

New Bryozoans from the Devonian of Afghanistan and the Carboniferous of Iran

R. V. Gorjunova

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: rgoryunova@mail.ru

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Abstract—A new family, Vidronovellidae, with a new genus, *Vidronovella*, and its type species *V. fastigata* sp. nov., and a new species, *Europora gerirudensis*, are described from the Famennian of Afghanistan, and the new species *Primorella iranica*, *Heloclema magnificum*, and *Worthenopora elbursensis* are described from the Viséan of Iran.

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INTRODUCTION

The Paleozoic bryozoans of Afghanistan are still little known and poorly studied. The French husband and wife paleontologists Termier and Termier (1971) were the first to provide information on them. In addition to the predominant Permian bryozoans, they described several species of Carboniferous fenestellides and a single bryozoan from the Frasnian Stage of this country.

The Afghan bryozoans that are described in this paper were collected and deposited in the Paleontological Institute by the geologist V.I. Dronov in the early

1970s. They come from the Famennian Stage (Etroeungtian Zone, Strunian Stage), which is exposed south of the Harirud River, between the villages of Tulak and Chaghcharan, in channels of small intermittent streams and lakes in western Afghanistan (Fig. 1).

The collection includes representatives of virtually all orders of Paleozoic bryozoans: Cystoporida, Trepostomida, Fenestellida, and Rhabdomesida. The taxonomic composition of the bryozoans belonging to the first three orders either closely resembles or, in many instances, is identical to that of Late Famennian bryo-

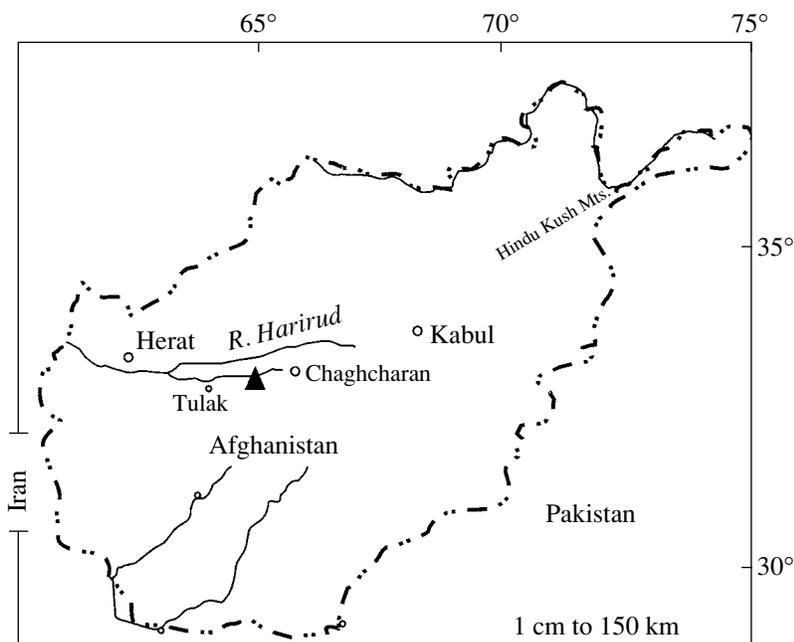


Fig. 1. Schematic map of the bryozoan locality in Afghanistan (marked by a dark triangle).

zoans of Kazakhstan, Kuznetsk Basin, Altai, and Siberia (identified by I.P. Morozova and the author). In contrast, the rhabdomesides are represented by forms with quite peculiar morphology; unfortunately, they are limited in number, many are known only from single specimens of isolated fragments of colonies. Thus, their study has been postponed. However, after 35 years of waiting, our hopes of enriching the collection of rhabdomeside bryozoans from Afghanistan have faded. Nevertheless, this collection still retains its interest for scientists, despite the fact that Paleozoic bryozoans as a whole have been well studied. In addition, the necessity of considering the Afghan bryozoans stems from their stratigraphic position at the Devonian–Carboniferous boundary. It is remarkable that during this time interval, when ecologically related faunal groups declined in number under the adverse conditions caused by marine regression at the end of the Devonian, bryozoans, especially rhabdomesides, were able to expand, i.e., they filled the ecological niches left vacant (Gorjunova et al., 2004).

New taxa from Afghanistan described in this paper improve our knowledge of the distribution of rhabdomesides and of the biodiversity of Paleozoic bryozoans.

The Viséan bryozoans from Iran are also of interest. These were collected by the late I.A. Gretschishnikova (Moscow State Geological Prospecting Institute, now Academy) during an expedition to the eastern Elburz Mountains (Fig. 2) in the early 1970s, and are now deposited in the Paleontological Institute.

Examination of this collection has showed that its chief interest lies in rhabdomesides and cryptostomides. However, these, and Afghan bryozoans have not been described until now. The identification of some of them as members of the genus *Primorella*, previously known only from Permian deposits (Romantchuk and Kiseleva, 1968), was then in doubt.

However, members of *Primorella* are now known not only from the Lower Carboniferous (Gorjunova, 1988) but also from the Middle and Upper Devonian of Poland (Morozova et al., 2003). The genus *Heloclema* from the Serpukhovian Stage of the Russian Platform has remained monotypic until now (Schulga-Nesterenko, 1955). A new species of this genus recorded from earlier (Viséan) deposits of Iran may be important for improving knowledge of the center of evolutionary diversification and geography of *Heloclema* species, as well as for phylogenetic and paleogeographic reconstructions of both rhabdomesides and the Paleozoic bryozoans as a whole. Although the genus *Worthenopora* was discovered many years ago (Miller, 1889), its species are limited in number (no more than four) and are distributed predominantly in the Viséan deposits of North America (Hageman, 1991; Gorjunova and Lavrentjeva, 1993) and the Kasimovian Stage of the Russian Platform (Makhlina et al., 2001). A new Iranian species, *W. elbursensis*, shows that the distribution of this genus was wider.

