

Some Studies on the New Zealand Oysters

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Abstract

Two species of *Ostrea* Linnaeus are present in New Zealand: *Ostrea lutaria* Hutton (the mud-oyster) and *Ostrea heffordi* Finlay (the southern rock-oyster). The Auckland rock-oyster, currently referred to *Saxostrea glomerata* Gould is a species of *Crassostrea*, probably *Crassostrea commercialis* Iredale and Roughley (the Sydney rock-oyster). Studies on *Ostrea lutaria* show that it is distinct from the South Australian mud-oyster, *Ostrea angasi* Sowerby, but has *Ostrea charlottae* Finlay as a synonym. *Ostrea lutaria* is larviparous and hermaphroditic, spawning for at least eight months of the year between August and March at temperatures as low as 10.0°C, it is probably protandric with regular alternating female and male phases, and it becomes hermaphroditic after the second or third breeding season. Fecundity is about 1,000,000, egg size 200 μ –270 μ . Larvae are incubated for about 20 days; are released when fully developed and settle when they measure approximately 0.44mm x 0.34mm. No free-swimming oyster larvae have been found in plankton collected from Evans Bay, Wellington. The large size of the veliger and the absence of larvae from the plankton suggests that the free swimming phase is extremely short, probably only a few days. The settling larva exhibits an exploratory phase; does not appear to be photosensitive and when approximately 5.5mm in length has all the gills present.

DESPITE the economic importance of the New Zealand mud-oyster, there has been little previous work on this animal, other than that of systematic accounts. A one-day survey of a Foveaux Strait oyster-bed carried out by Fleming (1952) resulted in a list of animals associated with the oyster-bed, and this list was then compared with other animal communities of Auckland Harbour and with Pliocene shell beds. Powell (1957) referred to the breeding habits of the mud-oyster, suggesting that they were similar to those of the oviparous Auckland rock-oyster. Further mention of the mud-oyster has been made by Korringa (1941, p. 7), Orton (1937, p. 93), and Roughley (1933, p. 281), who have listed it for the purpose of comparison with other species. Korringa, Orton and Roughley in their lists of incubatory and larviparous oysters refer to the New Zealand mud-oyster as *Ostrea lutaria*. Thus at the commencement of this study there were conflicting opinions regarding the type of larval development and nothing had been published on the anatomy of the soft-parts or reproduction.

This paper is primarily concerned with the systematic status, reproduction and development of the mud-oyster. Considerable difficulty was experienced in determining the status of this oyster and it was necessary to investigate the systematic status of all the known New Zealand oysters, before a decision was reached. The anatomy of the mud-oyster is essentially typical of the genus *Ostrea*.

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1. THE SYSTEMATIC STATUS OF THE NEW ZEALAND OYSTERS

At the time of this account there is considerable difference of opinion concerning the systematic status of the New Zealand oysters, more especially the mud-oyster. This has arisen in the main because previous authors have relied entirely on shell characters and some species were described from single shell valves alone.

The first description of the genus *Ostrea* based on shell characters was that of Linnaeus, who included in the genus the true oysters and also the pectens, the limas and the amusiums. The work of Orton (1928) who based his classification on the shell characters but included also features of the life history, was a major step forward in the revision of the genus *Ostrea*. Orton separated living oysters into two major divisions which he referred to as 'type 1' and 'type 2,' and his classification has provided a basis for all following workers.

Type 1 was based on *Ostrea edulis* in which "the shell is subcircular; the egg is large; the adult larviparous; the individual is hermaphrodite; spawning occurs at medium temperatures round 15.0°C.; and the species flourish in temperate regions." The known species included by Orton in this type are: *Ostrea edulis* (the European oyster), *Ostrea lurida* (the British Columbia oyster) and *Ostrea angasi* (the South Australian mud-oyster). Type 2 was based on *O. virginica*, a species in which "the shell is elongated in the anterodorsal and posteroventral direction; the egg is small; the adult non-larviparous; the individual of one sex only; spawning occurs at moderately high temperatures, around 20.0°C.; and the species flourish in sub-tropical or tropical regions." The known species included by Orton in this type are: *O. virginica* (the eastern North American oyster), *O. angulata* (the Portuguese oyster) and *O. cucullata* (of world-wide distribution in sub-tropical and tropical regions).

Further, Orton (1928, p. 321) suggested that 'type 1' oysters should belong to a new genus, *Monoeciostrea* and 'type 2' oysters to the new genus *Dioeciostrea*, but at the same time considered that these genera should not be adopted until definition could be made "founded on adequate information." Orton's two genera are invalid and have not been accepted since earlier names are available.

Nelson (1938, p. 1) in his review of Orton's work noted that the latter did not take into account the promyal chamber and that geographical limitations were unreliable where the American species *O. equestris* of type 1 is concerned because it ranges into sub-tropical water, and *O. virginica* of type 2 ranges from the sub-tropical to the more temperate waters of Nova Scotia. Nelson regarded *O. denselamellosa* of Japan and *O. equestris* as of Orton's type 1 (their spawning temperatures however, were unknown to him). In the main, Nelson agreed with Orton's divisions but recognised type 2 oysters as belonging to the genus *Gryphaea* Sacco and proposed to relate all deeply cupped oviparous oysters with the promyal chamber to this genus and the flat, larviparous oysters which lack the promyal chamber to the genus *Ostrea*.

Lamy (1929) working on the extant oysters in the Paris Museum collections, used only shell characters for identification. He recognised only one genus, namely *Ostrea*, but within the genus included 12 subgenera and 'sections.' Lamy's classification is not generally accepted.

Ranson (1948) used the type of crenulations found on the larval shell (prodissoconch) when he reviewed the recent oysters and concluded that these were clearly recognisable as belonging to three genera, *Pycnodonte* Fischer de Waldheim, *Gryphaea* Sacco and *Ostrea* Linnaeus. The characters of the prodissoconch have proved to be completely reliable for generic identification and on occasion are also reliable for specific identification. However, in adult shells, the prodissoconch may be weathered away. Then only a preliminary diagnosis based on other shell and soft part characters can be given until the prodissoconch is finally observed either on adult shells or in the larva.

Gunter (1950, p. 442) reviewed shell characteristics and soft parts and extended the description of the characters given by Orton for type 1 and type 2 oysters. Gunter regarded type 1 oysters as possessing larger eggs, the upper limit produced at one spawning around 1,000,000; the eggs are retained; fertilisation and larval development take place within the mantle chamber; the gill ostia are large; the animals live in sea water of high salinity; the muscle scar is unpigmented and near the centre of the shell; the lower valve is flatter and fairly constantly of subcircular shape; the prodissoconch hinge is long with two crenulations at each end; the ligament is at the level of the cardinal plateau. In type 2 oysters, the eggs are shed into the water; fertilisation and larval development take place in the sea water; the eggs are small; the upper limit produced at one spawning around 50,000,000; gill ostia are small; promyal chamber present; live in estuaries and brackish water with low salinity; muscle scar pigmented; lower valve more cupped; shell shape more elongated and variable; prodissoconch hinge short with two crenulations at each end; ligament anterior and outside the cardinal plateau.

As a result of this work, Gunter (1950, p. 443) came to the same conclusion as Ranson (1948) regarding the generic status of oysters, namely that there are three genera, *Ostrea*, *Pycnodonte* and *Crassostrea* (= *Gryphaea* of older authors—now used only for fossil shells).

The genera *Ostrea* and *Crassostrea* only are known from New Zealand waters. *Ostrea* is represented by *O. lutaria* Hutton, the mud-oyster and *O. heffordi* Finlay, the southern rock-oyster. Both these species show clearly the characters described for the genus *Ostrea* by Orton and later workers. The genus *Anodontostrea* proposed by Suter (1917) for the New Zealand mud-oyster has been shown by Ranson (1948, p. 11) and Gunter (1950, p. 443) to be a synonym of *Ostrea* Linnaeus.

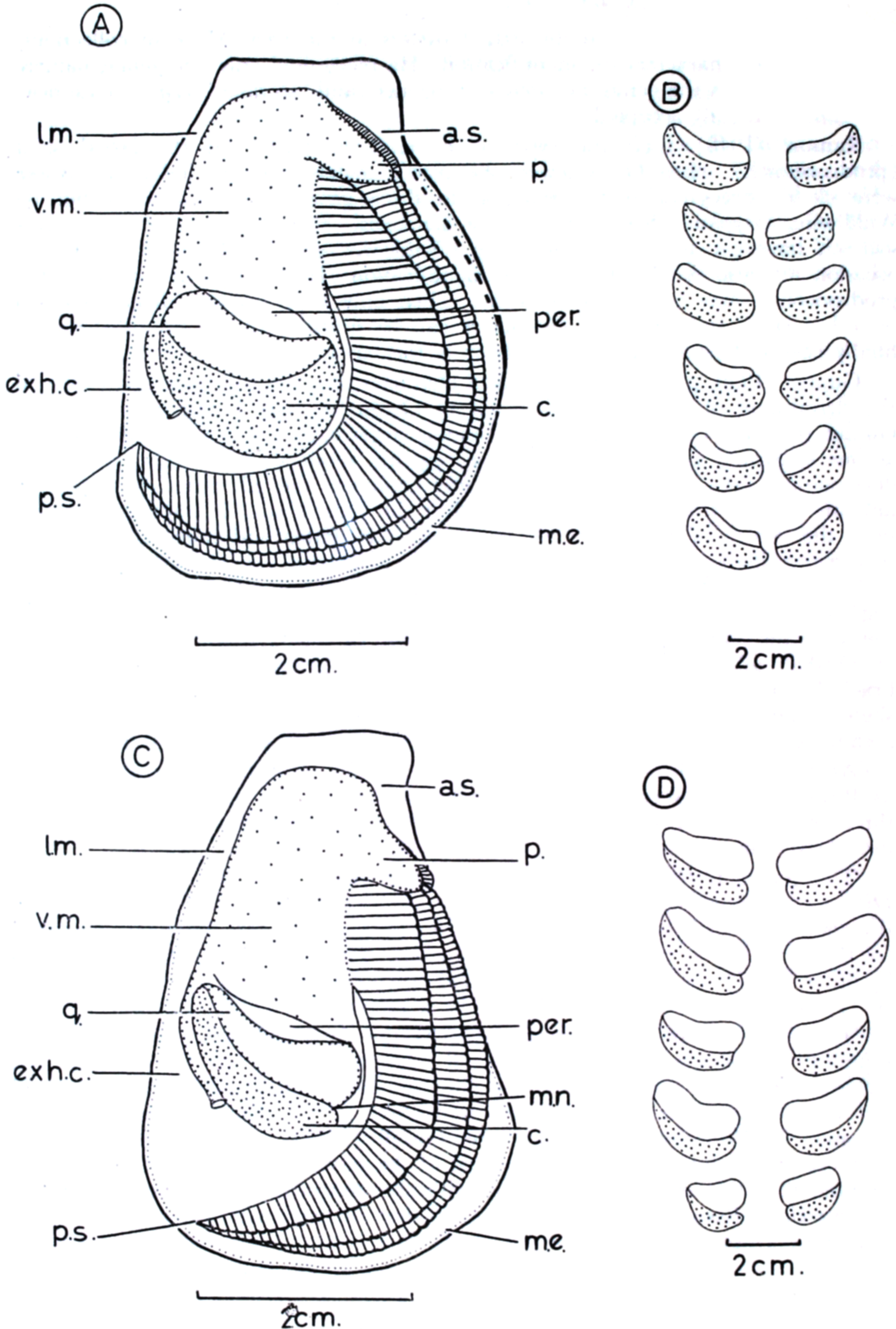
The genus *Crassostrea* is represented by the Auckland rock-oyster at present referred to *Saxostrea glomerata* Gould. Gunter (1950, p. 447) states that "*Saxostrea* differs from *Crassostrea* only in shell characteristics, which should not be considered valid grounds for separation . . . therefore, *Saxostrea* is a synonym of *Crassostrea*." Furthermore, Powell (1957) notes that the Auckland rock-oyster is oviparous, a feature typical of the genus *Crassostrea*. It would seem possible that this oyster is conspecific with the Australian rock-oyster *Crassostrea commercialis* Roughley and Iredale, 1933, but further investigations are needed before a decision can be made.

THE GENUS *Ostrea* Linnaeus, 1758 IN NEW ZEALAND (Pls. 1, 2 and 3)

Genotype (by subsequent designation Schmidt, 1818)

Ostrea edulis Linnaeus, 1758.

