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Taxonomy, Nomenclature, and Evolution of the Early Schubertellid Fusulinids

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Introduction

Schubertella Staff and Wedekind, 1910 and Eoschubertella Thompson, 1937 are quite common Pennsylvanian and Permian foraminiferal taxa. As noted by many fusulinid workers, both genera possess similarities in morphology and the latter genus has often been synonymized under the former one (Rauser-Chernousova et al. 1951; Rosovskaya 1975). Nevertheless, both names are used quite widely in the literature. However, the name Eoschubertella has been employed mostly using the concept of “practicality”. As stated by Groves (1991: 80) “In practice, western specialists apply the name Schubertella to Permian specimens and Eoschubertella to Middle–Late Pennsylvanian ones, with intervening Upper Pennsylvanian specimens referred by various authors to either genus”. Eoschubertella, however, has been reported from Lower, Middle and even Upper Permian deposits (Suleimanyan 1949; Leven 1998a; Kobayashi 2006) and therefore the concept of “biostratigraphic convenience” (Ueno in Fohrer et al. 2007) has not always been applied. The genus Schubertina Marshall, 1969 is not well known to specialists as it was described in a local journal that is not readily available outside of the USA. The writer, for example, was not aware about this genus until very recently. Besides, this genus was commonly considered to be a junior synonym of Eoschubertella (Groves 1991; Fohrer et al. 2007). The aim of this paper is to clarify the concept of Schubertella and related genera based on analyses of the types and toptotypes of Schubertella, Eoschubertella, Schubertina and some related taxa.

Institutional abbreviations.—SUI, University of Iowa Paleontology Repository, Keosauqua, USA; SUPTC, Stanford University Paleontological Type Collection, Stanford, USA; TGUR, Repository of Department of Geology, Koganei School, Tokyo Gakugei University, Tokyo, Japan; YPM, Peabody Museum of Natural History, Yale University, New Haven, USA.

Systematic paleontology

In the author’s recent study (Davydov 1997, 2009; Davydov et al. 2001; Davydov and Arefifard 2007; Davydov and Khodjanyazova 2009) of Schubertella and related genera in Donets Basin, Central Asia, Nevada, and Spitsbergen five groups of Schubertella-related forms that have already been reported in the literature are recognized:

1. Very small ovoid forms with test possessing 3–4 volutions, less than 0.3 mm in length with poorly differentiated microgranular wall and skewed initial 2–3 volutions. These forms best fit with concept of Schubertina Marshall, 1969, but more often they have been referred to as Eoschubertella.
(2) Similar to previous group, but with a nautiloid shape, i.e., with form ratio less than one. Recently this type was described as the genus *Grovessella* by Davydov and Areffard (2007).

(3) Medium size and fusiform schubertellids larger than 0.3 mm but less than 1 mm in length, with 4 or more volutions, a three layered wall and skewed initial involutions. This group possesses features of *Schubertella* Staff and Wedekind, 1910.

(4) Advanced large schubertellids usually over 1 mm in length with thick wall developed, multi-layered wall assigned to *Mesoschubertella* Kanuma and Sakagami, 1957.

(5) Very large schubertellids over 1.5–2 mm in length with a thick wall with coarse mural pores often referred to as kerotheca, but lacking features characteristic for the latter such as branching pores. These schubertellids, known as *Biwaella* Morikawa and Isomi, 1960, are usually considered as being Permian, but also occur in the Gzhelian of the Donets Basin (see below in this paper).

Please note that the synonymy lists for genera include also chresonyms (see e.g., Smith and Smith 1973).

Superfamily Fusulinoidae von Möller, 1878
Family Schubertellidae Skinner, 1931
Genus *Schubertella* Staff and Wedekind, 1910
1910 *Schubertella* gen. nov.; Staff and Wedekind 1910: 121, pl. 4: 8.
1937 *Schubertella* Staff and Wedekind; Thompson 1937: 120–121.

Type species: *Schubertella transitoria* Staff and Wedekind, 1910, the exact location unknown (see discussion below), Spitsbergen, Carboniferous–Permian transition, collection of Alfred G. Nathorst, 1882, Tempel Bay, and Wedekind, 1910, the same plane as the thin-section and thus all volutions looked planispiral on the drawing. Staff and Wedekind (1910) mentioned two localities, Tempel Bay and Klas Billen Bay from which the samples they studied came, but they did not specify the exact location.

