INTRODUCTION

Bivalve larvae constitute an important and distinctive part of tropical marine and estuarine plankton communities (Ockelmann 1994). However, studies of their distribution have been hampered by the inability of investigators to identify species in plankton samples. Rearing larvae from known parents in the laboratory eliminates this problem but authors employing this technique have usually only described individual species with little attempt to make interspecific comparisons.

Ockelmann (1965) described three developmental types (planktotrophic, lecithotrophic and direct development larvae) in marine bivalves and their distribution along the Atlantic coast and showed that there are relationships between egg size and the size of embryonic shells. Besides, he also found that the egg and prodissoconchs of Ostrea chilensis Philippi, 1845 and O. lurida Carpenter, 1864 are considerably larger than those of other species, which brood their larvae. Such species are called brooders or incubatory species.

Ranson’s important studies (1939, 1948, 1949, 1960) on the morphology of larval shells of the Ostreidae and Gryphaeidae brought into focus the usefulness of this complex structure for generic separation. Ranson recognized only three living genera, Ostrea, Crassostrea and Pycnodonta (=Pycnodonte), based on the features of prodissoconch II. Although he illustrated differences between several species on the same basis, his publications were not very well received or were even misunderstood. He gave

Steenstrupia 32 (2): 95–162.
the following definitions of the genera. Genus *Ostrea*: Prodissoconch with long hinge; two denticles at each end, the anterior pair frequently reduced; the ligament is internal at the level of the hinge, at the centre, and between the center and anterior end. Genus *Crassostrea*: Valves of the prodissococonch unequal; hinge with two teeth at each end; internal anterior ligament extends beyond the hinge. Genus *Pycnodonte*: Valves of prodissococonch equal; hinge with five teeth arranged over its entire length; internal anterior ligament immediately after the hinge; 10 small

Fig 1. Sampling stations (dots) of oyster larvae in the Andaman Sea and Gulf of Thailand.
denticles at the edge of each valve anteriorly to the ligament (Ranson 1967).

According to Galtsoff (1964) “comparison of Ranson’s illustrations of closely related species... indicated no significant differences”. In a later publication, Ranson (1967) provided photographs of the larval shells, but as with his earlier work, there were no descriptions or explanations. The exhaustive list of larval shells as parts of type specimens examined by Ranson provide a useful list of synonyms of several species of oysters and also indicated the depth of his studies.

Ranson (1948, 1960) regarded the form of the fully developed prodissoconch II as useful in distinguishing genera and species of ostreids. This was later discussed by Galtsoff (1964). Ranson’s (1960) figures of 34 species indicate fairly consistent generic differences which are most pronounced in the left valves. He showed that the left valve is somewhat heart-shaped in Crassostrea because the beaks are directed posteriorly (opisthogyrous). In Ostrea the left valve is teardrop shaped, more symmetrical and nearly orthogyrous and the beaks (tip of umbo) are relatively blunt.

Morphological characters in oyster larvae have been used in the systematics of higher taxa. Stenzel (1971) divided the Ostreacea into two families, Ostreidae and Gryphaeidae, based on the characters of the shell (larval and adult) and on the heart/intestine relationships. One of the main diagnostic characters that he used to separate the two families is the structure of the prodissoconch. In the Ostreidae “the hinge bear on each valve four unequal tooth precursors and their corresponding sockets, split by a long smooth median gap into two equal groups”. In the Gryphaeidae, “the hinge carries an interrupted series of alternating tooth precursors and sockets”. Malchus (2000) used fossil larval characters to investigate evolutionary aspects in the Ostreidea.

Morphological differences between oyster genera have in some cases been pointed out by others. Forbes (1967) described prodissoconchs of larvae reared from parents identified as C. virginica (Gmelin, 1791), O. equestris Say, 1834 and O. frons Linnaeus, 1758 from the Gulf of Mexico. Prodissoconchs of O. frons and O. equestris were indistinguishable from each other, but differed markedly from those of C. virginica. Definitive prodissoconchs of Ostrea possessed broad, blunt, orthogyrous beaks in contrast to the hooked, acute, opisthogyrous beaks of C. virginica. Dinamani (1976) studied the morphology of the larval shell of Saccostrea glomerata (Gould, 1850) and found some differences when compared to 3 Crassostrea species: C. virginica, C. angulata (Lamarck, 1819), and C. gigas (Thunberg, 1793). The differences are that it is equilateral, has an orthogyrate umbo, and symmetrical teeth on the provinculum. Such a hinge is characteristic of the cucullata group of oysters which Stenzel (1971) regarded as a separate genus, Saccostrea. Stenzel based his view on characters of the adult shell, mainly on the chomata and the insertions of small muscles in the pallial region, which constitute a disjunct pallial line. The characters of the prodissoconch fully support Stenzel’s view.

Species groups within genus have been demonstrated by Dinamani (1973) who studied the embryonic and larval development of the New Zealand rock oyster, Crassostrea glomerata. He found that it is distinctive and different from other species of Crassostrea figured by Ranson (1967), including C. cucullata (Born, 1778) which Ranson regarded as synonymous with C. glomerata. Ranson (Dinamani’s pers. communication with Ranson in 1971, cited in Dinamani, 1976) confirmed that the larval shell of C. glomerata is distinctive and different from that of C. cucullata. However, the fully developed prodissoconch of C. glomerata and C. cucullata share the common features of processing a broad provinculum and symmetrical shell and teeth, in contrast to C. virginica, C. angulata and C. gigas, all of which have a modified provinculum and a symmetrical shell.

There are no published reports on the larval shell morphology of any oyster species occurring in Thai waters apart from that of Ranson (1967) where he published photos of larvae of the species Pycnodonte hyotis (Linnaeus, 1758), Crassostrea lugubris (Sowerby, 1871), C. belcheri (Sowerby, 1871), C. cucullata, C. caparti Ranson, 1967, Ostrea futamensis Seki, 1929, O. deiformis Lamarck, 1819, O. rivularis (Gould, 1861), O. folium (Linnaeus, 1758), O. sandwicensis Sowerby, 1871 and O. bartschi Ranson, 1967. His descriptions of
Table 1. Oyster larvae found at different stations along the coasts of Thailand. Numbers correspond to species; see list below table.

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1 = *Crassostrea belcheri*; 2 = *Crassostrea iridalei*; 3 = *Crassostrea* sp.; 4 = *Saccostrea forskali*; 5 = *Saccostrea echinata*; 6 = *Saccostrea* sp. 1; 7 = *Saccostrea* sp. 2; 8 = *Saccostrea* sp. 3; 9 = *Saccostrea* sp. 4; 10 = *Saccostrea* sp. 5; 11 = *Ostrea futamiensis*; 12 = *Dendrostrea folium*; 13 = *Dendrostrea cf. folium*; 14 = *Dendrostrea sandvichensis*; 15 = *Dendrostrea* sp.; 16 = *Nanostrea exigua*; 17 = *Planostrea pestigris*; 18 = *Lopha cristagalli*; 19 = *Hyotissa hyotis*. 
the new species *C. caparti* and *O. bartschi* were based only on larvae collected at Ko Chang, Gulf of Thailand. There are generally few studies on the morphology of oyster larvae in the region around Thailand, but Tanaka (1960; 1980-1981) described several species from Japan. Some of them are also found in Thailand.

In Thailand, Ockelmann (1994) proposed a project to study the late larvae of all oyster species found in the region of Southeast Asia. Preliminary sampling by Ockelmann in 1986 showed that larvae of at least 13 different oyster species were found in the water just outside Phuket Marine Biological Center (PMBC).

The aim of this study is to describe and compare the oyster larval morphology for 4 cultured species from Thailand and to describe the morphology of the species of wild oyster larvae collected in Thai waters, in order to identify morphological characters that can be used for species identification and systematic studies of oysters in the region.

This study describes the development of laboratory-reared larvae of oysters through metamorphosis. The results should enable the identification of larvae in the plankton and the determination of developmental stages. Data derived from this study should help in establishing a good spat fall program, which is an essential aspect of the culture and farming of this valuable food resource.

**MATERIAL AND METHODS**

**Larval culture**

Mature oysters of 3 commercial species, *Crassostrea belcheri*, *C. bilineata* (Röding, 1798), and *Saccostrea forskali* (Gmelin, 1791) brought from Thailand (Khok Krai, Phang-nga) were artificially induced to spawn at the oyster hatchery of Muka Head Marine Station, Universiti Sains Malaysia, Penang. A fourth species, *Dendrostrea folium* was induced to spawn at Sri Racha Marine Station, Kasetsart University, Chonburi (broodstock collected at Ang Sila, Chonburi). Techniques following Loosanoff & Davis (1963) were used in culturing the larvae. Photomicrographs of living specimens were taken after a drop of 15% magnesium chloride was added to a cavity slide to arrest larval movements.

**Measurements and terminology**

For an explanation of morphological terms used for oyster larvae, see Figs 4, 5, 6, 7, 8, 9A and the section on terminology below.

All dimensions of larvae were measured using a grid ocular calibrated with a stage micrometer. The descriptive terminology follows Chanley & Andrews (1971).

**Field sampling of oyster larvae**

Plankton sampling near the islands and coastal sea in Thailand, both in the Gulf of Thailand and the Andaman Sea (Fig. 1), were carried out by plankton net (200 µm mesh size, 60 cm diameter) towed by snorkelling, from long tail boat or rubber boat or from bridges where strong tidal currents occurred (Table 1). Samples were made during rising tide and the net was towed obliquely through most of the water column.

