

# Systematic revision and phylogenetic assessment of the foraminiferal family Globivalvulinidae

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We present a systematic and phylogenetic revision of the Carboniferous–Permian subfamilies usually included within the family Globivalvulinidae (superfamily Biseriamminoidea), based for the first time on the interrelation between a morphological/structural approach (traditionally used for this fossil group) and a cladistic analysis (rarely applied to Palaeozoic Foraminifera). The systematic review of the globivalvulinid genera defines a new composition of the already existing four subfamilies of Globivalvulinidae (Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae). The phylogenetic analysis of the Globivalvulinidae is aimed at understanding and reconstructing the relationships between its four subfamilies. The resulting phylogenetic tree is obtained by means of fifteen qualitative and one quantitative characters. The analysis shows that the Globivalvulinidae represents a monophyletic clade having the subfamily Globivalvulininae as the first taxon to branch out. The close affinity between the Dagmaritinae and Paradagmaritinae is confirmed.

Key words: Foraminifera, Biseriamminoidea, Globivalvulinidae, cladistics, phylogeny, taxonomy, Palaeozoic.

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## Introduction

Biserially coiled to uncoiled biseriamminoids represent one of the most interesting groups, both from a stratigraphic and an evolutionary point of view, among Palaeozoic smaller foraminifers. According to Vachard et al. (2006), their biostratigraphic value is probably underestimated during the Carboniferous (Perret 1993; Pinard and Mamet 1998), and some genera such as *Tenebrosella* Villa and Sanchez de Posada, 1986 and *Verispira* Palmieri, 1988, remain poorly known and are rarely cited in the literature. Within biseriamminoids, some members of the family Globivalvulinidae Reitlinger, 1950 (order Endothyrida) are important biostratigraphical and palaeogeographical markers in the middle–late Permian together with other families such as the Pseudovidalinidae Altner, 1988 (order Archaediscida) and the Hemigordiopsidae Nikitina, 1969 (order Cornuspirida). The high biostratigraphic significance of these taxa is due to their wide palaeogeographical distribution and rapid evolution (Vachard et al. 2006, 2017; Gaillot and Vachard 2007; Gaillot et al. 2009; Altner and Özkan-Altner 2010; Vachard 2016b).

The taxonomic composition and evolution of biseriamminoid foraminifers is a long-standing debate. It started

when Schubert (1921) introduced the genus *Globivalvulina* choosing *Valvulina bulloides* Brady, 1876 as the type species, and later Chernysheva (1941) erected the genus *Biseriammina* (type species *Biseriammina uralica* Chernysheva, 1941) and assigned it to the family Biseriamminidae Chernysheva, 1941. Loeblich and Tappan (1964) recognised the family Biseriamminidae as composed of the only subfamily Biseriammininae Chernysheva, 1941 considering Globivalvulininae (sic!) Reitlinger, 1950 = Globivalvulininae Pokorny, 1958 as synonyms. Zaninetti and Altner (1981) divided the Biseriamminidae into two subfamilies Biseriammininae and Dagmaritinae Bozorgnia, 1973, to which the third subfamily Louisettitinae was added by Loeblich and Tappan (1984). Marfenkova (1991) and Gaillot and Vachard (2007) included three families into the superfamily Biseriamminoidea Chernysheva, 1941: Biseriamminidae, Koktjubinidae Marfenkova, 1991, and Globivalvulinidae. Subsequently, Hance et al. (2011) introduced the superfamily Globivalvulinoidea Reitlinger, 1950 moving the Biseriamminidae to the superfamily Mstinoidea Lipina, 1989. Cózar and Sommerville (2012) challenged this systematic interpretation and included two families into the superfamily Biseriamminoidea: Biseriamminidae (microgranular wall with agglutinated grains) and Globivalvulinidae (wall

microgranular or differentiated with diaphanoteca, sensu Cózar and Sommerville 2012). Finally, Vachard (2016a) revised the Globivalvulinoidea as composed of three families: Globivalvulinidae, ?Biseriamminidae, and ?Koktjubinidae.

Herein, we focus on the family Globivalvulinidae with the aim to review its taxonomic composition and to better define its systematics. The phylogenetic relationships of its subfamilies are tentatively proposed by means of a cladistic approach, which is not commonly applied to Palaeozoic foraminifers.

