

The Brachiopod Succession Through the Silurian—Devonian Boundary Beds at Dnistrove, Podolia, Ukraine

Author: Baliński, Andrzej

Source: *Acta Palaeontologica Polonica*, 57(4) : 897-924

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0138>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The brachiopod succession through the Silurian–Devonian boundary beds at Dnistrove, Podolia, Ukraine

ANDRZEJ BALIŃSKI



Baliński, A. 2012. The brachiopod succession through the Silurian–Devonian boundary beds at Dnistrove, Podolia, Ukraine. *Acta Palaeontologica Polonica* 57 (4): 897–924.

In the classic section across the Silurian–Devonian boundary at Dnistrove (Podolia, Ukraine) the brachiopod fauna has never been studied in detail. This paper presents results of research on brachiopods from this important locality and time interval. Bed-by-bed collecting has enabled the detailed distribution of brachiopod taxa through the boundary beds to be revealed. Generally, the reference section at Dnistrove yields rather scarce but often well preserved brachiopods. *Dayia bohémica* and *Dnestrina gutta* can be regarded as characteristic species for the uppermost Silurian. A relatively high-diversity but low-abundance brachiopod fauna occurs in the lowest 1.8 m of the earliest Devonian. Only three forms have been found to cross the Silurian–Devonian boundary: the strophomenide *Plectodonta (Plectodonta) mariae pantherae* subsp. nov., the atrypide *Gracianella (Sublepida) paulula* sp. nov., and the spiriferide *Howellella (Howellella) latissinuata*. A relatively narrow brachiopod-rich interval at 5.5 m above the Silurian–Devonian boundary yields 16 brachiopod species which probably indicate a setting near the lower limit of the photic zone equivalent to the Benthic Assemblage 3–4 boundary. Two new species and one new subspecies are described: *Skenidioides tatyanae*, *Plectodonta (Plectodonta) mariae pantherae*, and *Gracianella (Sublepida) paulula*.

Key words: Brachiopoda, palaeoenvironments, Silurian–Devonian boundary, Podolia, Ukraine.

Andrzej Baliński [balinski@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Received 9 September 2011, accepted 1 December 2011, available online 13 January 2012.

Copyright © 2012 A. Baliński. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Silurian–Devonian sequence in Podolia is regarded as one of the most important extensively exposed sections across this boundary interval, in both its palaeogeography and palaeontology. The succession is exposed at many localities along the valleys of the Dniester River and its tributaries and has been studied by many geologists and palaeontologists since the 19th Century (see overview by Nikiforova 1954). Of particular interest are the Upper Silurian and Lower Devonian strata, which record a complete upward transition from open-marine (fossiliferous Pridoli limestone) through marginal-marine to fluvial (upper Lochkovian–?lower Pragian redbeds) facies. Notwithstanding the long history of investigation of the Podolian sections, many aspects of this Silurian–Devonian reference sequence remain poorly known. In recent years several paleontological investigations have broaden and deepen our knowledge of the Silurian–Devonian faunas and floras of Podolia (e.g., Baliński 2010; Drygant and Szaniawski 2012; Filipiak et al. 2012; Krzemiński et al. 2010; Olempska et al. 2012; Olempska et al. 2012; Voichyshyn 2011; Voichyshyn and Szaniawski 2012).

Although a review of all papers on the Silurian–Devonian brachiopods of Podolia is beyond the scope of the present study, there is no doubt that the classic and pioneering monograph of Kozłowski (1929) is the most important. Unfortunately, the entire Kozłowski's (1929) collection, including the type specimens of new species, was destroyed in Warsaw during the Second World War. The review by Nikiforova et al. (1985) of the brachiopod fauna described by Kozłowski (1929), including establishment of neotypes of his new species, was an important contribution to modern knowledge of the Silurian–Devonian brachiopods of Podolia.

The main aim of the present paper is to study the detailed distribution of the brachiopod fauna through the Silurian–Devonian boundary beds at the key section at Dnistrove village (former Volkovtsy; 48°32'16.9"N, 26°14'21.4"E). All the material was collected bed-by-bed in this section, which is the only locality known at present where the boundary beds crop out (Figs. 1, 2). The exposure was densely covered and overgrown by vegetation but has been improved by excavation during the present investigation. Although the faunal occurrences were listed from the Silurian–Devonian key sections of Podolia by Nikiforova et al. (1972), the

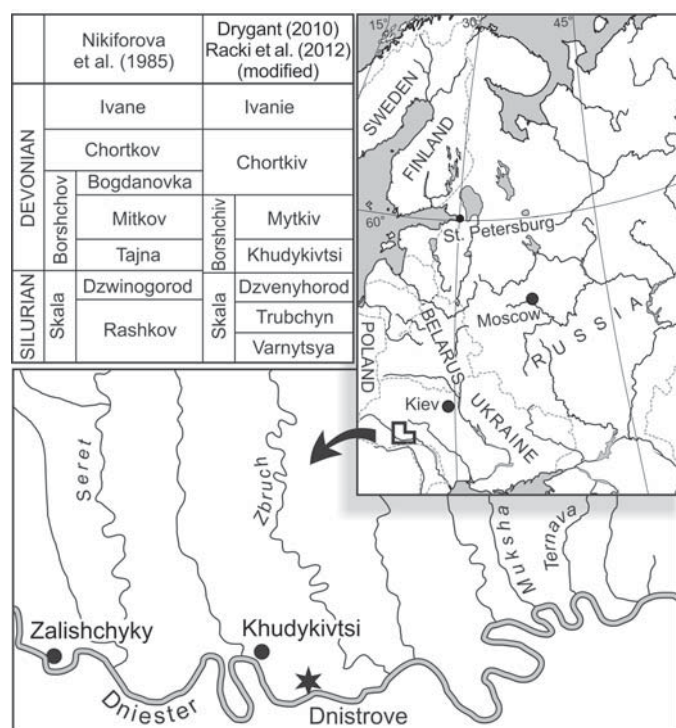


Fig. 1. General map of Eastern Europe and more detailed map of Podolia showing the valleys of the Dniester River and its tributaries. The reference section at Dnistrove (Volkovtsy) is marked by an asterisk. In the upper left corner a stratigraphic scheme of the Late Silurian to Early Devonian succession of Podolia shows the correlation of old and new terminology.

brachiopods from the S–D boundary interval at Dnistrove were not studied in detail.

The spelling of geographic names and names of stratigraphic units based on them in the Podolian sequence has changed through time according to adoption from Russian, Polish, or Ukrainian languages. Efforts to stabilize these names have failed, unfortunately. Recently, a new Ukrainian transliteration has been introduced and this nomenclature is used in the present paper (see Fig. 1).

Institutional abbreviations.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Other abbreviations.—BA, Benthic Assemblage; S–D, Silurian–Devonian.

Geological setting

The Late Silurian to Early Devonian succession of Podolia forms a continuous phase of marine sedimentation terminating in the Middle Devonian by erosional hiatuses. During Pridoli times, differential subsidence and sedimentation rates resulted in 700–800 m thickness of rocks in the southwestern part of Podolia and 150–160 m thick deposits in its eastern regions. Early Devonian sedimentation was characterised by gradual regression with shrinking marine environments and increasing terrigenous input in western areas (Drygant 2003).

The Silurian sequence terminates with the Trubchyn (upper part of the former Rashkov Beds) and Dzvenyhorod (former Dzvinogorod) beds of the upper part of the Skala Horizon (Figs. 1, 2). They are mostly calcareous, with 19 m thick, dark-grey, fossiliferous, nodular limestone predominating in the topmost interval. The Silurian–Devonian boundary is placed 3.2 m above this interval, in the middle part of a sequence of interbedded greenish-grey argillaceous shale and marl beds containing dark-grey limestone nodules (Małkowski et al. 2009; Drygant and Szaniawski 2012) and representing the lowermost part of the Khudykivtsi Beds. The index graptolite species *Monograptus uniformis angustidens* Přibyl, 1940 was recovered in shale interbeds within the nodular limestone layers at the reference Dnistrove section (Nikiforova et al. 1972; Nikiforova 1977). It appears that the Silurian–Devonian boundary at Dnistrove can be correlated quite reliably with the boundary at the stratotype section at Klonk, Czech Republic (Chlupač and Hladil 2000).

The fossil-rich, open-marine Lochkovian suite is an uninterrupted continuation of the Silurian marine deposits. The suite starts with the 180 m thick Borshchiv Horizon, which includes the Khudykivtsi (former Tajna) and Mytkiv (former Mitkov) beds (Figs. 1, 2). At the Dnistrove section only the lower part of the Khudykivtsi Beds and the uppermost part of the Dzvenyhorod Beds are exposed (Figs. 2, 3). The former consists of platy limestone and variably interbedded dark-grey argillaceous shale, marl, and marly to micritic limestone whereas the Dzvenyhorod Beds consists of dark-grey, nodular limestone interbedded with greenish-grey argillaceous shale and marl (Małkowski et al. 2009; Racki et al. 2012).

Although generally the reference section at Dnistrove yields rather scarce and sometimes poorly preserved brachiopods, a limited brachiopod-rich interval in beds 47–48, (i.e., at 5.5 m above the S–D boundary) is distinguished by a diverse, abundant, and well preserved fauna (Fig. 3). Podolian geochemical data (Małkowski et al. 2009; Małkowski and Racki 2009; Racki et al. 2012; Fig. 3) show a major positive $\delta^{13}\text{C}$ shift beginning in the late Pridoli that reached peak values as strong as +4‰ in the Khudykivtsi Beds (earliest Lochkovian). The secular pattern of $\delta^{18}\text{O}$ values recorded in the Podolian sections probably documents climatic changes: Małkowski and Racki (2009) suggest considerable cooling in the latest Silurian, together with possible hypersalinity and strongly limited primary production. This may explain, to some extent, the low frequency of brachiopod specimens preserved in the lowest part of the section at Dnistrove. Interestingly, a low frequency but relatively diverse brachiopod fauna occurs in the lowest 1.8 m of the Early Devonian. This interval correspond to an initial phase of the positive C-isotopic excursion recorded in the section (Fig. 3).

Material and methods

I sampled the section at Dnistrove during the spring seasons of 2004, 2005, 2008, and 2009. Macrofossils (predominantly



Fig. 2. Field photo of the section at Dnistrove village. The trenched interval reveals the clayey-calcareous Silurian–Devonian boundary beds. Numbers refer to the beds from which brachiopod material was collected (see also Fig. 3).

brachiopods) were collected bed-by-bed by splitting them out of the rock. In addition, samples of approximately 2 kg each were taken from fossiliferous beds and then dissolved in dilute acetic acid to obtain phosphatic shells of inarticulate brachiopods. These are represented almost exclusively by one species of *Opsiconidion* Ludvigsen, 1974.

The bed-by-bed collecting of specimens shows precisely the distribution of brachiopod taxa in the S–D boundary beds (Fig. 3). Although the sediments are similar throughout the greater part of the section (see above), the differing brachiopod faunas indicate that the environment must have varied slightly.

Distribution of brachiopods and palaeoenvironments across the Silurian–Devonian boundary

The brachiopod fauna described here was collected from the interval spanning from the topmost 1.6 m of the uppermost Silurian to about 12.3 m of the lowermost Devonian (Khudykivtsi Beds of the Borshchiv Horizon). The fauna consists of 22 species and genera including two new species and one new subspecies, i.e., *Skenidioides tatyanae*, *Plectodonta* (*Plecto-*

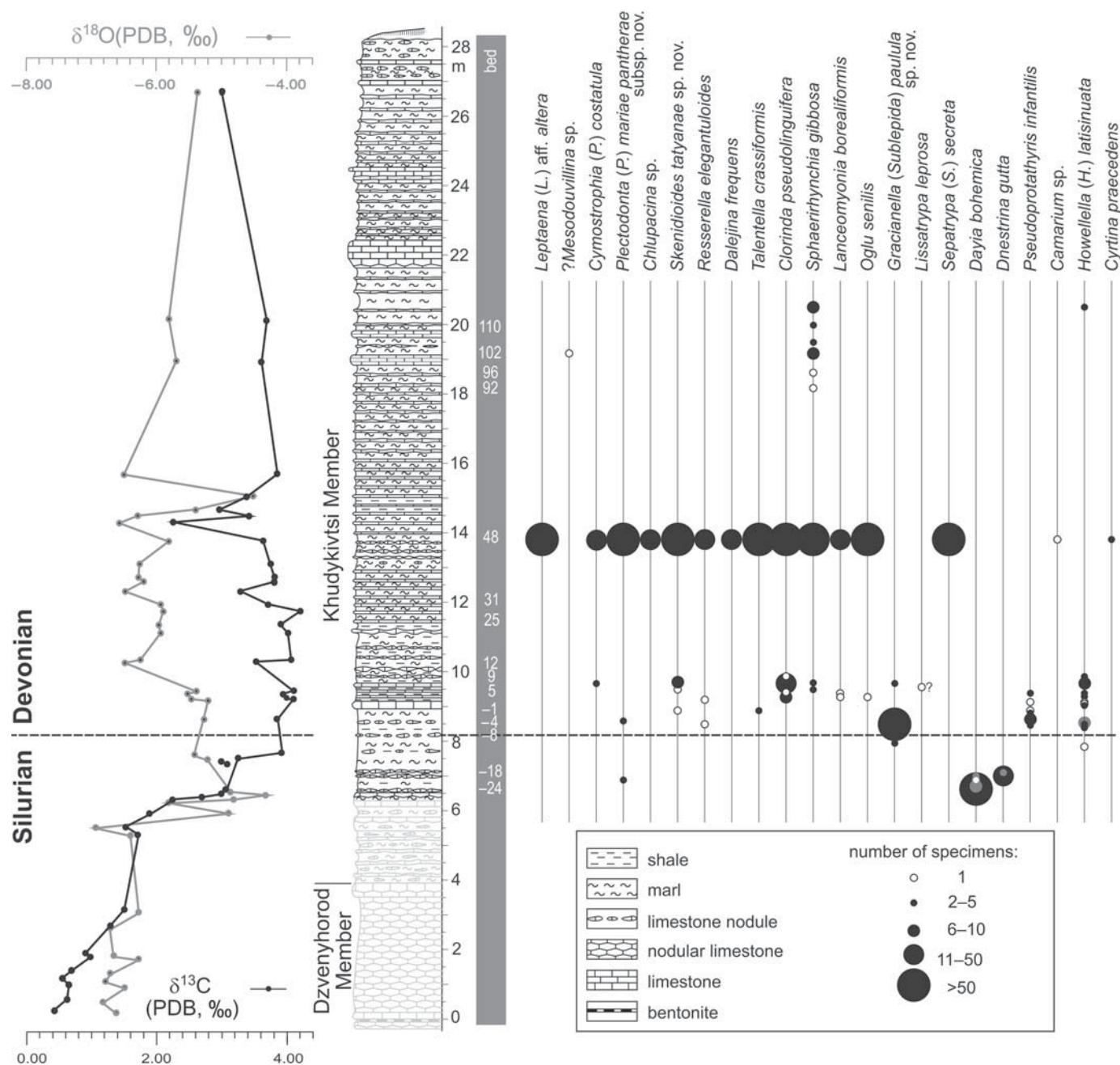


Fig. 3. Distribution of brachiopod species and their frequency in the section at Dnistrove village. Secular pattern of $\delta^{13}\text{C}$ (black curve) and $\delta^{18}\text{O}$ (grey curve) values after Małkowski and Racki (2009) and Racki et al (2012). Lithology after Nikiforova et al. (1972: fig. 82).

donta mariae pantherae, and *Gracianella* (Sublepidia) *paulula*. Four other forms are reported for the first time from Podolia. These are *Leptaena* (*Leptaena*) aff. *altera* Rybnikova, 1966, *Chlupacina* sp., *Oglu senilis* Havlíček 1987, and *Camarium* sp.

The topmost part of the Silurian exposed in the studied section contains brachiopods that are poorly differentiated taxonomically but nevertheless very characteristic for the time interval. The oldest species found in the section is *Dayia bohemia* Bouček, 1941. It is confined to the thin bedded nodular limestone occurring at about 1.3–1.6 m below the S–D boundary. It is especially numerous in bed -24 (1.6 m

below the boundary) where the species forms monospecific nest-like clusters. *D. bohemia* is known from several sections of the Pridoli Formation in Bohemia and from the Pridoli of Estonia, Lithuania, and Latvia (Havlíček and Štorch 1990; Rubel 1977). According to Havlíček and Štorch (1990: 42) *D. bohemia* is a characteristic species for the uppermost layers of the Pridoli Series and it does not cross the S–D boundary. It seems that the species occurs in the exactly the same stratigraphic position both in Bohemia and Podolia. In Bohemia the species occurs in brachiopod banks for which Havlíček and Štorch (1990) proposed the *Dayia bohemia* Subcommunity. Earlier Boucot (1975) noted that *Dayia*

forms a low-diversity, single brachiopod genus community in quiet-water settings within Benthic Assemblage (BA) 3.

About 0.3 m higher in the section at Dnistrove *Dnestrina gutta* Nikiforova and Modzalevskaya, 1968 is distinctive and is confined to a few cm thick shale. A very similar species described as *Dnestrina* cf. *gutta* has been recorded in the topmost layers of the Niushiping Formation (uppermost Pridoli) in the Renheqiao section in western Yunnan, China (Jahnke et al. 1989). It seems that *Dnestrina* might be widespread geographically but restricted stratigraphically. The Eifelian “*Dnestrina* n. sp. A” (see Langenstrassen 1972; Cocks 1978) from Sauerland (Germany) and *Dnestrina?* *mawei* (Davidson, 1881) from the Wenlock of Great Britain are insufficiently known forms. Thus, both the species from Dnistrove, *D. bohémica* and *D. gutta*, do not cross the Silurian–Devonian boundary in the section and can be regarded, at least locally, as guide species for the uppermost Silurian. Besides these two species the topmost Silurian faunule shows also the first appearances of very sporadic *Plectodonta* (*Plectodonta*) *mariae pantherae* subsp. nov., *Gracianella* (*Sublepidia*) *paulula* sp. nov., and *Howellella* (*Howellella*) *latisinuata* Kozłowski, 1929. It should be noted that all these forms are characterised by small shell size rarely exceeding 5 mm in length. This latest Silurian assemblage represents a stressed and impoverished, relatively deep-water environment characterised by interbedded greenish-grey argillaceous shale and marl. Although no evident change in environmental conditions has been noted in the lowermost Devonian, *Dnestrina gutta* and *Dayia bohémica* do not cross the S–D boundary. Boucot (1975) proposed a low-diversity high dominance, quiet-water *Gracianella* Community in the Silurian non-reef communities (BA 4–5, partially BA 3) of the Uralian-Cordilleran and North Atlantic Regions. In the Dnistrove section Racki et al. (2012) described a closely analogous low diversity, quiet water *Dnestrina gutta* Community for the assemblages dominated by that brachiopod.

An interval about 1.8 m thick immediately succeeding the Silurian–Devonian boundary consists of graptolite shale at the bottom, shale, marl with limestone nodules, and limestone, yielding a brachiopod fauna that is more prolific and taxonomically diverse, although numerically low-abundance, and usually poorly preserved. These strata indicate a prolonged influence of the open marine facies in which small brachiopods still predominate. The fauna includes 13 species (Fig. 3) of which *Gracianella* (*Sublepidia*) *paulula* sp. nov. occurs in large numbers in the shell bed -4 (about 0.4 m above the boundary). Only 3 species of those characteristic for the lowermost Devonian cross the S–D boundary and have their first appearance just below it. These are the strophomenide *Plectodonta* (*Plectodonta*) *mariae pantherae* subsp. nov., the atrypide *Gracianella* (*Sublepidia*) *paulula* sp. nov., and the spiriferide *Howellella* (*Howellella*) *latisinuata* Kozłowski, 1929. *P. (P.) mariae pantherae* is numerous higher in the section in the fossiliferous marly limestone beds 47–48 (about 5.5 m above the S–D boundary) and is distinguished by the preservation of an unique shell colour pattern

(Baliński 2010) which can also be easily recognised in specimens from shell bed -4 (0.4 m above the boundary), and thus appears to be an useful supplementary taxonomic feature even for specimens derived from different facies sediments.

The lowermost 1.8 m of the Devonian strata at Dnistrove contains a total of 13 species. Ten of them are more common in slightly higher intervals and can be regarded as characteristic for the lower Devonian: *Skenidioides tatyanae* sp. nov., *Resserella elegantuloides*, *Talentella crassiformis*, *Cymostrophia* (*Protocymostrophia*) *costatula*, *Clorinda pseudolinguifera*, *Sphaerirhynchia gibbosa*, *Lanceomyonia borealiformis*, *Oglu senilis*, *Lissatrypa leprosa*, and *Pseudoprotathyris infantilis*.

