



Identity of the enigmatic oyster *Saccostrea cucullata* (Bivalvia: Ostreidae)

Siong Kiat Tan¹, Fred E. Wells^{2,3}, Koh Siang Tan⁴, Sherralee S. Lukehurst², Melissa Morgan⁵ and Seema Fotedar⁶

¹Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore;

²School of Molecular and Life Sciences, Curtin University, PO Box U1987, Bentley, WA, Australia;

³Negaunee Integrative Research Center, Field Museum of Natural History, Lake Shore Drive, Chicago, IL, USA;

⁴St John's Island National Marine Laboratory, Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore;

⁵Conservation and Fisheries Directorate, Ascension Island Government, Airhead Road, Georgetown, Ascension Island; and

⁶Diagnostic and Laboratory Services, Sustainability and Biosecurity, Department of Primary Industries and Regional Development, Western Australian Government, 3 Baron-Hay Court, South Perth, WA, Australia

Correspondence: F. Wells; e-mail: fred.wells@curtin.edu.au

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ABSTRACT

Oysters (family Ostreidae) are a key group in shallow water tropical and warm temperate communities throughout the world. Many species are ecosystem engineers of considerable economic and environmental importance. The subfamily Saccostreinae currently contains the single genus *Saccostrea*. Species taxonomy is poorly understood, with numerous species having been described. As many were thought to be synonyms, *Saccostrea cucullata* was generally accepted to be a widespread species in the Indo-West Pacific and South Atlantic Ocean. Recent DNA studies have however demonstrated the “species” is actually a complex of different genetic lineages. We provide the first DNA sequences of *S. cucullata* from the type locality of Ascension Island in the central South Atlantic Ocean and demonstrate that it is distinct from all other published lineages. The present paper presents useful data for developing a better understanding of this complex genus.

INTRODUCTION

Oysters (family Ostreidae) are a key sessile group in tropical and warm temperate communities throughout the world. Many species are ecosystem engineers, forming dense populations on intertidal shorelines and shallow subtidal environments. Oyster reefs provide several ecosystem services. Their three-dimensional structure is a nursery habitat for economically valuable fish and crabs (Coen *et al.*, 2007). They are important in nutrient recycling (Newell, 2004) and reducing eutrophication (Kemp *et al.*, 2005; Pagenkopp Lohan *et al.*, 2015). A number of oysters are important aquaculture species that are easily cultured, fast growing, feed naturally and are commercially valuable. There is a global annual aquaculture production of about six million tonnes (Botta *et al.*, 2020).

Unfortunately, the attributes that make oysters suitable for aquaculture can also cause them to be detrimental to the marine environment. There is a growing concern over the negative effects of invasive species globally (e.g. Katsanevakis *et al.*, 2014; Crowe & Frid, 2015; McDonald *et al.*, 2020; Salimi *et al.*, 2021) and several oyster species are considered to be invasive marine species (DPIRD, 2016; NIMPIS, 2022). The introduction of oysters into a new environment, whether deliberate or accidental, also risks introducing diseases and other species living on or in the oysters (Ruesink *et al.*, 2005; Petton *et al.*, 2021).

With their ecological and commercial importance, considerable research has been undertaken on oyster systematics, but unfortu-

nately determining the identity of oyster species is incredibly difficult. Shell morphology is naturally variable and is often modified by available space or the presence of adjacent individuals (Wilk & Bieler, 2009). The ranges of many species overlap naturally or have been extended deliberately for aquaculture or inadvertently through other anthropogenic activities (Pagenkopp Lohan *et al.*, 2015). Huber (2010) stated that there are about 500 available names. Sowerby II (1871) figured over 80 species, but Harry (1985) recognized only 30 extant ostreids. Torigoe (2004) and Huber (2010) both considered Harry's 30 species to be an underestimate. Torigoe (2004) recognized 70 species. Huber (2010) included newly described species and increased this to 75. The World Register of Marine Species (WoRMS; MolluscaBase eds., 2024) recognizes 76 ostreid species.

Harry (1985) developed an ostreid supraspecific classification of four subfamilies that is incorporated into WoRMS (MolluscaBase eds., 2024). The Saccostreinae has the single genus *Saccostrea* with 13 recognized species. Huber (2010: 610) conceived *Saccostrea* as a homogenous grouping based on *Saccostrea cucullata* (Born, 1778), which is generally considered to have a broad distribution in West Africa and the Indo-Pacific (Gofas, Afonso & Brandão, 1985; Harry, 1985; Lam & Morton, 2004, 2006; Huber, 2010; Cosel & Gofas, 2019) though Huber (2010) restricted the species to West Africa and the western Indian Ocean. It is not worldwide as stated by Cernohorsky (1978). Using DNA data, Lam & Morton (2006) rec-

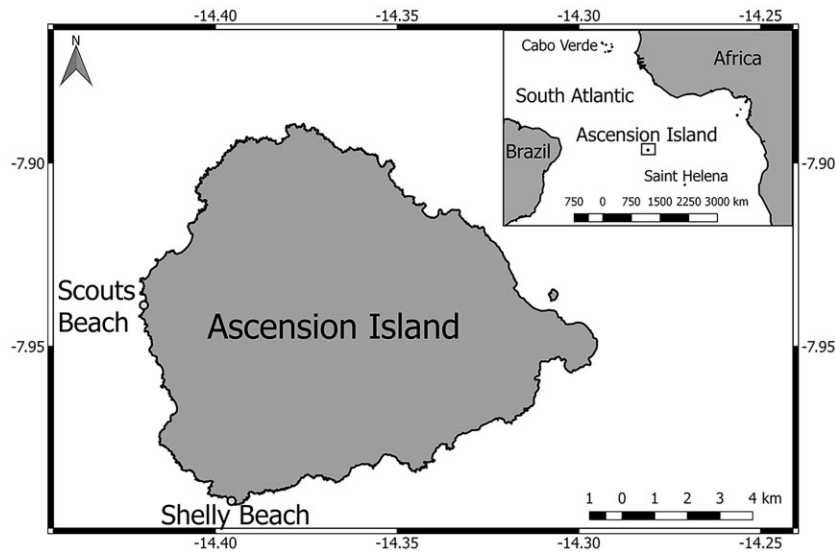


Figure 1. Map showing the location of Ascension Island in the South Atlantic Ocean and sampling sites on the island.

ognized *S. cucullata* as an Indo-Pacific ‘superspecies’ with seven lineages designated by letters (e.g. *S. cucullata*-A–G). Sekino & Yamashita (2016) found a further three distinct lineages H, I and J, and the present designation is simply *Saccostrea*-A, etc. (Snow *et al.*, 2023). The *S. mordax* oysters have been grouped into three lineages with two lineages (A and B; Lam and Morton, 2006), currently referred to as *S. scyphophilla* (F. Péron & Leseur, 1807) and lineage C (Sekino & Yamashita, 2013) now known as *S. mordoides* Z.-M. Cui *et al.*, 2021 (Cui *et al.*, 2021).

Thus, determining the “true” *S. cucullata* is essential in improving our scientific understanding of the genus *Saccostrea* and its species. We present below the first description of *S. cucullata* from the type locality of Ascension Island in the South Atlantic Ocean. Information on their shell morphology together with the DNA sequences of the species are provided as a first step towards determining the species relationships in the genus.

MATERIAL AND METHODS

Specimens were collected at Shelly Beach, Ascension Island (07°59.533’S, 014°23.734’W) on 9 November 2023 and at Scouts Beach, Ascension Island (07°56.327’S, 014°25.181’W) on 12 November 2023 (Figs 1, 2). Oysters were carefully harvested from rock beds using a sharp implement, with only intact and closed oysters being retained. The selected specimens were individually placed in sample bags on ice and transported to a sterile laboratory within 3 h. Upon arrival at the laboratory, each oyster was photographed and assigned a unique identification number before undergoing further processing. Using an oyster shucking tool, the oysters were opened and additional photographs taken. A section of the adductor muscle was then excised and placed into a small tube containing 95% molecular grade ethanol. Subsequently, the entire specimen was immersed in 95% ethanol for a minimum of 24 h. After the ethanol treatment, the specimens were carefully removed, wrapped in ethanol-soaked absorbent paper and vacuum-sealed in bags. To comply with air freight restrictions, the sealed bags were placed within a secondary sealed bag.

A small piece of absorbent cloth was inserted into each vial containing the adductor muscle samples and the vial drained and sealed. The oysters and vials containing the DNA samples were packed and hand carried to a laboratory in the UK, where they were shipped by air to Curtin University in Perth, Western Aus-

tralia with the necessary documentation. In Perth, the vials were removed, and the oysters were forwarded to the Lee Kong Chian Natural History Museum (LKCNHM) of the National University of Singapore, where they have been accessed into the mollusc section of the Zoological Reference Collection (ZRC) with accession numbers ZRC.MOL.29981–29990.

At Curtin, the vials containing the tissue samples were frozen until they could be analysed. The tissue from each vial was thawed and DNA extracted using DNeasy Blood and Tissue Kit (Qiagen Inc., USA) following the manufacturer’s instructions. PCR amplification of approximately 450 bp of the mitochondrial 16S ribosomal RNA (rRNA) region was done for each specimen, using primers 16Sar and 16Sbr (Simon *et al.*, 1994). PCR amplification of *c.* 650 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 a 25 µl volume containing 3 µl DNA (*c.* 20 ng), 1x Invitrogen Platinum Green Hot Start PCR master mix (containing 1.5 mM MgCl₂ and 0.2 mM of each dNTP), 0.5 mg/ml bovine serum albumin (Fisher Biotech, Australia) and 0.6 µM of each primer. PCR conditions consisted of an initial incubation at 95 °C for 3 min, followed by 35 cycles of 94 °C for 45 s, 52 °C for 90 s and 72 °C for 45 s, and a final extension step of 72 °C for 10 min.

