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Demarcation problem in fusuline classification: A case for *Verella/Eofusulina* discrimination

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ABSTRACT

The eofusulinin genera *Verella* and *Eofusulina* formed an important lineage among fusulines to define the Bashkirian/Moscovian transitional interval in the Pennsylvanian (Upper Carboniferous) subsystem. We studied morphologies of *Verella transiens*, a highly evolved form in the genus, and the first *Eofusulina* species from the Los Tornos section in the Cantabrian Zone of northern Spain, to understand the discriminating diagnosis of these two genera. We conclude that *Eofusulina* is distinguishable from *Verella* in having stronger septal fluting, lesser development of secondary deposits, generally larger proloculus, absence of early tightly coiled volutions, and with some lesser extent slightly larger diameter of shell and absence of polar torsion. No single morphological character provides a reliable criterion to distinguish the two genera, but rather only a combination of all these morphological criteria enables reliable generic discrimination. In order to better understand the morphology, we emphasise the usefulness of non-oriented specimens in this study. They have potential to show some morphological features that are sometimes not easy to perceive based only on well-oriented axial and sagittal sections. In regional biostratigraphic aspects, we propose a minor modification on the FAD of *Eofusulina* in the Los Tornos section, and

RESUMEN

La evolución de *Verella* hacia *Eofusulina* presenta un gran interés para caracterizar paleontológicamente el intervalo de transición entre los pisos Bashkiriense y Moscoviense (Pensilvánico/Carbonífero superior). En este trabajo hemos estudiado detalladamente la morfología de *Verella transiens*, especie avanzada de este género, en ejemplares procedentes de la sección de Los Tornos (Zona Cantábrica, norte de España). El objetivo ha sido fijar con claridad los criterios de separación entre *Verella* y *Eofusulina*, concluyendo que *Eofusulina* se puede distinguir de *Verella* por presentar plegamiento septal más intenso, menor desarrollo de los depósitos secundarios, prolóculo generalmente de mayor talla, ausencia de arrollamiento apretado en las vueltas iniciales, y, en menor grado, diámetro de la concha ligeramente mayor y ausencia de torsión polar. Ninguno de estos criterios es suficiente por sí mismo para distinguir estos dos géneros, sino que una identificación fiable ha de basarse en la combinación de los anteriormente expuestos y, en este sentido, destacamos la gran utilidad que pueden presentar las secciones no perfectamente axiales, ya que muestran rasgos que, con frecuencia, pasan desapercibidos en las secciones axiales y sagitales. Con respecto a la bioestratigrafía de la sección de Los Tornos, señalamos la primera aparición de *Eofusulina*

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lower it about 5 m stratigraphically. We also perform a comprehensive taxonomic review of *Verella* and *Eofusulina*. Two replacement names, *Verella zhenanensis* and *V. ivanovae*, are proposed for *Pseudowedekindellina fusiformis* Sun and *V. fusiformis* Ivanova, which are subjective and objective junior synonyms of *V. fusiformis* Bensh, respectively. Moreover, we deem *V. varsanofievae* as a correct original spelling of the type species of *Verella*, in accordance with the International Code of Zoological Nomenclature.

Keywords: Carboniferous, Pennsylvanian, fusuline morphology, thin section, taxonomy.

unos 5 m por debajo del nivel que se había indicado en trabajos anteriores. También hemos realizado una revisión de la taxonomía de estos dos géneros, proponiendo los nombres *Verella zhenanensis* y *V. ivanovae* para las especies descritas originalmente como *Pseudowedekindellina fusiformis* Sun y *V. fusiformis* Ivanova, ya que ambas deben ser consideradas como sinónimos de *Verella fusiformis* Bensh. Finalmente, de acuerdo con los requisitos establecidos en el Código de Nomenclatura Zoológica, se propone *V. varsanofievae* como nombre correcto de la especie tipo del género.

Palabras clave: Carbonífero, Pensilvánico, morfología de fusulinas, lámina delgada, taxonomía.

1. INTRODUCTION

Fusulines are the first group of larger foraminifera to appear in the history of foraminiferal evolution (e.g., BouDagher-Fadel, 2008). They constructed many chambers through growth, which are systematically arranged in an enrolling manner around the constant axis of coiling. Because of their innate large test size, commonly several millimetres in length but sometimes up to a few centimetres, planispiral chamber arrangement, and more complicated internal shell structures compared to rather simple outer morphologies, as well as their exclusive occurrence from consolidated limestones, fusulines are usually studied with thin-sectioned specimens under the microscope. For better taxonomic investigation and identification, it is especially important to prepare oriented specimens, such as axial and sagittal (cross) sections, which are cut through the first chamber (proloculus) in parallel or perpendicular to the axis of coiling (Dunbar & Henbest, 1942). In making fusuline thin sections, tangential and parallel sections (which cut shells in parallel or perpendicular to the axis of coiling but do not pass through the proloculus) are considered to have relatively minor importance, and oblique sections which cut fusuline shells randomly are even less valuable.

Thin-section study of fusulines, based especially on abundant axial and sagittal sections, provides a firm basis to clarify internal shell morphologies and their ontogenetic changes through growth (Dunbar & Henbest, 1942; Miklukho-Maklay *et al*., 1959). Accordingly, fusuline micropalaeontologists usually pay more attention to study such well-oriented specimens and tend to illustrate them more in their publications. However, some three-dimensional morphological characters can be difficult to understand when studying only oriented specimens. The nature and intensity of septal fluting is one such character that the study of non-oriented specimens has provided a broader understanding.

Moreover, a number of morphological characters often change continuously in varied degrees not only within the same species (e.g., Ozawa, 1975) but also between two phylogenetically consecutive taxa (e.g., Davydov, 1990). Such phyletic gradualism has been documented in various clades in fusuline foraminifera (e.g., Ozawa, 1970; Davydov, 1988; Groves, 2005), and it can make the discrimination of closely-related species quite difficult.

The two early fusuline genera *Verella* and *Eofusulina* appeared around the Bashkirian/Moscovian boundary interval. They both have elongate to highly elongate fusiform shells (Fig. 1) which are distinctive among fusuline genera seen in this interval, and formed a single evolutionary continuum (Miklukho-Maklay *et al*., 1959; Leven, 1979; Ivanova, 2008). Because of these morphological, phylogenetic, and biostratigraphic peculiarities, the *Verella*-*Eofusulina* transition is considered to be a potential marker that can assist in the recognition of the Bashkirian/Moscovian boundary in the Pennsylvanian (Upper Carboniferous) subsystem (Ivanova, 2008, 2015a; Groves & Task Group, 2011). It is considered that these two genera differ mainly in the degree of septal fluting. Septal fluting in *Verella* usually is weak and restricted to the poles and lateral slopes, whereas in *Eofusulina* septal fluting is stronger and extends across the entire length of the test (Groves & Task Group, 2011). In addition to the difference in the intensity of septal fluting, *Eofusulina* generally has a larger shell with a larger proloculus and lesser-developed secondary deposits than *Verella*. Because these characters changed gradually in the course of phylogenetic evolution in the *Verella*-*Eofusulina* lineage, it is known to occur transitional forms, such as *V. transiens* van Ginkel & Villa *in* van Ginkel (1987) from the Cantabrian Zone of Northern Spain, which possess shell characters intermediate between *Verella* and *Eofusulina*. This makes morphological distinction of these two genera somewhat controversial in some cases.