The brachiopod content of the Silurian–Devonian boundary beds at Dnistrove indicates a gradual shallowing-upward depositional environment. At about 3 m above the S–D boundary poorly fossiliferous, rhythmic marl and limestone beds start to prevail. In the exposed section the most fossiliferous beds 47–48 appears without easily recognisable environmental change, as indicated by the rocks. These beds yield brachiopod assemblage consisting of 16 species of which 10 possessed medium- to large-sized shells. The increased size of the elements of the assemblage indicates more favourable environmental conditions. The most numerous are *Septatrypa* (*Septatrypa*) *secreta* (27% of the assemblage), *Plectodonta* (*Plectodonta*) *mariae pantherae* subsp. nov. (13%), *Sphaerirhynchia gibbosa* (12%), *Clorinda pseudolinguifera* (11%), and *Talentella crassiformis* (7%). The assemblage is represented by members of 9 orders and is characterised by a variety of morphologic types and ecological adaptations (e.g., small to large, concavo-convex, biconvex to globose, smooth, ribbed to frilled, with or without functional pedicle). The brachiopods are well preserved with chiefly articulated specimens. The disarticulation of the shells and rarity of dorsal valves of *Clorinda pseudolinguifera* indicates current sorting, although the sorting was limited. The preservational characteristics of *C. pseudolinguifera* may indicate a mechanically weaker hinge structure which was more prone to disarticulation—as in majority of the pentamerides—of the deltidodont type. In contrast, many other articulate brachiopods co-occurring in the beds 47–48 possessed cyrtomatodont dentition, i.e., rhynchonellides, atrypides, athyridides, and spiriferides.

The occurrence of numerous specimens of the colour-patterned *Plectodonta* (*Plectodonta*) *mariae pantherae* subsp. nov. in the assemblage from bed 47–48 seems to have a potential value in characterising some environmental settings of the fauna. Baliński (2010) suggested that the assemblage with colour-banded shells inhabited shallow-water depths related to the photic zone of roughly tropical–subtropical or warm–temperate belt. The dominance of *S. (S.) secreta* in beds 47–48 suggests that this assemblage may be compared to the Silurian non-reef quiet-water *Dubaria* (= *Septatrypa*) Community of Boucot (1975). According to Racki et al. (2012) the brachiopod and associated fauna from beds 47–48 at Dnistrove probably indicates a setting near the lower limit of the photic zone correlated with equivalent to the BA 3–4 boundary.

Systematic palaeontology

The majority of species reported here are well known from other sections in Podolia and were described in details in the several papers (e.g., Kozłowski 1929; Nikiforova 1954; Modzalevskaya 1968; Nikiforova et al. 1985). In consequence, there is no necessity to repeat detailed descriptions of the species reported in the previous papers, so that only short comments and photographic documentation are provided. New species and inadequately known as well as those not described from the section before are described in details.

Phylum Brachiopoda Dumerill, 1806

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Rafinesquinidae Schuchert, 1893

Subfamily Leptaeninae Hall and Clarke, 1894

Genus *Leptaena* Dalman, 1828

Subgenus *Leptaena* (*Leptaena*) Dalman, 1828

Type species: *Leptaena rugosa* Dalman, 1828; *Dalmanitina* beds, Ashgil, Ordovician; Fårödalaberg (Varvsberget), Västergötland, Sweden.

Leptaena (*Leptaena*) aff. *altera* Rybnikova, 1966

Fig. 4A–J, L.

Material.—27 shells, partly embedded in sediment, 5 ventral valves, 4 dorsal valves, and about 60 fragments; all from beds 47–48 of the studied section, i.e., at 5.5 m above the S–D boundary.

Description.—Shell rather small, attaining usually 12–14 mm in width, transversally subrectangular outline, with length approaching 51–62% of width; anterior margin weakly arched, lateral margins straight to weakly concave, cardinal extremities extend forming pointed alae.

Ventral valve with a very gently convex posterior region and concave the rest of the disk, sometimes with a very weak median longitudinal elevation; peripheral rim elevated, anterolaterally forming often swellings or bulges; trail geniculated medially at 70–90° from commissural plane, attaining 51–91% of disk length, medially gently concave (emarginate); umbo small, with distinct supra-apical hollowed outgrowth (pedicle tube); interarea very low, ranging 0.4–0.8 mm in height, apsacline, medially triangular, laterally sublinear, delthyrium covered apically by short convex pseudodeltidium, rest of delthyrium filled up with massive chilidium (Fig. 4E–G).

Dorsal disk flattened, but with very shallow median sulcus and gently convex flanks; trail separated from disk with a shallow peripheral trough which anterolaterally forms two shallow hollows corresponding to the bulges on the ventral valve; trail frequently with very weak medial convexity; interarea very low, 0.2–0.3 mm in height, linear, anacline; notothyrium covered by a convex, medially deeply grooved chilidium.

Interior of the ventral valve with subcircular muscle field, bounded laterally by ridges and divided in its anterior half by

a short median ridge (Fig. 4I, J); dental plates obsolescent by secondary shell material, developed as thickened ridges (Fig. 4I, J); teeth small, wide, crenulated (Fig. 4J₂); internal surface outside the muscle area covered by sparse pustulae arranged in radial rows.

Dorsal interior with sub-triangular cardinal process lobes divided by a deep slit and expanding in width anteriorly; sockets triangular, usually shallow, broad, bounded posteriorly by the edge of the interarea and medially by sharp and straight inner socket ridges (Fig. 4L); adductor scars deeply impressed posteriorly in the thickened shell wall, poorly delineated anteriorly, and medially separated by wide, thickened myophragm (Fig. 4L); internal surface of the disk with thick tubercles around muscle field and much finer anteriorly and laterally.

Ornament multicostellate, costellae faint, delicate, 3.5–4.5 per mm, those on lateral parts of the trail sometimes thinner, up to 7 per mm; rugae usually weak, sometimes imperceptible.

Remarks.—The species differs from the majority of other leptaenids in having small shell dimensions, a transverse, subrectangular outline, usually straight to gently concave (emarginate) anterior margin, inconspicuous to absent concentric rugae, rather weak radial costellae, and an elevated peripheral rim on the ventral valve frequently forming swellings at anterolateral corners. A well preserved, distinct, supra-apical hollowed outgrowth (pedicle tube) on the studied ventral valves (Fig. 4C₂) is very similar to that described and illustrated by Kozłowski (1929: 92, fig. 26) in *Glossoleptaena emarginata* (Barande, 1879) from the middle part of the Borshchiv Horizon. The studied specimens differ from *G. emarginata* in not having a strongly emarginate anterior margin, which is one of the diagnostic features of the latter taxon.

Externally the specimens from Dnistrove are almost identical to *Leptaena* (*Leptaena*) *altera* Rybnikova, 1966 from the Pagėgiai Formation (Ludlow) of Ezere borehole and the Wenlock of Akniste borehole, Latvia (Rybnikova 1966). Musteikis and Cocks (2004: fig. 4H–O) re-illustrated two of the three type specimens of Rybnikova's paper and figured several other specimens from the Telychian–Ludfordian of Lithuania. Rubel (2011) described and illustrated several specimens of the species from the Wenlock of Estonia, and Telychian–Ludfordian of Lithuania. The authors have also shown the external variability of *L. (L.) altera*. Although the holotype of the species (Rybnikova 1966: pl. 1: 4; Musteikis and Cocks 2004: fig. 4H) is slightly larger and has a more semicircular shell outline than the specimens from Dnistrove, all other specimens of *L. altera* from the Baltic region illustrated by Musteikis and Cocks (2004) and Rubel (2011) show the same details of the external morphology and interior as the material here studied. The remarkable similarity between these forms is very suggestive despite evident difference in their stratigraphic ranges. This is the main reason that the present earliest Devonian material from Dnistrove is described as only related to the Llandovery–Ludlow *L. altera*.

The Podolian specimens show also some resemblance to *Letagonia joachimiana* Havlíček, 1967 from the Liteň and

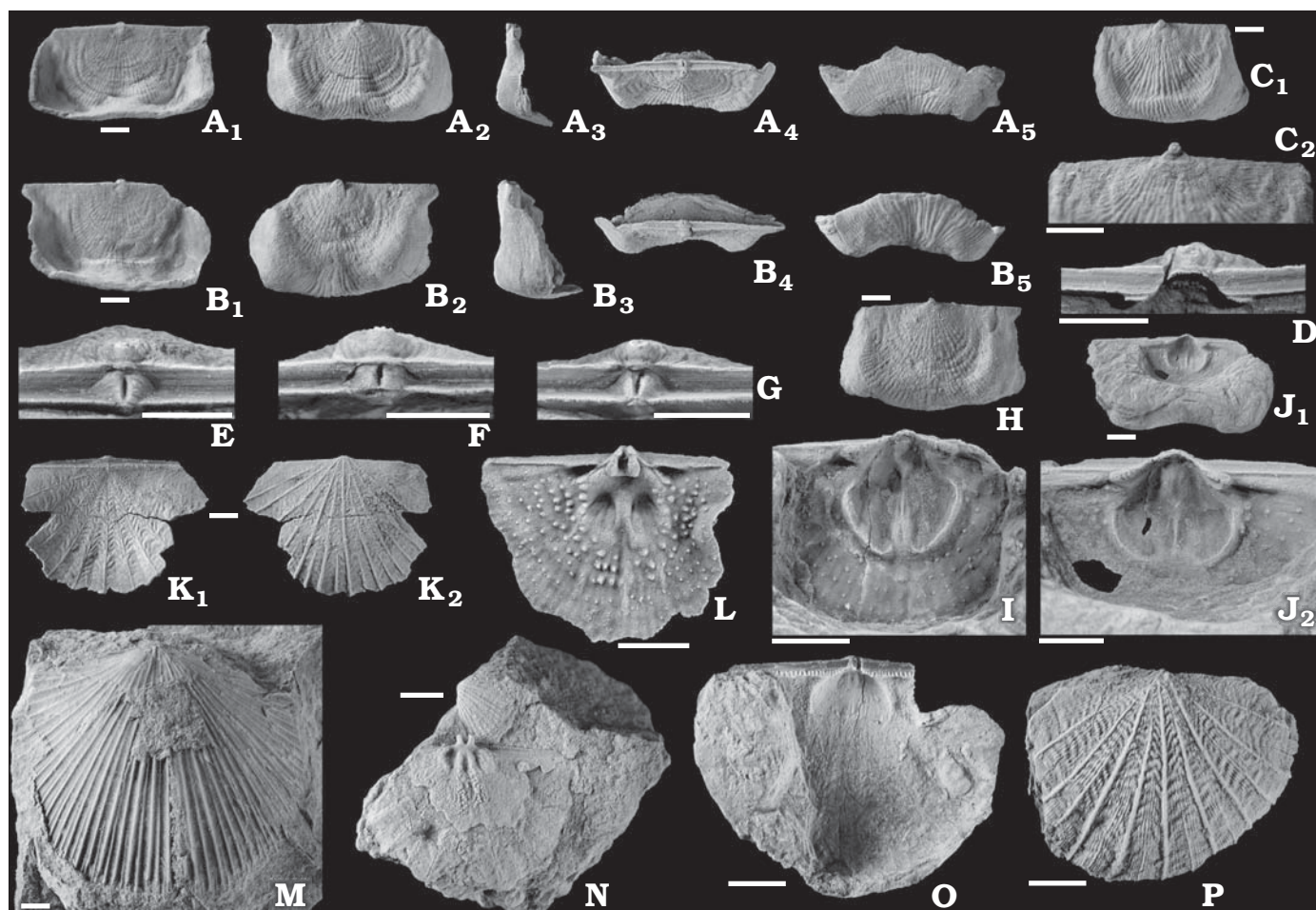


Fig. 4. Strophomenide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A–J, L.** *Leptaena* (*Leptaena*) aff. *altera* Rybnikova, 1966. **A, B.** Two nearly complete shells, ZPAL Bp. 56/42 (**A**) and ZPAL Bp. 56/43 (**B**), in dorsal (**A**₁, **B**₁), ventral (**A**₂, **B**₂), lateral (**A**₃, **B**₃), posterior (**A**₄, **B**₄), and anterior (**A**₅, **B**₅) views. **C.** Shell ZPAL Bp. 56/46 in ventral view (**C**₁) and enlargement showing the pedicle tube (**C**₂). **D.** Enlargement of the posterior region of the ventral valve ZPAL Bp. 56/32d showing interarea, delthyrium, and well preserved teeth. **E–G.** Enlargement of the posterior region of three shells, ZPAL Bp. 56/32c (**E**), ZPAL Bp. 56/32b (**F**), and ZPAL Bp. 56/32a (**G**); ventral valves uppermost. **H.** Almost complete shell ZPAL Bp. 56/45 in ventral view. **I.** Enlargement of the interior of ventral valve ZPAL Bp. 56/32e. **J.** Ventral valve ZPAL Bp. 56/44 with partially shown interior in general (**J**₁) and enlarged (**J**₂) views. **L.** Interior of incomplete dorsal valve ZPAL Bp. 56/32f. **K, N–O.** *Cymostrophia* (*Protocymostrophia*) *costatula* (Barrande, 1847). **K.** Incomplete shell ZPAL Bp. 56/18 in dorsal (**A**₁) and ventral (**A**₂) views. **N.** Interior of dorsal valve ZPAL Bp. 56/21. **O.** Interior of an incomplete ventral valve ZPAL Bp. 56/19. **P.** Exterior of an incomplete ventral valve ZPAL Bp. 56/20. **M.** ?*Mesodouvillina* sp.; exterior of ventral valve ZPAL Bp. 56/53. Beds 47–48 (**A–L, N–P**), 102 (**M**). Scale bars 2 mm.

Kopanina formations (Silurian) of Bohemia (Havlíček 1967: 105–106, pl. 19: 7–9, 12, 13, 17–20, fig. 41A; Havlíček and Štorch 1990: 77, pls. 13: 3, 15: 6, 7). The differences between the two species seem to be minor and are expressed mainly in a more rectangular shell outline of the former. It is possible that both species are also closely related although the latter is again older stratigraphically.

Family Amphistrophiidae Harper, 1973

Subfamily *Mesodouvillininae* Harper and Boucot, 1978

Genus *Mesodouvillina* Williams, 1950

Type species: *Stropheodonta* (*Brachypirion*) *subinterstitialis seretensis* Kozłowski, 1929; Chortkiv Horizon (Early Devonian); Bogdanovka, Podolia (Ukraine).

?*Mesodouvillina* sp.

Fig. 4M.

Material.—One slightly incomplete ventral valve with preserved exterior. Bed 102, 11 m above the S–D boundary.

Remarks.—A single, strongly exfoliated ventral valve was recovered from the upper part of the studied section. Unfortunately, its internal structure and details of shell ornamentation cannot be assessed, making generic determination of the specimen somewhat tentative.

Family Douvillinidae Caster, 1939

Subfamily Protodouvillininae Harper and Boucot, 1978

Genus *Cymostrophia* Caster, 1939

Type species: Leptaenas stephani Barrande, 1879; Koněprusy Limestone, Pragian (Lower Devonian); Koněprusy, Bohemia.

**Subgenus *Cymostrophia* (*Protocymostrophia*)
Harper and Boucot, 1978**

Type species: Strophomena ivanensis Barrande, 1879; Kotýs limestone (Lochkov, Lower Devonian); Svatý Jan pod Skalou, Bohemia.

***Cymostrophia* (*Protocymostrophia*) *costatula*
(Barrande, 1847)**

Fig. 4K, N–P.

1847 *Leptaena costatula* Barrande; Barrande 1847: 65, pl. 21: 17.

1929 *Stropheodonta* (*Brachyprion*) cf. *costatula* (Barrande); Kozłowski 1929: 100, pl. 3: 33.

1967 *Mesodouvillina costatula* (Barrande, 1848); Havlíček 1967: 170–171, pl. 34: 7, 9–12; fig. 69.

1968 *Mesodouvillina costatula* (Barrande); Modzalevskaya 1968: pl. 27: 2, 3.

1985 *Mesodouvillina costatula* (Barrande); Nikiforova et al. 1985: 22.

Material.—47 specimens, mostly fragmentary, embedded in rock. The species occurs scarcely at 1.5 m (bed 7) above the S–D boundary, but becomes much more common at 5.5 m (beds 47–48) above the S–D boundary.

Remarks.—Specimens from the studied interval at Dnistrove appear to be conspecific with *Stropheodonta* (*Brachyprion*) cf. *costatula* from the Khudykivtsi Beds of Myszkowce as illustrated by Kozłowski (1929: pl. 3: 33). More recently, Podolian collections from the same stratigraphic interval were attributed to *Mesodouvillina costatula* (Modzalevskaya 1968; Nikiforova et al. 1985). The latter authors discussed the relationship of the Podolian material with the type specimens of *C. (P.) costatula* from the lower Devonian of Bohemia, as well as with *C. (P.) costatuloides* (Johnson, Boucot, and Murphy, 1973) from the Pridoli of Nevada. According to Nikiforova et al. (1985), the specimens described by Nikiforova (1954) from the Malinovtsy and Skala horizons are probably more closely related to *C. (P.) costatuloides*, whereas specimens from the Khudykivtsi Beds are conspecific with *C. (P.) costatula*. This may also apply to two specimens reported (but not illustrated) by Kozłowski (1929) from the Dzwiniogorod Beds of the Skala Horizon.

Stratigraphic and geographic range.—The species was originally described from the Kotýs limestone (Lochkov, Lower Devonian) of Bohemia (Barrande 1847; Havlíček 1967). Recently Iordan (1999) found the species in the Silurian (Wenlock) of the Bătrânești borehole, Romania. Similar form is listed as *Mesodouvillina* aff. *costatula* by Berdan et al. (1969) from the upper Silurian of Nevada. In Podolia the species occurs in the Khudykivtsi Beds of the Borshchiv Horizon.

Superfamily Plectambonitoidea Jones, 1928

Family Sowerbyellidae Öpik, 1930

Subfamily Öpik, 1930

Genus *Plectodonta* Kozłowski, 1929

Type species: Plectodonta mariae Kozłowski, 1929; Mytkiv Beds, Borshchiv Horizon (Lower Devonian); Krivche, Podolia (Ukraine).

**Subgenus *Plectodonta* (*Plectodonta*) Kozłowski,
1929**

***Plectodonta* (*Plectodonta*) *mariae* Kozłowski, 1929**

***Plectodonta* (*Plectodonta*) *mariae pantherae* subsp.
nov.**

Fig. 5A–J, M–P.

1978 *Plectodonta* aff. *maria* Kozłowski; Modzalevskaya 1968: pl. 27: 39.

2010 *Plectodonta* sp.; Baliński 2010: 696, figs. 1, 2, 3A.

Etymology. After the spotted colour pattern resembling that in the panther.

Holotype. Complete articulated shell ZPAL Bp. 56/99; illustrated in Fig. 5A.

Type locality. Trench east of Dnistrove village, Podolia, Ukraine. Coordinates 48°32'16.9"N, 26°14'21.4"E.

Type horizon. Beds 47–48, Khudykivtsi Beds of the Borshchiv Horizon (Early Devonian).

Diagnosis.—Shell small, attaining 5.6 mm in width, transversely subrectangular to semicircular, with slightly alate cardinal extremities; ventral sulcus and dorsal fold; inner pair of the dorsal side septa diverge at 31°, beginning at some distance from the socket plates; ornament parvicostellate, about 70 to 100 costellae in adult specimens and 3–9 fine costellae between each major costella.

Material.—Two isolated shells and 175 specimens (mostly ventral valves) embedded in sediment. The subspecies is quite common at 5.5 m above the S–D boundary (beds 47–48). Two specimens have been revealed also at 0.4 m above the boundary and 3 other at 1.15 m below the boundary.

Description.—Shell small up to about 4.6 mm in length and 5.6 mm in width, with a length to width ratio of 0.51–0.70, having concavoconvex, transversely subrectangular alate to semicircular outline; anterior commissure rectimarginate, anterior margin arched, lateral margins rounded, usually weakly concave near the hinge line forming short, pointed ears or, less frequently, cardinal extremities angular; hinge line straight and wide, usually equals the greatest width of the shell, finely denticulate.

Ventral valve gently convex in lateral profile with slightly swollen umbonal region; beak small, blunt; interarea low, up to ca. 0.4 mm in height, apsacline, almost flat to weakly concave, margins of delthyrium diverge at about 88°, apically closed by small convex pseudodeltidium; supraapical forament very small, bordered by slightly elevated ring; sulcus wide but poorly delimited laterally, with a median primary costa, on some specimens better marked at about midlength (about 0.5–2 mm from the beak, i.e., where lateral borders of the sulcus accommodate side septa of the dorsal valve), variable in profile from U- to V-shaped in cross-section, starting at umbo.

