Taxonomy, nomenclature, and evolution of the early schubertellid fusulinids

VLADIMIR I. DAVYDOV

Davydov, V.I. 2011. Taxonomy, nomenclature, and evolution of the early schubertellid fusulinids. *Acta Palaeontologica Polonica* 56 (1): 181–194.

The types of the species belonging to the fusulinid genera *Schubertella* and *Eoschubertella* were examined from publications and type collections. *Eoschubertella* in general possesses all the features of *Schubertella* and therefore is a junior synonym of the latter. However, the concept of *Eoschubertella* best describes the genus *Schubertina* with its type species *Schubertina curculi*. *Schubertina* is closely related to the newly established genus *Grovesella* the concept of which is emended in this paper. Besides *Schubertella*, *Schubertina*, and *Grovesella*, the genera *Mesoschubertella*, *Biwaella* are reviewed and three new species, *Grovesella nevadensis*, *Biwaella zhikalyaki*, and *Biwaella poletaevi,* are described. The phylogenetic relationships of all Pennsylvanian–Cisuralian schubertellids are also proposed. Barrel-shaped *Grovesella* suggested being the very first schubertellid that appears sometimes in the middle–late Bashkirian time. In late Bashkirian it is then developed into ovoid to fusiform *Schubertina*. The latter genus gave rise into *Schubertella* in early Moscovian. First *Fusiella* derived from *Schubertella* in late Moscovian, *Biwaella*—in early Gzhelian and *Boultonia*—in late Gzhelian time. Genus *Mesoschubertella* also developed from *Schubertella* at least in Artinskian, but may be in late Sakmarian.

Key words: Foraminifera, Fusulinida, Schubertellidae, evolution, taxonomy, Permian, Carboniferous.

Vladimir I. Davydov [vdavydov@boisestate.edu], Permian Research Institute, Department of Geosciences, Boise State University, Boise, ID, 83725, USA.

Received 26 February 2010, accepted 28 July 2010, available online 16 August 2010.

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 (Suleimanov 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 topotypes 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, Vale 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*.

doi:10.4202/app.2010.0026

(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 *Grovesella* by Davydov and Arefifard (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 volutions. This group possesses features of *Schubertella* Staff and Wedekind, 1910.

(4) Advanced large schubertellids usually over 1 mm in length with thick well developed, multi-layerd 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 keriotheca, 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 chresonymes (see e.g., Smith and Smith 1973).

Superfamily Fusulinoidea 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.
1937 *Eoschubertella* Thompson; Thompson 1937: 123–124.

Type species: *Schubertella transitoria* Staff and Wedekind, 1910, the exact location unknown (see discussion below), Spitsbergen, Carboniferous–Permian boundary transition.

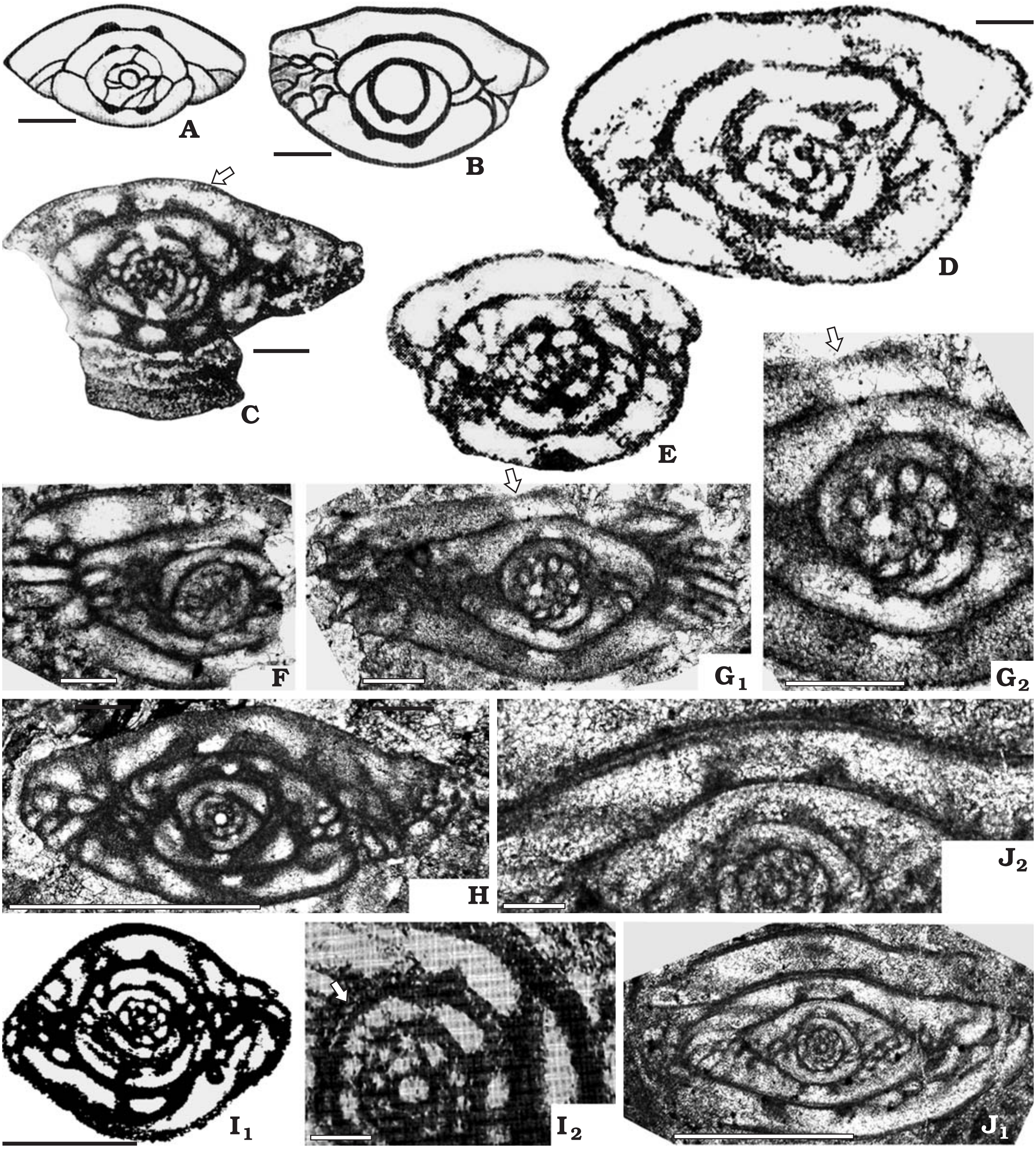
Description.—Test small, usually less than 1–1.5 mm in length, ovoid to elongate fusiform with convex lateral slopes and sharply to bluntly pointed poles. The initial one-two volutions are nautiloid in outline with form ratio less than 1.0. They are coiled in one plane, but always skewed at large, but variable angles in regards to the following planispiral volutions. Mature forms consist of four-six volutions, 0.5 to 1.5 mm in length and 0.3 to 0.9 mm in width. Form ratio typically is 1.5–2.0 sometimes up to 3.0. The ratio of diameter of proloculus vs diameter of final volution of the test is 1:10 to 1:20 (proloculus/test ratio). The wall is composed of a primatheca (dark tectum and lighter lower layer), lighter upper layer on the chamber floors (upper tectorium). On well preserved specimens, small and straight (mural) pores penetrating entire wall can be seen (Fig. 1C, H, I). Septa are numerous (up to 20 at maturity) and straight throughout the length of the test, except at the axial ends where they are sometimes slightly wavy. Chomata developed weakly to moderately and outlined the tunnel.

