



A new fossil species of *Clypeaster* (Echinoidea) from Malaysian Borneo and an overview of the Central Indo-Pacific echinoid fossil record

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Abstract

A complete, but fractured and crushed, echinoid corona from early to middle Miocene of Sarawak, Malaysia, is described as a new species, *Clypeaster sarawakensis* nov. sp. Although similar to modern *C. rarispinus*, the new species shows a distinct set of characters including petal length, periproct position and gut coiling. The discovery of a new *Clypeaster*, a genus characterised by a high preservation potential, illustrates that little is known about echinoid evolution and diversification in the Central Indo-Pacific, which features as a biodiversity hotspot since the Oligocene. Besides describing *Clypeaster sarawakensis*, we also compiled the known Central Indo-Pacific echinoid fossil record and used it to examine the Cenozoic diversity of echinoids. The overall diversity throughout the Cenozoic, and especially the rapid diversity increase at the Oligocene–Miocene boundary, corresponds to diversity trends observed in other taxa from the region.

Keywords Hotspot · Tethys · Miocene · Cenozoic · Preservation potential · Computed tomography

Introduction

The Central Indo-Pacific has been a hotspot of marine biodiversity for the last 28 My (Mihaljević et al. 2017). The high diversity of corals (Wallace and Rosen 2006), as well as foraminifera (Renema et al. 2008), molluscs (Kay 1996; Harzhauser et al. 2002, 2008) and mangroves (Ellison et al. 1999; Morley 2000), has shifted from the West Tethyan marine biodiversity hotspot (middle Eocene and older), through an Arabian hotspot (late Eocene–early Miocene), and finally to the Central Indo-Pacific region where it was

well established by the early Miocene (Harzhauser et al. 2007; Renema et al. 2008). Shallow water, tropical coral reefs provided the foundation for its diversity by offering habitats for a myriad of vertebrate and invertebrate species, each of which has a specific function within the ecosystem. Echinoids (Echinodermata: Echinoidea), for example, are important herbivores in the reef ecosystems; however, they are also known to be linked to major ecosystem shifts. A classic example is the decline in Caribbean urchin densities due to the introduction of pathogens in the 1980s, which led to a significant reduction in their herbivory and a dramatic phase shift from coral- to algal-dominated habitats (Hughes 1994). Conversely, urchin population booms can cause excessive herbivory and shift healthy ecosystems to barren habitats (Bellwood et al. 2004). Overall, stable sea urchin populations promote biodiversity on reefs (Sammarco 1982).

Global Cenozoic diversity of echinoids is characterised by a peak in the Eocene which is preceded and followed by much lower diversities in the Paleocene and Oligocene (Kier 1974; McKinney et al. 1992, 2014). These evolutionary patterns seem to be driven by global sea temperatures (McKinney and Oyen 1989) on one hand, but also appear to be tightly linked with the rock record (Smith et al. 2012; Smith and Benson 2013). The same general pattern has been reported for the Indo-Pacific despite a lack

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of systematic analysis of its echinoid fossil record (Ali 1983; McKinney et al. 1992). In contrast, regional echinoid diversity in Australia does not show a decline after the Eocene, but rather a continuous increase in diversity. This special situation was caused by the tectonic northwards movement of Australia into warmer, tropical waters that overall promote higher diversity (McKinney et al. 1992). By contrast, Mediterranean Eocene and Oligocene faunas were shared with the Middle East, India and Malaysia, creating a great tropical Indo-Mediterranean realm (Stefanini 1924; Ghiold and Hoffman 1986; Harzhauser et al. 2007; Ghiold 2013), which was separated by the early Miocene due to the closure of the Mediterranean sea (Tethys) creating a distinct Indo-Pacific fauna (Rosen and Smith 1988). Therefore, diversity hotspots for echinoids, along with those of corals, foraminifera, molluscs and mangroves, gradually shifted from the Western Tethys to the current biodiversity hotspot in the coral triangle. Unfortunately, in contrast to Australian, North American, European and North African faunas, very little is known about echinoid evolution and diversification in the Central Indo-Pacific biodiversity hotspot, and a systematic review of the region's echinoid fossil record is urgently needed.

Lack of knowledge of echinoid evolution and diversification in the Central Indo-Pacific has little to do with preservation potential as usually echinoids have excellent fossil records and are one of the most studied fossil benthic invertebrate groups (Mooi 2001; Kroh and Nebelsick 2010). However, there is a difference in preservation potential between regular and irregular echinoids. Regular echinoids are less likely to be preserved due to their less strongly interconnected coronal plates and hence higher susceptibility to disarticulation, specifically with elevated temperature or turbulence (Kidwell and Baumiller 1990; Greenstein 1991). Experimental studies show that the tests of regular echinoids can disintegrate to individual plates within 10–12 days (Greenstein 1991). Substrate (rocky, sandy, muddy) and the mode of life (infaunal or epifaunal) contribute to the preservation potential (Kier 1977; Smith 1984). Additionally, sand-dollar-like irregular echinoids have internal buttressing, a skeletal structure that provides stability to their discoidal test. It has been shown that skeletal stability (durability) is more important than life habitat in determining preservation potential (Greenstein 1993). A good example of this is the irregular echinoid genus *Clypeaster*, one of the most common fossil echinoids of the Cenozoic (Michelin 1855), characterised by a rather sturdy test and well-developed internal buttressing (e.g. Mortensen 1948; Roman 1952). Yet herein, we describe a new species of *Clypeaster* from the early Miocene of Malaysia, suggesting undersampling of the echinoid fauna in the Central Indo-Pacific. To test this hypothesis, we

provide an overview of the fossil record of echinoids in the Central Indo-Pacific.

