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RE-NEW OPINION ARTICLE

Beneath the surface: the overlooked subtidal reef-building oysters of the east coast of Australia

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Molecular and morphological evidence has reshaped our understanding of oyster diversity, distributions and phylogeny, revealing widespread misidentifications and undescribed species. On Australia's east coast the Sydney rock oyster, *Saccostrea glomerata*, traditionally thought to be reef-building both intertidally and subtidally, is likely a predominantly intertidal species. Examination of museum specimens and historical literature indicates that subtidal *S. glomerata* identifications are likely incorrect and instead represent multiple species, all with reef-building capacity. Broadly, clarifying species identities and distributions by tidal zone and depth will be an essential first step for guiding subtidal oyster reef restoration in tropical and subtropical areas. Given this re-interpretation, the threatened status of *S. glomerata* reefs should be re-assessed to reflect their true, predominantly intertidal distribution.

Key words: ***Magallana dactylena*, oyster reef restoration, oyster taxonomy, *Saccostrea subtrigona*, subtidal oyster reef**

Implications for Practice

- *Saccostrea glomerata* is likely an intertidal species which may explain why subtidal restoration attempts have been unsuccessful.
- Subtidal reef-building oysters historically identified as *S. glomerata* likely belonged to multiple different species.

Introduction

Once a common marine ecosystem worldwide, oyster reefs have now collapsed in many regions (Beck et al. 2011). There is an urgent need for their restoration, but efforts in many tropical and subtropical systems remain constrained by limited understanding of reef-building species and their ecology (Richardson et al. 2022). In these warmer regions molecular tools are essential for species identification, which has subsequently changed our understanding of oyster diversity, distributions and phylogeny, driving major taxonomic revisions (Salvi & Mariottini 2016; Sekino & Yamashita 2016). For example, *Saccostrea cuccullata*, once thought to occur across Australia and the Indo-Pacific, is now recognized as a species known only from Ascension Island in the Atlantic Ocean (Tan et al. 2025). While molecular work has begun to clarify the taxonomy of many intertidal species, the identity of subtidal oysters remains far less understood.

On the southeast coast of Australia, the Sydney rock oyster (*Saccostrea glomerata*) is the predominant reef-building species, and has previously been reported across tropical Australia (Ogburn et al. 2007). However, molecular work has shown that these past tropical identifications actually represent multiple species of *Saccostrea*, none of which are *S. glomerata* (Lam & Morton 2006; Snow et al. 2023; McDougall et al. 2024). Historical records also describe *S. glomerata* as occurring both intertidally and subtidally to depths of 10 m (Saville-Kent 1891), but modern observations reporting subtidal occurrences have been restricted to very shallow depths. For example, *S. glomerata* spat recruited subtidally in the Noosa River estuary at 0.7 m; however, recruitment was low, mortality was high, and no subtidal adults were observed in the system (Richardson et al. 2025b). Similarly, presumed *S. glomerata* spat recruited subtidally at 0.6 m in Pumicestone Passage, however, mortality was high and recruitment was hindered by sedimentation (Diggles 2017). Although *S. glomerata* may recruit to shallow subtidal depths, recruitment alone is not a reliable indication of species distributions as no naturally-occurring adult *Saccostrea* have been definitively identified subtidally. Following decades of intense overharvesting, the absence of subtidal *S. glomerata* reefs in the present day continues to be attributed to sedimentation, mudworm, and QX disease (Ogburn et al. 2007;

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Diggles 2013). However, the persistence of widespread intertidal *S. glomerata* reefs (see https://www.arcgis.com/apps/mapviewer/index.html?webmap=e81158f553324b12a3487dae4a4f6f22), suggests that environmental conditions no longer support subtidal reef formation across the entire range of the species (Diggles 2013; Gillies et al. 2015). Extrapolating results from recruitment studies conducted in highly modified seascapes in <1 m depths to support unconfirmed historical claims that *S. glomerata* formed reefs at 10 m depths is problematic. While environmental degradation is nevertheless a key problem for conservation and management regardless of the species, we present evidence which suggests that historical drift/dredge oysters may have been misidentified as *S. glomerata*.

