European Journal of Taxonomy 1043: 33–61
https://doi.org/10.5852/ejt.2026.1043.3207

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2026 · Okuyucu C. & Akbaş M.

Received: 28 April 2025 • *Accepted: 4 December 2025* • *Published: 25 February 2026*

Topic editor: Denis Audo • *Desk editor: Pepe Fernández*

Research article

urn:lsid:zoobank.org:pub:0252EFBA-E174-442B-BB29-FA1F4EE6E761

Systematic revision and phylogenetic assessment of the family Neodiscidae (Foraminifera) and new Capitanian foraminiferal genera from the Ankara region, central Türkiye

Cengiz OKUYUCU [1,*] & Melikan AKBAŞ [2]

[1]Ankara Hacı Bayram Veli University, School of Land Registry and Cadastre, 06500, Ankara, Türkiye.
[2]Konya Technical University, Department of Geological Engineering, 42250, Konya, Türkiye.

[*]Corresponding author: cengiz.okuyucu@hbv.edu.tr
[2]Email: makbas@ktun.edu.tr

Abstract. Among Paleozoic foraminifers, miliolids represent one of the most diverse groups, which reached their highest diversity during the Middle to Late Permian. Notably, many taxa within the family Neodiscidae emerged during the Guadalupian epoch. In this study, two fossiliferous Middle Permian blocks were studied for their foraminiferal assemblages around Kutludüğün Yayla (east of Ankara, Türkiye) from the Elmadağ Olistostrome. We present a systematic and phylogenetic revision of the subfamilies Neodiscinae and Agathammininae, and propose the erection of Globidiscinae subfam. nov. included within the family Neodiscidae. The foraminiferal genera *Kamurana*, *Globidiscus*, and *Agathammina* are taxonomically re-evaluated and emended based on newly described miliolid taxa, in conjunction with a reassessment of previously published data. The composition and taxonomic status of the subfamily Neodiscinae is revised. The subfamily Agathammininae and family Neodiscidae are emended. The genus *Neodiscus* derives from *Praeneodiscus* in the Capitanian, and *Kamurana*, *Globidiscus*, *Rectogordiopsis* gen. nov., *Davanela* gen. nov. and *Kaganella* gen. nov. derived probably from *Neodiscus* in the late Capitanian. The new taxa are Globiscinae subfam. nov.; *Rectogordiopsis* gen. nov.; *Davanella* gen. nov. and *Kaganella* gen. nov., *Rectogordiopsis kamuranaeformis* gen. et sp. nov., *Rectogordiopsis ovaliformis* gen. et sp. nov., *Davanella ankaraensis* gen. et sp. nov., *Davanella acuminata* gen. et sp. nov., *Kaganella tekini* gen. et sp. nov.

Keywords. Foraminifera, Neodiscidae, phylogeny, taxonomy, Permian, Türkiye.

Okuyucu C. & Akbaş M. 2026. Systematic revision and phylogenetic assessment of the family Neodiscidae (Foraminifera) and new Capitanian foraminiferal genera from the Ankara region, central Türkiye. *European Journal of Taxonomy* 1043: 33–61. https://doi.org/10.5852/ejt.2026.1043.3207

Introduction

The Permian period is an important time in Earth's history which was characterized by a pronounced paleobiogeographic subdivision and evolution to the effects of both paleogeographic reorganization

and climatic warming after the Late Paleozoic glaciation (Isbell *et al.* 2003, 2012; Montañez 2022). Paleozoic miliolids are widespread during the Permian and they have existed from the latest/earliest Mississippian or Pennsylvanian time (Groves & Altıner 2005; Vachard 2018; Krainer *et al*. 2019). In the Early Permian, Cisuralian epoch, their diversity is already significant, and it continuously rises during the Middle Permian, Guadalupian epoch, when giant forms such as hemigordiopsids and neodiscids emerge (Vachard 2018). The Guadalupian (Capitanian)–Lopingian episode exhibits the highest diversity and abundance of hemigordiopsids and neodiscids (Vachard 2018; Krainer *et al*. 2019). The morphologically complex fusulinoideans were eliminated by the end-Guadalupian extinction event. The evidence suggests that miliolids with complex morphology like *Shanita* Brönnimann, Whittaker & Zaninetti, 1978, *Nikitinella* Sosnina, 1983 and *Pseudobaisalina* Sosnina, 1983 were also adversely impacted by this extinction (e.g., Vachard 2018).

In the original description of subfamily Neodiscinae its main characteristics were described as discoidal to lenticular test composed of a second tubular chamber with initially irregular streptospiral then planispirally coiling by Lin (1984). Based on this diagnosis five genera have been included in this subfamily by Lin (1984): *Septagathammina* Lin, 1984, *Neodiscus* Miklukho-Maklay, 1953, *Multidiscus* Miklukho-Maklay, 1953, *Eodiscus* Vdovenko, 1970 and *Brunsia* Mikhailov, 1935. Later, in the study of Gaillot & Vachard (2007), the subfamily Neodiscinae of Lin (1984) was raised to family rank (Neodiscidae) with the following emended diagnosis: "Large Miliolida tests composed of a spherical proloculus followed by an undivided tubular chamber, diversely coiled: entirely glomospiral, initially glomospiral and then planispiral (or aligned) and involute, glomospiral becoming planispiral evolute or semi-involute, planispirally involute compressed or inflated agathamminoid, i.e., pseudoquinqueloculine. The chamber is semicircular in section (some flosculinisations are observable); the thick wall is still re-inforced by buttresses at the contact with the preceding whorl. Aperture terminal simple" (Gaillot & Vachard 2007: 94). According to Gaillot & Vachard (2007), the family Neodiscidae was composed of the genera *Neodiscus*, *Crassiglomella* Gaillot & Vachard, 2007, *Graecodiscus* Vachard, 1993, *Neohemigordius* Wang & Sun, 1973, *Uralogordius* Gaillot & Vachard, 2007, *Multidiscus*, *Brunsispirella* Gaillot & Vachard, 2007, *Crassispirellina* Vachard & Le Coze, 2019, *Neodiscopsis* Gaillot & Vachard, 2007, *Septagathammina* Baisalina Reitlinger, 1965, and *Pseudomidiella* Pronina-Nestell, 2001. Following Gaillot & Vachard (2007)'s taxonomic revision, several genera previously assigned to the family Neodiscidae were transferred to other families or subfamilies (e.g., Vachard *et al*. 2008; Vachard 2018; Hayward *et al*. 2021; Vachard & Le Coze 2024). Recently, Vachard & Krainer (2022) revised the composition of the family Neodiscidae and proposed a new composition, which includes the subfamilies Baisalininae Loeblich & Tappan, 1986, Multidiscinae Vachard & Krainer, 2022, ?Septagathammininae Mikhalevich, 1988, and Neodiscinae, along with the description of a new subfamily (Multidiscinae) and a new taxon within it.

Despite numerous significant studies on the composition and morphological characteristics of porcelaneous large miliolids (e.g., the family Neodiscidae), several aspects remain controversial. The character of thick porcelaneous wall in the family Neodiscidae can be reinforced by buttresses at the contact with the preceding whorl and/or may show a perforation due to neosparitization. This perforation structure on the wall originally named and shown by Gargouri & Vachard (1988) as "en dent de peigne" (comb teeth-shaped) in a single specimen of *Hemigordiopsis renzi* Reichel, 1945 (Gargouri & Vachard 1988: pl. 1 fig. 7). Since then, the comb teeth-shaped structure observed on the wall of a specimen of *Hemigordiopsis* Reichel, 1945 – or any taxon within the family Hemigordiopsidae Nikitina, 1969 – has neither been documented nor cited in subsequent studies except in the study of Gaillot & Vachard (2007) where it was cited under the emended diagnosis of the family Hemigordiopsidae.

Considering the information provided above, there are serious disagreements and confusions regarding the definition, morphological characteristics, and even wall structures of the genera within the family Neodiscidae including the studies of researchers and even the same author at different times.

The foraminiferal taxa recovered from the Elmadağ Olistostrome near Kutludüğün Yayla (east of Ankara, Türkiye) provides new insights into the family Neodiscidae Lin, 1984. In the light of these new findings, the purpose of this paper is to describe the new Capitanian miliolids within the Neodiscidae and give their taxonomic status and morphologic properties (e.g., wall structure, coiling type, shape, size of test). In addition, the clarification of the taxonomic composition and phylogenetic assessment of the family Neodiscidae are discussed.

Geological setting

The Ankara region, a part of the Sakarya Zone (Okay 1989) or Sakarya Composite Terrane (Göncüoğlu *et al*. 1997), located between the remnants of the northern Neotethyan Oceanic branches, represented by the Intra-Pontide (IP) and Izmir-Ankara-Erzincan (IAE) suture zones (Fig. 1A). The geological history of the Ankara region has been the subject of many studies since the beginning of the 20th century (e.g., Philipson 1919; Chaput 1931; Erol 1956; Akyürek *et al*. 1984; Koçyiğit 1991).

The rock units in the study area were originally designated by Erol (1956) as the "Elma Dağı Exotic-Block Series". Recently, Tekin *et al.* (2024, 2025) described these rock units as a sedimentary mélange which originated from the Neotethyan Intra-Pontide realm and named as Elmadağ Olistostrome. The Elmadağ Olistostrome is composed of different types of blocks (mainly platform carbonates and rare pelagic carbonates/cherts) with various sizes within a calcareous clastic to clayey carbonate matrix.

