PART N
BIVALVIA

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VOLUME 3

OYSTERS

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INTRODUCTION

The oysters are very successful biologically, if one may measure success by number of individuals living and by territory they occupy. Several species are important as food and as raw materials for high-purity lime used in the chemical and cement industries and have been studied intensively. Fortunately therefore, many biological data are available.

In the geological sciences oysters are useful or important in stratigraphic zonation, in paleoecologic interpretations, in phylogenetic studies, and as the makers of sediments (oyster biostromes and self-sedimentation). Many of the problems concerning oysters in biologic and geologic sciences have defied analysis, notably their evolution, phylogeny, and classification, partly because problems were attacked either with purely neontological or purely paleontological methods. Evidently both sources of information have to be tapped. For this reason the interdisciplinary approach is used here to reach for solutions to these problems.

A major result is the discovery that the oysters, as commonly understood by various authors, are not one monophyletic family but very probably are diphyletic. In other words, the oysters consist of two families: 1) Ostreidae *sensu stricto,* herewith emended to exclude the three subfamilies Gryphaeinae VYALOV, 1936 (*emend.* STENZEL, 1959), Pycnodonteinae STENZEL, 1959, and Exogyrinae VYALOV, 1936, and 2) Gryphaeidae [*nom. transl.* STENZEL herein (*ex* Gryphaeinae VYALOV, 1936, *emend.* STENZEL, 1959)] to comprise the three above-mentioned subfamilies. As far as this chapter is concerned, the vernacular name "oysters" includes two separate families.

Modern summaries of the biology of a few commercially important living species have been published by GALTSOFF (1964), KORRINGA (1952-53), LOOSANOFF (1965), RANSON (1943a), and YONGE (1960). Extensive bibliographies covering living species have been assembled by BAUGHMAN (1948), KORRINGA (1952-53), and RANSON (1952). Paleontological works covering larger groups of species are by COQUAND (1869), JOURDY (1924), SCHÄFLE (1929), VYALOV (1948a), WHITE (1884), and WOODS (1913). Living species were described by LAMY (1929-30) and SOWERBY (1870-71) in REEVE.

I wish to acknowledge with gratitude the generous support given before February, 1967, by Shell Development Company, a Division of Shell Oil Company, Houston, Texas, and by Louisiana State University since that time.

Extensive collections and good libraries are prerequisites to the present work. For many years both were not available to me and progress in this work was painfully slow. Were it not for the help and cooperation received from many colleagues at other institutions and in foreign countries the present work hardly could have been completed.

Thanks and appreciation are extended to all these who have given me a helping hand. They are too numerous to list all here in this space. However, I wish to thank specifically: Dr. R. TUCKER ABBOTT formerly of the Academy of Natural Sciences of Philadelphia; Dr. CARLOS C. AGUAYO of the Universidad de Puerto Rico; Dr. VAN REGTEREN ALTENA of Teyler's Museum in Haarlem, Netherlands; Dr. F. BROTZEN of the Swedish Museum of Natural History in Stockholm; Prof. R. M. CARTER of the University of Otago at Dunedin, New Zealand; Prof. W. J. CLENCH of the Museum of Comparative Zoology at Harvard University; the late Dr. L. R. COX of the British Museum (Natural History); Mr. DENNIS CURRY of Northwood in Middlesex, England; Mr. WILLIAM DEMORAN of the Gulf Coast Research Laboratory at Ocean Springs, Miss.; Prof. E. J. DENTON of the

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ORIENTATION AND AXES

Common normal Bivalvia are capable of moving about on or in a substratum, and while they move forward their sagittal plane of symmetry stands vertical. Direction of movement, hinge axis, mouth-anus axis, and axis through the centers of the two large adductor muscles are parallel or close to parallel. For that reason, it is easy to orient these bivalves anatomically, that is, one can define anterior, posterior, dorsal, and ventral sides readily (Fig. J1).

Not so the oysters. They are permanently immobilized, pleurothetic on the left side, and have no direction of movement. The earliest known fossil oysters show no trace of the anterior adductor' muscle, which probably had disappeared in the ancestors before oysters had evolved, and the axis through the centers of the two adductor muscles cannot be drawn. The two remaining axes form a large angle between them and thereby they present conflicting evi-

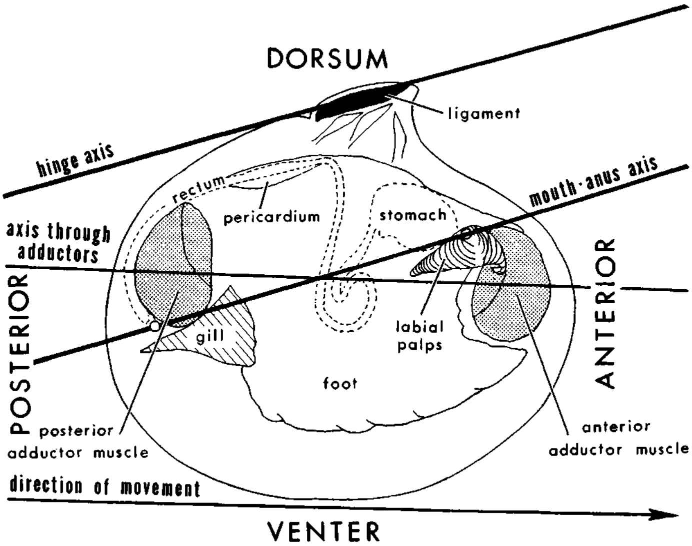

FIG. J1. Principal axes of orientation in common normal isomyarian bivalve as exemplified by *Astarte*, ×1.6 (after Saleuddin, 1965).

The RV has been removed and visceral mass is shown as transparent so that stomach, intestine, and pericardium are visible. Positions of mouth and anus are shown by circles.

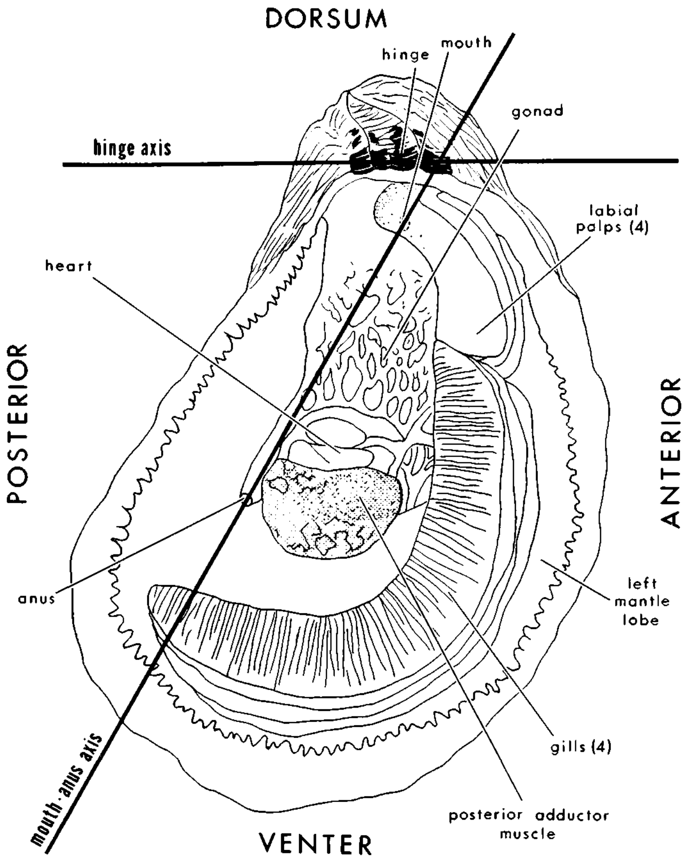

FIG. J2. Principal axes of anatomical orientation in oysters as exemplified by *Crassostrea virginica* (GMELIN, 1791), ×1.6 (Stenzel, n).

The oyster lies on its left side with RV removed so that soft parts are visible, position of mouth indicated, although it is hidden among labial palps; visceral mass shown partly transparent so that heart and gonad are visible.

dence for anatomical orientation of the animal. A choice must be made between these two axes as the means of orienting the mollusk (Fig. J2).

As concerns the animal and its survival, both axes have great functional importance, and one cannot claim that one is more significant than the other. Mouth and anus are part of the indispensable alimentary system, and the hinge is part of the mantle/shell protecting the animal. Rather, it is a question of practicability and general agreement.

If the hinge axis is the guide to anatomical orientation, that is, if it is equated with the anterior-posterior axis, hinge and umbonal region are the dorsum and the valve margins opposite the hinge are the venter of the animal. This is the orientation accepted in all conchological and paleontological literature and by some modern neozoologists, notably GALTSOFF (1964).

Since 1888 several neozoologists (JACKSON, 1888; LEENHARDT, 1926; PELSENEER in NELSON, 1938, p. 7; NELSON, 1938, p. 8; YONGE, 1953) have advocated using the mouth-anus axis instead. This orientation, or modifications of it, has been accepted by many authors since 1938. If one tries to apply the mouth-anus axis precisely, the hinge becomes not quite the anterior and the opposite valve margins become the ventroposterior side of the animal; in other words, many anatomical locations must

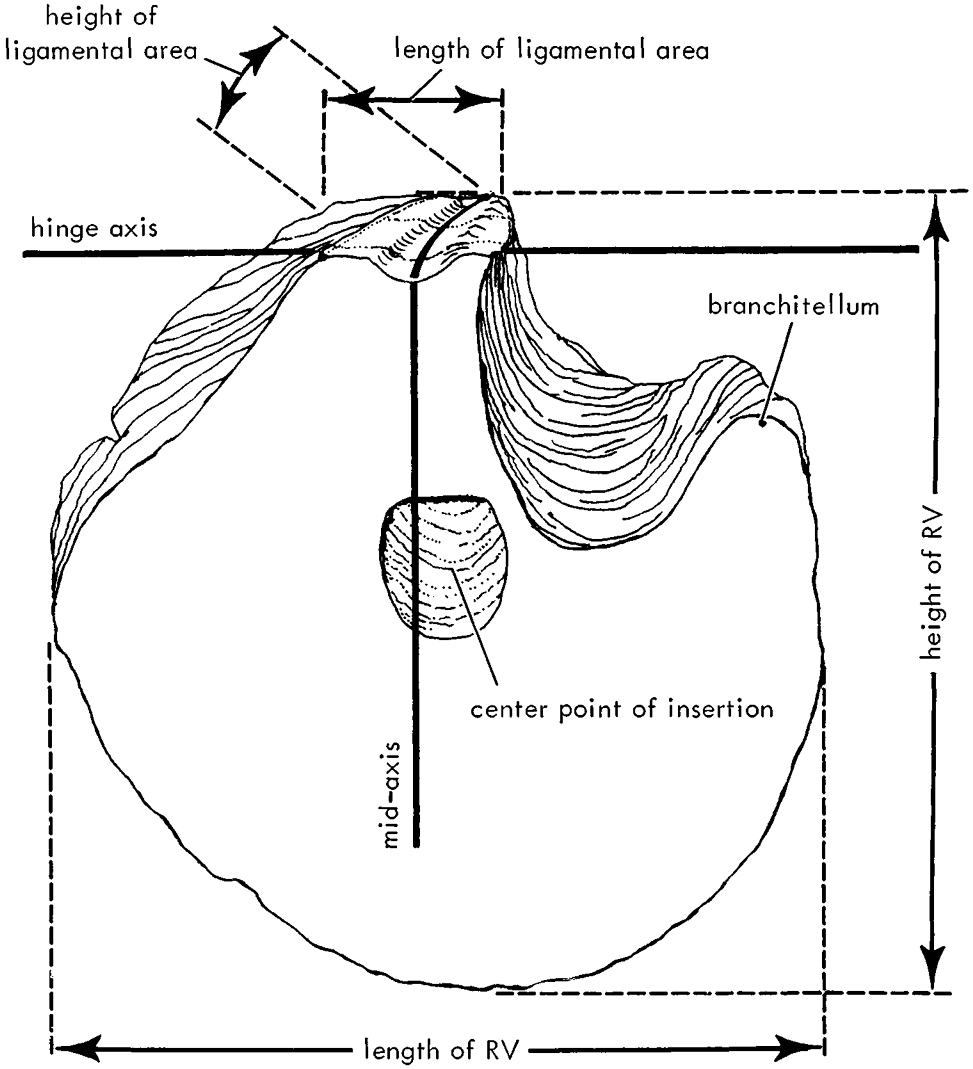

FIG. J3. Height, length, and mid-axis of an oyster as exemplified by RV of *Deltoideum*, ×0.9 (Stenzel, n). The aragonite pad at insertion of posterior adductor muscle has been leached, so that growth layers of the outer ostracum show through the hole.

have rather long, awkward descriptive terms. In order to simplify them, many neozoologists call the hinge simply the anterior and the opposite valve margins the posterior. The fact that this or other such changes are deemed necessary makes this choice of an axis a poor one.

In fossil oysters, one can locate the mouth-anus axis approximately. The mouth is near the imprint of the Quenstedt muscle (see p. *N*965), and the anus is at the margin of the posterior adductor muscle imprint (Fig. J2, see J4). However, some imprecision is involved. These anatomical landmarks can be found only if the shells at hand are in excellent condition. On the other hand, the hinge axis can be located with ease and precision on both living and fossil oysters. In short, the hinge axis is the better choice as the definitive guide for locating the anteroposterior axis of the animal.

The terms length, height, and width are

defined as follows. **Length** is the largest dimension obtained by projecting the extremities of the shell onto the hinge axis. **Height** is the largest dimension obtained by projecting the extremities onto the mid-axis of the shell. **Width** is the largest dimension obtained by projecting the outline of the shell onto a line that is at right angles to both the hinge axis and the mid-axis. The **mid-axis** is a straight line drawn in the commissural plane at right angles to the hinge axis and begins at the mid-point of the ventral margin of the resilifer (Fig. J3).

Length of the ligamental area is the length of its ventral border. **Height of the ligamental area** is measured along the middle of the resilifer following its curves from the umbo to the ventral margin (Fig. J3).

ANATOMY

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The oyster is composed of two major interconnected subdivisions: 1) **Visceral mass,** containing all those organ systems that must receive protection, namely, the whole digestive, excretory, and reproductive systems and most of the musculature and much of the nervous and circulatory systems. 2) **Gills and mantle/shell.** The latter is composed of a hard portion, the shell, which protects all other organs and a soft portion, the mantle, which carries sense organs and lesser parts of the musculature and of the nervous and circulatory systems. The term mantle/shell, coined by Yonge (1953, p. 443), emphasizes that it is an integral organ unit consisting of both soft and hard parts just as the arm of a vertebrate consists of soft and hard parts (muscles, blood vessels, nerves, hair, fingernails, bones, etc.).

VISCERAL MASS

The visceral mass extends from the hinge to the big adductor muscle, which is part of it. In it are concentrated, in the smallest possible space, organs indispensable to survival of the individual and of the species itself. For protection the visceral mass is as far removed as possible from the open margins of the valves and is tucked behind the adductor muscle, which forms a stout pillar connecting the two valves giving protection to organs lying between it and the hinge (Fig. J4).

A **visceral pouch** enclosing the hairpin loop of the intestine and carrying the urogenital openings wraps around the anterior flank of the adductor muscle.

DIGESTIVE SYSTEM

A detailed description of the digestive system of *Ostrea edulis* Linné, 1758, was given by Yonge (1926).

The **mouth** is at the dorsal end of the groove, and the tips of the gills are at the ventral end of the groove which is flanked by labial palps. There are two pairs of labial palps. Their outline is hatchet-shaped and slightly different in each genus. A short esophagus leads from the mouth to an elaborate stomach. The intestine leaves from the opposite side of the stomach, descends to the visceral pouch, forms a tight hairpin curve in the pouch, returns to form a wide loop around the stomach, and finally leads toward the dorsal flank of the adductor muscle. This terminal part of the intestine is the **rectum** and skirts the dorsal and posterior flanks of the adductor muscle. The anus is at the tip of a papilla at the posteroventral flank of the muscle, where it opens into the cloacal passage of the exhalant mantle chamber (Fig. J4).

In all living oysters, except the Pycnodonteinae, the rectum skirts the dorsal flank of the pericardium. In the Pycnodonteinae, the rectum passes through the pericardium and the ventricle of the heart, and the anal papilla projects more. These relative positions of rectum and ventricle in oysters are of great importance (Fig. J5).

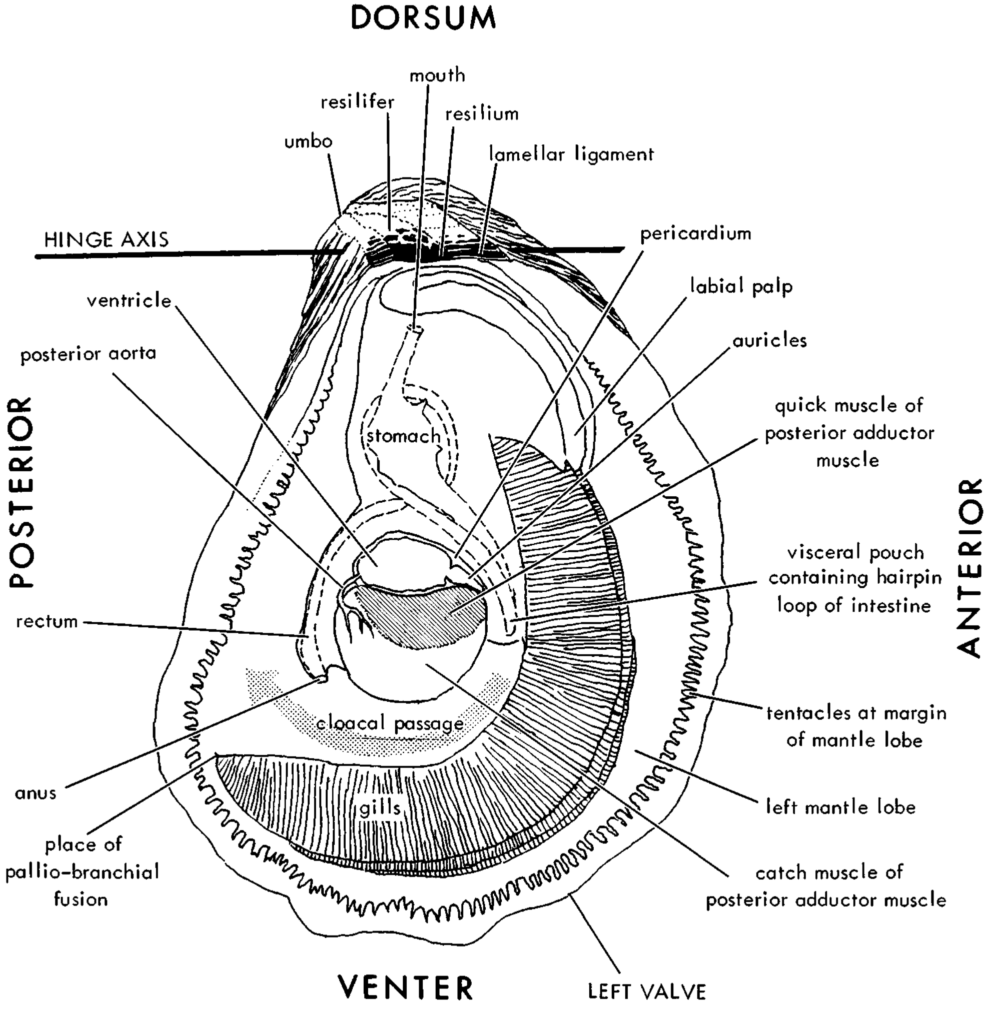

FIG. J4. Anatomy of an oyster as exemplified by *Crassostrea virginica* (GMELIN), ×0.8 (Stenzel, n). This is the common commercial oyster of eastern and southern coasts of North America. The animal rests on its left side; RV and mantle lobe removed and visceral mass depicted as partly transparent; shaded arrow indicates exhalant water current in cloacal passage.

EXCRETORY SYSTEM

The **kidneys,** or organs of BOJANUS, are two highly contorted tubules encased in a blood-filled sinus, located at the anterior flank of the adductor muscle. The blood coursing through this sinus loses its metabolic waste products to the tubules, which carry the liquid excreta out into the cloacal passage. The tubules discharge by way of a pair of small pores, each located near a genital pore in a short and slitlike urogenital cleft, which is located on the visceral pouch.

REPRODUCTIVE SYSTEM

The reproductive system is quite simple, because the eggs of oysters are very small and comparatively simple. The reproductive system is composed of two **gonads.** Each is an arborescent system of ciliated ducts ending with a canal at the genital pore.

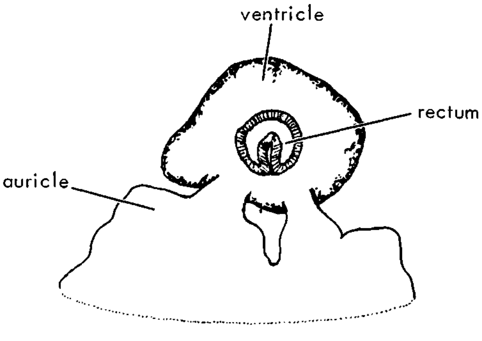

Fig. J5. Features of oyster anatomy. In living Pycnodonteinae rectum passes through both pericardium and ventricle of the heart, as shown in *Hyotissa hyotis* (Linné, 1758) *forma imbricata* (Lamarck, 1819), ×8 (after Pelseneer, 1911).

Because of this simplicity of structure, the oyster can and does change sex several times in its life. Changeover from male to female requires more vital resources and is slower than the reverse. As one sex phase fades away, the next one starts developing so that the two overlap. For example, during sex change from male to female, gonads carry simultaneously ripe spermatozoa and developing eggs and during the other change gonads carry residual spermatozoa and ripe eggs. In those genera of the Ostreidae that incubate their fertilized eggs and young larvae, one can find at certain times individual oysters that carry simultaneously unfertilized eggs, spermatozoa, and incubating larvae (Menzel, 1955) (Fig. J6). Young oysters begin their sexually mature life as males. Oysters are protandric alternating hermaphrodites.

Among natural, crowded populations sex change is influenced by food (starvation slows the change), by prevailing temperatures (cold slows it), and by neighboring individuals (old females influence young oysters to remain in the male stage). Old, large oysters are nearly all females.

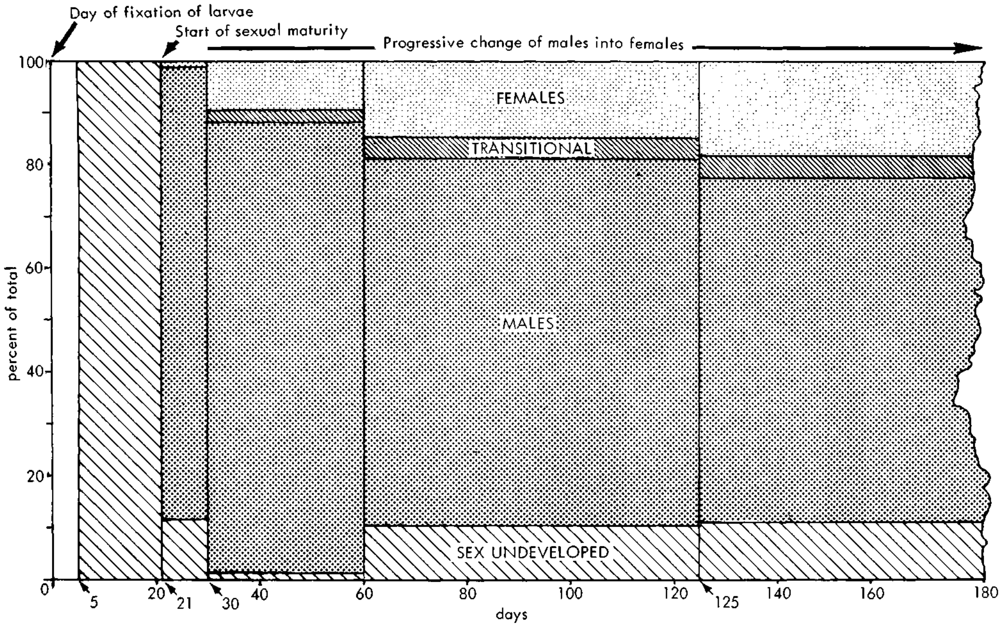

Fig. J6. Sexuality and sex change from male to female in young and small individuals of the incubatory species *Ostrea equestris* Say, 1834 (=*O. spreta* d'Orbigny, 1846) from Aransas Pass, Texas, USA (Stenzel, n).

Five age groups are shown, respectively, 5-21, 22-30, 31-60, 61-125, and over 125 days old, counting from day they became attached to substratum. Transitional stage includes individuals carrying sperm and eggs, sperm and incubating larvae, or sperm, eggs, and larvae. (From data on 439 individuals given by Menzel, 1955.)

MUSCULATURE

The many muscles in the body of the oyster are discussed here in two sets: muscles inserted on the valves at one or both ends and muscles not inserted on the valves. The former set generally leave traces of insertion on the valves and, therefore, are more important in paleontology than the latter. In adult oysters the former set consists of three: 1) The large solitary posterior **adductor muscle,** 2) the pair of small **Quenstedt muscles,** and 3) a group of several anterior **pallial muscles.** The first two are in the visceral mass and are discussed below. The last are in the mantle/shell and are discussed under that heading (Fig. J7).

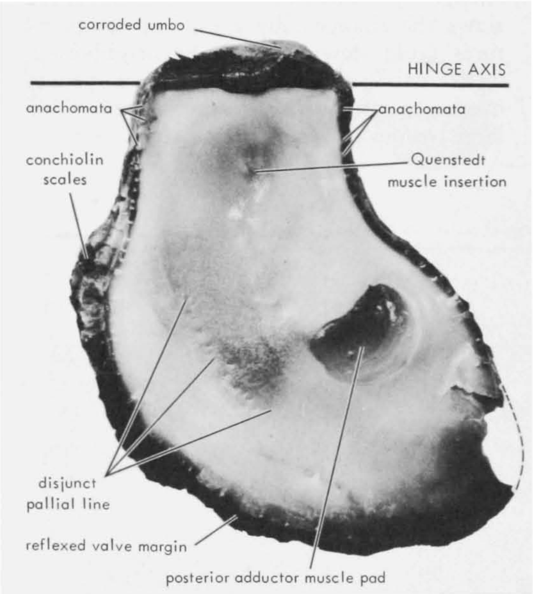

Fig. J7. Muscle insertions on valves of oysters as exemplified by RV of *Saccostrea echinata* (Quoy & Gaimard, 1835), living attached to rock surfaces on coast of Queensland, Australia, ×0.73 (Stenzel, n).

ADDUCTOR MUSCLE

Adult oysters are **monomyarian;** they have only one adductor muscle. On the other hand, the full-grown larva, before it affixes itself to its substratum, has an anterior and a posterior adductor muscle like all other normal dimyarian bivalves and their full-grown larvae (see Fig. J38). During metamorphosis from larva to young attached oyster, or spat, the anterior muscle of the larva shifts position and atrophies quite rapidly, leaving no trace whatsoever. This metamorphosis has been followed many times under the microscope so that there is no question that the solitary adductor muscle of the adult oyster is the posterior one.

Nevertheless, several authors have claimed either that some adult living oysters retain an additional adductor muscle, a vestigial anterior adductor muscle, or that some fossil oysters carry an imprint made by such an additional muscle. All these cases are in error and are based on misinterpretation of the Quenstedt muscles or their imprints on the valves.

Jaworski (1913) at first described *Heterostrea* (see Fig. J147) from the Jurassic of Peru as a new taxon of the Ostreidae that was supposedly heteromyarian, that is, had two unequal adductor muscles. Later he corrected himself (Jaworski, 1951) by discovering that this Peruvian fossil was incorrectly placed in the oysters and was really a *Myoconcha* J. de C. Sowerby, 1824 (see family Permophoridae, p. N547). Among the oysters, even among the most ancient ones described so far, there is no case known that would prove that anyone of them had a vestige of the anterior adductor muscle of their dimyarian bivalve ancestors.

The posterior adductor muscle is short and stout; it connects the two valves directly. Contraction of the muscle closes the two valves against the elastic expansion pressure of the ligament and keeps them shut for long periods of time, if need be.

The muscle is differentiated over its whole length into two coalescent subdivisions (Fig. J4): 1) the **catch muscle,** white opalescent and opaque in live oysters, composing the ventral or distal part of the muscle and 2) the **quick muscle,** flesh-colored and semitranslucent, composing the dorsal or proximal part of the muscle. The catch muscle is a tonic muscle similar to the tonic muscle fibers in the walls of arteries and intestines of vertebrates. It contracts slowly and can maintain the tension for long periods, even against the pull of outside forces. The quick muscle is phasic; it reacts quickly but does not endure. The two perform together in a division of labor when they contract and close the valves. The relative positions of the two subdivisions in the adductor muscle are the same in all bivalves. The quick muscle is always in proximal position. (See also Fig. J36.)

The relative sizes of the two subdivisions differ from genus to genus. *Ostrea* has a larger catch muscle than *Crassostrea* and *Saccostrea; Hyotissa* has the smallest. The two subdivisions cannot be distinguished in fossils.

Quick action of this muscle is of utmost importance to the survival of the oyster and requires the best possible supply of blood. There are many blood-filled gaps (sinuses) between the fibers of the adductor muscle, and the heart is located next to the muscle so that the artery supplying it is as short as possible (Fig. J4).

Each end of the adductor muscle is inserted on a thin film or pad composed of aragonite, which is deposited by the end of the muscle directly onto the calcitic outer ostracum of the valve. As the animal grows in size the muscle adds more fibers at its ventral flank and simultaneously retreats at its dorsal flank so that the successive aragonite pads grow with delicate growth lines subparallel to the ventral margin of the pad. Thick-shelled individuals have the muscle imprints deeply sunk in the face of the valve. Thin-shelled ones have them flush with that face so that they may be difficult to discern.

The planes of the opposing muscle imprints are tilted so that they converge in distal direction (see Fig. J13). The tilt is greater in more deeply cupped valves and usually the left has greater tilt than the right imprint. In many oysters there is also a tilt toward the posterior side, making the two imprints converge on that side. This tilt depends on the position of the imprint on the valve and on the cuppedness of the individual valve. In many thick-shelled morphs of *Gryphaea, Texigryphaea,* and *Hyotissa* the tilt of the muscle imprint is emphasized by a buttressed ventral border of the imprint which is raised considerably above the adjoining face of the valve (see Fig. J73,*2a,* Fig. J74,*3b,c*).

The adductor muscle and its imprints are on the posterior part of the mantle shell. If one draws the mid-axis on a valve the adductor muscle imprint, or at least the geometric center of it, falls on the posterior side of the mid-axis (Fig. J3). Within this limit there is considerable diversification as to position of the imprint among various genera.

The adductor muscle is more nearly central on the valve in the larger species of *Ostrea s.s.* than in other oysters (see Fig. J23, J109). *Crassostrea* has it closer to the ventral and posterior valve margins (Fig. J8; see Fig. J44). Advanced species of *Flemingostrea* and *Odontogryphaea* have it unusually close to the ventral and posterior valve margins (Fig. J9). *Arctostrea* and *Rastellum* have the imprint very close to the hinge. In the Gryphaeinae and Pycnodonteinae the imprint sits closer to the hinge than to the ventral valve margin (see Fig. J74,*3b*).

The outline of the imprint, which is simultaneously the cross-sectional shape of the muscle, depends very much on the individual shape of the valve (Fig. J8). In other words, the imprints of various individuals of a species are not the same in a strict geometric sense, but their proportions referred to the valve shape are much alike, as is the case with the locations of the imprints on the individual valves.

Outlines of imprints make up two major classes (Fig. J9): the concave class and the convex or orbicular class. 1) The former has concave or nearly rectilinear dorsal margins and imprints are generally longer than high (Fig. J9,*2*). The following outlines belong here: a) crescentic or shaped like crescent moon, ends sharp and concavity deep; b) semilunar or shaped like half moon, ends sharp and concavity shallow (Fig. J7); c) comma-shaped, only one end sharp and concavity deep (see Fig. J133); d) ribbon-shaped, very long and shaped like a curved ribbon (see Fig. J124); e) reniform or shaped like a kidney, ends well rounded and concavity gentle (Fig. J8; see Fig. J23, J109,*1b*).

2) The convex or orbicular class of imprint outlines has convex dorsal margins and is generally as long as it is high. It is characteristic of the Gryphaeidae (Fig. J9,*1*) The following outlines belong here: a) circular, length and height equal (see Fig. J74,*3b;* J76,*1;* J83); b) vertical-oval, height exceeding length (see Fig. J75,*4d*); c) horizontal-oval, length exceeding height (see Fig. J76,*5*); d) oblique-oval, longer

axis placed oblique in valve (see Fig. J9, *1a*).

The outlines and positions of the adductor muscle imprints are indicative of the interior anatomical topography of oysters. For this reason they are of utmost importance in the classification of fossil oysters. This was first pointed out and utilized in classification by Stenzel (1959). Some indications of this idea were noted in a special case of a living Australian oyster species by Thomson (1954, p. 135).

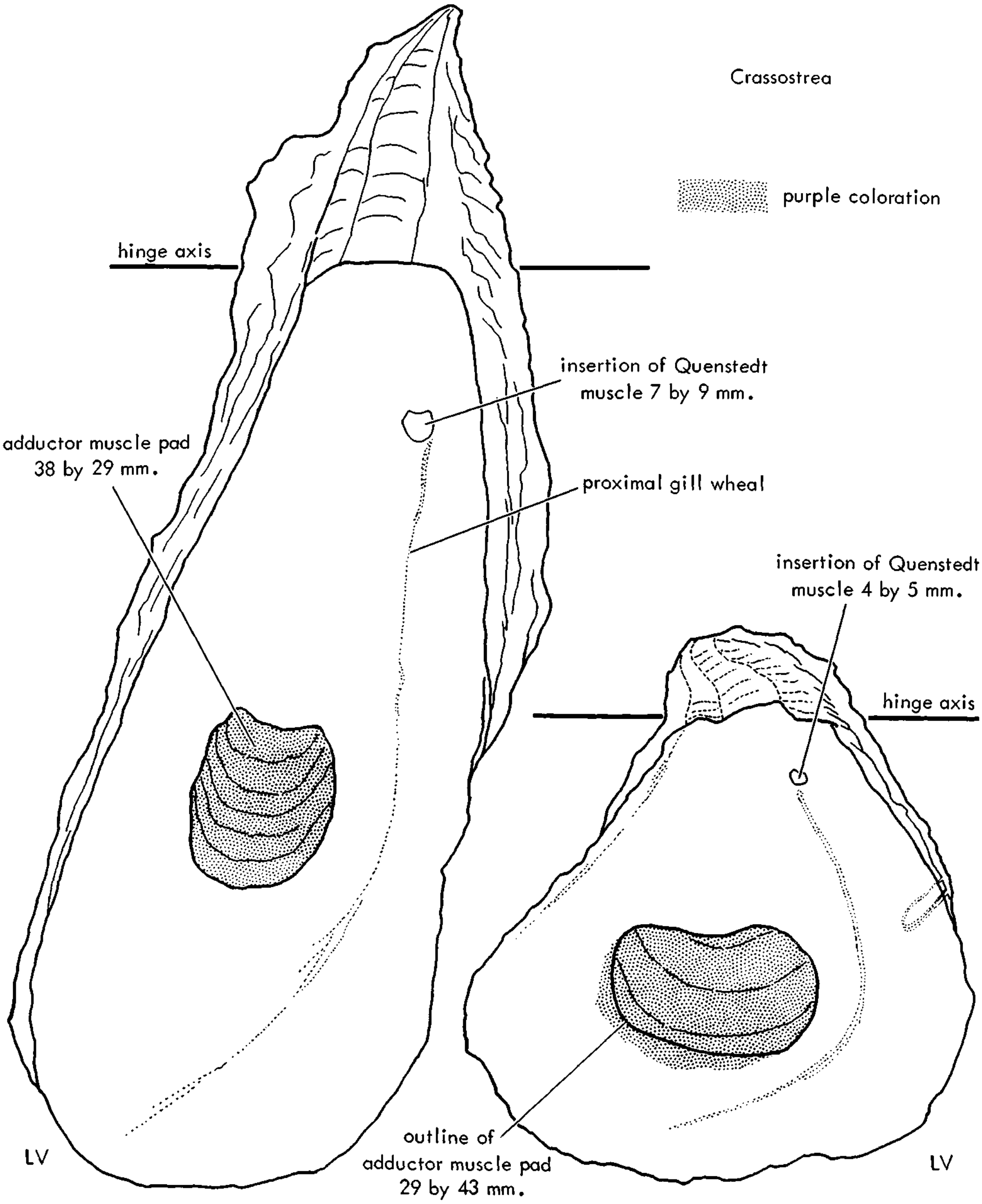

Fig. J8. Influence of valve outline on outline of adductor muscle pad, as shown by *Crassostrea virginica* from coast of New England, USA, ×0.55 (Stenzel, n. Specimens from Branford, Conn., and Providence, R.I., in Museum of Comparative Zoology).