Materials and methods

Study site

A single *Clypeaster* specimen was collected from the Sibuti Formation in north-west Sarawak, Miri Division, Malaysia (4°3'25.27"N 113°48'33.12"E) (Fig. 1). The Sibuti Formation consists mainly of shales, but is locally calcareous with thin lenses of limestone and sandstone (Liechti 1960; Wilford 1961; Haile 1962; Hutchison 2005). It overlies the Subis (Tangap) Limestone Formation, and is stratigraphically located below the sandstones and mudstones of the middle Miocene Lambir Formation (Simmons et al. 1999; Hutchison 2005). Studies of the large benthic foraminifera, planktonic foraminifera and pollen of the Sibuti Formation indicate an early Miocene to earliest middle Miocene age (Large benthic foraminifera zone Te5-Tf1) (Liechti 1960; Simmons et al. 1999). The Sibuti Formation is also referred to as the Sibuti Member or Sibuti facies and is included within the Setap Shale Formation by some workers (Hutchison 2005). The Sibuti Formation is interpreted as inner to outer neritic with water depths less than 50 m (Liechti 1960; Simmons et al. 1999). Other than the *Clypeaster* specimen described herein, solitary corals (*Cycloseris*, *Heterocyathus*), fragments of echinoid spines and loose large benthic foraminifera were also found on the site. The fossil site was a small, natural outcrop recognised only as a clearing of vegetation along the road from Bekenu to Bungai Beach. It had been discovered during a reconnaissance trip in February 2011 conducted by the University of Queensland team working on marine biotic evolution in SE Asia.

Fossil *Clypeaster* taxonomic description

The taxonomic description of a single *Clypeaster* specimen presented herein follows the 28 taxonomic characters identified and described by Mihaljević et al. (2011) (Table 1). The terminology of the echinoid endoskeleton used follows Mortensen (1948), Durham (1955) and Mooi (1989). Computed tomography (CT) was used to non-destructively obtain information on internal buttressing and on the proportions of the digestive tract, an important taxonomic character (e.g. Mortensen 1948; Roman 1952; Mihaljević et al. 2011). The classification used follows Kroh and Smith (2010).

The whole specimen was scanned using a 16-slice helical CT scanner (Toshiba Medical Systems Corporation, Tochigi-ken, Japan) with volumes acquired using the

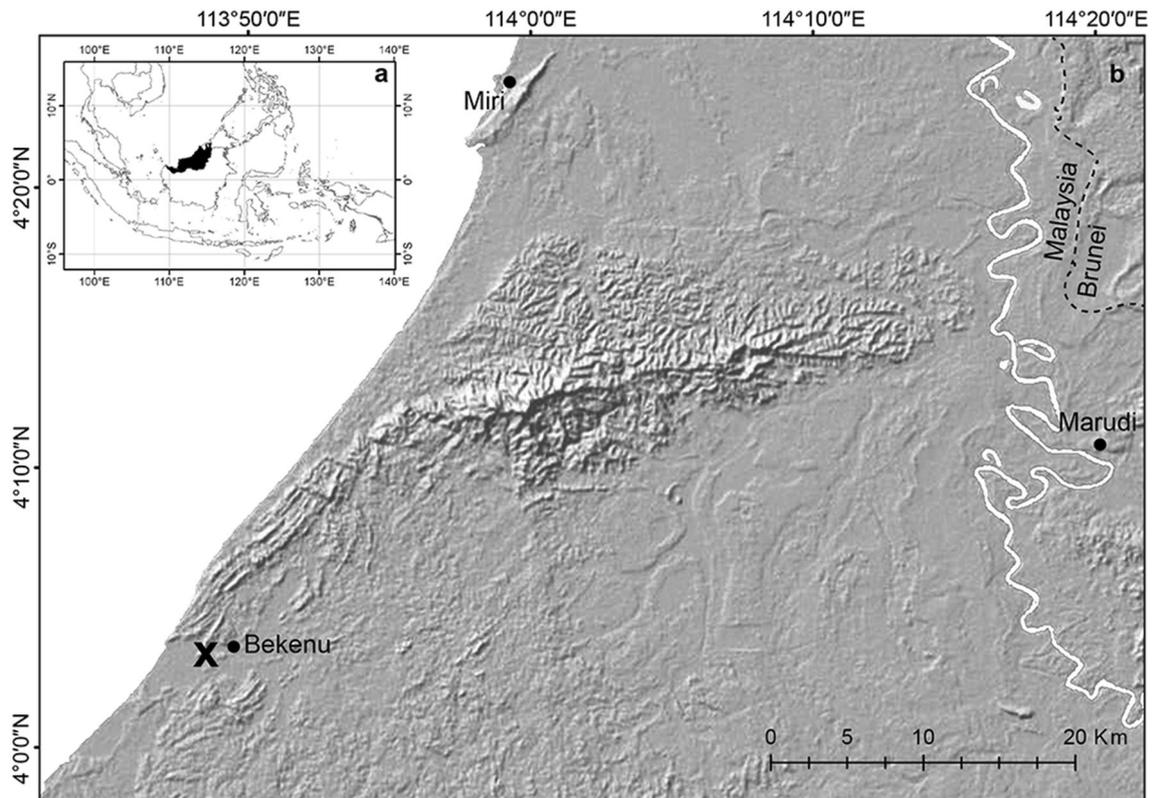


Fig. 1 Map of study site where the new fossil species of *Clypeaster* was found. **a** Map of the Central Indo-Pacific region with Sarawak marked in black. **b** northern part of Sarawak with marked study site (X)

following parameters: 100 kV, 100 mA, 1.5 s, 0.5 mm slice thickness, pitch factor 0.688/helical pitch 11, rotation time 2.0, smallest possible scan field of view (180 mm) and small focal spot, reconstruction interval 0.4 mm, and bone algorithm (WL 1100; WW, 4500). The CT study was viewed in Digital Imaging and Communications in Medicine (DICOM) format, and volumetric data reconstruction was performed using OsiriX MD image viewing software (v.9.0.1, Pixmeo, Geneva, Switzerland). The *Clypeaster* specimen is stored in the paleontological collections of the Queensland Museum in Brisbane, Australia, with the registration number QMF58959.

