Annales Societatis Geologorum Poloniae (2025), vol. 95: ...–... https://doi.org/10.14241/asgp.2025.10

A SYSTEMATIC REVIEW OF PALEOGENE AGGLUTINATED FORAMINIFERA WITH INTERNAL STRUCTURES (SUBFAMILY PAVONITININAE) FROM THE EOCENE OF NORTHWESTERN SAUDI ARABIA

Asmaa KORIN[1, 2], Sherif ALLAM[1], Sinatrya PRAYUDI[1], Iyad S. ZALMOUT[3, 4], Abdullah MEMESH[3], Mohammed I. ALNAJJAR[3], Ahmed A. BAHAMEEM[3] & Michael A. KAMINSKI[1 *]

[1] *Geoscience Department, College of Petroleum Engineering and Geoscience, King Fahd University of Petroleum and Minerals, Dhahran, 31261, Saudi Arabia*
[2] *Geology Department, Faculty of Science, Port Said University, Port Said, 42526, Egypt*
[3] *Survey and Exploration Center, Saudi Geological Survey, Jeddah, Saudi Arabia*
[4] *Museum of Paleontology, Research Museum Center, The University of Michigan, 3600 Varsity Drive, Ann Arbor, Michigan 48108-2228 USA; e-mail: kaminski@kfupm.edu.sa*
* *Corresponding author*

Korin, A., Allam, S., Prayudi, S. D., Zalmout, I. S., Memesh, A., Alnajjar, M., Bahameem, A. & Kaminski, M. A., 2025. A systematic review of Paleogene agglutinated foraminifera with internal structures (subfamily Pavonitininae) from the Eocene of northwestern Saudi Arabia. *Annales Societatis Geologorum Poloniae*, 95: xx–xx.

Abstract: Agglutinated foraminifera with complex internal structures represent key components of deep-marine benthic assemblages and are important tools for biostratigraphic and palaeoenvironmental reconstructions. The subfamily Pavonitininae, which includes the genera *Pavonitina* and *Pavopsammia*, previously has been documented mainly from Oligocene to Miocene successions of the central Paratethys, West Africa, and the Atlantic margins. This study reports the first stratigraphically well-constrained record of Pavonitininae from the upper Eocene (Biozone E14) Rashrashiyah Formation in the Sirhan-Turayf Basin of northwestern Saudi Arabia. The recovered assemblage includes *Pavopsammia flabellum*, *Pavonitina styriaca*, *Pavonitina biarritzensis*, and *Pavonitina kiscelliana*. The morphological characteristics of these species, preserved in marly limestones and calcareous claystones, show transitions from an initially coiled arrangement to biserial and uniserial arrangements, reflecting different evolutionary phases of the group. Their co-occurrence extends their known stratigraphic range into the Priabonian and shows that important morphological modifications emerged earlier than previously thought, providing the oldest reliably dated record of the Pavonitininae. Palaeoceanographic changes, such as carbonate compensation depth deepening and oxygen minimum zone expansion, along with the Sirhan-Turayf Basin's palaeogeographic location along the southern Tethyan margin, probably encouraged diversification of the Pavonitininae and their dispersal towards the Paratethys and Atlantic Ocean. These findings refine the evolutionary history, palaeobiogeography, and palaeoecological significance of the Pavonitininae, and improve their application in biostratigraphic and palaeoenvironmental studies of Paleogene deep-marine deposits.

Key words: Pavonitininae, agglutinated foraminifera, Eocene, Paleogene, Saudi Arabia.

Manuscript received 16 May 2025, accepted 25 August 2025

INTRODUCTION

Agglutinated foraminifera are unicellular benthic marine microorganisms that use detrital sediments (organic and/or inorganic) to construct their external chamber walls. Many species are important for biostratigraphy and for interpreting the deep-sea palaeoenvironment (Seiglie *et al*., 1986; Kaminski and Gradstein, 2005). The family Pavonitinidae, which was established by Loeblich and Tappan (1961) and later revised by Cimerman (1969), Seiglie and Baker (1983), and Sztràkos (1987), has distinct genera, such as *Pavonitina* and *Pavopsammia*. The family is characterized by compressed, palmate test and chamber configurations, which often change from triserial to biserial or uniserial stages and have partially completed alveolar partitions.

The stratigraphic distribution of the Pavonitinidae conventionally has been confined to the early to middle Oligocene, on the basis of findings from West Africa (notably Angola and Cameroon; Seiglie and Baker, 1983) and various locations in Europe, including Austria (Schubert, 1914; Rögl and Müller, 1976), Poland (Łuczkowska, 1990), Romania (Popescu, 1999), and northern Croatia (Vrsaljko *et al.,* 2006). Their widespread distribution throughout the Tethys and Paratethys is supported by additional discoveries, made in the middle Miocene of India (Govindan, 2004).

Pavonitinidae are thought to have descended from triserial ancestors, resembling *Verneuilina* (see Seiglie and Baker, 1983) and *Flabellogaudryina* (see Kaminski and Korin, 2025). Their morphology evolved toward simplified chamber arrangements and the development of alveolar partitions, interpreted as adaptations to low-oxygen, deep-marine environments (Seiglie *et al.*, 1986). Although they are well-documented in Oligocene–Miocene bathyal sediments along the Atlantic margins, where their biostratigraphic utility is established (Alegret and Thomas, 2009), late Eocene occurrences are rare. Sztràkos (1987) described *Pavonitina biarritzensis* from the Priabonian of France, and Bubík (2009) reported additional material from the Czech Republic. These findings indicated an earlier origin for the group, but their evolutionary and taxonomic framework remained unclear. Another taxonomic problem is the uncertain status of *Phyllopsammia adanula* Małecki, 1954, described from the Miocene of Wieliczka, in southern Poland. Cimerman (1969) regarded it as indistinguishable from *Pavonitina*, whereas Seiglie and Baker (1983) retained it as a separate genus, despite weak diagnostic criteria.

Here, the present authors report the first stratigraphically well-constrained Priabonian (E14 Biozone) occurrences of Pavonitininae from the Rashrashiyah Formation in the Sirhan-Turayf Basin, northwestern Saudi Arabia. The recovered assemblage, *P. styriaca*, *P. biarritzensis*, *P. kiscelliana*, and *P. flabellum*, provides the oldest well-dated record of the subfamily worldwide. This discovery significantly extends the stratigraphic range of Pavonitinidae into the late Eocene and confirms that their evolutionary history began earlier than previously was assumed, refining both their palaeobiogeographic significance and their role in Paleogene biostratigraphy.

GEOLOGIC SETTING

The Sirhan-Turayf Basin (Fig. 1A), also referred to as the Azraq-Sirhan Basin, is a broad synclinal structure, situated in the northwestern Arabian Peninsula, extending across northern Saudi Arabia into eastern Jordan (Meissner *et al.*, 1987). This basin recorded a continuous marine sedimentary sequence from the Late Cretaceous to the Paleogene and is of particular geological significance for understanding regional palaeoenvironmental evolution. Among its most important lithostratigraphic units is the Rashrashiyah Formation, which was first named by Meissner *et al.* (1987) after a prominent escarpment, located approximately 16 km north of An-Nabk (31.466667°N, 37.283333°E). The formation attains a thickness of approximately 75 m near the Al Qurayyat Water Well and is well exposed along erosional scarps and hills, providing excellent access for geological analysis.

The Rashrashiyah Formation has a varied rock structure that shows it was formed in a fairly deep-sea environment. The bottom section consists of chalky limestone, interlaced with bituminous calcareous marls, whereas the intermediate interval contains thin layers of siliceous limestone. The upper portion of the formation changes into calcareous claystones, indicating fluctuations in sediment supply and alterations to marine conditions. The lithological features indicate a depositional habitat, extending from outer shelf to upper bathyal settings, supported by the microfaunal content (Aljahdali *et al.*, 2020; Wade *et al.*, 2021; Allam *et al.*; 2025; Kaminski and Korin, 2025; Korin *et al.*, 2025).

