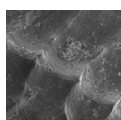


# Early Devonian polygnathids of Northeast Asia and correlation of Pragian/Emsian strata of the marginal seas of Angarida

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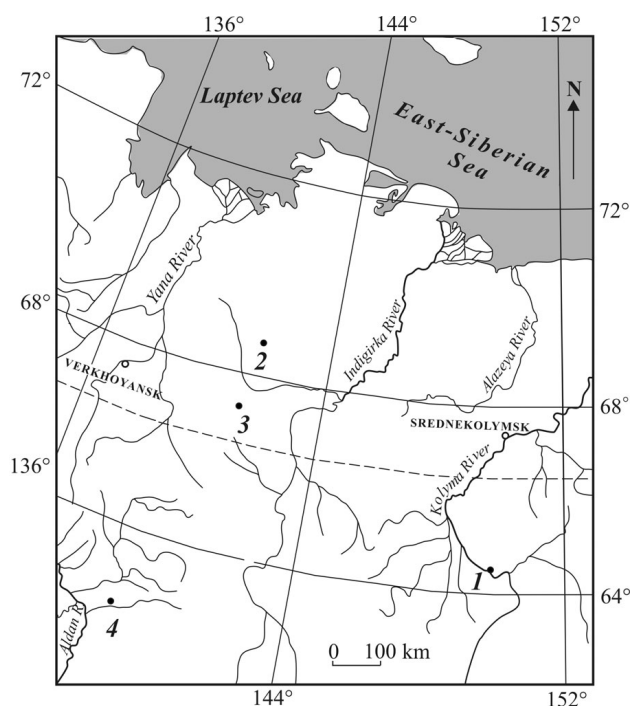
In late Pragian and early Emsian strata of the Izvestkovyi Karier – II section of Northeast Asia is found a continuous sequence of representatives of the family Polygnathidae which testify to the synthetic nature of the currently used conodont zonal scales. In this time interval are recognized three phylogenetic lineages of polygnathids: *Polygnathus sobolevi* → *Po. ivanowskyii*, *Polygnathus kitabicus* → *Po. bardashevi* and *Polygnathus settedabanicus* → *Po. nothoperbonus*. Fifteen species of polygnathids including mostly newly described taxa are documented here: *Polygnathus alkhovikovae* sp. nov., *Po. arthuri* sp. nov., *Po. bardashevi* sp. nov., *Po. dehiscens* (Philip & Jackson, 1967) late morphotype, *Po. excavatus* (Carls & Gandl, 1969), *Po. ivanowskyii* sp. nov., *Po. karsteni* sp. nov., *Po. kitabicus* (Yolkin *et al.*, 1994), *Po. lezhoevi* sp. nov., *Po. michaelmurphyi* sp. nov., *Po. nothoperbonus* (Mawson, 1987), *Po. perbonus* (Philip, 1966), *Po. sobolevi* Bardashev, Weddige & Ziegler, 2002, *Po. settedabanicus* sp. nov., and *Po. yakutensis* sp. nov. Early Emsian time in Northeast Asia is characterized by an intense speciation and radiation within its conodont fauna during a relatively short interval between the *Polygnathus excavatus* and *Polygnathus nothoperbonus* zones. The Pragian Stage (Middle Early Devonian) is characterized by a maximum transgression that led to increased migration of faunal associations of tabulate and rugose corals, brachiopods and conodonts in the marginal seas of Angarida. The position of the lower and upper boundaries of the Pragian Stage in this region is clarified and their correlations are shown with the adjoining Verkhoyansk-Chukotsk (Kolyma region), Taimyr, West Siberian, and Altai-Sayan marginal seas. • Key words: Early Devonian, eopolygnathids, Pragian, Emsian, correlation, Northeast Asia, marginal seas, Angarida.

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The late Pragian and early Emsian polygnathids are the most important group for dating boundaries between stages, as well as for the zonation and global correlation of the Lower Devonian strata in deeper-water settings. In shallow-water settings alternative conodont groups can be used – e.g., icriodontids and pelekysgnathids. For more than 40 years several attempts have been made to suggest phylogenetic schemes of early polygnathids from different continents as a basis for zonations: Australia (Philip & Jackson 1967; Mawson 1987, 1995, 1998; Mawson *et al.* 1992), North America (Klapper *et al.* 1978, Lane & Ormiston 1979, Klapper & Johnson 1980, Uyeno & Klapper 1980), Europe (Bultynck 1989), Central Asia (Bardashev & Ziegler 1992; Yolkin *et al.* 1989, 1994, 2011). Bardashev *et al.* (2002) reviewed most known occurrences of early poly-

gnathids and offered a new model of the phylogeny of early polygnathids (eopolygnathids) and conodont zonation of the Emsian Stage. Recently, the International Subcommission on Devonian Stratigraphy (SDS) came to the conclusion that the base of the Emsian is stratigraphically placed at a too low level and that a redefinition of the boundary is necessary (Carls *et al.* 2008a, Becker 2009, Becker *et al.* 2012). The *kitabicus* boundary of Yolkin *et al.* 1994 (*i.e.*, the current Emsian base) is currently considered as an important marker for the prospective subdivision of the Pragian Stage (see discussions e.g., in Carls *et al.* 2008b, Valenzuela-Ríos & Carls 2010, Slavík *et al.* 2011 and Jansen 2012). Yolkin *et al.* (1994) proposed a zonation for the late Pragian and the early Emsian that includes a succession of four zones: *pireneae*, *kitabicus*, *excavatus* and



**Figure 1.** Schematic map showing locations of the sections: 1 – Izvestkovyi Karier – II section, Kolyma River, 2 – Gon section, Selennyakh Range, 3 – Geremgandzha-Ger section, Tas-Khayakhtakh Ridge, 4 – Tikhyi section, Sette-Daban Ridge.

*nothoperbonus*. Yolkin *et al.* (2011) believed that the index species of each of these zones represents one phylogenetic step. However, in the opinion of Bardashev *et al.* (2002) and according to our interpretations of data given below, the phylogenies and the zonation suggested by Yolkin *et al.* (1994, 2011) may have an alternative basis.

The Pragian time is, however, much reduced because of the unsuitable definition of the base of the Emsian (the *kitabicus* boundary). The conodont material that has been obtained from Northeast Asia and which is presented herein shows that the former morphophylogenetic models cannot be applied in the studied region. One of the problematic questions of the stratigraphy of the Pragian Stage in the marginal seas of Angarida is the recognition of the lower and upper stage boundaries (Baranov & Blodgett 2012). In the stratotype area of the Pragian Stage its lower boundary is based on the first occurrence of an eognathodontid specimen found by Weddige (1987) (*i.e.*, *Eognathodus* “*sulcatus*” = *Eognathodus irregularis*) despite the fact that specimens with a clear “sulcus” have been found slightly below its base (Slavík & Hladil 2004). But scarcity of eognathodontids lead to an alternative correlation of the early Pragian based on icriodontids and pelekysgnathids (Slavík *et al.* 2007; see Fig. 4). In the marginal seas of Angarida *Eognathodus* “*sulcatus*” is found only in the Verkhoyansk-Chukotsk (Kolyma) region in deeper-water facies, while it is absent in shallow-water en-

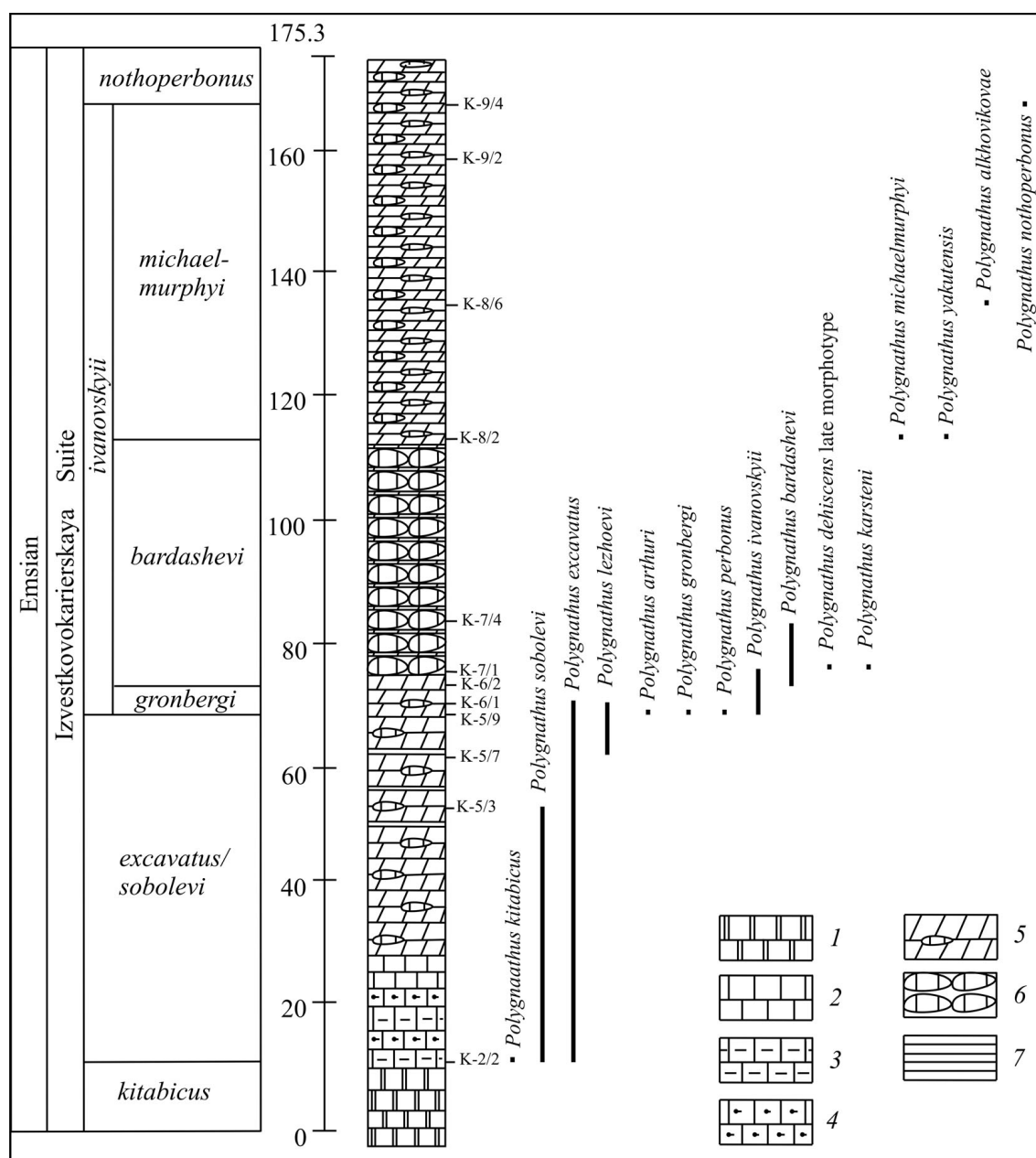
vironment. Therefore, for the biostratigraphic correlation of the lower Pragian an alternative shallow-water icriodontid morphophylogenetic lineage, *Gagievodus* → *Vjaloviodus*, is used (Alkhovik & Baranov 2001, Baranov 2012). In addition, for the correlation of the polyfacial beds in the Verkhoyansk-Chukotsk Marine Basin a composite biozonal scheme based on the stratigraphical distribution of rugose and tabulate corals, brachiopods and conodonts was developed. The lower boundary of the Pragian Stage was established regionally at the base of the *Tryplasma altaica*-*Yacutiopora innae*-*Sulcataechia tichiensis*, *Howellella prima*-*Eognathodus* “*sulcatus*”, *Gagievodus marinae* Assemblage Zone. Statistics showed what exactly occurred at the base of the zone. The structure of the association in these four faunal groups has been updated. In addition, this boundary coincides with the base of the lower Pragian cyclicity (Baranov 2009a). The recognition of the GSSP-defined basal Emsian boundary both in the Barrandian and in the marginal seas of Angarida, and, as well in other areas of the world raises problems. A corresponding discussion is provided in this present paper.

## Material

The material presented here has been obtained from three sections of late Pragian and early Emsian strata in Northeast Asia (Figs 1, 2). The dissolution of limestone samples was made using acetic acid (7%). The subsequent separation of conodont elements was based on using heavy liquids. In total, approximately 600 kg of carbonate rock samples was processed from which 1319 conodont elements were obtained. The majority of samples (571 kg) come from the Izvestkovyi Karier – II section. Additional sampling has been carried out in other three localities: 14 kg samples are from Tas-Khayakhtakh Ridge, 10 kg from Selennyakh Range, and 5 kg from Sette-Daban Ridge (see Fig. 1 for location). Together with the conodont faunas, previously described brachiopods, tabulate and rugose corals from the Pragian of Northeast Asia (Alkhovik & Ivanowskyi 1988, Alkhovik & Baranov 2001) are used for correlation.

## Geological setting

The Izvestkovyi Karier – II section is located on the right bank of Kolyma River in the southwestern part of Kolyma Uplift (Northeast Asia). It consists of middle Paleozoic rocks, which were deposited unconformably upon the Upper Proterozoic or Ordovician strata (Menner *et al.* 1973). The Lower Devonian here is composed of four suites: Zhelezninskaya (lower Lochkovian), El'geneskaya (Lochkovian–Pragian), Izvestkovokarierskaya (lower Emsian) and Sakhinskaya (upper Emsian). The Zhelezninskaya



**Figure 2.** Izvestkovyi Karier section – II column with distribution of selected taxa and its biostratigraphic interpretation: 1 – dolomite, 2 – limestone, 3 – shaly limestone, 4 – sandy limestone, 5 – lenses of fragmental limestone in calcareous shale, 6 – fragmental limestone, 7 – argillite.

Suite in its lower part consists of red-colored conglomerates, gravels, and red, green and grey sandstones. The upper part consists of grey thick beds of dolostones and sandstones. The early Lochkovian age is indicated by the presence of “*Ozarkodina*” ex gr. *remscheidensis* (Ziegler) (Gagiev 1987, Gagiev *et al.* 1990). Its total thickness varies from 320 up to 515 m. The Elgeneskskaya Suite is exposed in two tectonic blocks and is composed of folded thick-bedded and massive limestones alternating with layers of clay limestones, marls, sandstones and siltstones. In its lower part are found the conodonts *Pandorinellina boucoti*

(Klapper), *P. philipi* (Klapper) and in its upper part are found “*Eognathodus*” *sulcatus sulcatus* (Philip) and “*Eognathodus*” *sulcatus juliae* Lane & Ormiston. Its total thickness is 800 m. The Izvestkovokarierskaya Suite was established by Pepelyaev & Simakov (1974). The type section consists of marls, argillites and sedimentary limestone breccia with *Belodella resima* (Philip), *B. triangularis* (Stauffer), *Latericriodus sigmoidalis* (Carls & Gandl), *Pandorinellina philipi* (Klapper), *P. steinhornensis steinhornensis* (Ziegler), *Pelekysgnathus klamathensis* Savage, *Vjaloviodus taimyricus* (Kuzmin) (Al’khovik & Baranov

2001), and the polygnathids described in the present article. In the lower part of the Izvestkovokarierskaya Suite (at 15 and 26 m above its base) were found the dacryoconarid tentaculites *Turkestanella* (*Nowakia*) *acuaria* (Richter) and *Viriatella* aff. *hercynica* (Bouček). The suite varies in thickness from 160 to 200 m. A detailed lithological description of the Izvestkovyi Karier – II section with reference to the fauna present is described by Alkhovik & Baranov (2001, pp. 139–140). The Sakhinskaya Suite is represented by dark-grey and grey dolostones, limestones, sandstones, siltstones and marls. Conodonts are not present. The thickness of the suite varies from 250 up to 320 m.

### **Morphophylogenetic relationships of polygnathids according to data from the Devonian sequence at the Izvestkovyi Karier – II section (right bank of Kolyma River)**

Phylogenetic relationships of polygnathids have been considered by many conodont workers (*e.g.*, Klapper & Johnson 1975; Weddige 1977; Weddige & Ziegler 1979; Sweet 1988; Mawson 1987; Bultynck 1985, 1989; Bardashev & Ziegler 1992; Bardashev *et al.* 2002; Yolkin *et al.* 1994; Martínez-Pérez *et al.* 2010; Martínez-Pérez *et al.* 2011; Yolkin *et al.* 2011). A comprehensive review of the taxonomy was proposed by Bardashev *et al.* (2002). They based their revision on published figures and established a large number of new taxa. Mainly because their procedure disregards intraspecific variability and thus results in serious discrepancies of taxonomy and biostratigraphic zonation, their concept has been criticized by many authors, *e.g.*, Mawson & Talent (2003), Murphy (2005), Slavík *et al.* (2007) or Becker (2012). The last author tried to compile a list of all taxa that belong to or are related to the genus *Polygnathus*. The comprehensive list with almost 650 names evidently pleads for a generic subdivision of the “megagenus” *Polygnathus* as Becker pointed out. However, the problem remains as a clear grouping of morphological changes on both the aboral and oral surfaces of the platform at the generic or subgeneric level. It is not an easy task, especially with respect to evolution as shown by the data presented herein from Northeast Asia. Although the phylo-morphogenetic concept of Bardashev *et al.* (2002) includes several new polygnathid genera, the main emphasis in the diagnoses was put on the oral surface and general appearance (shape) of the platform element. Most problematic is the application of the proposed generic splitting for definition of time-specific intervals which is the main task for taxonomy of early polygnathids. Therefore we do not follow the taxonomical concept of Bardashev *et al.* (2002), although we agree that future subdivision of the “all-embracing” genus *Polygnathus* is necessary. An important

aspect that cannot be neglected is ontogenetic and intraspecific variation. Such types of variability have recently been demonstrated in Emsian polygnathid taxa by Klapper & Vodrážková (2013).

