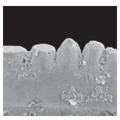
Morphologically distinct P_1 elements of *Zieglerodina* (Conodonta) at the Silurian–Devonian boundary: review and correlation

Aneta Hušková & Ladislav Slavík



The P_1 elements of the conodonts *Zieglerodina paucidentata* Murphy & Matti, 1982, and *Zieglerodina petrea* Hušková & Slavík, 2020, share similar gap in their denticulation, a characteristic easily recognizable among rather morphologically similar spathognathodontids from near the Silurian–Devonian boundary. The ambiguity in the diagnosis of *Z. paucidentata* (an earliest Lochkovian species) may affect precision in the recognition of the boundary. New geographic occurrences of *Z. petrea* in the Cellon section from the Carnic Alps, and *Z.* cf. *paucidentata* from the Atrous section in Morocco is reported. The revised data have shown that some specimens previously described as *Z. paucidentata* or *Z.* cf. *paucidentata* probably belong to other taxa; and therefore, their applicability for correlation of the Silurian–Devonian boundary is limited. • Key words: Silurian–Devonian boundary, conodonts, biostratigraphy.

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In many parts of the world, the base of the Devonian is generally characterized by the prevailing onset of carbonate sedimentation. The index fossil for the base of the Lochkovian is the graptolite *Monograptus uniformis* Přibyl, 1940; however, because of dominating carbonates, the lowermost Devonian stratigraphy must rely on other faunal groups, especially conodonts. Owing to their abundance in carbonate successions and their global distribution, in many cases conodonts are the only faunal group that permits recognition of the Silurian–Devonian boundary (corresponds to the conodont *hesperius–optima* Zone). In many studies over the past decades conodont zonations for the uppermost Přídolí and the lowermost Lochkovian had been established (*e.g.*, Walliser 1964, Klapper 1977, Ziegler 1979, Jeppsson 1988, Aldridge & Schönlaub 1989, Nowlan 1995, Corradini & Serpagli 1999, Corriga & Corradini 2009, Corradini & Corriga 2012, Slavík *et al.* 2012, Schönlaub *et al.* 2017, Slavík *in* Vacek *et al.* 2018, Spiridonov *et al*. 2020; for a detailed overview see Hušková & Slavík 2020).

In spite of the general consensus of the biostratigraphical importance of the entry of *Icriodus* Branson & Mehl, 1938, and recognition of the *hesperius* or *hesperius–optima* zones for the lowermost Lochkovian (Corradini & Corriga 2012, Slavík *et al.* 2012, Schönlaub *et al.* 2017, Slavík *in* Vacek *et al.* 2018), in some sections these important markers are missing due to paleoenvironmental constrains. The frequent absence of icriodontids, which were dependent on a shallower-water environment and less tolerant to water depth (*cf.* Hušková & Slavík 2020), makes biostratigraphical correlation of the boundary problematic (see Jeppsson 1988 1989; Corradini & Corriga 2010; Zhao & Zhu 2014; Slavík 2017). As a consequence, some recent studies were focused on the ozarkodinids (family Spathognathodontidae) and its potential for the improvement of the global conodont biostratigraphy of the Silurian–Devonian boundary (*e.g.*, Murphy *et al.* 2004, Carls *et al.* 2007, Slavík 2011, Slavík *et al.* 2012, Corradini & Corriga 2012, Peavey 2013, Hušková & Slavík 2020). Representatives of this conodont family are critical for the biostratigraphic subdivision of both the Přídolí: *e.g.*, *Zieglerodina zellmeri* Carls *et al.*, 2007; *Z. ivochlupaci* Carls *et al.*, 2007; "*Ozarkodina*" *eosteinhornensis* s.s. (Walliser, 1964); *Z. klonkensis* Carls *et al.*, 2007 (Slavík *in* Vacek *et al.* 2018); *Z. eladioi* (Valenzuela-Ríos, 1994); and the Lochkovian *O. optima* (Moskalenko, 1966); *Z. remscheidensis* (Ziegler, 1960); *Wurmiella excavata* (Branson et Mehl, 1933); and others (*cf.* Slavík *et al.* 2012).

The genus *Zieglerodina* Murphy, Valenzuela-Ríos & Carls, 2004 includes critical species for biostratigraphy previously placed in the "*remscheidensis* Group" of ozarkodinids (*e.g.*, *Z. remscheidensis*, *Z. klonkensis*, *Z. ivochlupaci*, *Z. zellmeri*, and *Z. eladioi*). The species recently added to this genus are *Z. paucidentata* Murphy & Matti, 1982, re-classified by Drygant & Szaniawski (2012), and *Z. petrea* Hušková & Slavík, 2020. In this paper the lowermost Devonian occurrences of these two taxa are discussed, including the material from Otto Walliser's collection, which was studied at Göttingen University. The aim of the present paper is to compare the conodont succession in the samples from the different sections with a focus on the distinct denticulation in spathognathodontid platform elements of *Zieglerodina* and their potential for biostratigraphical correlation of the Silurian–Devonian boundary. The specimens studied come from several sections of different areas of the world; *e.g.*, Cellon section (Carnic Alps, Austria), Altrous 3 section (Anti-Atlas, Morocco), and Klonk section (Prague Synform, Czech Republic). The conodont specimens were also compared with those from the Praha-Radotín and Na Požárech sections (Prague Synform, Czech Republic).

Silurian–Devonian boundary – Historical overview

Barrande (1846) included the lowermost Lochkovian beds with a dominance of carbonates in his "Étage Ee2", while the overlying "Étage Ff1" unites sequences of shales and carbonate beds. These "Étages" were identified in the Prague Synform and have been used all over the world until close to the end of the 20th century. In 1984 (Kříž *et al.* 1986), modern subdivisions were established – including Přídolí (for the uppermost Silurian) and Lochkovian (for the lowermost Devonian).

