

# *In situ*-preservation of jaws in the upper Turonian acanthoceratid ammonite *Prionocyclus germari* (Reuss, 1845): Palaeobiological and taphonomic aspects

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## ABSTRACT

Cephalopod mandibles are rare in the Bohemian Cretaceous Basin (BCB) of Central Europe, occurring only as isolated jaw elements, the sole exception being a specimen of *Yezoites bladenensis* found with a lower jaw *in situ* in the second half of the 19th century. Here, we present a second record, a specimen of the acanthoceratoid ammonite *Prionocyclus germari* (Upper Cretaceous, upper Turonian). The ammonite preservation shows similarities to ammonoids from Solnhofen-type Lagerstätten, including phosphatised siphuncles, while the flattened ammonite conch is poorly preserved or fully dissolved. The lower jaw of *P. germari* is referred to the genus *Praestriptychus*. Linking the jaw apparatus with an index ammonite taxon of the uppermost Turonian fills a gap in our knowledge of Upper Cretaceous acanthoceratoid ammonite jaw anatomy. The preservation of altered (secondarily carbonised) organic matter has been revealed by Raman spectroscopy analysis at the tip of the aptychus.

The associated fauna and flora, consisting of complete crustaceans, fish, chondrichthyans and gymnosperm plant remains, reflect an unusual and unique preservational/taphonomic window within the BCB.

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## 1. Introduction

During the last decades, cephalopod jaw research produced a wealth of new aspects on ammonite morphology and palaeobiology, summarised by Tanabe et al. (2015). The application of new methods such as SEM, MicroCT, Synchrotron, etc., enabled a very detailed inside view into buccal mass organisation and jaw apparatuses (Kruta et al., 2011, 2015). This progress in ammonite jaw research accelerated in the last years, showing also different modes of preservation of the buccal mass not only in the “classical” Konservat-Lagerstätten (Klug et al., 2020, with references therein), including also non-mineralised jaws with preserved organic matter. In spite these advances, the finds of jaw apparatuses *in situ* are

rare, why it is often difficult to relate isolated jaw elements to a distinct cephalopod taxon in some stratigraphic intervals, in particular in the Upper Cretaceous. An overview on Upper Cretaceous jaw apparatuses related to its species can be found in Tanabe et al. (2015), and from this compilation (with references) it becomes apparent that scaphitids, in particular, have a good documentation. Aptychi of the Acanthoceratoidea, on the other hand, have a rather poor fossil record. From Japan *Subprionocyclus minimus* (Hayasaka and Fukada, 1951) with associated jaws was recorded (Tanabe and Fukuda, 1987). Kennedy and Klinger (1972) described a *Spinaptychus-Texanites soutoni* (Baily, 1855) association from the Santonian of Zululand (South Africa), and Ifrim (2013) documented *Pseudaspidoceras flexuosum* Powell, 1963 (lower Turonian, northern Mexico) in association with an aptychus. Finally, Landman et al. (2019) documented *Spathites puercoensis* (Herrick and Johnson, 1900) with an aptychus *in situ* from the Turonian of New Mexico (USA). Isolated jaw apparatuses, potentially corresponding to the Acanthoceratoidea, were figured by Wippich (2005) from Cenomanian/Turonian black shales of

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Westphalia (Germany) and by Everhart (2005) from the Santonian of the Western Interior Seaway of the USA (*Texanites?*).

Although cephalopods occur frequently in Upper Cretaceous claystone, marl and limestone of the Central European Bohemian Cretaceous Basin, BCB (Fritsch and Schlönbach, 1872; Wiese et al., 2004a; Košťák et al., 2018; Fig. 1A), their jaw elements are also rare. Exceptions are nearshore or shallow-water carbonate settings, which provided a number of calcitic rhyncholites and conchrohynchids from nautilids (Fritsch and Schlönbach, 1872; Fritsch, 1883; Till, 1909; Košťák et al., 2004). Rare isolated aptychi were described from fine-grained marly siltstone (?lower Turonian of Kučlín; lower to middle Coniacian of Brezno) by Fritsch and Schlönbach (1872), and were, more recently, mentioned from the upper Cenomanian of the Pecínov quarry (Košťák et al., 2018).

On the other hand, during almost 200 years of intensive research, only a single specimen of an ammonite with a lower jaw (aptychus) preserved *in situ* was recorded: Fritsch and Schlönbach (1872, pl. 13, fig. 8) described and figured a specimen of *Scaphites auritus* [= *Yezoites bladenensis* (Schlüter, 1871); see Wilmsen & Nagm, 2014] from the lower/middle Coniacian of northern Bohemia (refigured here on Fig. 5H), which fits the comparatively

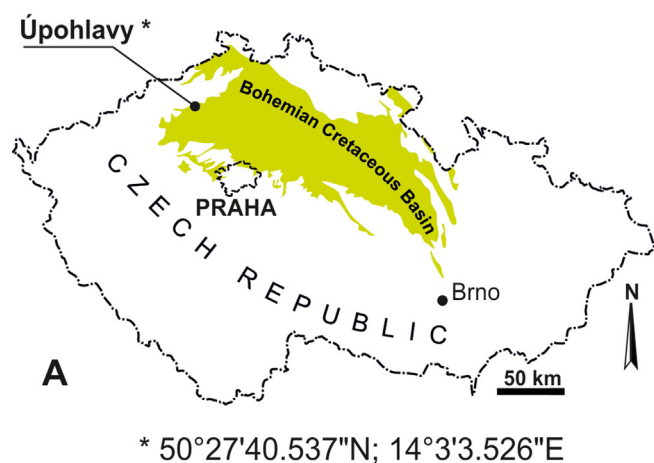
frequent occurrence of jaws in scaphitid ammonites elsewhere (Tanabe et al., 2015).

To contribute to the rare records of *in situ* jaw apparatuses in the Acanthoceratoidea, we present here an association of *Prionocyclus germari* (Reuss, 1845) together with its aptychi from the upper Turonian Úpohlavy working quarry (comp. Wiese et al., 2004; Figs. 1B–C, 2) in northern Bohemia. It is the second *in situ* record from the BCB. We applied Raman spectroscopy to the jaws in order to test for the preservation of organic matter. Linking the jaw apparatus to an upper Turonian index ammonite taxon fills a gap in our knowledge on Upper Cretaceous Acanthoceratoidea ammonite jaw anatomy.

Furthermore, we comment briefly on the possible taphonomy of the peculiar find situation, suggesting the presence of an unknown taphonomic window within the BCB.

## 2. Geological and stratigraphical framework

The Turonian strata near Úpohlavy (Fig. 1B, 2) are located in the SW–NE-trending Ohře Graben (northern Bohemia near Teplice). A first lithologic description of the Úpohlavy working quarry was



**Fig. 1.** A. Geographical position of the Bohemian Cretaceous Basin (green) within the Czech Republic and location of the Úpohlavy working quarry (\* coordinates), map from Košťák et al. (2018). B. Overview over the Úpohlavy working quarry. C. The incised channel (with dark phosphatic pebbles), cutting into the top of Bed 15 *sensu* Wiese et al. (2004a). In the middle part of the figure, the infill of burrows is well visible above the arrow. Scale bar equals 10 cm.