The material from the Northeast Asia is relatively rich and includes a number of very distinct forms that can be partly attributed to formally established taxa, while some taxa are newly proposed. We are aware of the fact that the material of several of the herein proposed taxa includes only a few specimens and, thus, intraspecific variability is an issue that must be considered. But the time distribution of the new taxa seems to be of stratigraphic meaning, especially when more material from this or other parts of the world is available. Therefore, at this stage, we have chosen the way of “specific splitting”, believing that in general it is a much easier procedure to split such distinctive forms which are poor in number, rather than split taxonomically lumped forms in the future. The degree of precision in biostratigraphic correlation is driven by the degree of recognition of very detailed morphological characters. Moreover, biostratigraphic correlation is largely hindered especially by usage of too liberal taxonomic concepts when “zonal names” are implied.

In this paper we put emphasis not only on the evolution of the basal cavity (lower surface), but also on the differentiation of transverse ridges and the development of sharp nodes as important diagnostic criteria for early polygnathid evolution.

In spite of their great importance for mid-Early Devonian stratigraphy, the eopolygnathids cannot be easily used in stratotype areas of the Pragian and Emsian Stages. Due to facies constraints, conodonts are very rare in the Emsian of the Ardennes-Rhine region (Germany) where the Emsian Stage was established. And, due to unfavorable paleobathymetric conditions, the early polygnathids are very scarce in the Prague Synform (Barrandian area, Czech Republic), where the Pragian Stage has been defined. Accordingly the correlation is alternatively established by means of icriodontids (Slavík 2004a, b) and/or other faunal groups (*e.g.*, dacryoconarids, for summary see Chlupáč *et al.* 1998). Therefore, the section in the Zinzilban Gorge in the Kitab State Reserve (Uzbekistan) has been chosen as the basal Emsian GSSP (Yolkin *et al.* 1997), as it was believed to contain a continuous sequence of polygnathids. The phylogenetic lineage that has been suggested allowed the recognition of the following sequence of zones, *Polygnathus pireneae* → *Polygnathus kitabicus* → *Polygnathus excavatus* → *Polygnathus nothoperbonus* (Yolkin *et al.* 2011). Exceptionally good conditions for the future recognition of the Pragian/Emsian boundary were found in the Pyrenees where both stratigraphically important conodont groups – polygnathids and icriodontids are present and occur in sufficient numbers (Martínez-Pérez 2010; Martínez-Pérez *et al.* 2010, 2011).



The study of late Pragian and early Emsian polygnathids of Northeast Asia suggests that representatives of the species *Polygnathus excavatus* and *Polygnathus nothoperbonus* may belong to different phylogenetic lineages. This alternative had earlier been postulated by Bultynck (1989) and Bardashev et al. (2002). In Northeast Asia a continuous sequence of eopolygnathids is established in the Izvestkovyi Karier – II section. Additional data were obtained from several stratigraphical levels in the sections of the Lower Devonian of the Tas-Khayakhtakh Ridge, Selennyakh Range and Sette-Daban Ridge (Southeast Siberian Platform); these data supplement the proposed conodont sequence.

The lower boundary of the Emsian Stage in the Verkhoyansk-Chukotsk Basin represents one of the most significant boundaries during which a major rearrangement of the ecosystem and a great diversification occurred in all faunal groups including conodonts. The origination of new ecological niches during the early Emsian can be explained by one of the largest transgressions that have been recognized in the northern hemisphere. It caused mixing and migration of conodont faunas from adjacent marine basins. Also, an increased diversification in nutrient supply may have triggered rapid changes of oral surface morphology in polygnathid platform elements. This led to the appearance of several new, possibly endemic taxa described in the present paper (see Figs 7–15).

The morphophylogenetic development of the early Emsian polygnathids in Northeast Asia can be characterized by three lineages: *Polygnathus sobolevi* → *Po. ivanowskyii*, *Polygnathus kitabicus* → *Po. bardashevi* and *Polygnathus settedabanicus* → *Po. nothoperbonus* (see Figs 3, 4).

The *sobolevi* → *ivanowskyii* lineage is represented by two nominal species: *Polygnathus sobolevi* and *Polygnathus ivanowskyii*. *Polygnathus sobolevi* appeared simultaneously at the base of the Emsian in Northeast Asia, southeast Alaska, northwest Canada, South China, Australia and Novaya Zemlya. It is possible to consider its ancestor as *Polygnathus pireneae* Boersma, which has not been found in the upper Pragian rocks of Northeast Asia. The aboral surface of *Polygnathus ivanowskyii* acquired a subtrigonal shape. There were no major changes in the structure of the basal cavity of this species group during the early Emsian (see Fig. 3).

The *kitabicus* → *bardashevi* lineage. *Polygnathus kitabicus* appears at the base of the Emsian and its most probable ancestor is *Polygnathus pireneae* Boersma (see systematic section), compared with which it has a more progressive structure of the aboral part of platform in the presence transverse ridges and grooves. *Polygnathus excavatus*, which was separated from *Po. kitabicus* in the lower part of the Emsian, is characterized by a larger platform and deeper adcarinal grooves reaching to mid-length,

platform margins which are ornamented by ridges, and a tongue occupied by interrupted or semi-crossed and transverse ridges bearing weakly expressed nodes. In the youngest species of the branch, *Po. excavatus*, there is observed an even greater differentiation of transverse ridges. *Po. lezhoevi* sp. nov. separated from its possible ancestor in the upper part of *excavatus* Zone. It has a platform, which is characterized by an oval outline and a flat upper surface. *Polygnathus gronbergi* is probably derived from *Po. excavatus* as shown in other areas (cf. Bardashev et al. 2002). *Po. gronbergi* has a sharply inverted and restricted basal cavity and differs from its ancestor *Eoc. excavatus* in the presence of transverse ridges bearing sharp nodes on the inner side of the platform, a semi-crossed tongue and in having nodes on the end of tongue. Probable descendants of *Po. gronbergi* have not yet been found in the Emsian beds of Northeast Asia. An evolutionary trend in the differentiation of transverse ridges into nodes is clearly observed in the descendants of *Po. excavatus*, in *Po. bardashevi* sp. nov. and *Po. karsteni* sp. nov. The last representatives of *Po. excavatus* gave rise to two phylogenetic branches: *Po. excavatus* → *Po. bardashevi* and *Po. arthuri* → *Po. alkhovikovae*. In comparison with its ancestor, *Po. bardashevi* sp. nov. has a much more inverted basal cavity than *Po. excavatus*, exceeding more than one half of its length, and also differs by a change in the ornamentation of the upper part of the platform. *Po. bardashevi* sp. nov. has transverse ridges only on the inner margins of the platform, the remaining part is occupied by nodes. In comparison with *Po. excavatus*, *Po. karsteni* sp. nov. is characterized by a strong differentiation of the transverse ridges into nodes, and the narrower posterior part of the basal cavity. *Po. arthuri* sp. nov. is probably a descendant of *Po. excavatus*. According to the structure of the basal cavity it does not differ from *Po. excavatus*, but the platform margins are ornamented by nodes or short ridges, and in the posterior part it has long transverse ridges differentiated by weakly to strongly expressed nodes. The youngest species of the lineage, *Po. alkhovikovae* sp. nov., is characterized by a medial displacement of the nodes at the bending of the platform, an increase in the length of the tongue, and by rough transverse grooves of the platform margins.

The *settedabanicus* → *nothoperbonus* lineage. The earliest representative in this lineage is *Polygnathus settedabanicus*. It is found at the base of *excavatus* Zone, its ancestor is unknown but it might coincide with the radiation of the early polygnathids close to the basal Emsian boundary. The relation of *Polygnathus perbonus*, which appears later in this lineage, with possible ancestors and descendants is not clear. The probable ancestor of *Po. perbonus* would appear to be an early representative of *Polygnathus dehiscens* (Mawson 1987). In Northeast Asia *Polygnathus dehiscens* late morphotype appears at 68 m above the top of the *kitabicus* Zone and below the base of

the *nothoperbonus* Zone at the same stratigraphical level as in Australia (Mawson 1987) or in northwestern France (Bultynck 1989). For several decades the species *Polygnathus dehiscens* Philip & Jackson was largely accepted as the index species of the oldest conodont zone of the Emsian Stage. The problems with the age of the taxon *Po. dehiscens* and the history of the *dehiscens* Zone have been discussed at length by Carls & Valenzuela-Ríos (2000) and by Carls *et al.* (2008). Our study of conodonts from the Izvestkovyi Karier – II section suggests (Fig. 3) that the *kitabicus* and *nothoperbonus* conodont zones can be extended also to Northeast Asia, along with evidence of a great variety of polygnathids. It can also be assumed that representatives of *Polygnathus excavatus* may belong to the local phylogenetic lineage *Polygnathus kitabicus* → *Polygnathus bardashevi* (see below). In the same manner, Bultynck (1989) and Bardashev *et al.* (2002) also considered that *Polygnathus excavatus* and *Polygnathus nothoperbonus* belonged to different phylogenetic branches. Mawson (1987) and Bultynck (1989) believed that the ancestor of *Polygnathus nothoperbonus* was *Polygnathus dehiscens*, while Bardashev *et al.* (2002) considered that its ancestor was *Polygnathus foveolatus* Philip & Jackson (= *perbonus* in multi-element taxonomy). However, in the Izvestkovyi Karier – II section in the interval between *Polygnathus dehiscens* late morphotype and *Polygnathus nothoperbonus* are found representatives of *Po. michaelmurphyi* sp. nov. that are possible ancestors of *Po. nothoperbonus*. *Polygnathus michaelmurphyi* sp. nov. differs from its ancestor *Po. dehiscens* in the prolongation of the tongue and platform and by a shorter carina and adcarinal grooves. *Po. nothoperbonus* differs from its suggested ancestor *Po. michaelmurphyi* sp. nov. by a stronger deflection of the platform, deeper adcarinal grooves, and the inversion of the basal cavity. An additional species derived from *Po. michaelmurphyi* sp. nov. is *Po. yakutensis* sp. nov., which differs from its ancestor by the transition of anterior transverse ridges on the tongue into sharp and distinct nodes, and a narrower basal cavity.

### Zonation of the upper Pragian and lower Emsian strata in Northeast Asia

The regional biostratigraphic schemes of the upper Pragian and lower Emsian in different parts of the world were developed mostly on the basis of eopolygnathids: Nevada (Klapper & Johnson 1975), Canada (Fähræus 1971, Lane & Ormiston 1979), Barrandian, Czech Republic (Klapper & Johnson 1980), Eifelian Hills and Eastern Rhenish Slate Mountains, Germany (Weddige & Ziegler 1977), France (Bultynck 1989, only *gronbergi* Zone), Canadian Arctic Archipelago (Uyeno & Klapper 1980, Uyeno 1990), Arctic regions of Eurasia (Baranov 2012), Tadzhikistan and Uz-

bekistan (Central Asia) (Bardashev & Ziegler 1992, Yolkin *et al.* 1994), Salair Ridge (Izokh 1998), and south-eastern Australia (Mawson *et al.* 1992). Recently, zonations of the Lower Devonian of the Arctic regions of Eurasia were completed; they are based also on the studies of past thirty years in adjacent areas, *e.g.*, the Kolyma River Basin by Gagiev (1987, 1996) and Gagiev *et al.* (1987), South Verkhoyanie, Tcherskyi Mountains, Yukagirskay Plateau and Selennyakh Range by Tarabukin (1989, 1992), Baranov (1991, 2004) and Alkhovik & Baranov (2001), for Novaya Zemlya and Taimyr by Sobolev (1984, 1994) and Koren' (2006) and for Arctic regions of Eurasia by Baranov (2012). We have obtained new data on the systematics of polygnathids in the Izvestkovyi Karier – II section and the collections of polygnathids from the others regions of Northeast Asia that allow improvement of this zonation. The lower Emsian includes the *kitabicus* and *excavatus/sobolevi* zones, the *ivanowskyii* Zone with three Subzones (*gronbergi*, *bardashevi* and *michaelmurphyi*) and the *nothoperbonus* Zone (Figs 2, 3).

The *kitabicus* Zone contains 5 genera and 7 species: *Polygnathus kitabicus* Yolkin *et al.*, *Gigantholus privus* (Baranov), *Panderodus simplex* (Branson & Mehl), *P. unicostatus* (Branson & Mehl), *Pandorinellina philipi* (Klapper), *Vjaloviodus hastatus* Baranov, *V. taimyricus* (Kuzmin). Only *Gigantholus privus* and *Vjaloviodus hastatus* are endemic, the remaining species are characterized in having a broad global geographical distribution. The early Emsian age of the zone is justified by the zonal species-index. This zone corresponds to the *Scoliopora crassicaulis-Embolophyllum aggregatum-Trigonirhynchia ventricosa* Assemblage Zone (Alkhovik & Baranov 2001). Of the above species, *Po. kitabicus* and *Po. excavatus* define the early Emsian time.

The *excavatus/sobolevi* Zone contains 8 genera and 14 species: *Polygnathus excavatus* Carls & Gandl, *Po. kitabicus* Yolkin *et al.*, *Po. lezhoevi* sp. nov., *Po. sobolevi* Bardashev *et al.*, *Po. settedabanicus* sp. nov., *Belodella devonica* (Stauffer), *B. resima* (Philip), *B. triangularis* (Stauffer), *Gigantholus repostus* Baranov & Alkhovik, *Spathognathodus steinhornensis steinhornensis* Ziegler, *Panderodus simplex* (Branson & Mehl), *P. unicostatus* (Branson & Mehl), *Pandorinellina philipi* (Klapper), and *Vjaloviodus taimyricus* (Kuzmin). This zone corresponds to the *Polygnathus "dehiscens"-Caliopora parva, Scoliopora clara-Spongonaria philoctetes-Marijaella graciosa, Yanetechia delecta* and former *Polygnathus gronbergi-Sibirirhynchia alata-Yanetechia limata* Assemblage zones (Alkhovik & Baranov 2001).

The *ivanowskyii* Zone is divided into three subzones: *gronbergi*, *bardashevi* and *michaelmurphyi*. The *gronbergi* Subzone contains 3 genera and 6 species: *Polygnathus lezhoevi* sp. nov., *Po. ivanowskyii* sp. nov., *Po. arthuri* sp. nov., *Po. gronbergi* Klapper & Johnson,

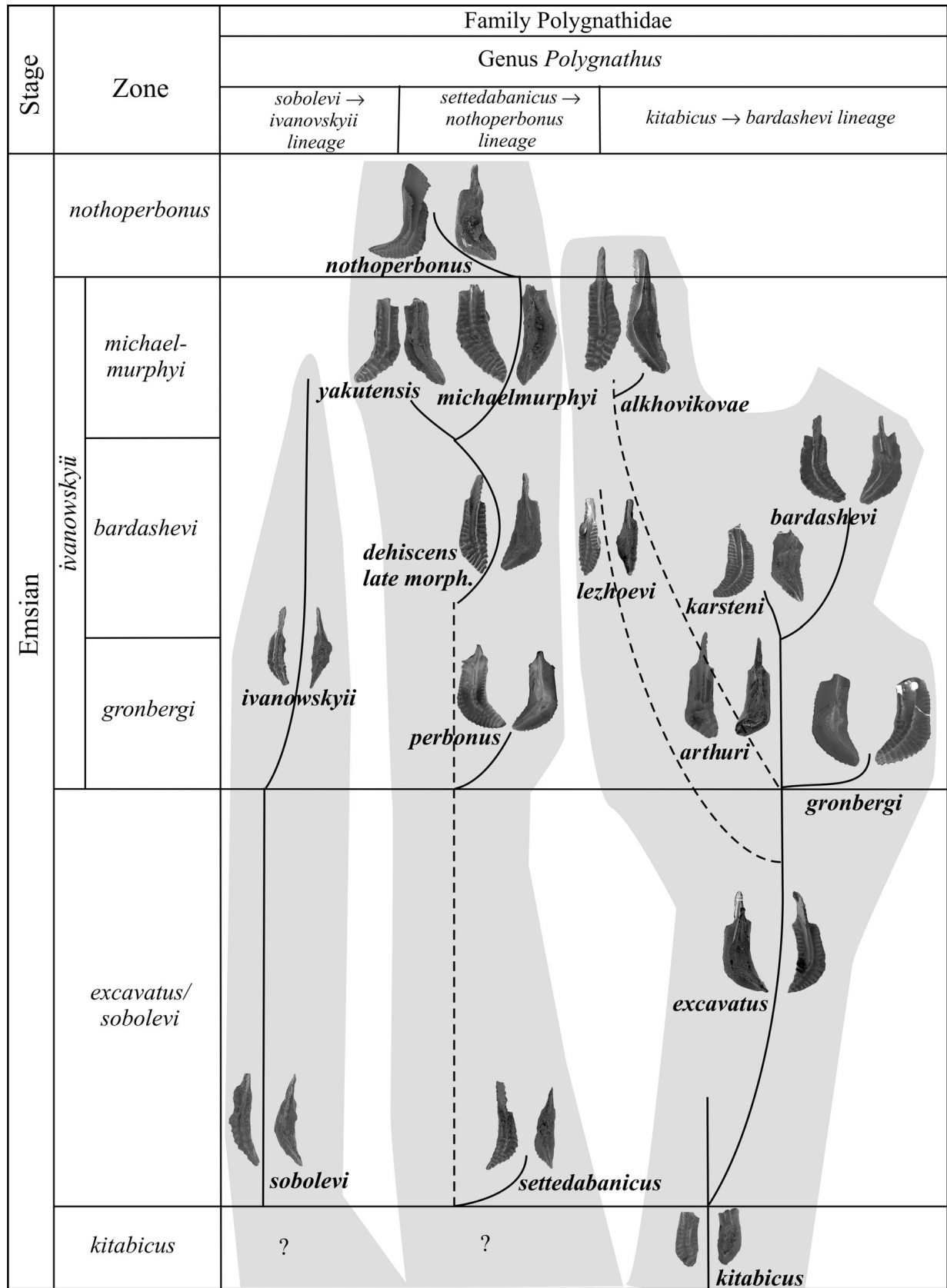


Figure 3. Phylomorphogenetic development of polygnathids of Northeast Asia.

