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New foraminifera from the Changhsingian (Upper Permian) of the Taurides (southern Turkey) with remarks on their evolutionary origins

Demir Altıner,[1] Jonathan L. Payne,[2]* Daniel J. Lehrmann,[3] Serdar Görkem Atasoy,[1] and Sevinç Özkan-Altıner[1]

[1]Department of Geological Engineering, Middle East Technical University, Üniversiteler Mahallesi, Dumlupınar Bulvarı No: 1, 06800 Çankaya Ankara, Turkey <demir@metu.edu.tr>, <altiner@metu.edu.tr>, <satasoy@metu.edu.tr>
[2]Department of Geological Sciences, Stanford University, Stanford, CA 94305, USA <jlpayne@stanford.edu>
[3]Department of Geosciences, Trinity University, San Antonio, TX 78212, USA <dlehrmann@trinity.edu>

Non-technical Summary.—New calcareous foraminifera are described from the uppermost Permian (Changhsingian; about 254–252 million years ago) carbonates of southern Turkey and their evolutionary schemes are discussed within the middle to late Permian time frame. Comprising *Retroseptellina*, *Septoglobivalvulina*, and *Paraglobivalvulinoides*, the Retroseptellininae new subfamily originated in the Wordian with thin and dense micrgranular walls and became diverse and abundant in Changhsingian strata. *Paraglobivalvulina*? *intermedia* new species gave way to completely involute tests of Paraglobivalvulininae and survived into the Changhsingian. From the class Miliolata, Midiellidae new family is characterized by sigmoidal coiling and *Pseudomidiella sahini* new species is interpreted as the youngest Changhsingian descendant of this family. *Glomomidiellopsis*? *okayi* new species is interpreted as an evolutionary link between Capitanian *Hemigordiopsis* and Lopingian *Glomomidiellopsis* and survived into the Changhsingian. In Nodosariata, from the fully coiled *Robuloides* lineage of Robuloididae, two smaller species, *R. lens* and *R. acutus*, are each interpreted as ancestral to additional Changhsingian species. *Robuloides lata* new species and *Plectorobuloides taurica* new genus new species most likely originated from *R. lens* in the Changhsingian. The R. *acutus* lineage, characterized by the reduction of laterally thickened hyaline wall and the appearance of evolute coiling, yielded *Robuloides*? *rettorii* new species in the early Lopingian, and *Pseudorobuloides reicheli* new genus new species in the Changhsingian. Among the remaining new Changhsingian taxa, *Calvezina anatolica* new species and *Eomarginulinella galinae* new species belong to evolutionary lineages of weakly coiled Robuloididae, whereas *Pseudocryptomorphina amplimuralis* new genus new species requires further study to determine its precise taxonomic placement. From the family Pachyphloiidae, *Robustopachyphloia farinacciae* new species is a descendant belonging to one of the lineages of *Pachyphloia* in the Changhsingian. The presence of canal-like pores in the walls of some *Pachyphloia* specimens is suggestive of a new morphological structure in the evolutionary history of the Changhsingian foraminifera.

Abstract.—Several new foraminiferal taxa are described from the Changhsingian carbonates of southern Turkey, and their evolutionary relationships are discussed within the middle to late Permian time frame. Comprising *Retroseptellina*, *Septoglobivalvulina*, and *Paraglobivalvulinoides*, Retroseptellininae n. subfam. originated in the Wordian with thin and dense micrograpular walls and became diverse and abundant in Changhsingian strata. *Paraglobivalvulina*? *intermedia* n. sp. appeared in the late Capitanian, survived into the Changhsingian, and gave way to completely involute tests of Paraglobivalvulininae. From the class Miliolata, Midiellidae n. fam., consisting of *Midiella* and *Pseudomidiella*, is characterized by sigmoidal coiling, and *Pseudomidiella sahini* n. sp. is probably the youngest known Changhsingian descendant. *Glomomidiellopsis*? *okayi* n. sp., which is interpreted as an evolutionary link between Capitanian *Hemigordiopsis* and Lopingian *Glomomidiellopsis*, survived into the Changhsingian. In the class Nodosariata, from the fully coiled *Robuloides* lineage of Robuloididae, *Robuloides lata* n. sp. and *Plectorobuloides taurica* n. gen. n. sp. most likely originated from *R. lens* in the Changhsingian. The *R. acutus* lineage, characterized by the reduction of laterally thickened hyaline wall and the appearance of evolute coiling, yielded *Robuloides*? *rettorii* n. sp. and *Pseudorobuloides reicheli* n. gen. n. sp. *Calvezina anatolica* n. sp. and *Eomarginulinella galinae* n. sp. are interpreted to have evolved from weakly coiled lineages in Robuloididae, whereas *Pseudocryptomorphina amplimuralis* n. gen. n. sp. is a poorly understood taxon and requires further study. *Robustopachyphloia farinacciae* n. sp. is interpreted as a descendant of some species within the genus *Pachyphloia.* The presence of canal-like pores in the wall of some

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*Corresponding author

Pachyphloia specimens is suggestive of a new morphological structure in the evolutionary history of the Changhsingian foraminifera.

Introduction

In the description of new foraminiferal taxa, it has been always useful to propose tentative evolutionary models or schemes depicting the phyletic relationships of new forms to closely related taxa for stimulating further hypothesis testing around evolutionary relationships. The middle to late Permian smaller foraminiferal inventory and their assemblage composition have been continuously enriched and renewed by the description of new taxa since the mid twentieth century (e.g., Reichel, 1946; Miklukho-Maklay, 1954; Crespin, 1958; Gerke, 1961; Reitlinger, 1965; Sellier de Civrieux and Dessauvagie, 1965; Zhao et al., 1981; Gaillot and Vachard, 2007). As the number of described species passed a minimum threshold, studies testing the evolutionary relationships of new taxa to previously described late Paleozoic smaller foraminifera increased notably in the last 50 years (Altıner, 1981, 1988, 1997, 1999; Zaninetti and Altıner, 1981; Zaninetti et al., 1982; Palmieri, 1983, 1994; Gargouri and Vachard, 1988; Vachard and Razgallah, 1988; Vachard et al., 1994, 2003, 2005, 2006, 2008, 2010; Pinard and Mamet, 1998; Altıner and Özkan-Altıner, 2001, 2010; Mohtat-Aghai and Vachard, 2003; Gaillot and Vachard, 2007; Gennari et al., 2018; Gennari and Rettori, 2019, 2020). These studies considerably advanced understanding of the major taxonomic units, especially at the family rank, which includes several distinct genera and their species. Recently, Vachard (2016, 2018) modified and revised the taxonomic framework of late Paleozoic smaller foraminifera developed by Loeblich and Tappan (1988), Vdovenko et al. (1993), Rauzer-Chernousova et al. (1996), and Ross (1999), and presented an up-to-date classification, focusing particularly on Permian smaller foraminiferal families and the genera classified within them.

This study, following Vachard (2018), aims to enrich the taxonomic framework of Permian calcareous foraminifera with the description of new taxa recovered from 17 stratigraphic sections measured at 10 localities of the Taurus Belt in southern Turkey. The new taxa comprise one new family from the Class Miliolata Saidova, 1981, one new subfamily from the Class Fusulinata Gaillot and Vachard, 2007, three new genera from the Class Nodosariata Mikhalevich, 1993, and 11 new species from Miliolata, Fusulinata, and Nodosariata. A discussion with figures depicting proposed phyletic relations of new taxa is given in the second part of the manuscript in order to consolidate the validity of new taxa within the taxonomic framework of Vachard (2018).

Geological setting

The present foraminiferal study is based on samples from stratigraphic sections measured on Changhsingian outcrops of the Southern Biofacies Belt in Turkey. This belt, previously recognized and described by Altıner et al. (2000, 2021a) as part of the middle–late Permian paleogeography in Turkey, is characterized by low-energy, micritic, inner-platform deposits exposed both in the Taurides (southern Turkey) and the Arabian Platform (southeastern Anatolia). It was, in fact, part of a vast carbonate platform of middle to late Permian age extending from northern Gondwana to the southern continental margin of the Paleotethys (Altıner et al., 2000). Outcrops of the Southern Biofacies Belt (Fig. 1) occur today as tectonic slices in the Taurides, which formed during the Late Cretaceous to Tertiary orogeny that was related to the nearly complete closure of the Neotethys (Özgül, 1976, 1984; Şengör and Yılmaz, 1981; Altıner and Özgül, 2001).

The Southern Biofacies Belt is characterized by the *Eopolydiexodina* Province unaccompanied by neoschwagerinid and verbeekinid fusulines and the *Shanita* Province in the middle Permian, and the *Paradagmarita* Province in the Changhsingian (upper Permian) (Şengör et al., 1988, 2023; Altıner et al., 2021a). The *Paradagmarita* Province, containing the areas where the new foraminiferal taxa are described in this study, extends from the Taurides, via southeastern Anatolia, to the Zagrides in Iran, Oman, and Saudi Arabia, and constitutes an endemic faunal province in the Changhsingian of western Gondwana.

Stratigraphic sections

The studied Changhsingian sections come from outcrops of the three major tectonic units in the central and eastern Taurides. The Gazipaşa, Demirtaş, Olimpus, Kesmeboğazı, Çürükdağ, and Koçular–Barak sections are from the Antalya Nappes. The Hadim, Taşkent, and Aygörmez Dağı sections belong to the Aladağ Nappe. The Köserelik Tepe section is from the Geyik Dağı Unit, which constitutes the parautochthon/autochthon of the Taurus Belt (Fig. 1).

Antalya Nappes.—Mainly composed of algal and foraminiferal limestones, the Changhsingian constitutes the uppermost part of the middle to upper Permian rocks (Özgül, 1984; Şahin and Altıner, 2019; Altıner et al., 2021a). Capped by an ooidal limestone level less than 1 m thick, the Changhsingian carbonates are conformably overlain by microbial limestones or stromatolites of the Kokarkuyu Formation (Altıner, 1981) of Griesbachian age in the Gazipaşa, Demirtaş, Çürükdağ, and Koçular–Barak sections and unconformably overlain by the variegated shales of the Akıncıbeli Formation of Olenekian age at the Olimpus sections (Fig. 1). The lower boundary of the Changhsingian stage with the underlying Wuchiapingian strata was observed only in the Gazipaşa and Olimpus sections.

Coordinates of the bases of the measured sections are as follows: Gazipaşa ASRTP: 36°21′33″N, 32°22′39″E; ÖRCN: 36°19′60″N, 32°21′37″E. Demirtaş TRLR: 36°28′57″N, 32°15′05″E; DD: 36°28′36″N, 32°14′36″E. Olimpus OLP-1/1: 36°23′05″N, 30°27′31″E; OLP-1/2: 36°23′26″N, 30°27′35″E; OLP-3: 36°23′35″N, 30°27′25″E. Kesmeboğazı KSMBGZ: 36°36′01″N, 30°29′12″E. Çürükdağ ÇÜ-1: 36°41′30″N, 30°27′38″E. Koçular–Barak BRK-1: 37°44′44″N, 31°05′58″E.

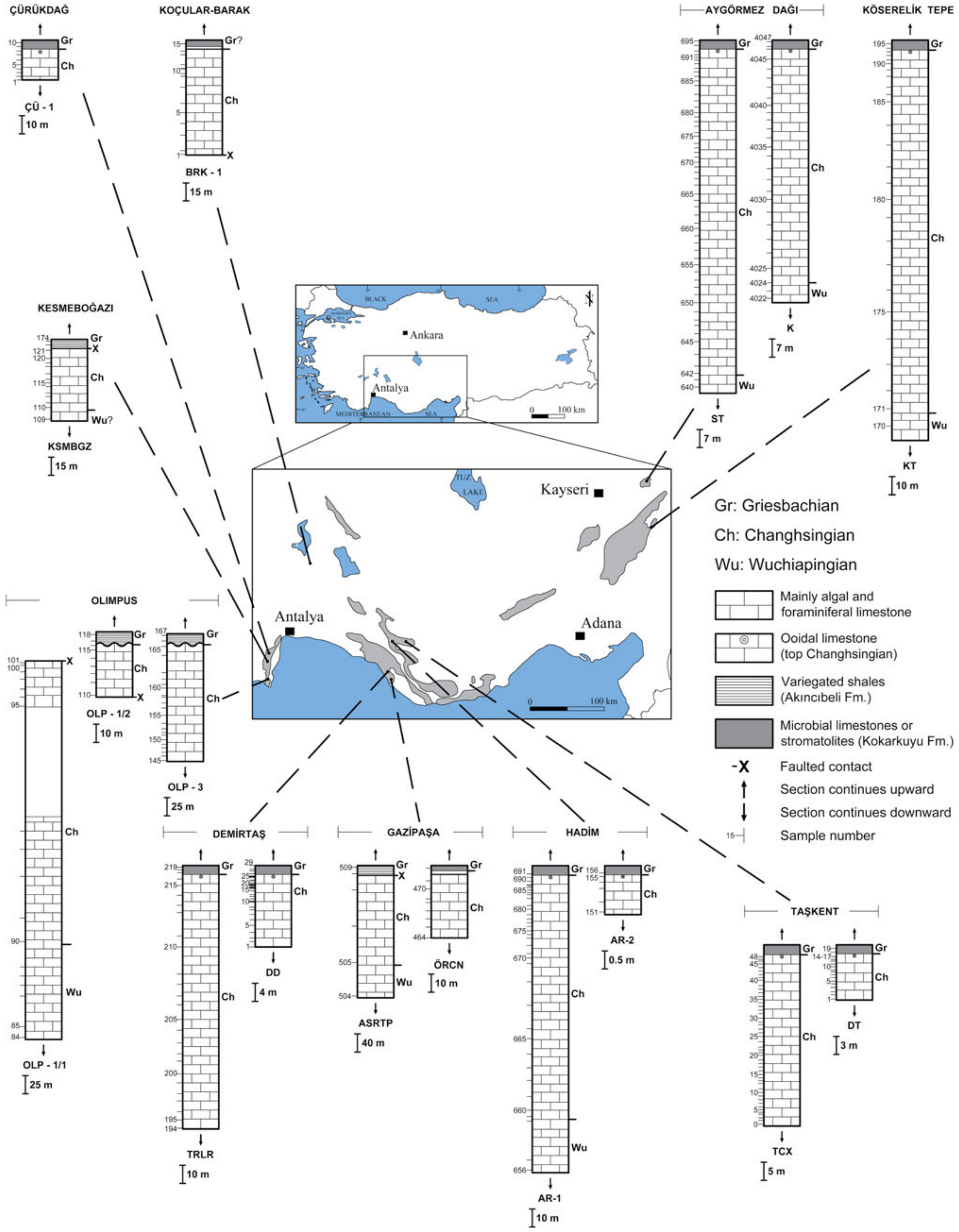


Figure 1. Location map and Changhsingian carbonate sections measured in the outcrops (gray areas) of the Southern Biofacies Belt (Altıner et al., 2000) in southern Turkey.

Aladağ Nappe.—The Changhsingian stage in the Hadim, Taşkent, and Aygörmez Dağı sections, like in the Antalya Nappes, conformably overlies the Wuchiapingian carbonates (Fig. 1). Entirely composed of algal and foraminiferal micritic limestones, the last 60 cm of the Changhsingian is composed of ooidal limestone. At the Permian–Triassic boundary, the youngest oolitic bed is overlain by the lowermost Griesbachian stromatolites and microbial limestones (Altıner, 1981; Özgül, 1997; Altıner and Özgül, 2001).

Coordinates of the base of measured sections in the Aladağ Nappe are as follows: Hadim AR-1: 36°53′08″N, 32°23′01″E; AR-2: 36°52′51″N, 32°23′26″E. Taşkent TCX: 36°48′42″N, 32°33′03″E; DT: 36°48′22″N, 32°33′18″E. Aygörmez Dağı ST: 38°46′12″N, 36°13′05″E; K: 38°45′16″N, 36°14′10″E.

Geyik Dağı Parautochthon/Autochthon.—Located in the eastern segment of the Taurides, the Changhsingian carbonates (coordinates of the base of the section: Köserelik Tepe KT: 38°14′47″N, 36°21′47″E) overlie the Wuchiapingian without any obvious unconformity (Fig. 1) and are capped by an ooidal limestone layer, which is the typical lithology indicating the top of the Permian System in the Southern Biofacies Belt (Altıner et al., 2000). Microbial limestones and stromatolites of the Griesbachian Kokarkuyu Formation (Altıner, 1981) of the Katarası Group (Özgül et al., 1973) overlie the Changhsingian carbonates.

Materials

We collected 341 samples for foraminiferal taxonomy and biostratigraphy from the stratigraphic sections measured in the Changhsingian strata of the Southern Biofacies Belt of Altıner et al. (2000) that crop out in the central and eastern Taurides. Thin sections were prepared from all samples in order to recover smaller foraminifera embedded in the carbonate lithology. Nearly all thin sections contain at least 10 randomly sectioned foraminiferal specimens. The total number of foraminiferal specimens was too large to count, but probably exceeded 5000, of which 112 specimens were illustrated for the description of new taxa in the figures of this manuscript.