Although Thompson (1937) designated the lectotype from Staff and Wedekind’s (1910) publication, he found that the original material was lost. Thus, Thompson (1937) studied samples from several localities in Spitsbergen from which the collections obtained by Alfred G. Nathorst in 1882 and studied by Staff and Wedekind (1910) came. One collection came from Tempel Bay which Thompson thought could be from where one of the topotypes of *S. transitoria* came. He found there a specimen (Thompson 1937, refigured herein as Fig. 1C) that since has been used as an illustrative reference to *S. transitoria* in many publications (Miklucho-Maklay et al. 1959; Thompson 1964; Loeblich and Tappan 1988). In the same paper in which he described the topotype of *S. transitoria*, Thompson (1937) erected the new subgenus *Eoschubertella* Thompson, 1937 with *Schubertella lata* Lee and Chen in
volution of this specimen. **D.** *Schubertella lata* Lee and Chen in Lee et al., 1930. **D, E.** *Schubertella lata* Lee and Chen in Lee et al., 1930. **F.** The Huanglungshan, Lungtan, S. China, Huanglung Limestone, Moscovian, repository unknown, axial section of holotype (as designated by Thompson 1937), from Lee et al. (1930: pl. 6: 9). **E.** Lower part of the Huanglung Limestone, the Huanglungshan, Lungtan, S. China, repository unknown, axial section of paratype, from Lee et al. (1930: pl. 6: 10). **I.** *Mesoschubertella thompsoni* Sakagami in Kanuma and Sakagami, 1957; limestone pebbles of the Tamanouchi limestone conglomerate from Hinode-mura, Nishitama-gun, Kanto massif, Japan. 23918−A holotype (I₁); 23918−A (I₂) enlarged internal volutions of holotype showing the structure of the wall (arrow pointed to diaphanotheca) from Kanuma and Sakagami (1957: pl. 8: 6, 7). **J.** *Mesoschubertella mullerriedi* (Thompson and Miller, 1944); Secret Canyon section, 270.1 meters above the base of the section, Artinskian, Nevada. SUI 114209, sample WS8973; axial section (J₁), enlarged internal volutions (J₂) showing the structure of the wall with diaphanotheca. Scale bars A–G, I₁ and J₁ 0.1 mm; H and J₂ 0.5 mm.
Lee et al. (1930) as the type species (refigured herein Fig. 1D, E). The concept of this genus was somewhat loose at the beginning. Eoschubertella as described possesses many features of Schubertella except, as stated by Thompson (1937), it lacks a four-layered wall with diaphanotheca. However, later Thompson (1964) and more recently Groves (1991) recognized that Schubertella has a three-layered wall. The other major difference between Eoschubertella and Schubertella according to the original description is the minute size and ellipsoidal to subglobular outline in the former as opposed to the fusiform and generally larger size in the latter (Thompson 1937; Groves 1991). Furthermore, Thompson (1937) specifically mentioned that Eoschubertella is early Pennsylvanian in age. Since that time fusulinid workers have had reread early-middle Pennsylvanian minute ellipsoidal to subglobular forms to Eoschubertella. I agree with the concept of considering minute globose to ellipsoidal forms as a separate genus. The irony, however, is that the type species of Eoschubertella, Schubertella lata Lee and Chen, 1930 is substantially larger than either the lectotype of Schubertella transitoria in Staff and Wedekind (1910) or specimens from Spitsbergen in Thompson (1937) (Fig. 1A–E, herein). Schubertella lata, however, was printed with ×30 magnification, whereas specimens of Thompson (1937) from Spitsbergen were printed nearly three times larger, with ×84 magnification making S. lata appear as a “miniature” form. In the original description of S. lata (Lee et al. 1930: 111) the authors mentioned the elliptical outline of the loosely coiled test with a total length 0.6–0.75 mm and form ratios 1.5–1.75, coiling of the first volute at nearly 90° in regards to outer volutes, small but distinct chomata and slightly wavy septa at the polar ends; the thin wall (20 μm) is three-layered, with a tectum and two distinct chomata and slightly wavy septa at the polar ends; the thick wall (30 μm) is three-layered, with a tectum and two tectoria. As stated by the authors (Lee and Chen in Lee et al. 1930: 111): “The absence of the light, transparent layer or diaphanotheca is, however, a fact beyond doubt”. All features of S. lata suggest its close resemblance to Schubertella transitoria at the generic level. Thus, in my opinion Eoschubertella is a junior synonym of Schubertella.