MATERIAL AND METHODS

The microfossil content and depositional history of the Rashrashiyah Formation were assessed using micropalaeontological analysis on 23 samples, obtained from an 11-metre-thick succession at Outcrop-C near Al-Qurayyat during the 2024 field trip (Fig. 1B–D). The field work was carried out with the assistance of the Saudi Geological Survey. Each 100 g sample was disaggregated by boiling in a detergent solution for approximately two hours, with the treatment durations being altered, depending on the hardness of the sample. The residues were desiccated in an oven at 50–70°C after being wet-sieved through a 63 µm screen. Benthic foraminiferal specimens were selected, using an Olympus SZX7 stereomicroscope, and photographed, using a ZEISS Axio Zoom V16 system, at the College of Petroleum Engineering and Geosciences, the King Faud University of Petroleum and Minerals (KFUPM). Taxonomic classification and species identification were conducted according to published sources, including Małecki (1954), Seiglie and Baker (1983), Loeblich and Tappan (1987), Sztràkos (1987), Mikhalevich (2004), Kaminski and Gradstein (2005), Kaminski (2014), and BouDagher-Fadel (2018). The authors utilized the typical tropical to subtropical planktonic foraminiferal framework established by Wade *et al.* (2011) for biostratigraphic zonation to determine the age of the studied interval, consistent with the age interpretation, presented in Korin *et al.* (2025). All microscope slides will be permanently archived in the European Micropalaeontological Reference Centre, Kraków, Poland.

SYSTEMATIC PALAEONTOLOGY

This study follows the updated classification of agglutinated foraminifera, proposed by Kaminski (2014), which refines the earlier morphological scheme of Loeblich and Tappan (1987) by incorporating newly described taxa and reorganizing suprageneric groups.

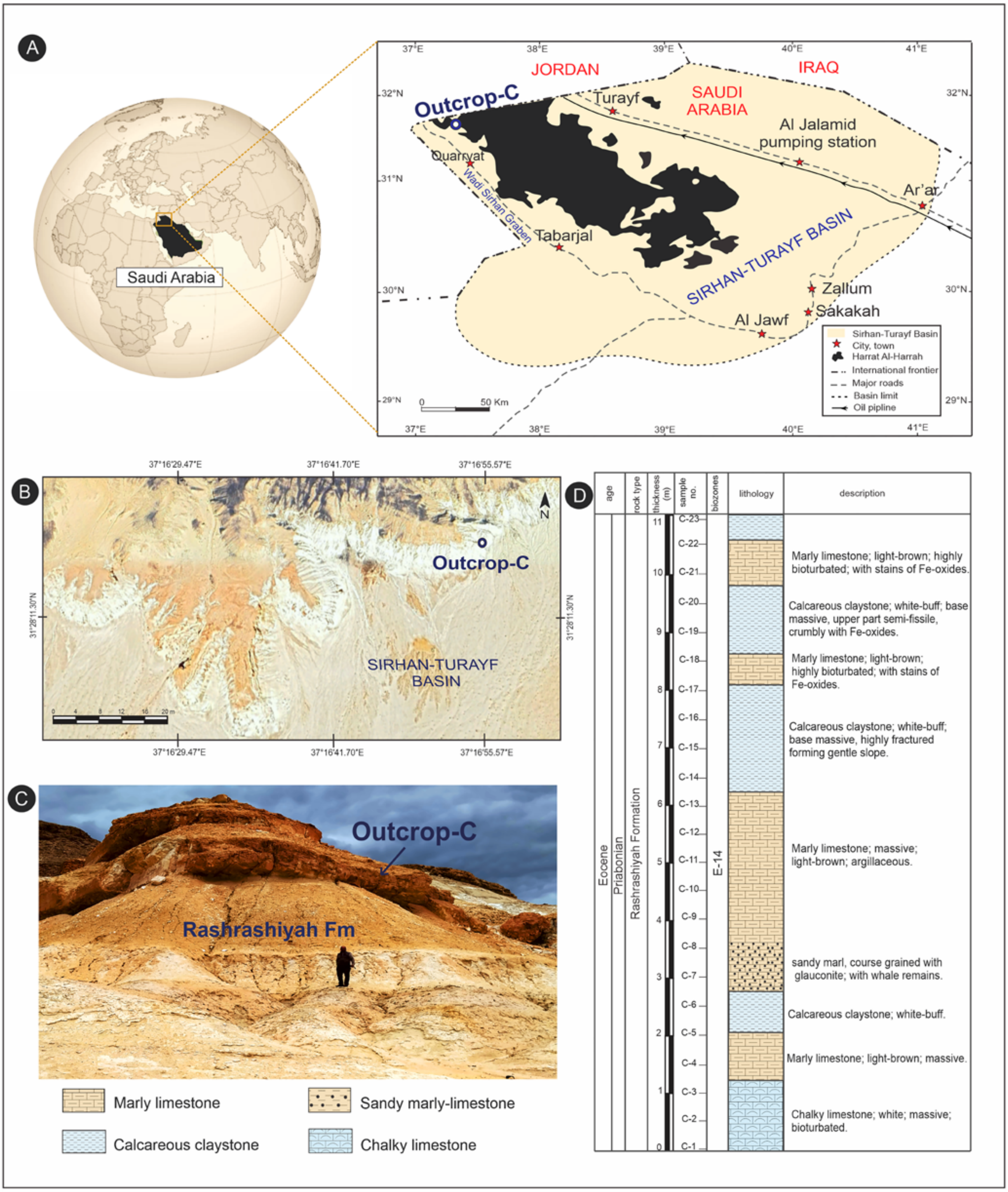

Fig. 1. Location, field view, and stratigraphy of Outcrop-C in the Sirhan-Turayf Basin. **A.** Location map, showing the position of Outcrop-C within the Sirhan-Turayf Basin, northwestern Saudi Arabia, near the Jordanian border. **B.** Google Earth satellite image, pointing to the location of Outcrop-C (31°28′12″N, 37°16′51″E) in the central part of the basin. **C.** Field photograph of Outcrop-C, showing the exposed section of the Rashrashiyah Formation, characterized by alternating marly and chalky limestone beds. **D.** Stratigraphic log of the 11-metres-thick section at Outcrop-C, illustrating the vertical distribution of lithologies and key facies.

Phylum Foraminifera d'Orbigny, 1826
Class Globothalamana Pawłowski,
Holzmann and Tyszka, 2013
Order Lituolida Lankester, 1885
Suborder Spiroplectamminina Mikhalevich, 1992
Superfamily Pavonitinoidea Loeblich and Tappan, 1961
Family Pavonitinidae Loeblich and Tappan, 1961

Diagnosis: Tests are initially coiled and exhibit a chamber arrangement that may be biserial, or uniserial in later growth stages. The internal structure of the chambers is characterized by numerous vertical partitions (septula or beams) projecting downward from the roof, and in some cases, a few horizontal connections (rafters) may also be present. These forms are recorded from the Late Cretaceous and then reappear in the fossil record from the late Eocene to the Pliocene (modified after Loeblich and Tappan, 1961; BouDagher-Fadel, 2018).

Subfamily Pavonitininae Loeblich and Tappan, 1961

Diagnosis: Tests are palmate in shape and triangular in cross-section, with early growth stages exhibiting initial coiling with biserial to uniserial chamber arrangement. The internal chamber structure is partially subdivided by numerous vertical partitions (septula or beams), projecting downward from the chamber roof, and in some cases, a few horizontal connections (rafters) may also be present. Apertures are terminal and may be single or multiple. These forms are known from the late Eocene to the Pliocene (BouDagher-Fadel, 2018; this study).