Fossil and modern distributions

The Central Indo-Pacific (here defined as 20°S–20°N, 90°–180°E) echinoid fossil record used in this study was obtained from the Paleobiology Database (PBDB, <http://paleobiodb.org>), a non-profit public resource containing a global compilation of the spatial and temporal observations of taxa in the fossil record. Data were downloaded from the PBDB on 28 February 2017. The PBDB fossil record was supplemented further by data from published monographs (Fritsch 1877; Martin 1880; Vredenburg 1919; Gerth 1922; Vredenburg 1922; Gerth 1927; Jeannet 1935; Jeannet and

Martin 1937; Kier 1964) and more recent literature (Lindley 2001, 2003, 2004; Donovan et al. 2010, 2012; Donovan and Renema 2015) not yet included in the PBDB. Validity of names of fossil genera was checked through the WoRMS Match Taxa (Kroh and Mooi 2017) function on 28 February 2017. Modern echinoid distribution was obtained from the Ocean Biogeographic Information System (OBIS, iobis.org) and supplemented with other published literature (De Meijere 1903; Mortensen 1948; Clark and Rowe 1971). Using both fossil and modern echinoid distributions in the Central Indo-Pacific, we estimated echinoid diversity through the Paleogene and Neogene (65 My–2.58 My).

To assess if the difference in preservation potential between regular and irregular echinoids affected their occurrence in the Central Indo-Pacific fossil record, a rarefaction curve was generated by plotting the number of echinoid collections against the number of genera/higher taxa. The rarefaction curve was generated using R, Version 2.15.2 software (R Development Core Team 2017). From the literature, we extracted information on the skeletal elements preserved and used for echinoid identification and description to make further inferences about the difference in preservation potential between regular and irregular echinoids.

Table 1 Comparison of morphological characters in *Clypeaster sarawakensis* nov. sp. with *Clypeaster* species present in (a) the Central Indo-Pacific fossil record, and (b) the modern Central Indo-Pacific and analysed in Mihaljević et al. (2011)

Morphological characters	<i>Clypeaster sarawakensis</i> ^F	<i>Clypeaster amandalei</i> ^M	<i>Clypeaster blumenthali</i> ^F	<i>Clypeaster brevipetalus</i> ^F	<i>Clypeaster fervens</i> ^M	<i>Clypeaster humili</i> ^{F, M}	<i>Clypeaster latissimus</i> ^{F, M}
Marginal buttressing							
Extent of marginal buttressing	Series of walls forming a wide buttressed zone	Series of walls forming a wide buttressed zone	NA	NA	Single internal wall around part or all of test*	Series of walls forming a wide buttressed zone	Series of walls forming a wide buttressed zone
Ambulacral buttress organization	Bar(s)	Aligned pillars*	NA	NA	Aligned pillars*	Bar(s)	Bar(s)
Internal wall effectively forming a double wall with microcanal system	?No	No	NA	NA	No	No	No
Radial bars projecting in from test margin along adradial sutures	Absent	Absent	NA	NA	Along just posterior interambulacrum (periproctal)*	Absent	Absent
Central buttressing							
Central buttressing structures	Present	Present	NA	NA	Present	Present	Present
Central buttressing of interambulacral zones	Infill of relatively fine pillars + bars in interradiar zone	Dominated by large adradial bars/pillars bounding lower ends of petals*	NA	NA	Infill of relatively fine pillars + bars in interradiar zone	Dominated by large adradial bars/pillars bounding lower ends of petals*	Infill of relatively fine pillars + bars in interradiar zone
Central buttressing fused to form an almost continuous curtain enclosing petaloid area:	No	No	NA	NA	No	No	No
Petals							
Central ambulacral zones within petals	Fine pillars only	No buttressing*	NA	NA	Fine pillars only	No buttressing*	Fine pillars only
Distance from distal end of petal III to ambitus vs. length of petal III:	~ 0.46 (petals end midway to ambitus)	0.35–0.65	0.35–0.65	> 0.7—petals from ambitus*	0.35–0.65	0.35–0.65	0.35–> 0.7
Petal III opened or closed - distance between inner pore-pairs vs. max broadness of inner 1-petals	~ 0.25 (relatively closed)	0.76–0.95—widely open*	0.76–0.95—widely open*	< 0.15—almost closed*	0.76–0.95—widely open*	< 0.15—almost closed*	< 0.15—almost closed*
Petal II opened or closed - distance between inner pore-pairs vs. max broadness of inner petals	~ 0.25 (relatively closed)	0.15–0.75	0.76–0.95*	< 0.15*	< 0.15*	< 0.15*	< 0.15*
Number of occluded plates in petal II	NA	1–6	?1–6	?1–6	>6	>6	>6
Demi-plates in petals	Present	Present	?Present	?Present	Present	Present	Present

Table 1 (continued)

Morphological characters	<i>Clypeaster cf. malumbangensis</i> ^F	<i>Clypeaster minicaceus</i> ^M	<i>Clypeaster pateriformis</i> ^M	<i>Clypeaster phyllodes</i> ^F	<i>Clypeaster rarispinus</i> ^M	<i>Clypeaster reitculatus</i> ^{F, M}	<i>Clypeaster saipanicus</i> ^F
Marginal buttressing							
Extent of marginal buttressing	NA	Series of walls forming a wide buttressed zone	Series of walls forming a wide buttressed zone	?Series of walls forming a wide buttressed zone*	Series of walls forming a wide buttressed zone	Absent*	NA
Ambulacral buttress organization	NA	Bar(s)	Bar(s)	NA	Bar(s)	-	NA
Internal wall effectively forming a double wall with microcanal system	NA	No	No	NA	No	No	NA
Radial bars projecting in from test margin along adradial sutures	NA	Along just posterior interambulacrum (periproctal)*	Absent	NA	Absent	Along just posterior interambulacrum (periproctal)*	NA
Central buttressing structures	NA	Present	Present	NA	Present	Present	NA
Central buttressing of interambulacral zones	NA	Dominated by large adradial bars/pillars bounding lower ends of petals*	Infill of relatively fine pillars + bars in interradial zone	NA	Infill of relatively fine pillars + bars in interradial zone	Dominated by large adradial bars/pillars bounding lower ends of petals*	NA
Central buttressing fused to form an almost continuous curtain enclosing petaloid area:	NA	No	No	NA	No	No	NA
Central ambulacral zones within petals	NA	No buttressing*	Fine pillars only	NA	Fine pillars only	No buttressing*	NA
Petals							
Distance from distal end of petal III to ambitus vs. length of petal III:	> 0.7—petals end far from ambitus*	> 0.7—petals end far from ambitus*	> 0.7—Petals end far from ambitus*	> 0.7—Petals end far from ambitus*	> 0.7—Petals end far from ambitus*	0.35–0.65	0.35–0.65
Petal III opened or closed - distance between inner pore-pairs vs. max breadth of inner 1-petals	< 0.15—Almost closed*	0.76–0.95—Widely open*	< 0.15—Almost closed*	? < 0.15—Almost closed	< 0.15—Almost closed*	< 0.15—Almost closed*	NA
Petal II opened or closed - distance between inner pore-pairs vs. max breadth of inner petals	< 0.15*	< 0.15*	< 0.15*	0.15–0.75	< 0.15—Almost closed*	< 0.15*	0.15–0.75

