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Diversity of sea stars (Echinodermata: Asteroidea) in Singapore

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Abstract. Sea stars (Echinodermata: Asteroidea) are diverse members of marine benthic communities, and many species play crucial roles as keystone species in maintaining the ecological balance of various ecosystems. Globally, sea stars face multiple threats due to environmental changes driven by anthropogenic activities and, for some species, overharvesting, but information on their diversity is incomplete and our understanding of their phylogeny remains limited. Traditional taxonomic methods have relied predominantly on morphological characteristics, yet the application of molecular approaches has uncovered significant inconsistencies in the taxonomic classification of certain groups of asteroids such as *Astropecten* and *Luidia*. While several morphology-based studies have documented the Asteroidea fauna of Southeast Asia, their molecular diversity and phylogenetic relationships remain understudied. Our study addresses this gap by combining morphological examination with molecular phylogenetic analysis of the cytochrome c oxidase subunit I gene on sea star specimens collected from Singapore's coastal waters. Our molecular findings support morphology-based identifications for 18 distinct sea star species out of the 22 collected in this study. Additionally, this study marks *Pentaceraster mammillatus* (Audouin, 1826), first observed here in 2008, as a new species record for this locality. While resolution of phylogenetic relationships among sea stars at the family and higher levels requires better gene sampling, this study represents a significant step towards advancing our understanding of sea star diversity in the Southeast Asian region.

Key words. COI, DNA barcoding, integrative taxonomy, marine biodiversity, phylogenetic analysis, Southeast Asia

INTRODUCTION

Sea stars (Echinodermata: Asteroidea) are a group of marine invertebrates that exhibit remarkable diversity, encompassing nearly 1,900 extant species organised into seven orders, 39 families, and approximately 370 genera (Mah, 2024; see also Mah & Blake, 2012). They inhabit a wide range of oceanic depths, ranging from intertidal and subtidal habitats such as rocky shore, kelp forest, seagrass beds, and tropical coral reefs down to the abyssal zone (Blake, 1990).

Sea stars exhibit a wide range of feeding behaviours from generalist to specialist predation (with diets comprising gastropods, bivalves, cnidarians, and other macroinvertebrates), to detrital feeding (Jangoux, 1982; Gaymer et al., 2004). Their abundance and roles in various habitats and food webs often distinguish them as keystone species (Menge et al., 1994). Nonetheless, they are susceptible to climate change, global warming in particular, as higher temperatures have adverse effects on their feeding and growth rates (Petes et al., 2008; Pincebourde et al., 2008). Furthermore, the sea star wasting disease, responsible for mass mortalities in several sea star species along the Pacific coast of North America (Dungan et al., 1982; Bates et al., 2009), has been known to have intensified effects in elevated sea temperatures (Bates et al., 2009). In addition to these challenges, coastal urbanisation and climate change have contributed to increased runoff pollution and ocean acidification respectively, which can result in disease and negatively affect the growth of sea stars (Keppel et al., 2014; Miner et al., 2018). The cumulative impacts of these anthropogenic threats, particularly for keystone species, underscore the pressing need for monitoring and management as their well-being is intricately linked to the overall health of the marine ecosystems they inhabit (Jordán, 2009; Johnson et al., 2017). Well-studied sea stars include *Pisaster ochraceus*, which has been pivotal in ecological research on competition, reproduction, and community structure (Paine, 1969, 1974; Menge, 1972, 1975), and *Acanthaster planci*, whose population outbreaks have raised concerns for coral reef health (Chesher, 1969; Birkeland & Lucas, 1990; Brodie et al., 2005). While these species have been extensively studied, the majority of sea stars remain poorly understood.

Sea stars are generally characterised by a dorsoventrally flattened body, generally with multiple arms radiating from a central disk, but body shapes can vary from spherical to pentagonal, or from highly inflated to extremely flattened