The genus Schubertina Marshall, 1969, although not known widely, has always been placed in synonymy with Eoschubertella (Loeblich and Tappan 1988; Groves 1991; Ueno in Fohrer et al. 2007), because it best fits the concept proposed by Thompson for Eoschubertella. However, since the type-species of the latter genus is a junior synonym of Schubertella, Schubertina becomes a valid taxon.

Another new genus Pseudoschubertella also has been erected by Marshall (1969: 124–125) with type-species Pseudoschubertella fusiforma Marshall, 1969. The author agrees with Groves (1991) and Ueno in Fohrer et al. (2007) that Schubertina and Pseudoschubertella are very similar and belong to the same genus, and thus the latter is a synonym of the former.

Thompson (1948: 19) specifically pointed out that advanced Schubertella have a spirotheca composed of a tectum and relatively thick lower clear layer that he sometimes called the diaphanotheca. This group of schubertellids is also characterized by a relatively large test that usually exceeds 1–1.5 mm in length, has large chomata and septa strongly fluted in the polar ends. This group best fits the concept of Mesoschubertella Sakagami in Kanuma and Sakagami, 1957 (see below).

Stratigraphic and geographic range.—Schubertella is distributed globally within the tropics-subtropics and known from Moscovian to Wordian (Rausser-Chernousova et al. 1951; Skinner and Wilde 1966; Leven 1998a, b).

Genus Schubertina Marshall, 1969

1964 Eoschubertella Thompson; Loeblich and Tappan 1964: C401 (pars).
Type species: Schubertina circulus Marshall, 1969, Bird Spring Formation, Clark County Nevada; Horquilla Limestone; Blue Mountain, Arizona; early Desmoinesian (middle Moscovian), Pennsylvanian.
Type material: Schubertina circulus Marshall, 1969: 122–123, pl. 1: 38–41 (holotype fig. 39; refigured herein as Fig. 2T) that is a junior syn-

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**Description.**—Test small subgloboso-ovoid to ovoid-fusiform, with two, to three and a half volutions. The initial volution always coiled at large angle in respect to the following volutions. The initial chamber is relatively large with outside diameter 30–70 μm. The proloculus/test ratio is 1:4 to 1:6 as opposed to 1:10 to 1:30 in *Schubertella*. Volutions coiled loosely, except for the first one that is tight. Chomata are very small to nearly undetectable. Septa are straight throughout. Wall is thin, often poorly differentiated. In well preserved specimens it is two-layered protheca with a thin, dark tectum and thicker, light lower layer (tectorium). A discontinuous upper tectorium observed in some specimens.

**Remarks.**—The author agrees with Groves (1991) who considered *Schubertina circuli* Marshall, 1969 as a junior synonym of *Eoschubertella bluensis* Ross and Sabins, 1965. Both species possess quite similar morphology such as a subgloboso outline, similar size of the proloculus, and overall test, character of coiling, and straight septa. Besides, they both appear close to the same chronostratigraphic horizon (middle Pennsylvanian). However, according ICZN, Article 67.1.2. “…the name of a type species remains unchanged even when it is a junior synonym or homonym, or a sup-nomen, even when it is a junior synonym or homonym, or a sup-nomen.” Thus, the type species of *Schubertina* is *S. circuli* Marshall, 1969 but at the same time it is a synonym of *Schubertina bluensis* (Ross and Sabins, 1965) and should be used under this taxonomy.

*Schubertina* differs from *Schubertella* in its much smaller overall test size, subgloboso to ovoid outline, relatively large proloculus, smaller number of volutions (two-three in *Schubertina* and four-six in *Schubertella*), two-layered wall, poorly developed secondary deposits and straight septa. *Schubertella* possesses a fusiform outline, at least four volutions, relatively small proloculus, three-layered wall, always prominent chomata and weakly fluted septa at the polar ends. Wall structure in both genera could appear similar in cases of poor preservation.

*Schubertina* is closely related to and somewhat resembles *Grovesella* Davydov and Arefifard, 2007. Their comparison is provided below in the re-description of *Grovesella*.

