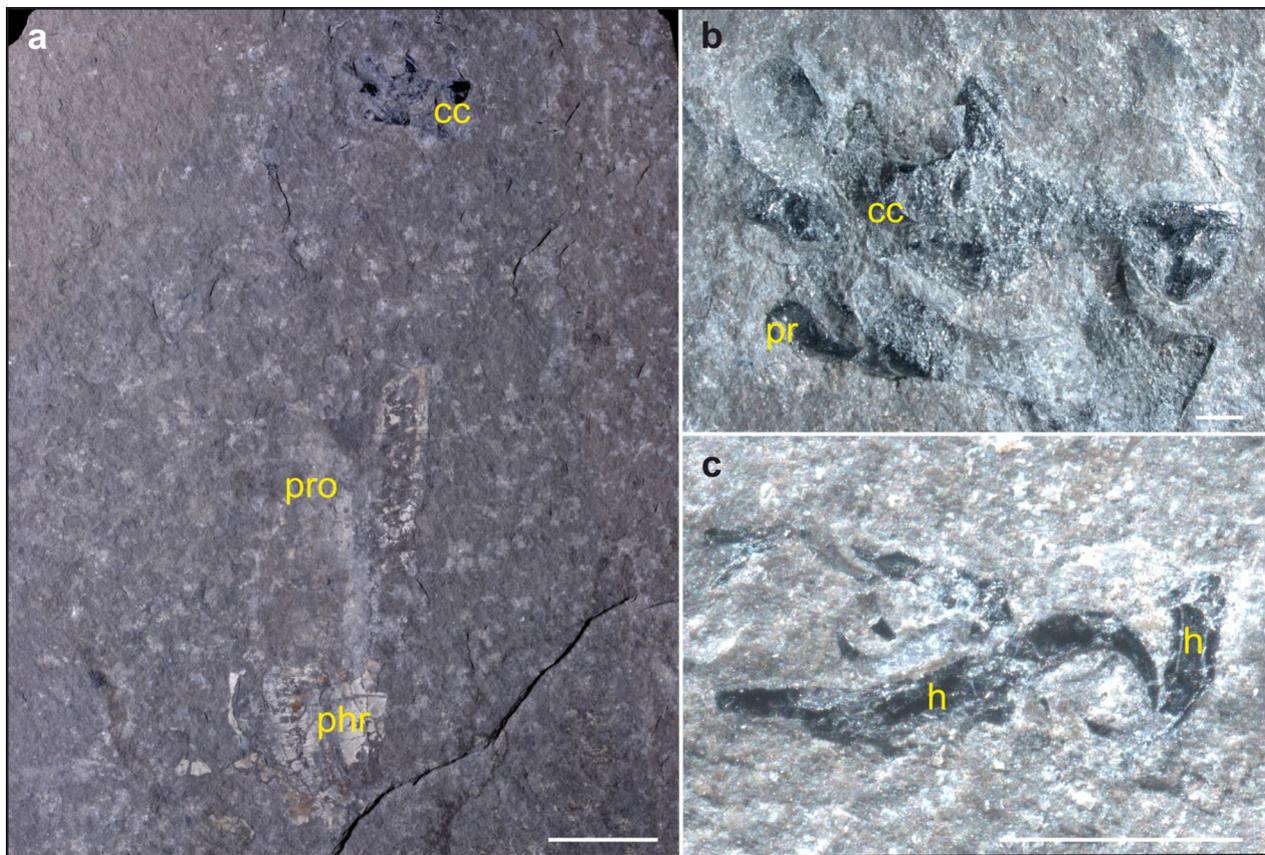


Fig. 7 Holotype of *P. polzbergensis* nov. sp. from the Reingraben shales of the Polzberg *Konservat-Lagerstätte*. **a** Specimen includes phragmocone and three-lobed proostracum with a L-shaped cephalic cartilage just anterior to the proostracum. **b** Detail of furcate cephalic cartilage, exhibiting angular c-structure and slightly curved processus. **c** Type 2 and type 5 arm hooks are scattered within the area of the cephalic cartilage. cc cephalic cartilage; h hooks; phr phragmocone; pr processus; pro proostracum. Scale bars **a** 1 cm; **b**, **c** 1 mm

shows—certainly insufficient for a meaningful delimitation at species or genus level. In our view, the species is a subjective junior synonym of *P. bisinuata*.

A complete specimen of *P. bisinuata* (NHMW 2006z0235/0054) was reported from “Schindelberg” (Doguzhaeva & Summesberger, 2012: Fig. 1), which is equivalent to the Polzberg locality. However, the figured specimen comes from Cave del Predil (see also Bronn, 1866; Mojsisovics von Mojsvar, 1882; Suess, 1865; Zittel, 1885), whose sedimentological properties, faunal composition and preservation type resemble those of Polzberg. Figure 2c in Lukeneder & Lukeneder (2022b) includes a large specimen of *P. cf. bisinuata* preserving phragmocone, proostracum and the cephalic cartilage.

Regional distribution: Cave del Predil (northern Italy).

Stratigraphic range: *P. bisinuata* is known from the lower Carnian (Julian 2, *Austrotrachyceras austriacum* Zone, Late Triassic) of Italy.