The GSSP section of the Silurian–Devonian boundary was defined in 1972 at the Klonk section in the Prague Synform. Since then, many biostratigraphic studies have been performed including the very detailed paleontological studies on trilobites by Chlupáč (1971, 1983); brachiopods by Havlíček & Štorch (1990), Havlíček (1999); bivalves by Kříž (1998, 1999); cephalopods by Manda (2001), Manda & Frýda (2010); gastropods by Frýda & Manda (1997); chitinozoa by Paris *et al.* 1981, Fatka *et al.* (2006), *etc.*; conodonts by Barnett (1972), Mehrtens & Barnett (1976), Jeppsson (1988, 1989), Slavík (2004a,b, 2011, 2017), Carls *et al.* (2005, 2007, 2008), Slavík *et al.* (2009, 2010, 2012), Slavík & Carls (2012), Slavík & Hladil (2020); as well as sedimentological and geochemical studies by Hladil (1991, 1992), Crick *et al.*, (2001), Frýda *et al.* (2002), Buggisch & Mann (2004), Vacek (2007), Lehnert *et al.* (2007), Vacek *et al.* (2010), Koptíková *et al.* (2010a, 2010b), Manda & Frýda (2010), Munnecke *et al.* (2011), Gocke *et al.* (2012), and Vacek *et al.* (2018).

There are many regions where the Silurian–Devonian boundary has been documented: Australia – New South Wales and Victoria (Garratt & Wright 1988, Packham *et al.* 2001, Vérard 2009); Argentine – Precordillera (García-Muro *et al.* 2014); Algeria (Kermandji 2007); Canada – Canadian Arctic islands, Ontario and Yukon Territory (Lenz 1968, 1982, 1988; Telford 1988; Märss *et al.* 1998); China – Yunnan Province and Guangxi Province (Zhao & Zhu 2010, 2014; Zhao *et al.* 2015); England (Holland & Richardson *in* Martinsson *et al.* 1977); Greenland (Blom 1999); Germany – Frankenwald (Carls *et al.* 2007); Italy – Carnic Alps and Sardinia (Corriga & Corradini 2009; Corradini & Corriga 2010, 2012; Corriga *et al.* 2016); Kazakhstan (Bandaletov & Mikhajlova 1971); Libya (Rubinstein & Steemans 2002); Morocco – Anti-Atlas (Crick *et al.* 2001, Lubeseder 2008, Corriga *et al.* 2014); Mexico – Sonora (Boucot *et al.* 2008); Poland – Bardzkie Mountains (Porębska & Sawłowicz 1997); Russia – South Urals (Mavrinskaya & Slavík 2013); Spain – East Iberian Chains and Guadarrama (Carls *in* Martinsson 1977); Turkey – Hazro Area (Kranendonck 2004); Thailand (Burret *et al.* 1986); USA – Alaska (Blodgett *et al.* 1988), Nevada (Klapper & Murphy 1975, Murphy & Matti 1982), Appalachian Mountains (Saltzman 2002); Ukraine – Podolia (Paris & Grahn 1996; Drygant & Szaniawski 2009, 2012; Małkowski *et al.* 2009; Wrona 2009; Drygant 2010; Baliński 2012; Racki *et al.* 2012).

Paleogeographic distribution of Spathognathodontid conodonts

Spathognathodontid conodonts are abundant in strata around the Silurian–Devonian boundary. They have been described from many areas: *e.g.*, Australia – Queensland, New South Wales (Simpson 2000, Farrell 2004); Austria – Carnic Alps (Suttner 2009); Baltica – Lithuania (Spiridonov 2020); Czech Republic – Prague Synform (Walliser 1964, Schönlaub *in* Chlupáč *et al.* 1980, Kříž *et al.* 1986, Carls *et al.* 2007, Slavík 2011, Slavík *et al.* 2012, Hušková & Slavík 2020); Germany – Frankenwald (Carls *et al.* 2007); Italy – Carnic Alps and Sardinia (Walliser 1964; Corradini 2007; Corriga & Corradini 2009; Corradini & Corriga 2010, 2012; Corriga *et al.* 2016; Schönlaub *et al.* 2017); Mexico – Sonora (Boucot *et al.* 2008); Morocco – Anti-Atlas (Corriga *et al.* 2014); Pakistan – Peshawar Basin (Mawson *et al.* 2003); Spain – East Iberian Chains and Guadarrama (Carls *in* Martinsson 1977); USA – Alaska (Blodgett *et al.* 1988), Nevada (Klapper & Murphy 1975,