**Genus Grovesella** Davydov and Arefifard, 2007

**Description.**—Test very small (0.09–0.2 mm in length and 0.2–0.3 mm in diameter), discoidal to barrel-shaped, with broadly rounded periphery and weakly to slightly umbilicate flanks. Proloculus is quite large. The proloculus/test ratio is 1:3 to 1.5, sometimes up to 1.7. Coiling planispiral or nearly planispiral with half or full first volution coiled at small angle in respect to following volutions. Length of the test is equal or significantly less than the width and consequently the means of form ratio is equal or less than one. Wall thin, its internal structure poorly visible. Wall probably two-layered with a darker thin tectum and slightly lighter structureless layer below the tectum. Chomata are not observed.

**Remarks.**—*Grovesella* is probably the ancestral taxon to all schubertellids. It closely resembles *Schubertina* in its small test size and relatively large proloculus, but differs from the latter in its barrel-shaped outline and planispiral or nearly planispiral coiling as opposed to the subgloboso to ovoid outline and strongly skewed coiling in *Schubertina*. It also lacks chomata. *Grovesella* probably evolved from *Semistaffella* or *Eostaffellina* stocks as they all possess a similar barrel-shaped outline. *Grovesella* differs from *Semistaffella* in its much smaller size, two-layered wall as oppose to undifferentiated wall in *Semistaffella*, planispiral coiling and absence of chomata. Although *Grovesella* is similar to *Eostaffellina* in the outline, it differs from the latter in its loosely coiled volutions, larger proloculus and consequently a smaller proloculus/test ratio that is 1:3 to 1:5 in *Grovesella* and 1:15 to 1:30 in *Eostaffellina* and in the lack of chomata or pseudochomata that are always present in *Eostaffellina*.

Because *Schubertina* was unknown to the writer in 2007, several specimens belonging to *Schubertina* were included in the original description of *Grovesella* (Davydov and Arefifard 2007: 5–6), i.e., *Schubertina mosquensis* (Rausser-Chernousova in Rauser-Chernousova et al. 1951); *Schubertina compressa* (Rausser-Chernousova in Rausser-Chernousova et al. 1951); *Schubertina miranda* (Leonovich in Rausser-Chernousova et al. 1951); *Schubertina globulosa* (Safonova in Rausser-Chernousova et al. 1951); *Schubertina borealis* (Rausser-Chernousova in Rausser-Chernousova et al. 1951)— all from the Moscovian of Russian Platform and surrounding areas. Now that, the genus *Grovesella* is restricted to barrel-shaped forms with planispiral coiling the above mentioned species are considered to belong to *Schubertina*.

The presence of a barrel-shaped test with a large proloculus and planispiral coiling make *Grovesella* homeomorphic to Permian *Levenella* Ueno, 1991 and *Zarodella* Sosnina, 1981. The latter genus has never been reported beyond the occurrence of the topotype in Far East Russia. Besides, it belongs
to staffellids i.e., possesses specific wall structure with glassy luminotheca that is easily re-crystallized. Typical *Grovesella* sometimes identified as *Levenella* (for example Leven 1995: pl. 1: 3) as both genera possess similar morphology. The wall structure of these genera during ontogenesis, however, is quite different. It is structureless one-layered initially in *Levenella* (Ueno 1991b), but two-layered in *Grovesella*. In the outer involutions the wall in *Levenella* becomes two layered with dark tectum and fine alveolar keriotheca, whereas it does not changed in *Grovesella*. Besides this, the test size of *Levenella*
three times greater than those of *Grovesella*. It might be that *Grovesella* and *Levenella* are related each other and thus the *Levenella, Pamirina*, and *Misellina* are originating from Schubertellida.

**Stratigraphic and geographic range.**—*Grovesella* is poorly known. Because of its very small size (> 0.2 mm) it might be overlooked in Permian rocks where workers generally look for large fusulinids. On the other hand, these forms are perhaps often considered as juvenile forms of *Schubertella* and therefore were ignored. *Grovesella* is distributed globally from Peri-Gondwana up to Panthalassa shelves and ranged from the middle Bashkirian up to Wordian.

**Grovesella nevadensis** sp. nov.

Fig. 2J–T.

**Etymology:** After the state Nevada (USA) where numerous specimens of the species were recovered.

**Type material:** Holotype: SUI 114224 (Fig. 2Q), axial section; para-types: SUI 114217 (Fig. 2F), axial section; SUI 114218 (Fig. 2K), axial section; SUI 114219 (Fig. 2LJ), axial section; SUI 114220 (Fig. 2M), axial section; SUI 114221 (Fig. 2N), axial section; SUI 114222 (Fig. 2O), axial section; SUI 114223 (Fig. 2P), axial section; SUI 114225 (Fig. 2R), axial section; SUI 114226 (Fig. 2S), axial section; SUI 114227 (Fig. 2T), axial section.

