

Ontogenetic and intraspecific variation in the late Emsian – Eifelian (Devonian) conodonts *Polygnathus serotinus* and *P. bultyncki* in the Prague Basin (Czech Republic) and Nevada (western U.S.)

GILBERT KLAPPER¹ AND STANISLAVA VODRÁŽKOVÁ²

¹Gilbert Klapper, Department of Earth and Planetary Sciences, Northwestern University, Evanston, IL 60208, USA. E-mail: g-klapper@northwestern.edu

²Stanislava Vodrážková, GeoZentrum Nordbayern, Fachgruppe Paläoumwelt, Friedrich-Alexander-Universität Erlangen-Nürnberg, Loewenichstr. 28, Erlangen, Germany and Czech Geological Survey, P.O.B. 85, 118 21 Prague 1, Czech Republic. E-mail: stana.vodrazkova@seznam.cz

ABSTRACT:

Klapper, G. and Vodrážková, S. 2013. Ontogenetic and intraspecific variation in the late Emsian – Eifelian (Devonian) conodonts *Polygnathus serotinus* and *P. bultyncki* in the Prague Basin (Czech Republic) and Nevada (western U.S.). *Acta Geologica Polonica*, **63** (2), 153–174, Warszawa.

Samples from populations of *Polygnathus serotinus* Telford 1975 and *P. bultyncki* Weddige 1977 from the Prague Basin and Nevada display normal variation for Devonian conodont species. A considerable number of previous authors, however, have proposed unnecessary synonyms of these two species, primarily because they have not recognized ontogenetic variation. In contrast, we interpret the variation as ontogenetic as well as intraspecific and present detailed synonymies as a result. A third species, *P. praetrigonicus* Bardashev 1992, which has been carried in open nomenclature for many years, is an important indicator of the basal *costatus* Zone in the Prague Basin, New York, and Nevada. We review the stratigraphic distribution of these three species and the conodont zonation across the Emsian-Eifelian (Lower-Middle Devonian) boundary. *Polygnathus pseudocostatus* sp. nov. (*partitus-costatus* zones, central Nevada) is described herein. We have observed a decrease in the pit size during ontogeny in *P. bultyncki* although we have not measured enough specimens to rule out intraspecific versus ontogenetic variation.

Key Words: Devonian; Emsian-Eifelian conodont zonation; Ontogenetic and intraspecific variation; Taxonomic revision.

INTRODUCTION

In what must be regarded as a seminal paper, Hass (1941) described the accretionary mode of growth of the lamellar microstructure of conodonts and concluded that “species of conodonts are quite variable entities, the individual changing greatly in ontogenetic development.”

The significance of ontogenetic variation for conodont taxonomy has been sporadically supported (e.g., Müller 1956; Scott and Collinson 1959, who, however, focused their paper mainly on intraspecific variation; and Dzik 2006). It is fair to say, nevertheless, that ontogenetic series of conodont species have only infrequently been presented (some examples are in papers by Müller and

Clark 1967; Sandberg and Ziegler 1973; Dzik 2002, 2006; Miller 2007). The reason for this may be that a microfossil collection is not always encountered from which an ontogenetic series can be reconstructed based on specimens that each represent a single growth stage. It is thus not surprising that supposedly new conodont species have been proposed by authors who have not taken ontogenetic variation into consideration.

On the subject of ontogeny in an overview of palaeontological taxonomy, Forey *et al.* (2004, p. 645) wrote: "Palaeontologists, in general, are hampered by the lack of knowledge of ontogenetic variation. Growth stages of individual taxa have received separate names, which may spuriously increase apparent diversity." . . . "but the problem is far more acute in the fossil record and can only be solved by fortuitous finds." However, study of micropalaeontological collections that yield either a single species of one genus or just two species of distinctly different morphology may potentially allow more frequent reconstruction of ontogenetic series than is generally possible with macrofossils. That is, we are referring to those macrofossils in which single specimens do not preserve the record of ontogeny, as opposed, for example, to single specimens of ammonoids which may do so.

In his general paper on conodont taxonomy, Müller (1956, p. 1331) discussed intraspecific variation within a population in addition to ontogenetic variation. As a result of the recognition of these two types of variation, he advocated acceptance of a broad concept for species. One of the best examples of intraspecific variation within the platform (Pa) element of a conodont species is the study of Koike (1992) on the Early Triassic *Spathoicriodus collinsoni* (Solien, 1979, p. 302–303). The amount of intraspecific variation within this species as illustrated by Koike (1992, text-figs 9, 12, 13) is highly instructive. Unfortunately in our opinion, this example and the implications derived from it have not influenced much current taxonomic practice.

In this paper we focus on two Lower-Middle Devonian (late Emsian-Eifelian) species, *Polygnathus serotinus* Telford 1975, and *Polygnathus bultyncki* Weddige 1977. The high abundances of each species in restricted stratigraphic intervals and in the same samples allowed us to recognize the different morphological forms, corresponding to different ontogenetic stages. As our synonymy lists indicate, nine different names have been applied to *P. serotinus* and six to *P. bultyncki*. These names refer either to early ontogenetic stages or to intraspecific variants of mature stages of the two species. The importance of recognizing both kinds of variation not only for a reasonable taxonomy but also for diversity studies is clearly apparent.

Polygnathus serotinus was named by Telford (1975, as a subspecies of *P. foveolatus* Philip and Jackson 1967) based on specimens from the Broken River Embayment in north Queensland, Australia. Telford (1975, p. 43–44, pl. 7, figs 1–8) illustrated an ontogenetic series of specimens, the largest of which was the holotype. A few months later, Snigireva (1975; her paper was presumably in press when Telford's paper was published in July) proposed two new species, *Polygnathus foliformis* and *P. totensis*. Both Weddige (1977) and Klapper (1977) independently recognized that the illustrated specimens of *P. totensis* (Snigireva 1975, pl. 4, figs 3, 4) represent a slightly earlier ontogenetic stage of *P. serotinus* and raised that taxon to specific status. This opinion was followed by several later authors who also treated *P. totensis* as a junior synonym (see Remarks under *P. serotinus*). Weddige (1977, p. 319) further questioned whether *P. foliformis* might be an additional junior synonym. Several later authors (see Synonymy under *P. serotinus*) have recognized *P. foliformis* as a valid species, but this cannot be supported in the light of ontogenetic evidence. As a result of the research presented herein, we conclude that the types of *P. foliformis* (Snigireva 1975, pl. 4, figs 1, 2) represent an early ontogenetic stage of *P. serotinus* and that those of *P. totensis* represent a later ontogenetic stage approaching maturity.

Bardashev *et al.* (2002) recognized six separate species that are here considered as intraspecific variants of *Polygnathus serotinus* (five of which were newly proposed in their paper in addition to *P. declinatus* Wang 1979); all were based on mature Pa elements reillustrated from previous literature without illustrating any new material of their own. They further recognized *P. foliformis* and *P. totensis* as valid species, but these are ontogenetic variants of *P. serotinus* as concluded above. These nine named species are allocated to three genera in the taxonomy proposed by Bardashev *et al.* (2002).

In another instance, these same authors recognized four separate species allocated to two genera, which again are either intraspecific or ontogenetic variants of the equally well known Emsian-Eifelian species *Polygnathus bultyncki* Weddige 1977. Details are given under these two species in the Systematic Palaeontology section.

Bardashev *et al.* (2002) have not recognized intraspecific and ontogenetic variation in their taxonomy. The artificiality of their splitting of the genus *Polygnathus* into seven genera is in question, at least insofar as several of the genera share intraspecific variants of the same species. Substantial criticism of the Bardashev *et al.* (2002) paper on these and other grounds has been detailed by Mawson and Talent (2003, p. 344–346), Murphy (2005, p. 191–193), and Slavík *et al.* (2007, p. 500).

In this paper in addition to the two main cited species, we also describe and discuss *Polygnathus pseudocostatus* sp. nov. and *P. praetrigonicus* Bardashev 1992 (both Middle Devonian, Eifelian) and their biostratigraphic significance.

ONTOGENY OF PIT IN *POLYGNATHUS BULTYNCKI*

Juvenile specimens of *Polygnathus bultyncki* are characterized by a relatively large basal pit (Text-fig. 1A, B), whereas adult specimens (Text-fig. 1E) possess a much smaller pit, apparently indicating a decrease in pit size during ontogeny. This is also supported by measurements of 23 specimens in our material representing various growth stages, showing enlargement of the pit in early growth stages and a subsequent decrease in later stages. However, the number of specimens measured is not large enough in our opinion to rule out intraspecific variability as a cause of the apparent decrease in pit size. A larger number of specimens should be measured to test: (1) whether the pit stopped enlarging at a certain point in the early growth stages and subsequently decreased in size in later stages, during which the platform continued to increase in size, or (2) whether the pit ceased to enlarge at a certain point and remained unchanged in size while the platform continued to enlarge in later stages, as suggested by Clark and Müller (1968, p. 564). As a full biometric study is beyond the scope of the present paper, we leave this question open. It should be noted however, that confirmation of the first hypothesis would have implications for the mode of formation of the “inverted cavity” (Lindström 1964; Lindström and Ziegler 1971), termed a “zone of recessive basal margin” (Sweet 1981, p. W9; Sweet 1988, text-figs 2.1, 2.5), or an “everted” basal cavity (von Bitter *et al.* 1986, p. 35; also p. 6–7).

BIOSTRATIGRAPHY

Upper Emsian–Lower Eifelian conodont zonation

The conodont zonation across the Lower (Emsian)–Middle Devonian (Eifelian) boundary was established in a series of papers in the 1970s. The *serotinus*, *patulus*, and *costatus* zones were proposed formally by Weddige (1977) based primarily on the sequence in the Eifel Mountains, Germany, but with reference to successions elsewhere (e.g., the Ardennes, Bultynck 1970; New York, Klapper 1971; among others, see Weddige 1977, table 3). Note that once the

costatus Zone was dropped as a name for an upper Famennian standard conodont zone (Ziegler and Sandberg 1984), the Eifelian zone came to be termed simply the *costatus* Zone (Johnson *et al.* 1986, p. 179). Weddige (1977, table 2) recognized lower and upper informal subdivisions of the *patulus* Zone and Klapper *et al.* (1978, text-fig. 3) strengthened this with the finding of the first occurrence of their new subspecies, *P. costatus partitus*, at the base of the upper *patulus* Zone in the Prague Basin [*P. patulus*, *P. partitus*, and *P. costatus* were established as separate species by Vodrážková *et al.* (2011)]. Weddige *et al.* (1979) proposed the *partitus* Zone for the informal upper *patulus* Zone and the *patulus* Zone thus became restricted to the equivalent of the informal lower *patulus* Zone. This usage is still followed.

The first occurrence of *P. partitus*, and consequently the base of the *partitus* Zone, were accepted as the defining level for the Lower (Emsian) – Middle Devonian (Eifelian) boundary by the International Commission on Stratigraphy in 1982 (Cowie *et al.* 1989, p. 81). The boundary stratotype was selected at the Weteldorf Richtschnitt, Prüm Syncline, Eifel Mountains (Ziegler and Klapper 1982, p. 9; Weddige 1982) and the Prastav Quarry, Holyně in the Prague Basin was designated as the parastratotype section (Chlupáč 1982, p. 89; Berkyová 2009, p. 668, text-fig. 2).

Polygnathus serotinus and *P. bultyncki* have first occurrences in the *serotinus* Zone, the former as the defining species for the lower boundary of the zone, but both range as high as the *costatus* Zone (e.g., Johnson *et al.* 1996, table 2; Berkyová 2009, text-fig. 2B). Similarly *P. patulus* and *P. partitus*, each defining species for the lower boundary of their respective zones, both range as high as the *costatus* Zone. Thus as opposed to spot samples having one or more of these four named species, it is necessary instead to have a detailed sequence of closely spaced samples through several zones for confident zonal identification.

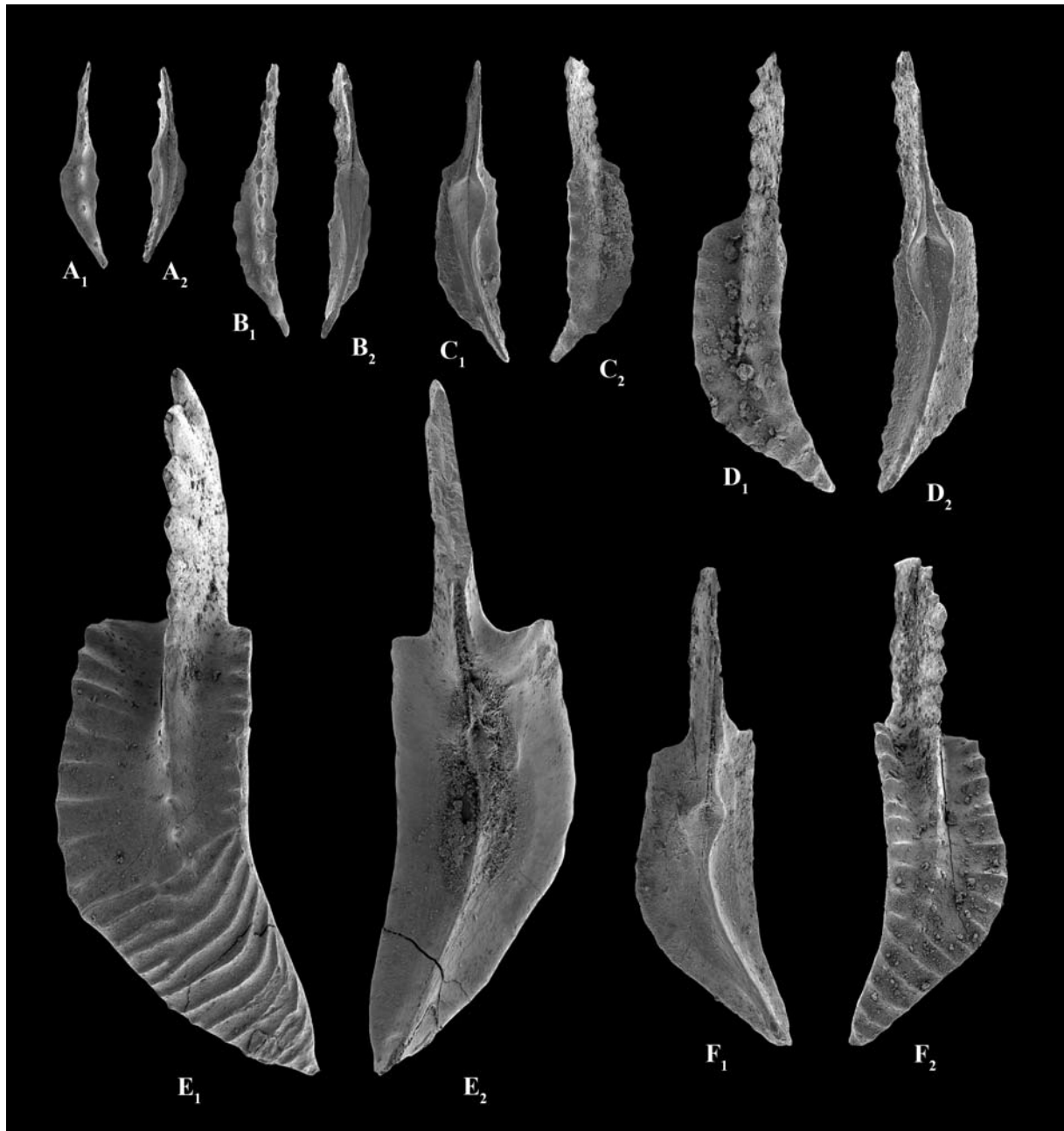
Stratigraphic distribution of *Polygnathus serotinus* and *P. praetrigonicus*

Polygnathus serotinus represents the most common species of the *serotinus*, *patulus*, and *partitus* zones in the Prague Basin (Daleje-Třebotov Formation). Klapper *et al.* (1978, text-fig. 1) recorded the highest occurrence of *P. serotinus* in the basal *costatus* Zone (Choteč Limestone at Chýnice) and Berkyová (2009, text-fig. 2B) showed the highest occurrence at the same zonal level but near the top of the Třebotov Limestone at the Barrandov road cut. There is a flood occurrence of juvenile specimens of *P. serotinus* associated with *P.*

praetrigonicus at 0.10 m above the base of the *Acanthopyge* Limestone at the Red Quarry (Červený Lom) near Suchomasty (collected by GK with Ivo Chlupáč in 1974 and identified by GK and SV in 2008). At other sections in the Prague Basin, the highest occurrence of this species is in the *partitus* Zone (e.g., Prastav Quarry,

Klapper *et al.* 1978, text-fig. 1; Berkyová 2009, text-fig. 2A) in the upper part of the Třebotov Limestone.