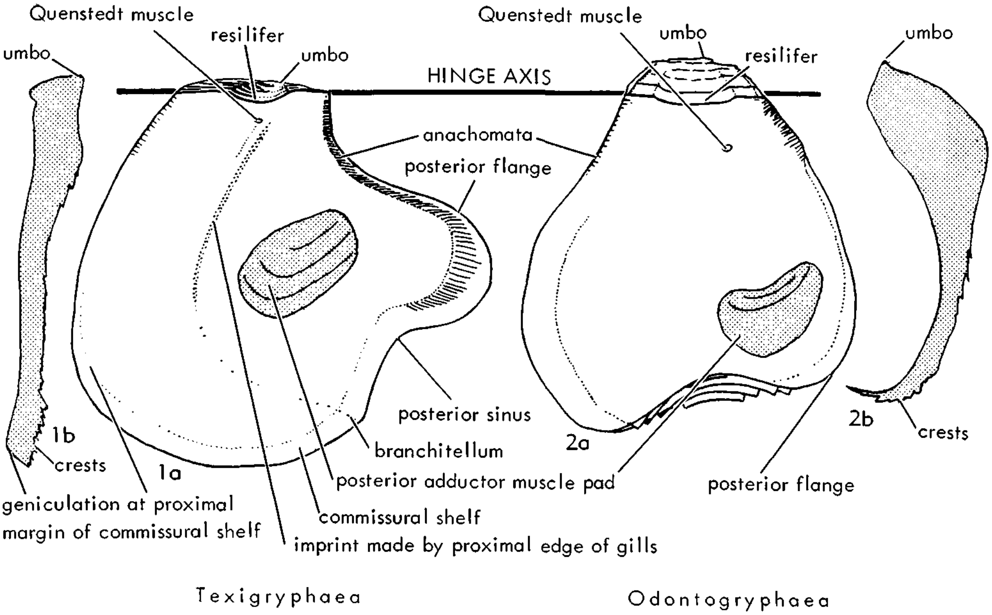

FIG. J9. Outlines and anatomical positions of posterior adductor muscle pads in RV of oysters (Stenzel, 1959).

In *Texigryphaea roemeri* (MARCOU, 1862) (family Gryphaeidae) (*1a,b*) from Grayson Marl (Cenoman.) of Texas outline of muscle pad is convex, orbicular, or oblique-oval. In *Odontogryphaea thirsae* (GABB, 1861) (*Gryphaea* homeomorph belonging in family Ostreidae) from Nanafalia Formation (Sparnac.) of Alabama (*2a,b*) it is concave or reniform.

In all studies of the adductor muscle imprints one should use only shells that have the aragonite adductor muscle pad and its surroundings perfectly preserved. In many fossil oysters the aragonite pad and the hypostracum are leached, leaving cavities that are either collapsed by rock pressure or are filled with secondary crystalline material or with sediment matrix (see Fig. J24-J26). In many Recent oyster shells the surroundings of the pad are damaged because the calcitic shell cover at the dorsal side of the imprint is very delicate. In all such cases the outline of the muscle imprints may be modified seriously.

QUENSTEDT MUSCLES

Quenstedt muscles are a pair of tiny muscles, each one attached at one end to a valve and ending with the other end among the adoral parts of the gills (Fig. J10). They were so named (STENZEL, 1963b) in honor of their discoverer. QUENSTEDT (1867, p. 598) noted a tiny muscle imprint between hinge and adductor muscle imprint on shells of *Gryphaea arcuata* LAMARCK, 1801, a common fossil of the European Liassic, but he misinterpreted it as the imprint of the vestigial anterior adductor muscle (Fig. J7-J9; see Fig. J23).

These muscles, or their imprints, have been noticed on many oyster species, fossil and living; it seems safe to assume they are present in all oysters. Being inconspicuous they have been forgotten or overlooked by many authors, only to be rediscovered several times. DALL (1880), one of the authors who rediscovered them, was the first to interpret them correctly as probably homologous with the pedal muscles of dimyarian bivalves. The best description is given in HERDMAN & BOYCE (1899, p. 10-12, pl. 2), who dissected *Crassostrea virginica* (GMELIN, 1791 [1790]), a species living on the east and south coasts of North America (Fig. J10).

Each muscle is thickest at its insertion on the valve and thins as it extends inward. It rises at about 50° from its insertion, extends obliquely in ventral direction,

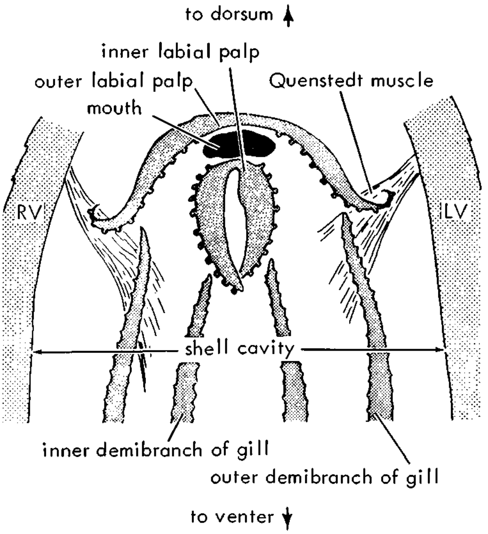

Fig. J10. Diagram depicting anatomical position of the two Quenstedt muscles in *Crassostrea virginica* (Gmelin), viewed looking in anteroposterior direction (mantle lobes and visceral mass omitted) (after Herdman & Boyce, 1899).

passes close to the bottom of the groove that separates the mantle fold from the outer labial palp, turns forward and splits to spread out mostly among the connective tissues between the inner and outer lamellae of the outer demibranch at the dorsal or adoral end of the gills. The insertion of the muscle on the valve is quite near the position of the animal's mouth. Thus Quenstedt muscle imprints come close to revealing in fossil species where the animal's mouth was located.

Although the two opposing Quenstedt muscles of an oyster converge toward the commissural plane and come close to each other, they do not merge. Each one is firmly attached to its valve and no mantle epithelium separates the muscle fibers from the valve as is also true for the posterior adductor.

Quenstedt muscles are modified anterior pedal muscles *(protractores* or *elevatores pedis),* now modified to perform a totally different function, because adult oysters have no trace of a foot left. Probably they adjust the positions of the dorsal, or adoral, ends of the gills and of the labial palps and aid in the transfer of food particles from gills to mouth. It is inadvisable to call them pedal muscles, because they no longer function as such and because it is uncertain with which particular pair of the several pairs of pedal muscles in normal bivalves they are homologous.

Many authors have interpreted them as vestiges of the anterior adductor muscle. This interpretation is regarded as erroneous for several reasons. They are not continuous from one valve to the other and they are not rectilinear; the anterior adductor should be continuous and rectilinear. They reach the adoral tip of the gills, that is, the region ventral of mouth and esophagus; the anterior adductor of normal bivalves is wholly on the dorsal side of the mouth and esophagus. During evolution, it would have been a difficult feat for the anterior adductor to cross the alimentary canal from the dorsum to its venter.

CIRCULATORY SYSTEM

Detailed descriptions of the circulatory system were given by Leenhardt (1926) for *Crassostrea angulata* (Lamarck, 1819), a living oyster of southwestern Europe, and by Awati & Rai (1931) for *Saccostrea cuccullata* (von Born, 1778), which is a complex superspecies widespread in the Indo-Pacific seas.[1]

The colorless blood of oysters does not contain any respiratory pigments, and the paths taken by the blood are rather uncertain because much of the circulation is through irregular intercommunicating blood sinuses, that is, blood-filled gaps between organs and tissues. Both conditions make for a rather inefficient circulatory system.

A blood-filled, thin-walled sac (**pericardium**) encloses the elongate heart, which has a pair of thin-walled contractile auricles leading into a single larger ventricle sheathed with muscles. The various genera show considerable differences in the configuration of the auricles. The pericardium is on the dorsal flank of the adductor muscle, where this stout muscle protects it from damage by predators and where it is close to organs that need the best possible supply of blood (Fig. J4).

Oxygenation takes place in the gills and in the mantle lobes. Freshly oxygenated

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[1] This species was described at first (von Born, 1778) as *Ostrea cuccullata*, then the name was changed to *O. cucullata* by von Born, 1780. The earlier spelling must stand, although it is objectionable.

blood flows from the gills and mantle lobes to the auricles and passes through valves into the ventricle. Contraction forces the blood from the ventricle into two aortas. The very short posterior aorta leads to the adductor muscle so that this muscle, which must act quickly for the survival of the animal, has a copious supply. The anterior aorta has many branches leading to blood sinuses and also supplies other parts of the animal. Two of the distal branches of the anterior aorta are the large arteries that circle along the margin of each mantle lobe (right and left circumpallial arteries). Venous blood flows back to the kidneys on one side and the gills on the other. Efferent circulation then reaches the auricles.

Circulation of the blood is helped whenever anyone of the muscles contracts, because most of them are surrounded by blood sinuses. Each time one of the muscles contracts some blood is squeezed from a sinus into other blood vessels. Such circulation is mostly oscillatory because there are no valves to direct it. Oscillatory blood movements in the mantle lobes facilitate oxygenation of the blood. In this way the mantle lobes become important to the respiration of the oysters.

NERVOUS SYSTEM

The nervous system of *Crassostrea angulata* was described by Leenhardt (1926) and that of *Saccostrea cuccullata* by Awati & Rai (1931).

The central nervous system of an adult oyster consists of loops of nerve strands connecting two pairs of ganglia. The smaller, dorsal pair (cerebropleural ganglia) is between the bases of the labial palps, and each arises from the fusion of two ganglia in the larva. They innervate mouth, stomach, and dorsal parts of gills and mantle lobes. The larger, ventral pair of visceral ganglia is at the adductor muscle and innervates the adductor muscle, nearly all the visceral mass, and most of the gills and mantle lobes. This pair grows to be the chief nerve center of the adult; it receives the nerves coming from the sense organs and sends out nerves to those muscles that must react quickly to outside stimuli, that is, the adductor muscle and the pallial muscles.

It is noteworthy that in the oysters the cerebral ganglia are no longer connected to chief sense organs of the animal, because like all the Bivalvia oysters are encased by a protective shell and have lost their heads and cephalic sense organs. It is also noteworthy that, unlike other Bivalvia, the adult oysters have lost all traces of a foot, including the pedal ganglia. This is a consequence of their immobilization.

GILLS AND MANTLE/SHELL

GILLS

The two gills, or branchiae, together form an elaborate strainer structure partitioning the mantle cavity into an inhalant and an exhalant mantle chamber. They are placed so that water cannot flow from one chamber into the other without passing through countless tiny holes, or ostia, of the gills.

The tip of the gills is between the labial palps, a short distance ventral of the mouth. They curve convexly and subparallel to the valve margins and end at the **palliobranchial fusion,** where the end of the gills and the two opposing mantle lobes are united (Fig. J4).

The gills are made of two pairs of demibranchs, one pair at each side of the animal. Each pair of demibranchs is composed of four lamellae joined in form of a W. However, the W is asymmetrical, because the inner two of the four demibranchs are wider, and the left inner demibranch is the widest of all four. In the mid-line the two gills are united by their adjacent edges, and the proximal edge of the outermost lamella of each gill is united with the adjacent mantle lobe. In this fashion the gills separate inhalant from exhalant chamber, leaving the mouth, surrounded by its four labial palps, to open into the inhalant chamber.

The gills carry many microscopic cilia which whip the water driving it through the ostia from inhalant to exhalant chamber. The cilia establish the water current.

MANTLE

The mantle is the soft tissues of the mantle/shell, which completely encloses the adult oyster when it has shut the mantle/shell. On the visceral mass the mantle forms merely a surface membrane, but peripherally to this mass the mantle extends to form two lobes (**mantle lobes** or **pallial lobes**). The two mantle lobes reach to the valve margins and are completely free of each other, except at two places: 1) along the hinge, where they join in the **mantle isthmus** and form a sort of cowl over the mouth and the dorsal ends of the labial palps and 2) at the place of palliobranchial fusion located at the posteroventral edge of the valves.

The mantle lobes of an adult oyster are thick and somewhat solid. They lack the large blood sinuses found in those Bivalvia that have a large active foot and open their valves partly by hydrostatic pressure of the blood in these sinuses.

Peripherally the margins of each mantle lobe carry three parallel small folds. The inner one is the highly mobile **pallial curtain,** well supplied with muscles and blood sinuses, carrying tentacles at its free edge. The middle one is the **tentacular fold** and has many tentacles of two sizes, disposed in two rows at its free edge. The outer one is the **shell fold** and is separated from the tentacular fold by the periostracal groove; lacking tentacles, it lies directly on the surface of the valve. In the periostracal groove, at the base of the outer fold, are the periostracal glands exuding a sheet of conchiolin which is the base layer of the periostracum.

The outer face of each mantle lobe rests loosely on the inner face of the adjoining valve. Along the valve margin this space is closed off from the surrounding sea water by the periostracum, which breaks easily. Firm attachments between shell and soft parts are provided only at those few places where muscles are inserted on the valves, that is, at the insertions of adductor muscle, Quenstedt muscles, and some pallial retractor muscles. The narrow space between mantle lobe and shell wall is called the **extrapallial space;** it is filled with a mucus-laden liquid secreted by various gland cells in the mantle epithelium. It is in this space that deposition and growth of the shell take place.

MANTLE MUSCULATURE

The mantle lobes have many muscle strands, some arranged in concentric and others in radial patterns. They are well developed at the valve margins where the pseudosiphons form.

The radial muscle strands serve as **pallial retractor muscles** and extend within the mantle lobes from the vicinity of the visceral mass out to the margins of the mantle lobes, where some of them end in the tentacles on the mantle folds. Each of these muscle strands is surrounded by a pulsating blood sinus. Near the margins of the mantle lobes, in particular, the strands and their surrounding blood sinuses tend to show as radial ridges on the outer face of the mantle lobes. Some of the configuration of the shell at the periphery of the valves may be caused by these ridges (JAWORSKI, 1928).

The **pallial line** on the inner face of the valves of isomyarian bivalves is a continuous or nearly continuous line, of nearly uniform width, extending from one adductor muscle insertion to the other and is made from the coalescent insertions of many radial pallial retractor muscles. These muscles extend within the mantle lobe from the pallial line radially outward to margins of the lobe. When they contract, they withdraw the margins so that the two valves can be closed tightly without any part of the mantle lobes being caught between the two valves.

The anisomyarian bivalves have a **disjunct pallial line.** Their mantle retractor muscles are inserted on the valves in bunches of unequal sizes, producing a series of unequal muscle insertions lined up in a crude sequence from one adductor muscle insertion to the other.

In most oyster genera, there is not even a crude sequence of separate muscle insertions, because the retractor muscles begin and end within the mantle lobes. In *Ostrea* and *Crassostrea,* for instance, the mantle retractor muscles that extend to the anterior edge of the mantle lobe are few and thin; their proximal beginnings are near the gills. Those pallial retractor muscles that extend to the ventral edge of the mantle lobes are more numerous and thicker; their proximal beginnings are inserted within the mantle lobes around the ventral flank of the posterior adductor muscle.

Only in one genus (e.g. *Saccostrea*) are the mantle retractor muscles attached directly to the valves and a disjunct pallial line very similar to that of anisomyarian bivalves is developed. As far as this one feature is concerned, this genus is more archaic than other oyster genera, because it still retains the disjunct pallial line of the anisomyarian ancestors of the oysters (Fig. J7; see Fig. J105,*2b, 2d*).

INHALANT MANTLE CHAMBER

The **inhalant** (or incurrent or infrabranchial) **mantle chamber** is simpler in configuration and about four times larger than the other chamber. At the distal margin it is closed at times by the opposing pallial curtains of the mantle lobes along the anterior and ventral valve margins (Fig. J2, J4). On the right and left sides the two mantle lobes enclose it. On the proximal side are the gills, mouth and labial palps. It reaches in a roughly crescentic shape from the mantle cowl and mantle isthmus at the hinge to the palliobranchial fusion.

EXHALANT MANTLE CHAMBER

The **exhalant** (or excurrent or suprabranchial) **mantle chamber** has several special passages and is more complex than the inhalant one.

The gills contain four passages at their adoral end. Each is enclosed by the wall of the visceral mass on one side and by two lamellae of a demibranch on the other. The passages are closed off at the tips of the gills but in the other direction they widen into two larger passages, each of which is enclosed by the wall of the visceral mass and by the four lamellae of a gill. The two branchial passages open into the cloacal passage, which curves around the ventral flank of the adductor muscle and opens into the main part of the exhalant mantle chamber, lying along the posterior valve margin.

The **cloacal passage** receives excretions of the kidneys and genital products from the pair of urogenital clefts on the visceral pouch. The anus projects into the cloacal passage well downstream from the urogenital clefts.

Another **(promyal) passage** was first noted by KELLOGG (1892, p. 396-397). NELSON (1938) was the first to recognize its significance and to elucidate its function. It was named by him the promyal chamber and distinguished by him from the "opisthomyal exhalent chamber," which is here called the cloacal passage of the exhalant chamber. The position taken here is that the oysters, in common with many other Mollusca, have only two mantle chambers, the exhalant and the inhalant one. All others are merely subdivisions, that is, passages.

The promyal passage is present in one group of living oyster genera and absent in another group (Fig. J11). Unfortunately not all living genera have been investigated in this respect so that information is not as securely founded as might be wished. The genera that have a promyal passage are the nonincubatory genera (e.g., *Crassostrea, Hyotissa, Neopycnodonte, Saccostrea, Striostrea*). Genera that lack a promyal passage are incubatory (e.g., *Alectryonella, Lopha, Ostrea*) (Fig. J11).

The promyal passage separates the right mantle lobe from the visceral mass over the region of the pericardium and between the adductor muscle and the hinge. It connects the branchial passages directly with the main part of the exhalant chamber and bypasses the cloacal passage, allowing an efficient disposal of the waste water current from the gills. There is no counterpart to it on the left side.

SENSE ORGANS

Adult oysters have but few kinds of sense organs: sensory cells in the epithelium of gills and mantle lobes, tentacles at the edges of two of the three mantle folds, and a pair of chemoreceptors in the cloacal passage. The last are asymmetrical; the one on the right side is the larger (AWATI & RAI, 1931, p. 73) and can be seen with the naked eye; the left one is often overlooked (PELSENEER, 1911, p. 27; ELSEY, 1935, p. 152). This heritable anatomical asymmetry indicates that oysters are permanently adapted to a pleurothetic attitude and cannot change from attachment on the left to attachment on the right side.

HARD PARTS

The hard parts of the mantle/shell are the **ligament** and the **shell,** which has two unequal valves. They consist of three organogenic substances: 1) calcite, an allomorph of calcium carbonate crystallizing in the rhombohedral system; 2) aragonite, another allomorph of the same substance, crystallizing in the orthorhombic system, and 3) conchiolin, a complex organic sub-

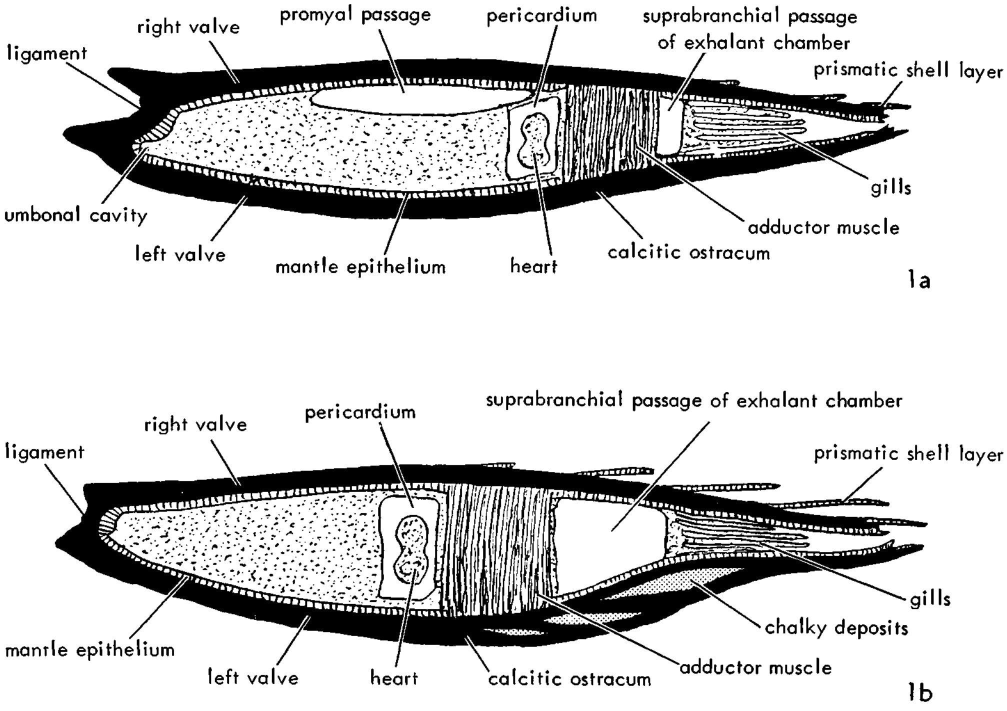

FIG. J11. Anatomical differences between nonincubatory and incubatory oysters, as exemplified by *Crassostrea* and *Ostrea* (from Korringa, 1956).

1a. Crassostrea, a nonincubatory oyster.
1b. Ostrea, an incubatory oyster.

[Diagrammatic sections are approximately along mid-line of shell from umbo at left to ventral margin at right.]

stance containing a mixture of mucopolysaccharides, polypeptides, and scleroprotein fractions. The three organogenic substances are found in different proportions in the various hard parts of the oyster.

Conchiolin is the chief or even exclusive component of the periostracum, the conchiolin scales, lamellae, and fringes of the valves, the ligament, and the delicate internal supports in the gills. Conchiolin is also present in small amounts within the calcareous parts of the valves. A filmy conchiolin network of microscopic thickness envelops each crystal of calcite or aragonite within the valves. As long as this conchiolin film remains untouched by decomposition, it protects the enclosed calcium-carbonate crystals from leaching. The structure of conchiolin matrix and calcium-carbonate enclosures is so tight that permeating water and invading bacteria are kept out and leaching or bacterial decay are retarded.

The amino acids of conchiolin in *Crassostrea angulata* (LAMARCK, 1819), a living species of southwestern Europe, are in percent of total protein: arginine 0.45, histidine 0, lysine 3.55, glycine 15.70, leucine 0.51, tryptophan 0, tyrosine 3.27, valine 0.95, cystine 0, and methionine 1.77. Those of *Ostrea edulis* (LINNÉ, 1758), a species living from Norway to Morocco, are: arginine 2.90, histidine 0.65, lysine 4.30, glycine 15.70, leucine —, tryptophan 0.47, tyrosine 3.05, valine —, cystine 0.98, and methionine 1.62 (ROCHE, RANSON & EYSSERIC-LAFON, 1951).

LIGAMENT

The ligament is strong and flexible within limits. It permits the bivalve to open or shut its two valves. Most Bivalvia have a hinge plate on each valve furnished with interlocking teeth and sockets. So does the oyster larva. However, the adult oyster lacks hinge plates, teeth, and sockets, and no

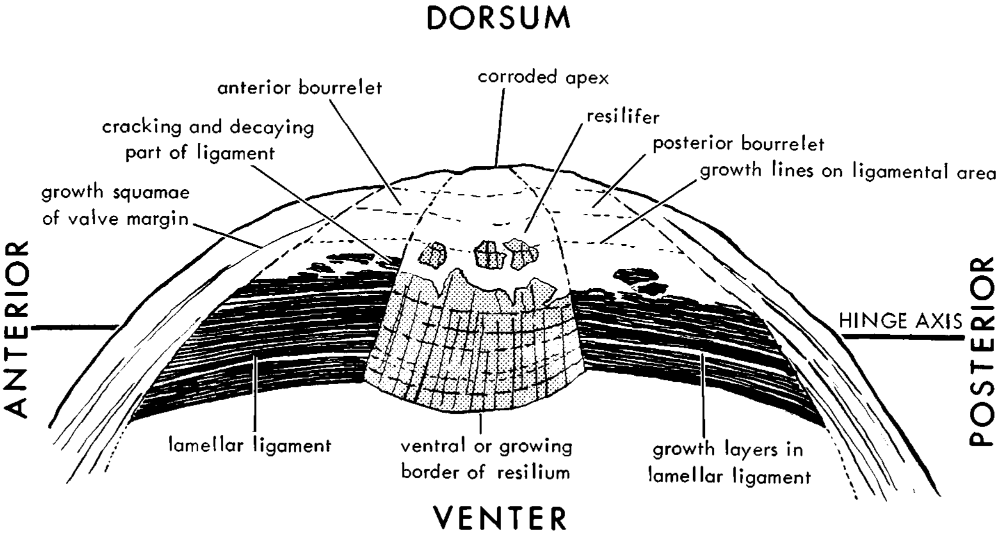

FIG. J12. Ligament and ligamental area on RV of *Ostrea edulis* LINNÉ (Stenzel, n).

vestiges of them are left. Thus the ligament is the sole hinge structure remaining on adult oysters.

The ligament of adult *Ostrea edulis* has been described by BERNARD (1896), RANSON (1940b), and TRUEMAN (1951). It is less modified than that of other genera, for example, *Exogyra,* and serves here as a model (Fig. J12).

It is alivincular and divided into three adjoining parts, lying side by side. 1) The **resilium** (=fibrous ligament of NEWELL, 1937, =inner layer of TRUEMAN, 1951) is in the middle and is fibrous, whitish gray, and semitranslucent. Its fracture pattern is fibrous. Its very fine fibers run parallel to the height of the ligament and about normal to the ventral, or growing, border of the ligament. The fibers are crossed by some light brown growth layers. It is made of naturally tanned protein complexes enclosing very fine white fibers of aragonite (STENZEL, 1962). These white fibers produce the whitish gray overall color. Under compressive stress it is strong, but under tension it is weak. 2) **Lamellar ligament** (of NEWELL, =outer layer of TRUEMAN, =tensilium of OLSSON, 1961, p. 41, 42, 51) composes the two flanking parts of the ligament and is nonfibrous, dark brown, and more translucent. Its fracture pattern is conchoidal. It lacks aragonite and fibrous structure and is for that reason more translucent. It is made of quinone-tanned protein complexes and is strong under bending stresses.

Some authors have called the resilium the elastic ligament and the lamellar ligament the inelastic one. However, both are elastic and respond well to stresses. Their elastic responses are specialized to different kinds of stresses.

The valves, whenever they open or close, pivot around an axis (**hinge axis,** pivotal axis, cardinal axis) which is parallel to the ventral, or growing, border of the ligament and lies within the ligament itself, about 2 mm. from that border. In fossil oysters, which have lost the ligament through bacterial decay, the ventral border of the ligamental area suffices for locating the hinge axis. During movements of the valves, the resilium is compressed and the lamellar ligament is bent whenever the valves close. Both return to a less strained condition when the adductor muscle relaxes and the valves part. However, even when the muscle is relaxed in a living oyster, the ligament remains under some compression and the valves do not open very wide. Only if the muscle is cut do the valves open really wide.

The ventral border of the resilium juts out a little into the shell cavity; the project-

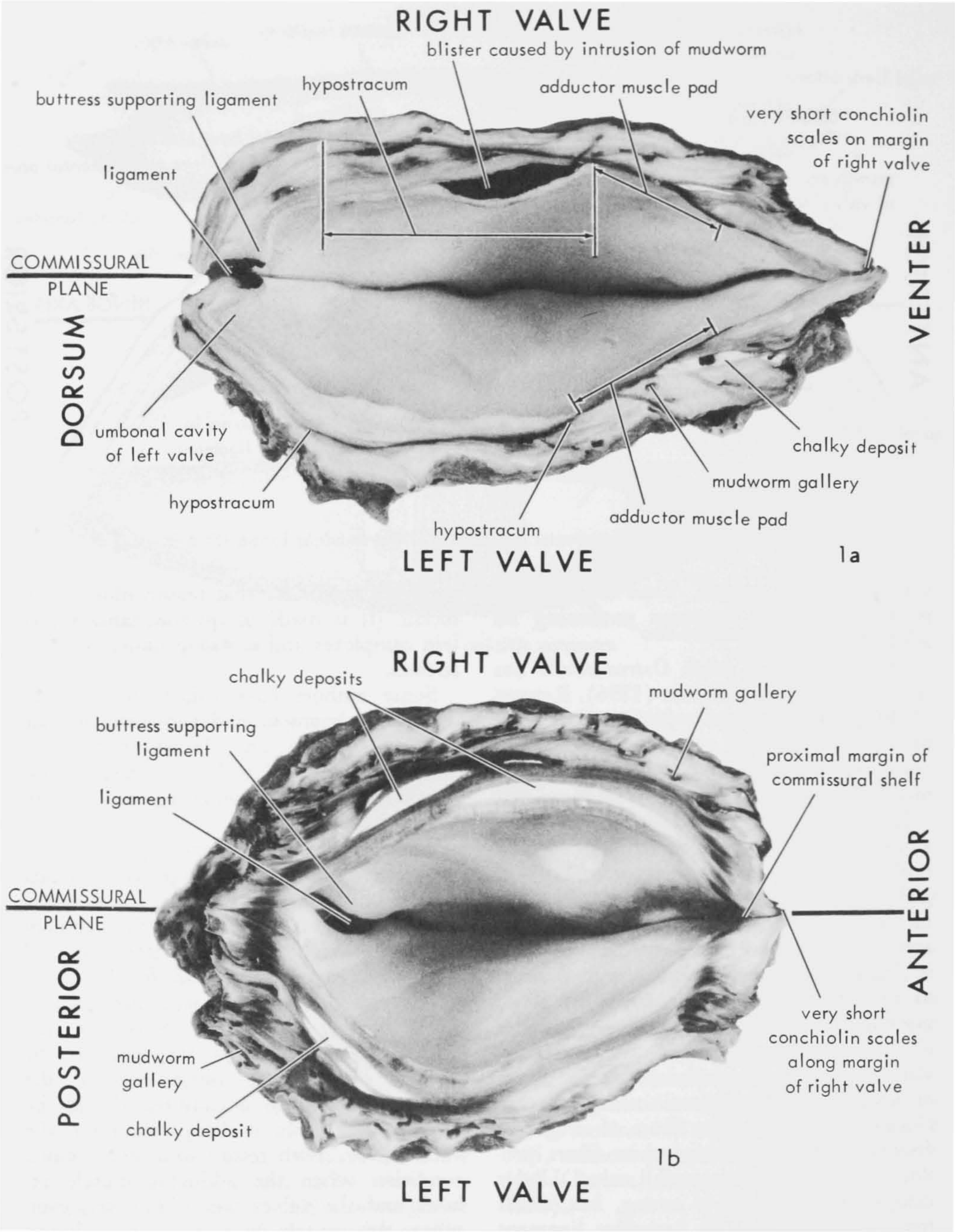

FIG. J13. Sections through shell of *Crassostrea virginica* (GMELIN), specimens from coast of Texas (Stenzel, n).

1a. Dorsoventral section, viewed looking toward anterior edge of shell, ×1.3.

1b. Anteroposterior section, viewed looking toward hinge which is visible at end of shell cavity.

[In this species a purple-colored layer lies immediately beneath the hypostracum so that the latter shows on the photographs as a dark line ending with the adductor muscle pad.]

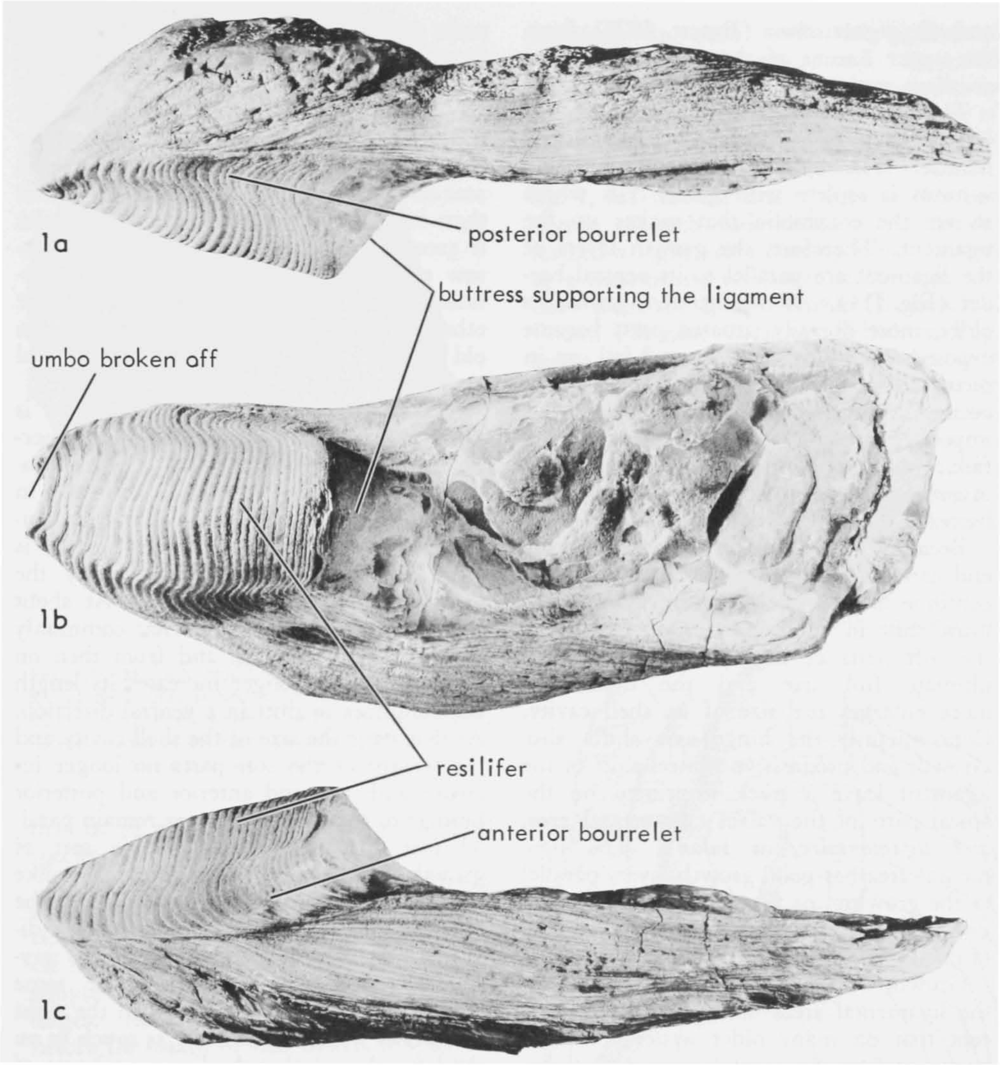

FIG. J14. Umbonal region of RV of *Crassostrea titan* (CONRAD, 1853), Mio., USA(Calif.), showing annual growth layers. [Specimen furnished by courtesy of U. S. GRANT and TAKEO SUSUKI, Univ. California (Los Angeles).]

