



# Global controversy in oyster systematics and a newly described species from SE Asia (Bivalvia: Ostreidae: Crassostreinae)

Julia D. Sigwart<sup>1,2</sup> · Nur Leena W. S. Wong<sup>3,4</sup> · Yuzine Esa<sup>3,4</sup>

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## Abstract

The diversity of native oysters in many regions is overshadowed by the global dominance of a few economically important species. Here we describe the Muar Oyster, *Crassostrea (Magallana) saidii* sp. nov., first reported as an established local fishery renowned for exceptional and distinctive flavour over 160 years ago by British colonial officials in Malaysia, but as yet never formally named or described as a species. This new species has a subtle but clear morphological diagnosis dependent on three-dimensional characters, which has long been recognised by local fishers to differentiate the new species from co-occurring *C. (M.) belcheri* (G. B. Sowerby II, 1871). The Indo-Pacific clade *Magallana* Salvi & Mariottini, 2016 in Salvi and Mariottini 2017 is a phylogenetically distinct group that nonetheless cannot be morphologically separated from the broader genus *Crassostrea* Sacco, 1897. Fossils or species known only from shell specimens, though morphologically distinct species, cannot be classified as *Magallana*, *Talonostrea* Li & Qi, 1994, or *Crassostrea s.s.*; therefore, we revise these groups as subgenera within *Crassostrea*. Our analysis of the COI barcoding fragment from previously published sequences of all available *Magallana* species found that gene is not sufficient to separate several economically important species, and revealed more than 5% of sequences in GenBank represent identification errors. The new species *Crassostrea (Magallana) saidii* sp. nov., which is genetically, morphologically, and gastronomically distinct, is known from only one population under potential threat from urbanisation. Many more global species of *Magallana* remain undescribed. The systematics of this group is critical to understand the diversity of global oysters, and to understand the sustainable use of species grown worldwide for centuries as our food.

**Keywords** *Crassostrea* · Phylogenetics · DNA taxonomy · Integrative taxonomy · Cryptic taxa · Tropical biodiversity · Malaysia · *Magallana* · *Talonostrea*

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- ✉ Julia D. Sigwart  
julia.sigwart@senckenberg.de; j.sigwart@qub.ac.uk
- ✉ Nur Leena W. S. Wong  
nurleena@upm.edu.my

- <sup>1</sup> Department of Marine Zoology, Senckenberg Research Institute and Museum, Frankfurt, Germany
- <sup>2</sup> Queen's University Belfast, Marine Laboratory, Portaferry, Northern Ireland
- <sup>3</sup> Department of Aquaculture, Universiti Putra Malaysia, Serdang, Selangor, Malaysia
- <sup>4</sup> International Institute of Aquaculture and Aquatic Sciences, Universiti Putra Malaysia, Teluk Kemang, Port Dickson, Negeri Sembilan, Malaysia

## Introduction

Oysters have provided food for humans for at least 100,000 years (Baily and Milner, 2008). The family Ostreidae includes around 70 species found worldwide (Horton et al. 2020), all of which are probably edible, many that are harvested at local scales, and a few that represent a global aquaculture industry worth billions (van der Schatte Olivier et al., 2018). Recently, systematic revision for this family changed names of multiple important aquaculture species native to Asia, in a genus *Magallana* Salvi & Mariottini, 2016 in Salvi and Mariottini 2017 that was recognised based on molecular characteristics (Salvi & Mariottini, 2017, 2020). Systematics has a function in highlighting the evolutionary relatedness of species, and this in turn has a wide range of scientific implications outside of taxonomy and phylogenetics. It is important to have clear genus and family

groups in under-studied clades, where many new species are being actively described, such that newly described species can be placed into a meaningful taxonomic framework.

## On *Magallana*

There are two main radiations within this subfamily Crassostreinae, one primarily in Asia and the other on the coasts of Europe and North America, which has been known since early molecular phylogenetic studies of these oysters (O’Foighil et al., 1995; O’Foighil & Taylor, 2000; Wang, Xu et al., 2004a, b; Lam & Morton, 2004). One of these two subgroups was named as a new genus based on a molecular diagnosis (Salvi & Mariottini, 2017). *Magallana* and *Crassostrea* s.s. are unambiguously phylogenetically distinct and represent separate biogeographic regions (Indo-Pacific and Atlantic, respectively). Yet these clades or radiations within *Crassostrea* Sacco, 1897 cannot be separated with any known morphological diagnosis that unites either group.

The authors who described *Magallana* have further made exaggerated claims that morphological diagnoses are inapplicable to oysters (Salvi & Mariottini, 2020), although species have clear morpho-anatomical diagnoses. In addition to the living species, there are many fossil species classified in *Crassostrea*. Without genus-level morphological characters, it is impossible to determine which extinct species belong to *Crassostrea* or *Magallana* (Harzhauser et al., 2016). This is why a transferable, preferably morphological diagnosis is an essential aspect of taxonomic best practice for groups above the species level (e.g. Vences et al., 2013; Sigwart, 2018). Based on this evidence—clearly separated clades of living species that nest within a morphologically coherent group of living and fossil species—we here recognise these clades as subgenera within *Crassostrea* applicable to Recent (i.e. living) species.

The use of the new name for one species in this genus, *Magallana gigas* (Thunberg, 1793), formerly *Crassostrea gigas*, provoked negative reactions among shellfish biologists (Bayne et al., 2017, 2019; Guo et al. 2018). The majority of recent articles on *M. gigas* have rejected the use of this revised (and at that time valid) binominal name. At least one leading journal in fisheries and aquaculture has implemented an explicit editorial policy to retain the use of *C. gigas* (S. Shumway pers. comm., August 2019; Bayne et al. 2019). Experts opposed to the change cite issues of stability, confusion among non-taxonomists, and that there is no morphological diagnosis of the new genus. But prior to the present study, the genus *Magallana* was the valid *status quo*, because no alternative hypothesis had been presented or justified in the form of a formal taxonomic revision (Willan 2021).

## Understanding oyster diversity

A strong supra-specific taxonomic framework is important to understand the diversity and the diversification of global oysters. Many oyster species remain undiscovered or undescribed (e.g. Liu et al., 2011; Thach, 2018). The subfamily Crassostreinae includes around 23 valid species and a number of other unresolved names (*nomina dubia* and *taxa inquirenda*). Assigning species names to less familiar oysters is challenging in part because shelled molluscs were historically described on the basis of shell characters, and this group has very high morphological plasticity (Harry, 1985). However, individual species do have morphological diagnoses. New species are often described from morphological evidence alone (e.g. Thach, 2018). These diagnoses are more clear when the morphology is considered in terms of overall three-dimensional shape rather than historically traditional descriptions of outline or linear measurements.

There is a further confounding factor, equally important but more often overlooked, which is that most type material and historical collections that would provide definitive comparative identification are located in Europe or North America. Most newly discovered species are in other regions. The necessary taxonomic infrastructure and comparative specimen collections are not readily accessible to scientists in the native range of many undescribed species. In the absence of both unambiguous descriptions and reference specimens, misinterpretation can be propagated through multiple scientific generations.

Molecular identification presents many pitfalls that are well known to taxonomists. If there is foundational confusion about species identification, then species names attached to sequences in public databases will be wrong, and perpetuate misidentifications based on sequence comparisons. Unusually for marine invertebrates, sequence data are available from at least one individual of most *Crassostrea* s.l. species (Salvi & Mariottini, 2017; Li et al., 2017), as well as a complete genome assembly for one (Zhang et al., 2012) and genomic reference sets for several species. Unfortunately, the genetic diagnosis for *Magallana* depends on RNA secondary structure of the ITS2 region (Salvi & Mariottini, 2017), and potentially mitochondrial gene order, which still are not known for most species. Thus data are not available to test the applicability of this diagnosis.

Oysters in particular represent a marine invertebrate group where the interest in these species is driven by a large global audience that is not directly engaged with taxonomy. Within Crassostreinae, barcode fragments are already known to be relatively ineffective at separating lineages (Liu et al. 2011). Yet the reality is that dependency on these techniques will continue to grow, and we consider it useful to examine

where the COI barcode marker can and cannot help distinguish species in the *Magallana* clade.