Dorsal valve weakly concave, with the greatest concavity in the posterior region near fairly prominent, elongate dorsal protegular node; fold well marked and wide occupying about

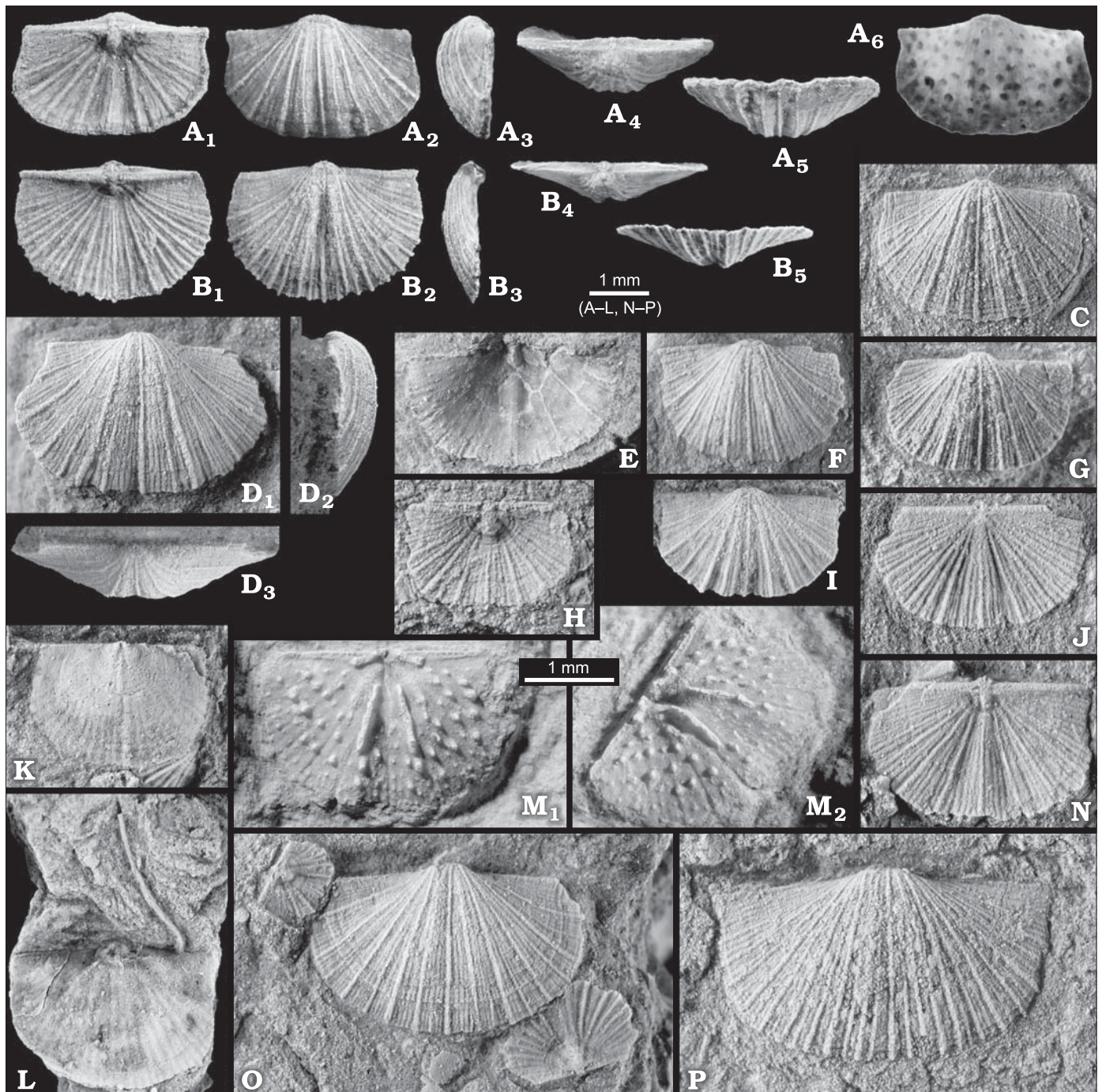


Fig. 5. Strophomenide *Plectodonta* (*Plectodonta*) *mariae pantherae* subsp. nov. (A–J, M–O) and chonetoid *Chlupacina* sp. (K, L) from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A.** Holotype ZPAL Bp. 56/99 in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views, and ventral view of an uncoated shell (A₆) to show colour pattern. **B.** Complete shell ZPAL Bp. 56/108 in dorsal (B₁), ventral (B₂), lateral (B₃), posterior (B₄), and anterior (B₅) views. **C, F, G, I.** Four specimens, ZPAL Bp. 56/102 (C), ZPAL Bp. 56/93 (F), ZPAL Bp. 56/103 (G), and ZPAL Bp. 56/104 (I), in ventral exterior view. **D.** Ventral valve ZPAL Bp. 56/94 in exterior (D₁; same as Baliński 2010: fig. 1C₂), lateral (D₂), and posterior (D₃) views. **E.** Slightly incomplete ventral valve ZPAL Bp. 56/106 in interior view. **H, J, N.** Three dorsal valves, ZPAL Bp. 56/107 (H), ZPAL Bp. 56/98 (J), and ZPAL Bp. 56/95 (N), in exterior view (N, same as Baliński 2010: fig. 1D₂). **M.** Interior of dorsal valve ZPAL Bp. 56/105 in general (M₁) and oblique lateral (M₂) views. **O.** Ventral valve ZPAL Bp. 56/91 in external view showing well preserved ornamentation; two other small shells in dorsal view visible near upper left and lower right corner of the photograph. **P.** Large ventral valve ZPAL Bp. 56/101 in exterior view. **K, L.** *Chlupacina* sp. **K.** Shell ZPAL Bp. 56/151 in ventral exterior view. **L.** Slightly damaged shell ZPAL Bp. 56/152 in ventral view. Beds 47–48.

1/4–1/3 of the valve width, triangular in cross-section; inter-area very low, linear, flat, hypercline; chilidium not preserved.

Dorsal interior visible on one juvenile specimen 1.8 mm long (Fig. 5M), with papillose surface; papillae coarse on the

central region, fine peripherally; socket plates small, widely divergent; two prominent side septa diverge at 31°, beginning posteriorly at a distance of 0.4 mm from the socket plates; second pair of side septa very weak and shorter, almost imperceptible due to the immaturity of the specimen; cardinal process trifold in posterior view, occupying large portion of the delthyrium.

Ventral interior poorly preserved, but a short and thick median septum in the most posterior region of a valve is visible; surface finely papillose (Fig. 5E).

Shell ornament unequally parvicostellate; about 70 to 100 costellae in adult specimens at the anterior margin and 3–9 fine costellae between each major costella (usually 3–5); growth lines sometimes visible, rather weak (Fig. 5C, O).

Remarks.—The subspecies from Dnistrove is common in the lowermost Devonian, but a few specimens also occur in the uppermost Silurian, i.e., just immediately below the S–D boundary. It is most closely related to the nominative subspecies of the type species of the genus, i.e., *Plectodonta* (*P.*) *mariae mariae* which seems to be a direct descendant of the former. *P. (P.) mariae mariae* occurs abundantly in the succeeding Mytkiv Horizon of several localities in Podolia (Kozłowski 1929; Nikiforova et al. 1985). The new subspecies differs from the nominative subspecies by a smaller, less transversely extended shell, a better marked ventral sulcus and dorsal fold, greater number of radial costellae (70 to 100 in *P. [P.] mariae pantherae*, 45–50 in *P. [P.] mariae mariae*; Jahnke et al. 1989, however, give a total number of 95–100 costellae for the Kozłowski's [1929] subspecies), wider interspaces between major costellae, and more numerous fine costellae between each major costella (3–9 in *P. [P.] mariae pantherae*, 2–4 in *P. [P.] mariae mariae*). Internally both subspecies seem also very similar. The internal features of a single available dorsal valve of *P. mariae pantherae* are less pronounced than those in large specimen of Kozłowski's nominate subspecies (see Kozłowski 1929: fig. 34A), but they appear virtually identical with those in juvenile specimen of *P. (P.) mariae mariae* representing the same individual stage of growth (see Kozłowski 1929: fig. 36C) as the former shown here on Fig. 5M.

The present subspecies differs from *Plectodonta* (*P.*) *micica* (Barrande, 1879) from the Lochkovian of Bohemia (Havlíček 1967) in being somewhat smaller and by having a slightly more rectangular and alate shell outline and dorsal inner side septa appearing further anteriorly. According to Jahnke et al. (1989: 155) the Bohemian form should be regarded as a subspecies of *P. (P.) mariae*. The inadequately known *Plectodonta moderatrix* Havlíček and Storch, 1990 from the Kopanina Formation (Ludlow) of Bohemia (Havlíček and Storch 1990) is stratigraphically much older than *P. mariae pantherae* and differs in having less numerous costellae. *Plectodonta petila* Amsden, 1958 from the Haragan Formation (Lower Devonian) of Oklahoma (USA; see Amsden 1958) is slightly larger than *P. (P.) mariae pantherae* and has rounded cardinal extremities. *P. (P.) sanglangensis* Xian, 1978 from the Tangxiang Formation of Guangxi, South

China (Vogel et al. 1989) differs from the present subspecies in being smaller and having a longitudinal median furrow on the interior of the dorsal valve. *P. (P.?) heterosinus* Vogel, Xu, and Langenstrassen, 1989 and *P. (P.) biplexa* Xu, 1979, both from the same formation (see Vogel et al. 1989), are readily distinguished from the new subspecies by the extremely transverse and alate outline and narrow, strong sulcus and fold of the former, and by the elongate shell of the latter. *P. (P.) orientalis* Vogel, Xu, and Langenstrassen, 1989 also from the same formation and area, differs in having fascicostellate ornamentation.

Order Productida Sarycheva and Sokolskaya, 1959

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1862

Family Strophochonetidae Muir-Wood, 1962

Subfamily Strophochonetinae Muir-Wood, 1962

Genus *Chlupacina* Havlíček and Racheboeuf, 1979

Type species: Chlupacina longispina Havlíček and Racheboeuf, 1979; Choteč Formation, Eifelian (Middle Devonian); Praha-Holýne, Bohemia.

Chlupacina sp.

Fig. 5K, L.

Material.—11 mostly incomplete specimens embedded in rock was found at 5.5 m above the S–D boundary (beds 47–48).

Remarks.—The collection is small and poorly preserved. The specimens show radial ornament which is weak to absent posteriorly and better developed peripherally. The characteristic stronger median costa is usually well developed and reaches the anterior margin. On one specimen a 2.8 mm long (117% of the valve length), proximally cyrtomorph intraverse and distally gently arched spine is well preserved (Fig. 5L). Although preservation of spines on the studied specimens is rare, it seems that they are developed on the right side of the ventral valve only.

The present specimens differ from all chonetoid species known from the Siluro–Devonian of Podolia. The former resembles externally *Pseudostrophochonetes mediocostalis* (Kozłowski, 1929) from the lower Chortkiv Horizon (former Bogdanovka Beds) in having distinct median costa, but differs mainly in thicker shell ribbing and a much older stratigraphic range. Small shell dimensions, presence of distinct median costa, and long spine developed on one side of the hinge line only suggest that the specimens from the studied section may be *Chlupacina*. Unfortunately, the paucity of the material and unknown internal shell structure does not allow for a more detailed determination.

Order Protorthida Schuchert and Cooper, 1931

Superfamily Skenidioidea Kozłowski, 1929

Family Skenidiidae Kozłowski, 1929

Genus *Skenidioides* Schuchert and Cooper, 1931

Type species: *Skenidioides billingsi* Schuchert and Cooper, 1931; Black River Formation, Sandbian, Ordovician; near the Ottawa River, Quebec, Canada.

Skenidioides tatyanae sp. nov.

Fig. 6.

1929 *Scenidium Lewisii* (Davidson); Kozłowski 1929: 47–50, pl. 1: 20, 21; figs. 5–7, 37I.

1968 *Skenidioides lewisi* Davidson; Modzalevskaya 1968: pl. 27: 4–7.

1985 *Skenidioides* sp. nov.; Nikiforova et al. 1985: 9.

Etymology: Species dedicated to Tatyana Lvovna Modzalevskaya in recognition of her work on Podolian brachiopods.

Holotype: Complete shell ZPAL Bp. 56/118; illustrated in Fig. 6A.

Type locality: Trench east of Dnistrove village, Podolia, Ukraine. Coordinates 48°32'16.9"N, 26°14'21.4"E.

Type horizon: Beds 47–48, Khudykivtsi Beds of the Borshchiv Horizon (Early Devonian).

Diagnosis.—*Skenidioides* with unisulcate anterior commissure, obtuse to gently rounded cardinal extremities, apsacline and usually concave ventral interarea, delthyrial angle attaining 31–38°, 26–31 costellae at the anterior margin; dorsal septalium deep, dorsal median septum reaching about 68% of the valve length.

Material.—Three complete shells, 57 ventral and 32 dorsal valves. Dimensions of the holotype (in mm): length 3.3, width 4.2, thickness 2.3, height of ventral interarea 1.2, width of hinge margin 3.7. The species is quite common at about 5.5 m (beds 47–48) above the S–D boundary. A few specimens have been also found 1.5 m (bed 7), 1.3 m (bed 5), and 0.7 m (bed -1) above the boundary. The species was also found in the Khudykivtsi beds at the Khudykivtsi village.

Description.—Shell small, up to about 5 mm in length, ventribiconvex, transversely elliptical to subpentagonal in outline; anterior commissure gently unisulcate, anterior margin arched to slightly emarginate, hinge margin straight and wide but narrower than maximum shell width, cardinal extremities obtuse to gently rounded, lateral margins rounded. Ventral valve sub-pyramidal with rather blunt beak, interarea high, apsacline, concave to only slightly concave, delthyrium open, sides diverging at 31–38°. Dorsal valve transversely elliptical, weakly convex, with wide, shallow, and poorly bounded laterally median sulcus occupying about 1/3 of the valve width; dorsal interarea wide and low, flat, anacline to nearly catacline.

Shell covered by strong, rounded costellae increasing by rare bifurcations or intercalations; ventral valve frequently with wider median intercostal space in which very thin, delicate single or paired costellae are usually developed; 26–31 costellae at the anterior margin. Growth lamellae rare, poorly developed, but anteriorly more obvious and crowded. Micro-ornamentation of very fine, dense concentric lines, about 60 per 1 mm.

Ventral interior with deep, concave spondylium supported apically by wide, septum-like median thickening (Fig. 6N); teeth plate-like, wide (Fig. 6G, I). Dorsal valve with

deep septalium bisected by thin median septum and triangular, elongated cardinal processes at apex; median septum high, reaching about 68% of the valve length (Fig. 6M, O).

Remarks.—The specimens studied here are most probably conspecific with those described in great details and illustrated by Kozłowski (1929: 47–50, figs. 5–7, 37I; pl. 1: 20, 21) from the middle part of the Borshchiv Horizon as *Scenidium lewisi* (Davidson, 1848). Boucot et al. (1966: 364) suggested that cardinalia of the specimens from Podolia are of *Skenidioides* rather than *Skenidium*. Modzalevskaya (1968: pl. 27: 4–7) illustrated one shell from the Tajna beds (= Khudykivtsi Beds) at Dnistrove as *Skenidioides lewisi*. Nikiforova et al. (1985) suggested that Kozłowski's (1929) material, as well as their own new collections from the upper Khudykivtsi and Mytkiv beds, represent a new species that differ from Wenlock–Ludlow *S. lewisii* in a number of features. Indeed, *Skenidioides lewisii* (Davidson, 1848) from the Wenlock Limestone and Wenlock Shale of Dudley and Walsall (England) re-described by Bassett (1972: 35–37, pls. 5: 10, 6: 1–12) differs from the species here described in having more restricted dorsal sulcus, higher and less concave ventral interarea, narrower delthyrium, narrower dorsal septalium, proportionally longer dorsal median septum, and usually thicker costellae.

From *Skenidioides robertsensii* Johnson, Boucot, and Murphy, 1973 described from the Early Devonian of central Nevada (Johnson et al. 1973: 15, 16; pl. 10: 1–13) the new species differs in having a less transverse shell, narrower hinge margin with less acute cardinal extremities, and more concave, apsacline ventral interarea. The latter is readily distinguishable from *Skenidioides operosa* Johnson, Boucot, and Murphy, 1976 from the Ludlovian of central Nevada (Johnson et al. 1976: 23, 24, pl. 29: 1–15), the Wenlock of Arctic Canada (Zhang 1989), and the Mackenzie Mountains of northwestern Canada (Jin and Chatterton 1997) in having less transverse shell, less acute cardinal extremities, shorter dorsal median septum, and finer, more numerous costellae. *Skenidioides polonicus* (Gürich, 1896) from the Middle Devonian of the Holy Cross Mountains, Poland, which was redescribed by Biernat (1959: 16–25, pl. 1: 1–9, figs. 6–8; text-plates 1–2) and Halamski (2009: 72–74, pls. 10: 1–38, 12: 30; fig. 10) differs from the species described here mainly by having much thicker shell costellation, longer dorsal median septum, and more acute, frequently mucronate cardinal extremities. *Skenidioides tatyanae* sp. nov. shows great external similarity to *Skenidioides henryhousensis* Amsden, 1958 from the Henryhouse Formation (late Silurian) of Oklahoma, USA (see Amsden 1958), but differs from the latter by shorter and more rounded cardinal extremities, more concave ventral interarea, and narrower and stronger dorsal sulcus.

As suggested Nikiforova et al. (1985) the Silurian species described by Kozłowski (1929) from the Skala Horizon as *Scenidium orthisiforme* Kozłowski, 1929 probably belongs to *Skenidioides*. This form is poorly known and thus a nomen dubium (Nikiforova et al. 1985). It differs from the species

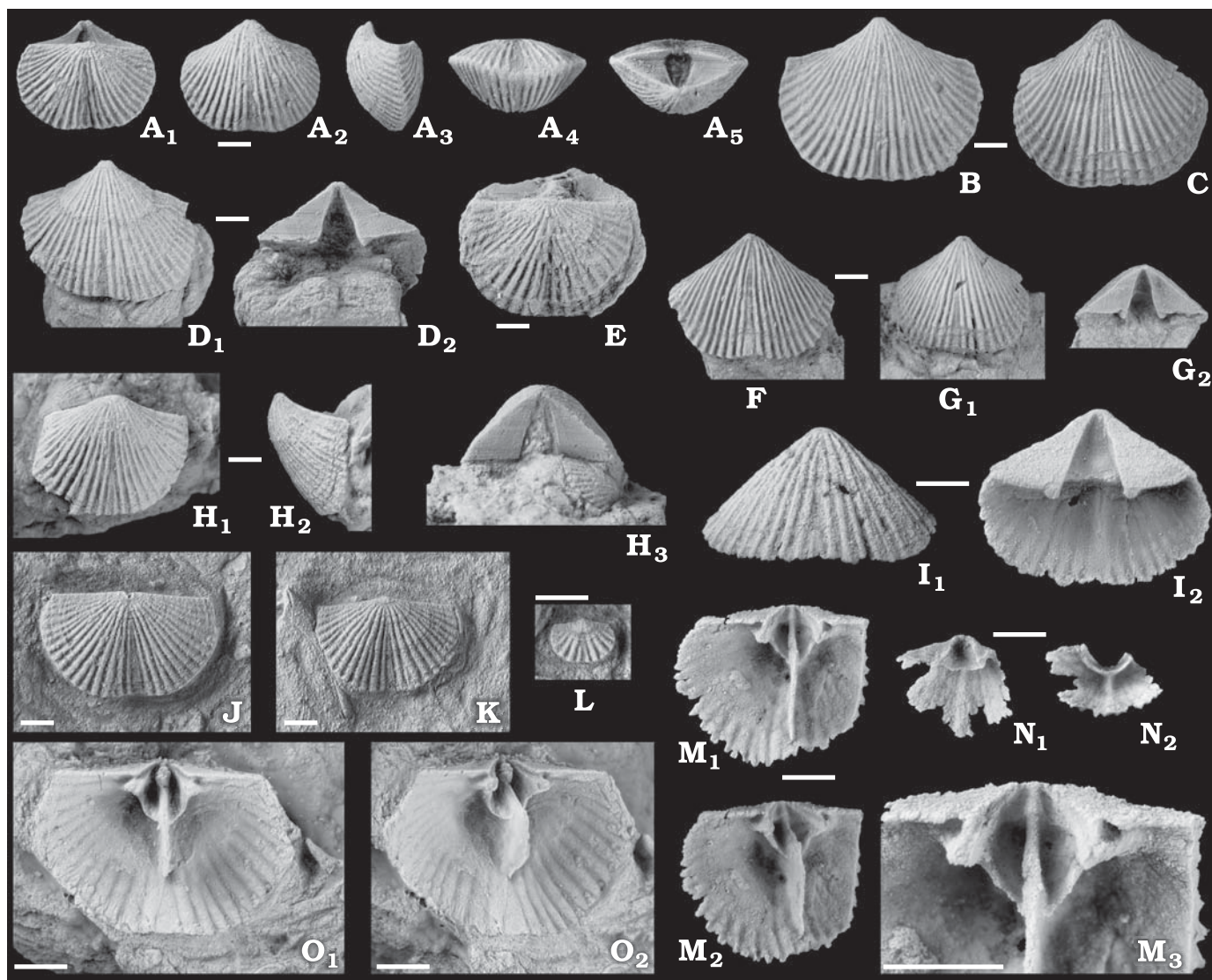


Fig. 6. Protorthide *Skenidioides tatyanae* sp. nov. the Silurian–Devonian boundary beds at Dnistrove (A–L, O) and Khudykivtsi (M, N), (Podolia, Ukraine). A. Holotype ZPAL Bp. 56/118 in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views. B, C, F. Three ventral valves, ZPAL Bp. 56/119 (B), ZPAL Bp. 56/120 (C), and ZPAL Bp. 56/123 (F), in exterior view. D. Ventral valve ZPAL Bp. 56/121 in exterior (D₁) and oblique posterior (D₂) views. E. Slightly damaged shell ZPAL Bp. 56/122 in dorsal view. G. Ventral valve ZPAL Bp. 56/124 in exterior (G₁) and posterior views (G₂). H. Ventral valve ZPAL Bp. 56/125 in exterior (H₁), lateral (H₂), and posterior (H₃) views. I. Ventral valve ZPAL Bp. 56/126 in anterior (I₁) and interior (I₂) views. J, K. Two dorsal valves, ZPAL Bp. 56/2 (J) and ZPAL Bp. 56/1 (K) in exterior view. L. Small dorsal valve ZPAL Bp. 56/127 in exterior view. M. Dorsal valve ZPAL Bp. 56/129 in interior (M₁) and oblique interior (M₂) views and enlargement of cardinalia (M₃). N. Incomplete ventral valve ZPAL Bp. 56/130 in internal (N₁) and anterior (N₂) views. O. Dorsal valve ZPAL Bp. 56/128 in interior (O₁) and oblique interior (O₂) views. Dnistrove, beds 7 (J, K) and 47–48 (A–I, L, O); Khudykivtsi (M, N). Scale bars 1 mm.

here described by a more convex dorsal valve, the absence of the dorsal median sulcus, more rounded lateral margins, lower ventral interarea, and finer costation.