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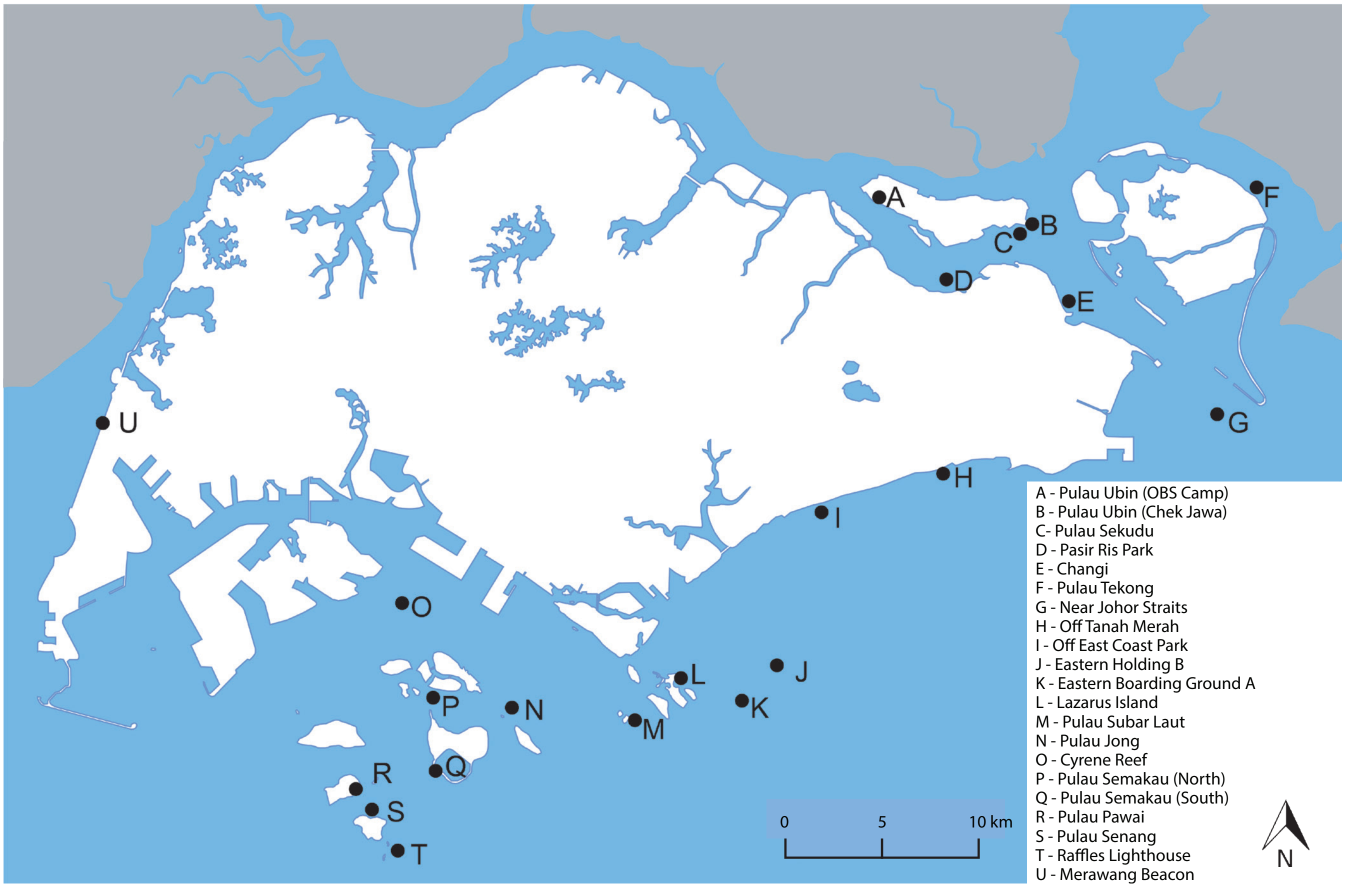

Fig. 1. Collection sites in Singapore.

(Mah & Blake, 2012). Traditional taxonomic methods for categorising species and their relationships rely heavily on morphological characteristics (see Blake, 1987). However, over the past two decades, there have been multiple attempts to resolve higher-level asteroid relationships using molecular data (Knott & Wray, 2000; Janies et al., 2011; Mah & Blake, 2012; Linchangco et al., 2017). Notable family- and genus-level revisions include the reclassification of *Fromia* from Ophidiasteridae to Goniasteridae (Mah & Foltz, 2011) and the transfer of 12 *Asterina* species into the genus *Aquilonastra* (O'Loughlin & Rowe, 2006), respectively. However, challenges have emerged when classifying sea star species according to morphological differences, especially in cases where substantial phenotypic variation are exhibited. These variabilities have prompted several descriptions of new species, such as in *Linckia* and *Luidia*, but which have been later found to lack support from molecular data analysis as noted by Williams (2000) and Xiao et al. (2013) respectively. Species complexes in genera *Linckia* and *Astropecten* have also been highlighted by Williams (2000) and Zulliger & Lessios (2010) respectively.

Singapore is situated in tropical Southeast Asia, a region globally recognised for its rich marine biodiversity and diverse ecosystems (Burke et al., 2002; Roberts et al., 2002). To date, 31 Asteroidea species have been recorded in Singapore (VandenSpiegel et al., 1998; see also Davison et al., 2024) but only a few of these records have been validated with molecular data. To plug this knowledge gap, this study aims to characterise the diversity and phylogenetic placements of sea stars in Singapore's waters by studying specimens collected from various localities. Through DNA sequencing of the cytochrome c oxidase subunit I (COI) gene and morphological observations of specimens, we positively identified species of Asteroidea and described the diversity of sea stars in Singapore.

MATERIAL AND METHODS

Collection and sampling. A total of 67 Asteroidea specimens from various localities were studied (Fig. 1). Of these, 61 specimens were collected during the Comprehensive Marine Biodiversity Survey (CMBS) between 2010 and 2015 via intertidal surveys, scuba diving, and trawling. Tube feet tissue samples were cryopreserved at the Lee Kong Chian Natural History Museum (Table 1). The remaining six specimens were obtained from intertidal surveys conducted in 2023, with tube feet likewise preserved in 100% molecular-grade ethanol at -20°C. Preliminary identification was performed based on morphological characteristics described by VandenSpiegel et al. (1998).

DNA extraction, PCR amplification, and sequencing. Tissue samples were digested in 180µl of buffer ATL and 20µl of proteinase K at 56°C until tissue was completely lysed. DNA was subsequently extracted using the Qiagen DNeasy Blood and Tissue kit, following manufacturer recommendations.

Table 1. Species and specimens at the Lee Kong Chian Natural History Museum that have been examined in this study. Asterisks denote specimens without precise locality information recorded.