1a-c. Posterior side, view from left, anterior side, ×0.4 (Stenzel, n). Specimen somewhat weathered and corroded, ventral part missing. Annual growth layers of ligamental area indicate that animal was 33 years old at cessation of growth.

ing part of the resilium of the right valve is strengthened by a supporting **buttress** rising from the right valve (Fig. J13). Through this arrangement the newest and best part of the resilium is placed in the inside of the shell cavity, that is, ventral to the hinge axis. There it becomes subject to compression greater than that of the rest of the ligament. Thus the resilium has improved leverage to open the valves whenever the adductor muscle relaxes. In those oysters which have a particularly great compressive load to overcome when they open their valves, the supporting buttress is outstanding and the ventral border of the resilium is strongly convex. Very good examples are found in the giant elongate oyster shells of certain species of *Crassostrea,* for example, *C. gryphoides* (VON SCHLOTHEIM, 1813) from the Miocene of the Tethyan region, and *C. gigantissima* (Finch, 1823) from the upper Eocene of the southeastern and southern states of the USA (Fig. J14).

The ligament grows only at its ventral border, the only border in contact with the mantle. The epithelium of the mantle isthmus is replete with gland cells which secrete the conchiolin that makes up the ligament. Therefore, the growth layers of the ligament are parallel to its ventral border (Fig. J14). As the ligament grows, its older, more dorsally situated parts become exposed to sea water, crack, and fall out in pieces. The deterioration is brought about because continuous mechanical employment imposed upon it induces elastic fatigue failure and cracking and because there is invasion of bacteria from the sea water and bacterial decay of the organic substance.

Because the deterioration at its dorsal end cannot be stopped, the ligament must continue to grow at its ventral margin and must shift in ventral direction, even after the soft parts of the oyster have reached ultimate full size and the oyster no more enlarges the size of its shell cavity. Concomitantly the hinge axis shifts also. Growth and progressive ventral shift of the ligament leave a track imprinted on the apical parts of the valves (**ligamental area,** *aire ligamentaire,* or *talon*). The ligamental area has good growth layers parallel to the growing, or ventral, border and may grow to great height, up to 15 cm. or so (Fig. J14; see Fig. J30).

Growth of the ligament is recorded on the ligamental areas of the two valves, except that on many older oysters the umbones, and the ligamental areas with them, are destroyed by a combination of bacterial decay and chemical corrosion (Fig. J14). The ligamental area is divided into three parts, which are growth tracks of the three parts of the ligament. The **resilifer,** in the middle, is the track of the resilium, and its ventral end is the temporarily functioning seat of the resilium during life of the animal. On each side of the resilifer are the growth tracks of the lamellar ligaments, called here the **anterior** and **posterior bourrelets.**

In their simplest forms the resilifer and the two bourrelets are triangles. These shapes are usually greatly modified by individual growth and variability and by generic and subfamilial characteristics. Configuration of the ligamental areas is a feature useful in classification. In all the genera of the Exogyrinae except two, the ligamental area is curved in a consistently regular spiral. The height of the ligamental area of the Exogyrinae is very much greater than its length, and the posterior bourrelet is greatly reduced in length to form a narrow crest (see Fig. J26). The two exceptional genera of the Exogyrinae are like the others in their earlier growth stages, but in old age they cease to have a regular spiral and the posterior bourrelet widens.

The growth and size of the ligament is and stays adjusted to the work it has to perform in lifting the upper valve. The ligament must grow in size, that is, mainly in length of its ventral border, as the load increases. In the first two years growth is rapid; beginning with approximately the third year, growth is less rapid. At about the seventh year, the oyster has commonly reached its full growth and from then on the ligament no longer increases its length but continues to shift in a ventral direction. At that stage the size of the shell cavity and the weight of the soft parts no longer increase with age and anterior and posterior borders of the ligamental area remain parallel (see Fig. J104, J105). This sort of growth gives rise to the high, straplike ligamental areas especially noticeable on the left valves of elongate oysters of great individual age. Examples are *Crassostrea gryphoides* and other species of the same genus. As a rule, the ligament on the right valve does not shift ventrally as much as on the left valve, so that the ligamental area of the right valve is nearly always less high than that of the left. The contrast between the ligamental areas on the left and on the right valve is not large in the Exogyrinae and is very large in the rudistid-like morphs of *Saccostrea* (see Fig. J104, J105).

Multiple Resilifers

More than one resilifer on the ligamental areas of a shell has been found in several unrelated species of oysters. Such individuals, while they were alive, had two or more resilia functioning side by side. Such multiple resilifers are found locally in exceptional individuals among many more normal ones that have only one resilifer,

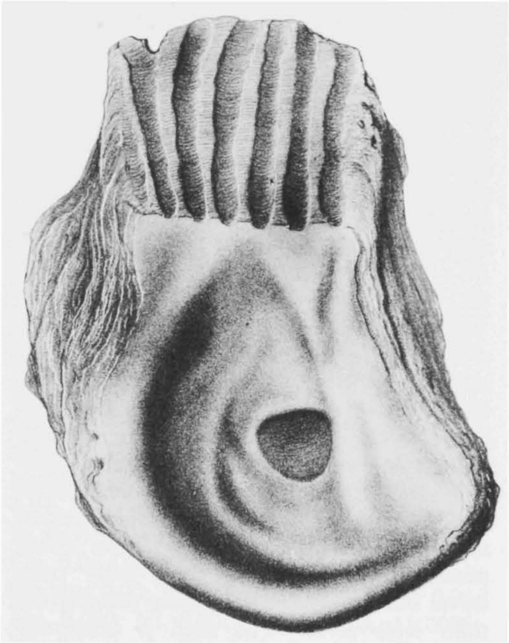

FIG. J15. Multiple resilifers and corroded umbo on RV of *Pernostrea luciensis* (D'ORBIGNY, 1850) (lectoholotype of *P. bachelieri* MUNIER-CHALMAS, 1864), Callov., Sainte-Scolasse-sur-Sarthe, France, ×0.7 (from Munier-Chalmas, 1864).

that is, in exceptional variants of a given species.

One individual of *"Ostrea" wiedeyi* HERTLEIN, 1928, from the Vaqueros Formation (early Miocene) of San Miguel Island, off the coast of southern California, had a simple, single resilium in early growth stages. Rather suddenly, about 20 years before the death of this oyster, it split into two subequal resilia. The two resilifers were small and far apart at first; they lengthened gradually and came close to coalescing before the end (Fig. J16).

A specimen of *Lopha semiarmata* (BÖSE, 1906, pl. 2, fig. 1) from the Cardenas Formation (Maastrichtian) of Cardenas, State of San Luis Potosí, Mexico, has unusually thick shell walls and a ligamental area 8 cm. high. Its resilifer divided three times in its early growth, and near the end two of the four resilifers coalesced. The animal probably lived about five years.

In the Bathonian-Callovian deposits of England and France are a few localities at which some shells of a species have been found that have multiple (up to nine) resilifers. In these shells the ligamental areas appear to be enormously elongated because the umbones are much corroded so that the early parts and the beginnings of the multiple resilifers are amiss (Fig. J15; see Fig. J78). LYCETT (1863, p. 108, pl. 34, fig. 1, 1a) was the first to surmise the true nature of such individuals when he described a right valve bearing nine resilifers as a monstrosity of *Ostrea wiltonensis* LYCETT from the Forest Marble (Bathon.) of Pound Pill near Corsham, Wiltshire, England. It had been found associated with several large and normal specimens of *O. wiltonensis*. Nonetheless, MUNIER-CHALMAS (1864, p. 75) bestowed the name *Pernostrea crossei* onto this extraordinary right valve and proposed the new genus *Pernostrea* for oysters with multiple resilifers. MUNIER-

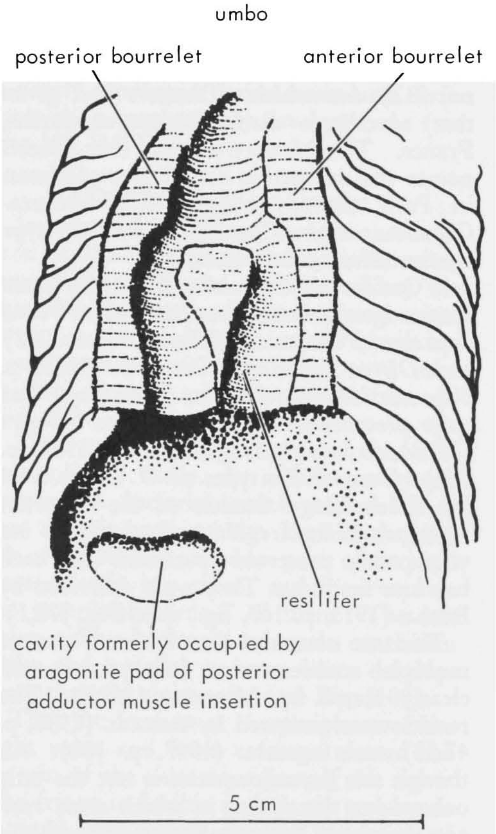

FIG. J16. Multiple resilifers in LV of specimen of *"Ostrea" wiedeyi* HERTLEIN (1928), from Vaqueros Formation (low.Mio.) of San Miguel Island, off coast of southern California, USA (Stenzel, n; specimen from Coll. San Francisco Acad. Nat. Sci.).

Chalmas described altogether six "species" of the new genus *Pernostrea,* each based on minor differences in shell outline (see Fig. J78). Most were founded on one single valve each. Three of the "species" were from the same locality. Munier-Chalmas probably coined the name *Pernostrea* because the genus *Perna* too has several resilifers and a greatly elongate ligamental area. He may have been influenced by Darwin's work to search for missing links to evolution.

Fischer (1864, 1865, 1880/87) agreed with Munier-Chalmas as to the biological validity of *Pernostrea* as a genus, but pointed out that *P. bachelieri* Munier-Chalmas, for which Munier-Chalmas had given *"Hab.? (collection de la Sorbonne)"* as the only locality information and for which Munier-Chalmas had failed to give references to an earlier name and description of the species, was nothing else than *Perna bachelieri* d'Orbigny (1850, p. 341, no. 212), for which d'Orbigny had given the locality Sainte-Scolasse-sur-Sarthe, France. The identity of the two species names and inspection of the type specimen in Paris strongly suggest that Munier-Chalmas used d'Orbigny's labeled type specimen for his description.

D'Orbigny had described the very same species from two separate localities as *Perna bachelieri* d'Orbigny (1850, p. 341, no. 212) and *Ostrea luciensis* d'Orbigny (1850, p. 315, no. 341), so that the latter name has page precedence and priority over Lycett (1863), as accepted by Stenzel (1947, p. 180). Two of the types of *O. luciensis* at the Paleontology Section of the Museum National d'Histoire Naturelle in Paris are very poorly preserved specimens and each has four resilifers. They were described by Boule (1913, p. 167, fig.) (see Fig. J78,*1*).

The true nature of these isolated cases of multiple resilifers was first proved and clearly stated by Mercier (1929). The results were reviewed by Arkell (1933, p. 47-48) and Stenzel (1947, p. 180). Although this Jurassic species is not the only one among the oysters in which arose variants furnished with multiple resilifers, it is remarkable that such variants of this species have been found in at least five places.

To summarize, the genus *Pernostrea* Munier-Chalmas, 1864, as defined by this author and Fischer is based on variants of a species which have two to nine resilifers. These variants are associated with and rarer than normal variants that have only one resilifer. The name of the species is *P. luciensis* (d'Orbigny) [=*Perna bachelieri* d'Orbigny, 1850 =*Pernostrea Bachelieri*+*P. Heberti*+*P. Ferryi*+*P. Fischeri*+*P. Pollati*+*P. Crossei* Munier-Chalmas, 1864].

SHELL

Oyster shells have two unequal valves which fit together without any gape whatsoever. Lack of a gape distinguishes the Gryphaeidae and Ostreidae from the Malleidae, some of which are quite similar and have been confounded with the Ostreidae. All oysters, except two or three species and some individuals of a few other species, are firmly attached by cementation either permanently or during their early postlarval life. They are invariably attached by their left valves. The shell is bilaterally asymmetrical and in many species highly asymmetrical. In general, most of the Gryphaeinae and Exogyrinae and many of the Pycnodonteinae are highly asymmetrical; the Lophinae approach bilateral symmetry the most (see Fig. J132, J139).

In most Bivalvia, the shell wall has four layers. The periostracum is at the outside. The hypostracum and the inner and outer ostracum are inside of the periostracum cover and compose the hard, light-colored shell substance of calcium carbonates encased in a bonding matrix of conchiolin. The **hypostracum** is deposited as a succession of aragonite pads on which the adductor and pallial retractor muscles are inserted. It divides the ostracum into an **inner** and an **outer ostracum.** The latter is between the periostracum and hypostracum; the former between the hypostracum and shell cavity. In most Bivalvia all these layers are composed of the allomorph aragonite. Oysters deviate from this scheme in many ways (Fig. J13; see Fig. J24, J25).

Chemical Composition

The shell is composed of calcium carbonates and minor amounts of conchiolin. The two allomorphs of calcium carbonate, aragonite and calcite, are present, the latter in greater abundance. Adventitious inclusions are found in cavities produced by boring parasites and consist of clay or silt. On heating, such organic components as conchiolin are burned and disappear so that oyster shells are an excellent source of high-purity lime for various industries.

A modern chemical analysis of the shell of freshly killed *Crassostrea virginica,* ground to pass a 100-mesh screen and dried at 110°C. before analysis, is as follows: loss 1000°C. (gravimetric) 43.79 and 43.77; SiO_2 (gravimetric), 1.1, 1.1, and 1.0; R_2O_3 (gravimetric), 1.1 and 1.0; CaO (gravimetric), 54.00 and 53.99; Mg (gravimetric), 0.19 and 0.20; Na (flame photometric), 0.34; K (flame photometric), 0.04; SO_3 (turbidimetric), 0.0; total halides calculated as chloride (turbidimetric), 0.02; metallic constituents (spectrochemical): Al, 0.03; Sb, 0.0; As, 0.; Ba, 0.002; Be, 0.000; Bi, 0.00; B, 0.0; Cd, 0.0; Cr, 0.001; Co, 0.001; Cb, 0.0; Cu, 0.007; Ga, 0.00; Ge, 0.0; Au, 0.0; In, 0.00; Fe, 0.09; Pb, 0.00; Mn, 0.01; Mo, 0.000; Ni, 0.001; Pd, 0.00; Ag, 0.0005; Na, 0.1; Sr, 0.; Ta, 0.00; Sn, 0.00; Ti, 0.00; W, 0.; V, 0.000; Zn, 0.0; Zr, 0.0.

Partial analyses of oyster shells, species unidentified, showed (Chave, 1954, p. 272) 1.30 and 1.80 (spectrographic) $MgCO_3$.

Several modern oyster shells have been analyzed for strontium (Asari, 1950, p. 157; Odum, 1957; Thompson & Chow, 1955, p. 32). The ratio of Sr:Ca (atoms) was found to be 1.01-1.90:1000. Fossil oyster shells (Odum, 1957; Kulp, Turekian, & Boyd, 1952, p. 707; Turekian & Armstrong, 1961, p. 1821) showed 0.81-1.83:1000. These authors were unaware that aragonite as well as calcite are present in oyster shells and that aragonite has a special distribution in them. Strontium is probably concentrated in the aragonite. It is, therefore, quite important to know which particular part of the shell was analyzed and whether the aragonite was leached in the fossil oysters or not. In the absence of any such information the data given by these authors are unreliable.

Periostracum

The periostracum consists exclusively or nearly so of conchiolin; it is very dark, horny in appearance, flexible, and resistant to leaching by sea water, but subject to bacterial decay. As long as it is intact it protects the underlying calcareous shell. It originates from two sources. The primary source is the periostracal glands located at the base of the outer one of the three folds of the mantle lobe and within the periostracal groove, the groove between the middle and the outer fold. These glands produce the outer layer of the periostracum. This layer in the oysters is a very thin, delicate, soft, hyaline, and elastic sheet. Because it is so fragile it tears easily. It is so delicate and hyaline that it is difficult to find and has been overlooked by many.

As the periostracum is secreted by the glands the sheet folds over to join the edge of the calcareous shell and to close off the extrapallial space. Deposition of the calcareous shell material takes place within the mucus-filled extrapallial space and for that reason the periostracum must come to cling to the outer face of the calcareous shell.

Among the various oysters, *Hyotissa* has a poorly developed periostracum and *Striostrea* has a very strongly developed one (see Fig. J85, J107).

Conchiolin Scales and Lamellae

In many of the oysters, margin and outer face of the right valve carry imbricating conchiolin scales and lamellae. They are thin, flexible, elastic, delicate, olive-green to dark brown, semitranslucent to horny appearing. Each of them is 0.5 to 1 mm. thick at the base and tapers to its free end (Fig. J7).

They are not firmly attached to the valve and split off easily. In addition, they are exposed to bacterial attack and decay so that they do not last long. Even during the life of the animal, the older parts of the shell have already lost them, and fossil oysters are completely devoid of them. The left valve either is devoid of such conchiolin scales and lamellae or has a lesser development than the right valve (see Fig. J107).

They are freshest at the periphery of the right valve and form a fringe around the margin of the calcareous part of the valve. The fringe is flexible and elastic and bends to mold itself tightly onto the inner face of the slightly larger left valve providing a water-tight closure when the shell is shut.

Douvillé (1920) and Astre (1922, p. 163) pointed out that many fossil oyster species have a right valve that is smaller than the left, which extends much beyond the periphery of the other valve (Fig. J17; see Fig. J117,*1a*). They explained this phenomenon by postulating that the right valve of these species had originally a very extensive conchiolin fringe reaching to the periphery of the left valve but that this fringe was lost post-mortem. The discrepancy in the size of the calcareous portions of the two valves is great in *Ostrea* and closely related genera. Examples are *Cubitostrea wemmelensis* (Glibert) (1936, p. 60-63, pl. 2, fig. 4a) from the Wemmel Sands (early Barton.) of Belgium and *C. petropolitana* Stenzel & Twining (Stenzel, Krause, & Twining, 1957, pl. 11, fig. 10) from the Stone City beds (middle Eocene) of Texas, which have quite small shells but have the right valve 8 to 15 mm. shorter than the left (Fig. J17). These conchiolin scales and lamellae can be called part of the periostracum.

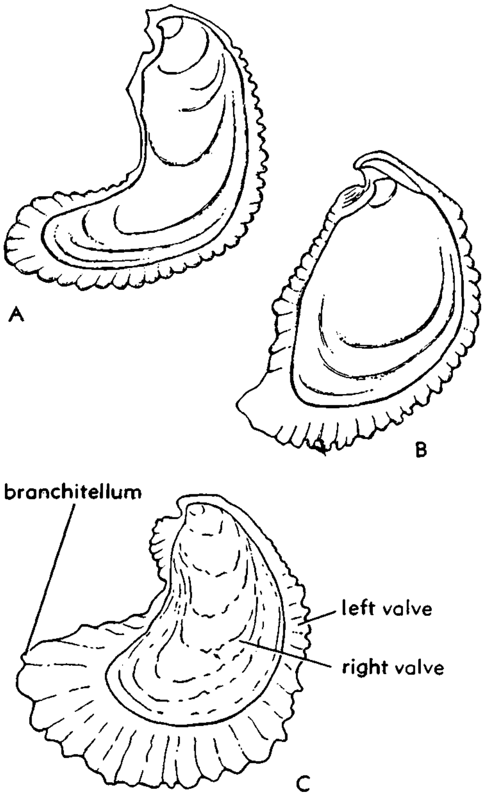

Fig. J17. Size discrepancy of calcareous portion of valves in fossil oysters revealed after decay of conchiolin fringe on RV, as shown in *Cubitostrea,* from Eoc. (Auvers.-Barton.), ×1 (Glibert, 1936).—*A. C. cubitus* (Deshayes, 1832), Paris basin, France.—*B. C. plicata* (Solander in Brander, 1766), Hampshire basin, England.—*C. C. wemmelensis* (Glibert, 1936), Sables de Wemmel, Belgium.

Prismatic Shell Layer

The flexible conchiolin scales merge at their bases into rigid calcareous layers of equal thickness. Although the two are continuous, the transition between the distal conchiolinous and the proximal calcareous part of a layer is quite abrupt. The calcareous part is composed of closely packed parallel prisms of calcite in a matrix of conchiolin. The prismatic layers are less opaque and contain more conchiolin than the other calcitic layers of the shell wall. If one dissolves the calcium carbonate with the aid of a chelating agent, the residue is a delicate coherent honeycomb of conchiolin (see Fig. J19, J20, J73, J109, J113).

Under the petrographic microscope (Schmidt, 1931) the prismatic layer of *Ostrea edulis* is seen to consist of long prismatic calcite units enveloped by a thin wall of conchiolin (Fig. J18, J19). The calcite units have the shape of parallel, curved, tapering prisms and have irregular polygonal cross sections of various sizes. The tapering curved ends are at an inclination of about 45° to the outer face of the prismatic layer and their taper points toward the outer face. As a prism unit is traced from its tapering outside point toward the interior of the shell cavity, it bends convexly away from the margin of the right valve and in doing so it achieves gradually a steeper inclination angle to become nearly vertical with reference to the shell wall. Simultaneously the size of the cross section increases, because there is more space available for each prism unit. The prism units evidently did not grow at a uniform rate; for there are darker growth layers that transect uniformly a great many neighboring prisms and are parallel with the inner face of the layer.

Each prism is one crystal of calcite. Most of them have the main optic axis (axis c) approximately normal to the layer. However, the optic axis changes attitude gradually from one end of the prism to the other. There are a few prisms that have a different orientation of the optic axis (Fig. J19, J20).

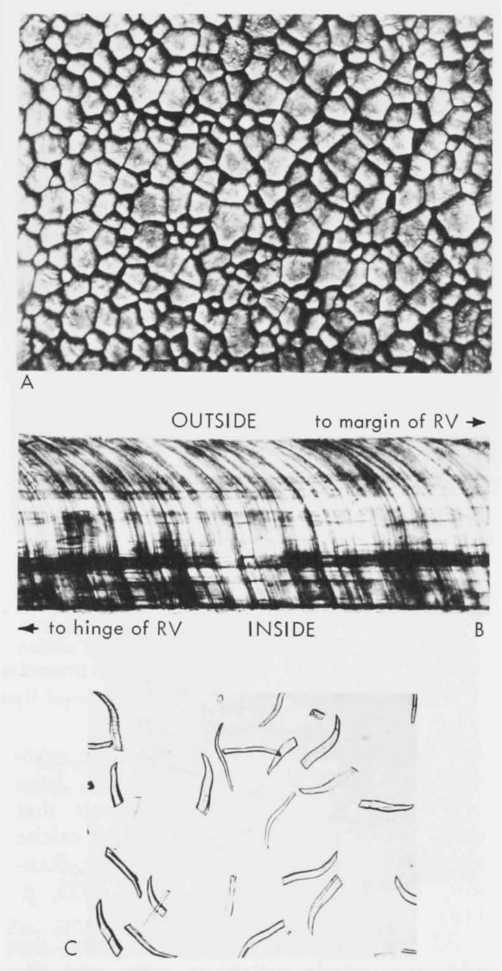

Fig. J18. Prismatic shell layer in oyster shells as exemplified by RV of *Ostrea edulis* Linné (from Schmidt, 1931).—*A*. Horizontal thin section through layer, ×185.—*B*. Vertical thin section through layer, ×185.—*C*. Individual calcite prisms, ×48.

Size and shape of the prism units show considerable differences from genus to genus (Ranson, unpublished data). *Ostrea* has prisms that are more curved than those of *Crassostrea,* which are long, straight, sharp and needle-like. *Flemingostrea* has very long conspicuous prisms (Fig. J20; see Fig. J124). *Hyotissa* does not have any, but *Neopycnodonte* has. As a rule, genera that have well-developed conchiolin scales and lamellae also have well-developed calcite prism layers.

Several oysters that have prominent conchiolin lamellae and calcite prism layers also have many fine delicate radial riblets on a surficial layer of the right valve (Fig. J21). This layer is thin and delicate and flakes off readily. In fossil species only a few exceptionally well-preserved specimens retain it on the outer face of the right valve (see Fig. 107,*1c*). Commonly the layer is dark-colored because it is either made entirely of conchiolin or is a prismatic calcite layer rich in conchiolin. Riblets are restricted to this surficial layer, and the immediately underlying, more calcareous and lighter-colored layer shows a faint trace of them at best. Because of its delicate consistency the riblet-bearing layer is better preserved in very young and still fragile oyster shells and dehisces in older individuals. Old individuals may show riblets only on the marginal conchiolin fringes.

The riblet-bearing surficial layer is well developed in young individuals of *Striostrea margaritacea* (Lamarck, 1819); this living species of East Africa is the type species of *Striostrea* Vyalov, 1936 (see Fig. J107, J108). Korringa (1956, p. 34-35) indicated that this layer is well developed on very young individuals, 17 mm. or less high, and makes it possible to distinguish them from young individuals of other, sympatric oyster species. Deshayes (1860-66, v. 2, p. 106) described the riblet-bearing surficial layer of *Striostrea(?) lamellaris* (Deshayes) in detail under the redescription of *Ostrea lamellaris* (Deshayes, 1832) (in Deshayes, 1824-37, v. 1, p. 372, pl. 54, fig. 3-4). [The type locality of this species is in doubt, and there may be some confusion as to it and other species between the two works of Deshayes; the original description was based on only the right valve; it is probably from the Bartonian of the Paris Basin.] *Striostrea alabamiensis* (Lea) [=*Ostrea lingua canis* Lea, 1833 (=*O. pincerna* Lea, 1833, p. 91-93, pl. 3, fig. 71-73)] from the Gosport Sand (Auvers.), Claiborne Group, of Claiborne Bluff, Ala., has these riblets which were shown but not explained by Harris (1919, p. 8, pl. 1, pl. 2, fig. 1-3, pl. 6, fig. 1, not pl. 3-5, see particularly pl. 6, fig. 1).

Hypostracum

In the Bivalvia the hypostracum is deposited as a succession of thin pads of ara-

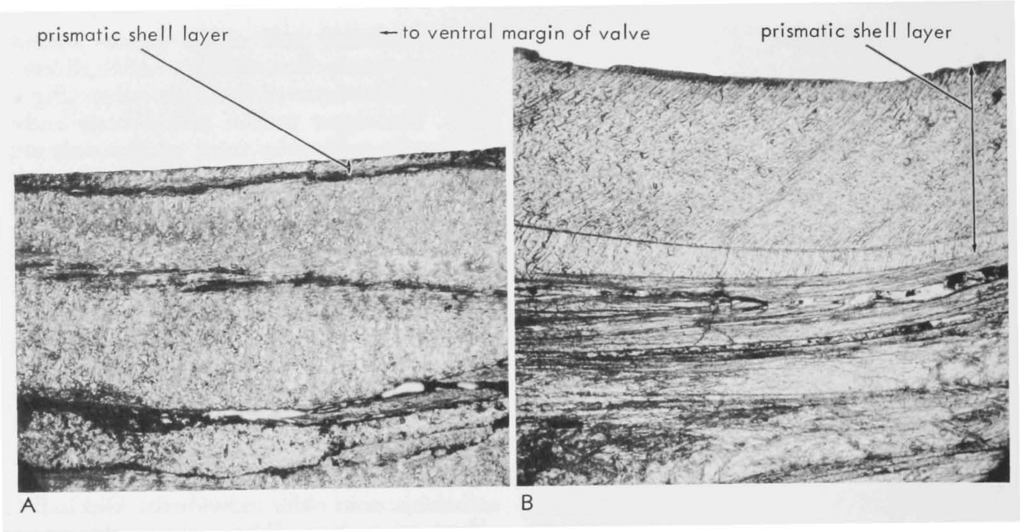

Fig. J19. Prismatic shell layer in oysters, ×21 (Stenzel, n).

A. Parlodion peel on outside face of RV of *Pycnodonte* sp. from Saratoga Chalk (Maastricht.) near Washington, Hempstead County, Ark. USA. [Prism layer is 0.1 mm. thick.]

B. Thin section on outside face of LV of *Flemingostrea subspatulata* (Forbes, 1845) from Ripley Formation (Maastricht.) of Braggs, Lowndes County, Ala., USA. [Prism layer is 1.35 mm. thick. Specimen by courtesy of Ernest E. Russell, Miss. State Univ.] [Peel and thin section made under supervision of Otto Majewske, Shell Development Co.]

gonite, stacked up one on another, on the last one of which the adductor and various pallial muscles are inserted. The hypostracum of the oysters is modified very much, because they have only one adductor muscle and few, if any, pallial retractor muscles attached to the shell wall. Thus, the hypostracum of most oysters is reduced to only one element, the succession of pads on the last of which the posterior adductor is inserted. It might be better to call it the **adductor myostracum** (Oberling, 1955a,b, 1964) (Fig. J13, J22).

The pad, or the muscle imprint, can be recognized on fresh shells of modern species by its slightly greater translucency, by its color, which in many species differs from that of the surrounding valve, by its luster, which is mostly brighter and more glistening, differing from that of the rest of the valve, and by its own special growth lines. The growth lines are very fine and subparallel to the ventral margin of the pad (Fig. J7; see Fig. J27, J31, J44).

The last pad and the entire adductor myostracum of the oysters are made of aragonite, whereas the surrounding parts of the valve are made of calcite (Stenzel, 1963b). The fact that the adductor myostracum is made of aragonite has been overlooked generally and statements that oyster shells are made entirely of calcite are erroneous (Bøggild, 1930, p. 30; Ranson, 1939-41, p. 469; Galtsoff, 1955, p 118).

As the oyster shell grows in size, the adductor muscle too must grow and the area of the pad must increase. In addition, the muscle must shift position in ventral direction in order to retain its relative location in the shell cavity. Therefore, additional aragonite is deposited on the ventral side of the old pad, new muscle fibers grow onto it, and simultaneously a dorsal part of the pad is vacated by the muscle and covered by freshly deposited calcite (Fig. J23). The first deposit at the dorsal side may be hyaline and exceedingly thin, but additional calcite soon piles up over it. For this reason the growth lines of the pad are parallel only to its ventral border and the hypostracum is buried in calcitic shell material except at the muscle.

If one were able to remove the entire adductor myostracum from a valve, one would see a thin curved sheet of aragonite

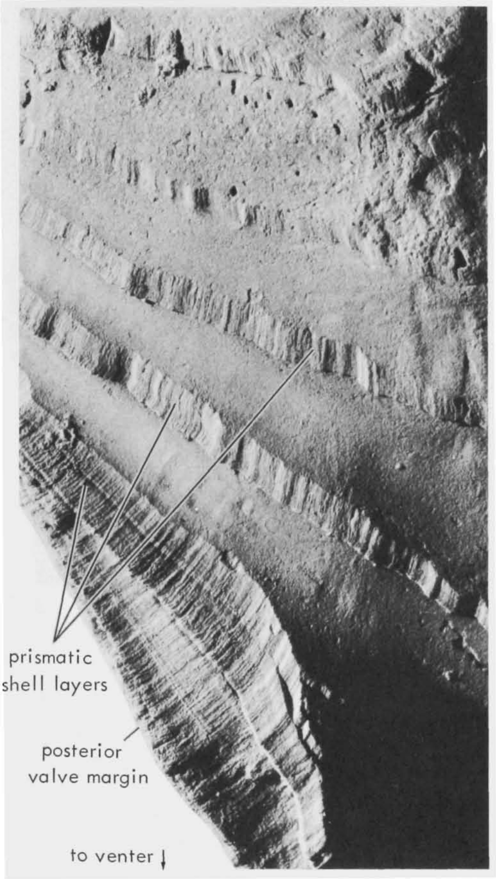

Fig. J20. Prismatic shell layers in *Flemingostrea.* Posterior slope of exterior of RV of *Flemingostrea subspatulata* (Forbes, 1845) from Ripley Formation, U. Cret. (Maastricht.), near Braggs, Lowndes County, Ala., showing prismatic shell structures at the broken ends of several successive growth squamae, ×2 (Stenzel, n).

in the shape of a slender and acute triangle with a convexly curved base line. The base line is the ventral border of the last pad and the tip of the triangle is at the prodissoconch. The plane of the triangle is curved to conform with the dorsoventral curvature of the valve. In the Exogyrinae the adductor myostracum is curved in a spiral conforming with the spirality of the valve. If a shell of an exogyrine oyster is cut normal to the commissural plane the hypostracum is seen to spiral in and out of the cut surface and may be cut twice along its path (Fig. J24, J25).

The hypostracum of dead or fossil oyster shells is prone to selective leaching, because it is made of aragonite and surrounded by calcite. Aragonite is the less stable of the allomorphs of calcium carbonate. Instead of the hypostracum, many fossil oysters have either a cavity (Fig. J26) or a filling composed of fine-grained sediment or a filling of secondary minerals, for instance, crystals of calcite (Fig. J22). In the second case, the hypostracum was leached selectively before the surrounding oozy sediment had a chance to solidify so that it could flow into the cavity (Fig. J24). This is common in chalks and marls. In the last case, the surrounding sediment either had already solidified before the leaching could take place or consisted of a sediment too coarse to penetrate into the cavity or the cavity was so narrow that the sediment could not penetrate. Wherever oyster-bearing sediments do not contain any aragonitic fossils (isomyarian bivalves, gastropods, scaphopods, ammonites, or others), it is most likely that selective leaching of aragonite has taken place, that the oysters have lost the hypostracum, and that the aragonitic fossil remains have disappeared. This is the case in most Mesozoic oyster-bearing deposits. Many authors in describing fossil oysters have either failed to recognize or failed to

Fig. J21. Surficial riblet-bearing layer on exterior of RV of *Pycnodonte vesicularis* (Lamarck, 1806) from "tuffeau de Maestricht," U.Cret.(Maastricht.), St. Pietersberg south of Maastricht, Netherlands, ×2.25 (Stenzel, n).

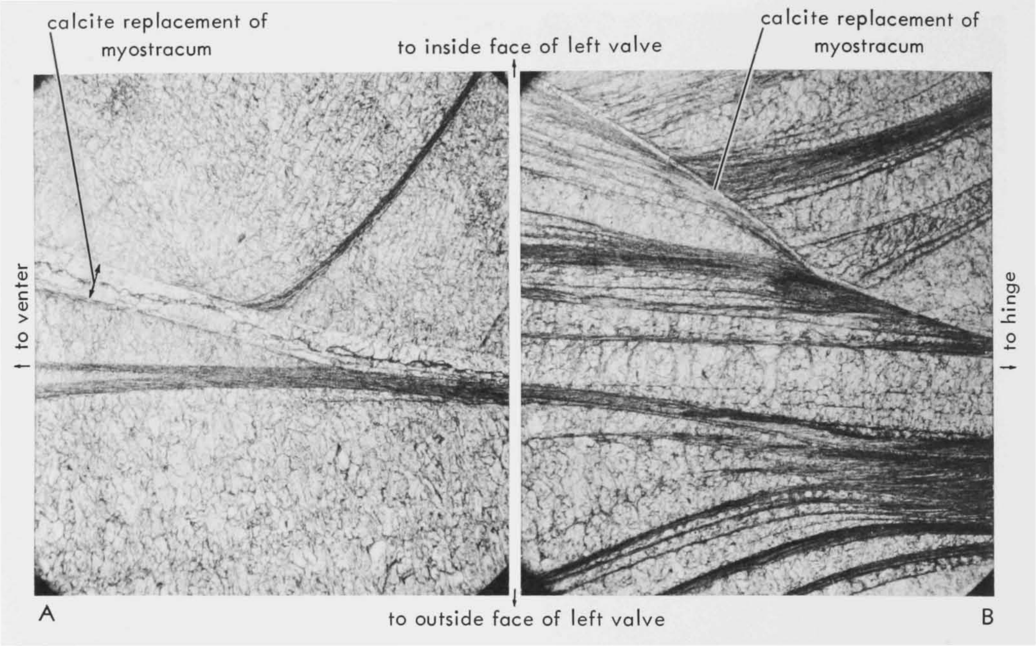

FIG. J22. Shell preservation in *Pycnodonte* sp., ×21.5 (Stenzel, n).