Foraminifers recovered from the samples collected along the Changhsingian sections were first used by Altıner et al. (2021a) for the description of a new dagmaritin foraminifer, *Paynita*, and other dagmaritin foraminifers associated with *Paynita*. The scope of our research is, however, distinct from and more comprehensive than the dagmaritin taxonomy and phylogeny given in Altıner et al. (2021a). The current study is mainly focused on the taxonomic descriptions of some new taxa from Fusulinata, Miliolata, and Nodosariata and their phyletic relations with the previously described Permian foraminifera.

Repositories and institutional abbreviations.—Types, figures, and other specimens examined in this study are deposited in the thin-section laboratory in the Department of Geological Engineering, Middle East Technical University, with the following catalog abbreviations: Gazipaşa (ASRTP and ÖRCN), Demirtaş (TRLR and DD), Olimpus (OLP-1/1, OLP-1/2, and OLP-3), Kesmeboğazı (KSMBGZ), Çürükdağ (ÇÜ-1), Koçular–Barak (BRK-1), Hadim (AR-1 and AR-2), Taşkent (TCX and DT), Aygörmez Dağı (ST and K), and Köserelik Tepe (KT).

Systematic paleontology

Following Altıner et al. (2021b), we largely use the studies of Vachard (2016, 2018) for generic and suprageneric classification of foraminifera. This classification deals with the hierarchical grouping of distinct populations, from species to families, based on wall structure and composition, and other morphological characters. Following the taxonomic notes in Altıner et al. (2021b), higher intermediate taxonomic ranks, including superfamily, suborder, and order, have not been used in this study because these ranks are less stable in their use across taxonomic studies of foraminifera. For the largest groups of foraminifera that include families with similar wall microstructure, we largely follow the classes defined in Vachard (2016, 2018).

Phylum Foraminifera d'Orbigny, 1826
nom. translated Cavalier-Smith, 2002 (subphylum) and 2003 (phylum)
Class Fusulinata Gaillot and Vachard, 2007

Remarks.—Class Fusulinata, possessing a microgranular low-Mg calcite wall, commonly to frequently occurs in the Changhsingian Stage of the Southern Biofacies Belt in Turkey (Altıner et al., 2000). Among smaller foraminiferal families of Fusulinata, Endothyridae Rhumbler, 1895, and Bradyinidae Reitlinger, 1950, are rare and sporadic; Paleotextulariidae Galloway, 1933, Endotebidae Vachard et al., 1994, and Tetrataxidae Pokorny, 1958, are absent. However, Globivalvulinidae Reitlinger, 1950, is diverse and abundant, represented by several genera and species.

Family Globivalvulinidae Reitlinger, 1950, emend. Gaillot and Vachard, 2007

Remarks.—As previously stated by Altıner et al. (2021a), globivalvulinid foraminifera evolved rapidly and split into subgroups with distinct evolutionary trends during the middle to late Permian. This evolution occurred in two major lineages: (1) the globivalvulins, which exhibit globular chambers; and (2) the dagmaritins, which exhibit angular chambers. From these two lineages, the globivalvulins, comprising *Globivalvulina* Schubert, 1921, and all allied genera, were subdivided into two subfamilies by Gaillot and Vachard (2007): Globivalvulininae Reitlinger, 1950, and Paraglobivalvulininae Gaillot and Vachard, 2007. Vachard (2018) directly adopted this taxonomy. In this study, we propose Retroseptellininae new subfamily, grouping some of the phylogenetically related taxa previously included either in Globivalvulininae or Paraglobivalvulininae. The second taxon that we describe as *Paraglobivalvulina*? *intermedia* n. sp. is considered to be an early lineage and to represent the ancestral state in the evolution of the subfamily Paraglobivalvulininae.

Subfamily Retroseptellininae new subfamily

Type genus.—*Retroseptellina* Gaillot and Vachard, 2007.

Other genera.—*Septoglobivalvulina* Lin, 1978; *Paraglobivalvulinoides* Zaninetti and Jenny-Deshusses, 1985.

Diagnosis.—A subfamily of Globivalvulinidae mainly characterized by a thin, dense, and simple microgranular wall; earlier irregularly coiled biserial taxa evolute and semi-involute with long apertural flaps and septa curved backward; later taxa involute, with almost entirely enveloping last chamber, hooklike apertural flaps, and interseptal secondary partitions.

Occurrence.—Wordian–Changhsingian, Tethys (Lin, 1978; Zaninetti and Jenny-Deshusses, 1985; Köylüoğlu and Altıner, 1989; Gaillot and Vachard, 2007; Vachard, 2018).

Remarks.—In many of the earlier and some of the recent studies, the specimens belonging to retroseptellinin foraminifera were identified either under the genus *Globivalvulina* or the genus *Paraglobivalvulina* Reitlinger, 1965, of biserially enrolled globivalvulinid stock (Bozorgnia, 1973; Lys et al., 1980; Altıner, 1981; Johnson, 1981; Zaninetti and Altıner, 1981; Jenny-Deshusses, 1983; Kotlyar et al., 1984, 1989; Pasini, 1985; Noe, 1987; Köylüoğlu and Altıner, 1989; Ueno and Sakagami, 1993; Kobayashi, 1997, 2004; Pronina-Nestell and Nestell, 2001; Ünal et al., 2003; Jenny et al., 2009; Koehrer et al., 2010; Nestell et al., 2011). In the taxonomic revision of the family Globivalvulinidae and its genera, Gaillot and Vachard (2007) recognized *Retroseptellina* as a member of the subfamily Globivalvulininae, and placed *Septoglobivalvulina* and *Paraglobivalvulinoides* in the subfamily Paraglobivalvulininae. In subsequent studies, these authors did not strictly follow this classification. Gaillot et al. (2009) placed *Retroseptellina*, *Septoglobivalvulina*, and *Paraglobivalvulinoides* in the subfamily Globivalvulininae. Vachard (2018) preferred to keep *Retroseptellina* and *Septoglobivalvulina* in the subfamily Globivalvulininae and placed *Paraglobivalvulinoides* in the subfamily Paraglobivalvulininae.

In the description of Retroseptellininae n. subfam., comprising *Retroseptellina* (*R. decrouezae* [Köylüoğlu and Altıner, 1989], Fig. 2.1–2.5; *R. globosa* [Wang in Zhao et al., 1981], Fig. 2.6–2.8), *Septoglobivalvulina* (*S. distensa* [Wang in Zhao et al., 1981], Fig. 2.9–2.12; *S. guangxiensis* Lin, 1978, Fig. 2.13–2.15), and *Paraglobivalvulinoides* (*P. gracilis* [Zaninetti and Altıner, 1981], Fig. 2.16–2.19; *P. septulifer* [Zaninetti and Altıner, 1981], Fig. 3.1), the morphologic changes within a certain lineage characterized by a distinct wall structure are considered as the main criteria to define this new subfamily, rather than classifying these genera under two previously defined subfamilies, as seen in the study of Gaillot and Vachard (2007).

The evolution of the retroseptellinin lineage separately from globivalvulinins and paraglobivalvulinins, with a thin and simple microgranular wall, a long and folded apertural flap, and irregular coiling, was first proposed by Altıner and Özkan-Altıner (2001), who considered *Retroseptellina* (given there as *Globivalvulina decrouezae* Köylüoğlu and Altıner, 1989, the type species of *Retroseptellina* Gaillot and Vachard, 2007) as the root stock of this evolution. Altıner and Özkan-Altıner (2001) further stated that even highly evolved *Paraglobivalvulinoides* could be linked to the evolutionary lineage of *Retroseptellina* and *Septoglobivalvulina* characterized by a very fine-grained, thin- and single-layered microgranular wall. Thus, following Altıner and Özkan-Altıner (2001), this group of thin and microgranular wall-bearing foraminifera comprising forms characterized by evolute to semi-involute to completely involute tests are gathered together within Retroseptellininae n. subfam. in this study. We agree again with Altıner and Özkan-Altıner (2001) in interpreting that the completely involute, globular chambered, true paraglobivalvulinid forms were derived from the *Globivalvulina graeca*–*Globivalvulina vonderschmitti* lineage characterized by the granular aspect of their multilayered walls (see also the description of the walls of the types of the *Globivalvulina* species in Reichel, 1946). *Globivalvulina vonderschmitti* Reichel, 1946 (Fig. 3.2) and *Paraglobivalvulina mira* Reitlinger, 1965 (Fig. 3.3) from our Changhsingian material clearly display the granular aspect of the wall structure of globivalvulinins and paraglobivalvulinins, which is markedly different from the compact, dense, and thin microgranular wall structure of retroseptellinin genera. Thus, the globivalvulinids, which are characterized by globular chambers in the middle to late Permian, are divided into two distinct groups distinguished by wall composition and structure: Globivalvulininae (including the paraglobivalvulinins of Gaillot and Vachard, 2007) and Retroseptellininae n. subfam. In a recent study, Gennari and Rettori (2019), agreeing with the scheme proposed by Altıner and Özkan-Altıner (2001), also considered the *Retroseptellina*–*Septoglobivalvulina* lineage as a separate evolutionary trend derived from a *Globivalvulina* ancestor.

Subfamily Paraglobivalvulininae Gaillot and Vachard, 2007

Genus *Paraglobivalvulina* Reitlinger, 1965

Type species.—*Paraglobivalvulina mira* Reitlinger, 1965, from the territory of Transcaucasus.

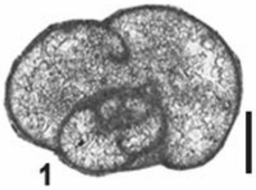
Paraglobivalvulina? *intermedia* new species

Figure 3.4–3.11

1970	*Globivalvulina graeca* Reichel; Canuti et al., fig. 14.1.
1981	*Globivalvulina vonderschmitti* Reichel?; Altıner, p. 286–287, pl. 36, fig. 12.
1981	*Paraglobivalvulina mira* Reitlinger; Zaninetti and Altıner, pl. 1, figs. 3, 4, 6, 7, 9.
1981	*Paraglobivalvulina mira*; Zaninetti, Altıner, and Çatal, p. 8, pl. 10, figs. 6, 8, 10–12, 14.
1989	*Paraglobivalvulina mira*; Köylüoğlu and Altıner, pl. 7, fig. 1.
2005	Aberrant morphologies for *Paraglobivalvulina*; Jenny and Guex, fig. 3c.
2007	*Paraglobivalvulina mira*; Gaillot and Vachard, p. 61, pl. 32, figs. 3, 19; pl. 39, figs. 4–7.
2015	*Paraglobivalvulina mira*; Nejad et al., p. 18, fig. 10.11.

Holotype.—The specimen is from sample ST 666, thin section B (Aladağ Nappe, Aygörmez Dağı, ST section) (Fig. 3.4).

Diagnosis.—A species doubtfully assigned to *Paraglobivalvulina* with evolute to semi-involute coiling,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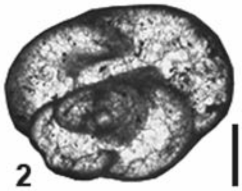
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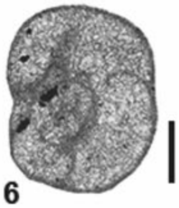
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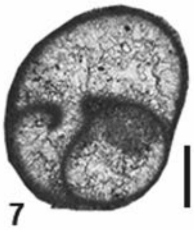
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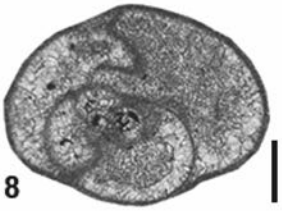
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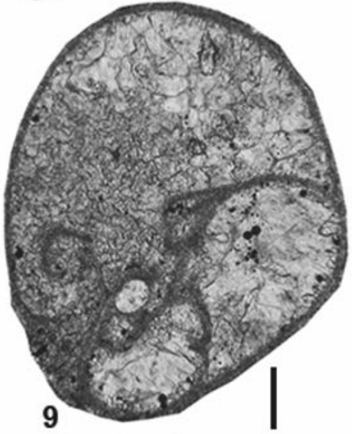
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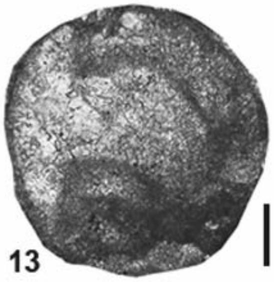
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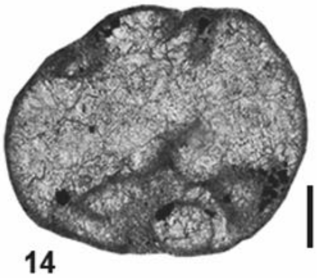
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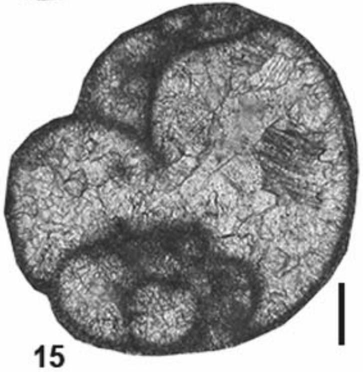
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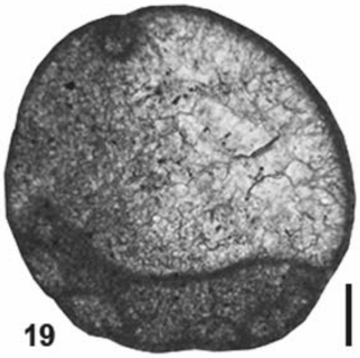
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Figure 2. Specimens belonging to Retroseptellininae new subfamily from Changhsingian carbonates of southern Turkey. (**1–5**) *Retroseptellina decrouezae* (Köylüoğlu and Altıner, 1989); (**6–8**) *Retroseptellina globosa* (Wang in Zhao et al., 1981); (**9–12**) *Septoglobivalvulina distensa* (Wang in Zhao et al., 1981); (**13–15**) *Septoglobivalvulina guangxiensis* Lin, 1978; (**16–19**) *Paraglobivalvulinoides gracilis* (Zaninetti and Altıner, 1981). (**1**) TCX 40.5; (**2**) TCX 47; (**3**) ST 660; (**4**) TCX 35; (**5**) DT 1; (**6, 16**) TK 2.05 (equivalent of DT 14); (**7**) TCX 4; (**8, 14**) DD 6; (**9**) AR-1 666; (**10**) BRK 9; (**11**) ST 683; (**12**) DT 11; (**13**) DT 12; (**15**) ST 662; (**17**) ST 663; (**18**) ST 664; (**19**) DT 5. Scale bars = 100 μm.

apertural flaps displaying either hook-shaped or planar, straight sections defining sometimes narrow V-shaped structures between the opposing chambers and weakly developed interseptal secondary partitions.

Occurrence.—Changhsingian. ST, TCX, AR-1, and DT sections of the Aladağ Nappe in the eastern and central Taurides, Turkey (Fig. 1). Earliest known occurrence is from the upper Capitanian of the Hakkari region, SE Anatolia (Köylüoğlu and Altıner, 1989).

Description.—The evolute to semi-involute test of *Paraglobivalvulina*? *intermedia* n. sp. consists of three to four pairs of biserial chambers coiled in 1–1.5 whorls. Globular to subglobular chambers increase rapidly in height. Early chambers are semi-involute, last pair of chambers are nearly evolute, not embracing the previous chambers. Apertural flaps in the second and third pairs of chambers are sometimes short and hook-shaped or in the form of long, straight planes attached to septal edges. In axial or tangential sections, the apertural flaps define a narrow V-shaped structure between the opposing chambers of the last pair. Poorly developed interseptal secondary partitions are visible in some sections. The wall, with a thin hyaline outer layer, is granular, sometimes thick, like that of the typical *Paraglobivalvulina*.

Etymology.—We have used the species name '*intermedia*' in order to define the transitional character of the new species between *Globivalvulina* and *Paraglobivalvulina*.

Materials.—Samples ST 658, 659, 666; TCX 40.5, 43, 45; AR-1 678; DT 11 (Changhsingian, Fig. 1). More than 30 specimens, eight of which are illustrated in Figure 3.4–3.11.

Microfossil association.—Several foraminiferal species occur in association with *Paraglobivalvulina*? *intermedia* n. sp. The most commonly encountered species are *Paynita permotaurica* Altıner et al., 2021a, *Paradagmarita monodi* Lys in Lys and Marcoux, 1978, *P. planispiralis* Gaillot and Vachard, 2007, *Paradagmacrusta callosa* Gaillot and Vachard, 2007, *Louisettita elegantissima* Altıner and Brönnimann, 1980, *Septoglobivalvulina distensa*, *Okimuraites linae* (Vachard and Gaillot in Vachard et al., 2005), *Ichthyofrondina latilimbata* (Sellier de Civrieux and Dessauvagie, 1965), *I. palmata* (Wang in Nanjing Institute of Geology and Paleontology, 1974), *Nestellorella acus* (Pronina, 1989), *Nodosinelloides sagitta* (Miklukho-Maklay, 1954), *Robuloides lens* Reichel, 1946, *R. acutus* Reichel, 1946, *Calvezina ottomana* Sellier de Civireux and Dessauvagie, 1965, and *Aulacophloia martiniae* Gaillot and Vachard, 2007.