Genus *Pavonitina* Schubert, 1914

Type species: *Pavonitina styriaca* Schubert, 1914.

Pavonitina styriaca Schubert, 1914
Fig. 2A–FF

1914 *Pavonitina styriaca* – Schubert, p. 143, pl. 4, figs 1–8.
1969 *Pavonitina styriaca* Schubert – Cimerman, p. 112, pl. 1, figs 1–7.
1983 *Pavonitina styriaca* Schubert – Seiglie and Baker, fig. 9.
1987 *Pavonitina styriaca* Schubert – Sztràkos, p. 131, pl. 2, fig. 5, pl. 3, fig. 8.
1990 *Pavonitina styriaca* Schubert – Łuczkowska, pl. 5, fig. 9.
1999 *Pavonitina styriaca* Schubert – Popescu, p. 413, pl. II, figs 6, 7, 10.
2008 *Pavonitina styriaca* Schubert – BouDagher-Fadel, p. 299, pl. 6.1, fig. 8.

Material: 29 specimens from sample C-21, 46 spm. from sample C-22, and 37 spm. from sample C-23.

Description: Test elongate, thin, palmate in shape, with a leaf-like outline. The initial portion exhibits slight coiling, which gradually transitions into a biserial arrangement, followed by a uniserial stage in the adult form. Chambers are semi-triangular in the early part, moderately compressed, and arranged in a linear series. Sutures are distinct and slightly depressed; they appear curved in the early portion and become strongly inverted and V-shaped in the later stages. The wall is finely agglutinated, composed of fine- to medium-grained particles, and characterized by sharply defined margins. The aperture is terminal, subcircular, and situated on a low, poorly developed neck; however, it is frequently indistinct or poorly preserved. Internal structures, such as secondary septa or chamber subdivisions, are very faint or not clearly discernible in the examined specimens.

Remarks: *Pavonitina styriaca*, the type species of the genus, was originally described by Schubert (1914), on the basis of material from the Miocene Schlier Formation in Austria. Subsequent work by Cimerman (1969), using better-preserved specimens from Slovenia, reaffirmed Schubert's interpretation and provided additional insights into internal morphological features. Among the original specimens from Laubegg (the type locality of the species) that are housed at the Geologische Bundesanstalt in Vienna, Cimerman (1969) examined three megalospheric forms. These specimens exhibit a relatively large spherical proloculus, followed by four pairs of biserial chambers and two uniserial chambers. Oblique septula are present in both the later biserial and uniserial portions of the test, consistent with observations from the Dobje material and Schubert's original figures. One of the diagnostic features of *P. styriaca* is thus the presence of these oblique septula in both biserial and uniserial stages.

Palaeoenvironment and stratigraphic distribution: According to Schubert (1914), *Pavontina styriaca* is interpreted to have inhabited outer neritic to upper bathyal environments, as indicated by its occurrence alongside diverse agglutinated benthic foraminiferal assemblages within fine-grained marls of the Miocene Schlier Formation in Austria. The thin, delicate test and the presence of internal septula are consistent with deposition in a low-energy, deeper-marine setting, where hydrodynamic activity probably was minimal (Cimerman, 1969). In the material of the present authors, *P. styriaca* occurs within calcareous claystone and marly limestone beds, further supporting a calm, low-energy depositional setting. Stratigraphically, these occurrences are confined to the upper part of the E14 Biozone in outcrop C of the authors.

Pavonitina biarritzensis Sztràkos, 1987
Fig. 3A–D

1987 *Pavonitina biarritzensis* sp. nov. – Sztràkos, p. 129, pl. 1, figs 1–3, pl. 3, figs 1–3.

Material: 4 specimens from sample C-15.

Description: Test free, elongate, and laterally compressed, with an overall outline resembling a leaf or palmate structure. The early growth stage begins with a short initial coil, which passes into a biserial chamber arrangement and subsequently transitions into a uniserial configuration in the adult portion. Chambers in the biserial stage are semi-triangular to subrectangular, moderately compressed, and arranged in

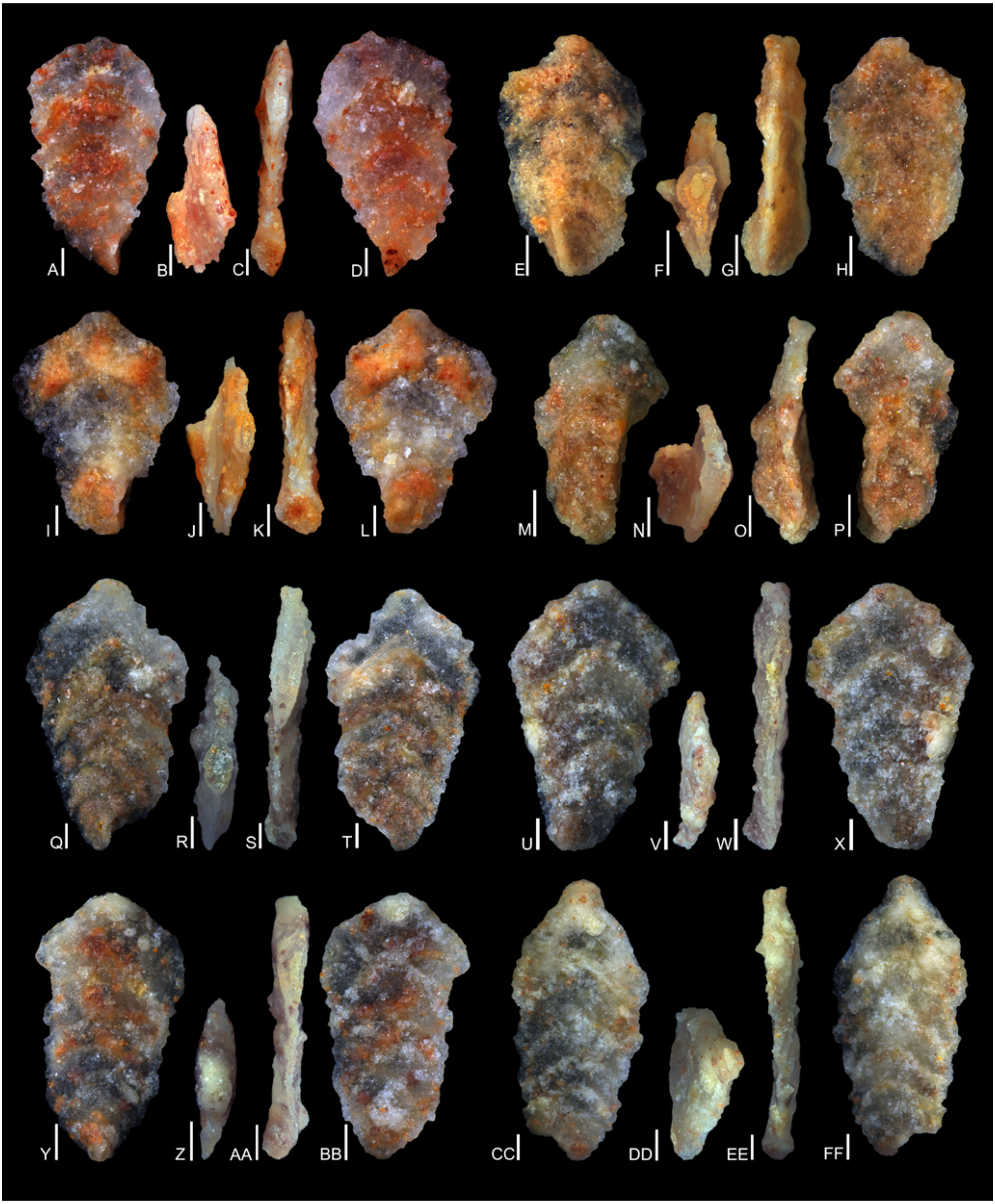

Fig. 2. *Pavonitina styriaca* Schubert, 1914 from the upper Eocene deposits from the Sirhan-Turayf Basin, northwestern Saudi Arabia. **A–P.** Specimens from sample C-23 in anterior, apertural, lateral, and posterior views. **Q–T.** Specimens from sample C-22. **U–FF.** Specimens from sample C-21. All specimens show the characteristic palmate test with transition from triserial to uniserial chamber arrangement and are illustrated in anterior, apertural, lateral, and posterior views, respectively. Scale bars equal 100 µm.

a linear series. Sutures are distinct and slightly depressed and curved. The wall is finely agglutinated, composed of well-selected fine to medium-sized grains, and displays sharply defined outer margins. The terminal aperture is subcircular and located on a short, weakly developed neck. In many specimens, the aperture is poorly preserved and difficult to discern. Internal structures, such as flabelliform (fan-shaped) septula may be present, though often faint and variably preserved among specimens.