"Shell subcircular, relatively constant in shape within the species; lower valve shallow not recessed under the hinge; muscle scar subcentral, upper valve may be flat and opercular,



TEXT-FIG. 1.—General systematics of *O. angasi* and *O. lutaria*. Fig. A—General diagram of *O. lutaria*. Fig. B—Variation of the posterior adductor muscle scar in *O. lutaria*. Fig. C—General diagram of *O. angasi*. Fig. D—Variation of the posterior adductor muscle scar in *O. angasi*.

ABBREVIATIONS: a.s., anterior suture; c., catch muscle; exh.c., exhalent chamber; l.m., left mantle notch; p., palps; per., pericardium; p.s., posterior suture; q., quick muscle; v.m., visceral mass.

or domed and subequal to the lower, and it may or may not have denticles along the margin laterally to the hinge which fits into pits in the lower valve. Prodissoconch with a long hinge, two denticles at each end, of which the anterior pair are reduced; ligament at the centre or displaced slightly anteriorly. Without a promyal chamber, gill ostia and the eggs are relatively large, fecundity relatively low; auricles of the heart unite broadly, the ventricle not penetrated by the rectum; 'catch' area of the adductor muscle more than 50% of the area. Incubatory forms. Usually totally submerged or baring only on spring tides, in high saline waters free from turbidity."—Thomson (1954, p. 141).

O. lutaria Hutton, 1873 (Pl. 2) the mud-oyster and *O. heffordi* Finlay, 1928 (Pl. 3), the southern rock-oyster are here recognised as the only representatives of the genus *Ostrea* in our waters. Hutton (1880, 1884, 1904), Cox (1883), Suter (1913), Oliver (1923), Finlay (1928), and Thomson (1954) regard the New Zealand mud-oyster as conspecific with the South Australian mud-oyster. Iredale (1924, p. 191) referred the South Australian mud-oyster to *O. sinuata* Lamarck and Finlay (1928) referred the New Zealand mud-oyster to this genus also. Until the present paper the New Zealand mud-oyster has been diagnosed as *O. sinuata*. Lamy (1924, p. 84) clearly shows that *O. sinuata* Lamarck is a species of *Crassostrea* with a recess under the hinge, a feature not possessed by the Australian or New Zealand mud-oyster. Furthermore, the New Zealand mud-oyster is not recognised here as a synonym of the South Australian mud-oyster. Reasons for regarding the South Australian mud-oyster as distinct from the New Zealand mud-oyster are based on Sowerby's original description of *O. angasi* (1873, pl. 13) and examination of shells and soft parts of *O. angasi* from Port Phillip and Cronulla, Australia.

In his description Sowerby made no reference to the ligament, muscle shape and the presence or absence of denticles and his illustration does not show these structures. Nonetheless, it can be seen from the illustration that the lower valve extends beyond the upper valve and that both valves are fluted and crenulated. New Zealand shells are distinctive in that both valves meet around the entire free margin and the edges of the valves may sometimes be waved but are never crenulated. Taken together, the short description and illustration of *O. angasi* Sowerby, demonstrate that the New Zealand mud-oyster is not to be regarded as conspecific with *O. angasi*.

Moreover, oyster shells from Port Phillip show that the muscle impression is distinctly different from the New Zealand mud-oyster. The impression of the 'quick' area of the posterior adductor muscle is always 50% larger than the impression of the 'catch' area in Port Phillip shells, whereas in New Zealand shells, it is the 'catch' area impression that is always 50% or more larger than the 'quick' area. There is also a very definite notch between the 'catch' and 'quick' muscle area on the ventral surface of the muscle both in the meat and in the impression on the shell, but in New Zealand mud-oyster shells, the constriction, if present, is minute and only discernible on examination of the meat (Text-fig. 1, B and D).

The upper valve of the South Australian mud-oyster shell has narrow scales in close imbricating rows (Pl. 1, fig. 2) whereas the scales on the New Zealand shells (Pl. 2, fig. 2) are broader in comparison and less closely packed together. The Australian shells are in general much thicker and heavier than the New Zealand shells. The rate of calcium deposition, however, may be controlled by environmental conditions and too much reliance should not be placed on this latter feature for specific identification.

The South Australian shells are blue-grey to deep purple. In contrast, the New Zealand shells are dark brown or dark grey and shells from less than three fathoms are a pale green-ochre.

Several features of the gross anatomy of the South Australian mud-oyster are also seen to be different from those in the New Zealand mud-oyster. In shape the

soft parts are elongate in the former, in contrast to the round form found in the New Zealand oysters (Text-fig. 1, A and C). The mantle lobes are more translucent, suggesting histological differences in the mantle tissue. The mantle hood covering the palps is more open and loose whereas in the New Zealand oysters the mantle hood completely encloses the palps. In some specimens of the South Australian mud-oyster, the visceral mass was not fused to the anterior suture. Further discernible differences found in the mantle structure are the arrangement of the tentacles on the middle and inner folds. The middle fold in the South Australian mud-oyster has two rows of tentacles: an outer row of small bulbous tentacles closely placed to each other and an inner row of tentacles which are 2-3 times longer than their basal width, with 1 or 2 smaller tentacles of the outer row to every larger tentacle. In the New Zealand mud-oyster the larger tentacles are much further apart, there being at least 3-5 smaller tentacles to each larger tentacle.

The inner fold in the South Australian oyster consists of regular bulbous tentacles, 4 times longer than their basal width, regularly arranged and separated one from the other by a space equal to their width, or even further apart, whereas the tentacles of the inner fold in the New Zealand oysters are 6 times longer than their basal width and are never more than their own basal width apart.

In all 48 specimens of the South Australian mud-oysters examined, there were no well-developed pseudofaecal tracts. However, this could be a reflection of the feeding conditions at the time of collection and more observations on the tract in the living animal will be necessary to give a decision on the permanent presence of this feature. Accessory hearts are present in the New Zealand mud-oyster but have not been observed in any specimens examined from South Australia.

The posterior suture is greatly displaced from the posterior adductor muscle in the Australian mud-oyster (Text-fig. 1, C) so that the opening of the supra-branchial chamber into the exhalent chamber is very wide, in fact twice as wide as in the New Zealand mud-oyster. In the latter species, the gills follow very closely the posteroventral curvature of the adductor muscle and terminate at the posterior suture which is much closer to the muscle, so that the opening of the supra-branchial chamber into the exhalent chamber is narrower than in the Australian mud-oyster (Text-fig. 1, A).

All these readily recognisable differences of the shell and soft parts of the New Zealand mud-oyster show this oyster to be a distinct species here referred to *O. lutaria* Hutton, 1873, the first valid name available for the New Zealand mud-oyster. The first cited locality from which this species was taken is Pelorus Sound.

O. charlottae was proposed by Finlay (1928, p. 265) as a new name for *O. hyotis* Suter non Linnaeus. This species includes all those New Zealand mud-oysters that possess lateral and marginal frills on the lower valve. Dell (1960, p. 143) using shell characters only, recognises oysters with frills as a subspecies of the mud-oyster which he refers to *O. sinuata charlottae*.

The present study of approximately 2,000 shells from a wide range of localities has shown that the possession of imbricate marginal and lateral frills is not sufficient to distinguish this sub-species from the mud-oyster, *O. lutaria*. Frilled shells are more characteristic of deeper water where they are found free on the substrate which is usually composed of mud or sand. Shells with well-developed frills are especially common in depths greater than 20 fathoms off Otago, Kaikoura, and in Tasman Bay (pers. comm. Dr R. Dell, Mr J. Graham and Mr J. H. Choat). Non-frilled shells are more common in the shallower water but a complete gradation from frilled shells to non-frilled shells has been found in every bed examined.

The anatomy of the soft parts and the life-history of oysters with frilled shells characteristic of *O. sinuata charlottae* also support the view that this is a growth form of *O. lutaria* Hutton.

Ostrea lutaria Hutton, 1873 (Pl. 2)

- 1873 (non) *Ostrea purpurea* Hanley. Hutton, p. 84.
 1873 *Ostrea lutaria* Hutton. Hutton, p. 84.
 1873 (non) *Ostrea virginica* Lamarck. Hutton, p. 84.
 1880 (non) *Ostrea edulis* Linnaeus. Hutton, p. 175.
 1880 (non) *Ostrea discoidea* Gould. Hutton, p. 175.
 1884 (non) *Ostrea edulis purpurea* Hanley. Hutton, p. 533.
 1884 (non) *Ostrea edulis angasi* Hutton. Hutton, p. 533.
 1884 (non) *Ostrea discoidea* Gould. Hutton, p. 533.
 1904 (non) *Ostrea angasi* Sowerby. Hutton, p. 93.
 1904 (non) *Ostrea purpurea* Hanley. Hutton, p. 93.
 1913 (non) *Ostrea angasi* Sowerby. Suter, p. 888.
 1913 (non) *Ostrea hyotis* Linnaeus. Suter, p. 889.
 1923 (non) *Ostrea angasi* Sowerby. Oliver, p. 182.
 1928 (non) *Ostrea sinuata* Lamarck. Finlay, p. 264.
 1928 *Ostrea charlottae* Finlay. Finlay, p. 265 (*nom. nov.* for *O. hyotis* Suter non Linnaeus).
 1957 (non) *Ostrea sinuata* Lamarck. Powell, p. 78.
 1957 *Ostrea charlottae* Finlay. Powell, p. 78.

DESCRIPTION: Shell shape generally subtriangular in outline ranging from a subcircular form when growing in uncrowded conditions to an elongate form when growing in crowded conditions. Oysters found in shallow beds have thinner shells than those found in deeper beds, the shells being imbricate and frilled when growing recumbent on a shifting substrate such as mud or sand. Right upper valve flat, sometimes domed just under hinge; distally the valve bears dark brown imbricating prismatic scales which are broad and not crowded together. The scales extend to the outer margin of lower valve so that both distal margins meet. Edges of valves not known to be crenulated. Internally valve colour is white or greenish-yellow and there may or may not be a darker brown band on the distal margin of the valve. Ligament triangular, slightly raised from surface of valve and dark brown in colour. Posterior muscle scar is central in position, broadly lunate, anteroventral region extending further forward. Impression of 'catch' muscle at least 50 per cent or more larger in area than impression of 'quick' muscle area.

The left lower valve is the valve by which the oyster is attached, but in adult specimens the attachment is usually lost and the oyster lies free on the substrate. Valve moderately convex, usually smooth but low distinct radiating ribs and prominent imbricate frills may be present. Beaks usually blunt but may sometimes be more acute; very common on lower left valve whereas in right upper valve they tend to be quickly worn away. In Wellington Harbour oysters, colour of left valve is greenish-white whereas in oysters from Foveaux Strait valve is yellow to dark brown. Internally valve is nacreous or dull, greenish-white. Muscle impression may be slightly larger or smaller than that found in right valve. Ligament is winged laterally so that it is triangular, also elevated.

Denticles occasionally present in young specimens and in oysters that have been growing attached to wharf piles in a crowded condition. Denticles vary in number from three to seven and are on one or both sides of right valve only. Pits corresponding to denticles are present on lower left valve.

Palps and gills creamish-white; posterior suture well dorsal. Tentacles of the mantle fold are generally unpigmented. Middle fold has two rows of tentacles; an outer row with tentacles three to four times longer than their basal width and

an inner row of tentacles twice as long as they are broad. There are at least three to five smaller tentacles to each large tentacle. The inner fold has regular tentacles four to six times longer than their basal width and very closely placed. There are fewer and smaller tentacles towards the hinge region. There are 11–13 bars per plica of gill.

Mature oyster larviparous and hermaphroditic, spawning for at least eight months of the year between August and March at temperatures as low as 10.0°C.; is probably protandric with regular alternating female and male phases; becomes hermaphroditic after second or third breeding season. Fecundity about 1,000,000; egg size at liberation, 200 μ –270 μ . Larvae are incubated for about 20 days; are ready to settle when they measure approximately 0.44mm x 0.34mm. The free swimming larva has not yet been identified in plankton collections. Settling larvae exhibit an exploratory phase; spat measuring 5.5mm in length have total complement of gills present.

TYPE LOCALITY: Pelorus Sound; Catlin River (= Catlins River).

DISTRIBUTION: *Ostrea lutaria* Hutton is recorded from Port Pegasus, Stewart Island; Waitangi Beach, Chatham Islands; Foveaux Strait, East Coast and Golden Bay, South Island; Wellington Harbour, Pauatahanui Inlet, Waitarere Beach, Patea, Napier, Firth of Thames, Auckland Harbour and Bay of Islands, North Island.

VERNACULAR NAMES: Stewart Island oyster; Foveaux Strait oyster; Bluff oyster; mud-oyster; deep-water oyster; dredge oyster.