Sections of LV from Saratoga Chalk (Maastricht.) near Washington, Hempstead County, Ark., USA, showing recrystallized calcite replacement of aragonitic myostraca. Sections are cut along tracks of myostraca. The vesicles of the vesicular shell structure are filled completely with secondary calcite. [Thin sections made under supervision of OTTO MAJEWSKE, Shell Development Co.]—*A*. Adductor myostracum.—*B*. Myostracum of Quenstedt muscle.

state that the hypostracum is leached (compare PFANNENSTIEL, 1928, p. 396, figure 8) (see Fig. J74).

Chalky Deposits

Patches of soft, chalky-white, opaque, and porous shell material, so-called **chalky deposits,** are visible on the inner face of the valves in many oysters. They appear amorphous, can be cut and powdered easily by a knife, and consist of microscopic crystals of calcite (MEDCOFF, 1944; KORRINGA, 1951) (Fig. J13; see Fig. J109).

Their sizes vary greatly and their outlines are irregular, although rounded. Many larger patches are apparently confluent smaller patches. Their diameters vary from 1 mm. to several centimeters. Their cross section is flat and thin, tapering to their margins; at their margins many are puffed up above the level of the surroundings. Their distribution is erratic, and patches on the two opposing valves do not match. They are never large enough to

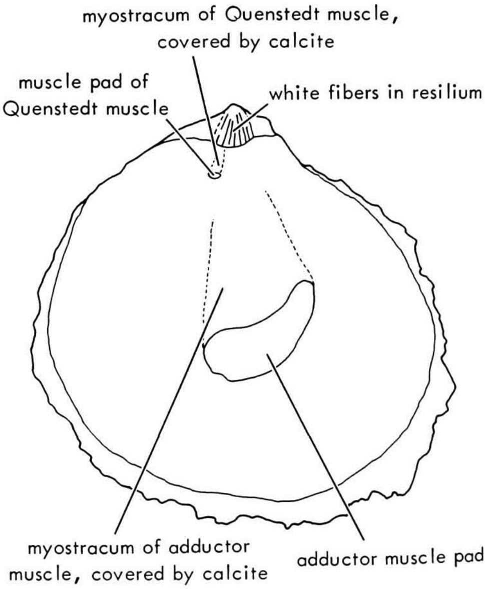

FIG. J23. Aragonite in shell of oysters as exemplified by RV of living species *Ostrea edulis,* ×0.7 (Stenzel, n).

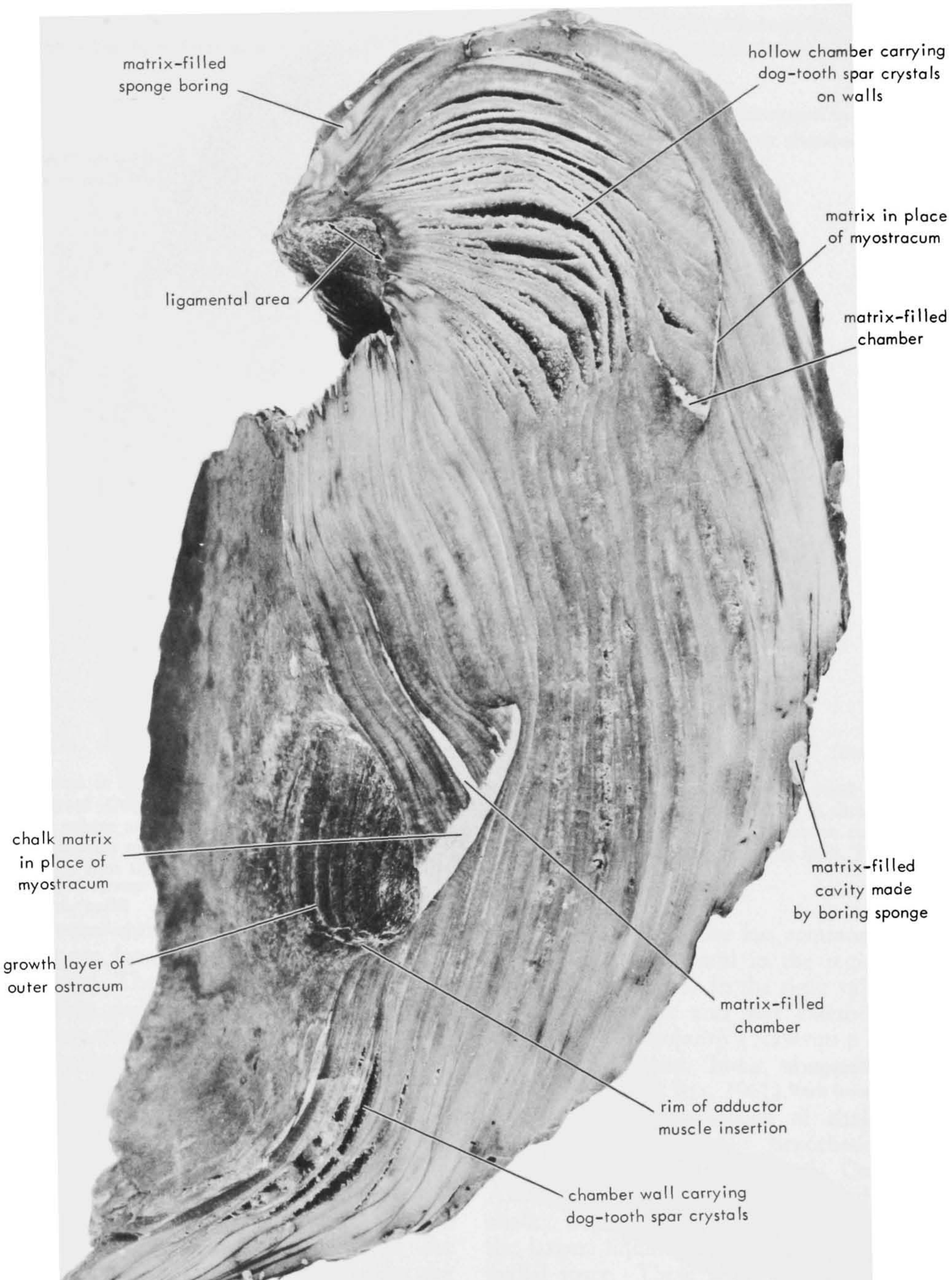

FIG. J24. Shell preservation in *Exogyra*, ×1.2 (Stenzel, n).

Section through LV of *E. (E.) erraticostata* STEPHENSON (1914), from Pecan Gap Chalk (Campan.) of Travis County east of Austin, Texas, USA. Section is cut at right angles to commissural plane through ligamental area and ventral valve margin. Chalk matrix was able to penetrate far into valve, because aragonite composing the adductor muscle pad and adductor myostracum had been leached before the surrounding chalk ooze had lithified. Intruded chalk matrix is cut twice because of spiral arrangement.

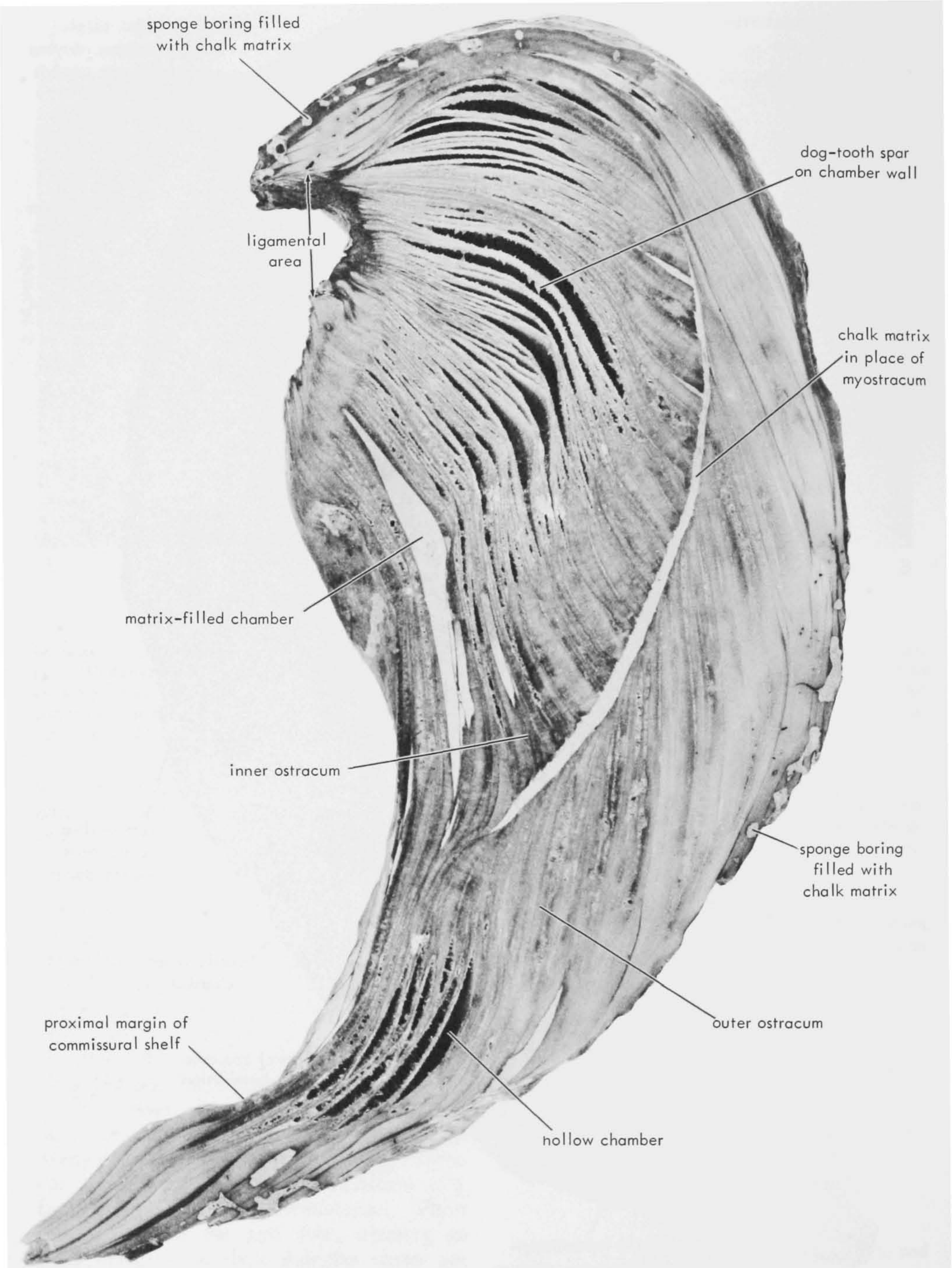

FIG. J25. Shell preservation in *Exogyra,* ×1.2; section through same LV shown in Fig. J24, cut parallel to other section but in plane 2 cm. in front of it. Chalk matrix is intersected in only a single place, because the myostracum spiral is cut near its outside curve (Stenzel, n).

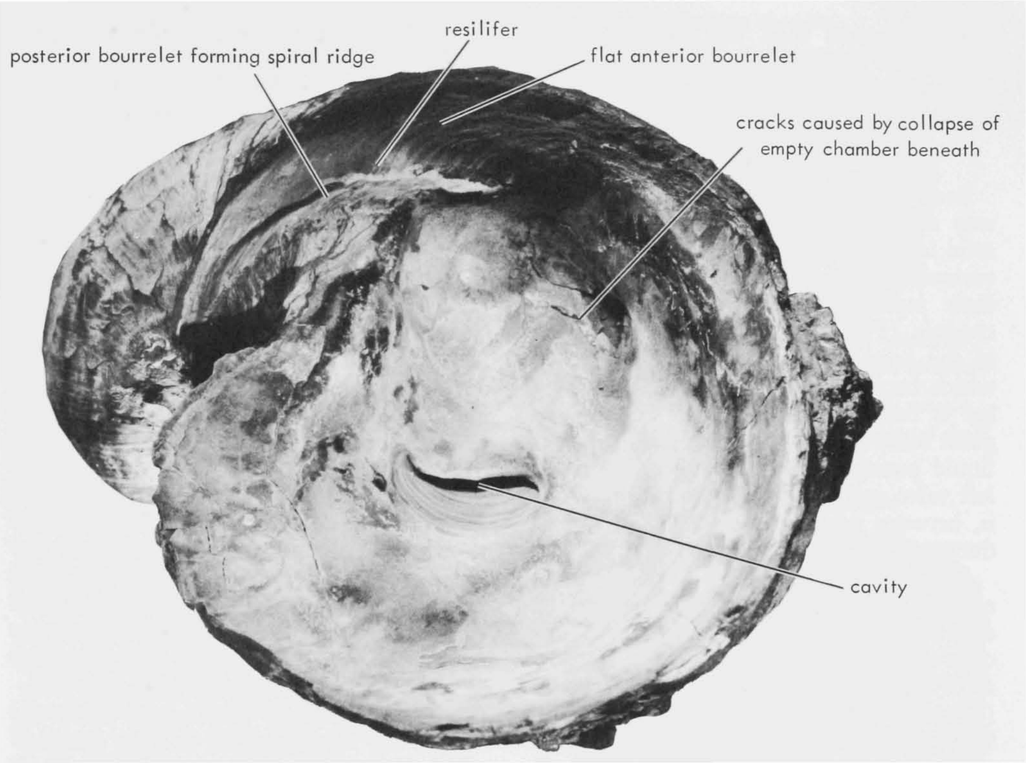

FIG. J26. Shell morphology of *Exogyra (Exogyra) erraticostata* STEPHENSON (1914), ×0.7 (Stenzel, n). Specimen is LV from Brownstown Marl (Santon.) of Lamar County, Tex., showing 3 mm. thick cavity where aragonite of the adductor muscle pad and adductor myostracum has been leached; oblique view up into shell cavity. [Growth lines visible at muscle imprint are growth layers of outer ostracum of valve, beneath. Imprint outline is distorted because of oblique perspective. (Specimen courtesy of Mrs. GERRY KIENZLEN, Arcadia Park, Tex.)]

cover the entire face of a valve and they never are found in the aragonitic parts of the valve. They never are found within the aragonite pad under the adductor muscle, but they can be present at its ventral border where they gradually become covered by the growth of the pad. They form intermittently and become covered by other, more solid shell deposits; new chalky deposits may form again above.

In *Ostrea edulis* chalky deposits form in all possible places on the face of the left valve, but are least common under the visceral mass and most abundant under the exhalant chamber (ORTON & AMIRTHALINGAM, 1927). They are much less frequent and much less extensive on the right valve, but have the same average distribution.

In *Crassostrea virginica* the center of distribution of chalky deposits is under the visceral mass. They are less common under the cloacal passage and in the region surrounding the center. In the right valve they are less common and less extensive. In *Crassostrea cuttackensis* (NEWTON & SMITH, 1912) of Bombay, India, the pattern is similar (DURVE & BAL, 1961).

The mode of formation of chalky deposits is enigmatic, but hypothetical explanations have been proffered. ORTON & AMIRTHALINGAM (1927) assumed that chalky deposits are laid down rapidly in the larger, liquid-filled spaces of the extrapallial space. These larger gaps originated when the visceral mass had shrunk after spawning. Chalky deposits are concentrated in the region of the cloacal passage because there the mantle tends to sag away from the shell wall. However, this explanation would run counter to the fact that the upper, or right, valve has fewer and smaller chalky deposits than the left. Whatever the correct explanation may be, chalky deposits do not require as much shell material as solid shell layers.

Chambers

Some oysters build their shells in such a way as to leave hollow chambers between solid layers repeatedly. The chambers have various sizes and are thin and lenticular; their tapered margins run into narrow crevices (Fig. J24, J25). During the life of the animal they are filled with liquid, which becomes entombed when the chamber is finished. If the liquid contains organic materials, such as mucus, the occluded liquid putrefies. Most chambers are in the left valve and under the visceral mass, that is, between umbo and insertion of the adductor muscle.

Thin walls enclosing the chambers break easily; accordingly, in fossil oysters the chambers are either crushed in by the load of overlying sediment (Fig. J24, J26) or are filled or partly filled with dog-tooth spar (calcite) or other secondary minerals. They become filled with fine-grained rock matrix if the chamber walls get broken while the surrounding sediment has not yet lithified and is able to invade the chamber.

Chambers occur in the Exogyrinae, all of which lived in euhaline waters and many on the sea bottom beyond shallow nearshore waters. In this subfamily, and perhaps even in all, changes of salinity cannot have been responsible for the formation of chambers within the shell.

Evidence indicates that chambers make appearance preferentially. The more deeply cupped shell shape becomes, the more readily chambers form. Extreme chamber building in the umbonal half of the left valve is a conspicuous and characteristic feature of those ecomorphs of *Saccostrea* that grow to a high conical shape and resemble rudists. Their right valve is simple, flat, operculiform and free of chambers.

Although one would expect chambers to be abundant in the umbonal half of the left valves of *Gryphaea* and its homeomorphs, they are not seen in this polyphyletic group of genera. Rather, the umbonal halves of the left valves in these separate and unrelated genera are filled solidly with shell material (see Fig. J73). The absence of chambers in this place appears to be an adaptation to their particular mode of life.

The origins of chamber construction are explained here by the following hypothesis. In oysters, the calcium carbonate for the shell is not derived from their food and does not become available to the mantle lobes of the animal by way of the digestive system. Rather, calcium ions enter the mantle lobes directly from sea water flowing through the mantle cavity, and travel from inner to outer face of the mantle lobes where they enter the extrapallial space and accumulate to become available for shell deposition. Therefore, growth of the oyster shell and additional deposition of shell layers is independent of the intake of food and of the growth of the fleshy parts of the animal. In some environments favorable to shell formation, shell building can outpace the growth of the internal, fleshy parts of the animal. In that case, the size of the shell cavity may become too large for the fleshy parts it harbors. The fleshy parts, however, must stay connected to the valve margins by the edges of the mantle lobes. In order to do so, the fleshy parts must move up toward the valve margins as these margins grow and must vacate a corresponding space within the shell cavity. The vacating is done preferentially in the far interior of the shell cavity, that is, between the visceral mass and the umbo of the left valve. After the vacating has been accomplished the mantle cover on the visceral mass deposits a shell layer forming the partition that closes off the cavity and a chamber is formed. During all these shifts the mantle isthmus must remain in position resting against the ligament, because this must grow and function continuously.

If this hypothesis is found to be correct, the chambers signify temporary rapid shell growth at the margins of the valve affected. Oysters that show numerous chambers (e.g., *Saccostrea*) live in environments where rapid shell growth is possible and where rapid growth of the valve margins to form deeply cupped shell shapes is an adaptive advantage to the survival of individual oysters. Crowding by competitors might produce such a situation.

Vesicular Shell Structure

Although vesicular shell structure must have been seen by Lamarck, when he named the fossil oyster from the Chalk

(Campan.) at Meudon near Paris *Ostrea vesicularis* LAMARCK (1806a, p. 160-161; 1806b, p. 266), he did not describe or mention the structure, and over 100 years elapsed before its significance came to light.

The structure consists of shell layers resembling a sort of foam or spongy honeycomb built up as a network of paper-thin partitions enclosing countless small cavities or vesicles (Fig. J27, J28). The vesicles are taller than wide and have irregular polygonal cross sections of varying sizes. Normally the vesicles of museum specimens are empty. It is entirely unknown, however, whether the vesicles in living oysters are filled with gas or liquid.

The vesicular shell layers are separated from each other by normal horizontal lamellae of solid shell material. The lamellae vary from paper-thin to several millimeters thick, and the proportion of vesicular to lamellar layers is variable from species to species and from local environment to local environment in each species.

Extreme in this respect is *Pycnodonte (Pycnodonte) gigantica* (SOLANDER in BRANDER, 1766) from the Barton Beds (Barton.) of Barton Cliff, Hampshire, England. Most of its lamellar layers are paper-thin; some reach 1 mm. thickness. The vesicular layers are 2 to 9 mm. thick and predominate. Because the vesicles are air-filled in this fossil, the shell is extremely light. The other extreme is seen in *P. (Crenostrea) wuellerstorfi* (ZITTEL, 1864) from the Duntroonian (Oligo.) of New Zealand, which has few vesicular layers.

Vesicular shell structure is found only in the Pycnodonteinae and is an important character for identification of this subfamily (STENZEL, 1959, p. 16, 29-30). In most cases it is readily seen either on a cross break of the shell or on accidentally abraded parts of the valves or on their commissural shelf where it was growing. In some Pycnodonteinae of Cretaceous age, notably in *Texigryphaea,* the vesicles are completely filled with secondary crystalline calcite,

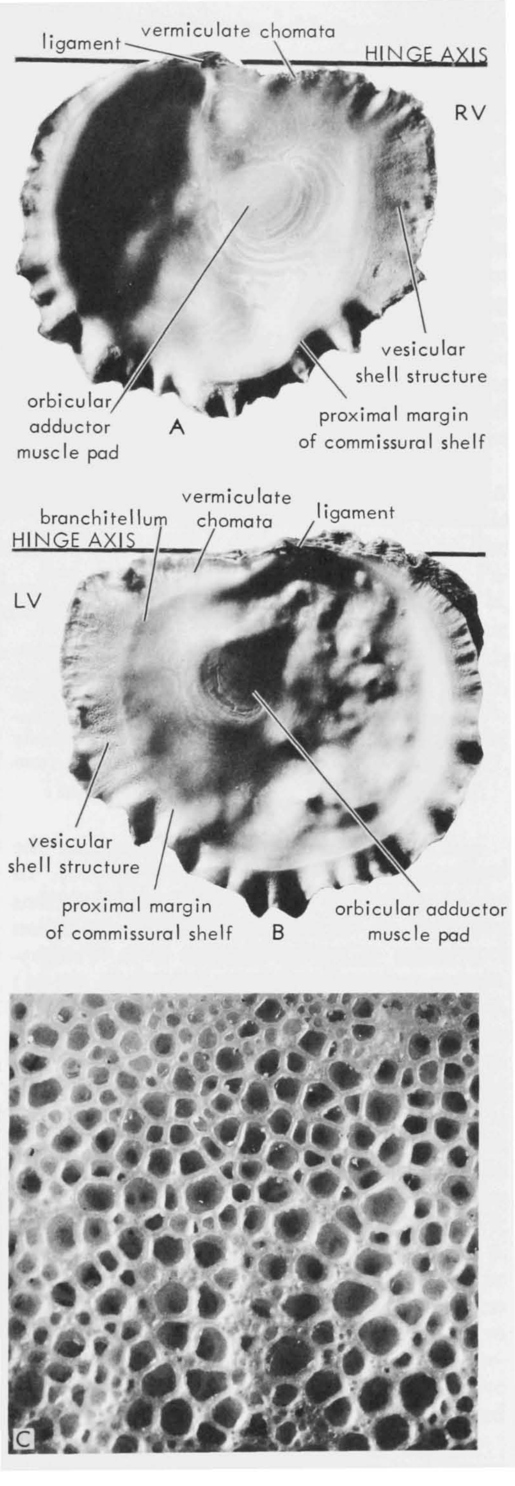

FIG. J27. Vesicular shell structure in *Hyotissa thomasi* (McLEAN, 1941), dredged alive off Key West, Fla. (Stenzel, n). [Specimen by courtesy of R. TUCKER ABBOTT, Philadelphia Acad. Nat. Sci.]—*A-B.* Interior faces of valves, ×0.7.—*C.* Part of commissural shelf, ×10. [Stage of growth is close to end of the construction of vesicles. Lumen of vesicles is partly constricted at the cross walls by hyaline beginnings of a foliated layer.]

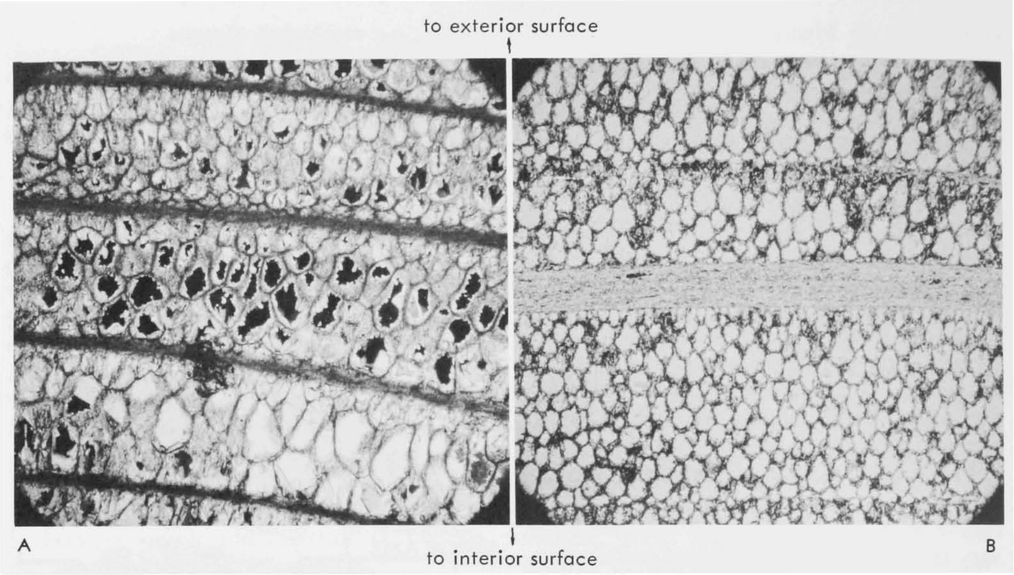

Fig. J28. Vesicular shell structure filled with secondary calcite, LV of *Pycnodonte (Phygraea) vesicularis* (Lamarck, 1806), U.Cret., Lüneburg, West Germany, ×20 (Stenzel, n).

[Alternating thin foliated and thick vesicular layers. Growth of shell wall progressed in direction of interior surface of valve and often began with a layer of small vesicles. Many vesicles have small beginnings and bulbous ends. Several vesicles are partly empty, and secondary crystals have grown from vesicle wall into the lumen.]

A. Thin section under crossed nicols of petrographic microscope valve cut in anteroposterior direction and at right angles to commissural plane.

B. Liquid peel in ordinary light, valve cut at right angles to section shown in *A*, that is, in dorsoventral direction and at right angles to a commissural plane.

making it quite difficult to recognize the structures with the naked eye (Fig. J28). In such cases one needs to study thin sections under the microscope. For that reason Stenzel failed to observe it in *Texigryphaea,* although Ranson (1939-41, p. 64) had already indicated the presence of vesicular shell structure in some species that later were placed in *Texigryphaea* by Stenzel (1959, p. 22-29).

Lamarck completely ignored the vesicular shell structure, except that he named one species *Ostrea vesicularis.* He probably never used this structure to recognize the species, for he described the same species from the same type locality under two different generic names and under three different species names (*Ostrea vesicularis* Lamarck, 1806; *O. deltoidea* Lamarck, 1806; and *Podopsis gryphoides* Lamarck, 1819; see Clerc & Favre, 1910-18, pl. 14, fig. 46-47; pl. 26, fig. 94-95). He probably did not attribute much importance to this structure. The first to describe the structure was Defrance (1821, p. 23). Dall (1898, p. 676-677) guessed that rapid growth produced vesicular shell structure and asserted that vesicular shell structure rarely attains constancy sufficient to entitle it to systematic significance on even as low as the species level and failed to notice it in several species he described. At first Douvillé (1907, p. 100, fig. 3-4) seems to have confounded vesicular shell structure with prismatic shell layers and with chalky deposits, naming the three *"couches prismatiques"* or *"structure prismatique."* However, he became later on the first (Douvillé, 1936b) to see the importance of it as a definitive supraspecific characteristic. Ranson (1939-41; 1941) followed Douvillé and greatly expanded our knowledge of this structure firmly establishing its value in classification.

Douvillé (1936b), Ranson (1939-41; 1941), and Nestler (1965) believed that the vesicular shell structure is some form of chalky deposits, that is, that the two are homologous. If that were true, the distributions of the two should be alike. The chalky deposits have their center of distribution under the visceral mass, when they are freshly formed, but the vesicular structure grows chiefly on the commissural shelves.

Although several living species have vesicular shell structure, nothing is known of its origin and growth. The following explanation is entirely hypothetical. All deposits of the calcareous shell wall, including the vesicular structure, grow in the extrapallial space, which is the mucus-filled narrow gap between mantle lobe and calcareous shell wall. The spongy honeycomb must grow in that mucus, and there must be a mechanism by which growth is regulated so that only thin honeycomb-like walls are formed. The most likely process is that the mantle lobes at times release tiny gas bubbles into the extrapallial space. These gas bubbles accumulate in the extrapallial space, because they cannot escape. Gradually they become crowded to form a sort of foam. The gas bubbles crowd each other, but the viscous mucus forms bubble walls that do not rupture easily. By crowding, the bubbles lose their spherical shapes and become irregularly polyhedral, and their cross sections become polygonal. Calcitic shell material crystallizes in the mucus gradually replacing the mucus so that the vesicular calcitic shell structure is a replacement replica of the original foam composed of gas bubbles in mucus. Crystallization and deposition of calcitic shell material begins at the distal flank, at the shell wall, which acts as a seed bed of crystal nuclei, and progresses toward the proximal side.

Fingerprint Shell Structure

In describing a new living species, *Ostrea cumingiana,* Dunker in 1846 (Dunker in Philippi, 1845-47, *Ostrea* p. 82), was the first to describe a unique shell structure, so far known only from that species: "Besides, one notices here and there partly straight, partly swirled sinuous or irregularly dichotomizing somewhat raised lines of brown coloration, which seem to be characteristic of this species . . ."[translated from German].

The fingerprint shell structure is visible in patches on the internal face of the valves. The patches vary in size and are situated on either valve between hinge and adductor muscle and between adductor muscle and valve margin. They consist of countless narrow curving threads, about 0.3 mm. wide, which are unbranching in some places, confluent in others, and dichotomous in still others. The threads consist of light brown, translucent material, presumably conchiolin. They form a set in a plane conforming to the shell layers. Within each set the threads are equidistant from and parallel with each other in a swirling pattern resembling in size and arrangement the raised lines on a man's fingers. The thread-bearing layers are visible in patches only, because the layers are mostly covered by shell layers free of threads (Fig. J29; see J134, J135).

The fingerprint structure has been seen in only one species, *Alectryonella plicatula* (Gmelin, 1791) (Fig. J29), living in the Red Sea, Indian Ocean, southwestern Pacific, and around southern Japan, that is, in the seas of the tropical and arid climatic belts. Junior synonymous names of this species are: A. *plicatula* (Lamarck, 1819), =A. *cumingiana* (Dunker, 1846), =A. *lactea* (G. B. Sowerby, 1871). It is the type species of *Alectryonella* Sacco, 1897. The origin of this structure is enigmatic.

Interior Topography

Several more or less well-circumscribed features are visible on the inner faces of the valves. Their importance lies in that they are the only means we have to reconstruct parts of the soft anatomy of extinct oysters. The features are (Fig. J7, J8): 1) a pair, right and left, of imprints at the two insertions of the large adductor muscle (see p. *N*962); 2) a pair of imprints at the insertions of the two Quenstedt muscles (see p. *N*965); 3) a pair of serial imprints left by the insertions of several pallial retractor muscles (see p. *N*968); 4) a pair of imprints left by the bulk of the gills (see next paragraph); 5) a pair of commissural shelves (see p. *N*990); 6) marginal ridgelets and pits, or **chomata** (see p. *N*990-*N*994); 7) a buttress supporting the resilifer of the right valve (see p. *N*974); 8) an umbonal cavity beneath the ligamental area of the left valve (see p. *N*994); and 9) parasite-induced features (not discussed here).

The gills are somewhat bulky and firmer than the neighboring fleshy parts of the animal, because they are folded over eightfold and internally stiffened with conchiolin fibers. By their bulk they exert some pressure onto the mantle lobes to either side of them and thereby they tend to reduce locally the width of the extrapallial space and the volume of fluid contained therein. Wherever such a pressure is present, the extrapallial space locally cannot furnish enough calcium carbonate and the shell wall there fails to keep up with carbonate deposition elsewhere. The result is a shallow crescentic basin in the form of the gills on the face of the valve. The basin is bounded distally by the inner curb of the commissural shelf and proximally by a faint wheal or curb or by a more pronounced fold, first noted by Reis (1914) and called *Branchialfältchen* or *Hauptkiemenschwelle* (Pfannenstiel, 1928). This **proximal gill wheal** (Fig. J8, J9; see Fig. J113) sweeps from the vicinity of Quenstedt muscle in a simple curve past the anterior border of the adductor muscle imprint to the palliobranchial fusion. If the shell has a projecting tip end, or branchitellum, at its posteroventral end, the end of the gill wheal points toward it.

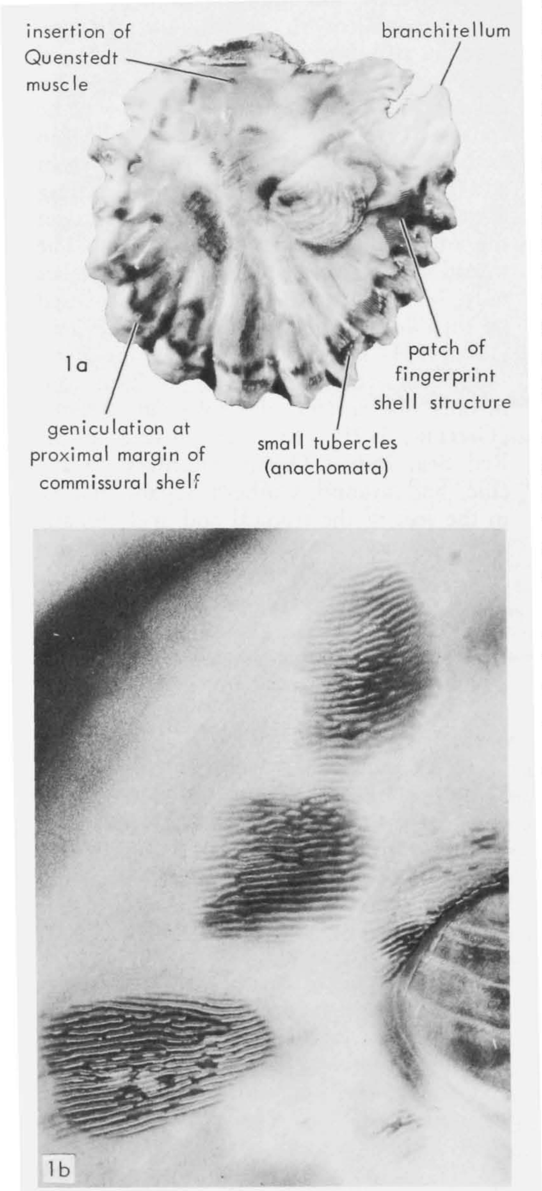

Fig. J29. Fingerprint shell structure on inside face of RV of *Alectryonella plicatula* (Gmelin), living species from Nosi-Bé, Madagascar. [Specimen by courtesy of R. Tucker Abbott, Philadelphia Acad. Nat. Sci.]

1a. RV inside face showing patches of fingerprint shell structure, ×0.7.

1b. Same valve showing fingerprint shell structure in vicinity of adductor muscle pad, ×2.1.

