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NEW GROUP OF TOURNAISIAN ADVANCED *SIPHONODELLA* (CONODONTS, LOWER CARBONIFEROUS)

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Abstract. A new morphological group of advanced *Siphonodella* with diagonal or/and longitudinal ribbed ornamentation on the upper side of the platform of the P1 elements was identified and described based on the author's paleontological material from the Polar Urals and published data from East European, Central, and Northeast Asian successions. The group includes two valid species *Siphonodella nandongensis* Li and *Siphonodella vladimirovi* Plotitsyn nom. nov. Due to the low representativeness of the paleontological material, eight taxa are described in an open nomenclature under the species names *Siphonodella* sp. A-H. *Siphonodella vladimirovi* is described as a nomen novum in accordance with the recommendations of the International code of zoological nomenclature (previously identified species appeared under the invalid species names *Siphonodella diagonalica* Pazukhin or *Siphonodella zeravshanica* Bardasheva). It is assumed that the species *Siphonodella nandongensis* Li, *Siphonodella vladimirovi* Plotitsyn, and *Siphonodella* sp. A-H came from morphologically similar species from the cosmopolitan group or as descendants of the East European group.

Introduction

Conodonts of the *Siphonodella* genus are of great stratigraphic importance at the terminal Famennian-Tournaisian. The different variants of global zonations have been developed based on the phylomorphogeny of siphonodellids (Sandberg et al. 1978; Ji 1985; Kaiser et al. 2009; Becker et al. 2016; Corradini et al. 2017; Hogancamp et al. 2019; Zhuravlev et al. 2021). Along with global variants of zonations, a number of regional zonal scales have been developed based on the phylomorphogeny of endemic shallow-water groups of the *Siphonodella* (Ji & Ziegler 1992; Zhuravlev 2017b). Moreover, *Siphonodella sulcata* (Huddle) is a biostratigraphic marker of the base of the Carboniferous (Paproth et al. 1991). The great research interest in this group of conodonts has led to a significant expansion of the taxonomic composition of siphonodellids. A number of new species of advanced (possessing rostrum) siphonodellids have been described only in last decade (Kaiser et al. 2017; Zhuravlev 2017a; Zhuravlev & Plotitsyn 2017; Zhuravlev 2019; Souquet et al. 2020) and taxonomical revisions carried out in the last decade (Zhuravlev & Plotitsyn 2017; Zhuravlev et al. 2021). At the same time, the emergence of specific specimens has been noted, which

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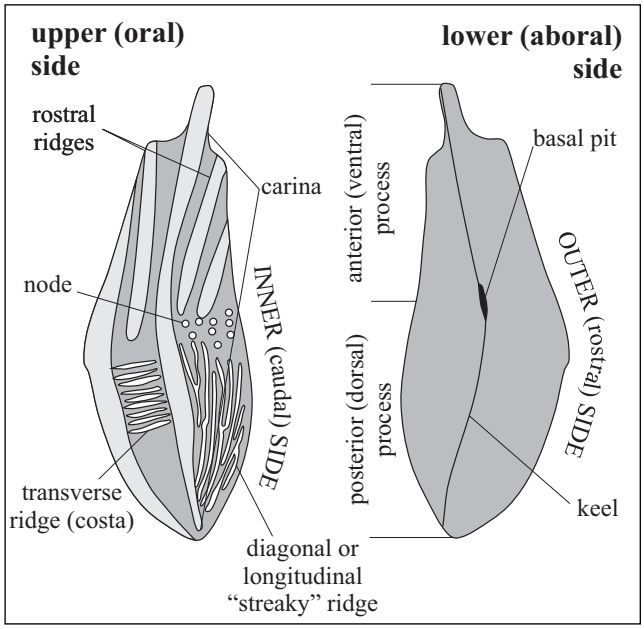

Fig. 1 - Main morphological features of the P1 element of the advanced *Siphonodella*.

differ morphologically from already known and previously described species.

Traditionally, morphological features such as the type of ornamentation of the outer (rostral) and inner (caudal) sides of the upper (oral) side of the platform, platform outlines, morphological features of the lower (aboral) side of the platform, as well as the development and structure of the rostrum are important in the taxonomic diagnosis of the *Siphonodella* species (Fig. 1).

The *Siphonodella* species were subdivided into different groups according to their morphological features and geographic or facies distribution. Sandberg et al. (1978) subdivided siphonodellids into groups based on the morphology of the lower side of the P1 element (pseudokeel, keel, depressed keel). The same trait was used by Ji (1985) for subdividing the genus on subgenera: *Eosiphonodella* having a pseudokeel and *Siphonodella* possessing a keel. Several groups of advanced siphonodellids (possessing a rostrum) were distinguished on the basis of the structure of the rostrum (Zhuravlev & Plotitsyn 2017). Two groups of siphonodellids were also recognised on the basis of their ecology (shallow-water and deep-water taxa) (Ji & Ziegler 1992) and their palaeogeographic distribution (endemics and taxa of global distribution) (Zhuravlev 2017b). Siphonodellids can further be subdivided into the following groups based on the features of ornamentation of the upper side of the platform and features of paleogeographic distribution: a group of cosmopolitans characterised by thin ornamentation of P1 elements mainly from nodes and transverse ridges; a group of endemic "Chinese" smooth siphonodellids (the area of distribution is limited by the epicontinental seas of the eastern part of the Paleotethys); a group of endemic "East European" smooth or roughly ornamented representatives of the genus (range - epicontinental seas of the western part of the Paleotethys) (Fig. 2).

The group affiliation of *Siphonodella kalvodai* Kaiser, Kumpan & Cigler*, S. leiosa* Souquet, Corradini & Girard, and *S. belkai* Dzik is unclear. The ornamentation of *Siphonodella kalvodai* Kaiser, Kumpan & Cigler is close to that of the East European group. However, this species has not been found in the type localities (Donetz, Moscow, and Pechora basins) of representatives of this group. *Siphonodella leiosa* Souquet, Corradini & Girard is insufficiently studied, since it has only been described at a single location at Puech de la Suque section, Montagne Noire, France (Souquet et al. 2020). This ornamentation of this species resembles more closely that of the group of cosmopolitans, since the forms, especially, at the late stages of ontogeny bear thin ornamentation in the form of nodes and short transverse ridges (Fig. 2, D-H; Souquet et al. 2020). For example, *Siphonodella lanei* Zhuravlev & Plotitsyn (= *S. crenulata* (Cooper) M2) or some *S. obsoleta* Hass have a similar thin reduced ornamentation. Despite the lack of ornamentation, and due to its wide paleogeographic distribution (Kaiser et al. 2017), *S. belkai* Dzik is more similar to the cosmopolitan group. In the group of cosmopolitans, there are taxa which have no or greatly reduced ornamentation (for example, *S. isosticha* (Cooper), some late *S. obsoleta* Hass and *S. lanei* Zhuravlev & Plotitsyn). Despite this, the species *Siphonodella kalvodai* Kaiser, Kumpan & Cigler*, S. leiosa* Souquet, Corradini & Girard, and *S. belkai* Dzik have not been assigned to any group and are included on the paleogeographic map separately as species with unclear group affiliation (Fig. 2).

Rare siphonodellids with specific diagonal or/and longitudinal ribbed ornamentation on the inner side of the platform stand out among the already known *Siphonodella* species.

Of all the known siphonodellids with diagonal or/and longitudinal ribbed ornamentation, only *Siphonodella nandongensis* Li has been described (Li et al.