**Transportation of samples**

Plankton samples with oyster larvae intended for live studies were cooled to 10–15 °C in an ice box during transportation over long distances and sorted out as quickly as possible under a stereo microscope after arrival at the PMBC laboratory or sorted at provincial hotels after daily sampling, in the cases of longer field trips.

**Preservation**

Oyster larvae were fixed in Carriker’s solution prepared several days before being used (Ockelmann 1994). The recipe for preparation was as follows: 100 g cane sugar + 10 ml of formaldehyde (40 % pro analysi) is dissolved in enough seawater of 30‰ salinity to make 1 litre of solution. This is buffered with a few grams of sodium tetraborate (Borax) to pH 8.5–9.0 and filtered. The pH of the preserved sampled should not be allowed to drop below 8.0 since even slightly acid media quickly destroy larval shells. Samples were stored in darkness in order to delay bleaching of the larval colour.

Another set of oyster larvae of each species was preserved in 70% alcohol for DNA sequence analysis in order to match them with adult species occurring in the area (See Bussarawit *et al.* 2006).
Larval shell preparations for photography

Living larvae of each species were sorted and photographed at the PMBC laboratory by the use of a NIKON SMZ10 zoom stereomicroscope, a compound microscope NIKON Optiphot and NIKON Coolpix 990 digital camera. Correct orientation of the larval valves is important because the shell shape (outline) is characteristic for each species. However, this is very difficult because of irregular shell morphology and skewed centre of gravity. All larvae therefore tend to tilt in one or the other direction. This problem could to some degree be solved if the larva was mounted in a hanging droplet (Fig. 9B). A larva was put in a small water droplet on a coverslip. The right valve was positioned downwards. Small amounts of Vaseline were attached to the coverslip corners. The coverslip was quickly turned upside-down and positioned on a cavity slide so that the larva was hanging in the droplet, now with the left valve downwards. The curvature of the droplet helped to orient the larva in a better position and could to some degree be modified by adjusting the diameter and volume of the droplet (Fig. 9B).

For close study and photography of larval shells, the soft parts were removed from some of the samples. Fresh as well as preserved material was used for this purpose. Samples preserved in Carriker’s solution were briefly washed in distilled water before being transferred to other media. Soft parts were dissolved in a 5% sodium hypochlorite solution in distilled water. Under such conditions, the valves will gape and eventually fall apart. This treatment may effect the shell surface if they are left in the solution too long. The process was therefore monitored under the microscope and terminated when the larval shells just begin to gape, usually within 1-3 minutes. After repeated washing in distilled water, the clean valves were mounted in glycerine on coverslips for examination of hinge structures and photographed in an inverted microscope (Zeiss Axiovert 135M). This method results in a perfect orientation of each valve: the plane separating the valves will be perpendicular to the optical axis, and the valve is seen from the inside. Shells should not be left in glycerine for more than a day, since glycerol also has a slow etching effect. Shell valves to be photographed were mounted with their edges toward the slide so that they are in a defined position. We found that some microscopes mirrored the image but others did not. It is very important to be aware of this when asymmetrical animals are studied (Berland 1982).

Scanning Electron Microscopy (SEM)

Preserved oyster larvae and left and right valves of the same developmental stage were prepared and cleaned in distilled water and an acetone series (30, 60, 80 and 100 %), positioned on a stub by carbon tape, and dried in an exsiccator with silica gel overnight. Samples were coated with approximately 600 Å of gold-palladium (Edwards S150B sputter coater) and photographed for minute details of shell morphology such as

Fig. 4. Different stages of oyster larvae and juveniles. A. Veliger larva, also called D-shaped larva or straight-hinge larva. B. Veliconcha made up of prodissoconch I (Prod. I) and prodissoconch II (Prod. II). C. Early bottom-living stage showing prodissoconch (P) and dissoconch (D), the juvenile shell. Redrawn from Rees (1950).
Fig. 5. Terminology used to describe oyster larvae. The posterior end is usually blunter and shorter than the anterior and has higher shoulders. Modified after Chanley & Andrews (1971).
hinge teeth and shell texture using a CamScan Maxim 2040S at the Department of Astronomy and Physics, University of Aarhus, Denmark and a Jeol 5900LV housed at the SEM Service Equipment Center, Kasetsart University, Bangkok, Thailand.

Terminology and characters used in the descriptions

Marine bivalve larvae develop a shell (prodissoconch), secreted as a unit by the shell gland, 18–30 hours after fertilization. It is called pro-

Fig. 6. Terminology used to describe oyster larvae.
dissoconch I (Prod I) (Werner 1939). The shell of Prod I is uniform in texture with the dorsal margin or hinge forming a straight line. It can be recognized in empty valves at all stages of larval development. The prodissoconch I is a cast of the interior of the egg and so, represents the size of the egg. The subsequent stage with additional shell material, deposited by the mantle, is called Prodissococonch II (Prod II). The Prod II is sharply delineated from Prod I and shows growth lines. The differences in appearance between Prod I and Prod II can be seen in many of the photomicrographs of larval hinge structure presented here. These 2 terms correspond roughly with the
European designation of veliger and velioconcha stages. They are frequently used to refer to the shell only. The postlarval shell, the bottom-living stage after metamorphosis, is called dissoconch. It is usually sharply delineated from the larval shell (prodissoconch) and of different texture.

The dorsal area of the shell where the 2 valves are permanently attached is called hinge line. The morphology of the larval shell, especially the hinge structure, was illustrated and pointed out by Dinamani (1976) as an important character in the systematics of the family Ostreidae, particularly at the generic level. The thickened dorsal area of the shell that bears the hinge teeth, when they are present, is called provinculum. For purposes of identification, larvae are separated into 2 groups based on shape. Early stages in most bivalves are D-shaped (Prod I as well as Prod II) and here called "straight hinge" larvae. The later stages are called "umbo" larvae. Straight-hinge larvae are defined as those having a hinge line along at least half the total length (maximum anterior-posterior length). Umbo larvae are those with a hinge line less than half the total length or with well-developed umbones.

Total length in Prod I larvae is usually 15-30 µm greater than hinge line length. Prod I size is an important identification aid for larvae with a straight hinge because this measurement does not increase during larval development. The hinge line becomes obscured in umbo larvae, and the shape of the umbo becomes an important feature. Umbonal shapes are illustrated in Fig. 22. Umbones tend to be "round" and "indistinct" in early development.

Umbones may appear continuous with the rest of the shell, as in the types we call "round", "broadly round" and "angular", or discontinuous, as in the types we call "knobby" and "skewed" (Fig. 5). A broad and rounded umbo is common and well known among most larval venerids. Some species with this type of umbo do not go through the round or indistinct stage. Knobby umbones, such as those found in pholadids and anomids, are also common. Frequently other types of umbones become knobby just prior to metamorphosis. The skewed umbo is a variant of the knobby type and is found only in the genus Crassostrea. Intermediate and transitional shapes occur frequently.

Larvae with two valves of the same shape and size are called equivale. Larvae with parts of shell anterior and posterior to beaks equal in length or almost so are called equilateral. The depth is the maximum distance through the larva from left to right. Depth is called thickness or convexity by some authors. The hight of a shell is the greatest distance in the dorso-ventral plane perpendicular to the length. Hight is called width by some authors.

Relative length and shape of anterior and posterior ends of valves can also be used to identify larvae. Relative lengths of ends can be estimated from an imaginary line drawn perpendicular from the middle of the hinge to the ventral margin (Fig. 5). Slope and length of anterior and posterior shoulders are important features. Usually the point of sharpest turn or "break" in the contour of larval shapes occurs at the higher level on the posterior shoulder (Fig. 5). The shoulders may be straight or rounded. Umbones and shoulders may be from 1/3 to more than 1/2 the total height (maximum dorso-ventral dimension). An orthogyrous shell is curved so that the beak (umbo) points at right angle to hinge axis. An opisthogyrous shell is curved so that the beak (umbo) points in posterior direction. The prodissocochns of the genus Saccostrea have orthogyrate umbones and symmetrical teeth whereas in the genus Crassostrea the prodissocochns have inequilateral growth, with posterior teeth modified and with the umbones tending to be opisthogyrate (Dinamani 1976).

The fasciole is a distinct character in some larvae. It is a groove on the posterior dorsal side of umbo as a result of a deviation of the growth lines on the shell margin. Another distinct larval character is the eyespot. It is a conspicuous pigment spot evident near center of outline of many species of larvae as they approach metamorphosis.

Veliger is technically a general term, meaning with a velum. It is used to describe the shelled pelagic stages of gastropod and pelecypod larvae. Werner (1939) used this term to describe the stage of development from fertilization through the Prodissocochn I stage. The term veliconcha was applied to later stages after the shell has grown beyond the original shell deposited by the shell gland. In this stage, the shell is marked with growth lines. The term pediveliger, proposed by
Carriker (1961) refers to metamorphosing larvae that possess both functional velum and foot. It is now widely used.

Fig. 9. A. Prodissoconch II (veliconcha) larva of oyster (Crassostrea) viewed from the left side. Redrawn from Eble & Scro (1996). B. Living oyster larvae were observed in a hanging droplet under a compound microscope.
tion of larvae. With practice, size, shape, umbo type and special characteristics are integrated by the eye, and recognition of similar larvae in a sample is possible. One must always consider distinctive features in relation to the size of the larvae, and measurements with an ocular micrometer are strongly recommended. Hinge structure and internal anatomy as well as soft part colours can also be used to identify larvae.