In the Eifel Mountains (Weddige 1977, tables 2, 5; Weddige 1982, text-fig. 3a) *Polygnathus serotinus* ranges to the top of the *patulus* Zone at the Wetteldorf Richtschnitt, but into the lower *costatus* Zone at adjacent



Text-fig. 1. Ontogenetic series of *Polygnathus bulynecki* Weddige; all specimens are Pa elements from the Prague Basin. **A₁, A₂** – upper and lower views of SB 27, 1550 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone. **B₁, B₂** – upper and lower views of SB 28, 460 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, lowermost *partitus* Zone. **C₁, C₂** – lower and upper views of SB 29, 960 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone. **D₁, D₂** – upper and lower views of SB 30, 450 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone. **E₁, E₂** – upper and lower views of SB 31, 960 cm below the base of the Choteč Limestone, Barrandov road cut at Prague, *serotinus* Zone. **F₁, F₂** – lower and upper views of SB 32, 960 cm below the base of the Choteč Limestone, Barrandov road cut at Prague, *serotinus* Zone. All magnifications are $\times 46$

sections (Weddige 1982, text-fig. 3b). In the Anti-Atlas Mountains of southern Morocco, the species occurs in the *serotinus* and *patulus* zones, but apparently not higher (Bultynck 1986, text-figs 5, 6, 8, 11, 12). However, in the Anti-Atlas regional composite developed through graphic correlation, *P. serotinus* ranges from the *serotinus* Zone into the lower part of the *partitus* Zone (Belka *et al.* 1997, text-fig. 3).

The highest occurrence of *Polygnathus serotinus* in the northern Antelope Range, central Nevada, is in the basal *costatus* Zone (Johnson *et al.* 1996, section V, table 2, seven samples in the lower 2.6 m of the zone). This is closely comparable to the highest occurrence noted above for the Prague Basin. But the species ranges higher in the *costatus* Zone in the Roberts Mountains of central Nevada (Vodrážková *et al.* 2011, p. 741, text-fig. 3, appendix 3). Note that in section V of the northern Antelope Range the *patulus* Zone is missing, whereas in the Roberts Mountains both the *patulus* and the *partitus* zones are missing (Vodrážková *et al.* 2011, p. 739–741).

Pyle *et al.* (2003, p. 103–104, text-fig. 5) reported occurrences of *Polygnathus serotinus* relatively high within the *costatus* Zone in the Deserters Formation in British Columbia. The anomalous occurrences of *P. linguiformis linguiformis* recorded from the *serotinus* and *costatus* zones in the Deserters Formation are perhaps explained by the fact that the one illustrated specimen is identified herein as *P. bultyncki* (see systematic description and synonymy for that species). The reported occurrences of *P. serotinus* in the lower part of the *australis* Zone in Central Asia (Bardashev 1990, p. 34; 1992, p. 46, 47) also seem anomalous. It is possible that these high occurrences represent *P. dobrogensis* Mirăuță (1971), a species discussed by Weddige (1977, p. 319–320, text-fig. 4) under *P. serotinus*.

Polygnathus serotinus is not present in the Schoharie-Onondaga succession of New York, where the Schoharie-Bois Blanc and the Edgecliff Member, the lowest member of the Onondaga Limestone, are entirely in the *Icriodus* biofacies lacking all species of *Polygnathus* (Klapper 1981, p. 58–59). Although the evidence is tenuous at best as it is based only on the occurrence of *Icriodus latericrescens robustus*, the Schoharie-Bois Blanc may represent the *serotinus* Zone and the Edgecliff, either the *patulus* Zone or the lower part of the *partitus* Zone, because the base of the overlying Nedrow Member is within the *partitus* Zone (Klapper and Oliver 1995, p. 1072).

Polygnathus praetrigonicus Bardashev 1992 (= *P. aff. P. trigonicus* Bischoff and Ziegler *sensu* Klapper 1971, and later authors, see synonymy) was first described from what is now recognized as the basal *costa-*

tus Zone in the New York succession. This occurrence is in the uppermost part of the Moorehouse Member and in the overlying Seneca Member of the Onondaga Limestone (Klapper 1971, tables 3, 4). However, in that paper an anomalously low occurrence of three specimens of *P. costatus* was reported well below the Moorehouse Member in the upper part of the underlying Nedrow Member at one locality (Klapper 1971, table 1) and well below abundant occurrences of *P. costatus* in the Seneca Member at the top of the Onondaga. Restudy of these Nedrow specimens in 2011 demonstrated, however, that they do not belong to either *P. costatus* or *P. partitus*. The latter species does occur at the base of the Nedrow Member as mentioned previously, meaning that the whole of the Nedrow is within the *partitus* Zone.

The lowest occurrence of *Polygnathus praetrigonicus* in the Prague Basin is in the basal *costatus* Zone with the nominal species of the zone in the lower part of the Choteč Limestone at Chýnice and the Barrandov road cut (Berkyová 2009, text-figs 4B, 2B). Klapper *et al.* (1978, text-fig. 1) reported the same association of these two species in the lower Choteč at Chýnice, but in the same study *P. praetrigonicus* occurs without *P. costatus* in the lower Choteč at the Prastav quarry and the correlative part of the *Acanthopyge* Limestone at the

series	stage	conodont zonation	<i>P. serotinus</i>	<i>P. bultyncki</i>	<i>P. praetrigonicus</i>
Middle Devonian	Eifelian	<i>costatus</i>			
		<i>partitus</i>	—		—
		<i>patulus</i>			
Lower Devonian	Emsian	<i>serotinus</i>	—		

Text-fig. 2. Generalized stratigraphic ranges for *Polygnathus serotinus*, *P. bultyncki*, and *P. praetrigonicus* in terms of the upper Emsian – lower Eifelian conodont zonation. These approximate maximum ranges, but the best way they could be given with precision is through Graphic Correlation, which is beyond the scope of our present research. For details of the ranges in the various areas discussed, however, consult the text under Biostratigraphy

Red Quarry near Suchomasty. These lowest occurrences of *P. praetrigonicus* may be taken as a working hypothesis to represent the basal *costatus* Zone in the Prague Basin as they do in the New York succession. In the northern Antelope Range, central Nevada, *P. praetrigonicus* ranges from the uppermost part of the *partitus* Zone into the basal *costatus* Zone. This was not reported in Johnson *et al.* (1996, section V, table 2), but nonetheless *P. praetrigonicus* occurs in three samples: VH 16 and 17 in the uppermost *partitus* Zone and VG25 in the basal *costatus* Zone. Bardashev (1992, p. 57) also reported this species from the *partitus* and *costatus* zones in Central Asia. Other geographic occurrences of *P. praetrigonicus* are in less constrained parts of the *costatus* Zone (see synonymy). For generalized stratigraphic ranges of *Polygnathus serotinus*, *P. bultyncki*, and *P. praetrigonicus* see Text-fig. 2.

SYSTEMATIC PALAEOONTOLOGY

The extent of the posterior carina is a matter of intraspecific variation within both *Polygnathus pseudocostatus* sp. nov. and *P. angusticostatus* Wittekindt (see especially Sparling 1981, pl. 1, figs 11, 14, 17, 22, 23). This also obtains iteratively in other species of *Polygnathus* throughout its evolutionary history. The genus *Ctenopolygnathus* Müller and Müller (1957, p. 1084) was based solely on the carina extending beyond the main part of the posterior platform in the Pa element. After their paper, this genus was treated as a junior synonym of *Polygnathus* by most authors. Yet *Ctenopolygnathus* was revived by Bardashev *et al.* (2002, p. 412) apparently unaware that this minor morphologic character supposedly diagnostic of the genus proves to be either present or absent as a result of intraspecific variation.

In the text-figure explanations, specimens labeled SB are housed in the Czech Geological Survey, Prague, and those labeled SUI are in the collections at the University of Iowa, Iowa City.

Polygnathus serotinus Telford 1975
(Text-figs 3A–G, 4A–H, 5A–F)

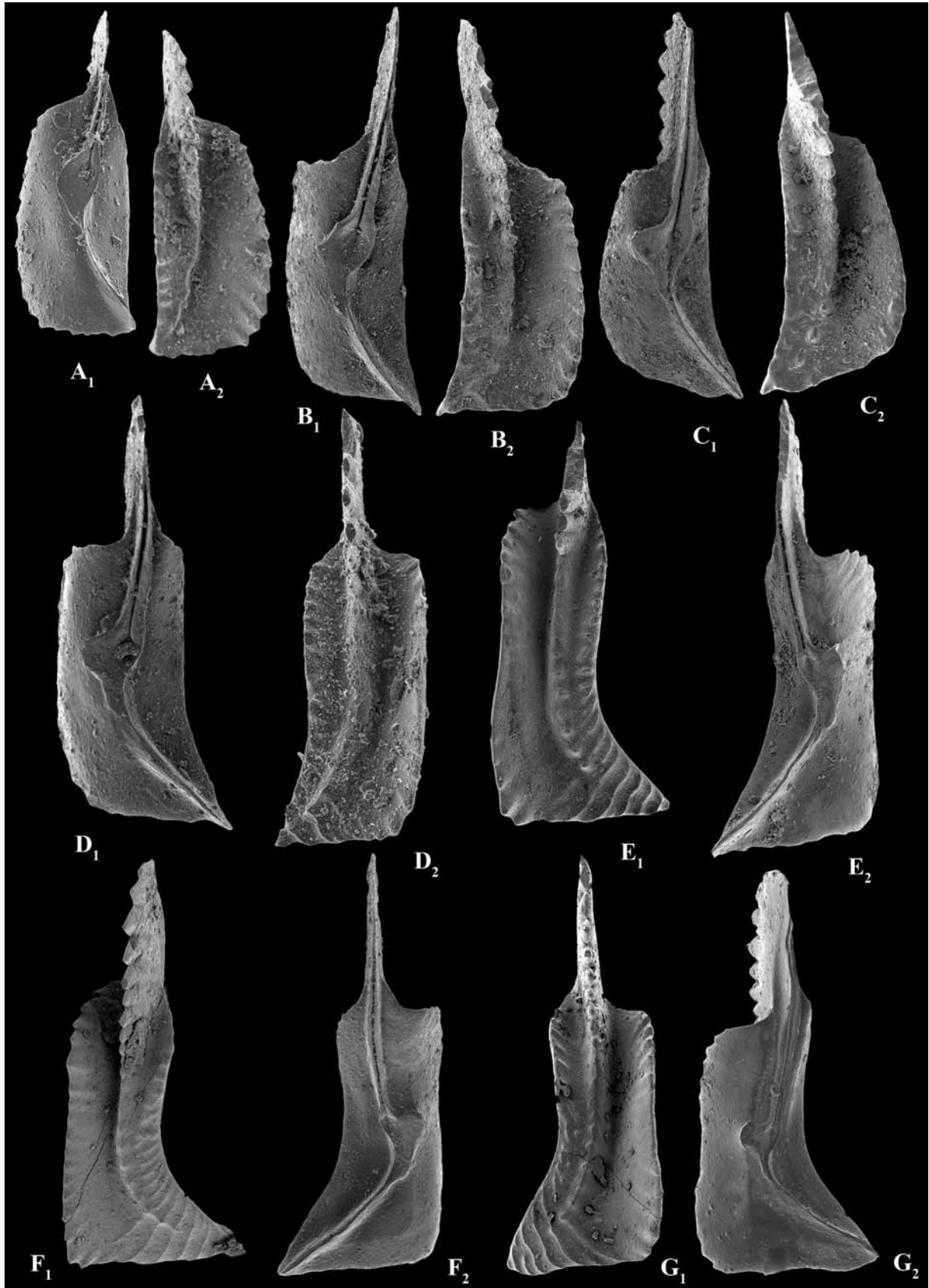
1974. *Polygnathus perbonus* new subspecies D. Perry, Klapper, and Lenz, 1089, 1091, pl. 8, figs 9–13, 15, 16.
1975. *Polygnathus foveolatus serotinus* subsp. nov. Telford, 43–44, pl. 7, figs 1–8 [figs 5, 6 = holotype].
1975. *Polygnathus* sp. nov. D. Klapper and Johnson, 74–75, pl. 3, figs 1, 2, 8–10.
1975. *Polygnathus foliformis* sp. nov. Snigireva, 26, pl. 4, figs 1, 2.
1975. *Polygnathus totensis* sp. nov. Snigireva, 27, pl. 4, figs 3, 4.
1976. *Polygnathus serotinus* Telford; Bultynck, 63–64, pl. 10, fig. 23; pl. 11, fig. 21.
1977. *Polygnathus serotinus* Telford; Weddige, 319–320, pl. 4, figs 77–79; text-fig. 4, no. 34.
1977. *Polygnathus serotinus* Telford; Klapper, 495–496, *Polygnathus* pl. 9, figs 4, 5 [fig. 5 = reillustration of holotype].
1978. *Polygnathus perbonus* new subsp. D. Perry *et al.*; Pickett, 101, pl. 1, figs 23–25; pl. 2, fig. 18.
1978. *Polygnathus serotinus* Telford; Klapper, Ziegler, and Mashkova, 112, pl. 1, figs 9, 10, 30, 31.
1978. *Polygnathus serotinus* Telford; Apekina and Mashkova, 46, pl. 76, fig. 9, pl. 77, figs 1, 2, 6.
1978. *Polygnathus foliformis* Snigireva; Apekina and Mashkova, 47, pl. 77, fig. 7, pl. 78, figs 1, 4, 7, 10.
1979. *Polygnathus serotinus* Telford; Lane and Ormiston, 63, pl. 8, figs 2, 6, 8–10, 13–16, 19–22, 32–35 [not pl. 7, figs 13, 37 = *P. inversus* transitional with *P. serotinus*].
1979. *Polygnathus serotinus* Telford; Lane, Müller, and Ziegler, 220, pl. 1, figs 5, 6, 20, 21.
1979. *Polygnathus declinatus* sp. nov. Wang, 401–402, pl. 1, figs 12–20.
1980. *Polygnathus serotinus* Telford; Klapper and Johnson, 454.
1980. *Polygnathus serotinus* Telford; Uyeno and Klapper, 87, pl. 8.1, figs 17–20.
1980. *Polygnathus serotinus* Telford; Bultynck and Hollard, 45, pl. 2, figs 8, 12, 13.
1980. *Polygnathus serotinus* Telford; Xiong, 97–98, pl. 23, figs 1–8; pl. 25, figs 5–20, 23, 24, 27, 28.
1980. *Polygnathus foliformis* Snigireva; Xiong, 92, pl. 25, figs 1–4, 21, 22, 25, 26.
1982. *Polygnathus serotinus* Telford; Weddige, 34, pl. 1, fig. 12.
1982. *Polygnathus serotinus* Telford; Brown, 45–46, pl. 4, figs 1–5.
1983. *Polygnathus serotinus* Telford; Wang and Ziegler, 102, pl. 6, figs 16–18.
1984. *Polygnathus serotinus* Telford; Apekina, 85, pl. 22, fig. 11.
1984. *Polygnathus foliformis* Snigireva; Apekina, 81, pl. 22, fig. 3.
1985. *Polygnathus serotinus* Telford; Austin *et al.*, 140, pl. 4.2, figs 12, 13.
1985. *Polygnathus serotinus* Telford; Schönlaub In: Feist, Schönlaub, and Bultynck, 94, pl. 2, figs 14, 15.