Phragmoteuthis polzbergensis nov sp.

(Figures 7, 8, 9, 11a, b).

non 2022b *Phragmoteuthis bisinuata* (Bronn).
Lukeneder & Lukeneder (2022b), p. 273; Figs. 1B, 3, 4.

non 2007b *Phragmoteuthis bisinuata* (Bronn).
Doguzhaeva & Summesberger (2007b), p. 273; Figs. 2, 3B–D.

<http://zoobank.org/46869B54-F172-462D-AE2A-5E2B1912FAC5>

Etymology: Named after the type locality, the Polzberg *Konservat-Lagerstätte* (Lower Austria).

Holotype: NHMW 2006z0005/0021 is the only specimen with a proostracum, differentiated arm hooks and a cephalic cartilage preserved.



Fig. 8 Specimen of *P. polzbergensis* nov. sp. from the calcareous beds (layer 0, –50 cm to 0 cm) of the Polzberg section. **a** NHMW 2021/0123/0090 is one of the most complete phragmoteuthid specimens from recent bed-by-bed collections at the Polzberg *Konservat-Lagerstätte*. Nine armoured arms, equipped with hooks are visible (compare with Fig. 9, which shows a cumulative reconstruction of the part and counterpart). **b** Drawing of all preserved elements. Inferred position of the arms are indicated by numbers 1 to 9. Scale bars 1 cm

Type locality and horizon: Reingraben shales at Polzberg main section at 0 cm to –50 cm, Carnian, Late Triassic.

Material: Eight specimens from recent excavations, at the lowermost 3 m of the Reingraben Shales at Polzberg, from sequence Po –50 cm to Po 320 cm, inventoried at the NHMW (NHMW 2021/0001/0002; NHMW 2021/0016/0400; NHMW 2021/0123/0005, 0013, 0057, 0090, 0218, 0424); eight specimens from historical NHMW collections; NHMW 2005z/0005/0021, 0040; NHMW 2012/0117/0011, 0025; NHMW 2012/0228/0495, 0512; NHMW 2020/0033/0003; NHMW 2021/0124/0038. No mantle remains are

preserved. If preserved, the oval-shaped carbonised ink sac is located near the centre of the specimens.

Description: Shell complex: Phragmocones and proostraca are flattened as in the type locality of *P. bisinuata*; width measurements and indices are therefore equivocal. Phragmocone lengths range from 14.17 to 22.63 mm, proostracum lengths were measured from 20.41 to 88.31. The ratio phragmocone length to proostracum length varies between 0.65 and 0.75. Opening angles cannot be determined exactly because of compaction; they range between about 25° and 30°

Sutures appear simple and densely spaced, but statements about septal spacing are speculative.

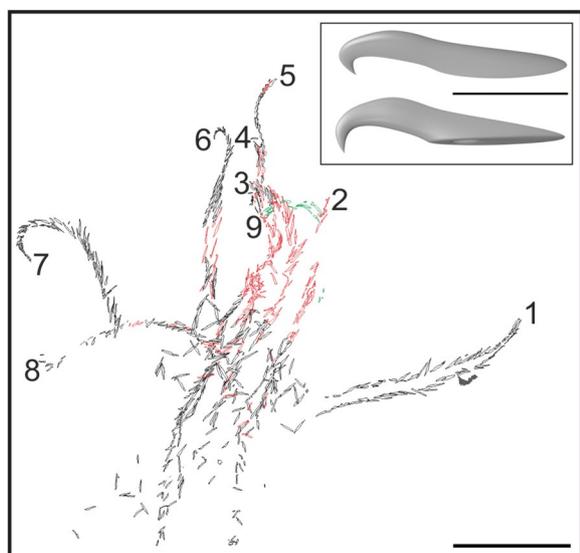


Fig. 9 Cumulative reconstruction of the arm crown from part and counterpart of *P. polzbergensis* nov. sp. (NHMW 2021/0123/0090), Hooks associated with nine arms are visible. Black lines part; red lines counterpart; green lines inferred ninth arm; dashed green line arm hooks visible on counterpart. Black rectangle inset: 3D reconstruction of stylet hook type 5; top: anterolateral view, base: ventrolateral view. Scale bar 1 cm. Scale bar hook reconstructions 250 μ m

The proostracum can be subdivided into a median field and adjacent hyperbolar zones and lateral fields. The anterior margin of the median field is rounded. Dorsolaterally, the retracted hyperbolar zones are evenly arcuated and occupy c. 83% of the total shell length (ratio hyperbolar zone length to total shell length=0.83). The projected lateral fields are likewise evenly rounded and take c. 88% of the total shell length.

Arm complex: NHMW 2021/0123/0021 stems from the lower, calcareous part of the section and comprises the proostracum, the cephalic cartilage and parts of a differentiated arm crown. The proostracum of the specimen NHMW 2021/0123/0090 only appears poorly preserved, but includes the complete arm crown with differentiated hooks, as well as both beaks. The specimen's total length is 88.3 mm, with a maximum width of 28.2 mm. The arm crown of NHMW 2021/0123/0090 is also preserved in situ and consists of different arm hook types (type 3, 5).

