

THE OYSTERS OF HONG KONG (BIVALVIA: OSTREIDAE AND GRYPHEIDAE)

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ABSTRACT. – In this revision of the oysters of Hong Kong, twelve species of Ostreidae and Gryphaeidae are described in terms of their shell characters and habitats. Of these, *Crassostrea ariakensis*, *Saccostrea mordax*, *Dendostrea crenulifera*, *Ostrea denselamellosa*, *Crassostrea lugubris* and *Crassostrea angulata* are new records for Hong Kong. Since species identification based on shell characters alone are inadequate, the identities of Hong Kong *C. lugubris* and *C. angulata* were determined by subjecting their mitochondrial DNA cytochrome oxidase I (COI) gene sequences to phylogenetic analyses. Other species from Hong Kong such as *Saccostrea cucullata*, *Saccostrea mordax*, *Planostrea pestigris*, *Dendostrea folium* and *Hytissa imbricata* are also identified, as is *Crassostrea hongkongensis*, a recently described new species.

KEY WORDS. – Ostreidae, Gryphaeidae, oysters, cytochrome oxidase I, Hong Kong.

INTRODUCTION

Oyster shell morphology is typically plastic and creates difficulties in classification. The effect of the environment upon valve morphology in oysters can be pronounced (Seilacher et al., 1985). Oysters are thus notorious for profound nomenclatorial confusion regarding species identities. About thirty nominal species of oysters have been recorded from the coast of China (Bernard et al., 1993). Some of these names have been synonymized by Tchang & Lou (1956) and Torigoe (1981). Morris (1985) prepared a preliminary guide to the common species of oysters which occur intertidally and in the shallow waters of Hong Kong. Six species, belonging to six genera were identified by following the classification and diagnosis of Stenzel (1971) and Torigoe (1981). These were *Crassostrea gigas* (Thünberg, 1793), *Saccostrea cucullata* (Born, 1778), *Ostrea pestigris* Hanley, 1846, *Alectryonella haliotidaea* (Lamarck, 1819), *Dendostrea glaucina* (Lamarck, 1819) and *Hytissa sinensis* (Gmelin, 1791). Descriptions provided by Morris (1985) were based entirely on conchological characters. Morton & Morton (1983) have described the general distributions of various oysters, including *C. gigas*, *Crassostrea rivularis* and *S. cucullata*, on Hong Kong shores. Scott (1994) described *A. haliotidaea*, *O. pestigris* and

Hytissa sinensis as occurring in the southern subtidal waters of Hong Kong. Fifteen species of oysters have been recorded from Hong Kong in a checklist of marine bivalve molluscs identified from the published literature between 1971-2000 (Scott, 2003). While these researches provide habitat data and identify basic shell characters for Hong Kong's oysters, identification is still difficult because of an inherent plasticity in shell form and a fast-changing nomenclature for the Ostreidae and Gryphaeidae (Stenzel, 1971; Torigoe, 1981; Harry, 1985; Morris, 1985; Bernard et al., 1993; Carriker & Gaffney, 1996; Coan et al., 2000). Some species may also have different colour morphs or ecotypes (Morris, 1985; Lam, 2003).

Problems in Hong Kong oyster taxonomy remain controversial. Examples include: the identity of the locally cultured oyster, a species of *Crassostrea*, in Deep Bay, the taxonomic status of the intertidal rock oyster, a species of *Saccostrea*, and the identification of subtidal oysters. Between 2000 and 2002, an extensive survey of the distribution of oysters within Hong Kong waters was carried out with species identifications based primarily on shell morphology complemented by molecular genetics. The results showed that two species of cultured oyster were present in the oyster farms of Hong Kong. One is a genetically identified new species,

C. hongkongensis Lam & Morton, 2003 (Lam & Morton, 2003a), whereas the other is a new record, *C. ariakensis* Fujita, 1913, (Lam et al., 2003). Three subtidal oysters, i.e. *Planostrea pestigris*, *Dendostrea folium* (Linnaeus, 1758) and *Hytissa imbricata* (Lamarck, 1819), were also identified from a trawl survey in 2001 which was conducted at 29 stations in local coastal waters (Lam & Morton, 2003b). During a marine cave expedition in 2002, two more subtidal oysters, i.e. *Dendostrea crenulifera*, Sowerby, 1871 and *Hytissa sinensis* (Gmelin, 1791), were collected by the authors. Individuals of the rock oyster, *Saccostrea* sp., collected from Indo-Pacific shores, including Hong Kong, have also been subjected to mtDNA sequences analysis. The results, not yet published by Lam & Morton, confirm that two superspecies are present in Hong Kong, i.e. *S. cucullata* (Born, 1778) and *S. mordax* (Gould, 1850).

In this updated revision to the oysters of Hong Kong, twelve species of Ostreidae and Gryphaeidae are described. Of these, *Crassostrea ariakensis*, *Saccostrea mordax*, *Dendostrea crenulifera*, *Ostrea denselamellosa* and two unidentified species of *Crassostrea* are first recorded from Hong Kong. *Crassostrea hongkongensis* is a new species genetically identified and described. The specific identity of the two problematic species of *Crassostrea* were determined by

comparing the genetic distances of mitochondrial DNA sequences, i.e. partial cytochrome oxidase I (COI) genes, from other *Crassostrea* species. The sequence of this gene has been used extensively as a molecular marker in distinguishing problematic ostreid taxa, especially species of *Crassostrea* (Banks et al., 1993; O'Foighil et al., 1995, 1998; Jozefowicz & O'Foighil, 1998).

MATERIALS AND METHODS

Sample collection. – Samples from the wild populations of local oysters were collected from intertidal habitats in Hong Kong. Figure 1 is a map of Hong Kong showing the locations where oysters were collected. Those from subtidal waters were obtained by SCUBA diving. The samples were identified using shell characters. These were: (1), general size; (2), shape and surface sculpture; (3), hinge line and ligament position and extent; (4), attachment area of the left valve; (5), presence and pattern of chomata; (6), position, colour and relative size of the adductor muscle scar and (7), external and internal shell colour. Details of habitat and biogeography were based mainly on the authors' personal observations, complemented by published material.

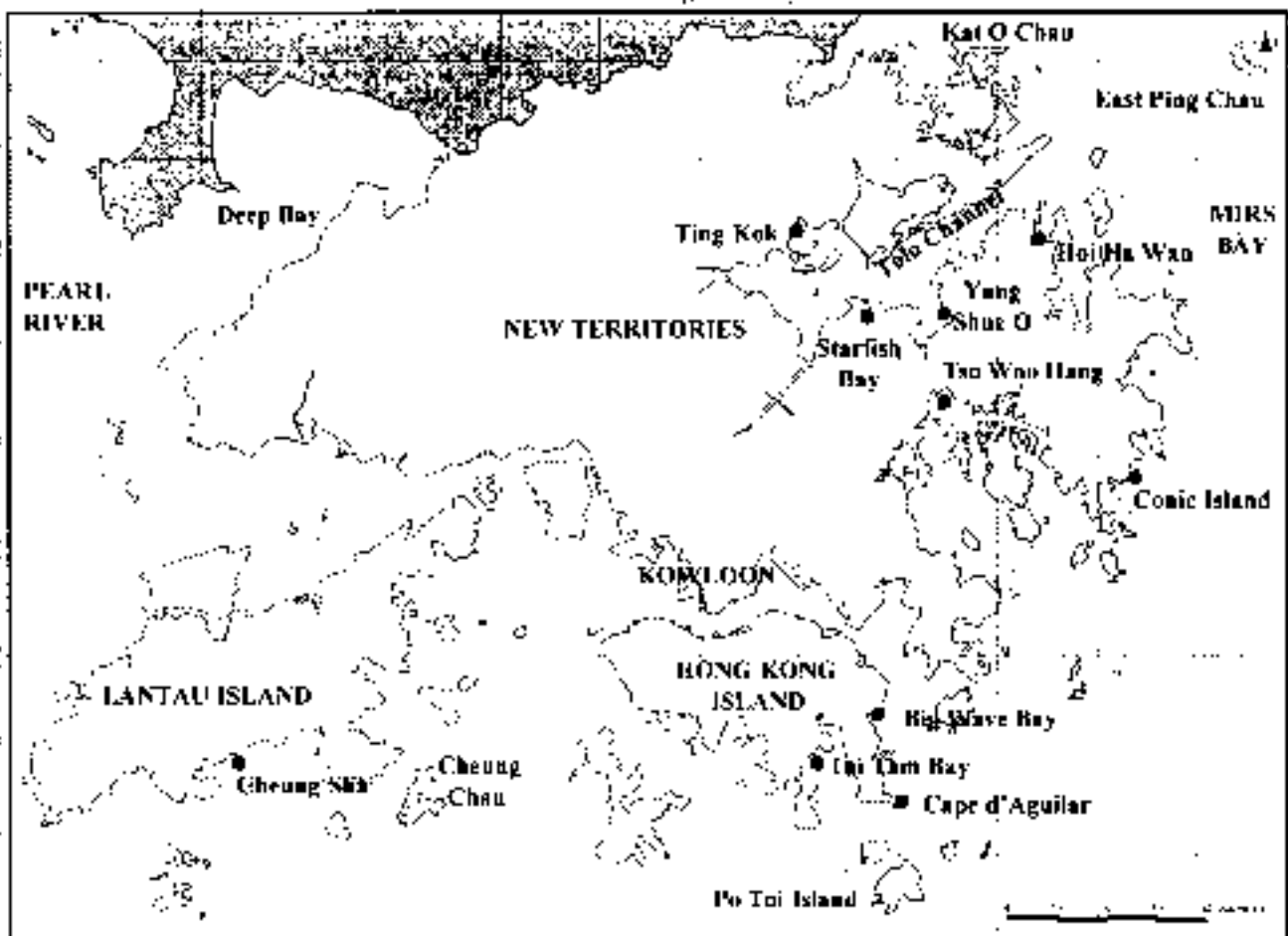


Fig. 1. A map of Hong Kong showing the locations where oysters were collected.