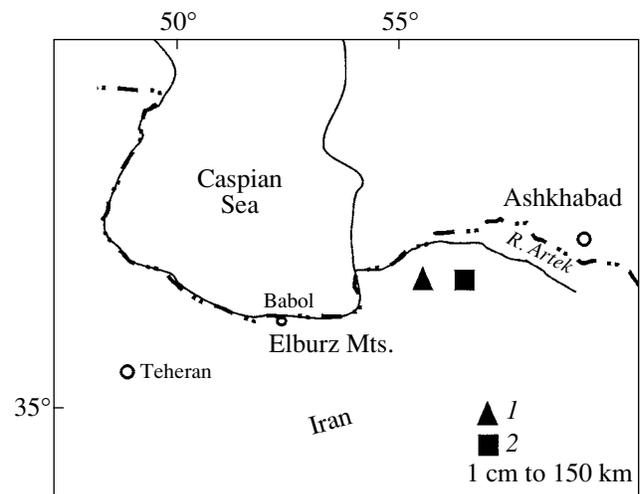


Fig. 2. Schematic map of the bryozoan localities in Iran: villages of (1) Bidestan and (2) Tue.

This paper contains diagnoses of the genera *Europora*, *Primorella*, *Heloclema*, and *Worthenopora* for a number of reasons: firstly, their diagnostic characterization is refined and augmented based on thoroughly studied morphology and using modern terminology; secondly, the latest data on their species composition are taken into account; and thirdly, their geochronology and paleogeography are substantially improved.

MATERIAL

The collection studied is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), no. 1613.

MORPHOLOGY AND CLASSIFICATION OF BRYOZOANS

The bryozoans studied are characterized by a distinctive pattern of slender, slim, and fairly delicate dendroid colonies, varying from 0.70 to 1.50 mm in diameter. Four of the described species, i.e., *Europora gerirudensis* sp. nov., *Vidronovella fastigata* gen. et sp. nov., *Primorella iranica* sp. nov., and *Heloclema magnifericum* sp. nov., belong to the order Rhabdomesida. Only one species, *Worthenopora elbursensis* sp. nov., belongs to the order Cryptostomida.

The Famennian (Etroungtian Zone) of Afghanistan has yielded representatives of two genera: *Europora* and *Vidronovella*.

The genus *Europora*, which is characterized by slim dendroid colonies, was discovered by Chinese bryozoologists from the Lower Carboniferous (Tournaisian) of Hunan province (Yang et al., 1988). Its elongate tubular autozoecia are strongly curved at the endozone–exozone boundary. This boundary is marked by the fact

that each autozoecium has a diaphragm and hemiseptum. The autozoecia open at the surface of colonies through elliptical apertures arranged in regular, longitudinal and diagonally intersecting rows: hence the spiral body plan, showing that the genus *Europora* belongs to rhabdomesides (Pl. 2, fig. 1). In the *Europora* species the growth of autozoecia strictly followed a spiral pattern with a constant locus of budding, but without any central axis in the colony. According to the author's classification (Gorjunova, 1996), the absence of a central axis is a key character of the suborder Goldfussitrypina, which includes the family Nicklesporidae, including the genus *Europora*.

The new genus *Vidronovella* is especially noteworthy in having a peculiar morphology, unique among Paleozoic bryozoans. I place it into the new family Vidronovellidae (order Rhabdomesida). This genus features the thinnest dendroid colonies, circular in cross section, with elliptical apertures arranged in longitudinal and diagonal rows on the colony surface, providing evidence of the spiral body plan (Pl. 2, figs. 2a, 2c). All these characters of the new genus quite fit the diagnosis of the order Rhabdomesida. The vidronovellids resemble the bryozoans of the order Cryptostomida in the elliptical shape and arrangement of apertures on the colony surface. However, vidronovellids essentially differ from the frondose-dendroid, symmetrically bilaminar Cryptostomida in the cylindrical shape of the colony.

The determination of the position of the new genus in the system of the order Rhabdomesida presents many difficulties. I tentatively place the Vidronovellidae into the suborder Nikiforovellina. Doubts are primarily cast upon the difference in the internal structures of these groups. The true Nikiforovellina are characterized by a central axis at the center of the endozone. The new genus has, instead of the central axis, a short median wall (mesotheca) at the very center of the colony, which can be seen in the cross sections (Pl. 2, fig. 2c). The mesotheca corresponds to the central axis genetically but not morphologically. In the longitudinal sections it is shaped like an irregular broken line (Fig. 3, Pl. 2, fig. 2b). A similar type of the zoarial pattern is only known in the Ordovician genus *Otoseetaxis* Bassler, 1952. In contrast to the mesotheca of symmetrically bilaminar Cryptostomida, which is a symmetry plane of frondose-dendroid colonies, the mesotheca of the genus *Vidronovella* apparently functioned as a central axis; i.e., controlled the direction of the vertical growth of small cylindrical branches (Pl. 2, fig. 2c). These differences in the morphology of the endozone are most likely due to the shape of autozoecia, the morphology of which prevented the formation of a lineal axis in the process of budding, but favored the formation of a shorter median wall, or mesotheca (Pl. 2, fig. 2c).