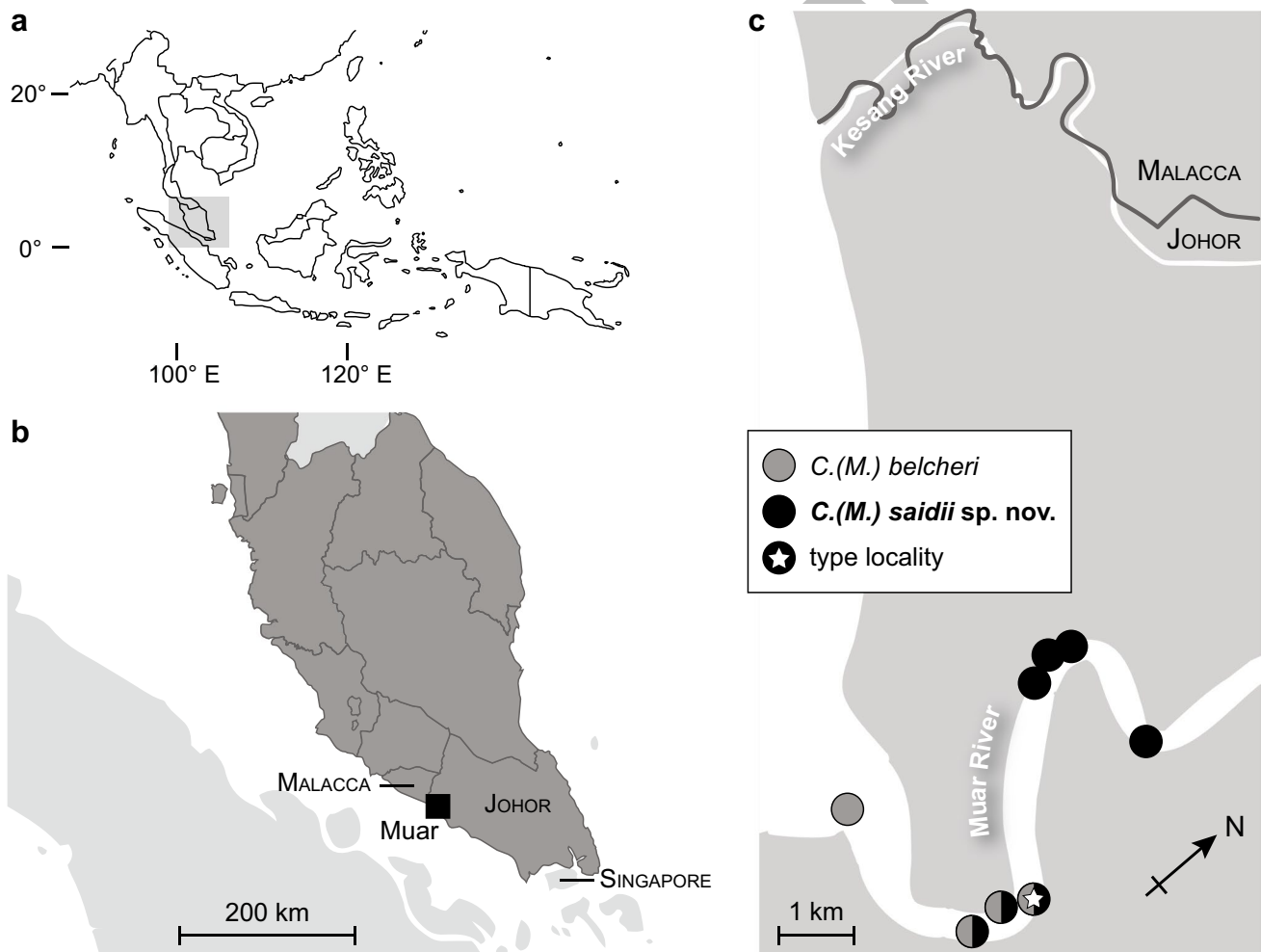
Not only are there cryptic and undescribed species of oysters, there are undescribed species which are exploited and even cultivated. We identified a new species of estuarine oyster in the *Magallana* clade found in a single population in the state of Johor, Malaysia. The presence of a distinctive variety of oyster in this location has been documented for over 160 years, but the species was never described. Indeed, this oyster was reported to have such excellent flavour that it was consumed only by the Sultan of Johor and his senior officers (Macpherson, 1858). The habitat for the remaining population is now under potential threat from urbanisation, and a second potential population noted in historical accounts could not be re-collected during this study.

Here we describe this species, and revise the clade *Magallana* to be recognised at sub-generic rank, noting that it lacks any morphological diagnosis but does reflect an important phylogeographically distinct clade. We also

consider the utility of the COI barcode for distinguishing the new species compared to other species in the *Magallana* clade, and the implications for using barcode identification approaches in this region. This case study illustrates how taxonomy—the recognition of species and informative species groups—serves as the foundation of not only phylogeny, but also conservation biology, and food traceability.

## Material and methods

Specimens were collected from Muar River, Muar, Johor, Malaysia (02° 03' 36" N, 102° 34' 18" E) by local workers collecting the oysters for sale (Fig. 1). This analysis includes specimens of the new species and co-occurring *Magallana belcheri* (Sowerby, 1871) collected on two occasions: an initial collection on May 23, 2019, and the type series collected on Feb 18, 2020. We note that the local fishers keep track of the separate stocks of the two species and refer to



**Fig. 1** (a) Regional map of Southeast Asia. (b) Peninsular Malaysia, indicating location of Muar. (c) Region of the type locality for *C.(M.) saidii* sp. nov. indicating distribution of *C.(M.) saidii* (black circles) and co-occurring *C.(M.) belcheri* (grey circles)

them as *Tiram Putih* (White Oyster) or *Tiram Kapak* (Axe Oyster, *M. belcheri*). There is a local practice of continuously discarding oyster shells (“cultch”) to specific beds to encourage larval settlement, and these sites now have the highest density of living oysters.

Oysters were opened alive to examine anatomy of the soft parts, and a small piece of mantle tissue was preserved intact in 100% ethanol for sequencing. The remaining flesh was either removed and specimens kept as dry shells, or preserved in 100% ethanol. PCR followed standard protocols using primers LCO1490 and HCO2198 (Folmer et al., 1994) with an annealing temperature of 51 °C for COI, primers 16Sg and 16S1 (Romano & Palumbi, 1997) with an annealing temperature of 56 °C for 16S, and primers D1F and D6R (Park and O’Foighill 2000) with an annealing temperature of 55 °C for 28S. Resulting sequences were cross-checked in NCBI GenBank using BLAST to exclude potential contamination. New sequences were deposited in GenBank with accession numbers MW349666-87 (28S), MW349625-48 (COI), and MW354028-42 (16S) (Online Resource 1).

Phylogenetic reconstruction used three loci for 64 ingroup tips in 24 nominal species obtained from GenBank in Crassostreinae and Striostreinae and 19 specimens of the new species (Online Resource 1). Substitution models for each marker were selected using jModelTest ver 2.1.6 for each alignment: HKY + gamma (16S), HKY + I + gamma (COI), GTR + gamma (28S). A combined phylogenetic analysis was conducted using maximum likelihood in RaxML ver 8.2.12 (Stamatakis 2014) and with Bayesian inference in MrBayes ver 3.2.7a (Huelsenbeck & Ronquist, 2001), using 2 runs of 4 chains over 5 million generations sampling every 1000 generations discarding an a priori burn in of 25%, resulting in a total of 7500 sampled trees. Substitution model testing and phylogenetic reconstruction were run via the CIPRES Science Gateway (Miller et al., 2010).

We used the COI barcoding fragment to test whether any previously published sequences matched the new species described herein, and to investigate the reliability of molecular identification for other less studied oysters. A haplotype network was constructed from 1122 previously published sequences for *Magallana* spp., plus our 19 specimens of the new species, using a selection of sequences for *M. gigas*, all available sequences for all other species in *Magallana*, unidentified *Magallana* sp., and unidentified sequences attributed to *Crassostrea* (Online Resource 2). Fragments that were determined by comparison not to belong to known species in the *Magallana* clade (i.e. those that were *Crassostrea* s.s., or contaminated) were discarded from the final haplotype network analysis, generated using TCS network inference (Clement et al., 2002) in PopArt (<http://popart.otago.ac.nz>).