The **commissural shelf** is a flattish band along the periphery of the valve along which opposing mantle lobes touch each other, when the shell is closed and the mantle lobe margins are not withdrawn toward the interior of the shell cavity. A circumferential curb delimits the commissural shelf proximally and encircles the deeper, main part of the shell cavity. The two opposing shelves of a shell and their curbs are better developed in the dorsal than in the ventral half and are the least distinct at the posteroventral part of the shell. Shelves are better developed and have neater curbs in the Exogyrinae, Gryphaeinae, and Pycnodonteinae than in other oysters (Fig. J27; see Fig. J83, J90). In many of the Exogyrinae the commissural shelf of the right valve is reflexed strongly along the anterior valve margin; there the circumferential shelf curb is exaggerated into a sort of internal keel paralleling the right anterior valve margin.

Small ridgelets and pits opposing them are near the hinge on the commissural shelves of many oyster genera. The ridgelets, called here **anachomata,** are on the right and the pits, called **catachomata,** on the left valve. Collectively they are called **chomata.** Although they are mostly in the

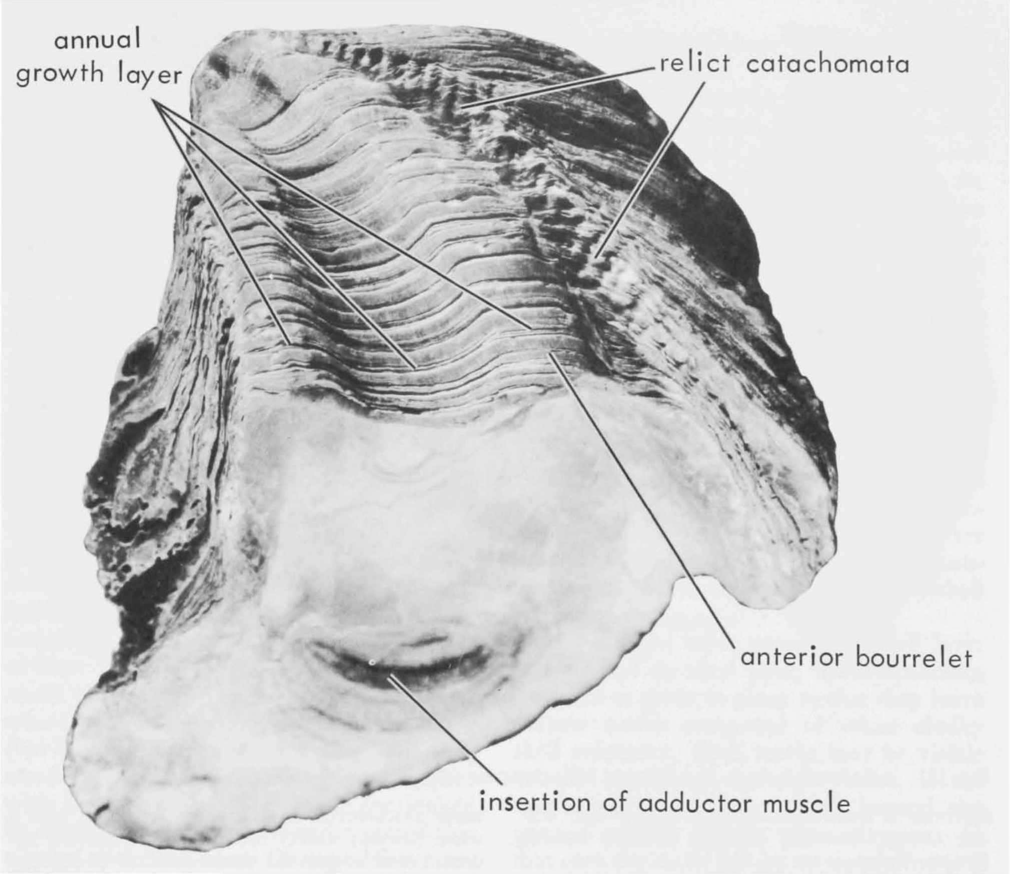

FIG. J30. Annual growth layers on ligamental area of LV of *Ostrea (Turkostrea) duvali* GARDNER (1927), ×1.4 (Stenzel, n).

Specimen is from Caldwell Knob Oyster Bed, Wilcox Group, low.Eoc., of Moss Branch, Bastrop County, Texas. [The oyster is estimated to have been about 15 years old. Pits or catachomata flanking the margin of the anterior bourrelet are relicts of former growth stages. Ligamental area is bent back from plane of valve commissure.]

vicinity of the hinge, they are neither homologous nor analogous to the teeth and sockets on the hinge plates of normal dentate Bivalvia. For that reason, the terms dents or denticles, used by many authors, are inappropriate and downright misleading (Fig. J30, J31; see Fig. J113, J127).

If the anachomata were homologous to the teeth, they would have to have the same or a similar derivation, that is, they would have to grow out of the larval teeth and hinge structures on the prodissoconchs as the teeth and sockets of adult normal Bivalvia do. Repeated studies on individual ontogenies of oysters *(Ostrea edulis* and other species of *Ostrea s.s.)* from the larval to the young adult stage have shown that the chomata are new, postlarval features independent of any hinge features on the prodissoconchs. In normal dentate Bivalvia true teeth and sockets are both found on each valve, but the anachomata of oysters are only on the right and the catachomata only on the left valves. Also, some oysters have chomata all around the peripheries of their valves, including valve margins directly opposite the hinge. True teeth are never found on valve margins opposite the hinges in the Bivalvia.

Functionally also, they do not correspond to teeth and sockets, that is, they are not analogous. True teeth and sockets are inter-

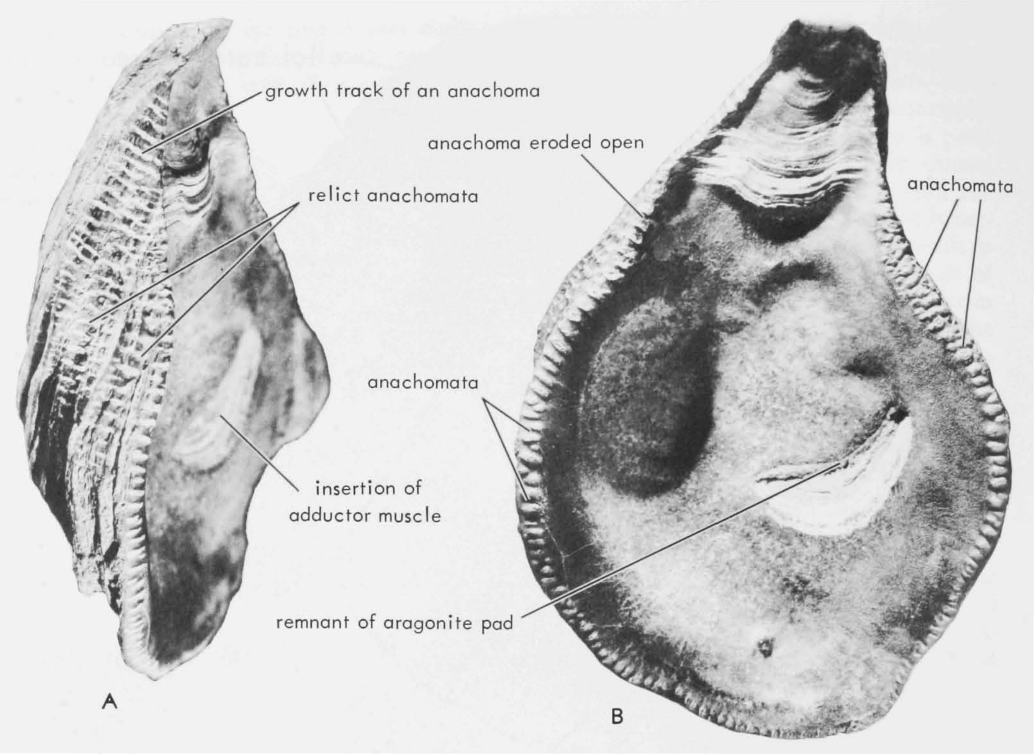

FIG. J31. Anachomata along periphery of RV of *Ostrea (Turkostrea) duvali* GARDNER, ×1 (Stenzel, n).

Specimen is from Caldwell Knob Oyster Bed, Wilcox Group, low.Eoc., of Moss Branch, Bastrop County, Texas.
A. RV viewed from anterior side.
B. Same RV viewed from left side.
[The anterior flank of the valve carries relict anachomata of several preceding growth stages and continuous or nearly continuous growth tracks of many anachomata. Each anachoma is filled with a white powdery chalky deposit. The aragonitic adductor muscle pad has deteriorated to a crumbly mass, which has broken off exposing the growth layers of the supporting calcitic shell wall, except at the dorsal margin of the muscle imprint where the original aragonitic material is still intact.]

locking devices for the continuous guidance of the valves during their movements. Their guidance prevents the valves from closing askew, and in order to accomplish that function in live bivalves they must remain in contact with each other even when the shells are fully opened. Bivalvia that have a large, hydrostatically expandable foot (e.g., Cardiidae) must open their valves rather wide to let the foot move about freely. They have deep sockets and highly projecting teeth that do not lose contact with each other when the animal opens the valves wide. In the oysters, however, chomata lose contact as soon as the animal opens its valves a little. If they exert guidance at all, it can be only minor and restricted to the final stage of shutting the valves. In short, chomata are a novel evolutionary accomplishment of the oysters and their allies that arose during the phylogeny of the superfamily.

The chomata have various characteristic shapes. All Gryphaeinae, *Gryphaeostrea* of the Exogyrinae, and *Crassostrea* of the Ostreinae are entirely devoid of them (see Fig. J101). The genus *Saccostrea* has strongly developed chomata (Fig. J7), high and strong tubercles on the right and deep pits on the left valves along the whole periphery of the valves. In *Ostrea, Cubitostrea, Odontogryphaea,* and other related Ostreinae, the anachomata range in size from simple, low and round tubercles to straight, slightly elongate (up to 3 mm.), unbranching ridgelets.

In *Ostrea* the anachomata are commonly restricted to the vicinity of the hinge. Some species of the genus have only one to five of them, others have a goodly number (10 to 15) in the dorsal half of the right valve. Finally there are species that have great many of them (100 or more), and many individuals of such species have these features encircling the entire or nearly the entire valve. Examples of the latter are *Ostrea (Ostrea) crenulimarginata* GABB, 1860 (p. 398, pl. 68, fig. 40-41), from the Midway Group (Dan.) of the northern coastal plain of the Gulf of Mexico, and *O. (O.) marginidentata* S. V. WOOD, 1861 (p. 27-28, pl. 5, fig. 2) from the lower Brackelsham Beds (Division N of FISHER, Palate Bed, Cuis.) at Brackelsham Bay, Sussex, southern England. These two appropriately named species are closely related, that is, they are members of the same minor phyletic branch in *Ostrea (Ostrea)*. Their chomata are stronger and longer than is usual for *Ostrea s.s.* In contrast, *O. (O.) lutraria* HUTTON, 1873, living off the coasts of New Zealand, has exceedingly few very small, round, tubercle-like anachomata and corresponding catachomata near its hinge (see Fig. J113). In some individuals they are difficult to find and may even disappear with advanced age. They were overlooked by SUTER (1917, p. 86) when he placed this species, under the name *O. angasi* SOWERBY, at the head of his original list of species composing the subgenus *Ostrea (Anodontostrea)*, which he proposed because it differed supposedly from *Ostrea (Ostrea)* by the lack of chomata. The species was later designated the type species of *Anodontostrea* SUTER by FINLAY (1928b, p. 264). Thus *Anodontostrea* differs only quantitatively but not significantly from other species of *Ostrea (Ostrea)* and is best regarded as a junior subjective synonym. *Ostrea s.s.* consists of many extinct and living species that may be arranged in a morphological series on the basis of relative abundance of chomata, and there is no significant gap in this series. Nevertheless, the underlying idea of SUTER's that the presence or absence of chomata is significant in the taxonomy of oysters is sound, even if his observations were incomplete and his examples ill-chosen.

In some species the anachomata project slightly to the outside, beyond the general contour of the right valve. For example, *Odontogryphaea thirsae* (GABB, 1861, p. 329-330) from the Nanafalia Formation and other homotaxial formations (Sparnac.) in the northern coastal plain of the Gulf of Mexico and *Ostrea (Turkostrea) duvali* GARDNER (1927, p. 366, fig. 1-4) from the Caldwell Knob Oyster bed (Sparnac.) of the Wilcox Group in central Texas (Fig. J30, J31) have anachomata projecting a fraction of a millimeter beyond the general margin of their right valves so that they are visible from the outside. In contrast, the corresponding left valves have the catachomata a slight distance proximally from the valve margins so that they are not visible except on the inside face of the valves. In these species the very core of each anachoma consists of white, chalky, opaque shell substance and neighboring anachomata are separated by darker, nonchalky, semitranslucent, grayish or brownish, laminated shell substance.

As the right valve grows and shell layer is deposited on shell layer, the anachomata continue to grow in place so that they leave narrow tracks composed of white chalky shell substance. Such tracks may be visible on the outside of the right valve, if the anachomata projected to and beyond the general outline of the valve margins. In that case the track left by an anachoma is a white, narrow, opaque, chalky ridge (Fig. J31). From these ridges it can be deduced that during growth the number of anachomata increases only slightly by dichotomy and intercalation. On the other hand some chomata play out. Because chomata continue to grow in place, the growing ligament seat often bypasses some of them so that the valves have relict chomata on the flanks of their respective ligamental areas (Fig. J30).

Because the chalky cores of the anachomata are less resistant to mechanical and chemical corrosion, they can become corroded or leached in sea water and their tracks can become narrow, sharply defined grooves visible on the outside of the right valves. No such features can be found on the left valves. These features can be used to distinguish left from right valves (see Fig. J128,*1h*).

All Pycnodonteinae have chomata of a special character. In early, primitive genera of this subfamily (e.g., *Texigryphaea*), most species have low, narrow, short (1.5-2.0 mm.), crowded ridgelets and corresponding grooves. On first inspection they are quite similar to those found in many Ostreinae. However, they differ in that they are crowded (about 20 per cm.) and set in series and in that the difference between the right and the left valves is obliterated, that is, the ridgelets cannot be distinguished from the pits because they are so crowded. In addition there is a tendency for some of the ridgelets to join or branch in a simple fashion.

A few species of *Texigryphaea* (e.g., *T. belviderensis*) (Hill & Vaughan, 1898, p. 56, pl. 9-10) from the Kiowa Shale (Alb.) of Belvidere, Kiowa County, Kansas, have wider commissural shelves and longer (up to 5 mm.) anachomata, some of which are branched and break up into irregular tubercles. Their ridgelet patterns approach the vermiculate patterns of *Pycnodonte.*

Most of the later, more advanced Pycnodonteinae, with the exception of *P. (Crenostrea),* have on both their valves wide commissural shelves carrying a vermiculate pattern of ridgelets (see Fig. J83, J84). These are irregular, tortuous (or vermiculate), crowded, and longer (up to 15 mm.); repeatedly they branch away from adjoining ridgelets or coalesce with them and break up into irregular rows of round tubercles.

This pattern has been commented on and figured by many authors. The first to recognize its importance in taxonomy of the oysters was Fischer de Waldheim (1835). He established the genus *Pycnodonte* chiefly on the basis of this pattern and named it accordingly (*πυκνός*, Greek adjective, thick, crowded; *ὀδους*, *ὀδόντος*, Green noun, masculine gender, the tooth). Later authors to contribute to the evaluation of the vermiculate pattern in taxonomy were Douvillé (1911, p. 635) and Ranson (1939-41, p. 61; 1941, p. 82). Thanks to their efforts the pattern is recognized now as definitive for a large but well-defined group of species which many authors prefer to regard as a single species-rich and diversified genus and call *Pycnodonta* G. B. Sowerby (1842). However, *Pycnodonta* is an unjustified emendation of the original validly introduced name *Pycnodonte* and the large diversified group of species breaks easily into several well-defined groups separated by morphological gaps. It seems clear that more than one genus is involved and the large diversified group is really a subfamily, the Pycnodonteinae Stenzel (1959, p. 16, 29-30).

The origin of the chomata is obscure. They are certainly not modified hinge teeth. Jaworski (1928) tried to explain them as imprints of radial pallial muscle strands situated at the margins of the mantle lobes. Such strands are indeed present in live oysters and stand out as rounded ridges on the outer face of the mantle lobes. Klinghardt (1922, p. 21) tried to explain the vermiculate patterns of the Pycnodonteinae as imprints left by the tentacles that rise from the margins of the mantle lobes. Jaworski (1928, p. 345) refuted this assumption by pointing out that tentacles are too small to produce such imprints, are too mobile to stay in place long enough to have much effect, and are held most of the time in a position vertical to the commissural plane of the shell while the oyster is alive. One would expect radial pallial muscle strands and tentacles to produce elongate grooves on both valves. They could not produce ridges on one valve and grooves on the opposite valve. In short, the chomata cannot be explained today.

Only the left valve has an **umbonal cavity.** Several genera of oysters commonly have an open cavity beneath the platform that carries the ligament and ligamental area of the left valve. The cavity changes shape and size during the growth of the oyster; at times it may be entirely obliterated by shell deposits or by the formation of chambers. Although it is so variable in size, its average appearance is distinctive (Stenzel, 1963a).

The deepest umbonal cavities and the most chambers are found in *Saccostrea,* particularly in the high-conical rudist-like ecomorphs of the living complex superspecies *S. cuccullata* (von Born, 1778) from the tropical IndoPacific (see Fig. J104-J106). Lesser umbonal cavities are found in *Crassostrea.* No umbonal cavities or few and generally shallow ones are found on *Ostrea.* Very shallow umbonal cavities are present in the Gryphaeinae and Exogyrinae, although their greatly extended left beaks would seem to favor their growth. An important feature of the homeomorphs of *Gryphaea* is that they have only very shallow umbonal cavities and that their extensive spiralling left beaks have no chambers but are filled with solid shell material (see Fig. J73).

Distinction Between Valves

To be able to distinguish the right from the left valve is of practical importance in the study of dead and fossil oyster shells. The following methods are useful for that purpose.

1) If one draws the mid-axis on a valve, the center of the adductor muscle falls to one side of it (see p. *N*963). The center falls to the left side on the inner face of the left valve and to the right side on the right valve (Fig. J3).

2) The left valve is the larger one. If both valves of the same individual are placed together in their natural positions, margins of the left extend beyond those of the right to a slight or considerable amount, provided the marginal conchiolin scales are discarded (see Fig. J113,*2c;* J117,*1a*).

3) The left valve is the more convex. The rule applies if the attachment area is small compared with the size of the whole left valve. If it is large, the opposite may be the case. These conditions vary from one to the other individual and may even reverse during growth of an individual. Individual shells that have grown with a large attachment area on a large flat substratum and have a left valve not much larger than its attachment area have xenomorphic sculpture (see p. *N*1021) in the form of a smooth convex right valve opposed to the flat attachment area of the left valve (see Fig. J75,*1*).

Differences in convexities between the two valves are quite large in most Exogyrinae, Gryphaeinae, and Pycnodonteinae, and also in *Saccostrea* and homeomorphs of *Gryphaea.* They are moderate in most Ostreinae and highly variable in *Crassostrea.* Almost equal convexities prevail in the Lophinae and in *Ceratostreon* (Exogyrinae) (see Fig. J92), *Ostreonella* (Ostreinae) (see Fig. J128) and *Hyotissa* (Pycnodonteinae) (see Fig. J85), and in the extremely flat-valved *Deltoideum* and *Platygena* (see Fig. J76, J120).

4) The attachment area is on the left valve in all the oysters. However, to recognize the attachment area one needs to have well-preserved material.

5) The umbonal cavity, if present, is on the left, and the buttress under the resilifer is on the right valve.

Fig. J32. Lack of attachment area on umbo of LV of young *Ilymatogyra arietina* (Roemer, 1852) from Grayson Clay, Cenoman., near Austin, Travis County, Texas, USA, ×4.8. [The recurved pointed calcitic inner mold of the prodissoconch is seen at tip of the umbo. This specimen is a variant which is costulated in youth.]

6) Anachomata are present near the hinge of the right valve. The corresponding catachomata are on the left valve. This method is useless in those genera that lack chomata altogether and in most Pycnodonteinae, in which the two cannot be distinguished.

7) The left valve is the heavier. This distinction is quite variable so that it can be used only on a statistical basis.

Attachment

With exceedingly few exceptions, oysters must become attached to a firm substratum at the end of their larval stage. They may remain attached during their entire postlarval life. Some individuals may break loose and continue to live lying loose on the bottom. Some species grow attached to a small fragment of shell and soon grow bigger and heavier than the fragment so that they become virtually free-lying. This is the case in the gryphaeas and their homeomorphs.

The only species discovered so far which grow from their earliest larval stage to old age without ever becoming attached to a substratum are (Fig. J32-J34; see Fig. J64):

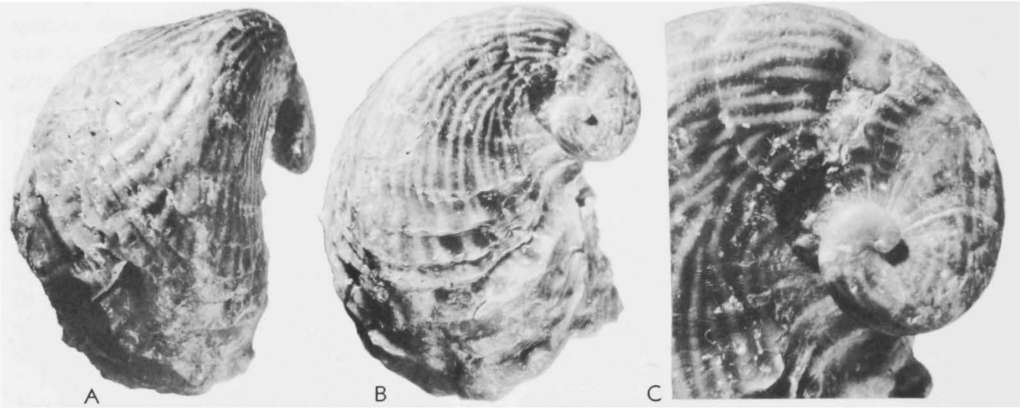

FIG. J33. Traces of coloration, lack of attachment area, and slender polygyral umbo on LV of *Exogyra (Exogyra) tigrina* STEPHENSON (1929) (Stenzel, n).

Specimen is topotype from uppermost bed of Austin Chalk (L.Campan.) of Little Walnut Creek, east of Austin, Travis County, Texas, USA.

A-B. Exterior views of LV, ×0.85.

C. Tip of LV umbo showing lack of attachment area and semiglobular calcitic internal mold of prodissoconch, ×1.7. [The prodissoconch itself is leached because it consisted of aragonite.]

Ilymatogyra arietina (ROEMER, 1852), from the Grayson Clay (Cenoman.) of Texas and northern Mexico (Fig. J32); *Odontogryphaea thirsae* (GABB, 1861) from the Nanafalia Formation (Sparnac.) of Alabama to Mexico and other species of the genus; and many individuals of *Rhynchostreon suborbiculatum* (LAMARCK, 1801) [=*Ostracites ratisbonensis* VON SCHLOTHEIM, 1813 (=*Gryphaea columba* LAMARCK, 1819, =*Ostrea mermeti* COQUAND, 1862, =*Rhynchostreon chaperi* BAYLE, 1878)] from the Cenomanian and Turonian of Europe, North Africa, and the Near East (see Fig. J97). These oysters are specially adapted, and their shells show no attachment areas at the umbones (see also Fig. J94).

All oysters are attached by their left valves. In no case has it been possible to prove that an oyster had become attached by the right valve. Those cases in which it had been claimed that the right rather than the left valve was attached have been proved to be or are very likely errors of some sort. SAVILLE-KENT (1893, p. 246) claimed that the living Australian species *"Ostrea glomerata"* [COX, 1883, not GOULD, 1850, =*Saxostrea commercialis* (IREDALE & ROUGHLEY, 1933), =*Saccostrea cuccullata* (VON BORN, 1778) subsp. *commercialis* (I. & R., 1933)] . . . "is . . . invariable affixed by its right one" (see Fig. J105). This claim is no longer supported by modern Australian authors. ROLLIER (1917, p. 587) distinguished the Jurassic genus *Deltoideum* from *Ostrea s.s.* because he surmised it was attached by its right valve. ARKELL (1932-36, p. 149, footnote 1) expressly refuted this claim. The genus has very flat valves and the two valves are most difficult to distinguish. ROLLIER probably mistook the right for the left valve (see Fig. J76).

NELSON (1938, p. 45, footnote 9) noted, among hundreds of normal newly set *Crassostrea virginica* (GMELIN), the living oyster of the North American east coast, one single one attached supposedly by its right valve. He did not illustrate it nor did he offer any proof. Innumerable newly set spat of this species have been seen by many other authors, but no one has duplicated NELSON'S observation. Presumably it was erroneous.

Size of the attachment area is quite variable from one to the next individual, even in the same vicinity. It is mostly quite small (diameter of 2 mm.) in *Gryphaea* and its homeomorphs. SWINNERTON (1939, p. xliv and lii; 1940, p. xcviii, fig. 8; 1964, p. 419-420) measured the longest diameter of the attachment area on 658 specimens of *Gryphaea arcuata* LAMARCK (1801) from clay shales in the Zone of *Schlotheimia angulata* (VON SCHLOTHEIM, 1820) in the Granby Limestones, latest Hettangian, Lias-

Fig. J34. Traces of coloration in LV of *Odontogryphaea thirsae* (Gabb, 1861) from Nanafalia Formation (Sparnac.) of Alabama, USA, ×1.5 (Stenzel, n).

sic, near Granby, Lincolnshire, England. The average of these 658 diameters, calculated from Swinnerton's data, is about 2.1 mm. and the average size of the attachment areas is less than 4.5 square mm. Only 2.9 percent of the specimens had diameters in excess of 10 mm. (Fig. J35). Oysters grown onto very small objects or fragments soon become heavier than their substratum. On toppling over, they lift the substratum up from the floor of the sea and become virtually free-lying but continue to grow.

The attachment area has the negative configuration of the substratum. In fossil oysters the configuration of the attachment area is an important clue to the nature of the substratum. In many places, one finds well-preserved fossil oyster shells that grew originally on aragonitic mollusk shells, but these are no longer preserved, because aragonite is subject to selective leaching. The configuration of the attachment area lets one identify the now no-longer-present mollusk shell with some confidence (see Fig. J45).

Some oyster genera also produce clasping shelly processes on the left valve. These processes grow out from the valve margin of the left valve periodically to embrace or enclose the substratum. Most of the Lophinae grow them, also *Gryphaeostrea* of the Exogyrinae. Many of the Lophinae that produce clasping processes grow on live gorgonacean coral stems (see Fig. J47, J129).

Pigmentation

The oysters have many pigmentation patterns. A common pattern is radial streaks of dark colors on the outer faces of the valves. The streaks begin as narrow bands near the umbones and widen concomitantly with growth of the shell. Another common pattern found in tropical oysters is a wide circumferential band of dark color (black, dark brown, or dark purple) along the margins on the inner faces of the valves (see Fig. J85).

Oysters living in warm and tropical regions have darker, more vivid, more varied, and more extensive colorations than those living in cooler climates. This rule applies to all species but is particularly noticeable in those having a large north-south geographic range extending from cool to hot climates. For example, northern populations of *Crassostrea virginica,* living north of Cape Cod along the east coast of North America, have whitish to grayish yellow (5Y 8/4) colors on the inner faces of the valves and have grayish red purple (5RP 4/2) to very dusky red purple (5RP 2/2) muscle imprints. The same species living in the northern part of the Gulf of Mexico has large areas of the inner faces light brown (5YR 6/4) to grayish purple (5P 4/2) and only a few patches remain whitish; the muscle imprints have approximately the same colors.

On the basis of coloration it is possible to distinguish geographic subspecies among living species that have a wide enough range. However, coloration, even traces of it, is rarely found in fossil oysters.

Traces of coloration in fossil oysters are in the form of radial brownish streaks on the exterior of the shell. The brownish color is probably the result of deterioration of purplish. Such brownish streaks are found on *Ilymatogyra arietina* (Roemer, 1852), from the Grayson Shale (Cenoman.) of Texas and northeastern Mexico; *Exogyra (Exogyra) tigrina* Stephenson, 1929 (Fig. J33) and *Exogyra (Exogyra) laeviuscula* Roemer, 1849, both from the top of the

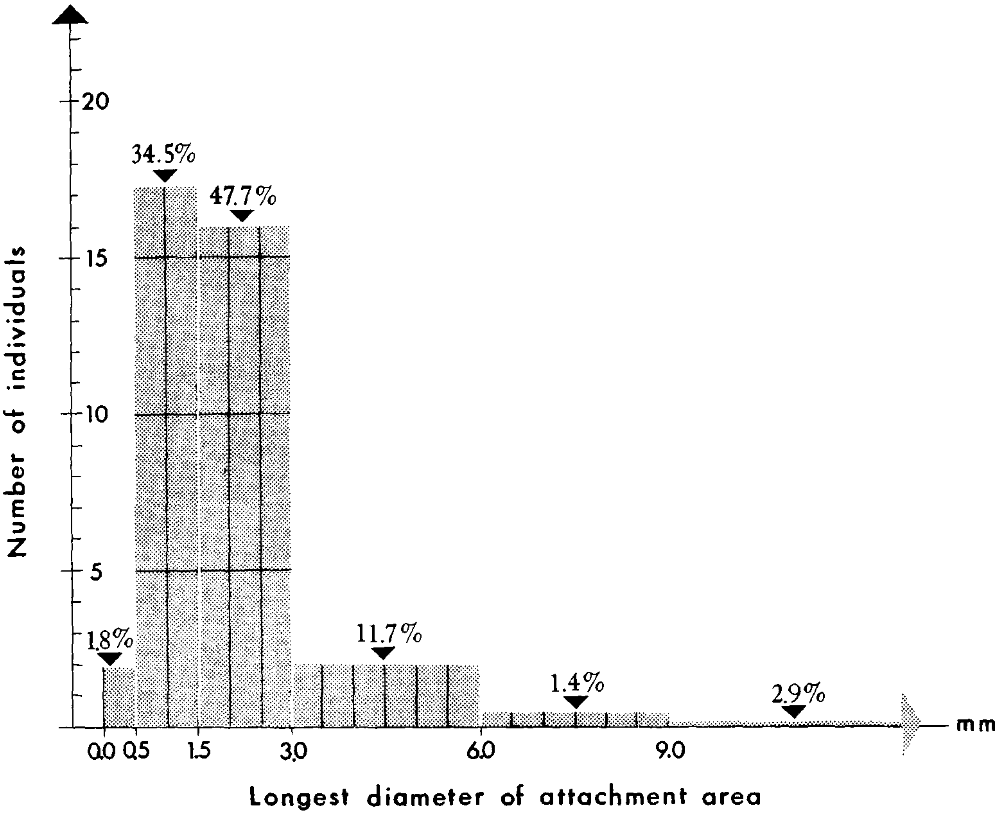

FIG. J35. Size of LV attachment area of *Gryphaea arcuata* LAMARCK (1801) (Stenzel, n; data from Swinnerton, 1964).

Specimens studied come from Granby Is. (latest Hettang., Lias.) south of Granby, Lincolnshire, Eng. Size of attachment area is indicated by length of its longest diameter measured on 658 individuals.

Dessau Chalk (Santon.), Austin Chalk Group, of central Texas; *Odontogryphaea thirsae* (GABB, 1861) (Fig. J34) from the Nanafalia Formation (Sparnac.) of Alabama to northeastern Mexico; and *Rhynchostreon suborbiculatum* (LAMARCK, 1801) from the Cenomanian and Turonian of Europe, North Africa, and the Near East. The last-mentioned species and its color bands has been figured by GOLDFUSS (1826-44, pl. 86, fig. 9c,d), COQUAND (1869, pl. 45, fig. 8-9), and BAYLE (1878, pl. 138, fig. 3) and specimens showing them have been found from County Antrim, Ireland, to the Postelberg in Bohemia, Czechoslovakia. Radial color bands are more common in the Exogyrinae than in other fossil oysters.

Colors in the shell wall of oysters are probably organic metabolic waste products. The kind of food available to the oysters probably determines their coloration. Purple pigments are probably acid-soluble bile pigments.

PHYSIOLOGY

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FUNCTIONS OF ADDUCTOR MUSCLE

The adductor muscle serves to move and close the two valves. It does so against the elastic reaction of the ligament, which is always under compression and pushes the valves apart. So important to the survival of the animal is the adductor muscle and so much work does it perform that it must be supplied with oxygenated blood at all times and in the best possible way. Therefore, the artery supplying it is very short and the heart is right next to the muscle on its more protected, dorsal flank. Thus heart and muscle are functionally tied together. If evolutionary adaptive change induce the muscle to shift position, the heart must follow it inexorably and remain next to it (see p. *N*1058).

Both quick reactions and long continued contraction are required. These two separate faculties have necessitated specialization of the muscle into two subdivisions side by side.

The tonic subdivision (catch muscle) holds the shell closed against the unceasing push of the ligament and it can do that for long periods of time, if need arises. Oysters can starve or suffocate and die while they hold the shell shut tight. Live oysters can remain shut for 20 to 30 days (Marceau, 1936, p. 952).

The phasic subdivision (quick muscle) acts frequently. Oysters never keep their valves in the same positions for long while they are feeding. Throughput of the water current through gills and mantle cavity is regulated by the pallial curtains and the degree to which the muscle lets the valves open. The water current bears suspended food particles and dissolved oxygen for breathing. A series of rapid contractions expels the newly issuing unfertilized eggs from the cloacal passage through the ostia of the gills into the inhalant mantle chamber. Similar movements eject the eggs of the nonincubatory oysters into the surrounding waters. The incubatory oysters eject their half-grown larvae at the end of their incubation period in a similar fashion. Self-cleansing of the mantle cavity depends on the quick muscle and the pallial curtains (see p. *N*1001).

ALIMENTATION

FOOD

Nannoplankton, that is, various microscopic plants or animals less than 10 microns large, are the food of oysters. Most of it is various one-celled plants or animals, such as algae, bacteria, diatoms, flagellates, and protozoans. Microscopic metazoa such as copepods, free-living nematodes, polychaetes, rotifers, and even tiny fish eggs are also taken. Larvae of oysters or many other sea animals are taken in too.

However, oysters cease to feed while they are ejecting their sex products.

FEEDING

While the oyster is feeding it must open its mantle/shell sufficiently to let in the water current which it establishes itself. Yet, the opening must be kept as small as possible to keep out predators. The extent to which oysters open their mantle/shell while feeding is astoundingly small. The opened gap is 2-3.5 mm. wide at the ventral valve margins of full-grown individuals (shells 80-110 mm. high) of *Crassostrea virginica* (data kindly supplied by Mr. W. J. Demoran of the Gulf Coast Research Laboratory at Ocean Springs).

The gills are covered with cilia. Cilia on the gills, particularly those at or near the ostia, beat regularly and thereby set in motion a water current that passes through the ostia from the side of the inhalant chamber to that of the exhalant chamber. No water can go from one chamber to the other without passing through the ostia of the gills. Therefore, the water is strained efficiently and nannoplankton and other particles are collected on the gills. The oyster is a ciliary suspension-feeder.

The gills perform two functions, respiration and food straining. However, respiration is also taken care of elsewhere. The mantle lobes are well supplied with blood vessels and have large epithelial surfaces exposed to the inhalant oxygen-carrying water current. Their help in respiration freed the gills to some extent so that they were able to become efficiently adapted to food-straining.

