THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* GMELIN

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CHAPTER I

TAXONOMY

The family Ostreidae consists of a large number of edible and nonedible oysters. Their distribution is confined to a broad belt of coastal waters within the latitudes 64° N. and 44° S. With few exceptions oysters thrive in shallow water, their vertical distribution extending from a level approximately halfway between high and low tide levels to a depth of about 100 feet. Commercially exploited oyster beds are rarely found below a depth of 40 feet.

The name "Ostrea" was given by Linnaeus (1758) to a number of mollusks which he described as follows:

"Ostrea. Animal Tethys, testa bivalvis inaequivalvis, subaurita. Cardo edentulus and fossula cava ovata, striisque lateralibus transversis. Vulva anusve nullus." The name Tethys (from Greek mythology and also refers to the sea) applies to the type of marine animals, living either within the shells or naked, that Linnaeus listed under a general name "Vermes" which includes worms, mollusks, echinoderms, and others. The translation of Linnaeus' diagnosis reads as follows: Shell bivalve, unequal, almost ear-shaped. Hinge toothless, depression concave and oval-shaped, with transverse lines on the sides. No vulva or anus.

This broad characterization included a number of genera such as scallops, pen shells (Pinnidae), limas (Limidae) and other mollusks which obviously are not oysters. In the 10th edition of "Systema Naturae," Linnaeus (1758) wrote:

"Ostreae non omnes, imprimis Pectines, ad cardinem interne fulcis transversis numerosis parallelis in utraque testa oppositis gaudentiquae probe distinguendae ab *Arcis polypleptoginglymis*, cujus dentes numerosi alternatim intrant alterius sinus." i.e., not all are oysters, in particular the scallops, which have many parallel ribs running crosswise inward toward the hinge on each shell on opposite sides; these should properly be distinguished from *Arca polyleptoginglymis* whose many teeth alternately enter between the teeth of the other side.

In the same publication the European flat oyster, *Ostrea edulis*, is described as follows: "Vulgo *Ostrea* dictae *edulis*. *O. testa* semiorbiculata membranis imbricatis undulatis: valvula altera plana integerrima." i.e., commonly called edible oyster; shell semicircular, outer valve with wavy grooves; the other small valve completely flat. With a minor change Linnaeus' diagnosis is repeated by Gmelin (1789).

Lamarck (1801) restricted the family Ostreidae to the species of the genus *Ostrea* which was characterized by him as follows: Adhering shell, valves unequal, irregular, with divergent beaks which with age become very unequal; the upper valve becomes misplaced. Hinge without teeth. Ligament half internal, inserted in the cardinal lunule of the valves; the lunule of the lower valve and the beak grow with age and sometimes reach great length.

Great confusion in the usage of the generic name of living oysters resulted, however, from

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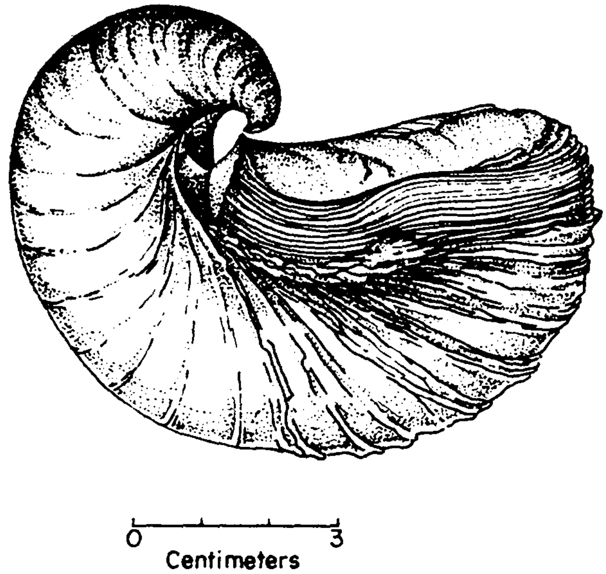

FIGURE 1.—*Gryphaea arcuata*, Jurassic fossil. Specimen No. 283 from the Museum of Comparative Zoology, Harvard University. Dimensions: height 8.5 cm., depth 3.5 cm.

Lamarck's (1801) allocation of extinct and recent species of oysters to the genus *Gryphaea*. Under this generic name, which was published with a diagnosis, Lamarck included nine nominal species, some of which at the time of publication were "nomina nuda" since they lacked diagnosis, but other species were validated by citation of bibliographical references (Hemming, 1951). Lamarck had not designated the type species, and a selection of "types" was made by Anton (1839), who designated fossil *Gryphaea arcuata* (fig. 1) as type. Dall (1898) and Anthony (1906) also selected *G. arcuata* as type. A living species, *Gryphaea angulata*, was included by Lamarck (1801) but without a diagnosis.

Lamarck (1819) further confused the nomenclature of the genus *Ostrea* when he again described the genus *Gryphaea*. A longer list of species included common oyster of Portugal and Mediterranean, *Gryphaea angulata*, this time, however, with a diagnosis (fig. 2). It was assumed by Children, Grey, Fisher, Tryon, Stoliczka, and Sacco (quoted from Dall, 1898: 671–688) that *G. angulata* is Lamarck's type species, an opinion entirely without foundation. Anatomical and embryological studies have demonstrated that *G. angulata* has no characteristics of the fossils *Gryphaeidae*. The species is simply another type of oyster similar to the American species (*C. virginica*), with a slightly twisted beak which only remotely resembles the curved beak of the *Gryphaea*.

Oysters are frequently found so closely adhering to the substratum that their shells faithfully reproduce the configurations and detailed structures of the objects upon which they rest. For instance, under the name of *Ostrea tuberculata*, Lamarck (1819) described a shell from the Timor Sea (Netherland Indies) grown on a coral of the family Astraeidae; this particular shell repeated the tubercles and other structural elements of the coral upon which it was resting. Other specimens of the same species, but grown on a smooth surface, were listed as different species. *O. haliotidea* of Australia, another Lamarckian species assumed a shape of the abalone shell to which it was attached. Oysters adhering to the shells of *Trochus maculatus* repeated the granular structure of this gastropod (Smith, 1878), while those grown on branches of mangrove trees usually formed a groove between the folds of the shell facing the branch while the same species attached to the trunk of the tree did not develop such structure (Gray, 1833). *O. equestris* found growing on navigation buoys (Galtsoff and Merrill, 1962) repeated the configurations of bolts and shells of barnacles upon which they happened to attach themselves.

The influence of other factors of the environment on the shape and sculpture of oyster shell has been reported by many investigators who noticed that specimens growing in calm water on flat surfaces have a tendency to acquire a round shape and to have poorly developed umbones. On soft bottom and overcrowded reefs the same species tend to form long and slender, laterally compressed bodies with hooklike umbones. Lamy (1929) observed that oysters attached to a pebble or shell and, therefore, slightly raised above the bottom, had deep lower valves, more or less radially ribbed. This type of structure, according to Lamy, offered greater resistance to dislodgment by currents or wave action.