Hutton (1800, p. 175, 1884, p. 533, 1904, p. 93) with some doubt referred the Dunedin rock-oyster to *O. reniformis* Sowerby and gave on each occasion Sowerby's description. The systematic status of the Dunedin rock-oyster was queried by Suter (1913, p. 889) who referred it to *O. tatei* and another oyster from Auckland Harbour to *O. reniformis* Sowerby. Oliver (1923, p. 182) recognised the *O. reniformis* of Suter as a synonym of *O. corrugata* Hutton non Brocchi and said that the "use of the name *O. reniformis* shows how persistently names once introduced into a fauna are retained. Hutton used it for the Dunedin rock-oyster but Sowerby's description does not agree with any New Zealand species. The locality from which it was collected is unknown and the name is best rejected as indeterminable". Oliver (1923, p. 182) further recognised the Dunedin rock-oyster as an intertidal variant of the mud-oyster. However, this view has never been accepted by other systematists.

Suter (1913, p. 889) referred the Dunedin rock-oyster to *O. tatei*, a new name for *O. hippopus* Tate non Lamarck, an Australian shell present only in the Eocene, not applicable to a recent New Zealand shell and as Finlay (1928, p. 265) has said, the name *O. tatei* can only be used as a substitute for *O. hippopus* Tate non Lamarck. However, the description is still valid and Finlay (1928, p. 265) renamed the oyster *O. hefferdi* (incorrect spelling for Hefford) and selected as his neotype a shell from Dunedin Harbour. Powell (1957) followed Finlay in keeping the Dunedin rock-oyster separate from the mud-oyster as also does this account.

Ostrea hefferdi Finlay, 1928 (Pl. 3. figs. 3-8)

- 1880 (non) *Ostrea reniformis* Sowerby. Hutton, p. 175.
 1884 (non) *Ostrea reniformis* Sowerby. Hutton, p. 533.
 1904 (non) *Ostrea reniformis* Sowerby. Hutton, p. 93.
 1913 *Ostrea tatei* Suter (in part). Suter, p. 889.
 1928 *Ostrea hefferdi*. Finlay, p. 265, *nom. nov.* for *O. tatei* Suter (in part).
 1957 *Ostrea hefferdi* Finlay. Powell, p. 78.

DESCRIPTION: Shell shape regularly subtriangular, valves thin and delicate. Right upper valve flat, sometimes domed beneath hinge. Distally the upper valve bears dark, concentrically laminated prismatic scales. Three to six dark bands are sometimes present crossing the valve to the outer margin. Ligament raised, triangular and winged laterally. Umbos are blunt on young shells and usually absent on older shells. Muscle scar lunate with anteroventral region extending further forward and lying alongside ventral margin of valve rather than centrally; slightly excavated on posteroventral margin. Colour of internal surface generally white, sometimes pink or yellowish-green; a conspicuous blue or purple band extends around distal posterior free margin.

Left lower valve is the valve by which the oyster is attached to the rock and the attachment scar occupies one half of the total area of the valve. Distally from the region of attachment, the valves turn upwards so that shell becomes either erect or lies at an angle to the rock. The distal free area is smooth with occasional low radiating ribs extending to the margin, ribs never projected into frills; distal shell margin moderately crenulated. External surface of left valve is grey to bluish-purple, occasionally pale brown. Internally the ligament is slightly raised, triangular in shape and winged laterally. Muscle scar identical in position to that of right valve, but not always the same size. Internally the free margins have a broad bluish-purple band, slightly wider than in upper valve. A few shells examined had no marginal colouration at all. Denticles occur regularly, there being between one and eight placed on either side of valve just posterior to the hinge; pits corresponding to the denticles are present on the upper valve.

TYPE: Suter's type (*Ostrea tatei*) and Finlay's neotype (*Ostrea heffordi*) are both held at the Geological Survey, Lower Hutt.

DISTRIBUTION: *Ostrea heffordi* is known from the rocks at Dunedin and Lyttelton.

VERNACULAR NAMES: Dunedin rock-oyster; Southern rock-oyster.

2. REPRODUCTION AND DEVELOPMENT OF *O. LUTARIA*

Ostrea lutaria reproduces for at least eight months of the year, between August and March and possibly for longer when favourable conditions are present. Sections of the gonads show that sexual products are present all the year and that a variety of sexual phases are represented including hermaphrodite individuals. The first functional phase appears to be that of the male while the female phase does not develop until the third summer. When ovulation occurs, the eggs are shed from the gonad and retained in the inhalent mantle chamber where fertilisation and development take place. The New Zealand mud-oyster is thus an incubatory species.

During the present study, all stages of incubation were observed in oysters held in the laboratory which had been induced to liberate their larvae by a rise in sea water temperature. The larvae are liberated when they are provided with a shell and pigment spots and are capable of swimming. A study of the plankton was made to find free swimming larvae. This investigation was carried out over a period of one year, including two summers and resulted in the identification of the larvae of two species of mussel and four other bivalve larvae, but no oyster larvae. The process of settling and metamorphosis were also observed in the laboratory.

The larvae were studied in the first instance as live material and these observations were supplemented by whole mounts stained with acetic acid-alum-carmin. Attempts to section the embryo were unsuccessful.

MATURITY AND SEXUAL PHASES

Sexual cycles of many marine organisms are more often than not governed by the complexity of their reproductive organs and the environmental conditions during the spawning months. However, the anatomical simplicity of the reproductive organs of oysters and other bivalves in general reflects their simple sexual reactions.

Sperm balls are generally considered to be characteristic of hermaphroditic and larviparous species of oyster. Sperm balls are characteristic of *O. lutaria* so that it could be expected also to be hermaphroditic and larviparous; this proved to be the case. The argument that sperm balls indicate hermaphroditism and the larviparous condition in oysters that possess them is taken further to indicate that such oysters are also protandric, and have a rhythmical alternation of female and male phases throughout the remainder of their lives. As regards the last two characteristics, it must be mentioned here that although *O. lutaria* appears to be protandric it is not proven and although sex change does occur, the lack of tagged individuals has made it impossible at this stage to say whether the sex change is a rhythmical alternation.

The young were never observed to become sexually mature in the summer during which they attached themselves. Maturity was only reached during the second summer when oysters measured approximately 20mm in length. In general, this agrees with the observations of Sparck (1925) on *O. edulis* when he noted that the young of this species may in exceptional circumstances produce eggs in the second summer. Individuals of *O. lutaria* were in their third summer at least and more commonly in their fourth summer before egg development commenced.

Although no experiments were carried out with *O. lutaria* as regards temperature and time requirements for maturation, it is noted that an oyster collected in August at a water temperature of 10.0°C., liberated larvae in the laboratory. The fact that the surface water temperatures in the previous few weeks was below 10.0°C. (average 9.4°C.) clearly indicates that *O. lutaria* is capable of maturation and spawning at temperatures as low as 10.0°C. Whether this was an exceptional case of spawning is unknown and it can only be said here that during the course of this study no other oysters were collected which spawned at similar temperatures.

Sexual phases: During the course of this study several young oysters were collected. These young oysters ranged in size from 4mm to 25mm, the latter being about one year old. The gonads gave no appearance of development until the oyster was at least a year old, or 20mm in length. Smears made of these gonads produced on all occasions spermatids and mature sperm balls. Whether or not the primary gonad is bisexual is not known since the limited material was insufficient to enable the author to clarify this point. Protandry is considered to dominate the sexuality of larviparous and oviparous species of oysters (Stafford, 1913; Coe, 1931, 1932) and it would appear that further investigation on *O. lutaria* will prove it to be protandric.

The sequence of sexual phases is hard to study in the oyster for two reasons: (1) there is a need for tagged oysters so that an all year round check can be made on the gonads that were originally known to be either male or female, and (2) the sequence is further complicated by the fact that different regions of the same gonad may have different sexual phases at the same time. Thus, the tubules further away from the main area of proliferation, i.e., beneath the hinge, may be in an advanced state of spermatogenesis while the area of the gonad nearer the pericardium may contain ripe eggs.

In the present study sections and smears were made of just over 100 gonads to show the types of sexual phase exhibited by *O. lutaria*. The phases were as

follows: hermaphrodite individuals with ripe sperm and eggs; females but with some early proliferation of spermatogonia; males, with no trace of oogenesis; males with oogonia present; males with oocytes lining the wall of the follicles. From this list it can be seen that no females were observed which did not show some phase of spermatogenesis. Orton (1927, p. 976) regards all oysters in which ripe ova are present as essentially functional females, irrespective of the amount of spermatogenesis occurring in the secondary and primary follicles.

The number of sexual phases that *O. lutaria* may pass through in a year, or even in a life-time, is unknown. In *O. edulis* however, the indifferent phase is followed by spermatogenesis. Thus, the lack of eggs in young *O. lutaria* suggests that in the New Zealand mud-oyster also spermatogenesis succeeds an indifferent phase. The exact age of *O. lutaria* when oogonia begin to develop is unknown. Nonetheless, the gonads of oysters in their third summer exhibit a characteristic male phase with ripe sperm morulae in the lumen of the follicles and young oogonia and oocytes lining the walls of the follicles. The development of this first observed female phase proceeds concurrently with the development and further maturation of the sperm morulae.

In the transitional phase between male and female phases the developing oocytes enlarge, thus leaving the ripe sperm morulae isolated in the lumen of the follicles. Spermatogonia that would appear to belong to a subsequent male phase lie between the developing ova round the wall of the follicle. The fact that ripe sperm balls and mature eggs occur together in the same follicle does not mean that self-fertilisation will necessarily result, for the individual spermatozoa of the sperm ball are tightly held together until they are liberated by contact with the sea water. Only if the eggs and sperm are liberated simultaneously from the gonad will there be opportunity for self-fertilisation. If self-fertilisation does occur, then the ripe sperm and eggs have been developed in an hermaphrodite gonad.

Hermaphroditism: Coe (1932, p. 136) notes that hermaphroditism is not rare in the genus *Ostrea* as at least ten of the more than sixty described species are known to be monoecious and viviparous. There has been a suggestion that hermaphrodite oysters "are derived from individuals which spawned incompletely, at the end of the previous season leaving behind in the gonad a fair number of unripe eggs which were retained throughout the winter" (Cole, 1942). The true factors governing the formation of hermaphrodite follicles are still unknown. Cole's suggestion when considered relative to the presence of hermaphrodite follicles at the beginning of a season seems reasonable, but it is hard to see how it can account for hermaphrodite follicles being present all through the breeding season.

Korringa (1941, p. 46) notes that "as the eggs develop, the oysters remain functioning as males for a considerable time and often sperm production continues until about ten days before the discharge of the eggs. When we consider that a few days after the shedding of the eggs the gonad again contains sperm morulae, we may conclude that the purely female phase can be very short, about three weeks". In *O. lutaria* the follicles that possessed developing or mature eggs always possessed in addition developing spermatozoa. Thus the gonads of three year old and older oysters of *O. lutaria* always appeared to be hermaphroditic and in a variety of intersexual forms.

Gonads after ovulation: Serial sections were prepared of the gonads of oysters that had liberated larvae in the laboratory. Sections were also made of gonads while the parent oyster was still incubating veliger larvae. In all these sections it could be seen that the secondary follicles of the gonad had collapsed, having become very irregular in outline and considerably lessened in size. The

genital canal connecting the lumen of the secondary follicles was also noticed to be considerably narrower than that found in sexually mature oysters. Phagocytes were present throughout the primary and secondary follicles and in the surrounding connective tissue. A few degenerated eggs were noticed scattered in the follicles.

Orton (1927, p. 974) shows that it is normal for unspent eggs to be voided from the gonad after the initial main act of spawning. He also considered that if the residual ova were fertilised upon spawning, they would then give rise to a successful but spurious second spawning. Thus, two stages of developing larvae would be likely to be found within the inhalent chamber. Such a condition was not observed in *O. lutaria*.

Orton (1927, p. 974) suggests that in *O. edulis* degeneration with absorption of eggs usually and possibly always occurs, while Coe (1932, p. 133) states that in *O. lurida* the few remaining ripe ova may eventually undergo degenerative changes and phagocytosis. This latter course of development occurs in *O. lutaria* where phagocytes containing the nuclear material of the unspent ova occur in the lumen of the follicles and similar phagocytes without the nuclear contents occur in the surrounding connective tissue. Phagocytes were present in the follicles of oysters that had spawned some ten to fourteen days earlier. This persistence of phagocytes in the follicles of *O. lutaria* is in direct contrast to that recorded for other oysters.

Coe (1932) and Orton (1927) state in *O. edulis*, *O. lurida* and other incubatory oysters, spermatogenesis begins immediately after the eggs have been liberated from the follicles and that the follicles have abundant mature sperm balls at the time when the larvae are fully developed and ready to be liberated. Spermatogenesis in these oysters continues until approximately eight weeks after ovulation.