The characters of particular importance in each stage are as follows. Prodissoconch I: size and shape, length and height, outline, shell convexity and microsculpture, length of provinculum and origin of larval ligament. Prodissoconch II: LV (left valve) and RV (right valve) photographs, size variation at metamorphosis, convexity, sculpture, colouration, internal features (hinge, ligament, chomata), as well as some other special traits. Soft parts such as colouration, position of internal organ, lipid reserves, and position and size of the eyespot are also used.

RESULTS

DESCRIPTION OF OYSTER LARVAL DEVELOPMENT

Development of Crassostrea belcheri from the hatchery (Fig. 12)

The shells (D shaped) were fully developed in 24 hour old larvae (approximate shell length 87 µm, height 74 µm) at a temperature of 26–28 °C. At this stage, the shells were uniform in texture with the dorsal margin or hinge forming a straight line and a rounded ventral margin. The left and right valves of a D-shaped larva are nearly equal.

The D shape disappeared as umbones became rounded and obscured the hinge region. The valves then appeared almost spherical. Small teeth were formed on the central portion of the hinge and 3-4 larger rectangular teeth at the posterior and anterior ends. At this stage, there was only a slight difference between the left and right valves. The difference became more pronounced as the larvae reached the umbo stage.

When the umbo stage was reached, the umbones developed a knobby appearance. Growth of the valves then made them unequal as the result of the left valve becoming enlarged and extending beyond the dorsal margin of the right valve. At the same time, larval dimensions also changed as shell height began to exceed shell length. The central region of the cardinal plate was relatively smooth, with only small indentations. On either side of both of the valves, three denticles developed symmetrically.

As the larvae grew larger (measuring approximately 250 µm in shell height), the umbones became skewed. The unrolling of the left umbo affected the provinculum structure of the larva. Development of denticles at both ends became asymmetrical, although each end of the valve still contained 3 denticles. The anterior teeth appeared to be longer due to umbonal enlargement towards the posterior end of the left valve, while the posterior teeth were reduced. The right valve was similarly modified with the anterior teeth becoming longer.

In pediveliger larvae (measuring approximately 400 µm in shell height), inrolling of the left umbo resulted in the umbones being directed posteriorly giving rise to the opisthogyrate condition. The posterior set of teeth on the left valve became obscured by the folding of the valve margin, while the right valve flared posteriorly to accommodate the modified portion of the left valve. At the anterior end of both valves the denticles became more pronounced.

Main features of the larval development of C. belcheri (temperature 25–30 °C, salinity 18 ppt, pH 7.5-8.5) are:

D-shaped larva (day 1): shell length 63±3µm, height 52±5 µm. Umbo stage (day 7): shell length 106±11 µm, height 130±17 µm. Late umbo stage (day 14): shell length 209±19 µm, height 260±18 µm. Pediveliger stage (day 18): shell length 331±36 µm, height 379±37 µm.

Observation of larval behaviour

The larval behaviour of C. belcheri observed in the hatchery showed that it took 14–16 days for the pediveliger larvae to reach the settling stage. The velum was reduced and the foot was extended in search of a proper substrate to settle on. The larva was crawling in an anticlockwise direction and finalized settling by turning 180 degrees clockwise. The settling process was completed within 2–3 minutes.
Development of *Crassostrea bilineata* from the hatchery (Fig. 18)

Prodissoconch I was fully developed in 24 hour old larvae (length 70 µm, height 61 µm). At this stage, the valves were uniform in texture with the dorsal margin or hinge forming a straight line and a rounded ventral margin. The left and right valves of a D-shaped larva are nearly equal. After this stage the larval development was almost complete.
Main features of the larval development of *C. bilineata* (temperature: 25–30 °C, salinity: 25 ppt, pH: 7.1–8.2) are:

D-shaped larva (day 1): shell length 70±2 µm, height 61±3 µm. Umbo stage (day 7): shell length 100±7 µm, height 110±10 µm. Late umbo stage (day 12): shell length 136±13 µm, height 162±20 µm. Pediveliger stage (day 19): shell length 278±35 µm, height 320±38 µm.

**Development of Saccostrea forskali from the hatchery (Fig. 26)**

Prodissococonch I was fully developed in 24 hours old larvae. At this stage, the shells were uniform in texture with the dorsal margin or hinge forming a straight line and a rounded ventral margin. The left and right valves of a D shaped larva are equal. After this stage the larval development was almost identical to that of *C. belcheri*.

Main features of the larval development of *S. forskali* (temperature: 25–30 °C, salinity: 25 ppt, pH: 7.1–8.2) are:

D-shape larva (day 1): shell length 75± µm, height 70±µm. Early umbo (day 6): shell length 83±8 µm, height 87±10 µm. Umbo (day 10): shell length 134±12 µm, height 143±14 µm. Late umbo (day 15): shell length 165±16 µm, height 169±16 µm. Pediveliger (day 22): shell length 225±28 µm, height 228±28 µm.

**Development of Dendrostrea folium from the hatchery (Fig. 45)**

The shell was fully developed in 24 hours old larvae. At this stage, the shells were uniform in texture with the dorsal margin or hinge forming a straight line and a rounded ventral margin. The left and right valves of a D shaped larva are equal. After this stage the larval development was almost identical to that of *C. belcheri*.

Development differed from that in *C. belcheri* in the following way. The D shape disappeared as umbones become rounded and obscured the hinge region. The valves then appeared almost spherical. There are 2 larger rectangular teeth at the posterior and anterior ends. At this stage, there was only a slight difference between the left and right valves. When the umbo stage was

![Fig. 11. Crassostrea belcheri from aquaculture. Broodstock collected in Khok Krai, Phang-nga in Thailand in Feb 2000. A. Both valves in natural position. B. Both valves seen from the posterior end. The aberrant surface on the ventrolateral part of the left valve is material secreted during cementation after settling.](image)
reached, the umbones developed a knobby appearance. Growth of the valves with the left umbo becoming enlarged and extending a bit beyond the dorsal margin of the right valve. The larval shell length was greater than shell height. The provinculum is short and the two anterior teeth are reduced.

Main features of the larval development of *D. folium* (temperature: 25–30 °C, salinity: 30 ppt, pH: 7.0–8.0) are:

D-shaped larva (day 1): shell length 129±4 µm, height 117±7 µm. Early umbo stage (day 6): shell length 168±9 µm, height 159±9 µm. Umbo stage (day 8): shell length 216±12 µm, height 197±12 µm. Late umbo stage (day 12): shell length 243±10 µm, height 229±10 µm. Pediveliger stage (day 14): shell length 257±9 µm, height 234±6 µm.

**Description of fully-grown oyster larvae collected in nature**

Different types of oyster larvae were found in samples collected along the coastal areas of Thailand. The generic names given in this study follow the classification of Vaught (1989): *Crassostrea, Saccostrea, Ostrea, Dendrostrea, Nanostrea, Planostrea, Lopha* and *Hyotissa*.

**Family Ostreidae**

**Crassostrea belcheri** (Sowerby, 1871)

Figs 2A, 10–15


Material examined:

Description

Prodissoconch I total length 63 µm. D-shaped with the dorsal margin of hinge forming a straight line, the ventral margin is round. Anterior end is slightly less pointed than the posterior. Outer surface smooth and uniform in texture. Length of the hinge line 54 µm.

Prodissoconch II length, 351 µm, height 373 µm (left valve); length, 351 µm, height 329 µm (right valve). Rather round, opisthogyrate in outline where the umbo twisted to the posterior direction. Convexity 266 µm. Concentric outer growth lines with relative narrow interspaces. The left valve consists of 2-3 teeth at the anterior end of the hinge line. The right valve teeth were obscured.

Pediveliger shell thin. Left valve larger than the right valve and a prominent umbo projecting backwards above the hinge line (opisthogyrate). Right valve has a narrower umbo than the left valve; surface of the shell with concentric growth line and relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a

Fig. 13. *Crassostrea belcheri*. Drawing showing the main characters.
small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour red.

Soft parts contain a round dark eyespot, 10 µm in diameter, located anteriorly above the centre of the shell. Digestive gland red. Posterior adductor muscle larger than anterior and situated dorso-

Fig. 14. Crassostrea belcheri. Living individuals collected in nature (Khok Krai, Phang-nga, Thailand, 23 Jan 2002). Scale bars = 100 µm.
posteriorly. Colour of all soft parts red. Lipid droplets found in umbo of the left valve.

Remarks

Identification: The morphology of the larvae (wild and cultured) of this species fits well with Ranson (1967). Some larval specimens were sequenced and matched with adult individuals described by Bussarawit et al. (2006).

This species was recorded by H.M. Smith from the Gulf of Thailand: Bandon Bight, Thailand (361067, 361480a), Ko Prap, Thailand (361064) and his specimens are deposited at the Smithsonian Institution, United States National Museum, Washington D.C., and referred to by the numbers in parenthesis above (Ranson 1967).

**Crassostrea bilineata (Röding, 1798)**
Figs 2B, 16–19, 20A–D, F, G

*Ostrea bilineata* Röding, 1798: 170.

*Ostraea lugubris* Sowerby, 1871: sp. 63.