## Results

Phylogenetic analyses recovered a monophyletic Crassostreinae with clades corresponding to *Magallana*, *Talonostrea*, and *Crassostrea* (Fig. 2). *Talonostrea* is sister to *Magallana*, and these two together are sister to *Crassostrea*. Within the *Magallana* group, the new species collected in Muar is sister to a clade containing several species primarily found in the region of China and Japan. Within the *Crassostrea* group, *C. rhizophorae* the Mangrove Oyster is sister to *C. virginica*, and species from both coasts of Latin America form a separate sister clade.

For species in the *Magallana* clade, we determined that around 6% (n = 62 of 942) of examined COI sequences were misidentified or unidentified (Online Resource 2). Of these, most (n = 50) could be positively identified from our analysis (Fig. 3). This seems modest, but a large portion of available sequences (13% of these data) belong to the *bilineata* / *iredalei* / *madrasensis* complex. The species epithets *iredalei* (Faustino, 1932) and *madrasensis* (Preston, 1916) are considered to be junior synonyms of *bilineata* (e.g. Willan et al. 2021). Yet all of these names are widely used in the literature especially regarding aquaculture, and they resolve as separate but closely related clades in our phylogenetic analysis, and are likely separate species lineages (Fig. 2).

## Systematics

Phylum Mollusca

Class Bivalvia

Order Ostreida Férussac, 1822

Family Ostreidae Rafinesque, 1815

Subfamily Crassostreinae Scarlato & Starobogatov, 1979

Genus *Crassostrea* Sacco, 1897

**Subgenus *Magallana* Salvi & Mariottini, 2016 stat. nov.**

**Type species.** *Ostrea gigas* Thunberg, 1793 designated by Salvi & Mariottini 2016.

### Remarks.

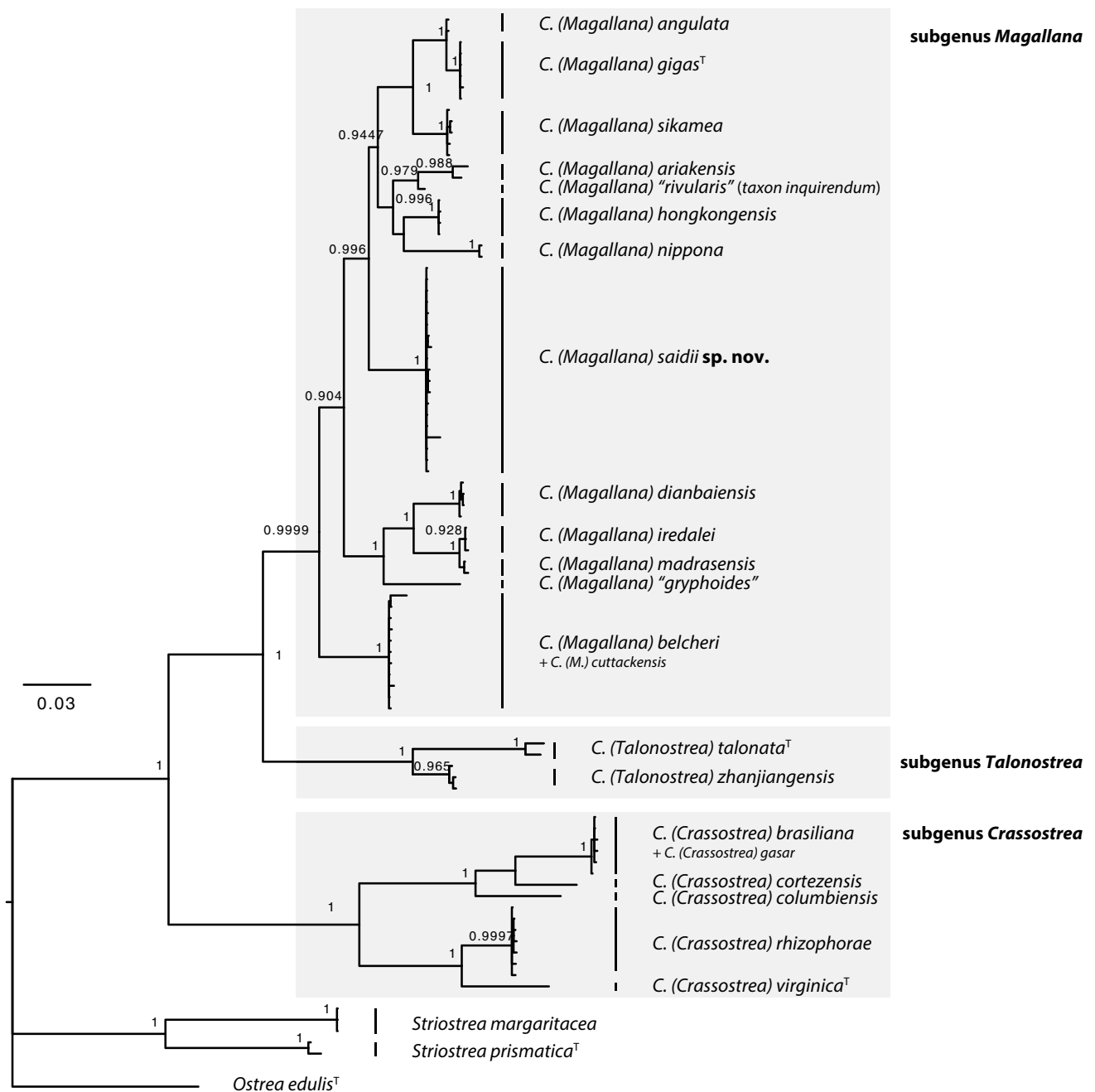
We recognise *Magallana* as a subgenus of *Crassostrea*, a phylogenetically and phylogeographically distinct unit within the genus *Crassostrea*. Members of the subgenus *Magallana* share genetic characteristics (Salvi & Mariottini, 2017) and a biogeographical origin in Asia. Members of this subgenus are native to the Western Pacific Ocean and northern Indian Ocean across Asia. Living species with biogeographic origins in this region are included in the subgenus, even where genetic data are not available.

### Members of the subgenus.

*Crassostrea (Magallana) gigas* (Thunberg, 1793)

*Crassostrea (Magallana) angulata* (Lamarck, 1819)

*Crassostrea (Magallana) ariakensis* (Fujita, 1913)