Order	Family	Species	Specimen	Site	GenBank accession
Paxillosida	Astropectinidae	*Astropecten indicus*	ZRC.ECH.2277; AST029	Merawang Beacon	PV210859
			ZRC.ECH.2278; AST030	Pulau Sekudu	PV210860
			ZRC.ECH.2279; AST031	Changi	PV210861
			ZRC.ECH.2280; AST054	Merawang Beacon	PV210874
			ZRC.ECH.2281; AST061	Changi	PV210879
		Astropecten novaeguineae	ZRC.ECH.2298; AST052	Pasir Ris Park	PV210872
			ZRC.ECH.2299; AST053	Pasir Ris Park	PV210873
		Craspidaster hesperus	ZRC.ECH.2289; AST034	Off Tanah Merah	PV210864
			ZRC.ECH.2212; AST036	Off East Coast Park	PV210866
	Luidiidae	*Luidia hardwicki*	ZRC.ECH.2264	Eastern Boarding Ground A	
			ZRC.ECH.2265	Eastern Holding B	
		Luidia maculata	ZRC.ECH.1265; AST026	Pulau Ubin (OBS Camp)	PV210857
			ZRC.ECH.2295; AST037	Eastern Boarding Ground A	MT444499
			ZRC.ECH.2296; AST073	Changi	PV210891
		Luidia penangensis	ZRC.ECH.2218; AST027	Pulau Ubin (OBS Camp)	PV210858
			ZRC.ECH.2282; AST032	Pulau Ubin (OBS Camp)	PV210862
			ZRC.ECH.2283; AST033	Near Johor Strait	PV210863
Valvatida	Archasteridae	*Archaster typicus*	ZRC.ECH.2287; AST016	Lazarus Island	PV210848
			ZRC.ECH.2288; AST023	Pulau Subar Laut	PV210854
	Asterinidae	*Aquilonastra anomala*	ZRC.ECH.2312; AST022	Pulau Jong	PV210853
		Aquilonastra coronata	ZRC.ECH.2273; AST002	Pulau Sekudu	PV210837
			ZRC.ECH.2310; AST005	Pulau Ubin (Chek Jawa)	PV210839
			ZRC.ECH.2274; AST008	Pulau Ubin (OBS Camp)	PV210841
			ZRC.ECH.2311; AST055	Changi	PV210875
			ZRC.ECH.2275; AST060	Pulau Sekudu	PV210878
			ZRC.ECH.2276; AST063	Pulau Ubin (OBS Camp)	PV210881
		Cryptasterina pentagona	ZRC.ECH.2224	Pulau Senang	
			ZRC.ECH.2225	Pulau Pawai	
		Nepanthia belcheri	ZRC.ECH.2315; AST004	Pulau Ubin (Chek Jawa)	MT476595
			ZRC.ECH.2246; AST015	Eastern Boarding Ground A	PV210847
		Nepanthia maculata	ZRC.ECH.2247; AST024	Raffles Lighthouse	PV210855
	Goniasteridae	*Goniodiscaster scaber*	ZRC.ECH.2313; AST006	Pulau Tekong	MT444497
			ZRC.ECH.2290; AST011	Eastern Boarding Ground A	PV210843
			ZRC.ECH.2291; AST058	Eastern Holding B	PV210876
			ZRC.ECH.2292; AST059	Eastern Holding B	PV210877
			ZRC.ECH.2314; AST068	Pulau Tekong	PV210886
			ZRC.ECH.2293; AST069	Eastern Boarding Ground A	PV210887
			ZRC.ECH.2297; AST071	Pulau Ubin (Chek Jawa)	PV210889
		Iconaster longimanus	ZRC.ECH.2256; AST012	Eastern Holding B	PV210844
			ZRC.ECH.2230; AST014	Raffles Lighthouse	PV210846
			ZRC.ECH.2251; AST046	Raffles Lighthouse	PV210867
			ZRC.ECH.2255; AST048	Eastern Holding B	PV210869
			ZRC.ECH.2250; AST049	Raffles Lighthouse	PV210870
			ZRC.ECH.2294; AST051	Pulau Semakau (North)	PV210871
			ZRC.ECH.2253; AST064	Pulau Semakau (North)	PV210882
			ZRC.ECH.2254; AST065	Pulau Semakau (North)	PV210883
			ZRC.ECH.2252; AST066	Pulau Semakau (South)	PV210884

Order	Family	Species	Specimen	Site	GenBank accession
		Stellaster childreni	ZRC.ECH.2233; AST010	Raffles Lighthouse	PV210842
			ZRC.ECH.2234; AST035	Off Tanah Merah	PV210865
	Ophidiasteridae	*Ophidiaster granifer*	ZRC.ECH.1621	Pulau Pawai	
			ZRC.ECH.1253	Pulau Subar Laut	NC_054227
	Oreasteridae	*Anthenea aspera*	ZRC.ECH.1622; AST003	Changi	PV210838
			ZRC.ECH.2284; AST007	Pulau Ubin (OBS Camp)	PV210840
			ZRC.ECH.2285; AST020	Cyrene Reef	NC_054230
			ZRC.ECH.2286; AST021	Eastern Boarding Ground A	PV210852
			ZRC.ECH.2309; AST062	Pulau Ubin (OBS Camp)	PV210880
			ZRC.ECH.2301; AST070	Pulau Ubin (Chek Jawa)	PV210888
		Culcita novaeguineae	ZRC.ECH.2317; AST019	Southern Shores*	PV210851
		Gymnanthenea laevis	ZRC.ECH.2239; AST001	Pulau Semakau (North)	PV210836
			ZRC.ECH.2300; AST072	Changi	PV210890
		Protoreaster nodosus	ZRC.ECH.2316; AST013	Cyrene Reef	PV210845
			ZRC.ECH.2320; AST017	Southern Shores*	PV210849
			ZRC.ECH.2321; AST018	Southern Shores*	PV210850
			ZRC.ECH.2319; AST025	Pulau Sekudu	PV210856
			ZRC.ECH.2322; AST047	Southern Shores*	PV210868
			ZRC.ECH.2318; AST067	Pulau Sekudu	PV210885
		Pentaceraster mammillatus	No voucher specimen	Cyrene Reef	NC_054225
Velatida	Pterasteridae	*Euretaster insignis*	ZRC.ECH.2207; AST028	Pulau Semakau (South)	NC_054231