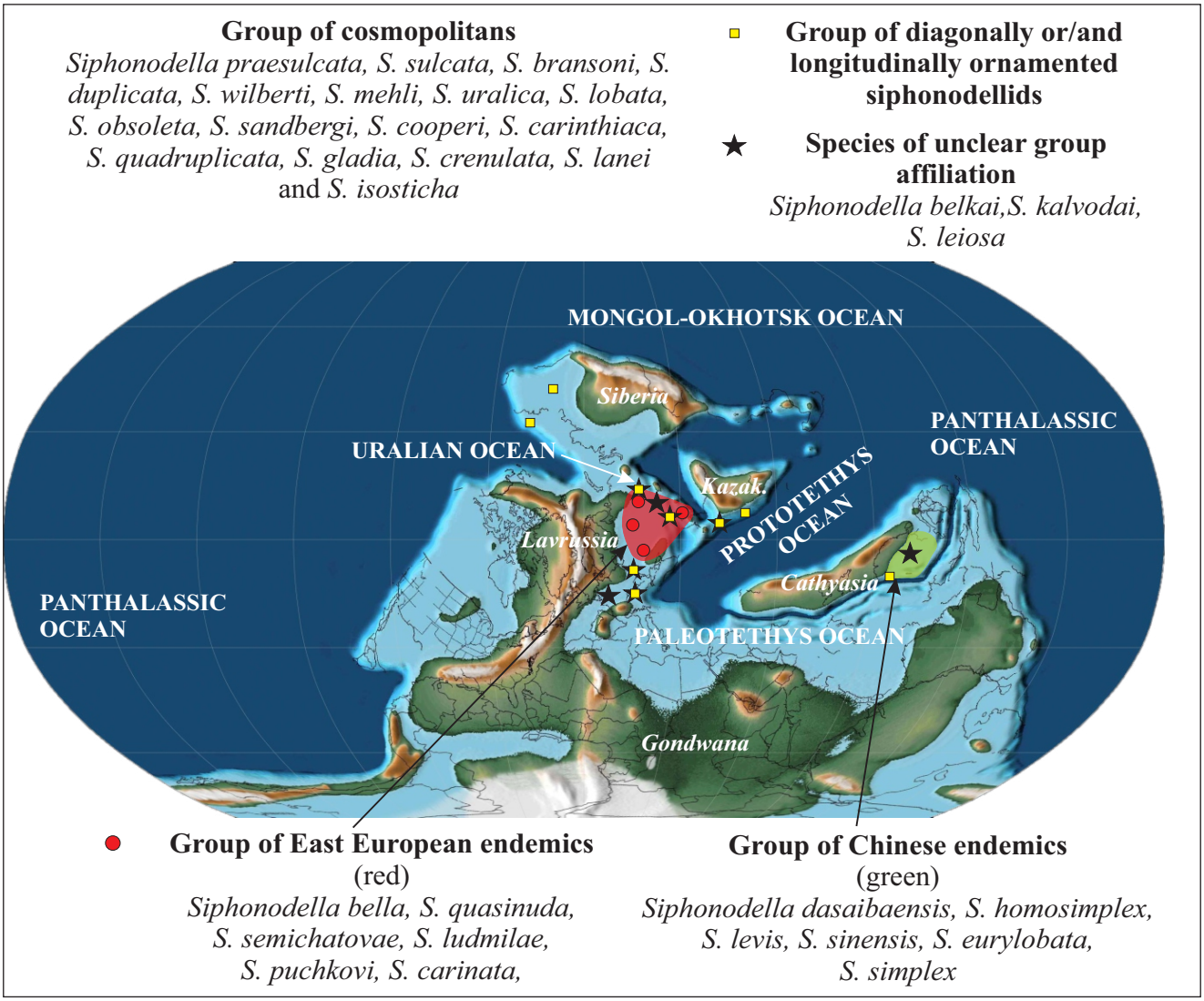

Fig. 2 - Taxonomic composition and paleogeographic distribution of *Siphonodella* groups on the base of Early Carboniferous paleogeographic map (Scotese 2016).

2014). *Siphonodella "diagonalica"* Pazukhin and *S.* aff. "*diagonalica*" Pazukhin were also mentioned in the article by Bardasheva et al. (2004). In addition, drawings of *Siphonodella diagonalica* Pazukhin and *S. zeravshanica* Bardasheva were published in the abstracts of PhD thesises by V.N. Pazukhin (Pazukhin 1989) and N.P. Bardasheva (Bardasheva 1997), respectively. Moreover, some siphonodellids from this group have often been diagnosed as other known species, which in turn has created a number of taxonomic problems, affecting the accuracy of biostratigraphy.

Thus, this article aims to systematise the author's and previously published data on the morphology, taxonomic composition, and stratigraphic ranges of the new group of diagonal or/and longitudinal ornamented representatives of the *Siphonodella*.

Materials

The author's studied materials derive from the Malaya Usa River section in the Polar Urals (part of the North Uralian region) in the northeast of the European part of Russia. During the Late Devonian-Early Carboniferous, the North Uralian region was a shelf area of the Uralian Ocean (paleostrait) which was located between the Laurussia and Kazakhstania paleocontinents (Puchkov 2010; Korobkin & Buslov 2011; Scotese 2016). The Devonian-Carboniferous boundary deposits of the epicontinental seas of Laurussia within the North Uralian region were formed under various conditions from a shallow carbonate platform to bathyal facies belts (Sobolev 2005; Zhuravlev 2003, 2012; Plotitsyn et al. 2018b). The geological structure of the Malaya Usa River basin dominated by Paleozoic carbonate sedimentary successions. Exposed Tournaisian deposits of the Malaya Usa River basin are represented mainly by two types of sections: 1) predominantly carbonate deposits with siliceous nodules of a shallow-water carbonate platform of the Vazhhanovey Formation (Shishkin et al. 2007; Zhuravlev & Plotitsyn 2017); 2) siliceous-carbonate relatively deep-water shelf deposits of the Buredan Formation (Kolesnik 1993; Shishkin et al. 2007; Plotitsyn et al. 2018a). The

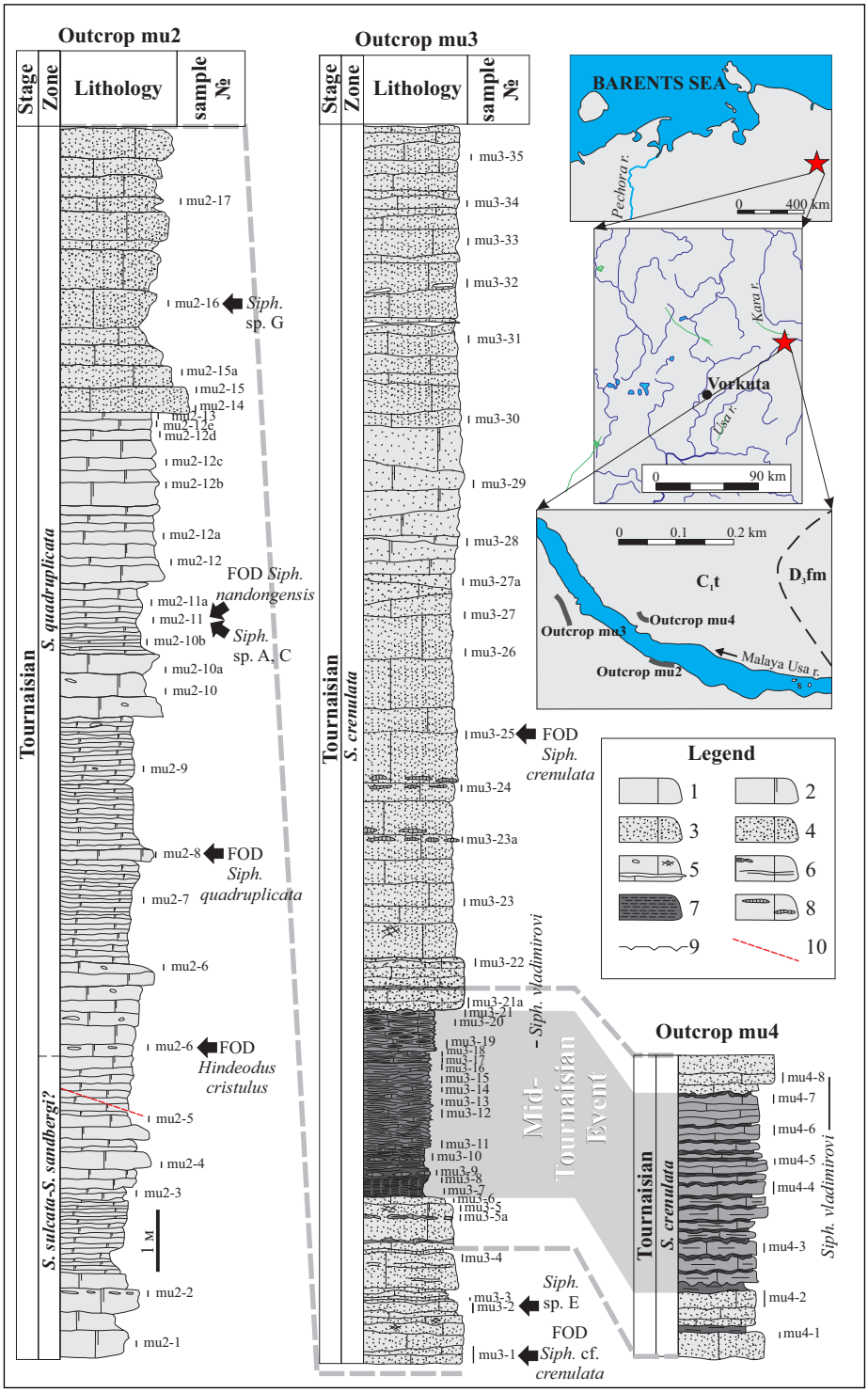

Fig. 3 - Lithological logs of the Tournaisian outcrops mu2, mu3, and mu4 in the upper reaches of the Malaya Usa River (Polal Urals, NE of the European part of Russia) with the occurrences of stratigraphically important *Siphonodella* species and siphonodellids with longitudinal or/and diagonal ornamentation (Plotitsyn et al. 2018a). Legend: 1 - limestone; 2 - recrystallized limestone, secondary dolomite; 3 - bioclastic limestone; 4 - calcarenite; 5 - calcite nests, veins and fine veins; 6 - clayey limestone; 7 - argillite; 8 - cherts, cherty nodules; 9 - supposed gap; 10 - small-amplitude fault. FOD - First Occurrence Datum.

material for this article was obtained from several outcrops located in the upper reaches of the Malaya Usa River (coordinates of outcrops: mu2 (67°39'42"N; 65°11'14"E), mu3 (67°39'47"N; 65°10'59"E); mu4 (67°39'42"N; 65°11'14"E)). The deposits exposed in these outcrops are dated to the *sulcata*(?)-*quadruplicata* (*crenulata*) conodont zonal interval (Fig. 3) (Plotitsyn et al. 2018a). Lithologically, they are represented by micritic, bioclastic limestones and, to varying degrees, their dolomitised varieties. There are few interbeds and members of massive calcarenites and calcareous argillites and black shales. The accumulation of sediments took place below the wave base under conditions of a likely gentle slope. At the same time, the Malaya Usa River section probably occupied an intermediate position between the sections of the shallow-water carbonate platform and deep-water sections of the shelf or continental slope (Plotitsyn et al. 2018a).