Mitochondrial DNA extraction, amplification, sequencing and analysis. – Two species of *Crassostrea*, collected from Yung She O, Hoi Ha Wan and Tai Tam, were difficult to identify based on shell morphology and were therefore subjected to phylogenetic analysis using COI gene sequences. Sixteen unidentified individuals of *Crassostrea* were taken to the laboratory alive. Genomic DNA was isolated from the oysters using the Dneasy™ Tissue Kit (Qiagen). A partial COI segment of the mtDNA was amplified by PCR using LCO1490 and HCO2198 as forward and backward primers, respectively (Folmer et al., 1994). PCR reactions were set up in a 50 ml volume composed of 0.1 mM of each primer, 1.255 mM MgCl₂, 0.1 mM dNTPs, 5 ml of 10× PCR buffer minus Mg and two units of *Taq* DNA polymerase: 0.2 mg of total genomic DNA was added as a template. The amplification cycles were started by denaturation at 94°C for two minutes. Another 35 cycles followed, with DNA being denatured at 94°C for 60 seconds, primers were annealed at 45°C for 60 seconds and the nucleotide chain extended with *Taq* DNA polymerase (Gibco BRL) at 72°C for 60 seconds, followed by a final extension for 10 minutes at 72°C. The PCR product

was purified using Sephaglas™ BandPrep Kit (Amersham Pharmacia Biotech Inc) and then sequenced using an ABI Prism™ dRhodamine Terminator Cycle Sequencing Ready Reaction Kit and a ABI 377 Perkin Elmer DNA sequencer. PCR primers were used for sequencing.

Cytochrome oxidase I sequences obtained in this study and those of other species of *Crassostrea* available from the GenBank were subjected to phylogenetic analysis. Initial alignments were performed using ClustalX 1.81 (Thompson et al., 1997) and then verified manually to minimize mismatches. Best trees were assessed with maximum parsimony (MP) and neighbour joining (NJ) optimality criteria (PAUP* 4.0b8, Swofford, 1998). Homologous partial COI sequences of *Ostrea chilensis* Philippi in Küster, 1844, [GenBank accession numbers AF112285] (O'Foighil et al., 1999) were used as outgroups as this has been identified as an appropriate outgroup species for the phylogenetic analysis of *Crassostrea* (O'Foighil et al., 1998). Analyses were performed as unweighted heuristic searches using random stepwise additions with 1000 replications. Inferred sequence

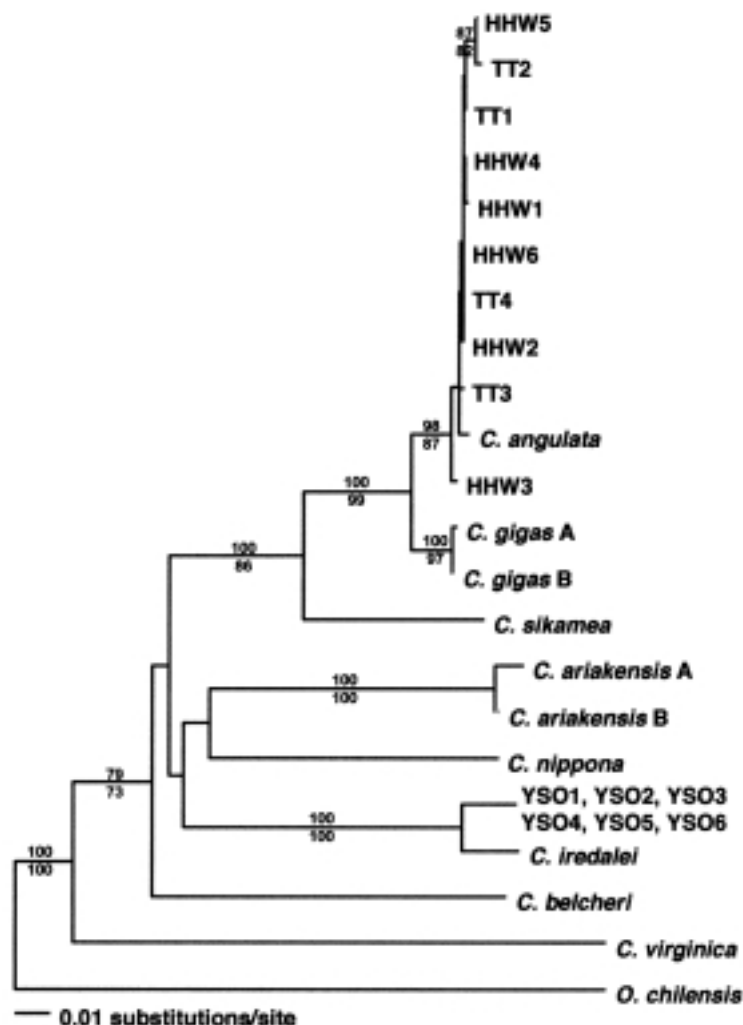


Fig. 2. Neighbour-joining tree based on Kimura 2-parameter distances with 1000 bootstraps using COI mtDNA partial sequences (~618 nt) of *Crassostrea*. The bootstrap percentages supporting each node of the neighbour-joining and most parsimonious trees are indicated above and below the branches, respectively. Only values >70 are shown. The scale represents percentage substitutions. *Ostrea chilensis* is employed as outgroups. YSO1 to 6, HHW1 to 6 and TT1 to 3 are samples collected from Yung Shue O, Hoi Ha Wan and Tai Tam, Hong Kong, respectively.

Table 1. Distance matrix COI among various *Crassostrea* species. Mean pairwise Ti/Tv and percentage Kimura 2-parameter (K2P) are given above and below the diagonal, respectively. NA = Ti/Tv ratios are not available when Tv equals 0.

Species/ populations	1	2	3	4	5	6	7	8	9	10	11
1. YSO1 to 6	-	8.23	2.09	2.17	1.92	2.68	2.83	3.04	1.79	1.23	1.53
2. <i>C. iredalei</i>	3.1	-	2.05	2.13	2.04	2.68	2.78	2.64	1.66	1.28	1.51
3. HHW1 to 6 & TT1 to 3	18.08	17.89	-	NA	13.83	5.68	3.82	4.39	2.54	1.11	1.49
4. <i>C. angulata</i>	18.08	17.93	0.43	-	13.83	3.53	3.89	4.32	2.5	1.11	1.46
5. <i>C. gigas</i>	17.51	18.25	2.75	2.55	-	7.16	3.42	3.79	2.48	1.07	1.36
6. <i>C. sikamea</i>	19.32	19.4	9.36	9.96	10.15	-	3.96	4.94	2.83	1.28	1.37
7. <i>C. ariakensis</i>	18.8	18.54	17.24	17.7	16.69	17.66	-	6.48	2.36	1.42	1.4
8. <i>C. nippona</i>	17.28	17.33	17.95	17.5	16.58	17.1	16.3	-	3.03	1.45	1.45
9. <i>C. belcheri</i>	19.35	19.79	18.61	19.14	18.91	19.01	19.29	19.78	-	1.26	1.18
10. <i>C. virginica</i>	25.66	27.16	25.35	25.64	25.57	26.73	29.29	26.2	27.7	-	1.27
11. <i>O. chilensis</i>	29.29	30.08	29.19	29.62	28.5	29.27	31.69	27.78	29.42	32.94	-

gaps were coded as missing characters and phylograms were constructed by PAUP*. Branch support levels were expressed as bootstrap values of 1000 replicates after 100 stepwise random additions were implemented in an heuristic search. Sequence divergences among species were expressed in terms of Kimura 2-parameter distances (Kimura, 1980) and transition/transversion values.

Abbreviations. – (NHM) The Natural History Museum, London, United Kingdom; (MNHN) Muséum National d'Histoire Naturelle, Paris, France; (UMMZ) Museum of Zoology, University of Michigan, United States; (NSMT) National Science Museum, Tokyo, Japan; (SBMNH) Santa Barbara Museum of Natural History, California, United States; (NMNH) National Museum of Natural History, Washington D. C., United States; and (AM) Australian Museum, Sydney, Australia.

RESULTS

Phylogenetic analysis. – Eight haplotypes were detected among the 16 oyster individuals sequenced for 618 homologous nucleotide COI positions without primer sequences on both the 3' and 5' ends. The number of haplotypes in the samples from Yung Shue O, Hoi Ha Wan and Tai Tam were one, five and four, respectively. Two of the samples, each collected from Hoi Ha Wan and Tai Tam, shared the same haplotype.

The sequences of the unidentified *Crassostrea* were subjected to phylogenetic analysis using the COI sequences of *C. ariakensis* (two haplotypes), *C. nippona*, *C. iredalei*, *C. gigas* (two haplotypes), *C. angulata*, *C. sikamea* and *C. virginica* [GenBank accession numbers AF300617, AF152569, AF300616, AY038078, AF280608, AF152565, AF152567, AF152568 and AF152566, respectively](O' Foighil et al., 1998; Lee et al., 2000; unpublished data by the research teams led by Klinbunga and Yu, respectively). Excluding the inferred gaps which were treated as missing data, a total of

262 sites were variable in our dataset and, of these, 176 were parsimony informative. Six most parsimonious (MP) trees (560 steps, CI = 0.679, RI = 0.683) were obtained by heuristic search with stepwise-addition options of the COI dataset. The topology of the MP and neighbour-joining (NJ) trees is similar with swapping of the positions of individual sequences within each clade. Figure 2 shows the phylogram of the NJ tree obtained by PAUP analyses of the COI dataset. The seven haplotypes of *Crassostrea* individuals from Hoi Ha Wan and Tai Tam, i.e. HHW1 to 6 and TT1 to 3, nested in a well-supported terminal clade with *C. angulata*. The haplotype of samples collected from Yung Shue O, i.e. YSO1-6 was grouped with *C. iredalei* in another terminal clade. Table 1 presents the K2P sequence divergence and transition/transversion values in the COI gene fragment for the above taxa. Combining the results of the phylogenetic analysis with the study on shell characters, the two unidentified *Crassostrea* are thus *Crassostrea lugubris* (Sowerby, 1871) and *Crassostrea angulata* (Lamarck, 1819).

The sequences obtained in this study have been deposited in the GenBank under accession numbers AY249023-AY249033.