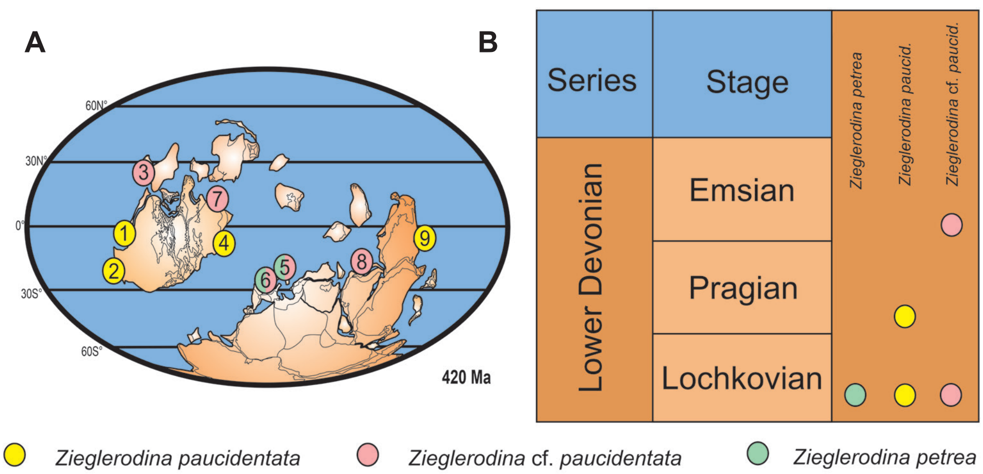

Figure 1. A – paleogeographic distribution of the *Zieglerodina paucidentata*, *Zieglerodina* cf. *paucidentata* and *Z. petrea* in the earliest Devonian. Legend: 1 – Coal Canyon, Nevada (Murphy & Matti 1982); 2 – Rancho Placeritos area, west–central Sonora, Mexico (Boucot *et al.* 2008); 3 – Mount Michelson, Alaska, USA (Blodgett *et al.* 1988); 4 – Podolia, Ukraine (Drygant & Szaniawski 2012); 5 – Prague Synform, Czech Republic (Hušková & Slavík 2020); 6 – Carnic Alps, Austria (Suttner *et al*. 2007, this contribution); 7 – South Urals, Russia (Mavrinskaya & Slavík 2013); 8 – Peshawar Basin, Pakistan (Mawson *et al.* 2003); 9 – Western New South Wales, Australia (Mathieson *et al.* 2016). • B – stratigraphic range of Lower Devonian taxa described as "*Zieglerodina paucidentata*", "*Zieglerodina* cf. *paucidentata*" and *Z. petrea*.

Murphy & Matti 1982), New York (Kleffner *et al.* 2009); Ukraine – Podolia (Drygant & Szaniawski 2009, 2012); Russia – South Urals (Mavrinskaya & Slavík 2013). Data from sections from Austria, Czech Republic, Germany, Missouri, and Nevada were incorporated into the novel taxonomic concept of Spathognathodontidae by Murphy *et al.* (2004), who re-classified many spathognathodontid taxa and established new genera. The latest Silurian spathognathodontids from North America were the subject of dissertation by Peavey (2013). Her study defined two different groups of taxa within the spathognathodontid family, which could be indicative of palaeoclimatic changes. Despite the representatives of the genus *Zieglerodina* that have been presented in all of above mentioned regions of the world, occurrences of *Z. paucidentata* and *Z. petrea* are also relatively widespread, but only in low numbers of specimens per sample (see Fig. 1 and Tab. 1 that show a global dispersal of taxa possessing a gap in denticulation = the "paucidentate morphology").

Material and methods

Conodont material described in this publication comes from four sections. Samples from the Praha-Radotín and Na Požárech sections were collected and processed using standard techniques employing 8% solution of formic or acetic acid and the residues were concentrated using heavy liquids (tribrommethane). Described elements and the rest of conodont material are deposited at the Institute of Geology of the Czech Academy of Sciences (Prague, Czech Republic). Material from the Cellon section (Carnic Alps) and Atrous 3 section (Morocco) was collected and processed by prof. Otto Walliser. This material was studied in the conodont collection at the Georg-August-Universität (Göttingen, Germany).

Zieglerodina petrea and *Z. paucidentata*: comparison and relationships

The paleogeographic distribution of *Zieglerodina petrea* and *Z. paucidentata* is not regular (Tab. 1). *Z. petrea* has been reported only from the southern margin of Gondwana, but *Z. paucidentata* has also been documented from Laurentia and Baltica. The restricted geographic distribution of *Z. petrea* may be a matter of few studies of this recently recognized taxon.

The stratigraphic ranges of these two species are also different. *Z. petrea* is only documented from the lowermost Lochkovian (*hesperius–optima* Zone). While specimens described as *Z. paucidentata* are known from sections of the lowermost Lochkovian (*hesperius–optima* Zone), as well as from both the Pragian (?*Caudicriodus steinachensis* Zone and *sulcatus* Zone) and the Emsian (*gronbergi* Zone) For more detailed information see Tab. 1.

The P_1 elements of *Z. paucidentata* and *Z. petrea* share a gap between the cusp and the denticles at the (conventional) posterior part of the element, but according to Murphy & Matti (1982), the gap in *Z. paucidentata* is followed by up to four reduced denticles. They are only slightly developed or absent; and followed by a two, three of four denticles on the posterior part, but none of

Table 1. Global paleogeographic and biostratigraphic distribution of *Zieglerodina paucidentata* Murphy & Matti, 1982; *Zieglerodina* cf. *paucidentata* Murphy & Matti, 1982; *Zieglerodina* aff. *paucidentata* Murphy & Matti, 1982; and *Zieglerodina petrea* Hušková & Slavík, 2020. Original names of biozones are given. Abbreviations: *Z.* = *Zieglerodina*; *O.* = *Ozarkodina*.