*Po. lezhoevi* sp. nov., and *Po. perbonus* Philip. The lower boundary of the subzone is based on the appearance of the zonal species-index *Polygnathus gronbergi* and *Polygnathus perbonus*. The *bardashevi* Subzone contains 6 genera and 7 species: *Belodella triangularis* (Stauffer), *Polygnathus ivanowskyi* sp. nov., *Po. bardashevi* sp. nov., *Po. dehiscens* Philip & Jackson late morphotype, *Po. karseni* sp. nov., *Caudicriodus sigmoidalis* (Carls & Gandl), and *Vjaloviodus taimyricus* (Kuzmin). *Caudicriodus sigmoidalis* usually appears in the upper part of the early Emsian, in addition to its type locality it is also known on Zemlya Island (Sobolev 1984), Morocco (Jansen *et al.* 2004) and southern Tien-Shan of Central Asia (Bardashev & Ziegler 1992). The *michaelmurphyi* Subzone contains 6 genera and 7 species: *Belodella devonica* (Stauffer), *Polygnathus alkhovikovae* sp. nov., *Po. michaelmurphyi* sp. nov., *Po. yakutensis* sp. nov., *Gigantholus kolymaensis* Baranov & Alkhovik, *Pandorinellina exigua* (Philip), and *P. expansa* Uyeno. The last species listed is widely distributed in Emsian beds of the Arctic regions of Eurasia and the Canadian Arctic.

The *nothoperbonus* Zone contains 2 genera and 2 species: *Polygnathus nothoperbonus* Mawson and *Pandorinellina expansa* Uyeno. The index-species of this zone is characterized by its wide global distribution.

### Global correlation of the “original Pragian” and the basal Emsian boundary

The definition of the Pragian Stage in the Prague Synform was originally intended to correspond with the complete succession of the well-defined (both lithologically and biostratigraphically) Praha Formation. The Praha Formation includes several facies types of carbonates with typical open-sea character, ranging from extremely shallow-water to relatively deeper water pelagic (e.g., nodular) limestones of rather medium sedimentation rates (~20–25 m/Ma). Planktonic and widespread, reliably correlated faunas are very abundant and the minor detrital input is indicative of open shelf conditions. Typical lithologies, the distribution of dactyloconarids, and even the long migration paths of several benthic faunal groups – e.g., corals, brachiopods and trilobites, enable biostratigraphic and paleoenvironmental/lithological correlations with peri-Gondwanan regions or even more distant areas. The correlation potential of the original Pragian is significant by its extraordinarily high degree of reconnaissance that dates back to the later half of 19<sup>th</sup> century, but also by numerous recent papers and monographs (e.g., Chlupáč *et al.* 1998; Slavík *et al.* 2007; Koptíková *et al.* 2010a, b; Hladil *et al.* 2011; Holcová & Slavík 2013). However, the present correlation with GSSP's is too different from the detailed correlation based on well-defined individual taxa or reliably dated horizons.

In principle, GSSP's are often based either on formalism of biostratigraphic zonations or on the first appearance of a single taxon or specimen that may have several limitations with respect to taxonomic definitions and global dispersal. The problems with the definition of the taxon (“*sulcatus*”) that was selected to define the base of the Pragian were discussed in Slavík & Hladil (2004) and Slavík *et al.* (2007). However, the base of the Pragian is a relatively minor problem. The major difficulty is the present position of the Pragian/Emsian GSSP that not only reduces significantly the original Pragian (= Praha Formation) but also very far from the base of the traditional German Emsian and classic Emsian bases in other regions.

The present valid, “official” delimitation of the Pragian Stage is thus far from the physical record of geological time of the Pragian in its stratotype area (Prague Synform, Barrandian). In this context it is necessary to summarize some important stratigraphic points concerning the original Pragian. 1. The Lochkovian/Pragian GSSP boundary definition in the Barrandian was based on the first “*Eognathodus sulcatus*” – a specimen with a clearly developed sulcus (i.e., a distinct evolutionary step). However, the recent concept of “unsulcated specimens” defining the boundary (Murphy 2005) does not correspond with the GSSP. In Barrandian sections “sulcate specimens” already appear slightly below the Lochkovian-Pragian GSSP (Slavík & Hladil 2004). 2. Due to the extreme scarcity and resulting biostratigraphic unreliability of eognathodontids and polygnathids in the Prague Synform, the former and the recent zonal concepts (developed by Bardashev *et al.* 2002 and Murphy 2005) cannot be applied in the stratotype area. No *Polygnathus kitabicus* (i.e., the GSSP defining species) has been reported so far from the Barrandian area; the oldest polygnathids described (in Chlupáč *et al.* 1980; Slavík 2001, 2004a, b) belong to the *Polygnathus pireneae* and *Polygnathus excavatus* groups. The regional zonation for the Pragian is based on icriodontids and pelekysgnathids (Slavík 2004a, Slavík *et al.* 2007). 3. Conodonts in the Praha Formation are relatively scarce and most species are largely confined to peri-Gondwana. Nevertheless, reliable inter-regional correlation is provided by abundant dactyloconarids. The major and abrupt change in dactyloconarid faunas is linked with the boundary between the Praha and the Zlíchov Formations (P. Lukeš, pers. comm.). 4. The current GSSP concept of the Pragian/Emsian (P/E) boundary, and, also the zonal concept of Bardashev *et al.* (2002, p. 451) have reduced the original Pragian enormously. Only a short lowermost part of the sedimentary succession of the Praha Formation belongs to the “official” Pragian. Accordingly, the majority of the Praha Formation belongs to the Emsian in the current SDS sense (cf. Carls & Valenzuela-Ríos 2000, Slavík *et al.* 2007, Carls *et al.* 2008). 5. The most promising marker for the lower Emsian boundary in the Prague Synform is *Icriodus*



Stage	Faraeus (1971) (zones)	Perry <i>et al.</i> (1974) (faunal unit)	Weddige & Ziegler (1977) (faunal unit)	Weddige (1977) (faunal unit)	Klapper (1977) (zones)	Lane & Ormiston (1979) (zones)	Klapper & Johnson (1980) (zones)	Yolkin & Izokh (1988) (zones)	Yolkin <i>et al.</i> (1994) (zones)	Mawson (1995) (zones)	Ziegler & Weddige (1999) (zones)
Emsian	<i>Po. foveolatus</i>	<i>Po. perbonus perbonus</i> late form (lower part)	<i>Po. gronbergi</i>	<i>Po. gronbergi</i>	<i>gronbergi</i>	<i>gronbergi</i>	<i>gronbergi</i>	<i>nothoperbonus</i> <i>gronbergi</i>	<i>nothoperbonus</i> <i>excavatus</i>	<i>nothoperbonus gronbergi/perbonus</i>	<i>gronbergi (excavatus)</i>
	<i>Po. dehiscens</i>	<i>Po. dehiscens</i>	<i>Po. dehiscens</i>	<i>Po. dehiscens</i>	<i>dehiscens</i>	<i>dehiscens</i>	<i>dehiscens</i>	<i>dehiscens</i>	<i>kitabicus</i>	<i>dehiscens</i>	<i>dehiscens (kitabicus)</i>
Pragian	<i>Sp. sulcatus</i> (U. Subzone)				<i>sulcatus</i> n. ssp.	<i>pireneae</i> <i>kindlei</i>	<i>kindlei</i>	<i>kindlei</i>	<i>pireneae</i>	<i>pireneae</i>	<i>pireneae</i>
										<i>kindlei</i>	<i>kindlei</i>

Stage	Bardashev <i>et al.</i> (2002)			Slavík <i>et al.</i> (2007) modif. (zones)	Yolkin <i>et al.</i> (2011) (zones)	This paper		
	<i>Eoectenopolygnathus</i> - <i>Ctenopolygnathus</i> trend	<i>Eocostapolygnathus</i> - <i>Costapolygnathus</i> trend	<i>Eolinguipolygnathus</i> - <i>Linguipolygnathus</i> trend			<i>sobolevii</i> - <i>ivanovskiyi</i> lineage	<i>settedabanicus</i> - <i>nothoperbonus</i> lineage	<i>kitabicus</i> - <i>bardashevi</i> lineage
Emsian	<i>mawsonae</i> , late	<i>philipi</i> , late	<i>nothoperbonus</i>		<i>nothoperbonus</i>		<i>nothoperbonus</i>	
	<i>mawsonae</i> , early	<i>philipi</i> , early	<i>foveolatus</i>		<i>excavatus</i>	<i>ivanowskyii</i>	<i>michaelmurphyi</i> <i>dehiscens</i> <i>perbonus</i>	<i>bardashevi</i> <i>gronbergi</i>
	<i>savagei</i>	<i>excavatus</i>	<i>dehiscens</i>	<i>excavatus</i> - <i>gracilis</i>		<i>sobolevi</i>	<i>settedabanicus</i>	<i>excavatus</i>
	<i>pireneae</i>	<i>kitabicus</i>	<i>pannonocinus</i> <i>yolkini</i>	<i>celtibericus</i>	<i>kitabicus</i>	?	?	<i>kitabicus</i>
	<i>zeravshnicus</i>	<i>trilinearis</i>		<i>brunsvicensis</i>	<i>pireneae</i> - <i>trilinearis</i>			
Pragian	<i>sulcatus</i>	<i>secus</i>		<i>steinachensis</i> beta morph	<i>kindlei</i> <i>juli</i>			

Figure 4. History of conodont zonal schemes for the late Pragian and early Emsian. Modified after Bardashev *et al.* (2002) with recent additions.

*bilatericrescens gracilis* Bultynck. This species is recorded in the uppermost part of the Praha Formation. It appears close below the “graptolite event” (for description of this level see Hladil *et al.* 1996, Hladil & Kalvoda 1997), within the range of *Polygnathus excavatus* and *Turkestanella (Nowakia) acuaria* and just below the acme of *Guerichina* ex gr. *strangulata* in the latest original Pragian (see Slavík 2004b). This taxon has been also reported in the very early Zlichovian in the Iberian Chain (Carls & Valenzuela-Ríos 2002). Based on dacryoconarid correlation (*cf.* Walliser & Kim 2001), the corresponding position of the “graptolite event” in Zinzilban might thus be within the interval from 114 and 134 m above the present basal Emsian GSSP. With respect to petrophysical correlation of magnetic susceptibility measurements both in the Prague Synform and Zinzilban

section, the level of the event correspond to 107 m above the GSSP (Hladil *et al.* 2011). Accordingly, the GSSP of the Pragian/Emsian boundary urgently needs revision.

### Correlation of the Pragian of the marginal seas of Angarida

The ancient continent of Angarida existed from early Paleozoic to middle Mesozoic time. Its outline on a modern map coincides with the Central Siberian Plateau and on tectonic maps with the territory of the Siberian Platform. Klets (2005) believed that the continent Angarida only appeared during Silurian time, though it would be more logical to connect its occurrence as well with the Archean and

Proterozoic as conditions of lagoons and shallow shelf already existed in the marginal seas environments during the Cambrian, Ordovician and Silurian (Nikiforova & Andreeva 1961, Egorova & Savitskyi 1969). Most the marginal seas of the Angarida were closed in the late Mesozoic when it was incorporated into the supercontinent Laurasia. During Early Devonian time it was surrounded to the east by the Verkhoyansk-Chukotsk Marine Basin, to the north and northwest by the Taimyr and West Siberian seas, and to the southwest by the Altai-Sayan marine basins. The southern boundary of Angarida at this time is the Mongol-Okhotsk Marine Basin (Fig. 5).

The status of the boundaries and correlation of the Pragian Stage of the marginal seas of Angarida remained debatable until now. The lower boundary of the Pragian Stage in Angarida had an unequivocal interpretation. In recent publications (Baranov 2009a, 2009b, 2009c; Baranov & Blodgett 2011, 2012) we correlated the lower Pragian beds of North Eurasia, Alaska and the marginal seas of Angarida. The main problem is the absence of eognathodontid conodonts in most sections. The boundary between the Lochkovian and Pragian Stages has been defined on the basis of the *E. sulcatus* (= *E. irregularis* in the sense of Murphy 2005) in the Velká Chuchle section in the Prague Synform (Barrandian area, Czech Republic; Chlupáč & Oliver 1989). In the marginal seas of Angarida the taxon has been found only in the Izvestkovyi Karier – I section on the Kolyma River. The conodont zonation of the lower boundary of the Pragian Stage in the northern regions of Eurasia was established at the base of the *Eognathodus sulcatus sulcatus*-Gagievodus *marinae* Zone (Baranov 2012). In Northeast Asia it coincides with the lower boundary of the Korotkinsky Regional Horizon (Alkhovik & Baranov 2001). Earlier, Baranov (2009a) noted that in the Verkhoyansk-Chukotsk Marine Basin the Lochkovian-Pragian boundary was marked by two large events – a change in sedimentological cyclicity and the reorganization of biocoenoses in all investigated faunal groups (tabulate and rugose corals, brachiopods and conodonts).

These events can be traced into the other marginal seas of Angarida (Verkhoyansk-Chukotsk, Taimyr, West Siberian, Altai-Sayan and Mongol-Okhotsk). In sections of the central Taimyr and in the northwestern Siberian Platform the lower boundary of the Pragian Stage can be recognized at the base of the Uryum Bed and Kureika Horizon. In the southeast part of the West Siberian Plate (Kulkov & Peregoedov 1990) it can be located at the base of the Lesnaya Series, according to the occurrence of the tabulate coral *Yacutiopora innae* Dubatolov (= *Yacutiopora dogdensis* Dubatolov), which in the Verkhoyansk-Chukotsk sea is the index-species of the lower Pragian regional tabulate zone (see Fig. 6). In addition, these beds are defined by the Pragian dacryoconarid *Turkestanella* (*Nowakia*) *acuaria* (Richter) and other species.

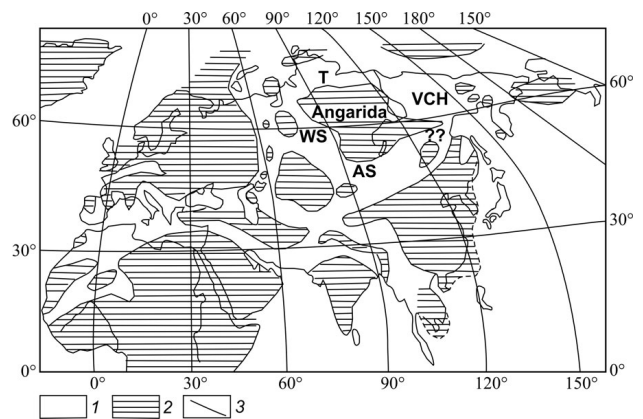
The question of where to define the lower boundary of the Pragian Stage in the Altai-Sayan Mountains remains very difficult. The placement of this boundary has repeatedly varied in the past few decades and is now placed at the base of the Malyi Bachat Horizon. In our opinion, this boundary may be lower, at the base of the Tom'Chymysh Horizon (Baranov & Blodgett 2012) or in its middle part.

Gagiev (1995) believed that the Pragian cycles in North-east Asia belonged to the Lower Devonian-Eifelian megacycle. However, Baranov (2009b, 2009c) showed that the initial stage of this megacycle begins in the early Přídolí (upper Silurian) and the maximum level of transgression can be observed in the Pragian and early Emsian time. In the present work we place the boundary between the Pragian and Emsian at the base of the Galkinsky Horizon based on the occurrence of *Polygnthaus kitabicus*. Thus, the Pragian Stage of the marginal seas of Angarida should be characterized mostly by deep-water facies. This sedimentological pattern is also present in the Taimyr sea. The Pragian there is represented mostly by deep-water facies (Uryum, Tolbat, Daksan and Yunkhond beds), overlying the Belyi Kamen' beds of the Lochkovian age which is a typically shallow-water facies with gypsum. These beds are succeeded by the Dolgan beds (early Emsian, *excavatus* Zone), which consists of lagoonal facies of the *Wijdeaspis arctica* Zone (Cherkesova 1994). The same sedimentological pattern is also observed in the northwestern Siberian Platform where the Pragian Stage consists of the Kureika and Razvedochny horizons (Matukhin *et al.* 1995). In the West Siberian Basin the Pragian beds have a greater thickness than the overlying deposits of Emsian-Eifelian age (Dubatolov *et al.* 1990, fig. 2).