Since Lamarck's inclusion of a living estuarine species, *G. angulata*, in one genus with the fossil Jurassic and Cretaceous Gryphaeas was not acceptable to many biologists, the question was submitted for ruling by the International Commission on Zoological Nomenclature. The retention of the name "*Gryphaea*" and the designation of *G. angulata* as the type species of the genus *Gryphaea* was favored by the "majority" of European zool-

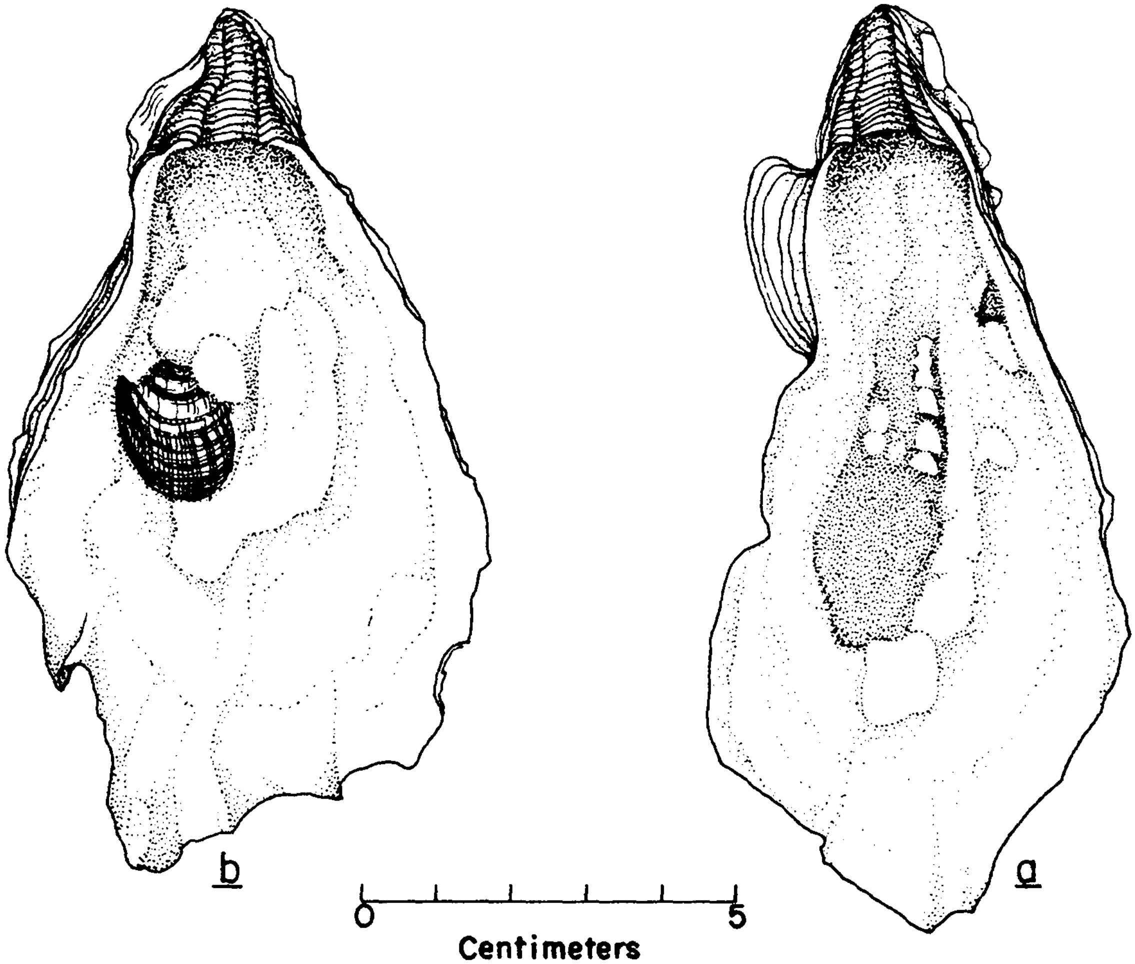

FIGURE 2.—(a) *Crassostrea angulata*, Arcachon, France. Dimensions: height 9 cm., length 5 cm.
(b) *C. virginica*, Brownsville, Tex. Dimensions: height 8.5 cm., length 4.5 cm.
Note similarity of the two forms.

ogists (Ranson, 1948a) who requested the International Commission to suppress the name "*Gryphaea*" (Lamarck 1801) as applied to fossil species and to validate the name "*Gryphaea*" (Lamarck 1819) which included the living oysters. The American zoologists (Gunter, 1950) were in favor of retaining the name "*Gryphaea*" for fossil forms.

The findings of the International Commission, published as Opinion 338 on March 17, 1955, are as follows:

Gryphaea Lamarck, 1801, is available for the purposes of the Law of Priority and has as its type species the Mesozoic Fossil species *G. arcuata* Lamarck, 1801, by selection by Anton (1839), and not *G. angulata* Lamarck, 1801, which was selected by Children in 1823, this latter name being a nomen nudum (not having been published with an indication for the recent species to which it is applicable until 1819).

"This nominal species *Gryphaea angulata* Lamarck, 1819, is not the type species of any nominal genus, but the generic name *Crassostrea* Sacco, 1897, is available for use for that species by those specialists who regard it as congeneric with *Ostrea virginica* Gmelin, (1790) (the type species of *Crassostrea* Sacco) and who do not refer both species to the genus *Ostrea* Linnaeus, 1758."

The names *Gryphaea* Lamarck, 1801, *Crassostrea* Sacco, 1897, *arcuata* Lamarck, 1801 (*Gryphaea*) and *angulata* Lamarck, 1819 (*Gryphaea*) were placed on the Official Lists of Generic Names and Specific Names respectively and the nomen nudum angulata Lamarck, 1801 (*Grypnaea*) was placed on the Official Index of Rejected and Invalid Names in Zoology.

TAXONOMIC CHARACTERS

According to the view shared today by all specialists on pelecypod taxonomy, the genus *Ostrea* (in a broad sense), as characterized by Lamarck, comprises several groups of oysters of the family Ostreidae sufficiently different to be considered as separate genera or subgenera (Lamarck, 1819; Thiele, 1935). There is, however, no general agreement about the validity of various genera and species. A uniform system of classification of oysters is lacking, and for the separation of genera and species various authors use the characters of different categories: namely, shape and structure of shell, anatomy, sex and spawning, habitat, and structure of the larval shell (prodissoconch).

SHELL

In spite of great variability, certain shell characters are generally constant although they may be obscured in grossly distorted specimens. Two characters of this category are important: the cavity of the valves and the structure of the shell.

The lower valve is usually deep and cup-shaped with a depression or recess of greater or lesser extent near the hinge area. The upper valve may be flat or curved and slightly bulging near the hinge.

The oyster shell consists of extremely thin outer periostracum, the median prismatic layer, which is well developed on the flat (right) valve, the inner calcitic ostracum that constitutes the major part of the shell thickness, and hypostracum, a very thin layer of aragonite (orthorhombic $CaCO_3$) pad under the place of attachment of the adductor muscle.[1] The prismatic layer of *Ostrea edulis* is confined to the intricate brown scales of the flat valve, while among the Australian oysters only one species, *O. angasi* Sowerby, has a well-developed prismatic layer (Thomson, 1954). In the genus *Pycnodonte* the shell is peculiarly vacuolated (Ranson, 1941). The white patches or so-called "chalky deposits" in the shells of many oysters are not significant as taxonomic characters.

Size, shape, curvature, and proportion of the beak, i.e., the pointed (dorsal) end of an oyster shell, are useful generic characters, but like other parts of the shell they are variable and cannot be entirely depended upon for identification.

The sculpture of the shell may be useful for recognizing some species (*O.* (*Alectryonia*) *megodon*, fig. 3) with valves reinforced by a number of prominences or folds (also called ribs, ridges, or flutings by various authors) which end in the crenulations at the edge of the shell. In American oysters this character varies greatly depending on local conditions but is rather constant in *O. equestris* (Galtsoff and Merrill, 1962).

The position of the muscle scar and its outline differs in various species and, therefore, is used as a taxonomic character.

ANATOMY

Anatomical characters are of limited usefulness to malacologists who have to base their identification primarily on shells alone. Consequently the anatomical characteristics have been ignored by the majority of taxonomists. Some of the anatomical differences are, however, important for the separation of the genera. Thus, the presence of the promyal chamber separates the *Ostrea*, in which this feature is absent in sufficiently studied species, *O. edulis*, *O. lurida*, *O. equestris*, from *Crassostrea* in which the chamber is well developed.