All of the specimens possess both the stylet shaped (type 3) and curved (type 5) arm hooks (Fig. 12a). Closer investigation reveals that the strongly curved hooks preferentially represent at least one modified arm pair, each of them equipped with complementary hook pairs of stylet shaped and curved hooks. The remaining arms are equipped with the stylet shaped hooks (Figs. 8, 9).

Head complex: The holotype shows a squashed, but determinable cephalic cartilage of type A. The well preserved cephalic cartilage of specimen NHMW 2012/0123/0057 with arm hooks identical to those of the holotype and NHMW 2021/0123/0090 confirms the presence of type A. Further cephalic cartilages of type A are present in specimens NHMW 2021/0001/0002; NHMW 2012/0117/0011, 0025; NHMW 2021/0016/0400 (Fig. 11a); NHMW 2021/0123/0013, 0424. The carbonised, furcate type of cartilage (Fig. 11a; supplementary S1c Figure; Type A cartilage) appears to be a bilaterally symmetric paired structure with a calcite-filled channel system, which follows the geometry of the fossil (see also Lukeneder & Lukeneder, 2022b). It is a distinct, characteristic "C-structure" with a prolonged processus (supplementary S1c Figure). Additional triangular-elongate "wing elements" (Fig. 10a) are located next to the C-shaped structure.

NHMW 2021/0123/0013 with the type A cartilage displays a carbonized upper beak illustrating the outline of the inner (lateral wall, crest) and outer lamella (rostrum, hood, wings).

Comparisons

The shell complexes of *P. polzbergensis* nov. sp. and *P. bisinuata* appear identical; we found no delimiting shell features. However, differences in the arm armature as well as the cephalic cartilage morphology are striking.

By contrast to the differentiated arms in *P. polzbergensis* nov. sp., there is no evidence of arm hook differentiation in *P. bisinuata* (GBA 2006/011/0001), whose arms are exclusively equipped with stylet-shaped hooks. Even more different are the cephalic cartilages of *P. polzbergensis* nov. sp. (type A) and *P. bisinuata* (type C). The cartilage of *P. bisinuata* is L-shaped and characterized by a slightly curved processus and an indistinct, more angular C-structure. Distinct wing elements as in type A are missing.

The studied specimens from Polzberg expand our knowledge of the Phragmoteuthida. A specimen with a tripartite proostracum and more than eight preserved arms (two of which appear modified) confirms that these phragmoteuthids had ten arms. Each of the two modified arms appears to be equipped with a series of stylet-shaped hooks and a series of curved hooks, with each curved hook having a complementary stylet-shaped hook. When preserved, the cephalic cartilage shows a furcate morphology. As specimens with arm hook differentiation occur in Polzberg (Fig. 11c, d) which cannot be clearly assigned to *P. polzbergensis* nov. sp., we conclude that a further subdivision according to the types of arm hooks and different head cartilage types is