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

Additional 16S rRNA and COX1 sequences for *Saccostrea cucullata* lineages were retrieved from GenBank and aligned with existing COX1 data from Australia using Geneious Prime 2022.1.1 software. Sequences that were not within the targeted region of the genes or were very short were removed. jModelTest v. 2.1.10 (Darriba *et al.*, 2012) was used to find the best evolutionary model of nucleotide substitution for the alignments. The 16S rRNA alignment was trimmed to 426 bp and we performed a Bayesian inference (BI) analysis using the MrBayes v. 3.2.6 (Huelsenbeck & Ronquist, 2001) plugin in Geneious Prime with the following param-

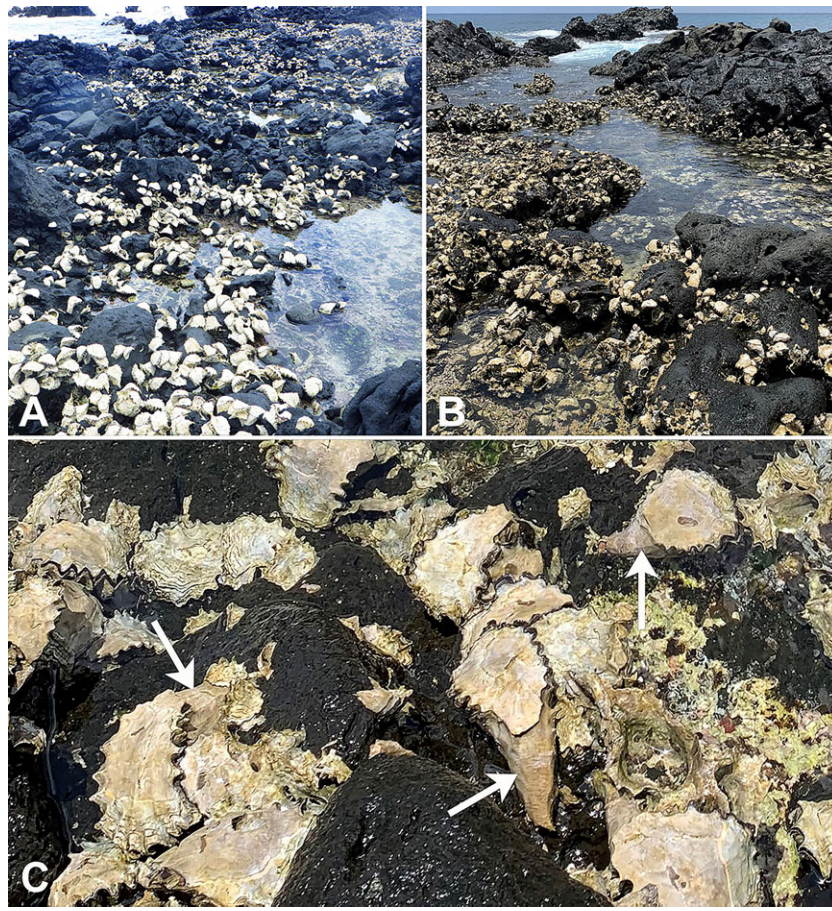


Figure 2. *Saccostrea cuccullata* in situ at Ascension Island. **A.** Shelly Beach. **B.** Scouts Beach. **C.** Detail of living individuals at Scouts Beach showing the elongate and tapered regions of the left valves (arrows) forming deep umbonal cavities within.

ters: HKY85 + I + G model with nucleotide sites partitioned for 1 million generations subsampling every 200 generations and a burn in of 100,000 generations. The COX1 alignment was trimmed to 561 bp and the BI analysis was performed with the following parameters: GTR + I + G model with nucleotide sites partitioned for 1 million generations subsampling every 200 generations and a burnin of 100,000 generations. For a subset of data, a 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 10%, posterior probability limit 0.5.

All maximum likelihood (ML) analyses were conducted in IQ-TREE v. 2.3.0 (Nguyen *et al.*, 2015) on the IQ-TREE web server (Trifinopoulos *et al.*, 2016). The software used ModelFinder (Kalyanamoorthy *et al.*, 2017) to automatically determine substitution models for each partition, with FreeRate heterogeneity. Ultra-fast bootstrap analyses (UFBoot, Hoang *et al.*, 2018) were conducted with 10,000 bootstrap replicates, as well as SH-aLRT branch tests with 10,000 replicates. All resulting phylogenetic trees were visualized in FigTree v. 1.4.4 (Rambaut *et al.*, 2018) with tree annotations added in Adobe Illustrator. Pairwise Kimura 2-parameter (K2P) distances (Kimura, 1980) between specimens was calculated using MEGA11 (Tamura, Stecher & Kumar, 2021).

Abbreviations: LV, left valve; RV, right valve; SL, shell length (maximum distance between ventral edge and hinge); MHNG, Muséum d'Histoire Naturelle de Genève, Switzerland; NHMW, Naturhistorisches Museum Wien, Austria; ZRC, Zoological Reference Collection, LKCNHM, National University of Singapore.

RESULTS

Molecular analyses

We obtained 10 16S rRNA sequences (corresponding to GenBank numbers PP842649–PP842658; see [Supplementary Material Table S1](#)) from the adductor muscles of 10 *Saccostrea* individuals (AS01–AS10) collected from Shelly Beach and Scouts Beach in Ascension Island. These were analysed together with a total of 55 identified 16S rRNA *Saccostrea* sequences from GenBank (see [Supplementary Material Table S2](#)). All 10 known *Saccostrea* lineages (A through to J) were represented, in addition to *S. glomerata* (Gould, 1850); *S. kegaki* Torigoe & Inaka, 1850; *S. mordoides*; *S. palmula* (P. P. Carpenter, 1857); and *S. scyphophilla*. The resulting ML and Bayesian phylogenetic trees (Figs 3, 4) using *Magallana* and *Ostrea* as outgroup taxa showed that the Ascension Island *Saccostrea* was genetically distinct from all other known lineages and species of *Saccostrea*. The K2P pairwise genetic distances ([Supplementary Material Table S3](#)) between Ascension *Saccostrea* (AS) and other *Saccostrea* lineages and species ranged between 0.057 and 0.113, in comparison to the within-group distances (0.003–0.025) and outgroup taxa (0.176–0.210). Both the ML and Bayesian trees suggested that AS was more closely related to the Indo-Pacific *Saccostrea* lineages I and J. They formed a clade (though with equivocal support) together with *S. mordoides* and *S. scyphophilla*. The eastern Pacific *S. palmula* was only distantly related to the AS clade, as were the recently discovered non-indigenous *Saccostrea* from the Caribbean and Brazil (KT970460; Fig. 3), which clustered with lineage F from the Indo-Pacific.

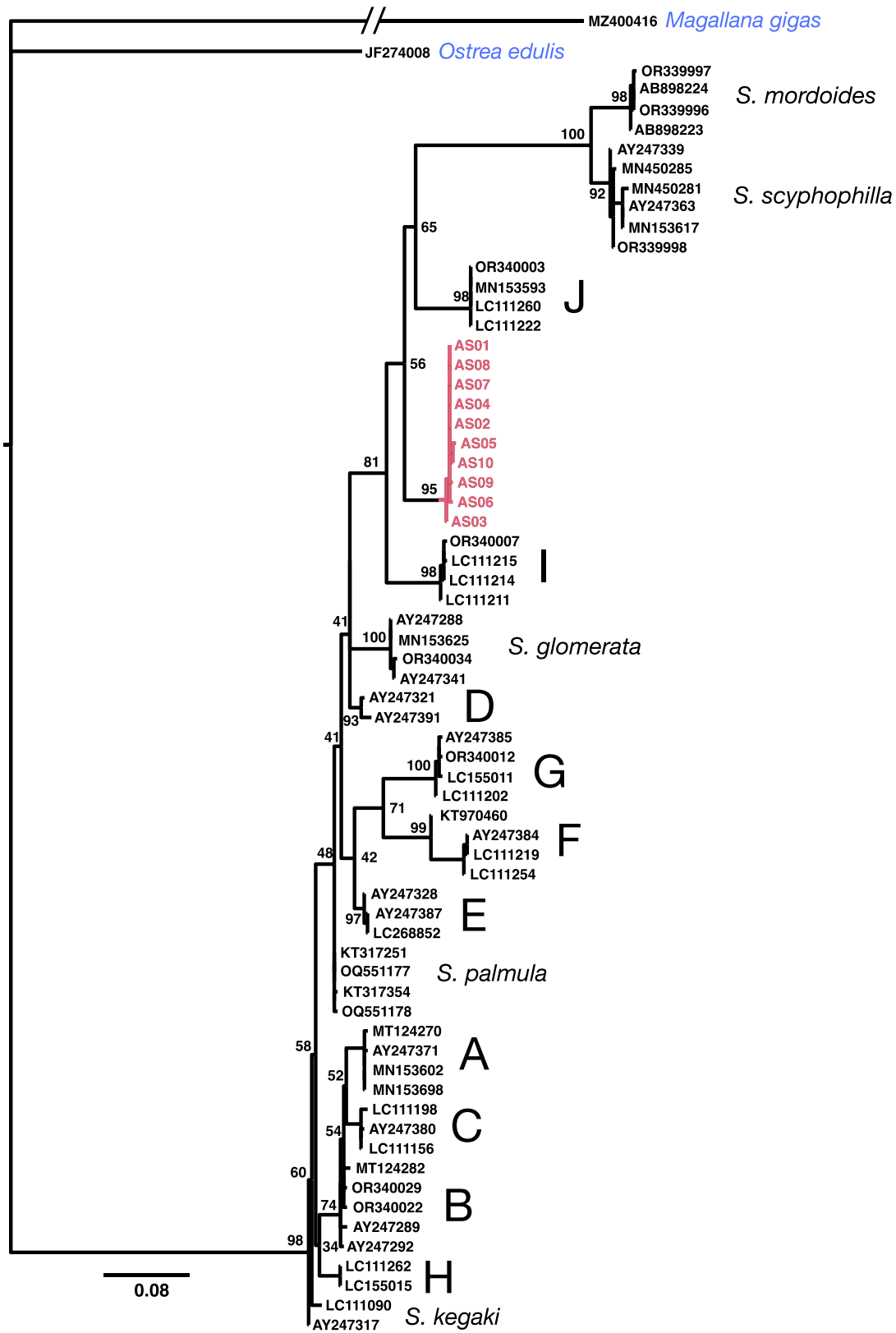


Figure 3. ML tree of *Saccostrea* species and lineages based on 16S rRNA data. Ascension *Saccostrea* are AS01–AS10. Clades corresponding to *Saccostrea* lineages are indicated in capital letters A–J. See [Supplementary Material Tables S1](#) and [S2](#) for locality data relating to GenBank sequences. Numbers at nodes indicate bootstrap support values.

