THE EASTERN OYSTER

Crassostrea virginica

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Crassostrea virginica

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Foreword

The Eastern Oyster is the first comprehensive review of the biology of the eastern oyster since Paul Galtsoff published his landmark work, *The American Oyster*, in 1964. For more than a generation, Galtsoff's book has served researchers, resource managers, and students well — it is a classic. *The Eastern Oyster* does not replace Galtsoff's work as much as it is a complement, bringing up-to-date some of the remarkable advances that scientists have made in our understanding of oyster biology, covering topics that had hardly been studied before, and adding topics that Galtsoff did not cover.

When a group of scientists first met to discuss a follow-on to *The American Oyster*, they agreed that a companion volume could no longer be written by one person because the field had become so large and complex. They decided to invite specialists to cover the various subjects and agreed that a new book should aim to update subject material in *The American Oyster* and to introduce important topics not covered there. We should note that *Crassostrea virginica* was designated as the eastern oyster by the Committee on Scientific and Vernacular Names of Molluscs of the Council of Systematic Malacologists (American Fisheries Society Special Publication 16). To help clarify some of these taxonomic and nomenclature problems, Chapter 1 in *The Eastern Oyster* provides a comprehensive catalog of the names of oyster species worldwide.

More than half of Galtsoff's book covered oyster anatomy, with detailed chapters on such topics as the shell, the mantle, the labial palps, and the gills as well as the circulatory, reproductive, and excretory systems. A number of chapters in *The Eastern Oyster* extend Galtsoff's findings and have added considerably to such well-covered details on anatomy, shell structure, and the circulatory system. The major thrust of this book, however, is holistic and reflects current approaches to biological processes. Thus, there are extensive scientific treatments of such topics as the physiology of feeding, population genetics, reproduction and larval biology, and diseases and mechanisms of defense. To address issues of the oyster as an important commercial and ecological resource, the book concludes with chapters on aquaculture, the effects of transferring oysters among ecosystems, and public management.

The Eastern Oyster is the first book to consolidate such an extensive range of knowledge about *Crassostrea virginica* — as with Galtsoff's work, we hope it will be of great value to scientists, managers, educators, and students.

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Chapter 1

A Catalogue of Selected Species of Living Oysters (*Ostreacea*) of the World

MELBOURNE R. CARRIKER AND PATRICK M. GAFFNEY

INTRODUCTION

A number of different species of living oysters are referred to by authors in the present volume on the eastern oyster. As a reference for readers, we have prepared the following catalogue of the more commonly used scientific names and synonyms of most living oysters of the world. Also included under "comments" are common names and size (where available), general geographic distribution, and references to the major systematic literature on the Ostreacea. The names of obscure and little known species of oysters have been omitted.

Students of ostreacean systematics recognize that the taxonomy of oysters is so tangled (Thomson 1954; Carreon 1969; Stenzel 1971; Ahmed 1975; Carriker 1976; Buroker et al. 1979a, b; Nikiforov 1979; Singarajah 1980; Torigoe 1981; Buroker 1982; Buroker et al. 1983; Harry 1985; Morris 1985; Angell 1986; Castillo-Rodríguez and García-Cubas 1986; Durve 1986; Harry 1986a, b; Mahadevan 1987; Arakawa 1990) that it is difficult to prepare a list of scientific names acceptable to most specialists. Our not unpleasant task of preparing the catalogue has been made vastly easier by the important syntheses of Lamy (1929-30), Thomson (1954), Tchang and Tse-kong (1956), Carreon (1969), Stenzel (1971), Ahmed (1975), Harry (1981, 1985, 1986a), Torigoe (1981), Bernard (1983), Durve (1986), Skoglund (1991); recent electrophoretic investigations on the population genetics of several species of oysters (Buroker et al. 1979a, b, 1983; Newkirk 1980; Hedgecock and Okazaki 1984); and the important volumes on bivalve culture edited by Menzel (1991) and Newkirk and Field (1991).

Several new generic names, which may be unfamiliar to some readers, have been introduced for oysters in recent years. Harry (1985), after an exhaustive study, found it necessary to extend the classification beyond that proposed by Stenzel (1971) in order to indicate the diversity and relationships of oyster species more precisely. This revised classification has resulted in the synonymization of names of oysters in several geographic regions that are simply different populations of one species.

A good example of this synonymization is the species *Ostrea puelchana* Orbigny, which, with a worldwide distribution in the southern hemisphere, is found on both coasts of South America, in New Zealand, the southern coast of Australia, and off South Africa (Harry 1986a). It has been identified in these different regions as *O. angasi*, *O. algoensis*, *O. chilensis*, or *O. lutaria*, among other names (see catalogue).