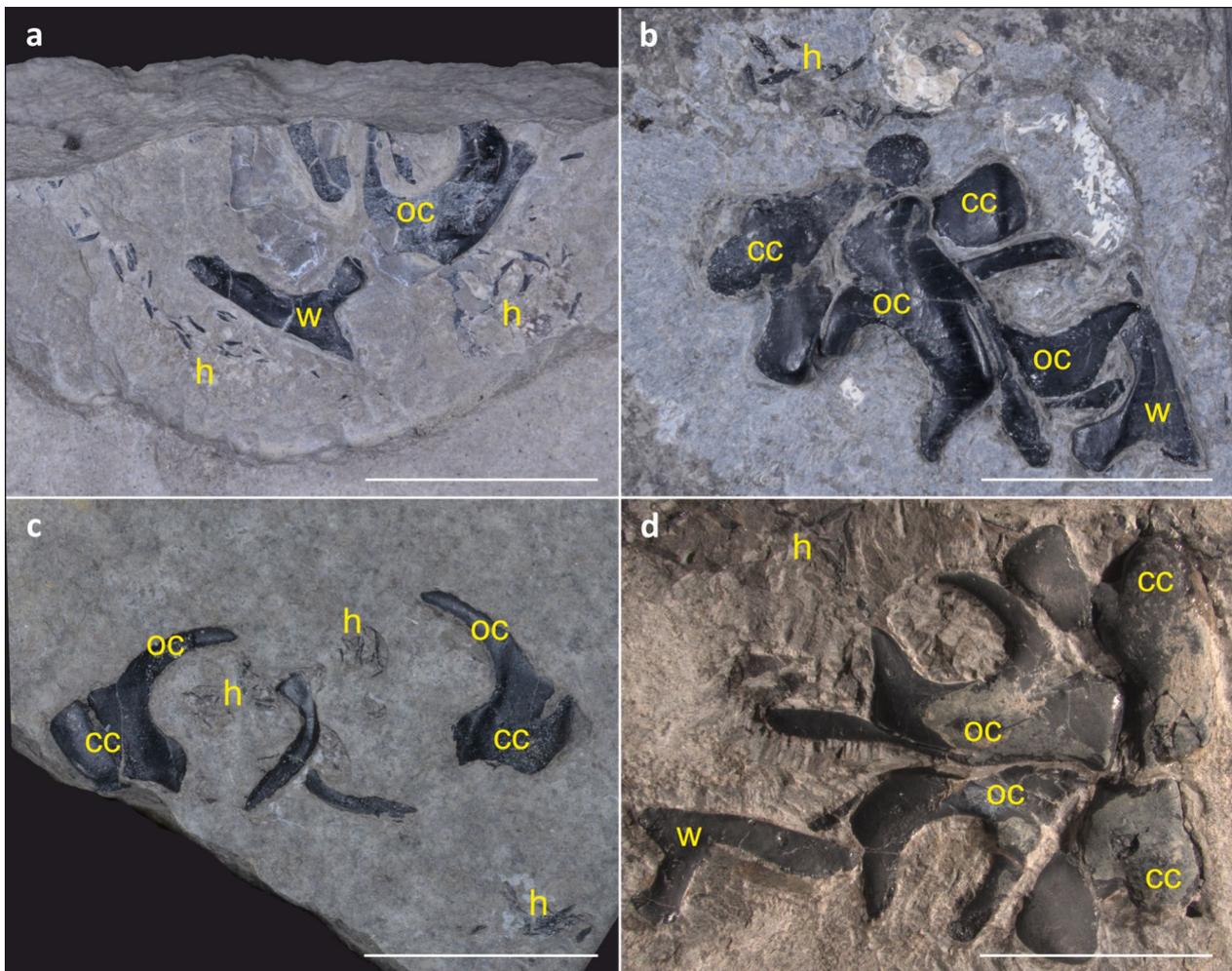


Fig. 10 Hooks and cephalic cartilage elements from phragmoteuthid specimens from the Polzberg *Konservat-Lagerstätte*. **a** Furcate (type A) cephalic cartilage of *Phragmoteuthis polzbergensis* nov sp. (NHMW 2012/0117/0025) associated with differentiated stylet and curved shaped coleoid hooks (type 1 and 3). **b** A massive type of stylet hooks in NHMW 2012/0001/0002, along with a furcate cephalic cartilage. **c** Type B cephalic cartilage (open ring) associated with ore fragile stylet shaped coleoid hooks (NHMW 2012/0124/0003). **d** NHMW 2012/0123/0057 with its differentiated arm hooks (thick type 3 hooks and type 5 hooks) and a furcate cephalic cartilage can be assigned to the newly described species *P. polzbergensis* nov. sp. h hooks; oc ocular cartilage as part of the cephalic cartilage. All scale bars 1 cm

necessary for a better understanding of the systematic relationships of the particular coleoid groups.

We propose that *P.?* *ticinensis* from the Grenzbitumenzone is unlikely to be a member of the genus *Phragmoteuthis* or even of the Phragmoteuthida. In the light of its curved hooks, it appears likely that *P.?* *ticinensis* is closer to *Mojsisovicsteuthis* although some overlap in hook shapes of transitional coleoid groups cannot be excluded.

Table 2 sums up the differences and similarities between *Mojsisovicsteuthis* sp., *P. bisinuata* and *P. polzbergensis* nov. sp.

Occurrence: Polzberg, Austria.

Stratigraphic range: *P. polzbergensis* is known from the lower Carnian (Julian 2, *Austrotrachyceras austriacum* Zone, Late Triassic) of Austria.

Discussion

Evolutionary implications

Origin of the proostracum

Despite enormous progress in past years, our understanding of the evolutionary development of the proostracum is still patchy (e.g., Doguzhaeva & Summesberger, 2012; Fuchs & Iba, 2015; Fuchs et al., 2007; Jeletzky, 1966). This uncertainty comes from the rarity of aulacoceratid body chambers and the lack of

