Zoological Studies **65:**21 (2026)
doi:10.6620/ZS.2026.65-21

Zoological Studies

Open Access

First Fossil *Faorina* (Echinoidea: Spatangoida) from the Bhuban Formation (Miocene), Northeastern India

Chia-Hsin Hsu[1], Lalramengi Fanai[2], Kongrailatpam M. Sharma[3], Malsawmtluanga[4], Jehova Malsawma[2], Paul Lalnuntluanga[2], Raghavendra P. Tiwari[5], Rajeev Patnaik[6], Ammu Sankar Senan[7], and Jih-Pai Lin[7],*

[1]School of Ocean and Earth Science, University of Southampton, Southampton, SO14 3ZH, UK.
E-mail: chiahsinhsu01@gmail.com (Hsu)
[2]Department of Geology, Mizoram University, Mizoram, 796004, India. E-mail: mami18fanai@gmail.com (Fanai); jmvalpuia@gmail.com (Malsawma); paultluanga@gmail.com (Lalnuntluanga)
[3]Department of Geology, Central University of South Bihar, Gaya, 824236, India. E-mail: milankumar.sharma@gmail.com (Sharma)
[4]Lunglei Government College, Government of Mizoram, Mizoram, 796701, India.
E-mail: mstmzu.gps@gmail.com (Malsawmtluanga)
[5]Department of Geology, Central University of Punjab, Bathinda, 151401, India.
E-mail: rptmzu@rediffmail.com (Tiwari)
[6]Department of Geology, Panjab University, Chandigarh, 160014, India.
E-mail: rajeevpatnaik@gmail.com (Patnaik)
*[7]Department of Geosciences, National Taiwan University, Taipei 106319, Taiwan. *Correspondence: E-mail: alexjplin@ntu.edu.tw (Lin).*
E-mail: ammusankars93@gmail.com (Senan)

urn:lsid:zoobank.org:pub:29A66379-FAC8-4E5F-8818-C9C1B3EB38C8
Received 13 October 2025 / Accepted 7 March 2026 / Published 13 May 2026
Communicated by Chien-Hsiang Lin

Heart urchins of the genus *Faorina* are now endemic to the Indo-West Pacific, but their fossils were previously known from the Miocene of Mediterranean, indicating a wider geographic distribution in the past. Here we describe *Faorina mizoramensis* sp. nov. from the Lower to Middle Miocene Bhuban Formation (Surma Group) in northeastern India, identified by their meridoplacous plating in interambulacrum 1 adorally. These fossils demonstrate that the distribution of *Faorina* had reached the eastern Indian Ocean (or Ceno-Tethys) by the Early to Middle Miocene. This study shows that *Faorina* likely expanded widely, extending into the Mediterranean during the Miocene. Following the closure of the Tethyan Seaway, they experienced local extinction. Today, they are restricted to Taiwan, southern China, Vietnam, Australia, Sulu Sea, Burma, and the Andaman Islands. We therefore hypothesize that *Faorina* may have originated in the Mediterranean, with the Indo-West Pacific later becoming a refugium for this genus and some of the tropical to subtropical Ceno-Tethyan echinoid faunas.

Keywords: Systematics, Echinoidea, Irregularia, Spatangoids, Tethys

BACKGROUND

Echinoderms are a group of marine invertebrates that exhibit unique modes of life through their development. They possess a free-swimming larval stage lasting from several days to weeks before settling onto the substrate and become benthic for the remainder of their lifespan (except for feather stars). With multiple modes of life ontogenetically, their spatial and temporal distributions are complex and striking (*e.g.*, Lefebvre et al. 2013; Zamora et al. 2013). These biogeographic patterns reveal aspects that are often difficult to extract

Citation: Hsu CH, Fanai L, Sharma KM, Malsawmtluanga, Malsawma J, Lalnuntluanga P, Tiwari RP, Patnaik R, Senan AS, Lin JP. 2026. First fossil *Faorina* (Echinoidea: Spatangoida) from the Bhuban Formation (Miocene), northeastern India. Zool Stud **65:**21. doi:10.6620/ZS.2026.65-21.

from the fossil record of other taxa (*e.g.*, Lin et al. 2018) and are commonly explained by plate tectonics, oceanic circulation, and seaway connections (*e.g.*, Oji 1990; Harzhauser et al. 2008; Lin et al. 2018; Ho et al. 2022; Thompson et al. 2022; Lee et al. 2023).

Because the fossil record is often fragmentary, the discovery of a few critical new fossils from key localities can dramatically reshape evolutionary scenarios. India, at the heart of southern Asia, undoubtedly serves as one of the major hubs of Cenozoic fossil echinoids. Positioned between two Cenozoic fossil echinoid hotspots: the Mediterranean (*e.g.*, Borghi and Garilli 2022) and the tropical western Pacific (*e.g.*, Hsu et al. 2024; Chen et al. 2025; Hsu and Chang 2025), the Indian fauna recorded the closure of the Ceno-Tethys Ocean (Rögl 1998 1999; Srivastava 2012), providing a unique window into interactions between Mediterranean and tropical western Pacific assemblages and the subsequent Cenozoic biodiversity hotspot shift from the former to the latter, as observed in many marine groups (*e.g.*, Harzhauser et al. 2024; Tian et al. 2024).

In this study, we focus on the enigmatic spatangoid genus *Faorina* Gray, 1851, which currently includes two extant species and three fossil species. Notably, the extant species are restricted to the Indo-West Pacific, whereas the fossil species are known only from the Early to Middle Miocene of the Mediterranean region (Stara and Borghi 2012). This striking contrast between fossil and modern distributions highlights an underexplored evolutionary history. Although sporadic unpublished reports and notes by citizen scientists have mentioned more fossil occurrences, none have undergone rigorous taxonomic examination (Huang 2011; Chuang 2020). Here, we describe new fossil species of *Faorina* and discuss how they contribute to explaining this interesting paleobiogeographic pattern.

Geological Setting

The fossil described herein was collected from the Bhuban Formation, part of the Surma Group, which is widely exposed across northeastern India and southeastern Bangladesh, especially in the Tripura-Mizoram region (Fig. 1). Geologically, this unit was deposited within the Surma Basin, associated with the subduction of the Indian Plate along the Arakan Yoma suture and the Indo-Burman Orogeny since the Eocene (Nandy 1972; Rangin et al. 2013). The evolution of the basin began in the Late Oligocene, with the deposition of Barail Group (Oligocene), Surma Group (Lower to Middle Miocene), and Tipam Group (Pliocene) from bottom to top (Karunakaran 1974; Dasgupta 1984).

In particular, the Surma Group, where the studied fossils were found, comprises a thick succession of shales, siltstones, and sandstones deposited in a tide-dominated deltaic system sourced from the eastern Himalayas (Johnson and Alam 1991). It can be subdivided into the Bhuban Formation and the Bokabil Formation. The Bhuban Formation can be further divided into three informal members: lower sandy, middle clayey, and upper sandy, representing fluctuations in foreshore to shoreface and offshore zones of a shallow marine, organic-rich setting (Singh et al. 2010; Tiwari et al. 2011; Rajkonwar et al. 2013 2014 2015; Bharali et al. 2017; Rose et al. 2021; Fanai et al. 2023) that were controlled by repeated transgressive and regressive cycles (Rahman et al. 2009; Tiwari et al. 2011).

The 158 m thick sampling section belongs to the Upper Bhuban Unit of the Bhuban Formation within the Surma Group (Fig. 1). It is mainly composed of a repetitive succession of argillaceous and arenaceous rocks. Three lithological units have been identified, in ascending order: brown sand with silt intercalation, shale with occasional lenses of sand, and shale-sandstone alternation. Fossils were found in the middle unit, which is characterized by brown, heterolithic sandstone at about 80 m above the base of the section. A fossil starfish was also discovered from the similar stratigraphic unit from a different locality (Fraga et al. in review).

In terms of fossil echinoid records from the Upper Bhuban Unit in this region, Jauhri et al. (2003) reported a hemiasterid echinoid associated with corals and foraminifers from a pocket of shell limestone within a siliciclastic sequence at a locality near Zemabawk, east of Aizawl. Srivastava et al. (2008) documented *Coelopleurus* (*Keraiaphorus*) sp. and *Schizaster* sp. from the South Hlimen Quarry, Aizawl, Mizoram. Numerous other studies have also mentioned fossil echinoids from this region, though generally without systematic descriptions or detailed geological information (La Touche 1891; Sinha et al. 1982; Satsangi and Patil 1988; Patil 1990 1991; Tiwari 1993; Mazumder 2004; Ralte 2009; Tiwari and Jauhri 2014).