1986. *Polygnathus serotinus* Telford; Ziegler and Wang, 30, pl. 1, figs 9, 10.
1986. *Polygnathus serotinus* Telford; Bardashev and Ziegler, 74, pl. 1, fig. 17.
1986. *Polygnathus serotinus* Telford; Bultynck, 278, 280, pl. 6, figs 3, 4 [not pl. 5, figs 17, 18 =? *P. inversus* transitional with *P. serotinus*].
1986. *Polygnathus serotinus* Telford; Schönlaub, 366, pl. 3, figs 23–26.
1986. *Polygnathus quadratus* Klapper, Ziegler, and Mashkova; Schönlaub, 366, pl. 3, figs 27–29.
- [not] 1987a. *Polygnathus serotinus* Telford ‘delta morphotype’ of Lane and Ormiston; Mawson, 278, 280, 282, pl. 33, figs 9–12; pl. 36, fig. 10 [= *P. inversus* transitional with *P. serotinus*].
- 1987b. *Polygnathus serotinus* Telford gamma morph of Lane and Ormiston; Mawson, 261, pl. 2, figs 12, 13.
- 1987b. *Polygnathus serotinus* Telford delta morph of Lane and Ormiston; Mawson, 261, pl. 2, figs 1–10.
1989. *Polygnathus serotinus* Telford; Mawson and Talent, 248, pl. 3, figs 1, 2.
1990. *Polygnathus serotinus* Telford; Uyeno, 86, pl. 7, figs 13, 14; pl. 9, figs 21, 22, 34, 35 [see for additional synonymy].
1990. *Polygnathus serotinus* Telford; Bardashev, 77, 79, pl. 2, fig. 3; pl. 6, fig. 6.
1991. *Polygnathus serotinus* Telford; Uyeno, 156, pl. 3, figs 8, 9.
1992. *Polygnathus quadratus* Klapper, Ziegler, and Mashkova; Bončeva, 41, pl. 6, figs 1–3 [= juvenile *P. serotinus*, not fig. 4 = *P. quadratus*].
1992. *Polygnathus serotinus* Telford; Bončeva, 41–42, pl. 6, figs 5–7.
- [?] 1992. *Polygnathus falcatus* sp. n. Bončeva, 42, pl. 5, figs. 1, 2 [not fig. 3 = ? *P. inversus* transitional with *P. serotinus*].
1992. *Polygnathus serotinus* Telford; Bardashev and Ziegler, 28, pl. 6, figs 12, 16, 17.
1992. *Polygnathus foliformis* Snigireva; Bardashev and Ziegler, 28, pl. 6, figs 19–21, 23–25.
1994. *Polygnathus serotinus* Telford; Bai, 182, pl. 17, figs 1–8.
- [not] 1994. *Polygnathus serotinus* Telford; Talent and Mawson, 78, pl. 2, figs 15–17 [= *P. inversus* transitional with *P. serotinus*].
1995. *Polygnathus serotinus* Telford; Sloan *et al.*, 56, pl. 5, figs 2–14.
1995. *Polygnathus serotinus* Telford; Mawson, Talent and Furey-Greig, 432–433, pl. 3, figs 1–5, 18.
2002. *Ctenopolygnathus totensis* (Snigireva); Bardashev, Weddige, and Ziegler, 414, text-fig. 13, no. 22.
2002. *Ctenopolygnathus foliformis* (Snigireva); Bardashev, Weddige, and Ziegler, 412–413, text-fig. 13, no. 23.
2002. *Costapolygnathus mariannae* sp. nov. Bardashev, Weddige, and Ziegler, 416, text-fig. 14, no. 26.
2002. *Costapolygnathus schenkae* sp. nov. Bardashev, Weddige, and Ziegler, 417, text-fig. 14, no. 27.
2002. *Costapolygnathus snigirevae* sp. nov. Bardashev, Weddige, and Ziegler, 418, text-fig. 14, no. 29, 30.
2002. *Linguiopolygnathus serotinus* (Telford); Bardashev, Weddige, and Ziegler, 424–425, text-fig. 15, no. 32 [= reillustration of holotype].
2002. *Linguiopolygnathus declinatus* (Wang); Bardashev, Weddige and Ziegler, 422, text-fig. 15, no. 33 [reillustration of holotype].
2002. *Linguiopolygnathus timofeevae* sp. nov. Bardashev, Weddige, and Ziegler, 426, text-fig. 15, no. 39.
2002. *Linguiopolygnathus wangi* sp. nov. Bardashev, Weddige, and Ziegler, 426–427, text-fig. 15, no. 40.
2003. *Polygnathus serotinus* Telford; Pyle, Orchard, Barnes, and Landry, 111, pl. 2, figs 14–15.
2009. *Polygnathus serotinus* Telford; Berkyova, 682, fig. 8 J.
2010. *Polygnathus serotinus* Telford; Meço, 180, pl. 2, figs 12, 17; pl. 3, figs 2, 4, 5, 8–11, 13, 15 [not fig. 7 = *P. bultyncki*].

MATERIAL: 270 specimens from the Prague Basin (for distributions see Berkyova 2009, figs 2–4). 2615 specimens were counted from 163 faunal slides from the northern Antelope Range, central Nevada. The 32 samples containing *P. serotinus* are listed in Johnson *et al.* 1996, section V, table 2. It was considered unnecessary to count an additional 116 slides from many of the same samples. Also, the northern Hot Creek Range samples were not counted for this species.

DIAGNOSIS: Representative Pa elements have a small pit located just anterior of the sharp inward deflection of the keel. A small, subcircular, shelf-like protuberance occurs on the outer side of the pit in mature specimens. Cavity entirely inverted posterior of pit. Flange-like anterior outer margin is distinctly higher than carina and inner margin, and separated from carina by a wide, deep adcarinal trough.

REMARKS: The distinctive shelf-like protuberance in combination with the small pit in mature Pa elements distinguishes *Polygnathus serotinus* from other species



of the genus. In ontogenetically small specimens of the species, however, the protuberance is characteristically not developed but is incipiently represented by a small flattening of the keel just posterior of the pit on the outer side. A complete gradation from this minor flattening of the keel in immature specimens to full development of the distinct protuberance in mature specimens has been observed in our material and in illustrations in the literature (well shown in Xiong 1980, pl. 25, figs 1–28 and in Bai 1994, pl. 17, figs 1–8). The immature specimens have been treated by several authors as separate species, *P. foliformis* and *P. totensis*, both proposed by Snigireva (1975, see synonymy), but Weddige (1977), Klapper (1977), Pickett (1978, p. 102), Klapper and Johnson (1980) and Mawson (1987a) recognized that *P. totensis* represents immature specimens of *P. serotinus*. Also, Lane and Ormiston (1979, pl. 8, figs 13–16, 19–22) included small, immature specimens, closely comparable to the types of *P. foliformis*, together with mature Pa elements within their morphotype gamma of *P. serotinus*. It is worth noting that Telford (1975, pl. 7, figs 1–4, 7, 8) included immature specimens like those of *P. foliformis* and *P. totensis* within his original concept of *P. serotinus*. In fact the only mature specimen he illustrated (Telford, pl. 7, figs 5, 6) was the holotype, but this has largely been ignored by later authors. Thus, it is clear that *P. foliformis* and *P. totensis* are best considered as immature ontogenetic stages of the Pa element of *P. serotinus*.

We recognize three informal morphotypes of *Polygnathus serotinus*, based on the character of the shelf-like protuberance on the outer side of the pit. In morphotype 1 the outer margin of the protuberance is sigmoidal in shape because of a small sinus (Text-fig. 3), whereas it is characteristically subcircular in morphotype 2 (Text-fig. 4), as in the holotype. Morphotype 3 (Text-fig. 5) has a protuberance that narrows and extends farther to the posterior end of the platform than in the other morphotypes, without a sinus as in Morphotype 1. The first two morphotypes are the most common, represented by several tens of specimens in the Prague Basin. These distinctive protuberances represent stable features during growth of the elements, although other features such as platform shape and formation of the tongue change substantially during ontogeny. This is also the reason why different growth stages of *P. serotinus* have been recognized as different species. *Polygnathus foliformis*

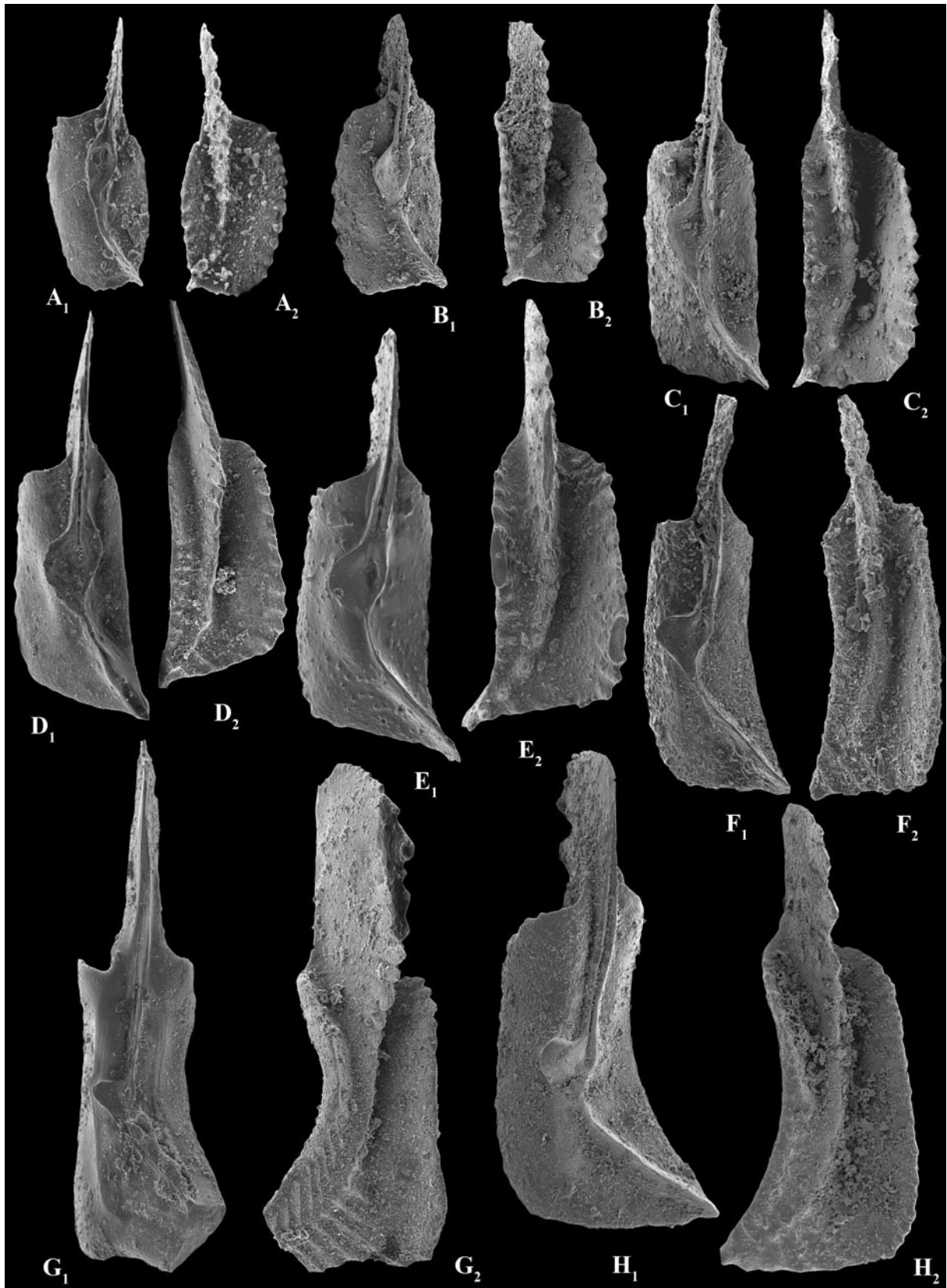
represents an early ontogenetic stage with a broader and rounder shape of the platform and a more anteriorly situated pit. *Polygnathus totensis* represents a somewhat later ontogenetic stage, wherein the pit is situated more posteriorly and the platform is more elongated.