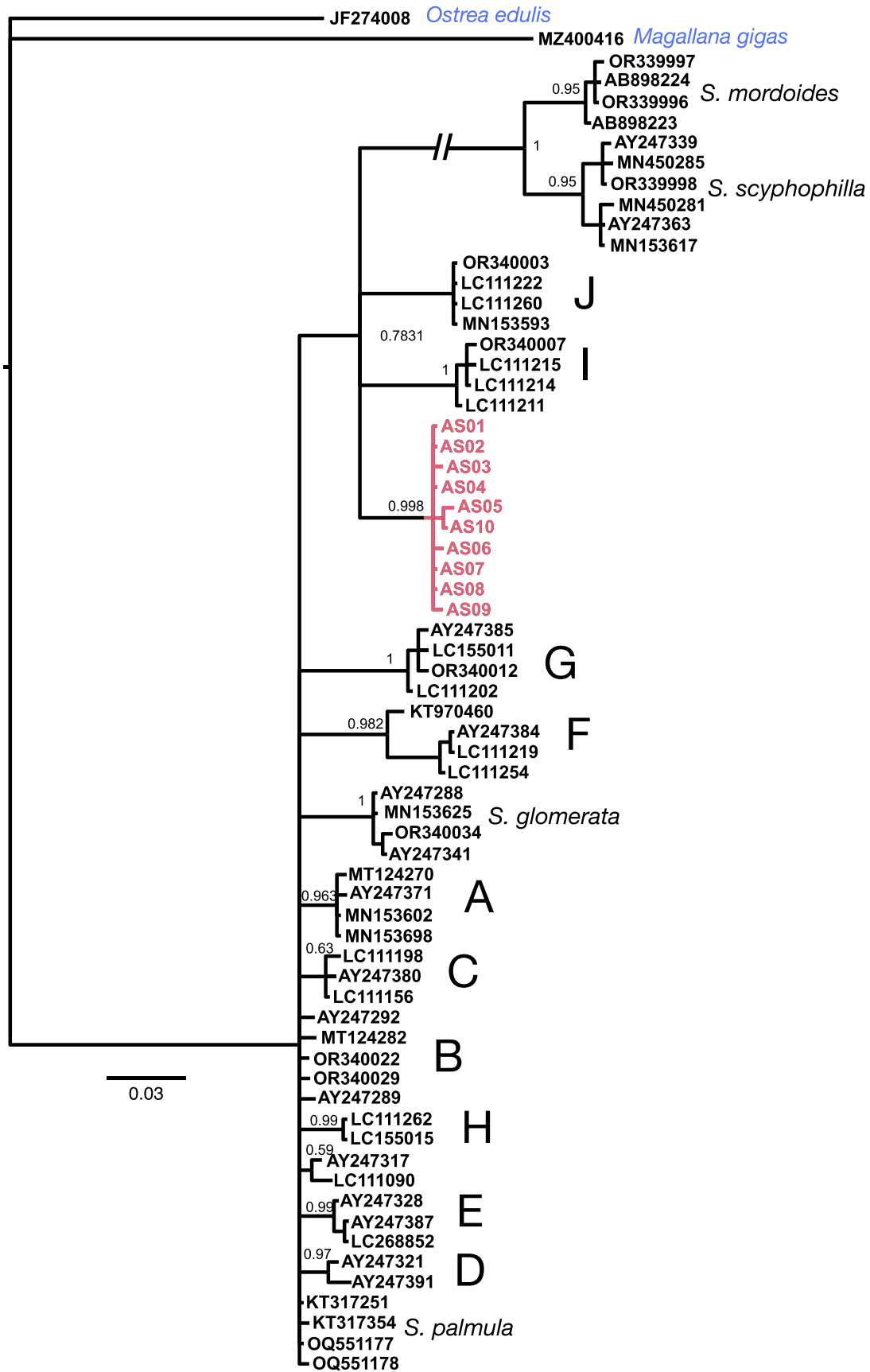


Figure 4. Bayesian tree of *Saccostrea* species and lineages based on 16S rRNA data. Ascension *Saccostrea* are AS01–AS10. Clades corresponding to *Saccostrea* lineages are indicated in capital letters A–J. See [Supplementary Material Tables S1](#) and [S2](#) for locality data relating to GenBank sequences. Numbers at nodes indicate Bayesian posterior probabilities.

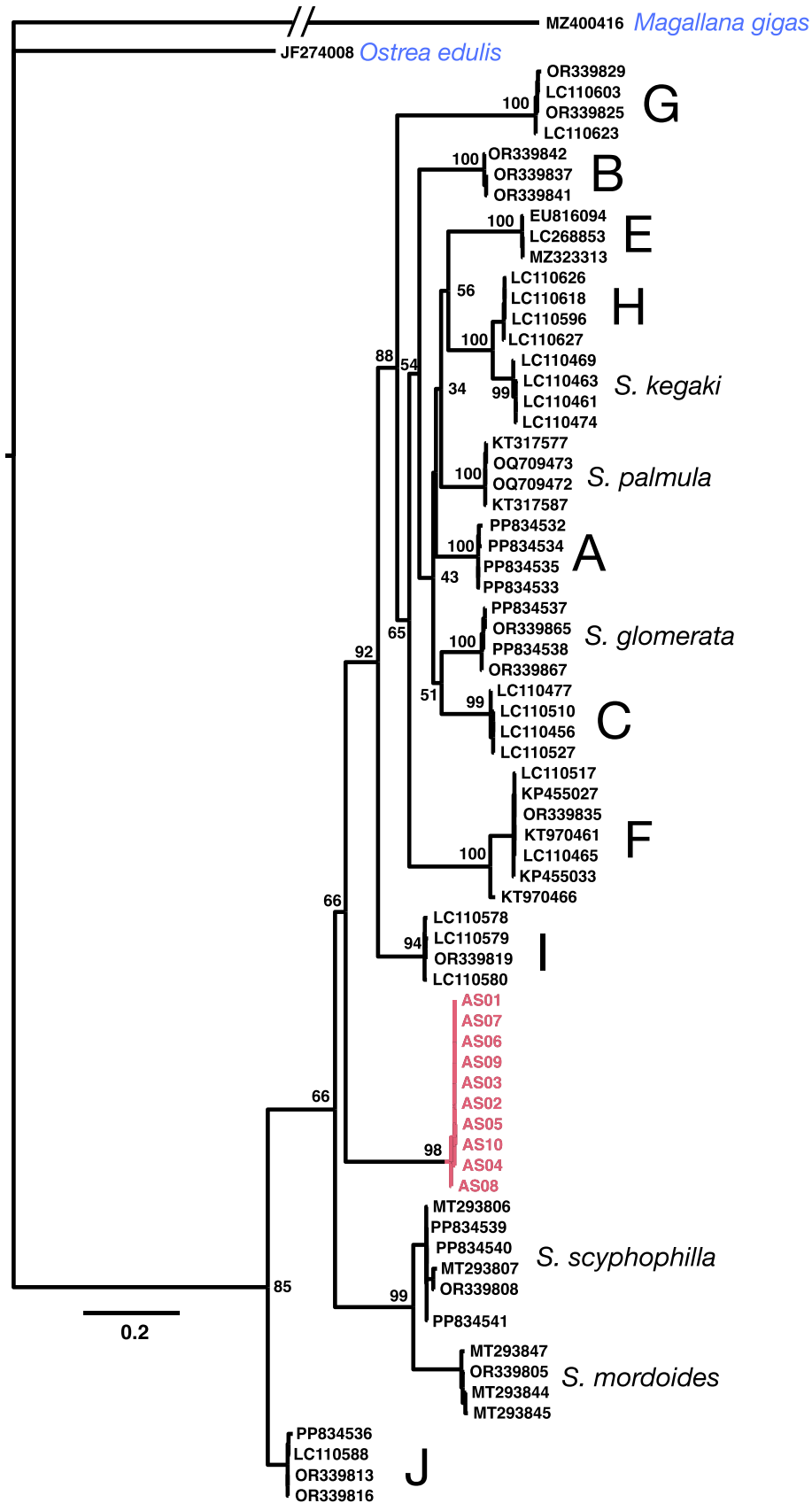


Figure 5. ML tree of *Saccostrea* species and lineages based on COX1 data. Ascension *Saccostrea* are AS01–AS10. Clades corresponding to known *Saccostrea* lineages are indicated in capital letters A–J. See [Supplementary Material Tables S1](#) and [S2](#) for locality data relating to GenBank sequences. Numbers at nodes indicate bootstrap support values.

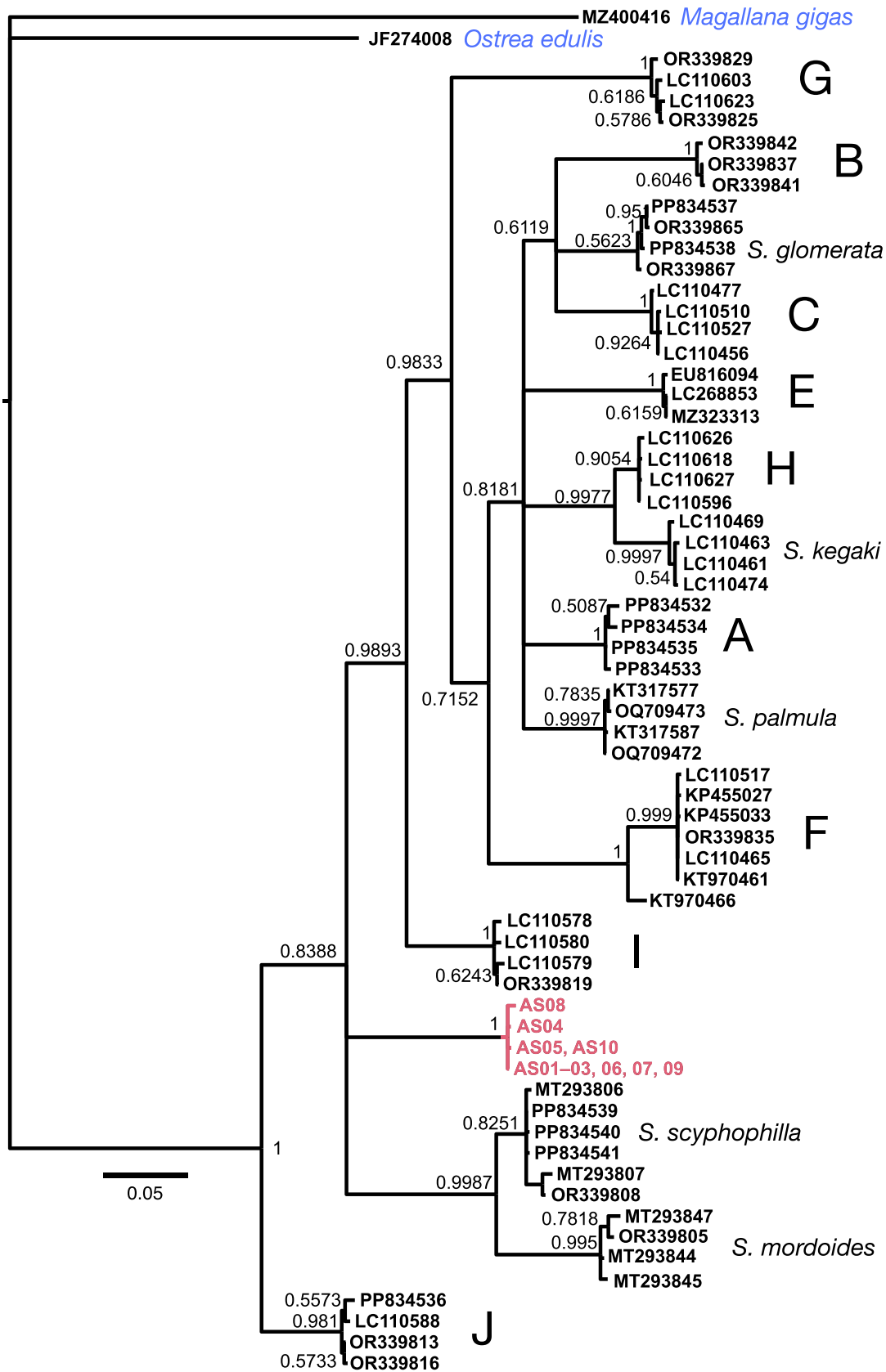


Figure 6. Bayesian tree of *Saccostrea* species and lineages based on COX1 data. Ascension *Saccostrea* are AS01–AS10. Clades corresponding to known *Saccostrea* lineages are indicated in capital letters A–J. See [Supplementary Material Tables S1](#) and [S2](#) for locality data relating to GenBank sequences. Numbers shown at nodes indicate Bayesian posterior probabilities.

