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A late Miocene record of the echinoid *Maretia* (Echinoidea, Spatangoida) from Victoria, Australia.

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An unlabelled group of irregular echinoids, donated to Museum Victoria, are identified as *Maretia* sp. aff. *planulata* (Lamarck, 1816) and their place of origin determined as the late Miocene Tambo River Formation at Swan Reach, East Gippsland. A comparison with the three extant species of the genus, *M. planulata* (Lamarck, 1816), *M. carinata* Bolau, 1873, and *M.*? *cordata* Mortensen, 1948, show *Maretia* sp. aff. *planulata* has a fair degree of similarity with the type species *M. planulata*. Because of this, and the lack of detail of certain diagnostic features on the specimens, the description has been left in open nomenclature. The fossil record of *Maretia*, currently considered to occur only within the Indo-Pacific region, is also listed and discussed.

Keywords Echinoidea, Spatangoida, *Maretia*, late Miocene, Australia.

Introduction

While searching through a large collection of invertebrate fossils donated to Museum Victoria by F. A. Cudmore between 1924 and 1950, an unlabelled box of irregular echinoids was noticed amongst material from the Glenelg River area of Western Victoria. The colour and composition of the attached matrix on the echinoids, as well as the type of preservation, immediately raised doubts as to their actual origin.

Examination of the specimens suggested that they belong to *Maretia*, a genus not previously recorded in the fossil record of Australia. Determining their place of origin thus rested on identification of the attached matrix, which contains small grains of glauconite. While this mineral is not uncommon in sediments containing fossil echinoids, its Australian presence in granular form is recorded from only one area, the Tambo River Formation in East Gippsland, Victoria.

A further search of the Cudmore Collection revealed a small assortment of fossils labelled as coming from Swan Reach, Victoria, the stratotype section for the above Tambo River Formation (fig.1). The matrix with these fossils, and a few fragments of associated echinoid tests, clearly matched the unlabelled specimens. Further support for the origin of the echinoids was provided by the presence in each group of fossils of a specimen of the brachiopod *Frenulina pumila* (Tate, 1899), the type locality of which is Swan Reach (Richardson, 1973).

Materials and methods

The specimens are housed in the Invertebrate Palaeontology Collection, Museum Victoria (NMV). Where meaningful measurements where possible they were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL).

Age and stratigraphy

The Tambo River Formation is late Miocene (Mitchellian, Tortonian-Messinian) in age, lying within International planktonic foraminiferal zones N16-N17. The section of the formation at Swan Reach, from which the specimens of *Maretia* are believed to have come, consists of six metres of fine orange-brown fine marly limestone containing numerous small grains of glauconite, with scattered bivalves and burrowed horizons occurring between discontinuous nodular cemented horizons. The presence of abundant bolivinids and other infaunal elements as well as the marly nature of the unit suggest a low energy palaeoenvironment, the coastal areas of the Formation representing transitional beds between the underlying middle Miocene Bairnsdale Limestone and the overlying late Miocene-Pliocene Jemmys Point Formation (Gallager and Holdgate, 1996, and papers cited therein). Strontium isotope dating of shells near the top of the Swan Reach road cutting have returned dates of 6.0 Ma (Dickinson, 2002).

Associated Fauna

Apart from the specimens of *Maretia* sp. aff. *planulata*, the only echinoids recorded from the Tambo River Formation are spines of *Goniocidaris murrayensis* Chapman and Cudmore, 1934, and *Phylacanthus clarki clarki* (Chapman and Cudmore, 1934); the latter identified by Crespin (1943) as *Phylacanthus duncani* Chapman and Cudmore, 1934.

The rarity of echinoids is unusual, considering the presumed low energy depositional environment of the formation and the abundance of *Clypeaster gippslandicus* M^{c}Coy, 1879, in the underlying Bairnsdale Limestone and of *Fellaster insisa* (Tate, 1893) in the overlying Jemmys Point Formation. However, the lack of any previous record of echinoids, other than spines, may simply be due to the paucity of surface exposures.

Systematic palaeontology

Order **Spatangoida** L. Agassiz, 1840

Family **Maretiidae** Lambert, 1905

Remarks. According to Smith and Kroh (2011) the family includes fourteen genera, three of them assigned with question: *Araeolampas*?, *Eupatagus, Granobrissoides, Gymnopatagus, Hemimaretia, Homolampas, Maretia, Mariania*?, *Mazettia, Murraypneustes, Nacospatangus, Pycnolampas, Spatagobrissus* and *Tripatagus*?

Excluding the reference to *Eupatagus*, which is now referred to the family Eupatagidae Lambert, 1905 (Kroh, 2014a), *Maretia* differs from other genera in the family by a combination of four primary features: lack of a peripetalous fasciole, sternal plates with small tubercules only in the posterior half, four gonopores, and the absence of a prominent sulcus.

Genus ***Maretia*** Gray, 1855

Type species. *Spatangus planulata* Lamarck, 1816, by original designation.

Other species (listed by Smith and Kroh, 2011). *Maretia carinata* Bolau, 1873, *M*.? *cordata* Mortensen, 1948, *M*.? *tuberculata* Agassiz and Clark, 1907, *M*. sp. of Henderson (1975), *M*.? *subrostrata* (Clark, 1915), and *M*.? *aequipetala* (Gregory, 1891).

