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Clarification of the identity of oysters in the genera *Magallana* and *Saccostrea* in the upper Gulf of Thailand based on 16S rRNA sequences

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Abstract. Oysters are ecologically important, often dominating shorelines and becoming habitat modifiers. They are a key group for molluscan aquaculture, with an estimated annual production of 8,000 tonnes in Thailand. Some species become invasive when introduced into new habitats. A variety of species have been recorded from Thailand, but identifications are uncertain. We examined oysters at 14 sites in the upper (northern) Gulf of Thailand in August 2023 and compared identifications made in the field using Thai literature with DNA sequences. Two species of *Magallana* and four species of *Saccostrea* were detected in the wild, and one species of each genus in aquaculture farms. The taxonomy of the species was clarified and their invasive potential evaluated.

Keywords. *Saccostrea*, *Magallana*, *Crassostrea*, invasive marine species, marine pests, Ostreidae, competition, bivalves

INTRODUCTION

Global aquaculture production has increased dramatically in recent decades and now contributes to more than 50% of the world supply of seafood. Molluscs were the second largest component of total production at 21% both by weight and value in 2016, with oysters dominating molluscan aquaculture production. Many oyster species are suitable for aquaculture as they are easily cultured, fast growing, feed naturally, and are commercially valuable. The total annual world aquaculture production is about six million tonnes, dominated by *Magallana gigas* (Thunberg, 1793). China is by far the largest producer, contributing 86% of the total global production, but very little is exported. A number of other countries such as France, United States of America, South Korea, Japan, and Canada have larger export markets (Botta et al., 2020).

Oyster aquaculture is the third most important shellfish culture in Thailand. The Thai Department of Fisheries reported a total estimated production of about 8,000 tonnes from 1,000 farms with a total area of 9.6 km^2 in 2022. Nearly 600 farms in eastern Thailand contribute about 85% of the total production (DoF, 2023). The key commercial species were listed as *Saccostrea commercialis* (Iredale & Roughley, 1933), *Crassostrea lugubris* (Sowerby II, 1871), and *Crassostrea belcheri* (Sowerby II, 1871) (Trivej & Kesjinda, 2018). Jeamsripong et al. (2022) estimated that oyster production in the Gulf of Thailand in 2021 was 13,101 tonnes with a value of THB 255.4 million; in contrast, production from the Andaman Sea coast was only 216 tonnes worth THB 24.5 million. The importance of oyster aquaculture to farming communities at Ang Sila in the upper Gulf of Thailand has been highlighted by Szuster et al. (2008).

The densely packed aggregations of many oysters cause considerable variations in shell form, making accurate taxonomic identification very difficult. Bussarawit & Cedhagen (2010) reported that previous studies on oysters in Thailand were scarce and there was considerable confusion regarding the scientific names with inconsistent taxonomic classification, making identifications of species reported in most published information uncertain. In some cases, unidentified or misidentified oysters were preserved in the collection of the Phuket Marine Biological Center (Nielsen, 1976; Tantanasiriwong, 1979); these were subsequently revised by Bussarawit & Cedhagen (2010). DNA analysis is the most reliable method for identifying species (Salvi & Mariottini, 2016; Willan et al., 2021). Bussarawit et al. (2006) and Klinbunga et al. (2000, 2001, 2002, 2003, 2005) studied the genetics of several species of Thai oysters but the taxonomy they used, primarily based on Harry (1985), is now outdated. There have been major changes to ostreid taxonomy in recent years (e.g., Huber, 2010; Salvi & Mariottini, 2016; Sekino & Yamashita, 2016; Sigwart et al., 2021). Bussarawit et al. (2006) used partial 16S rRNA sequences to show that specimens identified as *Saccostrea*

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forskahlii (Gmelin, 1791) and *Saccostrea* cf. *malabonensis* (Faustino, 1932) were genetically identical despite obvious morphological differences. Their results also indicated that a specimen identified as *Striostrea mytiloides* (Lamarck, 1819) belonged to the genus *Saccostrea*. Accordingly, the first goal of this paper is to use DNA sequencing to determine the identity of oysters in the genera *Magallana* and *Saccostrea* in the upper Gulf of Thailand and to, as far as possible, reconcile the current taxonomy with published records for the Gulf of Thailand.

In recent years, there has been increasing concern over the threat to global marine environments posed by invasive marine species (IMS, also known as introduced marine pests) (e.g., Johnson & Chapman, 2007; Molnar et al., 2008; Katsanevakis et al., 2014; Crowe & Frid, 2015; McDonald et al., 2020; Salimi et al., 2021). Unfortunately, the biological attributes that make oysters attractive for aquaculture also increase their IMS potential. Australian authorities have developed strong quarantine barriers to prevent the arrival of IMS to Australian waters (e.g., Vessel-Check, 2022) and monitoring strategies for species that penetrated the barriers (NIMPCG, 2010a, b; DPIRD, 2016). The introduction of oysters for aquaculture also brings risks of introducing diseases and other species living on or in the oysters (Ruesink et al., 2005; Herbert et al., 2016). The second goal of this paper is to determine what species of *Magallana* and *Saccostrea* are in fact present in the Gulf of Thailand and to assess their IMS risk to Australia.

MATERIAL AND METHODS

Sample collection. Oysters in the genera *Magallana* and *Saccostrea* were surveyed at 14 sites in the upper Gulf of Thailand in August 2023, in conjunction with a survey for the invasive mytilid *Mytella strigata* (Hanley, 1843) (Wells et al., 2024). The oyster survey commenced at Sriracha in Chonburi Province on the eastern side of the upper gulf on 1 August (Fig. 1; Table 1) and proceeded south to Kungkraben Bay. At most sites intertidal rocky shores were sampled on low spring tides. At Sriracha a small boat was used to inspect four commercial Asian green mussel aquaculture lines. At Kungkraben Bay a rocky shore was sampled near the base of the aquaculture demonstration facility, where hanging ropes in the facility were also inspected. Sites on the western side of the inner Gulf of Thailand were then examined, beginning at Klong Wan, then moving north back to Bangkok. The survey was completed on 8 August 2023.

At each site oysters were identified in the field as far as possible using Bussarawit & Cedhagen (2010) (see Table 2). Specimens of each presumed species and any doubtful species were removed by hand from the rocks using a hammer and chisel and were individually labelled. The oysters were opened, a small tissue sample was dissected from the adductor muscle, and preserved in 95% ethanol. The remaining tissue was discarded. Each oyster shell was then placed in a labelled plastic bag with bleach to remove any attached tissue.

Oyster specimens were collected in four markets in Chonburi in March 2024 (Fig. 1). These oysters were taken to the Kasetsart University Museum of Fisheries (Natural History) (KUMF) in Bangkok and were handled as described below.

Full details, including the museum and GenBank registration numbers of all specimens used in this study, are presented in Table 1.

Taxonomy. At the KUMF, the oyster shells were washed in freshwater, cleaned with a wire brush, dried, and photographed. Most specimens were deposited in the KUMF. Voucher representatives of each species were hand carried to Singapore and deposited in the Lee Kong Chian Natural History Museum (LKCNHM) of the National University of Singapore. Taxonomy in this paper follows the World Register of Marine Species (WoRMS) (MolluscaBase eds., 2024). Published literature was searched and all Gulf of Thailand records examined.

Other abbreviations are: ANG, Ang Sila; BAN, Bang Saen; PCR, Polymerase Chain Reaction; ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore; RV, right valve; LV, left valve.

DNA extraction, PCR amplification, and sequencing. Tissue samples were prepared for each species identified at each site. The adductor muscle was dissected with small pieces of tissue being removed and preserved in 95% ethanol in a small vial for DNA analysis. A small piece of absorbent cloth was inserted into each vial, and the vial drained and sealed. The vials were packed and hand carried with the necessary documentation to a laboratory at Curtin University in Perth. At Curtin the vials were frozen until analysis could be undertaken. For sequencing, the tissue from each vial was thawed and DNA extracted using the DNeasy Blood and Tissue Kit (Qiagen Inc., USA) following the manufacturer's instructions. PCR amplification of approximately 450 bases of the mitochondrial ribosomal RNA subunit 16S region (16S) was done for each specimen, using primers 16Sar and 16Sbr (Simon et al., 1994).

PCR reactions were conducted in 25 µl containing 3 µl DNA (~20 ng), 1× 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 0.6 µM of each primer. PCR conditions consisted of an initial incubation at 95ºC for 3 minutes, followed by 35 cycles of 94ºC for 45 seconds, 52ºC for 90 seconds, 72ºC for 45 seconds, and a final extension step of 72ºC for 10 minutes.

Bi-directional sequencing of unpurified PCR products was performed using the Sanger sequencing service provided by the Australian Genome Research Facility, Perth. Sequences were trimmed and edited using the Geneious Prime 2022.1.1 software (http://www.geneious.com). For each individual, species identification was verified by similarity-based searches on the NCBI BLAST database (Altschul et al.,

Fig. 1. Map of the upper (northern) Gulf of Thailand showing the locations of stations sampled in August 2023 and the aquaculture farms in Chonburi. ANG, Ang Sila; BAN, Bang Saen. Details of the locations are provided in Table 1.

1990). All sequences were submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and assigned individual accession numbers.