**Type locality:** Arrow Canyon section, Bird Spring Formation, Nevada, USA.

**Type horizon:** *Eoparafusulina linearis* beds, late Artinskian, Cisuralian.

**Diagnosis:**—Miniature test with nautiloid and broadly rounded periphery and nearly planispiral coiling, poorly visible but most probably two-layered wall; it is lacking chomata.

**Description:**—Test is very small, with 2–2.5 volutions, nautiloid with broadly rounded periphery and flat to mildly umbilicate flanks. Coiling is planispiral or nearly planispiral. The axis of initial volution in some specimens sometimes is at a small angle in respect of second volution.

Length of the test is 160–200 μm, diameter (width) 180–250 μm, with form ratio of 0.79–0.9. Outer diameter of proloculus is 25–60 μm. Wall thin, poorly visible, sometimes two-layers, a darker, thin tectum and slightly lighter, structureless lower tectorium can be observed. Thickness of the wall in the final volution is 3–10 μm. Chomata generally absent, but sometimes dark secondary deposits present on the chamber floor in the final volution (Fig. 2O). Because of lack of chomata, nether shape or size of the tunnel could be determined.

**Remarks:**—The species described here closely resembles *Grovesella staffeloides* (Suleimanov, 1949) from the late Asselian and Sakmarian of southern Urals but differs from it in smaller size of the test and the initial chamber, a smaller form ratio and lack of chomata. From *Grovesella tabasensis* Davydov and Arefifard, 2007 it differs in having a wider test and consequently a greater form ratio.

**Genus Mesoschubertella** Sakagami in Kanuma and Sakagami, 1957

**Type species:** *Mesoschubertella thompsoni* Sakagami in Kanuma and Sakagami, 1957; found in limestone pebble in Tamanouchi Limestone conglomerate together with Yakhhtsian (late Artinskian–Kungurian) fusulinids; Yagooki Valley, Tamanouchi, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

**Description:**—Medium to large elongate-fusiform to inflated-fusiform schubertellids with more than 4–5 volutions. The test lengths is exceed 1.0–1.5 mm. Proloculus/test ratio is 1:20 to 1:30 and is the greatest among the rest of genera discussed in this paper. Coiling is typical for schubertellids, i.e., the initial one or one and a half volutions are coiled at a large angle in respect to the following volutions. Wall is thick, with thin, dark tectum, well developed upper tectorium, lower tectorium and lighter layer between the tectum and lower tectorium (diaphanotheca). The latter layer often can be barely recognized due to poor preservation. Chomata are small to medium, always prominent. Septa straight, slightly fluted in the polar ends.

**Remarks:**—Thompson already noted the prominent features of Permian *Schubertella* that he called advanced (Thompson 1948: 33), such as a relatively large size and a large number of volutions. At the same time, he stated that there was a single-layered wall. It seems that preservation severely affects schubertellid’s wall structure, and sometimes the wall may appear as a single structureless layer. However, in sufficiently well preserved forms (Fig. 1L, M) four layers of the wall with diaphanotheca are commonly observed. Ueno (1996) call the light intermediate and less dense layer between dark tectum and dense lower tectorium, as protheca. He pointed that this layer is quite different from actual diaphanotheca of *Fususlinella, Beedeina*, and *Yangchienia*, but did not explain how exactly it is different. In my opinion the term diaphanotheca does not represent chemically or compositionally determined layer, but simply the descriptive term for the light and less dense layer between the two more dense layers (Rauser-Chernousova and Gerke 1971).

Nevertheless, the wall structure is not the only feature that allows separation of *Mesoschubertella* from *Schubertella*. *Mesoschubertella* also differs from *Schubertella* in its greater size, generally exceeding 1.0 mm, and greater number of volutions (4–6 versus 3–4 in *Schubertella*). The morphological features of *Schubertella* and *Mesoschubertella* overlap, as these genera are closely related to each other, and a taxonomic differentiation in some specimens could be difficult.

**Stratigraphic and geographic range.**—*Mesoschubertella* commonly is considered to be Tethyan form only, but as shown here it also occurs in Mexico and Nevada (Fig. 1L). Therefore, the genus is global in distribution and ranges from the Cisuralian (possibly the late Gzhelian) to the Guadalupian.