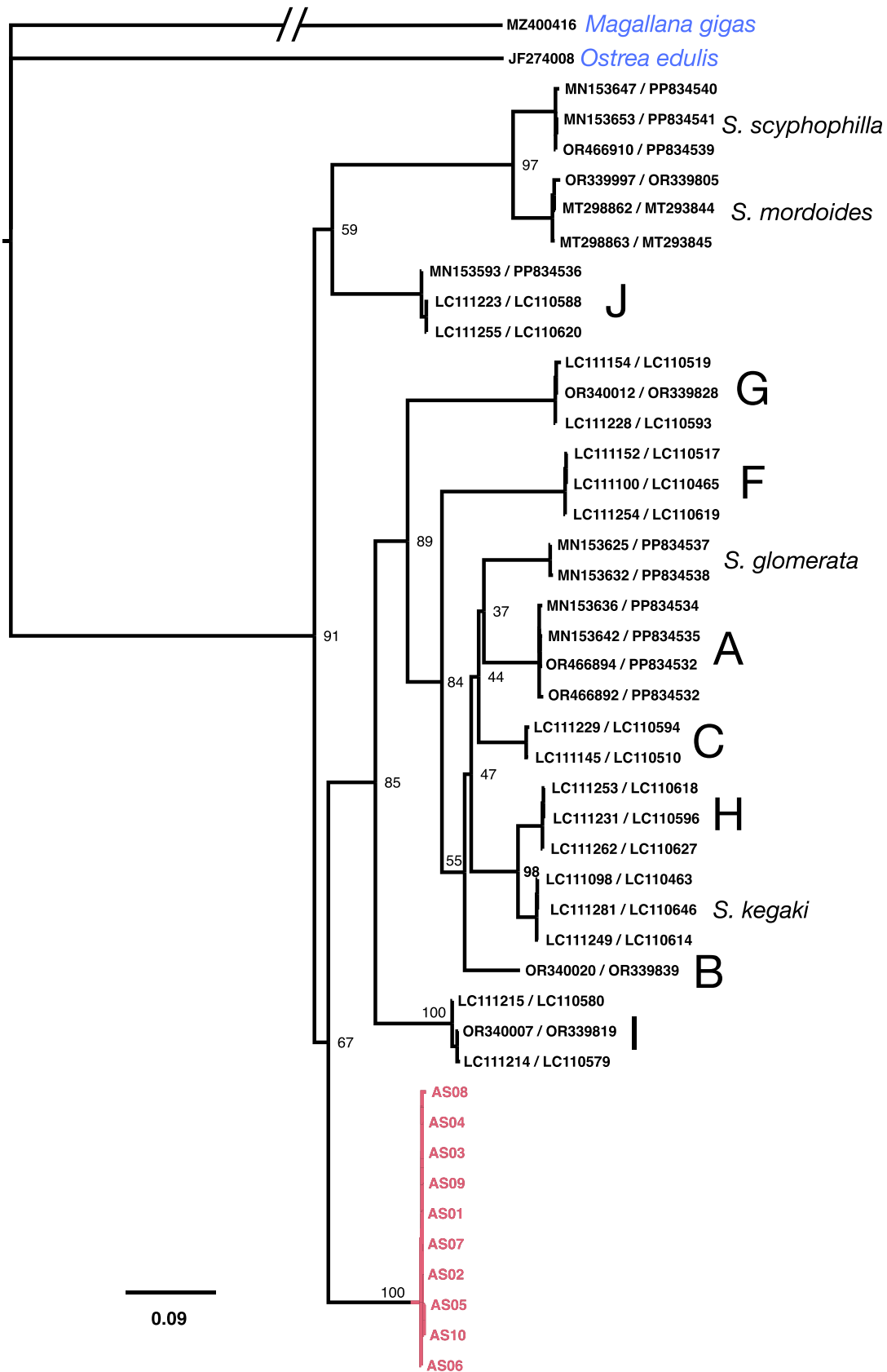


Figure 7. ML tree of *Saccostrea* species and lineages based on concatenated two-gene 16S rRNA + COX1 data (with *Magallana gigas* and *Ostrea edulis* as outgroups). Ascension *Saccostrea* are AS01–AS10. Clades corresponding to known *Saccostrea* lineages are indicated in capital letters A–J. See Supplementary Material Tables S1 and S2 for locality data relating to GenBank sequences. Numbers at nodes indicate bootstrap support values.

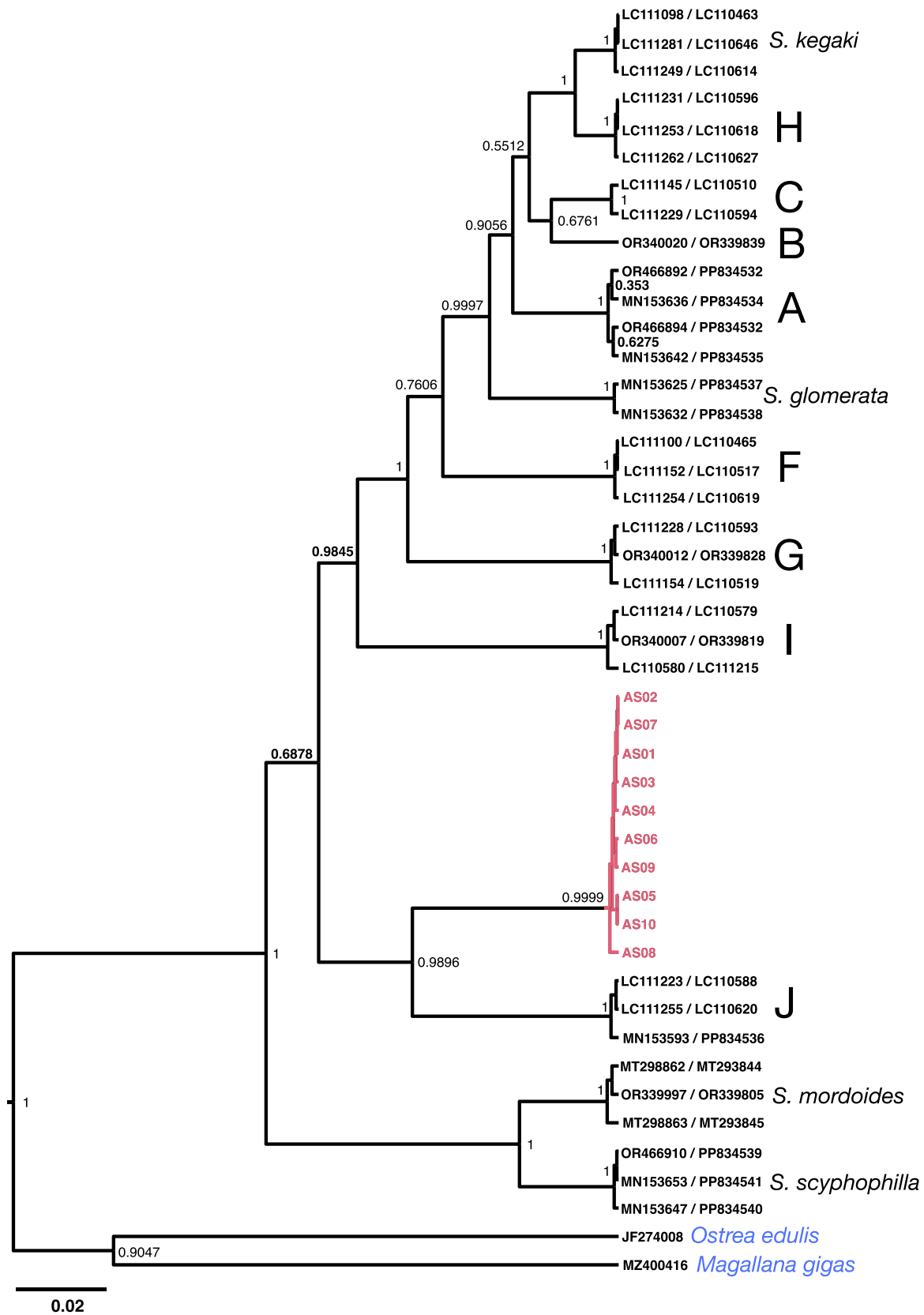


Figure 8. Bayesian inference tree of *Saccostrea* species and lineages based on concatenated two-gene 16S rRNA + COX1 data (with *Magallana gigas* and *Ostrea edulis* as outgroups). Ascension *Saccostrea* are AS01–AS10. Clades corresponding to known *Saccostrea* lineages are indicated in capital letters A–J. See [Supplementary Material Tables S1](#) and [S2](#) for locality data relating to GenBank sequences. Numbers at nodes indicate Bayesian posterior probability support values.

Ten COX1 sequences (corresponding to GenBank accession numbers PP834522–PP834531; see [Supplementary Material Table S1](#)) were also isolated from the same individuals (AS01–AS10) from Ascension Island. Another 59 COX1 *Saccostrea* sequences were selected from GenBank ([Supplementary Material Table S2](#)) representing nine *Saccostrea* lineages A–C and E–J (COX1 sequences from lineage D were not available in GenBank), together with *S. glomerata*, *S. kegaki*, *S. mordoides*, *S. palmula* and *S. scyphophilla*. ML and Bayesian trees ([Figs 5, 6](#)) using *Magallana* and *Ostrea* as outgroup taxa agreed with the results from the 16S rRNA dataset in that the AS clade was genetically distinct from other *Saccostrea* species and lineages. However, in the ML COX1 tree, the AS clade did not belong to the same clade as *Saccostrea* lineages I and J, *S. scyphophilla* and *S. mordoides*, while in the BI tree, the relationship of the AS lineage with other clades was unresolved. Nevertheless, it was clear that *S. palmula* and non-indigenous *Saccostrea* recently reported from the Caribbean and Brazil were distantly related to AS. The K2P pairwise genetic distances ([Supplementary Material Table S3](#)) between AS and other *Saccostrea* lineages and species were generally higher than those for 16S rRNA, ranging between 0.149 and 0.233; this was paralleled by the within-group distances (0.002–0.055) and outgroup taxa (0.256–0.307).

Both ML and BI trees based on the concatenated 16S rRNA + COX1 sequences ([Figs 7, 8](#)) also showed that AS formed a well-supported and distinct clade. In the ML tree, the AS clade was sister to a clade containing *Saccostrea* lineages A–C and lineages F–I, as well as *S. glomerata* and *S. kegaki*. However, in the Bayesian tree, the AS clade was sister to *Saccostrea* lineage J with reasonably good support. This clade in turn was sister to other *Saccostrea* lineages A–C and lineages F–I, together with *S. glomerata* and *S. kegaki*.

SYSTEMATIC DESCRIPTIONS

Family OSTREIDAE Rafinesque, 1815

Subfamily SACCOSTREINAE Salvi and Mariottini, 2016

Genus *Saccostrea* Dollfus and Dautzenberg, 1920

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

Saccostrea cucullata (Born, 1778)

([Figs 2–10, 12A, B, 13](#))

Ostrea cucullata Born, 1778: 100.

Ostrea cucullata Born, 1780: 114, pl. 6, [Figs 11, 12](#).

Note that while the species is often spelled as “*cucullata*”, the original Born (1778) spelling was “*cuccullata*” (Stenzel, 1971: N1134; Morris, 1985). The misspelling appears to have originated with Born himself as Born (1780) later refers to *Ostrea cucullata*.

Syntypes: NHMW MO14118 (figured in Born, 1780); NHMW MO14119 (single LV).

Type locality: Born (1778) did not provide a type locality, nor is one included on the syntype label. Born (1780) stated “Habitat in Indiis Davila; ad infulam Ascensionis Martini”, which we regard as a clarification of the type localities, that is, the East Indies and Ascension Island (see Discussion).