Remarks.—There is a puzzling story associated with the type-species of *Schubertella*, *Schubertella transitoria* Staff and Wedekind, 1910. The authors originally presented drawings of two specimens (see Fig. 1A, B herein) that were regarded by them as dimorphic representatives of the species. Nevertheless, Thompson (1937: pl. 8: 4) designated only one of them (Fig. 1A herein) "… as typical of *S. transitoria*" (Thompson 1937: 122) designating that way the lectotype of the type-species of *Schubertella*. The second specimen as noted by Thompson (1937), which has a very large proloculus, planispiral coiling and symmetrical volutions does not even belong to the genus. In my opinion this specimen probably is a juvenile form of *Schellwienia* that co-occurs with *Schubertella* in the original sample.

The "microspherical" specimen possesses an endothyroid juvenarium, but on the drawing it appears planispiral. Although, Hans von Staff generally photographed fusulinids, in the case of *S. transitoria* only a drawing was provided (Staff and Wedekind 1910: pl. 4: 7, 8). Probably a magnification of over 100 times could not be technically accomplished by Hans von Staff at that time. Also, it might be that in the thin-section of the lectotype, the axis of the initial nautiloid volution was in 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 (Miklukho-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

Fig. 1. Types of *Schubertella*, *Eoschubertella*, and *Mesoschubertella*. **A**. *Schubertella transitoria* Staff and Wedekind, 1910, Tempel Bay in Spitsbergen, Carboniferous–Permian transition, repository unknown; the drawing of "microsphaerical" specimen from Staff and Wedekind (1910: pl 4: 8) assigned by Thompson (1937) as a lectotype. **B**. "*Schubertella transitoria*" Staff and Wedekind, 1910, Tempel Bay in Spitsbergen, Carboniferous–Permian transition, repository unknown; the drawing of "macrosphaerical" specimen from Staff and Wedekind (1910: pl. 4: 7), probably a juvenile of *Schellwienia* sp. **C**, **F**–**H**. *Schubertella transitoria* Staff and Wedekind, 1910. **C**. Tempel Bay in Spitsbergen, Carboniferous–Permian transition, collection of Alfred G. Nathorst, 1882, Tempe1 Bay, Spitsbergen; SUPTC No. 5942, axial section of specimen from topotype as proposed by Thompson (1937: pl. 22: 5); arrow shows mural pores in the final volution. **F**. Sabina Land, Gnomen Mnt. Spitsbergen; lower Asselian; SUI 114207, axial section, sample 70-6_2-1. **G**. Early Asselian, Sabina Land, Gnomen Mnt. Spitsbergen, coll. of Eugene P. Karnaushenko; SUI 114208, sample 70-6_2-8; nearly axial section (G_1); detail of G_1 (G_2); mural pores (arrow) well visible in the final volution. **H**. Tempelfjorden, Spitsbergen; lower Asselian; SUI 1185, axial section from Ross (1965: pl. 12: 1), mural pores are shown in the final →



volution of this specimen. **D**, **E**. *Schubertella lata* Lee and Chen in Lee at al., 1930. **D**. 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, Tokyo-to, Kwanto massif, Japan. 23918-A holotype (I_1); 23918-A (I_2) 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 (J_1), enlarged internal volutions (J_2) showing the structure of the wall with diaphanotheca. Scale bars A–G, I_2 and J_2 0.1 mm; H and J_1 0.5 mm.

doi:10.4202/app.2010.0026

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 reffered 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 volution at nearly 90° in regards to outer volutions, 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 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 (Rauser-Chernousova et al. 1951; Skinner and Wilde 1966; Leven 1998a, b).

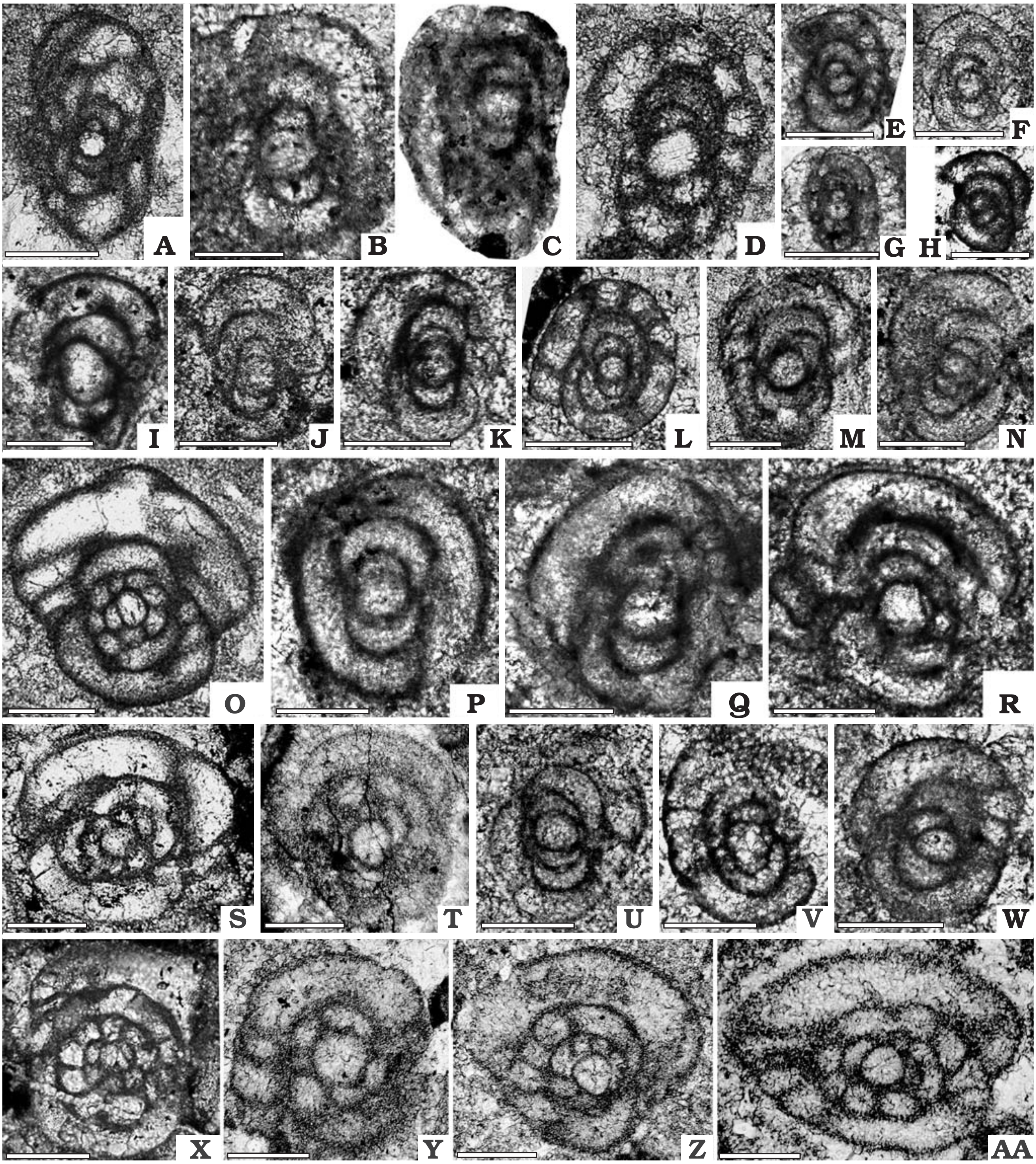
Genus *Schubertina* Marshall, 1969

1937 *Eoschubertella* Thompson, 1937: 123–124 (pars).
1964 *Eoschubertella* Thompson; Loeblich and Tappan 1964: C401 (pars).
1969 *Schubertina* gen. nov.; Marshall 1969: 121.
1969 *Pseudoschubertella* gen. nov.; Marshall 1969: 124–125.
1988 *Eoschubertella* Thompson; Loeblich and Tappan 1988: 258–259 (pars).
1988 *Quydatella* Liem, 1966; Loeblich and Tappan 1988: 257–258 (pars).
1996 *Eoschubertella* Thompson; Chediya in Rauser-Chernousova et al. 1996: 86 (pars).
2007 *Grovesella* Davydov and Arefifard, 2007: 5–6 (pars).

