

CONODONTS OF THE *POLYGNATHUS POLLOCKI* DRUCE GROUP (UPPER DEVONIAN, LOWER FRASNIAN) FROM THE EAST EUROPEAN PLATFORM

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Abstract. Conodonts of the *Polygnathus pollocki* Druce group are described from the Lower Frasnian shallow-water shelf deposits of the Main Devonian Field, East European Platform (Russia). One new species (*P. drucei* sp. nov.) is erected and two new species are described in open nomenclature (*Polygnathus* sp. nov. A and *Polygnathus* sp. nov. B). Two morphotypes of *P. pollocki* are recognized. Preliminary phylogenetic and ecological reconstructions for the group are considered.

Key words: Upper Devonian, Frasnian, conodonts, new species.

INTRODUCTION

The Early Frasnian polygnathids, known as taxa characterizing mainly the shallow-water facies, are represented by morphologically diverse forms. Many polygnathids of this age possess an elongate, lanceolate platform ornamented, as a rule, with weak transverse ridges. They are considered to belong to the *Polygnathus decorosus* stock (Ziegler, 1965; Huddle, 1970). Some of these species (with a strongly elongated platform) are regarded herein as the *P. pollocki* Druce group, which represents a lineage characterized by narrowing of the platform and development of longitudinal ornamentation. According to Druce (1976), this lineage probably evolved from the *P. decorosus* stock and displays symmetry class II *sensu* Lane (1968), in contrast to the *P. webbi* stock which is characterized by symmetry class III.

Conodonts of the *P. pollocki* lineage have been studied by the author from the Lower Frasnian shallow-water carbonate-siliciclastic sections of the Main Devonian Field (East European Platform, Russia). Most of the sections are located

| Stage | Standard conodont zone | Main Devonian Field | | |
|----------|------------------------|-------------------------|---------------------|--|
| | | Regional substage | Formation (Beds) | Local conodont zone (Zhuravlev et al., 1997) |
| Frasnian | U. hassi - jamieae | Rechitsian (lower part) | Snezha (lower part) | ? |
| | punctata - L. hassi | | | |
| | | Semilukian (upper part) | Buregi | <i>Polygnathus efimovae</i> |
| | | | Ilmen | <i>Polygnathus pollocki</i> |

Fig. 1. Stratigraphical chart.

in the Lake Ilmen region (Novgorod district) and provide abundant conodont associations commonly dominated by species of *Polygnathus* s. l. (for details see Zhuravlev et al., 1997). Conodont studies in this region were accompanied by facial, palaeoecological, and palaeotemperature investigations. The Ca/Mg ratios, measured by Dr L. Dorofeeva (VSEGEI, St Petersburg, Russia) in brachiopod shells (*Cyrtospirifer* and *Atrypa*), indicate the palaeotemperatures of about 19–20 °C.

In the present paper the correlation of the regional strata (such as the Semilukian Substage, Ilmen, Buregi, and Snezha formations) with the standard conodont zonation, suggested by Ovnatanova (1974), Aristov (1988), Ovnatanova & Kuz'min (1991), Ovnatanova & Kononova (1996), and Zhuravlev et al. (1997), is used with minor revision (Fig. 1). The sample numbers mentioned correspond to those in Zhuravlev et al. (1997).

SYSTEMATIC PALAEONTOLOGY

The following five species are regarded as belonging to the *Polygnathus pollocki* group: *P. pollocki* Druce (two morphotypes are recognized); *P. efimovae* Kononova, Alekseev, Barskov et Reimers, *P. drucei* sp. nov., *Polygnathus* sp. nov. A, and *Polygnathus* sp. nov. B (see Pls. I, II).

The species differ in proportions and ornamentation of the platform of the Pa element. The composition of the apparatus is difficult to reconstruct because of high taxonomic diversity (up to 20 formal species) of conodont associations studied.

The measurements of conodont elements mentioned in text are shown in Fig. 2. The collection studied is deposited in the F. N. Tschernyshev Central Geological Museum (CNIGR Museum), St Petersburg, Russia; collection Nos. 13019 and 13003 (one specimen). Holotype of *P. pollocki* Druce (Pl. II, fig. 4) is re-illustrated from Druce, 1976 (pl. 62, fig. 3b).