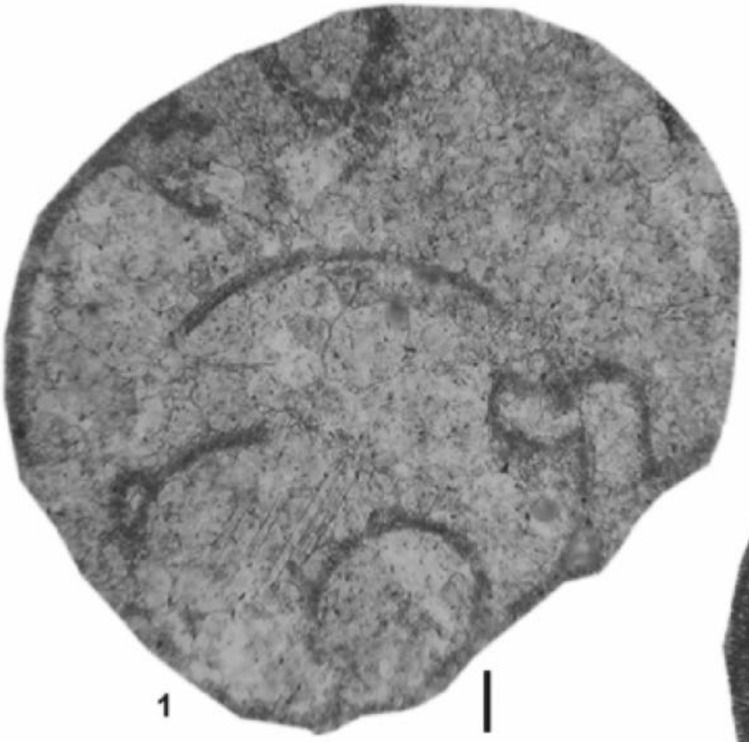
Dimensions.—Diameter of proloculus: 100–120 μm (holotype: 120 μm). Diameter of test: 520–780 μm (holotype: 780 μm). Width of test: 500–620 μm (holotype: 620 μm). Diameter/width: 1.04–1.27 (holotype: 1.26). Height of last chamber: 260–380 μm (holotype: 380 μm). Thickness of wall: 25–35 μm (holotype: 35 μm).

Remarks.—*Paraglobivalvulina*? *intermedia* n. sp. differs from *Paraglobivalvulina mira*, type species of the genus *Paraglobivalvulina* of Reitlinger (1965), in having semi-involute to evolute coiling instead of being totally involute. As can be seen in the specimen illustrated from the Changhsingian material (Fig. 3.3), *Paraglobivalvulina mira* is characterized by the resorption of the initial spire within the chambers of the last pair of the test. *Paraglobivalvulina*? *intermedia* n sp. differs also from the *Globivalvulina graeca*–*G. vonderschmitti* lineage (see Fig. 3.2, *G. vonderschmitti* Reichel, 1946), from which it probably originated, by the absence of the inner pseudofibrous layer in the wall structure, the presence of apertural flaps showing morphological variations from hook-shaped to straight, planar sections, and weakly developed interseptal secondary partitions. By these morphological features, *P.*? *intermedia* n. sp. is interpreted as an intermediate species establishing the evolutionary link between *Globivalvulina* and *Paraglobivalvulina*. The new species has been doubtfully assigned to *Paraglobivalvulina* because of the absence of a totally involute test.

Globivalvulina graeca Reichel, 1946, illustrated by Canuti et al. (1970, fig. 14.1) from the Hazro area (SE Anatolia, Turkey) should be referred to *P.*? *intermedia* n. sp. Several forms reported as *Paraglobivalvulina mira* in the morphological analysis of biserially enrolled involute foraminifera of Tethys by Zaninetti and Altıner (1981), from the Changhsingian of the Geyikdağı autochthon/parautochthon (eastern Taurides) by Zaninetti et al. (1981), and the middle–upper Permian of the Hakkari region (SE Anatolia) by Köylüoğlu and Altıner (1989) are synonyms of *Paraglobivalvulina*? *intermedia* n. sp. The specimen doubtfully referred to *G. vonderschmitti* from the Changhsingian of the Aladağ Nappe in the eastern Taurides by Altıner (1981) should also be considered as an intermediate form between *Globivalvulina* and *Paraglobivalvulina mira*. Forms illustrated as "aberrant morphologies for *Paraglobivalvulina*" in Jenny and Guex (2005, fig. 3c) also belong to *Paraglobivalvulina*? *intermedia* n. sp. Some of the *P. mira* specimens reported from the Changhsingian of the Kuh-e Surmeh section (Zagrides, Iran) by Gaillot and Vachard (2007, pl. 32, figs. 3, 19; pl. 39, figs. 4–7) also should be considered as *P.*? *intermedia* n. sp. because the last pair of chambers in these specimens does not strongly envelop the earlier ones and morphological variations in the apertural flaps of these forms are similar to our specimens.

Class Miliolata Saidova, 1981

Remarks.—This class, consisting of foraminifers with porcelaneous walls, occurs commonly to frequently in the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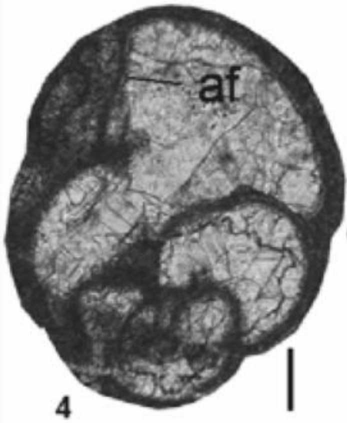

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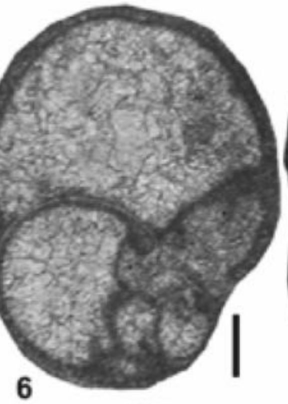
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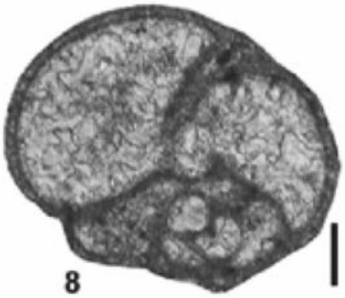
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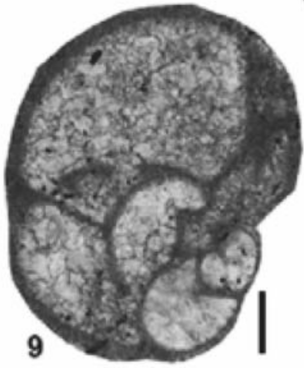
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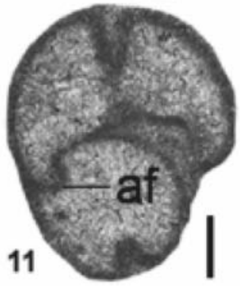

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Figure 3. Specimens belonging to Retroseptellininae new subfamily, Globivalvulininae, and Paraglobivalvulininae from Changhsingian carbonates of southern Turkey (af = apertural flap). (**1**) *Paraglobivalvulinoides septulifer* (Zaninetti and Altıner, 1981); (**2**) *Globivalvulina vonderschmitti* Reichel, 1946; (**3**) *Paraglobivalvulina mira* Reitlinger, 1965; (**4–11**) *Paraglobivalvulina*? *intermedia* new species, (**4**) holotype, sample ST 666, thin section B (Aladağ Nappe, Aygörmez Dağı, ST section). (**1**) DT 12; (**2**) AR-1 677; (**3**) K 4027; (**4, 8**) ST 666; (**5**) ST 658; (**6**) ST 659; (**7**) TCX 43; (**9**) TCX 40.5; (**10**) TCX 45; (**11**) AR-1 678. Scale bars = 100 µm.

Changhsingian material of the Southern Biofacies Belt in Turkey (Fig. 1). The morphologically primitive families Calcivertellidae Reitlinger in Vdovenko et al., 1993, Agathamminidae Ciarapica, Cirilli, and Zaninetti in Ciarapica et al., 1987, and Cornuspiridae Schultze, 1854, are generally sporadic; however, more-advanced families comprising Hemigordiidae Reitlinger in Vdovenko et al., 1993, Neodiscidae Lin, 1984, Baisalinidae Loeblich and Tappan, 1986a, and Hemigordiopsidae Nikitina, 1969, are common to frequent, sometimes in rock-forming abundance. Among new taxa described in this study, Midiellidae n. fam., characterized by sigmoidal coiling, adds to the taxonomic inventory of the families of Miliolata. *Pseudomidiella sahini* n. sp. belongs to this new family. The other new species, *Glomomidiellopsis*? *okayi*, belongs to the family Hemigordiopsidae, which encompasses the largest forms of the Paleozoic Miliolata.

Family Midiellidae new family

Type genus.—*Midiella* Pronina, 1988.

Other genera.—*Pseudomidiella* Pronina-Nestell in Pronina-Nestell and Nestell, 2001.

Diagnosis.—A family of the class Miliolata characterized by involute tests with lateral thickenings and sigmoidal coiling. In advanced genera, the second tubular chamber divided into pseudochambers by short, triangular pseudosepta. Aperture a simple opening at the end of the tubular chamber.

Occurrence.—Middle–upper Permian, Tethys (Altıner, 1978, 1981; Gaillot and Vachard, 2007; Vachard, 2018). Questionable occurrence in the lower Permian (Gaillot and Vachard, 2007).

Remarks.—Based on the types of *Hemigordius bronnimanni* Altıner, 1978 (re-illustrated in Altıner, 1981, 1984, and in a drawing in Altıner et al., 2003), Pronina (1988) established the genus *Midiella* for *Hemigordius*-like inflated forms characterized by sigmoidal coiling. Pronina-Nestell in Pronina-Nestell and Nestell (2001) classified *Midiella* and her newly created genus *Pseudomidiella* within the subfamily Hemigordiinae Pronina, 1994, of the family Hemigordiopsidae. In Vachard (2018), *Midiella* was questionably placed in the family Neodiscidae and *Pseudomidiella* in Baisalinidae. In this study, considering the phyletic relations of the porcelaneous foraminifera in the late Paleozoic, we group *Midiella* and *Pseudomidiella* within the same lineage and erect Midiellidae as a new family, housing these porcelaneous foraminifera with a sigmoidal coiling trend.

Genus *Pseudomidiella* Pronina-Nestell in Pronina-Nestell and Nestell, 2001

Type species.—*Pseudomidiella labensis* Pronina-Nestell in Pronina-Nestell and Nestell, 2001, from northwestern Caucasus, Severnaya Ravine, Nikitan calcareous lithofacies (algal-foraminiferal limestone).

Pseudomidiella sahini new species
Figure 4.7–4.12

1981 *Baisalina pulchra* Reitlinger; Altıner, pl. 45, figs. 7, 8.
1984 *Baisalina pulchra*; Altıner, pl. 2, fig. 8.

Holotype.—Sample K 4028, thin section B (Aladağ Nappe, Aygörmez Dağı, K section) (Fig. 4.8).

Diagnosis.—A species of *Pseudomidiella* with an inflated lenticular to ovate test consisting of six to eight whorls. *Midiella*-like sigmoidal coiling with three to five whorls in the early stage, tending later to become oscillating to planispiral. Five to six pseudochambers divided by triangular pseudosepta in the final whorl.

Occurrence.—Changhsingian. K and ST sections of the Aladağ Nappe in the eastern Taurides, Turkey (Fig. 1).

Description.—The population of *Pseudomidiella sahini* n. sp. consists of two different generations. The microspheric generation, following a small proloculus, is characterized by a *Midiella*-like sigmoidal coiling and consists of three to five whorls in the initial stage and sigmoidal to planispiral coiling in the last two to three whorls (Fig. 4.7, 4.8). The position of the coiling axis gradually changes, rotating 90° from the initial stage to the adult stage. In the megalospheric generation, the sigmoidal coiling, which is irregular in the initial stage, tends to become more regular in the adult stage (Fig. 4.9). The height of the tubular chamber increases more prominently toward the last whorls. The test is inflated lenticular to ovate in axial sections with considerable lateral thickenings. Pseudosepta are visible starting from the third whorl. The number of pseudochambers divided by triangular pseudosepta is generally five in the last whorl. The wall is thick, compared to the volume of the test, and the aperture is at the open end of the pseudochambers partly closed by pseudosepta.

Etymology.—*Pseudomidiella sahini* n. sp. is dedicated to the geologist Nazif Şahin from the Turkish Petroleum Corporation (TPAO) for his contributions to the understanding of tectonic structure and stratigraphy of the Tauride Belt in Turkey.

Materials.—Samples K 4028; ST 673 (Changhsingian, Fig. 1). More than 30 specimens recognized in oriented and unoriented sections. Six specimens from this population are illustrated in Figure 4.7–4.12.

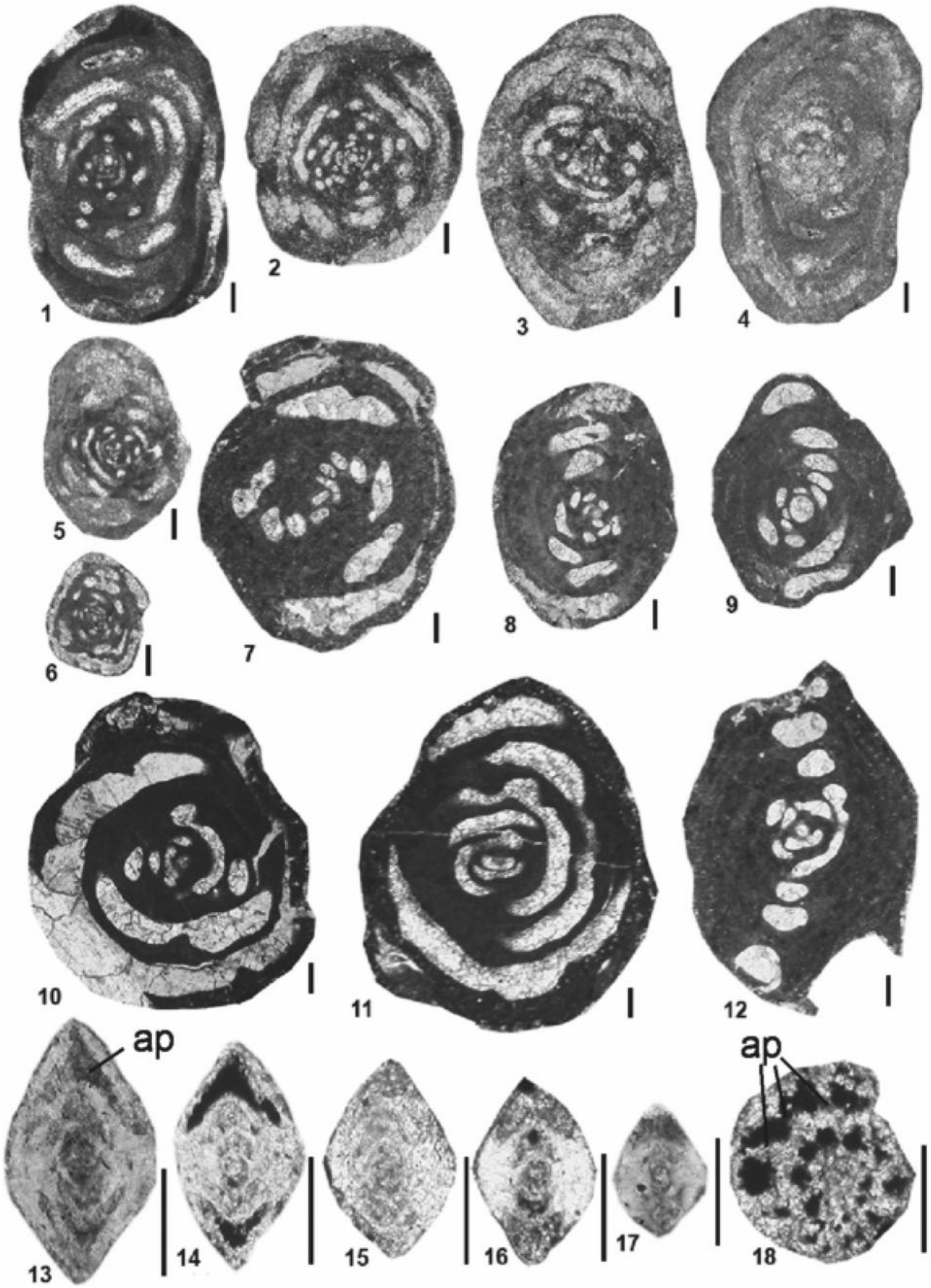
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Figure 4. Specimens belonging to Hemigordiopsidae, Midiellidae new family, and Robuloididae from Changhsingian carbonates of southern Turkey (ap = aperture). (**1–6**) *Glomomidiellopsis*? *okayi* new species, (**1**) holotype, sample ST 671, thin section C (Sarpkaya Tepe, ST section); (**7–12**) *Pseudomidiella sahini* new species, (**8**) holotype, sample K 4028, thin section B (Aladağ Nappe, Aygörmez Dağı, K section); (**13–18**) *Robuloides lata* new species, (**14**) holotype, sample DD 4, thin section number 1 (Antalya Nappes, Demirtaş area, DD section). (**1**) ST 671; (**2, 3, 9**) ST 673; (**4**) DD 10; (**5, 6**) ST 665; (**7, 8, 10–12**) K 4028; (**13**) TCX 40.5; (**14, 15**) DD 4; (**16, 18**) DD 6; (**17**) TCX 11. Scale bars = 100 μm.