MATERIALS AND METHODS

Three fossil echinoid specimens from the Miocene Upper Bhuban Formation were examined in this study. All specimens are internal molds recovered from a fine sandstone bed at Keifang Village, Mizoram, northeastern India (22°53'52.35"N, 92°52'14.91"E) (Fig. 1). The specimens are housed at Department of Geology, Mizoram University, India, under the registration numbers Ech/LGC/2025/001, Ech/LGC/2025/002, and

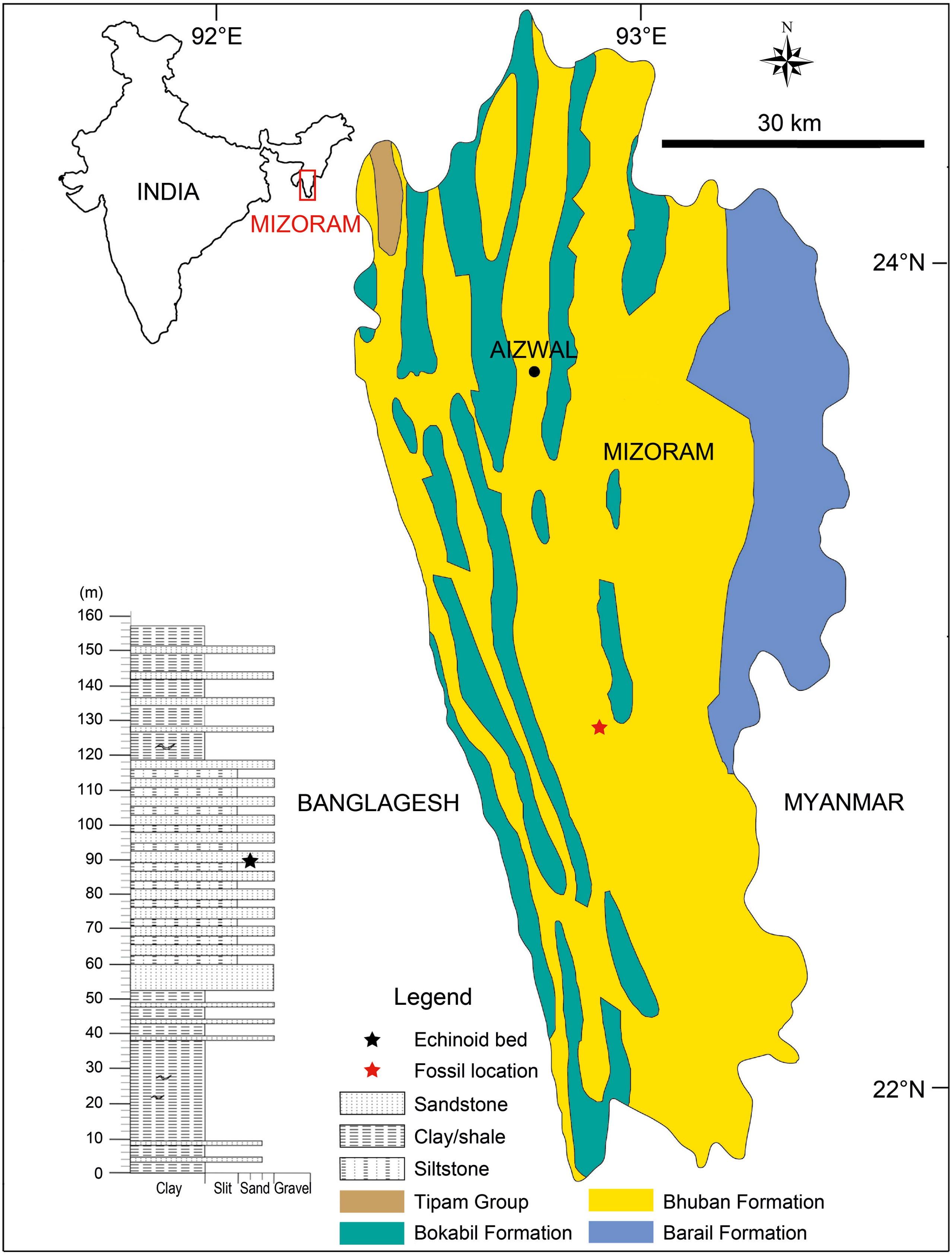

Fig. 1. Locality, geological map, and stratigraphy of the sampling bed.

Ech/LGC/2025/003. Two extant specimens of *Faorina chinensis* Gray, 1851, stored at the National Museum of Natural Science, Taichung, Taiwan (NMNS008510-00029 and NMNS008510-00030), were also included for comparisons.

To examine the effect of the closure of the Tethyan Seaway on the echinoid faunas of India, the Mediterranean, and the tropical western Pacific, we compiled available fossil occurrence data, spanning from the Oligocene to the present, from these regions and assessed the numbers of co-occurring genera as a proxy for faunal connections. Fossil data from India are based on Srivastava (2012) along with the new fossils described herein. Data from the Mediterranean are primarily from Borghi and Garilli (2022), with the missing records for the Oligocene and Early to Middle Miocene supplemented by the Paleobiology Database (PBDB; Uhen et al. 2023) downloaded on 27 September 2025. Fossil data for the tropical western Pacific are from Mihaljević and Rosenblatt (2018), originally downloaded from PBDB. Present-day distributions are from GBIF.org (2025) and OBIS (2025), and only genera with a fossil record in at least one of the regions are included. Classification strictly follows Kroh and Mooi (2025). Fossil occurrences with uncertain generic assignments or taxa regarded as *nomina dubia* were excluded, including records of *Brissopsis* (?), *Echinodiscus* (?), *Echinolampas* (?), *Goniocidaris* (?), *Hemipatagus* (?), *Opissaster* (?), *Schizobrissus* (?), *Moiropsis* (?), *Schizaster* (?), S*tomopneustes* (?), *Radiolus*, and *Spatangomorpha*. All records were carefully checked to minimize incorrect and redundant occurrences.

Taxonomic nomenclature follows Kroh and Mooi (2025). Morphological descriptions adhere to the terminology of Lewis and Donovan (2007). The ambulacral and interambulacral series are numbered according to Lovén's system (Lovén 1874). All measurements were taken with a digital caliper with a resolution of 0.01 mm and an accuracy of 0.03 mm.

SYSTEMATIC PALEONTOLOGY

Class Echinoidea Schumacher, 1817
Infraclass Irregularia Latreille, 1825
Order Spatangoida L. Agassiz, 1840
Suborder Paleopneustina Markov and Solovjev, 2001
Superfamily Paleopneustoidea A. Agassiz, 1904
Family Pericosmidae Lambert, 1905
Genus *Faorina* Gray, 1851

Type species: *Faorina chinensis* Gray, 1851, Recent, China, by subsequent designation of de Loriol 1875.

Species included: *Faorina chinensis* Gray, 1851, Recent, Indo-West Pacific (Stara and Borghi 2012; GBIF.org 2025); *Faorina callosa* (Manzoni, 1879), Miocene (early Langhian) of northern Italy and the San Marino; *Faorina maullui* Stara and Borghi, 2012, Miocene (Aquitanian–early Burdigalian) of Sardinia, Miocene (early Langhian) of northern Italy; *Faorina* sp. A (= *Pericosmus* sp. B in McNamara 1984 = *Faorina* sp. A in Stara and Borghi 2012), Recent, Australia; *Faorina* sp. B in Stara and Borghi 2012, Miocene (Aquitanian–early Burdigalian) of Sardinia; *Faorina mizoramensis* sp. nov., this study, Miocene (Lower–Middle) of northeastern India. (*F. lovisatoi* (Lambert, 1909) and *F. oppenheimi* (Lambert, 1909) from the Early Miocene (Aquitanian) of Sardinia are each based on a single, poorly preserved specimen, and their validity requires further confirmation due to the high morphological plasticity of Pericosmidae (Stara and Borghi 2012).)

Diagnosis: Pericosmid echinoids with meridoplacous plating in interambulacrum 1 adorally.

Remarks: Species of *Faorina* generally differ from *Pericosmus* in exhibiting a peripetalous fasciole that is not deeply indented behind the anterior petals, in typically lacking a marginal fasciole in adults, in having plates 1 in interambulacrum 1 and interambulacrum 4 adorally occluded from the peristome, and in possessing an elongated, wedge-shaped labrum pointing towards the sternal plates (Mortensen 1951; Markov and Solovjev 2001; Smith and Kroh 2011; Stara and Borghi 2012). However, these differences are not consistent, as many specimens show either intermediate or opposite conditions (Stara and Borghi 2012). The only reliable diagnostic feature recognized is the meridoplacous structure in interambulacrum 1 adorally, while the closely related genus *Pericosmus* L. Agassiz in L. Agassiz and Desor, 1847 exhibits amphiplacous plating (Stara and Borghi 2012).

Faorina mizoramensis sp. nov. Hsu and Lin

(Figs. 2, 3, 4C)
urn:lsid:zoobank.org:act:2C90A063-4AE4-41F8-82A9-15A1C211C30D

Material examined: Holotype: Ech/LGC/2025/001 (test length = 38.28 mm, test width = 50.53 mm, test height = 16.68 mm). Paratype: Ech/LGC/2025/002–Ech/LGC/2025/003.

Type locality and horizon: Mat River of Mizoram (northeastern India); Upper Bhuban Unit, Bhuban Formation, Surma Group (Early–Middle Miocene).

Etymology: The specific name is derived from the type locality, Mizoram (northeastern India), in reference to its distinct paleobiogeographic distribution compared with other known species.

Diagnosis: *Faorina* species with low test height; shallow frontal notch; truncated posterior margin; centrally positioned apical system; wide, elongate petals with narrow interporiferous zones; broad contact between first and second plates in interambulacrum 1; stout labrum ending at middle of second ambulacral plate.

Description: Test medium (test length = 36.17–49.69 mm, test width = 41.68–50.53 mm; Table 1), slightly angular, rounded to slightly heart-shaped, height low in profile (test height = 40–44% test length, mean = 42% test length). Maximum width slightly anterior; maximum height close to apical system (Fig. 3). Aboral surface slightly inflated, dome-shaped, not keeled posteriorly (Fig. 3); frontal groove wide and shallow. Oral surface flat, plastron slightly keeled posteriorly (Fig. 3). Posterior margin low and truncated (Fig. 3).

Apical disc centrally located aborally, with three gonopores (Fig. 2C1). Detailed plating structure unavailable.

Anterior ambulacrum non petaloid, straight, slightly sunken, wide, forming frontal groove anteriorly from apical disc to peristome (Fig. 2A, B).

