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Clarifying the identities of *Saccostrea scyphophilla* (Péron & Lesueur, 1807) and *S. mordax* (Gould, 1850) (Bivalvia: Ostreidae) from the Indo-Pacific

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Abstract

There have been numerous morphological and genetic studies of oyster taxonomy, but species relationships, particularly in the genus *Saccostrea*, are poorly understood. The present paper uses shell morphology and DNA sequences to demonstrate *Saccostrea scyphophilla* (Péron & Lesueur) and *S. mordax* (Gould) are distinct species. A neotype is designated for *S. scyphophilla*. Synonyms are *Saxostrea amasa* Iredale, *Ostrea mordax* var. *cornucopiaeformis* Saville-Kent and provisionally *Ostrea forskali* var. *sueli* Jousseaume, while *Saccostrea mordoides* Cui *et al.* is a synonym of *S. mordax*. The tropical oyster reef formed by *S. scyphophilla* at Point Quobba, Western Australia, is the first recorded reef constructed by this species. The present paper provides a basis for further work elucidating the species of *Saccostrea* in the Indo-West Pacific region.

Key words: 16S, COX1, Indo-Pacific, Singapore, Fiji

Introduction

True oysters (Family Ostreidae) are dominant molluscs on many tropical and temperate rocky shorelines throughout the world. Unfortunately, phenotypic plasticity within a species and congeneric species co-occurring on a single shoreline make unravelling the systematics of ostreids extremely difficult, particularly among Indo-West Pacific species of the genus *Saccostrea* Dollfus & Dautzenberg, 1920. Recently, Salvi & Mariottini (2016) erected the subfamily Saccostreinae after a molecular analysis of the Ostreidae. Previously, Harry (1985: 150) recognised a single variable species *S. cucullata* (*sic*) (Born, 1778) that "occurs along the tropical coast of West Africa and offshore islands, around the Cape of Good Hope and into the Indo-West Pacific to southern Japan, southeast Australia, northern New Zealand, and possibly somewhat eastward", but 12 species are currently recognised in the genus (MolluscaBase eds. 2026). In China, Chen *et al*. (2025) recently recorded five species of *Saccostrea* from Weizhou Island and Heng *et al*. (2025) found eight lineages of *Saccostrea* in Hainan Island whereas Huber (2010) conceived *Saccostrea* as a homogenous grouping based on *S. cuccullata.*

There are two major clades in *Saccostrea*: One of them is based around putative *S. cuccullata*, and the second involves *S. scyphophilla* (Peron & Leseur, 1807) and *S. mordax* (Gould, 1850). Of the two clades, *S. cuccullata* is

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by far the more complex. Lam & Morton (2006) considered them to be 'superspecies' and recognised two species *S. glomerata* and *S. kegaki*, together with seven *Saccostrea* lineages designated by letters, e.g. *S. cuccullata*-A through G. Sekino & Yamashita (2013, 2016) subsequently added three more lineages (H, I and J) to the *S. cuccullata* clade. The present designation is simply *Saccostrea*-A, etc. (Snow *et al.* 2023). More recently, Richardson *et al.* (2024) identified *Saccostrea*-J as *S. spathulata* (Lamarck, 1819). Tan *et al.* (2025) obtained DNA sequences of *S. cuccullata* sensu stricto from the type locality of Ascension Island in the South Atlantic Ocean and demonstrated that it is distinct from all other DNA sequences of Indo-Pacific forms previously identified as *S. cuccullata*. Even so, the systematics of this clade requires further clarification and remains largely unresolved in terms of phylogenetics and species taxonomy.

Regarding *S. scyphophilla/mordax* group, Lam and Morton (2006) observed that they can be separated from the other *Saccostrea* lineages using shell morphology and identified two genetic lineages (as *S. mordax*-A and -B). A third lineage, *S. mordax*-C, was discovered in Japan by Sekino & Yamashita (2013). The distinguishable shell characteristics of this group, notably the purple/pink external shell colouration, highly scalloped shell margins, and radial ribs on the right or upper valve, was further emphasised by McDougall *et al*. (2024). However, there is currently no consensus on the name applicable for the *S. mordax*-A and -B groups. Huber (2010) considered *S. mordax* and related species to be conspecific and pointed out that the earliest available name is *S. scyphophilla* described from Bernier Island in Shark Bay, Western Australia (WA). Arguing that Huber's (2010) recognition of *S. scyphophilla* was not based on molecular data and detailed morphological analyses, Cui *et al.* (2021) retained the use of *S. mordax* as the valid name of the species-group and described *S. mordax* lineage C (of Sekino & Yamashita 2013) as a new species *S. mordoides* from China.

At present, *S. scyphophilla*, *S. mordax* and *S. mordoides* are listed as valid in WoRMS (MolluscaBase eds. 2025) overlooking that the names are being arbitrarily applied by different authors to the same species (i.e. *S. mordax*-A & -B of authors). To clarify the confused taxonomy and nomenclature of the *S. scyphophilla*/*mordax* group, the present paper revisits both *S. scyphophilla* and *S. mordax* using shell morphology and DNA sequences from the type localities and elsewhere and designates a neotype for *S. scyphophilla* to objectively define the species. This provides a basis for further developing our knowledge of the relationships between *S. scyphophilla, S. mordoides* and *S. mordax*.

Materials and methods

Live oysters were collected from intertidal rocks at the type locality of Bernier Island, Shark Bay, Western Australia (24.927°S; 113.150°E) by staff of the WA Department of Biodiversity Conservation and Attractions (DBCA) on 26 June 2024. Samples were chilled and couriered to Curtin University in Perth for further analysis. At Curtin a small piece of tissue was dissected from the adductor muscle of each specimen, individually labelled and placed in a small vial of 100% ethanol. DNA was extracted using DNeasy Blood and Tissue Kit (Qiagen Inc., USA) following the manufacturer's instructions.

Polymerase Chain Reaction (PCR) amplification of approximately 450 base pairs (bp) of the mitochondrial ribosomal subunit 16S gene region was done for each specimen, using primers 16Sar and 16Sbr (Simon *et al.* 1994). PCR amplification of approximately 600 bp of the cytochrome c oxidase subunit I (COX1) gene region was done using the primers dgLCO-1490 and dgHCO-2198 (Meyer 2003). PCR reactions were conducted in 25 µl containing 3 µl DNA (~20ng), 1x Invitrogen Platinum Green Hot Start PCR master mix (containing 1.5 mM $MgCl_2$ and 0.2mM of each dNTP), 0.5 mg/ml bovine serum albumin (Fisher Biotec, Australia) and 0.6µM of each primer. PCR conditions consisted of an initial incubation at 95ºC for 3 min, followed by 35 cycles of 94ºC for 45s, 53ºC for 90s, 72ºC for 45s; and a final extension step of 72ºC for 10 min.

Bi-directional sequencing of unpurified PCR products was performed using the Sanger sequencing service provided by the Australian Genome Research Facility (AGRF, Perth). Sequences were trimmed and edited using the Geneious Prime® 2025.0.3 software (http://www.geneious.com). For each individual, species identification was verified by similarity-based searches on the NCBI BLAST database (Altschul *et al.* 1990). All individual sequences were submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and assigned individual accession numbers (Table 1).

TABLE 1. List of *Saccostrea scyphophilla* and *S. mordax* COX1 and 16S sequences obtained from oysters collected in this study and corresponding GenBank accession numbers, together with their specimen collection details and museum vouchers. Isolate codes (third column from left) correspond to those used in Figs. 1–3 and in the respective species descriptions. 16S isolates for FJ02, FJ06, FJ08, FJ13, FJ15–17, FJ19–20, FJ22–23,FJ26-27, FJ29, FJ31, FJ37, FJ41, FJ44, FJ47–50, FJ57–58 were all identical.

Saccostrea species	Gene	Isolate	Collector(s)	Date	Location	Geographical co-ordinates	Specimen voucher	GenBank accession number
scyphophilla	COX1	CN01	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	WAMS 95806	PV746236
scyphophilla	COX1	CN02	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	WAMS 95807	PV746235
scyphophilla	COX1	CN03	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	WAMS 95808	PV746234
scyphophilla	COX1	CN09	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	ZRC. MOL.32219	PV746233
mordax	COX1	FJ06	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32290	PV746232
mordax	COX1	FJ08	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32291	PV746231
mordax	COX1	FJ13	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32292	PV746230
mordax	COX1	FJ23	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32300	PV746229
mordax	COX1	FJ25	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32301	PV746228
mordax	COX1	FJ27	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32303	PV746227
mordax	COX1	FJ30	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32305	PV746226
mordax	COX1	FJ41	Nanise Levuwai	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32309	PV746225
mordax	COX1	FJ48	Nanise Levuwai	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32312	PV746224
mordax	COX1	FJ50	Nanise Levuwai	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32314	PV746223
mordax	COX1	FJ51	Sakiusa Kiti	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32315	PV746222
scyphophilla	16S	SB01–05	Evan Hallein, DBCA	26-Jun-2024	Australia: Bernier Island, WA	24.92744°S; 113.15013°E	WAMS 95800 to 95804	PV760169–PV760173
scyphophilla	16S	CN01–CN08	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	WAMS 95806 to 95813	PV760174–PV760181
scyphophilla	16S	CN09–CN11	F.E.Wells & S.S.Lukehurst	18-Oct-2024	Australia: Point Quobba, Carnarvon, WA	24.48712°S; 113.40962°E	ZRC. MOL.32219 to 32221	PV760182–PV760184
mordax	16S	FJ01, FJ02	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32288 and 32289	PV760185, PV760186

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TABLE 1. (Continued)

Saccostrea species	Gene	Isolate	Collector(s)	Date	Location	Geographical co-ordinates	Specimen voucher	GenBank accession number
mordax	16S	FJ06, FJ08	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32290 and 32291	PV760187, PV760188
mordax	16S	FJ13, FJ15	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32292 and 32293	PV760189, PV760190
mordax	16S	FJ16, FJ17	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32294 and 32295	PV760191, PV760192
mordax	16S	FJ19, FJ20	S. Kiti, R. Vuiyasawa, N. Levuwai & J. Dehm	02-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32296 and 32297	PV760193, PV760194
mordax	16S	FJ21–23	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32298 to 32300	PV760195–PV760197
mordax	16S	FJ25–27	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32301 to 32303	PV760198–PV760200
mordax	16S	FJ29, 30	S. Kiti & N. Levuwai	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32304 and 32305	PV760201, PV760202
mordax	16S	FJ31	S. Kiti, N. Levuwai & J. Dehm	03-Oct-2024	Fiji: USP School of Marine Studies Foreshore, Suva	18.150833°S; 178.453722°E	ZRC. MOL.32306	PV760203
mordax	16S	FJ37	Jasha Dehm, USP	03-Oct-2024	Fiji: USP Jetty, Suva	18.150806°S; 178.454222°E	ZRC. MOL.32308	PV760204
mordax	16S	FJ41, 44, 47–50	Nanise Levuwai	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32309 to 32314	PV760205–PV760210
mordax	16S	FJ51, 52	Sakiusa Kiti	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32315	PV760211, PV760212
mordax	16S	FJ57, 58	Sakiusa Kiti	04-Oct-2024	Fiji: FNU Fiji Maritime Academy Foreshore, Suva	18.151556°S; 178.452389°E	ZRC. MOL.32317	PV760213, PV760214
scyphophilla	16S	SG01, 04, 05	K.S. Tan, S.K. Tan, S.S. Lukehurst & F.E. Wells	20-Feb-2023	Singapore: Pulau Tekukor	1.231033°N; 103.838217°E	ZRC. MOL.27642	PV760215–PV760217
mordax	16S	SG12	K.S. Tan, S.K. Tan, S.S. Lukehurst & F.E. Wells	20-Feb-2023	Singapore: Lazarus-Seringat	1.228167°N; 103.849983°E	ZRC. MOL.27639	PV760218
scyphophilla	16S	SG28	K.S. Tan, S.K. Tan, S.S. Lukehurst & F.E. Wells	20-Feb-2023	Singapore: Lazarus-Seringat	1.227333°N; 103.847333°E	ZRC. MOL.27640	PV760219
scyphophilla	16S	SG31, 32	K.S. Tan, S.K. Tan, S.S. Lukehurst & F.E. Wells	21-Feb-2023	Singapore: Pulau Hantu	1.227717°N; 103.749333°E	ZRC. MOL.27646, ZRC. MOL.27720	PV760220, PV760221
scyphophilla	16S	SG45	K.S. Tan, S.K. Tan, S.S. Lukehurst & F.E. Wells	22-Feb-2023	Singapore: East Coast Park	1.293417°N; 103.896867°E	ZRC. MOL.27647	PV760222

DNA was successfully extracted from the specimens collected at the type locality of Bernier Island but after a week in transit the tissues were unsuitable for dissection. A second set of specimens of *S. scyphophilla* was then collected from the "Aquarium" just south of the Point Quobba blowholes, approximately 50km north of Bernier Island. They were maintained alive until they reached Perth. Most specimens were frozen at Curtin University until tissue samples were taken and treated according to the methods described above. The DNA sequencing of all tissue samples of the Point Quobba and Fiji oysters was undertaken as described above. Voucher specimens of *S. scyphophilla* from Bernier Island and Point Quobba were deposited in the Western Australian Museum (WAM). Additional specimens from Point Quobba were deposited in the Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum (LKCNHM), National University of Singapore.

In Fiji, 64 live specimens were collected from Laucala Bay, adjacent to the capital city of Suva. The oysters were taken from natural rock and concrete substrates between Suva Point (18.147°S; 178.456°E), the University of the South Pacific Marine Campus (18.151°S; 178.451°E) and the Fiji National University Maritime Campus (18.152°S; 178.452°E). Each oyster was carefully prized open, placed in an individually labelled sterile bag with 100% ethanol, and preserved for transport. With the appropriate documentation and permits from Fiji's Ministry of Fisheries, the specimens were couriered to the LKCNHM in Singapore for further dissection and analysis.

Additional 16S and COX1 sequences for *Saccostrea* lineages were retrieved from Lam & Morton (2006), Volatiana *et al*. (2015), Fakhri *et al*. (2020), Ghaffari *et al*. (2022), Snow *et al.* (2023), McDougall *et al*. (2024), Wells *et al.* (2024), Zhang *et al*. (2025) and GenBank (see Appendix A, B). They were aligned using Geneious Prime® 2025.0.3 software. Sequences that were not within the targeted region of the genes or were very short were removed. jModelTest v2.1.10 (Darriba *et al.* 2012) was used to find the best evolutionary model of nucleotide substitution in the alignments. 16S alignment was trimmed to 407 bp and a Bayesian Inference (BI) analysis was performed using the MrBayes v3.2.6 (Huelsenbeck & Ronquist 2001) plugin in Geneious Prime with the following parameters: GTR+I+G model with nucleotide sites partitioned for 1 million generations subsampling every 500 generations and a 100,000 burn-in length. COX1 alignment was trimmed to 407 bp this included sequence data from Fakhri *et al*. (2020) and Ghaffari *et al*. (2022). BI analysis was performed with the following parameters: GTR +I+G model with nucleotide sites partitioned for 1 million generations subsampling every 500 generations and a 100,000 burn-in length. For a subset of data, BI analysis of the two gene concatenated alignment was done with partitioning using BEAST2 (Bouckaert *et al*. 2014) with the following parameters: Beast Model Test, chain length 50 million generations, burn-in percentage to 10%, posterior probability limit to 0.5.

Maximum Likelihood (ML) analyses were conducted in IQ-TREE (Nguyen *et al.* 2015) on the IQ-TREE web server (Trifinopoulos *et al.* 2016) using *Magallana gigas* and *Ostrea edulis* as outgroup species. The software used ModelFinder (Kalyaanamoorthy *et al.* 2017) to automatically determine substitution models for each partition, with FreeRate heterogeneity. Ultrafast bootstrap analyses (UFBoot, Hoang *et al.* 2018) were conducted with 10,000 bootstrap replicates, as well as SH-aLRT branch tests (i.e., Shimodaira-Hasegawa-approximate Likelihood-based Ratio Test) with 10,000 replicates.

All resulting phylogenetic trees were visualised in FigTree v1.4.4 (Rambaut *et al.* 2018) with tree annotations added in Adobe Illustrator. Pairwise Kimura 2-parameter distances (Kimura 1980) between specimens were calculated using MEGA11 (Tamura *et al.* 2021).