## Historical background

Gaillot and Vachard (2007) raised the subfamily Globivalvulininae Reitlinger, 1950 to the family rank (Globivalvulinidae) defining the family as composed of Globivalvulininae, Dagmaritinae, Paradagmaritinae Gaillot and Vachard, 2007, and Paraglobivalvulininae Gaillot and Vachard, 2007. They introduced new genera belonging to three of the above cited four subfamilies: *Labioglobivalvulina* Gaillot and Vachard, 2007 (= *Siphoglobivalvulina* Gaillot, 2006) and *Retroseptellina* Gaillot and Vachard, 2007 to the Globivalvulininae; *Labiogadmarita* Gaillot and Vachard, 2007, *Bidagmarita* Gaillot and Vachard in Gaillot et al. (2009), and *Siphogadmarita* Gaillot and Vachard in Vachard et al. (2006) to the Dagmaritinae; and *Paremiratella* Gaillot and Vachard, 2007, *Paradagmaritella* Gaillot and Vachard, 2007, *Paradagmacrusta* Gaillot and Vachard, 2007, and *Paradagmaritopsis* Gaillot and Vachard in Gaillot et al. (2009) to the Paradagmaritinae. Partially in agreement with this latter interpretation and with some criticisms about the generic composition of subfamilies, Altner and Özkan-Altner (2010) reviewed the evolutionary relationships between the Paradagmaritinae and Dagmaritinae, indicating the former as a junior synonym of the Dagmaritinae. Cózar and Sommerville (2012) considered the superfamily Biseriamminoidea as composed of the family Globivalvulinidae and the family Biseriamminidae, considering the Koktjubinidae as a synonym of the Biseriamminidae. The latter authors synonymised the genera *Dzhamansorina* Marfenkova, 1991, *Admiranda* Marfenkova, 1991, and *Ulanbela* Marfenkova, 1991 with *Koktjubina* Marfenkova, 1991 on the basis of dubious differences between them. The latest taxonomic rearrange-

ment by Vachard (2016b) maintained the subfamily subdivisions as proposed in Gaillot and Vachard (2007).

The generic revision herein proposed led to suggest a revised taxonomic scheme of the family Globivalvulinidae and its subfamilies (Table 1). In this taxonomic scheme, the superfamily Biseriamminoidea is composed of two families: the Biseriamminidae sensu Cózar and Sommerville (2012) (Biseriammininae) and the Globivalvulinidae (Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae) on the basis of wall structure as stated by Cózar and Sommerville (2012) for Mississippian Biseriamminoidea.

The generic composition of the subfamily Globivalvulininae is modified by moving the genus *Septoglobivalvulina* Lin, 1978 to the subfamily Paraglobivalvulininae because its last chamber envelops the preceding ones. We also retain *Paremiratella* as valid, although morphologically it is close to *Globivalvulina*, because the differences in size of the tests (larger in *Paremiratella*) and number of chambers (more numerous in *Paremiratella*) are considered of specific taxonomic value. Furthermore, according to Altner and Özkan-Altner (2010), the genus *Paremiratella* (Paradagmaritinae in Gaillot and Vachard 2007) belongs to the Globivalvulininae because of its globular chambers and dark brown single-layered wall. Additionally, the genus *Lateenoglobivalvulina* introduced by Filimonova (2016) and placed into the Globivalvulininae, is not discussed herein because the holotype of the type species *Globivalvulina spiralis* Morozova, 1949 does not clearly show the generic diagnostic features (i.e., the type of wall and aperture) being also figured by Morozova (1949) as a drawing.

The genus *Sengoerina* Altner, 1999 (Dagmaritinae in Altner 1999), was assigned by Nestell and Nestell (2006) to globivalvulinids as later accepted by of Mikhalevich (2014). However, we follow Mohtat-Aghai and Vachard (2003) who evidenced the affinities between *Sengoerina* and *Paradagmarita* Lys in Lys and Marcoux, 1978, and include *Sengoerina*, as well as *Crescentia* Ciarapica, Cirilli, Martini, and Zaninetti, 1986, in the subfamily Paradagmaritinae. Both genera are characterised by a biserially enrolled initial stage and by chambers that become angular in the uncoiled stage. Based on the type of wall of the test and following Altner and Özkan-Altner (2010), we further reduce the generic composition of the Dagmaritinae, keeping outside of this subfamily

Table 1. New taxonomic arrangement of the family Globivalvulinidae proposed in this paper.

| Superfamily      | Families   | Subfamilies           | Genera  |
|------------------|--|-----------------------|---|
| Biseriamminoidea | Globivalvulinidae (this study)                     | Globivalvulininae     | <i>Globivalvulina</i> , <i>Charliella</i> , <i>Retroseptellina</i> , <i>Labioglobivalvulina</i> , <i>Biseriella</i> , <i>Tenebrosella</i> , <i>Verispira</i> , <i>Paremiratella</i> |
|                  |  | Paraglobivalvulininae | <i>Paraglobivalvulina</i> , <i>Paraglobivalvulinoides</i> , <i>Urushtenella</i> , <i>Septoglobivalvulina</i>  |
|                  |  | Dagmaritinae          | <i>Dagmarita</i> , <i>Danielita</i> , <i>Louissetita</i>  |
|                  |  | Paradagmaritinae      | <i>Paradagmarita</i> , <i>Paradagmacrusta</i> , <i>Paradagmaritopsis</i> , <i>Crescentia</i> , <i>Sengoerina</i>  |
|                  | Biseriamminidae (sensu Cózar and Sommerville 2012) | Biseriammininae       | <i>Biseriammina</i> , <i>Koktjubina</i> , <i>Parabiseriella</i>   |

the genera *Bidagmarita* and *Labiodagmarita*, which are probably closer to the family Palaeotextulariidae Galloway, 1933. Due to its coarse granular layer, the genus *Paradagmaritella* (Paradagmaritinae in Gaillot and Vachard 2007) is not referred to the Globivalvulinidae but in close proximity to the genus *Spireitlina* Vachard in Vachard and Beckary, 1991, as suggested by Altner and Özkan-Altner (2010).

