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Research paper

The mantle, ink sac, ink, arm hooks and soft body debris associated with the shells in Late Triassic coleoid cephalopod *Phragmoteuthis* from the Austrian Alps

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Abstract

Fragmentarily preserved shells – mainly pro-ostraca, in several cases also phragmocones – occurring together with arm hooks and the ink sac of the Carnian (Late Triassic) coleoid cephalopod *Phragmoteuthis bisinuata* (Bronn) from Lunz (Austria) are examined with the scanning electron microscope and energy-dispersive spectrometer. The pro-ostracum bears black, shiny, pitch-like sheets. The black sheets, the ink sac content and the arm hooks have a granular ultrastructure of 0.1–1 μm grain size. The arm hooks and black sheets are micro-laminated; each lamina consists of fibres. The ink consists of an agglomerate of grains. On the ventral (internal) side of the pro-ostracum, the black sheets occasionally bear agglomerates of homogeneous, ink-like material along with heterogeneous structures. The pro-ostracum has crystal-shaped units with lamello-columnar ultrastructure of the inner layer and plate ultrastructure of the outer layer. This resembles the Late Triassic *Lunzoteuthis* [Doguzhaeva, L.A., Mutvei, H., Summesberger, H., 2005a. A Late Triassic coleoid from the Austrian Alps: the pro-ostracum viewpoint. In: Kostak, M., Marek, J. (Eds.), Proceedings of the 2nd International Symposium on Coleoid Cephalopods Through Time. Short Papers/Abstracts Vol. Prague, 26–29 September, 2005, pp. 55–59] and Early Jurassic *Belemnotheutis* [Doguzhaeva, L.A., Donovan, D.T., Mutvei, H., 2005b. The rostrum, conotheca and pro-ostracum in the Jurassic coleoid Belemnotheutis Pearce from Wiltshire, England. In: Kostak, M., Marek, J. (Eds.), Proceedings of the 2nd International Symposium on Coleoid Cephalopods Through Time. Short Papers/Abstracts Vol. Prague, 26–29 September, 2005, pp. 45–49]. The black sheets, the material on their inner surface, the ink and the arm hooks consist of carbon, occasionally with minor amounts of sulfur. The shell is of calcium carbonate.

Based on their organic composition, position in the shell and lamello-fibrillar ultrastructure, the black sheets are considered to be remains of the mantle, sometimes with ink sac and soft body debris. The carbon composition and granular ultrastructure of arm hooks, ink, and soft tissue remains indicate that the non-mineralized structures are pseudomorphosed by carbon (carbonization), possibly due to C-accumulating bacteria.
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Keywords: Cephalopoda; Coleoidea; Triassic; Fossilization; Non-mineralized structures

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1. Introduction

The rare Late Triassic–Early Jurassic coleoid cephalopod genus *Phragmoteuthis* Mojsisovics is a significant taxon for elucidating the phylogeny of Coleoidea. It is characterized by tripartite, fan-like pro-ostracum (an anterior part of the shell covering the soft body dorsally and laterally) forming the largest portion of the shell and attached to about three-quarters of the circumference of the comparatively small phragmocone. Mojsisovics (1882) erected this genus and the family Phragmoteuthidae to clarify the concept, first introduced by Suess (1865), of the isolated taxonomic position of this genus that has the teuthid-like pro-ostracum and belemnoid-like phragmocone. Naef (1922) supported the idea of the isolated position of the phragmoteuthids.

Jeletzky raised the rank of the family to an order (Jeletzky in Sweet, 1964). He assumed that *Phragmoteuthis* shows how the external shell of bactritoids was transformed into the internal skeleton of coleoids, making it an ancestor of modern teuthids via "fossil squids" (Jeletzky, 1966).