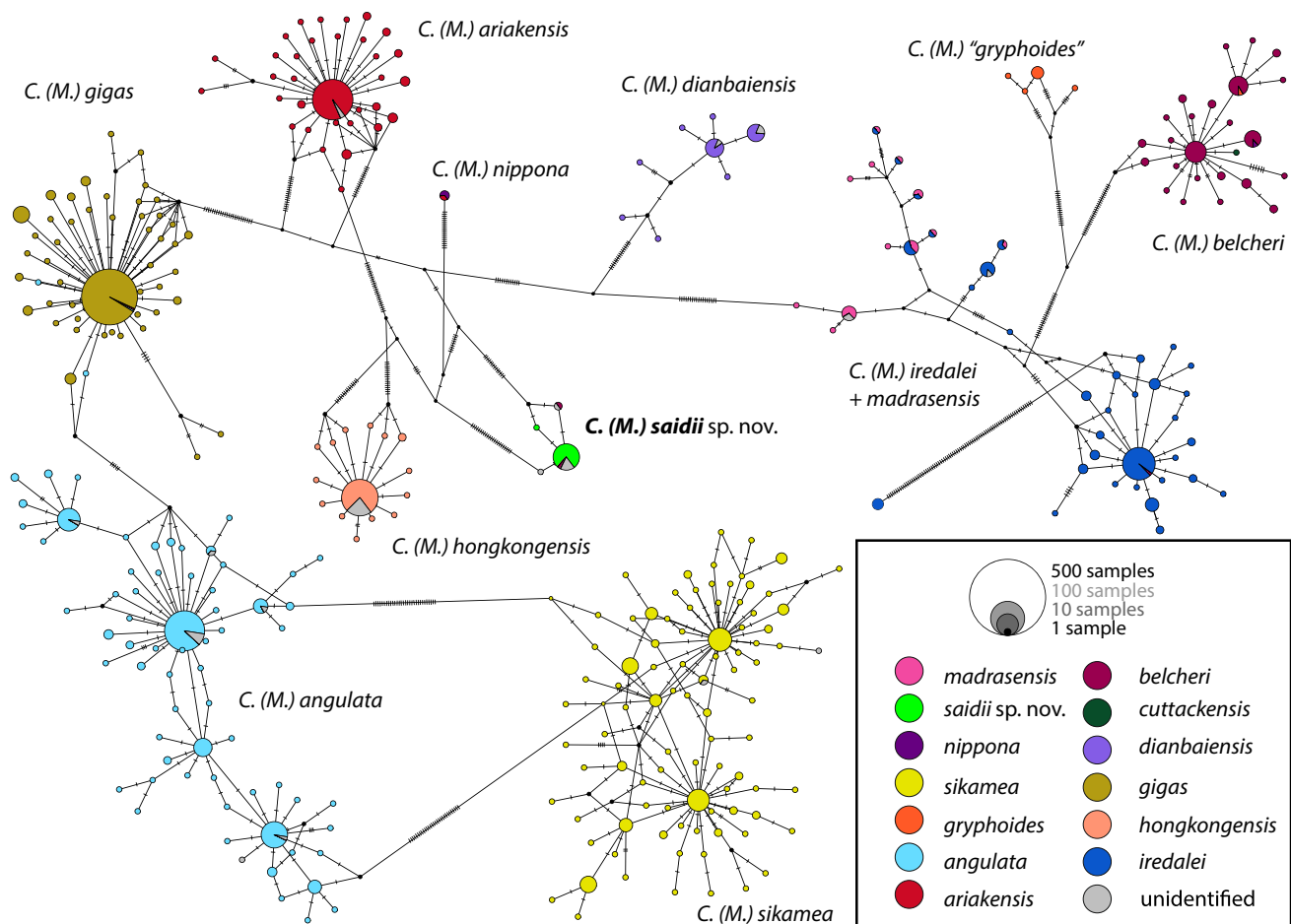


**Fig. 2** Multi-locus phylogenetic reconstruction for Crassostreinae. Nodal values indicate posterior probability from Bayesian analysis

*Crassostrea (Magallana) belcheri* (G. B. Sowerby II, 1871)  
*Crassostrea (Magallana) bilineata* (Röding, 1798)  
*Crassostrea (Magallana) dactylena* (Iredale, 1939)  
*Crassostrea (Magallana) dianbaiensis* (J Xia, X Wu, S Xiao & Z Yu, 2014)  
*Crassostrea (Magallana) hongkongensis* (Lam & Morton, 2003)

*Crassostrea (Magallana) markushuberi* Thach, 2018  
**comb. nov.**  
*Crassostrea (Magallana) nippona* (Seki, 1934)  
*Crassostrea (Magallana) sikamea* (Amemiya, 1928)  
*Crassostrea (Magallana) valentichscotti* Thach, 2018  
**comb. nov.**  
*Crassostrea (Magallana) cuttackensis* (Newton & E. A. Smith, 1912) (*taxon inquirendum*)





**Fig. 3** Haplotype network of the *Magallana* clade, reconstructed based on the COI gene. The size of circles and numbers within denote sampled frequency. Colours correspond to original species identity of sequence fragments from Genbank

*Crassostrea (Magallana) rivularis* (Gould, 1861) (taxon inquirendum)

*Crassostrea (Magallana) gryphoides tanintharyiensis* Li, Haws, Wang & Guo, 2017 (nomen nudum)

*Crassostrea (Magallana) gryphoides dwarkaensis* Li, Haws, Wang & Guo, 2017 (nomen nudum)

**non** *Crassostrea gryphoides* (Schlotheim, 1813) [extinct, *Crassostrea sensu lato*]

***Crassostrea (Magallana) saidii* sp. nov. Wong & Sigwart**  
<http://zoobank.org/CD3C3056-4BB7-44BB-866E-EF2BFCFA1DD4>  
 Figure 4

*Crassostrea* sp.: Nawawi, 1993, Suzana et al., 2011: Table 2, genbank accession numbers GU591442–7.

*Crassostrea belcheri*: Suzana 2011: genbank accession numbers JF915478–9.

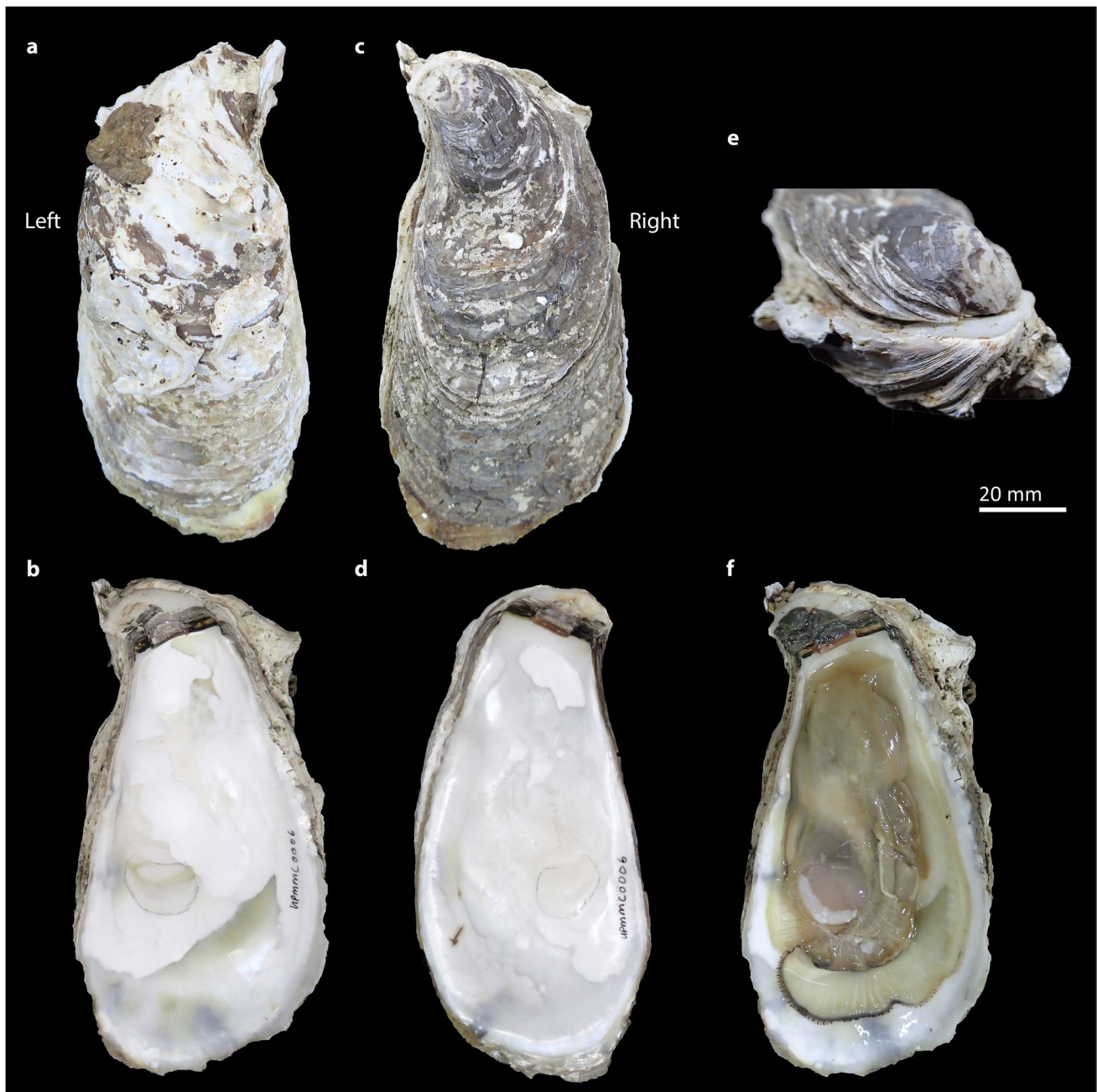
**Common names.** Muar Oyster (English). Tiram Putih (Malay).

**Abbreviations.** Universiti Putra Malaysia Marine Collection (UPMMC), National Museum Wales, UK (NMW.Z), Universiti

Malaysia Terengganu South China Sea Repository and Reference Centre (UMTMoll), National University of Singapore Lee Kong Chian Natural History Museum Zoological Reference Collection (ZRC.MOL), Senckenberg Museum, Frankfurt, Germany (SMF).