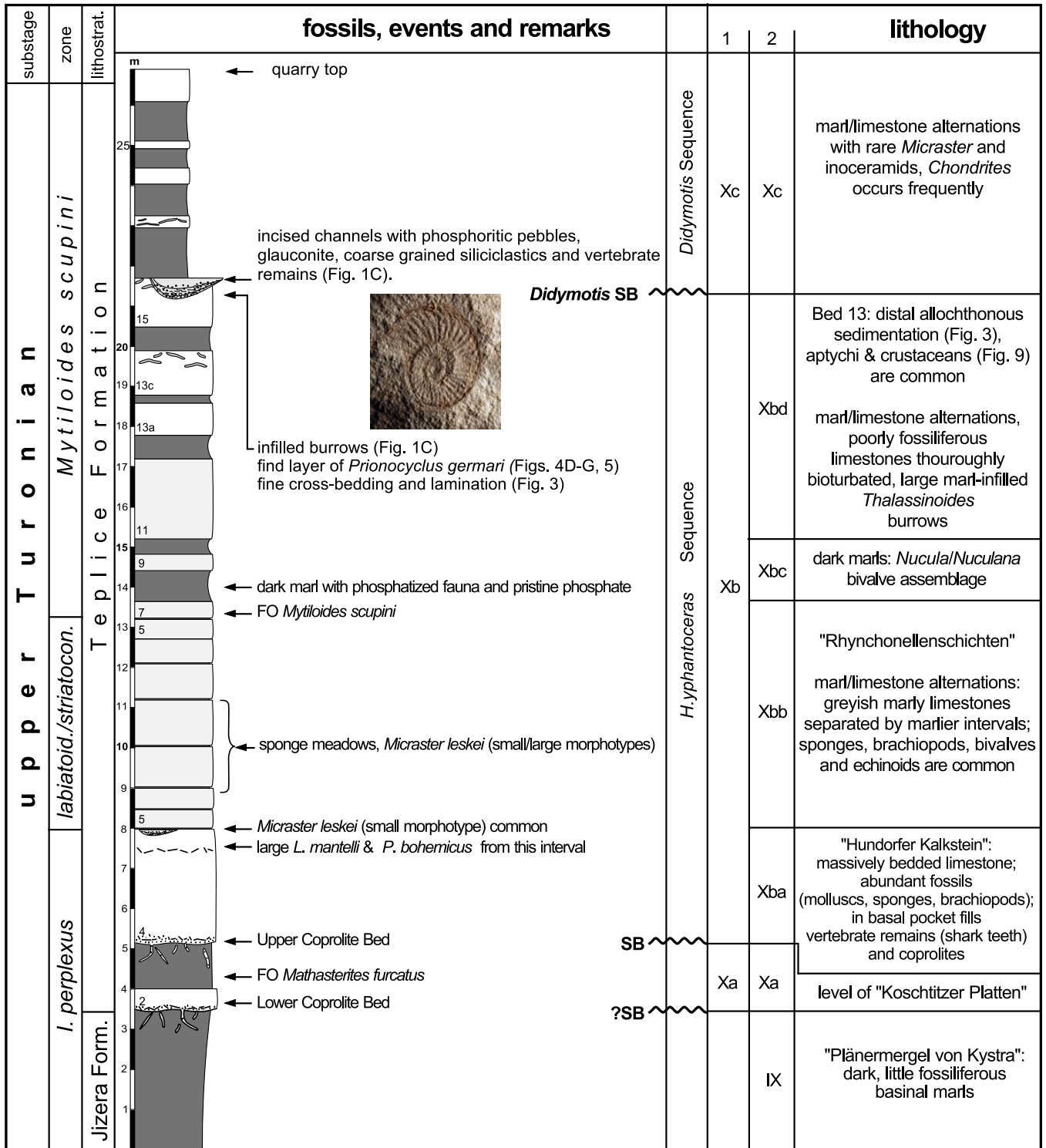


Fig. 2. Lithologic column of the upper Turonian Úpohlavý working quarry section, with data on litho-, biostratigraphy and remarks (changed after Wiese et al., 2004a). 1. Zahálka Beds (Zahálka, 1900a,b); 2. Refined lithostratigraphic subdivision of Váně in Krutský et al. (1975). Abbreviations: I: *Inoceramus*, labiatoid.: *M. labiatoidiformis*; striatocon.: *M. striatoconcentricus*; lithostrat.: lithostratigraphy.

given by Čech et al. (1996), Svobodová et al. (2002) and Wiese et al. (2004, with a historical account) presented data on lithology, biostratigraphy, sequence stratigraphy, palynology and stable carbon isotope stratigraphy. The cyclic nature of the succession, tied into a lateral correlation framework in a wider context, was

presented by Laurin and Uličný (2004). Phosphate occurrences and mineralisation were investigated by Al-Bassam et al. (2021). Contributions on the micro/macro fauna and isotopic analyses were presented in a number of further works (Hradecká, 1999; Foraminifera; Ekrt et al., 2001; Marine reptiles; Mikuláš, 2006; Trace

fossils; Ekrt et al., 2008: Teleost fish; Žítt and Vodrážka, 2008; Crinoids; Košťák and Wiese, 2011; Belemnites; Sklenář et al., 2013: Polychaetes; Chroustová and Pipík, 2019: Ostracods; Walliser et al., 2020: sclerochronological studies on *Inoceramus hercules*).

As shown in Figs. 1–2, the Úpohlavý section exposes ca. 27 m of marl, fossiliferous clayey limestone and marl/limestone alternations (beds 1–23, CaCO<sub>3</sub> content 50–85%), and the largest part of the section represents the Teplice Formation. Its base, and, likewise, the basal contact to the underlying Jizera Formation, is taken at the Lower Coprolite Bed (Bed 2 in Fig. 2). The informal regional lithostratigraphic subdivision into four lithological units and its members (IX, Xa, Xb<sub>α</sub>, Xb<sub>β</sub>, Xb<sub>γ</sub>, Xc) based on Zahálka (1900a,b), Váně (1976, 1979, 1999) and Váně in Krutský et al. (1975).

The top of Bed 15 marks the top a depositional sequence (*Hyphantoceras* Sequence). The associated sequence boundary (*Didymotis* Sequence Boundary of Wiese et al., 2018) is characterised by several shallow channel structures (Fig. 1C), occurring within the entire quarry at the same stratigraphic level. These represent the lowstand deposits of the succeeding *Didymotis* Sequence (comp. Wiese et al., 2004a,b; Wiese et al., 2018). The channel infills yield glauconite, phosphoritic pebbles, coarse-grained siliciclastics, frequent vertebrate remains – in particular fish and shark teeth – coprolites and larger benthic foraminifera. As seen in Fig. 1C, the sediments of the channels are locally infilled into open burrow systems (*Thalassinoides*), piping deeply down from the top of Bed 15 into the underlying sediment.

Although Bed 15 (Fig. 2) appears to be homogenous at first sight, it shows laterally and vertically discontinuous patches of weakly visible, shallow-angle cross-stratification and laminated intervals, which grade diffusely into the background sediment (Fig. 3). Sedimentary structures are indicative of fine-grained allochthonous sedimentation and are best understood as distal equivalents of the succeeding channel deposits and deposition from suspension clouds.

The preservation of ammonites from Bed 15 resembles that of Solnhofen-type Lagerstätten (cf. Seilacher, 1976; Keupp, 2007; ): The ammonites are flattened with weakly visible characters of the external shell ornament, and they exhibit a phosphatised siphununcle).

### 3. Material and methods

The material described here (Figs. 4–6) was collected *in situ* and comes from the upper part of Bed 15, which is a well-developed marly limestone of ca. 80 cm thickness (comp. Fig. 2). For comparison, we considered the original of *Scaphites auritus* Fritsch and Schlönbach (1872, pl. 13, fig. 8) from the Bohemian Brezno Formation (lower-middle Coniacian), housed in the collections of the National Museum, Prague (No. O3177; Fig. 5H).