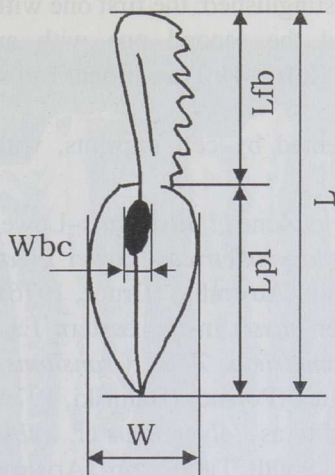


Fig. 2. Measurements of the Pa element: *L*, total length of the element; *Lfb*, length of the free blade; *Lpl*, length of the platform; *W*, width of the platform; *Wbc*, width of basal cavity flanks.

Genus *Polygnathus* Hinde, 1879
Polygnathus pollocki Druce, 1976
 Plate I, figures 1–4, 6, 7

- 1968 *Polygnathus* n. sp. A; Pollock, p. 436, pl. 62, figs. 32, 33, 38.
 1974 *Polygnathus* sp. B; Uyeno, pl. 5, fig. 8.
 1976 *Polygnathus pollocki* Druce, p. 198, pl. 79, figs. 2–4; text-fig. 24.
 1979 *Polygnathus pollocki* Druce; Balinski, pp. 80–81, pl. 23, figs. 7, 8.
 1985 *Polygnathus pollocki* Druce; Ovnatanova & Aristov, pl. 5, fig. 12.
 1992 *Polygnathus pollocki* Druce; Racki, fig. 32D,F.
 1993 ?*Polygnathus pollocki* Druce; Racki & Bultynck, pl. 4, figs. 4, 5 (*non* fig. 3, = *Polygnathus decorosus* Stauffer).
 1995 *Polygnathus* cf. *webbi* Stauffer; Shen Jian-Wei, pl. 2, figs. 15, 16.
 1996 *Polygnathus pollocki* Druce; Kononova et al., pl. 12, figs. 11, 12.
 1997 *Polygnathus pollocki* Druce; Zhuravlev et al., pl. I, figs. 5, 6.

Holotype. Sample BG 19543, Section 9, McPhee Knoll, Gogo Formation; CPC 12735.

Original diagnosis. A polygnathid with a very elongate and narrow platform (Druce, 1976).

Revised diagnosis. Polygnathid Pa element with elongate platform ($Lpl/W = 3-5$) having lateral margins bent inwards (omega-like transverse section of platform), and slightly undulated carina.

Material. More than 100 Pa elements of various preservation.

Remarks. Two morphotypes of *P. pollocki* can be distinguished: the first one with a platform ornamented by transverse ridges, and the second one with an unornamented platform (see Pl. I, figs. 1–4, 6, 7; Pl. II, fig. 4). Transitional forms also occur.

Micro-ornamentation of the platform is represented by cell imprints, with average size varying from 6.4 to 7.8 μm .

Occurrence. Upper Devonian, Frasnian, *asymmetricus* Zone (? *falsiovalis*–Lower *hassi*) in Alberta (Canada) (Pollock, 1968); Middle *asymmetricus*–Lower *gigas* zones (*punctata*–Lower *rhenana*) in the Canning Basin (Australia) (Druce, 1976); Middle–Upper *asymmetricus* Zone (*punctata*–Lower *hassi*) in the eastern East European Platform (Russia); Lower–Middle *asymmetricus* Zone (*transitans*–*punctata*) in the Holy Cross Mountains and Debnik area (Poland) (Balinski, 1979; Racki, 1992); *falsiovalis* Zone, South China (referred to as *Polygnathus* cf. *webbi* by Shen, 1995); *asymmetricus*–*gigas* zones in the South Tien Shan (Aristov, 1994).

Polygnathus pollocki Morphotype 1

Plate I, figures 1, 2, 6, 7

1974 *Polygnathus* sp. B; Uyeno, pl. 5, fig. 8.

1976 *Polygnathus pollocki* Druce, p. 198, pl. 79, figs. 2–4; text-fig. 24.

1979 *Polygnathus pollocki* Druce; Balinski, pp. 80–81, pl. 23, figs. 7, 8.

1985 *Polygnathus pollocki* Druce; Ovnatanova & Aristov, pl. 5, fig. 12.

1993 ?*Polygnathus pollocki* Druce; Racki & Bultynck, pl. 4, figs. 4, 5 (*non* fig. 3).