Microfossil association.—Pseudomidiella sahini n. sp. is associated with a large number of foraminiferal species including *Paradagmarita monodi*, *Dagmarita chanakchiensis* Reitlinger, 1965, *Louisettita elegantissima*, *Paraglobivalvulina mira*, *Codonofusiella* sp., *Glomomidiellopsis lysitiformis* Gaillot and Vachard, 2007, *Hemigordius irregulariformis* Zaninetti, Altıner, and Çatal, 1981, *Midiella bronnimanni* (Altıner, 1978), and *Polarisella elabugae* (Cherdyntsev, 1914).

Dimensions.—Diameter of proloculus: 50–60 μm (microspheric), 100 μm (macrospheric) (holotype 50 μm). Diameter of test: 730–1240 μm (holotype: 970 μm). Width of test: 600–860 μm (holotype: 710 μm). Diameter/width: 1.22–1.44 (holotype: 1.36). Height of lumen of last whorl: 100–120 μm (holotype: 100 μm). Thickness of wall: 30–40 μm (holotype: 30 μm).

Remarks.—Pseudomidiella sahini n. sp. differs from *Pseudomidiella labensis* by a more inflated test, smaller D/W ratio, and thicker wall. The sigmoidal coiling in the initial stage of *P. sahini* n. sp. is nearly identical to the sigmoidal coiling of *Midiella* both in size and number of whorls. However, *P. sahini* n. sp. is characterized in the adult stage by the presence of pseudosepta dividing the tubular chamber into pseudochambers.

Baisalina pulchra reitlingerae, introduced as a new subspecies by Lys in Lys et al. (1980) from a Changhsingian limestone block of the Lamayuru unit (Himalaya Ladakh) in the Induan suture zone, differs from *Pseudomidiella sahini* n. sp. by the absence of sigmoidal coiling in the initial stage and a greater number of pseudosepta in the final whorl. We argue that taxonomic revision is necessary to refine the Permian evolutionary lineages of larger, pseudosepta-bearing Miliolata, including the plexus of pseudosepta-bearing forms defined under *Baisalina pulchra* by Lys in Lys et al. (1980). Sections of *Baisalina pulchra* illustrated from the eastern Taurides (Turkey) by Altıner (1981) displaying pseudosepta are synonymized under *P. sahini* n. sp. *Neodiscus milliolides* Miklukho-Maklay, 1953, figured from the Changhsingian of Slovenia by Nestell et al. (2011, pl. 2, fig. 3), is close to some of the specimens of *P. sahini* n. sp. in having a sigmoidal coiling in the early stage and an inflated test. However, it is not certain whether this form has pseudosepta in the adult stage.

Family Hemigordiopsidae Nikitina, 1969
Genus *Glomomidiellopsis* Gaillot and Vachard, 2007

Type species.—Glomomidiellopsis tieni Gaillot and Vachard, 2007, from the Kuh-e Surmeh outcrop (Zagros, Iran).

Glomomidiellopsis? *okayi* new species
Figure 4.1–4.6

1979 *Kamurana*? sp., Nguyen, p. 104–106, pl. 12, figs. 1–10.
1981 *Hemigordius* sp. ‘en pelote’; Altıner, pl. 44, figs. 6–8.
1981 *Hemigordius* sp. ‘en pelote’; Zaninetti et al., pl. 6, figs. 3, 4.
1986 Hemigordius sp.; Ciarapica et al., pl. 3, figs. 2, 3.
1986 *Kamurana*? sp.; Vuks and Chediya, pl. 9, figs. 7–9; pl. 10, figs. 1, 2, 4–9.
1991 *Kamurana*? sp.; Vachard and Ferrière, pl. 4, fig. 3.
1996 *Kamurana*? sp.; Leven and Okay, pl. 9, fig. 37.
1997 *Kamurana* sp.; Pronina and Nestell, pl. 1, fig. 10.
1998 *Kamurana* or *Neodiscus* sp.; Altıner and Özkan-Altıner, pl. 4, fig. 19.
2006a *Kamurana* sp.; Kobayashi, pl. 2, figs. 39, 40, 44–50.
2006b *Kamurana*? sp.; Kobayashi, pl. 3, figs. 35, 36.
2007 *Glomomidiellopsis uenoi* Gaillot and Vachard, p. 106, pl. 55, fig. 14; pl. 70, fig. 10.
?2007 *Neodiscopsis specialis* (Lin, Li, and Sun); Gaillot and Vachard, p. 100–101, p. 58, figs. 3, 5, 7, 8, 14; pl. 66, figs. 4, 12, 16.
2007 *Glomomidiellopsis tieni* Gaillot and Vachard, p. 105–106, pl. 64, figs. 4, 10; pl. 67, figs. 14, 15.
2010 *Neodiscopsis* sp.; Koehrer et al., pl. 2, fig. 6.

Holotype.—The specimen comes from sample ST 671, thin section C (Fig. 4.1), Sarpkaya Tepe (ST) section.

Diagnosis.—A large and globular hemigordiopsid foraminiferal species comprising two stages of growth: an early streptospiral stage consisting of five to ten whorls and a later stage with widely oscillating four or five whorls and a marked increase in the height of the tubular chamber.

Occurrence.—Changhsingian. ST, TCX, and AR-1 sections of the Aladağ Nappe and the DD section of the Antalya Nappes in the Taurides, southern Turkey (Fig. 1). The earliest known well-dated occurrence is from the upper Capitanian of Cambodia (Nguyen, 1979).

Description.—The large, laterally compressed globular test is characterized by two stages of growth of the tubular chamber. Following a small and spherical proloculus, the initial stage of the test consists of five to ten streptospirally coiled whorls. Around the proloculus, the coiling is tight in the first three or four whorls. Later, the wall thickens due to flosculinization, and the initial stage appear to be a marked lump in the center of the test. The lumen of the tubular chamber hardly increases in height in this stage. The adult stage of the test consists of four to six widely oscillating whorls. The lumen of the tubular chamber increases markedly, twice or three times more than the height of the lumen of the initial stage. It usually appears in half-moon shaped sections. Slight constrictions or irregularities in the lumen of the tubular chamber are related either to the section orientation or diagenetic processes affecting the test. The aperture is probably an opening at the end of the tubular chamber.

Etymology.—Glomomidiellopsis? *okayi* n. sp. is dedicated to the late Prof. Dr. Aral I. Okay from the Istanbul Technical University, Turkey, for his great contributions to the petrology, stratigraphy, and tectonics of Turkey.

Materials.—Samples ST 660, 665, 671, 673; TCX 1, 7, 13, 18, 19, 28; AR-1 664, and DD 10 (Changhsingian, Fig. 1). More than 50 specimens, six of which are illustrated in Figure 4.1–4.6.

Microfossil association.—Glomomidiellopsis? *okayi* n. sp. is accompanied by many foraminiferal species, among which *Paynita permotaurica*, *Paradagmarita monodi*, *P. planispiralis*, *Paradagmacrusta callosa*, *Louisettita elegantissima*, *Paraglobivalvulina mira*, *Paraglobivalvulinoides gracilis*, *Glomomidiellopsis uenoi*, *G. lysitiformis*, *Nodosinelloides sagitta*, *Polarisella elabugae*, and *Robuloides lens* are the most common and important ones.

Dimensions.—Diameter of proloculus: 40–70 µm (holotype: 70 µm). Diameter of test: 1120–1500 µm (holotype: 1350 µm). Width of test: 840–1010 µm (holotype: 1000 µm). Diameter/width: 1.14–1.50 (holotype: 1.35). Height of lumen of deuteroloculus in initial stage: 30–40 µm (holotype: 40 µm). Height of lumen of deuteroloculus in adult stage: 70–100 µm (holotype: 100.µm). Thickness of wall: 30–60 µm (holotype: 60 µm).

Remarks.—Glomomidiellopsis? *okayi* n. sp. differs from *Kamurana bronnimanni* (type species of the genus *Kamurana* Altıner and Zaninetti, 1977, from the Changhsingian of eastern Taurides, Turkey) by the absence of the third stage of growth containing perforations in the wall. *Hemigordiopsis*? *speciosus* Nikitina, 1969, from the Capitanian of the southern Sikhote-Alin (Russia), superficially resembles *G.*? *okayi* n. sp. However, the former species is characterized by nearly planispiral coiling in the adult stage and more than ten rudimentary septa in the final whorl. In addition, the initial stage of the coiling is not clearly visible in the holotype of *H.*? *speciosus*, preventing conclusive taxonomic analysis.

In earlier studies, large porcelaneous forms characterized by streptospiral coiling and two stages of growth of the second chamber were classified as either *Hemigordius* sp. ‘en pelote’ (Altıner, 1981; Zaninetti et al., 1981; Ciarapica et al., 1986) or *Kamurana* sp. (Nguyen, 1979; Vuks and Chediya, 1986; Vachard and Ferrière, 1991; Leven and Okay, 1996; Pronina and Nestell, 1997; Kobayashi, 2006a, b). In Zaninetti et al. (1981), the specimens illustrated as *Hemigordius* sp. ‘en pelote’ comprise forms belonging either to *Neodiscopsis* of Gaillot and Vachard (2007) or to *G.*? *okayi* n. sp. Sections illustrated as *Kamurana*? sp. by Vachard and Miconnet (1990) from the upper Murgabian (= Wordian?) of the Monte Facito (southern Italy) are related neither to *G.*? *okayi* n. sp. nor to *Kamurana*. The specimen illustrated in Vachard and Miconnet (1990, pl. 2, fig. 11) is *Hemigordiopsis*, whereas the specimen illustrated in Vachard and Miconnet (1990, pl. 3, fig. 8) is probably a section of *Neodiscopsis*. *Glomomidiellopsis*? *okayi* n. sp., illustrated as *Kamurana* or *Neodiscus* sp. by Altıner and Özkan-Altıner (1998) from the Salamis Island (Greece), occurs together with several Changhsingian markers including *Baudiella stampflii* Altıner and Özkan-Altıner, 1998, *Nanlingella meridionalis* Rui and Sheng, 1981, *Reichelina cribroseptata* Erk, 1941, *Reichelina changhsingensis* Sheng and Chang, 1958, *Colaniella parva* (Colani, 1924), and *Colaniella leei* (Wang, 1966).

Some of the sections of foraminifera described and illustrated as *Glomomidiellopsis uenoi* and *G. tieni* from the Kuh-e Dena and Kuh-e Surmeh sections of Zagros (Iran) by Gaillot and Vachard (2007) should be attributed to *G.*? *okayi* n. sp. because they display a clear increase in the height of the tubular chamber corresponding to the second stage of growth of the new species. It should be noted here that although the increase in the height of the tubular chamber was given in the diagnosis of *G. tieni*, the holotype (Gaillot and Vachard, 2007, pl. 65, fig. 11) and paratypes (Gaillot and Vachard, 2007, pl. 65, figs. 1–6, 13) from the Lopingian of the Kuh-e Surmeh section do not clearly display this character. However, several other specimens identified as *G. tieni* by Gaillot and Vachard (2007) clearly display this character in the second stage of growth of the tubular chamber and are placed in synonymy under *G.*? *okayi* n. sp.

We describe *Glomomidiellopsis*? *okayi* with a question mark in the genus affiliation because of the presence of the second stage of growth in tubular chamber, which is clearly absent in the typical *Glomomidiellopsis* species, which are characterized by low chamber height throughout the ontogeny. We also interpret some sections of *Neodiscopsis specialis* (Lin, Li, and Sun, 1990) illustrated from the offshore Fars area (Iran) in Gaillot and Vachard (2007) as belonging to our new species, which is characterized by streptospiral coiling in the initial stage followed by widely oscillating whorls of the second chamber, which increases in height. In addition, *Neodiscopsis* sp. illustrated from the Guadalupian of the Saiq Formation of the Sultanate of Oman by Koehrer et al. (2010) is also *G.*? *okayi* n. sp.

We suggest the origination of *Kamurana* from *G.*? *okayi* n. sp., in contrast to Vachard et al. (2008), who considered *Neodiscopsis specialis* (Lin, Li and Sun, 1990) (given as *N. spectabilis*, which is an invalid species name) as the ancestor of *Kamurana bronnimanni* Altıner and Zaninetti, 1977. The basis for our suggestion is the presence of streptospiral coiling in the initial stage of *G.*? *okayi* n. sp., which closely resembles the initial stage of *K. bronnimanni*. The initial stage of *N. specialis* is characterized, on the contrary, by nearly aligned (planispiral) coiling.

Class Nodosariata Mikhalevich, 1993

Remarks.—This class, characterized by a pseudofibrous or fibrous hyaline wall and sometimes associated with a thin, inner dark lining probably made up of microgranular calcite, occurs frequently in the studied Changhsingian deposits of the Tauride Belt. Among the late Paleozoic families, Syzraniidae Vachard in Vachard and Montenat, 1981, Protonodosariidae Mamet and Pinard, 1992, Geinitzinidae Bozorgnia, 1973, Robuloididae Reiss, 1963, Frondinidae Gaillot and Vachard, 2007, Pachyphloiidae Loeblich and Tappan, 1984, and Ichthyolariidae Loeblich and Tappan, 1986b, are frequent. However, Nodosinellidae Rhumbler, 1895, Partisaniidae Loeblich and Tappan, 1984, and Colaniellidae Fursenko in Rauzer-Chernousova and Fursenko, 1959, are totally absent in the Changhsingiian. Most of the new taxa described in this study, including several new genera and species, belong to the highly diverse Robuloididae.

Family Robuloididae Reiss, 1963

Remarks.—Following Vachard (2018), all weakly or fully coiled Permian genera of the Class Nodosariata are lumped into this family in this study.

The taxonomy of the fully coiled group in the family Robuloididae, comprising *Robuloides* Reichel, 1946, *Hubeirobuloides* Lin, Li, and Zhang in Lin et al., 1990, and *Gourisina* Reichel, 1946, has been enriched by the addition of *Robuloides lata* n. sp., *Robuloides*? *rettorii* n. sp., and *Pseudorobuloides reicheli* n. gen. n. sp. *Plectorobuloides taurica* n. gen. n. sp., characterized by skewed coiling, is another taxon added to this group.

From the weakly coiled second group, including *Eocristellaria* Miklukho-Maklay, 1954, *Calvezina* Sellier de Civrieux and Dessauvagie, 1965, and *Cryptomorphina* Sellier de Civrieux and Dessauvagie, 1965, *Calvezina anatolica* n. sp., which is characterized by a large test tending to become rectilinear, is described from the Changhsingian of the Taurides. *Pseudocryptomorphina amplimuralis* n. gen. n. sp., doubtfully assigned to Robuloididae, is also added to this second group.

The third group in the Family Robuloididae comprises only the genus *Eomarginulinella* Sosnina, 1969, which is characterized by an incipiently coiled test followed by rectilinear, globular chambers. *Eomarginulinella galinae* n. sp. with its slender longitudinal sections is among the youngest known species in the genus.

Genus *Robuloides* Reichel, 1946

Type species.—*Robuloides lens* Reichel, 1946, from Hydra Island, Greece.

Robuloides lata new species
Figure 4.13–4.18

?1984	*Robuloides lens* Reichel; Lin, pl. 6, figs. 13, 14.
2007	*Robuloides lens*; Gaillot and Vachard, p. 134–135, pl. 82, fig. 11.
2009	*Robuloides* cf. *lens*; Nestell et al., pl. 2, fig. 26.

Holotype.—The specimen comes from sample DD 4, thin section number 1 (Antalya Nappes, Demirtaş area, DD section) (Fig. 4.14).

Diagnosis.—A species of *Robuloides* with a lozenge-shaped axial section, smaller dimensions, and a smaller diameter/width ratio.

Occurrence.—Changhsingian, DD section of the Antalya Nappes, DT and TCX sections of the Aladağ Nappe, Taurides, southern Turkey (Fig. 1).

Description.—The planispiral and involute test of the new species consists of a spherical proloculus and three to four whorls increasing rapidly in height. The final whorl, comprising nine to ten chambers, terminates with a sharp angle at the periphery of the test. The axial section is typically lozenge shaped. Lateral growth is very prominent and achieved by the lamellar thickenings symmetrically developed around the axis of coiling. Wall is hyaline, usually recrystallized and probably pseudofibrous. Septa are slightly curved, and the aperture is areal, located on the lower half of the septal face.

Etymology.—In Latin, one of the meanings of ‘*lata*’ is wide or broad, which describes the test morphology of the new species.

Materials.—Samples DD 4, 6; DT 13; TCX 11, 29, 40.5 (Changhsingian, Fig. 1). More than 10 well-oriented sections. Six of these specimens are illustrated in Figure 4.13–4.18.

