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The oral apparatus composition of the Early Carboniferous elictognathid conodont ‘*Siphonodella*’

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Conodont P_1 elements of ‘*Siphonodella*’ are the most important guide fossils for the Tournaisian and topmost Famennian. Hypotheses on the origin and evolution of the elictognathid (‘*Siphonodella*’) clade are based exclusively on the morphology of one pair of elements in the 15 element apparatus, because of difficulties with its reconstruction. An unusually rich sample taken from the Kowala Quarry in the Holy Cross Mountains, dominated by the core elictognathid species ‘*S.*’ *cooperi*, enables corroboration of the interpretation by Sandberg *et al.* (1978) and falsification of some more recent hypotheses. The elements P_1 and P_2 of ‘*S.*’ *cooperi* show a relatively narrow population variability and do not change morphologically in the course of their ontogeny. In contrast, elements S and M profoundly transformed their pattern of denticulation and general shape during growth. Juveniles are relatively underived and rather easily homologized with elements of other polygnathid apparatuses, but adults are of bizarre morphology unlike any other conodonts. Such a pattern of ontogenetic transformation makes it likely that small P_2 elements of relatively generalized morphology and mature *Dinodus*-type S elements associated with P_1 elements of ‘*S.*’ *praesulcata* in a Kowala sample taken from the topmost Famennian nodular limestone bed, belong together to the same apparatus. No Devonian conodont apparatus is known that could be compared with the highly derived ‘*Siphonodella*’ as its possible ancestor. Apparently, the elictognathid lineage immigrated to the Rheic Ocean realm from an unknown source near the end of the Devonian. ☐ *Conodont apparatuses, evolution, Famennian, palaeobiogeography, Tournaisian.*

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Although the apparatus composition is known for most of the conodont species represented in the fossil material exclusively by isolated elements, there are many biostratigraphically important taxa that still await reliable interpretation in terms of their whole apparatus evolution. Among them is the elictognathid clade (family Elictognathidae, including ‘*Siphonodella*’) of crucial importance to age correlation of the greater part of the Tournaisian (e.g. Sandberg *et al.* 1978; Becker *et al.* 2016; Corradini *et al.* 2017; Zhuravlev 2017, 2018). It is generally accepted that the ‘*Siphonodella*’ lineage emerged in the latest Famennian with the chronospecies ‘*S.*’ *praesulcata* Sandberg *et al.,* 1972. Its ancestry was proposed to be within *Alternognathus* (Ziegler & Sandberg 1984; Pazukhin 2008), *Immognathus* (Dzik 2006), or *Dasbergina* (Spalletta *et al.* 2011). These alternative phylogenetic hypotheses were based on morphological similarities between P_1 elements in the basal cavity geometry that are not especially informative and tends to be homoplastic. Knowledge of the complete composition of oral apparatuses would certainly strengthen the inference, but there have been very few attempts at apparatus studies concerning the elictognathids. Already Sandberg *et al.* (1978) suggested that the form-species *Elictognathus lacerata* Branson & Mehl, 1934 was the P_2 element of ‘*Siphonodella*’ whereas *Dinodus leptus* Cooper, 1939 represents the remaining elements of the apparatus. This was accepted by Sweet (1988) and Zhuravlev (2001), but Dzik (1997) supported such interpretation only in the case of ‘*S.*’ *lobata* (Branson & Mehl, 1934) but met difficulties with fitting it into the relatively rich material of ‘*Siphonodella*’ from the Dzikowiec locality in the Sudetes and Muhua in the Guizhou Province of China. For instance, sample Dz-46 from Dzikowiec, with 328 ‘*Siphonodella*’ elements P_1, has yielded no *Elictognathus* or *Dinodus* elements. Only P_1 elements identified as ‘*S.*’ *lobata* consistently co-occur in other samples with the *Elictognathus-Dinodus*-type elements and this species was transferred to *Dinodus* by Dzik (1997; *Elictognathus* Cooper, 1939 and *Dinodus* Cooper, 1939 are senior synonyms of *Siphonodella* Branson & Mehl, 1944). An alternative

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Table 1. Frequencies of conodont elements in samples from the latest Famennian and early Tournaisian of the Kowala Quarry.

Species	Element location	Sample Ko-276
Tripodellus ‘Palmatolepis’ gracilis	P$_1$	861
	P$_2$	55
	S$_0$	4
	S$_1$	17
	S$_2$	14
	S$_{3\text{-}4}$	39
	M	39
Branmehla suprema	P$_1$	210
Branmehla disparillis	P$_1$	88
Branmehla inornata	P$_1$	685
Branmehla sp.	P$_2$	16
	S$_0$	9
	S$_1$	8
	S$_2$	19
	S$_{3\text{-}4}$	53
	M	18
Pandorinella fragillis	P$_1$	92
	P$_2$	6
	S$_2$	2
	S$_{3\text{-}4}$	15
	M	2
Mehlina strigosa	P$_1$	109
	P$_2$	17
	S$_2$	4
	S$_4$	9
Pseudopolygnathus ‘Bispathodus’ ultimus	P$_1$	18
	P$_2$	8
Pseudopolygnathus ‘Bispathodus’ aculeatus	P$_1$	15
Idioprioniodus ruptus	P$_1$	1
	P$_2$	5
	S$_0$	13
	S$_1$	7
	S$_2$	12
	S$_3$	15
	M	4
Neopolygnathus communis (=Polygnathus communis)	P$_1$	26
	S$_{3\text{-}4}$	6
Jablonnodus sp.	P-S-M	74
Dasbergina ‘Pseudopolygnathus‘ trigonica	P$_1$	21
Dasbergina stabilis	P$_1$	1
‘Siphonodella’ praesulcata	P$_1$	15
	P$_2$	9
Dinodus	S	13
Species	Element location	Sample Ko-274
‘Siphonodella’ cooperi	P$_1$	857
Elictognathus	P$_2$	60
Dinodus	S-M	36
Neopolygnathus ‘Polygnathus’ subplanus	P$_1$	49
	P$_2$	11
	S$_1$	1
	S$_2$	3
	S3$_{-4}$	7
	M	3
Pandorinella laterigranosa	P$_1$	48
	P$_2$	6
	S$_2$	2
	S$_{3\text{-}4}$	15
	M	2
Pseudopolygnathus primus	P$_1$	44
	P$_2$	8
	S	9
	M	2
Weyerognathus ineaqualis	P$_1$	16
	S	5
Pinacognathus inornathus	P$_1$	4