Diagnosis. *Polygnathus pollocki*; platform margins of Pa element are ornamented by weak transverse ridges.

Material. 17 well-preserved Pa elements.

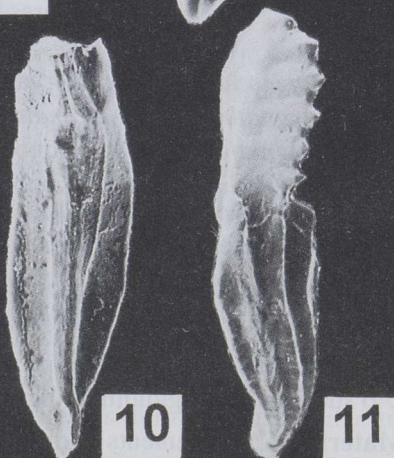
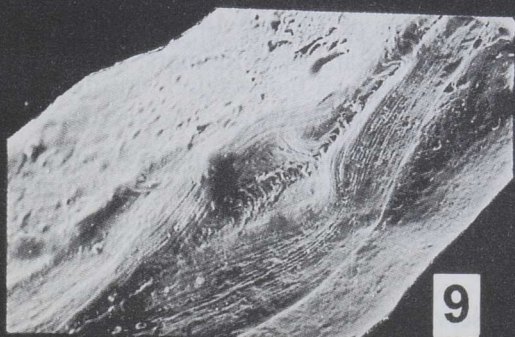
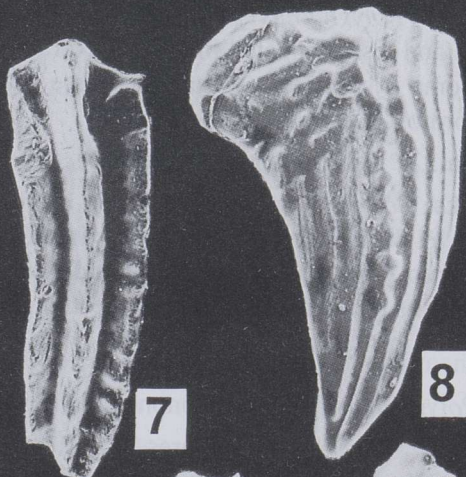
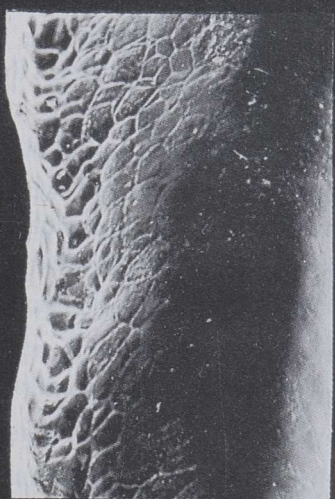
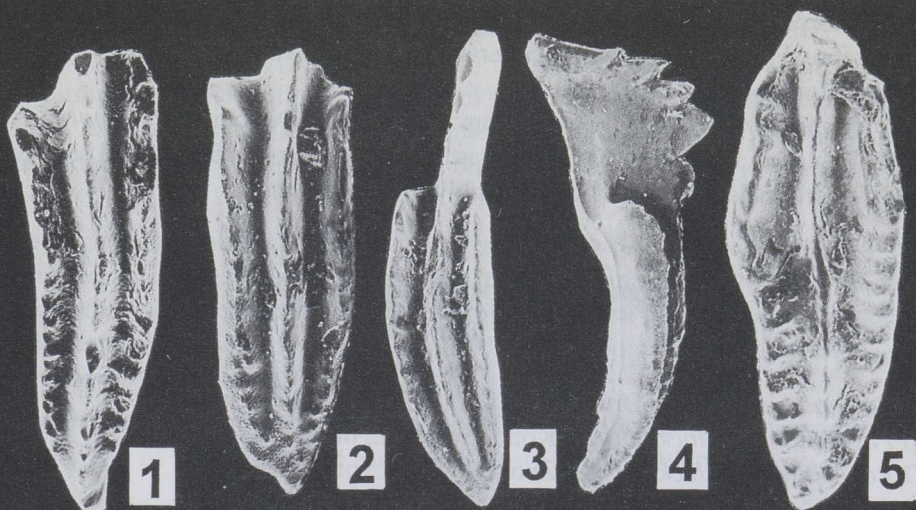
Explanation of Plate I