Morphological assessment of the DNA sequenced specimens was based on comparisons of the qualitative shell characters traditionally used for species delimitation. These include the shell sizes of putative adult or mature shells and their general form and shape, exterior shell sculpture, form of the shell margins and chomata, shape of the adductor muscle scar, and colouration of the exterior and interior of the shells and adductor muscle scars. Shell sections were obtained using a low speed saw (Buehler Isomet) equipped with a wafering blade.

Abbreviations: AMS, Australian Museum, Sydney; BI, Bayesian Inference; COX1, cytochrome c oxidase subunit I; FNU, Fiji National University; LV, left valve; MCZ, Museum of Comparative Zoology at Harvard University; ML, Maximum Likelihood; NHMUK, Natural History Museum (UK); SL, shell length (maximum distance between ventral edge and hinge); RV, right valve; USNM, National Museum of Natural History (Smithsonian Institution); USP, University of the South Pacific, Fiji; WAM, Western Australian Museum; ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum (LKCNHM), National University of Singapore.

Results

Molecular analysis

Both COX1 and 16S gene trees as well as their concatenated versions (Figs. 1–3) were in general topologically consistent with each other at the uppermost branches, although the lower branch configurations differed between the two genes. In both COX1 ML (Fig. 1A) and BI (Fig. 1B) trees, all major clades A through G were well supported. Clade A comprised most known *Saccostrea* species and lineages except lineage D whose sequences were not available. *Saccostrea* lineage J (as Clade G) was sister to the remaining *Saccostrea* lineages and species, which together formed clade B. Clade B in turn consisted of two well-supported Clades C and D. Clade C included *S. cuccullata* s.s., *S. glomerata*, *S. kegaki*, and *S. palmula*, as well as *Saccostrea* lineages A, B, C, E, F, G, H and I, whilst Clade D consisted of three groups, *S. scyphophilla* (lineages A and B; Clade E), *Saccostrea mordax* (Clade F) and Persian Gulf *S.* '*mordax*' COX1 sequences from Fakhri *et al*. (2020) and Ghaffari *et al*. (2022) as well as one sequence from Madagascar (Volatiana *et al*. 2015) in a third group within Clade D, that was clearly distinct from and sister to Clades E and F.

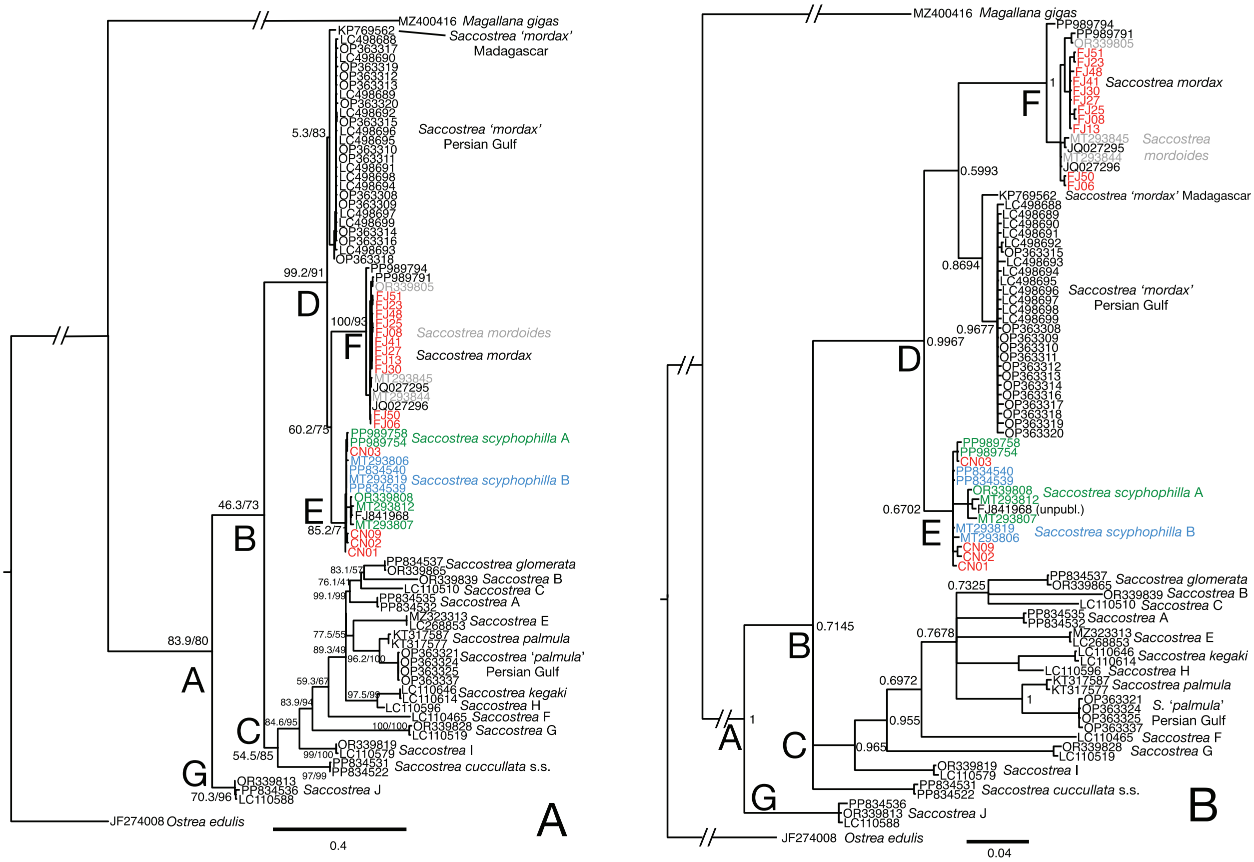

FIGURE 1. COX1 gene trees of *Saccostrea* species and lineages with the inclusion of species from the Persian Gulf based on Ghaffari *et al*. (2022). *Ostrea edulis* and *Magallana gigas* were used as outgroups. **1A**. Maximum Likelihood (ML) tree. **1B**. Bayesian Inference (BI) tree. Sequences based on material obtained in this study from Carnarvon, Western Australia (CN) and Fiji, Pacific Ocean (FJ) are in red font. Sequences of *Saccostrea scyphophilla* A and B are distinguished by green and blue font respectively. The remaining sequences utilised were selected from GenBank, with those identified as *S. mordoides* in grey font. Scale bars indicate substitutions per site. Numbers on ML tree nodes denote SH-aLRT (Shimodaira-Hasegawa-approximate Likelihood-based Ratio Test) support (%) / ultrafast bootstrap support (%) values, and those on BI tree nodes denote posterior probabilities. These values have been omitted from the uppermost branches for readability, and lengths of some branches are truncated (indicated with a double forward slash) for readability.

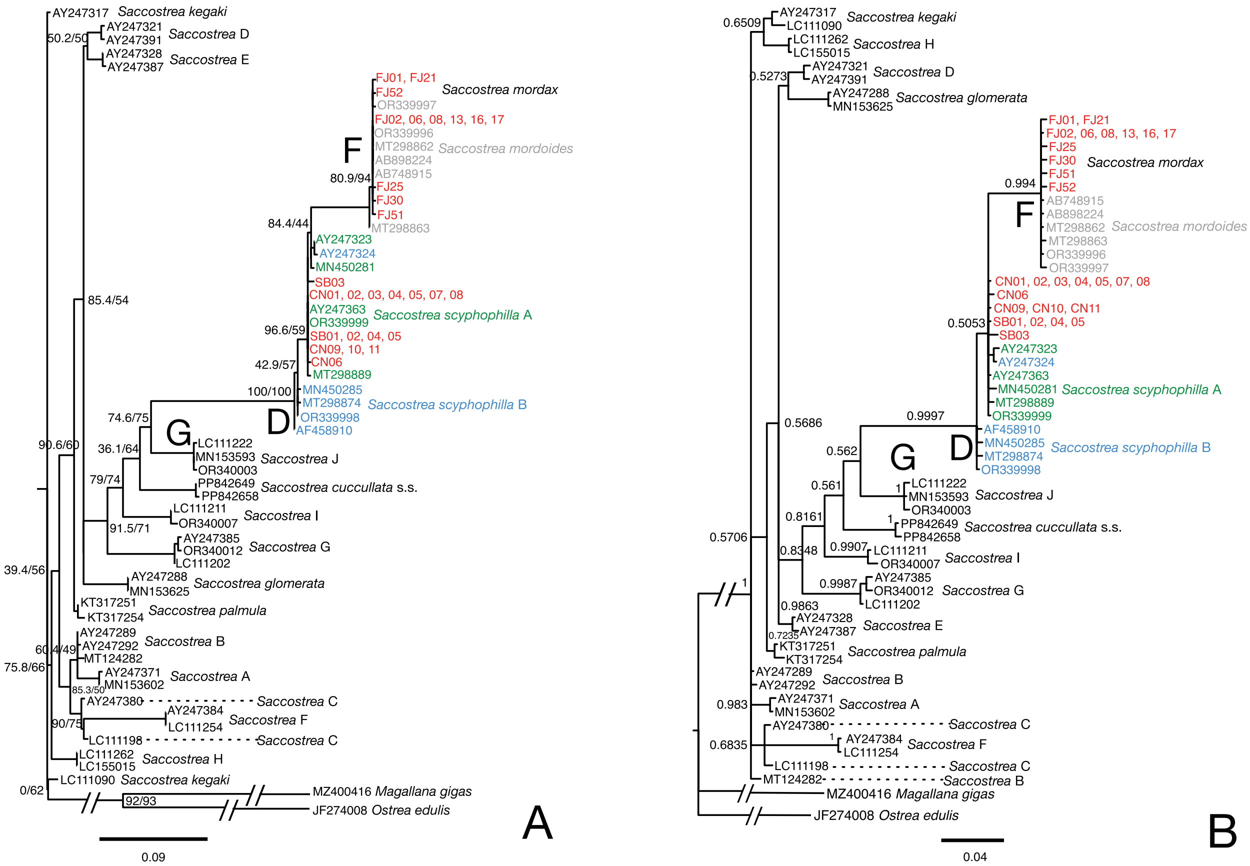

FIGURE 2. 16S gene trees of *Saccostrea* species and lineages, with *Ostrea edulis* and *Magallana gigas* as outgroups. 2**A**. Maximum Likelihood (ML) tree. 2**B**. Bayesian Inference (BI) tree. Sequences based on material obtained in this study from Bernier Island (SB), Carnarvon (CN) and Fiji (FJ) are in red font. Sequences of *Saccostrea scyphophilla* A and B are distinguished by green and blue font respectively. The remaining sequences utilised were selected from GenBank, with those identified as *S. mordoides* in grey font. Scale bars indicate substitutions per site. Numbers on ML tree nodes denote SH-aLRT (Shimodaira-Hasegawa-approximate Likelihood-based Ratio Test) support (%) / ultrafast bootstrap support (%) values, and those on BI tree nodes denote posterior probabilities. These values have been omitted from the uppermost branches for readability, and lengths of some branches are truncated (indicated with a double forward slash) and for readability.

In Clade E, the sequences from material obtained near the type locality of *S. scyphophilla* (CN01–03, CN09) were not distinct from the two lineages of *S. scyphophilla* from elsewhere in Australia and China (as *mordax* A and B). Sequences from Fiji (FJ06, FJ08, FJ13 etc.), the type locality of *S. mordax*, closely clustered with sequences identified as *S. mordoides* from Okinawa (Japan, as *mordax* C), China and Australia.

The 16S ML and BI trees (Fig. 2A, 2B) maintained similar topologies in the higher branches with COX1 trees in that the lineages and species were consistent, although the major clades resolved in the COX1 tree were absent in the 16S trees. Only Clades D, F and G can be detected, and while most *Saccostrea* lineages and species were clustered and distinct as expected, sequences of *Saccostrea* lineage C were paraphyletic to each other, as were those of *S. kegaki*. Support for the lower branches was also equivocal. Nevertheless, *S. mordax* (Clade F) was well-supported and formed a distinct clade that comprised of both *S. mordoides* from China and *S. mordax* from Fiji. *Saccostrea scyphophilla* sequences, which included those from its original type locality Bernier Island (SB01–05; see Fig. 2), were clustered together but clearly paraphyletic within Clade D.

In the COX1-16S concatenated trees (Fig. 3A, 3B), the lower branches had equivocal support, and the major clades differed in composition. In the ML concatenated tree, *Saccostrea* lineage J (Clade G) was sister to a well-supported Clade D (made up of *S. scyphophilla* and *S. mordax*). In contrast, Clade G was sister to *S. cucullata* s.s. in the BI tree, and they in turn were sister to the *Saccostrea* lineages A, B, F and I, as well as *S. glomerata* and *S. kegaki*. *Saccostrea* lineages D, E, and H, as well as *S. palmula* could not be included in the concatenated analysis due to lack of suitable sequences in GenBank. Even so, Clade D was clearly defined in both ML and Bayesian trees and concurred with the single gene trees in composition and topological structure, supporting two distinct clades comprising *S. scyphophilla* and *S. mordax*.

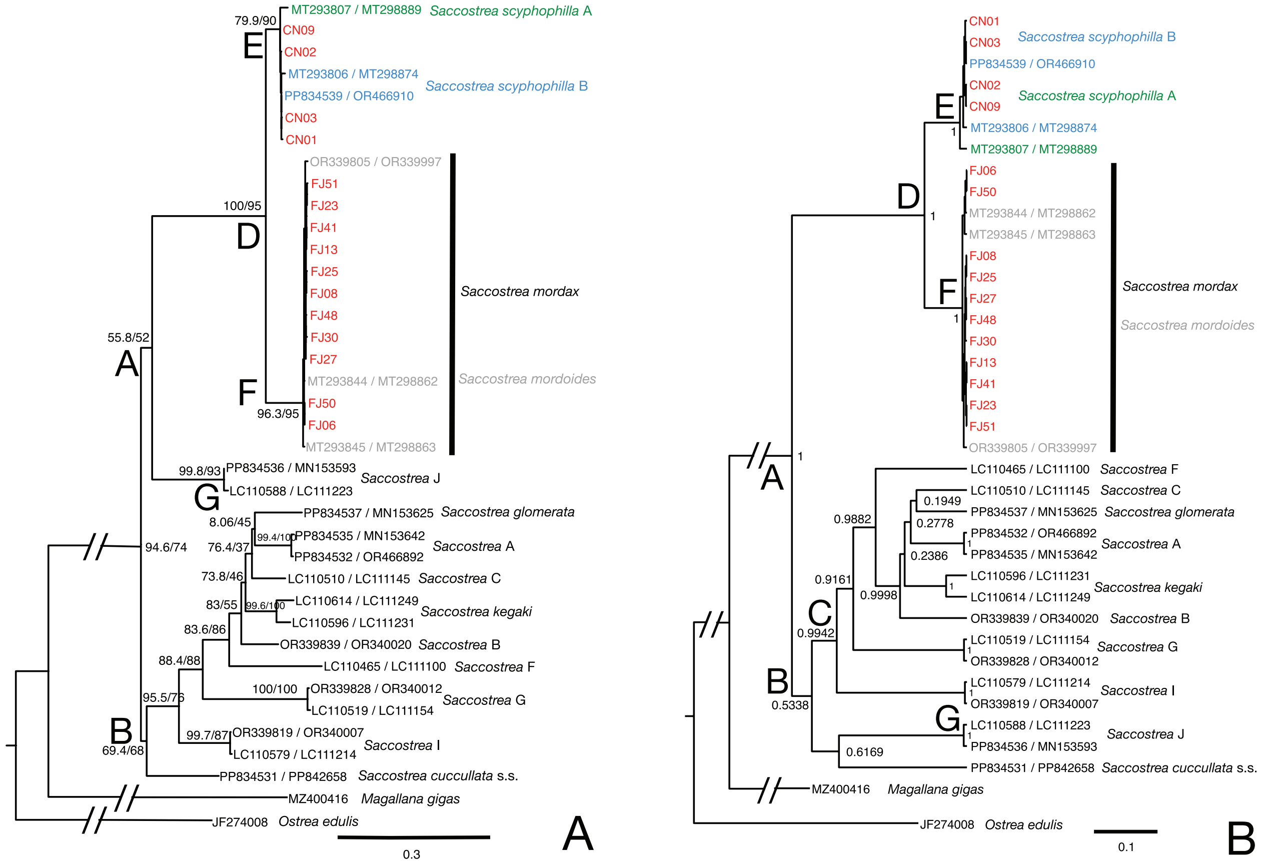

FIGURE 3. Concatenated COX1-16S gene trees of *Saccostrea* species and lineages, with *Ostrea edulis* and *Magallana gigas* as outgroups. 3**A**. Maximum Likelihood (ML) tree. 3**B**. Bayesian Inference (BI) tree. Sequences based on material obtained in this study from Carnarvon, Western Australia (CN) and Fiji, Pacific Ocean (FJ) are in red font. Sequences of *Saccostrea scyphophilla* A and B are distinguished by green and blue font respectively. The remaining sequences utilised were selected from GenBank, with those identified as *S. mordoides* in grey font. Scale bars indicate substitutions per site. Numbers on ML tree nodes denote SH-aLRT (Shimodaira-Hasegawa-approximate Likelihood-based Ratio Test) support (%) / ultrafast bootstrap support (%) values, and those on BI tree nodes denote posterior probabilities. These values have been omitted from the uppermost branches for readability, and lengths of some branches are truncated (indicated with a double forward slash) and for readability.