Individuals of *Crassostrea virginica* pump and strain for brief periods (5-15 minutes) at the rate of 41 liters per hours at the best and attain a sustained rate of 37.4 liters per hour when temperatures are 24.1 to 24.5°C. (Loosanoff, 1958, p. 62; Collier, 1959). They cease in cold waters. Allen (1962) measured filtration rates of *Ostrea edulis* by using a suspension of the unicellular alga *Phaeodactylum* labeled with radioactive phosphorus. The alga is 4 by 40μ in size and is readily accepted as food by filter-feeding bivalves. They remove the algae from surrounding waters, enabling one to calculate rates of filtration by measuring concentrations at intervals and the time intervals. *Mya arenaria* has a filtration rate of 0.8 milliliters per hour per milligram of dried tissues of all soft parts of the animal; *Ostrea edulis* has a much larger filtration rate than other bivalves and the rate is 6.6 milliliters per hour per milligram of dried tissues.

Nannoplankton strained by the gills becomes enshrouded in mucus and moved by cilia along special pathways over the gills to the adoral tip of the gills, where the food drops onto the labial palps. There unsuitable pieces are shunted aside but food continues to the mouth.

The unsuited particles dribble down to the mantle lobes. Any particles coming in with the inhalant current that are too large to be carried along to the gills have already dropped out and lodged on the mantle lobes. All the rejects are combined, enveloped in mucus, and moved by the cilia on the mantle lobes to discharge areas near the pallial curtains.

During this time the valves are kept quiet for no longer than a few minutes at a time. Repeatedly the adductor muscle contracts quickly and drives the water out from the mantle cavity. At that moment the combined rejects are forcibly ejected as **pseudofeces** from their discharge areas. Thus the self-cleansing mechanism keeps the complicated sieve structure of the gills from clogging.

The pallial curtains are equally mobile. By opening or closing they control the size and location of the expelled current carrying the pseudofeces. Normally the inhalant current is restricted by the pallial curtains and enters through a narrow gap, about 3 cm. long in full-grown oysters. This gap is usually present directly anterior to the adductor muscle or in a slightly more anteroventral position. This gap is the **inhalant pseudosiphon.**

An **exhalant pseudosiphon** is kept open at a location in direct line with the axis of the cloacal passage. This pseudosiphon is about 1.5 cm. long and gapes about 2 to 3 mm. Oysters that have a promyal passage have a third pseudosiphon opposite the axis of the passage.

DIGESTION

A detailed description of the digestive functions has been given by YONGE (1926; 1960). The entire intestinal tract from esophagus to anus is weakly acid, registering average pH concentration from 5.93 to 5.2. The most acid part is the stomach with 5.2-5.6. The mantle cavity itself contains water that is close to neutral (6.8-7.2 pH).

These acid liquids within the digestive system must have some chemical effect on clay minerals accidentally taken in and contained in the excrements (compare ANDERSON, JONAS, & ODUM, 1958).

SELF-CLEANSING AND SELF-SEDIMENTATION

Problems of sanitation confront oysters, because they are immobilized. Waste materials of two sorts accumulate in their mantle cavities and must be removed. Feces are discharged into the cloacal passage, but pseudofeces accumulate in the exhalant and inhalant mantle chambers, mainly on the pseudofecal discharge area of the latter chamber.

Feces, digested food particles enveloped in mucus, are retained for a short time in the rectum, where they become compacted into long and firm pellets or rods. Then they are expelled by the action of cilia through the anus into the cloacal passage. There they and pseudofeces are picked up by the exhalant water current. They are also moved along by cilia that cover the exposed faces of the mantle lobes. They move on special ciliated pathways that converge at the cloacal discharge area near the cloacal pseudosiphon. Finally they are expelled in a fairly continuous stream while the oyster is feeding.

Pseudofeces are built up from any particles that happen to enter the mantle cavity but are rejected as food or cannot reach the mouth. Most of them are in the inhalant mantle chamber. Balled up with mucus, they are moved by cilia against the inhalant water current toward the pallial curtains, where they accumulate in larger masses at the pseudofecal discharge area near the inhalant pseudosiphon. A sudden contraction of the adductor muscle forces water from the mantle cavity through the pseudosiphon. This squirt of water carries the pseudofeces with it. Such squirts have been observed to go for a distance of more than one meter.

These powerful cleansing streams are repeated whenever sufficient pseudofeces have accumulated at the discharge areas in the mantle cavity. In this fashion, the mantle cavity is kept from fouling and the delicate mechanism of the gills as a food strainer is kept from clogging. In addition, the immediate surroundings of a live oyster are squirted free and cleaned of encroaching freshly deposited silt, mud, feces, and pseudofeces.

The self-cleansing mechanism is a fine adaptation permitting many oysters to live in turbid, sediment-laden waters. Without it some of the genera, notably *Ostrea, Striostrea,* and *Crassostrea,* could not have been able to invade brackish coastal waters produced by mud-laden rivers and to move up into lagoons and river estuaries.

Materials carried in the waters in suspension are called **leptopel** and consist of living and dead nannoplankton and of colloidally or otherwise finely divided organic and inorganic detritus. Oysters quite efficiently extract the leptopel from the waters and convert it into feces and pseudofeces. Both are somewhat compacted and denser than the surrounding waters so that they tend to sink to the bottom in the general vicinity of the oysters that produce them. Thus oysters bring about **self-sedimentation** in their neighborhood and perform an enormous task of clearing turbid waters and depositing fresh sediments of very fine grain size and very rich in organic matter (LUND, 1957a; 1957b). Oyster beds in brackish, turbid waters, composed of thousands of live individuals, must be effective sediment accumulators, and such beds are local depocenters of rapid sedimentation.

Sediments accumulated in this way consist of 1) silt fine enough to be carried in suspension before being strained out by the oysters, 2) clay-size particles of various clay minerals and plant debris, and 3) organic substances, such as oyster excrements, various indigestible organic materials, 4) mucus, which envelops both feces and pseudofeces, and 5) any additional materials brought in separately by waves and currents. Accordingly, the sediments have prevailingly very fine grain sizes. Organic sulfur compounds are present in the organic ingredients of the sediments, and sulfur is correspondingly quite abundant.

Because the sediments are rich in organic components they have large amounts of free energy available for bacteria to engage in decomposition with high rates of oxygen consumption resulting in strongly reducing, anaerobic conditions within the sediments, which can be called a **sapropel.** Hydrogen sulfide (H_2S) and finely divided and dispersed black hydrotroilite ($FeS \cdot nH_2O$) is formed in the sapropel within four days even when aerated sea water passes over it (Lund, 1957a; 1957b). The iron sulfide gradually changes into FeS_2 (pyrite or marcasite). Both the organic components and the finely divided iron sulfide minerals impart dark colors to the sediments, which are mostly stink muds or stink silts with a strong odor of hydrogen sulfide.

The hydrogen sulfide rises in the sediment and reaches the sediment-water interface. There it is oxidized to sulfurous and sulfuric acid. This acid environment at the top of the sediment accounts for the corrosion many oyster shells show. Corrosion is most noticeable around the umbones, which are commonly etched and deeply pitted, because they have been exposed to the acid environment the longest. Nevertheless, waters above an oyster bed are nearly always alkaline ($pH=8.3$ to 7.7) because of the buffering action of the calcium carbonate of the shells (Wells, 1961, p. 244).

PROPAGATION

SEXUAL MATURITY

Sexual maturity, that is, ability to reproduce, is reached rather early in the life of the oyster. In most situations it is reached within a year after the larva has settled down and metamorphosed. The length of time required depends on prevailing temperatures and availability of food. Up to a limit, the warmer the waters, the more food is available, the more time the oyster spends feeding, the greater is its rate of pumping a water current, and the earlier the young attached oyster reaches sexual maturity. In tropical and hot temperate climates it takes merely 20 to 30 days. In cool climates it takes longer and in frigid climates it generally takes more than a year.

The size at which an oyster attains sexual maturity depends on the average size of adults of the species. If adults are generally small, maturity is reached at a small size. At Aransas Pass, Texas (Menzel, 1955, p. 84-85), *Ostrea equestris* Say, 1834, the small species living on the east coasts of the Americas, reaches maturity 22 to 30 days after fixation of the larvae, when its sizes are 0.5 to 1.0 cm. (Fig. J6). This species is incubatory and it is ready to incubate its own larvae 31 to 60 days after the parental oysters have become attached and are merely 0.8-1.0 cm. in diameter. Species that average a larger adult size, reach maturity at somewhat larger sizes, between 1 and 2 cm.

In any case, sexual maturity is attained while oysters are still very small. This fact is significant in the interpretation of such small fossil oysters as the Jurassic genus *Catinula* and in the evaluation of ideas proposed to explain the disappearance during the Liassic of the stock of *Gryphaea arcuata* Lamarck, 1801 (see p. *N*1075-*N*1076).

Early sexual maturity is a safety device for the survival of the species. Given a limited span of life of the individual oyster, the earlier it attains maturity the longer does it contribute gonadal products for the survival of the species.

FECUNDITY

The enormous fecundity of oysters is another safety device for the survival of the species. Oysters produce uncountable eggs and spermatozoa. The number of the gonadal products depends on the size of the gonads, which in turn depend on the amount of food available and the age and size of the oyster. As an oyster grows bigger, its fecundity increases correspondingly.

The nonincubatory oysters produce smaller and more numerous eggs than the incubatory oysters. Calculations show that full-grown oysters of the nonincubatory genus *Crassostrea* produce in one spawning season the following numbers of eggs: *C. gigas* (Thunberg, 1793) 11-92 million (Galtsoff, 1930a); *C. rhizophorae* (Guilding, 1828) 99-170 million (Mattox, 1949); and *C. virginica* (Gmelin, 1791) 15-115 million.

Fecundity of incubatory oysters is more difficult to estimate, because the eggs remain in the mantle cavity for incubation. Probably the number of larvae found incubating in the mantle cavity of an oyster is approximately the same as the number of eggs it had delivered. An individual of *Ostrea edulis* Linné, 1758, 4 years old and about 7.3 cm. in size, can have as many as 2.05 million larvae incubating at one time (Walne, 1964, p. 303).

Here again prevailing temperatures of the surrounding waters have some influence. Wherever the summer is long and warm, there is more than one spawning period. In tropical regions, oysters spawn intermittently throughout the year (Mattox, 1949, p. 352). In frigid regions, for instance the Kattegat, north of Denmark, waters may remain too cold for several years in succession and no spawning may take place in those years. In such areas, oysters are close to extinction and may survive only in narrow inlets which warm up better than the waters further out. Such areas are the limits of the geographic range of a given oyster species (see p. *N*1036).

SPAWNING

Sperm or eggs, depending on the sexual stage of the spawning individual, issue from the gonads through the urogenital clefts in the cloacal passage of the exhalant mantle chamber. However, beyond that point their paths are different.

In the male engaged in spawning, cilia on the walls of the urogenital passages move the sperm balls out into the cloacal passage. There the balls break up into spermatozoa which are carried away by the exhalant water current to form a milky stream issuing from the oyster. Discharge may continue for several hours.

In the female, eggs are delivered into the cloacal passage by the same means, but then they are pushed through the ostia of the gills into the inhalant mantle chamber. During this period the oyster ceases to feed and there is no regular water current going from the inhalant to the exhalant mantle chamber. Rather, successive spasmodic and strong contractions of the adductor muscle force water and eggs from the cloacal passage through the ostia into the inhalant mantle chamber.

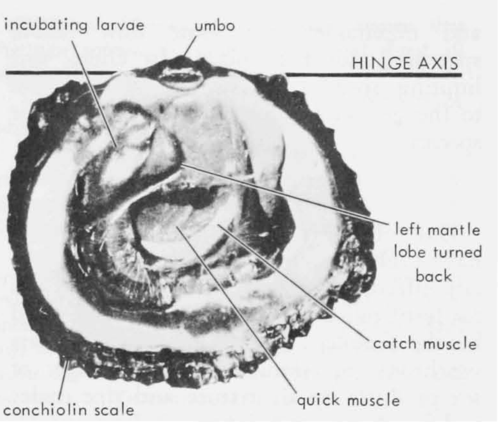

Fig. J36. Incubating oyster, *Ostrea (Ostrea) angassi* Sowerby, 1871, from South Australia, ×0.6 (Cotton, 1961). Left valve has been removed and left mantle lobe has been turned back to show mass of incubating larvae.

At this stage of female spawning incubatory genera begin to differ from nonincubatory genera. In the latter, the eggs accumulate in the inhalant mantle chamber near the inhalant pseudosiphon. Shortly afterward some more spasms of contraction of the adductor muscle expel a jet stream of water carrying the eggs through the pseudosiphon out for more than a meter. These forcible expulsions may last from a few minutes to two hours. Fertilization takes place in the surrounding water by haphazard meeting of egg and spermatozoon.

In incubatory oysters, the eggs remain in the inhalant chamber of the mother oyster and drop down onto her gills, labial palps, and mantle lobes. They are fertilized when spermatozoa are drawn into the inhalant mantle chamber by the pumping action of the mother oyster. Thus the chances of fertilization are somewhat better (Fig. J36).

Spawning depends very much on prevailing water temperatures. A certain specific limiting temperature must be attained and maintained for some time before spawning can take place. In effect, this limiting specific temperature sets a limit to the geographic distribution of an oyster species.

SYNCHRONY

One of the mechanisms which oysters have evolved to insure survival of the species effectuates the best possible conditions for fertilization of eggs as they are delivered by the females. This mechanism is mass synchrony or simultaneous discharge of sex products by all mature and ripe males and females in one neighborhood.

In an oyster bed many mature males and females become ready to discharge their individual sex products at about the same time. However, their discharge remains dormant for a time until they are triggered off by a special mechanism. This synchronization insures that as many individuals as possible participate at the same time.

If one male begins to discharge its sperm into water, 6 to 38 minutes later all the ripe males and females in the vicinity start discharging. The result is a maximal density of spermatozoa floating in the water when the eggs are discharged.

The sperm contains a powerful water-soluble stimulant and minute amounts of it suffice to stimulate a neighboring oyster that is drawing in the stimulant material with the inhalant current. Males can be stimulated also by eggs drawn in with the current. In this fashion stimulation can spread rapidly from oyster to oyster over a whole oyster bank, and tidal currents can spread action to neighboring oyster beds.

The stimulant is highly specialized. Sperm from *Ostrea* has no effect on *Crassostrea* species so that genetic isolation is maintained even if the two genera live side by side.

This mass reaction works best on densely settled oyster bottoms, and there must be a minimal population density below which this mass reaction is not attainable. Population density and sexual synchrony are interdependent adaptations in these animals. Because of synchrony the size of an actively and simultaneously interbreeding population of an oyster species tends to be enormously large.

INCUBATION

Several oyster genera incubate their larvae. Most incubatory species have an incubation period lasting 6 to 18 days. However, a species living on the Pacific coast of Chile, *Ostrea (Ostrea) chilensis* PHILIPPI, 1845, which delivers eggs unusually large for oysters, incubates for 5-6 weeks at temperatures of 13-15°C. (WALNE, 1963).

While they are incubating, eggs and larvae developing from them rest in the inhalant mantle chamber on the gills, labial palps, and mantle lobes of the incubatory adult (Fig. J36). They receive no nourishment from the adult except whatever they are able to gather from its inhalant water current. They depend on the original food (yolk) contained in the egg. For this reason eggs of incubatory oyster species are larger and richer in yolk. At the end of the incubation period, the adult oyster expels the larvae as a cloud, and the larvae begin their free-swimming larval periods. At the time of expulsion, the larvae already have bivalved shells, which furnish some protection.

Incubation has many advantages. For instance, fertilization of the eggs takes place under protection, in the inhalant mantle chamber of the mother, as spermatozoa are drawn in from the surrounding waters with the inhalant water current of the mother. The eggs have a better chance to become fertilized than would be possible if fertilization had to take place in the surrounding waters, as is the case in the nonincubatory oysters. Because of this aid, a larger percentage of eggs spawned become fertilized so that it is unnecessary for the mother oyster to produce as many eggs. Also, because the eggs are delivered under protection and the larvae remain protected while they incubate, the rate of their survival is much better. Rates of survival are estimated to be about 7 to 80 times as good in the incubatory as compared to the nonincubatory oysters.

These advantages allow the incubatory oysters to reduce the total amount, by weight, of their gonadal products. For this reason, incubatory genera need not have as large gonads in proportion to the entire visceral mass as the nonincubatory ones. As a rule, incubatory oysters have less capacious shell cavities, and their left valves are less deeply cupped. Some of the incubatory genera have flat, shallow left valves mostly devoid of deep umbonal cavities. Deep umbonal cavities prevailing in a genus are an indication that it is nonincubatory.

The only incontrovertible proof of the incubatory habit in a given oyster species is the presence of a brood of larvae within the inhalant mantle chamber of an adult. Such information is difficult to obtain, because incubation takes place only during a few months in a year. Only well-known commercially important oysters living on the coasts of scientifically advanced countries are likely to have been checked for this feature. In addition, it seems well established that nonincubatory genera have a promyal passage.

Incubating larvae have been found in the following genera:

1) *Alectryonella* (Lophinae). The single living species of this genus, *A. plicatula* (Gmelin, 1791) [=*Ostrea plicata* Chemnitz, 1785, =*O. plicatula* Lamarck, 1819, =*O. cumingiana* Dunker in Philippi, 1846, =*O. lactea* G. B. Sowerby, 1871] has been seen with incubating larvae (Amemyia, 1929; Wada, 1953).

2) *Lopha* (Lophinae). Wada (1953) reported *L. cristagalli* (Linné, 1758) with incubating larvae. According to Thomson (1954, p. 146-149), *L. cristagalli* is an ecomorph of *L. folium* (Linné) (see p. *N*1157), and the name is to be written *L. folium* (Linné) ecomorph *cristagalli* (Linné). Roughley found the *L. folium* (Linné) ecomorph *bresia* (Iredale) is incubatory (see Iredale, 1939, p. 397, and Thomson, 1954, p. 146-149).

3) *Ostrea* (Ostreinae). It is well known that the type species, *O. edulis* Linné, and about 10 other congeners are incubatory.

The following genera are known to be nonincubatory:

1) *Crassostrea* (Ostreinae). The type species, *C. virginica* (Gmelin, 1791), and about 8 other congeners are known to be nonincubatory (Cahn, 1950, p. 12, 17; Mattox, 1949; Paul, 1942, p. 9).

2) *Saccostrea* (Ostreinae). The Australian subspecies *S. cucullata* (von Born, 1778) subspecies *commercialis* (Iredale & Roughley, 1933) is nonincubatory according to Roughley (1933, p. 318) and so is the typical *S. cucullata* (von Born, 1778) according to Awati & Rai (1931, p. 38) and Someren & Whitehead (1961, p. 14).

3) *Striostrea* (Ostreinae). The type species, *S. margaritacea* (Lamarck, 1819), is nonincubatory (Korringa, 1956).

As to the other living genera, for example, *Hyotissa* and *Neopycnodonte* of the Pycnodonteinae, they have been investigated too little and nothing definite is known of the larval growth periods, although these two are scientifically very important because they are the last survivors of an important phyletic branch of the oysters. One must find anatomical features on them that are somehow linked with their incubatory or nonincubatory habit, as the case may be, in order to have an indication of their mode of larval growth. Such a feature seems to be the promyal passage of the exhalant mantle chamber. As to genera extinct today only features shown on the shell can be used. Here tenuous phylogenetic surmises can lead us to some conclusions.

ONTOGENY

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EGGS

Ripe unfertilized eggs are small and pear-shaped. They turn spherical as they are expelled and fertilized. Nonincubatory genera produce smaller eggs less rich in yolk. Their diameter is 0.046-0.09 mm. Eggs of incubatory oysters have a diameter of 0.09-0.323 mm. The smaller the eggs are the longer does the free-swimming larval period last.

The largest eggs known are produced by *Ostrea (Ostrea) chilensis* Philippi, 1845, living on the Pacific coast of Chile.

LARVAL STAGES

PROTOSTRACUM VELIGER STAGE

It takes fertilized eggs about 30 hours to 18 days to grow into the initial shell-bearing larval stage, depending on abundance of food and prevailing temperatures. This stage has two equal symmetrical equilateral D-shaped hyaline valves connected by a conchiolinous ligament located in the middle of the straight hinge. This is the straight-hinge veliger or protostracum veliger or phylembryo or D-shaped larval stage.

The anterior adductor is formed shortly before the posterior one. At first, the foot is a mere rudiment and a slight concavity between mouth and anus is the beginning of the exhalant mantle chamber.

A disc-shaped ciliated special larval organ, the **velum,** enables the larva to swim. It is located anteroventrally and completely retracts when the larva shuts its shell. In nonincubatory genera the eggs are released into the surrounding waters and grow there into planktonic and free-swimming protostracum larvae. Incubatory species let their fertilized eggs develop into protostracum veligers within the adult's inhalant mantle chamber.

At first, the straight valve margins at the hinge are only slightly thickened and are about half as long as the valves themselves. Later, these margins thicken and lengthen, forming the hinge plates of the prodissoconch, and rudiments of hinge teeth begin to grow as small thickenings. In the larvae of the Gryphaeidae, the thickenings or hinge teeth precursors are lined up in a continuous series all along the hinge, but in the Ostreidae precursors are only at each end of the hinge and a smooth gap separates them. Finally, the protostracum grows 0.095-0.235 mm. long; its height is about 7/8 of its length; its hinge extends for 5/7 of the length of the valves; the umbones are low and have not yet grown to rise above the hinge; the ligament remains in the middle of the hinge (see Fig. J37).

PRODISSOCONCH VELIGER STAGE

This is the stage commonly called umbo veliger larva, because the umbones of the shell are conspicuous. As this stage develops from the preceding protostracum veliger stage, the foot grows larger and more active. Its sole, near its heel-like base, now has a byssus gland. Both adductor muscles are present, and the rudiments of heart, kidneys, and gills make their appearances. A pair of black pigmented spots, or eyes, and a pair of otocysts grow in the wall of the visceral mass near the pedal nerve ganglia. These eyes are probably homologous with the cephalic eyes of other mollusks and appear shortly before the larva is ready to settle down (Fig. J38).

As the prodissoconch grows, its hinge thickens and the rudimentary swellings on the hinge grow into small, well-defined, rectangular, interlocking teeth or rather larval precursors of hinge teeth (Fig. J39). However, the hinge almost quits growing in length so that the valve margins gradually encroach upon and outflank the hinge ends. The valve margins grow progressively more inward, that is, toward the plane of symmetry between the opposing valves, so that the valves become more convexly tumid. The fastest growth is along the anteroventral valve margins, and the valves become quite inequilateral. By these growth tendencies the umbones rise above the level of the hinge and become more opisthogyral and bulgingly globose.

During this larval stage, that is, a considerable time before the larva is ready to settle down and metamorphose into a permanently fixed oyster, the left valve outgrows the right and becomes larger and more convex; its umbo grows more prominent than that of the right valve. This fact attests to the strong genetically fixed roots of the attachment habit of the oysters and

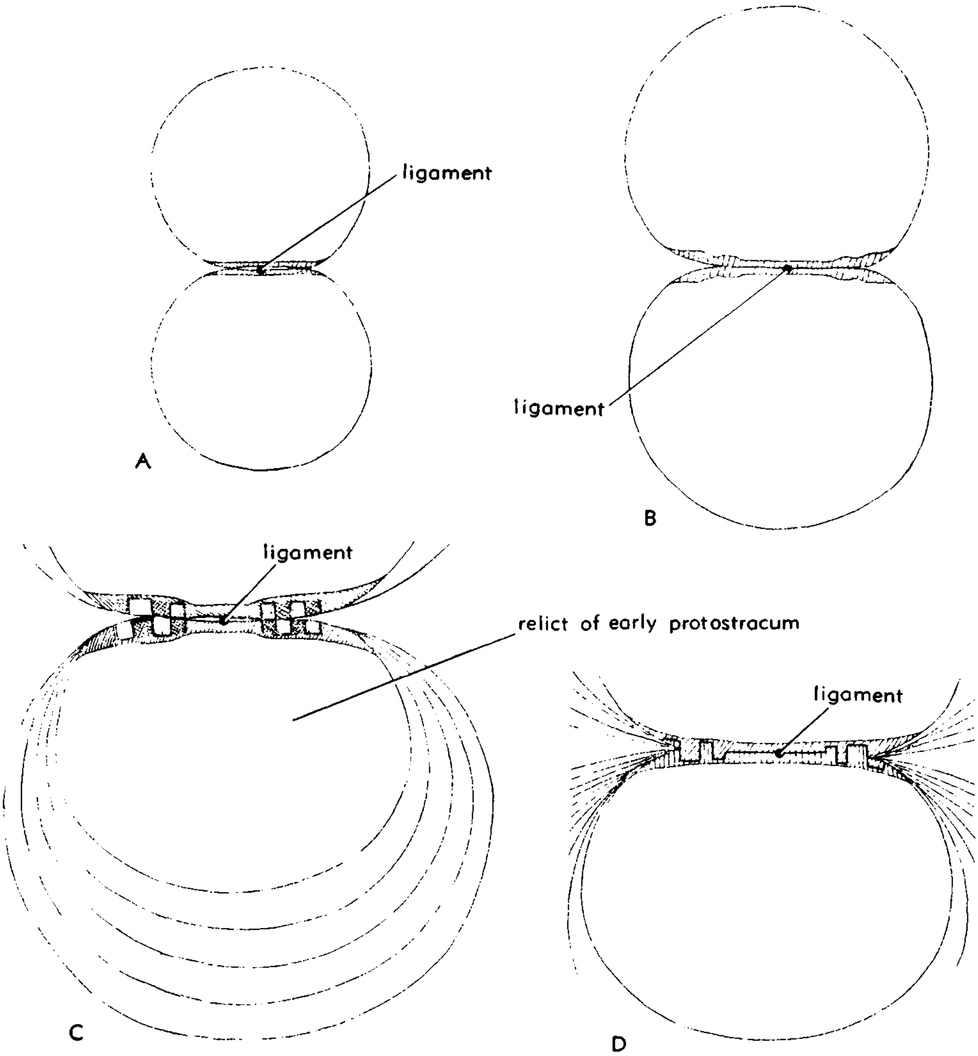

FIG. J37. Growth of larval shell (protostracum) of *Ostrea edulis*, ×170 (Ranson, 1939).

A. After 6 days of growth.

B. After 7 days, showing rudiments of larval hinge teeth and sockets.

C. After 20-25 days, showing well-formed larval precursors of teeth and sockets in arrangement characteristic of Ostreidae; valves are forced open.

D. Same, hinge in normal life attitude, not forced open, showing growth lines beyond ends of hinge.

explains why they attach themselves exclusively by their left sides.

At the end of this stage, prodissoconchs are 0.25-0.425 mm. long and there are many specific differences in the sizes and configurations of the prodissoconchs among the various species (RANSON, 1960a). There are also generic differences (FORBES, 1967).

BERNARD (1896) extended to the oysters his studies on the ontogenetic development of the hinge structures in the Bivalvia. Although he had available three oyster species, two of them living ones, his study was based only on a species from the Calcaire Grossier (Lutet.) of the Paris Basin, which he identified as *"Ostrea flabellula?"* [=*O.*

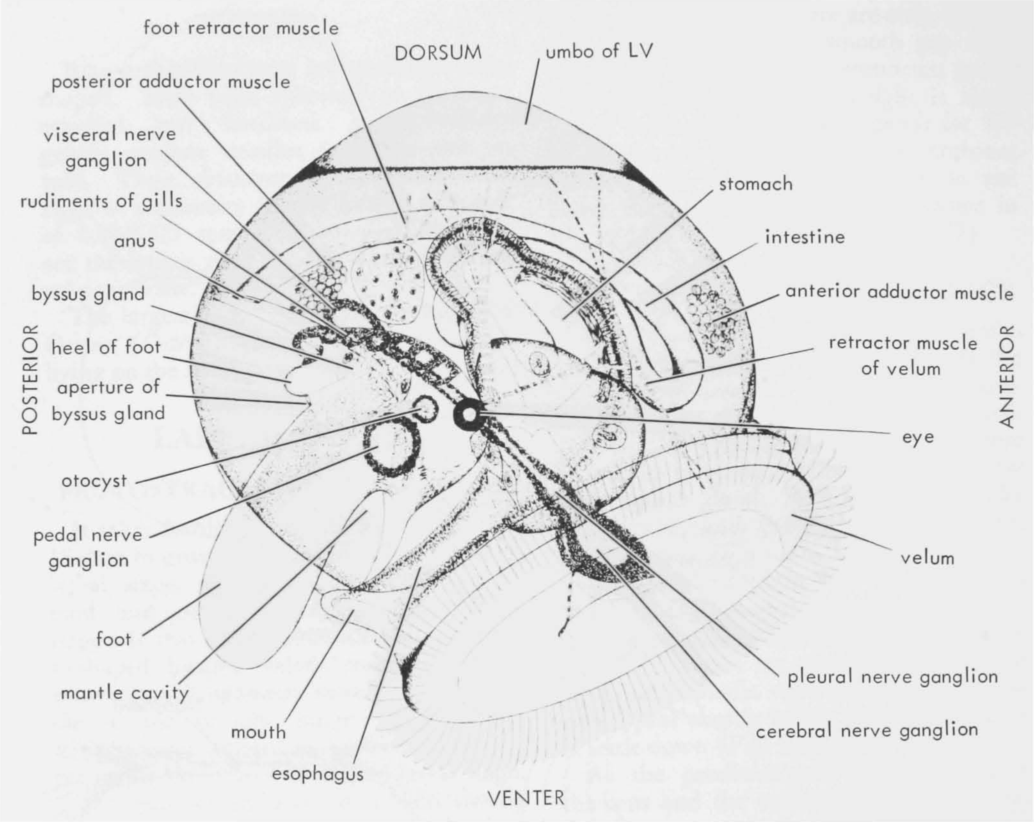

FIG. J38. Full-grown larva of *Ostrea edulis,* at end of prodissoconch veliger stage, ×335 (from Erdmann, 1934).

flabellula LAMARCK, 1806, =*Cubitostrea plicata* (SOLANDER in BRANDER, 1766)].

In so richly fossiliferous a sediment as the Calcaire Grossier, known to contain several sympatric oyster species, it is almost impossible to identify oyster prodissoconchs correctly and to try to relate prodissoconchs and very young attached oysters to fully grown adults of the same species. The young of one species may grow attached to the adults of another, and the more sympatric species are involved the more difficult is the task.

For that reason BERNARD's identification was only tentative. RANSON (1939a; 1941; 1942; 1948b; 1960a, fig. 1-16) demonstrated that the kind of prodissoconch illustrated by BERNARD (1896, p. 447, fig. 15) is found only in the Pycnodonteinae, that is, that BERNARD's identification was erroneous.

The hinge of the prodissoconch of the Pycnodonteinae differs considerably from that of the Ostreidae as was first recognized by RANSON. In the Pycnodonteinae the prodissoconch hinge carries an unbroken series of five interlocking teeth and no smooth gap occurs between them (Fig. J39).

In the Ostreidae, the prodissoconch hinge has two interlocking teeth at each end separated by a fairly long smooth gap. All these teeth are small, rectangular, interlocking, and somewhat higher than long. Each tooth fits into an opposing socket located on the other valve. In the common Ostreidae the anterior set of teeth is weaker than the posterior set. These teeth are larval structures and are the larval precursors of true teeth, homologous with the true teeth of adult eulamellibranchs. However, in oysters the larval tooth precursors never develop into true adult teeth. Strictly speaking, they should be called tooth precursors.

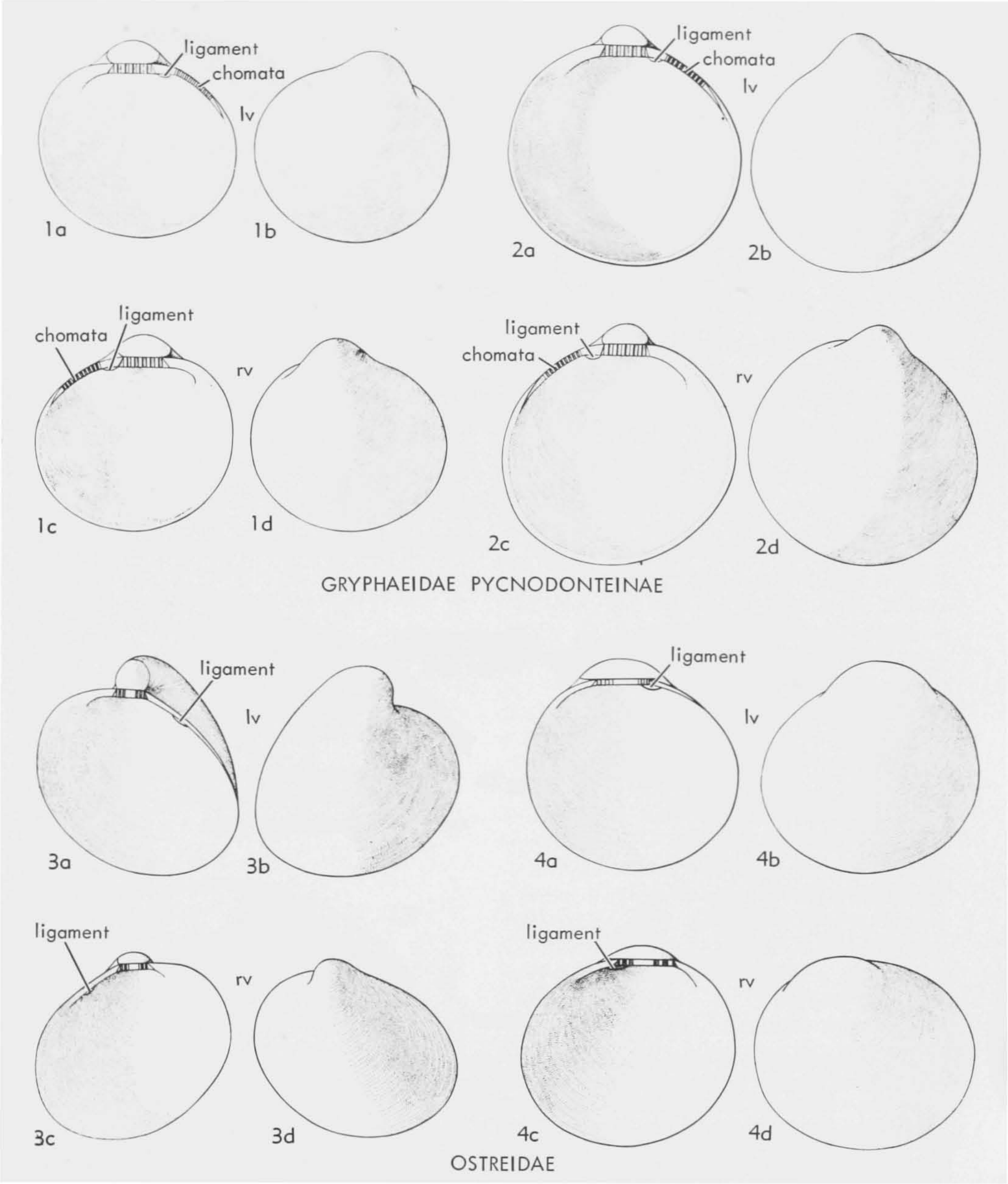

FIG. J39. Full-grown prodissoconchs of oysters, ×76 (Ranson, 1960a). All from living species.

1,2. Gryphaeidae-Pycnodonteinae. — *1a-d. Hyotissa hyotis* (LINNÉ), IndoPacific.—*2a-d. Neopycnodonte cochlear* (POLI), circumglobal.

3,4. Ostreidae.—*3a-d. Crassostrea virginica* (GMELIN), east and south coasts of North America. —*4a-d. Ostrea edulis* LINNÉ, west and south coasts of Europe, northwest Africa.