Fig. 3. Polished slab of Bed 15, showing cross-stratification, erosional features and laminated intervals. Scale bar equals 1 cm.

### 3.1. Optical observation, SEM and imaging

The macro-photos of specimens were taken using the camera Canon EOS 600D and a Keyence microscope. Photographs were improved by using CorelDRAW X7 and Corel Photo-Paint X7 (including an aptychus reconstruction, Fig. 6). The specimen of *P. germari* (Figs. 4–5) was investigated with a Keyence microscope (VHX-7000N, camera VHF-7020), using objective VH-Z20R/Z20T (20–200× magnification) and a standard optical binocular microscope.

The aptychus was examined at the Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague, by scanning electron microscope (SEM) JEOL-6380LV at 30 kV and at 0.33–2.2 k X magnification. A fragment of the aptychus was coated with gold and investigated in the high vacuum mode (Fig. 7).

### 3.2. Raman spectroscopy

Raman microspectroscopy (Fig. 8) analyses were performed at the Department of Inorganic Chemistry, Faculty of Science (Charles University, Prague), at several randomly selected locations in the dark (tip region) and light pigmented areas on the ammonite jaw, using a Thermo Scientific DXR Raman microscope coupled with an Olympus microscope. A diode laser ( $\lambda = 445$  nm) was used as excitation radiation. The laser power was limited to 1 mW at source to avoid thermal changes in the samples. Spectra were taken in the range 100–2000 cm<sup>-1</sup> with the following settings: 2 s time of one accumulation and 128 of these accumulations were recorded for the resulting spectrum with an optimised signal-to-noise ratio. The instrument was calibrated using a polystyrene standard. Spectra are reported without any processing.

### 3.3. Terminology and abbreviation

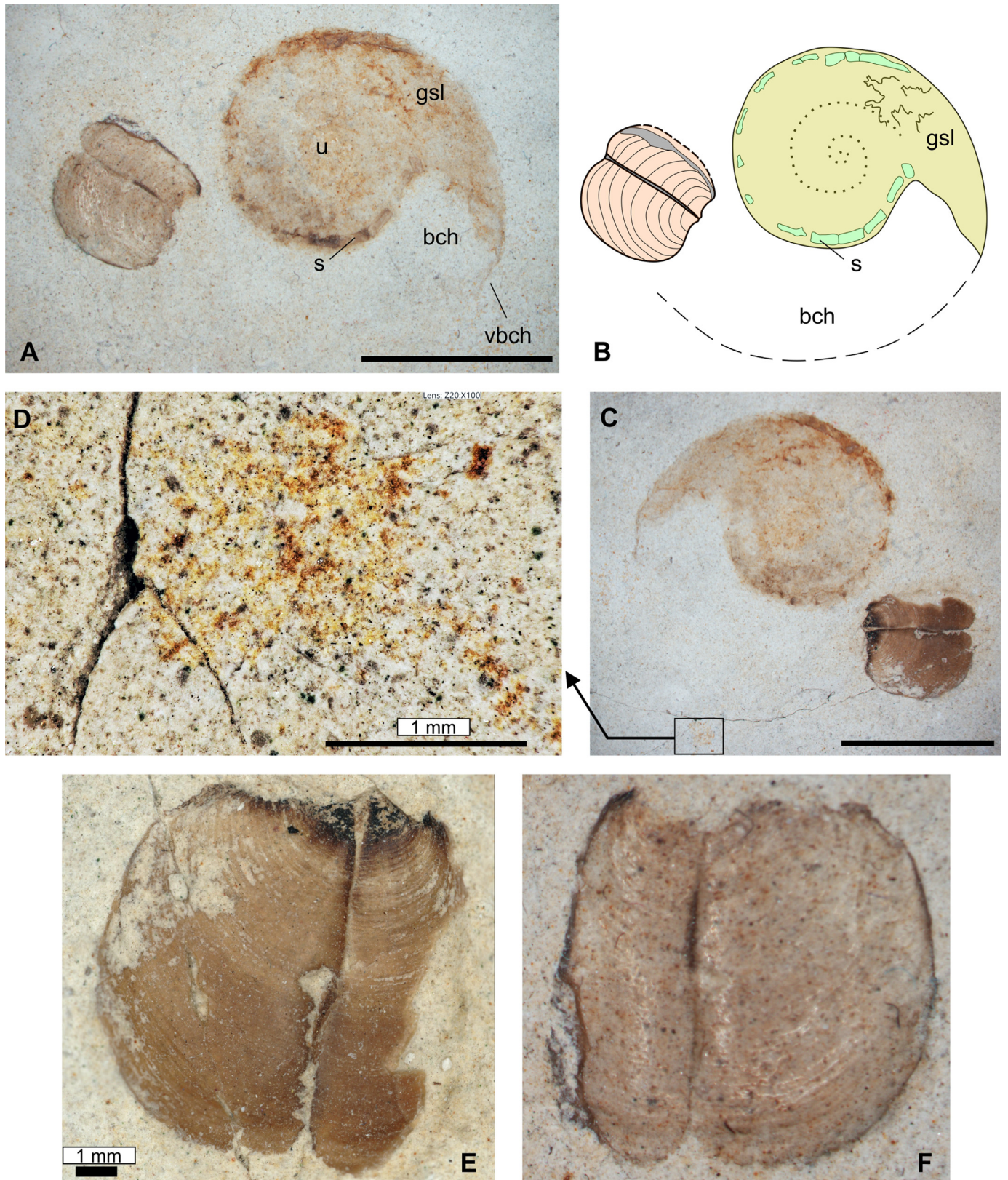
The terminology follows Engeser and Keupp (2002) and Tanabe et al. (2015).

Abbreviations: CHMZ – Chlupáč's Museum of Earth History, Faculty of Science, Charles University, Prague; NM – National Museum in Prague; D – diameter; U – umbilicus.