## Methods

The phylogenetic relationships within the Globivalvulinidae are herein investigated through a cladistic approach, by means of the analytical technique of maximum parsimony (Kolaczowski and Thornton 2004; Kannan and Wheeler 2012).

The use of cladistics for Foraminifera is not exempt from some restrictions and problems (Soldan et al. 2011). Some of these obstacles are related to intrinsic characteristics of each taxon. For instance, the relatively simple morphology of the earliest lagenids results in the difficulties to define a significant number of characters to analyse (Groves et al. 2003). In addition, morphological characters are not always recognisable on fossil samples, due to the destructive effects of diagenesis that often affect Palaeozoic sedimentary rocks. Worthy to note are also the limitations related to the two-dimensional microscopic analysis, commonly performed on Foraminifera of this time interval. This implies that some morphological features could not be easily identified, because observable only in 3D view (e.g., the ornamentations). Anyway, we believe that the phylogenetic relationships among Palaeozoic groups of foraminifers can be fruitfully determined, both at the genus and suprageneric level, starting from a correct recognition and definition of characters and character states.

In this study, the cladistic analysis is based on the taxonomic scheme showed in Table 1. The phylogenetic tree has been obtained by means of fifteen qualitative (descriptive) characters and one quantitative (numerical) character. Characters have been selected using original generic descriptions and diagnoses (Reitlinger 1965; Zaninetti and Jenny-Deshusses 1985; Ciarapica et al. 1986; Villa and Sanchez de Posada 1986; Loeblich and Tappan 1987; Palmieri 1988; Altner 1999; Altner and Özkan-Altner 2001; Pronina-Nestell and Nestell 2001; Nestell and Nestell 2006; Gaillot and Vachard 2007; Gaillot et al. 2009; Altner and Özkan-Altner 2010; Cózar and Sommerville 2012), without referring to any previous phylogenetic works. The descriptive characters are illustrated in Figs. 1 and 2, whereas the complete list of characters is provided in Appendix 1. The family Biseriamminidae has been designated as outgroup because it is closely related to the Globivalvulinidae due to the type of coiling, the arrangement and the shape of chambers, and the similarity of the aperture (Vachard et al. 2006; Cózar and Sommerville 2012). The ingroup is composed by the four Globivalvulinidae subfamilies