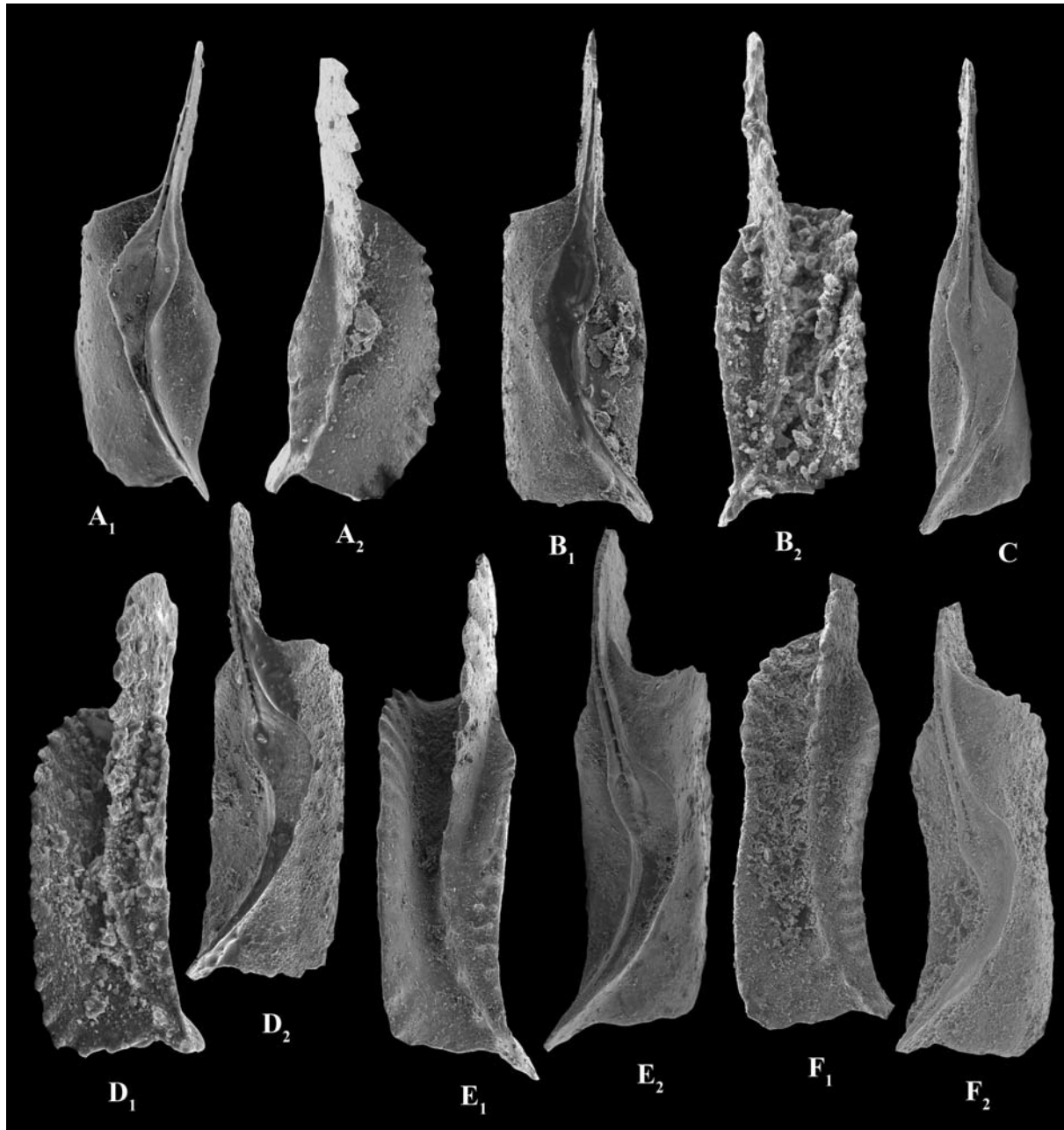
The different types of protuberances are stable and therefore distinguishable at all growth stages observed and as such have taxonomic value, which could allow us to treat it as a character at the subspecific level. However, all the types of the recorded protuberances are associated both geographically and stratigraphically in the Prague Basin, which is the main reason why we interpret them as intraspecific variants. We designate them as informal morphotypes only for clarity in the description, as the morphotypes have no biostratigraphic utility.

As mentioned above, the subcircular type of protuberance (morphotype 2) occurs in the holotype (also in morphotype delta of Lane and Ormiston 1979), whereas the sigmoidal protuberance (morphotype 1) has not been recognized by us in the literature so far, except for specimens illustrated by Mawson (1987b, pl. 2, figs 10 and 12 (identified by her as *P. serotinus* delta and gamma morphs *sensu* Lane and Ormiston 1979). Morphotype 3 may be represented by a specimen figured by Bončeva (1992, pl. 5, fig. 2) and named as *P. falcatus*. However, the quality of the photograph does not permit a certain identification.

There are specimens that are considered intermediate between *Polygnathus inversus* Klapper and Johnson and *P. serotinus* (for example, Klapper and Johnson 1975, p. 73, pl. 3, figs 19–22, 24–31; Uyeno and Klapper 1980, pl. 8.1, figs 13–16). Alternately, these were treated as an early morphotype of *P. serotinus* by Lane and Ormiston (1979, p. 63, pl. 7, figs 13, 37), their alpha morphotype. All of these “have an incipient development of a shelf-like protuberance on the outer side of the pit, but the protuberance characteristic of *P. serotinus* is more distinctly demarcated and smaller. . . Furthermore, the pit itself in *P. serotinus* is smaller than in the transitional form” (Uyeno and Klapper 1980, p. 89). The anterior outer margin is at more or less the same height as the inner margin and a flange-like outer margin is not developed in the transitional forms. There are additional specimens illustrated in the literature that fit this category, as well as others that are questionably related to these transitional forms, as indicated in the synonymy list.

Text-fig. 3. *Polygnathus serotinus* Telford, morphotype 1; all specimens are Pa elements from the Prague Basin. **A₁, A₂** – lower and upper views of SB 6, 250 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *partitus* Zone, × 135. **B₁, B₂** – lower and upper views of SB 7, 650 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone, × 110. **C₁, C₂** – lower and upper views of SB 8, 400 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnčice, *partitus* Zone, × 100. **D₁, D₂** – lower and upper views of SB 9, 400 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 130. **E₁, E₂** – upper and lower views of SB 10, 650 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone, × 85. **F₁, F₂** – upper and lower views of SB 11, 650 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone, × 70. **G₁, G₂** – upper and lower views of SB 12, 650 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone, × 80





Text-fig. 5. *Polygnathus serotinus* Telford, morphotype 3; all specimens are Pa elements from the Prague Basin. **A₁, A₂** – lower and upper views of SB 21, 330 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 175. **B₁, B₂** – lower and upper views of SB 22, 160 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 190. **C** – lower view of SB 23, 460 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, lowermost *partitus* Zone, × 122. **D₁, D₂** – upper and lower views of SB 24, 160 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 190. **E₁, E₂** – upper and lower views of SB 25, 1060 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 146. **F₁, F₂** – upper and lower views of SB 26, 960 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 136

Text-fig. 4. *Polygnathus serotinus* Telford, morphotype 2; all specimens are Pa elements from the Prague Basin. **A₁, A₂** – lower and upper views of SB 13, 160 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 175. **B₁, B₂** – lower and upper views of SB 14, 760 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 175. **C₁, C₂** – lower and upper views of SB 15, 200 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *partitus* Zone, × 175. **D₁, D₂** – lower and upper views of SB 16, 440 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 100. **E₁, E₂** – lower and upper views of SB 17, 250 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *partitus* Zone, × 150. **F₁, F₂** – lower and upper views of SB 18, 400 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 125. **G₁, G₂** – lower and upper views of SB 19, 90 cm below the base of the Choteč Limestone, Prastav quarry, *partitus* Zone, × 65. **H₁, H₂** – lower and upper views of SB 20, 960 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 125

As mentioned in the introduction to this paper and as expressed in the synonymy list, Bardashev *et al.* (2002) recognized nine species, which we regard as conspecific and which they allocated to three different genera in their taxonomy. Seven of these are minor intraspecific variants of the mature Pa element of *P. serotinus*, all of which have the diagnostic protuberance adjacent to the small pit, as well as the same platform outline and the flange-like outer anterior margin. The other two are those based on early ontogenetic stages of the Pa element of the same species, as discussed above.

Polygnathus karadjalis Vorontsova and Kuz'min (1984, see Mawson and Talent 1997, p. 216, 218, fig. 15, no. 15–24) is a Famennian homeomorph of *P. serotinus*, which differs by lacking the diagnostic protuberance adjacent to the pit and in having a distinctive arrow-shaped structure anterior of the pit.

RANGE: Lower boundary of *serotinus* Zone (by definition) to the lower *costatus* Zone (see discussion under Biostratigraphy section).

Polygnathus bultyncki Weddige, 1977
(Text-figs 1A–F, 6A–F)

1956. *Polygnathus linguiformis* Hinde; Ziegler, 103–104, pl. 7, figs 15–18 [not figs 11, 12, 19, 20 = *P. inversus* Klapper and Johnson, 1975].
1970. *Polygnathus linguiformis* Hinde alpha forma nova Bultynck, 126, pl. 9, figs 1–7.
1974. *Polygnathus linguiformis linguiformis* Hinde alpha morphotype Bultynck; Perry, Klapper, and Lenz, 1089, pl. 7, figs 8, 9, 11–14.
1977. *Polygnathus linguiformis linguiformis* Hinde alpha morphotype Bultynck; Klapper, 462, 492, *Polygnathus* – pl. 9, figs 6, 8 [= reillustration of Bultynck, 1970, pl. 9, figs 2, 1].
1977. *Polygnathus linguiformis bultyncki* n. ssp. Weddige, 313–314, pl. 5, figs 90–92 [fig. 91 = holotype]; text-fig. 4, no. 20.
1978. *Polygnathus linguiformis bultyncki* Weddige; Klapper, Ziegler, and Mashkova, 112, pl. 1, figs 21, 22, 26–29.
1978. *Polygnathus linguiformis* Hinde alpha forma (Bultynck) [sic]; Apekina and Mashkova, 47, pl. 77, figs 4, 5, 10 [not fig. 8 = *P. cracens* Klapper, Ziegler, and Mashkova, 1978].
1978. *Polygnathus linguiformis bultyncki* Weddige; Apekina and Mashkova, 47, pl. 78, figs 5, 6 [see Remarks].
1978. *Polygnathus kimi* sp. nov. Apekina and Mashkova, 47, pl. 78, figs 2, 3, 9 [nomen nudum].
1979. *Polygnathus linguiformis bultyncki* Weddige; Lane and Ormiston, 84, 86, pl. 7, figs 1, 2, 34, 38, 39; pl. 8, figs 11, 12, 23, 24.
1979. *Polygnathus linguiformis bultyncki* Weddige; Lane, Müller, and Ziegler, 222, pl. 1, fig. 22.
1980. *Polygnathus linguiformis bultyncki* Weddige; Klapper and Johnson, 453.
1980. *Polygnathus linguiformis linguiformis* Hinde alpha morphotype Bultynck; Bultynck and Hollard, 43, pl. 2, figs 14–16.
1980. *Polygnathus linguiformis bultyncki* Weddige; Xiong, 94, pl. 27, figs 6, 7.
1980. *Polygnathus* cf. *linguiformis* alpha morphotype Bultynck; Xiong, 94, pl. 27, figs 18, 19.
1980. *Polygnathus hanshanensis* sp. nov. Xiong, 93, pl. 27, figs 12–17, text-fig. 54.
1980. *Polygnathus hanshanensis obovatus* subsp. nov. Xiong, 93, pl. 27, figs 26, 27.
1980. *Polygnathus najiaoensis* sp. nov. Xiong, 95–96, pl. 27, figs 20–23, text-fig. 55.
1981. *Polygnathus kimi* sp. nov. Mashkova and Apekina, 146–147, text-fig. 1, figs a–p.
1981. *Polygnathus najiaoensis* sp. nov. [sic]; Xiong, 543, pl. 2, figs 11–16 [reillustration of the two specimens in Xiong in Xian *et al.*, 1980].
1982. *Polygnathus linguiformis bultyncki* Weddige; Weddige, 34, pl. 1, fig. 13.
1982. *Polygnathus linguiformis bultyncki* Weddige; Brown, 43, pl. 4, figs 6, 7, 9 [not fig. 8 = *P. linguiformis linguiformis* Hinde theta morphotype of Klapper in Johnson, Klapper, and Trojan, 1980].
1983. *Polygnathus linguiformis linguiformis* Hinde alpha morphotype Bultynck; Wang and Ziegler, 104, pl. 7, figs 16, 17.
- [not] 1983. *Polygnathus linguiformis bultyncki* Weddige beta and alpha morphotypes of Wang and Ziegler, 89, 100, pl. 5, figs 18, 19 [fig. 18 = ? *P. inversus* transitional with *P. serotinus*, fig. 19 = ?].
1984. *Polygnathus linguiformis bultyncki* Weddige; Apekina, 83–84, pl. 23, fig. 2.
1984. *Polygnathus kimi* Mashkova and Apekina; Apekina, 83, pl. 22, figs 1, 2.
1985. *Polygnathus linguiformis bultyncki* Weddige; Austin *et al.*, 138, pl. 4.2, figs 8, 9.
1985. *Polygnathus linguiformis bultyncki* Weddige; Schönlaub In: Feist, Schönlaub, and Bultynck, 94, pl. 2, figs 20, 23, 26.
- [not] 1986. *Polygnathus linguiformis bultyncki* Weddige beta morphotype of Wang and Ziegler; Ziegler and Wang, 30, pl. 1, fig. 15 [reillustration of pl. 5, fig. 18 of Wang and Ziegler, 1983].
1986. *Polygnathus linguiformis bultyncki* Weddige; Bultynck, 282, pl. 7, figs 2–4.