Type species: *Schubertina circuli* Marshall, 1969, Bird Spring Formation, Clark County Nevada; Horquilla Limestone; Blue Mountain, Arizona; early Desmoinesian (middle Moscovian), Pennsylvanian.

Type material: *Schubertina circuli* Marshall, 1969: 122–123, pl. 1: 38–41 (holotype fig. 39; refigured herein as Fig. 2T) that is a junior syn-

Fig. 2. *Grovesella* and *Schubertina* species. **A**. *Grovesella* aff. *tabasensis* Davydov and Arefifard 2007, SUI 114210, sample A-174_4, Bird Spring Formation, lower Atokan, Arrow Canyon section, Nevada. **B**–**E**, **G**, **I**–**K**. *Grovesella tabasensis* Davydov and Arefifard, 2007. **B**. SUI 114211, axial section, sample A-3/5-3b, Kalinovo section, N_3 Limestone, lower Kasimovian, Donets Basin, Ukraine. **C**. SUI 102982, axial section of holotype, sample M-49-3, Madbeiki section, Khan Formation, late Sakmarian–early Artinskian, Central Iran. **D**. SUI 114212, axial section, sample A-428m_4d, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **E**. SUI 114213, axial section, sample A-3/1-14b, Kalinovo section, N_1^1 Limestone, upper Moscovian, Donets Basin, Ukraine. **G**. SUI 114214, axial section, sample A3/31a_90, Kalinovo section, P_2 Limestone, lower Gzhelian, Donets Basin, Ukraine. **I**. SUI 114215, axial section, sample 9476_846_1-1, Bird Spring Formation, Arrow Canyon section, Nevada. **J**. SUI 114216, axial section, sample 9476_847_1-2, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **K**. SUI 103062, axial section of paratype (Davydov and Arefifard 2007: fig. 4.17), sample 9476_846_1-2, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **F**, **H**, **L**–**N**, **P**–**R**, **U**, **V**, **W**. *Grovesella nevadensis* sp. nov. **F**. SUI 114219, axial section of paratype, sample A-3/4-3b, Kalinovo section, N_2 Limestone, upper Moscovian, Donets Basin, Ukraine. **H**. SUI 114220, axial section of paratype, sample Gurk_M-9_21-4, Gurkova section, M_9 Limestone, upper Moscovian, Donets Basin, Ukraine. **L**. SUI 114217, axial section of paratype, sample A-3/31a-14, Kalinovo section, P_2^2 Limestone, lower Gzhelian, Donets Basin, Ukraine. **M**. SUI 114218, axial section of paratype, sample 9476_840_2-3, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **N**. SUI 114221, axial section of paratype, sample 9476_847_1-1, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **P**. SUI 114224, axial section of holotype, sample 9476_840_2-1, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **Q**. SUI 114223, axial section of paratype, sample 9476_840_1-1, Bird Spring Formation, Artinskian, →



Arrow Canyon section, Nevada. **R**. SUI 114222, axial section of paratype, sample 9476_840_1-2, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **U**. SUI 114227, axial section of paratype, sample 9476_840_2-2, Bird Spring Formation, Artinskian, Arrow Canyon section, Nevada. **V**. SUI 114226, axial section of paratype, sample O-1-101-2, Kalinovo section, O_1 Limestone, middle Kasimovian, Donets Basin, Ukraine. **W**. SUI 114225, axial section of paratype, sample Gurk_ M-9_21-2a, Gurkova section, M_9 Limestone, upper Moscovian, Donets Basin, Ukraine. **O**, **S**, **X**. *Schubertina bluensis* (Ross and Sabins, 1965). **O**. YPM 23432, axial section of holotype, from Ross and Sabins (1965: pl. 21: 29), locality DC-7, Dos Cabezas Mountains, Arizona, USA. **S**. YPM 22057, axial section of paratype, from Ross and Sabins (1965: pl. 21: 28), locality BM-3, Dos Cabezas Mountains, Arizona, USA. **X**. YPM 22057, axial section from the same thin-section as V; Horquilla Limestone, Middle Pennsylvanian, Arizona. **T**, **Y**, **Z**. *Schubertina curculi* Marshall, 1969. **T**. SUI 75266D, axial section of holotype, from Marshall (1969: pl. 1: 39), 26S-12E. **Y**. SUI 75272E, axial section of paratype, from Marshall (1969: pl. 1: 38), FCM 268-9L. **Z**. SUI 75273H, axial section of paratype, from Marshall (1969: pl. 1: 40), 26S-3H. Mountain Springs Pass section, Middle Pennsylvanian, S. Nevada. **AA**. *Pseudoschubertella fusiformis* (Marshall, 1969) (type species of *Pseudoschubertella* Marshall, 1969), SUI 75449H, axial section of holotype, from Marshall (1969: pl. 2: 1), FCM 302-1H, Mountain Springs Pass section, Middle Pennsylvanian, S. Nevada. Scale bars 0.1 mm.

doi:10.4202/app.2010.0026

onym of *Eoschubertella bluensis* Ross and Sabins, 1965: 184, pl. 21: 28 (paratype YPM 22057) and 29 (holotype YPM 23432) = *Schubertina circuli* Marshall, 1969: 122–123, pl. 1: 38–41.

Description.—Test small subglobose-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 subglobose 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 suppressed name." 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, subglobose 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*.

Stratigraphic and geographic range.—*Schubertina* similarly to *Schubertella* is distributed globally within the tropics-subtropics. It has been documented in the upper lower Bashkirian, Askynbashian Horizon in the Urals (Sinitsyna and Sinitsyn 1987), Donets Basin (Manukalova-Grebenyuk et al. 1969) and Timan-Pechora (Nikolaev 2005) and in early Atokan (late Bashkirian) in North America (Groves 1986, 1991). The upper range of *Schubertina* is not clear at the moment. Some forms that can be considered as *Schubertina* are reported from Wordian (early Midian), Capitanian (late Wordian) and Lopingian (Skinner and Wilde 1966; Leven 1998a).

Genus *Grovesella* Davydov and Arefifard, 2007

Fig. 2A–T.

2000 *Levenella*? Ueno, 1991; Vachard et al. 2000: 794.

2007 *Grovesella* gen. nov.; Davydov and Arefifard 2007: 5–6 (pars).

Type species: *Grovesella tabasensis* Davydov and Arefifard, 2007, Khan Formation, latest Sakmarian–early Artinskian, Madbeiki section, Kalmard area, East-Central Iran.