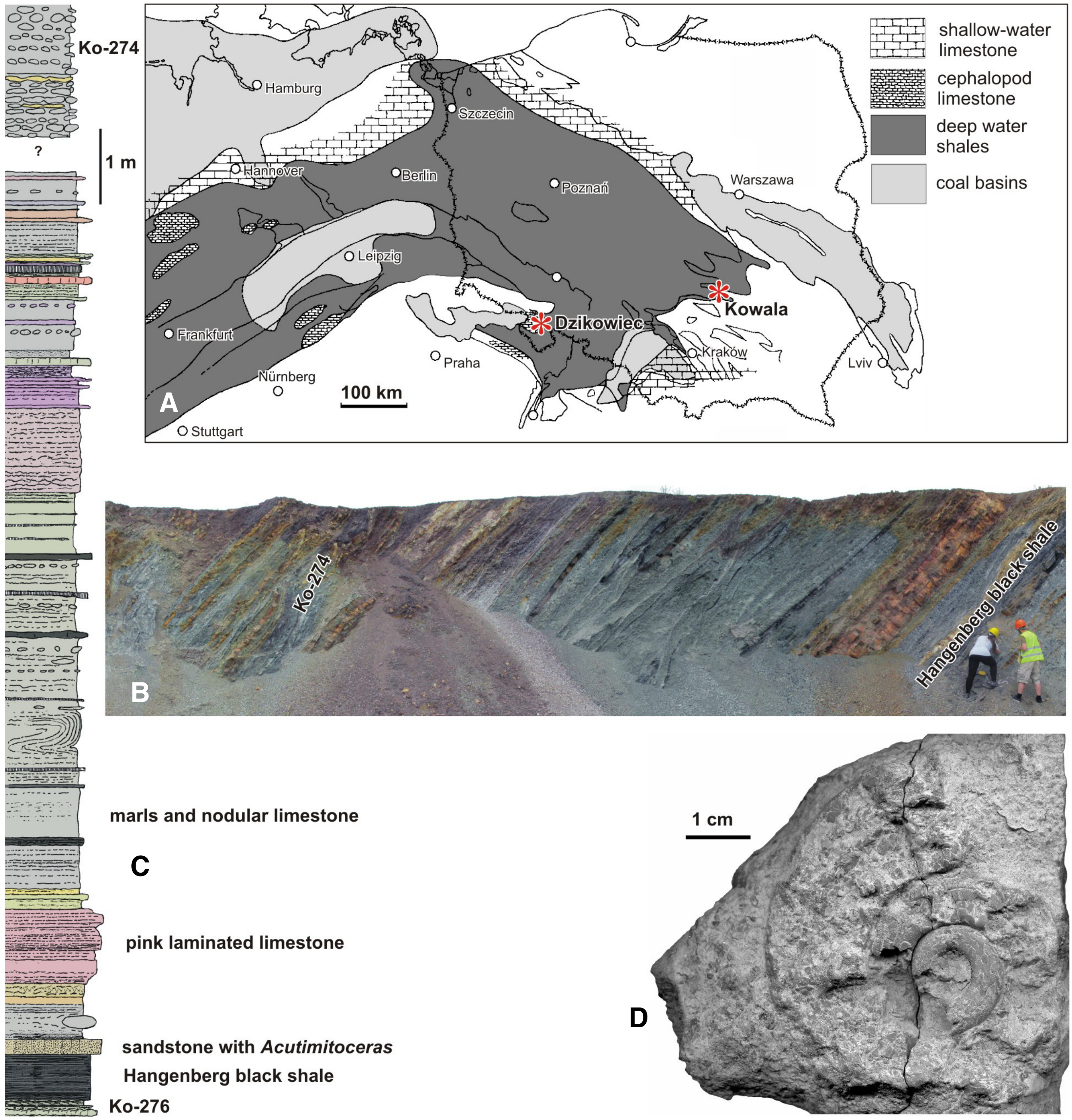

Fig. 1. Geological and geographical data of investigated locality. A, location of the Kowala Quarry shown on the non-palinspastic latest Devonian and earliest Carboniferous sedimentary facies distribution in Central Europe; extend of the late Carboniferous coal basins demarcates areas with intense late Palaeozoic subsidence (modified Dzik 1997). B, Devonian-Carboniferous transition strata exposed in the Kowala Quarry in 2019. C, position of the samples discussed in the text on the rock column of the Devonian-Carboniferous transition strata in the Kowala Quarry. D, prolecanitid ammonoid *Eocanites* sp. in a limestone concretion presumably from near the level of sample Ko-274. [Colour figure can be viewed at wileyonlinelibrary.com]

apparatus interpretation (apparently wrong) was forwarded for other '*Siphonodella*' species, to which minute, short-bladed, and sharply denticulated elements P_2 were tentatively attributed. Their origin from *Pinacognathus* was proposed.

The main difficulty with determining the apparatus composition of the Famennian and Tournaisian conodonts the imbalance within samples of their isolated elements – dominance of robust platform P elements over S and M ramiforms representing the same apparatus. To assemble a reasonable number of S and M elements, a large number of specimens has to be collected, which is usually difficult in the case of '*Siphonodella*.' Such an opportunity unexpectedly emerged with processing of sample Ko-274 from the otherwise rather unproductive (Dzik 1997) early