The Sukhoi beds of the northeastern Salair is correlated with the Belyi Kamen' Bed of the Taimyr and should be an equivalent to the Lochkovian Stage of the Lower Devonian. The overlying deposits of the Tom'Chymysh Horizon may comprise the basal beds of the Pragian though the age of these divisions remains one of the main problems for the stratigraphy of the region. Rare occurrences of conodonts described by Timofeeva (1973) do not give a definite answer for the age of the Tom'Chymysh horizon. "*Spathognathodus optimus*" Moskalenko (pl. 15, figs 14, 15) occurs in the third package of beds of the Tom'Chymysh Horizon and thus should indicate a Lochkovian age. However, it is not correctly assigned to this species. Rather it is the typical species *Pandorinellina philipi* (Savage) found in many regions of the world and occurring in strata spanning the upper Lochkovian to lower Emsian interval. In addition, occurrences of *Pandorinellina optima* (Moskalenko) in Northeast Asia (Gagiev 1995, Baranov 2012) are reported from the basal horizon of the Pragian Stage, and, in southeastern Alaska *Pandorinellina* cf. *P. optima* (Moskalenko) occurs in the lower Pragian together with *Eognathodus sulcatus* Philip (Savage 1981). It is also noteworthy that among the com-

plex of brachiopods of the Tom'Chumysh Horizon *Sibiritoechia convexa* Alekseeva (= *S. oblonga* Alekseeva, = *S. lata* Alekseeva), *Howellella mercuriformis* Kulkov, *Aldanispirifer kulkovi* (Gratsianova) and *Protathyris sibirica* Zintchenko (Gratsianova 1967, Kulkov 1963, Alekseeva et al. 1970) are present, all of which are known as well in Northeast Asia in lower Pragian beds (Korotkinsky Horizon). The tabulate corals *Yacutiopora innae* (Dubatolov) and *Striatopora minuscula* Tchudinova (Mironova 1974) are found in the Tom'Chumysh Horizon. The first species is an index-species of the lower Pragian regional tabulate zone of Northeast Asia, and second species occurs there as well. Thus, on the basis of the presence of the above-mentioned tabulates and brachiopods the Korotkinsky Horizon of Northeast Asia is correlated with the Tom'Chumysh Horizon of the Altai-Sayan Mountains and can be dated as early Pragian age. Occurrences in the Sukhoi Suite of *Pandorinellina exigua philipi* (Klapper) and *Pelekysgnathus* cf. *serratus* Jentzsch (Bakharev et al. 2013) indicate most probably a late Lochkovian age, as the first species in the other regions is of the upper Lochkovian - late Emsian, while the latter is left in open nomenclature and consequently cannot unequivocally determine the age as early Lochkovian. *P. exigua philipi* occurs in southeastern Alaska and northern California together with *Eognathodus "sulcatus"* (Savage 1977a, b; Savage et al. 1977). At Royal Creek, Yukon Territory (Canada) *P. exigua philipi* and *P. serratus* have been found also together with "*Spathognathodus sulcatus*" (Klapper 1969). The age determination of the top of the Tomskiy Zavod and Peetz Suite (Bakharev et al. 2013) as *eurekaensis* Zone is not clear, because the index species of the zone has been recognized only locally in Nevada and is no longer used worldwide (e.g., Murphy & Valenzuela-Ríos 1999, Corradini & Corrigan 2012, Slavík et al. 2012, Drygant & Szaniawski 2012, Mavrinskaya & Slavík 2013). The conodonts reported recently by Bakharev et al. (2013) are not decisive for the early Lochkovian age. On the other hand, the Tom'Chumysh Horizon is correlated with early Pragian brachiopods (Baranov & Blodgett 2012, this paper). The typical benthic and pelagic Lochkovian fauna may be expected below the Tom'Chumysh Horizon. In the Verkhoyansk-Chukotsk, Mongol-Okhotsk marine basins and Gornyi Altai equivalent beds correspond to the upper Lochkovian *Favosites socialis* Zone (Mironova 1974, Sharkova 1981, Alkhovik & Ivanowskyi 1988, Alkhovik & Baranov 2001).

Conodonts from the Lower Devonian of the Mongol-Okhotsk Marine Basin have not been studied yet. Accordingly, the correlation is made using only brachiopods and tabulates. The lower boundary of the Pragian Stage in the Mongolian Altai is marked by basal conglomerates of the Tikhiltinsky Bed. In the middle part of this unit the brachiopods *Trigonirhynchia ventricosa* Alekseeva, *Spinatrypina* (*Spinatrypina*) *margaritoides* Rzhonsnitskaya,



**Figure 5.** Index map showing the location of marginal seas of Angarida: AS – Altai-Sayan, MO – Mongol-Okhotsk, T – Taimyr, VCH – Verkhoyansk-Chukotsk, WS – West Siberian; 1 – land, 2 – sea, 3 – boundary between land and sea.

*Spirigerina supramarginalis* (Khalfin), *Carinatina minuta comatoida* Alekseeva & Kulkov (Alekseeva et al. 1981) occur, all described from the Krekov and Malyi Bachat horizons of the Altai-Sayan Mountains. In addition, the first and last species cited above are also found in the upper part of the Pragian Stage of Northeast Asia. It is necessary to note that Sharkova (1981) established the tabulate-based *Favosites socialis* Zone in the upper Lochkovian of Mongolia, equivalent to the same zone in Northeast Asia (Alkhovik & Baranov 2001). It indicates that close biogeographical connections already existed between the Verkhoyansk-Chukotsk and Mongol-Okhotsk marine basins during the Early Devonian.

The recognition of the upper boundary of the Pragian Stage is problematic in marginal seas of Angarida and in other regions. It is caused by endemism and biogeographical differentiation of conodonts. In Northeast Asia it coincides with the base of Krivoi Ruchi Horizon and their age analogues (Alkhovik & Baranov 2001, Gagiev 1995, Baranov 2012). The boundary has been based on the occurrences of *Polygnathus "dehiscens"*. In the lower Emsian of Northeast Asia *Polygnathus dehiscens* late form occurs stratigraphically very high, and *Polygnathus kitabicus* appears in the Galkiskiyi Horizon and goes into the Nikolaevskiyi Horizon in the base of which is found *Polygnathus excavatus*. Therefore, the upper boundary of the Pragian Stage is herein correlated with the appearance of *Polygnathus kitabicus* at the base of Galkiskiyi Horizon in association with a complex of tabulates, rugose corals and brachiopods (Alkhovik & Ivanowskyi 1988, Alkhovik & Baranov 2001). The upper boundary of the Pragian in the Taimyr Marine Basin coincides with the base of the Taribigai beds (Cherkesova 1994). Early Emsian brachiopods are also found in the northwest part of the Siberian Platform in the upper part of the Razvedochny Horizon (Krylova 1962, Matukhin et al. 1995). In the southeast

System	Series	Stage	Obsolete “standard conodont scale”	Comparison of stratigraphic schemes									
				Verkhoyansk- Chukotsk sea (Alkhovik & Baranov 2001; in this paper)	Taimyr sea				West Siberian sea		Altai-Sayan sea		Mongol- Okhotsk sea (Aleksееva <i>et al.</i> 1981; Sharkova 1981)
					Cherkesova (1994)	in this paper	Matukhin <i>et al.</i> (1995)	in this paper	Dubatolov <i>et al.</i> (1990)	in this paper	Reshenia... (1982); Regional... (2012)	in this paper	
Horizon	Layers	Layers											
DEVONIAN	LOWER	Emsian	<i>excavatus</i>	Nikolaevskiy	Dolgan	Dolgan	Razvedochniy	Manturovskiy (lower part)	Lesnaya	Chuziksk	Salairkinskiy	Belovo	<i>Anculipora angulita</i> , <i>Spinatrypina spinosaeformis</i>
			<i>kitabicus</i>	Galkinskiy		Taribigai						Taribigai	
		Pragian	<i>pireneae</i>	Lednikovskiy	Yunkhond	Yunkhond		Razvedochny		Lesnaya	Malyi Bachat	Malyi Bachat	Favosites <i>admirabilis</i> , <i>Stegerhynchus nympha</i>
			<i>kindlei</i>	Darskiy	Daksan	Daksan						Krekov	
			<i>sulcatus</i>	Korotkinskiy		Daksan						Tolbat	Peetz
												Uryum	Upper part of Tom'Chumysh (Tomskiy Zavod)

**Figure 6.** Schematic diagram showing correlation of the Lower Devonian beds of the marginal seas of Angarida. The obsolete “standard conodont scale” is used herein only with the purpose of traditional tentative correlation of local units with “global” conodont zones. However, no global zonation for the Pragian and early Emsian does exist.

part of the West Siberian Plate occurrences of *Taimyrrhynch taimyricus* are dated as Pragian in age, and those of *Trigonirhynchia ventricosa* as Emsian (Kulkov & Peregodov 1990). We believe that *Taimyrrhynch taimyricus* and *Trigonirhynchia ventricosa* are also of Emsian age as in the Verkhoyansk-Chukotsk Basin. In the Mongol-Okhotsk basins the stratigraphic range of *Trigonirhynchia ventricosa* terminates at the lower boundary of the Emsian.

Problems with the placement of the upper boundary of the Pragian also occur in the Altai-Sayan Mountains, where it traditionally has been correlated with the base of the Salairka Horizon, though the first appearance of *Polygnathus “dehiscens”* is established there only in the upper third of this horizon (Yolkin *et al.* 1987). Therefore, the age of the Lower Salairka and Middle Salairka beds should be reconsidered. In addition a direct contact between the Malyi Bachat and Salairka horizons has not been observed (Rzhonsnitskaya 1968). It is necessary to mention that Rzhonsnitskaya (1968) established a brachiopod zone with the index species “*Paraspirifer*” *gurjevskensis* Rzhonsnitskaya [= *Fimbispirifer* (?) *pseudoconcinnus* Nikiforova, 1960] in the Lower Emsian of the Kuznetsk Basin. In Northeast Asia as well as in Novaya Zemlya and Taimyr this species occurs in the early Emsian (*kitabicus* Zone) with the rhynchonellid *Taimyrrhynch taimyricus* (Nikiforova 1960) and it passes upward into overlapping beds of Emsian age. Baranov & Blodgett (2012) and Bakharev *et al.* (2013) put the boundary between the Pragian and Emsian on the base of Upper Salairka Subhorizon. It seems

logical to consider a Pragian age for the Lower and Middle Salairka Subhorizon.

The Early Devonian conodont fauna of the Mongol-Okhotsk Marine Basin has not been studied. The lower and upper boundaries of the Pragian Stage have been recognized there only provisionally (Alekseeva *et al.* 1981). Two local biostratigraphic zones have been established in the Pragian and the Lower Emsian: 1) *Favosites admirabilis*, *Stegerhynchus nympha* and 2) *Oculipora angulata*, *Spinatrypa spinosaeformis*. The clastic beds in the upper part of Pragian of the Mongol-Okhotsk Basin are assigned to the *Maoristrophia grandis* local zone, which is correlated with the Tom'Chumysh Horizon of the Altai-Sayan Mountains. According to the faunistic data the Lower and Middle Salairka Horizon corresponds to the Pragian.

## Conclusions

The phylogenetic models of eopolygonathids can be characterized mostly as a trend from a more open to an inverted large basal cavity, and then towards a small and constricted basal cavity, and at the same time, by a trend from discrete isolated nodes on the oral surface towards the development of fused nodes forming numerous transverse ridges as proposed by Yolkin *et al.* (1994). However, this concept may not necessarily work everywhere. The polygonathid faunas described from Northeast Asia enable a global correlation, but show a large variability that can be partly considered to



be the result of an increased degree of endemism. Our research suggests that the inversion of the basal cavity does not play an essential role in the evolution of early polygnathids of Northeast Asia, and that polygnathids with a partly inverted basal cavity may occur simultaneously in parallel phylogenetic lineages (e.g., *Polygnathus gronbergi* in the *kitabicus* → *bardashevi* and *Polygnathus perbonus* in the *settedabanicus* → *nothoperbonus* lineages). In addition, observations over changes in the structure of the basal cavity during growth in some polygnathid species show that juvenile specimens are characterized by a narrower basal cavity than senile specimens. The current conodont zonal scheme for the lower Emsian (*kitabicus-excavatus-nothoperbonus* zones) cannot be used globally. Although, these zones are distinguished in Northeast Asia, their index-taxa are probably not part of a single phylogenetic sequence. Secondly, in the Izvestkovyi Karier section (above 90 m in thickness) there was an intense radiation and speciation in the *kitabicus* → *bardashevi* and *settedabanicus* → *nothoperbonus* lineages between the *excavatus/sobolevi* and *nothoperbonus* zones. As a result, several new taxa are described above the disappearance of *excavatus* that are of stratigraphical significance. The rich conodont material from Northeast Asia enabled a new proposal of morphophylogenetic concept for the early polygnathids. The upper boundary of the Pragian Stage in Northeast Asia is situated just below the base of the *kitabicus* Zone (= base of Galkinskyi Horizon) and coincides with the upper boundary of the Pragian Stage in the Barrandian, which is currently within the lower part of the Praha Formation (= “original Pragian”). The prospective inclusion of the *kitabicus* Zone to the Pragian Stage would have solved many existing problems in Devonian stratigraphy including the global correlation of the Arctic regions of Northeast Asia. The regional conodont zonation of the Lower Emsian of Northeast Asia has been upgraded based on the new conodont data.

## Systematic palaeontology

All conodont material is housed in the Geological Museum of Diamond and Precious Metal Geology Institute, Siberian Department Russian Academy of Sciences Yakutsk, Sakha Republic (Yakutia), Russian Federation, under collection number 213.

Family Polygnathidae Bassler, 1925

### Genus *Polygnathus* Hinde, 1879

#### *Polygnathus alkhovikovae* sp. nov.

Figure 7A–F

*Holotype*. – GM IDPMG 3/213 2014 7 (illustrated).

*Paratypes*. – 2 specimens: GM IDPMG 1/213, GM IDPMG 4/2013 (illustrated).

*Type horizon and locality*. – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolykma River, 15 km southeast of the mouth of the Shamnikha River.

*Material*. – 3 Pa elements.

*Etymology*. – In honor of Dr. T.S. Al'khovik, who studied Devonian tabulate corals of Northeast Asia.

*Diagnosis*. – Representative Pa elements of *Polygnathus alkhovikovae* sp. nov. have an asymmetric, weakly curved platform with parallel margins, deeply developed adcarinal grooves and a slightly narrow anterior part. The outer margin of the platform is ornamented by coarse transverse ridges and in the anterior part is occupied by transverse ridges and nodes. The basal cavity is completely open with asymmetrical flanges.

*Discussion*. – *Polygnathus alkhovikovae* sp. nov. differs from its ancestor *Po. arthuri* in the presence of a narrower and weakly curved platform with a narrow anterior part; from *Po. kitabicus* it differs in having a rounded posterior end of the platform, deeply developed adcarinal grooves and smooth outlines of the basal cavity. Juvenile *Po. alkhovikovae* differs from *Po. savagei* (= *Polygnathus pirenae*; Mawson et al. 1992) by having parallel margins of the platform and a wider cavity on the posterior end; from *Po. mawsonae* (= *Polygnathus* sp. nov. A of Talent & Mawson 1999) it differs in having a basal cavity that is completely open and possesses asymmetrical flanges. Juvenile specimens of *Po. alkhovikovae* upon development of the strong transverse ridges on the platform margins differ from adult specimens in having a sharp posterior margin and narrower basal cavity in the posterior part.

*Occurrence*. – Izvestkovokarierskaya Suite, sample K – 8(6), *michaelmurphyi* Subzone.

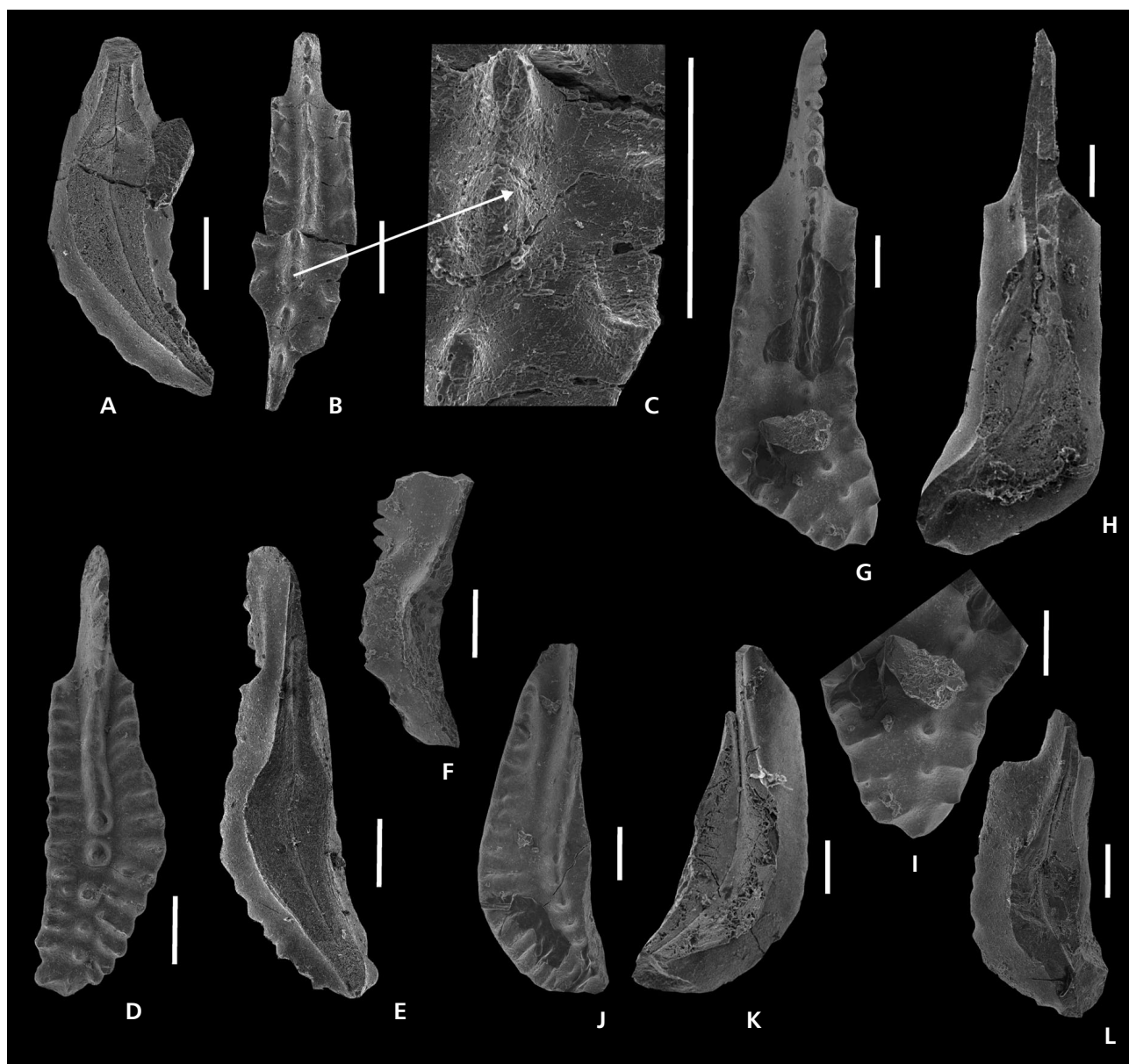
#### *Polygnathus arthuri* sp. nov.

Figure 7G–L

*Holotype*. – GM IDPMG 5/213 2014 7 (illustrated).

*Paratypes*. – 2 specimens: GM IDPMG 6/2013, GM IDPMG 7/213 (illustrated).