Rhabdomesides are characterized by tubular autozoecia that are elongated or shortened, constricted proximally, and variably curved in the exozone. In con-

trast, vidronovellids are characterized by boxlike rather than tubular autozoecia. Prior to the start of the upward growth of the colony, such autozoecia, being budded virtually at a right angle and oriented radially with respect to the mesotheca, assume a position perpendicular to the colony. In cross section they are shaped like isosceles triangles that are radially arranged with respect to the mesotheca and have the apex at the center of the endozone (Pl. 2, fig. 2c). In longitudinal section they represent elongated rectangles with rounded corners in the axial part of the colony (Pl. 2, fig. 2b). Distally they terminate in a short vestibule and open at the colony surface through elliptical apertures (Fig. 3; Pl. 2, fig. 2a). This vestibule is separated from the principal body cavity of an autozoecium by a long distal hemiseptum, which develops in the distal part of the autozoecium (Fig. 3; Pl. 2, fig. 2b).

The morphology of the new genus is distinctive in having conical structures packed in between the apertures in longitudinal rows (we here refer to them as fastigia: from the Latin *fastigium*, meaning "top, gable roof"). Fastigia are cap-shaped structures projecting beyond the general surface of the colony. Their peculiar morphology is most clearly seen in the longitudinal section of the colony (Fig. 3a). In side view fastigia are shaped like an avicularium (bird head) with a long slender neck and a beak. This beak enters the body cavity of autozoecia and has a position that corresponds to the proximal hemiseptum (Fig. 3a). The axial part of fastigia is composed of dark-colored vesicular tissue, which is an extension of the walls of neighboring autozoecia and is surrounded by amorphous homogeneous mass without any cavities or plates. In tangential sections vesicular tissue is usually marked by a dark-colored dot at the centers of the square spaces between the neighboring apertures (Pl. 2, fig. 2a). To my knowledge, neither rhabdomesides nor the Paleozoic bryozoans as a whole contain any structures analogous to fastigia; i.e., are devoid of any cavities, plates, or bars. Fastigia radically differ from acanthozoecia, stellatopores, and various rod-shaped and capillary structures known in rhabdomeside bryozoans. Each fastigium coupled with an autozoecium forms a complex module, which is regularly reproduced from generation to generation during colony growth. The interpretation of the functional role of fastigia in the colony is a rather difficult task. It is possible that they only passively performed some function: either to facilitate feeding through the control of water currents around the colony or to support lophophores during the feeding action.

I assume that the shape of autozoecia and the presence of fastigia are distinguishing characters of the new family Vidronovellidae. All the above characters taken together, including the boxlike shape of the autozoecia and the presence of short proximal and elongated distal hemisepta in the autozoecia, are characteristic of the genus *Vidronovella*.

