Middle Devonian (Eifelian, *australis–ensensis* zones) conodonts from the Jirásek quarry near Koněprusy (Barrandian area, Czech Republic) with special emphasis on the *Polygnathus pseudofoliatus* Group and notes on environmental changes related to the Kačák Episode

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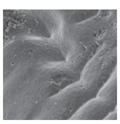

The Jirásek quarry in the Koněprusy area (Barrandian area, Czech Republic) represents a unique section, where the stratigraphic equivalent of the black shales of the Kačák Member (Srbsko Formation) is developed in a carbonate succession. Here we describe conodont faunas of the upper Acanthopyge Limestone (Choteč Formation, *australis–kockelianus* zones) and the Upper Dark Interval of the Acanthopyge Limestone referred to as UDI (Choteč Formation, *ensensis* Zone) with special emphasis on the *Polygnathus pseudofoliatus* Group. The following taxa are discussed in this paper: *Polygnathus pseudofoliatus* Wittekindt, *P. amphora* Walliser & Bultynck, *P.* sp. aff. *P. amphora* Walliser & Bultynck, *P. eiflius* Bischoff & Ziegler, *P. ensensis* Ziegler & Klapper *in* Ziegler *et al*., transitional forms among *P. pseudofoliatus–P. amphora*, *P. eiflius–P. amphora*, *P. pseudofoliatus–P. eiflius* and *P. eiflius–P. ensensis*, *P. benderi* Weddige, *P. abbessensis* Savage, *P. bagialensis* Savage, *Tortodus kockelianus* (Bischoff & Ziegler), *T. australis* (Jackson *in* Pedder *et al*.), *Tortodus* sp. A, *Tortodus* sp. B, *Tortodus* sp. aff. *T. weddigei* Aboussalam, *Tortodus* sp. aff. *T. caelatus* (Bryant), *Polygnathus* sp. A, *P. kluepfeli* Wittekindt, *P. trigonicus* Bischoff & Ziegler, *P. linguiformis* Hinde, *P. klapperi* Clausen, Leuteritz & Ziegler, *Polygnathus* sp. aff. *P. zieglerianus* Weddige, *Polygnathus* sp. aff. *P. alveolus* Weddige, *Polygnathus* sp. B, *Polygnathus* sp. C, *Polygnathus* sp. D, *Polygnathus* sp. E and *Polygnathus* sp. F. The occurrence of *P. amphora*, *P. benderi*, *P. abessensis* and *P. bagialensis* was recorded for the first time in the Barrandian area. The large morphological variability, occurrence of transitional forms and in most cases unknown ontogenetic variation within the *P. pseudofoliatus* Group, hampers using particular species of this group as zonally diagnostic taxa. It is emphasized herein that taxonomic and morphometric analysis of large collections with members of *P. pseudofoliatus* Group is highly needed in order to properly delineate species boundaries. The increased morphological variation within the group is discussed in the light of the contemporary environmental changes related to the Kačák Episode. • Key words: conodonts, Middle Devonian, Eifelian, *australis–ensensis* zones, *Polygnathus pseudofoliatus* Group, Kačák Episode, Barrandian area.

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The present study focuses on Eifelian (Middle Devonian) conodont faunas, with particular emphasis on the *Polygnathus pseudofoliatus* Group. The material comes from the Jirásek quarry at Koněprusy (Fig. 1), which represents a unique section in the Barrandian area where the *kockelianus–ensensis* boundary interval corresponding to the Kačák Episode, is developed in a carbonate succession. (Note: In this paper we use the designation Kačák Episode *sensu* Walliser & Bultynck 2011, which better reflects its polyphase nature). Conodonts from the Jirásek quarry were previously studied by Kalvoda & Zikmundová *in* Galle & Hladil (1991), Kalvoda (1992) and Kalvoda *in* Hladil & Kalvoda (1993a, b). The following conodonts were reported by the above mentioned authors from the section (only as lists of taxa, without description or photodocumentation; taxa names correspond to the original publications): *Polygnathus eiflius* Bischoff & Ziegler, *Polygnathus pseudofoliatus* Wittekindt, *Polygnathus linguiformis linguiformis* Hinde, *Polygnathus angustipennatus* Bischoff & Ziegler, *P. pseudofoliatus* Wittekindt–*P. ensensis* Ziegler & Klapper transitional forms, *P.* cf. *ensensis* Ziegler & Klapper, *Polygnathus* cf. *xylus* Stauffer, *Ozarkodina bidentata* Bischoff & Ziegler, *Polygnathus latus* Wittekindt, *Polygnathus* ex gr. *weddigei* Clausen, Leuteritz & Ziegler, *Polygnathus kluepfeli* Weddige, *Polygnathus* ex gr. *klapperi* Clausen, Leuteritz & Ziegler, *Tortodus caelatus* (Bryant), *Icriodus* sp., *Icriodus regularicrescens* Bultynck.

Hladil *et al*. (1993, p. 55) and Hladil & Kalvoda (1993a, p. 15) were the first to suggest that the topmost dark interval (referred to as "dark horizon", or "dark interval") of the Acanthopyge Limestone cropping out in the Jirásek quarry might represent a stratigraphic equivalent of the Kačák Member and thus could reflect the Kačák Episode (Kačák event *sensu* House 1985, *otomari* Event *sensu* Walliser 1985, Late Eifelian 1 Event *sensu* Walliser 2000). They based their conclusion on the presence of conodonts from the *kockelianus* and *ensensis* zones, the presence of *Nowakia otomari* Bouček & Prantl, a sudden change in benthic assemblages below and within the dark interval and also the sudden lithological change (onset of thin bedded, dark fine-grained packstones and grainstones). Budil (1995, p. 16.) regarded the correlation as "not fully proved, although very probable". Chlupáč (2003) argued that dark shales similar to the Kačák type also occur in the Koněprusy area and therefore left the question of correlation open. Similarly, Berkyová (2004) considered the correlation to be ambiguous mainly because of different morphotypes of *Nowakia otomari* occurring in UDI and black shales of the Kačák Member.

Geological setting

Acanthopyge Limestone in the Koněprusy area

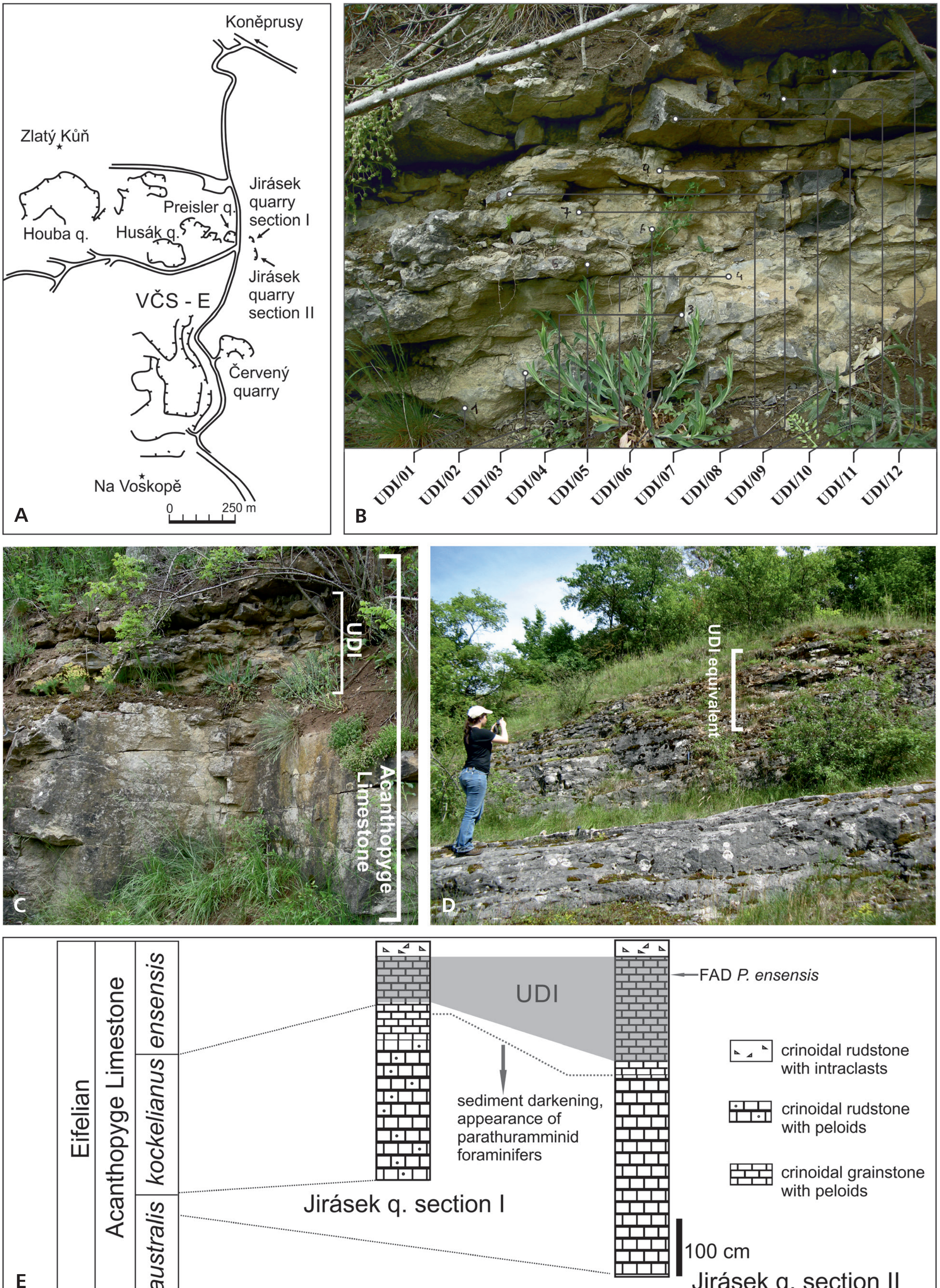
The Acanthopyge Limestone is a member of the Choteč Formation and represents a shallow-water equivalent of the offshore Choteč Limestone corresponding to the *costatus–kockelianus* conodont zones (Klapper *et al*. 1978; Kalvoda & Zikmundová *in* Galle & Hladil 1991; Kalvoda 1992; Kalvoda *in* Hladil & Kalvoda 1993a, b; Chlupáč *et al*. 1998). The occurrence of this unit is restricted to the Koněprusy area, where it is exposed in several quarries and small outcrops and also forms an infill of neptunian dykes transecting the stratigraphically older Suchomasty Limestone (Chlupáč 1996). The faunal content of this unit was studied since the 1950s of the 20th century (*e.g*., Svoboda & Prantl 1949; Chlupáč 1959; Přibyl 1978; Chlupáč & Turek 1983; Havlíček *in* Havlíček & Kukal 1990; Hladil 1993; Galle 1994; Mergl 2001, 2008, 2014, 2015, 2019; Holcová 2004).

Kukal (1963) and Kukal *in* Havlíček & Kukal (1990), who studied the sedimentology and petrography of the unit, described occurrences of features similar to grapestones known from the Bahamas and therefore interpreted the depositional environment of the Acanthopyge Limestone as shallow to extremely shallow. Berkyová & Munnecke (2010) and Vodrážková *et al*. (2013) reported intensively micritized grains, microproblematica and various grain alteration stages and linked the sudden occurrence of such features to increased bioerosion rates as a response to higher nutrification levels connected to the Basal Choteč Event (uppermost *partitus*–basal *costatus* Zone).

Acathopyge Limestone in the Jirásek quarry

The Jirásek quarry (known also as Acanthopyge quarry) is a small, abandoned quarry situated on the right side of a road from Bykoš to Koněprusy (Fig. 1). Acanthopyge Limestone cropping out in the Jirásek quarry was thoroughly studied with respect to its paleontological content and sedimentology. Systematic studies of fauna (apart from conodonts) from the Jirásek quarry were carried out by Hladil (1993, tabulatomorphs and stromatoporoids), Galle (1994, rugose corals), Berkyová (2004, dacryoconarid tentaculites), (Mergl *et al*. 2017, microvertebrate remains) and most recently by Mergl (2019, lingulate brachiopods) and Mergl & Budil (2019, rhynchonelliform brachiopods and trilobites). Detailed sedimentologic, petrographic and microfacies investigations were carried out by Hladil, Kalvoda *et al. in* Galle & Hladil (1991), Hladil & Kalvoda (1993a, b) and Budil (1995). Hladil & Kalvoda (1993a) recorded a change from light, crinoidal, coral-stromatoporoid rudstone of the Acanthopyge Limestone to dark, thin-bedded grainstone and packstone of the dark interval. The authors assumed that the deposition of the latter took place during sea level rise (Kačák Episode), preceded by sea-level fall, which

Figure 1. A – location of the sections studied (Jirásek quarry section I and section II). • B – detail of UDI in Jirásek quarry section I, with position of samples marked. • C – uppermost Acanthopyge Limestone and UDI in Jirásek quarry section I. The thickness of UDI is 75 cm. • D – Jirásek quarry section II with the probable equivalent of UDI marked. Abbreviations: q – quarry; VČS – E – Velkolom Čertovy schody – East. • E – simplified sketch of correlation between Jirásek quarry section I and II. See also explanation under Results.


Koněprusy
Zlatý Kůň
Jirásek
quarry
section I
Preisler q.
Houba q.
Husák q.
Jirásek
quarry
section II
VČS - E
Červený
quarry
Na Voskopě
0
250 m
A
UD1/01
UD1/02
UD1/03
UD1/04
UD1/05
UD1/06
UD1/07
UD1/08
UD1/09
UD1/10
UD1/11
UD1/12
B
UDI
Acanthopyge
Limestone
C
UDI equivalent
D
Eifelian
Acanthopyge Limestone
ensensis
kockelianus
australis
UDI
FAD P. ensensis
sediment darkening,
appearance of
parathuramminid
foraminifers
Jirásek q. section I
crinoidal rudstone
with intraclasts
crinoidal rudstone
with peloids
crinoidal grainstone
with peloids
100 cm
Jirásek q. section II
E

resulted in exposure of the seafloor, inferred from iron-bearing crusts and karst features they observed. They further concluded that within the dark interval, "each bed includes different types of sediments: tempestites/turbidites and shallow water contourites" (Hladil & Kalvoda, 1993a, p. 15). Deposition from contourite currents was also suggested by Oczlon (1992). Hladil & Kalvoda (1993a, b) and Budil (1995) reported from the dark interval, apart from ubiquitous crinoid ossicles, also very common dacryoconarid tentaculites, conodonts, land plant remains, bryozoan fragments, sponges, brachiopods, ostracods, trilobites, small lumps, *Girvanella* nodules, benthic foramininera, common calcispheres and pelletoids.

Aims of the study

The main aim of this paper is to provide a detailed taxonomic description of conodont faunas from the Jirásek quarry. Special attention is drawn to the *Polygnathus pseudofoliatus* Group and the interspecific and intraspecific variability within the group. Several authors recorded significant morphological variation and occurrence of transitional morphotypes (see below), which has a significant impact on the biostratigraphic correlations as *Polygnathus ensensis* and *Polygnathus eiflius* represent zonally diagnostic taxa. Furthermore, attention was focused on the environmental changes related to the Kačák Episode.

Material and methods

Conodont samples from the Jirásek quarry were sampled within the 2009–2016 period from Jirásek quarry sections I and II (Fig. 1, GPS coordinates for Jirásek quarry section I: N 49° 54′ 50.2″, E 14° 04′ 34.2″, Jirásek quarry section II: N 49° 54′ 49.2″, E 14° 04′ 33.9″). Section I represents the original section, where the dark interval was first described and studied by Hladil, Kalvoda *et al. in* Galle & Hladil (1991). Representative 2–10 kg from each interval were sampled, few specimens were provided by M. Mergl (Czech University of Life Sciences, Prague), who concurrently studied lingulate brachiopods from both sections (Mergl 2019). The limestones were crushed to small fragments of ca 3 × 5 cm and phosphatic microfossils were extracted using 6% acetic acid (SV) and 5% formic acid (TS). The residues were sieved, dried, separated using sodium polytungstate heavy liquid (density 2.79 g/cm^3), handpicked using a binocular microscope and photodocumented using a scanning electron microscope Tescan Mira 3GMU in the Czech Geological Survey (Prague, Czech Republic) and Vega Tescan 2 XMU in GeoZentrumn Nordbayern, Friedrich-Alexander-Universität (Erlangen, Germany). The conodont collection is stored in the Czech Geological Survey under designation SV1–SV121.

Results

Lithology and biostratigraphy

The succession of the Acanthopyge Limestone in the Jirásek quarry section I begins with massive, amalgamated beds of light, poorly sorted, crinoidal rudstone with fragmentarily preserved fauna, especially stromatoporoids, brachiopods, tabulate corals and bryozoans (Fig. 2A). Peloids occur in the grainstone peloidal matrix occasionally together with microproblematica (calcispheres). Starting at 270–280 cm above the base of the section, finer grained and darker crinoidal grainstones with common occurrence of peloids, calcispheres and parathuramminid foraminifers occur. The succeeding UDI (starting at 300 cm above the base of the section, Fig. 2B–D) is formed by 12 thin beds, representing an event deposits (calciturbidites), with dark, crinoidal grainstone with peloids and brachiopods forming the bases of the beds and peloidal grainstones with calcispheres and parathuramminds forming fine-grained tops of each bed as a result of hydrodynamic sorting. Micritited grains, peloids and microproblematica such as calcispheres and parathuramminid foraminifers are commonly reported from the shallow water, photic zone of restricted shelf settings, lagoons and back-reef areas (*e.g.*, Vachard *et al*. 2010, Berkyová & Munnecke 2010 and references therein) and their presence in dark, fine-grained crinoidal grainstones with fauna typical for an open marine habitat (crinoids, brachiopods, dacryoconarid tentaculites and conodonts) suggests their transport to open sea *e.g.*, during storm surges. Although deposition from turbidite currents is suggested for UDI herein, it is well plausible that these were initiated by storms.

The beds above UDI are light, skeletal rudstones with peloidal grainstone matrix, with tabulate and rugose corals, stromatoporoids, bryozoans, brachiopods, green algae and intraclasts. Conodonts in these beds (samples 385, 395 and 410) were recovered only rarely and due to the presence of common intraclasts it is well plausible that they were reworked.

The fining upward succession, sediment darkening in the proximity of UDI and a dark color within the UDI together with the change in faunal composition (from stromatoporoid–crinoid–brachiopod within the Acanthopyge Lm. to crinoid–microproblematica in the UDI) all point to progressive deepening. Because the onset of the deepening coincides with the appearance of *Polygnathus ensensis* (Fig. 3) and *Nowakia otomari*, it is correlated with the eustatic Kačák Episode.

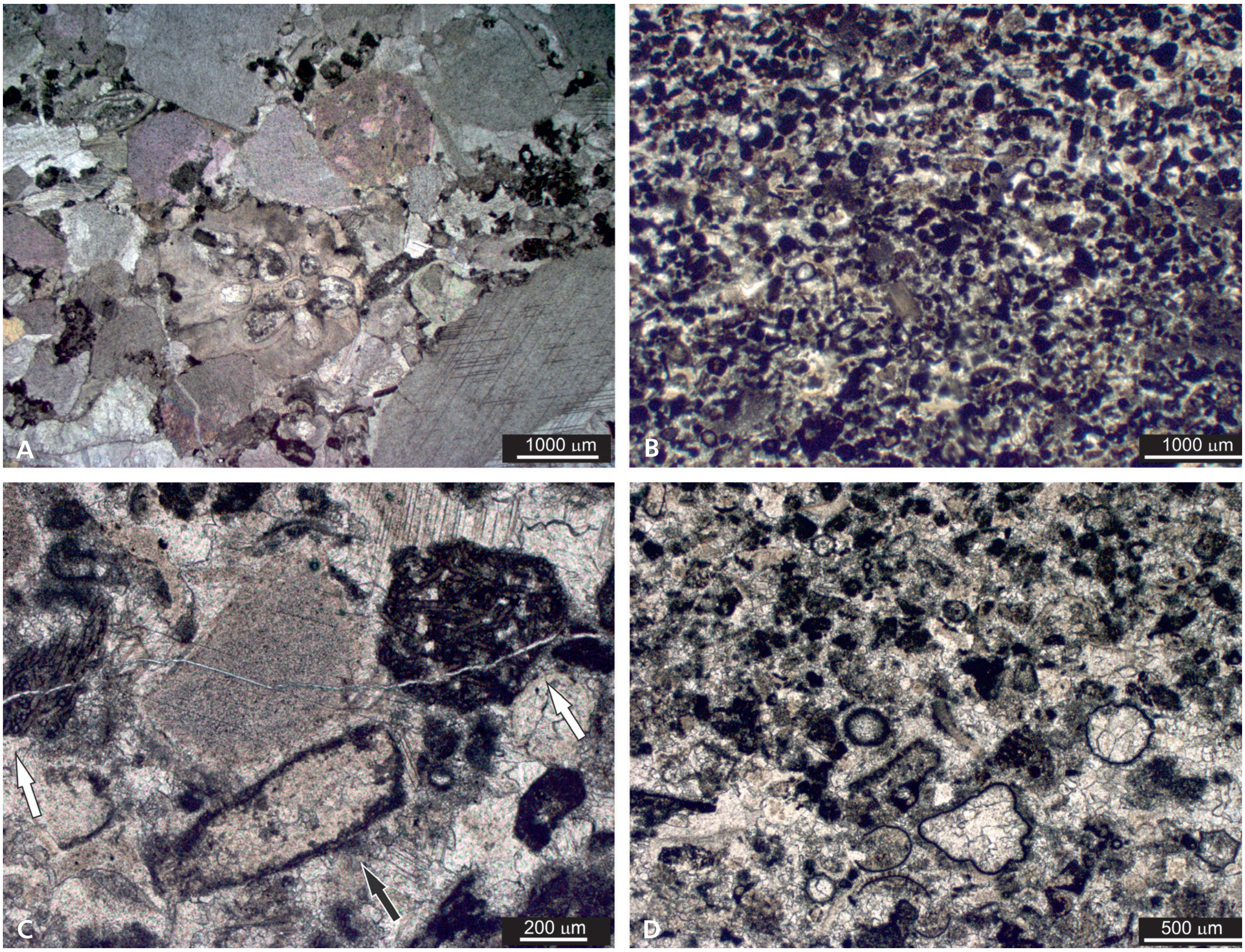


Figure 2. **A** – crinoidal rudstone with peloidal grainstone matrix (bryozoan fragment in the centre). Sample 60, Jirásek section I, Acanthopyge Limestone, *kockelianus* Zone. • B – peloidal grainstone with crinoids and microproblematica (calcispheres and parathuramminids). Sample UDI 4, Jirásek section I, *ensensis* Zone. • C – crinoidal grainstone with peloids. White arrows point to *Girvanella* clasts, black arrow points to example of centripetal micritization of crinoid osscicle (stadium of micritic envelope), base of bed UDI 6, Jirásek section I, *ensensis* Zone. • D – peloidal grainstone with microproblematica (parathuramminids and calcispheres), topmost part of bed UDI 6, Jirásek section I, *ensensis* Zone.

Tortodus kockelianus, the diagnostic taxon for the *kockelianus* Zone, was found in the topmost part of the Acantopyge Limestone (only 2 specimens, Fig. 3). However, given that the typical conodont associations of the *australis* Zone are missing, it is highly probable that the entire accessible succession of Acanthopyge Limestone cropping out below the UDI in the Jirásek quarry section I, belongs to the *kockelianus* Zone.

The lithological development of the Jirásek quarry section II (Jirásek II) is slightly different from the Jirásek quarry section I (Jirásek I), although both sections are in very close proximity (Fig. 1A, E). The section at Jirásek II starts with light-gray peloidal grainstones (*australis* Zone) and the change to dark peloidal grainstone is rather gradual. This section was sampled by the authors in 50 cm intervals and also by M. Mergl (University of West Bohemia, Pilsen), who studied lingulate brachiopods from both sections and provided conodonts for the purpose of this study. In comparison with Jirásek I, conodonts recovered from Jirásek II are far less numerous and also less diversified with higher representation of juvenile growth forms, except for the base of the section (first 100 cm of the section), which provided a diversified and rich conodont association with *Tortodus australis*, *Tortodus* sp. B., *Polygnathus abessensis*, *P. benderi*, *P. trigonicus*, *P. eiflius*, *P. linguiformis* and *P. amphora*. As mentioned above, the succeeding beds were rather poor in conodonts, but judging from the conodont association present in the sample 0 m and 100 cm with a common occurrence of typical representatives of the *australis* zone, namely *T. australis* and *P. benderi,* and their lack in the overlying beds, it seems very probable that the base of the Jirásek II section represents the top of the *australis* Zone. *Tortodus kockelianus* was not recorded in Jirásek II, which is not surprising given the sparse occurrence of conodonts in this section (except for its base) and rare occurrence of this particular species in the Barrandian area (Berkyová 2009).