Species	Publication	Significant associated conodont taxa	Location/section	Stratigraphy
Ozarkodina paucidentata	Murphy & Matti (1982)	*Icriodus woschmidti hesperius* Klapper & Murphy, 1975; *Oz. remscheidensis* (Ziegler, 1960).	Central Nevada, Coal Canyon; N Simpson Park Range	lowermost Lochkovian (*woschmidti–eurekaensis* Zone)
Ozarkodina paucidentata	Boucot *et al.* (2008)	Sample 2: only *Oz. paucidentata* (Murphy & Matti, 1982). Sample 3: *Oz. paucidentata* (Murphy & Matti, 1982) together with *Icriodus woschmidti* Ziegler, 1960 and *Oz.* cf. *Oz. pandora* (Murphy *et al*., 1981).	Mexico, San Miguel Fm., Rancho Placeritos area, west-central Sonora	lowermost Lochkovian (*woschmidti* Zone)
Zieglerodina paucidentata	Drygant & Szaniawski (2012)	Sample 52/510 m: only with *Z.* cf. *paucidentata* (Murphy & Matti, 1982).	Podolia, Ivanye Zolote section	lowermost Pragian (?*Caudicriodus steinachensis* Zone)
Ozarkodina paucidentata	Mathieson *et al.* (2016)	*Caudicriodus ampliatus* Mathieson *et al*., 2016; *Eognathodus sulcatus lanei* Mathieson *et al*., 2016; *Oz. selfi* Lane & Ormiston, 1979; *Panderodus unicostatus* (Branson & Mehl, 1933); *Wurmiella excavata* (Branson & Mehl, 1933); *Z. remscheidensis* (Ziegler, 1960).	Australia, Cobar Supergroup, western New South Wales	Pragian (*sulcatus* Zone)
Ozarkodina cf. *paucidentata*	Blodgett *et al.* (1988)	*Polygnathus* aff. *perbonus* (Philip, 1966), above the sample with the *Oz.* cf. *paucid*. (Murphy & Matti, 1982).	USA, Alaska, Mt. Michelson	lower Emsian (*gronbergi* Zone)
Ozarkodina cf. *paucidentata*	Mawson *et al.* (2003)	*Oz. r. remscheisensis* (Ziegler, 1960); *Oz. excavata excavata* (Branson & Mehl, 1933); *Ozarkodina* sp. Branson & Mehl, 1933.	Pakistan, Peshawar basin, Nowshera, Kandar-Pir Sabak area	lower Lochkovian (*woschmidti* Zone)
Zieglerodina cf. *paucidentata*	Drygant & Szaniawski (2012)	Sample 52/490 m: *Z. serrula*; *Z. mashkovae*; *Z. paucidentata* (Murphy & Matti, 1982); *Pedavis* cf. *breviramus* Murphy & Matti, 1982, *Pandorinellina praeoptima* (Mashkova, 1972); *Pelekysgnathus csakyi* (Chatterton & Perry, 1977); ?*Pandorinellina parva* Drygant & Szaniawski, 2012. Sample 52/510 m: only with *Z. paucidentata* (Murphy & Matti, 1982)	Podolia, Ivanye Zolote section	lowermost Pragian (?*Caudicriodus steinachensis* Zone)
Zieglerodina cf. *paucidentata*	This contribution		Austria, Carnic Alps, Cellon Section	lowermost Lochkovian (*hesperius–optima* Zone)
Zieglerodina cf. *paucidentata*	This contribution		Morocco, Anti-Atlas, Atrous 3 section	lowermost Lochkovian (*hesperius–optima* Zone)
Ozarkodina aff. *O. paucidentata*	Suttner (2007)	*Oz. rems. remscheidensis* (Ziegler, 1960); *Oz. excavata excavata* (Branson & Mehl, 1933); *Lanea telleri* (Schulze, 1968); *Lanea eoeleanorae* Murphy & Valenzuela-Ríos, 1999; *Oz.* aff. *Oz. pandora alpha* and *beta* morph (Murphy *et al*., 1981).	Austria, Carnic Alps, Rauchkofel formation, Seewarte section	lowermost Lochkovian (?*A. delta* Zone)
"*Ozarkodina*" aff. *paucidentata*	Mavrinskaya & Slavík (2013)	*Pelekysgnathus serratus* cf. *guadarramensis* Valenzuela-Ríos, 1994.	Russia, South Urals, Mindigulovo Section	Lochkovian (*eoeleanor.–eleanor.* Zone)
Zieglerodina petrea	Hušková & Slavík (2020)	*Z.* cf. *zellmeri* Carls *et al*., 2007; *Z.* cf. *remscheidensis* (Ziegler, 1960); *Zieglerodina* sp.; *Ozarkodina* sp.; *Icriodus hesperius* Klapper & Murphy, 1975; *Icriodus* cf. *w. woschmidti* Ziegler, 1960.	Czech Republic, Prague Synform, Radotín section	lowermost Lochkovian (*hesperius–optima* Zone)
Zieglerodina petrea	Hušková & Slavík (2020)	*Oz.* cf. *optima* (Moskalenko, 1966); *Zieglerodina* sp.; *Icriodus hesperius* Klapper & Murphy, 1975.	Czech Republic, Prague Synform, Na Požárech section	lowermost Lochkovian (*hesperius–optima* Zone)
Zieglerodina petrea	This contribution		Austria, Carnic Alps, Cellon Section	lowermost Lochkovian (*hesperius–optima* Zone)

them are more distinct than the cusp. The total number of denticles in mature elements is around 15. The basal cavity is situated in the central part of the element, and the lobes are open widely and circular. The base lobes can be symmetrical or slightly asymmetrical (for more details also see Figs 2 and 3 as well as the systematic part below). Compared to that, the P_1 elements of *Z. petrea* differ from the previous taxon: on the posterior part of element is only a small gap followed by two denticles, from which one of them is usually comparable to the cusp in size. *Z. petrea* also has a lower number of denticles – usually around 12 or 13 in mature elements. The basal cavity is situated in the posterior part, and its lobes are open widely and asymmetrical.

It is possible that the replacement of the denticles with the gap is not connected with just one stratigraphic level. Hence, *Z. paucidentata* from the lowermost Lochkovian may not be related to the "paucidentate" (= possessing a gap) forms from the younger biostratigraphic levels. They emerge at stratigraphic levels, where specific paleoecological conditions may change more rapidly than continuous change of temperature from the colder Přídolí to warmer Lochkovian, chemical changes in ocean water and global sea level fluctuation (*e.g.*, Crick *et al*. 2001, Spiridonov *et al*. 2020), and the organisms had to adapt to the new conditions or migrate. The conodont diversity above the base of the Devonian increased. Not only the diversity of the spathognathodontids is there slightly higher, but also the new genus *Icriodus* enters. This marks a striking change in icriodontids that were dominantly represented during the Silurian by the genus *Pedavis* Klapper & Philip, 1971. The entry of *Icriodus* was a global event. Slavík & Hladil (2020) introduced the *Icriodus* Event that represents the origin and rapid global dispersal of the genus. This should not be mistaken by the often misused Klonk Event by Jeppsson (1998) that has been recently misunderstood by Barrick *et al.* (2021). The origin of the early Devonian taxa of the family Icriodontidae is also uncertain, as is the exact phylogenetic relationships among the youngest *Icriodus* species [*e.g.*, *I. hesperius* Klapper & Murphy, 1975; *I. woschmidti* Ziegler, 1960; and *I. postwoschmidti* (Mashkova, 1968); Carls *et al.* 2007, and the recently described new taxa from Laurentia by Barrick *et al.* 2021].