**Genus Biwaella** Morikawa and Isomi, 1960

Figs. 3–5.

1960 *Biwaella* gen. nov.; Morikawa and Isomi 1960: 300–301.
1964 *Biwaella* Morikawa and Isomi; Thompson in Loeblich and Tappan 1964: C418.

1965 *Biwaella* Morikawa and Isomi; Skinner and Wilde 1965: 95.


1996 *Biwaella* Morikawa and Isomi; Chediya in Rauser-Chernousova et al. 1996: 114.

**Type species**: *Biwaella omiensis* Morikawa and Isomi, 1960; Minamitoba, near Lake Biwa, Shiga Prefecture, Japan; ?Artinskian.

**Description**.—Test large for schubertellids, inflated fusiform to subcylindrical, with broadly rounded axial ends, usually exceeds 1mm in length. Proloculus is relatively small, its outside diameter is around 100–150 μm. Proloculus/test ratio is 1:8 to 1:15. The axis of initial subglobose tightly coiled volution is typically at a large angle to the axis of other volutions. Second volution is ovoid. Following volutions ex-
pand rapidly in length and height, especially starting from third volution. Form ratios in first volution are around 1.0, in third—2.5–4.0, in the final volution it varies from 3.0 to 4.5. Wall is thin in early volutions 10–15 μm. It increases in thickness rapidly and in the final volution it becomes very thick, up to 100 μm. Wall in first volutions consists of two layers: a thin, dark tectum and a thicker and lighter lower structureless tectorium. A rarely observed upper tectorium is not typical for the genus. Wall in the final volution perforated with coarse mural (simple, branchless) pores. The pores may reach a diameter of 10 μm. The porosity, however, does not develop into keriothecal type, i.e., pores are straight and never join each other as in true keriotheca (Davydov 2007). Therefore, no differentiation of lower and upper keriotheca can be observed (Figs. 4B, 5B).

Septa are widely spaced, nearly straight throughout the length of the test and slightly fluted in axial ends. Chomata are small to prominent in all volutions except for the final one.

Remarks.—Biwaella closely resembles elongate Schwageriniformis and Obsoletes, but differs from both of these genera in having a much smaller test, skewed initial volution and, most important, a wall with mural pores only in final volution as opposed to keriothecal wall with lower and upper keriotheca that are developed in all volutions in Schwageriniformis and Obsoletes. Davydov (1984) has shown that although Biwaella and its descendant genus Dutkevichites possess coarse porosity, these genera are schubertellids. Nevertheless they both are often included in the schwagerinids (Loeblich and Tappan 1988; Rauser-Chernousova et al. 1996). Traditionally, a wall with coarse pores (Figs. 3B, D, 4B, 5B) is called keriotheca. It has been demonstrated (Thompson 1964; Davydov and Krainer 1999; Forke 2002; Leppig et al. 2005; Davydov 2007) that there is a principal difference between a true keriothecal wall developed in the family Schwagerinidae and a wall with coarse mural pores. A keriothecal wall possesses two sets of “piped” pores that are joined with each other and form a lower and upper keriotheca. In the lower part of the keriotheca the “pipes” are coarser than in the upper part of the keriotheca (Fig. 5E, G, F). In paraxial sections of keriothecal wall, two sets of pores (or “pipes”) of different size are clearly seen (Fig. 5F). Pores in the Biwaella wall are uniform in diameter throughout the thickness of the wall and in oblique sections only uniform pores can be observed (Fig. 5B). Late Gzhelian Dutkevichites Davydov, 1984, which probably evolved from Biwaella, differs from the latter in fluting of the septa developed throughout the length of the test.

Stratigraphic and geographic range.—Similar to the rest of the Schubertellidae described here this genus is distributed globally within tropics-subtropics. It appeared in the early Gzhelian and continued to develop throughout the Cisuralian.

Biwaella zhikalyaki sp. nov.

Fig. 3A–L.

Etymology: The species named after the Director of Artemgeology, Ukraine, Dr. Nikolay Vasilevich Zhikalyak who supports my study in the Donets Basin.

Type material: Holotype: SUI 114229 (Fig. 3C), axial section; para−types: SUI 114228 (Fig. 3A), axial section; SUI 114230 (Fig. 3E), axial section; SUI 114231 (Fig. 3F), axial section; SUI 114232 (Fig. 3G), axial section; SUI 114233 (Fig. 3H), axial section; SUI 114234 (Fig. 3I), axial section; SUI 114235 (Fig. 3J), axial section; SUI 114236 (Fig. 3K), axial section; SUI 114237 (Fig. 3L), axial section.