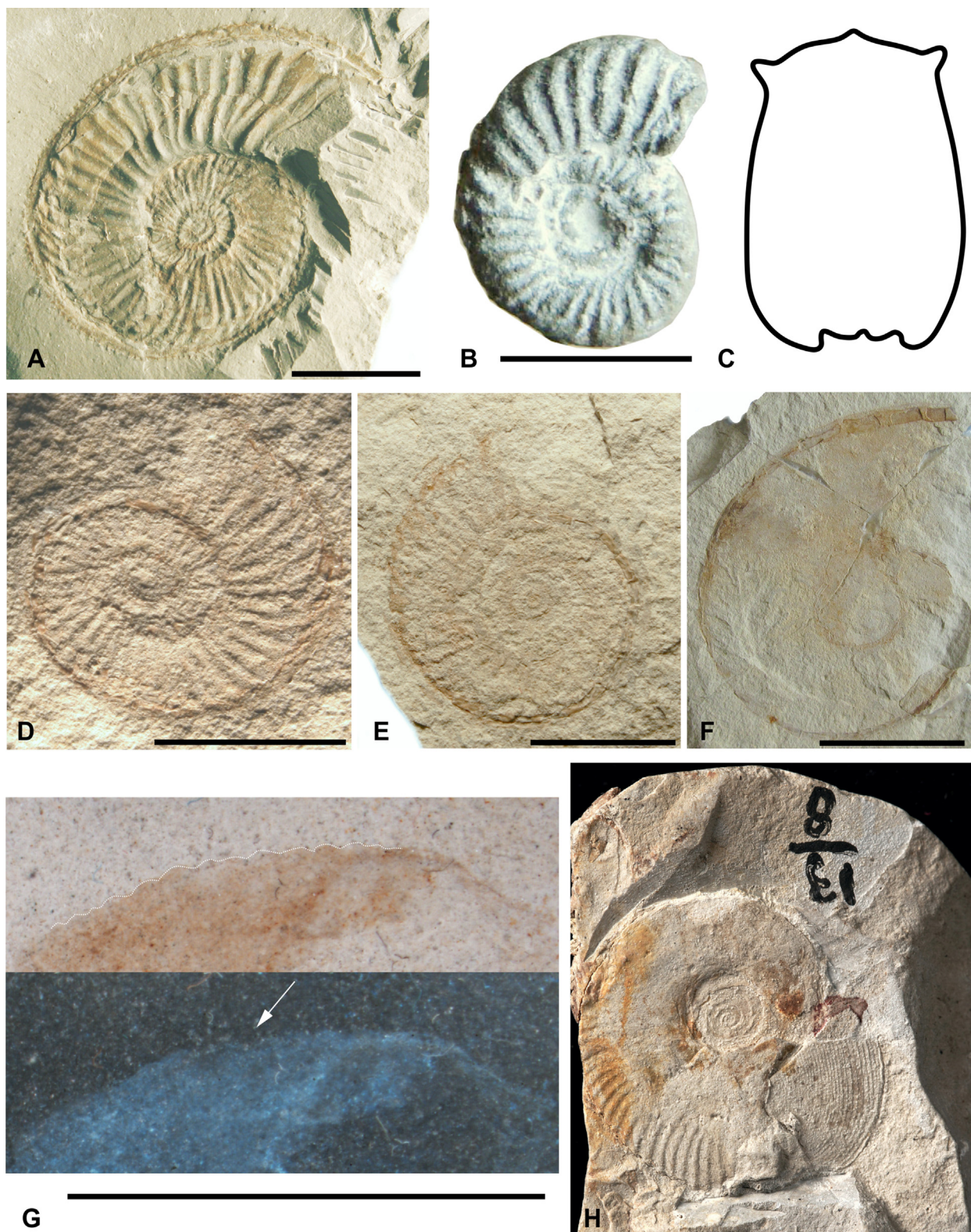
## 4. Systematic account

### 4.1. Ammonites

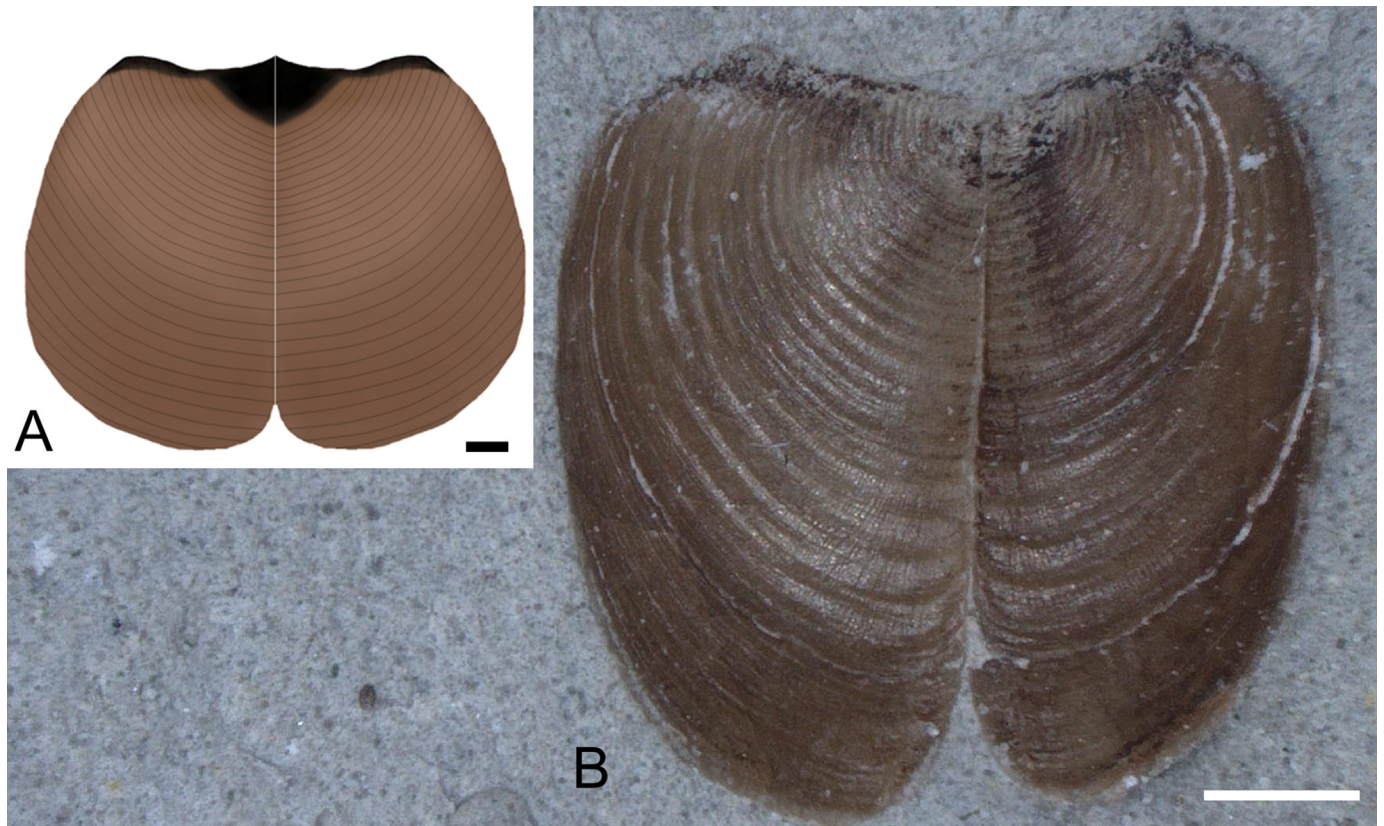
Ammonoidea Zittel, 1884  
 Acanthoceratoidea de Grossouvre, 1894  
 Collignoniceratidae Wright & Wright, 1951  
 Collignoniceratinae Wright & Wright, 1951



**Fig. 4.** A–C. *P. germari* specimen No. CHMZ 23-4358a, b with the preserved aptychus. A, C. No. CHMZ 23-4358a; part (C) and CHMZ 23-4358b: counter part (A). B. Schematic drawing indicating preserved morphological features within the specimen. C. CHMZ 23-4358a - counter part with indicated debris accumulation of debris located closely to the body chamber. D. Detail of debris (square in Fig. 4C) of phosphatic particles (?crustaceans). E. Calcitic *Praestriptychus* (concave) with preserved original organic matter at the tip (dark brown–black, CHMZ 23-4358a). F. Counter part (convex) of the *Praestriptychus*, CHMZ 23-4358b. Abbreviations: u – umbilicus, s – siphuncle, bch – body chamber, gsl – remains of the suture lines preserved as a ghost-like structures. Scale bars equal 1 cm unless otherwise indicated.