**Type material.** Holotype UPMMC0006 (Fig. 4; genbank accession numbers MW349630, MW354033, MW349671). Paratypes: UPMMC0001 (height 106 mm MW349625, MW349666, MW354028); UPMMC0002 (height 118 mm MW349626, MW349667, MW354029); UPMMC0003 (height 122 mm MW349629, MW349670, MW354032); UPMMC0004 (height 116 mm MW349633, MW349674, MW354036); UPMMC0005 (height 102 mm MW349634, MW349675, MW354037); UMTMoll 1816 (height 122 mm MW349627, MW349668, MW354030); ZRC.MOL.016549 (height 103 mm MW349628, MW349669, MW354031); SMF 360,799 (height 108 mm MW349631, MW349672, MW354034); NMW.Z.2021.007.00001 (height 116 mm MW349632, MW349673, MW354035).

**Other material examined.** Collected in the course of this study: *C.(M) belcheri* UPMMC0007–0011 (collected



**Fig. 4** The holotype of *C.(M.) saidii* sp. nov. (a, b) Left valve; (c, d) right valve; (e) dorsal view showing flat hinge line; (f) soft parts in live animal with right valve removed

from the study site co-occurring with *C. (M.) saidii* sp. nov.; Online Resource 1, genbank accession numbers MW349635-9, MW349676-8, MW354038-42), and additional material for morphological comparisons, *C.(M.) belcheri* UPMMC0015-0016, 0025–0029, SMF 363,104; *C. (M.) bilineata* UPMMC0012-0014, SMF 363,105; *C.(M.) saidii* sp. nov. UPM0017-0024.

**Type locality.** Muar River (Sungai Muar), Johor, Malaysia, depth 3 m, 02° 03' 36.8" N, 102° 34' 18.7" E.

**Distribution.** Known only from the region of the type locality, from the river mouth to approximately 6 km upstream in the Muar River, in brackish waters at depths from 2 to 9 m.

**Etymology.** Named for Md Saidi Bin Mohamed, from Muar, Malaysia, who has been actively promoting research and conservation for the sustainability of this oyster since 2013. This name recognises his dedication, commitment, passion, and discovery of the new species.

**Diagnosis.** Shell compressed, relatively flat, elongate. Hinge curving toward posterior in lateral view tapering to a sharp angle at the dorsal margin. Interior hinge surface of left (lower) valve is flat, parallel to sagittal plane. Adductor muscle scar tinged pale golden, darker than surrounding white chalky shell inside pallial line. Flesh cream to light brownish.

# Description.

Holotype height 120 mm; length 60 mm; inflation 43 mm.

Exterior characteristics: Elongated ovate valves, ventral margin rounded, dorsal margin narrow. Overall shape ovate-elongate to slightly ovoid, curved toward posterior at dorsal end. Valve surface lamellate. Thin, pigmented and brownish growth scales densely formed on the outer valve, from dorsal to ventral margins. Scales brownish, whitish on eroded sections.

Left valve thicker and more convex than right valve. Substratum attachment area small, rarely exceed one third of height. Right valve compressed and thin, light in weight.

Interior characteristics: Hinge area flat, parallel to valve, sagittal area forming almost 90° turn posteriorly. Posterior adductor muscle scar kidney shaped, slightly concave anterodorsally, closer to ventral margin than to hinge. Scar pale-coloured, whitish with pale golden line across scar of left valve. Internal valves chalky white and partially pearly, not nacreous, whitish with pale golden tinge.

Soft parts and adductor muscle scar cream to pale brownish. Ventral mantle with thin black marginal line.

# Ecological observations.

The species is limited within brackish water in the Muar River estuary. The river is tidal, and salinity of oyster beds ranged from 8 to 20. It is mainly found off the river banks on the river bottom, at curves of the river where currents are strong, possibly due to lower sedimentation in fast currents. The specimens examined herein were collected in the location where shells are traditionally returned as cultch; other sites within the river have lower population densities. The oysters grow vertically with ventral margins directed upward. A local oyster diver observed that oysters are apparently able to survive during unusual high sedimentation fluxes, buried under sediment with only the ventral margin gape open to water column.

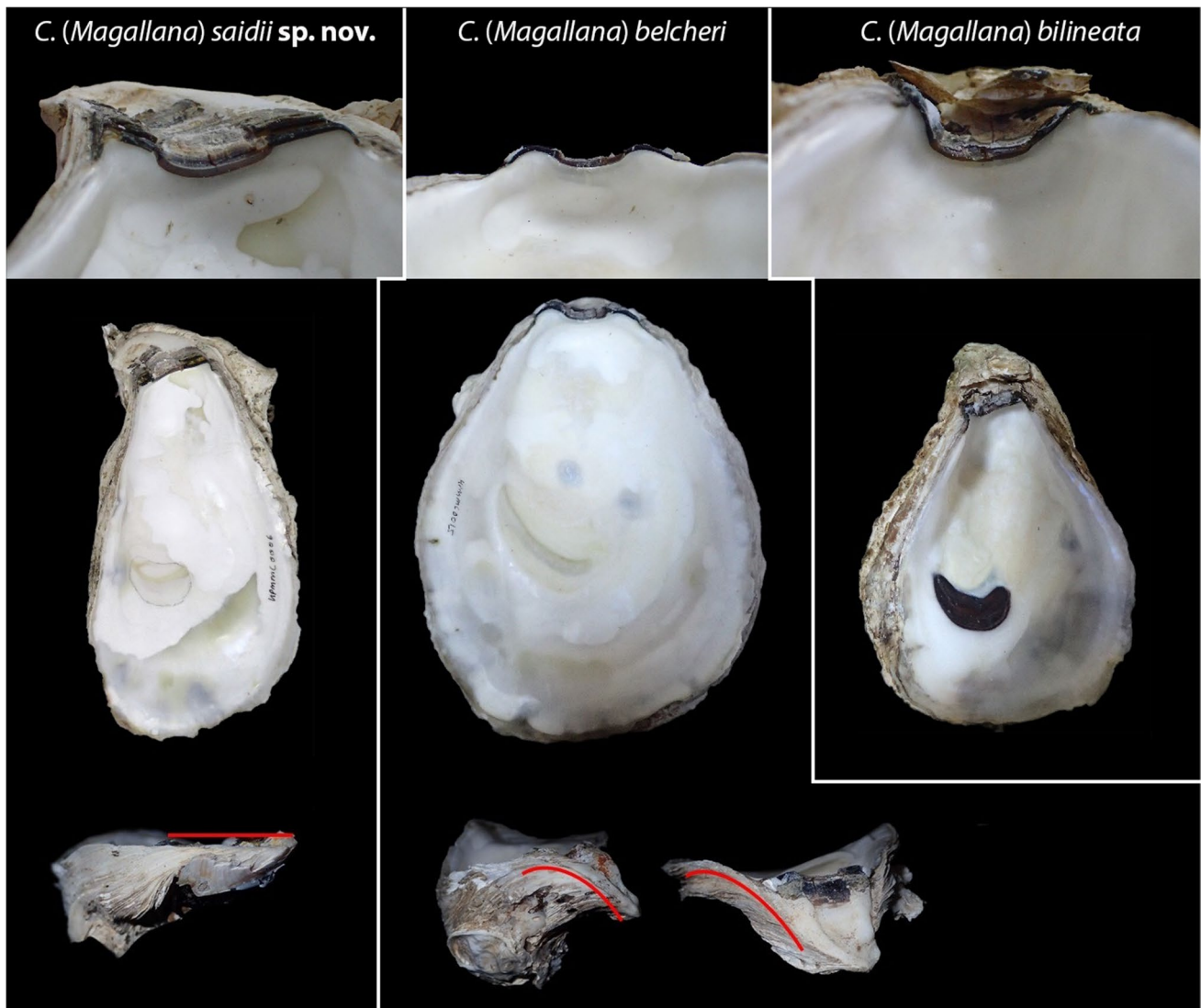
# Comparative remarks.