Additional 16S sequences for East Asian *Magallana* and *Saccostrea* species were retrieved from GenBank and aligned using the Geneious Prime 2022.1.1 software. Sequences that were not within the targeted region of the 16S rRNA gene 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 for the alignments. Specimens identified as *Magallana* species were aligned with *Magallana* sequences retrieved from GenBank and this alignment was trimmed to 418 bp. For this alignment we performed a Bayesian Inference analysis using the MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001) plugin in Geneious Prime with the following parameters: HKY85 gamma model with nucleotide sites partitioned for 1 million generations subsampling every 500 generations and a 100,000 burn-in length. Likewise, all remaining sequences were aligned with *Saccostrea* sequences retrieved from GenBank and this alignment was trimmed to 435 bp. For this alignment, we performed a Bayesian Inference analysis using the MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001) plugin in Geneious Prime with the following parameters: HKY85 invgamma model with nucleotide sites partitioned for 1 million generations subsampling every 500 generations and a 100,000 burn-in length. For both Bayesian inference analyses, *Ostrea edulis* Linnaeus, 1758 was used as an outgroup. All resultant trees were processed in FigTree v. 1.4.4 (Rambaut et al., 2018) with tree annotations added in Adobe Illustrator.

Full details of all sequences used in this study are included in Table 1 and Appendix 1.

TAXONOMY

Eighty-nine oysters were collected from 14 stations in the upper Gulf of Thailand in August 2023; partial 16S rRNA sequences were obtained from 67 oysters. Additionally, 46 oysters from farms in Chonburi were bought in four markets; 33 of these were sequenced.

Table 1. Site locations and specimens used in this study. The sequence identification codes (SIC) correspond to those used in Figs. 2 and 3.

Site no.	Location	Latitude and longitude	Date	Habitat	Species detected				
					Bussarawit & Cedhagen (2010)	DNA sequence			
						Species	SIC	Specimen voucher number	GenBank accession number
1	Kasetsart University Fisheries Research Center, Sriracha	13°10.728′N; 100°55.258′E	1 August 2023	Hanging ropes	*C. bilineata*, *S. cucullata*	*M. bilineata*	TH01	KUMF-MOLL 1207	PP836532
						M. bilineata	TH02	ZRC.MOL.028369	PP836533
						M. bilineata	TH03	ZRC.MOL.028370	PP836534
						Saccostrea F	TH08	ZRC.MOL.028371	PP836535
						Saccostrea F	TH10	KUMF-MOLL 1213	PP836536
2	Samaesan and Seafood market	12°35.955′N; 100°56.948′E	2 August 2023	Rocky shore	*S. cucullata*, *S. echinata*, *Ostrea* sp.	*M. belcheri*	TH26	ZRC.MOL.028372	PP836537
						M. belcheri	TH27	KUMF-MOLL 1214	PP836538
					C. belcheri in market	*M. belcheri*	TH28	KUMF-MOLL 1215	PP836539
						S. spathulata	TH35	KUMF-MOLL 1216	PP836540
						S. spathulata	TH36	KUMF-MOLL 1217	PP836541
						S. spathulata	TH37	KUMF-MOLL 1218	PP836542
						S. spathulata	TH38	ZRC.MOL.028373	PP836543
						S. spathulata	TH39	ZRC.MOL.028374	PP836544
						S. spathulata	TH41	KUMF-MOLL 1220	PP836545
						S. spathulata	TH42	ZRC.MOL.028375	PP836546
						S. scyphophilla	TH43	KUMF-MOLL 1221	PP836547
						S. scyphophilla	TH44	KUMF-MOLL 1222	PP836548
						S. scyphophilla	TH45	–	PP836549
						Saccostrea B	TH46	ZRC.MOL.028376	PP836550
						S. scyphophilla	TH48	KUMF-MOLL 1224	PP836551
						Saccostrea B	TH49	ZRC.MOL.028377	PP836552
3	Ta Kuan Beach	12°40.295′N; 101°09.887′E	2 August 2023	Rocky shore	*S. forskahlii*	*Saccostrea* B	TH58	ZRC.MOL.028378	PP836553
						Saccostrea B	TH59	KUMF-MOLL 1226	PP836554
						Saccostrea F	TH61	–	PP836555
4	Mae Rum Peung Beach	12°36.638′N; 101°23.028′E	2 August 2023	Rocky shore	*Striostrea* sp., *S. cucullata*, *S. echinata*	*Saccostrea* B	TH65	KUMF-MOLL 1228	PP836556
						Saccostrea B	TH66	KUMF-MOLL 1229	PP836557
						Saccostrea B	TH68	KUMF-MOLL 1231	PP836558
5	Hin Khrong north of Kungkraben Bay	12°36.475′N; 101°52.205′E	3 August 2023	Rocky shore	*S. cucullata*, *Striostrea* sp.	*Saccostrea* B	TH69	KUMF-MOLL 1232	PP836559
						Saccostrea B	TH72	KUMF-MOLL 1235	PP836560
						Saccostrea B	TH74	KUMF-MOLL 1237	PP836561

Site no.	Location	Latitude and longitude	Date	Habitat	Species detected				
					Bussarawit & Cedhagen (2010)	DNA sequence			
						Species	SIC	Specimen voucher number	GenBank accession number
6	Mouth of Kungkraben Bay	12°35.213′N; 101°53.062′E	3 August 2023	Rocky shore	*S. echinata*, *S. forskahlii*, *C. bilineata*	*M. bilineata*	TH88	KUMF-MOLL 1238	PP836562
						M. bilineata	TH90	KUMF-MOLL 1240	PP836563
						Saccostrea B	TH92	KUMF-MOLL 1242	PP836564
						Saccostrea B	TH93	–	PP836565
						Saccostrea F	TH94	KUMF-MOLL 1243	PP836566
						Saccostrea F	TH95	ZRC.MOL.028379	PP836567
7	Kungkraben Bay adjacent to Sea Farming Demonstration Unit	12°34.898′N; 101°53.507′E	3 August 2023	Rocky shore and wall	*C. bilineata*, *S. cucullata*, *S. forskahlii*, *Striostrea* sp.	*M. bilineata*	TH98	KUMF-MOLL 1246	PP836568
						M. bilineata	TH99	KUMF-MOLL 1247	PP836569
						Saccostrea B	TH102	ZRC.MOL.028380	PP836570
						Saccostrea B	TH105	ZRC.MOL.028381	PP836571
						Saccostrea F	TH106	ZRC.MOL.028382	PP836572
						Saccostrea B	TH108	KUMF-MOLL 1253	PP836573
						Saccostrea B	TH109	KUMF-MOLL 1254	PP836574
8	Kungkraben Bay, Sea Farming Demonstration Unit	12°34.898′N; 101°53.507′E	3 August 2023	Hanging ropes	*S. cucullata*	None collected as it is a research area.			
9	Pattaya	12°58.422′N; 100°53.373′E	4 August 2023	Rocky shore and wall	*C. bilineata*, *S. cucullata*, *S. forskahlii*, *Striostrea* sp.	*M. bilineata*	TH117	KUMF-MOLL 1258	PP836575
						M. bilineata	TH118	KUMF-MOLL 1259	PP836576
						Saccostrea F	TH121	ZRC.MOL.028383	PP836577
						Saccostrea B	TH123	KUMF-MOLL 1263	PP836578
						Saccostrea B	TH126	ZRC.MOL.028384	PP836579
						Saccostrea B	TH128	KUMF-MOLL 1267	PP836580
						Saccostrea F	TH130	KUMF-MOLL 1269	PP836581
						Saccostrea B	TH132	KUMF-MOLL 1271	PP836582
10	Klong Wan Pier	11°44.133′N; 99°46.915′E	6 August 2023	Jetty	*S. forskahlii*, *Striostrea* sp.	*Saccostrea* F	TH134	KUMF-MOLL 1273	PP836583
						Saccostrea B	TH137	KUMF-MOLL 1276	PP836584
						Saccostrea F	TH139	KUMF-MOLL 1278	PP836585
						Saccostrea B	TH140	KUMF-MOLL 1279	PP836586
11	Khao Ta Mong Lai Forest Park	11°50.198′N; 99°49.807′E	6 August 2023	Rocky shore	*S. forskahlii*, *S. cucullata*	None collected as it is a national park.			

