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THE FIRST RECORD OF *NEMKOVELLA DAGUINI* (NEUMANN, 1958) FROM THE MIDDLE-UPPER EOCENE OF OMAN (ARABIAN PENINSULA) AND MEGHALAYA (INDIAN SUBCONTINENT) AND ITS SIGNIFICANCE IN TETHYAN CORRELATIONS AND PALEOBIOGEOGRAPHY

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Abstract. *Nemkovella daguini* (Neumann, 1958) is a small-sized orthophragminid species previously reported from the Lutetian to lower Priabonian shelf deposits of the peri-Mediterranean region (Western Tethys). This species, originally established from the Aquitaine Basin (France), differs significantly from typical nemkovellas and other orthophragminids by having isolated adauxiliary and orbitoidal chamberlets that progressively give rise to the formation of typical annular chambers in the neanic stage. We record here for the first time this species from the lower Priabonian Tahwah Formation in the Arabian Peninsula and from the transitional middle-upper Eocene Prang Formation in Meghalaya (India), giving a detailed description and biometry. This expands the geographic range of *N. daguini* to the Eastern Tethys, allowing us to provide an enhanced scheme for the correlation of peri-Mediterranean deposits with those from the South Asia. In previous studies the majority of the larger benthic foraminiferal (LBF) fauna from this region were considered to belong to the Indo-Pacific bioprovince. The LBF in Tahwah Formation, on the other hand, are here considered to have greater affinity with those of Western Tethys based on the occurrence of *Heterostegina reticulata*, *Nummulites hormoensis*, *Assilina* gr. *schwageri-alpina*, and *Silvestriella tetraedra*. The occurrence of *Pellatispira* in this unit, represented by at least two species, shows Indo-Pacific influence in Oman.

Introduction

Orthophragminids, often associated with nummulitids, alveolinids and rotaliids, are major contributors to the upper Paleocene-Eocene benthic faunas in Tethyan shelves and platforms (Less 1987). In spite of the numerous data from the peri-Mediterranean region, the spatial and temporal records throughout the Tethys do not permit broad taxonomic, stratigraphic and paleobiogeographic evaluations. Inhomogeneous geographic distribution of data points from a large area and scarcity of taxonomic studies hamper an overall synthesis. The records of orthophragminids from the Arabian Peninsula, which occupies a transitional geographic position between the Western Tethys and the Indo-Pacific domains, are sparse and inadequate (El-Khayal 1974; Racey 1995; Beavington-Penney et al. 2006; Özcan et al. 2016; Erbay et al. 2018). Orthophragminids from the Indian subcontinent are, however, better known, but only from middle Eo-

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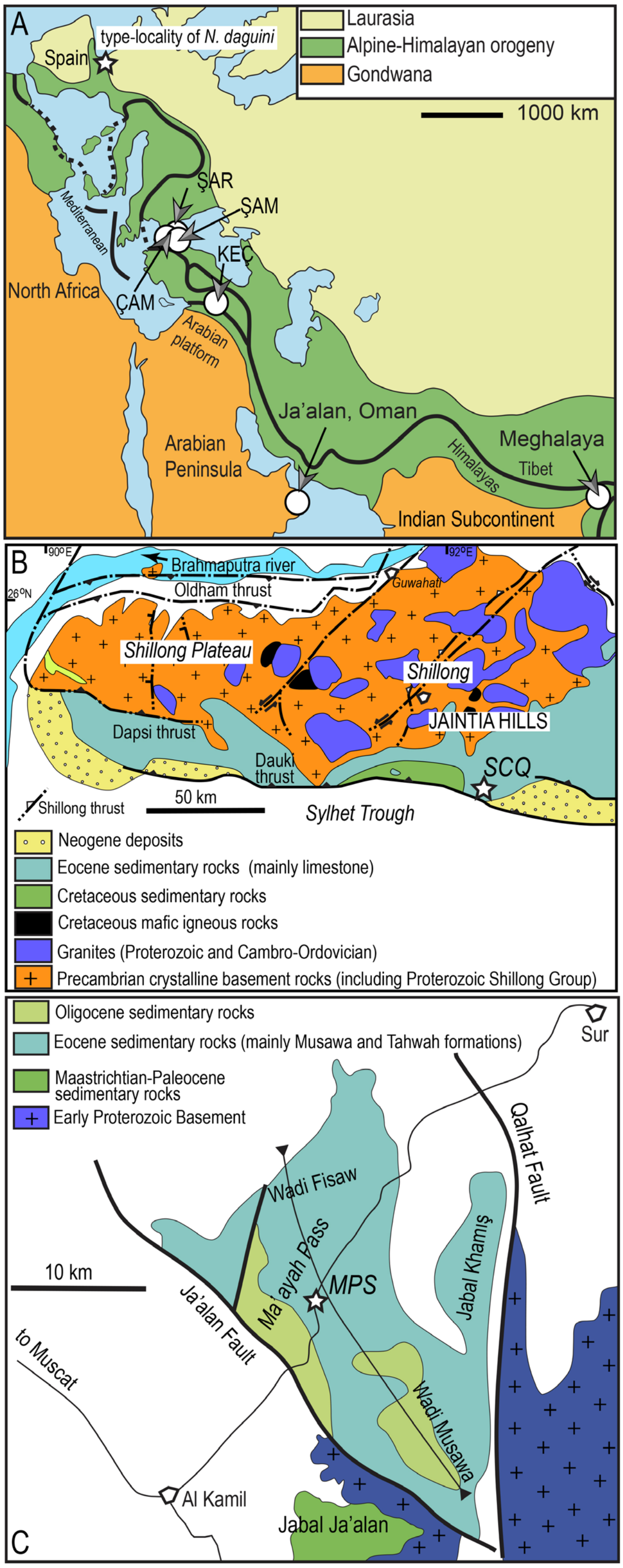


Fig. 1 - A) Alpine-Himalayan belt and location of Ja'alan region in East Oman and Star Cement Quarry in Meghalaya, North-east India. Locations of shallow-marine sections with the record of *Nemkovella daguini* in Turkey (abbreviated as ŞAR, ŞAM, ÇAM and KEÇ) and type-region of this species from the Aquitaine Basin are shown. B) Geological map of the Shillong Plateau (simplified from Yin et al. 2010). C) Geological map of the Ja'alan region to the south of Sur (simplified from Roger et al. 1991).

cene deposits, owing to the widespread middle Eocene transgression that led to the deposition of the 'Kirthar Series' with abundant orthophragminids in Pakistan and India (Sen Gupta 1963; Samanta 1964, 1965; Samanta & Lahiri 1985). The overall poor records could be explained by the fact that random sections from hard rock samples do not yield species-level taxonomic information, which requires the investigation of the morphological features in the equatorial layer of the test. This is achieved by the investigation of loose specimens, which, unfortunately, may not be available. Our recent studies of loose orthophragminid specimens from regionally widespread middle Eocene units (i.e. Fulra Limestone and Drazinda Formation) in W India and Pakistan (Özcan et al. 2018; Ali et al. 2018) and available data from the upper Middle Eocene to Priabonian Prang and Kopili formations from Meghalaya in East India (Samanta 1964, 1965) point to a significant taxonomic isolation between the Indian Subcontinent (Eastern Tethys) and the peri-Mediterranean region (Western Tethys). Studies on the Drazinda Formation and Fulra Limestone suggest that almost half of the fifteen species (lineages) in the late middle Eocene are specific to the Indian subcontinent (Özcan et al. 2018; Ali et al. 2018). The non-uniform LBF faunas along the almost E-W trending Tethyan realm, on the other hand, hamper accurate stratigraphic correlations and the establishment of a unified biostratigraphy along the Tethyan shelves and platforms. Therefore, it is important to search for faunas with a widespread latitudinal and longitudinal geographic distribution for a robust biostratigraphy and thus for more reliable Tethyan correlations.

Here, we present our records of *Nemkovella daguini* from the transitional middle-upper Eocene and lower Priabonian beds in Meghalaya (NE India) and Oman, respectively, based on the study of isolated specimens. The identification and description of the specimens relies on external and internal quantitative and qualitative features as well as the biometry of the embryos and equatorial chambers. The new records contribute to establishing and constraining the poorly known distribution of the orthophragminids in the Tethys during this time interval and provide new tools for large-scale Tethyan correlations in the light of significant longitudinal faunal variation and interactions between the 'Mediterranean' (Western Tethys) and 'Indo-Pacific' (Eastern Tethys) bioprovinces.