The first *Polygnathus ensensis* in the Jirásek II was recorded in our sample 550 cm (550 cm above the base of the section). We observed sediment darkening already from the level 350 cm above the base of the section and petrographic examination proved common presence of parathuramminid foraminifers in this level (next to peloids and calcispheres), the onset of whose was recorded 20 cm below UDI at Jirásek section I. It seems therefore that the level of 350 cm from Jirásek section II could be correlated with close proximity of UDI from the Jirásek section I (see Fig. 1E for simplified sketch of correlation). Until microfacies analysis together with detailed stable isotope analysis ($\delta^{13}C$, $\delta^{18}O$) are finished at Jirásek section II, and also – more conodonts are recovered, the correlation among Jirásek section I and II will remain only approximate.

Systematic part

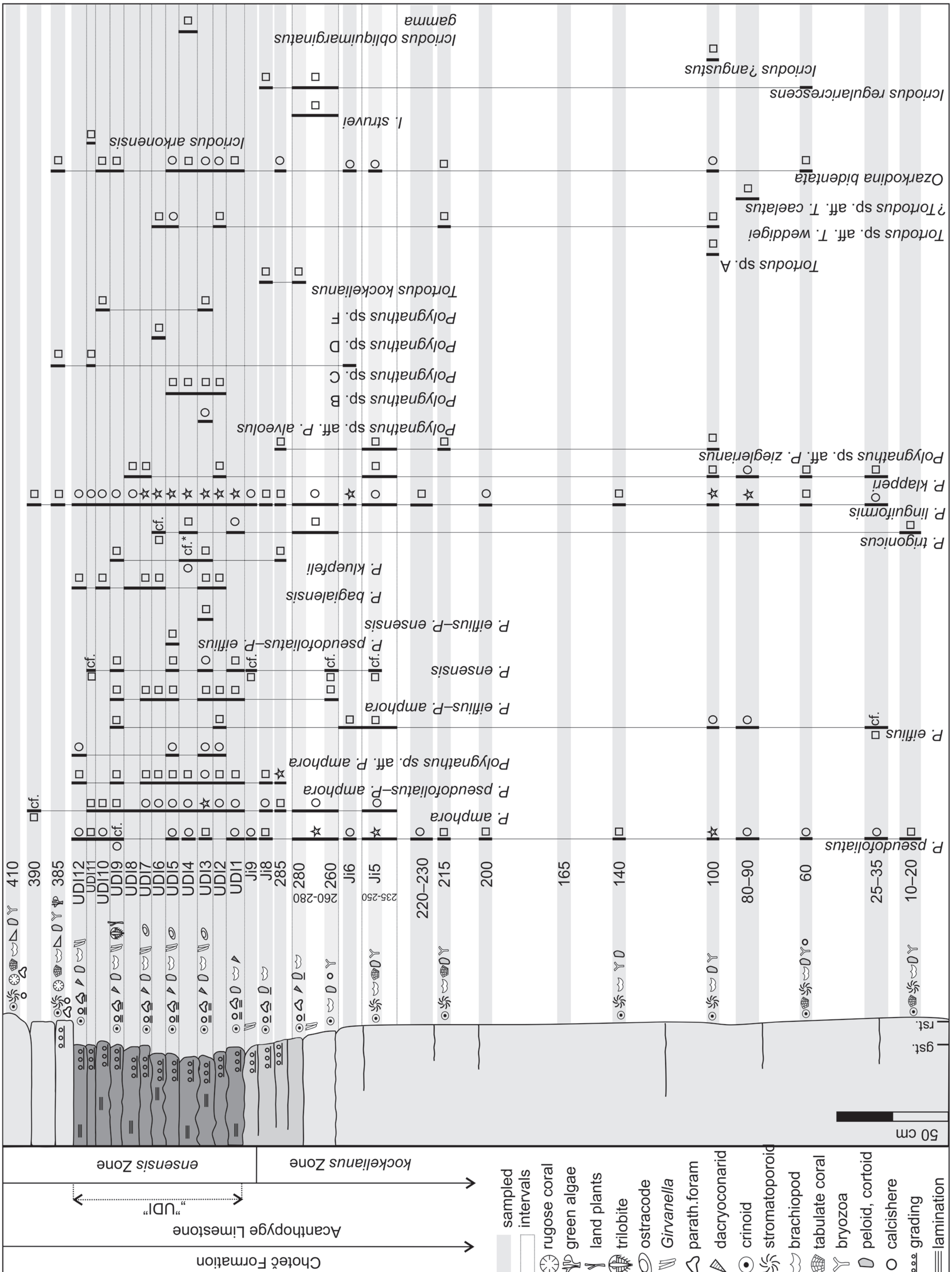
Notes to the systematic part: Purnell *et al*. (2000) introduced new terms for orientations and elemental notations, which reflected true biological orientation in the conodont apparatus. Although we acknowledge their findings, we decided to use the conventional terms in order to enable comparisons with previous descriptions. We therefore use 'lower view' instead of 'aboral', 'upper' instead of 'oral', 'posterior' instead of 'dorsal', 'anterior' instead of 'ventral', 'inner' instead of 'caudal' and 'outer' instead of 'rostral' in the Pa elements. Geographic distribution of taxa was summarized on the basis of publications where the particular taxon was figured, if not mentioned otherwise. It was not our intention to provide complete synonymy listings, in this respect we only focused on taxa that we regarded as problematic in respect to species delimitations, which applies mainly to representatives of the *P. pseudofoliatus* Group. Representatives of the genus *Icriodus* Branson & Mehl and *Belodella* Ethington are not discussed herein and will be part of an ongoing study of the working group of K. Narkiewicz (Polish Geological Institute, Warsaw) and M.A. Murphy (University of California, Riverside), respectively. In this paper we elevate certain taxa to species level (*P. ensensis*, *P. linguiformis*, *P. klapperi*, *Tortodus kockelianus*, *T. australis*) as we do not regard the taxonomic designation of subspecies meaningful in these cases, and continue thus in a practice initiated by Bultynck (1987) and Vodrážková *et al*. (2011).

For the stratigraphic distribution of the studied taxa from the Jirásek quarry see Fig. 3.

***Polygnathus pseudofoliatus* Group**

Sparling (1995) considered *P. pseudofoliatus* to be ancestral to, and most probably genetically conspecific with *P. ensensis*, *P. eiflius*, *P. amphora* (*P. pseudofoliatus* subsp. A *sensu* Sparling) and *P. pseudoeiflius* (synonymized with *Polygnathus* aff. *P. eiflius sensu* Klapper 1971 by Walliser & Bultynck 2011) and included the above mentioned species within the *Polygnathus pseudofoliatus* Group. In his opinion, the representatives of the group "belong to a conspecific mixture of ecotypic variants living in behavioral isolation yet interbreeding with sufficient frequency to reshuffle the genes from time to time" (Sparling 1995, pp. 1128, 1129). This seems to be a reasonable conclusion, taking into account the wide range of morphological variability, identical stratigraphic ranges, occurrence of transitional forms integrating characteristics of two and more different species and the difficulty, in some cases impossibility, to discern between intraspecific and interspecific features. The wide range of morphological variability within the group and occurrence of transitional forms has been noticed also by other authors (*e.g*., Philip 1966, Klapper 1971, Mawson & Talent 1989, Walliser 1991, Uyeno *in* Norris & Uyeno 1998, Walliser & Bultynck 2011, Uyeno *et al*. 2017, Gouwy *et al*. 2019). We include the following species to the *Polygnathus pseudofoliatus* Group: *Polygnathus pseudofoliatus* Wittekindt, 1966; *Polygnathus amphora* Walliser & Bultynck, 2011; *Polygnathus eiflius* Bischoff & Ziegler, 1957; *Polygnathus ensensis* Ziegler & Klapper *in* Ziegler *et al*., 1976 and *Polygnathus pseudoeiflius* Walliser & Bultynck, 2011. The characteristics common for the species in the group can summarized as follows: the platform is rather asymmetric (almost symmetric in *P. amphora*) – the expansion of the outer platform margin tends to be greater to various extent. Except for *P. ensensis*, the free blade tends to form less than a half of the unit. Carina tends to continue to platform posterior in forms of nodes. Adcarinal grooves in the posterior part of the platform are shallower (to various extent) in comparison to platform anterior.

Figure 3. Stratigraphic ranges of taxa and simplified lithological column of Acanthopyge Limestone and UDI in Jirásek quarry section I. Occurrence of *P. ensensis*–*P. amphora* transitional form is not marked (single specimen in UDI 3). Explanation of designation cf.* at *Polygnathus kluepfeli* in the sample UDI 4: 1 specimen of *Polygnathus kluepfeli* and 3 specimens of *P.* cf. *kluepfeli*. Numbers of representative specimens recovered is marked as follows: square = 1–2 specimens; circle = 3–10 specimens; asterisk = more than 10 specimens.


Choteč Formation
Acanthopyge Limestone
"UDI"
ensensis Zone
kockelianus Zone
50 cm
gst.
rst.
sampled intervals
rugose coral
green algae
land plants
trilobite
ostracode
Girvanella
parath.foram
dacryoconarid
crinoid
stromatoporoid
brachiopod
tabulate coral
bryozoa
peloid, cortoid
calcishere
grading
lamination
410
390
385
UDI12
UDI11
UDI10
UDI9
UDI8
UDI7
UDI6
UDI5
UDI4
UDI3
UDI2
UDI1
Ji9
Ji8
285
280
260
Ji6
Ji5
260-280
235-250
220–230
215
200
165
140
100
80–90
60
25–35
10–20
P. pseudofoliatus
P. amphora
P. pseudofoliatus–P. amphora
Polygnathus sp. aff. P. amphora
P. eiflius
P. eiflius–P. amphora
P. ensensis
P. pseudofoliatus–P. eiflius
P. eiflius–P. ensensis
P. bagialensis
P. kluepfeli
P. trigonicus
P. linguiformis
P. klapperi
Polygnathus sp. aff. P. ziegleriansus
Polygnathus sp. aff. P. alveolus
Polygnathus sp. B
Polygnathus sp. C
Polygnathus sp. D
Polygnathus sp. F
Tortodus kockelianus
Tortodus sp. A
Tortodus sp. aff. T. weddigei
?Tortodus sp. aff. T. caelatus
Ozarkodina bidentata
Icriodus arkonensis
I. struvei
Icriodus regularicrescens
Icriodus ?angustus
Icriodus obliquimarginatus gamma
cf.

Genus *Polygnathus* Hinde, 1879

Type species. – *Polygnathus dubius* Hinde, 1879.

Polygnathus pseudofoliatus Wittekindt, 1966
Figure 4A–K

1957 *Polygnathus foliata* Bryant 1921. – Bischoff & Ziegler, pl. 4, figs ?1, ?2, ?3 (oblique views only), 4.

1966 *Polygnathus* sp. nov. B. – Philip, pp. 158, 159, pl. 2, figs ?4, 5–7, ?8, 9.

partim 1966 *Polygnathus pseudofoliata* n. sp. – Wittekindt, pp. 637, 638, pl. 2, figs 20–22, ?23 (except for fig. 22 only oblique views are shown), *non* fig. 19 (= *P. eiflius*).

1970 *Polygnathus pseudofoliatus* Wittekindt. – Jackson *in* Pedder *et al*., pl. 16, figs ?3, 13.

partim 1970 *Polygnathus pseudofoliata* Wittekindt. – Bultynck, pp. 127, 128, pl. 14, figs 5, 8, *non* fig. 2 (= *Polygnathus* sp.), *non* figs 1, 3 (= *P. pseudofoliatus* transitional with *P. amphora*), *non* fig. 7 (= *Polygnathus pseudoeiflius*).

1970 *Polygnathus pseudofoliatus* Wittekindt. – Klapper *et al*., pl. 3, figs 7–19.

1971 *Polygnathus pseudofoliatus* Wittekindt. – Klapper, pp. 63, 64, pl. 2, figs 8–13.

1975 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Telford, pp. 50, 51, pl. 9, figs 1–6, ?7, ?8, 9–12.

1976 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Ziegler & Klapper *in* Ziegler *et al*., pl. 3, figs 2, 3, 12, 13.

1977 *Polygnathus pseudofoliatus* Wittekindt 1966. – Weddige, p. 317, pl. 4, figs ?68, 69, 70.

partim 1978 *Polygnathus pseudofoliatus* Wittekindt. – Orchard, pl. 108, figs 1, 4, 5, 7, ?8 (juvenile form), *non* fig. 3.

partim 1979 *Polygnathus pseudofoliatus* Wittekindt. – Chatterton, p. 199, pl. 3, figs 1–6, 8–10, 15–18, *non* fig. 7 (= *Polygnathus* cf. *P. holynensis* Vodrážková *et al*., 2011).

1980 *Polygnathus pseudofoliatus* Wittekindt, H., 1966. – Bultynck & Hollard, pl. 5, figs 13, 14.

1983 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Klug, p. 108, pl. 10, figs m–r.

partim 1983 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Sparling, pl. 11, figs ad, ae, pl. 12, figs k–m, pl. 13, figs x, y, ak, al, *non* pl. 11, figs s, t (= juvenile form of *Polygnathus* sp.).

1983 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Wang & Ziegler, pl. 6, figs 14, 15.

1985 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Bultynck, pl. 7, fig. 13.

partim 1987 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bultynck, pl. 8, fig. 8 (*non* figs 15–18, see under *P. amphora* and *P. eiflius* synonymy lists).

1988 *P. pseudofoliatus* Wittekindt. – Sparling, pl. 11, fig. 9, pl. 15, fig. 11, pl. 17, fig. 5, pl. 18, fig. 13.

1989 *Polygnathus pseudofoliatus* Wittekindt. – Mawson & Talent, p. 237, pl. 4, figs 16–19, ?20, ?21.

partim 1990 *Polygnathus pseudofoliatus* Wittekindt, 1965. – Lazreq, pl. 2, figs 10, 11, ?12, *non* fig. 13 (= *P. eiflius*).

partim 1992 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Bardashev, pl. 5, figs 1, 3, ?5, 6, *non* fig. 2 (= *P. amphora*).

partim 1992 *Polygnathus eiflius* Bischoff & Ziegler. – Bardashev, pl. 5, figs 4, 7, 8, *non* fig. 10 (= *P. eiflius*), *non* fig. 9 (= *P.* cf. *pseudoeiflius*).

1994 *Polygnathus pseudofoliatus* Wittekindt. – Mawson & Talent, pl. 2, figs 19, 20.

1995 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Sparling, pl. 2, figs 1–8, (figs 7, 8 treated as transitional form between *P. pseudofoliatus* and *P. xylus ensensis* in the original publication).

partim 1998 *Polygnathus pseudofoliatus* Wittekindt. – Uyeno *in* Norris & Uyeno, pp. 164, 165, pl. 11, figs 11, ?20 (probably transitional with *P. ensensis* as mentioned by the author), pl. 12, figs 5, 15, 17, fig. ?14 (anterior margins seem to be distinctly serrated, probably transitional form between *P. pseudofoliatus* and *P. ensensis*), *non* fig. 13 (= *P.* sp. aff. *P. amphora*), pl. 14, ?fig. 19 (lateral view missing and anterior serration seems to be prominent, probably transitional form with *P. ensensis*), pl. 14, fig. 20.

partim 1999 *Polygnathus pseudofoliatus* Wittekindt. – Sparling, p. 899, pl. 3, figs 17, 18, *non* fig. 19 (= *P. pseudoeiflius* Walliser & Bultynck, 2011).

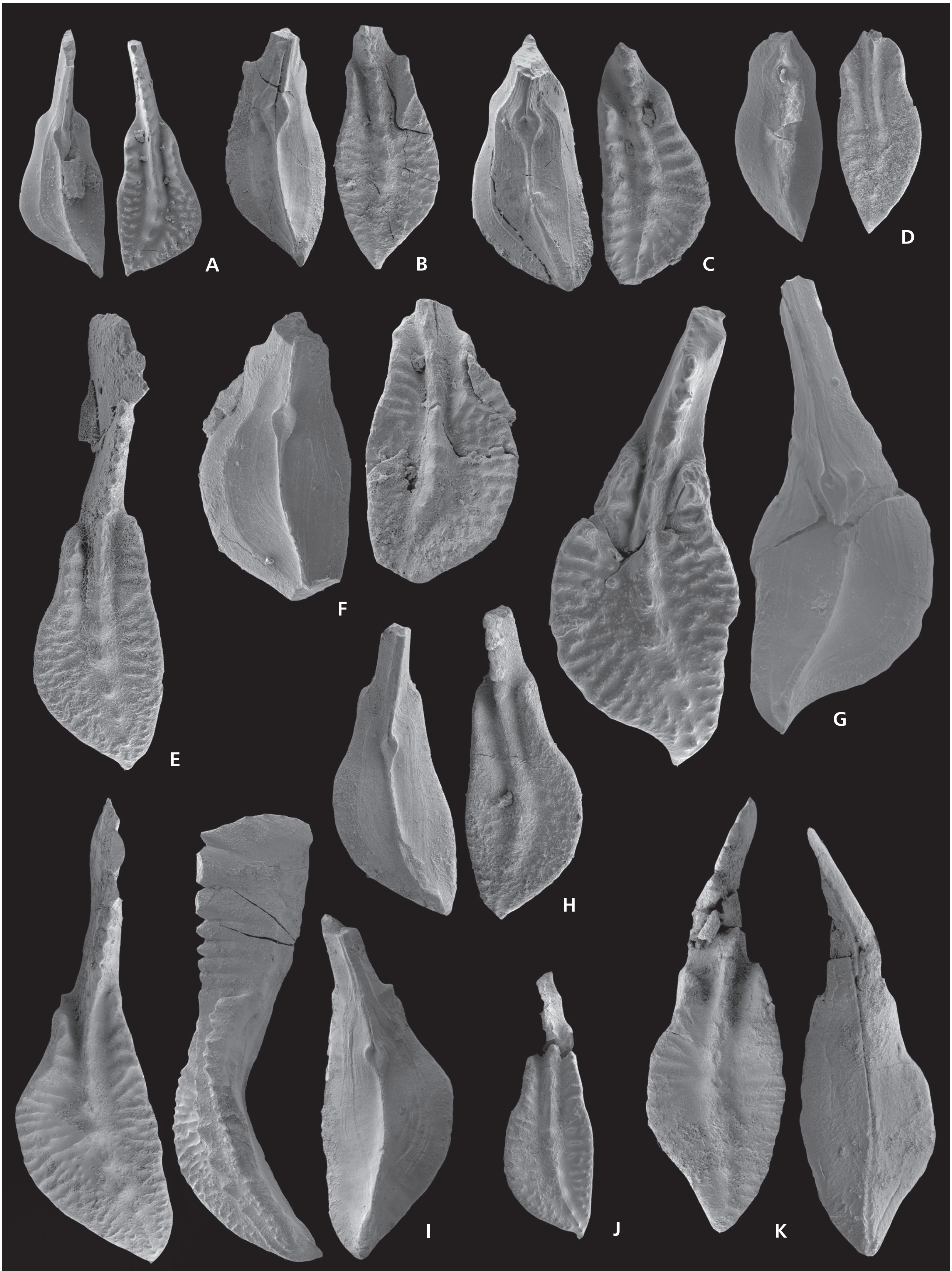
2001 *Polygnathus pseudofoliatus* Wittekindt, 1965. – Liao *et al*., p. 34, pl. 3, figs 1–5, 7, 10 –12, ?14, ?15, 16, 17.

2001 *Polygnathus* aff. *pseudofoliatus* Wittekindt, 1965. – Liao *et al*., pl. 3, figs 18, 19 (juvenile form).

partim 2003 *Polygnathus pseudofoliatus* Wittekindt 1966. – Aboussalam, p. 186, pl. 28, fig. 5, *non* fig. 10 (= ?).

2007 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Benfrika *et al*., pl. 9, fig. i.

Figure 4. *Polygnathus pseudofoliatus* Wittekindt. A – lower and upper view of SV1, sample UDI 5, *ensensis* Zone; B, E, H – sample 100, *kockelianus* Zone, B – lower and upper view of SV2, E – upper view of SV5, H – lower and upper view of SV8; C – lower and upper view of SV3, sample 25–35, *kockelianus* Zone; D – lower and upper view of SV4, sample UDI 1, *ensensis* Zone; F, G – sample 280, *kockelianus* Zone, F – lower and upper view of SV6, G – upper and lower view of SV7; I – upper, lateral and lower view of SV9, sample JI/100 of Mergl (2019, fig. 2), *ensensis* Zone, Jirásek section II (free blade broken during specimen manipulation); J – upper view of SV10, sample 80–90, *kockelianus* Zone. K – upper and lower view of SV11, sample 60, *kockelianus* Zone. Magnification of all specimens ×50.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2009 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Berkyová, pp. 678, 679, pl. 8, figs a–g.
2011 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Walliser & Bultynck, p. 11, pl. 1, figs 1, 2.
non 2012 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Liao & Valenzuela-Ríos, pl. 6, figs Ae-af (= *Polygnathus* sp.)
2013 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Gouwy *et al*., pl. 4, fig. e.
2015 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Bahrami *et al*., pl. 10, figs 11–13.
2017 *Polygnathus pseudofoliatus* Wittekindt 1966. – Uyeno *et al*., p. 398, pl. 1, fig. 8.
2019 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Gouwy *et al*., pl. 6, figs g, i.

Material. – 102 specimens of *P. pseudofoliatus*, 21 specimens of *P. pseudofoliatus*–*P. amphora*, 1 specimen of *P. pseudofoliatus*–*P. eiflius*.

Diagnosis. – (free translation from German original, Wittekindt 1966, p. 637): "A species of *Polygnathus* with the platform and the free blade being approximately of the same length. The platform bears shallow troughs; it is somewhat asymmetric and becomes uniformly narrower towards anterior and posterior ends."

The description in the original publication continues as follows (p. 637): from the lateral view, the platform is only weakly arched downward, the outer platform margin is strongly convex, and the inner platform margin is either straight or weakly convex. The anterior end is narrow, with deep grooves. The posterior end of platform is pointed but can also be somewhat rounded. The platform is ornamented with ridges, especially on the anterior margins. In the posterior platform nodes and/or nodes with irregular ridges can be developed. The carina is developed as a ridge in the anterior platform, followed by separated nodes, which become smaller towards the posterior end and can be connected with a low ridge.

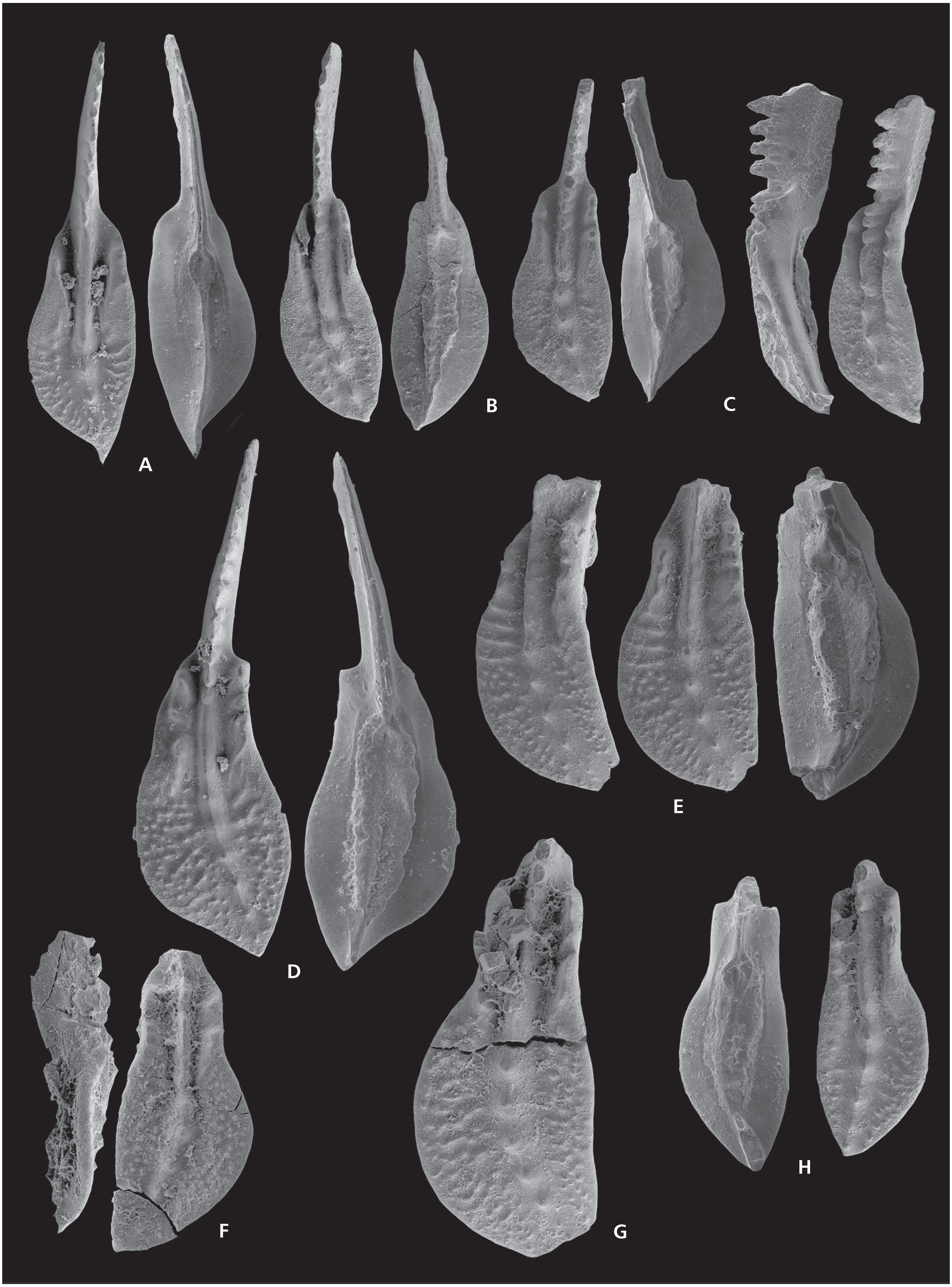
Unfortunately, only one of four figured specimens in the original publication shows the upper view oriented perpendicular to the free blade and carina. Others, including the holotype, show the specimens from oblique views, from which the diagnostic characteristics cannot be clearly assessed. In addition, the type material is currently inaccessible due to collection transfer in the Senckenberg research institute (P. Königshof, personal communication 2018).