Remarks: *Pavontina biarritzensis* was first described by Sztràkos (1987) from the Priabonian deposits of the Biarritz region (France). It is distinguished by its flattened test and the chamber arrangement that transitions from a short, initially coiled stage to biserial, and finally to a uniserial adult stage.

The morphology of *P. biarritzensis* closely resembles that of *Phyllopsammia adanula* Małecki (1954), particularly in its fan-shaped septula. However, as noted by Cimerman (1969), *Phyllopsammia* is not a valid genus, and Sztrákos (1987) further emphasized that these forms should be included within *Pavonitina*. In this study, the authors therefore follow Cimerman (1969) and Sztrákos (1987) and treat *P. adanula* as a morphological variant of *Pavonitina*.

Palaeoenvironment and stratigraphic distribution: *Pavontina biarritzensis* is believed to inhabit outer neritic to upper bathyal environments, as indicated by its association with other deep-marine agglutinated foraminifera in the Priabonian strata of the Biarritz region, in southwestern France, as noted by Sztràkos (1987). Adaptation to low-energy depositional environments with relatively calm bottom conditions is indicated by the flattened, elongate test morphology and the presence of weakly developed internal structures. The recovery of *P. biarritzensis* from fine-grained marls and calcareous mudstones in the present study is consistent with an outer shelf or upper slope environment beneath the storm wave base. Its stratigraphic distribution is limited to the lower Priabonian in outcrop C in this study, where it is documented within the upper part of *Globigerinatheka semiinvoluta* (E14) Biozone.

Pavonitina kiscelliana (Sztràkos, 1987)
Fig. 3E–L

1979 *Ammospirota kiscelliana* sp. nov. – Sztràkos, p. 59, pl. 3, fig. 6.

1982 *Ammospirota kiscelliana* – Sztràkos, pl. 2, fig. 6.

1987 *Pavonitina kiscelliana* (Sztràkos) – Sztràkos, p. 130, pl. 1, figs 4–8, pl. 3, figs 4–6.

1998 *Pavonitina kiscelliana* (Sztràkos) – Cicha *et al.*, p. 116, pl. 6, figs 2–4.

Material: 2 specimens from sample C-15.

Description: Test thin, laterally compressed, and broadly fan-shaped to palmate in general outline. The early portion of the test shows a short initial coil, transitioning into a biserial chamber arrangement, which gradually becomes uniserial toward the adult stage. Chambers are slightly arcuate, overlapping one another gently, and are delineated by well-defined, depressed sutures. The wall is finely agglutinated, constructed of well-sorted grains, and exhibits a smooth external surface. Internally, the chambers display weakly developed vertical septula that descend from the roof of the chamber in a radial or fan-like pattern. The aperture is terminal, subcircular, and located in a shallow depression, though it is frequently poorly preserved and difficult to discern in many specimens.

Remarks: *Pavonitina kiscelliana* was first described by Sztràkos (1979) as *Ammospirota kiscelliana* from the Kiscell Clay Formation in Hungary and later reassigned to the genus *Pavonitina,* on the basis of its distinctive internal features, including faint, radially arranged flabelliform septula. The species is distinguished by its thin, laterally compressed, fan-shaped test and a chamber arrangement that starts with a brief coiled phase, succeeded by biserial growth and a short uniserial phase. This study interprets the specimens classified as *P. kiscelliana* as juvenile forms, due to their diminutive size and underdeveloped uniserial stage. Morphologically, it closely resembles *P. biarritzensis*, although it is distinguished by a more advanced uniserial stage, accelerated chamber enlargement, and more distinct internal septation (Sztràkos, 1987).

Palaeoenvironment and stratigraphic distribution: *Pavontina kiscelliana* is typically associated with outer neritic to upper bathyal environments, as inferred from its occurrence in the deep-marine clays of the Kiscell Formation in Hungary and equivalent Oligocene deposits in the central Paratethys region. Its thin, compressed test and weakly developed internal septula indicate adaptation to low-energy, oxygen-poor settings characteristic of distal shelf to upper slope environments. The species has also been recorded from the upper Eocene to lower Oligocene transition, including material from Hungary and Spain (Poignant and Sztràkos, 1986), indicating a relatively broad stratigraphic range across the late Eocene–early Oligocene. In the present study, *P. kiscelliana* occurs in fine-grained marls, interpreted as representing calm, hemipelagic conditions below the storm wave base. Its stratigraphic occurrence in this study is confined to the lower Priabonian interval of outcrop C, where it is recorded from the upper portion of the Globigerinatheka semiinvoluta (E14) Biozone.

Genus *Pavopsammia* Seiglie and Baker, 1983

Type species: *Pavopsammia flabellum* Seiglie and Baker, 1983.

Pavopsammia flabellum Seiglie and Baker 1983
Fig. 3M–FF

1983 *Pavopsammia flabellum* – Seiglie and Baker, p. 393, pl. 1, figs 6a–8.

1987 *Pavopsammia flabellum* Seiglie and Baker – Loeblich and Tappan, p. 119, pl. 127, figs 7–9.

2008 *Pavopsammia flabellum* Seiglie and Baker – BouDagher-Fadel, p. 299, pl. 6.1, fig. 9.

Material: 56 specimens from samples C-13 and C-23.

Description: Test compressed, palmate to fan-shaped in outline, with chambers arranged successively in triserial, then biserial, and finally uniserial arrangement. Chambers