Black shales in outcrop mu3 are considered as transgressive black shales of the Lower Alum Shale event or so-called Mid-Tournaisian event (Plotitsyn 2016; Plotitsyn et al. 2018a). The level of the Mid-Tournaisian event is noted within the *S. quadruplicata* Zone near the first occurrence datum (FOD) of *Siphonodella crenulata* (Cooper) and is marked by lithological data and by carbonate carbon isotope variations. The transgressive phase of the Mid-Tournaisian event (within the *S. quadruplicata* Zone or at the base of the *S. crenulata*

Zone) is marked by a lighter carbon isotopic composition (within 1–2 ‰), similar to data from other sections of the Ural region (Sobolev 2011; Plotitsyn 2016; Plotitsyn et al. 2018a; Mizens et al. 2015; Zhuravlev et al. 2020) and some other regions of the world (Buggisch et al. 2008; Yao et al. 2015).

All specimens of *Siphonodella* with diagonal or/and longitudinal type of ornamentation from the Polar Urals sections are deposited in the A.A. Chernov Museum of the N.P. Yushkin Institute of Geology Komi SC UrB RAS, Syktyvkar, Russia (collection nos. 333/26, 333/29, 512/1, 512/20).

Taxonomic notes

First of all, it should be said that the longitudinal or/and diagonal ornamentation of the inner side of the platform is observed in siphonodellids, which can be attributed to the group of cosmopolitans and the East European group. The presence of similar ornamentation suggests the kinship of these groups. Traditionally, in the species diagnostics of the *Siphonodella*, a change in the type of ornamentation on the outer or inner sides of the platform is a sign of interspecific variability. The first most significant event in the evolution of the genus is the appearance of nodose ornamentation on the inner side of the platform due to the division of the ribs into rows of nodes and the subsequent randomisation of their location. This is clearly demonstrated during the evolutionary transition from *Siphonodella duplicata* (Branson & Mehl) to *S. wilberti* Bardasheva, Bardashev, Weddige & Ziegler, which is confirmed by the presence of transitional forms (Zhuravlev et al. 2021). The *Siphonodella crenulata* (Cooper) – *S. lanei* Zhuravlev & Plotitsyn transition demonstrates the reduction of ornamentation as well. In this regard, all specimens of diagonally or/and longitudinally ornamented siphonodellids with individual morphological features will be considered as independent taxa.

V.N. Pazukhin described *Siphonodella diagonalica* in an unpublished PhD thesis (1989). Later, also in an unpublished PhD thesis, N.P. Bardasheva (1997) described the species *Siphonodella zeravshanica*, which is similar in its morphological features to the *S. diagonalica* described by Pazukhin. However, both taxonomic names with descriptions were not published in the open press, making them invalid in accordance with Article 11.1 of ICZN (1999). Later, N.P. Bardasheva with co-authors (2004) gave the diagnosis and description of the taxa under the species name *Siphonodella "diagonalica"* Pazukhin, 1989. However, the authors noted that they had no information about whether V. Pazukhin had published his materials. They considered it possible to use the species name V. Pazukhin gave to these very characteristic forms, however the invalid status of a previously unavailable name cannot be changed by its mere citation (see Article 11.5.2 in ICZN, 1999). A later publication of V.N. Pazukhin (2008) does not use an invalid species name, but incorporates *Siphonodella diagonalica* on the phylogeny scheme of *Siphonodella* as *S.* sp. 1. Thus, guided by Article 13.1.3 of the ICZN (1999), it is necessary to describe the *Siphonodella diagonalica* under a new species name (nomen novum). In this article, this taxon is described under the species name *Siphonodella vladimirovi* nom. nov.

In the article by Bardasheva and coauthors (2004), a different specimen with similar ornamentation characteristics (see pl. 1, Fig. 37) is also presented under the specific name *Siphonodella "diagonalica"* (=*Siphonodella vladimirovi* nom. nov.). This specimen bears signs of a less developed rostral structure, with dimensions similar to that of *Siphonodella vladimirovi* nom. nov. (pl. 1, Fig. 37 and Fig. 38). Morphologically close forms were described by V.N. Pazukhin in an unpublished PhD thesis (1989) as *Siphonodella kochetkovae*. On V.N. Pazukhin's phylomorphogenetic scheme of *Siphonodella* (Pazukhin 2008), these forms appear as *S.* sp. 2. According to the assumption of V.N. Pazukhin *S.* sp. 2 is a descendant of *S. vladimirovi* nom. nov., from which they were formed by the reduction of the rostral structure (Pazukhin 2008). Due to the lack of paleontological material for a reliable description of this species, it is described in the open nomenclature as *Siphonodella* sp. D.

Other published representatives of the *Siphonodella* with diagonal or/and longitudinal ribbed ornamentation appear as known species of the genus, namely: *S. sandbergi* Klapper (Fig. 10, pl. 45, Shilo et al. 1984; Figs. 5-9, pl. 4, Bardasheva et al. 2004), *S. carinthiaca* Schönlaub (A, Fig. 16, Dzik 1997), *S. quadruplicata* (Branson & Mehl) (12, Fig. 5, Kalvoda et al. 2015), and *S. isosticha* (Cooper) (Fig. 4, pl. VI, Danukalova et al. 2019). Often such specimens are diagnosed in the open nomenclature: *Siphonodella* sp. B (Lipnjagov 1979), *S.* cf. *sandbergi* Klapper (Fig. 13, pl. 3, Bardasheva et al. 2004), *S.* aff. *quadruplicata* (Branson & Mehl) (Fig.

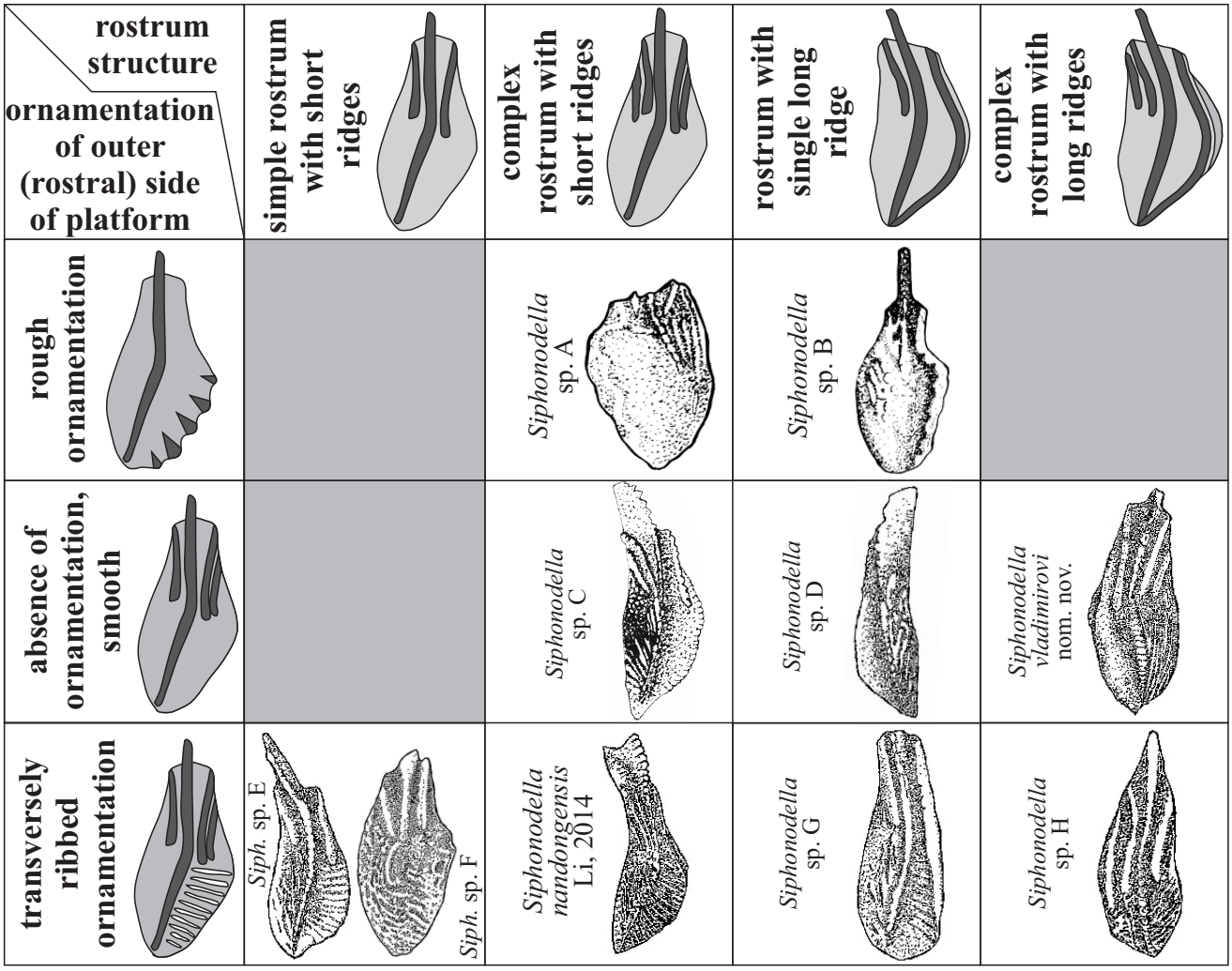

Fig. 4 - Morphological diversity of known specimens diagonally or/and longitudinally ornamented siphonodellids. Drawings of *Siphonodella* sp. A, *S*. sp. C, *S*. *vladimirov*i nom. nov., *S*. sp. E, and *S*. sp. G are based on authors materials. Drawings of *Siphonodella* sp. B, *S*. sp. D, *S*. *nandongensis* Li (holotype), *S*. sp. F, and *S*. sp. H are based on published photos (Lipnjagov 1979; Shilo et al. 1984; Bardasheva et al. 2004; Li et al. 2014).