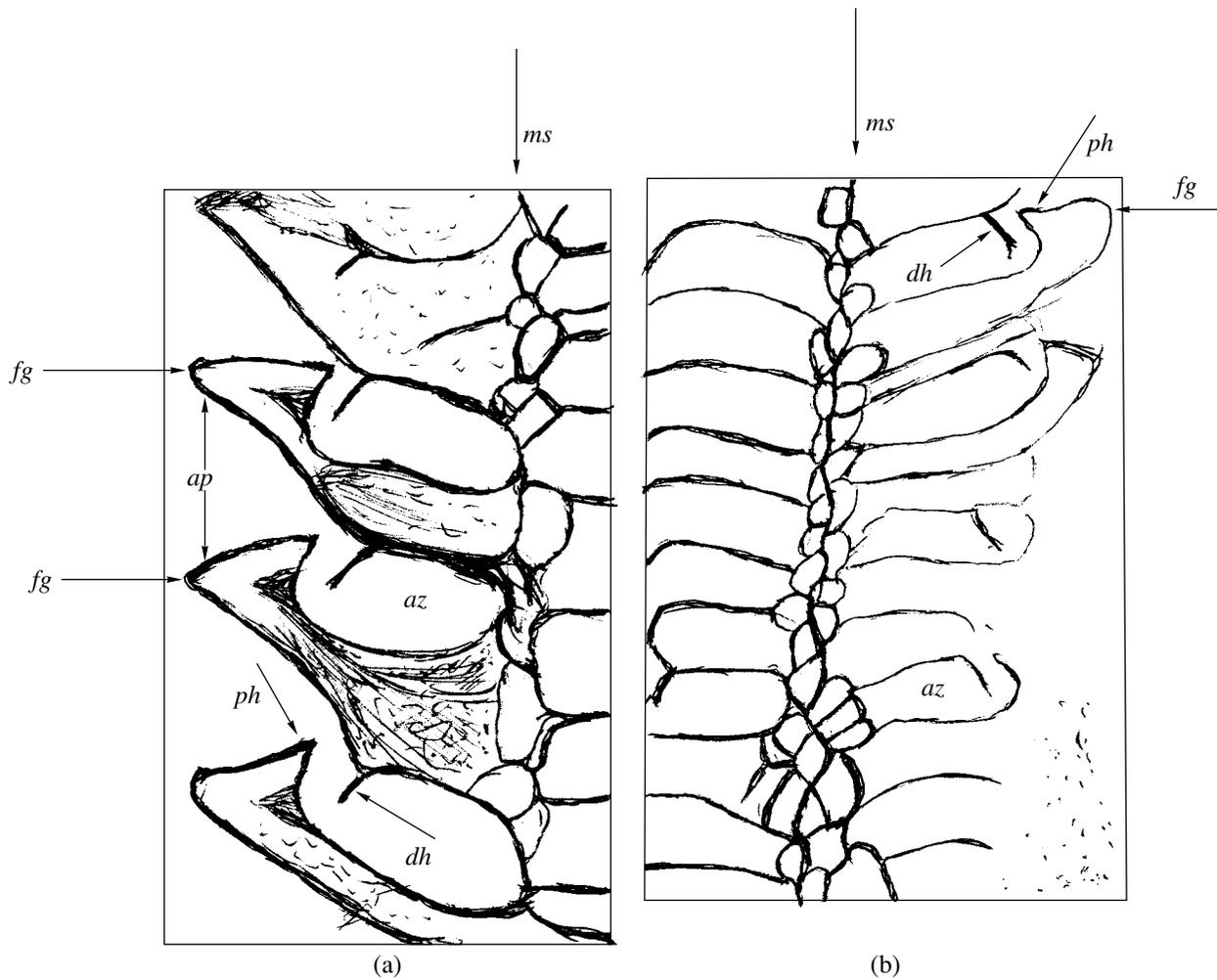


Fig. 3. *Vidronovella fastigata* sp. nov.; holotype PIN, no. 1613/389: (a) longitudinal section of the colony showing a vertically directed zigzag mesotheca (*ms*) on the right side of the figure, to the left of this mesotheca there are boxlike autozooeccia (*az*), distal hemiseptum (*dh*, short arrow), proximal hemiseptum (*ph*, long arrow), fastigia arranged in a single row (*fg*), and aperture (*ap*), $\times 90$; (b) longitudinal section showing the morphology of the same colony when fastigia (*fg*) are destroyed (left) or poorly preserved (right), $\times 60$; Harirud River, between the villages of Tulak and Chaghcharan; Famennian.

It is worth noting that during the burial of colonies, fastigia could be partly destroyed. Thus, sections of any type should be prepared more carefully. For example, the morphology of fastigia can be only partly traced in the longitudinal section of the colony (Fig. 3b). The presence of fastigia should be inferred from other characters, although at first sight these characters may appear indirect. The boxlike shape of the autozooeccia, which have a long distal hemiseptum, and a portion of the base of the fastigia preserved (although poorly) (shown at the right in the figure), clearly demonstrate that this bryozoan belongs to the genus *Vidronovella*.

Morphologically, the new species *Heloclema magnificum* very closely resembles the type species *H. spirale*; however, the latter differs from the former, in addition to other characters, in the pores arranged in pairs at the distal edge of the apertures and in the

minute capillaries clustered together between the apertures and arranged in longitudinal rows, referred to as valves by Schulga-Nesterenko (Fig. 4).

The new cryptostome species *Whortenopora elbursensis* is also of interest. This has dendroid colonies with an elliptical cross section, the thinnest sinusously curved mesotheca, and flask-shaped autozooeccia with semicircular apertures that are truncated proximally. The apertures in the longitudinal rows are separated by interspaces shaped like triangles with the acute apex pointed toward the distal edge of the apertures (Pl. 2, fig. 5). The morphogenesis of these structures has not been adequately studied because of the limited number of *Whortenopora* species and the poor state of preservation of their rather fragile colonies, which are characterized by a narrow and, therefore, poorly calcified exozone.

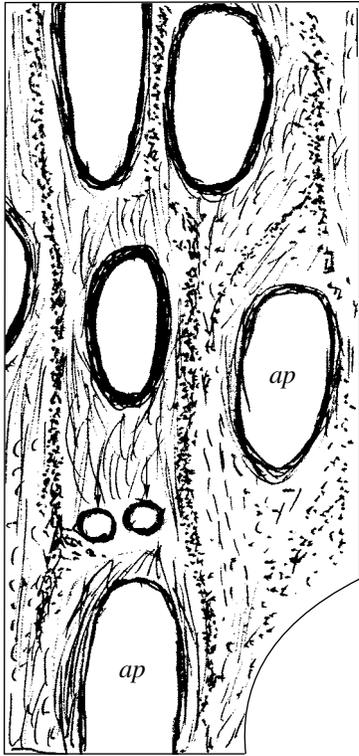


Fig. 4. *Heloclema magniferum* sp. nov.; holotype PIN, no. 1613/370 (2); tangential section showing morphology and the position of pores arranged in pairs (short arrows) near the distal edge of the apertures (ap), $\times 90$; eastern Elburz Mountains; Viséan.

SYSTEMATIC PALEONTOLOGY

Order Rhabdomesida

Suborder Goldfussitrypina

Family Goldfussitrypidae Gorjunova, 1985

Subfamily Nicklesoporinae Gorjunova, 1985

Genus *Europora* Yang, Hu, et Xia, 1988

Europora: Yang et al., 1988, p. 135.

Type species. *E. similomesoporis* Yang, Hu, et Xia, 1988; Lower Carboniferous, Tournaisian, Lower Aikuanian, Shaodon Formation; central China, Hunan.

Diagnosis. Colonies thinly branched, quite often dichotomously branching, differentiated into

endo- and exozone, dimorphic. Autozooezia elongate tubular, narrowed proximally and moderately widened distally, strongly (almost at a right angle) curved at boundary with exozone, marked by the presence of a single diaphragm or hemiseptum. Budding along spiral, without formation of central axis. Apertures elliptical, subelliptical, or subcircular to subelliptical, arranged in longitudinal and diagonal rows. Walls of autozooezia in exozone pierced by numerous microacanthostyles. Neither acanthozooezia, nor pores, nor stellatopores, nor capillaries.