Another striking example of synonymization is that of *Crassostrea virginica* (Gmelin), which is distributed in the Western Atlantic from Brazil northward through the Caribbean and Gulf of Mexico, including the Antilles, to the St. Lawrence River estuary in eastern Canada, a range of some 8,000 km. Harry (1985) has concluded that names of all populations of this species, such as *C. brasiliana, C. floridensis, C. guyenensis, C. lacerata, C. rhizophorae,* and others should be replaced by *C. virginica.* An especially debated species names is *C. rhizophorae.* Some workers (Ahmed 1975) have suggested that this "species" is simply an ecological variant in the southernmost part of the range of *C. virginica.* Others suggest that it could be a subspecies (i.e., *C. v. rhizophorae,* see Newball and Carriker 1983), or a species (Abbott 1974). Hedgecock and Okazaki (1984) concluded that despite their chromosomal and morphological similarity and their ability to produce viable F_1 hybrids in artificial crosses, *C. virginica* and *C. rhizophorae* have clearly evolved protein differences characteristic of old and well-separated biological species. This view is supported by a recent comparison of large subunit ribosomal DNA sequence data (Littlewood 1994). The close similarity of the valves and the broad plasticity of populations of *C. virginica* have resulted in a wide range of variability in shell characters, which makes it difficult to separate the geographic populations into species or subspecies — other than on the basis of geographic distribution (Newball and Carriker 1983).

An example of a thoroughly confusing nomenclatural problem begging for resolution is that of apparently one species being variously called either *ariakensis, discoidea, palmipes, paulucciae,* or *rivularis* in the literature. As *Ostrea discoidea* it is reported in India (Awati and Rai 1931; Ahmed 1971); as *O. rivularis,* in Japan (Cahn 1950); as *Crassostrea ariakensis* in Japan (Torigoe 1981), and as *C. rivularis* in India (Durve 1986; Mahadevan 1987; Rao 1987), Japan (Quayle and Newkirk 1989), and Pakistan, China, and Japan (Tchang and Tse-kong 1956; Rao 1987; Cai and Li 1990). Torigoe (1981) considered *Crassostrea rivularis* and *C. ariakensis* the same species, but this is probably incorrect usage (Coan et al. 1995). Ahmed (1975) noted that *C. rivularis* and *C. gigas* do not interbreed experimentally and probably not in nature, so they are probably not synonymous. Harry (1985, 1986b) concluded that *rivularis* is a junior synonym of *pestigris,* and placed *pestigris* in the new genus *Planostrea.* Although *C. gigas* and *C. ariakensis* are genetically distinct at both the allozyme level (Buroker et al. 1979b) and DNA sequence level (Littlewood 1994), they are capable of producing viable hybrids in the laboratory (Allen and Gaffney 1993). We concur with Coan et al. (1995) that this species, called by various names, should be *Crassostrea ariakensis* Fujita, 1913, and we follow this usage in this catalogue. *Crassostrea ariakensis* is commercially important and is cultivated widely in the western Pacific (Cahn 1950; Quayle and Newkirk 1989; Cai and Li 1990; Nie 1991), and with some success is being developed commercially in Oregon and Washington, USA (Quayle 1988; Robinson and Langdon 1992; Coan et al. 1995).

Because Harry (1985, 1986a) based his recent synthesis on a careful study of the morphology of the shell and soft parts of the oysters of the world, we have followed primarily his classification in this catalogue. Where available, we also have included information resulting from electrophoretic investigations.

We began preparation of this synthesis by checking the scientific names of oysters published in the *Zoological Record* for the years 1973 to 1990. We compared these names with those published in the recent systematic literature (see References), and from this collation selected the principal synonyms recorded in the catalogue.

The catalogue is alphabetically arranged, presenting the reader with specific names, scientific names (genus, species, authority, year), the most common synonyms, and, in a few cases, older scientific names in common usage in some countries. Although many scientific names (a total of 54) and synonyms (approximately 70) are listed in the catalogue, we did not attempt to include all that have been proposed — Korringa (1952) provides many more.

If undisturbed in an optimal environment, oysters will continue to grow for some years. Galtsoff (1964), for example, recorded a maximal height (from umbo to shell margin) of the shell of *Crassostrea virginica* of 36 cm; yet, commercial heights range about 8 to 10 cm. Thus, because maximal size (height) of oysters shells is highly variable, we give only relative size (small, medium, large) and the maximal dimension (usually height) recorded (if any) in the literature for each species of oyster included in the catalogue.

CATALOGUE

A

***adriatica*, *Ostrea*.** Variety of *Ostrea edulis* (according to Lamy 1929-30).

***aequatorialis*, *Crassostrea*.** Synonym: *Crassostrea columbiensis.*

***Alectryonella plicatula* (Gmelin, 1790)*.** Plicate kitten's paw oyster, chichikategaki, zhe muli. Has also been placed in *Dendostrea, Ostrea, Saccostrea, Saxostrea* (Torigoe 1981; Harry 1985). Synonyms: *Ostrea cumingiana, O. dubia, O. plicata, O. solida,* and others (Lamy 1929-30).