14, pl. 2, Plotitsyn et al. 2018a), *S*. aff. *nandongensis* Li (Fig. 7, pl. 3, Zhuravlev & Plotitsyn, 2017), *S*. aff. *semichatovae* Kononova & Lipnjagov (Fig. 5, pl. 2, Plotitsyn et al. 2018a), *S*. aff. *obsoleta* Hass (Fig. 8, pl. 45, Shilo et al. 1984), *S*. aff. *zeravshanica* Bardasheva (Fig. 28, pl. 1, Neyevin & Alexeiev 2021), and *S*. sp. nov. A (Fig. 24, pl. I, Li et al. 2014). The analysis of the rostrum structure and ornamentation of the outer side of the platform of known diagonally or/and longitudinally ornamented specimens of siphonodellids, with the exception of two already known species (*Siphonodella nandongensis* Li and *S*. *vladimirovi* nom. nov.), demonstrate the existence of at least eight potential new species of *Siphonodella* (Fig. 4). All potential new species, due to their rare occurrence, are described in an open nomenclature under the species names *Siphonodella* sp. A-H.

Systematic paleontology

Class **CONODONTA** Pander 1856
Order **Ozarkodinida** Dzik 1976
Family *Elictognathidae* Austin & Rhodes 1981
Genus *Siphonodella* Branson & Mehl 1944

Siphonodella vladimirovi nom. nov.

Figs. 5A-E

1984 *Siphonodella* aff. *obsoleta* Hass - Shilo et al., pl. 45, Fig. 8;
1984 *Siphonodella sandbergi* Klapper - Shilo et al., pl. 45, Fig. 10;
2004 *Siphonodella "diagonalica"* Pazukhin - Bardasheva et al., p. 243-244, pl. 1, Fig. 38;
2004 *Siphonodella* aff. "*diagonalica*" Pazukhin - Bardasheva et al., p. 244, pl. 1, Figs. 39-42.

Holotype: The sinistral P1 element of *Siphonodella vladimirovi* illustrated in figure 5B, mu4-6, Malaya Usa River section, Polar Urals.

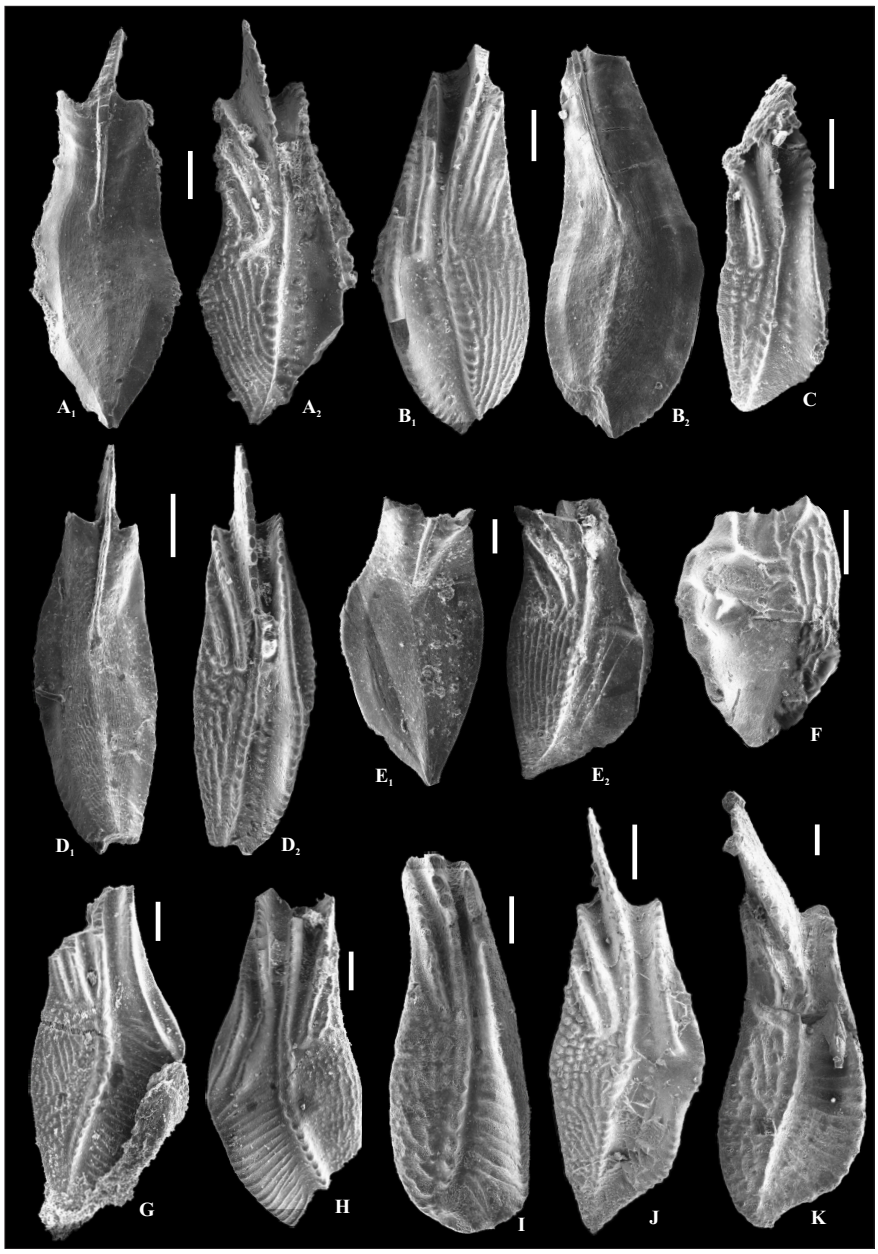

Fig. 5 - Diagonally or/and longitudinally ornamented siphonodellids from the Tournaisian (*S. quadruplicata* and *S. crenulata* zones) of the Polar Urals. A-E - *Siphonodella vladimirovi* nom. nov.: A - coll. № 512/20-3, sample № mu4-6, *S. crenulata* Zone; B - holotype, coll. № 512/20-4, sample № mu4-6, *S. crenulata* Zone; C - coll. № 512/1-45, sample № mu3-19, *S. crenulata* Zone; D - coll. № 512/20-8, sample № mu4-8, *S. crenulata* Zone; E - coll. № 512/20-5, sample № mu4-7, *S. crenulata* Zone; F - *Siphonodella* sp. A, coll. № 512/3-19, sample № mu2-11, *S. quadruplicata* Zone; G, H - *Siphonodella nandongensis* Li: G - coll. № 512/1-39, sample № mu3-13, *S. crenulata* Zone; H - coll. № 512/1-23, sample № mu3-11 *S. crenulata* Zone; I - *Siphonodella* sp. G, coll. № 333/26-74, sample № mu2-16, *S. quadruplicata* Zone; J - *Siphonodella* sp. C, coll. № 333/29-23, sample № mu2-11, *S. quadruplicata* Zone; K - *Siphonodella* sp. E, coll. № 512/1-52, sample № mu3-2, *S. crenulata* Zone. Length of the scale bar - 0.2 mm.

Coll. no. 512/20-4, A. A. Chernov Museum of the N.P. Yushkin Institute of Geology Komi SC UrB RAS, Syktyvkar (Russia).

Etymology: The name comes from the first name of the discoverer of the species - Vladimir Nikolaevich Pazukhin.

Diagnosis: Advanced species of *Siphonodella* possessing lanceolate, an asymmetrical platform ornamented by longitudinal or/and diagonal ribs on the inner side of the platform. The outer side of platform is smooth. Up to five long and short rostral ridges compose the rostrum. The lower side of the platform is characterised by a small basal pit in the anterior (ventral) half and depressed keel.

Material: Six specimens with varying degree of preservation from limestones of the Malaya Usa River section (Polar Urals) and seven published images of specimens from the Shishkat (Tien Shan), Sikambr, and Bazov (Omolon region) sections.

Range and occurrence: Tournaisian, *S. crenulata* Zone of the Polar and Southern Urals (according to the unpublished PhD thesis and published work (Pazukhin 2008) of V.N. Pazukhin); Lower *crenulata* Zone of Southern Tien Shan; *Gnathodus delicatus* Zone (roughly comparable to the Upper *crenulata-isosticha* Zone) of the Omolon region.