Size of the gill ostia, large in the larviparous species and relatively small in oviparous ones, is of generic significance. The relation of the rectum and the heart is of importance since in the genus *Pycnodonte* the ventricle is penetrated by the rectum, a unique feature not found in other Ostreidae.

Convolution of the edge of the mantle with three folds in the majority of the species and only two in some Japanese species (Hirase, 1930) has been mentioned by some investigators as a specific character. The existence of two or three folds may be significant, but other characters such as ridges of the mantle, pigmentation of the tentacles and their size and spacing are variable and, in my opinion, have no taxonomic value.

SEX AND SPAWNING

On the basis of sexual habits, oysters fall into two distinct categories of nonincubatory (or oviparous) species, (*Crassostrea* spp.) i.e., those in which the eggs discharged into the water are fertilized outside the organism; and the incubatory or larviparous species (*Ostrea* spp.) in which fertilization takes place in the gill cavity, and the larvae are incubated and discharged after having reached an advanced stage of development. Incubatory oysters, as for example *O. edulis*, *O. lurida*, and *O. equestris*, are bisexual

[1] The author is grateful to H. B. Stenzel for the information on aragonite in oyster shells.

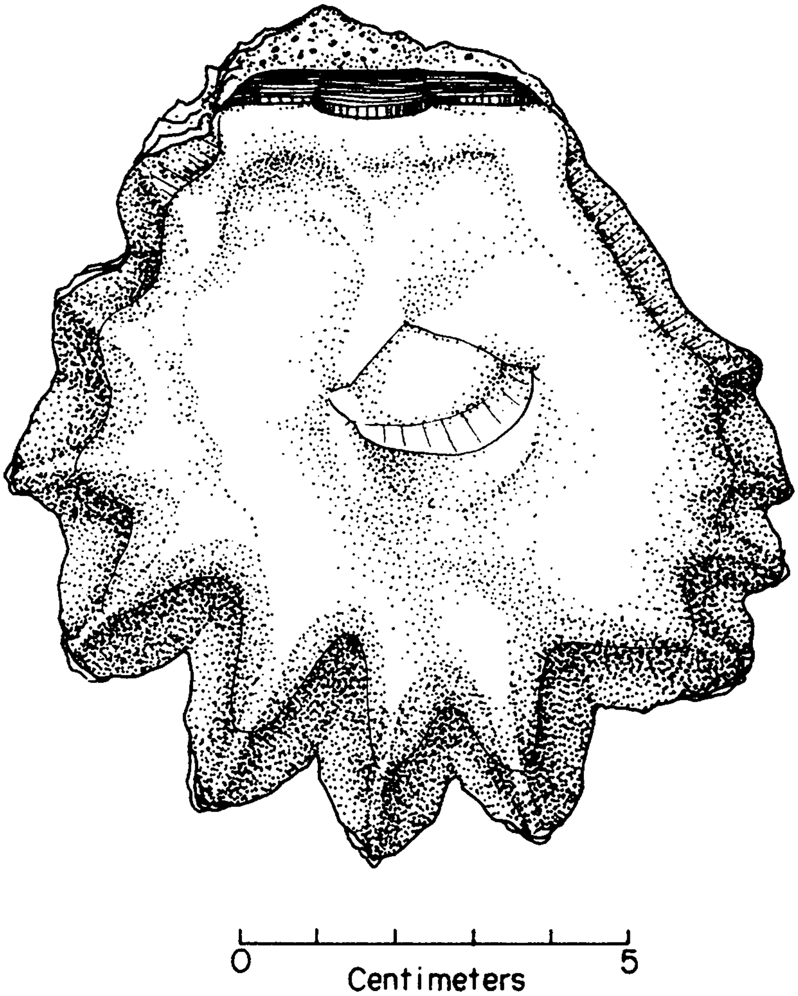

FIGURE 3.—*O.* (*Alectryonia*) *megodon.* Pearl Islands, Panama. Dimensions: height 17 cm., length 16 cm.

(hermaphroditic). The gonad of a bisexual oyster produces eggs and sperm simultaneously, but the relative quantity of sex cells of one or another type alternates periodically from male to female and vice versa.

The sexes of nonincubatory (oviparous) oysters (*C. virginica*, *C. gigas*, *C. angulata*) are separate. Instances of hermaphroditism in this group are very rare. The sexes are, however, unstable and once a year a certain percentage of oysters change their sex. This change takes place after spawning during the indifferent phase of gonad development. Alternation of sex (discussed in ch. XV) has been studied in detail only for a few species.

HABITAT

Salinity, turbidity, and depth of water are frequently mentioned in the brief statements that accompany the descriptions of various species. Ecological data are, however, of no help to classification. With the exception of a few commercial species, which have been more adequately studied, little is known about the environmental requirements of the populations of other species. In a general way it can be stated that *C. virginica*, *C. gigas*, and probably *C. angulata* are more tolerant to diluted sea water than are *O. lurida* and *O. edulis*. The two latter species survive better in more saline and less turbid environment. Geographical distribution of *O. equestris* suggests the preference of this species to the waters of full oceanic salinity (about 35°/oo). The same is true for many tropical oysters living along the continental shores and in the lagoons of oceanic islands where the salinity of water changes but little or remains constant throughout the year. Tolerances of these tropical species to lowered salinity have not been studied.

LARVAL SHELL (PRODISSOCONCH)

The difficulty in identifying a species by its shell led Ranson (1948b) to base the classification of oysters entirely on the features of a "definite" prodissoconch, i.e., the shell of a fully developed larva. He claims that distinctive crenulations of prodissoconchs are sufficient for the separation of species and that these specifically larval characters can be detected in well-preserved adult shells and even in fossils. In a brief paper comprising only 6 incomplete pages of text and 35 pages of drawings of 34 species of oyster larvae Ranson (1960) summarizes the basic idea of his classification. He states that a lamellibranch larval shell passes through two distinct stages, the first one is a "primitive" prodissoconch with undifferentiated hinge and the second phase, which he calls "definite" prodissoconch, is characterized by the development of hinge teeth. At the first phase all lamellibranchs have similar prodissoconchs, but at the second phase the hinge becomes differentiated. This makes it possible to distinguish the families and the genera. He maintains, without giving substantiating evidence, that the general shape of a definite prodissoconch is absolutely constant even if the size of the larva varies and that each species of oysters can be recognized by the shape of its larval shell and its structural characteristics.

Ranson's system of classification recognizes the following three genera of oysters: *Pycnodonte* (*Pycnodonta* in Ranson's spelling), *Crassostrea*, and *Ostrea*. His diagnoses of the prodissoconchs of these genera are given in the following section of this chapter. Unfortunately, the diagnoses of the larvae of 34 species of oysters studied by Ranson are lacking, and the prodissoconchs are shown only by diagrammatic drawings, some of which are reproduced in chapter XVI of the book. My attempts to locate the prodissoconchs on the shells of fully grown *C. virginica* (from 3 to 8 years old) were not successful. On a few occasions the prodissoconchs were faintly visible, but the structure of the hinge, and the number and location of hinge teeth could not be detected. Final decision regarding the possibility of identifying adult oysters by their larval characters must wait, however, until Ranson's system is given a fair trial by malacologists. His suggestion that identification can be made by observing spat attached to the shell of the adult is not valid because in many places several species of oysters live together in the same locality and the larvae settle indiscriminately on any shell or other object available at the time of setting.

THE GENERA OF LIVING OYSTERS

There is an obvious need for a complete taxonomic revision of the family Ostreidae. This revision should cover all the principal species of living oysters and must be supplemented by morphological, anatomical, and ecological observations which at present are available only for a few commercially utilized species. In the absence of these data for the large majority of species of living oysters, it is at present impossible to propose a logical taxonomical system for the family.