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 subglobose 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* (Rauser-Chernousova in Rauser-Chernousova et al. 1951); *Schubertina compressa* (Rauser-Chernousova in Rauser-Chernousova et al. 1951); *Schubertina miranda* (Leontovich in Rauser-Chernousova et al. 1951); *Schubertina globulosa* (Safonova in Rauser-Chernousova et al. 1951); *Schubertina borealis* (Rauser-Chernousova in Rauser-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

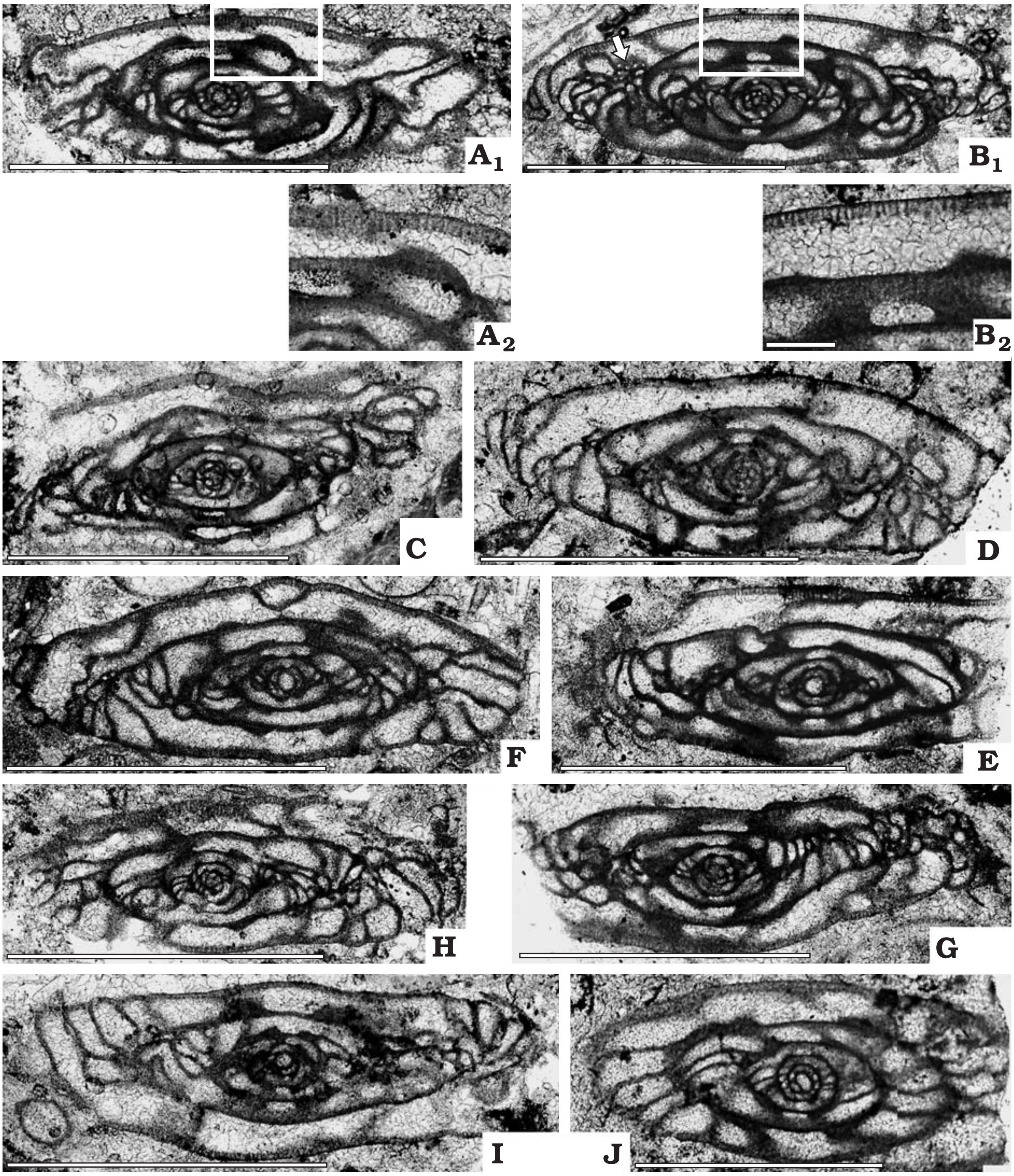


Fig. 3. *Biwaella zhikalyaki* sp. nov. from Kalinovo section, P_2^2 Limestone, lower Gzhelian, Donets Basin, Ukraine. **A**. SUI 114228, sample A-3/31a-2; axial section of paratype (A_1), box indicates the enlarged part of final volution in A_1, showing coarse mural pores (A_2). **B**. SUI 114229, sample A-3/31a-14; axial section of holotype (B_1) arrow pointed into septal pores, box indicates the enlarged part of final volution in B_1 showing coarse mural pores (B_2). **C**. SUI 114230, sample A-3/31a-93; axial section of paratype. **D**. SUI 114231, sample A-3/31a-79; axial section of paratype. **E**. SUI 114232, sample A-3/31a-97; axial section of paratype. **F**. SUI 114233, sample A-3/31a-21; axial section of paratype. **G**. SUI 114234, sample A-3/31a-77; axial section of paratype. **H**. SUI 114235, sample A-3/31a-84; axial section of paratype. **I**. SUI 114236, sample A-3/31a-88; axial section of paratype. **J**. SUI 114237, sample A-3/31a-101; axial section of paratype. Scale bars: A_1, B_1, C–J 1 mm, B_2 0.1 mm.

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 volutions 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*

doi:10.4202/app.2010.0026

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; paratypes: SUI 114217 (Fig. 2J), 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 broadely rounded periphery and nearly planispiral coiling, poorly visiable 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 staffelloides* (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.

Stratigraphic and geographic range.—Moscovian, Pennsylvanian through Artinskian, Cisuralian in Nevada and Donets Basin.

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 Yakhtashian (late Artinskian–Kungurian) fusulinids; Yagooki Valley, Tamanouchi, Hinode-rnura, Nishitamagun, 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.

