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Frasnian Conodonts from the Eastern Russian Platform

N. S. Ovnatanova[a] and L. I. Kononova[b]

[a]*All-Russia Research Geological Oil Institute, sh. Entuziastov 36, Moscow, 105118 Russia*
e-mail: ovnatanova@mail.ru
[b]*Department of Paleontology, Faculty of Geology, Moscow State University, Vorob'evy gory, Moscow, 119899 Russia*
e-mail: conodont@mail.ru

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Abstract—The Frasnian conodonts of the eastern Russian Platform from the Timan in the north to the Orenburg Region in the south are characterized in detail both paleontologically and stratigraphically. This paper is a continuation of a previously published monograph (Ovnatanova and Kononova, 2001) on the Frasnian conodonts of the shallow-water strata of the central Russian Platform, where polygnathids prevail. The conodont assemblages from the shallow-water and basinal sections of the Volga–Ural province and Southern Timan are analyzed. Problems and difficulties associated with the correlation of the shallow-water and deep-water Frasnian sections of the eastern Russian Platform and their correlation with the existing zonal conodont scales are discussed. The correlation between the deep-water Mendym deposits and the shallow-water Rechitza and Voronezh strata of the Volga–Ural province with the Vetlasyan and Sirachoi deposits of the Southern Timan is substantiated. The stratotype of the Semiluki Regional Stage of the Central Devonian Field contains equivalents of the lowermost beds of the Domanik Formation (unit 1), based entirely on polygnathids. Phylogenetic reconstructions for *Palmatolepis* and *Polygnathus* are suggested based on the ontogenetic series for some species of these two genera and the presence of transitional forms between some of the species. Based on these phylogenetic reconstructions, conodont zonal scales for the shallow-water and deep-water sections of the Frasnian Stage of the Russian Platform are proposed and their correlation with the existing conodont zonal scales is also adduced. Some aspects of biofacies control are considered based on the distribution of conodonts in the sections studied. In Systematic Paleontology, 91 conodont species of the genera *Ancyrodella*, *Mesotaxis*, *Palmatolepis*, and *Polygnathus* are described, including the new species *Palmatolepis menneri, P. kaledai, P. acutangularis*, and *Polygnathus reitlingerae*.

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CONTENTS

DEDICATION

To the blessed memory
of the outstanding geologist
Vladimir Vladimirovich Menner

INTRODUCTION

The authors of the present monograph were pioneers in the study of conodonts in the USSR that started in the 1960s. By this time in Western Europe the great importance of conodonts for the sequence and correlation of Paleozoic and especially of Upper Devonian deposits had already been demonstrated. The patterns in the development of conodont assemblages were revealed mainly in the stratotypical sections (Bischoff, 1956; Ziegler, 1958, 1962a, 1962b, etc.). Ziegler's work (1971) on erecting a series of thin closely spaced conodont zones in the Upper Devonian clay-with-cherts deposits of the Rhenish Slate Mountains was of fundamental importance: thus, a triumphant progress of this scale throughout the world, including the USSR, began (Bouckaert et al., 1972; Schulczewski, 1971, etc.). Even the earliest results of the study of conodonts in the USSR revealed their great stratigraphic significance for the subdivision and correlation of the Upper Devonian deposits of the eastern Russian Platform.

The present paper is a result of a longstanding study of Frasnian conodonts from the Volga–Ural province and Southern Timan. Conodonts from various facies of the Frasnian Stage of the Volga–Ural province and from most of the Frasnian stratotypical sections of the Timan–Pechora province in the Ukhta region were studied. In addition, the succession of the Frasnian conodont assemblages was studied for the Southern Urals (sections on the Sikaza and Ryauzyak Rivers, collection of L.I. Kononova). Here assemblages from various facies are described and analyzed (only Pa elements); problems connected with the use of the existing zonal scales for subdivision of the Frasnian basinal deposits of the eastern Russian Platform are discussed; a local conodont scale for the deep-water deposits of the eastern Russian Platform is outlined; for the first time the shallow-water zonal scale for the Frasnian of the eastern Russian Platform is proposed; and the problems of correlation with the existing zonal scales are discussed. It is known that zonal scales (Ziegler, 1962a, 1971; Ziegler and Sandberg, 1990; Klapper, 1988, etc.) are very difficult to correlate. One of the reasons for that is the ambiguous interpretation of the concept of some zonal and characteristic species. If the identification of the nominal species is uniform, the correlation is usually possible. Thus the correlation of scales and attempts to harmonize views of different authors seem to be less promising than a detailed study of the conodont succession without attempts to strengthen somebody's scheme.

The genus *Palmatolepis* is the most abundant taxon in the Late Devonian deep-water basins. The zonal conodont scale was based on the succession of its species. The phylogeny of the Frasnian palmatolepids was most fully described by Ziegler and Sandberg (1990). However, the number of species described has increased considerably during the last two decades; thus, we feel the need to revise and refine the previously proposed relationships. We suggest a scheme of the phylomorphogenetic development of the genus *Palmatolepis*; the scheme includes eight branches comprising groups of related genera. Each group contains species possessing one character in common.

Based on the eastern Frasnian polygnathids the previously established phylomorphogenetic relationships that provide a basis for the shallow-water zonal scale were confirmed (Ovnatanova and Kononova, 2001).

Another equally important aspect of this paper is the correlation of the heterofacies Frasnian deposits based on the newly proposed and previously developed zonations.

The most stratigraphically important representatives of the conodont genera studied are described. Morphological terms used in the descriptions were explained by I.S. Barskov et al. (1975).

The work was conducted in the All-Russia Research Geological Oil Institute (VNIGNI) and Moscow State University.

CHAPTER 1. MATERIAL

Most of the material came from boreholes from the Volga–Ural Province and also from outcrops and boreholes from Southern Timan.

In the Volga–Ural region, conodonts from the following sections of Tatarstan were studied: Melekess borehole 1, Ulyanovskaya borehole 1, Bugrovka area boreholes 18, 19, 20, Prikazanskaya area boreholes 113, 115, 120, 121, and 138, and Severnyi Kupol boreholes 71 and 166. In addition, conodonts from some levels of the Prikazanskaya borehole 69 and Severnyi Kupol boreholes 106, 142, and 220 were studied.

In the Orenburg Region, sections of the Shuvalovskii area boreholes 4, 6, and 19, Romanovskaya area borehole 2, and Kolgany area boreholes 17 and 23 were studied. In addition, the author's data on conodont distribution at some levels of the sections of the Krasnogor'e boreholes 94 and 95, Chutyr' (Udmurtia) borehole 152, Rekhino borehole 9, Uni borehole 3, Syr'yany boreholes 21 and 24, and Neopol'e boreholes 1 and 2 (Kirov Region), Terengul borehole 1, Severnaya Filippovka (Ulyanovsk Region) borehole 1, Malakhovskaya borehole 400, Zarinskaya borehole 350 (Orenburg Region), etc., were used in the analysis of the fauna. Most of the samples from the above-mentioned sec-

tions were collected by the authors, or were also passed to them for the study of conodonts by A.I. and G.P. Lyashenko, I.G. Gassanova, O.A. Lotsman, V.S. Gubareva, and S.P. Makarova.

We also describe and analyze conodonts from the outcrops and boreholes of the Ukhta region of Southern Timan. Most of the samples from the borehole sections were passed by A.I. Lyashenko and V.V. Menner to the authors at different times for the conodonts to be studied. A.I. Lyashenko, V.V. Menner, and A.V. Baranova repeatedly studied the sections of the Domanik Formation in the outcrops along the Ukhta, Chut', and Domanik Rivers. They passed their samples to VNIGNI for the study of conodonts. If the conodont fauna figured in the paleontological plates was collected by the above-listed authors, their numbering of the outcrops is adduced in the plate captions and the number of the outcrop indicated on the map and accepted in the paper is mentioned in parentheses. In the analysis of fauna, we also used results of the study of conodonts from the sections of the Shudayag borehole 1003, Balneologicheskaya borehole 3B, borehole 2056 (Ovnatanova and Kuzmin, 1991), boreholes 2040, 2051, and 2060 of the Ukhta expedition (Kuzmin and Ovnatanova, 1989), and also from the sections of the boreholes 2068 and 2023 (Klapper et al., 1996). An additional faunal survey of conodonts was carried out in the last two sections; the results are adduced in the present paper.

In addition, V.V. Menner passed samples from outcrops 2–4 on the Chut' River, from outcrop 9 on the Ukhta River, outcrops 10–13 in the cuttings of the road near the water-intake for the village of Shudayag, and Domanik Formation outcrops 1351, 1353, 1355,1903, and 1904 on the Lyaiol' River. Earlier V.S. Yudin passed to N.S. Ovnatanova samples from outcrops 1905, 1906, and 1355 on the Lyaiol' River for determination of conodonts. During the International field trip to Southern Timan in 1994, N.S. Ovnatanova collected samples from the sections on the Ukhta, Chut', Yarega, and Domanik rivers, from outcrop 3A at the town of Sirachoi, outcrop 2A near the village of Vetlasyan, and also from the parastratotype section of the Lyaiol' Formation on the Vezha-Vozh River (outcrops 8, 9, and 10). At the request of V.V. Menner, conodonts from the section of the Timanskaya borehole 10 (collected conjointly by V.V. Menner and A.V. Kuzmin, collection of A.V. Kuzmin) were studied.

The conodont fauna (only Pa elements) from the above-listed sections of Southern Timan and also from the Volga–Ural province is figured in the paleontological plates.

Along with the conodonts that are figured in the present paper for the first time, some species of *Palmatolepis* from the previous papers of the authors are reillustrated (Kononova, 1969; Gubareva et al., 1988; Ovnatanova et al., 1999; Ziegler et al., 2000; Klapper et al., 1996). Most of these collections are stored in the VNIGNI and PIN under collection numbers indicated in the plates captions numbers. Holotypes and some lectotypes of *Palmatolepis* are also reillustrated in the plates. As the concept of some *Palmatolepis* species of *Palmatolepis* was recently widened considerably, characteristic palmatolepid species found beyond the boundaries of the area studied (South Urals and Central Timan–Pechora province) are figured in the plates. Some *Palmatolepis* species of *Palmatolepis* from the outcrop of the Mendym and Askyn regional stages on the Sikaza River of the Southern Urals (materials of L.I. Kononova) are figured since it is especially important for the correlation of the Mendym and Askyn deposits. As for the polygnathids, holotypes of the *Polygnathus* species that were described on the territory of the former USSR and then in Russia are figured in the paleontological plates along with the specimens found in the area studied . In addition, some Givetian and Lower Famennian species that are not described in Systematic Paleontology are also figured.

CHAPTER 2. STRATIGRAPHY OF THE FRASNIAN DEPOSITS

The range of the Frasnian Stage is accepted here according to the Resolutions of the International Subcommission on the Devonian System (SDS). The boundaries of the stages are accepted according to the conodont zonation (Ziegler, 1962a; Ziegler and Sandberg, 1990) (Table 1).

2.1. Lower Boundary of the Frasnian Stage

In 1982 the International Commission on Stratigraphy approved the Resolution of the International Subcommission on Devonian Stratigraphy (SDS) to draw the boundary between the Middle and Upper Devonian (or Givetian and Frasnian Stages) at the base of the Lower *asymmetricus* conodont zone (Ziegler and Klapper, 1985) based on the co-occurrence of *Polygnathus asymmetricus* and *Ancyrodella rotundiloba* and up to the first appearance of *Palmatolepis punctata.* The boundary stratotype was selected in the Montagne Noire Mountains in the south of France. In the Russian Platform, this level coincides with the base of the Sargaevo Regional Stage on the western slope of the Urals and in the eastern Russian Platform, or with the base of the Ust'-Yarega Formation of Southern Timan. This level is considerably higher than the lower boundary of the Frasnian Stage accepted in the Unified Stratigraphical Schemes of the Paleozoic of the Russian Platform (*Resolution*…, 1990) at the base of the Pashiya Regional Stage. The latter corresponds approximately in conodont zonation to the *Schmidtognathus hermanni–Polygnathus cristatus* Zone (Ovnatanova and Kononova, 1984; *Resolution*…, 1990).

However, it was subsequently found that the boundary point in the Montagne Noire stratotype was not based on the appearance of typical *Ancyrodella rotundiloba*, but on the appearance of its older varieties,

which appeared within the Lowermost *asymmetricus* Zone. The revision of *Ancyrodella* and polygnathids revealed this level inside the Early *falsiovalis* Zone (Sandberg et al., 1989), i.e., within the previous Lowermost *asymmetricus* Zone (Table 1).

It is difficult to establish the exact position of this level on the eastern Russian Platform. Most likely *Mesotaxis falsiovalis* has not been found below the Sargaevo Regional Stage because of the facies features, and for the same reason *Ancyrodella pristina* and *A. binodosa* are represented by isolated specimens in the upper part of the Timan Regional Stage in the Volga–Ural region.

In Southern Timan, the Timan Regional Stage is composed of shallow-water deposits and thus only polygnathids are found there, while *Mesotaxis* and *Ancyrodella* are absent.

Isolated specimens of Givetian polygnathids are known from the lower part of the Regional Stage. Conodonts found in the upper part of the Timan Regional Stage (only polygnathid assemblage) were also found in the lower part of the Ust'-Yarega Regional Stage. In the Ust'-Yarega Formation, conodont assemblages are more diverse and contain *Ancyrodella rotundiloba.* For this reason the lower boundary of the Frasnian Stage in Southern Timan was established at the base of the Sargaevo (Ust'-Yarega) Regional Stage. Subsequently, on the grounds of the revision of the conodont assemblage in the stratotype of the Montagne Noire and establishment of the boundary inside the Early *falsiovalis* conodont zone (Sandberg et al., 1989), an additional study of the Timan and Ust'-Yarega formations was carried out (Kuzmin, 1995). Although there are no direct data on the correlation of the Upper Timan Formation with the Early *falsiovalis* Zone, some indirect evidence on the presence of *Ancyrodella* in the lower part of the Ust'-Yarega Formation suggests that the lower boundary of the Frasnian Stage should be placed at the base of the Upper Timan Subformation. This position of the Middle–Upper Devonian boundary is also confirmed by the results of the study of conodonts from the Chernyshev Ridge and Subpolar Urals.

Table 1. Correlation of the conodont zonal scales of Ziegler and Sandberg (1990), with the indication of positions of boundaries of the Frasnian Stage accepted according to the resolution of the International Subcommission on the Devonian System (SDS)

	Stage	Standard conodont zonation after Ziegler and Sandberg (1990)	Conodont zonation after Ziegler (1962a, 1971)
	Famennian	Late *triangularis*	Upper *triangularis*
		Middle *triangularis*	Middle *triangularis*
SDS, 1987		Early *triangularis*	Lower *triangularis*
	Frasnian	*linguiformis*	Uppermost *gigas*
		Late *rhenana*	Upper *gigas*
		Early *rhenana*	Lower *gigas*
		jamieae	*Ancyrognathus triangularis*
		Late *hassi*	
		Early *hassi*	Unzoned
			Upper *asymmetricus*
		punctata	Middle *asymmetricus*
		transitans	Lower *asymmetricus*
SDS, 1987		Late *falsiovalis*	
	Givetian	*Early falsiovalis*	Lowermost *asymmetricus*
		disparilis	

2.2. Upper Boundary of the Frasnian Stage

The upper boundary of the Frasnian Stage or the boundary between the Frasnian and Famennian stages at the base of the *Palmatolepis triangularis* conodont zone was approved by the Devonian Subcommission of the International Commission on Stratigraphy in 1987 during the International Symposium on the Devonian System (Dineley, 1988) in Calgary (Table 1).

In spite of the long discussions, the main argument for the acceptance of this boundary level was the fact that abrupt sea-level changes level and one of the great mass extinctions of organisms occurred here (MacLaren, 1988; MacLaren and Goodfellow, 1990).

On the Russian Platform, the Frasnian–Famennian boundary recently became especially important as the Volgograd Regional Stage was established at the base of the Famennian Stage in the Volgograd Volga region based on palynological data (Mantsurova and Tsygankova, 1995, Mantsurova et al., 2003). It was also found out that the Volgograd Regional Stage corresponds to the Early–Middle *triangularis* conodont zones (Galushin and Kononova, 2004). This conclusion has been already confirmed in some sections of the eastern Russian Platform.

Now the status of the Volgograd Regional Stage and its position at the base of the Famennian Stage is

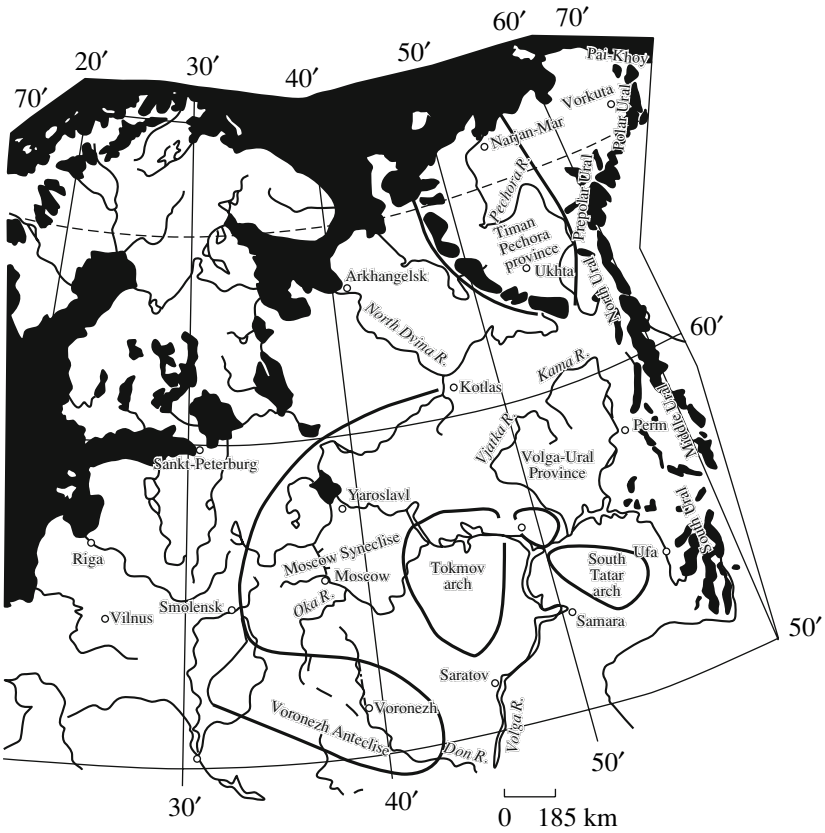


Fig. 1. Schematic map of the regions studied and mentioned, with the main tectonic structures.

approved (*Resolution*…, 1999, p. 41). Previously the Famennian Stage in the Unified Stratigraphical Scheme began with the Zadonsk Regional Stage (*triangularis* and *crepida* zones); the lower boundary of the *triangularis* Zone was not shown in the scheme.

The Frasnian deposits are subdivided based on the Unified Scheme of the Russian Platform (*Resolution*…, 1990) with changes concerning the correlation of different facies that were accepted by the authors.

CHAPTER 3. VOLGA–URAL PROVINCE

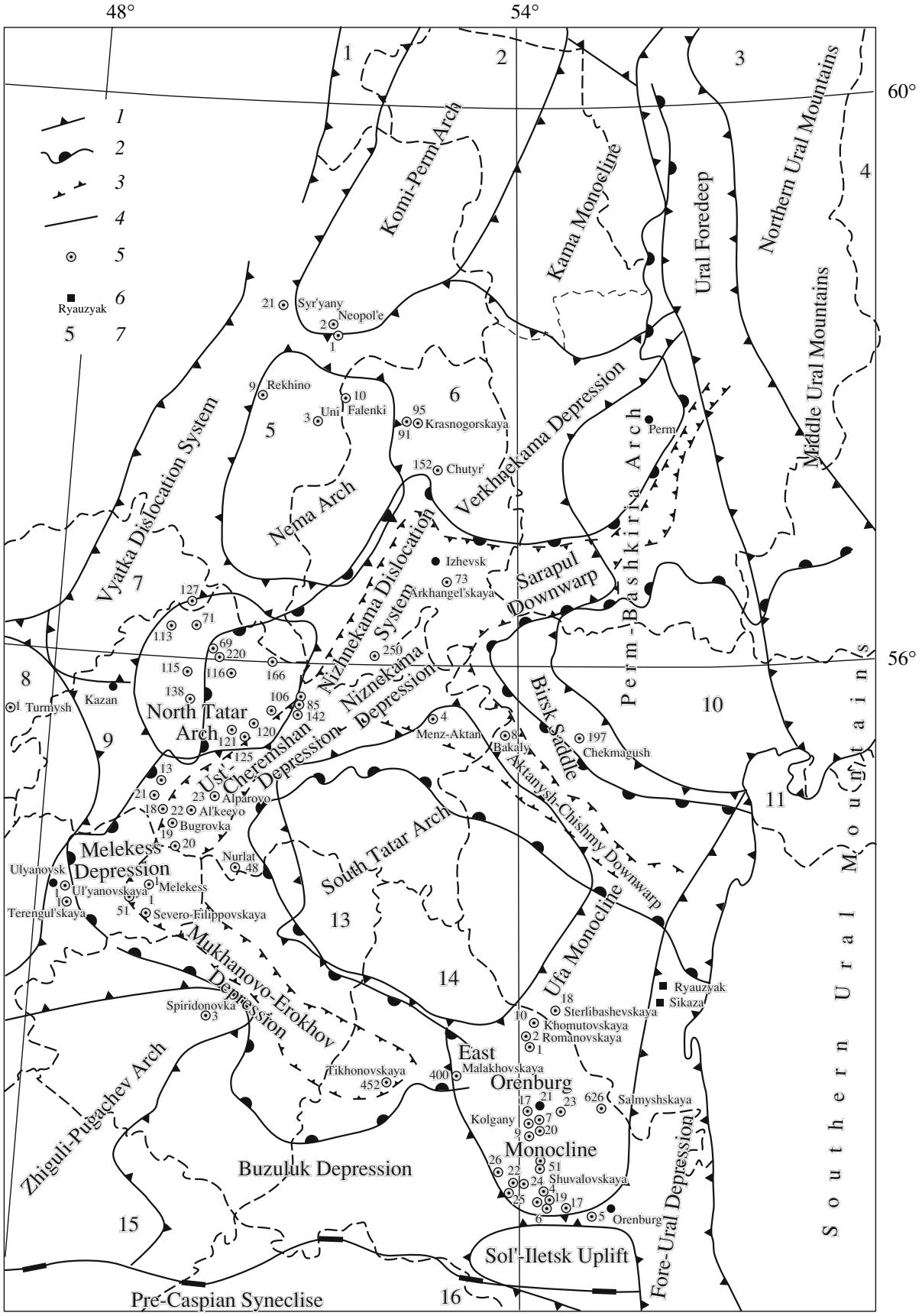
The Volga–Ural oil-bearing province is located on the southeastern Russian Platform and is bordered to the west by the Voronezh anteclise and the Moscow syneclise, to the north by the Timan–Pechora province, to the east by the Cis-Urals foredeep and Ural fold belts, and to the south by the Caspian depression (Fig. 1).

The main structural elements of the province in Fig. 2 are given after the paper "Oil-and-Gas-bearing…" (1970), in which the scheme of the deep tectonics of the Volga–Ural province compiled under the editorship of V.A. Klubov is produced. Data on the tectonic zonation of the region were also used (Mirchink et al., 1965; Mirchink, 1974; Garetskii et al., 1990).

The sections of the Kama–Kinel trough system are major tectonic elements of the Volga–Ural province. The most important troughs are the Mukhanovo-Erokhov, Ust'-Cheremshan, Nizhnekamskii, Mozhga, Aktanysh-Chishma, Sarapul, and Fokino troughs. Fauna from these locations is discussed in the present paper. The relative position of troughs and the arches conjugated with them and the location of the boreholes studied by the authors are shown in Fig. 2.

In 1950s–1960s, the deep drilling activity (including key boring) in the Volga–Ural region increased and

Fig. 2. Tectonic map of the Volga–Ural Province showing the localities of the sections studied and mentioned (based on the data from "Oil-and-Gas-bearing…", 1970; Mirchink et al., 1965; Mirchink, 1974; Garetskii et al., 1990, with the map of the Kama–Kinel Trough System); most important sections described are marked in the map. Designations: (*1*) outline of the first order structures, (*2*) outer borderline of the Kama–Kinel Trough System, (*3*) inner borderline of the Kama–Kinel Trough System, (*4*) Pre-Caspian Syneclise border, (*5*) boreholes and their nos., (*6*) outcrops, and (*7*) Russian republics and regions and Kazakhstan are marked by numbers: (1) Komi Republic, (2) Komi–Nenets Autonomous Okrug, (3) Perm Region, (4) Sverdlovsk Region, (5) Kirov Region, (6) Udmurtia, (7) Mari Republic, (8) Chuvashia, (9) Tatarstan, (10) Bashkiria, (11) Chelyabinsk Region, (12) Ulyanovsk Region, (13) Samara Region, (14) Orenburg Region, (15) Saratov Region, and (16) Kazakhstan.


48°
54°
60°
56°
Komi-Perm Arch
Kama Monocline
Ural Foredeep
Northern Ural Mountains
Middle Ural Mountains
Vyatka Dislocation System
Nema Arch
Verkhnekama Depression
Perm-Bashkiria Arch
Niznekama Dislocation System
Sarapul Downwarp
Niznekama Depression
North Tatar Arch
Ust'-Cheremshan Depression
Birsk Saddle
Aktanysh-Chishmy Downwarp
South Tatar Arch
Melekess Depression
Mukhanovo-Erokhov Depression
Ufa Monocline
East Orenburg Monocline
Zhiguli-Pugachev Arch
Buzuluk Depression
Sol'-Iletsk Uplift
Fore-Ural Depression
Pre-Caspian Syneclise
Southern Ural Mountains
Ryauzyak
Syr'yany
Neopol'e
Rekhino
Uni
Falenki
Krasnogorskaya
Chutyr'
Perm
Izhevsk
Arkhangel'skaya
Turmysh
Kazan
Menz-Aktan
Bakaly
Chekmagush
Alparovo
Al'keevo
Bugrovka
Nurlat
Ulyanovsk
Ul'yanovskaya
Melekess
Terengul'skaya
Severo-Filippovskaya
Spiridonovka
Sterlibashevskaya
Sikaza
Khomutovskaya
Romanovskaya
Tikhonovskaya
Malakhovskaya
Salmyshskaya
Kolgany
Shuvalovskaya
Orenburg

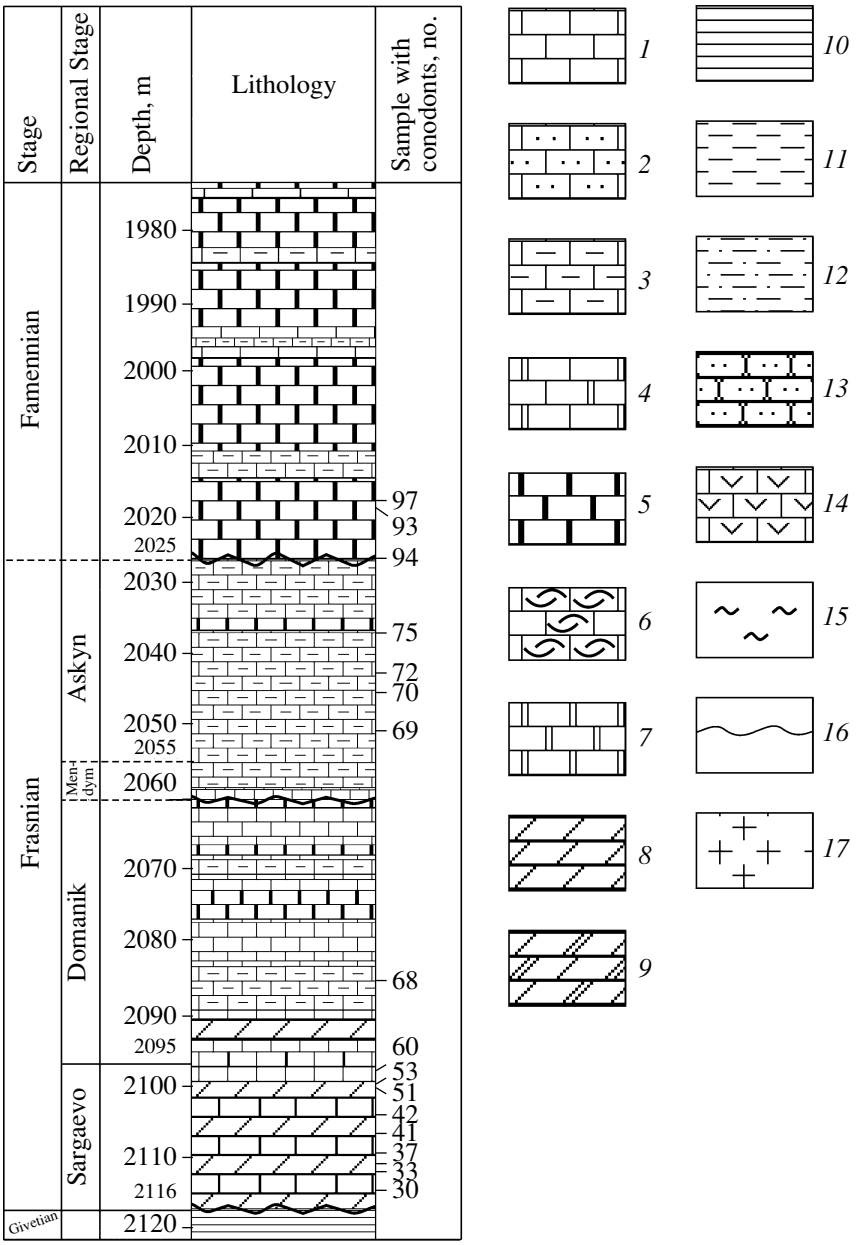


Fig. 3. Section of Frasnian and Famennian deposits in Melekess, borehole no. 1 (after Filippova and Aronova, 1957), modified. Designations: (*1*) limestone, (*2*) sandy limestone, (*3*) clayey limestone, (*4*) dolomitized limestone, (*5*) silicified bituminous limestone; (*6*) organogenous detrital limestone, (*7*) dolomite, (*8*) marl, (*9*) dolomitized marl, (*10*) clay, (*11*) argillite, (*12*) aleurolite, (*13*) sandstone, (*14*) sulphate carbonaceous deposits, (*15*) shale, (*16*) stratigraphical lacuna, (*17*) crystalline basement.

comprehensive investigations of Devonian core samples were carried out by large collectives of scientists. Brachiopods, ammonoids, ostracodes, pollen and spores, and then coniconchs were studied. Later the study of conodonts began. The most complete summaries of the Volga–Urals were produced in monographs (*Oil-and-Gas-bearing*…, 1970; Aliev et al., 1972). The Devonian deposits of Tatarstan were described by Gubareva (2003).

3.1. Lithostratigraphy of the Frasnian Deposits of the Kama–Kinel Trough System

The complicated history of the geological development of the Volga–Ural province determined the facies diversity of deposits. Thus the unified stratigraphic scheme cannot be used for the whole territory. Beginning with the Domanik level, peculiar conditions of sedimentation existed on the eastern Russian Platform and were accompanied by the development of starved

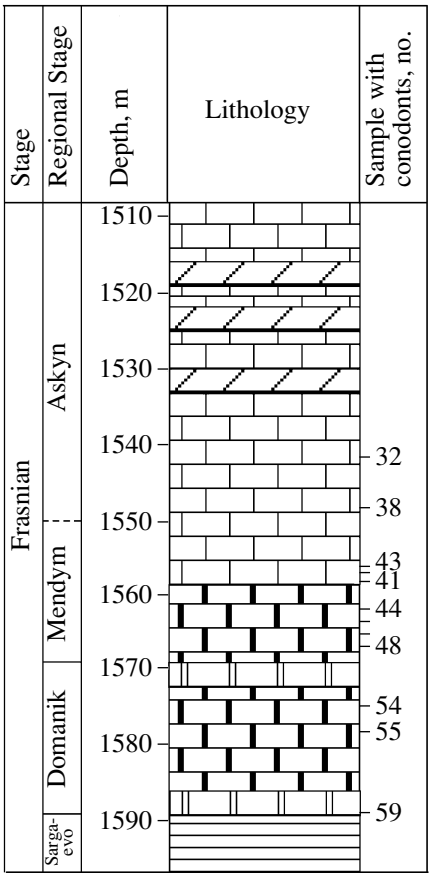


Fig. 4. Section of Frasnian deposits in Severnyi Kupol, borehole no. 166.

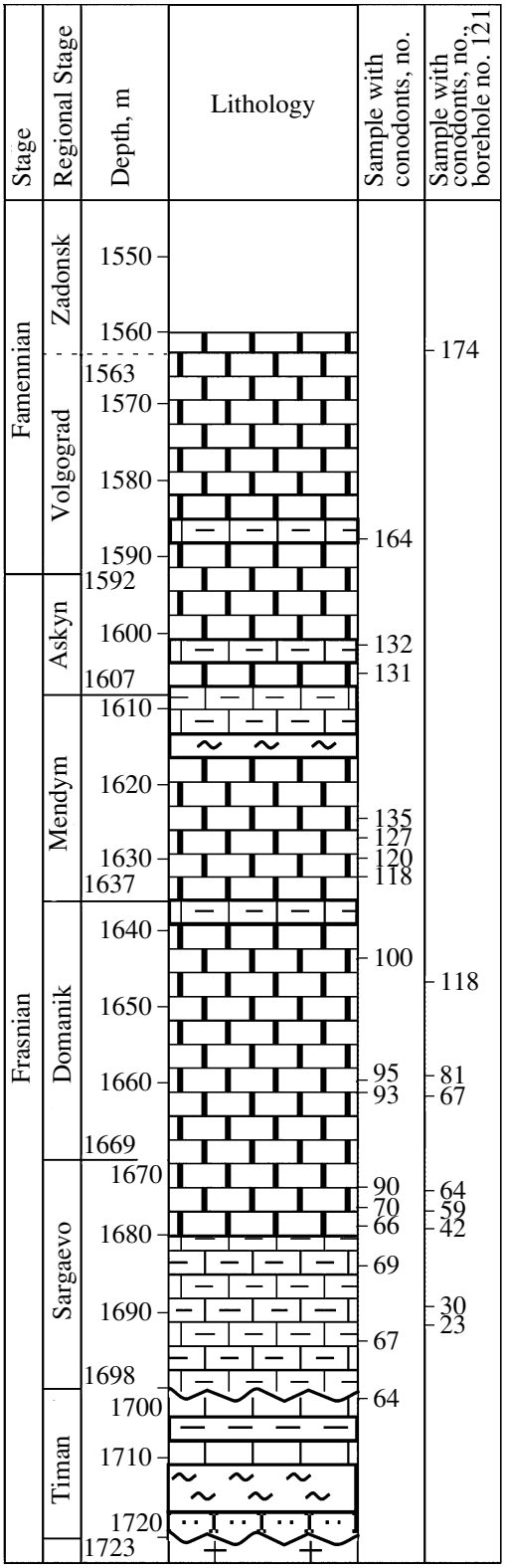


Fig. 5. Section of Frasnian and Lower Famennian deposits in the Prikazanskaya, boreholes nos. 120 and 121.

troughs. This was the reason for forming types of sections with strongly differentiated facies, specifically shallow-water and basinal. Facies differentiation of deposits is better pronounced from the Domanik time onward. For this reason the characterization of the Timan and Sargaevo regional stages is common for both types of the sections and is produced in the description of the shallow-water type of the section, while the characterization of the basinal sections is described beginning with the Domanik time.

Along the Ust'-Cheremshan downwarp, we studied the section of borehole Melekess 1 (Fig. 3). Within the Nizhnekamskii downwarp, the fauna from the basinal Frasnian sections of borehole 166 of Severnyi Kupol (Fig. 4) and boreholes 120 and 121 of the Prikazanskaya area (Fig. 5) was analyzed. Interesting sections and conodont assemblages were found within the north Tatar arch. If the Frasnian conodonts in the section of Severnyi Kupol 71 (Fig. 6) still preserve peculiarities typical for the basinal section, conodont assemblages from the sections of Prikazanskaya 113 and 115 consist mostly of shallow-water forms. Fauna from the section of Prikazanskaya 138 (Fig. 7) of the Tatar arch and from Ul'yanovskaya 1 (Fig. 8) of the Tokmovo uplift was also studied. In addition, data on conodonts from Terengul borehole 1, Turmysh borehole P-1 (Tokmovo uplift) and Prikazanskaya 113 and 115 on the north Tatar arch were used in the analysis of assemblages.

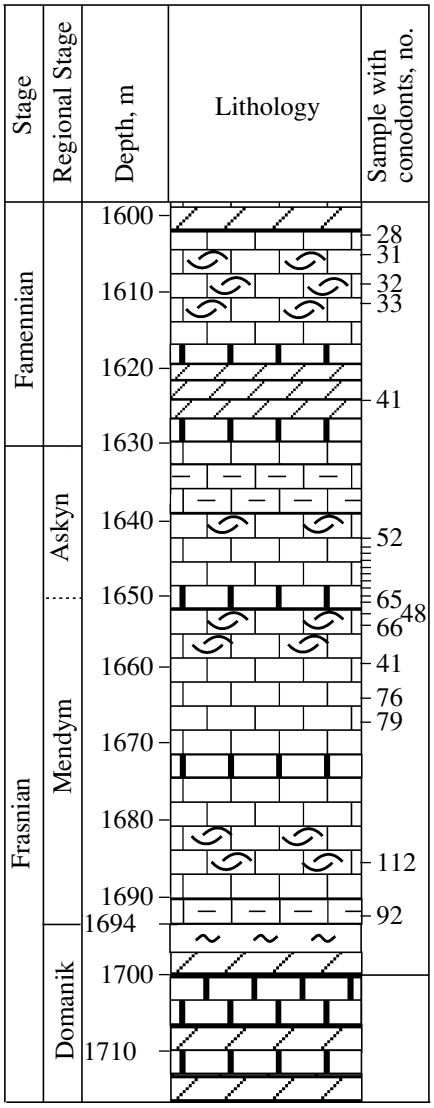


Fig. 6. Section of Frasnian and Lower Famennian deposits in Severnyi Kupol, borehole no. 71.

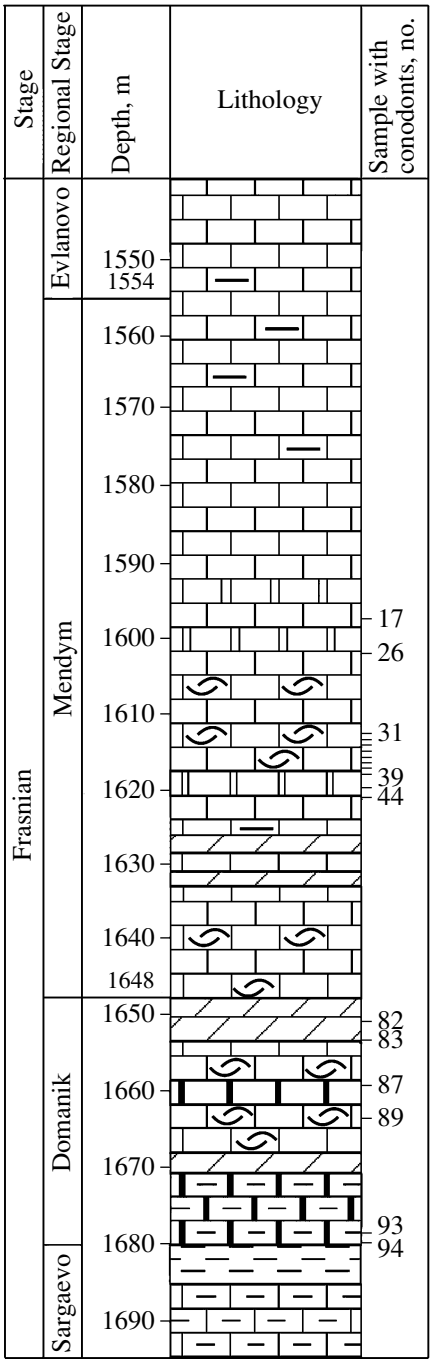


Fig. 7. Section of Frasnian deposits in Prikazanskaya, borehole no. 138.

Before proceeding to the lithostratigraphy, we shall mention again that the Frasnian Stage on the studied territory corresponds to the interval from the upper part of the Timan Regional Stage to the Livny Regional Stage inclusive.

Frasnian deposits in the western Volga–Ural province of the subregional part of the unified scheme (*Resolution*…, 1990) are consecutively divided into the Timan, Sargaevo, Semiluki, Rechitsa (=Petino), Voronezh, Evlanovo, and Livny regional stages. In the eastern basinal regions, Timan, Sargaevo, Domanik, Mendym, and Askyn regional stages are distinguishable (Table 2). It is important that here we assume a correlation that is absolutely different from the unified scheme correlation of the Mendym and Askyn deposits. The Mendym Regional Stage of the eastern regions we correlate to the Rechitsa and Voronezh regional stages of the western Volga–Ural province and the central Russian Platform and also with the Vetlasyan and Sirachoi regional stages of Southern Timan; Askyn Regional Stage of the eastern regions we correlate with the Evlanovo and Livny regional stages of the western Volga–Ural province and the central Russian Platform, and also to the Ukhta Formation of Southern Timan.

In most of the sections studied the Famennian Stage begins with the Zadonsk Regional Stage. The Volgograd Regional Stage has only rarely been found (completely or partly) in the basinal sections studied.

3.2. Shallow-Water Type of Sections

Shallow-water sections preserved all characteristics of the Frasnian section of the central Russian Platform, which consists of partly recrystallized and dolomitized organogenous and organoclastic limestones and usually calcareous dolomites, which contain inclusions of gypsum and anhydrites. The section is up to 250 m thick and rich in stromatoporates, crinoids, corals, cyanobacteria, brachiopods, and conodonts.

This type of section we considered based on the example of sections of the Tokmovo uplift (Ul'yanovskaya 1, which was also described in the literature as Okhotnich'ya borehole 1) (Fig. 8) and of the Tatar arch (Prikazanskaya 138) (Fig. 7).

3.2.1. Timan Regional Stage

The Lower–Upper Timan boundary is usually placed at the base of the Upper Timan limestone. However, it is often difficult to distinguish between the Lower and Upper Timan regional substages due to the scanty material. The Timan Regional Stage is less than 40 m thick and is usually composed mainly of the clayey and carbonate rocks. Most of the Lower Timan regional substage is probably absent in sections.

The Timan Regional Stage overlies the underlying deposits either conformably or with a gap. On the Tatar arch (Prikazanskaya 125 and 120, Severnyi Kupol 107, and other areas), it occurs on the crust of weathering of the Archean rocks of the basement. Timan deposits are absent in Ul'yanovskaya 1 of the Tokmovo uplift.

3.2.2. Sargaevo Regional Stage

The Sargaevo Regional Stage is present everywhere. Contact with the underlying deposits varies; it overlies either conformably or with a small gap the Upper Timan deposits and overlaps transgressively the rocks of the crystalline basement of the Tokmovo uplift (Ulyanovskaya 1 and Terengul 1).

On the Tokmovo uplift (Ulyanovskaya 1, interval 1951–1924 m (Fig. 8), Terengul 1, interval 2130–2090 m), Sargaevo Regional Stage is 27–40 m thick, composed of clayey limestones with varying clay content and admixture of silt material and subsidiary interbeds of marls, and contains brachiopods and rare conodonts. At the northern top of the Tatar arch (Prikazanskaya area), the Sargaevo deposits are richer in carbonate; the regional stage varies from 8 to 50 m in thickness, and its fauna includes brachiopods, ostracodes, bactrites, and conodonts.

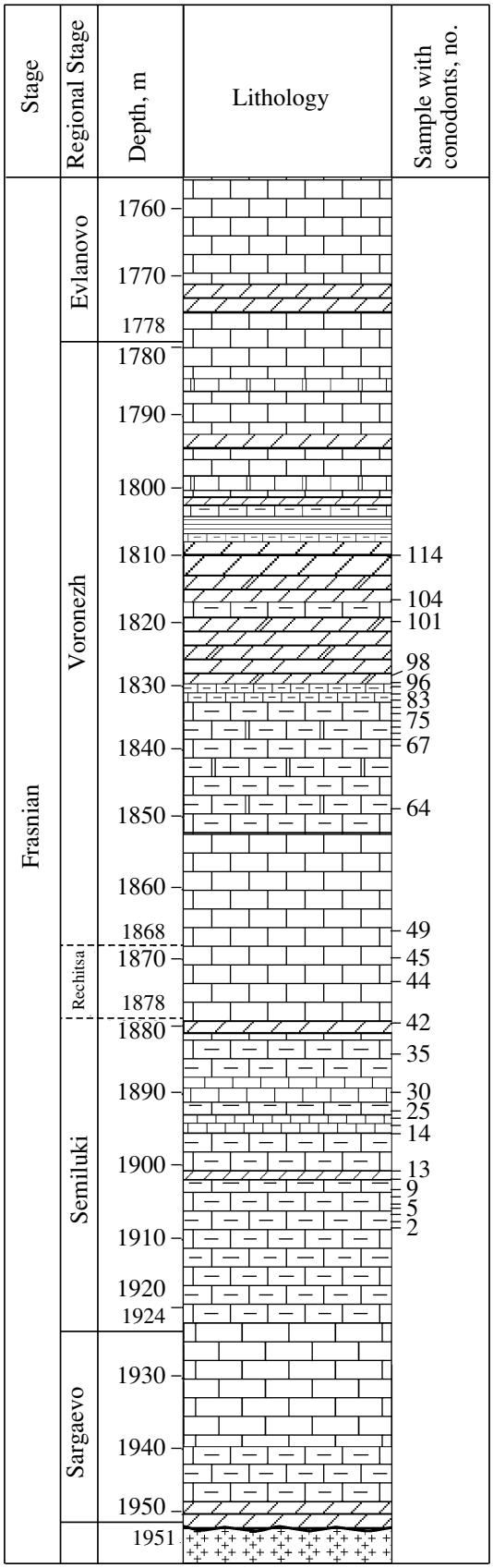


Fig. 8. Section of Frasnian deposits in Ul'yanovsk (Okhotnich'ya), borehole no. 1.

Table 2. Stratigraphic scheme showing the divisions of shallow-water and basinal Frasnian deposits of the Volga–Ural Province accepted in the present study

	Shallow-water type of section		Basinal type of section	
Stage	Regional stage, regional substage			
Famennian	Zadonsk		Zadonsk	
			Volgograd	
Frasnian	Livny		Askyn	
	Evlanovo			
	Voronezh		Mendym	
	Rechitsa (Petino)			
	Semiluki		Domanik	
	Sargaevo		Sargaevo	
	Timan	Upper	Timan	Upper
Givetian		Lower		Lower

3.2.3. Semiluki Regional Stage

The regional stage was studied in two sections of the Tokmovo Uplift (Ulyanovskaya 1, interval 1878–1924 m (Fig. 8) and Terengul 1, interval 2070–2090 m) and on the North Tatar Arch. The rock is exclusively carbonate in composition. It was studied in detail by Filippova et al. (1958) in the section of the Ulyanovskaya key borehole. The lower part of the section was earlier identified as Rudkino beds. The regional stage is composed of gray unevenly clayey limestones with interbeds of dark gray marls. In the sections of the north Tatar arch, the limestones in the upper part of the regional stage are of lighter color, massive, recrystallized, and dolomitized, with occasional bioclastic and crinoid varieties with glauconite. Fossils include brachiopods and rare corals, echinoderms, gastropods, and conodonts. The deposits are 25–40 m thick.

3.2.4. Rechitsa (= Petino) Regional Stage

The regional stage was studied in the Ulyanovskaya 1 of the Tokmovo Uplift (interval 1852–1878 m). It is composed of slightly clayey, microgranular, compact, partially dolomitized limestones with rare interbeds of clayey limestones and marls. Brachiopods, foraminifers, corals, and rare conodonts were found. The regional stage is 25 m thick. It is possibly present in the shallow zone of the North Tatar Arch where we included it in the Rechitsa–Voronezh undivided deposits.

3.2.5. Voronezh Regional Stage

On the Tokmovo Uplift (Ulyanovskaya 1 (Fig. 8) and Turmysh P-1) and in the shallow zone of the North Tatar Arch (Prikazanskaya 113, 115, and 138), the lower part of the Voronezh Regional Stage is composed of the gray and dark gray limestones interbedded with marls. The upper part of the section is composed mainly of light-colored, microgranular, organogenous, organoclastic, biomorphic, and partially recrystallized and dolomitized limestones and often of calcareous dolomites with inclusions of gypsum and anhydrite. Interbeds of calcareous conglomerates are also present. Of faunal remains, brachiopods, corals, crinoids, ostracodes, bryozoans, and conodonts are typical. The regional stage is 45–90 m thick.

3.2.6. Evlanovo Regional Stage

The regional stage is characterized by biomorphic organogenous and organodetrital limestone varieties with interbeds of clayey limestones and marls at the base. The fauna consists of numerous remains of algae, corals, foraminifers, brachiopods, and rare conodonts. The regional stage is about 50 m thick.

3.2.7. Livny Regional Stage

The regional stage is represented by organogenous and organoclastic, spheroid algae, strongly dolomitized limestones, which may contain inclusions of gypsums and anhydrites. The fauna is diverse: brachiopods, ostracodes, and rare oniconchs and conodonts. Corals and algae are abundant. The Livny Regional Stage is 30–50 m thick.

3.2.8. Famennian Stage

Deposits of the Famennian Stage are distributed almost everywhere. They are difficult to subdivide because of the facies variability of the deposits and scanty core material. The lowermost deposits of the stage (Volgograd Regional Stage) are still unknown in the shallow-water type of the sections. The Lower Famennian deposits are composed of organogenous and organoclastic (spheroid algae), carbonate, and strongly dolomitized rocks, which may contain inclusions of gypsums and anhydrites. The total thickness of the Famennian deposits is up to 200 m.

3.3. Basinal Type of Section

This type of section is characterized by materials from the Ust'-Cheremshan and Nizhnekamskii system of downwarps.

The Domanik, Mendym, and Askyn regional stages are distinguishable in those parts of the sections that overlie the Sargaevo Regional Stage (Table 2). The name "Askyn Horizon" is taken from the Urals stratigraphic scheme.

3.3.1. Domanik Regional Stage

The regional stage is characterized by the alternation of clayey carbonate and clayey siliceous-carbonate bituminous rocks. Fossil include coniconchs, ammonoids, bivalves, radiolarians, ostracodes, brachiopods (*Lingulas* and *Liorynchus*) and numerous conodonts. The regional stage is from 12 to 36 m thick.

3.3.2. Mendym Regional Stage

The regional stage is composed of the microgranular, cherty, and bituminous limestones, dark gray dolomitized limestones and dolomites, which upward in the section change into light-colored spheroid limestones. Limestones with pebbles are known at the base of the presumed Mendym Regional Stage in the Melekess 1 section. Coniconchs, radiolarians, and ammonoids *Manticoceras intumescens* Beyr. were found in the lower part of the horizon; algae and rare conodonts were found in its upper part. The Mendym Regional Stage is 7–42 m thick.

3.3.3. Askyn Regional Stage

Deposits of the Askyn Regional Stage in the domanik facies of the Volga–Ural region are developed within the Kama–Kinel trough system. It was provisionally identified for the first time as an Upper Frasnian Substage by Filippova and Aronova (1957) in the section of the Melekess key borehole between the fossiliferous Mendym and Famennian deposits with *Posidonomia venusta* Münst. Unfortunately, cores from this interval were rarely taken and thus it is poorly known and some errors have been made in its subdivision. The study of conodonts from the section revealed the presence of the Askyn Regional Stage or possibly only of its lower part, which corresponds to the Evlanovo Regional Stage.

The Askyn Regional Stage is composed of microgranular, bituminous, slightly dolomitized limestones with interbeds of bituminous argillites and silicified marls with remains of radiolarians, ostracodes, spiculae of sponges, and fragments of algae. Layers of silicites occur in the interbedding rocks. The thickness varies from 10 to 60 m. Shales and marls of the domanik type alternate with the reef limestones in some sections. Sometimes bituminous rocks prevail in the alternation and sometimes light-colored recrystallized carbonate varieties with interbeds of organoclastic limestones and calcareous sandstones are widely developed. In this case the Askyn Regional Stage is up to 100 m thick.

3.3.4. Famennian Stage

Filippova and Aronova (1957) were first to report the presence of Famennian deposits in the basinal facies in the description of the section of the Melekess key borehole. The peculiarity of the section is the interbedding of dark, almost black, strongly bituminous, clayey limestones with marls and siliceous shales. Sections of this basinal type are developed within the Kama–Kinel trough system, where the Famennian Stage is from 25 to 90 m thick. Filippova and Aronova (1957) mentioned that in the axial part of the depression, the section is composed mainly of shales, sometimes with thin interbeds of tuffaceous rocks. Subsequently, the presence of *Cheiloceras* Zone in the sections of domanik type was shown by finds of bivalves, ostracodes, and brachiopods (Lyashenko et al., 1970). The subsequent study of conodonts from this section testified to the presence of the Volgograd Regional Stage and, possibly, a part of Zadonsk Regional Stage in the Melekess 1 section. Their presence was established in some other sections, specifically in the Bugrovka area.

3.4. Lithostratigraphy of the Frasnian Deposits of the Eastern Orenburg Monocline

Oil geologists study in detail the Upper Devonian deposits of the eastern Orenburg Region since the strata are very distinctive in that the deposits show strong horizontal and vertical variations, contain organogenous structures, and above all have a thick terrigenous Kolgany Member in the south of the region. Within the eastern Orenburg monocline, the sections of the Kolgany and Shuvalovskii areas are better studied. These sections are interesting in the presence of the terrigenous Kolgany Member overlying the Domanik deposits. The Kolgany Member varies in stratigraphic range over the territory and is characterized by a distinctive shallow-water conodont assemblage.

Some of the sections of the Shuvalovskii area are shown in Figs. 9–11. The sections of the Shuvalovskii area are also interesting in the conodont assemblages revealed in the domanikoid deposits of the Timan Regional Stage.

3.4.1. Timan Regional Stage

The organogenous limestones of the Timan Regional Stage are developed immediately above the terrigenous unit of the Pashiya age (Givetian Stage) in the Romanovskaya, Sharlyk, and Kolgany areas of the northern and central parts of the East Orenburg Region (Fig. 2). The lower part of the Regional Stage in the Kolgany area is 20–25 m thick and is composed mainly of gray or light gray algae-stromatoporate, unevenly recrystallized limestones with brachiopods, ostracodes, and coniconchs. The middle part of the regional stage consists of 3–10 m thick clay-silt unit. The upper part of the section of the Timan Regional Stage is composed of 7- to 10 m-thick series of microgranular limestones. The boundary between the Lower and Upper Timan regional substages is most probably located at the base of this clay-silt unit. The Timan Regional Stage thickens up to 41–45 m in some sections of the Kolgany area.

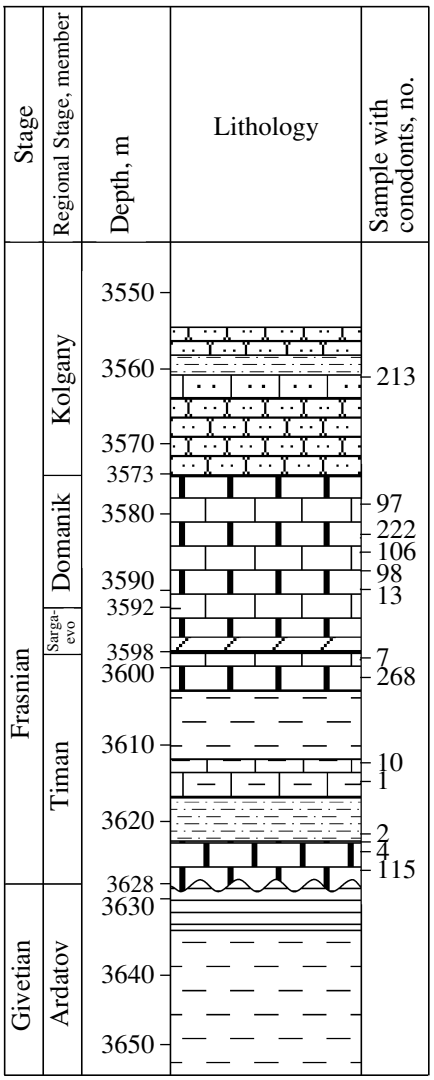


Fig. 9. Section of Givetian–Frasnian deposits in Shuvalovskaya, borehole no. 4.

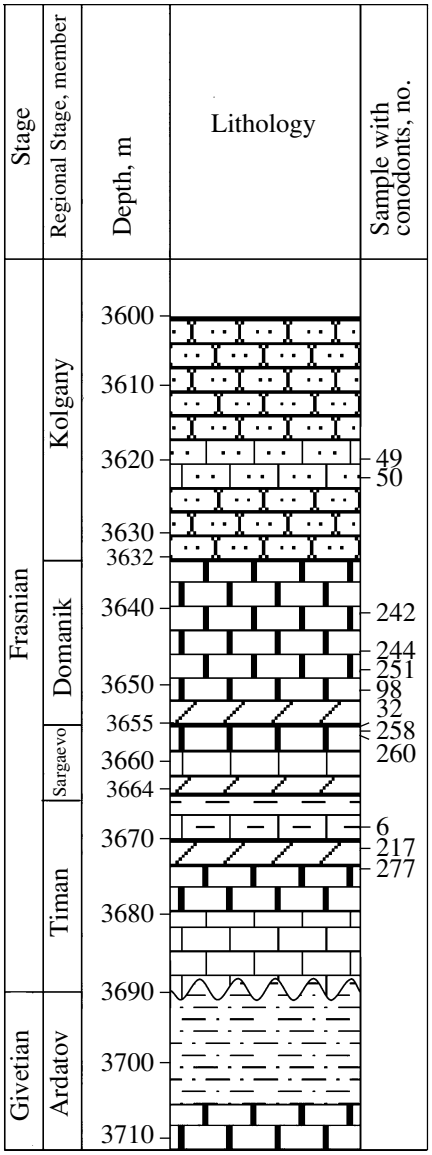


Fig. 10. Section of Givetian–Frasnian deposits in Shuvalovskaya, borehole no. 6.

Further south, in the Shuvalovskii area, the Timan Regional Stage rests unconformably on the Staryi Oskol deposits of the Givetian Stage. In the sections of boreholes 4, 6, and 19 (Figs. 9, 10, 11), it is represented by the domanikoid deposits containing ostracodes and conodonts. The Timan Regional Stage deposits are structured here in the following way: the lower part (12–13-m thick) is composed of thin interbedding of black coniconchous and microgranular, unevenly silicified, bituminous limestones; the middle part (13–14-m thick) is composed of thin interbedding of the same limestones, limestone-dolomitic marls, and argillites; similar limestones (1–2 m thick) constitute the top. The middle part of the Timan Regional Stage in borehole 6 (Fig. 10) consists of the interbedding of siltstones, argillites, rare limestones and marls; in the section of borehole 5 on the northern slope of the Sol'-Iletsk uplift, the Timan Regional Stage is represented by carbonate terrigenous rocks. The thickness of the regional stage varies from 27 to 32 m.

3.4.2. Sargaevo Regional Stage

In the northern part of the monocline, the regional stage is about 7–8 m thick and is composed of carbonate deposits. Further south, on the Kolgany area and in the section of Shuvalovskaya 5, it is composed of 3–15 m thick carbonate and carbonate terrigenous deposits, and in the sections of Shuvalovskaya 4 and 6 (Figs. 9, 10) it is composed of domanikoid deposits. The latter are represented by interbedding of inequigranular, unevenly pyritized, clayey, and slightly bituminous limestones and marls. The deposits are 5–8 m thick.

3.4.3. Domanik Regional Stage

The regional stage is represented by dark gray, almost black, platy, unevenly bituminous limestones with interbeds of marls. The thickness of deposits varies from 11 to 16 m in the northern part, reduces up to 3–6 m on the Kolgany area, and then increases further south up to 18–23 m (Shuvalovskaya 4, 6, and 19) (Figs. 9–11).

3.4.4. Mendym Regional Stage

In the northern part of the eastern Orenburg monocline, the regional stage is represented by 40 m thick limestones with interbeds of marls.

3.4.5. Kolgany Member

The thick (up to 170 m in the section of Shuvalovskaya 3) terrigenous Kolgany member is composed of coarse-grained sandstones transforming into gravelstones. It is developed on the south of the region, in the sections of the Shuvalovskii area between the top of the Domanik Regional Stage and the base of the Upper Famennian Substage (Shuvalovskaya 4, 6, and 19) (Figs. 9–11). On the Kolgany area, the member is composed of the interbedding of siltstones, limestones, and argillites. Here the member includes Mendym and partly Askyn deposits. The member is dated based on palynological data and also on the ostracodes and conodonts. The thickness of the member varies from 80 m in the section of Kolgany 4 and up to 30 m in the section of borehole 17 and 10–15 m in sections Kolgany 7, 21, and 22.

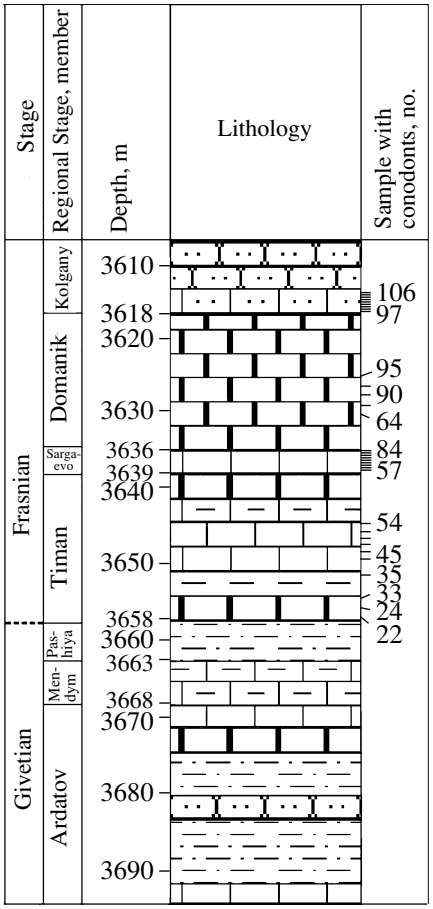


Fig. 11. Section of Givetian–Frasnian deposits in Shuvalovskaya borehole no. 19.

3.4.6. Askyn Regional Stage

In the northern part of the monocline, the horizon is represented by 35–40 m thick limestones with interbeds of marls. In the central part of the monocline on the Kolgany area, the limestones are gray, black in interbeds, microgranular, organoclastic, variously recrystallized and dolomitized; the lower part may be terrigenous (Kolgany 9 and 20). The age of the series is based on the ostracodes and conodonts.

On the south of the monocline, on the Shuvalovskii area, the Askyn deposits belong to the Kolgany series and are represented by terrigenous facies composed mainly of arks inequigranular sandstones and gravelstones.

The thickness of the Askyn deposits within the eastern Orenburg monocline varies from 35 to 40 m and decreases to 20 m in section Shuvalovskaya 5.

3.4.7. Lower Famennian

The lowermost part of the Famennian Stage (Volgograd Regional Stage) is established in section Romanovskaya 1 in the northern part of the monocline. In the central part of the monocline, the section is carbonate and consists of microgranular and spheroidally clotted limestones with subsidiary interbeds of marls; on the Shuvalovskii area, it is terrigenous carbonate and its lower part (20–30 m) is composed only of arkose sandstones with interbeds of marls.

3.5. Historical Review of the Study of Frasnian Conodonts of the Volga–Ural Province

The study of conodonts of the Volga–Ural province began in the 1970s. The possibility of using the zonal conodont scale (Ziegler, 1971) for the subdivision of the Upper Devonian deposits of the Volga–Ural region was confirmed by investigations conducted by Khalymbadzha and Chernysheva (1969, 1970); Khalymbadzha, (1981); Ovnatanova (1969, 1972, 1976; 1978); Ovnatanova and Makarova (1981); and Gubareva et al. (1980, 1985, 1988). It is worth noting that all of the above-mentioned papers subdivided the sections based on the conodont scale elaborated for the sections of the Rhenish Slate Mountains (Ziegler, 1971), except the lowermost Frasnian Stage and up to the lower part of the Domanik Regional Stage. The local conodont zones

Ancyrodella binodosa, Ancyrodella rotundiloba, and *Polygnathus timanicus* were distinguished in this interval in conformity with the peculiarities of conodont development during this period (Chernysheva and Khalymbadzha, 1978). The upper boundary of the local *Polygnathus timanicus* Zone coincided well with the top of the Upper *Polygnathus asymmetricus* Zone of the Rhenish Slate Mountains and thus all the following zones of Frasnian and Famennian stages could be stratigraphically allocated to it. The *Ancyrognathus triangularis, Palmatolepis gigas*, and *Palmatolepis triangularis* zones were distinguished within the Upper Frasnian deposits and the *crepida*, *rhomboidea*, and *marginifera* zones were distinguished in the lower part of the Famennian Stage. The Lower, Middle, and Upper *gigas* zones and the lower, middle, and upper *triangularis* zones were not distinguished during the first stage of conodont study due to the scanty core material and widely interpreted scope of some species (first of all *Palmatolepis subrecta, Pa. hassi*, and *Pa. foliacea*). It is known that at least the Lower and Middle *triangularis* zones (Ziegler, 1962a, 1971) were referred to the Frasnian Stage before the official establishment of the Frasnian–Famennian boundary at the base of *Palmatolepis triangularis* Zone in 1987.

Before the 1990s the conodont assemblages of the basinal part of the section in the Volga–Ural region overlying the Mendym Horizon were poorly known for various reasons (including scanty core material). Conodonts from the shallow-water Evlanovo–Livny deposits of the Volga–Ural province are represented mainly by poorly known polygnathid assemblages. Therefore a number of errors were made in the correlation with the conodont zonation (Khalymbadzha, 1981; Ovnatanova and Kononova, 1984).

3.6. Conodont Assemblages

Before proceeding to the characterization of the assemblages, it is worth noting that representative conodont assemblages are unknown from some levels of the Frasnian deposits of the Volga–Ural region (especially in the upper part of the section) due to the scanty core material and specific facies features. To make the conodont record of some levels more complete, we used conodont collections from some sections of the Volga–Ural province that are not considered here in full. The distribution of conodonts in the most completely studied sections is shown in Tables 3–11.

3.6.1. Frasnian Conodont Assemblages from the Shallow-Water Deposits of the Volga–Ural Province

Lower Timan conodont assemblage was studied in a very small number of localities of the Volga–Ural region. On the Tokmovo uplift, it was found in the section of Severnaya Filippovka 1 (interval 2215–2232 m), where it contains *Polygnathus xylus, Po. xylus* → *Po. praepolitus, Linguipolygnathus* sp. and rare *Icriodus expansus* and *Icriodus* ex. gr. *subterminus.* Isolated specimens of conodonts *Polygnathus varcus, Polygnathus webbi*, and *Icriodus nodosus* are known on the Zhigulev-Pugachev Arch (Spiridonovka borehole 3, interval 2964–2958 m).

The correlation of the Lower Timan assemblage with any of the existing conodont zones is impossible. The assemblage is dated as Givetian due to the absence of typically Frasnian species.

Upper Timan assemblage is slightly more diverse but also consists of polygnathids. On the Tokmovo uplift (Terengul 1, interval 2128–2131 m), *Po. ljaschenkoi, Po. alatus*, and *Po. xylus* were found; polygnathids *Polygnathus alatus, Po. xylus, Po. ljaschenkoi, Po. posterus, Po. angustidiscus*, and *Po. pennatus* presumably characterizing the Upper Timan assemblage were determined somewhat higher up the section (interval 2116–2131 m).

In the Nizhnekamskii downwarp (Prikazanskaya 120, interval 1695–1702 m) *Polygnathus xylus, Po. denisbricea,* and *Linguipolygnathus* sp. were found. *Po. pseudoxylus* was found in the section of borehole 125 (sample23, interval 1696.1–1692.1 m). *Polygnathus ljaschenkoi* was determined in Udmurtia (Reshetniki 250, interval 1715.3–1710.8 m).

Sargaevo assemblage. *Po. xylus, Po. pseudoxylus*, and *Po. ljaschenkoi* were identified in the section of Severnyi Kupol 142 (interval 1714.2–1710.8 m) of the Nizhnekamskii downwarp. *Linguipolygnathus* sp., *Polygnathus ljaschenkoi, Po. pennatus*, and *Klapperina ovalis* were found in borehole 127 (interval 1697–1694 m). *Ancyrodella rotundiloba* and *Mesotaxis asymmetricus* are known from the Vyatka system of dislocations (Syr'yany borehole 21, interval 1303.6–1308.3 m). In Prikazanskaya 120 (interval 1674–1679.6 m) of the Nizhnekamskii downwarp, this assemblage contains *Ancyrodella rugosa, Polygnathus xylus, Mesotaxis asymmetricus, M. falsiovalis, Klapperina ovalis*, and *Polygnathus dubius* and, upward in the section, *Ancyrodella alata, Palmatolepis transitans, Mesotaxis asymmetricus*, and *M. falsiovalis* (Table 8). *Po. xylus, Po. ljaschenkoi, Po. dubius*, and *Icriodus* sp. and isolated specimens of *Klapperina ovalis* and *Ancyrodella binodosa* were found in the section of Prikazanskaya 121 (interval 1691.7–1688 m).