Stratigraphic and geographic range.—Kozłowski (1929: 50) found this species in several other localities from Podolia representing “l’étage de Borszczów”. Nikiforova et al. (1985: 9) collected new specimens representing this species from the Khudykivtsi and Mytkiv beds.

Order Orthida Schuchert and Cooper, 1932

Suborder Dalmanellidina Moore, 1952

Superfamily Dalmanelloidea Schuchert, 1913

Family Dalmanellidae Schuchert, 1913

Subfamily Resserellinae Walmsley and Boucot, 1971

Genus *Resserella* Bancroft, 1928

Type species: *Orthis canalis* Sowerby, 1839; Coalbrookdale Formation, Wenlock, Silurian; Herefordshire, England.

Resserella elegantuloides (Kozłowski, 1929)

Fig. 7A.

1929 *Dalmanella elegantuloides* sp. n.; Kozłowski 1929: 63–67, pl. 2: 1–16; figs. 9A, 10, 11.

1985 *Resserella elegantuloides* (Kozłowski, 1929); Nikiforova et al. 1985: 10–12, pl. 1: 1–3 [full synonymy herein].

2003 *Resserella elegantuloides* (Kozłowski, 1929); Brock 2003: 118–119; pls. 7: 13–14, 8: 4–5.

Material.—Three complete shells, 19 ventral and 7 dorsal valves. The species was found 5.5 m above the S–D boundary (beds 47–48); single specimens were also recovered 0.4 and 0.95 m above the boundary (beds -4 and 1.5).

Remarks.—The species was described in great detail, both externally and internally, by Kozłowski (1929). Nikiforova et al. (1985) selected a neotype from the Mytkiv Beds of Verkhnyakovtsy. The present specimens from Dnistrove fully agree externally with *Resserella elegantuloides* described by those authors.

Stratigraphic and geographic range.—The species is reported from the Khudykivtsi and Mytkiv beds of the Borshchiv Horizon. It was also found in the lower Devonian of Nevada, USA (Johnson 1973: 1019, pl. 1: 16–20; Johnson et al. 1973: 17–18, pl. 14: 121) and New South Wales, Australia (Savage 1974: 16, 17; pl. 1: 25–29; Brock 2003: 118–119; pls. 7: 13–14, 8: 4–5).

Family Rhipidomellidae Schuchert, 1913

Subfamily Rhipidomellinae Schuchert, 1913

Genus *Dalejina* Havlíček, 1953

Type species: *Dalejina hanusi* Havlíček, 1953; Dvorce Limestone, Pragian; Prague Basin, Bohemia.

Dalejina frequens (Kozłowski, 1929)

Fig. 7B.

1929 *Rhipidomella frequens* sp. n.; Kozłowski 1929: 83–86, pl. 3: 4–22; figs. 21B, 22, 23.

1985 *Dalejina frequens* (Kozłowski, 1929); Nikiforova et al. 1985: 17, pls. 2: 7, 3: 1–4 [full synonymy herein].

Material.—Four shells (2 of them slightly damaged), 4 dorsal and 4 ventral valves. The present material was recovered from the Khudykivtsi Beds at Dnistrove at 5.5 m (beds 47–48) above the S–D boundary.

Remarks.—The studied specimens from Dnistrove, although rather scarce, are externally indistinguishable from specimens illustrated by Kozłowski (1929), Nikiforova (1954), and Nikiforova et al. (1985). The only difference is generally smaller shell size (not exceeding 8 mm in length) attained by the specimens reported here. In this respect they are similar to *Dalejina staszici* Kozłowski, 1929, but the latter has a thicker shell with a more pentagonal outline resulting from narrower hinge margin. *D. staszici* is a rare and stratigraphically older species, occurring only in the Skala Horizon.

According to Nikiforova et al. (1985) *D. frequens* is abundant in and restricted to the Mytkiv Beds (upper part of the Borshchiv Horizon). The present material, although not numerous, indicates that the species also occurs in the Khudykivtsi Beds.

Stratigraphic and geographic range.—Kozłowski (1929) found the species to range through the Borshchiv Horizon of

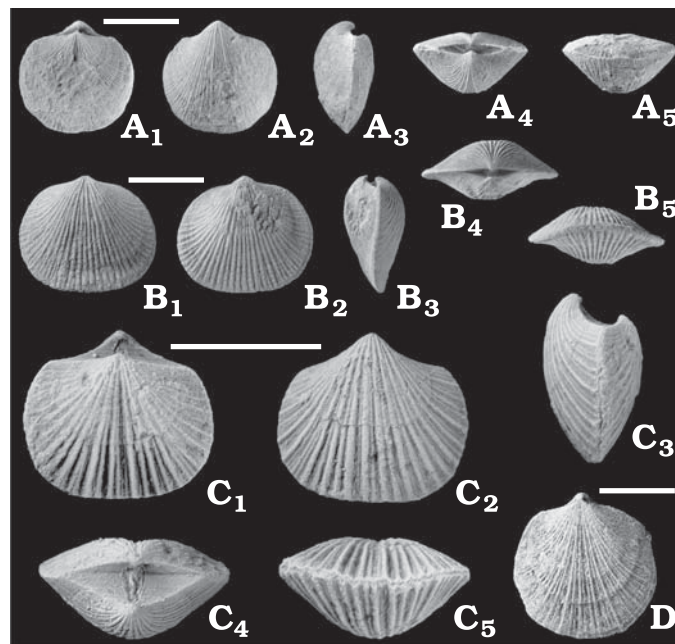


Fig. 7. Orthide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A.** *Resserella elegantuloides* (Kozłowski, 1929), complete shell ZPAL Bp. 56/41 in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views. **B.** *Dalejina frequens* (Kozłowski, 1929), complete shell ZPAL Bp. 56/35 in dorsal (B₁), ventral (B₂), lateral (B₃), posterior (B₄), and anterior (B₅) views. **C.** *Talentella crassiformis* (Kozłowski, 1929), articulated shell ZPAL Bp. 56/30 in dorsal (C₁), ventral (C₂), lateral (C₃), posterior (C₄), and anterior (C₅) views. Beds 47–48. Scale bars 5 mm.

Podolia. Nikiforova et al. (1985) reported it only from the Mytkiv Beds. Similar form described as *D. aff. frequens* was reported by Savage (1974: 19–20; pl. 3: 18–32; fig. 8A, B) from the lower Devonian of New South Wales (Australia).

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Talentella* Johnson, 1990

Type species: *Salopina submurifer* Johnson, Boucot, and Murphy, 1973; Lochkovian, Lower Devonian; Nevada, USA.

Talentella crassiformis (Kozłowski, 1929)

Fig. 7C.

1929 *Dalmanella crassiformis* sp. n.; Kozłowski 1929: 67–69, pl. 1: 30, 31; figs. 12A, 13.

1969 *Salopina crassiformis* (Kozłowski); Walmsley et al. 1969: 507–09.

1985 *Salopina crassiformis* (Kozłowski, 1929); Nikiforova et al. 1985: 12–14, pl. 1: 4.

Material.—7 shells, 53 ventral and 42 dorsal valves. The species occurs scarcely at 0.7 m (bed -1) above the S–D boundary but becomes much more common at 5.5 m (beds 47–48) above the boundary.

Remarks.—Describing the external variability of the species, Kozłowski (1929: 68) reported only 8 shells from 5 localities. During the present investigation 7 additional shells have

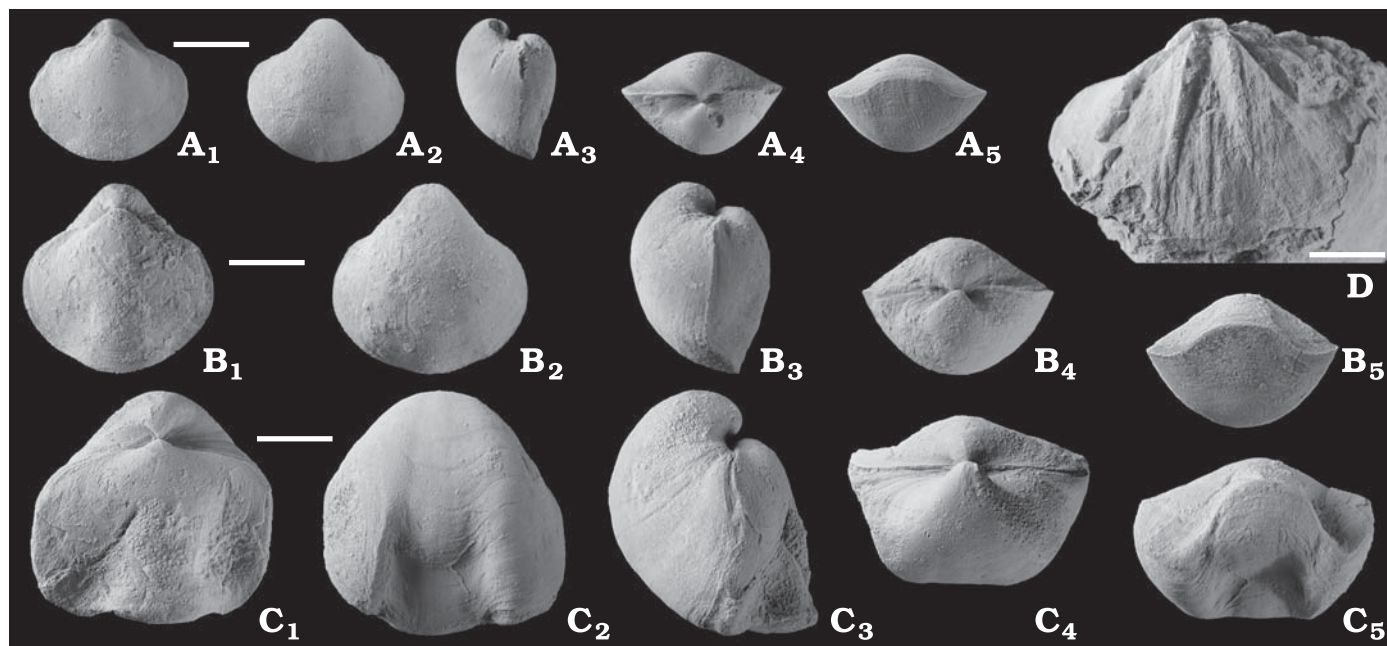


Fig. 8. Pentameride *Clorinda pseudolinguifera* Kozłowski, 1929 from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). A–C. Three shells, ZPAL Bp. 56/48 (A), ZPAL Bp. 56/49 (B), and ZPAL Bp. 56/50 (C), of different size in dorsal (A₁, B₁, C₁), ventral (A₂, B₂, C₂), lateral (A₃, B₃, C₃), posterior (A₄, B₄, C₄), and anterior (A₅, B₅, C₅) views. D. Exterior view of extensively decorticated ventral valve ZPAL Bp. 56/51 showing cast of the internal morphology of the valve. Beds 47–48. Scale bars 5 mm.

been recovered from the trench at Dnistrove. Nikiforova et al. (1985) selected a neotype from the Khudykivtsi Beds at Tselyuev-Myshakovtsy. Thus, this is a rather rare, small-sized (rarely exceeds 7 mm in length) species in Podolia.

The present specimens fully agree externally with those described by Kozłowski (1929) from the Borshchiv Horizon as *Dalmanella crassiformis*. More recently Nikiforova et al. (1985) assigned the species to *Salopina* Boucot, 1960, but eventually it was attributed by Johnson (1990) to his new genus *Talentella* Johnson, 1990. According to Kozłowski (1929) the species also occurs in the Malinovtsy and Skala horizons (Silurian) but Nikiforova et al. (1985) noted that it can be identified with certainty only from the Khudykivtsi Beds of the Borshchiv Horizon.

Stratigraphic and geographic range.—The species has been found in several localities in Podolia, all representing Khudykivtsi Beds of the Borshchiv Horizon. Walmsley et al. (1969: 509) reported the species from the lower Devonian of Nevada and northern Yukon Territory.

Order Pentamerida Schuchert and Cooper, 1931
Suborder Pentameridina Schuchert and Cooper, 1931
Superfamily Clorindoidea Rzhonsnitskaya, 1956
Family Clorindidae Rzhonsnitskaya, 1956
Subfamily Clorindinae Rzhonsnitskaya, 1956
Genus *Clorinda* Barrande, 1879

Type species: *Clorinda armata* Barrande, 1879; Zlichov Limestone, Emsian (Lower Devonian); Hlubočepy, Bohemia.

Clorinda pseudolinguifera Kozłowski, 1929

Figs. 8, 9.

1929 *Barrandella* (*Clorinda*) *pseudolinguifera* sp. n.; Kozłowski 1929: 137, pl. 6: 4–13; fig. 37: IV, fig. 40.

1967 *Clorinda pseudolinguifera* Kozłowski; Gratsianova 1967: 63–64; pl. 5: 3; fig. 18.

1985 *Clorinda pseudolinguifera* Kozłowski, 1929; Nikiforova et al. 1985: 33–34; pl. 9: 1, 2. [synonymy therein]

1990 *Clorinda pseudolinguifera* Kozłowski, 1929; Havlíček and Štorch 1990: 121; pl. 33: 8.

Material.—Six complete shells and more than 150 fragmentary valves and shells. Dimensions of the complete shells are given in Fig. 9. In the studied section the oldest (although fragmentary) specimens were recovered at about 1.0–1.7 m above the S–D boundary (beds 2, 5, 7, and 9). It becomes quite common at 5.5 m above the boundary (beds 47–48).

Remarks.—Contrary to the majority of species of the studied material from Dnistrove, *Clorinda pseudolinguifera* is mostly characterised by disjoined valves. This taphonomic characteristic can be explained by different mechanical resistance between cyrtomatodont and deltidiodont hinge teeth. The latter, characteristic for majority of Pentamerida (including *Clorinda*), are much more susceptible to mechanical damage and disarticulation.

This species from the Borshchiv Horizon was described in great detail by Kozłowski (1929), including its internal shell structure and the variability of the external morphology, and Podolian material have been considered by Nikiforova (1954), Modzalevskaya (1968), Gauri and Boucot (1968), and Nikiforova et al. (1985). Nikiforova et al. (1985) selected the neotype

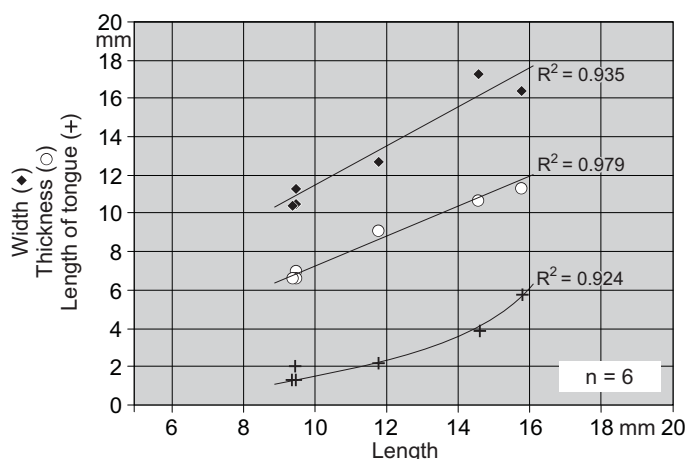


Fig. 9. Scatter diagram of shell width, thickness, and length of tongue to shell length ratios in *Clorinda pseudolinguifera* Kozłowski, 1929. Dnistrove, beds 47–48.

from the Mitkov beds cropping out at the mouth of Tsyganka stream. The new material contains adult as well as young shells, which illustrate some growth changes in the external morphology of the species (Figs. 8A–C, 9).

Stratigraphic and geographic range.—According to Nikiforova et al. (1985: 33), *C. pseudolinguifera* occurs through the Khudykivtsy Horizon, becoming common in the lower Mitkov Horizon where it sometimes forms shell banks up to 30–40 mm thick. Conspecific material has been reported from the early Devonian of the Urals (Gauri and Boucot 1968) and Altai Mountains (Gratsianova 1967) as well as from the top of Silurian and the lowest Lochkov of Bohemia (Havlíček and Štorch 1990).

Order Rhynchonellida Kuhn, 1949

Superfamily Uncinuloidea Rzhonsnitskaya, 1956

Family Hebetoechiidae Havlíček, 1960

Subfamily Sphaerirhynchiinae Savage, 1996

Genus *Sphaerirhynchia* Cooper and Muir-Wood, 1951

Type species: *Terebratula wilsoni* Sowerby, 1816; Elton Formation, Ludlow, Silurian; Mordiford, Herefordshire, England.

Sphaerirhynchia gibbosa (Nikiforova, 1954)

Figs. 10, 11, 12A–E.

1929 *Camarotoechia* (*Wilsonia*) *Wilsoni* (Sowerby); Kozłowski 1929: 159, pl. 7: 27–33 (not 34 = *Sphaerirhynchia wilsoni*?); fig. 50.

1954 *Wilsonella wilsoni* (Sowerby) var. *gibbosa* var. nov.; Nikiforova 1954: 110; pl. 11: 5.

1968 *Sphaerirhynchia gibbosa* (Nikiforova); Modzalevskaya 1968: pl. 27: 40–43.

1978 *Sphaerirhynchia gibbosa* (Nikiforova); Rubel and Teller 1978: 477; pl. 2: 16–18.

1985 *Sphaerirhynchia gibbosa* (Nikiforova, 1954); Nikiforova et al. 1985: 37.

Material.—86 complete and 109 fragmentary or deformed shells. Statistical analysis of the main shell dimensions is given in Fig. 10. *Sphaerirhynchia gibbosa* is one of the most characteristic species in the studied section at Dnistrove. The

first specimens appear in the interval at 1.3–1.5 m above the S–D boundary (beds 5 and 7). Slightly higher in the section (5.5 m above the boundary; beds 47–48) it becomes one of the most numerous taxa in the assemblage. Sporadically it occurs in beds 92, 96, 102, 105, 110, and 115.

Description.—Shell attaining about 18 mm in width, strongly dorsibiconvex in profile, subelliptical to subpentagonal in outline, globose, slightly wider than long; commissure serrate, moderately to strongly uniplicate. Ventral valve regularly convex in both lateral and anterior profiles; umbo massive but low, beak incurved; sulcus poorly defined, shallow, developed in anterior half, anteriorly forms subtrapezoidal to subrectangular tongue. Dorsal valve regularly and strongly convex with greatest convexity at about midvalve or slightly posteriorly; fold very low, poorly defined in anterior half of the valve.

Ribs fine, simple, extending from beaks, those at the anterior margin medianly grooved; 6–8 ribs on fold, 5–7 in sulcus, one pair of parietal ribs frequently present.

Interior of ventral valve with short, thin subparallel dental plates. In dorsal valve thin median septum attains less than half of the valve length and supports V-shaped septalium.

Dental plates slightly laterally convex, thin and short; outer hinge plates flat and horizontal; V-shaped septalium and median septum short; crura fairly long, slightly divergent, curving ventrally, with anterior surface concave distally (Fig. 11A, C).

Remarks.—Kozłowski (1929) described *Camarotoechia* (*Wilsonia*) *wilsoni* (Sowerby, 1816) (= *Sphaerirhynchia wilsoni*) from the Skala and Borshchiv horizons. Later, Nikifo-

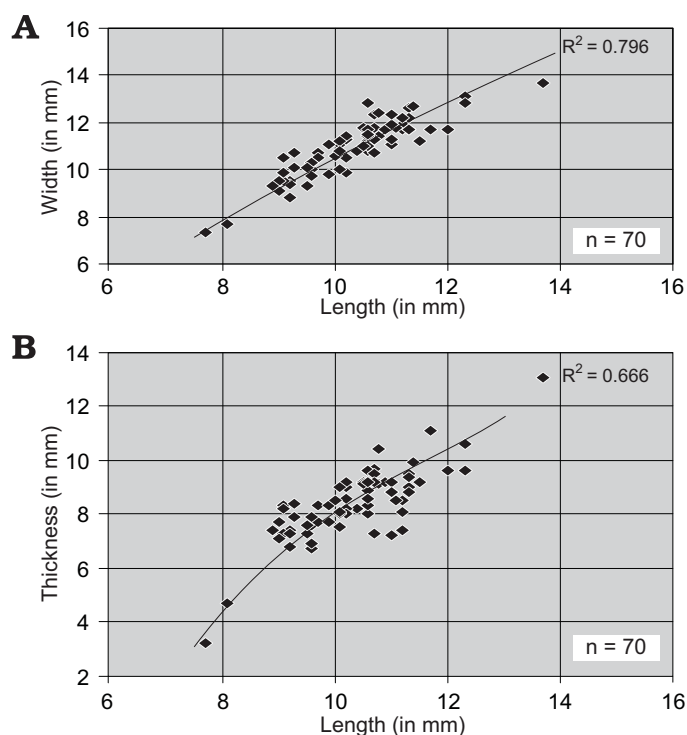


Fig. 10. Scatter diagrams of shell width (A) and shell thickness (B) to shell length ratios in *Sphaerirhynchia gibbosa* (Nikiforova, 1954). Dnistrove, beds 47–48.