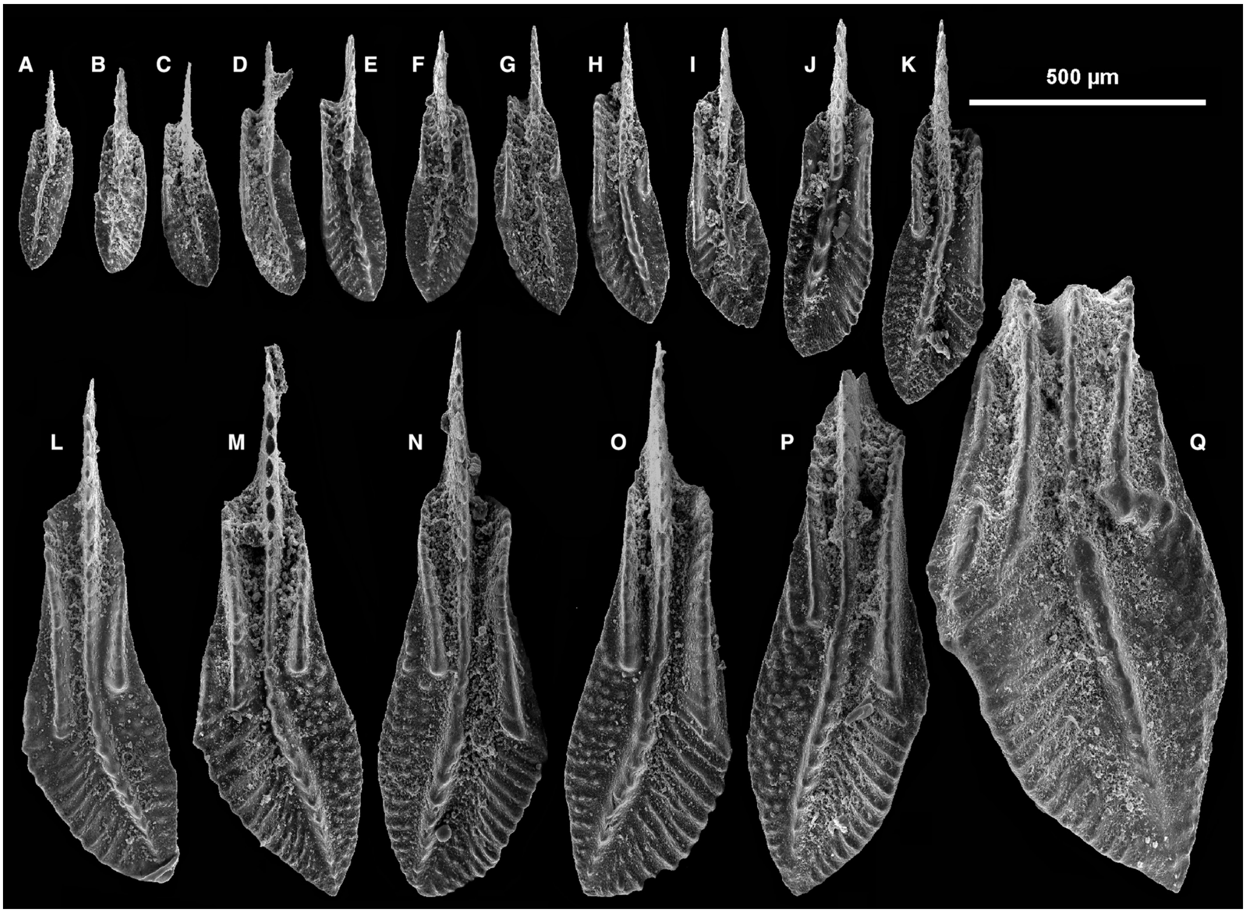

Fig. 2. '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland. A–Q, growth series of P_1 elements, specimens ZPAL C16/3024–3040, respectively.

Tournaisian part of the Kowala Quarry in the Holy Cross Mountains (Table 1). The impressive number of 857 P_1 elements associated with many ramiforms offers a chance to test the Sandberg *et al.* (1978) hypothesis on the '*Siphonodella*' apparatus composition more reliably than before, as well as to determine the range of its population variability and the course of ontogeny of particular apparatus elements.

Geological setting

The material studied comes from the Kowala Quarry in the Holy Cross Mountains in south-central Poland (Fig. 1A). The strata cropping out there represent the southern part of the Gałęzice-Bolechowice syncline (one of the main tectonic structures in the region) and range in age from the Givetian to the Tournaisian. The Givetian is represented by a stromatoporoid-coral massive limestone. The bedded limestone above, with strata rich in siliceous sponges, radiolarians and silicified cephalopods at the top, is of Frasnian age, corresponding to the Kellwasser event. The claystone with limestone intercalations and concretions represents the Famennian. The rhythmic succession of thin limestone beds in shale was proposed to record there the Milankovitch cyclicity (De Vleeschouwer *et al.* 2013).

During deposition of these strata there were several anoxic events that manifest themselves as black shales, including the Kellwasser (Joachimski *et al.* 2001; Racki *et al.* 2002; Bond *et al.* 2004), annulata (Bond & Zatoń 2003; Racka *et al.* 2010; Hartenfels 2011), and Hangenberg ones (Marynowski & Filipiak 2007; Marynowski *et al.* 2012; Myrow *et al.* 2014). A sandstone bed with *Acutimitoceras* and laminated limestone with *Protognathodus*, followed by a shale with limestone concretions and black radiolarite, show the transition to the Tournaisian (Berkowski 1991; Dzik 2006; De Vleeschouwer *et al.* 2013). Kowala is the source of very well-preserved fossils (Marynowski *et al.* 2011) and owing to a complete, continuous sedimentary succession enabled studies of evolution on the population level (Dzik 2006,

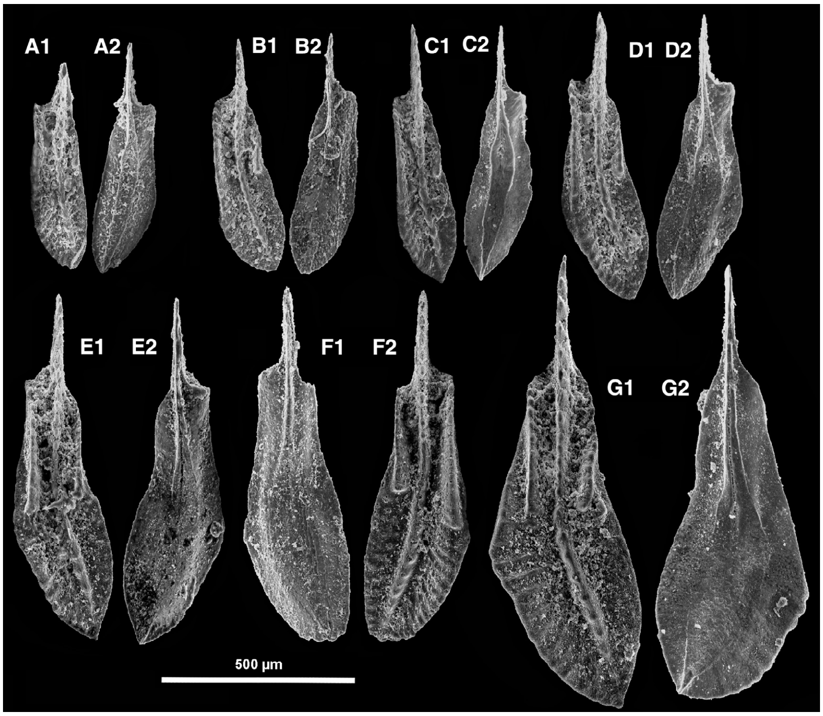

Fig. 3. '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland. A–G, P_1 elements shown from occlusal and aboral sides, specimens ZPAL C/16/3041–3048, respectively.