Opinions vary regarding the number of genera of living oysters of the family Ostreidae. Stenzel (1947) recognizes 12 valid generic names, some of which, as was shown by Gunter (1950), are synonymous. The latter author admits the existence of three definite genera (*Ostrea*, *Crassostrea* and *Pycnodonte*) and three others (*Dendostrea* Swainson, *Alectryonia* Fisher de Waldheim, and *Striostrea* Vialov) of doubtful validity.

Ranson (1941, 1948b, 1960) merges the three doubtful genera of Gunter in *Ostrea* and recognizes only the three definite genera listed above. This opinion, based primarily on structure of prodissoconchs, is shared by Thomson (1954) and is supported by the evidence accumulating from morphological and biological data. It can be, therefore, stated with a certain degree of assurance that on the basis of present knowledge, the living Ostreidae comprise three genera: namely, *Ostrea* Linnaeus; *Crassostrea* Sacco; and *Pycnodonte* Fisher de Waldheim. The genus *Lopha*, named by Bolton in 1798, without definition and described as a subgenus only in 1898 by Dall (1898), is undoubtedly a synonym of *Ostrea*. The distinctive feature upon which this genus was founded was the sharply crenulated nature of the shell margin, a very poor distinguishing character.

The three genera of oysters can be defined as follows:

Genus *Ostrea* Linné, 1758. Genotype: *O. edulis* L.

Shell subcircular; lower valve shallow, not recessed under the hinge; upper valve flat, opercular, sometimes domed; muscle scar subcentral. Promyal chamber absent. Gill ostia relatively large. Incubatory.

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 center, and between the center and anterior end (Ranson, 1960, fig. 350, ch. XVI).

Genus *Crassostrea* Sacco, 1897. Genotype: *C. virginica* Gmelin

Shell very variable, usually elongated; lower valve cuplike, deep, and recessed under the hinge; upper valve flat, opercular. Muscle scar displaced in dorsolateral direction. Large promyal chamber on the right side of the body. Gill ostia and eggs relatively small. Nonincubatory. Excellent illustrations of the species can be found in the monographs of Lister (1685) and Chemnitz (1785).

This genus includes species formerly known as *O. virginica*, *O. gigas*, and *G. angulata*. The separation of the cuplike oysters (*Crassostrea*) from the flat ones (*Ostrea*) is justified because of the anatomical differences (promyal chamber, size of the ostia) and spawning habits. The name "*Crassostrea*" (Sacco, 1897) is validated in accordance with the rules of the International Commission on Zoological Nomenclature (1955).

Valves of the prodissoconch unequal; hinge with two teeth at each end; internal anterior ligament extends beyond the hinge (Ranson, 1960). (Fig. 348, ch. XVI).

Genus *Pynodonte* Fisher de Waldheim, 1835. Genotype: *P. radiata* F. de W.

Shells large and heavy; lower valve slightly recessed under hinge; both shells lack sculpture except for sharp crenulations along the tip; hinge very broad. Inner sides of valves chalky white or greenish; row of small denticles along the edges of valves on both sides of the hinge; muscle scar white, elevated on a shelflike projection; the adductor muscle is oval in outline and rounded on the hinge side; the gonads are bright orange; the ventricle of the heart surrounds the rectum, which runs posteriorly beyond the adductor muscle almost to the junction of the mantle. Nonincubatory.

Valves of prodissoconch equal; hinge with five teeth arranged over the entire length of it; internal anterior ligament, immediately after the hinge; 10 small denticles at the edge of each valve anteriorly to the ligament (Ranson, 1960).

The following species of living oysters are known from the coastal waters of the continental United States and from the State of Hawaii:

C. virginica Gmelin, Eastern oyster, Atlantic oyster. This is the principal edible oyster of the Atlantic and Gulf Coasts of the U.S.A. (fig. 4). Its range of distribution extends from the Gulf of St. Lawrence to the Gulf of Mexico and the West Indies. The species was introduced in the waters of San Francisco Bay, Puget Sound, Willapa Bay, and Oahu Island but failed to establish itself, although occasionally single specimens can be found in these waters.

The right (upper) valve smaller than the left. The beaks elongated and strongly curved. The valve margins straight or only slightly undulating. The muscle scar usually deeply pigmented. The adductor muscle located asymmetrically, well toward the posterodistal border. Large promyal chamber on the right side. Nonincubatory, discharging eggs and sperm directly into the water.

Adults vary from 2 to 14 inches in height (dorsoventral direction) depending on age and environment. Shape, sculpture, and pigmentation of inner side of the shell and along the edges of the mantle and tentacles vary greatly.

Crassostrea rhizophorae Guilding. Light, thin, foliaceous, and deeply cupped shell with smaller flat upper valve fitting to the lower one (fig. 5). The inner margins straight and smooth with considerable purple coloration especially around the left valve. The beaks twisted dorsally. Muscle scar near the dorsal margin. Promyal chamber present. Nonincubatory, discharging eggs and sperm directly into the water.

Similar to *C. virginica* from which it differs by the following characters: lower left valve is less plicated than in *virginica;* the muscle scar is more rounded and often unpigmented. (Prodissoconch shown in fig. 349, ch. XVI).

Adults may reach 4 inches in height. Frequently attached to the aerial roots of the mangrove *Rhizophora mangle*. Inhabits Caribbean region including Puerto Rico and Cuba where the species is commercially exploited.

Crassostrea gigas Thunberg, Japanese oyster, Pacific oyster (fig. 6) Cuplike shells of large size with coarse and widely spaced concentric lamellae and coarse ridges on the outside; shells usually much thinner than those of *C. virginica*. Upper (right) valve flat and smaller than lower (left)