Site no.	Location	Latitude and longitude	Date	Habitat	Species detected				
					Bussarawit & Cedhagen (2010)	DNA sequence			
						Species	SIC	Specimen voucher number	GenBank accession number
12	Sirinart Rajini Mangrove Ecology Learning Center	12°23.573′N; 99°58.944′E	7 August 2023	*Rhizophora* mangroves	*Striostrea* sp., *S. forskahlii*	None collected as it is a national park.			
13	Khao Ta Kiab Pier	12°30.812′N; 99°58.840′E	7 August 2023	Jetty	*Striostrea* sp., *S. forskahlii*, *S. cuccullata*	*Saccostrea* F	TH141	KUMF-MOLL 1280	PP836587
						Saccostrea F	TH142	KUMF-MOLL 1281	PP836588
						Saccostrea B	TH143	KUMF-MOLL 1282	PP836589
						Saccostrea B	TH145	KUMF-MOLL 1284	PP836590
						Saccostrea F	TH146	KUMF-MOLL 1285	PP836591
						Saccostrea F	TH147	KUMF-MOLL 1286	PP836592
						Saccostrea B	TH148	KUMF-MOLL 1287	PP836593
						Saccostrea F	TH149	KUMF-MOLL 1288	PP836594
14	Institute of Marine Science, Burapha University (Cha Am Substation)	12°52.283′N; 100°01.067′E	8 August 2023	Rock wall	*Striostrea* sp., *S. forskahlii*	*Saccostrea* B	TH152	KUMF-MOLL 1291	PP836595
						Saccostrea B	TH153	KUMF-MOLL 1292	PP836596
						Saccostrea B	TH155	KUMF-MOLL 1294	PP836597
						Saccostrea B	TH156	KUMF-MOLL 1295	PP836598
Market 1	Chonburi market	13°18.664′N; 100°54.784′E	1 March 2023		*C. bilineata*; *S. forskahlii*	*Saccostrea* F	TH157	KUMF-MOLL 1306	PP836599
						M. bilineata	TH158	KUMF-MOLL 1304	PP836600
						M. bilineata	TH159	KUMF-MOLL 1303	PP836601
						Saccostrea F	TH160	KUMF-MOLL 1297	PP836602
						Saccostrea F	TH161	KUMF-MOLL 1299	PP836603
						Saccostrea F	TH162	KUMF-MOLL 1302	PP836604
						Saccostrea F	TH185	KUMF-MOLL 1300	PP836627
						Saccostrea F	TH186	KUMF-MOLL 1305	PP836628
Market 2	Chonburi market	13°18.830′N; 100°55.003′E	1 March 2023		*C. bilineata*; *S. forskahlii*	*Saccostrea* F	TH163	KUMF-MOLL 1308	PP836605
						Saccostrea F	TH164	KUMF-MOLL 1310	PP836606
						Saccostrea F	TH165	KUMF-MOLL 1309	PP836607
						M. bilineata	TH166	KUMF-MOLL 1314	PP836608
						M. bilineata	TH167	KUMF-MOLL 1316	PP836609
						M. bilineata	TH168	KUMF-MOLL 1318	PP836610
						Saccostrea F	TH181	KUMF-MOLL 1313	PP836623
						M. bilineata	TH182	KUMF-MOLL 1315	PP836624
						M. bilineata	TH189	KUMF-MOLL 1317	PP836631

Site no.	Location	Latitude and longitude	Date	Habitat	Species detected				
					Bussarawit & Cedhagen (2010)	DNA sequence			
						Species	SIC	Specimen voucher number	GenBank accession number
Market 3	Chonburi market	13°19.003′N; 100°55.122′E	1 March 2023		*C. bilineata*; *S. forskahlii*	*Saccostrea* F	TH169	KUMF-MOLL 1321	PP836611
						Saccostrea F	TH170	KUMF-MOLL 1322	PP836612
						Saccostrea F	TH171	KUMF-MOLL 1326	PP836613
						M. bilineata	TH172	KUMF-MOLL 1329	PP836614
						M. bilineata	TH173	KUMF-MOLL 1330	PP836615
						M. bilineata	TH174	KUMF-MOLL 1332	PP836616
						Saccostrea F	TH183	KUMF-MOLL 1324	PP836625
						M. bilineata	TH184	KUMF-MOLL 1328	PP836626
Market 4	Chonburi market	13°19.937′N; 100°55.382′E	1 March 2023		*C. bilineata*; *S. forskahlii*	*M. bilineata*	TH175	KUMF-MOLL 1333	PP836617
						Saccostrea F	TH176	KUMF-MOLL 1335	PP836618
						Saccostrea F	TH177	KUMF-MOLL 1337	PP836619
						M. bilineata	TH178	KUMF-MOLL 1340	PP836620
						M. bilineata	TH179	KUMF-MOLL 1339	PP836621
						M. bilineata	TH180	KUMF-MOLL 1341	PP836622
						M. bilineata	TH187	KUMF-MOLL 1338	PP836629
						Saccostrea F	TH188	KUMF-MOLL 1334	PP836630

Figs. 2 and 3 show the phylogenetic relationships of the *Magallana* and *Saccostrea* species respectively, based on material collected in the upper Gulf of Thailand and other GenBank registrations of species in both genera from Southeast Asia. The European *Ostrea edulis* was used as the outgroup. Two species of *Magallana* were recorded: *Magallana belcheri* (Sowerby II, 1871) and *Magallana bilineata* (Röding, 1798). Four genetic lineages of *Saccostrea* were collected in the wild: *Saccostrea* lineages B and F, *Saccostrea spathulata* (Lamarck, 1819) (= lineage J), and *Saccostrea scyphophilla* (Péron & Lesueur, 1807). Only two species were recorded from the farmed aquaculture specimens: *Magallana bilineata* and *Saccostrea* lineage F.

Bussarawit et al. (2006) sequences were excluded from the Bayesian Inference analysis since they were shorter than the rest of the dataset. However, during the alignment of sequences, it was noted that the sequences assigned to *Saccostrea forskahlii* (EF122388) and *S.* cf. *malabonensis* (EF122391) were 99.8–100% matches to specimens collected in this study that made up the *Saccostrea* lineage F clade (Fig. 3). *Saccostrea cucullata* (Born, 1778) (EF122389) sequence was 99.4–100% match to specimens that are part of the *Saccostrea scyphophilla* clade (Fig. 3) and *Saccostrea echinata* (Quoy & Gaimard, 1835) (EF122390) sequence was 99.4–100% match to specimens in the *Saccostrea spathulata* (Lamarck, 1819) clade. Even though Bussarawit et al. (2006) had a small sample size, they had similar species/lineage detections in Thailand based on partial 16S rRNA sequences.

Family Ostreidae Rafinesque, 1815

Subfamily Crassostreinae Scarlato & Starobogatov, 1979

Genus *Magallana* Salvi & Mariottini, 2016

Members of the well-known genus *Crassostrea* Sacco, 1897 were defined based on shell morphology and included species from the Pacific, Indian, and Atlantic Oceans. The genus included several commercially and ecologically important species, particularly *Crassostrea gigas* (Thunberg, 1793) in the Pacific and *Crassostrea virginica* (Gmelin, 1791) in the Atlantic. *Crassostrea gigas* was also regarded as an invasive marine species (NIMPCG, 2010a, b; DPIRD, 2016). However, with the development and use of DNA techniques it became clear that there were consistent genetic differences between extant species of *Crassostrea* in the Indo-Pacific and the Atlantic (Ó'Foighil et al., 1995; Lam & Morton, 2004; Wang et al., 2004a, b). Salvi et al. (2014) and Salvi & Mariottini (2016) proposed the separation of *Crassostrea* into three genera: *Crassostrea* sensu

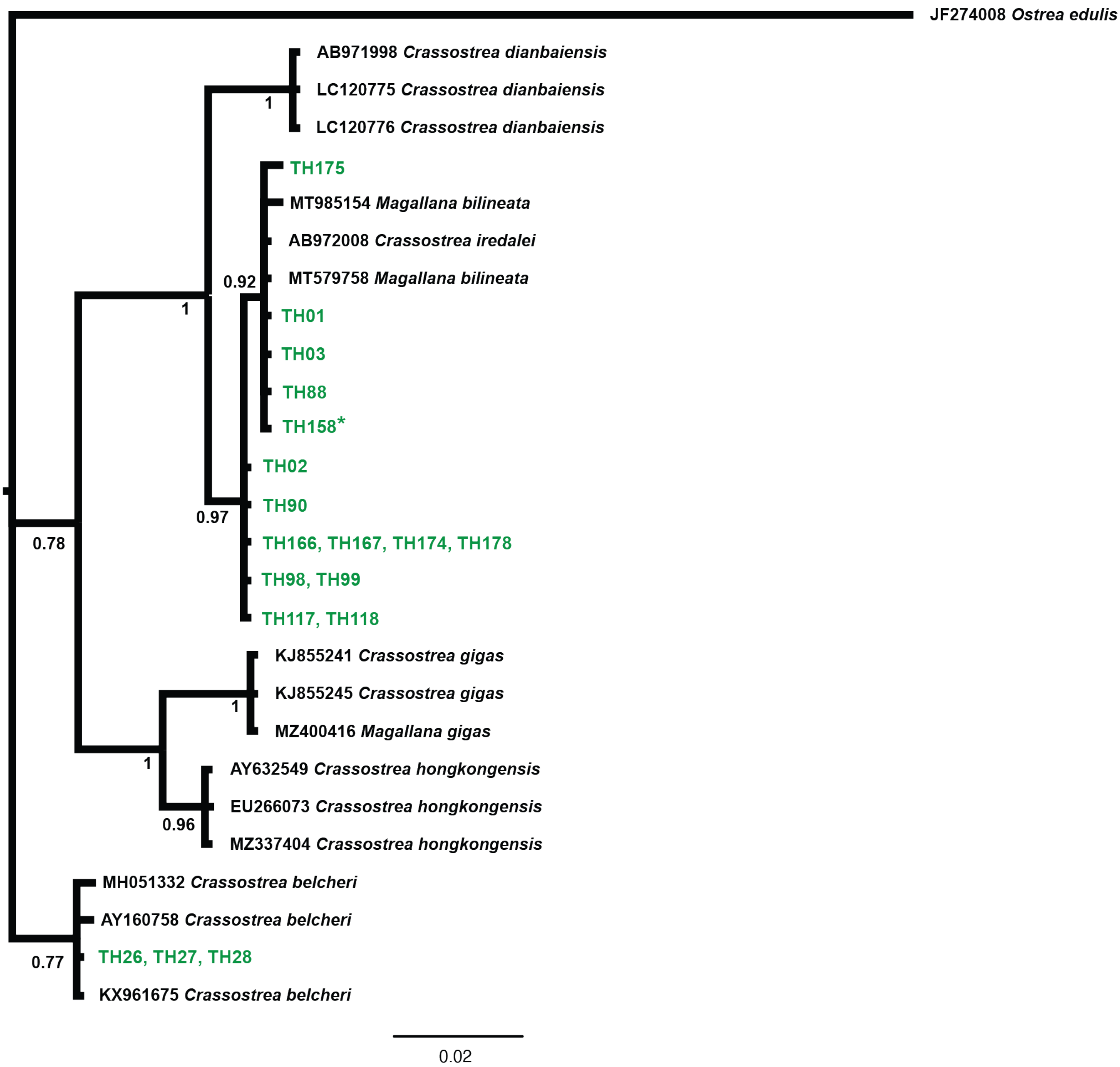

Fig. 2. 16S Bayesian inference tree of Southeast Asian *Magallana* species using *Ostrea edulis* as the outgroup. Genus names shown are those associated with the GenBank accession numbers. Sequence identification codes with prefixes TH in green font represent individuals sequenced in this study. Bootstrap values are shown at the nodes. TH158* (*Magallana bilineata*) represents specimens TH158, TH159, TH168, TH172, TH173, TH179, TH180, TH182, TH184, TH187, and TH189.