Ambulacra I, II, IV, V petaloid aborally, significantly sunken, with nearly constant width from adapical to terminal ends, extending approximately 70–80% between apical disc and margin in planar view (Fig. 3), with interporiferous zones and single pore-pair column equal in width (Figs. 2A1, B1, C1); anterior petals and posterior petals approximately equal in length (Figs. 2A1, B1, C1).

Anterior petals diverge at about 115–120°, with about 28 double-series pore pairs in similar size (Fig. 2). Posterior petals diverge at about 70–90°, with about 29 double-series pore pairs in similar size (Fig. 2).

Interambulacrum 1 meridoplacous, interambulacrum 4 amphiplacous adorally (Fig. 4C).

Plastron lanceolate, greatest width close to posterior margin; mesamphisternous, with nearly symmetric sternal plates and biserially offset episternal plates (Fig. 4C). Labrum elongated, stout, reaching second adjoining ambulacral plate (Fig. 4C). Sternal plates elongated, sutured with episternal plates posteriorly, about a quarter of test length from posterior margin (Fig. 4C).

Peristome kidney-shaped, situated about 15% test length from anterior margin (Fig. 2A2, B2, C2). Periproct oval, located at top of posterior truncated surface.

Distribution: Upper Bhuban Unit, Bhuban Formation, Surma Group (Early-Middle Miocene), section along Mat River of Mizoram, northeastern India (22°53'52.35"N, 92°52'14.91"E). Known only from the type locality and horizon.

Remarks: Although the internal molds do not preserve some important features such as the fasciole, the oral plating sutures are very clear in specimen Ech/LGC/2025/001 (Figs. 2A2, 4C), which allows reliable identification. Because the plating in interambulacrum 1 is meridoplacous adorally, the specimens can be assigned to the genus *Faorina*.

Compared with other known *Faorina* species, the main difference is in the petals, which are much wider and longer, especially the posterior petals. The stout contact between the first and second plates in interambulacrum 1, together with the stout labrum, also separates these specimens from most species of *Faorina*, where the two plates usually only slightly contact (except *Faorina* sp. B; Stara and Borghi 2012) and the labrum is wedge-shaped and points toward the sternal plates. Additional differences are also present. The studied specimens differ from the type species *F. chinensis* (Fig. 5) and *Faorina* sp. A of McNamara (1984) in having a lower test, a more central apical system, and narrower interporiferous zones; from *F. callosa* in having a lower test, a shallower frontal notch, and narrower interporiferous zones; and from *F. maullui* in having a shallower frontal notch, a truncated posterior margin, narrower interporiferous zones. The studied specimens are most similar to *Faorina* sp. B of Stara and Borghi (2012), but still differ in their wider test, lower height, and shorter labrum. These differences show that the studied specimens do not belong to any known species of *Faorina* (Table 2). Together with a distinct stratigraphic and geographic distribution, these fossils are therefore described herein as a new species.

However, since the long-standing confusion

Table 1. Biometric measurements of *Faorina mizoramensis* sp. nov.

Specimen	Test Length (mm)	Test Width (mm)	Test Height (mm)
Ech/LGC/2025/001 (holotype)	38.28	50.53	16.68
Ech/LGC/2025/002 (paratype)	36.17	45.42	15.18
Ech/LGC/2025/003 (paratype)	49.69	41.68	19.89

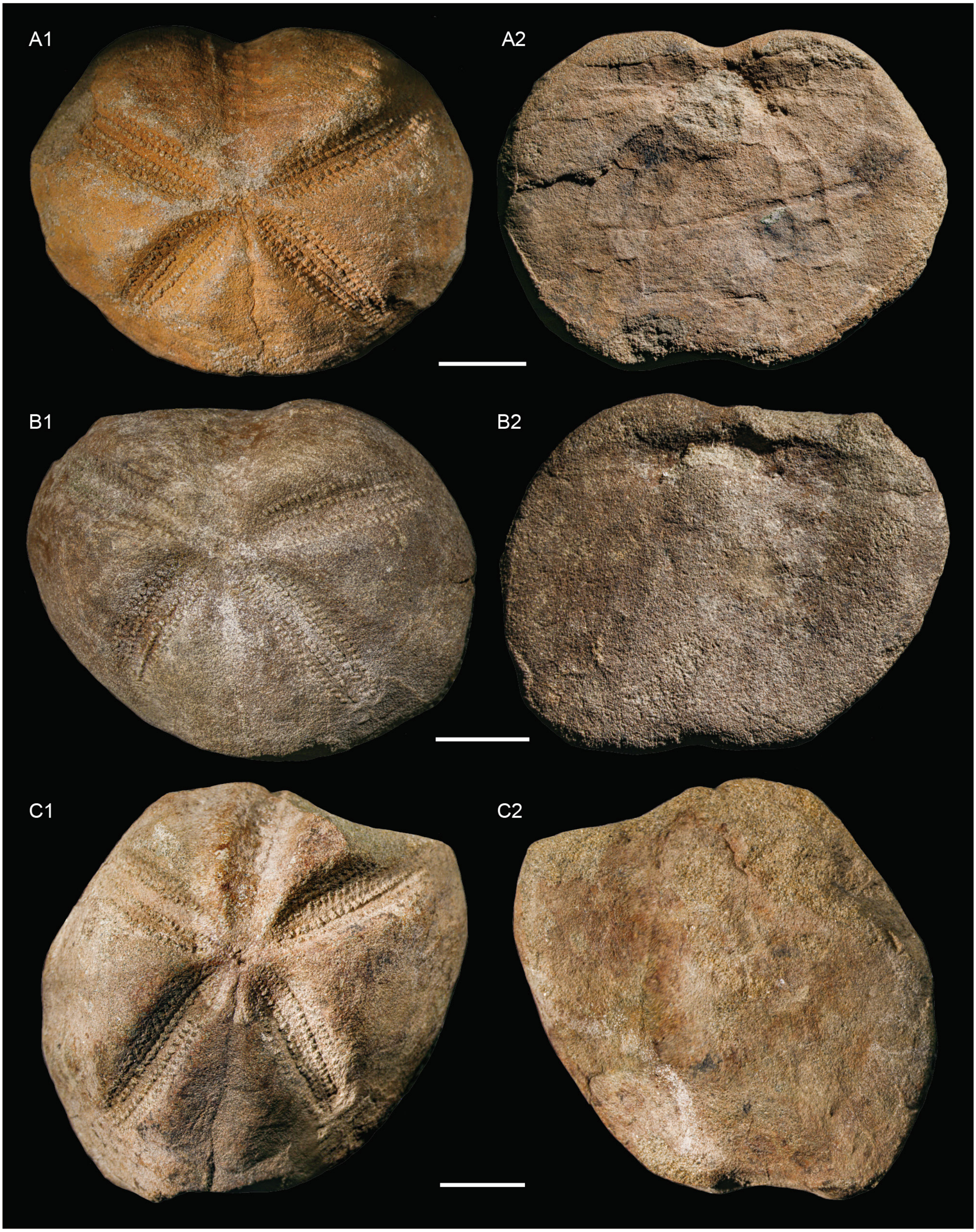

Fig. 2. *Faorina mizoramensis* sp. nov. from the Lower to Middle Miocene Bhuban Formation (Surma Group), northeastern India. A, Ech/LGC/2025/001. B, Ech/LGC/2025/002. C, Ech/LGC/2025/003. In aboral (A1–C1) and oral (A2–C2) views. Scale bar = 10 mm.

between the genera *Faorina* and *Pericosmus* has only recently been clarified, many species currently assigned to *Pericosmus* may actually belong to *Faorina* (Stara and Borghi 2012). For example, *Pericosmus hsui* Wang, 1984 from the Miocene of northern Taiwan most likely belongs to *Faorina*, based on the plating structure illustrated in the original description (Huang 2011; Chen et al. 2025), although type material and additional specimens are still required for confirmation. With more than 30 extant and fossil species currently placed in *Pericosmus* (Kroh and Mooi 2025), thorough re-examination will be required to clarify their true spatial and temporal diversity patterns.

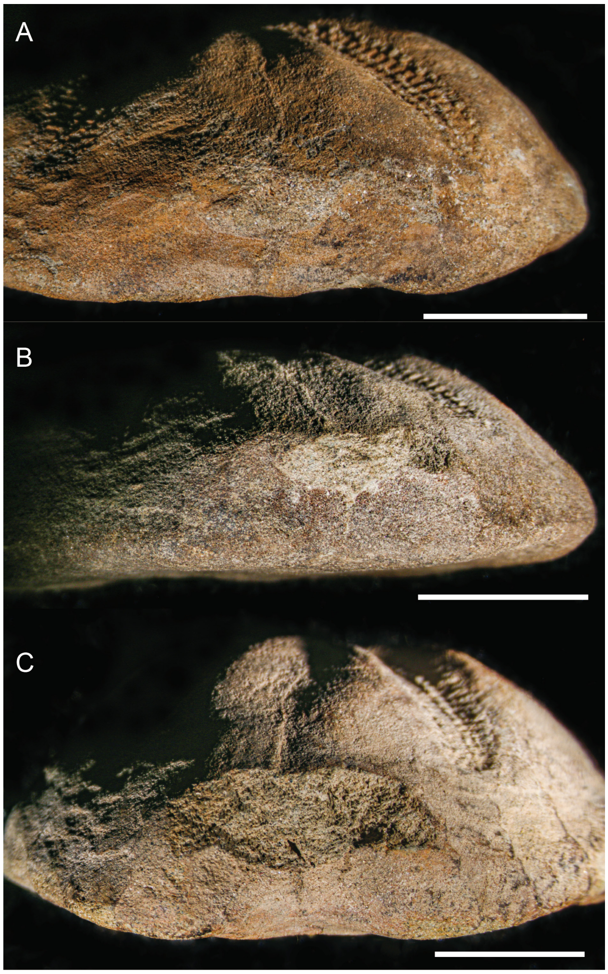

Fig. 3. Lateral view of interambulacrum 5 of *Faorina mizoramensis* sp. nov. from the Lower to Middle Miocene Bhuban Formation (Surma Group), northeastern India. A, Ech/LGC/2025/001. B, Ech/LGC/2025/002. C, Ech/LGC/2025/003. Scale bar = 10 mm.