K2P genetic distances obtained for sequences of the COX1 gene ranged between 0.06 to 0.25 amongst *Saccostrea* species and lineages (Table 2). However, the distances amongst *S. scyphophilla* A, *scyphophilla* B and sequences from material obtained near the type locality of *S. scyphophilla* (CN01–03, CN09; grouped as '*scy*' in Table 2) were all less than 0.03 suggesting their close relationship. Similarly, distances between sequences of *S. mordoides* (=*mordax* lineage C; as '*mdds*' in Table 2) from China and Australia as well as from material collected in Fiji, the type locality of *S. mordax* (as '*mrdx*'), were all less than 0.01. In contrast, genetic distances between '*mordax*' from the Persian Gulf and those of '*mdds*' and '*mrdx*' ranged between 0.10 and 0.13, suggesting the distinctness of the Persian Gulf species. The genetic distances between *S. scyphophilla* (as well as its lineages A and B) and *S. mordax* (=*mordoides*) were in the range of 0.11 to 0.12, again reflecting their distinct identities.

TABLE 2. Ranges of the number of base substitutions per site between COX1 (cytochrome c oxidase subunit 1) gene sequences of *Saccostrea* species based on the K2P (Kimura 2-Parameter) model using *Magallana gigas* and *Ostrea edulis* as outgroups. Sample sizes of the sequences used for each species are indicated in the first column. Abbreviations used: *cucc*—*cuccullata* s.s.; *glom*—*glomerata*; *kega*—*kegaki*; Lin—lineage; *Maga*—*Magallana*; *mdds*—*mordoides* (=*mordax* C) from China (n=2) and Australia (n=1); *mrdx*—*mordax* from Fiji (n=11), Indonesia (n=2) and Taiwan (n=2); *mrdx* (PG)—'*mordax*' from Persian Gulf; Ostr—*Ostrea*; *palm*—*palmula*; *scy*A—*scyphophilla* A; *scy*B—*scyphophilla* B; *scy*—*scyphophilla* from Carnarvon (n=4) and China (n=1).

Saccostrea spp.	*scy*A	*scy*B	*scy*	*mdds*	*mrdx*	*mrdx* (PG)	*glom*	*kega*	*palm*	Lin A	Lin B	Lin C	Lin E	Lin F	Lin G	Lin H	Lin I	Lin J	*cucc*	*Maga*	*Ostr*
*scy*A (n=5)	0.0020–0.0251																				
*scy*B (n=4)	0.0020–0.0200	0–0.0049																			
scy (n=5)	0–0.0251	0 –0.0049	0.0049–0.0074																		
mdds (n=3)	0.1056–0.1116	0.1056–0.1086	0.0996–0.1116	0.0049–0.0124																	
mrdx (n=15)	0.1056–0.1205	0.1056–0.1116	0.0996–0.1116	0 –0.0099	0–0.0099																
mrdx (PG) (n=25)	0.0680–0.1265	0.0597–0.0680	0.0624–0.0765	0.1081–0.1234	0.0991–0.1262	0–0.0099															
glom (n=2)	0.1693–0.1967	0.1663–0.1693	0.1693–0.1756	0.1957–0.1991	0.1926–0.2029	0.1994–0.2099	0–0.0025														
kega (n=2)	0.1834–0.2178	0.1868–0.1902	0.1834–0.1936	0.0996–0.1116	0.2107–0.2219	0.1936–0.2111	0.1423–0.1485	0–0.0025													
palm (n=2)	0.1822–0.2022	0.1789–0.1856	0.1789–0.1822	0.1988–0.2057	0.1789–0.1822	0.2060–0.2202	0.1391–0.1420	0.1423–0.1485	0–0.0049												
Lin A (n=2)	0.1536–0.1792	0.1567–0.1599	0.1536–0.1631	0.1693–0.1726	0.1691–0.1756	0.1599–0.1663	0.1268–0.1302	0.1427–0.1492	0.1363–0.1395	0–0.0025											
Lin B (n=1)	0.1663–0.1858	0.1663–0.1729	0.1631–0.1696	0.1759–0.1792	0.1565–0.1828	0.1856–0.1991	0.1423–0.1452	0.1642–0.1676	0.1350–0.1350	0.1517–0.1550	0										

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TABLE 2. (Continued)

Saccostrea spp.	*scy*A	*scy*B	*scy*	*mdds*	*mrdx*	*mrdx* (PG)	*glom*	*kega*	*palm*	Lin A	Lin B	Lin C	Lin E	Lin F	Lin G	Lin H	Lin I	Lin J	*cucc*	*Maga*	*Ostr*
Lin C (n=1)	0.2054–0.2198	0.2088–0.2088	0.2123–0.2054	0.2127–0.2234	0.2095–0.2234	0.2375–0.2450	0.1228–0.1256	0.1510–0.1543	0.1684–0.1684	0.1388–0.1420	0.1503–0.1503	0									
Lin E (n=2)	0.2002–0.2242	0.1895–0.1963	0.1998–0.2033	0.2134–0.2206	0.2134–0.2174	0.2033–0.2174	0.1680–0.1709	0.1583–0.1617	0.1591–0.1659	0.1420–0.1452	0.1908–0.1908	0.1743–0.1743	0								
Lin F (n=1)	0.1892–0.2057	0.1957–0.2026	0.1991–0.2127	0.2022–0.2057	0.2022–0.2060	0.2068–0.2174	0.1757–0.1757	0.1821–0.1856	0.1754–0.1754	0.1497–0.1529	0.1925–0.1925	0.1680–0.1680	0.2030–0.2030	0							
Lin G (n=2)	0.2306–0.2553	0.2343–0.2343	0.2306–0.2380	0.2515–0.2553	0.2482–0.2592	0.2270–0.2343	0.2147–0.2178	0.2017–0.2053	0.2051–0.2051	0.2080–0.2115	0.2151–0.2151	0.1831–0.1831	0.2160–0.2160	0.2223–0.2333	0						
Lin H (n=1)	0.1767–0.2036	0.1800–0.1800	0.1767–0.1834	0.2002–0.2036	0.1971–0.2040	0.1834–0.1936	0.1456–0.1485	0.0740–0.0769	0.1492–0.1492	0.1205–0.1236	0.1445–0.1445	0.1478–0.1478	0.1617–0.1617	0.1523–0.1523	0.1878–0.1878	0					
Lin I (n=2)	0.1504–0.1820	0.1473–0.1536	0.1442–0.1504	0.1721–0.1787	0.1719–0.1820	0.1636–0.1895	0.1777–0.1807	0.1875–0.1909	0.1392–0.1423	0.1491–0.1556	0.1577–0.1609	0.1936–0.1971	0.1707–0.1707	0.1814–0.1848	0.1770–0.1737	0.1773–0.1807	0–0.0049				
Lin J (n=3)	0.1636–0.2005	0.1940–0.1940	0.1871–0.1905	0.1636–0.1734	0.1631–0.1704	0.1905–0.2160	0.2071–0.2103	0.2071–0.2178	0.2142–0.2142	0.1831–0.1933	0.1764–0.1831	0.1865–0.1898	0.2260–0.2260	0.2002–0.2107	0.2469–0.2546	0.2036–0.2036	0.1933–0.2002	0–0.0049			
cucc (n=2)	0.1767–0.1998	0.1734–0.1804	0.1701–0.1800	0.1895–0.1963	0.1829–0.1933	0.1636–0.1878	0.1943–0.1978	0.2017–0.2084	0.1577–0.1579	0.2192–0.2233	0.1542–0.1572	0.2192–0.2197	0.2160–0.2192	0.1886–0.1890	0.2002–0.2005	0.1743–0.1773	0.1550–0.1582	0.1856–0.1886	0–0.0025		
Maga (n=1)	0.2919–0.3243	0.3195–0.3195	0.3115–0.3155	0.2957–0.2995	0.2916–0.2957	0.3239–0.3409	0.2954–0.2990	0.3075–0.3115	0.3115–0.3115	0.3036–0.3075	0.3115–0.3115	0.3075–0.3075	0.3043–0.3043	0.3399–0.3399	0.3371–0.3414	0.3115–0.3115	0.3004–0.3004	0.3112–0.3151	0.3036–0.3039	0	
Ostr (n=1)	0.2369–0.2730	0.2689–0.2689	0.2652–0.2727	0.2507–0.2581	0.2510–0.2581	0.2621–0.2696	0.2881–0.2916	0.3009–0.3049	0.2621–0.2621	0.2720–0.2758	0.2714–0.2714	0.2929–0.2929	0.2959–0.2959	0.2897–0.2897	0.3261–0.3261	0.2889–0.2889	0.2783–0.2821	0.2625–0.2700	0.2811–0.2815	0.3125	0

TABLE 3. Ranges of the number of base substitutions per site between 16S gene sequences of *Saccostrea* species based on the K2P (Kimura 2-Parameter) model using *Magallana gigas* and *Ostrea edulis* as outgroups. Sample sizes of the sequences used for each species are indicated in the first column. Abbreviations used: *cucc*—*cucullata* s.s.; *glom*—*glomerata*; *kega*—*kegaki*; Lin—lineage; *Maga*—*Magallana*; *mdds*—*mordoides* from Japan (n=2), China (n=2) and Australia (n=2); *mrdx*—*mordax* from Fiji (n=30, 6 haplotypes); Ostr—*Ostrea*; *palm*—*palmula*; *scy*A—*scyphophilla* A; *scy*B—*scyphophilla* B; *scy*—*scyphophilla* from Bernier Island (n=5) and Carnarvon (n=11).

Saccostrea spp.	*scy*A	*scy*B	*scy*	*mdds*	*mrdx*	*glom*	*kega*	*palm*	Lin A	Lin B	Lin C	Lin D	Lin E	Lin F	G	H	I	J	*cucc*	*Maga*	*Ostr*
*scy*A (n=5)	0–0.0155																				
*scy*B (n=5)	0–0.0155	0–0.0025																			
scy (n=16)	0.0025–0.0129	0.0025–0.0155	0–0.0077																		
mdds (n=6)	0.0393–0.0475	0.0420–0.0503	0.0393–0.0503	0–0.0124																	
mrdx (n=6)	0.0419–0.0503	0.0419–0.0503	0.0419–0.0503	0–0.0099	0–0.0051																
glom (n=2)	0.1152–0.1184	0.1152–0.1184	0.1152–0.1215	0.1059–0.1089	0.1028–0.1089	0–0.0025															
kega (n=2)	0.1214–0.1373	0.1214–0.1372	0.1091–0.1373	0.1121–0.1215	0.1091–0.1215	0.1423–0.1485	0–0.0052														
palm (n=2)	0.1000–0.1092	0.1000–0.1092	0.1000–0.1123	0.0969–0.0999	0.0939–0.0998	0.0402–0.0459	0.0210–0.0319	0–0.0052													
Lin A (n=2)	0.1092–0.1154	0.1123–0.1182	0.1123–0.1185	0.1060–0.1121	0.1060–0.1121	0.0402–0.0430	0.0346–0.0401	0.0211–0.0293	0–0.0026												
Lin B (n=3)	0.1215–0.1279	0.1155–0.1247	0.1219–0.1282	0.0420–0.1154	0.0419–0.1185	0.0429–0.1152	0.0237–0.0318	0.1000–0.1061	0.0157–0.0211	0–0.0026											
Lin C (n=2)	0.1184–0.1247	0.1214–0.1279	0.1029–0.1279	0.1089–0.1120	0.1089–0.1151	0.0401–0.0429	0.0264–0.0373	0.0265–0.0319	0.0292–0.0319	0.0184–0.0210	0–0.0078										

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TABLE 3. (Continued)

Saccostrea spp.	*scy*A	*scy*B	*scy*	*mdds*	*mrdx*	*glom*	*kega*	*palm*	Lin A	Lin B	Lin C	Lin D	Lin E	Lin F	G	H	I	J	*cucc*	*Maga*	*Ostr*
Lin D (n=2)	0.1029–0.1060	0.1029–0.1060	0.1029–0.1091	0.0998–0.0998	0.0968–0.1028	0.0374–0.0374	0.0324–0.0457	0.0238–0.0292	0.0429–0.0430	0.0459–0.0486	0.0401–0.0429	0									
Lin E (n=2)	0.1029–0.1152	0.1029–0.1182	0.1121–0.1373	0.0998–0.1089	0.0968–0.1151	0.0374–0.0401	0.0345–0.0401	0.0238–0.0292	0.0292–0.0430	0.0265–0.0291	0.0401–0.0429	0.0265–0.0265	0–0.0085								
Lin F (n=2)	0.1187–0.1219	0.1217–0.1250	0.1187–0.1250	0.1064–0.1095	0.1033–0.1095	0.0684–0.0684	0.0681–0.0769	0.0568–0.0625	0.0596–0.0625	0.0540–0.1187	0.0512–0.0540	0.0682–0.0682	0.0567–0.0567	0							
Lin G (n=3)	0.1099–0.1187	0.1129–0.1217	0.1099–0.1224	0.1008–0.1068	0.0977–0.1068	0.0684–0.0831	0.0681–0.0890	0.0627–0.0655	0.0540–0.0773	0.0540–0.0742	0.0684–0.0742	0.0655–0.0683	0.0540–0.0568	0.0742–0.0771	0–0.0052						
Lin H (n=2)	0.1244–0.1244	0.1274–0.1274	0.1244–0.1307	0.1059–0.1059	0.1028–0.1089	0.0512–0.0512	0.0237–0.0291	0.0318–0.0373	0.0318–0.0345	0.0345–0.0345	0.0372–0.0372	0.0458–0.0458	0.0429–0.0429	0.0651–0.0651	0.0859–0.0918	0					
Lin I (n=2)	0.1034–0.1067	0.1064–0.1096	0.1034–0.1129	0.1092–0.1093	0.1061–0.1123	0.0623–0.0680	0.0621–0.0794	0.0537–0.0593	0.0709–0.0766	0.0622–0.0623	0.0593–0.0649	0.0565–0.0621	0.0621–0.0621	0.0795–0.0795	0.0771–0.0829	0.0764–0.0764	0–0.0052				
Lin J (n=3)	0.0990–0.1074	0.1019–0.1103	0.0990–0.1135	0.1013–0.1128	0.0984–0.1158	0.0710–0.0794	0.0768–0.0912	0.0652–0.0736	0.0653–0.0766	0.0769–0.0797	0.0739–0.0768	0.0681–0.0709	0.0739–0.0824	0.1037–0.1125	0.0923–0.1012	0.0855–0.0855	0.0739–0.0824	0–0.0076			
cucc (n=2)	0.1026–0.1056	0.1055–0.1086	0.1056–0.1087	0.1024–0.1055	0.0994–0.1086	0.0652–0.0681	0.0624–0.0711	0.0711–0.0799	0.0681–0.0711	0.0595–0.0623	0.0623–0.0652	0.0739–0.0739	0.0681–0.0710	0.0946–0.0976	0.0832–0.0923	0.0681–0.0710	0.0652–0.0681	0.0731–0.0760	0–0.0026		
Maga (n=1)	0.2306–0.2343	0.2341–0.2380	0.2306–0.2343	0.2158–0.2194	0.2158–0.2228	0.2037–0.2037	0.2003–0.2038	0.2038–0.2074	0.2038–0.2075	0.2306–0.2306	0.1934–0.1934	0.2072–0.2072	0.2180–0.2180	0.2225–0.2225	0.2372–0.2445	0.2180–0.2180	0.2109–0.2109	0.2109–0.2075	0.2111–0.2147	0	
Ostr (n=1)	0.2009–0.2044	0.2078–0.2080	0.2044–0.2080	0.1999–0.2034	0.1965–0.1999	0.2090–0.2090	0.1844–0.1879	0.1776–0.1810	0.1949–0.1984	0.1951–0.2044	0.1880–0.1951	0.1951–0.1951	0.1951–0.1951	0.2028–0.2028	0.1918–0.1952	0.1880–0.1880	0.1951–0.2020	0.2141–0.2144	0.2094–0.2131	0.2188–0.2188	0

Genetic distances for the 16S gene reflected the trends shown for the COX1 gene although the absolute values were generally smaller. Sequences of both *S. scyphophilla* A and *scyphophilla* B were not distinguishable from those based on specimens from Bernier Island, the original type locality of *S. scyphophilla* (as '*scy*' in Table 3), with values that ranged between 0.003 to 0.016. In the case of *S. mordoides* (=*mordax* C) and *S. mordax* from Fiji, the distances were in the region of 0.001 to 0.005, again reflecting their closeness. Distances amongst the various *Saccostrea* species and lineages A–J were typically in the order of 0.02 to 0.13 (Table 3). The genetic distances between *S. scyphophilla* (as well as its lineages A and B) and *S. mordax* (=*mordoides*) were consistently in the range of 0.04 to 0.05.