**Fig. 5.** A–B, D–F. Different types of preservation of *P. germari* from various localities in the BCB. A. The most common state of preservation from silty marlstone (Úhřetice, specimen No. CHMZ 23-RV001). B. A pyritised three-dimensionally preserved specimen from the type locality of *P. germari* (Lenešice, NM – O46). C. Whorl section from a pyritised specimen. D–G. *P. germari* from Bed 15 (Úpohlavy). D. The best preserved specimen (No. CHMZ 23-2093) under extremely low angle of light. E. Specimen No. CHMZ 23-4664 with a partly preserved phosphatised siphuncle. F. Ghost-like preservation lacking almost all external morphological features but exhibiting a phosphatised siphuncle (specimen No. CHMZ 23-5042). G. Weakly visible ribs and the crenulated keel preserved close to the body-chamber (No. CHMZ 23-4358b; highlighted by very thin dashed white line – upper part of the figure; the best visible part indicated by an arrow in the inverted colours, lower part of the figure). The specimen is strongly compressed and partly dissolved (the crenulated keel, ribs and ventrolateral tubercles are compacted). H. The sole specimen of scaphitid ammonite with an aptychus preserved in the BCB [*Scaphites auritus* Fritsch and Schlönbach, 1872, Tab. 13, Fig. 8; Březno Fm., Lower-Middle Coniacian; = *Yezoites bladenensis* (Schlüter, 1871) coll. NM – No. O3177; photo by Ing. Lenka Váchová (NM), with courtesy of author]. Scale bars equal 1 cm.



**Fig. 6.** A–B. Comparison of aptychi from Bed 15. A. *Praestriptychus* together with *P. germari* (reconstruction drawing). B. *Striptychus* (scaphitid-like type, specimen No. CHMZ 23-5227). Scale bars equal 1 mm.

### *Prionocyclus* Meek, 1876

Type species: *Prionocyclus wyomingensis* Meek, 1876 (comp. Kennedy et al., 2001)

#### *Prionocyclus germari* (Reuss, 1845)

(Figs. 4–5)

- 1845 *Ammonites Germari* Reuss: p. 22, pl. 7, fig. 10.  
 1872 *Ammonites Germari* Reuss: Schlüter, p. 41, pl. 11, figs 15–17.  
 1872 *Ammonites Germari* Reuss: Fritsch & Schlönbach, pl. 14, figs 1–2.  
 1893. *Schlönbachia Germari* Reuss: Fritsch, p. 74, fig. 50.  
 1988 *Prionocyclus germari* (Reuss, 1845): Kaplan, p. 37, pl. 3 figs 1–3, p. 43, pl. 6 fig 1.  
 1988 *Subprionocyclus normalis* (Anderson, 1958): Kaplan, p. 40, pl. 5, fig. 5.  
 1998 ? *Prionocyclus* cf. *germari* (Reuss); Küchler, pl. 11, fig. 4.  
 2000 *Prionocyclus germari* (Reuss, 1845): Robaszynski et al., p. 442, pl. 1, figs 7–8.  
 2001 *Prionocyclus germari* (Reuss, 1845): Braunberger & Hall: p. 1125, pl. 3, figs 1–18.  
 2001 *Prionocyclus germari* (Reuss, 1845): Kennedy, Cobban & Landman, fig. 108A,B, D–F, fig 109–119, with additional synonymy.  
 2003 *Prionocyclus germari* (Reuss, 1845): Kennedy, Phansalkar & Walaszczyk, p. 435, fig. 2.  
 2005 *Prionocyclus germari* (Reuss, 1845): Andrade, pl. 11, fig. 2.  
 2009 *Prionocyclus germari* (Reuss, 1845): Wiese, pl. 1, figs A–J,  
 2012 *Prionocyclus* cf. *germari* (Reuss, 1845): Diebold, p. 167, pl. 3, figs 1–5.  
 2018 *Prionocyclus germari* (Reuss, 1845): Diebold et al., p. 379, fig. 4A–J.

2019 *Prionocyclus germari* (Reuss, 1845): Kennedy & Kaplan, pl. 36, figs 9–10; pl. 37, figs 2–5, 7.

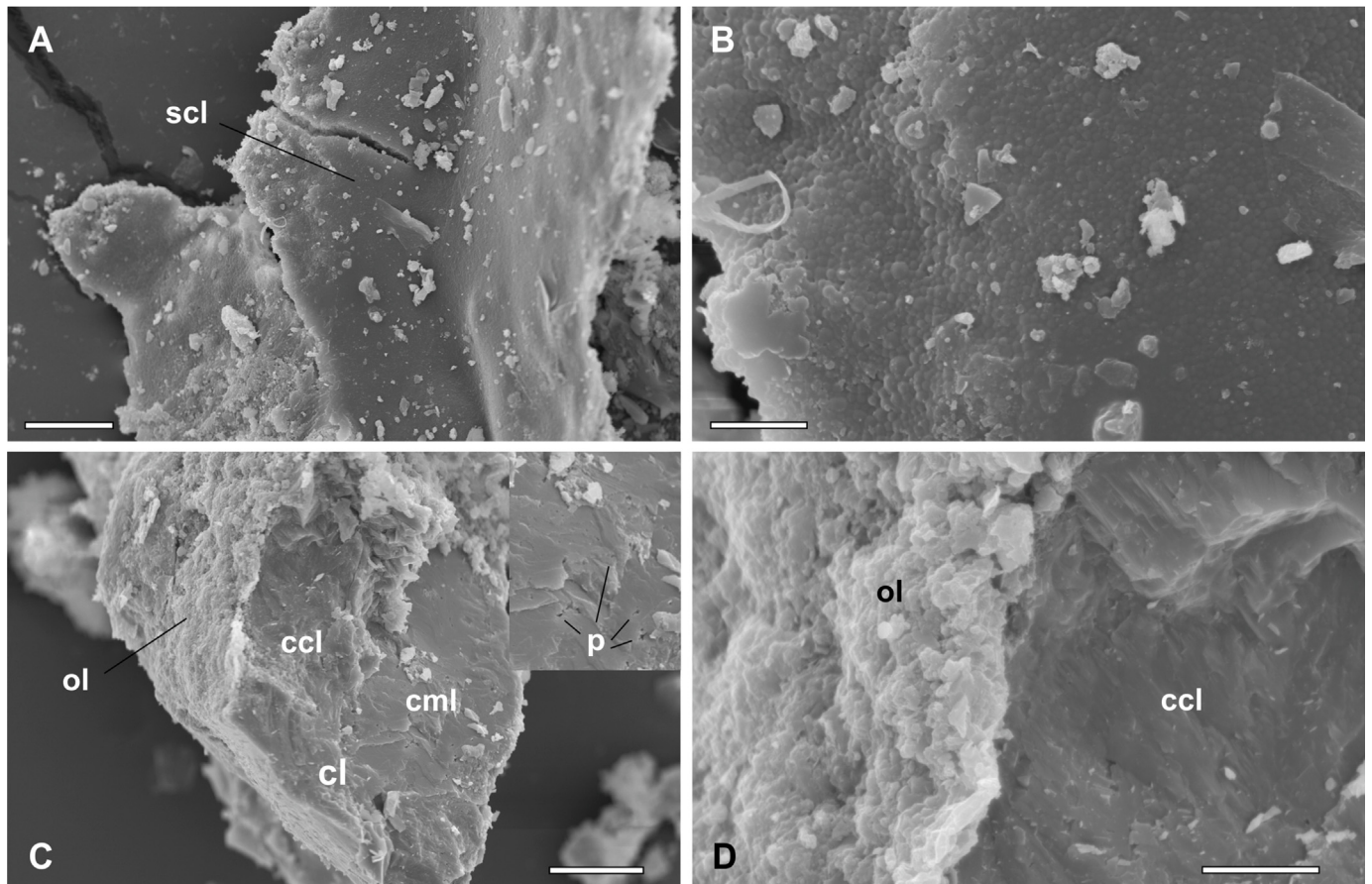
Type. Lectotype is the original of Reuss (1845, pl. 7, fig. 10), designated by Kennedy et al. (2001).