Figs. 1–4, 6, 7. *Polygnathus pollocki* Druce, 1976. 1, Morphotype 1, 10/13019, $\times 85$, 5101/6; 2, Morphotype 1, 4/13019, $\times 68$, 5101/4; 3, Morphotype 2, 13/13019, $\times 57$, 5101/3; 4, Morphotype 2, 8/13019, $\times 52$, 5101/6; 6, Morphotype 1, micro-ornamentation in the left posterior part of the platform, 5/13019, $\times 570$, 5101/7; 7, Morphotype 1, 5/13019, $\times 57$, 5101/7.

Fig. 5. *Polygnathus* sp. nov. A, 12/13019, $\times 48$, 5102/1.

Fig. 8. *Polygnathus* sp. nov. B, 7/13019, $\times 48$, 5119/4.

Figs. 9–11. *Polygnathus efimovae* Kononova, Alekseev, Barskov et Reimers, 1996. 9, basal cavity, 9/13019, $\times 230$, 5103/10; 10, lower view, 9/13019, $\times 58$, 5103/10; 11, 6/13019, $\times 62$, 5103/10.



Remarks. The holotype of *Polygnathus pollocki* Druce (1976, pl. 79, fig. 4) belongs to this morphotype, but the original description (Druce, 1976, p. 198) is closer to Morphotype 2 which has smooth platform margins (see below). Platform ornamentation varies from weak to moderate, transitional forms from Morphotype 1 (M1) to Morphotype 2 (M2) exist.

Polygnathus pollocki M1 differs from the Middle Devonian *P. timorensis* Klapper, Philip et Jackson in having inwardly bent platform margins and shorter free blade. Otherwise these species are highly homeomorphic.

Polygnathus pollocki Morphotype 2

Plate I, figure 3

1992 *Polygnathus pollocki* Druce; Racki, fig. 32D,F.

1996 *Polygnathus pollocki* Druce; Kononova et al., pl. 12, fig. 12.

1997 *Polygnathus pollocki* Druce; Zhuravlev et al., pl. I, fig. 6.

Diagnosis. *Polygnathus pollocki*; Pa element with non-ornamented platform margins and less elongated platform (average $Lpl/W = 3$) than in Morphotype 1. Only some specimens bear transverse ridges, or elongated nodes, in the posteriormost part of the platform.

Material. 21 well-preserved Pa elements.

Remarks. *Polygnathus pollocki* M2 is a probable ancestor of *P. drucei*, which evolved by developing the lateral rims in the platform margins. This morphotype is similar to *P. decorosus* Stauffer, but differs in having a platform with inwardly bent margins (omega-like transverse section of the platform).

Polygnathus efimovae Kononova, Alekseev, Barskov et Reimers, 1996

Plate I, figures 9–11; Plate II, figures 2, 10

1985 *Polygnathus ordinatus* Bryant; Ovnatanova & Aristov, pl. 5, figs. 10, 11.

1988 *Polygnathus* ex. gr. *ordinatus* Bryant; Aristov, pl. 2, figs. 1–3, 5.

1996 *Polygnathus efimovae* Kononova et al., p. 96, pl. 12, figs. 14–17.

1997 *Polygnathus efimovae* Kononova, Alekseev, Barskov et Reimers; Zhuravlev et al., pl. I, figs. 11, 13.

Holotype. Sample 128, borehole 1 Gavrilov-Yam, Semilukian Substage; Palaeontological Department, Moscow State University 272/26.

Diagnosis. Polygnathid Pa element with arched elongate lenticular platform bearing 2–6 subparallel longitudinal ridges.

Material. 82 Pa elements of different preservation.

Description. Polygnathid Pa element characterized by elongate lenticular platform, arched and slightly bowed laterally. The platform bears 2 to 6 subparallel longitudinal smooth or slightly nodose ridges. Carina smooth or nodose and S-like bent. Free blade short ($L_{fb}/L = 0.3-0.5$) in adult specimens. Average size of the cell imprints on the platform varies from 4.6 to 7.3 μm . Keel sharp and distinct. A small basal cavity is located in the anterior third of the platform. It has poorly developed flanks in adult specimens, but is large and flanked in immature specimens.