Taxonomy

Family Ostreidae Rafinesque, 1815

Subfamily Saccostreinae Salvi & Mariottini, 2016

Genus *Saccostrea* Dollfus & Dautzenberg, 1920

Type species: *Ostrea saccellus* Dujardin, 1837 (a fossil species).

Saccostrea scyphophilla (Péron & Lesueur, 1807)

Figs. 4–7

Original description: *Ostrea scyphophilla* Péron & Lesueur, 1807 [in Péron, 1807–1816]: 119. Type locality: Bernier Island ("l'île Bernier"), Western Australia, Australia.

Synonyms

Saxostrea amasa Iredale, 1939: 399, plate VII, fig. 8. Type locality: Caloundra, Queensland.
Ostrea forskali var. *sueli* Jousseaume, 1925 in Lamy (1925): 192. Type localities: Obock in Djibouti, Perim Island and Aden in Yemen ("Obock, Perim, Aden"). Uncertain synonym.
Ostrea mordax var. *cornucopiaeformis* Saville-Kent, 1893: 248, Chromo-plate xiv, figs. 3, 4. Type locality: Rocky Island, off Keppel Bay, Queensland, Australia.

Type material: Neotype of *Ostrea scyphophilla* (WAMS_95811), Point Quobba Blowholes, Western Australia; syntype of *Ostrea mordax* var. *cornucopiaeformis* (AMS C271), no other data; holotype of *Saxostrea amasa* (AMS C90526), Caloundra, Queensland.

Other material examined: Australia: 1 LV (NHMUK [1901.12.20.90]), Shark Bay, Western Australia; 3 ex. (NHMUK uncatalogued [D. G. Reid Colln. 2341]), Wistari Reef, near Heron Island, Queensland, coll. 12 January 1981; 1 ex. (ZRC.MOL.3414), Waterfall Bay, Christmas Island, coll. 23 Mar.2011; 5 ex. (WAMS_95800–95804 [DNA]), Bernier Island, Western Australia, coll. 26 June 2024; 8 ex (WAMS_95805–95810 [DNA], WAMS_95812–95813 [DNA], 5 ex. (ZRC.MOL.32219–32221 [DNA]), Point Quobba Blowholes, Western Australia, 24.487°S 113.410°E, coll. 18 October 2024. **Indonesia**: 2 ex. (ZRC.MOL.35009), Tanjung Sading, Pulau Bintan, Riau, coll. 11 May 1993; 2 ex. (ZRC.MOL.27077), Teluk Kombal, Lombok. **Malaysia**: 2 ex. (ZRC.MOL.35007), Pasir Bogak, Pulau Pangkor, Perak; 5 ex. (ZRC.MOL.28265), south of Teluk Nipah, Pulau Pangkor, coll. 26 April 2013. **Singapore**: 1 ex. (ZRC.MOL.31659), Raffles Lighthouse pier, coll. 3 May 1962; 2 ex. (ZRC.MOL.9786), Raffles Lighthouse, coll. 1963; 1 ex. (ZRC.MOL.34378), Pulau Salu, coll. 4 Nov.1968; 2 ex. (ZRC.MOL.34624), Tanjung Teritip, coll. Jan.–Feb.1969; 1 ex. (ZRC.MOL.8620), Pulau Semakau, coll. 4 January 2011; 2 ex. (ZRC.MOL.8619), Pulau Semakau, coll. 22 January 2011; 1 ex. (ZRC.MOL.8618), Pulau Semakau, coll. 19 February 2011; 2 ex. (ZRC.MOL.9113), East Coast Park, coll. 16 November 2016; 4 ex. (ZRC.MOL.24729, Tanjong Rimau, Sentosa, coll. 12–16 July 2021; 8 ex. (ZRC.MOL.209365), Raffles Lighthouse, Pulau Satumu, coll. 15–17 November 2020;

5 ex. (ZRC.MOL.27640 [DNA], ZRC.MOL.27641), Lazarus Island, 1°13.640'N 103°50.840'E, coll. 20 February 2023; 3 ex. (ZRC.MOL.27738), Lazarus Island-Pulau Seringat (St John's Island), N1°13.661' E103°50.879', coll. 20 February 2023; 7 ex. (ZRC.MOL.27642–27644 [DNA], ZRC.MOL.27645), Pulau Tekukor, 1°13.862'N 103°50.293'E, coll. 20 February 2023; 2 ex. (ZRC.MOL.27646 [DNA], ZRC.MOL.27720 [DNA]), Pulau Hantu, 1°18.583'N 103°55,038'E, coll. 21 February 2023; 2 ex. (ZRC.MOL.27647 [DNA], ZRC.MOL.27739), East Coast Park, 1°17.605'N 103°53.812'E coll. 22 February 2023. **Taiwan**: 1 ex. (ZRC.MOL.20740), Penghu, Aimen, coll. 3 Nov.2020.

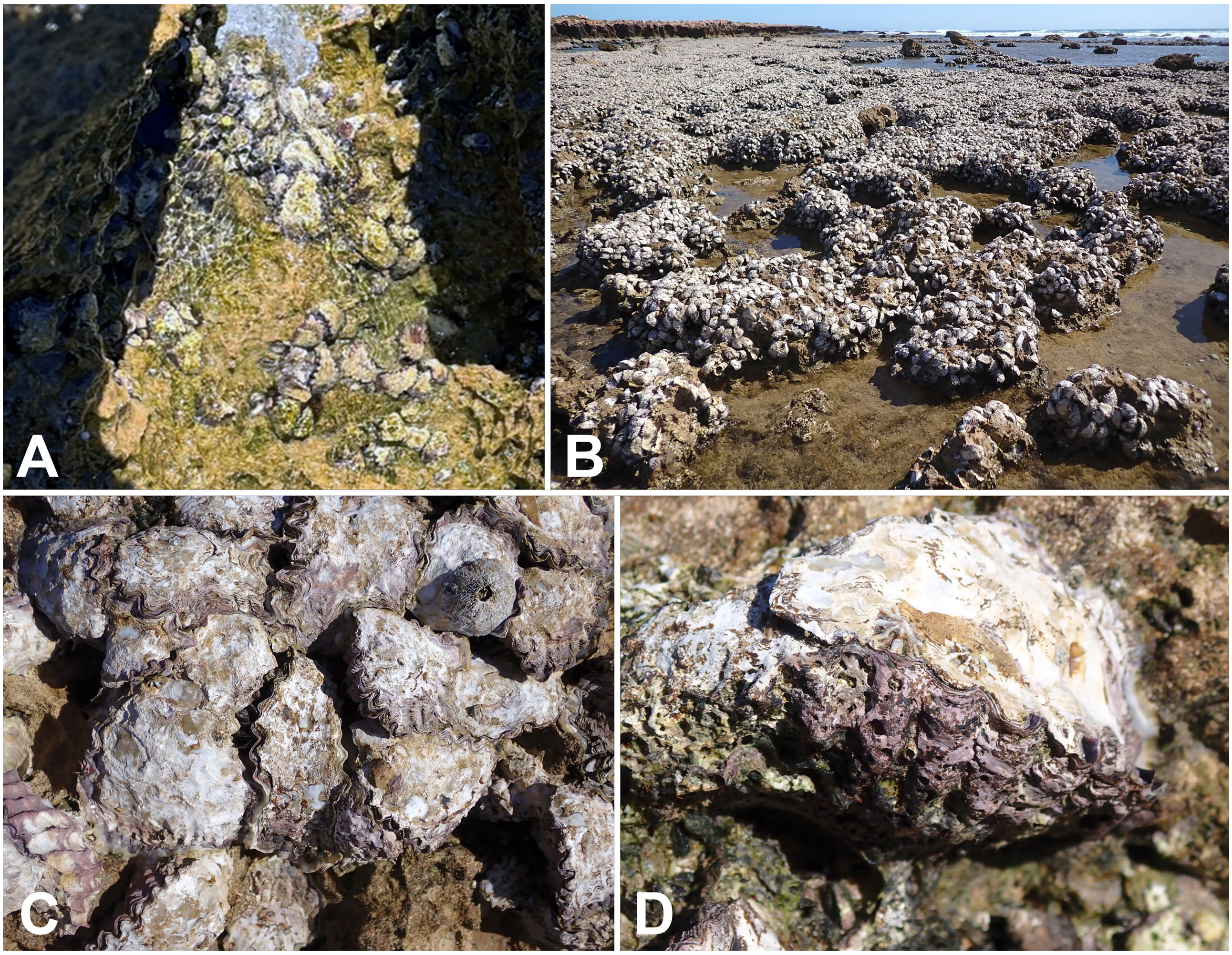

FIGURE 4. *Saccostrea scyphophilla*. **A.** On intertidal rocks at the original type locality of Bernier Island, Shark Bay, Western Australia. **B–D.** Oyster beds at the new type locality, the "Aquarium" at Point Quobba, Western Australia.

Description: Shell medium to large (c. 40–110 mm [160–190 mm stated in Péron & Lesueur, 1807]; SL of largest RV examined = 81.6 mm); form highly variable, from rather flat circular or triangular (e.g., Figs. 5C–F; 7S–U; 7V–X) to cornet-like or cylindrical (e.g., Figs. 5A, B; 7D–F); thick and solid. Shell exterior purplish black to reddish purple, usually with corroded/eroded patches of white. LV only slightly larger than RV and usually shallowly cupped when attached on flat surfaces, distinctly larger and very deeply cupped if growing in crowded conditions; posterior edge typically very thick and prominently raised from the attached substate, if not of the cornet-like or cylindrical form. RV exterior surface with many crowded, sometimes scaly, closely set radial ribs (e.g., Figs. 5D; 7W); often corroded/eroded, with irregularly concentric dark brown lines of the conchiolin layers except ventral edge usually with many distinct lines formed by the grooves between the ribs (e.g., Figs. 6I; 7N). Shell margins along the anterior and posterior edges scalloped, zigzagging or undulating, but sometimes hardly so along the ventral edge (e.g., 5F; 7X). Shell interior white, often with darker cloudy patches (e.g., 6C; 6J), occasionally with dark greenish brown spots and blotches (e.g., 6O; 7C; 7AA). Interior margin usually with thick purplish black border at posterior edge of LV, sometimes also present at anterior; often thin and interrupted in RV. Umbonal cavity shallow to very deep, depending on shape of LV. Chomata variable, prominent around the entire margin (e.g., 7U; 7AA) to very sparse, usually only near the hinge, and nearly non-existent (e.g., 6R; 7X). Adductor muscle scar of LV usually white; RV white with scarcely any hint of darker lines (e.g., Figs. 5F; 7R; 7X) to having purplish brown bands (e.g., Figs. 7I; 7U) to fully black (e.g., Figs. 6F; 6R), often slightly raised, especially towards the ventral side (see Figs. 12C; 12D).

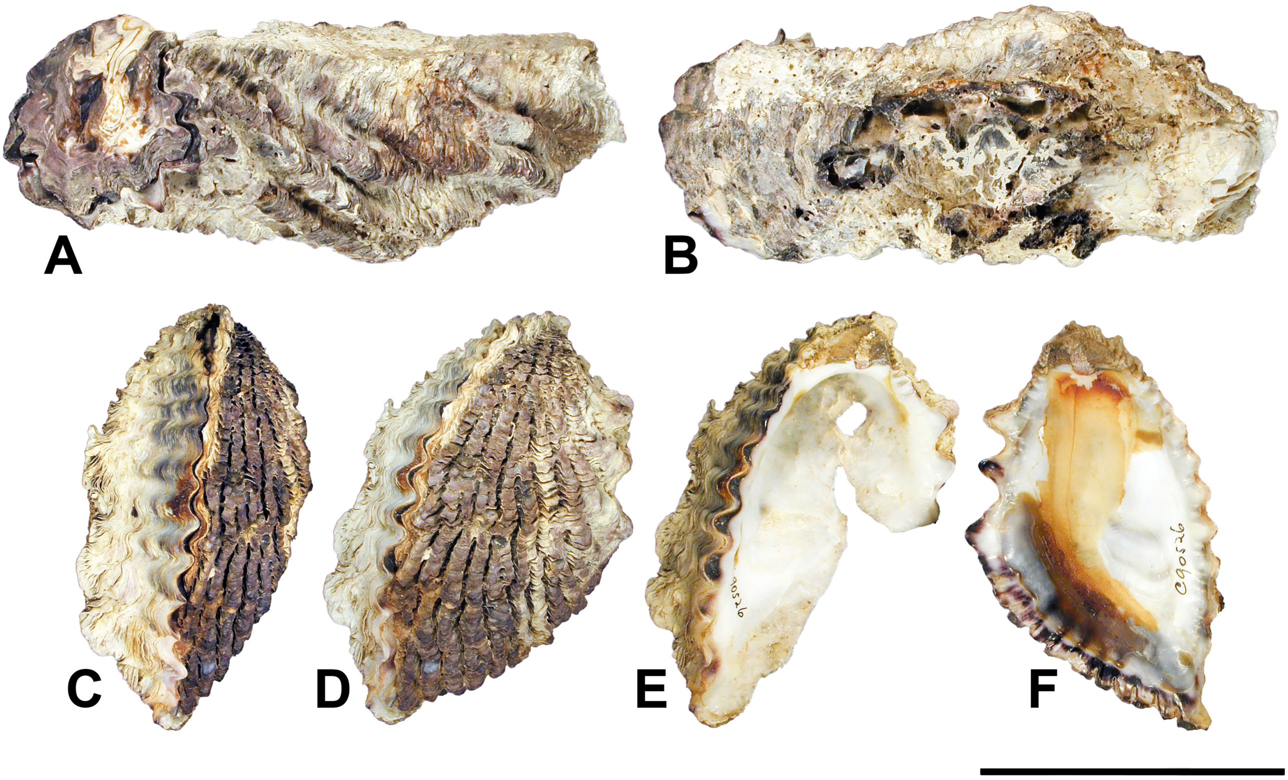

FIGURE 5. *Saccostrea scyphophilla*. **A–B,** Syntype (AMS C271) of *Ostrea mordax* var. *cornucopiaeformis* Saville-Kent, 1893 (dorso-lateral view [**A**], and ventral view [**B**]). **C–F.** Holotype (AMS C90526) of *Saxostrea amasa* Iredale, 1939 (posterolateral view [**C**], exterior of RV [**D**], interior of LV [**E**], and interior of RV [**F**]). Images by the ©Australian Museum. Scale bar: 50 mm.

Habitat: *Saccostrea scyphophilla* lives in the mid to upper intertidal region of a wide variety of hard bottoms including rocky shorelines, isolated rocks, mangroves and artificial structures. It occurs in sheltered areas, but reaches its highest densities on open, exposed coasts.

Previous records in Western Australia verified by DNA sequences (Fig. 13): Lam & Morton (2006): Vlamingh Head, north of Exmouth; Quobba; Barrow Island; Kalbarri (all as *S. mordax* (Gould, 1850)). Snow *et al.* (2023): King George River; Bonaparte Archipelago; Ngalanguru Island; Montebello Islands; Flying Foam Passage, north of Burrup Peninsula; Dampier Archipelago; Serrurier Island; Exmouth; Shark Bay; Carnarvon; Kalbarri; Yallabatharra; Geraldton; Houtman Abrolhos Islands. Wells *et al.* (2024): Ashburton Port area: Direction Island; East end Thevenard Island; Ashburton Island; Salt Creek; Old Onslow jetty, Beadon Point. Dampier Port area: Withnell Bay; Southern entrance to King Bay; Norbill Bay, Rosemary Island; Whalers Bay, Malus Island; Marney Bay, Malus Island; High Point, Whittaker Island; North side of East Intercourse Island. Port Hedland Port area: Public boat ramp; Finucane Island.