Primers tRNAasn42F (5′-AACGGCCAATYGCCTTTCCATTAGG-3′) and ValvaCOI-770R (5′-TATACYTCKGGGTGGCCAAAGAATC-3′) were used to amplify an 866-bp region of the mitochondrial cytochrome c oxidase subunit I (COI) gene (Crandall et al., 2008). Polymerase chain reaction (PCR) was carried out with cycling parameters as follows: initial denaturation at 94°C for 2 min, 39 repeats of 94°C for 30s, 60°C for 30s, and 72°C for 60s, followed by a final extension of 72°C for 3 min (Crandall et al., 2008). PCR products were outsourced to Axil Scientific (Singapore) for amplicon purification using magnetic beads clean up kit and Sanger sequencing on an Applied Biosystems 3730XL DNA Analyser.

Sequence alignment and phylogenetic analysis. DNA sequences were compiled, checked, and assembled into contigs in Geneious Prime v2022.01 (Kearse et al., 2012). Preliminary species identification was performed using the Basic Local Alignment Search Tool (BLAST), matching against the National Centre for Biotechnology Information (NCBI) GenBank database (Clark et al., 2016; Sayers et al., 2019). Along with the sequences obtained from our collections, additional sequences of the genera examined here were downloaded from NCBI GenBank to be incorporated into our analysis (Hart et al., 1997; Waters et al., 2004; Matsubara et al., 2005; Crandall et al., 2008; Ward et al., 2008; Xiao et al., 2013; Kim et al., 2017; Pernet et al., 2017; Cobb et al., 2019; Ip et al., 2019; Janies et al., 2019; Quek et al., 2019; Adeli et al., 2020; Collin et al., 2020; Quek et al., 2021; Nugroho et al., 2022; Shilling et al., 2022; Sonet et al., 2022; Galván Villa et al., 2023; Kogure et al., 2023; Lee, 2023) (Table 1). Sequence data were assembled in Mesquite v3.81 (Maddison & Maddison, 2023) and aligned using MAFFT v7.520 (Katoh & Standley, 2013) under default parameters.

In reference to all hypothesised topologies which grouped Paxillosida and Valvatida in a monophyletic clade (Knott & Wray, 2000; Janies et al., 2011; Mah & Blake, 2012; Linchangco et al., 2017), topology was constrained with all specimens from the orders Paxillosida and Valvatida specified as the ingroup. *Asterias amurensis*, *Aphelasterias japonica*, *Distolasterias nipon* (Order: Forcipulatida), and *Freyastera benthopila* (Order: Brisingida) sequences were obtained from NCBI GenBank and added as outgroups (Matsubara et al., 2005; Tang et al., 2014; Lee & Shin, 2018a; Mu et al., 2018).

Phylogenetic analyses based on maximum likelihood (ML) and Bayesian inference (BI) were conducted. ML analysis was performed using RAxML 8.2.13 (Stamatakis, 2014) under the GTRGAMMA model with 50 random starting trees and 1,000 bootstrap replicates to generate the best tree. For BI, jModelTest v2.1.10 (Guindon & Gascuel, 2003; Darriba et al., 2012) was used to obtain the best-fit model GTR+I+G under the Akaike information criterion and Bayesian information criterion. MrBayes v3.2.7a (Ronquist et al., 2012) was utilised for two runs of four Markov chains running for 12 million generations. A tree was logged for every 100 generations, with the initial 20,001 trees discarded as burn-in. All phylogenetic trees were visualised in FigTree v1.4.4 (Drummond & Rambaut, 2007).