Comments. Large (up to 12 cm high, Torigoe 1981). Indo-West Pacific region: Madagascar to Philippines, East and South China Seas, Ryukyu Islands, and western Caroline Islands (Torigoe 1981; Harry 1985). Warm water species most commonly cultivated in the People's Republic of China (Nie 1991) where oyster production is derived both from this species and *Crassostrea ariakensis* (see *Planostrea pestigris*) (Cai and Li 1990).

***algoensis*, *Ostrea*.** Synonym: *Ostrea puelchana.*

***amara*, *Ostrea*.** Synonym: *Saccostrea palmula.*

***amasa*, *Crassostrea*.** Synonym: *Saccostrea mordax.*

***amasa*, *Saccostrea*.** Synonym: *Saccostrea mordax* and *S. glomerata.*

***angasi*, *Ostrea*.** Synonym: *Ostrea puelchana.*

***angelica*, *Lopha*.** Now in genus *Myrakeena* (Harry 1985).

***angelica*, *Myrakeena*.** See *Myrakeena angelica.*

***angelica*, *Ostrea*.** Now in genus *Myrakeena* (Harry 1985).

***angulata*, *Crassostrea*.** See *Crassostrea angulata.*

***arakanensis*, *Ostrea*.** Synonym: *Crassostrea madrasensis.*

***ariakensis*, *Crassostrea*.** See *Crassostrea ariakensis.*

***auriculata*, *Ostrea*.** Synonym: *Ostrea denselamellosa.*

B

***belcheri*, *Crassostrea*.** See *Crassostrea belcheri.*

***belcheri*, *Ostrea*.** See *Crassostrea belcheri.*

***brasiliana*, *Crassostrea*.** Synonym: *Crassostrea virginica.*

***brasiliana*, *Ostrea*.** Synonym: *Crassostrea virginica.*

***bresia*, *Ostrea*.** Synonym: *Dendostrea folium.*

C

***cerrosensis*, *Ostrea*.** Synonym: *Undulostrea megadon.*

***chilensis*, *Ostrea*.** Synonym: *Ostrea puelchana.*

***chilensis*, *Tiostrea*.** Synonym: *Ostrea puelchana.*

***circumpicta*, *Striostrea*.** See *Striostrea circumpicta.*

***cochlear*, *Neopycnodonte*.** See *Neopycnodonte cochlear.*

***columbiensis*, *Crassostrea*.** See *Crassostrea columbiensis.*

***commercialis*, *Crassostrea*.** Now in genus *Saccostrea*; see *Saccostrea commercialis* and *S. cucullata.*

***commercialis*, *Ostrea*.** Now in genus *Saccostrea.*

***conchaphila*, *Ostreola*.** See *Ostreola conchaphila.*

***cornucopia*, *Ostrea*.** Synonym: *Saccostrea cucullata*

***corteziensis*, *Crassostrea*.** Synonym: *Crassostrea columbiensis.*

***corteziensis*, *Ostrea*.** Synonym: *Crassostrea columbiensis.*

***crasa*, *Crassostrea*.** Synonym: *Crassostrea virginica.*

Crassostrea angulata* (Lamarck, 1819). Portuguese oyster. Synonym: *Crassostrea angulata* crosses easily with *C. gigas* to yield viable hybrids in the laboratory, and morphologically and genetically closely resembles *C. gigas* (Menzel 1974, 1987; Ahmed 1975; Arakawa 1990), suggesting that *C. angulata* could be a synonym of *C. gigas*, or that *C. angulata* is a subspecies of *C. gigas* (Menzel 1987). Gaffney and Allen (1993) note that

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* An asterisk following the year of a scientific name indicates that the taxon was recognized by Harry (1985, 1986a).

although these two taxa traditionally have been classified as distinct species, they probably are not because they are indistinguishable in terms of protein polymorphisms, karyotype, and larval morphology. On the other hand, Héral and Deslous-Paoli (1991), on the basis of physiological reproductive characteristics, contend that the Pacific and Portuguese oysters are two separate species.

Comments. Large (up to 18 cm high, Tebble 1976). Eastern Atlantic from equator north to Mediterranean and Atlantic coast of Iberian Peninsula; introduced into southwestern France (Harry 1985); imported as young oysters to Great Britain, where they do not reproduce. A common, commercially important edible species, widely cultivated in southern Europe (Héral and Deslous-Paoli 1991). Menzel (1974) suggested that the Pacific oyster, *C. gigas*, could have been introduced accidently into Portugal, but Stenzel (1971) believes *C. gigas* and *C. angulata* arose from a common parent (Ahmed 1975). Buroker et al. (1979a) conclude *C. angulata* should be classified as a geographical isolate of *C. gigas* (also see Parenzan 1974).