Published distribution based on DNA analyses: Okinawa, Taiwan, Hong Kong, China, Malaysia (Lam & Morton 2009 as *S. mordax*; see also Zhou *et al*., 2025), Singapore (this study, GenBank PV760215–PV760217, PV760219–PV760222; Table 1), Thailand (Duangdee *et al*. 2025), Indonesia (Manado; Zhang *et al*. 2025); northern Australia (Western Australia, Northern Territory, Queensland, New South Wales) (Lam & Morton 2006 (as *S. mordax*); McDougall 2020; McDougall *et al*. 2020; 2024; Snow *et al*. 2023; Wells *et al*. 2024); Bangladesh (Chowdhury *et al*., 2021, as *S. mordax*); Maldives (Salvi *et al*. 2014).

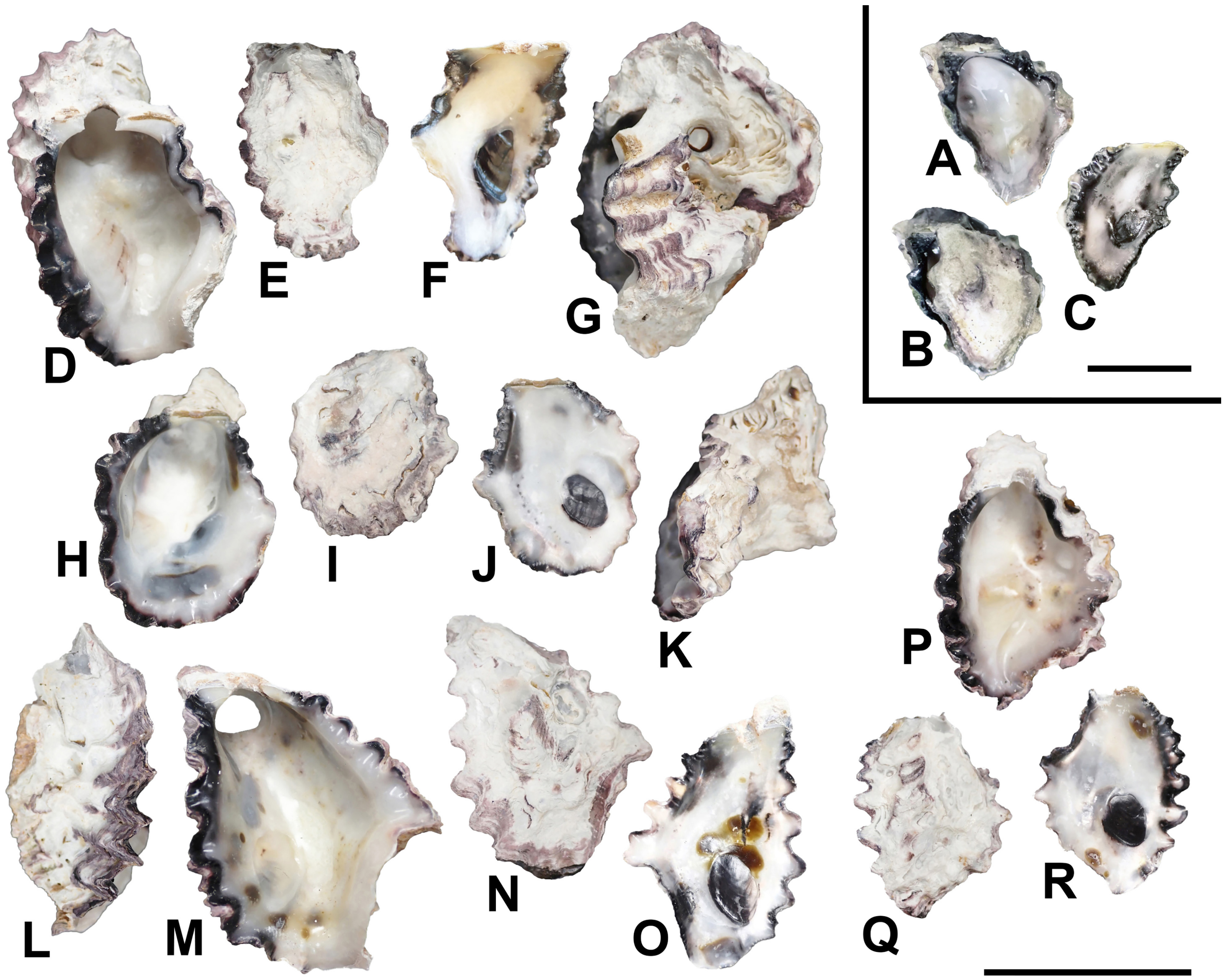

FIGURE 6. *Saccostrea scyphophilla* from Bernier Island (**A–C**) and Point Quobba (**D–R**), Western Australia showing the general shell morphology and colouration of the interior of LV (**A, D, H, M, P**]), exterior of RV (**B, E, I, N, Q**), interior of RV (**C, F, J, O, R**), anterior of LV (**G, K**), and posterior of LV (L). **A–C**, WAMS_95804; **D–G**, neotype WAMS_95811; **H–K**, WAMS_95805; **L–O**, WAMS_95808; **P–R**, WAMS_95807. Scale bars: 10 mm (A–C); 50 mm (D–R).

Published records not based on DNA analysis

Crassostrea amasa (Iredale, 1939).
Ostrea mordax Gould, 1850: Saville-Kent (1891; 1893).
Ostrea cornucopiae Lamarck, 1819: Saville-Kent (1891).
Saccostrea mordax (Gould, 1850): Torigoe (1981; 2004).
Saccostrea scyphophilla (Péron & Lesueur, 1807): Huber (2010); Beechey (2025).
Saxostrea (*cornucopiaeformis*) Saville-Kent, 1893: Iredale (1939).
Saxostrea scyphophilla (Péron, 1807): Iredale (1949).
Saccostrea cuccullata (Born, 1778): Wells & Bryce (1986); Lamprell & Healy (1998).
Crassostrea amasa (Iredale, 1939): Allan (1950); Thomson (1954).
Crassostrea tuberculata (Lamarck, 1819): Thomson (1954).
Crassostrea scyphophilla Peron (sic): Cotton (1961).

Other records not based on DNA sequences: Australia: Queensland, Wistari Reef (this study), Christmas Island (Wells *et al*., 1990 [as *S. cucullata*] and this study); Brunei: near Bandar Seri Begawan (Lee *et al.* 2024 [(as *S. mordax*]); India: Kerala, Asthamudi estuary (Ravinesh *et al.*, 2021 [as *S. cucullata*]); Tamil Nadu, Gulf of Manaar (Patterson-Edward *et al*., 2022); Indonesia: Pulau Bintan, Riau (this study), Lombok, Teluk Kombal (this study);

Sri Lanka (Fernando, 2018 [as *S. cucullata*]); Malaysia: Pulau Pangkor (this study); Taiwan: Penghu (this study); Thailand: Ranong, Kham Yai Island (Bussarawit & Cedhagen, 2010 [as *S. cucullata*]); Gulf of Aden (Lamy, 1925 [following Huber, 2010]).

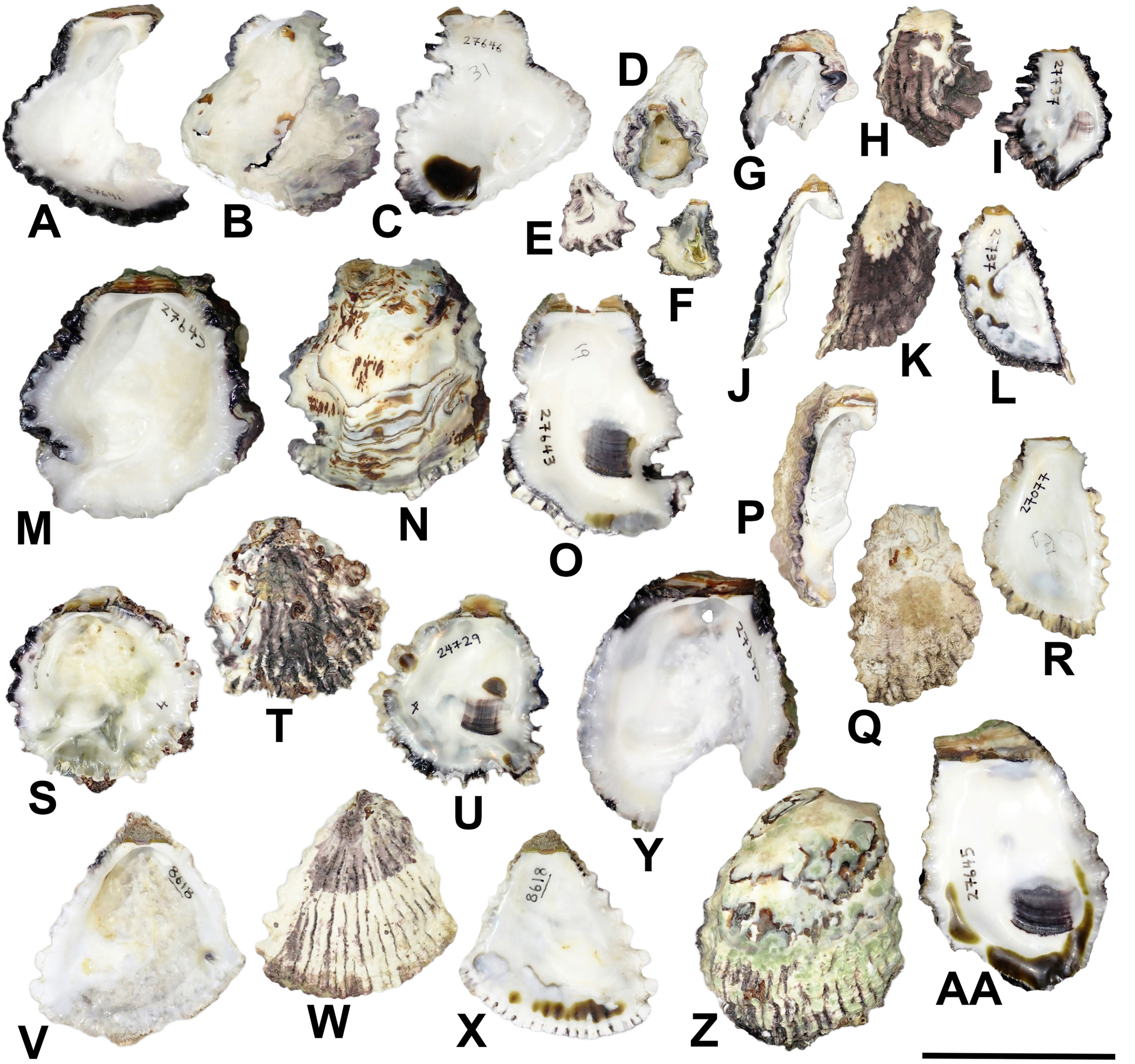

FIGURE 7. *Saccostrea scyphophilla* from Singapore (**A–C, G–O, S–AA**), Malaysia (**D–F**), and Indonesia (**P–R**) showing some variations of the shell morphology and colouration of the interior of LV (**A, D, G, J, M, P, S, V, Y**), exterior of RV (**B, E, H, K, N, Q, T, W, Z**), and interior of RV (**C, F, I, L, O, R, U, X, AA**). **A–C**, ZRC.MOL.27646 (Pulau Hantu, Singapore); **D–F**, ZRC.MOL.28265 (Pulau Pangkor, Malaysia); **G–L**, ZRC.MOL.27737 (Lazarus Island-Pulau Seringat, Singapore); **M–O**, ZRC.MOL.27643 (Pulau Tekukor, Singapore); **P–R**, ZRC.MOL.27077 (Lombok, Indonesia); **S–U**, ZRC.MOL.24729 (Sentosa, Singapore); **V–X**, ZRC.MOL.8618 (Pulau Semakau, Singapore); **Y–AA**, ZRC.MOL.27645 (Pulau Tekukor, Singapore). Scale bar: 50 mm.

Remarks: *Ostrea scyphophilla* was described by Péron & Lesueur (1807) as having a cornet-like lower valve attached to rocks by its point and one of its sides (for an English translation, see also Iredale 1949). In agreement with Iredale (1949), Huber (2010) associated *scyphophilla* with *cornucopiaeformis* and considered *amasa* and *mordax* conspecific, thus rendering the latter two names to be subjective synonyms with *scyphophilla* being the earliest available and valid name. However, the identity of *O. scyphophilla* remains open to subjective interpretation because of the lack of accompanying illustrations in the original description. The whereabouts of the specimens that formed the basis of the description in Péron & Lesueur (1807), if any, are not known and there appears to be no mention of the material or possible repositories by subsequent authors.

The designation of a neotype with DNA sequences is therefore necessary to establish the identity of this taxon in accordance with the Code (ICZN, 1999 [Article 75]), and to clarify its relationship with other related taxa. We have selected a neotype (WAMS_95811) from Point Quobba Blowholes (24.487°S; 113.410°E), located some 50 km north of Bernier Island (24.927ºS; 113.150ºE) in the same geographical region, Western Australia, because of the better condition and genetic data of the material from there. Specimens from Bernier Island were small and decomposed. However, we were still able to obtain 16S sequences from a few small individuals from Bernier Island, and these could not be distinguished from material collected at Point Quobba. Consequently, Point Quobba Blowholes, Western Australia, becomes the new type locality following this neotype selection (ICZN, 1999 [Article 76.3])

Saccostrea scyphophilla is well known in Australia but has been recorded under several names, including *S. cucullata* (Born, 1778). Tan *et al.* (2025) demonstrated that the true *S. cucullata* is restricted to the type locality of Ascension Island in the South Atlantic Ocean, nearby islands and possibly the west coast of Africa. The DNA sequence of *S. cucullata* has not been recorded from the Indo-Pacific region to date. On the other hand, *S. scyphophilla* was described from Bernier Island in Shark Bay in Western Australia, while two other oyster taxa were described from Queensland: *Ostrea mordax* var. *cornucopiaeformis* Saville-Kent, 1893; and *Saxostrea amasa* Iredale, 1939. Note that Saville-Kent (1893) described *cornucopiaeformis* as a variety of *S. mordax*, which in Saville-Kent (1891) was referred to as the *O. cornucopiae* of Lamarck and other authors. The *O. cornucopia* [sic] attributed to Saville-Kent (1891) in Huber's (2010) listing of species (row 4980 in the Excel sheet) and consequently listed in WoRMS (MolluscaBase eds. 2025) cannot be located and is in all probability an error. All of the Queensland names are now regarded as synonyms of *S. scyphophilla* (Huber 2010; MolluscaBase eds. 2025). McDougall (2020) and McDougall *et al.* (2020; 2024) reported *S. scyphophilla* based on extensive genetic data from Queensland and the Northern Territory. The only other species in the *S. mordax* group were two records of *Saccostrea 'mordax'* C (= *Saccostrea mordoides* Cui *et al.* 2021) from northeastern Queensland (McDougall *et al.* 2024: Richardson *et al.* 2024).

Thomson (1954) confused the issue in his revision of the Australian oysters. He did not include either *scyphophilla* or *mordax*. Instead, two species were recognised in northern Australia. *Crassostrea amasa* was reported as occurring in Queensland from the Great Barrier Reef to the Gulf of Carpentaria and probably the Northern Territory. *Ostrea mordax* Saville-Kent (1891) (*non* Gould, 1850) and *Ostrea forskali* var. *mordax* Lamy, 1929, were listed as synonyms. Thomson (1954) suggested the species might be the same as *Ostrea lingua* Lamarck from Timor but noted that the type specimens of *lingua* are severely weathered and were apparently beach-collected material; WoRMS (MolluscaBase eds. 2025) lists *O. lingua* as a nomen dubium. As a result, it is impossible to distinguish the original characteristics of the shells. Thomson (1954) further stated that whether the oysters he recognised as *C. amasa* were in fact *Ostrea mordax* (Gould, 1850) was uncertain due to the poor original description.

In Western Australia, Thomson (1954) recognised *Crassostrea tuberculata* (Lamarck, 1819) from the Abrolhos Islands to at least Broome. However, this species is recognised by WoRMS (MolluscaBase eds. 2025) as *Pustulostrea australis* (Lamarck, 1819) from Timor. Thomson (1954) did state that *Crassostrea scyphophylla* (Peron) "may be an ecomorphic form of this species, although Iredale (1949) has regarded it as valid."