1986. *Polygnathus linguiformis bultyncki* Weddige; Schönlaub, 368, pl. 4, fig. 26.
- 1987b. *Polygnathus linguiformis bultyncki* Weddige; Mawson, 259, pl. 1, fig. 10.
- [not] 1989. *Polygnathus linguiformis bultyncki* Weddige; Mawson and Talent, 252, pl. 5, figs 4, 5.
1989. *Polygnathus labiosus mawsonae* n. subsp. Long and Burrett, 126, 128, 129, figs 5.1–5.9, 6.1–6.3, 7.1–7.12, 10.1–10.10.
1990. *Polygnathus linguiformis bultyncki* Weddige; Uyeno, 84–85, pl. 18, figs 1, 2, 8.
1992. *Polygnathus linguiformis bultyncki* Weddige; Bončeva, 39–40, pl. 5, figs 5–7.
1992. *Polygnathus linguiformis bultyncki* Weddige; Bardashev and Ziegler, 28, pl. 6, figs 27, 28.
1992. *Polygnathus linguiformis bultyncki* Weddige; Bardashev, 66, pl. 3, figs 1–3, 9.
1994. *Polygnathus linguiformis bultyncki* Weddige; Bai, 179, pl. 18, figs 1, 2.
1994. *Polygnathus linguiformis linguiformis* Hinde morphotype alpha Bultynck; Bai, 179–180, pl. 18, figs 3–6.
1994. *Polygnathus neoserotinus* n. sp. Bai, 180, pl. 18, figs 7–9.
1995. *Polygnathus linguiformis bultyncki* Weddige; Sloan *et al.*, 60, pl. 7, figs 5, 6.
1999. *Polygnathus bultyncki* Weddige; Belka *et al.*, pl. 2, fig. 6.
2002. *Ctenopolygnathus najiaoensis* (Xiong); Bardashev, Weddige, and Ziegler, 413, text-fig. 13, no. 20.
2002. *Ctenopolygnathus kimi* (Mashkova and Apekina); Bardashev, Weddige, and Ziegler, 413, text-fig. 13, no. 21.
2002. *Linguipolygnathus anastasiae* sp. nov. alpha morphotype Bardashev, Weddige, and Ziegler, 419, text-fig. 15, no. 30 [= reillustration of Apekina and Mashkova, 1978, pl. 77, fig. 10].
2002. *Linguipolygnathus bultyncki* (Weddige); Bardashev, Weddige, and Ziegler, 420, text-fig. 15, no. 34 [= reillustration of holotype].
2003. *Polygnathus linguiformis bultyncki* Weddige; Pyle, Orchard, Barnes, and Landry, 111, pl. 2, figs 9, 10.
2003. *Polygnathus linguiformis linguiformis* Hinde; Pyle, Orchard, Barnes, and Landry, 111, pl. 2, fig. 11.
2009. *Polygnathus linguiformis bultyncki* Weddige; Berkyová, 682, fig. 8H [not fig. I = *P. cracens* Klapper, Ziegler, and Mashkova, 1978].
2010. *Polygnathus serotinus* Telford; Meço, 180, pl. 3, fig. 7 [only].
2011. *Polygnathus bultyncki* Weddige; Vodrážková, Klapper, and Murphy, 760, figs 13H, I.
2012. *Polygnathus linguiformis bultyncki* Weddige; Martínez-Pérez and Valenzuela-Ríos, 198–199, pl. 1, figs 3, 4.

MATERIAL: 127 specimens from the Prague Basin (for distribution, see Berkyova 2009, figs 2–4. 1365 specimens were counted from 163 faunal slides (32 samples) from the northern Antelope Range, central Nevada (samples are listed in Johnson *et al.* 1996, section V, table 2). The same protocol used with *Polygnathus serotinus* applies to *P. bultyncki* in terms of the number of uncounted slides and lack of counts for the northern Hot Creek Range samples.

DIAGNOSIS: Representative Pa elements have a moderately large pit located just anterior of the inward deflection of the keel. Well developed tongue covered by strong transverse ridges. Outer posterior margin just anterior of tongue about at same height as carina and inner margin. Outer margin flange not developed.

REMARKS: *Polygnathus bultyncki* is distinguished from Pa elements of *P. serotinus* by commonly lacking a protuberance on the outer side of the pit and the lack of a high, flange-like outer margin anterior of the tongue. Furthermore, the tongue is generally set with stronger, more numerous transverse ridges than in *P. serotinus*. The two species are clearly distinguishable on the basis of the upper surface characteristics just mentioned. However, as noted in the original diagnosis and relationships of *P. bultyncki* by Weddige (1977, p. 314, 416, pl. 4, fig. 92) a protuberance may be developed in some specimens, but that of his illustrated figure is different in shape from the protuberance of *P. serotinus*. A protuberance is not present in our Nevada specimens but it has been observed in some of the Czech material (e.g., Text-fig. 6B₁). The two mature specimens of *P. bultyncki* illustrated by Apekina and Mashkova (1978, pl. 78, figs. 5, 6) are also unusual in having a shelf-like protuberance but again it is of different shape from that of *P. serotinus*. The protuberance in these specimens is directed slightly to the posterior whereas it is directed straight laterally or slightly to the anterior in mature Pa elements of *P. serotinus*. The specimens of Bai (1994, p. 180, pl. 18, figs 7–9) that formed the basis of his species, *P. neoserotinus*, have an identical protuberance to the specimen of Apekina and Mashkova (1978, pl. 78, fig. 6). We regard the exceptional occurrence of this protuberance in *P. bultyncki* as an intraspecific development.

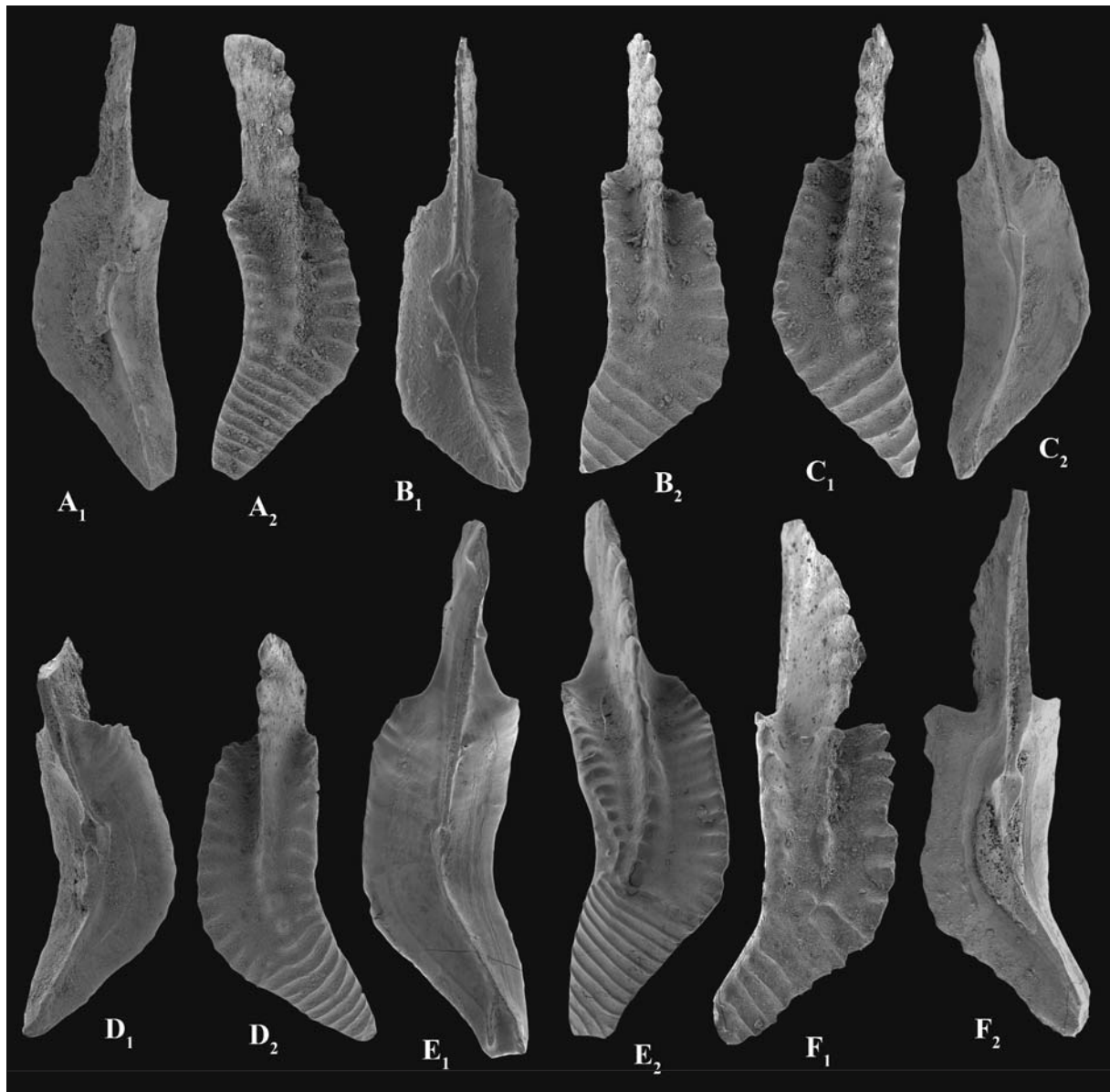
The specimen illustrated by Apekina and Mashkova (1978, pl. 78, fig. 6) was reillustrated by Bardashev *et al.* (2002, text-fig. 15, no. 31) as representative of their beta morphotype of *Linguipolygnathus anastasiae*, but the

holotype of that species (Apekina and Mashkova 1978, pl. 77, fig. 10) is a typical Pa element of *P. bultyncki*.

Polygnathus bultyncki differs from *P. linguiformis* s.s. (that is, *P. linguiformis linguiformis* gamma morphotype of authors) by lacking the high, flange-like outer margin immediately anterior of the tongue (Klapper 1971, p. 64). As the specimen illustrated by Pyle *et al.* (2003, pl. 2, fig. 11) lacks that morphologic feature, it is better identified as *P. bultyncki*. We do not treat *P. bultyncki* as a subspecies of *P. linguiformis*, following

the usage of Belka *et al.* 1999 and Vodrážková *et al.* 2011.

The smallest immature specimens of *Polygnathus bultyncki* have not yet developed the tongue and accompanying transverse ridges. That appears to be why a number of names, *P. kimi*, *P. hanshanensis*, *P. hanshanensis obovatus*, and *P. najiaoensis*, have been proposed as separate species based on very small specimens. Our material from the Prague Basin and central Nevada indicates that there is a complete ontogenetic continuum



Text-fig. 6. *Polygnathus bultyncki* Weddige; all specimens are Pa elements from the Prague Basin. **A₁**, **A₂** – lower and upper views of SB 33, 1080 cm below the base of the Choteč Limestone, Barrandov road cut at Prague, *serotinus* Zone, × 32. **B₁**, **B₂** – lower and upper views of SB 34, 450 cm below the base of the Choteč Limestone, Na Škrábku quarry at Choteč, *patulus* Zone, × 50. **C₁**, **C₂** – upper and lower views of SB 35, 1550 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 50. **D₁**, **D₂** – lower and upper views of SB 36, 1270 cm below the base of the Choteč Limestone, Barrandov road cut at Prague, *serotinus* Zone, × 32. **E₁**, **E₂** – lower and upper views of SB 37, 200 cm below the base of the *Acanthopyge* Limestone (equivalent of the Choteč Lm.), Červený Lom near Suchomasty, *partitus* Zone, × 32. **F₁**, **F₂** – upper and lower views of SB 38, 760 cm below the base of the Choteč Limestone, Jelínek mill quarry at Chýnice, *serotinus* Zone, × 40

from small specimens without a tongue and transverse ridges, to slightly larger specimens that have the beginnings of a tongue and a few transverse ridges, to the large specimens with a well developed tongue and numerous, strong transverse ridges (Text-fig. 1). These later ontogenetic stages of the Pa element have consistently been identified as *P. bultyncki* in the relevant literature.

Polygnathus labiosus mawsonae proposed by Long and Burrett (1989) is not closely related to *P. labiosus* Mawson (1987a, p. 274, pl. 35, figs 1–9; pl. 36, figs 3, 4), the platform element of which has a relatively large basal cavity. In contrast, *P. labiosus mawsonae* has a moderately large pit identical to that of *P. bultyncki*. This is evident, for example, in Long and Burrett's specimen (1989, fig. 5.8) where part of the basal plate material has been broken away revealing the pit. Other of their specimens, where the basal plate is not preserved (figs 5.9, 7.6, 7.7, 7.10), show a pit instead of a basal cavity. [For the standard terminology used here, see Clark and Müller (1968) and Sweet (1981, 1988)]. In their description and figure captions, Long and Burrett (1989) have termed basal plate material (or basal filling) as "basal cavity." Their proposed subspecies is synonymous with *P. bultyncki*.

RANGE: *serotinus* Zone to *costatus* Zone.