Diagnosis. (Modified from Smith and Kroh, 2011). Test moderate in size, ovate tapering posteriorly, with or without slight anterior depression, weakly arched to depressed in profile, oral surface flat except for low posterior keel; ambitus low and moderately sharp. Apical disk slightly anterior of centre, ethmolytic with 4 gonopores, genital plate 2 projecting far to the posterior of posterior oculars. Anterior ambulacrum narrow and flush adapically, pore-pairs small, isopores simple. Other ambulacra petaloid and flush. Anterior paired petals bowed, with adapical pore-pairs in anterior column rudimentary; remainder large and semi-conjugate. Posterior petals bowed to lanceolate, converging distally. Periproct on short steeply undercut truncate face; peristome wider than long, kidney-shaped, with adoral ambulacra forming a distinct phyllode. Labral plate narrow and elongate, just contacting sternal plates adjacent to the posterior half of adjoining third ambulacral plates; paired sternal plates narrow and triangular with tuberculation confined to the posterior. Aboral tuberculation heterogenous, with scattered sunken primary tubercules on interambulacra 1-4 varying markedly in density and generally missing in interambulacrum 5. On oral surface lateral tubercles arranged in distinct rows with slightly sunken areoles and spiral parapet. Subanal fasciole shield shaped, and generally well developed.

Remarks. According to Mortensen (1951: 26), in the previous 100 or so years no less than 40 fossil species, ranging in age from Eocene to Recent, have been assigned to *Maretia* or *Hemipatagus*; the two at times being considered synonymous. Most of the confusion in separating the two genera has been rectified by Kroh (2007) who listed species of *Hemipatagus*, *Maretia,* and presumed related spatangoids, accompanied by details of synonymy, type species and locality, and occurrence and age. Based on this information and cladistic analysis of specimens, the suggested taxonomic placement of these species was discussed in detail.

However, the seven species of *Maretia* listed by Smith and Kroh (2011) include four assigned to the genus with question: *M*.? *cordata*, because of it's prominent cordate outline and distinct anterior sulcus; *M*.? *tuberculata,* considered a juvenile specimen possibly assignable to *Lovenia*; *M*.? *subrostrata*, a species containing many features in common with *Hemipatagus*; and *M*.? *aequipetala*, because the type material is too poorly preserved for a positive identification. Of the remaining three species, even the illustrations of *M*. sp. from New Zealand suggest it is most likely related to *M*.? *cordata*.

Maretia sp. aff. ***planulata*** (Lamarck, 1816)

Figures 2A-F, 3A-H, Table 1

Material. Specimens NMV P324331–P324338 from the stratotype locality of the late Miocene Tambo River Formation (Mitchellian, Tortonian-Messinian) at Swan Reach, Victoria [NMV locality PL3110]. A quantity of disarticulated plates together with a sample of matrix found with these specimens are numbered NMV P322439.

Description. Test ovate to sub-pentagonal tapering to a semi-truncated posterior margin, slightly flattened adjacent to anterior depression, and weakly arched adapically with apex approximately central; margins rounded. Interambulacrum 5 mildly raised on the aboral surface at the interradial suture, and on the adoral surface swollen to form a posterior keel. Length of specimens range from 50-55 mm with width varying from 78-88%TL. Apical system showing 4 gonopores partially preserved on only one specimen (fig.3A); no detail of plate structure or hydropores can be discerned. Centre of apical disk 40-43.5%TL from anterior ambitus.

Anterior ambulacrum III, narrow and flush aborally, slightly depressed at ambitus and on adoral surface; no detail of pores. Anterior paired petals quite indistinct and possibly rudimentary but, based on ambulacrual plate suture, appear flush, straight sided, narrow and with maximum width only 3/5 that of posterior pair; detail of pores and tuberculation too poorly preserved to describe. Posterior paired petals,

Table 1. Comparison of diagnostic features of the late Miocene *Maretia* sp. aff. *planulata* (Lamarck, 1816) from Swan Reach, Victoria, with the extant *Maretia planulata* (Lamarck, 1815), based on specimens from the Philippines, and *M. carinata* Bolau, 1873, and *M. cordata* Mortensen, 1948, based on descriptions in Mortensen (1951) and Schultz (2005 and 2009).