Description. – specimens herein assigned to *P. pseudofoliatus* possess a free blade, which in adult forms characteristically is less than one half of the unit length. The platform outline is a variable characteristic as a result of both intraspecific and ontogenetic variation. In specimens representing adult growth forms, the platform is asymmetric, anterior platform margins widen gradually; the outer margin is more expanded than the inner margin. Platform ornamentation characteristically consists of a combination of transverse ridges in the anterior platform half and nodes and/or short ridges in the posterior half. Carina continues to the posterior tip most commonly in form of nodes. In adult specimens, the basal pit is small, symmetric, situated approximately at the end of the first anterior third of the platform.

Intermediate forms: Specimens figured in Fig. 5A–D are regarded as *P. pseudofoliatus*–*P. amphora* intermediates as the anterior margins are gradually widening, which is typical of *P. pseudofoliatus* but the ridges on the anterior platform and deep adcarinal grooves that shallow abruptly are typical of *P. amphora*. The specimens in Fig. 5A–C do not represent the fully adult growth stages but comparing with similar growth stages as represented by specimens assigned herein to *P. amphora* (compare with Fig. 7E); the anterior margins of the latter tend to be longer and parallel already in earlier growth stages. Immature specimen in Fig. 8C represents an example of *Polygnathus pseudofoliatus*–*P. eiflius* intermediate form. It possesses a platform outline typical for *P. pseudofoliatus* and a diagonal rostral ridge typical of *P. eiflius*.

Morphological and ontogenetic variability as recorded by previous authors: Immature forms of *P. pseudofoliatus* were described and figured by Klapper *et al*. (1970) from New York and by Telford (1975) from Australia; however, neither of these publications show earlier ontogenetic stages represented by morphotypes with poorly developed platforms and large basal pits situated outside the platform (such as shown herein in Fig. 7A, B). Earlier ontogenetic stages of *P. pseudofoliatus* are therefore unknown. Chatterton (1979) states that most of the specimens he assigned to *P. pseudofoliatus* are close to the holotype, however, some of them exhibit characteristics that are typical for *P. eiflius*, such as strongly nodose ornamentation and expansion of the posterior platform, which was earlier noted also by Philip (1966). A wide range of morphological variation within 399 Pa elements of *P. pseudofoliatus* from 106 localities

Figure 5. A–D – *Polygnathus pseudofoliatus* Wittekindt–*Polygnathus amphora* Walliser & Bultynck; A – upper and lower view of SV12, sample 285, *kockelianus* Zone; B, C – sample UDI 3, *ensensis* Zone, B – upper and lower view of SV13, C – upper, lower, lateral and oblique lateral view of SV14; D – upper and lower view of sample Ji 8, topmost *kockelianus* Zone. • E–H – *Polygnathus* sp. aff. *P. amphora*; E, G – sample UDI 3, *ensensis* Zone, E – oblique lateral, upper and lower view of SV16, G – upper view of SV18; F – lateral and upper view of SV17, sample UDI 5, *ensensis* Zone; H – lower and upper view of SV19, sample UDI 2, *ensensis* Zone. Magnification of all specimens ×70.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in Australia was recorded by Mawson & Talent (1989), including "variation on the anterior constriction of the platform, surface ornamentation and the nature of the platform margins" (p. 237). The latter authors planned to study the intraspecific variability of *P. pseudofoliatus*. Walliser & Bultynck (2011) recognized two morphotypes of *P. pseudofoliatus*: alpha morph corresponding to the holotype and beta morph (not recorded herein), which differs from the first by having a slender platform, a more distinctly developed rostrum and adcarinal troughs, and transverse ridges as a main platform ornamentation.

Occurrence. – In the Barrandian area, apart from the Jirásek quarry, this species was recorded in the Choteč Limestone from Na vyhlídce at Hostím and Barrandov road-cut in Prague (Berkyová 2009), in the uppermost Choteč Limestone in Hlubočepy railway cut and Vysoká quarry in Hlubočepy (Chlupáč *et al*. 1977, not figured). The stratigraphic range is from the uppermost *costatus* Zone (Bultynck & Hollard 1980) up to the *expansus* Zone *sensu* Narkiewicz & Bultynck (2010), the latter reported by Bahrami *et al*. (2015) from Iran (corresponds to lower *Sch*. *hermanni* Zone, upper Givetian). Occurrence from the *hermanni* Zone was also reported by Aboussalam & Becker (2007, p. 263, tab. 6, no specimen figured therein). As mentioned under *P. eiflius*, the specimen figured by Narkiewicz & Königshof (2018, pl. 5, fig. u) from Vietnam resembles *P. pseudofoliatus* in the platform outline and as such may represent the highest stratigraphic occurrence reported (*disparilis* Zone). *Polygnathus pseudofoliatus* further occurs in Nevada, New York, Ohio, Canada, Alaska, Morocco, Germany, Belgium, Australia (Klapper & Johnson 1980, tabs 8–10; Klug 1983; Sparling 1995), SW England (Orchard 1978), Spain (*e.g*., Liao *et al*. 2001), Iran (Bahrami *et al*. 2015), Tajikistan (*e.g*., Bardashev 1992) and South China (*e.g*., Wang & Ziegler 1983).

***Polygnathus amphora* Walliser & Bultynck, 2011**
Figures 6A–K, 7D–F

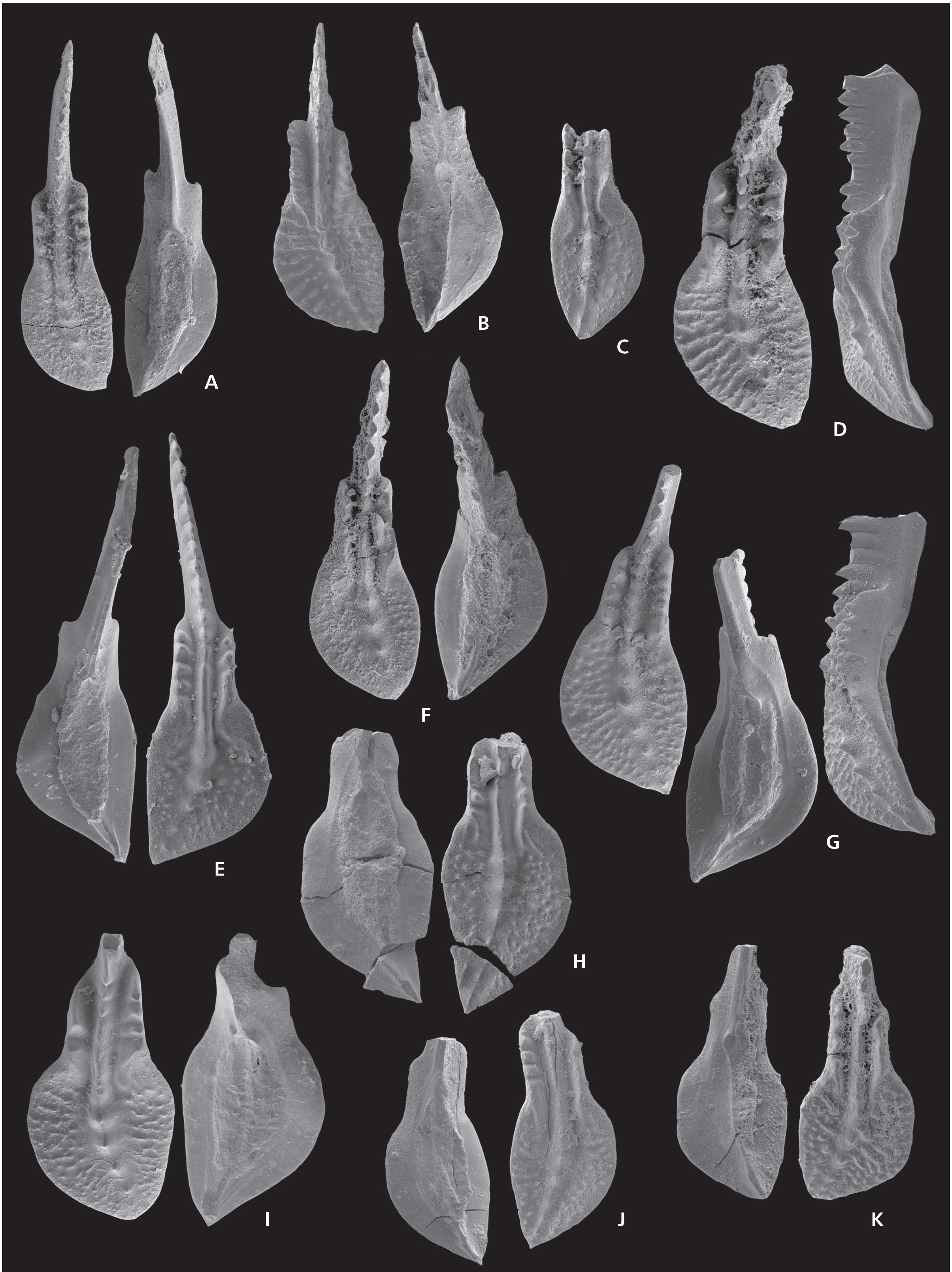
1980 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bultynck & Hollard, pl. 5, fig. 15; pl. 6, fig. 5.
cf. 1987 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bultynck, pl. 8, figs 15, 16, *non* fig. 8 (= *P. pseudofoliatus*), *non* fig. 17 (= *P. eiflius*), *non* fig. 18 (= probably *P. pseudofoliatus–P. amphora* transitional form).
partim 1992 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Bardashev, pl. 5, fig. 2 (see under *P. pseudofoliatus* synonymy list).
partim 1995 *Polygnathus pseudofoliatus* Wittekindt subsp. A. – Sparling, pl. 3, figs 15–22; *non* figs 10–14 (= transitional forms with *P. pseudofoliatus*).
2011 *Polygnathus amphora* n. sp. – Walliser & Bultynck, p. 12, pl. 1, figs 19,20 (fig. 20 = juv. form).
2017 *Polygnathus amphora* Walliser & Bultynck, 2011. – Gouwy *in* Kabanov & Gouwy, fig. 13a.

Material. – 81 specimens of *P. amphora,* 3 specimens of *P.* cf. *amphora,* 21 specimens of *P. pseudofoliatus–P. amphora,* 10 specimens of *P. eiflius–P. amphora,* 2 specimens of *P*. *ensensis–P. amphora*.

Diagnosis. – "The new species can be easily distinguished from the α and β morphotypes of *P. pseudofoliatus* by the long rostrum with parallel margins and representing one third to half of the total platform" (Walliser & Bultynck 2011, p. 12).

Description. – Specimens from the present study possess a long rostrum with parallel margins that most commonly extend over one-third of the platform length. In adult specimens, distinct, thick ridges in the anterior platform (rostrum) run almost perpendicular to the carina, from which they are separated by very deep and narrow adcarinal grooves. Termination of the ridges form distinctly serrated anterior margins, as visible especially from the lateral view (Figs 6D, G; 7E, F). Three denticles on both margins or three denticles on inner and two denticles on outer anterior margins were most commonly observed, followed by four denticles on inner and two-three denticles on the outer margin. In the posterior termination of the rostrum, a flattened and thickened area of the platform can be observed, which almost reaches the carina (see *e.g.*, Fig. 6C, E). It is also observed in not fully adult forms (Fig. 7E). Such flattened margins may be mistaken for rostral ridges in oblique view. Regular diagonal rostral ridges are observed in some specimens (Fig. 6F, H, J, K; see also pl. 1, fig. 20 in Walliser & Bultynck 2011). Adcarinal grooves, which are very deep in the anterior platform, are getting abruptly shallow posteriorly. Hence, the platform

Figure 6. *Polygnathus amphora* Walliser & Bultynck. A, J – sample UDI 9, *ensensis* Zone, A – upper and lower view of SB20, J – lower and upper view of SB29; B – upper and lower view of SV 21, sample 0 m, *australis* Zone, Jirásek section II; C – upper view of SV22, sample UDI 11, *ensensis* Zone; D – upper and lateral view of SV 23, sample 285, *kockelianus* Zone; E – lower and upper view of SV24, sample Ji 8, topmost *kockelianus* Zone; F, H – sample UDI 2, *ensensis* Zone, F – upper and lower view of SV 25, H – lower and upper view of SV27; G – upper, lower and lateral view of SV26, sample UDI 3, *ensensis* Zone; I, K – sample UDI 6, *ensensis* Zone, I – upper and lower view of SV28, K – lower and upper view of SV30. Magnification of all specimens ×60.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of adult specimens is almost flat in the posterior platform half. The posterior half of the platform is ornamented mainly by nodes and/or short irregular transverse ridges. Both inner and outer platform margins tend to expand in a strong convex curve, the expansion of the latter tends to be larger. The overall platform shape is suggestive of the Greek vase, amphora, as mentioned in the original publication. The carina reaches the posterior end of the platform in the form of nodes. The unit is mostly only slightly arched in lateral view (but see Fig. 7E for an exception). The free blade forms *ca* 40% of the element length. In adult specimens, the basal pit is small, symmetric and situated approximately in the area of the platform margin expansion. Intermediate forms with *P. eiflius*, *P. pseudofoliatus* and *P. ensensis* are identified (see under respective species).

Remarks. – Intraspecific variability and relations: The long rostrum with parallel platform margins, distinct serration of the anterior platform margins and deep adcarinal grooves that tend to shallow rather abruptly proved to be the most consistent and stable characteristics throughout the section; it can be observed also in immature specimens (see Fig. 7) and therefore regarded as true interspecific characteristics. Representative specimens of *Polygnathus pseudofoliatus* most commonly do not possess serrated anterior margins and if they do (20% in this study), the serration is more subtle in comparison to *P. amphora* (Fig. 4I). Moreover, *P. pseudofoliatus* does not possess a long rostrum with parallel margins. On the contrary, the anterior margins gradually widen. Adcarinal grooves of *P. pseudofoliatus* are not as deep as in *P. amphora* and shallow gradually toward the posterior platform end, unlike adcarinal grooves of the latter, which are very deep in the rostral area and then shallow rather abruptly. Another closely related species, *P. ensensis* has a different platform outline and possesses a posterior platform that is strongly down-arched, but more importantly, the serrated anterior platform margins are distinctly high, which is observed also in immature specimens (*e.g.*, Fig. 10A, D). Specimens E–H in Fig. 5, herein treated as *Polygnathus* sp. aff. *P. amphora*, can be regarded as intermediate with *P. pseudofoliatus* but for pragmatic reasons are separated here, because comparable specimens were recorded also elsewhere from different stratigraphic levels and eventually could be treated as a separate species.

Ontogenetic variability (Fig. 7): Species assignment of representatives of the earliest ontogenetic stages is doubtful as most diagnostic characteristics are formed gradually during ontogeny due to centrifugal growth of the element. As long as ontogenetic variation is not known in all the representatives of the *P. pseudofoliatus* Group, the species identification of not fully developed elements will always be only tentative.

The specimen figured in Fig. 7A has a poorly developed platform with parallel margins and discrete carina denticles. The anterior platform margins are smooth. The following growth stage represented by specimen in Fig. 7B already shows differentiation in adcarinal groove depth in the anterior and posterior platform, carina denticles are fused in the platform anterior and there are subtle bulges developed on the anterior platform margins. As the growth proceeds, the anterior margin serration is more pronounced and the anterior ridges are more numerous (Fig. 7C, D). As a result of the centrifugal growth, the denticles of the free blade become denticles of the carina, the part of the carina with fused denticles thus moves posteriorly, and so does the basal pit (compare the basal pit's position in Fig. 7A and D). The expansion of posterior platform margins is only a little in immature specimens, so the platform is slender in comparison to adult growth stages but the difference between narrow anterior and broader posterior is already apparent, as well as more or less symmetrical shape of the platform. The specimen in Fig. 7E represents a growth stage very close to maturity. The number of anterior transverse ridges and numbers of isolated carina denticles situated anteriorly from the fused denticles are comparable to those recorded in adult representatives, also the posterior platform is already flat, only the size of the basal pit is still quite large and the posterior platform is not fully developed.

Occurrence. – Within this study *P. amphora* was recorded from the *australis* Zone (single specimen from Jirásek section II) to *ensensis* Zone. The occurrence from the *australis* Zone represents the lowest stratigraphic occurrence recorded so far. The species was further reported from (compare also with the synonymy listing): Morocco (*kockelianus–timorensis* zones, *e.g.*, Walliser & Bultynck 2011), Ohio (*timorensis* Zone, Sparling 1995), Canada (*timorensis* Zone, Gouwy *in* Kabanov & Gouwy 2017) and Tajikistan (*ensensis* Zone, Bardashev 1992).

***Polygnathus* sp. aff. *P. amphora* Walliser & Bultynck, 2011**
Figure 5E, H

partim 1998 *Polygnathus pseudofoliatus* Wittekindt. – Uyeno *in* Norris & Uyeno, pl. 12, fig. 13 (only).
2008 *Polygnathus eiflius* Bischoff and Ziegler 1957. – Liao & Valenzuela-Ríos, pl. 3, figs q, r.
partim 2013 *Polygnathus pseudoeiflius* Walliser & Bultynck, 2011. – Gouwy, pl. 2, fig. 7 (only).
2019 *Polygnathus amphora* Walliser and Bultynck, 2011. – Gouwy *et al.*, pl. 6, fig. h.

Material. – 25 specimens.

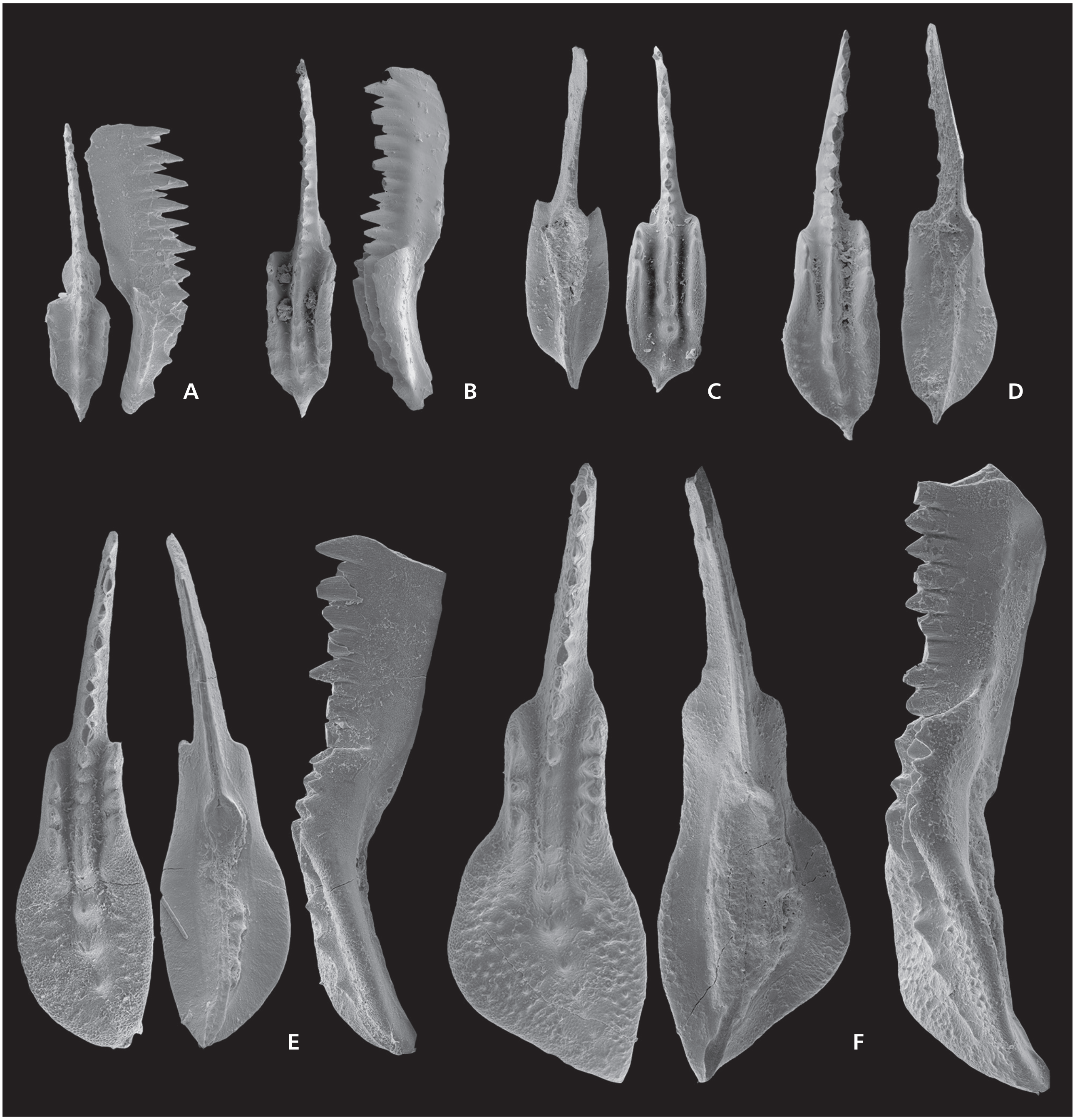


Figure 7. **A**–C – *Polygnathus* cf. *amphora* Walliser & Bultynck (juvenile growth stages); A – upper and oblique lateral view of SV31, sample UDI 3, *ensensis* Zone; B – upper and lateral view of SV32, sample UDI 9, *ensensis* Zone; C – lower and upper view of SV33, sample 390, ?*ensensis* Zone; D–F – *Polygnathus amphora* Walliser & Bultynck, D – upper and lower view of SV34, sample UDI 6, *ensensis* Zone, E, F – sample UDI 3, *ensensis* Zone, E – upper, lower and lateral view of SV35, F – upper, lower and lateral view of SV36. Magnification of all specimens ×90.

Remarks. – Representative specimens share diagnostic features with *P. amphora* Walliser & Bultynck, 2011, but possess a rather straight inner margin. Only for practical reasons are such forms separated here. Future studies may either suggest assignment of this form to a new species, or will confirm that such morphotype lie within the limits of variability of *P. amphora*.

Occurrence. – From the *ensensis* Zone up to the *rhenanus*/*varcus* zones (representative of the latter figured by Liao & Valenzuela-Ríos 2008, pl. 3, figs q, r). Morphotypes conforming to *Polygnathus* sp. aff. *P. amphora* are recorded in Spain (Liao & Valenzuela-Ríos 2008, pl. 3, figs q, r), Sardinia (Gouwy 2013, pl. 2, fig. 7), Canada (Uyeno *in* Norris & Uyeno 1998, pl. 12, fig. 13; Gouwy *et al*. 2019, pl. 6, fig. h).