Species composition. Five species: *E. gerirudensis* sp. nov. from the Famennian of Afghanistan; *E. unilaminata* Yang, Hu, et Xia, 1888; *E. bilaminata* Yang, Hu, et Xia, 1988; *E. similomesoporis* Yang, Hu et Xia, 1988; and *E. peculiaris* Yang, Hu, et Xia, 1988 from the Tournaisian of central China.

Comparison. This genus differs from the most closely related genus *Nicklesopora* Bassler, 1952 in the strongly curved autozooezia, the presence of a diaphragm or hemiseptum at the inflection of autozooezia, the presence of microacanthostyles in the exozone, and in the absence of pores; it differs from the genus *Paranicklesopora* Gorjunova, 1988 (Gorjunova, 1988) in the different shape of the autozooezia, the absence of paired hook-shaped hemisepta in autozooezia, and in the exozone not pierced by stellatopores.

Europora gerirudensis Gorjunova sp. nov.

Plate 2, fig. 1

Etymology. From the Harirud River.

Holotype. PIN, no. 1613/386; Afghanistan, south of the Harirud River, between the villages of Tulak and Chaghcharan; the Upper Devonian, Upper Famennian (Etroeungtian Zone).

Description. The colonies are thinly branched, straight or dichotomously branching, 1.25–1.50 in diameter, more rarely with encrusting layers 0.36–0.56 mm thick. The endozone is about 1 mm in diameter, the exozone is 0.13–0.15 mm thick. The autozooezia, which budded along the spiral, are elongate tubular and are strongly, almost at a right angle, curved where they emerge from the colony surface at the boundary with the exozone. They contain only single diaphragms and only sporadically. At the inflection of autozooezia

Explanation of Plate 2

Fig. 1. *Europora gerirudensis* sp. nov.; holotype PIN, no. 1613/386: (1a) tangential section, $\times 60$; (1b) longitudinal section, $\times 40$; Afghanistan, south of the Harirud River, between the villages of Tulak and Chaghcharan; Famennian (Etroeungtian Zone).

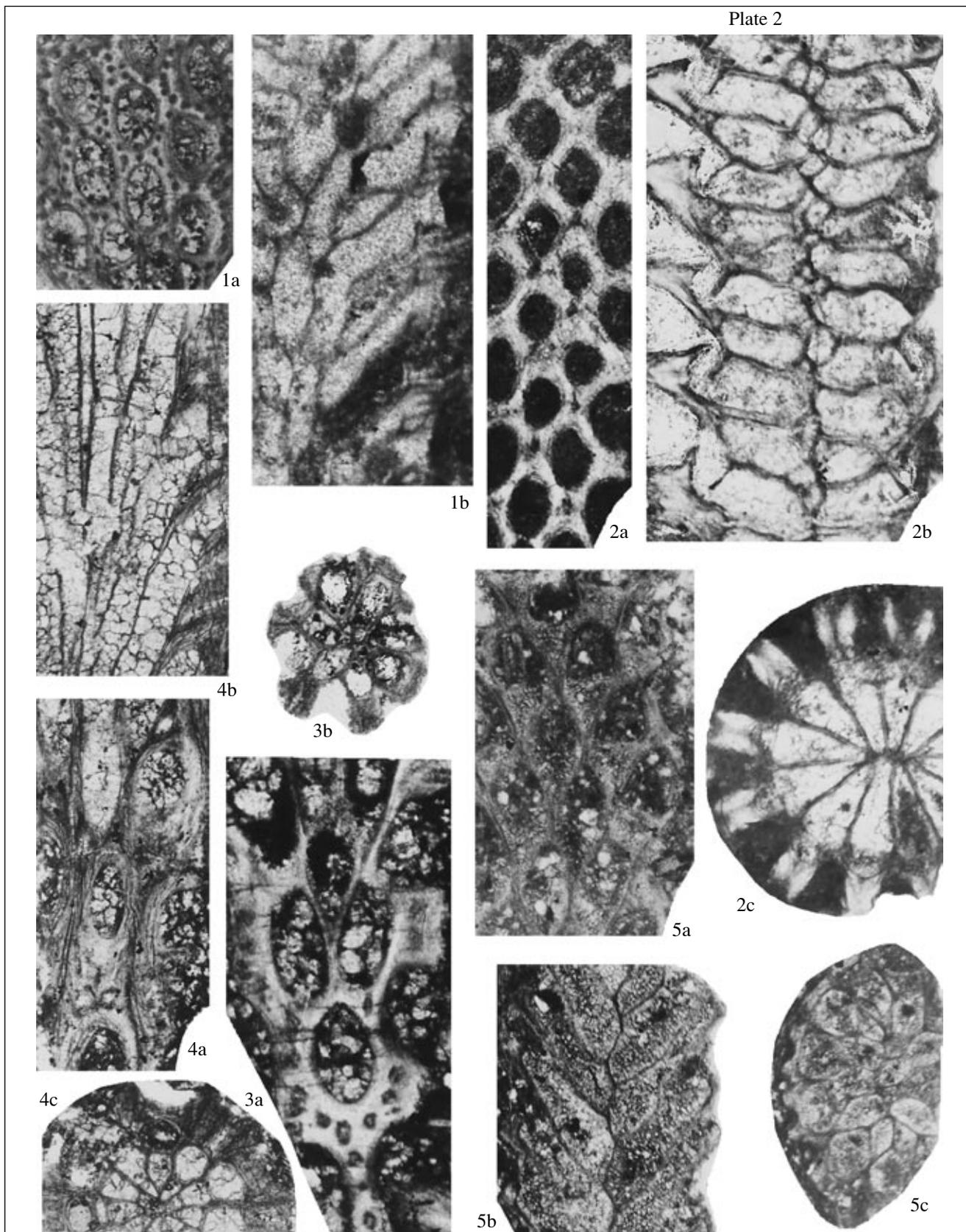
Fig. 2. *Vidronovella fastigata* sp. nov.; holotype PIN, no. 1613/389, $\times 60$: (2a) tangential section, (2b) longitudinal section, (2c) cross section; locality and age as in Fig. 1.