The conodont assemblage of the non-stratified Middle–Upper Sargaevo part of the section is quite uniform. *Ancyrodella rotundiloba, Polygnathus pennatus, Po. pollocki, Mesotaxis asymmetricus, M. bogoslovskyi*, and *Klapperina ovalis* were found in the sections of the Prikazanskaya area (borehole 121, interval 1677.3–1671.1 m) and *Ancyrodella alata, Palmatolepis transitans, Mesotaxis asymmetricus, M. falsiovalis*, and *Polygnathus xylus* were determined in the upper part of the horizon, section of borehole 120 (interval 1676.6–1674 m). In the upper part of the section of borehole 127 (interval 1683–1661 m) *Palmatolepis*

Table 3. Distribution of conodonts in Semiluki–Voronezh deposits of the Frasnian Stage in Ulyanovsk (Okhotnich'ya) borehole no. 1

Regional stage, regional substage	Semiluki																Rechitsa			Lower Voronezh														Upper Voronezh		
Sample, no.	2	3	4	5	7	8	9	10	13	14	20	21	25	30	35	42	44	45	47	49	64	67	68	69	73	75	78	80	83	85	90	96	98	101	104	114
Depth, m	1898–1908									1887–1898							1875	1870	1869	1867	1839–1851	1829–1839												1817–1829		1806–1817
Species																																				
Icriodus symmetricus Br. et M.	x	x					x																													
Polygnathus xylus xylus Stauffer			x															x																		
Po. pseudoxylus Kononova et al.			x																																	
Po. pennatus Hinde				x																																
Po. azygomorphus Aristov										x		x	x																							
Po. pollocki Druce										x		x	x	x	x																					
Po. efimovae Kononova et al.												x	x	x	x	x																				
Po. pollocki ⟶ *Po. azygomorphus*													x																							
Po. praepolitus Kononova et al.													x						x																	
Mesotaxis asymmetricus Bisch. et Ziegler												x		x																						
Po. brevilamiformis Ovn.															x			x																		
Po. aspelundi Savage et Funai																	x		x																	
Po. subincompletus Ovn. et Kononova																			x					x												
Po. churkini Savage et Funai																				x																
Palmatolepis semichatovae Ovn.																				x	x		x	x	x	x	x	x	x		x	x	x			
Po. politus Ovn.																					x						x	x		x		x	x		x	
Po. aff. *maximovae* Ovn. et Kon.																						x														
Po. unicornis Müll. et Müll.																				x							x				x					
Po. ex. gr. *angustidiscus* Youngq.																												?x								
Po. alvenus Ovn. et Kon.																																		x		
Po. colliculosus Aristov																																				x
S elements				x	x	x		x	x	x	x			x																						

Table 4. Distribution of conodonts in Domanik–Mendym deposits of Prikazanskaya borehole no. 138

Regional stage	Domanik						Mendym											
Sample, no.	94	93	89	87	83	82	44	41	39	38	37	36	35	34	32	31	26	17
Depth, m / Species	1681–1685	1677–1681	1663–1665	1659–1663	1651–1655		1618–1621		1614–1618					1612–1614			1601–1606	1596–1600
Mesotaxis falsiovalis Sand., Ziegl. et Bult.	x	x																
M. johnsoni Kl., Kuzm. et Ovn.		x	x															
M. falsiovalis ⟶ *Pa. transitans*	x	x																
Palmatolepis transitans Müll.	x		x															
Polygnathus vjalovi Zver.	x																	
Po. dubius (Hinde)	x	x	x															
Po. uchtensis Ovn. et Kuzm.	x		x															
Po. xylus Stauf.	x																	
M. asymmetricus (Bisch. et Z.)	x	x																
Po. pollocki Druce	x	x																
Po. timanicus Ovn.	x																	
Pa. punctata (Hinde)			x	x		x												
Pa. bohemica Kl. et Fost.				x														
Po. sp.			x															
Icriodus symmetricus Br. et M.			x															
Pa. ormistoni Kl. Kuzm. et Ovn.				x	x	x												
Pa. domanicensis Ovn.				x	x	x												
Pa. lyaiolensis Khrusch. et Kuzm.										x								
Pa. proversa Ziegler					x	x												
Po. praepolitus Kon. et al.							x											
Pa. kireevae Ovn.										x					x			
Po. politus Ovn.										x				x				
Pa. sp. indet.											x	x						x
Pa. muelleri Kl. et Fost.										x		x						
Po. subincompletus Ovn. et Kon.										x		x	x	x				
Po. maximovae Ovn. et Kon.													x			x	x	
Pa. timanensis Kl., Kuzm. et Ovn.											x	x	x					
Belodella sp.												x						
Po. aff. *maximovae* Ovn. et Kon.															x			
Po. ex. gr. *angustidiscus* Young												x			x			x
Pb elements							x			x								
M elements	x						x											
S elements	x				x		x											

transitans, Polygnathus xylus, and *Mesotaxis asymmetricus* were identified. Section of Melekess borehole 1 (interval 2112.3–2096.3 m) contains *Icriodus symmetricus*, *Mesotaxis asymmetricus, M. falsiovalis, Klapperina ovalis, Polygnathus pennatus*, and *Po. angustidiscus* → *Po. posterus*. The unrepresentative assemblages of the last two sections probably result from the scanty core material, which was used for conodont determination. The conodont assemblage of the middle and upper parts of the Sargaevo Regional Stage was also studied

Table 5. Distribution of conodonts in Frasnian–Lower Famennian deposits of Melekess borehole no. 1

Stage	Frasnian																Famennian	
Regional stage	Sargaevo										Domanik	Askyn					Zadonsk–Elets	
Sample, no.	30	33	35	36	37	41	42	51	53	60	68	69	70	72	75	94	93	97
Depth, m	2112–2116	2108–2112				2104–2108		2104	2099	2096–2099	2085–2089	2048–2053	2041–2048		2035–2041	2018–2024		
Icriodus symmetricus Br. et M.	x																	
Mesotaxis asymmetricus (Bisch. et Z.)		x	x	x		x				x								
Klapperina ovalis (Ziegl. et Klap.)				x														
Polygnathus angustidiscus ⟶ *Po. posterus*					x													
Po. pennatus Hinde					x			x										
Po. aff. *sculptilis* Kuzm.					x													
Palmatolepis kireevae Ovn.											x	x	x					
Pa. gyrata Kuzm.												x						
Pa. jamieae Ziegler et Sandberg													x					
Pa. foliacea Youngquist														x		x		
Pa. sp.														x				
Pa. subrecta Miller et Youngquist												x				x		
Po. krestovnikovi Ovn.															x			
Po. maximovae Ovn. et Kon.																x		
Pa. minuta Br. et M.																		x
Pa. glabra Ulrich et Bassler																	x	
Pa. distorta Br. et M.																		
Po. sp.															x			
S elements							x	x				x						
Pb element								x	x									

in the Nema arch of the Kirov Region (Rekhino 9, interval 2055.7–2043 m; Uni 3, interval 1960–1964 m) and in the northern Verkhnekamskaya depression of Udmurtia (Krasnogor'e 95, interval 2041–2037 m). *Ancyrodella alata, Icriodus symmetricus, Mesotaxis asymmetricus, M. falsiovalis,* and *Klapperina ovalis* were found in all samples studied from these localities. The presence of *Polygnathus reimersi* at this level (Uni 3, interval 1960–1964 m) is quite important as it is widespread in the synchronous deposits of the central Russian Platform together with *Ancyrodella alata* and *Mesotaxis asymmetricus.*

In the upper part of the regional stage within the eastern Orenburg monocline, *Ancyrodella alata, Palmatolepis transitans, Mesotaxis asymmetricus, M. falsiovalis, M. dengleri, Polygnathus dubius*, and *Klapperina ovalis* were found in the sections of the Kolgany (borehole 7, interval 3437–3439 m, borehole 21, interval 3417–3422 m). Although the coring was minimal on the Shuvalovskii area and the regional stage is 5–8 m thick there, a relatively representative assemblage was identified, probably from the lowermost part of the regional stage in the section of borehole 19 (Table 9): *Mesotaxis asymmetricus* and *M. falsiovalis* were found together with *Polygnathus xylus, Po. alatus, Po. ljaschenkoi, Po. dubius*, and *Po. pollocki.*

The Sargaevo assemblage in the lower part of the section is generally characterized by *Polygnathus alatus, Po. dubius, Po. xylus, Po. pseudoxylus, Po. webbi, Po. pennatus, Po. ljaschenkoi, Po. posterus*, and isolated specimens of *Klapperina ovalis, Ancyrodella binodosa, Ancyrodella rotundiloba*, and *Mesotaxis asymmetricus.* The appearance of the latter is probably connected with the deepening of the basin at different

Table 6. Distribution of conodonts in Frasnian deposits of Severnyi Kupol borehole no. 166

Regional stage	Domanik			Mendym							Askyn	
Sample, no.	59	55	54	48	47	46	44	43	42	41	38	32
Depth, m / Species	1578–1589	1575–1578	1571–1575	1563–1567				1559–1563			1556–1559	1548–1552
Polygnathus pseudoxylus Kon. et al.	x											
Po. timanicus Ovn.	x	x										
Ancyrodella mouravieffi Garcia-Lopez	x	x										
Icriodus symmetricus Br. et M.	x	x										
Mesotaxis johnsoni Kl., Kuzm. et Ovn.		x										
Ad. sp. indet.		x										
Po. decorosus St.		x										
Pa. kireevae Ovn.			x					x	x			
Ad. nodosa Ulrich et Bassler			cf		x							
Pa. semichatovae Ovn.				x	x	x	x					
Pa. timanensis Klap., Kuzm. et Ovn.				x	x				x		x	x
Pa. ormistoni Klap., Kuzm. et Ovn.				x	x			x			x	
Pa. ljaschenkoae Ovn.				x	x							
Pa. hassi Müll. et Müll.				x				x		x		
Pa. plana Z. et Sandb.					x							
Ancyrognathus triangularis San.					x							
Pa. aff. *delicatula* Br. et M.									x			
Pa. foliacea Youngq.											x	
Pa. ex gr. *rhenana* Bishoff											x	

periods of the Sargaevo time. The assemblage of the middle and upper parts of the Sargaevo Regional Stage is characterized by the appearance of *Polygnathus pollocki* and *Ancyrodella alata* in the middle part and *Palmatolepis transitans* in the uppermost Sargaevo Regional Stage.

The assemblages listed above provide a correlation of the Sargaevo Regional Stage with the Lower *asymmetricus* Zone of the previous scale (Ziegler, 1971) and possibly with the part of the Lowermost *asymmetrica* Zone by the position in the section. The upper part of the Sargaevo Regional Stage is undoubtedly correlated with the *transitans* Zone of Ziegler and Sandberg's scale (1990). The lower and middle parts of the Sargaevo Regional Stage are provisionally referred to the Late *falsiovalis* Zone.

Semiluki assemblage. The sharp differentiation of sections that is observed beginning with the Domanik level is especially pronounced in the Semiluki Regional Stage on the Tokmovo uplift, where a sequence very similar to the stratotype section of the Semiluki Regional Stage in the Central Devonian Field was revealed. Unfortunately, the available material on conodont distribution is rather scanty.

In the lower part of the section of Ulyanovskaya 1 (interval 1898–1908 m, earlier interpreted as Rudkino beds), the assemblage is composed of *Icriodus symmetricus, Polygnathus pennatus, Po. efimovae, Po. xylus*, and *Po. pseudoxylus. Mesotaxis asymmetricus, Polygnathus brevilamiformis, Po. azygomorphus, Po. efimovae, Po. praepolitus, Po. pollocki*, and *Po. pollocki* → *Po. azygomorphus* were identified in the interval 1887.7–1898.5 m. *Po. efimovae* was found at the depth of 1878–1887.7 m.

Polygnathus brevilamiformis and *Palmatolepis transitans* were identified in the lowermost Semiluki Regional Stage of the section of Terengul 1 (interval 2092–2100 m).

It is important that *Polygnathus brevilamiformis, Po. efimovae*, and *Po. praepolitus* appear in the lowermost part of the section. Although the records of *Mesotaxis asymmetricus* are rare, their presence up to the top of the Semiluki Regional Stage is also significant.

Rechitsa assemblage is poorly known. *Po. xylus, Po. praepolitus*, and *Polygnathus brevilamiformis* are still present and *Polygnathus subincompletus* and

Table 7. Distribution of conodonts in Mendym–Askyn deposits of the Frasnian and Lower Famennian Stages in Severnyi Kupol borehole no. 71

Substage, regional stage	Mendym							Askyn										Lower Famennian				
Sample, no.	92	112	79	76	71	66	48	65	64	63	62	60	59	58	57	53	52	41	33	32	31	28
Depth, m	1691–1697	1680–1685	1666–1669	1662–1666	1659–1662	1651–1654		1649–1651				1646–1649		1642–1649				1622–1626	1607–1611			1600–1604
Species																						
Pa. semichatovae Ovn.	x	x				x							x			x						
Polygnathus lodinensis Pölster	x	x							x	x	x				x							
Palmatolepis proversa Ziegler	x	x																				
Pa. plana Z. et Sandb.		x																				
Pa. anzhelae Khrustcheva et Kuzm.		x																				
Pa. barba Ziegler et Sandberg		x		x	x																	
Pa. timanensis Klap., Kuzm. et Ovn.		x		x	x	x	x		x	x	x											
Pa. mucronata Klap., Kuzm. et Ovn.		x								x					x							
Pa. muelleri Klap. et Foster		x	x	x					x	x	x	x	x									
Pa. kireevae Ovn.	x			x		x			x	x	x		x			x						
Pa. ormistoni Klap., Kuzm. et Ovn.				x									x									
Po. xylus Stauffer				x																		
Po. maximovae Ovn. et Kononova				x		x																
Pa. menneri sp. nov.				x	x																	
Pa. elegantula Ji				x	x																	
Pa. ljaschenkoae Ovn.	x			x		x																
Pa. orbicularis Ovn. et Kuzm.						x																
Pa. hassi Müll. et Müll.						x		x	x	x					x	x						
Icriodus interjectus Kuzm. et Ovn.						x																
Po. subincompletus Ovn. et Kononova						x																
Pa. ederi Ziegler et Sandberg							x				x	x	x									
Pa. brevis Ziegler et Sandberg							x		x	x		x	x	x								
Pa. gyrata Kuzm. et Meln.								x	x		x	x	x		x		x					
Po. krestovnikovi Ovn.						x		x	x													
Pa. subrecta Mill. et Youngq.									x	x	x		x		x	x	x					
Pa. foliacea Youngq.									x	x												
Pa. orlovi Khr. et Kuzm.									x	x			x		x	x	x					
Belodella sp.									x	x												
Po. macilentus Kuzm.										x												
Po. politus Ovn.										x												
Ancyrodella nodosa Ulrich et Bassler										x	x		x			x						
Pa. praetriangularis Ziegl. et Sandb.											x		x			x						
Pa. nasuta Müll.												x	x	x	x							
Pa. lyaiolensis Khrustcheva et Kuzm.						x						x	x		x							
Pa. rhenana Bishoff													x		x	x						
Pa. jamieae Ziegler et Sandberg										x			x			x						
Pa. juntianensis Han													x	x								
Pa. rotunda Ziegler et Sandberg													x									
Po. brevis Mill. et Youngq.										x	x		x		x							
A. ioides Ziegler													x									
Pa. minuta minuta B. et M.																		x	x	x		
Pa. glabra Ulrich et Bassler																			x	x		
Pa. glabra acuta Helms																					x	
Pa. glabra prima Ziegler et Huddle																						x
Pa. glabra lepta Ziegler et Huddle																						x
Pb elements	x		x					x	x	x	x											
M elements	x					x																
S elements	x					x	x	x					x									

Table 8. Distribution of conodonts in Upper Devonian deposits of Prikazanskaya boreholes nos. 120 and 121

Borehole	120																	121										
Stage	Frasnian															Famennian		Frasnian										Famennian
Regional stage	Timan	Sargaevo					Domanik			Mendym				Bottom of the Askyn		Volgograd	Zadonsk	Sargaevo						Domanik				Zadonsk
Sample, no.	64	67	69	66	70	90	93	95	100	118	120	127	135	131	132	164	191	23	30	37	42	59	64	67	71	81	118	174
Depth, m	1695–1702	1695–1700	1685–1690	1677–1679	1674–1676	1669–1674	1659–1662		1645–1650	1630–1633			1624.8–1627	1604–1610	1604–1607	1587–1591.7	1555–1560	1688–1692		1684–1688.2	1680.8–1684	1674.8–1677	1671–1674.8	1667–1671	1667–1669	1655.6–1659.6	1627–1632	1559–1563.7
Species																												
Polygnathus xylus Stauf.	x	x	x		x		x											x										
Linguipolygnathus sp.	x																											
Po. denisbriceae Bult.	x																											
Ad. rugosa Br. et M.		x	x																									
Mesotaxis asymmetricus Bisch. et Ziegl.		x	x	x	x	x	x	x													x	x		x	x			
Klapperina ovalis (Ziegl. et Kl.)		x	x		x	x		x											x			x						
Po. dubius (Hinde)		x																			x							
M. falsiovalis Sandb., Ziegl. et Bult.					x																					x		
Ad. alata Glen. et Kl.					x	x																						
Palmatolepis transitans Müll.					x	x																						
Po. timanicus Ovn.							x																	x				
Pa. punctata (Hinde)									x																			
Pa. kireevae Ovn.									x	x	x	x																
Pa. proversa Ziegl.									x	x	x		x														x	
Pa. hassi Müll. et Müll.											x	x																
Pa. timanensis Kl., Kuzm. et Ovn.											x	x			x													
Pa. ljaschenkoae Ovn.													x	x	x												x	
Pa. ormistoni Kl., Kuzm. et Ovn.													x															
Pa. mucronata Kl., Kuzm. et Ovn.														x														
Pa. subrecta Mill. et Young.														x	x													
Pa. ederi Ziegl. et Sandb.															x													
Pa. orlovi Khr. et Kuzm.															x													
Pa. subperlobata subperlobata Br. et M.																x												x
Pa. triangularis San.																x												
Pa. delicatula Br. et M.																x												
Pa. minuta minuta Br. et M.																	x											
Pa. quadrantinodosalobata San.																	x											
Po. ljaschenkoi Kuzm.																		x										
Icriodus sp.																		x	x									
Ancyrodella binodosa Uyeno																		x										
Ad. sp. indet.																				x			x					
Ad. rotundiloba Bryant																						xcf						
Po. pennatus (Hinde)																							x					
M. bogoslovskyi Ovn. et Kuzm.																							x					
Po. pollocki Druce																							x					
Po. reimersi Kuzm.																							x					
Pa. domanicensis Ovn.																											x	
Pa. glabra prima Ziegl. et Huddle																												x
S elements													x					x	x			x		x				

Table 9. Distribution of conodonts in Frasnian deposits of Shuvalovskaya borehole no. 19; (RW) reworked conodonts

Regional stage, substage, member	Upper Timan								Sargaevo											Domanik						Kolgany								
Sample, no.	22	24	33	35	45	50	52	54	57	59	60	65	65a	68	69	78	80	81	84	64	90	91	92	93	95	97	99	101	102	102a	103	104	105	106
Depth, m	3657–3660		3651–3657		3643–3649										3639–3643			3633–3639		3625–3633					3617–3625	3610–3617								
Species																																		
Polygnathus dubius (Hinde)	cf. x												x	x						x							x		x					x
Po. pollocki Druce													x	x																				
Po. ljaschenkoi Kuzm.			x	x			x			x	x																							
Po. praepolitus Kon. et al.				x																														
Po. xylus ⟶ *Po. pollocki*				x																														
Po. xylus Stauf.				3			x			x	x			x																				
Icriodus sp.				x	x	x											x				x													
Po. denisbriceae Bult.				x																														
Po. webbi Stauf.																				x														
Belodella sp.								x																										
Mesotaxis dengleri Bish. et Z.									x				x																					
Po. alatus Huddle										x		x		x																				
Po. pennatus Hinde				x										x							x													
Po. pseudoxylus Kon. et al.											x			x																				
Ozarkodina semialternans Z.															x		x	x	x															
M. falsiovalis S., Z. et Bult.																	x		x		x		x											
Pa. triquetra Kuzm.																				x														
Pa. maximovae Kuzm.																				x														
Pa. punctata (Hinde)																				x							x						cf. x	
Pa. ormistoni Kl., Kuzm. et Ovn.																				x							x							
Pa. sp. indet.																				x														
"*Po. foliatus*" Bryant																				x														
Po. brevilamiformis Ovn.																				x	x													
M. sp. indet.																x				x														
Po. sp. indet.										x		x		x									x					x	x	x	x		x	

Table 9. (Contd.)

Regional stage, substage, member	Upper Timan								Sargaevo											Domanik						Kolgany								
Sample, no.	22	24	33	35	45	50	52	54	57	59	60	65	65a	68	69	78	80	81	84	64	90	91	92	93	95	97	99	101	102	102a	103	104	105	106
Depth, m / Species	3657–3660		3651–3657		3643–3649										3639–3643			3633–3639		3625–3633					3617–3625	3610–3617								
Ancyrodella rugosa Br. et M.																					x													
M. bogoslovskyi Ovn. et Kuzm.																					x													
I. symmetricus Br. et M.																					x	x	x	x			x	x				x		x
A. alata Glen. et Klap.																					x					RW	x							
M. asymmetricus Bish. et Z.										x											x	x	x											
M. johnsoni Kl., Kuzm. et Ovn.																					x													
Po. timanicus Ovn.																					x		x											
Po. uchtensis ⟶ *Po. timanicus*																							x											
Po. vjalovi Zvereva																							x											
I. sp.				x	x																		x											
Ancyrognathus ancyrognathoideus Z.																							x											
Po. uchtensis Ovn. et Kuzm.																				x	x		x		x	x		x						
Po. siratchoicus Ovn. et Kuzm.																										x	x	x	x	x		x	x	x
Pa. timanensis Kl., Kuzm. et Ovn.																					x					x								
Po. decorosus Stauf.																										x	x				x	x	x	x
Pa. ederi Z. et Sandb.																											x		x	x				x
Po. aequalis Kl. et Lane																											1							
Pa. proversa Z.																												x						
Po. aspelundi Sav. et Fun.																												x						
Po. seraphimae Ovn. et Kon.																												x						
Po. sp.			x										x														x							
Pb elements												x	x		x					x	x	x	x			x	x		x					x
S elements								x									x			x	x	x	x			x	x		x					x
Gen. et sp. indet.		x	x	x	x	x		x	x	x		x	x	x		x	x	x		x	x	x	x		x	x	x	x	x	x		x	x	x

Table 10. Distribution of conodonts in Frasnian deposits of Shuvalovskaya borehole no. 4; (RW) reworked conodonts

Regional stage, member	Timan								Domanik					Kolgany
Sample, no.	115	4	3	2	1	10	268	7	13	98	106	222	97	213
Depth, m / Species	3618–3626				3604–3618				3589–3593				3582–3589	3560–3567
Polygnathus xylus Stauffer	x	x	x		x	x	x							
Po. alatus Huddle							x							
Po. denisbriceae Bult.					x									
Schmidtognathus sp.		x												
Linguipolygnathus sp.			x											
Ancyrodella binodosa Uyeno				x			x							
Po. (?) *cristatus* Hinde					x									
Icriodus sp.					x		x							
Po. ljaschenkoi Kuzm.					x									
Po. cristatus Hinde					x									
Po. pennatus (Hinde)							x							
Po. uchtensis Ovn. et Kuzm.									x	x			x	
I. symmetricus Br. et M.									x	x	x		x	x
Po. timanicus Ovn.									x	x	x			
Mesotaxis asymmetricus Bisch. et Z.									x	x	x			xRW
M. johnsoni Kl., Kuzm. et Ovn.										x	x			
Klapperina ovalis (Z. et Kl.)									x	x				
Po. pollocki Dr.										x				
Palmatolepis transitans Müll.										x		x	x	
Po. brevilamiformis Ovn.										x	x		x	
Belodells sp.										x				
M. sp. indet.										x	x			
M. falsiovalis S., Z. et Bult.											x			
Pa. gutta Kuzm.												x		
Pa. punctata (Hinde)													x	
Po. praepolitus Kon. et al.													x	
Po. evidens Kl. et Lane														x
"Po. foliatus" Bryant														x
Po. seraphimae Ovn. et Kon.														x
Po. sp.			x								x			x
Pb elements					x		x			x	x			
S elements			x		x	x	x	x		x	x			
Gen. et sp. indet.			x	x	x					x	x			

Po. aspelundi appear in the section of Ulyanovskaya 1 (interval 1866–1878 m) of the Tokmovo uplift.

Voronezh assemblage. *Polygnathus churkini, Po. politus*, and *Po. subincompletus* were identified in the section of Ulyanovskaya 1 (interval 1851–1866 m) on the slope of Tokmovo uplift in the Lower Voronezh shallow-water deposits. *Palmatolepis semichatovae* is present in all samples from that interval. *Polygnathus subincompletus, Po. politus, Po. unicornis,* and *Palmatolepis semichatovae* were found upward in the section (interval 1829–1839 m). In the section of Turmysh 1-P

Table 11. Distribution of conodonts in Frasnian deposits of Shuvalovskaya borehole no. 6; (RW) reworked conodonts

Regional stage, substage, member	Timan		Sargaevo			Domanik					Kolgany	
Sample, no.	277	6	260	258	32	98	251	244	242	1	49	50
Depth, m / Species	3670–3674	3661–3665	3651–3655			3645–3651			3639–3645		3619–3624	
Polygnathus denisbriceae Bult.	x											
Po. xylus Stauf.	x											
Ancyrodella binodosa Uyeno		x										
A. alata Glen. et Klap.			x	x								
Mesotaxis falsiovalis Sandb., Ziegl. et Bult.				x		x		x				
M. asymmetricus Bisch. et Ziegl.				x		x	x	x	cf. x		x RW	
Palmatolepis punctata (Hinde)						x						
Po. pollocki Druce						x						
Pa. proversa Ziegl.											x	
Po. evidens Kl. et Lane											x	
Po. imparilis Kl. et Lane											x	
Mesotaxis bogoslovskyi Ovn. et Kuzm.										x		RW x
Pa. sp. indet.					x							
Pb elements			x	x								
S elements			x							1		
Gen. et sp. indet.			x	x	x						x	

(interval 1550–1570 m), the presence of *Palmatolepis semichatovae* and *Po. subincompletus* testify to the Voronezh age of the deposits. *Po. alvenus, Po. colliculosus*, and *Po. politus* were found in the upper part of the Voronezh Regional Stage (Ulyanovskaya 1, interval 1806–1829 m).

The small specimens of *Palmatolepis proversa* and *Pa. punctata* were found in the section of Prikazanskaya 113 (interval 1613–1621 m) of the Tatar arch against a background of *Polygnathus churkini, Po. politus, Po. praepolitus, Po. evidens*, *Po. colliculosus*, and *Po. krestovnikovi* in the upper part of the section and isolated representatives of *Ancyrodella* and *Belodella*. Within the eastern Orenburg monocline, the base of the Kolgany Member (Shuvalovskii area) overlies the deposits of the Domanik Regional Stage and is composed mainly of coarse-grained sandstones transforming into gravelstones. *Polygnathus siratchoicus, Po. evidens, Po. seraphimae*, and also *Icriodus symmetricus* were identified in the rare interbeds of limestone (Shuvalovskaya 4, interval 3560–3567 m) (Table 10). *Palmatolepis proversa, Polygnathus evidens*, and *Po. imparilis* (Table 11) were found in the section of borehole 6 (interval 3619–3624 m). *Icriodus symmetricus, Polygnathus siratchoicus, Po. seraphimae*, and *Po. krestovnikovi* along with small *Palmatolepis ederi, Pa. proversa, Pa. timanensis*, and *Pa. ormistoni* were discovered in the section of borehole 19 (interval 3610–3617 m) (Table 9).

Palmatolepis hassi and *Palmatolepis* cf. *nasuta* are present at the base of the Kolgany Member of the Kolgany area (borehole 17, interval 3369–3374 m). *Palmatolepis semichatovae, Ancyrognathus triangularis*, and *Ancyrodella gigas* were also found (borehole 23, interval 3363–3370 m).

Evlanovo and Livny assemblages. The coring was poor and facies were unfavorable for conodont presence in this part of the section. Thus the data on conodonts are scanty here. In essence, the available limited information was only obtained from the deposits of the Evlanovo Regional Stage. Data on the Livny Regional Stage of the Volga–Ural region are almost absent. The rock samples from the Tokmovo and Tatar arches yielded almost no conodonts. Only isolated records of *Po. krestovnikovi* were made in the Evlanovo deposits (Prikazanskaya 113, interval 1565–1561 m).

On the southeast of the platform, *Polygnathus brevis* was found in the Kolgany Member (Kolgany 17, interval 3360–3365 m) within the eastern Orenburg monocline. *Palmatolepis subrecta* and *Polygnathus unicornis, Po. brevis,* and *Polygnathus politus* were identified in deposits overlying the Kolgany Member, the range of which is reduced here (borehole 17, interval 3275–3280 m). Polygnathids *Polygnathus krestovnik-*

Table 12. Distribution of conodonts in shallow-water Frasnian and Lower Famennian deposits of the Volga–Ural Province

Species \ Regional stage	Timan (upper part)	Sargaevo	Semiluki	Rechitsa	Voronezh	Evlanovo	Livny	Zadonsk
Polygnathus webbi Stauf.	———							
Po. xylus Stauf.	- - -	- - -	———	———				
Po. alatus Huddle	- - -	———						
Po. ljaschenkoi Kuzm.	———	———						
Po. posterus Kuzm.		———						
Po. pennatus Hinde	- - -	———	———					
Po. angustidiscus Young s. l.		———	———					
Po. pseudoxylus Kon. et al.		- - -	———					
Po. denisbriceae Bult.	———	———						
Po. pollocki Druce			———					
Ancyrodella alata Glen. et Kl.		———						
Mesotaxis asymmetricus (Bisch. et Z.)		- - -	———					
Palmatolepis transitans Müller		———						
Polygnathus dubius Hinde sensu Kl. et Ph.			- - -	- - -	———			
Po. ilmenensis Zhuravlev			———					
Po. reimersi Kuzm.		———						
Po. praepolitus Kon. et al.			———	———	———			
Po. efimovae Kon. et al.			———					
Po. brevilamiformis Ovn.			———	———				
Po. azygomorphus Aristov			———					
Po. aspelundi Sav. et Fun.			———	———	———			
Po. aequalis Kl. et Lane			- - -	- - -	———			
Po. subincompletus Ovn. et Kon.				———	———			
Po. churkini Sav. et Fun.				———	———			
Po. unicornis Müll. et Müll.					———			
Po. politus Ovn.					———	———	- - -	
Po. alvenus Ovn. et Kon.					———	———		
Po. evidens Kl. et Lane					———	———		
Po. colliculosus Aristov					———			
Po. imparilis Kl. et Lane					———			
Palmatolepis semichatovae Ovn.					———			
Pa. punctata (Hinde)					———			
Pa. proversa Z.					———			
Polygnathus maximovae Ovn. et Kon.					———	———		
Po. siratchoicus Ovn. et Kuzm.					———			
Po. seraphimae Ovn. et Kon.				- - -	———			
Po. krestovnikovi Ovn.					———	———	———	
Po. brevis Mil. et Young.						———	- - -	
Icriodus iowaensis Young. et Peter.								———
I. cornutus San.								———
Polygnathus brevilaminus Br. et M.								———
Pelekysgnathus planus San.								———
Palmatolepis wolskae Ovn.								———

ovi (borehole 21, interval 3329–3335 m) and *Po. brevis* are abundant in the Evlanovo deposits of the other sections of Kolgany area; isolated specimens of *Palmatolepis hassi* are also present.

Lower Famennian conodont assemblage was studied in the sections of the Volgograd Volga region (Galushin and Kononova, 2004) and contains *Icriodus iowaensis, I. cornutus, Polygnathus brevilaminus, Palmatolepis wolskae, Pa. circularis*, and *Pelekysgnathus planus.*

The distribution of conodonts in the shallow-shelf Frasnian and Lower Famennian deposits of the Volga–Ural province is shown in Table 12. The assemblages described have much in common with the sections of the central Russian Platform. Therefore the zonation previously outlined for this region may also be applicable to the shallow-shelf Frasnian sections of the Volga–Ural province.

3.6.2. Frasnian Conodont Assemblages from the Basinal Deposits of the Volga–Ural Province

Timan conodont assemblage. The assemblage is composed of *Ancyrodella binodosa, Polygnathus? cristatus*, and *Schmidtognathus hermanni*, along with *Po. pennatus, Po. dubius, "Po. foliatus," Po. ljaschenkoae*, etc., and was first established in the domanikoid deposits of the Timan Regional Stage in the sections of Shuvalovskii area of the eastern Orenburg Region. The distribution of conodonts in the sections of Shuvalovskii area is shown in Tables 9–11. We also recorded isolated *Schmidtognathus hermanni* in the sections of Bashkiria (Itkineevo borehole 1, interval 1961–1964 m; borehole 2, interval 2004–2007 m), where it was found together with "*Polygnathus foliatus*" and *Po. dubius*, and in Tatarstan (Bugrovskaya 13, interval 1831.2–1825.9 m; Prikazanskaya 125, interval 1696–1692 m). Isolated *Schmidtognathus hermanni* along with *"Polygnathus foliatus," Po. dubius, Icriodus nodosus*, and *I. expansus* were discovered in the north of the province in the Komi-Nenets Autonomous Okrug (Neopol'e borehole 2, interval 2016–2009 m) and in the Kirov Region (Uni, interval 1976–1980 m) that is probably connected with the deepening of the basin in separate intervals of the Late Timan time.

Sargaevo conodont assemblage. In contrast to shallow-shelf deposits, the sections, where interbeds of silicibituminous rocks are occasionally developed, contain an identical conodont assemblage. However, *Ancyrodella* and *Mesotaxis* species are more diverse and usually appear earlier in this assemblage in comparison with the shallow-shelf sections.

Domanik assemblage. Two radically different assemblages are identified within the Domanik Regional Stage. The first assemblage characterizes its lower part and the second assemblage characterizes the middle and upper parts of the regional stage. The Domanik assemblages were established in the sections of the Kirov, Kuibyshev, and Orenburg regions, and also in Udmurtia and Tatarstan. In the east and southeast of the Volga–Ural region, these assemblages were established in the sections of the Shuvalovskii area of the Orenburg Region (borehole 4, intervals 3589–3593 and 3582–3589 m; borehole 6, interval 3639–3651 m; borehole 17, interval 3605–3616 m; borehole 19, interval 3625–3633 m). The first assemblage in the section of borehole 6 (interval 3639–3651 m) is represented by *Mesotaxis asymmetricus, M. falsiovalis, Palmatolepis punctata*, and *Polygnathus pollocki.* The second assemblage in the section of borehole 17 (interval 3605–3616 m) is represented by *Ancyrognathus ancyrognathoideus, Palmatolepis punctata, Pa. kireevae, Polygnathus uchtensis*, and *Po. xylus. Polygnathus praepolitus* along with *Palmatolepis punctata* and *Pa. kireevae* were identified in the section of borehole 24 (interval 3661–3668 m). *Po. dubius* abounds there. Detailed lists of the conodont composition in boreholes 4 and 19 are shown in Tables 9 and 10. The second assemblage was also found in the north (Sharlyk borehole 1, interval 2753–2763 m) and in the Kolgany area of the central eastern Orenburg monocline (borehole 7, interval 3427–3432 m), where *Pa. kireevae, Pa. proversa, Pa. punctata, Ancyrodella gigas*, and *Ancyrognathus* sp. were determined. The richest first Domanik assemblage was established in the section of Tikhonovskaya 452 (interval 3589–3593 m) of the Buzuluk depression of the Orenburg Region, where *M. asymmetricus, Palmatolepis transitans, Po. efimovae, Po. timanicus, Po. pollocki, Po. dubius*, and *Po. brevilamiformis* were identified. The second assemblage was found upwards in the same interval. It includes *Palmatolepis punctata* and *Pa. kireevae* and completely lacks representatives of *Mesotaxis*.

In Tatarstan, the first Domanik assemblage was established in Prikazanskaya 69 (interval 1689.7–1686.2 m), 138 (interval 1681–1677 m), 121 (interval 1659–1655 m), 127 (interval 1640–1624 m), 138 (interval 1663–1685 m), and in the section of Severnyi Kupol 166 (interval 1575–1579 m). The second Domanik assemblage was recorded in the sections of Prikazanskaya 138 (interval 1651–1655 m), 120 (interval 1645–1650 m), 121 (interval 1632–1627 m), and also in the section of Severnyi Kupol 166 (interval 1571–1575 m). The distribution of conodonts in the deposits of Domanik regional stage in boreholes 138 and 166 is shown in Tables 4 and 6. The richest first assemblage in the section of the Prikazanskaya 69 (interval 1689.7–1686.2 m) includes *Mesotaxis asymmetricus, M. johnsoni, M. costalliformis, M. bogoslovskyi, Palmatolepis transitans, Palmatolepis punctata, Polygnathus pollocki, Po. efimovae, Po. timanicus, Po. xylus*, and *Po. azygomorphus.*

In the Kirov Region (Uni 3, interval 1938–1945 m), *Mesotaxis asymmetricus, Polygnathus pollocki, Po. ilmenensis*, and *Po. timanicus* were found. *Polygnathus rudkinensis* was recorded for the first time in the

first Domanik assemblage of the section of Rekhino 9 (interval 2034–2038 m). It was earlier described from the Rudkino beds and was unknown outside the central Russian Platform.

The Domanik Regional Stage was for a long time correlated with the Middle–Upper *asymmetricus–Ancyrognathus triangularis* zones of the conodont scale (Ziegler, 1971).

Mendym assemblage. The most representative assemblages of the Mendym Regional Stage were found and studied in the sections of borehole 166 (interval 1567–1559 m) and Severnyi Kupol 71 (interval 1680–1651 m) of the Tatar arch in Tatarstan. Detail lists of faunal changes with depth of these two sections are shown in Tables 6 and 7. It is very significant that *Palmatolepis semichatovae, Ancyrognathus triangularis, Palmatolepis anzhelae,* and *Pa. timanensis* along with rare but typical *Palmatolepis hassi* appear in these sections. The Mendym assemblage was also recorded in Prikazanskaya 120 (interval 1624.8–1633 m), where it includes *Palmatolepis hassi, Pa. ljaschenkoae, Pa. ormistoni*, and *Pa. timanensis*, and in the section of Severnyi Kupol 220 (interval 1578.9–1593 m), where *Ancyrognathus triangularis, Palmatolepis hassi, Pa. muelleri, Pa. timanensis, Pa. brevis*, and the only polygnathid *Polygnathus lodinensis* were found. *Palmatolepis proversa, Pa. barba, Pa. mucronata, Pa. domanicensis, Pa. ormistoni, Pa. orbicularis, Pa. ederi*, and *Pa. ljaschenkoae* along with *Belodella* sp. were identified in the section of Prikazanskaya 115 (interval 1649–1647 m). Many palmatolepids are small. Rare and isolated *Palmatolepis hassi, Pa. proversa, Pa. timanensis*, and *Pa. kireevae* (often small and poorly preserved) together with polygnathids *Polygnathus politus* and *Po.* aff. *brevilamiformis* were found in the lower part of the section of borehole 138 (interval 1614–1618 m). Palmatolepids almost disappear upward the section as the basin was becoming shallower, and the assemblage becomes mainly polygnathid; rare *Belodella* sp. are also present (Prikazanskaya 138, depth 1614 m, Table 4). Subsequently a shallow-water environment with accumulation of carbonate and clayey-carbonate oozes settled here.

Palmatolepis ljaschenkoae, Pa. kireevae, Pa. barba, and *Pa. mucronata* were identified in the section of the Mullovka borehole 50 (interval 2024–2027 m).

In the Orenburg Region (Malakhovskaya 400, interval 3245–3252 m), the Mendym assemblage is composed of *Palmatolepis hassi, Pa. ormistoni, Pa. kireevae, Pa. semichatovae*, and *Polygnathus krestovnikovi.* In the section of Zarinskaya 350 (interval 3591–3600 m), it comprises *Ancyrodella nodosa, Ancyrognathus asymmetricus, Icriodus symmetricus, Palmatolepis punctata, Pa. hassi, Pa. proversa*, *Pa.* ex. gr. *gigas*, *Polygnathus unicornis*, and *Po. dubius.*

In the northern and northeastern regions of the Volga–Ural province (Udmurtia and Kirov Region), the Mendym conodont assemblage was established in the sections of Krasnogor'e 91, Chutyr' 152, and Rekhino 9. *Ancyrognathus triangularis, Pa. ljaschenkoae, Pa. punctata, Pa. semichatovae, Pa. kireevae, Polygnathus* aff. *brevilamiformis*, and *Po. unicornis* were found in the Krasnogor'e 91 (interval 2010–2013 m). *Pa. ormistoni* and *Po. unicornis* were found slightly up the section (borehole 91, interval 2005–2008 m). The Mendym assemblage of Chutyr' 152 (interval 2093–2096 m) contains *Pa. ormistoni, Pa. semichatovae, Pa. kireevae*, and *Polygnathus brevilamiformis. Polygnathus praepolitus, Po. krestovnikovi, Po. praepolitus* → *Po. maximovae, Po. webbi* → *Po. zinaidae*, together with *Pa. semichatovae, Pa. kireevae, Pa. ederi,* and *Pa. proversa* typical of the Mendym assemblage were identified in the Rekhino 9 (interval 2016–2020 m).

Based mainly on the presence of *Palmatolepis semichatovae*, the Mendym assemblage was earlier correlated with the Lower *gigas* Zone and then with the Early *rhenana* Zone.

Askyn assemblage. The coring of these intervals in the territory studied was poor and therefore the conodonts are not numerous here. In Tatarstan, conodonts from the section of the Severnyi Kupol 71 (interval 1646–1656 m) and 166 (interval 1548–1562 m) were studied. The distribution of conodonts in these boreholes is shown in Tables 6 and 7. Here we shall only notice that *Palmatolepis subrecta, Pa. jamieae, Pa. foliacea, Pa. gyrata*, and *Pa.* ex gr. *rhenana* were found in the lowermost Askyn Regional Stage and *Pa. juntianensis* appears in its middle part. *Pa. juntianensis*, *Pa.* aff. *subrecta*, and *Polygnathus lodinensis* were identified in the section of Severnyi Kupol 106 (interval 1651–1647 m), and *Pa. juntianensis* and *Polygnathus lodinensis* were found in the section of Severnyi Kupol 142 (interval 1618–1614 m). *Pa. foliacea* and *Pa. orlovi* were found in the section of Zimnitskaya 51 (interval 1966–1970 m). Within the eastern Orenburg monocline, *Palmatolepis subrecta, Pa. foliacea, Polygnathus brevis*, and *Po. krestovnikovi* were identified in the Romanovskaya 2 (interval 2571–2591 m); *Palmatolepis praetriangularis* was found in the upper part of the interval.

In the lower part of the previously presumed continuous (Filippova and Aronova, 1957) Upper Frasnian–Famennian series in the section of Melekess 1, we determined Askyn species *Palmatolepis foliacea* and *Pa. subrecta* (interval 2018–2024 m; see Table 5); immediately upward in the same depth interval *Palmatolepis glabra* and *Pa. minuta* were found. This shows that the Late *crepida* Zone is present beginning with the lowest part of the Famennian section, i.e., that the Volgograd, lowermost Zadonsk, and possibly the upper part of the Askyn Regional Stage fall out from the section.

The assemblage of the Askyn Regional Stage correlates with the Middle–Upper *gigas* Zones.

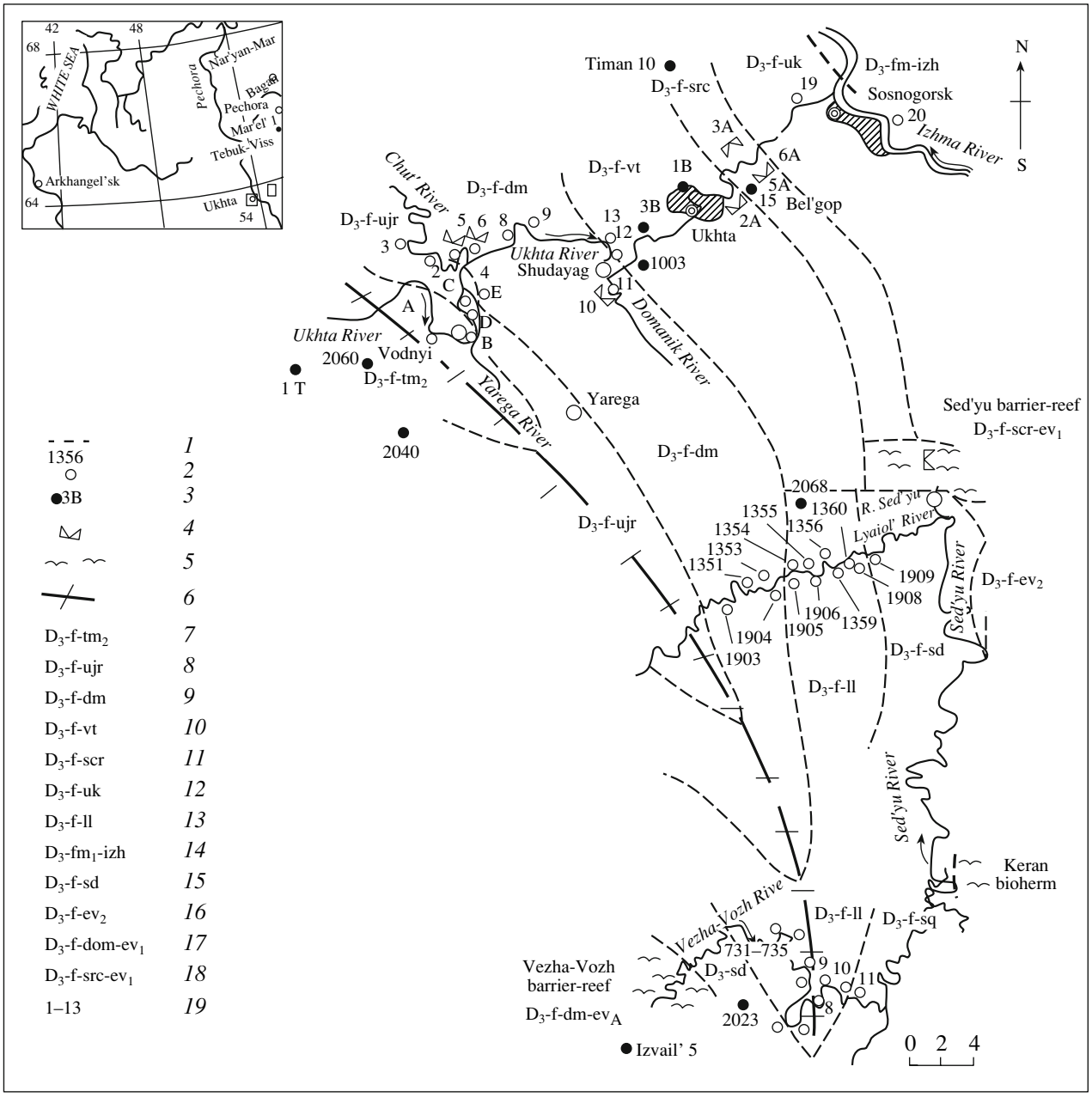
Lower Famennian conodont assemblages. Here we consider only those Lower Famennian assemblages that belong to the Volgograd Regional Stage.

Table 13. Distribution of conodonts in basinal deposits of the Frasnian and Lower Famennian stages of the Volga–Ural Province

Stage	Frasnian					Famennian
Regional Stage / Species	Timan (upper part)	Sargaevo	Domanik	Mendym	Askyn	Volgograd
Ancyrodella binodosa Uyeno	—	—				
A. rugosa Br. et M.		—	—			
A. alata Glen. et Klap.		—	—			
A. rotundiloba (Bryant)	—	—	—			
Klapperina ovalis (Z. et Kl.)		—				
Mesotaxis asymmetricus (Bisch. et Z.)		—	—			
M. falsiovalis Z., Sandb. et Bult.		—	—			
Polygnathus denisbriceae Bult.	—					
Po. xylus Stauf.	—	—	—			
Po. ljaschenkoi Kuzm.	—	—				
Mesotaxis johnsoni Kl., Kuzm. et Ovn.			—			
M. costalliformis (Ji)			—			
M. bogoslovskyi Ovn. et Kuzm.		—	—			
Polygnathus decorosus Stauf.			—	—		
Po. alatus Huddle	—	—				
"*Po. foliatus*" Bryant			—	—		
Po. dubius Hinde sensu Kl. et Ph.		—	—	—		
Po. efimovae Kon. et al.			—			
Po. timanicus Ovn.			—			
Po. azygomorphus Aristov			—			
Po. pollocki Druce		—	—			
Po. pennatus Hinde	—	—	—			
Po. brevilamiformis Ovn.			—	—		
Po. pseudoxylus Kon. et al.		—	—	—		
Palmatolepis transitans Müller		—	—			
Pa. maximovae Kuzmin			—			
Pa. punctata (Hinde)			—	—		
Pa. spinata Ovn. et Kuzm.			—			
Pa. gutta Kuzm.			—			
Pa. triquetra Kuzm.			—			
Ancyrodella gigas Young.			— - - -	- - -		
Polygnathus vjalovi Zvereva			—			
Palmatolepis proversa Z.				—		
Pa. bohemica Kl. et Fost.			—			
Polygnathus uchtensis Ovn. et Kuzm.			—	—		
Palmatolepis domanicensis Ovn.			—			
Pa. menneri sp. nov.				—		
Pa. kireevae Ovn.			—	—	—	
Pa. orbicularis Ovn. et Kuzm.			- - -	—		
Ancyrognathus ancyrognathoideus Z.			—			

Table 13. (Contd.)

Stage	Frasnian					Famennian
Regional Stage / Species	Timan (upper part)	Sargaevo	Domanik	Mendym	Askyn	Volgograd
Polygnathus praepolitus Kon. et al.						
Po. lodinensis Pölster						
Palmatolepis ljaschenkoae Ovn.						
Ancyrodella nodosa Ulr. et Basll.						
Palmatolepis muelleri Kl. et Fost.						
Pa. ormistoni Kl., Kuzm. et Ovn.						
Pa. semichatovae Ovn.						
Pa. anzhelae Khr. et Kuzm.						
Pa. timanensis Kl., Kuzm. et Ovn.						
Pa. brevis Z. et Sandb.						
Pa. ederi Z. et Sandb.						
Pa. hassi Müll. et Müll.						
Pa. plana Z. et Sandb.						
Pa. barba Z. et Sandb.						
Pa. mucronata K., Kuzm. et Ovn.						
Polygnathus unicornis Müll. et Müll.						
Po. maximovae Ovn. et Kon.						
Po. zinaidae Kon. et al.						
Po. politus Ovn.						
Po. subincompletus Ovn. et Kon.						
Ancyrognathus triangularis Young.						
Palmatolepis foliacea Young.						
Polygnathus krestovnikovi Ovn.						
Palmatolepis gyrata Kuzm. et Meln.						
Pa. jamieae Z. et Sandb.						
Polygnathus macilentus Kuzm.						
Palmatolepis subrecta Mill. et Young.						
Pa. lyaiolensis Khr. et Kuzm.						
Pa. orlovi Khr. et Kuzm.						
Polygnathus brevis Mill. et Young.						
Pa. rotunda Z. et Sandb.						
Pa. nasuta Müll.						
Pa. praetriangularis Sandb. et Z.						
Pa. juntianensis Han						
Ancyrodella ioides Z.						
Palmatolepis linguiformis Müller						
Pa. triangularis San.						
Pa. delicatula delicatula Br. et M.						
Pa. delicatula platys Z. et Sandb.						
Pa. subperlobata Br. et M.						
Pa. weddigei Ji et Z.						



Volgograd assemblage was studied in a very restricted number of sections: in the northern Orenburg Region (Romanovskii area) and in some basinal sections of Tatarstan (Bugrovka area). *Palmatolepis triangularis, Pa. delicatula*, and *Pa. quadrantinodosalobata* were identified in the northeastern Orenburg monocline (Romanovskaya 2, interval 2530–2538 m). In the Ust'-Cheremshan downwarp, *Palmatolepis triangularis, Pa. delicatula*, and *Pa. subperlobata* were found in the section of Bugrovskaya 18 (interval 1824–1821 m) and *Palmatolepis triangularis, Pa. delicatula delicatula, Pa. delicatula platys, Pa. subperlobata*, and *Pa. minuta wolskae* were found in the Bugrovskaya 20 (interval 1936–1940 m).

The regional stage is correlated with the Lower–Middle *triangularis* zones. The Lower, Middle, and Upper *triangularis* zones are hardly distinguishable due to the scanty material. The distribution of conodonts in the basinal deposits of the Frasnian Stage (from the Upper Timan Regional Stage and up to the Askyn Regional Stage) and the lowermost Famennian Stage (Volgograd Regional Stage) of the Volga–Ural province is shown in Table 13.

CHAPTER 4. TIMAN–PECHORA PROVINCE

The Timan–Pechora province is located in the extreme northeastern Russian Platform and is bor-

Fig. 12. Map of the Ukhta Region; incut shows the location of Ukhta, Bagan, and Tebuk-Vis regions. Outcrops of the Timan and Ust'-Yarega formations are in the village of Vodnyi and Yarega River. Outcrops A, B, and C (=outcrop 18, 13A, 14, and 16 in *Reference Sections*…, 1997): Outcrop A (=18), right bank of the Ukhta River, 0.3 km downstream from the mouth of the Neft'iol River; outcrop B (=13A), right bank of the Ukhta River, 0.8 km downstream from the mouth of the Polovinnyi Iol' River; outcrop C (=14) right bank of the Ukhta River, 0.5 km upstream from the mouth of the Yarega River; outcrop D (=16K after Yatskov and Kuzmin, 1997), right bank of the Yarega River, right tributary of the Ukhta River, 3.3 km from the mouth; outcrop E (=outcrop 16) village of Vodnyi, right bank of the Yarega River, right tributary of the Ukhta River, 3 km from the mouth. (1–13) outcrops and quarries of the Domanik Formation with conodonts near the town of Ukhta. Outcrop 1 (=outcrop 7 after *Reference Sections*…, 1997), left bank of the Chut' River, tributary of the Ukhta River, immediately upstream from the new bridge; outcrop 2 (=15b after Bogoslovskii, 1969), right bank of the Chut' River, 5.5 km upstream from the bridge; outcrop 4 (=28), mouth of the Chut' River, left bank; outcrop 5, Bogatskogo quarry; outcrop 6, quarry near the old road to the Chut' River; outcrop 9 (=39 after Bogoslovskii, 1969), left bank of the Ukhta River, 500 m downstream from the mouth of the Krokhal' River; outcrop 10, left bank of the Domanik River, tributary of the Ukhta River, quarry in 0.5 km from the mouth; outcrop 11 (=21 after *Reference Sections*…, 1994, 1997), right bank of the Domanik River, 0.5 km from the mouth; outcrop 12, left bank of the Ukhta River near the hospital in the village of Shudayag; outcrop 13, left bank of the Ukhta River, upstream from the village of Shudayag. Outcrop 2A, Podgornyi quarry, near railroad station of Vetlasyan; outcrop 3A, Sirachoi Mountain, airport region, right bank of the Ukhta River, 3.0 km upstream from the railroad station; outcrop 5A, "Old" quarry, Sirachoi Mountain, airport region, small quarry; outcrop 6A, "New" quarry, Sirachoi Mountain, functioning quarry on the right bank of the Ukhta River; outcrop 19, left bank of the Ukhta River, near the mouth; outcrop 20, right bank of the Izhma River near the town of Sosnogorsk. Sections of the Lyaiol' Formation along the Vezha-Vozh River. Outcrop 8, left bank of the Vezha-Vozh River, 3.2 km from the mouth; outcrop 9, left bank of the Vezha-Vozh River, 0.4 km downstream from outcrop 8; outcrop 10, left bank of the Vezha-Vozh River, 2.2 km from the mouth. Sections 1354, 1905, 1355, 1906, 1357, 1358, 1359, 1360, and 1908 of the Lyaiol' Formation on the Lyaiol' River. Designations: (*1*) geological boundary, (*2*) outcrop, (*3*) boreholes, (*4*) quarry, (*5*) outcrop of reef massifs, (*6*) axis of the Ukhta Anticline, (*7*) Upper Timan unit, (*8*) Ust'-Yarega Formation, (*9*) Domanik Formation, (*10*) Vetlasyan Formation, (*11*) Syrachoi Formation, (*12*) Ukhta Formation, (*13*) Lyaiol' Formation, (*14*) Izhma Formation, (*15*) Sed'yu Formation, (*16*) Upper Evlanovo, reef massifs: (*17*) Domanik–Lower Evlanovo, (*18*) Syrachoi–Lower Evlanovo, and (*19*) outcrops and quarries of the Domanik Formation with studied conodonts near the town of Ukhta.

dered by the Timan Ridge in the west, Ural folded system in the east, and Volga–Ural province in the south (Fig. 1).

Here we consider only those sections of Southern Timan (Ukhta region) where the stratotypes of most regional stages of the Frasnian Stage are located. All studied sections of boreholes and accepted in the paper numeration of the outcrops are shown on the map of the Ukhta region (Fig. 12). Corresponding numbers of the outcrops in the guidebook (*Reference Sections*…, 1994, 1997) are indicated in the figure captions of the map.

4.1. Ukhta Region

The Devonian System was established in Southern Timan in 1843 by A. Keyserling. He made the first geological description of the oil-bearing Ukhta region. Likharev (1931) and Tikhonovich (1930, 1941) proposed a paleontologically based subdivision of the Upper Devonian of the Ukhta region in 1930–1931. Most of the local stratigraphic subdivisions proposed by Tikhonovich are now considered as stratotypes for the regional stages in the stratigraphic schemes of the Devonian of Timan–Pechora subregion. In succeeding years, the stratigraphy of the Upper Devonian deposits of the Ukhta River basin was described in a number of papers (Lyashenko, 1956, 1973; Maksimova 1970; Fokin 1975, 1977; Kushnareva et al., 1974, 1978; Khalymbadzha, 1981; Ovnatanova and Kuzmin, 1991; Menner et al., 1992, 2001; Kuzmin, 1995; Kuzmin and Yatskov, 1997; House et. al., 2000).

4.2. Lithostratigraphy of the Frasnian Deposits of the Ukhta Region

Seven regional stages are distinguishable in the Frasnian Stage (from bottom to top): Timan (only the Upper Timan regional substage is referred to the Frasnian), Sargaevo, Domanik, Vetlasyan, Sirachoi, Evlanovo, and Livny (Table 14). In the sections of Southern Timan, Ust'-Yarega Formation corresponds to the Sargaevo Regional Stage. Sections are considerably differentiated beginning with the Domanik Regional Stage, upward in the section the Vetlasyan and Sirachoi formations are distinguishable, which correspond to the regional stages of the same name. In this region, the term "Ukhta Formation" designates the shallow-water Evlanovo and Livny deposits.

The basinal type of the section above the Sargaevo deposits is subdivided into the Domanik and Lyaiol' formations. They are overlain by the infilling clayey Sed'yu Formation. Deposits analogous to the sulfate member of the Ukhta Formation overlie the Sed'yu Formation in this type of the section and accomplish the sedimentation cycle of the Frasnian Stage.

Sections of the Timan and Ust'-Yarega formations are shown in Fig. 13. Sections of the Domanik Formation are not shown as they were illustrated in numerous papers, including those of one of the authors (Ovnatanova and Kuzmin, 1991; Ovnatanova et al., 1999; Becker et al., 2000). Sections of the Lyaiol' Formation in outcrops 8, 9, and 10 on the Vezha-Vozh River are shown in Fig. 14.

Material from the stratotype of the Lyaiol' Formation on the Lyaiol' River (collected by V.V. Menner, 2000) is also analyzed. This section was earlier

Table 14. Stratigraphic divisions of Frasnian deposits of the Ukhta Region

Stage	Regional stage, formation		Formation	Unit
Frasnian	Ukhta Formation	Livny		
		Evlanovo		
			Sed'yu (clayey member)	
			Lyaiol'	4
				3
	Sirachoi			2
	Vetlasyan			1
	Domanik		Domanik	3
				2
				1
	Sargaevo		Ust'-Yarega	
Givetian	Timan		Timan	

described by A.N. Orlov (VNIGNI). In 2000 Menner took samples on conodonts from this section; he used numbers of the layers proposed by A.N. Orlov. This numeration is used for the sections of the Lyaiol' Formation in outcrops 1906, 1359, 1360, 1908, etc. (Fig. 14). The parastratotype of the Lyaiol' Formation on the Vezha-Vozh River is also shown in Fig. 14. The location of samples in this section is shown according to the guidebook (*Reference Sections*…, 1994; 1997). The section of the Timanskaya 10 is shown in Fig. 15.

4.3. Shallow-Water Type of Sections

This type of the section is known mainly from the sections of boreholes 2040, 2060, Timanskaya 10, and from a number of outcrops of the Timan, Ust'-Yarega, Vetlasyan, and Sirachoi formations in the sections along the Ukhta, Chut', and Yarega Rivers, outcrop 3A in the town of Sirachoi, and outcrop 2A near the village of Vetlasyan.

4.3.1. Timan Regional Stage

The Timan Regional Stage is represented by the Timan Formation composed of gray, dark gray, greenish gray, and brownish gray argillites with a small number of interbeds of siltstones, sandstones, limestones, and tuffites.

It was studied in the sections of outcrops A and B on the Ukhta River (Fig. 13) and Balneologicheskaya 1 (depth 239.5–307 m). Type sections of the Timan Formation are divided into two subformations. The Lower Subformation is 50–70 m thick and upper is 30–70 m thick. The Timan Regional Stage together with the Sargaevo Regional Stage corresponds to the *C. optivus–S. krestovnikovi* Zone of the miospore zonation (Avkhimovich et al., 1996).

4.3.2. Sargaevo Regional Stage

In the Timan–Pechora province, the sections of Ust'-Yarega Formation in Southern Timan are the lectostratotype of the Sargaevo Regional Stage. Sections on the Ukhta and Yarega rivers (outcrops C (= 14), D (=16k) and E (=16) and on the Chut' River (outcrop 1 (=7) and outcrops 2 and 3 (=15b and 15c)), in which the uppermost part of the regional stage is exposed, were studied. The Lower Ust'-Yarega Subformation is mainly composed of clays with interbeds of siltstones and clays; in the middle part appear limestones, abound in ostracodes, brachiopods, and other benthic animals. The number of limestone interbeds considerably increases in the upper member. Ammonoids of the *Hoeninghausia nalivkini* Zone were found in most of the middle part of the regional stage and *Timanites keyserlingi* Zone was identified in the uppermost middle part (layer 2 in the guidebook (*Reference Sections*…, 1988, 1994)) (Becker et al., 2000). The last zone also characterizes the lower part of the upper member. The total thickness of the Ust'-Yarega Formation is 50–70 m.

4.3.3. Domanik Regional Stage

The equivalents of the Domanik Regional Stage in the shallow-water facies are developed in the sections of the adjacent western territories. In Middle Timan, clayey-carbonate shallow-shelf deposits of the back-reef zone are identified as the Kraipol Formation. These deposits are not recognized as an independent stratigraphic subdivision in Southern Timan. Eastwards the shallow-shelf sections give way to the sections with the lower part composed of the dark-colored Ezhvador Formation (base of the reef massifs), and the upper part is composed of the Timan barrier reef or structures of the lowermost Vezha-Vozh reef massif and basinal deposits of the Domanik Formation (Table 15). In the boreholes, the interval of the Domanik Formation is distinguished by very high values of resistivity logging.

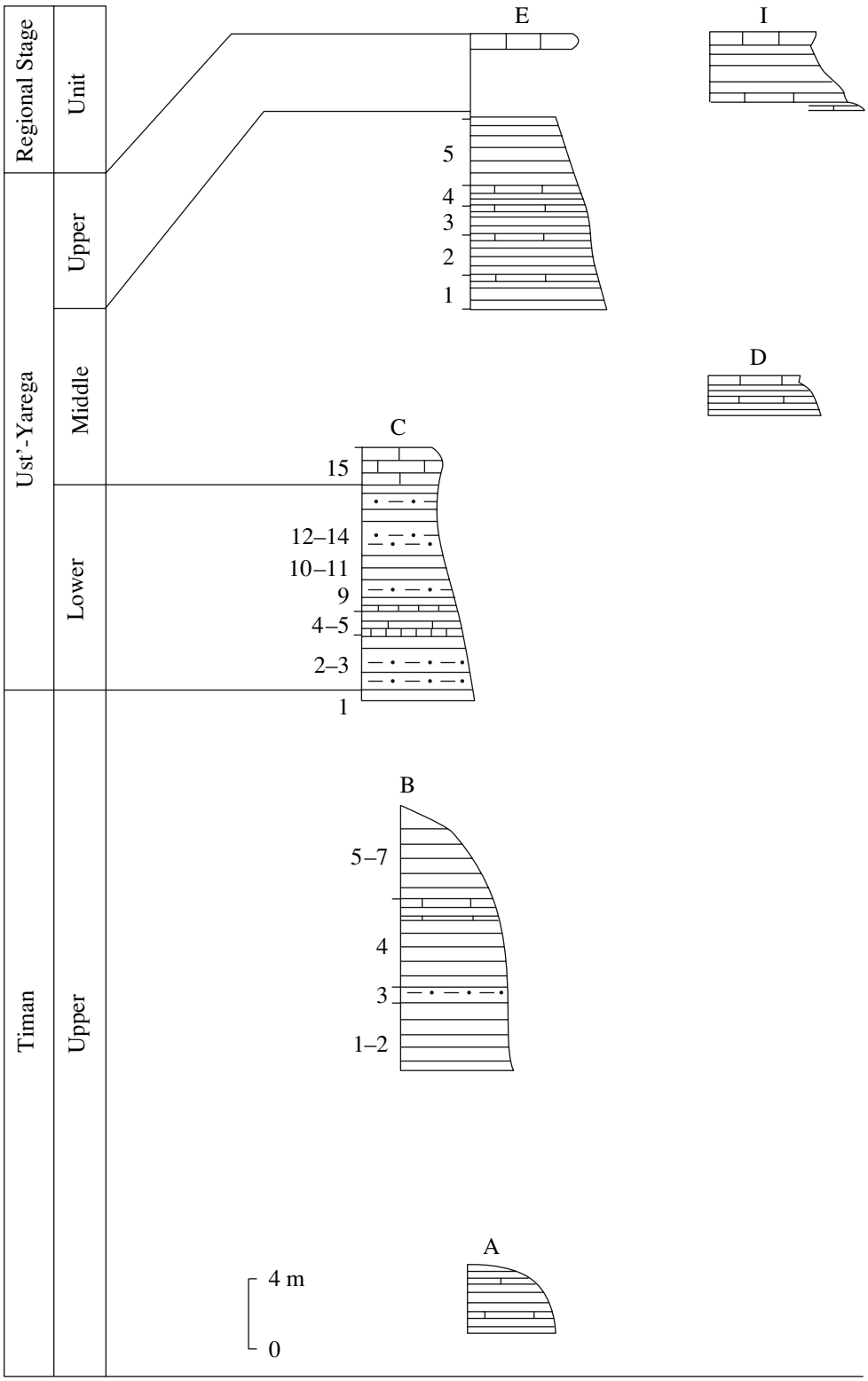


Fig. 13. Sections of the Timan and Ust'-Yarega formations on the Ukhta, Yarega, and Chut' rivers; samples with conodonts were collected from the limestone interbeds.

4.3.4. Vetlasyan Regional Stage

The regional stage corresponds to stratigraphic gaps or to thin clayey layers of the shallow-shelf sections. In front of the Domanik barrier reefs, the Vetlasyan Regional Stage corresponds to the clayey clinoform—infilling series—the Vetlasyan Formation. The clino-

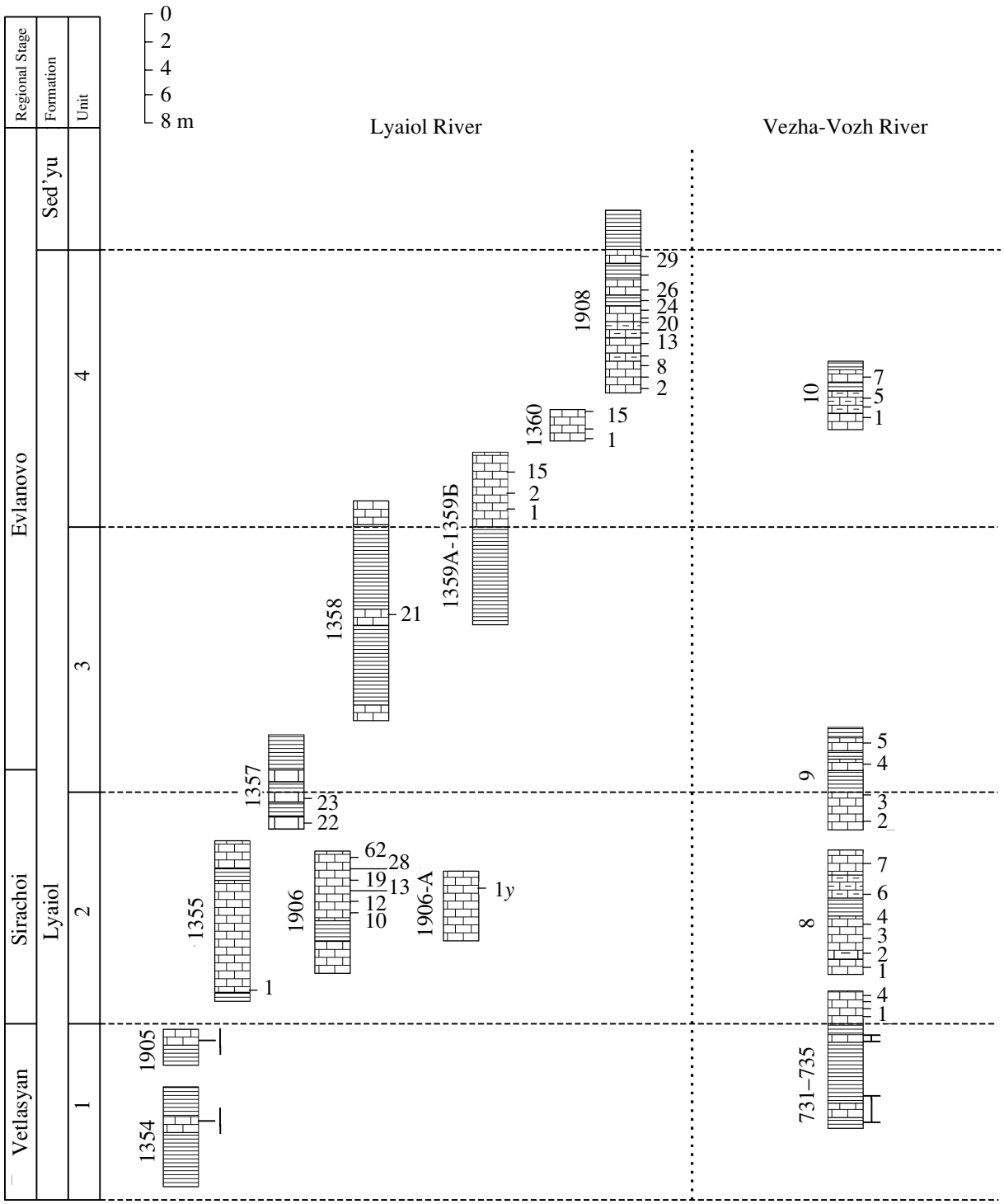


Fig. 14. Section of Frasnian deposits on the Lyaiol' and Vezha-Vozh rivers. In the section on the Lyaiol' River, levels with conodonts are marked in outcrops 1354, 1905, and 1355; in outcrops 1906, 1906A, and 1908, the positions of beds are indicated; and in outcrops 1357, 1358, and 1360, the positions of specimens with conodonts are shown. In outcrop 1359B, nos. 1 and 2 correspond to sample no.; and 15 designates bed no. In the section on the Vezha-Vozh River, all nos. designate the positions of samples.

form may be up to 250 m thick. Deep into the basin it is replaced by the 20–30 m thick clayey member, which is recognized as member 1 of the Lyaiol' Formation.

The formation was studied in the sections of boreholes 2040 and 2060 and in outcrop 2A on the right bank of the Ukhta River near the station of Vetlasyan, where its middle part is apparently exposed. The deposits of the Vetlasyan and upper horizons of the Frasnian Stage are shown in the section of Timanskaya 10 (Fig. 15).

4.3.5. Sirachoi Regional Stage

The Sirachoi Formation is the stratotype of the regional stage. It is 80–100 m thick and is represented by the shallow-shelf, back-reef, clayey-carbonate lithofacies. In southeastern Ukhta region, the carbonate strata of the Sirachoi Regional Stage constitute the lower part of the Sed'yu barrier-reef massif and in southwestern Ukhta region, they form the middle part of the Vezha-Vozh barrier reef. The basin facies of the Sirachoi Regional Stage deposits are represented by member 2 and the lower part of member 3 of the Lyaiol' Formation (Table 15). Conodonts from the Sirachoi Regional Stage were studied from outcrops 2A, 3A, and 5A on the Sirachoi Mountain and from the sections of boreholes 2040, 2060, and 2051 and Timanskaya 10.

4.3.6. Ukhta Formation

The Ukhta Formation with type sections in the lower reaches of the Ukhta River is up to 200–250 m thick and corresponds to the Evlanovo and Livny regional stages in the shallow-shelf sections. The formation is divided into two members. The upper is sulfate-bearing and the lower underlies it (subsulfate) (*Reference Sections…*, 1994, 1997). Limestones, marls, and clays are rhythmically interbedded in its lower 100-m-thick part; this member contains more clays than the Sirachoi Formation and a lesser number of fossils, the taxonomic composition of which is also poorer because of deviation from the normal salinity. This member is replaced east- and southwards by the reef structures forming the upper part of the Sed'yu and Vezha-Vozh barrier-reef massifs (Table 15). The middle and upper parts of the type section of the shallow-water Ukhta deposits are classed as sulfate-bearing strata and are composed of the carbonate-clayey member at the bottom and contain layers with gypsums and anhydrites, which are rhythmically interbedded with limestones, secondary dolomites, and marls, at the top.

The Frasnian–Famennian boundary in the Ukhta region coincides with the surface of discontinuity dividing the Ukhta and Izhma formations.

4.4. Basinal Type of the Section

As was previously mentioned, the sections are strongly differentiated beginning with the Domanik Formation. This type of the section is described using numerous sections of boreholes and outcrops of the Ukhta region.

4.4.1. Domanik Formation

The Domanik Formation is usually described using the outcrops on the Chut', Domanik, Ukhta, and Yarega rivers. It was found out (Menner et al., 1992) that composite sections of the Domanik Formation were incomplete and the correlation of outcrops was sometimes incorrect (Kushnareva et al., 1978; *Reference Sec-*

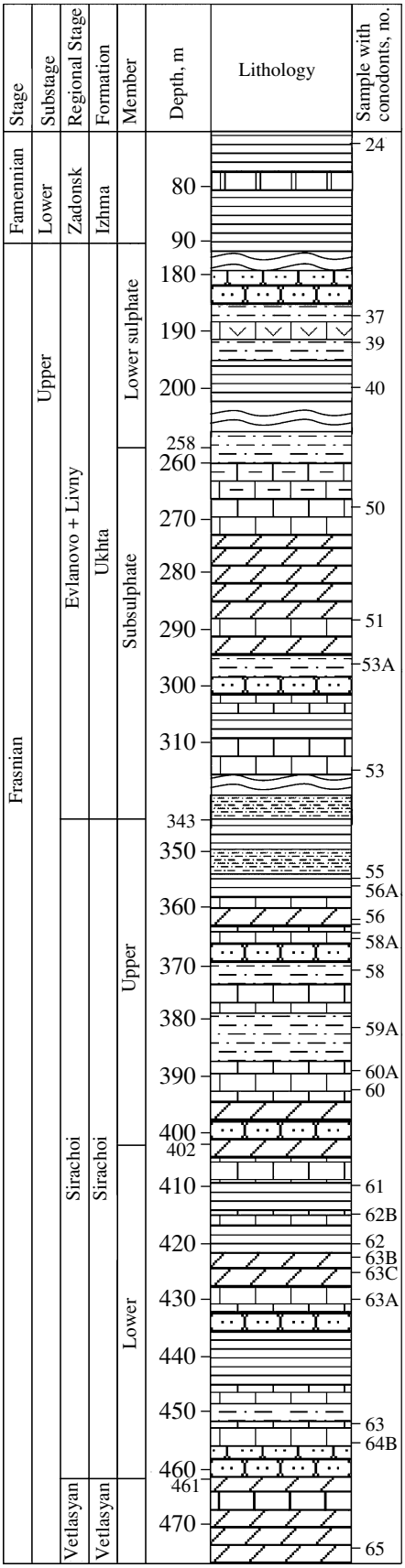


Fig. 15. Section of Frasnian and Lower Famennian deposits in Timanskaya, borehole no. 10.