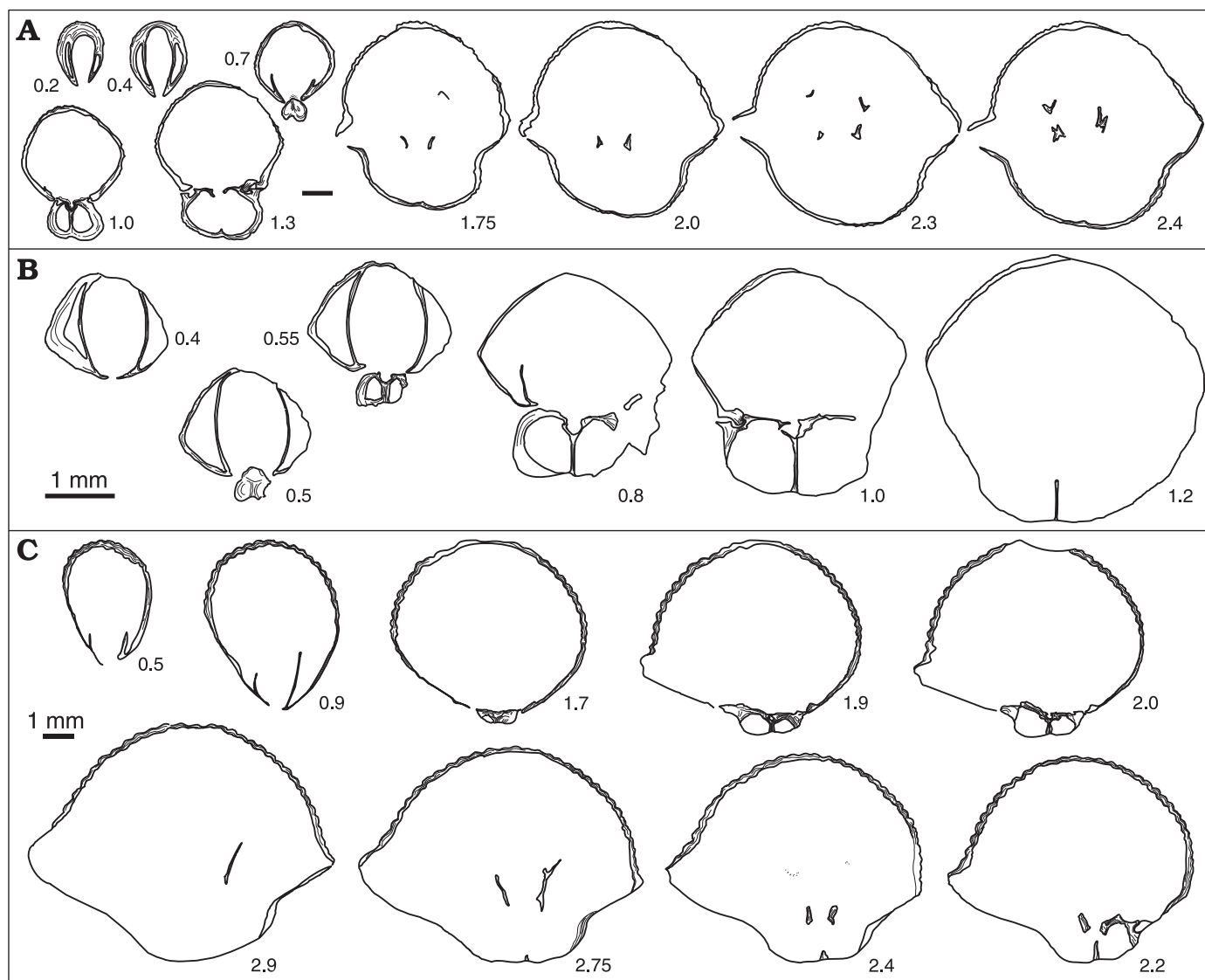


Fig. 11. Transverse serial sections through three shells of *Sphaerirhynchia gibbosa* (Nikiforova, 1954). **A.** ZPAL Bp. 56/64-3. **B.** ZPAL Bp. 56/64-2. **C.** ZPAL Bp. 56/64-1. Numbers refer to distance in mm from ventral umbo. Dnistrove, beds 47–48.

rova (1954) also collected the species from the older Malinovtsy Horizon. She found morphological differences between specimens from the Malinovtsy and Borshchiv horizons, and named the younger form as a new variety *gibbosa*. Nikiforova et al. (1985) then confirmed that specimens of *Sphaerirhynchia gibbosa* from the Khudykivtsi Beds of the Borshchiv Horizon are separable from true *S. wilsoni* as recovered by Nikiforova (1954) from the Malinovtsy horizon.

Stratigraphic and geographic range.—According to Nikiforova et al. (1985), this is a common species in the Khudykivtsi Beds. *S. gibbosa* was also reported by Johnson et al. (1973) from the lower Devonian of Nevada.

Subfamily Hebetoechiinae Havlíček, 1960

Genus *Lanceomyonia* Havlíček, 1960

Type species: *Terebratula tarda* Barrande, 1847; Pridoli, Silurian; Dvorce, central Bohemia.

Lanceomyonia borealiformis (Siemiradzki, 1906)

Fig. 12F–H.

1906 *Rhynchonella borealiformis* Szajnocha; Siemiradzki 1906: 171, pl. 7: 3–5.

1978 *Lanceomyonia borealiformis* (Siemiradzki, 1906); Rubel and Teller 1978: 477–478, pl. 3: 8–9.

1985 *Lanceomyonia borealiformis* (Siemiradzki, 1906); Nikiforova et al. 1985: 38 [full synonymy herein].

Material.—9 complete shells and 7 fragments of shells and single valves. In the studied section the stratigraphically oldest specimens come from 1.0 m and 1.5 m above the S–D boundary (bed 2 and 5, respectively). Other specimens were recovered 5.5 m (beds 47–48) above the boundary and from a loose block representing the uppermost part of the section.

Description.—Shell up to 16.4 mm in length, dorsibiconvex, transversely subelliptical to subcircular in outline, slightly wider than long, uniplicate. Ventral valve regularly convex

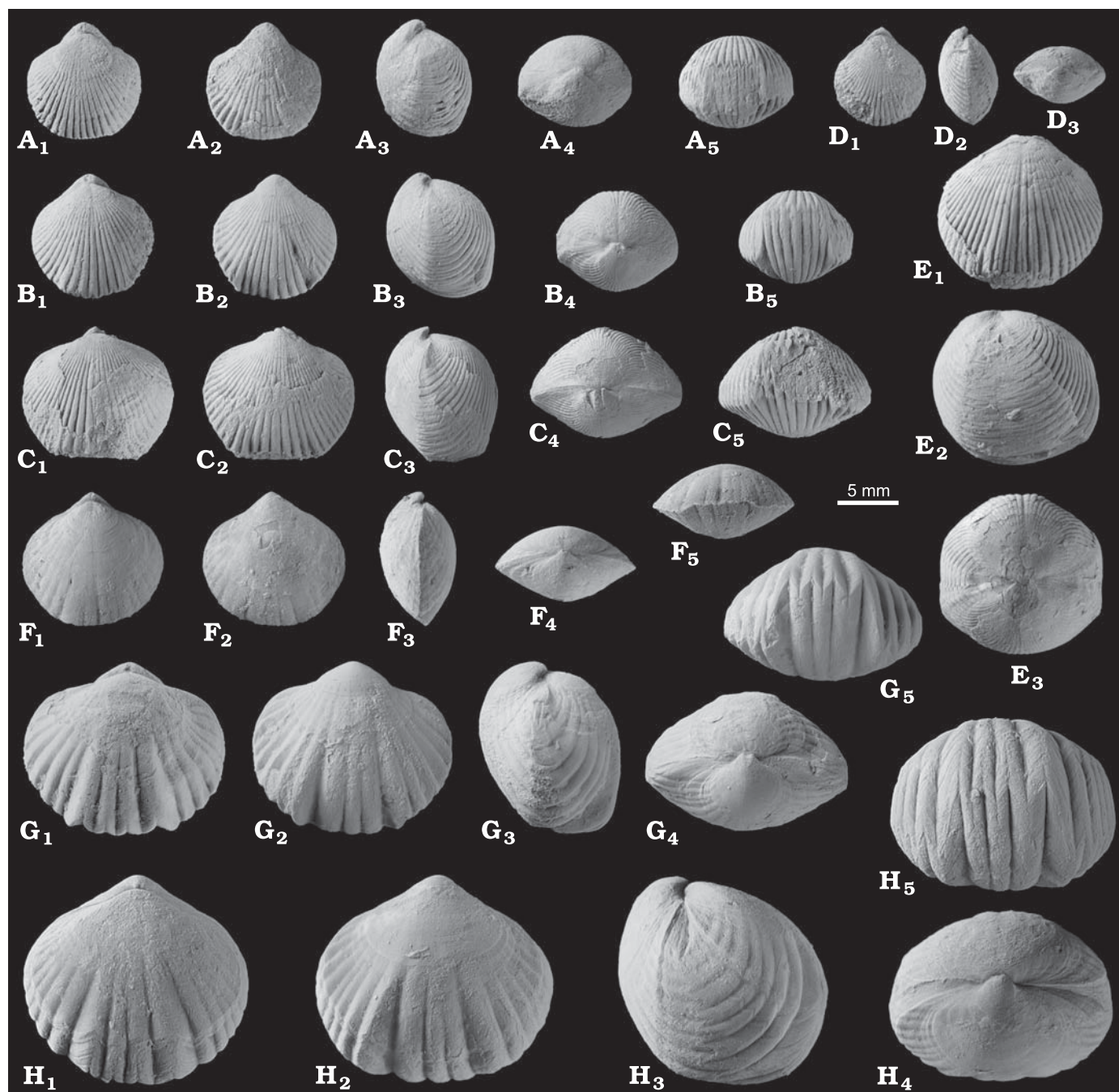


Fig. 12. Rhynchonellide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A–D.** *Sphaerirhynchia gibbosa* (Nikiforova, 1954). **A–C.** Three complete shells ZPAL Bp. 56/59 (**A**), ZPAL Bp. 56/60 (**B**), and ZPAL Bp. 56/61 (**C**) in dorsal (**A**₁, **B**₁, **C**₁), ventral (**A**₂, **B**₂, **C**₂), lateral (**A**₃, **B**₃, **C**₃), posterior (**A**₄, **B**₄, **C**₄), and anterior (**A**₅, **B**₅, **C**₅) views. **D, E.** Juvenile, ZPAL Bp. 56/62 (**D**) and gerontic, ZPAL Bp. 56/63 (**E**) shells in dorsal (**D**₁, **E**₁), lateral (**D**₂, **E**₂), and posterior (**D**₃, **E**₃) views. **F–H.** *Lanceomyonia borealiformis* (Siemiradzki, 1906), three well preserved shells ZPAL Bp. 56/65 (**F**), ZPAL Bp. 56/66 (**G**), and ZPAL Bp. 56/67 (**H**), in different individual age in dorsal (**F**₁, **G**₁, **H**₁), ventral (**F**₂, **G**₂, **H**₂), lateral (**F**₃, **G**₃, **H**₃), posterior (**F**₄, **G**₄, **H**₄), and anterior (**F**₅, **G**₅, **H**₅) views; all from beds 47–48.

in lateral profile with strongly incurved beak in large shells; sulcus appears at about 7–8 mm from the umbo, rather shallow but clearly separated from flanks by slightly stronger ribs; tongue long, with convex bottom. Dorsal valve strongly convex; fold appears 5–6 mm from umbo, rather low, but clearly delimited laterally by slightly stronger bordering ribs. Posterior 5–9 mm of the shell surface smooth, anteriorly ra-

dially ribbed; ribs simple, rounded, very variable in number; 4–5 ribs on fold, 3–4 in sulcus, and 7–11 ribs on each flank.

Remarks.—This species was reported by Kozłowski (1929), as *Camarotoechia* (*Wilsonia*) *tarda* (Barrande, 1847), from the Borshchiv and Chortkiv horizons. Nikiforova et al. (1985) identified the species with certainty, however, only

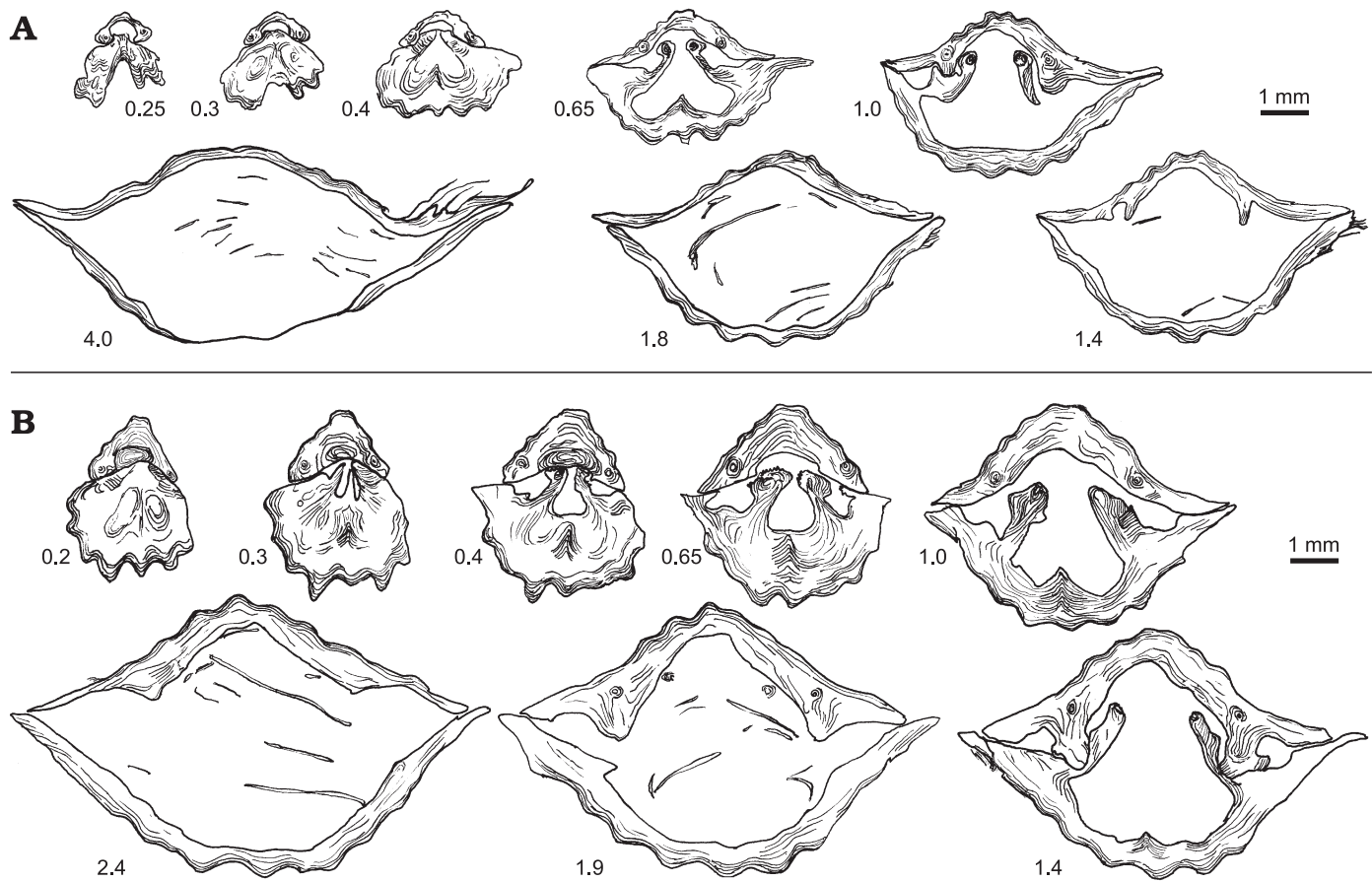


Fig. 13. Transverse serial sections through shell of *Oglu senilis* Havlíček, 1987. **A.** ZPAL Bp. 56/88. **B.** ZPAL Bp. 56/89. Numbers refer to distance in mm from ventral umbo. Dnistrove, beds 47–48.

from the Khudykivtsi and Mytkiv beds of the Borshchiv Horizon. The specimens studied here from the Dnistrove section agree closely with those illustrated by Kozłowski (1929: pl. 7: 26) from the Borshchiv Horizon. He described the species in great detail, both externally and internally, and gave the statistic range of its morphologic variability.

Stratigraphic and geographic range.—Nikiforova (1954) reported the species from several localities in Podolia from the Borshchiv Horizon. Although Kozłowski (1929) and Nikiforova (1954) reported the species from many localities in Podolia they did not list Dnistrove among them. Later, however, Nikiforova et al. (1972) mentioned *L. borealiformis* from Volkovtsy (= Dnistrove).

Order Atrypida Rzhonsnitskaya, 1960
Suborder Atrypidina Moore, 1952
Superfamily Atrypoidea Gill, 1871
Family Atrypidae Gill, 1871
Subfamily Spinatrypinae Copper, 1978
Genus *Oglu* Havlíček, 1987

Type species: *Terebratula semiorbis* Barrande, 1847; Koněprusy Limestone, Pragian (Lower Devonian); Koněprusy, Bohemia.

Oglu senilis Havlíček, 1987

Figs. 13, 14H–J, M.

1987 *Oglu senilis* sp. n.; Havlíček 1987: 83–84, pls. 2: 7, 4: 1.

Material.—51 complete and 37 damaged shells. The species is quite common in beds 47–48 (5.5 m above the S–D boundary); a single specimen was also collected at 1 m above the boundary (bed 2), and another was found in a loose block from the uppermost part of the section (lower part of the Khudykivtsi Beds).

Description.—Shell rather small, usually up to 15 mm in length, slightly elongate to transverse, circular to shield-shape in outline, dorsibiconvex; hinge line short, nearly straight to slightly angular; maximum width posterior to midlength; anterior commissure rectimarginate to very weakly and broadly arched distally.

Ventral valve convex posteriorly, laterally and anteriorly planar to weakly concave; beak minute, incurved, interarea poorly defined, low, anacline; sulcus absent or very weak, almost imperceptible. Dorsal valve convex to strongly convex, greatest convexity slightly posterior to midvalve, fold not developed.

Ribs relatively coarse, undulose, especially posteriorly; 8 and 7 ribs near hinge margin on ventral and dorsal valves,

respectively; ribs increasing usually by intercalation on dorsal and bifurcation on ventral valve; at anterior margin the total number of ribs ranges 17–20, exceptionally up to 25; ventral midrib pair slightly raised; growth lamellae undulating, extending into short trails and spines, the latter developed on both valves reaching up to 3.5 mm in length.

Interior of ventral valve with recognisable dental nuclei, thick pedicle callist developed into a collar in one of the sectioned shells (Fig. 13B); teeth stubby, subdorsally directed, with well-developed lateral lobes. Dorsal valve with distinct subtriangular in section median ridge; hinge plate umbonally lined with comb-like layer.

Remarks.—This rather small-sized atrypid is characterised by its shield shaped, dorsibiconvex shell ornamented by thick ribs, weakly undulating growth lamellae, and numerous short to quite long spines on both valves (Fig. 14M). The studied specimens externally resemble *Spinatrypa* Stainbrook, 1951, in shell shape, convexity, and spinose ornamentation, but they differ in their less undulose ribs, absence of dental plates, and by their occurrence much below the known stratigraphic range of the latter genus. Externally, the Podolian specimens also resemble *Isospinatrypa* Struve, 1966, in many respects, differing by having an evident dorsibiconvex shell instead of a biconvex to weakly dorsibiconvex profile as in the latter genus. They are also very similar externally and internally to inadequately known genus *Oglu* Havlíček, 1987 (see remarks in Copper 2002: 1412). It seems that Podolian species is conspecific with *O. senilis* Havlíček, 1987, which was described from a corresponding time interval (lowermost part of the Lochkov Formation) in central Bohemia (Havlíček 1987). The differences between them appear rather minor and are expressed in the presence of spinosity on both valves and slightly larger shell of the specimens from Dnistrove, which are up to 16 mm in width (in comparison to 12.5 mm in the Bohemian species; Havlíček 1987: 83). According to Havlíček (1987) the spinose ornament in *Oglu* occurs on dorsal valves only, but it seems probable that the absence of spines on the ventral valves may be related to the preservation. Because these differences seem rather minor, the specimens here described are regarded as conspecific with the Bohemian *Oglu senilis* Havlíček, 1987.

Stratigraphic and geographic range.—This species was not described from Podolia either by Kozłowski (1929) nor Niki-forova (1954). Originally the species was described by Havlíček (1987) from the lowermost part of the Lochkov Formation (Kotýs Limestone, Lochkov) in central Bohemia.