The Los Tornos section in the Cantabrian Zone of northern Spain was recently reported by Villa & Merino-

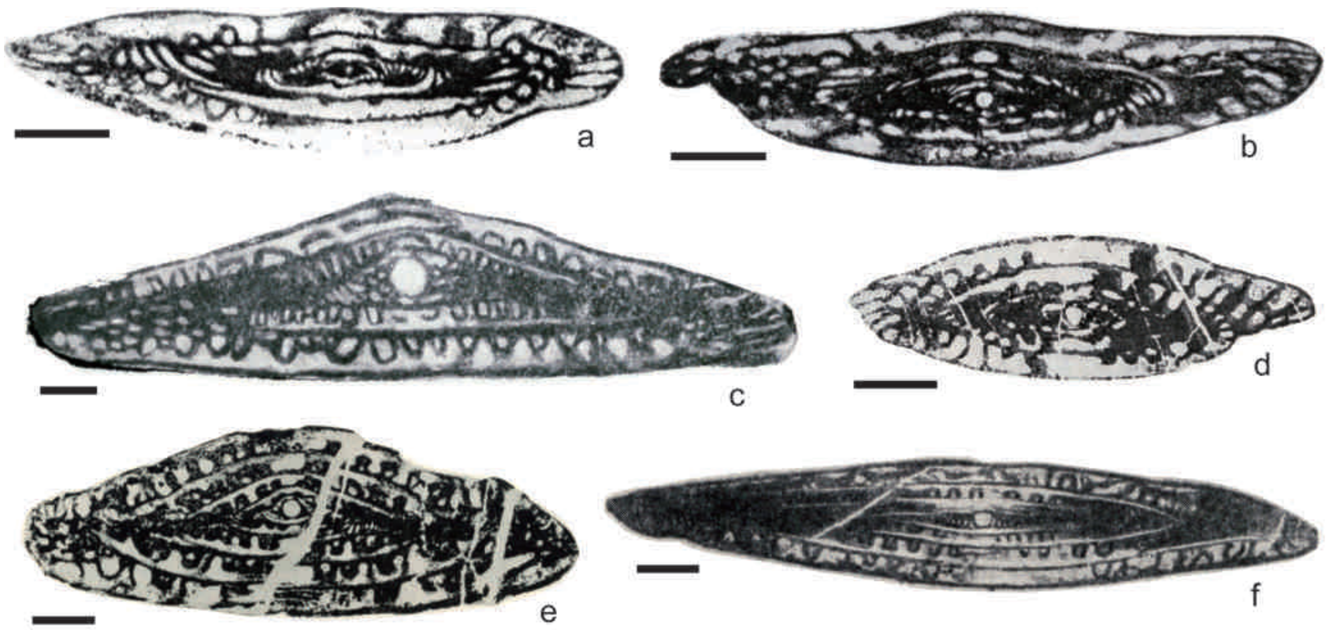


Figure 1. Type species of *Verella* and *Eofusulina*, and their synonymous genera. **a)** *Verella varsanofievae* Dalmatskaya, 1951 (specific name originally spelled as *warsanofievie*; see text for details), the type species of *Verella* Dalmatskaya, 1951. **b)** *Pseudowedekindellina prolixa* Sheng, 1958, the type species of *Pseudowedekindellina* Sheng, 1958 (= *Verella*). **c)** *Fusulina triangula* Rauzer-Chernousova & Beljaev *in* Rauzer-Chernousova *et al*., 1936, the type species of *Eofusulina* Rauzer-Chernousova *in* Rauzer-Chernousova *et al*., 1951. **d)** *Akiyoshiella ozawai* Toriyama, 1953, the type species of *Akiyoshiella* Toriyama, 1953 (= *Eofusulina*). **e)** *Eofusulina figurata* Ivanova *in* Chuvashov & Ivanova, 1980, the type species of *Postverella* Ivanova, 2008 (= *Eofusulina*). **f)** *Eofusulina* (*Paraeofusulina*) *trianguliformis* Putrja, 1956, the type species of *Eofusulina* (*Paraeofusulina*) Putrja, 1956. All scale bars equal to 0.5 mm.

Tomé (2016) as showing a good and relatively continuous fusuline record across the Bashkirian/Moscovian boundary. Importantly, the section has both occurrences of advanced *Verella*, *V. transiens*, and the early *Eofusulina* at several levels (Villa & Merino-Tomé, 2016, fig. 5), so it is promising to investigate the problem on how to put the morphological boundary between these two genera. These authors presented a number of good axial-sectioned fusuline specimens around the boundary interval. With respect to *V. transiens*, however, they did not show specimens from its last few occurrences.

In this study, we reexamined materials from the Los Tornos section used in Villa & Merino-Tomé (2016), in order to make clear morphological differentiation between the genera *Verella* and *Eofusulina*. Our investigation revealed that randomly oriented specimens, which are usually considered less important for fusuline taxonomy, can be utilised for understanding some key morphological features of these genera. Moreover in the last part of this article, we make a taxonomic review of *Verella* and *Eofusulina*, in consideration of the present state that quite few papers made taxonomic overview of these genera. All the illustrated specimens from the Los Tornos section are deposited in the micropalaeontological collection of the Departamento de Geología, Universidad de Oviedo, Spain.

2. STRATIGRAPHY AND STUDY MATERIALS

The study materials were originally prepared for a study of the Los Tornos section by Villa & Merino-Tomé (2016). The geological background of the section and the details of stratigraphy and fusuline faunal succession are described in that paper. We briefly summarise some important geological outlines of the section below.

The Los Tornos section is situated at about 30 km southeast of Oviedo, in the Central Asturian Coalfield, northern Spain (Fig. 2a). Geologically it is in the middle of the Bodón-Ponga Unit in the central part of the Cantabrian Zone (Alonso *et al*., 2009). The section is about 850 m thick, and consists of the Fresnedo, Levinco, and Llanón units in ascending order (Fig. 2b), which represent informal (local) stratal packages conventionally used for coal-mining industry. In this section, there are nine limestone intervals, including the 50-m-thick Peña Redonda Limestone at the base of the Levinco unit. The Los Tornos section consists entirely of marine siliciclastics, marls, and limestones, and represents cyclic sedimentation showing distinctive transgressive-regressive cycles (cyclothem). There are several levels of subaerial exposures with the occurrence of paleosols, which correspond to recognizable hiatuses.

The samples examined in this study came from the second, third, fifth, sixth, and seventh limestone intervals from the base of the section (Fig. 2b).

3. OBSERVATIONS

We examined thin sections from totally 13 samples (LT25, LT-26, LT-27, LT-28, LT-29, LT33, LT36, LT42, LT44, LT-45, LT-47, LT-49, and LT-51; Fig. 2b), which contain eofusulinin species with elongate to highly elongate fusiform shells. Of them, Villa & Merino-Tomé (2016) illustrated axial sections of *Verella transien*s from LT-26, LT-27, and LT-29, and those of *Eofusulina* sp. from LT-45, LT-49, and LT-51. In this study, we also paid special attention to observe non-oriented specimens in order to understand the entire morphological features of these species.