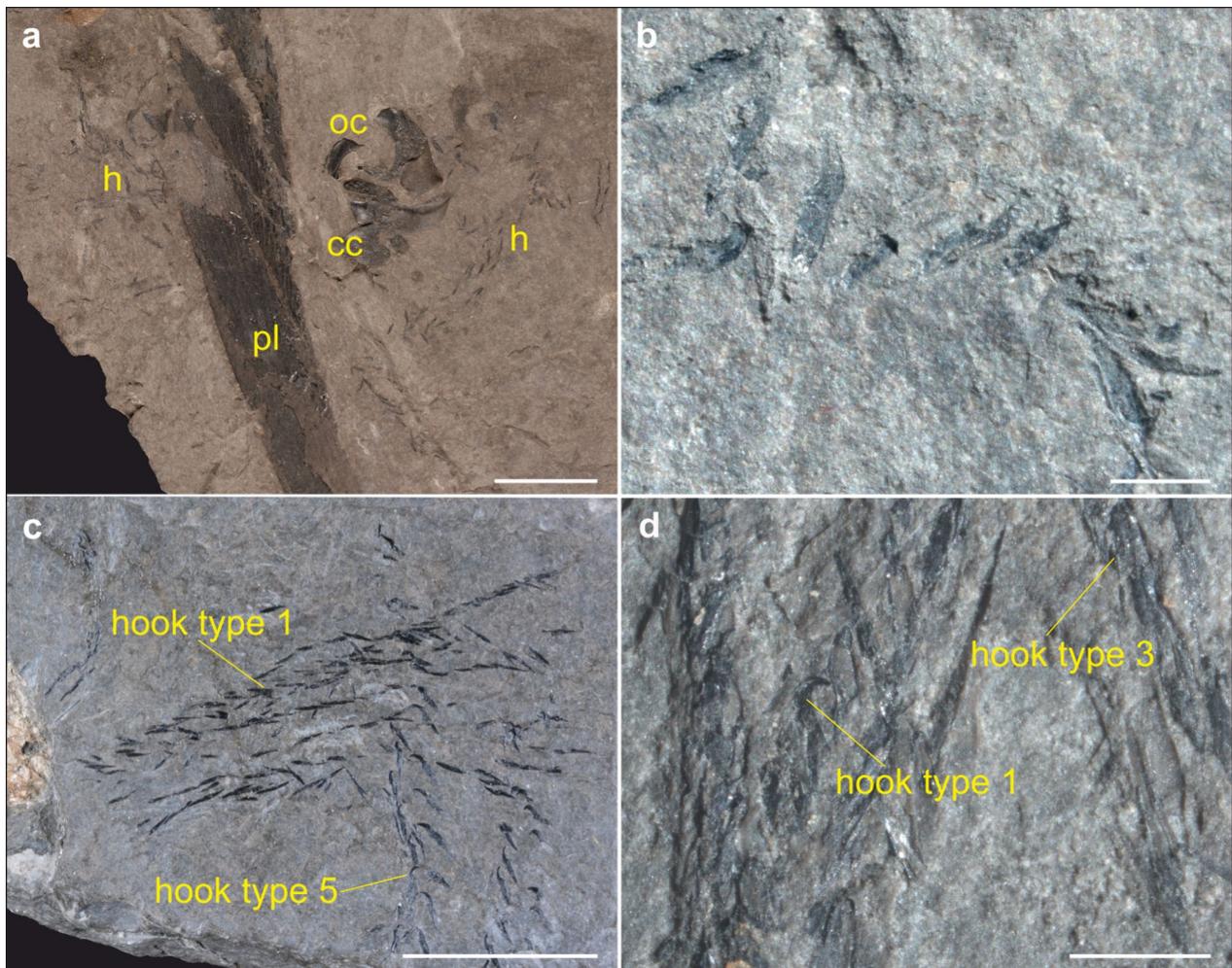


Fig. 11 Phragmoteuthid hooks and cephalic cartilages from the calcareous beds of the Polzberg section. **a** Furcate cephalic cartilage (type A) and partly preserved arm crown containing differentiated arm hooks (NHMW 2021/0016/0400) of *P. polzbergensis* nov. sp. **b** Detail showing stylet shaped (type 3) and long-based (type 5) arm hooks. **c** NHMW 2021/0001/0003 with its differentiated arms exhibiting two hook types (type 3 and type 5). Hooklets point to a phragmoteuthid relationship, without clear species assignment. **d** Differentiation of arm hooks (type 3, 5) in phragmoteuthid specimen NHMW 2005z/0005/0040. cc cephalic cartilage sensu stricto; h hooks; oc ocular cartilage; pl plant remain. Scale bars **a**, **c** 1 cm; **b**, **d** 1 mm

Table 2 Comparison of *Phragmoteuthis bisinuata* (GBA 2006/011/0001), *P. polzbergensis* nov. sp. and *Mojsisovicsteuthis* sp. from Polzberg and Cave del Predil

Features	<i>Phragmoteuthis bisinuata</i> (Cave del Predil)	<i>Phragmoteuthis polzbergensis</i> nov. sp. (Polzberg)	<i>Mojsisovicsteuthis</i> sp. (Polzberg)
Body size including arms (cm)	20	20	35
Shell complex	Phragmocone with tripartite proostracum; ratio proostracum length to phragmocone length 0.65 to 0.75	Phragmocone with tripartite proostracum; ratio proostracum length to phragmocone length 0.65 to 0.75	Phragmocone with tubular final chamber; ratio body chamber length to phragmocone length 1
Phragmocone opening angle	25–30°	25–30°	10–20°
Arm hook differentiation	Absent (only stylets; Type 3)	Present (stylet and curved; Type 3 and 5)	Present (curved), Type 1, 4
Cephalic cartilage	L-shaped (Type C)	Forked (Type A)	Open ring (Type B)

The differentiation of arm hooks and cephalic cartilage types appears to be the most obvious differences

fossil evidence showing the transitional stages between the ventrally closed (tubular) body chamber, and the more derived, ventrally opened chamber equivalent with a forward projecting dorsal proostracum. Morphologically, the body chambers examined in the study sample appear to be indistinguishable from those known in aulacoceratids though it is possible that there is a chemical difference (e.g. in the degree of mineralisation) between the taxa. Aulacoceratid body chambers are known to be fully mineralised. Doguzhaeva et al. (2007b) analysed the chemistry of the specimens NHMW 2006z0235/0007 to NHMW 2006z0235/0011 with Energy dispersive X-ray Spectroscopy (EDS-SEM), and concluded that the body chamber of *Mojsisovicsteuthis* sp., though misidentified as the proostracum of *P. bisinuata*, was rich in organics and only weakly mineralised (Doguzhaeva et al., 2007b). If our systematic attribution is correct and the analysis of Doguzhaeva et al. (2007b) can be confirmed, the tubular, weakly mineralised body chamber of *Mojsisovicsteuthis* would portray an intermediate evolutionary stage between a fully mineralised body chamber (like in *Gordoniconus*; see Klug et al., 2019) and a purely organic proostracum. Unfortunately, the analyses in Doguzhaeva et al. (2007b) are problematic and cannot be confirmed, as the given inventory numbers are not assigned at the NHMW and the repository of the material itself is unknown.