The Overlooked Subtidal Reef-Builders

On Australia's east coast, intertidal ("bank") and subtidal ("drift" or "dredge") oysters were historically described as morphologically distinct, even when considered to be conspecifics (Tenison-Woods 1882; Cox 1883; Saville-Kent 1891). Given that species within the same genus are challenging to distinguish and require molecular tools for identification (McDougall et al. 2024; Richardson et al. 2024), it is unlikely that morphologically distinct subtidal morphs are *S. glomerata*. Indeed, early ecologists initially shared this notion. In 1871, *Ostrea subtrigona* (from "Australia") was described from two disparate syntype specimens, one elongate shell (now missing from collections) and one triangular-shaped specimen (paired valves) (Sowerby 1871). This species name was subsequently applied to the drift/dredge oyster of Moreton Bay and New South Wales, a subtidal reef-building species that occurred in moderately deep water below the zones of both *S. glomerata* and *Ostrea angasi* and was considered one of Australia's most important commercial oysters (Tenison-Woods 1882; Cox 1883).

While morphology alone is insufficient for definitive species identifications, certain characteristics can be useful for distinguishing different genera. For example, *Saccostrea* are generally characterized by thick, irregular shells with strongly denticulated lateral margins known as chomata, a feature typical of this genus that is often found around most of the shell margins, though its expression can be variable and may, in rare cases, be reduced or absent in some individual shells (Sekino & Yamashita 2016; McDougall et al. 2024; Richardson et al. 2025a). Chomata are present in both *O. subtrigona* syntype specimens; however, the extent of the chomata differs markedly between them, being poorly developed and restricted to the hinge area of the upper valve only in the paired specimen (Fig. 1A), but present for half the length of the elongate valve (missing specimen) (Fig. 1B). It is therefore possible that Sowerby's specimens represent two different species. *Ostrea subtrigona* has since been reassigned to *Saccostrea* and currently is recognized as a valid species (*Saccostrea subtrigona*—adopted herein; Huber 2010). However, we note that if the surviving syntype is eventually designated as the lectotype of the species, then its poorly developed chomata likely indicate a position outside of the genus *Saccostrea* (all of which have very well developed chomata).

In the late 1800s it was proposed that *S. subtrigona* and *S. glomerata* (both previously included in the genus *Ostrea*) were the same species, and morphological differences were attributed to whether the oyster grew in intertidal or subtidal environments (Tenison-Woods 1882; Saville-Kent 1891). Some early ecologists vehemently disagreed, and Cox (1883) maintained that these species were different and criticized translocation efforts, stating that, "Our rock oyster has been placed in a similar position to the natural beds of *Ostrea subtrigona* but always with disappointment; when our rock oysters are placed in such a position they will not thrive and fatten, and in fact will not live very long, but will live longer than if the drift oyster is placed in the natural position of the rock oyster". Nevertheless, the interpretation that "bank," "dredge," and "drift" oysters represented a single species gained broad acceptance (Tenison-Woods 1882; Saville-Kent 1891).

Examination of Saville-Kent's (1891) illustrations of intertidal and subtidal *S. glomerata* shells indicates two different species. The subtidal morph was described as "a form very prevalent from deep water or dredge sections, and in which the prolongation and smoothness of the component shells are more conspicuously pronounced than in the typical dredge or drift variety associated in the foregoing diagnosis with the title of '*Ostrea subtrigona*.'" This suggests a second subtidal species in addition to *S. subtrigona*, but Saville-Kent (1891) presumed that this species was also synonymous with *S. glomerata*, proposing that, "the mollusc would grow upwards towards the light, much after the manner of a light starved plant." However, this growth form is atypical of *Saccostrea*, which normally grows broadly attached by the lower valve against a hard substrate (McDougall et al. 2020). Iredale 1939 reported similar specimens on Lindeman Island in north Queensland, but considered them morphologically distinct enough to warrant naming (as "*Saxostrea commercialis dactylena* ecomorph nov") (Fig. 1E). The accepted name for this species is now *Magallana dactylena*, but without molecular data and comparative morphological analyses of live specimens its phylogenetic placement is uncertain. Notably, chomata are absent in the genus *Magallana* (Salvi & Mariottini 2021). Chomata were not noted in Iredale's 1939 descriptions and are absent on all *M. dactylena* specimens observed by us in the Queensland Museum, confirming that this species is taxonomically distinct from the genus *Saccostrea*. However, chomata are present on one subtidal morph at the hinge of the shell depicted in one of Saville Kent's sketches (Fig. 1C). This inconsistency suggests an additional subtidal species which may have been reef-forming, however, there is not enough evidence to taxonomically place this species as several oyster genera display chomata (Salvi et al. 2022). *M. dactylena* also exhibits reef-building capacity through gregarious settlement, as shown in Saville-Kent's (1891) illustrations (Fig. 1D) and Queensland Museum specimens dredged from the mouth of the Brisbane River (1929–1939) (Fig. 1F). Recent collections of (dead) shells and gregarious clusters from tropical Queensland (Fig. 1H–J) support current consensus that *M. dactylena* has a broad distribution along the Queensland