Diagnostic feature	***Maretia planulata*** (Lamarck)	***Maretia carinata*** Bolau	***Maretia cordata*** Mortensen	***Maretia* sp. aff. *planulata*** (Lamarck)
Test shape	Ovate, with or without slight anterior depression, flattened or low arched adapically. Plaston and adjacent anbulacra form distinct keel posteriorly. Margin rather sharp.	Ovate with mere trace of anterior depression, high arched with posterior surface of interamb. 5 raised to form prominent keel on aboral surface. Margin rounded.	Generally smaller, broader and distinctly cordate. Anterior depression wider and deeper. Adapical surface low arched.	Basically ovate with moderate anterior depression, low arched adapically, both aboral and adoral surface of interamb. 5 swollen posteriorly. Margin more rounded.
Width as % test length	Av. 82.7%TL (based on 3 extant specimens).	Approx 85%TL (based on published figures).	Over 90%TL (based on published figures).	Approx 85%TL (based on 4 specimens).
Apical system	Approx. 40%TL from anterior ambitus, ethmolytic, with 4 gonopores and genital plate 2 extending to rear of oculars 4 and 5.	Approx. 38.5% TL from anterior ambitus, otherwise as for *M. planulata* (generic feature)	Approx. 43.5% TL from anterior ambitus, otherwise as for *M. planulata* (generic feature)	Approx. 41.5%TL from anterior ambitus. Only partially preserved on one specimen which appears to shows 4 gonopores.
Anterior ambulacrum	Narrow, flush, or slightly depressed at anterior ambitus. Pore pairs small to rudimentary in single longitudinal column.	No specific information	Plates longer and fewer than *M. planulata* and sunken towards frontal depression.	Appears as for *M. planulata* based on what little preservation occurs on specimens.
Anterior paired petals	Straight, wide, lanceolate, distal end nearly closed. Rudimentary pore-pairs in anterior column adapically for about 1/3 length.	Well-formed, shorter, with corresponding reduction in number of pore-pairs compared to *M. planulata* of similar size.	Distinctly broader, pore-pairs fewer compared to M. planulata of similar size. In anterior column only 4 plates have rudimentary or no pore-pairs proximally.	Preservation very poor in all specimens, however they appear fairly rudimentary, much narrower, straight sided and more obtuse than *M. planulata*.
Posterior paired petals	Longer and broader than anterior pair, straight or slightly S-shaped,	Well-formed, shorter and broader than M. planulata.	More like *M. carinata* than *M.. planulata*..	Marginally shorter and not as broad as *M. planulata*
Petals generally	Inter pore zone wide, slightly raised and covered with varying sized tubercles. Pairs not strictly conjugate.	Similar to *M. planulata*.	Inter pore zone not raised and sculpture between pore-pairs more elaborate than in *M. planulata*.	Pore zones contain more miliary granules; otherwise similar to *M. planulata*.
Periproct	Longer than wide with both ends distinctly pointed, situated in mildly concave, short, steeply undercut face.	Posterior face only mildly undercut and slightly concave. More like *M. cordata* than *M. planulata*..	About as long as wide and nearly round. Posterior margin rounded not undercut.	Not well preserved on any specimen but appears to be similar to *M. planulata*.
Peristome	Reniform, wider than long and sunken, but only in relation to raised projecting labrum. Groups of small tubercules occur around the peristome at junction of interambs 1-4.	Published illustrations suggest projection of labrum not as prominent.	Not strictly reniform, more rounded pentagonal in shape, no projection of labrum.	Preservation poor but raised projecting labrum suggests similarity to *M. planulata*. Small tubercules at junction of interanb's and peristome also visible on most specimens.
Phyllodes	Reasonably well developed, lateral 8-10, anterior 6.	Less developed than *M. planulata*	Longer and broader than *M. planulata*.	Poorly preserved - most plates missing or weathered.

Diagnostic feature	***Maretia planulata*** (Lamarck)	***Maretia carinata*** Bolau	***Maretia cordata*** Mortensen	***Maretia* sp. aff. *planulata*** (Lamarck)
Labrum	Narrow, very elongated, contacting sternal plates near posterior end of adjacent 3rd ambulacral plates. Anterior edge forms prominent lip above peristome,	Relatively broad, extending just posterior to centre of adjoining 3rd ambulacral plates. Anterior edge slightly curved at junction with peristome.	Narrower, marginally broader mid length. No projection at junction with peristome; otherwise similar to *M. planulata*.	Similar to *M. planulata*..
Sternal plates	Paired, long, narrow and triangular. Posterior 35-45% covered with small tubercles.	Paired but broader and conspicuously raised compared with *M. planulata*.	Paired, shorter & wider than *M. planulata*.	Similar to *M. planulata*.
Episternal plates	Tuberculated and sharply undercut by marked increase in width of plate 6 of adjoining ambulacra.	As *M. planulata* (familial feature)	As *M. planulata* (familial feature)	Assumed similar, but not clearly defined due to cracking across plates.
Subanal fasciole	Outline reniform, continuous below periproct, rising adorally over ambulacral plates 6-9 and across episternals.	Details of subanal fasciole do not appear to have been recorded.	Generally well developed but recorded as sometimes rather indistinct, posterior side straight, not re-entrant.	Extent indeterminate due to poor preservation of test. Only two specimens show a small section of fasciole, one of which is re-entrant.
Primary tubercules	Perforate, crenulate, areoles moderately sunken, heterogeneous on aboral surface except on interamb. 5 which has only a few small tubercles. Margin, including plates adjacent periproct, covered with closely spaced small tubercules increasing in size adorally in interambs 1 & 4 to form radiating rows of very closely spaced primaries with ear shaped areoles.	Primary aboral tubercules somewhat less numerous than in *M. planulata* specimens of similar size .Tubercules on aboral surface of interambulacrum 5 fairly large but not considered primary.	Primary aboral tubercules similar in density to *M. planulata* specimens of similar size but in larger specimens interamb. 5 contains a number of large tubercles.	Generally as for *M. planulata* but with primary aboral tubercules on interambs 1 & 4 somewhat less numerous (as in *M. carinata*) and with some large tubercles in interamb. 5 of size similar to those in interambs 1-4. Adoral primary tubercles considerably more widely spaced.

lanceolate, closing distally, wider and longer than anterior pair, pores eye shaped, outer and inner appear to be similar in size, not strictly conjugate but each side of plate sutures between pairs angularly sunken. Interporiferous zone covered with randomly placed small tubercles and numerous miliary granules, the latter extending across the pore zones (fig. 2F).