Fig. 3. *Primorella iranica* sp. nov.; holotype PIN, no. 1613/370 (1) $\times 60$: (3a) tangential section, (3b) cross section; Iran, eastern Elburz Mountains, village of Tue; Viséan.

Fig. 4. *Heloclema magnificum* sp. nov.; holotype PIN, no. 1613/370 (2): (4a) tangential section, $\times 60$; (4b) longitudinal section, $\times 40$; (4c) cross section, $\times 40$; locality and age as in Fig. 3.

Fig. 5. *Worthenopora elbursensis* sp. nov.; holotype PIN, no. 1613/379, $\times 60$: (5a) tangential section, (5b) longitudinal section, (5c) cross section; Iran, eastern Elburz Mountains, village of Bidestan; Viséan.

Plate 2



there is usually one hemiseptum, located on the proximal side. The hemisepta are flat, entering the body cavity of an autozoecium 0.02 mm deep. The walls of the autozoecia are slender in the endozone (0.01 mm thick) and thicker in the exozone (up to 0.03 mm thick). The microstructure of the walls consists of longitudinal fibers. The apertures are subcircular to subelliptical, 0.13–0.16 mm long and 0.10–0.11 mm wide, and are arranged in longitudinal and diagonally intersecting rows. The distance along the colony surface between the centers of apertures is 0.23–0.25 mm in longitudinal rows and 0.20–0.21 mm in diagonal rows. A 2-mm stretch of the colony surface contains 7–8 apertures both in longitudinal and diagonal directions. The microactinostyles are 10–15 μm in diameter, pierce the exozone, form virtually a single row of 18–20 microactinostyles around each autozoecium, and form no hexagonal contours around the apertures.

Comparison. The new species resembles *E. peculiaris* in the morphological features of the internal structure of colonies and in the relationship between the endo- and exozone but differs from the latter in the smaller diameter of colonies (1.25–1.50 mm instead of 3.00–3.50 mm), the subcircular to subelliptical apertures, the length of apertures (0.13–0.16 mm instead of 0.16–0.26 mm), and in the chaotic arrangement of microacanthostyles.

Material. Holotype (sample 6194, collected by V.I. Dronov).

Suborder Nikiforovellina

Family Vidronovellidae Gorjunova, fam. nov.

Type genus. *Vidronovella* gen. nov.

Diagnosis. Colonies thinly branched, perhaps rod-shaped, circular or slightly elliptical in cross section, with short mesotheca in axial region, formed by radially-spiral budding of autozoecia, without differentiation into endo- and exozone, dimorphic. Mesotheca zigzag in longitudinal section, straight and short in cross section, dividing colony into symmetrical parts. Autozoecia short tubular, boxlike, slightly narrowed proximally and slightly curved at colony surface, without diaphragms. Autozoecia bear proximal and distal hemisepta. Proximal hemiseptum hook-shaped, short, located near proximal wall; distal hemiseptum long, slender, directed at an obtuse angle away from distal to proximal wall, overlapping two-thirds of body cavity of autozoecia. Autozoecia contain no diaphragms. Aperture rounded or rounded-rhombic, arranged in longitudinal and diagonally intersecting rows. Fastigia occur between apertures in longitudinal rows, fastigia and apertures alternate. Above colony surface, fastigia shifted toward proximal edge of apertures. Heterozoecia absent. Stellatopores, actinostyles, and capillaries absent.

Composition. Type genus.

Comparison. The new family differs from all the other families of the suborder Nikiforovellina in the radially spiral body plan of the colony with a shortened mesotheca, the boxlike shape of autozoecia, and the presence of fastigia. It resembles the family Arthroclemididae in having dimorphic colonies. However, the presence of a shortened mesotheca restricted to the endozone region instead of the lineal axis characteristic of the Arthroclemididae and the boxlike shape of autozoecia are important distinguishing characters of the new family.

Genus *Vidronovella* Gorjunova, gen. nov.

Etymology. In memory of Viktor Ivanovich Dronov, who discovered this bryozoan.

Type species. *V. fastigata* sp. nov.

Diagnosis. The same as for the family.

Species composition. Type species.

Vidronovella fastigata Gorjunova, sp. nov.

Plate 2, fig. 2

Etymology. From the Latin *fastigatus* (sharp, peaked).

Holotype. PIN, no. 1613/389; western Afghanistan, south of the Harirud River, between the villages Tulak and Chaghcharan; the Upper Devonian, Famenian (Etroeungian Zone).