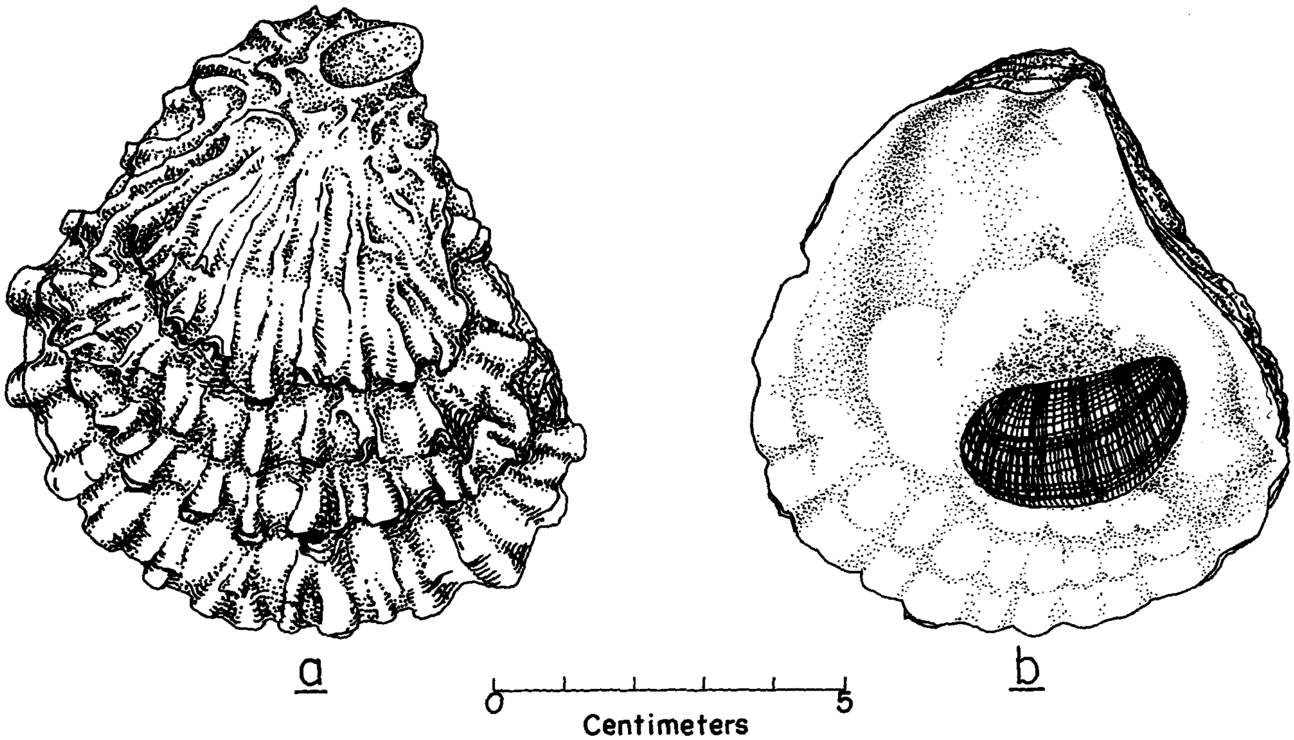

FIGURE 4.—*C. virginica.* Wellfleet Harbor, Mass. Dimensions: height 9.5 cm., length 8 cm. (a) lower (left) valve; (b) inside of upper (right) valve.

valve. Interior surface white, often with faint purplish stain over the muscle scar or near the edges. Large promyal chamber on the right side. Edges of the mantle deeply pigmented. Nonincubatory, discharging a very large number of eggs and sperm directly into the water. Introduced from Japan into the waters of British Columbia, western states of the United States, and Alaska (Ketchikan). Small number of specimens of *C. gigas* were at various times planted in Mobile Bay, Ala., and in Barnstable Bay, Mass.

Highly variable. Typical *C. gigas* is a long, straplike oyster. The form *C. laperousi* (considered by Japanese malacologists as a separate species) has round, highly ridged shells.

C. commercialis (Iredale and Roughley), Sydney rock oyster, commercial oyster. This Australian species (fig. 7) was imported to Hawaii about 1925–28 and planted along the shores of the western end of Kaneohe Bay, in Oahu Island. In 1930 several of the imported specimens were examined by the author and found to be ripe and spawning. During World War II the small population of this species was destroyed by dredging operations.

Valves markedly unequal and variable. The left valve deep and cup-shaped, recessed under the hinge, slightly fluted; the edge weakly crenulated. The upper valve flattened. Inner side of valves chalky white, frequently with bluish or creamy markings on the upper valve; muscle scar usually not pigmented. Edges of valves with small denticles extending about half way around the valve. Sexes are separate; nonincubatory.

Usually grows to 3 to 4 inches in height, but cultivated specimens have been reported to reach 10-inch size. Normal range of distribution New South Wales and Queensland; frequently found in the intertidal zone attached to rocks, sticks, and shells.

C. rivularis Gould (fig. 8). This Japanese species has been planted in waters of Puget Sound with the shipments of seed of *C. gigas*. In Japan the oyster is known as "suminoegaki" (Hirase, 1930).

The shell orbicular; strong and large, adult specimens reaching 6 inches in height. Left, lower, valve slightly concave, upper valve shorter and flat. The left valve with generally indistinct lamellae of pale pink color with radiating striae. The lamellae of the right valve are thin and al-

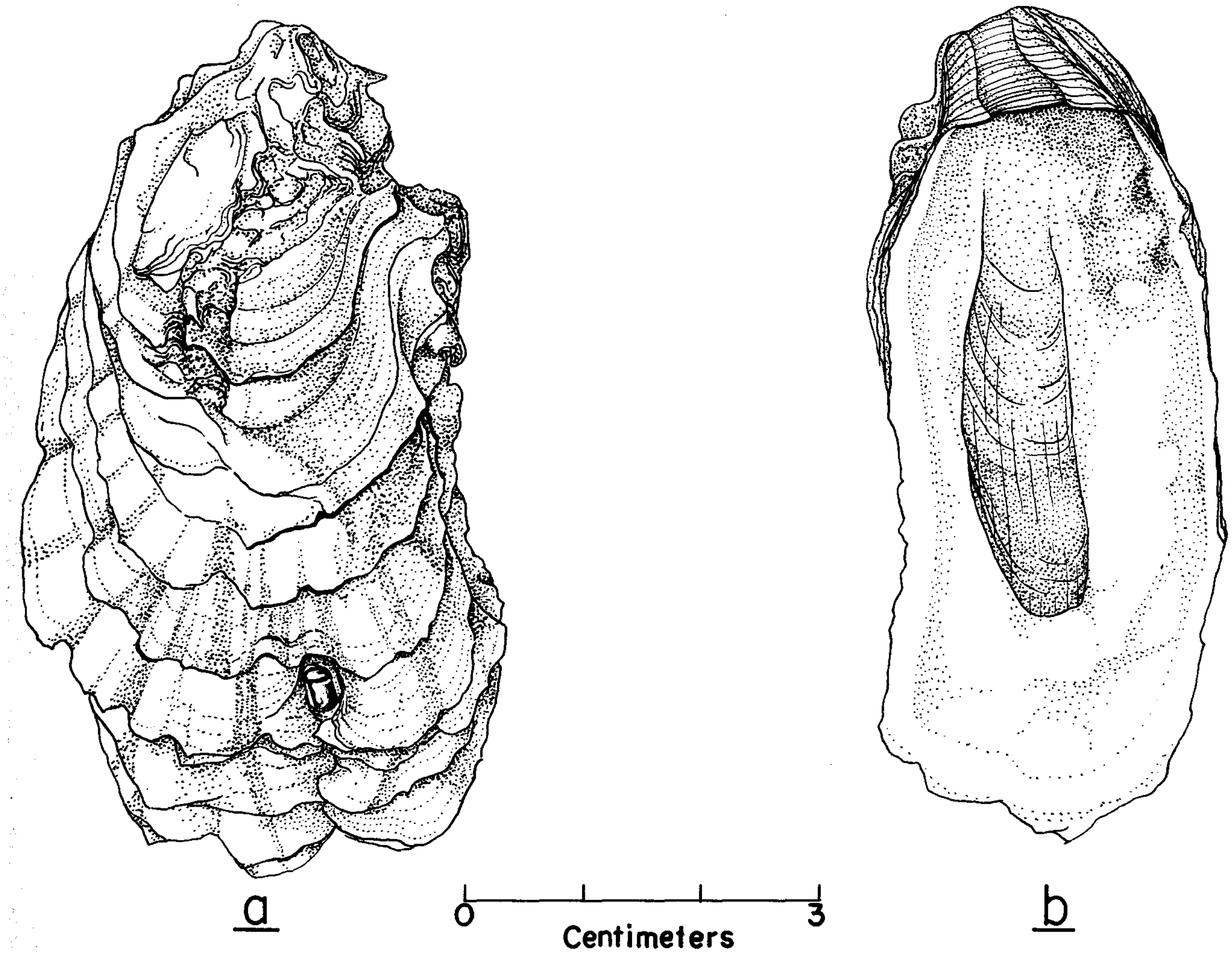

FIGURE 5.—*C. rhizophorae.* On mangrove roots, Florida Keys. Dimensions: height 7 cm., length 3.7 cm. (a) exterior; (b) interior of the shell.

most smooth, sometimes covered with tubular projections. The color of the right valve is cream buff with many radial chocolate bands; their arrangements greatly variable. Muscle scar, situated near the center or a little dorsally, is white, occasionally with olive-ochre spots. Margin of the mantle is dark violet; the tentacles are arranged in two rows; those of the outer row are of irregular size; the inner tentacles in a single row are slender.

The species, described from China by Gould, occurs in Ariake Bay and in the bays of Okayama Prefecture, Japan. It has established itself in Puget Sound.