Table 1 (continued)

Morphological characters	<i>Clypeaster</i> cf. <i>malumbangensis</i> ^F	<i>Clypeaster</i> <i>miniacicus</i> ^M	<i>Clypeaster</i> <i>pateriformis</i> ^M	<i>Clypeaster</i> <i>phyllodes</i> ^F	<i>Clypeaster</i> <i>rarispinus</i> ^M	<i>Clypeaster</i> <i>reticulatus</i> ^{F, M}	<i>Clypeaster</i> <i>saipanicus</i> ^F
Number of occluded plates in petal II	?1–6	1–6	?1–6	?1–6	1–6	1–6	?1–6
Demi-plates in petals	Present	Present	Present	Present	Present	Present	?Present
Sunkenness of oral surface	NA	Flat outer region with intumed test close to the peristome	Flat outer region with intumed test close to the peristome	Flat outer region with intumed test close to the peristome	Flat outer region with intumed test close to the peristome	Test with broad adoral concavity*	Test with broad adoral concavity*
Angle of peristome to point of contact	NA	5°–10°	?5°–10°*	5°–10°	0°*	5°–10°	? > 10°*
Peripheral swollen rim	Absent*	Absent*	Absent*	Absent*	Present	Present	Absent*
Thickness of the test edge	?Rounded	Rounded*	?Thin/sharp*	Rounded	Rounded	Rounded	Rounded
Food grooves	Present on oral surface only	Present on oral surface only	Present on oral surface only	Present on oral surface only	Present on oral surface only	Present on oral surface only	Present on oral surface only
S/T ratio (distance of distal end of the food groove to ambitus vs. distance of peristome to ambitus)	NA	0.4–0.7*	< 0.35—Food groove extends almost to ambitus	NA	< 0.35—Food groove extends almost to ambitus	> 0.7—Food groove confined to adoral region	? > 0.7—Food groove confined to adoral region*
Combed area	NA	Absent	Absent	Absent	Absent	Absent	Absent
Tubercle differentiation along ambulae	NA	Present, pores in distinct V-shaped region on each plate	?Absent; pores scattered across plates	?Absent; pores scattered across plates	Resent, pores in distinct V-shaped region on each plate	Absent; pores scattered across plates	?Absent; pores scattered across plates
Periproct	NA	0.8–1.5	> 1.5*	0.8–1.5	< 0.8	0.8–1.5	0.8–1.5*
Situated between plates	NA	5b and 4a	NA	NA	4b and 3a	4b and 3a	NA
Situated	On oral surface	On oral surface	On oral surface	On oral surface	On oral surface	On oral surface	On oral surface
Gut coiling	NA	runs anteriorly and loops back before reaching perradius of ambulacrum III	runs anteriorly and loops back before reaching perradius of ambulacrum III	NA	Comes out slightly left of centre and loops around front (crosses perradius of ambulacrum III)*	Comes out slightly left of centre and loops around front (crosses perradius of ambulacrum III)	NA
digestive system							

Table 1 (continued)

Morphological characters	<i>Clypeaster</i> cf. <i>malumbangensis</i> ^F	<i>Clypeaster</i> <i>miniacus</i> ^M	<i>Clypeaster</i> <i>pateriformis</i> ^M	<i>Clypeaster</i> <i>phylloides</i> ^F	<i>Clypeaster</i> <i>rarispinus</i> ^M	<i>Clypeaster</i> <i>reticulatus</i> ^{F M}	<i>Clypeaster</i> <i>saipanicus</i> ^F
Apical disc	Number of gonopores 5	5	5	5	5	5	?5
Lantern support structures	?Paired	Paired	?Paired	?Paired	Paired	Paired	?Paired
Interambulacral plates	Ambulacral and interambulacral columns of plates	Ambulacral and interambulacral columns of plates	Ambulacral and interambulacral columns of plates	Ambulacral and interambulacral columns of plates	Ambulacral and interambulacral columns of plates	ambulacral and interambulacral columns of plates	Ambulacral and interambulacral columns of plates

Detailed description of morphological characters used can be found in Mihaljević et al. (2011)

NA refers to characters that were not available due to poor preservation of the fossil specimen