3.1. Samples LT-25 to LT-29

These five samples were collected in the second limestone interval from the base of the section (Fig. 2b). All the *Verella transiens* specimens illustrated by Villa & Merino-Tomé (2016) are from this limestone member (samples LT-26, LT-27, and LT-29), where they were associated with species of *Profusulinella* and *Aljutovella*. As they described, those specimens have very elongate fusiform shells with bluntly pointed polar ends, and broadly arched central part. Chomata are present from the first to penultimate or the last volutions, and supplementary deposits are well recognised especially in the axial regions, but do not fill the entire chambers. They have moderate-sized proloculus (90-170 µm in outside diameter). Septa are unfluted in the early volutions, and are moderately but not very regularly fluted in the outer ones. All these features well fit with the diagnosis of *V. transiens* originally reported by van Ginkel (1987) from the Lena Formation near Puebla de Lillo, about 30 km to the southeast of Los Tornos, in the same Bodón-Ponga Unit in the central part of the Cantabrian Zone.

We supplement here further observations with additional illustrations from these sample levels. In two sagittal sections (Figs 3g, 3j), a relatively small proloculus is followed by one and a half to two, slightly tightly coiled early volutions, which make an indistinct juvenarium. A similar feature is also seen in some axial sections illustrated by Villa & Merino-Tomé (2016). Six tangential sections (Figs 3a-3d, 3h-3i), which cut variously distant positions from the proloculus, demonstrate the degree of septal fluting and the approximate positions where septa are fluted. Some of these specimens show that septa are moderately fluted along lateral slopes, forming incipient septal chamberlets (Figs 3b-3c), but septal loops are semicircular and only as high as half the chamber height (e.g., Figs 3b, 3d, 3h-i). Two other specimens (Figs 3a, 3e) exhibit septa that are unfluted at the polar end of the shells. Moreover, they clearly show polar torsion in the very end of the polar region.

In two sagittal sections (Figs 3g, 3j), we can observe that septa are numerous (number of septa counted to be 32 in the fifth volution in the specimen illustrated on Figure 3j) and they are rather narrowly spaced in this species. Judging from the presence of well-developed secondary deposits of chomata at the base of volutions, the specimens on Figures 3f and 3k are parallel sections that probably cut around the position of the one-third from the proloculus to the axial end, almost perpendicularly to the coiling axis. In these sections, septa are very narrowly spaced and often weakly bending anteriorly (and sometimes posteriorly) at the lower part of the volutions, but a peak and a trough of two adjacent fluted septa seldom join each other, forming a peculiar “V-shaped” connection (compare these specimens to that illustrated on Figure 3v obtained from a much higher level in the sixth limestone interval, which develops a greater number of these “V-shaped” features, suggesting a stronger degree of septal fluting).

3.2. Sample LT-33

This level corresponds to the upper part of the limestone interval from which samples LT-25 to LT-29 were collected (Fig. 2b). In this sample, Villa & Merino-Tomé (2016) reported the occurrence of *Verella transiens*, but did not illustrate any specimens. Only one, probably immature tangential section, showing well-developed axial fillings, is available from this sample (Fig. 3l). It has weakly fluted septa on the lateral slopes and plane septa at the very end of the polar region, in probably the third (or third and a half?) volution. This specimen is very similar to that illustrated on Fig. 3h from sample LT-29.

3.3. Sample LT-36

Villa & Merino-Tomé (2016) also cited the occurrence of *Verella transiens* without illustration from this level, in the lower part of the third limestone interval from the base of the Los Tornos section (Fig. 2b). One tangential section is examined in the present study (Fig. 3m). Though poorly oriented, this specimen has somewhat similar features as those illustrated on Figures 3d and 3i from samples LT-26 and LT27, in having a very elongate shell, dense axial fillings in the polar region, plane septa in the central part of the early volutions, and weakly fluted septa on the lateral slopes.