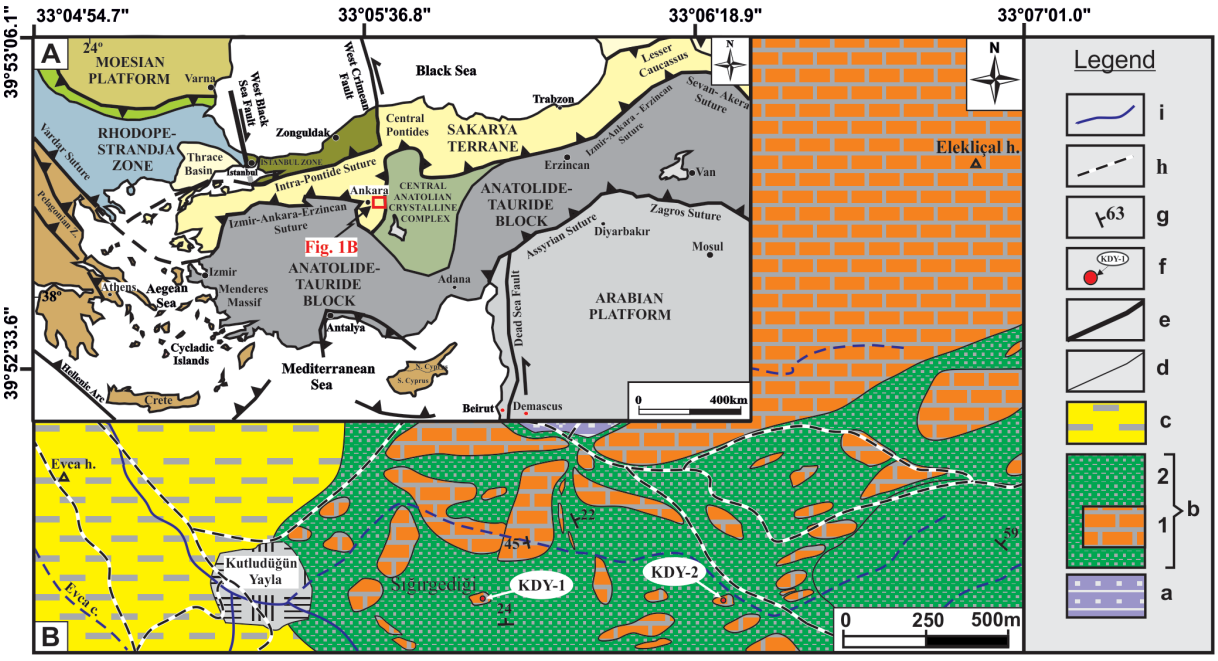

Fig. 1. A. Tectonic map of Türkiye and surrounding areas within major suture zones/terranes and location of the studied region to the SE of Ankara city center (slightly revised after Okay & Tüysüz 1999; Okay & Göncüoğlu 2004). **B**. Geological map of the area around the Kutludüğün Yayla, showing the locations of studied individual samples. Legend: a = Middle Anisian to upper Ladinian (Middle Triassic) Dikmen Graywacke consisting of clastics and volcanoclastics/volcanic breccia; b = Upper Cretaceous Elmadağ Olistostrome composed of foreland flysch deposits of the Intra–Pontide Ocean: 1 = blocks of Permian detrital and platform limestones; 2 = Upper Cretaceous carbonaceous clastic and clayey carbonate matrix of the Elmadağ Olistostrome; c = Tertiary clastics; d = stratigraphic contact; e = structural contact; f = sampling point; g = dip and strike; h = main roads; i = drainage system (simplified after Tekin *et al.* 2025).

Whereas a part of the Elmadağ Olistostrome includes Jurassic–Cretaceous limestone blocks, the other part consists of older limestone blocks of Carboniferous–Permian ages (Tekin *et al*. 2024, 2025). This finding is extremely important since this Upper Cretaceous Elmadağ olistostrome is very similar to the so-called Triassic Upper Karakaya Complex (Okay & Göncüoğlu 2004). Studied Middle Permian blocks, from which the samples were collected, were mapped previously as the Upper Karakaya Complex by Akyürek *et al*. (1984).

In this study, two Middle Permian blocks within the Elmadağ Olistostrome around the Kutludüğün Yayla (east of Ankara, Türkiye) (Fig. 1B), were examined in detail for their foraminiferal assemblages.

Material and methods

This study has been carried out on two rich fossiliferous carbonate samples, KDY–1 (coordinates: 39°52′11.0″ N, 33°05′51.4″ E) and KDY–2 (coordinates: 39°52′07.4″ N, 33°06′23.4″ E), both from the Elmadağ Olistostrome (Ankara, Türkiye) (Figs 1B, 2) representing one sample from each block. For the systematic paleontological studies, 19 randomly oriented thin sections were prepared from samples and a transmitted light microscope was used for the examination of the thin sections and taking microphotographs of the foraminifers.The systematics of foraminifers used in this paper is based on the classification of the Paleozoic foraminifera proposed by Vachard (2018) and Vachard & Le Coze (2024).

Institutional abbreviations

KTÜN = Konya Technical University, Türkiye

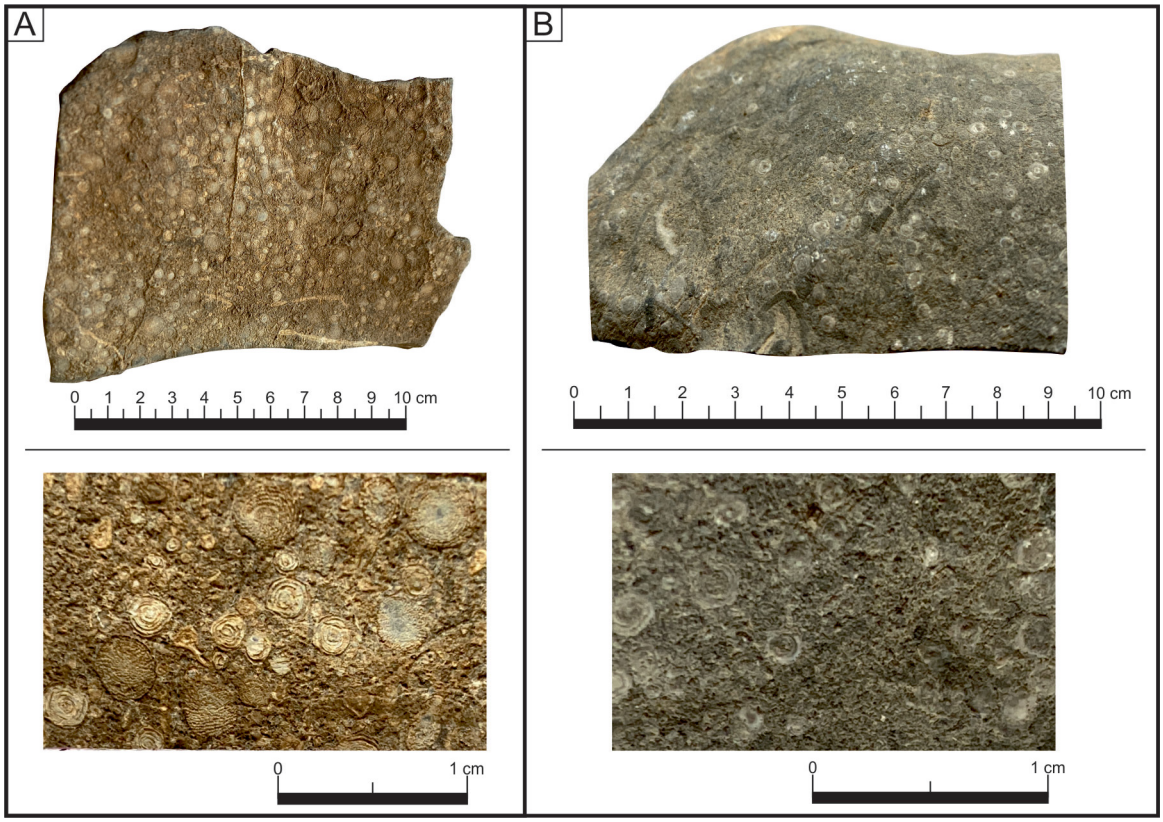

Fig. 2. The general and close up view of the fossiliferous hand samples from the isolated carbonate blocks with new Permian miliolid genera. **A**. KDY–1. **B**. KDY–2.

Anatomical abbreviations

D = diameter
n.w. = number of whorls
w = width

Results

Systematic paleontology

Phylum Foraminifera d'Orbigny, 1826 emend. Cavalier-Smith 2003
Class Miliolata Saidova, 1981
Order Cornuspirida Mikhalevich, 1980
Suborder Cornuspirina Jirovec, 1953
Superfamily Cornuspiroidea Bogdanovich, 1981

Family **Neodiscidae** Lin, 1984 nom. translat. and emend. Gaillot & Vachard 2007; emend. herein

Description (emended)

Medium- to large-sized miliolid composed of a spherical proloculus followed by an undivided deuteroloculus with different types of coiling: entirely glomospiral, initially glomospiral and then planispiral (or aligned) involute, glomospiral becoming planispiral evolute or semi-involute, glomospiral then irregular planispiral involute/semi-evolute(?), initially quinqueloculinoid then planispiral involute or evolute. The following chamber is semicircular in axial section and sometimes with flosculinisations. Pseudosepta present in few genera. Thick porcelanaceous wall with buttresses and sometimes with perforations similar to comb teeth-shaped structure. Aperture terminal, simple.

Subfamilies

Neodiscinae Lin, 1984; Baisalininae Loeblich & Tappan, 1986 nomen translat. Pronina 1994; Agathammininae Ciarapica, Cirilli & Zaninetti, 1987; Multidiscinae Vachard & Krainer, 2022; Globidiscinae subfam. nov.

Subfamily **Neodiscinae** Lin, 1984

Original description

Neodiscidae medium- to large-sized, undivided or with weak pseudosepta, involute or with a short evolute terminal stage of coiling, and devoid of flosculinisation.

Remarks

In the original description, the genus *Praeneodiscus* is tentatively included in the family Neodiscidae by Vachard *et al*. (2015). After the acceptance of the original taxonomic position of *Praeneodiscus* under the family Neodiscidae by Vachard (2018), it was later transferred to the subfamily Cornuspirinae Schultze, 1854 nom. translat. Rhumbler 1904 within the family ?Cornuspiridae Schultze, 1854 by Krainer *et al*. (2019). Recently, the genus *Praeneodiscus* was placed tentatively in the subfamily Hemigordiinae Reitlinger in Vdovenko *et al*., 1993 (nomen translat. Pronina 1994 pro family) of the family Hemigordiidae Reitlinger in Vdovenko *et al*. (1993) by Vachard & Krainer (2022). In this study, even the taxonomic status of the genus *Praeneodiscus* is still controversial, it is concluded that it should be included in the subfamily Neodiscinae due to its test shape, coiling type and devoid of flosculinisation.

Included genera

Praeneodiscus Vachard, Krainer & Lucas, 2015; *Neodiscus* Miklukho-Maklay, 1953; *Crassiglomella* Gaillot & Vachard, 2007; *Crassispirellina* Gaillot, Vachard & Le Coze, 2019; *Graecodiscus* Vachard, 1993; *Neohemigordius* Wang & Sun, 1973; *Pseudomidiella* Pronina-Nestell, 2001; *Uralogordiopsis* Vachard, 2019; *Uralogordius* Gaillot & Vachard, 2007 (= *Arenovidalina* sensu Baryshnikov, Zolotova & Kocheleva, 1982, non Ho, 1959).

Subfamily **Agathammininae** Ciarapica, Cirilli & Zaninetti, 1987 emend. herein

Septagathammininae Mikhalevich, 1988: 88.

Description (emended)

Medium-sized miliolid with spherical proloculus followed by a tubular chamber, initially quinqueloculinoid then planispiral involute, sometimes with evolute last whorls. The tubular chamber sometimes shows pseudosepta. Porcelanaceous wall with perforations similar to comb teeth-shaped structure. Aperture terminal, simple.

Included genera

Agathammina Neumayr, 1887; *Septagathammina* Lin, 1984.

Genus ***Agathammina*** Neumayr, 1887 emend. Wolanska 1959, emended herein

Type species

Agathammina pusilla (Geinitz, 1848) (type by subsequent designation).

Description (emended)

Test ovate, globular proloculus followed by enrolled undivided tubular second chamber of few gradually enlarging whorls, initially quinqueloculinoid then planispiral involute sometimes with evolute last whorls without septation; wall calcareous, porcelaneous with perforations similar to comb teeth-shaped structure. Aperture terminal, simple.