2008; Świś 2019). The Holy Cross Mountains were located within the tropical palaeolatitudes in the Late Devonian and Early Carboniferous (Golonka *et al.* 1994; Racki 2005) and the fossil assemblages do not significantly differ from those from elsewhere within this climatic zone.

The sample Ko-274, from which most of the material to this work comes, was a concretion of grey micritic limestone collected about 12 metres above the Hangenberg black shale horizon in the northern wall of the quarry (Fig. 1B, C). The shale and marl sequence there is split by numerous faults and

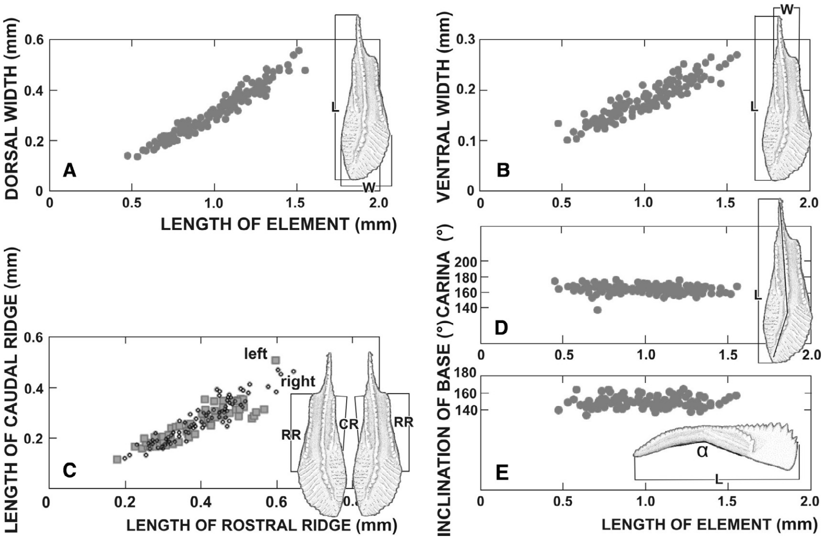

Fig. 4. Biometric tracing of the ontogeny of P_1 element of '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland (162 randomly chosen specimens measured). A, increase of elongation in mature element. B, isometric growth of the platform. C, mirror symmetry of elements as expressed by the proportion between rostral ridge and caudal ridge. D, a slight decrease in angulation of the dorsal and ventral branches of carina. E, unchanging basal curvature.

tectonic discontinuities. One of such tectonic pockets yielded a flat calcareous concretion with the prolecanitid ammonoid *Eocanites* sp. (Fig. 1D). Unlike sample Ko-274, no conodonts were found in the acid-resistant residue from the concretion. Generally, the Tournaisian part of the Kowala sections is not especially productive in fossils (Dzik 1997, tables 2, 3).

Material

The material used in this work comes from samples Ko-274 and 276 collected in 2017 (Table 1). They are housed in the Department of Paleobiology and Evolution of the University of Warsaw where they were processed in the routine way, using diluted formic acid to dissolve the rock and the Franz laboratory electromagnetic separator to enrich the residue. Specimens, picked out by hand, are held in the Franke cells, usually all elements of one species in one cell, which makes examining them from all sides easier than in case of gluing them to the cardboard slides. SEM photographs were taken of specimens mounted on stubs with washable in water UHU® glue stick, which enables relatively easy remounting of specimens. They were coated with carbon and gold. Camera lucida drawings and tracings of the photographs with a graphic tablet were used to make restorations of elements and to count growth increments. All the measurements were undertaken on pictures with the ImageJ software. The conodont elements extracted from sample Ko-274 are generally well preserved. All collected elements are not taphonomically altered and their colour is light amber, which located them in the 1st class of the Color Alteration index (Epstein *et al.* 1977). Altogether there are 1238 elements in the sample, 857 of them are P_1 elements of '*Siphonodella*'. In sample Ko-276, the total number of elements is 2654 and only 15 of them were recognized as P_1 '*Siphonodella*'.

Ontogeny of P_1 elements

Identification of many '*Siphonodella*' species remains problematic because of the small number of elements that were used to establish them. Some of the diagnostic traits may actually be within the range of population or ontogenetic variability of earlier known species. Discrete classes may represent growth stages (Dzik 2008; Plotitsyn & Zhuravlev 2016; Shirley *et al.* 2018) and growth differences may to some degree recapitulate earlier evolution. All this may blur differences between species. The Kowala sample Ko-274 offers an opportunity to clarify such issues.

Juvenile P_1 elements of advanced '*Siphonodella*' species have their platform of almost uniform width along the carina (e.g. Dzik 1997, fig. 18G) which makes them similar to the probable ancestor of the clade, the latest Famennian '*S.*' *praesulcata*. The smallest elements found in the Kowala sample Ko-274 are of such morphology as well. The elements are symmetrical and lenticular in outline, with a relatively short free blade (Fig. 2A).

In subsequent ontogeny, the distinction between the ventral ('anterior' in conventional, non-anatomical terminology) portion of the platform developed, with two high ridges parallel to the carina on the occlusal surface of the platform, and the dorsal ('posterior' in conventional terminology) part with low transverse ridges. They are better developed on the rostral (anterior) side of the element. As a result, the element gradually became strongly asymmetrical in the course of its ontogeny. The platform sides at the pit level are of more or less equal width but the carina is bent caudally under a wide angle. The rostral edge of the platform in its dorsal part is raised higher than in its caudal part. In the next ontogenetic stage, the uplifting of the platform edge continued and the ventral part of the platform became more and more narrow and asymmetrical. The ventral branch of the carina became much more inclined in respect to the dorsal part of the element.

In the last stage of the ontogeny additional ventral ridges developed near the edges of platform. That on the caudal side is always significantly longer than the other ones. In the wide dorsal ('posterior') part of the platform, each side is ornamented differently. The lobes of platform started then to form new ledges that expand towards sides of the element. A short additional area may develop near the edge of the platform, where parallel ridges are developed. The costae on the caudal side divided and developed nodes approximately at the level of the basal pit. Elements reaching this stage may bear more than three ridges, but only one specimen in the sample represents such status (Fig. 2Q).