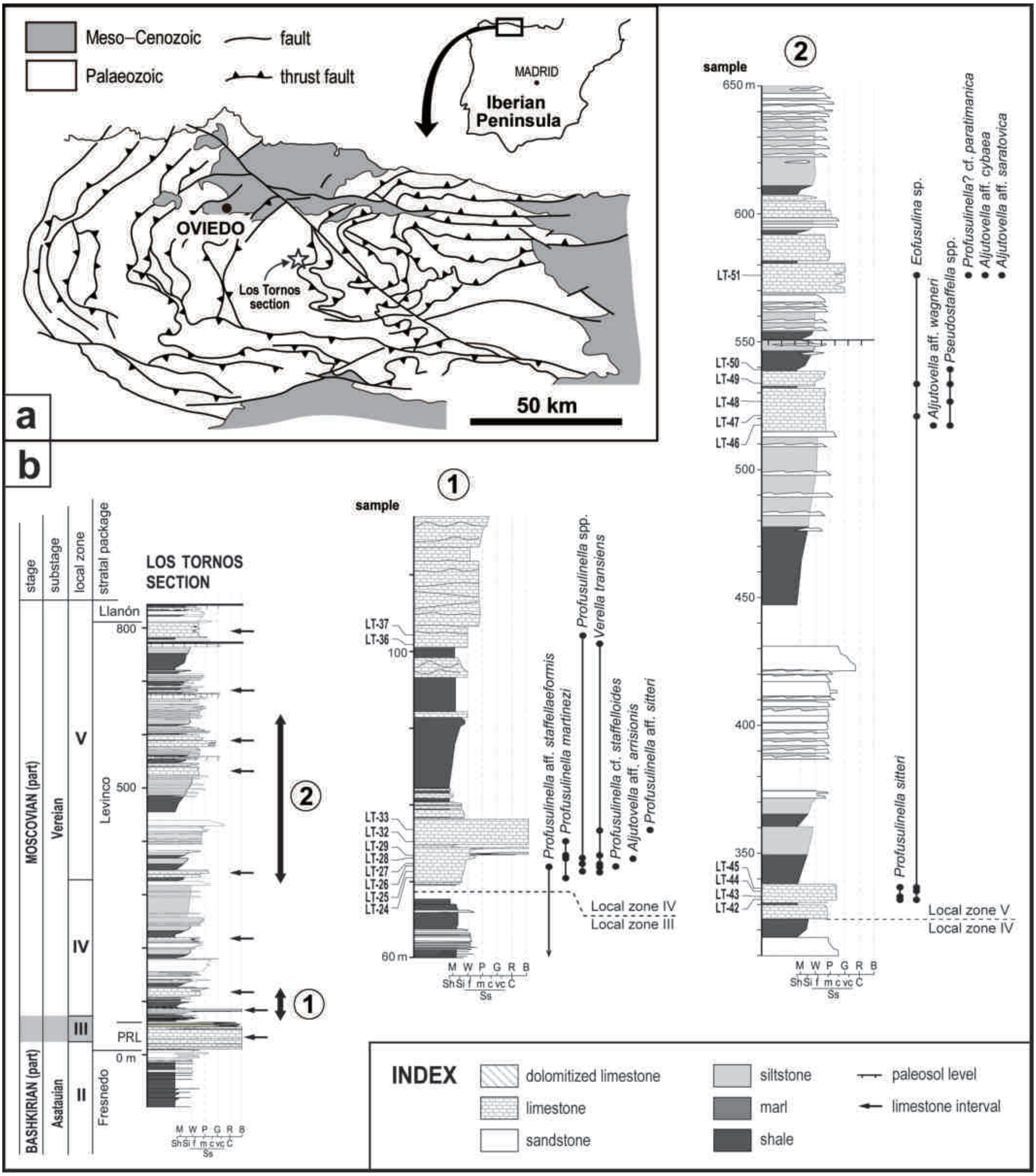
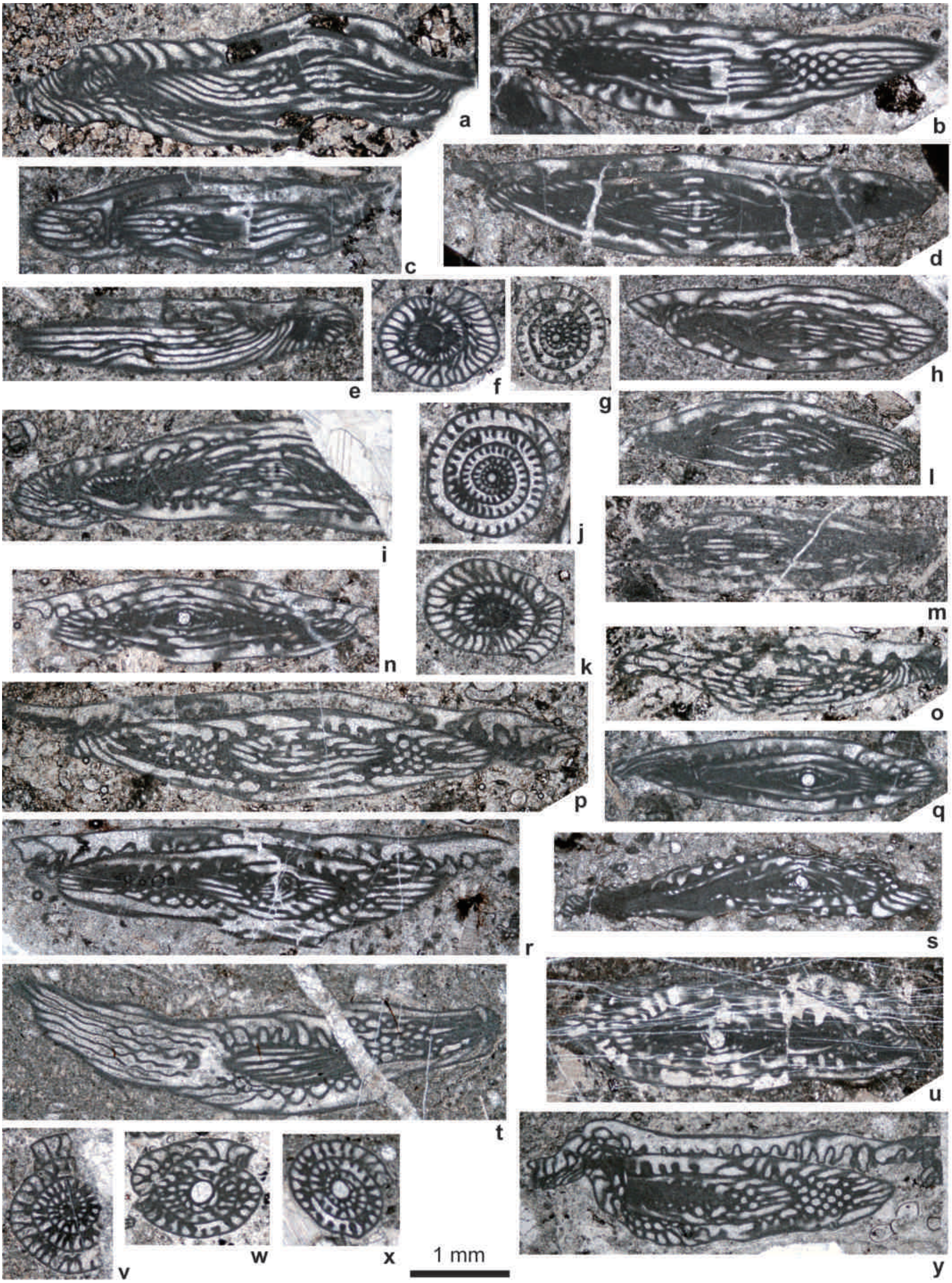


Figure 2. Index map and stratigraphic logs of the Los Tornos section. **a)** Structural sketch and the distribution of Paleozoic strata in the Cantabrian Zone of northern Spain, with the location of the Los Tornos section (star mark). **b)** Stratigraphy, major fusuline occurrences, and sample levels of the Los Tornos section, with the subdivision of local biostratigraphic zones and their correlation (adapted from Villa & Merino-Tomé, 2016). PRL: Peña Redonda Limestone. Some occurrences of *Verella transiens* and *Eofusulina* sp. are modified from the original, following the observation of this study, and accordingly the boundary between local zones IV and V is slightly lowered. Shaded band (corresponding to local zone III) represents the Bashkirian/Moscovian transitional interval (see Villa & Merino-Tomé, 2016 for further details). Subdivision of limestone microfacies and scale for grain size; M: lime mudstone; W: wackestone; P: packstone; G: grainstone; R: rudstone; B: boundstone; Sh: shale; Si: siltstone; Ss: sandstone (f: fine; m: medium; c: coarse; vc: very coarse); C: conglomerate.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3.4. Samples LT-42 and LT-44

These two samples came from the upper part of the fifth limestone interval from the base of the section. They correspond to at 330-340 m levels from the base of the section, and about 240 m stratigraphically higher than the last, lower, *Verella*-bearing sample (LT-36; Fig. 2b). In the present two levels, the occurrence of *Verella transiens* was documented by Villa & Merino-Tomé (2016) but specimens were not illustrated.

In fact, two, probably non-full-matured specimens (Figs 3n, 3q) are reminiscent of axial sections of *V. transiens*, except for the weaker development of chomata and slightly more intense septal fluting in the former. But other associated eofusulinin specimens in these samples (Figs 3o-3p, 3r-3s) clearly demonstrate stronger septal fluting, especially in the lateral slopes and polar regions, sometimes forming high and narrow (and occasionally irregular) septal loops. In tangential sections, septal chamberlets made by the connection of neighbouring peaks and troughs out of phase are well exhibited (Fig. 3p). Thus overall, it can be said that septa become more intensely fluted in these specimens compared to those of eofusulinines from the second and third limestone intervals. Moreover, these specimens have less developed secondary deposits, shown as axial fillings and chomata, compared to eofusulinin (*V. transien*s) specimens in lower sample levels (see also Villa & Merino-Tomé, 2016, fig. 14 for comparison).

3.5. Sample LT-45

This is the level of the first *Eofusulina* species by Villa & Merino-Tomé (2016), from which one axial section was illustrated (Villa & Merino-Tomé, 2016, fig. 14.11). It is also in the same fifth limestone interval from which samples LT-42 and LT44 were collected (Fig. 2b). One additional axial section is examined in this study (Fig. 3u). Both axial-sectioned specimens have four and a half volutions and large proloculi (200 and 220 µm in outside diameter, respectively), and expand regularly from the first volution, lacking a tightly coiled inner part. They are characterised by relatively regularly and strongly fluted septa and weaker axial fillings.