Periproct longer than wide situated on steep undercut truncate face, exact shape indistinct. Peristome also poorly preserved in all specimens but clearly wider than long with convex anterior lip of labrum overhanging posterior side. Phyllodes and groups of small tubercules at termination of interambulacra with peristome partially visible on some specimens (fig. 3B).

Labrum narrow and very elongate, just contacting sternal plates adjacent posterior end of adjoining third ambulacral plates, and with a number of small tubercles on anterior lip, similar to those at end of adoral interambulcra (fig. 3D,E). Sternal plates paired, long, narrow and triangular, extending to posterior end of adjoining fifth ambulacral plates. The posterior ends of the plates are covered with small tubercles for 40-45% of their length and possess a ventral apex at the centre just anterior of the posterior sutures (fig. 2E)**.** Episternal plates**,** covered with small tubercles, are probably triangular and undercut by re-entrant sixth ambulacral plates; junction with sub-anal plates indeterminate. Due to extensive posterior damage, the subanal fasciole is partially visible on only two specimens; a small indistinct section crossing the episternal plates (fig. 3G), and a re-entrant section adjoining the periproct (fig. 3H).

Heterogeneous, moderately spaced, perforate and crenulate, primary tubercles with sunken areoles as well as occasional small tubercles occur on the aboral surface of interambulacra 1-4 (fig. 3C). Several small tubercles and a few primaries, the latter generally towards the posterior ambitus, occur on interambulacrum 5. Small closely spaced tubercules immediately below the ambitus in ambulacra 1-4 increase in

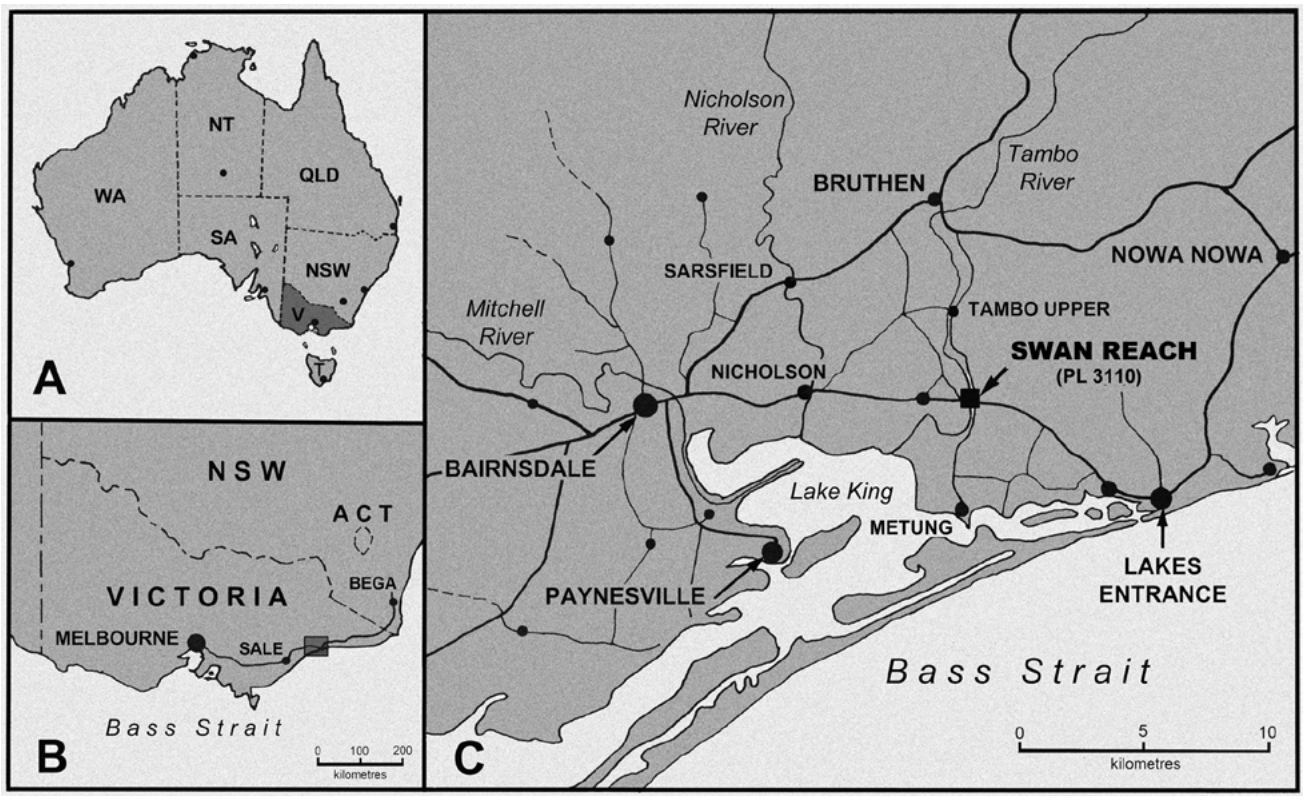

Figure 1. A, B, general location maps; C, map of East Gippsland, Victoria, from Bairnsdale to Lakes Entrance, showing locality NMV PL3110 at Swan Reach.

size but reduce in quantity adorally to form distinct radiating rows of primary tubercles. Plates surrounding the periproct are also covered with small tubercles.