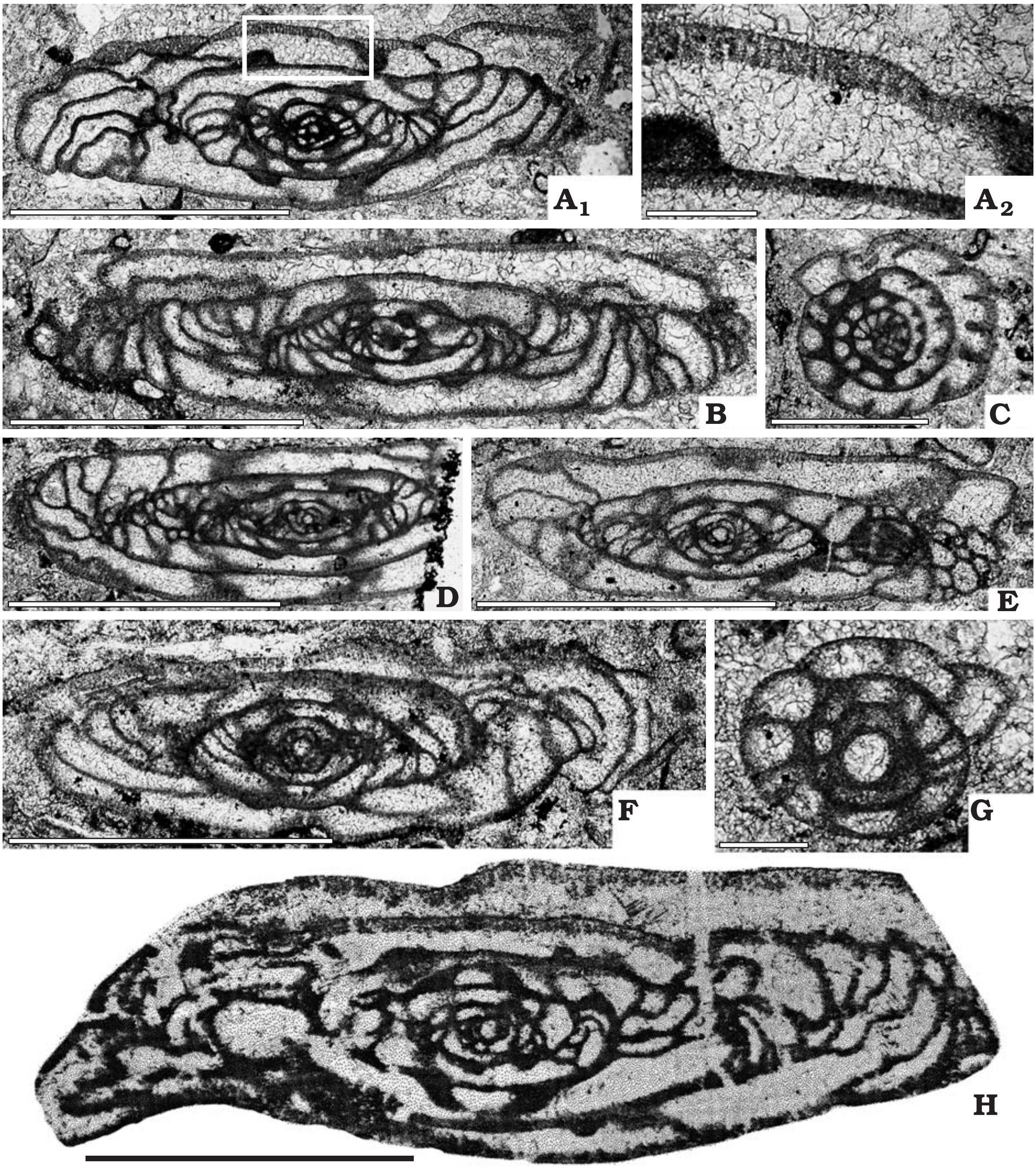


Fig. 4. Type of *Biwaella* and *Biwaella poletaevi* sp. nov. **A**–**H**. *Biwaella poletaevi* sp. nov. **A**–**G**. Kalinovo section, P_2^2 Limestone, Donets Basin, Ukraine. **A**. SUI 114238, sample A-3/31a-8, axial section of paratype (A_1), box indicates the enlarged part of final volution in A_1 showing coarse mural pores (A_2). **B**. SUI 114239, sample A-3/31a-5, axial section of paratype. **C**. SUI 114240, sample A-3/31a-77; sagital section of paratype. **D**. SUI 114241, sample A-3/31a-83, axial section of holotype. **E**. SUI 114242, sample A-3/31a-84, axial section of paratype. **F**. SUI 114243, sample A-3/31a-96, axial section of paratype. **G**. SUI 114244, sample A-3/31a-8; sagital section of paratype. **H**. *Biwaella omiensis* Morikawa and Isomi, 1960, repository unknown, axial section of holotype, from Morikawa and Isomi (1960: pl. 54: 1); ?Artinskian; Minamitoba, near Lake Biwa, Shiga Prefecture, Japan. Scale bars: A_1, D–F, H 1 mm, C 0.5 mm, A_2 0.1 mm, G 0.1 mm.

1964 *Biwaella* Morikawa and Isomi; Thompson in Loeblich and Tappan 1964: C418.
1965 *Biwaella* Morikawa and Isomi; Skinner and Wilde 1965: 95.
1988 *Biwaella* Morikawa and Isomi; Loeblich and Tappan1988: 280.
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-

doi:10.4202/app.2010.0026

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 Vasilievich Zhikalyak who supports my study in the Donets Basin.

Type material: Holotype: SUI 114229 (Fig. 3C), axial section; paratypes: 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 P_2, *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 Shcherbovich 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 Shcherbovich, 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.