Description. A *Siphonodella* that has a lanceolate narrow asymmetrical platform that becomes wider and more asymmetrical (up to a pear-shaped form) at the late ontogenetic stages. The outer side of the platform is smooth and a small number of nodes ordered in a row in the adcarinal part may be characterised at the late ontogenetic stages. The edge of the long ridge on the outer side or the platform margin on the outer side can be denticulated. The inner side of the platform is ornamented with longitudinal or/and diagonal "streaky" ribs, which in the anterior part of the platform can disintegrate into the nodes. The angle between the ornamentation direction and the carina can range from 0° (longitudinal ornamentation - the line of the orna-

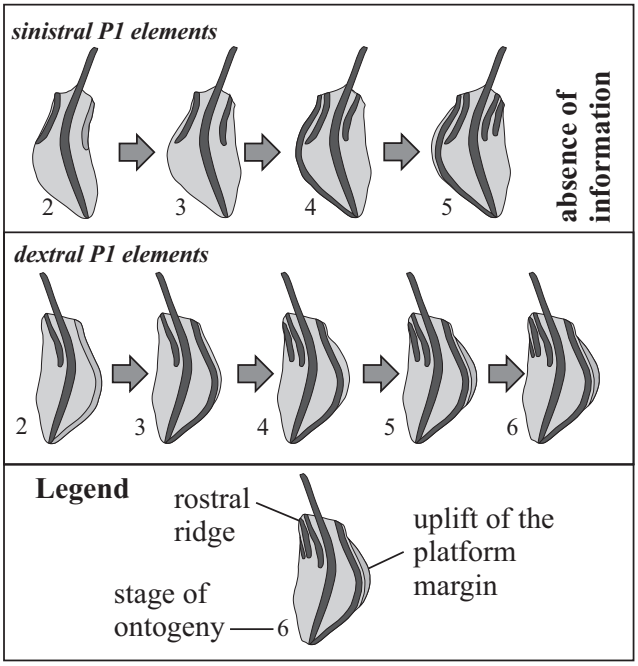

Fig. 6 - Peculiarities of transformation of the rostrum structure of the sinistral and dextral P1 elements of S*iphonodella vladimirovi* nom. nov. during ontogeny. Stages of *Siphonodella* ontogeny according to Zhuravlev & Plotitsyn 2017.

mentation direction is parallel or sub-parallel to the carina) to 30° or possibly more (diagonal ornamentation). The ornamentation at the posterior part of the platform can reach and merge with the carina (Fig. 5A, B), forming an extension of the carina similar to *Siphonodella carinthiaca* Schönlaub. The inner side of the platform is raised almost to the level of the axial ridge height. The rostrum on the inner side is always composed of short ridges. The outer side of the platform possesses the long ridge or adcarinal short and outer long ridges. Similarly to representatives of the subgroup 4 of the rostrum development (see Zhuravlev & Plotitsyn 2017), the first adcarinal rostral ridge in ontogeny appears on the outer side in the sinistral elements and on the inner side in the dextral ones (Fig. 6). The lower part of the P1 element is characterised by a narrow and small basal pit in the anterior half of the platform (or in the middle of the P1 element) and depressed keel.

Remarks. *Siphonodella vladimirovi* nom. nov. with longitudinal ornamentation on the inner side platform at the late stages of ontogeny is similar to *Siphonodella sandbergi* Klapper, in which nodes arranged in rows can be observed on the inner side (for example, Figs. 10, 11, pl. 4, Klapper 1966). *Siphonodella vladimirovi* nom. nov. is characterised by a less developed rostrum structure and specific longitudinal or/and diagonal "streaky" ornamentation of the inner side platform. The similarity of the structure of the rostrum morphologically brings together *Siphonodella vladimirovi* nom. nov. in the early stages of ontogeny and *S. obsoleta* Hass. However, *S. obsoleta* Hass. has a nodular ornamentation on the inner side of the platform.

Siphonodella nandongensis Li, 2014

Fig. 5G, H

2014 *Siphonodella nandongensis* sp. nov. - Li et al., p. 31-32, pl. 1, Figs. 19-23 (fig. 20 is photo of holotype);
2015 *Siphonodella quadruplicata* (Branson & Mehl) - Kalvoda et al., Fig. 5, 12;
2017 *Siphonodella nandongensis* Li - Zhuravlev & Plotitsyn, p. 462, pl. 3, Fig. 6.

Diagnosis: Advanced *Siphonodella* with the narrow, lanceolate asymmetrical platform ornamented transverse ridges on the outer side and diagonal or/and longitudinal "streaky" ribs of the inner side platform. The rostrum is characterised by up to 5-6 short rostral ridges. The thin keel in the anterior part of the platform becomes depressed in the posterior part.

Material: Two specimens from the Malaya Usa River section (Polar Urals) and six published images of specimens from the Baping Formation in Nandong (Guangxi Autonomous Region) and Anaklety section (Moravian Karst).

Range and occurrence: Tournaisian, *S. quadruplicata* and *S. crenulata* zones of South China, North Russia, and Central Europe.

Remarks. Morphologically (with the exception of diagonal or/and longitudinal ornamentation), the upper side of the platform *Siphonodella nandongensis* Li is similar to *S. quadruplicata* (Branson & Mehl). It was previously noted that *Siphonodella nandongensisis* Li also demonstrates a rostrum development in ontogeny similar to that of *S. quadruplicata* (Branson & Mehl) (Zhuravlev et Plotitsyn 2017). *Siphonodella nandongensis* Li at early stages of ontogeny demonstrates some similarity with *S. cooperi* Hass. Ornamentation of the inner side of the platform of *Siphonodella nandongensis* Li is a distinctive feature.

***Siphonodella* sp. A**

Fig. 5F

Diagnosis: Advanced species of *Siphonodella* with the P1 element that has a spoon-like, thick, asymmetrical platform which is ornamented by longitudinal ribs on the inner side of the platform. The outer side of the platform is characterised by wide, coarse, fan-like transverse ridges which formed a platform margin. The rostrum consists of up to three (?) short rostral ridges. The morphology of the lower side of the platform is unclear.

Material: One specimen from the Malaya Usa River section (Polar Urals, Russia).

Range and occurrence: Tournaisian, *quadruplicata* Zone of the Polar Urals.

Remarks. Morphologically (with the exception of longitudinal ornamentation), the upper side of the platform *Siphonodella* sp. A is similar to that of *S. carinata* Zhuravlev. Some morphological similarities can be found with *Siphonodella puchkovi* Zhuravlev and some late forms of *S. quasinuda* Gagiev, Kononova & Pazuhin. However, unlike *Siphonodella* sp. A, *S. puchkovi* Zhuravlev and late *S. quasinuda* Gagiev, Kononova & Pazuhin bears up to two rostral ridges at the late stages of ontogeny. Also, *Siphonodella* sp. A differs from *S. puchkovi* Zhuravlev and *S. quasinuda* Gagiev, Kononova & Pazuhin by having wide, coarse, fan-like transverse ridges on the outer side of the platform.

Siphonodella sp. B

1979 *Siphonodella* sp. A - Lipnjagov, pl. 2, Fig. 2.

Diagnosis: Advanced species of *Siphonodella* with the P1 element possessing a thick, asymmetrical pear-shaped platform with a simple (up to two rostral ridges) rostrum. The outer side of the platform is characterised by a long rostral ridge which merges with the lateral platform margin and has rough tuberous or wavy ornamentation. The rostral ridge on the inner side is short. The inner side is ornamented by diagonal ribs. The morphology of the lower side of the platform is unclear.

Material: One published image of a specimen from the Styla section (or Mokraya Volnovakha River section) (Donetz Basin, Donbas region).

Range and occurrence: Tournaisian of the Donetz Basin.

Remarks. Morphologically the upper side of the platform *Siphonodella* sp. B is similar to that of *S. puchkovi* Zhuravlev. With a significant similarity of the structure of the rostrum, the inner side of the platform of *Siphonodella puchkovi* Zhuravlev doesn't bear features of ornamentation. A thick platform, which is characteristic of all advanced representatives of the East European group, distinguishes *Siphonodella* sp. B from other siphonodellids bearing a long ridge on the outer side of the platform (*Siphonodella obsoleta* Hass, *S.* sp. D, early *Siphonodella vladimirovi* nom. nov.).

Siphonodella sp. C

Fig. 5J

Diagnosis: Advanced species of *Siphonodella* with P1 element that has a lancet-like, thin, slightly asymmetrical platform. The ornamentation of the outer side of the platform is smooth. The inner side is characterised by nodes on the central part and diagonal ribs on the posterior part of the platform. The rostrum consists of numerous (three or more) short rostral ridges. The outer margin of the platform is denticulate. The morphology of the lower side of the platform is unclear.

Material: One specimen from the Malaya Usa River section (Polar Urals).

Range and occurrence: Tournaisian, *S. quadruplicata* Zone of the Polar Urals.

Remarks. Morphologically the upper side of the platform *Siphonodella* sp. C is most similar to that of *S. kalvodai* Kaiser, Kumpan & Cigler. Except for the diagonal ornamentation of the platform, *Siphonodella* sp. C doesn't bear typical for *S. kalvodai* Kaiser, Kumpan & Cigler crenulated and undulated outer margin of the platform. The smooth outer side of the platform distinguishes *Siphonodella* sp. C from *S. quadruplicata* (Branson & Mehl) and *S. nandongensis* Li, which have transverse ridges.