Remarks. All specimens are to some degree deformed, often incomplete, with some of the plates cracked and their sutures opened up. Nevertheless it is possible to compare individual features of the specimens with those of the three extant species of *Maretia*: *M. planulata, M. carinata, and M.*? *cordata* (Table 1).

Apart from primary generic characteristics present in all four species compared in the table, approximately 70 percent of the listed diagnostic features are common to both *M.* sp. aff. *planulata* and the type species *M. planulata*. Comparison with *M. carinata* is more difficult to summarise as two important diagnostic features that distinguish it from *M. planulata*, the number of pore pairs in paired petals and the development of the phyllodes, are not preserved in the fossil specimens. Excluding the generic characteristics and these latter features, *M.* sp. aff. *planulata* has only about 30 percent of its diagnostic characteristics in common with *M. carinata*. Similarity between *M.* sp. aff. *planulata* and *M.*? *cordata* is quite minimal.

In descriptions of *Maretia* species, the density of tubercles on parts of the test has been used as a diagnostic feature; particularly the density of primary tubercles on aboral interambulacra 1-4. However, based on the extant specimen from the Philippines (fig. 2G) and numerous published photographs of *M. planulata* (e.g. Mortensen, 1951; Fisher, 1966; Schultz, 2005; Kroh, 2007; Smith and Kroh, 2011), there appears to be considerable variation in density and arrangement of these tubercles, making comparison of this feature between species of the genus, somewhat tenuous.

Fossil record of *Maretia*

Extant species of *Maretia*, principally *M. planulata*, are currently considered to occur in two distinct Indo-Pacific marine zones:

1. East Africa, from Mozambique north to Egypt and Saudi Arabia on the Red Sea; and the western Indian Ocean Islands, particularly Madagascar, Mauritius and the Seychelles.

2. From southern India and Sri Lanka, eastwards across the Indo-Malayan Archipelago, Indonesia, the Philippines, Papua New Guinea, north and east Australia, and the western Pacific Islands from Japan in the north to Fiji and New Caledonia in the south, and as far east as Hawaii.

The fossil record of species, currently assigned to the genus, is consistent with the present-day distribution of extant forms, with one exception, but is restricted to less than a dozen specific localities (fig.4).

East Africa. *M. ovata* (Leske, 1778) from three localities in the Pliocene Zanzibar Series, Zanzibar (Unguja) Island,