In the twelve post-spawned gonads that were sectioned, there was complete absence of spermatogenesis and oogenesis. The twelve gonads were representative of early summer and late summer spawners. Since there were no adequate facilities for keeping the spawned oysters alive indefinitely, the interval between ovulation and the commencement of spermatogenesis is unknown. The length of time elapsing between the first and second female phase is also unknown.

Resting period and wintering condition: After the ripe sperm balls and eggs have been discharged the appearance of the body alters considerably, for the tissues become flabby, watery and translucent. This translucent condition which enables the brownish digestive diverticular tubules to be observed, remains until the next sex phase is entered upon. Oysters that appeared to be in a resting phase were observed throughout the year but with more frequency during the months of March, April, May, June and July. During these months, the resting condition may last longer than in the summer months. Sections of the gonads during these months showed that oogenesis and spermatogenesis still occurred but not to the point where ripe eggs and sperm were present. Cole (1942, p. 343) notes that the "stage at which an individual passes the winter is conditioned by the phase it reaches at the close of the previous season".

The duration of the spawning season for *O. lutaria* is eight months at least and possibly all the year round when favourable conditions are present. Thus there is never a long period of over-wintering but rather a resting period with the spermatocytes and oocytes ready to mature when the conditions become more favourable. Since mature eggs and sperm were never found in the sections made of over-wintering gonads, in *O. lutaria* it may be assumed that phagocytes have broken down and absorbed any ripe products left from the previous season. The functional sexual phase in the following season will be that of the dominant sex cells in the resting follicles.

SPAWNING AND FECUNDITY

Spawning in the oyster involves the discharge of eggs and sperm from the gonads into the sea. The sperm pass down the suprabranchial chamber and enter the sea by way of the exhalent chamber. The eggs, however, pass immediately from the suprabranchial chamber through the spaces of the gills and the gill ostia into the inhalent chamber. The eggs lie on the gill plates, just posterior to the labial palps; the inhalent chamber thus acts as a brood chamber. The length of time during which the eggs are retained is dependent on the larvae reaching a certain stage of development and on external factors such as temperature.

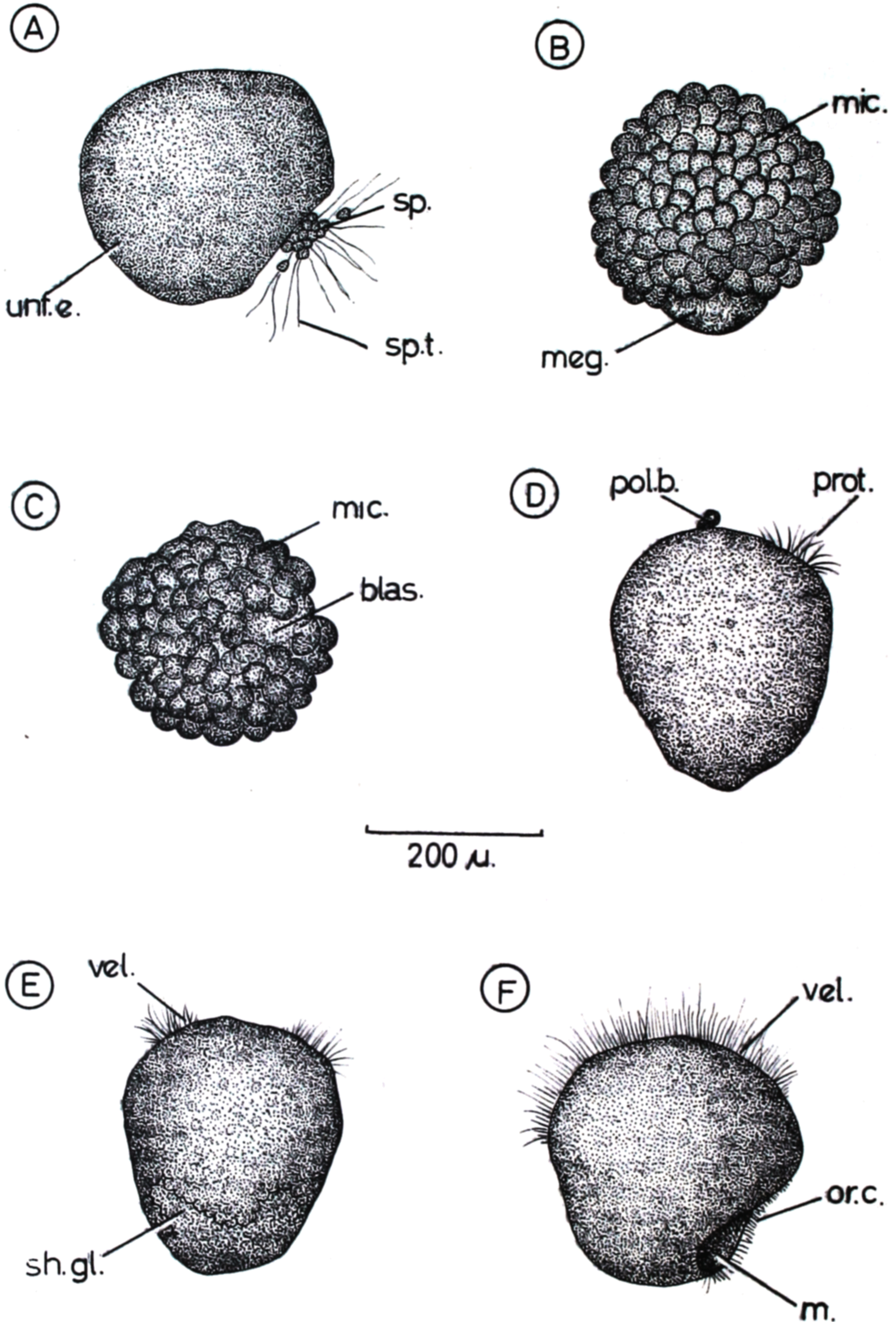
Korringa (1941) refers to the liberation of larvae from the inhalent chamber to the sea as "swarming" and considers that this is in effect only the delayed completion of the spawning act. The release of eggs from the gonads in incubatory oysters has never been observed, observations being confined to the liberation of developed larvae.

The spawning season of an oyster varies in length according to local conditions and can only be observed in incubatory oysters by a regular examination of adults throughout the summer season. The first oysters examined from Wellington Harbour were collected on 18/12/60, the water temperature being 11.0°C. The gonads of all the oysters were undeveloped and appeared to be in an "overwintering" or resting period. However, from this date, the water temperature rose steadily to 18.5°C. by 28/12/60 when approximately 36 oysters were collected from Evans Bay; two of these oysters liberated larvae on the following day. Further examination of the adults showed that spawning continued until early March. The last collection of oysters that contained larvae was on 1/3/61, at a water temperature of 16.0°C. Examination of over 100 oysters during the following weeks failed to produce any incubating oysters or even oysters with well developed gonads.

Examination of adults was recommenced on 22/8 61 when the water temperature was as low as 10.0°C. This collection of oysters followed a succession of severe southerly storms that lasted for several weeks. The average water temperature during this cold weather was 9.4°C. as already mentioned above. Of the 31 oysters examined from this collection, one only was carrying larvae. The appearance of the gonads of the remaining oysters suggested various stages of development; some ripe, others less so. This is notable for two reasons: (1) the gonads were actually capable of maturation at temperatures as low as 10.0°C. and (2) oysters were spawning for at least eight months of the year, that is, from August to March.

It would seem possible then, since the water temperature rarely goes very far below 10.0°C. in Wellington Harbour (lowest record was 8.8°C. on 11/8/61) that spawning takes place throughout the year. This does not mean that spawning takes place with the same frequency and regularity throughout the year, but rather will there be periods of more active spawning during the summer months when there are higher water temperatures. Before it is possible to state with certainty that *O. lutaria* spawns throughout the year, it will be necessary to examine oysters collected from April to July. It is equally possible that any of these months and maybe all of them will be found to be periods of overwintering, but maturation of the gonads and spawning would be possible during warmer months.

A spawning season of eight months is considerably longer than recorded for other incubatory oysters, except where oysters occur in warmer water (i.e., the Mediterranean) than in New Zealand and spawning takes place over the whole year.



TEXT-FIG. 2.—Fig. A—Unfertilised egg with sperm at the receptive spot. Fig. B—Late morula. Fig. C—Gastrula. Fig. D—Early trochosphere. Fig. E—Slightly older trochosphere. Fig. F—Trochosphere with mouth and velum developed.

ABBREVIATIONS: blas., blastopore; m., mouth; meg., megamere; mic., micromere; or.c., oral cilia; pol.b., polar body; prot., prototroch; sh.gl., shell gland; sp., sperm; sp.t., sperm tail; unf.e., unfertilised egg; vel., velum.

Korringa (1941, p. 93) reviews the little that has been written on the number of larvae that may be spawned by incubatory and non-incubatory species of oysters. There have been no estimates of the number of eggs or larvae produced by *O. lutaria* until the present account but marketable oysters (approximately four to five years old), produce between one million and two million larvae while oysters of two or three years produce about 500,000. At the end of the breeding season, oysters of three and four years may produce as few as 2,000 larvae. It is possible that these oysters were spawning at the time of collection and that consequently only the remaining larvae were spawned in the laboratory. In general however, there is a tendency for oysters to produce fewer larvae at the end of the breeding season.

FERTILISATION AND CLEAVAGE

Fertilisation and cleavage in *O. lutaria* take place in the inhalent chamber of the parent oyster. The sperm balls rotate rapidly and move through the sea water by means of the lashing sperm tails. After a few minutes in contact with the sea water, the spermatozoa begin to break free from the sperm ball. The heads of the spermatozoa become detached from the central mass of the ball and move outwards and away; the sperm tail is the last part of the spermatozoon to break free. The complete disintegration of a single sperm ball containing approximately 2,000 spermatozoa takes about five minutes. These observations were made by teasing a small portion of a male gonad into a watch glass containing fresh sea water and observing under a microscope.

As fertilisation has never been observed in incubatory oysters, it is assumed that the spermatozoa enter the mantle cavity of a female oyster with the inhalent water current and subsequently fertilise any eggs lying on the gill plates. Three separate attempts at artificial fertilisation of the eggs of *O. lutaria* were unsuccessful and likewise attempts by other workers to fertilise the eggs of incubatory species of oysters have also been unsuccessful.

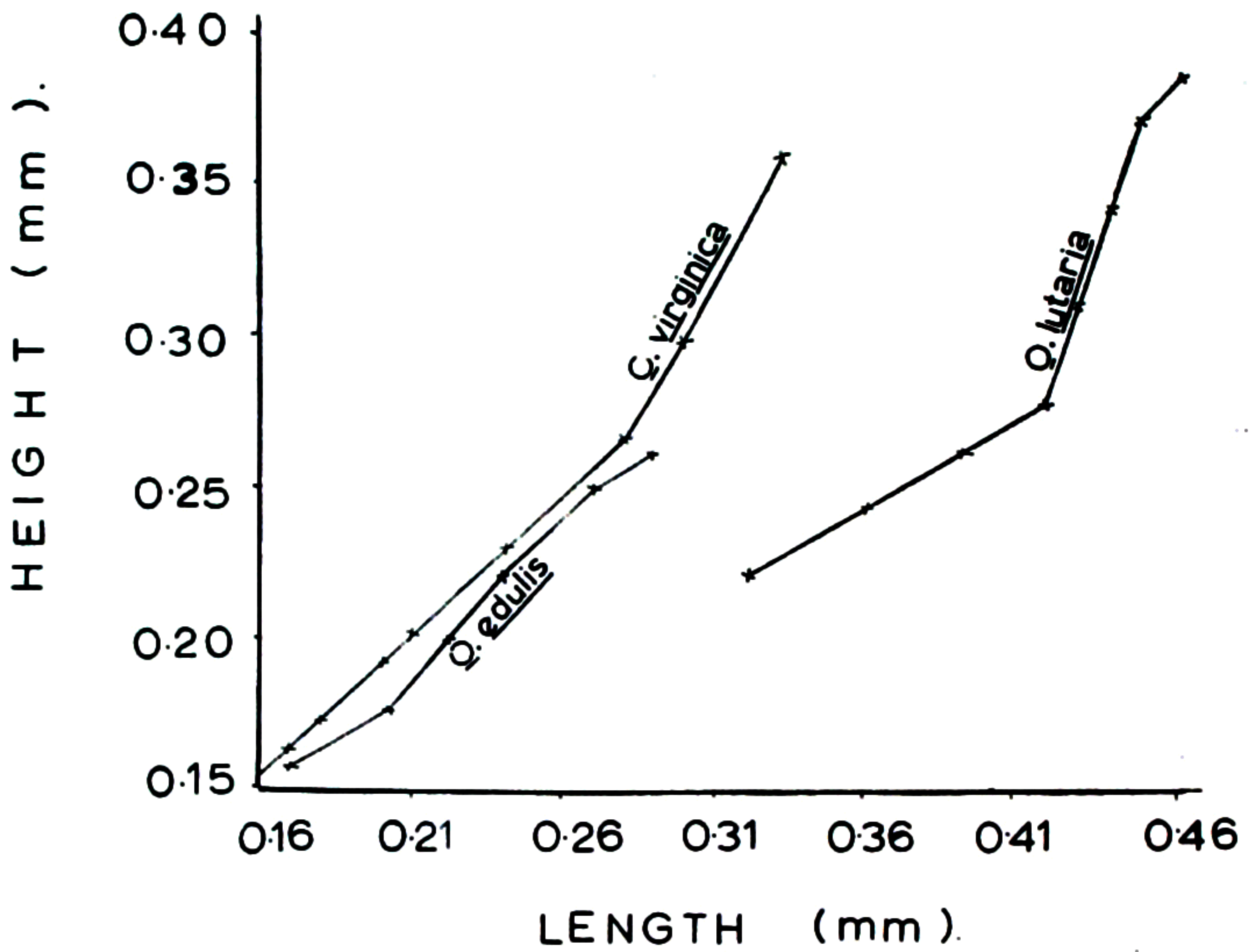
However, on one of these three attempts, sperm were noticed clustered around a particular area of each egg. This area corresponds to the flat surface of the egg that had been lying next to the wall of the follicle. This area is thought to correspond to the receptive spot (Text-fig. 2, A).