***Crassostrea ariakensis* Fujita, 1913.** Suminoe oyster, suminoegaki. Earlier placed in *Ostrea*. Synonyms: Torigoe (1981) listed *Ostrea rivularis* as a synonym of *Crassostrea ariakensis*, but this is probably incorrect usage (Coan et al. 1995). What has been called *C. discoidea* by Awati and Rai (1931), Rao (1987) considers to be *C. rivularis*. By some, *C. ariakensis* is considered conspecific with *C. gigas*, but electrophoretic and DNA analyses show that they are different species (Buroker et al. 1979b; Torigoe 1981; Littlewood 1994); this conclusion is supported by the fact that it is difficult to cross these two species (Imai 1977, but see Allan and Gaffney 1993). Furthermore, the shell of *C. ariakensis* is heavier and more rounded than that of *C. gigas* (Coan et al. 1995).

Comments. Large (up to 20 to 24 cm high, Cahn 1950, Torigoe 1981). According to Awati and Rao (1931) and Ahmed (1971), *Ostrea discoidea* (possibly *Crassostrea ariakensis*) occurs in the littoral zone in Bombay, India; *Crassostrea rivularis* is common along the Gujarat coast in India (Mahadevan 1987), occurs in Pakistan, China, and Japan (Rao 1987), and all along the Chinese coast (Tchang and Tse-kong 1956). This species is common on intertidal hard grounds and in muddy creeks in warm water habitats (Rao 1987), is an important commercial oyster cultivated in China (Cai and Li 1990; Nie 1991) and Japan (Cahn 1950; Quayle and Newkirk 1989), and is regularly harvested in India (Rao 1987). According to Angell (1986) populations of *C. ariakensis* are cultivated in deep bays. These many authors may be writing about a species we here call *C. ariakensis* — though considering the confusion of nomenclature, this is not a certainty. Commercial development of *C. ariakensis* has begun successfully in Oregon and Washington, USA (Robinson and Langdon 1992).

***Crassostrea belcheri* (Sowerby, 1871).** Synonym: *Crassostrea belcheri* could be the same species as *C. nippona* according to Torigoe (1981); morphological differences between them are very small.

Comments. Large (up to 25 cm high, Torigoe 1981). Southeast Asia, including the Philippines, Vietnam, Malaysia, and Indonesia; India (Awati and Rai 1931; Angell 1986). A large, rapidly growing oyster that has been experimentally cultured (Angell 1986), this is the principal commercial species in southeast Asia (Quayle and Newkirk 1989).

Crassostrea columbiensis* (Hanley, 1845). Columbian oyster, ostion de mangle. Has also been placed in *Ostrea*. Synonyms: *Ostrea aequatorialis*, *O. corteziensis*, *O. ochracea*. Long erroneously called *O. chilensis* (Lamy 1929-30).

Comments. Large (up to 25 cm, Abbott 1974). Eastern Pacific from Chile north to Gulf of California. Common, adhering to rocks or mangrove roots principally in the mid-intertidal zone, and on other solid substrata. Is the main commercial species from the Gulf of California to Panama (García-Cubas et al. 1987; Quayle and Newkirk 1989), is harvested in the wild, and has been raised experimentally (Angell 1986; Hernández 1990). In Mexico attempts have been made to culture the species and an important natural fishery is being replaced slowly by aquacultural practices (Baqueiro 1991). The names *Ostrea corteziensis* and *Crassostrea columbiensis* have long been given to the same species, but *C. corteziensis* is now considered the junior synonym (Harry 1985). Menzel (1987) readily crossed *C. corteziensis* with *C. virginica*, obtaining F_1, F_2, and backcrosses with no abnormal chromosomal behavior, and tentatively considered *C. corteziensis* a subspecies of *C. virginica* (Baqueiro 1991).

Crassostrea gasar **(Adanson, 1757).** West African mangrove oyster. Synonyms: *Crassostrea tulipa.* According to Lamy (1929-30), Adanson described *Ostreum gasar* in 1757, and Lamarck named the same species *Ostrea tulipa* in 1819.

Comments. Large. Central West Africa, Senegal to Angola (Ajana 1980; Quayle 1980; Angell 1986). Common. Attaches to roots and branches of mangroves in the intertidal zone and on muddy bottoms of the brackish region of estuaries. Of considerable economic importance to natives, especially in Gambia. Harvested from wild populations. Some experimental culture in Senegal (Quayle 1980; Angell 1986; Cham 1991).