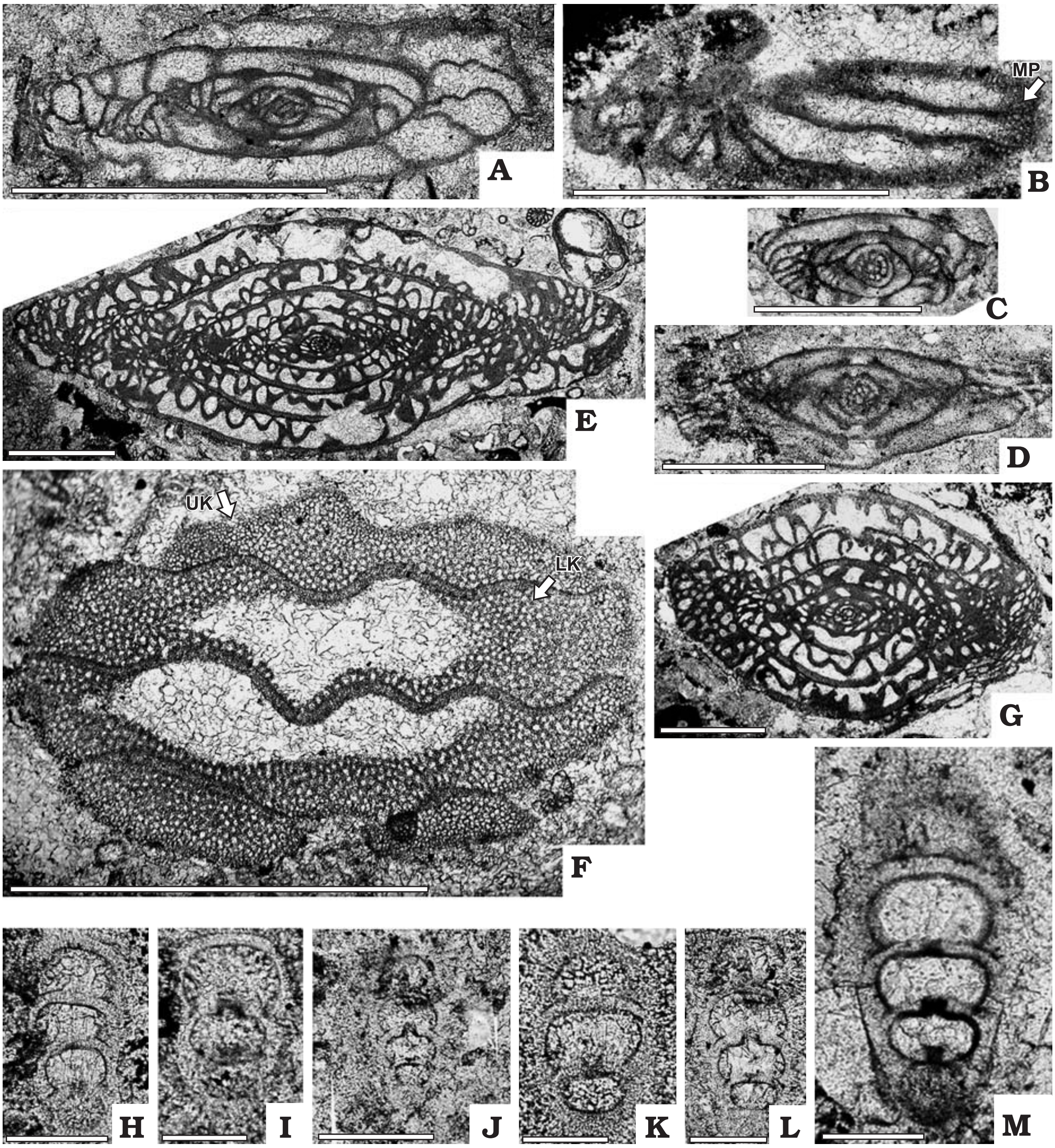


Fig. 5. The types of porosity in keriothecal and non-keriothecal wall. All specimens from Kalinovo section, P_2^2 Limestone, lower Gzhelian, Donets Basin, Ukraine. **A**. *Biwaella poletaevi* sp. nov., SUI 114245, axial section of paratype, sample A-3/31a-3. **B**. *Biwaella* sp., SUI 114246, oblique section, arrow points to coarse mural pores MP; the diameter of the pores is the same elsewhere within the wall; sample A-3/31a-86. **C**, **D**. *Schubertella subkingi* Putrja, 1939. **C**. SUI 114247, axial section, sample A-3/31a-9. **D**. SUI 114248, axial section, sample A-3/31a-73. **E**. *Darvasoschwagerina archaica* (Leven and Scherbovich, 1978), SUI 114249, axial section, sample A-3/31a-22. **F**. *Darvasoschwagerina* sp., SUI 114250, oblique section, arrows point to the two different types of pores: UK - fine pores in upper keriotheca, LK - coarse pores in lower keriotheca; sample A-3/31a-22. **G**. *Darvasoschwagerina satoi* (Ozawa, 1925), SUI 114251, axial section, sample A-3/31a-9. **H**–**M**. *Nodosinelloides* sp. **H**. SUI 114252, axial section, sample A-3/31a-16. **I**. SUI 114253, axial section, sample A-3/31a-84. **J**. SUI 114254, axial section, sample A-3/31a-4. **K**. SUI 114255, axial section, sample A-3/31a-5. **L**. SUI 114256, axial section, sample A-3/31a-5. **M**. SUI 114257, axial section, sample A-3/31a-104. Scale bars A, B, E, G 1 mm, C, D, F 0.5 mm, H–M 0.1 mm.

Type material: Holotype: SUI 114241 (Fig. 4E), axial section; paratypes: SUI 114238 (Fig. 4A), axial section; SUI 114239 (Fig. 4C), axial section; SUI 114240 (Fig. 4D), axial section; SUI 114242 (Fig. 4F), axial 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 P_2,*Darvasoschwagerina donbassica*–*Schagonella proimplexa* beds, early Gzhelian, Pennsylvanian.

Diagnosis.—Large elongate-subcylindrica test with rounded polar ends, nearly unifome coiling, wavy septae, poorly developed chomata that are often absent in the final volution.

doi:10.4202/app.2010.0026

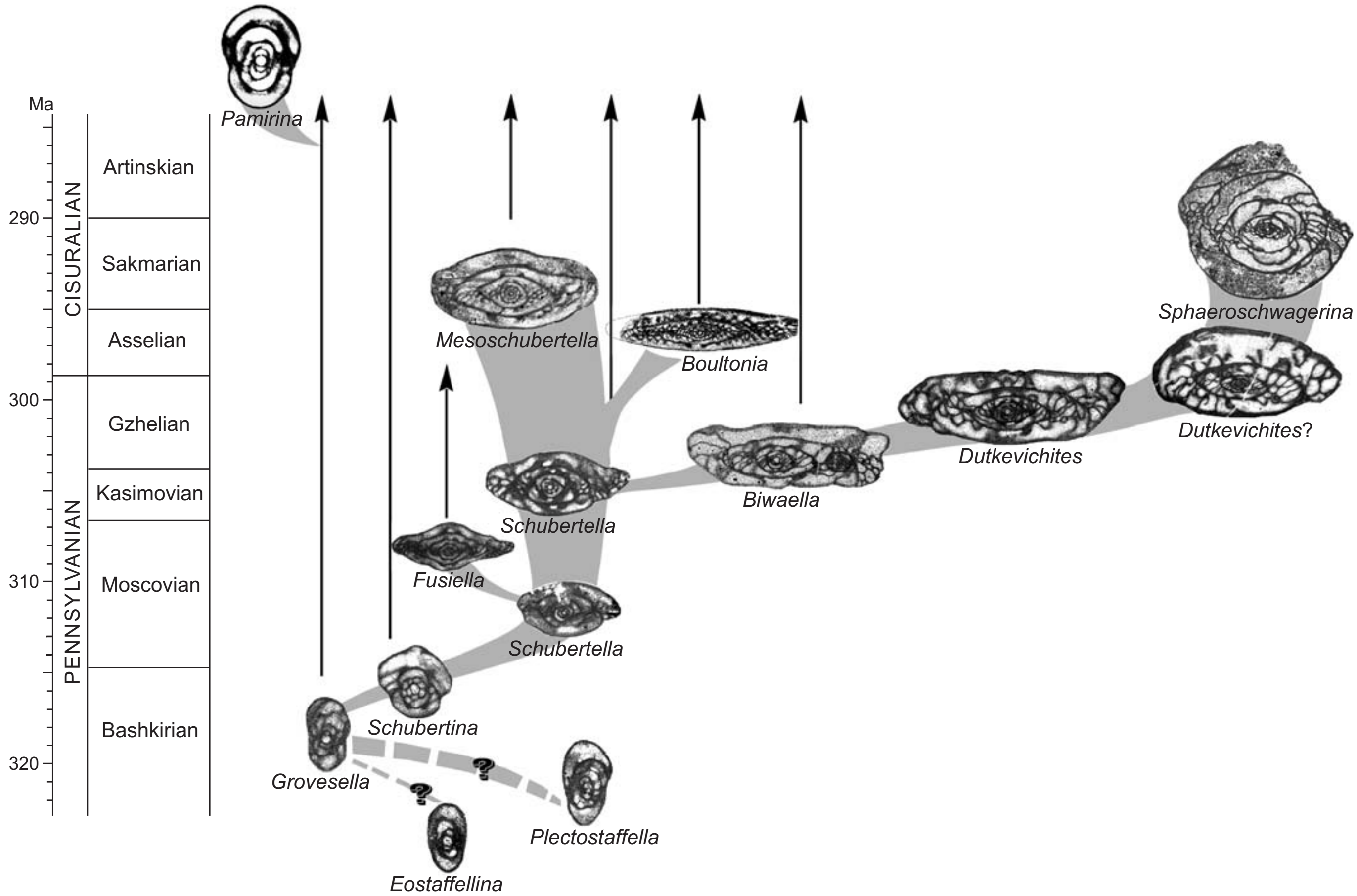


Fig. 6. Phylogenetic relationship of *Schubertella* and related genera.

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.

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 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.