^FCharacters that differ to *Clypeaster sarawakensis*

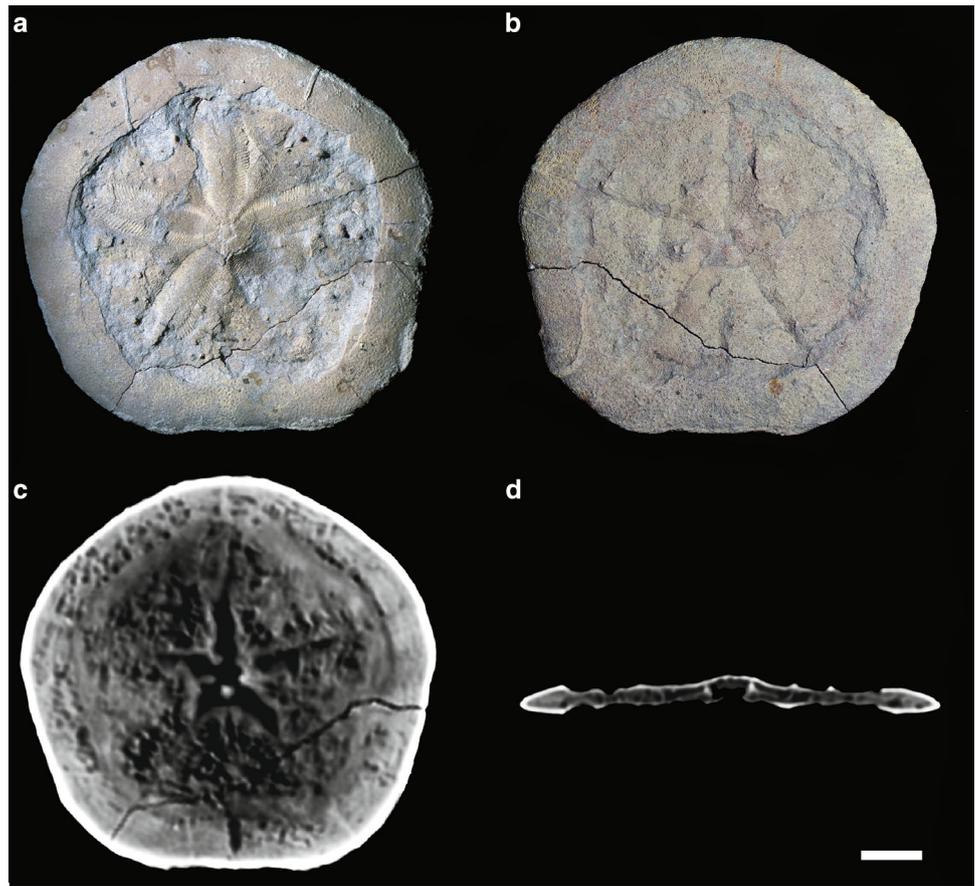
— Inapplicable

? indicates uncertainty in character scoring

^FFossil species

^MModern species

Fig. 2 *Clypeaster sarawakensis* nov. sp., QMF58959, holotype. **a** Aboral side, **b** oral side, **c** and **d** computed tomography (CT) images showing internal buttressing - **c** dorsoventral view, and **d** transversal view. Scale bar represents 10 mm



Systematic palaeontology

Class Echinoidea Leske, 1778

Subclass Euechinoidea Bronn, 1860

Infraclass Acroechinoidea Smith, 1981

Irregularia Latreille, 1825

Microstomata Smith, 1984

Neognathostomata Smith, 1981

Order Clypeasteroidea Agassiz, 1835

Suborder Clypeasterina Desor, 1857

Family Clypeasteridae Agassiz, 1835

Diagnosis Clypeasterina echinoids with five gonopores in the apical disc and peristome generally sunken, with surrounding infundibulum (Smith and Kroh 2011a, b).

Range. Late Eocene to Recent, worldwide in depths from 0 to 550 m.

Genus *Clypeaster* Lamarck, 1801

Type species. *Echinus rosaceus* Linnaeus 1758, from the tropical western Atlantic by subsequent designation (Rowe and Gates 1995).

Diagnosis Clypeasteridae, which are ovate to subpentagonal with rounded or thin/sharp margin and central apical disc with 5 gonopores. Internal buttressing usually well-developed around periphery. Petals well-developed; plating compound with every other plate a demiplate. All interambulacra disjunct on oral surface. Periproct oral, towards posterior margin; positioned between third and fifth pairs of post-basicoronal interambulacral plates. Food grooves a simple strong perradial trunk; unbranched and confined to oral surface. Pores and tubercles irregularly scattered (Smith and Kroh 2011a, b).

Clypeaster sarawakensis nov. sp.

Figure 2, Table 1.

Holotype A complete, but fractured and crushed corona (Queensland Museum QMF58959).

Type locality North-west Sarawak, Miri Division, Malaysia (4°3'25.27"N 113°48'33.12"E).

Type stratum Sibuti Formation, early Miocene to earliest middle Miocene (Large benthic foraminifera zone Te5-Tf1).

Diagnosis. *Clypeaster* with pentagonal outline, digestive tract looping back before Amb III, and relatively closed petals which extend ~ 70% of the corresponding test radius to the ambitus.

Description Test pentagonal with rounded edge, 670 mm in length and 696 mm in width. Test dorsoventrally crushed, thus its height might be underestimated (measured at 7 mm). Most of oral surface flat (angle of peristome to point of contact is 5°–10°), only area closest to the peristome sunken, forming a small infundibulum. Peripheral swollen rim present and the test edge is rounded.

Petals well developed and relatively closed (ratio of distance between inner pore-pairs and maximum width of inner petals for both petal II and III ~ 0.25). Petals not reaching ambitus, extending ca. two-thirds of the corresponding test radius (based on petal I (ratio of distance from distal end of petal III to ambitus and length of petal III ~ 0.46). Neither petals nor the petalodium as a whole are markedly inflated; instead, they are almost level with the interambulacra. Area around apical disc slightly inflated, causing a slightly concave profile of the petals in lateral view.

Food grooves present only on oral surface and extending almost to the ambitus (ratio of distance of distal end of the food groove to ambitus and distance of peristome to ambitus ~ 0.33). Combed areas absent.

Periproct situated on the oral surface close to the ambitus (ratio of distance to ambitus from periproct and periproct length ~ 0.64). Tract of digestive system runs anteriorly and loops back before reaching perradius of ambulacrum III. Lantern support structure is paired.

Marginal buttressing is well developed. Series of walls form a wide buttressed zone on the margin. Ambulacral buttressing comprises bar(s). Internal wall does not seem to form a double wall with microcanal system, although a double wall might be infilled by syntaxial rim cement. Radial bars projecting in from test margin along adradial sutures are absent. Central buttressing made of infill of relatively fine/delicate pillars and bars in the interradiol zone. Central buttressing is not fused and, therefore, does not form a continuous curtain enclosing petaloid area. In the central ambulacral zones within the petals, only fine pillars are present.