Table 15. Correlation of heterofacies Frasnian deposits of the Ukhta Region after Menner et al. (1992), supplemented

Stage	Regional stage	Northwest		Northeast			Southwest	Southeast	South		
Famennian	Zadonsk	Izhma Formation		Izhma Formation, shallow-water facies							shallow-water facies
	Volgograd			Clayey bed							
Frasnian	Livny	Ukhta Formation	Shallow-water facies	Ukhta Formation	Sulphate member	Sulphate unit	Sulphate unit				
	Evlanovo					Carbonaceous clayey unit			Sed'yu Formation		
			Shallow-water back-reef facies		Subsulphate member		Vezha-Vozh barrier-reef	Sed'yu barrier-reef	Lyaiol' Formation	4 3	slope facies
	Sirachoi	Sirachoi Formation		Sirachoi Formation						2	basin facies
	Vetlasyan	Clayey bed		Vetlasyan Formation (filling strata)				Vetlasyan Formation		1	
	Domanik	Timan barrier-reef		Domanik Formation (basin facies)				Domanik Formation			
		Ezhvador Formation					Ezhvador Formation				
	Sargaevo	Ust'-Yarega Formation									
Givetian	Timan	Timan Formation (partly)									

tions…, 1994, 1997). In the present paper we describe the stratotype of the Domanik Formation based on boreholes 1003, 3B, and 2068, which exposed the complete sections of the formation. The upper boundary of the Domanik Formation was recently uncovered in the excavation works on the right and left banks of the Ukhta River near the village of Shudayag (outcrop 13).

Sections of the Domanik Formation were previously discussed in a number of papers (Ovnatanova and Kuzmin, 1991; Ovnatanova et al., 1999; Kuzmin and Yatskov, 1997; Klapper et al., 1996). In the latter conodonts from the Domanik and Lyaiol' formations are analyzed based on the sections of boreholes 2023 and 2068. Here we describe for the first time conodont assemblages from the Domanik Formation of the Lyaiol' River.

The lower boundary of the Domanik Formation is at the top of the calcareous bed with the ammonoids *Komioceras stuckenbergi* (Holz) and *Tornoceras typum* (G. and F. Sandb.). This bed completes the section of the Ust'-Yarega Formation and was found in the outcrops on the Ukhta and Chut' Rivers; however, it is sometimes poorly apparent in the logging diagrams of the boreholes.

Komioceras stuckenbergi were identified from the basal layers of the lower unit, and higher up in the section various species of *Ponticeras* (previously identified as *Probeloceras*) were found. The genera *Koenenites* and *Timanites* disappear at this level. Most of the lower unit corresponds to the *Ponticeras domanicensis* Zone and *Ponticeras auritum* Subzone may be separated from its upper part (Becker et al., 2000). Earlier the lower unit of the Domanik Formation was correlated with the *Probeloceas domanicensis* Zone (Yatskov and Kuzmin, 1992; *Reference Sections*…, 1994, 1997).

The upper boundary of the Domanik Formation is established at the top of the last thick carbonate bed, overlain by the clay of the Vetlasyan Formation. The level of the upper boundary is well defined by coring and logging of the boreholes but almost unknown in the outcrops.

Complete sections of the Domanik Formation revealed that the boreholes are divided into three units.

The lower unit starts with a thin bed of greenish gray and gray argillites, which contain the spores of *Geminospora semilucensa–Perotriletes donensis* Zone, which define the lower part of the Domanik Regional Stage (Obukhovskaya, 1996). Upward in the section the lower unit is represented by a 22- to 24 m-thick series of dark gray thin-laminated limestones, silicic limestones, oil shales with lenses of dark gray cherts, carbonate nodules and three beds of limestones with ammonoids, straight nautiloids, *Tentaculites*, and sometimes *Buchiola*. The upper boundary of the unit is established at the base of a thin (0.3–1.5 m) clayey bed, which is readily traceable in the outcrops and boreholes. The lower unit is exposed in outcrop 1 on the Chut' River near the new highway bridge, as well as upstream of outcrop 1 (outcrops 2 and 3), and on the Ukhta River near the mouth of the Chut' River (outcrop 4). This lower unit on the Chut' River was earlier divided by Kushnareva (Kushnareva et al., 1978) into three units; however, in other areas this subdivision is difficult.

The middle part of the Domanik Formation is 17–22 m thick and is represented by the platy silicic limestones, oil shales, cherts, and limestones containing a small number of thin (0.1–1 m) layers of clays at the base and in the middle part of the unit. Layers with large calcareous nodules are present in the middle and upper parts of the section. The concretions contain shells of ammonoids, nautiloids, and *Buchiola*. The ammonoid assemblage is impoverished due to the disappearance of *Ponticeras* and *Probeloceras*. *Manticoceras ammon* (Keys.) and *Tornoceras simplex* Buch were recorded in the upper part of the middle unit on the Domanik River (Bogoslovskii, 1969). The middle and upper units of the Domanik Formation were referred to the *Nordiceras timanicum* Zone (Becker et al., 2000). This interval (middle and upper units) contains spore assemblages of the *Spelacotriletes bellus* Subzone of the *Archaeoperisaccus ovalis–Verrucososporites grumosus* Zone (Obukhovskaya, 1996; Avkhimovich et al., 1996).

The middle unit more often than the lower unit contains benthic fossils. The outcrops of the middle unit are located on several separated areas of the eastern limb of the Ukhta anticline. The first area is located near the head and in the upper reaches of the Chut' River and includes outcrops 1, 2, 3, and 4 (Fig. 12) and quarries near these outcrops (sites 5 and 6). The 4- to 10 m-thick lower part of the unit is exposed here. The next area the middle unit is exposed is on the Ukhta River near Krokhal' Creek. The upper part of the middle unit is exposed in the outcrops and quarry on the Domanik River and along the banks of the Ukhta River near the village of Shudayag (outcrops 10–13).

The structure of the upper unit of the Domanik Formation was previously known mainly from the sections of boreholes. During the last decade it was also fairly well studied using the road and building excavations in the outskirts of the village of Shudayag.

The lowermost third unit is exposed in the small outcrops on the left bank of the Ukhta River near the hospital at the village of Shudayag; its middle and upper parts are exposed in the ditch of the water-intake and excavations in the road on the left bank of the Ukhta River upstream of the village of Shudayag. Recently the upper boundary of the Domanik Formation was exposed by the excavation works on both banks of the Ukhta River near the village of Shudayag (outcrop 13). Ammonoids were determined from the upper part of the unit in the outcrops along the Ukhta River and borehole 1904 on the Lyaiol' River. In the section of bore-

hole 1904, *Lobotornoceras trangulatum* (Keis.) *Manticoceras ammon* (Keys.), *M. lamed,* etc. were identified (Becker et al., 2000). Earlier the middle and upper parts of the Domanik Formation were correlated with the *Manticoceras ammon* Zone (*Reference Sections*…, 1994).

The upper part of the Domanik Formation is divided into four strata (from bottom to top):

(1) greenish-gray and gray clays 3–4 m thick;

(2) interbedding of platy silicic limestones, limestones, and oil shales with rare, thin (up to 6 m) interbeds of clays;

(3) gray or dark gray clays with interbeds of limestones in the upper parts up to 4.5 m thick;

(4) dark gray, thin-laminated silicic limestones,, and oil shales with rare carbonate nodules up to 8 m thick. The total thickness is 20–23 m. Uncertain exposures of these rocks are located near the mouth of the Domanik River.

The correspondence between the Lyaiol' Formation and the interval of Vetlasyan, Sirachoi, and subsulfate member of the Ukhta Formation in the sections of basinal type was established based on the spore spectra and ostracodes (Fokin, 1977; Kushnareva and Raskatova, 1980) and then confirmed based on conodonts (Menner et al., 1992). Earlier (Lyashenko, 1956; Tsyu and Kosovoi, 1973; Kushnareva et al., 1974; Deulin, 1987; *Stratigraphical Dictionary*…, 1975, etc.) the Mendym Regional Stage was correlated only with the lowermost Upper Frasnian Substage in the stratigraphic scheme of the Volga–Urals province, and thus it was placed below the Voronezh Regional Stage. Therefore the Lyaiol' Formation was initially correlated with this level as its position was mistakenly determined between the Domanik and Vetlasyan formations. In this stratigraphic interval researchers made ill-founded attempts to trace the Lyaiol' Formation in the sections of the northern and central areas of the Ukhta region. In the stratotype section on the Lyaiol' River, the clayey series overlying the Lyaiol' Formation was for a long time considered to be the Vetlasyan Formation. Only Kushnareva and Raskatova (1980) identified it as an independent Sed'yu Formation of the Evlanovo age. The Lyaiol' Formation rocks are basinal (domanikoid) and slope facies and contain a rich assemblage of conodonts that should allow correlation with global conodont scales.

4.4.2. Lyaiol' Formation

The formation was studied in the outcrops on the Lyaiol' River south of the Ukhta River and in numerous exposures on the Vezha-Vozh River (Fig. 12). An almost complete section of the Lyaiol' Formation was exposed by borehole 2068 and described by Klapper et al. (1996). The formation is rich in ammonoids, nautiloids, and ostracodes. *Manticoceras intumescens* (Beyr.), *M. cordatum* (Sandb.), *Tornoceras simplex* (Buch), *Carinoceras menneri* G. Ljasch., *Virginoceras ljaschenkoae* Bogosl., etc. are typical. Initially the formation was fully referred to the *Manticoceras intumescens* Zone (Lyashenko, 1957; Kushnareva et al., 1978); later a more detailed zonal subdivision was carried out (Becker et al., 2000). The stratotype of the formation was defined using outcrops on the Lyaiol' River. The Lyaiol' Formation is divided into four units (Kushnareva and Raskatova, 1980).

Unit 1 conformably overlies the Domanik Formation and is up to 35 m thick in the section of borehole 2068. It is composed of dark gray or greenish gray clays with rare interbeds of limestones and is characterized by miospores of the *Cymbosporites vetlasjanicus* Subzone of the *Archaeoperisaccus ovalis–Verrucosisporites grumosus* Zone of the Vetlasyan Regional Stage (Avkhimovich et al., 1996). Typical Domanik ammonoids disappear at this level; *Carinoceras* sp. are rare.

Unit 2 (outcrops 1355, 1906, and 1357) is 25–35 m thick. It is composed of thin interbedding of dark gray thin-laminated limestones, silicic limestones, and sometimes oil shales. The limestones contain numerous nautiloids, ammonoids, tentaculites, ostracodes, and rare brachiopods. Of ammonoids, *Carinoceras menneri, Manticoceras solnzevi,* and *M. latisellatum* are typical along with the zonal species *Virginoceras ljaschenkoae.* Miospores of the Sirachoi Regional Stage were determined in the clayey interbeds. These are typical basin facies.

Unit 3 (Lyaiol' River, outcrops 1357, 1358, and 1359) is up to 26 m thick. It is composed of deposits of the continental-slope facies: gray or greenish gray clays with interbeds of gray thin-laminated and nodular limestones with brachiopods. The Lower Evlanovo spore assemblage was determined from the upper part of the unit.

Unit 4 (Lyaiol' River, outcrops 1359, 1360, and 1908) is up to 30 m thick. It is represented by interbedding of nodular and thin-laminated limestones (sometimes of domanikoid appearance) with gray or greenish gray clays. The limestones prevail in the lower part of the unit; the upper part is composed of the interbedding of clays and limestones. The Evlanovo spore assemblage was encountered in these clays. Ammonoids are numerous in the lower part of unit 4. Units 3 and 4 correspond to the *Manticoceras lyaolensis* Zone (Becker et al., 2000). The Lyaiol' Formation is overlain by the clayey Sed'yu Formation containing the Upper Evlanovo spore assemblage (*Auraspora speciosa* Subzone of the *Cristatisporites deliquescens–Verrucosisporites evlanensis* Zone (Avkhimovich et al., 1996).

Another group of the exposures of the Lyaiol' Formation and the Sed'yu Formation that overlies the latter is located further south, downstream of the Vezha-Vozh River (outcrops 8, 9, 10, and 11; Fig. 12). The outcrops are located along the axis of the Ukhta fold, which is gently rising to the north. The lowest layers of the Lyaiol' Formation and the uppermost layers of the

Domanik Formation are not exposed. All four units of the Lyaiol' Formation are possibly present in the outcrop, but their borders are hardly distinguishable. The clayey material was less abundant in the Vezha-Vozh part of the paleobasin than in the region of the Lyaiol' River. It was established using the sections of boreholes 2023, 2024, and 2027 that the only comparatively thick clayey unit is unit 1. Its thickness is 15–20 m. In addition, deposits of the Lyaiol' Formation in the Vezha-Vozh area were accumulated under less deep-water conditions than that in the Lyaiol' area. This somewhat obscures the litho- and biofacies differences between the rocks of units 2, 3, and 4. Deposits of unit 2 and possibly unit 1 are represented in outcrops 731–735. Outcrops 8, 9, 10, and 11 are located downstream and confined to the axis of the Ukhta anticline and its eastern margin. Deposits analogous to the sulfate member of the Ukhta Formation overlie the Sed'yu clays. The latter complete the depositional cycle of the Frasnian Stage. As the conodonts are almost absent in these deposits, they were studied based on the sections in the Tebuk-Vis region of the Izhma–Pechora depression (Kuzmin et al., 1998), located east of the Ukhta region, where sections of the Upper Frasnian and lower part of the Famennian Stage were exposed in the basin and continental-slope facies.

4.5. Historical Review of the Study of Frasnian Conodonts from Southern Timan

Frasnian conodonts from Southern Timan have previously been analyzed in the literature (Kushnareva et al., 1974; Kushnareva et al., 1978; *Reference Sections*…, 1994, 1997; Ovnatanova, 1972; Ovnatanova and Kononova, 1984; Ovnatanova and Kuzmin, 1991; Khalymbadzha, 1981; Kuzmin, 1995, 1998; Kuzmin and Ovnatanova, 1989; Klapper et al., 1996; Khrushcheva and Kuzmin, 1996; Ziegler et al., 2000, etc.).

Most of the above-mentioned papers were devoted to the conodonts from the basin deposits, including the Domanik Formation (Ovnatanova and Kuzmin, 1991; Kuzmin and Yatskov, 1997; Kuzmin et al., 1997). The scheme of the correlation of the heterofacies Middle- and Upper Frasnian deposits of the Ukhta region, including all type sections of the subregional horizons was proposed (Menner et al., 1992). The position of the lower boundary of the Frasnian Stage is discussed based on the conodont assemblages from the type sections of the Timan and Ust'-Yarega formations (Kuzmin, 1995). The composite conodont scale, which was originally established for the Frasnian sections of Montagne Noire, was tested and accepted as valid first for the sections of North America (Kirchgasser, 1994; Kralick, 1994) and Canada (McLean and Klapper, 1998) and than for the Timan sections (Klapper, 1988).

The succession of the conodont assemblages was established using the sections of the boreholes and outcrops of Southern Timan, including the stratotypes of the Frasnian Stage in the Ukhta region (Ovnatanova et al., 1999a, 1999b). The proposed succession of the conodont assemblages was initially regarded by the authors as a preliminary stage of elaborating the local zonal conodont scale. Later this succession was correlated with the spore zonation (Menner et al., 2001).

The revision of ammonoid stratigraphy of the Frasnian Stage of Southern Timan, including the correlation of the newly elaborated ammonoid scale with the conodont succession elaborated for the Ukhta region, was quite important (Becker et al., 2000). Conodonts from the shallow-shelf sections are very poorly known at present (Kuzmin and Ovnatanova, 1989; Menner et al., 1992). The use of previously described assemblages (Kushnareva et al., 1974, 1978; *Reference Sections*…, 1994, 1997) seems to be impossible as these papers lack paleontological plates. Ziegler et al. (2000) listed and analyzed the polygnathids (conodonts) of the Ukhta region and presented comparative plates showing polygnathids that occur both in this region and in the sections of the conodont zones of the Rhenish Slate Mountains. The Frasnian conodont assemblages from the shallow-shelf and basin sections of the Ukhta region are described below. The species composition of conodonts in the specific sections is shown in Tables 16–18.

4.5.1. Frasnian Conodont Assemblages from the Shallow-Water Sections of the Ukhta Region

The Lower Timan assemblage was determined from the top of the Lower Timan Subformation in the section of Balneologicheskaya 1 (depth of 239.5–241 m). It is composed of polygnathids *Polygnathus xylus* and *Po. webbi.* According to V.G. Khalymbadzha, *Icriodus nodosus, Polygnathus varcus*, and *Po. webbi* were determined down the section in borehole 1, at the depth of 300–297 m (*Reference Sections*…, 1994, 1997). We referred the Lower Timan conodont assemblage to the Givetian Stage based on its position in the section and the absence of typical Frasnian forms. Earlier it was described as Timan–Pechora assemblage TP-0 (Ovnatanova et al., 1999a, 1999b).

Upper Timan assemblage. The lowest part of the Upper Timan Subformation was exposed in outcrop A, near the village of Vodnyi. L.N. Mel'nikova determined *Polygnathus alatus, Po. webbi, "Po. foliatus," Icriodus expansus*, etc., from the lowermost limestone interbed. Kuzmin (1995) identified conodonts *Icriodus expansus, Polygnathus alatus, Po. angustidiscus, Po. pennatus, Po. webbi*, and *Po. lanei* from the upper limestone interbed (Fig. 13, sample 2). *Polygnathus angustidiscus, Polygnathus alatus, Po. pennatus, Po. webbi, Po. lanei, Po. posterus*, and *Po. ljaschenkoi* were found in outcrop C on the right bank of the Ukhta River, where the upper part of the Timan Formation is exposed.

Table 16. Distribution of conodonts in the stratotype of the Lyaiol' Formation on the Lyaiol' River (collected by V.V. Menner in 1996 and 2000) (the sample numbers are often given after those beds in the unpublished section of the Lyaiol' River of A.N. Orlov)

Outcrop	1354	1905	1355	1906							1906-A, upper part	1357, lower part		1358	1359B			1360			1908													
Unit	1		2											3	4																				
Bed				10	12	13	19	28			1y						15				2	6	8	9	13	15	20	22	24	25	26		28		29
Sample, no.			1						1 m below Bed 62	3 m above Bed 62		22	23	21	1	2		1	3	15		E					H	11d–11z		z-2	g-1	g-2	d-1	d-2	
Palmatolepis plana Z. et Sandb.	x	x	x								x																								
Icriodus symmetricus Br. et M.	x	x																																	
Pa. proversa Ziegler	x	x			x				x																										
Pa. barba Z. et Sandb.	x																																		
Pa. amplificata Klapper, Kuzm. et Ovn.	x	x							?x	x																									
Palmatolepis punctata (Hinde)		x				x																													
Pa. orbicularis Ovn. et Kuzm.		x											x																						
Po. dubius Hinde		x																																	
Pa. hassi Müll. et Müll.		x										s.l.	s.l.		x	x		x			x	x		x		x					x	x	x		
Ad. gigas Youngq.	x	x										x																							
Pa. menneri sp. nov.			x	x					x																										
Pa. semichatovae Ovn.			x					x		x	x	x	x	x																					
Pa. timanensis Klapper, Kuzm. et Ovn.	x		x	x	x			x	x	x		x																							
Ag. triangularis Youngq.		x	x															x																	
Po. lodinensis Pölsl.	x	x	x	x				x		?x		x	x	x	x		x	x	x					x			x			x					
Pa. ederi Ziegler et Sandberg		x	x				x	x	x																										
Pa. ljaschenkoae Ovn.	x		x	x				x	x	x																									
Pa. kireevae Ovn.		x		x	x			x	x	x		x	x		x			x	x	x			x	x											
Pa. mucronata Klapper, Kuzm. et Ovn.	x	x		x				x	x						x						x							x					x	x	
Pa. ormistoni Klapper, Kuzm. et Ovn.					x	x		x										x	x													cf			
Pa. muelleri Klapper et Foster	x				x				x	x		x			x	x	x	x	x								x				x			x	
Belodella sp.					x			x		x																									
Ozarkodina trepta Ziegler						x		x																											
Ag. ancyrognathoideus Ziegler						x																													
Ad. curvata early form Br. et M.						x																													
Po. krestovnikovi Ovn.						x																													
Pa. elegantula Wang et Z.	x								x								x			x									x						
Pa. anzhelae Khruscheva et Kuzm.											x																x	x					x		

Table 16. (Contd.)

Outcrop	1354	1905	1355	1906							1906-A, upper part	1357, lower part		1358	1359B			1360			1908														
Unit	I		II											III	IV																				
Bed				10	12	13	19	28			1y						15				2	6	8	9	13	15	20	22	24	25	26		28		29
Sample, no. / Species			1						1 m below Bed 62	3 m above Bed 62		22	23	21	1	2		1	3	15		E					H	11d–11z		z-2	g-1	g-2	d-1	d-2	
Pa. simpla Ziegler et Sandberg											x																								
Po. imparilis Kl. et L.														x																					
Pa. subrecta Mill. et Youngq.															x	x	x	x		x	x	x				x		x		x		x	x	x	
Pa. nasuta Müller															x		x		x			x	x	x	x				x		x	x	x		
Pa. foliacea Youngq.															x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x
Pa. gyrata Kuzm.															x	x	x	x	x										x	x					
Po. subincompletus Ovn. et Kononova															x																				
Pa. brevis Ziegler et Sandberg	x															x																			
Pa. jamieae Ziegler et Sandberg																x				x		x						x						x	
Pa. juntianensis Han																x				x		x				x		x					x	x	
Pa. orlovi Khrustcheva et Kuzm.																	x				x				x	x			x			x	x		
Pa. rotunda Ziegler et Sandberg																	x																		
Ancyrodella nodosa Br. et M.																		x				x		x				x						x	
Po. alvenus Ovn. et Kononova																		x															x		
Po. politus Ovn.											x							x																	
Po. macilentus Kuzm.																		x						x							x				
Ag. amana Müll. et Müll.																		x				x									x				
Ad. ioides Ziegler																		x				x						x						x	
Po. siratchoicus Ovn. et Kuzm.																				x												x			
Pa. jamieae ⟶ *Pa. juntianensis* Han																						x													
Polygnathus brevilamiformis Ovn.		x																																	
Icriodus interjectus Kuzm. et Ovn.																													x				x	x	
Pa. praetriangularis Ziegler et Sandberg																												x						ex gr	
Pa. rhenana Bisch.																			cf												x		cf		cf
Pa. sp.							x							x																					
Pb elements																																			

Table 17. Distribution of conodonts in the parastratotype on the Lyaiol' Formation on the Vezha-Vozh River

Outcrop	731	732	733	734	735				8						9				10			
Unit	1				2										3				4			
Sample, no. / Species					1	2	3	4	1	2	3	4	6	7	2	3	4	5	1	3	5	7
Palmatolepis amplificata Klapper, Kuzm. et Ovn.	x	x										x		x								
Ancyrodella nodosa Ulr. et Basl.	x				x				x	x	x	x			x	x				x		x
Pa. luscarensis Klapper et Foster	x	x																				
Pa. barba Z.					x			x														
Pa. orbicularis Klapper, Kuzm. et Ovn.	x																					
Pa. menneri sp. nov.					x							x										
Pa. ljaschenkoae Ovn.	x	x	x			x	x	x	x	x	x	x	x									
Polygnathus uchtensis Ovn. et Kuzm.	x	x																				
Pa. proversa Ziegler		x			x		x	x														
Pa. hassi Müll. et Müll.		x			x	x	x			x	x	x	x		x	x	x	x				
Pa. kireevae Ovn.		x		x	x		x				x	x	x	x	x	x	x	x	x	x	x	
Pa. timanensis Klapper, Kuzmin et Ovnatanova		x		x	x	x	x		x	x	x	x	x		x	x	x					
Pa. ormistoni Klapper, Kuzm. et Ovn.		x				x	x	x			x											
Pa. semichatovae Ovn.						x	x		x	x	x	x	x		x	x	x					
Pa. mucronata Klapper, Kuzm. et Ovn.					x		x	x	x	x	x	x	x		x	x	x					
Pa. brevis Ziegler et Sandberg					x		x	x														
Pa. anzhelae Khruscheva et Kuzm.					x		x									?x						
Pa. ederi Ziegler et Sandberg					x		x			x		x	x		x							
Pelekysgnathus planus Sannemann					x										x							
Pa. plana Ziegler et Sandberg						x				x	x		x									
Po. lodinensis Pölsl.						x	x		x		x	x	x	x	x	x	x	x	x	x	x	
Pa. muelleri Klapper et Foster							x		x	x	x	x	x	x	x	x		x	x		x	
Ancyrognathus triangularis Youngq.							x		x		x	x				x	x					
Po. webbi Stauffer									x													
Ag. ancyrognathoideus Ziegler									x													
Ag. sp. indet.															x	x						
Pa. nasuta Muller										x	x	x			x		x	x		x	x	
Po. politus Ovn.											x			x	x						x	
Po. brevilamiformis Ovnatanova															x							
Po. unicornis Müll. et Müll.											x											
Pa. lyaiolensis Khruscheva et Kuzm.												x					x					
Pa. gyrata Kuzm.															?x							
Pa. rhenana Bisch.																			cf.x			
Pa. foliacea Youngq.																	x	x	x	x	x	x
Pa. jamieae Ziegler et Sandberg																	x	x				x
Ad. gigas Youngq.																x						
Ad. curvata Br. et M.										x												
Pa. subrecta Mill. et Youngq.																	x	x		x		x
Pa. aff. *coronata* Müll.																	x					
Pa. orlovi Khrustcheva et Kuzm.																	x	x	x	x	x	x
Pa. juntianensis Han.																				x		x
Pa. acutangularis sp. nov.																				x		
Pa. kaledai sp. nov.																				x		x
Pa. elegantula Wang et Ziegler																				x	x	
Pa. rotunda Ziegler et Sandberg																				x		
Po. brevis Mil. et Youngq.																				x		
Po. politus Ovnatanova														x							x	

Table 18. Distribution of conodonts in Frasnian and Lower Famennian deposits of Timanskaya, borehole no. 10 (collected by V.Vl. Menner and A.V. Kuzmin in 1989)

Regional Stage, substage, formation, member	Vetlasyan	Lower Sirachoi								Upper Sirachoi										Ukhta							Izhma
																				subsulphate member				lower sulphate member			
Sample, no.	65	64B	63	63A	63B	63C	62	62B	61	60	60A	59A	58	58A	57	57M	56	56A	55	53	53A	51	50	40	39	37	24
Depth, m / Species	474	456–457	450–452	430	422	421–426	420–421	415	410	392–393	388–390	382	370–371	366–367	363	365	362–363	356–357	354–355	314–315	295–297	287–289	268–269	200	191	188	72–73
Polygnathus webbi Stauffer	x	x											60														
Po. subincompletus Ovn. et Kon.			x	x			x	x	x	x	x		6														
Po. zinaidae Kon. et al.			x	x														x	x								
Po. aequalis Klap. et Lane			x			x				x																	
Po. churkini Sav. et Fun.			x			x					x			x					x	x	x				x		
Po. praepolitus Kon. et al.			x																								
Po. planarius Kl. et Lane				x	x																						
Icriodus symmetricus Br. et M.					x																						
Po. unicornis Müll. et Müll.					x					x cf									x	x							
Po. politus Ovn.					x	x	x	x			x				x		x			x						x	
Po. alvenus Ovn. et Kon.					x																						
Belodella sp.								x																			
Po. aspelundi Sav. et Fun.											x		x	x		x			x	x							
Po. maximovae Ovn. et Kon.											x		x		x			x	x	x			x	x	x		
Po. imparilis Kl. et Lane											?x																
Po. krestovnikovi Ovn.												x		x													
Po. evidens Kl. et Lane															x												
Po. torosus Ovn. et Kon.																x			x	x							
Po. azygomorphus Aristov																x											
Po. komi Kuzm. et Ovn.																x			x	x							
Po. costulatus Aristov																	x									x	
Palmatolepis semichatovae Ovn.																	x		x	x							
Po. brevis Müll. et Müll.																						x					
Po. dentimarginatus Kuzm.																								x	x	x	
Pelekysgnathus peejae Druce																											x
I. cornutus San.																											x
Po. tichonovitchi Kuzm																											x

Sargaevo conodont assemblage. A species assemblage identical to the assemblage of the upper part of the Timan Regional Stage was found in the lower unit of the Ust'-Yarega Formation in outcrop C on the Ukhta River. Representatives of *Ancyrodella* are absent in the assemblage possibly due to the facies reasons. It is known as assemblage TP-1 typical of the upper part of Timan and lowermost Ust'-Yarega formations.

The lower boundary of the Frasnian Stage was established at the border of the Lower–Upper Timan subformations.

Representatives of *Ancyrodella* (*A. africana, A. rugosa, A. recta*, and *A. rotundiloba*) and *Mesotaxis* (*M. asymmetrica, M. falsiovalis, M. costalliformis*) appear in the assemblage in the middle part of the Ust'-Yarega Formation (outcrop D on the Ukhta River and outcrop E on the Yarega River). *Polygnathus xylus, Po. webbi*, and *Po. angustidiscus* are also present. Earlier the assemblage was described as TP-2.

Palmatolepis transitans and *Mesotaxis bogoslovskyi* appear in the upper part of the Ust'-Yarega Formation (outcrop D on the Yarega River and outcrop 1 on the Chut' River) and *A. africana, A. alata, M. asymmetrica, M. falsiovalis, M. costalliformis, Po. webbi*, and *Po. angustidiscus* persisted in the assemblage. The assemblage was previously called TP 3. It is correlated with the *transitans* Zone (Ziegler and Sandberg, 1990).

Domanik assemblage. Conodonts from the shallow-water analogues of the Domanik Regional Stage are virtually unknown.

Polygnathus efimovae characterizes the reef-rock lower part of the Domanik Regional Stage near the western border of the Ukhta region; its upper part contains solitary *Polygnathus aequalis, Po. prepolitus, Po. webbi,* and *Palmatolepis punctata.* Further west, in Middle Timan, the analogues of the Domanik Regional Stage (Kraipol Formation) are represented only by polygnathid biofacies. In this region, *Polygnathus brevilamiformis, Po. pollocki*, and *Po. efimovae* were found in the lower subformation and *Polygnathus zinaidae* and *Po. webbi* were found in the upper subformation (Kuzmin, 2001).

Vetlasyan assemblage. Palmatolepids prevail in the conodont assemblage from the lower part of the Vetlasyan Formation, as is typical for relatively deep-water sedimentation conditions. *Pa. kireevae, Pa. transitans, Pa. punctata, Pa. proversa*, and *Pa. amplificata* were found in the sections of borehole 2060 (depth 225 m), 2040 (interval 345–360 m), Shudayag 1003 (interval 50–63 m), and Balneologicheskaya 3 (interval 50–55 m). *Pa. amplificata* was previously treated as *Pa. gigas* (Ovnatanova and Kuzmin, 1991) or as *Pa.* aff. *rhenana* (Kuzmin and Ovnatanova in Menner et al., 1992). *Ancyrodella nodosa, Polygnathus aequalis*, and *Po. politus* were also identified in these sections.

In the middle and upper parts of the Vetlasyan Formation, the polygnathids dominate. *Ancyrodella nodosa, Icriodus symmetricus, Po. aequalis, Po. evidens*, and numerous *Polygnathus reitlingerae* sp. nov. were found in outcrop 2A on the right bank of the Ukhta River near the village of Vetlasyan, where possibly the middle part of the Vetlasyan Regional Stage is exposed. *Polygnathus webbi* was identified in Timanskaya 10 at a depth of 474 m within the Vetlasyan deposits. *Polygnathus praepolitus* and *Po. subincompletus* were found in the upper part of the formation (borehole 2060, depth 85–86 m). On the whole, the Vetlasyan Regional Stage corresponds to the interval of the lower part of the Lower *gigas* conodont Zone (= Early *rhenana*).

Lower Sirachoi assemblage. Conodonts from the stratotype of the Lower Sirachoi Subformation are small in number and are represented by polygnathid biofacies. *Polygnathus komi, Po. subincompletus, Po. politus*, and *Po. krestovnikovi* were found in the lower part of the regional stage in outcrop 2A, Podgornyi Quarry, near the Vetlasyan railway station. *Po. zinaidae* and numerous *Polygnathus subincompletus* are known from the lowermost section (bed 1 in *Reference Sections*…, 1994, 1997) in outcrop 3A on the right bank of the Ukhta River, near the airport, 3 km downstream from the railway station. Juvenile *Palmatolepis kireevae* were found up the section in bed 4. At the top of the outcrop (bed 5), we identified *Po. unicornis, Polygnathus politus*, and *Po. subincompletus.* Conodonts of the Lower Sirachoi Formation were also studied in sections of boreholes 2040 and 2060 (Kuzmin and Ovnatanova, 1984), where *Palmatolepis* cf. *semichatovae* (borehole 2060, depth 65 m), *Palmatolepis punctata, Pa. hassi, Polygnathus unicornis, Polygnathus aequalis*, and *Ancyrodella nodosa* were identified. *Po. subincompletus, Po. zinaidae*, and *Po. churkini* prevail in the section of Timanskaya 10 (interval from 450–452 m up to 392–393 m). More detailed lists of the distribution of conodonts in the section of Timanskaya 10 are given in Table 18.

Upper Sirachoi assemblage. Data on the assemblage of conodonts in the stratotype of the Upper Sirachoi Subformation are restricted to records of *Polygnathus colliculosus* and *Po. churkini* from outcrop 6A "Novyi Kar'er" on Mt. Sirachoi (determination by A.V. Kuzmin). More representative assemblages are known from the sections of boreholes 2040, 2060, and 2051. The latter borehole contains *Polygnathus komi, Po. churkini, Po. politus*, and *Po. evidens* within an interval of 43–60 m. *Polygnathus subincompletus, Po. komi, Po. unicornis*, and *Palmatolepis semichatovae* were found in the section of borehole 2040 (interval 182–193 m). A rich assemblage was recorded in the section of Timanskaya 10 (interval from 388–390 m up to 354–355 m) and borehole 2060 (interval 15–42 m), where *Polygnathus maximovae, Po. sublatus, Po. siratchoicus*, and *Po. imparilis* appeared. Of palmatolepids, rare *Palmatolepis semichatovae* were found. The Sirachoi Regional Stage corresponds to the upper part of the conodont Early *rhenana* Zone.

The *Ukhta assemblage* is considerably poorer than the Sirachoi Formation assemblage. A.V. Kuzmin identified conodonts *Polygnathus* cf. *churkini* and *Palmatolepis* cf. *semichatovae* in the series underlying the sulfate-bearing series in outcrop 19 on the left bank of the Ukhta River. *Polygnathus unicornis, Po. churkini, Po. subincompletus, Po. komi, Po. alvenus*, and *Po. sublatus* were recorded in the lower part of the formation in the section of borehole 2060 (interval 9.5–11 m). A closely related assemblage of polygnathids was identified in the section of Timanskaya 10 (Table 14). In the strata underlying the sulfate-bearing strata, *Palmatolepis semichatovae* (interval 314–315 m) and *Polygnathus brevis* (borehole 10, interval 287–292 m) were found. Conodonts are rare in the lowermost sulfate-bearing member. *Polygnathus dentimarginatus, Polygnathus churkini*, and *Po. costulatus* were identified in the section of Timanskaya 10 (interval 191–200 m). The same assemblage was recorded in the section of Bel'gop 4 (148–154 m). Conodonts are unknown from the upper part of the sulfate-bearing member.

Izhma assemblage. Only *Polygnathus brevilaminus, Icriodus iowaensis, I. cornutus*, and *I. alternates* were found in the stratotype of the Izhma Formation, outcrop 20.

The distribution of conodonts in the shallow-shelf deposits of the Frasnian–lowermost Famennian Stages of the Ukhta region is shown in Table 19. The succession of assemblages here is similar to that of the sections of the central Russian Platform and Ural–Volga region. The joint distribution of conodonts in the shallow-shelf Frasnian–Lower Famennian deposits of the two studied regions is shown in Table 20.

4.5.2. Frasnian Conodont Assemblages from the Basinal Sections of Southern Timan

As the sections and assemblages are well differentiated beginning with the Domanik level, and the assemblages of the Timan and Sargaevo regional stages are described in the previous chapter on the shallow-water assemblages; here we consider the assemblages of Domanik and Lyaiol' formations. The sections of the Domanik Formation and the distribution of conodonts in them were repeatedly discussed in the literature (Ovnatanova and Kuzmin, 1991; Kuzmin and Yatskov, 1997; Menner et al., 1992; Ovnatanova et al., 1999a, 1999b; Klapper et al., 1996; Becker et al., 2000). The Lyaiol' Formation is described in detail in this chapter in the description of the stratotype and parastratotype of the Lyaiol' Formation (Tables 16, 17). The upper part of the Evlanovo Regional Stage and the Livny Regional Stage are described based on the sections of the Izhma–Pechora depression (Kuzmin et al., 1998).

In the lower unit and basal clayey bed of the middle unit of the Domanik Formation, *Palmatolepis punctata* appear at the base of the section, and slightly upward in the section *Ancyrodella gigas, Pa. gutta, Po. timanicus, Po. vjalovi*, and *Mesotaxis johnsoni* appear. *Po. brevilamiformis* and *Po. strictus* also appeared. *Palmatolepis transitans* and *Klapperina ovalis* (lower part of the section) persisted. *Polygnathus pollocki, Po. pennatus, Po. dubius*, and *Mesotaxis* (*M. asymmetricus, M. falsiovalis, M. dengleri, M. bogoslovskyi*) are also present, and here became extinct. The assemblage was established in numerous outcrops in the lower reaches of the Chut' River (outcrop 1) and upstream (outcrops 2 and 3) and on the right bank of the Ukhta River in the mouth of the Chut' River. Earlier the assemblage was called TP 4. From this point on the Timan–Pechora (TP) assemblages are numbered according to Ovnatanova et al. (1999).

Ancyrognathus ancyrognathoideus, Anc. primus, Ancyrodella curvata, Palmatolepis domanicensis, Pa. orbicularis, Pa. spinata, Pa. bohemica, Ozarkodina trepta, Pa. kireevae, Pa. ljaschenkoae, and *Pa. proversa* appear successively in the assemblage in the upper part of the middle unit of the Domanik Formation (except the basal clayey bed). *Pa. punctata, Pa. transitans*, and *Po. brevilamiformis* are still present. *Po. uchtensis* and *Po. lodinensis* appear. The conodont assemblage of the middle unit of the Domanik Formation was established based on a number of outcrops in the lower reaches of the Chut' River, quarries and outcrops near the Ukhta River downstream of the mouths of the Chut' and Krokhal' rivers, on the Ukhta River near the hospital at the village of Shudayag, on the Domanik River, and in boreholes 2068, 1003, and 3B. Earlier it was known as assemblage TP 5. Outside the outcrops on the Chut' and Ukhta rivers, the assemblage of the middle member was also identified in outcrops 1351 and 1903 on the Lyaiol' River (collected by V.Vl. Menner, 2000). *Pa. orbicularis, Pa. transitans, Pa. punctata*, and *Polygnathus uchtensis* were found in outcrop 1351 and *Pa. orbicularis, Pa. punctata, Po. uchtensis, Ancyrognathus amplicavus, Anc. ancyrognathoideus, Pa. kireevae, Pa. kuschnarevae*, and *Pa. proversa* were found in outcrop 1903. It is worth noting that *Pa. spinata* is absent in the assemblage.

Within the Ukhta and Chut' rivers, in the lower part of the third unit of the Domanik Formation, the assemblage is almost identical to the above TP 5 assemblage. However, it lacks *Pa. spinata* and *Pa. bohemica.* A single specimen of *Ozarkodina nonaginta* was found in the sections of the Ukhta region. The assemblage was earlier described as TP 6.

In the upper part of the third unit, *Pa. amplificata, Pa. ederi, Pa. mucronata, Pa. plana, Pa. ormistoni*, and *Pa. timanensis* appear. *Ancyrognathus ancyrognathoideus, Palmatolepis domanicensis, Pa. orbicularis, Pa. punctata, Pa. proversa, Pa. ljaschenkoae, Pa. kireevae*, and *Po. uchtensis* are still present. The assemblage was earlier described as TP 7. The conodont assemblages of unit 3 were identified in the sections of boreholes 2056, 3B, and 1003 (lower part of the unit) and in the outcrop on the left bank of the Ukhta River

Table 19. Distribution of conodonts in shallow-water deposits of the Frasnian and the bottom of the Famennian in the Ukhta Region

Stage	Frasnian							Famennian
Regional Stage	Timan (upper part)	Sargaevo	Domanik	Vetlasyan	Sirachoi	Evlanovo	Livny	Zadonsk
Formation	Timan	Ust'-Yarega	Ezhvador	Vetlasyan	Sirachoi	Ukhta		Izhma
Strata / Species						subsul-phate	sulphate	
Polygnathus alatus Huddle	———	——— - - -	- - -					
Po. pennatus Hinde	———	———	——— - - -	- - -				
Po. xylus Stauf.	———	——— - - -	- - -					
Po. webbi Stauf.	———	———	———	———	———			
Po. angustidiscus Young.	———	———	———					
Po. pollocki Druce		———	———					
Po. posterus Kuzm.	———	———						
Po. ljaschenkoi Kuzm.	———	———						
Po. dubius Hinde sensu Klapper et Ph.		———	———					
Mesotaxis dengleri Bisch. et Z.		———	———					
M. bogoslovskyi Ovn. et Kuzm.		———	———					
Ancyrodella rugosa Br. et M.		———	———					
Ad. rotundiloba (Bryant)		———	———					
Ad. recta Kralick		———	———					
Ad. africana Garcia-Lopez		———	———					
Ad. alata Glen. et Kl.		———	———					
Mesotaxis falsiovalis Z., Sandb. et Bult.		———	———					
M. costalliformis (Ji)		———	———					
Klapperina ovalis (Z. et Kl.)		———	———					
Mesotaxis distinctus Ovn. et Kuzm.		———	———					
M. asymmetrica (Bisch. et Z.)		———	———					
Palmatolepis transitans Müller		———	———					
Polygnathus efimovae Kon. et al.			———					
Po. uchtensis Ovn. et Kuzm.			———					
Polygnathus timanicus Ovn.			———					
Po. praepolitus Kon. et al.			———	———	———			
Palmatolepis punctata (Hinde)			- - - ———	- - - - - -	———			
Polygnathus brevilamiformis Ovn.			———	- - - - - -	- - -			
Po. aequalis Kl. et Lane			- - -	- - - - - -	———	———		

Table 19. (Contd.)

Stage	Frasnian							Famennian
Regional Stage	Timan (upper part)	Sargaevo	Domanik	Vetlasyan	Sirachoi	Evlanovo	Livny	Zadonsk
Formation	Timan	Ust'-Yarega	Ezhvador	Vetlasyan	Sirachoi	Ukhta		Izhma
Strata / Species						subsul-phate	sulphate	
Po. azygomorphus Aristov								
Palmatolepis proversa Z.								
Polygnathus subincompletus Ovn. et Kon.								
Po. reitlingerae sp. nov.								
Ancyrodella nodosa Ulr. et Bassl.								
Polygnathus aspelundi Sav. et Fun.								
Po. politus Ovn.								
Po. unicornis Müll. et Müll.								
Po. brevis Mill. et Joung.								
Po. evidens Kl. et Lane								
Po. macilentus Kuzm.								
Po. zinaidae Kon. et al.								
Po. imparilis Kl. et Lane								
Palmatolepis semichatovae Ovn.								
Polygnathus churkini Sav. et Fun.								
Po. colliculosus Aristov								
Po. maximovae Ovn. et Kon.								
Po. krestovnikovi Ovn.								
Po. alvenus Ovn. et Kon.								
Po. komi Kuzm. et Ovn.								
Po. torosus Ovn. et Kon.								
Po. siratchoicus Ovn. et Kuzm.								
Po. sublatus Ulr. et Bassl.								
Po. costulatus Aristov								
Po. dentimarginathus Kuzm.								
Po. brevilaminus Br. et M.								
Pelekysgnathus peejae Druce								
Polygnathus tichonovitchi Kuzm. et Meln.								
Icriodus cornutus San.								

Table 20. Distribution of conodonts in shallow-water deposits of the Frasnian and bottom of the Famennian of the Volga–Ural Province and Ukhta Region of southern Timan

Volga–Ural regional stages	Timan (upper part)	Sargaevo	Semiluki	Rechitsa	Voronezh	Evlanovo	Livny	Zadonsk
Southern Timan formations	Timan	Ust'-Yarega	Ezhvador	Vetlasyan	Sirachoi	Ukhta		Izhma
Species								
Polygnathus xylus Stauf.								
Po. alatus Huddle								
Po. webbi Stauf.								
Po. angustidiscus Young. s. l.								
Po. posterus Kuzm.								
Po. ljaschenkoi Kuzm.								
Po. dubius Hinde sensu Klapper et Phil.								
Po. pollocki Druce								
Po. pennatus Hinde								
Po. pseudoxylus Kon. et al.								
Po. denisbriceae Bult.								
Klapperina ovalis (Z. et Kl.)								
Mesotaxis asymmetricus (Bisch. et Z.)								
M. falsiovalis Z., Sandb. et Bult.								
M. bogoslovskyi Ovn. et Kuzm.								
M. distinctus Ovn. et Kuzm.								
Ancyrodella binodosa Uyeno								
Ad. rotundiloba (Bryant)								
Ad. rugosa Br. et M.								
Ad. recta Kralick								
Ad. africana Garcia-Lopez								
Ad. alata Glen. et Kl.								
Palmatolepis transitans Müller								
Polygnathus reimersi Kuzm.								
Mesotaxis dengleri Bisch. et Z.								
M. costalliformis (Ji)								
Palmatolepis punctata (Hinde)								
Polygnathus praepolitus Kon. et al.								
Po. efimovae Kon. et al.								
Po. brevilamiformis Ovn.								
Po. azygomorphus Aristov								
Po. zinaidae Kon. et al.								
Po. aspelundi Sav. et Fun.								
Po. reitlingerae sp. nov.								

Table 20. (Contd.)

Volga–Ural regional stages	Timan (upper part)	Sargaevo	Semiluki	Rechitsa	Voronezh	Evlanovo	Livny	Zadonsk
Southern Timan formations / Species	Timan	Ust'-Yarega	Ezhvador	Vetlasyan	Sirachoi	Ukhta		Izhma
Palmatolepis proversa Z.								
Pa. semichatovae Ovn.								
Polygnathus ilmenensis Zhuravlev								
Po. aequalis Kl. et Lane								
Po. uchtensis Ovn. et Kuzm.								
Po. timanicus Ovn.								
Po. subincompletus Ovn. et Kon.								
Ancyrodella nodosa Ulr. et Bassl.								
Polygnathus politus Ovn.								
Po. evidens Kl. et Lane								
Po. imparilis Kl. et Lane								
Po. churkini Sav. et Fun.								
Po. sublatus Ulr. et Bassl.								
Po. siratchoicus Ovn. et Kuzm.								
Po. torosus Ovn. et Kon.								
Po. maximovae Ovn. et Kon.								
Po. seraphimae Ovn. et Kon.								
Po. krestovnikovi Ovn.								
Po. unicornis Müll. et Müll.								
Po. colliculosus Aristov								
Po. alvenus Ovn. et Kon.								
Polygnathus komi Kuzm. et Ovn.								
Po. brevis Mill. et Young.								
Po. macilentus Kuzm.								
Po. costulatus Aristov								
Po. dentimarginathus Kuzm.								
Po. brevilaminus Br. et M.								
Pelekysgnathus peejae Dr.								
Pel. planus San.								
Polygnathus tichonovitchi Kuzm. et Meln.								
Icriodus cornutus San.								
I. iowaensis Young. et Pet.								
Palmatolepis wolskae Ovn.								

Table 21. Distribution of conodonts in Frasnian basinal deposits of southern Timan

Regional stage	Domanik			Vetla-syan	Sirachoi		Evlanovo		Livny
Formation	Domanik			Lyaiol'				Ukhta	
Species / Unit	1	2	3	1	2	3	4		
Palmatolepis transitans Müller									
Pa. punctata (Hinde)									
Pa. gutta Kuzm.									
Pa. rotundilobata Kuzm.									
Pa. maximovae Kuzm.									
Pa. triquetra Kuzm.									
Pa. keyserlingi Kuzm.									
"*Polygnathus foliatus*" Bryant									
Po. strictus Ovn. et Kuzm.									
Po. webbi Stauf.									
Po. uchtensis Ovn. et Kuz.									
Po. olgae Ovn. et Kuzm.									
Po. timanicus Ovnat.									
Po. vjalovi Zver.									
Po. brevilamiformis Ovn.									
Po. pollocki Druce									
Po. pennatus Hinde									
Ancyrodella gigas Young.									
Polygnathus dubius Hinde sensu Kl. et Ph.									
Mesotaxis asymmetricus (Bisch. et Z.)									
M. distinctus Ovn. et Kuzm.									
M. falsiovalis Z., Sandb. et Bult.									
M. dengleri Bisch. et Z.									
M. johnsoni Kl., Kuzm. et Ovn.									
M. bogoslovskyi Ovn. et Kuzm.									
Polygnathus lodinensis Pölster									
Ozarkodina trepta Z.									
Oz. nonaginta Kl., Kuzm. et Ovn.									
Palmatolepis menneri sp. nov.									
Pa. orbicularis Ovn. et Kuzm.									
Pa. spinata Ovn. et Kuzm.									
Pa. ljaschenkoae Ovn.									
Pa. bohemica Kl. et Foster									
Pa. hassi Müll. et Müll.									
Pa. domanicensis Ovn.									
Pa. kuschnarevae Ovn. et Kuzm.									
Ancyrognathus ancyrognathoideus Z.									
Anc. primus Ji									
Palmatolepis nasuta Müll.									
Pa. barba Z. et Sandb.									
Pa. ormistoni Kl., Kuzm. et Ovn.									

Table 21. (Contd.)

Regional stage	Domanik			Vetla-syan	Sirachoi		Evlanovo		Livny
Formation	Domanik			Lyaiol'				Ukhta	
Species / Unit	1	2	3	1	2	3	4		
Klapperina ovalis (Z. et Kl.)	—	—							
Palmatolepis proversa Ziegl.		—	—	—	—	—			
Pa. amplificata Kl., Kuzm. et Ovn.			—	—	—	—			
Pa. mucronata Kl., Kuzm. et Ovn.			—	—	—	—	—		
Pa. kireevae Ovn.		—	—	—	—	—	—	—	
Ancyrodella nodosa Ulr. et Basll.			—	—	—	—	—	—	
Palmatolepis semichatovae Ovn.					—	—	- -	- -	
Pa. plana Z. et Sandb.				—	—	—			
Pa. ederi Z. et Sandb.				—	—				
Pa. muelleri Kl. et Fost.				—	—	—	—	—	
Ancyrognathus triangularis Young.				—	—	—	—		
Palmatolepis elegantula Wang et Z.					—	—	—		
Pa. anzhelae Khr. et Kuzm.					—	—	—	—	
Pa. timanensis Kl., Kuzm. et Ovn.					—	—	—		
Pa. brevis Z. et S.				—	—	—	—		
Pa. gyrata Kuzm. et Meln.						—	—	—	
Pa. foliacea Young.						—	—	—	—
Pa. subrecta Mill. et Young.						—	—	—	—
Pa. lyaiolensis Khrusch. et Kuzm.					—	—	—	—	
Pa. jameae Z. et Sandb.						—	—	—	
Pa. orlovi Khrusch. et Kuzm.						—	—	—	—
Pa. kaledai sp. nov.							—	—	
Pa. acutangularis sp. nov.							—	—	
Icriodus interjectus Kuzm. et Ovn.					—	—	—	—	
Palmatolepis rotunda Z. et Sandb.									—
Pa. juntianensis Han.							—	—	
Pa. praetriangularis Sandb. et Z.									—
Pa. rhenana Bisch. et Z.							- -	- -	—
Polygnathus unicornis Müll. et Müll.				—	—	—	- -	- -	
Po. brevis Mil. et Young.							—	—	
Po. politus Ovn.					—	—	—	—	
Po. alvenus Ovn. et Kon.							—		
Po. macilentus Ovn.							—	—	
Po. krestovnikovi Ovn.					—	—			
Po. subincompletus Ovn. et Kon.							—		
Po. zinaidae Ovn. et Kon.		—							
Po. siratchoicus Ovn. et Kuzm.							—	—	
Po. imparilis Kl. et Lane						—	—		
Palmatolepis linguiformis Müll.									—
Ancyrodella ioides Z.									—
Timan–Pechora assemblages	4	5	6	7	8	9	10		11

Table 22. Distribution of conodonts in basin deposits of the Frasnian and the bottom of Famennian of the Volga–Ural Province and southern Timan

Region	Stage	Frasnian								Famennian
Volga–Ural	Regional stage	Timan	Sargaevo	Domanik	Mendym		Askyn			
Southern Timan	Regional stage	Timan (upper part)	Sargaevo	Domanik	Vetla-syan	Sirachoi	Evlanovo		Livny	Volgograd
	Formation	Timan	Ust'-Yarega	Domanik	Lyaiol'					
Species \ Unit					1	2	3	4		
Ancyrodella binodosa Uyeno										
A. rugosa Br. et M.										
A. alata Glen. et Klap.										
A. rotundiloba (Bryant)										
Klapperina ovalis (Z. et Kl.)										
Mesotaxis asymmetricus (Bisch. et Z.)										
M. falsiovalis Z., Sandb. et Bult.										
Polygnathus denisbriceae Bult.										
Po. xylus St.										
Pa. ljaschenkoae Kuzm.										
Po. olgae Ovn. et Kuzm.										
Mesotaxis distinctus Ovn. et Kuzm.										
M. dengleri Bisch. et Z.										
M. johnsoni Kl., Kuzm. et Ovn.										
M. costalliformis (Ji)										
M. bogoslovskyi Ovn. et Kuzm.										
Polygnathus decorosus Stauf.										
Po. webbi Stauf.										
Po. alatus Huddle										
"Po. foliatus" Bryant										
Po. dubius Hinde sensu Kl. et Ph.										
Po. efimovae Kon. et al.										
Po. timanicus Ovn.										
Po. azygomorphus Aristov										
Po. pollocki Druce										
Po. pennatus Hinde										
Po. brevilamiformis Ovn.										
Po. pseudoxylus Kon. et al.										
Po. strictus Ovn. et Kuzm.										
Palmatolepis transitans Müller										
Pa. maximovae Kuzm.										
Pa. punctata (Hinde)										
Pa. spinata Ovn. et Kuzm.										
Pa. gutta Kuzm.										
Pa. keyserlingi Kuzm.										
Pa. triquetra Kuzm.										
Ancyrodella gigas Young.										
Palmatolepis rotundilobata Kuzm.										
Polygnathus vjalovi Zver.										
Palmatolepis proversa Z.										
Pa. bohemica Kl. et Foster										
Polygnathus uchtensis Ovn. et Kuz.										
Palmatolepis domanicensis Ovn.										
Pa. menneri sp. nov.										
Pa. kuschnarevae Ovn. et Kuzm.										
Pa. kireevae Ovn.										
Pa. orbicularis Ovn. et Kuzm.										
Ancyrognathus ancyrognathoideus Z.										
Anc. primus Ji										
Polygnathus praepolitus Kon. et al.										

Table 22. (Contd.)

Region	Stage	Frasnian								Famennian
Volga–Ural	Regional stage	Timan	Sargaevo	Domanik	Mendym		Askyn			
Southern Timan	Regional stage	Timan (upper part)	Sargaevo	Domanik	Vetla-syan	Sirachoi	Evlanovo		Livny	Volgograd
	Formation	Timan	Ust'-Yarega	Domanik	Lyaiol'					
Species / Unit					1	2	3	4		
Po. lodinensis Pölster										
Palmatolepis ljaschenkoae Ovn.										
Ozarkodina trepta Z.										
Oz. nonaginta Kl., Kuzm. et Ovn.										
Ancyrodella nodosa Ulr. et Basll.										
Palmatolepis muelleri Kl. et Fost.										
Pa. ormistoni Kl., Kuzm. et Ovn.										
Pa. semichatovae Ovn.										
Pa. anzhelae Khr. et Kuzm.										
Pa. timanensis Kl., Kuzm. et Ovn.										
Pa. brevis Z. et S.										
Pa. ederi Z. et Sandb.										
Pa. hassi Müll. et Müll.										
Pa. amplificata Kl., Kuzm. et Ovn.										
Pa. plana Z. et Sandb.										
Pa. barba Z. et Sandb.										
Pa. mucronata Kl., Kuzm. et Ovn.										
Polygnathus unicornis Müll. et Müll.										
Po. maximovae Ovn. et Kon.										
Po. zinaidae Kon. et al.										
Po. imparilis Kl. et Lane										
Po. politus Ovn.										
Po. subincompletus Ovn. et Kon.										
Ancyrognathus triangularis Young.										
Palmatolepis foliacea Young.										
Polygnathus krestovnikovi Ovn.										
Palmatolepis gyrata Kuzm. et Meln.										
Pa. jamieae Z. et Sandb.										
Polygnathus macilentus Kuzm.										
Palmatolepis subrecta Mill. et Young.										
Pa. lyaiolensis Khr. et Kuzm.										
Pa. orlovi Khr. et Kuzm.										
Icriodus interjectus Kuzm. et Ovn.										
Polygnathus brevis Mill. et Joung.										
Palmatolepis rotunda Z. et Sandb.										
Polygnathus alvenus Ovn. et Kon.										
Palmatolepis elegantula Wang et Z.										
Pa. nasuta Müll.										
Pa. kaledai sp. nov.										
Pa. acutangularis sp. nov.										
Polygnathus siratchoicus Ovn. et Kuzm.										
Palmatolepis rhenana Bisch.										
Pa. praetriangularis Sandb. et Z.										
Pa. juntianensis Han										
Ancyrodella ioides Z.										
Palmatolepis linguiformis Müller										
Pa. triangularis San.										
Pa. delicatula delicatula Br. et M.										
Pa. delicatula platys Z. et Sandb.										
Pa. subperlobata Br. et M.										
Pa. weddigei Ji et Z.										

near the hospital at the village of Shudayag; in the middle and upper parts of the member, they were identified in the ditch of the new water-intake structure and in the road cuttings on the left bank of the Ukhta River upstream of the village of Shudayag. They were also found in outcrops 1353 and 1903 on the Lyaiol' River.

Conodonts from the Upper Frasnian interval were identified from the outcrops of Lyaiol' Formation (Lyaiol' and Vezha-Vozh rivers). Carbonate and clayey deposits of the lower units (1 and 2) of the Lyaiol' Formation are the basin facies; units 3 and 4 are slope facies.

The richest assemblage of unit 1 of the Lyaiol' Formation was found in outcrops 1354 on the Lyaiol' River. Conodonts *Palmatolepis mucronata, Pa. elegantula, Pa. timanensis, Pa. barba, Pa. proversa, Pa. mulleri, Pa. ljaschenkoae, Pa. brevis*, and *Pa. kireevae* were identified in the lower limestone interbed. Of polygnathids, only *Polygnathus lodinensis* was found. Isolated specimens of *Ancyrodella gigas* and *Belodella* sp. were also identified. A rich palmatolepid assemblage consisting of *Palmatolepis proversa, Pa. punctata, Pa. orbicularis, Pa. ederi, Pa. kireevae, Pa. mucronata*, and *Pa. plana* was found in the calcareous interbed of outcrop 1905 on the Lyaiol' River. *Ancyrognathus triangularis* and *Polygnathus unicornis* appear. Of polygnathids, *Polygnathus lodinensis* develops significantly.

Palmatolepis elegantula and *Ancyrognathus triangularis* appear in the carbonates of unit 2 and the lowermost unit 3 (Sirachoi Regional Stage). *Palmatolepis semichatovae, Pa. timanensis*, and *Pa. anzhelae* appear beginning with the middle of unit 2. *Palmatolepis plana, Pa. kireevae, Pa. ormistoni, Pa. amplificata*, etc., were also found. The assemblage was earlier called TP 8.

In the upper part of unit 3 and in unit 4 of the Lyaiol' Formation (lower part of the Evlanovo Regional Stage), *Palmatolepis gyrata, Pa. foliacea, Pa. subrecta*, and *Pa. hassi* appear. *Palmatolepis jamieae, Pa. nasuta*, and *Pa. orlovi* appear beginning with the base of unit 4. *Palmatolepis elegantula, Pa. amplificata*, etc., persist. *Ancyrodella nodosa, Ancyrognathus amana*, and *Icriodus interjectus* are rare. The assemblage was earlier known as TP 9.

The stratigraphical range of conodonts in the upper part of the Evlanovo Regional Stage and in the Livny Regional Stage is given according to Kuzmin et al. (1998), based on the sections of the Tebuk-Vis District of the Izhma–Pechora depression.

The upper part of the Evlanovo Regional Stage is characterized by the appearance of *Palmatolepis juntianensis, Pa. rotunda*, and *Pa.* cf. *rhenana* (assemblage TP 10).

The Livny Regional Stage is determined above all by the appearance of *Palmatolepis linguiformis. Palmatolepis subrecta, Pa. rhenana, Pa. rotunda, Palmatolepis juntianensis*, and *Pa. orlovi* continue to exist. The assemblage was earlier called TP 11. Assemblages corresponding to the *triangularis–crepida* zones of the standard scale of the Famennian Stage were recognized in stratigraphically higher layers in a number of basinal sections of the Izhma–Pechora depression of Southern Timan.

The distribution of Frasnian–Lower Famennian conodonts in the basinal sections of Southern Timan is shown in Table 21. The revealed succession of species is only partly confirmed based on the sections of the Volga–Ural province primarily due to poor coring. The summary table of the distribution of the Frasnian–Lower Famennian conodonts in the basinal sections of the two regions considered above is shown in Table 22.

CHAPTER 5. CORRELATION OF THE FRASNIAN DEPOSITS OF THE EASTERN RUSSIAN PLATFORM WITH THE CONODONT ZONAL SCALES

The conodont zones that were established by Ziegler (1962a, 1971) for the basinal sections of the Upper Devonian of the Rhenish Slate Mountains, were then used for a long time for the Russian Platform. Subsequently, the zones of the standard conodont zonation established by Ziegler and Sandberg (1990) were also used. This zonation was worked out on the same Frasnian sections of the Rhenish Slate Mountains and on the sections of Nevada (North America) and was based on the phylomorphogenesis of the genus *Palmatolepis*. However, isolated levels that were difficult to correlate were frequently revealed on the Russian Platform and therefore local conodont zones were often established at these levels (Chernysheva and Khalymbadzha, 1978; Ovnatanova and Kononova, 1984). In fact, the boundaries of some zones of the standard scale (*transitans, punctata, linguiformis*) are confidently defined. Some other zones (Early and Late *hassi, jamieae*, Late *rhenana*) are difficult and sometimes (Lowermost *asymmetricus*) impossible to determine because of the facies peculiarities of the lower part of the Frasnian Stage (only polygnathid biofacies are developed).

The Early *hassi* Zone was established by Ziegler and Sandberg (1990) within the range of the Upper *asymmetrica* Zone of the former conodont scale of Ziegler (1971). However, only numerous *Mesotaxis asymmetricus* have been recorded at this level by many investigations in the Volga–Ural region and Timan–Pechora province; *Palmatolepis hassi* has not been found. It is very rare and appears only up the section at the level corresponding to the Late *hassi* Zone.

The Late *hassi* Zone is defined by the first appearance of *Ancyrognathus triangularis.* However, the latter was not found at this level on the east of the platform and was only once encountered upward in the section at the level corresponding to the former Lower *gigas* Zone.

Palmatolepis jamieae is an index species of the zone with the same name. It was very rarely found in the

Table 23. Frasnian zonal conodont scale for relatively deepwater deposits of the eastern Russian Platform and correlation with the regional stages, Timan–Pechora assemblages (TP 1–TP 11), and other conodont scales

Stage	Volga–Urals (relatively deep-water type of section)	Southern Timan			Frasnian conodont zonal scale for relatively deepwater sections of the eastern Russian Platform (Ovnatanova et al., 2000, modified)	TP assem-blages (Ovnatanova et al., 1999)	Correlative levels (hatched)	Conodont zonation	
		regional stage	formation	unit				Ziegler, 1962a, 1971	Ziegler and Sandberg, 1990
Famen-nian	Volgograd		Savinobor		*Pa. triangularis*			Middle *triangularis*	
								Lower *triangularis*	
Frasnian	Askyn	Livny			*Pa. linguiformis*	11		Uppermost *gigas*	*linguiformis*
		Evlanovo			*Pa. juntianensis*	10		Upper *gigas*	Late *rhenana*
			Sed'yu						
			Lyaiol	4					
				3	*Pa. gyrata*	9			
	Mendym	Sirachoi		2	*Pa. elegantula–Pa. semicha-tovae*	8		Lower *gigas*	Early *rhenana*
		Vetlasyan		1		7			
	Domanik		Domanik	3	*Pa. mucronata–amplificata*	6		*Ancyrognathus triangularis*	*jamieae*
				2	*Anc. ancyrognathoideus–Pa. orbicularis*	5			Late *hassi*
								unzoned	Early *hassi*
				1	*Po. efimovae–Pa. punctata*	4		Upper *asymmetricus*	
								Middle *asymmetricus*	*punctata*
	Sargaevo		Ust'-Yarega		*A. alata–M. bogoslovskyi*	3		Lower *asymmetricus*	*transitans*
					A. rotundiloba–A. africana	2			Late *falsiovalis*
	Timan		Timan		*Po. pennatus–Po. ljaschenkoi*	1		lowermost *asymmetricus*	Early *falsiovalis*
Give-tian						0			

Table 24. Frasnian zonal conodont scale for shallow-water deposits of the eastern Russian Platform and correlation with the regional stages of the Russian Platform and other conodont scales

Stage	Regional stages of the Russian Platform (Volga–Ural and southern Timan regions)		Frasnian conodont zonal scale for shallow sea deposits (Ovnatanova and Kononova, 2001, modified)		Correlative levels (hatched)	Zonal conodont scales: Ziegler, 1962a, 1971	Zonal conodont scales: Ziegler and Sandberg, 1990
Frasnian	Livny	Ukhta Formation	Beds with *Po*. aff. *brevilaminus*			Uppermost *gigas*	*linguiformis*
	Evlanovo		*Po. maximovae*	Beds with *Po. brevis–Po. macilentus*		Upper *gigas*	Late *rhenana*
	Voronezh	Sirachoi		Beds with *Po. churkini–Po. komi*		Lower *gigas*	Early *rhenana*
	Rechitsa	Vetlasyan	*Po. subincompletus*				
	Domanik (Semiluki)		Beds with *Po. aspelundi*			*Anc. triangularis*	*jamieae*
							Late *hassi*
						unzoned	Early *hassi*
			Po. efimovae			Upper *asymmetricus*	
						Middle *asymmetricus*	*punctata*
	Sargaevo		*A. alata–M. bogoslovskyi*			Lower *asymmetricus*	*transitans*
			A. rotundiloba–A. africana				Late *falsiovalis*
	Timan		*Po. pennatus–Po. ljaschenkoi*			lowermost *asymmetricus*	Early *falsiovalis*
Give-tian							

regions studied and only at higher stratigraphical levels, where *Palmatolepis foliacea, Pa. subrecta*, and *Pa. nasuta* were also identified.

The base of the overlying Early *rhenana* Zone (index species of the *Pa. nasuta* Zone) coincides with the base of the former Lower *gigas* Zone. Unfortunately, the index species of the *Pa. nasuta* Zone is very rare in the collections from the Volga–Ural region and Timan–Pechora province and was only found upward in the section together with *Pa. subrecta* and *Pa. jamieae*. This is probably due to the facies peculiarities as this species is widespread in the flinty strata of the Polar Urals. Earlier the Lower *gigas* Zone was established based on palmatolepids with an elongated lateral lobe, which are now referred to *Pa. amplificata* and *Pa. mucronata.*

The Late *rhenana* Zone is determined by the first appearance of *Pa. rhenana.* Unfortunately, this species is almost unknown on the Russian Platform. Earlier this zone was established based on the species *Pa. subrecta* and *Pa. juntianensis*, which occur in association with *Pa. rhenana*, in the upper part of the Late *rhenana* Zone.

The *linguiformis* Zone of the standard scale of Ziegler and Sandberg (1990) completes the section of the Frasnian Stage. This zone and the overlying Lower Famennian *triangularis–crepida* zones are easily traced.

The correlation of these assemblages (TP 1–TP 11), which were previously established in Southern Timan (Ovnatanova et al., 1999), with the zonal conodont scales of the Frasnian Stage (Ziegler, 1962a, 1971; Ziegler and Sandberg, 1990) is shown the Table 23 (right part).

The correspondence with the scale of Ziegler (1962a, 1971) is as follows:

Assemblages TP 2 and TP 3 correspond to the Lower *asymmetricus* Zone; assemblage TP 4 corresponds to the Middle–Upper *asymmetricus* Zone. The correlation of assemblages TP 5–7 with the scale is impossible. It may be assumed that assemblage TP 5 belongs to the "unzoned" interval after the disappearance of *Mesotaxis,* TP 6 belongs to the *Ancyrognathus triangularis* Zone, and interval TP 7 to the lower part of the Lower *gigas* Zone. Assemblage TP 8 is correlated with the Lower *gigas* Zone based on the presence of *Palmatolepis semichatovae*; TP 9 and TP 10 with the Upper *gigas* Zone, and TP 11 with the Uppermost *gigas* Zone.

The correlation with the zones of the standard conodont scale of Ziegler and Sandberg (1990) is as follows: there are no data for the correlation of TP 1 and TP 2; TP 3 correlates with *transitans*; TP 4 correlates with *punctata*; correlation of TP 5 and TP 6 with intervals of the *hassi–jamieae* zones is unclear; TP 7 is presumably correlated with the lower part of the Early *rhenana* Zone; TP 8 correlates with the Early *rhenana* Zone; TP 9 and TP 10 correlate with the Late *rhenana* Zone; and TP 11 correlates with the *linguiformis* Zone (Table 24).

The conodont succession studied is also correlated with the scale of Montagne Noire (Klapper, 1988). MN Zones 4–13 were established in Southern Timan (Klapper et al., 1996). At the same time MN Zones 7 and 8 are hardly traced. The following study of the material from outcrops of the Ukhta region revealed additional difficulties in the tracing of MN Zones 7–10. The difficulties were connected with the fact that *Palmatolepis domanicensis* was chosen as an index species of MN Zone 10. This species was first described from Southern Timan, where it appears below the level MN 10, which was indicated in the scale, i.e., in the second unit of the Domanik Formation, which corresponds to the MN Zone 6. The determination of the MN Zone 11 (index species *Pa. jamieae*) was also obscure and therefore the zone was traced using the index species *Palmatolepis semichatovae* (Klapper et al., 1996). The MN scale was somewhat improved based, among other things, on the revision of the Timan material (Klapper and Becker, 1999). Now the following correlation of the MN zones with the local zonal assemblages seems to be possible (Table 24): TP 2 with MN 3; TP 3 with MN 4; TP 4 with MN 5; TP 5 with MN 6; TP 6 was tentatively correlated with the interval of MN Zones 7–10. Based on the presence of rare *Pa. elegantula*, assemblages TP 7 and TP 8 are correlated with MN 11; TP 9 with MN 12; TP 10 and TP 11 with MN 13. The MN scale and conodont scale of Ziegler and Sandberg (1990) are hardly correlated. The base of MN Zone 4 corresponds to the base of the *transitans* Zone, and the base of MN Zone 5 corresponds to the base of the *punctata* Zone. The base of MN Zone 11 possibly correlates with the base of the Early *rhenana* Zone, and MN Zone 12 correlates with the base of Late *rhenana* Zone. The above-mentioned problems of correlation were the reason for elaborating local Frasnian zonal scales for the basinal and shallow-water Frasnian deposits of the eastern Russian Platform.

CHAPTER 6. FRASNIAN CONODONT ZONAL SCALE FOR THE SHALLOW-WATER DEPOSITS OF THE EASTERN RUSSIAN PLATFORM

Earlier (Ovnatanova and Kononova, 2001) a zonal polygnathid scale was proposed based on material from the central Russian Platform for the subdivision of the shallow-water Frasnian deposits. The scale was based on the morphogenetic changes of *Polygnathus* representatives and includes five zones and two levels that were characterized as beds with fauna on account of the scanty material. The scale was correlated with the regional stages, the stratotypes of which were earlier established in the region. The accumulated material on the east of the platform allows slight changes in the existing zonation. The changes concern mainly the lower part of the Frasnian Stage. The stratotypes of the subdivisions of the latter are located in the east of the platform. The zonation developed for the shallow-water sections of the central Russian Platform is consistently

applied beginning with the Semiluki Regional Stage (Table 24). The data presented below were previously briefly outlined in the paper on the correlation of the various Frasnian facies of the eastern Russian Platform (Ovnatanova and Kononova, 2007).

The *Polygnathus pennatus–Po. ljaschenkoi* Zone. The lower boundary of the zone is determined by the appearance of *Polygnathus posterus, Po. angustidiscus, Po. pseudoxylus*, and *Po. denisbriceae* along with the zonal species. *Polygnathus xylus* and *Po. webbi* still exist. *Polygnathus varcus* and *Linguipolygnathus* sp. terminate their development. The zone characterizes deposits of the upper part of the Timan–lower part of the Sargaevo regional stages of the Volga–Ural region and Ukhta region of Southern Timan.

Many species of the assemblage of the *Polygnathus pennatus–Po. ljaschenkoi* Zone are also present in the *Po. alatus* Zone, which was established in the uppermost Timan Regional Stage of the central regions. These species are *Polygnathus posterus, Polygnathus pennatus*, and *Po. ljaschenkoi.*

The correlation of the ***Polygnathus pennatus–Po. ljaschenkoi* Zone** with the conodont scale (Ziegler, 1962a, 1971) and with the scale of Ziegler and Sandberg (1990) is impossible due to the peculiarity of the lowermost Frasnian assemblages (mainly polygnathids are present) and the absence (possibly because of the facies peculiarities) of the zonal species *Mesotaxis falsiovalis* and *Ancyrodella rotundiloba*, the presence of which indicates the lower boundary of the Frasnian Stage within the Early *falsiovalis* Zone.