3.6. Samples LT-47 to LT-51

These samples were collected from the sixth and seventh limestone intervals from the base of the section, which are closely situated to each other stratigraphically but separated by a distinct paleosol horizon (Fig. 2b). Villa & Merino-Tomé (2016) reported *Eofusulina* from LT-47, LT-49, and LT51, from which two axial sections were illustrated from the latter two sample levels. Here we additionally illustrate two tangential (Figs 3t, 3y), two sagittal (Figs 3w, 3x), and one parallel (Fig. 3v) sections. The tangential sections clearly possess stronger septal fluting, which extends to the lateral slope and the middle part of shell, with the septa forming high and narrow septal loops. In the parallel section, the "V-shaped" (or "Y-shaped" when septal fluting is stronger) connection of two successive septa are more often observed compared to *Verella transiens* from the second limestone interval, suggesting that the specimens from the sixth and seventh limestone intervals have definitely stronger septal fluting. Sagittal-sectioned specimens have large proloculi (220 and 250 µm in outside diameter), followed by regularly expanding volutions, and do not show juvenile tight coiling that can be seen in *V. transiens* (Figs 3g, 3j; and see also specimens illustrated on fig. 14 in Villa & Merino-Tomé, 2016).

4. DISCUSSION AND CONCLUDING REMARKS

The above-mentioned observations with respect to the *Verella-Eofusulina* lineage from the Los Tornos section indicate that, as Villa & Merino-Tomé (2016) concluded, the eofusulinin specimens from the second limestone interval of the section (samples LT-25 to LT-29) are assignable to *Verella transiens*, which is considered as a highly evolved member of the genus *Verella* (van Ginkel, 1987). This interval denotes the basal part of the local zone IV (Villa & Merino-Tomé, 2016) (Fig. 2b). Although they are poorly oriented, two tangential sections obtained from overlying levels (samples LT-33 and LT-36) in the same and next adjacent limestone intervals, examined in this study are also highly probably included in the

Figure 3. Eofusulinin specimens from the Los Tornos section of northern Spain (materials used in Villa & Merino-Tomé, 2016, but not illustrated in that paper). **(a-m)** *Verella transiens* van Ginkel & Villa *in* van Ginkel, 1987. **(a, g, k)** Specimens from sample LT-25: **a)** tangential section; **g)** sagittal section; **k)** parallel section. **(b-d, j)** Specimens from LT-26: **b-d)** tangential sections; **j)** sagittal section. **(e-f, i)** Specimens from sample LT-27: **e)** oblique section; **f)** parallel section; **i)** tangential section. **h)** Specimen from sample LT-29 (tangential section). **l)** Specimen from sample LT-33 (tangential section). **m)** Specimen from sample LT-36 (tangential section). **(n-y)** *Eofusulina* sp. **n-p)** Specimens from sample LT-42: **n)** axial section, **o-p)** tangential sections. **(q-s)** specimens from sample LT-44: **q, s)** axial sections; **r)** tangential section. **t)** Specimen from LT-49 (tangential section). **u)** Specimen from sample LT-45 (axial section). **(v, x-y)** specimens from sample LT-47: **v)** parallel section; **x)** sagittal section; **y)** tangential section. **w)** Specimen from sample LT-51 (sagittal section).

same species (Fig. 2b). All these specimens suggest that septa in *V. transiens* are moderately fluted along lateral slopes (e.g., Figs 3d, 3h, 3i) but become unfluted toward both the median part of shell and polar ends (Figs 3a-d). Important to note is the intensity of septal fluting in the lateral slope areas. They form semicircular septal loops but in parallel sections, two adjacent septa seldom contact each other to form the "V-shaped" connection described earlier, even though their space is very narrow (Figs 3f, 3k). This species makes septal chamberlets in the lateral slope parts (Figs 3b-3c), but their nature is still incipient. These are good lines of evidence that the septa of *V. transiens* are indeed fluted but are not very intense, which would be described as "moderately fluted" at the most. Moreover, some random-sectioned specimens exhibit polar torsion at the axial ends (Figs 3a, 3e). Other morphological features to note are the relatively heavy development of the secondary deposits. In *V. transiens*, chomata are well discernible through growth, and axial fillings are relatively heavy (Villa & Merino-Tomé, 2016). This species also exhibits slight tight coiling in the early one or two volutions, forming an indistinct juvenarium with relatively small to moderate proloculus (Figs 3g, 3j).

Higher up the section, separated by an about 240-m-thick siliciclastic-dominant interval from the sample level LT-36, two samples (LT-42 and LT-44) in the fifth limestone interval of the Los Tornos section were originally placed at the top of the local zone IV, which is defined by the occurrence of *Profusulinella rhomboides* group, several typical Vereian *Aljutovella* species, and *Verella transiens* (Villa & Merino-Tomé, 2016). Eofusulinine specimens available from these two samples yielded axial sections of immature individuals (Figs 3n, 3q, 3s), which are reminiscent of *Verella transiens* that lacks outermost one volution, by their very elongate fusiform shells. Moreover, they have slightly tightly coiled early volutions. But they show more intense septal fluting and less developed chomata, compared to the typical specimens of *V. transiens* from the second limestone interval. Additionally, some tangential-sectioned specimens (Figs 3p, 3r) from samples LT-42 and LT-44 show definitely stronger septal fluting than those of *V. transiens*, in forming distinct septal chamberlets in the axial parts and high and narrow septal loops in the lateral slopes. Thus, they can be related to *Eofusulina* rather than *Verella*, which more typically occurs from the next higher sample LT-45, and further higher limestone intervals of the Los Tornos section (Fig. 2b). Based on these morphological features, especially on the nature of stronger septal fluting, we judge that sample LT-42 is the first appearance datum (FAD) of *Eofusulina* in the Los Tornos section (Figs 2, 4).

Of eofusulinines in higher levels (samples LT-45 to LT-51), septal fluting becomes stronger and extends nearly over the entire shell except the central part of it; the proloculus becomes larger; and secondary deposits (chomata and axial fillings) become less developed. Moreover, there is no polar torsion and no early slightly tightly coiled volutions seen in *Eofusulina* sp. from the fifth to seventh limestone intervals (samples LT-42 to LT-51), which are observed in *Verella transiens*. Thus, specimens from samples LT-45 to LT-51 are clearly assignable to the genus *Eofusulina*, as Villa & Merino-Tomé (2016) considered.

In the unerlying part of the Los Tornos section, *Verella* cf. *normalis* Rumyantseva, 1962 was reported from the upper part of the first limestone interval (the Peña Redonda Limestone in the basal part of the Levinco stratal package). This species is a typical, moderately evolved *Verella*, especially in its weaker septal fluting. Moreover, elsewhere in the Central Asturian Coalfield further ancestral *Eowedekindellina* species (*E. solovievae* Villa *in* Villa & Merino-Tomé, 2016 and *E.* sp.) were reported from lower stratigraphic levels (in the local zones II and III) of the Santo Firme section located to the north of Oviedo (Villa & Merino-Tomé, 2016). These species, together with *Verella transiens* and *Eofusulina* sp., are considered to form a single phylogenetic lineage in the Cantabrian Zone during late Bashkirian-early Moscovian time (Fig. 4).