Most of the elements that were previously classified as *Zieglerodina paucidentata* resemble those of this species in the gap between the cusp and the remaining denticles but differ in other aspects. These include the number of denticles in mature elements and the proportions of the basal cavity. Several groups of elements previously described as *Z. paucidentata* and *Z. petrea* that differ morphologically have been distinguished (Fig. 2). The first group strictly follows the characteristics of *Z. petrea*. The second group includes elements, which resemble

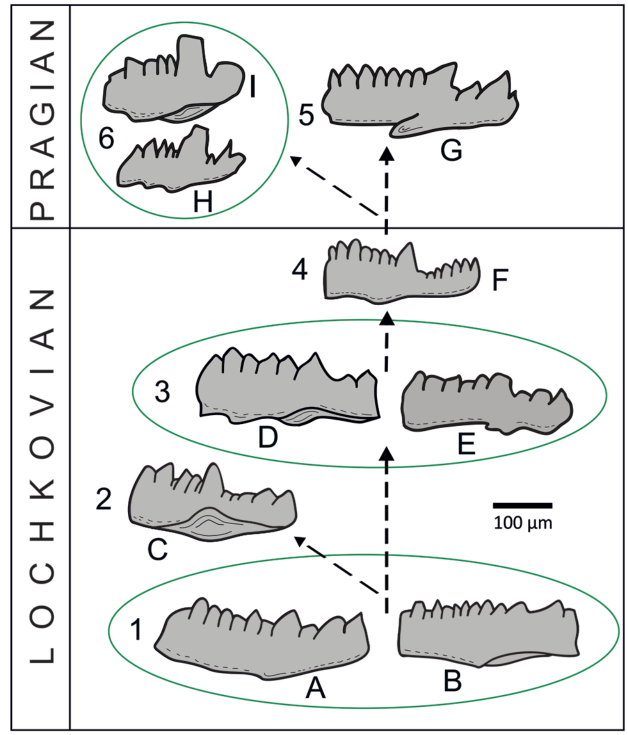

Figure 2. Drawing of selected spathognathodontids P_1 elements with distinct gap clustered into groups (1, 2, 3, 4, 5, 6) based on morphological similarities, with tentative interpretation of their phylogeny. Group 1 strictly follows the characteristics of *Z. petrea*. Group 2 and 3 includes elements, which occurs in Lower Lochkovian and resemble *Z. petrea* and *Z. paucidentata.* Group 4 bears the characteristics of *Z. paucidentata*. Group 5 and 6 occurs in the Pragian and resemble *Z. petrea* and *Z. paucidentata.* For details see text. Legend: A – *Zieglerodina petrea* Hušková & Slavík, 2020, Na Požárech section, sample POZ5, cat. No. POZ-5-001, lower Lochkovian; B – *Zieglerodina petrea* Hušková & Slavík, 2020, holotype, Radotín Section, published *in* Hušková & Slavík (2020, fig. 6e), lower Lochkovian; C – "*Ozarkodina*" aff. *paucidentata* Murphy & Matti, 1982, published *in* Mavrinskaya & Slavík (2013, fig. 6j), Mindigulovo Section, Lochkovian; D – *Ozarkodina* cf. *paucidentata* Murphy & Matti, 1982, published *in* Mawson *et al.* (2003, pl. 4, fig. 19), Kandar–Pir Sabak area, Lower Lochkovian; E – *Zieglerodina* cf. *paucidentata* Murphy & Matti, 1982, sample Wa3722–22, Atrous 3 section, cat. No. GZG.MP.4987, lower Lochkovian; F – *Zieglerodina paucidentata* Murphy & Matti, 1982, published *in* Murphy & Matti (1982, pl. 1, fig. 25), Coal Canyon section, Lower Lochkovian; G – *Ozarkodina paucidentata* Murphy & Matti, 1982, published *in* Mathieson *et al.* (2016, fig. 32i), section western New South Wales – Trundle, Pragian; H – *Zieglerodina* cf. *paucidentata* Murphy & Matti, 1982, published *in* Drygant & Szaniawski (2012, fig. 11t), Ivanye Zolote section, Pragian; I – *Zieglerodina* cf. *paucidentata* Murphy & Matti, 1982, published *in* Drygant & Szaniawski (2012, fig. 11r), Ivanye Zolote section, Pragian.

Z. petrea and *Z. paucidentata* with other traits, but the gap between the denticles is not so prominent. It can be considered as incipient, still possessing small denticles in the critical part of the posterior part of the element. The third group shows more of the characteristics of *Z. petrea* than of *Z. paucidentata*; the gap is followed by only two denticles, the total number of denticles is low (around 10), and the basal lobes are asymmetrical. This group also has a few characteristics that resemble *Z. paucidentata*, these being: denticles visibly smaller than the cusp, and the basal cavity almost in the middle part of element. The fourth group bears the characteristics of *Z. paucidentata*. These groups have representatives in the Lochkovian. The fifth group has traits more characteristic for *Z. paucidentata* – mainly the presence of a smaller denticle or denticles in the gap, the basal cavity is in the middle part of the element; but it also shows some similarity to *Z. petrea* – as the total number of denticles is around 10. However, an element of the fifth group occurs in the Pragian, which means it is several million years younger than the morphologically convergent earliest Devonian specimens. The sixth group stands apart from the previous ones as it is different from the others. It only shares the gap between denticles. The other parameters are completely different – the size of the element (although it can be influenced by the maturity of the element), the number of denticles, and the constricted basal platform. Elements allocated to this group are younger as well and occur in the Pragian. The differences in morphology of the figured specimens can also be the result of intraspecific variation reflecting paleoenvironmental conditions at the regional level.