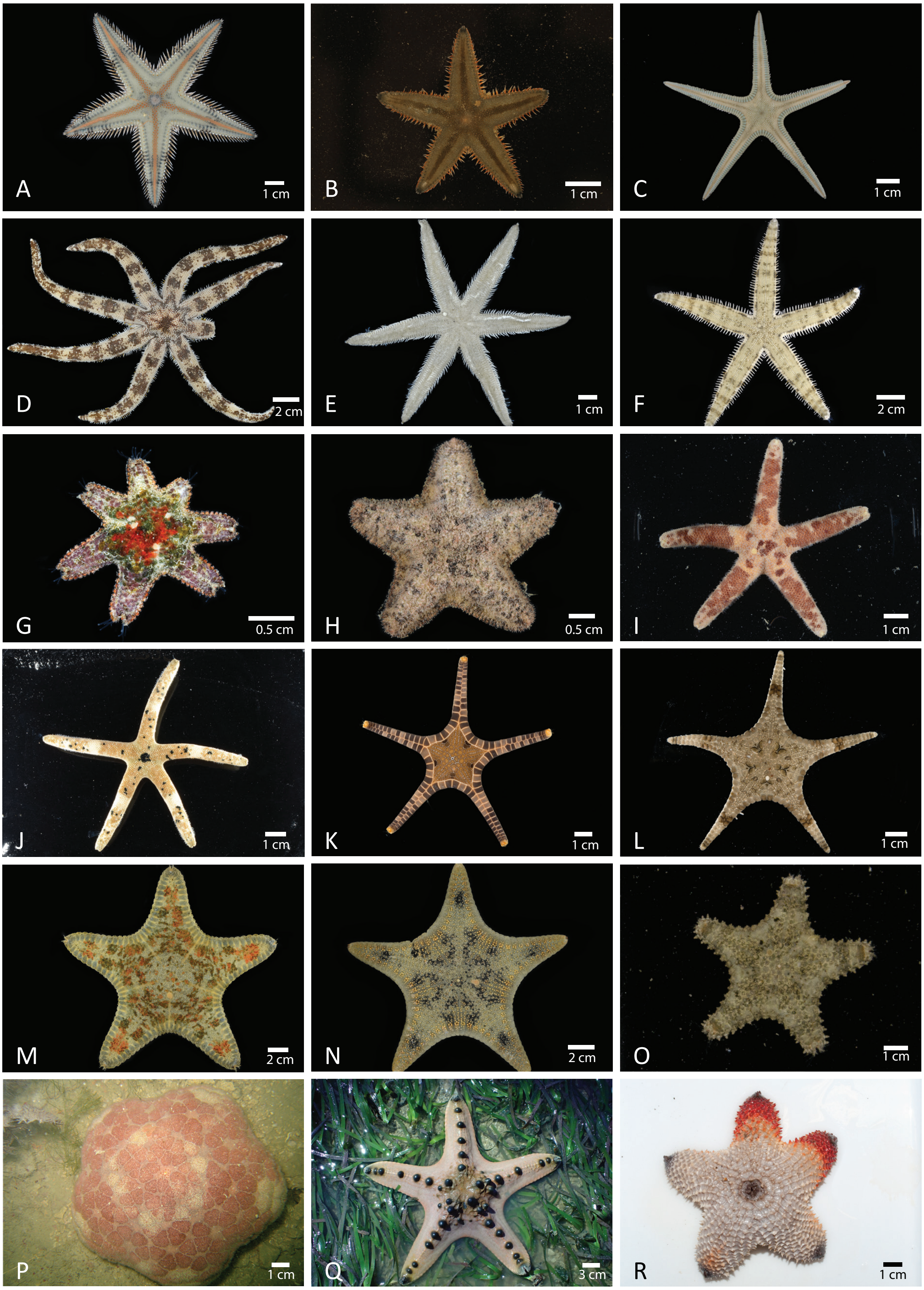

Fig. 2. Asteroidea species sequenced in this study. A, *Astropecten indicus* (ZRC.ECH.2277). B, *Astropecten novaeguineae* (ZRC.ECH.2298). C, *Craspidaster hesperus* (ZRC.ECH.2289). D, *Luidia maculata* (ZRC.ECH.2295). E, *Luidia penangensis* (ZRC.ECH.2283). F, *Archaster typicus* (ZRC.ECH.2287). G, *Aquilonastra anomala* (ZRC.ECH.2312). H, *Aquilonastra coronata* (ZRC.ECH.2276). I, *Nepanthia belcheri* (ZRC.ECH.2246). J, *Nepanthia maculata* (ZRC.ECH.2263). K, *Iconaster longimanus*. L, *Stellaster childreni*. M, *Anthenea aspera* (ZRC.ECH.2286). N, *Goniodiscaster scaber* (ZRC.ECH.2313). O, *Gymnanthenea laevis* (ZRC.ECH.2300). P, *Culcita novaeguineae*. Q, *Protoreaster nodosus*. R, *Euretaster insignis* (ZRC.ECH.2207). Images for *Culcita novaeguineae* (P) and *Protoreaster nodosus* (Q) were provided by the Reef Ecology Study Team, National University of Singapore. All other images, unless otherwise stated, were taken by the Comprehensive Marine Biodiversity Survey, Lee Kong Chian Natural History Museum.

RESULTS

A total of 21 species were identified through morphological examination (Fig. 2; Table 1), with 18 sequenced and confirmed using BLAST comparisons. Molecular data were not obtained for *Luidia hardwicki*, *Cryptasterina pentagona*, and *Ophidiaster granifer* for this study, but *Ophidiaster granifer* was previously sequenced by Quek et al. (2021) and incorporated in this study's phylogenetic analysis. *Pentaceraster mammillatus* was first observed in Singapore by Lane et al. (2008), and subsequently reported and sequenced by Quek et al. (2021), though without a preserved voucher. This raised the total number of recently recorded (2010–2023) sea star species in Singapore to 22 (Table 2). The phylogenetic trees constructed from ML and BI consensus were generally congruent, so the ML tree topology is shown (Fig. 3). Out of the eighteen species sequenced in this study, sixteen species were separately recovered as strongly supported monophyletic groups, with the exceptions being *Aquilonastra doranae* nested within the *Aquilonastra anomala* clade (ML/BI: 100/1) and *Luidia magnifica* nested within the *Luidia maculata* clade (ML/BI: 100/1).