Crassostrea gigas **(Thunberg, 1793).*** Giant Pacific oyster, Japanese oyster, Miyagi oyster, magaki. Has also been placed in *Ostrea.* Synonyms: Species names *laperousii*, *sikamea*, and *talienwhanensis* have been considered synonyms of *gigas* but Coan et al. (1995) lists *C. sikamea* as a separate species. In Japan, *C. gigas* consists of four well-defined forms, regarded as races. The Hiroshima oyster is *C. laperousii* and the Kumamoto oyster, *C. sikamea* (Ahmed 1975). In the Kumamoto prefecture, two species of *Crassostrea* are found: *C. gigas* and *C. sikamea.* This geographical overlap has made it difficult to evaluate published reports. The two species are genetically distinct but capable of partial hybridization (see Buroker et al. 1979b; Allen and Gaffney 1993; Hedgecock et al. 1993). Species *C. gigas*, *C. laperousii*, and *C. posjetica* in the Southern Maritime Territory of Russia are not different electrophoretically; hence Nikiforov (1979) concludes they are all *C. gigas.*

Comments. Large (up to 40 cm, Cahn 1950; 45 cm, Torigoe 1981). Indo-West Pacific from Pakistan to Japan and Korea and the Philippine Islands, Borneo, and Sumatra; all along the Chinese coast (Tchang and Tse-kong 1956). Introduced to west coast of Canada, United States, Mexico, as well as to Chile, Korea, Taiwan, New Zealand, Australia, and coastal European countries — indeed, throughout much of the world (Parenzan 1974; Quayle and Newkirk 1989; Dix 1991). Common in shallow protected waters in optimal salinities of 23 to 28 ppt. *Crassostrea gigas* is one of the most important food oysters in many parts of the world and is widely cultivated, especially in Japan, Korea, the west coasts of the United States, Canada, and Europe (Héral and Deslous-Paoli 1991; Kusuki 1991). Since its accidental arrival in New Zealand, the Pacific oyster, in about 7 years, has taken over as the sole commercial oyster in the north (Dinamani 1991b). It also is being produced commercially in Brazil, Chile, and Ecuador (Hernández 1991).

Crassostrea gryphoides **(Schlotheim, 1813).** Has also been placed in *Ostrea.* Synonym: The validity of the species name *gryphoides* has been questioned, and the name *cuttakensis* has been proposed instead (see Ahmed 1975; Angell 1986; Nagabhushanam and Mane 1991).

Comments. Large (up to 17 cm size, Rao 1987). Northwestern coast of India, especially in Bombay area. Common, of commercial importance. Populations are harvested periodically, and bottom culture is carried out by fisherfolk (Manhadevan 1987; Rao 1987; Nagabhushanam and Mane 1991). Occurs in intertidal zone to 7 m depth in euryhaline coastal waters.

Crassostrea iredalei **(Faustino, 1932).** Slipper-shaped oyster, talabang tsinelas. Has also been placed in *Ostrea.* Synonym: Although superficially similar to *C. gigas*, electrophoretic studies show it to be a distinct species (Buroker et al. 1979b), even though Harry (1981) considered it a possible *C. gigas*.

Comments. Large. Philippines, southeast Asia (Angell 1986; Quayle and Newkirk 1989). Common in sheltered bays and estuaries (Rosell 1991). Important fishery on east coast of Malaysia, widely cultivated in the Philippines, a main commercial species in southeast Asia (Quayle 1980; Angell 1986; Quayle and Newkirk 1989, Rosell 1991).

Crassostrea madrasensis **(Preston, 1916).** Has also been placed in *Ostrea*. Synonyms: *Ostrea arakensis, O. cucullata, O. virginica*. In India and Pakistan, *C. madrasensis* could be synonymous with *C. virginica* (Ahmed 1971, 1975), but until further research is done, it should be considered a separate species (Rao 1987). According to Stenzel (1971), *C. madrasensis* is a junior synonym of *C. cattuckensis*, as is also *C. gryphoides* (see Nagabhushanam and Mane 1991).

Comments. Large (up to 21 cm, larger in estuaries, Rao 1987). In estuaries and embayments along the east coast and up to Karwar on the west coast of India and to South China Sea coasts (Angell 1986; Durve 1986) and Pakistan (Rao 1987). A main commercial species in India and Sri Lanka, flourishing in estuaries from the mid-littoral to 16 m (Nagabhushanam and Mane 1991). Shells are collected for industrial purposes, and subfossil shells are mined (Mahadevan 1987). The species provides a seasonal fishery for coastal villagers. Some culture has been attempted near Bombay (Rao 1987).

Crassostrea nippona **(Seki, 1934).** Iwagaki. Has also been placed in *Ostrea*. Synonyms: The only morphological differences between *Crassostrea nippona* and *C. belcheri* are shape and sculpture of growth squamae; more information is needed to determine if these are separate species (Torigoe 1981). *Crassostrea nippona* was originally identified as *Ostrea circumpicta* (by Cahn 1950) and *O. multistriata* (by Imai 1977).

Comments. Large (up to 25 cm high, Imai 1977; Torigoe 1981). Western Pacific, Japan (Cahn 1950; Torigoe 1981). Uncommon. Fast growing and has good flavor. Gathered by dredging or diving. Not successfully cultured (Torigoe 1981).

Crassostrea paraibanensis **(Singarajah, 1980).** Synonyms: According to Singarajah (1980), this is a separate species and quite different morphologically from other species of *Crassostrea*. Was previously confused with, and is still locally called, *C. brasiliana*. *Crassostrea paraibanensis* is closely related morphologically to *C. angulata* and *C. virginica*.