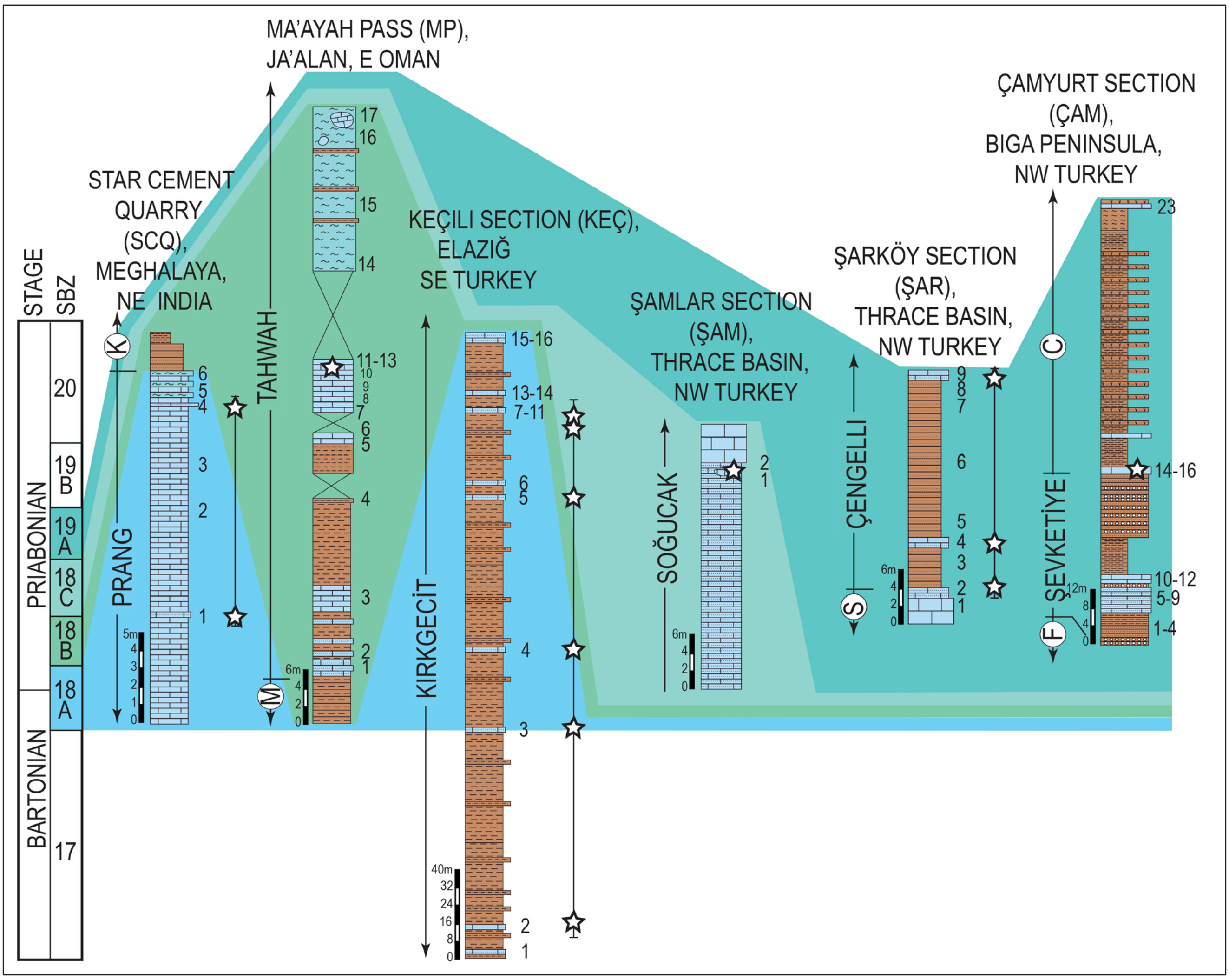


Fig. 2 - Lithostratigraphic columns of the Prang and Tahwah formations from Meghalaya (NE India) and Oman, and Kırkgeçit, Çengelli, Soğucak and Şevketiye formations from Turkey. Stratigraphic position and ranges of *N. daguini* are shown by stars. SBZ zones by Serra-Kiel et al. (1998), updated for Bartonian-Priabonian interval by Less & Özcan (2012). Boundaries of SBZ zones with respect to geological time scale after Papazzoni et al. (2017).

Geological Setting and stratigraphy

Meghalaya

The Shillong Plateau of Meghalaya, NE India consists of a Precambrian basement and Cretaceous and Cenozoic sedimentary deposits at its southern part, and forms a raised topography in the foreland of the Himalayas (Fig. 1A, B) (Biswas et al. 2007). The Paleogene succession exposed in the Southern Shillong Plateau is represented by the Paleocene fluvio-deltaic Langpar and Therria formations, consisting of fine calcareous shales with occasional limestone bands and a thick sandstone succession, and by the overlying Sylhet Limestone Group subdivided into the Lakadong, Umlatdoh and Prang formations intercalated with two mainly sandstone units (Lakadong Sandstone and Narpuh Sandstone) (Wilson & Metre 1953). These units were previously interpreted to record three marine transgressions in the late Paleocene, the early Eocene and the middle Eocene and are overlain by the upper Eocene Kopili Formation (Nagappa 1959; Jauhri & Agarwal 2001; Jauhri et al. 2016). The Prang Formation, with a variable thickness ranging between 20 and 200 meters, comprises highly fossiliferous limestone beds and argillaceous limestone at its upper part in the Jaintia Hills. In addition to LBF, coralline algae are major biotic constituents of the unit (Kishore et al. 2007; Matsumaru & Sarma 2010; Ghosh & Sarkar 2013; Jauhri et al. 2016).

Oman

Cenozoic rocks in Oman are widely exposed around Jabal Ja'alan and Wadi Musawa area. These

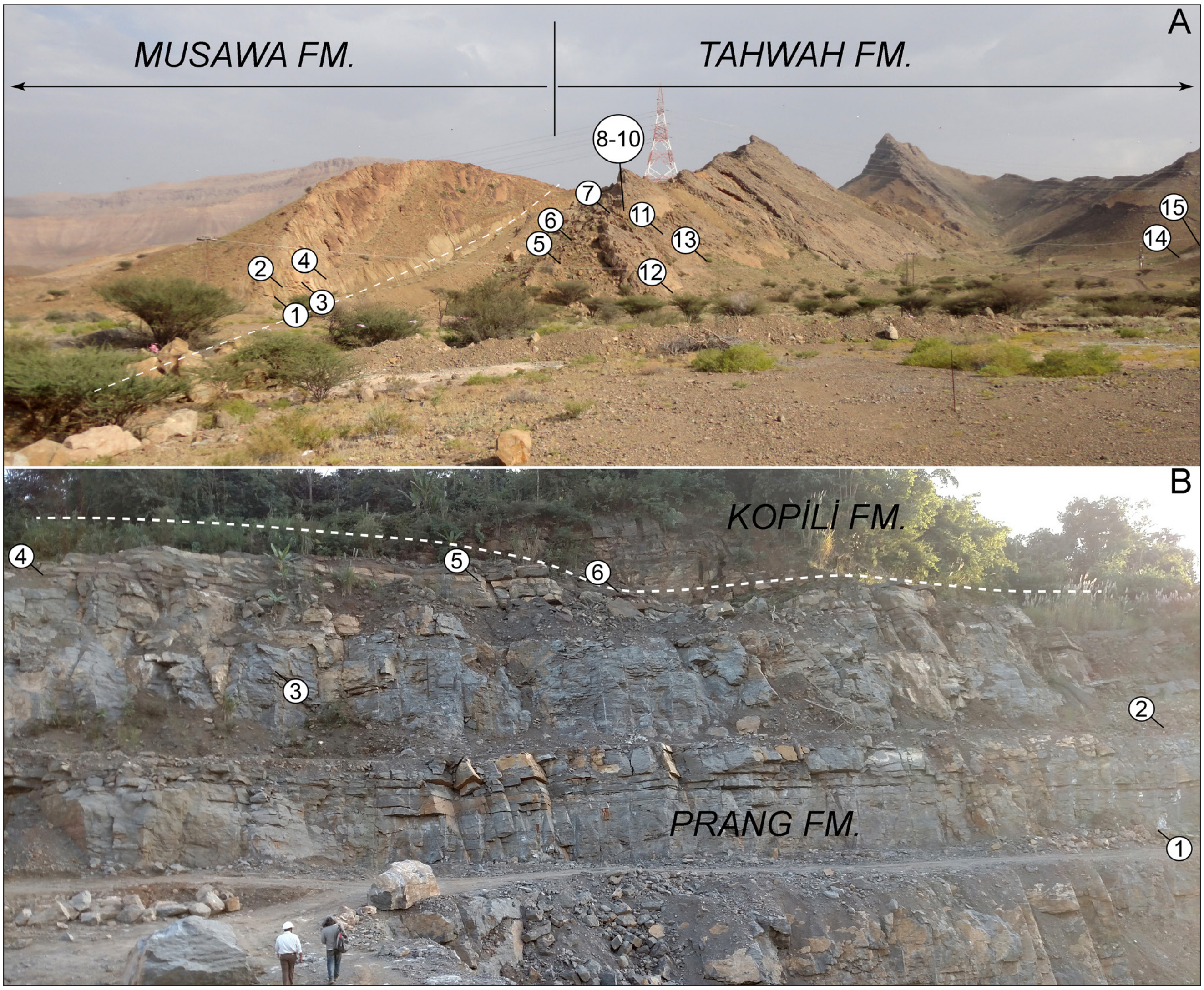


Fig. 3 - Lower part of the Tahwah (A) and upper part of the Prang formations (B) in Oman (Ma'ayah Pass, Sur) and NE India (Star Cement Quarry, Lumshnong, Meghalaya) and position of the samples.

comprise a series of carbonate and siliciclastic mixed carbonate sequences with a combined thickness of > 2000 m. At Ma' ayah Pass, the Cenozoic rocks occupy a broad syncline known as Wadi Fisaw-Wadi Musawa syncline (Fig. 1C). The Wadi Fisaw-Wadi Musawa syncline contains very thick (~1300 m) carbonate and siliciclastic-carbonate mixed rocks of the Abat, Musawa and Tahwah formations (Roger et al. 1991). The Tahwah Formation is characterized by slope deposits comprising green marl, fossiliferous calcarenite, polymictic breccia, conglomerate and olistoliths of Priabonian-early Oligocene age (Racey 1995). At Ma'ayah Pass section, the formation is over 1500 m thick. Here, the lower part of the formation comprises fine-grained calcarenite and shale-siltsone intercalations that pass to a thick calcarenitic unit with abundant LBF. Marl-siltstone alternations consisting of pelagic fauna, and olistholiths with corals and LBF are found in the upper part of the studied section.