Type locality: Kalinovo section near Kalinovo village, Luganskaya County, western Donets Basin, Ukraine.

Type horizon: Limestone P2 Darvasoschwagerina donbassica–Schagonella proimplexa beds, early Gzhelian, Pennsylvanian.

Diagnosis.—Large elongate-fusiform test with pointed polar ends, tight coiling initially and loose at maturity, wavy septae, small but prominent chomata in all volutions and wide tunnel.

Description.—Large, elongate-fusiform test with roundly pointed polar ends possessing 5–6 volutions. First–second volutions are nearly globular. Starting from the third volution, test elongates quite rapidly and reaches elongate-fusiform outline in fourth and following volutions. Initially tight coiling becomes much looser starting from the fourth volution. The initial volution coiled with large to very small angle in respect to outer volutions. In some forms coiling is planispiral or nearly planispiral. Test with length of 1.4–1.96 mm and diameter 0.48–0.65 mm producing form ratio 2.6–3.1 in the final volution. Outer diameter of proloculus varies between 45 and 80 μm, but generally is around 50–60 μm. Wall thin initially (15–20 μm), gradually becomes very thick and reaches thickness 40–45 μm in final volution. It is two-layered with thin dark tectum and thick lighter lower tectorium. Wall in the final volution penetrated by coarse pores up to 7–8 μm in diameter. Pores can be observed also in the volution before the final, but not elsewhere. Septa are straight or slightly wavy throughout the length except at the polar ends where they are fluted. Chomata very small initially are not always present in the final volution. Tunnel low and narrow initially becomes quite wide in the final volution.

Remarks.—The described species somewhat resembles the undescribed Biwaella sp. No 1 from the late Asselian of Darvas, Central Asia (Leven and Schcherbovich 1978: 87) and Sakmarian of Afghanistan (Leven 1971), but differs in having a smaller more elongate test, and consequently greater form ratios, better developed chomata in the internal volutions, and in fluting of the septa in the polar ends.

Stratigraphic and geographic range.—Darvasoschwagerina donbassica–Schagonella proimplexa Zone, early Gzhelian, Pennsylvanian, Donets Basin.

Biwaella poletaevi sp. nov.

Figs. 4A–H, 5A.

1978 Biwaella ex gr. omiensis; Leven and Schcherbovich, 1978: 87, pl. 1: 15.
1978 Biwaella sp. No. 2; Leven and Scherbovich, 1978: 88, pl. 1: 16.

Etymology: In honor of my friend and great Donets geologist and paleontologist Vladislav Innokent’evich Poletaev.
Type material: Holotype: SUI 114241 (Fig. 4E), axial section; para−
types: SUI 114238 (Fig. 4A), axial section; SUI 114239 (Fig. 4C), axial
section; SUI 114240 (Fig. 4D), axial section; SUI 114242 (Fig. 4F), ax−
ial section; SUI 114243 (Fig. 4G), axial section; SUI 114243 (Fig. 4H),
axial section.

Type locality: Kalinovo section near Kalinovo village, Luganskaya
County, western Donets Basin, Ukraine.

Type horizon: Limestone P₂ Darvasoschwagerina donbassica–Scha−
gonella proimplexa beds, early Gzhelian, Pennsylvanian.

Diagnosis.—Large elongate−subcylindrica test with roun−
ded polar ends, nearly unifome coiling, wavy septae, poorly
developed chomata that are often absent in the final vulotion.
**Description.**—Large, subcylindrical test of 5–6 volutions with broadly rounded polar ends. Test elongates quite rapidly starting from the third volution and becomes subcylindrical in outline in the two outer volutions. The coiling is planispiral or nearly planispiral. Initial volution is coiled tight then expands uniformly but rapidly. The final volution is loosely coiled. Test with length of 2.0–2.5 mm and diameter 0.57–0.65 mm producing form ratio 3.2–4.1 in the final volution. Outer diameter of proloculus is 40–60 μm. Wall is thin initially, reaching thickness up to 20–30 μm in the final volution. Its internal structure is the same as in *Biwaella zhikalyaki* sp. nov. Septa are straight or slightly wavy throughout the length except at the polar ends where they are fluted. Chomata in early volutions are prominent, but absent in two outer volutions. Tunnel is moderate in height and width throughout the growth.