Microfossil association.—In the studied Changhsingian samples, *Robuloides lata* n. sp. co-occurs with a great number of foraminiferal species. The most characteristic species include *Paynita permotaurica*, *Paradagmarita monodi*, *P. planispiralis*, *Louisettita elegantissima*, *Septoglobivalvulina distensa*, *S. guangxiensis*, *Paraglobivalvulinoides gracilis*, *Robuloides lens*, *Robuloides acutus*, and *Polarisella elabugae*.

Dimensions.—Diameter of proloculus: 20–30 µm (holotype: 25 µm). Diameter of test: 120–230 µm (holotype: 210 µm). Width of test: 90–150 µm (holotype: 150 µm). Diameter/width: 1.33–1.53 (holotype: 1.4). Height of last chamber: 30–50 µm (holotype: 50 µm). Thickness of wall: 10–20 µm (holotype: 20 µm).

Remarks.—*Robuloides lata* n. sp. differs from *Robuloides lens* in having a lozenge-shaped axial section, instead of being lenticular or inflated lenticular, and a smaller diameter/width ratio.

Specimens identified as *R. lens* by Lin (1984) from the Yangtze Gorge area (China) probably belong to *R. lata* n. sp. The specimen illustrated as *Robuloides lens* from the Hazro area (Arabian Platform, SE Turkey) by Gaillot and Vachard (2007) is nearly identical to the holotype of *Robuloides lata* n. sp. *Robuloides* cf. *R. lens* reported from the uppermost Changhsingian of northwestern Serbia by Nestell et al. (2009) should also be included into the population of *R. lata* n. sp.

Robuloides? *rettorii* new species
Figure 5.8–5.15, 5.16?

2007	*Robuloides* sp.; Gaillot and Vachard, p. 136, pl. 79, fig. 26.
2011	*Robuloides* sp.; Korchagin, pl. 2, figs 25, 26.
2011	*Robuloides acutus* Reichel, 1946; Nestell et al., pl. 2, fig. 26.
2018	*Robuloides acutus*; Ke et al., fig. 9.10, 9.11.

Holotype.—The specimen comes from sample AR-1 682 (Fig. 5.8), Aladağ Nappe, Hadim AR-1 section.

Diagnosis.—A species of robuloidid foraminifer of smaller dimensions with a lenticular, involute test becoming evolute in the final whorl.

Occurrence.—Changhsingian, AR-1, DT, and TCX sections of the Aladağ Nappe and DD section of the Antalya Nappes, central Taurides, Turkey (Fig. 1).

Description.—The test, planispiral and lenticular with laterally compressed sides, is composed of a spherical and medium-sized proloculus and three whorls, rather rapidly increasing in height. The initial 2–2.5 whorls are involute with poorly developed lamellar thickenings. At this stage, the coiling axis could be slightly oblique to the coiling axis of the final whorl. The final half whorl is evolute, never extends to overlap the inner involute whorls in axial sections and forms a lateral thickening on the sides of the test. The final whorl typically contains nine chambers. Wall is hyaline and pseudofibrous. Septa are curved, probably undulating close to the test wall in the involute part. The aperture is areal, a rounded hole located on the lower half of the septal face.

Etymology.—*Robuloides*? *rettorii* n. sp. is dedicated to Prof. Dr. Roberto Rettori from the University of Perugia, Italy, for his contributions to the taxonomy of Permian and Triassic foraminifera.

Materials.—Samples AR-1 674, 682, 689; DD 1, 3, 5, 6, 7, 11; DT 1, 13; TCX 11, 16, 22, 26, 28, 30, 35, 38.5, 40, 40.5 (Changhsingian, Fig. 1). More than 50 oriented sections. Nine of these specimens are illustrated in Figure 5.8–5.16.

Microfossil association.—*Robuloides*? *rettorii* n. sp. occurs in association with a great number of foraminiferal species in the Changhsingian samples. The most commonly encountered species are *Paradagmarita monodi*, *P. planispiralis*, *Paradagmacrusta callosa*, *Dagmarita chanakchiensis*, *Louisettita elegantissima*, *Septoglobivalvulina distensa*, *Globivalvulina lukachiensis* Nestell et al., 2011, *Robuloides lens*, and *Rectostipulina quadrata* Jenny-Deshusses, 1985.

Dimensions.—Diameter of proloculus: 20–35 µm (holotype: 30 µm). Diameter of test: 135–235 µm (holotype: 150 µm). Width of test: 50–100 µm (holotype: 70 µm). Diameter/width: 2.0–2.7 (holotype: 2.14). Height of last chamber: 35–50 µm (holotype: 40 µm). Thickness of wall: 5–10 µm (holotype: 10 µm).

Remarks.—Gaillot and Vachard (2007) reported for the first time the presence of specimens becoming evolute at the end of the coiling. *Robuloides* sp., illustrated from the Lopingian of Zagros by Gaillot and Vachard (2007, pl. 79, fig. 26), is placed as a synonym under *Robuloides*? *rettorii* n. sp. We insert a question mark in the genus affiliation because this evolute character of *Robuloides*? *rettorii* n. sp. does not fit the description of the genus *Robuloides*, which is characterized by involute coiling. This character of exhibiting an evolute last whorl is probably an intermediate step in the evolution of robuloidid forms from *R*.? *rettorii* n. sp. to *Pseudorobuloides* n. gen. Poorly illustrated specimens as *Robuloides* sp. from the Global Stratotype (GSSP) of the Permian–Triassic boundary, Bed 27, Meishan, South China by Korchagin (2011, pl. 2, figs. 25, 26) also belong to *Robuloides*? *rettorii* n. sp.

Among previously described *Robuloides* species, *Robuloides acutus* seems to be morphologically close to *R*.? *rettorii* n. sp. However, *R. acutus* (Fig. 5.6, 5.7) differs from our new species in having a completely involute test where the last whorl overlaps the inner whorls with a lamellar thickening. Moreover, in *R*.? *rettorii* n. sp., the last whorl terminating on the sides of the test does not embrace the inner whorls. Even a specimen sectioned parallel to the equatorial plane displays the evolute character of the last whorl (Fig. 5.13). In the involute part of the test, septa extend toward the center of the test, whereas in the evolute final half whorl, septa do not extend to overlap the inner involute whorls. The specimens illustrated as *R. acutus* from the upper Changhsingian of Slovenia by Nestell et al. (2011, pl. 2, fig. 26) and the Meishan D section, Zhejiang, China by Ke et al. (2018, fig. 9.10, 9.11) should be referred to *R*.? *rettorii* n. sp. because the evolute coiling is clearly visible in the axial sections of these specimens.

Genus *Pseudorobuloides* new genus

Type species.—*Pseudorobuloides reicheli* new species.

Diagnosis.—A small, discoidal, biumbilicate and planispiral robuloidid test with sharply angular periphery. Involute coiling in the early stage, later semi-involute to evolute. Lateral lamellar thickenings completely absent in the involute stage.

Occurrence.—Changhsingian of the Antalya Nappes, Aladağ Nappe and the Geyik Dağı parautochthon/autochthon of Taurides (southern Turkey). Lopingian of Zagros (Iran) (Gaillot and Vachard, 2007) and the Changhsingian of the Julfa area (southwestern Iran) (Mohtat-Aghai et al., 2009).

Etymology.—The prefix *pseudo-* is used to name this new genus that superficially appears to be *Robuloides*.

Remarks.—The new genus *Pseudorobuloides* differs from *Robuloides* of Reichel (1946) in having a biumbilicate and discoidal test, absence of lateral thickenings in the involute stage, and a tendency to become evolute at the end of the ontogenesis. The change in coiling style of smaller robuloidid foraminifera broadly evokes the evolution of the genus *Millerella* Thompson, 1942, with an involute to evolute test from the genus *Eostaffella* Rauzer-Chernousova, 1948, characterized by an involute to slightly evolute test in the Carboniferous ozawainelloid foraminifera (see the phylogenetical reconstruction of Maslo and Vachard, 1997, fig. 1).

Pseudorobuloides reicheli new species
Figure 5.17–5.31, 5.32?, 5.33?

2007 *Robuloides* sp.; Gaillot and Vachard, p. 136, pl. 78, figs. 6, 27; pl. 84, fig. 11.
2009 *Robuloides* sp.; Mohtat-Aghai et al., pl. 2, fig. 28.

Holotype.—The specimen is from sample TCX 30, thin section number 2 (Fig. 5.17, 5.18), Aladağ Nappe, Taşkent TCX section.

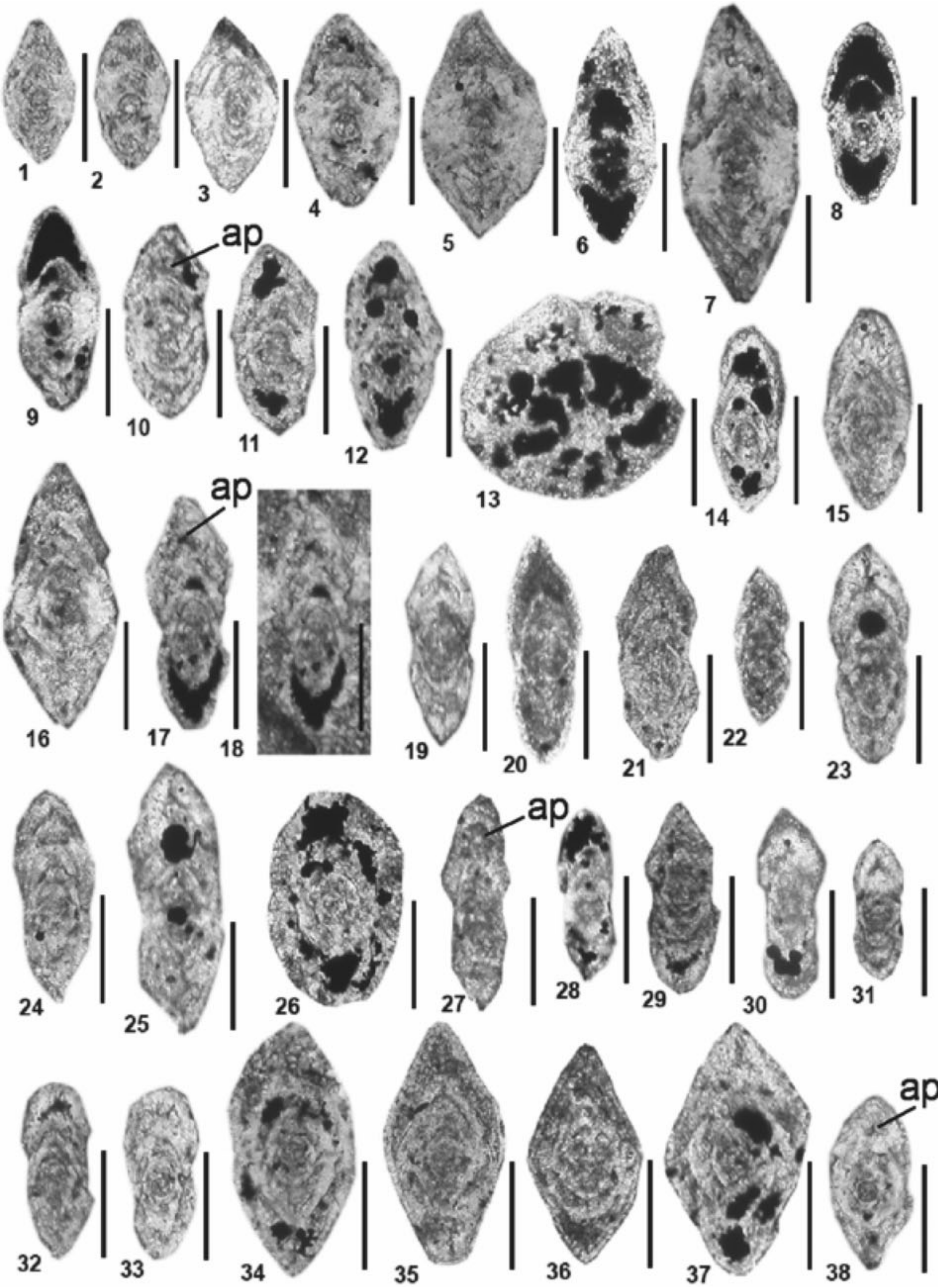
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Figure 5. Specimens belonging to Robuloididae from Changhsingian carbonates of southern Turkey (ap = aperture). (**1–5**) *Robuloides lens* Reichel, 1946; (**6, 7**) *Robuloides acutus* Reichel, 1946; (**8–16**) *Robuloides*? *rettorii* new species, (**8**) holotype, sample AR-1 682 (Aladağ Nappe, Hadim AR-1 section); (**17–31, 32?, 33?**) *Pseudorobuloides reicheli* new genus new species, (**17, 18**) holotype, sample TCX 30, thin section number 2 (Aladağ Nappe, Taşkent TCX section); (**34–38**) *Plectorobuloides taurica* new genus new species, (**34**) holotype, sample TCX 32, thin section number 2 (Aladağ Nappe, Taşkent TCX section). (**1**) DD 3; (**2**) DT 13; (**3**) DT 3; (**4**) TCX 4; (**5, 7, 13, 16**) TCX 40.5; (**6**) DD 6; (**8**) AR-1 682; (**9, 28**) TCX 11; (**10**) TCX 22; (**11, 23**) TCX 38.5; (**12, 15**) TCX 35; (**14, 19, 31, 33**) DT 1; (**17, 18, 26**) TCX 30; (**20**) K 4034; (**21**) DT 12; (**22**) TCX 41; (**24**) DT 8; (**25**) TCX 39.5; (**27**) KT 190; (**29, 32**) TCX 36; (**30**) TCX 38; (**34**) TCX 32; (**35**) TCX 34; (**36**) TCX 42.5; (**37**) TCX 47.5; (**38**) DT 11. Scale bars = 100 μm.

Diagnosis.—Type species of *Pseudorobuloides* n. gen. with a small, discoidal, and subcarinate test including three involute to evolute, planispiral whorls, eight to nine chambers in the last whorl, and a high diameter/width ratio.

Occurrence.—Changhsingian. TCX, DT, AR-1, K, and KT sections of the Aladağ Nappe and DD section of the Antalya Nappes, Taurides, southern Turkey (Fig. 1).

Description.—The test is discoidal and biumbilicate with a sharply angled periphery defining a somewhat keeled margin. Following a small proloculus, the coiling is planispiral with three whorls, rapidly increasing in height in the final whorl. The initial two whorls are involute, never forming a lamellar thickening on the sides of the test, contrary to the presence of lamellar thickenings in the genus *Robuloides*. The final whorl is semi-involute to evolute and consists of eight to nine chambers. The wall is hyaline, similar to that of *Robuloides* and usually recrystallized. The aperture is rounded and located on the lower half of the slightly curved septal face.

Etymology.—*Pseudorobuloides reicheli* n. sp. is dedicated to the late Prof. Manfred Reichel (Switzerland) for his great contribution to the taxonomy of Paleozoic, Mesozoic, and Cenozoic foraminifera, including the discovery of the genus *Robuloides* from the Permian of Hydra Island, Greece.

Materials.—Samples AR-1 676, 685, 688, 689; AR-2 151; DD 6, 7; DT 1, 11, 12, (TK 2.15) 13; K 4034; KT 190; TCX 11, 28, 30, 36, 38, 38.5, 39.5, 40.5, 41, 42.5, 47.5 (Changhsingian, Fig. 1). More than 100 oriented sections. Sixteen of these specimens are illustrated in Figure 5.17–5.33.

Microfossil association.—*Pseudorobuloides reicheli* n. sp. is found in association with more than 100 species of foraminifera in the Changhsingian samples from southern Turkey. The most commonly encountered species are *Paradagmarita monodi*, *Paynita permotaurica*, *Paradagmacrusta callosa*, *Louisettita elegantissima*, *Retroseptellina decrouezae*, *Septoglobivalvulina distensa*, *S. guangxiensis*, *Glomomidiellopsis lysitiformis*, *Rectostipulina pentamerata* Groves, Altıner, and Rettori, 2005, *Polarisella elabugae*, *Nestellorella acus*, *Nodosinelloides mirabilis caucasica* (Miklukho-Maklay, 1954), *Eomarginulinella typica* (Sosnina, 1967), *Robuloides lens*, and *Frondina permica* Sellier de Civrieux and Dessauvagie, 1965.

Dimensions.—Diameter of proloculus: 15–25 μm (holotype: 25 μm). Diameter of test: 140–225 μm (holotype: 220 μm). Width of test: 50–75 μm (holotype: 70 μm). Diameter/width: 2.4–3.14 (holotype: 3.14). Height of last chamber: 35–60 μm (holotype: 50 μm). Thickness of wall: 5–10 μm (holotype: 7 μm).

Remarks.—Specimens illustrated as evolute *Robuloides* from the Lopingian of Zagros (Iran) by Gaillot and Vachard (2007) are morphologically very similar to *Pseudorobuloides reicheli* n. gen. n. sp., characterized by the absence of laterally thickened lamellae, discoidal tests, and involute to evolute coiling.