The ligament is at first, during the protostracum veliger stage and at the beginning of the prodissoconch veliger stage, in the middle of the hinge so that the two valves open up with the opposing umbones remaining close together (Fig. J37). Grad-

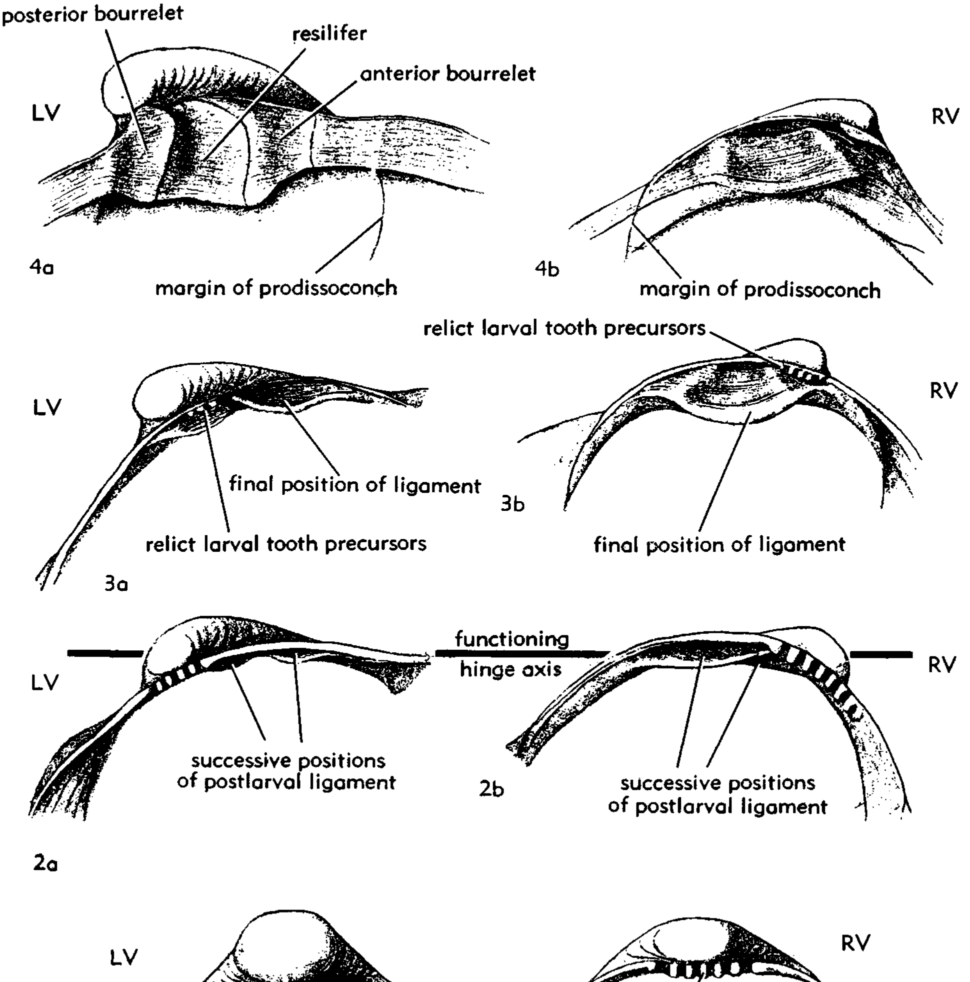

Fig. J40. Metamorphosis of hinge structures during growth from prodissoconch larval stage to early post-larval stage in oysters. An indeterminate species of pycnodonteine oyster (called *Ostrea flabellula*(?) in Bernard) from Calcaire Grossier (mid.Eoc.) of France, ×130 (Bernard, 1896).

1a,b. Prodissoconch showing well-developed larval tooth precursors in pattern characteristic of Pycnodonteinae.

2a,b-4a,b. Successive early postlarval stages showing obliteration of the larval tooth precursors and growth of ligamental area with progressive shift of positions of the functioning ligament.

ually, as the valves become more inequilateral and their umbones more prominent, the ligament migrates along the hinge toward the anterodorsal valve margins, leaving the umbones and tooth precursors behind in their own places. The shift of the ligament takes place smoothly; at no time is the shell without a well-functioning ligament. At the end of this shifting, the ligament joins what had been the anterodorsal margins of the valves and the original umbones, the hinge, and the tooth precursors come to lie posterior of the ligament (Fig. J40, J41).

Judging by the arrangement of ligament and tooth precursors in the full-grown

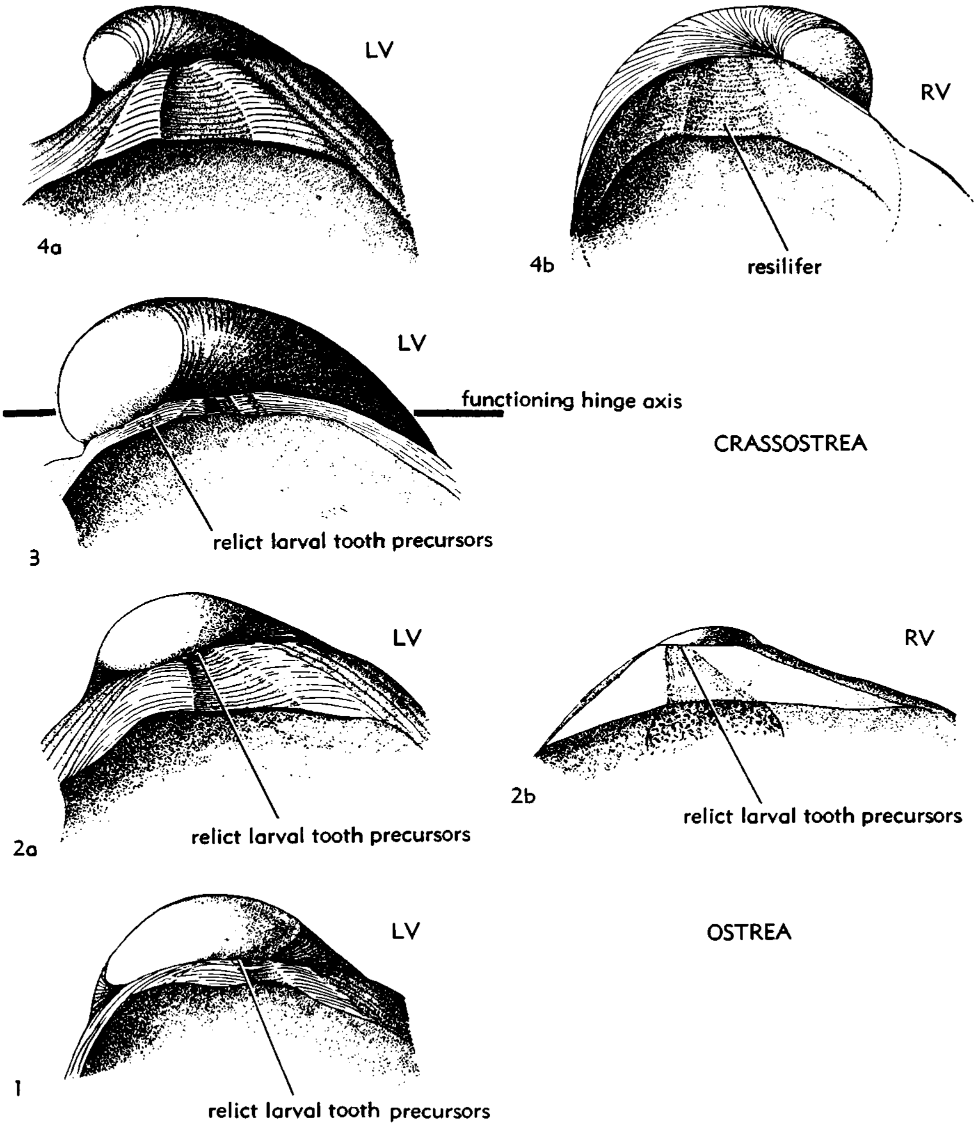

FIG. J41. Metamorphosis of hinge structures during early postlarval growth in oysters (Ranson, 1940).

1-2a,b. Ostrea edulis (LINNÉ, 1758), ×250, three, five, and five days old.

3-4a,b. Crassostrea angulata (LAMARCK, 1819), ×250, ×150, and ×250, two, five, and five days old.

prodissoconch, BERNARD concluded that in the oysters all the tooth precursors represent only the posterior half of the set normally found in Bivalvia and that the hinge structure of larval oysters would have to be called a demiprovinculum (or half-provinculum), because it differed profoundly from the provinculum of other Bivalvia. However, RANSON pointed out that the earlier larval stages of the oysters have a provinculum like other Bivalvia in that they have two sets of tooth precursors, one to each flank of the ligament.

Oyster larvae remain planktonic and free-swimming up to 33 days (ERDMANN, 1934, p. 7). Incubatory oysters have shorter free-swimming larval periods than nonincubatory ones. Shortest free-swimming periods are recorded (Walne, 1963; Millar & Hollis, 1963; Hollis, 1963) for *Ostrea (Ostrea) chilensis* Philippi, living on the coast of Chile, and *O. (O.) lutraria* Hutton, 1873, living on the coasts of New Zealand. They have free-swimming larval periods of a few hours to a few days. These extremes are thought to be special local adaptations of species living in exposed situations among strong currents, where longer periods would allow the larvae to be carried on out to sea into dangerous environments. The adaptations prevent excessive larval mortalities. Durations of larval periods depend also on prevailing temperatures and availability of food for the larvae. Warm and plankton-rich waters accelerate growth.

FIXATION

As the end of the prodissoconch veliger larval stage approaches, the larva becomes ready to attach itself to a substratum and undergoes extensive internal changes and rearrangements of its organs (metamorphosis). Nearly all oyster larvae must become attached to a firm substratum or perish.

Exceptions are few. Rarely do a few larvae of the living species *Ostrea (Ostrea) edulis* and *O. (O.) chilensis* succeed in growing into adults without becoming firmly attached (Walne, 1963). Only a few extinct species have been discovered that were able to settle on a very soft substratum, such as ooze. All or nearly all their larvae grew into adults lying loose on the sea bottom, and the adults became sexually mature and propagated the species. Such species seen by me are:

1) *Exogyra laeviuscula* Roemer, 1849, from the top chalk layer of the Dessau Formation (early Campan.) at the top of the Austin Chalk in central Texas.

2) *Ilymatogyra arietina* (Roemer, 1852), from the Grayson Marl (Cenoman.) and other homotaxial formations of Texas and northeastern Mexico (Fig. J32; see Fig. J94).

3) *Rhynchostreon suborbiculatum* (Lamarck, 1801) [=*R. columba* (Lamarck, 1819)], Cenomanian and Turonian of Europe and Syria (see Fig. J97).

These three exogyrine oysters have very slender left beaks noticeably more spirogyral than those of other exogyrine oysters which commonly have fairly large attachment imprints.

4) *Odontogryphaea thirsae* (Gabb, 1861) from the Nanafalia Formation and other homotaxial formations (Sparnac.) of Alabama. Louisiana, and northern Mexico (Fig. J34; see Fig. J64).

These exceptional species are divisible into two categories: very specialized Exogyrinae (1-3 of above) and homeomorphs of *Gryphaea* (4). Such species, for some unknown reason, have traces of coloration preserved. They are in the form of brownish radial streaks (see "Pigmentation," p. *N*997, and Fig. J33, J34). Their shells have no visible attachment imprints at the left umbo. They may have incidental attachment imprints at other places caused by crowding of neighboring shells.

The full-grown oyster larva can swim with its velum and crawl about with its foot in search of a suitable location, when it is ready to become affixed to a substratum. Normally the substratum must be firm and clean, free of a film of mud, and free of the slimy gelatinous cover growing algae produce. The larva in search of a suitable location prefers close proximity of young adults of the same species (Knight-Jones, 1951). This preference tends to maintain live oyster reefs and is essential to successful propagation.

Finally, the larva settles down with its umbones held up and its foot and ventral valve margins resting against the substratum. After some irregular movements, the final attitude is assumed: the right valve is on top, the mid-ventral margin of the left valve is pressed flat against the substratum and the commissural plane of the valves is inclined about 30° to it (see Fig. 78, p. *N*94). The byssus gland on the sole of the foot then excretes a drop of liquid which spreads in the narrow space between left valve and substratum. By natural tanning, the sticky liquid turns fairly rapidly into horny, no longer water-soluble conchiolin, firmly cementing the left valve of the larva to the substratum. This is the end of the larval stage and the beginning of rapid metamorphosis of the animal into a young adult.

All oyster larvae, except those of the Exogyrinae, assume approximately the same final attitude with reference to the substratum when they are full-grown and ready to affix themselves. Larvae of the Exogyrinae settle with the posterior margin of the left valve pressed flat onto the substratum so that rapid growth of the free anteroventral margin of the left valve, outgrowing the rest, initiates a spiral growth pattern immediately after fixation. This tilted fixation attitude of larvae of all Exogyrinae at the moment the larvae assume their final attitude just before fixation attests to the monophyletic origin of the subfamily and is one of the justifications for regarding them as a natural taxon and as a subfamily.

Because larvae of normal oysters can settle only where firm and solid substrata are available to them, oysters can inhabit only certain restricted brackish and marine habitats and are unable to occupy large sea-bottom areas that are covered exclusively by soft mud or ooze. Special adaptations are necessary for the oysters to be able to occupy sea bottoms that have only tiny shell fragments scattered on an ooze bottom or are composed of ooze exclusively. The four species listed above were adapted to the last-mentioned, highly specialized situation (compare p. *N*1071).

METAMORPHOSIS

The shell of the full-grown larva is composed of aragonite (Stenzel, 1964). As soon as the oyster has become attached, it begins depositing new shell material at the valve margins. This new ring is composed of calcite and shows special shell structures, for instance, the prismatic shell layer of the right valve. Henceforth, the major part of the shell deposited by the oyster is made of calcite.

Rapid and radical changes among the organs take place as soon as the larva has become fixed. Organs no longer needed disappear, making room for other needed organs to grow in size and to shift into more favorable positions.

The velum is a bulky locomotor organ in the larva, which is located anteroventrally. By its size it tends to push aside mouth and foot, away from the anterior adductor muscle. Because locomotion is no longer possible after fixation of the larva, the velum and the foot with its byssus gland atrophy rapidly during metamorphosis. Thus a large space, formerly occupied by the velum, becomes available for other organs to expand or shift into.

Its fixed position prevents the young adult oyster from going after its food; rather, it must gather its food as it passes by. This the oyster does by using the gills as a sieve. As filter-feeding is adopted, the gills must become larger.

However, the mouth must remain near the anterior end of the sieve structure of the gills in order to be in correct position for receiving food from the gills. As the gills grow allometrically, the mouth must shift with them correspondingly. When the velum disappears, the mouth is free to shift forward, toward and against the anterior adductor muscle.

Because the gills have become so long that the mouth lies against the anterior adductor muscle, this muscle must become confined. It can neither shift nor grow in size; its fate is sealed.

In contrast, the posterior adductor muscle becomes unrestricted and can grow in size; it also can shift position to occupy the space vacated by atrophy of the foot and velum and by the shift of the mouth. Thus the posterior adductor muscle gets to occupy a more favorable position as to leverage, effectiveness, and ability to grow in size. Very soon it takes over the work of both adductor muscles and the anterior one disappears. The eyes of the larvae disappear also.

The foot, being a locomotor organ, becomes useless and disappears completely except for some anterior pedal muscles which take on new, as yet poorly understood functions and become the Quenstedt muscles of the adult oyster.

One of the results of the shifts among the organs is that the mouth-anus axis has to rotate counterclockwise during metamorphosis. If the pivotal axis of the hinge is chosen as a fixed reference line for the purpose of measuring the amount of torsion of the mouth-anus axis, that axis in the full-grown larva is at minus 70° and in the adult oyster at plus 47° to the pivotal axis; the total amount of torsion is 117° counterclockwise.

Metamorphosis of hinge structures was first investigated by BERNARD (1896) on fossil material. RANSON (1939a, 1940b) added to these observations, corrected them and gave the metamorphoses of the hinges on two living European oysters, *Crassostrea angulata* (LAMARCK, 1819) and *Ostrea edulis* LINNÉ (Fig. J41).

The structure of the hinge had already undergone considerable change during the growth of the prodissoconch veliger larva. The ligament had shifted from its original position in the provinculum, midway on the hinge, to a position considerably anterior to the larval tooth precursors. In that position the ligament and hinge structure supporting it grow vigorously during and after metamorphosis. The larval tooth precursors have become devoid of function and are left more and more behind, to become obscured by growth of the ligament and its supports. Their obliteration is finished during metamorphosis.

POSTLARVAL STAGE

GROWTH

Rate of growth of the postlarval oyster is influenced by local food supply, prevailing temperatures, and the amount of time the animal is able to keep its shell open and feed.

Most rapid growth is in the first three months after fixation. After that the growth rate declines gradually. Toward the end of a long life (after about eight years), the oyster individual ceases to grow in size as concerns the soft parts of its body so that volume of the shell cavity occupied by the soft parts remains nearly constant, but the shell continues to grow and the whole animal gains weight, except that destruction of the shell by bacterial corrosion and by attacks of shell parasites continues all the time.

Growth rates are smaller in winter than in summer, and growth may cease altogether in severe winters. Consequences of their climatic effect make it possible to estimate the age in years of an individual oyster.

Crassostrea madrasensis (PRESTON, 1916) [better named *C. cuttackensis* (NEWTON & SMITH, 1912)], living in Madras Harbor on the tropical Indian coast in waters of 26.2-29.6°C., has shell growth rates of 0.27-0.62 mm. a day (PAUL, 1942). This is the fastest growth rate recorded for the shell of an oyster.

LIFE SPAN

Very few oysters have been observed individually for more than one to five years in their natural habitat so that direct observations of the life span are exceedingly scarce. However, there is a record (BJERKAN, 1918) of one old, extra-large individual of *Ostrea edulis* from near Bergen, Norway, which had been watched off and on for 20 years and which must have been 25 or more years old. Its valves weighed 251 gr. (left) and 204 gr. (right valve).

Two methods of estimating the age in years of an individual oyster through inspection of its shell are noted. Because the shell ceases to grow, or nearly so, during the winter, either one large or a group of closely spaced imbrications are produced on the valves in winter. They show better on the left than on the right valve. Thus the age in years should equal the number of such markers found on the left valve.

In a mild winter, however, imbrications may fail to show up altogether. On the other hand, extended or repeated storms and rainy years with long periods of too low salinities may produce additional, nonannual imbrications. This method of estimating the age of an individual oyster is obviously exceedingly difficult or even unreliable (MASSY, 1914) (see Fig. J42).

A better method, first used by POISSON (1946, p. 6), is based on the annual growth layers visible on the ligamental area. The consistency and composition of the shell material deposited in a year changes seasonally. In the colder season, during slow shell growth, the material deposited is darker and richer in organic matter; the shell substance deposited in the warmer months is lighter-colored, less rich in organic matter, and more solid and stronger. These annual layers can be seen when the shell is cut through in dorsoventral direction (BJERKAN, 1918). It is much easier without any sectioning, however, to see the annual layers on the ligamental area. Visi-

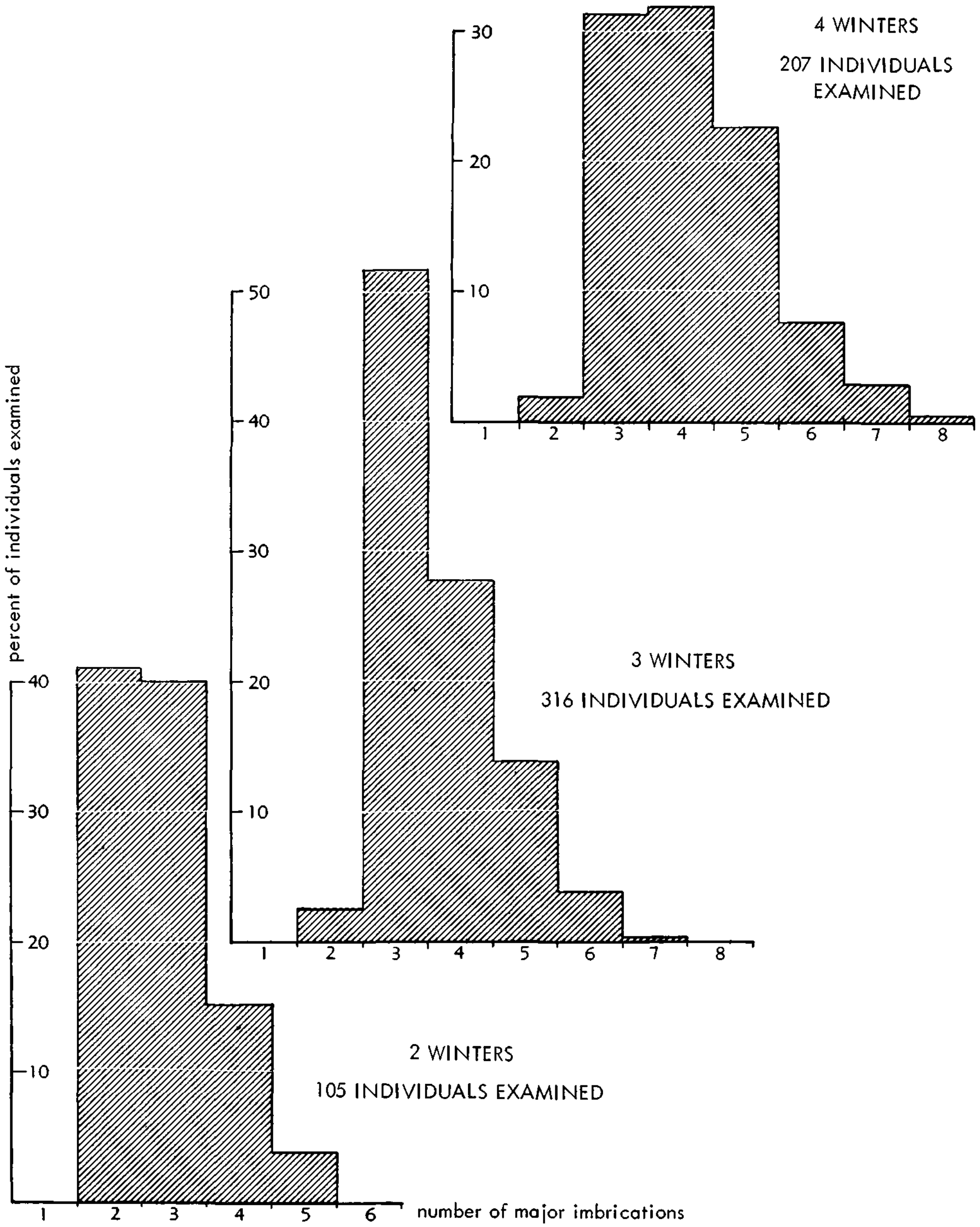

FIG. J42. Number of major imbrications on LV of *Ostrea edulis,* from Ireland, as related to number of winters survived by the animals, given in percentages of individuals examined (Stenzel, n. From data given by Massy, 1914).

bility of the annual layers on the ligamental area can be improved by a slight amount of buffing or washing with dilute hydrochloric acid. Even this method used on old and large shells gives an incomplete estimate, because generally the first-grown part of older shells is lost through corrosion during the animal's lifetime (Fig. J14, J30; see Fig. J124).

The oldest oyster seen by me is a specimen of *Crassostrea bourgeoisii* (Rémond, 1863) from the Temblor Formation (Mio.) in California (Calif. Acad. Sci., no. 33269), which has a ligamental area 2.0 cm. long and 13.1 cm. high, as measured along the curves of the mid-line. The apex of the ligamental area is missing; the remainder shows 43 annual layers. Counting the annual layers of the ligamental area on the left valve of *Crassostrea gryphoides* (von Schlotheim, 1813) from the Miocene of Europe, Haranghy, Balázs, & Burg (1965) determined the life span of this oyster as more than 47 years.

SHAPE, FORM, AND SIZE OF SHELL

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Function of the shell of free-moving, normal Bivalvia, including the distant and unknown ancestors of oysters, is to protect all soft parts of the animal, including the foot. Shape of the shell and its capacity must be adapted to the animal's activities and locomotion and must be adequate to let the foot retract completely when the animal shuts its shell.

Because oysters are sedentary, they have lost the organ of locomotion, the foot. There is no need for their shell to enclose a foot and to be adapted to any kind of locomotion. The absence of these two necessities allows other factors to assume importance and to determine significant features of the shell. There are many such factors and they cause a bewildering profusion of shapes, forms, and sizes.

CONSEQUENCES OF SEDENTARY MODE OF LIFE

Sedentary animals tend to have rounded outlines, that is, cylindrical, conical, or globular shapes, and they tend to develop radially arranged organs. Oysters have the same tendencies, but cannot develop them much.

Ostrea (Ostrea) equestris SAY, 1834, living on the east coast of the Americas, tends to grow in orbicular outline, that is, the height becomes almost equal to the length of its shell, if the individual is not obstructed in its growth by neighboring shells or irregularities of the substratum (GALTSOFF & MERRILL, 1962, p. 238). Many other oyster species follow this pattern.

Sedentary animals have no weight problems; they do not have to move their bulk and support of it is not difficult in most cases. For that reason, sedentary Bivalvia are commonly larger than mobile ones and have thicker and heavier shells. Many oysters follow this pattern.

INFLUENCE OF GILLS

Influence of the gills on the shapes of shells is proportionately larger in the oysters than in Bivalvia that have a large foot. This is so because oyster gills are proportionately larger and, in addition, their gills do not have to share the mantle/shell cavity with a foot.

The following features indicate influence of the gills: 1) Anterior and ventral valve margins are subparallel to the distal edges of the gills in all oysters. 2) The shells as a whole are noticeably curved to conform with the curved outline of the gills in all oysters. 3) The shell has a more or less conspicuously projecting posteroventral tip end, the branchitellum. It is close to the palliobranchial fusion, and the aboral end of the gills points toward it.

These features are most strongly emphasized in oysters that have a sickle-shaped outline. In them the gills are long and narrow, curved and strap-shaped, and the visceral mass is very small so that the gills determine outline of the shell.

The following genera have sickle-shaped outlines: *Agerostrea* VYALOV, 1936, *Rastellum* FAUJAS-SAINT-FOND [1802?], and *Cubitostrea* SACCO, 1897 (see Fig. J116, J117, J133, J138, J139).

In addition, species of other genera approach or have sickle shapes, although congeneric species do not. Here belongs *"Ostrea"* [probably new genus] *quadriplicata* SHUMARD, 1860, from the Fort Worth Limestone to Mainstreet Limestone, Washita Group (late Alb.) of north-central Texas. Many species of the Exogyrinae related to *Ceratostreon* BAYLE, 1878, or placeable in that genus are narrow and sickle-shaped. An example is *Exogyra* [*sensu latissimo*] *sigmoidea* REUSS, 1844 (v. 2, p. 180), from the basal conglomerate (late Cenoman.-early Turon.) of the vicinity of Praha, Czechoslovakia (ZÁRUBA, 1965).

Agerostrea is related to *Rastellum* and differs from the latter by the smooth median area restricting the plications to the flanks of the shell. It is connected to *Rastellum* by transitional species. *Rastellum* has subequal valves, both ribbed; the zigzag commissure has many long tapering acute-angle points. The muscle pad is comma-shaped and much closer to the hinge than to the branchitellum. *Rastellum,* in turn, is connected to *Lopha* of the Triassic and Jurassic by many transitional species. There seems to be no room for doubt that the three genera have close relationships.

Cubitostrea has a ribbed, but not plicate, left valve and a flat nonribbed right valve; the right valve is considerably smaller than the left. It is closely related to *Ostrea,* from which it arose in Eocene time.

Thus, the sickle-shaped oysters originated from at least two roots. They are a polyphyletic convergent collective group. They are nonestuarine, euhaline, warm-water oysters apparently restricted to very fine-grained sediments, more or less rich in lime.

INFLUENCE OF PSEUDOSIPHONS

INHALANT PSEUDOSIPHON

Much, or even all, of the inhalant water current enters the mantle/shell cavity through the inhalant pseudosiphon, whenever the oyster has its shell open and is feeding (see p. *N*1000). The part of the gills that is nearest to the inhalant pseudo-

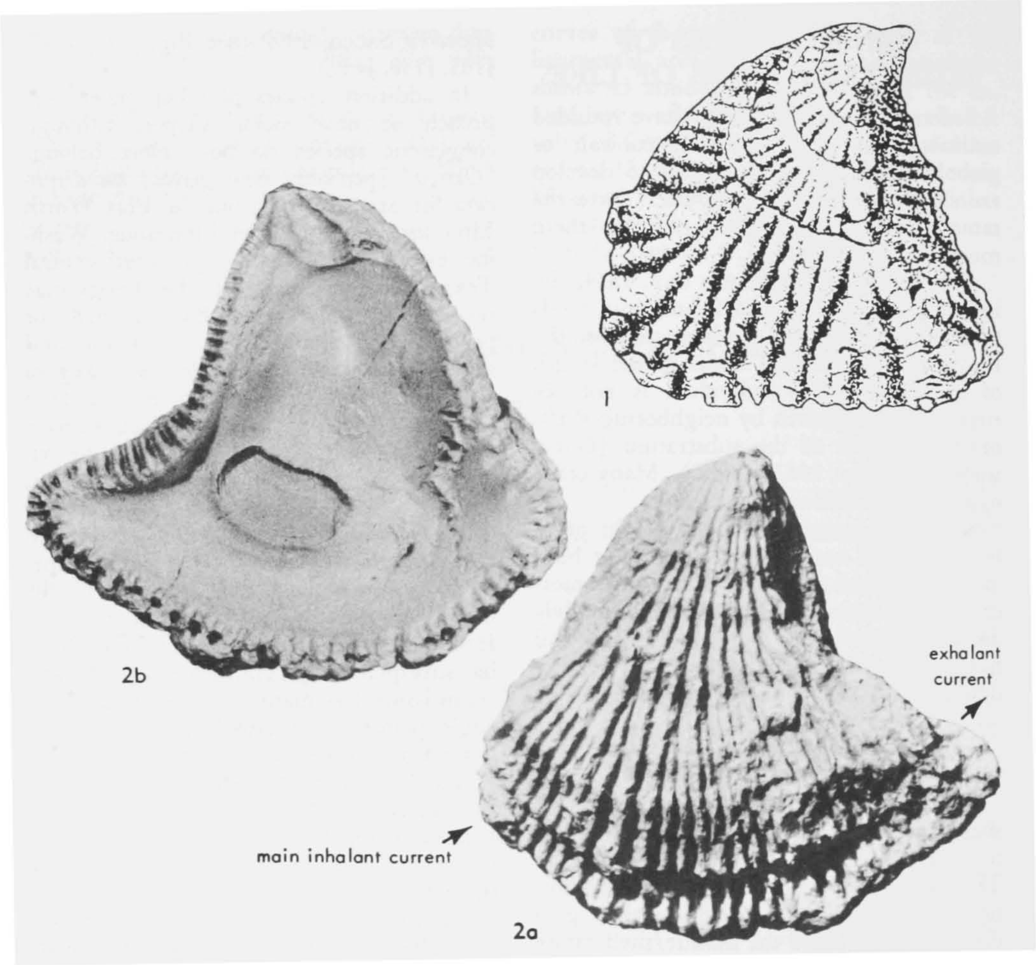

FIG. J43. Triangular shell outlines in oysters.

1. Cubitostrea perplicata (DALL, 1898), Tallahatta Formation, mid.Eoc.(Lutet.), Alabama, USA, exterior of LV, ×0.7 (Stenzel, 1949).

2. "Lopha" villei (COQUAND, 1862), U.Cret.(Maastricht.), Chouf Motta, Algeria; *2a,b,* LV, ext., int., ×0.7 (Stenzel, n. Specimen by courtesy of C. W. DROOGER, Univ. of Utrecht, Netherlands).

siphon is in the best position for receiving the current and for collecting food particles. It is to advantage of the animal to provide the best catchment area of the gills at that place. For this reason, the gills of all oysters are widest there and taper thence to both ends of the gills.

How rapidly the gills taper from their widest place depends on the stability, site, and size of the pseudosiphon. If it remains small and opens up at the same place every time the oyster is feeding, the taper of the gills is likely to be rapid and the gills will have the outline of a low elongate triangle curved in conformity of the shell and the widest place on the gills, the apex of the triangle, will be well defined. On the other hand, if the pseudosiphon is a long slit and opens up variably in a general vicinity, the taper of the gills likely will be much less rapid and there will be no narrowly defined widest place on the gills.

In the first case the shell will have a projecting anteroventral rounded corner. Such shells are more or less clearly triangular in outline: *"Lopha" villei* (COQUAND, 1862), Maastrichtian of N.Africa (Fig. J43); *Cubitostrea perplicata* (DALL, 1898) from the upper Tallahatta Formation (Lutet.) of Alabama, USA (see STENZEL, 1949, fig. 3; GEKKER, OSIPOVA, & BELSKAYA, 1962, v. 2, fig. 24-1) (see Fig. J116, J117); *C. prona* (S. V. WOOD, 1861) from the Lattorfian beds of England. Triangular shapes are possibly restricted to oysters that have no promyal passage and in which the convexities of the two valves are subequal.

EXHALANT PSEUDOSIPHON

The exhalant pseudosiphon takes care of most of the exhalant water current of the oysters, and metabolic waste products are expelled through it. These waste products present problems of sanitation; they must be disposed of in such a fashion that they cannot by any chance reenter the mantle cavity of the animal.

The Gryphaeidae are the only oysters in which the exhalant pseudosiphon has great influence on the configuration of the shell. Their left valves are divided by a radial **posterior sulcus** into a main part and a smaller **posterior flange** (see Fig. J74, J83, J84, J87).

In most species the sulcus is a deep groove, in others it is shallow; in some, notably in *Gryphaea arcuata* LAMARCK, 1801, from the Liassic of western Europe, it is evanescent as a groove, but remains indicated by a flexure in the trend of the growth lines. In the strongly plicate genus *Hyotissa* of the Pycnodonteinae the sulcus is difficult to discern from the other sharp plications of the shell. However, it makes a deeper and broader groove on the left valve than the other plications do, and the corresponding radial fold on the right valve is a broader, higher, and more prominently upturned ridge than the other plication ridges in this genus.

At the posteroventral margin of the left valve the sulcus ends with an obtuse, rounded angulation shown by the growth lines of the valves. This angulation tends to become more obscure with age. This angulation is the branchitellum of the Gryphaeidae (see Fig. J74,*3e,f*).

The posterior flange of the left valve has a convex or highly convex cross section differing in shape from species to species. The terminus of the posterior flange at the valve margin is the place at which the exhalant pseudosiphon was located and at which the organic waste products of the oyster were ejected while the animal was alive. The posterior flange is the growth track of the successive positions the exhalant pseudosiphon occupied during the growth of the animal.

LEOPOLD VON BUCH (1835) was the first to attempt an explanation for the posterior flange and sulcus, which he had noticed on *Gryphaea.* According to his explanation the pull of the posterior adductor muscle caused formation of the sulcus. This hypothesis is hardly valid, however, because the shell morphology is determined by the attitude of the shell-secreting edges of the mantle lobes, that is, at the very edges of the valve margins, and these are well removed from the insertion of the adductor muscle. Be it to his credit that he was the first to recognize in print that there is a problem of explaining the feature.

INFLUENCE OF SUNLIGHT

MEDCOF (1949) experimented with *Crassostrea virginica,* growing two sets side by side, one exposed to sunlight and the other shaded. Specimens exposed to sunlight grew (linear growth rate of shell) about 30 percent slower than shaded ones and their shell walls were thinner and had fewer chalky deposits than the shaded set. Those exposed to sunlight had stronger, harder, and denser shells and their shell walls had higher specific gravities.

Oysters growing in the shade had flat or concave right valves mostly; many of those growing in the sunlight had convex right valves. Oysters exposed to sunlight had more chunky compact shells and their left valves were more convex.