*Type horizon and locality*. – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right side of the



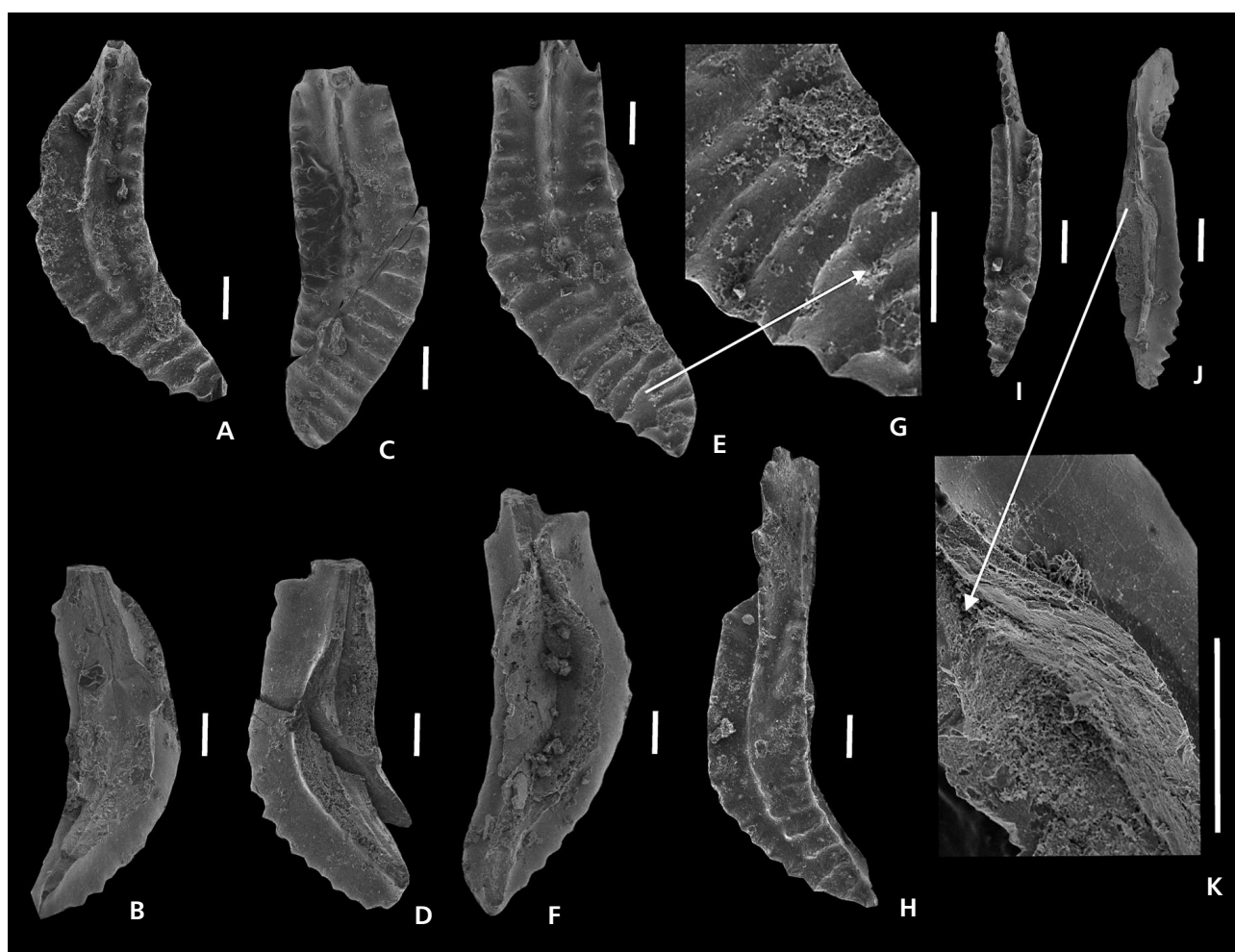
**Figure 7.** A–F – *Polygnathus alkhovikovae* sp. nov., Pa elements. • A – lower view of paratype GM IDPMG 1/213, sample K – 8/6. • B, C – upper view and its fragment of paratype GM IDPMG 1/213, sample K – 8/6. • D, E – upper and lower views of holotype GM IDPMG 3/213, sample K – 8/6. • F – lateral view of paratype GM IDPMG 4/213, sample K – 8/6. • G–L – *Polygnathus arthuri* sp. nov., Pa elements. • G, H – upper and lower views and I – fragment of sculpture on tongue of holotype GM IDPMG 5/213, sample K – 5/9. • J, K – upper and lower views of paratype GM IDPMG 6/213, sample K – 5/9. • L – lower view of paratype GM IDPMG 7/213, sample K – 8/6; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.

Kolyma River, 15 km southeast of the mouth of the Shamaniha River.

**Material.** – 4 Pa elements.

**Etymology.** – In honor of Dr. Arthur J. Boucot, who has contributed much to our knowledge of Silurian and Devonian faunas.

**Diagnosis.** – Representative Pa elements *Polygnathus arthuri* sp. nov. have a long asymmetrical curved platform with sub-parallel margins, in the anterior part it is ornamented by nodes or short ridges, and in the posterior part it has long transverse ridges differentiated by weakly to strongly expressed nodes. The basal cavity is completely open with asymmetrical flanges. The basal pit is centrally located and has an oval shape.



**Figure 8.** *Polygnathus michaelmurphyi* sp. nov., Pa elements. • A, B – lower and upper views of paratype GM IDPMG 8/213, sample K – 8/2. • C, D – lower and upper views of paratype GM IDPMG 9/213, sample K – 8/2. • E, F – upper and lower views, G – fragment of sculpture on tongue of holotype GM IDPMG 10/213, sample K – 8/2. • H – upper view of paratype GM IDPMG 11/213, sample K – 8/2. • I, J – upper and lower views, K – detail of the lower surface of paratype GM IDPMG 12/213, sample K – 8/2; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler makes 100 microns.

**Remarks.** – *Polygnathus arthuri* sp. nov. differs from all morphotypes of *Eulinguipolygnathus dehiscens* (see Bardashev *et al.* 2002) in the presence of a single line of weakly differentiated nodes located on the posterior part of platform along its outer margin.

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 5(9), *gronbergi* Subzone.

***Polygnathus bardashevi* sp. nov.**

Figure 9A–C, F–H

**Holotype.** – GM IDPMG 15/201 2014 9 (illustrated).

**Paratypes.** – 1 specimen: GM IDPMG 13/213 (illustrated).

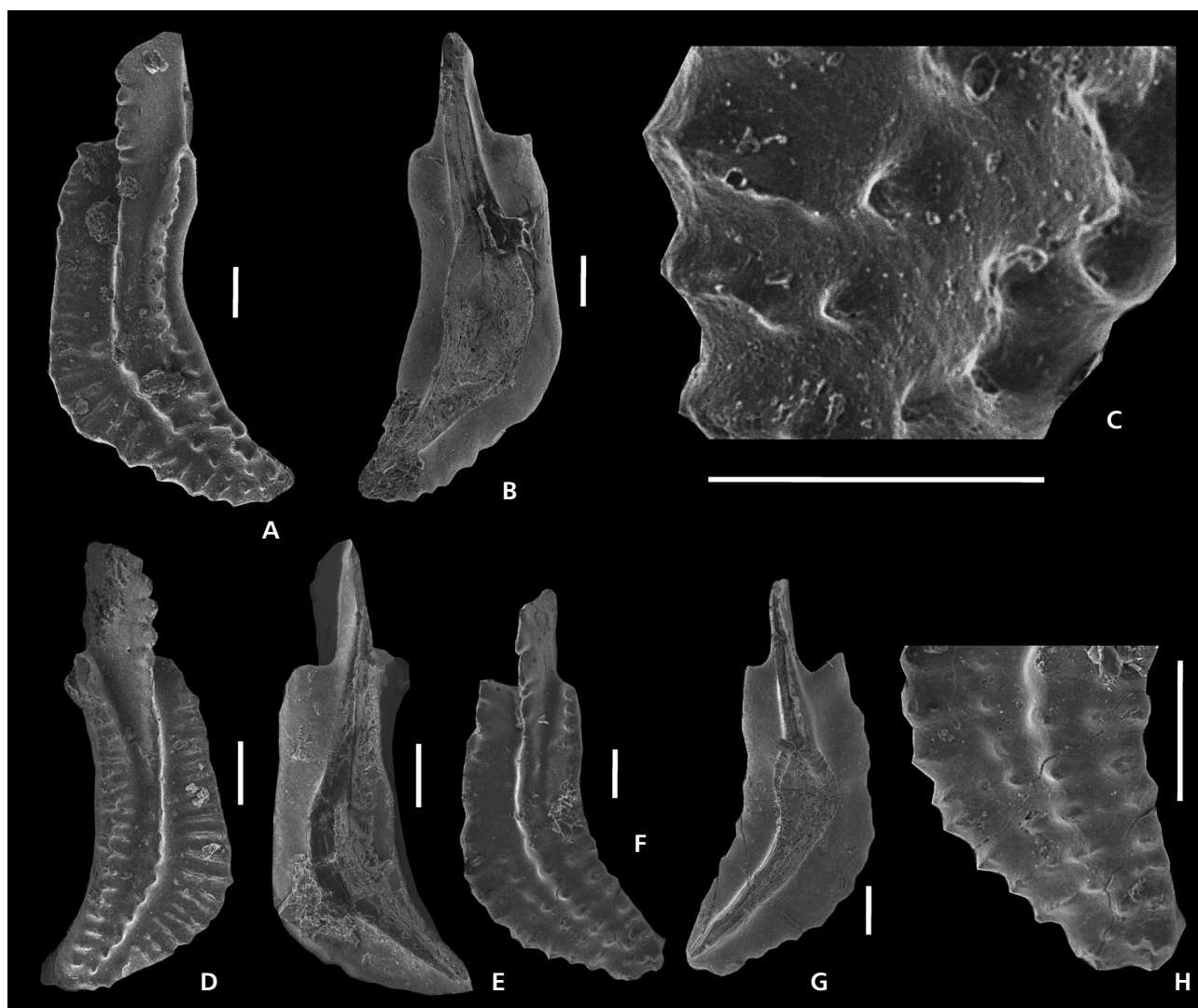
**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolyma River, 15 km southeast of the mouth of the Shamarnikha River.

**Material.** – 4 Pa elements.

**Etymology.** – In honor of I.A. Bardashev, who has studied the Devonian conodonts of central Asia.

**Diagnosis.** – Pa elements of *Polygnathus bardashevi* sp. nov. have a long asymmetrical curved platform with deep adcarinal grooves and subparallel margins. The margins and posterior half of the platform are ornamented by nodes and short transverse ridges. The anterior blade bears five denticles. The basal cavity is completely open with





**Figure 9.** A–C, F–H – *Polygnathus bardashevi* sp. nov., Pa element. • A – upper view, B – lower view, C – detail of the upper surface of platform of paratype GM IDPMG 13/213, sample K – 7/4, F – upper, G – lower views and H – detail of the upper surface of platform of holotype GM IDPMG 15/213, sample K – 6/2. • D, E – *Polygnathus excavatus* Carls & Gandl 1969, Pa element. • D – upper view, E – lower view of GM IDPMG 14/213, sample K – 5/9; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.

asymmetrical flanges, and has a narrow and flat posterior extension of the cavity with a small oval basal pit displaced forward of the center.

**Discussion.** – *Polygnathus bardashevi* sp. nov. differs from *Po. hindei* Mashkova & Apekina, 1980 in the presence of nodes only in the posterior part of platform and a narrow and flat posterior extension of the cavity, as well as in the absence of radial rostra; from *Po. lezhoevi* sp. nov. it differs in having a long asymmetrically curved platform with deep adcarinal grooves and in the presence of nodes on the margins of the posterior half of platform and in its much shorter free blade; from *Po. richi* (Bardashev *et al.* 2002) (= *Polygnathus* cf. *P. gronbergi* Lane & Ormiston,

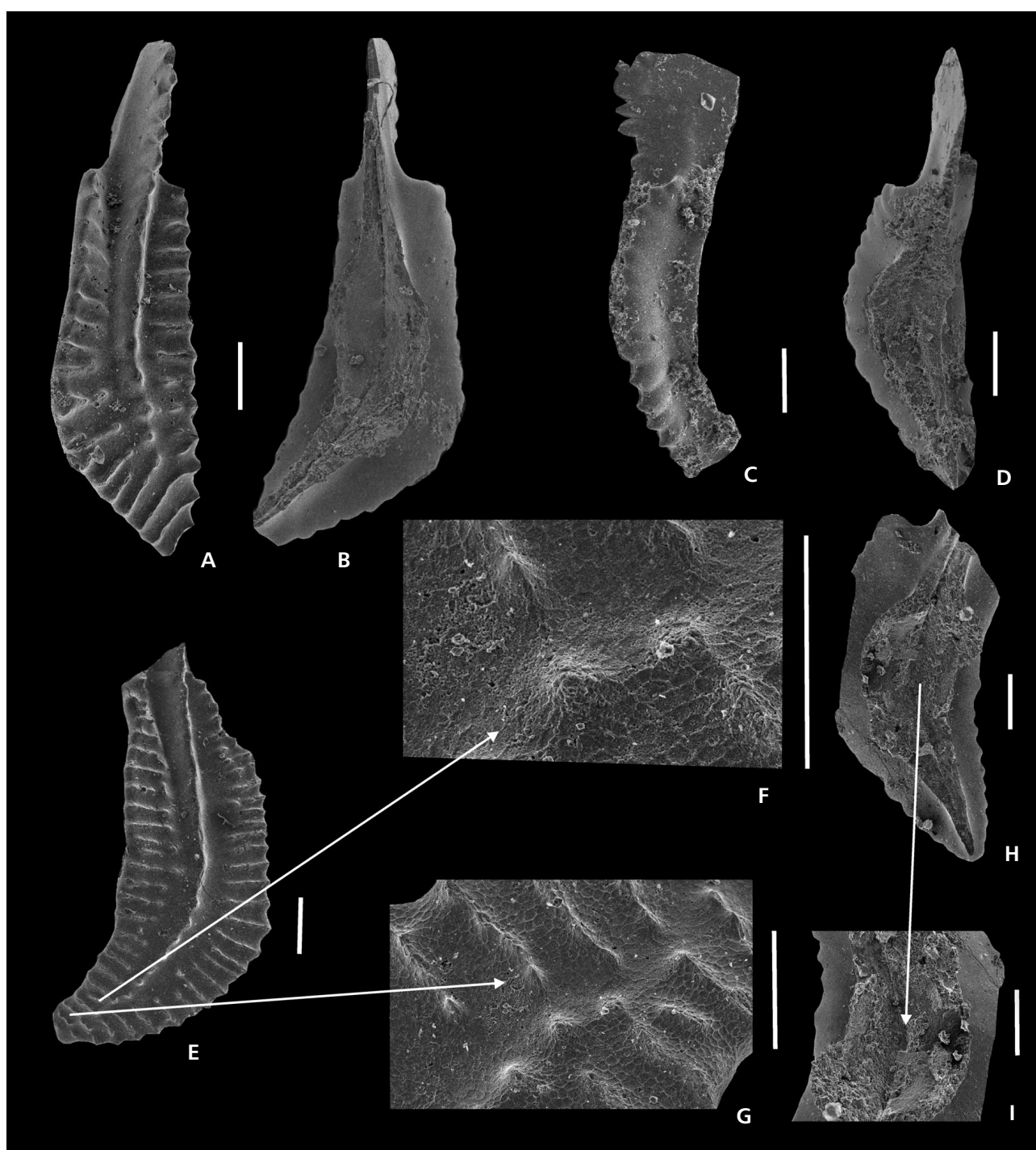
1979) it differs in the presence a long asymmetrical curved platform with subparallel margins and a basal pit displaced forward of the center. Adult specimens of *Po. bardashevi* have a wider basal cavity than juvenile specimens.

**Occurrence.** – Izvestkovokarierskaya Suite, samples K – 6(2), K – 7(4), *bardashevi* Subzone.

***Polygnathus dehiscens* Philip & Jackson, 1967, late morphotype**  
Figure 10A–D

**Material.** – 2 Pa elements.





**Figure 10.** A–D – *Polygnathus dehiscens* Philip & Jackson, 1967, late morphotype, Pa elements. • A, B – upper and lower views of GM IDPMG 16/213, sample K – 7/1. • C – lateral view of GM IDPMG 17/213, sample K – 7/1. • D – lower view of GM IDPMG 18/213, sample K – 7/1. • E–I – *Polygnathus karsteni* sp. nov. E – upper view, F and G – fragment of sculpture of tongue of holotype GM IDPMG 18/213, sample K – 7/1; H – lower view and I – basal pit of paratype GM IDPMG 19/213, sample K – 7/1; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.

**Discussion.** – Representative Pa elements *Polygnathus dehiscens* Philip & Jackson, 1967 late morphotype have an asymmetrical curved platform with strong transverse ridges and nodes on its posterior part and have a single line of weakly

differentiated nodes located on the exterior part of the outer margin. The basal cavity is completely open with symmetrical flanges and grooves passing from the pits to the anterior and posterior edges of the basal cavity. *Polygnathus dehiscens*

Philip & Jackson, 1967, late morphotype differs from the other morphotypes of *Po. dehiscens* (Bardashev *et al.* 2002) in the presence of a single row of weakly differentiated nodes located in the posterior part of the platform along its outer margin and strong transverse ridges and nodes on its posterior part.

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 7(1), *bardashevi* Subzone.