The tangential section identified as *Robuloides* sp. from the Changhsingian of the Zal section of the Julfa area (northwestern Iran) by Mohtat-Aghai et al. (2009, pl. 2, fig. 28) also should be referred to *P. reicheli* n. sp. in having a discoidal test and the absence of laterally thickened lamellae.

Genus *Plectorobuloides* new genus

Type species.—Plectorobuloides taurica new species.

Diagnosis.—A small, lenticular to inflated-lenticular robuloidid genus displaying an abrupt change in the direction of coiling during the early stage of ontogeny, later becoming planispiral and involute.

Occurrence.—Changhsingian of the Aladağ Nappe and the Antalya Nappes, Taurides (southern Turkey).

Etymology.—The prefix *plecto*- from Latin means twist, turn, or bend. It is used in the name of *Plectorobuloides* n. gen. in order to express its coiling character.

Remarks.—*Plectorobuloides* n. gen. differs from *Robuloides* Reichel, 1946, by an abrupt change in the direction of coiling and the absence of lateral lamellar thickenings. The evolution of *Plectorobuloides* n. gen. within the robuloidid foraminifera late in the Permian, with its twisted coiling, resembles the evolution of Carboniferous ozawainelloid foraminifera (Maslo and Vachard, 1997). Although there are differences in detail between robuloidid and ozawainelloid foraminiferal stocks, the derivation of *Plectostaffella* Reitlinger, 1971, with twisted coiling from an eostaffellid stock in the late Serpukhovian to early Bashkirian (more precisely from the genus *Eostaffellina* Reitlinger, 1963), is similar to the derivation of *Plectorobuloides* n. gen. in the late Changhsingian from the robuloidid stock. This change in coiling mode seems to be a common event in the evolution of lenticular, multilocular, and planispiral stocks of late Paleozoic foraminifera.

Plectorobuloides taurica new species

Figure 5.34–5.38

?2007 *Robuloides lens* Reichel; Gaillot and Vachard, p. 134–135, pl. 82, fig. 12.

Holotype.—The specimen is from sample TCX 32, thin section number 2 (Fig. 5.34), Aladağ Nappe, Taşkent TCX section (Fig. 1).

Diagnosis.—A species of *Plectorobuloides* n. gen. characterized by a small, lenticular to inflated-lenticular test with a sharply angled periphery. Coiling, with three to four whorls, twisted in the early stage of the test, later planispiral and involute.

Occurrence.—Late Changhsingian, TCX and DT sections of the Aladağ Nappe and DD section of the Antalya Nappes, Taurides, southern Turkey (Fig. 1).

Description.—The lenticular to inflated-lenticular test with a sharply angled periphery consists of three to four whorls. Following a rounded proloculus of moderate size, the initial whorl is tightly coiled. A slight change in the position of the coiling axis of the second whorl is succeeded by a more accentuated change in the coiling direction in the third whorl, giving the test a highly asymmetric profile in the axial section. In the last whorl, the coiling axis returns to coincide more or less with the coiling axis of the initial whorl and the test becomes planispiral and involute. The number of the chambers in the last whorl is not known. The wall is similar to that of *Robuloides*, hyaline, pseudofibrous, and usually recrystallized. The aperture is a rounded hole in the lower part of the septal face.

Etymology.—The species name '*taurica*' refers to the chain of Taurus Mountains where the type locality of the new species is located.

Materials.—Samples TCX 32, 34, 42.5, 47.5; DD 6, 7, 15; DT 11 (Changhsingian, Fig. 1). More than 10 oriented sections; five of these specimens are illustrated in Figure 5.34–5.38.

Microfossil association.—*Plectorobuloides taurica* n. gen. n. sp. co-occurs with a great number of foraminiferal species in the Changhsingian. From these forms, the most commonly encountered are *Paynita permotaurica*, *Paradagmarita monodi*, *P. planispiralis*, *Paradagmacrusta callosa*, *Paraglobivalvulina mira*, *Retroseptellina decrouezae*, *Paraglobivalvulinoides gracilis*, *Sphaerulina crassispira* Lee, 1934, *Midiella zaninettiae* (Altıner, 1978), *Rectostipulina quadrata*, *Robuloides lens,* and *Frondina permica*.

Dimensions.—Diameter of proloculus: 20–30 µm (holotype: 25 µm). Diameter of test: 150–245 µm (holotype: 210 µm). Width of test: 80–140 µm (holotype: 120 µm). Diameter/width: 1.72–1.94 (holotype: 1.75). Height of last chamber: 35–60 µm (holotype: 45 µm). Thickness of wall: 8–10 µm (holotype: 10 µm).

Remarks.—The specimen illustrated as *Robuloides lens* from the Lopingian of the Hazro area (Arabian Platform, SE Anatolia) by Gaillot and Vachard (2007, pl. 82, fig. 12) seems to display a change in the coiling direction in the earlier whorls and is questionably assigned to the population of *P. taurica* n. gen. n. sp.

Genus *Calvezina* Sellier de Civrieux and Dessauvagie, 1965

Type species.—*Calvezina ottomana* Sellier de Civrieux and Dessauvagie, 1965, from south of the Village of Çukurköy (Akseki, southern Turkey).

Calvezina anatolica new species
Figure 6.1–6.4

?2007 *Calvezina* sp.; Gaillot and Vachard, p. 133–134, pl. 90, fig. 15.

Holotype.—Sample DT 1, thin section number 2 (Fig. 6.1), Aladağ Nappe, Taşkent DT section (Fig. 1).

Diagnosis.—An elongate test of large dimensions, ovate in transverse section. Early marginuline-like stage with three to four arcuate chambers, followed by two uniserial rectilinear chambers.

Occurrence.—Changhsingian. DT, TCX, AR-1, and AR-2 sections of the Aladağ Nappe and DD section of the Antalya Nappes, central Taurides, southern Turkey (Fig. 1).

Description.—Large test consists of a small proloculus followed by six chambers rapidly increasing in height in two distinct stages. The initial stage is marginuline-like and characterized by three to four weakly coiled chambers. In longitudinal frontal section, these chambers appear arcuate and asymmetrical with thin septa. In the late stage of ontogeny, the chambers are rectilinear, uniserial, and symmetrical and they do not show any sign of coiling. The test is ovate in transverse section. The wall is hyaline, pseudofibrous, and usually recrystallized, either plesio-monolamellar or atelo-monolamellar. Aperture areal, terminal with a rounded to ovate outline.

Etymology.—The species name '*anatolica*' refers to the Anatolian Peninsula, which constitutes the Asian portion of Turkey where the type locality of the new species is located.

Materials.—Samples TCX 0, 7, 17, 22; DD 7, 8, 11; DT 1, 8, 12, 13; AR-1 665; AR-2 152 (Changhsingian, Fig. 1). More than 20 oriented and unoriented sections, four of which are illustrated in Figure 6.1–6.4.

Microfossil association.—*Calvezina anatolica* n. sp. is accompanied by a large number of foraminiferal species. The most commonly encountered species are *Paynita permotaurica*, *Paradagmarita monodi*, *P. planispiralis*, *Paradagmacrusta callosa*, *Septoglobivalvulina guangxiensis*, *Louisettita elegantissima*, *Reichelina* sp., *Sphaerulina crassispira*, *Glomomidiellopsis uenoi*, *G. lysitiformis*, *Polarisella elabugae*, *Nodosinelloides sagitta*, and *Nestellorella dorashamensis* (Pronina, 1989).

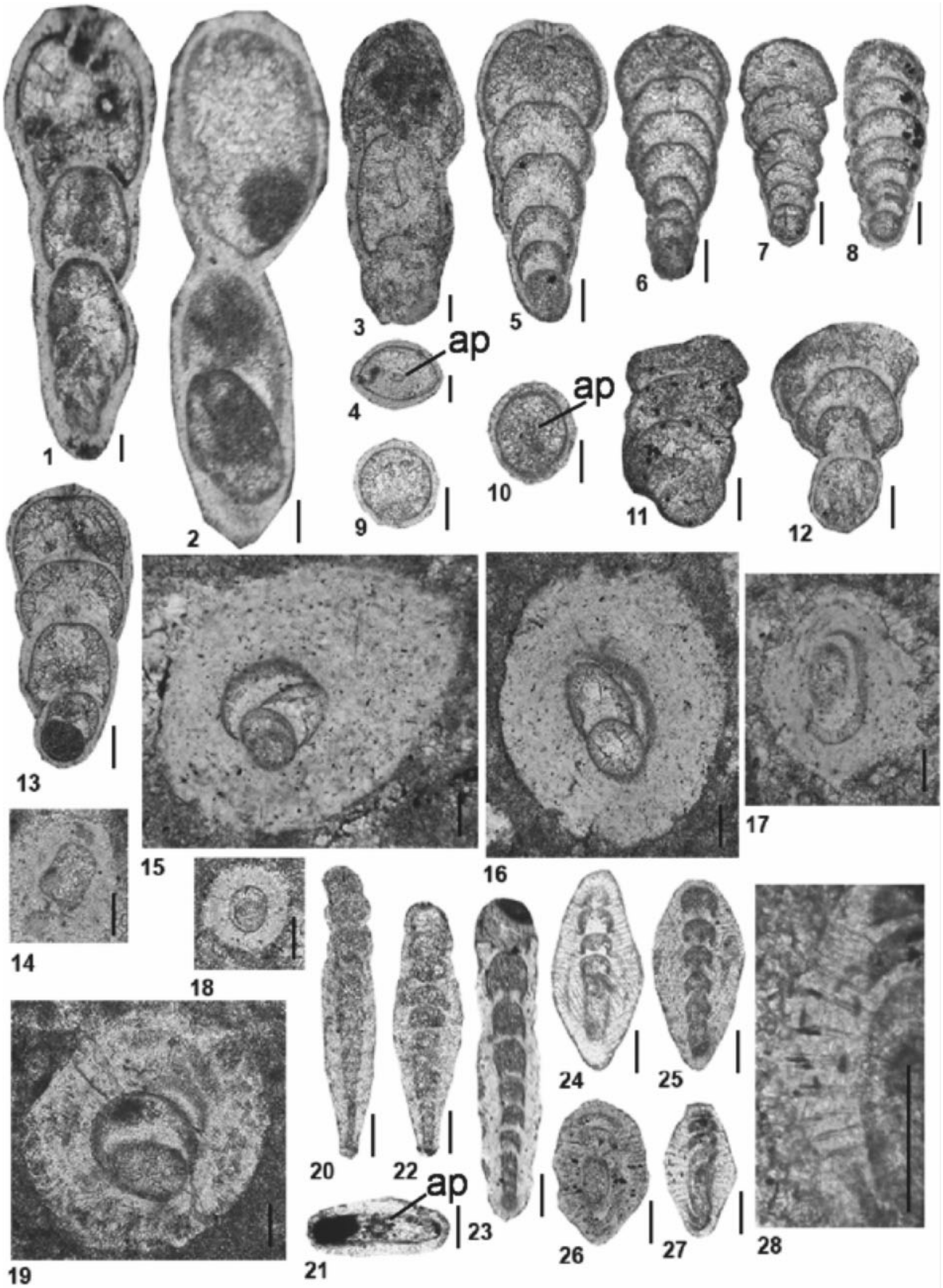
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Figure 6. Specimens belonging to Robuloididae and Pachyphloiidae from Changhsingian carbonates of South Turkey (ap = aperture). (**1–4**) *Calvezina anatolica* new species, (**1**) holotype, sample DT 1, thin section number 2 (Aladağ Nappe, Taşkent DT section); (**5–10**) *Eomarginulinella galinae* new species, (**5**) holotype, sample DT 11, thin section number 1 (Aladağ Nappe, Taşkent DT section); (**11, 12**) *Eomarginulinella typica* (Sosnina, 1967); (**13**) *Eomarginulinella* sp.; (**14–19**) *Pseudocryptomorphina amplimuralis* new genus new species, (**15**) holotype, sample TCX 8, thin section number 2 (Aladağ Nappe, Taşkent, TCX section); (**20, 21, 22?, 23**) *Robustopachyphloia farinacciae* new species, (**20**) holotype, sample TRLR 194 (Antalya Nappes, Demirtaş TRLR section); (**24–27**) new pachyphloiidid genus?; (**28**) higher magnification of part of (**27**); notice regularly spaced canal-like pores crossing the successive laminae. (**1**) DT 1; (**2**) TCX 0; (**3**) TCX 7; (**4**) TCX 17; (**5, 8, 9, 12**) DT 11; (**6**) AR-1 669; (**7**) AR-1 681; (**10**) AR-1 664; (**11**) TCX 38; (**13**) TK 1.06 (equivalent of DT 13); (**14**) TCX 10; (**15**) TCX 8; (**16**) TCX 21; (**17**) TCX 17; (**18**) DD 8; (**19**) ST 656; (**20**) TRLR 194; (**21, 23**) DD 15; (**22**) TRLR 206; (**24**) ST 663; (**25**) K 4034; (**26**) DT 4; (**27, 28**) TCX 11. Scale bars = 100 μm.

Dimensions.—Diameter of proloculus: 50 μm (holotype: 50 μm). Height of test: 1660–2150 μm (holotype: 2090 μm). Width of test: 500–650 μm (holotype: 650 μm). Height/width: 3.19–3.21 (holotype: 3.21). Height of last chamber: 500–680 μm (holotype: 680 μm). Thickness of wall: 30–55 μm (holotype: 55 μm).

Remarks.—*Calvezina anatolica* n. sp. differs from *Calvezina ottomana* Sellier de Civrieux and Dessauvagie, 1965, in having larger dimensions and having rectilinear and symmetrical last two chambers, as seen in the longitudinal frontal section of the holotype (Fig. 6.1). The large specimen illustrated as *Calvezina* sp. from the Lopingian of the Hazro area (Arabian Platform, SE Turkey) by Gaillot and Vachard (2007, pl. 90, fig. 15) is probably *Calvezina anatolica* n. sp.

Genus *Eomarginulinella* Sosnina, 1969

Type species.—*Eomarginulinella typica* (Sosnina, 1967) from southern Primorye (USSR).

Eomarginulinella galinae new species
Figure 6.5–6.10

2005 *Calvezina ottomana* Sellier de Civrieux and Dessauvagie; Groves et al., p. 31–32, fig. 23.30 only.

Holotype.—The specimen occurs in sample DT 11, thin section number 1 (Fig. 6.5), Aladağ Nappe, Taşkent DT section (Fig. 1).

Diagnosis.—A species of *Eomarginulinella* with a slender test and uniformly growing five to seven chambers. The initial one or two chambers incipiently coiled or curvilinear, succeeding ones rectilinear.

Occurrence.—Changhsingian, DT and TCX sections of the Aladağ Nappe and DD section of the Antalya Nappes, central Taurides, southern Turkey (Fig. 1).

Description.—Slender test consists of a rather large and spherical proloculus and five to seven chambers gradually and regularly increasing in height. Initial one or two chambers are weakly coiled and curvilinear. Succeeding chambers are rectilinear, globular, or subglobular with depressed sutures. Slight morphological differences in some specimens are probably related to the orientation of longitudinal-frontal and longitudinal-lateral sections cutting through the slightly compressed subglobular chambers with different height/width ratios. The wall is atelo-monolamellar, calcareous, hyaline, and pseudofibrous with a thin, dark inner lining, probably made up of microgranular calcite. Aperture is a simple, areal, terminal opening accompanied by a slight thickening of the wall.

Etymology.—*Eomarginulinella galinae* n. sp. is dedicated to Prof. Galina P. Nestell from the University of Texas at Arlington, USA, for her great contributions to the taxonomy and biostratigraphy of Permian foraminifera.

Materials.—Samples DT 1, 11, 12 (TK 1.05, 2.15); DD 19; AR-1 664, 666, 669, 681, 682; TCX 5, 10, 23.5, 29, 46 (Changhsingian of the Aladağ Nappe and Antalya Nappes, Fig. 1). More than 30 recognizable sections, six of which are illustrated in Figure 6.5–6.10.

Microfossil association.—The most common species found in association with *Eomarginulinella galinae* n. sp. in the Changhsingian are *Paradagmarita monodi*, *P. planispiralis*, *Paynita permotaurica*, *Septoglobivalvulina distensa*, *Paraglobivalvulinoides gracilis*, *Labiodagmarita vasleti* Gaillot and Vachard, 2007, *Sphaerulina crassispira*, *Nankinella* cf. *N. quasihunanensis* Sheng, 1963, *Neodiscus milliolides*, *Midiella zaninettiae* (Altıner, 1978), *Multidiscus padangensis* Lange, 1925, *Rectostipulina pentamerata*, *Protonodosaria exploita* Trifonova, 1978, *Nodosinelloides sagitta*, *Ichthyofrondina palmata*, *Tauridia pamphyliensis* Sellier de Civrieux and Dessauvagie, 1965, *Eomarginulinella typica*, and *Robuloides lens*.

Dimensions.—Diameter of proloculus: 75–100 μm (holotype: 100 μm). Height of test: 400–810 μm (holotype: 650 μm). Width of test: 160–310 μm (holotype: 270 μm). Height/width: 2.24–2.61 (holotype: 2.40). Height of last chamber: 85–250 μm (holotype: 200 μm). Thickness of wall: 15–25 μm (holotype: 25 μm).