Acknowledgements

Thanks to prompt help from Tiffany S. Adrain (Collections Manager from the University of Iowa Paleontology Repository, Keosauqua, USA) and Susan H. Butts (Collections Manager, Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University New Haven, CT, USA) the author was able to study and photograph the original collections of Marcus L. Thompson and Charles A. Ross from Spitsbergen and Arizona. I'm in debt to Calvin H. Stevens (San Jose University, California, USA) for his help in improving the taxonomy and English. Critical reviews of Daniel Vachard (UFR Sciences de la Terre, Université de Lille 1, France), Folger Forke (Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany), and Merlynd and Galina Nestell (both The University of Texas at Arlington, USA) significantly enhanced the paper. This study supported by NSF grants EAR-0545247 and EAR-0746107.

References

Baranova, D.V. and Kabanov, P.B. 2003. Facies distribution of fusulinoid genera in the Myachkovian (Upper Carboniferous, upper Moscovian) of southern Moscow region. *Rivista Italiana di Paleontologia e Stratigrafia* 109: 225–239.

Davydov, V.I. 1984. On the problem of origin of schwagerins [in Russian]. *Paleontologičeskij žurnal* 4: 3–16.

Davydov, V.I. [Davidov, V.I.] 1997. Fusulinid biostratigraphy of the Upper Paleozoic of the Kolguev Island and Franz Josef Land Archipelago [in Russian]. *In*: M.D. Belonin, A.I. Kiričkova, and G.E. Kozlova (ed.), *Biostratigrafiâ neftegazonosnyh basseinov. Trudy pervogo meždunarodnogo simpoziuma*, 40–59. VNIGRI, St. Petersburg.

Davydov, V.I. 2007. *Protriticites* foraminiferal fauna and its utilization in the Moscovian–Kasomovian boundary definition. *In*: T.E. Wong (ed.), *Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy, Utrecht, the Netherlands, 10–16 August 2003*, 456–466. Royal Netherlands Academy of Arts and Sciences, Amsterdam.

Davydov, V.I. 2009. Bashkirian-Moscovian transition in Donets Basin: the key for Tethyan-Boreal correlation. *In*: V.N. Puchkov (ed.), *The Carboniferous Type Sections in Russia, Potential and Proposed Stratotypes. Proceedings of the International Conference*, 188–192. Institute of Geology, Bashkirian Academy of Science, Ufa.

Davydov, V.I. and Arefifard, S. 2007. Permian fusulinid fauna of Gondwanan affinity from Kalmard Region, east-central iran and its significance for the tectonics and paleogeography. *Paleontologia Electronica* 2: 1–40. http://palaeo-electronica.org/2007_2/00124/index.html

Davydov, V.I. and Khodjanyazova, R. 2009. Moscovian-Kasimovian transition in Donets Basin: fusulinid taxonomy, biostratigraphy correlation and paleobiogeography. *In*: V.N. Puchkov (ed.), *The Carboniferous Type Sections in Russia, Potential and Proposed Stratotypes. Proceedings of the International Conference*, 193–196. Institute of Geology, Bashkirian Academy of Science, Ufa.

Davydov, V.I. and Krainer, K. 1999. Fusulinid assemblages and facies of the Bombaso Fm. and basal Meledis Fm. (Moscovian–Kasimovian) in the central Carnic Alps (Austria/Italy). *Facies* 40: 157–196. [CrossRef]

Davydov, V.I., Nilsson, I., and Stemmerik, L. 2001. Fusulinid zonation of the Upper Carboniferous Kap Jungersen and Foldedal Formations, southern Amdrup Land, eastern north Greenland. *Bulletin of the Geological Society of Denmark* 48: 31–77.

Fohrer, B., Nemyrovska, T.I., Samankassou, E., and Ueno, K. 2007. The Pennsylvanian (Moscovian) Izvarino section, Donets Basin, Ukraine; a multidisciplinary study on microfacies, biostratigraphy (conodonts, foraminifers, and ostracodes), and paleoecology. *Journal of Paleontology* 81 (Supplement 5): 1–85. [CrossRef]

Forke, H.C. 2002. Biostratigraphic subdivision and correlation of uppermost Carboniferous/Lower Permian sediments in the southern Alps; fusulinoidean and conodont faunas from the Carnic Alps (Austria/Italy), Karavanke Mountains (Slovenia), and Southern Urals (Russia). *Facies* 47: 201–275. [CrossRef]

Groves, J.R. 1986. Foraminiferal characterization of the Morrowan–Atokan (lower Middle Pennsylvanian) boundary. *Geological Society of America Bulletin* 97: 346–353. [CrossRef]

Groves, J.R. 1991. Fusulinacean biostratigraphy of the Marble Falls Limestone (Pennsylvanian), western Llano region, central Texas. *Journal of Foraminiferal Research* 21: 67–95.

Kanuma, M., and Sakagami, S. 1957. *Mesoschubertella*, a new Permian fusulinid genus from Japan. *Transactions and Proceedings of the Paleontological Society of Japan, New Series 26*: 41–46.

Kobayashi, F. 2006. Middle Permian foraminifers of the Izuru and Nabeyama Formations in the Kuzu area, central Japan; Part 2, Schubertellid and ozawainellid fusulinoideans, and non-fusulinoidean foraminifers. *Paleontological Research* 10: 61–77. [CrossRef]

Lee, J.S., Chen, S., and Chu, S. 1930. Huanglung Limestone and its Fauna. *Natural Research Institute of Geology Memories* 9: 90–136.

Leppig, U., Forke, H.C., Montenari, M., and Fohrer, B. 2005. A three- and two-dimensional documentation of structural elements in schwagerinids (superfamily Fusulinoidea) exemplified by silicified material from the Upper Carboniferous of the Carnic Alps (Austria/Italy): a comparison with verbeekinoideans and alveolinids. *Facies* 51: 559–571. [CrossRef]

Leven, E.Y. 1971. Les gisements permiens et les fusulinides de l'Afghanistan du Nord. The Permian beds and fusulinids of northern Afghanistan. *Notes et Memoires sur le Moyen-Orient* 12 (1):1–35.

Leven, E.J. 1995. Lower Permian fusulinids from the vicinity of Ankara (Turkey). *Rivista Italiana di Paleontologia e Stratigrafia* 101: 235–248.

Leven, E.Y. 1998a. Permian fusulinids assemblages and stratigraphy of the Transcaucasia, *Rivista Italiana di Paleontologia e Stratigrafia* 104: 299–328.

Leven, E.Y. 1998b. Stratigraphy and fusulinids of the Moscovian Stage (Middle Carboniferous) in the southwestern Darvaz (Pamir). *Rivista Italiana di Paleontologia e Stratigrafia* 104: 3–42.

Leven, E.Y. and Shcherbovich, S.F. [Ŝerbovič, S.F.] 1978. *Fuzulinidy i stratigrafiâ assel'skogo ârusa Darvaza*. 162 pp. Nauka, Moskva.

Loeblich, A.R. Jr. and Tappan, H. 1964. Sarcodina, chiefly "thecamoebians" and Foraminiferida. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology Part C, Protista 2. Vol. 1*, C1–C510; *Vol. 2*, C511–C900. The Geological Society of America and The University of Kansas, Boulder.

Loeblich, A.R. Jr., and Tappan, H. 1988. *Foraminiferal Genera and Their Classification*. 970 pp. Van Nostrand Reinhold, New York.