Materials and Methods

The Tahwah Formation was logged at Ma'ayah pass, located between Al Kamil and Sur in East Oman (base of the section: 22°20'13.32"N, 59°18'43.80"E, top of the section: 22°20'2.36"N, 59°18'38.18"E) (Figs 2, 3). The outcropping succession (abbreviated here as MP) is about 70 m thick and consists of shale, siltstone, calcarenite, marl and olistoliths. *Nemkovella daguini* occurs only in sample MP11.

The Prang Formation was sampled in the Star Cement Quarry (abbreviated here as SCQ) to the southeast of Lumshnong in Meghalaya, (base of the section: 25° 9'57.86"N, 92°24'12.20"E, top of the section: 25° 9'57.30"N, 92°24'12.82"E) (Figs 2, 3). The sampled portion of the unit corresponds to the upper 20 meters of the Prang Formation and is overlain by the Kopili Formation, barren in LBF. *Nemkovella daguini* was identified only in samples SCQ1 and SCQ 4. In addition, some specimens from three sections, Şarköy (ŞAR) and Şamlar (ŞAM) in the Thrace Basin and Çamyurt (ÇAM) in the Biga Peninsula in NW Turkey, and from one section, Keçili (KEÇ) in eastern Turkey, were used in this study for the comparison of the species from Western and Eastern Tethys (Fig. 2). The detailed information on the biometry of this species from Turkey, associated LBF and age of the units are given in Özcan et al. (2006, 2018) and Less et al. (2011).

Specimens extracted from the shale, and calcarenite beds were studied for their external and internal features in equatorial and axial sections. Oriented equatorial sections of megalospheric specimens (A forms) were prepared because the most diagnostic taxonomic and evolutionary parameters are observed in this part of the test (Less 1987; Ferràndez-Cañadell 1998). Microspheric specimens were not identified in the studied material. Morphometric measurements and counts were carried out on equatorial sections of the megalospheric specimens based on Less (1987, 1998). All the studied material is deposited in the collections of Ercan Özcan at İstanbul Technical University.

Associated fauna and age of the studied sections

The Prang Formation was dated as either (late) middle Eocene (Bartonian) or middle to Late Eocene (Bartonian-Priabonian) based on the records of LBF such as *Nummulites pengaronensis* Verbeek, *N. beaumonti* d'Archiac and Haime, *Nummulites obtusus* (Sowerby), *N. acutus* (Sowerby), *Assilina papillata* Nuttall, *Discocyclina dispansa* (Sowerby), *D. undulata* (Nuttall), *D. sowerbyi* (Nuttall), *Orbitolites complanatus* Lamarck, *Alveolina* sp., *Pellatispira* spp. *Linderina* sp. (Nagappa 1959). Jauhri et al. (2016) have reported *Nummulites beaumonti* d'Archiac and Haime, *N. perforatus* (de Montfort), *N. acutus* (Sowerby), *N. striatus* (Bruguière), *Discocyclina dispansa* (Sowerby), *Alveolina elliptica* (Sowerby) in the lower part, and *N. striatus* (Bruguière), *Discocyclina dispansa* (Sowerby) and *Pellatispira* sp. in the upper part of the unit, assigning a late Eocene age (SBZ 18-19) to the upper part of the Prang Formation. Samanta (1968) studied the Siju Limestone in Garo Hills in the western Meghalaya, a carbonate unit equivalent to the Prang Limestone, and reported the associations of *Asterocyclina matanzensis* Cole, *Discocyclina javana* (Verbeek), *Discocyclina omphalus* (Fritsch), *Nummulites beaumonti* d'Archiac and Haime, *N. pengaronensis* Verbeek, *N.* sp. cf. *gizehensis* (Forskal) and *N.* sp. cf. *perforatus* from the upper part of the unit. Samanta (1968) has also reported various *Pellatispira* species such as *P. inflata* Umbgrove, *P. madaraszi* (Hantken), *P.* sp. cf. *P. irregularis* Umbgrove, and *P.* sp. cf. *P. orbitoidea* (Provale) from the overlying late Eocene Kopili Formation, suggesting a strong influence from the Indo-Pacific bioprovince in Meghalaya region. Among the orthophragminids, *Discocyclina omphalus* is the most common species, known only from Indo-Pacific region. This species was not recorded from time-equivalent units in Pakistan (Ali et al. 2018) and West India (Özcan et al. 2018). We have identified *Discocyclina omphalus* (Fritsch), *Discocyclina dispansa* (Sowerby), *Discocyclina* sp. (possibly a new stock of discocyclinids of Indo-Pacific affinity), *Asterocyclina alticostata* (Nuttall), *Pellatispira* cf. *madaraszi* (Hantken) and some small-sized *Pellatispira* sp., *Linderina* sp., *Sphaerogypsina* sp., *Operculina* sp. from the upper part of Prang Formation, which may tentatively be assigned to SBZ 18A sensu Less & Özcan (2012), suggesting an age close to the middle-upper Eocene boundary. In addition, *Nummulites* spp. and rotaliids occur abundantly. Some LBF species from the Prang Formation are illustrated in Figure 4.

Roger et al. (1991) reported *Nummulites fabianii* (Prever in Fabiani), *N. garnieri* (de la Harpe), *Silvestriella tedraedra* (Gümbel) and *Spiroclypeus* sp. in the same region of our study section, assigning a Priabonian age to the Tahwah Formation. Racey (1995) did not use this formation name in his study, but informally referred to slope and turbidite beds in the Ma'ayah Pass area as the Ma'ayh Beds. Racey assigned these beds a late middle Eocene-Oligocene (?) age based on LBF assemblages, but he did not provide details at the species level. We have identified *Heterostegina reticulata* (Rütimeyer), *Nummulites hormoensis* Nuttall & Brighton, *Silvestriella tetraedra* (Gümbel), *Discocyclina* spp., *Asterocyclina sireli* Özcan & Less, *Assilina* gr. *schwageri* Silvestri-*alpina* (Douvillé), *Linderina* sp. and two types of *Pellatispira, P. madaraszi* (Hantken) and *P.* cf. *inflata* Umbgrove in the studied section of the Tahwah Formation (Fig. 4). We also identified *Spiroclypeus*, a marker genus for the Priabonian in the Western Tethys, in another locality from the same unit, but not in the studied material. On morphometric grounds, *H. reticulata* belongs to a primitive developmental stage of the species, *H. reticulata* ex. interc. *hungarica-tronensis* after Less & Özcan (2012). The records of primitive members of *Heterostegina reticulata* lineage and morphometric features of reticulate *Nummulites* (assigned to *N. hormoensis* with mean proloculus diameters of 167.0 and 157.4 µm based on 5 and 23 specimens from samples MP11 and MP12 respectively) suggest SBZ 18B (lowermost Priabonian) for the studied part of the Tahwah Formation.