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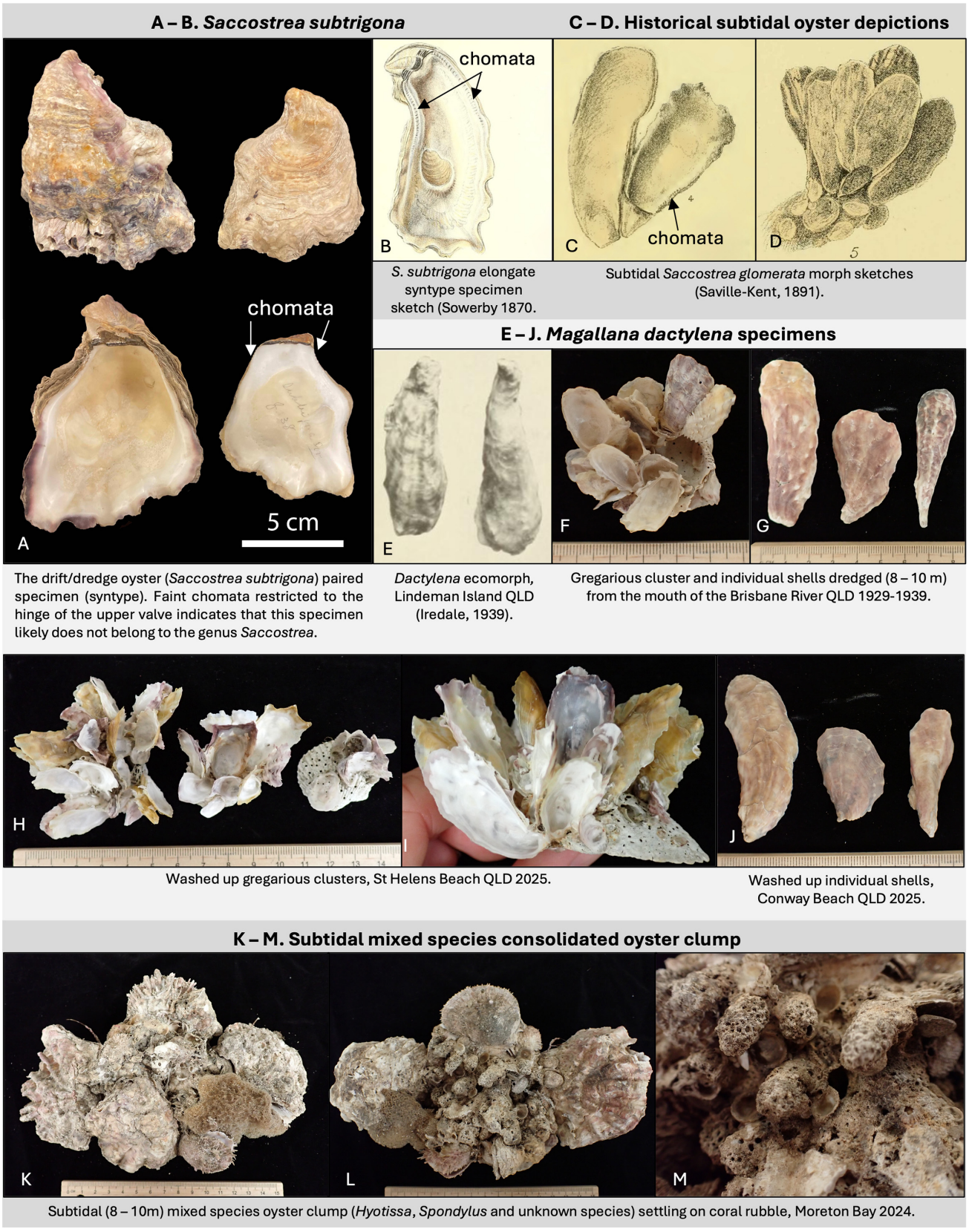