### ***Polygnathus excavatus* Carls & Gandl, 1969**

Figures 9D, E, 11E–Q, 15A–O

- 1969 *Polygnathus webbi excavatus* n. ssp.; Carls & Gandl, pp. 193–195, pl. 18, fig. 11 (holotype).
- 1978 *Polygnathus* sp. – Mashkova & Apekina in Kim *et al.*, pl. 73, fig. 1.
- 1978 *Polygnathus dehiscens* → *Polygnathus gronbergi*. – Mashkova & Apekina in Kim *et al.*, pl. 74, fig. 10.
- 1978 *Polygnathus gronbergi* Klapper & Johnson. – Mashkova & Apekina in Kim *et al.*, pl. 75, fig. 5 (only); non pl. 75, figs 4, 6.
- 1984 *Polygnathus* cf. *gronbergi* Klapper & Johnson. – Sobolev, pl. 3, fig. 7.
- 1985 *Polygnathus dehiscens* Philip & Jackson. – Ziegler & Wang, pl. 1, fig. 1.
- 1986 *Polygnathus dehiscens* Philip & Jackson. – Barca *et al.*, pl. 29, figs. 3–5.
- 1988 *Polygnathus gronbergi* Klapper & Johnson. – Yolkin & Izokh, pl. 1, figs 3, 4.
- 1990 *Polygnathus dehiscens* Philip & Jackson. – Rzhonsnitskaya *et al.*, pl. 9, figs 6, 7.
- 1994 *Polygnathus dehiscens* “*excavatus*” Carls & Gandl. – García-Lopez & Alonso-Menendez, p. 97, pl. 3, figs 7, 8.
- 2002 *Eocostapolygnathus excavatus* (Carls & Gandl), alpha morphotype. – Bardashev *et al.*, p. 402, text-figs 9, 14.11.
- 2002 *Eocostapolygnathus excavatus* (Carls & Gandl), beta morphotype. – Bardashev *et al.*, p. 402, text-figs 9, 14.12.
- 2004a *Polygnathus excavatus* Carls & Gandl. – Slavík, p. 465, figs 11.26–11.29.
- 2007 *Polygnathus excavatus* Carls & Gandl. – Erina in Kim *et al.*, p. 289, pl. 126, fig. 6.

2011 *Polygnathus excavatus* Carls & Gandl. – Izokh *et al.*, p. 51, pl. 1, figs 11–14.

2011 *Polygnathus foveolatus* Philip & Jackson. – Izokh *et al.*, p. 54, pl. 3, figs 21–24.

**Material.** – 17 Pa elements.

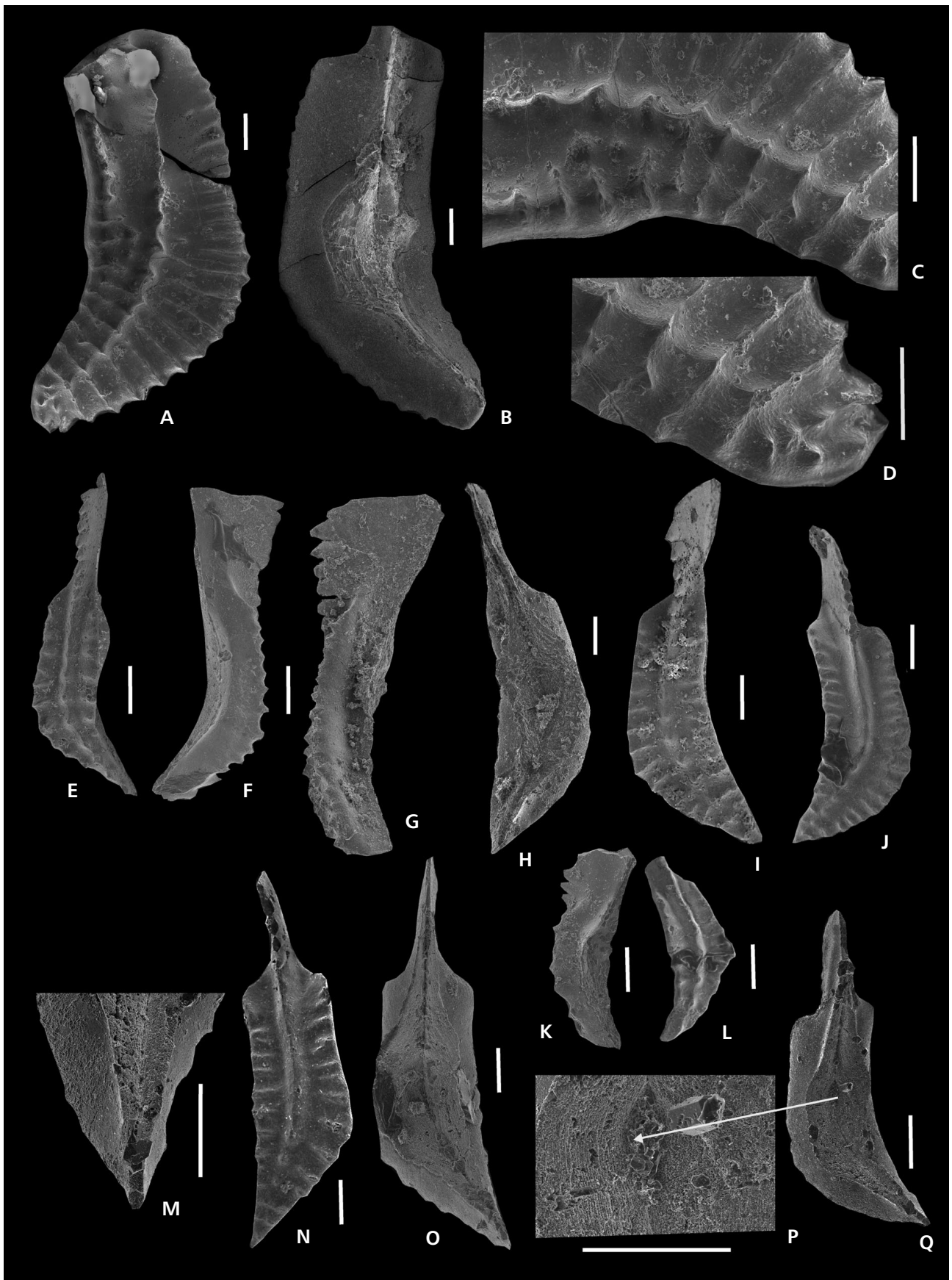
**Discussion.** – Representative Pa elements of *Polygnathus excavatus* have a relatively wide platform with weak narrow or subparallel anterior margins and deep adcarinal grooves reaching to the mid-length of the platform. Margins of the platform are ornamented by ridges and the tongue is occupied by interrupted or semi-crossed (*sensu* Yolkin *et al.* 1994) transverse ridges bearing weakly expressed nodes. The basal cavity is completely open with weakly asymmetrical flanges. The oval-shaped basal pit is slightly displaced anteriorly from the center. The representatives of species *Polygnathus excavatus* described from the Kolyma River Basin do not differ from *Po. excavatus* as specified in the synonymy. *Po. excavatus* differs from *Po. pannonicus* alpha morphotype (= *Po. pannonicus* Mashkova & Apekina 1980, p. 138, fig. 2), *Po. dehiscens* Philip & Jackson and *Po. foveolatus* Philip by the presence of interrupted transverse ridges bearing weakly expressed nodes. The shallow basal cavity and the mode of denticulation (the semi-crossed ridges at the posterior part of the platform) are very close to *Polygnathus* ssp. 114 from Mariposas Formation in Celtiberia (see Carls *et al.* 2008). This taxon has potential to be a prospective basal Emsian marker after redefinition of the respective GSSP. Juvenile specimens of *Po. excavatus* differ from adult specimens in having a narrower platform, a sharp posterior end, and a more narrow basal cavity in its posterior part. In some adult specimens can be observed differentiation of transverse ridges with the formation of nodes on the posterior part of the platform.

**Occurrence.** – Nikolaevskaya Suite, sample C – 108, and Izvestkovokarierskaya Suite, samples K – 2(2), K – 5(3), K – 5(7), K – 5(9), *excavatus/sobolevi* Zone.

### ***Polygnathus gronbergi* Klapper & Johnson, 1975**

- 1975 *Polygnathus gronbergi* sp. nov.; Klapper & Johnson, p. 73, pl. 1, figs 17, 18, 21–28 [non figs 19, 20 = *Eulinguipolygnathus perbonus*].

**Figure 11.** A–D – *Polygnathus gronbergi* Klapper & Johnson, 1975, gamma morphotype, Pa element. • A – upper view; B – lower view of GM IDPMG 20/213; C, D – fragmental details of platform, sample K – 5/9. • E–Q – *Polygnathus excavatus* Carls & Gandl 1969, Pa elements: E – upper view; F – lateral view of GM IDPMG 21/213, sample K – 5/3. • G – lateral view of GM IDPMG 22/213, sample K – 5/3. • H, I – lower and upper views of GM IDPMG 23/213, sample K – 5/3. • K, L – upper and lower views of GM IDPMG 24/213, sample K – 5/3. Pa elements: • J – upper view, M, P, Q – lower (fragmentary) views of GM IDPMG 25/213, sample K – 5/7. • N – upper view, O – lower view of GM IDPMG 26/213, sample K – 5/7; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovy Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.





- 1977 *Polygnathus gronbergi* Klapper & Johnson. – Ziegler (ed.), p. 449, pl. 8, figs 1, 5.  
 1979 *Polygnathus gronbergi* Klapper & Johnson. – Lardeux & Morzades, pl. 1, fig. 2.  
 1980 *Polygnathus gronbergi* Klapper & Johnson. – Bultynck & Hollard, pl. 2, fig. 6, 7.  
 1983 *Polygnathus gronbergi* Klapper & Johnson. – Wang & Ziegler, pl. 5, fig. 10 (only).  
 1985 *Polygnathus gronbergi* Klapper & Johnson. – Schönlaub, pl. 3, fig. 16.  
 1986 *Polygnathus gronbergi* Klapper & Johnson. – Barca *et al.*, p. 314, text-fig. 2.  
 1986 *Polygnathus gronbergi* Klapper & Johnson. – Bardashev, pl. 5, fig. 2 (only).  
 1989 *Polygnathus gronbergi* Klapper & Johnson. – Bultynck, p. 182, pl. 1, fig. 12 (only); pl. 3, figs 2–4; pl. 4, fig. 12.  
 1991 *Polygnathus gronbergi* Klapper & Johnson. – Bardashev, p. 239, pl. 111, fig. 11 (only).  
 1991 *Polygnathus gronbergi* Klapper & Johnson. – Barskov *et al.*, p. 50, pl. 11, figs 3–6.  
 1992 *Polygnathus gronbergi* Klapper & Johnson. – Bardashev & Ziegler, figs 28–32, 38, 39.  
 2002 *Polygnathus gronbergi* Klapper & Johnson, alpha morphotype. – Bardashev *et al.*, p. 403, text-figs 9, 14.14.  
 2002 *Polygnathus gronbergi* Klapper & Johnson, beta morphotype. – Bardashev *et al.*, p. 403, text-figs 9, 14.15.

**Diagnosis (emended).** – Representative Pa elements of *Polygnathus gronbergi* have a variable form of the platform ranging from suboval, slightly narrowing anteriorly to elongate with subparallel margins. The outer margin of the platform is ornamented by long transverse ridges and the inner margin and tongue is ornamented by short transverse ridges differentiated by nodes. The outer margin is more than twice as wide than the inner margin.

**Remarks.** – Bardashev *et al.* (2002) distinguished two morphotypes (alpha and beta) of *Polygnathus gronbergi* based on the degree of variability of the basal cavity, which differ only in the degree of inversion of the basal cavity.

***Polygnathus gronbergi* Klapper & Johnson, 1975, gamma morphotype**

Figure 11A–D

**Material.** – 2 Pa elements.

**Discussion.** – Representative Pa elements of *Polygnathus gronbergi* Klapper & Johnson, 1975 gamma morphotype have an asymmetrical, strongly curved platform with parallel margins in its anterior part and a long tongue occupied by semi-crossed transverse ridges, with the exception of its posterior end on which are located sharp nodes. Posterior part of the basal cavity is completely closed, and a sharp keel is present behind the large basal pit. A narrow groove extends from the basal pit to the anterior margin. *Polygnathus gronbergi* Klapper & Johnson, 1975, gamma morphotype differs from *Po. gronbergi* Klapper & Johnson, 1975, alpha and beta morphotypes (Bardashev *et al.* 2002) in having a platform with subparallel long margins and a single row of sharp nodes located on its posterior part.

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 5(9), *gronbergi* Subzone.

***Polygnathus ivanowskyi* sp. nov.**

Figure 12A–E

- 1979 *Polygnathus pireneae* Boersma, 1973. – Lane & Ormiston, p. 62, pl. 3, figs 15–17.  
 1984 *Polygnathus* sp. No. 1. – Sobolev, pl. 4, fig. 11.  
 2012 *Polygnathus pireneae* Boersma, 1973. – Baranov, pl. 3, figs 10–14.

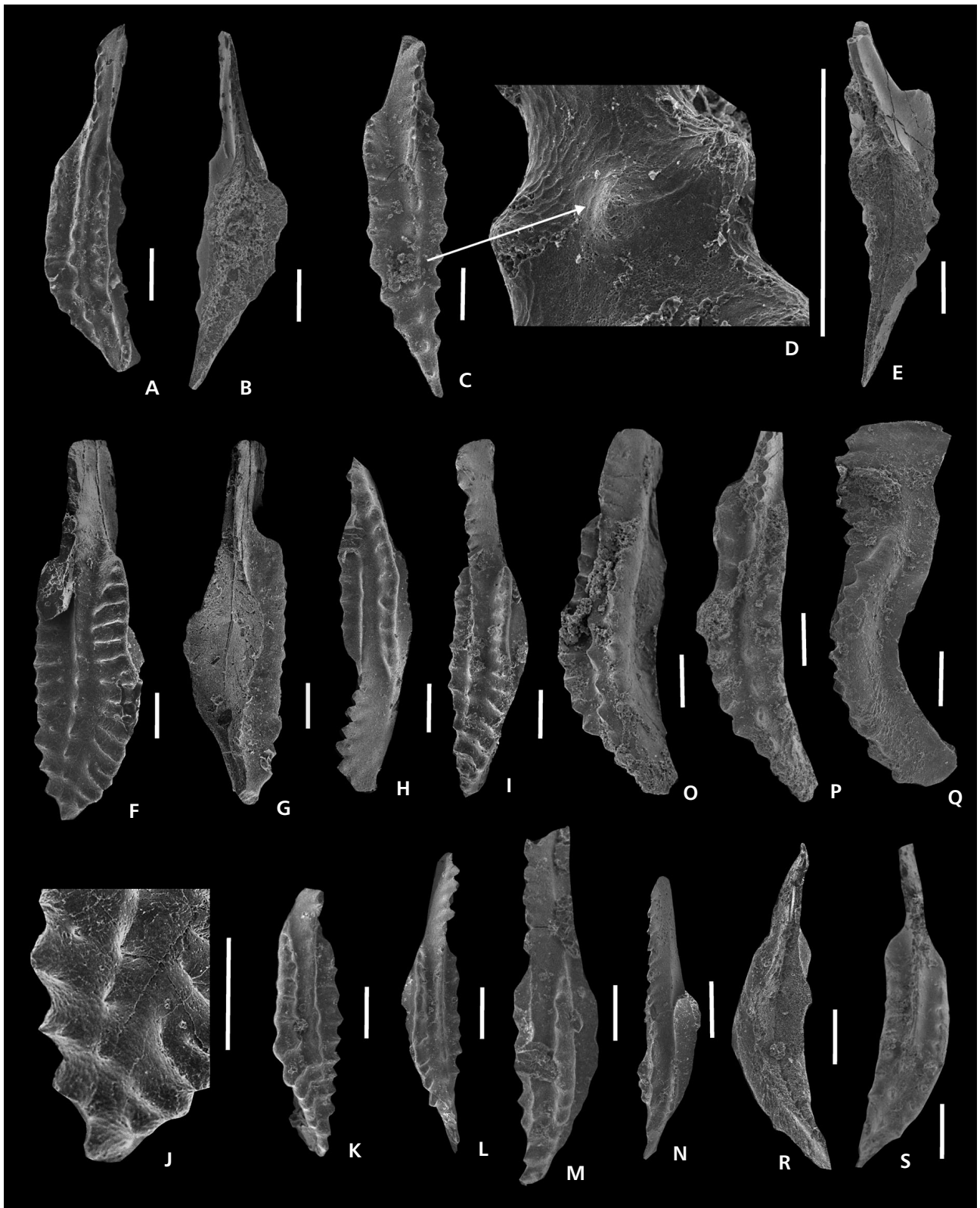
**Holotype.** – GM IDPMG 28/213 2014 12 (illustrated).

**Paratype.** – 1 specimen: GM IDPMG 27/213 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolyma River, 15 km southeast of the mouth of the Shamnikha River.

**Figure 12.** A–E – *Polygnathus ivanowskyi* sp. nov., Pa elements. • A, B – upper and lower views of paratype GM IDPMG 27/213, sample K – 7/1. • C, D – upper and E – lower views of holotype GM IDPMG 28/213, sample K – 7/1. • F–N – *Polygnathus lezhoevi* sp. nov., Pa elements: F, J – upper and G – lower views of holotype GM IDPMG 29/213, sample K – 5/7. • H – lateral view of paratype GM IDPMG 30/213, sample K – 5/7. I – upper view of paratype GM IDPMG 31/213, sample K – 8/2. • K – upper view of paratype GM IDPMG 32/213, sample K – 6/1. • L – upper view of paratype GM IDPMG 33/213, sample K – 6/1. • M – lateral view of paratype GM IDPMG 34/213, sample K – 6/1. • N – lateral view of paratype GM IDPMG 35/213, sample K – 6/1. • O–S – *Polygnathus sobolevi* (Bardashev, Weddige & Ziegler, 2002), Pa elements. • O–Q – upper, lower and lateral views of GM IDPMG 36/213, sample K – 2/2. • R, S – upper and lower views of GM IDPMG 37/213, sample K – 2/2; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovy Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.





**Material.** – 7 Pa elements.

**Etymology.** – In honor of A.B. Ivanowskyi, who studied the Devonian rugose corals of Siberia.

**Diagnosis.** – Representative Pa elements *Polygnathus ivanowskyi* sp. nov. have a subtrigonal narrow platform with narrow adcarinal grooves. The margins of the platform are ornamented by short ridges and nodes. The posterior end of the platform is sharp. The subtrigonal basal cavity is completely open with a large oval basal pit in its anterior part.