*Material studied.* Specimens Nos CHMZ 23-4358a and CHMZ 23-4358b (part and counter parts), CHMZ 23-4664, CHMZ 23-5093, CHMZ 23-4664, CHMZ 23-5042 (Coll. Souček), CHMZ 23-RV001, and specimen No. NM O3177.

*Description.* A very small specimen (D: 1.7 cm, D/U = 2.8), consisting of part and counter part (CHMZ 4358a, b). The flattened (dissolved) shell shows only weak ornament like shadows of ribbing on the ventral side, a phosphatised siphuncle and ghost-like suture lines on the last chambers. The body chamber is weakly visible in its posterior part (Fig. 4A), where faint ribbing and a crenulated keel are developed (Fig. 5G).

*Discussion and remarks.* The ammonite assemblage from the Bed 15 consists of the heteromorphic taxa *Scaphites*, *Allocrioceras* and *Hyphantoceras* plus the desmoceratid *Puzosia*. From that, our find differs by its ribbing and the crenulated keel, which identifies the specimen as *P. germari*. The suture lines are preserved as ghost-like sutures and are in accordance with this taxon (cf. Braunberger and Hall, 2001). Compared to better preserved specimens of *P. germari* from Bed 15, the D/U ratio shows almost identical values (CHMZ-4664 D/U = 2.7 and CHMZ-5098, slightly compressed specimen, D/U = 2.6). An accumulation of crustacean debris located closely the body chamber (Fig. 4C–D) may represent a random accumulation as we did not find any relevant evidences for the existence of a stomach content.

*P. germari* is fairly abundant in the BCB and shows different types of preservation in different lithologies. Pyritised and 3D-preserved individuals occur in dark marlstone of Reuss's type locality Lenešice



**Fig. 7.** A–D. SEM image of *Praestriptychus* microstructures. A. Surface of the calcitic layer (**scl**) at the contact with the organic layer; scale bar equals 50  $\mu\text{m}$ . B. Detail of the granulated surface; scale bar equals 10  $\mu\text{m}$ . C. Preserved (internal) organic layer – **ol**; the calcitic layer (**cl**): outer part of the calcitic layer – **ccl** with calcitic oblique crystal microstructure; **cml** – compact massive layer of the **cl** with irregularly arranged pores – **p** (detail in the right upper corner); scale bar equals 50  $\mu\text{m}$ . D. Detail of the boundary between **ol** and **cl** (**ccl**) showing oblique lamination of the calcitic part of the aptychus; scale bar equals 10  $\mu\text{m}$ .

(Fig. 4B), flattened but nicely preserved specimens occur in central parts of the BCB (siltstone to marlstone, Fig. 5A), and poorly preserved specimens, mainly lacking morphological details of the outer shell surface, are found in laminated limestone like presented here (Fig. 5D–F).

**Stratigraphic occurrence.** Upper Turonian, *P. germari* Zone, *Mytiloides scupini* Zone.

#### 4.2. *Aptychus* (lower jaw sensu Tanabe et al., 2015, fig. 10.11 c)

##### *Praestriptychus* Trauth, 1927

Type species: *Praestriptychus gerzensis* Trauth, 1930, Tab. V, figs. 14–15, designated by Schweigert (2000, p. 698).

##### *Praestriptychus* sp.

**Material studied.** A single specimen preserved as part and counterpart (Nos CHMZ 23-4358a and CHMZ 23-4358b, Coll. Souček, Figs. 4E–F, 5G, 6A).

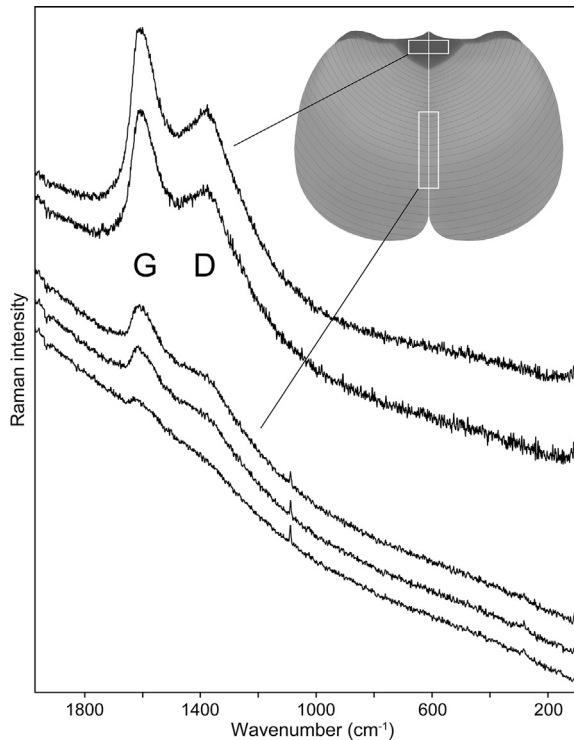
**Description.** The lower jaw is located in the most proximal part of the body chamber in a position, which is assumed to be close to the aperture. It is preserved in a butterfly position. The length of the aptychus is 7 mm. The well-preserved left wing is 5 mm wide; the right wing is partly incomplete (the total width is calculated to be 10 mm). Both valves are only slightly concave. The aptychus has an almost semi-circular shape with refined and concentric fine ribs.

No harmonic facets are developed. Striae are very fine. The calcitic parts are well preserved, displaying a light brown colour. It consists of well-distinguished calcitic layer (Fig. 7) and altered organic matter in the apical part of the aptychus (see Raman spectrometry, Fig. 8). The SEM analysis (Fig. 7A–D) shows two distinct layers, an inner organic layer (**ol**) and a calcitic layer (**cl**: **ccl** – calcitic layer formed by oblique fibrillar crystals and **cml** – calcitic massive layer, Fig. 7C–D). The contact of the **cl** (**ccl**) with organic matter (forming **ol**) shows a granulation (partly missing the **ol**), which is well visible in a 1.8k x magnification (Fig. 7B). While the outer part of the **cl** is formed by oblique calcitic crystals (Fig. 7D), the middle part of the layer (**cml**) shows a rather homogenous character with dispersedly distributed micropores (Fig. 7C).

Raman spectroscopy confirms that the apical part of the aptychus is rich in organic matter, as documented by a strong signal of the G and D bands of carbonaceous matter (top two spectra in Fig. 8). The bottom three spectra illustrate a lower content of organic matter in the lighter region near the centre of the aptychus, where the Raman signal of calcite and associated fluorescence are more prominent. The high concentration of organic matter at the tip of aptychus is presumably linked to the original lower jaw anatomy, i.e., a thicker chitinous layers in this part of the mandible.