The basal pit in smallest specimens is located at a distance of two-thirds from the dorsal end of platform (Fig. 3A). The basal cavity is conical only in the early ontogeny of P_1 elements. Soon after, it gradually changes into a flat area delimited by an escarpment referred to as a pseudokeel (Fig. 3C). The pseudokeel is well-developed in the Kowala specimens especially in their ventral ('posterior') parts. After reaching the level of basal pit, it blurs and

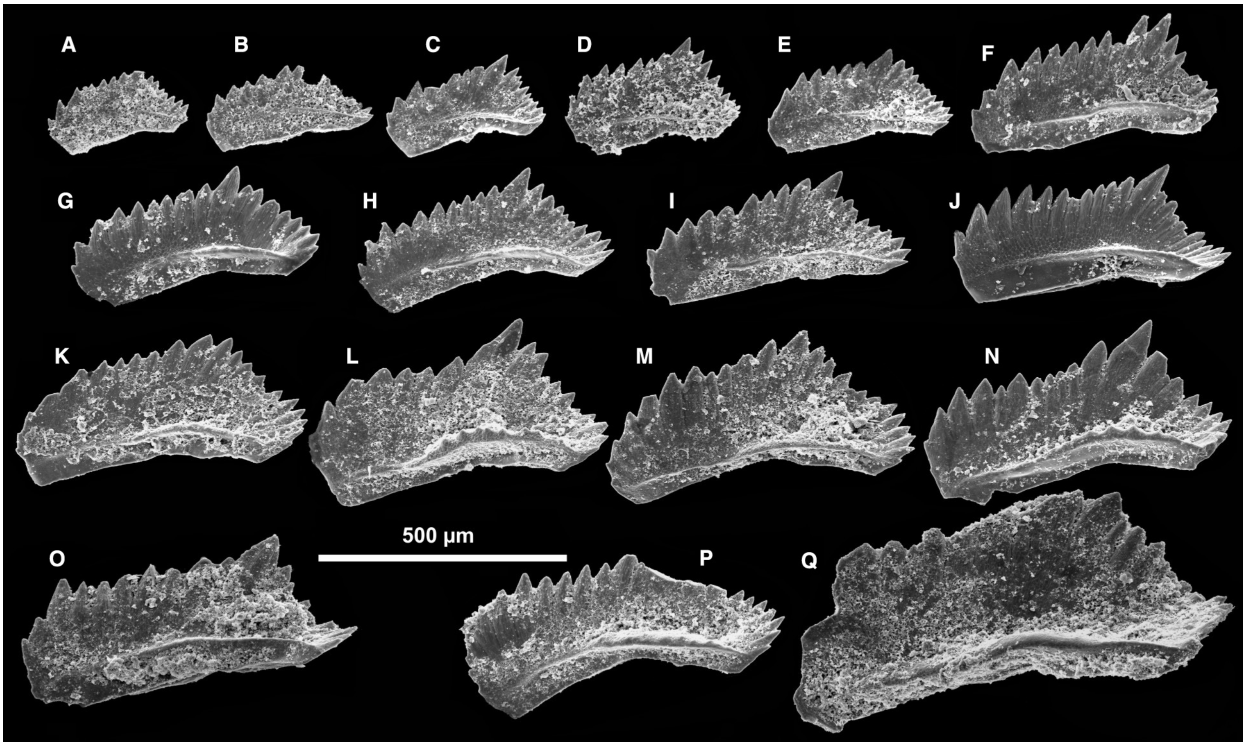

Fig. 5. '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland. A–Q, growth series of P_2 (*Elictognathus*) elements, specimens ZPAL C16/3061–3077, respectively.

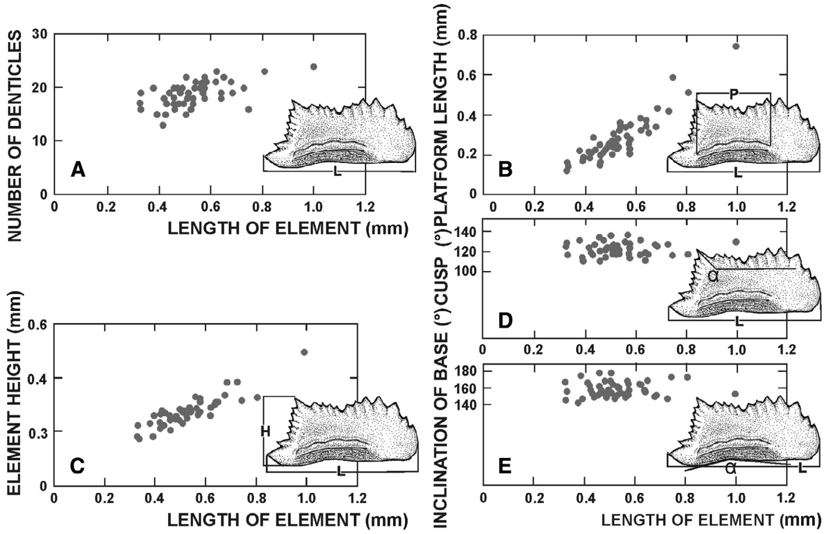

Fig. 6. '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland, biometrics of P_2 (*Elictognathus*) element (51 specimens measured). A, gradual increase in number of denticles. B, gradual increase in length of the platform. C, isometric growth of the element. D, unchanging inclination of the cusp in the ontogeny. E, unchanging inclination of the base.

expands in its further course, changing into a flat lanceolate surface, the edge of which reaches the dorsal ('posterior') end of the element (Fig. 3C).

The flat part of the basal cavity of largest specimens is widest in the middle of dorsal part of the element, where its margin is blurred. The conical basal cavity extends as a steep furrow from the central pit to the ventral tip of the free blade. It narrows just behind the basal pit in the ventral part.

The course of ontogeny of the Kowala species from sample Ko-274 is closely similar to observations of Boersma (1973) based on the occlusal side of