Subfamily **Globidiscinae** subfam. nov.
urn:lsid:zoobank.org:act:9BC6E72C-D473-47DD-9681-51754BC42BAE

Type genus

Globidiscus Okuyucu, 2021.

Description

Large miliolid tests composed of a spherical proloculus followed by an undivided tubular chamber, diversely coiled: initially glomospiral and finally planispiral involute, initially glomospiral then irregular planispiral involute/semi-evolute(?). Sometimes one or two sided ogival shape of the last whorls. No septa or pseudosepta. Lumen with common flosculinisation. The thick wall with perforations similar to comb teeth-shaped structure. Neosparitization rare to common. Umbilicus slightly depressed or absent. Aperture terminal, simple.

Comparison

Globidiscinae differ from Neodiscinae by the test shape of the last whorls which has one- or two-sided ogival-shaped last whorls, and is of a coiling type initially glomospiral and finally planispiral involute, initially glomospiral then irregular planispiral involute/semi-evolute(?) and with common

flosculinisation; from Baisalininae and Agathammininae by a larger test and devoid of septa/pseudosepta; and from Multidiscinae by a test which has one- or two-sided ogival-shaped last whorls, a larger test and common flosculinisation.

Remarks

In the original description of the genus *Kamurana* it was tentatively attributed to the family Hemigordiopsidae Nikitina, 1969 instead of Milioliporidae Brönnimann & Zaninetti, 1971 by Altıner & Zaninetti (1977) due to the probable absence of septation and a homeomorph of the irregular forms of the genus *Hemigordius* Schubert, 1908. Besides, as indicated by the authors, the presence of perforations in the wall at the adult stage of the genus *Kamurana* makes its attribution to the Hemigordiopsidae problematic. In this study, after a detailed investigation of the wall structure of the genus *Kamurana* in the original description compared with recovered well-preserved material, it is clearly shown that the wall of *Kamurana* does not feature a perforation structure in the adult stage in the sense of authors. This structure is clearly comb teeth-shaped which developed on the porcelaneous wall related to the neosparitization. For this reason, the taxonomic position of the genus *Kamurana* should be located under the subfamily Globidiscinae subfam. nov.

Included genera

Kamurana (sensu Altıner & Zaninetti 1977); *Globidiscus* Okuyucu, 2021; *Rectogordiopsis* gen. nov., *Davanella* gen. nov. and *Kaganella* gen. nov.

Genus ***Globidiscus*** Okuyucu, 2021 emend. herein

Type species

Globidiscus fragilis Okuyucu, 2021 (type by original designation).

Description (emended)

Test free, very large, bilocular, involute, inflated, lenticular in axial section and subglobular in transverse section with tapering last whorls, sometimes with sharp triangular protrusions. Coiling initially glomospiral and planispiral in the terminal part. A well-developed flosculinisation fills the base of the lumen and generally exceeds the two-thirds height of the chamber. Thick porcelaneous wall with perforations (comb teeth-shaped) related to neosparitization and without buttresses. Aperture simple, terminal.

Included species

Globidiscus fragilis Okuyucu, 2021 and *G. flexus* Okuyucu, 2021.

Range and distribution

Discovered in the Middle Permian (late Capitanian) of the Karakaya Complex (= Elmadağ Olistrostrome, this study), northwest Anatolia, Türkiye.

Genus ***Kamurana*** Altıner & Zaninetti, 1977 emend. herein

Type species

Kamurana bronnimanni Altıner & Zaninetti, 1977 (type by original designation).

Description (emended)

Test free, large and spherical to ovoid, formed of a globular proloculus and a undivided tube. Coiling initially glomospiral then irregular planispiral involute/semi-evolute(?). Thick porcelaneous wall often neosparitized with perforations (comb teeth-shaped). Aperture simple, terminal.

Remarks

Compared to the type species of *Kamurana* (*Kamurana bronnimanni*), the position of *K. chatalovi* Trifonova, 1984 from the Lower Triassic strata in the Sveti Iliya Ridge, southeastern Bulgaria is more controversial. Additionally, Trifonova (1984) reassigned *Kamurana*, previously considered in the family Hemigordiopsidae, to the family Milioliporidae due to its coarse perforation on the wall in the adult stage. Besides, she also noted that her new species differed from *K. bronnimanni* by its phylogenetically reduced first volutions, whereas *K. chatalovi* is characterized by the first 2–3 irregular coils compared to about 12 glomospirid coils in *K. bronnimanni.* As indicated above by Trifonova (1984), the typical coiling type of *Kamurana* (glomospirid-type with more initial volutions) is not observed in the specimens of *K. chatalovi*. It is also clear that the perforation of the wall in *K. bronnimanni* (sensu Altıner & Zaninetti 1977) is not a typical structural element (e.g., septa), whereas it is a structure formed by the neosparatization of the thick porcelanous wall. For this reason, *K. chatalovi* of Trifonava (1984) is excluded from the genus *Kamurana* in this study. In the original study, Altıner & Zaninetti 1977 stated that the taxonomic position of *Kamurana* was provisionally based on the difference in the descriptions of the linked families. For the reasons detailed above, the genus *Kamurana* is included in the Globidiscinae subfamily, which includes many genera with similar characteristics.

Included species

Kamurana bronnimanni Altıner & Zaninetti, 1977.

Range and distribution

Kamurana bronnimanni was described from the Upper Permian (Upper Dzhulfian) of the Eastern Taurus, Türkiye. Discovered in the Middle Permian (late Capitanian) (this study) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Genus ***Rectogordiopsis*** gen. nov.
urn:lsid:zoobank.org:act:53AA5ECF-1580-4176-BF8A-9C4BE232DCD5

Type species

Rectogordiopsis kamuranaeformis gen. et sp. nov.

Etymology

From the Latin '*rectus*' (= 'straight') because of the many planispiral coils and the Latin '*gordiopsis*' because of the similarity to the genus *Hemigordiopsis* Reichel, 1945.

Description

Test free, very large and globular. Proloculus spherical followed by a tubular undivided chamber. First whorls numerous tightly streptospiral and following whorls planispiral involute. Flosculinisation well developed. Thick porcelaneous wall often neosparitized with perforations (comb teeth-shaped). Aperture simple terminal.

Comparison

Rectogordiopsis gen. nov. differs from the other genera of the Neodiscidae by the type of coiling (initially glomospiral and finally planispiral) involute test, the well-developed flosculinisation, the long streptospiral initial stage and devoid of buttresses. It differs from the morpholocically closest genus *Kamurana* by a larger and more globular test with planispiral involute coiling without any oscillation in the last whorls. It is also similar to *Globidiscus* but differs by the last whorls not tapering. *Hemigordiopsis* can be easily differentiated from the new genus *Rectogordiopsis* by the varying test shape (globular to discoidal), the very dark or even black porcelaneous wall, the absence of a comb teeth-shaped structure on the wall and a very low and broad lumen.

Included species

Rectogordiopsis kamuranaeformis gen. et sp. nov., *R. ovaliformis* gen. et sp. nov.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Rectogordiopsis kamuranaeformis gen. et sp. nov.
urn:lsid:zoobank.org:act:E13B6453-85E7-4A7B-AAF0-A323C865B17F
Fig. 3

Kamurana bronnimanni – Altıner & Zaninetti, 1977: 2, pl. 1 figs 3–4.
Hemigordiopsis renzi – Gargouri & Vachard 1988: 60–61, pl. 1 fig. 7.

Diagnosis

Large globular *Rectogordiopsis* gen. nov. with rounded periphery.

Etymology

Referring to its morphology relatively similar to *Kamurana.*

Material examined

Fifty specimens were observed. 1 holotype and 11 paratypes are illustrated.

Holotype (Fig. 3A–B)
TÜRKİYE – **Ankara** • SE of Kutludüğün village, Kutludüğün Yayla, sample KDY–1; 39°52′11.0″ N, 33°05′51.4″ E; 20 Jun. 2023; Okuyucu and Akbaş leg.; KTÜN.CO–KDY1, KDY1.2–36.

Paratypes (Fig. 3C–M)
TÜRKİYE – **Ankara** • 6 specs; same data as for holotype; KTÜN.CO–KDY1, KDY1.2–3, KDY1.2–35, KDY1.3–29, KDY1.5–48, KDY1.7–15, KDY1.7–27 • 5 specs; same data as for holotype, sample KDY–2; 39°52′07.4″ N, 33°06′23.4″ E; KTÜN.CO–KDY2, KDY2.1–14, KDY2.2–24, KDY2.4–10, KDY2.4–11, KDY2.4–24.

Description

Test large to very large, involute, globular with rounded periphery. Coiling initially glomospiral and finally planispiral. Spherical proloculus, 0.087–0.100 mm in diameter, followed by second chamber slowly enlarging in height through whorls. Initial part consists of at least 15–17 whorls, thin-walled and tightly coiled. In the terminal part (5–8 whorls) the height of the chamber increases gradually. Adult specimens measure: D = 2.08–3.25, w = 1.88–3.00 mm, the ratio w/D = 0.74–1.04, n.w. = 20–25. Wall