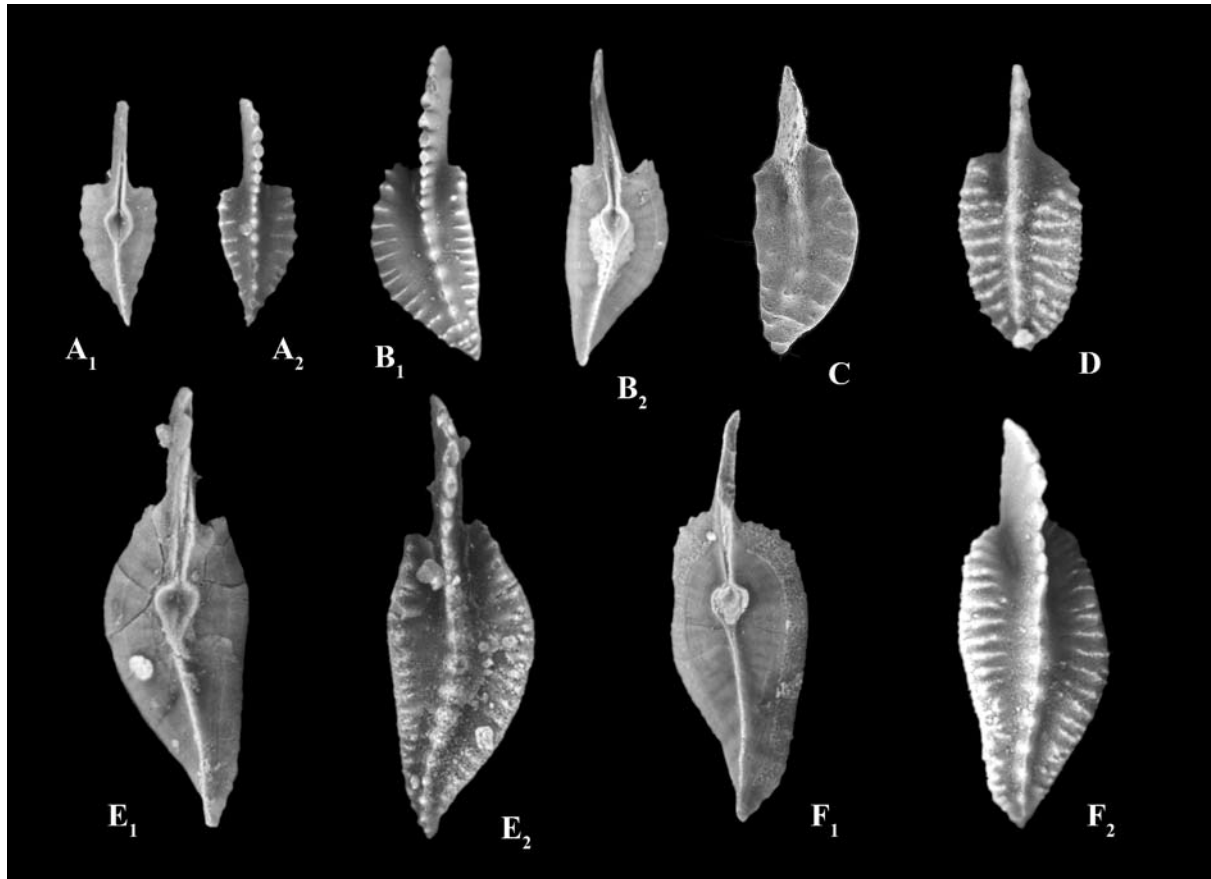
Polygnathus praetrigonicus Bardashev, 1992
(Text-fig. 7A–F)

1971. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Klapper, 66, pl. 3, figs 1–6.
1974. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Perry, Klapper, and Lenz, 1091, pl. 8, fig. 14.
1978. *Polygnathus* sp. aff. *P. trigonicus* Bischoff and Ziegler; Klapper, Ziegler, and Mashkova, 110, pl. 2, figs 32, 33.
1980. *Polygnathus* sp. aff. *P. trigonicus* Bischoff and Ziegler; Klapper and Johnson, p. 454.
1980. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Bultynck and Hollard, 46, pl. 3, figs 11, 12.
1980. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Xiong, 98, pl. 26, figs 17, 18, pl. 27, figs 4, 5.
1981. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Xiong, 542, pl. 2, figs 27–29 [reillustration of specimen in preceding paper, pl. 26, figs 17, 18].
1982. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Uyeno, in Uyeno, Telford, and Sanford, 30, pl. 2, figs 1–6.
1983. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler of Klapper; Sparling, 859, figs 10 L–Q, AD–AI, AV, 11 AH–AQ [not figs 12 A–C].
1986. *Polygnathus* sp. aff. *P. trigonicus* Bischoff and Ziegler; Schönlaub, 368, pl. 4, figs 27, 28.
1988. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler of Klapper; Sparling, 9, figs 10.5, 11.6 [reillustration of Sparling, 1983, figs 10 AD, 11 AI].
1992. *Polygnathus praetrigonicus* sp. nov. Bardashev; 56–57, pl. 2, figs 32–34.
- [not] 1994. *Polygnathus* sp. aff. *P. trigonicus* Bischoff and Ziegler; Mawson and Talent, 54, pl. 2, fig. 16.
2005. *Polygnathus* sp. aff. *P. trigonicus* (Bischoff and Ziegler) [sic]; Mawson and Talent, 380, figs 4 N, O [not figs 4 C, D].
2009. *Polygnathus* sp. aff. *P. trigonicus* Bischoff and Ziegler; Berkyová, 679, 681, fig. 6 L.
2010. *Polygnathus* aff. *P. trigonicus* Bischoff and Ziegler; Machado *et al.*, 445, pl. 2, fig. J.

MATERIAL: Five specimens from the Prague Basin: 40 cm above the base of the Choteč Limestone, Na Škrábku quarry at Choteč (two specimens, 20 cm above the base of *Nowakia (Dmitriella) sulcata sulcata* Zone); 400 cm above the base of the Choteč Limestone, Na Škrábku quarry at Choteč (one specimen); 500 cm above the base of the Choteč Limestone, Na Škrábku quarry at Choteč (one specimen, sample with the first occurrence of *Polygnathus costatus*); 30 cm above the base of the Choteč Limestone, Barrandov road-cut (one specimen, 150 cm above the base of the *costatus* Zone). Eleven specimens from the northern Antelope Range section V: VH-16 (3 specimens), VH-17 (4 specimens), uppermost *partitus* Zone; VH-18 (one specimen), VG-22 (one specimen), VG-25 (2 specimens), all from the lower *costatus* Zone (Johnson *et al.* 1996, table 2). An additional eight specimens are from the Prague Basin from the *Acanthopyge* Limestone at the Red Quarry near Suchomasty, four at 0.10 m above the base and four at 1.12–1.37 m above the base of that formation, basal *costatus* Zone.

DIAGNOSIS: Representative Pa elements have a moderately large pit located somewhat anterior of midlength. Platform more or less triangular in outline set with strong transverse ridges, which are commonly separated from the carina by adcarinal troughs anteriorly narrowing to adcarinal grooves posteriorly. Anterior margins meet short free blade at almost right angles.

REMARKS: The carina commonly reaches the posterior tip, but there are exceptions in which a few transverse ridges are developed near the posterior end. Diagonal ridges are developed anteriorly in just a few specimens of this variable species (e.g., Bultynck and Hollard 1980, pl. 3, fig. 11, these ridges converge posteriorly).

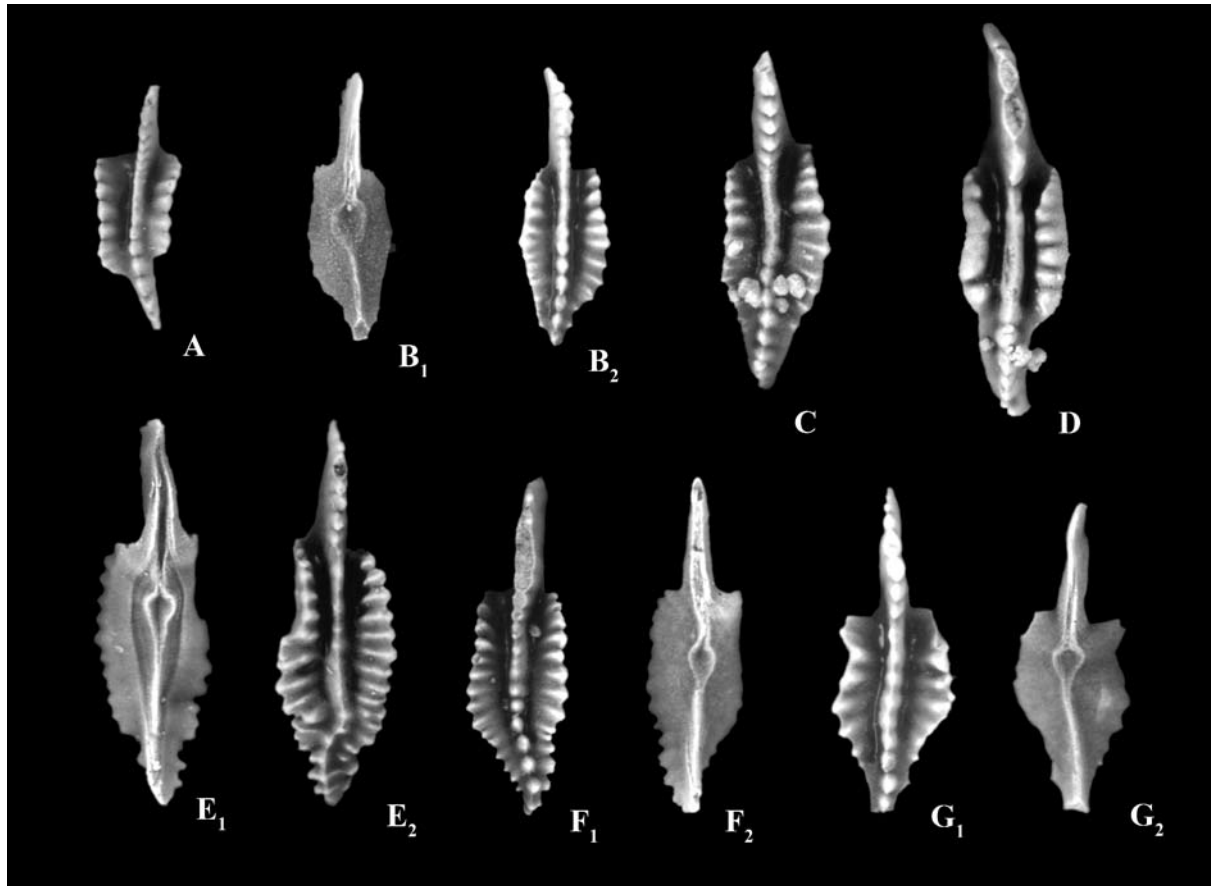


Text-fig. 7. *Polygnathus praetrigonicus* Bardashev; all specimens are Pa elements. **A₁, A₂** – lower and upper views of SUI 133901, 1.12–1.37 m above base of *Acanthopyge* Limestone, Red Quarry (Červený Lom) near Suchomasty, Prague Basin (collected by Willi Ziegler with Ivo Chlupáč in 1976; see Klapper *et al.* 1978, text-fig. 1), basal *costatus* Zone. **B₁, B₂** – upper and lower views of SUI 133902, same sample and locality as A, note fragmentary basal plate around part of pit and beginning of posterior keel. **C** – upper view of SB 39, 40 cm above the base of the Choteč Limestone, Na Škrábku quarry at Choteč, Prague Basin, *costatus* Zone. **D** – upper view of SUI 133903, an atypical specimen with adcarinal grooves instead of troughs, northern Antelope Range, central Nevada, section V, sample VG-25 (Johnson *et al.* 1996, table 2), basal *costatus* Zone. **E₁, E₂** – lower and upper views of SUI 133904, northern Antelope Range, section V, sample VH-17, uppermost sample of *partitus* Zone (Johnson *et al.* op. cit.). **F₁, F₂** – lower and upper views of SUI 133905, same locality as E but sample VH-16, 0.3 m below VH-17, upper *partitus* Zone. All magnifications are $\times 40$

This species has been carried in open nomenclature for a long time, with many consistently identified specimens (see synonymy); it was formally named by Bardashev (1992). The principal distinction between *Polygnathus praetrigonicus* and *P. trigonicus* Bischoff and Ziegler (1957, p. 97–98, pl. 5, figs 1–6; Klapper 1973, p. 387–388) is that the pit is at or extremely close to the anterior end of the platform in the latter species. The platform outlines of the two are similar, but in *P. praetrigonicus* the strong transverse ridges are commonly shorter and separated from the carina by wider adcarinal troughs anteriorly. There are exceptions to this distinction, however, in which relatively narrow anterior grooves instead of troughs are present in rare specimens of *P. praetrigonicus* (e.g., Text-fig. 7D). Diagonal rows of nodes are commonly developed anteriorly in *P. trigonicus* (e.g., Wittekindt 1966, pl. 3, fig. 1), whereas diagonal ridges in the same position are only

rarely developed in *P. praetrigonicus*, as noted above. The illustrated Pa element of Mawson and Talent (1994, pl. 2, fig. 16) has a much narrower platform than in the present species and that of Mawson and Talent (2005, figs 4 C, D) has a quite different platform outline.

Savage (1995, p. 550, figs. 8.8, 8.9) named a new species from the Wadleigh Limestone of Alaska as *Polygnathus praetrigonicus*, including earlier specimens that he had identified as *P. trigonicus* (Savage 1977, p. 1353, pl. 1, figs 1–12). As the name proposed by Bardashev (1992) has priority, Savage (2011) proposed *P. bagialensis* as the replacement name for the Wadleigh species. Wadleigh Pa elements differ from those of *P. trigonicus* in that the pit lies distinctly posterior of the anterior platform margin. They differ from those of *P. praetrigonicus* Bardashev in that the platform in mature Pa elements is relatively longer and narrower and there are a few randomly distributed but prominent nodes an-



Text-fig. 8. *Polygnathus pseudocostatus* sp. nov.; all specimens are Pa elements from central Nevada. Specimens in figs. A, C-E are from the northern Antelope Range, section V, sample VH-8, *partitus* Zone (Johnson *et al.* 1996, table 2, see revision of zonal identifications in Vodrážková *et al.* 2011, p. 739). Specimens in figs. B, F, G are from the same locality as A, but from sample VH-7, 0.5 m above base of *partitus* Zone and 0.1 m below VH-8. A – upper view of SUI paratype 133906, juvenile specimen. B₁, B₂ – lower and upper views of SUI paratype 133907. C – upper view of SUI paratype 133908. D – upper view of SUI paratype 133909. E₁, E₂ – lower and upper views of SUI paratype 133910. F₁, F₂ – upper and lower views of SUI holotype 133911. G₁, G₂ – upper and lower views of SUI paratype 133912. All magnifications are $\times 40$

teriorly. Furthermore, the Wadleigh species has narrow adcarinal grooves anteriorly rather the commonly wide adcarinal troughs seen in Bardashev's species.

RANGE: The lowest occurrences of *Polygnathus praetrigonicus* in the Prague Basin and in New York are in the basal *costatus* Zone. In the northern Antelope Range, central Nevada, the species ranges from the uppermost part of the *partitus* Zone to the basal *costatus* Zone. Elsewhere the species is in unconstrained parts of the *costatus* Zone (see discussion under Biostratigraphy).

Polygnathus pseudocostatus sp. nov.
(Text-fig. 8A–G)

HOLOTYPE: SUI 133911, illustrated on Text-fig. 8F, from the northern Antelope Range, central Nevada, section V, sample VH-7, *partitus* Zone.

MATERIAL: Thirty-three specimens from the northern Antelope Range, central Nevada: VH-6 (one specimen), VH-7 (eight specimens), VH-8 (14 specimens), VH-9 (8 specimens), all from the *partitus* Zone; VB-1 (one specimen), VG-25 (one specimen), lower *costatus* Zone (Johnson *et al.* 1996, table 2; see revision of zonal identifications discussed in Vodrážková *et al.* 2011, p. 739). Three specimens from the northern Hot Creek Range, central Nevada, Summit 8782 section, 10A (two specimens, Johnson *et al.* 1986, table 8; Vodrážková *et al.* 2011, p. 741), probable *partitus* Zone, 8A (one specimen), *costatus* Zone.