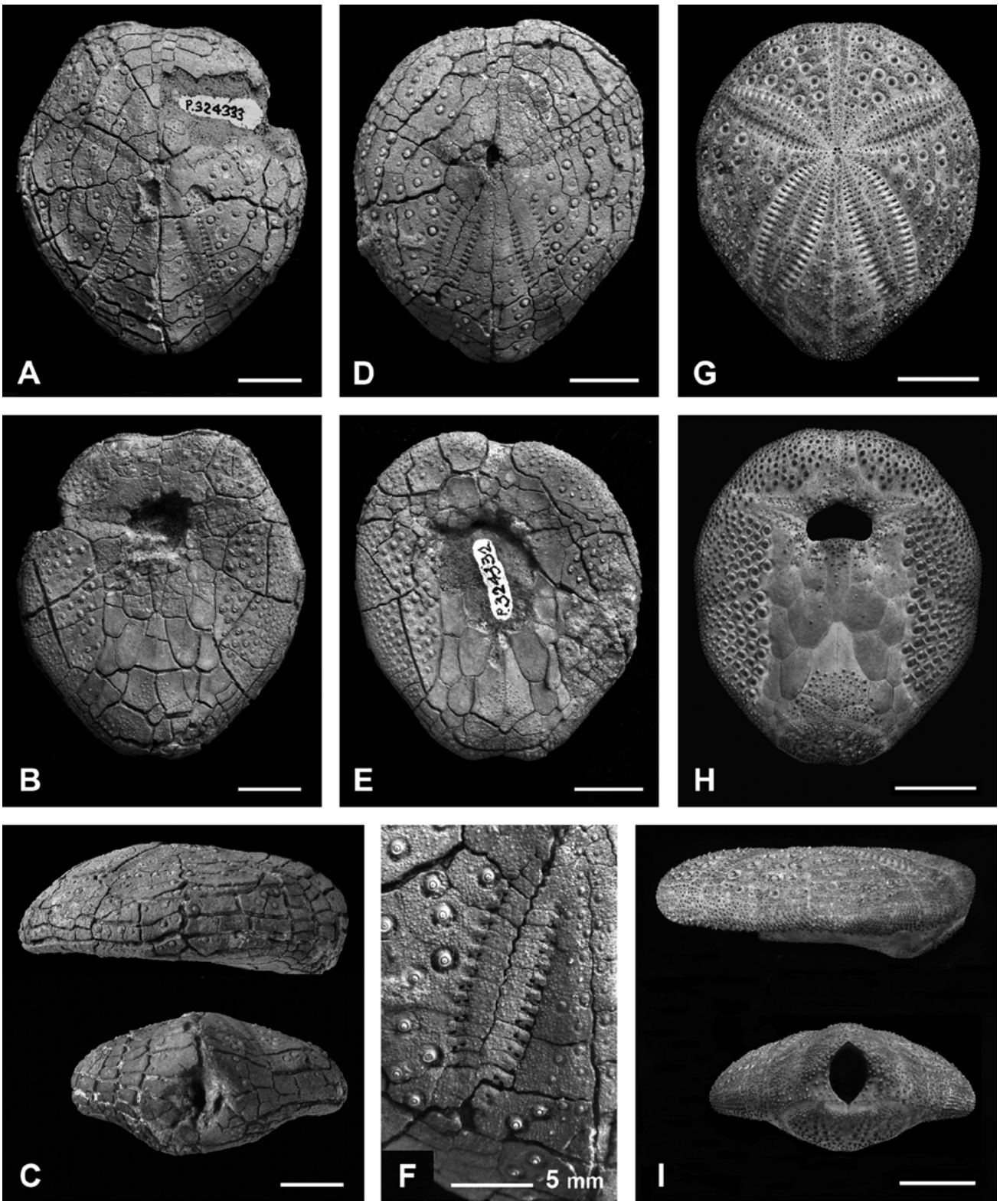

Figure 2. *Maretia* sp. aff. *planulata* (Lamarck, 1816): A-C, adapical, adoral, left lateral and posterior views of NMV P324333; D, E, adapical and adoral views, and F, aboral ambulacrum V detail of NMV P324332, both specimens from the late Miocene, Tambo River Formation, Swan Reach, Victoria. G-I, adapical, adoral, left lateral and posterior views of extant specimen of *Maretia planulata* from the Philippines. Scale bar 10 mm unless otherwise stated.