The Paxillosida and Valvatida groups were recovered as ingroups. However, basal splits above the family level displayed limited support. Family-level clades, where present, were moderately supported, with only Asterinidae being recovered as a well-supported clade (ML/BI: 81/1). Among genera with more than one species, namely *Luidia*, *Astropecten*, *Protoreaster*, *Nepanthia*, and *Aquilonastra*, all formed clades except for *Luidia*. *Nepanthia* (ML/BI: 100/1) and *Aquilonastra* (ML/BI: 80/0.99) clades had high support values. While *Astropecten* formed a clade, there was poor support for this grouping. *Protoreaster* formed a well-supported clade (ML/BI: 88/1), but three *Pentaceraster* species (*Oreaster occidentalis* is the junior synonym of *Pentaceraster cumingi*) were nested within the clade as a strongly supported subclade (ML/BI: 100/1). *Luidia*, the only genus in the family Luidiidae, was polyphyletic and divided into four distinctive clades, albeit with limited support and long branches suggesting poor sampling with respect to taxa and molecular markers.

The *Gymnanthenea laevis*/*Anthenea aspera*/*Goniodiscaster scaber*/*Stellaster childreni* clade was well supported (ML/BI: 88/1), with *Gymnanthenea laevis* and *Anthenea aspera* identified as sister species with maximum support (ML/BI: 100/1). Interestingly, *Stellaster childreni* belongs to a different family, the Goniasteridae, in contrast to the other three species within this well-supported clade, but was moderately supported as a sister group to *Goniodiscaster scaber* (ML/BI: 54/0.96).

DISCUSSION

This study analysed 18 species from 14 genera that form strongly supported clades (Fig. 3), which are also supported by morphological identification (Fig. 2). Interestingly, several species exhibit population genetic differentiation between regions of sampling, including *Craspidaster hesperus*, *Luidia maculata*, *Culcita novaeguineae*, *Stellaster childreni*, and *Aquilonastra coronata*. Most notably, *Culcita novaeguineae* is known for its extensive colour variation (Sim et al., 2009). These variations are indicative of geographic differences between populations for several species.

Our findings indicate that *Gymnanthenea laevis* and *Anthenea aspera* are sister groups. The genus *Gymnanthenea* H.L. Clark, 1938 is recognised as a separate genus from *Anthenea* Gray, 1840. This differentiation is primarily based on the number of subambulacral spine rows, with *Gymnanthenea* having one row in contrast to the two rows in *Anthenea* (Clark, 1938). Additionally, *Gymnanthenea* is characterised by the absence of upper-end spines on the superomarginal plates, a feature otherwise present in *Anthenea* (Clark, 1938). Presently, only three species are included in *Gymnanthenea*, with two of them having been reclassified from *Anthenea* by Clark (1938) and later by Fujita & Marsh (2004), providing substantial evidence of the close relationship between these two genera. Past suggestions to consider *Gymnanthenea* as a synonym of *Anthenea* (Liao & Clark, 1995) have remained disregarded, possibly due to substantial morphological differences, a view also agreed upon by Fujita & Marsh (2004). While there are currently three recognised species in *Gymnanthenea* and 23 recognised species in *Anthenea* (Mah, 2024), COI sequences for the remaining species within both genera are unavailable, thus preventing a comprehensive account of these two genera.

Astropecten is recognised as one of the most species-rich genera among sea stars with 104 described species (Mah, 2024). Due to the high phenotypic variability of this genus, morphological characters in *Astropecten* are not easily assessed (Zulliger & Lessios, 2010). In our analysis, the monophyly of all *Astropecten* species lacks robust support owing to poor phylogenetic resolution provided by COI and incomplete taxon sampling. However, the two deepest branching clades of the genus exhibit geographical alignment, with one exclusively comprising specimens from the Indo-Pacific region and the other from the Neotropics. This division aligns with the ecological convergence findings of Zulliger & Lessios (2010). In the present study, two *Astropecten* species, *Astropecten novaeguineae* and *Astropecten indicus*, have been identified. Zulliger & Lessios (2010) suggested potential cryptic speciation within *Astropecten indicus* in Southeast Asia, although a conclusive assessment remains to be carried out due to the absence of sequence data for comparison. Notably, *Astropecten novaeguineae* was exclusively collected during the 2023 intertidal survey and was absent from CMBS collections. This may indicate that *A. novaeguineae* is either restricted to specific habitats or underreported in past surveys due to morphological similarities with *Astropecten indicus.* However, more detailed surveys over a longer period of time are needed for a more accurate assessment of this species' distribution and abundance. Species identification between these two species primarily relies on the morphological characteristics of the superomarginal plates and the paxillae rather than coloration or patterning, as these latter traits are highly variable and often unreliable for distinguishing species.