CHECKLIST OF HONG KONG OYSTERS

The following is a list and taxonomic description of oysters identified from Hong Kong. Ten species of Ostreidae and two species of Grypheididae are herein identified. All the figured specimens have been deposited in the NHM, London.

Suborder Ostreina Férussac, 1822

Superfamily Ostreoidea Rafinesque, 1815

Family Ostreidae Rafinesque, 1815

Subfamily Crassostreinae Torigoe, 1981

Genus *Crassostrea* Sacco, 1897

Crassostrea lugubris (Sowerby, 1871)

Crassostrea angulata (Lamarck, 1819)

Crassostrea hongkongensis Lam & Morton, 2003

Table 2. Comparison of general shell morphological characteristics of the twelve species of oysters recorded from Hong Kong.

Taxa	Chomata	Shape	Sculpture	Maximum height (mm)
<i>Crassostrea lugubris</i>	Absent	Elongated and slipper-shaped	Right valve covered by flat conchiolin scales with pointed margins	93
<i>Crassostrea angulata</i>	Absent	Spatulate to oval	Both valves have radial ribs and right valve covered with calcareous growth squamae	60
<i>Crassostrea hongkongensis</i>	Absent	Spatulate	Right valve covered with flat conchiolin lamellae	180
<i>Crassostrea ariakensis</i>	Absent	Oval to spatulate	Right valve covered with erect conchiolin lamellae	230
<i>Saccostrea cucullata</i>	Present	Oval to subtriangular	Right valve covered by growth squamae with hyote spines	40
<i>Saccostrea mordax</i>	Present	Triangular or elongate D-shape	Parallel grooves run from hinge to ventral margin	60
<i>Planostrea pestigris</i>	Present	Oval	Flat and smooth	75
<i>Dendostrea folium</i>	Inconspicuous	Orbicular to oval	Smooth, covered by dichotomous ribs	80
<i>Dendostrea crenulifera</i>	Present	Variable form, usually oval	Heavily eroded, white calcareous layer exposed	30
<i>Ostrea denselamellosa</i>	Inconspicuous	Subtriangular to oval	Right valve covered by thin conchiolin scales	70
<i>Hytissa imbricata</i>	Present	Circular	Dichotomous ribs, growth squamae and occasion hyote spines on both valves	150
<i>Hytissa sinensis</i>	Present	Circular	Shell thick and heavy, with radial ribs	150

Crassostrea ariakensis Fujita, 1913
 Genus *Saccostrea* Dollfus & Dautzenberg, 1920
Saccostrea cucullata (Born, 1778)
Saccostrea mordax (Gould, 1850)
 Genus *Planostrea* Harry, 1985
Planostrea pestigris (Hanley, 1846)
 Genus *Dendostrea* Swainson, 1835
Dendostrea folium (Linnaeus, 1758)
Dendostrea crenulifera Sowerby, 1871
 Genus *Ostrea* Linnaeus, 1758
Ostrea denselamellosa Lischke, 1869
 Family Gryphaeidae Vyalov, 1936
 Subfamily Pycnodontinae Stenzel, 1959
 Genus *Hytissa* Stenzel, 1971
Hytissa imbricata (Lamarck, 1819)
Hytissa sinensis (Gmelin, 1791)

TAXONOMY

A comparison of shell morphological characteristics of the twelve herein identified species of Hong Kong oysters is shown in Table 2. The following are detailed descriptions of the species.

FAMILY OSTREIDAE

SUBFAMILY CRASSOSTREINAE

Crassostrea Sacco, 1897

Crassostrea Sacco, 1897: 15; Dall, 1898: 671; Hirase, 1930: 41; Stenzel, 1971: N1128-N1131; Torigoe, 1981: 304, 325; Harry, 1985: 152, 156; Coan et al., 2000: 216.
Dioeciostrea Orton, 1928: 320.

Type species. – *Crassostrea virginica*, Gmelin, 1791, by original designation.

Description. – Size varies among species and populations and can be up to 60 cm in height. Outline is variable among individuals but is usually high, slender and spatulate. Shell rough externally with many nonappressed, irregularly spaced growth squamae which are either simple or frilled along their free ends. Rounded radial ribs on some individuals, more common on left than on the right valve and tend to end as undulating ventral shell margins. Chambers are common. Well-developed umbonal cavity on left valve. No chomata. Adductor muscle scar close to postero-ventral valve margin. Ligamantal area on left valve well-developed with dense growth foliations. This always give rise to a well-developed, convex resilifer and ligamantal area on the right valve. Nonincubatory. Cosmopolitan.

Crassostrea lugubris (Sowerby, 1871)

Common name: Black-scar oyster
(Figs. 3A-C)

Ostrea lugubris Sowerby, 1871: Fig. 63.

Ostrea iredalei Faustino, 1932: 546-547, 550, Pl. 1; Talavera & Faustino, 1933: 49-50, Pls. 1-2.

Crassostrea iredalei - Carreon, 1969: 109-110, Pl. IV; Yoosukh & Duangdee, 1999: 367, Fig. 5.

Material examined. – Holotype – dry shells (length by height = 77.57 by 53.23 mm)(NHM 1900.2.13.30), ‘‘North America’’, coll. Hanley (1819-1899), no date.

Description. – Shell outline variable but typically elongated and slipper-shaped when grown singly either on or close to the bottom. Margin non or only weakly plicate. Right valve is flat and covered with dense layers of flat, brown scales with finely pointed margins. Left valve is purple or yellowish white, more deeply cupped (especially those grown in clusters) and with a more produced ligamental area than the right one. The hinge line is straight and short. Ligament area is short. Shell background is internally shiny white with colour patches varying from yellow, orange to purple. Patches of chalky white calcium carbonate may be present on the internal surfaces of the valves, near the dorsal shell margin. No chomata. Muscle scar is deep purple on both valves, reniform and displaced postero-dorsally.

Distribution. – In Hong Kong, this species is restricted to shores along Tolo Channel, e.g. the sandy shore of Starfish Bay (= Hoi Sing Wan), mangroves at Ting Kok and the sandy shore at Yung Shue O. This species has not been documented from Hong Kong because of its limited distribution and difficult-to-access habitats. Individuals usually grow either singly or in clusters on sandy or muddy bottoms at lower intertidal levels.

Remarks. – The holotype of *Ostrea lugubris* shows very similar shell characters to the type specimen of *C. iredalei* (figured as drawings in Faustino, 1932: 550, Pl. 1, and

photographs in Talavera & Fautino, 1933: 49-50, Pls. 1-2). *Ostrea lugubris* is considered to be synonymous with *C. iredalei* (Yoosukh & Duangdee, 1999). *Ostrea lugubris* differs from other *Crassostrea* species in having patches of colour, which may be either brownish-yellow, purple or light orange, on the valve interiors. It is also characterised by the purple left valve being sculptured with weak, dense, discontinuous radial ribs which is unusual in the genus.

The result of the phylogenetic analysis confirmed that the collected samples from Yung She O, Hong Kong, are *Crassostrea lugubris* (= *C. iredalei*). Hong Kong samples and *C. iredalei* from Thailand [GenBank accession number AY038078] show a divergent K2P sequence divergence, in terms of partial COI gene, i.e. 3.1%. This value is greater than that between *C. gigas* and *C. angulata*, i.e. 2.55%. Two populations of New Zealand *Ostrea chilensis* have also shown pronounced sequence divergence for a 609 nucleotide fragment of COI gene, i.e. 3.1%. The mitochondrial dichotomy between Hong Kong *C. lugubris* and Thai *C. iredalei* may be due to the geographical isolation of the former population. *Crassostrea iredalei* has been reported to occur in the Philippines and Thailand (Yoosukh & Duangdee, 1999) but there is no other identified *C. lugubris* population in Hong Kong and adjacent waters. The holotype of *C. lugubris* was collected by Hanley from the China coast but no specific location was given.

Crassostrea angulata (Lamarck, 1819)

Common name: Portuguese oyster
(Figs. 3D-F)

Gryphaea angulata Lamarck, 1819: 198.

Crassostrea angulata Ranson, 1967: 127-199; Lam, 2003: 107-108, Pls. 3-6.

Material examined. – Holotype – right valve only (length 103 mm)(MNHM, no registration number, from Lamarck’s collection), no locality, coll. Sallé, 1819.

Description. – Hong Kong individuals up to ~60mm in height. Shell outline variable with usually spatulate to oval individuals. Attachment area of left valve depends on the substratum. Both valves concave with left more deeply cupped and hence a deep umbonal cavity. Both valves have dichotomous radial ribs from the umbo; the tops of the ribs are well-rounded and radial ribs with growth squamae are recognisable on both valves. The older part of the right valve, i.e. the dorsal surface, is usually eroded. Wavy plications along the shell margins reflect the positions and height of the ribs. No chomata. Adductor muscle scar reniform, antero-dorsal border concave and close to the postero-ventral shell margin from the centre of the valve. External coloration of both valves is variable from white and light purple with deep purple lines radiating from the umbo. Internally, the shell is white with patches of chalky deposits and hollow chambers. The muscle scar is colourless with occasional purple growth lines.

Distribution. – This species originated in Taiwan and was introduced into Portugal and Spain for cultivation. It is one of the important commercial oyster species in Taiwan and Western Europe. Although this species is cultured in Taiwan extensively, it occurs as wild populations and in low abundance in Hong Kong. Only two bays with constant freshwater inputs, i.e. Hoi Ha Wan and Tai Tam Bay, have been identified as local habitats.