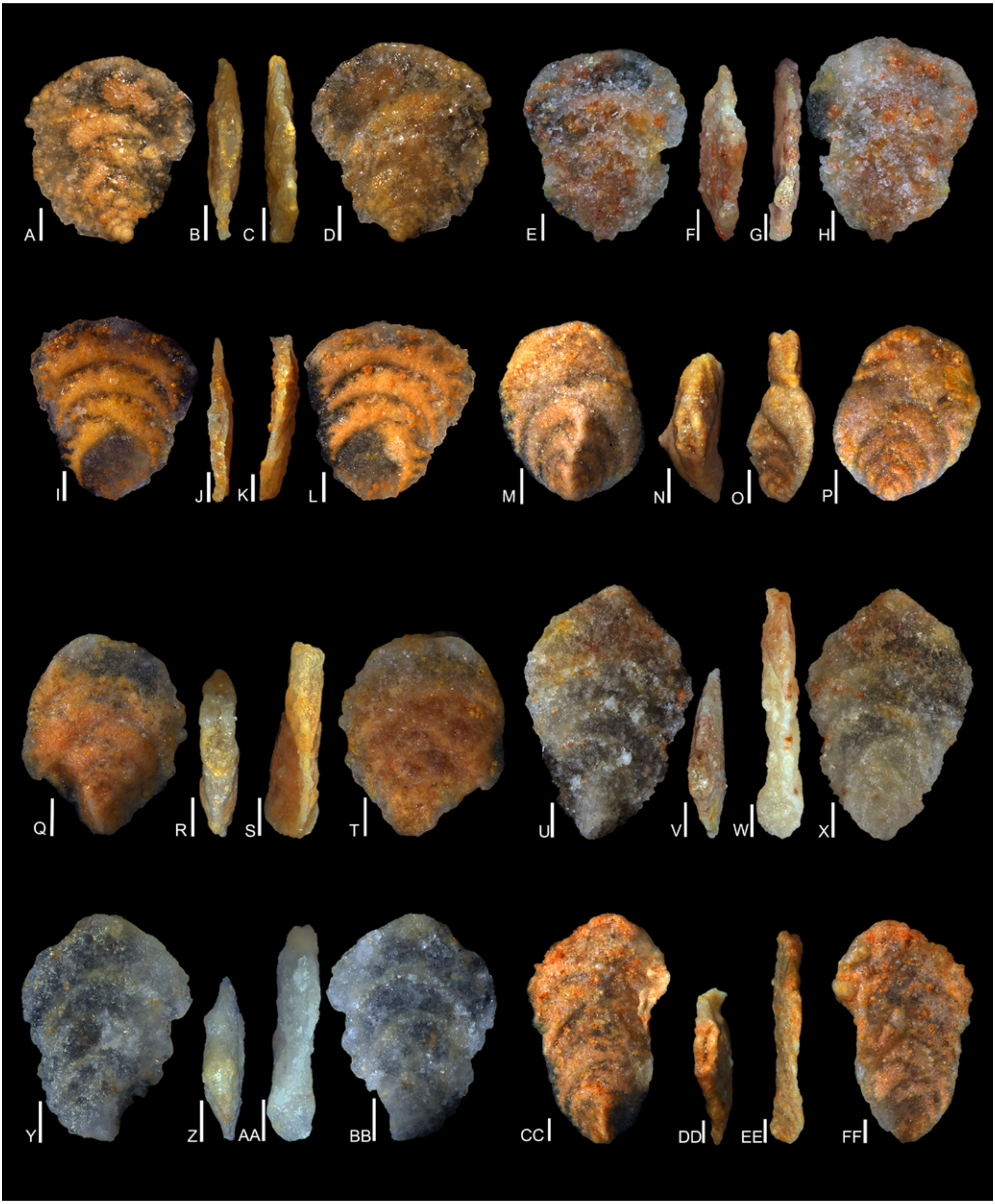

Fig. 3. *Pavonitina biarritzensis* Sztràkos, 1987, *Pavonitina kiscelliana* (Sztràkos, 1987), *Pavopsammia flabellum* Seiglie and Baker, 1983 from the upper Eocene deposits in the Sirhan-Turayf Basin, northwestern Saudi Arabia. **A–D.** *Pavonitina biarritzensis* from samples C-15. **E–L.** *Pavonitina kiscelliana* (juvenile) from samples C-23 (E–H) and C-15 (I–L). **M–FF.** *Pavopsammia flabellum* Seiglie and Baker, 1983 from sample C-19 (M–P, Q–T, CC–FF) and C-21 (U–X), and C-22 (Y–BB). All specimens are illustrated in anterior, apertural, lateral, and posterior views, respectively, and display fan-shaped to flabelliform outlines with mixed chamber arrangements. Scale bars equal 100 µm.

are subrectangular to crescentic in shape and increase gradually in size. Sutures are depressed and often marked by slightly coarser agglutinated grains. The interior of the chambers is subdivided by numerous incomplete vertical partitions (septula or beams), projecting from the upper chamber wall in a fan-shaped pattern. The wall is composed of fine agglutinated particles. Aperture terminal, elongated semi-rounded, located at the end of the final chamber, often within a shallow depression.

Remarks: *Pavopsammia flabellum* was established by Seiglie and Baker (1983) as the type species of the genus *Pavopsammia*, on the basis of material from the Oligocene of west Africa. Its chamber arrangement progresses from an initial triserial stage, through a biserial phase, and terminates in a short uniserial portion. Internally, the presence of fan-shaped (flabelliform) vertical septula further supports its intermediate morphology. As illustrated in the lineage chart, *P. flabellum* occupies a pivotal position between earlier triserial and triserial-biserial genera, such as *Verruculina*-like forms and *Flabellogaudryina*, and more specialized coiled biserial-uniserial taxa, such as *Pavonitina*. These features indicate that *P. flabellum* may represent an evolutionary link, bridging primitive and more specialized deep-water agglutinated foraminiferal morphotypes in the late Eocene.

Palaeoenvironment and stratigraphic distribution: *Pavopsammia flabellum* is typically associated with deep-marine settings, particularly outer neritic to upper bathyal environments. Its thin, compressed test and fan-shaped internal septula are interpreted as morphological adaptations to low-energy, oxygen-depleted conditions on the continental slope. Seiglie and Baker (1983) originally described the species from the Oligocene of offshore west Africa, where it was found with other deep-water agglutinated foraminifera. In this study, *P. flabellum* is recorded from the lower part of the Priabonian, within the *Globigerinatheka semiinvoluta* (E14) biozone. Its stratigraphic occurrence and evolutionary position show that it played a transitional role between older triserial-biserial taxa and later-evolving biserial-uniserial forms, indicating environmental continuity and faunal turnover during the late Eocene in deep-water depositional settings.

DISCUSSION

This study of the upper Eocene Rashrashiyah Formation in the Sirhan-Turayf Basin presents valuable new data to refine the evolutionary history of Pavonitinidae Loeblich and Tappan, 1961. The study is based on a well-preserved assemblage of deep-marine agglutinated foraminifera, allowing for detailed morphological and taxonomic analysis. The classification applied herein adopts the revised systematic framework, proposed by Kaminski (2014), which refines the traditional taxonomy of Loeblich and Tappan (1987) by integrating new insights into test structure, chamber arrangement, internal features, and palaeobiogeographic and biostratigraphic distributions.

Four pavonitinid taxa (Fig. 4) are recognized in this study: *Pavonitina styriaca*, *Pavonitina biarritzensis*, *Pavonitina kiscelliana*, and *Pavopsammia flabellum*. *P. styriaca*, first identified in the Miocene Schlier Formation of Austria (Schubert, 1914; Cimerman, 1969), is distinguished by a test that commences with initial coiling, progresses to biserial growth, and ends in a uniserial phase, which includes significantly inverted V-shaped sutures and increasingly pronounced oblique septula in the later chambers. *P. biarritzensis* and *P. kiscelliana*, both delineated by Sztràkos (1987), exhibit a comparable coiled-biserial-uniserial progression. However, they differ in significant morphological characteristics: *P. kiscelliana* generally exhibits a prolonged uniserial phase and more pronounced internal septula, while *P. biarritzensis* is characterised by its thin, leaf-like test and less robust internal structures. The resemblance of *P. biarritzensis* to *Phyllopsammia adanula* has long been noted (Cimerman, 1969; Seiglie and Baker, 1983). While Seiglie and Baker (1983) retained *Phyllopsammia* as a separate genus, subsequent authors (Cimerman, 1969; Sztrákos, 1987) argued that its diagnostic features are insufficient. The present results agree with the latter interpretation, and the authors therefore consider *Phyllopsammia* a junior synonym. *P. flabellum*, the type species of the genus *Pavopsammia* (Seiglie and Baker, 1983), is especially notable for its triserial-biserial-uniserial chamber progression and fan-shaped vertical septula. These features indicate a transitional evolutionary position between earlier triserial forms (e.g., *Verneuilina*-like taxa according to Seiglie and Baker, 1983) and *Flabellogaudryina* (Kaminski and Korin, 2025) and the more specialized uniserial morphotypes of *Pavonitina*. The presence of these septula indicates structural adaptation to low-oxygen bathyal environments and supports the interpretation of *Pavopsammia* as a key intermediate form in the lineage, leading to more specialized pavonitinids (BouDagher-Fadel, 2018).