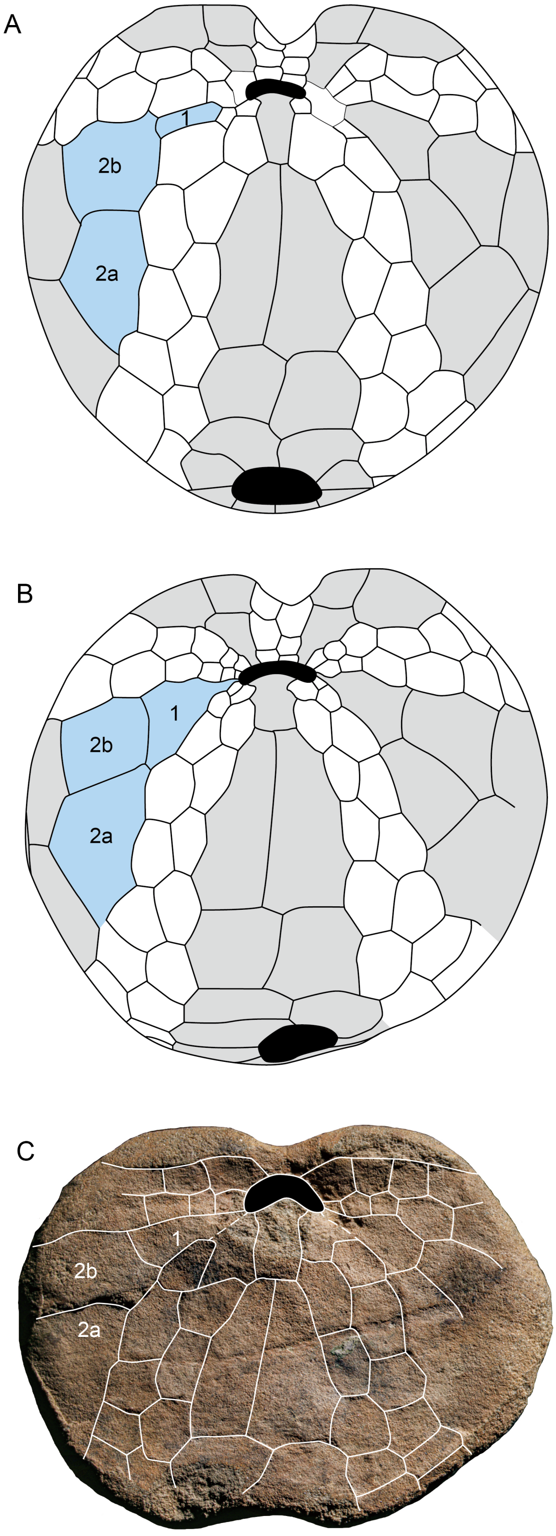

Fig. 4. Oral plating patterns. A, Genus *Faorina* (*Faorina maullui* Stara and Borghi, 2012; modified from Stara and Borghi 2012). B, Genus *Pericosmus* (*Pericosmus latus* Agassiz and Desor, 1847); modified from Stara and Borghi 2012). C, *Faorina mizoramensis* sp. nov. (Ech/LGC/2025/001). Shallow shaded areas represent ambulacral regions. Only clearly defined sutures are illustrated.

DISCUSSION

The diversity and distribution pattern of marine faunas have always been closely related to paleogeographic changes throughout the Phanerozoic, mostly reflected by oceanic connections and isolations (*e.g.*, Cao et al. 2017; Balembois et al. 2025). During the Late Mesozoic and Cenozoic, one of the most important paleogeographic event, the closure of the Tethys Ocean, has been demonstrated to have thoroughly reshaped the present-day spatial patterns of marine faunas (*e.g.*, Yasuhara et al. 2022). Since the Late Cretaceous (~80 Ma), the northward movement of the African, Indian, and Australian plates resulted in a continuous narrowing of the vast Tethys Ocean and its eventual complete closure and formed present-day Mediterranean, with successively diminishing connections among adjacent regions (*e.g.*, Harzhauser et al. 2008 2024; Yasuhara et al. 2022). These palaeogeographic events contributed to numerous faunal turnover events (*e.g.*, Lin et al. 2017), including the reduction of faunal exchange with the western Atlantic and Caribbean during the Late Oligocene (BouDagher-Fadel and Price 2010; Perrin and Bosellini 2012) and

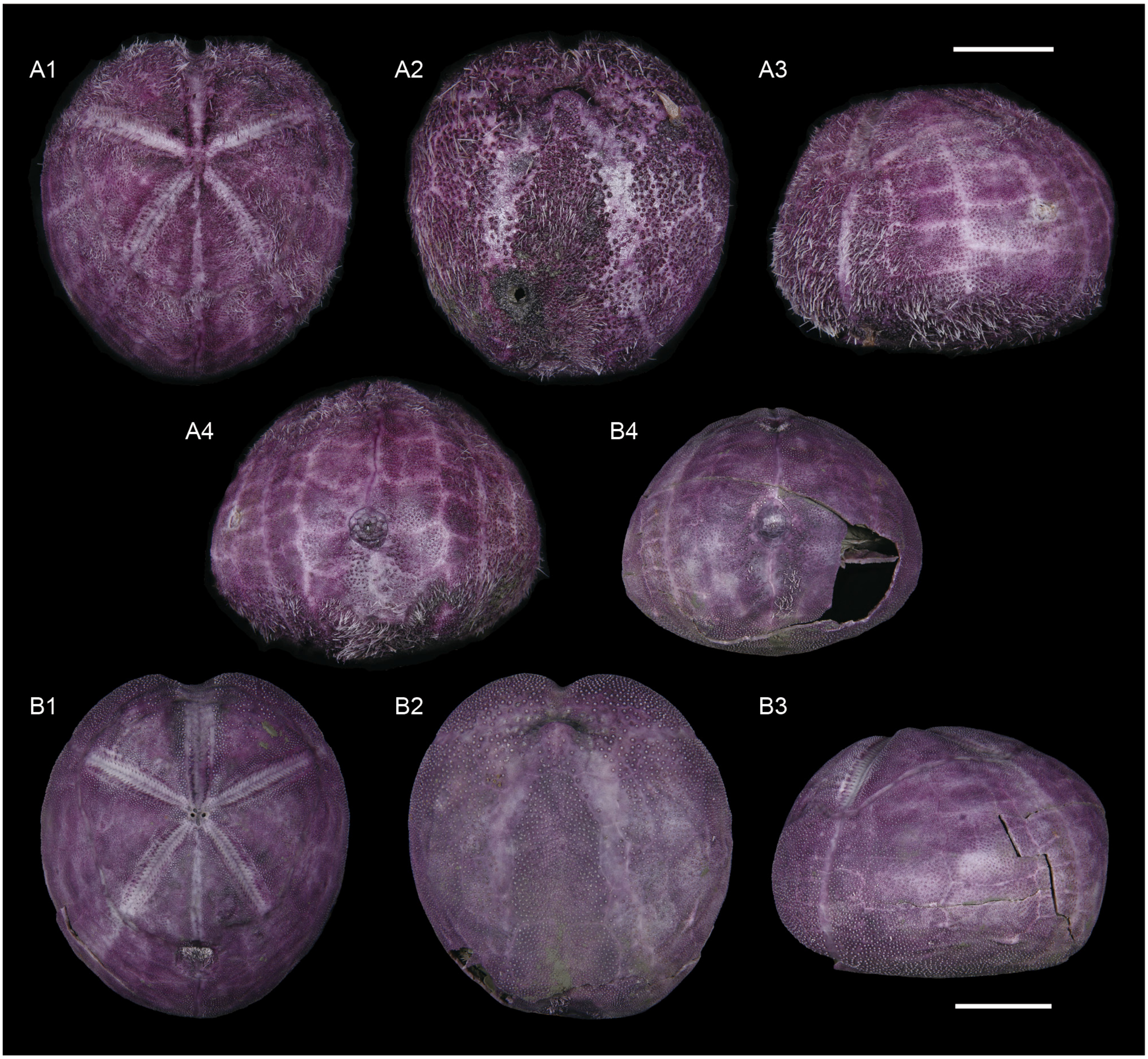

Fig. 5. Extant specimens of *Faorina chinensis* Gray, 1851 collected from Donggang Harbor Pingtung, Taiwan (22°27'58.0"N, 120°26'38.6"E). A, NMNS008510-00029. B, NMNS008510-00030. In aboral (A1–B1), oral (A2–B2), lateral (A3–B3), and posterior (A4–B4) views. Scale bar = 20 mm.

with the Indian Ocean from the late Oligocene to middle Miocene as the Tethyan Seaway completely closed (Harzhauser et al. 2007; Reuter et al. 2009; Hall 2012; Bialik et al. 2019; Lokho et al. 2026).