*Ostrea iredalei*. – Faustino 1932: 546, pl. 1, fig. 1–4. – Blanco *et al.* 1951: 53.

Fig. 15. *Crassostrea belcheri* collected in nature (Khok Krai, Phang-nga, Thailand, 23 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 μm.


Material examined:

**Description**

Prodissoconch I length 58 µm. D-shaped larva with the dorsal margin of hinge forming a straight line, and with a round ventral margin. Anterior end is slightly less pointed than the posterior. Outer surface smooth and uniform in texture.

Prodissoconch II length 317 µm, height 350

Fig. 16. *Crassostrea bilineata*. Fully developed veliconcha from hatchery. Broodstock sampled in Khok Krai, Phang-nga in Thailand in Feb 2000. A. Left valve. B. Right valve. C. Both valves seen from the umbo (posterior end with fasciole to the left). D. Both valves in natural position. Scale bars = 100 µm.
µm (left valve); length, 317 µm, height 342 µm (right valve). Shape ventrally elongated, opisthogyrate in outline where the umbo twisted to the posterior direction, but less than in *C. belcheri*. Convexity 188 µm. Concentric growth lines with relatively broader interspaces than in *C. belcheri*. The left valve consists of 3 teeth at the anterior end of the hinge line. The posterior teeth were partially modified by the opisthogyrate umbo growth.

Pediveliger shell thin. Left valve larger than the right. The prominent umbo is skewed and projecting backwards above the hinge line (opisthogyrate). Height exceeding length in both valves, but is more pronounced in the left. Right valve umbo narrower than the left umbo, surface of the shell with concentric growth lines and relatively broader interspaces than in *C. belcheri*. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour dark red.

Soft parts contain an oval dark eyespot that is dorso-ventrally elongated and 14–21 µm. It is located anteriorly, above the centre. Digestive gland dark red. Posterior adductor muscle larger than the anterior and situate dorso-posteriorly. Colour of most soft parts dark red and grey. Lipid droplets in umbo of the left valve.

**Remarks**

The shell shape fits well with the picture illustrated by Ranson (1967) under the name *Ostrea lugubris*. This species is known to have a wide geographical distribution in Thailand. The nomenclature follows Yoosukh and Duangdee.

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**Fig. 17. Crassostrea bilineata.** Drawings showing the characters. A, C. Left valves. B, D. Right valves.

Fig. 19. *Crassostrea bineata* collected in nature (Khok Krai, Phang-nga, Thailand, 23 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
Fig. 20. A–D, F, G. *Crassostrea bilineata*. Living individuals collected in nature (Khok Krai, Phang-nga, Thailand, 23 Jan 2002). E, H. *Crassostrea* sp. Living individual collected at the PMBC pier 20 Jan 2002. This species has a smaller eyespot and a more triangular shell shape than *C. bilineata*. The eyespot has been marked on the photos in the bottom row (F–H). Scale bars = 100 μm.
Some larval specimens were sequenced and matched with adult individuals described by Bussarawit et al. (2006).

This species was recorded by Vignal; dated 28 Oct 1884 in Thailand (No. 223 in Ranson 1967) and his specimens are deposited at the Institut Royal des Sciences Naturelles de Belgique, Bruxelles. This species was also collected by Th. Mortensen in 1900 (Thailand) (No. 537 in Ranson 1967) and his specimens are deposited at the Zoological Museum, University of Copenhagen, Denmark (Ranson 1967).

Ver (1986) studied the early development of *Crassostrea bilineata* (Röding, 1798) from the Philippines with notes on the structure of the larval hinge. The larval hinge structure consists of minute denticles on the central portion of the provinculum and large rectangular teeth on both its ends. These teeth become obscured in advanced larvae due to the skewed development of the umbo.

**Crassostrea sp.**

Figs 2C, 20E, H, 21–23

Material examined:
PMBC pier, Phuket, 20 Jan 2002.

![Fig. 21. *Crassostrea* sp. collected in nature (PMBC pier, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.](image-url)
Fig. 22. *Crassostrea* sp. collected in nature (PMBC pier, 20 Jan 2002). A. Left valve. B. Right valve. C. Both valves seen from posterior end. D. Both valves seen from the dorsal (umbonal) side; posterior end with the fasciole is to the left. E. Both valves in natural position. Scale bars = 100 µm.
Description

Prodissococonch I length around 50 µm. D-shaped with the dorsal margin of hinge forming a straight line, the ventral margin is round. Outer surface smooth.

Prodissococonch II length 405 µm, height 450 µm (left valve); length 384 µm, height 413 µm (right valve). Ventrally elongated shape, opisthogyrate in outline where the umbo twisted to the posterior direction, but less than in *C. belcheri*. Convexity 118 µm. Concentric growth lines indistinct. The left valve consists of 2–3 teeth at the anterior end of the hinge line. The right valve teeth were obscured.

Pediveliger shell thin. Left valve larger than the right valve. The prominent umbo is skewed.

Fig. 23. *Crassostrea* sp. Collected in nature (PMBC pier, 20 Jan 2002). This photo of a living individual shows the characteristic very small eyespot. Scale bar = 100 µm.

and projecting backwards above the hinge line (opisthogyrate). Height exceeding length in both valves, but is more pronounced in the left. Right valve umbo narrower than the left umbo, surface of the shell with non-distinct concentric growth lines and relatively broader interspaces than in *C. belcheri*. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour: orange.

Soft parts contain an eyespot that is round, dark, 7 µm in diameter and positioned anteriorly above the centre. Digestive gland dark orange. Posterior adductor muscle larger than the anterior and situated dorso-posteriorly. Colour of soft parts orange. Lipid droplets found in umbo of the left valve.

**Remarks**

This species resembles *C. bilineata*, but can be distinguished by its smaller eyespot and more triangular shell shape. The 16S rDNA sequence analysis showed that it is different from *C. belcheri* and *C. bilineata* (as *C. iredalei*; Bussarawit et al. 2006).

**Saccostrea forskali** (Gmelin, 1791)

Figs 2D, 24–29

*Ostrea Forskålii* Gmelin, 1791: 3336, no. 110.

*Ostrea cucullata* var. *barclayana* Lyng, 1909: 64.


*Ostrea cucullata* var. *forskali*. – Lyng 1909: 64.


Material examined:

Ang Sila, Chonburi, 23 Feb 2000; Sarasin Bridge, Phuket, 23 Jan 2002.

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Fig. 25. *Saccostrea forskali*. Veliconcha from hatchery. Broodstock sampled in Ang Sila, Chonburi in Thailand in Feb 2000. A. Both valves seen from the posterior end. B. Both valves in natural position, posterior end to the left. Scale bars = 100 µm.
Fig. 27. *Saccostrea forskali*. Drawing showing the main characters. A, B, E, G. Left valve. C, D, F, H. Right valve.
Description

Prodissoconch I length 58 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Anterior end is slightly less pointed than the posterior end. Outer surface smooth. Length of the hinge line 52 µm.

Prodissoconch II length 359 µm, height 395 µm (left valve); length 355 µm, height 377 µm (right valve). Orthogyrate in outline, equi- valve. Left valve higher than right valve, with distinctly broader umbo. Shell rather broaded in the middle of antero-posterior line. Convexity 239 µm. Concentric growth line ridges with narrower interspaces. The left valve has 3 teeth at the anterior end and 2 at the posterior end. Short ridge on the middle of provinculum. Ligament positioned anteriorly on the shell and outside the provinculum.

Pediveliger shell thin. Left valve larger than the right valve with prominently broad umbo projecting upward above the hinge line and slightly twisted to the posterior direction (orthogyrate). Right valve umbo is lower than the left umbo. Surface of the shell with concentric growth lines with relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargina-

Fig. 28. Saccostrea forskali collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
tation at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour brown to yellow brown.

Soft parts contain a dark irregular or rather rectangular eyespot 6–11 µm in diameter, and positioned anteriorly in the centre. Digestive gland orange. Posterior adductor muscle equal to anterior and situated dorso-posteriorly. Colour of soft parts yellow brown. Lipid droplets found under the left valve umbo.

Fig. 29. *Saccostrea forskali*. Living individuals collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). Scale bars = 100 µm.
Remarks

This species is distinct from *Crassostrea* larvae in being rather equivate and having an orthogyrate umbo, but with a very slight twisting of the left valve to the posterior.

The larval character of the genus *Saccostrea* to be used to distinguish from *Crassostrea* was first reported by Dinamani (1976) (orthogyrous and opisthogyrous, respectively). The species called *Saccostrea cucullata* in the literature could...
be a species complex with more than one species within its global distribution.

The 16S rDNA sequence analysis showed our specimens to be identical to the adults of the species *S. forskali* occurring in the area (Bussarawit et al. 2006).

*Saccostrea echinata* (Quoy & Gaimard, 1835)

Figs 2E, 30, 31

*Ostrea echinata* Quoy & Gaimard, 1835: 445.


*Ostrea forskali*. – Sowerby 1871: 79.


Material examined:
PMBC pier, Phuket, 20 Jan 2002.

Description

Prodissocochnch I total length 67 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Outer surface smooth and uniform in texture. Length of the hinge line 48 µm.

Fig. 31. *Saccostrea echinata* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
Prodissocochn II left valve length 333 µm, height 383 µm; right valve length 341 µm, height 364 µm. Orthogyrate. Ovate in outline, elongate dorso-ventrally, height excess length, equivalue. Left valve higher than right valve, with a distinct broad umbo. Convexity 270 µm. Concentric growth line ridges broad with narrower interspace grooves. The left valve has 2 teeth at the posterior and 3 teeth at the anterior end where the anterior was most reduced. Short ridge on the middle of provinculum.