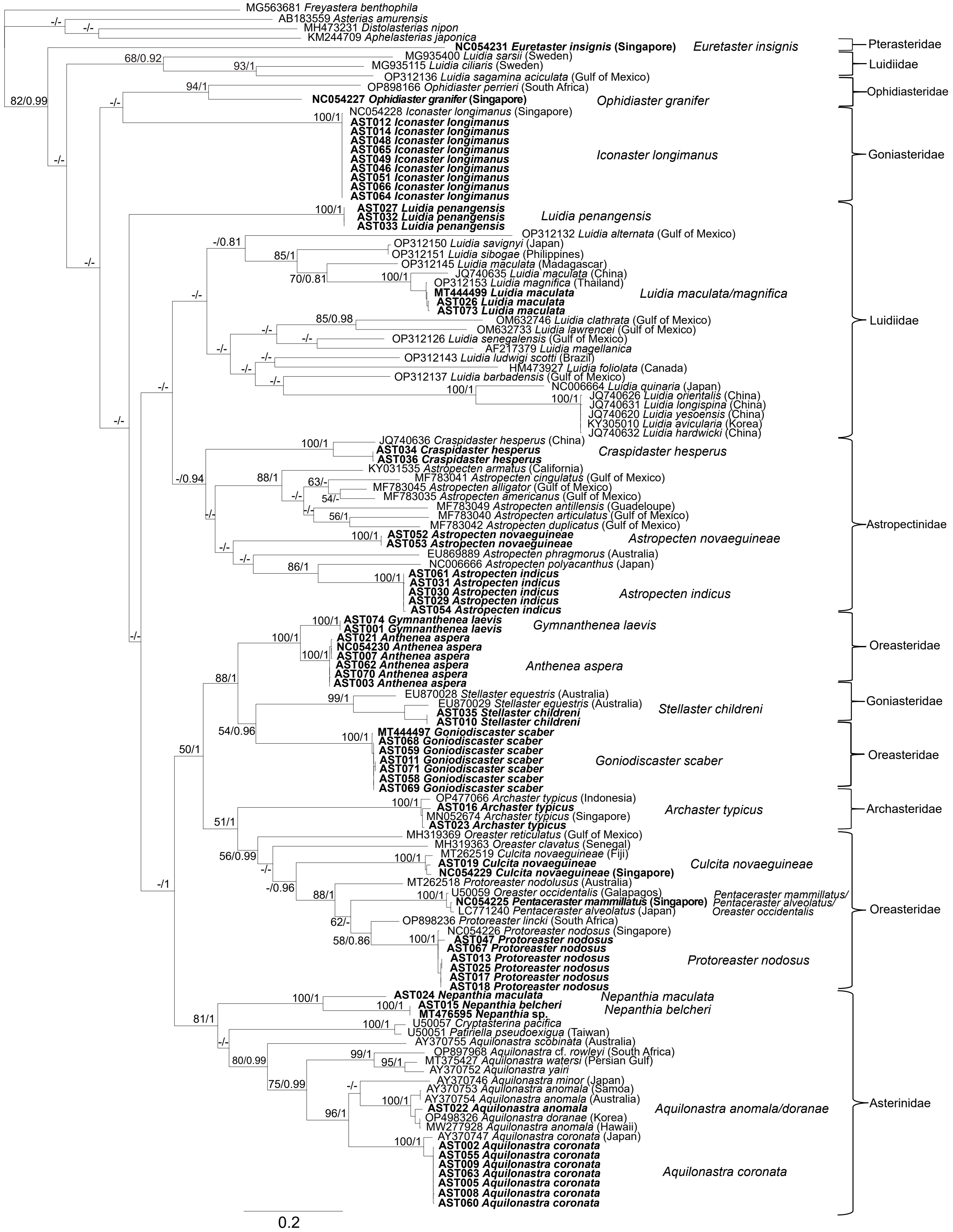

Fig. 3. Phylogenetic reconstruction of Asteroidea based on maximum likelihood (ML) analysis of aligned cytochrome c oxidase subunit I sequences, with *Freyastera benthopila*, *Asterias amurensis, Aphelasterias japonica*, *Distolasterias nipon*, and *Euretaster insignis* as outgroups. Branch support values are indicated as ML/BI, where bootstrap proportions for ML ≥ 50 and posterior probabilites for BI ≥ 0.8 are stated. Sequences obtained from this study are in bold, including those that were previously sequenced in Quek et al. (2021).

Table 2. Species list of Singapore asteroids based on VandenSpiegel et al. (1998) and this study. Synonymies appearing in the preceding paper are shown in square brackets.

Species	**VandenSpiegel et al. (1998)**	**Recent (2010–2023)**
Order Paxillosida		
Family Astropectinidae		
Astropecten bengalensis Döderlein, 1917	x	
Astropecten indicus Döderlein, 1888	x	x
Astropecten novaeguineae Döderlein, 1917	x	x
Craspidaster hesperus (Müller & Troschel, 1840)	x	x
Family Luidiidae		
Luidia chefooensis Grube, 1876 nomen dubium	x	
Luidia hardwicki (Gray, 1840)	x	x
Luidia longispina Sladen, 1889	x	
Luidia maculata Müller & Troschel, 1842	x	x
Luidia penangensis deLoriol, 1891	x	x
Order Valvatida		
Family Archasteridae		
Archaster typicus Müller & Troschel, 1840	x	x
Family Asterinidae		
Anseropoda rosacea (Lamarck, 1816)	x	
Aquilonastra anomala (H.L. Clark, 1921)	x	x
Aquilonastra coronata (von Martens, 1866)	x	x
Cryptasterina pentagona (Müller & Troschel, 1840) [= *Patiriella pseudoexigua* Dartnall, 1971]	x	x
Nepanthia belcheri (Perrier, 1875)	x	x
Nepanthia maculata Gray, 1840	x	x
Disasterina ceylanica Döderlein, 1888 [= *Tegulaster ceylanica* (Döderlein, 1888)]	x	
Family Goniasteridae		
Fromia monilis (Perrier, 1869)	x	
Goniodiscaster scaber (Möbius, 1859)	x	x
Iconaster longimanus (Möbius, 1859)	x	x
Stellaster childreni Gray, 1840 [= *Stellaster equestris* (Bruzelius, 1805)]	x	x
Family Oreasteridae		
Anthenea aspera Döderlein, 1915	x	x
Culcita novaeguineae Müller & Troschel, 1842	x	x
Gymnanthenea laevis H.L. Clark, 1938	x	x
Pentaceraster mammillatus (Audouin, 1826)		x
Protoreaster nodosus (Linnaeus, 1758)	x	x
Family Ophidiasteridae		
Ophidiaster granifer Lütken, 1871	x	x
Tamaria fusca Gray, 1840	x	
Order Velatida		
Family Pterasteridae		
Euretaster insignis (Sladen, 1882)	x	x
Order Spinulosida		
Family Echinasteridae		
Echinaster callosus Marenzeller, 1895	x	
Echinaster stereosomus Fisher, 1913	x	
Metrodira subulata Gray, 1840	x	

This approach aligns with the broader taxonomic practices in Paxillosida, where structural features of the paxillae serve as key diagnostic traits (Blake, 1990).