Comments. Large (25 cm or more, Singarajah 1980). Northeastern Brazil (Singarajah 1980, Angell 1986). Common. A main commercial species in northeastern Brazil (Quayle and Newkirk 1989) where it is cultured commercially (Angell 1986). Occurs on muddy estuarine bottoms, whereas *Crassostrea brasiliana* is found intertidally.

Crassostrea rhizophorae **(Guilding, 1828).** Gureri, mangrove oyster, ostra, ostra-gaiteira (Boffi 1979). Has also been placed in *Ostrea*. Synonyms: *Crassostrea rhizophorae* and *C. virginica* are closely similar, in fact, almost identical morphologically (McLean 1941; Abbott 1974; Newball and Carriker 1983; Arakawa 1990). Some workers believe *C. rhizophorae* is an ecotype, or at most a subspecies of *C. virginica* (Ahmed 1975; Newball and Carriker 1983; Menzel 1987); others that it is a junior synonym (Harry 1985). It crosses readily with *C. virginica* (Menzel 1983, 1987). However, Hedgecock and Okazaki (1984) consider that *C. virginica* and *C. rhizophorae* are old, well-separated biological species. Synonyms given in the literature for *C. rhizophorae* include *Ostrea arborea, O. adsociata, O. braziliana, O. parasitica*, and *C. virginica* (Lamy 1929-30). Compare with *C. virginica* in this catalogue.

Comments. Large (up to 15 cm, Arakawa 1990). Gulf of Mexico, Caribbean, Brazil (Castillo-Rodríguez and García-Cubas 1986). Common intertidally, on roots and branches of mangrove trees in high salinity seawater. Buroker (1983) notes that *C. rhizophorae* replaces *C.*

virginica in high salinity regions of their range, *C. rhizophorae* remaining in the more saline, mainly mangrove areas (Nascimento 1991). *Crassostrea rhizophorae* is important commercially and is cultivated on Caribbean sea coasts (Quayle and Newkirk 1989; Arakawa 1990) but does not yet represent a large fishery (Hernández 1991). It is nonetheless an important source of income for the poorer communities of the Caribbean (Vélez 1991). Cuba is the only country with a working commercial program (Frías and Rodríguez 1991; Nascimento 1991; Vélez 1991). In Brazil *C. rhizophorae* is cultivated on a pilot scale by family enterprises (Hernández 1990).

Crassostrea rivularis **(Gould, 1861).** Synonym: *Planostrea pestigris.* See also p. 2

Crassostrea sedea **(Iredale, 1939).**

Comments. Small (4 cm size, Thomson 1954). Australia. Has been mistaken for young *C. commercialis.* Lives on partially and fully submerged surfaces.

Crassostrea virginica **(Gmelin, 1791).*** Eastern oyster. Has also been placed in *Ostrea.* Synonyms: Harry (1985) recognized only four species in the genus *Crassostrea: C. angulata, C. virginica, C. columbiensis,* and *C. gigas.* Ease of hybridization and chromosomal patterns in the hybrids suggested to Menzel (1987) that *C. virginica, C. columbiensis,* and *C. rhizophorae* should be considered the same species, *C. columbiensis* and *C. rhizophorae* being subspecies of *C. virginica. Crassostrea v. guyenensis* and *C. v. lacerata* reported from Venezuela are subspecies of *C. virginica* (Ahmed 1975), and *C. crassa, C. brasiliana,* and *C. floridensis* are synonyms of *C. virginica* (Abbott 1974; Quayle 1980; Castillo-Rodríguez and García-Cubas 1986). Ahmed (1971, 1975) believes that *C. madrasensis* in India and Pakistan is the same species as *C. virginica* because of very close morphological similarities. Many other synonyms (Lamy 1929-30).

Comments. Large (up to 36 cm high, Galtsoff 1964). Form highly variable (McLean 1941). Western Atlantic from the Gulf of St. Lawrence in Canada to the Gulf of Mexico, Caribbean, and coasts of Brazil and Argentina (Newball and Carriker 1983; García-Cubas et al. 1987; Andrews 1991). Common in estuaries and coastal areas of reduced salinity. Still occurs naturally in some areas as extensive reefs on hard to firm bottoms, intertidally and subtidally. Very important commercially, and extensively exploited, being widely cultivated in many areas of its range (Galtsoff 1964; García-Cubas et al. 1987; Quayle and Newkirk 1989; Andrews 1991; Menzel 1991; Nascimento 1991 [who calls it *C. brasiliana*]). Has been introduced to the west coast of North America, Hawaii, Australia, England, Japan, and possibly other areas, but generally has not become established there (Quayle 1988; Arakawa 1990).