Based on the material examined and published distribution, this species is probably widely distributed in the tropical Western and Southern Pacific. In Australia, *S. scyphophilla* appears to be primarily restricted to tropical locations (Snow *et al.*, 2023; McDougall *et al.* 2024; Wells *et al.* 2024) although it has been recorded south of the Tropic of Capricorn (Fig. 13).

Ostrea forskali var. *sueli* Jousseaume in Lamy, 1925 is tentatively retained as a synonym of *S. scyphophilla* following Huber (2010). It may prove to be a valid species of the Western Indian Ocean. We were unable to obtain material or DNA data from the Gulf of Aden and adjacent areas for confirmation.

***Saccostrea mordax* (Gould, 1850)**

Figs. 8C, D, 9–11, 12A, B

Original description: *Ostrea mordax* Gould, 1850: 346. Type locality: Fiji ("Feejee Islands").

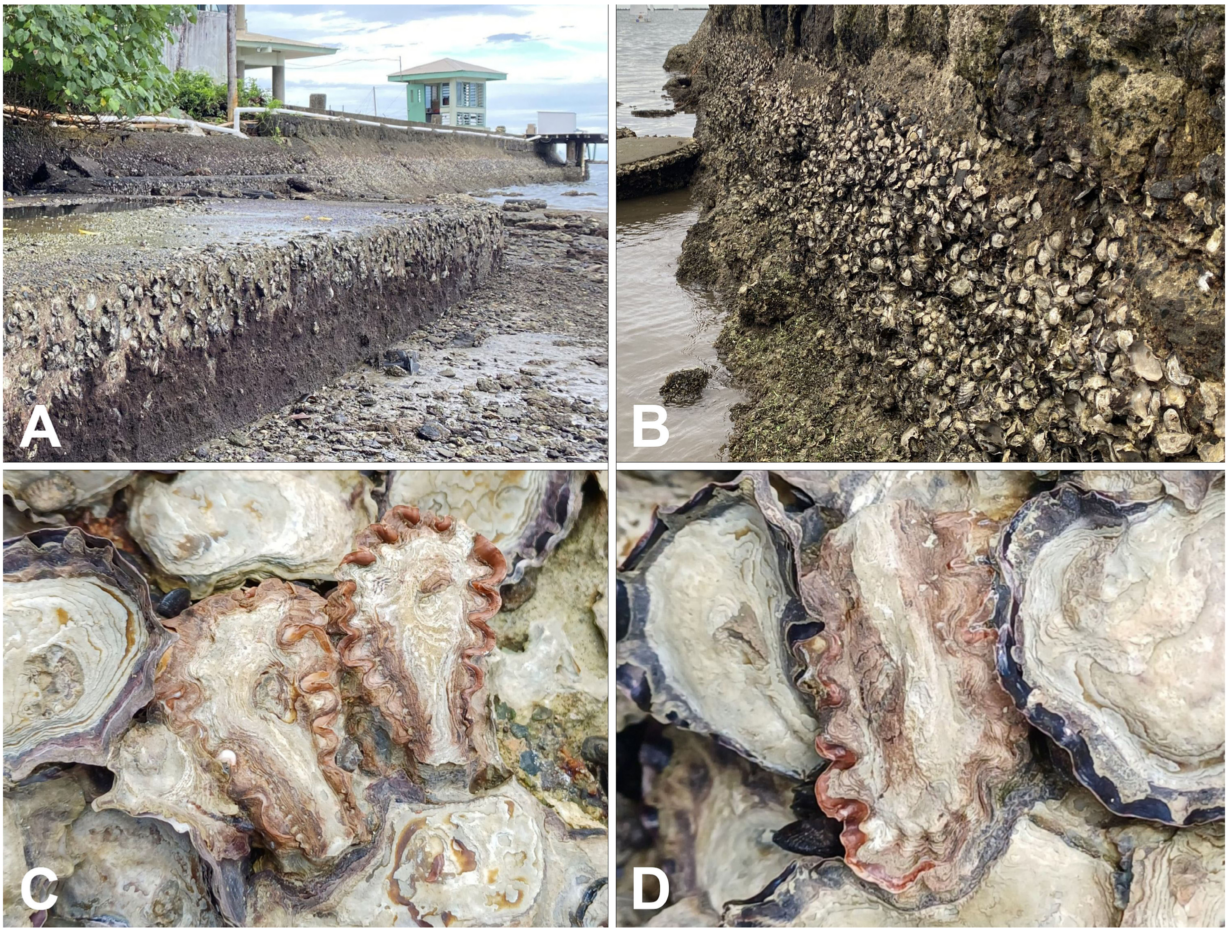

FIGURE 8. A–B, Oysters, including *Saccostrea mordax*, on intertidal structures between Suva Point, the USP Marine Campus and the FNU Fiji maritime foreshore in Laucala Bay, Suva, Fiji. **C–D**, *Saccostrea mordax* nested among other oysters at USP School of Marine Studies Jetty (**C**) and at FNU Fiji maritime foreshore (**D**).

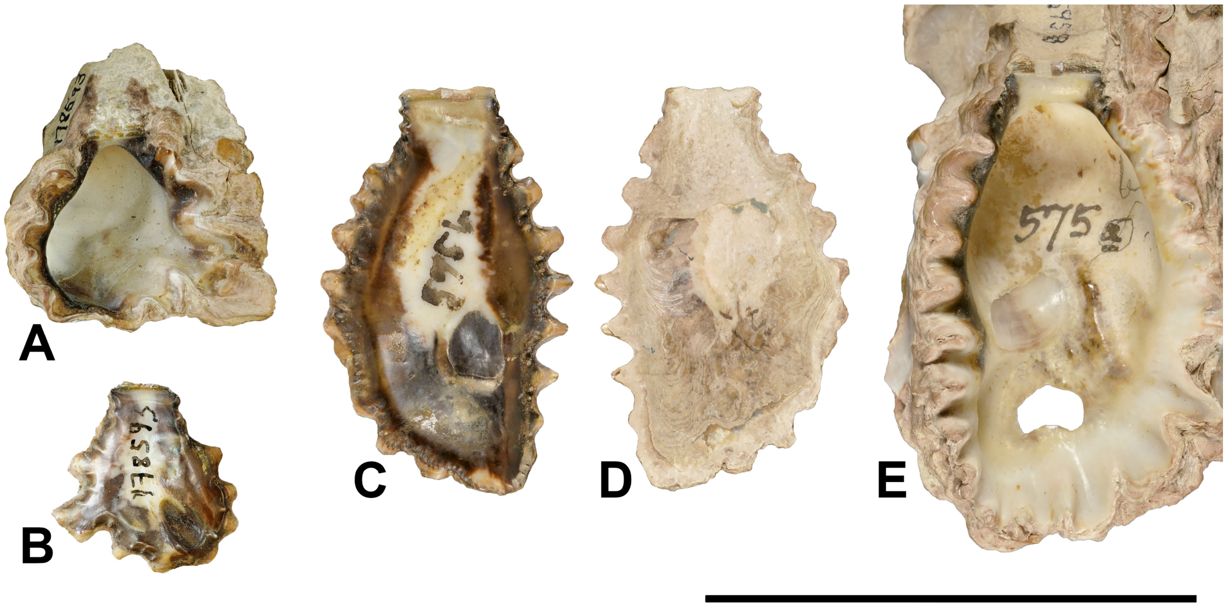

FIGURE 9. *Saccostrea mordax* **A–E,** Syntypes (MCZ: Mala: 178593 [**A, B**]; USNM 5958 [**C–E**]) of *Ostrea mordax* Gould, 1850; showing interior of LV (**A, E**), interior of RV (**B, C**), and exterior of RV (**D**). Images from SIGNIFY, LKCNHM (https://signifynaturalhistory.sg/specimens/MCZ178593_*Ostrea_mordax*_syntype [Museum of Comparative Zoology, Harvard University; ©President and Fellows of Harvard College]), and Smithsonian National Museum of Natural History (http://n2t.net/ark:/65665/39f0daf6e-9d41-4e24-ab56-5c3bcd653c04). Scale bar: 50 mm.

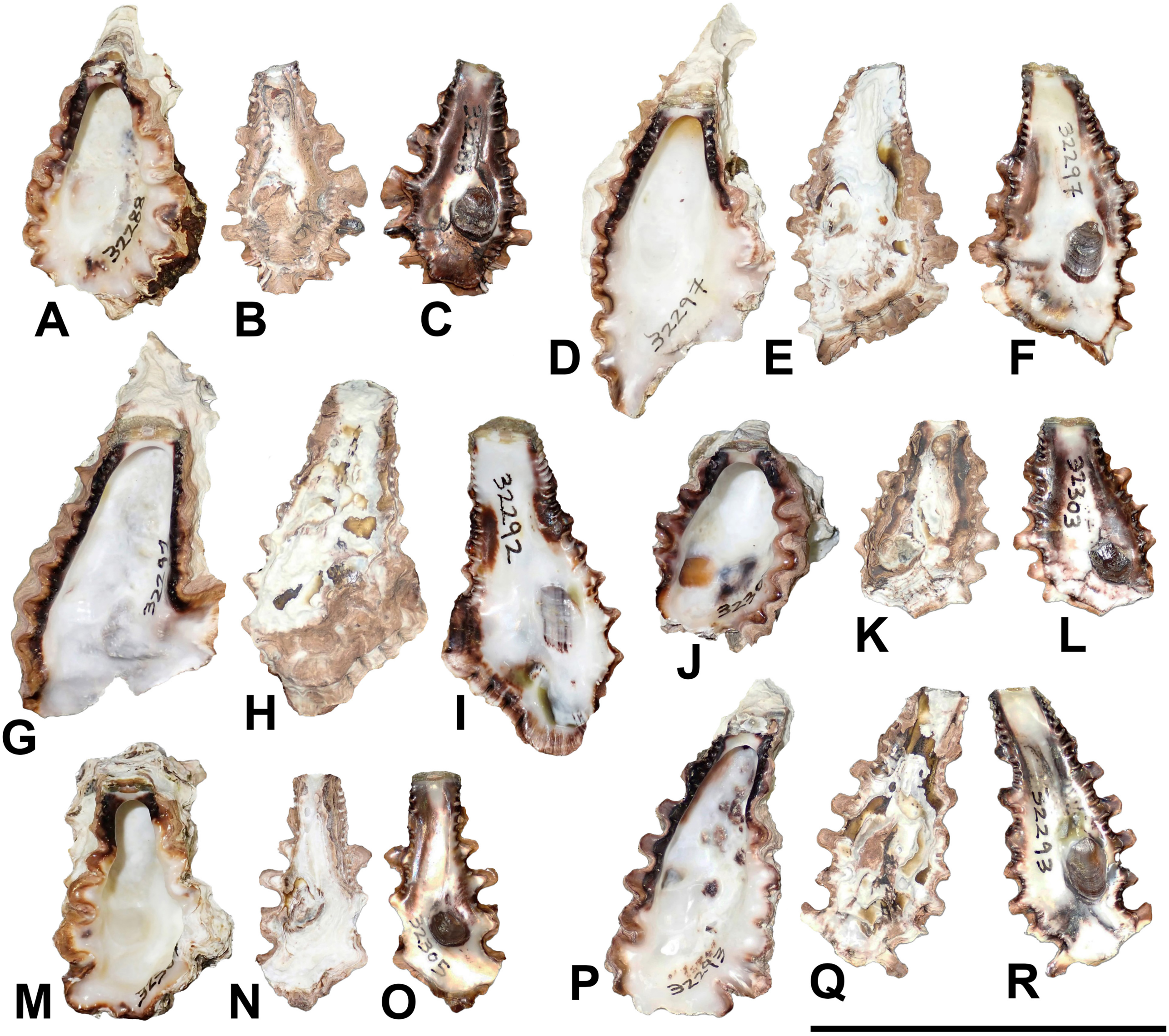

FIGURE 10. *Saccostrea mordax* from Fiji showing the general shell morphology and colouration of the interior of LV (**A, D, G, J, M, P**), exterior of RV (**B, E, H, K, N, Q**) and interior of RV (**C, F, I, L, O, R**). **A–C**, ZRC.MOL.32288; **D–F**, ZRC.MOL.32297; **G–I**, ZRC.MOL.32292; **J–L**, ZRC.MOL.32203; **M–O**, ZRC.MOL.32305; **P–R**, ZRC.MOL.32293. Scale bar: 50 mm.

Synonym: *Saccostrea mordoides* Cui *et al.*, 2021: 70–71, fig. 4. Type locality: Haitang Bay, Hainan Province, China. New synonym.

Type material: Syntypes (USNM 5958; MCZ: Mala: 178593), Fiji.

Other material examined: Fiji: 19 ex. (ZRC.MOL.32263–32272, ZRC.MOL.32288–32297 [DNA]), USP School of Marine Studies, Suva, 18°09'03.0"S 178°27'13.4"E, coll. 2 October 2024; 3 ex. (ZRC.MOL.32273–32274, ZRC.MOL.32308 [DNA]), USP School of Marine Studies Jetty, Suva, 18°09'02.9"S 178°27'15.2"E, coll. 3 October 2024; 3 ex. (ZRC.MOL.32275–32276, ZRC.MOL.32306 [DNA]), USP School of Marine Studies Foreshore, Suva, 18°09'01.6"S 178°27'18.6"E, coll. 3 October 2024; 9 ex. (ZRC.MOL.32277, ZRC.MOL.32298–32305 [DNA]), USP School of Marine Studies Jetty, Suva, 18°09'02.9"S 178°27'15.2"E, coll. 3 October 2024; 10 ex. (ZRC.MOL.32278–32281, ZRC.MOL.32309–32314 [DNA]), FNU Fiji Maritime Foreshore, Suva, 18°09'05.6"S 178°27'08.6"E, coll. 4 October 2024; 10 ex. (ZRC.MOL.32282–32287, ZRC.MOL.31315–32318 [DNA]), FNU Fiji Maritime Foreshore, Suva, 18°09'05.8"S 178°27'08.2"E, coll. 4 October 2024. **Indonesia**: 1 ex. (ZRC.MOL.35008), Tanjung Gemal, Pulau Bintan, coll. 11 May 1993. **Malaysia**: 6 ex. (ZRC.MOL.35005), Tanjung Layar, Pulau Tioman, coll. 2

Jul.1987; 3 ex. (ZRC.MOL.32211), Pulau Babi Kechil, off Mersing, no coll. date. **Philippines**: 1 ex. (NHMUK 20080637), Island of Luzon, no coll. date. **Singapore**: 4 ex. (ZRC.34376 [3 halves], ZRC.MOL.34377), Pulau Salu, coll. 4 Nov.1968; 1 ex. (ZRC.MOL.34623), Tanjong Teritip, coll. Feb.1969; 6 ex. (ZRC.MOL.27639 [DNA], ZRC.MOL.33319), Lazarus Island-Pulau Seringat, 1°13.690'N 103°50.999'E, coll. 20 February 2023.

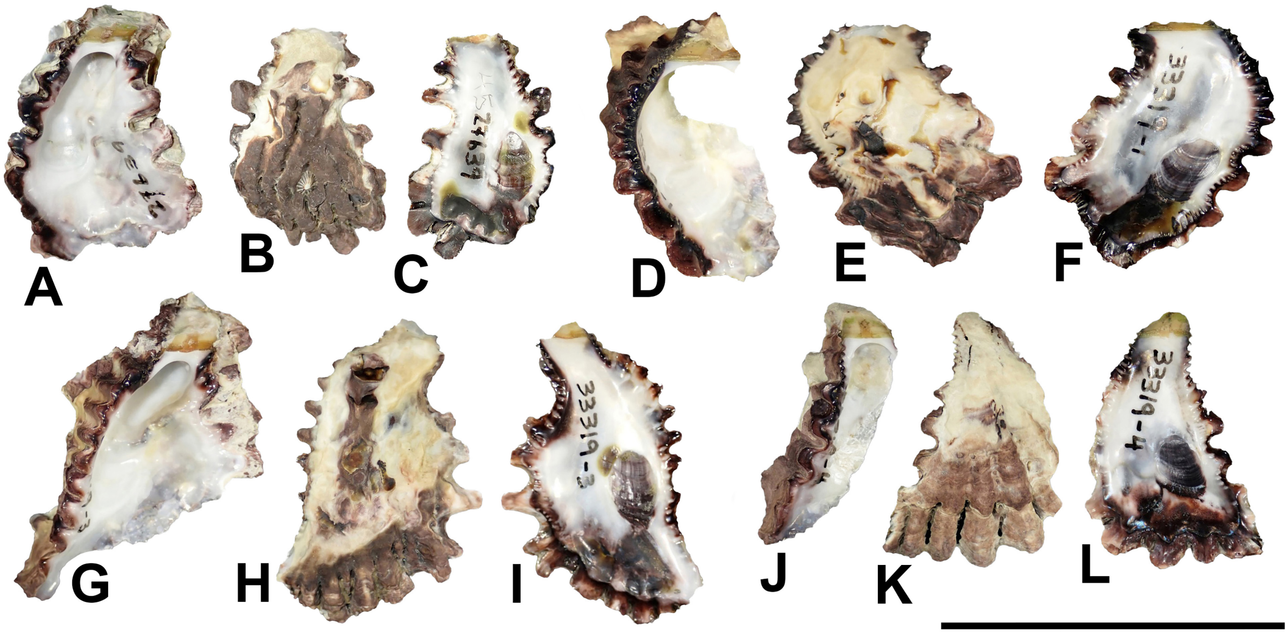

FIGURE 11. *Saccostrea mordax* from Lazarus Island-Pulau Seringat, Singapore, showing some variations of the shell morphology and colouration of the interior of LV (**A, D, G, J**), exterior of RV (**B, E, H, K**), and interior of RV (**C, F, I, L**). **A–C**, ZRC.MOL.27639; **D–L**, ZRC.MOL.33319. Scale bar: 50 mm.