***Ancyrodella rotundiloba–Ancyrodella africana* Zone.** Its lower boundary is determined by the appearance in the assemblage of representatives of the genus *Ancyrodella* (*A. africana, A. rugosa, A. recta, A. rotundiloba*, sometimes rare *A. binodosa*) and the species *Polygnathus pollocki* and *Po. praepolitus*, and representatives of *Mesotaxis* (*M. asymmetrica, M. falsiovalis*, and *M. costalliformis*). *Polygnathus pennatus, Po. xylus, Po. webbi*, and *Po. angustidiscus* continue to exist. *Polygnathus posterus* and *Po. ljaschenkoi* terminate their development. The zone is in the middle part of the Sargaevo (Ust'-Yarega) Regional Stage.

***Ancyrodella alata–Mesotaxis bogoslovskyi* Zone.** Its lower boundary is determined by the appearance of *Mesotaxis distinctus, Polygnathus reimersi*, and *Palmatolepis transitans* along with the zonal species. *Ancyrodella africana, A. alata, Mesotaxis asymmetrica, M. falsiovalis, M. costalliformis, Polygnathus webbi*, and *Po. angustidiscus* continue to exist. The zone characterizes the upper part of the Sargaevo (Ust'-Yarega) Regional Stage. The last two *Ancyrodella rotundiloba–Ancyrodella africana* and *Ancyrodella alata–Mesotaxis bogoslovskyi* zones are correlated with the *Polygnathus reimersi* Zone, which was established earlier in the Sargaevo deposits of the central Russian Platform. Unfortunately, up to recently the findings of the zonal species *Polygnathus reimersi* on the east of the platform are rare and thus we had to distinguish local zones within the deposits of the same name of the Volga–Ural and Southern Timan. It is worth noting that in the *reimersi* Zone together with *M. asymmetrica* and *M. falsiovalis* isolated specimens of *A. rotundiloba* were found in the middle part, and *A. alata* was found in the upper part of the Sargaevo Regional Stage together with *Mesotaxis asymmetricus, M. falsiovalis,* and *Klapperina ovalis.* One specimen of *Palmatolepis transitans* was found in the uppermost part of the section. This allows us to establish the *transitans* Zone (Ziegler and Sandberg, 1990) in the uppermost part of the Sargaevo Regional Stage. The *Ancyrodella rotundiloba–Ancyrodella africana* and *Ancyrodella alata–Mesotaxis bogoslovskyi* zones are correlated with the Lower *asymmetricus* Zone of the Ziegler scale (Ziegler, 1962a, 1971).

The *Polygnathus efimovae* Zone was established in the stratotype of the Semiluki Regional Stage in the Central Devonian Field and also in the sections of boreholes of the Semiluki Regional Stage in the topotype area. The lower boundary of the zone was established by the appearance of the zonal species. Isolated records of *Ancyrodella gigas, Palmatolepis punctata*, and *Polygnathus vjalovi* in the lower part of the section (Rudkino beds), the successive appearance of *Polygnathus seraphimae* and *Po. zinaidae*, and the appearance, somewhat upward in the section, in the Semiluki layers, of *Ancyrognathus ancyrognathoideus* and *Polygnathus azygomorphus* are also important. In the Volga–Ural region, the *Polygnathus efimovae* Zone was found only within the Tokmovo uplift, where *Polygnathus brevilamiformis, Po. azygomorphus*, and *Mesotaxis asymmetricus* were found together with the zonal species.

In the Volga–Ural region, the *Polygnathus efimovae* Zone is easily correlated with the lower part of the Domanik Formation that was earlier correlated with the *Polygnathus timanicus* Zone or with unit 1 of the Domanik Formation in the Ukhta region of Southern Timan.

The assemblage of the *Polygnathus efimovae* Zone is partly present near the western border of the Ukhta region. There the lower part of the Domanik Regional Stage is characterized by *Polygnathus efimovae*, and its upper part contains isolated specimens of *Polygnathus aequalis, Po. prepolitus, Po. webbi*, and *Palmatolepis punctata.* Eastward (Izvail'), the shallow-shelf sections are replaced by the sections in which the lower part is composed of the dark-colored Ezhvador Formation (base of the reef massifs) with a rich assemblage of conodonts of the *Polygnathus efimovae* Zone: *Polygnathus timanicus, Po. pollocki, Po. uchtensis, Po. azygomorphus, Po. brevilamiformis, Po. efimovae*, and *Palmatolepis keyserlingi.* The *Polygnathus efimovae* Zone is correlated with the Lower and Upper *asymmetricus* zones of the scale (Ziegler, 1962a, 1971) or possibly (judging by isolated records of *Palmatolepis*

punctata) with the *punctata* Zone (Ziegler and Sandberg, 1990).

Beds with ***Polygnathus aspelundi*** were established in the upper part of the Semiluki Regional Stage in the Moscow Syneclise. These layers are superimposed on the section of the Semiluki Regional Stage stratotype and are determined by the first appearance of *Polygnathus aspelundi.* The species *Polygnathus seraphimae, Po. zinaidae*, and *Po. prepolitus*, which continue to exist, are also typical. Isolated records of *Palmatolepis spinata* were made only within these beds and allow us to correlate them with unit 2 of the Domanik Formation of Southern Timan. The correlation with the international scales (Ziegler, 1962a, 1971; Ziegler and Sandberg, 1990) is impossible.

The *Polygnathus subincompletus* Zone was established in the Rechitsa (Petino)–Lower Voronezh deposits of the central Russian Platform. The lower boundary of the zone is determined by the appearance of the zonal species; if it is absent, then by the appearance of *Polygnathus politus. Polygnathus alvenus, Po. torosus, Po. unicornis*, and *Palmatolepis semichatovae* first appeared in this zone and also characterize it. *Po. costulatus* and *Po. churkini* appeared in the upper part of the zone. *Ancyrognathus ancyrognathoideus, Polygnathus azygomorphus*, and *Po. aspelundi* continue to exist. *Po. zinaidae* becomes extinct. The assemblage of the ***Polygnathus subincompletus* Zone** corresponds to the Rechitsa–Lower Voronezh deposits in the sections of the Volga–Ural region and to the Lower Sirachoi and possibly Vetlasyan deposits of Southern Timan. The zone correlates with the Early *rhenana* Zone.

The *Polygnathus maximovae* Zone was distinguished in the central Russian Platform within the range of the upper part of the Voronezh Regional Stage and Evlanovo Regional Stage (Ovnatanova and Kononova, 2001). The lower boundary of the zone is determined by the appearance of the zonal species. Other important species that appeared in this zone are *Po. sublatus* and *Po. siratchoicus. Polygnathus politus, Po. unicornis*, and *Po. costulatus* continue to exist.

In the future, with sufficient material accumulated, the zone may be divided into lower and upper parts based on the presence of *Po. brevis* in the upper part of the zone at the base of the Evlanovo Regional Stage. *Po. brevis* was found in the shallow-shelf deposits beginning with the base of the Evlanovo Regional Stage everywhere in the Russian Platform. It was also recorded in the basinal sections of the Volga–Ural province at the base of the Askyn Regional Stage and in Southern Timan in member 4 of the Lyaiol' Formation (= Evlanovo Regional Stage). Earlier (Ziegler et al., 2000), *Polygnathus brevis* was reported from the Benner Bicken and Steinbruch Schmidt sections in the deposits of the Late *rhenana* Zone together with *Polygnathus alvenus, Po. krestovnikovi*, and *Polygnathus politus.* Tracing the *maximovae* Zone in the shallow-shelf sections of the Ukhta region of Southern Timan and Volga–Ural province allows us to distinguish beds with *Po. churkini–Po. komi* in its lower part and beds with *Po. brevis–Po. macilentus* in its upper part.

Beds with *Po. churkini–Po. komi* are represented by the newly appearing *Polygnathus maximovae* and *Po. komi*, as well as by quite uncommon *Po. sublatus* and *Po. siratchoicus* and still persisting *Po. aspelundi, Po. politus, Po. subincompletus, Pa. semichatovae*, and *Po. unicornis*. The beds characterize the Upper Sirachoi Subformation of the Ukhta region and the lower part of the sulfate-bearing series of the Ukhta Formation, where *Polygnathus dentimarginatus* appeared and *Polygnathus krestovnikovi, Po. maximovae, Po. politus, Po. costulatus*, and *Po. macilentus* continued to exist.

Beds with *Po. brevis–Po. macilentus* are represented by the newly appearing *Po. brevis* and *Po. macilentus. Polygnathus alvenus, Po. churkini, Po. komi, Po. maximovae, Po. subincompletus, Pa. semichatovae*, and *Po. unicornis* continue to exist. *Po. aspelundi* became extinct. The beds characterize the lower subsulfate member of the Ukhta Formation in the Ukhta region. Although the conodont characterization of the Upper Voronezh and Evlanovo deposits of the Volga–Ural province is weak, isolated records of *Polygnathus maximovae, Po. krestovnikovi*, and *Po. politus* beginning with the base of the Upper Voronezh deposits together with records of *Po. brevis* in the Evlanovo deposits allow us to establish the *Polygnathus maximovae* Zone in this region.

Beds with *Polygnathus* aff. *brevilaminus* were previously established (Ovnatanova and Kononova, 2001) within the range of the Livny Regional Stage. The assemblage is rather poor. It consists mainly of the species that appeared in the lower layers. *Polygnathus krestovnikovi, Po. politus, Po. costulatus*, and *Po. unicornis* were recorded. The assemblage is almost unknown in the Volga–Ural region and Southern Timan; correlation with other conodont scales is impossible. Those intervals with the most substantiated correlation with other conodont scales are hatched in Table 24.

CHAPTER 7. FRASNIAN ZONAL CONODONT SCALE FOR THE BASINAL DEPOSITS OF THE EASTERN RUSSIAN PLATFORM

The range and correlation of the previously proposed local conodont zones (Ovnatanova et al., 2000) are improved as the data are accumulated. The zonation was elaborated mainly on the best studied sections of the Ukhta region. Most of the zones were traced in the Volga–Ural province. The supposed Frasnian conodont zonation for the basinal deposits of the eastern Russian Platform and its correlation with the regional stages, Timan–Pechora assemblages (TP 1–TP 11), and other conodont scales is shown in Table 23. Those intervals with the most substantiated correlation with other conodont scales are hatched. The lower Frasnian Zones *Polygnathus pennatus–Po. ljaschenkoi*, *Ancyrodella*

rotundiloba–A. africana, and *A. alata–Mesotaxis bogoslovskyi* and the shallow-water scale are given in Chapter 6. The zone characteristics beginning with the Domanik Formation are as follows.

***Polygnathus efimovae–Palmatolepis punctata* Zone**; the lower boundary of the zone is defined by the appearance of *Palmatolepis punctata, Polygnathus efimovae,* and *Po. brevilamiformis* and slightly upward in the section of *Ancyrodella gigas, M. johnsoni, Palmatolepis gutta, Polygnathus timanicus*, and *Po. vjalovi. Palmatolepis transitans* and *Klapperina ovalis* (in the lower part of the section), *Polygnathus pollocki, Po. pennatus, Po. dubius*, and *Mesotaxis* (*M. asymmetricus, M. falsiovalis, M. dengleri, M. bogoslovsky*) continue to exist. *Polygnathus pennatus* became extinct here. The zone characterizes the lower member and basal clayey bed of the Middle Subformation of the Domanik Formation of Southern Timan, and the lower part of the Domanik Formation of the Volga–Ural region. It is correlated with the Middle and Upper *asymmetricus* zones of Ziegler (1962a, 1971) or with the *punctata* and the lowermost part of the *hassi* zones of Ziegler and Sandberg (1990).

The *Ancyrognathus ancyrognathoideus–Palmatolepis orbicularis* Zone is defined by the appearance of the zonal species; if the latter are absent, then by the appearance of *Pa. domanicensis. Ancyrognathus primus, Pa. bohemica, Pa. spinata, Pa. plana, Pa. ljaschenkoae*, rare *Pa. proversa, Pa. kireevae, Ozarkodina trepta*, etc., also appear in this interval. *Ancyrodella gigas, Palmatolepis transitans, Pa. punctata, Polygnathus webbi, Po. brevilamiformis*, etc., continue to exist. All *Mesotaxis* representatives became extinct in this zone. An assemblage essentially identical to the assemblage of the middle unit of the Domanik Formation was found in the lowermost unit 3 of the Domanik Formation. *Pa. domanicensis, Pa. ljaschenkoae, Pa. proversa, Pa. kireevae, Pa. orbicularis, Pa. transitans, Pa. punctata, Pa. amplificata, Ozarkodina trepta*, etc., continue to exist here. The only difference is the disappearance of *Palmatolepis bohemica* and *Pa. spinata* that may be connected with the facies peculiarities of the basin. This part of the section was also provisionally referred to the ***Ancyrognathus ancyrognathoideus–Palmatolepis orbicularis* Zone**.

This zone characterizes unit 2 of the Domanik Formation (without basal clayey bed) and possibly the lower part of unit 3 in the Ukhta region and the middle part of the Domanik Formation in the Volga–Ural region. Earlier this zone was established as *Ancyrognathus ancyrognathoideus–Palmatolepis domanicensis* (Ovnatanova et al., 2000). However, the concept of *Pa. domanicensis* (see description of the species) is ambiguous; in addition, it was mistakenly established as a zonal species of the MN Zone 10 (Klapper and Foster, 1993). Therefore it became necessary to establish *Pa. orbicularis* as a zonal species instead of *Pa. domanicensis.*

The *Palmatolepis mucronata–Pa. amplificata* Zone is defined by the first occurrence of the zonal species; if the latter are absent, then by *Palmatolepis ormistoni. Pa. ederi* and *Pa. timanensis* also appear in this interval. *Ancyrognathus triangularis, Palmatolepis orbicularis, Pa. punctata, Pa. proversa, Pa. ljaschenkoae, Pa. kireevae*, and *Po. uchtensis* continue to exist. Earlier the interval of the upper carbonate member of the Domanik Formation together with the lowermost Vetlasyan Formation was referred to the *Palmatolepis proversa–Pa. amplificata* Zone (Ovnatanova et al., 2000). The *Palmatolepis mucronata–Pa. amplificata* Zone characterizes member 3 of the Domanik Formation in Southern Timan. This zone cannot be established in the Volga–Ural province due to the limited coring from these intervals. However, the presence of this zone may be assumed based on the records of *Palmatolepis ormistoni* together with *Ancyrognathus ancyrognathoideus* in the upper part of the Domanik Regional Stage.

The correlation of the local *Ancyrognathus ancyrognathoideus–Palmatolepis orbicularis* Zone and *Palmatolepis ormistoni–Pa. amplificata* Zone with the interval of the *hassi–jamieae* zones of Ziegler and Sandberg scale (1990) is problematic.

The *Palmatolepis elegantula–Palmatolepis semichatovae* Zone is defined by the appearance of the zonal species and *Palmatolepis brevis* and *Ancyrognathus triangularis*; *Palmatolepis semichatovae* and rare *Pa. nasuta* and *Pa. anzhelae* appear somewhat upward in the section, beginning with the middle of unit 2 of the Lyaiol' Formation (Sirachoi Regional Stage). *Palmatolepis plana, Pa. kireevae, Pa. ormistoni, Pa. mucronata*, etc. continue to exist. *Pa. amplificata* became extinct in the middle part of unit 2. Of polygnathids, isolated specimens of *Po. unicornis* were found in units 1 and 2, and *Po. politus* and *Po. krestovnikovi* were found in unit 2 of the Lyaiol' Formation. In the Volga–Ural province, rare polygnathids are represented by *Po. unicornis* in the lower part and *Po. maximovae, Po. subincompletus*, and *Po. politus* were found in the upper part of the Mendym Regional Stage. The *Palmatolepis elegantula–Palmatolepis semichatovae* Zone characterizes deposits of the Vetlasyan (unit 1 of the Lyaiol' Formation) and Sirachoi regional stages (units 2 and lowermost unit 3 of the Lyaiol' Formation) in Southern Timan and Mendym Regional Stage in the Volga–Ural province. The *Pa. elegantula–Pa. semichatovae* Zone is correlated with the Early *rhenana* Zone of Ziegler and Sandberg scale (1990).

The *Palmatolepis gyrata* Zone. The lower boundary of the zone is defined by the appearance of *Palmatolepis gyrata, Pa. foliacea, Pa. subrecta, Pa. hassi*, and *Polygnathus brevis*; *Palmatolepis jamieae, Pa. nasuta*, and *Pa. orlovi* appear beginning with the base of unit 4. *Palmatolepis elegantula* and rare *Ancyrodella nodosa, Ancyrognathus amana*, and *Icriodus interjectus* continue to exist. In Southern Timan, isolated records of

polygnathids *Po. politus, Po. alvenus*, and *Po. subincompletus* in the slope facies and isolated specimens of *Po. macilentus* in the upper part of the Evlanovo Regional Stage are also noteworthy. Earlier the assemblage was called TP 9. The zone characterizes the upper part of units 3 and 4 of the Lyaiol' Formation in Southern Timan and the lower part of the Askyn Regional Stage in the Volga–Urals province.

The *Palmatolepis juntianensis* Zone. *Palmatolepis juntianensis* and *Pa. rotunda* appear in the uppermost part of the Evlanovo Regional Stage and thus these layers and the overlying Sed'yu Formation of Southern Timan (with the Upper Evlanovo spore assemblage) can be referred to the interval of assemblage TP 10.

Most of the Askyn Regional Stage of the Volga–Ural region corresponds to the *gyrata* and *juntianensis* zones. The *gyrata* and *juntianensis* zones are correlated with the Late *rhenana* Zone based on the presence of *Pa. subrecta* and of *Palmatolepis juntianensis* in the upper part of the zone.

The *linguiformis* Zone of Ziegler and Sandberg scale (1990) completes the section of the Frasnian Stage. It is determined first of all by the appearance of the zonal species. *Palmatolepis subrecta, Pa. rhenana, Pa. juntianensis*, and *Pa. orlovi* continue to exist. This zone corresponds to the Livny Regional Stage; in the Volga–Ural region, it corresponds to the upper part of the Askyn Regional Stage.

The scale proposed for the basinal Frasnian deposits (Table 23) will be improved and specified as new data will be accumulated.

CHAPTER 8. CORRELATION OF DIFFERENT FRASNIAN FACIES OF THE EASTERN RUSSIAN PLATFORM

The correlation of the shallow-water and basinal Frasnian sections was carried out based on the above data on conodont distribution and on Frasnian conodont zonations of the eastern Russian Platform (Table 25).

Unfortunately, the lower boundary of the Frasnian Stage still remains problematic in the Russian Platform. Although we accept its position at the base of the Upper Timan Subformation, data for the foundation of such position are still insufficient. It is especially obvious for the shallow-water facies as the boundary is determined on the zonal species *Mesotaxis falsiovalis* and early *Ancyrodella* and these species were found only upward in the section beginning with the middle of the Sargaevo level together with more progressive forms. Unfortunately, the position of the boundary in the sections of the Southern Urals is also obscure. *Ancyrodella binodosa* was only identified in the Kedzyrschor Formation of the deep-water sections on the Chernyshev Ridge, which corresponds to the international level of the Givetian-Frasnian boundary. At the same time, the characteristics of the Frasnian deposits and their correlation within the Russian Platform and at separate levels with other conodont zonations are gradually refined as the information is obtained. The increasing role of *Mesotaxis* in the assemblage of shallow-water polygnathid biofacies and then the appearance of palmatolepids considerably contribute to this process.

The study of the Frasnian polygnathids from the central and eastern parts of the Russian Platform revealed for the first time large capacity of this group of conodonts for the correlation of heterofacies Frasnian deposits. Study of polygnathids from the conodont zones of the sections of the Rhenish Slate Mountains that was earlier conducted by the authors was also important (Ziegler et al., 2000).

Now only polygnathids allow us to correlate assemblages of epicontinental deposits with the elaborated conodont zones. The use of polygnathids enabled us to specify intervals of the stratigraphic interruptions in the Upper Devonian of the Central Devonian Field and to prove for the first time that the stratotype of the Semiluki Regional Stage corresponds only to unit 1 of the Domanik Formation in the Ukhta region of Southern Timan.

The Timan–Sargaevo deposits are easily correlated within the platform. The *Polygnathus alatus* Zone was initially established within the central Russian Platform and is correlated based on the presence of shared species with *Polygnathus pennatus–Po. ljaschenkoi* Zone, which was established in the deposits of the Upper Timan Regional Stage and lowermost Sargaevo Regional Stage of the eastern Russian Platform. However, its correlation with other conodont scales (Ziegler, 1962a, 1971; Ziegler and Sandberg, 1990) is impossible.

The *reimersi* Zone was established based on isolated records of *Mesotaxis asymmetricus, M. falsiovalis*, and *Ancyrodella rotundiloba* in the middle part and *A. alata* in the upper part of the Sargaevo Regional Stage in the central Russian Platform. It is correlated with the *Ancyrodella rotundiloba–Ancyrodella africana* and *Ancyrodella alata–Mesotaxis bogoslovskyi* zones, which can only be outlined on the east of the platform, where the zonal species *reimersi* is unfortunately very rare. The only record of *Palmatolepis transitans* was made in the upper part of the Sargaevo Regional Stage. It is obvious that the future trend is to establish a unified zone or zones for the shallow-shelf Sargaevo deposits of the Russian Platform. Now the elaborated zones are correlated with the Lower *asymmetricus* Zone of Ziegler's scale (Ziegler, 1962a, 1971) and the upper part of the Sargaevo Regional Stage is correlated with the *transitans* Zone (Ziegler and Sandberg, 1990).

The *Polygnathus efimovae* Zone was established in the stratotype of the Semiluki Regional Stage and in the sections of numerous boreholes in its topotypical area of the Central Devonian Field. This zone is correlated with the Lower and Middle *asymmetricus* zones (=*punctata*) based on the presence in the assemblage of *Polygnathus timanicus, Po. vjalovi*, and *Po. brevilami-*

Table 25. Correlation of heterofacies Frasnian deposits of the eastern Russian Platform

Shallow-water type of section				Basinal type of section										
Conodont zonal scale for shallow-water deposits of the eastern Russian Platform (Ovnatanova and Kononova, 2001, modified)	Southern Timan		Volga–Ural Province	Volga–Ural Province	Southern Timan			Conodont zonal scale for basinal sections of the eastern Russian Platform (Ovnatanova et al., 2000, modified)	TP assemblages (Ovnatanova et al., 1998)	Correlative levels (hatched)	Conodont zonation		Stage
	regional stage	formation, strata	regional stage	regional stage	regional stage	formation	unit				Ziegler, 1962a, 1970	Ziegler and Sandberg, 1990	
	Volgograd			Volgograd		Savinobor		*Pa. triangularis*			Middle *triangularis* / Lower *triangularis*		Famennian
Beds with *Po.* aff. *brevilaminus*	Livny	Ukhta Formation, sulphatebearing strata	Livny	Askyn	Livny			*Pa. linguiformis*	11		Uppermost *gigas*	*linguiformis*	Frasnian
Po. maximovae: Beds with *Po. brevis*–*Po. macilentus*	Evlanovo	Ukhta Formation, subsulphate strata	Evlanovo		Evlanovo	Sed'yu		*Pa. juntianensis*	10		Upper *gigas*	Late *rhenana*	
						Lyaiol'	4	*Pa. gyrata*	9				
Po. maximovae: Beds with *Po. churkini*– *Po. komi*	Sirachoi	Sirachoi Formation	Voronezh	Mendym	Sirachoi		3	*Pa. elegantula*–*Pa. semichatovae*	8		Lower *gigas*	Early *rhenana*	
Po. subincompletus	Vetlasyan	Vetlasyan Formation	Rechitsa (Petino)		Vetlasyan		2		7				
Beds with *Po. aspelundi*	Domanik (Semiluki)	reef massif	Semiluki	Domanik		Domanik	1	*Pa. mucronata*– *amplificata*	6		*Ancyrognathus triangularis*	*jamieae*	
							3	*Anc. ancyrognathoideus*–*Pa. orbicularis*				Late *hassi*	
							2		5		unzoned	Early *hassi*	
Po. efimovae		Ezhvador Formation					1	*Po. efimovae*–*Pa. punctata*	4		Upper *asymmetricus* / Middle *asymmetricus*	*punctata*	
A. alata–*M. bogoslovskyi*	Ust'-Yarega	Ust'-Yarega Formation	Sargaevo	Sargaevo		Ust'-Yarega		*A. alata*–*M. bogoslovskyi*	3		Lower *asymmetricus*	*transitans*	
A. rotundiloba–*A. africana*								*A. rotundiloba*–*A. africana*	2			Late *falsiovalis*	
Po. pennatus–*Po. ljaschenkoi*	Timan	Timan Formation	Timan	Timan		Timan		*Po. pennatus*–*Po. ljaschenkoi*	1		Lowermost *asymmetricus*	Early *falsiovalis*	
									0				Givetian

formis together with *Mesotaxis asymmetricus* and *M. johnsoni*, which are present up to the top of the Semiluki Regional Stage in its stratotype.

In the Volga–Ural province, the *Polygnathus efimovae* Zone was established in the Semiluki deposits of the Tokmovo uplift. *Polygnathus efimovae* together with *Po. timanicus, Palmatolepis punctata*, etc., were found in the basinal deposits of the lower part of the Domanik Regional Stage. The *Polygnathus efimovae* Zone evidently characterizes the lower part of the Kraipol Formation of Middle Timan and the lower part of the Domanik Formation of Southern Timan near the western border of the Ukhta region. Eastward (Izvail'), the *Polygnathus efimovae* Zone was established at the base of the reef massifs (Ezhvador Formation).

Within the Main Devonian Field, the *Po. efimovae* Zone probably includes not only the Buregi beds of the Semiluki Regional Stage, in which it was earlier distinguished (Zhuravlev et al., 1997) but also the Porkhov-Svinord beds (*Po. pollocki* Zone) and the Il'men' beds (*Po. ilmenensis* Zone) (Sokiran et al., 1999; Zhuravlev et al., 2006). Even the impoverished conodont assemblage of these beds does not contradict this possibility: *Polygnathus pollocki, Po. mosquensis*, and *Po. zinaidae* were found in the Porkhov-Svinord beds and *Ancyrognathus ancyrognathoideus, Po. strictus, Po. uchtensis,* and *Po. ilmenensis* were found in the Il'men' beds. *Po. efimovae* appears in the section only beginning with the base of the Buregi beds probably due to extremely shallow-water facies conditions of the basin and still scanty information on conodonts inhabiting the basin. Nevertheless, the use of the zonal species *Po. efimovae* for part of the Semiluki Regional Stage is unacceptable. It seems to be more appropriate to establish in this basin a local conodont zonation. Its correlation with other conodont scales is still difficult. Nevertheless, the literary data (Sokiran et al., 1999; Zhuravlev et al., 2006) and conodonts collected by the authors (unpublished) prove that analogues of the Semiluki Regional Stage on the Main Devonian Field are developed within the range of its stratotype in the Central Devonian Field, i.e., within the range of units 1–3 of the Domanik Formation in the Southern Timan according to Kushnareva et al. (1978) or within the range of unit 1 of the Domanik Formation (Menner et al., 1992).

The section of the stratotype of the Semiluki Regional Stage in the Moscow Syneclise is overbuilt by the beds with *Polygnathus aspelundi.* Although the assemblage is very distinctive it may be correlated with the middle part or with the lowermost upper unit (*Ancyrognathus ancyrognathoideus–Palmatolipis orbicularis* Zone) of the Domanik Formation based on the presence of rare *Palmatolepis spinata.* In the Volga–Ural region, this level was only recorded on the Tokmovo uplift.

The *Palmatolepis mucronata–Palmatolepis amplificata* Zone was established in the middle and upper parts of unit 3 of the Domanik Formation of Southern Timan. Its analogues are unknown in the shallow-shelf sections, this may be explained by the sedimentary gap in this period on most of the Russian Platform. It is evident that of all the sections studied, the Domanik Formation is most fully preserved in the sections of Southern Timan. Abramova (1999) presented interesting data on the distribution of conodonts in the section on the Ryauzyak River of the Southern Urals (conodonts were determined by V.N. Baryshev). She correlated the Domanik Regional Stage with the *Palmatolepis punctata–Pa. jamieae* conodont zones (Ziegler and Sandberg, 1990).

Unfortunately, this paper lacks paleontological plates and thus the conclusion cannot be fully assessed. However, the scope of the Domanik in Bashkortostan may be larger than in the Ukhta stratotype.

Since the first work on Upper Devonian conodonts of the Russian Platform (Ovnatanova, 1972), it has been apparent that correlation of the Mendym and Voronezh regional stages may be possible based on records of *Palmatolepis semichatovae.* In contrast with the Unified Scheme of the Russian Platform (*Resolution*…, 1990), which exists to the present day, the authors suggested (Ovnatanova and Kononova, 1984) correlation of the Mendym and Voronezh deposits. This was also suggested by Kononova's (1969) study of conodonts from the topotypical area of the Mendym deposits of the Southern Urals (section on the right bank of the Sikaza River against the village of Kuk-Karauk; Ryauzyak section), where conodonts *Palmatolepis rhenana nasuta* were found together with goniatities *Manticoceras intumescens* Beyr. (Ovnatanova and Kononova, 1984, p. 38; Kononova, 1969). Later the correlation of Mendym and Voronezh deposits was confirmed (Abramova, 1999, p. 20) as the trenching sampling of the whole interval of the Mendym Regional Stage on the Ryauzyak River revealed that zonal ammonoids *Manticoceras intumescens* Beyr. appear almost simultaneously with the conodonts *Palmatolepis rhenana nasuta* (Abramova, 1999, p. 20).

The *subincompletus* Zone corresponds to the Rechitsa–Lower Voronezh deposits of the central regions. Of the shallow-shelf sections, it corresponds to the Rechitsa–Lower Voronezh deposits of the Volga–Ural region and the Lower Sirachoi and possibly Vetlasyan deposits of Southern Timan. The level of the Vetlasyan Regional Stage usually corresponds to the stratigraphic gap or to the thin clayey members with impoverished assemblages of polygnathid biofacies. The correlation of the Lower Voronezh and Lower Sirachoi deposits is based first of all on the records of *Palmatolepis semichatovae* and also of *Polygnathus subincompletus, Po. unicornis, Po. politus*, and *Po. krestovnikovi. Po. subincompletus* and *Po. unicornis* were also found in the section of the Mendym Regional Stage and in the stratotype of the Early *rhenana* Zone; however, the number of polygnathids in the Mendym Regional Stage is smaller than in the interval of the

Domanik Regional Stage. In the basinal sections, the *subincompletus* Zone is correlated with the *Palmatolepis elegantula–Palmatolepis semichatovae* Zone (units 1 and 2 and the lowermost unit 3 of the Lyaiol' Formation) in Southern Timan and with the Mendym Regional Stage of the Volga–Ural region. The zone is correlated with the Lower *rhenana* Zone of Ziegler and Sandberg scale (1990).

The *Polygnathus maximovae* Zone was established in the upper part of the Voronezh and Evlanovo regional stages of the central Russian Platform and corresponds to the regional stages of the same name in the Volga–Ural province. In Southern Timan, the *Polygnathus maximovae* Zone characterizes the upper part of the Sirachoi Formation and the lower part of the Ukhta Formation (subsulfate and lowermost sulfate-bearing strata). Species common for these regions include the zonal species, *Polygnathus krestovnikovi, Po. politus*, and *Po. brevis* (beds with *Po. brevis–Po. macilentus* at the base of the Evlanovo Regional Stage). As previously mentioned, the latter species was also found in the Late *rhenana* conodont Zone of the sections of the Rhenish Slate Mountains (Ziegler et al., 2000).

The lower part of the *Polygnathus maximovae* Zone (beds with *Po. churkini–Po. komi*) along with the *subincompletus* Zone is correlated with the Early *rhenana* Zone, while the upper part of the ***Polygnathus maximovae* Zone** corresponds to the Late *rhenana* Zone. The *gyrata* and *juntianensis* zones and *linguiformis* Zone of Ziegler and Sandberg scale (1990) were established at this level in the basinal sections of the eastern Russian Platform.

In the Volga–Ural region, the lower part of the Askyn Regional Stage (=Evlanovo Regional Stage) corresponds to the *gyrata* and *juntianensis* zones and its upper part (= Livny Regional Stage) corresponds to the *linguiformis* Zone. In the Ukhta region, the *gyrata* Zone is correlated with the uppermost unit 3 and part of unit 4 of the Lyaiol' Formation. *Palmatolepis juntianensis* appears in the uppermost unit 4; thus the latter together with the overlying Sed'yu clayey series (with the Upper Evlanovo spore assemblage) may be referred to the *Pa. juntianensis* Zone correlative with the upper part of the Late *rhenana* Zone. This zone is correlated with the upper part of the ***Polygnathus maximovae* Zone (*Po. brevis–Po. macilentus* beds)** based first of all on the presence of *Po. brevis.*

The uppermost Frasnian assemblage of the Ukhta region probably corresponds to the *Polygnathus* aff. *brevilaminus* beds, which were earlier established in the central regions within the range of the Livny Regional Stage.

Conodont assemblages corresponding to the *triangularis–crepida* zones of the Famennian Stage were established up the basinal sections of the Volga–Ural province and in the sections of the Tebuk-Vis area of the Izhma–Pechora depression of the Izhma–Pechora province (Kuzmin et al., 1998).

CHAPTER 9. BIOFACIES CONTROL OF CONODONT DEVELOPMENT

Recently conodonts have been regularly used not only for subdivision and correlation of sections but also for establishment of various sedimentary settings. It was initially concluded that as the conodonts were found in all types of marine rocks including littoral sandstones and deep-water siliciclayey deposits, they were independent from facies. However, from the 1980s, it became apparent that the distribution of conodonts is related to sedimentary settings (Druce, 1973, 1976; Seddon, 1970; Sandberg et al, 1992; Ziegler and Sandberg, 1984, etc.). The term "biofacies" appeared and came to be used to designate various assemblages of the same age with domination of certain genera or species depending on the sedimentation conditions. Most of the conodonts are widespread; on the contrary, some conodonts are restricted either geographically or environmentally.

Here we analyze the taxonomic diversity of the assemblages based on the sections of the Ukhta region. Data on conodonts from the sections of the boreholes of South and North Timan–Pechora province (Kuzmin et al., 1998; Ovnatanova et al., 1993) and outcrops of the Subpolar Urals and Chernyshev Ridge were also considered. Substantial differences in the taxonomic composition and in the types of conodont distribution in various facies are revealed. Two large contrasting biofacies are established, *Mesotaxis–Palmatolepis* and *Polygnathus,* the distribution of which was governed by the changes in the basin depth.

The *Mesotaxis–Palmatolepis* biofacies corresponds to the most deep-water areas (slope and basinal facies). The conodont content of samples from this biofacies is high, 100 or more specimens per kilogram of rock. The *Mesotaxis–Polygnathus* biofacies is composed mainly of members of *Mesotaxis* and *Polygnathus*; sometimes *Ancyrodella* also become important (biofacies *Mesotaxis–Ancyrodella*). The biofacies is dated to the uppermost Sargaevo Regional Stage and the lower part of the Domanik Regional Stage. Of polygnathids, *Polygnathus timanicus, Po. brevilamiformis,* and *Po. webbi* are especially typical.

The *Palmatolepis* biofacies contain 80–100% of palmatolepids. It characterizes deposits from the upper part of the Domanik Regional Stage and up to the top of the Livny Regional Stage in the basinal and slope facies. The former assemblage may be completely composed of *Palmatolepis*. Sometimes rare polygnathids *Polygnathus lodinensis, Po. decorosus*, and *Po. politus* occur, and also *Po. macilentus* may appear in the upper part of the Frasnian Stage. In the continental-slope facies, the proportion of palmatolepids decreases due to the appearance in the assemblage of representatives of other genera, including *Polygnathus, Ancyrodella*, and *Icriodus*. Their proportion is usually less than 20%. For instance, the *Palmatolepis* constitute up to 95% of the assemblage of units 1 and 2 of the

Lyaiol' Formation on the Lyaiol' River, which are composed of the deposits of the basinal facies. Of polygnathids, usually only *Polygnathus lodinensis* is present in large numbers. Units 3 and 4 of the Lyaiol' Formation characterize the continental-slope facies. The number of polygnathids increases upward in the section; they are represented by *Polygnathus lodinensis* and also by *Polygnathus uchtensis, Po. brevilamiformis, Po. krestovnikovi,* etc., although they are often represented by isolated specimens. The same regularities exist in the section of the Lyaiol' Formation on the Vezha-Vozh River. The relative increase in the numbers of polygnathids (in comparison with the section on the Lyaiol' River) and also the presence of representatives of the genus *Belodella*, an indicator of reef facies, are noteworthy. Most likely this is due to the influence of Vezha-Vozh reef massif. Usually the numbers of *Mesotaxis* and *Palmatolepis* decrease and the numbers of polygnathids increase towards the region of the linear reef zones (Ovnatanova and Kuzmin, 1991). The numbers of *Ancyrodella* remain approximately the same or somewhat increase.

The *Polygnathus* biofacies is developed within the back-reef and shallow-shelf deposits. The number of conodonts in the samples is tens of specimens per kilogram of rock. The biofacies mainly consists of smooth and ornamented polygnathids. *Polygnathus alatus, Po. praepolitus, Po. efimovae*, and solitary *Palmatolepis punctata* are typical for the lower part of the Frasnian Stage and in the upper part of the section most typical are *Polygnathus politus* and *Po. macilentus*; and sometimes *Palmatolepis semichatovae* is abundant, which is adapted to the conditions of the shallow-water zone.

The number of conodonts in the marginal reef zones is very small. Isolated representatives of *Belodella* (*B. triangularis* Stauf., *B. dentata* Chal. et Tchern.) and *Ancyrodella* (*A. curvata, A. nodosa*) occur in the reef. Isolated polygnathids (*Polygnathus politus, Polygnathus alatus*, and *Po. efimovae*) and rare palmatolepids (*Palmatolepis punctata, Pa. ljaschenkoe, Pa. kireevae*, and single *Pa. subrecta*) also were found. Members of organoclastic limestones at the base of the reef massifs are the richest in conodonts. They often contain *Palmatolepis* and thus the beginning of the phases of the reef building may be sufficiently exactly dated. On the whole, the marginal reef zones are a peculiar kind of ecological barrier dividing regions with different biofacies.

Another pattern of conodont distribution takes place in the sections of banks formed in the shallow parts within a starved depression. Although the number of samples with conodonts was small, representatives of *Ancyrodella, Palmatolepis*, and *Mesotaxis* often occur and thus the reefs may be sufficiently precisely dated. The assemblage is hardly referred to any of biofacies and is essentially compound.

The biofacies differentiation in the section of the Frasnian Stage seems to be as follows. The Timan Formation and the lowermost Ust'-Yarega Formation are developed over a considerable part of the Timan–Pechora province as the shallow-water polygnathid biofacies. The absence of *Ancyrodella* is possibly connected with the facies peculiarities of the section. Sections of the Subpolar Urals and Chernyshev Ridge are different; the *Ancyrodella–Polygnathus* biofacies prevail there. The upper part of the Ust'-Yarega Formation is everywhere represented by the *Mesotaxis–Ancyrodella* biofacies. The lower part of Domanik deposits is composed of two biofacies: *Mesotaxis–Palmatolepis* for the basinal and *Polygnathus* for the shallow-water facies. Two contrasting biofacies, *Palmatolepis* and *Polygnathus*, are developed beginning with the upper part of the Domanik Regional Stage and upwards up to the top of the Frasnian Stage.

CHAPTER 10. PHYLOMORPHOGENESIS OF THE FRASNIAN PALMATOLEPIDS AND POLYGNATHIDS

Palmatolepis is one of the most abundant conodont taxa in Late Devonian deep-water basins. Therefore the zonal conodont scale of the Upper Devonian (Ziegler, 1962a; Ziegler and Sandberg, 1984, 1990) was based on the phylogenetic succession of its species. *Palmatolepis* apparatus consists of Pa, Pb, M, and S elements. Types of the *Palmatolepis* apparatuses were repeatedly described in the literature (Boogard and Kuhry, 1979; Dzik, 2002; Klapper and Foster, 1993; Metzger, 1994; Schülke, 1995, 1997; Puchkov et al., 1981; etc.). Pa elements had the highest evolutionary morphological variability. They are the most informative part of the apparatus and thus are the basis for the species diagnostics. The first phylogenetic scheme of *Palmatolepis* for the whole Late Devonian was based on the morphological changes of Pa element (Helms, 1963). This scheme became the basis for all following developments (Ziegler and Sandberg, 1984, 1990; Khalymbadzha, 1987; Ji and Ziegler, 1993; etc.).

The number of described *Palmatolepis* species increased considerably during the last two decades. New species were described in many papers (Wang, 1989; Ziegler and Sandberg, 1990; Irwin and Orchard, 1991; Ovnatanova and Kuzmin, 1991; Kuzmin and Mel'nikova, 1991; Ji and Ziegler, 1992, 1993; Klapper and Foster, 1993; Schülke, 1995; Klapper et al., 1996; Khrushcheva and Kuzmin, 1996; Kuzmin, 1998). We conducted the present study in order to place new species in the phylogenetic tree and rethink earlier suggested relationships. The results were partly published by L.I. Kononova, N.S. Ovnatanova, and M.V. Vasil'eva (2005) and are presented in chapter 10. 1.

The first investigations of the phylogeny of Frasnian polygnathids were published in the early 1980s (Huddle, 1970; Khalymbadzha, 1987). In 1993 Q. Ji and W. Ziegler published a monograph, in which phylogenetic relationships of many Frasnian polygnathids

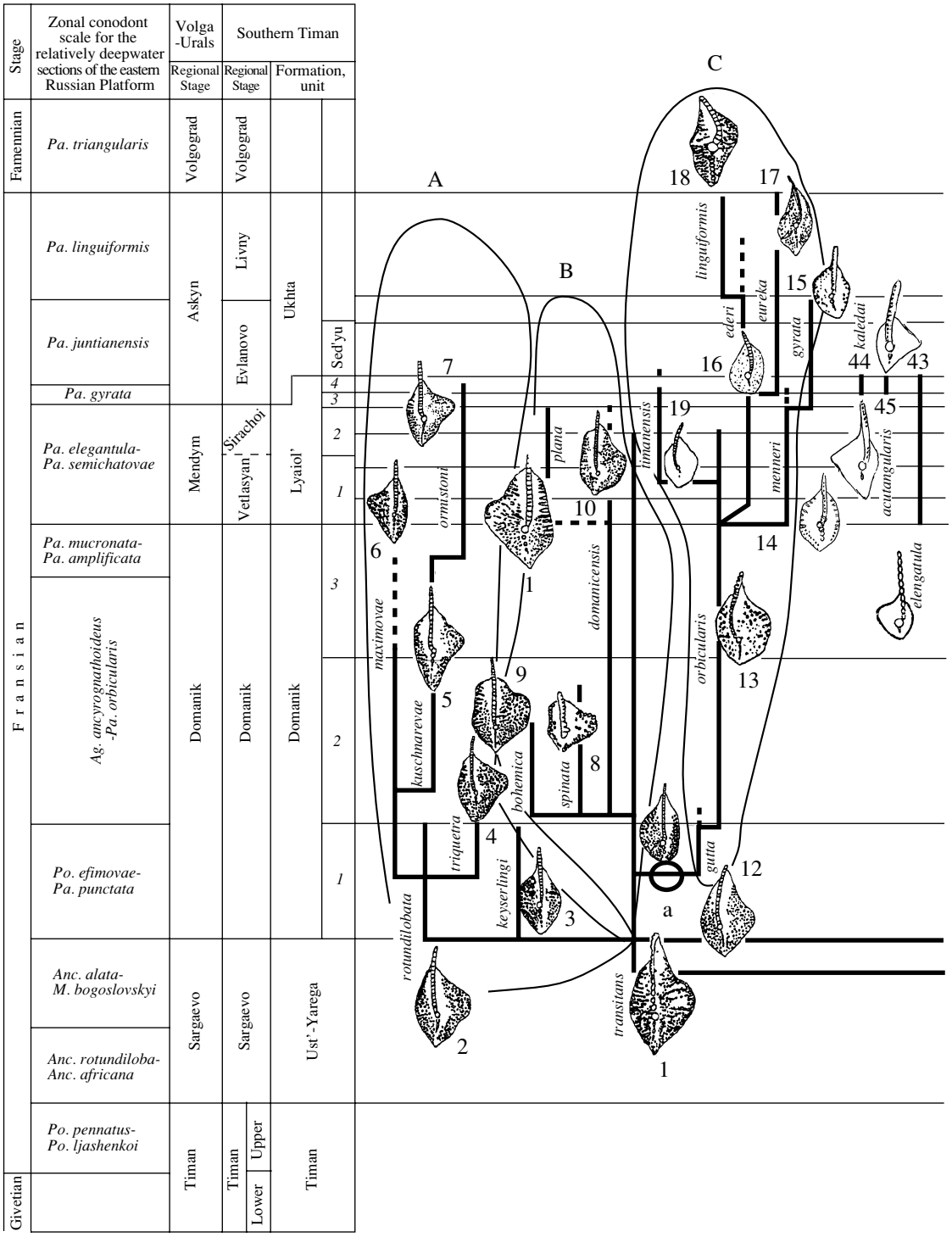


Fig. 16. Phylomorphogenetic scheme of Frasnian palmatolepids. Designations: *(1)* stratigraphic range of species in Frasnian; (*2*) transitional forms: (a) *Palmatolepis transitans* Müller → *Pa. gutta* Kuzmin; (b) *Pa. punctata* Hinde → *Pa. proversa* Ziegler; (c) *Pa. jamieae* Ziegler et Sandberg → *Pa. foliacea* Youngquist; and (d) *Pa. hassi* Müller et Müller → *Pa. anzhelae* Khrustcheva et Kuzmin; (*3*) possible phylogenetic connections; (*4*) sketches (contoured photographs) of the holotypes designated by numbers; (A–H) phylogenetic lineages: (1) *Pa. transitans* Müller, 1956, ancestor of the genus *Palmatolepis*; Branch A: (2) *Pa. rotundilobata* Kuzmin, 1998, (3) *Pa. keyserlingi* Kuzmin, 1998, (4) *Pa. triquetra* Kuzmin, 1996, (5) *Pa. kushnarevae* Ovnatanova et Kuzmin, 1992, (6) *Pa. ormistoni* Klapper, Kuzmin et Ovnatanova, 1996, (7) *Pa. maximovae* Kuzmin, 1998; Branch B: (8) *Pa. spinata* Ovnatanova et Kuzmin, 1991, (9) *Pa. bohemica* Klapper et Foster, 1993, (10) *Pa. domanicensis* Ovnatanova, 1976, (11) *Pa. plana* Ziegler et Sandberg, 1990; Branch C: (12) *Pa. gutta* Kuzmin, 1998, (13) *Pa. orbicularis* Ovnatanova et Kuzmin, 1991, (14) *Pa. menneri* sp. nov., (15) *Pa. gyrata* Kuzmin et Melnikova, 1991, (16) *Pa. ederi* Ziegler et Sandberg, 1990, (17) *Pa. eureka* Ziegler et Sandberg, 1990, (18) *Pa. linguiformis* Müller, 1956, (19) *Pa. timanensis* Klapper, Kuzmin et Ovnatanova; Branch D: (20) *Pa. punctata* (Hinde, 1879), (21) *Pa. jamieae* Ziegler et Sandberg, 1990, (22) *Pa. juntianensis* Han, 1987, (23) *Pa. foliacea* Youngquist, 1945;

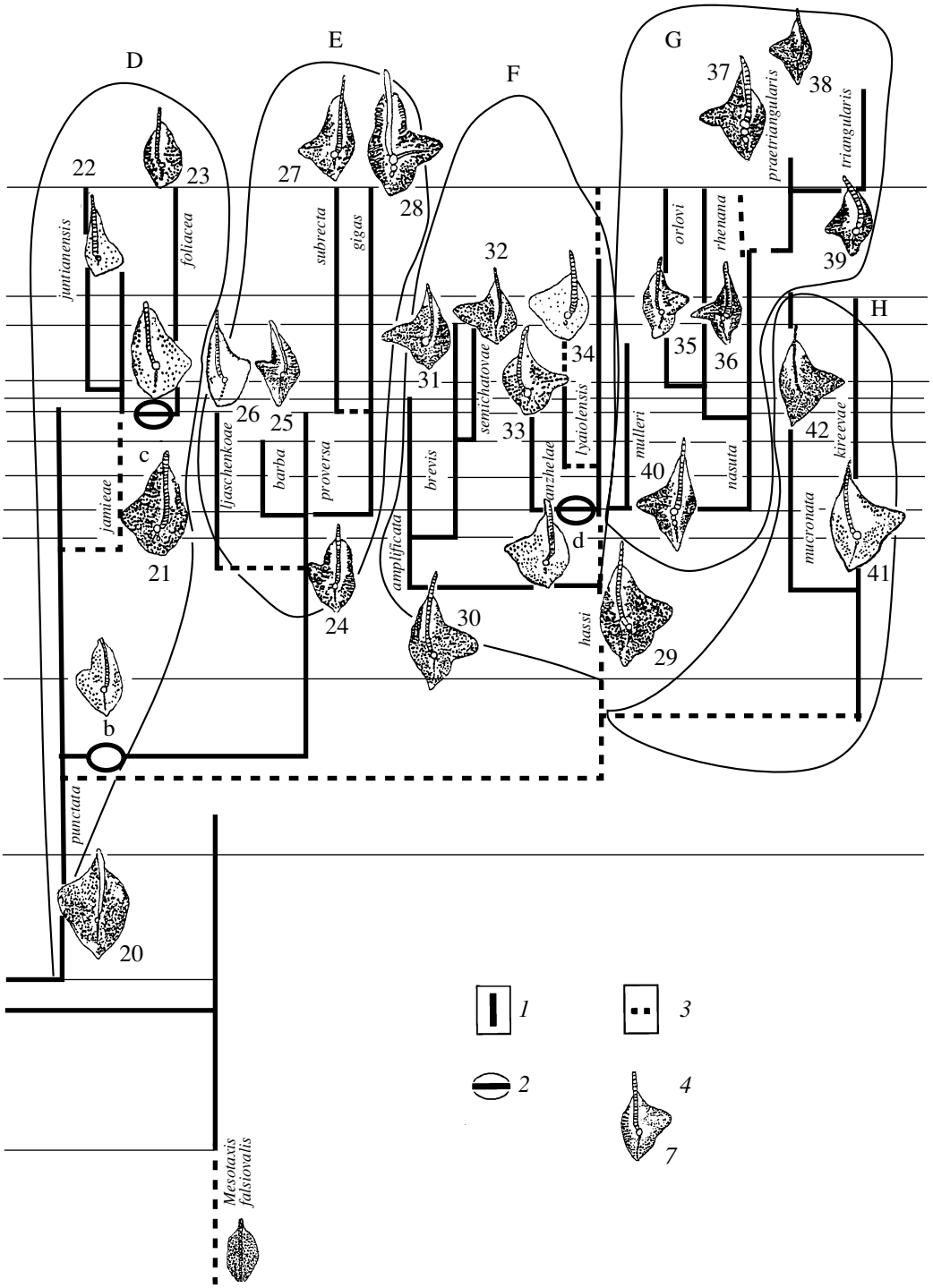


Fig. 16. (Contd.). Branch E: (24) *Pa. proversa* Ziegler, 1958, (25) *Pa. barba* Ziegler et Sandberg, 1990, (26) *Pa. ljaschekoae* Ovnatanova, 1976, (27) *Pa. gigas* Miller et Youngquist, 1947, (28) *Pa. subrecta* Miller et Youngquist, 1947; Branch F: (29) *Pa. hassi* Müller et Müller, 1957, (30) *Pa. amplificata* Klappet, Kuzmin et Ovnatanova, 1996, (31) *Pa. brevis* Ziegler et Sandberg, 1990, (32) *Pa. semichatovae* Ovnatanova, 1976, (33) *Pa. anzhelae* Khrustcheva et Kuzmin, 1996, (34) *Pa. lyaiolensis* Khrustcheva et Kuzmin, 1996; Branch G: (35) *Pa. orlovi* Khrustcheva et Kuzmin, 1996, (36) *Pa. rhenana* Bischoff, 1956, (37) *Pa. nasuta* Müller, 1956, (38) *Pa. praetriangularis* Ziegler et Sandberg, 1988, (39) *Pa. triangularis* Sanneman, 1957, (40) *Pa. mulleri* Klapper et Foster, 1993, (41) *Pa. kireevae* Ovnatanova, 1976, (42) *Pa. mucronata* Klapper, Kuzmin et Ovnatanova, 1996; separated branches with unknown phylogenetic connections: (43) *Pa. elegantula* Wang et Ziegler, 1983, (44) *Pa. kaledai* sp. nov., (45) *Pa. acutangularis* sp. nov.

(groups *Polygnathus webbi, aequalis, decorosus*, etc.) were considered. Later Ovnatanova and Kononova (2001) refined and supplemented the phylogeny of Frasnian polygnathids by the material from the shallow-shelf Frasnian deposits of the central Russian Platform. The phylogenetic relationships of most species were determined by the creation of ontogenetic rows. Similar investigations were previously conducted by Wolska (1967). Finds of forms transitional between some species contributed to the tracing of the direction of the morphological changes from an ancestor to the descendant. Five phylogenetic branches were distinguished based on this strategy (Ovnatanova and Kononova, 2001): *Polygnathus xylus, Polygnathus dubius, Polygnathus pennatus, Polygnathus uchtensis*, and *Polygnathus angustidiscus.*

10.1. Phylomorphogenesis of the Frasnian Palmatolepids

We compiled a phylogenetic scheme of the genus *Palmatolepis* based on material from the eastern Russian Platform (Fig. 16, right). The scheme is allocated to the local conodont zones and stratigraphic subdivisions of the Russian Platform (Fig. 16, left). Correlation of the suggested scheme with other conodont zones is shown in Tables 24 and 25.

Pa. transitans Müller, 1956, is the oldest species of the genus *Palmatolepis*. It is an ancestor for the three branches designated by the letters A, B, and C and was first recorded within the Russian Platform in the Late Sargaevo time (*A. alata–M. bogoslovskyi* Zone). *Pa. transitans* originated from *Mesotaxis falsiovalis* Sandberg, Ziegler et Bultynck, 1989, and inherited a straight median ridge. Formation of the species' features includes developing of the lobe on the inner platform that changed the outline of the platform from oval to oviform triangular, enlarging of the node on the median ridge located over the basal cavity up to the transforming into the azygous node, decreasing the basal cavity to a dot, and loss of flanks contouring the basal cavity. Rise of *Pa. transitans* indicated transition from *Mesotaxis* to *Palmatolepis*. *Palmatolepis* developed in the Frasnian Age in several directions. Changes in the platform outline resulted in the appearance of species united into the A, C, and D phylogenetic branches (Fig. 16). Branches B and E were formed by the changing of the shape of the anterior part of the platform (Fig. 16). Enlarging of the lobe characterizes F, G, and H phylogenetic schemes. Distinguished phylogenetic branches are composed of groups of related species. Each group includes species with one feature in common. The groups were named after their oldest member. The groups were constituted based on the law of "equalizing variability" of the English entomologist Walsch (cited after Vavilov, 1967, pp. 11–12): "If any feature varies within one species of the group, it will exhibit a tendency to changing also in the other relative groups; and if any feature is absolutely constant within one species of the group, it will endeavor to be constant in the related species."

Branch A or rotundilobata group. Elongated triangular platform characterizes all species of this branch.

Branch B or domanicensis group. Its peculiar feature is a short rostrum with wide troughs in the anterior part of the platform.

Branch C or gutta group. Irregularly rounded platform is typical.

Branch D or punctata group. Rounded triangular platform characterizes all species of the branch.

Branch E or proversa group. All species of the branch have an elongated rostrum with narrow troughs in the anterior part of the platform.

Branch F or hassi group. The platform is convex behind the posterior sinus in all species of the branch.

Branch G or nasuta group. Narrow pointed lobe is typical.

Branch H or kireevae group. Long lobe with poorly developed posterior sinus characterizes all species of the branch.

Let us consider each branch in detail.

Branch A (*rotundilobata* group, Fig. 16a). Except *Palmatolepis rotundilobata* Kuzmin, 1998, the branch includes *Pa. keyserlingi* Kuzmin, 1998, *Pa. triquetra* Kuzmin, 1998, *Pa. kuschnarevae* Ovnatanova et Kuzmin, 1992, *Pa. ormistoni* Klapper, Kuzmin et Ovnatanova, 1996, and *Pa. maximovae* Kuzmin, 1998.

Pa. rotundilobata and *Pa. keyserlingi* originated from *Pa. transitans* at the beginning of the Domanik time (at the base of the *efimovae–punctata* Zone). Their distribution was restricted to the lower unit of the Domanik Formation. *Pa. keyserlingi* appears by the changing of platform outline from rounded triangular to elongated triangular and elongated rhombic. It inherits from *Pa. transitans* a straight median ridge and poorly developed lobe. *Pa. rotundilobata* inherits from *Pa. transitans* a lobe located ahead of the level of the azygous node. *Pa. rotundilobata* rises on the account of separation of the lobe with poorly developed posterior sinus and appearance of slightly sigmoidally curved median ridge.

Pa. triquetra and *Pa. maximovae* originated from *Pa. rotundilobata* in the Domanik time (*Po. efimovae–punctata Zone*). *Pa. triquetra* inherits from the ancestor a triangular platform and slightly sigmoidally curved median ridge. The following development included the loss of the posterior sinus. *Pa. maximovae* appeared by the narrowing of the platform and lobe and forming the anterior sinus. *Pa. triquerta* disappears at the end of the early Domanik time (*Po. efimovae–punctata* Zone);

Pa. maximovae became extinct within the terminal stage of the Domanik time.

Pa. kuschnarevae originated from *Pa. maximovae* in the Domanik time (beginning of the *Ancyrognathus ancyrognathoideus–Palmatolepis orbicularis* Zone). Its Pa element inherited from the ancestor a straight median ridge, poorly developed small lobe located ahead of the level of the azygous node. Platform of *Pa. kuschnarevae* becomes irregularly lanceolate due to the further extension and lengthening of its posterior part. This species became extinct in the terminal stage of the Domanik time.

Pa. ormistoni originates from *Pa. kuschnarevae* at the end of the Domanik time by the enlarging the lateral lobe and forming weakly developed sinuses. Almost straight median ridge and elongated posterior part of the platform were inherited from the ancestor. *Pa. ormistoni* became extinct during the Early Askyn time (lowermost *gyrata* Zone).

In this branch (*rotundilobata* group of species), the relationships that were earlier suggested by Kuzmin (1998) are confirmed between *Pa. keyserlingi* and *Pa. rotundilobata*, which originated from *Pa. transitans* and *Pa. maximovae* and *Pa. triquetra*, the descendants of *Pa. rotundilobata.*

Branch B (*domanicensis* group, Fig. 16b) unites species with a short and wide rostrum located in the anterior part of the platform. This branch includes *Palmatolepis spinata* Ovnatanova et Kuzmin, 1991, *Pa. bohemica* Klapper et Foster, 1993, *Pa. domanicensis* Ovnatanova, 1976, and *Pa. plana* Ziegler, Sandberg, 1990.

Pa. spinata, Pa. bohemica, and *Pa. domanicensis* originated from *Pa. transitans* in the Domanik time (*Ancyrognathus ancyrognathoideus–Pa. orbicularis* Zone). They inherited a straight median ridge. *Pa. spinata* was formed by forming a short rostrum and wide troughs, enlarging the lobe, which was removed to the level of the azygous node, and nodes arranged along the platform margins. *Pa. bohemica* is characterized by a short, wide rostrum, deepening anterior sinus, and widening lateral lobe. *Palmatolepis spinata* and *Pa. bohemica* became extinct in the middle of the Domanik time. *Pa. domanicensis* has a short and wide rostrum, poorly pronounced lobe, and pear-shaped posterior part of the platform with an extended posterior ending. This species disappears at the end of the Domanik time.

Pa. plana originated from *Pa. domanicensis* at the end of the Domanik time (*mucronata–amplificata* Zone). *Pa. plana* inherited a wide, short rostrum, but its lobe is enlarged. This species became extinct in the Mendym time (*elegantula–semichatovae* Zone). Phylogenetic relationships of the species of the *domanicensis* group (Fig. 16b) are established for the first time. The only exception is *Pa. plana*, which was previously supposed to be a descendant of *Pa. transitans* (Ziegler and Sandberg, 1990).

Branch C (*gutta* group, Fig. 16b) unites the species with an irregularly rounded platform and weakly developed lobe located in front of the azygous node. Except *Pa. gutta* Kuzmin, 1998, this branch comprises *Pa. orbicularis* Ovnatanova et Kuzmin, 1991, *Pa. gyrata* Kuzmin et Melnikova, 1991, *Pa. ederi* Ziegler et Sandberg, 1990, *Pa. eureka* Ziegler et Sandberg, 1990, *Pa. linguiformis* Müller, 1956, *Pa. timanensis* Klapper, Kuzmin et Ovnatanova, and *Pa. menneri* Ovnatanova et Kononova sp. nov.

The short lived *Pa. gutta* originated from *Pa. transitans* in the Early Domanik time (*Po. efimovae–punctata* Zone) and inherited a poorly pronounced lobe with a weakly developed anterior sinus. We discovered transitional forms *Pa. transitans* → *Pa. gutta* (Fig. 16a) with a triangular rounded platform bearing a straight median ridge. The following development of *Pa. gutta* includes widening of the platform and forming of the rounded poorly pronounced lobe with a hardly noticeable anterior sinus and slightly curved median ridge.

Pa. orbicularis originated from *Pa. gutta* in the Domanik time. It has an irregularly rounded to trapezoid rounded platform. The median ridge is more sigmoidally curved than that of the ancestor. *Pa. orbicularis* disappears in the Mendym time (*elegantula–semichatovae* Zone).

Pa. timanensis, Pa. menneri, and *Pa. ederi* originated from *Pa. orbicularis* in the Mendym time (*elegantula–semichatovae* Zone). The latter is an ancestor of several species. *Pa. timanensis* inherited from *Pa. orbicularis* a rounded platform and sigmoidally curved median ridge. Formation of *Pa. timanensis* is characterized by the loss of nodes and developing of a shagreened surface of the platform.

Pa. menneri inherits from *Pa. orbicularis* the irregularly rounded platform. It loses most of the ornamentation and has a straight median ridge. This species disappears at the beginning of the Evlanovo time. *Pa. gyrata* originated from *Pa. menneri* at the beginning of the Evlanovo time and inherited a poorly ornamented platform but the outline of the platform changed from widely oval to lanceolate.

Pa. ederi inherited from *Pa. orbicularis* a poorly pronounced lobe and ornamentation of nodes. The platform changed to oval and median ridge became slightly sigmoidally curved. The position of the posterior end of the platform also changed with respect to the horizontal plane. Unlike most of the Frasnian species of *Palmatolepis* with a descending posterior end of the platform, *Pa. ederi* has a lifted posterior end. This species became extinct in the Late Askyn time (within the *linguiformis* Zone). *Pa. eureka* originated from *Pa. ederi* in the Early Askyn time (*gyrata* Zone) and *Pa. linguiformis* originated in the Late Askyn time.

Pa. eureka inherited from *Pa. ederi* an elongated oval platform and sigmoidally curved median ridge.

Pa. linguiformis inherited from *Pa. ederi* an oval platform and sigmoid median ridge. The changes consist of the development of a small and weakly pronounced lobe bordered with hardly visible anterior and posterior sinuses, in abrupt decrease of the free blade length, and in the development of better pronounced nodes. *Pa. eureka* and *Pa. linguiformis* became extinct at the terminal stage of the Askyn time (top of the *linguiformis* Zone).

The *gutta* group unites species, the phylogenetic relationships of which have not been thoroughly analyzed. This branch is of the greatest interest as it clarifies connections between *Pa. ederi, Pa. eureka*, and *Pa. linguiformis.* Ziegler and Sandberg (1990) supposed *Pa. ederi* to originate from *Pa. hassi*, and *Pa. linguiformis* from *Pa. rhenana rhenana.* These relationships were specified by the introduction of new species into the phylogenetic scheme (Fig. 16c).

Branch D (*punctata group*) unites species with a rounded triangular platform. The ancestor of the branch is *Pa. punctata* (Hinde, 1879). The branch consists of *Pa. jamieae* Ziegler et Sandberg, 1990, *Pa. juntianensis* Han, 1987, and *Pa. foliacea* Youngquist, 1945.

Pa. punctata originated from *Pa. transitans* in the Early Domanik time (base of the *efimovae–punctata* Zone). It inherited an almost straight median ridge and a poorly developed lobe. The changes consist of the widened platform and lobe removed anteriorly to the level of the azygous node. *Pa. punctata* became extinct in the end of the Mendym time (top of the *elegantula–semichatovae* Zone).

Pa. jamieae probably originated from *Pa. punctata* in the Early Askyn time (base of the *gyrata* Zone). It inherited a rounded triangular platform and well developed nodes. The transitional forms *Pa. punctata* → *Pa. jamieae* (Fig. 16c) demonstrate changes in the size of the anterior and posterior parts of the platform as the anterior part becomes considerably longer. The lobe removes to the level of the azygous node, the ridge becomes sigmoidally curved. Then the lobe of *Pa. jamieae* becomes better pronounced and contoured by well developed anterior and posterior sinuses. *Pa. jamieae* became extinct in the Late Askyn time (*linguiformis* Zone).

Pa. foliacea originated from *Pa. jamieae* in the Early Askyn time (*gyrata* Zone). It inherited a slightly sigmoidally curved median ridge and ornamentation of nodes. The species formed as a result of the disappearance of sinuses contouring the lobe and formation of the irregularly ellipsoid platform.

Pa. juntianensis originated from *Pa. jamieae* in the Late Askyn time (*juntianensis* Zone). It inherited a triangular platform; but the anterior part of its platform abruptly elongates and extends; the lobe enlarges and removes to the level of the azygous node in the posterior part of the platform. The posterior sinus and ornamentation of nodes disappear; the platform surface becomes shagreened and the median ridge straight. *Pa. foliacea* and *Pa. juntianensis* became extinct in the Late Askyn time (top of the *linguiformi*s Zone).

The phylogenetic line from *Pa. jamieae* to *Pa. juntianensis* suggested by Ziegler and Sandberg (1990) was on the whole confirmed in our investigations. It was earlier supposed that *Pa. foliacea* originates from *Pa. punctata* (Ziegler et Sandberg, 1990).

Branch E (*proversa* group) unites species with an elongated anterior part of the platform and elongated narrow rostrum formed by the raised lateral margins of the platform. Except *Pa. proversa* Ziegler, 1958, the group includes *Palmatolepis barba* Ziegler et Sandberg, 1990, *Pa. ljaschenkoae* Ovnatanova, 1976, *Pa. gigas* Miller et Youngquist, 1947, and *Pa. subrecta* Miller et Yongquist, 1947.

Pa. proversa originated from *Pa. punctata* in the Domanik time (*Ancyroghathus ancyrognathoideus–Pa. orbicularis* Zone). It inherits almost straight median ridge, lobe located anterior to the azygous node, and ornamentation of nodes. The transitional forms from *Pa. punctata* to *Pa. proversa* (Fig. 16b) have a lateral lobe with a well-pronounced anterior sinus.

Later on the axis of the lobe changes its direction from the lateral (in *Pa. punctata*) to the anterior end (in *Pa. proversa*). The end of the lobe points and the anterior sinus deepens; rostrum with deep troughs and well-developed rostral ridges appear. *Pa. proversa* became extinct in the Mendym time (top of the *elegantula–semichatovae* Zone).

Pa. ljaschenkoae possibly originated from *Pa. proversa* in the Domanik time (*Ancyroghathus ancyrognathoideus–Pa. orbicularis* Zone). Both of them have an elongated anterior part of the platform and axis of the lobe directed upwards. But *Pa. ljaschenkoae* lacks troughs and rostral ridges, its anterior sinus shallows, and ornamentation of nodes disappears over the whole platform except some nodes along its margins. This species became extinct in the Late Mendym time (*elegantula–semichatovae* Zone).

Pa. barba and *Pa. gigas* originated from *Pa. proversa* in the Early Mendym time. All of them have elongated anterior part of the platform, narrow rostrum, well-pronounced lobe, and ornamentation of nodes. But the lobe axis of *Pa. gigas* becomes laterally directed, the lobe removes to the level of the azygous node, and the posterior sinus deepens; meanwhile *Pa. barba* preserves the outline of the platform of its ancestor, but the troughs shallow and position of the posterior end of the platform changes with respect to the horizontal plane. Unlike most of the Frasnian species, the posterior end of the platform of *Pa. barba* is raised with respect to the horizontal plane. This species

became extinct in the Late Mendym time (*elegantula–semichatovae* Zone).

Pa. subrecta originated from *Pa. gigas* in the Early Askyn time (*gyrata* Zone). It inherited rostrum, anterior and posterior sinuses, and ornamentation of nodes. *Pa. subrecta* was formed by the shortening of the lobe, shallowing of the troughs, and disappearance of the rostral ridges. The parapet developed on the outer platform may be considered as a rudiment of the rostral ridge. This species disappears in the Late Askyn time (top of the *linguiformis* Zone).

Due to the transitional forms of this branch, the origin of *Pa. proversa* from *Pa. punctata* (not from *Pa. transitans*, as was previously supposed (Ziegler and Sandberg, 1990)) was demonstrated. The assumed connections (Ziegler et Sandberg, 1990) from *Pa. proversa* to *Pa. barba* and from *Pa. proversa* to *Pa. simpla* (=*Pa. ljaschenkoae*) were confirmed. Heretofore *Pa. proversa* was supposed to originate from *Pa. transitans* and *Pa. subrecta* from *Pa. hassi.*

Branch F (*hassi* group) includes conodonts with well-developed sinuses and convex margin of the platform behind the posterior sinus. This branch includes *Pa. hassi* Müller et Müller, 1957, *Pa. amplificata* Klapper, Kuzmin et Ovnatanova, 1996, *Pa. brevis* Ziegler et Sandberg, 1990, *Pa. semichatovae* Ovnatanova, 1976, *Pa. anzhelae* Khruschova et Kuzmin, 1996, and *Pa. lyaiolensis* Khrustcheva et Kuzmin, 1996.

Pa. hassi is the ancestor of the branch. According to Ziegler and Sandberg (1990), it appeared at the base of the zone with the same name that corresponds approximately to unit 2 of the Domanik Formation of Southern Timan. Unfortunately, the range of *Pa. hassi* was noticeably widened recently and also by the authors of the conodont zonation (Ziegler and Sandberg, 1990) and thus the use of the scale was considerably hampered. Isolated records of *Pa. hassi* s.l. are known only in the uppermost Domanik Formation (member 3) of the Volga–Ural province and Southern Timan; this species is abundant at the Mendym level. *Pa. hassi* originated from *Pa. punctata* by the lengthening of the lobe and its removing closer to the azygous node, appearance of the sigmoid curvature of the median ridge, and well-developed anterior and posterior sinuses. *Pa. hassi* inherited from *Pa. punctata* a relatively wide subtriangular platform and well-pronounced ornamentation of nodes. This species became extinct at the end of the Frasnian Age.

Pa. amplificata originated from *Pa. hassi* in the second half of the Domanik time by the development one or two parapets in the anterior third of the platform, which are arranged parallel to the median ridge, lengthening of the lobe, and pointing of the posterior end of the platform. It inherited a well-pronounced lobe with deep anterior and posterior sinuses, convex margin of the platform behind the posterior sinus, and ornamentation of nodes. *Pa. amplificata* disappeared in the Early Askyn time (base of the *gyrata* Zone).

Pa. brevis originated from *Pa. amplificata* in the Early Mendym time (*elegantula–semichatovae* Zone). It inherited long, contoured by anterior and posterior sinuses, and located at the level of the azygous node lobe, convex anterior margin of the platform behind the posterior sinus, and ornamentation of nodes uniformly covering the platform surface. The changes consist of the disappearance of parapets, pointing of the lobe ending, and widening of the posterior end of the platform. *Pa. brevis* became extinct in the Early Askyn time (*juntianensis* Zone).

Pa. semichatovae branched off *Pa. brevis* in the Mendym time (inside the *elegantula–semichatovae* Zone). It inherited a long rounded triangular lobe with well-developed anterior and posterior sinuses, convex margin of the platform behind the posterior sinus, and rounded posterior end of the platform. The changes consist of the developing one or two low parapets in the anterior third of the platform, which are parallel to the median ridge and separated from the latter by narrow troughs; the lobe removed anteriorly with respect to the azygous node. *Pa. semichatovae* became extinct in the Evlanovo time (*juntianensis* Zone).

Pa. anzhelae originated from *Pa. hassi* in the Early Mendym time (*elegantula–semichatovae* Zone). It inherited a rounded triangular platform, convex margin of the platform behind the posterior sinus, and well-pronounced ornamentation of nodes. The changes consist of the considerable narrowing and lengthening of the lateral lobe. The revealed transitional forms demonstrate the process of the gradual narrowing of the lateral lobe (Fig. 16d).

Pa. lyaiolensis originated from *Pa. hassi* in the Mendym time (*elegantula–semichatovae* Zone). It inherited subtriangular platform, lobe located in front of the azygous node, sigmoid median ridge, and convex margin of the platform behind the posterior sinus. The platform widens and becomes rounded triangular; posterior sinus becomes shallow; size of the nodes decreases and they become extremely small; the platform surface is often shagreened. *Pa. lyaiolensis* becomes extinct in the Evlanovo time (*juntianensis* Zone).