All four taxa were recovered in this study from the upper part of the *Globigerinatheka semiinvoluta* (E14) Biozone, constraining their occurrence to the lower Priabonian (Korin *et al*., 2025). This represents the oldest stratigraphically well-documented occurrence of the Pavonitinidae globally. Previous reports placed *Pavontina styriaca* in the Miocene Schlier Formation (Austria), *P. flabellum* in the Oligocene of offshore west Africa (Seiglie and Baker, 1983), and *P. kiscelliana* in the Oligocene Kiscell Clay of Hungary (Sztràkos, 1987; Cicha *et al*., 1998). *P. biarritzensis* previously was known only from the upper Eocene of France (Sztràkos, 1987), but never in association with the other taxa. The co-occurrence of all four species in the same stratigraphic interval at Sirhan-Turayf thus significantly extends the known temporal range of Pavonitinidae and indicates that their key morphological innovations originated earlier than previously was assumed.

In the late Eocene, the Sirhan-Turayf Basin was situated in a strategic palaeogeographic position along the southern margin of the Western Tethys Seaway (Fig. 5). This region was connected to the Indo-Pacific, Arabian, and Atlantic marine provinces by westward-flowing warm surface currents (Haq, 1981). These dominant oceanic channels most likely enabled the early radiation and spread of deep-marine agglutinated foraminifera, such as Pavonitinidae members. The co-occurrence of *Pavontina styriaca*, *P. biarritzensis*, *P. kiscelliana*, and *Pavopsammia flabellum* within the

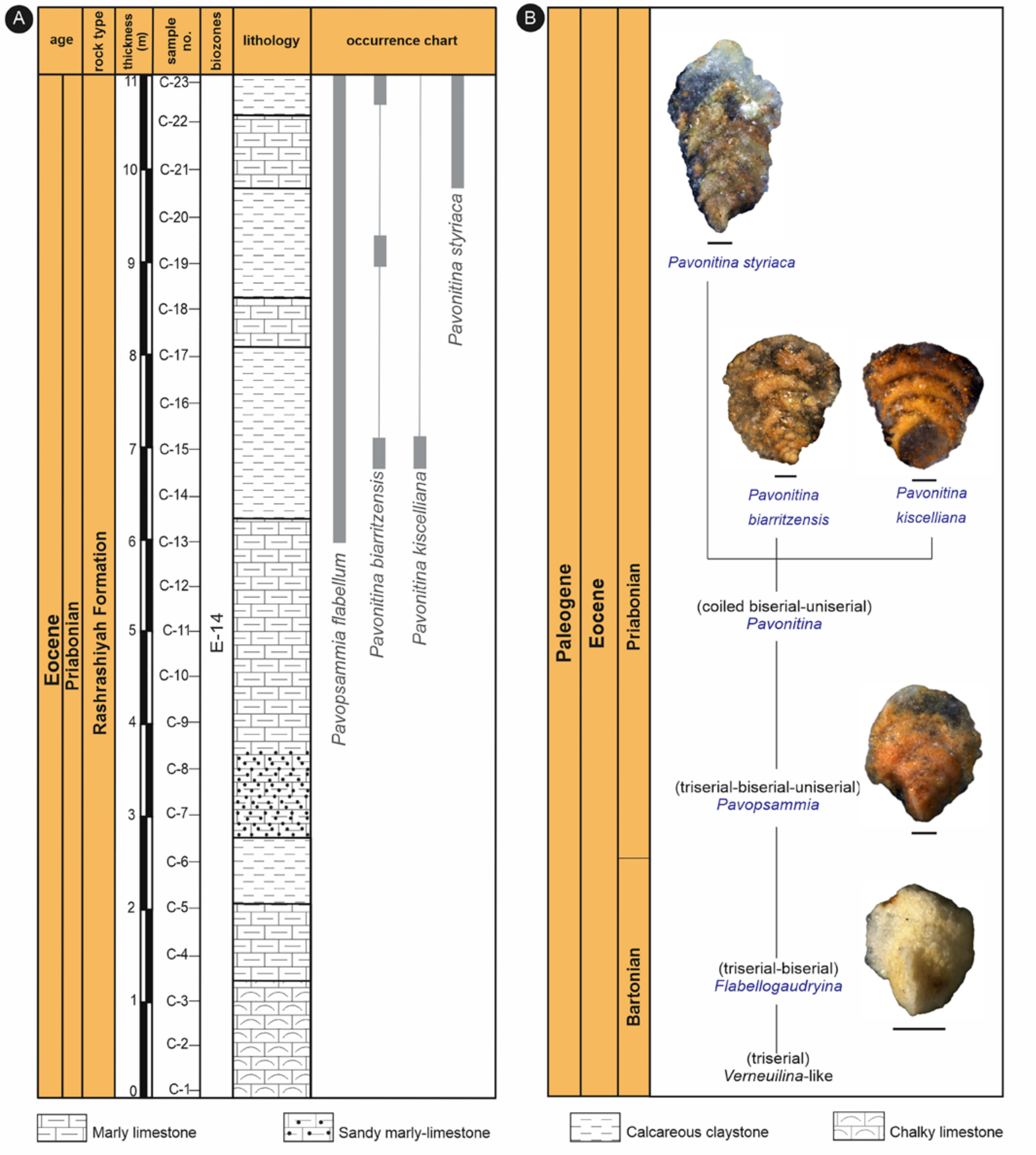

Fig. 4. Stratigraphic distribution and evolutionary context of Pavonitinidae from the upper Eocene Rashrashiyah Formation, Sirhan-Turayf Basin, northwestern Saudi Arabia. **A.** Lithostratigraphic column of the Priabonian succession with occurrence chart of *Pavopsammia flabellum*, *Pavonitina biarritzensis*, *Pavonitina kiscelliana*, and *Pavonitina styriaca*, calibrated to planktonic foraminiferal Biozone E14. **B.** Evolutionary framework of Pavonitinidae, showing representative specimens from the study area and illustrating morphological trends from triserial *Verneuilina*-like ancestors through triserial-biserial *Flabellogaudryina*, to triserial-biserial-uniserial *Pavopsammia* and coiled biserial-uniserial *Pavonitina*. Scale bars equal 100 µm.

Priabonian strata of the Rashrashiyah Formation in Saudi Arabia provides strong evidence for a southern Tethyan origin of the group. Each species has a documented palaeogeographic connection: *P. styriaca* from the Miocene Schlier Formation in Austria, *P. biarritzensis* from the Priabonian of Biarritz (France), *P. kiscelliana* from the Oligocene Kiscell Clay of Hungary, and *P. flabellum* from the Oligocene of Cabinda and Cameroon in west Africa. This region served as both an evolutionary centre and a point of origin for broader geographic expansion, as evidenced by their collective presence in the Sirhan-Turayf Basin. The arrival of these taxa is concurrent with substantial palaeoceanographic changes, including the deepening of the carbonate compensation depth (CCD), the expansion of oxygen minimum zones, and the increased stratification of the water column (Van Andel, 1975; Zachos *et al*., 2001; Pälike *et al*., 2012). These conditions likely established habitats that favoured agglutinated forms over calcareous benthic taxa. Particularly regarding chamber architecture and internal septation, the morphological variation among these pavonitinids is probably indicative of an evolutionary response to these environmental pressures.

Taken together, the pavonitinid assemblage from the upper Eocene Rashrashiyah Formation provides a valuable window into the early evolution and geographical dispersial of deep-marine agglutinated foraminifera. The co-occurrence of *Pavontina styriaca*, *P. biarritzensis*, *P. kiscelliana,* and *P. flabellum* within the well-dated lower Priabonian interval (E14 Biozone; Korin *et al*., 2025) represents the oldest firmly established record of the family Pavonitinidae. These species exhibit a range of test shapes and internal features, reflecting distinct evolutionary stages already developed by the late Eocene. Their presence in a single deep-marine setting indicates that the Sirhan-Turayf Basin may have acted as an early centre for the diversification and expansion of this group. The organic-rich, fine-grained sediments, where these forms are preserved, further support their adaptation to low-energy, oxygen-depleted environments. Overall, this study offers important fossil evidence that helps clarify the timing, environmental preferences, and early distribution patterns of Pavonitinidae, contributing to a broader understanding of the Paleogene oxygen minimum zone environment.