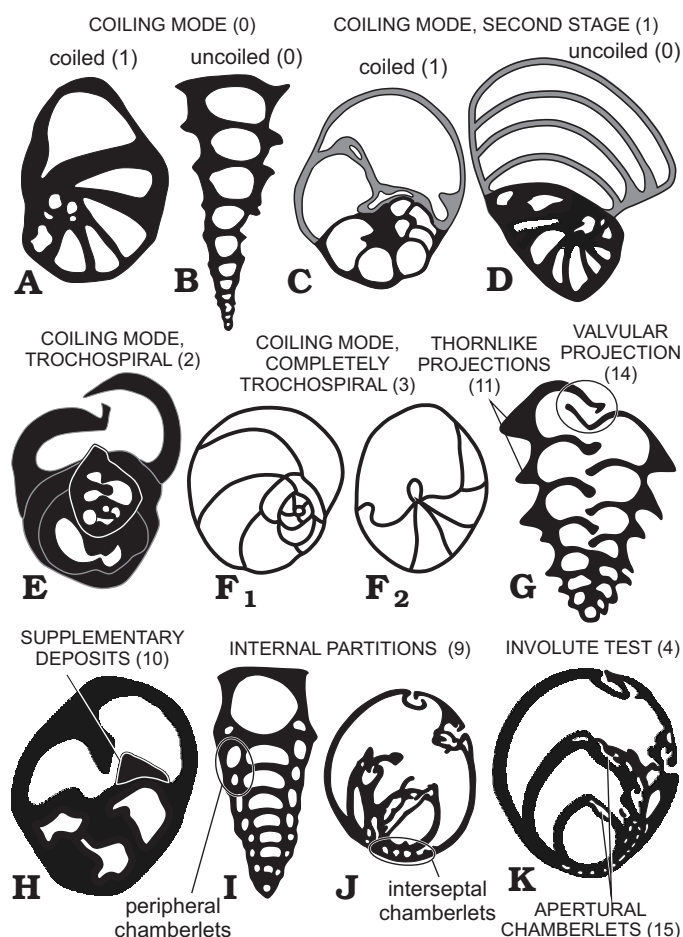


Fig. 1. Graphic explanation of descriptive morphological characters on which the cladistic analysis is based. **A.** *Charliella rossae* Altner and Özkan-Altner, 2001 (Altner and Özkan-Altner 2001: pl. 1: 2). **B.** *Danielita gailloti* Altner and Özkan-Altner, 2010 (Altner and Özkan-Altner 2010: pl. 2: 20). **C.** *Globivalvulina* sp. 1 (Nestell and Nestell 2006: pl. 6: 1). **D.** *Paradagmarita flabelliformis* Zaninetti, Altner, and Catal, 1981 (Altner 1981: pl. 39: 1). **E.** *Tenebrosella asturica* Villa and Sanchez de Posada, 1986 (Villa and Sanchez de Posada 1986: holotype, pl. 1: 1). **F.** *Verispira jelli* Palmieri, 1988 in spiral (F<sub>1</sub>) and umbilical (F<sub>2</sub>) views (modified from Palmieri 1988: fig. 8). **G.** *Dagmarita* sp. (Nestell and Pronina 1997: pl. 1: 6). **H.** *Labioglobivalvulina baudi* Gaillot and Vachard, 2007 (Gaillot and Vachard 2007: holotype, pl. 12: 10). **I.** *Louissetta elegantissima* Altner and Brönnimann, 1980 (Loeblich and Tappan 1987: holotype, pl. 231: 7). **J.** *Paraglobivalvulinoides septulifer* Zaninetti and Altner, 1981 (Zaninetti and Altner 1981: holotype, pl. 1: 15). **K.** *Paraglobivalvulinoides septulifer* Zaninetti and Altner, 1981 (Zaninetti and Altner 1981: pl. 1: 19). Area in gray in C and D indicates the second stage of coiling. Not to scale.

(Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae), since one of the aims of the work is to reconstruct the phylogenetic relationships within the family and to evaluate the systematic validity of its subfamilies.

A matrix of five taxa and sixteen characters has been constructed (Appendix 1). All characters have been treated as unordered and unweighted. The data matrix has been processed with the software PAUP\* version 4.01 (Swofford 2002). Nodal support has been calculated performing 1000 bootstrap analyses (Felsenstein 1985) using branch and bound searches.

## Systematic palaeontology

Phylum Foraminifera d'Orbigny, 1826

Class Fusulinata Gaillot and Vachard, 2007

Subclass Fusulinana Maslakova, 1990 nom. correct.  
Vachard et al. (2010)

Order Endothyrida Fursenko, 1958

Superfamily Biseriamminoidea Chernysheva, 1941

Families included: Biseriamminidae Chernysheva, 1941; Globivalvulinidae Reitlinger, 1950.

**Description.**—Test biserial, globular, subglobular or elongated in shape, evolute/semi-evolute or involute/semi-involute, rounded or pinched peripheral outline, from coiled, coiled to uncoiled, to uncoiled. Endoskeletal partitions and supplementary deposits can be present. Test wall microgranular, with agglutinated grains, undifferentiated or poorly layered or microgranular, single layered or plurilayered. Presence of hyaline layer in inner, median or outer position or pseudoalveolar median layer. Perforations of the wall can be present. Aperture narrow, simple or with valvular projection.

**Stratigraphic and geographic range.**—Late Tournaisian (Mississippian, Carboniferous) to latest Changhsingian (Lopingian, Permian); cosmopolite.

Family Biseriamminidae Chernysheva, 1941

Genera included: *Biseriammina* Chernysheva, 1941; *Koktjubina* Marfenkova, 1991; *Parabiseriella* Cózar and Sommerville, 2012.

**Description.**—Test biserial, globular, subglobular or elongated in shape, evolute, rounded peripheral outline, low trochospirally or planispirally coiled, with the tendency to uncoil in the terminal part. Test wall microgranular, with “adventitious grains, undifferentiated or poorly layered” (Cózar and Sommerville 2012: 217). Aperture simple, narrow, rarely depressed with a valvular projection (in *Parabiseriella*).

**Stratigraphic and geographic range.**—Late Tournaisian (Mississippian, Carboniferous) to ?early Bashkirian (Pennsylvanian, Carboniferous) of the Palaeotethys and Panthalassa (Urals and North America).

Family Globivalvulinidae Reitlinger, 1950

Subfamilies included: Globivalvulininae Reitlinger, 1950; Paraglobivalvulininae Gaillot and Vachard, 2007; Dagmaritinae Bozorgnia, 1973; Paradagmaritinae Gaillot and Vachard, 2007.

**Description.**—Test biserial, globular, subglobular or elongated in shape, evolute/semi-evolute or involute/semi-involute, rounded or pinched peripheral outline, coiled, coiled to uncoiled, uncoiled. Endoskeletal partitions and supplementary deposits can be present. Test wall microgranular, single layered or plurilayered. Presence of hyaline layer in inner, median or outer position or pseudoalveolar median layer. Perforations of the wall can be present. Aperture interior-marginal depressed and protected by a valvular projection.