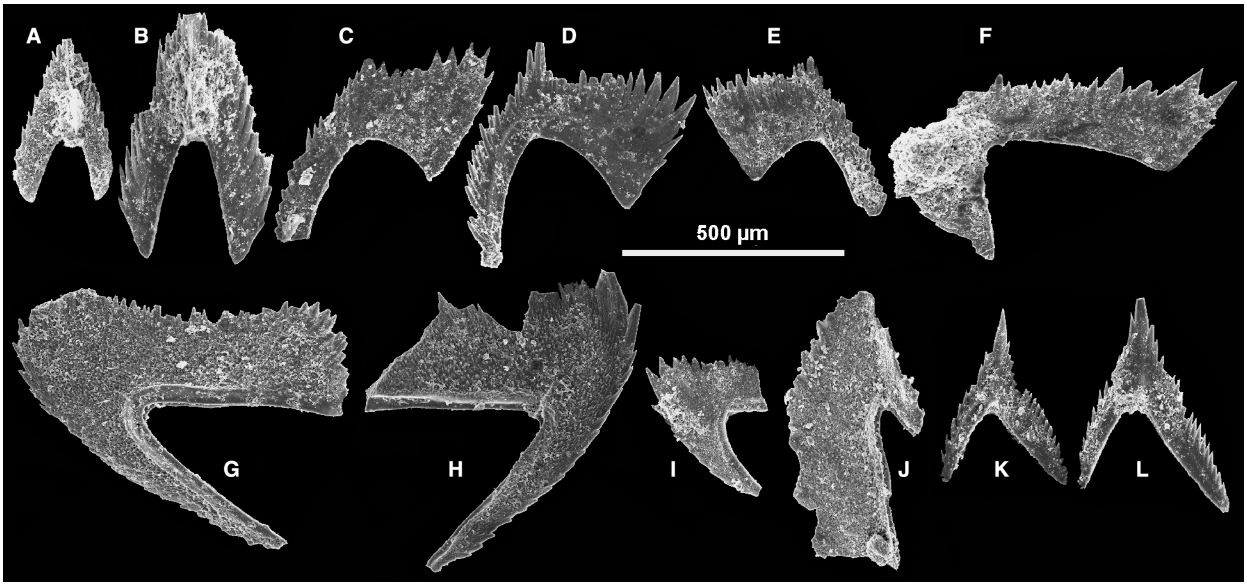

Fig. 7. '*Siphonodella*' *cooperi* Hass, 1959 from sample Ko-274, early Tournaisian of the Kowala Quarry, Holy Cross Mountains, Poland, ramiform elements of the apparatus ('*Dinodus*'). A–L, specimens ZPAL C/16/3049–3060, respectively; A–B, elements S_0, C–E, elements S_1, F, element S_2?, G–I, elements S_{3-4}, I–L, elements M.

elements of '*S.*' *cooperi*. The Kowala material enabled extension of the study to the smallest specimens. They are still symmetrical compared to adult ones. It is probably a recapitulation of the course of evolution in the ontogeny. In '*S.*' *quadruplicata* studied by Zhuravlev & Plotitsyn (2019) even the youngest stages have already developed the both rostral ridges. Presumably, the stage with symmetrical platform shifted towards even earlier stage in result of acceleration of early ontogeny.

The P_1 element elongation decreased at the subadult stage in respect to juvenile ones, which means that the dorsal part of the platform widened faster than the carina increased its length (Fig. 4A). Such growth allometry has already been identified in the Triassic *Gondolella*, in which additional denticles were added to the ventral end of carina during the element growth (Dzik & Trammer 1980). This does not concern the ventral region of the platform, which grew isometrically (Fig. 4B).

We also checked if there is any sign of the apparatus asymmetry in the left and right elements that is recognizable in the associated *Pseudopolygnathus* and its cavusgnathid relatives. It appears that there is no significant difference in the proportion of caudal to rostral ridges length between left and right elements (Fig. 4C).

The angle between the dorsal and ventral branches of the carina slightly decreased in the course of the P_1 element ontogeny (Fig. 4D). It ranges from 138° to 176° but the distribution is clearly unimodal. The inclination of the element is stable and ranges from 133° to 164° (Fig. 4E), which does not depend on the length of element.

It appears that in all aspect of the morphology of P_1 elements, the distribution of variability is unimodal throughout their ontogeny. This refers also to characters that are unmeasurable, for instance to the outline of free blade. The most common morphotype shows a rounded tip with the largest denticle relatively distant from it and a strongly inclined aboral ledge. Free blades with angular, concave or triangular outlines are less frequent. There is a continuity between various morphologies and no evidence for heterogeneity of the sample has been detected.

The variability shown by the '*Siphonodella*' P_1 elements from sample Ko-274 is relatively low compared to other platform-bearing polygnathid conodonts. This supports interpretations of species ranges and the '*Siphonodella*' phylogeny proposed by earlier authors (e.g. Sandberg *et al.* 1978; Zhuravlev 2018).

'*Siphonodella*' oral apparatus

'*Siphonodella*' P_1 elements dominate the sample Ko-274, with 857 elements that make 72% of the total number of 1185 specimens and 84% of all 1018 P_1 elements. They are determined as '*Siphonodella*' *cooperi* Hass, 1959 based on the diagnosis by Hass (1959) and description by Klapper (1966) who pointed out transverse ridges on the outer platform and nodes on the inner platform, which are well developed in our specimens. The elements are elongated and the outer platform rostral ridge bends to its margin in mature specimens. The pseudokeel was not included in the original concept of '*S.*' *cooperi* but some workers suggested that a thin keel is typical for the species (Klapper 1966; Sandberg *et al.* 1978). Possibly, we are dealing with an early population of '*S.*' *cooperi* that preserved the pseudokeel structure inherited after '*S.*' *duplicata* or, alternatively, the basal cavity is variable within the species.

Other P_1 elements in sample Ko-274 belong to *Pseudopolygnathus primus* Branson & Mehl, 1934, *Neopolygnathus subplanus* Voges 1959, *Weyerognathus inaequalis* Voges 1959, and *Pandorinellina laterigranosa* Gedik, 1968 (Table 1). The second highest number of specimens of an element type is 60 P_2 elements traditionally classified in *Elictognathus* that make 5% of the total number of conodont elements and 71% of all P_2 elements. The remaining P_2 elements are of generalized ozarkodinid morphology. Most of them represent *Neopolygnathus* and *Pseudopolygnathus.* It seems to be of special importance that among the P_2 elements found in Ko-274 there is only one that is somewhat similar to those proposed by Dzik (1997) to be a part of most the non-'*Siphonodella*' *lobata* elictognathid apparatuses. So low frequency makes unlikely its correspondence to the P_1 elements of '*S.*' *cooperi.* More likely, it is a part of an apparatus of a *Neopolygnathus* species not necessarily represented in the sample by P_1 elements. Admittedly, such minute P_2 elements associated with '*S.*' *duplicata* P_1 elements in the Sudetes locality Dzikowiec grade morphologically into juvenile P_2 elements of *Neopolygnathus purus* or *N. vogesi* (Dzik 1997, p. 88).