crenulifera, Dendostrea, and ***Ostrea mordax*** and ***Saccostrea mordax*** are synonyms of *Pustulostrea tuberculata.*

cristagalli, Lopha. See *Lopha cristagalli.*

cristata, Ostrea. Synonym: *Ostreola equestris.*

crynusi, Ostrea. See *Ostrea crynusi.*

Cryptostrea permollis **(Sowerby, 1844).*** Sponge oyster. Has also been placed in *Ostrea.* Synonym: *C. weberi.*

Comments. Medium (up to 7.6 cm, Abbott 1974). Northeastern Gulf of Mexico, off coast of North Carolina to Florida and West Indies. Records from West Indies need verification (Harry 1985). Moderately common, living embedded in bread sponge or under rocks, low tide to about 3 m (McLean 1941). *Cryptostrea weberi* is an ecologic form. One of the most thoroughly studied of the noncommercial oysters (Abbott 1974; Harry 1985).

cucullata, Crassostrea. Now in genus *Saccostrea.*

cucullata, Ostrea. Now in genus *Saccostrea.*

cucullata, Saccostrea. See *Saccostrea cucullata.*

cumingiana, Ostrea. Synonym: *Alectryonella plicatula.*

cuttakensis, Crassostrea. See *Crassostrea gryphoides.*

D

dalli, Ostrea. Synonym: *Dendostrea folium.*

Dendostrea folium **(Linné, 1758).*** Bronze oyster, cox-comb oyster, flat oyster, imbricated oyster, leaf oyster, wanigaki. Has also been placed in *Lopha, Mytilus, Ostrea.* Synonyms: *Lopha folium, Mytilus frons, Ostrea folium, O. serra, O. dalli, O. bresia.*

Comments. Medium (up to 10 cm, Thomson 1954). Widely distributed in Indo-West Pacific region (Harry 1985). Moderately common, intertidal and submerged, on mangrove roots in lower estuaries, solitarily attached to floating twigs. Not of commercial interest. Experimentally cultured in Malaysia. Some harvesting from wild populations in the Morocco to Gabon area of western Africa (Thomson 1954; Angell 1986; Rao 1987).

Dendostrea frons **(Linné, 1758).*** Frons oyster. Has also been placed in *Ostrea.* Synonyms: *Ostrea limacella, O. rubella.*

Comments. Small (up to 5 cm, Abbott 1974). Tropical western Atlantic and probably also in eastern Atlantic (Harry 1985). Common, often on mangrove roots south of the United States (Galtsoff 1964).

Dendostrea mexicanum **(Sowerby, 1871).***

Comments. Tropical and warm temperate seas in eastern Pacific, coast of Baja California. Moderately common, in shallow subtidal depths in protected waters of normal salinity. Often associated with gorgonians and stony corals (Harry 1985).

denselamellosa, Ostrea. See *Ostrea denselamellosa.*
discoidea, Ostrea. Synonym: *Planostrea pestigris.*
dubia, Ostrea. Synonym: *Alectryonella plicatula.*

E

echinata, Crassostrea. Now in genus *Saccostrea.*
echinata, Ostrea. Now in genus *Saccostrea.*
echinata, Saccostrea. See *Saccostrea echinata.*
edulis, Ostrea. See *Ostrea edulis.*
equestris, Ostrea. Now in genus *Ostreola.*
equestris, Ostreola. See *Ostreola equestris.*
expansa, Ostrea. Synonym: *Ostreola conchaphila.*

F

fischeri, Crassostrea. Synonym: *Hyotissa hyotis.*
fisheri, Ostrea. Synonym: *Hyotissa hyotis.*
floridensis, Ostrea. Synonym: *Crassostrea virginica.*
folium, Crassostrea. Now in genus *Dendostrea.*
folium, Dendostrea. See *Dendostrea folium.*
folium, Lopha. Now in genus *Dendostrea.*
folium, Ostrea. Now in genus *Dendostrea.*
forskali, Ostrea. Synonym: *Saccostrea cucullata.*
forskali, Saccostrea. Synonym: *Saccostrea cucullata.*
frons, Dendostrea. See *Dendostrea frons.*
frons, Mytilus. Now in genus *Dendostrea.*
frons, Ostrea. Now in genus *Dendostrea.*

G

gallus, Ostrea. Synonym: *Undulostrea megadon.*
gasar, Crassostrea. See *Crassostrea gasar.*
gigas, Crassostrea. See *Crassostrea gigas.*
glomerata, Crassostrea. Now in genus *Saccostrea.*
glomerata, Ostrea. Now in genus *Saccostrea.*
glomerata, Saccostrea. See *Saccostrea commercialis.*
gryphoides, Crassostrea. See *Crassostrea gryphoides.*
gryphoides, Ostrea. Now in genus *Crassostrea.*
gundata, Ostrea. Synonym: *Ostreola equestris.*
guyenensis, Crassostrea virginica. See *Crassostrea virginica.*

H

hyotis, Hyotissa. See *Hyotissa hyotis.*
hyotis, Mytilus. Now in genus *Hyotissa.*
hyotis, Ostrea. Now in genus *Hyotissa.*
hyotis, Pycnodonte. Now in genus *Hyotissa.*

Hyotissa hyotis **(Linné, 1758).*** Honeycomb oyster, hyoid oyster, giant oyster, shakogaki. Has also been placed in *Crassostrea, Ostrea, Pycnodonte.* Synonyms: *Crassostrea fischeri, Mytilus hyotis, Ostrea fisheri, O. sinensis, O. jacobaea, O. thomasi, O. turbinata,* and many others (Torigoe 1981; Skoglund 1991).