Systematic paleontology

Class Conodonta Eichenberg, 1930 *sensu* Sweet & Donoghue (2001)
Order Ozarkodinida Dzik, 1976
Family Spathognathodontidae Hass, 1959

Genus *Zieglerodina* Murphy, Valenzuela-Ríos & Carls, 2004

Type species. – *Spathognathodus remscheidensis* Ziegler, 1960.

Remarks. – Genus *Zieglerodina* was established by Murphy *et al.* (2004) to include the ozarkodinids of the "*remscheidensis* Group". The diagnosis of "*Ozarkodina*" *remscheidensis* Ziegler, 1960 was restricted to morphs very similar to the holotype (Ziegler 1960, pl. 13, fig. 2). Afterwards, Carls *et al*. (2007) introduced three new species to discriminate forms from the Přídolí (*Z. klonkensis* Carls *et al.*, 2007; *Z. ivochlupaci* Carls *et al.*, 2007; and *Z. zellmeri* Carls *et al.*, 2007). Drygant (2010) described *Z. podolica* Drygant, 2010, and moved *Ozarkodina mashkovae* (Drygant, 1984), *Oz. serrula* (Drygant, 1984), as well as "*Oz.*" *planilingua* (Murphy & Valenzuela-Ríos, 1999) to *Zieglerodina*. The assignment of the latter species to *Zieglerodina* has been confirmed by Corriga *et al.* (2014) on the basis of a reconstruction of the apparatus. Corriga (2007, 2011) considered *Ozarkodina eladioi* (Valenzuela-Ríos, 1994) as a species of *Zieglerodina*, which was later confirmed in Corriga & Corradini (2019) by description of its completed apparatus. Drygant & Szaniawski (2012) moved *Oz. prosoplatys* (Mawson *et al.*, 2003) and *Oz. paucidentata* (Murphy & Matti, 1982) to the genus *Zieglerodina*, and Corriga *et al.* (2016) also added *Pandorinellina formosa* (Drygant, 2010) to the genus.

However, it should be noted that the generic attribution of all of the species mentioned above would only be confirmed when the complete apparatuses are reconstructed (as has been done for *Zieglerodina eladioi* by Corriga & Corradini 2019).

***Zieglerodina* cf. *paucidentata* (Murphy & Matti, 1982)**
Figures 2D, E, I; 3C, F

? 1964 *Spathognathodus steinhornensis remscheidensis* Ziegler. – Walliser, pl. 20, fig. 26.
1975 *Ozarkodina* n. sp. E. – Klapper & Murphy, p. 44, pl. 7, figs 6, 9, 10.
1977 *Ozarkodina* n. sp. E. Klapper & Murphy. – Klapper, p. 51.
cf. 1982 *Ozarkodina paucidentata* n. sp.; Murphy & Matti, p. 9–10, pl. 1, figs 25–32, 39, 40.
2003 *Ozarkodina* sp. cf. *O. paucidentata* Murphy & Matti. – Mawson *et al.*, p. 93, pl. 4, figs 19, 20.
2007 *Ozarkodina* aff. *O. paucidentata* Murphy & Matti. – Suttner, pp. 38, 39, pl. 18, fig. 10.
non 2012 *Zieglerodina paucidentata* (Murphy & Matti). – Drygant & Szaniawski, p. 851, fig. 11r.
non 2012 *Zieglerodina* cf. *paucidentata* (Murphy & Matti). – Drygant & Szaniawski, p. 851, fig. 11s, t.
non 2013 "*Ozarkodina*" aff. *paucidentata* (Murphy & Matti). – Mavrinskaya & Slavík, p. 291, fig. 6j–l.
non 2016 *Ozarkodina paucidentata* (Murphy & Matti). – Mathieson *et al.*, p. 643, fig. 32h, i.

Material. – 18 P_1 elements in samples from Cellon section, 12 P_1 elements from Atrous 3 section.

Description. – A species of *Zieglerodina* characterized by a P_1 element with distinctly lowered area in the posterior part. The lowered area adjacent to the cusp is filled with reduced denticles. High, conical cusp is not located in the center but slightly posteriorly. The platform lobes are almost circular from the upper view. Our material figured is very close to original material from Nevada, but there is not the real gap, but the area is filled up by reduced denticles instead. Therefore the figured specimens are treated herein in open nomenclature.