Remarks. This species differs from *Polygnathus ordinatus* Bryant in having many longitudinal ridges which are parallel to the carina, and in having S-shaped undulation of the carina. From morphologically close *P. rudkinensis* Ovnatanova et Kononova *P. efimovae* differs in smoother longitudinal ridges and in the general form of the platform.

Occurrence. Upper Devonian, Frasnian; Buregi and lowermost Snezha formations (upper part of the Semilukian Substage), East European Platform.

Polygnathus drucei sp. nov.

Plate II, figures 1, 3, 5-9

1996 *Polygnathus pollocki* Kononova et al., pl. 12, fig. 13.

Holotype. Sample 5101/7, CNIGR Museum, St Petersburg, No. 1/13019.

Type locality. Lake Ilmen region, section 5101 (see Zhuravlev et al., 1997 for the description and location of the section).

Type horizon. Upper Devonian, Lower Frasnian, Semilukian, Ilmen Beds (Formation).

Derivation of name. In honour of Dr E. C. Druce.

Diagnosis. Polygnathid Pa element with lanceolate elongate platform bearing (on each side of platform) one or two longitudinal ridges separated from platform margins by rims.

Material. 19 well-preserved Pa elements and 27 strongly broken elements.

Description. Polygnathid Pa element with a lanceolate elongate platform, which is arched and slightly bowed laterally. Platform bears, mainly in the posterior part, one or two narrow lateral rims, nodose in some specimens. The rims separate longitudinal ridges (one or two) from platform margins. Adcarinal troughs are deep and narrow. Average size of the cell imprints on the platform margins varies from 6.5 to 8.3 μm . Keel sharp and distinct. Basal cavity moderate, with poorly developed flanks. Width of basal cavity flanks decreases during ontogeny due to growing over.

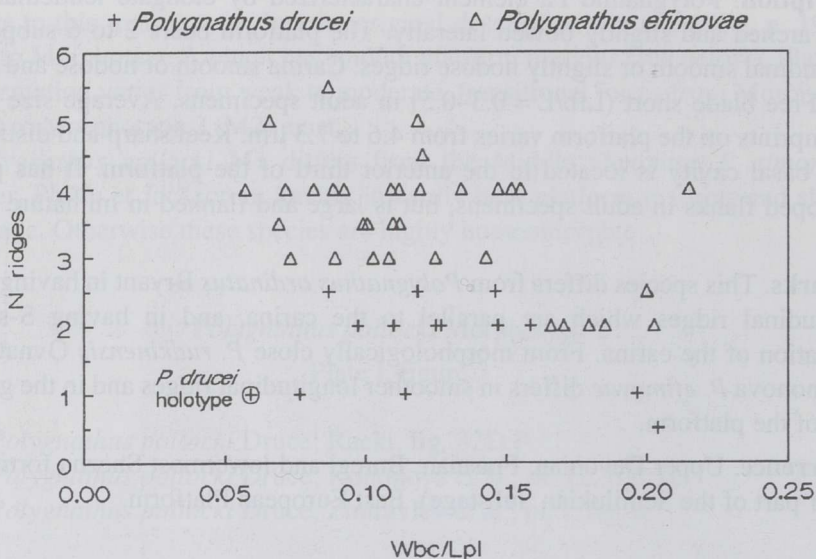


Fig. 3. Scattered plot diagram showing biometric differences between *Polygnathus efimovae* Kononova, Alekseev, Barskov et Reimers and *P. drucei* sp. nov. N ridges – number of longitudinal ridges on the platform.

Remarks. This species is close to the immature forms of *P. efimovae*, but differs in having smaller flanks of the basal cavity and poorly developed longitudinal ridges (only two ridges even in adult specimens). Certain correlation between the number of longitudinal ridges and relative width of the basal cavity flanks forms the biometrical diagnostic feature (see Fig. 3). Also, the basal cavity is located closer to the midpoint of the platform than in *P. efimovae*.

Morphologically similar *P. lingulatus* Ovnatanova differs from the new species in having rather nodose longitudinal ornamentation, a nodose carina, as well as a rounded posterior tip of the platform.