***Polygnathus eiflius* Bischoff & Ziegler, 1957**
Figure 9A–F

v. 1957 *Polygnathus eiflia* n. sp.; Bischoff & Ziegler, pp. 89, 90, pl. 4, figs 5–7.
partim 1966 *Polygnathus pseudofoliata* n. sp. – Wittekindt, pl. 2, fig. 19, *non* figs 20–23 (= *P. pseudofoliatus*).
1966 *Polygnathus eiflia* Bischoff and Ziegler. – Philip, p. 157, pl. 1, figs 5, 6.
partim 1966 *Polygnathus eiflia* Bischoff & Ziegler. – Wittekindt, p. 633, pl. 1, fig. 21, *non* fig. 20 (= probably *P. pseudofoliatus* transitional with *P. amphora*).
1970 *Polygnathus eiflius* Bischoff & Ziegler. – Jackson *in* Pedder *et al*., pl. 15, figs 18, 20, 23.
non 1970 *Polygnathus eiflia* Bischoff & Ziegler. – Bultynck, *non* pl. 14, fig. 4 (= *P. pseudofoliatus–P. eiflius* intermediate form), *non* fig. 6 (= *P. pseudofoliatus*).
1977 *Polygnathus eiflius* Bischoff & Ziegler 1957. – Weddige, pp. 311, 312, pl. 4, figs 66, 67.
non 1980 *Polygnathus eiflius* Bischoff, G. et Ziegler, W., 1957. – Bultynck & Hollard, pl. 5, fig. 15, pl. 6, fig. 5 (= *P. amphora*).
aff. 1985 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bultynck, pl. 7, fig. 17 (rostrum not developed, compare with *P. uyenoi* Bardashev, 1992).
partim 1987 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bultynck, pl. 8, fig. 17, *non* figs 15, 16 (*P.* cf. *amphora*), *non* fig. 18 (= probably *P. pseudofoliatus–P. amphora* transitional form).
1989 *Polygnathus eiflius* Bischoff & Ziegler. – Mawson & Talent, pl 3, fig. 13.
partim 1990 *Polygnathus pseudofoliatus* Wittekindt, 1965. – Lazreq, pl. 2, fig. 13, *non* figs 10–12 (figs 10, 11 = *P. pseudofoliatus*; fig. 12 = possibly *P. pseudofoliatus–P. eiflius* transitional form).
partim 1992 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Bardashev, pl. 5, fig. 10, *non* figs 4, 7, 8 (= *P. pseudofoliatus*), *non* fig. 9 (= *P.* cf. *pseudoeiflius*).
partim 1994 *Polygnathus eiflius* Bischoff & Ziegler. – Mawson & Talent, pl. 3, figs 7–9, *non* fig. 10 (= *P.* cf. *amphora*).
aff. 1995 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Sparling, p. 1135, pl. 2, figs 31–38.
non 1995 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Savage, p. 545, pl. 3, figs 18–20 (= *P.* cf. *pseudoeiflius*).
2001 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Liao *et al*., pp. 27, 28, pl. 3, figs 6, 8, 9, 13.
aff. 2007 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Benfrika *et al*., pl. 9, fig. h.
aff. 2011 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Walliser & Bultynck, pl. 1, fig. 6.
aff. 2013 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Gouwy *et al*., p. 329, pl. 4, fig. i.
non 2018 *Polygnathus eiflius* Bischoff & Ziegler, 1957. – Narkiewicz & Königshof, pl. 5, fig. u (*P.* cf. *pseudofoliatus*).

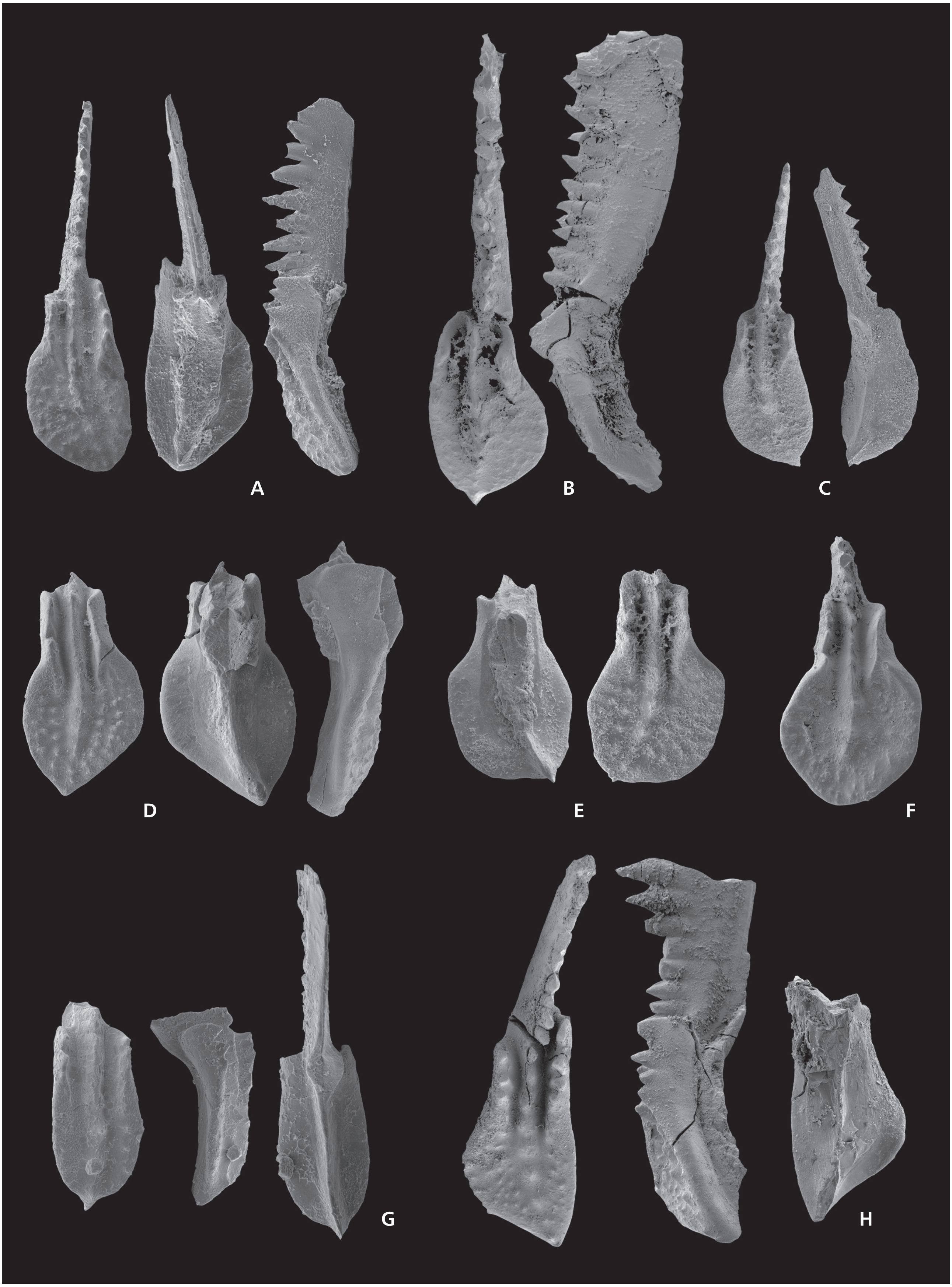
Material. – 12 specimens of *P. eiflius*, 1 specimen of *P.* cf. *eiflius*, 10 specimens of *P. eiflius–P. amphora*, 1 specimen of *P. pseudofoliatus–P. eiflius*, 2 specimens of *P. eiflius–P. ensensis*.

Diagnosis. – "A species of the genus *Polygnathus* with a densely granulated upper surface of the platform and with two diagonal ridges, which accompany the blade at the anterior margin of the platform" (translation of German original, Bischoff & Ziegler 1957, p. 89).

Description. – The platform is conspicuously constricted anteriorly, the outer margin is strongly expanded, forming almost a semi-circular outline, the inner margin forms a convex curve. The anterior platform, when preserved, is developed in the form of short (*ca* ¼ of the platform length) rostrum. The diagonal ridge(s) in the rostral area are rather weak but distinguishable. Deep, narrow adcarinal grooves are only present in the rostral area and shallow abruptly toward the posterior. The posterior platform is almost flat, ornamented by nodes and/or very short, irregular ridges. The free blade (preserved in these collections in a single specimen) forms ca one third of the total length of the unit. A small, symmetrical basal pit is situated approximately between platform midlength and anterior platform end. The morphological and ontogenetic variability could not be assessed herein due to low numbers of recovered specimens.

Intermediate forms: The three specimens in Fig. 8 D, E, F have the platform outline typical of *P. amphora* (narrow rostrum with parallel margins and both plat-

Figure 8. A, B – *Polygnathus eiflius* Bischoff & Ziegler–*Polygnathus ensensis* Ziegler & Klapper; A – upper, lower and lateral view of SV37, sample UDI 3, *ensensis* Zone; B – upper and lateral view of SV38, sample TM9 of Mergl (2019, fig. 2), *ensensis* Zone. • C – *Polygnathus pseudofoliatus* Wittekindt–*Polygnathus eiflius* Bischoff & Ziegler, upper and lower view of SV39, sample UDI 5, *ensensis* Zone. • D– F – *Polygnathus eiflius* Bischoff & Ziegler–*Polygnathus amphora* Walliser & Bultynck; D – upper, lower and lateral view of SV40, sample UDI 3, *ensensis* Zone; E – lower and upper view of SV41, sample UDI 5, *ensensis* Zone; F – upper view of SV42, sample UDI 1, *ensensis* Zone. • G, H – *Polygnathus ensensis* Ziegler & Klapper–*Polygnathus amphora* Walliser & Bultynck; G – upper, oblique lateral and lower view of SV 43, sample UDI 3, *ensensis* Zone; H – upper, lateral and lower view of SV44, sample JI/99 of Mergl (2019, fig. 2), *ensensis* Zone, Jirásek section II (free blade broken during specimen manipulation). Magnification of all specimens ×60.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form margins strongly expanded), however, unlike for *P. amphora*, the rostrum of these specimens is not ornamented by strong, transverse ridges. Rostral diagonal ridges occur, which are typical for *P. eiflius* but can also occur in *P. amphora*. These forms are treated as *P. eiflius*–*P. amphora* intermediate. For intermediate forms with *P. pseudofoliatus* and *P. ensensis* see under the respective species.

Remarks. – Pictures of representative specimens of *P. eiflius* figured by Bischoff & Ziegler (1957) in pl. 4, figs 5–7 show either lower sides of the platforms, lateral or oblique lateral views. Hence, the platform shape and the rostral ridges are not well visible. Personal examination (SV, 2012) of the original collection confirms the presence of only weakly developed rostral ridges in specimen figured in pl. 4, fig. 5, but very prominent ridges developed in the holotype, figured in pl. 4, fig. 7 in the original publication. The holotype possesses a narrow and short rostrum with prominent rostral ridges, an expanded outer platform and strongly nodose ornamentation of the platform. The rostral margins are only subtly serrated. Walliser & Bultynck (2011, p. 11) described relatively high and mostly serrated anterior margins in *P. eiflius*; however, the specimen figured therein (pl. 1, fig. 6) does not seem to possess any of these characteristics, as far as can be judged from the figured upper view. A specimen with rostral ridges and prominent serrated anterior margins assigned to *P. eiflius* was recorded by Gouwy *et al*. (2013). A comparable specimen was figured by Lazreq (1990, pl. 2, fig. 13; assigned to *P. pseudofoliatus* therein).

Relations: According to Bischoff & Ziegler (1957), *P. eiflius* can be distinguished from *P. pseudofoliatus* (treated as *P. foliata* Bryant in the original publication) by the presence of the rostral ridges and thinner anterior platform. Wittekindt (1966) considered the presence of two diagonal rostral ridges as less important and emphasized the contrasting proportions of the strikingly narrow anterior and broadly expanded posterior platform. Bultynck (1970) and Klapper (1971) noticed the different conception of the taxon and the latter author suggested using a combination of characteristics in order to distinguish both species: *P. eiflius* can be distinguished from *P. pseudofoliatus* by having the rostral ridges and much greater expansion of the posterior outer platform. Telford (1975) suggested synonymization of both species because of the occurrence of transitional forms, the rarity of unquestionable rostral ridges and almost identical stratigraphical ranges. The problem of ambiguous conception of the species has not been solved so far, *e.g.*, Weddige (1977) follows the concept of Wittekindt (1966), and Sparling (1995), on the other hand, regarded the presence of rostral ridges as the most important for species delimitation and included into *P. eiflius* also forms that have a platform outline typical for *P. pseudofoliatus* but bear diagonal ridges in the platform anterior (pl. 2, figs 31–38 therein). In this study, the following combination of characteristics was used for determination of *P. eiflius*: short rostrum (*ca* ¼ of platform length), presence of 1–2 rostral ridges, platform outline (narrow anterior, strongly expanded posterior outer platform, convex curve formed by inner platform margin) and ornamentation (mainly nodes).

The presence of one or two diagonal ridges was recorded also in some representative specimens of *P. amphora* (see Walliser & Bultynck 2011, pl. 1, fig. 20; Sparling 1995, pl. 3, figs 16, 20; herein Fig. 6F, H, J, K). However, *P. amphora* differs from *P. eiflius* by having a narrow rostrum with parallel margins, which mostly forms at least $^{1}/_{3}$ of the total platform length, and is ornamented by distinct transverse ridges oriented perpendicular to the carina. Also, both platform margins tend to be strongly expanded in adult forms of *P. amphora*, so the platform shape is rather symmetrical, unlike in *P. eiflius*. The specimens figured by Sparling (1995, pl. 2, figs 31–38) seem to intergrade characteristics typical of *P. pseudofoliatus* (platform shape), *P. eiflius* (diagonal ridges) and *P. amphora* (parallel anterior platform margins, presence of strong transverse ridges on the anterior platform).

Occurrence. – From the *australis* Zone (Eifelian), reported by Weddige 1977 (tab. 18, p. 394) and this study, up to the Lower *varcus* Zone reported by Liao *et al*. (2001). Abboussalam (2003) marks the occurrence (with question mark) also in Upper *varcus* Zone (text-fig. 4a); however, no specimen is figured therein. Narkiewicz & Königshof (2018) reported *P. eiflius* from *disparilis* Zone from Vietnam. However, the specimen figured therein (pl. 5, fig. u) has a platform outline typical for *P. pseudofoliatus* and the reported rostral ridge parallel with carina is difficult to discern from the picture. If the specimen proves to be representative of *P. pseudofoliatus*, it would represent the highest stratigraphic occurrence reported for this species. The occurrence of *Polygnathus eiflius* was further reported from Germany (*e.g.*, Bischoff & Ziegler 1957, Weddige 1977 and Wittekindt 1966), Spain (*e.g.*, Liao *et al*. 2001), Belgium (Gouwy & Bultynck 2003, not figured), Morocco (Bultynck 1987), Nevada (Klapper & Johnson 1980), Australia (*e.g.*, Philip 1966, Mawson & Talent 1989). From the Barrandian area *P. eiflius* was recorded in Jirásek quarry by Kalvoda & Zikmundová *in* Galle & Hladil (1991) and from neptunian dykes infill from the Voskop quarry by Berkyová (2004, determined by L. Slavík). Within this study *P. eiflius* was recorded from the upper *australis* Zone to the lower *ensensis* Zone from Jirásek quarry sections I and II.

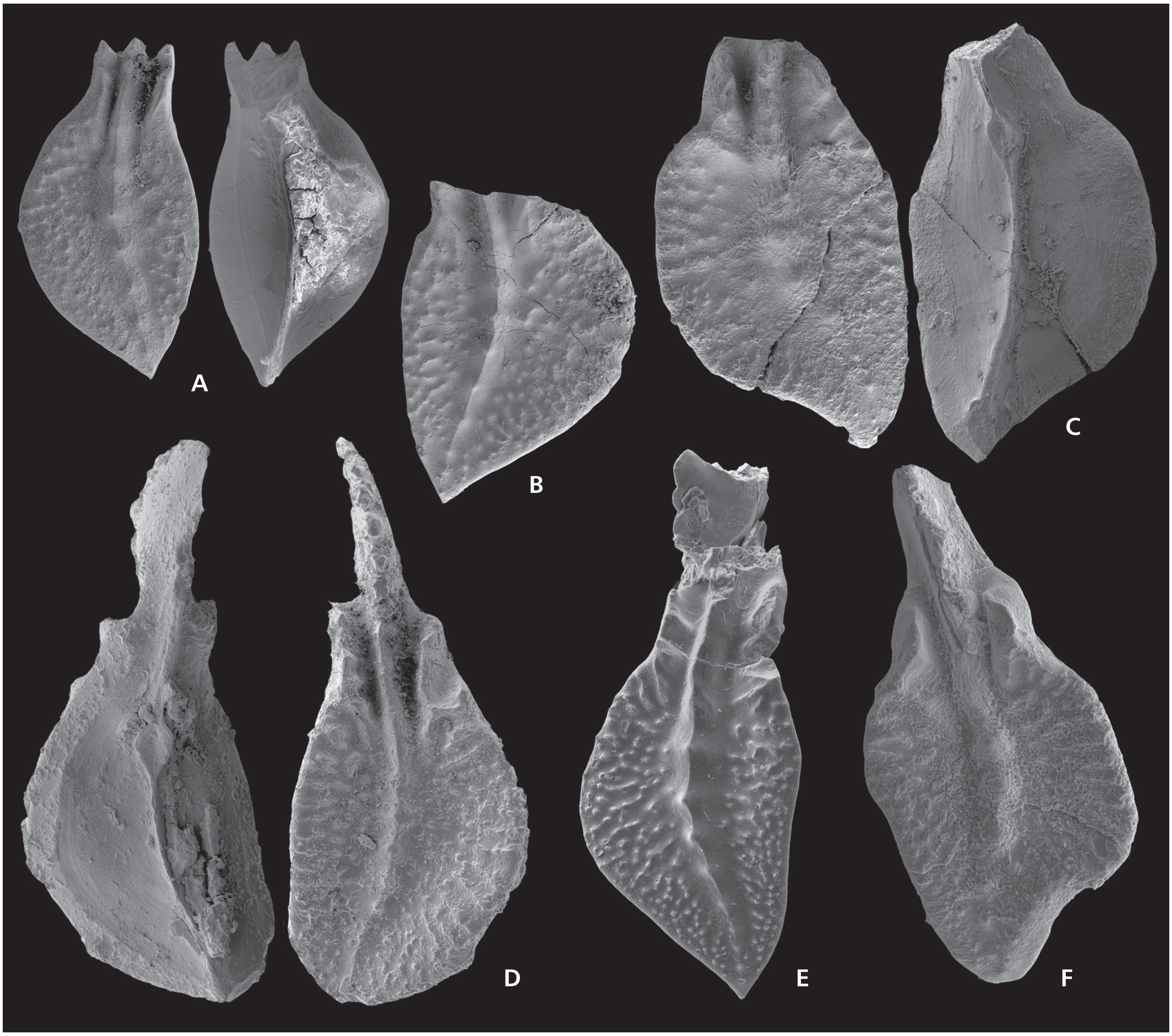


Figure 9. *Polygnathus eiflius* Bischoff & Ziegler. A – upper and lower view of SV 45, sample UDI2, *ensensis* Zone; B – upper view of SV46, sample TM3 of Mergl (2019, fig. 2), *ensensis* Zone; C – upper and lower view of SV47, sample 235–250, *kockelianus* Zone; D – lower and upper view of 48, sample 0 m, *australis* Zone, Jirásek section II; E – upper view of SV49, sample UDI 9, *ensensis* Zone; F – upper view of SV50, sample Ji 6, *kockelianus* Zone. Magnification of all specimens ×60.

***Polygnathus ensensis* Ziegler & Klapper *in* Ziegler *et al.*, 1976**
Figure 10A–C, G

1970 *Polygnathus xylus* Stauffer. – Klapper, Phillip & Jackson, pp. 659–662, pl. 2, figs 10–12.
1976 *Polygnathus xylus ensensis* n. subsp. – Ziegler & Klapper, pp. 125–127, pl. 3, figs 4–9.
partim 1977 *Polygnathus xylus ensensis* Ziegler & Klapper 1976. – Weddige, pp. 321, 322, pl. 4, figs 62, 64, 65, *non* fig. 63 (= *P. pseudofoliatus*).
1978 *Polygnathus xylus ensensis* Ziegler and Klapper. – Orchard, pl. 108, figs ?2 (lateral view missing), 21, 25.
1980 *Polygnathus* aff. *P. xylus ensensis* Ziegler, W. et Klapper, G., 1976. – Bultynck & Hollard, pl. 6, fig.1.
non 1980 *Polygnathus xylus ensensis* Ziegler & Klapper – Schönlaub, pl. 9, fig. 22 (= *Polygnathus* sp).
? 1980 *Polygnathus xylus ensensis* Ziegler & Klapper. – Johnson *et al*., pl. 4, fig. 4 (lateral view missing, treated as *P. pseudofoliatus*–*P. ensensis* transitional form in the original publication).
? 1983 *Polygnathus xylus* cf. *ensensis* Ziegler & Klapper, 1976. – Wang & Ziegler, pl. 6, fig.12, (lateral view missing).
1985 *Polygnathus xylus ensensis* Ziegler & Klapper, 1976. – Ziegler & Wang, pl. 1, fig. 24.

partim 1987 *Polygnathus ensensis* Ziegler & Klapper, 1976. – Bultynck, p. 161, pl. 7, figs 1, ?3 (juv.), 6, *non* figs 2, 4, 5.

? 1989 *Polygnathus xylus ensensis* Ziegler & Klapper. – Mawson & Talent, pl. 4, figs 1, 2.

partim 1989 *Polygnathus ensensis* Ziegler & Klapper. – Bultynck, pl. 2, figs ?12, ?13, 14, 15, 19, 20, ?21, *non* figs 16–18.

1990 *Polygnathus xylus ensensis* Ziegler & Klapper, 1976. – Lazreq, pl. 2, fig. 18.

1994 *Polygnathus xylus ensensis* Ziegler and Klapper. – Mawson & Talent, pl. 3, figs ?11 (oblique lateral view only), 12, ?18 (lateral views missing).

1995 *Polygnathus xylus ensensis* Ziegler and Klapper, 1976. – Sparling, p. 1137, pl. 2, figs ?20 (lateral view missing), 22–24, pl. 8, figs 5, 6.

1995 *Polygnathus pseudofoliatus* Wittekindt, 1966. – Sparling, p. 1137, pl. 2, figs 17–19, (treated as transitional form between *P. pseudofoliatus* and *P. ensensis* in the original publication).

? 1995 *Polygnathus xylus ensensis* Ziegler and Klapper *in* Ziegler *et al.*, 1976. – Savage, pl. 3, figs 1–6 (juv.).

1998 *Polygnathus xylus ensensis* Ziegler and Klapper. – Uyeno *in* Norris & Uyeno, pl. 12, figs ?4, ?16 (close to juv. form of *P. amphora*), pl. 14, figs 28, ?26, ?27, ?29 (lateral view missing).

? 2011 *Polygnathus ensensis* Ziegler & Klapper, 1976. – Walliser & Bultynck, p. 12, pl. 1, figs 21, 22 (juv.).

? 2013 *Polygnathus ensensis* Ziegler & Klapper, 1976. – Gouwy *et al.*, pl. 4, fig. o.

2015 *Polygnathus ensensis* Ziegler, Klapper and Johnson, 1976. – Bahrami *et al.*, pl. 10, figs 20a, b, ?21.

2017 *Polygnathus ensensis* Ziegler & Klapper, 1976. – Gouwy *in* Kabanov & Gouwy, pl. 13, fig. e.

2017 *Polygnathus ensensis* Ziegler and Klapper 1976. – Uyeno *et al.*, p. 398, pl. 1, fig. 15.

2017a *Polygnathus ensensis* Ziegler and Klapper 1976. – Suttner *et al.*, p. 38, fig. 3b.

2018 *Polygnathus xylus ensensis* Ziegler & Klapper, 1976. – Narkiewicz & Königshof, pl. 5, figs g, h.

2019 *Polygnathus xylus ensensis* Ziegler & Klapper, 1976. – Gouwy *et al.*, pl. 6, figs e, ?f, ?m, (latteral views missing).

Material. – 9 specimens of *P. ensensis*, 5 specimens of *P.* cf. *ensensis*, 3 specimens of *P. eiflius–P. ensensis*, 2 specimens of *P. ensensis–P. amphora*.