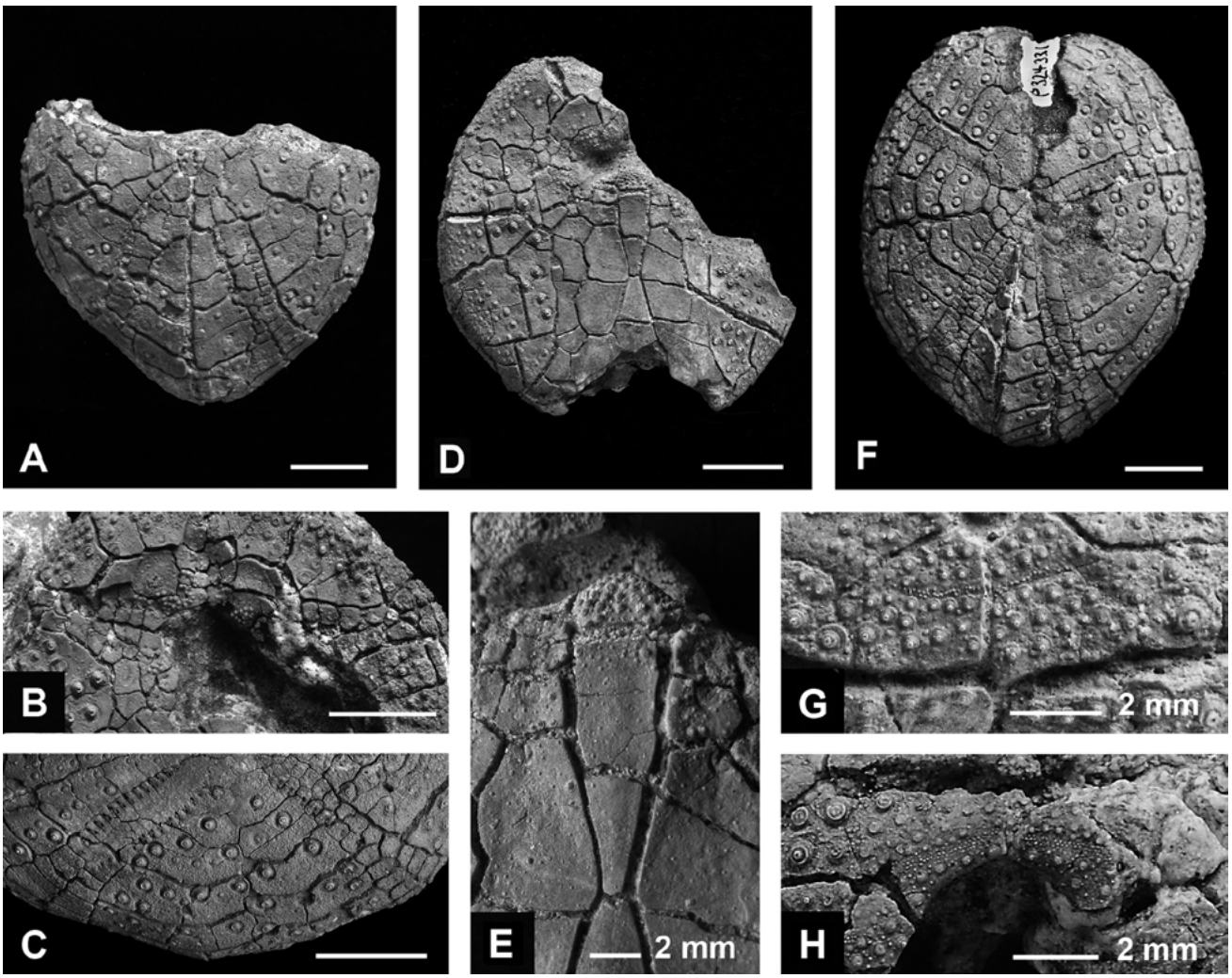

Figure 3. *Maretia* sp. aff. *planulata* (Lamarck, 1816): A, adapical view of NMV P324337 recording presence of four gonopores; B, partial adoral view of NMV P324338 showing phyllodes and small tubercules at termination of interambulacra with peristome; C, partial adapical view of NMV P324332 showing interambulacra 1 and ambulacrun I and II; D, E, adoral view and labrum detail of NMV P324336; F, adapical view of NMV P324331; G, partial adoral view of NMV P324332 showing an indistinct section of subanal fasciole crossing episternal plates; H, partial posterior view of NMV P324333 with re-entrant section of subanal fasciole adjoining the periproct. Specimens from the late Miocene, Tambo River Formation, Swan Reach, Victoria. Scale bar 10 mm unless otherwise stated.

Tanzania (Stockley, 1927: 117). However, Eames and Kent (1955: 342) revised the age of these Pliocene deposits to early Miocene, and in a footnote state "Comparison, in the British Museum Natural History, of the Zanzibar Lower Miocene *Clypeaster*, *Maretia* and temnopleurids with recent material indicates that they are not attributable to the species to which they have been assigned." The Tanzanian fossil specimens of *Maretia* assigned to the taxon *M. ovata* (Leske) by Stockley, is almost certainly the result of *Spatangus planulatus* Lamarck, 1816, being synonymised with *Spatangus ovatus* Leske, 1778 (H.L.Clark 1917: 248 and 1925: 226). Mortensen (1951: 37) recounts in considerable detail the history of this synonymy, clearly stating that there is no real foundation for any change; the figures and description of *Spatangus ovatus* being poor and of unknown affinity. The taxon is now cited in the World Register of Marine Species (Kroh, 2014b) as *Maretia ovata* H.L.Clark, 1917; a subjective junior synonym of *M. planulata* (Lamark, 1816).

Red Sea. *M. ovata* (Leske) from four localities in the Pliocene basal beds of the Marly Limestone Series, Farsan Islands, Saudi Arabia (Brighton, 1931: 332). In referring to the specimens as *M. ovata* (Leske), Brighton appears to have followed the synonymy in Stockley (1927) without question.

Red Sea. *M. planulata abbassi*, Ali, 1985: 294, a new subspecies from the lower Pliocene of Wadi Abu Abraiki, Egypt, based primarily on differences in the aboral ambulacra. However, no reference was made to the sternal plates having a distinct contact with adjoining ambulacral plates 6a and 6b, as