Explanation of Plate II

Figs. 1, 3, 5–9. *Polygnathus drucei* sp. nov. 1, 11/13019, × 85, 5101/6; 3, 2/13019, × 60, 5101/5C; 5, micro-ornamentation of holotype, 1/13019, × 570, 5101/7; 6, upper view of holotype, 1/13019, × 48, 5101/7; 7, oblique lateral view of holotype, 1/13019, × 48, 5101/7; 8, lateral view of holotype, 1/13019, × 48, 5101/7; 9, micro-ornamentation, 11/13019, × 620, 5101/6.

Figs. 2, 10. *Polygnathus efimovae* Kononova, Alekseev, Barskov et Reimers, 1996. 2, 3/13019, × 90, 5103/10; 10, 13/13003, × 37, 5103/9.

Fig. 4. *Polygnathus pollocki* Druce. Holotype, × 58, re-illustration from Druce, 1976 (pl. 62, fig. 3b).



1



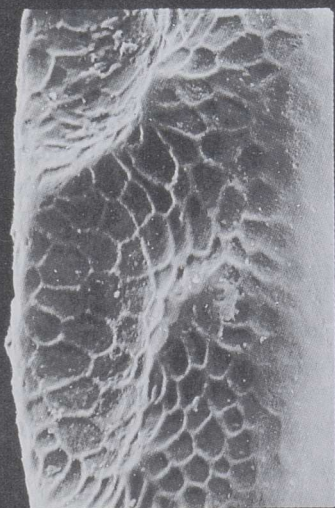
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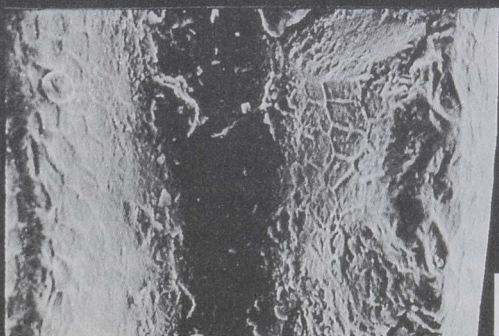
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8



9



10

Polygnathus drucei is distinguishable from *P. pollocki* M2 in having a lateral rim (or rims), relatively wider platform (average $Lpl/W = 3$), and different position of the basal cavity.

The proposed phyletic succession from *P. pollocki* M2 through *P. drucei* to *P. efimovae* demonstrates the heterochrony process (hypermorphosis) *sensu* McKinney (1986).

Occurrence. Upper Devonian, Lower Frasnian, Semilukian Substage, Ilmen and Buregi formations, East European Platform.

Polygnathus sp. nov. A

Plate I, figure 5

Diagnosis. Polygnathid Pa element with elongate platform whose posterior part is ribbed. The platform has S-shaped lateral bowing in its middle part. Adcarinal troughs are deep anteriorly and become shallower in the posterior part of the platform. Platform margins are elevated in the anterior part of the platform and form here a rostrum-like structure.

Material. 3 specimens from different samples.

Remarks. This species differs from *P. pollocki* M1 in having a rostrum-like anterior elevation of platform margins and in the absence of deep adcarinal troughs in the posterior part of the platform.

Occurrence. Upper Devonian, Lower Frasnian, upper part of the Semilukian Substage, Ilmen Formation, East European Platform.

Polygnathus sp. nov. B

Plate I, figure 8

Diagnosis. Polygnathid Pa element with elongate subtriangular platform bearing a number of subparallel longitudinal ridges and possessing a nodose ornamentation on the outer antero-lateral lobe.

Material. 4 Pa elements of poor preservation.

Remarks. These forms seem to belong to a new species, but are not aberrant specimens of *P. efimovae*. However, due to the small number of specimens (only 4) and their poor preservation, these forms are described in open nomenclature.

Occurrence. Upper Devonian, Lower Frasnian, upper part of the Buregi Formation and the lowermost part of the Snezha Formation, East European Platform.

REMARKS AND CONCLUSIONS

Conodont zonation for the shallow-water *Polygnathus* biofacies of the Frasnian is not yet developed. Thus the precise correlation of evolutionary events in the *P. pollocki* lineage is difficult. The preliminary phylogenetic reconstruction is based mainly on morphological similarities of the species, without precise stratigraphic control.