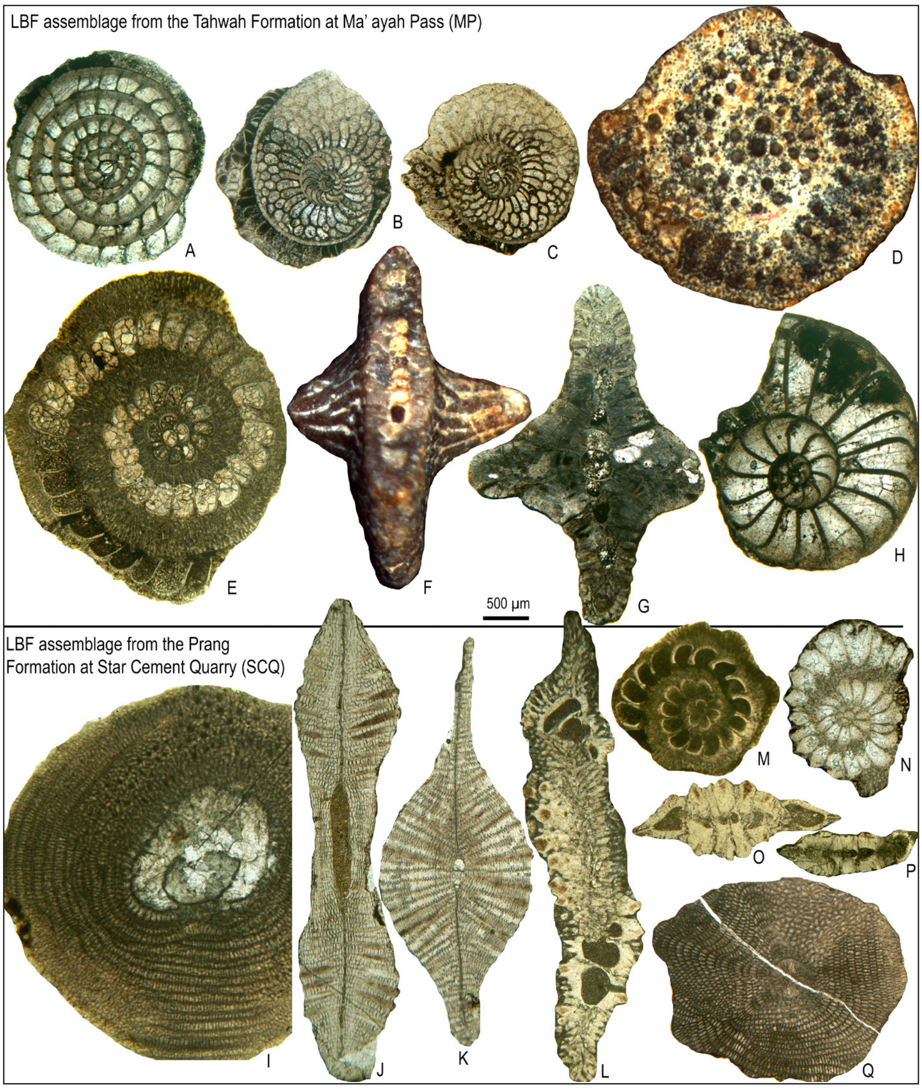


Fig. 4 - Stratigraphically important LBF from the Tahwah (A–H) and the Prang formations (I–Q). A) *Nummulites hormoensis* Nuttall & Brighton, MP11-94. B-C) *H. reticulata* ex. interc. *hungarica-tronensis* Less, Özcan, Papazzoni, Stockar, B: MP12-63, C: MP12-14. D-E) *Pellatipira madaraszi* Hantken, external view and equatorial section of the same specimen, MP12-5. F-G) *P.* cf. *inflata* Umbgrove, external view and equatorial section of the same specimen, MP12-38. H) *Assilina* gr. *schwageri* Silvestri-*alpina* (Douvillé), MP12-38. I-J) *Discocyclina omphalus* (Fritsch), I: equatorial section, SCQ5-2, J: axial section, SCQ4-21. K) *Discocyclina dispansa* (Sowerby), SCQ6-28. L) *P.* cf. *madaraszi* Hantken, microspheric (?) form, SCQ2-25. M-P) *Pellatispira* sp. 2 (with small test and proloculus), megalospheric forms, M, N: equatorial, O, P: axial sections. M: SCQ1-80, N: SCQ2-26, O: SCQ2-2, P: SCQ1-74. Q) *Asterocyclina alticostata* (Nuttall), SCQ1-1.

Morphology of *Nemkovella daguini*

Nemkovella daguini has a typical orthophragminid test with a smooth test surface (without ribs). The species consists of equatorial and lateral layers with chambers, chamberlets, and pillars (piles) piercing the lateral layers on both sides of the test (Less 1987; Özcan et al. 2006). Though this species do not possess ribs on the exterior of the test, equatorial sections reveal a characteristic wavy pattern, as observed in the ribbed orthophragminid species. Some unribbed orthophragminid taxa, such as *Orbitoclypeus varians* (Kaufmannn), also develop wavy pattern in the equatorial layer in the lack of ribs (Özcan et al. 2006). Although *Nemkovella daguini* shares the similar overall morphologic features with most Tethyan orthophragminids, it differs from them in:

a) having few (1 to 3) isolated adauxiliary chamberlets arising from the deuteroconch, and short spiral chambers on the protoconchal side (Fig. 5A-C). Except for some species of genus *Asterocyclina* Gümbel, which is characterized by the ribs in the test, almost all known orthophragminids species possess a number of adauxiliary chamberlets connected to each other by a common wall (Less 1987).

b) having characteristic orbitoidal chamberlets (similar to chamberlets in the Late Cretaceous genus *Orbitoides*) before the development of annular chambers in the equatorial layer. These chamberlets are isolated, not sharing a common wall. Thus, annular chambers, typically formed at the very early stage in most orthophragminids, are lacking here and substituted by orbitoidal chamberlets.

Similar orbitoidal chamberlets are only known from *Nemkovella stockari*, an earliest Eocene species in Tethys (Özcan et al. 2016), which has been recently referred to genus *Hexagonocyclina*

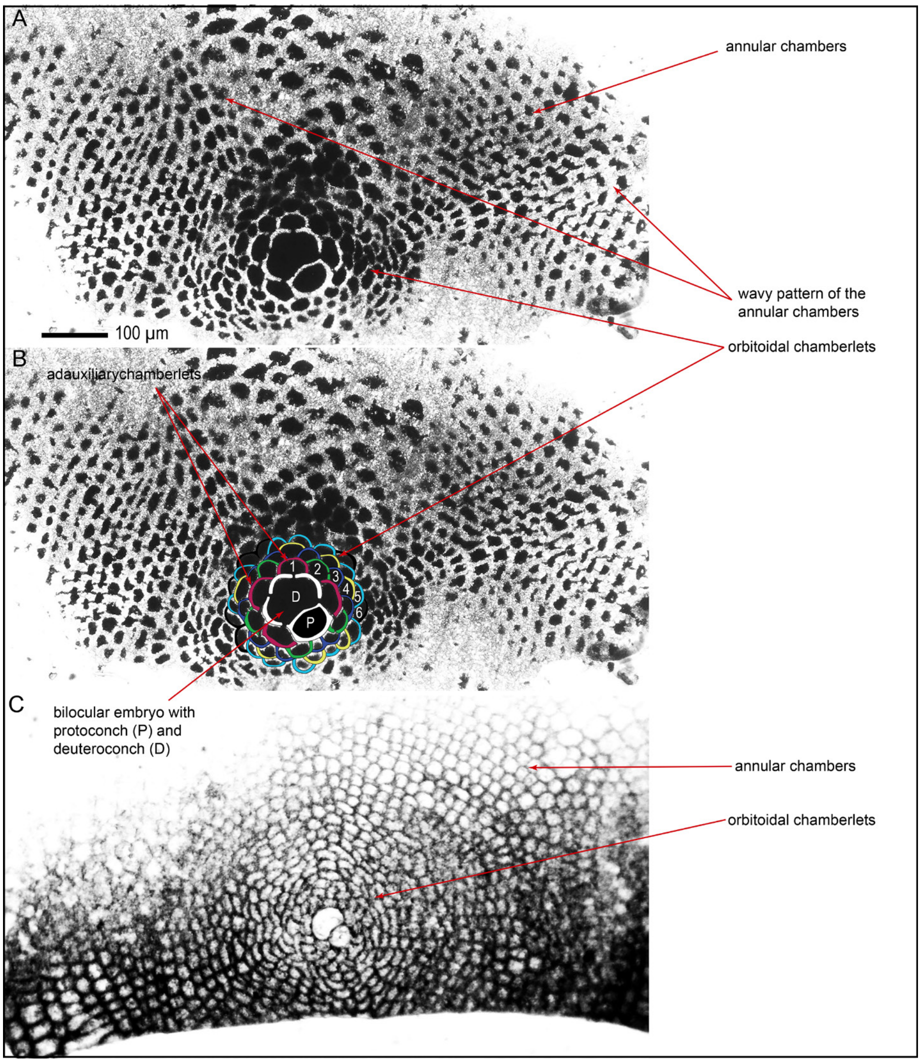


Fig. 5 - Sections through the equatorial layers of megalospheric *Nemkovella daguini* (Neumann) showing the small almost isolepidine-type embryo, early orbitoidal chamberlets, and transition from orbitoidal chamberlets to annular chambers (A–C). Orbitoidal chamberlets formed at one growth step (up to 6^{th} growth step) are illustrated by the same colour in B. These specimens possess two isolated adauxiliary chamberlets. All specimens are from the Bartonian-Priabonian Kırkgeçit Formation, Keçili Section, Turkey. A-B) KEÇ11-8. C) KEÇ3-49.

Caudri from the Caribbean bioprovince (Özcan et al. in press). In fact, *N. daguini* differs from true nemkovellas by the presence of orbitoidal chamberlets, while its microspheric generation with a discocyclinid type embryo and hexagonal equatorial chamberlets both in megalo and microspheric specimens suggest an affinity with the genus *Nemkovella* Less, 1987.

Systematic Paleontology

The suprageneric classification of orthophragminids by Less (1987, 1998) and Özcan et al. (2006) has been followed herein.

Order **Foraminiferida** Eichwald, 1830
Family Discocyclinidae Galloway, 1928
Genus *Nemkovella* Less, 1987

Nemkovella daguini (Neumann, 1958)

Figs 5A–C, 6A–H, 7A–K, 8, 9A–H, 10A–I, 11A–E

1958 *Discocyclina daguini* n. sp; Neumann, p. 89, pl. 17, figs. 7–10.
1987 *Orbitoclypeus daguini* (Neumann, 1958); Less, p. 222-224, pl. 36, figs. 1–6, text figs. 31 a and b (with synonymy).
1989 *Orbitoclypeus daguini* (Neumann, 1958); Less, pl. III, figs. 1, 2.
2006 *Nemkovella daguini* (Neumann, 1958); Özcan et al., pl. 2, figs. 1-4, pl. 3, fig. 14, pl. 5, fig. 6, text fig. 12.
2011 *Nemkovella daguini* (Neumann, 1958); Less et al., fig. 34k.
2012 *Nemkovella daguini* (Neumann, 1958); Less & Özcan, fig. 10c.
2018 *Nemkovella daguini* (Neumann, 1958); Özcan et al., fig. 14H.