Preservation. The test is dorsoventrally flattened with the peripheral rim supported by very dense marginal buttressing. This dorsoventral flattening might have impacted the test profile; thus, the test height is reported as an underestimated value. As a consequence of collapsed test height,

the angle of peristome to point of contact (measure of the flatness of the oral surface) has also been impacted. However, from the transversal view (Fig. 2d), it is clear that the oral surface of the studied specimen is neither as flat as in *Clypeaster annandalei* nor as convex as in *C. rosaceus* (Mihaljević et al. 2011). Thus, the angle of peristome to point of contact measures 5°–10°. The test flattening has resulted in a circular fracture of the test along the inner edge of marginal buttressing. During the fossilisation process, sediment has accumulated and lithified along the fracture concealing some of the taxonomical informative characters, including: (a) tips of the petals-creating uncertainty in some petal measurements, and (b) occluded plates-preventing counting of the plates. The oral side of the specimen is not as well preserved. The periproct is almost undetectable on the specimen but it is clearly visible using the CT images (Fig. 2c). Thus, the distance of the periproct from the ambitus was measured on the CT image. Additionally, due to the poor preservation, determination of (a) plates between which the periproct is situated, and (b) tubercle differentiation along ambulacra could not be made. Despite the state of preservation, 25 out of 28 characters described in Mihaljević et al. (2011) could be determined.

Remarks. The genus *Clypeaster* is characterised by a rather sturdy test, ovate to subpentagonal outline with rounded margin and internal buttressing. These features facilitate not only a high preservation potential, but also identification on generic level. However, subdividing *Clypeaster* taxonomically has proven difficult, largely because its approximately 400 nominal species show extensive gradation in test shape. A recent study re-evaluated taxonomic characters employed in previous attempts to subdivide the genus (Agassiz 1863; Pomel 1887; Lambert 1912; Serafy 1970; 1971; Hopkins 1988; Mooi 1989; Schultz 2006) and systematically assessed test architecture (internal buttressing) as a taxonomically informative character for distinguishing between species (Mihaljević et al. 2011).

Only 33 *Clypeaster* occurrences, of which eight are nominal species, are known from the Central Indo-Pacific fossil record: *C. blumenthali* (Jeannet and Martin 1937), *C. brevipetalus* (Jeannet and Martin 1937), *C. humilis* (Gerth 1922; Jeannet and Martin 1937), *C. latissimus* (Lindley 2003), *C. cf. malumbangensis* (Jeannet and Martin 1937), *C. phyllodes* (Fritsch 1877), *C. reticulatus* (Jeannet and Martin 1937; Lindley 2003, 2004) and *C. saipanicus* (Cooke 1957). Three of these (*C. humilis*, *C. latissimus* and *C. reticulatus*), together with 5 other *Clypeaster* species (*C. annandalei*, *C. fervens*, *C. miniaceus*, *C. pateriformis* and *C. rarispinus*), have been reported from the modern Central Indo-Pacific. We compared the Malaysian specimen described herein with the eight fossil species and five

Fig. 3 Echinoid genera/higher taxa rarefaction curves for all regular (dashed line) and irregular (solid line) echinoid collections from the Central Indo-Pacific

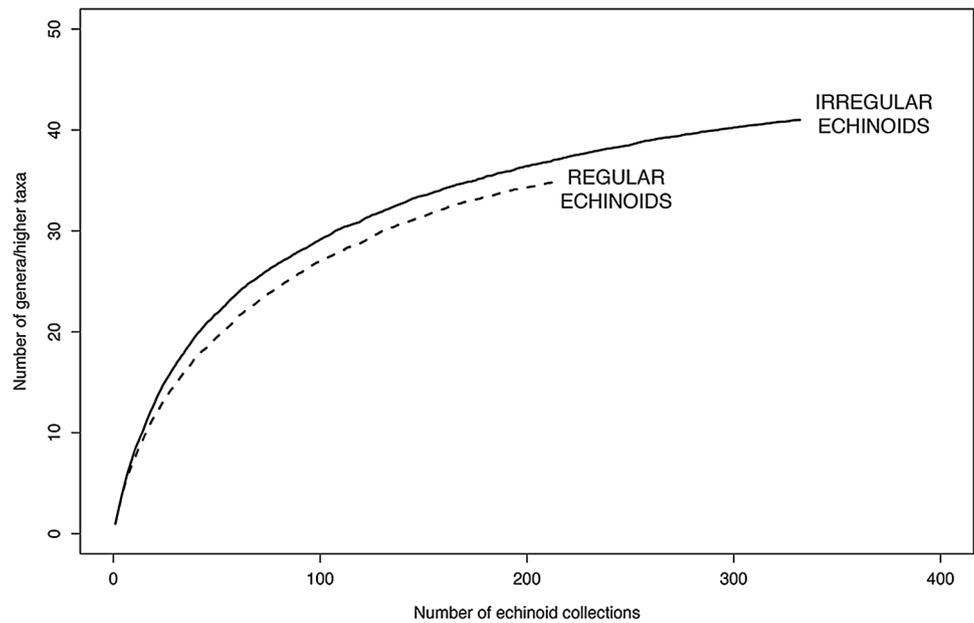


Table 2 Number of echinoid genera and higher taxa relative to the number of collections found in each time interval

Time interval	Number of occurrences	Number of genera and higher taxa
Neogene undifferentiated	18	13
Eocene	5	3
Oligocene	10	7
Miocene	278	83
Pliocene	114	35
Pleistocene	15	13

exclusively modern Central Indo-Pacific *Clypeaster* species (Table 1). Most of the fossil species lack any description of the internal structures, thus the comparison was not possible in these cases. From 28 accessed taxonomic traits, most traits (25) could be accessed in only eight out of the 13 Central Indo-Pacific *Clypeaster* species (Table 1). From all these species, the specimen described herein most closely resembles *Clypeaster rarispinus*. *Clypeaster rarispinus* is unknown from the Central Indo-Pacific fossil record but is common in coastal (shallower) regions of the modern north-western Indian Ocean and the Central Indo-Pacific (De Meijere 1903; Mortensen 1948; Clark and Rowe 1971). However, the following five morphological characters differentiate the studied specimen