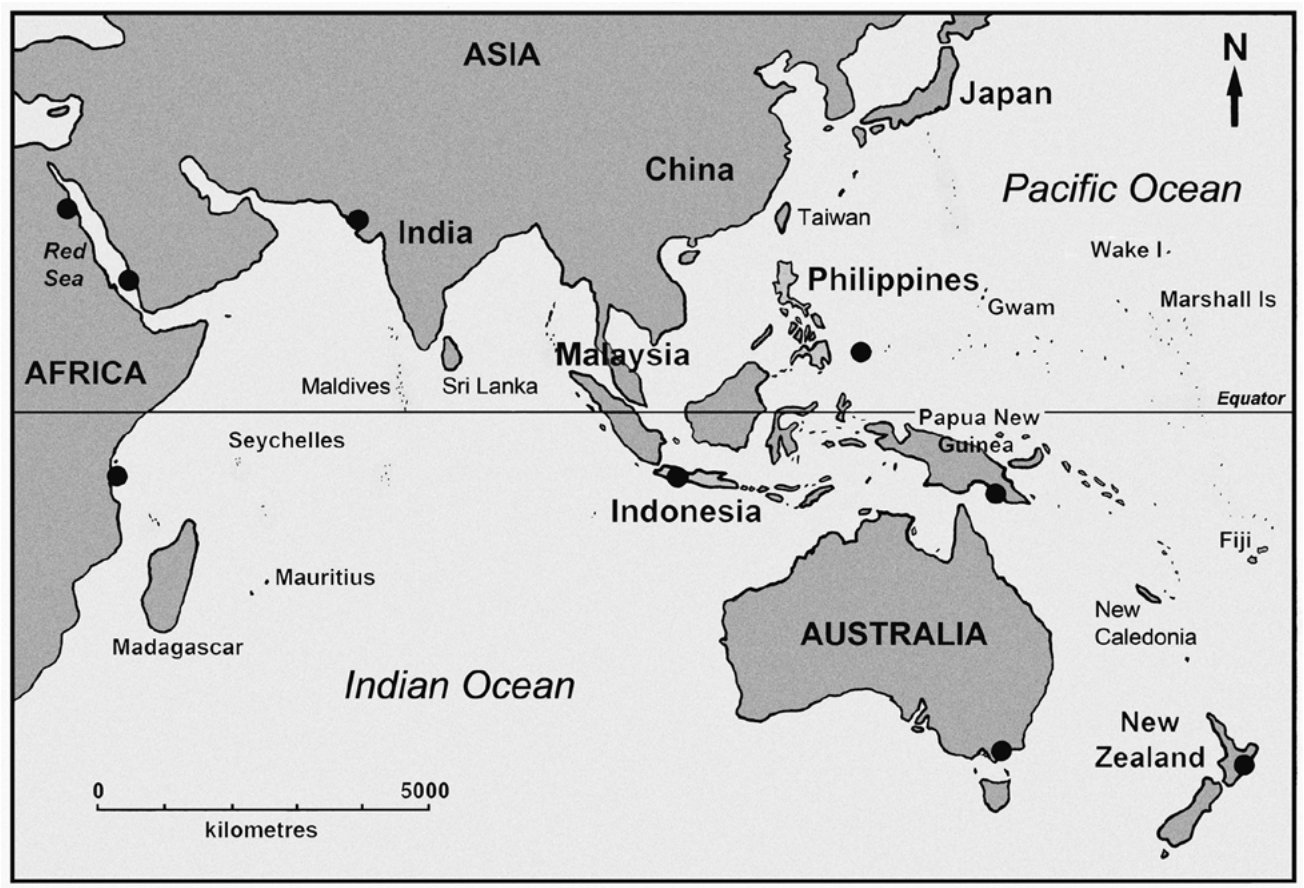

Figure 4. Generalised map of the Indo-Pacific Region showing localities where fossil specimens attributable to *Maretia* have been found (•).

shown on the oral view of the holotype. This feature is unusual, as contact of these latter plates is normally with the episternals. As only the holotype is recorded, it is not possible to determine if this feature is simply an anomaly.

India. *M. ranjitpurensis* Jain, 2002: 130, a questionable species from the Raj Formation (? Burdigalian), Kathiawar, Gajarat, western India. Described from eight specimens, it differs from *M planulata* only in the far smaller number of aboral primary tubercles and the wider angle of the anterior paired ambulacra. It appears to be the first record of the genus, either fossil or extant, from the area that separates the two distinct marine zones referred to above; the State of Gajarat bordering Pakistan.

Indonesia. *Spatangus praelongus* Herklots, 1854: 11, a species from the Miocene of Tjidamar, western Java. Subsequent authors considered this species synonymous with *M. planulata* and of Pliocene age (Mortensen 1951: 37).

Papua New Guinea. *M. planulata* (Lamarck, 1816), a partial test from the lower Pliocene Kairuku Formation, Yule Island, Central Province (Lindley, 2003: 160). Also recorded were two specimens of *M. cordata* from the same general location.

South Sea Islands. *M. planulata* (Lamarck, 1816), a single internal mould from the Pleistocene Younger Angaur Limestone of Angaur Island, Palao Island Group, Micronesia (Nisiyama, 1968: 205).

New Zealand. *Maretia* sp. of Henderson (1975: 33). Two partially preserved specimens from the upper Miocene (Kapitean) of Tawhiti Hill, north Tokomaru Bay, east coast of North Island.

United Kingdom. *Agassizia aequipetala* Gregory, 1891: 39, from the Pliocene Coralline Crag, Aldborough, Suffolk. Although this has been tentatively assigned to *Maretia* (Sullivan, 2007), it's origin, and the information on which this identification was made are considered inadequate for it to be included in the currently accepted distribution of both fossil and extant species of *Maretia*.

The earliest occurrence of *Maretia*, considered to be in the Pliocene (Kroh, 2007: 173), needs to be revised to take account of the late Miocene record of *M.* sp. aff. *planulata* from the Tambo River Formation. However, the early to middle Miocene age given for the Indian specimens from the Raj Formation and the revision of the age of the Zanzibar Series specimens from Pliocene to early Miocene, if correct, would extend the known range of the genus further back in time by several million years.

Because of poor preservation and general lack of detail in many of the above fossils, and the possibility that there may be

differences in both fossil and extant populations of *M. planulata* between the two distinct marine zones in the Indo-Pacific region, description of the specimens from the Tambo River Formation has been left in open nomenclature. Features common to both *M. planulata* and *M. carinata* (Table 1) are those most likely to be preserved in older fossil specimens, often making specific identification problematical. Currently, extant specimens of both of these species are found from the Indo-Malayan Archipelago to the western Pacific Islands, and include the north Queensland coast of Australia (Cannon et al., 1987).

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