Number of phragmoteuthid arms

Lack of morphological evidence has fuelled the debate on the number of arms in the past (Fuchs & Donovan, 2018). Although without direct evidence, Jeletzky (1966) and most previous authors regarded the Phragmoteuthida as ten-armed belemnoids. This idea was based on the outdated view that teuthid squids directly arose from phragmoteuthids. Mesozoic gladius-bearing coleoids were dealt as the descendents of phragmoteuthids (Bandel & Leich, 1986), but these admittedly squid-shaped coleoids possess only eight hook-less arms and are therefore today classified within the Octobranchia (Fuchs, 2020, and references therein).

A few years after the work of Jeletzky (1966), the ten arm-hypothesis received additional support through Rieber (1970), who presented a Triassic arm crown consisting of ten arms. He determined his specimen from the Anisian of Monte San Giorgio (Switzerland) as “*Phragmoteuthis ticinensis*” (PIMUZ 3784), although a three-lobed proostracum, the key character of phragmoteuthids, was missing. Historical specimens of *P. bisinuata* as well as our specimens of *P. polzbergensis* nov. sp.

with their three-lobed proostracum demonstrate that the stylet-shaped hooks and thus the entire arm armature is fundamentally different from the curved hooks of Rieber’s Anisian specimen.

A similar confusion about the phragmoteuthid arm morphology was caused by Jurassic *Clarkeiteuthis* (“*Phragmoteuthis*”) *conocauda* and *C. (“P.”) montefiorei*, both of which were ultimately revealed to exhibit spatula-shaped proostraca and articulated hook series (Fuchs et al., 2013).

In summary, although previous statements about the number of phragmoteuthid arms were solely based on doubtful classifications (e.g., Donovan, 1977, 2006; Doyle et al., 1994; Engeser, 1990), it is today accepted that the Phragmoteuthida were ten-armed coleoids (Fuchs & Donovan, 2018). In this respect, they retain the plesiomorphic state that was documented for the Carboniferous early branching coleoid *Gordoniconus* (Klug et al., 2019). Specimen NHMW 2021/0123/0090 from Polzberg finally confirms that (at least characteristic) phragmoteuthids possessed 10 arms, including one modified arm pair. Nevertheless, note that, if Doyle et al. (1994) are correct and Octobranchia derived from the Phragmoteuthida, it is conceivable that aberrant phragmoteuthids show evidence of a rudimentary arm pair. If Octobranchia arose from ten-armed phragmoteuthids, the reduction of the second dorsal arm pair would have occurred early on the octobranchian lineage (see Fuchs et al., 2024 for a more detailed discussion). In any case, the studied arm crowns from Polzberg demonstrate a remarkable variability of arm hooks, suggesting distinct arm differentiation, particularly compared to the uniform hook shapes reported from some belemnites (e.g., *Passaloteuthis*, from which two megahooks and uniform microhooks are reported) (Fuchs et al., 2021; Hoffmann & Stevens, 2020; Stevens, 2010).

Ecological implications

Various types of fossil predation signs help to reconstruct fossil food-webs, including bromalites (including, e.g., coprolites and regurgitalites), shell damage (holes, shell fragments, bite marks, complementary scars, angular fragments), and repair scars of sublethal injuries (Klompaker et al., 2019; Kowalewski, 2002). Such food-webs can become very complex because many predators also act as facultative scavengers (Mellard et al., 2021). Coleoids including Mesozoic ones (e.g., Jenny et al., 2019) are mostly regarded as predators, less often as facultative

scavengers, whereby predators and scavengers interact strongly (Mellard et al., 2021) and both modes of life strongly influence the local food-web.

The deposits at the Polzberg *Konservat-Lagerstätte* yielded evidence for various types of (direct or indirect) trophic interactions:

- 1) Indirect evidence for belemnoids as prey is documented by the occurrence of phragmoteuthid remains (mainly arm hooks, shell hash, but also cephalic cartilage) within bromalites (produced by larger fish; see also Lukeneder et al., 2020).
- 2) Stylet shaped hooks are rarely found in coprolites. The hook types 1 are exclusively found within coprolites or, when isolated, may stem from predated specimens of *Mojsisovicsteuthis*. This, in turn, may indicate that these coleoids were a much easier prey to capture in this environment.
- 3) The accumulation of primitive hooks (type 1 and 2) in coprolites suggests that predators in the Polzberg locality were able to successfully hunt primitive coleoids such as *Mojsisovicsteuthis*, which still had a body chamber and thus lack a free muscular mantle that enables powerful jet propulsion.
- 4) Until now, no larger predators have been recorded from the deposits of the Carnian Polzberg sea. The assumption is therefore that fish such as *Saurichthys calcaratus* and belemnoids were the main active carnivores in the water column here.
- 5) Abundant small thylacocephalans (*Atropicaris striata*) are frequently found close to coleoid remains. Sometimes multiple thylacocephalan specimens are recorded in association with one belemnoid fossil. As it appears difficult to determine the lifestyle of these small arthropods, the co-occurrences of the thylacocephalans with coleoid remains may support the hypothesis of a scavenging life mode for this arthropod (see also Lukeneder & Lukeneder, 2021).
- 6) We observed a reduction in the fragment size over time, which is related to a deepening of the Polzberg Basin. Since these fragments can not be determined more precisely, we can not document any changes in the species composition through time.