With the tectonically mediated geographic changes, a series of echinoid faunal distribution shifts have been observed in the fossil record, particularly in the eastern Tethys Ocean. At the species level, the Arabian fauna, located east of the Tethyan Seaway and between the Mediterranean and Indian faunas, showed changing affinities from the Mediterranean to the Indian regions from the Late Cretaceous to the Middle Miocene, indicating that faunal exchange between the Mediterranean and Indian Oceans had become increasingly difficult since the Oligocene (Roman et al. 1989). In contrast, at the generic level, the affinities between the two oceans largely overlapped (Rosen and Smith 1988; Harzhauser et al. 2007).

The new fossils described herein represent the first fossil record of *Faorina* outside the Mediterranean region, helping to bridge the apparent gap between its fossil and modern distributions and providing a new perspective for ongoing paleobiogeographic discussions. These specimens indicate that the genus had already reached the eastern Indian Ocean at the time of its earliest known fossil occurrence, prior to the complete closure of the Tethyan Seaway between the Mediterranean and the Indian Ocean (ca. 13.8 Ma; Bialik et al. 2019; Fig. 6). This observation is consistent with previous studies that reported close generic-level affinities between the two faunas, reflecting long-term faunal connections. It strongly suggests that *Faorina* was once widely distributed, from at least the eastern Indian Ocean to the Mediterranean region. Following the closure of the Tethyan Seaway, Mediterranean populations went extinct, and the genus became restricted to its modern Indo-West Pacific distribution. Interestingly, similar patterns have also been observed in other echinoderm groups. For example, Kroh (2004) described fossil "snake stars" (Ophiuroidea: Euryalidae) from the Mediterranean, but this group is now restricted to the Indo-Malayan region and around Australia, highlighting that comparable extinction events also occurred in the Mediterranean.

Furthermore, we combine our new fossil evidence with Cenozoic echinoid records from the Mediterranean (Borghi and Garilli 2022; Uhen et al. 2023), India and Pakistan (Srivastava 2012), and the tropical western Pacific (Mihaljević and Rosenblatt 2018) to improve the discussions of the broader biogeographic pattern. Although these data are potentially affected by uneven sampling and database biases, they provide an overview of general patterns. Based on these data, we hypothesized a broader faunal similarity pattern that seems to be strongly shaped by the closure of the Tethyan Seaway (Fig. 7; Table 3). During the Oligocene and Miocene, when the Mediterranean remained connected to the Indian Ocean, several genera co-occurred across these regions but were absent from the tropical western Pacific in our dataset (two genera in the Oligocene; five in the Miocene), suggesting relatively high connection between the Mediterranean and Indian faunas. Since the Pliocene-Pleistocene, however, following the complete closure of the Tethyan Seaway, Indian echinoid faunas have become increasingly dissimilar to those of the Mediterranean, and there are no genera whose distribution is limited only to those two regions in our dataset. At the same time, all genera present in the Indian Ocean can also be found in the tropical western Pacific, including many that are shared

Table 2. Trait comparisons between *Faorina* species

Species	*Faorina mizoramensis* sp. nov.	*F. chinensis*	*F. callosa*	*F. maullui*	*Faorina* sp. A	*Faorina* sp. B
Reference	this study	Mortensen 1951	Stara and Borghi 2012 (holotype)	Stara and Borghi 2012	McNamara 1984 (*Pericosmus* sp. B)	Stara and Borghi 2012
Test length	36–50 mm	30–96 mm	48 mm	35–82 mm	39 mm	46 mm
Test width	84–132% TL	89–94% TL	111% TL	100–106% TL	92% TL	83% TL
Test height	40–44% TL	70–83% TL	78% TL	37–42% TL	72% TL	70% TL
Frontal notch	shallow	shallow	deep	deep	shallow	shallow
Posterior margin	truncated	truncated	truncated	oblique	truncated	truncated
Apical system	central	slightly anterior	central	central	slightly anterior	central
Petal	long	medium	long	medium	medium	medium
Interporiferous zones	narrow	wide	wide	wide	wide	narrow
1st and 2nd plates in IA 1	broad contact	narrow contact	narrow contact	narrow contact	narrow contact	broad contact
End of labrum	middle of 2nd AP	middle of 2nd AP	middle of 2nd AP	middle of 2nd AP	middle of 2nd AP	end of 2nd AP

TL = test length; IA = interambulacrum; AP = ambulacral plate.

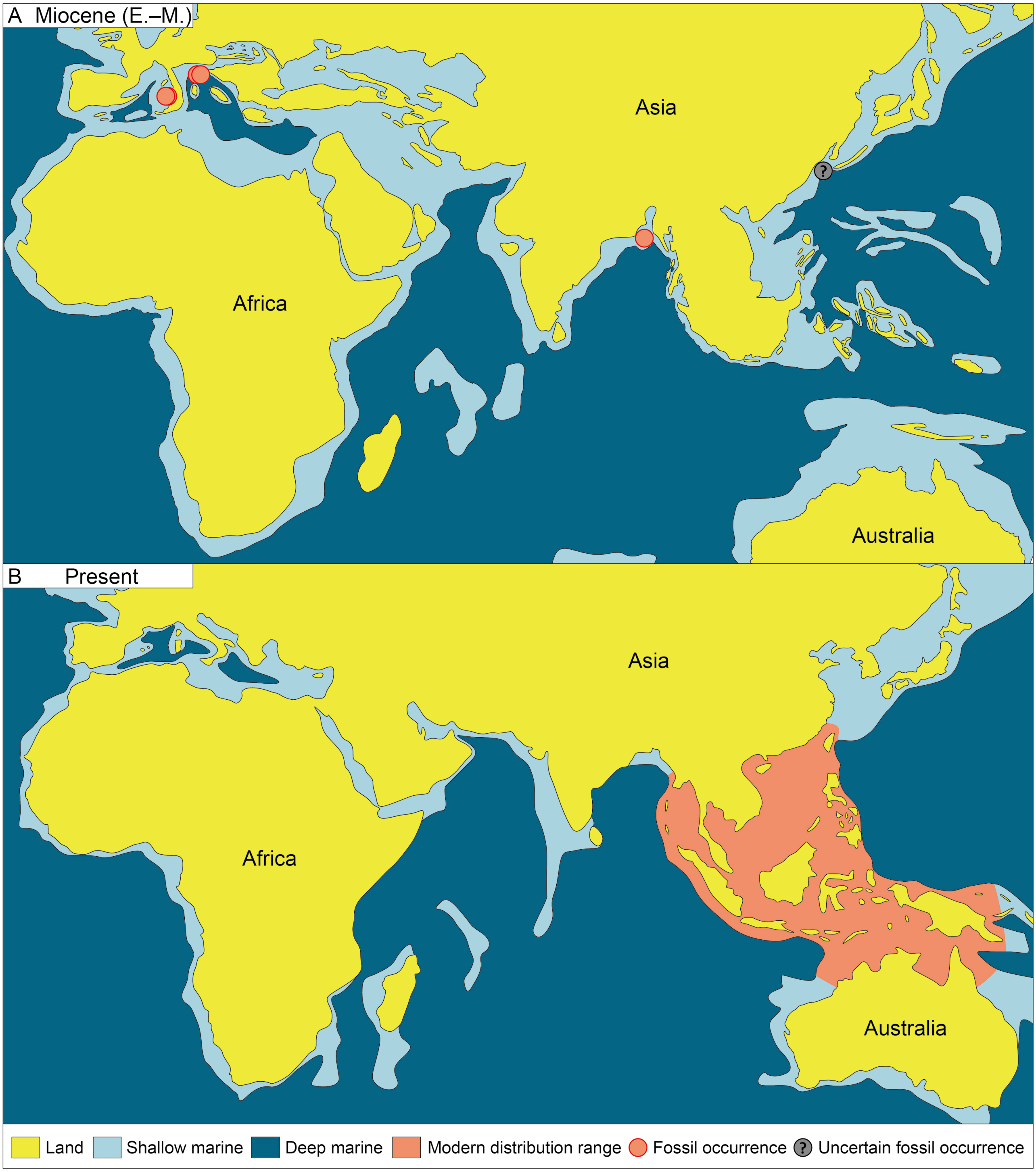

Fig. 6. Fossil occurrences and present-day distributions of genus *Faorina*. A, Early-Middle Miocene (paleogeography is modified from Cao et al. 2017). B, Present day (geography is modified from Scotese and Wright 2018). Fossil occurrences are listed in systematic paleontology section. Present-day distributions are from GBIF.org (2025) and OBIS (2025).