Description. The colonies are dendroid, 1.00–1.10 mm in diameter. The autozoecia are short, tubular, and boxlike in longitudinal section and are shaped like isosceles triangles, slightly narrowed at the proximal ends of the axial part of the colony in cross section. The autozoecia are 0.25–0.26 mm long and 0.03 and 0.11 mm wide at the proximal and distal tips, respectively. The walls are straight, smooth, slender (0.01 mm thick), uniform along the entire length, with a microstructure consisting of longitudinal fibers. Diaphragms are absent. The distal hemiseptum is straight, this is directed upward at an obtuse angle to the dorsal wall and enters the body cavity of autozoecia 0.06–0.08 mm deep. The fastigia, which are slightly inclined upward along the growth direction of the colony, are 0.21 mm high at the center and 0.025 mm in diameter at the base. The proximal slope of the fastigia is 0.15 mm long, the distal slope is 0.13 mm long, with the lower edge terminating in a 0.03-mm-long proximal hemiseptum. The apertures are subcircular or rounded-rhombic in deeper sections, which measure 0.13 \times 0.11 mm and 0.18 \times 0.12 mm. The distance between the centers of apertures is 0.28 mm in longitudinal rows and 0.20 mm in diagonal rows. A 2-mm stretch of the colony surface contains seven apertures in longitudinal rows and ten apertures in diagonal rows. Zooecia show no polymorphism. Stellatopores and capillaries are absent.

Material. Holotype (sample 2435/1, collected by V.I. Dronov).

Family Arthroclemidae Simpson, 1897**Subfamily Primorellinae Gorjunova, 1985****Genus *Primorella* Romantchuk et Kiseleva, 1968**

Primorella: Romantchuk and Kiseleva, 1968, p. 57; Gorjunova, 1975, p. 63; 1985, p. 90; Morozova, 1981, p. 44; Blake, 1983, p. 580; Morozova et al., 2003, p. 102.

Type species. *P. polita* Romantchuk et Kiseleva, 1968; Upper Permian, Kazanian Stage; Primorskii krai.

Diagnosis. Colonies thinly branched, differentiated into endo- and exozone, dimorphic. Body plan of colonies spiral. Central axis clearly defined. Autozoecia short tubular, with infrequent diaphragms, without hemisepta. Exozone abundant in stellatopores.

Species composition. Seventeen species from the Middle Devonian–Upper Permian of Europe and Asia. Two species are known from the Devonian: *P. nitida* Morozova et Weis, 2002 from the Upper Givetian of Poland and *P. indigena* Morozova et Weis, 2002 from the Frasnian of Poland. Five species come from the Carboniferous: *P. iranica* sp. nov. from the Viséan of Iran, *P. mera* Gorjunova, 1988 from the Viséan of southern Mongolia, *P. elegans* Ariunchimeg, 1992 from the Viséan–Serpukhovian of northern Mongolia, *P. tatianae* Gorjunova, 1988 from the Bashkirian Stage of southern Mongolia, and *P. ivanovi* (Schulga-Nesterenko, 1955) from the Gzhelian Stage of the Russian Platform. The checklist of Permian species is provided by Gorjunova (1985).

Comparison. This genus differs from the most closely related genus *Hexites* Schulga-Nesterenko, 1955 in the more elegant shape of colonies and elongate tubular shape of autozoecia.

***Primorella iranica* Gorjunova, sp. nov.**

Plate 2, fig. 3

Etyymology. From Iran, the place of its discovery.

Holotype. PIN, no. 1613/370 (1); Iran, eastern Elburz Mountains, village of Tue; Lower Carboniferous, Viséan.

Description. The colonies are thinly branched, dimorphic, 0.80 mm in diameter. The endozone is 0.45 mm in diameter, the exozone is 0.17 mm thick. The autozoecia are elongate tubular, bud off along the spiral, and form a lineal axis at the center of the colony. No diaphragms have been observed in the autozoecia. The walls, which have a microstructure of longitudinal fibers, are slender (0.025 mm thick) in the endozone and 0.12 mm thick in the exozone. The apertures are elliptical, 0.30 mm long, 0.16 mm wide. The distance between the centers of apertures is 0.58–0.60 mm in longitudinal rows and 0.36 mm in diagonal rows. A 2-mm stretch of the colony surface contains five apertures in longitudinal rows and six apertures in diagonal rows. The stellatopores are large, 0.03–0.05 mm in diameter, and surround each aperture by a single row of 8–12 stellatopores.

Comparison. This species differs from the most closely related species *P. mera* in the larger diameter of colonies, larger apertures (0.30 mm × 0.16 mm instead of 0.20 × 0.13 mm), the number of apertures per 2 mm (five or six instead of seven or eight in *P. mera*), and the larger number of stellatopores around the apertures (8 to 12 instead of 6 to 8).

Material. Holotype (sample 2/7, collected by I.A. Gretchishnikova).

Subfamily Helocleminae Gorjunova, 1985**Genus *Heloclema* Schulga-Nesterenko, 1955**

Heloclema: Schulga-Nesterenko, 1955, p. 139; Schulga-Nesterenko et al., 1960, p. 92; Blake, 1983, p. 559; Gorjunova, 1985, p. 93.

Type species. *H. spirale* Schulga-Nesterenko, 1955; Lower Carboniferous, Serpukhovian; Russian Platform.

Diagnosis. Colonies thinly branched, differentiated into endo- and exozone, dimorphic. Body plan of colony spiral, central axis formed. Autozoecia elongate tubular with or without hemisepta. Diaphragms virtually absent. Apertures subcircular or elliptical, with pores arranged in pairs at distal edges. Longitudinal rows of autozoecia separated by ridges projecting beyond colony surface. Ridges pierced by stellatopores arranged in longitudinal rows in exozone. Except for stellatopores, exozone contains abundant capillaries.