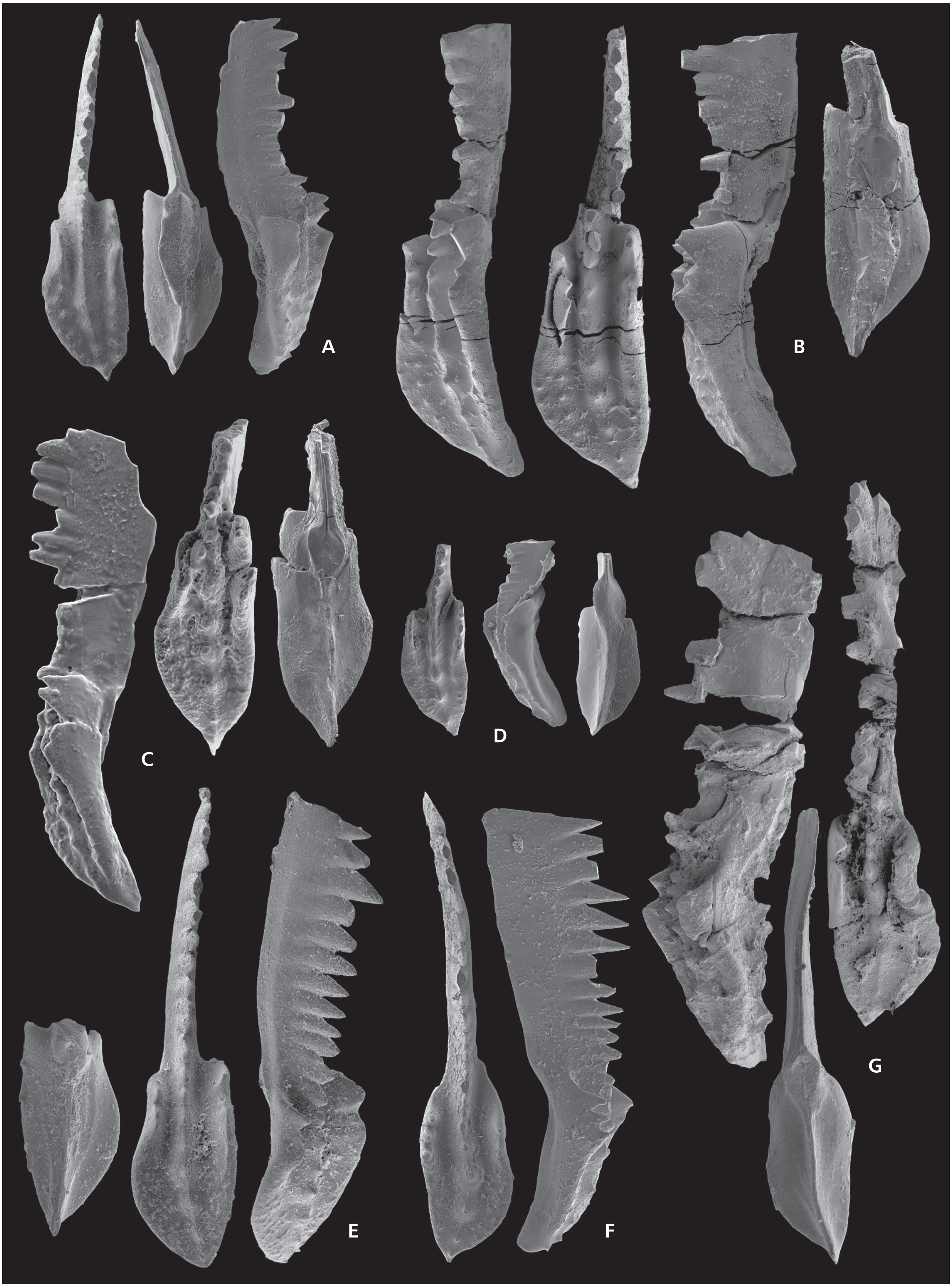
Diagnosis. – *P. ensensis* was originally described as a subspecies of *P. xylus* Stauffer by Ziegler & Klapper *in* Ziegler *et al*. (1976). According to the amended diagnosis of *P. xylus* in Klapper *et al*. (1970, p. 660) and Ziegler *et al*. (1976, p. 125), the representatives of the species are characterized by a more or less symmetrical platform, with the geniculation points situated opposite and essentially parallel platform margins.

Original diagnosis: "Representative specimens of *P. xylus ensensis* have platform margins that are distinctly serrated just posterior of geniculation point. Characteristically there are three to five serrations on both sides, but in phyletically late forms, there are two to three on the inner side and none to one on the outer side. The platform posterior of the serrations is strongly arched downward" (Ziegler *et al*. 1976, pp. 126, 127).

Description. – Specimens assigned herein to *P. ensensis* have distinct serrations on the high anterior platform margins (2–3 serrations on both sides), well visible in lateral view. The posterior platform is down-arched. The outer posterior platform margin forms a convex curve; the inner margin tends to be more or less straight or forms a weak convex curve. The size and position of the basal pit (close to the anterior platform margin) points to immaturity of the figured specimens. The free blade consists of strong and isolated denticles and forms approximately half of the platform length or more. Specimens figured herein in Fig. 10E, F are treated herein as *Polygnathus* sp. aff. *P. ensensis*. They all possess high, serrated anterior platform margins, strongly serrated free blade and asymmetric platform. The size and position of the basal pit points to immaturity of the specimens, however the size seems to be too large to represent juvenile growth stage (their size corresponds to size of mature specimens figured in the original publication). In addition, the free blade is rather long for *P. ensensis*.

Intermediate forms: two specimens (Fig. 8A, B) sharing diagnostic features of *P. ensensis* (distinctly serrated and high anterior platform margin, posteriorly down-arched platform) and *P. eiflius* (presence of a weak diagonal rostral ridge and flat, nodose posterior platform) are treated here as *Polygnathus eiflius–Polygnathus ensensis* intermediate. The immature specimen in Fig. 8G is very close to the specimen figured by Uyeno (Uyeno *in* Norris & Uyeno 1998, pl. 12, fig. 16, assigned

Figure 10. A–C, G – *Polygnathus ensensis* Ziegler & Klapper; A – upper, lower and oblique lateral view of SV51, sample UDI 3, *ensensis* Zone; B – oblique lateral, upper, lateral and lower view of SV52, sample JI/99 of Mergl (2019, fig. 2), *ensensis* Zone, Jirásek section II; C – lateral, upper and lower view of SV53, sample Ji 9, base of the *ensensis* Zone; G – lateral and upper view of SV57, sample TM9 of Mergl (2019, fig. 2), *ensensis* Zone. • D – *Polygnathus* cf. *ensensis* (juvenile), upper, lateral and lower view of SV54, sample 260, *kockelianus* Zone (?*ensensis* Zone). • E, F – *Polygnathus* sp. aff. *P. ensensis*; E – lower, upper and oblique lateral view of SV55, sample UDI 9, *ensensis* Zone; F – upper, lateral and lower view of SV56, sample UDI 3, *ensensis* Zone. Magnification of all specimens ×70.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to *P. ensensis* therein) in the platform outline, position of fused denticles on the carina and development of anterior margin serration. Due to presence of a high and serrated anterior margin it can be viewed as *Polygnathus ensensis–Polygnathus amphora* intermediate. Similarly, the specimen in Fig. 8H possesses strongly serrated, high anterior margins, typical of *P. ensensis*, strong transverse ridges in the anterior platform and deep adcarinal groves that shallow abruptly, which is typical of *P. amphora*.

Remarks. – Anterior platform margins: All the specimens figured in Ziegler *et al.* (1976, pl. 3, figs 4–9) possess serrated anterior platform margins, which are distinctly high although the height is not mentioned in the original description. The height of the serrated anterior margins was stressed later by Weddige (1977, 1989). The inception of "*ensensis* serration" was regarded by Weddige (1989) as the most striking morphologic event in the conodont faunas from the Eifelian–Givetian boundary and *P. ensensis* was suggested to represent an index species for the Eifelian–Givetian boundary at that time. According to Weddige (1977 and personal communication in 2012) first forms of *P. ensensis* that appear in the upper *kockelianus* Zone bear just small denticles on the rostral margins. Above the *kockelianus* Zone, forms with strikingly tall, serrated rostral margins appear. However, only specimens from the *ensensis* Zone are figured in Weddige (1977). Bultynck (1989) noted that the development of the serrations on the platform margins in Moroccan specimens is not so distinctly developed as in the holotype, which was described from the *ensensis* Zone from the Benner quarry near Bicken in Rhenish Slate Mountains (Klapper & Johnson 1980). Bultynck (1987) furthermore stressed that most of the Moroccan specimens possess two or three weak or distinct serrations on the inner side and none or one-two serrations on the outer side and without stratigraphic evidence that those would represent late forms (compare with original diagnosis). A similar observation was made by Uyeno *in* Norris & Uyeno (1998), who also did not regard the serration pattern to be of stratigraphic significance. On the other hand, Walliser (1991) described and figured the range of variability of anterior margin serrations and noted that representatives of early morphotype of *P. ensensis*, possessing only weak serrations on one side and no serrations on the other side, occur in the uppermost *kockelianus* Zone in Morocco. Weddige (1977) also noted serrated anterior margins in specimens of *P. pseudofoliatus* and stressed that these "always turn into irregular ridges toward the centre…"(p. 318), which is in accordance with observations made here.

Free blade denticulation: Similar denticulation as recorded herein, thus isolated, strong, pointed (when well preserved) denticles were also figured by Ziegler *et al.* (1976, pl. 3, figs 4–6), Weddige (1977, pl. 4, fig. 62), Ziegler & Wang (1985, pl. 1, fig. 24), Bultynck (1987, pl. 7, fig. 3), Mawson & Talent (1994, pl. 3, fig. 11), Uyeno *in* Norris & Uyeno (1998, pl. 14, fig. 28) and Narkiewicz & Königshof (2018, pl. 5, fig. g). On the other hand, they seem to be fused rather than isolated (although mostly poorly preserved) in specimens figured by Kabanov & Gouwy (2017, pl. 13, fig. e), Klapper *et al.* (1970, pl. 2. figs 10, 12), Bultynck (1987, pl. 7, fig. 1b), Mawson & Talent (1989, pl. 4, fig. 2). It appears that the characteristic of free blade denticulation might be of taxonomic significance, which would have to be confirmed by a study of larger collection(s).

Platform outline: According to Ziegler *et al.* (1976), the species possesses a "nearly straight outer margin" (p. 127), however, as stressed by Walliser & Bultynck (2011), the posterior outer margin of specimens figured in the original publication forms a convex curve, although it is not as anteriorly constricted as in *P. pseudofoliatus*. Forms with a posteriorly expanded outer platform margin typical for *P. pseudofoliatus* but possessing serrated anterior margins and a down-arched posterior platform diagnostic for *P. ensensis*, were described by Klapper *in* Johnson *et al.* (1980, p. 103, pl. 4, fig. 4) from the *ensensis* Zone in Nevada and regarded by them, together with forms from the *ensensis* and *varcus* zones figured by Weddige (1977, pl. 4, figs 62, 63, 65), as transitional between *P. pseudofoliatus* and *P. ensensis*. Sparling (1995) recorded these forms in the *timorensis* Zone in Ohio (upper *ensensis* Zone according to Sparling, *timorensis* Zone suggested by DeSantis *et al.* (2007) based on the presence of *P. xylus* and *Icriodus brevis*). All the specimens recorded within the present study assigned to *P. ensensis* conform to this morphotype.

Basal pit: The characteristics of the basal pit are not mentioned in the original publication (Ziegler *et al.* 1976), however, the paratype figured in pl. 3, fig. 9 therein possesses a small, symmetric pit situated approximately between platform mid-length and anterior end. In general, lower views of specimens identified as *P. ensensis* have only been scarcely figured in publications. In addition, available illustrations mostly represent juvenile specimens. Judging from the degree of platform development and basal pit position and size, juvenile forms identified as *P. ensensis* were figured by Savage (1995, pl. 3, figs 1–6), Walliser & Bultynck (2011, pl. 1, figs 21, 22), Uyeno *in* Norris & Uyeno (1998, pl. 12, fig. 16; the lower view is not shown but part of the pit can be seen from the upper view). More advanced, yet not adult growth stage is shown by Bahrami *et al.* (2015, pl. 10, fig. 20b), where the basal pit is still large, situated approximately between anterior platform margin and platform mid-length.

Summary: The low number of specimens did not allow assessing ontogenetic and morphological variability, nevertheless, the high and serrated anterior platform margins seem to be a consistent and stable characteristic, it was observed also in juvenile growth stages and therefore can be viewed as truly interspecific. The posterior outer platform outline and the degree of posterior platform down-arching seem to be more variable. However, unless large collections are processed quantitatively, the assessment of height of anterior platform margins and the degree of posterior platform down-arching depends on a subjective perspective by a taxonomist. The serrated anterior margin of *P. amphora* could be also considered as high in some cases and some specimens of *P. amphora* tend to have a down-arched posterior platform (Fig. 7E), which is also true for *P. pseudofoliatus* (Fig. 4I). *P. ensensis* is rather rare in the Barrandian, but Ziegler *et al*. (1976) reported over 50 and Weddige (1977) even over 100 specimens, which would be a solid base for quantitative assessment of the ontogenetic and morphologic variability.

Occurrence. – From the *ensensis* Zone up to the *expansus* Zone *sensu* Narkiewicz & Bultynck (2010) reported by Bahrami *et al*. 2015 from Iran (corresponds to lower *Sch. hermanni* Zone, upper Givetian). The species was reported from Germany (Ziegler *et al*. 1976, Weddige 1977), Spain (*e.g.*, Gouwy *et al*. 2013), SW England (Orchard 1978), Morocco (*e.g.*, Walliser & Bultynck 2011), Austria/Italy (Carnic Alps, Suttner *et al*. 2017a), Alaska (Savage 1995), Canada (*e.g.*, Uyeno *in* Norris & Uyeno 1998, Gouwy *et al*. 2019), Nevada (Johnson *et al*. 1980), Ohio (*e.g.*, Sparling 1995), Iran (Bahrami *et al*. 2015), Vietnam (Narkiewicz & Königshof 2018), South China (*e.g.*, Ziegler & Wang 1985) and Australia (Mawson & Talent 1994).

***Polygnathus pseudoeiflius* Walliser & Bultynck, 2011**

Diagnosis. – The original diagnosis is as follows: "The new species is characterized by a short rostrum with parallel margins and representing about one third or less of the total platform length. The outer margin forms a strong nearly half-circular expansion and the inner margin a weakly convex curve. The outer margin of the rostrum can be slightly diagonal..." (Walliser & Bultynck 2011, p. 11). Note that the diagnosis is partly overlapping with that of *P. amphora*, which is as follows: "The new species can be easily distinguished from...*Polygnathus pseudofoliatus* by the long rostrum with parallel margins and representing one third to half of the total platform" (Walliser & Bultynck 2011, p. 12). Walliser & Bultynck (2011) synonymized *P. pseudoeiflius* with the form described by Klapper (1971, pl. 2, figs 14, 15, 20) as *Polygnathus* aff. *P. eiflius* from New York, which the latter author considered to be intermediate between *P. eiflius* and *P. pseudofoliatus* because of the presence of an expanded posterior outer platform and rostral development but lack of rostral ridges. However, the two specimens shown therein (Klapper 1971, pl. 2, figs 15, 20) seem to possess a short and rather weak diagonal rostral ridge in the outer platform margin (which is a characteristic mentioned in the original diagnosis of *P. pseudoeiflius*). Gouwy *et al*. (2019) stressed, that the rostrum at *P. pseudoeiflius* is very short, in most cases forming about one quarter of the total platform length. The platforms of specimens figured therein are all ornamented by nodes, however, the specimens figured by Klapper (1971, pl 2, figs 14, 15, 20), which are synonymized by Gouwy *et al*. (2019) with *P. pseudoeiflius*, possess diagonal ridges, which is also mentioned in the original diagnosis in Klapper (1971, p. 63). Furthermore, the specimen illustrated by Klapper (1971, pl. 2, fig. 20) has rather long rostral area, expanded platform and strong ridges in the rostral area – characteristics diagnostic for *P. amphora*, but unlike in *P. amphora*, the adcarinal grooves continue in the posterior platform ornamented with ridges, whereas the posterior platform in *P. amphora* is rather flat and ornamented with nodes. Walliser & Bultynck (2011) further synonymized *P. pseudoeiflius* with the forms figured by Bultynck (1987, pl. 8, pp. 16–18). However, the specimen figured therein in pl. 8, fig. 16 possesses a rather long rostrum, typical for *P. amphora.* The specimens in pl. 8, figs 17, 18 are viewed herein as transitional forms between *P. pseudofoliatus* and *P. amphora*. Sparling (1995) regarded *Polygnathus* aff. *P. eiflius* of Klapper (1971) as possibly the only genetically distinctive species within the *P. pseudofoliatus* Group. Sparling had two specimens in his collection and the specimen figured in pl. 2 fig. 9 seems to conform to specimens figured by Klapper (1971, pl. 2, fig. 15), Bultynck (1970, pl. 14, fig. 7) and partly to specimens figured by Jackson *in* Pedder *et al*. (1970, pl. 15, figs 18, 20, 23, 26) in respect to platform outline but not that much in respect to platform ornamentation. The partly overlapping diagnoses for *P. pseudoeiflius* and *P. amphora* and the fact that some forms are herein interpreted as transitional with *P. amphora* illustrates further the variability within the *P. pseudofoliatus* group and the presence of overlapping morphologies leading to difficulties in deciphering between intraspecific and interspecific variation. It further demonstrates that if species boundaries are vaguely defined, and the observed variation in the population is not described, it can only lead to confusion and misidentification.

Remarks. – Representatives of this species were not recorded in the Jirásek quarry; however, it is discussed here as it belongs to the *Polygnathus pseudofoliatus* Group.

***Polygnathus benderi* Weddige, 1977**
Figure 11A–G

Material. – 9 specimens from Jirásek section II.

Diagnosis. – "*Polygnathus benderi* has a very flat, elliptical platform, which is ornamented by fine nodes on either side of the smooth adcarinal bands. Much more prominent are the conical carina denticles, which clearly rise above the flat platform plane. They are mostly isolated and only linked with fine, longitudinal ridges. On the lower side, the margins of basal pit and the keel posterior of it are faintly bulging and protruding" (free translation from German original, Weddige 1977, p. 308).

Description. – Representative specimens from the Barrandian area possess flat, elliptical platforms, ornamented by nodes and mostly by short, irregular ridges (see well developed transverse ridges in the anterior platform in Fig. 11B, C). Shallow adcarinal grooves are present only in the anterior part. Nodes in the anterior platform tend to be diagonally aligned in most of the specimens (Fig. 11A, D, E–G). The free blade forms *ca* $^{1}/_{3}$rd of the total platform length. Basal pit is situated close to the anterior platform margin. The specimen in Fig. 11G probably represents a gerontic growth stage, assuming from the platform size, its profound ornamentation and more posteriorly situated basal pit.

Relations: Weddige (1977) noted that the species may resemble *P. trigonicus* but it differs in not having a triangular platform outline and in lacking diagonally arranged anterior nodes. The specimen in Fig. 11F possesses more triangular platform and diagonally arranged anterior nodes, which suggests that *P. benderi* may have affinity to *P. trigonicus*. As mentioned above, most of the specimens assigned herein to *P. benderi* have diagonally arranged anterior nodes. *Polygnathus abbessensis* Savage, 2011 has a constricted anterior platform and a pointed posterior platform. Vodrážková *et al.* (2011) noted that the basal pit of *P. abbessensis* is situated closer to platform midlenght, contrary to *P. benderi*, that has a pit situated close to the anterior end. This is not the case for Barrandian specimens of *P. abbessensis*, in which the position of the basal pit is comparable to that of *P. benderi* (only two specimens of the first were recovered, however).

Remarks. – See synonymy in Vodrážková *et al*. 2011.

Occurrence. – upper *costatus* Zone in Germany (Weddige 1977), *australis* Zone in Australia (Mawson & Talent 1994), *australis* Zone in South China (Wang & Ziegler 1983), *australis* Zone in Nevada (Vodrážková *et al*. 2011). The species occurs in the the *australis* Zone in the Barrandian area (Jirásek II, sample 0 m).

***Polygnathus abbessensis* Savage, 2011**
Figure 11H, I

Diagnosis. – "*Polygnathus* in which Pa element has broad, flattened nodose platform extending three-quarters unit length and pinched posteriorly where it tapers to sharp point. Adcarinal grooves lacking. Posterior two-thirds of carina consists of nodes joined by thin, low ridges. Short high blade bears large fused denticles. Lower platform surface has moderately small pit situated midway between platform midlength and anterior" (Savage 1995, p. 550).

Description. – Only two specimens were recovered at the base of the Jirásek quarry section II (sample 0 m, *australis* Zone), both possessing an anteriorly constricted platform, which expands significantly immediately after constriction. The platform is posteriorly pointed. The platform is finely nodose, or bears short, irregular ridges, which in the anterior part tend to align diagonally. The free blade forms *ca* ¼th of total platform length. Basal pit is situated approximately between platform anterior and midlength. For comparisons with *P. benderi* see above.

Remarks. – See synonymy in Vodrážková *et al*. 2011.

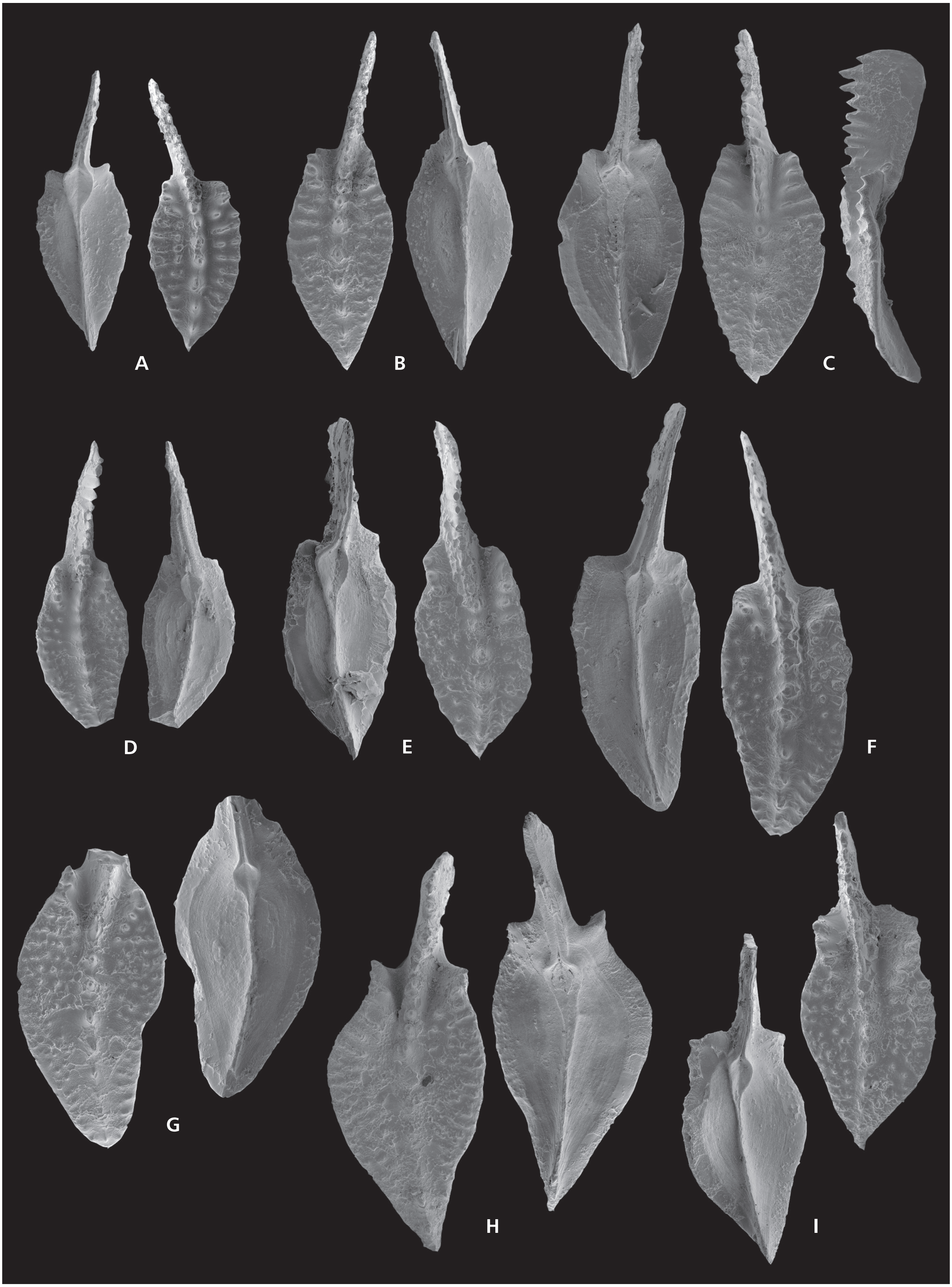
Occurrence. – *australis* and *kockelianus* zones in Alaska (Savage 1995), *australis* and *kockelianus* zones in Nevada (Klapper & Johnson 1980, tab. 8; Vodrážková *et al*. 2011), *australis* Zone in the Barrandian area (Jirásek II, sample 0 m).