stricto for Atlantic species, and *Talonostrea* Li & Qi, 1994 and *Magallana* Salvi & Mariottini, 2016 for Indo-Pacific species. The proposed separation of Atlantic and Indo-Pacific *Crassostrea* has been controversial. Several researchers (Bayne et al., 2017, 2019; Backeljau, 2018) argued for nomenclatural stability as *Crassostrea* is well understood and includes species that are ecologically and economically important. Salvi & Mariottini (2021), Willan (2021) and Salvi et al. (2022) believed the separation of *Crassostrea* should be accepted as the genetic data are clear and there have been numerous nomenclatural changes of economically and ecologically important species in other taxa as new information became available. Sigwart et al. (2021) observed that there are clearly identifiable extant and fossil species that, in the absence of genetic data, cannot be included in one of the three genera. They suggested retaining the genus *Crassostrea* and recognising three subgenera (*Crassostrea*, *Magallana*, and *Talonostrea*). WoRMS recognises the three as valid genera (MolluscaBase eds., 2024), a classification followed by Tan et al. (2024) for *Magallana* in Singapore. We have followed the WoRMS use of *Magallana* and the WoRMS recognised synonymy of the species.

Magallana species present in the upper Gulf of Thailand:

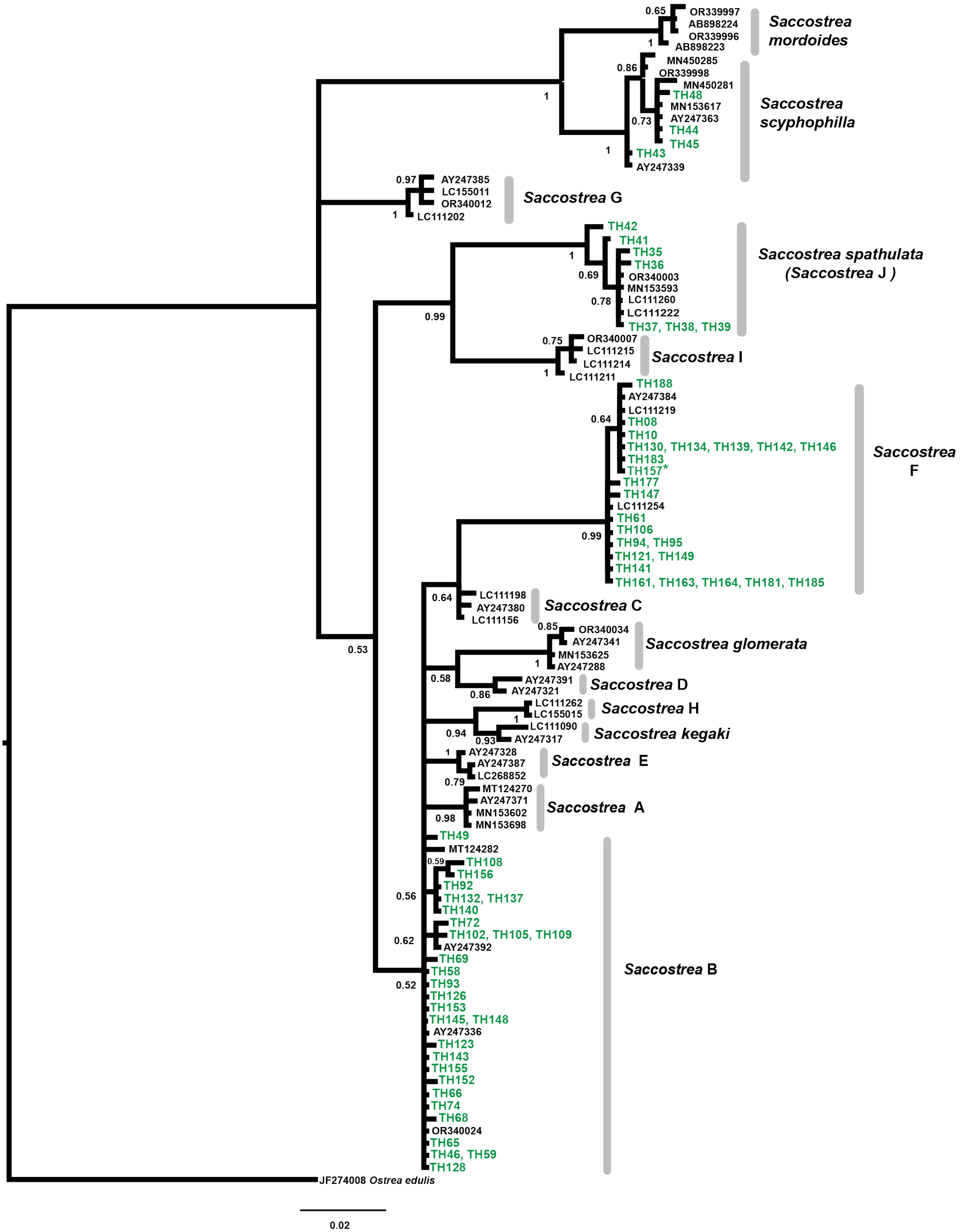

Fig. 3. 16S Bayesian inference tree of Asian *Saccostrea* species using *Ostrea edulis* as the outgoup. Sequence identification codes with prefixes TH in green font represent individuals sequenced in this study. Bootstrap values are shown at the nodes. TH157* (*Saccostrea* lineage F) represents specimens TH157, TH160, TH162, TH165, TH169, TH170, TH171, TH176, and TH186.

Magallana belcheri (Sowerby II, 1871)
(Fig. 4D–F)

Ostrea belcheri Sowerby II, 1871 (in 1870–1871): pl. 7, fig. 11 (type locality: "Eastern Seas?").
Ostrea siamensis Mörch, 1853: 62 (type locality: "Singapuhra")—nomen nudum.

Habitat. Not recorded in the wild in the upper gulf but included here for completeness.

Material examined. Site 2, Samaesan seafood market.

Published Gulf of Thailand records. *Crassostrea belcheri* (Sowerby II, 1871): Chaitiamwong et al. (1971); Aungtonya et al. (1999); Yoosukh & Duangdee (1999); Day et al. (2000); Klinbunga et al. (2000, 2001, 2002, 2003, 2005); Yoosukh (2000); Bussarawit & Simonsen (2006a); ONEP (2007); Nabhitabhata (2009); Bussarawit & Cedhagen (2010; 2012); Phuwan et al. (2018); Trivej & Kesjinda (2018); Ninwichian et al. (2021).

Geographic range. Native to Southeast Asia, with sequenced records from Pakistan, Myanmar, India, Thailand, Malaysia, Singapore, Vietnam, China, and Indonesia (Willan et al., 2021).

Remarks. This is an important aquaculture species on both sides of the Gulf of Thailand, particularly on the eastern side (Bussarawit & Cedhagen, 2010; Trivej & Kesjinda, 2018). Three specimens purchased in the Samaesan seafood market were field identified as *Crassostrea* sp. (Table 2). *M. belcheri* is known as the white scar oyster because its white adductor muscle scar differentiates it from *M. bilineata*, the black scar oyster with its black adductor muscle scar (see below).

Magallana bilineata (Röding, 1798)
(Figs. 4A–C, 6A, B)

Ostrea bilineata Röding, 1798: 170 (type locality: not stated).
Ostrea lugubris Sowerby II, 1871 (in 1870–1871): pl. 26, fig. 63 (type locality: "North America?").
Ostrea iredalei Faustino, 1932: 546, 547, pl. 1, figs. 1–4 (type locality: "Navotas, Malabon, Parañaque, and other places on Manila Bay", Philippines).
Ostrea madrasensis Preston, 1916: 33–35, figs. 11, 11a (type locality: "Ennur backwater, Madras", India).

Habitat. Recorded on rocky shores and aquaculture ropes.

Material examined. Site 1, Sriracha; Site 6, mouth of Kungkraben Bay; Site 7, south Kungkraben Bay; Site 9, Pattaya. *Magallana bilineata* was also identified from the aquaculture farms in Chonburi.

Published Gulf of Thailand records. *Crassostrea bilineata* (Röding, 1798): Nabhitabhata (2009); Bussarawit & Cedhagen (2010, 2012). *Crassostrea lugubris* (Sowerby II, 1871): Aungtonya et al. (1999); Murugan et al. (1999); Day et al. (2000); Trivej & Kesjinda (2018). *Crassostrea iredalei* Faustino, 1932: Aungtonya et al. (1999); Yoosukh & Duangdee (1999); Klinbunga et al. (2000, 2001, 2002, 2003, 2005); Yoosukh (2000); Lam & Morton (2004); Bussarawit et al. (2006); Bussarawit & Simonsen (2006a).