Before syngamy takes place and possibly just after the sperm nucleus has penetrated the egg, the formation of polar bodies takes place. In some eggs, great clusters of incompletely divided polar bodies were observed while other eggs had only one, two or three polar bodies present. In some instances the polar bodies were noticed to persist through the stages of cleavage and were present on the prototroch of the trochosphere (Text-fig. 2, D).

The two, four, eight celled stages of cleavage were not observed in *O. lutaria*; the earliest stage observed was the blastula. The result of the early stages of cleavage is that the oosperm becomes differentiated into a megamere (deutomere) surrounded by a large number of micromeres (blastomeres). Finally the micromeres increase to such an extent that they arch over and partly surround the megamere so that the gastrula is formed by epiboly (Text-fig. 2, B and C).

DEVELOPMENT AND LIBERATION

The micromere cells of the gastrula come together forming a smooth outer surface while the megamere divides and the resulting cells tend to occupy the central space of the gastrula. The cleavage cavity opens to the exterior on the undersurface by the blastopore. Shortly after gastrulation, long tufts of cilia appear



TEXT-FIG. 3.—The relationship of height to length in free-swimming larvae of *Crassostrea virginica*, *Ostrea edulis* and *O. lutaria*. Figures for *C. virginica* and *O. edulis* taken from Yonge (1960, pl. IV and V).

on the broader, anterior end of the embryo. These cilia are between 80μ and 100μ tall and encircle the polar bodies if the latter are still present. This anterior region forms the prototroch which later develops into the velum (Text-fig. 2, E and F). The invagination forming the mouth represents the ventral region. The next noticeable event observed was the formation of the shelled larva and thus the trochosphere develops into the veliger larva.

The Veliger

Larval shell: The valves of the shell appear on either side of the body on the dorsal surface. As the valves increase in size, they grow together and meet along the hinge line. The fully formed larval shell or prodissoconch is equivalvular, each valve being discoidal with a straight hinge line and moderately convex externally. Distinct concentric growth lines are present, some of which are more prominent than others. The edges of the valves are entire and distinct and further apart ventrally. As the larva approaches the settling stage, the straight hinge becomes slightly and evenly curled and the lower left valve becomes deeper so that both valves are no longer equivalvular.

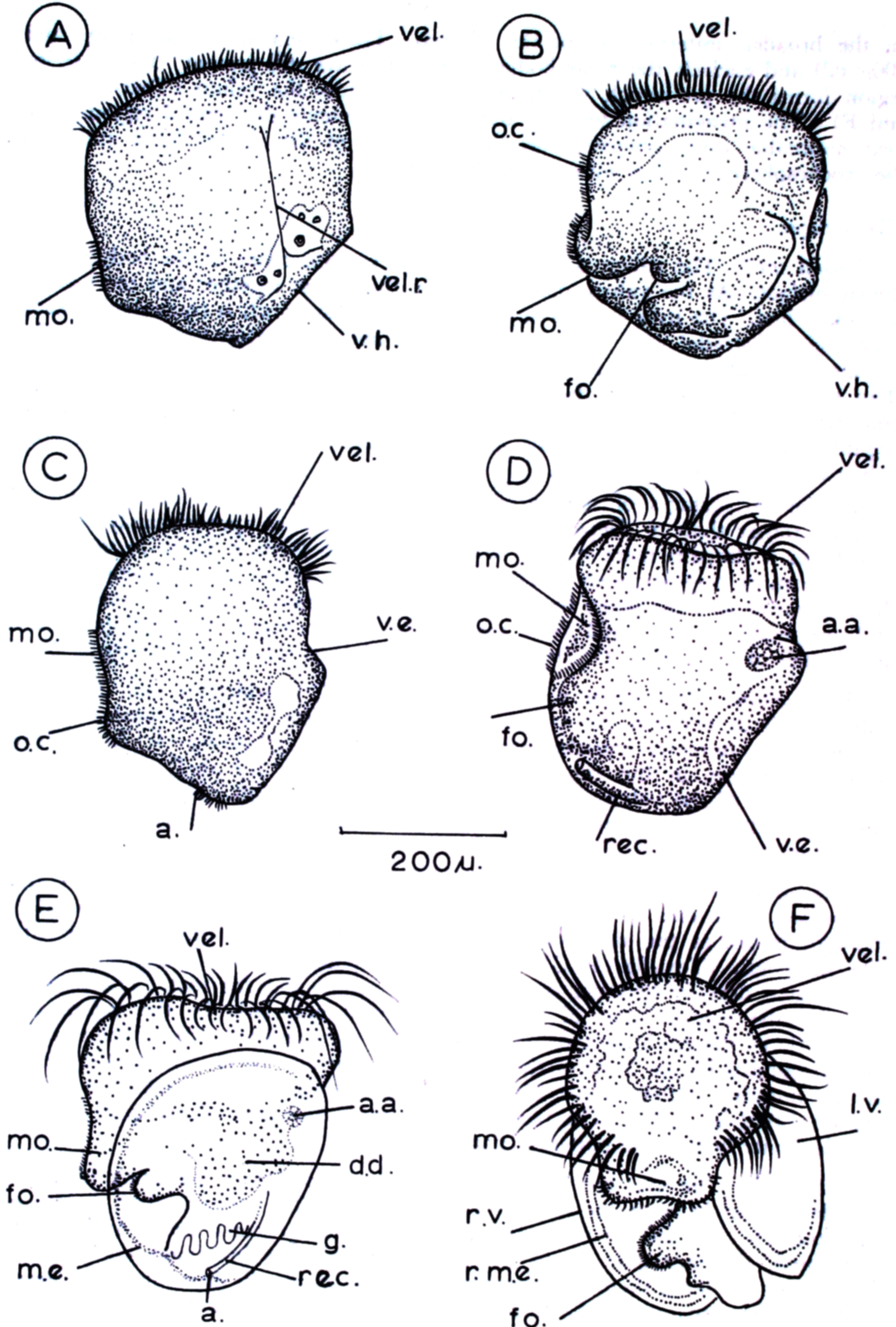
In the early stages of shell growth, the initial tendency is for the shell to elongate rather than to deepen. When the shell measures approximately $0.42\text{mm} \times 0.28\text{mm}$ it deepens more rapidly so that when the larva is ready to settle, the shell measures approximately $0.47\text{mm} \times 0.40\text{mm}$. These measurements are in direct contrast to those given for *C. virginica* and *O. edulis* where the lengthening and deepening of the shell keep pace. The height-length relationship of the larval shell of *O. lutaria*, *O. virginica* and *O. edulis* is shown in Text-fig. 3.

The velum: The velum is very well developed, conspicuous and protrudes anteriorly from between the valves of the shell. With the development of the velum, velar retractor muscles become differentiated (Text-fig. 4, A). These muscles originate in the velum and are inserted onto the shell. The general outer surface of the velum is ciliated as was the prototroch. The marginal cilia are 100μ tall and are more powerful than the cilia covering the outer surface of the velum (Text-fig. 4, E and F).

The alimentary canal: Associated with the velum is the mouth which is ventral in position. The cilia of the velum become continuous with the cilia surrounding the mouth but at the same time become noticeably shorter until they are only 20μ in length (Text-fig. 4, C). The mouth opens into the oesophagus which passes back dorsally between the base of the velum and the foot. The stomach occupies the central mass of the body bounded anteriorly by the velum and posteriorly by the gill buds and the rectum. The right and left sides of the stomach are surrounded by the lobes of the digestive diverticula. In *O. lutaria*, the coiling of the intestine is first visible where it passes downwards and backwards as the rectum (Text-fig. 4, E). The rectum terminates in the anus which opens into the mantle cavity behind the posterior mantle suture.

The gills: The gills are first visible as a series of knobs extending from the mantle margin beneath the foot to a position near the posteroventral margin of the stomach. As the larva develops, the gill knobs become more distinct and segmented, the outermost knobs being smaller than the innermost knobs. In a fully developed larva there are approximately nine or ten gill filaments in the series. The filaments separate at the time of settling, and active cilia were noted on the surfaces of the larger filaments.

Adductor muscles: The adductor muscles are developed in the same manner as recorded for other oysters. The strength of the anterior and posterior adductor



TEXT-FIG. 4.—Fig. A—Trochosphere with velar retractor muscle visible. Fig. B—Trochosphere with shell developing. Fig. C—Trochosphere at later stage. Fig. D—Trochosphere with position of alimentary canal visible. Fig. E—Straight-hinged veliger. Fig. F—Straight-hinged veliger in swimming position.

ABBREVIATIONS: A., anus; a.a., anterior adductor muscle; d.d., digestive diverticulum; fo., foot; g., gill; l.v., left valve; m.e., mantle edge; mo., mouth; o.c., oral cilia; rec., rectum; r.m.e., right mantle edge; r.v., right valve; v.e., hinge region of valve; vel., velum; vel.r., velar retractor muscle; v.h., hinge.

muscles was particularly noticed when a 20% solution of cocain was added to the sea water containing the larvae. The solution caused the adductor muscles to close the shell so tightly that the velum was cut off.

The mantle: In the veliger the first region of the mantle to be observed was the margin (the mantle lobes are not easy to observe until the larva has become fully developed). In the early veliger, the mantle margin is yellow and the mantle lobes can be seen in the living larva moving backwards and forwards beneath the valves of the shell.

The foot: In the early veliger, the foot is represented by a small projection on the ventral surface, beneath the mouth (Text-fig. 4, A). As the veliger develops, the foot lengthens until finally it is as long as the valves. When not in use, the foot is withdrawn and contained entirely within the mantle cavity beneath the mouth. As the foot begins to protrude, a groove becomes apparent on the under surface. This groove is ciliated as is the entire outer surface of the foot. The two sides of the groove are capable of coming together and closing over the groove, thus forming a canal. As the foot protrudes even further, the groove becomes shallower. The fully extended foot is long, slender and strap-shaped. It is capable of moving anteriorly over the velum, posteriorly behind the gills and over the outer surfaces of the valves. Posteriorly behind the foot, is a heel. This heel is only observed when the foot is fully extended. Stafford (1913, p. 46) refers to this heel as the byssus-papilla and although the byssus gland was found in *O. lutaria*, the duct leading to the papilla was not (Text-fig. 5, B).

Otocysts: Stafford (1913, p. 50) observed about a dozen small otoconia in each cyst. The right and left cysts are situated at the base of the foot near the surface of the first gill filament. On a few occasions when the veliger foot was fully extended, structures that could have been the otocysts were observed, but confirmation of the presence or absence of otocysts awaits further investigation.