Description: Shell small to medium (c. 30–60 mm; SL of largest RV examined = 54.5 mm); irregularly oval (e.g., Figs. 9A, B; 10J–L) to slender elongate triangular (e.g., Figs. 10G–I; 10P–R); LV quite thick and solid, RV distinctly thinner. Shell exterior pinkish brown, usually with corroded/eroded patches of white. LV larger than RV, shallowly cupped to very deeply cupped; posterior side often thicker and prominently raised from the attached substate in shallowly cupped specimens, or boxy with entirely margin strongly raised in deeply cupped ones (e.g., 10J; 10M). RV exterior surface with several broad radial ribs; often corroded/eroded especially around the centre with or without dark brown bands and lines of the conchiolin layers, usually rimmed with a pinkish brown border. Shell margin scalloped, often strongly undulating with prominent lobes. Shell interior white with pink tint, LV usually with darker cloudy patches, occasionally with dark greenish brown spots and blotches; RV usually with pinkish brown to dark chocolate brown blotches and bands; interior margin pinkish brown, usually with prominent chocolate brown line or band, ranging from being present only near the hinge (e.g., Figs. 10O; 10R) to around the entire margin of the RV (e.g., 10C). Umbonal cavity deep. Chomata usually prominent around entire margin, sometimes indistinct or absent along the ventral edge (e.g., Fig. 10O). Adductor muscle scar of LV usually white (e.g., Figs. 10D; 10G), rarely stained brown (e.g., Fig. 10J); RV usually dark brown to black (e.g., Fig. 9C; 10C), occasionally white streaked with brown lines and/or bands (e.g., Fig. 10I; 11C), often strongly raised, sometimes ridge-like, on ventral part (see Fig. 12A, B).

Habitat: In Laucala Bay, Fiji, *S. mordax* inhabits both natural rock substrates and artificial structures, thriving particularly on concrete surfaces such as seawalls, jetties, pylons, and pontoons in intertidal zones.

Published distribution based on DNA analyses: Okinawa, Japan (Sekino & Yamashita 2013; Hamaguchi *et al*. 2014 as *S. mordax*-C), Hainan province, China (Cui *et al*. 2021 as *S. mordoides*), Guangdong province, China (Zhang *et al*. 2025), Queensland, Australia (McDougall *et al*. 2024; Richardson *et al*. 2024), Singapore (this study, GenBank PV760218) and Indonesia (Zhang *et al*. 2025).

Other records not based on DNA sequences: Indonesia: Pulau Bintan, Riau (this study); Malaysia: Pulau Tioman (this study); Pulau Babi Kechil (this study); Philippines: Luzon (this study).

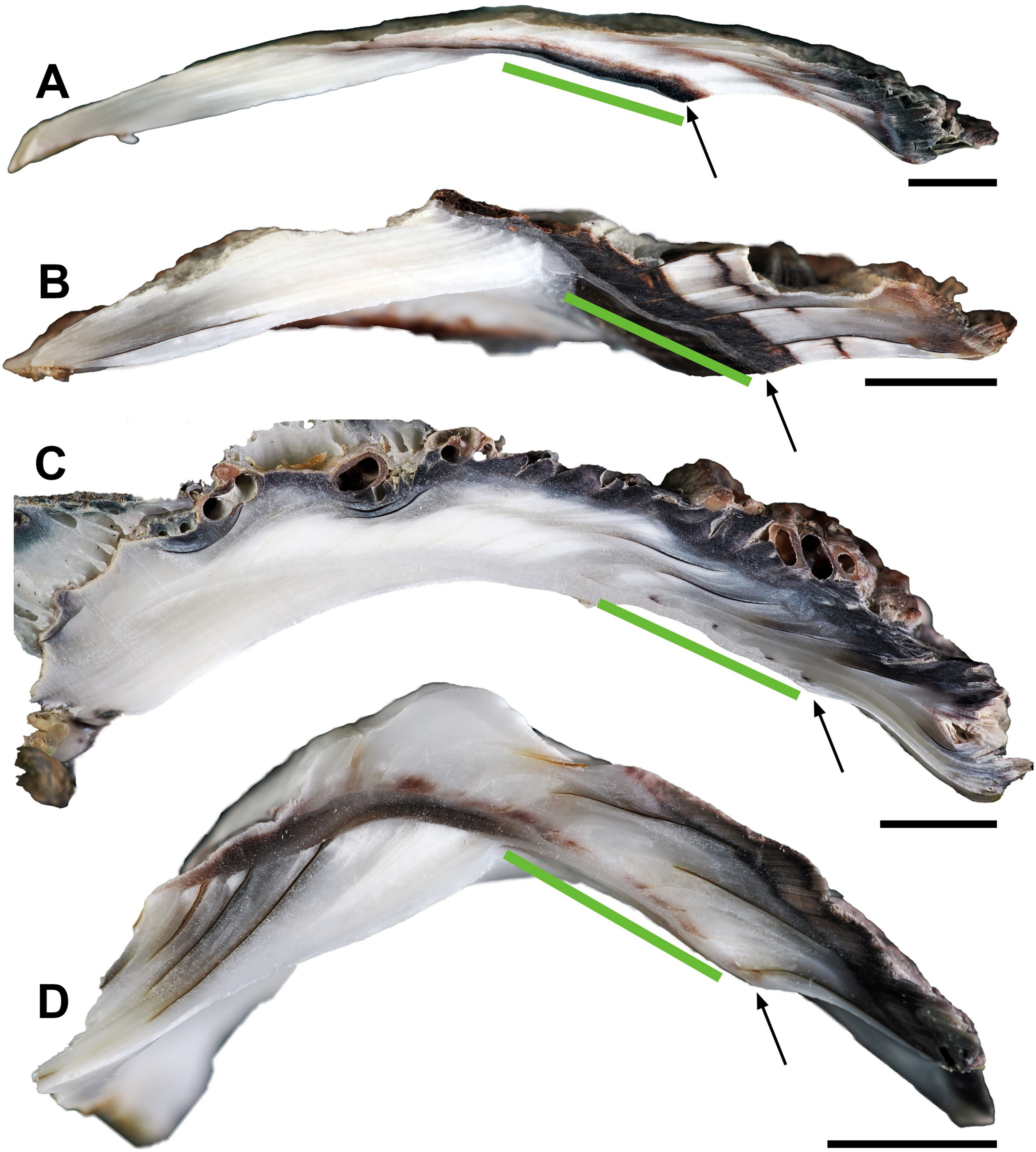

FIGURE 12. Shell sections of the right valves of *Saccostrea mordax* (**A, B**) and *S. scyphophilla* (**C, D**), cut across the adductor muscle scars dorso-ventrally. The hinge is to the left for all images. The green bars indicate the extent of the muscle scar along the inside surface of the valves, and the arrows show the ventral extremities of the scars, which are sharply angled in *S. mordax* but gently sloping in *S. scyphophilla*. **A**, ZRC.MOL.33319-5, Lazarus Island, Singapore; **B**, ZRC.MOL.32316, Suva, Fiji; **C**, ZRC.MOL.27641, Lazarus Island, Singapore; **D**, ZRC.MOL.32220, Point Quobba, Western Australia. Scale bars (in black): 5 mm.

Remarks: *Saccostrea mordax* can be distinguished from S. *scyphophilla* based solely on their shell morphology. Compared to *S. scyphophilla*, *S. mordax* is generally smaller, and has a distinctive pink shell margin, which is usually more highly scalloped with fewer protruding lobes. The interior of the valves tends to be more distinctively pinkish brown, often featuring chocolate brown bands and blotches especially along the anterior and posterior margins. The often brown adductor muscle scar on the RV is typically raised, either a bump or only along its ventral side, compared to that of *S. scyphophilla* which is usually not as prominently raised (Fig. 12). Our study has also provided evidence that topotypes of *S. mordax* from Fiji are genetically and morphologically indistinguishable from the recently described *S. mordoides* from China and hence suggest that the two species are synonymous.

Discussion

One of the main aims of this study is to clarify the identity and relationship of the species within the *S. scyphophilla* / *mordax* group (i.e., the *S. mordax* superspecies of Lam & Morton 2006 and the *S. mordax* lineages A–C of Sekino & Yamashita 2016). *Saccostrea scyphophilla* lineages A and B are herein provisionally treated as a single species because of the difficulty of morphologically and genetically separating the two (see Figs. 1–3 and Tables 1, 2) and follows the current consensus. Snow *et al*. (2023) provided DNA sequences of *S. scyphophilla* from a number of Western Australian (WA) localities, including Monkey Mia in Shark Bay, approximately 120 km southeast of Bernier Island. They concluded there was no requirement to recognise two DNA sequences of the species. Wells *et al*. (2024) followed this recommendation and provided additional records of the species in WA. This conclusion is further reiterated in our study here based on additional material from Bernier Island and Point Quobba in WA, its former and current type localities. However, Zhang *et al*. (2025) showed that the mean sequence divergence based on the COX1 gene between *scyphophilla* (as *mordax*) lineages A and B from populations sampled from southern China and Indonesia was 2.0%, a relatively small difference in this complex genus. Further study of more material from throughout their wide geographic range will be preferred to properly assess whether certain shell characteristics of *S. scyphophilla* could be of taxonomic significance. Preliminary observations of limited material suggest that the shells of lineage A possess shell margins that are elevated or elongated away from the substrate, whereas lineage B tend to be flatter, resembling *amasa*-like forms. In Singapore, the latter seem to be often isolated, occurring singly, or in small clusters of two or three individuals, so it may also be interesting to determine whether forms resembling lineage A occur in or form dense beds, or they assume these forms as a result of crowding.

Our study also demonstrated that *S. mordax* is clearly separable from *S. scyphophilla*. Genetically the two species are distinct, as shown consistently in the COX1 (Table 2; see also Zhang *et al*. 2025), 16S and their concatenated trees (Figs. 1–3). The two species can also be distinguished morphologically, as detailed in the descriptions given above, despite considerable intraspecific variation in shell form. Both species can co-occur in Southeast Asia and they appear to be widely distributed across the Indo-west Pacific region (Fig. 13). Based on shell morphology and DNA we recorded the two species co-occurring at Lazarus Island-Pulau Seringat in Singapore. From shell morphology alone, we also observed both species from Pulau Salu and Tanjong Teritip in Singapore, and Pulau Bintan in Indonesia. However, we do not have enough data to confirm whether they are syntopic. McDougall *et al*. (2024) suggested that where the two species co-occur, *S. mordax* is usually found in the lower intertidal zone, while *S. scyphophilla* is located above them. McDougall (2024) also documented the two species in the same general location (e.g., see fig. 3 [12 – Whitsunday Islands/Shute Harbour]). Cui *et al.*'s (2021) *mordoides* samples were among 47 oysters collected from the Haitang Bay (its type locality), the rest being their *S. mordax* A (n= 29) and B (n=13). They did not mention possible habitat differences.

DNA verified records of *S. scyphophilla* demonstrate that the species has a widespread distribution. It has been frequently recorded across northern Australia from the Houtman Abrolhos Islands, Western Australia to New South Wales on the east coast of the continent. It has also been recorded in Southeast Asia (Singapore, Thailand and Malaysia) and northwards along the east Asian coast (Zhang *et al*. 2025; Zhou *et al*., 2025) to Japan (as *mordax* A and/or B). The only DNA records for *S. scyphophilla* in the Indian Ocean are from Western Australia, Bangladesh (Chowdury *et al*., 2021 as *S. mordax*), and the Maldives (Salvi *et al*., 2014), together with a few matching (>99.4%) but unpublished GenBank sequences (OR830708 and OR831083) from the Andaman and Nicobar Islands that were submitted as '*S. cucullata*'. Isolated records from southern India, Sri Lanka and Yemen are based on shell photographs and need to be confirmed. In comparison, there are very few DNA confirmed records of *S. mordax*, all of which are in the western Pacific (Fig. 13). The species has been recorded from the type locality of Fiji and two isolated records on the Queensland coast. The distribution of the two species overlaps in Singapore, southern China and probably in the Ryukyu Islands. There is one record based on shell morphology in the Philippines. There is a considerable gap in our knowledge of the distribution of both species in Indonesia, Papua New Guinea and Oceania that needs to be rectified, but as it stands *S. scyphophilla* seems to have a wider latitudinal range. We have yet to find *S. mordax* in Western Australia, where *S. scyphophilla* appears to be a dominant species on exposed shores.

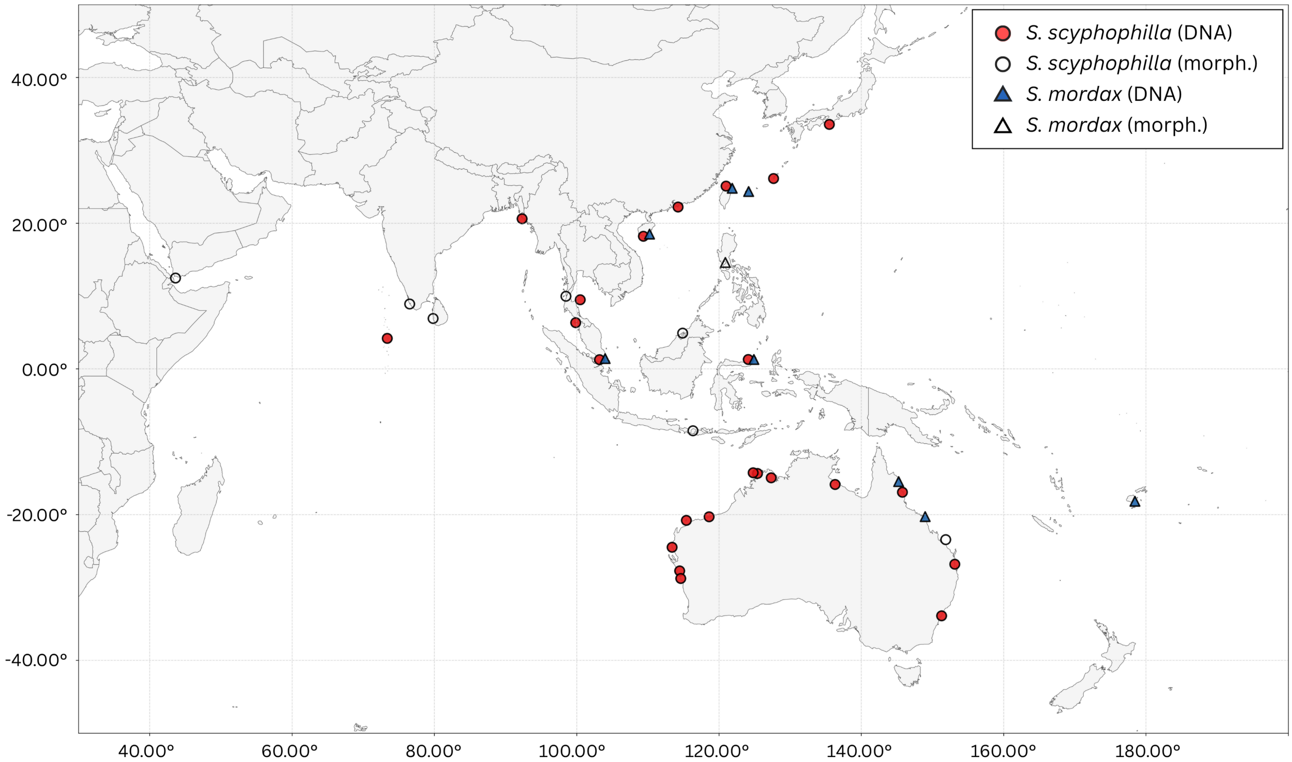

FIGURE 13. Distribution of the oysters *Saccostrea scyphophilla* and *S. mordax* based on DNA sequences and on morphological analysis. Sources of data are: *S. scyphophilla*: this study, Lam & Morton 2006 (as *S. mordax*); Bussarawit & Cedhagen 2010 (as *S. cucullata*); Hamaguchi *et al.* 2014 (as *S. mordax*-A); Fernando 2018 (as *S. cucullata*); Cui *et al.* 2021 (as *S. mordax*); Chowdhury *et al.* 2021 (as *S. mordax*); Patterson-Edward *et al*. 2022; Ravinesh *et al*. 2021 (as *S. cucullata*); Salvi *et al*. 2014; Snow *et al.* 2023; Lee *et al.* 2024 (as *S. mordax*); McDougall *et al.* 2024; Wells *et al.* 2024; Duangdee *et al.* 2025. *Saccostrea mordax*: this study (NHMUK 20080637); Hamaguchi *et al.* 2014 (as *S. mordax*-C); Cui *et al.* 2021 (as *S. mordoides*); McDougall *et al.* 2024 (as *S. mordoides*).