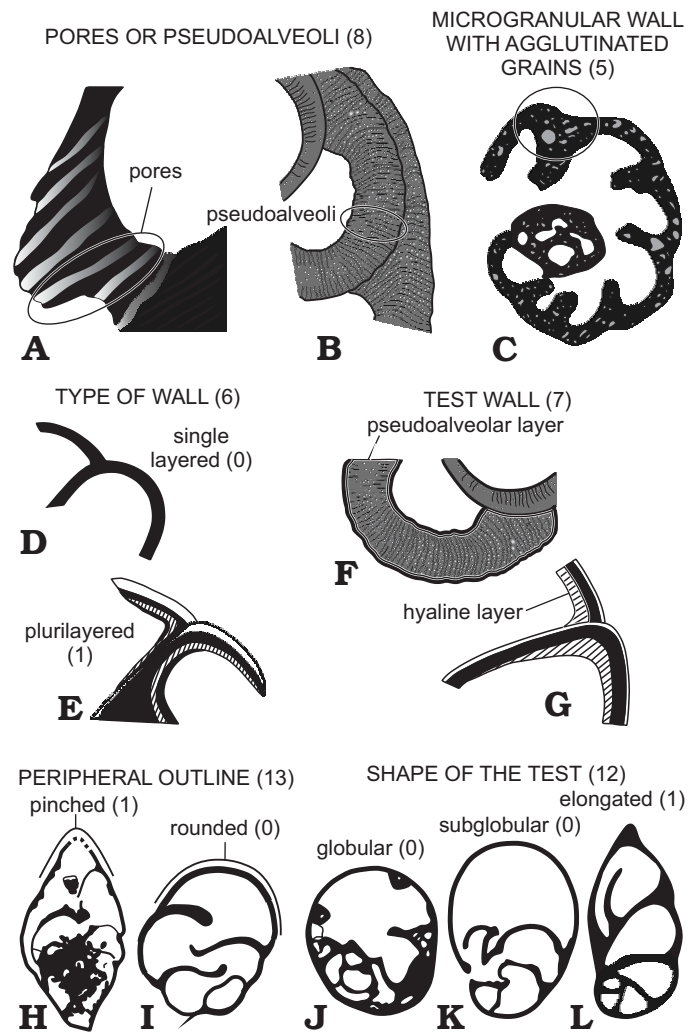


Fig. 2. Graphic explanation of descriptive morphological characters on which the cladistic analysis is based. **A.** *Danielita gailloti* Altner and Özkan-Altner, 2010 (Altner and Özkan-Altner 2010: pl. 1: 3). **B.** *Urushtenella latebroso* Pronina-Nestell, 2001 (Pronina-Nestell and Nestell 2001: pl. 5: 12). **C.** *Koktjubina windsorensis* (Mamet, 1970) (Mamet 1970: holotype, pl. 1: 11). **D.** *Retroseptellina decrouezae* (Köylüoğlu and Altner, 1989) (modified from Altner and Özkan-Altner 2001: fig. 2). **E.** *Charliella rossae* Altner and Özkan-Altner, 2001 (modified from Altner and Özkan-Altner 2001: fig. 2). **F.** *Urushtenella latebroso* Pronina-Nestell, 2001 (Pronina-Nestell and Nestell 2001: pl. 5: 12). **G.** *Globivalvulina graeca* Reichel, 1946 (modified from Altner and Özkan-Altner 2001: fig. 2). **H.** *Paradagmarita monodi* Lys in Lys and Marcoux, 1978 (Loeblich and Tappan 1987: holotype, pl. 230: 6). **I.** *Globivalvulina bulloides* (Brady, 1876) (Loeblich and Tappan 1987: pl. 230: 14). **J.** *Paraglobivalvulina mira* Reitlinger, 1965 (Loeblich and Tappan 1987: holotype, pl. 230: 10). **K.** *Septoglobivalvulina distensa* (Wang in Zhao et al., 1981) (Gaillot and Vachard 2007: pl. 37: 2). **L.** *Paradagmaritopsis kobayashii* Gaillot and Vachard, 2009 (Gaillot et al. 2009: holotype, fig. 6: 6). Not to scale.

**Stratigraphic and geographic range.**—Late Visean (Mississippian, Carboniferous) to latest Changhsingian (Lopingian, Permian); cosmopolite.

Subfamily Globivalvulininae Reitlinger, 1950

Genera included: *Globivalvulina* Schubert, 1921; *Charliella* Altner and Özkan-Altner, 2001; *Labioglobivalvulina* Gaillot and Vachard,

2007; *Retroseptellina* Gaillot and Vachard, 2007; *Tenebrosella* Villa and Sanchez de Posada, 1986; *Verispira* Palmieri, 1988; *Biseriella* Mamet in Armstrong and Mamet, 1974; *Paremiratella* Gaillot and Vachard, 2007.