Pediveliger shell rather oval along the antero-posterior axis. Right valve longer than the left valve, but lower than the left valve. The left valve with prominently broad umbo projecting upwards above the hinge line (orthogyrate).

Fig. 32. *Saccostrea* sp. 1 (*Saccostrea cf. cucullata*). Individuals collected in nature (PMBC pier, Phuket, Thailand, 15 Jan 2002. A. Left valve. B. Right valve. 

![Image](image-url)
Fig. 33. *Saccostrea* sp. 2. Collected in nature (Mai Thon Island, Phuket, Thailand, 19 Jan 2002). A. Left valve. B. Right valve. C. Both valves in natural position. D. Valves seen from posterior end. E. Valves seen from dorsal (umbonal) side, posterior to the left. Scale bars = 100 µm.
The right valve umbo lower than the left umbo. Surface of the shell smooth with distinct marked concentric growth lines with relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour greenish brown.

Soft parts contain a dark eyespot with irregular shape and therefore impossible to measure. It is positioned anteriorly above the centre. Digestive gland greenish in colour. Posterior and anterior adductor muscles are of similar size and situated near dorso-posteriorly. Colour yellow brown. Lipid droplets found in umbo of the left valve.

Remarks
The species was identified by the use of Tanaka (1960) and the adult of this species has also been found in Thailand by us (Bussarawit & Cedhagen 2011).

Fig. 34. Saccostrea sp. 2 collected in nature (Mai Thon Island, Phuket, Thailand, 19 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
**Saccostrea cf. cucullata (Born, 1778)**

Figs 2F, 32

*Ostrea cucullata* [sic] Born, 1778: 100.


*Ostrea cucullata*. – Sowerby 1871: sp. 34.


Material examined:

![Image of Saccostrea cf. cucullata](image_url)

Fig. 35. *Saccostrea* sp. 3. Collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). A, B. Right valves. C. Both valves seen in natural position. D. Both valves seen from posterior end. Scale bars = 100 µm.
Description

Prodissoconch I total length 82 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Outer surface smooth. Length of the hinge line 71 µm.

Prodissoconch II length 356 µm, height 406 µm (left valve); length 353 µm, height 405 µm (right valve). Orthogyrate in outline, equiva1ve. Left valve is of the same height as the right valve, with broad umbo. Distinctive concentric growth line ridges with similar interspaces. The left valve consists of 2–3 teeth at the anterior and posterior end. Short ridge on the middle of provinculum.

Fig. 36. Saccostrea sp. 4. Collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). A. Left valve. B. Right valve. C. Both valves seen in natural position, posterior to the left. Scale bars = 100 µm.
Pediveliger shell rather oval dorso-ventrally. Left valve larger or equal to the right valve and with broad umbo projecting upwards above the hinge line (orthogyrate). Right valve umbo equals the left umbo, and with a smooth shell surface with well marked concentric growth lines with relatively similar interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissococonch I, across prodissococonch II in left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Remarks

This species seems to belong to the genus *Saccostrea* as described by Dinamani (1976). It is rather oval dorso-ventrally and both valves are of equal height. This species was collected from the Gulf of Thailand (no. 394 in Ranson 1967) by Sir Robert Schomburgk and his specimens are deposited at British Museum of Natural History, London and by Th. Mortensen in 1900 from Ko Chang, (Thailand) (No. 487 in Ranson 1967) and his specimens are deposited at Zoological Museum, University of Copenhagen, Denmark (Ranson 1967).

*Saccostrea* sp. 2
Figs 2G, 33, 34

Material examined:

Description

Prodissococonch I total length 71 µm. D-shaped with the dorsal margin of hinge forming a straight line, with round ventral margin. Outer surface smooth. Length of the hinge line 57 µm.

Prodissococonch II length 326 µm, height 372 µm (left valve); length 313 µm, height 361 µm (right valve). Orthogyrate in outline, equivalve. The left valve is higher than the right valve, with broad umbo. Convexity 214 µm. Distinctive concentric growth line ridges with narrower interspaces. The left valve has 3 teeth at the anterior and 2 teeth at posterior end of the hinge. Short ridge on the middle of provinculum.

Pediveliger shell rather oval dorso-ventrally. Left valve higher than right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left umbo. Shell surface smooth with well marked concentric growth lines with relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of

Fig. 37. *Saccostrea* sp. 5. Individuals collected in nature (Mai Thon Island, Phuket, Thailand, 19 Jan 2002). Scale bars = 100 µm.
Fig. 38. *Ostrea futamiensis* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B. Right valve. C, D. Both valves in natural position, posterior end to the left. E. Both valves seen from the posterior end. The fasciole is clearly marked. Scale bars = 100 µm.
prodissococonch I, across prodissococonch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Remarks

This species seems to belong to the genus *Saccostrea* as described by Dinamani (1976). It is rather oval dorso-ventrally and both valves are of equal height.

**Saccostrea sp. 3**

Figs 2H, 35

Material examined:
Sarasin Bridge, Phuket, 23 Jan 2002.

Description

Prodissococonch I total length 65 µm. D-shaped with the dorsal margin of hinge forming a straight line, with round ventral margin. Outer surface smooth. Length of the hinge line 52 µm.

Prodissococonch II length 335 µm, height 357 µm (left valve). Orthogyrate in outline, equal-valve. The left valve is higher than the right valve, with broad umbo. Convexity 232 µm. Distinctive concentric growth line ridges with narrower interspaces. Hinge structure: The left valve has 3 teeth at the anterior and 2 teeth at the posterior hinge end. Short ridge on the middle of the provinculum.

Pediveliger shell rather oval dorso-ventrally. Left valve higher than right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left umbo. Surface of the shell smooth with well marked concentric growth lines with relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissococonch I, across prodissococonch II in left valve, and ends in a small emargination at

![Image of Ostrea futamiensis](image_url)

**Fig. 39. Ostrea futamiensis** collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. Scale bars = 100 µm.
the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Remarks
This species seems to belong to the genus *Saccostrea* as described by Dinamani (1976). It is rather oval dorso-ventrally. The size of the prodissoconch differs from that of other *Saccostrea* species.

*Saccostrea* sp. 4
Figs 21, 36

Material examined:

Description
Prodissoconch I total length 63 µm. D-shaped with the dorsal margin of hinge forming a straight

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Fig. 40. *Ostrea futamiensis*. Line drawing showing specific characters. A, B. Left valve. C, D. Right valve.
line, with round ventral margin. Outer surface smooth. Length of the hinge line 46 µm.

Prodissococonch II length 329 µm, height 392 µm (left valve); length 346 µm, height 350 µm (right valve). Orthogyrate in outline, equivale. The left valve is higher than the right valve, with broad umbo. Distinctive concentric growth line ridges with similar interspaces. The left valve has 3 teeth at the anterior and 2 teeth at posterior hinge end. Short ridge on the middle of provin-
culm.

Pediveliger shell rather oval dorso-ventrally. Left valve higher than right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left umbo, surface of the shell smooth with

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**Fig. 41. Dendrostrea folium** from hatchery. Age: 14 days. Broodstock collected in Ang Sila, Chonburi, Thailand, Feb 2000. A. Right valve. B. Left valve. C. Both valves in natural position. D. Both valves seen from the posterior end. Scale bars = 100 µm.
well marked concentric growth lines with similar interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Remarks
This species seems to belong to the genus *Saccostrea* as described by Dinamani (1976). It is rather oval dorso-ventrally with a distinct straight anterior shoulder. The right valve is much lower than the left.

*Saccostrea* sp. 5
Figs 2J, 39

Material examined:

Description
Prodissoconch I total length 50 µm. D-shaped with the dorsal margin of hinge forming a straight line, with round ventral margin. Outer surface smooth. Length of the hinge line 38 µm.

Prodissoconch II length 274 µm, height 329 µm (left valve); length 274 µm, height 296 µm (right valve). Orthogyrate in outline, equivale. The left valve is higher than the right, with broad umbo.

Pediveliger shell rather oval along the dorso-ventral axis. Left valve higher than right valve with broad umbo projecting upwards above the hinge line (orthogyrate). Right valve: The right umbo lower than the left. Shell colour red.

Remarks
This species seems to belong to the genus *Saccostrea* as described by Dinamani (1976). It is

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Fig. 42. *Dendrostrea folium* collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). A. Seen from the posterior end. B. Both valves in natural position. Scale bars = 100 µm.
rather oval dorso-ventrally and has a red colour, which is distinct from other *Saccostrea* species.

**Ostrea futamiensis** Seki, 1929  
Figs 2K, 38–40


Material examined:  
PMBC pier, Phuket, 20 Jan 2002.

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Fig. 43. *Dendrostrea folium*. Drawings showing characteristica of the shells of the veliconcha. A, B. Left valve. C, D. Right valve.
Fig. 44. *Dendrostrea folium* collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valves. B, D. Right valves. Scale bars = 100 µm.

Description

Prodissoconch I length 148 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Outer surface smooth with rising marginal edges. Length of the hinge line 89 µm.

Prodissoconch II length 293 µm, height 276 µm (left valve); length 284 µm, height 236 µm (right valve). Orthogyrate in outline, equi-va-lve.