Ostrea edulis Linné (fig. 9). This European flat oyster is the type species of the genus *Ostrea.* Shell round or oval; left valve larger and deeper, slightly bulging with 20 to 30 ribs and irregular concentric lamellae. Upper valve smaller, flat, without ribs, with numerous concentric lamellae. Beaks poorly developed. Ligament consists of three parts; the middle part is flat on the left valve and forms a projection on the right valve. Muscle scar is eccentrically located, unpigmented. Promyal chamber absent. Ostia and eggs relatively large. Hermaphroditic and incubatory mollusk, discharging eggs into the gill cavity. Small numbers of European flat oysters were introduced several years ago into the coastal waters of Maine in Boothbay Harbor where they survived and reproduced themselves. At present the population is too small to be used commercially. Recently the stock of European oysters in Maine waters was increased by planting seed raised from eggs fertilized and developed in the Bureau of Commercial Fisheries Biological Labora-

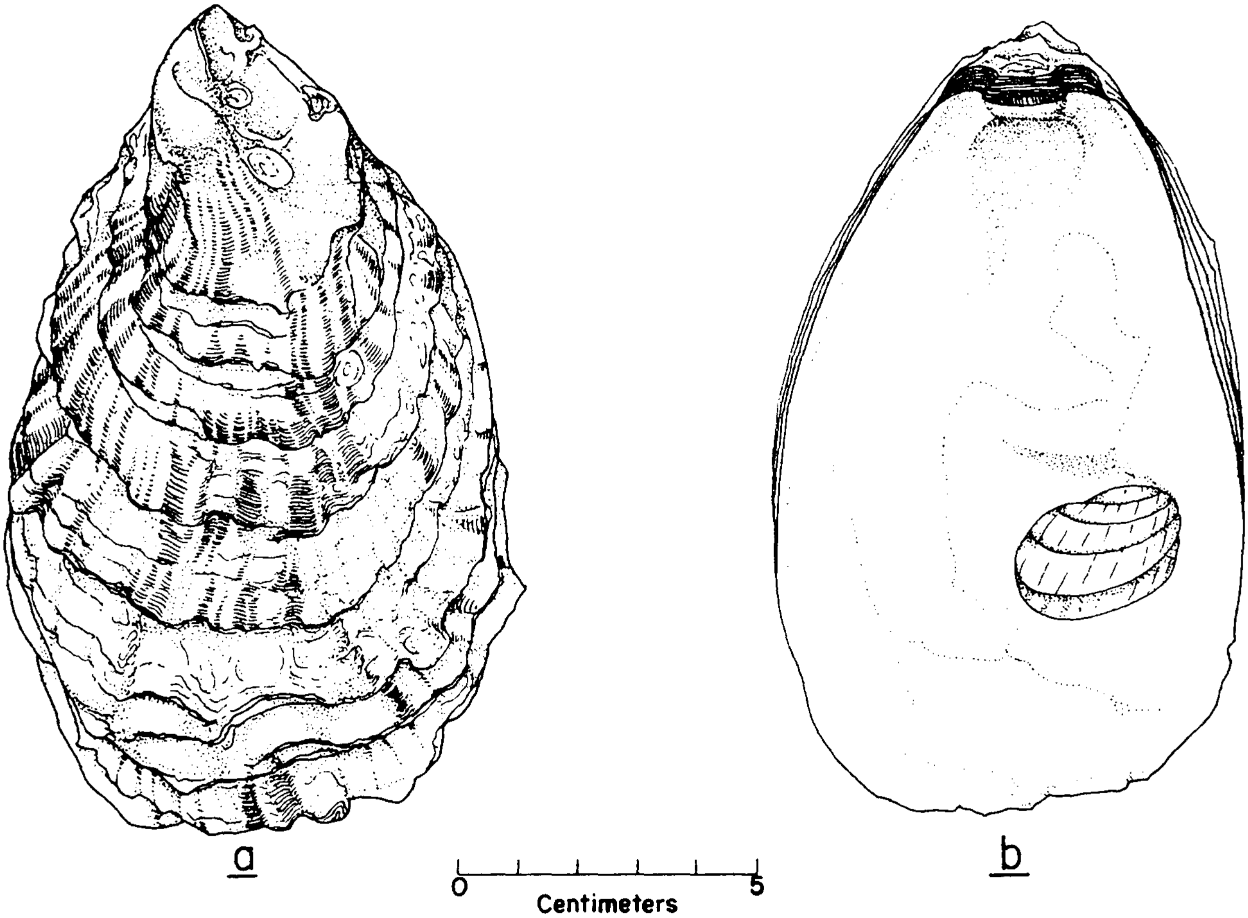

FIGURE 6.—*C. gigas*. Adult oyster grown in Willapa Harbor, Wash., from seed imported from Japan. Dimensions: height 14 cm., length 9 cm. (a) exterior of lower (left) valve; (b) interior of upper (right) valve.

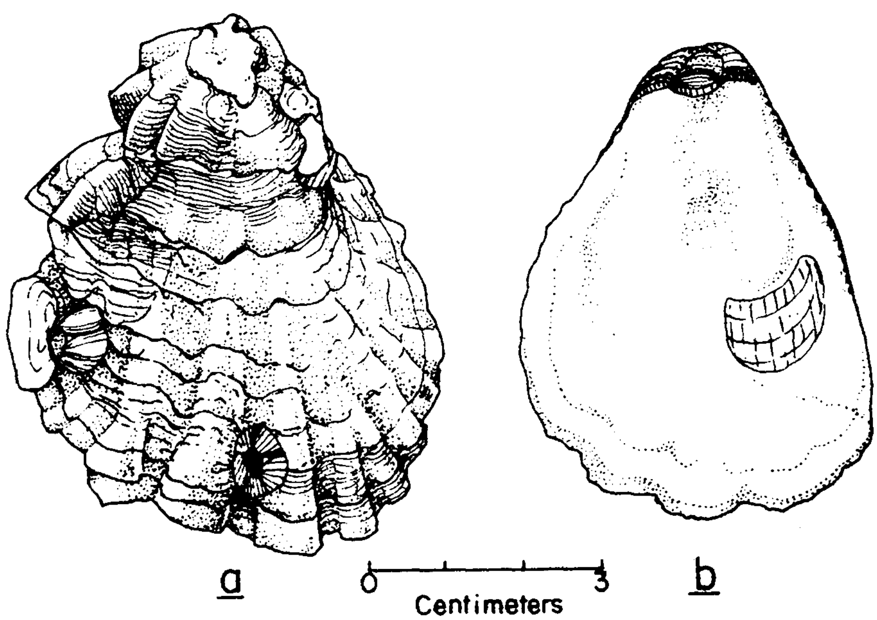

FIGURE 7.—*C. commercialis*. Kaneohe Bay, Oahu Island, Hawaii. Dimensions: height 7 cm., length 4.8 cm. (a) exterior of lower (left) valve; (b) interior of upper (right) valve.