Geographic range. Native to Southeast Asia, with sequenced records from: India, Thailand, Malaysia, Singapore, southern Japan, and Vietnam. Unsequenced records are from Pakistan and the Philippines (Tan et al., 2024). Introduced to Queensland, Australia (Willan et al., 2021).

Remarks. *Magallana bilineata* is known as the black scar oyster because its black adductor muscle scar differentiates it from *M. belcheri*, the white scar oyster, with its white adductor muscle scar. *Magallana bilineata* is well known in Thailand where it has been variously identified as *Crassostrea bilineata*, *C. lugubris*, and *C. iredalei*. Torigoe and Bussarawit (2010) clarified that there is a single species present in Thailand (*C. bilineata*), and *C. lugubris* and *C. iredalei* are synonyms. Identified in the field as *Crassostrea* sp. (Table 2). The species was introduced to aquaculture farms in the Sriracha area about 20 years ago from Kungkraben Bay and has now become naturalised in the region (Attawut Kuntavong, pers. comm.).

Published _Magallana_ records in the Gulf of Thailand rejected. *Saccostrea dactylena* (Iredale, 1939) was reported by van Gemert (2003) from Ko Samui in the southern Gulf of Thailand. *Saxostrea commercialis dactylena* Iredale, 1939 was described as an ecomorph from a specimen collected at Lindeman Island, Great Barrier Reef, Queensland. The species is accepted as valid by WoRMS (MolluscaBase eds., 2024) and is included in the genus *Magallana*. Van Gemert (2003) simply lists *S. dactylena* without a description or photograph. As there are no validated records from the Gulf of Thailand, the record is rejected.

Magallana gigas (Thunberg, 1793) was reported as *Crassostrea gigas* (Thunberg, 1793) by Aungtonya et al. (1999), Swennen et al. (2001), Robba et al. (2002), Printrakoon et al. (2008), and Sanpanich (2011). This is the Pacific oyster that has been widely introduced for aquaculture (Botta et al., 2020). It has also been reported from Singapore, but Tan et al. (2024) conducted a detailed investigation of intertidal oysters in Singapore and concluded the Singapore records of *M. gigas* were based on outdated taxonomy and the species is not present in Singapore. Similarly, the DNA sequences obtained for *Magallana* for the present paper were all *M. belcheri* and *M. bilineata*; *M. gigas* was not recorded.

Magallana rivularis (Gould, 1861) was reported as *Ostrea rivularis* Gould, 1861 by Lynge (1909). This species is considered a taxon inquirendum by WoRMS (MolluscaBase eds., 2024). Photographs of the Lynge specimens were obtained from the Natural History Museum of Denmark but were unidentifiable fragments.

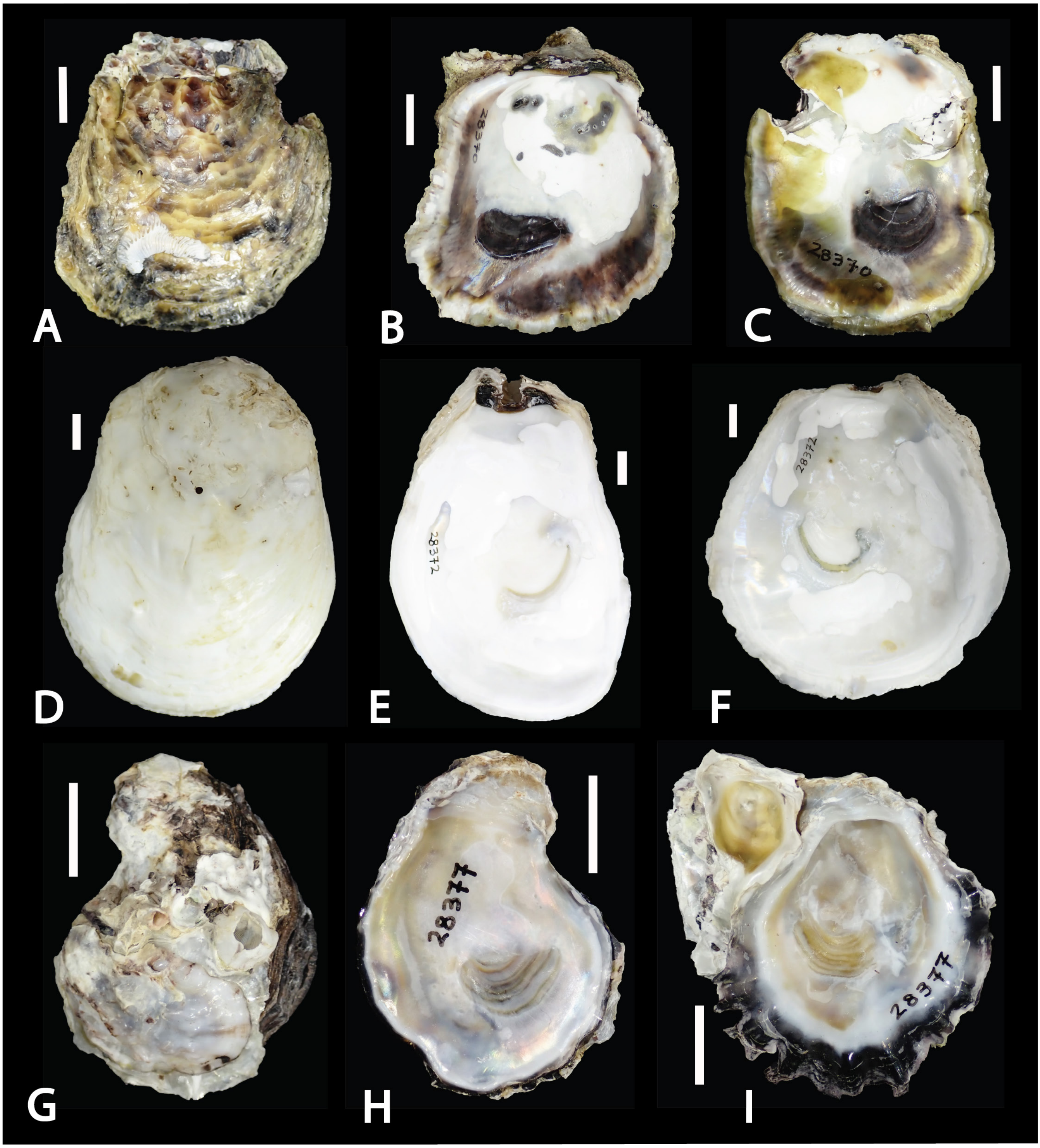

Fig. 4. *Magallana* and *Saccostrea* species collected in the upper Gulf of Thailand in August 2023. *Magallana bilineata* (A–C; ZRC.MOL.28370); *M. belcheri* (D–F; ZRC.MOL.28372); *Saccostrea scyphophilla* (G–I; ZRC.MOL.28377). For each species, the external surface of the upper (right) valve is on the left, the centre is the interior surface of the RV, and the right is the interior surface of the lower (left) valve. Scale bars are 1 cm.

Subfamily Saccostreinae Salvi & Mariottini, 2016

Genus *Saccostrea* Dollfus & Dautzenberg, 1920

Saccostrea is a widespread genus in the Indo-Pacific, with a number of species described largely on the basis of shell morphology, but *Saccostrea* taxonomy remains very confusing. Lam & Morton (2006) used genetic techniques in an attempt to differentiate the species. They proposed a 'superspecies' of *S. cucculata* and a separate clade based on *S. mordax* (Gould, 1850) (= *S. scyphophilla*; see Snow et al., 2023) to include all the different ecotypes and/or forms. Recent studies indicate that 10 distinct lineages are present within *Saccostrea* (non-*mordax*); these are all probably valid species. Sekino & Yamashita (2016) argued that they should not be included in *S. cuccullata*, but referred to them as