The phylogenetic relationships of the majority of the species of the branch F are adduced for the first time. Previously assumed relationship between *Pa. brevis* and *Pa. semichatovae* is confirmed.

Branch G (group *rhenana*) unites the species with a narrow lobe that is sharply bordered with anterior and posterior sinuses. The branch includes *Pa. muelleri* Klapper et Foster, 1993, *Pa. nasuta* Müller, 1956, *Pa. rhenana* Bischoff, 1956, *Pa. orlovi* Khrustcheva et Kuzmin, 1996, *Pa. praetriangularis* Ziegler et Sandberg, 1988, and *Pa. triangularis* Sannemann, 1955.

Pa. muelleri and *Pa. nasuta* simultaneously originated from *Pa. hassi* in the early Mendym time (*eleganula–semichatovae* Zone). Both of them inherited a long lobe, well-pronounced anterior and posterior sinuses, sigmoidally curved median ridge, and ornamentation of nodes. But the platform of *Pa. muelleri* becomes elongated triangular and its posterior end narrows while in *Pa. nasuta* the posterior end and lateral lobe become narrow.

Pa. rhenana originated from *Pa. nasuta* in the Early Askyn time (at the base of the *gyrata* Zone). It inherited a well-developed lateral lobe, well-pronounced anterior and posterior sinuses, sigmoidally curved median ridge, and ornamentation of nodes. The changes consist of the more sigmoidally curved median ridge, pointed and elongated posterior end of the platform, enlarged nodes of the median ridge, which are located near the azygous node, and pointed and narrowed lobe.

Pa. orlovi originated from *Pa. rhenana* in the Askyn time (*gyrata* Zone). It inherited a strongly sigmoidally curved median ridge, deep posterior sinus, and pointed posterior end of the platform. The changes consist of the widened and shorted lateral lobe. *Pa. orlovi, Pa. rhenana*, and *Pa. nasuta* became extinct in the Late Askyn time (top of the *linguiformis* Zone) and *Pa. muelleri* disappears in the Early Askyn time (within the *juntianensis* Zone).

Pa. praetriangularis branched off *Pa. nasuta* in the Late Askyn time (*linguiformis* Zone). It inherited a pointed lobe, sigmoidally curved median ridge, and ornamentation of nodes. The posterior end of the ancestor is descending, while in *Pa. praetriangularis* it is horizontal. *Pa. praetriangularis* also has a more sigmoidally curved median ridge and pointed posterior end of the platform and ending of the lobe. This species disappears in the lower part of the Famennian Stage (*triangularis* Zone).

Pa. triangularis originated from *Pa. praetriangularis* at the beginning of the Famennian (*triangularis* Zone). The changes consist of the uplift of the posterior end of the platform with respect to the horizontal plane. *Pa. triangularis* inherited a pointed posterior end of the platform, pointed lobe, sigmoid curvature of the median ridge, and ornamentation of nodes. *Pa. triangularis* became an ancestor for the majority of the Famennian species. Except *Pa. praetriangularis*, none of the species considered above survives beyond the Frasnian–Famennian boundary. Previously assumed connections between *Pa. rhenana* and *Pa. nasuta* were confirmed within the branch G. Other relationships are argued for the first time.

Branch H (group *kireevae*) includes *Pa. kireevae* Ovnatanova, 1976, and *Pa. mucronata* Klapper, Kuzmin et Ovnatanova, 1996, with a long and well developed lobe with a weakly pronounced posterior sinus. *Pa. kireevae* presumably originated from *Pa. hassi* in the middle of the Domanik time (*Ancyrognathus ancyrognathoideus–Palmatolepis orbicularis* Zone). It inherited a triangular platform, well-pronounced lobe, and pointed posterior end of the platform. The changes consist of the lengthened lobe, shallower posterior sinus, and decreased in sizes nodes. Posterior end of *Pa. mucronata* is narrower and ornamentation of nodes is better pronounced. The latter species became extinct in the Askyn time (top of the *juntianensis* Zone).

At the end of the review of the *Palmatolepis phylogeny*, we mention that there are three branches the ancestry of which for the present remain unknown: *Palmatolepis elegantula* Wang et Ziegler, 1987, *Pa. acutangularis* Ovnatanova et Kononova sp. nov., and *Pa. kaledai* Ovnatanova et Kononova sp. nov. *Pa. acutangularis* and *Pa. kaledai* are short-lived and were found only within unit 4 of the Lyaiol' Formation (beginning of the Evlanovo time). *Pa. elegantula* appears at the beginning of the Mendym time and disappears at the beginning of the Evlanovo time.

10.2. Ontogenetic Changes of Some Palmatolepis Representatives

In the study of the Frasnian palmatolepids, we succeeded in compiling ontogenetic rows for several species that were numerous in the collection.

Based on the sizes, small juvenile (0.2–0.3 mm), young (0.35–0.4 mm), large adult (0.5–0.6 mm), and senile (0.7–1.2 mm) forms were distinguished (Fig. 17).

The ontogenetic rows allow us to determine the peculiarities of the formation of species characteristic features and trace the species forming.

The majority of *Palmatolepis* specimens in the collection proved to be adult and senile forms. In the Fig. 17, the adult palmatolepids are the right units and senile are the left units. However, our collection contains adult and senile forms represented both by left and right forms. The stages of growth were distinguished by the length of the platform based on the received experience of the study of icriodid ontogeny (Kononova and Kim, 2001). Only five species in our collection are represented by the specimens on the young, adult, and senile stages. One species is characterized by all four stages: juvenile, young, adult, and senile (Figs. 17a–17d).

Juvenile and young specimens of *Pa. semichatovae* (Figs. 17a–17d) have a well-developed rounded posterior end of the platform, anterior and posterior sinuses, relatively long and rounded lobe, slightly arched in juvenile and slightly sigmoidally curved in young forms median ridge. The ornamentation of nodes at these stages is poorly developed. Some nodes are developed only in the anterior half of the platform. A characteristic feature of the species is the presence of low parapets parallel to the median ridge, which are absent at the early developmental stages. The low parapet appears at the adult stage. It consists of a chain of nodes

Stage / Species / Length, mm	Juvenile	Young	Adult	Senescent
	0.2–0.3	0.35–0.4	0.5–0.6	0.7–1.2 and more
Pa. semichatovae	(a) ×33	(b) ×33	(c) ×33	(d) ×33
Pa. barba		(e) ×40	(f) ×37	(g) ×42
Pa. gutta		(h) ×40	(i) ×35	(j) ×35
Pa. orbicularis		(k) ×27	(l) ×27	(m) ×27
Pa. lyaiolensis		(n) ×34	(o) ×34	(p) ×34
Pa. gyrata		(q) ×35	(r) ×35	(s) ×30

Fig. 17. Ontogenetic series of Frasnian representatives of *Palmatolepis:* (a–d) *Pa. semichatovae* Ovnatanova, 1976, specimens from the VNIGNI collection, no. ONS 7; southern Timan, Vezha-Vozh River, outcrop 9, sample 9/1; Lyaiol' Formation, unit 2; (e–g) *Pa. barba* Ziegler et Sandberg, 1990, specimens from the VNIGNI collection, no. ONS 40; southern Timan, Vezha-Vozh River, outcrop 735, sample K-6, sample 9/1; Lyaiol' Formation, unit 2; (h–j) *Pa. gutta* Kuzmin, 1998, specimens from the VNIGNI collection, no. ONS 6; southern Timan, Chut' River, outcrop 7 (1), sample 91, Domanik Formation, unit 1; (k–m) *Pa. orbicularis* Ovnatanova et Kuzmin, 1991: (k) PIN, no. OK-1033; southern Timan, Chut' River, outcrop 7, sample 5; Domanik Formation, unit 3 (collection of A.V. Kuzmin); (n–p) *Pa. lyaiolensis* Khruscheva et Kuzmin, 1996, specimens from the VNIGNI collection, no. ONS 7, Volga–Urals, Severnyi Kupol 71, sample 59, interval 1646–1649 m, upper part of the Askyn Regional Stage; (q–s) *Pa. gyratus* Kuzmin et Melnikova, 1991, specimens from the VNIGNI collection, no. ONS 7, Volga–Urals, Severnyi Kupol 71, sample 62, interval 1649–1651 m, upper part of the Askyn Regional Stage.

arranged almost parallel to the median ridge in the anterior third of the outer platform. The parapet is separated from the median ridge by a small trough. At the senile stage, the lobe enlarges and becomes rounded triangular, the sigmoid curvature of the median ridge increases, and the posterior end of the platform remains rounded. The nodes cover almost the entire platform surface. Low parapets appear in the anterior third of the platform. They are parallel to the median ridge and are separated from the latter by shallow troughs.

The young forms of *Pa. barba* (Figs. 17e–17g) have a well-developed, narrow, and rostrum-like elongated anterior end and pointed lobe with a deep anterior sinus. The platform surface is smooth and lacks ornamentation of nodes. The adult forms have all above-listed features but numerous nodes and ridges are developed along the platform margin. The senile specimens have more nodes along the platform margins. The posterior end of the platform is raised during all stages considered above.

Pa. gutta at the young developmental stages (Figs. 17h–17j) has a triangularly rounded platform, poorly developed lobe, straight median ridge, and ornamentation of fine nodes, or the platform surface is shagreened. These features are retained at the adult stage; in addition, the platform widens and the ornamentation of nodes becomes better pronounced; small nodes cover the whole platform surface except the area adjacent to the median ridge. In the senile forms, the lobe is better pronounced due to the marked anterior sinus; the ornamentation remains the same.

The young forms of *Palmatolepis orbicularis* (Figs. 17k–17m) have an irregularly rounded shagreened platform with a straight median ridge. At the adult stage, the platform becomes rounded trapezoid. The median ridge is sigmoidally curved. The ornamentation consists of small nodes irregularly arranged on the platform. At the senile stages, the platform is also irregularly rounded or rounded trapezoid but with a well-developed short, wide lobe and well-pronounced anterior sinus. The ornamentation consists of small nodes irregularly arranged on the platform but in its anterior half located closer to the margins.

The young specimens of *Pa. lyaiolensis* (Figs. 17n–17p) have a rounded triangular platform and slightly sigmoidally curved median ridge. The lobe is located in front of the azygous node. The platform surface is smooth. All the above-mentioned features are retained at the adult stage. In the senile forms, all adult features persist and the platform surface becomes shagreened.

Young specimens of *Pa. gyrata* (Figs. 17q–17s) have a lanceolate platform with a smooth surface and straight median ridge. The lobe is poorly pronounced and is located in the anterior part of the platform. At the adult stage, the above-mentioned features persist, and ornamentation of nodes develops; small nodes are arranged along the platform margins. In the senile forms, all adult features persist and the platform becomes widely oval.

Ontogenetic studies demonstrate that the main species features (outline of the platform, presence of the lobe, and curvature of the median ridge) are developed beginning with the earliest developmental stages. Although the ornamentation of nodes is developed beginning with the juvenile and young stages (*Pa. semichatovae* for instance), it becomes fully pronounced at the adult and senile stages.

10.3. Phylomorphogenesis of the Frasnian Polygnathids

The genus *Polygnathus* appeared in the Early Devonian, reached its peak in the Emsian and Eifelian, slightly slowed down the evolutionary rate in the Givetian, and again flourished in the Frasnian. The beginning of the Emsian was marked by a subdivision of this genus into three main phylogenetic lines *Polygnathus linguiformis, Po. cooperi*, and *Po. costatus* (Weddige, 1977). Later these three lines gave many additional lateral branches. Some of these branches survived up to the Givetian and became ancestors for Frasnian polygnathids.

The ontogenetic rows were compiled and presented based on the representative collections from the Frasnian deposits of the central Russian Platform (Ovnatanova and Kononova, 2001, figs. 11–13). In a number of cases, transitional forms between separate species were found.

The earlier assumed phylogenetic relationships are confirmed in the present paper and also some additions and changes are inserted.

Six phylogenetic lines, each having one specific feature in common, are shown in Fig. 18; transitional forms between separate species are also shown.

Branch *Polygnathus xylus* (Fig. 18, branch A) unites species with an elongated platform and raised lateral margins. Within this branch, the platform developed in two directions: loss of ornamentation (*praepolitus*, *politus*, and branch *Po*. sp. *B groups*) and developing of ornamentation (*pollocki* group and species of the branches *Po. pseudoxylus, Po. reimersi*, and possibly *Po. brevilamiformis*). The ancestor of this branch is *Polygnathus xylus* (Fig. 18.1) which has an elongated platform, poorly pronounced ornamentation, short transverse ridges, and long free blade bearing small spinous denticles. This species appeared in the Givetian Age and became extinct in the Frasnian (middle of the Domanik (Semiluki) time).

The *Praepolitus group* unites species with a smooth platform and long median ridge extending up to the posterior end of the platform. Except *Po. praepolitus*, this group includes *Po. maxomovae* and *Po. macilentus. Po. praepolitus* originated from *Po. xylus* at the beginning of the Sargaevo time (end of the *Po. pennatus–Po. ljaschenkoi* Zone) (Fig. 18.5). It inherited a

Fig. 18. Phylomorphogenetic scheme of Frasnian polygnathids. Designations: (*1*) stratigraphical range of the *Polygnathus* species in the Frasnian age, (*2*) transitional forms (a–n): (a) *Po. xylus* Stauffer → *Po. praepolitus* Kononova et al., (b) *Po. xylus* Stauffer → *Po. pseudoxylus* Kononova et al., (c) *Po. xylus* Stauffer → *Po. brevilamiformis* Ovnatanova, (d) *Po. pollocki* Druce → *Po. azygomorphus* Aristov, (e) *Po. pollocki* Druce → *Po. lingulatus* Ovnatanova, (f) *Po. lingulatus* Ovnatanova → *Po. rudkinensis* Ovnatanova et Kononova, (g) *Po. praepolitus* Kononova et al. → *Po. politus* Ovnatanova, (h) *Po. politus* Ovnatanova → *Po. alvenus* Ovnatanova et Kononova, (i) *Po. politus* Ovnatanova → *Po. subincompletus* Ovnatanova et Kononova, (j) *Po. praepolitus* Kononova et al. → *Po. maximovae* Ovnatanova et Kononova, (k) *Po. webbi* Stauffer → *Po. mosquensis* Litvinova in Ovnatanova et Kononova, (l) *Po. webbi* Stauffer → *Po. zinaidae* Kononova et al., (m) *Po. torosus* Ovnatanova et Kononova → *Po. brevis* Miller et Youngquist, (n) *Po. uchtensis* Ovnatanova et Kuzmin → *Po. timanicus* Ovnatanova; (*3*) possible phylogenetic connections; only fact of the presence of a transitional form is marked, the forms themselfes are figured in Ovnatanova and Kononova, 2001, text-figs. 11–13; (*4*) scetchs (contoured photographs) of the holotypes designated with numbers. (A–E) phylogenetic branches: (A) *xylus* branch: (1) *Polygnathus xylus* Stauffer, 1940, (2) *Po. reimersi* Kuzmin, 2001, (3) *Polygnathus* sp. B Ovnatanova et Kononova 2001, (4) *Po. pseudoxylus* Kononova, Alekseev, Barskov et Reimers, 1996, (5) *Po. praepolitus* Kononova, Alekseev, Barskov et Reimers, 1996, (6) *Po. alvenus* Ovnatanova et Kononova, 1996, (7) *Po. politus* Ovnatanova, 1969; (8) *Po. subincompletus* Ovnatanova et Kononova, 1996, (9) *Po. macilentus* Kuzmin in Obuchovskaya, Kuzmin, 1993, (10) *Po. maximovae* Ovnatanova et Kononova, 1996, (11) *Po. brevilamiformis* Ovnatanova, 1976, (12) *Po. azygomorphus* Aristov in Ovnatanova, Aristov, 1985, (13) *Po. pollocki* Druce, 1976, (14) *Po. ilmenensis* Zhuravlev, 2003, (15) *Po. efimovae* Kononova, Alekseev, Barskov et Reimers, 1996, (16) *Po. lingulatus* Ovnatanova, 1976, (17) *Po. rudkinensis* Ovnatanova et Kononova, 1996, (18) *Po. strictus* Kuzmin et Jurtchenkova, 1989; (B) *denisbriceae* branch: (19) *Po. denisbriceae* Bultynck, 1979, (20) *Po. ljaschenkoi* Kuzmin, 1995; (C) *dubius* branch: (21) *Po. dubius* Hinde, 1879, (22) *Po. olgae* Ovnatanova et Kuzmin, 1991, (23) *Po. alatus* Huddle, 1934, (24) *Po. reitlingerae* Ovnatanova et Kononova, sp. nov., (25) *Po. aequalis* Klapper et Lane, 1985, (26) *Po. decorosus* Stauffer, 1940, (27) *Po. komi* Kuzmin et Ovnatanova, 1989, (28) "*Po. foliatus*" Bryant, 1921, (29) *Po. webbi* Stauffer, 1938, (30) *Po. imparilis* Klapper et Lane, 1985, (31) *Po. evidens* Klapper et Lane, 1985, (32) *Po. planarius* Klapper et Lane, 1985, (33) *Po. churkini* Savage et Funai, 1980, (34) *Po. krestovnikovi* Ovnatanova, 1969, (35) *Po. mosquensis* Litvinova in Ovnatanova, Kononova, 1996, (36) *Po. zinaidae* Kononova, Alekseev, Barskov et Reimers, 1996, (37) *Po. seraphimae* Ovnatanova et Kononova, 1996, (38) *Po. aspelundi* Savage et Funai, 1980; (D) *pennatus* branch: (39) possible ancestor of *Po. pennatus* (*Linguipolignathus linguiformis* (Hinde, 1879)), (40) *Polygnathus* sp. A Ovnatanova et Kononova, 2001, (41) *Po. pennatus* Hinde, 1879, (42) *Po. torosus* Ovnatanova et Kononova, 1996, (43) *Po. unicornis* Müller et Müller, 1957, (44) *Po. sublatus* Ulrich et Bassler, 1926, (45) *Po. costulatus* Aristov in Ovnatanova, Aristov, 1985, (46) *Po. colliculosus* Aristov in Ovnatanova, Aristov, 1985, (47) *Po. brevis* Miller et Youngquist, 1947, (48) *Po. ettremae* Pickett, 1972; (E) *uchtensis* branch: (49) *Po. uchtensis* Ovnatanova et Kuzmin, 1991, (50) *Po. vjalovi* Zvereva, 1986, (51) *Po. timanicus* Ovnatanova, 1969, (52) *Po. lodinensis* Pölsler, 1969, (53) *Po. siratchoicus* Ovnatanova et Kuzmin, 1992; (F) *angustidiscus* branch: (54) *Po. angustidiscus* Youngquist, 1945, (55) *Po. posterus* Kuzmin, 1995, and (56) *Po*. aff. *brevilaminus* Branson et Mehl, 1934.

long median ridge reaching the posterior end of the platform. Transverse ridges gradually disappear in the development of *Po. praepolitus.* This species became extinct at the beginning of the Evlanovo time.

Po. maximovae originated from *Po. praepolitus* in the middle of the Voronezh time (Fig. 18.10). It inherited a long extended platform and long median ridge reaching the posterior end of the platform. Well-pronounced denticles are developed along the platform margins in its anterior part. *Po. maximovae* became extinct at the end of the Frasnian Age.

Po. macilentus originated from *Po. praepolitus* at the beginning of the Evlanovo time (Fig. 18.9). It was formed by the strong uplift of the platform lateral margins and inherited a long median ridge reaching the posterior end of the platform. This species became extinct at the end of the Livny time.

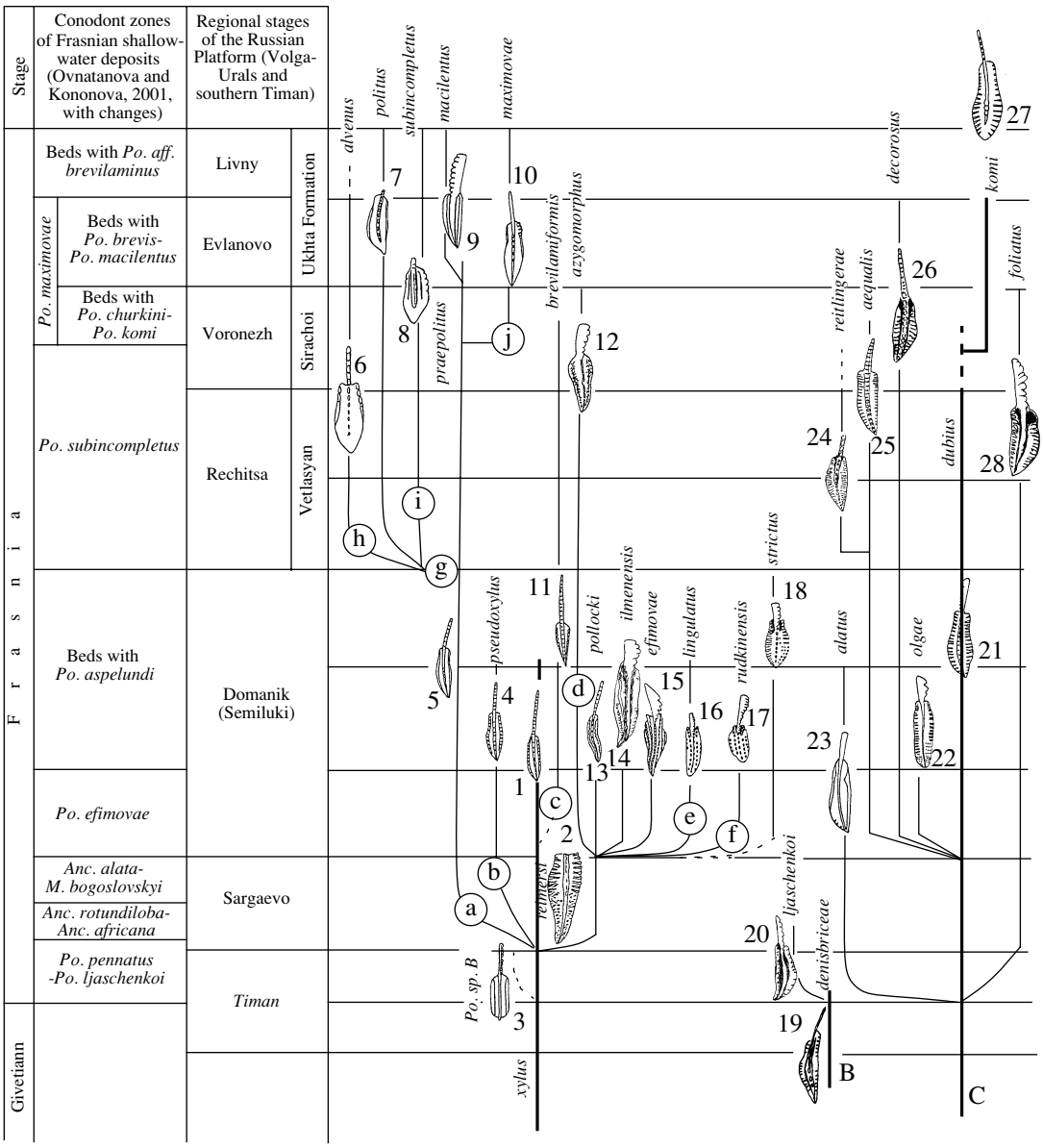
The *politus group* unites species with a smooth platform and short median ridge. The platform is smooth behind the median ridge. Apart from *Po. politus*, the group includes *Po. alvenus* and *Po. subincompletus.*

Po. politus (Fig. 18.7) originated from *Po. praepolitus* at the beginning of the Rechitsa time. It inherited a smooth platform surface. In the formation of the species features of *Po. politus*, the median ridge disappears in the smoothening of the posterior part of the platform. This feature is inherited by the descendants of *Po. politus*: *Po. alvenus* and *Po. subincompletus.* Both of these species appeared simultaneously at the beginning of the Rechitsa time (*Po. subincompletus* Zone). In *Po. alvenus* (Fig. 18.6), the height of the median ridge gradually decreases and short ridges appear on the lateral sides of the anterior part of the platform. *Po. alvenus* became extinct at the beginning of the Livny time. In *Po. subincompletus* (Fig. 18.8), the height of the median ridge increases and denticles are developed along the margins of the anterior part of the platform. This species became extinct at the end of the Livny time.

Another representative of the *xylus* branch with a smooth platform is *Po.* sp. *B* Ovnatanova et Kononova, 2001 (Fig. 18.3). This species appeared in the Timan time (at the beginning of the *Po. pennatus–Po. ljaschenkoi* Zone). It possibly originated from *Po. xylus* by the raising of the lateral margins of the platform and loss of ornamentation. The species was short-lived and became extinct at the end of the Timan time.

The *pollocki group* is characterized by the tucking up of the platform margins inwards and developing of the longitudinally extended ornamentation (ridges or chains of nodes). Except *Po. pollocki*, the group includes *Po. lingulatus, Po. rudkinensis, Po. ilmenensis, Po. efimovae*, and *Po. azygomorphus. Po. strictus* is provisionally included. *Po. xylus* is the ancestor of the *Po. pollocki* group of species. All representatives of the group inherited from *Po. xylus* a long median ridge reaching the posterior end of the platform.

Po. pollocki branched off *Po. xylus* at the beginning of the Sargaevo time (end of the *Po. pennatus–Po. ljas-*



chenkoi Zone). At the early developmental stages, *Po. pollocki* is almost similar to its ancestor in the platform outline and type of the ornamentation (Fig. 18.13). The margins are tucking up and S-shaped curvature of the median ridge forms in the development of *Po. pollocki.* This species disappears in the Domanik time. *Po. lingulatus* is phylogenetically connected with *Po. pollocki* (Fig. 18.16). It appeared at the beginning of the Semiluki time (base of the *Po. efimovae* Zone). In the development of *Po. lingulatus*, the margins of the platform lower and short transverse ridges along the margins transform into the small nodes along the median ridge. The transitional forms were revealed between *Po. lingulatus* and its descendant *Po. rudkinensis* (Fig. 18.17). *Po. rudkinensis* appeared at the beginning of the Semiluki time. In the formation of *Po. rudkinensis*, the platform widened and the number of the longitudinal rows of nodes on its upper surface increases. *Po. strictus* possibly originated from *Po. rudkinensis* at the beginning of the Semiluki time. Its development possibly included the reconstruction of the platform ornamentation that resulted in the developing of transversely extended chains of nodes and transverse ridges.

Po. ilmenensis originated from *Po. pollocki* at the beginning of the Domanik (Semiluki) time (Fig. 18.14) by the widening of the platform and developing of the longitudinal ridges. *Po. efimovae* branched off *Po. ilmenensis* at the beginning of the Domanik time also by the further increase in the number of longitudinal ridges (Fig. 18.15). Both species have a short

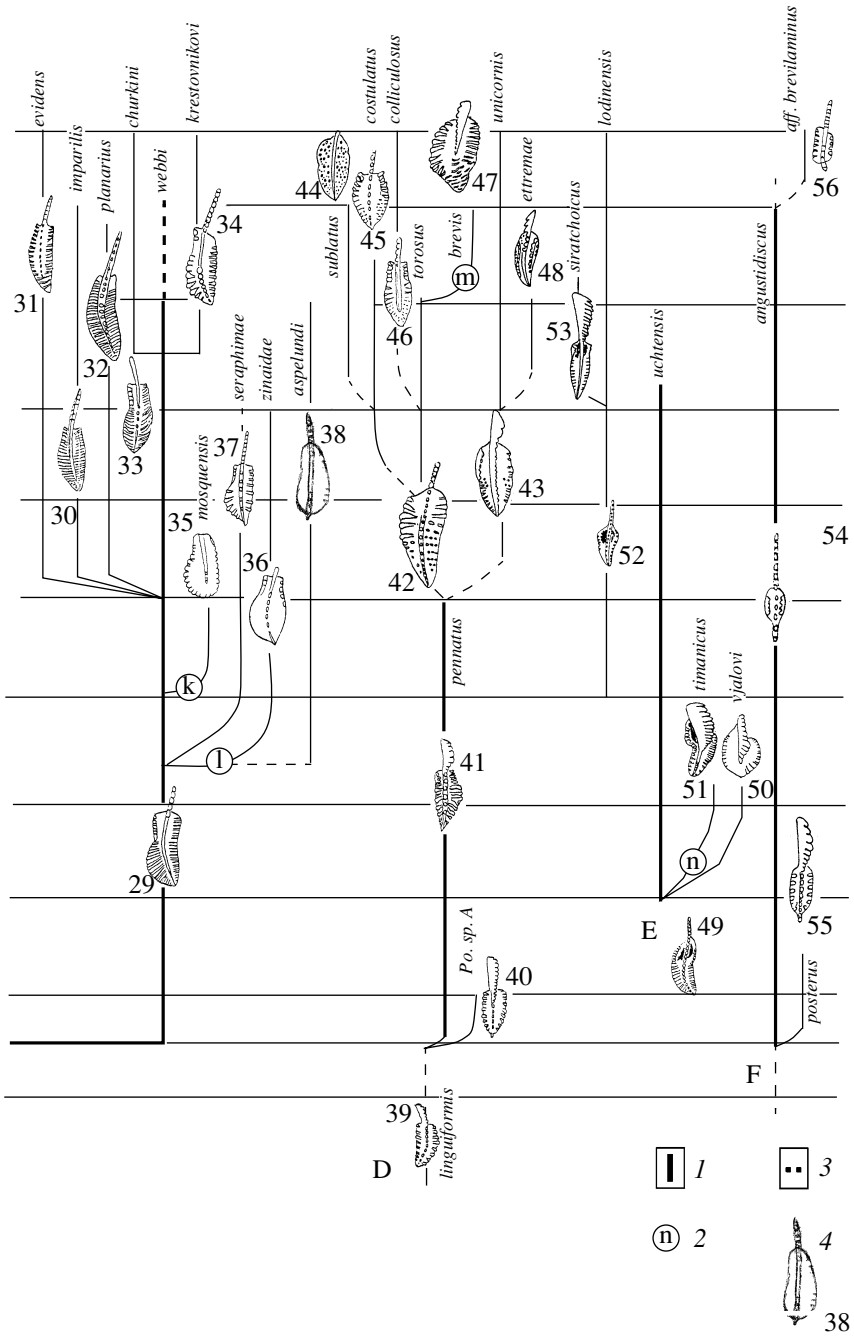

evidens
imparilis
planarius
churkini
webbi
krestovnikovi
costulatus
colliculosus
unicornis
lodinensis
aff. brevilaminus
ettremae
sublatus
torosus
brevis
stratchoicus
angustidiscus
uchtensis
seraphimae
zinaidae
aspelundi
mosquensis
pennatus
timanicus
vjalovi
Po. sp. A
posterus
linguiformis
D
E
F
1
2
3
4

Fig. 18. (Contd.)

period of duration and became extinct within the Domanik time.

Po. azygomorphus originated from *Po. pollocki* also at the beginning of the Domanik time (Fig. 18.12). The dotted sinuous transverse ridges comprised of the fused nodes were formed in the formation of the species. *Po. azygomorphus* became extinct at the beginning of the Evlanovo time (*Po. maximovae* Zone).

Po. pseudoxylus and *Po. brevilamiformis* possibly originated from *Po. xylus. Po. pseudoxylus* (Fig. 18.4) appeared at the beginning of the Sargaevo time (at the beginning of the *Ancyrodella rotundiloba–Ancyrodella africana* Zone). It inherited an elongated platform and long median ridge reaching the posterior end of the platform. In the development of *Po. pseudoxylus*, the free blade shortens, transverse ridges along the platform margins become better pronounced, and small lobe-shaped widening forms on the outer platform. *Po. pseudoxylus* becomes extinct in the second half of the Domanik time.

Po. brevilamiformis possibly originated from *Po. xylus* (Fig. 18.11) at the beginning of the Domanik (Semiluki) time (*Polygnathus efimovae* Zone). It inherited a long free blade with numerous small spinous denticles and long median ridge reaching the posterior end of the platform. Its peculiar feature is spear-shaped platform. *Po. brevilamiformis* became extinct at the end of the Voronezh time.

Po. reimersi (Fig. 18.2) appeared at the beginning of the Sargaevo time. Its possible ancestor was *Po. xylus*, from which it could originated by the widening of the platform and smoothening its margins. Smoothening of the platform margins starts near its posterior end and gradually spread for more and more of the platform. Numerous small nodes develop on the smoothened part of the platform. The margins in the anterior part of the platform remain raised and bear well-pronounced long transverse ridges. In *Po. reimersi*, platform is sharply divided in ornamentation into the anterior part with transverse ridges and posterior part covered with nodes. This species is short-lived and became extinct at the beginning of the Domanik time.

Several levels may be distinguished in the evolutionary rates of the *Po. xylus* branch. Each level is characterized by the outbursts of speciation. The first level is in the beginning of the Sargaevo time, when *Po. praepolitus, Po. pseudoxylus*, and *Po. reimersi* almost simultaneously originated from *Po. xylus.*

The second outburst of speciation is in the beginning of the Domanik (Semiluki) time, when *Po. efimovae, Po. lingulatus, Po. ilmenensis, Po. rudkinensis, Po. brevilamiformis, Po. azygomorphus*, and possibly *Po. strictus* appeared.

The third outburst of speciation is in the beginning of the Rechitsa time, when *Po. politus, Po. subincompletus*, and *Po. alvenus* appeared.

Branch Polygnathus denisbriceae (Fig. 18, branch B) unites two species with a beak-shaped posterior end. *Polygnathus denisbriceae* (Fig. 18.19) appeared in the uppermost Givetian Age. It is short-lived species and became extinct at the beginning of the Frasnian Age (in the second half of the Timan time). *Polygnathus denisbriceae* has an elongated platform with asymmetrically raised lateral margins and weakly developed ornamentation consisting of short transverse ridges. *Po. ljaschenkoi* originated from *Po. denisbriceae* in the second half of the Timan time (Fig. 18.20). It is also a short-lived species and became extinct at the beginning of the Sargaevo time. *Po. ljaschenkoi* inherited asymmetrically raised platform margins and beak-shaped posterior end. In the formation of the specific features of *Po. ljaschenkoi,* the platform shortens, the posterior end becomes less elongated, and the transverse ridges become more coarse.

Branch Polygnathus dubius (Fig. 18, branch C) unites species with lateral margins of the platform raised in the anterior part. This branch includes *Polygnathus webbi* and *Po. evidens* groups of species and also the species forming separate lateral branches, which are the direct descendants of *Polygnathus dubius.* We accept *Po. dubius* (Fig. 18.21) as *Po. dubius* sensu Klapper et Philip, 1971. It appeared at the end of the Givetian Age (at the beginning of the Late *hermanni–cristatus* Zone). Its peculiar features are lateral margins of the platform that are highly raised along the whole length and form a poorly pronounced rostrum in the anterior third. The median ridge is long and reaches the posterior end of the platform. The ornamentation consists of long and thin transverse ridges. This species disappears in the middle of the Voronezh time.

"*Po. foliatus*" and *Po. alatus* originated from *Po. dubius* in the Timan time (at the beginning of the *Po. pennatus–Po. ljaschenkoi* Zone). *Po. alatus* (Fig. 18.23) possibly was formed by the loss of the ornamentation. Although it sometime has a few transverse ridges in the posterior part of the platform, they may be regarded as a relic feature. *Po. alatus* became extinct in the Domanik time. The specific features of "*Po. foliatus*" (Fig. 18.28) are the better developed ornamentation and widened anterior half of the platform. This species disappears at the end of the Voronezh time.

Po. olgae, Po. decorosus, and *Po. aequalis* simultaneously originated from *Po. dubius* at the beginning of the Domanik time. *Po. olgae* (Fig. 18.22) is a short-lived species and exists only within the *Po. efimovae* Zone. It was possibly formed by the narrowing of the platform and shortening of the transverse ridges. *Po. decorosus* (Fig. 18.26) branched off *Po. dubius* possibly due to the intensification of ornamentation. *Po. decorosus* is a long-lived species and became extinct at the end of the Evlanovo time. *Po. aequalis* (Fig. 18.25) inherited lateral margins of the platform raised along their whole length and thin transverse ridges. It disappears in the middle of the Voronezh time. *Po. reitlingerae* (Fig. 18.24) possibly originated from *Po. aequalis* in the Rechitsa time. It was possibly

formed by the transformation of the sharply pronounced transverse ridges into the thinner dotted transverse ridges. The lateral margins of the platform smoothen in the posterior part. *Po. reitlingerae* became extinct at the beginning of the Voronezh time.

Po. komi originated from *Po. dubius* in the Voronezh time (at the end of the *subincompletus* Zone) (Fig. 18.27). It was possibly formed by the changing of the platform outline (from lanceolate in the ancestor to the elongated pear-shaped of the descendant) and shortening of the median ridge that does not reach the posterior end of the platform. *Po. komi* disappears at the end of the Evlanovo time (at the end of the *Po. maximovae* Zone).

Polygnathus webbi group unites species with a lobe-shaped widening on the outer margin of the platform. All species of the *webbi* group are referred to the 3b class of symmetry. The latter has a highly raised right margin with respect to the opposite side (both in the left and right forms) and better developed ornamentation in the left units. In the evolution of the species of this group, the platform developed in two directions: to the better developed ornamentation (*Po. krestovnikovi* and *Po. seraphimae*) and loss of ornamentation (*Po. zinaidae, Po. mosquensis*, and possibly *Po. aspelundi*). *Po. webbi* is the ancestor of the group (Fig. 18.29). It originated from *Po. dubius* in the Upper Timan time (at the beginning of the *Po. pennatus–Pa. ljaschenkoae* Zone) and inherited thin transverse ridges and a long median ridge reaching the posterior end of the platform. The lobe-shaped widening forms on the outer platform and the transverse ridges lengthen during development. *Po. webbi* became extinct in the Evlanovo time.

Po. seraphimae and *Po. zinaidae* originated from *Po. webbi* in the Domanik time. *Po. seraphimae* (Fig. 18.37) inherited a lobe-shaped widening of the outer margin of the platform. The changes consist of the shorter and coarser transverse ridges divided by enlarged interspaces. This species became extinct at the end of the Rechitsa time. *Po. zinaidae* (Fig. 18.36) inherited a lobe-shaped widening of the outer margin of the platform and median ridge reaching the posterior end of the platform. Almost the entire platform surface of this species becomes smooth except the anterior third, where weakly developed short transverse ridges persist. *Po. zinaidae* disappears at the end of the Rechitsa time.

Po. aspelundi possibly originated from *Po. zinaidae* in the Domanik time (Fig. 18.38). This species possibly appeared due to the raising of the platform margins and developing small denticles along its lateral margins. *Po. aspelundi* could have inherited a comparatively smooth platform surface. It became extinct at the end of the Voronezh time.

Po. mosquensis originated from *Po. webbi* in the Domanik time (Fig. 18.35) by the almost complete disappearance of the transverse ridges, which persist only along the platform margin. *Po. mosquensis* is a short-lived species; it became extinct at the end of the Domanik time. *Po. krestovnikovi* originated from *Po. webbi* in the Late Voronezh time (beds with *Po. churkini–Po. komi*) (Fig. 18.34). It inherited long transverse ridges and lobe-shaped widening of the platform outer margin. In the ontogeny of *Po. krestovnikovi*, the transverse ridges become high and coarse, especially along the platform margins, which thus became denticulate. The platform margins smoothen in its posterior part and the transverse ridges begin splitting. It is especially well pronounced at the late developmental stages. *Po. krestovnikovi* became extinct at the end of the Livny time.

The group of species with a lingulate posterior end of the platform originated from *Po. webbi* at the beginning of the Rechitsa time (*Po. subincompletus* Zone). This group of species was provisionally called *evidens*. Except *Po. evidens*, *evidens group* includes *Po. imparilis, Po. planarius*, and *Po. churkini*. According to Ji and Ziegler (1993, fig. 17), *Po. evidens* and *Po. planarius* are phylogenetically connected with *Po. dubius*, and *Po. imparilis* and *Po. churkini* are connected with *Po. webbi.* However, it is possible that not only *Po. churkini* and *Po. webbi*, but all species of the *Po. evidens* group are related with *Po. webbi.* All of them have long and thin transverse ridges reaching the median ridge. *Po. evidens* (Fig. 18.31) and *Po. churkini* (Fig. 18.33) became extinct at the end of the Frasnian Age and *Po. imparilis* (Fig. 18.32) disappeared at the end of the Evlanovo time.

Analysis of the evolution within the *Po. dubius* branch reveals gradual appearance of the raw of species *Po. reitlingerae, Po. komi, Po. churkini, Po. krestovikovi*, and *Po. mosquensis.* Several bursts of speciation were also distinguished. The first burst is in the middle of the Timan time, when *Po. alatus, "Po. foliatus,"* and *Po. webbi* simultaneously appeared. The second burst is at the beginning of the Domanik time and is connected with the appearance of *Po. aequalis, Po. decorosus*, and *Po. olgae.* The third burst is in the middle of the Domanik time, when *Po. seraphimae, Po. zinaidae*, and *Po. aspelundi* simultaneously appeared. The last burst at the beginning of the Rechitsa time is connected with the formation of the *Po. evidens* group of species.

The *pennatus branch* (Fig. 18, branch D) unites species with coarse transverse ridges. *Po. pennatus* is a possible ancestor of this group. It originated from the Givetian *Linguipolygnathus linguiformis* (Fig. 18.39). *Polygnathus pennatus* (Fig. 18.41) appeared in the middle of the Timan time and inherited a lanceolate platform and well-developed transverse ridges. The ridges became better pronounced and the separate "tongue" on the lingulate posterior end of the platform disappears in the development. *Polyganthus pennatus* became extinct at the beginning of the Rechitsa time.

Po. torosus possibly originated from *Po. pennatus* precisely at this time (Fig. 18.42). At the early developmental stages (small forms), *Po. torosus* has well-

developed coarse transverse ridges and long median ridge reaching the posterior end of the platform. In the adult forms, coarse transverse ridges persist only on the anterior half of the platform. On the posterior end, they disintegrate into small nodes but the structure of the transverse rows persists. *Po. torosus* became extinct at the beginning of the Evlanovo time.

Po. brevis originated from *Po. torosus* at the beginning of the Evlanovo time (Fig. 18.47). It inherited coarse transverse ridges in the anterior half of the platform and system of small nodes, which form dotted transverse ridges in the posterior half of the platform. The changes consist of the shortening of the median ridge and separating of the lingulate posterior end of the platform as in the distant ancestor *L. linguiformis* s.l. *Po. brevis* disappears at the end of the Evlanovo time. *Po. unicornis, Po. ettremae, Po. colliculosus, Po. costulatus,* and *Po. sublatus* are provisionally connected with the *pennatus* branch. These species appear gradually, and do not form the burst of specification. *Po. unicornis* (Fig. 18.43) appear at the beginning of the Rechitsa time and became extinct at the end of the Livny time.

Po. costulatus (Fig. 18.45) appeared in the second half of the Rechitsa time; *Po. colliculosus* (Fig. 18.46) and *Po. sublatus* (Fig. 18.44) appeared at the beginning of the Voronezh time. The latter disappears at the end of the Evlanovo time; *Po. colliculosus* became extinct at the end of the Livny time. *Po.* sp. *A* Ovnatanova et Kononova, 2001 (Fig. 18.40) (second half of the Timan time) and *Po. ettremae* (Fig. 18.48) (Voronezh time) are short-lived species. Species of the *pennatus* branch appear one after another and thus the branch lacks burst of specification.

The *uchtensis branch* (Fig. 18, branch E) unites species with a cup-shaped depression in the anterior half of the platform. The ancestors of the branch were not revealed. *Po. uchtensis* (Fig. 18.49) appeared at the beginning of the Domanik time (*efomovae* Zone) and became extinct at the beginning of the Voronezh time (*maximovae* Zone). It has an elongated asymmetrical platform with a small cup-shaped depression in the anterior half and short transverse ridges along the platform margins. *Po. timanicus* originated from *Po. uchtensis* at the beginning of the Domanik time. In *Po. timanicus* (Fig. 18.51), the anterior half of the platform widens, the cup-shaped depression deepens, and transverse ridges elongate. *Po. timanicus* inherited a cup-shaped depression in the anterior half of the platform. It became extinct in the Domanik time. The short-lived species *Po. vjalovi* (Fig. 18.50) possibly originated from *Po. timanicus* at the beginning of the Domanik time and inherited transverse ridges. Most of its platform surface is slightly curved like a cup. *Po. vjalovi* is known only from the lower part of the Domanik time.

Po. lodinensis (Fig. 18.52) originated from *Po. uchtensis* at the end of the Domanik time. It platform shortens and cup-shaped depression increases. *Po. lodinensis* became extinct in the Livny time.

Po. siratchoicus (Fig. 18.53) possibly originated from *Po. lodinensis* at the beginning of the Voronezh time. This species is short-lived and has an elongated triangular platform, small cup-shaped depression, and well-developed transverse ridges. *Po. siratchoicus* became extinct at the beginning of the Evlanovo time.

Species of the branch *Po. uchtensis* appear one after another.

The *angustidiscus* branch (Fig. 18, branch F). Its ancestors are unknown. This branch unites three species with a posterior free blade. *Po. angustidiscus* (Fig. 18.54) is the ancestor of the branch. It appears in the middle of the Timan time and became extinct at the beginning of the Livny time. The platform margins of this species are highly raised and bear short transverse ridges. The short-lived species *Po. posterus* (Fig. 18.55) appears in the middle of the Timan time. The platform margins of this species bear transverse ridges. *Po. posterus* inherited short posterior and long anterior free blades. This species disappears in the middle of the Sargaevo time. *Po.* aff. *brevilaminus* (Fig. 18.56) originated from *Po. angustidiscus* at the beginning of the Livny time. The species is described in the open nomenclature because of the small number of specimens in the collection. *Po.* aff. *brevilaminus* inherits highly raised platform margins and posterior free blade.

CHAPTER 11. SYSTEMATIC PALEONTOLOGY

Phylum Chordata

Subphylum Vertebrata

SUPERCLASS AGNATHA

CLASS CONODONTA PANDER, 1856

SUBCLASS CONODONTATA PANDER, 1856

Order Polygnathida Barskov, 1995[1]

Genus *Ancyrodella* Ulrich et Bassler, 1926

Ancyrodella: Ulrich and Bassler, 1926, p. 48; *Catalogue*…, 1973, pp. 21–22; Huddle and Repetski, 1981, p. B-19.

Ancyropenta: Müller et Müller, 1957, p. 1092.

Type species. *Ancyrodella nodosa* Ulrich et Bassler, 1926, p. 48; Upper Devonian, North America.

Diagnosis. Pa element planate; platform symmetrical or asymmetrical, from triangular to heart-shaped or alar in shape; with two lateral lobes directed anteriorly; posterior end pointed; lateral lobes narrow or wide. Laterally or posteriorly directed additional lateral lobes sometimes developed. Free blade well developed. Median ridge high. Secondary ridges locally bifurcating. Basal cavity from medium- to large-sized and rhombic; median keel and two or more lateral keels directed from basal cavity to ends of lateral lobes (Fig. 19).

[1] Classification follows Barskov (1995).

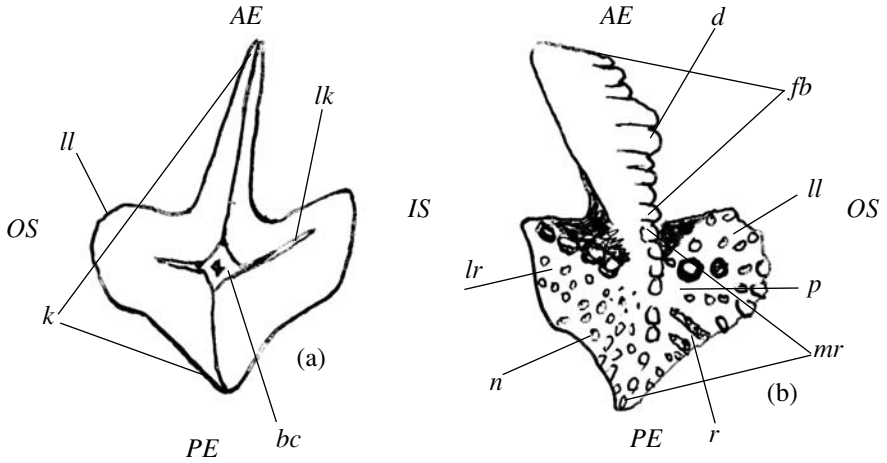


Fig. 19. Morphology of the genus *Ancyrodella*: (a) lower and (b) upper views. Designations: (*AE*) anterior end, (*IS*) inner side, (*OS*) outer side, (*PE*) posterior end, (*bc*) basal cavity, (*r*) ridge, (*d*) denticle, (*fb*) free blade, (*k*) keel, (*lk*) lateral keel, (*ll*) lateral lobe, (*lr*) lateral ridge, (*mr*) median ridge, (*n*) node, and (*p*) platform.

Comparison. This genus differs from *Ancyrognathus* Branson et Mehl, 1934 in the platform outline, the presence of the lateral lobes with anteriorly directed ends, and the rhombic basal cavity.

Species composition. *Ancyrodella africana* Garcia-Lopez, 1981, *Anc. alata* Glenister et Klapper, 1966, *Anc. binodosa* Uyeno, 1974, *Anc. buckeyensis* Stauffer, 1938, *Anc. crosbiensis* Kralick, 1994, *Anc. curvata* (Branson et Mehl, 1934), *Anc. devonica* Garcia-Lopez, 1986, *Anc. gigas* Youngquist, 1947, *Anc. huddlei* Ji et Ziegler, 1993, *Anc. ioides* Ziegler, *Anc. isabella* Garcia-Lopez, 1986, *Anc. lobata* Branson et Mehl, 1924, *Anc. mouravieffi* Garcia-Lopez, 1986, *Anc. nodosa* Ulrich et Bassler, 1926, *Anc. pramosica* Perri et Spalletta, 1981, *Anc. pristina* Khalymbadzha et Tchernyschova, 1970, *Anc. quadrata* Ji, 1986, *Anc. recta* Kralick, 1994, *Anc. rotundiloba* (Bryant, 1921), *Anc. rugosa* Branson et Mehl, 1934, *Anc. soluta* Sandberg, Ziegler et Bultynck, 1989, and *Anc. triangulata* Kralick, 1994.

Occurrence. Frasnian Stage, Middle *falsiovalis–linguiformis* Zone; North America, Australia, Western Europe, Africa; Russia (Central Russian Platform, Volga–Ural Province, Southern Timan, Ural Mountains).

Ancyrodella alata Glenister et Klapper, 1966

Plate 26, figs. 4 and 5

Ancyrodella rotundiloba: Bischoff and Ziegler, 1957, p. 42, pl. 16, figs. 5–12, 14, 16, and 17.

Ancyrodella rotundiloba rotundiloba: Ji, 1989, pl. 3, figs. 10–13.

Ancyrodella rotundiloba alata: Glenister and Klapper, 1966, p. 799, pl. 85, figs. 1–8; Khalymbadzha and Tchernyschova, 1970, p. 92, pl. 2, figs. 3–9 (only); Uyeno, 1974, p. 24, pl. 1, figs. 3 and 7; Perri and Spalletta, 1980, p. 293, pl. 2, fig. 1 (only); Bultynck and Jacobs, 1981, p. 18, pl. 10, figs. 10–I2; Huddle and Repetski, 1981, pl. 1, figs. 9, 10, 23–27, pl. 2, figs. 1–28; Bultynck, 1982, pl. 2, figs. 4–8 (only); Wang and Ziegler, 1983, pl. 1, fig. 4; Ji et al., 1986, pl. 1, figs. 1 and 2; Khalymbadzha et al., 1987, pl. 2, figs. 10 and 11; pl. 3, fig. 1.

Ancyrodella alata: Ziegler and Wang, 1985, pl. 3, fig. 9; Bultynck, 1986, pl. 1, figs. 10 and 11; Uyeno, 1991, pl. 4, figs. 4–6; Bardaschev, 1992, pl. 11, figs. 29, 30, 33–37; Ji et al., 1992, pl. 1, figs. 16–19; Norris et al., 1992, p. 72, pl. 15, figs. 11–14; Yatskov and Kuzmin, 1992, text-fig. 2, figs. 4 and 6; Ji and Ziegler, 1993, p. 51, pl. 1, figs. 1–3; text-fig. 8, fig. 12; Racki and Bultynck, 1993, pl. 9; figs. 1–4; Weary et Harris, 1994; pl. 2, figs. 11 and 12 (only); Kralick, 1994, figs. 3.1; 3.2?, 4.5, and 4.6.

Holotype. GSWA (Geological Survey of the Western Australia), no. 35803; outcrop Wapet D, isolated outcrop on the Lour Hill of the central Bugle Gap; western Australia, Frasnian Stage, Gogo Formation (Glenister and Klapper, 1966, pl. 85, figs. 7, 8).

Diagnosis. Pa element with strongly alar platform outline; two lateral lobes rounded. Posterior end pointed and arched downwards. Median ridge straight or slightly arched, reaching posterior end of platform. Free blade high, denticulated and as long as platform. Upper surface of platform covered with small nodes; some nodes constituting two weak lateral ridges near anterior end of platform. Median keel high and sharp; two secondary keels thin and terminating short of lobe margins; one of them longer than other. Basal cavity well developed, rhombic.

Comparison. This species differs from *Ancyrodella rotundiloba* (Bryant, 1921) in the strongly alar platform with small nodes covering the upper surface.

Occurrence. Frasnian Stage, Gogo Formation, western Australia, *transitans* and *punctata* zones of Europe, Late *falsiovalis–punctata* zones of southern China; Givetian–Frasnian boundary of Africa (Morocco); Russia: Sargaevo and Lower Domanik regional stages of the Volga–Ural Province, Ust'-Yarega Formation and bottom of the Domanik Formation of southern Timan.

Material. Volga–Ural Province, Tatarstan, Prikazanskaya 120, samples 70 and 90, interval 1669–1676 m, Sargaevo Regional Stage. Orenburg Region, Shuvalovskaya 6, samples 260 and 258, interval 3651–3655 m, Sargaevo Regional Stage; Shuvalovskaya 19,

sample 90, interval 3625–3633 m, Domanik Regional Stage; Shuvalovskaya 21, interval 3764–3768 m, Sargaevo Regional Stage. Southern Timan, outcrop D, right bank of the Yarega River, outcrop F, village of Vodnyi, Yarega River, Ust'-Yarega Formation; outcrop 1, Chut' River, Domanik Formation, unit 1; borehole no. 2056, interval 122–125 m, Ust'-Yarega Formation, depth of 120 m, Domanik Formation, unit 1; Shudayag 1003, depth of 130 m, Ust'-Yarega Formation.

Ancyrodella binodosa Uyeno, 1974

Plate 26, figs. 1–3

Ancyrodella rotundiloba binodosa: Uyeno, 1974, p. 24, pl. 1, figs. 2, 4–6, pl. 2, figs. 2, 3, and 5; Ovnatanova and Aristov, 1984, pl. 1, figs. 2 and 3.

Ancyrodella binodosa: Bultynck and Jacobs, 1981, p. 16, pl. 8, figs. 1–14; pl. 9, figs. 1–8; Bultynck, 1982, pl. 1, figs. 18–30; Ziegler and Wang, 1985, pl. 3, fig. 13; Sandberg et al, 1989, pl. 1, figs. 1 and 2; Racki and Bultynck, 1993, pl. 7, fig. 7.

Holotype. GSC (Geological Survey of Canada), no. 22819, station 181, Clearwater River, Calumet Unit, Waterways Formation, Alberta, Canada (Uyeno, 1974, pl. 2, figs. 2A and 2B).

Diagnosis. Pa element with triangular platform and small rounded lateral lobes. Posterior end of platform pointed. Median ridge straight or slightly arched. Free blade as long as platform, equipped with high denticles. Highest denticles located near anterior end of blade. Platform surface with two high nodes, one node on each side of median ridge; isolated smaller nodes rarely developed. Large basal cavity below, consisting of rhombic pit bordered by wide flat flanks, occupying most of lower surface of the platform. Median keel sharp; secondary keels poorly developed or absent.

Comparison. This species differs from *Ancyrodella rotundiloba* in the only two nodes developed on the upper platform surface (one node on each side of the median ridge) and in the large basal cavity, which occupies almost the whole lower surface of the platform.

Occurrence. Frasnian Stage, *falsiovalis* Zone; Canada, Western Europe; Givetian–Frasnian boundary beds of Morocco. Volga–Ural Province, Upper Timan Regional Substage and Sargaevo Regional Stage, Ust'-Yarega Formation; southern Timan.

Material. Volga–Ural Province, Tatarstan, Prikazanskaya 121, sample 23, interval 1688–1691.7 m; Frasnian Stage, Sargaevo Regional Stage. Orenburg Region, Shuvalovskaya 4, sample 2, interval 3618–3626 m and sample 268, interval 3604–3618 m, Upper Timan Regional Substage; Shuvalovskaya 6, sample 6, interval 3661–3665 m; Upper Timan Regional Substage. southern Timan, borehole no. 1003, depth of 128 m, Ust'-Yarega Formation; borehole no. 2056, depth of 124 m, Ust'-Yarega Formation.

Ancyrodella gigas Youngquist, 1947

Plate 26, figs. 6 and 8

Ancyrodella gigas: Youngquist, 1947, p. 96, pl. 25, fig. 23; Müller and Müller, 1957, p. 1091, pl. 142, fig. 1; Anderson, 1966, p. 403, pl. 48, figs. 10 and 14; Uyeno, 1974, p. 23, pl. 1, figs. 1, 8, and 9; Aristov and Belyi, 1976, text-fig. 1, fig. 10; Bultynck and Jacobs, 1981, pl. 9, figs. 9–11; Klapper, 1985, pl. 10, figs. 1–6, 9, 10, 13–16; Wang, 1989, pl. 1, figs. 1–4; Ji, 1989, pl. 3, figs. 1, 2, 4, and 5; Ji and Ziegler, 1993, p. 52, pl. 1, figs. 11 and 12, text-fig. 8, fig. 4; Ovnatanova and Kononova, 1999, text-figs. 2.17, 3.10, 3.11; 2001, pl. 12, fig. 19, pl. 5, figs.17 and 18; Racki, 1992, p. 151, fig. 34D; Pazukhin et al., 2007, pl. 1, fig. 9.

Holotype. SUI (Iowa State University of Science and Technology), no. 3358, North America, Iowa; Frasnian Stage, Johnson County, Iowa; North Liberty beds, (Youngquist, 1947, pl. 25, fig. 23).

Diagnosis. Pa element with narrow arrow-shaped platform; with well-developed lateral lobes concave at junction with median ridge; posterior end pointed. Median ridge denticulated, straight or slightly arched. Free blade high as long as platform. Secondary ridges distinct, positioned at acute angle to median ridge. Ornamentation composed of irregular nodes; some nodes arranged in rows. Basal cavity medium-sized; median and secondary keels well pronounced.

Comparison. This species differs from *Ancyrodella nodosa* Ulrich et Bassler, 1926 in the narrow and arrow-shaped platform.

Occurrence. Frasnian Stage, *punctata*–Early *rhenana* zones. North America, Western Europe, southern China. Russia: southern Timan, Domanik and Lyaiol' formations (unit 1–bottom of unit 3); Volga–Ural Province, Domanik Regional Stage.

Material. Volga–Ural Province, Orenburg Region, Kolgany 7, interval 3427–3432 m, Domanik Regional Stage. Southern Timan, Chut' River, outcrop 1, Domanik Formation, unit 1; borehole no. 1003, depth of 120 m, Domanik Formation, unit 2; borehole no. 3B, depth of 75 m, Domanik Formation.

Lyaiol' River, outcrops 1354 and 1905, Lyaiol' Formation, unit 1; outcrop 1357, sample 22, Lyaiol' Formation, unit 2; Vezha-Vozh River, outcrop 9, sample 3, Lyaiol' Formation, bottom of unit 3.

Ancyrodella nodosa Ulrich et Bassler, 1926

Plate 26, figs. 11–16

Ancyrodella nodosa: Ulrich and Bassler, 1926, p. 48, pl. 1, figs. 10–13; Youngquist and Miller, 1948, p. 441, pl. 68, figs. 13 and 14; Bischoff, 1956, p. 119, pl. 8, figs. 12 and 15; Ziegler, 1958, p. 44, pl. 11, fig. 1; Glenister and Klapper, 1966, pp. 798, 799, pl. 86, figs. 5–12; Khalymbadzha and Tchernyschova, 1970, p. 96, pl. 2, figs. 10–13; Aristov and Belyi, 1976, text-fig. 2, figs. 1 and 3; Ji et al., 1986, pl. 1, fig. 4; Khalymbadzha et al., 1987, pl. 3, fig. 10; Ji, 1988, pl. 1, figs. 1, 2, 5–10, 13–16; Ji, 1989, pl. 3, fig. 6; Ji et al., 1992, pl. 2, figs. 1 and 2; Norris et al., 1992, p. 72, pl. 16, figs. 1–6; Matyja, 1993, pl. 21, figs. 3 and 10; Ji and Ziegler, 1993, p. 53, pl. 2, figs. 11 and 12; text-fig. 8, figs. 8 and 9; Dong and Wang, 2006, pl. 24, fig. 12; Pazukhin et al., 2007, pl. 1, fig. 7.

Lectotype. The lectotype was designated by Ziegler (1958, p. 44) based on the paper of Ulrich and Bassler (1926, pl. 1, fig. 10), specimen USNM (Smithsonian National Museum of Natural History), no. 11303; Devonian, Rainstreet shales; New York State, United States.

D i a g n o s i s. Pa element with platform anchor-shaped and strongly narrowed posteriorly; two narrow lateral lobes well developed, directed anteriorly, and concave in anterior part of platform; posterior end pointed. Median ridge slightly arched; free blade almost as long as platform. Secondary ridges well developed, denticulate, and join median ridge at angle of 70–80°. Ornamentation consisting of short transverse ridges or nodes along platform margin. Basal cavity small; median and secondary keels sharp, well pronounced.

C o m p a r i s o n. This species described differs from *Ancyrodella gigas* in the strongly narrowed posterior part of the platform.

O c c u r r e n c e. Frasnian Stage, *hassi–linguiformis* zones of North America, Europe, Australia, and southern China. Russia: Volga–Ural Province: Domanik, Mendym, and Askyn regional stages; southern Timan, upper unit of the Domanik Formation–units 1–4 of the Lyaiol' Formation.

M a t e r i a l. Volga–Ural Province, Tatarstan, Severnyi Kupol 166, sample 47, interval 1563–1567 m, Mendym Regional Stage; Severnyi Kupol 71, interval 1714–1721 m, Domanik Regional Stage, samples 59, 62, and 64, interval 1646–1651 m, Askyn Regional Stage. Southern Timan, Lyaiol' River, outcrops 1360 and 1908, Lyaiol' Formation, unit 4; Vezha-Vozh River, outcrops 731, 735, 8, 9, and 10; Lyaiol' Formation, units 1–4.

Ancyrodella rotundiloba (Bryant, 1921)

Plate 26, fig. 10

Polygnathus rotundilobus: Bryant, 1921, pp. 26, 27, pl. 12, figs. 1–6; Huddle, 1934, p. 102, pl. 8, figs. 36 and 37.

Ancyrodella rotundiloba: Bischoff and Zigler, 1957, p. 42, pl. 16, fig. 15; Bultynck, 1986, pl. 1, figs. 9–12; Yatskov and Kuzmin, 1992, figs. 2 and 3; Racki and Bultynck, 1993, pl. 7, fig. 4; Kirchgasser, 1994, p. 129, pl. 2, figs. A–R, pl. 4, fig. A-1; Kralick, 1994, p. 1387, text-figs. 3.15–3.24, 4.7, 4.8, 5.3, 5.4, 5.7–5.11; Sandberg et al.,1994, pl. 1, fig. 7.

Ancyrodella rotundiloba rotundiloba: Glenister and Klapper, 1966, p. 799, pl. 85, figs. 9–13; Bultynck and Jacobs, 1981, p. 17, pl. 10, figs. 1–9; Ji et al., 1986, pl. 1, fig. 3.

Ancyrodella rotundiloba subsp. A: Uyeno, 1974, pp. 25, 26, pl. 2, figs. 1, 4, 6–9.

L e c t o t y p e. The lectotype was designated and figured by Ziegler (1958, p. 44, text-fig. 7) based on the collection of Bryant (1921, pl. 12, fig. 1). USNM, no. 135043; boundary beds of the Givetian–Frasnian stages, North Evans Limestone; United States.

D i a g n o s i s. Pa element with platform from triangular to heart-shaped in outline; lateral lobes directed upwards; posterior end pointed. Median ridge straight and denticulated. Free blade high, denticulated; highest denticles located in anterior part. Platform surface with high and coarse nodes, sometimes arranged in rows or weakly pronounced secondary ridges between median ridge and platform margins. Basal cavity rhombic, from small to medium-sized; secondary keels short and weakly pronounced.

C o m p a r i s o n. The species described differs from *Ancyrodella rugosa* Br. et M., 1934 in the poorly developed short secondary keels.

O c c u r r e n c e. Frasnian Stage, Montagne Noire, Lower *asymmetricus* Zone; North America, New Albany Shales (Indiana), North Evans Limestone (western New York). Volga–Ural Province, uppermost Timan Regional Stage and Sargaevo Regional Stage; Timan–Pechora Province, Ust'-Yarega Formation.

M a t e r i a l. Volga–Ural Province, Orenburg Region, Shuvalovskaya 21, interval 3764–3768 m; Frasnian Stage, Sargaevo Regional Stage, Shuvalovskaya 4, interval 3604–3618 m, Upper Timan Regional Substage; southern Timan, borehole no. 2056, depth of 123 m; Ust'-Yarega Formation, Shudayag 1003, depth of 130 m, Ust'-Yarega Formation.

Ancyrodella rugosa Branson et Mehl, 1934

Plate 26, fig. 7

Ancyrodella rugosa: Branson and Mehl, 1934, p. 239, pl. 19, figs. 15 and 17 (=holotype); Huddle, 1981, B21–22, pl. 3, figs. 1–19; Klapper, 1985, p. 30, pl. 11, figs. 1, 2, 5–14; text-fig. 3U; Yatskov and Kuzmin, 1992, text-fig. 2, fig. 2 (only); Racki and Bultynck, 1993, pl. 8, figs. 9–12; Ji and Ziegler, 1993, text-figs. 8–11; Uyeno, 1994, pl. 4, figs. 10 and 11; Kralick, 1994, p. 1393, text-figs. 3.7, 3.8, 3.13, 3.14, 4.9, and 4.10; Weary and Harris, 1994, pl. 1, figs. 14 and 15.

H o l o t y p e. University of Missouri, Cat. no. C 224-1, Grassy Creek Shale, Missouri (Branson and Mehl, 1934, pl. 19, figs. 15 and 17).

D i a g n o s i s. In Pa element, platform massive and rounded triangular; lateral lobes well pronounced, anteriorly directed, and rounded; posterior end pointed. Secondary ridges well developed. Median ridge straight or slightly arched, denticulated, reaching posterior end of platform. Denticles of median ridge usually fused at base. Free blade high, denticulate. Platform surface covered with many coarse and irregularly arranged nodes; sometimes nodes arranged in rows; in posterior part of platform, irregular secondary ridges occasionally formed. Secondary keels well developed. Basal cavity relatively small, with long secondary keels extending from it into lobes, sometimes bifurcated, forming third keel, which usually directed laterally.

C o m p a r i s o n. The species is distinguised from *A. rotundiloba* (Bryant, 1921) in the well-developed secondary keels.

O c c u r r e n c e. Europe, North America (Indiana), southern China, Frasnian Stage, *transitans–punctata* zones. southern Timan, Ust'-Yarega and Domanik Formation, unit 1; Volga–Ural Province, Sargaevo and Domanik regional stages.

M a t e r i a l. Volga–Ural Province, Tatarstan, Prikazanskaya 120, sample 67, interval 1695–1700 m, sample 69, interval 1685–1690 m, Sargaevo Regional Stage; Orenburg Region, Shuvalovskaya 19, sample 90,

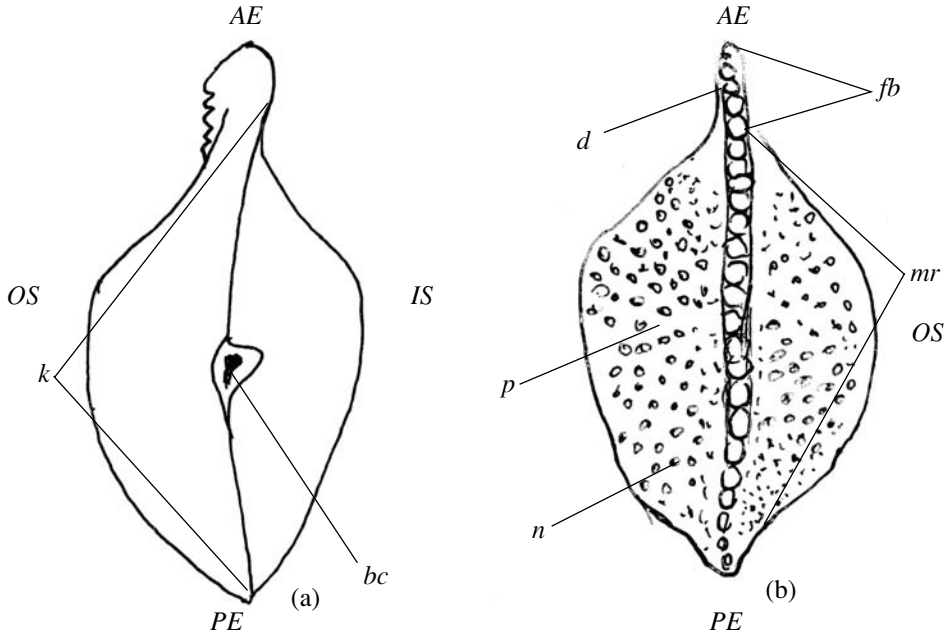


Fig. 20. Morphology of the genus *Klapperina*: (a) lower and (b) upper views. Designations: (*AE*) anterior end, (*IS*) inner side, (*OS*) outer side, (*PE*) posterior end, (*bc*) basal cavity, (*d*) denticle, (*fb*) free blade, (*k*) keel, (*mr*) median ridge, (*n*) node, and (*p*) platform.

interval 3625–3633 m, Domanik Regional Stage; southern Timan, outcrop C, sample 24, outcrop D, samples 2, 4, 5, and 27; Ust'-Yarega Formation, outcrop 2, sample b-2, Ust'-Yarega Formation; Chut' River, outcrop 1, Domanik Formation, unit 1.

Genus *Klapperina* Lane, Müller et Ziegler, 1979

Klapperina: Lane et al., 1979, pp. 217–218; Johnson et al., 1980, pp. 100, 101; Ziegler and Klapper, 1982, p. 466; Racki, 1985, p. 269; Ziegler and Lane, 1987, p. 155; *Catalogue*…, 1991, pp. 73, 74.

Type species. *Klapperina disparalvea* (Orr et Klapper, 1968).

Diagnosis. Pa element planate; platform flat and bladelike; anterior end rounded; posterior end pointed. Median ridge straight and denticulated. Free blade short, about one-fifth or one-sixth of platform length. Platform surface shagreened or covered with coarse nodes. Basal cavity large, distinctly asymmetrical, located in middle or, sometimes, in posterior part of lower platform surface, varying from triangular to L-shaped, with margins elevated above lower surface. Keel thin and filiform (Fig. 20).

Comparison. This genus differs from *Mesotaxis* Klapper et Philip, 1972 in the large and asymmetrical basal cavity.

Remarks. The genus *Klapperina* was initially established (Lane et al., 1979, pp. 217, 218) based on the palmatolepid species *Palmatolepis disparalvea* and *Pa. disparilis*, which have a large asymmetrical basal cavity and a weakly developed or absent azygous node. The genus was supposed to evolve from *Polygnathus cristatus* (Hinde).

Species composition. *Klapperina ovalis* (Ziegler et Klapper, 1964), *K. disparata* (Ziegler et Klapper), *K. disparalvea* (Orr et Klapper,1968), *K. disparilis* (Ziegler et Klapper, 1974), *K. ninae* Bardaschev, 1992, and *K. vysotskii* Bardaschev, 1992.

Occurrence. Europe: Poland, Germany, Belgium, Russia; North America: Indiana and Nevada; Asia: Central Asia (Tajikistan), southern China; Malaysia; Africa, Morocco; Givetian–Frasnian boundary beds, *disparilis–punctata* zones.

Klapperina ovalis (Ziegler et Klapper), 1964

Plate 25, figs. 2 and 3

Polygnathus asymmetricus ovalis: Ziegler and Klapper in Ziegler et al., 1964, pp. 422, 423.

Klapperina ovalis: Ovnatanova and Kuzmin, 1991, pl. 1, figs. 3 and 4; Bardaschev, 1992, pl. 10, figs. 21, 24–26, Orchard and McCracken, 1992, pl. 1, figs. 7 and 8; Racki and Bultynck 1993, pl. 5, figs. 8, 10–11.

Polygnathus dubia dubia sensu Bishoff and Ziegler: Ziegler, 1958, pl. 1, figs. 1 and 2.

Holotype. Department of Geosciences, Philipps University, Marburg, Germany, no. Zi 1958/1; Middle–Upper Devonian, Givetian–Frasnian, *asymmetrica* Zone (Ziegler, 1958, pl. 1, figs. 1, 2a, 2b).

Diagnosis. Pa element: platform symmetrical, phylloid, wide anteriorly and narrow posteriorly; anterior end rounded; posterior end pointed. Maximum width of platform located close to midlength. Median ridge denticulated and almost straight. Free blade relatively long in comparison with congeners. Basal cavity large, asymmetrical, located near center of platform, with elevated margins.