Siphonodella sp. D

2004 *Siphonodella* "*diagonalica*" Pazukhin - Bardasheva et al., pl. 1, Fig. 37;
2019 *Siphonodella isosticha* (Cooper) - Danukalova et al., pl. IV, Fig. 4.

Diagnosis: Advanced siphonodellid species with P1 element having a lancet-like, thin, slightly asymmetrical platform with simple (up to two long and short rostral ridges) rostrum. The outer side of the platform is smooth and characterised by a long rostral ridge which is presented in the form of a raised platform margin. The inner side of the platform is ornamented by diagonal or/and longitudinal ribs. A small basal pit is located in the anterior half of the platform. The keel is depressed.

Remarks. Morphologically (with the exception of diagonal ornamentation), the upper side of the platform *Siphonodella* sp. D is similar to *S. obsoleta* Hass and *S. vladimirovi* nom. nov. *Siphonodella* sp. D differs from the *S. obsoleta* Hass and *S. vladimirovi* nom. nov. in the less developed structure of its rostrum. *Siphonodella* sp. D possesses up to two rostral ridges at the latest stages of ontogeny. Moreover, the inner side of the platform of *Siphonodella obsoleta* Hass is usually ornamented by nodes.

Siphonodella sp. E

Fig. 5K

Diagnosis: Advanced species of *Siphonodella* with P1 element that has a lancet-like, asymmetrical platform with the widening of the outer part. The outer side of the platform is ornamented

by transverse ridges (costae). The inner side is characterised by diagonal "streaky" ribs on the posterior part of the platform. Based on the size of the P1 element, the rostrum at the late stages of ontogeny bears up to two short rostral ridges. The morphology of the lower side of the platform is unclear.

Material: One specimen from the Malaya Usa River section (Polar Urals).

Range and occurrence: Tournaisian, *S. crenulata* Zone of the Polar Urals.

Remarks. Morphologically *Siphonodella* sp. E is similar to the *S. wilberti* Bardasheva, Bardashev, Weddige & Ziegler - *S. crenulata* (Cooper) transitional forms, due to the presence of a slight widening of the outer part of the platform. The diagonal ornamentation of the inner side of the platform is a distinctive diagnostic feature.

Siphonodella sp. F

1997 *Siphonodella carinthiaca* Schönlaub - Dzik, p. 90, Fig. 16, A;
2004 *Siphonodella* cf. *sandbergi* Klapper - Bardasheva et al., pl. 3, Fig. 13.

Diagnosis: Advanced *Siphonodella* with a weakly asymmetric lenticular platform. The ornamentation is characterised by longitudinal-diagonal ribs on the inner side of the platform, which merge with the carina and form transverse ribs on the outer side of the platform. Due to the presence of such ornamentation, the carina can only be traced in the anterior part of the platform. The rostrum is represented by two short rostral ridges converging to the carina. The morphology of the lower side of the platform is unclear.

Material: Two published images of specimens from the Shishkat (Tien Shan) and Dzikowiec (Sudetes) sections.

Range and occurrence: Tournaisian, *quadruplicata* Zone of Southwest Poland and Southern Tien Shan.

Remarks. *Siphonodella* sp. F is similar to the *S.* sp. H by type of ornamentation, but bears a less developed rostrum consisting of short rostral ridges (only). *Siphonodella* sp. F differs from *S. carinthiaca* Schönlaub from the type locality (see Schönlaub, 1969) by the platform outlines (there is no or a weakly expressed rostral narrowing of the anterior part of the platform) and the ornamentation of the inner side of the platform (diagonal ribs instead of disordered tubercles).

Siphonodella sp. G

Fig. 5I

Diagnosis: Advanced *Siphonodella* with an asymmetrical pear-shaped platform. The platform is ornamented by nodes and diagonal ribs on the inner side of the platform. The outer side of the platform is characterised by transverse ridges. The rostrum bears up to two rostral ridges: a long ridge on the outer and a short ridge on the inner sides of the platform. The long rostral ridge is presented as an uplift of the platform margin. The morphology of the lower side of the platform is unclear.

Material: One specimen from the Malaya Usa River section (Polar Urals).

Range and occurrence: Tournaisian, *S. quadruplicata* Zone of the Polar Urals.

Remarks. Morphologically, *Siphonodella* sp. G is similar to the *S. gladia* Zhuravlev & Plotitsyn, from which, in addition to the diagonal ornamentation of the inner side of the platform, it differs in the specific pear-shaped form of the platform. Moreover, the rostral ridge on the outer side of the platform of *Siphonodella* sp. G is represented as an uplift of the platform margin.

Siphonodella sp. H

2004 *Siphonodella sandbergi* Klapper - Bardasheva et al., pl. 4, Figs. 1-9, 14-15.

Diagnosis: Advanced species of *Siphonodella* with P1 element that has a thin, lenticular, slightly asymmetrical platform. The inner side of the platform is ornamented with "streaky" diagonal ribs that pass through the carina and continue on the outer side of the platform in the form of transverse ribs. The rostrum is characterised by up to six rostral ridges: long ridges on the outer side and short ridges on the inner side of the platform. The lower side of the platform is characterised by a thin keel and small basal pit, which is located in the middle of the P1 element.

Material: One published image of a specimen from the Shishkat section (Tien Shan).

Range and occurrence: Tournaisian, *quadruplicata* Zone of Southern Tien Shan.

Remarks. Regarding the structure of the rostrum, the outline of the platform, and the structure of the lower side of the platform, *Siphonodella* sp. H is similar to *Siphonodella sandbergi* Klapper. However, they are very different in terms of ornamentation. Type specimens of *Siphonodella sandbergi* Klapper are characterised by nodes on the inner side of the platform, which can be arranged in rows (Klapper 1966). The outer side of the platform of *Siphonodella sandbergi* Klapper is usually not ornamented. Specimens with similar ornamentation, but with a less developed rostrum (presumably two short ridges) are illustrated in the articles by Dzik (1997, Fig. 16A) and Bardasheva et. al. (2004, pl. 3, Fig. 13) as *Siphonodella carinthiaca* Schönlaub and *S.* cf. *sandbergi* Klapper and are described here as *S.* sp. F. *Siphonodella* sp. F has a less developed rostrum, which presumably consists of up to two short rostral ridges.

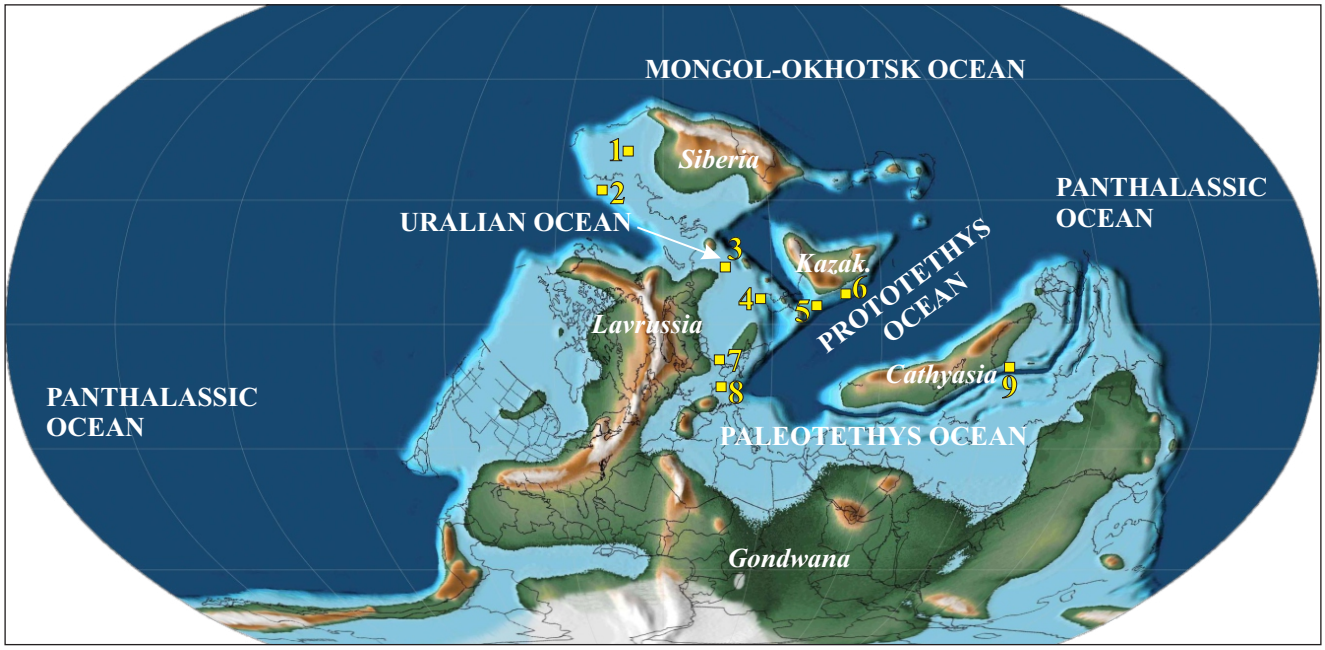

Fig. 7 - Paleogeographic distribution of the group of diagonally or/and longitudinally ornamented *Siphonodella* on the base of Early Carboniferous paleogeographic map (Scotese 2016). Legend: 1 - Omolon region (*Siphonodella vladimirovi* nom. nov.) (Shilo et al. 1984); 2 - New Siberian Islands (*Siphonodella* sp. D) (Danukalova et al. 2019); 3 - Polar Urals (*Siphonodella nandongensis* Li, *S. vladimirovi* nom. nov., *S.* sp. A, *S.* sp. C, *S.* sp. E, and *S.* sp. G) (Zhuravlev, Plotitsyn 2017; Plotitsyn et al. 2018a, and this article); 4 - Southern Urals (*Siphonodella vladimirovi* nom. nov., S. sp. D) (unpublished PhD thesis (1989) of V.N. Pazukhin); 5 - Southern Tien Shan (*Siphonodella vladimirovi* nom. nov., *S.* sp. D, *S.* sp. F, *S.* sp. H) (Bardasheva et. al. 2004); 6 - Southern Tien Shan (*Siphonodella* cf. *vladimirovi* nom. nov.) (Neyevin & Alexeiev 2021); 7 - Donbas region (*Siphonodella* sp. B) (Lipnjagov 1979); 8 - Moravia region (*Siphonodella nandongensis* Li) (Kalvoda et al. 2015); 9 - Guangxi region (*Siphonodella nandongensis* Li) (Li et al. 2014).