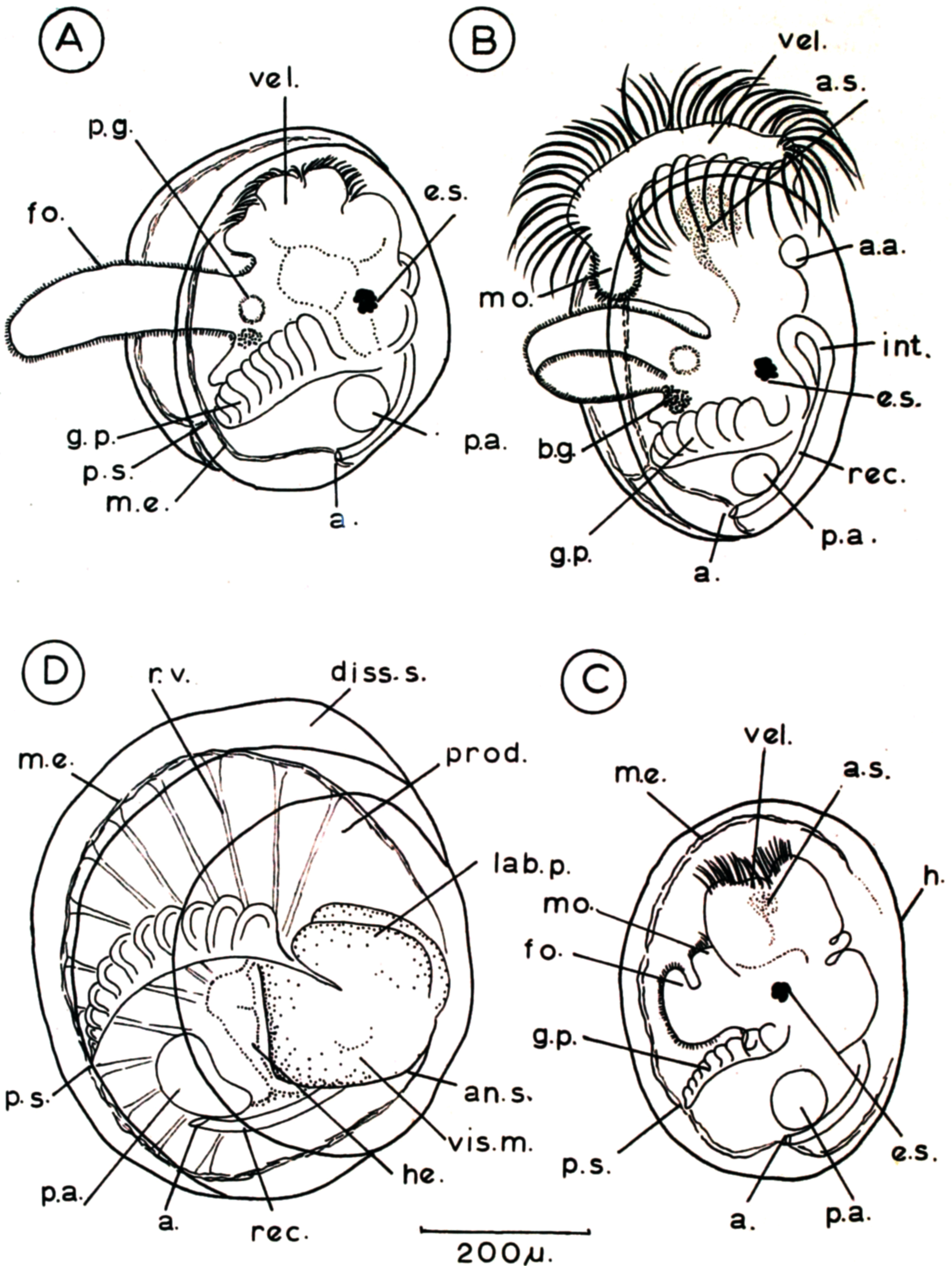
Nerve ganglia: The only nerve ganglia observed in *O. lutaria* were the pedal and cephalic ganglia. The former are situated in the proximal region of the foot and are only visible when the foot is fully extended. The cephalic ganglia are associated with the apical sensory organ which is situated in the central region of the velum (Text-fig. 5, A and B).

Pigment spots: The pigment spots are sometimes called eyespots but are better known as the former since their photosensitivity has not been confirmed. The pigment spots are paired, and lie on the lateral walls of the right and left mantle lobes just anterior to the proximal region of the gill buds. They are almost black in colour, irregular in outline and measure approximately 12μ in diameter (Text-fig. 5, A, B and C).

Duration of the incubation period.

Because artificial fertilisation was unsuccessful with *O. lutaria*, the duration of the incubation period was studied by regular examination and measurement of larvae liberated by oysters held in the laboratory.

A larva takes approximately five days from fertilisation to develop into an early veliger. The time of development between an early veliger and a middle veliger without pigment spots is approximately three days. The shell measurements of early veligers are 0.22mm x 0.18mm (length x height) and total measurements are between 0.32mm x 0.29mm and 0.33mm x 0.32mm. The shell measurements of the middle veliger are between 0.30mm x 0.22mm and 0.31mm x 0.19mm and total measurements are between 0.40mm x 0.29 and 0.35mm x 0.32mm. The



TEXT-FIG. 5.—Fig. A—Veliger with foot fully extended. Fig. B—Veliger with velum and foot in swimming position. Fig. C—Veliger with velum and foot withdrawn. Fig. D—Spat settled for approximately 72 hours.

ABBREVIATIONS: A., anus; a.a., anterior adductor muscle; an.s., anterior suture; a.s., apical sensory organ; b.g., byssus gland; diss.s., dissoconch shell; e.s., eyespot; fo., foot; g.p., gill plate; h., hinge; he., heart; int., intestine; lab.p., labial palp; m.e., mantle edge; mo., mouth; p.a., posterior adductor muscle; p.g., pedal ganglion; prod., prodissoconch; p.s., posterior suture; rec., rectum; r.v., radial vessel; vel., velum; vis.m., visceral mass.

total time taken for an early veliger to develop into a veliger with pigment spots is unknown, but observations made on oysters held in the laboratory in sea water between 18.0°C. and 20.0°C., suggest that it is five to eight days. A fully developed veliger measuring 0.47mm x 0.35mm is liberated after about a further six days. Thus the total time of development within the mantle chamber appears to be about 21 days.

The stage of development reached by the larva under natural conditions before it is liberated is discussed in the section on the free swimming larva, but briefly if *O. lutaria* follows other incubatory species of oysters, the larvae will be liberated when they have attained a size of about 0.32mm x 0.26mm. Larvae of *O. lutaria* with these measurements were liberated in the laboratory, but more fully developed larvae complete with foot and pigment spots were also observed being liberated from the parent indicating that if conditions are favourable the parent oyster will incubate the larvae through all the stages of development until the latter are ready to settle.

Liberation: In *O. lutaria* the developing larvae are liberated by violent contraction of the posterior adductor muscle of the parent. This fast closure of the shell forces the larvae out through a gap in the inner pallial fold as in other incubatory species.

Liberation of the larvae in some cases was completed within an hour; in other instances the liberation took as many as four days to complete. The only regular feature of liberation that was observed was that the majority of larvae were liberated in the first two or three rapid closures of the shell and that subsequent liberations yielded very much lower number of larvae. Towards the end of liberation, larvae appeared to "spill" out of the shell and over the left valve to the dish beneath. The last few larvae were always held in strands of mucus that was probably secreted by the gills during the process of feeding.

FREE SWIMMING LARVAE

No free swimming oyster larvae have so far been found in plankton collections studied from Wellington Harbour. Under laboratory conditions however, the larvae were observed to be released in various stages of development which may or may not be the case in the field. Oysters were collected from Evans Bay and were quickly removed to the laboratory where they were placed in 7½ in culture dishes (3-4 oysters per dish) and covered with sea water. The temperature of this sea water varied between 18.5°C. and 20.5°C. and was usually 2-4 degrees warmer than the temperature prevailing in Evans Bay. In every instance this rise in temperature of the sea water was sufficient to induce the oysters to liberate their larvae. All stages of development were liberated from parent oysters held in the laboratory including embryos and trochospheres, early straight-hinged veliger larvae and fully developed larvae possessing a pair of pigment spots and well developed foot.

The measurements of free swimming larvae of *O. edulis* vary between 0.16mm and 0.20mm (Erdmann, 1934, p. 6, and Korringa, 1941, p. 101) whereas larvae of *O. lutaria* at a comparable stage of development vary between 0.31mm and 0.33mm. Swimming in these latter larvae is by means of the velum and is restricted to horizontal movement on the bottom of the dish and short vertical movements. In the horizontal movement, the velum is uppermost and the larvae turn anti-clockwise. The movements as seen by the naked eye is very slow, almost imperceptible. The measurements of seven fully developed larvae of *O. lutaria* are given to show the size variations in height of larvae with similar length:

0.42mm x 0.28mm; 0.42mm x 0.35mm; 0.42mm x 0.36mm; 0.43mm x 0.31mm; 0.44mm x 0.34mm; 0.45mm x 0.37mm; 0.47mm x 0.39mm.

Since the size of the straight-hinged veliger of *O. lutaria* is greater than that of *O. edulis*, it could be anticipated that the fully developed larva of *O. lutaria* would be larger than that of *O. edulis*. Measurements of the larvae of *O. edulis* which have just developed the pigment spot vary between 0.26mm and 0.30mm (Cole, 1939, and Korringa, 1941) and larvae ready to settle measure between 0.27mm and 0.31mm (Erdmann 1934, Cole 1939, and Korringa 1941).

Fully developed larvae of *O. lutaria* (Text-fig. 5, A, B and C) liberated in the laboratory have been observed to swim rapidly in both horizontal and vertical directions, to rest on the surface of the water and to creep on the bottom of the dish. Larvae that are about to settle do not necessarily confine themselves to crawling and in fact they alternate swimming with crawling phases, always being in a crawling phase immediately prior to attachment. This last type of movement is the exploratory phase described by Cole (1938, p. 478) in which the foot serves as a locomotory organ on the substratum immediately prior to attachment and apparently acts as a tactile organ.

Furthermore, Cole (1938, p. 471), notes that in *O. edulis* the eyespot (pigment spot) develops only a few days before attachment. Thus it would appear, that if in *O. lutaria* the foot and pigment spots are also developed only a few days before attachment then the larvae of *O. lutaria* are ready to settle and become attached immediately after being liberated. Fully developed veliger larvae which do not settle have also been liberated. These larvae are easily recognised by their pigment spots but do not exhibit an exploratory phase which is typical of attaching larvae. These larvae are the same size as larvae that settle and become attached.

Duration of free swimming stage.

If it is assumed that under normal conditions the larvae of *O. lutaria* are liberated complete with well-developed foot and pigment spots, then it is apparent that the duration of the free swimming stage will be reduced accordingly. During the course of this study only three oysters of the 565 held from time to time in the laboratory liberated fully developed larvae which subsequently became attached. The free swimming larvae of these three oysters became attached as follows: one, five days after a temperature rise from 15.5°C. to 18.5°C.; the second, three days after a temperature rise from 18.0°C. to 20.0°C.; and the third, two days after a temperature change from 16.0°C. to 19.5°C. The temperature change was caused by removing oysters from Evans Bay to warmer sea water in the laboratory. In all cases mentioned, the rise in temperature was sufficient to induce oysters to liberate their larvae prematurely. In other instances, the successful attachment of the larvae depends on their state of development at the time of liberation.

During experiments some larvae were held at 21.5°C. Of these, a few became attached within two hours. The majority died and about 20 per cent were still in an exploratory phase 18 days later. This indicates that the larvae are capable of postponing attachment for some considerable length of time, but the experimental temperature of 21.5°C. is higher than that recorded in Evans Bay so that it is quite possible that the larvae behaved abnormally.

In conclusion, it seems reasonable to assume that any pelagic free swimming stage of the larvae of *O. lutaria* if it does exist, lasts a few days only, but that attachment may be postponed if suitable conditions are not present.

ATTACHMENT AND METAMORPHOSIS

The exploratory, crawling phase preceding attachment has already been mentioned. Several oysters liberated veliger larvae that subsequently became attached but the actual process of attachment was not observed. Larvae of *O. lutaria* were observed crawling above the surface water level and these larvae subsequently became firmly attached to the glass wall of the bowl. Also, larvae which became detached floated to the surface of the water and remained alive for as long as 24 hours. Such larvae, it was observed, never attempted resettlement, possibly because the byssus gland cement was secreted during the initial attempt at attachment. During the hours following attachment while the foot was still present, spat were observed defending their attachment area by means of the foot. If several spat settled in very close proximity they kept the foot fully extended. Consequently spat are never attached less than their own distance apart (which is also equal to the length of the foot).

The influence of light on the settling process.