Table 3. Fossil and present-day echinoid occurrences data in India, Mediterranean, and the tropical western Pacific. A total of 103 genera are recorded from the Oligocene to the Pleistocene, with 15 genera in the Oligocene, 87 in the Miocene, and 68 in the Pliocene to Pleistocene. Among 103 genera, 70 of them persist to the present day in these regions (Srivastava 2012; Mihaljević and Rosenblatt 2018; Borghi and Garilli 2022; Uhen et al. 2023; GBIF.org 2025; Kroh and Mooi 2025; OBIS 2025). I = India; M = Mediterranean; P = tropical western Pacific

Genus	Oligocene	Miocene	Plio-Pleistocene	Present
Acanthocidaris		P		I P
Amblypygus		M	M	
Amphiope	M	M	M	
Arbacia			M	I M P
Breynia	I P	I P	P	P
Brisaster	P	P	P	P
Brissopatagus		P		
Brissopsis	P	I M P	M	I M P
Brissus		I M P	I M P	I M P
Centrostephanus		M P	M	I M P
Chondrocidaris		P	P	P
Cidaris	I P	I M P	I M P	M
Clypeaster	I M P	I M P	I M P	I P
Coelopleurus	I	I P	P	I P
Conolampas		M		P
Ditremaster			P	
Echinarachnius			P	P
Echinocardium		M	M	I M P
Echinocyamus	I	M P	M	I M P
Echinodiscus		I P	I P	I P
Echinolampas	I M	I M P	M P	I P
Echinometra		P	P	I P
Echinoneus		M P	M P	I P
Echinostrephus		P	P	I P
Echinus		I M	M	I M P
Erbechinus			P	P
Eucidaris		I M P	M P	I P
Eupatagus	I M P	I M P		P
Faorina		I M		P
Fibularia	P	I P		I P
Genocidaris		M	M	M
Goniocidaris		I P	I P	I P
Gracilechinus			M	M
Grammechinus		I		
Gymnopatagus	I			
Hemiaster		M P		
Hemifaorina		P		
Hemipatagus		M		
Heterobrissus		M		P
Heterocentrotus		P	P	I P
Histocidaris		M	M	I P
Holanthus		M	M	P
Holaster		M		
Hypsoclypus		M	M	
Jacksonaster		P	P	I P
Javanechinus		P	P	
Koehleraster		M		
Laganum		P	I P	I P
Lovenia		I M P	I P	I P
Lytechinus		P	P	P

Table 3. (Continued)

Genus	Oligocene	Miocene	Plio-Pleistocene	Present
Mazettia			M	
Maretia		I P	P	I P
Metalia		I M		I P
Microcyphus		P	P	I P
Moiropsis		I		P
Mortonia		I		P
Oligophyma		M		
Oligopodia		P	P	I P
Opechinus		I P		P
Opissaster		M	M	
Ova		M	M	M P
Paracentrotus			M	M
Parasalenia		P		I P
Parascutella		M		
Peribrissus		M	M	
Pericosmus		M P	P	I P
Peronella		P		I P
Phyllacanthus		M P	P	I P
Placentinechinus			M	
Plagiobrissus		M	M	M
Plegiocidaris		M		
Platybrissus			P	P
Pliolampas		M		
Plococidaris			P	I P
Printechinus			P	I P
Prionocidaris		M P	M P	I P
Psammechinus		M	M	M
Rhopalocidaris			P	P
Salmacis		P	I P	I P
Sardocidaris		M		
Sardospatangus		M		
Schizaster	I M	I M P	I M P	I M P
Schizechinus		M	M	
Schizobrissus		I M	M	
Sculpsitechinus			P	I P
Scutella	M	M P	P	
Sismondia		P		
Spatangus		M	M	M P
Sphaerechinus			M	M
Stereocidaris		P		I P
Stirechinus		M	M	
Stomopneustes		P		I P
Studeria		M P		P
Stylocidaris		M P	M	I M P
Temnechinus		I P		
Temnopleurus		I P	I P	I P
Temnotrema		P	P	I P
Thylechinus	P			
Trachyaster		M		
Trachypatagus		M	M	
Tretocidaris		M		
Tripneustes		I M	M	I P
Tylocidaris		M		P

between the Indian and Pacific faunas but absent from the Mediterranean, a pattern that persists to the present day and characterizes the modern Indo-West Pacific biogeographic region as a whole.

The Indian echinoid fauna represents one of the most important hubs for understanding the temporal and spatial pattern of late Cenozoic echinoid radiations, providing an indispensable window for bridging the two well-studied and fossiliferous faunas of the Mediterranean and tropical western Pacific.

CONCLUSIONS

Faorina mizoramensis sp. nov. from the Early to Middle Miocene are described. These represent the first fossil record of the genus outside the Mediterranean region, implying that *Faorina* once had a wider distribution but later became restricted to the Indo-West Pacific, potentially due to the closure of the Tethyan Seaway, consistent with broader late Cenozoic echinoid biogeographic patterns of the Mediterranean, India, and the tropical western Pacific hypothesized based on our compiled dataset.

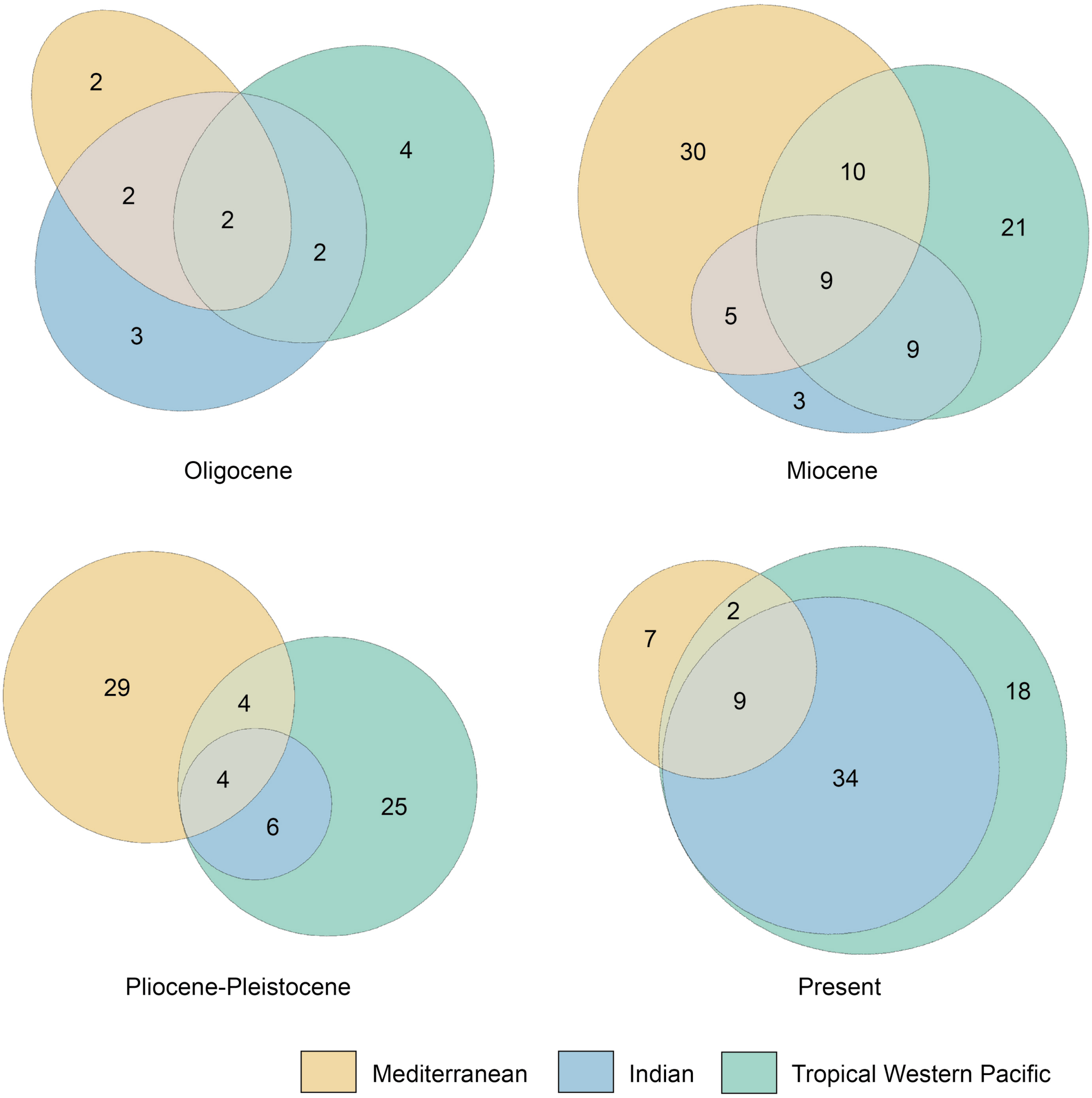

Fig. 7. Diversity distribution of echinoid faunas throughout the late Cenozoic. The numbers in the circles indicate the numbers of genera described in the corresponding regions. The numbers in the overlapping areas indicate the numbers of shared genera between regions. The pattern suggests that the Indian fauna became more similar to the tropical western Pacific fauna through time. Data from Srivastava (2012), Mihaljević and Rosenblatt (2018), Borghi and Garilli (2022), Uhen et al. (2023), GBIF.org (2025), Kroh and Mooi (2025), and OBIS (2025). The full dataset is provided in table 3.

Acknowledgments: We are grateful to editor-in-chief Benny Kwok Kan Chan, associate editor Chien-Hsiang Lin, reviewer Andreas Kroh (Naturhistorisches Museum Wien, Austria), and one anonymous reviewer for their comments, which greatly improved this manuscript. We thank Josep Quintana Cardona (Institut Català de Paleontologia Miquel Crusafont, Spain), Enrico Borghi (a Società Reggiana di Scienze Naturali, Italy), and Kai-Chun Chang (National Taitung University, Taiwan) for discussions; Hsin-Drow Huang (NMNS; National Museum of Natural Science, Taiwan), Ho-Tian Hung (NMNS), and Tzu-Ruei Yang (NMNS) for their assistance in examining extant echinoids at the National Museum of Natural Science, Taiwan. Chia-Hsin Hsu is thankful to Ministry of Education, Taiwan for Overseas PhD Fellowship. K.M. Sharma is thankful to SERB-ANRF for the research grants (sanctioned no. CRG/2021/004627). Jih-Pai Lin is thankful to NSTC for the research funding (NSTC 114-2116-M-002-017).