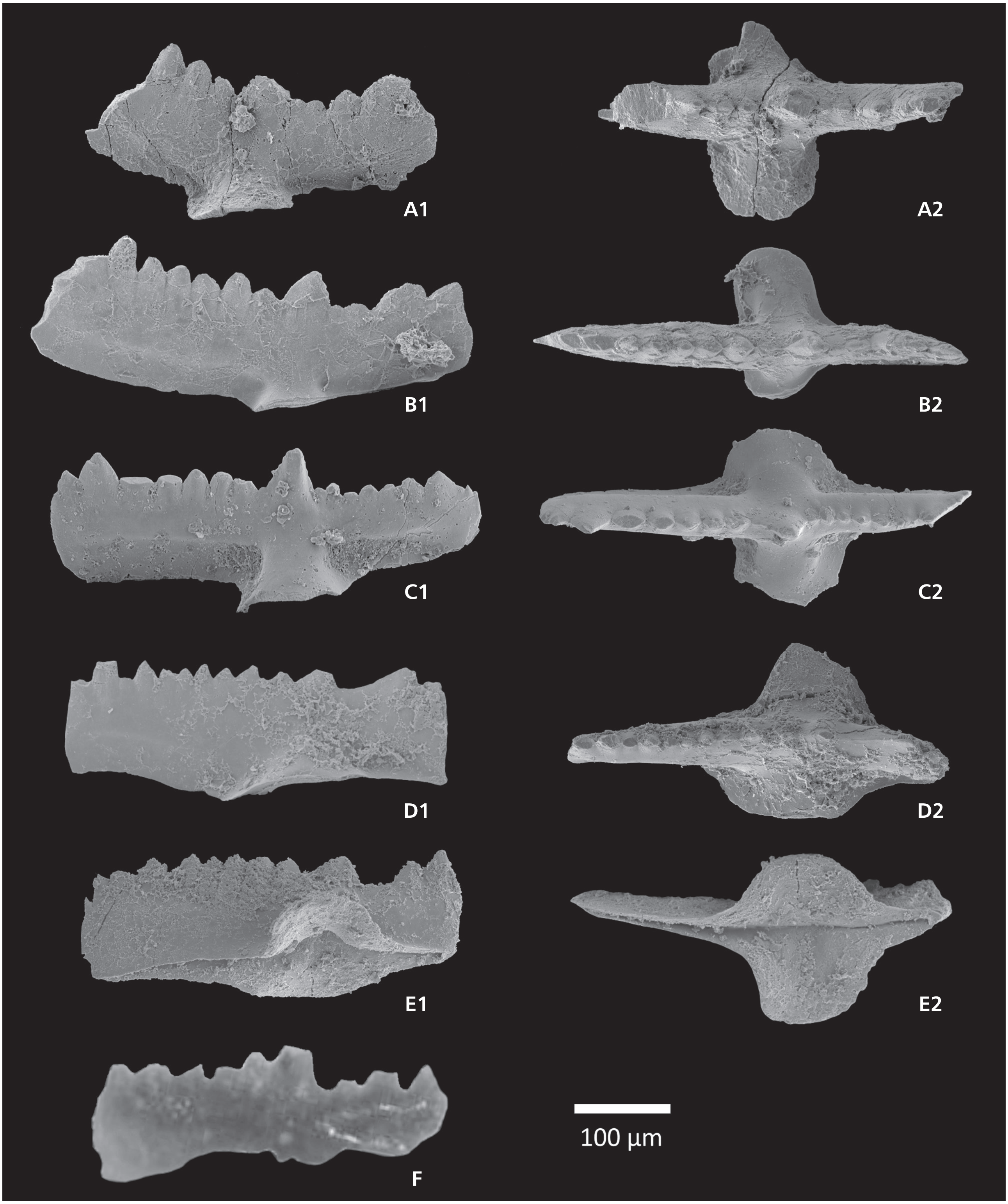

Figure 3. SEM images of selected conodont P_1 elements of *Zieglerodina petrea* Hušková & Slavík, 2020, *Zieglerodina* cf. *paucidentata* Murphy & Matti, 1982. All specimens are to the same scale. • A, B, D, E – *Zieglerodina petrea* Hušková & Slavík, 2020, lower Lochkovian; A – sample Wa547, Cellon section, cat. No. GZG.MP.4989, A1 – lateral view, A2 – upper view; B – sample POZ5, cat. No. POZ–5–001, B1 – lateral view, B2 – upper view; D – published *in* Hušková & Slavík, 2020, holotype, Radotín Section, Prague Synform, sample RAD1, cat. No. RAD–1–001, D1 – lateral view, D2 – upper view; E – published *in* Hušková & Slavík (2020), paratype, sample RAD1, cat. No. RAD–1–002, E1 – lateral view, E2 – upper view. • C, F – *Zieglerodina* cf. *paucidentata*, lower Lochkovian; C – sample Wa548, Cellon section, cat. No. GZG.MP.4988, upper view; F –sample Wa3722–22, Atrous 3 section, cat. No. GZG.MP.4987, F1 – lateral view, F2 – lower view.

Remarks. – This species was originally diagnosed and named by Murphy & Matti (1982, p. 9) based on material previously documented but left in open nomenclature by Klapper & Murphy (1975). The diagnosis included the rudimentary nature of denticle development on the posterior process, but also stated that the number of reduced denticles was three or four (for more details see Fig. 2F). However, few P_1 elements of this species appear to have only two reduced denticles on the posterior part of element (Murphy & Matti 1982, pl. 1, figs 31, 32, 39, and 40). This diagnosis also denotes the almost circular nature of platform lobes in the upper view. While this could be true of the holotype, other specimens show a distinct asymmetry of the lobes (*e.g.*, Murphy & Matti 1982, pl. 1, figs 31 and 40). The specimens from Podolia described by Drygant & Szaniawski (2012) also greatly differ from the holotype – they have a comparatively small size, high cusp, and differentiated height of the blade sections, of which the anterior one is much higher (for more details see Fig. 2H, I). The three elements have 8 to 10 denticles. In comparison, the elements described in Murphy & Matti (1982) have 13 to 14 denticles at variable size. A similar element was mentioned in the study of Mavrinskaya & Slavík (2013), where it is left in open nomenclature as "*Ozarkodina*" aff. *paucidentata* (see Fig. 2C). This P_1 element is relatively bigger, the lobes are strongly asymmetrical, and the "rudimentary denticle" or gap is not as wide and distinct as in the holotype species. The study of Mathieson *et al.* (2016) as a diagnosis of this taxon includes the "unifying characteristic of the relatively low posterior process". Accordingly, *Zieglerodina paucidentata* seems to be a species that clusters together several slightly different morphotypes, which only share one characteristic – rudimentary or missing denticles in the posterior part of element (see Fig. 2G). Also, this species is documented from two different stratigraphic positions – from the lowermost part of the Lochkovian (*hesperius*–*optima* Zone) and the Pragian (*sulcatus* Zone) (see Tab. 1). A question remains whether these "different morphotypes" of *Z. paucidentata* still belong to the same species, reflecting rather intraspecific variations. We think that these stratigraphically contrasting specimens need to be reclassified as different taxa at least at the (sub)species level, however, these are treated here for the purpose of this review.