Manukalova-Grebenyuk, M.F. [Manukalova-Grebenûk, M.F.], Il'ina, M.T., and Serezhnikova, T.D. [Serežnikova, T.D.] 1969. Atlas of middle Carboniferous foraminifera of the Dnieper-Donets basin [in Russian]. *Ukrainskij Naučno-Issledovatel'skij Geologorazvedočnyj Institut, Trudy* 20: 1–287.

Marshall, F.C. 1969. Lower and Middle Pennsylvanian fusulinids from the Bird Spring Formation near Mountain Springs Pass, Clark County, Nevada. *Brigham Young University Geology Studies* 16: 97–154.

Miklukho-Maclay, A.D. [Mikluho-Maclay, A.D.], Rauser-Chernousova, D.M. [Rauser-Černousova, D.M.], and Rosovskaya, S.E. [Rosovskaâ, S.E.] 1959. *Fusulinida* order [in Russian]. *In*: A.V. Rauser-Černousova and A.V. Fursenko (eds.), *Osnovy Paleontologii, Prosteishie 1*, 201–215. Nauka, Moskva.

Morikawa, R. and Isomi, H. 1960. A new genus, *Biwaella*, *Schwagerina*-like *Schubertella*. *Science Reports of the Saitama University. Series B: Biology and Earth Sciences* 3: 301–305.

Nikolaev, A.I. 2005. Foraminifers and zonal stratigraphy of Bashkirian Stage in the east of Timan-Pechora province [in Russian]. *Bûlleten' paleontologičeskih kollekcyj VNIGRI* 2: 1–120.

Putrja, F.S. [Putriâ, F.S.] 1939. The materials on stratigraphy of the Upper Carboniferous of eastern part of Donets Basin [in Russian]. *In*: (anonymous editor), *Materialy po geologii i poleznym iskopaemym, Vol. 8*, 97–156. Azovo-Černomorskoe geologičeskoe upravlenie, Rostov.

Rauser-Chernousova, D.M. [Rauser-Černousova, D.M.] 1950. Facies of upper Carboniferous and Artinskian deposts of Sterlitamak-Ishimbai Preurals (based on fusulinids study) [in Russian]. *Trudy, Geologičeskij Institut, Akademiâ Nauk SSSR* 119 (43): 1–108.

Rauser-Chernousova, D.M. [Rauser-Černousova, D.M.] and Gerke, A.A. 1971. *Terminologičeskij spravochnik po stenkam rakovin foraminifer*. 192 pp. Nauka, Moskva.

Rauser-Chernousova, D.M. [Rauser-Černousova, D.M.], Gryslova, N.D., Kireeva, G.D., Leontovich, G.E. [Leontovič, G.E.], Safonova, T.P., and Chernova, E.I. [Černova, E.I.] 1951. *Srednekamennougol'nye fuzulinidy Russkoy Platformy i sopredel'nyh oblastej. Spravočnik-opredelitel'*. 380 pp. Geologičeskij Institut, Akademiâ Nauk SSSR, Izdatel'stvo Akademii Nauk SSSR, Moskva.

Rauser-Chernousova, D.M. [Rauser-Černousova, D.M.], Bensh, F.S. [Benš, F.S.], Vdovenko, M.V., Gibshman, N.B. [Gibšman, N.B.], Leven, E.Y., Lipina, O.A., Reitlinger, E.A., Solov'eva, M.N., and Chediya, I.O. [Chediâ, I.O.] 1996. *Spravočnik po sistematike foraminifer paleozoâ*. 204 pp. Nauka, Moskva.

Rosovskaya, S.E. [Rosovskaâ, S.E.] 1975. Composition, phylogeny and system of the order Fusulinida [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 149: 1–267.

Ross, C.A. 1965. Fusulinids from the Cyathophyllum limestone, central Vestpitsbergen. *Contributions from the Cushman Foundation for Foraminiferal Research* 16(2): 74–86.

Ross, C.A. and Sabins, F.F. Jr. 1965. Early and Middle Pennsylvanian fusulinids from southeast Arizona. *Journal of Paleontology* 39: 173–209.

Sinitsyna, Z.A. [Sinicyna, Z.A.] and Sinitsyn, I.I. [Sinicyn, I.I.] 1987. *Biostratigrafiâ baškirskogo ârusa v stratotipe*. 72 pp. Baškirskoe otdelenie Akademii Nauk SSR, Baškirsij Intitut geologii, Ufa.

Skinner, J.W. and Wilde, G.L. 1965. Lower Permian (Wolfcampian) fusulinids from the Big Hatchet Mountains, southwestern New Mexico. *Contributions from the Cushman Foundation for Foraminiferal Research* 16 (3): 95–104.

Skinner, J.W. and Wilde, G.L. 1966. Permian fusulinids from Sicily. *The University of Kansas Paleontological Contributions* 8: 1–16.

Smith, H.M. and Smith, R.B. 1973. Chresonymy ex synonymy. *Systematic Zoology* 21 (for 1972): 1–445.

Staff, H.V. and Wedekind, R. 1910. Der oberkarbonische Foraminiferen-Sapropelit Spitzbergens. The Upper Carboniferous foraminiferal sapropelite of Spitsbergen. *Bulletin-Uppsala Universitet, Mineralogisk-geologiska Institut* 10: 81–123.

Suleimanov, I.S. 1949. New fusulinid species of subfamily Schubertellinae Skinner from Carboniferous and Lower Permian deposits of Bashkirian Preurals [in Russian]. *In*: D.M. Rauser-Černousova (ed.), Novye vidy fuzulinid podsemeistva Schubertellinae Skinner iz kamennougol'nyh i nižnepermskih otloženij Baškirskogo Priural'â. *Trudy Instituta Geologičeskih Nauk, Geologičeskaâ Seriâ* 105 (35): 22–43.

Teodorovich, G.I. [Teodorovič, G.I.] 1949. The carbonate facies of upper Carboniferous–lower Permian of the Uralo-Volga area [in Russian]. *Materialy k poznaniu geologičeskogo stroeniâ SSSR. Novaâ seriâ* 13 (17): 1–304.

Thompson, M.L. 1937. Fusulinids of the subfamily Schubertellinae. *Journal of Paleontology* 11: 118–125.

Thompson, M.L. 1948. *Studies of American Fusulinids*. 184 pp. University of Kansas, Topeka.

Thompson, M.L. 1964. Fusulinacea. *In*: A.R. Jr. Loeblich and H. Tappan (eds.), *Treatise on Invertebrate Paleontology; Part C, Protista 2, Sarcodina, Chiefly 'Thecamoebians' and Foraminiferida*, C358–C436. Geological Society of America and University of Kansas Press, New York.

Ueno, K. 1991. Early evolution of the families Verbeekinidae and Neoschwagerinidae (Permian Fusulinacea) in the Akiyoshi Limestone Group, Southwest Japan. *Transactions and Proceedings of the Palaeontological Society of Japan. New Series* 164: 973–1002.

Ueno, K. 1996. *Mesoschubertella* (Permian Fusulinacea) from the Akiyoshi Limestone Group, Southwest Japan. *Bulletin of the Akiyoshi-Dai Museum of Natural History = Akiyoshidai Kagaku Hakubutsukan Hokoku* 31: 21–31.

Vachard, D., Lemus, M.V., Fourcade, E., and Requena, J. 2000. New Early Permian fusulinid assemblage from Guatemala. *Compte Rendus de l'Académie des Sciences de Paris* 331: 789–798.