**Remarks.** According to its morphological features and, in particular, due to the absence of harmonic facets, we relate this aptychus to *Praestriptychus* Trauth, 1927. *Praestriptychus* corresponds to the calcitic “Aptychus” sensu Tanabe et al. (2015). In the BCB, only two formal genera, *Praestriptychus* and *Striptychus* Trauth, 1927 are





**Fig. 8.** Raman microspectroscopy. Two broad Raman bands at  $1595$  and  $1370\text{ cm}^{-1}$  (G, D bands) correspond to carbonaceous matter (organic carbon) content of the inner (organic) layer of the jaw. The black matter preserved at the tip of the aptychus proves the presence of original (however altered) organic matter or primary pigments. Vertical axis – Raman intensity, horizontal axis – Wavenumber ( $\text{cm}^{-1}$ ). Higher concentration of organic matter at the tip of the aptychus may reflect an enlarged thickness of original? chitinous layers in this part of the jaw.

recorded so far. Both genera can easily be separated by the harmonic facets in *Striptychus*. Striptychi are typical of the Scaphitidae Gill, 1871 (Figs. 5H, 6B), Baculitidae Gill, 1871, Nostoceratidae Hyatt, 1894 and the Ancyloceratidae Meek, 1876. The earliest record of *Striptychus*-type jaw is reported from *Ancyloceras matheronianum* d'Orbigny, 1840 from the early Aptian (Baraboshkin and Shumilkin, 2018). Generally, *Striptychus*-type jaws are more rounded and show a more variable morphology, including the shape of the valves (oval: e.g., *Baculites*, rounded: e.g., *Scaphites*, elongated: e.g., *Sciponoceras*). Ribbed lines can be very narrowly spaced. Starting at the apex, the space between them increases sometimes. The concentric lines in the *Striptychus* type are accompanied by radial striae, well seen in Fig. 6B (scaphitid-like type of aptychus, Bed 15). This morphological feature is absent in *Praestriptychus* associated with *P. germari*.

## 5. Discussion

### 5.1. *Praestriptychus* – its role and occurrence

The oldest aptychi in the form of the ribbed *Cornaptychus* Trauth, 1927 are early Toarcian in age and are related to the Hildoceratidae (Keupp, 2000; Tanabe et al., 2015). The earliest record of a *Praestriptychus* comes from the body chamber of the stephanoceratoid ammonite genus *Normannites* Munier-Chalmas, 1892 (Middle Jurassic, Bajocian, Westermann, 1954). There is, however, the possibility that praestriptychi evolved earlier from the poorly known *Laevicornaptychus* Trauth, 1936 (Lower Jurassic, Toarcian),

the latter differing from *Cornaptychus* by the presence of a smooth, unsculptured calcitic surface layer (e.g., Farinacci et al., 1976). Praestriptychi were, most likely, a plesiomorphy of the superfamily Stephanocerataceae, while the *Lamellaptychus* Trauth, 1927 in the Haplocerataceae evolved directly from *Cornaptychus* (Engeser and Keupp, 2002).

Several further types of aptychi evolved from *Praestriptychus* still during the Jurassic, differing by surface and internal structures of the calcitic layer such as *Granulaptychus* Trauth, 1927 in the Kosmocerotidae and Garantianinae (Trauth, 1930; Mitta and Mironenko, 2021), *Strigogranulaptychus* Schweigert, 2000 in the Lithacoceratinae (Schweigert, 2000) and *Laevaptychus* Trauth, 1927 in the Aspidoceratinae (Trauth, 1930). The main lineage of praestriptychi, however, persisted in many perisphinctoid ammonites, and a number of Cretaceous ammonite families inherited this type of aptychus (see Engeser and Keupp, 2002 for more details).

#### 5.1.1. Acanthoceratoidea

Apart from *P. germari*, *Praestriptychus* seems to be also present in *Subprionocyclus minimus* (Tanabe and Fukuda, 1987). Lacking harmonic facets, the aptychi in *P. flexuosus* (lower Turonian, Ifrim, 2013) and *S. puercoensis* (middle Turonian, Landman et al., 2019) can also be tentatively referred to as *Praestriptychus*. Similarly, aptychi in some Placenticeratidae (Hoplitioidea) (Summesberger et al., 1996; Landman et al., 2006), referred to as striptychus-like aptychus by Engeser & Keupp (2002), seem also to lack harmonic facets and are best included into *Praestriptychus*. We therefore support the idea that the Acanthoceratoidea and Hoplitioidea could have been characterised by the presence of a *Praestriptychus* as a plesiomorphic character. This would be in accordance with the phylogenetic tree of ammonoids by Engeser & Keupp (2002, p. 92, fig. 8), based on the presence/absence of different types of aptychi.

The lower jaws of the Texanitinae (Acanthoceratoidea: Collignoniceratidae), on the other hand, show some affinities to the striptychi at first sight (see specimens figured in Kennedy and Klinger, 1972, pls. 72, 73), and there exist also some similarities with aptychi from the Desmocerotidae (possessing similar apical angle and facets). However, there are significant differences in the mode of ribbing (e.g., wider spaced ribs in desmocerotids) and the presence of a tuberculation. These aptychi are referred to as *Spinaptychus* Trauth, 1930. Morphologically, this type of aptychus is characterised by an open apex and nodules/granules more or less irregularly distributed between the growth-lines. The latter morphological feature, however, is not necessarily developed in all specimens. Where associated with ammonites (Kennedy and Klinger, 1972; Klinger and Kennedy, 1980, figs 263–265), *Spinaptychus* occurs only in the Texanitinae. *Spinaptychus* is known to occur from the Coniacian to the Campanian (Trauth, 1930; Kennedy and Klinger, 1972), which mirrors the stratigraphic range of the Texanitinae. The presence of *Spinaptychus* in the Texanitinae reflects, therefore, possibly an apomorphic character of the group.

The function of aptychi still remains controversial. Despite some unique records studied by synchrotron (Kruta et al., 2011), suggesting explicitly its role as a jaw element (see also Tanabe et al., 2015; Klug et al., 2020; and others), some other authors point out their (additional) protective function, judging from the identical shape of the aptychus and the aperture (Lehmann and Kulicky, 1990; Mironenko, 2014). The shape of *Praestriptychus* in *P. germari* equals well the outline of the aperture of the conch (Fig. 5C; specimen No. NM – O46), which represents a similar size as the specimen described herein. Mironenko (2018) assumed a decreasing role of

protective function during ontogeny, explaining disproportions between the size of aptychus and the size of aperture.

The eco-functional role of morphology was widely discussed by Tanabe et al. (1980) and others, leading to the assumption that large morphological variations within the aptychi is linked to the diversity in dietary habits (e.g., predatory, scavenging, microphagous). This interpretation may explain also different types of aptychi in the Acanthoceratoidea, in which smaller and large ammonite taxa of different habitats are known.