Discussion

The diagonal or/and longitudinal ornamentation of the inner side of the platform of P1 elements is not often observed. This type of ornamentation is known among some Famennian and Tournaisian *Polygnathus*, *Tanaissognathus, Polylophodonta,* and *Rhodalepis*. Moreover, conodonts with this type of ornamentation are found in deposits of a wide facies spectrum: from shallow-water shelf (for example, *Polylophodonta pergyrata* (Holmes), *Polylophodonta talenti* Drygant, *Tanaissognathus businovensis* Lipnjagov, some representatives of *Polyganthus nodocostatus* group (see Lipnjagov 1979; Shilo et al. 1984; Drygant 2010, etc.)) to deep-water shelf and bathyal zones (for example, *Polyganthus znepolensis* Spasov, *Pol. extralobatus* Schäfer, *Pol. obliquicostatus* Ziegler, some deviate *Pol. siphonellus* Druce (see Sandberg & Ziegler 1979; Çapkınoğlu 2000; Corradini 2003; Dzik 2006; Hartenfels 2011; Plotitsyn et al. 2014; Weiner & Kalvoda 2016, Neyevin & Alexeiev 2021, etc.)). Diagonal or/and longitudinal ornamentation in Famennian taxa is more often presented in the form of distinct ribs or it covers the entire platform (both the outer and inner sides of the platform), unlike in most siphonodellids. Similarly to the Famennian species of *Polygnathus*, *Tanaissognathus, Polylophodonta,* and *Rhodalepis*, siphonodellids with diagonal or/and longitudinal ornamentation have a wide facies distribution from a shallow-water carbonate platform (*Siphonodella* sp. B, *S.* sp. D (see Lipnjagov 1979, Shilo et al. 1984)) to a deep-water shelf slope (*S. vladimirovi* nom. nov., *S. nandongensis* Li, *S.* sp. C, *S.* sp. E, *S.* sp. G (see Plotitsyn & Vevel 2018)). The possibility of reworking of conodont elements from other facies zones into deep-water shelf conditions is not excluded. Thus, a reliable differentiation of species or individual species groupings of diagonally or/and longitudinally ornamented *Siphonodella* along individual facies belts is not presented. The main reasons are the rare occurrence of representatives of this group and a small number of localities from which such taxa have been described.

Siphonodella with diagonal or/and longitudinal ornamentation are known from a geographically wide number of sections of the Southern and Polar Urals, Donbass, Omolon region, Southern China, Southern Tien Shan, and Central Europe, which,

in paleogeographic terms, were widespread in the epicontinental seas of E-NE Laurussia, Western Siberia, Southern Kazakhstania and Southeastern Cathyasia (Fig. 7). This wide paleogeographical distribution allows the use of this group of siphonodellids in biostratigraphic reconstructions.

Siphonodella vladimirovi nom. nov. and *S. nandongensis* Li are found in a number of sections around the world and their stratigraphic distribution is relatively well known (Pazukhin 2008; Li et al. 2014; Kalvoda et al. 2015; Zhuravlev & Plotitsyn 2017; Plotitsyn & Vevel 2018). Data on the stratigraphic ranges of *S.* sp. A, *S.* sp. C, *S.* sp. E, and *S.* sp. G have previously been obtained from the Malaya Usa River section (Polar Urals). These findings are shown in Fig. 3 relative to the FODs of stratigraphically important taxa *Hindeodus cristulus* (Youngquist & Miller), *Siphonodella quadruplicata* (Branson & Mehl), and *S. crenulata* (Cooper). The stratigraphic distribution of *Siphonodella* sp. B, *S.* sp. D, *S.* sp. F, and *S.* sp. H requires additional analyses.

Siphonodella sp. B is found only in the Mokraya Volnovakha River section (Styla settlement) in the conodont association characterising the $C_1^tb_1$ subzone of the Donetz Basin (Lipnjagov 1979). The lower boundary of the Tournaisian in the Mokraya Volnovakha River section has not been established (see Fig. 2, Lipnjagov 1979). Based on the conodont associations, the base of the Carboniferous should be established by the appearance of *Patrognathus* with nodose ornamentation, which was diagnosed by O.M. Lipnjagov as *Patr. andersoni* Klapper. According to the latest data (Plotitsyn & Zhuravlev 2020), the range of the *Patrognathus andersoni* Klapper is approximately comparable to the interval of zones from the upper part of the *S. wilberti* to the *S. isosticha* zones. However, the specimen pictured by O.M. Lipnjagov as *Patrognathus andersoni* Klapper (see Fig. 11, pl. 2, Lipnjagov 1979) is morphologically more similar to *Patr. crassus* Kononova & Migdisova. *Patrognathus crassus* Kononova & Migdisova is the ancestor of *Patr. andersoni* Klapper within the phyletic line *Patr. ourayensis* Sandberg & Ziegler, 1979 → *Patr. donbassicus* Lipnjagov (Kozitskaya et al. 1978) → *Patr. crassus* Kononova & Migdisova → *Patr. variabilis* Rhodes, Austin & Druce → *Patr. andersoni* Klapper (Barskov et al. 1984; Zhuravlev 2007; Plotitsyn & Zhuravlev 2020). O.M. Lipnjagov diagnosed *Patrognathus crassus* Kononova & Migdisova as *Patr. andersoni* Klapper in a 1979 publication because *Patr. crassus* Kononova & Migdisova was not described and published about until later in 1984 (Barskov et al. 1984). The joint finding of early representatives of the *Siphonodella* (*S. sulcata* (Huddle), *S. praesulcata* Sandberg, *S. semichatovae* Kononova & Lipnjagov), and *Patrognathus crassus* Kononova & Migdisova suggests that *S.* sp. B begins its distribution slightly above the base of the Tournaisian. At the same time, similar in rostrum structure *Siphonodella puchkovi* Zhuravlev ranges in the sections of the Cis-Urals approximately from the upper part of *S. sandbergi* or *S. crenulata* Zones (Zhuravlev 2019). A more accurate determination of the stratigraphic distribution of *Siphonodella* sp. B is currently impossible.

The stratigraphic distribution of *Siphonodella* sp. D within the *isosticha* Zone (approximately comparable to the upper part of the Lower *crenulata* Zone and possibly the *isosticha*-Upper *crenulata* Zone) is provided in the article by V.N. Pazukhin (2008), where *S.* sp. D is diagnosed as *S.* sp. 2. The first appearance of *Siphonodella* sp. D probably corresponds to the base of the Lower *crenulata* Zone, because this taxon is found within the Lower *crenulata* conodont zone in the Shishkat section (Southern Tien Shan, Tajikistan) (Bardasheva et al. 2004).

Siphonodella sp. F is known from the upper part of the *S. carinthiaca* Zone at the Dzikoviec sections in Southwest Poland (Dzik 1997) and *sandbergi* Zone of the Shishkat section in Southern Tien Shan (Bardasheva et al. 2004). According to conodont associations of the upper part of *Siphonodella carinthiaca* Zone (see sample no. DZ-22, Table 1, Dzik 1997) this interval corresponds to the *S. quadruplicata* Zone. Sample no 9-0-16, in which *Siphonodella* sp. F is hosted in the Shishkat section, contains poor conodont assemblages, but the FOD of *Siphonodella quadruplicata* (Branson & Mehl) is noted as being stratigraphically below (see Table 2.3, Bardasheva et al. 2004). Thus, *Siphonodella* sp. F is known from the *S. quadruplicata* Zone.