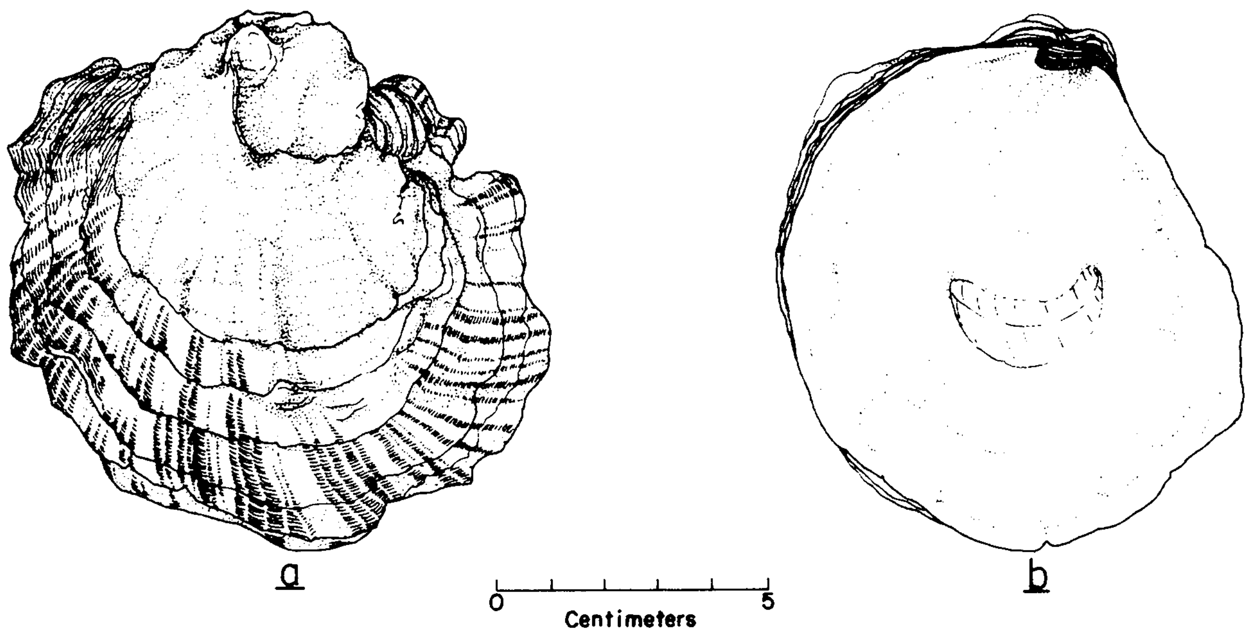

FIGURE 8.—*C. rivularis.* Puget Sound. Introduced from Japan with the seed of *C. gigas.* Dimensions: height 10.7 cm., length 10.5 cm. (a) exterior of lower (left) valve; (b) interior of upper (right) valve.

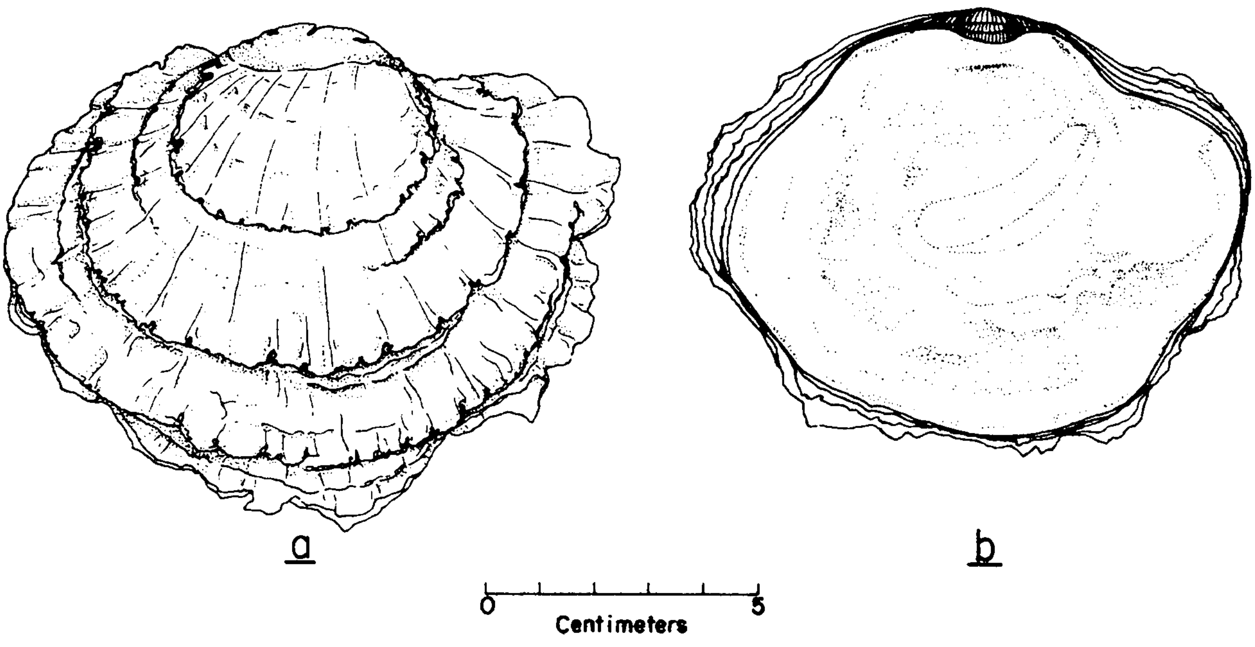

FIGURE 9.—*O. edulis,* European flat oyster introduced from Europe to Boothbay Harbor, Maine. Dimensions: height 9 cm., length 11 cm. (a) exterior of the left (lower) valve; (b) interior of the right (upper) valve.

tory at Milford, Conn. Prodissoconch shown in fig. 350 ch. XVI.

O. lurida Carpenter (fig. 10). Shells from 2 to 3 inches in height, with coarse concentric lines. Inner side of valves usually olive-green. Promyal chamber absent. Hermaphroditic, incubatory, eggs retained in the gill cavity until fully developed larvae are formed and discharged into the water. Inhabits the tidal waters of the Pacific Coast of North America from Alaska to Lower California. (Prodissoconch shown in fig. 351, ch. XVI.).

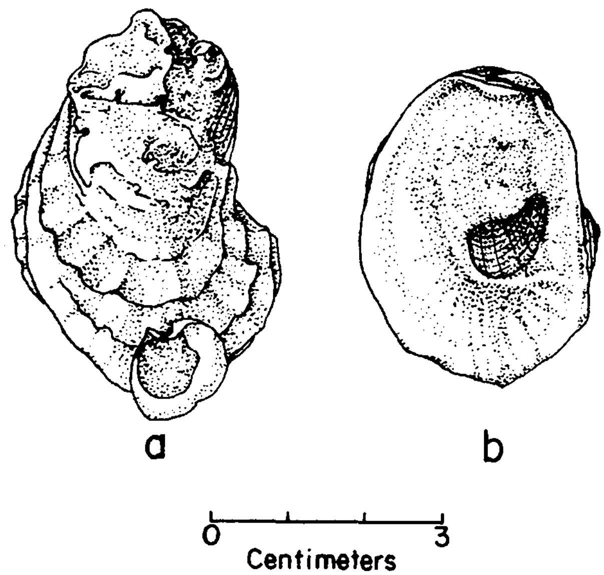

FIGURE 10.—*O. lurida* from Puget Sound. Left (a) and right (b) valves. Height 5.5 cm.; length 3 cm.

O. equestris Say, horse oyster, crested oyster (fig. 11). This small, noncommercial oyster of the South Atlantic states, Gulf of Mexico, and West Indies is often mistaken by laymen for young *C. virginica*. Its average size is about 2 inches, but occasionally specimens measuring up to 3½ inches in height are found. Say (1834), who described the species, lists the following identifying characters: Shell small, with transverse wrinkles, and more or less deeply and angularly folded longitudinally; ovate-triangular, tinted with violaceous; lateral margins near the hinge with from 6 to 12 denticulations of the superior valve; superior valve depressed but slightly folded; inferior valve convex, attached by a portion of its surface, the margins elevated, folds unequal, much more profound than those of the superior valve; hinge very narrow, and curved laterally and abruptly.

The shape of the oyster shell is very variable depending on crowding and type of substratum. The most significant combination of features by which *O. equestris* can be distinguished from small *C. virginica* and from *O. frons* are as follows: a rather high vertical and crenulated margin of the lower valve; off-center position of the adductor muscle scar; a dull greenish color of the interior surface; and the presence of a single row of denticles of the upper valve with the corresponding depression on the lower valve (Galtsoff and Merrill, 1962). The number of denticles and their size very variable. Ranson (1960) does not include *O. equestris* in the drawings of prodissoconchs reproduced in his publication. A rough sketch of the prodissoconch of *O. equestris*, not showing the details of hinge structure, is given by Menzel (1953).