## 5.2. Microstructure

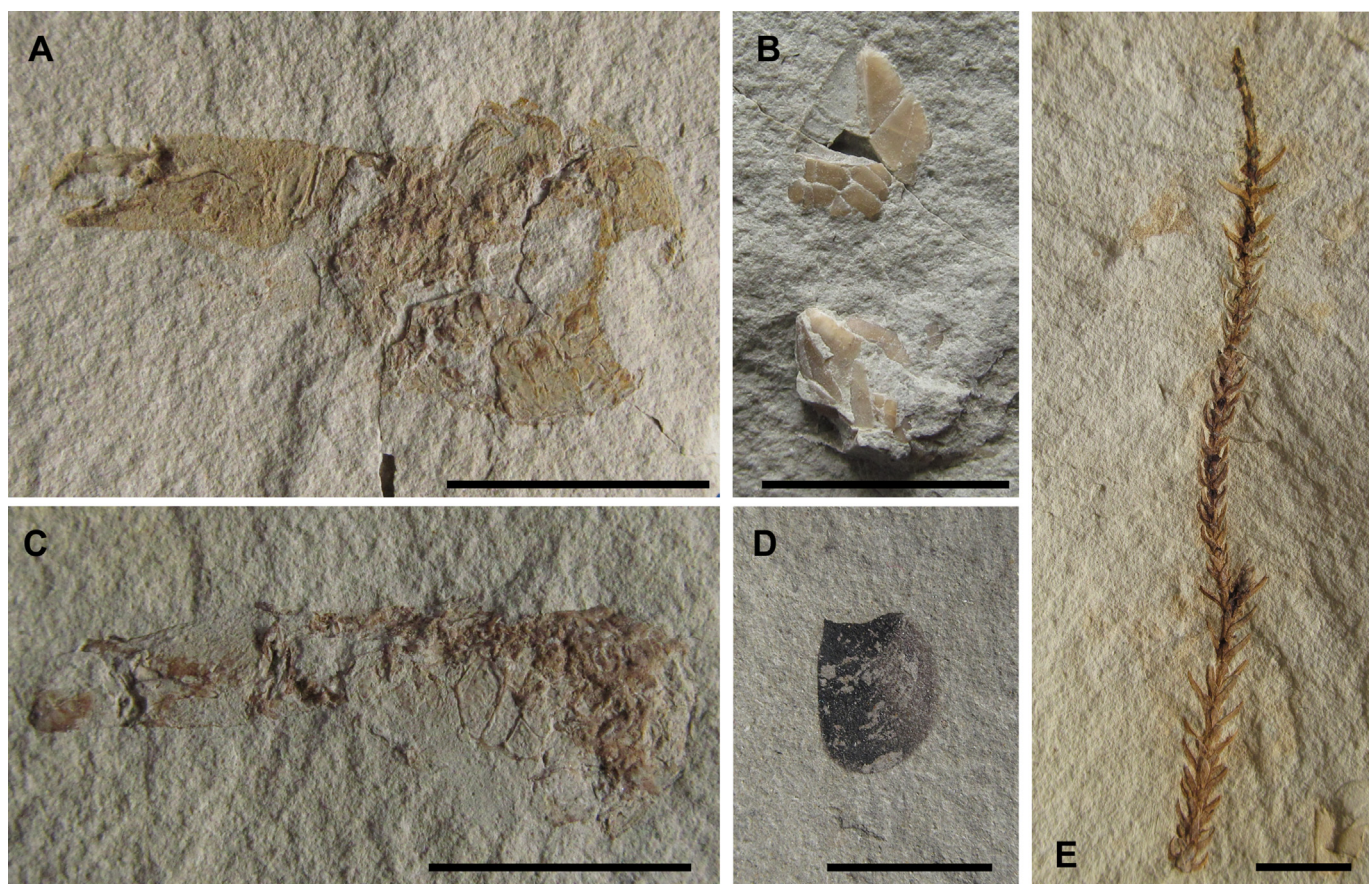
The microstructure of the aptychus was subject of numerous investigations (Farinacci et al., 1976; Dagys et al., 1989; Doguzhaeva and Mikhailova, 2002; Kruta et al., 2009; Mironenko, 2018). The SEM investigation of our aptychus (Figs. 7A–D) revealed a well-preserved microstructure, comparable to exceptionally well preserved aptychi figured by Mironenko (2018, 2021) and Landman et al. (2019). The aptychus microstructure of *P. germari* shows similar features of the calcitic layer compared to those in *Spathites puercoensis*, figured by Landman et al. (2019, fig. 4). We observed an oblique arrangement of calcitic (fibrous) crystals (Fig. 7D) in the outer part of the **cl**. The middle part of calcitic layer is characterised by the massive microstructure possessing well-developed micropores. This massive part is thicker (than the part with fibrous crystal), reaching of about 80  $\mu\text{m}$ . The overall thickness of both (e.g., the part of layer with oblique lamination and the part with massive

microstructure) is about 145  $\mu\text{m}$  (Fig. 7C), i.e., slightly thinner than in the *Spathites puercoensis* aptychus (190  $\mu\text{m}$ ; Landman et al., 2019).

The calcitic layer (Fig. 7C, D) exhibits widely-spaced micropores. However, the porosity in these type of aptychi is poorly known (Mironenko, 2018). Similar but probably not identical structures are well-developed in placenticeratid jaws in the calcitic layer (at the outer surface therein), figured by Landman et al. (2006, Fig. 29A). A black organic layer preserved at the tip of the aptychus was also described by Landman et al. (2006). According to their interpretation, this layer represents an original organic (assumed as originally chitinous) lamella forming a part of the inner lamella. However, in thin aptychi, the chitinous layer may be exposed at the surface (Landman et al., 2006).

## 5.3. Preservation

The dark inner layer is preserved in the apical part of the aptychus (Figs. 4E, 5G, 6A), still exhibiting an organic matter signal (Fig. 8). Therefore, we assume a very low level of diagenesis and degradation of the originally organic origin of this layer. The carbonaceous matter can be interpreted as a product of diagenesis and carbonification of the original organic matter (presumably chitin; Landman et al., 2006). The original organic matter was especially concentrated at the tip and frontal margin of the aptychus and, to a lesser extent, in its more distal parts. Raman spectroscopy and other optical methods confirmed similar pattern in



**Fig. 9.** A–E. Samples of unusual preservation from Bed 15, corresponding to the preservation in Solnhofen-type Lagerstätten. A. The decapod crustacean *Mesostylus* sp. (specimen No. CHMZ-20-B15001). B. An articulated specimen of the cirriped *Stramentum pulchellum* (G.B. Sowerby, 1843); figured in Kočová Veselská et al., 2020 (specimen No. CHMZ-20-5282). C. An indetermined decapod crustacean (specimen No. CHMZ-20-B15002). D. Carbonised? scaphitid-type aptychus (specimen No. CHMZ-20-B15003). E. An indetermined gymnosperm plant remain (specimen No. CHMZ-20-B15004). Scale bars equal 1 cm.

the fossilised material. Therefore we conclude that the detected carbonaceous matter is the remnant of the original (however altered – carbonificated) organic matter.

The exceptional preservation of other fossil remnants in Bed 15 is shown in Fig. 9, supporting the idea of the existence of a new taphonomic window in central European BCB. This fauna (and flora) is currently under investigation.

## 6. Conclusions

Our main conclusions are summarised as follows:

A *Prionocyclus germari* (Reuss, 1845) with an aptychus *in situ* is the second record of an ammonite with its jaws preserved *in situ* in the BCB. We include the aptychus in *Praestriptychus* Trauth, 1927. It is only the sixth record of an acanthoceratid ammonite with its aptychus *in situ*.

Using Raman spectroscopy, we recognised that altered organic matter is still present in the inner part of the aptychus resulting from degradation (carbonification) of presumably original chitinous parts of the jaw. Larger accumulation of the organic matter with stronger Raman signal is observed at the tip and frontal part of the lower jaw.

Based on a review of literature data we speculate that *Praestriptychus* is a plesiomorphic feature of a part of the Acanthoceratoidea. Within the Acanthoceratoidea, the ammonite subfamily Texanintinae (Acanthoceratoidea: Collignoniceratidae, Coniacian to lower Campanian) appears to be characterised by the presence of a *Spinptychus*, which then reflects an apomorphy.

Being the index zonal taxon, isolated aptychi of *P. germari* might be also of stratigraphical importance.

The preservation of the ammonites corresponds to that in Solnhofen-type Lagerstätten.

Exceptionally preserved fossils, including mineralised organic/soft parts, reveal probably a new taphonomic window in the central European BCB (currently under investigation).

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