**Description.**—Test free, globular or subglobular in shape, evolute or semi-evolute, rounded peripheral outline, biserial, coiling planispiral to slightly trochospiral, or trochospiral (helicoidal? in *Biseriella*). Chambers globular, subglobular to angular. Septal supplementary nodular formations (in *Labioglobivalvulina*). Test wall dark microgranular, single layered or plurilayered with white inner hyaline layer, sutural fine perforations in *Verispira*. Aperture interiomarginal depressed and protected by a valvular projection.

**Stratigraphic and geographic range.**—Late Visean (Mississippian, Carboniferous) to latest Changhsingian (Lopingian, Permian); cosmopolite.

### Subfamily Paraglobivalvulininae Gaillot and Vachard, 2007

**Genera included:** *Paraglobivalvulina* Reitlinger, 1965; *Paraglobivalvulinoides* Zaninetti and Jenny-Deshusses, 1985; *Urushtenella* Pronina-Nestell in Pronina-Nestell and Nestell 2001; *Septoglobivalvulina* Lin, 1978.

**Description.**—Test free, globular or subglobular in shape, semi-involute or involute, rounded peripheral outline, biserial, planispirally to trochospirally coiled. Chambers globular to subglobular. Auxiliary interseptal and apertural chamberlets can be present. Test wall dark, microgranular, single layered or plurilayered with pseudoalveolar structure (in *Urushtenella*). Aperture interiomarginal depressed and protected by a valvular projection.

**Stratigraphic and geographic range.**—Capitanian (Guadalupian, Permian) to late Changhsingian (Lopingian, Permian) of the Palaeotethys and Neotethys.

### Subfamily Dagmaritinae Bozorgnia, 1973

**Genera included:** *Dagmarita* Reitlinger, 1965; *Louissetita* Altner and Brönnimann, 1980; *Danielita* Altner and Özkan-Altner, 2010.

**Description.**—Test free, elongated in shape, evolute, rounded peripheral outline, biserial, uncoiled. Subspheric chambers, semi-circular to semi-ellipsoidal in axial section. Presence of outer thornlike projections of the test wall. Endoskeletal septal partitions (peripheral chamberlets) are present in *Louissetita*. Test wall plurilayered composed of dark microgranular and white median or outer hyaline layer. The microgranular layer described with perforations (in *Danielita*). Aperture interiomarginal depressed and protected by a valvular projection.

**Stratigraphic and geographic range.**—Roadian (Zheng 1986) (Guadalupian, Permian) to late Changhsingian (Lopingian, Permian) of the Palaeotethys, the Neotethys, and the Panthalassa (Japan and North America).

The first appearance datum (FAD) of the Dagmaritinae is based on the FAD of the genus *Dagmarita*. Zheng (1986)

recorded the first appearance of this taxon in the sample D40 of the Chihhsia (= Qixia) Formation (South China), which has been referred to the *Verbeekina grabau* Zone. This biozone corresponds to the Roadian *Neoschwagerina simplex* Zone (Nestell and Nestell 2006; Angiolini et al. 2015).

### Subfamily Paradagmaritinae Gaillot and Vachard, 2007

**Genera included:** *Paradagmarita* Lys in Lys and Marcoux, 1978; *Paradagmacrusta* Gaillot and Vachard, 2007; *Paradagmaritopsis* Gaillot and Vachard in Gaillot et al., 2009; *Crescentia* Ciarapica, Cirilli, Martini, and Zaninetti, 1986; *Sengoerina* Altner, 1999.

**Description.**—Test free, elongated in shape, pinched peripheral outline, biserial, involute initial stage, generally slightly trochospiral and later followed by an uncoiled biserial stage. Chambers are globular at the beginning and later angular or inflated. Crustae at the roof of the chambers are present in *Paradagmacrusta*. Test wall dark, microgranular or plurilayered with white outer hyaline layer. Aperture interiomarginal depressed and protected by a valvular projection.

**Stratigraphic and geographic range.**—Capitanian (Guadalupian, Permian) to late Changhsingian (Lopingian, Permian) of the Palaeotethys, the Neotethys, and the Panthalassa (Japan and North America).

## Results

The phylogenetic analysis produced a single tree of 19 steps (Fig. 3), with a Consistency Index of 0.842 and a Retention Index of 0.571.

The monophyletic clade of Globivalvulinidae has the Globivalvulininae as the first taxon to have branched off, characterised by one autapomorphy: presence of supplementary deposits (nodular structures). Then, a monophyletic clade composed of the Paraglobivalvulininae and Dagmaritinae plus Paradagmaritinae, is recognised. This clade is supported by one synapomorphy: absence of a completely trochospiral coiling mode (although this character is inapplicable for Dagmaritinae; see Appendix 1). The sister-group relationship between Dagmaritinae and Paradagmaritinae is evidenced by three synapomorphies: uncoiled test in the second stage, predominance of plurilayered genera, and elongated shape of the test (Fig. 3; Appendix 1).