We conclude that *Verella* and *Eofusulina* can be distinguished by the following features: 1) stronger septal fluting in *Eofusulina*, 2) lesser development of chomata in *Eofusulina*, 3) generally stronger axial fillings in *Verella*, 4) generally larger proloculus in *Eofusulina*, and 5) absence of inner tightly coiled volutions in *Eofusulina*. To the lesser extent, *Eofusulina* may have a slightly larger shell diameter and lacks polar torsion. No single character among these features, however, alone can be the conclusive diagnosis to distinguish these two genera, although as noted above, the degree and nature of septal fluting are important for identifying *Eofusulina*. The combination of all these morphological criteria substantially produces more reliable and stable identification of these genera. As a contribution to regional biostratigraphic aspects, this study slightly modified the result of Villa & Merino-Tomé (2016) with respect to the first occurrence of *Eofusulina* in the Los Tornos section, and lowered it about 5 m stratigraphically, in the same fifth limestone interval of the section (compare fig. 6 in Villa & Merino-Tomé (2016) and Fig. 4 in this study). More importantly, we have demonstrated the practical usefulness of tangential, parallel, and oblique sections, which usually are not paid much attention and thus are not illustrated often in the studies of fusuline taxonomy and classification. In some cases, these sections give us clues to understand morphological features that sometimes are not easily perceived based only on well-oriented axial and sagittal sections, such as the intensity (degree) of septal fluting and the presence of polar torsion.

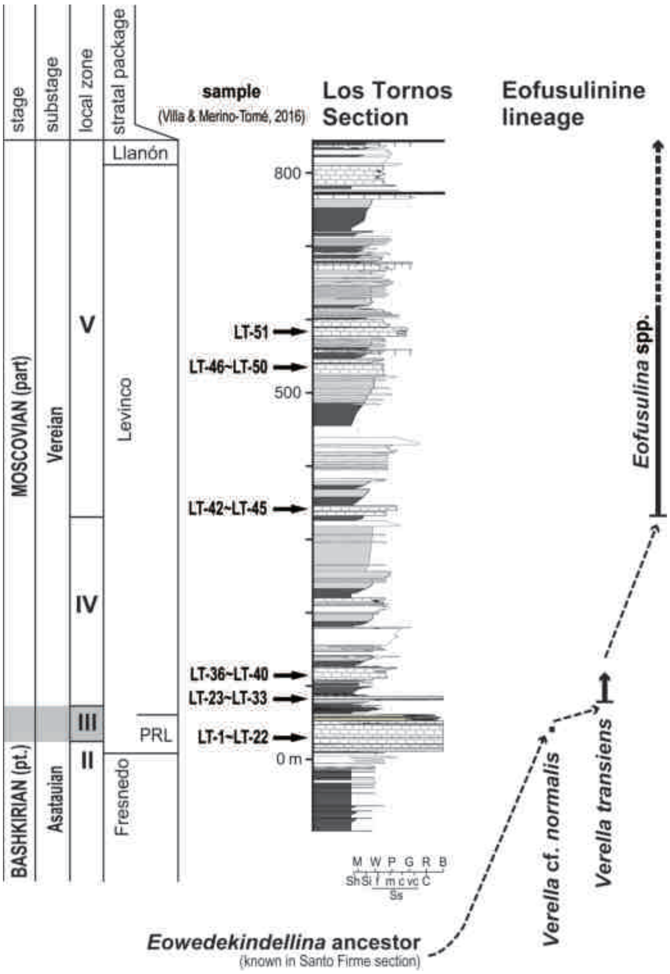

Figure 4. Diagram showing stratigraphic occurrences of eofusulinin species in the Los Tornos section (adapted from Villa & Merino-Tomé, 2016). The first occurrence datum (FAD) of *Eofusulina* in the Los Tornos section is placed at sample LT-42 in the fifth limestone interval from the base of the section, following observation in this study. This level is about 5 m lower than the FAD of the genus presented by Villa & Merino-Tomé (2016) originally. See Fig. 2 for the index of geologic log and other abbreviations.

5. TAXONOMIC REVIEW OF *VERELLA* AND *EOFUSULINA*

The genera *Verella* and *Eofusulina* are very peculiar in having elongate to highly elongate fusiform shells, among late Bashkirian-early Moscovian fusuline faunas, which are usually dominant in *Pseudostaffella*, *Neostaffella*, *Profusulinella*, *Aljutovella*, and *Fusulinella* with spherical, oval, ellipsoidal, rhomboidal, and fusiform shells. In spite of such noticeable morphology, however, these two eofusulinin genera tend to be represented as subordinate faunal elements because of their minor occurrences in the stratigraphic records (both in quantity and frequency). Accordingly their taxonomy is less progressed compared to coeval pseudostaffellin and fusulinellin genera mentioned above. On that account, we supplement to this article a systematic review of *Verella* and *Eofusulina* to describe their basic morphological features and taxonomic characterization.

Superfamily **Fusulinoidea** von Möller, 1878

Family **Fusulinidae** von Möller, 1878

Subfamily **Eofusulininae** Rauzer-Chernousova & Rozovskaya *in* Miklukho-Maklay, Rauzer-Chernousova & Rozovskaya, 1959

Genus *Verella* Dalmatskaya, 1951

1951 *Verella* Dalmatskaya, p. 195.

1958 *Pseudowedekindellina* Sheng, p. 29, 87-88.

1985 not *Verella* Goryunova, (established for a Silurian bryozoan genus with *Verella sytovae* Goryunova, 1985 as type species; junior homonym of *Verella* Dalmatskaya, 1951)

Type species. *Verella varsanofievae* Dalmatskaya, 1951 (Fig. 1a). As discussed below, we deem the specific name *varsanofievae* as a correct original spelling of this taxon although Dalmatskaya (1951) originally spelled it as *warsanofievie*.

Diagnosis. Shell is medium-sized in eofusulinines, elongate to highly elongate fusiform with nearly straight to slightly curved axis of coiling, nearly straight to slightly convex lateral slopes, broadly arched to nearly flattened median part of shell, and bluntly pointed axial regions. It consists usually of up to around 5-5.5 volutions. Axis of coiling is constant, and early volutions are coiled slightly more tightly than outer volutions. Proloculus is spherical and relatively small to medium in size. Wall consists of a tectum, primatheca (lower less dense layer), and outer tectorium that may be discontinuous. Septa are numerous, nearly plane in early volutions but are weakly fluted in outer ones. They may be moderately fluted in mainly lateral slopes in outer volutions of some advanced forms, forming incipient septal chamberlets, but even in this case, septa become nearly plane in the central part of shell and extreme polar regions. Chomata are small and massive in inner volutions, but usually well discernible and asymmetrical in outer ones, extending gently toward axial regions and nearly vertical or overhanging to tunnel sides. Axial fillings are moderately developed in most forms. Tunnel is narrow to moderate. Polar torsion may be observed in some forms.

Discussion and remarks. As has been discussed by Villa & Merino-Tome (2016), *Verella* is larger and has a more elongate shell with a slightly larger form ratio than its ancestral *Eowedekindellina* Ektova, 1977. Secondary deposits (axial fillings and upper tectorium) are more prominent in the latter genus. Moreover, *Verella* has weakly to moderately fluted septa, while they are essentially plane in *Eowedekindellina*.

Rozovskaya (1975), Sheng (1988), Rauzer-Chernousova *et al*. (1996), and Ivanova (2008) demonstrated that *Pseudowedekindellina* Sheng, 1958 (type species; *Pseudowedekindellina prolixa* Sheng, 1958; Fig. 1b) can be regarded as a junior synonym of *Verella*. Their essentially similar, elongate fusiform shells with weakly fluted septa, three-layered spirotheca, and late Bashkirian occurrences all support this interpretation.

Goryunova (1985) established the Silurian bryozoan genus *Verella* with *V. sytovae* Goryunova, 1985 as type species. In the same publication, she also described another species, *V. kogulensis* in the same bryozoan genus. That genus is, however, a junior homonym of fusuline *Verella*, which was established earlier, and thus the bryozoan genus *Verella* is regarded as invalid.