Authors' contributions: Conceptualization CH Hsu (CHH); Data Curation CHH; L Fanai (LF), KM Sharma (KMS), JP Lin (JPL); Formal Analysis CHH; Funding Acquisition JPL; Investigation CHH, LF, KMS, Malsawmtluanga (M), J Malsawma (JM), P Lalnuntluanga (PL), RP Tiwari (RPT), R Patnaik (RP), AS Senan (ASS), JPL; Methodology CHH; Project Administration CHH, KMS, JPL; Resources CHH, LF, KMS, M, JM, PL, RPT, RP, JPL; Software CHH; Supervision JPL; Validation CHH; Visualization CHH; Writing – Original Draft Preparation CHH; Writing – Review & Editing CHH, LF, KMS, M, JM, PL, RPT, RP, ASS, JPL.

Competing interests: Authors declare no competing interests.

Availability of data and materials: All data are available in the paper. Examined fossil specimens were deposited in the Department of Geology, Mizoram University, India.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Agassiz A. 1904. The Panamic deep sea echini. Mem Mus Comp Zool Harvard Coll **31:**1–243.

Agassiz L. 1840. Catalogus Systematicus Ectyporum Echinodermatum Fossilium Musei Neocomiensis, O. Petitpierre, Neuchâtel. Jent and Gassmann, Solothurn.

Agassiz L, Desor PJE. 1847. Catalogue raisonné des familles, des genres, et des espèces de la classe des échinodermes. Ann Sci Nat Zool **8:**5–35, 355–380.

Balembois A, Pohl A, Lefebvre B, Servais T, Lunt DJ et al. 2025. Unravelling the drivers of marine biodiversity across the Phanerozoic. Nat Commun **16:**8498. doi:10.1038/s41467-025-63428-9.

Bharali B, Borgohain P, Bezbaruah D, Vanthangliana V, Phukan PP, Rakshit R. 2017. A geological study on Upper Bhuban Formation in parts of Surma Basin, Aizawl, Mizoram. Science Vision **17:**128–147. doi:10.33493/scivis.17.03.02.

Bialik OM, Frank M, Betzler C, Zammit R, Waldmann ND. 2019. Two-step closure of the Miocene Indian Ocean Gateway to the Mediterranean. Sci Rep **9:**8842. doi:10.1038/s41598-019-45308-7.

Borghi E, Garilli V. 2022. Climate-driven diversity changes of Mediterranean echinoids over the last 6 Ma. Acta Palaeontol Pol **67:**781–805. doi:10.4202/app.00993.2022.

BouDagher-Fadel MK, Price GD. 2010. Evolution and paleogeographic distribution of the lepidocyclinids. J Foraminifer Res **40:**79–108. doi:10.2113/gsjfr.40.1.79.

Cao W, Zahirovic S, Flament N, Williams S, Golonka J, Müller RD. 2017. Improving global paleogeography since the late Paleozoic using paleobiology. Biogeosciences **14:**5425–5439. doi:10.5194/bg-14-5425-2017.

Chen H-K, Hsu C-H, Lin J-P. 2025. Three echinoid assemblages with the earliest cidaroid (Echinodermata: Echinoidea) fossil record from the Middle Miocene of Taiwan. Geobios **88–89:**35–48. doi:10.1016/j.geobios.2024.05.010.

Chuang SC. 2020. Study of the Echinoid Fossils from Yujing Area, Tainan, Taiwan. MSc dissertation, National Cheng Kung University, Tainan.

Dasgupta S. 1984. Tectonic trends in Surma Basin and possible genesis of the folded belt. Rec Geol Surv India **113:**58–61.

de Loriol P. 1875. Echinologie helvétique. Description des échinides tertiaires de la Suisse. Troisième partie. Mém Soc Paléont Suisse **2:**1–88.

Fanai L, Lalnuntluanga P, Malsawma J, Lalhruaitluanga, Lalremruatfela C. 2023. A comparative study of ichnofossils from Upper and Middle Bhuban Unit of Bhuban Formation (Surma Group), Aizawl, Mizoram to decipher the depositional environment. Indian J Sci Technol **16:**134–147. doi:10.17485/ijst/v16sp1.msc20.

Fraga MC, Sharma KM, Lin J-P, Fanai L, Zoramthara C, Lalremruatfela C, Lalnuntluanga P, Tiwari RP, Patnaik R. *in review*. A new starfish (Asteroidea, Echinodermata) from the Miocene of India.

GBIF.org. 2025. GBIF Home Page. Available at: https://www.gbif.org. Accessed 27 Sept. 2025.

Gray JE. 1851. New genera and species of Spatangidae in the British Museum. Ann Mag Mat Hist **2:**34–38.

Hall R. 2012. Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean. Tectonophysics **570–571:**1–41. doi:10.1016/j.tecto.2012.04.021.

Harzhauser M, Kroh A, Mandic O, Piller WE, Göhlich U et al. 2007. Biogeographic responses to geodynamics: A key study all around the Oligo – Miocene Tethyan Seaway. Zool Anz **246:**241–256. doi:10.1016/j.jcz.2007.05.001.

Harzhauser M, Landau B, Mandic O, Neubauer TA. 2024. The Central Paratethys Sea – Part of the tropical eastern Atlantic rather than gate into the Indian Ocean. Glob Planet Change **243:**104595. doi:10.1016/j.gloplacha.2024.104595.

Harzhauser M, Mandic O, Piller WE, Reuter M, Kroh A. 2008. Tracing back the origin of the Indo-Pacific mollusc fauna: Basal Tridacninae from the Oligocene and Miocene of the sultanate of Oman. Palaeontology **51:**199–213. doi:10.1111/j.1475-4983.2007.00742.x.

Ho S-L, Wang J-K, Lin Y-J, Lin C-R, Lee C-W et al. 2022. Changing surface ocean circulation caused the local demise of echinoid *Scaphechinus mirabilis* in Taiwan during the Pleistocene-Holocene transition. Sci Rep **12:**8204. doi:10.1038/s41598-022-11920-3.

Hsu C-H, Chang K-C. 2025. Sea urchins of Hong Kong: Corrections of misidentifications and an updated species list. Zootaxa **5683:**142–150. doi:10.11646/zootaxa.5683.1.9.

Hsu C-H, Lin J-P, Lin C-H. 2024. A spatangoid echinoid assemblage from the Gutingkeng Formation (Early Pleistocene) of Taiwan and its paleoenvironmental and geological implications. Geobios **87:**9–23. doi:10.1016/j.geobios.2024.09.003.

Huang C-C. 2011. Taiwanese Fossil Echinoids I. Private Press, Taichung.

Jauhri AK, Mandaokar BD, Mehrotra RC, Tiwari RP, Singh AP. 2003. Corals and foraminifera from the Miocene (Upper Bhuban Formation) of Mizoram, India. J Palaeontol Soc India **48:**135–138. doi:10.1177/0971102320030110.

Johnson SY, Alam AMN. 1991. Sedimentation and tectonics of the Sylhet trough, Bangladesh. Geol Soc Am Bull **103:**1513–1527. doi:10.1130/0016-7606(1991)103<1513:satots>2.3.co;2.

Karunakaran C. 1974. Geology and mineral resources of the states of India. Misc Publ Geol Surv India **30:**93–101.

Kroh A. 2004. First fossil record of the family Euryalidae (Echinodermata: Ophiuroidea) from the Middle Miocene of the central Mediterranean. *In*: Heinzeller T, Nebelsick JH (eds) Echinoderms. Proceedings of the 11th International Echinoderm Conference, Munich/Germany/6–10 October 2003. Taylor & Francis, London, pp. 447–452.

Kroh A, Mooi R. 2025. World Echinoidea Database. Available at: https://www.marinespecies.org/echinoidea. Accessed 27 Sept. 2025.

La Touche THD. 1891. Note on the geology of the Lushai Hills. Rec Geol Surv India **24:**83–141.

Lambert J. 1905. Notes sur quelques échinides éocéniques de l'Aude et de l'Hérault. In catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Annls Univ Lyon Nouv Sér I Sci Méd **17:**129–164.

Lambert J. 1909. Descriptions des échinides fossiles des terrains miocèniques de la Sardaigne - 2me partie. Mém Soc Paléont Suisse **35:**74–141.

Latreille PA. 1825. Families Naturelles du Règne Animal Exposées Succinctement et dans un Ordre Analytique, avec l'Indication de Leurs Genres. J.B. Baillière, Paris.

Lee H, Lee K-S, Hsu C-H, Lee C-W, Li C-E et al. 2023. Phylogeny, ancestral ranges and reclassification of sand dollars. Sci Rep **13:**10199. doi:10.1038/s41598-023-36848-0.

Lefebvre B, Sumrall CD, Shroat-Lewis RA, Reich M, Webster GD et al. 2013. Palaeobiogeography of Ordovician echinoderms. *In*: Harper DAT, Servais T (eds) Early Palaeozoic Biogeography and Palaeogeography. Geological Society, London, Memoirs, London, pp. 173–198. doi:10.1144/m38.14.

Lewis DN, Donovan S. 2007. A standardized method of describing fossils, using Echinoidea as an example. Scr Geol **134:**109–118.

Lin C-H, Brzobohatý R, Nolf D, Girone A. 2017. Tortonian teleost otoliths from northern Italy: taxonomic synthesis and stratigraphic significance. Eur J Taxon **322:**1–44. doi:10.5852/ejt.2017.322.

Lin J-P, Ausich WI, Balinski A, Bergström SM, Sun Y. 2018. The oldest iocrinid crinoids from the Early/Middle Ordovician of China: possible paleogeographic implications. J Asian Earth Sci **151:**324–333. doi:10.1016/j.jseaes.2017.10.041.

Lokho K, Carrasco JF, Bhandari A, Biswal S, Whiso K. 2026. Additional Eocene echinoids from the Sylhet Limestone of Mikir Hills, Assam, Northeast India: Deeper insights into Neo-Tethys palaeobiogeography. J Palaeontol Soc India **0:**1–11. doi:10.1177/05529360251408963.