Synonymy: As would be expected for a species considered to be so abundant and widespread, many names have been synonymized with it. There are currently seven subjective synonyms of *S. cucullata* listed in WoRMS (MolluscaBase eds., 2024). Only *Ostrea cornucopiae* Gmelin, 1791 appears to be unequivocally synonymous after an assessment. Considering the confused taxonomy, however, a taxonomic review beyond the scope of this study will be required

to properly reassess the current statuses of the other associated species. Our comments on the seven objective synonyms are as follows:

- (1) *Ostrea purpurea* [Lightfoot], 1786: 53, 91, 139, 174, 177 (type localities: “New Holland” [Australia], China and “South Seas”): *Ostrea purpurea* is apparently a Solander manuscript name made available by [Lightfoot] (1786) (see also Dance, 1962) via indication to the figures in Born (1780: pl. 6, figs. 11, 12). Born’s figured syntype is therefore syntypic with the specimens listed in [Lightfoot] (1786). However, this implies that the type-series is heterogenous since the real *S. cucullata* does not occur in the Indo-Pacific (this study). The original Portland Museum specimens seen by [Lightfoot] are probably the species currently known as *S. scyphophilla* but confirmation is impossible because the present whereabouts of those specimens are unknown. In the interest of stability, the existing syntype (i.e. the figured syntype of *O. cucullata* [NHMW MO14118]) is here selected as the lectotype of *O. purpurea* [Lightfoot], 1786 to fix the identity of this species. This makes it a junior objective synonym of *O. cucullata*.
- (2) *Ostrea cornucopiae* Gmelin, 1791: 3336 (type locality: “Oceano indico et africano” [Indian Ocean and Africa]). There is little doubt that this is synonymous with *O. cucullata* Born, 1778, which was included under this species in Gmelin’s original description, validating Chemnitz’s unavailable *Ostrea cornucopiae*. The original illustrations in Chemnitz (1785: pl. 72, figs 679a–b) agree well with *S. cucullata sensu stricto* as currently defined.
- (3) *Ostrea forskahlii* Gmelin, 1791: 3336 (type locality: “mari rubro” [Red Sea]). Gmelin’s description is a validation of Chemnitz’s unavailable *Ostrea forskahlii* [sic]. The original illustrations in Chemnitz (1785: pl. 72, figs 671a–c), presumably different views of the valves of the same individual, show a deeply cupped left shell with a deep umbonal cavity and only slightly wavy shell margins on both valves. Chemnitz’s plate 72, figure 671c also suggests the presence of a large kidney-shaped adductor muscle scar, and the general form of the shell margins is more reminiscent of the non-*mordax* lineages. The images are decidedly not representative of the *Saccostrea cucullata sensu stricto*, thus this name should be removed from the synonymy of *O. cucullata*.
- (4) *Ostrea stellata* Gmelin, 1791: 3337 (type locality: “Guineam” [Guinea], West Africa). Whether this species group-name is synonymous with *O. cucullata* is debatable. The figures in Schröter (1786: pl. 9, figs 7a, b) referred to as a basis for the species by Gmelin show a shell with a distinctly larger lower valve with a somewhat leafy and expanded shell margin with distinct projections. It may not even be a *Saccostrea*, as currently understood, so further verification with West African material will be needed to clarify its taxonomic status.
- (5) *Ostrea gibbosa* Lamarck, 1819: 209 (type locality: not stated). The shell characteristics of the holotype (MHNG-MOLL-50836), such as the thin and generally smooth free shell margin and relatively large adductor muscle scar, are clearly dissimilar to *S. cucullata sensu stricto*, and should be removed from its synonymy.
- (6) *Ostrea turbinata* Lamarck, 1819: 212 (type locality: “l’Océan indien?” [Indian Ocean?]). The Lamarck syntype (MHNG-MOLL-50848) is a shell with sharp zigzagging shell margins and relatively large kidney-shaped adductor muscle scar. It is nothing like *S. cucullata* as currently defined, and *O. turbinata* should be excluded from its synonymy.
- (7) *Dioeciostrea subtropica* Orton, 1928: 321 (type locality: not stated). Orton (1928) proposed several new names as being more ‘useful’ for delineating oysters. Detailed descriptions were not provided by Orton, but he clearly considered *D. subtropica* to be the “*O. cucullata*” of authors. The broad definition of this *D. subtropica* with a world-wide distribution in the subtropical and tropical areas would include most, or all, of the known *Saccostrea* species.

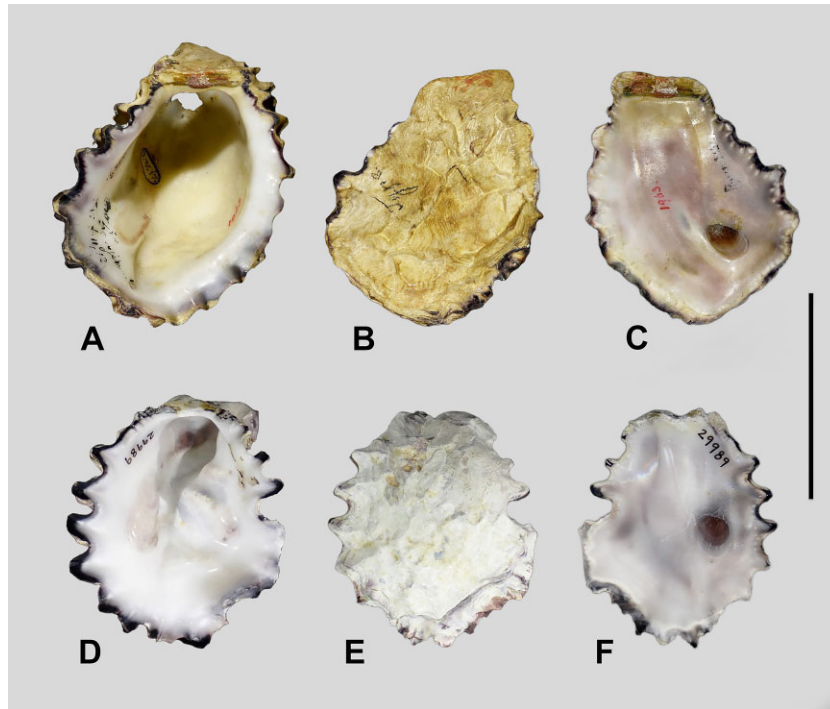


Figure 9. *Saccostrea cuccullata* (Born, 1778). **A–C.** Syntype of *Ostrea cuccullata* (NHMW MO14118) figured in Born (1780). **D–F.** A specimen from Ascension (ZRC.MOL.29989) for comparison. Scale bar = 5 cm.

Material examined: Shelly Beach, Ascension Island (07°59.533'S, 014°23.734'W), 9 November 2023: ZRC.MOL.29981, ZRC.MOL.29982, ZRC.MOL.29983, ZRC.MOL.29984, ZRC.MOL.29987, ZRC.MOL.29988 and ZRC.MOL.29989. Scouts Beach, Ascension Island (07°56.327'S; 014°25.181'W), 12 November 2023: ZRC.MOL.29985, ZRC.MOL.29986 and ZRC.MOL.29990. GenBank accession numbers: PP842649-PP842658 (16S rRNA) and PP834522-PP834531(COX1).

Shell morphology: Shell medium sized (c. 60–70mm; SL of largest RV examined = 57.5 mm), teardrop or pear shaped, relatively thick and solid, LV deeply cupped, sometimes significantly larger and longer than RV (see e.g. Fig. 2C). Shell margin scalloped, zig-zagging or undulating. Shell exterior surface typically corroded/eroded into shallow pits with angular lines and points, greyish white with some purplish-brown markings near shell margins, commarginal grooves sometimes present near edges. Umbonal cavity deep to very deep. Shell interior white with a slight purplish tinge, with nebulous purplish grey patches, occasionally with darker brownish purple spots. Interior margin with black line that may be interrupted, bright white line behind the black sometimes present. Chomata distinct near hinge, nearly non-existent to sparsely present in groups of two to four around most of the margin. Adductor muscle scar small in relation to area of internal shell surface, purplish brown on RV, usually with progressively paler crescent shaped bands, noticeably paler in LV, often only slightly darker than surrounding, usually with small purplish grey spots; shape somewhat asymmetrical, circular or oval on RV, slightly kidney-shaped or trapezoidal on LV and often with a coloured 'trail' or 'wake' of previous attachments making discernment of the eventual size and shape of the muscle attachment difficult.

Remarks: The exterior of the shells of the AS appears to be consistently corroded in a manner that is identical to the syntypes. Internally, the relative size, colour and shape of the adductor muscle scars; the diffused purplish brown or grey blotches; and the thin black border along the strongly undulating shell edges all agree very well with the syntypes (Figs 9, 10). In addition, the left

valve of the Ascension oysters and Born's syntypes have a prominent 'beak' and a correspondingly deep umbonal cavity under the hinge.

DISCUSSION

Determining the type locality of *Saccostrea cuccullata* is critical to correctly identifying the species and establishing relationships with closely related species. Clarification is particularly important as the type species of *Saccostrea*, *Ostrea saccellus* Dujardin, 1837, is a fossil and no DNA information can be obtained from it. Unfortunately, Born (1778) did not provide a type locality nor is there any indication on the syntype labels. As mentioned previously, it was two years after the publication of his original description when Born (1780) stated the species occurs in the Indies and Ascension Island, which we regard as a subsequent clarification. These localities have been interpreted by subsequent authors in a number of ways: as the East Indies, West Indies and/or Ascension Island.

Brittanica (2024) provides three interpretations for the term "East Indies". The most commonly used, and most restrictive, is the present Republic of Indonesia and the island of New Guinea. An intermediate usage is the whole of Southeast Asia including the Malay Archipelago and the Philippines. The broadest usage for "East Indies" is the region from India to Southeast Asia and Papua New Guinea. The Singapore *Saccostrea* material we have examined (Fig. 11) was thus collected at the margin of the most restrictive usage of "East Indies".

Lam & Morton (2006) stated in their introduction that "[t]he type specimen of *S. cuccullata* sensu stricto was from India, where the species is known as the Bombay oyster." However, they did not provide references, so the basis for their statement is unclear, and we note that India is included only in the broadest usage of "East Indies".