DIAGNOSIS: Representative Pa elements have a relatively long and narrow platform set with strong transverse ridges separated from the carina by adcarinal grooves. Platform margins in posterior half commonly strongly corrugated with prominent furrows. Posterior carina commonly twisted or sig-

moidal. Moderately large pit lies somewhat anterior of platform midlength.

REMARKS: The extent of the carina varies from terminating coincident with the posterior margin of the platform to extending one denticle beyond. In an early ontogenetic specimen (Text-fig. 8A) it extends several denticles beyond the posterior margin of the platform. The exact termination of the carina is thus a highly variable intraspecific character.

Polygnathus pseudocostatus differs from *P. angusticostatus* Wittekindt (1966, p. 631, pl. 1, figs 15–18; Klapper 1971, pl. 3, figs 21–25; Weddige 1977, pl. 6, figs 102–104; Sparling 1981, p. 309, 311, pl. 1, figs 11, 13–18, 21–23), in which the platform margins in the posterior half are smooth and not set with corrugations. Furthermore, the carina is not twisted or sigmoidal as in some specimens of *P. pseudocostatus*. Whereas specimens of *P. angusticostatus* commonly have the carina extending several denticles beyond the posterior margin of the platform, there are some specimens in which the carina terminates at the posterior platform margin (e.g., Bultynck and Hollard 1980, pl. 3, fig. 17; Sparling 1981, pl. 1, fig. 17, 22).

RANGE: *partitus* Zone to *costatus* Zone.

CONCLUSIONS

- (1) High abundances of *Polygnathus serotinus* and *P. bultyncki* in restricted stratigraphic intervals allow us to recognize significant intraspecific and ontogenetic variation within samples from populations of these two prominent Emsian-Eifelian conodont species. Nine different names have been applied to *P. serotinus* and six to *P. bultyncki* by previous authors. We synonymize all these names because they represent either early ontogenetic stages or intraspecific variants of mature stages of the two species.
- (2) We recognize three different types of the diagnostic shelf-like protuberance on the outer side of the pit in the Pa element of *Polygnathus serotinus*. These three types are ontogenetically stable and occur consistently both in terms of geography and stratigraphy within the Prague Basin. Since they have no demonstrated biostratigraphic utility, and from a taxonomic viewpoint are most reasonably regarded as intraspecific variants, they are treated herein as informal morphotypes of *P. serotinus*.
- (3) An enlargement of the pit in early growth stages of *P. bultyncki* and a subsequent size decrease in later stages has been observed in 23 measured speci-

mens. However, we consider that this number of specimens is not large enough to rule out intraspecific variation as the cause of our observations. Thus, our study does not resolve this question.

- (4) The conodont zonation across the Emsian-Eifelian (Lower-Middle Devonian) boundary from the *serotinus* and *patulus* zones through the *partitus* Zone (basal Eifelian) into the *costatus* Zone is well developed in the Prague Basin. The Czech succession is comparable to that in central Nevada, with the exception that the *patulus* Zone is missing there due to a regional unconformity (Vodrážková *et al.* 2011, p. 739–741). The nominal species that define the lower boundaries of the first three zones all range into the *costatus* Zone, requiring a detailed sequence of closely spaced samples through several zones for confident zonal identification. The lowest occurrence of *Polygnathus praetrigonicus* may be taken as a working hypothesis to represent the basal *costatus* Zone in the Prague Basin as it does in the revised New York succession.

Acknowledgements

The order of authorship is alphabetical as we contributed equally to the paper. The study was begun in 2008 at the University of Iowa on S.V.'s meeting with G.K. and her study of the collections there. S.V.'s research was supported by the Czech Science Foundation (P210/12/2018), Alexander von Humboldt Foundation and the Czech-American Cooperation Program (Kontakt ME08011). S.V. also received support from the SYNTHESYS Project <http://www.synthesys.info/> which is financed by the European Community Research Infrastructure Action under the FP7 „Capacities“ Program.“ Z. Belka (Adam Mickiewicz University, Poznań), P. Bultynck (Royal Belgian Institute of Natural Sciences, Brussels) and C. Spalletta (University of Bologna) are to be thanked for their thorough reviews. J. Dzik (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) is gratefully acknowledged for discussion of the mode of growth of conodonts. S.V. thanks P. Bultynck and K. Weddige (Senckenberg Research Institute, Frankfurt am Main) for discussions on taxonomy of Lower and Middle Devonian conodonts. G.K. thanks C.A. Sandberg (U. S. Geological Survey, Denver) for taxonomic discussions involving this paper. The interpretations expressed in this paper, however, are solely those of the authors. This is our contribution to IGCP 596.

REFERENCES

- Apekina, L.S. 1984. Biostratigrafiya Devona Zerafshano-Gissarskoy Gornoy oblasti. *Tashkent*, 73–87. [In Russian]

- Apekina, L.S. and Mashkova, T.V. 1978. Conodonts. In: B.S. Sokolov (Ed), Atlas of the Paleontological Plates: Supplement to a Guide of the Field Excursions. Tashkent, pls 73–78.
- Austin, R.L., Orchard, M.J. and Stewart, I.J. 1985. Conodonts of the Devonian System from Great Britain. In: A.C. Higgins and R.L. Austin (Eds), A stratigraphical index of conodonts. *Ellis Horwood Limited, Chichester, West Sussex*, 93–166.
- Bai, S.L. 1994. Systematic Paleontology, Part 1. Conodonts and Miscellaneous. In: Bai, S.L., Bai, Z.Q., Ma, X.P., Wang, D.R. and Sun, Y.L. Devonian Events and Biostratigraphy of South China. Peking University Press, 161–195, 276–298.
- Bardashev, I. A. 1990. Konodonty i stratigrafiya eifel'skikh otlozheniy Tsentral'nogo Tadzhikistana. In: V.G. Khalymbadza (Ed), Konodonty eifel'skogo yarusa SSSR., pp. 25–40. Izdatel'stvo Kazanskogo Universiteta. [In Russian]
- Bardashev, I.A. 1992. Conodont stratigraphy of Middle Asian Middle Devonian. *Courier Forschungsinstitut Senckenberg*, **154**, 31–83.
- Bardashev, I.A. and Ziegler, W. 1986. Conodonts from a Middle Devonian section in Tadzhikistan (Kalagach Fm., Middle Asia, USSR). *Courier Forschungsinstitut Senckenberg*, **75**, 65–77. [date of imprint, 1985]
- Bardashev, I.A. and Ziegler, W. 1992. Conodont biostratigraphy of Lower Devonian deposits of the Shishkat section (southern Tien-Shan, Middle Asia). *Courier Forschungsinstitut Senckenberg*, **154**, 1–29.
- Bardashev, I. A., Weddige, K. and Ziegler, W. 2002. The phylogenesis of some Early Devonian platform conodonts. *Senckenbergiana lethaea*, **82**, 375–451.
- Bełka, Z., Kaufmann, B. and Bultynck, P. 1997. Conodont-based quantitative biostratigraphy for the Eifelian of the eastern Anti-Atlas, Morocco. *Geological Society of America Bulletin*, **109**, 643–651.
- Bełka, Z., Klug, C., Kaufmann, B., Korn, D., Döring, S., Feist, R. and Wendt, J. 1999. Devonian conodont and ammonoid succession of the eastern Tafilalt (Ouidane Chebbi section), Anti-Atlas, Morocco. *Acta Geologica Polonica*, **49**, 1–23.
- Berkyová, S. 2009. Lower-Middle Devonian (upper Emsian-Eifelian, *serotinus-kockelianus* zones) conodont faunas from the Prague Basin, the Czech Republic. *Bulletin of Geosciences* **84**, 667–686.
- Bischoff, G. and Ziegler, W. 1957. Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, **22**, 136 pp.
- Bončeva, I. 1992. Emsian representatives of the conodont genus *Polygnathus* Hinde, 1879 from southwest Bulgaria. *Geologica Balcanica*, **22**, 33–45.
- Brown, J.O. 1982. Search for a western North American stratotype for the Lower-Middle Devonian boundary in Eureka County, Nevada. Unpublished M.S. thesis, Oregon State University, 75 pp.
- Bultynck, P. 1970. Révision stratigraphique et paléontologique (Brachiopodes et Conodontes) de la Coupe type du Couvinien. *Mémoires de l'Université de Louvain*, **26**, 152 pp.
- Bultynck, P. 1976. Le Silurien supérieur et le Devonien inférieur de la Sierra de Guadarrama (Espagne centrale). Troisième partie: éléments icriodiformes, pelekysgnathiformes et polygnathiformes. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique*, **49**, 74 pp.
- Bultynck, P. 1986. Lower Devonian (Emsian) – Middle Devonian (Eifelian and lowermost Givetian) conodont successions from the Ma'der and the Tafilalt, southern Morocco. *Courier Forschungsinstitut Senckenberg*, **75**, 261–285. [date of imprint, 1985]
- Bultynck, P. and Hollard, H. 1980. Distribution compare de Conodontes et Goniatites dévoniens des plaines du Dra, du Ma'der et du Tafilalt (Maroc). *Aardkundige Mededelingen*, **1**, 73 pp.
- Chlupáč, I. 1982. Preliminary submission for Lower – Middle Devonian boundary stratotype in the Barrandian area. *Courier Forschungsinstitut Senckenberg*, **55**, 85–95.
- Clark, D.L. and Müller, K.J. 1968. The basal opening of conodonts. *Journal of Paleontology*, **42**, 561–570.
- Cowie, J.W., Ziegler, W. and Remane, J. 1989. Stratigraphic Commission accelerates progress, 1984 to 1989. *Episodes*, **12**, 79–83.
- Dzik, J. 2002. Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, **47**, 565–650.
- Dzik, J. 2006. The Famennian “Golden Age” of conodonts and ammonoids in the Polish part of the Variscan Sea. *Palaeontologica Polonica*, **63**, 359 pp.
- Forey, P.L., Fortey, R.A., Kenrick, P. and Smith, A.B. 2004. Taxonomy and fossils: a critical appraisal. *Philosophical Transactions of the Royal Society of London*, **B 359**, 639–653.
- Hass, W. H. 1941. Morphology of conodonts. *Journal of Paleontology*, **15**, 71–81.
- Johnson, J.G., Klapper, G. and Elrick, M. 1996. Devonian transgressive-regressive cycles and biostratigraphy, northern Antelope Range, Nevada: Establishment of reference horizons for global cycles. *Palaaios*, **11**, 3–14.
- Johnson, J.G., Klapper, G., Murphy, M.A. and Trojan, W.R. 1986. Devonian Series boundaries in central Nevada and neighboring regions, western North America. *Courier Forschungsinstitut Senckenberg*, **75**, 177–196. [date of imprint, 1985]
- Klapper, G. 1971. Sequence within the conodont genus *Polyg-*

- nathus* in the New York lower Middle Devonian. *Geologica et Palaeontologica*, **5**, 59–79.
- Klapper, G. 1973. *Polygnathus trigonicus* Bischoff and Ziegler. In: W. Ziegler (Ed), Catalogue of conodonts, **I**, pp. 344, 387–388. E. Schweizerbart'sche Verlagsbuchhandlung; Stuttgart.
- Klapper, G. 1977. *Polygnathus linguiformis linguiformis* Hinde alpha morphotype Bultynck; *Polygnathus serotinus* Telford. In: W. Ziegler (Ed), Catalogue of conodonts, **III**, pp. 462, 492, 495–496. E. Schweizerbart'sche Verlagsbuchhandlung; Stuttgart.
- Klapper, G. 1981. Review of New York Devonian conodont biostratigraphy. In: W. A. Oliver, Jr. and G. Klapper (Eds), Devonian biostratigraphy of New York, Part 1. Text, pp. 57–66. International Union of Geological Sciences, Subcommittee on Devonian Stratigraphy.
- Klapper, G. and Johnson, D.B. 1975. Sequence in conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. *Geologica et Palaeontologica*, **9**, 65–83.
- Klapper, G. and Johnson, J.G. 1980. Endemism and dispersal of Devonian conodonts. *Journal of Paleontology*, **54**, 400–455.
- Klapper, G. and Oliver, W.A., Jr. 1995. The Detroit River Group is Middle Devonian: Discussion on “Early Devonian age of the Detroit River Group, inferred from Arctic stromatoporoids.” *Canadian Journal of Earth Sciences*, **32**, 1070–1073.
- Klapper, G., Ziegler, W. and Mashkova, T.A. 1978. Conodonts and correlation of Lower-Middle Devonian boundary beds in the Barrandian area of Czechoslovakia. *Geologica et Palaeontologica*, **12**, 103–115.
- Koike, T. 1992. Morphological variation in Spathian conodonts *Spathoicriodus collinsoni* (Solien) from the Taho Limestone, Japan. In: K. Ishizaki and T. Saito (Eds), Centenary of Japanese Micropaleontology. *Terra Scientific Publishing Company, Tokyo*, 355–364.
- Lane, H.R. and Ormiston, A.R. 1979. Siluro-Devonian biostratigraphy of the Salmontrout River area, east-central Alaska. *Geologica et Palaeontologica*, **13**, **39**, 39–95.
- Lane, H.R., Müller, K.J. and Ziegler, W. 1979. Devonian and Carboniferous conodonts from Perak, Malaysia. *Geologica et Palaeontologica*, **13**, 213–225.
- Lindström, M. 1964. Conodonts, 196 pp. Elsevier; Amsterdam, London, New York.
- Lindström, M. and Ziegler, W. 1971. Feinstrukturelle Untersuchungen an Conodonten. 1. Die Überfamilie Panderodontacea. *Geologica et Palaeontologica*, **5**, 9–33.
- Long, J.A. and Burrett, C.F. 1989. Early Devonian conodonts from the Kuan Tung Formation, Thailand: Systematics and biogeographic considerations. *Records of the Australian Museum*, **41**, 121–133.
- Machado, G., Hladil, J., Slavik, L., Koptikova, L., Moreira, N., Fonseca, M. and Fonseca, P. 2010. An Emsian-Eifelian calciturbidite sequence and the possible correlatable pattern of the basal Choteč event in western Ossa-Morena Zone, Portugal (Odivelan Limestone). *Geologica Belgica*, **13**, 431–446.
- Martínez-Pérez, C. and Valenzuela-Ríos, J.I. 2012. Polygnathids (Conodonta) around the lower/upper Emsian boundary from the La Guardia d'Àres section (Lower Devonian, Spanish Central Pyrenees). *Bollettino della Società Paleontologica Italiana*, **51**, 193–202.
- Mashkova, T.V. and Apekina, L.S. 1981. Novye Devonskie konodonty *Polygnathus kimi* iz zony *patulus* Zeravshanskogo khrebt. *Paleontologicheskii Zhurnal*, **1981**, 145–147. [In Russian]
- Mawson, R. 1987a. Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology*, **30**, 251–297.
- Mawson, R. 1987b. Documentation of conodont assemblages across the Early Devonian – Middle Devonian boundary, Broken River Formation, north Queensland, Australia. *Courier Forschungsinstitut Senckenberg*, **92**, 251–273.
- Mawson, R. and Talent, J.A. 1989. Late Emsian – Givetian stratigraphy and conodont biofacies – carbonate slope and offshore shoal to sheltered lagoon and nearshore carbonate ramp – Broken River, north Queensland, Australia. *Courier Forschungsinstitut Senckenberg*, **117**, 205–259.
- Mawson, R. and Talent, J.A. 1994. The Tamworth Group (mid-Devonian) at Attunga, New South Wales: conodont data and inferred ages. In: P. Königshof and R. Werner (Eds), Willi Ziegler – Festschrift I, *Courier Forschungsinstitut Senckenberg*, **168**, 37–59.
- Mawson, R. and Talent, J.A. 1997. Famennian – Tournaisian conodonts and Devonian – Early Carboniferous transgressions and regressions in northeastern Australia. In: G. Klapper, M.A. Murphy, and J.A. Talent (Eds), Paleozoic sequence stratigraphy, biostratigraphy, and biogeography: Studies in honor of J. Granville (“Jess”) Johnson. *Geological Society of America, Special Paper* **321**, 189–233.
- Mawson, R. and Talent, J.A. 2003. Conodont faunas from sequences on or marginal to the Anakie Inlier (central Queensland, Australia) in relation to Devonian transgressions. *Bulletin of Geosciences*, **78**, 335–358.
- Mawson, R. and Talent, J.A. 2005. Conodont data and correlations: In: Taube, A., Mawson, R., and Talent, J.A., Repetition of the Mount Morgan stratigraphy and mineralization in the Dee Range, northeastern Australia: Implications for exploration. *Economic Geology*, **100**, 375–384.
- Mawson, R., Talent, J.A. and Furey-Greig, T.M. 1995. Coincident conodont faunas (late Emsian) from the Yarrol and Tamworth belts of northern New South Wales and central Queensland. In: R. Mawson and J.A. Talent (Eds), Contributions to the First Australian Conodont Symposium (AUSCOS 1) held in Sydney, Australia, 18–21. July 1995. *Courier Forschungsinstitut Senckenberg*, **182**, 421–445.