The pigment spots of fully-developed larvae are eye-like structures as shown by Cole (1938) and Erdmann (1934). The black colour of the spots is due to heavy pigmentation in the epithelium. The spherical cup formed by the epithelium is filled with a gelatinous matrix, the aperture being closed by a lens-like body. The function of the eyespots has been the subject of considerable controversy. To date, observations on *O. edulis* and *O. lurida* indicate that the pigment spots are not light sensitive at all. On several occasions, fully-developed larvae of *O. lutaria* were placed in a glass tube and subjected to a bright light; half of the tube being shaded. The larvae did not exhibit a negative phototaxi. In contrast, the larvae of *C. virginica* have been demonstrated by some authors to be photosensitive. The larvae when stimulated continue to move away from the light until they reach a shaded site, and this is thought to account for the preference shown by the settling larvae for attachment in shade.

Experiments investigating the influence of light on settling and attachment have been carried out by many authors on various oysters and as yet there is no general agreement on the subject. Korringa (1941, p. 192) concludes that "although light appears to be no orientating factor in the settling behaviour of *O. edulis* under field conditions, it is not impossible that light influences the settling process in cases where the intensity of the light exceeds a certain degree."

Metamorphosis.

Knowledge of the metamorphosis of the larva of the American oyster, *V. virginica*, is considerable, owing mainly to the work of Stafford (1913). Cole (1937, 1938) describes the less well-known metamorphosis of incubatory oysters. The following is a brief account of the anatomical reorganisation of the spat of *O. lutaria* when it takes on the fixed life of the adult oyster.

The shell: The dissoconch is the post larval shell; it is formed during the 24 hours following attachment. It appears around the distal margin of the prodissoconch, but is very thin and indefinite at first. The dissoconch shell growth can be divided into two phases, (1) the silphologic (spat) phase, and (2) the adult shell phase. The silphologic shell phase has further been divided into five stages by Jackson (1888) most of which have been identified in *O. lutaria*. The lower left valve as it grows, becomes closely attached to the attachment area by becoming flattened. Lateral wings appear on the valves, usually on the anterior side. Growth continues until the lower valve reaches the margin of its attachment when it

proceeds to grow upwards so that the general form of the adult shell with concave lower valve and flattened upper valve is soon apparent. Another feature of the dissoconch silphologic stages is the subnacreous layer which is formed unevenly at first until it covers the entire inside lining of both valves.

The foot: The foot persists for the first 24 hours following attachment but then rapidly degenerates and is carried forward by the rotation of the mouth until it reaches a mid-ventral position. The statocysts are thought to persist in the adult oyster of other species but no trace was ever found of them in *O. lutaria*.

The velum: The velum persists as an identifiable organ for about 12 hours following attachment. It is contained within the valves and the movement of the cilia is quite clear. The velum finally collapses and shrinks in size, becoming converted eventually into the outer palps of the adult oyster (Text-fig. 5, D). Cole (1938) describes how the velum of *O. edulis* shrinks after attachment and is carried forward and upward by the rotation of the body so that about 24 hours after attachment, the velar remnants "consist of a little of the typical epithelium of the thickened edge and some of the muscle fibres of the interior . . . subsequently the much thickened upper lip spreads out laterally and gives rise to short rounded lobes which project, one on each side, at the upper corners of the mouth". These are the rudiments of the outer palps of the adult oyster. The outer palps are initially large but gradually shorten as the inner palps are formed. The beginning of the formation of the inner palps was never observed in *O. lutaria* and as far as the writer is aware, has not been observed in other species of oysters. However, they are present in spat measuring 5.5mm in length.

The mantle: The mantle edge is visible in a fully-developed larva and in the attached spat. Associated with the mantle lobes are prominent radiating vessels (Text-fig. 5, D) and in spat measuring 5mm they appear to act as pulsating vessels or accessory hearts. Tentacles were not observed in recently settled spat. In older spat measuring 5mm the mantle lobes are well defined being united anteriorly beneath the hinge and posteriorly with the gills. The mantle margin has three folds as in the adult but the similarity ends there. The outer fold has no tentacles and is unpigmented, and the middle fold is more well-developed, being tentacular. There are two types of tentacles arranged in no particular order. The majority are small and regular, as tall as they are broad and the remainder are twice as tall as they are broad and are scattered amongst the smaller more regular tentacles. Both types of tentacles are brown apically. The inner fold which is the pallial curtain is present as a simple flap, smaller than the outer fold and similarly without tentacles.

The gills: At the time of attachment, the larva has between eight and ten gill filaments (Text-fig. 5, C). This is in contrast to the six filaments recorded for *O. edulis* by Erdmann (1934) and seven filaments recorded by Cole (1937, p. 413). Cole further notes that eyed-spat have eight gill filaments; spat measuring 0.35mm have ten gill filaments and that the 11th, 12th and 13th gill filaments appear on the left side before the spat is 90 hours old. Such spat measure approximately 0.6mm in diameter. At this stage there are also seven gill filaments on the right side. Spat of *O. lutaria* measuring 0.6mm (Text-fig. 5, D) in diameter have been settled for only 72 hours in contrast to the 90 hours of *O. edulis* described by Cole (1937). Such spat have 11-12 gill filaments on the left and about five gill filaments on the right (not figured). Thus the larvae of *O. lutaria* possess more gill filaments at the time of attachment than *O. edulis*, which is in keeping with the much larger size of the settling larvae of *O. lutaria*. Yonge (1926) figures a spat of *O. edulis* which had probably been settled for five or six days, 1.2mm in length, with 20 gill

filaments on the left and 13 gill filaments. Spat of *O. lutaria* of a similar stage were never found. However, spat measuring 5mm in diameter had 90 gill filaments on the left. The filaments were simple and similar in structure, there being no transitional or principal filaments or even any indication of plication. The filaments are spaced their own distance apart and are ciliated laterally and apically and are connected apically to adjacent filaments by a thin membrane. In these spat the filaments had split longitudinally so as to form the respective inner and outer lamellae. This splitting did not include the head of the filament. Two rows of interfilamentar junctions are present on the left inner demibranch but none could be seen on the corresponding right demibranch. The interfilamentar junctions transform the linear filamentous spaces into a series of fenestrae.

Stafford (1913, p. 68) stated that weight and pressure acting unequally upon the two sides of the gill soon effects a marked difference in the gill growth rate. The left gill in *O. lutaria* grows much faster than the right gill. The right and left gills of a recently settled spat correspond to the inner demibranchs of the adult. The measurements of a spat with the beginnings of the right outer demibranch are unknown but the left outer demibranch is seen to appear from the mantle and the gill axes of the left inner demibranch in a spat measuring 5mm x 5.5mm. The appearance of the left outer demibranch in other incubatory species of oysters is unknown as far as the author is aware. Stafford (1913, p. 68) also mentions that in *C. virginica* the right outer demibranch is formed when the spat is 2.5mm tall and the left outer demibranch is formed when the spat is 3mm tall. A spat 3mm tall has 50 gill filaments in the left inner gill. This is considerably less than the 90 filaments that *O. lutaria* has when the outer left demibranch appears.

Stafford furthermore notes that a spat of *C. virginica* 1.5mm in height has 23 gill filaments which is very similar to the 1.2mm spat of *O. edulis* which has 20 gill filaments. Therefore it is quite reasonable to estimate that a spat of *O. edulis* measuring about 3mm in height will show incipient left outer demibranch. In contrast, the spat of *O. lutaria* takes longer to develop all the demibranchs even though it settles at a much larger size and possesses more gill filaments at the time of attachment.

Adductor muscles: The fully developed larva possesses an anterior and posterior adductor muscle more or less symmetrically placed with regard to the hinge and of similar size. However, after attachment the anterior adductor muscle is moved upwards and outwards towards the edge of the prodissoconch where it finally disappears (Text-fig. 5, D). The posterior adductor muscle moves downwards and towards the centre of the viscera. In a spat measuring about 0.5mm in height, the posterior adductor muscle is situated between the edge of the prodissoconch and the dissoconch, until it finally moves entirely onto the dissoconch (Text-fig. 5, D). As the muscle moves centrally, it enlarges but does not as yet show any differentiation into quick and catch areas. The muscle is also becoming characteristically lunate as it moves ventrally on to the dissoconch.

Pigment spots: The pigment spots are lost during the 20 hours immediately following attachment.

Spat axes: In the larva, the mouth and the anus develop ventrally but when the larva becomes attached the anus moves dorsally. The mouth also rotates dorsally to rest against the ventral side of the anterior adductor muscle, and the posterior adductor muscle develops on the ventral side of the intestine. The palps and gills have also rotated dorsally from a former ventral position. The hinge of the prodissoconch is dorsal but after metamorphosis a reorientation of the body takes place so that the hinge becomes anterodorsal.

DISCUSSION

Reproduction and development in the New Zealand mud-oyster is essentially typical of the genus *Ostrea* being larviparous (incubatory) and hermaphroditic. Species of this genus are also held by some workers to be protandric, having a rhythmical alternation of female and male phases following the initial male phase and having the spermatozoa liberated in clusters. Certainly the New Zealand mud-oyster has sperm balls and appears to be protandric but further work is needed to determine the actual sequence of sexual phases, the duration of phagocytosis after female spawning and the length of time elapsing between the female phase and the following male phase. In other species of the genus *Ostrea*, spermatogenesis is well advanced and the oyster is capable of maturing as a male while larvae are still being held in the mantle cavity. Rapid proliferation of the spermatogonia while larvae were being liberated was not observed in *Ostrea lutaria*.

A comparison of *O. lutaria* with other incubatory and non-incubatory species of oysters shows several noteworthy contrasting features. The eggs and larvae of *O. lutaria* are considerably larger than those of other species. The larvae appear to be incubated for a much longer period than that recorded for other incubatory species and that they may be retained within the mantle cavity until they are fully developed. This is of great significance since the larvae of other incubatory species of oysters do not become fully developed until they have passed through a free swimming phase of several days.

An examination of the plankton of Evans Bay collected over a period of one year failed to identify any free swimming oyster larvae. The plankton did show, however, that several other bivalves were breeding all the year round in Wellington Harbour. It is therefore possible that the mud-oyster in Wellington Harbour may also breed for more than the eight months noted in this study.

Larvae are considered fully developed when they possess pigment spots, a well-developed foot and about seven gill filaments. Until this account, the fully-developed larvae of non-incubatory species of oysters such as *C. virginica* have always been found to be larger than those of incubatory species. The results of this study show that the larvae of *O. lutaria* are considerably larger and more fully developed than the larvae of any non-incubatory species of oyster. Fully-developed larvae of the New Zealand mud-oyster when liberated from the mantle cavity possess pigment spots, a well-developed foot and at least ten gill filaments. Furthermore, these larvae exhibit the characteristic exploratory phase immediately on liberation and settle within the following few days. Larvae of all other incubatory species of oysters do not exhibit the exploratory phase until they have been in the plankton for some considerable length of time. The pigment spots and seven gill filaments of such oysters are produced during the last 24 hours of the free swimming phase.

The attached larva (spat) of *O. lutaria* is consequently much larger than the metamorphosing spat of other incubatory and non-incubatory oysters. Other oyster spat of both types measure 2mm in length when the four gills are developed whereas the spat of *O. lutaria* are at least 5mm in length before the fourth gill (left outer demibranch) is developed. The young oysters of *O. lutaria* were never observed to be sexually mature before the second summer (this includes the summer during which they become attached). Thus it appears that even though the larvae are more fully developed and of a larger size at the time of settlement, they subsequently develop more slowly than all other incubatory and non-incubatory species of oysters.

It therefore seems that either *O. lutaria* follows a unique pattern of reproduction and development, or, it follows a pattern similar to that of many other invertebrate

animals of south temperate regions in which the larva is large and the pelagic phase very short. If the latter is the case, then other incubatory species of oysters inhabiting latitudes greater than 40°S. could also be expected to possess large larvae and a short pelagic life. The oyster species known from these latitudes are *O. angasi*, the South Australian mud-oyster, *O. heffordi*, the Dunedin rock-oyster, and *O. chilensis*, the South American oyster. *O. nomades*, the Australian green oyster, extends from Port Jackson to the Gulf of Carpentaria and is only included in this list because of its southern range (where *O. angasi* also occurs).

No information was available to the author with regard to the reproduction and development of the South American oyster and very little is known about *O. angasi*. Thomson (1954, p. 145) notes that Ranson has investigated the prodissoconch of *O. angasi* but the results are not yet available. Roughley (1925, p. 15) states that the larvae of *O. angasi* are about 1/150th of an inch long when ready to be liberated. This is similar to other species of *Ostrea*.

During the present study brief observations were made on *O. heffordi* while specimens of this oyster were being studied with regard to its systematic status. Specimens of this oyster collected in winter had very young spat attached to the older oyster shells. In a total of about 100 specimens examined throughout the year, no incubatory specimens were observed.