Remarks. – The shell and anatomy of this species cannot be

distinguished morphologically from *Crassostrea gigas*. The *C. angulata* specimens collected from Hong Kong have been genetically identified using mitochondrial DNA sequences. *Crassostrea angulata* from Hong Kong (this study) and Portugal [GenBank accession number AF152567] (O’ Foighil et al., 1998) showed an intraspecific K2P sequence divergence value of 0.43%. Hong Kong *C. angulata* morphologically resembles and occurs in low abundance at the same shore level as the rock oyster, *Saccostrea cucullata*. This may be why *C. angulata* has not been recorded from Hong Kong

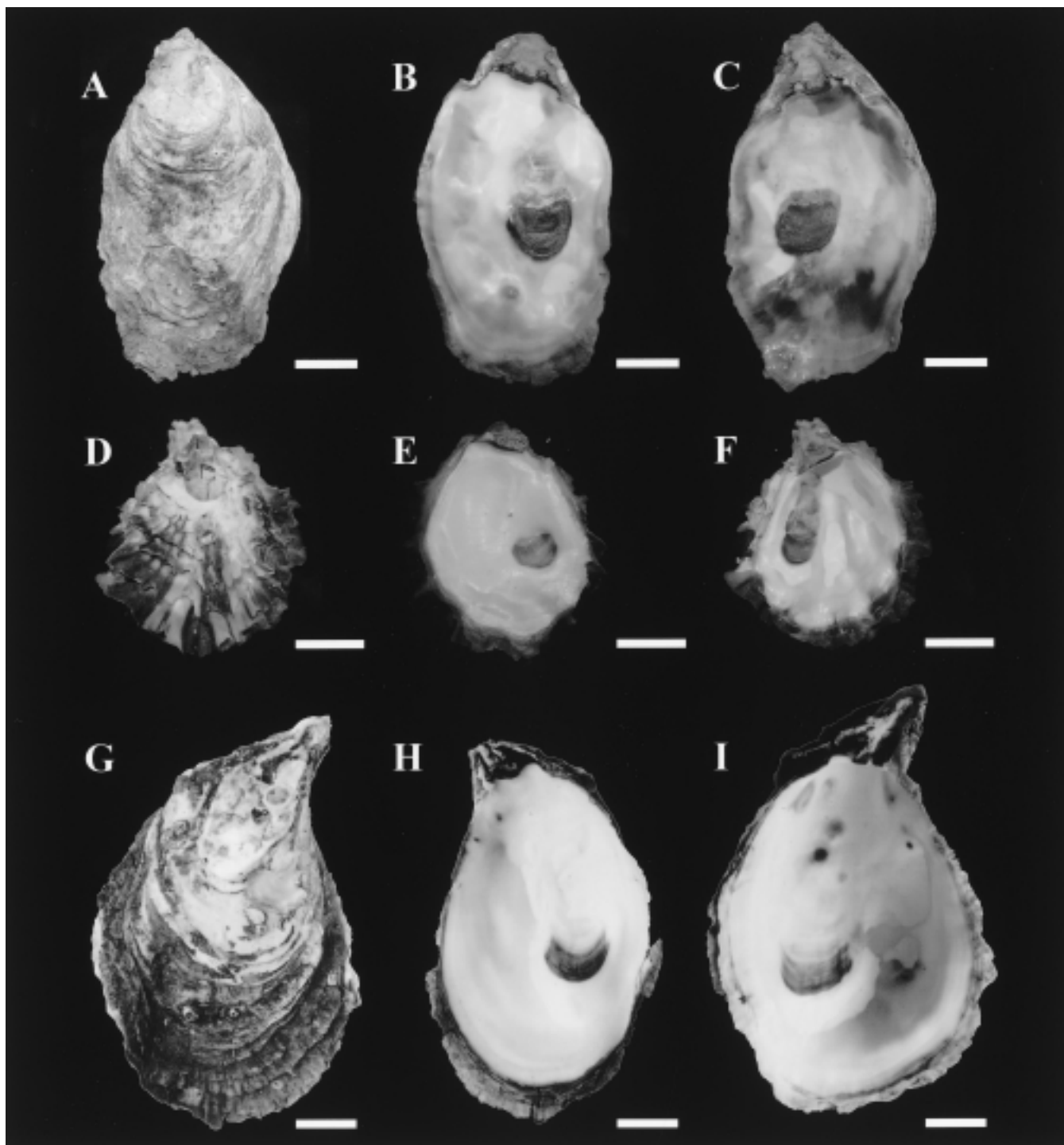


Fig. 3. *Crassostrea* from Hong Kong showing external and internal views of the right valves and the internal views of the left valves. A-C. *C. lugubris* (NHM 20030490). D-F. *C. angulata* (NHM 20030491). G-I. *C. hongkongensis* (NHM 20020501). Scale bars = 20 mm.

hitherto. The two can be distinguished by examining the eroded dorsal side of the right valve. Alternate white calcareous and brown conchiolin layers are exposed in *S. cucullata* whereas only white calcareous layers occur in *C. angulata*.

Crassostrea hongkongensis Lam & Morton, 2003

Common name: Hong Kong cultured oyster
(Figs. 3G-I)

Crassostrea gigas – Morton & Wong, 1975: 139-149, Pls. 14-16;
Morris, 1985: 123-125, Pl. 2, Figs. A-F.

Crassostrea hongkongensis Lam & Morton, 2003a: 1-13, Fig. 3.

Material examined. – Holotype – One dry shell and preserved tissues (135 by 82.5 mm)(NHM 20020501), ‘‘Lau Fau Shan, Deep Bay, Hong Kong, 837 500N 816 950E’’, coll. K. Lam, 9 Feb.2001.

Paratypes – Three dry shells and preserved tissues (largest 160 by 93 mm)(NHM 20020502, UMMZ 3000076, NSMT-Mo 73486), same data as holotype.

Others – Ten dry shells and preserved tissues (largest 129 by 76 mm)(NHM 20020503), same data as holotype; 10 dry shells and preserved tissues (largest 161 by 68 mm)(SBMNH 348407-348416), same data as holotype.

Description. – Shell elongate dorsoventrally with a spatulate form, being broader towards the ventral margin and tapering dorsally. Right valve is slightly convex. Left valve is cupped. No ribs on the surface of either the right or left valves. The surface is encrusted with smaller oysters and barnacles and the shell is bored by polychaetes, sponges and the bivalve *Aspidopholas obtecta* (Wong, 1975). Concentric growth increment lines spreading from the umbone of the right valve give rise to brownish-yellow and brittle conchiolin lamellae. Unbroken lamellae have radiating rays which end in the slightly undulating ventral shell margin. The soft flaky lamellae of the outer prismatic layer at the ventral margin forms a flexible edge. At the older parts of the shell, i.e. near the umbones, the lamellae are eroded with the white chalky layer of the shell often exposed. The left valve is covered with white growth squamae. During life, the left dorsal shell margin grows towards the right, producing commarginal and slightly erect layers of old ventral margins during each season of faster growth. Attachment area is small and appears as a patch at the umbone with the rest of the left valve surface unattached.

The hinge line is short and slightly curved. The ligament is large, occupying the full length of the hinge line. The resilifer is typically greatly elongated in both valves with a deep channel formed by the growth increments of the inner fibrous layer of the ligament. The interior of the shell is translucent white with patches of opaque white chalky deposits. The adductor muscle scar is large, D-shaped and white with light purple growth lines. The adductor muscle scar is located towards the posterior side between the middle and ventral third of the pallial area. Chomata on the inner shell margin and commissural shelf are not developed.

Distribution. – This species is cultivated in the Pearl River Delta, Guangdong Province, China, i.e. under estuarine conditions. In Hong Kong, it occurs only in Deep Bay (= Hau Hoi Wan). It is cultured in oyster farms but also occurs as wild individuals on intertidal and subtidal rocks along the shoreline of Deep Bay. This species may also be cultured in oyster farms along the shores of the Pearl River Delta, and elsewhere in China. Deep Bay, Hong Kong is, however, the only known locality for this species.

Remarks. – In the Pearl River Delta, the cultivation of species of *Crassostrea* is reputed to have a ~700 year history, the industry in Hong Kong currently being centred around the village of Lau Fau Shan in Deep Bay. There are two methods of oyster cultivation employed in Deep Bay. One involves the collection of spat on concrete tiles (25×13×1.5 cm) or posts deployed on the lower shore and sublittoral mud (Morton & Wong, 1975) whereas the other is the more recently developed raft culture. Shucked oysters cultivated in Deep Bay are usually either sold fresh to Hong Kong markets or sun-dried for export. Part of the harvest is sold to make oyster sauce, a popular Chinese seasoning.

Crassostrea ariakensis Fujita, 1913, ex Wakiya MS

Common name: Suminoe oyster
(Figs. 4A-C)

Ostrea rivularis Lischke, 1869: 176, Pl. 14, Figs. 2, 3.

Ostrea ariakensis Fujita, 1913: 519, ex Wakiya MS; Wakiya, 1929: 363-364, Pl. 9, Figs. 1, 2.

Crassostrea ariakensis - Torigoe, 1981: 377, Pl. 15; Lam, 2003: 109-110, Pls. 9, 10.

Material examined. – Type not examined, its location being unknown (K. Torigoe, pers. comm.).

Description. – Shell outline is orbicular to spatulate; outline tongue-shaped. External surface is whitish with broken rays of purplish brown. The scales of the outer shell layer radiating from the dorsal side are brown to light brown. This species is sympatric with *Crassostrea hongkongensis* and is, thus, bored and heavily encrusted by other marine invertebrates in a similar way. Left valve deeply cupped. Right valve usually either flat or slightly convex dorsally and slightly concave near the ventral margin. Internally whitish with hollow chambers of irregular size and position. Hinge line short; the ligament occupying its full length. Attachment area of the left valve is variably small, usually not more than half the shell height. Adductor muscle scar is D-shaped with the outline on the dorsal side being concave and with light to dark purplish growth lines which vary in colour among individuals. Colour may be different on right and left valves in the same individual.

Distribution. – This species is cultivated in the Pearl River Delta, Guangdong Province, China, i.e. under estuarine conditions. In Hong Kong, it occurs only in oyster farms in Deep Bay and is thus cultured with *Crassostrea hongkongensis* but in lower numbers. The species is reported

to occur naturally in Japan and along the southern coast of China to Vietnam. It is also cultivated in Oregon and Washington, the United States of America (Robinson & Langdon, 1992).

Remarks. – *Crassostrea ariakensis* has been called *C. rivularis*, which has been determined to be invalid (Torigoe, 1981). This is because the holotype of *Ostrea rivularis* Gould, 1861, from the East China Sea was in fact a species of *Lopha*

and is different from *O. rivularis* as described by Lischke, 1869 (Habe & Kosuge, 1967). It is difficult to separate *C. ariakensis* and *C. hongkongensis* using external shell characters. In general, however, the former is more rounded and scales on both valves are generally more erect. The definitive morphological distinction between the two is the shape of the adductor muscle. In *C. ariakensis*, the adductor muscle scar is crescent-shaped, whereas in *C. hongkongensis* the outline of the muscle on the dorsal side is straight to slightly convex.