Fig. 46. *Dendrostrea cf. folium*. Collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). This species is similar to *D. folium* but is probably a different species. A. Left valve. B. Right valve. C. Both valves seen from the posterior end. D. Both valves seen from the dorsal (umbonal) end, posterior to the left. Scale bars = 100 µm.
Fig. 47. *Dendrostrea sandwichensis* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B. Right valve. C–E. Entire individuals. F. Entire individual seen in oblique dorsal (umbonal) view, anterior to the right. Scale bar in F = 100µm.
Left valve higher than right, with distinct broad umbo upward, but the right valve is slightly longer than the left. Convexity, rather broad, 241 µm. Distinctive concentric growth line ridges with larger interspaces. Hinge structure: The left valve has 2 posterior and 2 anterior teeth. The anterior are somewhat reduced. Short ridge on the middle of provinculum. The right valve has 2 posterior and 2 anterior teeth. The anterior are somewhat reduced.

Pediveliger shell rather oval in the antero-posterior plane. Left valve larger than the right valve with prominently broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left. Surface of the shell smooth with well marked concentric growth lines with relative larger interspaces. The fasciole is a conspicuous tract, that extends from the posterior end of prodissoconch I, across prodissoconch II in left valve, and ends in a small emargination at the posterior margin of the lar-

Fig. 48. *Dendrostrea sandvichensis* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Entire individual seen in oblique dorsal (umbonal) view. Anterior end to the left.

Fig. 49. *Dendrostrea sandvichensis* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
val shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour greenish brown.

Soft parts contain an eyespot, 21 µm, irregular in shape and positioned anteriorly above the centre. Digestive gland greenish. Colour of soft parts greenish brown. Lipid droplets found in umbo of the left valve.

Remarks
This species is easily distinguished from other oyster larvae by having a broad umbo directed upwards above the hinge, especially in the left valve. It has distinct growth line ridges and sharp marginal edges. It was identified by the use of Ranson (1967). However, the 16S rDNA sequences of the larva (no adults were found) indicated that this species probably does not fit very well in the genus Ostrea (Bussarawit et al. 2006) but this has to be studied further.

This species was recorded by Th. Mortensen from Kung Kaben, (Thailand) (no. 581 in Ranson 1967), Ko Chang, (Thailand) (no. 583 in Ranson 1967) and his specimens are deposited at the Zoological Museum, Copenhagen, Denmark (Ranson 1967).

**Dendrostrea folium** (Linnaeus, 1758)
Figs 2L, 41–45

*Ostrea folium* Linnaeus, 1758: 699, sp. 178.
*Ostrea folium.* – Sowerby, 1871: sp. 40, pl. 18, fig. 40.

![Fig. 50. Dendrostrea sp. collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.](image)
Fig. 51. *Nanostrea exigua* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B. Right valve. C. Both valves in natural position, anterior to the right. D–F. Living individuals showing the eye spot. Scale bars = 100 µm.
Description

Prodissoconch I length 120 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Anterior end is slightly less pointed than the posterior. Outer surface smooth. Length of the hinge line 73 µm.

Fig. 52. Planostrea pestigris collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). A. Left valve. B. Right valve. C. Both valves in natural position. D. Valves seen from the posterior end. Scale bars = 100 µm.
Prodissococonch II length 329 µm, height 333 µm (left valve); length 342 µm, height 320 µm (right valve). Orthogyrate in outline, equivaleve. Left valve higher than right valve, with distinct broad umbo. Convexity 282 µm. Distinctive concentric growth line ridges with larger interspaces. The arrangement of growth lines is conspicuous in this species. The left valve hinge has two posterior and two anterior teeth. Short ridge on the middle of the provinculum.

Pediveliger shell thin and rather oblong. Left valve is higher than the right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo is lower than the left. Surface of the shell with distinct concentric growth lines with relative large interspaces. The right valve margin covers the left margin.

The fasciole is a conspicuous tract that extends from the posterior end of prodissococonch I, across prodissococonch II in left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Soft parts contain an oblong eyespot, 30–40 µm. It is positioned at the anteriorly centre of the valve. Digestive gland dark brown. Colour of soft parts brown. Lipid droplets found in the left valve umbo.

Remarks
Ranson (1960, 1967) referred larvae of this species to the genus *Ostrea*. However, the 16S rDNA sequences of the larva indicated that this species probably does not fit very well in the genus

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![Fig. 53. Planostrea pestigris collected in nature (Sarasin Bridge, northern end of Phuket Island, Thailand, 23 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.](image-url)
Ostrea (Bussarawit et al. 2006). We tentatively place the species in the genus *Dendrostrea* as they found it to clusters together with other *Dendrostrea* species within an unresolved polytomy, but this has to be studied further.

This species was collected by H.M. Smith from Ko Samet (Thailand) (no. 384107, Sri Racha, (Thailand) (no. 363566 in Ranson 1967), Leam Sing, (Thailand) (no. 361032 in Ranson 1967), Ban Don Bay, (Thailand) 361506b, Pak Nam Khan, (Thailand) (no. 360845 in Ranson 1967) and his specimens are deposited at the Smithsonian Institute, United States National Museum, Washington DC (Ranson 1967).

*Dendrostrea* cf. *folio*um

Figs 3A, 46

Material examined:
Sarasin Bridge, Phuket, 23 Jan 2002.

Description

Prodissoconch I length 126 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Anterior end is slightly less pointed than the posterior end. Outer surface smooth. Length of the hinge line 67 µm.

Prodissoconch II length 343 µm, height 357 µm (left valve); length 347 µm, height 320 µm (right valve). Orthogyrate in outline, equivaile. Left valve higher than right valve, with broad umbo. Convexity 270 µm. Distinctive concentric growth line ridges with larger interspaces. The arrangement of growth lines is conspicuous in this species. The left valve hinge has 2 teeth at the posterior end and two reduced teeth in the anterior end. Short ridge on the middle of the provinculum.

Pediveliger shell thin and rather oblong. Left valve is higher than the right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left umbo. Surface of the shell with distinct concentric growth lines with relatively large interspaces. The right valve margin covers the left margin. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. The transparency of the shell disappears in preserved specimens.

Soft parts contain an elongated eyespot, 30-35 µm, positioned at the centre of the valve. Digestive gland dark brown. Posterior adductor muscle larger than anterior and situated dorso-posteriorly. Colour of soft parts brown. Large lipid droplets found in umbo of the left valve.

Remarks

We found larvae of this species to be very similar to larvae of the cultured *D. folium*, but the hinge teeth were different in having anterior teeth of much reduced size. DNA sequences could help to clarify identification in the future. Ranson (1960, 1967) referred larvae of *D. folium* to the genus *Ostrea*.

*Dendrostrea sandvichensis* (Sowerby, 1871)

Figs 3B, 47–49

*Ostreae*a *sandvichensis* Sowerby, 1871: sp. 66.


Ostrea sandvicensis. – Kay 1979: 539.
Material examined:
PMBC pier, Phuket, 20 Jan 2002.

**Description**

Prodissoconch I length 100 µm. D-shaped with the dorsal margin of hinge forming a straight line, rather oval with round ventral margin. Outer surface smooth. Length of the hinge line 70 µm.

Prodissoconch II left valve length 311 µm, height 311 µm; right valve length 320 µm, height 289 µm. Orthogyrate in outline, equivaleve. Left valve higher than the right, with distinct broad umbo. Distinctive concentric growth line with narrower interspaces. The left valve hinge carries 2 teeth at the posterior end and two smaller teeth anteriorly.

Pediveliger shell rather broad antero-posteriorly. Left valve higher than the right valve with prominently broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower, but longer than the left umbo. Surface of the shell with concentric growth lines with relatively narrow interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval

**Fig. 55. Planostrea pestigris.** Drawings showing characteristic of the shells of the veliconcha. A, B. Left valve. C, D. Right valve.
shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Soft parts contain a round dark eyespot, 30 µm. It is positioned at the centre of the valve. Digestive gland dark brown. Posterior adductor muscle larger than anterior and situated dorso-posteriorly. Colour brown.

Remarks
The identification follows Ranson (1967). This species, reported as *Ostrea sandwichensis*, was collected from Thailand by Th. Mortensen in 1900 and is deposited in the ZMUC, Copenhagen. It was collected at Kung Kaben, (Thailand) (no. 581 in Ranson 1967), Ko Chang, (Thailand) (no. 583 in Ranson 1967) (Ranson 1967). The adults of this species are also found in Thailand and were described by Bussarawit & Cedhagen (2011).

*Dendrostrea* sp.
Figs 3E, 50

Material examined:
PMBC pier, Phuket, 20 Jan 2002.

Description
Prodissoconch I length 114 µm. D-shaped with the dorsal margin of hinge forming a straight line. Rather oval with round ventral margin. Outer surface smooth. Length of the hinge line 69 µm.

Prodissoconch II length 341 µm, height 359 µm (left valve); length 342 µm, height 347 µm (right valve). Orthogyrate in outline, equivalve. Left valve higher than right valve, with distinct broad umbo. Distinctive concentric growth line ridges with larger interspaces. The arrangement of growth lines is conspicuous in this species. The left valve hinge has 2 teeth at the posterior end and two anterior teeth. Short ridge on the middle of the provinculum.