The P_2 elements are relatively variable and their morphology changes in the ontogeny (Fig. 5). This is expressed most clearly in the increase in number of denticles (Fig. 6A). As in the P_1 elements of gondolellids (Dzik & Trammer 1980), denticles are added in the ontogeny, although this is a highly variable aspect of the element shape. Even the smallest and largest elements may have the same number of denticles. Some change in proportions is also discernible in the extent of the platform (Fig. 6B), which is relatively longer and more prominent in large specimens. However, even the largest specimens do not develop as prominent and orally bent a platform as those associated with P_1 elements of *Siphonodella* in the Ruxton Formation in Queensland (Mawson & Talent 1999). Other aspects of the morphology, although variable, do not significantly change with growth. This concerns the inclination of cusp that ranges from 111° to 137° (Fig. 6D) and the basal bending, ranging from 142° to 178° (Fig. 6E).

Despite such an extent of variability, there is a continuity between all morphotypes of P_2 elements. The distribution of frequencies shows a normal distribution (Shapiro Wilk test $P = 0.9847$). Elements with the ventrally decreasing height of the blade and the rounded ventral edge dominate.

Regrettably, the contribution of the element types with different mechanical and hydrodynamic properties to conodont samples is usually unbalanced (Von Bitter & Purnell 2005). This is especially troubling in case of the late Palaeozoic conodont fossil assemblages. Probably mostly because the usually robust P_1 elements have a better chance to be preserved in the digestive tracts of potential predators and so the imbalance may be related to the increase of predation on conodonts. This refers also to '*Siphonodella.*' The only set of S and M elements that can be compared with the dominant P_2 and P_1 elements in sample Ko-274 is that usually classified in the form-genus *Dinodus.* They contribute 39% to all S and M elements in the sample. Bizarre elements of this kind are similar to associated elements of the form-genus *Elictognathus* in having their surface covered with tubercles presumably connected with imprints of cells and in developing acute denticulation that gives them a chainsaw apparition (Fig. 7).

Remarkably, the juvenile elements of *Dinodus*-type show a relatively regular denticulation with domination of the cusp (e.g. Fig. 7A, D, E, K, and L), which allows their homology to be traced with elements of underived polygnathid conodonts, for instance *Pinacognathus* (Dzik 1997). An alternation in denticle size developed in larger specimens (Fig. 7 F), the cusp became similar in size to other denticles and eventually large specimens attained a rounded outline and the bizarre morphology superficially similar to the Famennian prioniodinid *Guizhoudella.* Mature S and M elements from the Ruxton Formation illustrated by Mawson & Talent (1999) nicely show development of a rudimentary platform. An element M of the *Dinodus wilsoni* Druce, 1969 morphology was attributed by these authors to *S. lobata*, but closely similar and apparently homologous specimen from the same sample was labelled as Sa (that is S_0) of an undetermined siphonodellid. Another set of elements proposed to occupy locations Sb (S_1) and Sc ($S_{3\text{-}4}$) are here interpreted as just $S_{3\text{-}4}$, elements. Such morphotypes were referred to *Dinodus fragosus* (E.R. Branson 1934) by Druce (1969).

All this agrees with the interpretation of the elictognathid apparatus by Sandberg *et al.* (1978). To test rigorously this interpretation, one has to extend knowledge of the apparatus structure to the earliest members of the '*Siphonodella*' lineage.

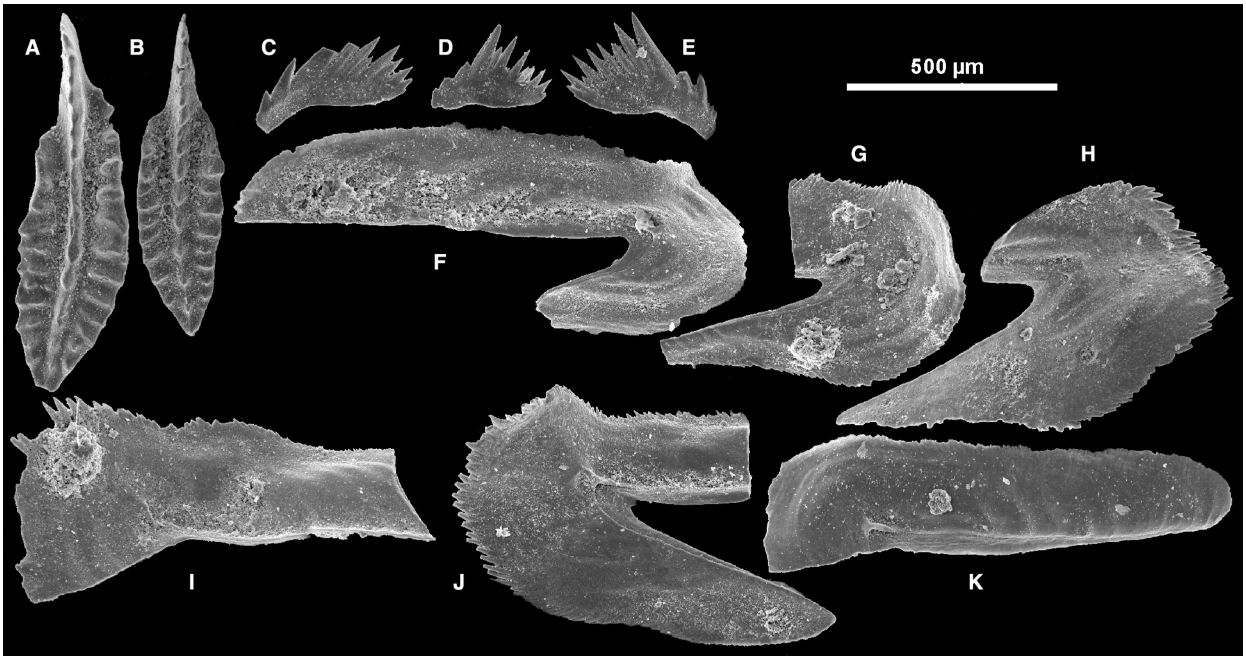

Fig. 8. '*Siphonodella*' *praesulcata* Sandberg, 1972 from sample Ko-276, latest Famennian of the Kowala Quarry, Holy Cross Mountains, Poland, specimens ZPAL C16/3078–3089, respectively. A, B, elements P_1. C–E, putative juvenile elements P_2. F–K, mature elements S and M.

Evolutionary roots of the '*Siphonodella*' lineage

In the cladistic analysis performed by Donoghue *et al.* (2008), the *Dinodus* apparatus (as reconstructed by Dzik 1997 for '*S.*' *lobata*) resolved as a sister clade to the Palmatolepididae and *Mesotaxis*. In fact, the whole apparatus composed of *Dinodus, Elictognathus*, and '*Siphonodella*' resembles a little some palmatolepidids, like *Klaperilepis* (see Dzik 2006). It is unlikely, however, that there is any direct evolutionary relationships between these clades and the similarity is apparently homoplastic.