Immature specimens of all species of the *P. pollocki* group are similar and resemble *P. pollocki* M2. The last one is considered to be the probable ancestor of the *P. pollocki* lineage. The second member of the lineage, *P. pollocki* M1, gave rise to *Polygnathus* sp. nov. A. *Polygnathus drucei* evolved from *P. pollocki* M2. Thus the morphotypes of *P. pollocki* probably represent an early morphological divergence in this lineage. Then (in the late Semilukian) *P. efimovae* arose from *P. drucei*, and some advanced forms of *P. efimovae* gave rise to *Polygnathus* sp. nov. B.

The lineage studied demonstrates strong homeomorphy (in general sense) with the *Polygnathus latifossatus*–*Schmidtognathus wittekindti* lineage (Kononova et al., 1996). The *P. pollocki* lineage shows also some common features with a number of other polygnathid lineages, namely, developing from the unornamented (or poorly ornamented) platform, through the platform ornamented by transverse ribs, to the platform ornamented by longitudinal ridges. This morphological trend can be observed in the Upper Devonian–Lower Carboniferous genus *Neopolygnathus* (*N. communis* (Branson et Mehl)–*N. dentatus* (Druce) – *N. talassicus* (Nigmatzhanov)), Lower Carboniferous genus *Siphonodella* (*S. sulcata* Huddle–*S. sandbergi* Klapper), and in some other conodont genera.

Palaeogeographically, the *P. pollocki* group inhabited the tropic and southern subtropic realms, mainly the Prototethys shelves. The oldest representatives of the *P. pollocki* group are known from South China (*P. pollocki* in the *falsiovalis* conodont Zone, figured by Shen as *P. cf. webbi*; Shen, 1995, pl. 2, figs. 15, 16) and the youngest ones from the South Tien Shan (*P. pollocki* in the *gigas (rhenana)* conodont Zone; reported by Aristov, 1994). Probably, the South China shelf was the centre of the origination of the *P. pollocki* group. The highest diversity of this group in the East European Platform has been detected in the Semilukian Substage (*punctata*–Lower *hassi* conodont zones). All the species of the group discussed occur there.

The conodonts of the *P. pollocki* group are abundant in the shallow-water facies and correspond to the *Polygnathus* biofacies *sensu* Klapper & Lane (1985). They were not strongly dependent on the palaeotemperature and inhabited both, the relatively cool water (19–20 °C in the East European Platform basin) and warm water (at least 24 °C in the Western Australian basin according to Compston, 1960) environments. The species of the *P. pollocki* group are most common in shallow-water clastic carbonates, in association with *P. lanei* Kuzmin, *P. webbi* Stauffer, *P. ljaschenkoi* Kuzmin, and *Mehlina gradata* Youngquist.

Polygnathus pollocki M2 is closely associated with *Icriodus subterminus* Youngquist as well. Thus the morphotypes of *P. pollocki* demonstrate not only morphological but also some ecological differentiation.

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**POLYGNATHUS POLLOCKI DRUCE RÜHMA KONODONDID
(ÜLEMDEVON, ALAM-FRASNES, IDA-EUROOPA PLATVORM)**

Andrei V. ŽURAVLJOV

On kirjeldatud Ida-Euroopa platvormi Alam-Frasnes'i madalveelist päritolu settekivimitest leitud uusi konodondiliike *Polygnathus drucei* sp. nov., *Polygnathus* sp. nov. A ja *Polygnathus* sp. nov. B ning liigi *P. pollocki* Druce koosseisus kaht uut morfotüüpi. Kõik kirjeldatud konodondid kuuluvad *P. pollocki* rühma. Lühidalt on käsitletud ka selle rühma konodontide arengut ja suhet keskkonnaga.

**КОНОДОНТЫ ГРУППЫ *POLYGNATHUS POLLOCKI* DRUCE
(ВЕРХНИЙ ДЕВОН, НИЖНИЙ ФРАН, ВОСТОЧНО-ЕВРОПЕЙСКАЯ
ПЛАТФОРМА)**

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Из нижефранских мелководно-шельфовых отложений Главного девонского поля (Восточно-Европейская платформа, Россия) описаны конodontы группы *Polygnathus pollocki* Druce. Выделен новый вид *Polygnathus drucei* sp. nov. и описаны в открытой номенклатуре два новых вида (*Polygnathus* sp. nov. A, *Polygnathus* sp. nov. B). Для *Polygnathus pollocki* установлено два морфотипа. Кратко обсуждаются предполагаемые филогения и экология рассматриваемой группы полигнатид.