The left valves of oysters exposed to sunlight had more prominent ornamentation. The left valves tended to become ribbed or fluted and to have a serrate margin. The right valves had more color streaks (Fig. J44).

Oysters exposed to sunlight had abundant sea lettuce *(Ulva)* growing on them but had fewer mussels (*Mytilus edulis* LINNÉ) and oyster spat attached. Shaded oysters had very little of sea lettuce, but had about three times as many mussels and spat growing on them, on the upper

Fig. J44. Shell features of *Crassostrea virginica* (Gmelin) taken alive in Tarpon Bay, Sanibel Island, Florida, USA, ×0.7 (Stenzel, n). [These oysters grew exposed to air at low tide and show the strong ribs characteristic of exposure to sunlight. Specimens courtesy of R. Tucker Abbott, Acad. Nat. Sci. Philadelphia.]—*1*. Outside view of LV.—*2a,b*. Inside and outside views of RV.—*3a,b*. Inside and outside views of LV, same individual.

as well as the lower surfaces. The upper surface of oysters exposed to sunlight was avoided by epibiotic animals.

Exposure to sunlight and different substrata possibly are the causes of extreme polymorphism in a case analyzed for the first time by Thomson (1954, p. 146-149, pl. 2, fig. 3-4, and pl. 3, fig. 1-4). The case involves the species which he called *Ostrea folium* Linné. He came to the firm conclusion that the names *Ostrea folium* Linné (1758, p. 699), *Mytilus crista galli* Linné (1758, p. 704), and *Ostrea (Pretostrea) bresia* Iredale (1939, p. 396) all stood for the same polymorphous species, which he chose to call *O. folium,* because it has page priority and because as to shape it is intermediate between the other two (see Fig. J47, J129, J130).

According to Thomson, individuals of that species which grow in intertidal situations and are attached to a flattish substratum or to each other develop long and strong hyote claspers and well-defined strong plications few in number; they are the ecomorph known as *Lopha cristagalli.* While individuals that remain completely submerged and grow preferentially on gorgonid corals develop a lanceolate outline, many small plications and many small and short claspers embracing the gorgonid stem. These ecomorphs are commonly called *Lopha folium* (Linné) and are intermediate between the other two as concerns plications. *Ostrea bresia* is founded on individuals of orbicular outline furnished with irregular, more rounded plications.

It so happened that *L. cristagalli* became the type species of *Lopha* Röding, 1798, *L. folium* the type species of *Dendostrea* Swainson, 1835, and *O. bresia* the type species of *Pretostrea* Iredale, 1939. Thus *Lopha* has clear priority and the other two become its junior subjective synonyms. As to the name for this polymorphous species, Thomson's choice must stand, because he is the discoverer of these relationships and the first reviser in the sense of Article 24.

The East African mangrove oyster *Saccostrea cuccullata* (von Born, 1778) has two distinct ecomorphs: 1) a chunky irregularly shaped oyster, commonly rounded and flat, with fairly thick shell walls and coarsely crenated valve margins, and 2) a spiked form that has thinner, more fragile shells with foliated shell shoots, up to 3 cm. long, extending outward from the shell margins. The spiked form grows at a higher intertidal level and is exposed to air and sunshine for 7.75 to 124 hours during low tides. The other becomes exposed 0 to 20 hours only. So different are the two, that Someren & Whitehead (1961) considered them different species. It is, however, more likely that they are ecomorphs of the same species (see Fig. J54).

INFLUENCE OF SUBSTRATUM

Shell shape is influenced by the substratum in two separate and fundamentally differing ways: 1) Fortuitous nonheritable indivdual effect produced by a local hard substratum resulting in xenomorphism on an individual oyster and 2) the mass effect produced by adaptations of large populations to special widespread facies of the substratum resulting in adaptive, heritable features.

XENOMORPHISM

The outside surface configuration of one valve closely imitating the configuration of the substratum under the other valve is called **xenomorphism** or xenomorphic sculpture. In some individual oysters the umbonal region of the right valve resembles closely the configuration of the hard substratum to which the left valve is or was originally attached. Xenomorphic sculpture is patterned after ammonites, belemnites, snails, trigonias or other bivalves, echinoids, echinoid spines, coral colonies, twigs of sea fans *(Octocorallia),* or other hard materials, depending on which animal or object the oyster was growing. Xenomorphism is found also in other attached shell-bearing animals, for example, *Anomia* (Stenzel, Krause, & Twining, 1957), *Myochama, Plicatula,* barnacles, brachiopods.

Xenomorphism in oysters was noted as an unexplainable curiosity by pre-Linnean authors, for instance, d'Argenville (1742, p. 316, pl. 22, fig. F), and has been described in innumerable cases (Judd, 1871; Schäfle, 1929; Saint-Seine, 1952; Stenzel, Krause, & Twining, 1957, p. 98-99). The first to give a good description was Defrance (1821, p. 21) and the first to explain it was Gray (1833, p. 780-784). Good bibliographies are given by Schäfle (1929) and Saint-Seine (1952).

The first to apply a definite term to it were Staff & Reck (1911, p. 166-167). They applied the German adjective allomorph [=allomorphic] to it, contrasting it with automorph. Neither term was defined by them, presumably because both were in current use in Germany in other situations. Although allomorphic has been adopted by several authors, it is inappropriate and is here replaced by xenomorphic.

It is derived from the Greek pronoun *ἄλλος*, another, that is, a person or thing of the same kind besides the one mentioned before, and the Greek noun *μορφη*, shape or form. Allomorph (noun) is used correctly in mineralogy and chemistry where it defines two or more different crystalline forms of the same chemical substance. Xenomorphism is derived from the Greek *ξενος*, strange (adjective) or stranger (noun).

Xenomorphism in oysters remains restricted to the umbonal region of the right valve. The area occupied by it is nearly always devoid of growth squamae or prominent growth lines and has exactly the same size and outline as the attachment area on the left valve of the same individual. In young, small, thin-shelled individuals it may occupy all of the right valve. In old, large, thick-shelled ones it is limited to the right umbonal region, and the rest of the valve has a configuration normal (idiomorphic) for the species and the inside of the valve is smooth (Fig. J45).

If the oyster shell is detached from its substratum, its left valve carries the negative impression of the substratum on its attachment area and the right valve has the corresponding positive xenomorphic configuration, which is a replica of the substratum. However, the replica is always less sharp than the impressions on the left valve. Points or ridges on the right valve are wider and more rounded, the corresponding pits or grooves on the left are sharper and have narrower crests (Staff & Reck, 1911).

Xenomorphism results in reversed convexities of the two valves in some cases. For example, if the substratum is a flat surface, the attachment area is flat too, but the corresponding xenomorphic area is convex. Thus the usual condition is reversed among the two valves. Were it not so, there would be no room for the soft parts of the animal.

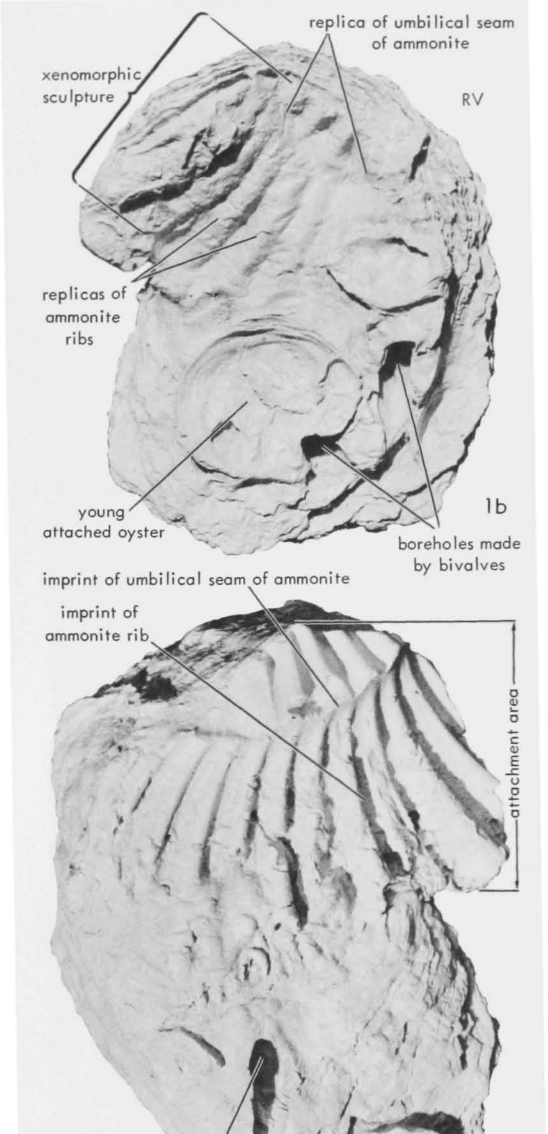

FIG. J45. Xenomorphism of oysters. *Ceratostreon texanum* (ROEMER, 1852), upper part Walnut Formation, L.Cret.(M.Alb.), Coryell County, Texas, USA, showing xenomorphic sculpture patterned after ammonite *Oxytropidoceras,* ×0.6 (Stenzel, n).—*1a.* Attachment area of LV.—*1b.* Xenomorphic sculpture on RV.

Xenomorphism is caused by simple passive molding while the shell is growing at the valve margins. As long as the oyster is young and its shell is very thin, it must grow closely appressed to its substratum. Were it to grow away from this, it would be too exposed to predators which could crush its shell all too easily. At the very thin growing shell margin, the left valve grows over the substratum and produces a detailed negative impression of it on the attachment area; the right valve margin must leave no gap at the valve commissure so must follow or mold over the left valve margin with all of its irregularities. In this way, the outside surface of the right valve is molded and reproduces the configuration of the substratum (Fig. J46).

As the oyster grows older and bigger, the mantle/shell margins start to turn up and away from the support, passive molding ceases, and the shell attains its specific (idiomorphic or automorphic) configuration. Only after that stage is reached, it becomes possible for growth squamae to diverge from the surface of the shell so that the xenomorphic portion remains free of them. Idiomorphic configuration is commonly accompanied by a thickening of the shell. Additional shell layers are deposited on the inside of the valves, making them thicker, and smoothing out any irregularities on the inside of the valves (Fig. J46).

Obviously xenomorphic sculpture is not heritable. Some oyster species, however, have a heritable predilection to become attached to selected substrata, for example, twigs of Octocorallia. Or in certain areas, there may be only one kind of firm substratum available so that all or most individuals of an oyster species will grow on the same kind of substratum and in this fashion they will all have similar xenomorphic sculptures. For these reasons, xenomorphic sculpture may appear to be a specific characteristic, and many misconceptions based on it are found in the literature.

Oysters growing on the cylindrical twigs of sea fans (Octocorallia) have rather unusual and prominent xenomorphism. It consists of a narrow rounded longitudinal ridge extending along the longest diameter of the right valve. The attachment area is a deep rounded channel, and the left valve has many shelly processes that clasp the twig. The twig of the octocoral, when it is dried out, becomes blackish and longitudinally wrinkled, looking very much like

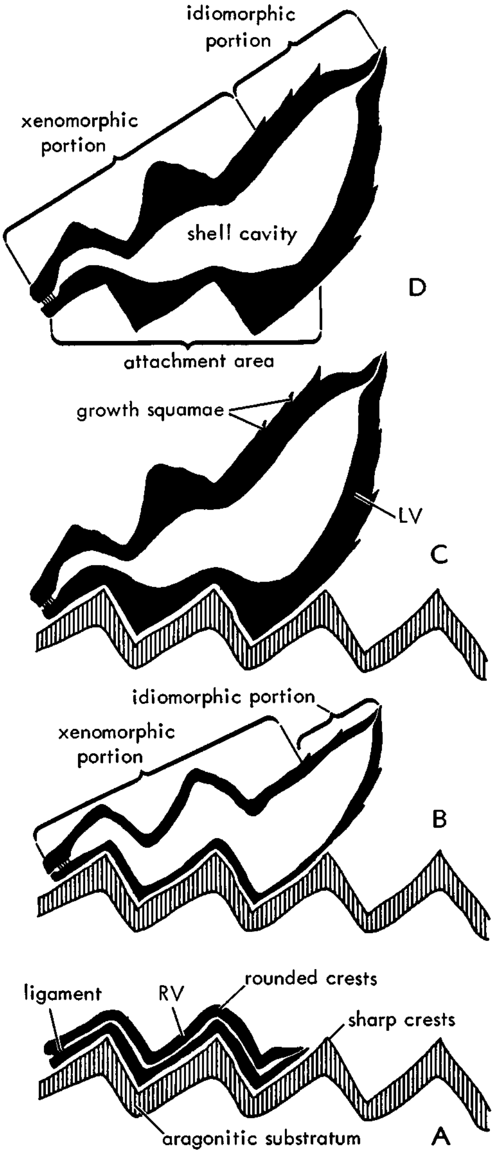

Fig. J46. Origin of xenomorphism on oyster shells (Stenzel, n).

A. Neanic stage of rapid uninterrupted growth showing thin shell walls, narrow shell cavity, lack of growth squamae, and growth closely appressed to substratum, which is here assumed to be a sharply plicated aragonitic shell.

B. Beginning of idiomorphic growth stage showing increasing size of shell cavity, first appearance of growth squamae by intermittent growth, and LV growing away from substratum.

C. Advanced idiomorphic growth stage showing thicker shell walls and more growth squamae, and smoothing out of inside faces of the two valves through progressive obliteration of their impressed configuration.

D. Freeing of shell from its substratum through disappearance by leaching of aragonitic substratum.

a plant twig or root. It is easy to mistake it for part of a woody plant.

The first such oyster to be noticed was a living tropical species figured by d'Argenville (1742, p. 316, pl. 22, fig. F), who described it as a *"feuille"* [leaf] and assumed that it had been attached to a *"morceau de bois"* [piece of wood]. Consequently, Linné (1758, p. 699, no. 178) named this species *Ostrea folium*. In many specimens the right valve looks like a lanceolate leaf with the xenomorphic longitudinal ridge as the midrib of the leaf (Fig. J47).

Swainson (1835, p. 39) later proposed the genus *Dendostrea* for these "tree oysters" and *Ostrea folium* was made the type species by Herrmannsen (1847, v. 1, p. 378).

Thomson (1954, p. 146-149 and letter dated December 14, 1966) insists that the three: *Lopha cristagalli* (Linné, 1758), which is the type species of *Lopha* (see Fig. J129); *Dendostrea folium* (Linné, 1758), which is the type species of *Dendostrea* (Fig. J47); and *Ostrea (Pretostrea) bresia* Iredale (1939, p. 396-397, pl. 7, fig. 4), which is the type species of *Pretostrea* (see Fig. J130) really are not three distinct species but actually are ecomorphs of one species. If this is so, *Dendostrea* and *Pretostrea* are junior synonyms of *Lopha* and it becomes clear that shell shape and outline may not be reliable generic features, at least in the Lophinae.

Examples of this sort of xenomorphism in fossil oysters are *"Ostrea" dorsata* Deshayes (1824-37, v. 1, p. 355, pl. 54, fig. 9-10; pl. 55, fig. 9-11; pl. 14, fig. 1-4) from Bartonian beds of the Paris Basin and *"O." russelli* Landes (Russell & Landes, 1940, p. 139-140, pl. 3, fig. 3-6) from the Late Cretaceous Pakowki Formation of Alberta, Canada.

DEFENSE ADAPTATIONS

In order to keep enemy intruders out of the mantle/shell cavity oysters have devel-

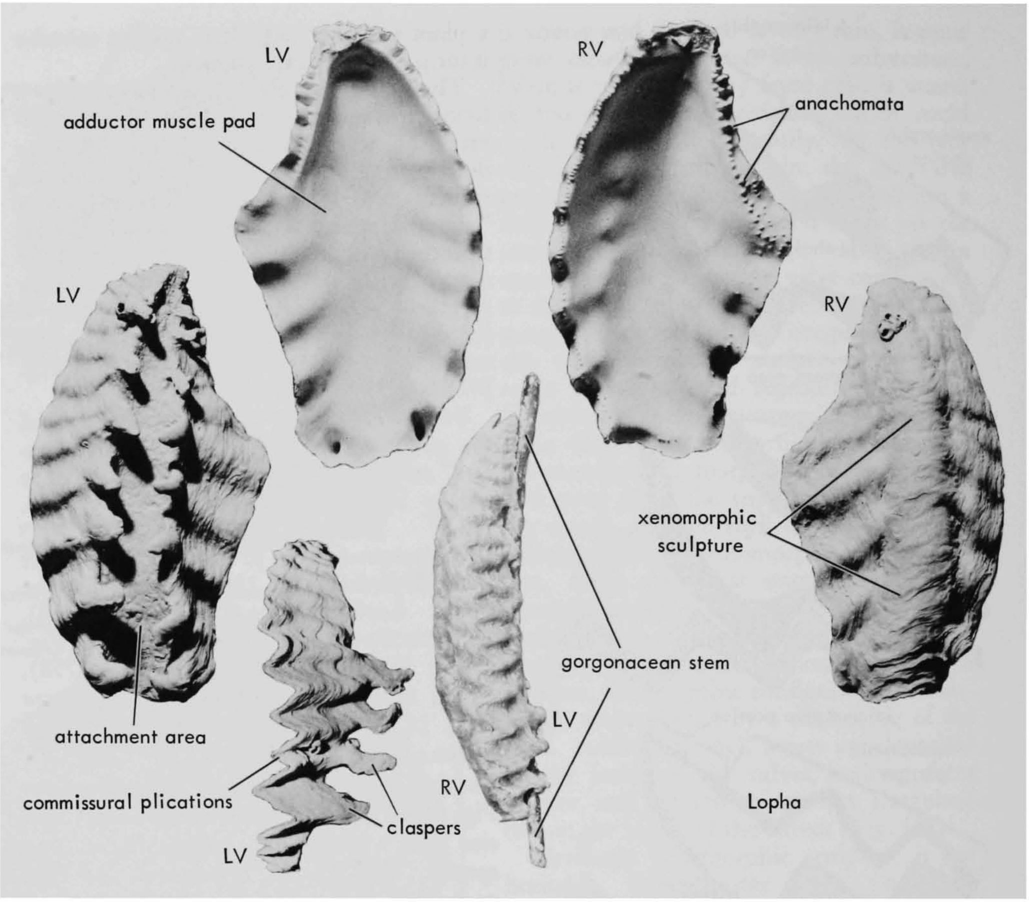

FIG. J47. Ecomorph (2) of *Lopha folium* (LINNÉ, 1758) attached to gorgonacean twig, showing shelly claspers and xenomorphic sculpture, W. Indies, ×0.7 (Stenzel, n. Specimens by courtesy of R. TUCKER ABBOTT, Philadelphia Acad. Nat. Sciences).

oped several defensive features: 1) complete shell closure, 2) commissural shelves, 3) commissural plications, and 4) hyote spines. All these features concern the valve margins or originate at them, where entry might be gained.

SHELL CLOSURE

Oysters can close their shells completely, leaving no gap or chink between the valves. Some of the other bivalves have such gaps; they are reserved for special organs or functions, for example, the byssus, the foot, or the two siphons. When ancestors of the oysters changed their method of attachment from a byssus to cementation of a valve, they gained the advantage of being able to close their valves tightly.

The closure is almost watertight because the thin, flexible conchiolin fringe around the right valve molds itself like a gasket onto the interior surface of the calcareous valve margin of the left. Thus oysters are able to shut out enemies and to survive periods of unfavorable environmental conditions.

For example, the rock oyster *Saccostrea cuccullata* (VON BORN, 1778), growing on sea cliffs, is able to survive exposed to air and tropical sun during low tide (MACNAE & KALK, 1958) (see Fig. J50, J51). Many other species are able to survive exposure to air during low tides under less severe conditions. Prolonged periods of unfavorable salinities, either too low or too high, can be survived in the same way.

COMMISSURAL SHELVES

The commissural shelf of a valve is a flattened band along the valve margins. It is better developed on the dorsal than on the ventral half of the valve. It is narrower near the dorsum and widens toward the venter. It is set off from the shell cavity proper by an angulation, which is gentle on the ventral half and strong on the dorsal half of the valve.

The Pycnodonteinae have the best developed shelves (see Fig. J83). In some Exogyrinae (particularly *Exogyra s.s.*), the anterior margin of the right valve has the commissural shelf reflexed at an angle of about 40° from the general plane of the valve (see Fig. J89, J92, J96). This condition makes itself manifest on the outside of the valve by a succession of sharp parallel upstanding concentric crests or growth squamae and on the inside of the valve by a sharply defined commissural shelf delineated proximally by a well-defined smooth ridge.

A commissural shelf makes it more difficult for certain predators to reach the soft parts in the shell cavity. Predators that break pieces of the shell margins in order to gain entry (margin breakers) must break through the entire width of the commissural shelf before they reach the bulk of the soft parts. The commissural shelf is of some use also against small parasites that wait to sneak in while the oyster has its shell open. Quick shutting of the valves may not exclude them, but may catch them before they can finish crossing the shelf.

COMMISSURAL PLICATIONS

Commissural plications take the form of acute-angular zigzags or rounded sinuous undulations of the shell margin at which the opposing valves fit into each other, when the shell is shut. All Lophinae have them, except that some genera (e.g., *Agerostrea*) attain some size before plications show up (see Fig. J133). *Hyotissa* of the Pycnodonteinae commonly has several zigzag plications and the living southwestern Pacific growth form *H. hyotis* (Linné, 1758) *forma sinensis* (Gmelin, 1791) is quite strongly plicate (see Fig. J85). No commissural plications have been found on the Exogyrinae and Gryphaeinae.

The most acute and numerous plications are found on *Rastellum* and in particular on *R. (Arctostrea) carinatum* (Lamarck, 1806), originally described from Cenomanian beds near Le Mans, Département Sarthe, France, but distributed over most of the globe. The species has a plication prong angle (2α) of about 30° and about 3.5 prongs per cm. along the valve margins.

Plications on oyster shells are positioned in such a way that the bisectrix of each prong angle at the valve margin is normal to the generalized commissural plane of the shell. Therefore, as the valves are opened, the width of the slit opened between them remains the same on each side of a given prong.

The plication angles of the various successive prongs on a shell are unequal and form a progressive graded series; the most acute angle of such a series is the one the farthest away from the hinge axis and the least acute is the one nearest. In plicate oysters that are not or little crescentically curved the graded series progresses with continuously decreasing plication angles from the hinge to the region of the branchitellum.

In the highly crescentic and recurved species of *Rastellum (Arctostrea)* and *Agerostrea* the branchitellum reapproaches the hinge axis and the angles of the prongs around the branchitellum are less acute than those halfway between hinge and branchitellum, at the convex outside curve of the shell. Thus in progressing from the hinge to the branchitellum the prong angles first become more acute and then less acute.

Wherever the sizes of the plication angles differ greatly from one plication to the next, the flanks of the plications are curved in order to accommodate the change without interfering with the normal attitude of the bisectrices of the angles. This situation is noticeable in species with few and large prongs around the periphery. In such shells one flank is convex and the other concave; the concave flank always faces the hinge axis.

These rules follow from the geometry of the valves and their rotational movements when the valves open or close and were

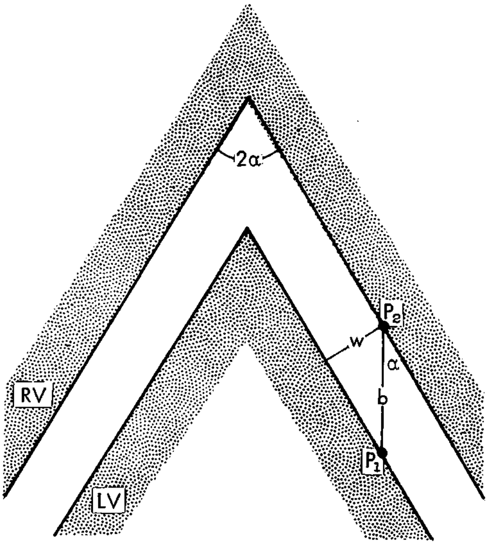

FIG. J48. Geometry of a plication on the margins of an oyster shell (Stenzel, n).

first investigated by RUDWICK (1963, p. 138, fig. 3A). CUMINGS (1903, p. 131-132) was the first to suggest that plicate valve commissures in brachiopods and in oysters are either adaptations for defense against predators trying to enter or reach into the mantle/shell cavity or adaptations to make it impossible for overly large particles to be carried into the mantle/shell cavity. These ideas have been explored further by HERTA SCHMIDT (1937, p. 27-30) and RUDWICK (1964).

Two neighboring points (P_1 and P_2), each on an opposite valve, become separated by the distance *b,* when the plicate oyster opens its valves. Because the commissure is plicate the slit that opens between the valves is narrower than *b*. The width *(w)* of the slit is $w = \sin \alpha \times b$. The sin α is always smaller than 1, if the angle α is less than 90°. Therefore, sin $\alpha \times b$ is always smaller than *b,* and the width *(w)* of the slit is smaller, the smaller angle α may be, that is, the more acute the plication angle (2α) (Fig. J48).

HYOTE SPINES

Hyote spines are tubular outgrowths, hollow and cylindrical, that arise periodically from thin edges of the shell margins of oysters. They are open distally, at their tips as well as along their distal flanks. Their tips are rounded ear-shaped openings. They start as accentuations of ridges or costae on the shell. As the shell margins continue to grow, they become closed off at the base and new ones are formed farther on. The older ones are followed by newer ones in radial rows. As long as they are not closed off an extension of the mantle lobe occupies them, lining their shell wall (Fig. J49).

They are best developed on and named after *Hyotissa hyotis* (LINNÉ, 1758), the pycnodonteine oyster living in the Indo-Pacific (see Fig. J85). Other plicate or costate oysters have such spines too, for example, *Exogyra (Exogyra) spinifera* STEPHENSON, 1941, from the Peedee Formation (Maastricht.) of Robinson's Landing on Cape Fear River, North Carolina.

As long as they are not closed off at the bottom and have a lining of sensitive mantle lobe tissues, they act as sensory organs extending the reach of sensitivity of the mantle edges (RUDWICK, 1965). All of them are deterrents to predators making access to live tissues more difficult.

SIZE

Extraordinary shell size and corresponding thickness of the shell wall show up either individually or as a minor generic characteristic.

An individual oyster may reach great size, if by good fortune it manages to survive much longer than its neighbors. Such a case is the individual (listed below on p. N1028) of *Ostrea edulis* from near Bergen, Norway, which probably reached an age of

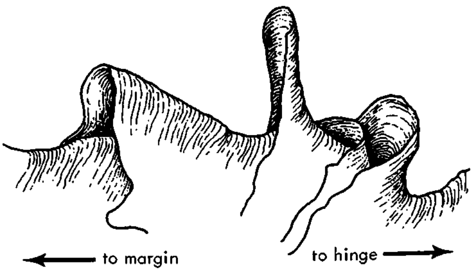

FIG. J49. Hyote spines. Four hyote spines arising from radial rib on RV of *Hyotissa hyotis* (LINNÉ, 1758) *forma imbricata* LAMARCK, 1819, living at 30 fathoms off southern Japan, ×2 (Stenzel, n).

26 or 27 years, much of it under observation (Bjerkan, 1918). Survival of such large specimens today has become quite unlikely, as human populations have increased and oyster fishing has become intensified. For this reason fossil oysters generally tend to be larger than those of today.

After about eight years the soft parts of an oyster cease to increase in size and the volume of the mantle/shell cavity remains constant, but shell deposition does not cease. The shell increases in weight and size, but the shell cavity does not enlarge. Accordingly, after about eight years the length of the ligament does not increase, but the ligament continues to shift from the dorsum toward the venter and the ligamental area increases in height, if not in length.

Among various oyster genera, *Crassostrea* seems to be capable of growing fastest. Species of this genus tend to reach larger sizes, although there are some that do not grow particularly large. The living northeast Asian *C. gigas* (Thunberg, 1793) grows large rapidly. This species is probably the direct descendant of the giant Miocene species *C. gryphoides* (von Schlotheim, 1813, p. 52). This well-known, widespread, and conspicuous species (Rutsch, 1955) ranged in the Miocene Tethys Sea from Spain, southern France, Switzerland, Swabia, northern Africa, Somalia, and Cilicia in Asia Minor to Japan. Because of its wide geographic range the species has received numerous, supernumerary names. It appears to have crossed the Pacific, for in California there is the giant *C. titan* (Conrad, 1853) from the late Miocene. The group of large crassostreas was discussed by Dollfus (1915) and Dollfus & Dautzenberg (1920, p. 465-469). However, Dollfus erroneously included several species of *Ostrea* and *Pycnodonte* and his claim that *Crassostrea* and *Ostrea,* as well as *Crassostrea* and *Gryphaea,* are connected through transitional species is unacceptable.

MAXIMAL SIZES AND WEIGHTS

The largest oyster shell on record has a left valve 32 by 76 cm. in size (Awati & Rai, 1931, p. 9) and is an individual of *Saccostrea cucculata* (von Born, 1778); presumably it was collected near Bombay, India. The species is a complex superspecies living widely distributed in the Indo-Pacific.

Many extraordinary sizes reported in the literature are estimates made in the field without benefit of a tape measure and most of them are exaggerated. The following list gives data believed to be trustworthy (H=height; L=length; T=thickness; W=width; Wt=weight).

1) *Aetostreon couloni* (Defrance, 1821) [=*Exogyra sinuata* (Sowerby, 1822)], Lower Greensand (late Apt.), Perthe du Rhone, France: 17.7 by 20.5 cm. [Quenstedt, 1867].
2) *Crassostrea blanpiedi* (Howe, 1937), Chickasawhay Formation (early Miocene), Wayne County, Mississippi, USA: H, 30.5 cm.; L, 15.3 cm.; W, 12.8 cm.; ligamental area, 3.8 by 7.7 cm. [Howe, 1937].
3) *Crassostrea cuttackensis* (Newton & Smith, 1912) [=*C. madrasensis* Preston, 1916], living (Rec.), Pulicat Lake (ca. 70 km. north of Madras), India: H, 43.2 cm.; L, 17.8 cm. [Moses, 1927, p. 552].
4) *Crassostrea gigas* (Thunberg, 1793), living (Rec.), Enoshima Island (near Yokohama), Japan: H, 44.8 cm.; L, 9.5 cm.; H, left ligamental area, 9.5 cm. [Pilsbry, 1890, p. 95].
5) *Crassostrea gryphoides* (von Schlotheim, 1813) [=*Ostrea grandis* Serres, 1843], Miocene marnes argilocalcaires, Tessan (near Béziers), Dépt. Hérault, France: H, 59-60 cm.; L, 7-8 cm.; T (shell wall in center of valve), 4.5-5.0 cm. [Serres, 1843, p. 143-147, pl. 2, fig. 1].
6) *Crassostrea gryphoides* (von Schlotheim, 1813) [=*Ostrea ponderosa* Serres, 1843], Miocene marnes argilocalcaires, Gremian (near Montpelier), Dépt. Hérault, France: Wt, 4.45-4.85 kg.; T (shell wall), 15 cm.+ [Serres, 1843, p. 143, 150-151].
7) *Crassostrea titan* (Conrad, 1853), Neroly Formation (late Miocene), near Bitter Creek, Santa Barbara County, California, USA: H, 44.4 cm.; W,

22.9 cm. (Fig. J14). [Eaton, Grant, & Allen, 1941, expl. pl. 4, fig. 3].

8) *Crassostrea virginica* (Gmelin, 1791), subfossil from shell mound (Pleist.), Damariscotta River, southern Maine, USA: H. 35.5 cm.; L, 11 cm. [Ingersoll, 1881, p. 82, pl. 30, fig. 22].

9) *Crassostrea virginica* (Gmelin, 1791), living (Rec.), Boothbay Harbor, Lincoln County, Maine, USA: distance from hinge to ventral border, 20.6 cm.; H (left ligamental area), 5.5 cm.; H (right ligamental area), 4.5 cm.; L, 9.7 cm.; W (near hinge), 6.5 cm.; Wt (shell), 1175 gm.; Wt (soft parts), 35.8 gm.; Wt (enclosed liquid), 19.2 gm.; Wt (total), 1230 gm. [Galtsoff, 1964, p. 20-21].

10) *Exogyra (Exogyra) erraticosta* Stephenson (1914), Pecan Gap Chalk (Campan.), Austin-Manor road, Travis County, Texas, USA: max. dimension, 20.1 cm.; Wt (both valves and internal mold), 3939.5 gm. [Stenzel, personal collection].

11) *Hyotissa hyotis* (Linné, 1758), living (Rec.), New Caledonia: H, 28.5 cm.; L, 23.4 cm.; W, 19.0 cm. [Mus. Natl. Hist. Nat., Paris, France].

12) *Hyotissa hyotis* (Linné, 1758) [= *Ostrea cristagalli* Roughley, 1931 (*non* Linné, 1758)], living (Rec.), Great Barrier Reef, Queensland, Australia: H, 24.8 cm.; L, 15.6 cm.; W, 11.4 cm.; Wt (shell), 1885 gm. [Roughley, 1931].

13) *Hyotissa hyotis* (Linné, 1758), living (Rec.), Direction Island (Cocos-Keeling Is.), Indian Ocean, depth 10-20 ft.: H, 28 cm.; L, 28 cm.; W, 15 cm.; Wt (right valve), 1673 gm.; Wt (left valve), 2750 gm. [Philadelphia Acad. Nat. Sci.].

14) *Ostrea edulis* Linné (1758), living (Rec.), estimated age 26-27 yrs., near Bergen, Norway: Wt (shell), 1228 gm.; Wt (soft parts), 55 gm.; Wt (enclosed liquid), 67 gm.; Wt (total), 1350 gm. [Bjerkan, 1918].

15) *Ostrea edulis* Linné (1758), living (Rec.), age 10+ yrs., Salcombe Estuary near Salstone, Devonshire, England: H, 17.6 cm.; L, 19.8 cm.; W, 5.9 cm.; Wt (shell), 1038 gm.; Wt (soft parts), 94 gm.; Wt (enclosed liquid), 133 gm.; Wt (total) 1265 gm.; mantle cavity volume, 130 cm^3. [Orton & Amirthalingam, 1930].

16) *Rastellum (Arctostrea) aguilerae* (Böse, 1906) [=*Arctostrea atkinsi* Raymond, 1925], Habana Formation (Maastricht.), 1 km. NW of Dos Hermanos on road to Abreus, Santa Clara Prov., Cuba: diameter tip to tip, 23.5 cm.; W (right valve), 7.0 cm. [Sohl & Kauffman, 1964, p. 414-419].

TERMS, CHIEFLY MORPHOLOGICAL, APPLIED TO OYSTERS

Terms regarded most important are in boldface type (as **adductor muscle**); use is not recommended of those printed in italics (as *epidermis*). Some nonmorphological terms have been included for aid to biologists and zoologists who may not be familiar with them. These are enclosed by square brackets. Many terms have general application to Bivalvia (*Treatise,* p. N102); additional ones considered by H. B. Stenzel to be especially applicable to oysters are accompanied by an asterisk (*).

aboral*. Pointing away from mouth.

adductor muscle*. Single posterior muscle connecting the 2 valves, tending to close them.

adoral*. Pointing toward mouth.

alate. With wings or auricles.

alivincular. Type of ligament not elongated in longitudinal direction nor necessarily situated entirely posterior to beaks, but located between cardinal areas (where present) of respective valves, with lamellar layer both anterior and posterior to fibrous layer; example, *Ostrea.*

[**allochthonous***.] In structural geology, pertaining to rock masses that tectonic forces have transposed to rest on a strange base.

allometric growth*. Growth by unequal rates in different parts of an animal.

[**allomorph** (noun)*.] Any of 2 or more diverse crystalline forms of the same chemical substance.

[*allomorphic* (adj.)*.] Pertaining to allomorphs. *See* xenomorphic.

allomorphism. *See* xenomorphism.

allopatric*. Pertaining to 2 or more species living in different regions.

amphidetic. Extending on both anterior and pos-