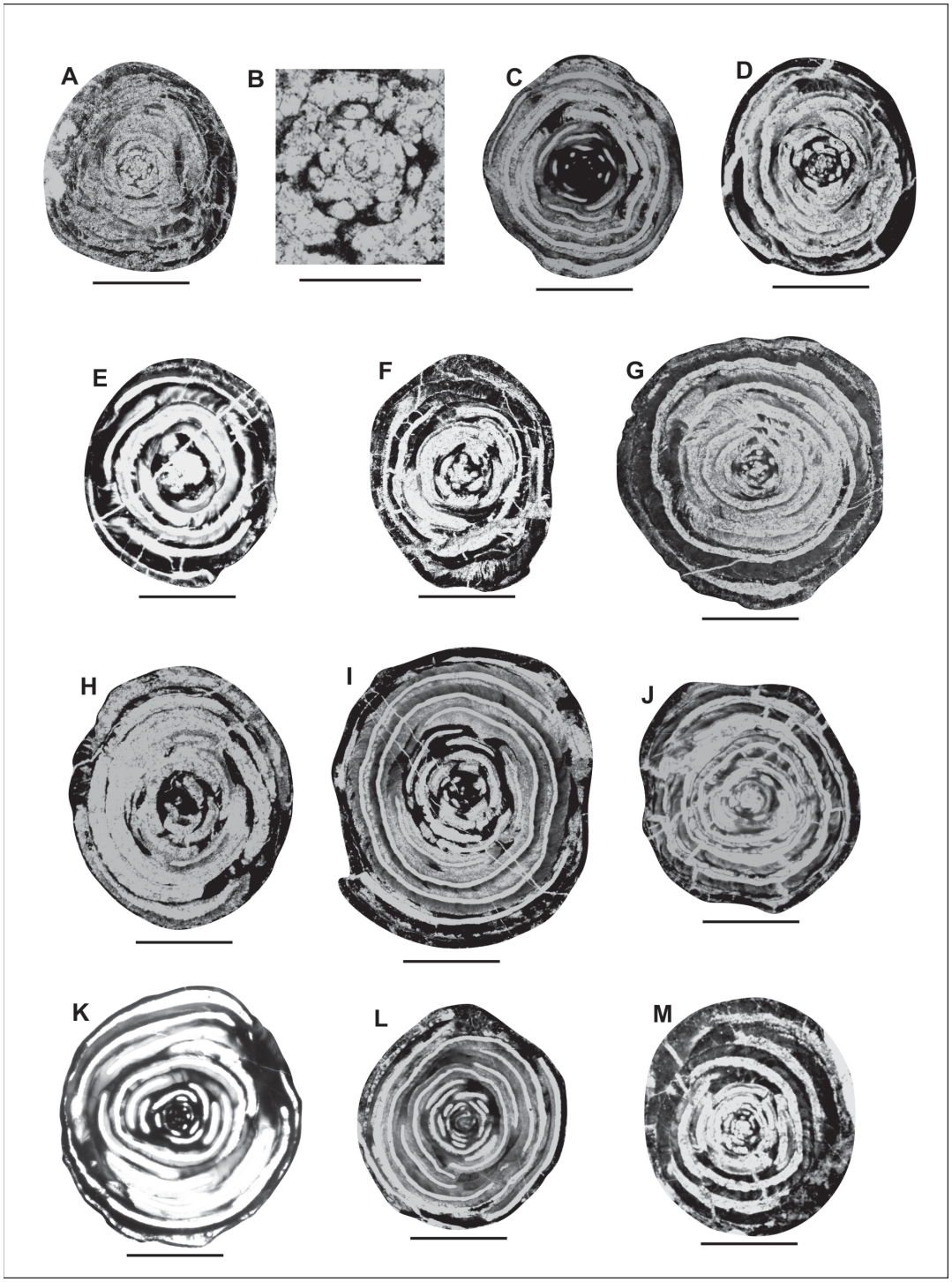

Fig. 3. Microphotographs of the *Rectogordiopsis kamuranaeformis* gen. et sp. nov. **A–B**. Holotype, KTÜN.CO–KDY1.2–36. **A**. Axial section. **B**. Detail view of the inner volutions, showing the proloculus. **C–M**. Paratypes. **C**. Axial section, KTÜN.CO–KDY2.4–24. **D**. Axial section, KTÜN.CO–KDY1.5–48. **E**. Transverse section, KTÜN.CO–KDY1.3–29. **F**. Axial section, KTÜN.CO–KDY1.7–27. **G**. Transverse section, KTÜN.CO–KDY1.2–3. **H**. Subaxial section, KTÜN.CO–KDY2.2–24. **I**. Axial section, KTÜN.CO–KDY2.4–10. **J**. Subaxial section, KTÜN.CO–KDY1.7–15. **K**. Axial section, KTÜN.CO–KDY2.1–14. **L**. Axial section, KTÜN.CO–KDY2.4–11. **M**. Subaxial section, KTÜN.CO–KDY1.2–35. Scale bars: A, C–M = 1 mm; B = 0.25 mm.

Table 1 (continued on next page). List of the foraminiferal taxa described herein from the studied carbonate blocks KDY–1 and KDY–2.

Foraminifers	Sample		Illustrations
	KDY–1	KDY–2	
Neoschwagerina craticulifera		•	Fig. 4A–B
Neoschwagerina pinguis		•	Fig. 4C
Neoschwagerina sp.	•		Fig. 4D
Yabeina sp.		•	Fig. 4E
Chusenella tieni		•	Fig. 4F
Postkwantoella goekcehueyuekensis		•	Fig. 4G
Leella armenica		•	Fig. 4H–I
Codonofusiella sp.	•		Fig. 4J
Kahlerina sp.	•		Fig. 4K
Nankinella orientalis	•	•	Fig. 4L–M
Nankinella acuta	•	•	Fig. 4N–O
Nankinella aff. *chongyangensis*		•	Fig. 4P
Nankinella sp.		•	Fig. 4Q
Reichelina sp.	•		Fig. 4R–S
Globivalvulina vonderschmitti		•	Fig. 5A
Globivalvulina cyprica		•	Fig. 5B–C
Charliella rossae	•	•	Fig. 5D–E
Sengoerina argandi	•		Fig. 5F
Paraglobivalvulina mira		•	Fig. 5G–H
Retroseptellina decrouezae		•	Fig. 5I
Dagmarita chanakchiensis		•	Fig. 5J–L
Hemigordius schlumbergeri		•	Fig. 5M
Cornuspira kinkelini		•	Fig. 5N
Cornuspira sp.		•	Fig. 5O
Calcivertella sp.	•		Fig. 5P
Geinitzina sp.		•	Fig. 5Q
Nodosinelloides camerata	•		Fig. 5R
Pachyphloia sp.	•		Fig. 5S
Langella sp.	•		Fig. 5T
Robuloides lens	•		Fig. 5U
Rectostipulina quadrata	•		Fig. 5V–W
Rectostipulina hexamerata	•		Fig. 5X
Kamurana bronnimanni	•		Fig. 6A–B
Globidiscus flexus	•		Fig. 6C–D
Globidiscus fragilis	•		Fig. 6E–G
Baisalina akasakensis	•	•	Fig. 6H–L
Baisalina sp.		•	Fig. 6M

Table 1 (continued). List of the foraminiferal taxa described herein from the studied carbonate blocks KDY–1 and KDY–2.

Foraminifers	Sample		Illustrations
	KDY–1	KDY–2	
Agathammina sp.	•	•	Fig. 6N–O
Neodiscus sp.	•		Fig. 6P–R
Midiella broennimanni		•	Fig. 6S–T
Midiella irregulariformis	•		Fig. 6U
Rectogordius sp.		•	Fig. 6V
Multidiscella langei	•		Fig. 6W
Multidiscella zaninettiae	•		Fig. 6X
Hemigordiopsis luquensis	•		Fig. 6Y–Z
Hemigordiopsis renzi	•		Fig. 6AA–AB
Glomomidiella sp.		•	Fig. 6AC
Rectogordiopsis kamuranaeformis gen. et sp. nov.	•	•	Fig. 3
Rectogordiopsis ovaliformis gen. et sp. nov.	•	•	Fig. 7
Davanella ankaraensis gen. et sp. nov.	•		Fig. 8A–G
Davanella acuminata gen. et sp. nov.		•	Fig. 8H–L
Kaganella tekini gen. et sp. nov.	•	•	Fig. 8M–R

calcareous, porcelaneous with perforations (comb teeth-shaped). The lumen of the tube is relatively high with frequent flosculinisation in adult stage. Aperture simple, terminal.

Comparison

Rectogordiopsis kamuranaeformis gen. et sp. nov. differs from *Kamurana bronnimanni* by the planispiral involute coiling without any oscillation.

Microfossil association

The associated foraminiferal fauna is listed in Table 1 and illustrated in Figs 4–6.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Rectogordiopsis ovaliformis gen. et sp. nov.
urn:lsid:zoobank.org:act:F4124BCF-5B42-495B-B5C8-FE3DB60FAEDF
Fig. 7

Indeterminate *Miliolina* – Kobayashi & Altıner 2011: pl. 1 fig 30.

Diagnosis

Very large oval *Rectogordiopsis* gen. nov. with flattened to slightly rounded periphery.

Etymology

From the overall oval shape of the test.