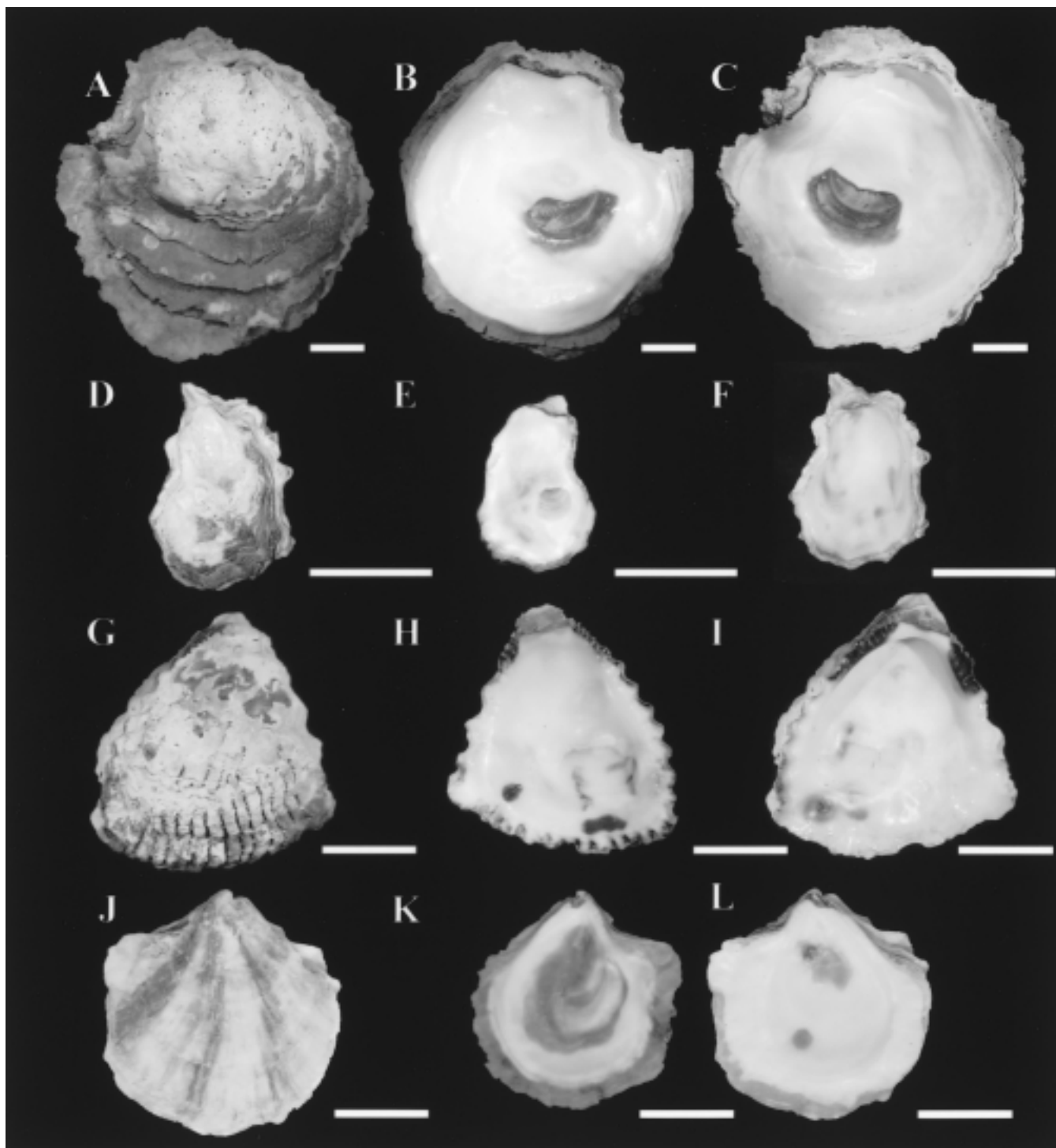


Fig. 4. *Crassostrea*, *Saccostrea* and *Planostrea* from Hong Kong showing external and internal views of the right valves and the internal views of the left valves. A-C. *C. ariakensis* (NHM 20030470). D-F. *S. cucullata* (NHM 20030496). G-I. *S. mordax* (NHM 20030492). J-L. *P. pestigris* (SBMNH 345716). Scale bar = 20 mm.

Saccostrea Dollfus & Dautzenberg, 1920

Saccostrea Dollfus & Dautzenberg, 1920: 471; Stenzel, 1971: N1134-N1135; Torigoe, 1981: 306, 327-328; Harry, 1985: 150.

Type species. – *Ostrea saccellus* Dujardin, 1835, by monotypy.

Description. – Small to medium-sized. Shell shape varies from spatulate and oval ostreiform to abnormal rudistiform. There may be a small, operculiform right valve and a large, conical, cornucopia-like left valve carrying a large ligamental area. Left valve attaches to hard substrata such as bare rock surfaces or mangrove roots and stems and carries layers of growth squamae and rough irregular rounded dichotomous radial ribs. Size of umbonal cavity depends on attachment area of left valve and thus varies among individuals. Right valve is flat with scaly growth squamae of conchiolin. Chomata present, usually stronger along the posterior and anterior margins but faded ventrally or encircling the entire valve. Chomata may be very weak in some individuals. Nonincubatory. Geographic distribution includes the Indo-Pacific, Indian Ocean and Mediterranean Sea.

***Saccostrea cucullata* (Born, 1778)**

Common name: Rock oyster (Spiny oyster for the ‘*echinata*’ morpho- or ecotype)
(Figs. 4D-F)

Ostrea cucullata Born, 1778: 100; 1780: 114, Pl. 6, Figs. 11, 12; Awati & Rai, 1931: 1-107.

Ostrea echinata Quoy & Gaimard, 1835: 455, Pl. 76, Figs. 13, 14.

Ostrea commercialis Iredale & Roughley, 1933: 278.

Saccostrea cucullata Stenzel, 1971: N1134-N1135, Fig. J106; Morris, 1985: 125-128, Pl. 3, Figs. E, F, G; Lam, 2003: 110-112, Pls. 11, 12.

Material examined. – Born’s type is deposited in the Naturhistorisches Museum, Vienna (Morris, 1985): data unknown.

Description. – Shell small, up to ~ 40 mm in length and ~ 30 mm in width, with an oval to subtriangular outline, depending upon substratum and available space. Hinge line is straight, short, with the ligament occupying its total length. Ligamental area short. The external surfaces of both left and right valves are white to lilac with a dark purple coloration at the shell margin. White radiating stripes occur on the right valves of some specimens.

The attachment area of the left valve, i.e., the one attached to the substratum, is usually at least half the shell length, and is often complete. Commissural shelf not obvious. The surface of the left valve has up to about 15 ribs radiating from the umbone. Concentric layers of weak flaky growth squamae with hyote spines at rib-intersecting points occur in specimens in which the left valve is raised above the substratum and sheltered from erosion. Fine crenulations along the ventral shell margin identify the number of ribs present. They form a flaky shell margin patterned black, white and yellow. For individuals with a complete attachment area, the flat left

valves are slightly larger than the right, shallowly cupped and have slightly raised margins with dense growth squamae.

The flat to slightly convex right valve is covered with concentric layers of dense, flaky lamellar scales radiating from the ligament. These scales are usually eroded along the ligamental side and where concentric growth squamae are revealed. They end as black or yellow conchiolin scales along the ventral shell margin. The shell margin is crenulate reflecting the number and position of the radial ribs. The marginal plications are small, usually regularly-spaced and sharply-rounded.

The right valve of the ‘*echinata*’ ecotype of *Saccostrea cucullata* is slightly convex. External surface is eroded but there may be between 10-30 closely spaced radial to sub-parallel ribs and short, hollow, black hyote spines. Ribs not raised; may retain thick, overlapping, dark greenish-black, conchiolin scales. Where the conchiolin scales are eroded, the exterior surface is either white or purplish black with white streaks radiating from the umbone and at the margins. Shell margin crenulate to irregularly plicate with flaky scales fitting closely within the margin of the left valve. The right valve of juveniles is circular, black and covered densely with short hyote spines.

Interiors of both valves are usually iridescent bluish green or opalescent white with patches of bluish green, or olive to yellowish green. The adductor scar is large, D-shaped, and may have purple or yellow growth bands paralleling the width of the shell. The scars on the left and right valves of the same specimen are of the same shape, size, and colour. The scar is positioned in the posterior ventral third of the pallial area. Chomata and gutters may be present in young individuals. These are well developed from the hinge region to the adductor muscle, but fade beyond.

Distribution. – This oyster dominates the eulittoral zone of sheltered rocky shores such as Hoi Ha Wan, Starfish Bay, Tso Woo Hang, Deep Bay and Tai Tam Bay and mangroves such as Ting Kok (Morton, 1990; Chiu, 1997, 1998). It forms a clear visible oyster zone restricted by the level of Mean High Water Neap Tides (MHWNT). It is rare on exposed shores such as Cheung Sha and Cape d’Aguilar. It also occurs on submerged, sheltered concrete structures of the pier on East Ping Chau and is scattered individually among the barnacle zone at Big Wave Bay, Hong Kong Island. This species is distributed in both the subtropical and tropical Indo-West Pacific, from southern Japan to Australia (authors’ unpublished data).

Remarks. – Because of shell plasticity, the taxonomy of *Saccostrea* has been problematic. Some *Saccostrea cucullata* “forms” have been cross-referred to using different names by different authors, e.g. *S. echinata*, *S. mordax* and *S. glomerata*. Mitochondrial DNA sequence analysis of these oysters has shown that *S. cucullata* is a superspecies with *S. glomerata* as a component species and *S. echinata* as a morpho- or ecotype (authors’ unpublished data).

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

Common name: Crenulate rock oyster
(Figs. 4G-I)

Ostrea cucullata Lamarck, 1819: 200.