Family Atrypinidae McEwan, 1939

Subfamily Atrypinae McEwan, 1939

Genus *Gracianella* Johnson and Boucot, 1967

Type species: *Gracianella lisumbra* Johnson and Boucot, 1967; Robert Mountains Formation, Ludlow (Silurian); Robert Mountains, Nevada, USA.

Subgenus *Gracianella* (*Sublepida*) Mizens and Sapelnikov, 1982

Type species: *Terebratula sublepida* Verneuil, 1845; Pridoli, Upper Silurian; the Urals, Russia.

Gracianella (*Sublepida*) *paulula* sp. nov.

Fig. 14A–G.

Etymology: From Latin *paulula*, in reference to the very small shell.

Holotype: Complete shell ZPAL Bp. 56/183; illustrated in Fig. 14F.

Type locality: Trench east of Dnistrove village, Podolia, Ukraine. Coordinates 48°32'16.9"N, 26°14'21.4"E.

Type horizon: Bed -4, lowest part of the Khudykivtsi Beds of the Borshchiv Horizon (Early Devonian).

Diagnosis.—Very small, lenticular, subcircular in outline with pointed ventral beak; distinct, apsacline to nearly orthocline ventral interarea, delthyrium open; ribs thick, about 8–10 on each flank, increasing by intercalation and bifurcation on both valves; ventral midrib pair prominent, divided by deep interspace with a thin, thread-like median costella; dorsal valve with well marked, wide sulcus and thick and simple median rib; lacking distinct concentric lamellose ornamentation.

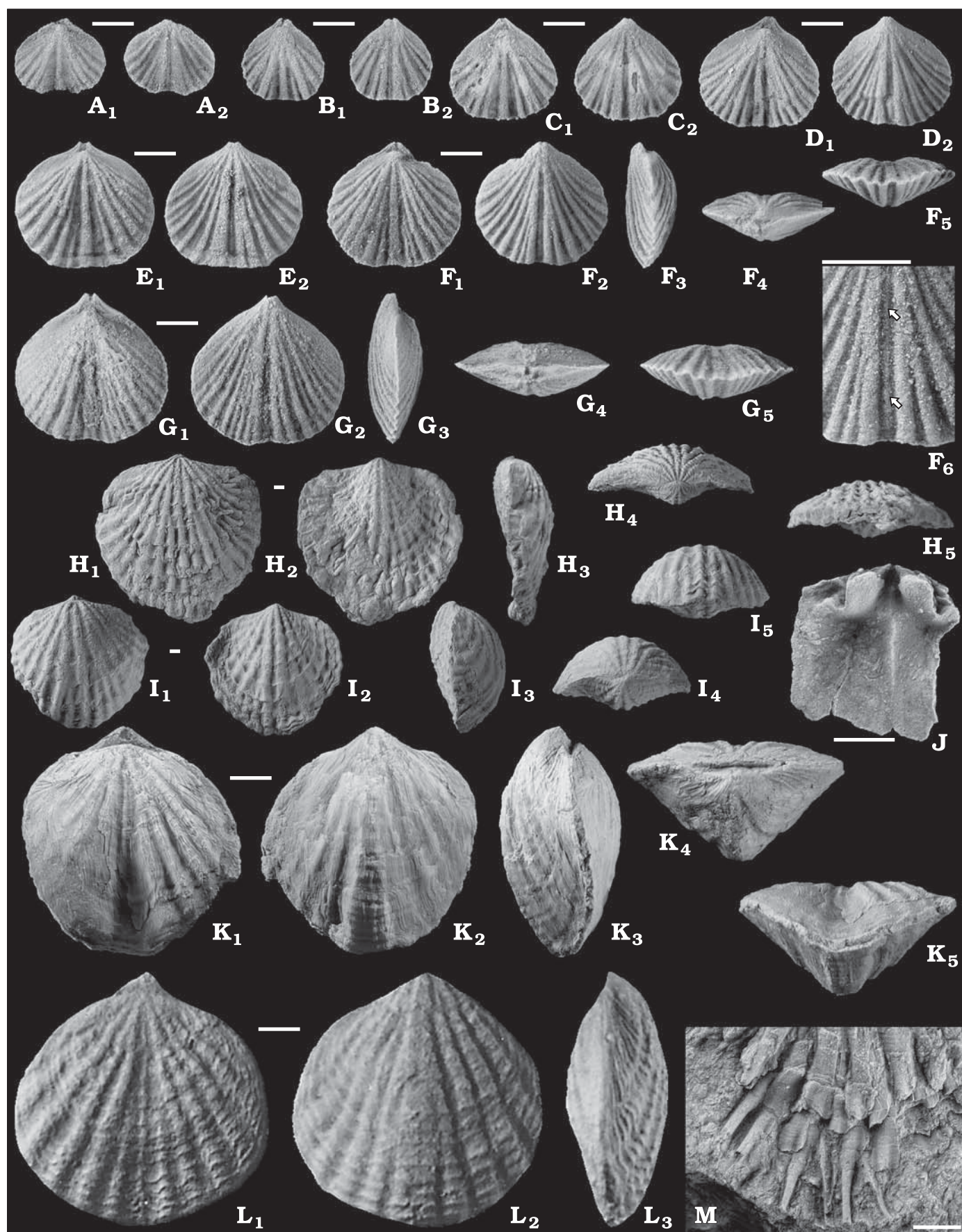
Material.—109 complete shells and 53 fragmentary specimens. This species is quite common in the shale at 0.4 m (bed -4) above the S–D boundary. A few specimens were also found at 1.5 m (bed 7) above the boundary, as well as 0.2 m (bed -10) below it. In the studied section this short-ranging species occurs about 1.1 m above the last occurrence of *Dnestrina gutta* and 1.2 m above *Dayia bohémica* (see Fig. 3).

Description.—Shell small, up to about 4 mm in length, biconvex, lenticular, subtriangular posteriorly and subcircular anterolaterally in outline, approximately as wide as long or slightly wider, widest slightly anteriorly to midlength; anterior margin rounded to weakly emarginate, hinge line short, almost straight, anterior commissure weakly sulcate.

Ventral valve weakly convex, slightly carinate, subtriangular in anterior profile; ventral beak pointed, interarea distinct, flat, apsacline to nearly orthocline, up to 0.6 mm in height; delthyrial cover not preserved. Dorsal valve weakly convex, subcircular to transversely elliptical, with weak to moderate median sulcus originating near umbo and widening markedly anteriorly.

Shell ornamented with thick radial ribs originating near umbos and delicate concentric, non-lamellose growth lines; ribs thickening anteriorly, separated by equal in width interspaces, increasing by intercalation and bifurcation on both valves; about 8–10 ribs on each flank; ventral midrib pair slightly carinate, thicker and more strongly elevated than lateral ribs, bifurcating laterally usually 3–4 times, separated by deeper and wider median interspace, the bottom of the interspace with a simple, very thin and low thread-like median costella; dorsal median rib simple, thicker than lateral ones, rarely with a very weak median furrow.

Remarks.—The main features of the specimens are very small and prominently ribbed shell, generally rounded outline with



gently rounded to slightly emarginate anterior commissure, weakly carinate ventral midrib pair with deep median interspace occupied by thin median costella, sulcate dorsal valve with distinct simple median rib, apsacline to orthocline ventral interarea, and open delthyrium. Although the specimens are numerous they are frequently compressed by sediment compaction and sparitic filling of the interior, making study of the shell interior impossible. The small shell dimensions and character of the shell ribbing suggest assignment to *Gracianella* (*Sublepida*) Mizens and Sapelnikov, 1982.

While erecting *Gracianella* (*Sublepida*), Mizens and Sapelnikov (1982) included four species within the subgenus, *Terebratulula sublepida* Verneuil, 1845 (type species), *Gracianella plicumbra* Johnson and Boucot, 1967, *G. crista* Johnson and Boucot, 1967, and *G. cryptumbra* Johnson, Boucot, and Murphy, 1973. The type species *G. (Sublepida) sublepida* was originally described by Verneuil (1845) from the uppermost Silurian of the east slope of the Urals, Russia (a probable topotype shell is shown here in Fig. 14K; see also Mizens and Sapelnikov 1982; Breivel and Breivel 1988). Conspecific specimens have been reported by Modzalevskaya (1968: pl. 15: 4–7) and Nikiforova et al. (1972: 89, 227) from the uppermost Silurian beds of the section at Dnistrove as *Atrypa sublepida* and *Zygospiraella sublepida*, respectively. It should be noted, however, that *Gracianella* (*Sublepida*) *sublepida* occurs at Dnistrove about 0.6–3.6 m below the S–D boundary (see Nikiforova 1977: fig. 3), whereas *G. (S.) paulula* sp. nov. was found in the interval spanning from 1.5 m above the boundary to 0.2 m below it. Due to the poorly exposed lowermost part of the section at Dnistrove, *G. (S.) sublepida* was not found during the present investigations; however, one shell of the species from the locality from the Tatyana Modzalevskaya's (1968) collection is here presented for comparison (Fig. 14L). Thus, the ranges of the two species mentioned do not overlap, but are separated by an interval about 0.4 m thick in which *Dnestrina gutta* is very characteristic (Fig. 3; see also Nikiforova 1977: fig. 3). *G. (S.) paulula* sp. nov. differs from *G. (S.) sublepida* mainly in having a smaller shell, different ribbing pattern (presence of distinct ventral midrib pair divided by deep interspace), open delthyrium, and the absence of conspicuous, undulating growth lamellae.

G. (S.) paulula sp. nov. seems to be most similar externally to *Arctispira canadensis* Smith, 1980 described from the Early Lochkovian of the Canadian Arctic Archipelago (Smith 1980:

66, pls. 27: 42, 48; 28: 1–32). The former differs in having a shell which is more expanded laterally, a shorter hinge margin, and in the greatest shell width situated slightly more anteriorly. Furthermore, the presence of a ventral median costella, which is very characteristic for the new species, was not mentioned in the original description of *A. canadensis* nor could be discernible on the figures in Smith (1980). Recently the genus *Arctispira* was considered as a possible subjective synonym of *Ogilviella* Lenz, 1968 (Copper 2002: 1432).

The present species differs from *Gracianella plicumbra* Johnson and Boucot, 1967 from the Ludlow of the Robert Mountains (Nevada, USA: Johnson and Boucot 1967; Johnson et al. 1976) and Bohemia (Havlíček and Štorch 1990), and the Pridoli of Yukon Territory (Canada: Jackson et al. 1978; Lenz 1982) in having a wider shell, less rounded anterior commissure, wider dorsal sulcus with strong median rib, and a distinct midrib pair on the ventral valve. From *Gracianella crista* Johnson and Boucot, 1967, from the Ludlow of the Robert Mountains (Nevada, USA: Johnson and Boucot 1967; Johnson et al. 1976) and Bohemia (Havlíček and Štorch 1990), the new species is distinguished by a more circular instead of subrhomoidal shell outline, weaker ribs, a wider dorsal sulcus with strong median rib, and clearly divided median ventral ribs. Some finely ribbed specimens of a highly variable *G. cryptumbra* Johnson, Boucot, and Murphy, 1973 from the Pridoli of the Robert Mountains (Nevada, USA: Johnson et al. 1973) and Yukon Territory (Canada: Lenz 1977; Jackson et al. 1978) resembles *G. (S.) paulula* sp. nov., but the latter can be easily distinguished by its ribbing pattern. More often, however, the shells of the former species have fewer rather weak, and sometimes coalescent ribs, and a very broad, low median ventral rib.

Suborder Lissatrypidina Copper, 1996

Superfamily Lissatrypoidea Twenhofel, 1914

Family Lissatrypidae Twenhofel, 1914

Genus *Lissatrypa* Twenhofel, 1914

Type species: Lissatrypa atheroidea Twenhofel, 1914; Jupiter Formation, Llandovery, Silurian; Anticosti Island, Canada.

Lissatrypa leprosa Kozłowski, 1929

Fig. 15C.

1929 *Lissatrypa leprosa* sp. n.; Kozłowski 1929: 167–169, pl. 5: 15–21; figs. 54, 55.

← Fig. 14. Atrypide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine; A–J, L, M) and the Urals (Russia; K). **A–G.** *Gracianella* (*Sublepida*) *paulula* sp. nov. **A–D.** Five shells, ZPAL Bp. 56/178 (**A**), ZPAL Bp. 56/179 (**B**), ZPAL Bp. 56/180 (**C**), ZPAL Bp. 56/181 (**D**), and ZPAL Bp. 56/182 (**E**), of different size in dorsal (**A**₁, **B**₁, **C**₁, **D**₁, **E**₁) and ventral (**A**₂, **B**₂, **C**₂, **D**₂, **E**₂) views. **F.** Holotype ZPAL Bp. 56/183 in dorsal (**F**₁), ventral (**F**₂), lateral (**F**₃), posterior (**F**₄), and anterior (**F**₅) views and enlargement of a median sector of the ventral valve (**F**₆) showing thin, thread-like median costella (arrowed). **G.** Shell ZPAL Bp. 56/182a in dorsal (**G**₁), ventral (**G**₂), lateral (**G**₃), posterior (**G**₄), and anterior (**G**₅) views. **H–J, M.** *Oglu senilis* Havlíček, 1987. **H, I.** Two shells, ZPAL Bp. 56/86 (**H**) and ZPAL Bp. 56/87 (**I**), in dorsal (**H**₁, **I**₁), ventral (**H**₂, **I**₂), lateral (**H**₃, **I**₃), posterior (**H**₄, **I**₄), and anterior (**H**₅, **I**₅) views. **J.** Incomplete dorsal valve ZPAL Bp. 56/90b showing interior. **M.** Enlargement of the anterior region of the dorsal valve ZPAL Bp. 56/90a showing details of ornamentation. **K.** *Gracianella* (*Sublepida*) *sublepida* (Verneuil, 1845) from the uppermost Silurian of the east slope of the Urals, Russia, in dorsal (**K**₁), ventral (**K**₂), lateral (**K**₃), posterior (**K**₄), and anterior (**K**₅) views. **L.** *G. (Sublepida) sublepida* (Verneuil, 1845) from the uppermost Silurian of Dnistrove, Russia, in dorsal (**L**₁), ventral (**L**₂), lateral (**L**₃), posterior (**L**₄), and anterior (**L**₅) views (photographs courtesy of Tatyana Modzalevskaya). Scale bars 1 mm.

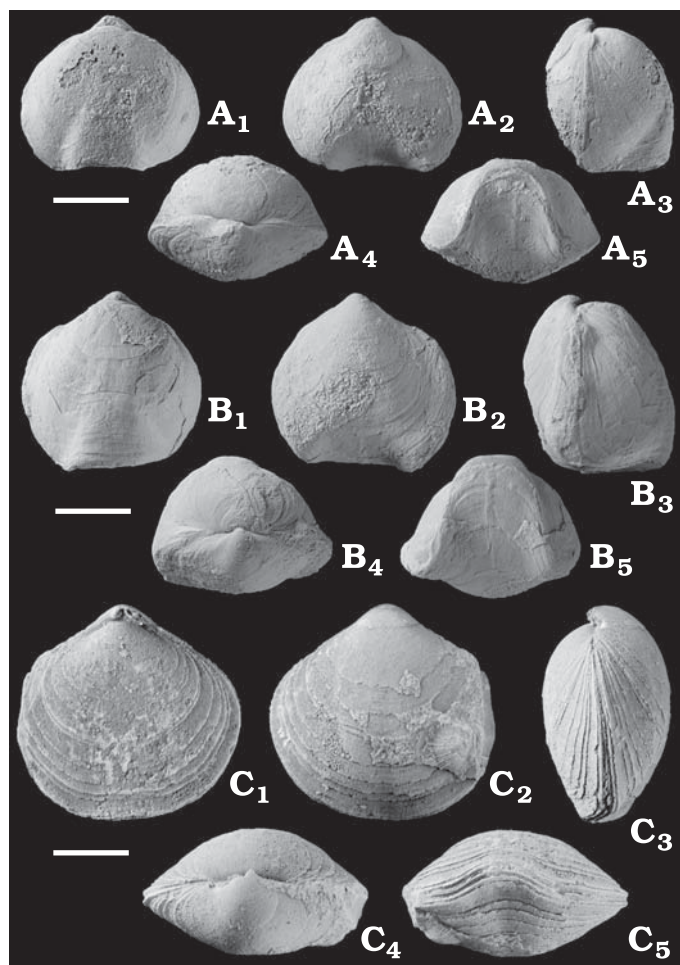


Fig. 15. Atrypide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A, B.** *Septatrypa (Septatrypa) secreta* Kozłowski, 1929. Two shells ZPAL Bp. 56/74 (**A**) and ZPAL Bp. 56/75 (**B**) in dorsal (**A**₁, **B**₁), ventral (**A**₂, **B**₂), lateral (**A**₃, **B**₃), posterior (**A**₄, **B**₄), and anterior (**A**₅, **B**₅) views. **C.** *Lissatrypa leprosa* Kozłowski, 1929; shell ZPAL Bp. 56/100a in dorsal (**C**₁), ventral (**C**₂), lateral (**C**₃), posterior (**C**₄), and anterior (**C**₅) views. Beds 47–48 (**A**, **B**) and loose block between the trench and well (**C**). Scale bars 1 mm.

1968 *Lissatrypa leprosa* Kozl.; Modzelevskaya 1968: pl. 27: 44–47.

1984 *Lissatrypa neglecta* sp. n.; Havlíček 1984: 220, pl. 1:6, 7; pl. 2: 3–8.

1985 *Lissatrypa leprosa* Kozłowski, 1929; Nikiforova et al. 1985: 42–44, pls. 10: 4, 5; 11: 1–8; fig. 5.

1989. *Lissatrypa leprosa* Kozłowski 1929; Jahnke et al. 1989: 162–163, pls. 1: 19–21; 2: 1–3; fig. 23.

1990 *Lissatrypa leprosa* Kozłowski, 1929; Havlíček and Štorch 1990: 193, pl. 65: 9.

Material.—One almost complete shell was found in a loose block of limestone near the bottom of the Khudykivtsi Beds together with *Clorinda pseudolinguifera* Kozłowski, 1929 and *Sphaerirhynchia gibbosa* (Nikiforova, 1954).

Remarks.—Although the single available specimens can not be studied internally, its exterior is indistinguishable from that of *L. leprosa* Kozłowski, 1929. Nikiforova et al. (1985) selected a neotype of the species from the Mytkiv (= Mitkov)

Beds of the Borshchiv Horizon at Ustje and re-figured several well-preserved specimens externally and internally.

Copper (2004: 110–111) listed 41 species assigned tentatively to the genus *Lissatrypa* Twenhofel, 1914.

Stratigraphic and geographic range.—According to Nikiforova et al. (1985) the range of *L. leprosa* extends through the Khudykivtsi and lower Mytkiv beds. Havlíček and Štorch (1990) described the species in the top of the Pridoli Formation and the lowermost part of the Lochkov Formation in Bohemia. The species was also described by Jahnke et al. (1989) from the Lower Devonian of Yunnan Province, China.

Family Septatrypidae Kozłowski, 1929

Subfamily Septatrypinae Kozłowski, 1929

Genus *Septatrypa* Kozłowski, 1929

Subgenus *Septatrypa (Septatrypa)* Kozłowski, 1929

Type species: *Septatrypa secreta* Kozłowski, 1929; Khudykivtsi (former Tajna) Beds, Borshchiv Horizon, Lower Devonian; Olkhovtsy, Podolia, Ukraine.

Septatrypa (Septatrypa) secreta Kozłowski, 1929

Figs. 15A, B, 16.

1929 *Septatrypa secreta* sp. n.; Kozłowski 1929: 177, pl. 9:18–24; fig. 58.

1985 *Septatrypa secreta* Kozłowski, 1929; Nikiforova et al. 1985: 44–45, pl. 11: 9–11; fig. 6 [full synonymy herein].

2004 *Septatrypa secreta* Kozłowski, 1929; Copper 2004: 126–127, figs. 86, 87.

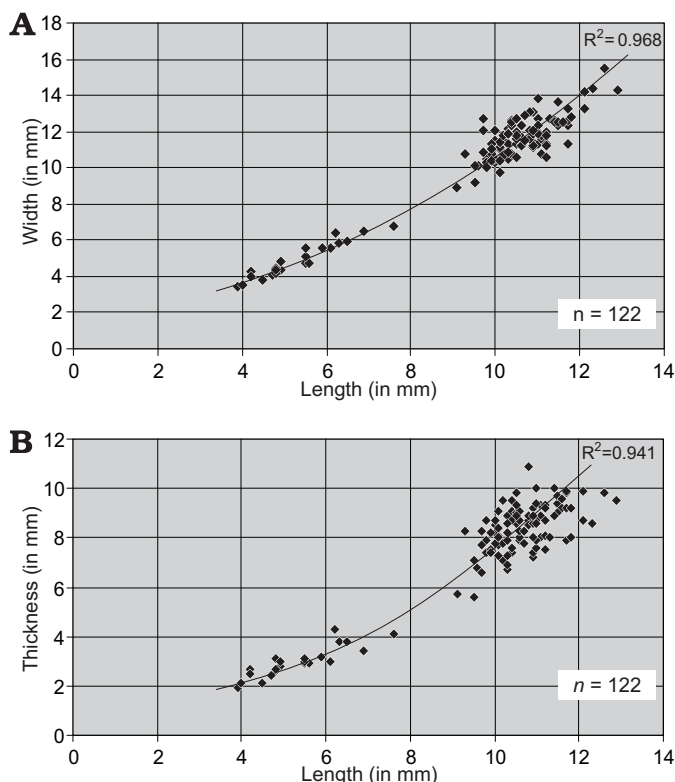


Fig. 16. Scatter diagrams of shell width (**A**) and shell thickness (**B**) to shell length ratios in *Septatrypa (Septatrypa) secreta* Kozłowski, 1929. Dnistrove, beds 47–48.