## Concluding remarks

The phylogenetic relationships within the Globivalvulinidae have been reconstructed in order to investigate the evolutionary history of this group of Foraminifera. The analysis has to be considered as preliminary because it should be expanded in the future with the inclusion of additional characters, and a larger taxonomic sampling.

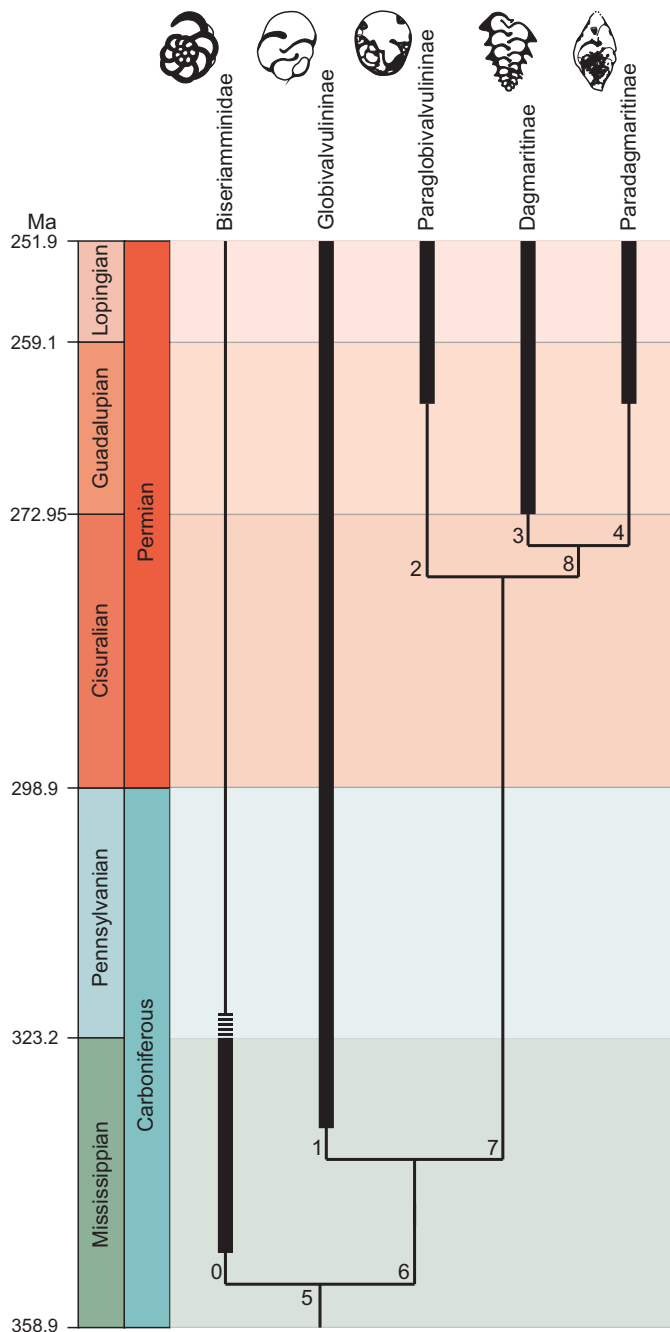


Fig. 3. Phylogenetic tree resulting from the cladistic analysis. Thick lines represent the known stratigraphic ranges of the considered taxa (dashed line indicates uncertain stratigraphic ranges). Nodes are numbered above branches. See text and Appendix 1 for details.

The obtained phylogenetic tree (Fig. 3) supports the validity of the four globivalvulinid subfamilies as they all resulted as monophyletic groups.

Within the Globivalvulinidae, the Globivalvulininae are the first group to branch out. This result is in agreement with biostratigraphic data, according to which representatives of this subfamily appear in the fossil record starting from the Mississippian (Gaillot and Vachard 2007; Cózar and Sommerville 2012; Vachard 2016b). However, the alleged relationship between the Globivalvulininae and

Paraglobivalvulininae (Altiner 1999; Altiner and Özkan-Altiner 2001; Vachard et al. 2006) is not supported by our results, since the latter subfamily is phylogenetically closer to the Dagmaritinae and Paradagmaritinae than to the Globivalvulininae (i.e., a hypothetical group including the Globivalvulininae and Paraglobivalvulininae would be paraphyletic). Conversely, we firmly confirm the close affinity between the Dagmaritinae and Paradagmaritinae as defined by Altiner (1997, 1999) and Altiner and Özkan-Altiner (2010), in the light of the sister-group relationship between the two subfamilies in our tree, supported by three synapomorphies (Fig. 3). We are aware that the separation between Globivalvulininae and the other three subfamilies (node 7) is relatively weak, being supported by a single synapomorphy (see Appendix 1), and that this weakness could implicitly strengthen the previous morphology-based phylogenetic views (Altiner 1999; Altiner and Özkan-Altiner 2001; Vachard et al. 2006). On the other hand, phylogenetic relationships between Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae are well supported in our tree (see Appendix 1), thus questioning the “traditional” phylogenetic proximity between Globivalvulininae and Paraglobivalvulininae. We hope that further phylogenetic investigations on these groups can provide significant contributions to support our reconstruction.