Siliculites was introduced by Fang (1988) in the subfamily Eofusulininae. *Siliculites euchomaticus* Fang, 1988 was designated as its type species, which came from the basal part of the Maping Formation of Guangxi, China. This level can be correlated to the Kasimovian (Late Pennsylvanian) as it contains *Obsoletes*, *Montiparus*, and *Triticites*. In the original description, that genus was compared to *Verella*, and also to *Eofusulina* to some extent, mainly because of its elongate fusiform shell and a similar spirothecal structure. *Siliculites*, however, is not regarded to be related to the eofusulinin lineage as its last member (*Neofusulina* Miklukho-Maklay, 1963) became extinct in a much lower level, at around the base of the late Moscovian (Leven, 1979). The gross shell morphology of *Siliculites* specimens illustrated by Fang (1988) suggests that it can possibly be referable to primitive schwagerinids, such as *Montiparus*, *Schwageriniformis*, or *Triticites*. Its apparent lack of keriothecal wall, which Fang (1988) considered diagnostic, is due probably to diagenetic alteration.

There is long-standing nomenclatural confusion about the correct spelling of the type species of *Verella*. Dalmatskaya (1951) originally named the type species as *V. warsanofievie*, dedicated to Вера Александровна Варсанофьева (Vera Aleksandrovna Varsanofieva). Later, Rauzer-Chernousova & Dalmatskaya (1954) and Miklukho-Maklay *et al*. (1959) proposed two variant spellings for the scientific name of that species, which were both attributed to the original author and date; they are *V. varsanofievae* and *V. warsanofievae*. These modifications were based probably on correct latinization of its suffix (-*ae* for feminine) and moreover, widely accepted transliteration from Cyrillic into Roman alphabet (transcription of Cyrillic “в” into Roman “v”, instead of “w”), but both are not justified under Article 32.5.1 of the International Code of Zoological Nomenclature (ICZN; International Commission on Zoological Nomenclature, 1999). Nevertheless the original spelling *warsanofievie* was seldom used in later publications (Thompson 1964 is the only instance in which we have found the use of the original spelling), while one of the two incorrect subsequent spellings, *varsanofievae*, has been definitely in prevailing usage since 1960s (Kireeva & Dalmatskaya, 1960; Rumyantseva, 1962, 1974; Miklukho-Maklay, 1963; Beligovskiy & Ektova, 1966; Saltovskaya, 1974; Rozovskaya, 1975; Dzhenchuraeva, 1975, 1979; Aliev *et al*., 1975; Granados *et al*., 1985; van Ginkel, 1987; Villa, 1995; Einor, 1996; Rauzer-Chernousova *et al*., 1996; Ivanova, 2000, 2008, 2015a, 2015b; Kim *et al*., 2007; Vodolazskaya *et al*., 2015; Kossovaya *et al*., 2016; Villa & Merino-Tome, 2016). The other subsequent incorrect spelling *warsanofievae* is lesser used (Yarikov, 1959; Pasini, 1965; Kahler & Kahler, 1966; Toriyama, 1970; Rui, 1983; Loeblich & Tappan, 1988; Sheng, 1988; Wang *et al*., 1992; Li & Lin, 1994; Wang *et al*., 1995; Fan, 1998; Zhang *et al*., 2010). Consequently, in accordance with ICZN Articles 33.3.1 and 33.5, we here deem *V. varsanofievae*, which was originally used in Rauzer-Chernousova & Dalmatskaya (1954), to be a correct original spelling for the taxonomic name of the type species of *Verella*.

As listed below, there have been some 30 species established in the genus *Verella* until now, in which *Pseudowedekindellina fusiformis* Sun *in* Sun *et al*., 1983 and *Verella fusiformis* Ivanova, 2000 are secondary and primary junior homonyms of *V. fusiformis* Bensh, 1969, respectively. We propose here *V. zhenanensis*, nomen novum for *P. fusiformis* Sun *in* Sun *et al*., 1983 and *V. ivanovae*, nomen novum for *V. fusiformis* Ivanova, 2000 as their new replacement names.

Species composition. *Verella varsanofievae* Dalmatskaya, 1951 (= *V. warsanofievie* Dalmatskaya, 1951 and *V. warsanofievae* Dalmatslaya, 1951); *Verella spicata* Dalmatskaya, 1951; *Pseudowedekindellina prolixa* Sheng, 1958; *Verella acuminata* Rumyantseva, 1962; *Verella imperplana* Rumyantseva, 1962; *Verella normalis* Rumyantseva, 1962; *Verella bosdonica* Rumyantseva, 1962; ?*Verella plicata* Rumyantseva, 1962; ?*Verella fusiformis* Bensh, 1969; *Verella muruntavica* Rumyantseva, 1974; *Verella sparsaplicata* Rumyantseva, 1974; *Verella grandicamerata* Saltovskaya, 1974; *Eofusulina serrata* Saltovskaya, 1974; *Verella bashkirica* Lebedeva *in* Stepanov *et al*., 1975; *Verella binhaiensis* Zhang & Rui, 1980; *Pseudowedekindellina antra* Xie, 1982; *Pseudowedekindellina paraprolixa* Xie, 1982; *Pseudowedekindellina*? *caudata* Xie, 1982; ?*Pseudowedekindellina obesa* Zhang *in* Wang *et al*., 1982; *Pseudowedekindellina fusiformis* Sun *in* Sun *et al*., 1983 (secondary junior homonym of *Verella fusiformis* Bensh, 1969; = *Verella zhenanensis*, nomen novum); *Verella guangdongensis* Lin, 1983; *Pseudowedekindellina lianpingensis* Lin, 1983; *Verella transiens* van Ginkel

& Villa *in* van Ginkel, 1987; *Pseudowedekindellina*? *zhungerensis* Zhuang, 1990; *Verella fuxianica* Wang, Wang & Zhang, 1992; *Verella tarimensis* Li & Lin, 1994; *Verella absidata* Sun *in* Wang *et al*., 1995; *Verella laxa* Sun *in* Wang *et al*., 1995; *Verella fusiformis* Ivanova, 2000 (primary junior homonym of *V. fusiformis* Bensh, 1969; = *Verella ivanovae*, nomen novum).

The following two species should be excluded from *Verella* as they were established as bryozoan species: *Verella sytovae* Goryunova, 1985; *Verella kogulensis* Goryunova, 1985. In the course of scrutinizing literature, moreover, we found the following three taxonomic names; *Verella kysilcumensis*, *Pseudowedekindellina yeongweolensis*, and *Pseudowedekindellina triangularis*. The first one was found in Solovieva (1963) and the latter two are in Lee & Na (1999). These taxa, if established formally, may have potential to be related to *Verella* in some way in the present taxonomy, but we could not find out their original references.

Distribution. Late Bashkirian and Bashkirian/Moscovian transitional interval; Tethys province.

Genus *Eofusulina* Rauzer-Chernousova *in* Rauzer-Chernousova, Kireeva, Leontovich, Gryzlova, Safonova & Chernova, 1951

1951 *Eofusulina* Rauzer-Chernousova *in* Rauzer-Chernousova, Kireeva, Leontovich, Gryzlova, Safonova & Chernova, p. 268-269.

1953 *Akiyoshiella* Toriyama, p. 251-253.