Late Triassic *Phragmoteuthis* (=*Belemnotheutis* in Bronn, 1859; =*Acanthoteuthis* in Suess, 1865) are known mainly by the unique specimens from the Carnian fish shales of Raibl (formerly Carinthia, now Cave del Predil, Northern Italy) (Bronn, 1859; Suess, 1865; Mojsisovics, 1882). The Raibl specimens of *Phragmoteuthis bisinuata* (Bronn) are preserved with tri-lobate pro-ostracum, arm hooks (in rare specimens still arranged to reflect the arm outlines), ink sacs ("bobbles" with narrow, long necks filled with black solidified ink) and a structure located at some distance to the anterior rim of the pro-ostracum, interpreted by Suess (1865) and Mojsisovics (1882) as mandibles. Since Mojsisovics's time, *Phragmoteuthis* from Raibl has been studied by Jeletzky (1966), Rieber (1970) and Riegraf (Riegraf, 1995; Riegraf et al., 1998).

As yet undescribed contemporaneous specimens of *Phragmoteuthis bisinuata* (Bronn) from Lunz (Lower Austria) are held by the Museum of Natural History in Vienna. The town of Lunz (Fig. 1) is located about 200 km northeast of Raibl, in the Northern Calcareous Alps (NCA) within an old coal-mining district which was abandoned in the 1950s. The fossil collecting history goes back to the 19th and early 20th century. Two tunnels were dug in the Carnian Raingraben shales of the Schindelberggraben at the Polzberg site close to Lunz. About 100 specimens of *Phragmoteuthis*, preserved with shells, arm hooks and ink sacs (Figs. 2A–C and 3A–F), are stored in the collection. Additionally, the pro-ostracum of the Raibl specimens bears black glossy sheets that were noticed yet not commented upon by Mojsisovics (1882, p. 305, pl. 94, fig. 7).

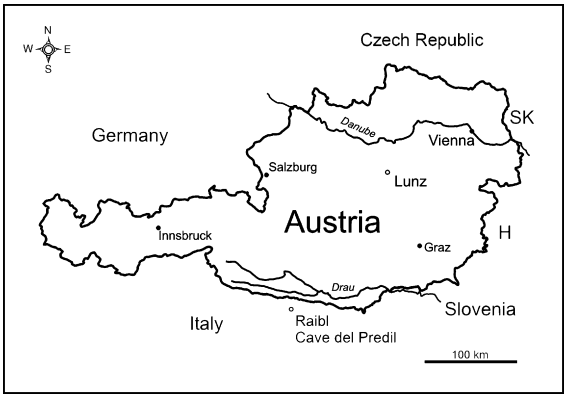

Fig. 1. Sketch map showing the position of the localities Lunz (Lower Austria) and Raibl (Cave del Predil, Italy) in relation to the Austrian border. H = Hungary, SK = Slovakia.

The well-preserved specimens of *Phragmoteuthis* from Lunz have been "forgotten" for a long time, mentioned only by Glaessner (1931) and Krystyn (1991). The present paper elucidates the origin of the black sheets on the pro-ostracum. Similar black material was observed in the body chamber of co-occurring ceratitid *Austrotrachyceras* and interpreted as the mantle and soft body tissue pseudomorphosed by carbon (Doguzhaeva et al., 2004a, 2007).

2. Geological setting, depositional environment and palaeogeographic background

2.1. Geological setting

During the Carnian the clastic Lunz Formation interrupted the sedimentation of shallow marine platform carbonates. The clastic deposition started with the fine-grained and silicate-rich Raingraben Shale Member, which is more or less even-bedded and thinly laminated. It contains in abundance the ceratitid *Austrotrachyceras* (Krystyn, 1991), fishes (Griffith, 1977), crustaceans and the bivalve *Halobia* (Glaessner, 1931). The middle Carnian of the Raingraben Member with *Phragmoteuthis* is defined by the occurrence of *Austrotrachyceras austriacum* (Mojsisovics, 1882). The subsequent Lunz Sandstone Member with coal seams is the dominating lithostratigraphical unit of the Lunz Formation. After its deposition, carbonate sedimentation started again with the fossil-rich Opponitz Limestone Member, followed by the re-established platform carbonate regime. Towards southwest the Lunz Formation is replaced by the relatively deep-water Hallstatt Limestone Facies

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