Description. The test is small, strongly inflated without ribs (Fig. 6A-C). Test diameter varies between 0.78 and 1.18 mm, with an average of 0.98 mm (based on 45 specimens) in Oman and between 0.82 and 1.31 mm, with an average of 1.12 mm (based on 18 specimens) in Meghalaya specimens. Test thickness varies between 0.5 and 0.6 mm. The pillars are ca. 60-70 µm in diameter in the central part of the test and polygonal in outline, they are

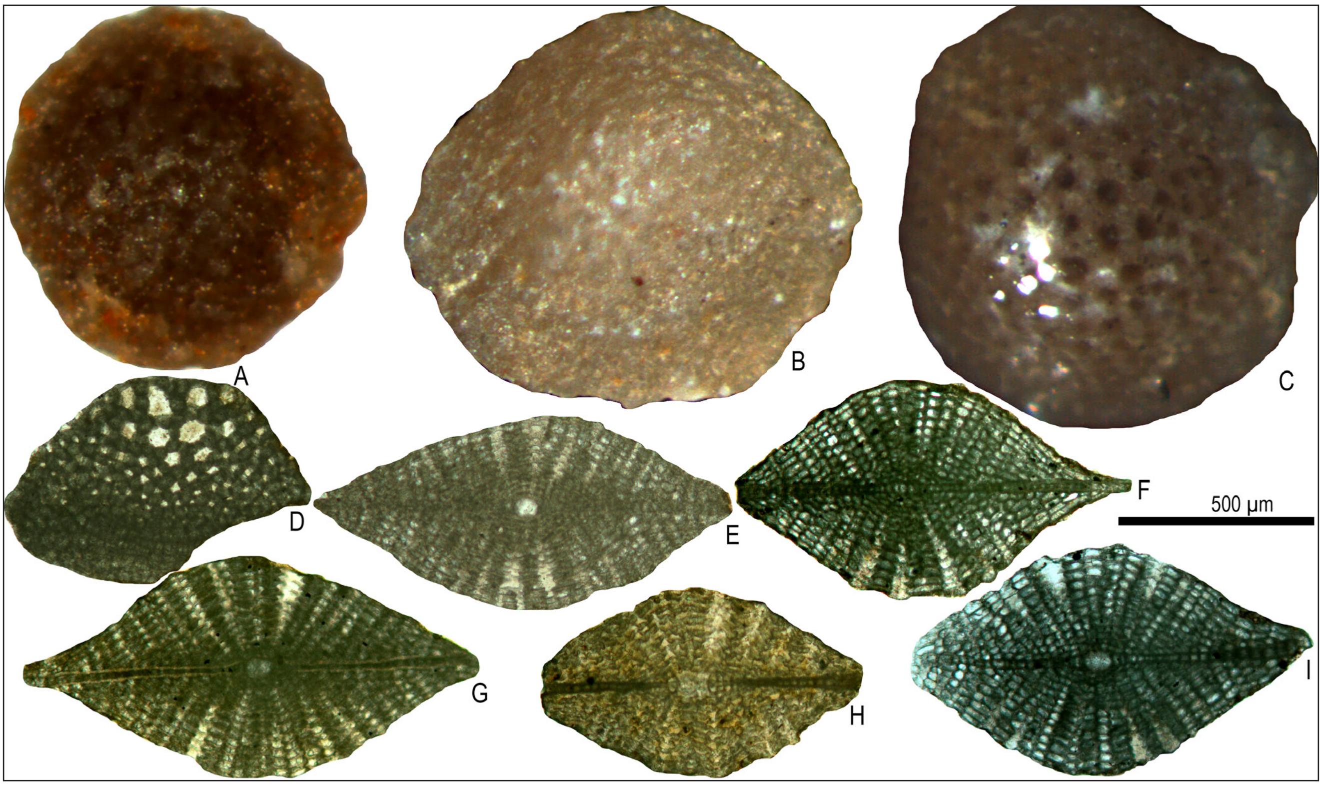


Fig. 6 - Megalospheric specimens of *Nemkovella daguini* (Neumann) from the Tahwah (A, F, I), Prang (B-E, G) and Çengelli (H) formations, A-C) external views. D) tangential section showing the polygonal pillars. E-I) axial sections. A: MP11-13, B: SCQ1-9, C: SCQ1-9, D: SCQ4-19, E: SCQ4-11, F: MP11-28, G: SCQ1-2a, H: ŞAR4-114, I: MP11-88. Note the coarser polygonal pillars on the central part of the test. Abbreviations: MP; Ma'ayah Pass, SCQ; Star Cement Quarry, ŞAR: Şarköy.

larger in the umbo and hardly observed at the peripheral part of the test (Fig. 6C, D). The embryo displays almost iso- to nephrolepidine type configuration with a very small, spherical protoconch varying in diameter between 30 and 70 µm, followed by a slightly larger deuteroconch varying in diameter between 50 and 100 µm (Table 1). The pre-annular stage includes auxiliary, adauxiliary and orbitoidal chamberlets. Two auxiliary chamberlets, comparatively larger than the nearby orbitoidal chamberlets at the junction of the protoconch and deuteroconch are tangentially elongated and similar in size and shape to the adauxiliary chamberlets. The adauxiliary chamberlets are arcuate in shape, radially low (10-25 µm), tangentially wide (25-50 µm), and are isolated from each other leading to the development of orbitoidal chamberlets. The number of adauxiliary chamberlets ranges between 1 (?) and 2 (most specimens have only 2 such chamberlets with only one specimen with questionable 3 such chamberlets). The chamberlets following the auxiliary chamberlets on the protoconchal side form very short spirals. The arrangement of the equatorial chamberlets around the deuteroconch is typically

		Outer cross diameter of the embryon				Adauxiliary chamberlets			Equatorial chamberlets		Species
		deuteroconch		protoconch		number	height	width	height	width	
SAMPLE	N	D		P		A	H	W	h	w	
		range	mean±s.e.	range	mean	range	range	range	range	range	
MP11	45	50-85	70.78±1.04	30-55	47.27	1?-2	10-25	25-45	30-80	15-30	*Nemkovella daguini*
SCQ1	18	50-100	77.50±2.70	35-70	51.11	2	20-25	25-50	30-90	12-30	

Tab. 1 - Statistical data for *Nemkovella daguini* (Neumann) from the Tahwah and Prang formations.
P and D: outer diameter of the protoconch and deuteroconch (including the wall thickness) perpendicular to their common axis; A: number of adauxiliary chamberlets; H and W: height and width of the adauxiliary chamberlets; and h and w: height and width of the equatorial chamberlets around the peripheral part of the equatorial layer. N denotes number of specimens.

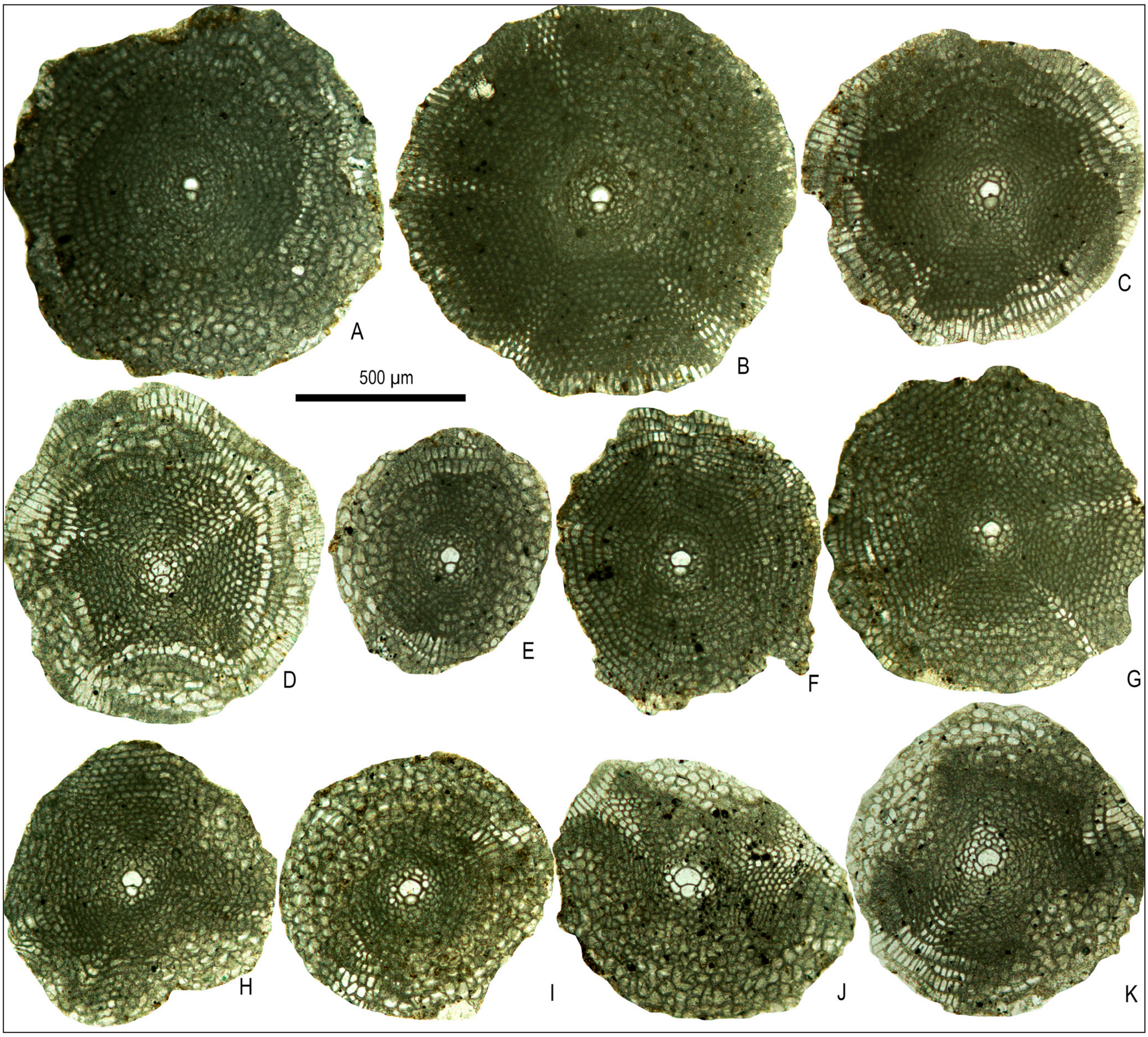


Fig. 7 - Megalospheric specimens of *Nemkovella daguini* (Neumann) from the Tahwah Formation in Ma'ayah pass, equatorial sections. A) MP11-98. B) MP11-25. C) MP11-136. D) MP11-126. E) MP11-118. F) MP11-122. G) MP11-129. H) MP11-125. I) MP11-124. J) MP11-134. K) MP11-128.