In referring to *S. cuccullata*, Iredale (1924) stated: "This species was described from the Mus. Caes. Vindob. without locality, but, when figured in the later work [Born, 1780], the locality was given as West Indies and the Isle of Ascension and is still included in lists

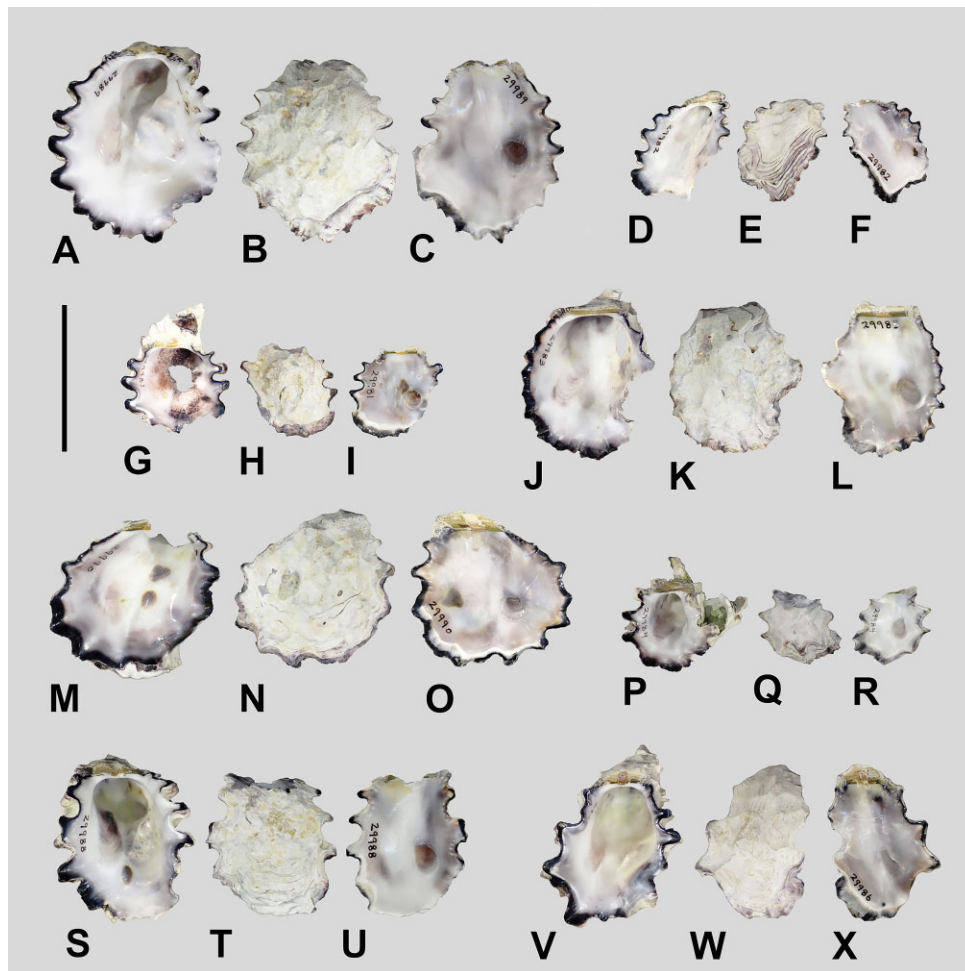


Figure 10. Examples of *Saccostrea cucullata* from Ascension Island. **A–C.** ZRC.MOL.29989. **D–F.** ZRC.MOL.29982; **G–I.** ZRC.MOL.29981. **J–L.** ZRC.MOL.29983. **M–O.** ZRC.MOL.29990. **P–R.** ZRC.MOL.29984. **S–U.** ZRC.MOL.29988. **V–X.** ZRC.MOL.29986. Views shown: interior of LV, **A, D, G, J, M, P, S** and **V**; exterior of RV, **B, E, H, K, N, Q, T** and **U**; interior of RV, **C, F, I, L, O, R, U** and **X**. Scale bar = 5 cm.

of these faunas”. He reiterated this as “... *cucullata* Born, introduced for a shell from Ascension Island and the West Indies ...” in the description of *Ostrea commercialis* Iredale & Roughley, 1933 (currently a synonym of *Saccostrea glomerata*) in Iredale & Roughley (1933). Sekino & Yamashita (2016) listed “West Indies and Ascension Island” as the type localities of *cucullata*, citing Born (1780), Iredale (1924) and Iredale & Roughley (1933). However, in seeking a westward trade route to India in 1492, Christopher Columbus reached a group of Caribbean islands he thought were near India and called them the “West Indies” (Oxford reference, 2020). Iredale misinterpreted Born’s (1780) term “Indies” to be the West Indies, when in fact it was the East Indies. Recently Pagenkopp Lohan *et al.* (2015) reported that *Saccostrea* had clearly been introduced to the Caribbean.

Lamy (1925) seems to be one of the earliest to argue that *cucullata* is a West African species. Interestingly, Rosewater (1975) lists the distribution of *cucullata* as the “West Coast of Africa; islands of Sao Thome, Principe, and Ascension (Nicklès, 1950: 182)”, but did not discuss the other *Saccostrea* species that are the *cucullata* of other authors.

With the recent development of DNA sequencing techniques there has been an increasing realization that oysters cannot be reliably identified using shell and anatomy; DNA analysis is the most reliable method for species identification (Salvi & Mariottini, 2016; Willan *et al.*, 2021). However, certain intraspecific shell characteristics are relatively consistent and are thus relevant to species de-

limitation. An integrative approach is therefore not only prudent but necessary for reassessing species described solely on the basis of their shells.

We have examined photographs of the syntypes of *S. cucullata*, literature illustrations of the species from Ascension Island, *Saccostrea* from the Indo-West Pacific region, and specimens of the lineages present in Singapore in the East Indies. We agree with Sekino & Yamashita (2016) that Born’s *cucullata* should be restricted to the *Saccostrea* species found at Ascension Island. The Ascension material in the ZRC matches well with images in Born (1778, 1780), Rosewater (1975: fig. 23) and Arkhipkin *et al.* (2017: fig. 2) from Ascension Island. It does not match illustrations of any species from the Indo-West Pacific (e.g. Lam & Morton, 2006; Bussawarit & Cedhagen, 2010; Sekino & Yamashita, 2016) or any of the examined material of other *Saccostrea* from Singapore (Fig. 11) and elsewhere deposited in the ZRC. On the other hand, the Ascension material appears to be similar to those from West Africa (Cosel & Gofas, 2019: figs 8.11.E, F, 8.12.F–H]) but not Brazil (Galvão, Alves & Hilsdorf, 2017: fig. 2; Amaral *et al.*, 2020: fig. 2) and the Caribbean coast of Panama (Pagenkopp Lohan *et al.*, 2015). Sequences of *Saccostrea* reported from Brazil and Panama clustered with those of lineage F (Figs 3–6), a group that is widely distributed in Southeast Asia, Japan and Australia (Lam & Morton, 2006; Hamaguchi *et al.*, 2014; Sekino & Yamashita, 2016; McDougall *et al.*, 2024).

Interestingly, the strong wavy shell margins and deep umbonal cavities of the *S. cucullata* syntypes and the Ascension specimens

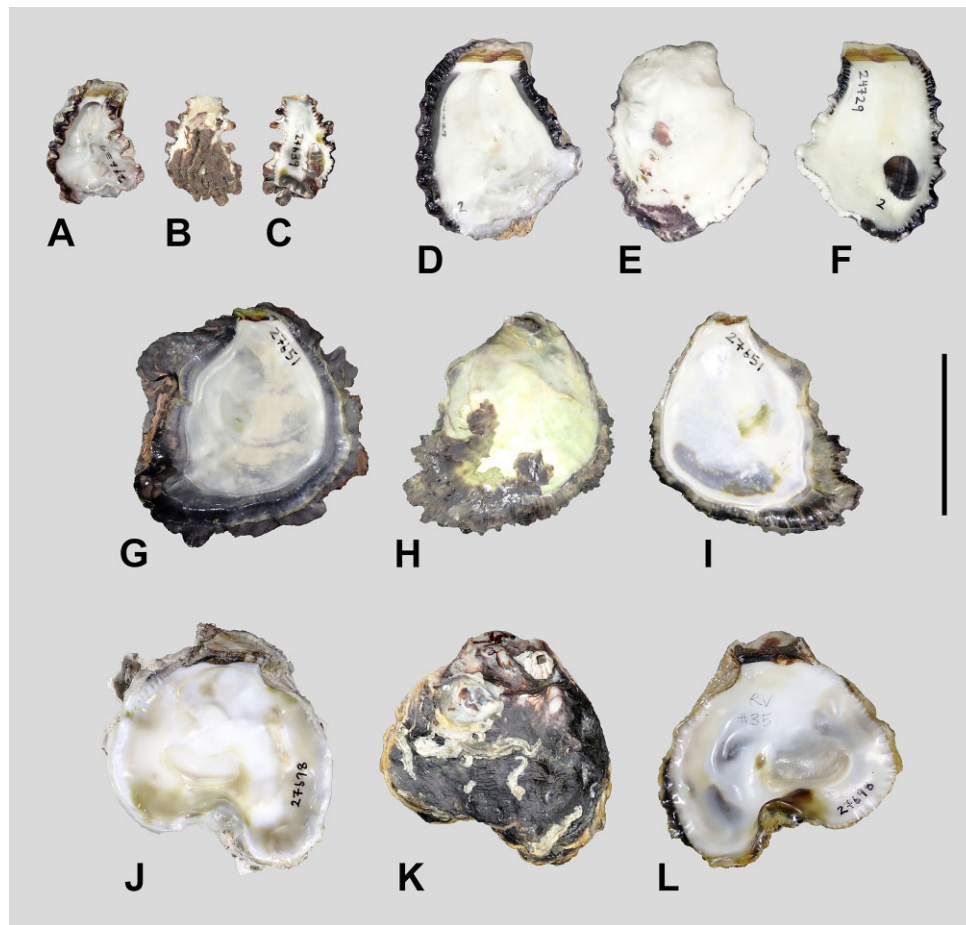


Figure 11. Examples of *Saccostrea* species from Singapore for comparison. **A–C.** *Saccostrea mordoides* (ZRC.MOL.27639). **D–F.** *Saccostrea scyphophilla* (ZRC.MOL.24729). **G–I.** *Saccostrea* lineage I (ZRC.MOL.27651). **J–L.** *Saccostrea spathulata* (ZRC.MOL.27698). Views shown: interior of LV, **A, D, G** and **J**; exterior of RV, **B, E, H** and **K**; interior of RV, **C, F, I** and **L**. Scale bar = 5 cm.

observed in this study (Fig. 2C) render them morphologically closer to the putative *S. scyphophilla* group than the *S. cucullata* of various authors (i.e. the non-*mordax* lineages of Sekino & Yamashita, 2016). The adductor muscle scars of all other *Saccostrea* examined are very large in comparison with those on the syntypes of *cucullata* and the Ascension material (see Figs 9–11), which appear small in relation to the internal surface area of the valves. In addition, the shells of *S. scyphophilla* and *S. mordoides* feel heavier or thicker (although this is difficult to quantify) and the umbonal cavities are usually not as deep. The so-called non-*mordax* lineages (i.e. the *S. cucullata* group of some authors) are even less similar to the syntypes and Ascension Island material, with a very shallow or non-existent umbonal cavity, different shell form, thin irregular wavy or zigzag free shell margins and large kidney-shaped adductor muscle scars (Figs 11, 12). On the exterior of the Ascension Island shells, only commarginal sculpture (of previous free shell margins) is present, and distinct radial sculpture, such as grooves commonly seen in *S. scyphophilla* and *S. mordoides* (e.g. Fig. 11B), is lacking (see the juvenile specimen in Fig. 13, which is relatively less weathered).

Huber (2010) considered there to be a group of species of *Saccostrea* with *S. cucullata* at its core. Lam & Morton (2006) recognized *S. cucullata* as an Indo-Pacific ‘superspecies’, but Sekino & Yamashita (2016) regarded the lineages as possibly distinct species. It is anomalous that while the group is distributed widely in the Indo-West Pacific, the true *S. cucullata* occurs in such an isolated locality in the middle of the South Atlantic Ocean, 2,200 km east of Brazil and 3,000 km west of Africa. The nearest land mass is

St Helena, about 1,300 km to the southeast; Smith (1890) records *Saccostrea* from St Helena. It is unlikely that *S. cucullata* is restricted to Ascension Island but it is not impossible. DeGrave *et al.* (2017) recorded 75 species of decapod crustaceans from the island, 11 of which are thought to be endemic. The range of *S. cucullata* is not yet known as the only genetic information is from Ascension Island. The species has been reported from other islands in the South Atlantic and the west coast of Africa (Nicklès, 1950; Rosewater, 1975; Gofas *et al.*, 1985; Cosel & Gofas, 2019) and Huber (2010) indicated the range as West Africa and the western Indian Ocean. Genetic analysis is required to determine the broader range of *S. cucullata*.