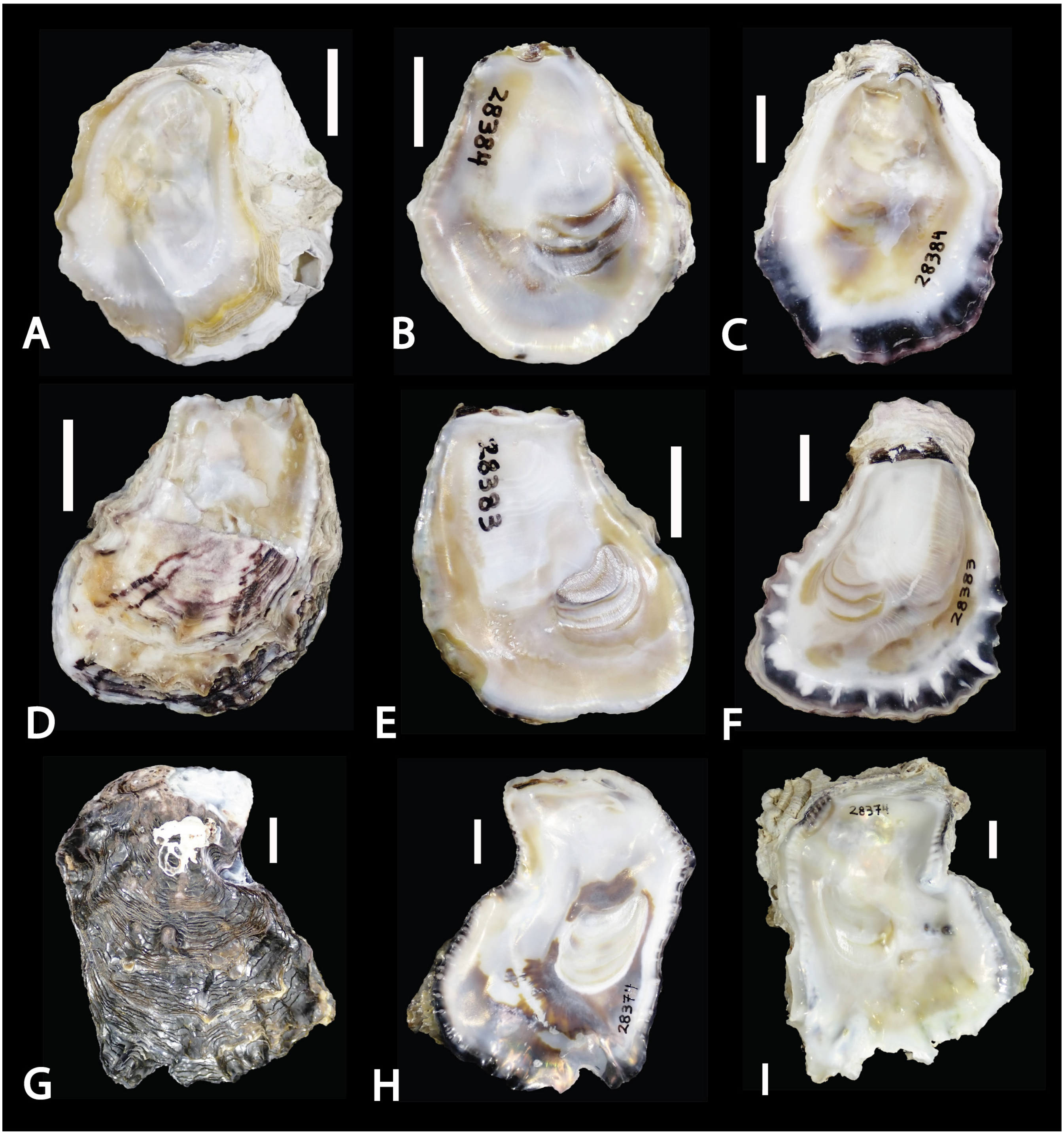

Fig. 5. *Saccostrea* species collected in the upper Gulf of Thailand in August 2023. *Saccostrea* B (A–C; ZRC.MOL.28384); *Saccostrea* F (D–F; ZRC.MOL.28383); *Saccostrea spathulata* (G–I; ZRC.MOL.28374). For each species, the external surface of the upper (right) valve is on the left, the centre is the interior surface of the RV, and the right is the interior surface of the lower (left) valve. Scale bars are 1 cm.

Saccostrea A–J. This terminology was used by Snow et al. (2023) and we have followed their recommendations. Tan et al. (in press) have recently demonstrated that *S. cuccullata* was described from Ascension Island in the South Atlantic Ocean and does not occur in the Indo-West Pacific.

Visootiviseth et al. (1998) pointed out the confused taxonomy of small oysters in the genus *Saccostrea* in Thailand and used a combination of electrophoretic and morphometric techniques to distinguish three species: A, B, and C. All three occurred in the Gulf of Thailand but were not named. Klinbunga et al. (2005) also recognised three groups (1–3) of *Saccostrea* in Thailand, with groups 1 and 3 occurring in the Gulf of Thailand. These results cannot be compared with the present study as Visootiviseth et al. (1998) used allozyme analysis and Klinbunga et al. (2005) used Polymerase Chain Reaction-Restriction Fragment Length Polymerase (PCR RFLP), vastly different molecular techniques from those used here.

Saccostrea species present in the upper Gulf of Thailand:

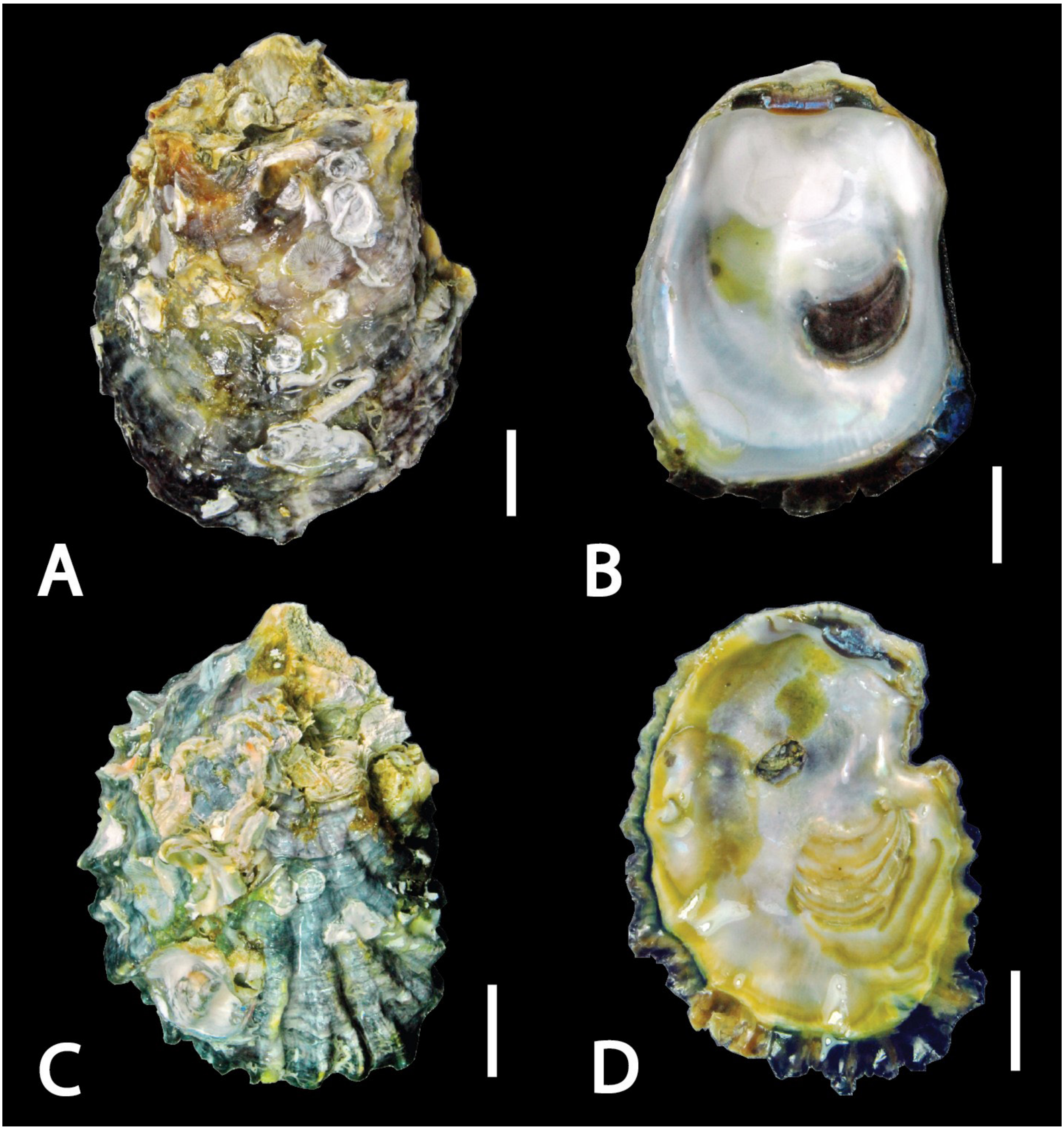

Fig. 6. Oysters from the Chonburi aquaculture farms bought in the markets in March 2024. *Magallana bilineata* (A, B; KUMF–MOLL 1333); *Saccostrea* F (C, D; KUMF–MOLL 1335). For each species, the external surface of the upper (right) valve is on the left, on the right is the interior surface of the lower (left) valve. Scale bars are 1 cm.

Saccostrea B species complex
(Fig. 5A–C)

Habitat. Rocky shores, rock walls, jetty.

Material examined. Site 2, Samaesan; Site 3, Ta Kuan Beach; Site 4, Mae Rum Peung Beach; Site 5, Hin Khrong; Site 6, mouth of Kungkraben Bay; Site 7, south Kungkraben Bay; Site 9, Pattaya; Site 10, Klongwan Pier; Site 13, Kao Ta Kiep; Site 14, Cha Am. Identified in the field as *S. echinata*, *S. forskahlii*, *Striostrea* sp., and *Saccostrea cuccullata* (Table 2).

Published Gulf of Thailand records. None.

Geographic range. Recorded by sequence data from Australia (Northern Territory, Queensland), China, Singapore, Vietnam, Taiwan (Lam & Morton 2006), and Kimberley, Western Australia (Snow et al., 2023).

Table 2. Summary comparison of oyster identifications in the upper Gulf of Thailand using Bussarawit & Cedhagen (2010) in the field and 16S rRNA sequencing.