Species composition. Two species: *H. spirale* Schulga-Nesterenko, 1955 from the Serpukhovian of the Russian Platform and *H. magnificum* sp. nov. from the Viséan of Iran.

Comparison. This genus differs from the genus *Pemoheloclema* Ozhgibesov, 1983 from the Upper Permian of Novaya Zemlya (Ozhgibesov, 1983) in the elongate tubular autozoecia, subcircular to subelliptical apertures, and the presence of stellatopores.

***Heloclema magnificum* Gorjunova, sp. nov.**

Plate 2, fig. 4

Etyymology. From the Latin *magnificus* (magnificent).

Holotype. PIN, no. 1613/370 (2); Iran, eastern Elburz Mountains, village of Tue; Lower Carboniferous, Viséan.

Description. The colonies are thinly branched, quite often dichotomously branching, circular in cross section, dimorphic. The colonies are 0.72 mm in diameter, the endozone is 0.42 mm in diameter, the exozone is 0.13–0.15 mm thick. The autozoecia are elongate tubular, narrowed proximally, with a gentle and moderate widening in the distal direction. They budded at an acute angle with respect to each other and formed a central axis. In the cross section near the base, the autozoecia are triangular, 0.04 mm in size, at the distal edge in the same section, they are trapezoidal, 0.10 mm in size. The walls of autozoecia, which have a micro-

structure of longitudinal fibers, are slender (0.009 mm thick) in the endozone and thicken up to 0.03–0.05 mm in the exozone. The diaphragms are infrequent, flat, very slender. Hemisepta are absent. The apertures are elliptical, 0.17 mm long (along the major axis) and 0.07–0.010 mm wide (along the minor axis). A 2-mm stretch of the colony surface contains six apertures in longitudinal rows. The exozonal walls are pierced by randomly arranged minute capillaries, no more than 3–4 μm in diameter. They form accumulations in the form of ridges, separating longitudinal rows of apertures. The pores arranged in pairs at the distal edge of the apertures are 0.03–0.04 mm in diameter. At the colony surface pores are occasionally covered by a dense calcareous layer. Zooecia show no polymorphism.

C o m p a r i s o n. This species differs from the very morphologically close species *H. spirale* in the autozoecia having a straighter tubular shape and lacking hemisepta, in the presence of capillaries arranged in regular rows, and in the absence of stellatopores.

M a t e r i a l. Holotype (sample 2/7, collected by I.A. Gretchishnikova).

Order Cryptostomida
Suborder Ptilodictyina

Family Worthenoporidae Ulrich, 1889

Genus Worthenopora Ulrich, 1889

Worthenopora: Ulrich in Miller, 1889, p. 330; Ulrich, 1890, p. 403; Simpson, 1897, p. 602; Bassler, 1953, p. 146; Hageman, 1991, p. 653; Gorjunova and Lavrentjeva, 1993, p. 79.

Type species. *Flustra spatulata* Prout, 1859; Lower Carboniferous, Tournaisian–Viséan of the United States.

D i a g n o s i s. Colonies dendroid, narrowed proximally, or lamellar. Mesotheca straight or sinuous, without capillaries. Autozoecia geniculate, flask-shaped, widened proximally and considerably narrowed near distal tip. Apertures bearing spines, semielliptical, truncated from below. Zooecia show no polymorphism.

S p e c i e s c o m p o s i t i o n. Five species: *W. spatulata* (Prout, 1859), *W. spinosa* Ulrich, 1890, and *W. valmeyerensis* Hageman, 1991 from the Lower Carboniferous of North America; and *W. rara* Gorjunova, 2001 from the Kasimovian Stage of the Russian Platform and *W. elbursensis* sp. nov. from the Viséan of Iran.

Worthenopora elbursensis Gorjunova, sp. nov.

Plate 2, fig. 5

E t y m o l o g y. From the Elburz Mountains.

H o l o t y p e. PIN, no. 1613/379; Iran, Eastern Elburz Mountains, near the village of Bidestan; Lower Carboniferous, Viséan.

D e s c r i p t i o n. The colonies are frondose-dendroid, lenticular in cross section, measure 0.90 mm along the major axis and 0.53 mm along the minor axis. The exozone is poorly defined; 0.05 mm thick. The

mesotheca is zigzag shaped, without capillaries, no more than 0.01 mm thick. The autozoecia are flask-shaped, widened proximally up to 0.16 mm and narrowed distally to 0.08 mm. The length of autozoecia varies within a range of 0.56–0.58 mm. The walls of autozoecia are slender (8 μm thick), with a lamellar microstructure consisting of parallel plates. The body cavities of autozoecia contain no diaphragms, but contain “terminal” hemiphragms near the distal tip. They cover one-third of the area of the aperture at the proximal edge. The apertures are elliptical, 0.25–0.26 mm long, and 0.10–0.11 mm wide. The distance between the centers of apertures is 0.50 mm in longitudinal rows and 0.20–0.21 mm in diagonal rows. A 2-mm stretch of the colony surface contains four or five apertures. Zooecia show no polymorphism.

C o m p a r i s o n. This species differs from the most closely related species *W. rara* (Makhlina et al., 2001) in the frondose-dendroid shape of the colony, flask-shaped shape of autozoecia, and smaller apertures (0.25–0.26 \times 0.10–0.11 mm instead of 0.30 \times 0.13–0.16 mm in *W. rara*).

M a t e r i a l. In addition to the holotype, specimen no. 1613/381 from the same locality (sample 1/4, collected by I.A. Gretchishnikova).

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