In the Persian Gulf and Western Indian Ocean however, there appears to be a third species that is closely related to *S. mordax* and *S. scyphophilla*, as shown in Fig. 1 based on a recent study by Ghaffari *et al*. (2022) and from a sequence obtained from Madagascar (Volatiana *et al*., 2015). We believe that a careful study of their morphology may prove its status as a distinct species, as are likely with at least some of the other *Saccostrea* lineages.

The Point Quobba reef formed by *S. scyphophilla* is the only known reef formed by that species and is worthy of further investigation.

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APPENDIX A. List of COX1 and 16S sequences retrieved from GenBank that were used to construct the phylogenetic trees shown in Figures 1 and 2.

Species	Location	GenBank accession number	Publication	Remarks
COX1				
Ostrea edulis	France	JF274008	Danic-Tchaleu *et al.*, (2011)	
Magallana gigas	Australia: Port Adelaide, SA	MZ400416	unpublished	
Saccostrea scyphophilla	China?	FJ841968	Wu *et al.*, (2009) unpubl.	submitted as *Saccostrea mordax*
Saccostrea scyphophilla A	Australia: Cow Bay, QLD	OR339808	McDougall *et al.*, 2024	
Saccostrea scyphophilla A	China	MT293807	Cui *et al.*, 2021	
Saccostrea scyphophilla A	China	MT293812	Cui *et al.*, 2021	
Saccostrea scyphophilla A	Indonesia: Manado	PP989758	Zhang *et al.*, 2025	
Saccostrea scyphophilla A	Indonesia: Manado	PP989754	Zhang *et al.*, 2025	
Saccostrea scyphophilla B	Australia: Ashburton Island, WA	PP834539	Tan *et al.*, 2025	
Saccostrea scyphophilla B	Australia: Carnarvon, WA	PP834540	Tan *et al.*, 2025	
Saccostrea scyphophilla B	China	MT293806	Cui *et al.*, 2021	
Saccostrea scyphophilla B	China	MT293819	Cui *et al.*, 2021	
Saccostrea mordax	Australia: Hook Island	OR339805	McDougall *et al.*, 2024	
Saccostrea mordax	China (Hainan)	MT293844	Cui *et al.*, 2021	
Saccostrea mordax	China (Hainan)	MT293845	Cui *et al.*, 2021	
Saccostrea mordax	Taiwan	JQ027295	Hsiao, unpublished	
Saccostrea mordax	Taiwan	JQ027296	Hsiao, unpublished	
Saccostrea mordax	Indonesia: Manado	PP989791	Zhang *et al.*, 2025	
Saccostrea mordax	Indonesia: Manado	PP989794	Zhang *et al.*, 2025	
Saccostrea lineage A	Australia: Karratha Bay, West Lewis Island, Dampier Archipelago, WA	PP834532	Tan *et al.*, 2025	
Saccostrea lineage A	Australia: Pelican Point, Carnarvon, WA	PP834535	Tan *et al.*, 2025	
Saccostrea lineage B	Australia: Hervey Bay, QLD	OR339839	McDougall *et al.*, 2024	
Saccostrea lineage C	Japan: Kagoshima, Amami-Oshima Island	LC110510	Sekino & Yamashita, 2016	
Saccostrea lineage E	Japan: Kochi	LC268853	unpublished	
Saccostrea lineage E	China	MZ323313	Li *et al.*, 2021	
Saccostrea lineage F	Japan: Kagoshima, Kakeroma Island	LC110465	Sekino & Yamashita, 2016	
Saccostrea lineage G	Australia: Percy Islands, QLD	OR339828	McDougall *et al.*, 2024	
Saccostrea lineage G	Japan: Kagoshima, Amami-Oshima Island	LC110519	Sekino & Yamashita, 2016	
Saccostrea lineage H	Japan: Okinawa	LC110596	Sekino & Yamashita, 2016	
Saccostrea lineage I	Australia: Orpheus Island	OR339819	McDougall *et al.*, 2024	
Saccostrea lineage I	Japan: Okinawa, Iriomote Island, Yaeyama	LC110579	Sekino & Yamashita, 2016	
Saccostrea lineage J	Australia: Cone Bay, Kimberley, WA	PP834536	Tan *et al.*, 2025	
Saccostrea lineage J	Australia: Shute Harbour, QLD	OR339813	McDougall *et al.*, 2024	

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APPENDIX A. (Continued)

Species	Location	GenBank accession number	Publication	Remarks
Saccostrea lineage J	Japan: Okinawa, Iriomote Island, Yaeyama	LC110588	Sekino & Yamashita, 2016	
Saccostrea glomerata	Australia: Oyster Harbour, Albany, WA	PP834537	Tan *et al.*, 2025	
Saccostrea glomerata	Australia: Minjerribah, QLD	OR339865	McDougall *et al.*, 2024	
Saccostrea kegaki	Japan: Okinawa	LC110614	Sekino & Yamashita, 2016	
Saccostrea kegaki	Japan: Wakayama, Honshu Island	LC110646	Sekino & Yamashita, 2016	
Saccostrea palmula	Mexico: Sonora, Guaymas	KT317577	Raith *et al.*, 2015	
Saccostrea palmula	Mexico: Baja California Sur, Bahia Concepcion	KT317587	Raith *et al.*, 2015	
Saccostrea '*palmula*' Persian Gulf	Iran (Persian Gulf)	OP363321	Ghaffari *et al.*, 2022	
Saccostrea '*palmula*' Persian Gulf	Iran (Persian Gulf)	OP363324	Ghaffari *et al.*, 2022	
Saccostrea '*palmula*' Persian Gulf	Iran (Persian Gulf)	OP363325	Ghaffari *et al.*, 2022	
Saccostrea '*palmula*' Persian Gulf	Iran (Persian Gulf)	OP363337	Ghaffari *et al.*, 2022	
Saccostrea cuccullata sensu stricto	Atlantic Ocean: Ascension Island, Shelly Beach	PP834522	Tan *et al.*, 2025	
Saccostrea cucullata sensu stricto	Atlantic Ocean: Ascension Island, Scouts Beach	PP834531	Tan *et al.*, 2025	
other "*mordax*"	Madagascar	KP769562	Volatiana *et al.*, 2016	
other "*mordax*"	Iran (Persian Gulf)	LC498688-LC498699	Fakhri *et al.*, 2020	
other "*mordax*"	Iran (Persian Gulf)	OP363308-OP363320	Ghaffari *et al.*, 2022	
16S				
Ostrea edulis	France	JF274008	Danic-Tchaleu *et al.*, (2011)	
Magallana gigas	Australia: Port Adelaide, SA	MZ400416	unpublished	
Saccostrea scyphophilla A	Australia: South of Onslow, WA	AY247363	Lam & Morton, 2006	
Saccostrea scyphophilla A	Taiwan: Shiman	AY247323	Lam & Morton, 2006	
Saccostrea scyphophilla A	Australia: Kalbarri, WA	MN450281	Snow *et al.*, 2023	
Saccostrea scyphophilla A	Australia: Seventeen Seventy, QLD	OR339999	McDougall *et al.*, 2024	
Saccostrea scyphophilla A	China	MT298889	Cui *et al.*, 2021	
Saccostrea scyphophilla B	Taiwan: Shiman	AY247324	Lam & Morton, 2006	
Saccostrea scyphophilla B	Australia: Bondi, Sydney, NSW	AF458910	Lam & Morton	submitted as *S. amasa*
Saccostrea scyphophilla B	Australia: Minjerribah, QLD	OR339998	McDougall *et al.*, 2024	
Saccostrea scyphophilla B	Australia: Kalbarri, WA	MN450285	Snow *et al.*, 2023	
Saccostrea scyphophilla B	China	MT298874	Cui *et al.*, 2021	
Saccostrea mordax	Australia: Hook Island	OR339997	McDougall *et al.*, 2024	
Saccostrea mordax	Australia: Orpheus Island	OR339996	McDougall *et al.*, 2024	
Saccostrea mordax	Japan: Okinawa, Ishigaki Island	AB898224	Hamaguchi *et al.*, 2014	

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APPENDIX A. (Continued)

Species	Location	GenBank accession number	Publication	Remarks
Saccostrea mordax	Japan: Okinawa, Kunigami, Onna, Yakata	AB748915	Sekino & Yamashita, 2013	
Saccostrea mordax	China (Hainan)	MT298862	Cui *et al.*, 2021	
Saccostrea mordax	China (Hainan)	MT298863	Cui *et al.*, 2021	
Saccostrea lineage A	Australia: Carnarvon, WA	AY247371	Lam & Morton, 2006	
Saccostrea lineage A	Australia: Dampier, WA	MN153602	Snow *et al.*, 2023	
Saccostrea lineage B	Singapore: Tanah Merak	AY247292	Lam & Morton, 2006	
Saccostrea lineage B	Australia: Darwin Harbour, NT	AY247289	Lam & Morton, 2006	
Saccostrea lineage B	Australia: Kimberley, WA	MT124282	Snow *et al.*, 2023	
Saccostrea lineage C	Japan: Okinawa	AY247380	Lam & Morton, 2006	
Saccostrea lineage C	Japan: Kagoshima, Amami-Oshima Island	LC111198	Sekino & Yamashita, 2016	
Saccostrea lineage D	Taiwan: Shiman	AY247321	Lam & Morton, 2006	
Saccostrea lineage D	China: Sanya (Hainan Id)	AY247391	Lam & Morton, 2006	
Saccostrea lineage E	Australia: Darwin Harbour, NT	AY247328	Lam & Morton, 2006	
Saccostrea lineage E	Taiwan: Shiman	AY247387	Lam & Morton, 2006	
Saccostrea lineage F	Taiwan: Shiman	AY247384	Lam & Morton, 2006	
Saccostrea lineage F	Japan: Okinawa, Iriomote Island, Yaeyama	LC111254	Sekino & Yamashita, 2016	
Saccostrea lineage G	Taiwan: Shiman	AY247385	Lam & Morton, 2006	
Saccostrea lineage G	Japan: Kagoshima, Amami-Oshima Island	LC111202	Sekino & Yamashita, 2016	
Saccostrea lineage G	Australia: Percy Islands, Queensland	OR340012	McDougall *et al.*, 2024	
Saccostrea lineage H	Japan: Okinawa, Iriomote Island, Yaeyama	LC111262	Sekino & Yamashita, 2016	
Saccostrea lineage H	Japan: Okinawa, Iriomote Island, Yaeyama	LC155015	Sekino & Yamashita, 2016	
Saccostrea lineage I	Japan: Okinawa, Iriomote Island, Yaeyama	LC111211	Sekino & Yamashita, 2016	
Saccostrea lineage I	Australia: Orpheus Island	OR340007	McDougall *et al.*, 2024	
Saccostrea lineage J	Japan: Okinawa, Iriomote Island, Yaeyama	LC111222	Sekino & Yamashita, 2016	
Saccostrea lineage J	Australia: Orpheus Island	OR340003	McDougall *et al.*, 2024	
Saccostrea lineage J	Australia: Cone Bay, Kimberley, WA	MN153593	Snow *et al.*, 2023	
Saccostrea glomerata	Australia: La Parouse, Sydney, NSW	AY247288	Lam & Morton, 2006	
Saccostrea glomerata	Australia: Oyster Harbour, Albany, WA	MN153625	Snow *et al.*, 2023	
Saccostrea kegaki	Japan: Morozaki	AY247317	Lam & Morton, 2006	
Saccostrea kegaki	Japan: Kagoshima, Kakeroma Island	LC111090	Sekino & Yamashita, 2016	
Saccostrea palmula	Mexico: Baja California Sur, Los Cabos	KT317251	Raith *et al.*, 2015	
Saccostrea palmula	Mexico: Sonora, Guaymas	KT317354	Raith *et al.*, 2015	

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APPENDIX A. (Continued)

Species	Location	GenBank accession number	Publication	Remarks
Saccostrea cucullata sensu stricto	Atlantic Ocean: Ascension Island, Shelly Beach	PP842649	Tan *et al.*, 2025	
Saccostrea cucullata sensu stricto	Atlantic Ocean: Ascension Island, Scouts Beach	PP842658	Tan *et al.*, 2025	

APPENDIX B. List of COX1 and 16S sequences retrieved from GenBank that were used to construct the phylogenetic trees shown in Figure 3.

Species	Location	GenBank accession number		Publication
		COX1	16S	
Ostrea edulis	France	JF274008	JF274008	Danic-Tchaleu *et al.*, 2011
Magallana gigas	Australia: Port Adelaide, SA	MZ400416	MZ400416	unpublished
Saccostrea lineage A	Australia: Karratha Bay, West Lewis Island, Dampier Archipelago, WA	PP834532	OR466892	Tan *et al.* 2025; Wells *et al.*, 2024
Saccostrea lineage A	Australia: Pelican Point, Carnarvon, WA	PP834535	MN153642	Tan *et al.*, 2025; Snow *et al.*, 2023
Saccostrea lineage B	Australia: Hervey Bay, QLD	OR339839	OR340020	McDougall *et al.*, 2024
Saccostrea lineage C	Japan: Kagoshima,Amami-Oshima Island	LC110510	LC111145	Sekino & Yamashita, 2016
Saccostrea lineage F	Japan: Kagoshima, Kakeroma Island	LC110465	LC111100	Sekino & Yamashita, 2016
Saccostrea lineage G	Australia: Percy Islands	OR339828	OR340012	McDougall *et al.*, 2024
Saccostrea lineage G	Japan: Kagoshima, Amami-Oshima Island	LC110519	LC111154	Sekino & Yamashita, 2016
Saccostrea lineage H	Japan: Okinawa	LC110596	LC111231	Sekino & Yamashita, 2016
Saccostrea lineage I	Australia: Orpheus Island	OR339819	OR340007	McDougall *et al.*, 2024
Saccostrea lineage I	Japan: Okinawa, Iriomote Island, Yaeyama	LC110579	LC111214	Sekino & Yamashita, 2016
Saccostrea lineage J	Australia: Cone Bay, Kimberley, WA	PP834536	MN153593	Tan *et al.*, 2025; Snow *et al.*, 2023
Saccostrea lineage J	Japan: Okinawa	LC110588	LC111223	Sekino & Yamashita, 2016
Saccostrea glomerata	Australia: Oyster Harbour, Albany, WA	PP834537	MN153625	Tan *et al.*, 2025; Snow *et al.*, 2023
Saccostrea kegaki	Japan: Okinawa	LC110614	LC111249	Sekino & Yamashita, 2016
Saccostrea cucullata sensu stricto	Atlantic Ocean: Ascension Island, Scouts Beach	PP834531	PP842658	Tan *et al.*, 2025
Saccostrea mordax	Australia: Hook Island	OR339805	OR339997	McDougall *et al.*, 2024
Saccostrea mordax	China	MT293844	MT298862	Cui *et al.*, 2021
Saccostrea mordax	China	MT293845	MT298863	Cui *et al.*, 2021
Saccostrea scyphophilla	China	MT293807	MT298889	Cui *et al.*, 2021
Saccostrea scyphophilla	China	MT293806	MT298874	Cui *et al.*, 2021
Saccostrea scyphophilla	Australia: Ashburton Island, WA	PP834539	OR466910	Tan *et al.*, 2025; Wells *et al.*, 2024