Findings of *Siphonodella* sp. H (figured as *S. sandbergi* Klapper, Figs. 1-9, 14-15, pl. 4, in Bardasheva et al. 2004) are recorded either as starting from the level of the FODs of *S. quadruplicata* (Branson & Mehl) (see Table 2.3 in Bardasheva et al. 2004), or slightly below (see Tables 3, 4.1 in Bardasheva et al. 2004). In the Shishkat section, the FODs of *S. sandbergi* Klapper and *S. quadruplicata* (Branson & Mehl) are actually comparable (see Ta-

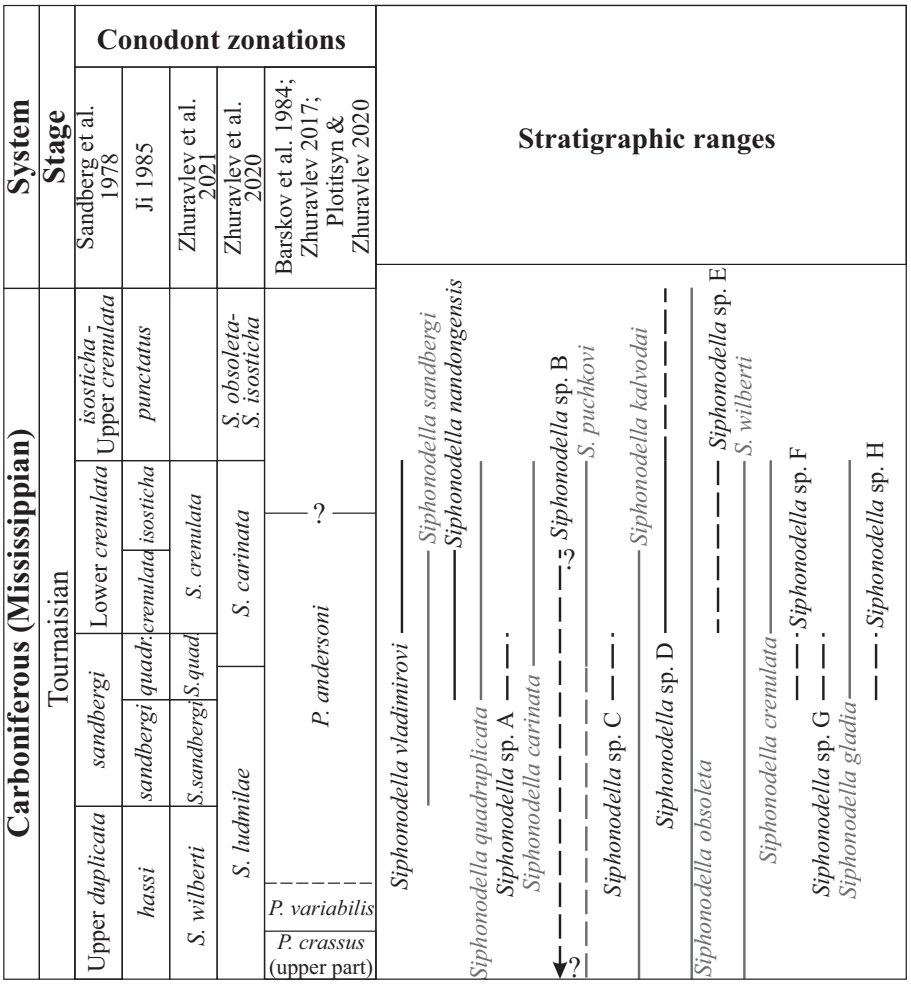

Fig. 8 - Stratigraphic ranges of the Tournaisian diagonally or/and longitudinally ornamented *Siphonodella* (painted black) and their morphological (by the structure of the rostrum) analogs (painted gray). Abbreviations: S. quad. - *Siphonodella quadruplicata*; quadr. - *quadruplicata*; *P.* - *Patrognathus*; *S.* - *Siphonodella*.

ble 5.2 in Bardasheva et al. 2004). Therefore, the *sandbergi* Zone identified by N.P. Bardasheva with coauthors can be correlated with the *S. quadruplicata* Zone.

The appearance of diagonal or/and longitudinal ornamentation atypical for advanced siphonodellids can be explained by several variants:

First, there may be a individual evolutionary branch, similar to the cosmopolitan group (thinly ornamented), the East European group (smooth or/and roughly ornamented), and the Chinese group (smooth). Individual evolutionary branch with diagonal or/and longitudinal ornamentation of the inner side of the platform of P1 elements, which is geographically distributed in Europe, Central, and East Asia. In paleogeographic terms, this corresponds to the northwestern and northeastern parts of the Paleotethys ocean (epicontinental seas of the eastern part of Lavrussia, southern part Kazakhstania, and southeast of Cathyasia) and northeastern part of the Panthalassic Ocean (Angayuchim sea) (Scotese 2016, 2017). However, this theory does not explain the presence of representatives within the group that have quite different platform morphologies. In particular, *Siphonodella* sp. A, B have similar platform morphologies as the smooth or/and roughly ornamented species of the East European group, and *S.* sp. C-H are closer to cosmopolitans in morphology.

Second, taxa represent intraspecific variability of already known species of *Siphonodella*, where variability is expressed by the change in the ornamentation of the inner side of the platform. However, this theory looks unreliable due to the fact that, in addition to the change in ornamentation in morphologically similar species, there are other differences between typical and deviant forms. In particular, these differences can be noted in the structure of the rostrum of *Siphonodella vladimirovi* nom. nov. and *S. sandbergi* Klapper or *S.* sp. D and *S. obsoleta* Hass; in the platform outlines of *S.* sp. G and *S. gladia* Zhuravlev & Plotitsyn or *S.* sp. F and *S. carinthiaca* Schönlaub; in the ornamentation of the outer side of the platform of *S.* sp. H and

S. sandbergi Klapper. Moreover, the stratigraphic ranges of the most studied representatives of the group of diagonally or/and longitudinally ornamented siphonodellids *Siphonodella nandongensis* Li and *S. vladimirovi* nom. nov. (assumed as deviated forms) and their morphological analogs *S. quadruplicata* (Branson & Mehl) and *S. sandbergi* Klapper (assumed typical forms) do not coincide (Fig. 8). In addition, as mentioned earlier, the change of ornamentation is traditionally considered as one of the most important mechanisms in the process of speciation during the evolution of the *Siphonodella* genus. Thus, forms with ornamentation that differ from typical species are considered as individual species.

Third, and most plausibly, species with diagonal or/and longitudinal ornamentation derived from morphologically similar species as descendants of the cosmopolitan group and East European group. The same scenario has previously been considered for *Siphonodella vladimirovi* nom. nov. (Pazukhin 2008). It was assumed that *Siphonodella vladimirovi* nom. nov. is a descendant of *S. carinthiaca* Schönlaub, in which the structure of the rostrum has become more complex and the type of ornamentation has changed (see *S. carinthiaca* Schönlaub - *S.* sp. 1 lineage in the phylogeny scheme in Pazukhin, 2008). Subsequently, a decreasing of number of rostral ridges in ontogeny (down to two) and a reduction in ornamentation of the outer side of the platform led to the formation of *Siphonodella* sp. D from *S. vladimirovi* nom. nov. (see *S.* sp. 1 - *S.* sp. 2 line in the phylogeny scheme in Pazukhin, 2008). In general, morphological transformations occurring during the transition from *Siphonodella vladimirovi* nom. nov. to *S.* sp. D appear plausible, since a similar mechanism has occurred in other evolutionary lineages of the genus. Morphological changes by the time of the final stage of development of the genus, against the background of the general taxonomic and quantitative depletion of conodonts within the *crenulata-isosticha* zones interval, are characterised by a reduction in the ornamentation of the upper side of the platform. Evolutionary branches in the group of cosmopolitans demonstrating reduction of ornamentation in phyletic lines: *Siphonodella crenulata* (Cooper) - *S. lanei* Zhuravlev & Plotitsyn, *S. cooperi* Hass - *S. isosticha* (Cooper). In this regard, this theory looks more appropriate at the present time. In addition, species with diagonal or/and longitudinal ornamentation were formed from morphologically similar taxa from the cosmopolitan group. Likely examples include *Siphonodella nandongensis* Li from *S. quadruplicata* (Branson & Mehl); *S. vladimirovi* nom. nov. from *S. sandbergi* Klapper or *S. obsoleta* Hass; *S.* sp. E from *S. wilberti* Bardasheva, Bardashev, Weddige & Ziegler or *S. crenulata* (Cooper); *S.* sp. G from *S. gladia* Zhuravlev & Plotitsyn; *S.* sp. H from *S. sandbergi* Klapper. In the East European group likely examples include *S.* sp. A from *S. carinata* Zhuravlev; *S.* sp. B from *S. puchkovi* Zhuravlev; and *S.* sp. C from *S. kalvodai* Kaiser, Kumpan & Cigler.

Conclusions

Advanced representatives of *Siphonodella* with diagonal or/and longitudinal ornamentation on the upper side of the platform of P1 elements are currently known from the middle of the early Tournaisian (*S. wilberti* Zone), when the ribbed type of ornamentation changed to other types of ornamentation (= second morphological event in the advanced evolution of *Siphonodella* after Zhuravlev & Plotitsyn 2017). The last representatives of the group are known from the final stage of the existence of siphonodellids from the level with surviving *Siphonodella isosticha*. The forms with a diagonal or/and longitudinal type of ornamentation are probably descendants of morphologically similar forms from the cosmopolitan and East European groups. The persistence of the appearance of diagonal or/and longitudinal ornamentation as a feature during speciation in different groups may indicate that it is adaptive. Indeed, this feature is probably adaptive to a specific food source (diet) within certain environments. The complication of the morphology of P1 elements in the conodont apparatus is hypothetically reflects complication of food processing (Donoghue, Purnell, 1999). Additional, the study of diagonally or/and longitudinally ornamented siphonodellids will allow the future use of these features in detailed stratigraphy studies, up to the creation of alternative variants of the zonal scales of narrow facies belts.

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