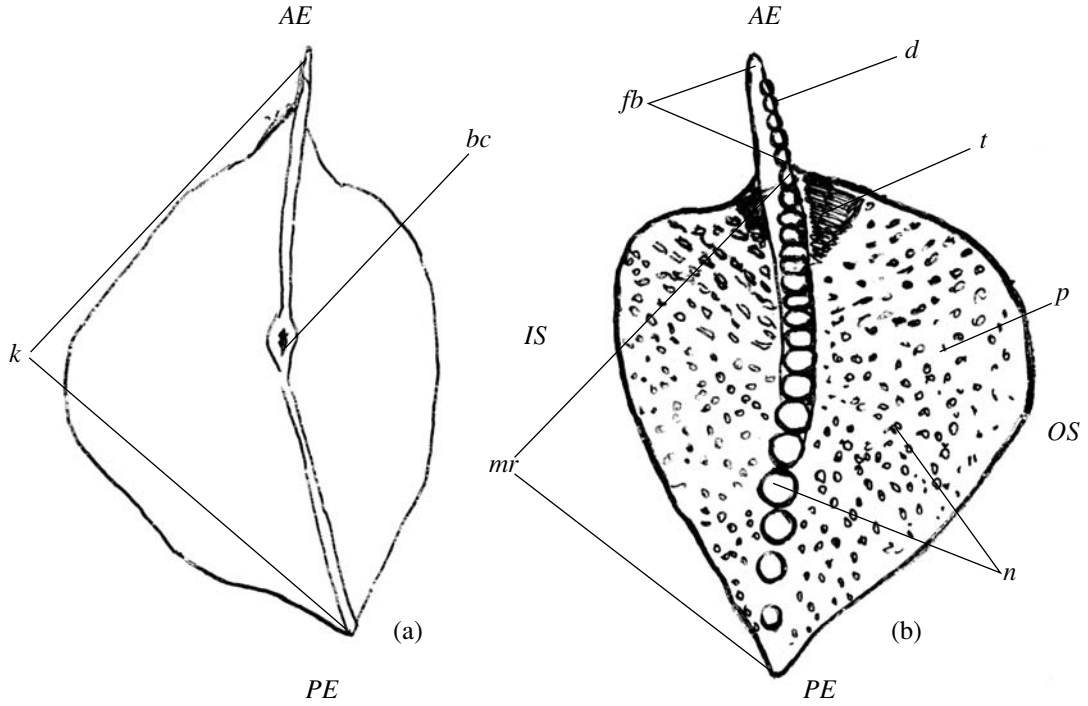


Fig. 21. Morphology of the genus Mesotaxis: (a) lower and (b) upper views. Designations: (*AE*) anterior end, (*IS*) inner side, (*OS*) outer side, (*PE*) posterior end, (*bc*) basal cavity, (*d*) denticle, (*fb*) free blade, (*k*) keel, (*mr*) median ridge, (*n*) node, (*p*) platform, and (*t*) trough.

C o m p a r i s o n. This species differs from known congeners in the symmetrical, wide anteriorly and narrow posteriorly platform and in the large and asymmetrical basal cavity located near the center.

R e m a r k s. *Klapperina ovalis* is similar in platform outline and ornamentation to *Mesotaxis*. This is the reason for discussions concerning the assignment of the species described to the genus *Klapperina* and concerning validity of this genus (Klapper in Johnson et al., 1980, p. 100; Klapper, 1988, p. 458).

O c c u r r e n c e. Germany, Poland, *transitans* Zone; Central Asia, *falsivalis* Zone. Russia, Sargaevo and Domanik regional stages.

M a t e r i a l. Volga–Ural Province: Tatarstan, Melekess 1, sample 36, interval 2108–2112 m, Sargaevo Regional Stage; Orenburg Region, Shuvalovskaya 6, interval 3651–3655 m; Sargaevo Regional Stage. southern Timan: borehole no. 2056, sample 3, depth of 121.5 m, Domanik Formation, unit 1, depth of 114 m, Domanik Formation, unit 1; Chut' River, Domanik Formation, unit 1.

Genus *Mesotaxis* Klapper et Philip, 1972

Mesotaxis: Klapper and Philip, 1972, p. 100.

T y p e s p e c i e s. *Polygnathus asymmetrica* Bischoff et Ziegler, 1957, Middle Devonian, uppermost Givetian, Padberger limestone, Germany.

D i a g n o s i s. Pa element planate; platform convex or flattened, widely ovate, symmetrical and asymmetrical; anterior end rounded or straight; posterior end pointed. Median ridge denticulated, low, straight or slightly arched. Free blade short, from one-eighth to one-third of platform length. Troughs short and poorly developed. Platform surface covered with nodes. Basal cavity small, lens-shaped, with symmetrical flanks, and located near center of platform or in its anterior third. Keel thin and low (Fig. 21).

C o m p a r i s o n. This genus differs from *Klapperina* Lane, Müller et Ziegler, 1979 in the small and symmetrical basal cavity.

S p e c i e s c o m p o s i t i o n. *Mesotaxis asymmetrica* (Bischoff et Ziegler, 1957), *M. bogoslovskyi* Ovnatanova et Kuzmin, 1991, *M. costalliformis* (Ji) 1986, *M. distinctus* Ovnatanova et Kusmin, 1991, *M. falsiovalis* Sandberg, Ziegler et Bultynck, 1989, *M. johnsoni* Klapper, Kuzmin et Ovnatanova, 1996.

O c c u r r e n c e. Cosmopolitan; upper part of the Givetian Stage, Middle Devonian–lower part of the Frasnian Stage, Upper Devonian.

Mesotaxis asymmetricus (Bischoff et Ziegler, 1957)

Plate 25, fig. 8

Polygnathus dubia asymmetrica: Bischoff and Ziegler, 1957, p. 88, pl. 16, figs. 20–22, pl. 21, fig. 3.

Polygnathus asymmetricus asymmetricus: Uyeno, 1974, p. 37, pl. 3, figs. 1, 3, 4, 6; Khalymbadzha and Tchernyschova, 1978,

pl. 11, figs. 1–3; Khalymbadzha, 1981, pl. 4, fig. 7; Huddle and Repetski, 1981, pp. 25, 26, pl. 7, figs. 11, 12, 19–21; Ziegler and Klapper, 1982, p. 469, pl. 1, figs. 7 and 8; Wang and Ziegler, 1983, pl. 5, fig. 25; Ziegler and Wang, 1985, pl. 3, fig. 5; Hou et al., 1995, pl. 3, fig. 7; Bardaschev and Ziegler, 1985, pl. 2, figs. 15 and 16; Aristov, 1988, pl. 4, fig. 19; Hou et al., 1995, pl. 3, fig. 7.

Mesotaxis asymmetricus asymmetricus: Klapper and Philip, 1972, p. 100, pl. 1, fig. 20; Druce, 1976, p. 180, pl. 68, fig. 1, pl. 69, figs. 1–3.

Mesotaxis asymmetricus: Ziegler and Sandberg, 1990, p. 44, pl. 1, figs. 5–7; Barskov et al., 1991, p. 71, pl. 18, figs. 1 and 2; Ji and Ziegler, 1993, p. 58, pl. 33, figs. 1–3, text-fig. 7, fig. 3.

Mesotaxis asymmetrica: Ovnatanova and Kononova, 2001, pl. 11, figs. 1–5; Bardaschev et al., 2006, pl. 1, fig. 37.

Mesotaxis asymmetrica: Dzik, 2002, P_1 element, figs. 30L, 30M? 30N, and 30O.

Holotype. Institute of Geology and Paleontology, Marburg, no. BiZi 1956/240, Padberger limestone, uppermost Givetian (Bischoff and Ziegler, 1957, pl. 16, fig. 20).

Diagnosis. Pa element: platform widely ovate and almost symmetrical; anterior end rounded; posterior end pointed and arched downwards. Median ridge slightly arched. Free blade one-fifth or one-sixth of platform length. Platform surface uniformly covered with small nodes. Basal cavity small, lens-shaped, symmetrical, located in anterior third of platform. Keel low and thin.

Comparison. This species differs from *M. johnsoni* Klapper, Kuzmin et Ovnatanova, 1996 in the upper surface of the platform almost uniformly covered with small nodes and in the almost symmetrical widely ovate platform.

Occurrence. Upper part of the Givetian–lower part of the Frasnian, *falsiovalis*–Early *hassi* zones; Australia, North America, Central Asia, China, Western Europe. Russia: central regions of the eastern European Platform, Semiluki Regional Stage, Frasnian Stage; Volga–Ural Region, Sargaevo and Lower Domanik regional stages; southern Timan, Ust'-Yarega Formation (middle and upper units) and bottom of the Domanik Formation (unit 1 and bottom of unit 2).

Material. Volga–Ural Province, Tatarstan, Ul'yanovskaya 1, samples 21 and 30, interval 1887–1898.5 m, Frasnian Stage, Semiluki Regional Stage; Melekess 1, interval 2108–2112 m, Sargaevo Regional Stage; Prikazanskaya 138, interval 1677–1685 m, lower part of the Domanik Regional Stage; Prikazanskaya 120, samples 67, 90, interval 1669–1700 m, Sargaevo Regional Stage, samples 93 and 95, interval 1659–1662 m, botton of the Domanik Regional Stage. Orenburg Region, Shuvalovskaya 19, sample 59, interval 3643–3649 m, Sargaevo Regional Stage, samples 90, 91, and 92, interval 3625–3633 m, Domanik Regional Stage; Shuvalovskaya 6, sample 258, interval 3651–3655 m, Sargaevo Regional Stage, samples 98, 251, and 244, interval 3645–3651 m, Domanik Regional Stage, Shuvalovskaya 4, samples 13, 98, and 106, interval 3589–3593 m, botton of the Domanik Regional Stage.

Southern Timan, outcrops D and E, Ust'-Yarega Formation, outcrop 1, botton of the section, Ust'-Yarega Formation; upward in the same section, unit 1 of the Domanik Formation; Shudayag 1003, interval 128–130 m, Ust'-Yarega Formation, interval 106–120 m, Domanik Formation, unit 1; borehole no. 3B, interval 120–122 m, Ust'-Yarega Formation, interval 98–118 m, Domanik Formation, unit 1, depth of 97 m, Domanik Formation, botton of unit 2.

Mesotaxis bogoslovskyi Ovnatanova et Kuzmin, 1991

Plate 25, figs. 9–11, 13

Mesotaxis bogoslovskyi: Ovnatanova and Kuzmin, 1991, p. 45, pl. 1, figs. 8–10; Barskov et al. 1991, p. 71, pl. 18, figs. 3–5; Ovnatanova et al., 1993, text-fig. 3, fig. 2a and 2b; Klapper et al., 1996, text-figs. 6.11 and 6.12; Over, 2007, text-fig. 10.17.

Holotype. VNIGNI (All-Russia Research Geological Oil Institute, Moscow), no. OK 1009, Komi Republic, Ukhta Region, borehole no. 2056, depth of 122.5 m; upper part of the Ust'-Yarega Formation, Lower *asymmetricus* Zone (Ovnatanova and Kuzmin, 1991, pl. 1, fig. 9).

Diagnosis. Pa element: platform elongated, ovate, flattened, and slightly asymmetrical; outer surface wider than inner surface; anterior end rounded; posterior end pointed. Median ridge slightly curved, composed of densely fused denticles in anterior part; its posterior part composed of large nodes separated by interspaces or fused at base. Free blade short, one-third or one-fourth of platform length. Ornamentation: upper surface of platform uniformly covered with small nodes. Basal cavity small, rounded, with symmetrical narrow flanks, and located in anterior third of platform.

Comparison. This species differs from *Mesotaxis asymmetricus* (Bischoff and Ziegler, 1957) in the elongated platform and asymmetry of the outer and inner platforms.

Occurrence. Upper Devonian, Frasnian Stage. North America, Tennessee; Russia: southern Timan, upper part of the Ust'-Yarega–lowermost Domanik Formation; Volga–Ural Province, Sargaevo and Lower Domanik regional stages.

Material. Volga–Ural Province: Tatarstan, Prikazanskaya 121, sample 64, interval 1671–1674.8 m; Sargaevo Regional Stage. Orenburg Region: Shuvalovskaya 4, sample 1, interval 3639–3645 m, Domanik Regional Stage, Shuvalovskaya 6, sample 1, interval 3639–3645 m, Domanik Regional Stage, Shuvalovskaya 19, sample 90, interval 3625–3633 m, lower part of the Domanik Regional Stage. Southern Timan: outcrop 1A, left bank of the Chut' River, 0.5 km from the mouth, Chut' River, outcrop 1, bottom of the Domanik Formation; borehole no. 2056, depth of 122.5 m, Ust'-Yarega Formation; Shudayag 1003, interval 106–120 m, Domanik Formation.

***Mesotaxis falsiovalis* Sandberg, Ziegler et Bultynck, 1989**

Plate 25, figs. 7, 12, and 14

Polygnathus dubia dubia: Ziegler, 1958, pl. 1, fig. 3 (only).

Polygnathus ovalis: Ziegler et Klapper, 1986, pl. 2, figs. 8 and 9.

Polygnathus asymmetricus subsp. nov.: Ziegler and Klapper, 1982, pl. 1, fig. 6; Orchard and McCracken, 1991, pl. 1, figs. 5 and 6.

Mesotaxis falsiovalis: Sandberg et al., 1989, p. 211; Ziegler and Sandberg, 1990, p. 44, pl. 1, figs. 1–4, 8; Yatskov and Kuzmin, 1992, text-fig. 2, figs. 10a and 10b.

Polygnathus asymmetricus ovalis: Szulczewski, 1971, pl. 17, figs. 1a and 1c; Aristov and Belyi, 1976, pl. 1, fig. 5; Vandelaer et al., 1989, pl. 3, fig. 6.

Holotype. Specimen figured by Ziegler (1958, pl. 1, fig. 3) and reillustrated by Ziegler and Klapper (1982, pl. 1, fig. 6).

Diagnosis. Pa element: platform flattened, ovate, and symmetrical; anterior and posterior ends pointed. Median ridge straight, reaching posterior end of platform. Free blade short, from one-eighth to one-sixth of platform length. Ornamentation: upper surface of platform uniformly covered with small nodes. Basal cavity small, lens-shaped, located near center of platform.

Comparison. This species differs from *M. asymmetricus* in the narrower platform, the pointed anterior and posterior ends, and the basal cavity located near the center of the platform.

Occurrence. Upper part of the Givetian Stage, Middle Devonian and lower part of the Frasnian Stage, Upper Devonian; North America, Western Europe, Africa, Central Asia, China. Russia: Sargaevo and Domanik regional stages of the Volga–Ural Province; Ust'-Yarega Formation and bottom of the Domanik Formation of southern Timan.

Material. Volga–Ural Province, Orenburg Region: Shuvalovskaya 6, sample 258, interval 3651–3655 m, Sargaevo Regional Stage, samples 98 and 244, interval 3645–3651 m, Domanik Regional Stage; Shuvalovskaya 4, sample 106, interval 3589–3593 m, Domanik Regional Stage; Shuvalovskaya 19, samples 80 and 84, interval 3633–3643 m, Sargaevo Regional Stage, samples 90 and 92, interval 3625–3633 m, Domanik Regional Stage. southern Timan, borehole no. 2056, depth of 122.5 m, Frasnian Stage, Ust'-Yarega Formation.

***Mesotaxis distinctus* Ovnatanova et Kuzmin, 1991**

Plate 25, figs. 4 and 5

Mesotaxis distinctus: Ovnatanova and Kuzmin, 1991, pl. 1, figs. 11 and 12.

Holotype. VNIGNI, no. OK 1011, Komi Republic, Ukhta Region; borehole no. 1003, depth of 120 m; lower part of the Domanik Formation, *punctata* Zone (Ovnatanova and Kuzmin, 1991, pl. 1, fig. 11).

Diagnosis. Pa element: platform flattened, wide, subsquare or rounded; outer side of platform somewhat wider than inner side; anterior end straight; posterior end semicircular. Median ridge straight, approaching but terminating short of reaching posterior end of platform. Free blade short, one-fourth or one-third of platform length. In anterior part of median ridge, denticles high, small, and fused at base; in posterior part of median ridge, denticles or nodes large and separate. Ornamentation: whole platform surface uniformly covered with small nodes, which occasionally fused along platform margins to form short transverse ridges. Basal cavity teardrop-shaped, with narrow symmetrical flanks, and located in anterior part of platform. Keel well pronounced over whole length.

Comparison. This species differs from *Mesotaxis asymmetricus* (Bischoff et Ziegler, 1957) in the subsquare platform and in the median ridge, which does not reach the posterior end of the platform.

Occurrence. Southern Timan, Frasnian Stage, *transitans–punctata* zones.

Material. Southern Timan, borehole no. 2056, depth of 125 m, Ust'-Yarega Formation; borehole no. 1003, depth of 120 m, Domanik Formation, unit 1.

***Mesotaxis johnsoni* Klapper, Kuzmin et Ovnatanova, 1996**

Plate 25, figs. 15–18

Mesotaxis sp. Q: Klapper and Lane, 1985, p. 474, pl. 2, figs. 10 and 11; Klapper and Lane, 1988, pl. 2; figs. 9–13.

Mesotaxis johnsoni: Klapper et al., 1996, p. 140, pl. 6, figs. 13–16.

Holotype. Geological Survey of Canada, no. GSC 90681; Canada, Alberta, outcrop Luscar 1, sample 10, Perdrix Formation. Reillustrated from Klapper and Lane, 1988, pl. 2, figs. 10 and 11.

Diagnosis. Pa element: platform trapezoid; outer side of platform wider than inner side; platform margins slightly raised; anterior end rounded or oblique; posterior end pointed and arched downwards. Median ridge arched, consisting of discrete nodes equal in size, reaching posterior end of platform. Free blade short, one-third or one-fourth of platform length. Ornamentation: nodes in anterior part of platform and along its margins large and sometimes fused to form short interrupted ridges; sometimes, nodes forming denticulation along platform margin. Basal cavity small, elongated, located in anterior third of platform.

Comparison. This species differs from *Mesotaxis asymmetricus* (Bischoff et Ziegler, 1957) in the trapezoid platform and larger nodes in the anterior part of the platform.

Occurrence. Canada, Australia, Central Russian Platform, southern Timan, and Volga–Ural Province. Upper Devonian, Frasnian Stage, *punctata* Zone; in the Volga–Ural Province and southern Timan, bottom of the Domanik Regional Stage.

Material. Volga–Ural Province, Tatarstan: Prikazanskaya 69, interval 1686.2–1689.7 m, Frasnian Stage, Domanik Regional Stage; Prikazanskaya 138, samples 89 and 93, interval 1633–1681 m, Domanik Regional Stage; Prikazanskaya 166, sample 55, interval 1575–1578 m, Domanik Regional Stage. Orenburg Region: Shuvalovskaya 4, samples 98 and 106, interval

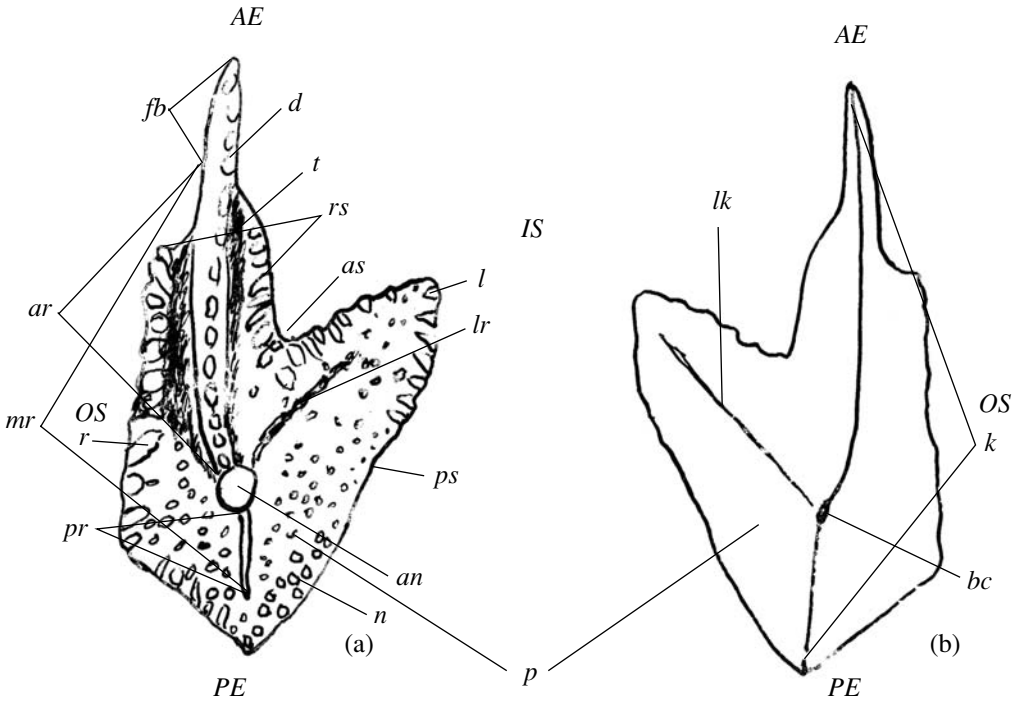


Fig. 22. Morphology of the genus *Palmatolepis:* (a) upper and (b) lower views. Designations: (*AE*) anterior end, (*IS*) inner side, (*OS*) outer side, (*PE*) posterior end, (*an*) azygous node, (*ar*) anterior ridge, (*as*) anterior sinus, (*bc*) basal cavity, (*r*) ridge, (*d*) denticle, (*fb*) free blade, (*k*) keel, (*l*) lobe, (*lk*) lateral keel, (*lr*) lateral ridge, (*mr*) median ridge, (*n*) node, (*p*) platform, (*pr*) posterior ridge, (*ps*) posterior sinus, (*rs*) rostrum, and (*t*) trough.

3589–3593 m; Domanik Regional Stage; Shuvalovskaya 19, sample 90, interval 3625–3633 m, Domanik Regional Stage. Southern Timan: outcrops 1 and 1A on the Chut' River, Domanik Formation, unit 1; borehole no. 2068, depth of 132 m, Domanik Formation.

Genus *Palmatolepis* Ulrich et Bassler, 1926

Palmatolepis: Ulrich and Bassler, 1926, p. 49; Klapper in *Catalogue*…, 1973, pp. 253–256.

Palmatolepis (*Palmatolepis*): Müller, 1956, p. 16.

Palmatolepis (*Manticolepis*): Müller, 1956, p. 16.

Palmatolepis (*Deflectolepis*): Müller, 1956, p. 16.

Palmatolepis (*Panderolepis*): Helms, 1963, p. 467.

Type species. *Palmatolepis perlobata* Ulrich et Bassler, 1926; Upper Devonian of the North America.

Diagnosis. Pa element planate; platform variously shaped, asymmetrical, ovate, subtriangular. Inner side wider than outer side, with short or long, rounded or pointed lobe bordered by anterior and posterior sinuses. Median ridge sigmoidal, sometimes straight. Azygous node dividing median ridge into anterior and posterior parts. Free blade short or long, occasionally absent. Upper surface of platform smooth, shagreened, or ornamented with nodes or ridges. Lower side with keel located opposite to median ridge of upper surface of platform. Basal cavity tiny, hardly visible, located under azygous node. Basal cavity lacking flanks; in some species, keel forming asymmetrical loop contouring basal cavity (Fig. 22).

Comparison. This genus differs from *Mesotaxis* Klapper et Philip, 1972 in the presence of lateral lobe and azygous node.

Species composition. More than forty species and subspecies from the Frasnian Stage.

Occurrence. North America, Africa, Europe, Asia, Australia. Upper Devonian, Frasnian and Famennian stages.

Palmatolepis acutangularis Ovnatanova et Kononova sp. nov.

Plate 16, figs. 5 and 6

Etymology. From the Latin *acutangularis* (acute-angled).

Holotype. PIN (Paleontological Institute, Russian Academy of Sciences, Moscow), no. 5255/86; southern Timan, Vezha-Vozh River, outcrop 10, sample 3; Frasnian Stage, Lyaiol' Formation, unit 4 (Pl. 16, fig. 5).

Diagnosis. Pa element: platform flattened and subtriangular; lobe large, triangular, with pointed end, without sinuses, and located in line with, or anteriorly to, azygous node. Anterior inner margin of lobe ranging from straight to slightly concave; posterior margin straight. Posterior end of platform pointed. Median ridge denticulated and almost straight. Posterior ridge with 1–3 conical nodes decreasing in size backwards. Azygous node large, high, and conical. Free blade one-

half or one-third of platform length. Platform surface smooth or finely shagreened.

Comparison. The new species differs from *Palmatolepis kaledai* sp. nov. in the pointed triangular lobe and straight median ridge. It differs from *Pa. ormistoni* Klapper, Kuzmin et Ovnatanova, 1996 in the flattened and wider platform, pointed triangular lobe lacking posterior sinus, and in the smooth or finely shagreened platform surface.

Occurrence. Southern Timan, Frasnian Stage, Lyaiol' Formation, unit 4.

Material. Four specimens from Vezha-Vozh River, outcrop 10, bed 3, sample 3; southern Timan, Frasnian Stage, Lyaiol' Formation, unit 4.

Palmatolepis amplificata Klapper, Kuzmin et Ovnatanova, 1996

Plate 9, figs. 1–9

Palmatolepis amplificata: Klapper et al., 1996, p. 140, pl. 7, figs. 1, 2, and 4; Ovnatanova et al., 1999b, pl. 2, figs. 7 and 10; Over, 2007, pl. 16, fig. 15.

Palmatolepis aff. *rhenana*: Klapper and Lane, 1988, pl. 1, figs. 10–13; Kuzmin and Ovnatanova in Menner et al., 1992, pl. 4, fig. 5.

Palmatolepis gigas: Ovnatanova and Kuzmin, 1991, pl. 3, fig. 18.

Holotype. PIN, no. 4551/38 (Klapper et al., 1996, p. 140, text-fig. 7.2); southern Timan, borehole no. 2068, sample 24, depth of 20 m; Lyaiol' Formation, unit 3.

Diagnosis. Pa element: platform triangular; posterior end pointed; lobe well pronounced, elongated, rounded, and contoured by well developed anterior and posterior sinuses. Platform margin convex behind posterior sinus. Median ridge usually slightly S-shaped, with large nodes anterior to azygous node and small hardly visible nodes behind it. Median ridge reaching or closely approaching posterior end of platform; sometimes, it terminating behind the azygous node (Pl. 9, fig. 9). Posterior ridge consisting of small nodes. Free blade one-third or one-fourth of platform length. Denticulated parapet well developed along outer margin of upper third of platform. Sometimes, parapets developed on each side of median ridge. Parapet (or parapets) usually parallel to median ridge. Ornamentation consisting of small nodes uniformly covering platform.

Comparison. This species differs from *Palmatolepis brevis* Ziegler et Sandberg, 1990 in the more elongated subtriangular platform, the presence of a parapet (or parapets), and posterior ridge consisting of a series of small nodes. It differs from *Palmatolepis gigas gigas* in the presence of one or two parapets (*Palmatolepis gigas gigas* has a rostrum) and in the pointed posterior end. It differs from *Palmatolepis mucronata* in the presence of a parapet and rounded lobe.

Occurrence. Upper Devonian, Frasnian Stage. North America (Iowa, Tennessee), Canada, Russia: southern Timan, Domanik Formation, unit 3, Lyaiol' Formation (unit 1–bottom of unit 3).

Material. Southern Timan, Shudayag outcrop 13, Domanik Formation, unit 3; Lyaiol' outcrop 1353, Domanik Formation, unit 3; outcrops 1354 and 1905 on the Lyaiol' River, outcrops 731 and 732 on the Vezha-Vozh River, Lyaiol' Formation, unit 1, outcrop 8, samples 4 and 7 (Lyaiol' Formation, unit 2), borehole no. 2023, depths of 177 and 189 m; Lyaiol' Formation, unit 2; borehole no. 2068, depth of 20 m; Lyaiol' Formation, unit 3.

Palmatolepis anzhelae Khruscheva et Kuzmin, 1996

Plate 5, figs. 4 and 5

Palmatolepis anzhelae: Khruscheva and Kuzmin, 1996, p. 91, pl. 11, figs. 12 and 13; Klapper, 2007, text-figs. 2–7.

Palmatolepis kireevae: Klapper and Lane, 1988, pl. 1, fig. 7.

Holotype. VNIGRI (All-Russia Research Institute of Oil and Geological Prospecting, St. Petersburg), no. KI/6, Komi Republic, Ukhta Region, Lyaiol' River, outcrop 1906, sample 56; Frasnian Stage, Lyaiol' Formation, bituminous unit (Khruscheva and Kuzmin, 1996, pl. 11, fig. 1).

Diagnosis. Pa element: platform rounded rhombic; posterior end rounded and arched downwards; lobe narrow, small, short, pointed, located at level of azygous node or somewhat higher, bordered by well pronounced anterior and posterior sinuses. Platform margin convex posterior to posterior sinus. Median ridge S-shaped, terminating short of reaching posterior end of platform. Azygous node large, well developed, located near center of platform. Posterior ridge short, with small nodes. Free blade one-fifth or one-sixth of platform length. Secondary ridge often present, extending from azygous node to lobe end. Ornamentation consisting of small nodes uniformly covering upper surface of platform.

Comparison. This species differs from *Palmatolepis hassi* in the rhombic platform with narrow, short, and pointed lobe.

Occurrence. Frasnian Stage, France, Luscar Mountain section, 146 m from the section base; Canada, upper part of the Perdrix Formation; Volga–Ural Province, Mendym Regional Stage; southern Timan, Lyaiol' Formation, unit 2–4.

Material. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, sample 112, interval 1680–1685 m, Mendym Regional Stage. Southern Timan: outcrop 1906A on the Lyaiol' River, Lyaiol' Formation, unit 2; outcrop 1908 on the Lyaiol' River, beds 20, 22, and 28, Lyaiol' Formation, unit 4; outcrop 735, sample 1 and outcrop 9, sample 3, Lyaiol' Formation, unit 2.

Palmatolepis barba Ziegler et Sandberg, 1990

Plate 10, figs. 9–15

Palmatolepis barba: Ziegler and Sandberg, 1990, p. 48, pl. 4, figs. 3, 4, and 8; Ziegler et al., 1992, pl. 3, fig. 8; Matyja, 1993, pl. 20, fig. 6; 2003, pl. 20, fig. 6; Ji and Ziegler, 1993, pl. 29, fig. 1; Ovnatanova et al., 1999a, pl. 2, fig. 5; Bultynck et al., 1998, pl. 1, fig. 8.

?Palmatolepis proversa: Klapper, 1988, pl. 2, figs. 14 and 15.

H o l o t y p e. NS (Naturmuseum Senckenberg, Frankfurt am Main), no. SMF 38693, sample 85; Bel-115, wackestone, 8 m higher than the upper part of the Lion mudstone; northeast of Tiene du Lion quarry), Belgium, Early *rhenana* Zone (Ziegler, 1958, pl. 4, fig. 4).

D i a g n o s i s. Pa element: platform well developed; lobe anteriorly directed, pointed, and bordered by well pronounced and deep anterior sinus; posterior end pointed and raised. Median ridge S-shaped like curved, terminating short of reaching posterior end of platform. Azygous node well pronounced and large. Posterior ridge composed of chain of small, often fused nodes, . Free blade from one-third to one-fifth of platform length. Rostrum and troughs rarely well developed. Ornamentation consisting of small nodes uniformly covering platform surface; occasionally, they irregularly arranged or fused to form small interrupted ridges.

C o m p a r i s o n. This species differs from *Palmatolepis proversa* in the raised posterior end of the platform and the weakly developed rostral ridges and troughs, which occasionally absent.

R e m a r k s. Ornamentation of the platform varies from almost smooth to variously ornamented. Species is known from the region of accumulation of reef and interreef facies.

O c c u r r e n c e. Frasnian Stage, Germany, France, Poland; Early *rhenana* Zone; Volga–Ural Province, Mendym Regional Stage; Timan–Pechora Province, Lyaiol' Formation, units 1 and 2.

M a t e r i a l. Volga–Ural Province, Tatarstan, Prikazanskaya 115, interval 1647.3–1649.7 m, Mendym Regional Stage; Severnyi Kupol 71, sample 112, interval 1680–1685, m and samples 71, 76, interval 1659–1666 m, Mendym Regional Stage; central regions of Timan–Pechora Province, Mar'el' borehole, 2595–2601 m (Lyaiol' Formation, unit 2); southern Timan, outcrop 1354 on the Lyaiol' River, Lyaiol' Formation, unit 1, outcrop 735 on the Vezha-Vozh River, Lyaiol' Formation, unit 2.

Palmatolepis bohemica Klapper et Foster, 1993

Plate 3, figs. 23 and 24; Plate 4, figs. 1 and 5

Palmatolepis bohemica: Klapper et Foster, 1993, p. 5, figs. 4.9–4.12, (Pa element) figs. 5.1–5.3, (Pa element); Klapper et al., 1996, p. 147, text-figs. 9.17 and 9.18; Pisarzowlska et al., 2006, fig. 14L; Klapper, 2007, text-figs. 5.17.

Palmatolepis transitans: Barskov et al., 1987, pl. 6, fig. 7 (only).

H o l o t y p e. GSWA, no. F48963, WCB 365-26; Western Australia, Canning Basin, section west of McPhee Knoll in Old Bohemia Valley (Klapper and Foster, 1993, fig. 5.3).

D i a g n o s i s. Pa element: platform subtriangular; posterior end slightly pointed; lobe rounded trapezoid, with well pronounced anterior sinus; posterior sinus absent. Median ridge straight and usually reaching posterior end of platform. Posterior ridge thin, composed of chain of small and fused at base nodes, and reaching posterior end. Azygous node well developed. Free blade short, one-fourth or one-fifth of platform length. Rostrum short; troughs developed in anterior third of platform. Ornamentation consisting of small nodes covering upper surface of platform.

C o m p a r i s o n. This species differs from *Palmatolepis spinata* Ovnatanova et Kuzmin, 1991 in the rounded trapezoid lobe with well pronounced anterior sinus and thin posterior ridge reaching posterior end of the platform. It differs from *Pa. domanicensis* Ovnatanova, 1976 primarily in the rounded trapezoid platform with well pronounced anterior sinus, while *Pa. domanicensis* has a pear-shaped platform.

O c c u r r e n c e. Frasnian Stage, Western Australia, Canning Basin, Zones 6 and 7 of the composite scale of G. Klapper. Russia: Timan–Pechora Province, Domanik Formation, unit 2; Volga–Ural Province, Domanik Regional Stage.

M a t e r i a l. Volga–Ural Province: Tatarstan, Prikazanskaya 138, sample 87, interval 1659–1663 m, Domanik Regional Stage; Orenburg Region, Shuvalovskaya 17, interval 3605–3616 m, Domanik Regional Stage; southern Timan, outcrops 2 and 3 on the Chut' River, outcrop 9 on the Ukhta River, outcrops 10 and 11 on the Domanik River, Domanik Formation, unit 2, borehole no. 2051, depth of 214 m, Domanik Regional Stage.

Palmatolepis brevis Ziegler et Sandberg, 1990

Plate 8, figs. 12–16; Plate 14, figs. 11 and 12

Palmatolepis gigas gigas: Barskov et al., 1987, pp. 32–33, pl. 8, figs. 3 and 5 (only).

Palmatolepis aff. *rhenana*: Klapper, 1988, pl. 1, figs. 10 and 12.

Palmatolepis rhenana brevis: Ziegler and Sandberg, 1990, pp. 56–57, pl. 13, figs.1 and 2.

Palmatolepis hassi: Müller and Müller, 1957, fig. 7 (only), text-fig. 9, fig. 16.

Palmatolepis brevis: Klapper et al., 1996, pp. 143 and 144, text-figs. 7.3, 7.5–7.8; Klapper, 2007, text-figs. 5.17; Over, 2007, pl. 17, fig. 14.

H o l o t y p e. NS, no. SMF 38766, sample WCD-2, Water Canyon, Diamond Mountains, White Pine County, Nevada, Early *rhenana* Zone (Ziegler and Sandberg, 1990, pl. 13, fig. 2).

D i a g n o s i s. Pa element: platform rounded triangular; lobe elongated; posterior end rounded, with extended tip. Lobe rounded pointed, long, and contoured by well pronounced anterior and posterior sinuses. Platform margin convex behind posterior sinus. Median ridge slightly arched, terminating in azygous node, disappearing posterior to it. Azygous node well developed. Free blade high, short, one-fourth to one-sixth of platform length. Ornamentation consisting of nodes uniformly covering platform surface. Occasionally, thin secondary ridge present.

C o m p a r i s o n. This species differs from *Palmatolepis mucronata* Klapper, Kuzmin et Ovnatanova, 1996 in the more rounded platform, the more rounded

lobe, and the poorly developed or undeveloped posterior ridge, while the posterior ridge of *Pa. mucronata* is always present and closely approaches the posterior end of the platform.

Occurrence. Upper Devonian, Frasnian Stage, Early *rhenana* Zone; North America (Nevada, Iowa, Tennessee), Europe: Germany, Belgium; Russia: Volga–Ural Province, Mendym Regional Stage and lower part of the Askyn Regional Stage; southern Timan, Lyaiol' Formation, units 1–4.

Material. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, sample 48, interval 1651–1654 m; Mendym Regional Stage, samples 59–62, interval 1646–1649 m, Askyn Regional Stage; Severnyi Kupol 220, interval 1574–1578.9 m, Askyn Regional Stage. Southern Timan: outcrop 1354 on the Lyaiol' River, Lyaiol' Formation, unit 1, outcrop 1359 on the Lyaiol' River, Lyaiol' Formation, unit 4 (lower part), outcrop 735 on the Vezha-Vozh River, Lyaiol' Formation, unit 2, borehole no. 2023, depth of 189 m, Lyaiol' Formation, unit 2.

Palmatolepis domanicensis Ovnatanova, 1976

Plate 3, figs. 17–22; Plate 4, figs. 6 and 7

Palmatolepis domanicensis: Ovnatanova, 1976, p. 109, pl. 9, figs. 1 and 2; Ovnatanova et Kuzmin, 1991, pl. 3, fig. 3 (only); Klapper et al., 1996, p. 145, text-fig. 9.12 (only; reillustration of the holotype).

Palmatolepis plana: Ziegler and Sandberg, 1990, pl. 3, figs. 2 and 3 (only).

Palmatolepis foliacea: Sandberg et al., 1992, pl. 3, fig. 6.

Mesotaxis ? domanicensis: Dzik, 2002, P_1 elements, figs. 32C, 32D, and 32E?.

Holotype. VNIGNI, no. 40/58, southern Timan, Domanik River, Frasnian Stage, upper part of the Domanik Regional Stage (Ovnatanova, 1976, pl. 9, fig. 2).

Diagnosis. Pa element: platform pear-shaped (spear-shaped in the original description); lobe from trapezoid to rounded in outline; anterior sinus poorly pronounced. Platform margins raised; rostrum short; troughs poorly pronounced. Posterior end of platform pointed, extended, and arched downwards. Median ridge straight and usually terminating short of posterior end of platform. Azygous node well developed and larger than nodes of median ridge. Free blade short, one-fifth or one-sixth of platform length. Upper surface uniformly covered with small nodes. Sometimes, nodes fused to form small interrupted ridges.

Comparison. This species differs from *Palmatolepis plana* Ziegler et Sandberg, 1990 in the pear-shaped platform with extended posterior end and poorly pronounced sinus. It differs from *Pa. bohemica* Klapper et Foster, 1993 in the pear-shaped platform with weakly developed lobe and extended, pointed, and arched downwards posterior end, while *Pa. bohemica* has a rounded lobe with a well pronounced anterior sinus.

Remarks. Ziegler and Sandberg (2000, p. 339, fig. 3) refer specimens that were interpreted earlier (Klapper et al., 1996, text-figs. 9.9, 9.10) as transitional from *Pa. domanicensis* to *Pa. foliacea* to the species *Pa. foliacea.* We strongly object to the assignment of the holotype of *Pa. domanicensis* to *Pa. foliacea* (Klapper et al., 1996, text-fig. 9.12). *Pa. domanicensis* differs from *Pa. foliacea* in the presence of the lobe and the attenuate posterior end of the platform. The two species also differ in the stratigraphic range. *Pa. domanicensis* appeared in unit 2 of the Domanik Formation (*punctata* Zone), while *Pa. foliacea* appeared stratigraphically higher (Late *rhenana* Zone).

Occurrence. Frasnian Stage, Early *rhenana* Zone of Germany, Benner Bicken quarry; Poland, Middle Frasnian, Wietrznia; North America (Nevada). Russia: Timan–Pechora Province, Domanik, Vetlasyan, and Lyaiol' (unit 2) formations; Volga–Ural Province, Domanik Regional Stage.

Material. Volga–Ural Province: Tatarstan, Prikazanskaya 138, depth of 1659–1663 and 1651–1655 m, Domanik Regional Stage; Prikazanskaya 121, interval 1627–1632 m, Domanik Regional Stage. Southern Timan: outcrop 11 on the Domanik River, Domanik Formation, unit 2; Shudayag outcrop 12, Domanik Formation, unit 2, outcrop 13, Domanik Formation, unit 3; borehole no. 2056, depth of 91 m, Domanik Formation, unit 2, depth of 64 m, Domanik Formation, unit 3; boreholes nos. 3B, 70, and 75 m, Domanik Formation, unit 2, depth of 63 m, Domanik Formation, unit 3, depth of 53 m, Vetlasyan Formation; borehole no. 2060, depth of 224.9 m, Vetlasyan Formation; borehole no. 2068, depth of 36.0 m, Lyaiol' Formation, unit 2.

Palmatolepis ederi Ziegler et Sandberg, 1990

Plate 11, figs. 17 and 18; Plate 12, figs. 3–8

Palmatolepis ederi: Ziegler and Sandberg, 1990, pp. 62–63, pl. 9, figs. 1–6, and 7?, pl. 10, figs. 7–10; Kuzmin and Mel'nikova, 1991, p. 69, pl. 1, figs. 10, 13, and 14; Orchard and McCracken, 1991, pl. 2, fig. 6; Ji and Ziegler, 1993, pl. 25, fig. 7 (only); Klapper et al., 1996, p. 145, pl. 9, figs. 5 and 6; Ovnatanova et al., 1999a, pl. 2, fig. 17; Gereke, 2004, pl. 1, fig. 7; Klapper, 2007, text-fig. 2.5.

Palmatolepis foliacea: Sandberg et al., 1994, pl. 1, fig. 11.

Mesotaxis simpla: Dzik, 2002, P_1 elements, figs. 32M, 34A?, 34L?, 34M.

Holotype. NS, no. SMF 38 749, *jamieae* Zone of the Martenberg section, Germany (Ziegler and Sandberg, 1990, pl. 10, figs. 8–10).

Diagnosis. Pa element: platform elongated relatively narrow, and ovate; lobe poorly developed; posterior end slightly pointed and raised. Median ridge slightly sigmoidal. Azygous node well developed. Behind azygous node, posterior ridge consisting of chain of nodes and terminating short of reaching posterior end of platform. Free blade high, relatively long, one-fifth or one-sixth of platform length. Ornamentation absent or consisting of nodes uniformly covering platform.

Comparison. This species differs from *Palmatolepis linguiformis* Müller, 1956 in the relatively long free blade and the slightly curved median ridge.

O c c u r r e n c e. Frasnian Stage, Germany, *jamieae*–Early *rhenana* zones; Poland, Middle Frasnian; North America (Indiana), Early *rhenana* Zone, New Albany Shale, Selmier unit; southern China, Xiangtian Formation, Early *rhenana* Zone. Russia: Volga–Ural Province, Mendym Regional Stage and bottom of the Askyn Regional Stage; Timan–Pechora Province, Lyaiol' Formation (units 1 and 2).

M a t e r i a l. Volga–Ural Province: Udmurtia, Krasnogor'e 91, interval 2010–2013 m, Mendym Regional Stage; Tatarstan, Prikazanskaya 115, interval 1647–1649 m, Mendym Regional Stage; Prikazanskaya 120, interval 1604–1607 m, bottom of the Askyn Regional Stage; Severnyi Kupol 71, samples 66 and 48, interval 1651–1654 m, Mendym Regional Stage, sample 62, interval 1649–1651 m and sample 60, interval 1646–1649 m, bottom of the Askyn Regional Stage. Orenburg Region, Shuvalovskaya 19, interval 3610–3617 m, bottom of the Kolgany Member. Southern Timan: outcrops 1354, 1905, and 1906 on the Lyaiol' River, Lyaiol' Formation, units 1 and 2; outcrops 735, 8, and 9 on the Vezha-Vozh River, Lyaiol' Formation, unit 2; borehole no. 2068, depth of 36 m, Lyaiol' Formation, unit 2.

Palmatolepis elegantula Wang et Ziegler, 1983

Plate 16, figs. 1–4

Palmatolepis minuta elegantula: Wang and Ziegler, 1983, p. 87, pl. 3, figs. 10a and 10b; Barskov et al., 1987, pl. 3, figs. 16–18 (only), text-fig. 3.A5.

Pa. elegantula: Khruscheva and Kuzmin, 1996, pl. 11, fig. 6.

H o l o t y p e. Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, no. HL-15g/75142, Liujing section, Hengxian County, Quangxi Province, Rongxian Formation, above the *asymmetricus* Zone, possibly *gigas* Zone (= *rhenana*) (Wang and Ziegler, 1983, pl. 3, figs. 10a and 10b).

D i a g n o s i s. Pa element always small; platform rounded and occupying half of element length; posterior end of platform rounded. Median ridge high, straight, and long. Posterior ridge low, consisting of one or two relatively small nodes. Azygous node high, conical, displaced relative to median ridge, and located in posterior part of platform. Free blade high, straight, with narrow peglike denticles almost equal in height; it gradually passing into median ridge but height of denticles remaining the same (Pl. 16, fig. 4). Platform surface smooth or finely shagreened.

C o m p a r i s o n. This species is similar to *Palmatolepis parva* Klapper et al., 2004 in the small size and differs in the rounded triangular platform, ovate lobe, and rounded posterior end of the platform, which is located in the horizontal plane; the posterior end of *Pa. parva* is slightly arched downwards.

O c c u r r e n c e. Upper Devonian, Frasnian Stage, China; Russia, southern Timan, Lyaiol' Formation (units 1–4).

M a t e r i a l. Southern Timan, Lyaiol' River, outcrops 1354, 1906, 1359, 1360, and 1908, Vezha-Vozh River, outcrops 8 and 10 (units 2–4).

Palmatolepis foliacea Youngquist, 1945

Plate 11, figs. 10–15, 16; Plate 12, figs. 1 and 2

Palmatolepis foliaceus: Youngquist, 1945, pp. 364, 365, pl. 56, figs. 11 and 12.

Palmatolepis (*Manticolepis*) *foliacea:* Müller and Müller, 1957, p. 1102, pl. 140, figs. 6, 7, and 8.

Palmatolepis foliacea: Ziegler and Sandberg, 1990, pp. 49–50, pl. 5, figs. 1, 2, 3, 4, and 6 (only, fig. 6 is a reillustration of the lectotype); Kuzmin and Mel'nikova, 1991, p. 69, pl. 1, fig. 6; Klapper et al., 1996, p. 145, text-figs. 9.7 and 9.8; Ovnatanova et al., 1999b, pl. 2, figs. 19 and 20.

L e c t o t y p e. The lectotype of *Palmatolepis* (*Manticolepis*) *foliacea* Youngquist was designated by Müller and Müller (1957) from the Youngquist's collection (1945, pl. 56, fig. 12); presently housed in State University of Iowa, no. 2949; Independence Shale (?), Middle Amana, Iowa.

D i a g n o s i s. Pa element: platform elongated and irregularly pear-shaped; posterior end arched downwards; lobe undeveloped. Platform widest in line with azygous node. Median ridge slightly S-shaped. Azygous node located in posterior part of platform. Posterior ridge consisting of several nodes and terminating near posterior end of platform. Free blade relatively small. Platform margins joining free blade at the same level. Platform covered with nodes, which often arranged mostly along platform margins.

C o m p a r i s o n. This species differs from *Palmatolepis jamieae* Ziegler et Sansdberg, 1990 in the elongated and irregularly pear-shaped platform and the poorly developed lobe.

O c c u r r e n c e. Frasnian Stage, Germany, Benner Bicken quarry, Early *rhenana* Zone; North America (Iowa), Sweetland Creek Shales, bottom of zones 12 and 13 of the composite scale; Volga–Ural Province, Askyn Regional Stage; southern Timan, Lyaiol' Formation, unit 4.

M a t e r i a l. Volga–Ural Province: Tatarstan, Melekess 1, sample 72, interval 2041–2048 m and sample 94, interval 2018–2024 m, Askyn Regional Stage; Severnyi Kupol 71, samples 63 and 64, interval 1649–1651 m, samples 59, 57, 53, and 52, interval 1642–1646 m, Askyn Regional Stage; Severnyi Kupol 166, sample 38, interval 1556–1559 m, Askyn Regional Stage. Southern Timan: outcrops 1359, 1360, and 1908 on the Lyaiol' River (Lyaiol' Formation, unit 4); upper part of outcrop 9 and outcrop 10 on the Vezha-Vozh River (Lyaiol' Formation, unit 4).

Palmatolepis gutta Kuzmin, 1998

Plate 2, figs. 3–10

Palmatolepis gutta: Kuzmin, 1998, p. 74, pl. 8, figs. 8–14; Ovnatanova et al., 1999b, pl. 1, fig. 16.

Palmatolepis sp.: Uyeno, 1991, pl. 3, figs. 24 and 25; pl. 4, figs. 1 and 2.

Holotype. PIN, no. 4551/108; Ukhta Region, Chut' River, outcrop 7; Frasnian Stage, Domanik Formation, lower unit, sample D-9213, (Kuzmin, 1998, pl. 8, fig. 8).

Diagnosis. Pa element: platform teardrop-shaped and flattened; lateral lobe rounded and weakly developed; located in posterior part of platform in line with azygous node; sinus poorly pronounced; posterior end slightly pointed and arched downwards. Median ridge slightly sigmoidal. Azygous node well developed and displaced to posterior end of platform. Posterior ridge consisting of 2–5 nodes and terminating short of reaching posterior end of platform. Free blade very short, one-eighth of platform length. Platform uniformly ornamented with small nodes.

Comparison. This species differs from *Palmatolepis timanensis* Klapper, Kuzmin et Ovnatanova in the teardrop-shaped platform and the lobe located in the posterior part of the platform in line with the azygous node.

Occurrence. Volga–Ural Province, bottom of the Domanik Regional Stage; southern Timan, Domanik Formation, unit 1.

Material. Upper Devonian, Frasnian Stage. Volga–Ural Province, Orenburg Region, Shuvalovskaya 4, sample 222, interval 3589–3593 m; bottom of the Domanik Regional Stage; southern Timan, Domanik Formation, unit 1. Southern Timan, Chut' River, outcrop 1; borehole no. 1003, interval 106–107 m; Domanik Formation, unit 1; borehole no. 2056, depth of 102.5 m, Domanik Formation, unit 1.

Palmatolepis gyrata Kuzmin et Melnikova, 1991

Plate 12, figs. 18–22; Plate 13, figs. 1–3

Palmatolepis gyratus: Kuzmin and Melnikova, 1991, p. 71, pl. 1, figs. 4 and 5; Ovnatanova et al., 1999b, pl. 2, fig. 15.

Holotype. TPD VNIGRI (Timan–Pechora Department of All-Russia Research Institute of Oil and Geological Prospecting, St. Petersburg), no. 6M/9; Khoreiver Depression, Bagan borehole no. 41, interval 3255.1–3259.4 m; Upper Frasnian Substage, analogues of the Upper *gigas* Zone (Kuzmin and Melnikova, 1991, pl. 1, fig. 5).

Diagnosis. Pa element: platform from widely ovate to lanceolate; outer side of platform narrow, with slightly elevated margin; inner side twice as wide as outer side and flattened. Maximum width of platform located anterior to azygous node. Posterior end pointed and arched downwards. Median ridge from straight to slightly sigmoidal. Posterior ridge consisting of two to four nodes and terminating short of reaching posterior end. Free blade one-fourth of conodont length. Platform covered with small nodes; sometimes, they fused, forming short interrupted ridges along platform margin. Central part of platform smooth or finely shagreened.

Comparison. This species differs from *Palmatolepis foliacea* Joungquist, 1945 in the lanceolate platform, pointed posterior end, and maximum width of the platform located in front of the azygous node.

Occurrence. Timan–Pechora Province, Khoreiver Depression, Upper Frasnian Substage; southern Timan, Lyaiol' Formation, units 4 and possibly 3; Volga–Ural Province, Askyn Regional Stage.

Material. Volga–Ural Province: Tatarstan, Melekess 1, sample 69, interval 2048–2053 m, Askyn Regional Stage; Severnyi Kupol 71, samples 64, 63, 58–60 from the interval 1642–1651 m, Askyn Regional Stage. Southern Timan: outcrops 1359, 1360, and 1908 on the Lyaiol' River, Lyaiol' Formation, unit 4; outcrop 9 on the Vezha-Vozh River, borehole no. 2023, depth of 140 m, Lyaiol' Formation, unit 4; borehole no. 2025, depth of 16 m, Lyaiol' Formation, unit 4.

Palmatolepis hassi sensu stricto Müller et Müller, 1957

Plate 4, figs. 10–14, 15; Plate 5, fig. 1

Palmatolepis hassi: Müller and Müller, 1957, pp. 1102–1103, pl. 139, fig. 2, pl. 140, figs. 2–4; Klapper and Foster, 1986, pl. 2, fig. 14 (Pa element); Klapper and Lane, 1988, pl. 1, fig. 7?; Klapper, 1988, text-figs. 1.4 and 1.5; Klapper and Foster, 1993, p. 22, text-figs. 15.1–15.9; Barskov et al., 1987, p. 34 (partly), pl. 7, fig. 18 (only); Ziegler and Sandberg, 1990, pp. 55–56, pl. 2, figs. 2, ?4, and 5 (only); Matyia, 1993, pl. 20, fig. 10; Bultynck et al., 1998, p. 58, pl. 2, figs. 5? and 6, pl. 3, figs. 1, 2?, 3–7, Ovnatanova et al., 1999b, pl. 1, fig. 25; Gereke, 2004, pl. 1, figs. 2 and 3; Klapper, 2007, text-figs. 3.1–3.6.

Palmatolepis kireevae Ovnatanova: Norris et al., 1992, pp. 74–75, pl. 12, figs. 10 and 11.

Holotype. SUI, no. SUI 9958, Amana beds of State Highway 220 near Middle Amana, Iowa, CoIowa, Layer 7 (Müller and Müller, 1957, pl. 140, fig. 4).

Diagnosis. Pa element: platform subtriangular; posterior end slightly pointed; lobe well developed, narrow, rounded triangular, located anteriorly to azygous node, and bordered by two deep sinuses. Platform margin behind posterior sinus strongly convex. Median ridge S-shaped and usually terminating short of reaching posterior end of the platform. Azygous node large. Free blade medium-sized, one-sixth of platform length. Its denticles gradually descending to anterior ridge of platform. Upper surface uniformly covered with small nodes.

Comparison. This species differs from *Palmatolepis kireevae* Ovnatanova in the rounded triangular lobe, the deep sinuses bordering the lobe, and the strongly convex platform margin behind the posterior sinus. The upper surface of the platform is uniformly covered with small nodes, while the platform of *Palmatolepis kireevae* is finely shagreened and bears widely spaced nodes.

Remarks. Unfortunately, the composition of *Palmatolepis hassi* was recently considerably widened, in particular, by the authors of the conodont zonation Ziegler and Sandberg (1990); this strongly embarrassed and sometimes made impossible the use of their scale for a number of levels. As follows from the above synonymy, we accept *Palmatolepis hassi* in the narrow sense. For instance, the species figured by Ziegler and

Sandberg as *Palmatolepis hassi* (1990, pl. 2, figs. 3, 6, 8, pl. 12, figs. 10, 11) are at most *Palmatolepis hassi* sensu lato rather than true *hassi*.

In the collections from the Timan–Pechora Province, *Palmatolepis hassi* Müller et Müller sensu stricto is abundant beginning from the level of the Lyaiol' Formation, which corresponds to the Early *rhenana* Zone. The older representatives, which were earlier referred to this species, are more likely *Palmatolepis hassi* sensu lato.

Occurrence. Frasnian Stage; Poland: Wietrznia section, Late Frasnian; France, Montagne Noire; North America, Iowa, Independence Formation; western Australia, Canning Basin, lower part of Zone 13 of the composite scale of Klapper; Volga–Ural Province, Mendym and Askyn regional stages; southern Timan, Lyaiol' Formation, units 1–4.

Material. Volga–Ural Province: Udmurtia, Krasnogor'e 91, interval 2005–2008 m, Mendym Regional Stage; Tatarstan, Severnyi Kupol 71, interval 1651–1654 m, Mendym Regional Stage, samples 63–65, interval 1649–1651 m, sample 57, interval 1642–1646 m, Askyn Regional Stage; Prikazanskaya 166, sample 48, 1567 m, samples 41 and 43, interval 1559–1563 m, Mendym Regional Stage; Prikazanskaya 120, samples 120 and 127, interval 1630–1633 m, Mendym Regional Stage; Severnyi Kupol 220, interval 1589–1593 m, Mendym Regional Stage. Central regions of the Timan–Pechora Province: Mar'el' 1, borehole 1, interval 2595–2601 m, Lyaiol' Formation, unit 2. Southern Timan: outcrops 1905, 1359, 1360, and 1908 on the Lyaiol' River, Lyaiol' Formation, units 1–4; outcrops 732, 735, 8, and 9 on the Vezha-Vozh River, Lyaiol' Formation, units 1–4; borehole no. 2068, depth of 46 m, Lyaiol' Formation, unit 2; borehole no. 2023, depth of 149 m, Lyaiol' Formation, unit 3.

Palmatolepis jamieae Ziegler et Sansdberg, 1990

Plate 10, figs. 16–18; Plate 11, figs. 1–4, 5? 6, 7?, 8, and 9; Plate 14, fig. 10

Palmatolepis jamieae: Ziegler and Sandberg, 1990, pp. 50–51, pl. 6, figs. 1–3, 9, and 10 (only); Helsen and Bultynck, 1992, pl. 3, fig. 6 and 7?; Ji et Ziegler, 1993, pl. 27, figs. 1–3; Matyja, 1993, pl. 21, fig. 7 (only); Ovnatanova et al., 1999b, pl. 2, fig. 13; Galushin and Kononova, 2004, figs. 8 and 5; Klapper, 2007, text-figs. 4.5–4.9.

Kielcelepis? (or *Lagovilepes*) *jamieae*: Dzik, 2002, P_1 elements, figs. 34B and 34D.

Holotype. NS, no. SMF 38 708, sample 84-GER-1, Steinbruch Schmidt section, Germany; Early *rhenana* Zone (Ziegler and Sandberg, 1990, pl. 6, fig. 1).

Diagnosis. Pa element: platform from slightly to strongly trapezoid, with anterior part (from anterior end to azygous node) considerably shorter than posterior part; posterior end rounded or roundly pointed; lobe short, laterally directed, located in line with, or slightly anteriorly to, azygous node, and bordered by anterior and posterior sinuses. Platform margin behind posterior sinus convex. Median ridge sigmoidal and denticulated. Denticles high. Azygous node well developed; posterior ridge behind it consisting of chain of several nodes gradually increasing in size posteriorly. Posterior ridge terminating short of reaching the posterior end of platform. Free blade short, with one or two high nodes, one-fifth to one-seventh of platform length. Ornamentation consisting of nodes; in young specimens, nodes usually located near platform margin; in adult specimens, they uniformly scattered over platform surface.

Comparison. This species differs from *Palmatolepis foliacea* Youngquist, 1945 in the trapezoid platform and the well developed lobe with two sinuses.

Remarks. On the Russian Platform, this species has not been recorded lower than the Late *rhenana* Zone and, thus, it is difficult to recognize the *jamieae* Zone in the east of the platform.

Occurrence. Frasnian Stage. Germany, Early *rhenana* Zone; Belgium, *jamieae*?–Early *rhenana* Zones; Poland, Late *rhenana* Zone; southern Timan, Lyaiol' Formation, unit 4; Volga–Ural Province, Askyn Regional Stage.

Material. Volga–Ural Province: Tatarstan, Melekess 1, interval 2041–2048 m, Askyn Regional Stage; Severnyi Kupol 71, samples 63, 59, 57, and 53, interval 1642–1649 m, Askyn Regional Stage. Southern Timan: outcrops 1359, 1360, and 1908 on the Lyaiol' River, Lyaiol' Formation, unit 4; outcrops 9 and 10 on the Vezha-Vozh River, Lyaiol' Formation, unit 4; borehole no. 2023, depth of 125 m, Lyaiol' Formation, unit 4.

Palmatolepis juntianensis Han, 1987

Plate 12, figs. 13–17

Palmatolepis juntianensis sp. nov.: Han, 1987, p. 186, pl. 1, figs. 15 and 16; Ziegler and Sandberg, 1990, p. 52, pl. 14, figs. 6 and 7; Kuzmin and Melnikova, 1991, pl. 1, figs. 7 and 8; Ji and Ziegler, 1993, pl. 26, figs. 5–11; Sandberg et al., 1994, pl. 2, fig. 5; Kuzmin et al., 1998, text-fig. 4, fig. 4; Klapper et al., 2004, p. 378, text-figs. 6.1–6.3; Abramova and Artyushkova, 2004, text-fig. 10a; Dong and Wang, 2006, pl. 21, fig. 15, pl. 24, fig. 15; Pazukhin et al., 2007, pl. 1, fig. 22.

Palmatolepis coronata juntianensis: Ji, 1989, pl. 1, figs. 18–20.

Holotype. Institute of Geology, Chinese Academy of Geological Sciences, no. 39448; southern China, Maanschan section, bottom of the Rongxian Formation (Frasnian Stage, upper part of the *gigas* Zone). Published by Han (1987, pl. 1, fig. 15.)

Diagnosis. Pa element; platform small, triangular, and flattened; its anterior part from anterior end to azygous node three or four times as long as posterior part. Lobe triangular, located in posterior part of platform at level of azygous node, and bordered only by anterior sinus. Posterior end of platform obtuse. Median ridge straight and terminating short of posterior end of platform. Azygous node large and somewhat displaced laterally from median ridge. Posterior ridge short, consisting of one or two nodes, or absent. Free blade one-fifth or one-sixth of platform length. Platform surface smooth or finely shagreened. Margins sometimes raised and covered with widely spaced nodes.

Comparison. This species differs from *Palmatolepis foliacea* Youngquist, 1945 in the triangular plat-

form, well pronounced lobe in the posterior part of the platform, and the strongly elongated anterior part of the platform.

Remarks. Transitional forms between *Palmatolepis jamieae* and *Pa. juntianensis* have been recorded.

Occurrence. Frasnian Stage. North America: Nevada, *linguiformis* Zone, New Albany Shale, Selmier unit; Indiana; southern China, Xiangtian Formation, Upper *gigas* Zone. Russia: southern Timan, Lyaiol' Formation, unit 4; Volga–Ural Province, Askyn Regional Stage; southern Ural Mountains, Askyn Regional Stage.

Material. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, samples 59 and 53, interval 1642–1649 m, Askyn Regional Stage; Severnyi Kupol 106, interval 1551–1547 m, Askyn Regional Stage; Severnyi Kupol 142, interval 1614–1618 m, Askyn Regional Stage. Southern Timan: outcrops 1359, 1360, and 1908 on the Lyaiol' River, Lyaiol' Formation, unit 4; outcrop 10 on the Vezha-Vozh River, Lyaiol' Formation, unit 4. Southern Ural Mountains, Sikaza River, outcrop 2, sample 2/2 (collected by L.I. Kononova), Askyn Regional Stage.

Palmatolepis kaledai Ovnatanova et Kononova sp. nov.

Plate 16, figs. 7–12

Etymology. In memory of the famous lithologist, Professor Gleb Aleksandrovich Kaleda.

Holotype. PIN, no. 5255/88; southern Timan, Vezha-Vozh River, outcrop 10, bed 3, sample 3a; Frasnian Stage, Lyaiol' Formation, unit 4 (Pl. 16, fig. 7).

Diagnosis. Pa element: platform flattened and subtriangular; lobe weakly developed, rounded, triangular, and lacking sinuses. Anterior inner margin of platform slightly concave and posterior margin slightly convex. Posterior end from slightly pointed to rounded. Median ridge S-shaped. Posterior ridge with one small node. Azygous node large and highly conical. Free blade half or one-third of platform length. Platform surface smooth and finely shagreened.

Comparison. This species differs from *Palmatolepis subminuta* Branson et Mehl, 1934 in the rounded triangular lobe and S-shaped ridge. It differs from *Pa. lyaiolensis* Khrustcheva et Kuzmin, 1996 in the subtriangular outline and the longer free blade.

Occurrence. Frasnian Stage, Lyaiol' Formation, unit 4.

Material. Five specimens from sample 3 and one specimen from sample 7 of outcrop 10, Vezha-Vozh River; southern Timan, Frasnian Stage, Lyaiol' Formation, unit 4.

Palmatolepis keyserlingi Kuzmin, 1998

Plate 1, figs. 9–15

Palmatolepis transitans: Vandelaer et al., 1989, p. 332, pl. 3, fig. 2.

Palmatolepis keyserlingi: Kuzmin, 1998, pp. 74–75, pl. 8, figs. 2–5; Ovnatanova et al., 1999b, pl. 1, figs. 17 and 18.

Holotype. PIN, no. 4551/102; Ukhta Region, Chut' River, outcrop 7; Frasnian Stage, Domanik Formation, lower unit, sample D-912 (Kuzmin, 1998, pl. 8, fig. 2).

Diagnosis. Pa element: platform elongated rhombic, with weakly developed rounded lobe bordered by hardly visible sinuses; sinuses often absent. Posterior end pointed and arched downwards. Median ridge straight or slightly sigmoid, reaching posterior end of platform. Azygous node well developed and located near center of platform. Free blade one-fourth of platform length. Lobe located at level of azygous node or anterior to it. Platform uniformly covered with small nodes.

Comparison. This species differs from *Palmatolepis transitans* in the elongated rhombic platform, slightly curved median ridge, and the longer free blade.

Remarks. Specimens with poorly pronounced sinuses bordering the lobe were also found.

Occurrence. Southern Timan, Frasnian Stage, Domanik Formation, lower unit.

Material. Southern Timan, Chut' River, outcrop 1, Domanik Formation, unit 1.

Palmatolepis kireevae Ovnatanova, 1976

Plate 4, fig. 16; Plate 5, figs. 6–11; Plate 14, fig. 6

Palmatolepis kireevae: Ovnatanova, 1976, p. 111, pl. 9, fig. 5; Barskov et al., 1987, pl. 11, fig. 1 (reillustration of the holotype); Klapper, 1988, p. 462, pl. 2, figs. 2 and 6; Klapper et al., 1996, p. 145, text-figs. 10.6–10.8; Ovnatanova et al., 1999b, pl. 2, fig. 9; Klapper, 2007, text-figs. 4.2–4.4.

?Palmatolepis hassi: Ovnatanova in Gubareva et al., 1988, pl. 1, figs. 31–33, 36?.

Palmatolepis hassi: Barskov et al., 1987, p. 34, pl. 7, figs. 8–12, 19 (only); Ji and Ziegler, 1993, pl. 28, figs.11 and 12.

Kielcelepis? (or *Lagovilepes*) *jamieae*: Dzik, 2002, P_1 element, figs. 34A, 34 K, and 34L.

Holotype. VNIGNI, no. 40/63b; Udmurtia, village of Krasnogor'e, borehole no. 91, interval 2010.5–2013.5 m; Frasnian Stage, lower part of the Mendym Regional Stage (Ovnatanova, 1976, pl. 9, fig. 5).

Diagnosis. Pa element: platform subtriangular, with slightly pointed and arched downwards posterior end. Lobe triangular, with poorly developed sinuses, located at level of, or anterior to, azygous node. Median ridge S-shaped and usually terminating short of reaching posterior end of platform. Posterior ridge thin, with from two to six small nodes. Azygous node large. Free blade one-fourth of platform length. Ornamentation consisting of small and widely spaced nodes on shagreened platform surface.

Comparison. This species differs from *Palmatolepis hassi* in the triangular lobe with poorly developed sinuses and shagreened platform surface bearing irregularly arranged nodes.

Remarks. The synonymy of *Palmatolepis kireevae* (figured in Klapper et al., 1996, p. 145, text-figs. 10.6–10.8, 10.6–10.8) with *Palmatolepis hassi*,

proposed by Ziegler and Sandberg (2000), appears to be unjustified. According to data on the ontogeny of a number of species, derived from the collections examined, the main features of a species appear at the initial developmental stage. The validity of these species is based primarily on the different shape of the platform. *Palmatolepis hassi* has a rounded lobe bordered by two deep sinuses and a convexity behind the lobe, while *Palmatolepis kireevae* has a triangular platform, with an almost straight margin from the lobe end to the posterior end of the platform. These features are present at the early developmental stages.

Occurrence. Frasnian Stage; France, Coumiac quarry. Volga–Ural Province: Domanik, Mendym, and Askyn regional stages; southern Timan, Domanik Formation, units 2? and 3, Lyaiol' Formation, units 1–4.

Material. Volga–Ural Province: Tatarstan, Melekess 1, sample 68, interval 2085–2089 m, Domanik Regional Stage, samples 69 and 70, interval 2041–2053 m, Askyn Regional Stage; Prikazanskaya 120, interval 1645–1638 m, upper part of the Domanik Regional Stage, interval 1630–1633 m, Mendym Regional Stage; Prikazanskaya 138, interval 1614–1618 m, Mendym Regional Stage; Severnyi Kupol 71, samples 92, 79, and 76, interval 1662–1697 m, Mendym Regional Stage, samples 59–64, interval 1646–1651 m, Askyn Regional Stage; Severnyi Kupol 166, sample 54, interval 1571–1575 m, Domanik Regional Stage, samples 43 and 42, interval 1559–1563 m, Mendym Regional Stage; Severnyi Kupol 220, interval 1581.1–1589 m, Askyn Regional Stage; Prikazanskaya 115, interval 1647.3–1649.7 m, Mendym Regional Stage; Prikazanskaya 120, interval 1645–1650 m, Domanik Regional Stage, interval 1630–1633 m, Mendym Regional Stage. Southern Timan: outcrop 1904 on the Lyaiol' River, Domanik Formation, unit 3, outcrops 1905, 1354, 1355, 1906, 1359, and 1360 on the Lyaiol' River, Lyaiol' Formation, units 1–4; outcrops 732, 734, 735, and 8–10 on the Vezha-Vozh River, Lyaiol' Formation, units 1–4; borehole no. 2023, depth of 148 and 177 m, Lyaiol' Formation, units 2 and 3.

Palmatolepis kuschnarevae Ovnatanova et Kuzmin in Menner et al., 1992

Plate 6, figs. 7 and 8

Palmatolepis sp. B: Ovnatanova and Kuzmin, 1991, pl. 3, figs. 10 and 11.

Palmatolepis kuschnarevae: Ovnatanova and Kuzmin in Menner et al., 1992, pp. 78–79, pl. 4, fig. 1.

Holotype. VNIGNI, no. OK-1048, Komi Republic, Ukhta Region, Domanik River, outcrop 7, sample 5; Frasnian Stage, Domanik Formation, upper unit (Ovnatanova and Kuzmin in Menner et al., 1992, text-fig. 4, fig. 1).

Diagnosis. Pa element: platform irregularly lanceolate; posterior part of platform elongated; posterior end lowered and rounded arched downwards; lobe short, triangular, directed laterally, located in front of azygous node. Median ridge slightly sigmoidal, almost straight. Azygous node well developed. Posterior ridge thin, consisting of many small nodes fused at base and decreasing in size posteriorly. Free blade one-fourth or one-fifth of platform length. Ornamentation consisting of irregularly arranged nodes on upper surface of platform; larger nodes located along outer margin of platform near its anterior end.

Comparison. This species differs from *Palmatolepis maximovae* in the lanceolate platform and its elongated posterior part.

Occurrence. Frasnian Stage, southern Timan, Domanik Formation, units 2 and 3.

Material. Southern Timan, Shudayag, upper part of outcrop 1, outcrops 12 and 13; Domanik Formation, units 2 and 3; borehole no. 3B, depth of 85 m, Domanik Formation, unit 2.

Palmatolepis ljaschenkoae Ovnatanova, 1976

Plate 5, figs. 12–17

Palmatolepis ljaschenkoae: Ovnatanova, 1976, pp. 111–112, pl. 9, fig. 6; Barskov et al., 1987, p. 25, pl. 4, figs. 10, 11, 16, and 17 (only); Menner et al., 1992, p. 81, pl. 4, fig. 2; Klapper and Foster, 1993, pp. 8 and 12, figs. 8.5 and 8.7 (only); Ovnatanova et al., 1999b, pl. 2, figs. 3 and 4; Galushin and Kononova, 2004, text-fig. 8, figs. 1 and 2?; Over, 2007, pl. 16, figs. 19 and 21.

Mesotaxis simpla: Dzik, 2002, P_1 elements, figs. 32N and 32O (only).

Holotype. VNIGNI, no. 40/65, southern Timan, Vezha-Vozh River, 15 km from the mouth; Frasnian Stage, bottom of the Lyaiol' Regional Stage, *Manticoceras intumescens* Zone (Ovnatanova, 1976, pl. 9, fig. 6).