**Discussion.** – *Polygnathus ivanowskyi* sp. nov. differs from *Po. lezhoevi* sp. nov., and *Po. pireneae* (Boersma, 1973) by the presence of a subtrigonal narrow platform without adcarinal grooves; from *Po. mawsonae* (Bardashev *et al.* 2002, pp. 399, 400) it differs in the presence of a completely open basal cavity with a large oval basal pit in its anterior part; from *Po. boersmai* it differs in having a subtrigonal narrow platform with narrow adcarinal grooves, and a subtrigonal cavity with a large oval basal pit in its anterior part.

**Occurrence.** – Izvestkovokarierskaya Suite, samples K – 4(6), K – 7(1), K – 8(6), *ivanowskyi* Zone.

***Polygnathus karsteni* sp. nov.**

Figure 10E–I

**Holotype.** – GM IDPMG 18/213 2014 10 (illustrated).

**Paratype.** – 1 specimen: GM IDPMG 19/213 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolykha River, 15 km southeast of the mouth of the Shamanikha River.

**Material.** – 3 Pa elements.

**Etymology.** – In honor of K. Weddige, Devonian conodont worker.

**Diagnosis.** – The platform elements of *Polygnathus karsteni* sp. nov. have a long asymmetrical, strongly curved platform. The rest of the platform is ornamented by transverse ridges that bear weakly or strongly expressed nodes. The carina is long but does not reach the posterior end of platform. The tongue is covered by short transverse ridges that bear three or four nodes. The posterior blade bears five nodes. The basal cavity is completely open with asymmetrical flanges. The basal pit is elongate, oval-shaped and located centrally.

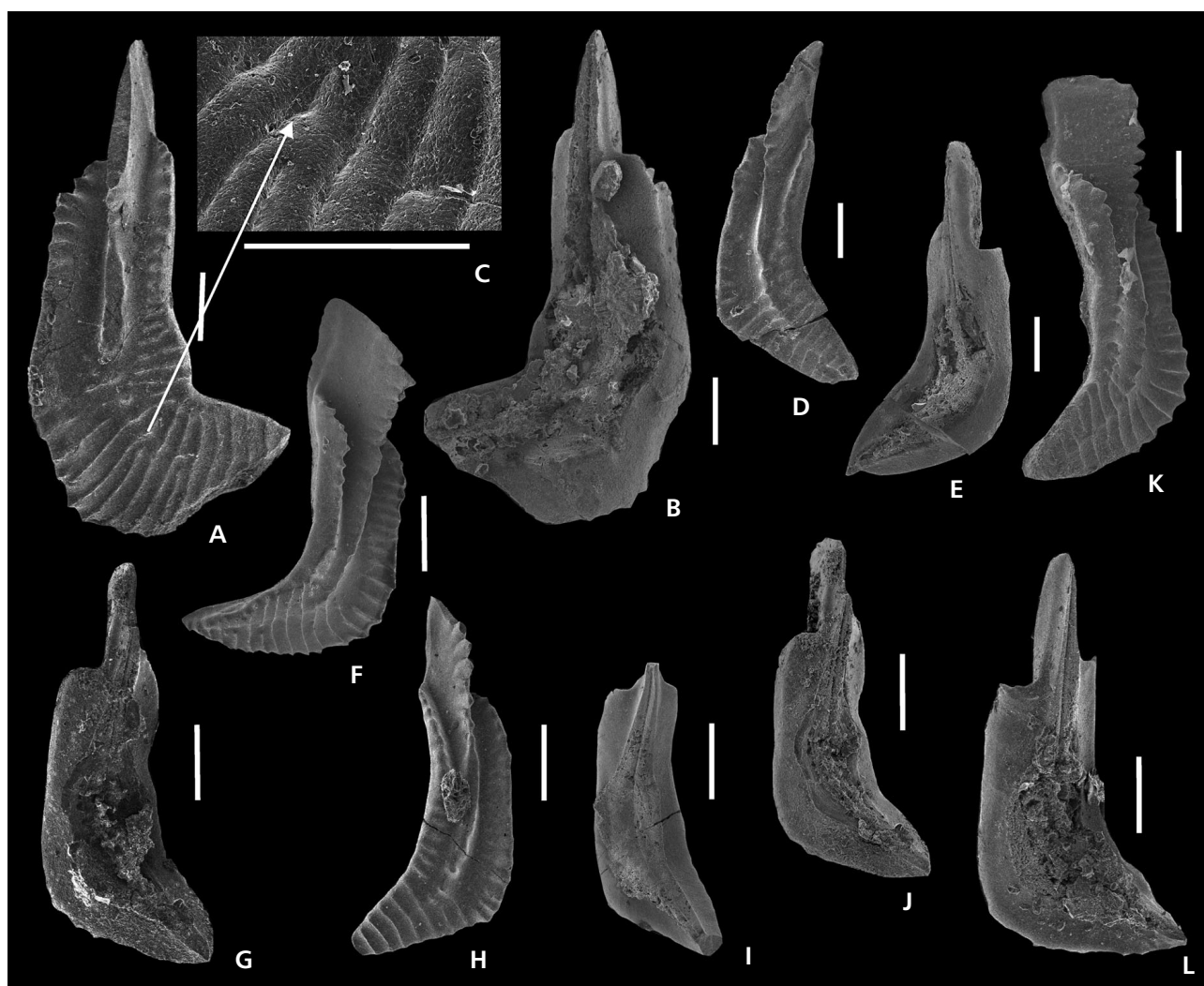
**Remarks.** – *Polygnathus karsteni* sp. nov. differs from *Po. excavatus* Carls & Gandl in having more differentiated nodes on the transverse ridges and a longer tongue.

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 7(1), *bardashevi* Subzone.

***Polygnathus kitabicus* Yolkin *et al.*, 1994**

Figure 14A–G

- 1972 *Polygnathus lenzi* Klapper. – McGregor & Uyeno, pl. V, figs 10–12.
- 1979 *Polygnathus pireneae* Boersma. – Lane & Ormiston, pl. 5, figs 2, 3 (only).
- 1979 *Polygnathus dehiscens* Philip & Jackson. – Lane & Ormiston, pl. 5, fig. 37 (only).
- 1980 *Polygnathus dehiscens* Philip & Jackson. – Uyeno & Klapper, p. 87, pl. 8.1, figs 1, 2 (only).
- 1982 *Polygnathus pireneae* Boersma. – Murphy & Matti, p. 265, p. 39, pl. 1, figs 33–38.
- 1984 *Polygnathus pireneae* Boersma. – Mastandrea, p. 265, pl. 1, figs 5, 6.
- 1985 *Polygnathus dehiscens* Philip & Jackson. – Savage *et al.*, pl. 1, figs 27, 28.
- 1989 *Polygnathus dehiscens* Philip & Jackson. Early form. – Yolkin *et al.*, p. 238, pl. 2, figs 3, 4.
- 1989 *Polygnathus pireneae* Boersma. – Yolkin *et al.*, p. 238, pl. 1, fig. 5, 6 (only).
- 1990 *Polygnathus dehiscens* Philip & Jackson. – Olivieri & Serpagli, p. 72, pl. 3, fig. 1 (only).
- 1990 *Polygnathus pireneae* Boersma. – Olivieri & Serpagli, p. 72, pl. 3, figs 4–6 (only).
- 1990 *Polygnathus dehiscens* Philip & Jackson. – Uyeno, p. 82, pl. 9, figs 1, 2 (only); pl. 17, figs 1, 2; pl. 19, figs 1–4.
- 1992 *Polygnathus pireneae* Boersma. – Weyant, p. 281, fig. 3.
- 1992 *Polygnathus dehiscens* Philip & Jackson. – Bardashev & Ziegler, p. 82, pl. 4, figs 22–24 (only).
- 1994 *Polygnathus kitabicus* Yolkin *et al.*, p. 149, pl. 1, fig. 1–4.
- 2000 *Polygnathus pireneae* Boersma. – Mawson *in* Talent *et al.*, p. 174, fig. 6, J.
- 2002 *Eocostapolygnathus kitabicus* (Yolkin *et al.*) – Bardashev *et al.*, p. 404, text-fig. 9, 14.12.
- 2005 *Polygnathus kitabicus* Yolkin *et al.* – Martínez-Pérez & Valenzuela-Ríos, p. 298, pl. 1, fig. 5 (only).
- 2005 *Polygnathus excavatus* (Carls & Gandl). – Martínez-Pérez & Valenzuela-Ríos, p. 298, pl. 1, fig. 9.
- 2011 *Polygnathus pireneae* Boersma *kitabiformis* morph. – Izokh *et al.*, p. 51, pl. 1, fig. 6.
- 2011 *Polygnathus kitabicus* Yolkin *et al.* – Izokh *et al.*, p. 51, pl. 1, figs 7–10.



**Figure 13.** *Polygnathus nothoperbonus* Mawson, 1987, Pa elements. • A, B – upper and lower views, C – fragment of sculpture of tongue of GM IDPMG 38/213, sample K – 9/4. • D, E – upper and lower views of GM IDPMG 39/213, sample K – 9/4. • F, G – upper and lower views of GM IDPMG 40/213, sample K – 9/4. • H, I – upper and lower views of GM IDPMG 41/213, sample K – 9/4. • J, K – upper and lower views of GM IDPMG 42/213, sample K – 9/4; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.

**Material.** – 4 Pa elements.

**Discussion.** – Representative Pa elements of *Polygnathus kitabicus* have a long symmetrical platform with subparallel margins and an inward deflection of the posterior part. The upper platform surface is ornamented by short transverse ridges in the adult specimens. A deep adcarinal groove is present only on the outer side of platform. The basal cavity is completely open with symmetrical flanges. The oral and aboral morphology of the platform elements of *Po. kitabicus* described here does not differ from the species listed in the synonymy.

**Occurrence.** – Nelichenskaya Suite, sample SI – 94, *kitabicus* Zone; Izvestkovokarierskaya Suite, sample K – 2(2), *excavatus/sobolevi* Zone.

***Polygnathus lezhoevi* sp. nov.**

Figure 12F–N

**Holotype.** – GM IDPMG 29/213 2014 12 (illustrated).

**Paratypes.** – 6 specimens: GM IDPGM 30/213 – GM IDPMG 35/213 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolyma River, 15 km southeast of the mouth of the Shamarnikha River.

**Material.** – 8 Pa elements.



**Etymology.** – In honor of V.K. Lezhoev, who has studied the Paleozoic stratigraphy of Northeast Asia.

**Diagnosis.** – Representative Pa elements *Polygnathus lezhoevi* have an oval, straight, symmetrically flat or weakly concave platform with shallow adcarinal grooves and a long free blade with seven denticles. The margins of platform and its tongue are ornamented by transverse ridges and nodes. Juvenile specimens bear weakly expressed nodes on the platform margins, adult specimens bear short ridges and nodes. The posterior blade extends to the posterior platform margin. The basal cavity is completely open with symmetrical flanges.

**Discussion.** – *Polygnathus lezhoevi* sp. nov. differs from *Po. yolkini* (Bardashev *et al.* 2002) in the presence of transverse ridges on the margins and on the posterior part of platform; from *Po. kitabicus* it differs in having an oval, symmetrically flat or weakly concave platform and a long free blade; from *Po. sokolovi* Yolkin *et al.* it differs in the presence of a straight platform and a transverse ridges on the platform margins and on the tongue; from *Po. yolkini erinae* it differs in the presence a straight platform, shallow adcarinal grooves and in the absence of diagonal rostra; from *Po. lenzi* (Bardashev *et al.*, 2002, p. 399) and narrow specimens of *Po. excavatus* Carls & Gandl it differs in the presence an oval, straight, symmetrically flat or weakly concave platform; from *Po. sobolevi* (Bardashev *et al.* 2002) and *Po. pireneae* Boersma it differs in the presence of an oval, symmetrically flat or weakly concave platform with shallow adcarinal grooves and a long free blade with seven denticles and in being ornamented by transverse ridges bearing weakly expressed nodes on the platform margins.

**Occurrence.** – Izvestkovokarierskaya Suite, samples K – 5(7), K – 6(1), K – 8(2), *excavatus/sobolevi* Zone – *gronbergi* and *bardashevi* subzones.

***Polygnathus michaelmurphyi* sp. nov.**

Figure 8A–K

**Holotype.** – GM IDPMG 10/213 2014 8 (illustrated).

**Paratypes.** – 4 specimens: GM IDPGM 8/213, GM IDPMG 9/213, GM IDPMG 11/213, GM IDPMG 12/213 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Izvestkovokarierskaya Suite, right bank of the Kolyma River, 15 km southeast of the mouth to the Shamnikha River.

**Material.** – 7 Pa elements.

**Etymology.** – In honor of M.A. Murphy, Silurian and Devonian conodont worker.

**Diagnosis.** – Representative Pa elements *Polygnathus michaelmurphyi* sp. nov. have a long narrow symmetrically curved platform with very short adcarinal grooves and carina, and a very long tongue crossed by ridges. The outer margin is ornamented by transverse ridges and the inner margin is occupied by nodes. The large basal cavity is completely open with asymmetrical flanges.

**Discussion.** – *Polygnathus michaelmurphyi* sp. nov. differs from *Po. pannonicus* (Mashkova & Apekina, 1980) in the absence of radial rostra; from *Po. dehiscens* late morphotype it differs in the presence of very short adcarinal grooves and carina, and a very long tongue crossed by ridges; from all other representatives of the genus *Polygnathus* it differs in the presence of very short adcarinal grooves and carina, and by a very long tongue crossed by ridges.

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 8(2), *michaelmurphyi* Subzone.

***Polygnathus nothoperbonus* Mawson, 1987**

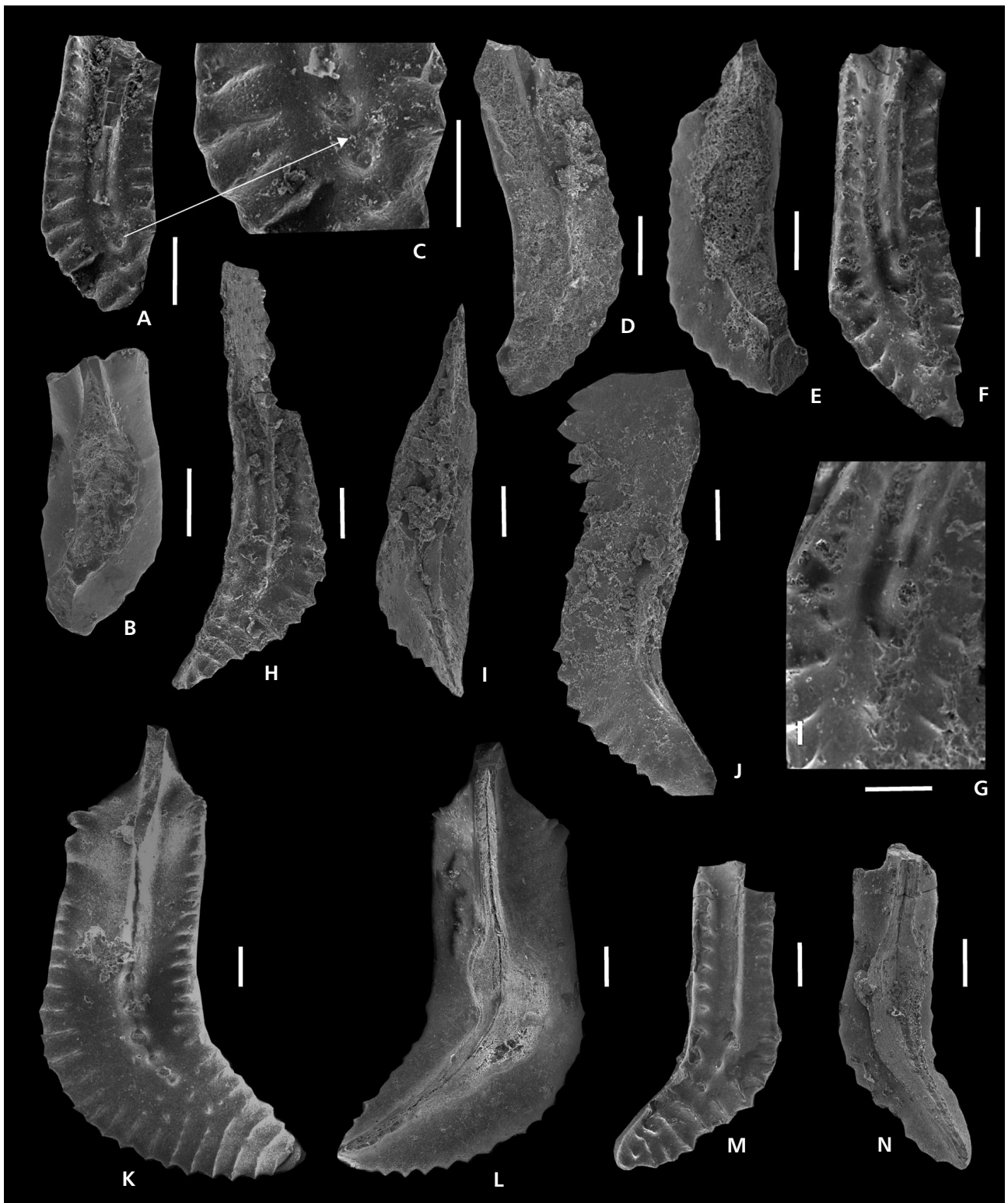
Figure 13A–L

1975 *Polygnathus* aff. *perbonus* Philip. – Klapper & Johnson, p. 74, pl. 2, figs 1–10.

1978 *Polygnathus perbonus* (Philip). – Mashkova & Apekina in Kim *et al.*, pl. 74, fig. 5; pl. 76, figs 1, 2.