DNA sequencing	Following Bussarawit & Cedhagen (2010)	Number of stations	Number sequenced
Magallana belcheri	*Crassostrea belcheri*	Market	3
Magallana bilineata	*Crassostrea* sp.	4	9
Saccostrea B	*S. cuccullata*; *S. forskahlii*; *S. echinata*; *Striostrea* sp.	10	29
Saccostrea F	*S. cuccullata*; *S. forskahlii*; *Striostrea* sp.	7	15
Saccostrea spathulata	*Ostrea* sp.	1	7
Saccostrea scyphophilla	*S. cuccullata*	1	4

Remarks. Published Gulf of Thailand records as *Saccostrea echinata* (Quoy & Gaimard, 1835): Aungtonya et al. (1999); Yoosukh & Duangdee (1999); Yoosukh (2000); Nabhitabhata (2009). Note: Bussarawit & Cedhagen (2010) considered Nielsen's (1976) identification of *Saccostrea cuccullata* as a misidentification of *Saccostrea echinata*. WoRMS (MolluscaBase eds., 2024) considers *S. echinata* to be a valid species, but the DNA sequences identified as *S. echinata* from the upper Gulf of Thailand were *Saccostrea* B. The 16S Bayesian inference tree of Asian *Saccostrea* (Fig. 3) suggests *Saccostrea* B is paraphyletic, with more than one species taxon present. More investigation of this possibility is required, however this is outside the scope of the present paper.

***Saccostrea* F**
(Figs. 5D–F, 6C, D)

Habitat. Hanging ropes, rocky shores and pier.

Material examined. Site 1, Sriracha; Site 3, Ta Kuan Beach; Site 6, mouth of Kungkraben Bay; Site 7, south Kungkraben Bay; Site 9, Pattaya; Site 10, Klongwan Pier; Site 13, Kao Ta Kiep. Identified in the field as *Saccostrea cuccullata*, *S. forskahlii*, and *Striostrea* sp. (Table 2). *Saccostrea* F was also identified from the aquaculture farms in Chonburi.

Published Gulf of Thailand records. None.

Geographic range. Taiwan and Singapore (Lam & Morton, 2006), Japan (Sekino & Yamashita, 2016), and Queensland (McDougall et al., 2024).

Remarks. Published Gulf of Thailand records as *Saccostrea forskahlii* (Bussarawit et al., 2006), specimen collected from Ang Sila Chonburi oyster farm.

***Saccostrea spathulata* (Lamarck, 1819)**
(Fig. 5G–I)

Habitat. Rocky shore.

Material examined. Site 2, Samaesan. Identified in the field as *Ostrea* sp. (Table 2).

Published Gulf of Thailand records. None.

Geographic range. Uncertain, sequenced records from Queensland, Western Australia, and Japan (McDougall et al., 2024).

Remarks. This is the species previously referred to as *Saccostrea* J. Sekino & Yamashita (2016), McDougall et al. (2024), and Richardson et al. (2024) all presented evidence to support their conclusion *Saccostrea* J is actually *S. spathulata*.

***Saccostrea scyphophilla* (Péron & Lesueur, 1807)**
(Fig. 4G–I)

Habitat. Rocky shore.

Material examined. Site 2, Samaesan. Identified in the field as *Saccostrea cuccullata* (Table 2).

Published Gulf of Thailand records. Reported as *Saccostrea mordax* (Gould, 1850) by Kurozumi et al. (1989) and Yoosukh (2000).

Geographic range. Australia (Western Australia to New South Wales), Japan, China, and Taiwan (Lam & Morton, 2006). Sekino & Yamashita (2013) showed a *S. cucullata* seq (AY038076) collected from Thailand was actually *S. mordax*, but *S. mordax* is considered to be a synonym of *S. scyphophilla* (MolluscaBase eds., 2024).

Remarks. There are numerous literature references of *S. mordax* on the more open Thai coastline on the Andaman Sea, but we could only find records in the Gulf of Thailand by Kurozumi et al. (1989) and Yoosukh (2000). We detected the species only on the rocky shore at Samaesan. *Saccostrea mordax* was originally described from Fiji. While there are GenBank sequences available for the species, there are none from the type locality. Huber (2010) discusses the taxonomic history of the species in detail. *Saccostrea scyphophilla* was described by Péron & Lesueur (1807) from Shark Bay, Western Australia, and Huber (2010) considers the species to be the same, with *S. scyphophilla* having priority. Our DNA sequences of specimens collected in Samaesan (Fig. 3) match those of Snow et al. (2023) and Wells et al. (2024), so we consider the Thai species to be *S. scyphophilla*.

Published *Saccostrea* records in the Gulf of Thailand rejected. There have been numerous reports of *S. cucullata* (Born, 1778) in the Gulf of Thailand, but unfortunately with no DNA sequences presented, it is not clear what species were actually reported. Published Gulf of Thailand records: *Ostrea cucullata* Born, 1778 reported by: Lynge, 1909. *Saccostrea cucullata* (Born, 1778) reported by: Amornjaruchit (1988); Nateewathana (1995); Sanpanich (1998, 2011); Aungtonya et al. (1999); Yoosukh & Duangdee (1999); Klinbunga et al. (2000, 2001, 2002, 2003, 2005); Yoosukh (2000); Swennen et al. (2001); Robba et al. (2002); van Gemert (2003); Bussarawit & Simonsen (2006b); Printrakoon et al. (2008); Nabhitabhata (2009); Bussarawit & Cedhagen (2010); Samakraman et al. (2010); Negri et al. (2014).

Saccostrea commercialis (Iredale & Roughley, 1933) reported by Trivej & Kesjinda (2018) is actually *S. glomerata* (Gould, 1850), but this is a misidentification.

Saccostrea forskahlii (Gmelin, 1791). Published Gulf of Thailand records as *Saccostrea forskahli*: Aungtonya et al. (1999); Klinbunga et al. (2000, 2001, 2005); Bussarawit et al. (2006); Bussawarit & Simonsen (2006b); Kasetsart University (2006); ONEP (2007); Nabhitabhata (2009); Bussarawit & Cedhagen (2010); Sanpanich (2011). As *S. forskahlii*: Yoosukh & Duangdee (1999). Note: Huber (2010) believes the *S. forskahlii* reported by Yoosukh & Duangdee (1999) is actually the Melanesian *S. circumsuta* (Gould, 1850). WoRMS considers *S. forskahlii* to be a synonym of *S. cucullata* (MolluscaBase eds., 2024), but it is not clear to which lineage *S. forskahlii* belongs. There are only two 16S sequences submitted to GenBank under the name *S. circumsuta*. One matches Lam & Morton (2006) lineage D and the other lineage C.

Striostrea mytiloides (Lamarck, 1819) was reported in the Gulf of Thailand by Yoosukh & Duangdee (1999) and Klinbunga et al. (2000, 2001, 2005), and *Striostrea* (*Parastriostrea*) *mytiloides* (Lamarck, 1819) by Kurozumi et al. (1989). Huber (2010) and WoRMS (MolluscaBase eds., 2024) recorded three other species of *Striostrea* Vialov, 1936: *S. denticulata* (Born, 1778) from West Africa; *S. margaritacea* (Lamarck, 1819) from South Africa and the Western Indian Ocean; and *S. prismatica* (Gray, 1825) from the Panamic Province. Huber (2010) believed *Ostrea rufa* Lamarck, 1819 from the Panamic Province may be a valid *Striostrea*, but WoRMS classifies it as *S. prismatica* (MolluscaBase eds., 2024). The Japanese *Ostrea circumpicta* Pilsbry, 1904 was included in *Striostrea* by Huber (2010) but was retained in *Ostrea* by WoRMS (MolluscaBase eds., 2024). Regardless of the final classification of these two species, the genus *Striostrea* has not been recorded from the Gulf of Thailand. *Ostrea mytiloides* Lamarck, 1819 is accepted as *Saccostrea echinata* (Quoy & Gaimard, 1835) by WoRMS (MolluscaBase eds., 2024), but there is no record of the DNA lineage of this species.

DISCUSSION

The two *Magallana* species, *M. bilineata* and *M. belcheri*, were correctly identified in the field, albeit with the earlier generic name *Crassostrea*. *Magallana bilineata* was recorded from nine sequences in the field and 16 in the markets. Field identifications of other taxa using Bussarawit & Cedhagen (2010) were inconsistent. *Saccostrea* B was identified in the field with four separate names: *S. cucullata*, *S. forskahlii*, *S. echinata*, and *Striostrea* sp. *Saccostrea* F was field identified variously as *S. cucullata*, *S. forskahlii*, and *Striostrea* sp. Both *Saccostrea* B and F were identified with more than one name on a single shoreline. *Saccostrea spathulata* and *S. scyphophilla* were found only at a single station and each was identified in the field by a single name, *Ostrea* sp. and *Saccostrea cucullata* respectively. *Saccostrea* B was the most widespread species, occurring at 10 of the 11 stations where specimens were collected, of which 29 were sequenced. *Saccostrea* F was recorded from 15 sequences in the field and 17 in the markets. *Magallana bilineata* and *Saccostrea* F occurred at all four of the markets surveyed.

There are numerous published references on the occurrence of *Saccostrea* species in the Gulf of Thailand. Unfortunately, there is no voucher material for most of these studies. Where vouchers are available, they are likely to be dry material or preserved in formalin. Visootiviseth et al. (1998) described the difficulty in assessing Thai *Saccostrea* species, distinguishing three species using allozyme and morphometric techniques. Klinbunga et al. (2005) also recognised three species of *Saccostrea*, two of which occurred in the Gulf of Thailand. However, neither of these studies can be reconciled with our DNA sequences as they used different molecular techniques. The present paper reports on the upper Gulf of Thailand; further work is required to extend the results into the lower Gulf of Thailand and the Andaman coast.

Similarly, it is difficult to compare the number of species of *Saccostrea* in the upper Gulf of Thailand with other geographic areas. While numerous studies have recorded *Saccostrea* species, the lack of genetic information means the number of species reported may be different from the actual number of species in a locality. McDougall et al. (2020, 2024) found eight *Saccostrea* on a lengthy part of the Queensland coastline. Three species occur in the Kimberley of Western Australia, but only two in the Pilbara (Snow et al., 2023; Wells et al., 2024).