Material.—122 complete and well preserved shells and 140 fragmentary specimens. In the studied section it appears at 5.5 m above the S–D boundary (beds 47–48) where it is the most numerous species, comprising 27% of the brachiopod assemblage. In addition, five specimens were recovered from loose blocks from the uppermost part of the section.

Remarks.—This is one of the most common brachiopod species in the studied section at Dnistrove. The studied material is clearly conspecific with *S. secreta* as described and illustrated in great detail by Kozłowski (1929: 177–179, fig. 58, pl. 9: 18–24), Nikiforova (1954: 128–129, pl. 14: 8–9), Nikiforova et al. (1985: 44–45, fig. 6, pl. 11: 9–11), Biernat and Godefroid (1992: 44–48, pl. 1: 57–67, figs. 1, 2) and Copper (2004: 126–127, figs. 86, 87) from Podolia. Statistical characteristics of the studied material from Dnistrove are given on Fig. 16.

Stratigraphic and geographic range.—According to Nikiforova et al. (1985) the species is confined to the lower part of the Borshchiv Horizon (Khudykivtsi Beds; former Tajna Beds).

Order Athyridida Boucot, Johnson, and Staton, 1964
Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Didymothyridinae Modzalevskaya, 1979

Genus *Pseudoprotathyris* Modzalevskaya, 1979

Type species: *Protathyris infantile* Kozłowski, 1929; Dzwinogorod beds, Skala Horizon, Silurian; Zvenigorod, Podolia.

Pseudoprotathyris infantilis (Kozłowski, 1929)

Figs. 17, 19G, H.

1929 *Protathyris infantile* sp. n.; Kozłowski 1929: 230, pl. 11: 47.

1978 *Protathyris infantile* Kozłowski, 1929; Rubel and Teller 1978: 479, pl. 3: 3, 4.

1985 *Pseudoprotathyris infantilis* (Kozłowski, 1929); Nikiforova et al. 1985: 54, pl. 14: 11 [full synonymy herein].

1986 *Pseudoprotathyris infantilis* (Kozłowski); Grunt 1986: 51, pl. 3: 2.

2002 *Pseudoprotathyris infantilis* (Kozłowski, 1929); Musteikis and Modzalevskaya 2002: 620, pl. 5: 1–7, fig. 16.

Material.—11 more or less complete shells and 6 fragmentary specimens. The species were found at Dnistrove in interval at 0.3–1.2 m 1.3 m above the S–D boundary (beds -5, -4, -3, -1, 1.5, and 4).

Dimension of the two figured shells (in mm; see Fig. 19G, H, respectively): length, 5.3, 5.7; width, 4.5, 5.2; thickness, 2.5, 2.6.

Remarks.—The specimens from Dnistrove found at the base of the Khudykivtsi Beds appear to be conspecific with *P. infantilis* as described by Kozłowski (1929: 230–231, pl. 11: 47) from the Dzvenyhorod Beds of the Skala Horizon (former Dzwinogorod Beds) and by Modzalevskaya (1979: 60–62, pl. 4: 6–8, text-fig. 11) from the Dzvenyhorod, Khudykivtsi, and

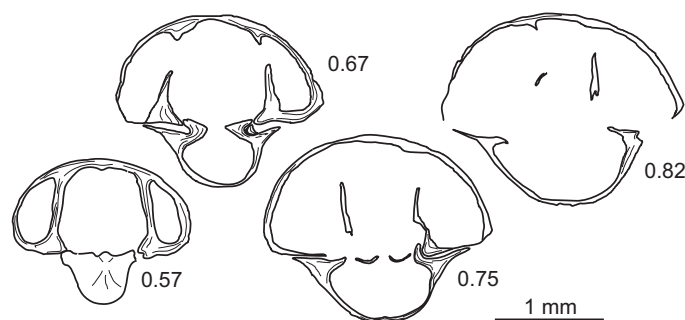


Fig. 17. Transverse serial sections through shell of *Pseudoprotathyris infantilis* (Kozłowski, 1929). ZPAL Bp. 56/186a. Numbers refer to distance in mm from ventral umbo. Dnistrove, bed -4.

Mytkiv beds. Nikiforova et al. (1985) noted that the species is most common through the Khudykivtsi Beds. They selected a neotype of the species (Nikiforova et al. 1985: 54, pl. 14: 11) from the Dzvenyhorod Beds at the village of Dzvenyhorod. Two shells from Dnistrove are illustrated here (Fig. 19G, H) together with serial sections of one shell (Fig. 17).

Stratigraphic and geographic range.—As noted by Nikiforova et al. (1985) *P. infantilis* appears in the Dzvenyhorod Beds (uppermost Silurian) and ranges through the Khudykivtsi and Mytkiv beds (lower Devonian).

Superfamily Meristelloidea Waagen, 1883

Family Meristidae Hall and Clarke, 1895

Subfamily Meristinae Hall and Clarke, 1895

Genus *Camarium* Hall, 1859

Type species: *Camarium typum* Hall, 1859; Lower Helderberg Group, Lochkovian, Early Devonian; Cumberland, Maryland, USA.

Camarium sp.

Figs. 18, 19I.

Material.—Two slightly damaged and three complete juvenile articulated shells. The specimens were recovered at 5.5 m above the S–D boundary (beds 47–48).

Remarks.—The present specimens resemble some meristids in the general shell shape and in the presence of a shoe-lifter, which can be seen as a result of shell exfoliation in the umbonal region of one ventral valve. That is also supported by serial sections (Fig. 18), which confirm the presence of dental plates and a shoe-lifter in the ventral valve, together with a long and high dorsal median septum supporting a narrow, Y-shaped septalium. The absence of mystrochial plates in the sectioned specimen indicates that this form most probably represents *Camarium*. The specimens are ventribiconvex, subcircular in outline and possess a strongly incurved ventral beak, an extremely weak dorsal fold and ventral sulcus, which result in a weak uniplication of the anterior commissure in large and thick individuals. Kozłowski (1929) identified several meristid specimens from the Mytkiv Beds (former Mitkov Beds) and a few from the Khudykivtsi Beds (former Tajna Beds) as *Merista passer* (Barrande, 1848).

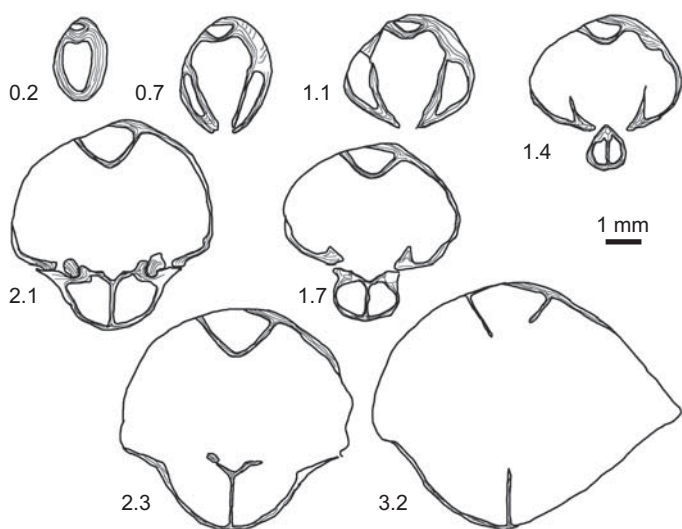


Fig. 18. Transverse serial sections through shell of *Camarium* sp. Numbers refer to distance in mm from ventral umbo. ZPAL Bp. 56/71a. Dnistrove, beds 47–48.

These differ from the specimens described here by their rather subpentagonal to subrhomboidal instead of circular shell outline, and their more weakly developed ventral sulcus. According to Nikiforova et al. (1985) *M. passer* is confined to the Mytkiv Beds, whereas rare specimens from the Khudykivtsi Beds appear to represent a new species. Unfortunately, the interiors of the sectioned specimens are incomplete or recrystallised, making impossible the investigations of brachiojugal structures and the material is too scarce to base a formal description of a new taxon.

Suborder uncertain

Superfamily Dayioidea Waagen, 1883

Family Dayiidae Waagen, 1883

Dayia Davidson, 1881

Type species: Terebratula navicula Sowerby, 1839; Leintwardine Formation, Ludlow, Silurian; Herefordshire, England.

Dayia bohémica Bouček, 1941

Fig. 19A–C.

1847 *Terebratula navicula* Murch.; Barrande 1847: 402, pl. 15: 4.

1879 *Atrypa navicula* Sow.; Barrande 1879: pls. 17–I: 1–7; 28–II: 1–16.

1929 *Dayia navicula* (Sowerby); Kozłowski 1929: 179–181, pl. 5: 22; fig. 59.

1941 *Dayia navicula bohémica* (nov.); Bouček 1941: 14, pl. 2: 1.

1977 *Dayia bohémica* Bouček, 1940; Rubel 1977: 215, pl. 3, 4; fig. 3.

1982 *Dayia bohémica* Bouček, 1940; Modzalevskaya and Nikiforova 1982: 111, pl. 1: 22.

1990 *Dayia bohémica* Bouček, 1941; Havlíček and Štorch 1990: 206, pl. 68: 9–11.

Material.—34 complete or slightly damaged shells and about 130 fragmentary specimens. The species occurs in the lowermost exposed there layers, i.e., 1.3–1.6 metres below the S–D boundary (beds -21 to -24).

Remarks.—*Dayia bohémica* was initially proposed by Bouček (1941) as a new subspecies of *D. navicula*. Subsequently, however, it has been elevated to the species rank by Rubel (1977) and Havlíček and Štorch (1990).

According to Nikiforova et al. (1985), the specimens from the Dzwynogorod Beds near Dnistrove described by Kozłowski (1929) and Nikiforova (1954) as *Dayia navicula* (Sowerby, 1839) represent *Dayia bohémica* Bouček, 1941, which is known from approximately contemporaneous beds in the Pridoli of Bohemia. In addition to *D. bohémica*, Nikiforova et al. (1985: 45) also reported the occurrence of typical *D. navicula* in slightly older horizons in Podolia, in the Grinchuk and Isakovtsy beds.

Stratigraphic and geographic range.—The species is known from several sections of the Pridoli Formation in Bohemia (Havlíček and Štorch 1990). Rubel (1977) reported it from Pridoli of Estonia, Lithuania, and Latvia. In Podolia the species was reported from the Dzvenyhorod Beds of the Skala Horizon from the vicinity of Dzvenyhorod and Dnistrove villages.

Superfamily Anoplothecoidea Schuchert, 1894

Family Anoplothecidae Schuchert, 1894

Subfamily Anoplothecinae Schuchert, 1894

Genus *Dnestrina* Nikiforova and Modzalevskaya, 1968

Type species: Dnestrina gutta Nikiforova and Modzalevskaya, 1968; Pridoli, Upper Silurian; Moldavia, Podolia.

Dnestrina gutta Nikiforova and Modzalevskaya, 1968

Fig. 19D–F, J.

1968 *Dnestrina gutta* sp. nov.; Nikiforova and Modzalevskaya 1968: 207–210; pl. 1: 1–14.

1968 *Dnestrina gutta* Nikif. et T. Modz.; Modzalevskaya 1968: pl. 15: 15–19.

1982 *Dnestrina gutta* Nikiforova et Modzalevskaya, 1968; Modzalevskaya and Nikiforova 1982: 106, pl. 2: 8.

Material.—Two complete although compressed shells, and about 20 specimens embedded in sediment, mostly fragmentary. The present material was found 1.3–1.35 metres below the S–D boundary (beds -21 to -21.5).

Description.—Shell small, up to about 6.2 mm in length, subcircular to subovate in outline, slightly wider than long to subequal, widest slightly anteriorly to midlength, weakly concavo-convex; antero-lateral margins rounded, apical angle 110–120°, hinge line short, almost straight, anterior commissure gently arched ventrally.

Ventral valve weakly convex, with almost imperceptible median carina; interarea flat, apsacline to nearly orthocline, up to 0.5 mm in height. Dorsal valve weakly concave, subcircular to slightly transversely elliptical, with poorly marked narrow, angular median sulcus originating near umbo.

Interior of the ventral valve with distinct subtriangular, elongated, bulbous median thickening, rising gradually in height and lanceolate anteriorly; valve margin forming dis-

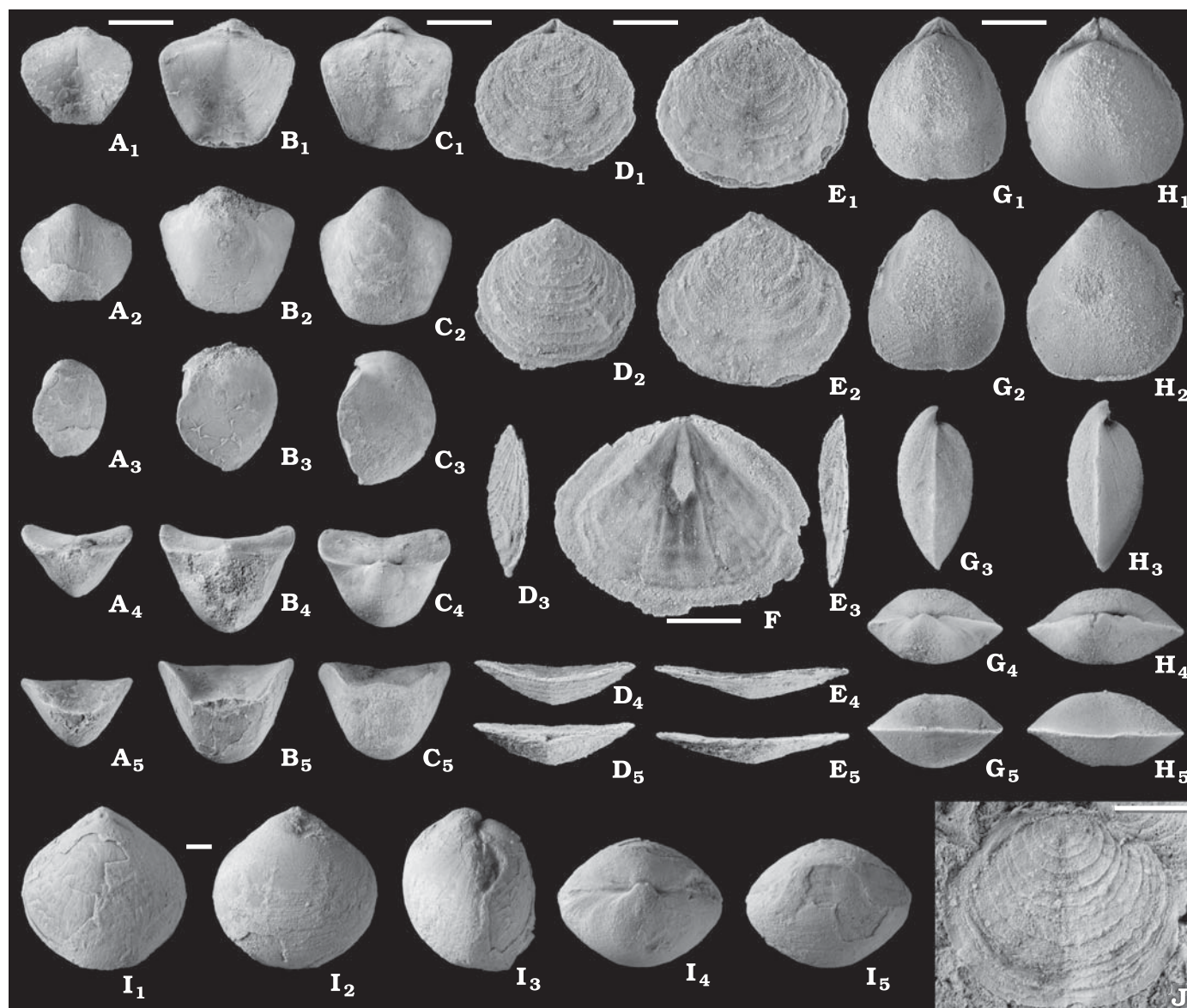


Fig. 19. Athyridide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A–C.** *Dayia bohémica* Bouček, 1941; three shells, ZPAL Bp. 56/200 (**A**), ZPAL Bp. 56/201 (**B**), and ZPAL Bp. 56/202 (**C**), in dorsal (**A**₁, **B**₁, **C**₁), ventral (**A**₂, **B**₂, **C**₂), lateral (**A**₃, **B**₃, **C**₃), posterior (**A**₄, **B**₄, **C**₄), and anterior (**A**₅, **B**₅, **C**₅) views. **D–F, J.** *Dnestrina gutta* Nikiforova and Modzalevskaya, 1968. **D, E.** Two shells, ZPAL Bp. 56/208 (**D**) and ZPAL Bp. 56/209 (**E**), in dorsal (**D**₁, **E**₁), ventral (**D**₂, **E**₂), lateral (**D**₃, **E**₃), posterior (**D**₄, **E**₄), and anterior (**D**₅, **E**₅) views. **F.** Interior view of slightly damaged ventral valve, ZPAL Bp. 56/210. **J.** Shell ZPAL Bp. 56/207b in dorsal exterior view. **G, H.** *Pseudoprotathyris infantilis* (Kozłowski, 1929); two shells, ZPAL Bp. 56/176 (**G**) and ZPAL Bp. 56/177 (**H**), in dorsal (**G**₁, **H**₁), ventral (**G**₂, **H**₂), lateral (**G**₃, **H**₃), posterior (**G**₄, **H**₄), and anterior (**G**₅, **H**₅) views. **I.** *Camarium* sp.; shell ZPAL Bp. 56/29 in dorsal (**I**₁), ventral (**I**₂), lateral (**I**₃), posterior (**I**₄), and anterior (**I**₅) views. Beds -24 (**A–C**), -21 (**D–F, J**), -4 (**G, H**), and 47–48 (**I**). Scale bars 2 mm.

tinct, flat and wide peripheral rim; mantle canals poorly impressed, radiating. Dorsal interior not preserved, but probably with crenulated dental sockets (Fig. 19J).

Shell surface smooth, but with distinct lamellose growth lines, usually 12–14 on adult specimens.

Remarks.—This characteristic form was originally described by Nikiforova and Modzalevskaya (1968) from the Dzvenyhorod Beds of the Skala Horizon of Moldavia and Podolia. The latter is confined to the vicinity of the Dnistrove village where the present material comes from. In the

studied section the species occurs approximately in the same layers as *Dayia bohémica*, i.e., in the lowermost beds exposed in the trench and representing the uppermost Silurian (Fig. 3).

Stratigraphic and geographic range.—The species is known from the the Dzvenyhorod Beds (uppermost Silurian) of Moldavia, Podolia, and Western Europe (Alvarez and Copper 2002). Similar form was described as *D. cf. gutta* by Jahnke et al. (1989) from the uppermost Silurian of Yunnan Province of China.

Order Spiriferida Waagen, 1883

Suborder Delthyridina Ivanova, 1972

Family Delthyrididae Phillips, 1841

Subfamily Howellellinae Johnson and Hou, 1994

Genus *Howellella* Kozłowski, 1946

Subgenus *Howellella* (*Howellella*) Kozłowski, 1946

Type species: *Delthyris elegans* Muir-Wood, 1923; Mulde Formation, Wenlock, Silurian; Gotland, Sweden.

Howellella (*Howellella*) *latisinuata* Kozłowski, 1929
Fig. 20A.

1929 *Spirifer* (?*Crispella*) *latisinuatus* sp. n.; Kozłowski 1929: 197, pl. 11: 1–7.

1985 *Howellella latisinuata* (Kozłowski, 1929); Nikiforova et al. 1985: 48, pl. 13: 1–3.

Material.—Four complete shells and 37 fragments of shells and single valves embedded in rock. The specimens were recovered from several beds in the interval extending from 0.2 m below the S–D boundary (bed -10) up to 12.3 m above the boundary (bed 115).

Remarks.—Fragmentary material from Dnistrove conforms with this species, which was described from the basal part of the Borshchiv Horizon (Kozłowski 1929: 197–198, pl. 11: 1–7; Nikiforova et al. 1985: 48, pl. 13: 1–3), in having a small shell and very few, weak radial plications. The largest complete shell in the present material (see Fig. 20A) measures 8.2 mm in length and 10.7 mm in width. Nikiforova et al. (1985) designated the neotype of the species from the Khudykivtsi Beds exposed at Olkhovtsy village (about 8 km NW from Dnistrove).

Stratigraphic and geographic range.—Nikiforova et al. (1985: 48) confirmed that the species is confined to the Khudykivtsi Beds (former Tajna Beds).

Suborder Cyrtinidina Carter and Johnson, 1994

Family Cyrtinidae Fredericks, 1911

Genus *Cyrtina* Davidson, 1859

Type species: *Calceola heteroclita* Defrance, 1824; Middle Devonian, France.