2008 *Postverella* Ivanova, p. 119-120.

Type species. *Fusulina triangula* Rauzer-Chernousova & Beljaev *in* Rauzer-Chernousova, Beljaev & Reitlinger, 1936 (Fig. 1c).

Diagnosis. Shell is medium to large in eofusulinines, elongate to highly elongate fusiform but rarely elongate ellipsoidal, with nearly straight to slightly curved axis of coiling, bluntly pointed axial regions, consisting usually of up to 4-5 volutions. Lateral slopes are straight to broadly convex. Shell expands gradually through growth, with constant axis of coiling. Proloculus is spherical but somewhat irregular in some forms, and medium- to large-sized (usually having 170-300 μm in outside diameter). Wall consists of a tectum, primatheca (lower less dense layer), and thin outer tectorium which tends to be diminished in outer volutions. Primatheca may look slightly translucent. Septa are strongly and regularly to irregularly fluted from the first or second volution, forming narrow and high septal loops that may reach to nearly the roof of chamber, and septal chamberlets in the middle of axial regions on both sides of tunnel. Small chomata are seen in the inner volutions, and usually diminished or even absent in the outer ones, or probably replaced by pseudo-chomata. Axial fillings are usually weak to moderate, but often more prominent especially in the subgenus *Paraeofusulina*. Narrow to moderately broad tunnel is observed, but is unclear in some forms due to inconspicuous chomata.

Discussion and remarks. *Eofusulina* can be distinguished from its ancestral *Verella* in having stronger septal fluting, lesser development of secondary deposits, a generally larger proloculus, absence of inner tightly coiled volutions, and to some extent a slightly larger shell diameter and absence of polar torsion. However, in the case of the subgenus *Paraeofusulina*, secondary deposits, especially axial fillings, are even stronger than *Verella*.

Ueno *in* Fohrer *et al*. (2007) recognised strong similarities between *Eofusulina* and *Akiyoshiella*, which was established by Toriyama (1953) with *A. ozawai* Toriyama, 1953 (but probably conspecific with *Schellwienia staffi* Ozawa, 1925) from the Akiyoshi Limestone of Japan as type species (Fig. 1e). He provisionally retained that genus as distinct from *Eofusulina*, due mainly to the uncertain phylogenetic origin of the former within the mid-oceanic Panthalassa paleobiogeographical province. However, considering the close similarity of both morphologies and stratigraphic occurrences of these two genera, *Akiyoshiella* should now be better treated as a junior synonym of *Eofusulina*.

Postverella was established by Ivanova (2008), with *Eofusulina figurata* Ivanova *in* Chuvashov & Ivanova (1980) from the Kashirian (upper Lower Moscovian; Middle Pennsylvanian) of the eastern slope of the Southern Urals, as type species (Fig. 1d). She noted that this genus can be distinguished from *Eofusulina* in having a smaller shell, three-layered wall, well-developed axial fillings, and mixed type of septal fluting, with plane septa in the first and second volutions but strongly fluted ones in the form of narrow and high loops in the subsequent volutions. However, all these features are considered to stay within the known morphological variations of *Eofusulina*. In this respect, we judge that *Postverella* is a junior synonym of *Eofusulina*.

Eofusulina can be subdivided into two subgenera: *Eofusulina* (*s.s.*) and *Paraeofusulina* Putrja, 1956 with the type species of *Eofusulina* (*Paraeofusulina*) *trianguliformis* Putrja, 1956 (Fig. 1f). The latter subgenus can be distinguished from the former by its more elongate shell, more compactly coiled volutions, usually slightly smaller proloculus, heavier axial fillings, and more regularly fluted septa with rounded septal loops.

Species composition. Subgenus *Eofusulina* (*s.s.*): *Schellwienia staffi* Ozawa, 1925; *Fusulina triangula*

Rauzer-Chernousova & Beljaev *in* Rauzer-Chernousova *et al.*, 1936; *Fusulina paratriangula* Putrja, 1939; *Fusulina triangula almasica* Manukalova, 1950; *Fusulina triangula finalis* Manukalova, 1950; *Akiyoshiella ozawai* Toriyama, 1953; *Akiyoshiella toriyamai* Thompson, Pitrat & Sanderson, 1953; *Eofusulina binominata* Putrja, 1956; *Eofusulina inusitata* Sheng, 1958; *Eofusulina triangula fusiformis* Grozdilova & Lebedeva, 1960; *Eofusulina corpulenta* Rumyantseva, 1962; *Verella postspicata* Bensh, 1969; ?*Verella postfusiformis* Bensh, 1969; *Eofusulina triangula gigas* Bensh, 1969; ?*Eofusulina crassa* Saltovskaya, 1974; ?*Eofusulina simplex* Saltovskaya, 1974; *Eofusulina rumjantzevae* Lebedeva *in* Stepanov *et al.*, 1975; *Akiyoshiella fusulinoides* Sosnina *in* Sosnina & Nikitina, 1976; *Eofusulina compacta* Li *in* Lin *et al.*, 1977; *Eofusulina pullata* Ivanova *in* Chuvashov & Ivanova, 1980; *Eofusulina figurata* Ivanova *in* Chuvashov & Ivanova, 1980; *Eofusulina*? *dualis* Ivanova *in* Chuvashov & Ivanova, 1980; *Eofusulina tashlensis* Malakhova, 1980 (*nomen nudum*; probably included in *E. triangula*); *Eofusulina fenghuangshanensis* Wang, 1981; *Eofusulina longipertica* Lin *in* Wang *et al.*, 1982; *Eofusulina xinjiangensis* Sun *in* Da & Sun, 1983; *Eofusulina hamiensis* Sun *in* Da & Sun, 1983; *Eofusulina megatriangula* Sun *in* Da & Sun, 1983; *Eofusulina triangula minima* Da *in* Da & Sun, 1983; *Eofusulina tumidoformis* Sun, 1992; *Akiyoshiella irregularis* Lee *in* Lee & Park, 1994. Moreover, we add one potential nude-name taxon to this subgenus; *Eofusulina tetis* Solovieva (MS), which was found in Dzhenchuraeva (1979, text-fig. 3, pl. 37, figs 4, 5). This is probably the same as *Eofusulina triangula tethys* Solovieva, illustrated by Orlov-Labkovsky & Bensh (2015, pl. 33, figs 8, 9; pl. 37, fig. 2). *Eofusulina fortis* Zhuang, 1984 and *Eofusulina duijiugouensis* Zhuang, 1990 were originally assigned to this subgenus, but should be included in *Quasifusulina* and *Beedeina* (or *Fusulina*), respectively.

Subgenus *Eofusulina* (*Paraeofusulina*): *Fusulina triangula rosdorica* Putrja, 1938; *Eofusulina* (*Paraeofusulina*) *trianguliformis* Putrja, 1956; *Paraeofusulina quadratoarcus* Rumyantseva, 1974; *Eofusulina angusta* Saltovskaya, 1974; *Eofusulina arcuata* Saltovskaya, 1974. Three species of this subgenus reported by Zhuang (1984), *Eofusulina* (*Paraeofusulina*) *quasifusulinoides*, *Eofusulina* (*Paraeofusulina*) *subcylindrica*, and *Eofusulina* (*Paraeofusulina*) *guizhouensis*, should be included in *Quasifusulina* by their basic morphologies.

Distribution. Lower Moscovian; Tethys, Panthalassa, Ural, and Arctic provinces.

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