Looking at the stratigraphic distribution of the analysed taxa (Fig. 3), it is worth noting that the range of the Dagmaritinae is slightly longer than expected on the basis of their phylogenetic position in the tree. In fact, a shorter stratigraphic range (i.e., coinciding at least with that of their sister taxon, the Paradagmaritinae) would be suggested by the tree topology. Pending on new significant palaeontological discoveries involving these groups (i.e., Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae) and/or new phylogenetic analyses of the Globivalvulinidae and related groups, this may be explained, hypothetically, by the fact that the Paraglobivalvulininae and Paradagmaritinae have ghost ranges, i.e., they appeared earlier than as known in literature (at least in the Roadian), so that their available fossil record is still incomplete. Furthermore, worthy to note is that the first appearance datum of Dagmaritinae is based on a single report of *Dagmarita* sp. recorded in the upper part of the Chihhsia Formation (Zheng 1986), whose reliability has already been questioned by Vachard (2016b).

Despite the relatively low number of considered taxa, our phylogenetic analysis has proven to convincingly solve the phylogenetic relationships between them (i.e., Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae). By providing the first reconstruction of the evolutionary history of the Globivalvulinidae through a cladistic approach, this paper also represents a methodological contribution, which could serve as a starting point for similar studies on other groups of fossil Foraminifera.

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## Appendix 1

Supplementary data regarding the phylogenetic analysis.

### Character list

Unordered and unweighted states for all characters.

0. Coiling mode: uncoiled (0); coiled (1).
1. Coiling mode, second stage: uncoiled (0); coiled (1).
2. Coiling mode, trochospiral: present (0); absent (1).  
*Remarks:* We assigned state 0 to Biseriamminidae, Globivalvulininae, Paraglobivalvulininae, and Paradagmaritinae which are at least composed by one genus having a test made by a trochospirally coiled stage; we assigned state 1 to subfamily Dagmaritinae, whose genera are never characterised by trochospirally coiled stage.
3. Coiling mode, completely trochospiral: present (0); absent (1).  
*Remarks:* We coded this character as inapplicable (–) for Dagmaritinae because this group never shows a trochospirally coiled stage (see character 2).
4. Involute test: present (0); absent (1).
5. Wall microgranular with agglutinated grains: present (0); absent (1).
6. Wall, number of layers: one (0); more than one (1).

### Character-taxon matrix

|                       | 0 | 1   | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12  | 13 | 14 | 15 |
|-----------------------|---|-----|---|---|---|---|---|---|---|---|----|----|-----|----|----|----|
| Biseriamminidae       | 1 | 0/1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1  | 1  | 0/1 | 0  | 0  | 1  |
| Globivalvulininae     | 1 | 1   | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0  | 1  | 0   | 0  | 1  | 1  |
| Paraglobivalvulininae | 1 | 1   | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1  | 1  | 0   | 0  | 1  | 0  |
| Dagmaritinae          | 0 | 0   | 1 | – | 1 | 1 | 1 | 0 | 0 | 0 | 1  | 0  | 1   | 0  | 1  | 1  |
| Paradagmaritinae      | 1 | 0   | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0  | 1  | 1   | 1  | 1  | 1  |

### Character state transformations at nodes on the most parsimonious tree

- Node 1: Char. 10: 1 > 0.  
 Node 2: Char. 4: 1 > 0; Char. 15: 1 > 0.  
 Node 3: Char. 0: 1 > 0; Char. 2: 0 > 1; Char. 11: 1 > 0.  
 Node 4: Char. 8: 0 > 1; Char. 10: 1 > 0; Char. 13: 0 > 1.  
 Node 7: Char. 3: 0 > 1.  
 Node 8: Char. 1: 1 > 0; Char. 6: 0 > 1; Char. 12: 0 > 1.

- Remarks:* The taxa showing state 0 include genera with predominantly single layered wall; the taxa showing state 1 include genera with predominantly plurilayered wall.
7. Wall, hyaline or pseudoalveolar layer: present (0); absent (1).
  8. Pseudoalveoli or pores: present (0); absent (1).
  9. Internal partitions, interseptal or peripheral chamberlets: present (0); absent (1).
  10. Supplementary deposits: present (0); absent (1).
  11. Thornlike projections: present (0); absent (1).
  12. Shape of the test: globular/subglobular (0); elongated (1).
  13. Peripheral outline: rounded (0); pinched (1).
  14. Valvular projection: absent (0); present (1).  
*Remarks:* We assigned state 0 to Biseriamminidae which are at least composed by one genus having a simple aperture without a valvular projection; we assigned state 1 to Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae, whose genera are characterised by an aperture protected by a valvular projection.
  15. Apertural chamberlets: present (0); absent (1).