CONCLUSIONS

This study documents the first stratigraphically well-constrained Priabonian (E14 Biozone) record of Pavonitininae from the Rashrashiyah Formation in the Sirhan-Turayf Basin, northwestern Saudi Arabia. The assemblage, comprising *Pavontina styriaca*, *P. biarritzensis*, *P. kiscelliana*, and *P. flabellum*, represents the oldest known occurrence of the subfamily and demonstrates that its evolutionary history originated in the late Eocene, rather than in the Oligocene. The observed morphological traits particularly chamber arrangement from an initial coil or triserial part to biserial and uniserial arrangements, and the development of fan-shaped septula record important evolutionary stages and confirm a close relationship with triserial-biserial ancestors, such as *Flabellogaudryina*. Their co-occurrence within fine-grained, deep-marine sediments emphasizes the role of

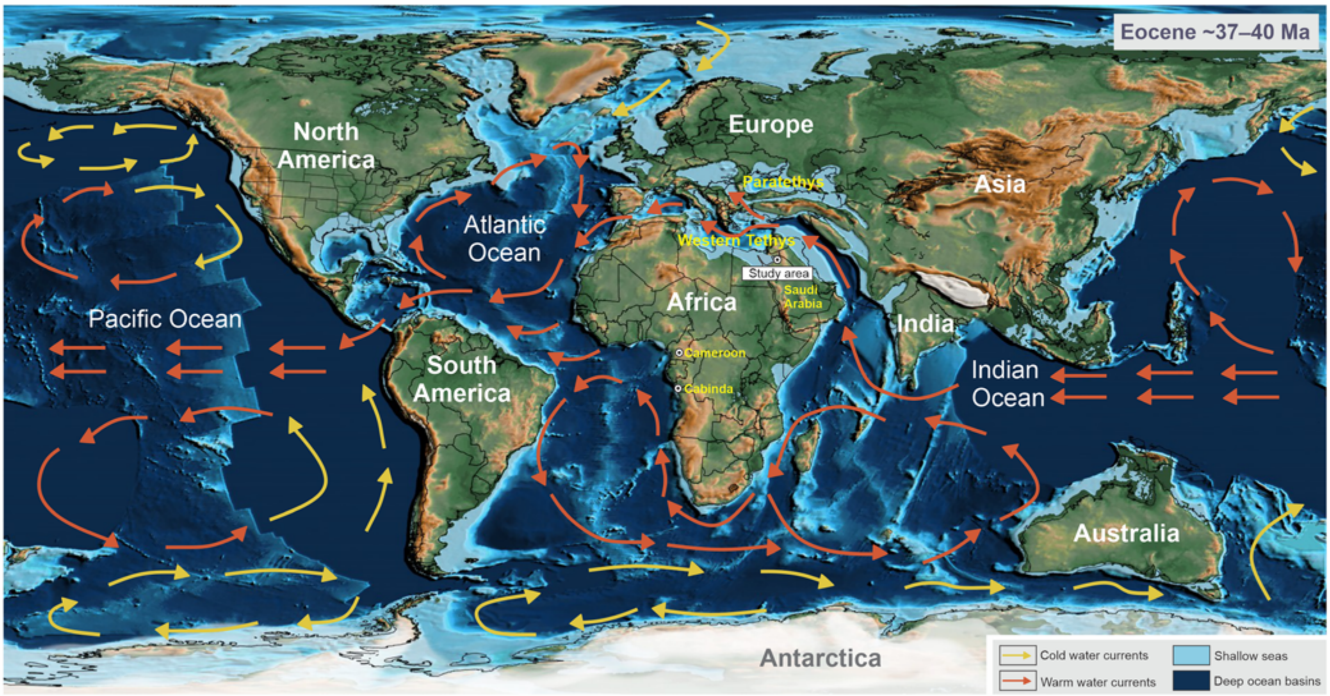

Fig. 5. Middle to upper Eocene palaeogeographic map reconstruction, showing paleo-surface ocean circulation patterns. Warm (red arrows) and cold (yellow arrows) currents; light and dark blue colours indicate shallow seas and deep ocean basins, respectively. Marked locations represent key Pavonitinidae occurrences, including the newly identified Sirhan-Turayf Basin, alongside some other localities in the Paratethys, Western Tethys, Cabinda, and Cameroon (modified after Haq, 1981; Scotese, 2021).

the southern margin of the Tethys as a centre of early diversification and dispersal. These results refine the age range, evolutionary history, and palaeobiogeographic significance of Pavonitininae, while also contributing to the biostratigraphic correlation and palaeoenvironmental interpretation of Paleogene deep-sea ecosystems.

ACKNOWLEDGEMENTS

We thank the College of Petroleum Engineering and Geosciences, King Fahd University of Petroleum and Minerals, and the Saudi Geological Survey for providing logistical and technical support and research resources, as well as Miroslav Bubík (Czech Geological Survey) and an anonymous reviewer for their helpful comments on an earlier draft of this paper.

REFERENCES

Alegret, L. & Thomas, E., 2009. Food supply to the seafloor in the Pacific Ocean after the Cretaceous/Paleogene boundary event. *Marine Micropaleontology*, 71: 1–5.

Aljahdali, M. H., Elhag, M., Mufrreh, Y., Memesh, A., Alsoubhi, S. & Zalmout, I. S., 2020. Upper Eocene calcareous nannofossil biostratigraphy: a new preliminary Priabonian record from northern Saudi Arabia. *Applied Ecology & Environmental Research,* 18: 5607–5625.

Allam, S., Korin, A., Herlambang, A., Humphrey, J. D., Alnajjar, M. I., Bahameem, A. A., Memesh, A. M., Zalmout, I. S. & Kaminski, M. A., 2025. Stable carbon and oxygen isotopes of benthic and planktonic foraminifera as paleoenvironmental and paleoclimatic proxies for the Bartonian–Priabonian in northwestern Saudi Arabia. *Geological Quarterly*, 69: 1–12.

BouDagher-Fadel, M. K., 2008. The Cenozoic larger benthic foraminifera: the Palaeogene. *Developments in Palaeontology and Stratigraphy*, 21: 297–545.

BouDagher-Fadel, M. K., 2018. *Evolution and Geological Significance of Larger Benthic Foraminifera*. Second Edition. UCL Press, London, 693 pp.

Bubík, M., 2009. Nové a málo známé aglutinované foraminifery z paleogénu jižní Moravy. *Zprávy o geologických výzkumech*, 2008: 82–84. [In Czech.]

Cicha, I., Rögl, F., Rupp, C. & Ctyroka, J., 1998. Oligocene–Miocene Foraminifera of the Central Paratethys. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 549: 1–325.

Cimerman, F., 1969. The genus *Pavonitina* Schubert (Foraminiferida) and its systematic position. *Micropaleontology,* 15: 111–115.

d'Orbigny, A. D., 1826. Tableau méthodique de la classe des Céphalopodes. *Annales des Sciences Naturelles*, 7: 96–169.

Google Earth, 2024. Satellite imagery of Outcrop-C, Sirhan-Turayf Basin, NW Saudi Arabia (31°28′12″N, 37°16′51″E). Google LLC. Available at: https://earth.google.com.

Govindan, A., 2004. Miocene deep-water agglutinated foraminifera from offshore Krishna-Godavari Basin, India. *Micropaleontology*, 50: 213–252.

Haq, B. U., 1981. Paleogene paleoceanography: Early Cenozoic oceans revisited. *Oceanologica Acta*, 4: 71–82.