Ostrea mordax Gould, 1850: 346; Sowerby, 1871, Pl. 15, Figs. 31a, b.

Ostrea forskali var. *mordax* Lamy, 1929: 159.

Ostrea amasa Iredale, 1939: 399, Pl. 17, Fig. 8.

Crassostrea amasa Thomson, 1954: 154, Pl. 7, Figs. 1, 2.

Crassostrea tuberculata Thomson, 1954: 157, Pl. 8, Fig. 3.

Saccostrea mordax Torigoe, 1981: 328, Pl. 17; Qi & Choe, 2000: 138-139, Figs. 3C-E; Lam, 2003: 112-113, Pl. 13.

Saccostrea cucullata - Morris, 1985: 125-128, Pl. 3, Figs. A, B, C, D.

Material examined. – Syntypes – three dry shells (NMNH 5958), ‘‘Feejee Islands’’ (Fiji), coll. United States Exploring Expedition, no date.

Description. – Shell medium, up to 60 mm in length, 40 mm in width. Outline triangular or an elongate D-shape depending upon substratum and space. The left valve is flat and completely attached. It is very thin and easily broken with a hard hit when a specimen is collected. The margin of the left valve is built up steeply along the anterior and posterior sides. The margins are thick, with packed layers of growth squamae running along the margin and perpendicular to these are closely and evenly spaced ribs ending as marginal crenulations. In most cases, where the oyster is growing on unlimited flat rock surfaces, the anterior margin is reduced so that the right valve is in touch with the substratum. When viewed along the mouth-anus axis, the shape of the oyster is almost a right-angled triangle with its height given by the height of the posterior margin and its base by the left valve. The hinge line is straight and short. The ligament area is elongated to form an obvious left beak. The left valve of juveniles is a thin white calcite pad attached completely to the substratum.

The right valve is convex and white with purple patches on the less eroded ventral area. It is usually eroded with exposed conchiolin scales near the dorsal end. Parallel grooves extend from half way along the dorso-ventral axis to the ventral shell margin. These grooves reveal uneroded growth lines on the right valve. They are also present on juveniles which have a fan-like, triangular shell. Evenly-spaced crenulations around the shell margin are more obvious anteriorly and posteriorly.

The interior of the shell is white with a shiny, pearly appearance. A band of dark green conchiolin usually occurs near the ventral margin of the right valve. This band may be absent in some specimens. It appears that the conchiolin and prismatic calcite layers are deposited alternatively at the right, inner, ventral shell margin. The adductor muscle scar is relatively large and positioned in the posterior ventral half of the pallial area. It is circular to elongate-oval according to the growth form of the shell and mostly white, slightly stained with growth bands or purple. The chomata are white, short and rod-shaped and arranged in a single line around the inner

margin. These are more prominent dorsally and fade out as they extend towards the ventral shell margin.

Distribution. – *Saccostrea mordax* occurs only on oceanic, exposed rocky shores such as Cape d’Aguilar and Big Wave Bay. At Big Wave Bay, it occurs as individuals among the *Septifer* and *Tetraclita* zone on rocky slopes. At Cape d’Aguilar, it occurs in rock pools frequently refreshed by strong waves. This species is widely distributed in the Indo-West Pacific, e.g. Japan, Korea, Taiwan, Hong Kong, South China Sea, Peninsula Malaysia, Singapore, Indonesia, New Hebrides and Australia.

Remarks. – *Saccostrea mordax* has been identified previously as *S. amasa* and *S. tuberculata* (Thompson, 1954). This species is often confused with *S. cucullata* because of similar shell characters. Like *S. cucullata*, *S. mordax* is probably a superspecies. Two genetic lineages of this species from the Indo-West Pacific have been differentiated by mitochondrial DNA sequences (authors’ unpublished data).

***Planostrea* Harry, 1985**

Planostrea Harry, 1985: 143.

Type species. – *Ostrea pestigris* Hanley, 1846, by original designation and monotypy.

Description. – Shell of moderate size (~ up to 75 mm in height), very compressed in one plane. The valves are weakly lamellose with few growth rests and little shell erosion. Thin, cylindrical and widely-spaced radial ribs on the left valve. The surfaces between the ribs are flat. Chomata are well developed, uniform and closely spaced along the posterior and anterior margins near the hinge. A wide commissural shelf on the left valve is flat, well-defined along the inner edge and regularly thickened with chalky deposits. The shell exterior is light to dark lavender with numerous darker radial stripes. Geographic distribution limited to certain Indo-Pacific areas, e.g. the Philippines (type locality), Hong Kong, Taiwan, Thailand, North Borneo, and Queensland, Australia.

***Planostrea pestigris* (Hanley, 1846)**

Common name: Flat oyster
(Figs. 4J-L)

Ostrea pestigris Hanley, 1846: 106-107; Morris, 1985: 129, Pl. 4A-D; Scott, 1994: 69, Pl. 5B.

Ostrea paulucciae Crosse, 1869: 188.

Ostrea palmipes Sowerby, 1871, sp. 56, Figs. a-c.

Planostrea pestigris Harry, 1985: 143, Fig. 22.

Material examined. – Holotype – dry shell (height, 75 mm)(U. S. National Museum, USNM 666809), ‘‘Isle of Luzon; on rocks’’, coll. H. Cuming, no date.

Other – Syntype of *Ostrea palmipes* – One dry shell (NHM 1907.10.28.77 & 1907.12.30.10-11), no other data.

Description. – Shell of moderate size, up to 80mm high. Outline subquadrate, attenuated dorsally. Shell laterally compressed, generally in one plane. The smaller right valve fits closely within the margin of the left. Right valve smooth, with the outer shell layer continuous and having few growth increments. Little shell erosion and few encrustations. Cream to yellowish, usually with dark lavender irregular rays. Left valve usually either light or white, with 6-10 low, widely-spaced ribs which may have obsolete hyote spines at some growth increments. Attachment area is small at the left umbo. Most are attached to shells of other gastropods and bivalves. Some are unattached. Chomata are small, uniform, closely-spaced and in straight lines along the anterior and posterior margins near the hinge. Hinge line straight and short. Ligament area slightly extended in both valves. Marginal commissural shelf on the left valve is wide and flat with a well-defined inner edge. The interior of the shell is white with a pearly nacre. Chalky deposits are prominent on the commissural shelf of the left valve only. The adductor muscle scar is white, large and elongate. It is positioned approximately at the middle of the shell, slightly towards the posterior.

Distribution. – Intertidal zone to 10m on rocks and corals. Indo-West Pacific, the Philippines, Taiwan, Thailand, North Borneo, Mauritius, South and East China Seas, Yellow Sea, Shandong Province, China to Honshu, Japan, Townsville, Queensland, Australia. Hong Kong; 8-10 m in Tolo Channel and southern waters of Hong Kong.

Remarks. – Harry (1985) proposed a new genus, *Planostrea*, exclusively for *Ostrea pestigris*. This genus is described as of moderate size (to 75 mm), very compressed in one plane, being non-lamellous and with a continuous outer shell layer. Well-developed chomata line up along the dorsal margins near the hinge, with a wide and flat marginal commissural shelf and a lavender outer surface with radial stripes. This species can be distinguished easily from other oysters because of the consistent shape of a smooth, flattened, circular disc. Unlike other oysters, it is usually free from encrustations and the influence of the substratum to which it is attached. This species has been synonymised with *Ostrea paulucciae* Cross, 1869 and *O. palmipes* Sowerby, 1871 in terms of similar shell characters (Tchang & Lou, 1956).

***Dendostrea* Swainson, 1835**

Dendostrea Swainson, 1835: 39; Torigoe, 1981: 315-316, 336; Harry, 1985: 137-138.

Type species. – *Ostrea folium* Linnaeus, 1758, by subsequent designation (Herrmannsen, 1847)

Description. – Shell small to medium, up to ~85 mm. Outline irregularly subcircular. Right valve usually more convex than the left. Rounded radial ribs may be present on both valves and ending at rounded and plicate ventral margins. Shell exterior usually smooth with a waxy texture and covered by occasional and weak growth squamae. Shell interior is white

with brown or light green patches. Chomata along margins restricted near hinge or extended to the ventral margin. Larviparous.

***Dendostrea folium* (Linnaeus, 1758)**

Common name: Foliate oyster
(Figs. 5A-C)

Ostrea folium Linnaeus, 1758: 699; Born, 1780: 112; Dodge, 1952: 190-191.

Dendostrea glaucina Lamarck, 1819: 212.

Dendostrea folium Swainson 1835: 39; Sowerby 1839: 137; Fig. 181; Iredale, 1939: 402, Pl. 7, Fig. 11; Torigoe 1981: 315-316, 336-337, Pl. 5, Fig. 2, Pl. 26; Harry, 1985: 137-138, Fig. 18; Carriker & Gaffney, 1996: 8; Lam, 2003: 113-114, Pl. 14.

Ostrea (Pretostrea) bresia Iredale, 1939: 396-397.

Lopha folium Stenzel, 1971: N1157, Fig. J47.

Material examined. – Type not studied. The type material is in the University Museum, Uppsala, Sweden (561, 991, 1043). This species is not represented in the Linnaean collection of the Linnean Society of London.

Description. – Shell of medium size, up to 80mm in height. Outline orbicular to oval, subequivalve. Both valves concave with dichotomous ribs radiating from the umbones and ending ventrally as either a zig-zagged or rounded undulating margin. Rib tops are rounded and bear obsolete hyote spines at some growth increments. There are two colour morphs, i.e. dark yellow and dark purple. Reddish-purple streaks may radiate from the umbones. Usually, the growth squamae on both valves are eroded and the shell is thus often smooth. The attachment area of the left valve extends halfway from the umbo to the ventral margin. Commissural shelf not developed. Umbonal cavity shallow. The ligament is short. Ligamental area not extended. Chomata usually either not present or restricted to both sides of the ligament and to half the shell height as small elongate tubercles and corresponding pits. The interior of the shell is lustrous white with iridescent bluish green patches particularly along ridges formed by the ribs. The interior shell margin is the same as that of the exterior. The adductor muscle scar is either reniform or crescentic and the same colour as the interior of the shell. It is positioned posterior to the centre of the pallial area.