Cyrtina praecedens Kozłowski, 1929
Fig. 20B, C.

1929 *Cyrtina praecedens* sp. n.; Kozłowski 1929: 207–211, pl. 11: 8–23; figs. 68, 70–75.

1985 *Cyrtina praecedens* Kozłowski, 1929; Nikiforova et al. 1985: 52–53, pl. 12: 3, 4 [full synonymy herein].

Material.—One complete but superficially corroded shell and one incomplete ventral valve, both from beds 47–48 (5.5 m above the S–D boundary) of the studied section at Dnistrove.

Remarks.—The species, as well as its variability, was described in great detail by Kozłowski (1929). More recently, Nikiforova et al. (1985) selected the neotype of the species from the Mytkiv Beds of Verkhnyakovtsy. The present material, although rather scanty, closely corresponds exter-

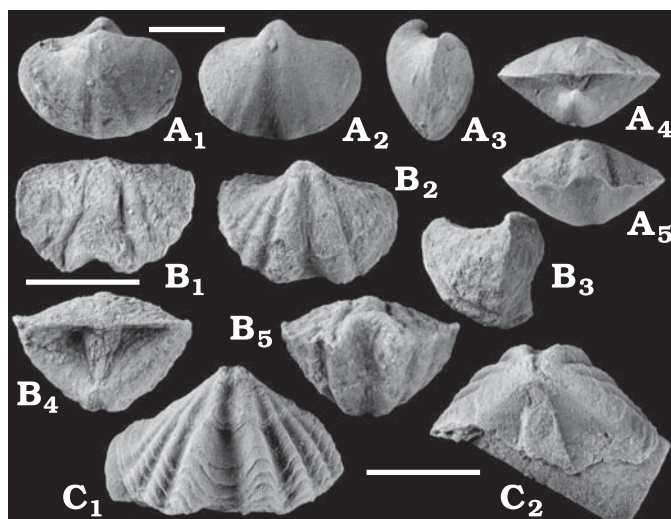


Fig. 20. Spiriferide brachiopods from the Silurian–Devonian boundary beds at Dnistrove (Podolia, Ukraine). **A.** *Howellella* (*Howellella*) *latisinuata* Kozłowski, 1929; shell ZPAL Bp. 56/26 in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views. **B.** *Cyrtina praecedens* Kozłowski, 1929. **B.** Slightly damaged shell ZPAL Bp. 56/37 in dorsal (B₁), ventral (B₂), lateral (B₃), posterior (B₄), and anterior (B₅) views. **C.** Incomplete ventral valve ZPAL Bp. 56/36 in ventral (C₁) and posterior (C₂) views. Dnistrove, beds 47–48. Scale bars 5 mm.

nally to *Cyrtina praecedens*. The studied specimens show clear punctation of the shell substance, pustulose micro-ornamentation, and presence of tichorhinum in the ventral valve.

Stratigraphic and geographic range.—According to Nikiforova et al. (1985), *C. praecedens* is one of the most common and characteristic species of the Borshchiv Horizon. It appears in the Khudykivtsi Beds but becomes especially common in the Mytkiv Beds. Savage (1969: 483–486, pl. 92: 1–44) described *C. praecedens* from the Lower Devonian (Siegenian) Mandagery Park Gormation of New South Wales and Drot (1964: 91) reported ?*Cyrtina praecedens* from the Geddinnian of Morocco.

Acknowledgements

Sincere thanks are extended to Mike Basset (National Museum of Wales, Cardiff, UK) for improvement of the English of an earlier version of the manuscript and Grzegorz Racki (Silesian University, Sosnowiec, Poland) for critical comments. To Tatyana L. Modzalevskaya (A.P. Karpinsky Russian Geological Research Institute, Sankt Petersburg, Russia) I owe my special thanks for the specimens of *Gracianella* (*Sublepida*) *sublepida* from Dnistrove and the Urals as well as for providing access to the collection from Podolia. The paper was greatly improved through reviews by Robin Cocks (Natural History Museum, London, UK) and Jisuo Jin (University of Western Ontario, London, Canada). This work has been supported by a grant on the geochemistry, stratigraphy, and palaeontology across the Silurian–Devonian transition in Podolia (No. N N307 057834) from the Ministry of Science and Higher Education to Hubert Szaniawski (ZPAL).

References

- Alvarez, F. and Copper, P. 2002. Uncertain. In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised 4*: 1604–1614. Geological Survey of America and University of Kansas Press, Boulder.
- Amsden, T.W. 1958. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region. Part II, Haragan articulate brachiopods. Part III, Supplement to the Henryhouse brachiopods. *Oklahoma Geological Survey Bulletin* 78: 1–144 (Part 2), 145–157 (Part 3).
- Baliński, A. 2010. First colour-patterned strophomenide brachiopod from the earliest Devonian of Podolia, Ukraine. *Acta Palaeontologica Polonica* 55: 695–700.
- Barrande, J. 1847. Über die Brachiopoden der silurischen Schichten von Boehm. *Naturwissenschaftliche Abhandlungen* 1: 357–475.
- Barrande, J. 1879. *Système Silurien du centre de la Bohême, 1ère partie, 5, Classe des Mollusques. Ordre des Brachiopodes*, 1–226. L'auteur, Prague, Paris.
- Bassett, M.G. 1972. The articulate brachiopods from the Wenlock Series of the Welsh Borderland and South Wales. Part 2. *Palaeontographical Society (London), Monograph* 126 (532): 27–78.
- Berdan, J.M., Berry, W.B.N., Boucot, A.J., Cooper, G.A., Jackson, D.E., Johnson, J.G., Klapper, G., Lenz, A.C., Martinsson, A., Oliver, W.A., Jr., Rickard, L.V., and Thorsteinsson, R. 1969. Siluro-Devonian boundary in North America. *Geological Society of America Bulletin* 80: 2165–2174.
- Biernat, G. 1959. Middle Devonian Orthoidea of the Holy Cross Mountains and their ontogeny. *Palaeontologia Polonica* 10: 1–78.
- Biernat, G. and Godefroid, J. 1992. Redescription des genres *Septatrypa* Kozłowski, 1929 et *Dubaria* Termier, 1936 (Brachiopoda, Atrypida, Lissatrypidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 62: 43–60.
- Bouček, B. 1941. O variabilitě ramenonožců *Dayia navicula* (Sow.) a *Cyrtia exporrecta* (Wahl.) a o použití metod variační statistiky v paleontologii. *Rozpravy České Akademie Věd, Třída II* 50 (22): 1–27.
- Boucot, A.J. 1975. Evolution and extinction rate controls. *Developments in Palaeontology and Stratigraphy* 1: I–XV, 1–427. Elsevier, Amsterdam.
- Boucot, A.J., Gill, E.D., Johnson, J.G., Lenz, A.C., and Talent, J.A. 1966. *Skenidioides* and *Leptaeniscia* in the Lower Devonian of Australia (Victoria, Tasmania) and New Zealand, with notes on other Devonian occurrences of *Skenidioides*. *Proceedings of the Royal Society of Victoria* 79: 363–369.
- Breivel, I.A. and Breivel, M.G. 1988. *Biostratigraphiä i Brahiopody Silura Vostočnogo Sklona Urala*. 204 pp. Nedra, Moskva.
- Brock, G.A. 2003. Lochkovian (Early Devonian) brachiopods from the Garra Limestone at Eurimbla, New South Wales, Australia, Part 1: Acrotretida, Strophomenida, Productida, Orthotetida, Orthida and Pentamerida. *Palaeontographica A* 269 (4–6): 93–136.
- Chlupáč, I. and Hladil, J. 2000. The global stratotype section and point of the Silurian-Devonian boundary. *Courier Forschungsinstitut Senckenberg* 225: 1–8.
- Cocks, L.R.M. 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Palaeontographical Society, Monograph* 131 (549): 1–256.
- Copper, P. 2002. Atrypida. In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised 4*, 1377–1474. Geological Survey of America and University of Kansas Press, Boulder.
- Copper, P. 2004. *Silurian (Late Llandovery-Ludlow) Atrypid Brachiopods from Gotland, Sweden, and the Welsh Borderlands, Great Britain*. 215 pp. NRC Research Press, Ottawa.
- Drot, J. 1964. Rhynchonelloidea et Spiriferoidea siluro-dévonien du Maroc Presaharien. *Notes et Mémoires du Service Géologique du Maroc* 178: 1–287.
- Drygant, D. 2003. About the problem of correlation and stratigraphic division of Lower Devonian deposits in the Volyn'-Podillja part of the East-European Platform [in Ukrainian with English summary]. *Naukovi Zapiski Deržavnogo Prirodopisnogo Muzeu* 18: 195–208.
- Drygant, D.M. 2010. *Devonian Conodonts from South-West Margin of the East European Platform (Volyn'-Podolian Ukraine)* [in Ukrainian]. 156 pp. Academperiodyka, Kyiv.
- Drygant, D.M. and Szaniawski H. 2012. Lochkovian conodonts from Podolia, Ukraine, and their stratigraphic significance. *Acta Palaeontologica Polonica* 57: 833–861.
- Filipiak, P., Zatoń, M., Szaniawski, H., Wrona R., and Racki G. 2012. Palynology and microfacies of Lower Devonian mixed carbonate-siliciclastic deposits in Podolia, Ukraine. *Acta Palaeontologica Polonica* 57: 863–877.
- Gauri, K.L. and Boucot, A.J. 1968. Shell structure and classification of Pentameracea M'Coy, 1844. *Palaeontographica A* 131: 79–135.
- Gratsianova, R.T. [Gracianova, R.T.] 1967. *Brahiopody i stratigraphiä nižnego devona Gornogo Altaia*. 177 pp. Nauka, Moskva.
- Grunt, T.A. 1986. Classification of brachiopods of the order Athyridida [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 215: 1–200.
- Halamski, A.T.H. 2009. Middle Devonian brachiopods from the northern part of the Holy Cross Mountains, Poland in relation to selected coeval faunas. Part one: Introduction, Lingulida, Craniida, Strophomenida, Productida, Protorthida, Orthida. *Palaeontographica* 287: 41–98.
- Havlíček, V. 1967. Brachiopoda of the Suborder Strophomenidina in Czechoslovakia. *Rozpravy Ústředního ústavu geologického* 33: 1–235.
- Havlíček, V. 1984. *Lissatrypa* (Brachiopoda; Silurian, Lower Devonian) in Bohemia. *Vestník Ústředního ústavu geologického* 59: 217–226.
- Havlíček, V. 1987. Lower Devonian and Eifelian Atrypacea (Brachiopoda) in central Bohemia. *Sborník geologických věd, Paleontologie* 28: 61–115.
- Havlíček, V. and Štorch, P. 1990. Silurian brachiopods and benthic communities in the Prague Basin (Czechoslovakia). *Rozpravy Ústředního ústavu geologického* 48: 1–275.
- Iordan, M. 1999. The Palaeozoic brachiopods of Romania. *Geo-Eco-Marina* 4/1999: 135–145.
- Jackson, D.E., Lenz, A.C., and Pedder, A.E.H. 1978. Late Silurian and Early Devonian graptolite, brachiopod and coral faunas from Northwestern and Arctic Canada. *Geological Association of Canada, Special Paper* 17: 1–159.
- Jahnke, H., Shi, Y., and Haude, R. 1989. The Silurian-Devonian boundary strata and the Early Devonian of the Shidian-Baoshan area (W. Yunnan, China). *Courier Forschungsinstitut Senckenberg* 110: 137–193.
- Jin, J. and Chatterton, B.D.E. 1997. Latest Ordovician–Silurian articulate brachiopods and biostratigraphy of the Avalanche Lake area, southwestern District of Mackenzie. *Palaeontographica Canadiana* 13: 1–167.
- Johnson, J.G. 1973. Mid-Lochkovian brachiopods from the Windmill Limestone of central Nevada. *Journal of Paleontology* 47: 1013–1030.
- Johnson, J.G. 1990. *Talentella*, a new Siluro-Devonian genus of enteletacean brachiopods. *Journal of Paleontology* 64: 489–490.
- Johnson, J.G. and Boucot, A.J. 1967. *Gracianella*, a new Late Silurian genus of atrypoid brachiopods. *Journal of Paleontology* 41: 868–873.
- Johnson, J.G., Boucot, A.J., and Murphy, M.A. 1973. Pridolian and early Gedinnian age brachiopods from the Roberts Mountains Formation of Central Nevada. *University of California Publications in Geological Sciences* 100: 1–75.
- Johnson, J.G., Boucot, A.J., and Murphy, M.A. 1976. Wenlockian and Ludlovian age brachiopods from the Roberts Mountains Formation of Central Nevada. *University of California Publications in Geological Sciences* 115: 1–102.
- Kozłowski, R. 1929. Les Brachiopodes gothlandiens de la Podolie Polonaise. *Palaeontologia Polonica* 1: 1–254.
- Krzemiński, W., Krzemińska, E., and Wojciechowski, D. 2010. Silurian synziphosurine horseshoe crab Pasternakevia revisited. *Acta Palaeontologica Polonica* 55: 133–139.
- Langenstrassen, F. 1972. Fazies und stratigraphie der Eifel-stufe im oestlichen Sauerland. *Göttinger Arbeiten zur Geologie und Paläontologie* 12: 1–106.
- Lenz, A.C. 1977. Upper Silurian and Lower Devonian brachiopods of Royal

- Creek, Yukon, Canada. Part 2: Spiriferida: Atrypacea, Dayiacea, Athyridacea, Spiriferacea. *Palaeontographica A* 159: 111–138.
- Lenz, A.C. 1982. New data on Late Silurian and Early Devonian brachiopods from the Royal Creek area, Yukon Territory. *Canadian Journal of Earth Sciences* 19: 364–375.
- Małkowski, K. and Racki, G. 2009. A global biogeochemical perturbation across the Silurian–Devonian boundary: Ocean–continent–biosphere feedbacks. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276: 244–254.
- Małkowski, M., Racki, G., Drygant, D., and Szaniawski, H. 2009. Carbon isotope stratigraphy across the Silurian–Devonian transition in Podolia, Ukraine: evidence for a global biogeochemical perturbation. *Geological Magazine* 146: 674–689.
- Mizens, L.I. and Sapelnikov, V.P. [Sapel'nikov, V.P.] 1982. *Rebristye Siluryjskie i Lohkovskie Atrypidy Vostochnogo Sklona Urala. Paleontologičeskij i Biostratigrafičeskij Srednego Paleozoja Urala*. 43 pp. Akademiā Nauk SSSR, Ural'skij Naučnyj Centr, Sverdlovsk.
- Modzalevskaya, T.L. [Modzalevskaā, T.L.] 1968. *Third international symposium on Silurian–Devonian boundary and Lower and Middle Devonian stratigraphy. Atlas of Silurian and early Devonian fauna of Podolia* (appendix to the guide). 37 pls. Ministry of Geology of the USSR, All-Union Scientific-Research Geological Institute (VSEGEI), Leningrad.
- Modzalevskaya, T.L. [Modzalevskaā, T.L.] 1979. On systematics of the Paleozoic athyridids [in Russian]. *Paleontologičeskij žurnal* 1979 (2): 48–63.
- Modzalevskaya, T.L. [Modzalevskaā, T.L.] and Nikiforova, O.I. 1982. Brachiopods of the Skala Horizon in Podolia [in Russian]. *Ežegodnik Vsesoūznogo Paleontologičeskogo Obšestva* 25: 98–121.
- Musteikis, P. and Cocks, L.R.M. 2004. Strophomenide and orthotetide Silurian brachiopods from the Baltic region, with particular reference to Lithuanian boreholes. *Acta Palaeontologica Polonica* 49: 455–482.
- Musteikis, P. and Modzalevskaya, T.L. [Modzalevskaā, T.L.] 2002. Some Silurian brachiopods from Lithuania and their palaeobiogeographical significance. *Palaeontology* 45: 595–626.
- Nikiforova, O.I. 1954. Stratigraphy and brachiopods of the Silurian deposits of Podolia [in Russian]. *Trudy Vsesoūznogo Naučno-Issledobatel'skogo Geologičeskogo Instituta (VSEGEI)* 1954: 1–218.
- Nikiforova, O.I. 1977. Podolia. In: A. Martinsson (ed.), *The Silurian–Devonian Boundary. Final Report of the Committee in the Silurian–Devonian Boundary within IUGS Commission on Stratigraphy and a State of the Art Report for Project Ecostratigraphy, IUGS, Series A, no. 5E*, 51–64. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Nikiforova, O.I. and Modzalevskaja, T.L. [Modzalevskaā, T.L.] 1968. A new brachiopod genus *Dnestrina* from the Silurian, Moldavia and Podolsk [in Russian]. *Ežegodnik Vsesoūznogo Paleontologičeskogo Obšestva* 18: 206–211.
- Nikiforova, O.I., Modzalevskaya, T.L. [Modzalevskaā, T.L.], and Basset, M.G. 1985. Review of the upper Silurian and lower Devonian articulate brachiopods of Podolia. *Special Papers in Palaeontology* 34: 1–66.
- Nikiforova, O.I., Predtechensky, N.N. [Predtečenskij, N.N.], Abushik, A.F. [Abušik, A.F.], Ignatovich, M.M. [Ignatovič, M.M.], Modzalevskaya, T.L. [Modzalevskaā, T.L.], Berger, A.Y. [Berger, A.Ā], Novoselova, L.S., and Burkov, Y.K. [Burkov, Ū.K.] 1972. *Opornyj Razrez Silura i Nižnego Devona Podolii*, 1–258. Izdatiel'stvo "Nauka", Leningrad.
- Olempska, E. 2012. Exceptional soft-tissue preservation in boring ctenostome bryozoans and associated "fungal" borings from the Early Devonian of Podolia, Ukraine. *Acta Palaeontologica Polonica* 57: 925–940.
- Olempska, E., Horne, D.J., and Szaniawski, H. 2012. First record of preserved soft parts in a Palaeozoic podocopid (Metacopina) ostracod, *Cytherellina submagna*: phylogenetic implications. *Proceedings of the Royal Society B* 279: 564–570.
- Racki, G., Baliński, A., Wrona, R., Małkowski, K., Drygant, D., and Szaniawski, H. 2012. Faunal dynamics across the Silurian–Devonian positive isotope excursion ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) in Podolia, Ukraine: Comparative analysis of the Ireviken and Klonk events. *Acta Palaeontologica Polonica* 57: 795–832.
- Rubel, M.P. 1977. Revision of Silurian Dayiacea (Brach.) from the North-East Baltic [in Russian]. *Eesti NSV Teaduste Akadeemia Toimetised (Keemia Geoloogia)* 26: 211–220.
- Rubel, M. 2011. Silurian brachiopods Dictyonellida, Strophomenida, Productida, Orthotetida, Protorthida and Orthida from Estonia. *Fossilia Baltica* 4: 1–64.
- Rubel, M.P. and Teller, L. 1978. Lower Devonian stratigraphy and brachiopods from boreholes Bachus 1 and Ursynow 1. *Acta Geologica Polonica* 28: 471–483.
- Rybnikova, M.V. 1966. Some Strophomenida brachiopods from the Upper Silurian rocks of Latvia [in Russian]. In: A.A. Grigelis (ed.), *Paleontologičeskij i stratigrafičeskij Pribaltiki i Belorussii*, vol. 1, 75–95. Mintis, Vilnius.
- Savage, N.M. 1969. New spiriferid brachiopods from the Lower Devonian of New South Wales. *Palaeontology* 12: 472–487.
- Savage, N.M. 1974. The brachiopods of the Lower Devonian Maradana Shale, New South Wales. *Palaeontographica A* 146: 1–51.
- Siemiradzki, J. 1906. Monografia warstw paleozoicznych Podola. *Sprawozdania Komisji Fizyograficznej oraz Materyaly do Fizyografii Kraju* 39: 87–196.
- Smith, R.E. 1980. Lower Devonian (Lochkovian) biostratigraphy and brachiopod faunas, Canadian Arctic Islands. *Geological Survey of Canada, Bulletin* 308: 1–155.
- Verneuil, E. de 1845. Paléontologie, mollusques, brachiopodes. In: R.I. Murchison, E. de Verneuil, and A. Keyserling (eds.), *Géologie de la Russie d'Europe et des Montagnes de l'Oural*. Vol. 2, Part 3: Paléontologie, 17–395. John Murray, London.
- Vogel, K., Xu, H., and Langenstrassen, F. 1989. Brachiopods and their relation to facies development in the Lower and Middle Devonian of Nandan, Guangxi, South China. *Courier Forschungsinstitut Senckenberg* 110: 17–59.
- Voichyshyn, V. 2011. The Early Devonian armoured agnathans of Podolia, Ukraine. *Palaeontologia Polonica* 66: 1–211.
- Voichyshyn, V. and Szaniawski, H. 2012. Acanthodian jaw bones from Lower Devonian marine deposits of Podolia, Ukraine. *Acta Palaeontologica Polonica* 57: 879–896.
- Walmsley, V.G., Boucot, A.J., and Harper, C.W., Jr. 1969. Silurian and Lower Devonian salopinid brachiopods. *Journal of Paleontology* 43: 492–516.
- Zhang, N. 1989. Wenlockian (Silurian) brachiopods of the Cape Phillips Formation, Baillie Hamilton Island, Arctic Canada: Part I. *Palaeontographica A* 206: 49–97.