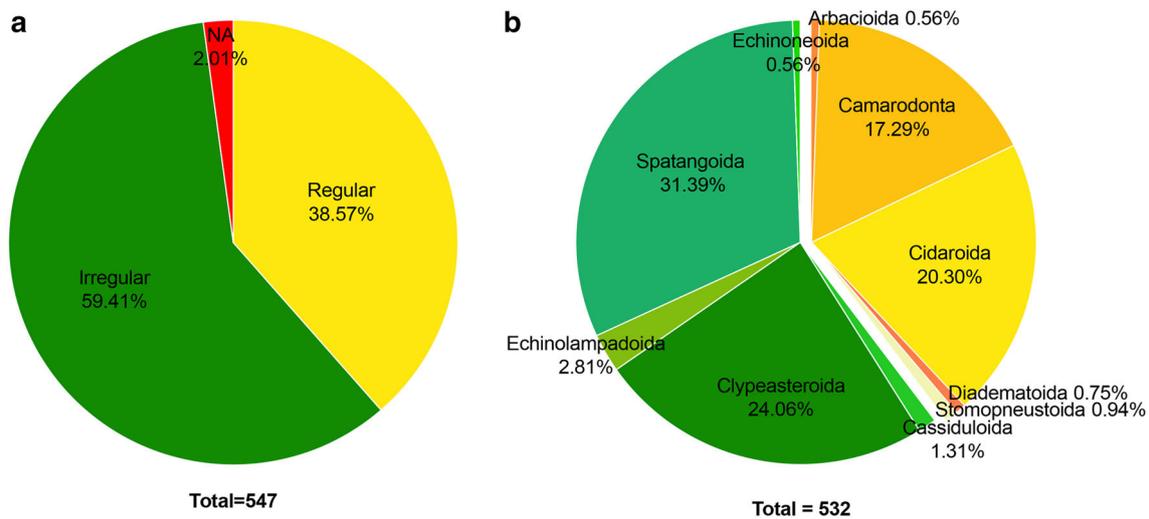


Fig. 4 Central Indo-Pacific echinoid fossil record. **a** Occurrences of irregular and regular echinoids, **b** occurrences of echinoid orders

Fig. 5 Diversity of Cenozoic echinoids in the Central Indo-Pacific: regular echinoids in yellow, and irregular echinoids in green. Abbreviations: *Eoc.* Eocene, *Mio.* Miocene, *P* Pleistocene

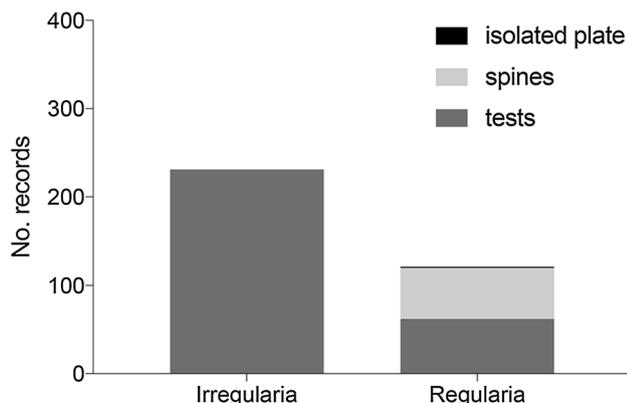
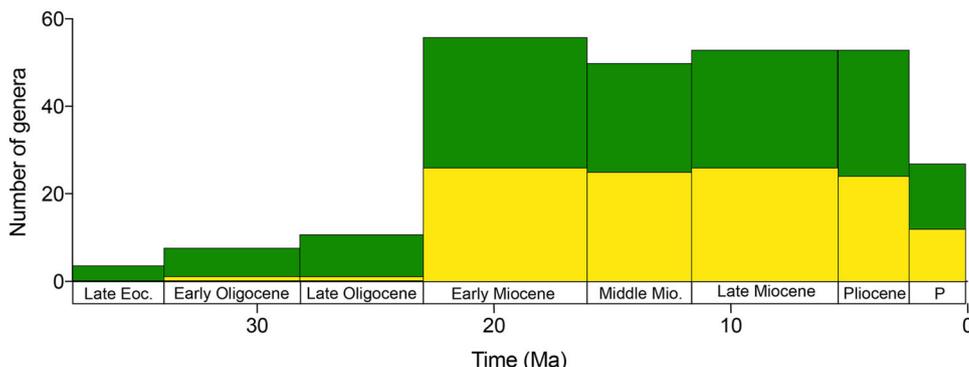


Fig. 6 The Central Indo-Pacific echinoid fossil record comprised of tests, spines and isolate plates. The presence of these skeletal elements in the fossil record differs between regular and irregular echinoids

from *C. rarispinus*: (a) petal III in *Clypeaster sarawakensis* nov. sp. extends further to ambitus than in *C. rarispinus*, (b) both petals II and III in *C. sarawakensis* nov. sp. are more open than in *C. rarispinus*, (c) oral surface in *C. sarawakensis* nov. sp. is less flat than in *C. rarispinus*, and (d) gut in *C. sarawakensis* nov. sp. runs anteriorly and loops back before reaching perradius of ambulacrum III, whereas in *C. rarispinus*, gut loops back after crossing perradius of ambulacrum III (Table 1).

Describing a new species based on a single specimen is problematic since no assessment of intraspecific variation can be made. This is particularly relevant in a species-rich genus such as *Clypeaster*, which also shows extensive gradation in test shape. In the past, new *Clypeaster* species were established based on minor shape differences in poorly preserved specimens, which has led to the inflation of the number of nominal species (Poddubiuk 1985). Moreover, a recent review of the clypeasteroid genus *Monostychia* shows high intraspecific variation and illustrates that to capture intraspecific variation assessment greater than 15 individuals are needed (Sadler et al. 2016). Nevertheless, following a robust taxonomic framework (Mihaljević et al. 2011), we could show that none of the

known species from the region are similar to our described Malaysian specimen. Thus, we are confident that it represents a new species.

Central Indo-Pacific echinoid fossil record

Data available

After combining the 96 records of fossil echinoids from the PBDB (Martin 1879; Ladd and Hoffmeister 1945; Abrard 1946; Beets 1947; Cloud et al. 1956; Martin and Braga 1993) and the 464 records extracted from the literature, the Central Indo-Pacific echinoid fossil record comprises 560 occurrences (Supplementary Table 1). These occurrences belong to 79 valid genera and 12 higher taxa (e.g. family, order; that is, not all fossil echinoids are described to genus level). Irregular echinoids contribute a larger number of taxa (43 of 307 samples) than regular echinoids (33 of 216 samples). Classification beyond the class Echinoidea is unknown for 11 occurrences. Neither of the rarefaction curves for regular or irregular echinoids have started to level off, but the curve for irregular echinoids is slightly more flattened, possibly indicating less undersampling (Fig. 3). Most records are from the Miocene of Indonesia (Table 2).