Among the early Tournaisian conodonts, the apparatus interpreted by Dzik (1997) as *Pinacognathus* is closest in the morphology of the S elements set to that of *Dinodus*. If truly related to the elictognathids it had a common Devonian ancestor with '*Siphonodella*', having similarly underived non-P elements of the apparatus. According to Zhuravlev (2018), the first elictognathid appeared in the Famennian of northern Russia, but no data on its apparatus are available. It represents the branch of '*Siphonodella*' with a robust or smooth platform that flourished in the Tournaisian of China (Qie *et al.* 2016). In the morphology of P_1 elements alone, these conodonts resemble a little the latest Famennian *Rhodalepis* (Komatsu *et al.* 2014).

The latest Famennian '*Siphonodella*' *praesulcata* is the oldest elictognathid in the Rheic realm. The evolutionary phyletic transition of '*S.*' *praesulcata* into '*S.*' *sulcata* (Huddle, 1934) has been proposed to delimit the Devonian-Carboniferous boundary (Paproth & Streel 1984; Paproth *et al.* 1991), although the validity of data on this transition has been repeatedly questioned (e.g. Ji 1989; Kaiser 2009; Mossoni *et al.* 2015). The point of disagreement is how to distinguish results of evolutionary transformation from aspects of population variability in the P_1 element morphology (Ziegler & Sandberg 1996; Kaiser & Corradini 2011) but in any case one may expect that the '*S.*' *praesulcata* apparatus structure should be of morphology ancestral for the clade.

To test this hypothesis, we dissolved several kilograms of dark concretions from the bed immediately underlying the Hangenberg black shale in the Kowala quarry (sample Ko-276; Table 1), expecting to find there apparatus elements of '*Siphonodella*' *praesulcata* there. Eventually, we found only 15 P_1 elements of '*S.*' *praesulcata* (Fig. 8A, B), but no P_2 element that could be compared with *Elictognathus*. In fact, *Elictognathus* is unknown from the Devonian. Only nine P_2 elements that could not be matched with any other associated polygnathids can be considered as belonging to the '*S.*' *praesulcata* apparatus (Fig. 8C–E). They show an incipient platform and some lateral bending but, unlike *Elictognathus*, have their ventral processes shorter than the dorsal one. Their attribution to a '*Siphonodella*' apparatus would require a rather profound evolutionary remodelling of their morphology. The most surprising aspect of the assemblage was the finding of 13 elements of *Dinodus* morphology, not less advanced and bizarre than that occurring in the Tournaisian. All these are mature S (and M?) elements of large size and similar to each other, which is consistent with the profound change and unification of *Dinodus* morphology during the ontogeny observed in the Tournaisian sample Ko-274. It appears thus that already in the Famennian the '*Siphonodella'* apparatus developed highly derived S and M series elements morphology but presumably the shape of P_2 elements remained primitive.

The origin of '*S.*' *praesulcata* and, by implication, the whole elictognathid lineage is still a matter of debate. The most widely accepted hypothesis places its origin in *Alternognathus*. This is based on a similarity between the shape of the basal cavity of P_1 elements between the early '*Siphonodella*' and *Alternognathus*. The oldest *Alternognathus* species, *A. pseudostrigosus* (Dreesen & Dusar, 1974) was proposed to be the ancestor of '*S.*' *praesulcata by* Ziegler & Sandberg (1984). Other member of the genus were also considered as possibly ancestral, for instance *A. regularis* Ziegler & Sandberg, 1984 (Pazukhin 2008). However, the apparatus of *Alternognathus* is rather basically different from that of the elictognathids (Dzik 2006; Świś *et al.* 2020), which precludes such relationship. An alternative hypothesis was forwarded by Spalletta *et al.* (2011) who saw another local faunal element, *Dasbergina brevipennata* (Ziegler, 1962), as the ancestor of '*Siphonodella*' but also in this case the difference in the apparatus structure is profound. Among the Famennian conodont apparatuses, those of *Immognathus* species may show a distant similarity in the morphology of P_1 elements to '*S.*' *praesulcata* and S elements to those of *Dinodus* (Dzik 2006). This relationship may find additional support in the similarity of S_2 elements associated with '*S.*' *praesulcata* in sample Ko-276 to those of *Immognathus*. Possibly a species of *Immognathus* or even a more primitive one of *Ctenopolygnathus* (Dzik 2006; Świś *et al.* 2020) was ancestral to '*Siphonodella*' but this requires a prolonged evolution before the lineage immigrated to the Rheic Ocean realm in the latest Famennian..

Conclusions

The contents of large sample Ko-274 dominated by P_1 elements of '*Siphonodella*' *cooperi* co-occurring with P_2 of the *Elictognathus* morphology, as well as S and M elements of *Dinodus*, falsifies the interpretation of typical '*Siphonodella*' species apparatuses forwarded by Dzik (1997) and supports the classic interpretation by Sandberg *et al.* (1978). The elements P_1 and P_2 of '*S.*' *cooperi* show a relatively narrow population variability and do not change morphologically in the course of their ontogeny. In contrast, elements S and M change profoundly the pattern of denticulation and general shape during their growth. Juveniles are relatively underived and rather easily homologized with elements of other polygnathid apparatuses but adults are bizarre and do not find analogies among other Palaeozoic conodonts except for the Famennian homeomorphic prioniodinid *Guizhoudella*.

Such a pattern of ontogenetic transformation makes it likely that small P_2 elements of a relatively generalized morphology and very large bizarre S elements associated with '*S.*' *praesulcata* in sample Ko-276 taken from the topmost nodular limestone bed in the Kowala Quarry belong to the same apparatus. This would mean that the non-P elements of the oldest known member of the '*Siphonodella*' lineage are advanced in their evolution as much as its early Tournaisian relatives. No close relative of '*S.*' *praesulcata* with such an apparatus has been encountered among Famennian conodonts in Europe. The '*Siphonodella*' lineage seems to have originated outside the Rheic Ocean realm and immigrated there from an unknown source near the end of the Devonian. Possibly, its subsequent diversification in the early Tournaisian (*Gattendorfia* Stufe) was connected with a replacement (or restoration) of niches previously occupied by the palmatolepidids with equally complex apparatus structure.

Confirmation of the apparatus reconstruction of '*S.*' *praesulcata* based on a sample large enough to yield statistically significant numbers of all element types and identification of the source region of the lineage would be the conclusive test for the Sandberg *et al.* (1978) hypothesis.

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