***Polygnathus bagialensis* Savage, 2011**
Figure 12A–C

partim 1977 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Savage, pl. 1, figs 9–12 (only).
1992 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Bardashev, pl. 2, figs 38, ?39, 40?
1995 *Polygnathus praetrigonicus* sp. nov. – Savage, pl. 8, figs 8, 9.
2011 *Polygnathus bagialensis* n. name. – Savage, p. 810.
2011 *Polygnathus bagialensis* Savage, 2011. – Vodrážková *et al*., figs 12j, k.

Material. – 6 specimens from UDI (Jirásek section I).

Figure 11. A–G – *Polygnathus benderi* Weddige, sample 0 m, *australis* Zone, Jirásek section II; A – lower and upper view of SV58; B – upper and lower view of SV59; C – lower, upper and lateral view of SV60; D – upper and lower view of SV61; E – lower and upper view of SV62; F – lower and upper view of SV63; G – upper and lower view of SV64. • H, I – *Polygnathus abbessensis* Savage, sample 0 m, *australis* Zone, Jirásek section II; H – upper and lower view of SV65; I – lower and upper view of SV66. Magnification of all specimens ×60.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Diagnosis. – "A species of *Polygnathus* with an elongate triangular platform ornamented with nodes that in large specimens merge into transverse ridges" (Savage 1995, p. 550).

Description. – Representative specimens have a robust, elongated platform, which is widest just posterior of mid-length (Fig. 12A, B) or possesses more or less triangular shape (Fig. 12C), with a short free blade comprised of very high denticles. Adcarinal troughs are rather wide and shallow, limited only to anterior platform. Carina continues to posterior end of platform either in form of nodes linked with a low but distinct ridge or isolated nodes. The platform is ornamented by numerous transverse ridges, which are rather irregular, wavy and most of the ribs are interrupted so they have the form of elongated nodes. The basal pit is of moderate size, possesses lips and is situated between platform anterior and midlength. The unit is strongly arched.

Stratigraphic and geographic occurrence. – *australis* Zone in southern Alaska (Savage 1977), central Asia (Bardashev 1992), Nevada (Vodrážková *et al*. 2011) and in the *ensensis* Zone in Barrandian area.

***Polygnathus* sp. A**
Figure 12D, E

Remarks. – Only 3 specimens were recorded, all from the base of the Jirásek II section (*australis* Zone). The element is massive, exceeding 2 mm in length. The platform anterior in widest and platform margins tapers both to the anterior and posterior ends. The free blade is very short. Adcarinal grooves may be deep in the platform anterior but shallow rather abruptly towards the platform posterior. The platform is ornamented by transverse ridges oriented perpendicular to the carina and also by nodes in the posterior platform; the transverse ridges terminate almost at the carina. The carina is formed by a series of nodes connected by a very low, indistinct ridge. Small, nearly isometric basal pit is situated in the end of anterior third. The unit is strongly arched.

***Polygnathus kluepfeli* Wittekindt, 1966**
Figure 13A, C, F

1966 *Polygnathus kluepfeli* n. sp.; Wittekindt, pp. 633, 634, pl. 2, figs 1, 2, 3, ?4, 5.
? 1980 *Polygnathus* n. sp. Klapper *in* Johnson, Klapper & Trojan. – Klapper *in* Klapper & Johnson, pl. 4, figs 11, 12, 16 (figs 11, 16 identical with *Polygnathus* n. sp. M Klapper *in* Johnson *et al*. 1980, pl. 4, figs 9, 10).
? 1980 *Polygnathus* n. sp. M. – Klapper *in* Johnson *et al*., pl. 4, figs 9, 10.
partim 1998 *Polygnathus linguiformis* Hinde predelta morphotype. – Uyeno *in* Norris & Uyeno, pl. 13, figs 10–12, ?8, 9, *non* figs 7, 13.
2011 *Polygnathus linguiformis weddigei*. – Walliser & Bultynck, pl. 3, figs 10, 11.
? 2017 *Polygnathus* n. sp. M of Klapper 1980 . – Uyeno *et al*., p. 398, pl. 1, fig. 5.
? 2019 "*Polygnathus* n. sp. M Klapper, 1980". – Gouwy *et al*., pl. 7, figs v, w.

Material. – 5 specimens of *P. kluepfeli* and 3 specimens of *P.* cf. *kluepfeli* from UDI (Jirásek section I).

Diagnosis. – "A species of *Polygnathus* with elongated, oval, strongly asymmetric platform, with only weakly developed troughs. The platform margins are ornamented by weak but distinct transverse ridges" (free translation from German, Wittekindt 1966, p. 634).

According to further description, the platform is strongly arched, pointed both anteriorly and posteriorly, the outer platform margin is more strongly convex than the inner margin and the outer platform reaches further anteriorly than the inner platform. The platform shape, tapering on both platform sides, is clearly visible only on the figured holotype (Wittenkindt 1966, pl. 2, fig. 1), other figures show oblique views.

Description. – Representative specimens assigned to *P. kluepfeli* possess a platform ornamented by sparse but distinct transverse ridges. The anterior margin terminations meet the free blade in an obtuse angle so the platform is tapering on both anterior and posterior ends. The outer platform is broader and more convex than the inner platform. The free blade is broken. The posterior carina consists of conspicuous nodes connected by a low, indistinct ridge. The basal pit is of medium size, possessing "lips" and situated approximately between anterior end and platform midlength. The unit is strongly arched.

Remarks. – The specimens assigned here to *Polygnathus* cf. *kluepfeli* (Fig. 13B, D, E) differ from the nominate species by the shape of the anterior platform margins, which are not tapering. Only a few specimens were recovered so the variability could not be assessed, it is possible that such a platform outline falls within the variability of *P. kluepfeli*. The free blade is very short and rather high in *P.* cf. *kluepfeli*, which seems to apply also to *P. kluepfeli* (see Wittekindt 1966, pl. 2, figs 2, 3, 5). The specimens in Fig. 13D, E share also some similarities with *P. praetrigonicus* Bardashev, 1992; especially in the nearly triangular platform outline and position of basal pit. The latter species was kept in an open nomenclature for a long time, firstly described by Klapper (1971, p. 66) as *Polygnathus* aff. *P. trigonicus* with stratigraphic

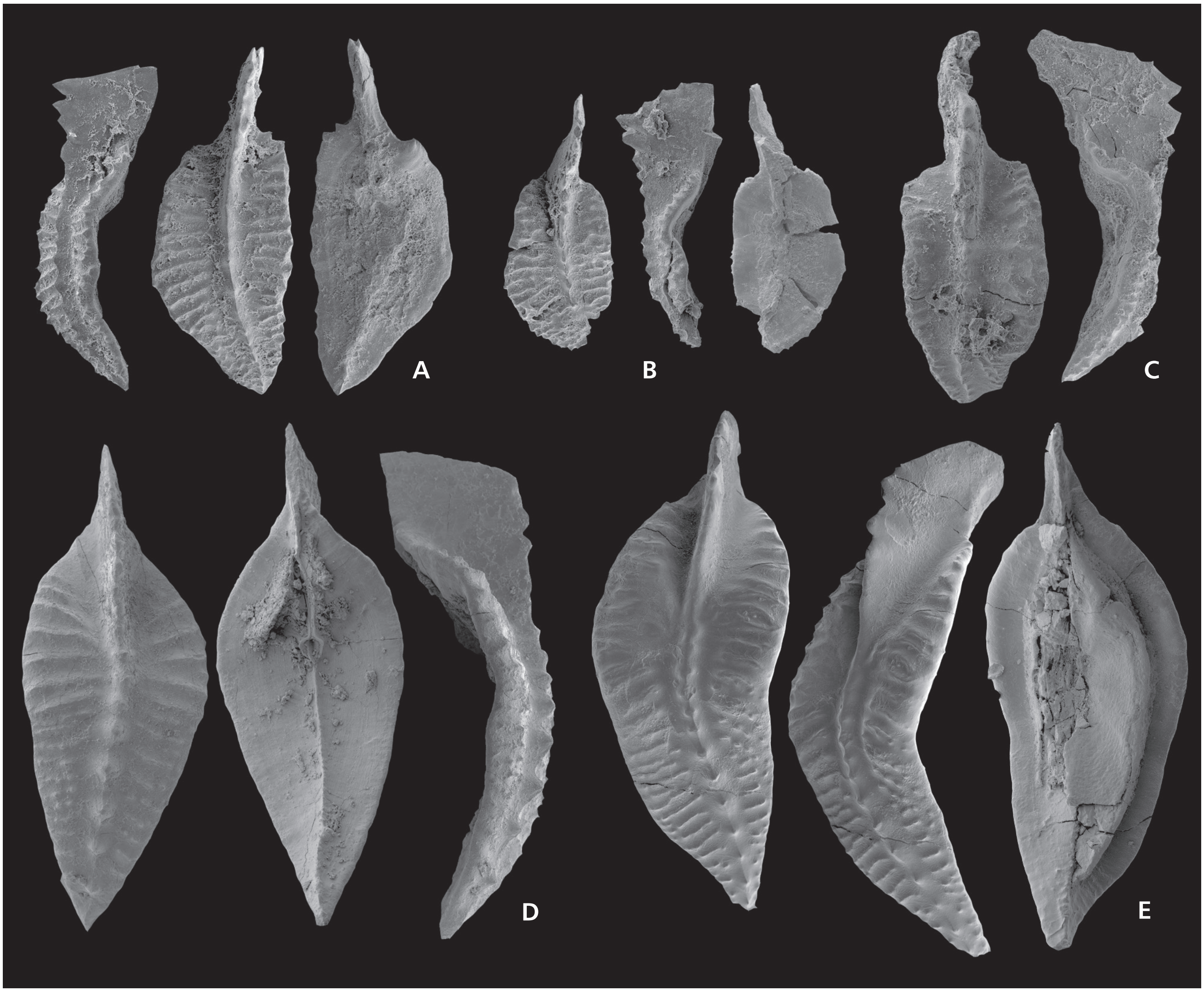

Figure 12. A–C – *Polygnathus bagialensis* Savage; A, B – sample UDI 2, *ensensis* Zone, A – oblique lateral, upper and lower view of SV67, B – upper, lateral and lower view of SV68; C – upper and lateral view of SV69, sample UDI 12, *ensensis* Zone. • D, E – *Polygnathus* sp. A, sample 0 m, *australis* Zone, Jirásek section II; D – upper, lower and lateral view of SV70; E – upper, oblique lateral and lower view of SV71. Magnification of all specimens ×30.

occurrence limited to the *costatus* Zone (basal *costatus* Zone in the Barrandian area). The specimen in Fig. 13B has a similar platform outline to *P. weddigei*, except for the shape of the anterior inner platform margin, which is strongly convex here, unlike in *P. weddigei*. The specimen in Fig. 13D is also similar to *Polygnathus weddigei* in the shape of anterior platform terminations and almost straight inner platform margin. The latter taxon was described by Ziegler *et al*. (1976) as a new (delta) morphotype of *P. linguiformis linguiformis* and eventually described as *P*. *linguiformis weddigei* by Clausen *et al*. (1979). Except for Clausen *et al*. (1979), who reported more than 100 specimens of *P*. *weddigei*, both taxa, *P. weddigei* and *P. kluepfeli* seem to occur rather rarely (Wittekindt 1966, Uyeno *in* Norris & Uyeno 1998, Klug 1983 and this study) so the range of morphological variability is not known. *Polygnathus weddigei* appears to occur stratigraphically higher than *P*. *kluepfeli* in the Rhenish Slate Mountains and Eifel Hills (Ziegler *et al*. 1976, Weddige 1977, Clausen *et al*. 1979) and Ziegler *et al*. (1976) suggested that *P*. *kluepfeli* may represent an extremely rare earlier morphotype of *P*. *weddigei*. *Polygnathus* n. sp. Klapper & Johnson (1980, pl. 4, figs 11, 12, 16; identical with *Polygnathus* n. sp. M Klapper *in* Johnson *et al*. 1980, pl. 4, figs 9, 10) from the *ensensis* Zone of Nevada seems also to have an affinity to *P*. *kluepfeli*, however, only 7 specimens of this taxon were recovered by the above mentioned authors, from which two were photodocumented, so further comparisons are difficult. Original collections with *P. kluepfeli* and *P. weddigei* should be re-studied and photodocumented, and the range of variability should be assessed in order to clarify the taxonomic concept of the two species.

Occurrence. – Clausen *et al*. (1979, tab. 7) who summarized information on stratigraphic distribution of conodonts from Ziegler *et al*. (1976), and Weddige (1977) and their own observations report the occurrence of *P. kluepfeli* from upper *ensensis* and lower *varcus* zones from Rheinisches Schiefergebirge and Eifel Hills. The specimens illustrated by Uyeno *in* Norris & Uyeno (1998) and Walliser & Bultynck (2011) synonymized herein with *P*. *kluepfeli* occur in the *ansatus* Zone (middle *varcus*) in Canada and the uppermost *ensensis–hemiansatus* zones in Morocco. The species was previously reported by Kalvoda *in* Hladil & Kalvoda (1993b) from UDI in the Jirásek quarry. Specimens from this study assigned to *P. kluepfeli* and *P*. cf. *kluepfeli* occur in the *ensensis* Zone in the Jirásek quarry section I.

***Polygnathus trigonicus* Bischoff & Ziegler, 1957**
Figure 13G–I

1957 *Polygnathus trigonica* n. sp.; Bischoff & Ziegler, pp. 97, 98, pl. 5, figs 1–6.
1966 *Polygnathus trigonica* Bischoff and Ziegler. – Philip, p. 158, pl. 1, fig. 7.
1966 *Polygnathus trigonica* Bischoff & Ziegler. – Wittekindt, p. 639, pl. 3, fig. 1.
1970 *Polygnathus trigonicus* Bischoff and Ziegler. – Jackson *in* Pedder *et al*., pl. 15, figs 11, 14, 15.
1970 *Polygnathus trigonica* Bischoff & Ziegler. – Bultynck, pp. 129, 130, pl. 15, figs 1, 3.
partim 1971 *Polygnathus trigonicus* Bischoff & Ziegler. – Klapper, pl. 3, figs 7, 8, 11, 12, *non* figs 9, 10 (= *Polygnathus* sp. aff. *P.* n. sp. M *sensu* Klapper *in* Johnson *et al*. 1980).
? 1977 *Polygnathus trigonicus* Bischoff & Ziegler 1957. – Weddige, pp. 320, 321, pl. 6, figs 98, 99.
non 1977 *Polygnathus trigonicus* Bischoff and Ziegler, 1957. – Savage, p. 1353, pl. 1, figs 1–12 [(= *P. bagialensis* Savage, 2011 (= *P. preatrigonicus* Savage, 1995)].
1980 *Polygnathus trigonicus* Bischoff, G. et Ziegler, W., 1957. – Bulltynck & Hollard, pl. 5, fig. 9.
1980 *Polygnathus trigonicus* Bischoff & Ziegler. – Klapper *in* Johnson *et al*., pl. 4, fig. 11.
1983 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Wang & Ziegler, pl. 7, figs 19, 20.
cf. 1992 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Bardashev, pl. 2, figs 39, 40 (ornamentation with strong, continuous ridges), *non* figs 37, 38.
1995 *Polygnathus trigonicus* Bischoff and Ziegler, 1957. – Savage, p. 550, pl. 2, figs 10–15.
2009 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Berkyová, pp. 680, 681, pl. 6, fig. d.
2011 *Polygnathus trigonicus* Bischoff & Ziegler, 1957. – Walliser & Bultynck, p. 13, pl. 2, fig. 6.

Material. – 8 specimens of *P. trigonicus* (Jirásek sections I and II), 1 specimen of *P*. cf. *trigonicus* (Jirásek section I).

Diagnosis. – "A species of genus *Polygnathus* with triangular platform, which is ornamented with nodes or discontinuous ribs or ridges" (free translation from German original, Bischoff & Ziegler 1957, p. 97).

The description in the original publication points out the anterior platform margins, which meet the free blade at an approximately right angle and anterior platform ornamentation, which consists of nodes that tend to be aligned diagonally and can form diagonal ridges, especially in adult forms. Large basal pit with rims is situated close to the anterior platform end. The free blade forms $^1/_2$ to $^1/_3$ of the total platform length.

Description. – The Barrandian specimens conform to specimens from the original collection of Bischoff & Ziegler (1957). Even the two morphotypes recognized by above mentioned authors are present – one with slender and more elongated platform (Fig. 13G) and the one conforming to the holotype (Fig. 13H). All the specimens recovered, including juvenile forms, have diagonally aligned nodes developed in the anterior platform, delicate in some specimens (Fig. 13G) and prominent in others (Fig. 13H). Except the nodes in the platform anterior, the platform is mostly ornamented by irregularly developed and interrupted transverse ridges. The carina continues to posterior end in forms of nodes, which are mostly isolated. The free blade is short, forming mostly less than $^1/_3$rd of total element length. The unit is arched posteriorly.

Remarks. – Relations: Wittekindt (1966, p. 639) and Bultynck (1970, p. 129) regarded the presence of diagonally aligned anterior nodes as diagnostic for *P. trigonicus*. Weddige (1977), on the other hand, noted that phylogenetically early forms do not possess distinctly developed diagonally arranged nodes. As noted herein under *P*. *benderi*, the two species may be related, as both

Figure 13. A, C, F – *Polygnathus kluepfeli* Wittekindt; A, C – sample UDI 4, *ensensis* Zone, A – upper and lower view of SV72, C – upper and lateral view of SV74; F – upper and lower view of SV77, sample UDI 3, *ensensis* Zone. • B, D, E – *Polygnathus* cf. *kluepfeli*, sample UDI 4, *ensensis* Zone; B – upper and lower view of SV73, D – upper and lower view of SV75, E – upper, lower and lateral view of SV76. • G–I – *Polygnathus trigonicus* Bischoff & Ziegler; G, I – sample 0 m, *australis* Zone, Jirásek section II, G – upper and lower view of SV78, I – lower and upper view of SV80; H – upper and lower view of SV79, sample 260–280, *kockelianus* Zone. Magnification of all specimens ×70.


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may possess diagonally aligned nodes and one Barrandian representative assigned to *P. benderi* possesses a nearly triangular platform shape (Fig. 11F). Representative specimens herein assigned to *P.* cf. *kluepfeli* also have a nearly triangular platform, none of them, however, possess diagonally arranged nodes in the platform anterior and also the basal pit of *P.*cf. *kluepfeli* is situated more posteriorly. *P. trigonicus* differs from *P. praetrigonicus* Bardashev, 1992 (= *Polygnathus* aff. *P. trigonicus sensu* Klapper 1971) mainly by the position of basal pit, which is situated more posteriorly in the latter. For further comparisons of these two species see Klapper & Vodrážková (2013, p. 168).

Occurrence. – The species occurs from the *australis–ensensis* zones in the Barrandian area (Berkyová 2009 and this study), *kockelianus* Zone in South China (Wang & Ziegler 1983). For further geographic distribution within the *australis–ensensis* zones see Klapper & Johnson (1980, tabs 8, 9).

***Polygnathus linguiformis* Hinde, 1879**
Figures 14A–F; 15D, F, G

Diagnosis. – "Plate elongate, one extremity produced into a tongue-like projection, bending downwards; the sides of the plate curving upwards, forming a central trough, from the bottom of which the keel rises, this extends some distance beyond the sides of the plate and has an expanded crenulated crest. The anterior tongue-like projection has several strongly-marked transverse ridges; the lateral surface has a few scattered tubercles…" (Hinde 1879, p. 367).

Description. – Representative specimens possess a characteristic, flange-like development of the outer margin, which is significantly higher than the inner platform and carina. Platform is already asymmetric in the earliest ontogenetic stages of development; with the outer platform being wider than the inner platform. Adcarinal troughs, especially in the outer platform are shallow in the earlies ontogenetic stages (Fig. 14A, B) and get very deep in later stages, as the platform continues to grow (Figs 14C–F; 15 D, F, G). The sharp, almost rectangular posterior outer platform margin develops in later ontogenetic stages (Figs 14D–F; 15 D, F, G); in earlier ontogenetic stages it is rather rounded. The tongue is not developed in the earliest ontogenetic stages – the more advanced the ontogenetic stage is, the better developed the tongue with more numerous transverse ridges is.

Remarks. – Wittekindt (1966), Bultynck (1970), Klapper (1971), Ziegler *et al*. (1976) and Weddige (1977) introduced several subspecies/morphotypes of *Polygnathus linguiformis*, which are treated herein as species of the genus *Polygnathus*. *Polygnathus linguiformis* is commonly reported as the most common taxon in Middle Devonian conodont collections, which is true also for the Barrandian area. Interestingly, this taxon appears to maintain its integrity within the stratigraphic record as only a subtle variation, mainly ontogenetic, was recorded herein. The morphotypes described by Walliser & Bultynck (2011) were not recognized within this study.

Occurrence. – This is a very long-ranging species occurring globally from the *costatus* Zone (Klapper & Johnson 1980, tab. 7) to *hermanni* Zone (Walliser & Bultynck 2011). Extensive information on geographic distribution can be found in Aboussalam (2003), who also mentioned occurrence of the species in early Frasnian *transitans* Zone recorded by Sandberg *et al*. (1989); however, caution should be taken as this material could be reworked (see Sandberg *et al*. 1989, pp. 207–209).

***Polygnathus klapperi* Clausen, Leuteritz & Ziegler, 1979**
Figure 15A–C, E

1970 *Polygnathus linguiformis* Hinde, forma nova. – Jackson *in* Pedder *et al*., pl. 16, fig. 17.
partim 1976 *Polygnathus linguiformis linguiformis* epsilon morphotype. – Ziegler *et al*., pp.123, 124, pl. 4, figs 3, 12, 24, *non* fig. 14 (= *Polygnathus* sp. aff. *P. klapperi*).
1977 *Polygnathus linguiformis* ssp. a – Weddige, p. 316, pl. 5, fig. 83.
partim 1979 *Polygnathus linguiformis klapperi* n. ssp. – Clausen *et al*., pl. 1, fig. 8, *non* fig. 7 (= *Polygnathus* sp. aff. *P. klapperi*).
1979 *Polygnathus linguiformis linguiformis* Hinde epsilon morphotype Ziegler & Klapper. – Savage & Amundson, pl. 1, figs 19–24.
partim 1980 *Polygnathus linguiformis linguiformis* Hinde, G.J., 1879, epsilon morphotype Ziegler, W. et Klapper, G. – Bultynck & Hollard, pl. 7, figs 3, 4, 7, 9, ?6, ?8 (juv. forms), *non* fig. 2 (= *Polygnathus* sp. aff. *P. klapperi*), *non* fig. 5 (= *P. linguiformis weddigei*).
non 1983 *Polygnathus linguiformis linguiformis* Hinde epsilon morphotype. – Wang & Ziegler, pl. 7, fig. 23 = *P. linguiformis*, fig. 24 = *Polygnathus* sp. aff. *P. klapperi*.
1983 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Klug, pl. 11, figs r–t.
1987 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler. – Bultynck, pl. 9, fig. 20.
partim 1989 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Mawson & Talent, pl. 5, fig. 11, *non* fig. 10 (= *Polygnathus* sp. aff. *P. klapperi*).