The only paper on the biology of *S. cucullata* in Ascension Island is that of Arkhipkin *et al.* (2017), who studied its age and growth. They found growth rates were slower but that the oysters lived longer than those in Southeast Asia. The Ascension oysters lived for up to 14–16 years, with the oldest individual estimated to have been 26 years old and 49 mm long. The slow growth rate was attributed to the oligotrophic conditions that prevail at Ascension Island.

We used genetic analysis to compare the partial DNA sequences of *S. cucullata* from Ascension Island with Indo-West Pacific lineages of *Saccostrea*. The Ascension Island material is unique (Figs 3–8). None of the currently recognized species and lineages cluster genetically with the AS. Based on the concatenated 16S rRNA + COX1 gene tree (Figs 7, 8), *Saccostrea* lineage J (= *S. spathulata* (Lamarck, 1819); see Sekino & Yamashita, 2016) appeared to be closest to

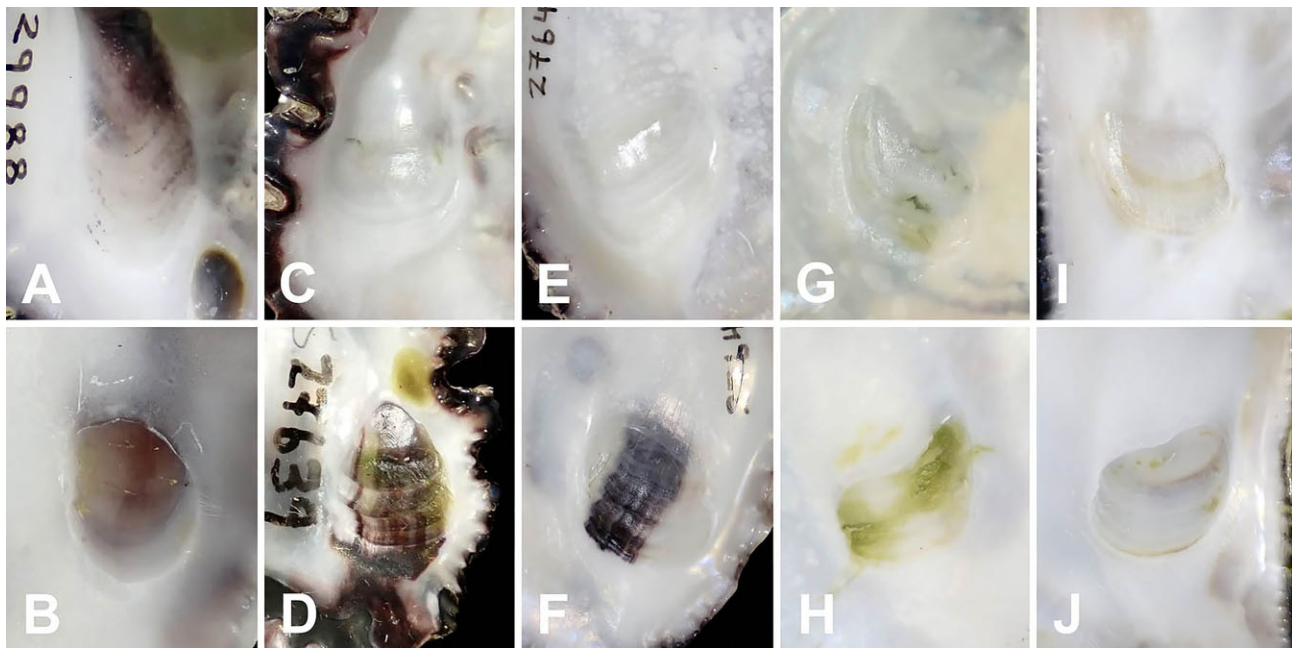


Figure 12. Comparison of the general shape and colouration of the adductor muscle scars of *Saccostrea* spp. The top row shows LVs; the bottom row RVs from Ascension Island (A, B) and Singapore (C–J). A, B. *Saccostrea cucullata* (ZRC.MOL.29988). C, D. *Saccostrea mordoides* (ZRC.MOL.27639). E, F. *Saccostrea scyphophilla* (ZRC.MOL.27642). G, H. *Saccostrea* lineage I (ZRC.MOL.27651). I, J. *Saccostrea spathulata* (ZRC.MOL.27686). Not to scale.

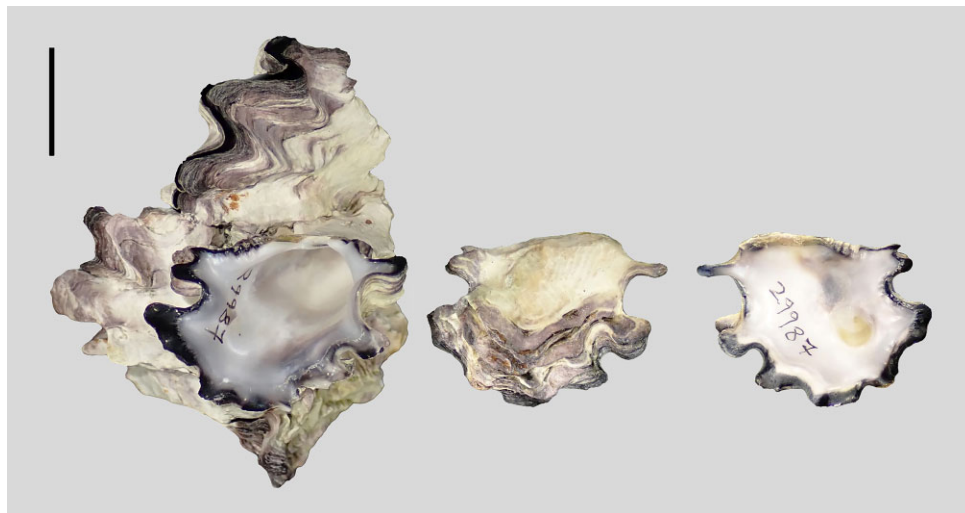


Figure 13. A small specimen of *Saccostrea cucullata* (ZRC.MOL.29987) from Ascension Island. From left to right: interior of LV; exterior of RV; and interior of RV. Scale bar = 1 cm.

AS, although in shell form and habitat preferences, they seem to be quite different. Now that DNA sequences for *S. cucullata* are available and do not match any of the other available sequences, the status of all the associated species and currently accepted synonyms needs to be re-examined. Many will likely be shown to be species that are distinct from *S. cucullata*, as defined here.

The taxonomy of *Saccostrea* is complex, with numerous taxa having been described in the *S. cucullata* group; most of these occur in the Indo-West Pacific and have been historically [mis]identified as or synonymized with *S. cucullata*. Determining the identity and relationships of the various species in the group requires an understanding of the DNA sequence of *S. cucullata* from the type locality of Ascension Island in the central South Atlantic Ocean. The present paper presents useful data for developing a better understanding of this complex genus.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY

Data not included in the paper are available from the corresponding author.

REFERENCES

- ALTSCHUL, S.F., GISH, W., MILLER, W., MYERS, E.W. & LIPMAN, D.J. 1990. Basic local alignment search tool. *Journal of Molecular Biology*, **215**: 403–410.
- AMARAL, V.S.D.O., SIMONE, L.R.L., DE SOUZA TÂMEGA, F.T., BARBIERI, E., CALAZANS, S.H., COUTINHO, R. & SPOTORNO-OLIVEIRA, P. 2020. New records of the non-indigenous oyster *Saccostrea cucullata* (Bivalvia: Ostreidae) from the southeast and south Brazilian coast. *Regional Studies in Marine Science*, **33**: 100924.
- ARKHIPKIN, A., BOUCHER, E., GRAS, M. & BRICKLE, P. 2017. Variability in age and growth of common rock oyster *Saccostrea cucullata* (Bivalvia) in Ascension Island (central-east Atlantic). *Journal of the Marine Biological Association of the United Kingdom*, **97**: 735–742.
- BORN, I. 1778. *Index Rerum Naturalium Musei Caesarei Vindobonensis*. Pars Ima. Testacea. Verzeichniß der natürlichen Seltenheiten des k. k. Naturalien Cabinets zu Wien. Erster Theil. Schalthiere. Ex Officina Krausiana, Vindobonae.
- BORN, I. 1780. *Testacea Musei Caesarei Vindobonensis*. quae jussu Mariae Theresiae Augustae disposuit et descripsit. Joannis Pauli Kraus, Vindobonae. <https://biodiversitylibrary.org/bibliography/11581>.
- BUSSARAWIT, S. & CEDHAGEN, T. 2010. *Field Guide to the Oyster Fauna of Thailand*. pp. 47. Kyoto University Press, Kyoto, Japan.
- BOTTA, R., ASCHE, F., BORSUM, J.S. & CAMP, E.V. 2020. A review of global oyster aquaculture production and consumption. *Marine Policy*, **117**: 103952.
- BOUCKAERT, R., HELED, J., KÜHNER, T.D., VAUGHAN, T., WU, C.-H., XIE, D., SUCHARD, M.A., RAMBAUT, A. & DRUMMOND, A.J. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, **10**: e1003537.
- BRITTANICA. 2024. *East Indies*. <https://www.britannica.com/place/East-Indies> (10 April 2024, date last accessed).
- CERNOHORSKY, W.O. 1978. *Tropical Pacific Marine Shells*. Pacific Publications, Sydney.
- CHEMNITZ, J.H. 1785. *Neues Systematisches Conchylien-Cabinet*. Achter Band. Gabriel Nicolaus Raspe, Nürnberg.
- COEN, L.D., BRUMBAUGH, R.D., BUSHEK, D., GRIZZLE, R., LUCKENBACH, M.W., POSEY, M.H., POWERS, S.P. & TOLLEY, S.G. 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, **341**: 303–307.
- COSEL, R.V.O.N. & GOFAS, S. 2019. Marine bivalves of tropical West Africa from Rio de Oro to Southern Angola. Service des publications scientifiques du Muséum. *Collection Faune et Flore Tropicales*, **48**: 1–1102.
- CROWE, T.P. & FRID, C.L.J. (eds). 2015. *Marine Ecosystems: Human Impacts on Biodiversity, Functioning and Services*. Cambridge University Press, Cambridge.
- CUI, Z., HU, L., CUI, L., ZHANG, Z., GUO, X. & WANG, H. 2021. Identification of *Saccostrea mordax* and a new species *Saccostrea mordoides* sp. nov. (Bivalvia: Ostreidae) from China. *Journal of Shellfish Research*, **40**: 63–75.
- DANCE, S.P. 1962. The authorship of the Portland catalogue (1786). *Journal of the Society for the Bibliography of Natural History*, **4**: 30–34.
- DARRIBA, D., TABOADA, G.L., DOALLO, R. & POSADA, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, **9**: 772.
- DE GRAVE, S., ANKER, A., DWORSCHAK, P.C., CLARK, P.F. & WIRTZ, P. 2017. An updated checklist of the marine decapoda of Ascension Island, central Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom*, **97**: 759–770.
- DOLLFUS, G.F. & DAUTZENBERG, P. 1920. Conchyliologie du Miocène moyen du Bassin de la Loire. 1re Partie: pélécy-podes (suite et fin). *Mémoires de la Société Géologique de France, Paléontologie*, **22**: 379–500.
- DPIRD. 2016. *Western Australian Prevention List for Introduced Marine Pests*. Department of Primary Industry and Regional Development, Perth. <https://www.fish.wa.gov.au> (25 May 2023, date last accessed).
- DUJARDIN, F. 1837. Mémoire sur les couches du sol en Touraine, et description des coquilles de la craie et des faluns. *Mémoires de la Société Géologique de France*, **2**: 211–311.
- GALVÃO, M.S.N., ALVES, P.M.F. & HILSDORF, W.S. 2017. First record of the *Saccostrea* oyster in Bertioga, São Paulo. *Boletim do Instituto de Pesca*, **43**: 638–645.
- GMELIN, J.F. 1791. Vermes. In: *Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Ed. 13. Tome 1(6)*. (J.F. Gmelin, ed.), pp. 3021–3910. GE Beer, Lipsiae, Leipzig, Germany. *Systema Naturae. Linnaeus (ed.)*. Ed. 13. 1: pars. 6.
- GOFAS, S., AFONSO, J.P. & BRANDÃO, M. 1985. *Conchas E Moluscos de Angola = Coquillages Et Mollusques D'Angola*. [Shells and molluscs of Angola]. Universidade Agostinho/Elf Aquitaine Angola, Angola.
- HAMAGUCHI, M., SHIMABUKURO, H., USUKI, H. & HORI, M. 2014. Occurrences of the Indo-West Pacific rock oyster *Saccostrea cucullata* in mainland Japan. *Marine Biodiversity Records*, **7**: e84.
- HARRY, H.W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia, Gryphaeidae and Ostreidae). *Veliger*, **28**: 121–158.
- HOANG, D.T., CHERNOMOR, O., VON HAESELER, A., MINH, B.Q. & VINH, L.S. 2018. UFBOT2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, **35**: 518–522.
- HUBER, M. 2010. *Compendium of Bivalves. A Full-color Guide to 3,300 of the World's Marine Bivalves. A Status on Bivalvia after 250 Years of Research*. Conchbooks, Hackenheim.
- HUELSENBECK, J.P. & RONQUIST, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754–755.
- IREDALE, T. & ROUGHLEY, T.C. 1933. The scientific name of the commercial oyster of New South Wales. *Proceedings of the Linnean Society of New South Wales*, **58**: 278.
- IREDALE, T. 1924. Result from Roy Bell's molluscan collections. *Proceedings of the Linnean Society of New South Wales*, **49**: 179–278.
- KALYAANAMOORTHY, S., MINH, B.Q., WONG, T.K.F., VON HAESELER, A. & JERMIN, L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, **14**: 587–589.
- KATSANEVAKIS, S., WALLENTINUS, I., ZENETOS, A., LEP-PÄKOSKI, E., ÇINAR, M.E., ÖZTÜRK, B., GRABOWSKI, M., GOLANI, D. & CARDOSO, A.C. 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, **9**: 391–423.