**Figure 14.** A–G – *Polygnathus kitabicus* Yolkin *et al.*, 1973, Pa elements. • A, B – upper and lower views, C – fragment of sculpture of tongue of GM IDPMG 43/213, sample S1 – 94. • D, E – upper and lower views of GM IDPMG 44/213, sample S1 – 94; Selennyakh Range, Northeast Asia, Russia, Gon section, Lower Nikolaevskaya Subsuite, lower Emsian. • F, G – upper view and fragment of sculpture of tongue of GM IDPMG 45/213, sample K 2/2; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, Lower Emsian, Upper Lower Devonian. • H–J – *Polygnathus settedabanicus* sp. nov., Pa element: upper, lower and lateral views of holotype GM IDPMG 46/213, sample S – 17/12; Sette-Daban Ridge, Northeast Asia, Russia, Tikhyi section, Middle Settedabanskaya Subsuite. • K–L – *Polygnathus perbonus* Philip 1966, Pa element: upper and lower views of GM IDPMG 47/213, sample K – 5/9. • M, N – *Polygnathus yakutensis* sp. nov., Pa element: upper and lower views of holotype GM IDPMG 48/213, sample K – 5/9; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.





- 1979 *Polygnathus* aff. *perbonus* Philip. – Lane & Ormiston, p. 62, pl. 8, figs 26, 27.
- 1980 *Polygnathus* aff. *perbonus* Philip. – Uyeno & Klapper, pl. 8.1, figs 5, 6; pl. 8.3, figs. 11, 12.
- 1981 *Polygnathus perbonus* Philip. – Wang, p. 403, fig. 1.
- 1983 *Polygnathus* aff. *perbonus* Philip. – Wang & Ziegler, pl. 2, fig. 17.
- 1983 *Polygnathus perbonus* Philip. – Wang & Ziegler, pl. 2, fig. 20.
- 1983 *Polygnathus perbonus* Philip. – Xiong, pl. 69, fig. 3 (only).
- 1985 *Polygnathus perbonus* Philip. – Ziegler & Wang, pl. 1, fig. 5 (only).
- 1987 *Polygnathus nothoperbonus* sp. n., Mawson, p. 276, pl. 32, figs 11–15; pl. 33, figs 1, 2; pl. 36, fig. 7.
- 1990 *Polygnathus nothoperbonus* Mawson. – Uyeno, p. 85, pl. 7, figs 4, 5; pl. 9, figs 5, 6, 13, 14.
- 1994 *Polygnathus nothoperbonus* Mawson. – Yolkin *et al.*, pl. 1, figs 16, 17.
- 1991 *Polygnathus nothoperbonus* Mawson. – Barskov *et al.*, p. 58, pl. 10, figs 3–5.
- 2002 *Eolinguiopolygnathus nothoperbonus* (Mawson). – Bardashev *et al.*, p. 411, text-figs 10, 15.18.
- 2003 *Polygnathus nothoperbonus* Mawson. – Mawson *et al.*, figs 7O–P.
- 2011 *Polygnathus nothoperbonus* Mawson. – Izokh *et al.*, p. 52, pl. 1, figs 15–17.
- 2011 *Polygnathus dehiscens* Philip & Jackson. – Izokh *et al.*, p. 55, pl. 3, figs 25–28.
- 2011 *Polygnathus nothoperbonus* Mawson. – Martínez-Pérez *et al.*, pp. 58–59, fig. 6, d1–d2, f1–f2.

**Material.** – 25 Pa elements.

**Discussion.** – Representative Pa elements *Polygnathus nothoperbonus* have an asymmetrical, strongly curved platform with deep adcarinal grooves and a very long tongue crossed by ridges. The margins are ornamented by transverse ridges. The basal cavity is less than half inverted and has asymmetrical flanges. *Polygnathus nothoperbonus* differs from its ancestor *Po. michaelmurphyi* sp. nov. in the presence of a basal cavity which is less than half inverted. Senile forms of *Po. nothoperbonus* do not differ from specimens described by Izokh *et al.* (2011) as *Po. dehiscens* Philip & Jackson from the *nothoperbonus* Zone of Kitab State Reserve (Zeravshan-Gissar Mountain Area, Uzbekistan).

**Occurrence.** – Geremgandzhinskaya Suite, samples T – 41(1), T – 43(3), T – 43(5), *nothoperbonus* Zone; Izvestkovokarierskaya Suite, sample K – 9(4), *nothoperbonus* Zone.

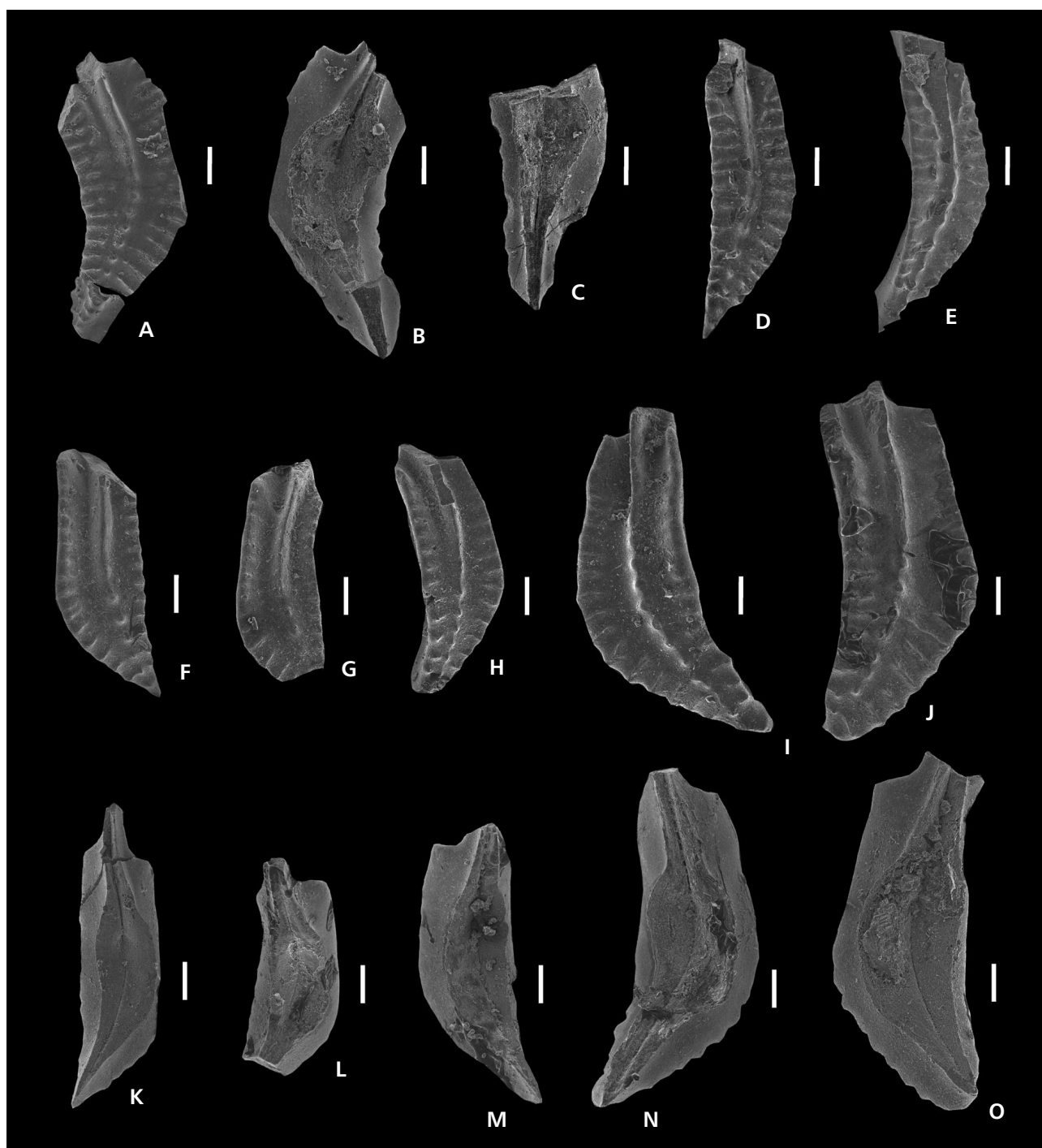
## ***Polygnathus perbonus* Philip, 1966**

Figure 14K–L

- 1966 *Roundya perbona* sp. nov.; Philip, pp. 448–449, pl. 2, figs 29–40, pl. 4, figs 7, 8.
- 1966 *Polygnathus linguiformis* Hinde; Philip, pl. 2, fig. 39.
- 1967 *Polygnathus linguiformis foveolata* n. subsp. – Philip & Jackson, p. 1265, text-figs 2d–g.
- 1972 *Polygnathus foveolatus* Philip & Jackson. – McGregor & Uyeno, pl. 5, figs 13, 14.
- 1976 *Polygnathus foveolatus* Philip & Jackson. – Bultynck, p. 62, pl. 11, figs 16–20.
- 1981 *Polygnathus perbonus* (Philip). – Mashkova & Apekina, p. 92, pl. 1, figs 7, 8.
- 1981 *Polygnathus gronbergi* Klapper & Johnson. – Mashkova & Apekina, p. 92, pl. 1, figs 11, 12.
- 1984 *Polygnathus perbonus* (Philip). – Apekina in Kim *et al.*, pl. 22, fig. 6.
- 1984 *Polygnathus gronbergi* Klapper & Johnson. – Apekina in Kim *et al.*, p. 81, pl. 22, fig. 9.
- 1987 *Polygnathus perbonus* (Philip). – Mawson, pp. 276–277, pl. 34, figs 8–13, pl. 36, fig. 2.
- 1991 *Polygnathus perbonus* (Philip). – Bardashev, p. 243, l. 109, figs 23–27.
- 1993 *Polygnathus perbonus* (Philip). – Brock & Talent, p. 233, fig. 9A–H.
- 2002 *Eolinguiopolygnathus foveolatus* alpha morph (Philip & Jackson). – Bardashev *et al.*, p. 409, text-figs 10, 15.10, 15.11.
- 2002 *Eolinguiopolygnathus foveolatus* beta morph (Philip & Jackson). – Bardashev *et al.*, p. 409, text-figs 10, 15.12.
- 2003 *Polygnathus perbonus* (Philip). – Mawson & Talent, pp. 276–277, pl. I, figs 5, 16–18, pl. II, figs 1–3, 6, 6.
- 2011 *Polygnathus foveolatus* Philip & Jackson. – Izokh *et al.*, p. 54, pl. III, figs 21–24.

**Material.** – 2 Pa elements.

**Discussion.** – Representative Pa elements *Polygnathus perbonus* Philip have a long symmetrical strongly curved platform with deep adcarinal grooves and parallel lateral margins. Lateral margins of platform are ornamented by transverse ridges. The tongue is occupied by semi-crossed and crossed transverse ridges. The basal cavity has weakly asymmetrical flanges and continues as a groove until the posterior and bears a small oval-shaped basal pit in the middle. Siberian representatives of *Polygnathus perbonus* Philip do not differ to any significant degree in the structure of the oral and aboral surfaces from platform elements of Australian representatives of this species. Some conodont workers (Klapper & Johnson 1975, Talent & Mawson 1999) believe that *Polygnathus foveolatus* is a junior synonym of *Polygnathus perbonus*. This thesis is substantiated



**Figure 15.** *Polygnathus excavatus* Carls & Gandl 1969, Pa elements. • A, B – upper and lower views of GM IDPMG 50/213, sample K – 2/2. • C – lower view of GM IDPMG 51/213, sample K – 2/2. • D, E – upper and upper-lateral views of GM IDPMG 52/213, sample K – 5/7; right bank of Kolyma River, Northeast Asia, Russia, Izvestkovyi Karier – II section, lower part of the Izvestkovokarierskaya Suite, lower Emsian, Upper Lower Devonian. • F, K – upper and lower views of GM IDPMG 53/213, sample SL – 108. • G, L – upper and lower views of GM IDPMG 54/213, sample SL – 108. • H, M – upper and lower views of GM IDPMG 55/213, sample SL – 108. • I, N – upper and lower views of GM IDPMG 56/213, sample SL – 108. • J, O – upper and lower views of GM IDPMG 57/213, sample SL – 108; Selennyakh Range, Northeast Asia, Russia, Gon section, Lower Nikolaevskaya Subsuite, lower Emsian, Upper Lower Devonian; the length of a ruler marks 100 microns.



by the fact that the Sc element of this species was described by Philip earlier (under the name *Royndia perbona*) than the P element of *Polygnathus linguiformis foveolatus* and according to the rules of priority one should use the first published name (Klapper & Philip 1971).

**Occurrence.** – Izvestkovokarierskaya Suite, sample K – 5(9), *gronbergi* Subzone.

***Polygnathus settedabanicus* sp. nov.**

Figure 14H–J

1971 *Polygnathus dehiscens* Philip & Jackson. – Fähræus, p. 677, pl. 77, fig. 2, 3 (only).

**Holotype.** – GM IDPMG 46/213 2014 14 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower Emsian, Settedabanskaya Subsuite, right bank of Tikhyi Creek, 1.5 from the mouth.

**Material.** – 2 Pa elements.

**Etymology.** – After Sette-Daban Ridge, Northeast Asia, Russia.

**Diagnosis.** – Representative Pa elements of *Polygnathus settedabanicus* sp. nov. have a sharply pointed posterior, asymmetrically curved platform with sub-parallel margins; the outer margin is occupied by transverse ridges of various lengths and the inner margin is ornamented by nodes or short ridges; tongue has crossed transverse ridges in the posterior part of platform in adult specimens. The free blade bears six to nine nodes. The basal cavity is completely open, narrow in the posterior part.

**Discussion.** – *Polygnathus settedabanicus* sp. nov. differs from *Po. lenzi* Klapper, *Po. pireneae* Boersma, *Po. kitabicus* (Yolkin *et al.*, and *Po. excavatus* Carls & Gandl by the presence of crossed transverse ridges in the posterior part of the platform and a long free blade with six to nine nodes; from *Po. sobolevi* (Bardashev *et al.*) it differs in having an oval, asymmetrically curved platform and transverse crossed ridges in the posterior part of the platform; from juvenile representatives of “*Polygnathus*” *dehiscens abyssus* (Mawson 1987, pl. 32, figs 1, 2) it differs in the presence the transverse ridges in the posterior part and on the outer margin of the platform, and in having regular transverse ridges in adult specimens.

**Occurrence.** – The Upper Settedabanskaya Subsuite, sample T – 17(12), *excavatus/sobolevi* Zone.

***Polygnathus sobolevi* (Bardashev, Weddige & Ziegler, 2002)**

Figure 12O–S

- 1977b *Polygnathus dehiscens* Philip & Jackson. – Savage, p. 59, pl. 1, figs 29–36.
- 1979 *Polygnathus pireneae* Boersma. – Lane & Ormiston, p. 62, pl. 3, figs 15–17; pl. 5, figs 27–34 (only).
- 1980 *Polygnathus dehiscens* Philip & Jackson. – Mashkova & Sobolev, pl. 1, figs 1, 2 (only).
- 1981 *Polygnathus dehiscens* → *Polygnathus gronbergi*. – Wang & Wang, pl. 2, figs 4, 5.
- 1985 *Polygnathus pireneae* Boersma. – Savage *et al.*, pl. 1, figs 21–26.
- 1990 *Polygnathus pireneae* Boersma. – Olivieri & Serpagli, p. 72, pl. 3, figs 2–6.
- 1992 *Polygnathus pireneae* Boersma. – Mawson, p. 42, figs 7E, F (only).
- 1994 *Polygnathus dehiscens* Philip & Jackson (→ *Polygnathus gronbergi* Klapper & Johnson). – Sobolev, p. 98, pl. 13, fig. 12 (only).
- 1998 *Polygnathus pireneae* Boersma. – Mawson, pl. 2, fig. 7 (only).
- 2002 *Eoectenopolygnathus sobolevi* Baradashev; Weddige & Ziegler, p. 401, text-figs 9, 13.9.

**Material.** – 6 Pa elements.

**Discussion.** – Representative Pa elements *Polygnathus sobolevi* have a very long symmetrical, narrow, slightly curved platform with a deeply developed adcarinal groove on the outer side of the platform. The margins of the platform are ornamented by nodes. Posterior blade extends to the platform margin. The basal cavity is completely open with symmetrical flanges.

*Polygnathus sobolevi* differs from *Po. pireneae* Boersma in the presence of a very long symmetrical, narrow, and slightly curved platform and by a less extended basal cavity that does not exceed the platform margin and a deeply developed adcarinal groove on the outer side of the platform.

**Occurrence.** – Izvestkovokarierskaya Suite, samples K – 2(2), K – 5(3), *excavatus/sobolevi* Zone.

***Polygnathus yakutensis* sp. nov.**

Figure 14M, N

?1986 *Polygnathus linguiformis bultyncki* Weddige. – Barca *et al.*, pl. 29, fig. 6.

**Holotype.** – GM IDPMG 48/213 2014 14 (illustrated).

**Type horizon and locality.** – Upper Lower Devonian, lower

Emsian, Izvestkovokarierskaya Suite, right bank of the Kolya River, 15 km southeast of the mouth of the Shamanikha River.

*Material.* – 2 Pa elements.

*Etymology.* – After Yakutia.

*Diagnosis.* – Representative Pa elements of *Polygnathus yakutensis* sp. nov. have a long symmetrical, narrow, strongly curved platform with parallel margins and a long tongue ornamented by transverse ridges of variable length and terminated by nodes. Platform margins bear transverse ridges. The basal cavity has symmetrical flanges inverted at the posterior tip. The large basal pit is elongate, oval-shaped and located centrally.

*Discussion.* – *Polygnathus yakutensis* sp. nov. differs from its ancestor *Po. michaelmurphyi* sp. nov. in the presence of a shorter tongue, parallel margins of the platform and a basal cavity weakly inverted in the posterior part; from *Polygnathus linguiformis bultyncki* (Weddige 1977, pl. 5, figs 90–92) it differs in the presence of a long narrow platform and long tongue ornamented by transverse ridges of variable length. *Polygnathus linguiformis bultyncki* described by Barca et al. (1986) does not differ from the platform of *Po. yakutensis* sp. nov.; from *Polygnathus linguiformis* (Philip, 1966, pl. 2, figs 32, 34, 35, 39) it differs in the presence a tongue ornamented by transverse ridges of variable length and terminated by nodes, and the large basal pit is elongate and oval-shaped.

*Occurrence.* – Izvestkovokarierskaya Suite, sample K – 8(2), *michaelmurphyi* Subzone.

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