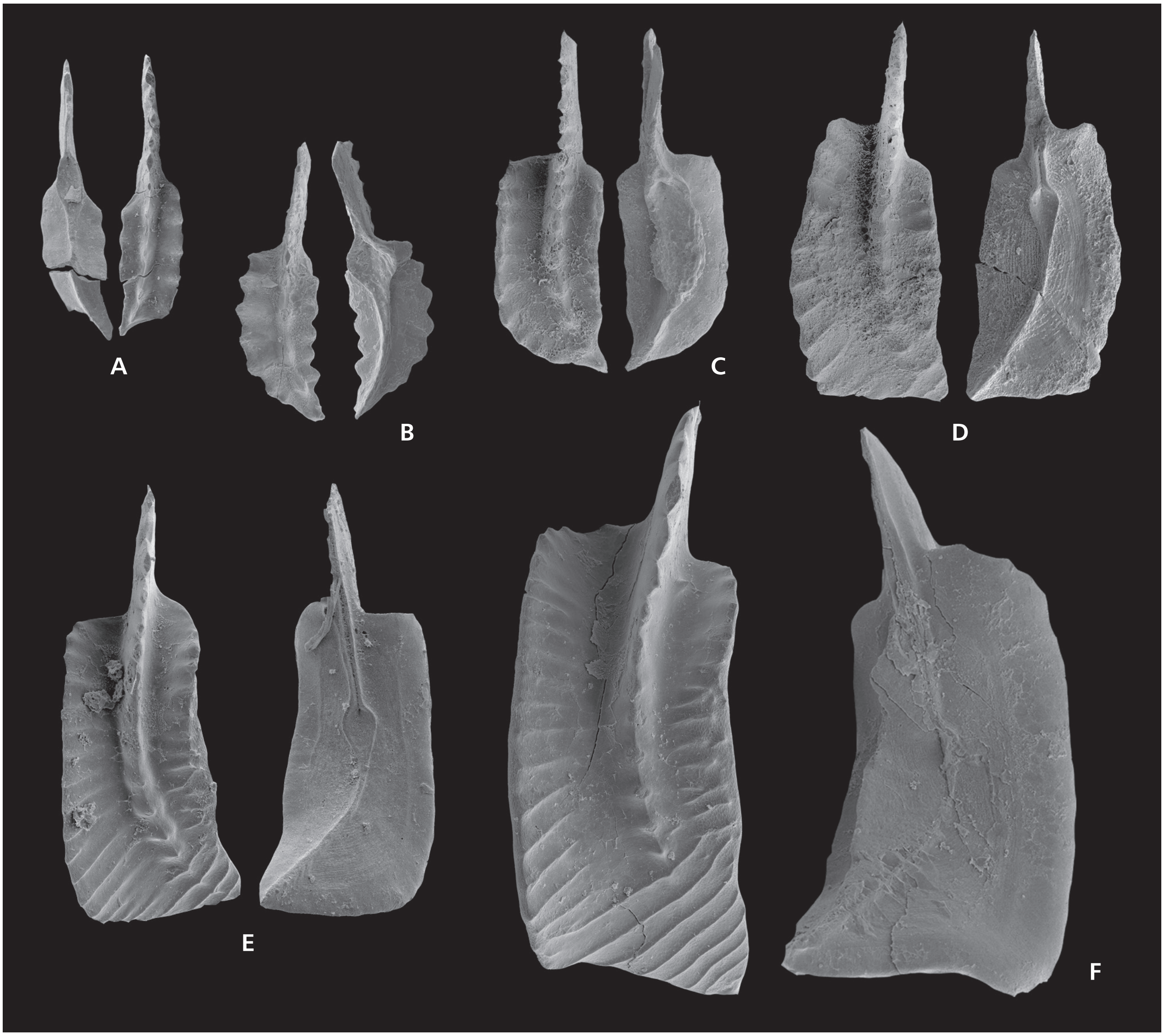


Figure 14. Ontogenetic series of *Polygnathus linguiformis* Hinde. A – lower and upper view of SV81, sample 390, *ensensis* Zone; B, C – sample UDI 3, *ensensis* Zone, B – upper and lower view of SV82, C – upper and lower view of SV83; D – upper and lower view of SV84, sample 260–280, *kockelianus* Zone; E, F – sample UDI 6, *ensensis* Zone, E – upper and lower view of SV85, F – upper and lower view of SV86. Magnification of all specimens ×70.

1992 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Bardashev, pl. 3, figs 10, 14, 20.

1998 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler. – Uyeno *in* Norris & Uyeno, pl. 13, figs 22–27, pl. 14, figs 1–11.

1999 *Polygnathus linguiformis* aff. *klapperi* Clausen, Leuteritz & Ziegler 1979. – Bultynck & Hollevoet, pl. 1, figs 11, 12.

non 2001 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Liao *et al*., pl. 2, figs 25–28 (= *P. linguiformis*).

2003 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Aboussalam, pl. 17, figs 7, ?8, 9, *non* fig. 10 (*Polygnathus* sp. aff. *P. klapperi*).

2008 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Liao & Valenzuela-Ríos, pl. 3, fig. b.

partim 2011 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Walliser & Bultynck, pl. 3, fig. 7, *non* fig. 8 (= *Polygnathus* sp. aff. *P. klapperi*).

non 2013 *Polygnathus linguiformis klapperi* Clausen, Leuteritz & Ziegler, 1979. – Liao & Valenzuela-Ríos, pl. 7, fig. m (= *Polygnathus* sp.).

2019 *Polygnathus linguiformis klapperi* s.l. *sensu* Uyeno *in* Norris & Uyeno, 1998. – Gouwy *et al*., pl. 6, fig. b.

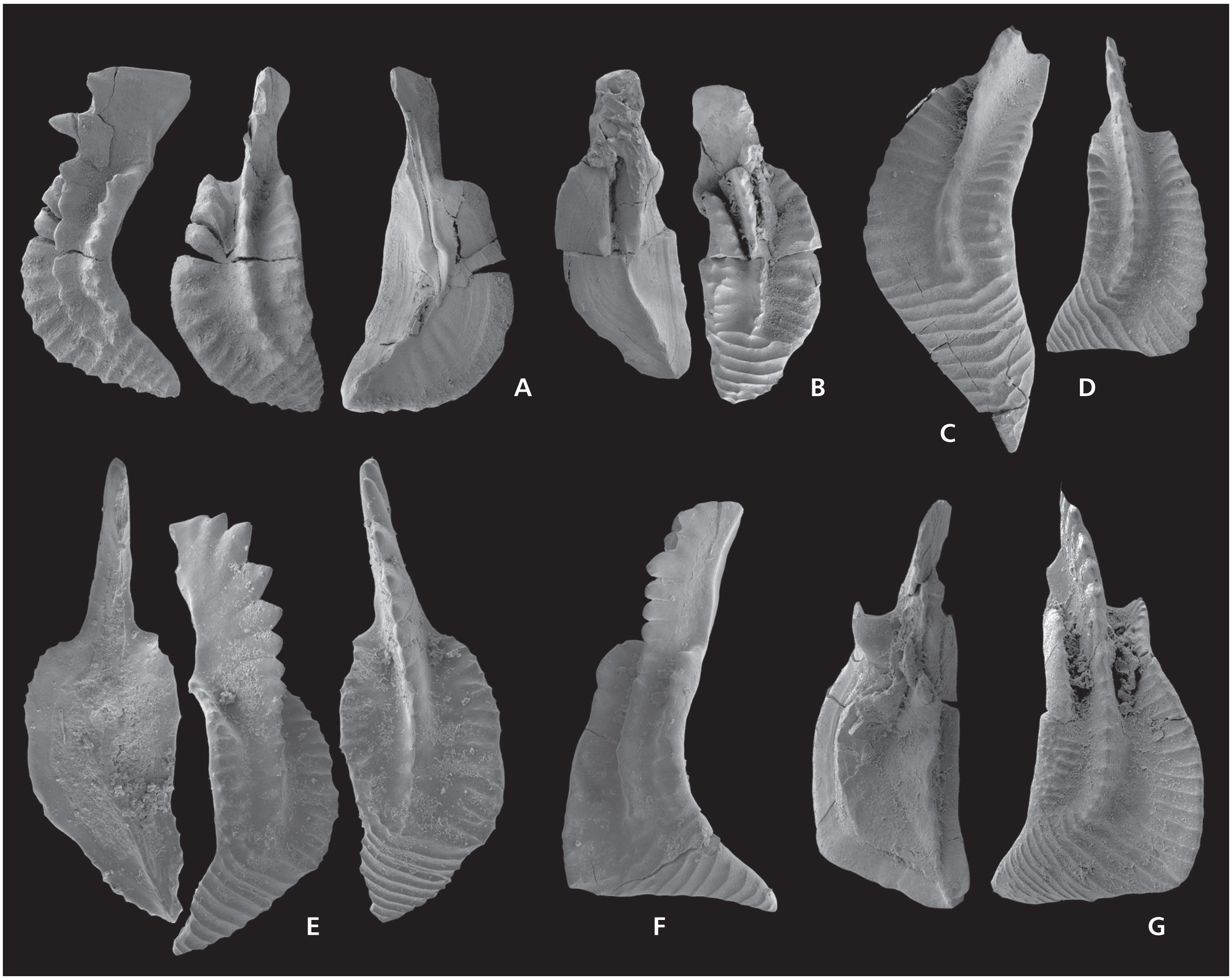


Figure 15. A–C, E – *Polygnathus klapperi* Clausen, Leuteritz & Ziegler, sample 80–90, *kockelianus* Zone; A – oblique lateral, upper and lower view of SV87; B – lower and upper view of SV88; C – upper view of SV89; E – lower, oblique and upper view of SV91. • D, F, G – *Polygnathus linguiformis* Hinde; D – upper view of SV90, sample UDI 9, *ensensis* Zone; F – upper view of SV92, sample UDI 10, *ensensis* Zone; G – lower and upper view of SV93, sample UDI 2, *ensensis* Zone. Magnification of all specimens ×30.

Material. – 11 specimens.

Diagnosis. – This taxon was firstly described by Ziegler *et al*. (1976) from the *varcus* Zone of the Solon Member, Cedar Valley Formation in Iowa, as a new (epsilon) morphotype of *Polygnathus linguiformis linguiformis* Hinde and eventually described as a subspecies of *P. linguiformis* by Clausen *et al*. (1979). The original diagnosis in the latter is identical to description of Ziegler *et al*. (1976), which is as follows: "Representative specimens of the epsilon morphotype are characterized by a strong development of transverse ridges on the well developed tongue. The outer anterior platform bears strong transverse ridges separated from the carina by an adcarinal trough or groove, but a high flange-like margin is characteristically not developed. The outer margin at the beginning of the tongue generally turns inward in a sharply rounded curve..." (Ziegler *et al*. 1976, pp. 123, 124). According to Clausen *et al*. (1979) the subspecies differs from *P. l. linguiformis*, in addition to the absent flange-like outer margin, by the curvature of the outer platform margin that is to be found at the beginning of the tongue, unlike in *P. l. linguiformis*, where the curvature includes the tongue.

Description. – Representative specimens of *P. klapperi* from the Barrandian area have a very well developed tongue, with strong, uninterrupted transverse ridges (in total number of 6–10 ridges per tongue in adult specimens). Both platform margins bear distinct transverse ridges that are separated from the carina by rather wide and shallow troughs, giving the platform almost a flat appearance. The free blade forms *ca* $^{1}/_{3}$ of the total unit length. The basal pit is of medium size, situated slightly above platform midlength. The tongue bends inward and the unit is arched. Due to the low number of the specimens recorded the intraspecific variability could not be assessed.

Remarks. – The specimen figured by Ziegler *et al*. (1976) in pl. 4, fig. 3, apparently representing a juvenile growth stage, possesses anterior platform margins that meet the free blade in an obtuse angel. Specimens with such a feature were also figured by other authors (*e.g*., Walliser & Bultynck 2011, pl. 3, fig. 7; Savage & Amundson 1979, pl. 1, figs 21, 22 and Uyeno *in* Norris & Uyeno 1998, pl. 13, figs 23, 24, pl. 14). Neither Ziegler *et al*. (1976) nor Clausen *et al*. (1979) mention the shape of the anterior platform margins in their descriptions. The holotype selected by Clausen *et al*. (1979, pl. 1, fig. 7, a reillustrated specimen figured by Ziegler *et al*. 1976) seems to possess a rather high outer platform margin and deeper troughs. This feature is seen also elsewhere (*e.g*., Bultynck & Hollard 1980, pl. 7, fig. 2; Wang & Ziegler 1983, pl. 7, fig. 24; Mawson & Talent 1989, pl. 5, fig. 10). It is questionable, whether these forms still lie within the range of variability of *P. klapperi*. As we regard the depth of adcarinal troughs and height of outer platform margin as diagnostic characteristics, together with posteriorly curved outer margin and strongly developed tongue, we treat such forms with higher outer margin and deeper troughs as *Polygnathus* sp. aff. *P. klapperi* (see synonymy).

Occurrence. – Iowa (*varcus* Zone, Ziegler *et al*. 1976); Central Oregon (*timorensis*, *rhenanus/varcus* or *ansatus* zones = Lower or Middle *varcus* zones in the publication, Savage & Amundson 1979); Indiana (*timorensis, rhenanus/ varcus* Zone = lower *varcus* Zone in the publication, Klug 1983); Canada (*ensensis–ansatus* zones, Uyeno *in* Norris & Uyeno 1998, Gouwy *et al*. 2019); Germany (*hemiansatus* Zone, Weddige 1977; uppermost *ensensis*–lower *hermanni* zones, Clausen *et al*. 1979); Belgium (uppermost *ensensis–hemiansatus* zones, Bultynck & Hollevoet 1999); Spain (*rhenanus*/*varcus* Zone, Liao & Valenzuela-Ríos 2008); New South Wales (*varcus* Zone,

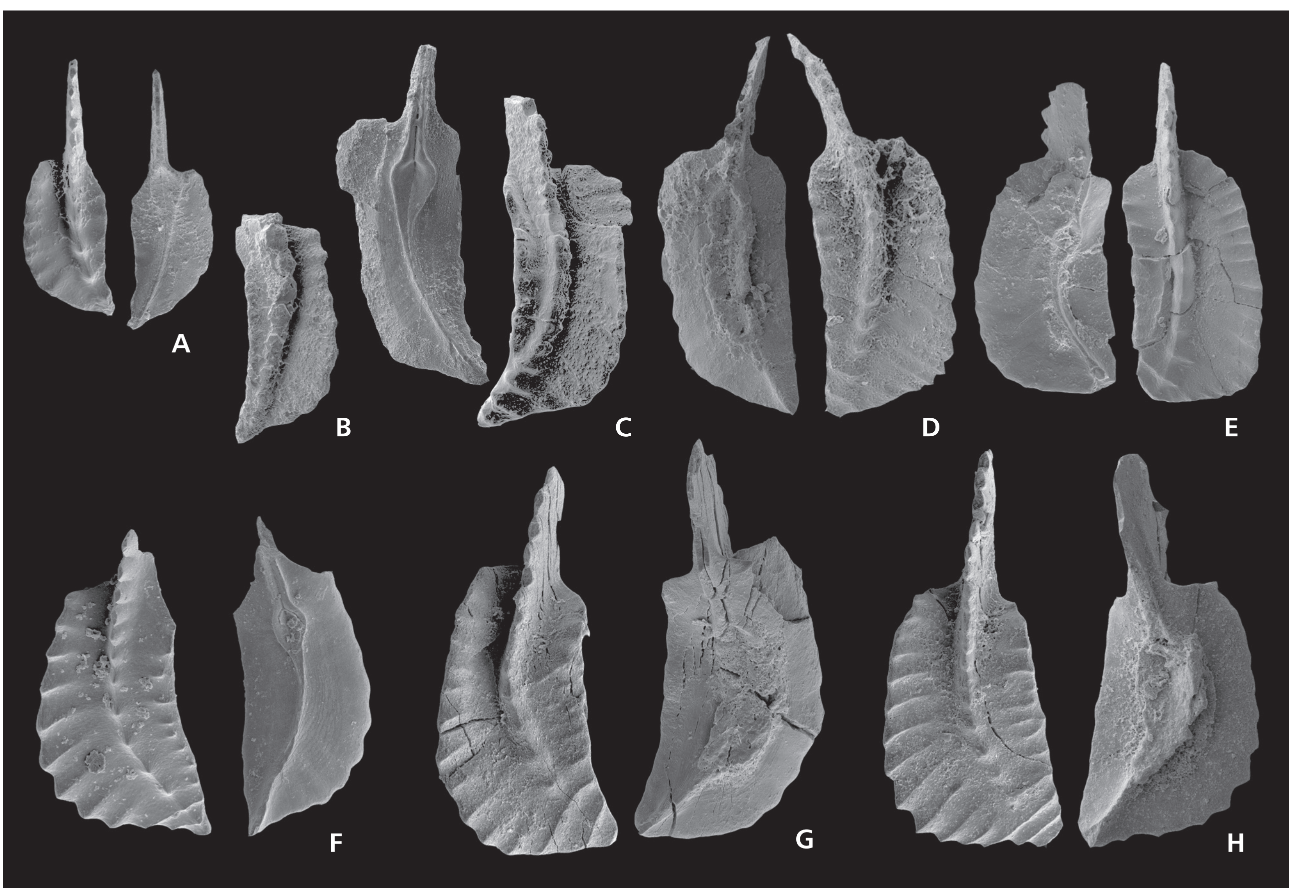


Figure 16. A–C – *Polygnathus* sp. aff. *P. zieglerianus* Weddige; A – upper and lower view of SV94, sample 285, uppermost *kockelianus* Zone (juvenile); B – upper view of SV95, sample 100, *kockelianus* Zone; C – SV97, sample 235–250, *kockelianus* Zone. • D, E – *Polygnathus* sp. aff. *P. alveolus* Weddige, sample UDI 3, *ensensis* Zone; D – lower and upper view of SV97; E – lower and upper view of SV98. • F–H – *Polygnathus* sp. B; F – upper and lower view of SV99, sample UDI 4, *ensensis* Zone; G – upper and lower view of SV100, sample UDI 3, *ensensis* Zone; H – upper and lower view of SV101, sample UDI 2, *ensensis* Zone. Magnification of all specimens ×70.

Pedder *et al*. 1970); Morocco (*kockelianus–semialternans/latifossatus* zones, Bultynck & Hollard 1980, Walliser & Bultynck 2011); Australia (*ensensis–semialternans/latifossatus* zones, Mawson & Talent 1989); Tajikistan (*ensensis–semialternans/latifossatus* zones, Bardashev 1992). The species was previously recorded by Kalvoda *in* Hladil & Kalvoda (1993b) in Jirásek quarry (not figured, treated as *Polygnathus* ex gr. *klapperi*).Within this study the species was recorded in the *kockelianus* and *ensensis* zones in the Jirásek quarry.

***Polygnathus* sp. aff. *P. zieglerianus* Weddige, 1977**
Figure 16A–C

Material. – 4 specimens.

Description. – The inner platform that terminates well before the platform posterior end resembles that of *P. zieglerianus*, however, the inner platform of the Barrandian specimens seems to be more poorly developed and narrower than that of *P. zieglerianus*. The latter species was described from the *partitus–costatus* zones and the occurrence of the Barrandian specimens is limited to the *kockelianus* Zone so it is possible that they represent a later morphotype of *P. zieglerianus*. The specimens figured herein in Fig. 16 represent different ontogenetic stages, with Fig. 16A representing a juvenile and Fig. 16C the more mature, although not fully adult growth stage, judging from the position and size of the basal pit.

***Polygnathus* sp. aff. *P. alveolus* Weddige, 1977**
Figure 16D, E

Material. – 4 specimens.

Description. – Only 4 specimens were recovered that resemble *P. alveolus* especially in the shape of the inner platform margin, which is straight and in the development of the carina, which is diagonal. The carina either continues to the posterior end of the platform disrupted by 1–2 transverse ridges, or there are 2 ridges, forming thus very indistinct tongue. The outer margin is nearly twice as wide as the inner margin. These specimens do not seem to have adcarinal troughs as deep as in *P. alveolus* and also the posterior outer margin is not rectangular in Barrandian specimens. The species occurs in the *ensensis* Zone in the Jirásek I section (sample UDI 3).

***Polygnathus* sp. B**
Figure 16F–H

Material. – 6 specimens.

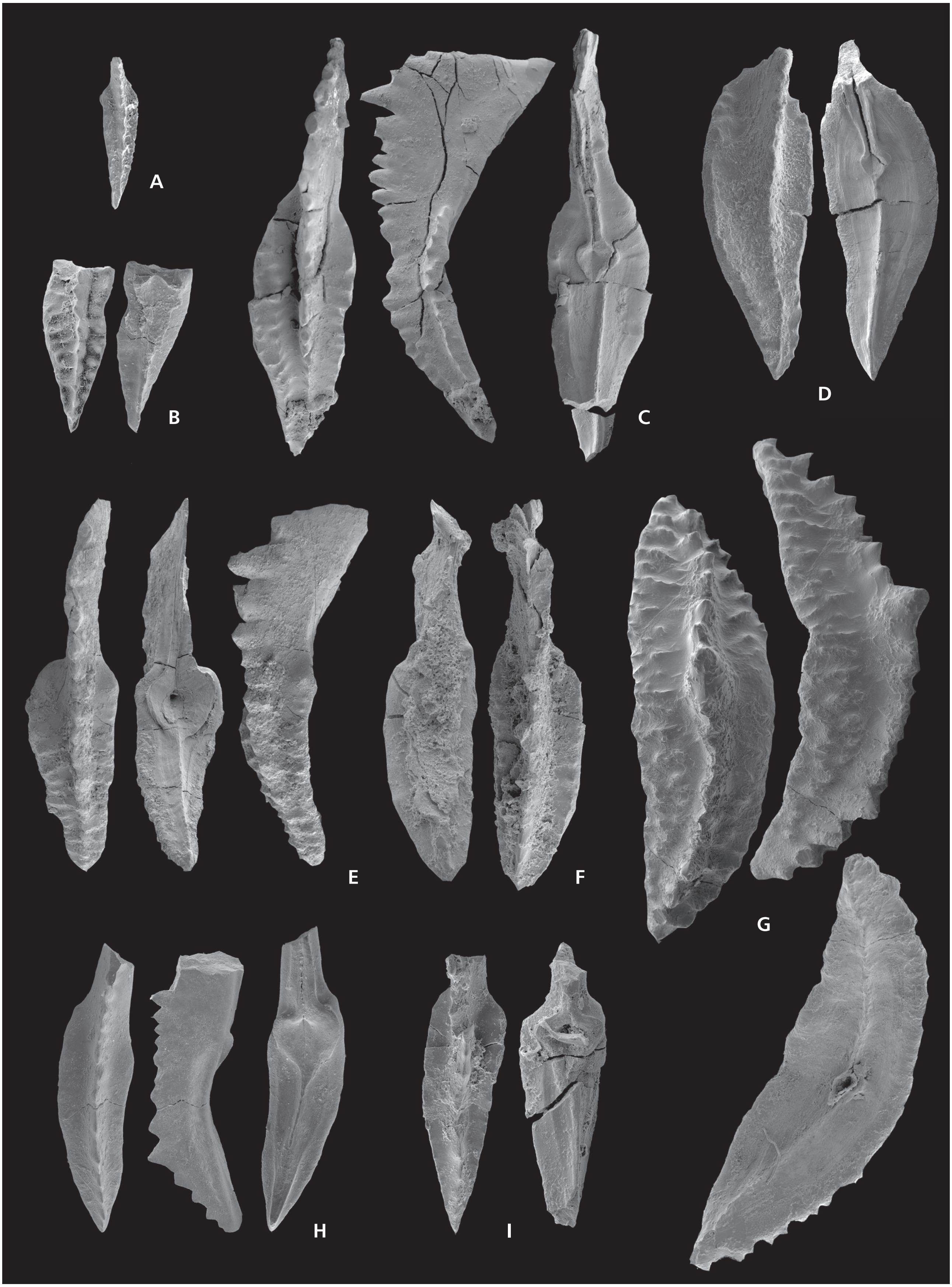
Description. – Representative specimens of this species have an indistinctly developed tongue, formed by two short, either complete or interrupted transverse ridges. The anterior two-thirds of the outer platform margin meets the posterior third in a curve, the posterior third is more or less perpendicular to the axis of the element. The adcarinal troughs are deep only in the platform anterior. The outer platform margin is strongly convex and widest in its posterior two-third. The flange-like outer margin is not developed. The inner platform margin more or less copies the course of the curved carina. Both inner and outer platforms are ornamented with distinct transverse ridges (11–14 ridges in the recovered specimens) that terminate shortly before the carina. The free blade is short and forms less than a third of the total platform length. The species occurs in the *ensensis* Zone in Jirásek I section.

***Polygnathus* sp. C**
Figure 17A–D

Material. – 4 specimens.

Description. – The figured specimens represent an ontogenetic series. The denticles of the free blade and carina are strikingly tall and conspicuous. The platform is ornamented by short, irregular transverse ridges that are, in specimens representing the adult growth stage, separated from the carina by rather wide adcarinal troughs, that shallow close to the platform posterior. Both platform margins taper to the posterior end, so the platform is rather pointed. The unit is strongly arched. The basal pit is rather large with thick rims, roughly heart-shaped, situated approximately between platform anterior and midlength. The species was recorded in the *kockelianus* and *ensensis* zones in the Jirásek I section and in the sample JI/99 provided by M. Mergl (Mergl 2019, fig. 2, *ensensis* Zone).