Remarks.—*Eomarginulinella*? sp. illustrated from the Midian stage of the USSR by Kotlyar et al. (1989, pl. 1, fig. 4) is close to *E. galinae* n. sp., but our form differs from the former in having a more slender longitudinal section. One of the specimens attributed to *Calvezina ottomana* by Groves et al. (2005, fig. 23.30) is identical to *E. galinae* n. sp. in having slightly arcuate one or two chambers followed by uniserial chambers. Similarly, *E. galinae* n. sp. differs from the holotype of *Eomarginulinella serbica* of Nestell et al. (2009) from the Changhsingian of northwestern Serbia in having a different growth rate of chambers in the uniserial stage and a slender test.

In our Changhsingian samples, *E. galinae* n. sp. is sometimes associated with *Eomarginulinella typica* (Sosnina, 1967), type species of the genus *Eomarginulinella* described as

Marginulinella typica Sosnina, 1969. The new species differs from *E. typica* illustrated in Figure 6.11 and 6.12 in having symmetrical and regularly growing chambers in the uniserial stage and a slender test. *Eomarginulinella* sp. (Fig. 6.13) is a specimen morphologically close to *E. galinae* n. sp. but differs by the sudden increase of the chamber height immediately following the initial arcuate stage.

?Family Robuloididae Reiss, 1963
Genus *Pseudocryptomorphina* new genus

Type species.—*Pseudocryptomorphina amplimuralis* new species.

Diagnosis.—A genus questionably assigned to Robuloididae, consisting of strongly overlapping chambers with abruptly changing axis of growth and abnormally thickened wall in the last stage of ontogeny.

Occurrence.—Changhsingian of the Aladağ Nappe and Antalya Nappes of the Taurides (southern Turkey).

Etymology.—We have used the prefix pseudo- to define the present genus as a fake or false form of the genus *Cryptomorphina* of Sellier de Civrieux and Dessauvagie (1965), a Permian genus characterized by a thick wall and described for the first time from the Antalya Nappes, Turkey.

Remarks.—*Pseudocryptomorphina* n. gen. differs from *Cryptomorphina* in having strongly overlapping chambers with an abruptly changing axis of growth and unusually thickened wall whose thickness is more than the maximum width of the chambers as seen in the holotype. A well-oriented longitudinal frontal section of *Cryptomorphina* has been illustrated by Groves et al. (2005, fig. 22.17), in which it is clear that the coiling is present in the initial arcuate stage of *Cryptomorphina* followed by uniserial rectilinear chambers. We think that Vachard (2018) was right to place this genus in the family Robuloididae, rather than in the uniserial groups of Permian foraminifera.

Pseudocryptomorphina amplimuralis new species
Figure 6.14–6.19

Holotype.—The specimen comes from sample TCX 8, thin section number 2 (Aladağ Nappe, Taşkent, TCX section) (Fig. 6.15).

Diagnosis.—A species of *Pseudocryptomorphina* n. gen., consisting of a large proloculus and strongly overlapping three chambers with axis of growth changing abruptly close to 90°. Wall unusually thick, made up of several laminae, successively added in the last stage of ontogeny.

Occurrence.—Changhsingian, TCX and ST sections of the Aladağ Nappe and DD section of the Antalya Nappes, Taurides, South Turkey (Fig. 1).

Description.—Test is composed of a rather large proloculus and three strongly overlapping chambers with an axis of growth shifting 90° as each chamber is added to the test structure. The height of the initial two chambers is more than their width. The third chamber becomes wider and partially overlaps the previous two chambers. The wall consists of a thin, microgranular inner layer and an outer hyaline fibrous layer. The fibrous layer tends to become thicker and partially occludes the cavities of chambers. The outer wall is unusually thick, even thicker than the maximum width of the space occupied by the cavities of chambers. It consists of several laminae successively added around the chambers. Aperture is unknown in the early two chambers, probably terminal, a rounded opening crossing the thickened laminar wall of the test.

Etymology.—We have used the trivial name *amplimuralis* to indicate the thick-walled character of our new population.

Materials.—Samples TCX 8, 10, 17, 20, 21; DD 8; ST 656 (Changhsingian, Fig. 1). More than 15 variously oriented sections, six of which are illustrated in Figure 6.14–6.20.

Microfossil association.—The most commonly encountered species of foraminifera associated with *Pseudocryptomorphina amplimuralis* n. gen. n. sp. are *Paradagmarita monodi*, *P. flabelliformis* Zaninetti, Altıner, and Çatal, 1981, *Septoglobivalvulina distensa*, *S. guangxiensis*, *Glomomidiellopsis eunoi*, *Hemigordius guvenci* Altıner, 1978, *Rectostipulina quadrata*, *Polarisella elabugae*, *Frondina permica*, and *Ichthyofrondina palmata*.

Dimensions.—Diameter of proloculus: 70–75 µm (holotype: 75 µm). Height of test: 510–600 µm (holotype: 510 µm). Width of test: 500–520 µm (holotype: 520 µm). Height/width: 0.98–1.24 (holotype: 0.98). Height of last chamber: 65–75 µm (holotype: 75 µm). Thickness of wall: 150–350 µm (holotype: 350 µm).

Remarks.—*Pseudocryptomorphina amplimuralis* n. gen. n. sp. differs from *Cryptomorphina limonitica* Sellier de Civrieux and Dessauvagie, 1965, in having a different chamber arrangement and a thicker wall. The specimens identified as *C. limonitica* by Groves et al. (2007, fig. 6.6, 6.8) from the Changhsingian of the Southern Alps are close to *P. amplimuralis* n. gen. n. sp. in having a similar chamber arrangement. However, *P. amplimuralis* n. gen. n. sp. differs from these specimens in possessing a thicker wall in the final stage of ontogeny.

Family Pachyphloiidae Loeblich and Tappan, 1984

Remarks.—From the family Pachyphloiidae, comprising the genera *Pachyphloia* Lange, 1925, *Robustopachyphloia* Lin, 1980, *Aulocophloia* Gaillot and Vachard, 2007, and *Sosninella* Sellier de Civrieux and Dessauvagie, 1965, we describe two new taxa from the Changhsingian of the Tauride Belt. *Robustopachyphloia farinacciae* n. sp. is characterized by a slender and compressed test and the “new pachyphloiidid genus?” with long and regularly spaced canal-like pores in the test crossing the successive laminae.

Genus *Robustopachyphloia* Lin, 1980

Type species.—Robustopachyphloia annectena Lin, 1980, from the Changhsing Limestone, Guangdong and Hubei provinces, China.

Robustopachyphloia farinacciae new species
Figure 6.20–6.21, 6.22?, 6.23

Holotype.—The specimen is from sample TRLR 194, Antalya Nappes, Demirtaş TRLR section (Fig. 1) (Fig. 6.20).

Diagnosis.—A species of *Robustopachyphloia* with a slender and compressed test comprising a small proloculus and up to 17 uniformly growing chambers. Chambers high and narrow, and septa arched throughout the test.

Occurrence.—Changhsingian, TRLR and DD sections of the Antalya Nappes and TCX and DT sections of the Aladağ Nappe, central Taurides, southern Turkey (Fig. 1).

Description.—Highly compressed, elongate, uniserial, and rectilinear test consisting of a small proloculus followed by 10 to 17 chambers progressively increasing in height. In the longitudinal-lateral section of the holotype, the initial four to five chambers appear to be beaded, forming a chain-like growth. Following high and narrow chambers with arched septa in the *Pachyphloia* stage increase more gradually in height. The last two or three chambers, devoid of lamellar thickening, are added to the test with depressed sutures. The wall is calcareous, radially fibrous, with a very thin, dark microgranular calcite inner layer. The aperture is terminal, rounded, and typically bordered by radial grooves in the *Pachyphloia* stage.

Etymology.—Robustopachyphloia farinacciae n. sp. is dedicated to the late Professor Anna Farinacci from the Sapienza University of Rome, Italy, for her contributions to the geology and paleontology of Turkey.

Materials.—Samples TRLR 194, 203, 206; DD 15; TCX 43; DT (TK 1.05). More than 10 variously oriented sections, four of which are illustrated in Figure 6.20–6.23.

Microfossil association.—Robustopachyphloia farinacciae n. sp. is found in association with several foraminiferal species. The most commonly encountered ones are *Paradagmarita monodi*, *P. flabelliformis*, *Paynita permotaurica*, *Louisettita elegantissima*, *Septoglobivalvulina distensa*, *Rectostipulina pentamerata*, *Nodosinelloides sagitta*, *Polarisella elabugae*, *Robuloides lens*, *Ichthyofrondina palmata*, and *I. latilimbata*.

Dimensions.—Diameter of proloculus: 20–35 μm (holotype: 20 μm). Height of test: 420–550 μm (holotype: 520 μm). Width of test: 90–125 μm (holotype: 105 μm). Height/width: 4.40–4.95 (holotype: 4.95). Height of last chamber: 50–100 μm (holotype: 60 μm). Thickness of wall: 15–20 μm (holotype: 15 μm).

Remarks.—Robustopachyphloia sp., illustrated by Gaillot and Vachard (2007, pl. 87, fig. 21) from the Lopingian of the Kuh-e Surmeh section of Iran, is similar to *Robustopachyphloia farinacciae* n. sp. in having high and narrow chambers with arched septa. However, it differs from *R. farinacciae* n. sp. by the lesser number of chambers. *Robustopachyphloia farinacciae* n. sp. differs also from *R. annectena* Lin, 1980, from the Changhsing Limestone of China and *R. texana* Nestell and Nestell in Nestell et al., 2006, from Capitanian deposits of the Guadalupe Mountains, West Texas (USA), in having high and narrow chambers with arched septa instead of having crescentiform chambers with flattened septa.

New pachyphloiid genus?
Figure 6.24–6.28

Remarks.—According to Groves et al. (2004) (see also the description of Sellier de Civrieux and Dessauvagie, 1965), the wall in *Pachyphloia* Lange, 1925, is thickened by secondary lamellae, suggesting plesio- or ortho-monolamellar construction. The hyaline and radially organized fibrous structure visible in this thickened lamellar wall is the most characteristic feature of the genus *Pachyphloia* that can be easily recognized in longitudinal lateral sections. In the Changhsingian of the Southern Biofacies Belt, several *Pachyphloia*-like specimens recovered from the Antalya Nappes (Olimpus: OLP-3 159; Demirtaş: DD 3, 11, 14, 19) and the Aladağ Nappe (Taşkent: TCX 4, 11, 14, 21, 22; DT 4, 5, 8, 13; Hadim: AR-1 662, 669; AR-2 153; Aygörmez Dağı: ST 671; K 4034) (Fig. 1) exhibit long and regularly spaced canal-like pores crossing the successive laminae (Fig. 6.28). Although several sections display the character that we define here, in order to give a correct taxonomic description, we need longitudinal-frontal sections and sections perpendicular to the radially organized pores crossing the lamellar system of these peculiar forms.

Phylogenetic assessment of new taxa

Retroseptellininae n. subfam.—According to Vachard (2018) and our recent observations, the genus *Retroseptellina*, the root stock of Retroseptellininae n. subfam., appeared as early as the Wordian and was widespread in the paleotethyan and neotethyan shelves of the Tethyan Realm. As stated in Altıner and Özkan-Altıner (2001), *Retroseptellina* (given there as *Globivalvulina decrouezae* Köylüoğlu and Altıner, 1989, the type species of *Retroseptellina*), which is characterized by a thin and simple microgranular wall, long and folded apertural flaps, and irregularly coiled biserial chambers with septa curved backward, evolved from the *Globivalvulina* stock around the Murgabian–Midian boundary, corresponding to the Wordian Stage in the standard timescale (Fig. 7). Close to the Wordian–Capitanian boundary, *Retroseptellina* gave way to the genus *Septoglobivalvulina*, characterized again by a thin and dense microgranular wall and semi-involute (*S. distensa*) to nearly completely involute (*S. guangxiensis*) populations with hook-shape apertural flaps. This lineage finally gave way to the genus *Paraglobivalvulinoides* in the Changhsingian (Fig. 7). Larger and completely involute tests of *P. gracilis* were succeeded by very large involute tests with interseptal partitions

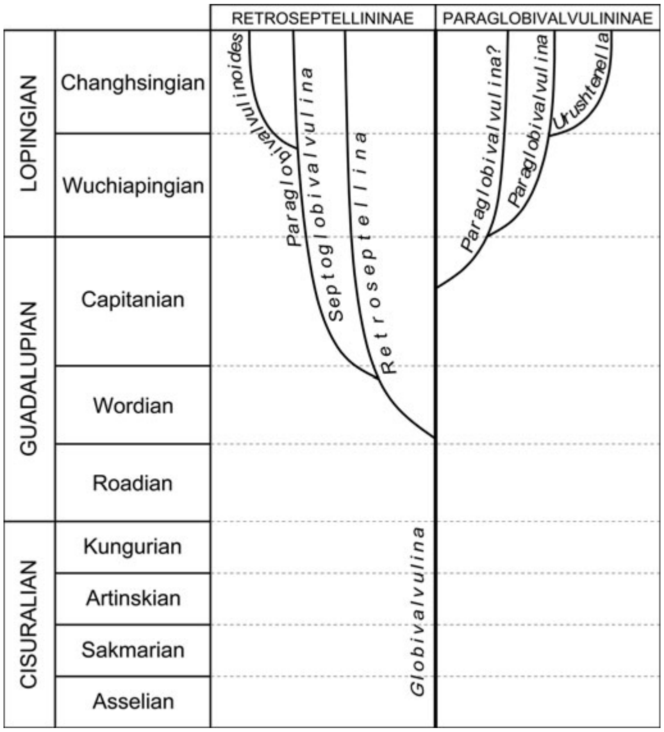

Figure 7. Tentative evolutionary scheme of Retroseptellininae new subfamily and Paraglobivalvulininae. Globivalvulinin genera (except *Globivalvulina*) and dagmaritins are not shown in the figure. For the tentative evolutionary scheme of dagmaritins, see Altıner et al. (2021a, fig. 12).

of the late Changhsingian *P. septulifer*. As indicated by this evolutionary interpretation, the taxonomy of Retroseptellininae n. subfam. is based on grouping of genera along a certain lineage, rather than classifying these genera into similar-looking, but phylogenetically unrelated subfamilies of the family Globivalvulinidae.

Paraglobivalvulina*? intermedia n. sp., root stock of Paraglobivalvulininae.*—In the evolutionary development of completely involute globivalvulinids, represented by Paraglobivalvulininae, *Paraglobivalvulina*? *intermedia* n. sp. constitutes the root stock of this phylogenetic lineage (Fig. 7). This new species, characterized by a well-developed apertural flap system and weakly developed interseptal secondary partitions, established the phylogenetic link between the genus *Globivalvulina* and the genus *Paraglobivalvulina* of Reitlinger (1965). *Paraglobivalvulina*? *intermedia* n. sp. appeared in the late Capitanian, following the mid-Capitanian extinction of schwagerinids in the Southern Biofacies Belt in Turkey (Köylüoğlu and Altıner, 1989; Altıner and Şahin, 2012). Close to the Capitanian–Wuchiapingian boundary, *P.*? *intermedia* n. sp. gave rise to *Paraglobivalvulina*, characterized by involute tests with well-developed interseptal partitions (Fig. 7). The last step in this lineage is represented by the genus *Urushtenella* of Pronina-Nestell in Pronina-Nestell and Nestell (2001), which evolved from *Paraglobivalvulina* in the Changhsingian by the development of a pseudoalveolar, porous wall structure.

Midiellidae n. fam. and Pseudomidiella sahini *n. sp., one of the last midiellid taxa in the Changhsingian.*—Although some of the previously described hemigordiopsid taxa from the early Permian have been assigned to the genus *Midiella* (e.g., *Midiella ovatus* of Gaillot and Vachard, 2007, originally described as *Hemigordius ovatus* Grozdilova, 1956), we argue that the true *Midiella* population appeared in the earliest Roadian (Fig. 8). The medium- to small-sized populations of *Midiella* with well-developed sigmoidal coiling became more frequent starting from the base of the Capitanian. *Midiella broennimanni* (Altıner, 1978) and *M. zaninettiae* (Altıner, 1978) appeared in this stage and survived until the end of the Changhsingian stage.

Pseudomidiella appeared earliest in the late Capitanian from a *Midiella* ancestor. One of the earliest forms was illustrated by Wignall et al. (2012) from the upper Capitanian of Hungary. *Pseudomidiella*, which is distinct from *Midiella* by the development of pseudochambers in the late stage of its ontogeny, is more frequently encountered in the Changhsingian. Together with the type species of the genus, *P. labensis* Pronina-Nestell in Pronina-Nestell and Nestell, 2001, *P. sahini* n. sp. is characterized by a more inflated and robust population and is the last known representative of the midiellid foraminifera.

Pseudomidiella was illustrated in Vachard et al. (2008) as the direct descendant of *Glomomidiella* Vachard et al., 2008. We do not share this opinion. The early stage of *Pseudomidiella* is characterized by a sigmoidal coiling, indicating that this mode of coiling was directly inherited from a *Midiella* ancestor.