**Remarks.**—This species strongly resembles *Biwaella ex gr. omiensis* Morikawa and Isomi and *Biwaella* sp. No. 2 from middle–late Asselian of Darvas, Tadzhikistan, Central Asia (Leven and Scherbovich 1978) in its subcylindrical outline in two outer volutions, weak septal fluting throughout the length of the test, intensive fluting in polar ends, and lack of chomata in the two outer volutions. *Biwaella omiensis* Morikawa and Isomi, 1960 possesses some similarities with the described species but the described species differs in its rather fusiform outline of the test, smaller size and much smaller chomata.

**Stratigraphic and geographic range.**—Schagonella proimplexa Zone, early Gzhelian, Pennsylvanian, Donets Basin; middle–late Asselian of Darvas, Central Asia.

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**Evolution and development of Schubertella and related genera**

The ontogeny of *Schubertella* and related genera suggests the following phylogenetic development and relationship. The earliest representative of the schubertellids, *Grovesella*, is very small and nautiloid, with a poorly developed wall and nearly planispiral coiling. It appeared in the Tethys sometimes in the mid-Bashkirian (Sinitsyna and Sinitsyn 1987, Nikolaev 2005) (Fig. 6). Probably, *Grovesella* evolved from *Semistaffella* or *Eostaffellina* stocks because all possess a similar barrel-shaped outline and small size. The proloculus/test ratio in *Grovesella* is 1:3 to 1:5. *Grovesella* probably was quite rare at that time as it has been reported from only a few localities in the western Tethys and Timan-Pechora (Manukalova-Grebenyuk et al. 1969; Sinitsyna and Sinitsyn 1987; Nikolaev 2005). In late Bashkirian (early Atokan) time, it
dispersed globally within the tropics-subtropics including North America (Thompson 1937; Groves 1986, 1991). It is generally rare in assemblages with two acmes in roughly Artinskian and Kungurian time and developed up to the Wordian (early Midian) (Kobayashi 2006).

The appearance of the genus Schubertina was a second step in the evolution of early schubertellids. It was derived from Grovesella almost immediately after its origination in mid–late Bashkirian time (Sinitsyna and Sinitsyn 1987; Nikolaev 2005). Schubertina is larger than Grovesella overall, it possesses more volutions and the early volutions coil at a large angle in respect of volutions at maturity. The proloculus/test ratio in Schubertina is 1:4 to 1:5, i.e., slightly larger but overlapping that of Grovesella. The wall of Schubertina is differentiated into two layers. Schubertina has a stratigraphic and geographic range similar to that of Grovesella, i.e., it survived for nearly 50 Ma from late Bashkirian up to Wordian.

It seems that true Schubertella, i.e., forms restricted to the type-species, first appeared in the Moscovian (Rauser-Chernousova et al. 1951). These forms are generally have fusiform outlines, at least 0.3–0.5 mm in length and have a significant number of volutions (generally 3–4, sometimes up to 6). Most important is that the ratio of proloculus-final volution diameter in Schubertella is greater than 1:10 which does not overlap that of Schubertina. The wall of Schubertella is differentiated into three layers which are penetrated by relatively coarse pores observed on well preserved specimens. Although Schubertella is generally rare in foraminiferal assemblages, sometimes it forms a specific schubertellid or staffellid-schubertellid facies in restricted or cooler/deeper water environments (Teodorovich 1949; Rauser-Chernousova 1950; Baranova and Kabanov 2003). Schubertella lived from the Moscovian through Lopingian with several acme zones in the Moscovian–Kasimovian, late Asselian–early Sakmarian and late Artinskian time.

In early Gzhelian time, the relatively large schubertellid Biwaella with a thick coarsely porous wall developed from Schubertella. The Biwaella morphotype once evolved was conservative overall and the genus survived through Artinskian–Kungurian time. In the latest Gzhelian Dutkevitchites, i.e., a Biwaella-like form with fluted septa, was derived from the latter. This highly specialized form is developed into Sphaeroschwagerina (Davydov 1984). All three genera, Biwaella, Dutkevitchites, and Sphaeroschwagerina form the subfamily Biwaellinae Davydov, 1984.

The exact time of appearance of another advanced schubertellid, Mesoschubertella, is not clear. It is documented in Artinskian through Murgabian time, but its origination could have been in the Sakmarian–Asselian or even in the late Gzhelian.

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