The new species is superficially similar to *C.(M.) belcheri*, which co-occurs (Fig. 1). We note that in the early stages of this investigation, we found it difficult to differentiate live animals of the two species; however, identification by local fishers who helped us collect specimens was always correct, as verified by DNA, even when we were wrong. This underscores the fact that the two species can be readily distinguished morphologically when observing the correct features and we have tried to articulate the relevant information in the diagnosis and description

**Table 1** Characteristics compared between three local oyster species at Malacca Strait

Origin of specimens examined	<i>C. (M.) saidii</i> sp. nov	<i>C. (M.) belcheri</i>	<i>C. (M.) bilineata</i>
	Wild population. Muar, Johor	Wild population. Muar, Johor	Farmed. Pantai Merdeka, Kedah
Shape	Elongated ovate, rounded ventral margin, narrow dorsal margin. Often inequivalved, growth curved toward posterior commonly observed at dorsal end	Ovate, broad ventral margin. Often equivalved. High plasticity in shape based on attached substrate	Roughly rounded, slightly triangular dorsally. Broad ventral margin, narrow dorsal margin (almost triangular). Often equivalved
Hinge	Hinge parallel to anterior–posterior axis	Hinge tip recurves downward (toward anatomical left)	Hinge parallel to anterior–posterior axis
Valve exterior	Valves lamellate, covered in pigmented brownish growth scales from dorsal to ventral margins. Whitish at eroded sections. Left valve convex, right valve flat and light weighted	Valve lamellate at ventral margin. Mostly whitish, pigmented growth scales at ventral margin of right valve. Valves compressed Left valve convex but shallow, right valve flat	Rarely lamellate, nearly smooth. Greyish white, may flushed with dark purplish along growth margins. Left valve deeply convex, often slightly wider than right valve. Right valve flat and light weighted
Valve interior	Chalky and partially pearly white. Adductor muscle scar whitish with pale golden tinge	Chalky and partially pearly white. Adductor muscle scar white	Chalky white, often with irregular areas of pale purplish, golden tinge often on valve margin if any. Adductor muscle scar dark purplish to black
Flesh	Cream to light brownish	Brownish	Cream to light brownish





**Fig. 5** Comparative photographs of specimens of *C.(M.) saidii* sp. nov. (left), *C.(M.) belcheri* (centre), and *C.(M.) bilineata* (right). Top, close up of the hinge ligament area; middle, inner left valves;

and bottom, hinge in lateral view. At bottom, red lines highlight the three-dimensional shape of the hinge, which is flat in *C. (M.) saidii* sp. nov. and recurved in *C. (M.) belcheri*

(Table 1). In *C.(M.) saidii* sp. nov., the hinge area is parallel to anterior–posterior axis, whereas in *C.(M.) belcheri*, the surface of the hinge area recurves downward (toward anatomical left). Furthermore, *C.(M.) belcheri* is more equivalve, whitish on the surface of the top valve, usually only pigmented at the ventral margin, and the terminal dorsal margin (behind the hinge) is comparatively more curved (Table 1; Fig. 5; Online Resource 3). The new species can be confused externally with *C. bilineata* (referred to locally as *C. iredalei*), but that species has a black adductor scar where the adductor scar in *C. (M.) saidii* is pale (Online Resource 3), and a black marginal line extending around the whole mantle perimeter.

Material identified as *C.(M.) “rivularis”* in the National Museum of Wales collected in the early twentieth century

(ca. 1932–1954) from “Singapore fish market” contains specimens of *C.(M.) saidii* sp. nov. (H. Wood, pers. comm. 2020). The meagre original description of *Ostrea rivularis* Gould, 1861 was supplemented by illustrations by Lischke 1869, and that species has a distinct foliose outer surface of the valve that is lacking in *C.(M.) saidii* sp. nov. More recently, the name *C. rivularis* was applied to commercial oysters in China and India (Wang, Guo et al., 2004a, b; Reece et al., 2008; see also Fig. 2), which have been recognised as comprising two separate species, *C.(M.) ariakensis* and *C.(M.) hongkongensis*, and neither conforms to the original description of *Ostrea rivularis* (Wang, Guo et al., 2004a, b). This species name is a *taxon inquirendum*, meaning that it is potentially valid but there is no clear way to determine which species is connected to the name.

The names “*C. gryphoides*” and *C.(M.) cuttackensis* are used to refer to species cultivated in India and surrounding countries. We are not entirely confident of the continuity of the original descriptions for these names with their current applications (see “**Discussion**” section); however, both the original descriptions lack features diagnostic for *C.(M.) saidii* sp. nov. which has thin valves that are distinctly curved toward the posterior on the dorsal end.

#### Subgenus *Crassostrea* Sacco, 1897 stat. nov.

**Type species.** *Ostrea virginica* Gmelin, 1791 by o.d.

**Remarks.** The subgenus *Crassostrea* represents a clade of Recent species within *Crassostrea* recognised by molecular phylogeny (Fig. 2; Salvi & Mariottini, 2017). Members of the subgenus are native to the Atlantic region with a range extending to both coasts of Latin America.

##### Members of the subgenus.

*Crassostrea (Crassostrea) virginica* (Gmelin, 1791)

*Crassostrea (Crassostrea) aequatorialis* (d’Orbigny, 1846)

*Crassostrea (Crassostrea) brasiliensis* (Lamarck, 1819)

*Crassostrea (Crassostrea) columbiensis* (Hanley, 1846)

*Crassostrea (Crassostrea) corteziensis* (Hertlein, 1951)

*Crassostrea (Crassostrea) mangle* Amaral & Simone, 2014

*Crassostrea (Crassostrea) praia* (Ihering, 1907)

*Crassostrea (Crassostrea) rhizophorae* (Goulding, 1828)

*Crassostrea (Crassostrea) tulipa* (Lamarck, 1819)

#### Subgenus *Talonostrea* Li & Qi, 1994 stat. nov.

**Type species.** *Talonostrea talonata* Li & Qi, 1994 by monotypy.

**Remarks.** The subgenus *Talonostrea* is currently restricted to two species, the type species and its sister species *C. (T.) zhanjiangensis*. These two species form a clade sister to the subgenus *Magallana*. The genus was recognised on the basis of anatomical characteristics (Li & Qi, 1994). Further examination may determine that this distinction is not concordant with synapomorphies of this subgenus and these species should be considered members of subgenus *Magallana*.

##### Members of the subgenus.

*Crassostrea (Talonostrea) talonata* (Li & Qi, 1994).

*Crassostrea (Talonostrea) zhanjiangensis* X Wu, S Xiao & Z Yu, 2013.

#### Genus *Crassostrea* Sacco, 1897 sensu lato

**Remarks.** The recognition of the above subgenera is based primarily on molecular characters. The classification of a fossil species into one of these groups is not possible. This includes, for example, *Crassostrea gryphoides* from Romania (Rakosd, middle Miocene, Badenium stage, ca. 19 million years ago).

## Discussion

The Muar Oyster, *Crassostrea (Magallana) saidii* sp. nov., is notable for having a longer than average “shelf life” from its first discovery to taxonomic description. Although spans of 20–30 years between discovery and description are typical in many groups (Fontaine et al., 2012), 160 years of documented history is unusual. Oyster species are difficult to distinguish, but this is more a product of the larger global problem of capturing local knowledge about biodiversity. This particular genus is also connected to recent controversy about systematics and phylogenetic structure within the genus *Crassostrea* and the utility of taxonomy in animals reared for human consumption.

## Phylogenetic systematics

The goal of systematic phylogenetics is to communicate information about the relatedness of species and species groups. Many authors have rejected taxonomic revision of *Magallana gigas*, but some arguments do not consider the whole clade, and are limited to the consideration of one species cultivated outside of its native range (Beninger and Backeljau, 2019). Other works do clearly retain *Crassostrea* for all *Crassostreinae* (Guo et al. 2018), but there has been disproportionate attention paid to the taxonomy of one species in the clade. The clade *Magallana* contains many other related species that are also commercially important, such as *M. belcheri*, *M. plicatula*, and *M. bilineata*, and presumably other undescribed species. In some published calls to retain the name “*Crassostrea gigas*” (Bayne et al. 2017, 2019; Beninger and Backeljau, 2019), it is unclear whether those authors reject the concept of the genus *Magallana* and expect all members of the clade to be called *Crassostrea* sp., or if they instead proposed retaining the name for *C. (M.) gigas* individually. Keeping a special name for *C. (M.) gigas* alone among this important clade de-emphasises its connection to the Asian clade *Magallana* and misleadingly unifies it to the predominantly European group *Crassostrea*.