Figure 1. Illustrations and photographs of subtidal reef-building oysters in Queensland, Australia. British Natural History Museum accession number: (A and B) NHMUK_1874.12.11.259; Queensland Museum accession numbers: (F and G) QMMO 79053; (H and I) QMMO 86467; and (J) QMMO 86469.

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coast, but has not been recorded in New South Wales (Beechey 2025).

Historical accounts described subtidal reefs as being comprised of mixed oyster assemblages. These assemblages were said to include *M. dactylena* morphs, *S. subtrigona* morphs and an oyster similar to intertidal *S. glomerata* in appearance (Saville-Kent 1891). However, Saville-Kent 1891 noted a considerable size difference between similar looking subtidal and intertidal morphs, stating that subtidally, "the tendency to develop an abnormally massive shell is especially noteworthy, instances occasionally occurring in which the lower valve weighs as much as half a pound." Given this considerable size difference, it is likely that these large oysters represent additional species yet to be documented as reef-building. In 2024, an aggregated clump of large oysters which closely resembles Saville-Kent's descriptions was collected subtidally (8–10 m) in Moreton Bay (Fig. 1K–M). Some of these oysters appear to belong to the genera *Hyotissa* and *Spondylus* while others are unknown; however, they do not appear to belong to the genus *Saccostrea*.

Limited knowledge of subtidal oyster species combined with severe population declines hinders assessment of key ecological traits such as reef-building potential, distribution, and preferred settlement substrates in tropical and subtropical regions. For example, while rock is a common substrate for intertidal oysters, *S. subtrigona* has been observed occurring in beds of unattached individuals, attached to one another by adhesion of the lower valve, or attached within masses of drift material (Tenison-Woods 1882). The mixed species oyster clump collected subtidally from Moreton Bay is attached to coral rubble, while all gregarious clusters of *M. dactylena* specimens are attached to Arcidae shells. These observations suggest that settlement preferences may differ for intertidal versus subtidal species; however, they could also reflect collection bias, as shells attached to consolidated substrates may be less easily washed ashore. Regardless, the disappearance of subtidal reefs may be due to both a collapse in larval supply and substrate availability as well as a decline in environmental conditions, as both live oysters and the substrates they settled on were historically targeted by dredging (Kirby 2004; Ogburn et al. 2007; Diggles 2013). This emerging evidence gives reason to challenge previously held assumptions about the ecology and identity of subtidal reef-building oysters on Australia's east coast.

Future Directions

Improving taxonomic resolution and understanding which species are reef-building will be critical for the conservation of tropical and subtropical subtidal oyster reefs. This requires increased sampling efforts and integrated genetic and morphological analyses, especially for lesser-known rock oysters within genera known to occur subtidally, such as *Ostrea*, *Nanostrea*, *Dendostrea*, *Booneostrea*, *Planostrea*, and *Hyotissa* (Lamprell & Healy 1998; Lam & Morton 2003; Chen et al. 2025). This will help to describe new species and resolve taxonomic ambiguities for taxa with broad geographic ranges where duplicate names exist. Assessing reef-building capacity is more complicated, however, as subtidal reefs may have collapsed and extant species may only exist in fragmented populations (Gillies et al. 2020). "Reef-building" may therefore need to be inferred from experimental recruitment traits and observations of gregarious settlement. Addressing these taxonomic and ecological gaps is essential for developing effective restoration strategies, as methods used in temperate subtidal systems may not suit tropical and subtropical species-specific requirements. Finally, if *S. glomerata* is indeed a predominantly intertidal species capable of naturally recruiting only in very shallow depths, its conservation status warrants reassessment.

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