Figure 17. A–D – ontogenetic series of *Polygnathus* sp. C; A – upper view of SV102, sample UDI 11, *ensensis* Zone; B – upper and lower view of SV103, sample 385, *ensensis* Zone; C – upper, lateral and lower view of SV104, sample JI/99 of Mergl (2019, fig. 2), *ensensis* Zone, Jirásek section II; D – upper and lower view of SV105, sample Ji 6, *kockelianus* Zone. • E–F – *Polygnathus* sp. D; E – upper, lower and oblique lateral view of SV106, sample JI/100 of Mergl (2019, fig. 2), *ensensis* Zone, Jirásek section II; F – lower and upper view of SV107, sample UDI 6, *ensensis* Zone. • G – *Polygnathus* sp. E, upper, oblique lateral and lower view (lower right corner) of SV108, sample 0 m, *australis* Zone, Jirásek section II. • H, I – *Polygnathus* sp. F; H – upper, lateral and lower view of SV109, sample UDI 3, *ensensis* Zone; I – upper and lower view of SV110, sample UDI 10, *ensensis* Zone. Magnification of all specimens ×50.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***Polygnathus* sp. D**
Figure 17E, F

Description. – The specimens are similar to *Polygnathus* sp. C in high and conspicuously developed free blade and carina denticles and in platform shape, but differ in lacking anterior grooves and especially in the development of platform lower side, which possess a largely opened, conical basal cavity completely inverted already before platform midlenth. The carina is straight. One specimen was recovered from the sample UDI 6 in Jirásek I section (*ensensis* Zone), one specimen was provided by M. Mergl from his sample Ji/100 (Mergl 2019, fig. 2).

? *Polygnathus* sp. E
Figure 17G

Description. – A single specimen from the base of the Acanthopyge Limestone from the Jirásek quarry II (*australis* Zone). A massive, strongly ornamented platform bearing irregular transverse ridges and nodes. It resembles *Tortodus caelatus* from which it differs by the presence of a relatively small basal pit situated in platform midlength.

***Polygnathus* sp. F**
Figure 17H, I

Description. – The specimens resemble *Polygnathus* sp. C and *Polygnathus* sp. D in having a carina with very high denticles but these are even higher and also more pointed than those of the mentioned species. The narrow platform is smooth and rather bulging. Large, heart-shape basal pit with thick rims is developed close to platform anterior. Only two specimens were recovered from UDI from Jirásek quarry, neither of which had a free blade preserved. The specimens referred here as to *Polygnathus* sp. C, *Polygnathus* sp. D and *Polygnathus* sp. F are similar to *Polygnathus angustipennatus* Bischoff & Ziegler in the high and conspicuously developed free blade and carina denticles that rise well above the platform but differ in having platform margins reaching the posterior end and lacking U-shape adcarinal troughs.

Genus *Tortodus* Weddige, 1977

Type species. – *Tortodus kockelianus* (Bischoff & Ziegler).

Description. – Representative specimens assigned to the genus *Tortodus* occur only rarely in the Jirásek quarry. The most common species is *Tortodus australis*, which was recovered only at the base of the Jirásek quarry section II (8 complete and several broken specimens, Fig. 18G, H.). Only 2 representatives of *Tortodus kockelianus* (Fig. 18I) were recovered from Jirásek quarry section I. Other specimens of *Tortodus*, herein assigned to *Tortodus* sp. aff. *T. weddigei*, ? *Tortodus* sp. aff. *Tortodus caelatus* (Bryant, 1921)*, Tortodus* sp. A and *Tortodus* sp. B, are almost all fragmentarily preserved, which together with their rare occurrence (single specimens in the two latter taxa) hampers species identifications. More robust and better preserved collections of future work (ongoing research of K. Narkiewicz) might resolve the species affiliation of these specimens.

***Tortodus* sp. A**
Figure 18A

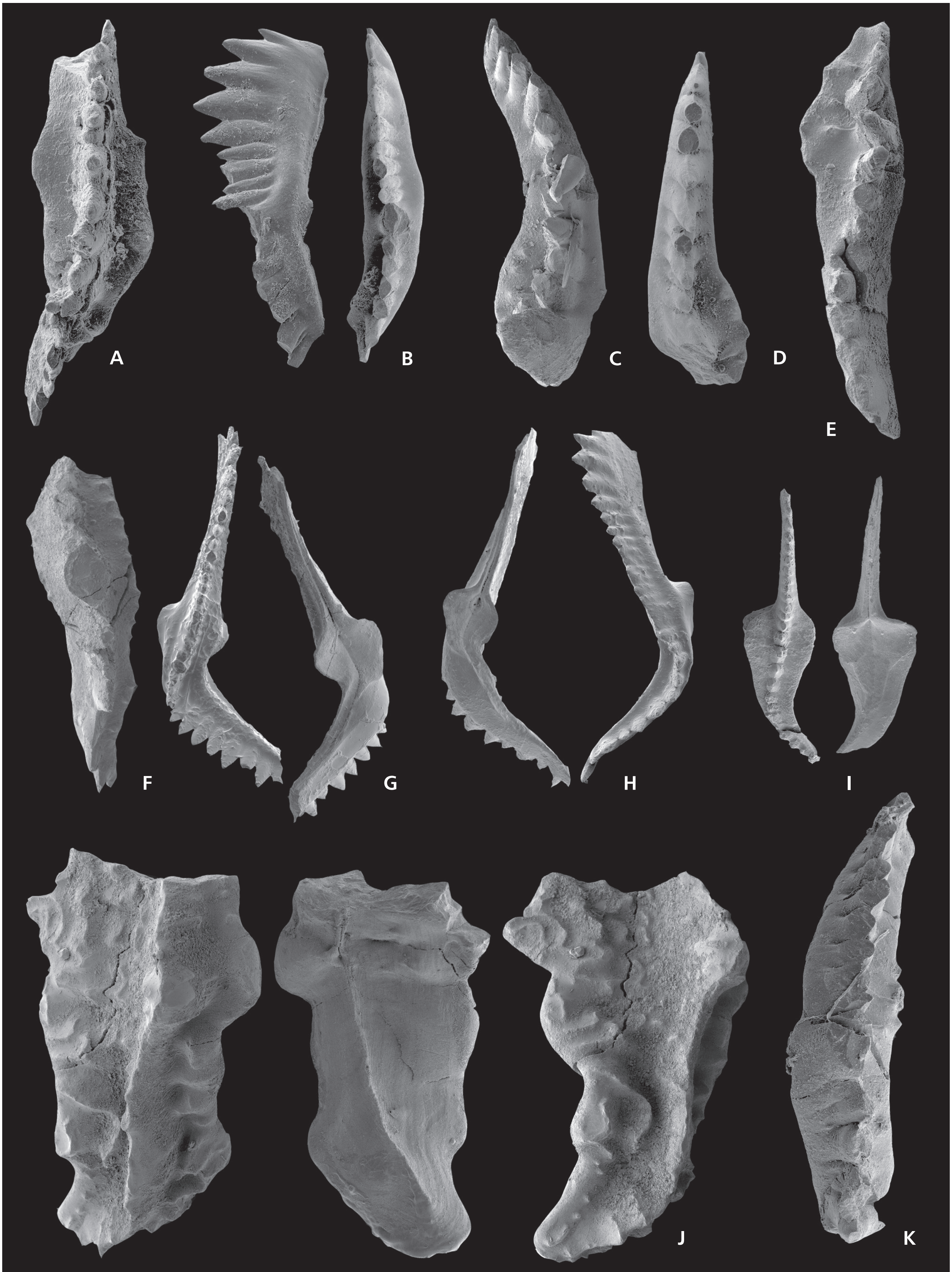
Description. – A single, partially preserved specimen from the upper part of the Acanthopyge Limestone from the Jirásek quarry I (probably *kockelianus* Zone) possesses a flat, smooth platform, with somewhat irregular margins.

***Tortodus* sp. aff. *Tortodus weddigei* Aboussalam, 2003**
Figure 18B–E, K

Material. – 10 specimens.

Description. – The specimens show some similarity with *Tortodus weddigei* Aboussalam, 2003 in respect to platform development, which is broadest around midlength, tapers to both platform ends and is ornamented with a few subtle nodes. Posterior blade denticles of *T. weddigei* are supposed to be isolated, in number of 3–4. As Barrandian specimens are partially preserved this could not be assessed, nevertheless the denticles in specimen B, which represents the most complete preservation, are more numerous and partly fused. The platform of specimens B and K seems to be smooth so they resemble *Tortodus* aff. *weddigei* sensu Aboussalam (2003). It is important to stress that the species *Tortodus weddigei* was described based on a single specimen, so the range of variability is unknown. It is well plausible that both smooth and ornamented platforms fall within the range of variability of one species. The

Figure 18. A – *Tortodus* sp. A, upper view of SV111, sample 100, *kockelianus* Zone. • B–E, K – *Tortodus* sp. aff. *T. weddigei* Aboussalam; B – lateral and upper view of SV112, sample UDI 5, *ensensis* Zone; C – upper view of SV113, sample 100, *kockelianus* Zone; D, K – sample UDI 2, *ensensis* Zone, D – upper view of SV114, K – upper view of SV121; E – upper view of SV115, sample UDI 6, *ensensis* Zone. • F – *Tortodus* sp. B, upper view of SV116, sample 0 m, *australis* Zone, Jirásek section II. • G, H – *Tortodus australis* Jackson *in* Pedder *et al*., sample 0 m, *australis* Zone, Jirásek section II; G – upper and lower view of SV117; H – lower and upper view of SV118. • I – *Tortodus kockelianus* Bischoff & Ziegler, upper and lower view of SV119, sample 280, *kockelianus* Zone. • J – ? *Tortodus* sp. aff. *T. caelatus* (Bryant), upper, lower and oblique lateral view of SV120, sample 80–90, *kockelianus* Zone. Magnification of all specimens ×50.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specimens are also similar to *Tortodus bultyncki* Aboussalam, 2003 but as far as can be judged from their fragmentary preservation, their blades do not appear to be as twisted as are the representatives of *T. bultyncki*. There is also similarity between the Barrandian specimens and *Tortodus* sp. B alpha and gamma morphotypes of Sparling (1999, pl. 5, figs 10–12, pl. 6, figs 5, 6) from the *ansatus* Zone in Ohio. The specimens with both the smooth and ornamented platforms come from the upper part of Acanthopyge Limestone in the Jirásek quarry (probably *kockelianus* Zone) and UDI (*ensensis* Zone). *T. weddigei* and *T.* aff. *weddigei* sensu Aboussalam (2003) were described from Morocco from the *ansatus* Zone and *semialternans* Zone respectively. *Tortodus bultyncki* was described from Morocco from the *ansatus–disparilis* zones (Aboussalam 2003).

***Tortodus* sp. B**
Figure 18F

Description. – A single, partially preserved specimen from the base of the Jirásek II section (*australis* Zone) with outer platform that seems to be more developed than the inner platform and that is ornamented by nodes aligned along the platform margin. The platform ornamentation – nodes aligned along the platform margin, resemble that of *Tordodus schultzei* Aboussalam, 2003 but the platform of the latter is better developed and ornamentated on both the inner and outer platform margins. Nevertheless, the species *T. schultzei* was described based on a single specimen.

? *Tortodus* sp. aff. *Tortodus caelatus* (Bryant, 1921)
Figure 18J

Description. – Only two specimens were recovered from the base of Jirásek section II (*australis* Zone) and 80–90 cm above the base of Jirásek section I (probably *kockelianus* Zone). Large and robust platforms are ornamented by irregular, wavy ridges and aligned nodes. Both specimens resemble *T. caelatus* (*Polygnathus beckmanni* of Bischoff & Ziegler 1957) in respect to the robust platform and massive, irregular ornamentation. However, unlike *T. caelatus*, the Barrandian specimens possess a small basal pit, therefore the genus affiliation is questioned here. Discussion on taxonomy of *Tortodus caelatus* can be found in Huddle (1981), Klug (1983) and Aboussalam (2003).

Discussion

Transitional forms within the *P. pseudofoliatus* Group

Forms with overlapping morphologies, transitional between *P. eiflius*, *P. pseudofoliatus*, *P. ensensis* and/or *P. amphora* have been figured by several authors from various stratigraphic levels. Forms integrating characteristics of *P. eiflius* (presence of rostral ridges), *P. amphora* (presence of long rostrum) and *P. pseudofoliatus* (less contrasting difference between the platform anterior and posterior width) were figured by Sparling (1995, pl. 2, figs 11–16) from the *timorensis* Zone in Ohio (for stratigraphic assignment see DeSantis *et al*. 2007), and by Walliser & Bultynck 2011 (pl. 1, fig. 6) from the upper *kockelianus* Zone in Morocco. Forms with platform outline typical for *P. pseudofoliatus* and rostral ridges typical for *P. eiflius* were figured by Bultynck (1970, pl. 14, fig. 4) from the Ardennes (probably basal *ensensis* Zone, see text-fig. 13 therein), Gouwy *et al*. 2013 (*eiflius–ansatus* zones, Spain), Lazreq (1990) from Morocco (*timorensis* Zone) and Benfrika *et al*. (2007) from Morocco (*hemiansatus* Zone). Forms with posteriorly expanded platform margins typical for *P. pseudofoliatus* but possessing serrated anterior margins and down-arched posterior platform diagnostic for *P. ensensis*, were described by Klapper *in* Johnson *et al*. (1980, pl. 4, fig. 4) from the *ensensis* Zone in Nevada and regarded, together with forms from the *ensensis* and *varcus* zones figured by Weddige (1977, pl. 4, figs 62, 63, 65), as transitional between *P. pseudofoliatus* and *P. ensensis*. Sparling (1995) recorded these forms from the *timorensis* Zone in Ohio (pl. 2, figs 17–19, upper *ensensis* Zone according to Sparling, *timorensis* Zone suggested by DeSantis *et al*. (2007) on the basis of presence of *P. xylus* and *Icriodus brevis*). Such transitional forms were further recorded from Canada by Uyeno *in* Norris & Uyeno (1998, pl. 11, fig. 20, *ensensis* Zone; pl. 14, figs 21, 22, Middle *varcus* Zone in the original publication), Uyeno *et al*. 2017 (pl. 1, fig. 4, *ensensis* Zone, Canada). Gouwy *et al*. (2019) recorded *P. pseudofoliatus* transitional to *P. amphora* (pl. 6, fig. j therein) and a *P. pseudofoliatus* transitional to *P. ensensis* (pl. 6, fig. k therein) in the *timorensis* Zone in Canada.

Variation within the *P. pseudofoliatus* Group and environmental changes at the level of Kačák Episode

From the above mentioned listing it is apparent that forms with overlapping morphologies commonly occur without spatial or stratigraphic restriction, from the upper *kockelianus* to *ansatus* zones. Most abundantly, these taxa are recorded from the *ensensis* to *timorensis* zones globally (Europe, US, Canada, North Africa). The appearance of new forms (*P. ensensis*, *P. amphora*, and *P. pseudoeiflius*) and the increased intraspecific variability within *P. pseudofoliatus*, *P. amphora*, *P. ensensis* and *P. eiflius* correlates with the global transgressive Kačák Episode. Walliser & Bultynck (2011) considered the

Kačák Episode mainly as an innovation period of the *Polygnathus pseudofoliatus* Group with the appearance of *P. amphora*, *P. ensensis* and later *P. hemiansatus*. It seems that environmental changes, such as the availability of new shallow marine habitats, could have promoted the increase of the morphologic variation within the *P. pseudofoliatus* Group due to non-existing intrinsic boundaries and unlimited gene flow, which blurred species boundaries. Similar significant morphological variations are observed for contemporaneous icriodontids, which show a reduced formation of lateral denticles (Suttner *et al*. 2017b). In addition, we recorded massive occurrences of parathuramminid foraminifers, peloids and calcispheres already 20 cm below the UDI. Similar features, *i.e.*, increased occurrence of microproblematica and peloids were reported in the Barrandian area within the upper *partitus*–basal *costatus* zones (Berkyová & Munnecke 2010, Vodrážková *et al*. 2013). In that case, the absence of such microbiota and micritization processes in the shallow-water Suchomasty Limestone (Emsian–Eifelian, *serotinus*–*partitus* zones) and their presence in the succeeding Acanthopyge Limestone (*costatus*–*kockelianus* zones) and its deeper water equivalent, the Choteč Limestone, lead the authors to conclude that massive accumulation of calcisperes and peloids is indicative for environmental changes, namely increased nutrient flux linked to sea-level fluctuations and increased atmospheric dust deposition, related to the Basal Choteč Event (Vodrážková *et al*. 2013, p. 442). In this respect it is important to stress that micritized grains and calcispheres are also known from the Acanthopyge Limestone from the underlying *costatus* Zone (Berkyová & Munnecke 2010, Vodrážková *et al*. 2013). However, here parathuramminid foraminifers were not recorded, except sparse occurrence of *Uralinella*, which was treated as radiosphaerid calcispere in Berkyová & Munnecke (2010), as pointed out by Vachard *et al*. (2018). It can either mean that parathuramminids were absent in the Barrandian area at that time (corresponding to the *costatus* Zone) or allochems preserved within UDI originate from different source area than allochems from the Acanthopyge Limestone. In any case, the very common occurrence of parathuramminids, which was recorded 20 cm below UDI and within the UDI, is suggestive of change(s) in certain paleoenvironmental parameter(s). Interestingly, Hladil *et al*. (2006) recorded significant anomalies in combined magnetic susceptibility and gamma-ray loggs above and at the event interval, which was interpreted as an increased flux of atmospheric dust at the level of the Kačák Episode. It therefore seems that enhanced nutrient delivery could have promoted the increased occurrence of microbiota recorded in both the Basal Choteč Event and Kačák Episode. In addition, the recorded increase in morphological variation within the *P. pseudofoliatus* Group in the *ensensis* Zone could also be a result of the shift in the ecosystem towards more nutrient-rich, if not eutrophic, environment. In the fossil record, an increased morphological variability within a population as a response to environmental change is a known feature (Hopkins 2011 and references therein), although this has not been thoroughly documented.

Species of *Polygnathus pseudofoliatus* Group as zonally diagnostic taxa

Among the requirements of the index fossil taxa are their limited stratigraphic occurrence, global distribution and easy identification. It is obvious that the last requirement will be the most difficult to be fulfilled in *P. pseudofoliatus* Group. Within this group, only the entry of *P. pseudofoliatus* represents a valuable marker as the species is easily distinguishable from *P. costatus*, which is also a reason why it was recently used by Becker *et al*. (2016) for a subdivision of the *costatus* Zone. *Polygnathus ensensis* has been suggested as a zonally defining taxon for the base of the *ensensis* Zone by Weddige (1977, p. 344), which was challenged by Narkiewicz *et al*. (2017), who pointed out the difficulties with species identification and suggested to use instead the stratigraphic range of *P. eiflius* for definition of the uppermost Eifelian zone. The latter species was proposed to define the base of the Upper *kockelianus* Subzone by Bultynck (1987) and later as a zonally diagnostic taxon for the base of the *eiflius* Zone by Belka *et al*. (1997). However, *P. eiflius* is not a common species and as stressed herein and also elsewhere, *P. eiflius* was treated rather ambiguously in the past (see under *P. eiflius*). *Polygnathus amphora* is a common species in the Prague Basin (81 specimens in Jirásek section I), and relatively common in Morocco (as far as can be judged from figs 3, 4 in Walliser & Bultynck 2011). The presence of a long, serrated rostrum with parallel margins, strongly developed transverse ridges in the rostral area and deep adcarinal grooves that abruptly shallow towards the posterior platform, proved herein to represent the most stable features and thus diagnostic for the species identification. This makes *P. amphora* a plausible candidate for upper Eifelian zonally diagnostic species, as in comparison to *P. ensensis* and *P. eiflius* the identification is easier. In addition, the various growth stages of *P. amphora* described here strongly contribute to species delimitation. However, as far as can be judged from the published occurrences (see synonymy list under *P. amphora*), this species does not seem to occur commonly. In addition, although the FAD of *P. amphora* was recorded in the *kockelianus* Zone in previous studies, we report its first occurrence from the upper *australis* Zone (single specimen from the sample 0 m Jirásek section II). However, this applies also to *P. eiflius*, FAD of which is commonly reported from the *kockelianus* Zone, but Weddige (1977) reported its occurrence from the upper *australis* Zone, which is in accordance with the present study (single occurrence in the sample 0 m Jirásek section II). The occurrence of both taxa in the *australis* zones complicates their usage as diagnostic for an upper Eifelian biozone above the *kockelianus* Zone. In the light this problem, a possibility to use stratigraphic ranges of *P. eiflius*, *P. ensensis* and *P. amphora* as an assemblage Zone seems reasonable. In any case, a taxonomic revision of large collections of members of the *P. pseudofoliatus* Group is highly needed in order to properly describe morphological variation, both intraspecific and ontogenetic by means of morphometric analysis and contribute thus to proper species delimitation, which is essential for a practical biostratigraphy.

Conclusions

Within the studied interval (*australis–ensensis* zones), a large variation, both morphologic and ontogenetic, was recorded within the *Polygnathus pseudofoliatus* Group. Deciphering between interspecific and intraspecific variation is difficult and in many cases impossible, as forms integrating characteristics regarded as diagnostic for different species, are fairly common. In addition, the transitional forms do not appear to have any stratigraphic and spatial significance, which applies also in the global context. One plausible attitude would be to view the representative specimens, which fulfill the combination of characteristics that are summarized in Fig. 19, as end-members of a broad spectrum of an intraspecific variation,

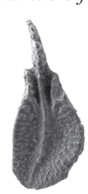
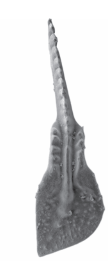
Polygnathus pseudofoliatus 	Asymmetric platform shape, short, constricted anterior margins, which widen gradually towards the posterior. Outer platform margin strongly convex, inner platform margin more or less straight or slightly convex. Platform ornamented by transverse ridges or by combination of transverse ridges and nodes especially in the platform posterior. Carina reaches the posterior platform tip mostly in the form of nodes. Adcarinal grooves deep in the anterior, gradually shallowing towards the posterior (but no tendency to form flat platform). Free blade forms usually less than a half of the total length.
Polygnathus eiflius 	Asymmetric platform shape, short and narrow rostrum, with significant difference between rostral and mid-platform width, deep adcarinal grooves that shallow abruptly, 1–2 rostral ridges, strongly expanded outer platform margin, inner platform margin forms convex curve. Anterior platform margins may be serrated. Platform posterior flat, ornamented with nodes. Posterior carina not continuous. Free blade approximately of the same length as the platform or less.
Polygnathus amphora 	Almost symmetric platform shape, narrow and long rostrum (mostly at least 1/3 of total platform length), with significant difference between rostral and mid-platform width, 1–2 rostral ridges can be present, rostrum ornamented with strong, transverse ridges, endings of which form distinct serrations of the anterior margins, which is approximately of the same height as the rest of the platform. Both posterior platform margins strongly expanded, posterior platform is flat, ornamented by nodes and/or short, irregular ridges. Posterior carina not continuous. Free blade forms usually less than half of the unit length.
Polygnathus ensensis 	High, distinctly serrated anterior platform margins, platform posterior down-arched. Outer platform margin may form a convex curve, inner platform margin tends to be more or less straight. Free blade approximately of the same length as the platform or longer.

Figure 19. Characteristic features of representatives of the *Polygnathus pseudofoliatus* Group.

which would be also supported by almost identical stratigraphic ranges. Such an attitude is not followed herein but it needs to be stressed that in large collections, which contain a sufficient number of specimens representing adult growth stages, quantitative morphometric analysis should be applied in order to test the species boundaries as are used herein. There is no doubt that accurate species delimitation is crucial, it is actually a cornerstone of palaeobiology and biostratigraphy. It is also clear that both morphological and ontogenetic intraspecific variability can only be understood, and therefore reasonable taxonomy can only be performed, in large collections of individuals with accurate stratigraphic assignment. And yet, descriptions of new species based on only a few specimens (or even a single specimen); inadequate and brief descriptions of observed variation and/or poor photo-documentation are commonly encountered in conodont literature.

The main conclusions can be summarized as follows:

1) Eifelian conodonts (*australis–ensensis* zones) from the Acanthopyge Limestone (Choteč Formation) from the Jirásek quarry near Koněprusy were studied. Jirásek quarry represents a unique section, where the stratigraphic equivalent of the black shales of the Kačák Member (Srbsko Formation) is developed in a carbonate succession (UDI).

2) Due to large morphological variability and occurrence of transitional forms within the *P. pseudofoliatus* Group, the particular species cannot be regarded as best candidates for zonally diagnostic taxa. As both *P. eiflius* and *P. amphora* were recorded already in the *australis* Zone, the usage of stratigraphical ranges of *P. eiflius*, *P. amphora* and *P. ensensis* as an assemblage Zone seems reasonable.

3) The following species were recorded in the Barrandian area for the first time: *P. amphora*, *P. benderi*, *P. abbessensis* and *P. bagialensis*.

4) Ontogenetic series for *P. amphora* and *P. linguiformis* were reconstructed, which adds to species boundaries delimitations.

5) In the proximity of the *ensensis* Zone, high accumulations of calcispheres and especially parathuramminid foraminifers were recorded and interpreted as a result of higher nutrification due to sea-level rise and/or increased aeolian input related to the Kačák Episode.

6) The increased morphological variation within the *pseudofoliathus* Group is interpreted as being causally linked with the contemporary environmental changes recorded, *i.e.*, availability of new shallow marine habitats and/or increased nutrification.

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