We accept the argument that morphological diagnosis is critically important for higher ranked groups (Vences et al. 2013), and that the use of the clade *Magallana* at genus level is therefore not justified. There are as yet no clear morphological or anatomical characters that readily separate *Magallana* and *Crassostrea*. That *Magallana* forms a distinct clade is well established and not controversial, and this information is relevant to phylogenetics but it is also important to the development of commercial fisheries, and to the taxonomy of oysters more generally.

The genus *Crassostrea* extends to at least the mid Jurassic in Asia (Komatsu et al., 2002). Dating of molecular phylogenetic studies estimated the most recent common ancestor

of *Magallana* and *Crassostrea* occurred in the Cretaceous ca. 83 million years ago (Ren et al. 2010; Salvi & Mariottini 2020). Thus, fossil species from the Cretaceous onward should be attributable to *Magallana*, *Crassostrea*, or *Talonostrea*. But this is not possible based on the shell characters preserved in fossils. Here we have restricted our interpretation of the three subgenera of *Crassostrea* to geologically Recent species. This is another reason to revise these clade names at subgenus rank: the genus *Crassostrea* sensu lato includes many fossil species, but these fossil species cannot be confidently assigned to the subgenera *Crassostrea* (*Crassostrea*), *Magallana*, or *Talonostrea*.

Although high intraspecific variation in shell characters is well known in oysters, it is actually not clear whether soft anatomical characters in oysters may be similarly plastic (Dutertre et al., 2009; Lodeiros et al., 2020). While the anatomy of a few species is well known (Li & Qi, 1994; Amaral and Simone 2014), several other common species remain very poorly studied and this hampers any attempts to identify anatomical synapomorphies. A redescription of the type species of *Magallana*, *C. gigas*, based on material from an introduced population in Argentina (Amaral & Simone, 2014) was later criticised as not representing global intraspecific variation (Bayne et al., 2017). To provide a reference point, re-descriptions should ideally depend on material from the type series or the type locality (Sigwart 2018), which in the case of *C. gigas* would be Japan; however we note that any high-quality anatomical descriptions are extremely valuable. It is possible that further studies with more comparative context may find anatomical synapomorphies that are distinct to these subgenera.

Another interesting aspect of the phylogenetic relationships within *Crassostrea* s.l. is the distinct phylogeographic trend of an Atlantic radiation in *Crassostrea* (*Crassostrea*) and an Indo-Pacific radiation in *Magallana* + *Talonostrea*. Among living species, this is confounded by the long history of frequent anthropogenic relocations of oysters. Many oysters occur outside their native ranges, and several are widespread invasives (e.g. Meistertzheim et al., 2013; Cavaleiro et al., 2019; Willan et al. 2021). Historical translocations of young oysters were often motivated mainly to provide a short-term supply of fresh (live) food, with less concern about multigenerational survival (Bromley et al., 2016).

The case of *C.(M.) saidii* sp. nov. is intriguing because of its extremely small known range and a long history of exploitation. There is no reason to assume that *C.(M.) saidii* sp. nov. is introduced; however, it is surprising that the species has apparently never been recorded elsewhere. It co-occurs with *C.(M.) belcheri*, which is broadly distributed across SE Asia. The position of *C.(M.) belcheri* as sister to all other sampled species in *Magallana* (Fig. 2) suggests a SE Asian origin of the clade, with a subsequent (re)invasion

of W Pacific coasts in China and Japan (*C.(M.) gigas*, *C.(M.) nippona*, and other species in the clade sister to *C.(M.) saidii* sp. nov.).

The subgenus *Talonostrea* is sister to *Magallana*; *Talonostrea* is also distributed in the W Pacific of China and Japan. The taxon was originally described as a distinct monospecific genus based on anatomical and shell features, with a type locality in Kiautschou Bay, Qingdao, which was a German leased territory from 1898 to 1914 (Li & Qi, 1994). *Talonostrea talonata* is now a widespread invasive and cultivated species in the SW Atlantic, extensively distributed in South America and an ecological competitor with native species (Cavaleiro et al. 2019). Specimens of the type species *T. talonata* were sequenced only in 2017, using material from Peru, and found as sister to *T. zhanjiangensis*, but those authors used the name *Crassostrea* for both species (Li et al., 2017). Salvi et al. (2014) recognised *Talonostrea* as a separate clade, sister to *Magallana*. *Talonostrea* spp. are phylogeographically Asian, as are *Magallana* spp., and there is no clear, reliable morphological synapomorphy or diagnosis for *Talonostrea* that is applicable to both species and not to other Crassostreinae. The molecular diagnosis of *Magallana* was based on the nuclear ITS2 region (Salvi and Mariottini 2017) and mitochondrial gene order (Salvi and Mariottini 2020). At present, the only nuclear DNA fragments published for *T. talonata* is one single fragment of 28S (KC847154, not used herein), and for *T. zhanjiangensis* there are only mitochondrial markers published. We note that this group should be considered to be within *Magallana*, if it shares the diagnostic features of ITS2. Until the ITS2 region is examined for those species, we retain the current *status quo* of recognising the two species in a separate clade (Salvi et al. 2014) but now at subgeneric rank.

## Historical range and use of the Muar Oyster

Historical reports that we interpret as records of *C.(M.) saidii* sp. nov. point to the high quality of the oyster meat, and to its habitat on the river bottom, which distinguish it from other oyster species in the region. The earliest historical report of the Muar Oyster, *C.(M.) saidii* sp. nov. noted: “The mouth of the river is famous for its oyster beds, the fish [i.e. oysters] being very large and of excellent flavour” (Macpherson, 1858). From context of the journey described, this 1858 narrative referred to the Kesang River, but the original report did not include any direct observation of specimens.

We have found no evidence of a population in the Kesang River now (Fig. 1), and local fishers relate no oral history of that second population within the last three generations of fishers who came before those now working. The Kesang River was formerly the border between the states of Malacca and Johor, and was historically referred to as part of the district of Muar in Johor, so historical reports of oysters from



“Muar” could be from either the Muar or Kesang rivers. The Kesang River is much smaller than the Muar River and has been partially canalised; the visibility in these rivers is poor and the persistence of a small relict population cannot be entirely excluded, but there is no evidence for a living second population.

A later account in 1908 specifically refers to town of Muar at the mouth of the Muar River: “The Muar Oysters are ... found in the bed of the river, some near the town of Banda Maharani [Muar], others nearer the mouth. The latter are bigger and better quality and are reserved for the Sultan and the officials” (Hanitsch, 1908). This apparently describes the co-occurrence of *C. (M.) belcheri* and the superior flesh of *C. (M.) saidii* sp. nov. The 1908 account also described the fishing method, with fishers heading out in small wooden boats (“kolehs”) and free-diving to the bottom (4.5–6-m depth) to hand-collect the oysters. The same method is practiced today, although the boats are fibreglass (M. Saidi, pers. comm.).

At that time, the Singapore market received its chief supply of oysters from Muar (Hanitsch, 1908). Yet the oyster industry in Johor was dismissed as “aenemic” in the early twentieth century in a British colonial report (Dover, 1929). Much later, a 1988 report documented the ongoing traditional use of oyster shells (cultch) to encourage spatfall for the Muar Oyster (Lovatelli, 1988). A further report noted the relatively high market price of oysters from Muar, still known to be distinct and listed as “*Crassostrea* sp.” (Nawawi, 1993). The population of *C. (M.) saidii* sp. nov. has been continuously exploited, using the same collection and mariculture methods, for over 160 years of recorded history.

The total known historical extent of occurrence for *C. (M.) saidii* sp. nov. is within an area of around 50 km<sup>2</sup>, including the Kesang River. The habitat extended to 18 ha (Lovatelli, 1988), but there is anecdotal evidence that the population has declined since then (M. Saidi, pers. comm. 2019). The IUCN Red List uses range as one criterion that contribute to the assessment of threatened species, and the threshold for a potential assessment as Critically Endangered is an extent of occurrence less than 100 km<sup>2</sup>, although other criteria apply to managed populations (IUCN, 2001).