Pediveliger shell thin and rather oblong. Left valve is higher than the right valve with broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo lower than the left umbo. Surface of the shell with distinct concentric growth lines with relative large interspaces. The right valve margin covers the left margin. Shell colour greenish.

Soft parts contain a round dark eyespot, 33 µm. It is positioned at the centre of the valve. Digestive gland greenish. Posterior adductor muscle larger than anterior and situated dorso-posteriorly. Colour of soft parts greenish brown. Large lipid droplets found in umbo of the left valve.

Remarks
The morphology of this species is similar to that of other species of the genus *Dendrostrea*, but the arrangement of the hinge teeth and pediveliger size is different from other members of the genus described in this paper. There is a possibility that this larva could represent the species *D. crenulifera* or *D. rosacea*. Both species are found as adults in Thailand.

**Nanostrea exigua** Harry, 1985
Figs 3D, 51


Material examined:
PMBC pier, Phuket, 20 Jan 2002.

Description
Prodissoconch I total length 140 µm. D-shaped with the dorsal margin of hinge forming a straight line, and has a round ventral margin. Anterior end is slightly less pointed than the posterior end. Outer surface smooth. Length of the hinge line 108 µm.

Prodissoconch II length 327 µm, height 288 µm (left valve); length 330 µm, height 261 µm (right valve). Orthogyrate in outline, equivalve. Left valve higher than right valve, with distinct broad umbo. Convexity: the ventral part of the left valve is very flat. Distinctive concentric growth line ridges with large interspaces. The left valve hinge has 2 teeth at the posterior end with reduced anterior teeth. Long ridge in the middle of the provinculum.
Pediveliger shell oval along the antero-posterior axis. Left valve larger than the right valve, with prominent broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo is much lower than the left umbo with straight dorsal line. Surface of the shell with well-marked concentric growth lines with relatively broad interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour greenish brown.

Soft parts contain a round dark eyespot, 21 µm. It is positioned at the centre of the valve. Digestive gland greenish brown. Posterior adductor muscle larger than anterior and situated dorso-posteriorly. Colour of soft parts greenish brown. Large lipid droplets found in umbo of the left valve.

Remarks
This species is easily distinguished from other oyster larvae by having a broad continuously round umbo of the left valve, which is markedly different from the right valve. Its umbo is rather flat and has much lower planes separating the valve. The growth line ridges are rather well defined. The marginal edge around the right valve is distinctly grooved and covers the left valve edges.

This species was collected by Th. Mortensen in 1900 from Thailand, 55 m (no. 582 in Ranson 1967), Ko Kun, 9 m (no. 586 in Ranson 1967) and Kung Kaban, 11 m (no. 591 in Ranson 1967) and his samples are deposited at Zoological Museum, University of Copenhagen, Denmark (Ranson 1967).

Ranson (1960, 1967) referred larvae of this species to the genus Ostrea. Harry (1985) gave separate generic status to this species under the genus name Nanostrea.

Planostrea pestigris (Hanley, 1846)
Figs 3E, 52–55

Ostrea pestigris Hanley, 1846: 106.
Ostraea palmipes Sowerby, 1871: sp. 78.

Ostrea paulucciae Ranson, 1960: 34, fig. 109–112.
Crassostrea palmipes. – Carreon 1969: 114.
Ostrea pestigris. – Morris 1985: 128.
Planostrea pestigris. – Harry 1985: 143. – Yoosukh 2000: 82, fig. 1.

Material examined:
Sarasin Bridge, Phuket, 23 Jan 2002.

Description
Prodissoconch I length 134 µm. D-shaped with the dorsal margin of hinge forming a straight line, with round ventral margin. Outer surface smooth and uniform in texture. Length of the hinge line 91 µm.

Prodissoconch II length 327 µm, height 288 µm (left valve); length 330 µm, height 261 µm (right valve). Orthogyrate in outline, equivale. Left valve higher than right valve, with distinct broad umbo of prodissoconch I, which is continuous from the anterior and posterior shoulders. Convexity rather large, 230 µm, with ventral part of left valve rather flat. Concentric growth line ridges with large interspaces. The left valve hinge has 2 teeth at the posterior end and reduced size of two anterior teeth. Long ridge in the middle of the provinculum.

Pediveliger shell medium thick. Rather triangular in general shell form and with a round and projecting umbo. Left valve larger than the right valve with prominently broad umbo projecting upwards above the hinge line (orthogyrate). The right valve umbo is much lower than the left. Surface of the shell with well-marked concentric growth lines with relatively large interspaces. The fasciole is a conspicuous tract that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour greenish red.

Soft parts contain a round, dark eyespot, 29 µm in size, and positioned at the centre of the valve. Digestive gland greenish red. Posterior adductor muscle larger than anterior and situated slightly dorso-posterioirly. Colour of soft parts greenish red. Lipid droplets found in umbo of the left valve.
Remarks
The larva of this species is similar to *Nanostrea exigua*, but can be separated by its narrower umbo and greater height. The shape is taller and the right valve umbo is more distinct than in *Nanostrea exigua*.

This species was collected by Th. Mortensen in 1900 from Thailand (no. 484, 488, 508, 536, 546, 556, 569, 570, 572, 574, 575, 576, 578, 588) and his samples are deposited at Zoological Museum, University of Copenhagen, Denmark (Ranson 1967).

Ranson (1960, 1967) referred larvae of this species to the genus *Ostrea*. Harry (1985) suggested that *O. deformis* is a junior synonym of *Planostrea pestigris* (Hanley, 1846), which is known from a limited area in the Indo-West Pacific. The only way to test this is by sequencing larvae and adults but we were unable to do that.

*Lopha cristagalli* (Linnaeus, 1758)
Figs 3F, 56

*Ostraea cristagalli*. – Sowerby 1871: sp. 22.
*Ostrea folium*, *cristagalli* type. – Thomson 1954: 146, pl. 3, fig. 1.

Material examined:
PMBC pier, Phuket, 20 Jan 2002.

Description
Prodissoconch I total length 133 µm. D-shaped with the dorsal margin of hinge forming a straight line, with round ventral margin. Outer surface smooth. Length of the hinge line 93 µm.

Prodissoconch II length 267 µm, height 257 µm (left valve); length 267 µm, height 227 µm (right valve). Orthogyrate in outline, equivaque. Left valve higher than the right, with low broad round umbo consisting of prodissoconch I. Concentric growth lines indistinct and with broad interspaces. The left valve hinge has 2–3 teeth at the posterior end and reduced size of the two anterior teeth. Very short ridge in the middle of the provinculum.

Pediveliger shell oval at antero-posterior line with rather sharp marginal edge. Left valve similar to the right valve with broad umbo above the hinge line (orthogyrate). The right valve umbo is slightly lower than the left. Surface of the shell with indistinct concentric growth lines with relatively large interspaces. The fasciole is a conspicuous tract, that extends from the posterior end of prodissoconch I, across prodissoconch II in the left valve, and ends in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve.

Remarks
This species is easily distinguished from other oyster larvae by having rather transparent and asymmetrical shell valves. It has broad overlapping growth line ridges.

Ranson (1960, 1967) referred larvae of this species to the genus *Ostrea*. This species is recorded from the Indian Ocean and Indo-China (Ranson 1967). Adults of this species have previously been recorded in Thailand (Yoosukh & Duangdee 1999). The larva is very similar to *Dendrostrea sandvichensis* but the size of Prod I is clearly different (larger).

Family Gryphaeidae

*Hyottissa hyotis* (Linnaeus, 1758)
Figs 3G, 57–59

*Ostraea hyotis*. – Sowerby 1871: sp. 7.
Fig. 56. *Lopha cristagalli*. Collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B, D. Right valve. C, E, F. Individuals seen from different positions. Scale bars = 100 µm.
Description

Prodissoconch I length 89 µm. D-shaped with the dorsal margin of the hinge forming a straight line, and with round ventral margin. Outer surface smooth. Length of the hinge line 64 µm.

Fig. 57. Hyotissa hyotis. Collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B. Right valve. C. Both valves in natural position, anterior to the left. D. Individual seen from the posterior end. Scale bars = 100 µm.
Prodissoconch II length 311 µm, height 324 µm (left valve); length 324 µm, height 333 µm (right valve). Orthogyrate in outline, inequivaleve. Right valve is higher than left valve. Convexity: 302 µm. Concentric growth line ridges are distinct with similar interspaces. The left and right valve hinges consist of 5 teeth with rather equal interspaces distributed along the provinculum. Additionally 10 minute denticular teeth are distributed at the dorso-anterior margin of the valve.

Pediveliger shell thick, with oval shape, length shorter than height. Left valve similar to the right valve with umbo above the hinge line (orthogyrate) and slightly directed to the posterior. The right valve umbo is slightly higher than the left umbo. Surface of the shell with distinct concentric growth lines with relatively large interspaces. The fasciole is a conspicuous tract, that extends from the posterior end of prodissoconch I, across prodissoconch II in left valve, and ends

Fig. 58. *Hyotissa hyotis*. Collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). A. Left valve. B. Right valve. C. Individual seen from the dorsal (umbonal) side, posterior to the left. D. Both valves in natural position. Scale bars = 100 µm.
in a small emargination at the posterior margin of the larval shell. A complementary sulcus also appears on the posterior aspect of the right valve. Shell colour pink.

Soft parts contain an eyespot, 31–62 µm, irregular or slightly rectangular in shape and positioned anterior of the centre of the valve. Digestive gland pink to violet. Posterior and anterior adductor muscles rather similar in size. Colour of soft parts pink to violet. Lipid droplets found under the left umbo.