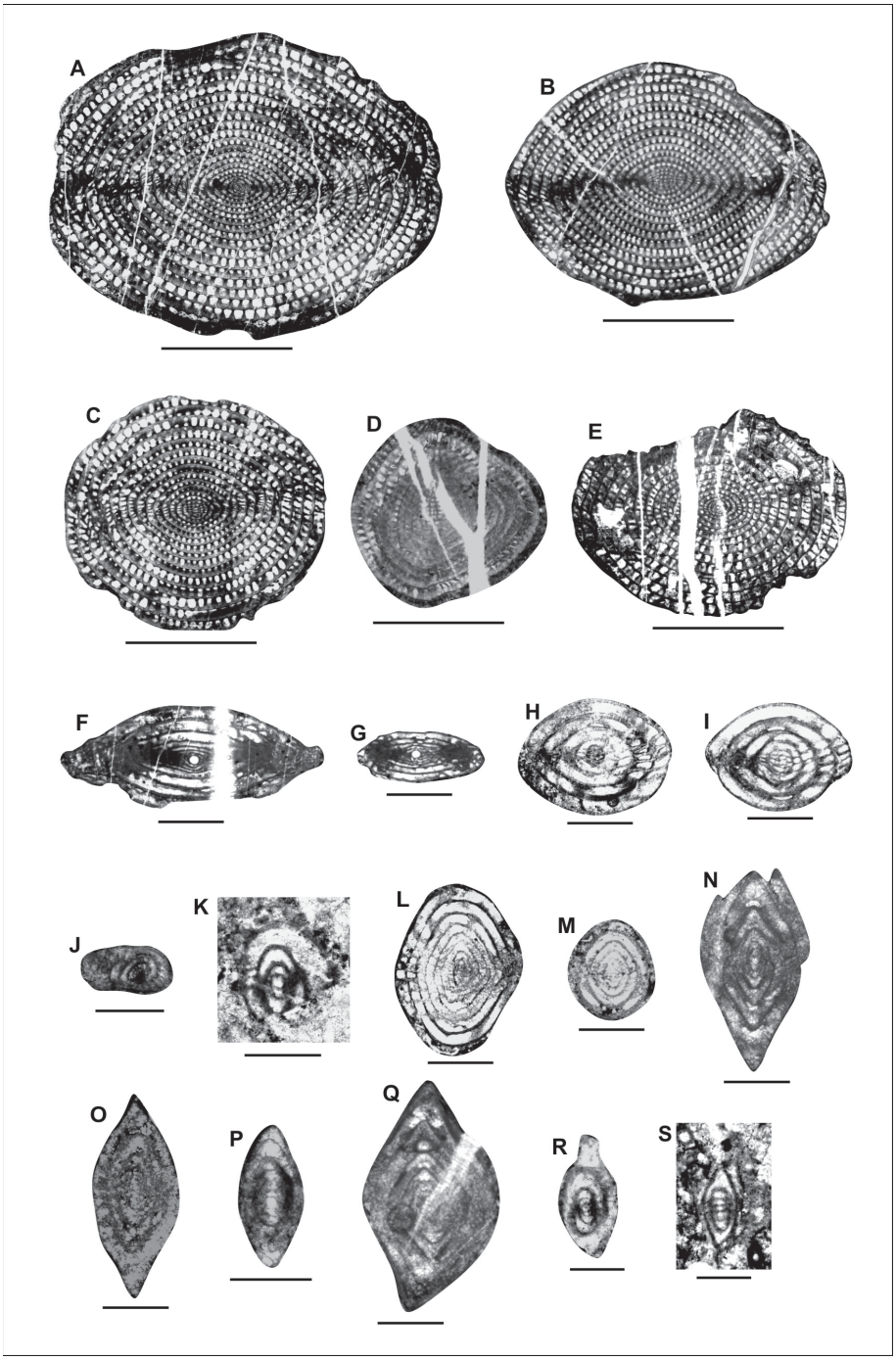

Fig. 4. Microphotographs of associated foraminiferal fauna identified in the studied Middle Permian (late Capitanian) blocks. **A–B**. *Neoschwagerina craticulifera* (Schwager, 1883). **A**. KDY2.2–32. **B**. KDY2.4–19. **C**. *Neoschwagerina pinguis* Skinner, 1969, KDY2.4–28. **D**. *Neoschwagerina* sp., KDY1.4–15. **E**. *Yabeina* sp., KDY2.1–1. **F**. *Chusenella tieni* (Chen, 1956), KDY2.1–30. **G**. *Postkwantoella goekcehueyuekensis* Okuyucu, 2022, KDY2.1–4. **H–I**. *Leella armenica* Rozovskaya, 1965. **H**. KDY2.1–54. **I**. KDY2.1–55. **J**. *Codonofusiella* sp., KDY1.8–20. **K**. *Kahlerina* sp., KDY1.8–27. **L–M**. *Nankinella orientalis* Miklukho-Maklay, 1954. **L**. KDY2.3–14. **M**. KDY1.5–11. **N–O**. *Nankinella acuta* Rui, 1979. **N**. KDY2.1–9. **O**. KDY1.2–20. **P**. *Nankinella* aff. *chongyangensis* Jing, 1992, KDY2.2–10. **Q**. *Nankinella* sp., KDY2.1–35. **R–S**. *Reichelina* sp. **R**. KDY1.5–30. **S**. KDY1.6–14. Scale bars: A–E = 2 mm; F–I, L–M = 1 mm; J, N–O, Q = 0.5 mm; K, P, R–S = 0.25 mm.

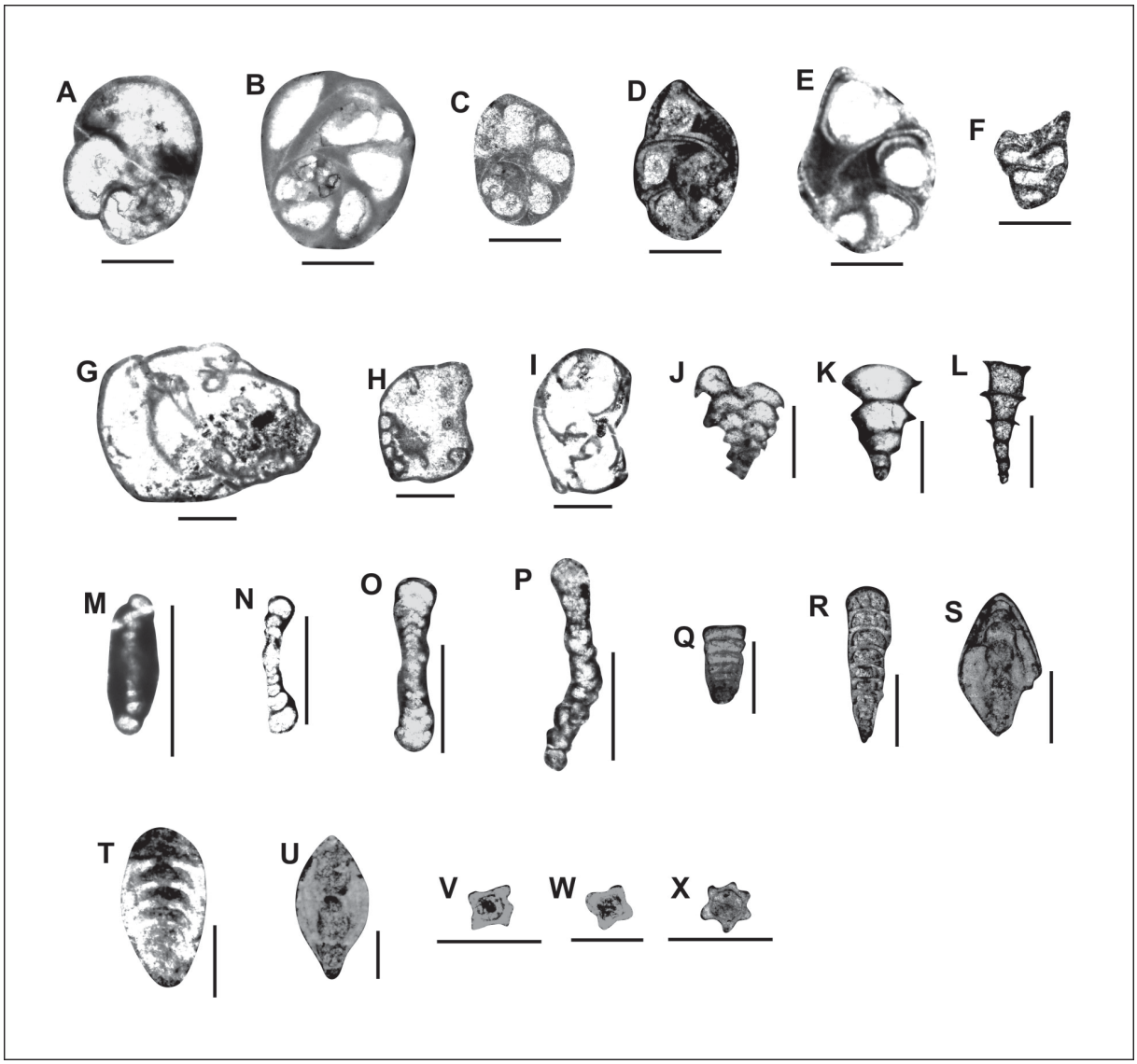

Fig. 5. Microphotographs of associated foraminiferal fauna identified in the studied Middle Permian (late Capitanian) blocks. **A**. *Globivalvulina vonderschmitti* Reichel, 1946, KDY2.2–34. **B–C**. *Globivalvulina cyprica* Reichel, 1946. **B**. KDY2.4–9. **C**. KDY2.1–37. **D–E**. *Charliella rossae* Altıner & Özkan-Altıner, 2001. **D**. KDY1.6–9. **E**. KDY2.2–38. **F**. *Sengoerina argandi* Altıner, 1999, KDY1.8–1. **G–H**. *Paraglobivalvulina mira* Reitlinger, 1965. **G**. KDY2.4–15. **H**. KDY2.2–13. **I**. *Retroseptellina decrouezae* (Köylüoglu & Altıner, 1989), KDY2.1–29. **J–L**. *Dagmarita chanakchiensis* Reitlinger, 1965. **J**. KDY2.1–10. **K**. KDY2.2–33. **L**. KDY2.1–16. **M**. *Hemigordius schlumbergeri* (Howchin, 1895), KDY2.4–25. **N**. *Cornuspira kinkelini* Spandel, 1898, KDY2.2–19. **O**. *Cornuspira* sp., KDY2.4–20. **P**. *Calcivertella* sp., KDY1.8–28. **Q**. *Geinitzina* sp., KDY2.3–3. **R**. *Nodosinelloides camerata* (Miklukho-Maklay, 1954), KDY1.1–26. **S**. *Pachyphloia* sp., KDY1.6–12. **T**. *Langella* sp., KDY1.4–7. **U**. *Robuloides lens* Reichel, 1946, KDY1.1–31. **V–W**. *Rectostipulina quadrata* Jenny-Deshusses, 1985. **V**. KDY1.8–2. **W**. KDY1.8–3. **X**. *Rectostipulina hexamerata* Song & Tong, 2009, KDY1.4–5. Scale bars: A–F, J–X = 0.25 mm; G–I = 0.5 mm.