- Meço, S. 2010. Litho-biostratigraphy and the conodonts of Palaeozoic/Triassic deposits in Albania. *Palaeontographica, Abteilung A*, **290** (4-6), 131–197.
- Miller, C.G. 2007. Growth in early species of the conodont *Ancyrodella* and implications for correlation of the Middle – Upper Devonian boundary. *Geological Quarterly*, **51**, 443–452.
- Mirăuță, E. 1971. Étude des Conodontes dévoniens de la Dobrogea septentrionale (Zone de Tulcea). *Mémoires Institut Géologique Romania*, **14**, 7–34.
- Müller, K.J. 1956. Taxonomy, nomenclature, orientation, and stratigraphic evaluation of conodonts. *Journal of Paleontology*, **30**, 1324–1340.
- Müller, K.J. and Clark, D.L. 1967. Early Late Devonian conodonts from the Squaw Bay Limestone in Michigan. *Journal of Paleontology*, **41**, 902–919.
- Müller, K.J. and Müller, E.M. 1957. Early Upper Devonian (Independence) conodonts from Iowa, part I, *Journal of Paleontology*, **31**, 1069–1108.
- Murphy, M.A. 2005. Pragian conodont zonal classification in Nevada, western North America. *Revista Española de Paleontología*, **20**, 177–206.
- Perry, D.G., Klapper, G. and Lenz, A.C. 1974. Age of the Ogilvie Formation (Devonian), northern Yukon: Based primarily on the occurrence of brachiopods and conodonts. *Canadian Journal of Earth Sciences*, **11**, 1055–1097.
- Phillip, G.M. and Jackson, J.H. 1967. Lower Devonian subspecies of the conodont *Polygnathus linguiformis* Hinde from southeastern Australia. *Journal of Paleontology*, **41**, 1262–1266.
- Pickett, J. 1978. Conodont faunas from the Mount Frome Limestone (Emsian/Eifelian), New South Wales. In: D.J. Belford and V. Scheibnerová (Eds), *The Crespian Volume: Essays in honour of Irene Crespian*. *Australia Bureau of Mineral Resources, Geology and Geophysics, Bulletin*, **192**, 97–107.
- Pyle, L.J., Orchard, M.J., Barnes, C.R. and Landry, M.L. 2003. Conodont biostratigraphy of the Lower to Middle Devonian Deserters Formation (new), Road River Group, northeastern British Columbia. *Canadian Journal of Earth Sciences*, **40**, 99–113.
- Sandberg, C.A. and Ziegler, W. 1973. Refinement of Standard Upper Devonian conodont zonation based on sections in Nevada and West Germany. *Geologica et Palaeontologica*, **7**, 97–121.
- Savage, N.M. 1977. Middle Devonian (Eifelian) conodonts of the genus *Polygnathus* from the Wadleigh Limestone, southeastern Alaska. *Canadian Journal of Earth Sciences*, **14**, 1343–1355.
- Savage, N.M. 1995. Middle Devonian conodonts from the Wadleigh Limestone, southeastern Alaska. *Journal of Paleontology*, **69**, 540–555.
- Savage, N.M. 2011. *Polygnathus bagialensis*, new name for the homonymous *P. praetrigonicus* Savage, 1995, and *Polygnathus abbessensis*, new name for the homonymous *P. borealis* Savage, 1995 (Conodontes, Polygnathidae). *Journal of Paleontology*, **85**, p. 805.
- Schönlaub, H.-P. 1985. Plates 1 and 2. In: Feist, R., Schönlaub, H.-P. and Bultynck, P., *Faciès et biostratigraphie (conodontes) du passage Dévonien inférieur-moyen dans la Montagne Noire (France)*. *Hercynica*, **1**, 81–97.
- Schönlaub, H.P. 1986. Devonian conodonts from section Oberbuchach II in the Carnic Alps (Austria). *Courier Forschungsinstitut Senckenberg*, **75**, 353–373. [date of imprint, 1985]
- Scott, A.J. and Collinson, C. 1959. Intraspecific variability in conodonts: *Palmatolepis glabra* Ulrich and Bassler. *Journal of Paleontology*, **33**, 550–565.
- Slavík, L., Valenzuela-Ríos, J.I., Hladil, J. and Carls, P. 2007. Early Pragian conodont-based correlations between the Barrandian area and the Spanish central Pyrenees. *Geological Journal*, **42**, 499–512.
- Sloan, T. R. *et al.* 1995. Conodont data from Silurian-Middle Devonian carbonate fans, debris flows, allochthonous blocks and adjacent autochthonous platform margins: Broken River and Camel Creek areas, north Queensland, Australia. In: R. Mawson and J.A. Talent (Eds), *Contributions to the First Australian Conodont Symposium (AUSCOS 1) held in Sydney, Australia, 18–21. July 1995*. *Courier Forschungsinstitut Senckenberg*, **182**, 1–77.
- Snigireva, M.P. 1975. Novye konodonty iz srednedevonskikh otlozheniy Severnogo Urala. *Paleontologicheskij Zhurnal*, **1975**, 24–30. [In Russian]
- Solien, M.A. 1979. Conodont biostratigraphy of the Lower Triassic Thaynes Formation, Utah. *Journal of Paleontology*, **53**, 276–306.
- Sparling, D.R. 1981. Middle Devonian conodont apparatuses with seven types of elements. *Journal of Paleontology*, **55**, 295–316.
- Sparling, D.R. 1983. Conodont biostratigraphy and biofacies of Lower Middle Devonian limestones, north-central Ohio. *Journal of Paleontology*, **57**, 825–864.
- Sparling, D.R. 1988. Middle Devonian stratigraphy and conodont biostratigraphy, north-central Ohio. *Ohio Journal of Science*, **88**, 2–18.
- Sweet, W.C. 1981. Macromorphology of elements and apparatuses. In: Clark, D.L. *et al.*, *Conodonts*. In: R.A. Robison (Ed), *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 2*. Geological Society of America and The University of Kansas, Lawrence, 202 p.
- Sweet, W.C. 1988. *The Conodonts: Morphology, Taxonomy, Paleoecology, and Evolutionary History of a Long-Extinct Animal Phylum*, 212 pp. Oxford, Clarendon Press; New York, Oxford.
- Talent, J.A. and Mawson, R. 1994. Conodonts in relation to age and environmental framework of the Burdekin Basin (Mid-

- Devonian), north-eastern Australia. In: P. Königshof and R. Werner (Eds), Willi Ziegler – Festschrift I, *Courier Forschungsinstitut Senckenberg*, **168**, 61–81.
- Telford, P. G. 1975. Lower and Middle Devonian conodonts from the Broken River Embayment, north Queensland, Australia. *Special papers in palaeontology*, **15**, 96 pp.
- Uyeno, T. T. 1982. Conodont study. In: Uyeno, T. T., Telford, P. G., and Sanford, B. V., Devonian conodonts and stratigraphy of southwestern Ontario. *Geological Survey of Canada, Bulletin*, **332**, p. 23–55.
- Uyeno, T.T., with contributions by U. Mayr and R.F. Roblesky. 1990. Biostratigraphy and conodont faunas of Upper Ordovician through Middle Devonian rocks, eastern Arctic Archipelago. *Geological Survey of Canada, Bulletin*, **401**, 211 pp.
- Uyeno, T.T. 1991. Pre-Famennian Devonian conodont biostratigraphy of selected intervals in the eastern Canadian Cordillera. In: M.J. Orchard and A.D. McCracken (Eds), Ordovician to Triassic conodont paleontology of the Canadian Cordillera. *Geological Survey of Canada, Bulletin*, **417**, 129–161.
- Uyeno, T.T. and Klapper, G. 1980. Summary of conodont biostratigraphy of the Blue Fiord and Bird Fiord formations (Lower-Middle Devonian) at the type and adjacent areas, southwestern Ellesmere Island, Canadian Arctic Archipelago. In: Current Research. Part C. *Geological Survey of Canada, Paper 80-1C*, 81–93.
- Vodrážková, S., Klapper, G. and Murphy, M. A. 2011. Early Middle Devonian conodont faunas (Eifelian, *costatus-kockelianus* zones) from the Roberts Mountains and adjacent areas in central Nevada. *Bulletin of Geosciences*, **86**, 737–764.
- von Bitter, P.H., Sandberg, C.A. and Orchard, M.J. 1986. Phylogeny, speciation, and palaeoecology of the Early Carboniferous (Mississippian) conodont genus *Mestognathus*. Royal Ontario Museum Life Sciences Contribution, **143**, 115 pp.
- Vorontsova, T.N. and Kuz'min, A.V. 1984. Rasprostranenie novykh vidov konodontov roda *Polygnathus* v Famenskikh otlozheniyakh Tsentral'nogo Kazakhstana. *Izvestiya Akademii Nauk SSSR, seriya geologicheskaya*, **1984**, 58–64. [In Russian]
- Wang, Cheng-Yuan 1979. Some conodonts from the Sipai Formation in Xiangzhou of Guangxi. *Acta Palaeontologica Sinica*, **18**, 395–407.
- Wang, Cheng-Yuan and Ziegler, W. 1983. Devonian conodont biostratigraphy of Guangxi, south China, and the correlation with Europe. *Geologica et Palaeontologica*, **17**, 75–107.
- Weddige, K. 1977. Die Conodonten der Eifel-Stufe im TYPUSgebiet und in benachbarten Faziesgebieten. *Senckenbergiana lethaea*, **58**, 271–419.
- Weddige, K. 1982. The Wetteldorf Richtschnitt as boundary stratotype from the view point of conodont stratigraphy. In: R. Werner and W. Ziegler (Eds), Proposal of a boundary stratotype for the Lower/Middle Devonian boundary (*partitus*-boundary). In: W. Ziegler and R. Werner (Eds), On Devonian stratigraphy and palaeontology of the Ardenno-Rhenish Mountains and related Devonian matters. *Courier Forschungsinstitut Senckenberg*, **55**, 26–37.
- Weddige, K., Werner, R. and Ziegler, W. 1979. The Emsian-Eifelian boundary: An attempt at correlation between the Eifel and Ardennes regions. *Newsletters on Stratigraphy*, **8**, 159–169.
- Wittekindt, H. 1966. Zur Conodontenchronologie des Mitteldevons. *Fortschritte in der Geologie von Rheinland und Westfalen*, **9**, 621–646. [date of imprint, 1965]
- Xiong, J. 1980. Conodonts. In: Xian, S. *et al.*, Nandan typical stratigraphy and paleontology of Devonian, in south China. *Guizhou Peoples Press, Guiyang*, 82–100, 150–154. [In Chinese]
- Xiong, J. 1981. Discovery of conodonts in the Najiao Formation of Guangxi. *Acta Palaeontologica Sinica*, **20**, 542–545.
- Ziegler, W. 1956. Unterdevonische Conodonten, insbesondere aus dem Schönauer und dem Zоргensis-Kalk. *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **84**, 93–106.
- Ziegler, W. and Klapper, G. 1982. Subcommission on Devonian Stratigraphy: Decisions since 1973 and present status. In: W. Ziegler and R. Werner (Eds), On Devonian stratigraphy and palaeontology of the Ardenno-Rhenish Mountains and related Devonian matters. *Courier Forschungsinstitut Senckenberg*, **55**, 7–11.
- Ziegler, W. and Sandberg, C.A. 1984. *Palmatolepis*-based revision of upper part of standard Late Devonian conodont zonation. In: D.L. Clark (Ed.), Conodont biofacies and provincialism. *Geological Society of America, Special Paper*, **196**, 179–194.
- Ziegler, W. and Wang, Cheng-Yuan. 1986. Sihongshan section, a regional reference section for the Lower-Middle and Middle-Upper Devonian boundaries in east Asia. *Courier Forschungsinstitut Senckenberg*, **75**, 17–37, [date of imprint, 1985]

Manuscript submitted: 31th January 2013

Revised version accepted: 25th April 2013

ADDENDUM: After this paper was submitted, an additional reference involving *Polygnathus serotinus* has been published: Klapper, G., Crônier, C., and Vodrážková, S. 2012. Conodont evidence for a latest Emsian to early Eifelian (Devonian) age for the phacopid trilobite *Plagiolaria kitabi* from Uzbekistan. *Memoirs of the Association of Australasian Palaeontologists*, **44**, 25–26.