Lovén S. 1874. Études sur les échinoïdées. Kungl Svenska Vetenskapsakad Handl **11:**1–91.

Manzoni A. 1879. Gli echinodermi fossili dello Schlier delle colline di Bologna. Denkschr Kaiserl Akad Wiss Math-Naturwiss Cl **39:**149–164.

Markov AV, Solovjev AN. 2001. Echinoids of the family Paleopneustidae (Echinoidea, Spatangoida): morphology, taxonomy, phylogeny. Geos **2001:**1–109.

Mazumder BI. 2004. A Study of Miocene Invertebrates from the area around Kolasib, Mizoram. PhD dissertation, Nagaland University, Kohima.

McNamara KJ. 1984. Living Australian species of the echinoid *Pericosmus* (Spatangoida: Pericosmidae). Rec West Aust Mus **11:**87–100.

Mihaljević M, Rosenblatt AJ. 2018. A new fossil species of *Clypeaster* (Echinoidea) from Malaysian Borneo and an overview of the Central Indo-Pacific echinoid fossil record. Swiss J Palaeontol **137:**389–404. doi:10.1007/s13358-018-0164-y.

Mortensen T. 1951. A Monograph of the Echinoidea. V, 2. Spatangoida II. Amphisternata II. Spatangidae, Loveniidae, Pericosmidae, Schizasteridae, Brissidae. C.A. Reitzel, Copenhagen.

Nandy DR. 1972. Style of folding in the Mio–Pliocene of Tripura and Mizoram area and possible role of Basement dislocation fabrics. Misc Publ Geol Surv India **31:**83–141.

OBIS. 2025. Ocean Biodiversity Information System. Available at: https://obis.org/. Accessed 27 Sept. 2025.

Oji T. 1990. Miocene Isocrinidae (stalked crinoids) from Japan and their biogeographic implication. Trans Proc Paleontol Soc Jpn **157:**412–429.

Patil RS. 1990. Palaeontology of the Upper Bhuban Formation of Lunglei District, Mizoram. Rec Geol Surv India **123:**168–169.

Patil RS. 1991. Palaeontology of the Bhuban rocks of parts of Lunglei District, Mizoram. Rec Geol Surv India **124:**227.

Perrin C, Bosellini FR. 2012. Paleobiogeography of scleractinian reef corals: Changing patterns during the Oligocene–Miocene climatic transition in the Mediterranean. Earth-Sci Rev **111:**1–24. doi:10.1016/j.earscirev.2011.12.007.

Rahman MJJ, Faupl P, Alam MM. 2009. Depositional facies of the subsurface Neogene Surma group in the Sylhet trough of the Bengal Basin, Bangladesh: record of tidal sedimentation. Int J Earth Sci **98:**1971–1980. doi:10.1007/s00531-008-0347-7.

Rajkonwar C, Fanai L, Malsawma J, Lalnuntluanga P, Lalremruatfela C et al. 2015. Ichnofossil assemblage of Bhuban Formation (Surma Group) from Zuangtui area, Aizawl, Mizoram. Science Vision **15:**164–177.

Rajkonwar C, Ralte VZ, Lianthangpui PC, Tiwari RP, Patel SJ. 2014. Miocene ichnofossils from Upper Bhuban Succession, Bhuban Formation (Surma Group), Mizoram, India. Spec Publ Paleontol Soc India **5:**247–255.

Rajkonwar C, Tiwari RP, Patel SJ. 2013. *Arenicolites helixus* isp. nov. and associated ichnofossils from the Bhuban Formation, Surma Group (Lower-Middle Miocene) of Aizawl, Mizoram, India. Himal Geol **34:**18–37.

Ralte VZ, Lalchawimawii, Malsawma J, Tiwari RP. 2009. Decapod fossils from the Bhuban Formation, Surma Group, Aizawl, Mizoram. Earth Science India **2:**196–210.

Rangin C, Maurin T, Masson F. 2013. Combined effects of Eurasia/Sunda oblique convergence and East-Tibetan crustal flow on the active tectonics of Burma. J Asian Earth Sci **76:**185–194. doi:10.1016/j.jseaes.2013.05.018.

Reuter M, Piller W, Harzhauser M, Mandic O, Berning B et al. 2009. The Oligo-/Miocene Qom Formation (Iran): Evidence for an early Burdigalian restriction of the Tethyan Seaway and closure of its Iranian gateways. Int J Earth Sci **98:**627–650. doi:10.1007/s00531-007-0269-9.

Rögl F. 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Ann Naturhist Mus Wien **99:**279–310.

Rögl F. 1999. Mediterranean and Paratethys: facts and hypotheses of an Oligocene to Miocene paleogeography: short overview. Geol Carpath **50:**339–349.

Roman J, Roger J, Platel J-P, Cavelier C. 1989. Les échinoides du Crétacé et du Paléogene du Dhofar (Sultanat d'Oman) et les relations entre les bassins de l'Océan Indien et de la Méditerranée. Bull Soc Géol France **5:**279–286. doi:10.2113/gssgfbull.v.2.279.

Rosen BR, Smith AB. 1988. Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from Late Cretaceous to Recent, using a new method. Geol Soc London Spec Publ **37:**275–306. doi:10.1144/gsl.sp.1988.037.01.19.

Rose E, Lalchawimawii, Lalrammuana A, Malsawma J, Lalnuntluanga P et al. 2021. Ichnofossils from the Middle Bhuban Unit, Bhuban Formation of Pachhy Lokah near Maubawk, Siaha District, Mizoram, India. Science Vision **21:**26–35. doi:10.33493/scivis.21.02.01.

Satsangi PP, Patil RS. 1988. Mega fossils from Bhuban Formation of Mizoram. Newsletter Geol Surv India NER **7:**1–11.

Schumacher CF. 1817. Essai d'un Nouveau Système des Habitations des Vers Testacés. Schultz, Copenghagen.

Scotese CR, Wright N. 2018. PALEOMAP paleodigital elevation models (PaleoDEMS) for the Phanerozoic. Paleomap Proj, pp. 1–26. doi:10.1130/abs/2016nc-275387.

Singh MC, Kundal P, Kushwaha RAS. 2010. Ichnology of Bhuban and Boka Bil Formations, Oligocene-Miocene deposits of Manipur Western Hill, northeast India. J Geol Soc India **76:**573–586. doi:10.1007/s12594-010-0118-5.

Sinha NK, Chatterjee BP, Satsangi PP. 1982. Status of palaeontological researches in the North-east States of India. Rec Geol Surv India **112:**66–88.

Smith AB, Kroh A. 2011. The Echinoid Directory. Available at: https://web.archive.org/web/20190430172545/http://www.nhm.ac.uk/ourscience/data/echinoid-directory/. Accessed 27 Sept. 2025.

Srivastava DK. 2012. An annotated bibliography of fossil echinoids (Echinodermata) of India and Pakistan. J Palaeontol Soc India **57:**163–203. doi:10.1177/0552936020120210.

Srivastava DK, Lalchawimawii, Tiwari RP. 2008. Echinoids from the Bhuban Formation (Surma Group), Mizoram. J Palaeontol Soc India **53:**221–226. doi:10.1177/0971102320080211.

Stara P, Borghi E. 2012. First fossil record of the genus *Faorina* (Echinoidea: Pericosmidae). Boll Soc Paleontol Ital **51:**85–98.

Thompson JR, Ausich WI, Cournoyer ME. 2022. The morphologic and paleobiogeographic implications of a new early Silurian echinoid from Anticosti Island, Quebec, Canada. Can J Earth Sci **59:**973–983. doi:10.1139/cjes-2022-0028.

Tian SY, Yasuhara M, Condamine FL, Huang H-HM, Fernando AGS et al. 2024. Cenozoic history of thetropical marine biodiversity hotspot. Nature **632:**343–349. doi:10.1038/s41586-024-07617-4.

Tiwari RP. 1993. Palaeontological and Biostratigraphic Studies of the Surma Group Rocks around Aizawl and Lunglei, Mizoram, India. PhD dissertation, Gauhati University, Guwahati.

Tiwari RP, Jauhri AK. 2014. Miocene palaeobiology of Mizoram: Present status and future prospect. Spec Publ Paleontol Soc India **5:**189–204.

Tiwari RP, Rajkonwar C, Lalchawimawii, Malsawma PLJ, Ralte VZ et al. 2011. Trace fossils from Bhuban Formation, Surma Group (Lower to Middle Miocene) of Mizoram India and their palaeoenvironmental significance. J Earth Syst Sci **120:**1127–1143. doi:10.1007/s12040-011-0131-0.

Uhen MD, Allen B, Behboudi N, Clapham ME, Dunne E et al. 2023. Paleobiology database user guide version 1.0. PaleoBios **40:**1–56. doi:10.5070/p9401160531.

Wang C-C. 1984. A new species of *Pericosmus* (Echinoidea) from the Miocene Nankang Sandstone of northern Taiwan. Spec Publ Cent Geol Surv MOEA **3:**249–256.

Yasuhara M, Huang HHM, Reuter M, Tian SY, Cybulski JD et al. 2022. Hotspots of Cenozoic tropical marine biodiversity. Oceanogr Mar Biol Annu Rev **60:**243–300. doi:10.1201/9781003288602-5.

Zamora S, Lefebvre B, Javier Alvaro J, Clausen S, Elicki O et al. 2013. Cambrian echinoderm diversity and palaeobiogeography. *In*: Harper DAT and Servais T (eds) Early Palaeozoic Biogeography and Palaeogeography. Geological Society, London, Memoirs, London, pp. 157–171. doi:10.1144/m38.13.