Conclusions

Our research on the fossil material collected bed-by-bed yielded new data not only on the coleoid fossils from Polzberg and Cave del Predil, but also on their

trophic relationships within the Carnian Polzberg Basin. Observations on the new coleoid material from the Polzberg *Konservat-Lagerstätte* include exceptionally preserved belemnoid remains preserving beaks and various types of arm hooks.

Our morphological comparisons have shown that species determinations of coleoid cephalopods are more complicated than previously thought; even non-related taxa can be difficult to be distinguished. We detected two new coleoids in Polzberg, while the occurrence of *P. bisinuata*—previously thought to be the only coleoid in this locality—is now unclear and restricted to Cave del Predil. Besides a new species of the genus *Phragmoteuthis*, our inventory revealed for the first time coleoids of the genus *Mojsisovicsteuthis*. The reconstructions in Fig. 12 compare the treated taxa.

Additional finds are identified here as questionable Phragmoteuthida indet. (see also supplementary S2 Table), some of them belong to a new species. The specimens furthermore indicate that *Mojsisovicsteuthis* sp. probably belonged to hook-bearing belemnoids (Fig. 12c), which can be regarded as prey that was easier to catch in this environment.

The examination of newly excavated coleoid arm crowns, especially the discovery of the first unambiguous phragmoteuthid fossil with ten arms, provides new data for studying the relationships between the various coleoid groups. Our results confirm that the late Triassic coleoid diversity from the Polzberg *Konservat-Lagerstätte* and Cave del Predil is higher than previously thought and must be re-evaluated. Specifically, the highly variable hook and cartilage shapes call for further attention in a detailed species assessment. A few specimens (see also supplementary Table S2) belong probably to an undescribed phragmoteuthid species, which should be studied in the future.

The examinations indicate that the taphonomic process mainly started with predatory activities in the water column above an extended temporally low-oxygen water system. Most of the collected belemnoid fragments likely represent the remains of individuals that were hunted and crushed during predations.

In many cases, coleoid carcasses reached the sea floor more or less intact, but due to the low-oxygen environment, they usually could not be accessed and fragmented by scavengers. Although fast burial is often associated with *Konservat-Lagerstätten*, there is no evidence (such as corresponding sedimentary structures) for it at