Diagnosis. Pa element: platform elongated, subtriangular, posterior end elongated ovate and slightly pointed; lobe rounded, small, located in front of azygous node, anteriorly directed, and bordered by well pronounced shallow anterior sinus and hardly visible (or absent) posterior sinus. Median ridge slightly sigmoidal and usually reaching posterior end of platform. Azygous node well developed and large. Posterior ridge with from three to seven nodes, gradually decreasing in size posteriorly. Free blade one-fourth or one-sixth of platform length. Ornamentation: most of platform surface shagreened. Small nodes arranged along platform margins and forming denticulated margin in anterior part.

Comparison. This species differs from *Pa. proversa* in the small lobe with shallow sinus and the poorly developed ornamentation of nodes.

Occurrence. Frasnian Stage; Poland, France (Montagne Noire), Canada (Alberta), Australia (Canning Basin). Southern Timan, Domanik Formation, units 2 and 3, Lyaiol' Formation, units 1–3; Volga–Ural Province, upper part of the Domanik, Mendym, and bottom of the Askyn regional stages.

Material. Volga–Ural Province: Tatarstan, Prikazanskaya 120, interval 1627.8–1624.8 m, Mendym Regional Stage, interval 1604–1610 m, bottom of the Askyn Regional Stage; Melekess 1, interval 2048–2053 m,

Askyn Regional Stage; Severnyi Kupol 71, sample 92, interval 1691–1697 m, samples 76 and 66, interval 1651–1666 m, Mendym Regional Stage; Severnyi Kupol 166, samples 47 and 48, interval 1563–1567 m, Mendym Regional Stage. Southern Timan: outcrop 5, Bogatskogo quarry, Domanik Formation, unit 2; Shudayag outcrop 12, Domanik Formation, unit 2, outcrop 13, Domanik Formation, unit 3; outcrops 731–735 and outcrop 8 on the Vezha-Vozh River, Lyaiol' Formation, units 1 and 2; outcrops 1354, 1355, and 1906 on the Lyaiol' River, Lyaiol' Formation, units 1 and 2, borehole no. 2068, depth of 36 m, Lyaiol' Formation, unit 2, depth of 20 m, Lyaiol' Formation, unit 3, borehole no. 2023, depth of 184 m, Lyaiol' Formation, unit 2.

Palmatolepis linguiformis Müller, 1956

Plate 12, figs. 9–12

Palmatolepis linguiformis: Müller, 1956, pp. 24–25, pl. 7, figs. 1–7; Szulczewski, 1971, p. 35, pl. 12, fig. 9, *Catalogue*…, 1973, p. 283, pl. 3, figs. 7 and 8; Khalymbadzha and Tchernyschova, 1978, p. 26, pl. 5, fig. 6; Barskov et al., 1987, p. 34, pl. 6, figs. 24–30; Han, 1987, pl. 1, fig. 1; Ji, 1989, pl. 1, figs. 12–14; Ziegler and Sandberg, 1990, pp. 59–60, pl. 14, figs. 8–10; Kuzmin and Melnikova, 1991, pl. 1, figs. 16 and 17; Ji and Ziegler, 1993, pl. 25, figs. 9–12; Sandberg et al., 1994, pl. 2, figs. 1–4; Bultynck and Martin, 1995, pl. 9, fig. 11; Kuzmin et al., 1998, text-fig. 4, fig. 1; Bultynck et al., 1998, pp. 58–59, pl. 5, figs. 1 and 2; Galushin and Kononova, 2004, text-fig. 9, fig. 6; Abramova and Artyushkova, 2004, text-figs. 3a and 10e; Klapper et al., 2004., p. 378, fig. 6.11; Gereke, 2004, pl. 1, figs. 8–10; Woroncowa-Marcinowska, 2006, text-figs. 3K and 6H; Klapper, 2007, text-fig. 2.6; Bardashev et al., 2006, pl. 2, figs. 8 and 9; Over, 2007, text-fig. 15.11.

Conditolepis? aff. *linguiformis*: Dzik, 2002, figs. 35B, 35C, and 35H–35J.

Holotype. NS, no. SMF XVI 210; Braunau Kellerwald, sample 82, upper part of the *Manticoceras* Stage (Müller and Müller, 1956, pl. 7, fig. 4).

Diagnosis. Pa element: platform elongated lingulate; anterior part raised; posterior part strongly varying from flattened to slightly elevated; lobe poorly developed or absent. Median ridge strongly arched. Azygous node well developed. Posterior ridge straight, consisting of chain of relatively large nodes, and terminating near the posterior end. Free blade short, one-seventh or one-eighth of platform length. Platform margins joining free blade at the same level. Anterior outer margin of platform strongly convex. Platform smooth or uniformly covered with nodes.

Comparison. This species differs from *Palmatolepis ederi* Ziegler et Sandberg, 1990 in the strongly curved median ridge in front of the azygous node, the short free blade, and the convex outer margin in the anterior part of the platform.

Remarks. This species is very rare in the area studied but widespread in the relatively deepwater sections of the southern and polar Ural Mountains (collection of the authors).

Occurrence. Frasnian Stage; Germany, *linguiformis* Zone, Belgium, Matagne Unit of the Neuville section (isolated specimens); North America (Indiana and Nevada), *linguiformis* Zone, New Albany Shale, Selmier unit; southern China, upper part of the Xiangian Formation, *linguiformis* Zone; southern Ural Mountains, Askyn Regional Stage; Volga–Ural Province, upper part of the Askyn Regional Stage, *linguiformis* Zone; Volga Region near Volgograd, Livny Regional Stage; Timan–Pechora Province, Late *rhenana* Zone (southern Khoreiver Depression).

Material. Southern Ural Mountains, Sikaza River, upper part of the Askyn Regional Stage.

Palmatolepis lyaiolensis Khrustcheva et Kuzmin, 1996

Plate 13, figs. 4–11

Palmatolepis lyaiolensis: Khruscheva and Kuzmin, 1996, p. 93, pl. 11, figs. 1 and 2.

Holotype. VNIGRI, no. K-1/1; Komi Republic, Ukhta Region, Lyaiol' River, outcrop 1906, sample 73; Upper Frasnian, Lyaiol' Formation, bituminous unit (Khruscheva and Kuzmin, 1996, pl. 11, fig. 2).

Diagnosis. Pa element: platform rounded triangular, with poorly differentiated lobe located above level of azygous node. Some large specimens with small posterior sinus. Posterior end pointed and arched downwards. Median ridge slightly sigmoidal. Azygous node displaced to posterior part of platform. Posterior ridge short, consisting of two or three nodes. Free blade long, one-third or one-fourth of platform length. Platform shagreened, sometimes, ornamented with small nodes.

Comparison. This species differs from *Palmatolepis hassi* Müller et Müller in the poorly developed lobe lacking well pronounced sinuses. It differs from *Palmatolepis anzhelae* in the poorly differentiated lobe.

Occurrence. Volga–Ural Province, Mendym and Askyn regional stages and their analogues; southern Timan, Lyaiol' Formation, units 2–4.

Material. Volga–Ural Province: Tatarstan, Prikazanskaya 138, sample 38, interval 1614–1618 m, Mendym Regional Stage; Severnyi Kupol 71, sample 66, interval 1651–1654 m, samples 53–60, interval 1642–1649 m, Askyn Regional Stage; southern Timan: outcrops 1906 A and 1908 on the Lyaiol' River, Lyaiol' Formation, units 2–4, outcrop 8 and lower part of outcrop 9 on the Vezha-Vozh River, Lyaiol' Formation, unit 2.

Palmatolepis maximovae Kuzmin, 1998

Plate 6, figs. 1–6

Palmatolepis maximovae: Kuzmin, 1998, p. 75, pl. 7, figs. 11–16.

Holotype. PIN, no. 4551/96; Ukhta Region, Chut' River, outcrop 7, Frasnian Stage, Domanik Formation, lower unit, sample D-914 (Kuzmin, 1998, pl. 7, fig. 12).

Diagnosis. Pa element: platform elongated triangular; posterior end pointed; lobe short, triangular, laterally and slightly anteriorly directed, and located anterior to azygous node. Posterior sinus occasionally present (Pl. 6, figs. 4 and 6). Median ridge from straight to slightly sigmoidal, terminating short of reaching posterior end of platform. Azygous node well developed.

Posterior ridge with from three to five small nodes. Free blade one-fourth or one-fifth of platform length. Outer lateral margin of platform slightly raised. Ornamentation: platform uniformly covered with small nodes, which sometimes fuse, forming interrupted ridges.

Comparison. This species differs from *Palmatolepis rotundilobata* in the small triangular lobe, while the lobe of *Palmatolepis rotundilobata* is wide and rounded. It differs from *Palmatolepis kuschnarevae* Ovnatanova et Kuzmin in the elongated triangular platform and the anteriorly directed lobe.

Occurrence. Southern Timan, Frasnian Stage, Domanik Regional Stage, Domanik Formation, units 1 and 2; Volga–Ural Province, Domanik Regional Stage.

Material. Volga–Ural Province: Orenburg Region, Shuvalovskaya 19, interval 3625–3633 m, Domanik Regional Stage. Southern Timan: Chut' River, outcrop 1, Domanik Formation, unit 1; Lyaiol' River, outcrop 1351, Domanik Formation, unit 2; borehole no. 2056, depth of 102.5 m; Domanik Formation, unit 1; borehole no. 2021, depth of 299 m, nonstratified middle–upper unit of the Domanik Formation.

Palmatolepis menneri Ovnatanova et Kononova sp. nov.

Plate 15, figs. 1–13

Palmatolepis foliacea Youngquist: Barskov et al., 1987, pl. 6, figs. 14–20.

Etymology. In memory of the outstanding geologist Vladimir Vladimirovich Menner.

Holotype. PIN, no. 5255/97; southern Timan, Vezha-Vozh River, outcrop 735, sample 735a; Frasnian Stage, Lyaiol' Formation, unit 2 (Pl. 15, fig. 3).

Diagnosis. Pa element usually small; platform flattened, wide, irregularly rounded, and teardrop-shaped; lobe absent. Maximum width of platform located in its anterior part, above level of azygous node. Anterior end of platform rounded or slightly pointed. Platform margins joining free blade at the same level. Posterior end ranging from pointed to rounded. Inner margin of platform rounded; inner side wider than outer side; outer margin gently arched. Median ridge straight. Azygous node occasionally displaced laterally (towards inner side). Posterior ridge consisting of from one to three nodes, almost equal in size and height to each other and to azygous node. Free blade short, from one-fourth to one-sixth of platform length. Platform smooth, finely shagreened, with small nodes and short, thin transverse ridges along margins.

Comparison. The new species differs from *Palmatolepis foliacea* Youngquist, 1945 in the wider and smoother platform and the maximum width of the platform located in its anterior part higher than the level of the azygous node.

Occurrence. Volga–Ural Province, Mendym Regional Stage; southern Timan, Frasnian Stage, Lyaiol' Formation, unit 2.

Material. Volga–Ural Province: Tatarstan, three specimens from the Severnyi Kupol 71, sample 71, interval 1659–1662 m, Mendym Regional Stage; one specimen from the Prikazanskaya 115, interval 1647–1649 m, Mendym Regional Stage; Southern Timan: two specimens from the Lyaiol' River, outcrop 1355, bed 1, four specimens from outcrop 1906, bed 10, four specimens from outcrop 1906, 1 m below bed 62; six specimens from the Vezha-Vozh River, outcrop 735, three specimens from outcrop 8, sample 4; Lyaiol' Formation, unit 2.

Palmatolepis mucronata Klapper, Kuzmin et Ovnatanova, 1996

Plate 7, fig. 16; Plate 8, figs. 1–11

Palmatolepis mucronata: Klapper et al., 1996, p. 147, text-figs. 7.9–7.13; Ovnatanova et al., 1999b, pl. 2, fig. 6; Klapper, 2007, text-figs. 5.16; Pazukhin et al., 2007, pl. 1, fig. 4.

Holotype. PIN, no. 4551/43; southern Timan, borehole no. 2068, sample 19A, depth of 46 m, Lyaiol' Formation, unit 2 (Klapper et al., 1996, text-fig. 7.10).

Diagnosis. Pa element: platform triangular; posterior end pointed; lobe sharply pointed, triangular, laterally directed, and bordered by anterior and posterior sinuses. Median ridge S-shaped, reaching posterior end of platform. Azygous node well developed. Posterior ridge positioned at obtuse angle to anteriour ridge; consisting of chain of very small, equal sized nodes. Free blade relatively short, one-fifth to one-seventh of platform length. Ornamentation: small nodes uniformly covering platform surface except its anterior part adjacent to median ridge. Thin lateral ridge occasionally present.

Comparison. This species differs from *Palmatolepis amplificata* in the pointed and triangular lobe. It differs from *Palmatolepis brevis* in the triangular platform and pointed posterior end.

Occurrence. Volga–Ural Province, Mendym and Askyn regional stages; southern Timan, Domanik Formation, unit 3; Lyaiol' Formation, units 2–4.

Material. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, sample 112, interval 1680–1685 m, Mendym Regional Stage, samples 63 and 57, interval 1646–1651 m, Askyn Regional Stage; Prikazanskaya 115, sample 87, interval 1647–1649 m, Mendym Regional Stage; Prikazanskaya 120, interval 1604–1610 m, bottom of the Askyn Regional Stage. Southern Timan: Shudayag outcrop 13, Domanik Formation, unit 3, Lyaiol' River, outcrops 1354, 1905, 1906, 1359, and 1908, Lyaiol' Formation, units 1–4; Vezha-Vozh River, outcrops 735, 8, and 9, Lyaiol' Formation, units 2 and 3; borehole no. 2023, depth of 89 m, Lyaiol' Formation, unit 2; borehole no. 2068, depth of 46 m, Lyaiol' Formation, unit 2.

Palmatolepis muelleri Klapper et Foster, 1993

Plate 7, figs. 12–15, Plate 14, fig. 5

Palmatolepis (*Manticolepis*) *wildungensis*: Müller, 1956, p. 22, pl. 5, figs. 21–23 (only).

Palmatolepis mulleri: Klapper and Foster, 1993, pp. 22, 24, text-figs. 16.2–16.9; Klapper et al., 1996, pp. 147–148, text-figs. 8.1 and 8.3; Bultynck et al., 1998, pl. 1, fig. 12; Ovnatanova et al., 1999b, pl. 2, fig. 16.

H o l o t y p e. SUI, no. F 48983, WCB 364-43; sample from the lowest well-developed stromatolite horizon in the Virgin Hills Formation correlative with the Montagne Noire Zone 13; Horse Spring, Canning Basin, Western Australia (Klapper and Foster, 1993, text-fig. 16.8).

D i a g n o s i s. Pa element: platform elongated triangular; posterior end pointed and arched downwards; lobe relatively wide, laterally directed, located almost at level of azygous node, and bordered by well developed sinuses. Platform margin slightly convex behind posterior sinus. Median ridge high, denticulated, slightly S-shaped, and usually reaching posterior end of platform. Azygous node well developed. Nodes of median ridge large near azygous node and equal in size to azygous node. Posterior ridge consisting of chain of nodes gradually decreasing in size. Free blade high, long, one-fourth of platform length. Upper surface uniformly covered with small nodes, which occasionally fused, forming interrupted ridges.

C o m p a r i s o n. This species differs from *Palmatolepis* (Manticolepis) *wildungensis* Müller, 1956 in the longer platform, better pronounced lobe, well developed anterior and posterior sinuses, and pointed posterior end of the platform. It differs from *Palmatolepis hassi* Müller et Müller, 1957 in the elongated triangular platform.

O c c u r r e n c e. Frasnian Stage. Volga–Ural Province, from Mendym to Askyn regional stages; southern Timan, Lyaiol' Formation, units 1–4.

M a t e r i a l. Volga–Ural Province: Tatarstan, Prikazanskaya 138, samples 36 and 38, interval 1614–1618 m, Mendym Regional Stage; Severnyi Kupol 71, samples 112, 79, and 76, interval 1662–1685 m, Mendym Regional Stage, samples 63, 60, and 57, interval 1642–1951 m, Askyn Regional Stage; Orenburg Region, Malakhovskaya 400, interval 3262–3272 m, Mendym Regional Stage. Southern Timan: Lyaiol' River, outcrops 1354, 1906, 1357, 1359, and 1360; Vezha-Vozh River, outcrops 735, 8, 9, and 10, Lyaiol' Formation, units 1–4; borehole no. 2068, depth of 15 m, Lyaiol' Formation, unit 3; borehole no. 2023, sample 17, depth of 129 m, Lyaiol' Formation, unit 4.

Palmatolepis nasuta Müller, 1956

Plate 7, figs. 1–8; Plate 14, fig. 9

Palmatolepis (*Manticolepis*) *nasuta*: Müller, 1956, p. 23, pl. 6, figs. 31–33, 34?, and 35; Bultynck et al., 1998, p. 59, pl. 5, figs. 3, 5–7; Galushin and Kononova, 2004, text-fig. 9, fig. 8.9.

Palmatolepis gigas: Szuczewski, 1971, pl. 2, fig. 1; Kuzmin and Melnikova, 1991, pl. 1, fig. 9.

Palmatolepis rhenana nasuta: Ziegler and Sandberg, 1990, p. 57, pl. 12, figs. 4–9, pl. 15, figs. 4 and 5 (only); Irwin and Orchard, 1991, pl. 3, fig. 1; Sandberg et al., 1992, pl. 2, fig. 7; Ji and Ziegler, 1993, pl. 28, figs. 2, 3, 4?, 5, and 8; Abramova and Artyushkova, 2004, text-fig. 10h.

Palmatolepis rhenana: Kononova, 1969, pl. 1, fig. 2.

Palmatolepis nasuta: Bardaschev et al., 2006, pl. 2, figs. 7, 12.

H o l o t y p e. NS, no. SMF XVI 1956, upper part of the *Manticoceras* Stage (Müller, 1956, pl. 6, figs. 31a–31c).

D i a g n o s i s. Pa element: platform triangular; posterior end pointed and arched downwards; lobe V-shaped, pointed, and triangular; posterior sinus deep. Platform margin behind posterior sinus slightly convex. Median ridge S-shaped and almost reaching posterior end of platform. Azygous node well developed. Posterior ridge consisting of chain of relatively large nodes, decreasing in size posteriorly. Free blade high, gradually passing into platform, one-fourth as long as platform. Ornamentation consisting of nodes uniformly covering platform surface; sometimes, they fused, forming small interrupted ridges. Lateral ridge rarely developed.

C o m p a r i s o n. This species differs from *Palmatolepis rhenana* Bischoff, 1956 in the wider platform. It is most similar to *Palmatolepis boogardi* Klapper et Foster, 1993; according to the authors of the species (Klapper and Foster, 1993, p. 18), *Palmatolepis boogardi* differs from all other representatives of *Palmatolepis* in the roughly triangular configurations of the platform outline and especially in the Pb elements. Unfortunately, we cannot describe Pb elements based on our material; however, we suppose that Pa elements of the two species are quite similar.

O c c u r r e n c e. Upper Devonian, Frasnian Stage, Late *hassi–linguiformis* zones; North America, Canada, China, Australia, Europe: Germany, Poland. Central Asia, Tajikistan; rarely, in the sections of southern Timan and Volga–Ural Province, abundant in the deep-water sections of the southern and polar Ural Mountains (collection of L.I. Kononova). Volga–Ural Province, Mendym–Askyn regional stages; southern Timan, Lyaiol' Formation, units 2–4.

M a t e r i a l. Southern Ural Mountains, Sikaza River, outcrop 1, Mendym Regional Stage, outcrop 2, Askyn Regional Stage. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, samples 57–60, interval 1642–1649 m, Askyn Regional Stage; Orenburg Region, Kolganskaya 17, interval 3369–3374 m, Mendym Regional Stage. Southern Timan: Lyaiol' River, outcrops 1359, 1360, and 908, Lyaiol' Formation, unit 4; Vezha-Vozh River, outcrops 8, 9, and 10, Lyaiol' Formation, units 2–4.

Palmatolepis orbicularis Ovnatanova et Kuzmin, 1991

Plate 3, figs. 1–5

Palmatolepis orbicularis: Ovnatanova and Kuzmin, 1991, p. 47, pl. 2, figs. 13–16; Klapper et al., 1996, p. 148, text-figs. 9.15 and 9.16; Ovnatanova et al., 1999b, pl. 1, fig. 19.

H o l o t y p e. VNIGNI, no. OK1035; Ukhta Region, Domanik River, outcrop 7, sample 5; Frasnian Stage, upper part of Domanik Formation, *Ancyrognathus triangularis* Zone (Ovnatanova and Kuzmin, 1991, pl. 2, fig. 15).

D i a g n o s i s. Pa element: platform irregularly rounded; posterior end of platform flattened or slightly arched downwards; lobe rounded and located anterior to azygous node; anterior sinus shallow; posterior sinus absent. Lateral margins of platform raised relative to its middle part. Median ridge slightly S-shaped and reaching posterior end of platform as thin posterior ridge consisting of small and fused at base three, four, or more nodes. Azygous node well developed and larger than nodes of median ridge. Free blade short, one-fifth to one-seventh of platform length. Small nodes covering platform and occasionally fused, forming thin interrupted ridges.

C o m p a r i s o n. This species differs from *Palmatolepis hassi* Müller et Müller, 1957 in the rounded platform and the small rounded lateral lobe lacking posterior sinus. It differs from *Palmatolepis timanensis* Klapper, Kuzmin et Ovnatanova, 1996 in the well developed lobe and small nodes on the upper surface of the platform.

R e m a r k s. In small specimens, small nodes are developed on the outer side of the platform along the anterior lateral margin, while the inner platform surface is smooth. The free blade of small specimens is longer than that of the large specimens. The lobe of large specimens is bordered by sinuses.

Ziegler and Sandberg (2000, p. 339, text-fig. 3) referred species that had previously been interpreted as *Palmatolepis orbicularis* (Klapper et al., 1996, text-figs. 9.15–9.16) to the early morphotype of *Pa. hassi* without any explanations. In the same paper *Palmatolepis timanensis* was also referred to the early morphotype of *Pa. hassi* (text-figs. 9.3–9.4).

O c c u r r e n c e. Southern Timan, Frasnian Stage, middle and upper units of the Domanik Formation, Vetlasyan Formation, Lyaiol' Formation, units 1 and 2; Volga–Ural Region, Mendym Regional Stage; southern China, upper part of the Fuhe Formation (correlative to the Middle *asymmetricus* Zone).

M a t e r i a l. Volga–Ural Province: Tatarstan, borehole no. 115, interval 1647–1649.7 m, Mendym Regional Stage; Severnyi Kupol 71, sample 66, interval 1651–1654 m, Mendym Regional Stage. Southern Timan: Chut' River, upper part of outcrop 1, Domanik River, outcrop 11, Shudayag, outcrop 12, Domanik Formation, unit 2, outcrop 13, Domanik Formation, unit 3, borehole no. 3B, depth of 85 m, Domanik Formation, unit 2, depth of 65 m, Domanik Formation, unit 3; Lyaiol' River, outcrop 1904, bed 14, sample 24, Domanik Formation, unit 3; borehole no. 2023, sample 5, depth of 209 m, Domanik Formation, units 2 and 3, borehole no. 2056, sample 13, depth of 64 m, Domanik Formation, unit 3, outcrop 1351, Domanik Formation, unit 2, outcrop 1903, Domanik Formation, unit 2, outcrop 1904, Domanik Formation, unit 3, borehole no. 2060, depth of 226 m, Vetlasyan Formation; outcrops 1905 and 1357, Lyaiol' Formation, units 1 and 2; Vezha-Vozh River, outcrop 731, Lyaiol' Formation, unit 1.

Palmatolepis orlovi Khruscheva et Kuzmin, 1996

Plate 6, figs. 15–19

Palmatolepis orlovi: Khruscheva and Kuzmin, 1996, p. 91–92, pl. 11, figs. 3–5; Ovnatanova et al., 1999b, pl. 2, fig. 14.

H o l o t y p e. PIN, no. 4551/81; Komi Republic, Ukhta Region, Lyaiol' River, outcrop 1908, sample 1; Upper Frasnian, Lyaiol' Formation, carbonaceous unit (Khruscheva and Kuzmin, 1996, pl. 11, fig. 5).

D i a g n o s i s. Pa element: platform irregularly elongated, ovate, and sigmoidal; posterior end pointed and arched downwards; lobe rounded triangular, short, bordered by shallow anterior and relatively deep posterior sinuses, laterally directed, and located slightly anteriorly to azygous node. Outer lateral margin of platform raised in anterior part. Median ridge sigmoidal and terminating short of reaching posterior end of platform. Azygous node high and conical. Posterior ridge consisting of three to five small nodes, decreasing in size posteriorly. Narrow groove developed on their continuation. Free blade one-fifth or one-sixth of platform length. Ornamentation consisting of small nodes uniformly covering upper surface of platform. Thin and short transverse ridges occasionally present along outer margin.

C o m p a r i s o n. This species differs from *Palmatolepis ljashenkoae* Ovnatanova, 1976 in the well pronounced lobe with deep posterior sinus. It differs from *Palmatolepis nasuta* Müller, 1956 in the shorter lobe and the sigmoidal platform.

O c c u r r e n c e. Volga–Ural Province, Askyn Regional Stage; southern Timan, Lyaiol' Formation, unit 4.

M a t e r i a l. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, samples 64 and 63, interval 1649–1651 m, sample 59, interval 1646–1649, sample 57, 53, and 52, interval 1642–1646 m, Askyn Regional Stage; Prikazanskaya 120, interval 1607–1604 m, Askyn Regional Stage. Southern Timan: Lyaiol' River, outcrops 1359 and 1908, Vezha-Vozh River, outcrops 9 and 10, Lyaiol' Formation, unit 4, borehole no. 2023, depth of 125 m, Lyaiol' Formation, unit 4.

Palmatolepis ormistoni Klapper, Kuzmin et Ovnatanova, 1996

Plate 6, fig. 9–14

Palmatolepis ormistoni: Klapper et al., 1996, p. 148, pl. 10, figs. 1–5.

Palmatolepis subrecta Miller et Youngquist → *Palmatolepis ljaschenkoae* Ovnatanova: Ovnatanova in Gubareva et al., 1988, pl. 1, fig. 29.

H o l o t y p e. PIN, no. 4551/69, southern Timan, borehole no. 2068, sample 19A, depth of 46 m; Frasnian Stage, Lyaiol' Formation, unit 2 (Klapper et al., 1996, pl. 10, fig. 4).

D i a g n o s i s. Pa element: platform more or less subtriangular; posterior end pointed; lobe rounded triangular, located anterior to azygous node, laterally and slightly anteriorly directed, and bordered by poorly developed anterior and posterior sinuses. Platform mar-

gin usually slightly widened behind posterior sinus. Median ridge denticulated and slightly sigmoidal. Azygous node well developed. Posterior ridge with from two to seven small nodes, decreasing in size posteriorly. Free blade high, one-third or one-fourth of platform length. Ornamentation: central part of platform shagreen; small nodes developed along platform margins.

Comparison. This species differs from *Palmatolepis maximovae* Kuzmin, 1998 in the shagreened surface of the central part of the platform. It differs from *Palmatolepis hassi* Müller et Müller, 1957 in the poorly developed anterior and posterior sinuses and finer ornamentation of the upper surface of the platform.

Occurrence. Volga–Ural Province, upper part of the Domanik–bottom of the Askyn regional stages; southern Timan, Domanik Formation, unit 3–Lyaiol' Formation, bottom of unit 4.

Material. Volga–Ural Province: Udmurtia, Krasnogor'e 91, interval 2010–2013 m, Mendym Regional Stage; Tatarstan, Prikazanskaya 138, samples 87, 83, and 82, interval 1651–1663 m, Domanik Regional Stage, Prikazanskaya 115, interval 1653.5–1649.7 m, Domanik Regional Stage, interval 1649.7–1647.3 m, Mendym Regional Stage, Prikazanskaya 120, sample 135, interval 1624.8–1627 m, Mendym Regional Stage; Severnyi Kupol 71, sample 76, interval 1662–1666 m, Mendym Regional Stage, sample 66, interval 1651–1654 m, Mendym Regional Stage, samples 62–64, interval 1649–1651 m and samples 59 and 53, interval 1642–1649 m, Askyn Regional Stage, borehole no. 166, interval 1563–1567 m, Mendym Regional Stage, interval 1559–1563 m, Mendym Regional Stage; Orenburg Region, Shuvalovskaya 19, interval 3625–3633 m, Domanik Regional Stage, interval 3610–3617 m, bottom of the Kolgany Member. Southern Timan: Lyaiol' River, outcrop 1353, uppermost Domanik Formation, outcrops 1906 and 1360, Lyaiol' Formation, units 2–4; Vezha-Vozh River, outcrops 732, 735, and 8, Lyaiol' Formation, units 1 and 2; borehole no. 2068, depth of 46 m, Lyaiol' Formation unit 1; town of Sirachoi, outcrop 3A, Lower Sirachoi Regional Substage (solitary).

Palmatolepis plana Ziegler and Sandberg, 1990

Plate 2, 15–17, 18?, 19?, 20, and 21; Plate 3, fig. 25; Plate 4, figs. 2–4, 8, and 9

Palmatolepis plana: Ziegler and Sandberg, 1990; p. 46, pl. 3, figs. 1?, 4–6, 8–10; Sandberg et al., 1992, pl. 2, fig. 10, pl. 3, fig. 10; Ji and Ziegler, 1993, pl. 26, fig. 4, pl. 31, figs. 2–7; Pisazowska et al., 2006, text-fig. 14G; Klapper, 2007, text-figs. 8.3 and 8.4.

Palmatolepis domanicensis: Klapper, 1988, pl. 1, figs. 1 and 2; Klapper and Foster, 1993, pp. 5, 8, text-figs.4.1–4.8, 6.10–6.13, 7.15 (only).

Holotype. NS, no. SMF 38 685; Belgium, sample 85-BEL-115 in a section of backmound beds on the northern side of the hill called Tiene du Lion, northeast of the Lion quarry (Ziegler and Sandberg, 1990, pl. 3, fig. 9).

Diagnosis. Pa element: platform relatively wide; lobe rounded, located anteriorly to azygous node, and contoured by well pronounced anterior sinus; posterior sinus absent. Platform margin between lobe and posterior end straight. Posterior end of platform pointed. Median ridge slightly S-shaped and terminating short of reaching posterior end of platform. Azygous node well developed. Posterior ridge consisting of two or three small nodes. Free blade short, one-seventh of platform length. Rostrum weakly developed and short. Troughs short and poorly pronounced. Upper surface uniformly covered with small nodes; sometimes, they fused, forming small interrupted ridges.

Comparison. This species differs from *Palmatolepis domanicensis* Ovnatanova, 1976 in the relatively wide platform with a rounded lobe, pronounced anterior sinus, and slightly S-shaped ridge, while *Palmatolepis domanicensis* has pear-shaped platform with an extended posterior end and poorly pronounced sinus. It differs from *Palmatolepis bohemica* Klapper et Foster, 1993 in the slightly curved median ridge, which terminates short of reaching the posterior end of the platform, in the short posterior ridge consisting of two or three nodes, while, in *Pa. bohemica*, the posterior ridge consists of a chain of small nodes and reaches the posterior end. It differs from *Palmatolepis spinata* in the elongated platform and the small nodes uniformly covering the platform.

Occurrence. Frasnian Stage, Germany, Martenberg section, Early *hassi*–Late *rhenana* Zones (Ziegler et Sandberg, 1990). According to Klapper and Becker (1999), *Palmatolepis plana* occurs in the Martenberg section only higher the Upper *hassi* Zone correlative to Zone 10 of the composite scale. In the la Serre section of Montagne Noire, this species was found in the Serre Formation in 6.32–6.38 m from the section base along with *Palmatolepis kireevae* and *Pa. proversa* (Zone 10 of the composite scale); it was also found in Canada (Mountains of Alberta). In southern China (Lali section), it is known from the upper part of the Laoyefen Formation. Southern Timan, Domanik Formation, unit 2; Lyaiol' Formation, units 1 and 2; Volga–Ural Province, Mendym Regional Stage.

Material. Volga–Ural Province: Udmurtia, Krasnogor'e 91, interval 1997–2002 m, Mendym Regional Stage; Tatarstan, Severnyi Kupol 71, sample 112, interval 1680–1685 m, Mendym Regional Stage, Severnyi Kupol 166, interval 1563–1567 m, Mendym Regional Stage. Southern Timan: Domanik River, outcrop 11, Domanik Formation; Vezha-Vozh River, outcrop 8, Lyaiol' Formation, unit 2; Lyaiol' River, outcrops 1354, 1355, 1905, 1906, and 1906 A, Lyaiol' Formation, units 1 and 2; borehole no. 2060, depth of 224.9 m, Vetlasyan Formation, borehole no. 2068, depth of 36 m, Lyaiol' Formation, unit 2, borehole no. 2023, depth of 177 m, Lyaiol' Formation, unit 2.

Palmatolepis proversa Ziegler, 1958

Plate 9, fig. 16; Plate 10, figs. 1–8

Palmatolepis proversa: Ziegler, 1958, pp. 62–63, pl. 3, figs. 11 and 12, pl. 4, figs. 2, 7, 9–14 (only); Klapper in *Catalogue*…, 1973,

p. 289, pl. *Palmatolepis* 2, fig. 5 (reillustration of the holotype); Khalymbadzha and Tchernyschova, 1978, p. 30, pl. 4, figs. 7 and 8; Barskov et al., 1987, pp. 38, 39, pl. 7, figs. 1–6; Khalymbadzha et al., 1987, pl. 4, fig. 6; Ji et al., 1986, pl. 2, fig. 4; Ji, 1988, pl. 2, figs. 1, 2, and 4; Klapper and Lane, 1988, pl. 1, figs. 3 and 4; Ziegler and Sandberg, 1990, p. 46, pl. 4, figs. 1, 2, 5, and 6; Orchard and McCracken, 1991, pl. 2, fig. 14; Ji and Ziegler, 1993, pl. 29, figs. 7–10, and 12 (only); Klapper and Foster,1993, p. 12, text-figs. 8.1 and 8.2 (only), text-figs. 9.1–9.8; Matyja, 1993, pl. 20, fig. 8; Bultynck et al., 1998, pl. 1, fig. 14; Ji et al., 1986, pl. 2, fig. 4; Pazukhin et al., 2007, pl. 1, fig. 2.

Palmatolepis aff. *proversa*: Irwin and Orchard, 1991, pl. 2, fig. 14.

Mesotaxis? proversa: Dzik, 2002, P_1 elements, fig. 32A.

Holotype. Departament of Geosciences, Philipps University, Marburg, Germany, no. Zi 1958/43; Martenberg section near Adorf, sample 7, purple goniatite-bearing limestone of Adorfstufe, *Manticoceras cordatum* Zone, bottom of the Upper Devonian, upper part of the *Pharciceras lunulicosta* Zone in the *Manticoceras cordatum* Zone (Ziegler, 1958, pl. 3, figs. 11a, 11c); reillustrated by G. Klapper (*Catalogue*…, 1973, pl. *Palmatolepis*-1, fig. 5).

Diagnosis. Pa element: lobe large, well developed, and anteriorly directed; anterior sinus deep and usually narrow; posterior end of platform pointed, sometimes, extended, and arched downwards. Median ridge slightly S-shaped and usually terminating short of reaching posterior end. Azygous node well developed. Posterior ridge consisting of from two to six nodes; nodes rarely absent. Free blade from one-fourth to one-sixth of platform length. Rostral ridges high, strengthened with nodes, and separated from median ridge by deep and long troughs. Ornamentation: small nodes uniformly or irregularly covering upper surface of platform; occasionally, largest nodes accumulated along margin or in rostral part of platform. Some nodes fused, forming small interrupted ridges.

Comparison. This species differs from *Palmatolepis ljashenkoae* Ovnatanova in the anteriorly directed lobe, the deep anterior sinus, the presence of rostrum, and the well developed ornamentation of nodes. The distinctions from *Palmatolepis barba* Ziegler are considered in the description of the latter.

Occurrence. Cosmopolitan (Northern Hemisphere and Australia), *punctata*–Early *rhenana* zones; Timan–Pechora and Volga–Ural provinces, Domanik and Mendym regional stages and their analogues.

Material. Volga–Ural Province, Prikazanskaya 115, interval 1653.5–1649.7 m, Domanik Regional Stage, interval 1649.7–1647.3 m, Mendym Regional Stage, Prikazanskaya 113, interval 1613–1617 m, Voronezh Regional Stage, Prikazanskaya 120, sample 100, interval 1645–1650 m, Domanik Regional Stage, samples 118, 120, and 135, interval 1624–1633 m, Mendym Regional Stage, Prikazanskaya 121, sample 118, interval 1627–1632 m, Domanik Regional Stage; Severnyi Kupol 71, samples 92 and 112, interval 1680–1697 m; Mendym Regional Stage; Orenburg Region, Shuvalovskaya 6, sample 49, interval 3619–3624 m, Frasnian Stage, Kolgany Member; central Timan–Pechora Province: Mar'el' borehole, interval 2595–2601 m, Lyaiol' Formation, unit 2; southern Timan, Shudayag outcrops 12 and 13, Domanik Formation, units 2 and 3; Lyaiol' River, outcrops 1354, 1905, and 1906, Vezha-Vozh River, outcrops 732 and 735, Lyaiol' Formation, units 1 and 2.

Palmatolepis punctata **(Hinde, 1879)**

Plate 2, figs. 11–14

Polygnathus punctatus: Hinde, 1879, p. 367, pl. 17, fig. 14 (lectotype).

Palmatolepis punctata: Branson and Mehl, 1934, pp. 149 and 151, pl. 11, fig. 6 (reillustration of the lectotype); Glenister and Klapper, 1966, p. 819, pl. 88, figs. 8 and 9; Ziegler, 1973, pp. 291–293, pl. 1, figs. 4 and 5 (fig. 5 is a reillustration of the holotype); Klapper, 1988, pl. 1, figs. 8 and 9; Ovnatanova and Kuzmin, 1991, pl. 3, fig. 1; Ji and Ziegler, 1993, pl. 31, figs. 6, 8, 10, and 11 (only); Klapper and Foster, 1993, p. 15, pl. 5, figs. 4–9; pl. 8, figs. 11 and 12; Kuzmin, 1998, pl. 7, figs. 2 and 3; Belka et al., 1999, pl. 3, figs. 1 and 2; Ovnatanova et al., 1999b, pl. 1, figs. 20, 21, 23, and 24; Bardaschev et al., 2006, pl. 1, fig. 39.

Palmatolepis martenbergensis: Müller, 1956, pp. 19 and 20, pl. 1, figs. 5b and 8 (only).

Mesotaxis punctata: Dzik, 2002, P_1 elements, figs. 31A and 31B.

Lectotype. British Natural History Museum, London, no. 4317; North Evans, New York, Genesse Shale, lower Upper Devonian, upper part of the *Pharciceras lunulicosta* Zone in the *Manticoceras cordatum* Zone, reillustrated by Klapper (*Catalogue*…, 1973, pl. *Palmatolepis*-1, fig. 5).

Diagnosis. Pa element: platform widely subtriangular; lateral lobe rounded, located anterior to azygous node, and bordered by well pronounced anterior sinus and weakly developed posterior sinus; posterior end arched downwards. Median ridge gently sigmoidal and usually terminating short of reaching posterior end of platform. Azygous node well developed and large. Posterior ridge occasionally consisting of three or four nodes. Free blade short, one-fourth as long as platform. Upper surface more or less uniformly covered with nodes.

Comparison. This species differs from *Palmatolepis transitans* in the well developed and bordered by sinuses lateral lobe and in the sigmoidal median ridge.

Occurrence. Frasnian Stage, lower and middle parts of the *Manticoceras* Zone; southern Timan, Ukhta Region, Domanik Formation, units 1–3, and Lyaiol' Formation, units 1 and bottom of unit 2; Volga–Ural and Timan–Pechora provinces, Domanik and Mendym regional stages.

Material. Volga–Ural Province: Tatarstan, Prikazanskaya 138, samples 89, 87, and 82, interval 1651–1665 m, Domanik Regional Stage, Prikazanskaya 120, sample 93, interval 1645–1650 m, Domanik Regional Stage, Prikazanskaya 113, interval 1617–1613 m, Voronezh Regional Stage; Orenburg Region, Shuvalovskaya 4, sample 97, interval 3582–3589 m, Domanik Regional Stage, Shuvalovskaya 6, sample 98, interval 3645–3651 m, Domanik Regional Stage, Shuvalovskaya 17, interval 3605–3616 m, Domanik Regional Stage, Shuvalovskaya 19, sample 64, interval

3625–3655 m, Domanik Regional Stage, sample 99, interval 3610–3617 m, bottom of the Kolgany Member. Southern Timan: Chut' River, outcrops 1, 2, 3, and 6; Domanik River, outcrop 11; Shudayag outcrop 12, Domanik Regional Stage; Lyaiol' River, outcrops 1905 and 1906, Lyaiol' Formation, unit 2.

Palmatolepis rhenana **Bischoff, 1956**

Plate 7, figs. 9–11; Plate 14, figs. 7 and 8

Palmatolepis rhenana: Bischoff, 1956, pp. 129 and 130, pl. 8, figs. 26–28, 30, pl. 10, fig. 7; Ziegler, 1958, pp. 63–64, pl. 4, figs. 15 and 16, pl. 5, fig. 2, 4, 5, 9, and 10, pl. 6, fig. 7, pl. 9, fig. 3 (only); Klapper, 1989, pl. 2, figs. 1 and 13; Klapper and Foster, 1993, p. 24, figs. 16.1, 17.3–17.10; Klapper et al., 1996, p. 148, text-figs. 8.7, 8.10, and 8.13; Kuzmin et al., 1998, text-figs. 4 and 5; Bultynck et al., 1998, pl. 4, fig. 12, pl. 5, fig. 4; Klapper, 2007, text-figs. 5.14 and 5.15.

Palmatolepis (*Manticolepis*) *prominens*: Müller, 1956, pp. 22–23, pl. 5, figs. 26 and 30 (only).

Palmatolepis rhenana rhenana: Ziegler and Sandberg, 1990, pp. 57 and 58, pl. 12, figs. 1–3, pl. 15, figs. 1, 3, 6, and 7?; Gereke, 2004, pl. 1, figs. 5 and 6.

Palmatolepis cf. *rhenana*: Khruscheva and Kuzmin, 1996, pl. 11, fig. 14.

Holotype. Marburg University, 1956/27, Rein Shale Mountains, Steinbruch Bicken section, upper part of Kelwasserkalk limestone (Bischoff, 1956, pl. 8, fig. 27).

Diagnosis. Pa element: platform narrow and more or less elongated triangular; lobe well developed, narrow, pointed, directed laterally or posteriorly, and bordered by well pronounced sinuses. Posterior end narrow, pointed, and arched downwards. Median ridge sigmoidal, with large nodes, reaching posterior end of platform. Near azygous node, nodes of median ridge large and almost as large as azygous node. Posterior ridge composed of chain of large and nodes gradually decreasing in size posteriorly. Free blade high, long. Ornamentation consisting of small nodes uniformly covering platform; sometimes, they fused, forming interrupted ridges. Secondary ridge rarely developed.

Comparison. This species differs from *Palmatolepis nasuta* in the narrow, elongated triangular, and sharply pointed lateral lobe, the narrow and pointed posterior end, and the long free blade.

Occurrence. Frasnian Stage, from the Mendym Regional Stage and its analogues to the top of the Frasnian Stage. The species is rare in the territory under study. In Timan–Pechora Province, it was found in the Tebuk-Vis unit (Frasnian Stage) of the Khoreiver Depression. *Palmatolepis rhenana* mostly occurs in the pelagic facies of the southern and polar Ural Mountains, where it is abundant.

Material. The specimens come mostly from the sections of the southern and polar Ural Mountains (collection of L.I. Kononova).

Palmatolepis rotundilobata **Kuzmin, 1998**

Plate 1, fig. 22; Plate 2, figs. 1 and 2

Palmatolepis rotundilobata: Kuzmin, 1998, p. 75, pl. 7, figs. 8–10.

Holotype. PIN, no. 4551/93; Ukhta Region, Chut' River, outcrop 7; sample D-914; Frasnian Stage, Domanik Formation, lower unit (Kuzmin, 1998, pl. 7, fig. 9).

Diagnosis. Pa element: platform triangular; lobe well developed, large, rounded, bordered by posterior sinus, and located anterior to azygous node; posterior sinus well developed; posterior end of platform pointed and lowered. Outer side of platform slightly raised. Median ridge straight or slightly sigmoidal and terminating short of reaching posterior end of platform. Azygous node well developed and displaced from middle of platform to its posterior end. Posterior ridge consisting of two or three nodes. Narrow grove developed along posterior ridge. Free blade one-fifth as long as platform. Platform uniformly covered with nodes; short transverse ridges occasionally present in its anterior part along outer margin.

Comparison. This species differs from *Palmatolepis triequetra* Kuzmin, 1998 in the rounded lobe with well pronounced posterior sinus.

Occurrence. Southern Timan, Frasnian Stage, Domanik Formation, lower unit.

Material. Southern Timan, Chut' River, outcrop 1; Domanik Formation, unit 1.

Palmatolepis semichatovae **Ovnatanova, 1976**

Plate 13, figs. 19–28

Palmatolepis gigas semichatovae: Ovnatanova, 1976, p. 110, pl. 9, figs. 3a and 3b; Ovnatanova and Aristov, 1985, pl. 7, fig. 3; Barskov et al., 1987, p. 32, pl. 8, figs. 12–16, 18; Aristov, 1988, pl. 7, figs. 20 and 21.

Palmatolepis firmus: Khalymbadzha and Tchernyschova, 1978, pp. 20–21, pl. 4, figs. 9–12.

Palmatolepis gigas: Szulczewki, 1971, pl. 11, fig. 3.

Palmatolepis semichatovae: Klapper and Lane, 1985, pl. 15, figs. 8–10; Klapper and Lane, 1988, pl. 1, figs. 6 and 9; Ziegler and Sandberg, 1990, p. 58, pl. 11, figs. 1 and 2, pl. 13, figs. 3–11; Day, 1990, p. 623, Pa element figs. 11.12, 11.13, and 11.19; Sandberg et al., 1992, pl. 3, figs. 1, 2, and 4; Ovnatanova et al., 1999b, pl. 2, fig. 8; Ovnatanova and Kononova, 1999, text-fig. 3, fig. 29; Galushin and Kononova, 2004, text-fig. 8, figs. 3 and 4; Klapper, 2007, text-fig. 2.9; Pazukhin et al., 2007, pl. 1, fig. 14; Bardaschev et al., 2006, pl. 2, fig. 10.

Holotype. VNIGNI, no. 40/60, Udmurtia, village of Krasnogor'e, borehole no. 91, interval 2010.5–2013.5 m; Frasnian Stage, lower part of the Mendym Regional Stage (Ovnatanova, 1976, pl. 9, figs. 3a and 3b).

Diagnosis. Pa element: platform irregularly rounded; lobe well developed, long, and bordered by anterior and posterior sinuses; posterior end rounded and arched downwards. Median ridge slightly sigmoidal, usually terminating short of reaching posterior end of platform, and consisting of one to five small and sometimes fusing nodes. Free blade from half to quarter as long as platform. Parapet (or parapets) developed in anterior part of platform. Parapet separated from median ridge by narrow and shallow trough terminating at azygous node. Ornamentation: small nodes uniformly or irregularly covering upper surface of platform.

C o m p a r i s o n. This species differs from *Palmatolepis gigas* in the rounded platform with rounded posterior end and in the presence of parapets (rather than the rostrum, as in *Palmatolepis gigas*).

R e m a r k s. *Palmatolepis semichatovae* is highly variable. The posterior end of the platform varies from rounded (Pl. 17, figs. 19–22) to pointed (Pl. 13, figs. 23, 26, 27). Ornamentation also varies from uniformly arranged nodes on the upper surface (Pl. 13, figs. 25, 26, 28) to nodes located only in its anterior part (Pl. 13, figs. 22, 24, 27). Additional ridge occasionally present (Pl. 13, figs. 21–24). The number of parapets varies from one (Pl. 13, figs. 21, 24) to two (Pl. 13, figs. 25, 27). The lobe outline varies from widely rounded (Pl. 13, fig. 24) to trapezoid (Pl. 13, fig. 26).

Palmatolepis semichatovae is widely spread in the shallow-water deposits, also occurs in the deepwater sections. This peculiarity of its distribution was the reason to recommend it as a pretender for determination of the substage boundary of the Frasnian Stage.

O c c u r r e n c e. Germany, United States (Arizona, Iowa, Nevada, Utah, and Montana), Early *rhenana* Zone; France, Luscar Mountain, section 1; Early *rhenana* Zone; Canada, Twin Falls Formation, Frasnian Stage; Poland, Holy Cross Mountains; Russia: Central Russian Platform, Voronezh Regional Stage; Volga–Ural Province, Mendym Regional Stage and the lower part of the Askyn Regional Stage; southern Timan, Lyaiol' Formation, units 2 and 3, shallow water deposits of the Sirachoi Regional Stage and bottom of the Ukhta Formation.

M a t e r i a l. Volga–Ural Province: Tatarstan, Ul'yanovskaya 1, samples 49 and 64, interval 1839–1867 m, samples 68–98, interval 1829–1839 m, Lower Voronezh Regional Stage; Turmysh 1, interval 1565–1570 m, Voronezh Regional Stage; Severnyi Kupol 71, samples 92 and 112, interval 1680–1697 m, Mendym Regional Stage, sample 59, interval 1646–1649 m, Askyn Regional Stage, Severnyi Kupol 166, samples 44–48, interval 1563–1567 m, Mendym Regional Stage; Udmurtia, Krasnogor'e 91, interval 2010–2013 m, Mendym Regional Stage; Orenburg Region, Kolgany 23, interval 3364–3370 m, Kolgany Member; Malakhovskaya 400, interval 3262–3272 m, Mendym Regional Stage. Southern Timan: Lyaiol' River, outcrops 1355, 1906, 1357, and 1358; Vezha-Vozh River, outcrops 735, 8, and 9, Lyaiol' Formation, units 2–bottom of unit 3, borehole no. 2060, depth of 32 m, Upper Sirachoi Regional Substage; Bel'gop 4, depth of 266 m, Upper Sirachoi Regional Substage; Timanskaya 10, interval 354–363 m, Upper Sirachoi Regional Substage, depth of 314–315 m, lower part of the Ukhta Formation.

Palmatolepis spinata Ovnatanova et Kuzmin, 1991

Plate 3, figs. 6–16

Palmatolepis spinatus: Ovnatanova and Kuzmin, 1991, pp. 47 and 49, pl. 3, figs. 4–7; Ovnatanova and Kononova, 1999, text-fig. 3, fig. 22; Ovnatanova et al., 1999b, pl. 2, figs. 1 and 2.

Palmatolepis spinata: Klapper et al., 1996, p. 148, text-fig. 9.13; Klapper, 2007, text-fig. 8.5.

H o l o t y p e. VNIGNI, no. OK-1043; southern Timan, Komi Republic, Ukhta Region, Domanik River, outcrop 6; sample 3; Frasnian Stage, upper part of the Domanik Formation (Ovnatanova and Kuzmin, 1991, pl. 3, fig. 6).

D i a g n o s i s. Pa element: platform short and subtriangular; lateral lobe well developed, located at level of, or slightly anteriorly to, azygous node, and bordered by anterior sinus. Outer lateral margin usually raised and denticulated. Posterior end of platform flattened, triangular, pointed, and arched downwards. Median ridge almost straight. Posterior ridge usually absent, replaced by thin groove or, rarely, one or two small nodes or denticles developed behind azygous node. Azygous node well developed. Free blade short, one-sixth or one-seventh of platform length. Troughs well pronounced and usually wide. Ornamentation consisting of small nodes scattered mostly at platform margins. Nodes elongated and spinous already in small (young) specimens.

C o m p a r i s o n. This species differs from *Palmatolepis punctata* in the lobe located at the level of the azygous node, in the triangular posterior end of the platform, and elongated spinous nodes, which are better developed along the platform margins.

R e m a r k s. The species is highly variable due to the additional secondary ridge consisting of a chain of small nodes directed from the azygous node (or near it) to the lobe margin (Pl. 3, figs. 6, 9, 10). The azygous node of some specimens is almost equal in size to the nodes of the median ridge. Short and slightly asymmetrical rostrum occasionally present.

According to Ziegler and Sandberg (2000, p. 339), *Pa. spinata* Ovnatanova et Kuzmin, 1991 is an early morphotype of *Palmatolepis plana*. Certainly, the two species are similar in platform outline; however, they differ in the straight median ridge of *Pa. spinata* and its platform margins spinous already at the early ontogenetic stages. In addition, they differ in stratigraphic distribution. On the Russian Platform, *Pa. spinata* is only known from the Domanik Regional Stage, i.e., confined to the *punctata* Zone, while, in Germany, *Palmatolepis plana* was registered within the Early *hassi*–Early *rhenana* zones.

O c c u r r e n c e. Frasnian Stage, North America, Western Australia (section west of McPhee Knoll). Central Russian Platform: Semiluki Regional Stage (isolated specimens); southern Timan, Domanik Formation, unit 2; Volga–Ural Province, Domanik Regional Stage (rare).

M a t e r i a l. Volga–Ural Province: Orenburg Region, Shuvalovskaya 1, interval 3618–3627 m, Domanik Regional Stage. Southern Timan: borehole no. 2056, depth of 91 m, Domanik Formation, unit 2, borehole no. 1003, depth of 92 m, borehole no. 3B, depth of 85 m, sample 149, depth of 75 m; Chut' River, outcrop 2,

right bank; Ukhta River, outcrop 9, left bank; Domanik River, outcrop 11; Shudayag, outcrop 12. All outcrops listed above belong to unit 2 of the Domanik Formation. Borehole no. 2060, depth of 241 m, Domanik Formation.

Palmatolepis subrecta Miller et Youngquist, 1947

Plate 9, figs. 12–14, 15?; Plate 14, fig. 2

Palmatolepis subrecta: Miller and Youngquist, 1947, pp. 513, 514, pl. 75, figs. 7–11; Müller and Müller, 1957, p. 1104, pl. 139, fig. 1; Glenister and Klapper, 1966, p. 823, pl. 88, figs. 1–3; Kononova, 1969, p. 135, pl. 1, fig. 1; Khalymbadzha and Tchernyschova, 1978, p. 35, pl. 3, figs. 12 and 13; Nasedkina and Plotnikova, 1979, p. 60, pl. 1, fig. 1; Khalymbadzha, 1981, pl. 4, figs. 10 and 11; Klapper and Foster, 1986, pl. 1, fig. 8, Pa element; Barskov et al., 1987, p. 42, pl. 7, fig. 23 (only), text-fig. 3, fig. B-8; Klapper and Lane, 1988, pl. 1, figs. 5 and 8; Ziegler and Sandberg, 1990, pp. 60–61, pl. 11, fig. 3 (reillustration of the lectotype), figs. 11 and 12 (only); pl. 15, fig. 8; Ji and Ziegler, 1993, pl. 27, figs. 7 and 10 (only); Sandberg et al., 1994, pl. 2, fig. 6; Ovnatanova et al., 1999, pl. 2, fig. 11; Gouwy and Bultynck, 2000, pp. 43–44, pl. 2, figs. 13? and 14.

Palmatolepis winchelli (Stauffer): Klapper, 1988, pl. 2, fig. 5; Klapper and Foster, 1993, pp. 24–31, text-figs. 13.1, 13.2, 18.2, 18.3, 18.5, and 18.6 (only).

Palmatolepis gigas gigas: Sandberg et al., 1994, pl. 1, fig. 10; Ji and Ziegler, 1993, pl. 27, fig. 4.

Manticolepis winchelli: Dzik, 2002, P_1 elements, figs. 39A, 39G, 39H?, and 42E.

Manticolepis gigas: Dzik, 2002, P_1 elements, figs. 36B and 36C.

Lectotype. University of Iowa, no. 5570, United States, Upper Devonian, Sweetland Creek shale. Müller and Müller (1957, p. 1104) designated the lectotype from the collection of the authors of the species (Miller and Youngquist, 1947, pl. 75, fig. 8). Later, the lectotype was rephotographed by Klapper and published in many papers, including the present paper (Pl. 9, fig. 12).

Diagnosis. Pa element: platform elongated triangular; posterior part relatively wide; posterior end pointed. Lobe small, directed laterally, located at level of azygous node, bordered by well-pronounced anterior and posterior sinuses. Median ridge slightly S-shaped and terminating short of reaching posterior end of the platform. Azygous node well developed. Posterior ridge consisting of two to five nodes gradually decreasing in size posteriorly. Free blade from one-fourth to one-sixth as long as platform. Parapet well developed in anterior half of platform, extending along platform margin in parallel to median ridge. Thin secondary ridge rarely developed. Ornamentation consisting of small nodes covering platform; sometimes, some nodes fused, forming small interrupted ridges along platform margin.

Comparison. This species differs from *Palmatolepis ljashenkoae* Ovnatanova, 1976 in the elongated platform with the lobe, which is distinctly bordered by sinuses, located at the level of the azygous node, and directedlaterally, in the presence of parapet, and the pointed posterior end of the platform. It differs from *Palmatolepis muelleri* Klapper et Foster, 1993 in the wide posterior part of the platform (posterior part of the platform of *Palmatolepis muelleri* is elongated) and in the presence of parapet. It differs from *Palmatolepis gigas* sensu stricto Miller et Youngquist, 1947 in the presence of parapet (instead of rostrum, as in *Palmatolepis gigas* sensu stricto) and in the narrower posterior part of the platform.

Remarks. Klapper and Foster (1993, pp. 31, 32) proposed to include *P. subrecta* in *Pa. gigas* because *Pa. gigas* was established based on a single large specimen from the type Sweetland Creek shale. Although precise stratigraphical allocation of *Palmatolepis subrecta* is not known, *Pa. subrecta* probably occurs in the same formation (possibly in 1.87–2.30 m upwards from its basement) based on the presence in the assemblage of other species, in particular, *Ancyrognathus calvini* (Klapper, 1990, p. 1006). According to Klapper, the lectotype of *Palmatolepis subrecta* possibly comes from the same collection and level as *Pa. gigas*. It may be that the lectotype of *Palmatolepis subrecta* and some specimens of *Palmatolepis winchelli* (Klapper and Foster, 1993, text-figs. 13.1, 13.2, 18.3, 18.5, 18.6) are merely small specimens of *Pa. subrecta.* Other specimens (Klapper and Foster, 1993, text-figs. 18.1, 18.9, reillustration of the holotype of *Palmatolepis gigas* Miller et Youngquist, and 18.10) have well developed rostrum and possibly belong to *Pa. gigas.* We suppose that *Pa. subrecta* and *Pa. gigas* are separate species. Unfortunately, we do not have specimens of *Pa. gigas* in our collection; however, it is widely known in literature. The main features of *Pa. gigas* are the presence of rostrum and the well developed lobe. Descriptions and figures of this species were provided by Miller and Youngquist (1947, pp. 512–513, pl. 75, fig. 1), Ziegler and Sandberg (1990, pl. 7, figs. 1, 2, pl. 8, figs. 6, 7?), Ji and Ziegler (1993, pl. 27, fig. 4), Klapper and Foster (1993, pp. 31–32, figs. 18.1, 18.9, 18.10), Dzik (2002, fig. 38A (only), P_1 element), and Galushin and Kononova (2004, text-fig. 9, fig. 18).

Occurrence. Upper Devonian, Frasnian Stage. North America, Iowa, Sweetland Creek shale; Germany, Steinbruch Schmidt section, Late *rhenana* Zone; South China, Lali section, upper part of the Xiangtian Formation, *linguiformis* Zone; southern Ural Mountains, Askyn beds; southern Timan, Lyaiol' Formation, units 3 and 4; Volga–Ural Province, Askyn beds.

Material. Volga–Ural Province: Tatarstan, Melekess 1, sample 69, interval 2048–2053 m, sample 94, interval 2018–2024 m (bottom of the interval), Askyn Regional Stage; Prikazanskaya 120, interval 1604–1610 m, Askyn Regional Stage; Severnyi Kupol 71, samples 64, 63, 59, 53, and 53, interval 1642–1649 m, Askyn Regional Stage. Southern Ural Mountains: Sikaza River. Southern Timan: Vezha-Vozh River, outcrops 9 and 10; Lyaiol' River, outcrops 1359, 1360, and 1908; borehole no. 2023, depth of 125 m, Lyaiol' Formation, unit 4.

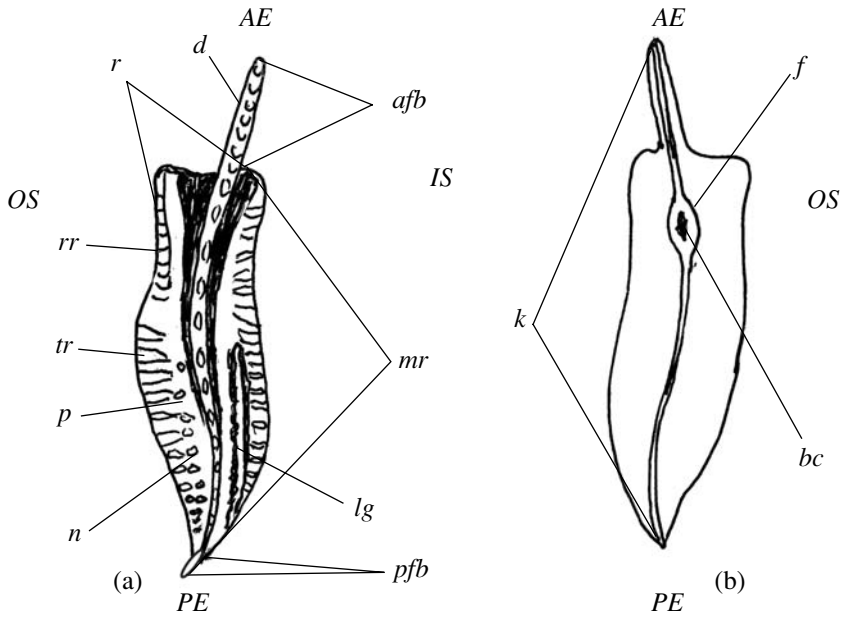


Fig. 23. Morphology of the genus *Polygnathus*: (a) upper and (b) lower views. Designations: (*AE*) anterior end, (*IS*) inner side, (*OS*) outer side, (*PE*) posterior end, (*afb*) anterior free blade (or free blade if the posterior free blade is absent), (*bc*) basal cavity, (*d*) denticle, (*f*) flank, (*k*) keel, (*lg*) longitudinal ridge, (*mr*) median ridge, (*n*) node, (*p*) platform, (*pfb*) posterior free blade, (*r*) rostrum, (*rr*) rostral ridge, (*tr*) transverse ridge.

Palmatolepis timanensis **Klapper, Kuzmin et Ovnatanova, 1996**

Plate 13, figs. 14–17, 18?

Palmatolepis timanensis: Klapper et al., 1996, p. 149, pl. 9, figs. 1–4; Ovnatanova et al., 1999b, pl. 2, fig. 18.

Holotype. PIN, no. 4551/8; southern Timan, borehole no. 2068, sample 24, depth of 20 m, Lyaiol' Formation, unit 3 (Klapper et al., 1996, pl. 9, fig. 2).

Diagnosis. Pa element: platform irregularly rounded; lobe weakly developed and located anteriorly to azygous node; sinuses almost absent; posterior end of platform pointed and arched downwards. Median ridge slightly S-shaped and terminating short of reaching posterior end of platform. Posterior ridge consisting of two or four nodes decreasing in size posteriorly. Free blade from one-third to one-fifth as long as platform. Platform smooth except rare nodes along margins.

Comparison. This species differs from *Palmatolepis lyaiolensis* Khrustcheva et Kuzmin, 1996 in the more rounded platform and the weakly developed lobe.

Remarks. Large specimens have poorly pronounced posterior sinus.

Occurrence. Southern Timan, Lyaiol' Formation, units 2 and 3; Volga–Ural Province, Mendym Regional Stage and bottom of the Askyn Regional Stage.

Explanation of Plate 1

Figs. 1–8. *Palmatolepis transitans* Müller, 1956: (1, 2) southern Timan, Chut' River, outcrop 7 (=1), sample 91, specimens: (1) VNIGNI, no. ONS 6/11, ×46; (2) VNIGNI, no. ONS 6/12, ×46; (3, 4) southern Timan, Domanik River, outcrop 6 (=11), sample 4/2; Frasnian Stage, Domanik Formation, unit 1, specimens: (3) PIN, no. 5255/1, ×84; (4) PIN, no. 5255/2, ×50; (5) specimen VNIGNI, no. OK-1016, ×36; southern Timan, borehole no. 1003, depth of 124 m, sample 4; Frasnian Stage, Ust'-Yarega Formation; (6) specimen PIN, no. 5255/3, ×46, Central Timan–Pechora Province, Mar'el' borehole, battering 20, interval 2595–2601 m; Frasnian Stage, Lyaiol' Formation, unit 2; (7) specimen PIN, no. 5254/1, ×45; Volga–Ural Province, Orenburg Region, Shuvalovskaya 4, interval 3589–3593 m, sample 13; Frasnian Stage, Domanik Regional Stage; (8) holotype, reillustration (after Müller, 1956, pl. 1, fig. 1, ×40).

Figs. 9–15. *Palmatolepis keyserlingi* Kuzmin, 1998: (9–11) southern Timan, Chut' River, outcrop 7 (=1), sample 91; Frasnian Stage, Domanik Formation, unit 1, specimens: (9) VNIGNI, no. ONS 6/13, ×37; (10) VNIGNI, no. ONS 6/14, ×36; and (11) VNIGNI, no. ONS 6/15, ×37; (12–14) southern Timan, Chut' River, outcrop 7 (=1), sample 97; Frasnian Stage, Domanik Formation, unit 1, specimens: (12) VNIGNI, no. ONS 6/16, ×35; (13) VNIGNI, no. 40/538, ×70; and (14) VNIGNI, no. 40/539, ×30; (15) holotype, reillustration after Kuzmin, 1998, pl. 8, fig. 2, ×45.

Figs. 16–21. *Palmatolepis triquetra* Kuzmin, 1998: (16–20) southern Timan, Chut' River, outcrop 1, sample 91; Frasnian Stage, Domanik Formation, unit 1, specimens: (16) holotype, reillustration after Kuzmin, 1998, pl. 7, fig. 5, ×45; (17) PIN, no. 5255/4, ×52; (18) PIN, no. 5255/5, ×49; (19) PIN, no. 5255/6, ×47; and (20) PIN, no. 5255/7, ×48; (21) specimen PIN, no. 5254/2, ×45; Volga–Ural Province, Orenburg Region, Shuvalovskaya 17, interval 3605–3616 m, sample 282; Frasnian Stage, Domanik Formation.

Fig. 22. *Palmatolepis rotundilobata* Kuzmin, 1998, holotype, reillustration (after Kuzmin, 1998, pl. 7, fig. 9, ×45).

Plate 1

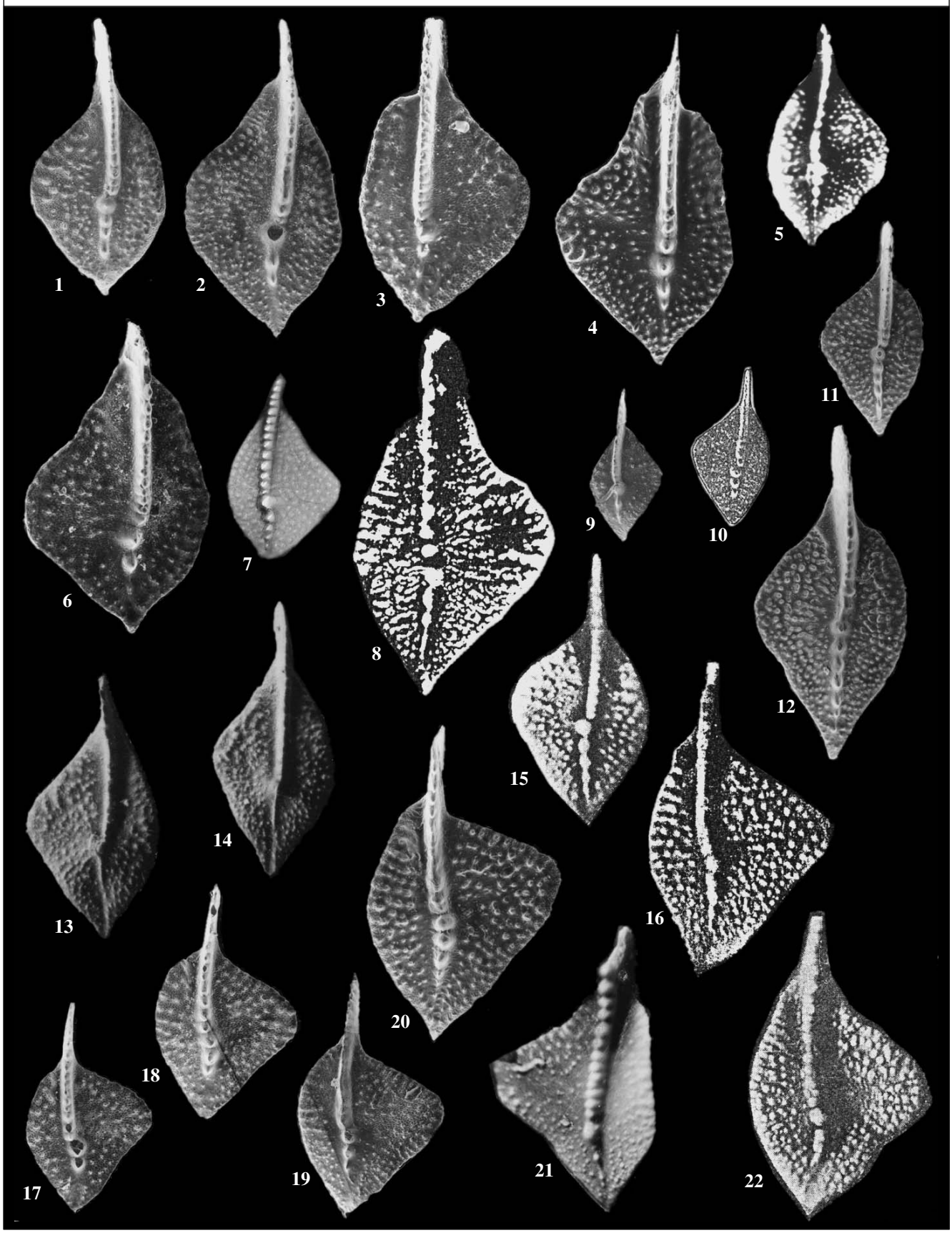
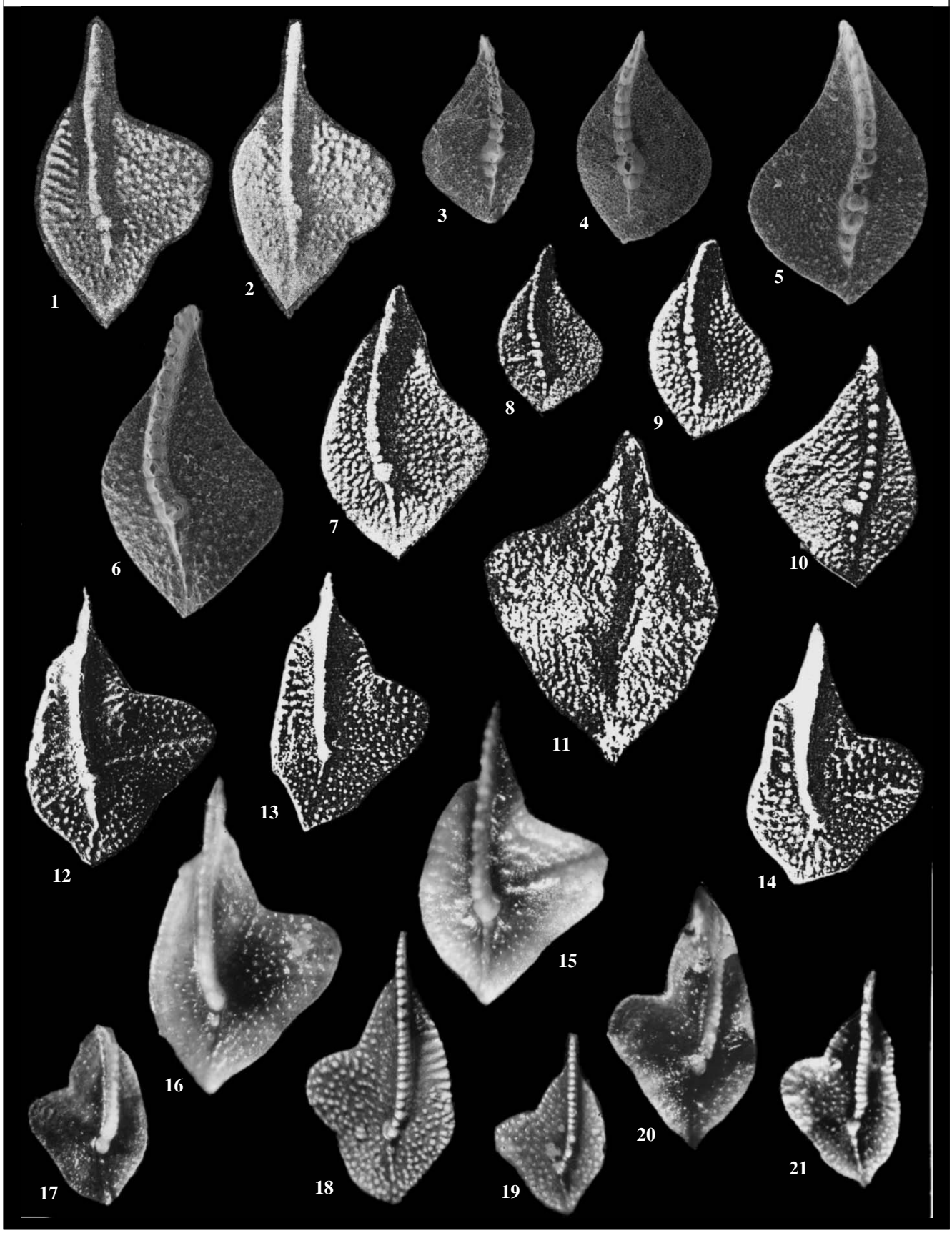


Plate 2



M a t e r i a l. Volga–Ural Province: Tatarstan, Prikazanskaya 120, samples 120 and 127, interval 1630–1633 m, Mendym Regional Stage; Severnyi Kupol 71, sample 112, interval 1680–1685 m, samples 76 and 71, interval 1662–1666 m and samples 66 and s48, interval 1651–1654 m, Mendym Regional Stage, samples 64 and 63, interval 1649–1651 m, bottom of the Askyn Regional Stage. Southern Timan: outcrops on the Vezha-Vozh and Lyaiol' rivers; borehole no. 2068, sample 24, depth of 20 m, sample 25, depth of 15 m, Lyaiol' Formation, unit 3.