### Problematic names of Asian oysters

Issues with problematic identifications make it extremely difficult to follow the historical literature about which species have been cultivated where in Asia. For example, cultivated oysters widely referred to as *C. (M.) “rivularis”* actually did not match the original description for that name, and were clarified as representing not just one but two species that were both undescribed (Wang, Guo et al., 2004a, b). This highlights the relevance of taxonomy for aquaculture: if species are lumped together, then the population could

have apparently unpredictable or unmanageable traits. One lumped-together group could have a wide range of responses to environmental change, which belies predictable but species-specific responses.

The name *C. “gryphoides”* is used regularly for oysters cultivated in several Asian countries (Trivedi et al., 2015; Li, Haws et al., 2017), but it is not clear what this species is. We suspect the use of the name *C. gryphoides* outside of India is attributable to a specific expert in India credited with identifying specimens from Penang, Malaysia (Dover, 1929), and the use of that misidentification has been passed on in the aquaculture profession. This is a widespread problem that has also been noted in scallop species (Serb, 2016), so *C. “gryphoides”* is an interesting case study in the propagation of an erroneous name.

The name *Crassostrea gryphoides* in fact correctly applies to a very distinctive European fossil species from the Miocene of Europe (Harzhauser et al., 2016). The name *C. gryphoides* should not be used for any extant oyster (Huber 2010; Harzhauser et al., 2016; Li, Haws et al., 2017). The name came into use because it was applied to fossil material from India, and subsequently those Indian fossils were considered to be identical with other live oysters also in India (Durve 1967). The live specimens compared to the Indian fossil *C. “gryphoides”* were classified in a separate subspecies, *gryphoides* var. *cuttackensis*. Thus, *C. (M.) cuttackensis* was originally described from Hukitola, Odisha, on the Indian coast of the Bay of Bengal (Newton & Smith 1912; Durve, 1967).

One review used the name *C. (M.) cuttackensis* as a replacement name for *C. “gryphoides”* in extant oysters (Huber 2010), but we have not followed this, as there is no evidence whether any of the specimens sequenced match the original description of *C. (M.) cuttackensis*. Our haplotype map (Fig. 2) includes specimens as they were identified by other authors: specimens identified as *C. cuttackensis* are clearly misidentified material belonging to *C. (M.) belcheri*. Other specimens called *C. (M.) “gryphoides”* are an unidentified species in the *Magallana* subgenus.

Another study also attempted to correct for the common use of this epithet for living oysters, by creating two new subspecies names for populations in the Arabian Sea and Bay of Bengal (Li, Haws et al., 2017). No type material was designated and no description was provided, although one specimen was figured and a later work referred to the existence of a specimen for one (Guo et al. 2018); these proposed names are currently unidentifiable *nomina nuda* and cannot be used. In any case, neither should not be a subspecies of *C. gryphoides*, since that is a fossil species. Finally, those two proposed subspecies are probably not separate lineages. Our haplotype analysis recovers one cluster of sequences of *C. (M.) non gryphoides* covering specimens combining both the Arabian Sea and Bay



of Bengal (Li, Haws et al., 2017; Reece et al., 2008), indicating they probably are all one species that currently has no valid species name. It is possible that these two *nomina nuda* are synonymous with the “real” *C. (M.) cuttackensis*, from its original description, which could be determined by comparison with the original type material in the Zoological Survey of India.

## Molecular identification

The problems with depending on public sequence databases such as Genbank are well known (Steinegger & Salzberg, 2020). There is a long standing, aggravating issue that the taxonomic affinity of sequences in Genbank can only be corrected by the researcher who submitted the record. Yet the names on sequences in Genbank are accepted as authoritative for other applications such as identifying environmental DNA (eDNA) samples. *Crassostrea* (sensu lato) is relatively well represented, and most valid species are represented in sequences deposited in GenBank (n = 20 of 26 names), providing hope that molecular barcodes could solve the persistent issues of morphological misidentification (e.g. Liu et al., 2011). We provide re-identifications of sequences analysed herein (Online Resource 2) but this does not mean that future work using GenBank directly has been improved.

The haplotype network found few clusters and cannot separate the species using COI alone (Fig. 3). It is not uncommon that COI has variable utility even among closely related species (Sigwart & Garbett, 2018). Other studies have proposed alternative markers such as 28S fragments for separating oyster species (Mazón-Suástegui et al., 2016). There is an ongoing taxonomic problem with *C. (M.) iredalei* and *C. (M.) madrasensis*, which are both formally considered to be junior synonyms of *C. (M.) bilineata*, but nonetheless these names are used routinely in aquaculture literature. There is not sufficient molecular data for *C. (M.) bilineata* from the type locality to include that species in a meaningful way in our multi-locus phylogeny.

On balance, it seems likely that *C. (M.) iredalei* is a valid separate species, but the COI barcode cannot separate the *bilineata* / *iredalei* / *madrasensis* complex. Although unresolved, this is important, because *C. bilineata* is identified as an invasive species (Willan et al. 2021), but feral populations cannot be identified to species level from mitochondrial barcode markers. Understanding the identity of *C. (M.) iredalei* requires further work with additional markers and material from the type localities of these closely-related species. The available reference data for the COI barcode fragment for *Magallana* are frequently wrong, and in one important case, it is ineffective for species discrimination.

## Conclusions

Clarifying the taxonomic nomenclature of the *Crassostrea* clade should improve communication and general understanding of the Asian phylogeography of this globally important group of oysters. Objections raised around the revision of *Magallana* were generally restricted to discussion of *Crassostrea (Magallana) gigas*. Other *Magallana* spp. are widely farmed and equally impacted by any taxonomic change: *C. (M.) belcheri* in Malaysia, *C. (M.) plicatula* in China, and *C. (M.) bilineata* in the Philippines (e.g. Lebata-Ramos et al. 2021). One thing that distinguishes *C. (M.) gigas* among these is its widespread presence as an invasive species that damages habitat and competes with native oyster species in Europe, Australia, North, and South America (e.g. Zwerschke et al., 2018; Willan et al., 2021). Triploid stocks of *C. (M.) gigas* grown for aquaculture have lower but non-zero reproductive capacity (Suquet et al., 2016), as evidenced by extensive escapes and global establishment of pest populations. Attempts to maintain the genus “*Crassostrea*” for this species misleadingly emphasise its similarity to native *Crassostrea (Crassostrea)* species in the Atlantic. We need separate names for the two clades *Crassostrea* and *Magallana*, in recognition that these are well known to be separate groups, to help understand the biology for the benefit of conservation and aquaculture, and to communicate honest information about the organisms. The name *Crassostrea (Magallana) gigas* broadcasts its differentness and separate origins even to non-taxonomists.

The present study demonstrates the importance and utility of morphological identification for oyster species, and local fishers can easily distinguish *C. (M.) saidii* sp. nov. from similar co-occurring species. However, there is no recognisable morphological diagnosis to separate larger clades within *Crassostrea* s.l., and it is appropriate to utilise these names at subgeneric rank, groups within the genus-level group characterised by distinctive morphology. The long history of oyster introductions and movements cast some doubt on the extent of the native range of most species. Ostreidae more broadly have a large fossil and subfossil record that are tied up in the history of human evolution (Baily & Milner, 2008). Recognising clearly established phylogenetic hypotheses with appropriate nomenclature is a first step to solving the complex and fascinating problems of oyster diversification.

Among living species, the economic value of oysters means that it is critical to accurately differentiate species, so that harvest rates can be managed appropriately. The isolated range of the Muar Oyster in a single estuarine location puts it at great risk of future urbanisation or pollution impacts in the Muar River. Describing *Crassostrea (Magallana) saidii*

sp. nov., 160 years after it was first reported, has highlighted the importance of basic taxonomy to phylogeography, conservation, and our food supply.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethical approval** All applicable international, national, and/or institutional guidelines for use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

**Data availability** The datasets generated during the current study are deposited in public databases (NCBI genbank, museums acknowledged herein) or are included in the supplementary materials; any further details are available from the corresponding author on reasonable request.

**Author contribution** NLWSW and JDS conceived the study, NLWSW conducted morphological analyses, YE and JDS conducted molecular analyses, NLWSW and JDS described the species, JDS drafted the manuscript, and all authors contributed to writing the manuscript.

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