For 532 occurrences, family level is known. Camarodonta and Cidaroida are the two most common orders in the fossil record among regular echinoids, and Clypeasteroida and Spatangoida are the most common for irregular echinoids in the study area (Fig. 4).

Diversity of echinoids in the Central Indo-Pacific

Echinoid diversity in the Central Indo-Pacific, based on the fossil record compiled herein, appeared to have improved slowly until the early Miocene when a sharp increase is recorded (Fig. 5). After the rapid increase in generic diversity, with 45 new genera originating, the diversity stayed relatively stable throughout the Neogene. Both

regular and irregular echinoids displayed similar patterns (Fig. 5).

Preservation

For 352 of 464 fossil records extracted from the literature, information about skeletal element preservation has been gathered. The fossil record of irregular echinoids is based on complete or fragmented tests. In regular echinoids, spines are a big contributor to the fossil record in addition to the tests (Fig. 6). The record includes a single report based on a disarticulated plate of the test.

Implications

Due to their sturdy test, members of the genus *Clypeaster* are some of the most common fossil echinoids in the Cenozoic (Michelin 1855). Yet, we describe here a new species of this genus from a single specimen found at the study location. Thus, the description of a new *Clypeaster* species suggests undersampling, lack of systematic collection and overall poor knowledge of fossil echinoids from the Central Indo-Pacific. With a few exceptions (Lindley 2001, 2003, 2004; Donovan et al. 2010, 2012; Donovan and Renema 2015), systematic collection and description of the Central Indo-Pacific echinoids ceased in the first half of the twentieth century after the comprehensive works of Martin (1880), Gerth (1922), and Jeannet and Martin (1937). The Central Indo-Pacific fossil record in general was poorly known until 2010 when the Indo-Pacific Ancient Ecosystem Group (IPAEG) was founded. The IPAEG's purpose is to document and understand the relationship between environmental and biotic changes of shallow tropical marine ecosystems in the Indo-Pacific. Despite the tremendous improvements in our understanding of the Cenozoic diversification of tropical faunas in the Central Indo-Pacific over the last few years (e.g. Bromfield and Pandolfi 2011; McMonagle et al. 2011; Johnson et al. 2015; Santodomingo et al. 2015, 2016; Mihaljević et al. 2017), our knowledge of the echinoid fossil record in this region remains largely unchanged.

This overview of the Central Indo-Pacific echinoid fauna suggests that the overall pattern of echinoid diversity and especially the rapid diversity increase at the Oligocene–Miocene boundary corresponds with trends seen in corals, foraminifera and molluscs (Wilson and Rosen 1998; Harzhauser et al. 2002; Wallace and Rosen 2006; Harzhauser et al. 2007, 2008; Renema et al. 2008). In corals, a rapid diversity increase is also observed from the Early to Late Oligocene, when the Central Indo-Pacific biodiversity hotspot originated (Wilson and Rosen 1998; McMonagle et al. 2011; Mihaljević et al. 2017). The later onset of diversification of Central Indo-Pacific echinoid faunas in

comparison to corals may have a variety of reasons, including research bias (i.e. Late Oligocene echinoids may be understudied) and the possibility that diversification of echinoids might have genuinely lagged behind corals. That is, it may have taken place only after the true reef framework and diversity of habitats was properly established. An increase in the functional redundancy of corals has been suggested as an important factor in the persistence of the Central Indo-Pacific biodiversity hotspots for over 28 My (Mihaljević et al. 2017). However, high and constant echinoid diversity throughout the Neogene has potentially also contributed to the overall health of ecosystems through herbivory, bioerosion, and bioturbation.

To truly uncover the evolutionary patterns of the Central Indo-Pacific echinoids, an in-depth revision of taxonomy and stratigraphy of the known echinoid fossil record is required. Additionally, new fossil collections gathered in a rigorous temporal and environmental framework are needed, because they provide empirical data for documenting past diversity (Adrain 2001; Jackson and Johnson 2001; Jackson and Erwin 2006). New fossil data can help calibrate molecular clocks by providing firm minimum ages of diversification events, and facilitate understanding of paleontological longevity and distribution of taxa over spatial scales (Alfaro et al. 2007; Benton and Emerson 2007; Donoghue and Benton 2007; Simpson et al. 2011). The value of fossil data for evolutionary studies depends on the quality and precision of taxonomic identifications (and descriptions) of new collections (Patterson 1981; Hedges et al. 1996; Blair and Hedges 2005). Moreover, when estimating past diversity and conducting paleontological sampling, geological processes need to be considered (Jackson and Johnson 2001; Smith and McGowan 2011), including the relationship between the number of samples and extent of the examined rock (i.e. size of outcrop), facies diversity and their abundance in the geological record, and the preservation potential of different taxa in different facies (Foote 2001; Jackson and Johnson 2001; McGowan and Smith 2008; Smith and McGowan 2011; Zuschin et al. 2011; Smith and Benson 2013). The latter is especially important to consider for the echinoids, as taphonomic challenges have led to discrepancies in reported diversity between regular and irregular echinoids (Kier 1977; Greenstein 1993) because disarticulated or broken fragments (more common in regular echinoids) are commonly ignored in studies of faunal diversity (Donovan 2001; Kroh 2007). It is, therefore, not surprising that so far twice as many occurrences of irregular echinoids have been reported compared to regular echinoids from the Central Indo-Pacific biodiversity hotspot.

Better understanding of the diversity, abundance and taphonomy of the Central Indo-Pacific echinoids throughout the Cenozoic would advance our knowledge of

relationships between the Mediterranean, Indo-Pacific and Australian echinoid faunas. Understanding these past relationships of echinoid faunas would supplement our knowledge of present day distributions and aid our attempt to predict future diversities and distributions (Keith et al. 2013). Hence, new fossil collections and detailed taxonomic descriptions are the only reliable way forward in studying the evolution of the Central Indo-Pacific echinoids and the longevity of this whole marine biodiversity hotspot.

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