This incubatory species frequently occurs in large numbers on commercial oyster beds in association with *C. virginica*. It thrives in waters of high salinity (35°/₀₀) but has been found in regions where salinity is about 20 to 25°/₀₀. The northernmost boundary of distribution established by Merrill is about half way between Delaware and Chesapeake Bays, (37°31′ N., 73°18′ W.) at the depth of 60 fathoms.

O. frons Linné (fig. 12). Small shells of 1 to 2 inches in height with radial plicated sculpture and sharply folded margins. Valves closely set with minute denticles almost around the entire circumference. Muscle scar near the hinge. Beaks slightly curved. Interior white, exterior usually purple-red. Frequently attached to branches or roots of mangrove trees by a series of hooked projections. Common in Florida, Louisiana, and the West Indies. Was found attached to navigation buoys off Port Royal, S.C., and off Miami Harbor, Fla. (personal communication of A. S. Merrill).

O. permollis Sowerby (fig. 13). This small oyster lives commensally, completely embedded in sponges with only the margins of the valves visible. The species is common along the west coast of Florida, north of Tarpon Springs, where it is constantly associated with the sponge *Stellata grubi* (fig. 14). Rarely exceeds 1.5 inches in size. Surface of valves soft and silky. Beaks twisted back into a strong spiral. Inner margins with numerous small denticles. Nonedible species. North Carolina to Florida and the West Indies.

Pycnodonte hyotis Linné. This species dredged from 300 feet of water off Palm Beach was described by McLean (1941) as *O. thomasi*, nova species, but identified by Ranson as *Pycnodonte hyotis*. It is characterized by the peculiar foam-like appearance of its shell structure, particularly at the margins. Shells circular, 3 to 4 inches in diameter.

Pycnodonte is frequently found on navigation buoys off Key West, Fla., and near the entrance to Miami Harbor (personal communication of A. S. Merrill).

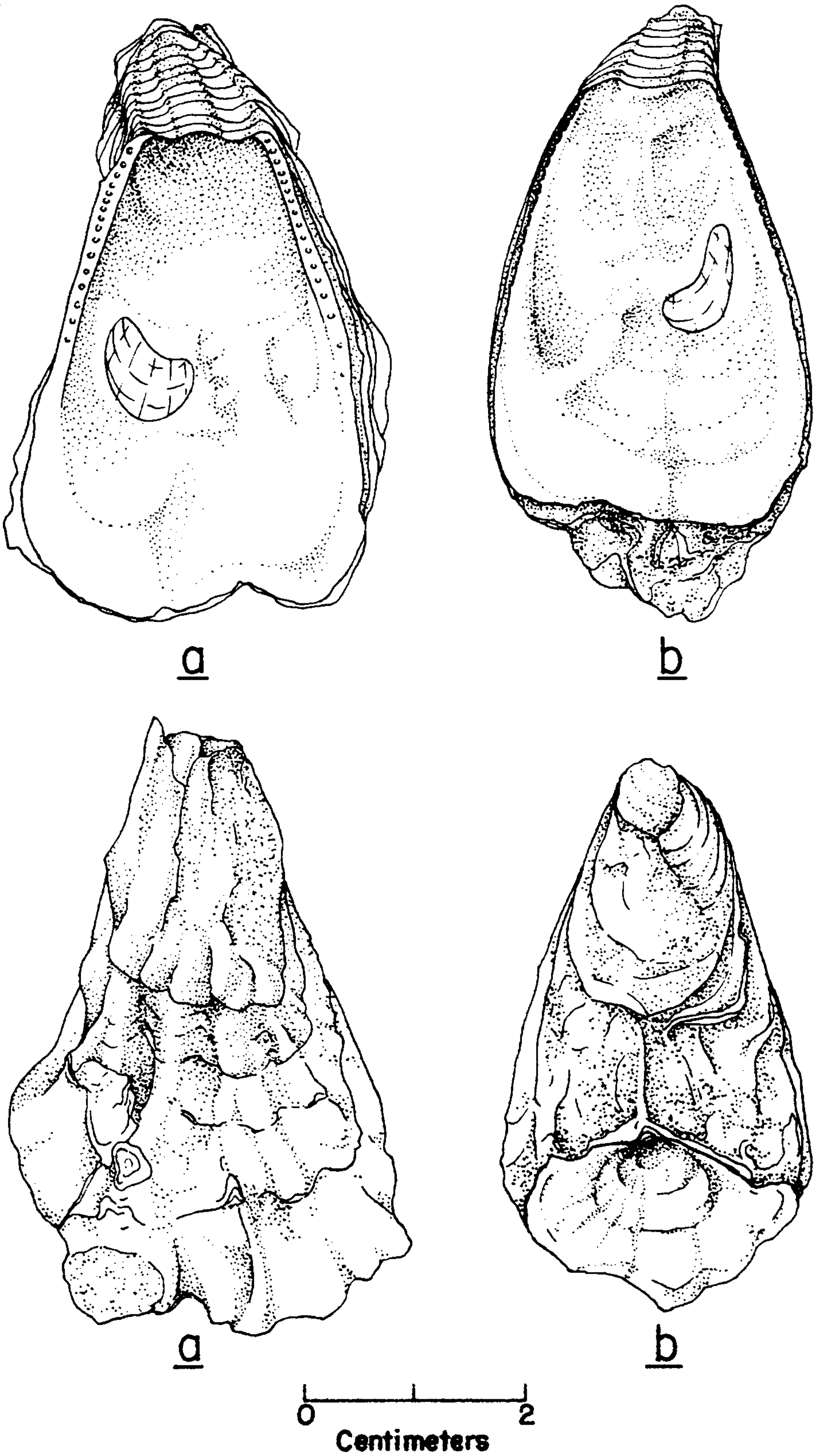

FIGURE 11.—*O. equestris*. Left (a) and right (b) valves. 5 cm. in height.

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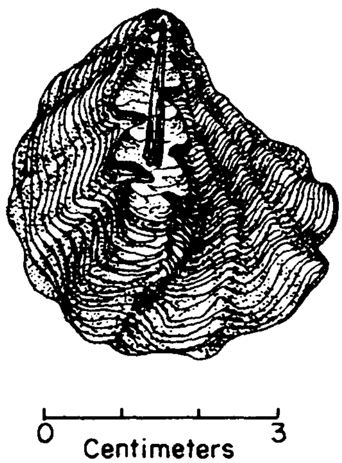

FIGURE 12.—*O. frons*. Key Biscayne, Florida. Natural size.

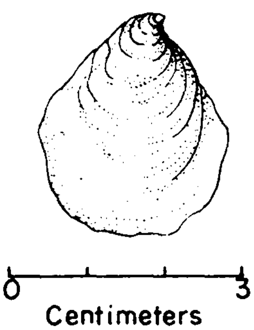

FIGURE 13.—*O. permollis*. West of Andote Light, Tarpon Springs, Fla., at 6 fathoms. Dimensions: height 3.5 cm., length 3 cm.

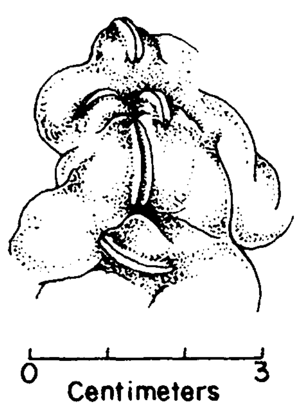

FIGURE 14.—*O. permollis* embedded in sponge *Stellata grubi*.

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