***Zieglerodina petrea* Hušková & Slavík, 2020**
Figures 2A, B; 3A, B, D, E

2020 *Zieglerodina petrea* n. sp.; Hušková & Slavík, fig. 6e1, e2, f1, f2.

Material. – 8 P_1 elements in samples from Na Požárech section, 4 P_1 elements from Praha–Radotín section, 5 P_1 elements in samples from Cellon section.

Description. – According to the original diagnosis, the platform P_1 element is straight, not very robust with open, asymmetrical basal cavity in the posterior part of the element. A small gap in denticulation is present between the main cusp and the posteriormost denticles (usually one or two), from which one of them is usually comparable to the cusp in size. Number of denticles is usually around 12 or 13 in mature elements. New material from the Cellon section and Morroco is visibly very close to original material from the Prague Synform. Even if some of the elements of *Z. petrea* from Cellon were broken, they can be identified because of the significant gap in posterior part of element. The basal cavity is widely open and asymmetrical and also the number of denticles corresponds. The P_1 elements from the Morocco have about 10 or 12 denticles and they are a bit shorter, than the ones from the Prague Synform and Cellon. All P_1 elements share the similar gap in posterior part and other proportions are corresponding to the holotype as well.

Remarks. – The taxon was recently described (Hušková & Slavík 2020) based on 6 P_1 elements from two sections in the Prague Synform. Although dispersal of this taxon could have been considered regionally restricted to that area, this paper shows more data on its occurrence (see Figs 2, 3). *Zieglerodina petrea* was recently also documented in the unpublished conodont material of O. Walliser's collection from the Cellon section (Carnic Alps), which confirms its wider regional occurrence in the peri-Gondwana. The recorded stratigraphical range of this species is very short; only occurring in the lowermost Lochkovian, usually together with the first entry of *Icriodus hesperius* Klapper & Murphy, 1975, for now (temporarily) the best conodont marker of the base of the Devonian. A phylogenetic relationship with *Zieglerodina paucidentata*, which is probably slightly younger, is highly probable.

Discussion

Almost half of the specimens possibly related to *Zieglerodina paucidentata* were left in open nomenclature and classified as *Z.* cf. *paucidentata* by authors of their descriptions. This points to the ambiguity of the classification. The question remains if the division of this taxon into two categories could solve this problem: a formal one, "*Z. paucidentata* sensu stricto" that fully complies with the original diagnosis, description, and holotype; plus an informal category "*Z. paucidentata* sensu lato", where the concept of the taxon is more liberal. A splitting it up into subspecies is probably needed.

Zieglerodina petrea shares the gap in denticulation in the posterior part of P_1 elements with *Z. paucidentata* but other aspects of their morphology are different (*e.g.*, the number of denticles, the size of the element, the position and shape of the basal lobes). However, the stratigraphic range of these two taxa is virtually the same – both occur in the lowermost Lochkovian. Moreover, forms described as *Zieglerodina paucidentata* are also recorded from the Pragian and Emsian (see Tab. 1). However, such a long range up to 13 Ma is rather improbable. The former concept of very long–ranging taxa; *e.g.*, *Wurmiella excavata*, which originally was of late Silurian to early Devonian in age, has been abandoned following a new spathognathodontid classification given by Murphy *et al*. (2004), who showed many differences in the "excavata" clade that enable the refinement and splitting of the former taxon. Therefore, the much younger specimens classified as *Z. paucidentata* of the Pragian or Emsian age, should be considered as different taxa. The occurrence of a gap in denticulation can be explained by recurrent morphological characteristics driven by specific paleoecological conditions.

Some of the elements appear morphologically transitional between *Zieglerodina paucidentata* and *Z. petrea* (see Fig. 2). Also, the relationship between the Lochkovian *Z. paucidentata* and the Pragian forms described as *Z. paucidentata* is uncertain. The small number of available specimens prevents recognition of the actual range of population variability and the proposed phylogenetic relationship between these species requires a follow up studies in the future.

Conclusions

Based on the biostratigraphic distribution of the conodont species *Zieglerodina petrea* (Hušková & Slavík, 2020) and *Z. paucidentata* (Murphy & Matti, 1982) in the early Devonian, these two taxa seem to have a great potential as promising biostratigraphic markers. However, their phylogenetic relationship remains uncertain and requires a follow-up study.

It is not possible to prove a continuous lineage from *Z. petrea* to *Z. paucidentata* in any of the studied sections and worldwide materials. A division into several different groups according to morphology, with a possible phylogenetic trend that reflects development from an incipient gap in older forms to a largely developed and distinct gap in younger specimens, is suggested as a preliminary concept (Fig. 2).

The same morphological characteristic – the presence of suppressed (paucidentate) denticles on P_1 elements as in the taxa *Zieglerodina paucidentata* and *Z. petrea* has evolved in more species within the spathognathodontid clade at different stratigraphic levels. A possibility of splitting of the taxon into (sub)species or morphotypes has to be considered. The occurrence of the oldest – Lochkovian "paucidentate" taxa of *Zieglerodina* is especially useful in the case of scarcity of other critical biostratigraphic markers – graptolites and the oldest taxa of the conodont genus *Icriodus* that indicate the Silurian–Devonian boundary.

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