- KEMP, W.M., BOYNTON, W.R., ADOLF, J.E., BOESCH, D.F., BOICOURT, W.C., BRUSH, G., CORNWELL, J.C., FISHER, T.R., GLIBERT, P.M., HAGY, J.D., HARDING, L.W., HOUDE, E.D., KIMMEL, D.G., MILLER, W.D., NEWELL, R.I.E., ROMAN, M.R., SMITH, E.M. & STEVENSON, J.C. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, **303**: 1–29.
- KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**: 111–120.
- LAM, K. & MORTON, B. 2004. The oysters of Hong Kong (Bivalvia: Ostreidae and Gryphaeidae). *Raffles Bulletin of Zoology*, **52**: 11–28.
- LAM, K. & MORTON, B. 2006. Morphological and mitochondrial DNA analysis of the Indo-West Pacific rock oysters (Ostreidae: *Saccostrea* species). *Journal of Molluscan Studies*, **72**: 235–245.
- LAMARCK, J.-B.M.d. 1819. *Histoire Naturelle Des Animaux Sans Vertèbres*. Tome 6. l'Auteur, Paris.
- LAMY, E. 1925. Les Huîtres de la mer Rouge (d'après les matériaux recueillis par le Dr Jousseume). *Bulletin du Muséum national d'histoire naturelle*, **31**: 190–196.
- LIGHTFOOT, J. 1786. *A Catalogue of the Portland Museum, Lately the Property of the Duchess Dowager of Portland, Deceased: Which Will be Sold by Auction, by Mr. Skinner & Co. Mr. Skinner & Co., London*.
- MCDONALD, J.I., WELLINGTON, C.M., COUPLAND, G.T., PEDERSEN, D., KITCHEN, B., BRIDGWOOD, S.D., HEWITT, M., DUGGAN, R. & ABDU, D.A. 2020. A united front against marine invaders: developing a cost-effective marine biosecurity surveillance partnership between government and industry. *Journal of Applied Ecology*, **57**: 77–84.
- MCDUGALL, C., NENADIC, N., RICHARDSON, M. & HEALY, J.M. 2024. Molecular identification of intertidal rock oyster species in north-eastern Australia reveals new candidates for aquaculture. *Aquaculture*, **587**: 740838.
- MEYER, C. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, **79**: 401–459.
- MOLLUSCABASE EDS. 2024. *MolluscaBase*. Various oyster species accessed through: World Register of Marine Species (WoRMS). <https://www.marinespecies.org/aphia.php?p=taxdetails&id=140656> (10 July 2024, date last accessed).
- MORRIS, S. 1985. Preliminary guide to the oysters of Hong Kong. *Asian Marine Biology*, **2**: 119–138.
- NEWELL, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research*, **23**: 51–61.
- NGUYEN, L.T., SCHMIDT, H.A., VON HAESELER, A. & MINH, B.Q. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution*, **32**: 268–274.
- NICKLÈS, M. 1950. *Mollusques testaces Marine De la cote Occidentale D'Afrique. Manuels Ouest-Africains. Volume 2*. Paul Lechevalier, Paris.
- NIMPIS 2022. *National Introduced Marine Pest Information System*, Canberra. <https://nimpis.marinepests.gov.au/species> (18 November 2022, date last accessed).
- ORTON, J.H. 1928. The dominant species of *Ostrea*. *Nature*, **121**: 320–321.
- OXFORD REFERENCE. 2020. *West Indies*. <https://www.oxfordreference.com/on> (10 April 2024, date last accessed).
- PAGENKOPP LOHAN, K.M., HILL-SPANIK, K.M., TORCHIN, M.E., STRONG, E.E., FLEISCHER, R.C. & RUIZ, G.M. 2015. Molecular phylogenetics reveals first record and invasion of *Saccostrea* species in the Caribbean. *Marine Biology*, **162**: 957–968.
- PETTON, B., DESTOUMIEUX-GARZÓ, D., PERNET, F., TOULZA, E., DE LORGERIL, J., DEGREMONT, L. & MITTA, G. 2021. The Pacific Oyster Mortality Syndrome, a polymicrobial and multifactorial disease: state of knowledge and future directions. *Frontiers in Immunology*, **12**: 630343.
- RAFINESQUE, C.S. 1815. *Analyse de la Nature Ou Tableau de L'univers et Des Corps Organisés*. Le nature es mon guide, et Linnéus mon maître. Privately published, Palermo.
- RAMBAUT, A., DRUMMOND, A.J., XIE, D., BAELA, G. & SUCHARD, M.A. 2018. Posterior summation in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, **67**: 901–904.
- ROSEWATER, J. 1975. An annotated list of the marine mollusks of Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*, **189**: 1–41.
- RUESINK, J.L., LENIHAN, H.S., TRIMBLE, A.C., HEIMAN, K.W., MICHELI, F., BYERS, J.E. & KAY, M.C. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics*, **36**: 643–689.
- SALIMI, P.A., CREED, J.C., ESCH, M.M., FENNER, D., JAAFAR, Z., LEVESQUE, J.C., MONTGOMERY, A.D., SALIMI, M.A., EDWARD, J.K.P., RAJ, K.D. & SWEET, M. 2021. A review of the diversity and impact of invasive non-native species in tropical marine ecosystems. *Marine Biodiversity Records*, **14**: 11.
- SALVI, D. & MARIOTTINI, P. 2016. Molecular taxonomy in 2D: a novel ITS2 rRNA sequence-structure approach guides the description of the oysters' subfamily Saccostreinae and the genus *Magallana* (Bivalvia: Ostreidae). *Zoological Journal of the Linnean Society*, **179**: 263–276.
- SCHRÖTER, J.S. 1786. *Einleitung in die Conchylienkenntniß nach Linné*. Dritter und letzter Band. Nebst zwey Kupfertafeln. Johann Jacob Gebauer, Halle.
- SEKINO, M. & YAMASHITA, H. 2013. Mitochondrial DNA barcoding for Okinawan oysters: a cryptic population of the Portuguese oyster *crassostrea angulata* in Japanese waters. *Fisheries Science*, **79**: 61–76.
- SEKINO, M. & YAMASHITA, H. 2016. Mitochondrial and nuclear DNA analyses of *Saccostrea* oysters in Japan highlight the confused taxonomy of the genus. *Journal of Molluscan Studies*, **82**: 492–506.
- SIMON, C., FRATI, F., BECKENBACH, A., CRESPI, B., LIU, H. & FLOOK, P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87**: 651–701.
- SMITH, E.A. 1890. On the marine Mollusca of Ascension Island. *Proceedings of the Zoological Society of London*, **1890**: 317–322.
- SNOW, M., FOTEDAR, S., WILSON, N.G. & KIRKENDALE, L.A. 2023. Clarifying the natural distribution of *Saccostrea* Dollfus and Dautzenberg, 1920 (edible rock oyster) species in Western Australia to guide development of a fledgling aquaculture industry. *Aquaculture*, **566**: 739202.
- STENZEL, H.B. 1971. Oysters. In: *Treatise on Invertebrate Paleontology. Part N Vol. 3, Mollusca 6, Bivalvia*. (L.R. Cox, N.D. Newell, D.W. Boyd & J. Weir, eds), pp. N953–N1224. University of Kansas and Geological Society of America, Inc, Lawrence, Kansas.
- TAMURA, K., STECHER, G. & KUMAR, S. 2021. MEGA 11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, **38**: 3022–3027.
- TORIGOE, K. 2004. Oysters in the world. Part 2. Systematic description of the recent oysters. *Bulletin of the Nishinomiyama Shell Museum*, **3**: 1–63.
- TRIFINOPOULOS, J., NGUYEN, L.T., VON HAESELER, A. & MINH, B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, **44**: W232–W235.
- WILK, J. & BIELER, R. 2009. Ecophenotypic variation in the flat tree oyster, *Isognomon alatus* (Bivalvia: Isognomonidae), across a tidal microhabitat gradient. *Marine Biology Research*, **5**: 155–163.
- WILLAN, R.C., NENADIC, N., RAMAGE, A. & MCDUGALL, C. 2021. Detection and identification of the large, exotic, crassostreine oyster *Magallana bilineata* (Röding, 1798) in northern Queensland, Australia. *Molluscan Research*, **41**: 64–74.