orbitoidal ("daguini" type of Less 1987). Annular growth is attained in the successive growth stages following the orbitoidal chamberlets. The annular chamberlets are low, hexagonal, progressively tend to become rectangular (15-30 µm wide and 90 µm high) towards the periphery. Most of the specimens possess wavy annuli, at least in the early part of development; their number varies between 4 and 6. This wavy pattern is attenuated with successive growth and latest equatorial chamberlets are in regular annuli with circular outline.

In axial section (Fig. 6D-H), the height of the protoconch and deuteroconch is about 60 and 65 µm, respectively. The equatorial layer is always flat, and its thickness increases progressively towards the periphery. The thickness of this layer is 20 µm in early stage and 40/45 µm at the peripheral chambers.

Microspheric generation was not found in this study. A single microspheric specimen was illustrated previously (Özcan et al. 2006; pl. 3, fig. 14) from the Şarköy Section in NW Turkey and suggests that this species should be attributed to genus *Nemkovella* Less rather that *Orbitoclypeus* Silvestri as suggested by Less (1987, 1998). The megalospheric specimens, however, differ from typical nemkovellas lacking orbitoidal chamberlets.

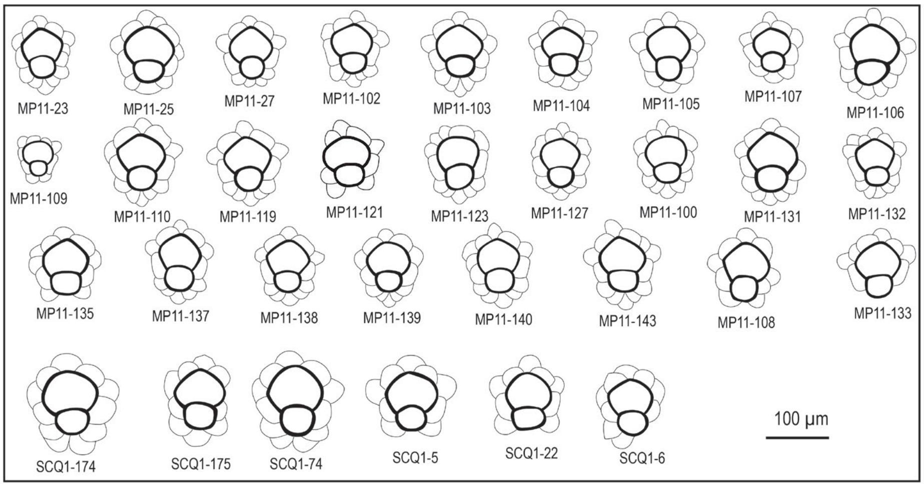


Fig. 8 - Embryo and peri-embryonic chambers/chamberlets and their variation in megalospheric *Nemkovella daguini* (Neumann) from the Tahwah and Prang formations.

Remarks. *Nemkovella daguini* has a complex taxonomic history as it was assigned to *Discocyclina* Gümbel, *Orbitoclypeus* Silvestri and *Nemkovella* Less by Neumann (1958), Less (1987), and Özcan et al. (2006) respectively. The adauxiliary chamberlets, peri-embryonic chambers, and thus, orbitoidal chamberlets, are not clearly seen in the equatorial section illustrated by Neumann. Due to lack of holotype, Less (1987) designated a lectotype illustrating the external view of the species from the Neumann's material (Less 1987; p. 222) and affiliated this species with genus *Orbitoclypeus* after observing that the species lacks the annular stolons. This species is distinct from most Tethyan orthophragminid taxa in having key morphological characters including the isolated adauxiliary chamberlets, and orbitoidal chamberlets of the equatorial layer, facilitating its recognition in the equatorial sections. Because the test is very small (representing one of the smallest-sized orthophragminid taxa in the Tethys), it is easily missed in thin sections studies. The placement of the species in the genus *Nemkovella* by Özcan et al. (2006) follows the discovery of a microspheric specimen from Priabonian deposits in Turkey with a discocyclinid- type juvenarium, although, otherwise, the megalospheric forms display different chamber development than the typical nemkovellas, lacking orbitoidal chamberlets. The wavy pattern in the equatorial layer in the genus *Nemkovella* was only illustrated from a ribbed species of the genus, *N. rota* Ferràndez-Cañadell (Ferràndez-Cañadell 1997), whereas unribbed species, such as, *N. strophiolata* (Gümbel, 1870) and *N. evae* Less, 1987, never display this feature. Thus, the assignment of this species to genus *Nemkovella* Less appears to remain controversial. In addition, the available information also suggests that all the other nemkovellas were confined only to the peri-Mediterranean region and never inhabited the Indian Subcontinent (Eastern Tethys) and Pacific region (Less 1987; Ali et al. 2018 and Özcan et al. 2018). Here, we maintain the taxonomic concept of Özcan et al. (2006) and provisionally accommodate our specimens in *Nemkovella* Less, providing that further studies, specifically on the microspheric generation, are required to reevaluate the taxonomic position of this species.

Nemkovella daguini shows some similarities in the equatorial section to *Discocyclina sulaimanensis* Özcan, Ali, Hanif, a Bartonian species known from Pakistan (Özcan et al. 2016), which is diagnosed to have a small, inflated test with a thick centrally- depressed umbo and an elevated ring-like structure (Özcan et al. 2016; fig. 11). Thus, the two species, despite being almost the same dimensions, are easily differentiated externally. In equatorial sections, the small embryo (with protoconch and deuteroconch diameters varying from 35 to 50 and 50 to 75 µm respectively) of this species is very similar to *N. daguini* in having a rounded to nearly- rounded protoconch and semi- rounded slightly larger deuteroconch displaying a semi-isolepidine or nephrolepidine type configuration (Fig. 10C-H). The pre-annular stage is characterized by notably large auxiliary chambers, elongated parallel to the common axis of embryonic chambers, and by the presence of few isolated adauxiliary chamberlet(s) (most commonly only one such chambers) (Fig. 10D, F, G-H). Contrary to *Nemkovella daguini*, orb-