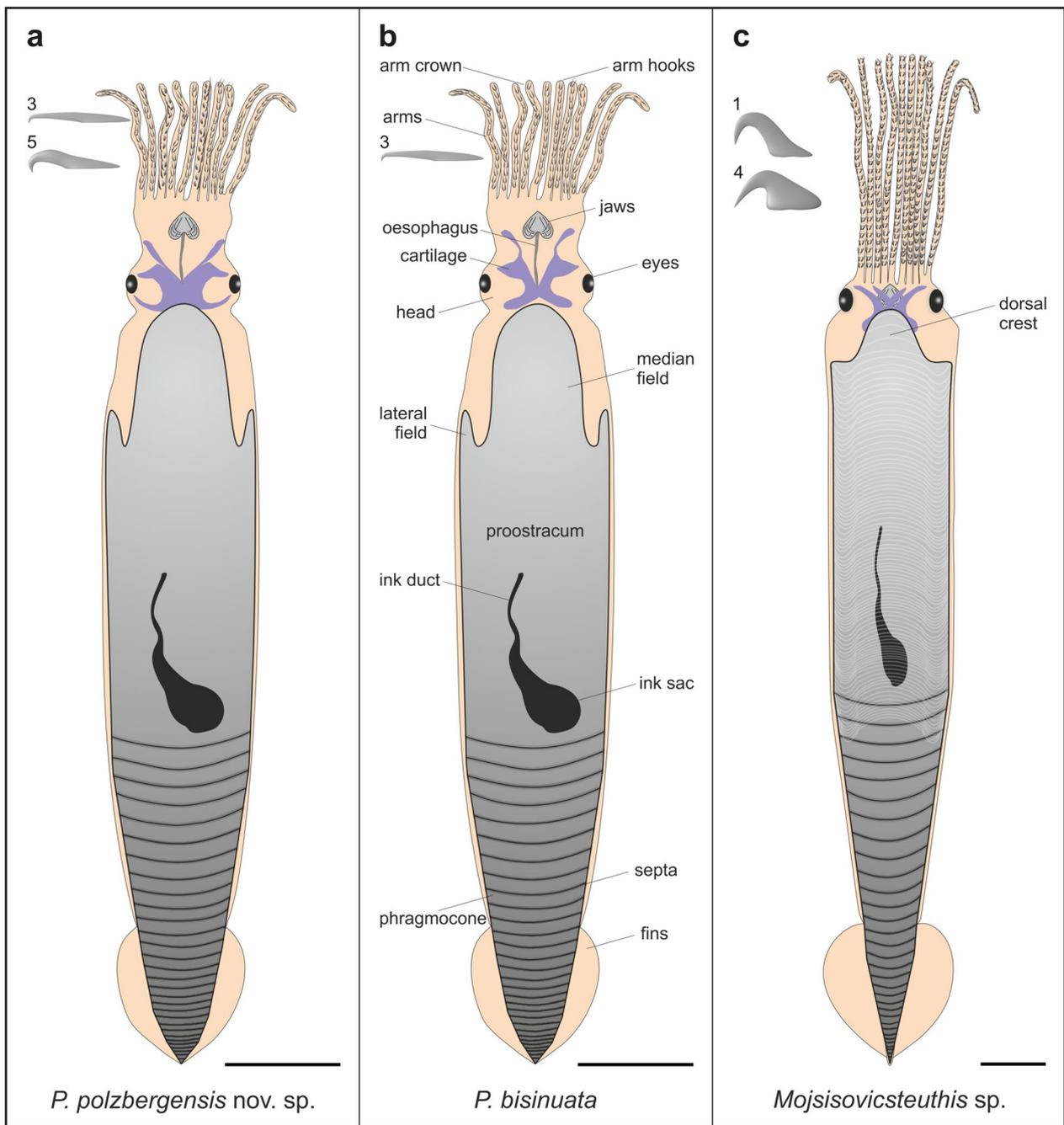


Fig. 12 Reconstructions of treated taxa including the most significant features such as size, hook types, phragmocone opening angles. Cephalic cartilages are indicated by purple structures. **a** *P. polzbergensis* nov. sp. with type 3 and 5 hooks. **b** *P. bisinuata* with type 3 hooks. **c** Note tubular body chamber and dorsal crest in *Mojsisovicsteuthis* sp. (hook types 1 and 4). Scale bars 1 cm

Polzberg. Instead, the carcasses likely remained on the sediment surface for longer time periods and small scavengers such as eunicid polychaetes and thylacocephalans that were adapted to these dysoxic environmental conditions were still able to access the coleoid remains. Such trophic contacts were not known from the historical

material and only came to light during these studies on the material from recent collections.

After death, the rapid mineralisation (phosphatisation) process of the belemnoid cephalic cartilages started early in the soft, upper sediment layers, with concurrent processes of initial decay and associated disarticulation

(see also e.g. Briggs & Wilby, 1996; Clements et al., 2017; Schiffbauer et al., 2014).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-024-00319-4>.

Supplementary Material 1: Supplementary Figure S1. Visualisation of all metrics. **a** Slightly compressed specimen of *Phragmoteuthis bisinuata* from Cave del Predil (Italy), exhibiting central field and two lateral fields with hyperbolic zones; l_{ch} chamber length, l_{pro} proostracum length, l_{phr} phragmocone length, l_{sp} specimen length, w_{phrmax} maximum phragmocone width, α_a apical angle of the phragmocone. **b** Hook measurements on two types of phragmoteuthid hooks; l_h total hook length. Compare also hooklet types in Fuchs et al. (2013). **c** Coleoid cephalic cartilage of *Ph. bisinuata*. Top: furcate cephalic cartilage (type A) from lateral view; base: open ring type B cartilage associated with differentiated arm hooks (thick lancet shaped hook type 3, type 5). cc cephalic cartilage sensu stricto; oc ocular cartilage with so-called C-structure; pr processus. Scale bar a 1 cm; b 200 μ m; c 1 cm.

Supplementary Material 2: Supplementary Table S2. Measurements obtained from specimens in collections of the Natural History Museum Vienna (NHMW), the Geosphere Austria (GBA), the University of Vienna (IPUW), the Montanuniversität Leoben (Austria) (MUL), the Museo Friulano di Storia Naturale, Udine (Italy) and the University of Heidelberg (Germany) (GEOW-HD). Compare hook types 1 to 5 in Fig. 3. b beak; car cartilage; cr dorsal crest; cop coprolite; is ink sac; h hook; phr phragmocone; pro proostracum; l_{pro} length proostracum; l_{phr} length of phragmocone; *indicates almost complete specimens of *Mojsisovicteuthis* sp.

Supplementary Material 3: Supplementary Data S3. Energy dispersive X-ray spectroscopy Scanning Electron Microscopy (EDX-SEM) geochemical data obtained from ink sac, black substance within belemnoid proostraca and microhooks. Samples: NHMW 2005z0005/0010 (ink sac from Polzberg); NHMW 2021/0016/0396 (ink sac from Cave del Predil); NHMW 2021/0123/0080 (black substance within belemnoid proostracum); NHMW 2021/0123/0404 (black substance within belemnoid proostracum); Hook from sieving sample NHMW 2021/0123/0430 (Polzberg main section, layer E); Hook from specimen NHMW 2021/0123/0015.

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Author contributions

PL designed the research. PL, DF, and AL documented the fossil material. PL wrote the first draft of the paper; PL, DF, and AL wrote parts of the paper; all authors edited and approved of the final version of the MS.

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Availability of data and materials

The datasets supporting the conclusions of this article are included within the article and its additional files.

Declarations

Competing interests

We have no competing interests.

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