Remarks

Ranson (1960, 1967) referred larvae of this species to the family Ostreidae and belonging to the genus *Pycnodonte*.

This species was collected by H.M. Smith from Thailand and his samples are deposited at the Smithsonian Institution, United States National Museum, Washington D.C. They were collected at Lam Sing, Gulf of Thailand (no. 367442 in Ranson 1967), Ko Tao, Gulf of Thailand (no. 367443) (Ranson 1967) and by Th. Mortensen in 1900 from whom the specimens are deposited at Zoological Museum, University of Copenhagen, Denmark. They were collected in Ko Kradat (no. 430 in Ranson 1967), Ko Kram, depth 55 m (no. 444 in Ranson 1967), and Thailand, depth 11 m (no. 452) (Ranson 1967).

Other species

Four more species of oyster larvae were found, see Figs 3H–K.

The first one (Fig. 3H) is probably *Alectryonella plicatula* because it resembles the photo given by Ranson (1967: 248, fig. 45), but it also

Fig. 59. *Hyotissa hyotis* collected in nature (PMBC pier, Phuket, Thailand, 20 Jan 2002). Shells are cleared in Chlorox, mounted in glycerol, and photographed in an inverted microscope. A, C. Left valve. B, D. Right valve. Scale bars = 100 µm.
shows some similarity to *Pustulostrea tuberculata*, also figured by Ranson (1967: 242, fig. 48). However, *P. tuberculata* has a more elongated shape (anterior-posterior axis) than our specimens.

The second one (Fig. 3I) is not at all described in the literature, but because of its general shape, we can say that it belongs to the genus *Dendrostrea*. The peculiar large eyespot has never before been described in the literature. Most oyster species have small eyespots and live in shallow waters. Our guess is that such an enormous eyespot could be used in deeper living species, which are never attracted by light but try to avoid it, but this has to be tested.

The third one (Fig. 3J) is not at all described in the literature, but from its general shape it is possible to place it in the genus *Dendrostrea*. It could be identical with the species from Thailand described as the new species *Ostrea bartschi* by Ranson 1967 (p. 243, fig. 40), but no information is given by him.

The fourth one (Fig. 3K) resembles *Dendrostrea folium*, but has a different colour.

**DISCUSSION**

Oysters are a quantitatively important component in various marine habitats in SE Asia and elsewhere (Ruesink et al. 2005). Large numbers of oyster species are reported from SE Asian countries in numerous publications, but we hesitate to summarize the literature because of the vast taxonomic confusion. Several species are also commercially important as fishery resources or in aquaculture. Some commercial oyster species have been introduced to neighbour countries, such as *Crassostrea gigas* to Malaysia and Singapore (Lam & Morton 2009). They have, however, not been introduced to Thailand or been found in Thai waters (Ruesink et al. 2005). Oysters in aquaculture in Thailand are mostly produced from local broodstock. However, one species with a high market value, *Crassostrea belcheri* has probably frequently been transplanted as spat between the Gulf of Thailand and the Andaman Sea so that regional differences have been wiped out. But such regional differences are still found in the closely related *C. bilineata* with such a low market value that transplantation is unprofitable (as *C. iredalei* in Bussarawit & Simonsen 2006).

Larvae of altogether 23 species recorded in Thailand are included in this study. Twelve of them have been identified to species, but the identity of the remaining eleven species needs to be clarified. In all, 17 species of adult oyster species have been found in Thailand (Bussarawit & Cedhagen 2011). The application of molecular methods is a promising method in order to clarify remaining problems regarding the identity of oysters and their larvae.

**Development**

The stages of hinge development in larvae of *C. belcheri* are essentially similar to those described for other *Crassostrea* species. The larvae of all *Crassostrea* species show large umbones rising above the hinge plane and becoming involuted over the hinge to become opisthogyrate. Growth is faster along the antero-ventral margin. Consequently, the valves become inequilateral. It has been suggested that such larval shells present a fundamentally different type than that of the orthogyrate larval shell of the genera *Saccostrea* (Dinamani 1973, 1976) and *Ostrea* (Loosanoff et al. 1966; Le Pennec 1980), where growth of the shell is fairly uniform on both the anterior and posterior regions of the hinge.

The morphology of the larval shell of *C. belcheri* and other *Crassostrea* species is distinctly different from that of the genus *Saccostrea* as described by Dinamani (1976). The species of *Saccostrea* described by him have equilateral prodissoconchs with orthogryral umbones, and symmetrical teeth on the provinculum.

The fully developed prodissoconchs of *C. belcheri* and *C. gigas* share a common feature in that the posterior teeth on the left valve are obscured by the folding of the valve margin. This is different from those of *C. virginica*, *C. rhizophorae* and *C. bilineata* pediveliger larvae, where the posterior teeth are only reduced (Aileen Tan, pers. comm.).

During the early stage of larval life, development of the hinge in *C. belcheri* is similar to that of *C. bilineata*. However, at the pediveliger stage, a number of differences exist between the two species:
a. The degree of inrolling of the left umbo in *C. belcheri* is greater than in *C. bilineata*.
b. The posterior region of the provinculum becomes modified with teeth being obscured in *C. belcheri*, whereas it is only partially modified in *C. bilineata* so that the teeth, though reduced, are still visible.
c. The shell shape in *C. belcheri* is round while in *C. bilineata* it is ventrally elongated.

In the present study we discovered and verified morphological criteria which allow one to reliably distinguish between commercial oyster species and other oyster larvae collected in nature. We could verify identification based on morphology of several larvae with a match of DNA sequences done on known adults (Bussarawit et al. 2006).

**Comparison of oyster larval shell morphology**

Oyster larvae can be identified to the family Gryphaeidae by the following characters; inequivalve; hinge with five teeth arranged over the entire length of it; internal anterior ligament occurs immediately after the hinge; 10 small denticles at the edge of each valve anterior to the ligament. This agrees with Ranson (1960, 1967). However, in his publication all Gryphaeidae species were included in the family Ostreidae. For the living oyster species, his genus *Pycnodonte (=Pycnodontia)* could be divided into the genera *Pycnodonta*, *Hyotissa* and *Parahyotissa*. In this paper we could describe only the larva of the species *Hyotissa hyotis*. However, the species *Parahyotissa imbricata*, and *P. sinensis* are all found as adults in Thailand so their larvae are also expected to be found there in the future.

The family Ostreidae can be identified by the following characters: inequivalve; hinge structure has teeth at both ends, around 2-3 teeth. The genus *Crassostrea* has inequivalent valves, skewed umbo (opisthogyrate); hinge with two teeth at each end; internal anterior ligament extends beyond the hinge. The two commercial species *C. belcheri* and *C. bilineata* differ in shell shape, level of skewness of the umbo, and hinge teeth structure.

Large numbers of a third species of *Crassostrea* were collected in nature. This species resembles *C. bilineata* but is bigger, has a smaller eyespot, and a more triangular shell shape. The separation of this species was verified by DNA sequencing (Bussarawit et al. 2006). However, it was impossible to identify it to species. An adult shell of an undescribed *Crassostrea* species in Thailand has also been noticed (Yoosukh, pers. communication).

The genus *Saccostrea* has a knobby umbo and the species of this genus are very similar. The colour of living individuals and knowledge about the size of prodissoconch I and II are needed in order to identify larvae of this genus.

Apart from *Pycnodonte* and *Crassostrea*, Ranson (1960, 1967) placed all the remaining species in the genus *Ostrea*. He described characters of the genus *Ostrea* as having prodissoconchs with a long hinge; two denticles at each end, the anterior pair frequently reduced; the ligament is internal at the level of the hinge, at the centre or between the centre and anterior end. In our study, oyster larvae belonging to more genera were found: *Dendrostrea*, *Lopha*, *Nanostrea*, and *Planostrea*. Differences in larval shell shape, umbo shape, and hinge teeth were described.

Comparison of oyster larval soft parts and their colour revealed clear differences between many species (see Figs 2–3).

During our study just a few prodissoconchs I of each species were measured. During a very late stage of our investigation, we understood the importance of measuring a large number of prodissoconch I in all available species. Prodissoconch I is formed during early development and its size or, rather, its volume, is closely related to egg size (Ockelmann 1965). Some species are incubatory which means that the adults brood the larvae in their gills. Such species have larger eggs and prodissoconch I size than the non-incubatory (non brooding) species. Careful measurements of prodissoconch I would therefore indicate the type of early larval development. The prodissoconch I size does not seem to vary very much within each species, so it is a useful character to distinguish between different species with similar morphology. We plan to study this more closely in the future.

About half of all living oyster species brood offspring in the inhalant chamber of their mantle cavity. They are released as early planktotrophic larval stages or even as advanced larvae capable
of immediate metamorphosis. The brooders are found within the subfamilies Lophinae and Ostreinae. The others are broadcast spawners, which release eggs and sperm in the water and do not engage in parental care of the young. The broadcast spawners belong to the subfamily Crassostreinae (Crassostrea and Saccostrea) of Ostreidae and the subfamily Pycnodonteinae of Gryphaeidae. The adults of the broadcast species are significantly larger than the brooders (Buroker 1985; O’Foighil & Taylor 2000). Our results show that the prodissocochn I is larger (often 100–150 µm) in brooding species than in the broadcasting species (about 60–90 µm).

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