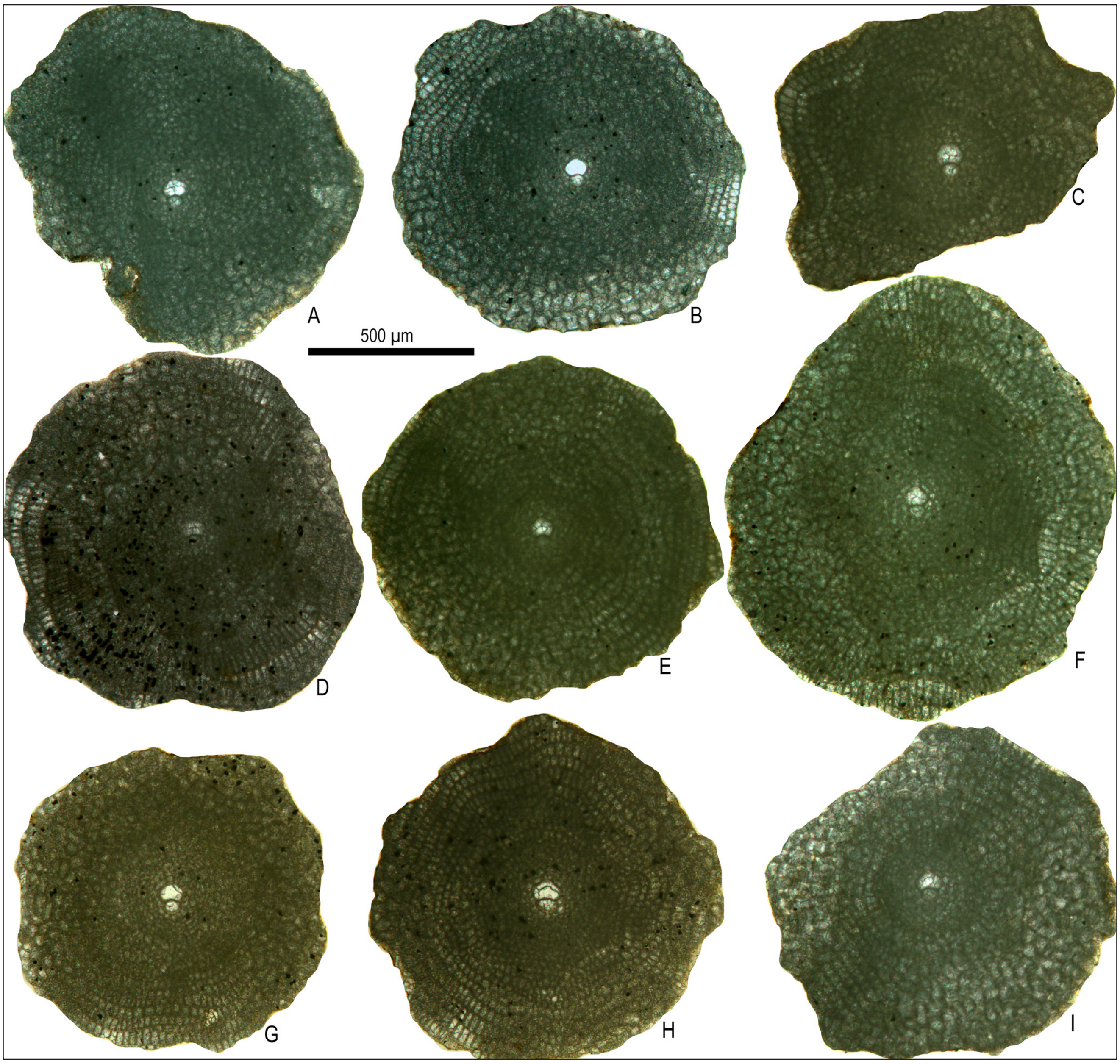


Fig. 9 - Megalospheric specimens of *Nemkovella daguini* (Neumann) from the Prang Formation, equatorial sections. A) SCQ1-5. B) SCQ1-6. C) SCQ1-10. D) SCQ1-9. E) SCQ1-13. F) SCQ1-26. G) SCQ1-23. H) SCQ1-25. I) SCQ1-14.

itoidal chamberlets are not formed in *D. sulaimanensis*. The first annulus is usually formed after the formation of auxiliary chambers (3 th growth stage), and occasionally it may be formed at the 4th stage. The annular chambers, in contrast to those of *N. daguini*, are regular and circular in outline (Fig. 10C, E). The adult equatorial chamberlets in *D. sulaimanensis* are rectangular (with straight distal sides) due to the presence of annular stolons (well visible in Figs 10D-E), while those of *N. daguini* are hexagonal because of the lack of such stolons.

Stratigraphic range of *N. daguini* and paleobiogeographic inferences

Neumann (1958) established *N. daguini* from Lutetian beds in Préchacq, Landes, France, proposing its stratigraphic range as Ypresian-late middle Eocene (Bartonian). All the illustrations given by the author (Fig. 24 and Pl. 13, figs. 7-10) are, however, from the upper Lutetian beds. The oldest record of this species with illustrations comes from Saint-Barthélémy, Maisonnave in France by

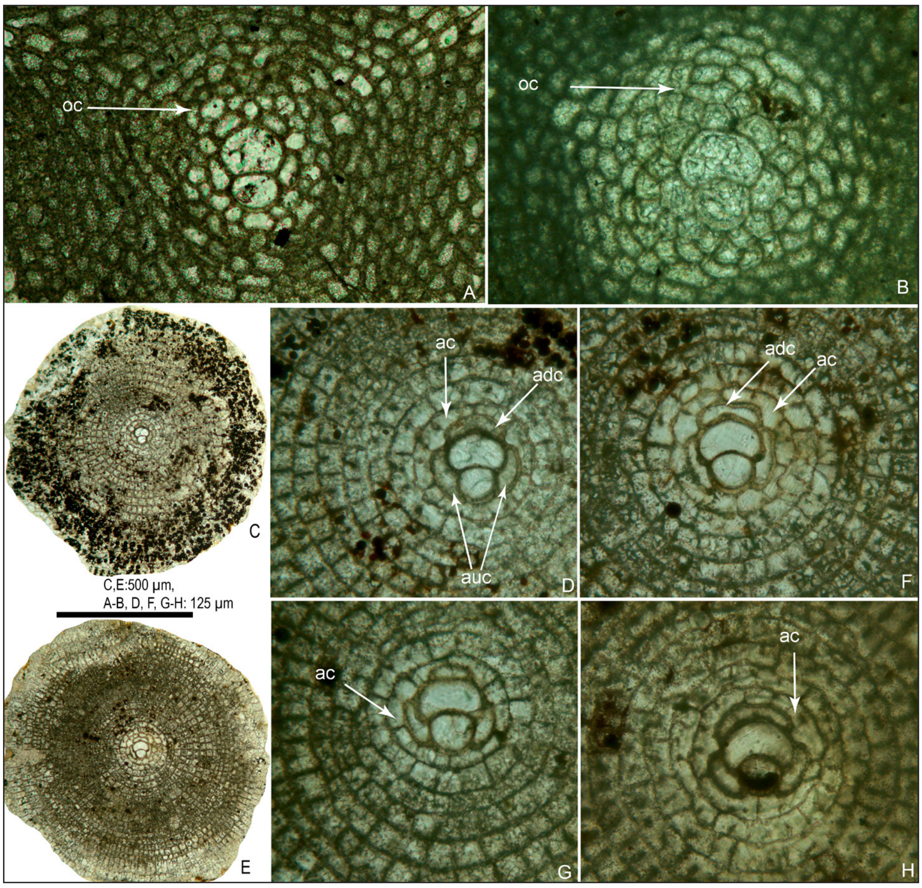
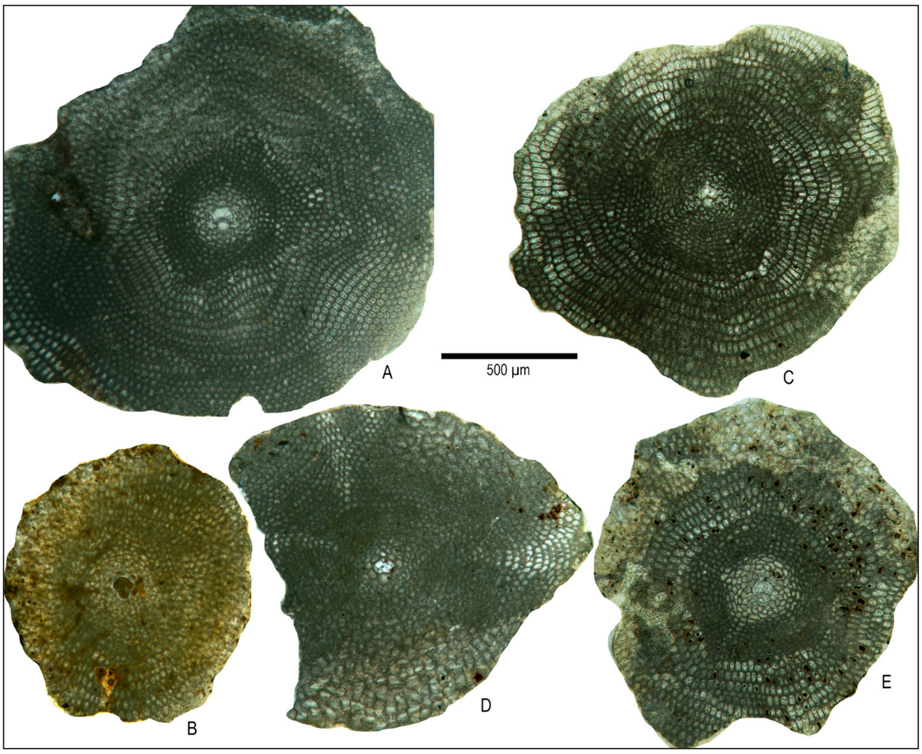


Fig. 10 - Comparison of the equatorial sections of *Nemkovella daguini* (Neumann) (A–B) and *Discocyclina sulaimanensis* Özcan, Ali, Hanif from the Bartonian of Pakistan (C–H). Note that the first annulus in *D. sulaimanensis* is formed as early as the 3th growth step following the auxiliary and adauxiliary chamberlets (also compare these with the chamber formation in *N. daguini* in Figure 5). A) MP11-126. B) KEÇ10-9. C-D) ZP10-1. E-F) ZP10-11. G) ZP10-8. H) ZP12-17. ac: annular chambers, oc: orbitoidal chamberlets, adc: adauxiliary chamberlets, auc: auxiliary chamberlets. ZP: Zinda Pir section in Ali et al. (2018).

Less (1987) who assigned these beds to the orthophragminid zone (OZ) 8a, implying a late Ypresian age. *Nemkovella daguini* was later recorded from the upper Lutetian-lower Priabonian (SBZ 16-18B) of Hungary (Less 1987, 1998; Less & Özcan 2012), from the lower Priabonian (SBZ 18) of Pyrenean foreland Basin, NE Spain (Serra-Kiel et al. 2003), and from the Bartonian- lower Priabonian (SBZ 17-19) of Thrace and Elazığ basins in Turkey (Özcan et al. 2006, 2018; Less et al. 2011). In addition, the occurrence of this species, though not published, was reported from the Priabonian (SBZ 19A) of Verona, Castel S. Felice (Italy) and from the Priabonian (SBZ 20) of Biarritz, Lou Cachaou (France) (per. com., Gyorgy Less 2018). Most of the records, thus, come from the Bartonian and Priabonian of the Western Tethys.