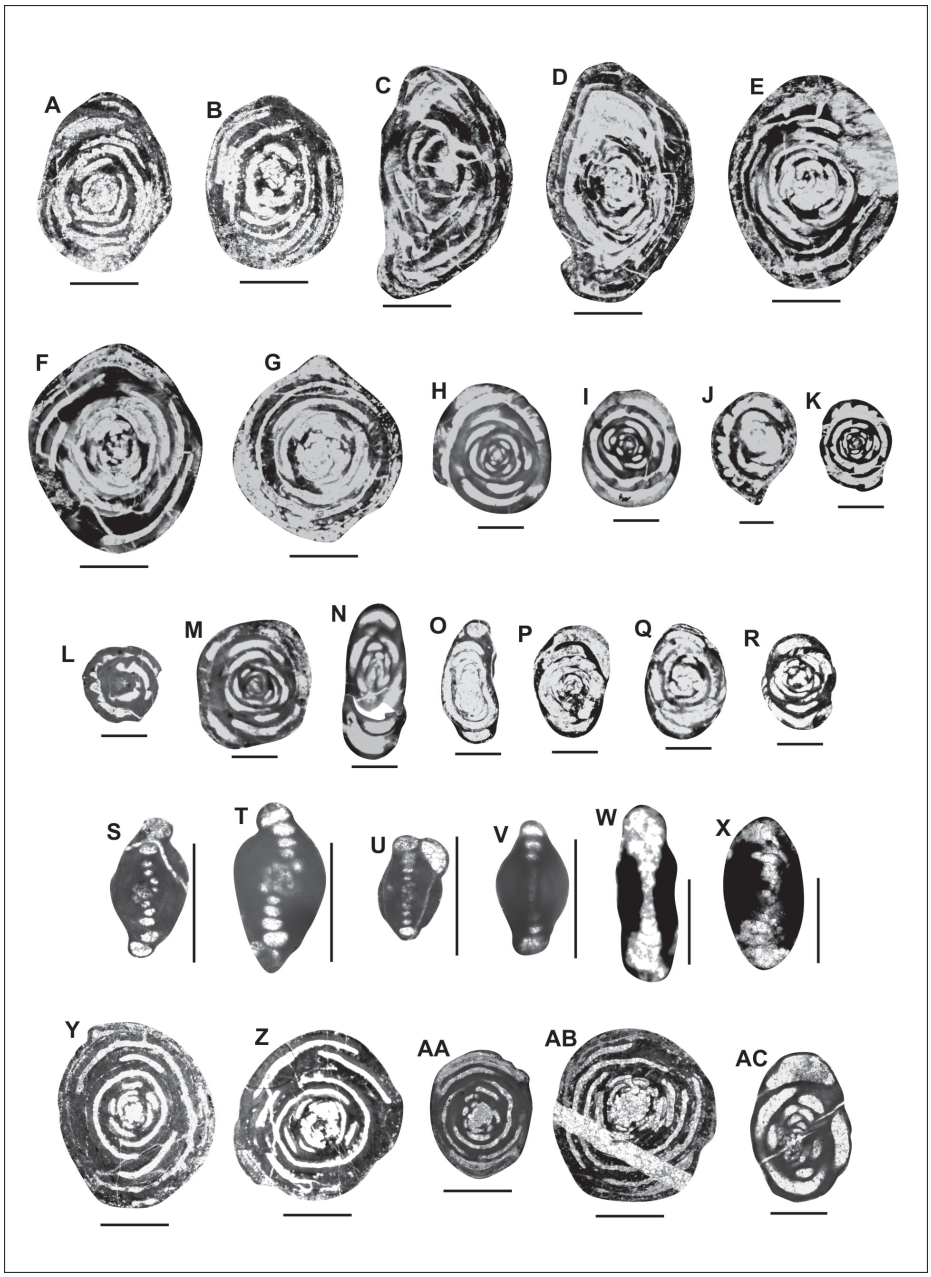

Fig. 6. Microphotographs of associated foraminiferal fauna identified in the studied Middle Permian (late Capitanian) blocks. **A–B**. *Kamurana bronnimanni* Altıner & Zaninetti, 1977. **A**. KDY1.6–44. **B**. KDY1.6–45. **C–D**. *Globidiscus flexus* Okuyucu, 2021. **C**. KDY1.1–5. **D**. KDY1.6–40. **E–G**. *Globidiscus fragilis* Okuyucu, 2021. **E**. KDY1.4–1. **F**. KDY1.4–9. **G**. KDY1.6–8. **H–L**. *Baisalina akasakensis* Kobayashi, 2012. **H**. KDY2.1–2. **I**. KDY2.3–13. **J**. KDY1.7–24 **K**. KDY2.2–18. **L**. KDY2.4–5. **M**. *Baisalina* sp., KDY2.3–10. **N–O**. *Agathammina* sp. **N**. KDY2.1–12. **O**. KDY1.5–51. **P–R**. *Neodiscus* sp. **P**. KDY1.8–30. **Q**. KDY1.7–10. **R**. KDY1.1–2. **S–T**. *Midiella broennimanni* (Altıner, 1978). **S**. KDY2.4–2. **T**. KDY2.4–7. **U**. *Midiella irregulariformis* (Zaninetti, Altıner & Çatal, 1981), KDY2.2–14. **V**. *Rectogordius* sp., KDY2.3–12. **W**. *Multidiscella langei* Vachard & Krainer, 2022, KDY1.3–21. **X**. *Multidiscella zaninettiae* Vachard & Krainer, 2022, KDY1.8–22. **Y–Z**. *Hemigordiopsis luquensis* (Wang & Sun, 1973). **Y**. KDY1.1–20. **Z**. KDY1.5–4. **AA–AB**. *Hemigordiopsis renzi* Reichel, 1945. **AA**. KDY1.6–22. **AB**. KDY1.6–34. **AC**. *Glomomidiella* sp., KDY2.1–33. Scale bars: A–G, Y–AB = 1 mm; H–R = 0.5 mm; S–X, AC = 0.25 mm.

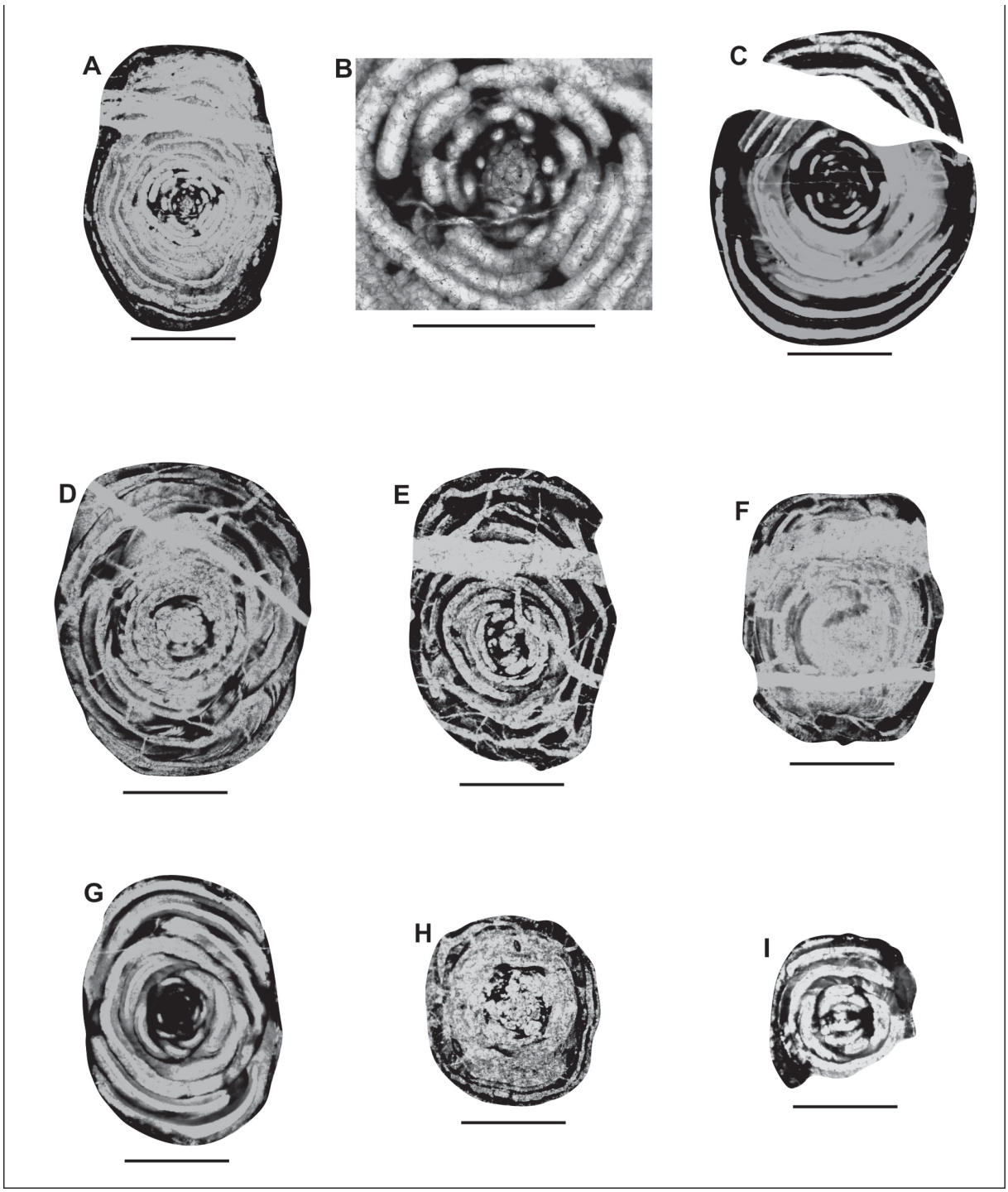

Fig. 7. Microphotographs of the *Rectogordiopsis ovaliformis* gen. et sp. nov. **A–B**. Holotype, KDY2.1–6, axial section. **B**. Detail view of the inner volutions, showing the proloculus. **C–H**. Paratypes. **C**. Axial section, KDY2.2–16. **D**. Subaxial section, KDY1.5–24. **E**. Axial section, KDY1.1–1. **F**. Tangential section, KDY1.2–19. **G**. Axial section, KDY2.1–52. **H**. Tangential section, KDY1.3–19. **I**. Subaxial/Tangential section, KDY1.6–28. Scale bars: A, C–I = 1 mm; B = 0.5 mm.

Material examined

Twelve specimens were observed. 1 holotype and 7 paratypes are illustrated.

Holotype (Fig. 7A)
TÜRKİYE – **Ankara** • SE of Kutludüğün village, Kutludüğün Yayla, sample KDY–2; 39°52′07.4″ N, 33°06′23.4″ E; 20 Jun. 2023; Okuyucu and Akbaş leg.; KTÜN.CO–KDY2, KDY2.1–6.

Paratypes (Fig. 7B–I)
TÜRKİYE – **Ankara** • 2 specs; same data as for holotype; KTÜN.CO–KDY2, KDY2.1–52, KDY2.2–1 • 5 specs; same data as for holotype, sample KDY–1; 39°52′11.0″ N, 33°05′51.4″ E; KTÜN.CO–KDY1, KDY1.1–1, KDY1.2–19, KDY1.3–19, KDY1.5–24, KDY1.6–28.

Description

Test large, involute, oval with slightly flattened to broadly rounded periphery. Coiling at the beginning tightly glomospiral and finally planispiral. Spherical proloculus, 0.06–0.08 mm in diameter, followed by second chamber slowly enlarging in height through successive whorls. The initial part consists of at least 25–30 whorls with thin-walled. In the terminal part (4–6 whorls) the height of the chamber increases gradually. Adult specimens measure: D = 1.95–3.43 mm, w =1.70–2.68 mm, the ratio w/D = 0.73–0.96, n.w. = 29–36. Wall thick, calcareous porcelaneous with perforations (comb teeth-shaped). The lumen of the tube is relatively narrow with some flosculinisation in adult stage. Aperture simple, terminal.

Comparison

This new species differs from the *Rectogordiopsis kamuranaeformis* gen. et sp. nov. mainly by narrower chamber height, flattened periphery and more tightly coiled inner glomospiroid whorls.

Microfossil association

The associated foraminiferal fauna is listed in Table 1 and illustrated in Figs 4–6.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Genus ***Davanella*** gen. nov.
urn:lsid:zoobank.org:act:6D884B23-E7D2-425E-A527-7C53DAEFC6E1

Type species

Davanella ankaraensis gen. et sp. nov.

Etymology

After the Dava spring in Kutludüğün Yayla, southeast of Kutludüğün village, Ankara City, Central Türkiye.

Description

Test free, involute, very large and globular to ovoid. Proloculus spherical followed by a tubular undivided chamber. First whorls numerous tightly streptospiral and adult whorls planispiral with depressed umbilicus on both sides. Flosculinisation well developed. Thick porcelaneous wall often neosparitized with perforations (comb teeth-shaped). Aperture simple, terminal.

Comparison

Davanella gen. nov. differs from the similar genus *Rectogordiopsis* gen. nov. by the depressed umbilicus on both sides of the test.

Included species

Davanella ankaraensis gen. et sp. nov., *Davanella acuminata* gen. et sp. nov.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Davanella ankaraensis gen. et sp. nov.
urn:lsid:zoobank.org:act:32686C24-35E1-49BD-9162-7204E5E84947
Fig. 8A–G

Diagnosis

Very large globular to ovoid *Davanella* gen. nov. with rounded periphery.

Etymology

Latin, from Ankara, the capital of Türkiye.

Material examined

Eight specimens were observed. 1 holotype and 5 paratypes are illustrated.

Holotype (Fig. 8E)
TÜRKİYE – Ankara • SE of Kutludüğün village, Kutludüğün Yayla, sample KDY–1; 39°52′11.0″ N, 33°05′51.4″ E; 20 Jun. 2023; Okuyucu and Akbaş leg.; KTÜN.CO–KDY1, KDY1.1–16.

Paratypes (Fig. 8A–D, G)
TÜRKİYE – Ankara • 5 specs; same data as for holotype; KTÜN.CO–KDY1, KDY1.2–2, KDY1.3–53, KDY1.8–4, KDY1.8–19, KDY1.8–25.