Distribution. – Usually shallow sublittoral fringe to 8-10m; might extend to 50m on rocks. Attached to other living sessile bivalves such as fan shells (*Pinna atropurpurea*) and *Isognomon ehippium*. Indo-West Pacific, Australia, the Philippines, South and East China Seas, Hainan, Taiwan to Kii Peninsula, Japan. Hong Kong; shallow sublittoral fringe to 8-10m in Tolo Channel and Mirs Bay.

Remarks. – Sometimes, species of *Hyotissa* may be confused with *Dendostrea folium* especially in terms of external shell characters. Internal shell characters are more reliable in distinguishing these two species. For example, the shape of the adductor muscle scar is the most important feature for identification: that of *Hyotissa* is large and circular while that

of *Dendostrea folium* is crescentic. Species of *Hyotissa* also have a well-developed commissural shelf and are whitish internally whereas *Dendostrea* does not have an obvious commissural shelf and internally the basal whiteness is always patterned with dark yellowish green patches showing the position of radial rays.

***Dendostrea crenulifera* (Sowerby, 1871)**

Common name: Crenulate oyster
(Figs. 5D-F)

Ostraea crenulifera Sowerby, 1871: 67, Pl. 27, Figs. 67a, b.
Dendostrea crenulifera Torigoe, 1981: 338-339, Pl. 28; Hayami, 2000: 926-927, Fig. 12.

Material examined. – Syntypes, two dry shells (largest 36.71 by 21.39 mm)(NHM 1879.2.26.242), ‘Red Sea’, coll. Lombe-Taylor, no date.

Description. – Shells are < 30mm in dorso-ventral height and of variable form, depending on the substratum. Attachment area varies among individuals. Shell margins usually crenulated: hence the name ‘*crenulifera*’. Some individuals have deep and regular plications whereas others have poorly-developed ones along the margins. The right valve is usually heavily eroded such that the white, chalky calcareous shell layer is exposed. Thin, reddish brown radial lines on the right valves can be observed on uneroded specimens. The left valve is also white. Small, rounded chomata are present either along the posterior and anterior margins or along the entire shell margin. The hinge line is straight and short. Ligament area

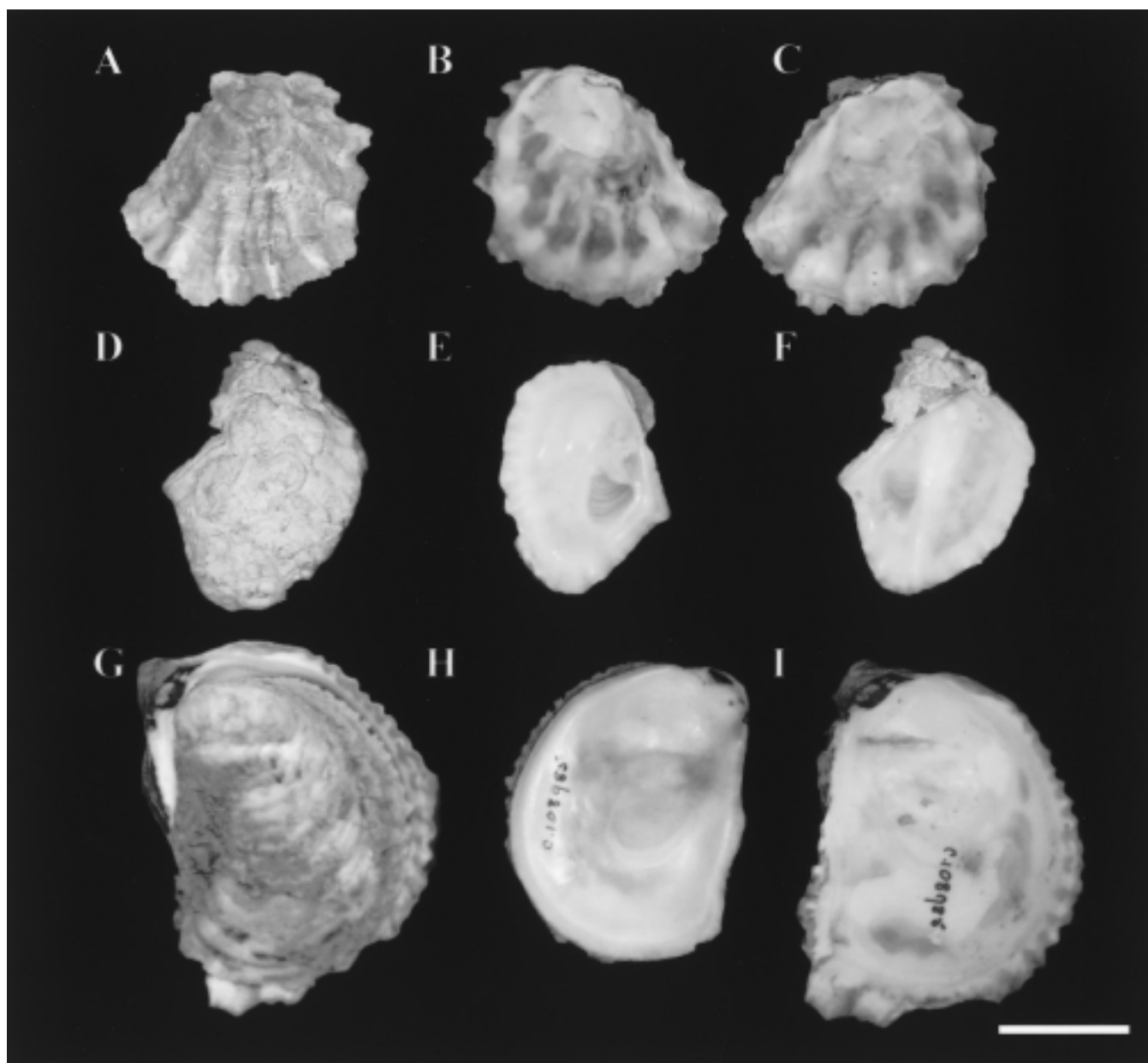


Fig. 5. *Dendostrea* and *Ostrea* from Hong Kong showing external and internal views of the right valves and the internal views of left valves. A-C. *D. folium* (SBMNH 345717). D-F. *D. crenulifera* (NHM 20030493). G-I. *O. denselamellosa* (AM 108985). Scale bar = 20 mm.

is short. The interior varies from lustrous white to pale green. The green-tinted interior of the shell is a particular character of this species. The adductor muscle scar is colourless, half-moon shaped or reniform. It is positioned in the posterior ventral third of the pallial area.

Distribution. – *Dendostrea crenulifera* occurs on subtidal (> 7m) boulders or is associated with hard corals in the eastern waters of Hong Kong such as Hoi Ha Wan. It also attaches to the walls of the marine cave at Conic Island. This species is probably stenohaline since it is not recorded from the western side of Hong Kong where salinities are much lower. This species is distributed in the Red Sea and from Japan south into the Indo-West Pacific.

Remarks. – Some authors consider *Dendostrea crenulifera* to be a synonym of *Saccostea mordax* and *Pustulostrea tuberculata* Lamarck, 1804. *D. crenulifera*, however, can be distinguished from these two species in having a green-tinted interior to the shell and occurring in subtidal waters.

Ostrea Linnaeus, 1758

Ostrea Linnaeus, 1758: 696; Sowerby, 1871: 1.
Monoeciostrea Orton, 1928: 320.

Type species. – *Ostrea edulis* Linnaeus, 1758, subsequent designation by Gray, 1847: 201.

Description. – Size medium to large (up to ~18 cm in height). Both valves not plicate and with a roughly orbicular outline. Right valve is flat to gently convex, covered by layers of flat conchiolinous growth squamae which end in a wide peripheral conchiolin fringe. The calcareous part of the right valve is smaller than that of the corresponding left. Left valve is slightly convex with a shallow umbone, covered by rounded radial ribs interrupted by weak, concentric growth squamae. Chomata inconspicuous and confined to posterior and anterior margins near the hinge. Adductor muscle scar reniform with rounded ends and located ~centrally. Distribution worldwide except polar regions.

Ostrea denselamellosa Lischke, 1869

Common name: Densely lamellated oyster
(Figs. 5G-I)

Ostrea denselamellosa Lischke, 1869: 177, Pl. 13, Figs. a, b, Pl. 14, Fig. 1; Torigoe, 1981: 333, Pl. 22.
Ostrea auriculata Sowerby, 1871, Pl. 25, Figs. 60a-c.
Ostraea multicostata Sowerby, 1871, Pl. 25, Fig. 61.

Material examined. – Type not studied. Probably in the Naturhistorisches Museum, Vienna, “prop Jedo et Nagasaki” (near Tokyo and Nagasaki).

Description. – Shells are ~70mm in dorso-ventral height, and subtriangular to oval. Attachment of the left valve is restricted

to a small area ventrally. The right valve is nearly flat and covered by dense layers of brown, overlapping, thin and brittle lamellae, or scales, arising from growth lines. The left valve is either white or purple, slightly cupped with radiating ribs ending in a densely plicate margin. Chomata are inconspicuous along the anterior and posterior margins near the hinge. The hinge line is straight and short. Ligament area short. The interior of the shell is white with yellow patches and has a pearly nacre. Small patches of white chalky deposits are prominent on the interiors of both the left and right valves. The adductor muscle scar is colourless, half moon-shaped with lightly coloured growth lines. It is positioned dorso-ventrally and slightly towards the posterior end of the shell.

Distribution. – *Ostrea denselamellosa* is a rarely-encountered species which occurs on the continental shelf (~ 20m) in the southern waters of Hong Kong, e.g. Cheung Chau, Po Toi Island. In a trawl survey of Hong Kong’s waters in 2002, only empty left valves were found. The only two existing complete specimens from Hong Kong have been deposited in the Australian Museum, Sydney (Registration number: c.108985). These were collected by fisherman at Cheung Chau in 1973. This species is common among the islands of Japan, Korea and along the northern coast of China (Torigoe, 1981; Lee et al., 2000). It is a palatable oyster but difficult to obtain and only by dredging. Attempted culture in Japan has been unsuccessful (Cahn, 1950).