Kaminski, M. A., 2014. The year 2010 classification of the agglutinated foraminifera. *Micropaleontology*, 60: 89–108.

Kaminski, M. A. & Gradstein, F. M., 2005. Atlas of Paleogene Cosmopolitan Deep-water Agglutinated Foraminifera. *Grzybowski Foundation Special Publication*, 10: 1–547.

Kaminski, M. A. & Korin, A., 2025. *Flabellogaudryina* n. gen, a new agglutinated foraminiferal genus from the Eocene of Saudi Arabia. *Micropaleontology*, 71: 94–100.

Korin, A., Allam, S., Humphrey, J. D., Amao, A. O., Ayranci, K., Najjar, M. I., Bahameem, A. A., Zalmout, I. S., Memesh, A. M. & Kaminski, M. A., 2025. The genus *Hantkenina* in Saudi Arabia: Implications for biostratigraphy and paleoecology across the Bartonian–Priabonian transition. *Revue de Micropaléontologie*, 87: 100844.

Lankester, E. R., 1885. Protozoa. In: Anon, E, (ed.), *The Encyclopaedia Britannica, 9th ed.* Adam and Charles Black, Edinburg and London, 36 pp.

Loeblich, A. R. & Tappan, H., 1961. Suprageneric classification of the Rhizopodea. *Journal of Paleontology*, 35: 245–330.

Loeblich, A. R. & Tappan, H., 1987. *Foraminiferal Genera and Their Classification*. Van Nostrand Reinhold, New York, 970 pp.

Łuczkowska, E., 1990. Stratigraphically important agglutinated foraminifera in the Badenian (Miocene M4) of Poland. In: Hemleben, C., Kaminski, M. A., Kuhnt, W. & Scott, D. B. (eds), *Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated Foraminifera. NATO ASI Series C: Mathematical and Physical Sciences*, 327. Kluwer Academic Publishers, Dordrecht, pp. 843–857.

Małecki, J., 1954. New genera of agglutinated foraminifera from the Polish Miocene. *Rocznik Polskiego Towarzystwa Geologicznego*, 22: 497–513.

Meissner, C. R., Jr., Riddler, G. P., van Eck, M., Aspinall, N. C., Farasani, A. M. & Dini, S. M., 1987. *Preliminary geologic map of the Turayf quadrangle, Sheet 31 C, and part of the An Nabk quadrangle, Sheet 31 B, Kingdom of Saudi Arabia*. US Geological Survey, Technical Report, Saudi Arabian Deputy Ministry for Mineral Resources, pp. 89–336.

Mikhalevich, V. I., 1992. *Makrosistema foraminifer*. Ph.D. Thesis. Zoological Institute of the Russian Academy of Sciences, St. Petersburg, 43 pp. [In Russian.]

Mikhalevich, V. I., 2004. On the heterogeneity of the former Textulariina (Foraminifera). In: Bubík, M. & Kaminski, M. A. (eds), *Proceedings of the Sixth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication*, 8: 317–349.

Pälike, H., Lyle, M. W., Nishi, H., Raffi, I., Ridgwell, A., Gamage, K., Moore, T. C., Klaus, A., Abelson, M., Anderson, L., Backman, J., Baldauf, J. G., Beltran, C., Bohaty, S. M., Bown, P. R., Busch, W., Channell, J. E. T., Chun, C. O. J., Delaney, M. L., Dewangan, P., Dunkley Jones, T., Edgar, K. M., Evans, H. F., Fitch, P., Foster, G. L., Gussone, N., Hasegawa, H., Hodell, D. A., Hovan, S. A., Hyland, E., Iijima, K., Ito, T., Kamikuri, S., Kimoto, K., Kuroyanagi, A., Leon-Rodriguez, L., Malinverno, A., Moore, J. L., Murphy, B. H., Murphy, D. P., Nakamura, H., Ogane, K., Ortiz, J. D., Pearson, P. N., Pusz, A., Rea, D. K., Rosenthal, Y., Sagawa, T., Santis, L. D., Scher, H. D., Schneider, L. J., Sexton, P. F., Shah, H., Shackford, J. K., Shields-Zhou, G., Shin, Y., Sluijs, A., Sugisaki, S., Thomas, E., Tian, J., Tsujimoto, A., Wade, B. S., Westerhold, T., Wilkens, R. H., Wilson, P. A., Yamamoto, Y., Yamamoto, S., Yamazaki, T. & Zeebe, R. E., 2012. A Cenozoic record of the equatorial Pacific carbonate compensation depth. *Nature*, 488: 609–614.

Pawłowski, J., Holzmann, M. & Tyszka, J., 2013. New supraordinal classification of Foraminifera: molecules meet morphology. *Marine Micropaleontology,* 100: 1–10.

Poignant, A. & Sztrákos, K., 1986. Les Foraminifères de l'Oligocène supérieur de la Formation "Ciudad Granada" (coupe de Barranco Blanco, province d'Almeria, Espagne). Comparaisons avec la microfaune de l'Oligocène hongrois. *Revista Española de Micropaleontologia,* 18: 115–129.

Popescu, G., 1999. Lower and Middle Miocene agglutinated foraminifera from the Carpathian area. *Acta Palaeontologica Romaniae*, 2: 407–425.

Rögl, F. & Müller, C., 1976. Das Mittelmiozän und die Baden-Sarmat Grenze in Walbersdorf (Burgenland). *Annalen des Naturhistorischen Museums in Wien*, 80: 221–232.

Schubert, R. J., 1914. *Pavonitina styriaca*, eine neue Foraminifere aus dem mittelsteirischen Schlier. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 64: 143–148.

Scotese, C. R., 2021. An atlas of Phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annual Review of Earth and Planetary Sciences*, 49: 679–728.

Seiglie, G. A. & Baker, M. B., 1983. Some West African Cenozoic agglutinated foraminifers with inner structures: taxonomy, age and evolution. *Micropaleontology*, 29: 391–403.

Seiglie, G. A., Fleisher, R. L. & Baker, M. B., 1986. Alveovalvulinidae, n. fam., and Neogene diversification of agglutinated foraminifers with inner structures. *Micropaleontology*, 32: 169–181.

Sztràkos, K., 1979. La stratigraphie, paléoécologie, paléogéographie et les Foraminifères de l'Oligocène du Nord-Est de la Hongrie. *Cahiers de Micropaléontologie*, 3: 1–95.

Sztràkos, K., 1982. Les Foraminifères de la Marne de Buda et la limite Éocène–Oligocène en Hongrie. *Cahiers de Micropaléontologie*, 4: 1–48.

Sztràkos, K., 1987. Le genre *Pavonitina* (foraminifère) dans le Cénozoïque européen. *Revue de Micropaléontologie,* 30: 128–138.

Van Andel, T. H., 1975. Mesozoic/Cenozoic calcite compensation depth and the global distribution of calcareous sediments. *Earth and Planetary Science Letters*, 26: 187–194.

Vrsaljko, D., Pavelić, D., Miknić, M., Brkić, M., Kovačić, M., Hećimović, I., Hajek-Tadesse, V., Avanić, R. & Kurtanjek, N., 2006. Middle Miocene (Upper Badenian/Sarmatian) palaeoecology and evolution of the environments in the area of Medvednica Mt. (North Croatia). *Geologia Croatica*, 59: 51–63.

Wade, B. S., Aljahdali, M. H., Mufrreh, Y. A., Memesh, A. M., AlSoubhi, S. A. & Zalmout, I. S., 2021. Upper Eocene planktonic foraminifera from northern Saudi Arabia: implications for stratigraphic ranges. *Journal of Micropalaeontology*, 40: 145–161.

Wade, B. S., Pearson, P. N., Berggren, W. A. & Pälike, H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Science Reviews*, 104: 111–142.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292: 686–693.