Oysters from aquaculture farms in Chonburi were a mixture of *M. bilineata* and *Saccostrea* F. The presence of *M. bilineata* in the aquaculture farms was to be expected, but *Saccostrea* F was unexpected as *Saccostrea* B was more widely distributed in the area and more individuals were present in the samples sequenced. Bussarawit et al. (2006) had *S. forskahli* listed from Chonburi, which turned out to be Lineage F. While important, oyster aquaculture in the upper Gulf of Thailand is on a small scale compared to further southeast at the mouth of the Welu River on the border between Trat and Chanthaburi provinces. The key commercial species were listed as *Saccostrea commercialis*, *Crassostrea lugubris*, and

C. belcheri by Trivej & Kesjinda (2018). The taxonomy of *C. lugubris* and *C. belcheri* can be updated to *Magallana bilineata* and *M. belcheri* respectively. The *Saccostrea* is not *S. commercialis*, as this is actually the Australian temperate species *S. glomerata* (Snow et al., 2023).

The Pacific oyster *M. gigas* has been recorded on numerous occasions in the Gulf of Thailand, but these records are based on outdated concepts of oyster systematics, particularly Harry (1985). Instead, two species of *Magallana*, *M. belcheri* and *M. bilineata*, were found in the upper Gulf of Thailand. The same finding was made in a recent study of the genus in Singapore (Tan et al., 2024). Harry (1985) recognised a single species of *Crassostrea* (now *Magallana*) *gigas* in the Indo-Pacific that occurred from Pakistan to Korea and Japan, and in the Philippines, Borneo, and Sumatra. *Magallana gigas* dominates the total annual world aquaculture production of about six million tonnes (Botta et al., 2020), but this statement is based on the opinion of Harry (1985) that there is one species of *Magallana* in the Indo-Pacific. WoRMS (MolluscaBase eds., 2024) recognised 13 species of *Magallana*, five of which were described subsequent to Harry (1985). It is likely that future DNA studies will show that the aquaculture production of the genus is more widespread than just *M. gigas*.

The introduction of oysters into new parts of the world oceans, either deliberately through aquaculture or accidentally via vessels, poses a number of threats. Species may escape from the aquaculture farms and become invasive as has happened with *M. gigas* in south-eastern Australia (NIMPIS, 2022a). Other organisms, such as oyster drills, boring polychaetes, sponges, and pea crabs can be attached to or in oyster shells, or in the mantle cavity (Haupt et al., 2010). Ruesink et al. (2005) estimated that 46% of marine species introductions in northern Europe and 20% in Australia were likely to have been introduced through oyster aquaculture. Another potential impact is the introduction of diseases with introduced oysters, such as Pacific Oyster Mortality Syndrome, which can cause significant mortality in *M. gigas* (Petton et al., 2021).

The absence of *M. gigas* in Thailand demonstrated here and in Singapore (Tan et al., 2024) is important as *M. gigas* is a known invasive marine species (IMS). For example, it is one of three oysters listed by DPIRD (2016) as being of concern to Western Australia. The other two are *M. ariakensis* (Fujita in Wakita, 1929) and *Crassostrea virginica*. Because of its wide reported distribution in Southeast Asia and known invasive characteristics, *M. gigas* was the primary concern. There is direct vessel traffic between the largest port in Thailand, Laem Chabang in the study area and northwestern Australia. The absence of *M. gigas* from the upper Gulf of Thailand is thus reassuring for Australian regulators.

Two other *Magallana* (*M. bilineata* and *M. ariakensis*) have recently been recorded in Queensland and are potential IMS threats to Australia (Willan et al., 2021; NIMPIS, 2022b; Biosec Qld, 2024). *Magallana bilineata* is also a known vector for oyster pathogens (Suja et al., 2020). Thus, while there is no risk of introducing the high-risk *M. gigas* to Australia from the upper Gulf of Thailand, there remains a lower risk of introductions from *M. bilineata* and *M. belcheri*.

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Appendix 1. List of 16S sequences retrieved from GenBank and utilised in the Bayesian Inference analysis, in addition to those provided in Table 1 (main text).

Species	GenBank accession number	Location	References
Ostrea edulis	JF274008	France	Danic-Tchaleu et al. (2011)
Magallana bilineata	MT985154	India	N/A
	MT579758	Australia: Cairns	Willan et al. (2021)
	AB972008	Japan: Okinawa, Nago, Haneji-naikai	Sekino et al. (20150
Magallana belcheri	KX961675	Myanmar	Li et al. (2017)
	MH051332	Vietnam	Gastineau et al. (2018)
	AY160758	China: Hong Kong	Lam & Morton (2004)
Magallana gigas	MZ400416	Australia: Port Adelaide, South Australia	N/A
	KJ855245	China: Haihua, Weifang, Shandong	Ren et al. (2016)
	KJ855241	Japan: Komaru	Ren et al. (2016)
Magallana dianbaiensis	LC120776	Japan: Wakayama, Shirahama, Tonda-River	N/A
	LC120775	Japan: Wakayama, Tanabe, Aidzu-River	N/A
	AB971988	Japan: Ehime, Minami-uwa, Misho Bay	Sekino et al. (2015)
Magallana hongkongensis	EU266073	China	Yu et al. (2008)
	MZ337404	China: Sanmen Bay, East China Sea	Lui et al. (2022)
	AY632549	China: Beihai	Wang et al. (2004b)
Saccostrea lineage A	AY247371	Australia: Carnarvon, Western Australia	Lam & Morton (2006)
	MN153602	Australia: Dampier, Western Australia	Snow et al. (2023)
	MN153698	Australia: Shark Bay, Western Australia	Snow et al. (2023)
	MT124270	Australia: Western Australia	Snow et al. (2023)
Saccostrea lineage B	MT124282	Australia: Kimberley, Western Australia	Snow et al. (2023)
	OR340024	Australia: Queensland	McDougall et al. (2024)
	AY247336	China: Cape D'Aguilar, Hong Kong	Lam & Morton (2006)
	AY247392	China: Sanya	Lam & Morton (2006)
Saccostrea lineage C	AY247380	Japan: Okinawa	Lam & Morton (2006)
	LC111198	Japan: Kagoshima, Amami-Oshima Island	Sekino & Yamashita (2016)
	LC111156	Japan: Kagoshima, Amami-Oshima Island	Sekino & Yamashita (2016)
Saccostrea lineage D	AY247321	Taiwan: Shiman	Lam & Morton (2006)
	AY247391	China: Sanya	Lam & Morton (2006)
Saccostrea lineage E	AY247328	Australia: Darwin Harbour, Northern Territory	Lam & Morton (2006)
	AY247387	Taiwan: Shiman	Lam & Morton (2006)
	LC268852	Japan: Kochi	N/A
Saccostrea lineage F	AY247384	Taiwan: Shiman	Lam & Morton (2006)
	LC111254	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	LC111219	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
Saccostrea lineage G	AY247385	Taiwan: Shiman	Lam & Morton (2006)
	LC111202	Japan: Kagoshima, Amami-Oshima Island	Sekino & Yamashita (2016)
	LC155011	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	OR340012	Australia: Percy Islands	McDougall et al. (2024)
Saccostrea lineage H	LC111262	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	LC155015	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
Saccostrea lineage I	LC111211	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	LC111214	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	LC111215	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	OR340007	Australia: Orpheus Island	McDougall et al. (2024)

Species	**GenBank accession number**	**Location**	**References**
Saccostrea lineage J	LC111222	Japan: Okinawa, Iriomote Island, Yaeyama	Sekino & Yamashita (2016)
	LC111260	Japan: Okinawa, Iriomote Islnd, Yaeyama	Sekino & Yamashita (2016)
	OR340003	Australia: Orpheus Island	McDougall et al. (2024)
	MN153593	Australia: Cone Bay, Kimberley, Western Australia	Snow et al. (2023)
Saccostrea kegaki	AY247317	Japan: Morozaki	Lam & Morton (2006)
	LC111090	Japan: Kagoshima, Kakeroma Island	Sekino & Yamashita (2016)
Saccostrea glomerata	AY247341	Australia: Albany, Western Australia	Lam & Morton (2006)
	AY247288	Australia: La Parouse, Sydney, New South Wales	Lam & Morton (2006)
	MN153625	Australia: Oyster Harbour, Albany, Western Australia	Snow et al. (2023)
	OR340034	Australia: Round Island Urangan	McDougall et al. (2024)
Saccostrea scyphophilla	AY247363	Australia: Quobba, Western Australia	Lam & Morton (2006)
	MN153617	Australia: South of Onslow, Western Australia	Snow et al. (2023)
	MN450281	Australia: Kalbarri, Western Australia	Snow et al. (2023)
	OR339998	Australia: Minjerribah, Queensland	McDougall et al. (2024)
	AY247339	Australia: Cooee Bay, Rockhampton, Queensland	Lam & Morton (2006)
	MN450285	Australia: Kalbarri, Western Australia	Snow et al. (2023)
Saccostrea mordoides	OR339997	Australia: Hook Island	McDougall et al. (2024)
	OR339996	Australia: Orpheus Island	McDougall et al. (2024)
	AB898224	Japan: Okinawa, Ishigaki Island	Hamaguchi et al. (2014)
	AB898223	Japan: Okinawa, Ishigaki Island	Hamaguchi et al. (2014)