Luidia stands as the sole recognised genus within the Luidiidae family, encompassing 49 species to date (Mah, 2024). This genus is distinguished by its characteristic long arms with pointed tips and paxillae-adorned upper surfaces (Gray, 1840). Döderlein (1920) classified *Luidia* into four primary groups based on ossicle system features, spine development, and pedicellariae. These groups are known as the Alternata-Group, Ciliaris-Group, Clathrata-Group, and Quinaria-Group (Döderlein, 1920). The structural organisation of these groups with respect to ossicle morphology was subsequently confirmed by Blake (1973). All four groups are present within the COI tree as separate clades although their interrelationships are not well-supported. The Ciliaris-Group branched early, separating from other Paxillosida and Valvatida sea stars. Meanwhile, the three remaining groups collectively form a monophyletic clade, albeit with weak supports and long branches that reduce confidence in their placements. *Luidia maculata* falls within the Alternata-Group, aligning with Döderlein's initial classification. However, *Luidia penangensis* does not appear to be recovered as closely related to other congeneric species. Interestingly, our phylogenetic analysis (Fig. 3) reveals low genetic divergence among several species, namely *Luidia quinaria*, *L. yesoensis*, *L. orientalis*, *L. avicularia*, *L. longispina*, and *L. hardwicki*, despite notable morphological differences according to Xiao et al. (2013), who also suggested that these species should be synonymised with *Luidia hardwicki* Gray, 1840 as the senior synonym.

Goniodiscaster scaber, *Stellaster childreni*, and *Iconaster longimanus*, which are all classified within Goniasteridae, are not supported as monophyletic. In particular, the *Stellaster childreni*/*Goniodiscaster scaber* clade is well supported within the *Gymnanthenea laevis*/*Anthenea aspera*/*Goniodiscaster scaber*/*Stellaster childreni* clade (Oreasteridae). While Goniasteridae is considered to be monophyletic in Mah & Foltz (2011), neither of the goniasterid species in this study was analysed by Mah & Foltz (2011). Indeed, Goniasteridae consists of over 300 species (Mah, 2024), and better sampling of such a large family can improve phylogenetic accuracy and inferences on their evolutionary relationships (Heath et al., 2008).

From 1991 to 1995, 27 species of asteroids were collected and examined (VandenSpiegel et al., 1998). The count was subsequently increased to 31 species by including additional species based on historical distributional data available at that time (Grube, 1876; Bedford, 1900; Tortonese, 1956). The four species added were *Luidia chefooensis*, *Luidia longispina*, *Astropecten bengalensis*, and *Anseropoda rosacea* (VandenSpiegel et al., 1998). Of these, *Luidia chefooensis* is a nomen dubium and considered indeterminate according to Döderlein (1920). Hence, the reliable count of asteroid species during that time should be considered 30, rather than 31. Additionally, six species collected between 1991 and 1995 were not observed during the CMBS conducted from 2010 to 2015 (Table 2). These species include *Disasterina ceylanica*, *Fromia monilis*, *Tamaria fusca*, *Echinaster callosus*, *Echinaster stereosomus*, and *Metrodira subuluta.* They were previously recorded from areas around Pulau Semakau and Sultan Shoal (VandenSpiegel et al., 1998). The absence of *Echinaster stereosomus* and *Fromia monilis* during the CMBS is not unexpected, as the survey did not overlap with their previous localities at the Sultan Shoal area. However, the other four species, which were recorded from the Southern Islands, were not found during the CMBS despite extensive sampling efforts in the region. It is important to note that these species are classified as Vulnerable, Endangered, or Not Evaluated according to the Singapore Red Data Book (Davison et al., 2024). Nevertheless, their absence in the survey does not necessarily indicate population declines but may instead reflect natural rarity.

Of the 31 historically documented asteroid species in Singapore, 22 are reported in the present study (Table 2). Our findings concur with the challenges associated with inferences at family and higher taxonomic levels that underscore the pressing need for further field sampling and multilocus analyses with the inclusion of additional markers such as 12S and 16S rRNA genes, mitogenomes, or even transcriptomes and genomes (Mah & Blake, 2012; Linchangco et al., 2017; Quek et al., 2021). The discrepancies between our results and the current asteroid classification also underscore the need for more detailed studies with improved taxonomic sampling. Such studies are essential for a more precise characterisation of the diversity and phylogeny of sea stars in Singapore and throughout Southeast Asia. Accurate species identification is crucial for effective implementation of biodiversity conservation efforts (Mace, 2004). Additionally, a robust phylogeny is essential for understanding evolutionary relationships among species, which can provide insights into their ecological roles, adaptive strategies, and potential vulnerabilities to environmental changes (Davis et al., 2010; Chamberlain et al., 2012).

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