Palmatolepis transitans Müller, 1956

Plate 1, figs. 1–8

Palmatolepis transitans: Müller, 1956, p. 18, pl. 1, fig. 1 (=holotype, only); Klapper in *Catalogue*…, 1973, p. 309, pl. 1, fig. 1 (only); Khalymbadzha and Tchernyschova, 1978, p. 37, pl. 4, fig. 13; Khalymbadzha, 1981, pl. 3, fig. 6 (only); Bultynck and Jacobs, 1981, pl. 7, figs. 15 and 16; Barskov et al., 1987, p. 43, pl. 6, figs. 1–5 (only); Aristov, 1988, pl. 7, figs. 12 and 13; Klapper, 1988, pl. 1, figs. 7 and 10; Orchard and McCracken, 1991, pl. 2, fig. 7; Irwin and Orchard, 1991, pl. 2, fig. 7; Ovnatanova and Kuzmin, 1991, pl. 1, fig. 17; Uyeno, 1991, pl. 3, figs. 22–23; Ji and Ziegler, 1993, pl. 30, figs. 10–12; Klapper et al., 1996, pp. 149–150, text-fig. 9.14; Kuzmin, 1998, pl. 7, fig. 1; Izokh et al., 2002, pl. 1, fig. 9; Klapper et al., 2004, figs. 6 and 7; Klapper, 2007, text-fig. 8.7.

Mesotaxis bohemica: Dzik, 2002, P_1 elements, figs. 31I and 31J?, 31M, and 31Q.

H o l o t y p e. NS, no. SMF XVI 127, Martenberg near Adorf, gray fine-grained limestone with red ironstone, *Pharciceras lunulicosta* Zone; lower part of the *Mancicoceras* Zone (Müller, 1956, pl. 1, figs. 1).

D i a g n o s i s. Pa element: platform slightly asymmetrical and rounded triangular; lobe not differentiated; posterior end pointed. Median ridge straight and terminating short of reaching posterior end of platform. Azygous node small and poorly distinguished between nodes of median ridge. Free blade short, one-sixth as long as platform. Lateral lobe poorly developed, rounded, and located at level of, or slightly anteriorly to, azygous node. Ornamentation consisting of abundant nodes, which sometimes fused, forming interrupted ridges along platform margin.

C o m p a r i s o n. This species differs from *Pa. keyserlingi* Kuzmin, 1998 in the rounded triangular platform. It differs from *Palmatolepis punctata* (Hinde, 1879) in the straight median ridge and the poorly developed lobe.

O c c u r r e n c e. Upper Devonian, Frasnian Stage, cosmopolitan. Southern Timan and central Timan–Pechora Province, upper part of the Sargaevo, Domanik, and Lyaiol' formations (units 1 and 2); Volga–Urals Province, Sargaevo and Domanik regional stages.

M a t e r i a l. Volga–Ural Province: Tatarstan, Prikazanskaya 138, samples 94 and 89, interval 1663–1685 m, Domanik Regional Stage, Prikazanskaya 120, samples 70 and 90, interval 1669–1676 m, Sargaevo Regional Stage; Orenburg Region, Shuvalovskaya 4, samples 98, 222, and 97, interval 3582–3593 m, Domanik Regional Stage; Zarinskaya 450, interval 3594–3601 m, Domanik Regional Stage. Southern Timan: Chut' River, outcrop 1; Ukhta River, outcrops 9 and 11; Shudayag, outcrop 12; borehole no. 1003, depth of 128 m, Ust'-Yarega Formation, depth of 92 and 120 m, Domanik Formation. Central Timan–Pechora Province: Mar'el' 1, interval 2595–2601 m, Lyaiol' Formation, unit 2.

Palmatolepis triquetra Kuzmin, 1998

Plate 1, figs. 16–21

Palmatolepis triquetra: Kuzmin, 1998, p. 75, pl. 7, figs. 4–7.

Palmatolepis aff. *triquetra*: Pisarzowska et al., 2006, text-fig. 14, fig. F.

H o l o t y p e. PIN, no. 4551/89; Ukhta Region, Chut' River, outcrop 7; Frasnian Stage, Domanik Formation, lower unit, sample D912 (Kuzmin, pl. 7, fig. 5).

D i a g n o s i s. Pa element: platform equilateral triangular; lobe rounded triangular and located at level of, or slightly anterior to, azygous node. Posterior end

E x p l a n a t i o n o f P l a t e 2

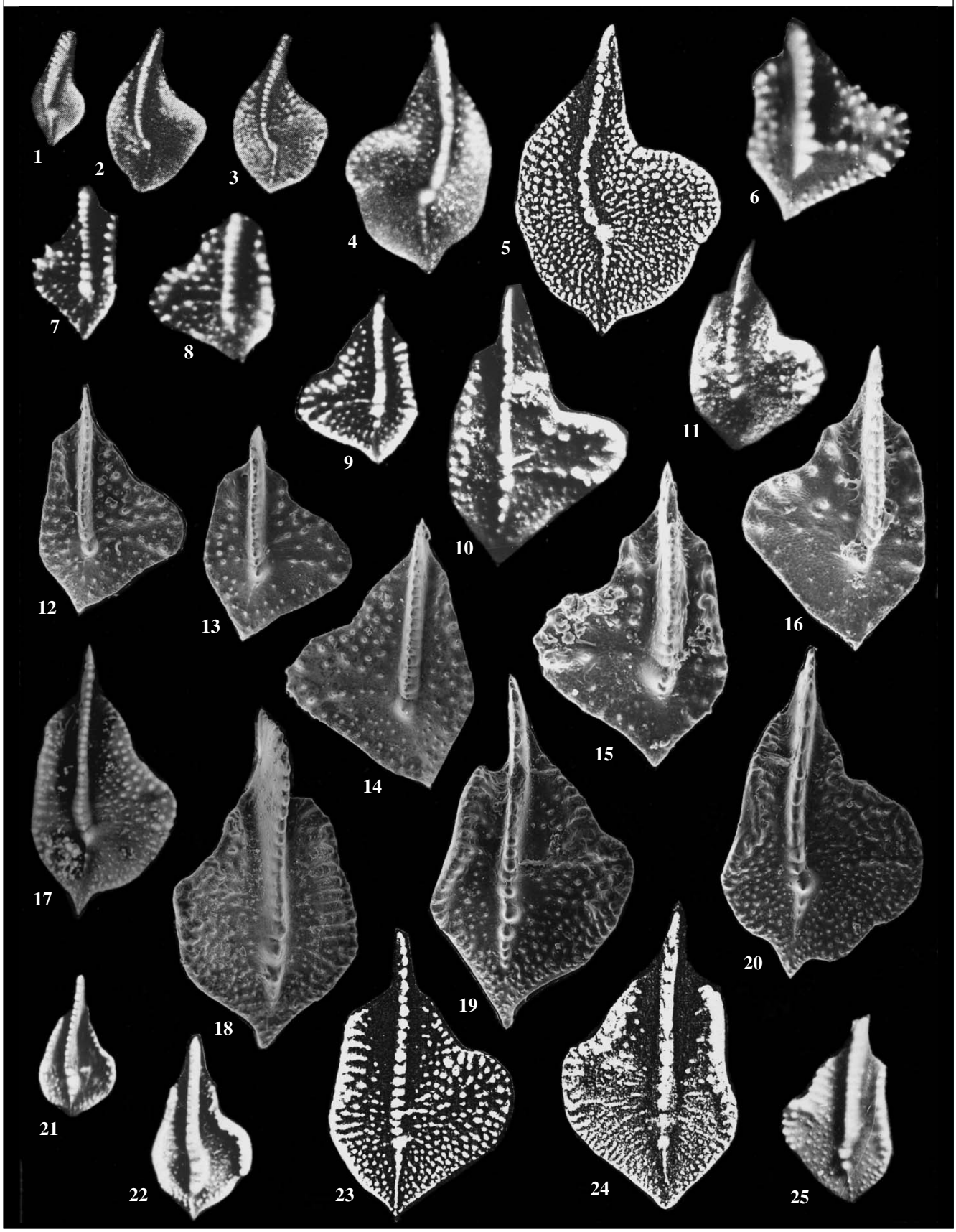
Figs. 1 and 2. *Palmatolepis rotundilobata* Kuzmin, 1998; outcrop 7 (=1), 1, sample D-914; Domanik Formation, unit 1: (1) reillustration after Kuzmin, 1998, pl. 7, fig. 10, ×45; (2) reillustration after Kuzmin, 1998, pl. 7, fig. 8, ×45.

Figs. 3–10. *Palmatolepis gutta* Kuzmin, 1998: (3–6) southern Timan, Chut' River, outcrop 7 (=1), 1, sample 91; Frasnian Stage, Domanik Formation, unit 1, specimens: (3) VNIGNI, no. ONS 6/23, ×78; (4) VNIGNI, no. ONS 6/24, ×69; (5) VNIGNI, no. ONS 6/25, ×72; and (6) VNIGNI, no. ONS 6/26, ×74; (7–10); outcrop 7 (=1), Domanik Formation, unit 1: (7) holotype, reillustration after Kuzmin, 1998, pl. 8, fig. 8, ×45; (8) reillustration after Kuzmin, 1998, pl. 8, fig. 10, ×45; (9) reillustration after Kuzmin, 1998, pl. 8, fig. 11, ×45; and (10) reillustration after Kuzmin, 1998, pl. 8, fig. 9, ×45.

Figs. 11–14. *Palmatolepis punctata* (Hinde): (11) lectotype, reillustration after Ziegler, 1973, *Palmatolepis*, pl. 1, fig. 5, ×35; (12) specimen VNIGNI, no. 40/539, ×50; southern Timan, Chut' River, outcrop 2; Domanik Formation, unit 1; (13) specimen VNIGNI, no. 40/540, ×55; southern Timan, left bank of the Ukhta River, outcrop 9, sample 1; Frasnian Stage, Domanik Formation, unit 3; (14) specimen VNIGNI, no. 40/541, ×45; southern Timan, Lyaiol' River, outcrop 1905; Frasnian Stage, Domanik Formation, unit 3.

Figs. 15–21. *Palmatolepis plana* Ziegler et Sandberg, 1990: (15, 16) southern Timan, Domanik River, outcrop 512 after A.I. Lyashenko (=11), sample 26; Frasnian Stage, Domanik Formation, unit 2, specimens: (15) PIN, no. 5255/8, ×45; (16) PIN, no. 5255/9, ×45; (17) specimen PIN, no. 5255/10, ×45; southern Timan, Domanik River, outcrop 512 after A.I. Lyashenko (=11), sample 22; Frasnian Stage, Domanik Formation; (18, 19) *?Palmatolepis plana*, Volga–Ural Province, Orenburg Region, Shuvalovskaya 17, interval 3605–3616 m, Domanik Regional Stage, specimens: (18) PIN, no. 5254/3, ×45; (19) PIN, no. 5254/4, ×45; (20) specimen PIN, no. 5255/11, ×45; southern Timan, Domanik River, outcrop 512 (=11), sample b13; Frasnian Stage, Domanik Formation, unit 2; (21) specimen VNIGNI, no. OK 1038, ×36; southern Timan, outcrop 6 (=11) in the mouth of the Domanik River; Frasnian Stage, Domanik Formation, unit 2.

Plate 3



slightly pointed and arched downwards. Median ridge slightly sigmoidal and terminating short of reaching posterior end of platform. Azygous node well developed. Posterior ridge short and consisting of three or four nodes. Narrow groove developed along posterior ridge. Free blade relatively long, one-fourth or one-third as long as platform. Platform uniformly covered with nodes; in its anterior part, nodes occasionally fused along outer margin, forming short and interrupted ridges.

Comparison. This species differs from *Palmatolepis rotundilobata* Kuzmin, 1998 in the rounded triangular lobe and the absence of sinuses. It differs from *Palmatolepis kireevae* Ovnatanova, 1976 in the rounded triangular lateral lobe and the less sigmoidal median ridge.

Occurrence. Volga–Ural Province, Frasnian Stage, lower part of the Domanik Regional Stage; southern Timan, Domanik Formation, units 1 and possibly 2.

Material. Volga–Ural Province: Orenburg Region, Shuvalovskaya 19, sample 64, interval 3625–3633 m, Domanik Regional Stage, Shuvalovskaya 17, interval 3605–3616 m, Domanik Regional Stage. Southern Timan: Chut' River, outcrop 1, Domanik Formation, unit 1; Lyaiol' River, outcrop 1351, Domanik Formation, possibly unit 2.

Genus *Polygnathus* Hinde, 1879 sensu lato

Polygnathus: Hinde, 1879, pp. 351–369; Klapper in *Catalogue*…, 1973, pp. 333–334; Barskov et al., 1991, pp. 4–8.

Type species. *Po. dubius* Hinde, 1879.

Diagnosis. Pa element planate. Lateral margins of platform raised or flattened. In anterior part, lateral margins sometimes compressed, forming rostrum and joining median ridge at one or different levels. Posterior end of platform pointed or arched downwards, sometimes lingulate. Median ridge straight or arched, reaching posterior end of platform extending beyond its edge in shape of posterior free blade, or terminating near posterior end of platform. Anterior free blade short or long, equal to, or much longer than platform. Troughs short or long, wide or narrow, shallow or deep. Upper surface of platform smooth or covered with transverse or longitudinal ridges and nodes. Lower side of platform with sharp keel opposed to median ridge and lens-shaped or rounded basal cavity with flanks located near middle or in anterior part of platform (Fig. 23).

Comparison. This genus differs from *Palmatolepis* Ulrich et Basler, 1926 in the absence of lobe, the presence of sharp keel, and the basal cavity with flanks.

Species composition. About 60 species in the Frasnian Stage.

Occurrence. North America, Africa, Europe, Asia, and Australia; Devonian–Lower Carboniferous.

Polygnathus aequalis Klapper et Lane, 1985

Plate 23, fig. 12

Polygnathus aequalis: Klapper and Lane, 1985, p. 930, pl. 16, figs. 7–14; Ziegler et al., 2000, pl. 7, figs. 13 and 14.

Holotype. Geological Survey of Canada, no. GSC 76747; Canada, outcrop on the High River; Frasnian Stage, 23.5 m upwards from the basement of the High River Formation (Klapper and Lane, 1985, text-figs. 16.11–16.13).

Explanation of Plate 3

Figs. 1–5. *Palmatolepis orbicularis* Ovnatanova et Kuzmin, 1991: (1, 2) southern Timan, Domanik River, outcrop 7 (=10), sample 5; Frasnian Stage, Domanik Formation, unit 2, specimens: (1) VNIGNI, no. OK 1033, ×36; (2) VNIGNI, no. OK 1034, ×36; (3) holotype, VNIGNI, no. OK 1035, ×36; reillustration after Ovnatanova and Kuzmin, 1991, pl. 2, fig. 15, ×36; (4) specimen VNIGNI, no. OK 1036, ×36; southern Timan, mouth of the Domanik River, outcrop 7 (=10), sample 5; Frasnian Stage, Domanik Formation, unit 2; (5) reillustration after Klapper et al., 1996, pl. 9, fig. 15, ×40; southern Timan, borehole no. 2023, sample 5; Frasnian Stage, Domanik Formation.

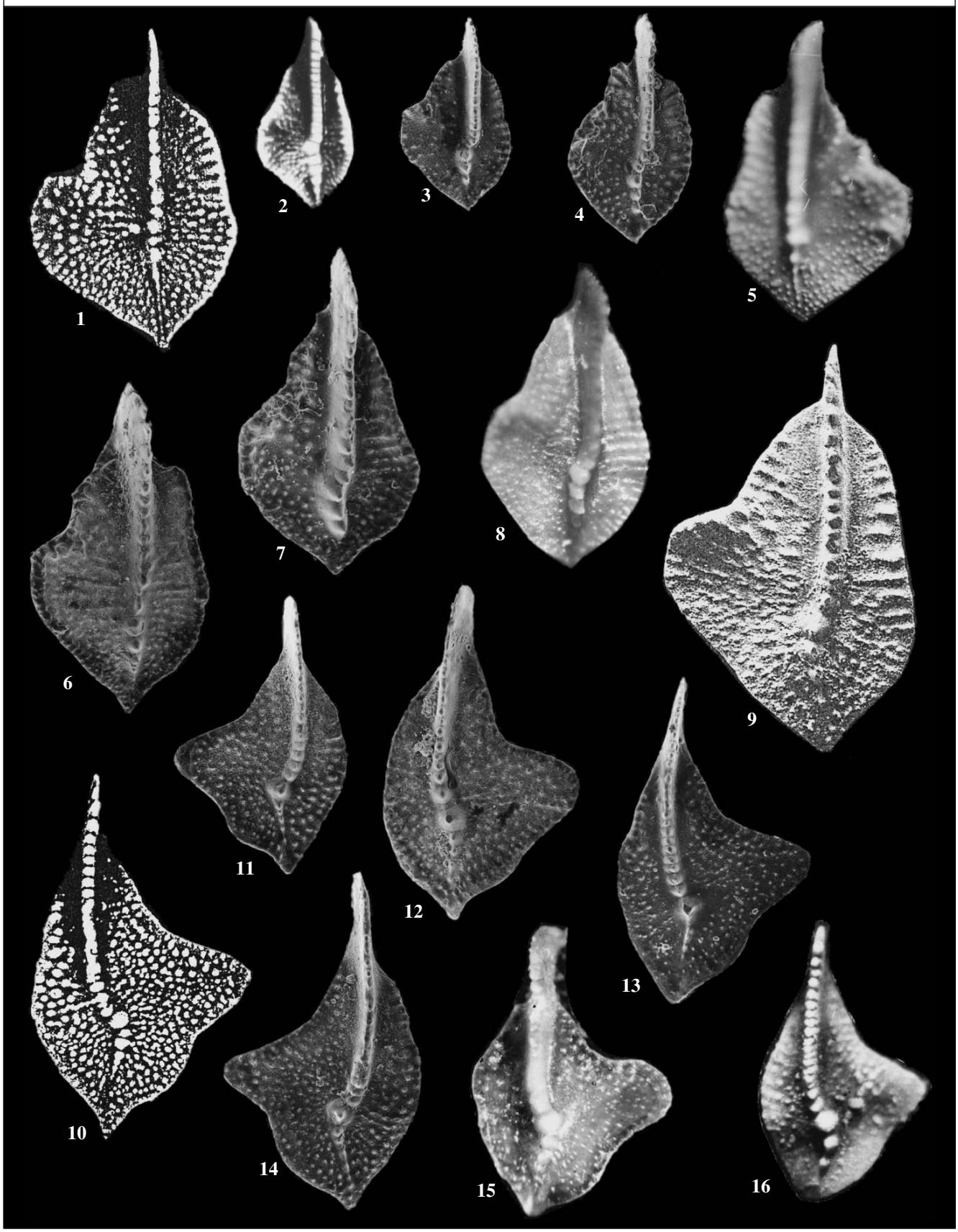
Figs. 6–16. *Palmatolepis spinata* Ovnatanova et Kuzmin, 1991: (6) holotype, ×36, reillustration after Ovnatanova and Kuzmin, 1991, pl. 3, fig. 6; (7, 8) mouth of the Domanik River, outcrop 6 (=11); Domanik Formation, unit 2; specimens: (7) VNIGNI, no. OK 1044, ×36, sample 4/2; (8) VNIGNI, no. OK 1042, ×36, sample 3; (9) specimen VNIGNI, no. OK 1044, ×36; southern Timan, borehole no. 2056, depth of 91 m, sample 9; Frasnian Stage, Domanik Formation, unit 2; (10, 11) Volga–Ural Province, Orenburg Region, Shuvalovskaya 1, interval 3618–3627 m, sample 38, Frasnian Stage, Domanik Regional Stage, specimens: (10) PIN, no. 5254/5, ×45; (11) PIN, no. 5255/34, ×45; (12–16) southern Timan, Domanik River, outcrop 6 (=11), sample 4/2; Frasnian Stage, Domanik Formation, unit 2, specimens: (12) VNIGNI, no. ONS 6/27, ×60; (13) VNIGNI, no. ONS 6/28, ×57; (14) PIN, no. ONS 6/28, ×58; (15) VNIGNI, no. ONS 6/31, ×96; and (16) VNIGNI, no. ONS 6/32, ×67.

Figs. 17–22. *Palmatolepis domanicensis* Ovnatanova, 1976: (17) holotype, ×40, reillustration after Ovnatanova, 1976, pl. 9, fig. 2; (18) specimen PIN, no. 5255/35, ×45; southern Timan, mouth of the Domanik River, outcrop 7e (=10), sample 2/2; Frasnian Stage, Domanik Formation, unit 2; (19) specimen PIN, no. 5255/36, ×43; southern Timan, Domanik River, outcrop 11, sample 4/2; Frasnian Stage, Domanik Formation, unit 2; (20) specimen PIN, no. 5255/37, ×33; southern Timan, Domanik River, outcrop 6 (=11), sample 4/2; Frasnian Stage, Domanik Formation, unit 2; (21, 22) Volga–Ural Province, Tatarstan, Prikazanskaya 138, sample 87, interval 1659–1663 m; Frasnian Stage, Domanik Regional Stage, specimens: (21) VNIGNI, no. 40/115, ×30; (22) VNIGNI, no. 40/112, ×30.

Figs. 23 and 24. *Palmatolepis bohemica* Klapper et Foster, 1993: (23) holotype, reillustration after Klapper et Foster, 1993, fig. 5.3, ×40; (24) reillustration after Klapper et al., 1996, pl. 9, fig. 17, ×40; southern Timan, borehole no. 2051, sample 1A, depth of 214 m; Frasnian Stage, Domanik Regional Stage.

Fig. 25. *Palmatolepis plana* Ziegler et Sandberg, 1990, specimen PIN, no. 5254/11, ×45; Volga–Ural Province, Tatarstan, Severnyi Kupol 166, interval 1563–1567 m, sample 47; Frasnian Stage, Mendym Regional Stage.

Plate 4



D i a g n o s i s. Pa element: platform elongated lanceolate; lateral margins equally raised in anterior part. Right-curved specimens wider than left-curved specimens. Posterior end of platform pointed and anterior end straight. Median ridge high, nodular, slightly arched, and reaching posterior end of platform. Free blade high, denticulated, half as long as platform. Highest denticles located in anterior part of blade. Troughs deep, narrow, and reaching posterior end of platform. Ornamentation varying from almost smooth to short transverse ridges, which better developed along platform margins; at posterior end of platform, ridges sometimes divided into nodes. Basal cavity relatively small, with narrow flanks, and located in anterior third of platform.

C o m p a r i s o n. This species differs from *Polygnathus webbi* Stauffer and *Polygnathus alatus* Huddle in the equally raised in the anterior part of the lateral margins of the platform, the longer free blade, and the ornamentation of short transverse ridges arranged along the platform margins.

O c c u r r e n c e. Canada, Upper Devonian, Frasnian Stage; Central Russian Platform, Semiluki Regional Stage; Volga–Ural Province, Voronezh Regional Stage and its analogues in southern Timan.

M a t e r i a l. Volga–Ural Province: Tatarstan, Prikazanskaya 113, interval 1613–1621 m, Voronezh Regional Substage; Orenburg Region, Shuvalovskaya 19, interval 3610–3617 m, Kolgany Member. Southern Timan: Timanskaya 10, sample 63, interval 450–452 m, sample 63B, interval 421–426 m, Lower Sirachoi Regional Substage, sample 60, interval 392–393 m, Upper Sirachoi Regional Substage.

***Polygnathus alatus* Huddle, 1934**

Plate 18, figs. 9–11

Polygnathus alata: Huddle, 1934, p. 100, pl. 8, figs. 19–20.

Polygnathus janetae: Druce, 1976, p. 192, pl. 76, figs. 3a–4c, text-fig. 23.

Polygnathus alatus: Klapper and Lane, 1985, p. 932, text-figs. 16.15–16.17; *Catalogue*…, 1991, pp. 133–134, pl. 14, fig. 11; Barskov et al., 1991, p. 13, pl. 2, figs. 17–21; Uyeno, 1991, pl. 5, fig. 7; Racki, 1992, text-figs. 30A–30C; Kuzmin, 1995, pl. 1, fig. 4; Kuzmin, 2001, pl. 10, fig. 18; Ziegler et al., 2000, pl. 6, fig. 3; Ovnatanova and Kononova, 2001, p. 40, pl. 1, figs. 3 and 4, pl. 3, figs. 11–12 (?), pl. 9, figs. 6–8.

H o l o t y p e. Indiana University, no. 1913; Indiana, near Prather, outcrop 30; shale in the lower part of the New Albany Formation (Huddle, 1934, pl. 8, figs. 19 and 20).

D i a g n o s i s. Pa element: platform asymmetrical (3b class of symmetry); posterior end of platform from slightly rounded to pointed. Free blade high, half as long as platform. Median ridge low, nodular, and reaching posterior end of platform or terminating near it. Troughs deep and narrow. Platform surface smooth, except poorly developed nodes or short ridges on lateral margins in posterior part of platform. Basal cavity small, lens-shaped, with narrow flanks, and located in anterior third of platform.

C o m p a r i s o n. This species differs from *Polygnathus webbi* Stauffer, 1938 in the almost smooth surface of the platform.

O c c u r r e n c e. Canada, Australia, Poland; Upper Devonian, Frasnian Stage. Germany, Heimberg and Martenberg sections, *punctata–jamieae* zones (zonation in these sections follows W. Ziegler). Russia: Central Russian Platform: Voronezh Anteclise and Moscow Syneclise, Upper Timan Regional Substage, Sargaevo and Semiluki regional stages; Volga–Ural Province: Upper Timan Regional Substage and Sargaevo Regional Stage; southern Timan, Upper Timan and Sargaevo regional stages; Middle Timan, Upper Kraipol Subformation; Main Devonian Field, Semiluki Regional Stage, Buregi beds.

E x p l a n a t i o n o f P l a t e 4

Figs. 1 and 5. *Palmatolepis bohemica* Klapper et Foster, 1993: (1) reillustration after Klapper et al., 1996, pl. 9, fig. 17, ×40; (5) specimen PIN, no. 5254/12, ×45; Volga–Ural Province, Orenburg Region, Shuvalovskaya 17, interval 3605–3616 m, sample 282; Frasnian Stage, Domanik Regional Stage.

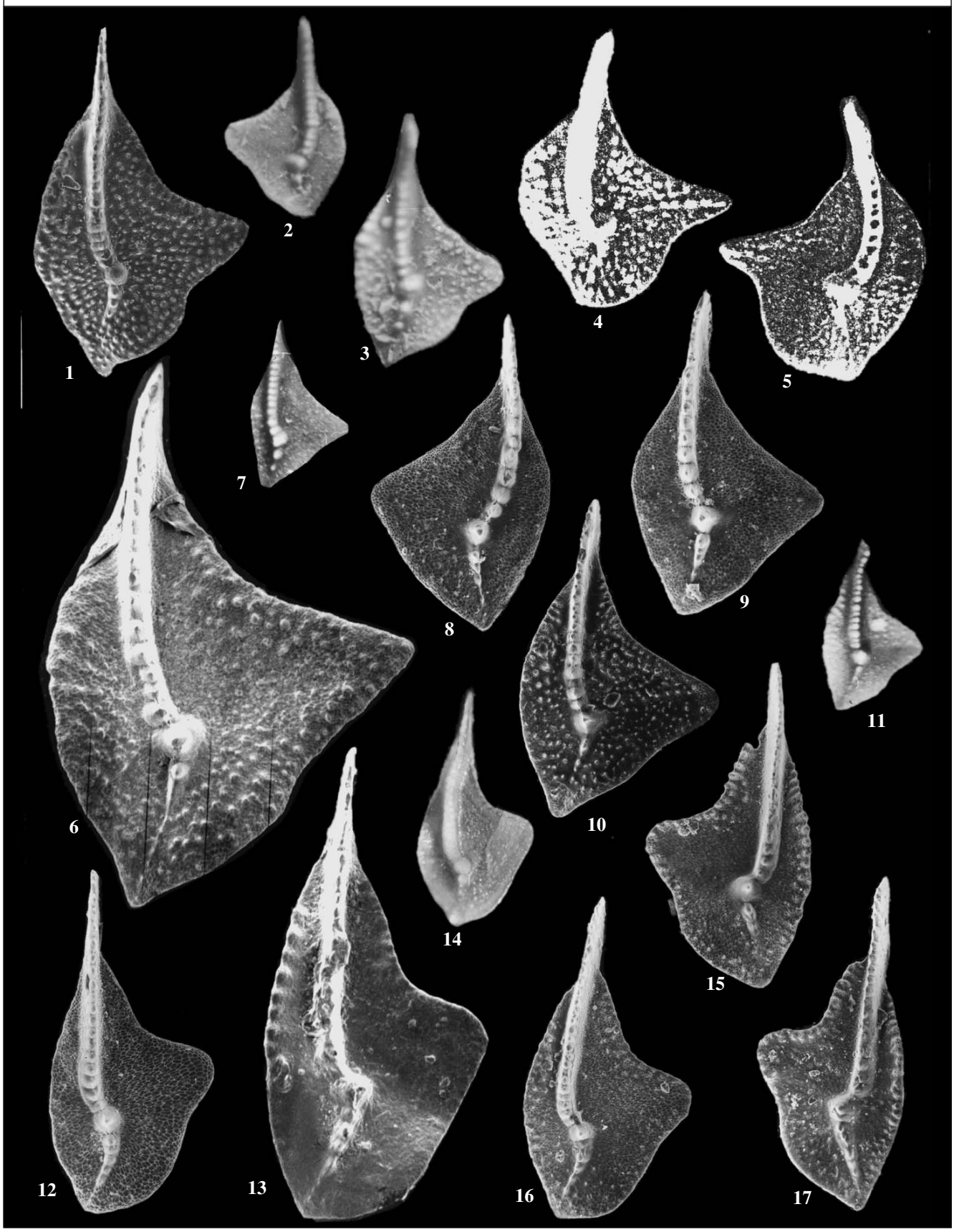
Figs. 2–4, 8, and 9. *Palmatolepis plana* Ziegler et Sandberg, 1990: (2) specimen VNIGNI, no. 40/113, ×30; Volga–Ural Province, Tatarstan, Severnyi Kupol 71, sample 112, interval 1680–1685 m; Frasnian Stage, Mendym Regional Stage; (3, 4) southern Timan, borehole no. 2023, depth of 177 m, sample 10A; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (3) PIN, no. 5255/38, ×42; (4) PIN, no. 5255/50, ×44; (8) specimen PIN, no. 5254/13, ×45; Volga–Ural Province, Udmurtia, Krasnogor'e 91, sample 73, interval 1997–2002 m; Frasnian Stage, Mendym Regional Stage; (9) holotype, reillustration after Ziegler et Sandberg, 1990, pl. 3, fig. 9, ×70.

Figs. 6 and 7. *Palmatolepis domanicensis* Ovnatanova, 1976: (6) specimen PIN, no. 5255/39, ×44; southern Timan, borehole no. 2060, depth of 224.9 m, sample 6B; Frasnian Stage, Vetlasyan Formation; (7) specimen PIN, no. 5255/40, ×53; southern Timan, borehole no. 2068, sample 20, depth of 36.0 m; Frasnian Stage, Lyaiol' Formation, unit 2.

Figs. 10–14 and 15. *Palmatolepis hassi* Müller et Müller, 1957: (10) holotype initially published by Müller et Müller, 1957, pl. 140, fig. 4, ×54, then rephotographed by Klapper; (11, 12) Central Timan–Pechora Province, Mar'el' 1, battering 20, interval 2595–2601 m; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (11) PIN, no. 5255/41, ×52; (12) PIN, no. 5255/42, ×52; (13) specimen PIN, no. 5255/43, ×50; southern Timan, borehole no. 2023, depth of 149 m, sample 14; Frasnian Stage, Lyaiol' Formation, unit 3; (14) specimen PIN, no. 5255/44, ×45; southern Timan, borehole no. 2068, sample 19A, depth of 46 m; Frasnian Stage, Lyaiol' Formation, unit 2; (15) specimen PIN, no. 5254/14, ×45; Volga–Ural Province, Udmurtia, Krasnogor'e 91, sample 55, interval 2005–2008 m; Frasnian Stage, Mendym Regional Stage.

Fig. 16. *Palmatolepis kireevae* Ovnatanova, 1976, specimen PIN, no. 5254/15, ×45; Volga–Ural Province, Melekess 1, sample 69, interval 2048–2053 m; Frasnian Stage, Evlanovo Regional Stage.

Plate 5



M a t e r i a l. Volga–Ural Province: Tatarstan, Terengul 1, interval 2128–2131 m, Sargaevo Regional Stage; Orenburg Region, Shuvalovskaya 1, interval 3649–3655 m, Timan Regional Stage, Shuvalovskaya 4, sample 268, interval 3604–3618 m, Upper Timan Regional Substage, Shuvalovskaya 19, samples 59, 65, and 68, interval 3643–3649 m, Sargaevo Regional Stage; southern Timan, Ukhta Region, right bank of the Ukhta River, outcrops A and B, Upper Timan Regional Substage.

Polygnathus alvenus Ovnatanova et Kononova, 1996

Plate 22, figs. 1–4

Polygnathus incompletus: Aristov, 1988, p. 87, pl. 3, fig. 8.

Polygnathus alvenus: Ovnatanova and Kononova, 1996, p. 54, pl. 5, figs. 3–7; Ziegler et al., 2000, pl. 3, fig. 4, pl. 4, figs. 30 and 31, pl. 9, figs. 7 and 8, pl. 10, figs. 17–21; Ovnatanova and Kononova, 2001, p. 40, pl. 16, figs. 2–8, 15 and 16, pl. 17, figs. 4–6, pl. 18, figs. 15–21, pl. 21, figs. 15–17, pl. 23, fig. 25, pl. 27, figs. 17–19.

Polygnathus cf. *procerus*: Sanz Lopez et al., 1999, pl. 1, fig. 11.

H o l o t y p e. VNIGNI, no. 40/117; Voronezh Region, right bank of the Don River near the village of Panskaya Gvozdevka, outcrop 5, sample 65; Frasnian Stage, Voronezh Regional Stage (Ovnatanova and Kononova, 1996, pl. 5, fig. 3).

D i a g n o s i s. Pa element: platform elongated trough-shaped; lateral margins raised within anterior two-thirds and flattened in posterior third of platform; posterior end rounded or slightly pointed. Median ridge low, nodular, straight or slightly arched, and abruptly terminating in posterior third of platform. Free blade half as long as platform, denticulated, with denticles gradually lowering towards posterior end. Troughs deep and flattened in posterior third of platform. Platform surface mostly smooth; only anterior one-third of platform having slightly denticulated margins. Basal cavity small, elongated, with narrow flanks, and located in anterior third of platform.

V a r i a b i l i t y. In the anterior half, the platform margins vary from slightly to distinctly denticulated. The nodes on the median ridge are poorly developed or absent.

C o m p a r i s o n. This species differs from *Polygnathus subincompletus* Ovnatanova et Kononova, 1996 in the low median ridge relative to the raised lateral margins of the platform. It differs from *Po. incompletus* Uyeno, 1967 in the trough-shaped platform with flattened in the posterior third lateral margins, the low median ridge, and the small basal cavity.

O c c u r r e n c e. Upper Devonian, Frasnian Stage, Germany, Late *rhenana* Zone (collection of W. Ziegler, Benner Bicken section, Bi-25, Bi-26). Russia: Central Russian Platform, Petino, Voronezh and Evlanovo regional stages; Volga–Urals Province, Upper Voronezh and Evlanovo regional stages; Timan, Sirachoi Formation and bottom of the Ukhta Formation; relatively deepwater sections, isolated specimens occur in unit 4 of the Lyaiol' Formation.

M a t e r i a l. Volga–Ural Province: Tatarstan, Ul'yanovskaya 1, sample 101, interval 1817–1829 m, Upper Voronezh Regional Substage; Orenburg Region, Salmysh 626, interval 3670–3677 m, Evlanovo Regional Stage; southern Timan, Bel'gop 4, depth of 266 m, Upper Sirachoi Regional Substage, depth of 239, 235, and 203–207 m, lower part of the Ukhta Formation; Lyaiol' River, outcrops 1360 and 1908, Lyaiol' Formation, unit 4.

Polygnathus aspelundi Savage et Funai, 1980

Plate 22, figs. 8 and 9

Polygnathus aspelundi: Savage and Funai, 1980, p. 812, pl. 2, figs. 18–33; Klapper and Lane, 1985, p. 934, text-fig. 16.1; Barskov et al., 1991 pp. 104–105, pl. 29, figs. 1–3; Klapper in *Catalogue*…, 1991, p. 139, pl. 14, fig. 1; Norris et al., 1992, pl. 15, fig. 4; Kuzmin, 2001, pl. 10, fig. 16; Ziegler et al., 2000, pl. 7, fig. 4; Ovnatanova

Explanation of Plate 5

Fig. 1. *Palmatolepis hassi* Müller et Müller, 1957, specimen PIN, no. 5255/45, ×43; southern Timan, borehole no. 2068, sample 19a, depth of 46 m; Frasnian Stage, Lyaiol' Formation, unit 2.

Figs. 2 and 3. *Palmatolepis* sp., Volga–Ural Province, Kazan Region, Severnyi Kupol 220, sample 16, interval 1589–1593 m; Frasnian Stage, Mendym Regional Stage: (2) specimen PIN, no. 5254/16, ×45; (3) specimen PIN, no. 5254/17, ×45.

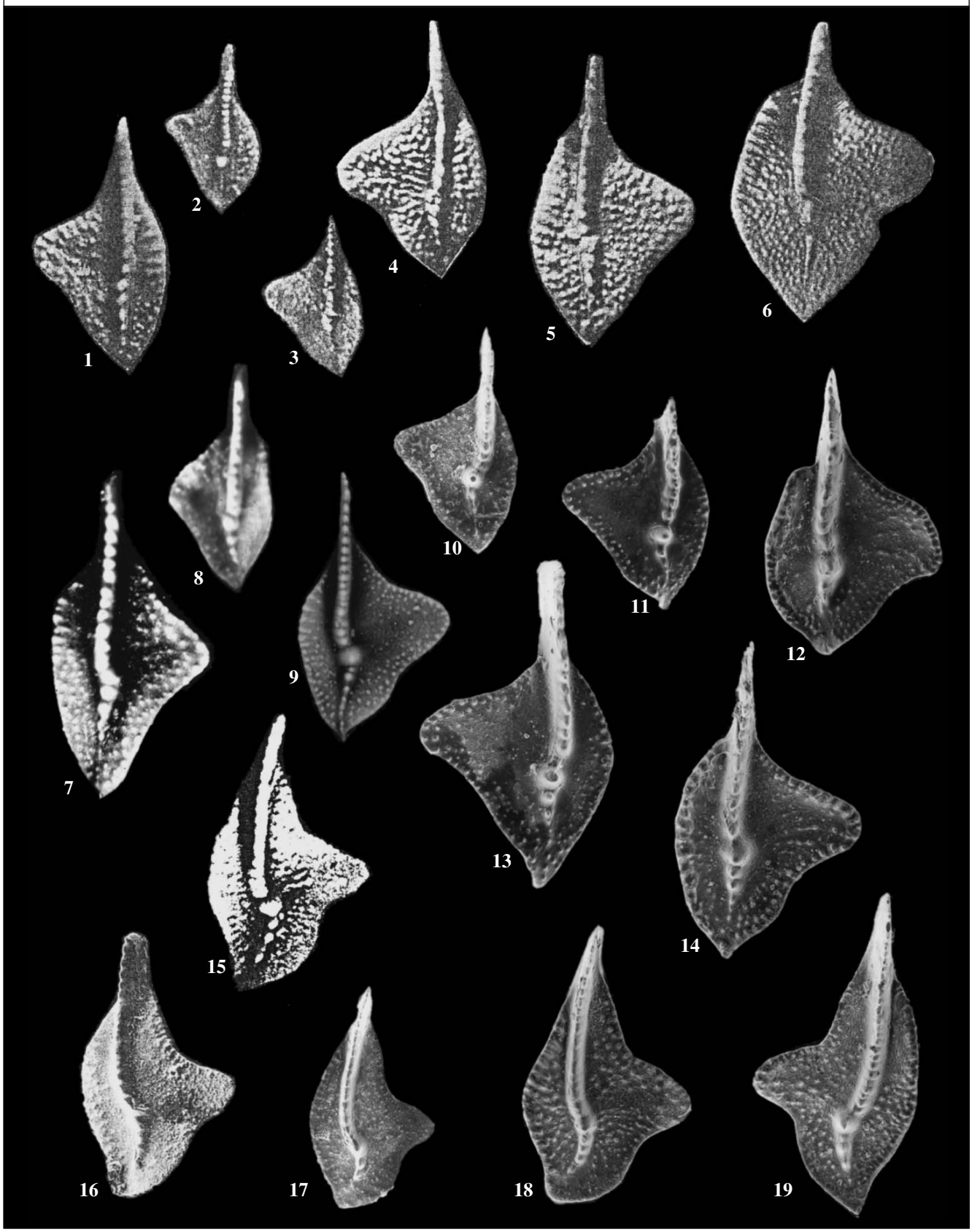
Figs. 4 and 5. *Palmatolepis anzhelae* Khruschova et Kuzmin, 1996: (4) holotype, reillustration after Khruscheva and Kuzmin, 1996, pl. 11, fig. 12, ×35; (5) reillustration after Khruscheva and Kuzmin, 1996, pl. 11, fig. 13, ×37.

Figs. 6–11. *Palmatolepis kireevae* Ovnatanova, 1976: (6) holotype, reillustration after Ovnatanova, 1976, pl. 9, fig. 5 (rephotographed in the laboratory of professor W. Ziegler), ×80; (7) specimen PIN, no. 5254/18, ×30; Volga–Ural Province, Prikazanskaya 115, sample 87, interval 1647.3–1649.7 m; Frasnian Stage, Mendym Regional Stage; (8–10) southern Timan, borehole no. 2023, depth of 177 m, sample 10A; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (8) VNIGNI, no. ONS6/57, ×82; (9) VNIGNI, no. ONS6/58, ×77; (10) VNIGNI, no. 6/60, ×66; (11) specimen VNIGNI, no. ONS6/59, ×30; Volga–Ural Province, Prikazanskaya 138, sample 38, interval 1614–1618 m; Frasnian Stage, Voronezh Regional Stage.

Figs. 12–14 and 16. *Palmatolepis ljaschenkoae* Ovnatanova, 1976: (12) specimen VNIGNI, no. ONS 6/62, ×83; southern Timan, Vezha-Vozh River, outcrop 8, sample 8/2; Frasnian Stage, Lyaiol' Formation, unit 2; (13) holotype, reillustration after Ovnatanova, 1976, pl. 9, fig. 5; ×80 (rephotographed in the laboratory of professor W. Ziegler); (14) specimen PIN, no. 5255/12, ×30; southern Timan, Vezha-Vozh River, outcrop 735a; Frasnian Stage, Lyaiol' Formation, unit 2; (16) specimen VNIGNI, no. ONS 6/64, ×66; southern Timan, Vezha-Vozh River, outcrop 8, sample 8/2; Frasnian Stage, Lyaiol' Formation, unit 2.

Figs. 15 and 17. *Palmatolepis ljaschenkoae* Ovnatanova → *Palmatolepis proversa* Ziegler; southern Timan, Vezha-Vozh River, outcrop 8, sample 8/2; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (15) VNIGNI, no. ONS 6/65, ×66; (17) VNIGNI, no. ONS 6/66, ×52.

Plate 6



and Kononova, 2001, pp. 40–42, pl. 17, figs. 1–3, pl. 21, figs. 8–10, pl. 23, figs. 15–24.

Holotype. USNM, no. 224249, right-side Pa element; southeastern Alaska, Coronados Island; possibly Lower Frasnian (Savage and Funai, 1980, pl. 2, figs. 22–25).

Diagnosis. Pa element: platform slightly asymmetrical and ovally pear-shaped. Lateral margins of platform highly raised over whole length. Anterior end semicircular or vaguely gradate; posterior end pointed. Median ridge low, smooth, straight or slightly arched, and slightly projecting beyond platform. Free blade moderately high, with maximum height in center; denticulated, consisting of seven to nine denticles, half or one-third as long as platform. Troughs narrow and deep in anterior part and flattened posteriorly. Ornamentation almost absent, or lateral margins of platform slightly denticulated in anterior part. Basal cavity small, lens-shaped, with narrow flanks, and located in anterior third of platform.

Comparison. This species differs from *Polygnathus politus* Ovnatanova, 1969 in the ovally pear-shaped platform, the low median ridge projecting beyond the posterior end of the platform, and in the denticulated lateral margins in the anterior part of the platform.

Occurrence. Upper Devonian, Frasnian Stage; United States (Alaska), Canada; Russia: Voronezh Anteclise, Voronezh–Evlanovo regional stages; Volga–Ural Province, Rechitsa Regional Stage, Kolgany Member; southern Timan, Upper Sirachoi Regional Substage and the bottom of the Ukhta Formation.

Material. Volga–Ural Province: Ulyanovsk (Okhotnich'ya) 1, samples 44 and 47, interval 1869–1875 m, Rechitsa Regional Stage; Orenburg Region, Shuvalovskaya 19, sample 101, interval 3610–3617 m, Kolgany Member. Southern Timan: Timanskaya 10, samples 60A, 58, 58A, 57H, and 55, interval 354–390 m, Upper Sirachoi Regional Substage, sample 53, interval 314–315 m, Lower Ukhta Subformation.

***Polygnathus azygomorphus* Aristov in Ovnatanova and Aristov, 1985**

Plate 20, figs. 10–12

Polygnathus azygomorphus: Aristov in Ovnatanova and Aristov, 1985, p. 33, pl. 6, figs. 6 and 7; Aristov, 1988, p. 83, pl. 6, figs. 8 and 9; Barskov et al., 1991 p. 72, pl. 26, figs. 7 and 8; Aristov, 1994, pl. 8, figs. 1–3; Ziegler et al., 2000, pl. 6, figs. 15–18; Ovnatanova and Kononova, 2001, p. 41, pl. 10, figs. 32–37, pl. 16, figs. 24–26, pl. 20, figs. 14 and 15, pl. 22, figs. 12–16.

Holotype. GIN (Geological Institute, Russian Academy of Sciences, Moscow), no. 4593/95; Voronezh Anteclise, village of Nizhnii Karachan, borehole no. 178, depth of 81.3 m; Frasnian Stage, Voronezh Regional Stage (Aristov in Ovnatanova and Aristov, 1985, pl. 6, fig. 7).

Diagnosis. Pa element: platform massive, narrow, elongated, and asymmetrically wedge-shaped; anterior end of platform semicircular; posterior end pointed, lateral margins slightly raised. Median ridge high, nodular, slightly S-shaped, and reaching posterior end of platform. Free blade high, inclined inwards, denticulated, half or more of platform length. Denticles of free blade large, with maximum height in middle of blade. Troughs narrow, deep in anterior part of platform and small in posterior part. Ornamentation consisting of sinuous interrupted transverse ridges formed by fused nodes. Basal cavity small, lens-shaped, with narrow flanks, and located in anterior third of platform.

Comparison. This species differs from *Polygnathus pollocki* Druce, 1976 in the transverse ridge formed by fused nodes.

Occurrence. Upper Devonian, Frasnian Stage; Russia: Voronezh Anteclise, Semiluki, Petino, and Voronezh regional stages; Volga–Ural Province, Domanik Regional Stage; southern Timan, Domanik and Sirachoi Formations.

Material. Volga–Ural Province: Tatarstan, Ulyanovsk (Okhotnich'ya) 1, samples 14, 21, and 25, interval 1887–1898 m, Semiluki Regional Stage; Prikazanskaya 69, interval 1686–1689 m, bottom of the

Explanation of Plate 6

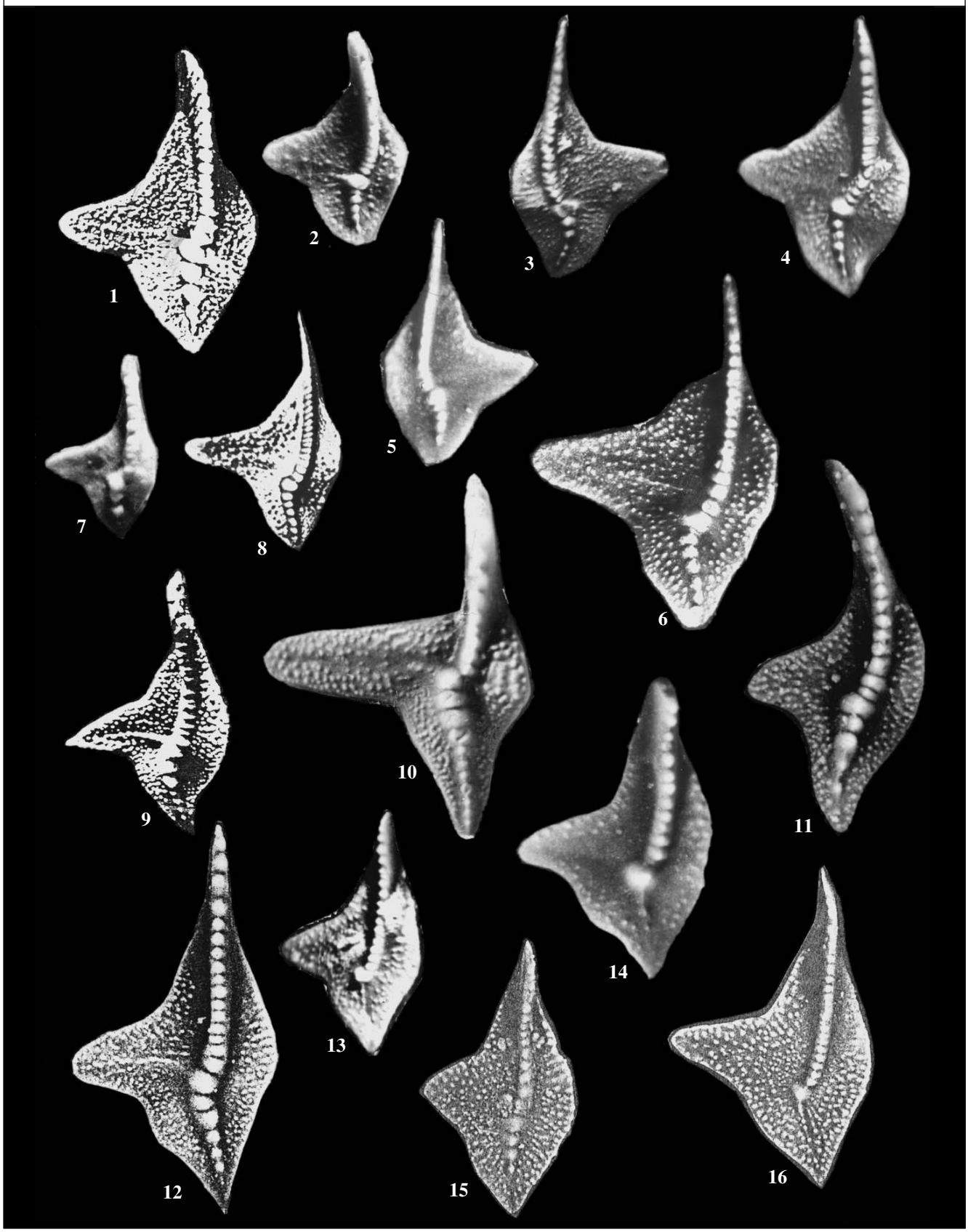
Figs. 1–6. *Palmatolepis maximovae* Kuzmin, 1998: (1) holotype, reillustration after Kuzmin, 1998, pl. 7, fig. 12, ×45; (2) reillustration after Kuzmin, 1998, pl. 7, fig. 13, ×45; Domanik Formation, unit 2; (3) reillustration after Kuzmin, 1998, pl. 7, fig. 14, ×45; southern Timan, borehole no. 2056, depth of 102.5 m; (4) reillustration after Kuzmin, 1998, pl. 7, fig. 15, ×45; southern Timan, Chut' River, outcrop 7 (1), sample D-912; (5) reillustration after Kuzmin, 1998, pl. 7, fig. 11, ×45; southern Timan, Chut' River, outcrop 7 (1), sample D-914; Domanik Formation, unit 2; (6) reillustration after Kuzmin, 1998, pl. 7, fig. 16, ×45; southern Timan, borehole no. 2021, depth of 299 m, sample 6; Frasnian Stage, nonstratified middle–upper units of the Domanik Formation.

Figs. 7 and 8. *Palmatolepis kuschnarevae* Ovnatanova et Kuzmin in Menner et al., 1992: (7) holotype, reillustration after Menner et al., 1992, text-fig. 4, fig. 1, ×45; (8) (= *Palmatolepis* sp. B) reillustration after Ovnatanova and Kuzmin, 1991, pl. 3, fig. 10, ×36; southern Timan, borehole no. 3B, sample 142, depth of 85 m; Frasnian Stage, Domanik Formation, unit 2.

Figs. 9–14. *Palmatolepis ormistoni* Klapper, Kuzmin et Ovnatanova, 1996: (9) holotype, reillustration after Klapper et al., 1996, text-fig. 10.4, ×40 (photographed by G. Klapper); (10–14) southern Timan, borehole no. 2068, sample 19A, depth of 46 m; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (10) PIN, no. 5255/13, ×48; (11) PIN, no. 5255/14, ×38; (12) PIN, no. 5255/15, ×41; (13) PIN, no. 5255/16, ×43; and (14) PIN, no. 5255/17, ×42.

Figs. 15–19. *Palmatolepis orlovi* Khruscheva et Kuzmin: (15) holotype, reillustration after Khruscheva and Kuzmin, 1996, pl. 11, fig. 5, ×40; (16) specimen PIN, no. 5255/18, ×45; southern Timan, Vezha-Vozh River, outcrop 10, sample 7; Frasnian Stage, Lyaiol' Formation, unit 4; (17, 18) southern Timan, borehole no. 2023, depth of 125 m, sample 18; Frasnian Stage, Lyaiol' Formation, unit 4, specimens: (17) PIN, no. 5255/19, ×40; (18) PIN, no. 5255/20, ×43; (19) specimen PIN, no. 5255/21, ×41; southern Timan, Lyaiol' River, outcrop 1908, sample 1; Frasnian Stage, Lyaiol' Formation, unit 4.

Plate 7



Domanik Regional Stage. Southern Timan: borehole no. 2060, depth of 236 m, Domanik Regional Stage, depth of 26 m, upper part of the Sirachoi Regional Stage.

Polygnathus brevilamiformis Ovnatanova, 1976

Plate 21, figs. 3–5

Polygnathus brevilamiformis: Ovnatanova, 1976, p. 114, pl. 9, figs. 9 and 10; Aristov, 1988, p. 83, pl. 2, figs. 4, 10–12; Barskov et al., 1991, p. 97, pl. 26, figs. 12–15; Ziegler et al., 2000, pl. 4, figs. 11 and 12; Ovnatanova and Kononova, 2001, p. 41, pl. 7, figs. 23–30, 34–42, pl. 15, figs. 30 and 31; Kuzmin, 2001, pl. 10, fig. 15.

Holotype. VNIGNI, no. 40/69; Middle Timan, Umba River; Upper Devonian, Frasnian Stage, Lower Verkhovskaya beds (Ovnatanova, 1976, pl. 7, figs. 23, 24).

Diagnosis. Pa element: platform symmetrical, elongated triangular, with highly raised lateral margins. Median ridge straight, high, denticulated, and sometimes projecting beyond posterior end of platform, forming short posterior free blade. Anterior free blade long and equal to platform in length, or slightly longer. Troughs shallow, wide in anterior part of platform, narrowing posteriorly, and reaching posterior end of platform. Ornamentation consisting of slightly denticulated lateral margins of platform or very short and small well pronounced transverse ridges along platform margin. Basal cavity small, with narrow flanks, and located near anterior end of platform.

Comparison. This species differs from *Polygnathus brevilaminus* Branson et Mehl, 1934 in the triangular platform and the short posterior free blade.

Occurrence. Germany, Upper Devonian, Frasnian Stage, Late *hassi* Zone (collection of W. Ziegler, Benner Bicken section, Bi-57). Russia: Voronezh Anteclise, Semiluki Regional Stage; Volga–Ural Province, Domanik, Rechitsa, and Mendym regional stages; southern Timan, Domanik Regional Stage and Lyaiol' Formation, units 1 and 2; Middle Timan, Lower Kraipol Subformation.

Material. Volga–Ural Province: Tatarstan, Terengul borehole, interval 2092–2100 m, Semiluki Regional Stage; Ulyanovsk (Okhotnich'ya) 1, sample 35, interval 1887–1898 m, Semiluki Regional Stage, sample 45, depth of 1870 m, Rechitsa (Petino) Regional Stage; Kirov Region, Rekhino 9, interval 2024–2029 m, Domanik Regional Stage; Udmurtia, Chutyr', 152, interval 2096.6–2093.6 m, Mendym Regional Stage; Orenburg Region, Shuvalovskaya 4, samples 98, 106, and 97, interval 3582–3593 m, Domanik Regional Stage, Shuvalovskaya 19, samples 64 and 90, interval 3625–3633 m, Domanik Regional Stage, borehole no. 17, interval 3605–3616 m, Domanik Regional Stage, Shuvalovskaya 25, interval 3680–3688 m, Domanik Regional Stage. Southern Timan: borehole no. 2060, depth of 241 m, Domanik Regional Stage; Lyaiol' River, outcrop 1905, Lyaiol' Formation, unit 1; Vezha-Vozh River, outcrop 9, Lyaiol' Formation, unit 2.

Polygnathus brevis Miller et Youngquist, 1947

Plate 23, figs. 8–11

Polygnathus brevis: Miller and Youngquist, 1947, p. 514, pl. 74, fig. 9; Szulczewski, 1971, pl. 19, fig. 3; 1972, p. 450, pl. 1, figs. 1–7, pl. 2, figs. 1–4; Klapper in *Catalogue*…, 1973, p. 341, pl. 1, fig. 2; Aristov, 1988, p. 84, pl. 3, figs. 9 and 10; Day, 1990, p. 623, fig. 11.18; Barskov et al., 1991, p. 44, pl. 14, figs. 3–6; Menner et al., 1992, text-fig. 4, fig. 8; Savage, 1992, p. 286, text-figs. 4.1, 4.2, 5.26–5.28; Norris et al., 1992, pl. 15, figs. 9 and 10; Schindler et al., 1998, pl. 5, fig. 34 (not fig. 35 = *Po. krestovnikovi* Ovn.); Ziegler et al., 2000, pl. 9, figs. 23 and 25; Klapper, 2007, text-fig. 7.11; Pazukhin et al., 2007, pl. 1, fig. 16.

Holotype. Department of Geology, the University of Iowa, no. SUI no. 5572; type section of Sweetland Creek shale, about four miles east of Muscantine, Iowa; Late Devonian (Miller and Youngquist, 1947, pl. 74, fig. 9).

Explanation of Plate 7

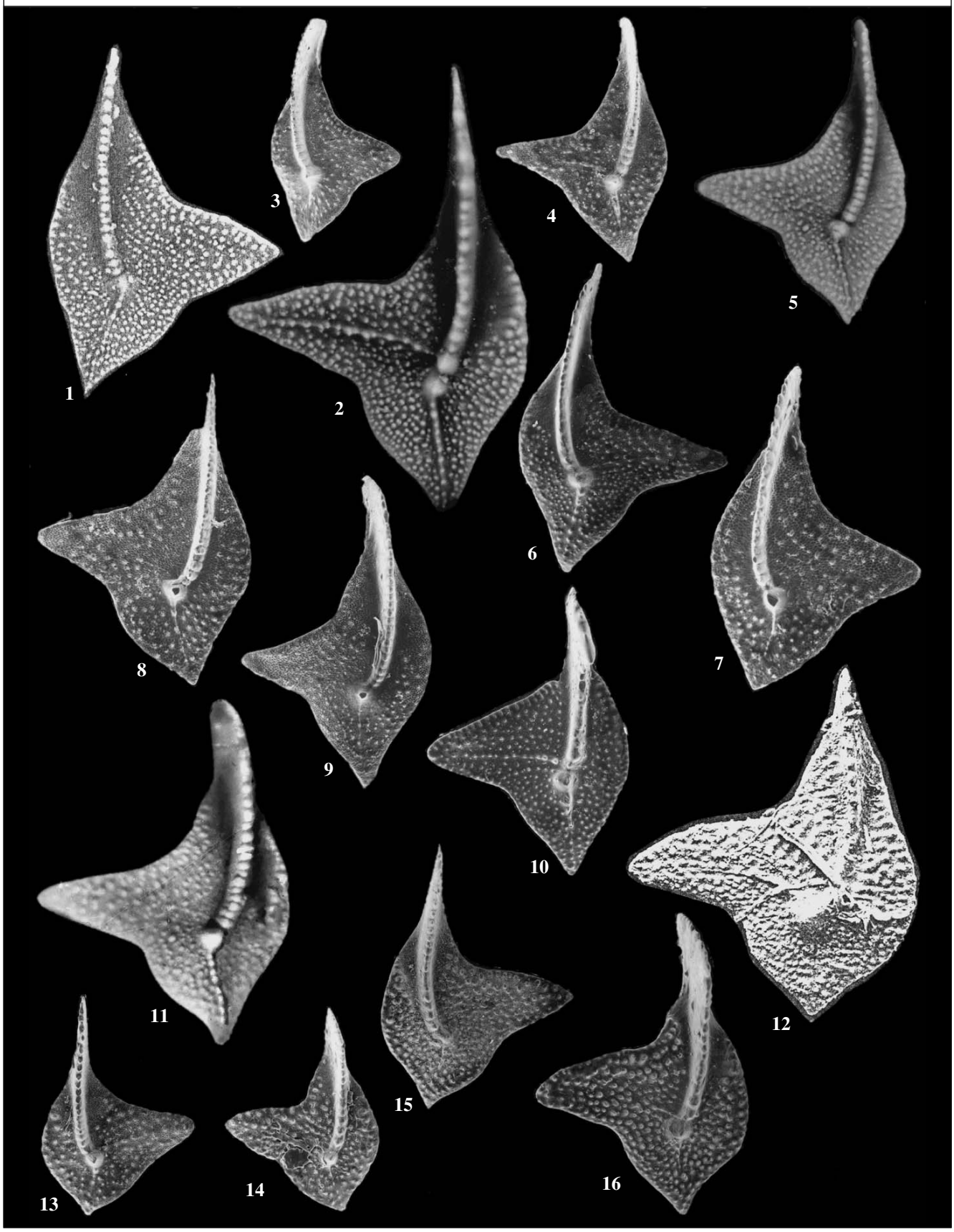
Figs. 1–8. *Palmatolepis nasuta* Müller et Müller, 1956: (1) holotype, reillustration after Müller, 1956, pl. 6, fig. 31, ×40; (2, 3) southern Ural Mountains, Sikaza River, khutor of Kuk-Karauk, opposite to the mouth of the stream, outcrop 1, sample 1/13; Frasnian Stage, Mendym Regional Stage, specimens: (2) PIN, no. 5255/22, ×45; (3) PIN, no. 5255/23, ×45; (4) specimen PIN, no. 5254/6, ×45; Volga–Ural Province, Orenburg Region, Kolgany 17, sample 94, interval 3369–3374 m; Frasnian Stage, Mendym Regional Stage; (5) specimen PIN, no. 5255/24, ×45; southern Ural Mountains, Sikaza River, outcrop 2, sample 2/3; Frasnian Stage, Askyn Regional Stage; (6) specimen PIN, no. 5254/7, ×45; Volga–Ural Province, Orenburg Region, Zarinskaya 350, interval 3591–3600 m; Frasnian Stage, Mendym Regional Stage; (7) specimen PIN, no. 5255/25, ×45; southern Ural Mountains, Sikaza River, opposite to the Kuk-Karauk Stream, outcrop 1, sample 1/13; Frasnian Stage, Askyn Regional Stage; (8) (= *Palmatolepis rhenana* Bisch.) reillustration after Kononova, 1969, pl. 1, fig. 2, ×45; southern Ural Mountains, Sikaza River, outcrop 2, sample 2/1; Frasnian Stage, Askyn Regional Stage.

Figs. 9–11. *Palmatolepis rhenana* Bischoff, 1956: (9) holotype, reillustrated after Bischoff, 1956, pl. 8, fig. 27, ×20; (10) specimen PIN, no. 5254/8, ×45; southern Ural Mountains, Sikaza River, opposite to the stream, khutor of Kuk-Karauk, outcrop 1, sample 1/13; Frasnian Stage, Askyn Regional Stage; (11) reillustrated after Klapper et al., 1996, text-fig. 8.7; Timan–Pechora Province, Khoreiver Depression, Bagan, borehole no. 3, sample 18-A, interval 3174.8–3178 m; Frasnian Stage, Askyn Regional Stage.

Figs. 12–15. *Palmatolepis mülleri* Klapper et Foster, 1993: (12) holotype, reillustrated after Klapper et Foster, 1993, fig. 16.8, ×40; (13) specimen PIN, no. 5254/9, ×45; Volga–Ural Province, Orenburg Region, Malakhovskaya 400, interval 3262–3272 m; Frasnian Stage, Mendym Regional Stage; (14) specimen PIN, no. 5254/10, ×45; Volga–Ural Province, Tatarstan, Severnyi Kupol 71, interval 1646.2–1649.7 m, sample 60; Frasnian Stage, Evlanovo Regional Stage; (15) reillustrated after Klapper et al., 1996, text-fig. 8.1, ×40; southern Timan, borehole no. 2068, sample 25, depth of 12 m; Frasnian Stage, Lyaiol' Formation, unit 3.

Fig. 16. *Palmatolepis mucronata* Klapper, Kuzmin et Ovnatanova, 1996, specimen PIN, no. 4551/41, ×40; southern Timan, borehole no. 2068, depth of 46 m; sample 19A; Frasnian Stage, Lyaiol' Formation, unit 2.

Plate 8



D i a g n o s i s. Pa element: platform wide, slightly asymmetrical and convex; lateral margins raised in anterior half of platform and flattened in posterior part; anterior end straight and posterior end turned inwards and arched downwards; lingulate in adults. Median ridge slightly arched, high, denticulated, and usually terminating near middle of platform. Free blade with four or five almost equally high denticles, one-fourth as long as platform. Troughs deep and wide in anterior part of platform and usually terminating in middle of platform. Ornamentation consisting of well pronounced and coarse transverse ridges in anterior half of platform and thin transverse ridges in posterior part. Lingulate posterior end of platform hatched with system of thin transverse ridges. Basal cavity small, with narrow flanks, and located in anterior third of platform. Keel low.

V a r i a b i l i t y. In small (young) specimens, the lateral margins of the platform are raised and the troughs are deep along the whole length up to its posterior end; the median ridge reaches the posterior end of the platform.

C o m p a r i s o n. This species differs from *Polygnathus torosus* Ovnatanova et Kononova, 1996 in the detached lingulate posterior end of the platform and in the lateral margins of the platform turned inwards and elevated in the anterior part.

O c c u r r e n c e. United States (Iowa State), Poland; Upper Devonian, Frasnian Stage; Germany, Late *rhenana* Zone (Benner Bicken and Steinburg Schmidt sections, collection of W. Ziegler); Australia (Canning basin); Russia: Voronezh Anteclise, Evlanovo Regional Stage; Volga–Ural Province, Tatarstan, Askyn Regional Stage; southern Timan, Lyaiol' Formation, unit 4; shallow-water deposits of the Ukhta Formation.

M a t e r i a l. Volga–Ural Province: Tatarstan, Severnyi Kupol 71, samples 63 and 59, interval 1646–1651 m, Askyn Regional Stage; Orenburg Region, Kolgany 17, interval 3275–3280 m, Evlanovo Regional Stage; Romanovskaya 2, interval 2578–2586 m, Askyn Regional Stage. Southern Timan: borehole no. 2060, depth of 9.5 m, Ukhta Formation; Timanskaya 10, sample 51, interval 287–289 m, Ukhta Formation, subsulphate strata; Vezha-Vozh River, outcrop 10, sample 3, Lyaiol' Formation, unit 4.

***Polygnathus churkini* Savage et Funai, 1980**

Plate 22, fig. 19

Polygnathus churkini: Savage and Funai, 1980, p. 809, pl. 1, figs. 1–14, pl. 2, figs. 1–5; Aristov, 1988, p. 85, pl. 3, figs. 13 and 14; Barskov et al., 1991, p. 45, pl. 15, figs. 8–11; Aristov, 1994, pl. 8, figs. 12 and 13; Ziegler et al., 2000, pl. 5, fig. 10, pl. 7, figs. 5 and 6; Ovnatanova and Kononova, 2001, p. 41, pl. 22, figs. 1, 2, 8, and 9, pl. 27, figs. 20, 26, and 27.

H o l o t y p e. USNM, no. 224238, Coronados Island, southeastern Alaska; Frasnian Stage, presumably Lower *asymmetricus* Zone (Savage and Funai, 1980, pl. 1, figs. 1–5).

D i a g n o s i s. Pa element: platform lanceolate and slightly laterally curved; lateral margins highly raised in anterior part and flattened posteriorly; outer margin higher than inner margin; posterior end of platform pointed. Median ridge straight, nodular, high in anterior half of platform and low in posterior part. Free blade high, denticulated, one-third as long as platform. Troughs narrow, deep in anterior part of platform; inner trough usually deeper. Ornamentation consisting of transverse ridges along margins in anterior part of platform and long and thin ridges obliquely directed to median ridge in posterior part. Basal cavity small, with narrow flanks, and located in anterior quarter of platform.

C o m p a r i s o n. This species differs from *Polygnathus brevis* Miller et Youngquist, 1947 in the lanceolate platform and transverse ridges located in the posterior half of the platform and directed obliquely to the median ridge.

R e m a r k s. This species was initially established based on specimens from Coronados Island of the southeastern Alaska presumably from the Frasnian beds of the Lower *asymmetricus* Zone. However, *Po. aspelundi* and *Po. politus* (=*Po. pacificus*) co-occurred with *Polygnathus churkini*; therefore, the deposits of Coronados Island (southeastern Alaska) should be dated as the Middle–Upper Frasnian rather than the Lower Frasnian. It is probably a shallow water analogue of the *rhenana* Zone. Similar assemblages are widespread in the deposits of the Voronezh and Evlanovo regional stages (shallow analogue of the Early and Late *rhenana* zones) of the Russian Platform.

O c c u r r e n c e. Upper Devonian, Frasnian Stage, analogue of the *rhenana* Conodont Zone. United States, Canada; Russia: Voronezh Anteclise, Voronezh and Evlanovo regional stages; Volga–Ural Province, Petino

E x p l a n a t i o n o f P l a t e 8

Figs. 1–11. *Palmatolepis mucronata* Klapper, Kuzmin et Ovnatanova, 1996: (1) holotype, reillustrated after Klapper et al., 1996, text-fig. 7–11, ×40; (2) specimen PIN, no. 4551/44, ×40; southern Timan, borehole no. 2068, sample 19A, depth of 46 m; Frasnian Stage, Lyaiol' Formation, unit 2; (3–5) southern Timan, borehole no. 2023, depth of 89 m, sample 7; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (3) PIN, no. 5255/26, ×35; (4) PIN, no. 5255/27, ×35; and (5) PIN, no. 4551/50, ×40; (6–10) southern Timan, borehole no. 2068, depth of 46 m, sample 19A; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (6) VNIGNI, no. ONS 6/51, ×32; (7) VNIGNI, no. ONS 6/47, ×63; (8) VNIGNI, no. ONS 6/48, ×54; (9) VNIGNI, no. ONS 6/49, ×45; and (10) PIN, no. 5255/28, ×45; (11) (=*Palmatolepis nasuta*) reillustrated after Menner et al., 1992, pl. 4, fig. 7, ×40.

Figs. 12–16. *Palmatolepis brevis* Ziegler et Sandberg, 1990: (12) holotype, reillustrated after Ziegler and Sandberg, 1990, pl. 13, fig. 2, ×45; (13–16) southern Timan, borehole no. 2023, depth of 189 m, sample 7; Frasnian Stage, Lyaiol' Formation, unit 2, specimens: (13) VNIGNI, no. ONS 6/42, ×35; (14) VNIGNI, no. ONS 6/43, ×35; (15) VNIGNI, no. ONS 6/44, ×40; and (16) VNIGNI, no. ONS 6/45, ×35.

Plate 9