Glomomidiellopsis*? okayi n. sp. within the evolutionary scheme of Hemigordiopsidae.*—Probably derived from a *Hemigordius* ancestor, the family Hemigordiopsidae, consisting of large porcelaneous foraminifera of the Permian, appeared in the Capitanian with flosculinized tests of *Hemigordiopsis* Reichel, 1945, with a low chamber lumen. According to our tentative evolutionary scheme (Fig. 8), *Hemigordiopsis* gave way to the appearance of three distinct taxa in the Capitanian. Pillared *Shanita* Brönnimann, Whittaker, and Zaninetti, 1972, and *Lysites* Reitlinger in Vdovenko et al., 1993, with a compressed test appeared in the late Capitanian. The third taxon, *Glomomidiellopsis*? *okayi* n. sp., previously reported under several taxa (e.g., '*Hemigordius* en pelote', *Kamurana*, *Neodiscus*, *Hemigordiopsis*, *Glomomidiellopsis*, or *Neodiscopsis*) evolved from *Hemigordiopsis* in the Capitanian by the increase of the height of the chamber lumen and widely oscillating whorls in the adult stage of the test. This taxon, questionably assigned to *Glomomidiellopsis* in this study, was a 'bridge' in the evolution from the Capitanian *Hemigordiopsis* to the Lopingian *Glomomidiellopsis* whose flosculinized test morphology is characterized by oscillating to streptospiral whorls. *Glomomidiellopsis*? *okayi* n. sp. gave way to *Kamurana* Altıner and Zaninetti, 1977, by the appearance of perforations in the porcelaneous wall in the late Changhsingian.

Contrary to the opinion of Gaillot and Vachard (2007) and Vachard et al. (2008), who considered *Neodiscopsis specialis* (Lin, Li, and Sun, 1990) as the ancestor of *Kamurana*, we select *G.*? *okayi* n. sp. as the ancestor of *Kamurana* based on the similarity between the streptospiral coiling in the initial stage of *G.*? *okayi* and that of the type of *Kamurana*, *K. bronnimanni*. However, *N. specialis* is a form characterized by a nearly aligned (planispiral) coiling in the initial stage.

Evolution of robuloidid genera.—When phyletic relations of previously known robuloidid genera (Vachard, 2018) are analyzed along with the new genera added in this study, three

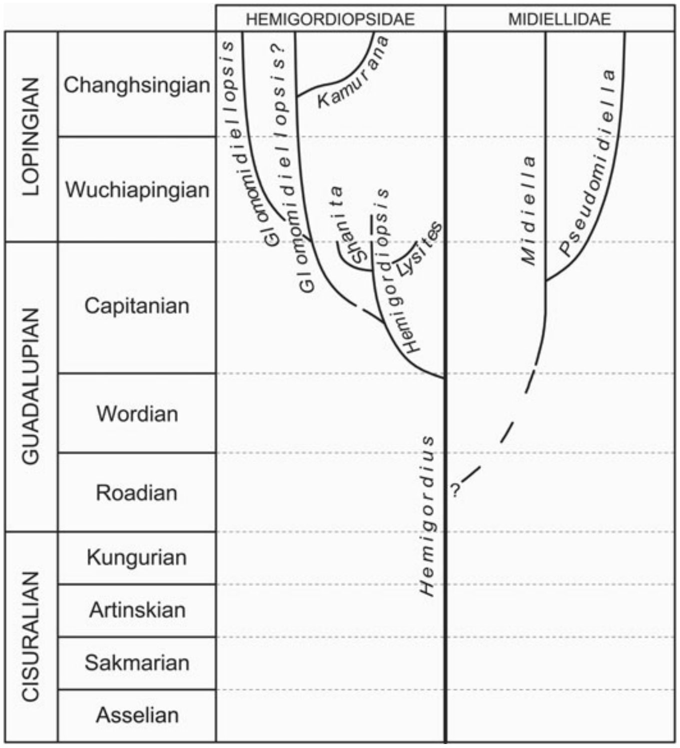

Figure 8. Tentative evolutionary scheme of Hemigordiopsidae and Midiellidae new family. Genera belonging to other families of Miliolata (Hemigordiidae, Neodiscidae, and Baisalinidae) that originated from the genus *Hemigordius* are not shown in the figure.

distinct groups emerge, which are probably related to one another by intermediate taxa that have not yet been identified and resolved (Fig. 9). Among these groups, the entirely coiled group appeared with *Robuloides* in the Capitanian, probably derived from an unknown ancestor that established the evolutionary link between *Robuloides* and *Eocristellaria* Miklukho-Maklay, 1954. *Robuloides* gave way to *Hubeirobuloides* Lin, Li, and Zhang in Lin et al., 1990, characterized by a test that uncoils following the fully coiled stage and a taxon called *Robuloides*? in this study, becoming evolute in the late stage of its ontogeny. The lineage terminated finally by the derivation of *Pseudorobuloides* n. gen. from *Robuloides*? with an involute to semi-involute to evolute discoidal test and completely reduced lateral lamellar thickenings. *Plectorobuloides* n. gen., which exhibits twisted coiling in the early stage of its ontogeny, and *Gourisina* Reichel, 1946, characterized by two serial chambers, could be added to this lineage in the Changhsingian; however, there must be some intermediate taxa that have yet to be discovered that would illustrate the sequence of morphological change between these two forms and the possible ancestor *Robuloides* (Fig. 9).

The second group of taxa of the family Robuloididae, represented by *Eocristellaria* (Fig. 9), appeared in the Wordian. With loosely coiled chambers increasing rapidly in breadth, *Eocristellaria* gave way to *Calvezina* Sellier de Civrieux and Dessauvagie, 1965, in the Capitanian, characterized by loosely coiled chambers in the initial stage of the test followed by rectilinear-elongate chambers in the adult stage. Finally, *Cryptomorphina* Sellier de Civrieux and Dessauvagie, 1965, was derived from *Calvezina* with the development of a thick wall in the late Capitanian. All taxa in this group and those included in the *Robuloides* lineage survived into the Changhsingian stage and disappeared very close to the Permian–Triassic boundary. *Pseudocryptomorphina* n. gen., doubtfully included in Robuloididae and characterized by a different chamber arrangement and a very thick wall, could be related to *Cryptomorphina*; however, we are not confident of this interpretation in the absence of an intermediate taxon (or taxa) illustrating the morphological transition.

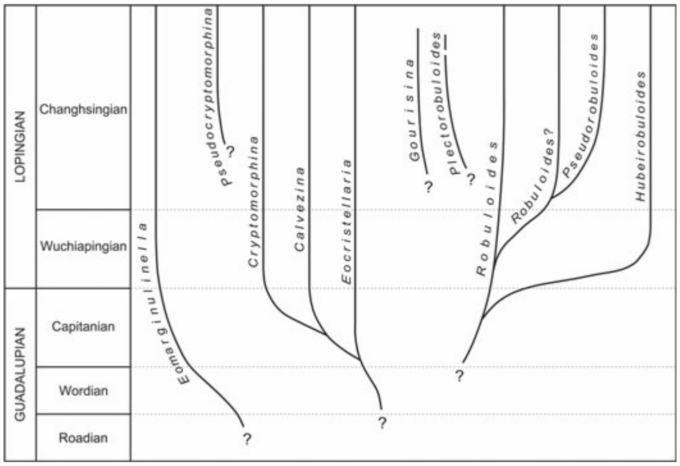

Figure 9. Tentative evolutionary scheme of Robuloididae including the new genera introduced in this study.

The third group in the evolution of robuloidid foraminifera is represented by *Eomarginulinella* Sosnina, 1969, and characterized by incipiently coiled chambers in the early stage, and rectilinear and globular chambers in the adult. *Eomarginulinella* is first known from the early Guadalupian and survived into the Changhsingian. It is distinguished from the second group by possessing circular transverse sections of its chambers instead of having oval shapes. The ancestors of both *Eomarginulinella* and *Eocristellaria* are not yet known in the Permian. Identification of an intermediate taxon would help to clarify the evolutionary relationship between *Eomarginulinella* and *Eocristellaria*.

Two different lineages (the Robuloides acutus–Robuloides*?* rettorii *n. sp.*–Pseudorobuloides reicheli *n. gen. n. sp. lineage, and the* Robuloides lens–Robuloides lata *n. sp. lineage) and* Plectorobuloides taurica *n. gen. n. sp. in robuloidid foraminifera.*—Morphologic variation and the frequent occurrence of smaller *Robuloides* species in the middle and upper Permian carbonate deposits of the Southern Biofacies Belt in Turkey reveal that these smaller species evolved in certain lineages with a pronounced proliferation in the latest Permian (Changhsingian). As was indicated by Vachard (2018), the earliest *Robuloides* appeared in the middle Permian (Capitanian) and two smaller *Robuloides* species, *R. lens* and *R. acutus*, split into two lineages and survived from the Capitanian to the end of the Changhsingian.

Robuloides? *rettorii* n. sp. appeared, with coiling becoming evolute in the last whorl, in the Wuchiapingian from the laterally compressed and involute tests of *R. acutus*, and continued to survive into the Changhsingian (Fig. 10). A major morphological modification in this lineage occurred close to the Wuchiapingian–Changhsingian boundary. Similar to the evolution of *Millerella* from the eostaffellid stock in the Carboniferous (Maslo

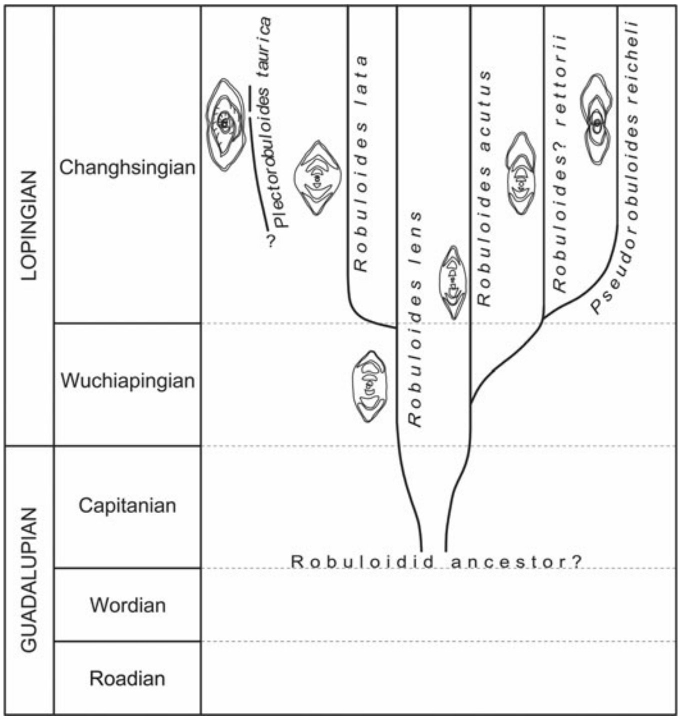

Figure 10. Tentative scheme depicting the evolution of smaller robuloidid genera and species in two different lineages originated from *Robuloides lens* and *R. acutus*.

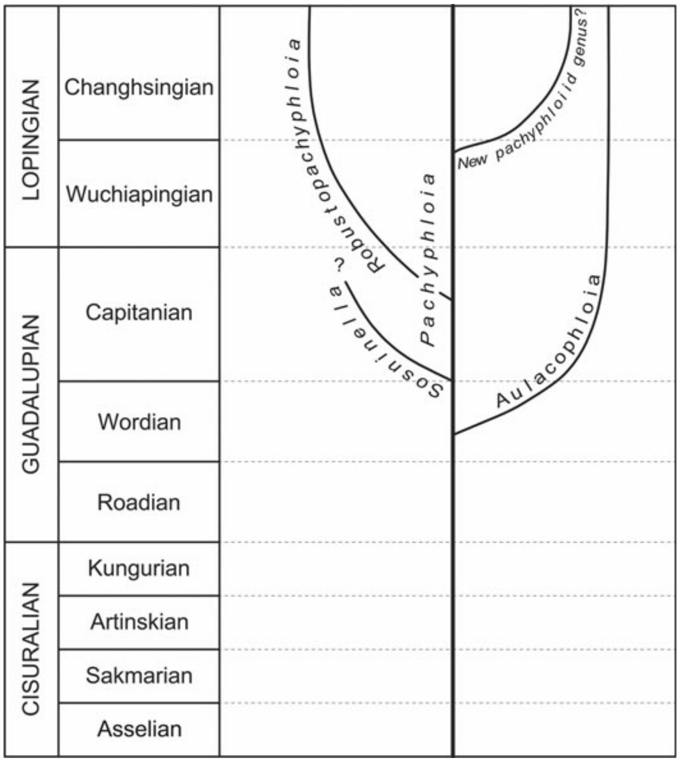

Figure 11. Tentative evolutionary scheme of Pachyphloiidae including the "new pachyphloiid genus?".

and Vachard, 1997), *Pseudorobuloides reicheli* n. gen. n. sp., with an involute to semi-involute to evolute discoidal test and completely reduced lateral lamellar thickenings, probably evolved from *R.*? *rettorii* n. sp. and survived up to the Permian–Triassic boundary.

The other lineage, represented mainly by *R. lens* with involute and lenticular to inflated-lenticular tests, remained morphologically unchanged up to the Wuchiapingian–Changhsingian boundary (Fig. 10). *Robuloides lata* n. sp., with lozenge-shaped axial sections and thus a smaller diameter/width ratio, evolved from *R. lens* in the Changhsingian. In the evolution of robuloidid foraminifera, the most distinct trend is the appearance of *Plectorobuloides taurica* n. gen. n. sp. in the Changhsingian. Characterized by changes in the coiling axis of the initial whorls, the ancestor of this taxon is not properly known. *Robuloides lens* may have been the ancestor, however, intermediate steps should be found filling the morphologic gap between *R. lens* and *Plectorobuloides taurica* n. gen. n. sp.

*Evolution of other robuloidid species (*Eomarginulinella galinae *n. sp.,* Calvezina anatolica *n. sp., and* Pseudocryptomorphina amplimuralis *n. gen. n. sp.).*—With current data, it is not possible to propose clear evolutionary hypotheses for these species. *Eomarginulinella*, comprising *E. galinae* n. sp. and some other species, such as *E. typica* and *E. serbica*, may be polyphyletic. For example, *E. galinae* n. sp. and *E. serbica* may have evolved from a *Pseudolangella* ancestor, whereas the type species, *E. typica*, may be directly related to the evolution of robuloidid foraminifera.

Calvezina anatolica n. sp., characterized by a large test and with a tendency to become rectilinear at the end its ontogeny, is closely related to *C. ottomana* and probably evolved from this latter species in the Changhsingian.

Among the new taxa described in this study, the most difficult taxon to assess phylogenetically is *Pseudocryptomorphina amplimuralis* n. gen. n. sp. Although this taxon superficially resembles *Cryptomorphina limonitica* in having a thick wall and few chambers, the chamber organization is different and it is difficult to relate it, at the moment, to a known evolutionary lineage.

Robustopachyphloia farinacciae *n. sp. and the new pachyphloiid genus? within the evolutionary frame of pachyphloiid genera*.—The genus *Pachyphloia*, which probably is derived from the *Syzrania* Reitlinger, 1950–*Nodosinelloides* Mamet and Pinard, 1992–*Geinitzina* Spandel, 1901, lineage, survived the entire Permian (Fig. 11). Although Vachard (2018) reported the first occurrence of *Pachyphloia* in the Kungurian, based on studies of Groves (1997) and Groves and Wahlman (1997), this genus most likely originated earlier in the Permian. *Pachyphloia* led to the evolution of some distinct taxa during the middle and late Permian. *Aulacopholia*, considered to be confined to the Changhsingian (Vachard, 2018), was derived from *Pachyphloia* in the late Wordian and survived up to the Permian–Triassic boundary, based on data from the eastern Taurides, Turkey (Altıner and Şahin, 2012). The genus *Sosninella* also was derived from *Pachyphloia* and currently is known only from the Capitanian. *Sosninella*, characterized by sigmoidal transverse sections and not very well known from the literature, makes its last appearance during the mid-Capitanian extinction event when schwagerinids became extinct in the eastern Taurides, Turkey (Altıner and Şahin, 2012) (Fig. 11). From the other pachyphloiids, the genus

Robustopachyphloia appeared in the late Capitanian and seems to have survived until the end of the Permian. Similar to some of the robuloidid species (e.g., *Eomarginulinella*) *Robustopachyphloia* species are probably polyphyletic. *Robustopachyphloia* is a clear descendent from the genus *Pachypholia*, but the species of *Robustopachyphloia* (e.g., *R. farinacciae* n. sp., *R. annectena*) may have descended from different species of *Pachyphloia*. This problem raises questions about the taxonomic validity of the genus *Robustopachyphloia*, if it houses species that evolved from different ancestors.

The taxon that we report in this study as "new pachyphloiid genus?", which is characterized by the appearance of canal-like perforations in the wall, surely is a descendent from the genus *Pachyphloia*, more precisely the type species *P. ovata*.

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Declaration of competing interests

The authors declare that have no competing interests.

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