Description

Test large to very large, involute, globular to ovoid with rounded periphery. A central depression or umbilicus well-developed in axial section. Spherical proloculus, measuring 0.07–0.09 mm in outside diameter, followed by second tubular chamber. Initial part consists of approximately 12–15 loosely coiled glomospiroid whorls. In all subsequent whorls the height of the chamber increases rapidly. Adult specimens measure: D = 2.13–3.43 mm, w =1.90–2.38 mm, the ratio w/D = 0.67–0.89, n.w. = 15–19. Wall thick, calcareous porcelaneous with perforations (comb teeth-shaped). A weak flosculinisation developed in adult stage. Aperture simple, terminal.

Comparison

Davanella ankaraensis gen. et sp. nov. differs from the species of the *Rectogordiopsis* gen. nov. by the presence of umbilicus.

Microfossil association

The associated foraminiferal fauna is listed in Table 1 and illustrated in Figs 4–6.

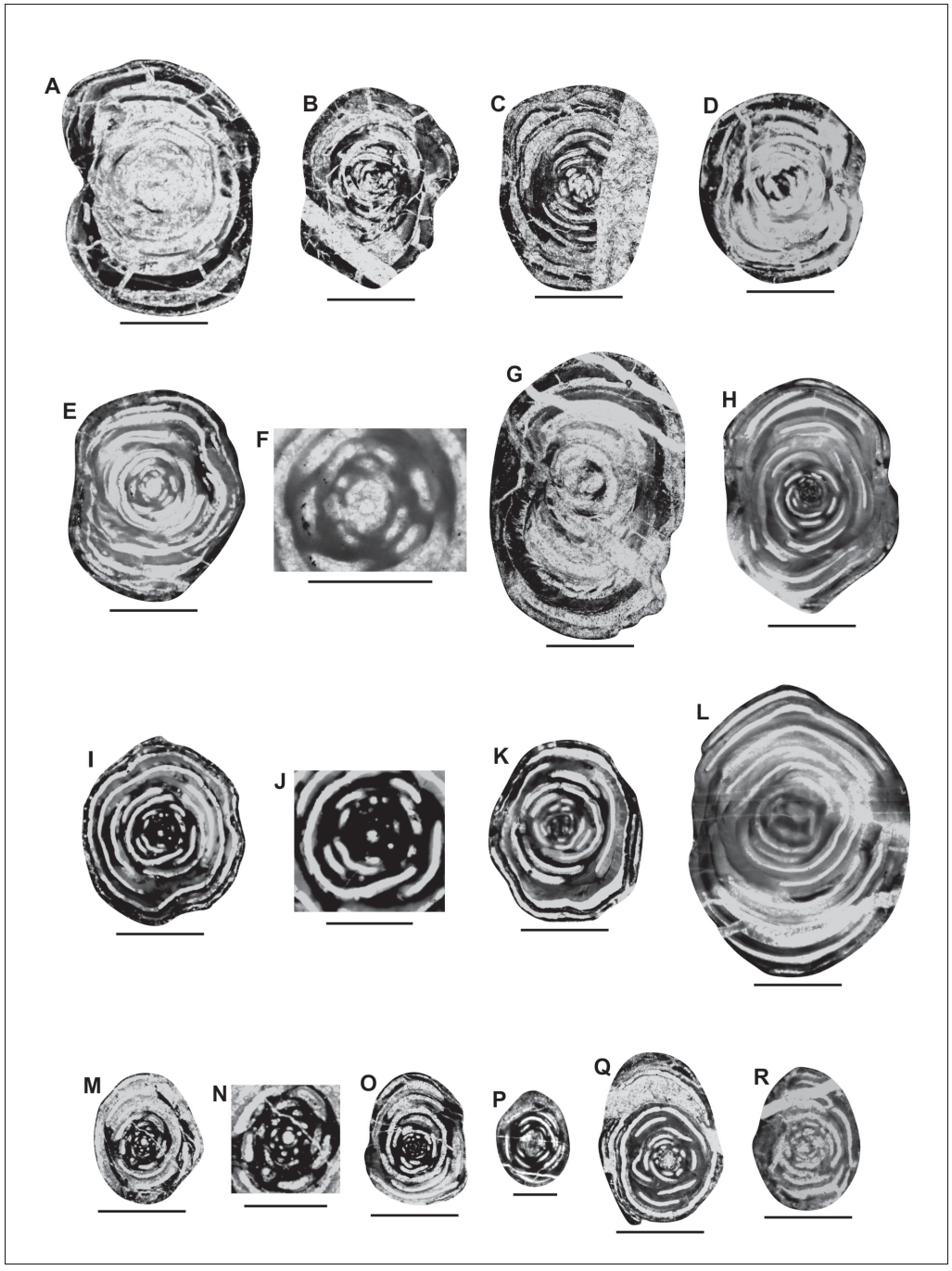

Fig. 8. Microphotographs. **A–G**. *Davanella ankaraensis* gen. et sp. nov. **A–D, G**. Paratypes. **A**. Subaxial section, KDY1.8–25. **B**. Subaxial section, KDY1.8–4. **C**. Axial section, KDY1.3–53. **D**. Subaxial section, KDY1.8–19. **E–F**. Holotype, KDY1.1–16. **E**. Axial section. **F**. Detail view of the inner volutions, showing the proloculus. **G**. Subaxial section, KDY1.2–2. **H–L**. *Davanella acuminata* gen. et sp. nov. **H, K–L**. Paratypes. **H**. Axial section, KDY2.1–49. **I–J**. Holotype, KDY2.1–17. **I**. Axial section. **J**. Detail view of the inner volutions, showing the proloculus. **K**. Subaxial section, KDY2.3–16. **L**. Transversal section, KDY2.1–48. **M–R**. *Kaganella tekini* gen. et sp. nov. **M–N**. Holotype, KDY2.2–2. **M**. Axial section. **N**. Detail view of the inner volutions, showing the proloculus. **O–R**. Paratypes. **O**. Axial section, KDY2.2–35. **P**. Subaxial section, KDY1.3–35. **Q**. Subaxial section, KDY1.2–40. **R**. Subaxial section, KDY1.2–27. Scale bars: A–E, G–I, K–M, O–R = 1 mm; F, J, N = 0.5 mm.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Davanella acuminata gen. et sp. nov.
urn:lsid:zoobank.org:act:C385F006-1FB6-4017-B23C-F70139AC58FA
Fig. 8H–L

Diagnosis

Very large globular to ovoid *Davanella* gen. nov. with pointed periphery.

Etymology

Latin, '*acuminatus*' (= 'sharp, pointed').

Material examined

Five specimens were observed. 1 holotype and 3 paratypes are illustrated.

Holotype (Fig. 8I–J)
TÜRKİYE – **Ankara** • SE of Kutludüğün village, Kutludüğün Yayla, sample KDY–2; 39°52′07.4″ N, 33°06′23.4″ E; 20 Jun. 2023; Okuyucu and Akbaş leg.; KTÜN.CO–KDY2, KDY2.1–17.

Paratypes (Fig. 8H, K–L)
TÜRKİYE – **Ankara** • 3 specs; same data as for holotype; KTÜN.CO–KDY2, KDY2.1–48, KDY2.1–49, KDY2.3–16.

Description

Test large to very large, involute, globular to ovoid with pointed periphery. Umbilicus slightly-developed on lateral sides. Spherical proloculus, 0.06–0.086 mm in diameter, followed by second tubular chamber. The quite tightly coiled glomospiroid initial part consists of approximately 25 whorls. The height of the chamber in planisipiral coiled part increases gradually. Adult specimens measure: D = 2.65–3.40 mm, w =2.03–2.63 mm, the ratio w/D = 0.76–0.77, n.w. = approximately 32. Wall relatively thick, calcareous, porcelaneous with perforations (comb teeth-shaped). A flosculinisation fills progressively the base of the chamber almost in all whorls. Aperture simple, terminal.

Comparison

Davanella acuminata gen. et sp. nov. differs from the *Davanella ankaraensis* gen. et sp. nov. by the pointed periphery, quite tightly coiled inner whorls and gradually developed test.

Microfossil association

The associated foraminiferal fauna is listed in Table 1 and illustrated in Figs 4–6.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Genus ***Kaganella*** gen. nov.
urn:lsid:zoobank.org:act:BC97972C-632D-4124-9D50-76CC24B5AE04

Type species

Kaganella tekini gen. et sp. nov.

Etymology

This genus is named after Professor Dr U. Kagan Tekin (Hacettepe University, Ankara, Türkiye), in honour of his contributions to the knowledge of Radiolarian biostratigraphy.

Description

Test involute moderate to large and globular. Proloculus spherical followed by a tubular undivided chamber. First whorls numerous, tightly glomosproid and following whorls planispiral. Flosculinisation poorly developed. Relatively thick porcelaneous wall neosparitized with rare perforations (comb teeth-shaped). Aperture simple terminal.

Comparison

Kaganella gen. nov. differs from the other genera of the subfamily Globidiscinae subfam. nov. by the weakly-developed flosculinisation, rare perforations (comb teeth-shaped) in neosparitized wall and smaller dimensions in similar number of whorls.

Included species

Kaganella tekini gen. et sp. nov.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Kaganella tekini gen. et sp. nov.
urn:lsid:zoobank.org:act:ABA3BE39-4E76-47C5-9AA9-A6D380B32B51
Fig. 8M–R

Diagnosis

Moderate to large rounded *Kaganella* gen. nov. with slightly pointed periphery.

Etymology

This species is named after Professor Dr U. Kagan Tekin (Hacettepe University, Ankara, Türkiye), in honour of his contributions to the knowledge of Radiolarian biostratigraphy.

Material examined

Five specimens were observed. 1 holotype and 4 paratypes are illustrated.

Holotype (Fig. 8M–N)
TÜRKİYE – **Ankara** • SE of Kutludüğün village, Kutludüğün Yayla, sample KDY–2; 39°52′07.4″ N, 33°06′23.4″ E; 20 Jun. 2023; Okuyucu and Akbaş leg.; KTÜN.CO–KDY2, KDY2.2–2.

Paratypes (Fig. 8O–R)
TÜRKİYE – **Ankara** • 1 spec.; same data as for holotype; KTÜN.CO–KDY2, KDY2.2–35 • 3 specs; same data as for holotype, sample KDY–1; 39°52′11.0″ N, 33°05′51.4″ E; KTÜN.CO–KDY1, KDY1.2–27, KDY1.2–40, KDY1.3–35.

Description

Test moderate to large, involute, globular with slightly pointed periphery. Coiling at the beginning tightly glomospiral and finally planispiral. Spherical proloculus, 0.06–0.10 mm in diameter, followed by second chamber slowly enlarging in height through successive whorls. Initial part consists of approximately

23–25 whorls with relatively thin-walled. In the terminal part (planispiral coiled 3–4 whorls) the height of the whorls increases gradually. Adult specimens measure: D = 1.23–2.38 mm, w = 0.9–1.25 mm, the ratio w/D = 0.64–0.87, n.w. = 26–29. Wall calcareous, porcelaneous with some neosparitizations mainly in last whorls. The lumen of the tube is relatively narrow with rare flosculinisations. Aperture simple, terminal.