Remarks. – Some authors considered *Ostrea futamiensis* Seki, 1929 to be an ecomorph of *O. denselamellosa*. The two species have, however, been separated in terms of egg diameter, larval colour, differences in adult shell characters and by differences in the electrophoretic analysis of adductor muscle proteins (Torigoe, 1981).

FAMILY GRYPHAEIDAE

SUBFAMILY PYCNODONTEINAE

Hyotissa Stenzel, 1971

Hyotissa Stenzel, 1971: N1107-N1108; Torigoe, 1981: 300, 320-321; Harry, 1985: 130.

Type species. – *Mytilus hyotis* Linnaeus, 1758: 704, no. 207, by original designation.

Description. – Shell size medium to large (up to ~28 cm in height). Both valves tend to be subequal and similar in sculpture. Shell shape suborbicular to oval. The left valve has a large attachment area and is more convex than the right. Commissural plications originate from dichotomous radial ribs, the tops of which are crossed by growth squamae that give rise to hyote spines. Vermiculate, fingerprint-like chomata restricted to a short length along the posterior and anterior margins next to the hinge. Distortion of shell shape and sculpture due to shape and size of settling substrata is common.

***Hyotissa imbricata* (Lamarck, 1819)**

Common name: Imbricated oyster
(Figs. 6A-C)

Ostrea imbricata Lamarck, 1819: 213.
Ostrea imbricata Sowerby, 1871, sp. 36, Pl. 17, Figs. 36a-b.
Dendostrea imbricata Habe, 1951: 93.
Pretostrea imbricata Habe & Kosuge, 1967: 138, Pl. 51, Fig. 14.
Hyotissa hyotis forma *imbricata* Stenzel, 1971: N961, N1026, Figs. 15, J49.
Hyotissa hyotis imbricata Habe & Okutani, 1975: 195.
Parahyotissa imbricata Harry, 1985: 130.

Material examined. – Type not studied. Probably in MNHN or in the Geneva, Switzerland, museum.

Description. – Shell large, up to 150mm in height. Outline either orbicular or semicircular, equivalve. Hinge line is long and straight and approximately equal to shell length in smaller individuals. Shell relatively thin and light in smaller individuals but becomes thicker and heavier in larger ones. Both valves have dichotomous ribs radiating from the umbo and which bear prominent growth squamae that increase in length to become hyote spines. In older, eroded individuals, hyote spines are obsolete but growth squamae are still

prominent at the newly-grown ventral margin. Attachment area varies from small and limited at the umbones, to large and encompassing the entire left valve. The shell margins of both valves are undulate, fitting into each other and, thus, reflecting the positions of the radial ribs. External coloration of both valves varies from white to cream in younger individuals to pink and purple with dark purple bands in older ones. The interior of the shell is white with pearly opalescent patches within the pallial area. The large commissural shelf is dull in texture because of the vesicular shell structure. The ligament is short and the ligamental area is usually not elongate. Umbonal cavity shallow. Chomata are absent. The adductor muscle scar is large, white or pink, approximately circular and positioned postero-dorsally from the centre of the valve.

Distribution. – This species can be obtained only by trawling in the southern and western waters of Hong Kong, e.g. near Po Toi Island and northern Lantau Island. It is an Indo-West Pacific species which occurs in the Philippines, Australia and South China Sea to the Boso Peninsula, Japan.

Remarks. – This species is distinguished from *Hyotissa sinensis* in having a white shell interior, obvious hyote spines and radiating ribs on both valves.

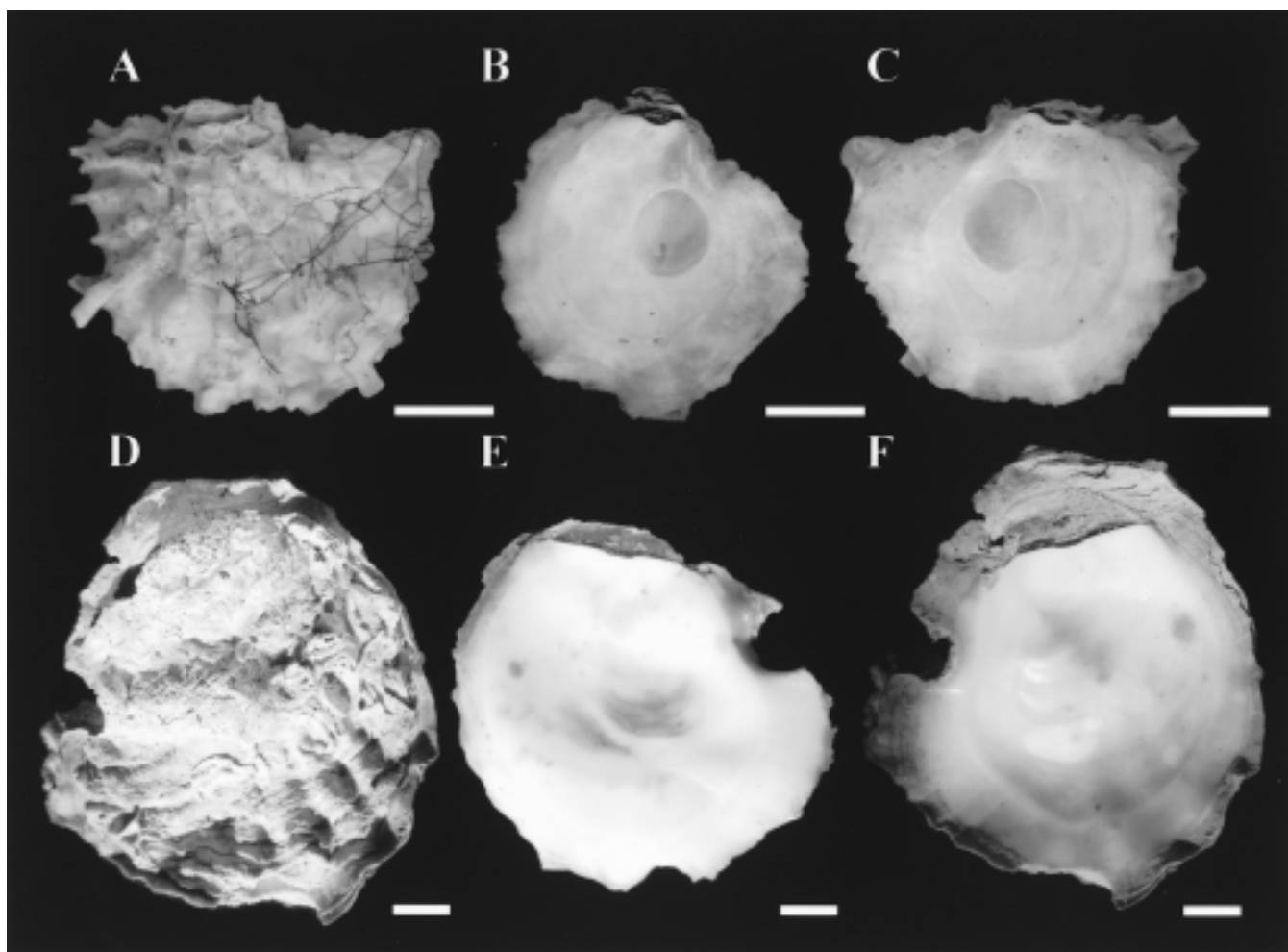


Fig. 6. *Hyotissa* from Hong Kong showing external and internal views of the right valves and the internal views of left valves. A-C. *H. imbricata* (SBMNH 345718). D-F. *H. sinensis* (NHM 20030494). Scale bar = 20 mm.

***Hyotissa sinensis* (Gmelin, 1791)**

Common name: Honeycomb oyster
(Figs. 6D-F)

Ostrea sinensis Gmelin, 1791: 3335; Sowerby 1871, Pl. III, Fig. 5.
Hyotissa sinensis Morris, 1985: p. 120-123, Pls. 1A, B; Scott, 1994:
70, Pl. 5D.

Material examined. – Type not studied, presumably in the Spengler Collection at the Zoologisk Museum, Copenhagen (ZMUC), Denmark, or in the Adanson Collection of the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Voucher – One dry shell, (height 78.2 mm)(NHM 1981130), Mirs Bay, Hong Kong, trawl, 10 m, coll. J. D. Taylor, 23 Mar.– 8 Apr. 1977; one dry shell (height 51.7 mm)(SBMNH 141713), southeastern waters of Hong Kong, trawl, 7-55 m, coll. P. H. Scott, 13 Apr.– 1 May. 1992.

Description. – Shell large, up to ~150mm in height, rounded to oval in outline. Shell is thick and heavy in large individuals. Surface irregularly folded with radial ribs on both valves. Shell margin with irregular wavy plications corresponding to rib positions. Attachment area on the left valve depends on substratum type. Two colour morphs are identified, i.e. pale yellow and deep purple. Chomata in a vermiculate pattern are restricted to the anterior and posterior hinge margins. Shell interior is white and covered by a layer of vesicular shell microstructure. Commisural shelf is broad and coloured either pale yellow or deep purple. The hinge line is straight and comparatively long. The adductor muscle scar is large, circular and positioned to the posterior side of the centre of the shell. It may be colourless, i.e. white, or cream or purplish brown depending on the individual and the presence of growth lines.

Distribution. – *Hyotissa sinensis* occurs in the sublittoral zone at Kat O Chau, Mirs Bay, at between 8 and 10 m, in the eulittoral zone of East Ping Chau and subtidal waters of southern Hong Kong. It also aggregates on the walls and ceiling inside the marine cave on Conic Island. This species favours marine salinities rather than estuarine conditions and is restricted to the Western Pacific from southern Japan, the coast of China to the Philippines and probably as far south as northern Queensland, Australia (Scott, 1994).

Remarks. – *Hyotissa sinensis* has been considered to be synonymous with *Hyotissa hyotis* by some authors (Morris, 1985). This species, however, can be distinguished from the latter by the weak irregular folding of the margins. *H. hyotis* has a sharp and acute plicate shell margin reflecting the shape and position of the well-defined, regularly-spaced radial ribs on both valves.

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