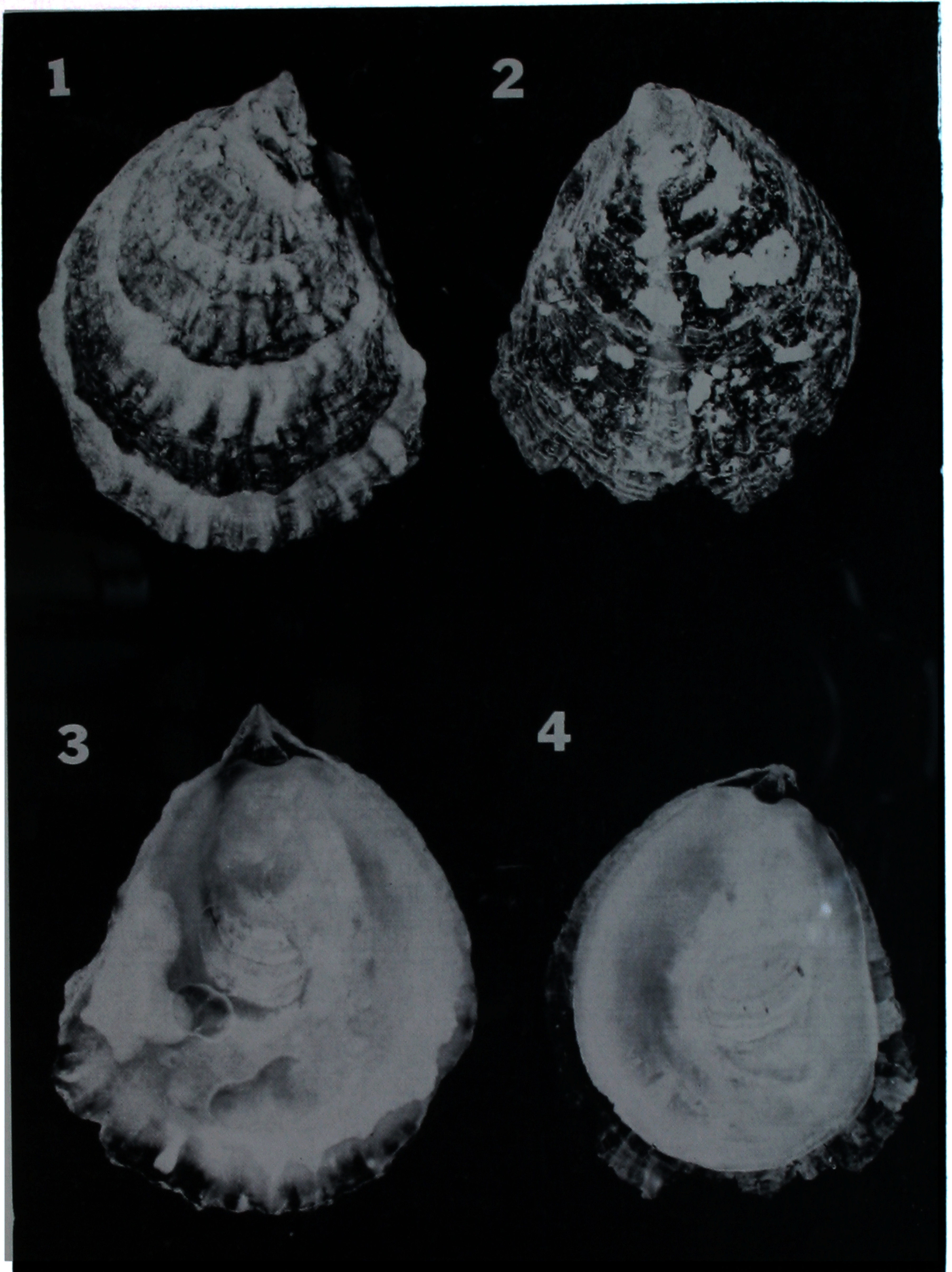
Thus, the greater size of the larvae and shorter pelagic phase of *O. lutaria* is at the moment unique with regard to all other oysters known. Whether or not other south temperate incubatory oysters also have a similar reproduction and development yet remains to be determined.

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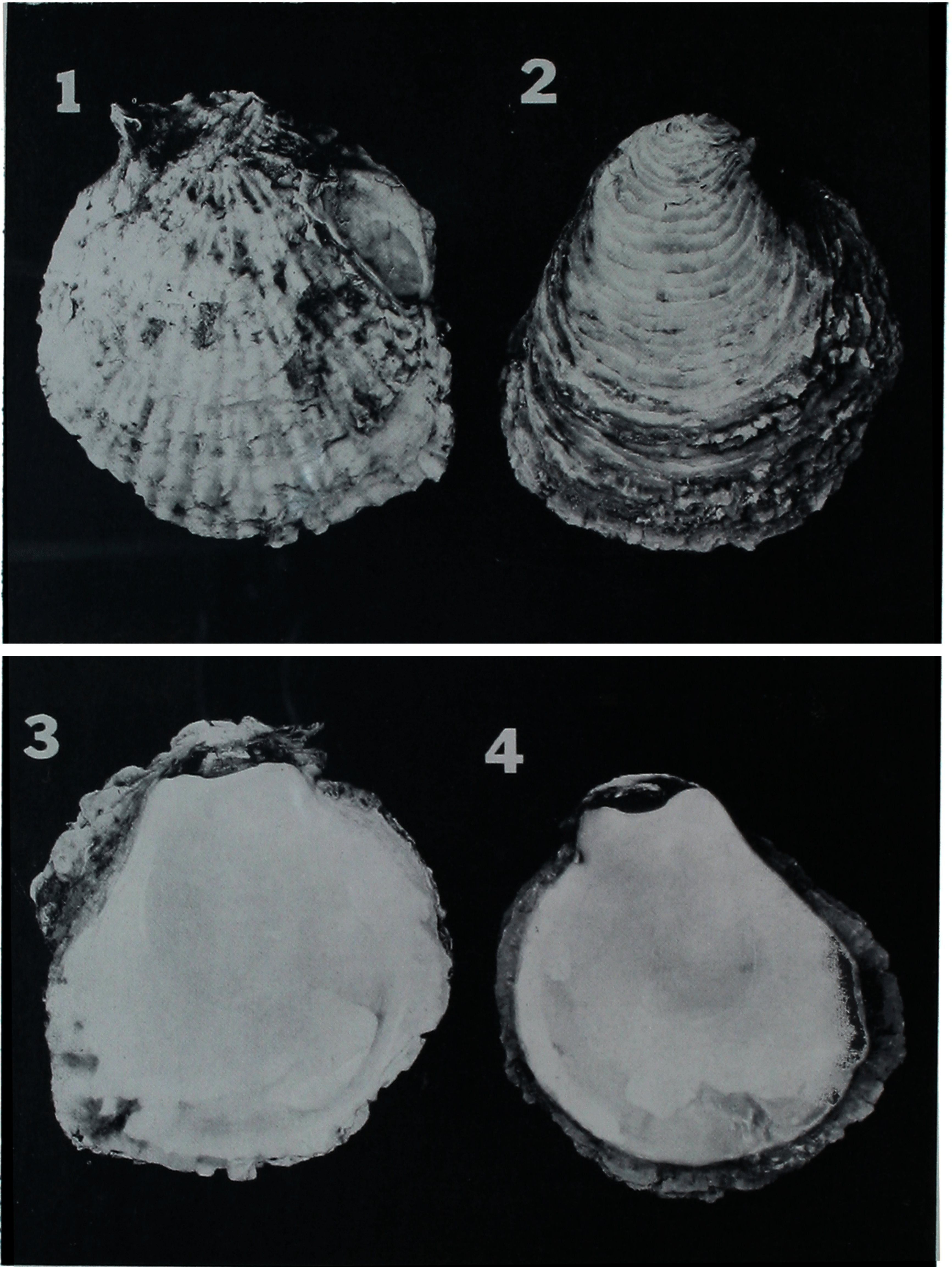
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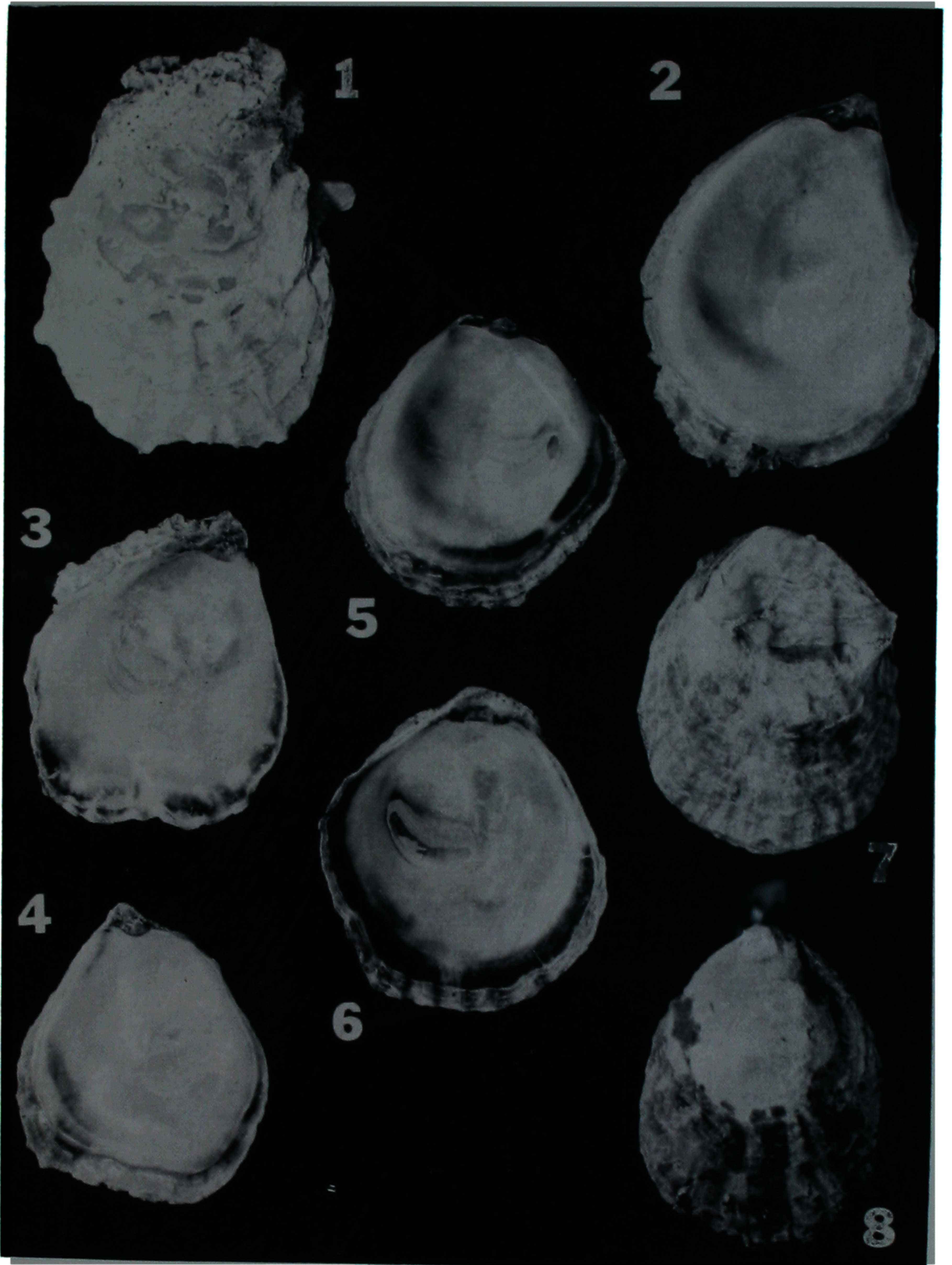
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Ostrea angasi Sowerby. Fig. 1, external surface of lower valve; 2, external surface of upper valve; 3, internal surface of lower valve; 4, internal surface of upper valve. Approx. $\frac{1}{2}$ natural size.



Ostrea lutaria Hutton. Fig. 1, external surface of lower valve; 2, external surface of upper valve; 3, internal surface of lower valve; 4, internal surface of upper valve. Approx. natural size.



Ostrea lutaria Hutton. Fig. 1. external of lower valve; 2, internal of upper valve. *Ostrea heffordi* Finlay. Fig. 3, internal surface of lower valve; 4, internal surface of upper valve; 5, internal surface of upper valve; 6, internal surface of lower valve; 7, external surface of lower valve; 8, external surface of upper valve. Approx. natural size.