The geographic distribution of middle to upper Eocene LBF in the Tethyan domain is poorly known at species-level, whereas the genus-level distribution has been comparably well-established (Adams 1983; Fleury et al. 1985; Serra-Kiel et al. 1998; Renema 2007). From previous studies, it appears that *Pellatispira* and some nummulitids are the most useful groups in the recognition of the Mediterranean and Indo-Pacific bioprovinces covering an area between the Mediterranean region to West Pacific (Samanta 1968a, b; Adams 1983; Fleury et al. 1985). Samanta (1968a) provided the most comprehensive data-set, although a species-level revision is certainly needed, for the orthophragminids from the Priabonian of Assam region (western Meghalaya) showing that certain species of this group belong to the Indo-Pacific fauna. Similarly, *Pellatispira* species recorded by Samanta (1968b), *P. inflata*, *P.* sp. cf. *P. irregularis*, *P. madaraszi*, *P.* sp. cf. *P. orbitoidea,* suggest Indo-Pacific affinity since only *P. madaraszi* occurs in the peri-Mediterranean region (Fleury et al. 1985; Serra-Kiel et al. 1998). Recently, the presence of a notable number of endemic species from the Indian Subcontinent was recorded from the Bartonian of the Sulaiman Range in Pakistan and the Kutch Basin in West India (Ali et al. 2018; Özcan et al. 2018). *Nemkovella daguini* was not recorded in these extensively studied regions. It is suggested here that this species may have immigrated to the South Asia in latest Bartonian-earliest Priabonian times. Adams (1983) differentiated three major LBF bioprovinces globally, the Mediterranean, Indo-West Pacific and Central American, for much of the Cenozoic (Ad-

Fig. 11 - Megalospheric specimens of *Nemkovella daguini* (Neumann) from the Çengelli, Şevketiye and Kırkgeçit formations in Turkey, equatorial sections, A) ÇAM14-25. B) ŞAR4-47. C) KEÇ6-1. D) KEÇ11-11. E) KEÇ10-9. Abbreviations: ÇAM: Çamyurt, ŞAR: Şarköy, KEÇ: Keçili.



ams 1983) (Fig. 12), though this scheme essentially reflects post-Eocene faunal provincialism. The boundaries of these bioprovinces were dynamic, with the most dramatic change after the closure of the Tethyan Sea way connecting the Mediterranean Sea and Indian Ocean during the early Miocene (Rögl 1999; Less et al. 2018). Our record of *N. daguini* from Oman and Meghalaya (NW India) expands its geographic range from the Aquitaine Basin in France as far as south of the Himalayan Range in South Asia, which belongs to Indo-Pacific province (Fig. 12). The occurrence of this species in the eastern part of the Indian Subcontinent (Eastern Tethys) is noteworthy as it provides a useful tool for Tethyan correlations in the light of the fact that Eocene LBF faunas of this region have most affinities to the Indo-Pacific bioprovince.

Discussion and Conclusions

Nemkovella daguini, a small-sized unribbed orthophragminid species previously known from the peri-Mediterranean region, is recorded for the first time from the upper Bartonian-lower Priabonian transitional (SBZ 18a) and earliest Priabonian (SBZ 18b) shallow marine beds from Meghalaya (NE India, South Asia) and Oman (Arabian Peninsula). This expands its geographic range in the Tethys, extending it from the Aquitaine Basin in France to Meghalaya in South Asia during late Bartonian-early Priabonian times. The occurrence of *N. daguini* in a wide area, both in Mediterranean and Indo-Pacific bioprovinces, enhances the possibility of stratigraphic correlations of the shallow marine deposits of this period. As the present shallow benthic zonation (SBZ of Serra-Kiel et al. 1998) mostly relies on the biostratigraphic data from the peri-Mediterranean region, a detailed description of orthophragminids as well as associated LBF from Indian Subcontinent would further contribute to the characterization of the coeval SBZ zones in Indo-Pacific region and their application in South Asia. The unribbed species *N. daguini* differs from typical nemkovellids and all species of the genera *Discocyclina* Gümbel, *Orbitoclypeus* Silvestri and *Asterocyclina* Gümbel in having orbitoidal chamberlets in the equatorial layer of the megalospheric specimens. *Nemkovella daguini* bears some resemblance only to the species of genus *Hexagonocyclina* Caudri, known from the Caribbean (Central American) bioprovince, that has been recently recorded from the peri-Mediterranean region after the assignment of *Nemkovella stockari* Özcan and Less to *Hexagonocyclina* (Özcan et al. in press). The microspheric generation of *Hexagonocyclina*, however, consists of a or-

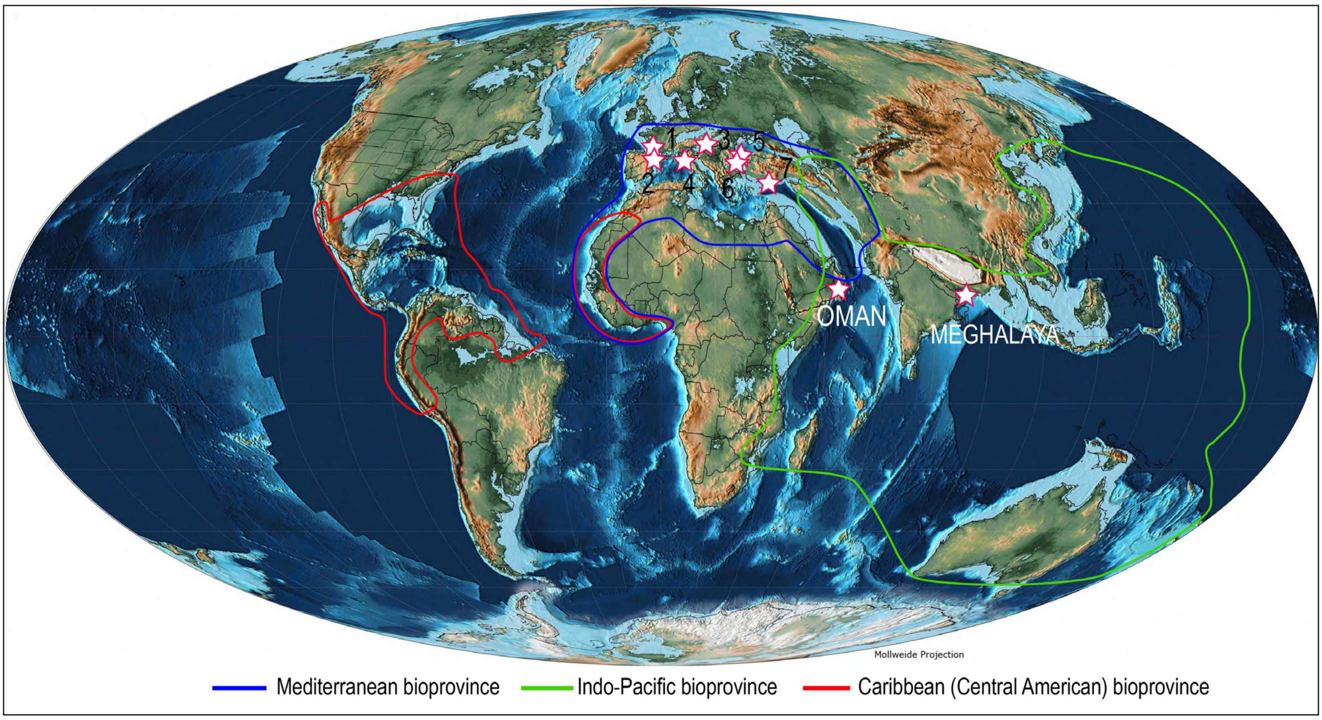


Fig. 12 - Paleogeographic distribution of *Nemkovella daguini* (Neumann) on late middle Eocene base map. LBF bioprovinces and their distribution during much of the Tertiary are from Adams (1983). 1) Aquitaine Basin, France: Neumann (1958). 2) Pyrenean Foreland Basin, Spain: Serra-Kiel et al. (2003). 3) Hungary: Less (1987, 1998), Less & Özcan (2012). 4) Verona, Italy: per. com. with G. Less, 2018. 5) Thrace Basin, NW Turkey: Özcan et al. (2006), Less et al. (2011). 6) Biga Peninsula, NW Turkey: Özcan et al. (2018). 7) Elazığ, E Turkey: Özcan et al. (2006). Position of Oman and Meghalaya localities are shown. Paleogeographic map is from Scotese (2014).

bitoclypeus-type juvenarium (Özcan et al. in press), whereas *N. daguini* consists of a discocyclinid-type. This species was assigned to the genus *Nemkovella* Less by Özcan et al. (2006) after observing the discocyclinid type juvenarium and the presence of spatulate to hexagonal chamberlets, characteristics for *Nemkovella* but not of *Discocyclina*. Further studies pending, *Nemkovella* presently appears to be the most appropriate genus to accommodate 'daguini' type specimens, even if they differ from typical nemkovellas such as *N. strophiolata* (Gümbel) and *N. evae* Less (Less 1987, 1998). Moreover, the typical nemkovellas have never been reported from South Asia. The lack of this genus in the Bartonian of Sulaiman Range in Pakistan and in the Kutch Basin (Özcan et al. 2018) further supports that other nemkovellas are only confined to the peri-Mediterranean region.

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