Comparison

Kaganella tekini gen. et sp. nov. differs from *Rectogordiopsis kamuranaeformis* gen. et sp. nov. by the smaller size of the test and rare perforations (comb teeth-shaped) in neosparitized wall which observed mainly in last whorls.

Microfossil association

The associated foraminiferal fauna is listed in Table 1 and illustrated in Figs 4–6.

Range and distribution

Middle Permian (late Capitanian) of the Elmadağ Olistostrome, Ankara City, Central Türkiye.

Discussion

Phylogenetic considerations

The comb teeth-shaped structure in the test wall can be readily observed in certain genera within the family Neodiscidae: genus *Baisalina* (*B. pulchra* Reitlinger, 1965: pl. 1 fig. 15; *B. akasakensis* Kobayashi, 2012: pl. 3 figs 1–30), genus *Pseudobaisalina* (*P. mirifica* Sosnina, 1983: pl. xv, fig. 13), genus *Septagathammina* (all new species of *Septagathammina* Lin, 1984: pl. 7 figs 11–16), genus *Agathammina* (*A. gigantea* Kobayashi, 2012: pl. 4 figs 20–23) and genus *Neodiscus* (*N.* aff. *millilolides* Miklukho-Maklay, 1953; Pronina 1988: pl. 1 fig. 15).

Based on newly recovered material and a re-evaluation of the calcareous porcelaneous wall of the genera within the family Neodiscidae and its subfamilies, the assessments regarding the phylogenetic relationships are given here. It is evident that the wall of the genus *Kamurana* possesses perforations related to neosparization (comb teeth-shaped) (Altıner & Zaninetti 1977: pl. 1 fig. 1; this study, Fig. 6A–B). This character of the wall is also consistent with the genus *Globidiscus* (e.g., Okuyucu 2021: pl. 1 fig. 13, *Globidiscus fragilis*; this study, Fig. 6E–G). Therefore, the genera *Kamurana* and *Globidiscus* are taxonomically assigned to the newly proposed subfamily Globidiscinae subfam. nov.

The main characteristics of the genera under the subfamily Globidiscinae are the spherical proloculus followed by an undivided diversely coiled tubular chamber, common flosculinisation and thick wall with perforations (comb teeth-shaped). Within the family Neodiscidae, the genus *Neodiscus* which was originally assigned to the subfamily Neodiscinae by Lin (1984) is the most comparable taxon to the newly proposed genera and previously described forms (*Globidiscus*, *Kamurana*) in terms of coiling type (initially glomospiral, later planispiral involute to semi-involute) and wall structure characterized by comb teeth-shaped features. Whereas the genera included in the subfamily Globidiscinae consisting of a long streptospiral and tightly coiled initial stage and larger tests with common flosculinisation, the similar genus *Neodiscus* has a short streptospiral and weakly coiled initial stage, a medium-sized test without flosculinisation. Consequently, a close phylogenetic relationship can be inferred between the genus *Neodiscus* and the genera assigned to the subfamily Globidiscinae, although they can be readily distinguished from one another based primarily on morphological characteristics (e.g., the degree of flosculinasation, development of comb teeth-shaped structure in the wall, the presence of umbilicus) (Fig. 9). The emergence of the genus *Neodiscus* is critical for understanding the diversification of various Permian miliolid lineages during the Capitanian. The genus *Neodiscus*, probably gave rise after its

occurrence in early Capitanian, to the genera included in the subfamily Globidiscinae in stratigraphically younger levels in the late Capitanian (Fig. 9) as indicated for the genus *Globidiscus* in the study of Okuyucu (2021).

Among Permian miliolids, the genus *Praeneodiscus*, originally described from the lower? Kungurian strata of New Mexico, USA, is the most similar to the genus *Neodiscus* in terms of test shape and the shape of the lumina (Fig. 9). Despite some differences (e.g., less ogival lumina, smaller dimensions, less whorls) there is a phylogenetic tendency from the genus *Praeneodiscus* to the genus *Neodiscus* (Fig. 9).

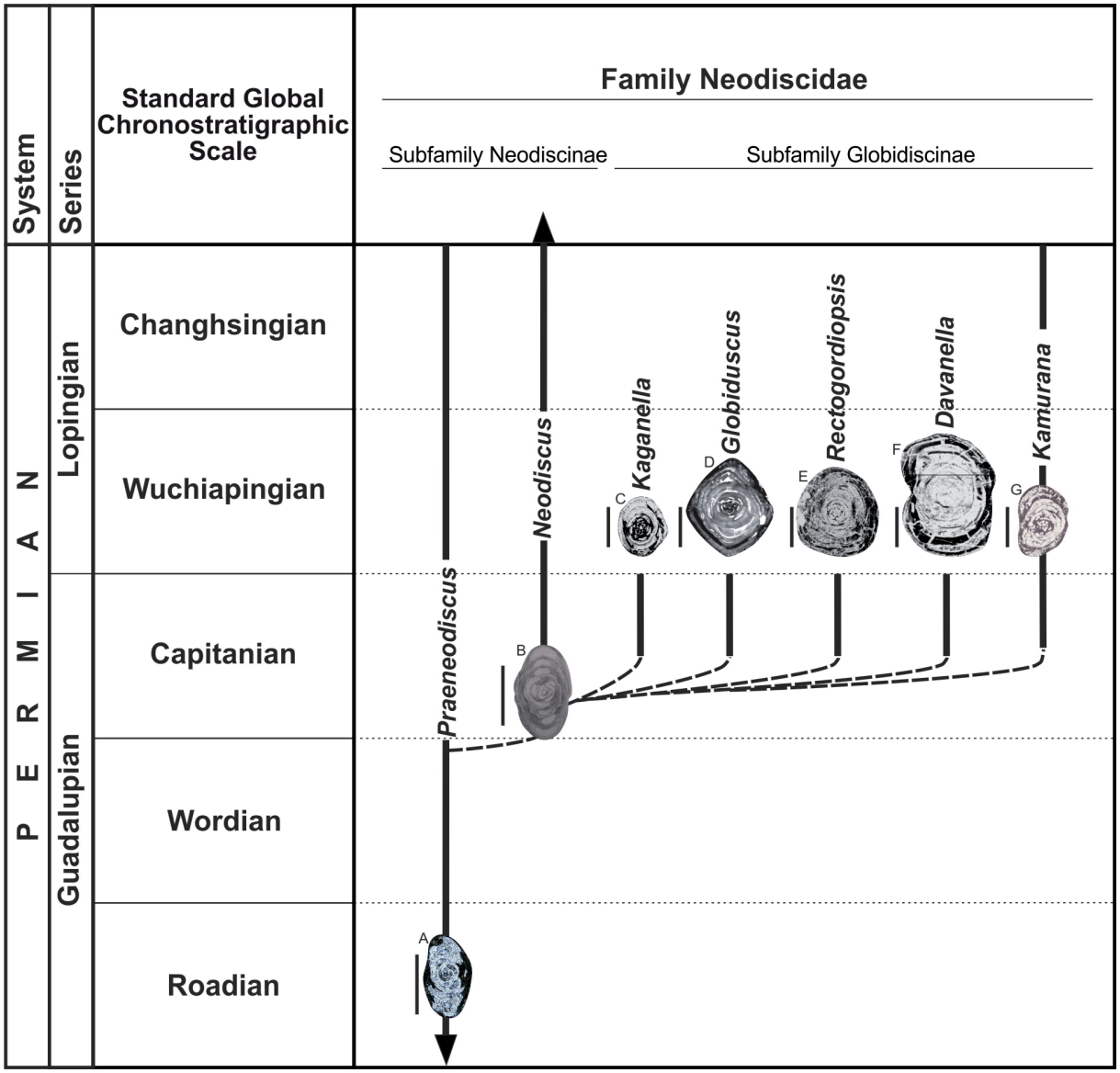

Fig. 9. The possible phylogenetic relationship of the subfamilies Neodiscinae Lin, 1984 and Globidiscinae subfam. nov. of the family Neodiscidae Lin, 1984 and related genera with their stratigraphic distribution. **A**. *Praeneodiscus convexus* Vachard, Krainer & Lucas, 2015, holotype. **B**. *Neodiscus milliloides* Miklukho-Maklay, 1953, holotype. **C**. *Kaganella tekini* gen. et sp. nov., holotype. **D**. *Globidiscus fragilis* Okuyucu, 2021, holotype. **E**. *Rectogordiopsis kamuranaeformis* gen. et sp. nov., holotype. **F**. *Davanella ankaraensis* gen. et sp. nov., holotype. **G**. *Kamurana bronnimanni* Altıner & Zaninetti, 1977, holotype. Scale bars: A–B= 0.5 mm; C–G = 1 mm.

Accordingly, the genus *Neodiscus* most likely originated from the genus *Praeneodiscus* at the beginning of the Capitanian (Fig. 9).

The genus *Praeneodiscus* likely represents the ancestral form of *Neodiscus*, having originated in the Early Permian and subsequently given rise to *Neodiscus* at the beginning of the Capitanian. The newly described foraminiferal taxa in this study, along with other genera included in the subfamily Globidiscinae, are interpreted to have diversified from *Neodiscus* during the late Capitanian, evolving into distinct genera along separate phylogenetic lineages (Fig. 9).

Conclusions

A rich Permian large miliolid assemblages recorded from late Capitanian blocks in the Ankara region were studied in detail. The conclusions obtained in this study are briefly given below.

Globiscinae subfam. nov. and new taxa (*Rectogordiopsis* gen. nov., *Davanella* gen. nov., *Kaganella* gen. nov.) within this subfamily are described.

These new large miliolid taxa are characterized by initially glomospirid then planispiral involute/semi-evolute(?) and a porcelenous wall with perforations corresponding to the "en dent de peigne" (comb teeth-shaped) aspect of Gargouri & Vachard (1988).

The descriptions of the genera *Kamurana*, *Globidiscus* and *Agathammina* were emended based on re-analyses of the previously published and recent data.

The taxonomic positions of the genera *Agathammina* and *Septagathammina* were changed based on coiling type and wall structures, and transferred to the subfamily Agathammininae because of the priority rule.

Based on the description of new miliolid taxa and the re-evaluation of the previously published data, the composition and taxonomic status of some subfamilies in the superfamily Cornuspiroidea was revised, and the family Neodiscidae emended.

The genus *Praeneodiscus* is likely the ancestor of the genus *Neodiscus*, and the previously determined genera *Kamurana* and *Globidiscus* along with the new genera *Rectogordiopsis* gen. nov., *Davanela* gen. nov. and *Kaganella* gen. nov. must have diversified from the genus *Neodiscus* in the late Capitanian.

Acknowledgments

We gratefully acknowledge Dr U. Kağan Tekin (Hacettepe University, Ankara, Türkiye) for his assistance during the field research. We are grateful to Dr Kaan Sayit (METU, Ankara, Türkiye) for his assistance in revising the English version of the text. Many thanks to the anonymous reviewers and topic editor D. Audo for their constructive remarks and very useful comments that significantly improved the manuscript.

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