Comments. Large (up to 30 cm long, Thomson 1954). Tropics of Indo-West Pacific and eastern Pacific (Thomson 1954; Harry 1985). Common, in shallow, subtidal depths, often on coral reefs. A main commercial species in the tropics. Harvested from wild populations (Torigoe 1981; Harry 1985; Angell 1986; Quayle and Newkirk 1989).

I

imbricata, Ostrea. Now in genus *Parahyotissa.*
imbricata, Parahyotissa. See *Parahyotissa imbricata.*
iredalei, Crassostrea. See *Crassostrea iredalei.*
iredalei, Ostrea. See *Crassostrea iredalei.*
iridescens, Crassostrea. See *Striostrea prismatica.*
iridescens, Ostrea. See *Striostrea prismatica.*
iridescens, Saccostrea. See *Striostrea prismatica.*

J

jacobaea, Ostrea. Synonym: *Hyotissa hyotis.*

K

kupua, Ostrea. Synonym: *Ostrea sandvicensis.*

L

lacerata, Crassostrea virginica. See *Crassostrea virginica.*
lamellosa, Ostrea. See *Ostrea lamellosa.*
laperousii, Ostrea. Synonym: *Crassostrea gigas.*
laticaudata, Ostrea. Synonym: *Ostreola conchaphila.*
limacella, Ostrea. Synonym: *Dendostrea frons.*

Lopha cristagalli* (Linné, 1758). Cock's comb oyster. Has also been placed in *Crassostrea, Mytilus,* and *Ostrea.* Synonym: *Ostrea townsendi.*

Comments. Medium (up to 10 cm, Torigoe 1981; Rao 1987). Mediterranean (Durve 1986), Indo-West Pacific, east coast of Africa and Red Sea to Ryukyu Islands, Philippines, Indonesia, and rare in northern Australian waters (Torigoe 1981; Harry 1985). Common to rare, limited to the tropics, associated with coral reefs at depths of a few meters (Harry 1985). Oysters consumed from the wild by local fisherfolk (Rao 1987).

lugubris, Crassostrea. Now in genus *Saccostrea.*
lugubris, Saccostrea. See *Saccostrea lugubris.*
lurida, Ostrea. Synonym: *Ostreola conchaphila.*
lutaria, Ostrea. Synonym: *Ostrea puelchana.*

M

madrasensis, Crassostrea. See *Crassostrea madrasensis* and *C. virginica.*
madrasensis, Ostrea. Now in genus *Crassostrea.* See *Crassostrea madrasensis* and *C. virginica.*
malabonensis, Ostrea. See *Saccostrea malabonensis.*
malabonensis, Saccostrea. See *Saccostrea malabonensis.*
manilai, Saccostrea. See *Saccostrea malabonensis.*
margaritacea, Crassostrea. Now in genus *Striostrea.*
margaritacea, Striostrea. See *Striostrea margaritacea.*
maura, Ostrea. Synonym: *Myrakeena angelica.*
mcgintyi, Parahyotissa. See *Parahyotissa mcgintyi.*
megadon, Ostrea. Now in genus *Undulostrea.*
megadon, Undulostrea. See *Undulostrea megadon.*
mexicanum, Dendostrea. See *Dendostrea mexicanum.*
mordax, Saccostrea. See *Saccostrea mordax.*
multicostata, Ostrea. Synonym: *Ostrea denselamellosa.*
multistriata, Ostrea. Synonyms: *Crassotrea nippona* and *Ostreola conchaphila.*

Myrakeena angelica* (Rochebrune, 1895). Has also been placed in *Ostrea* and *Lopha.* Synonym: *Ostrea maura.*

Comments. Medium (up to 10 cm, Keen 1971). Seems to be limited to Gulf of California, contrary to statements in the literature (Harry 1985). Moderately common, in water of normal oceanic salinity, in protected areas at low tide level and slightly deeper (Harry 1985).

mytiloides, Striostrea. See *Striostrea mytiloides.*

N

Neopycnodonte cochlear* (Poli, 1795). Deepsea oyster, spoon oyster, bekkogaki. Has also been placed in *Notostrea, Ostrea, Pycnodonte.* Synonyms: *Ostrea hiranoi, O. musashiana, Pycnodonta floribunda,* and several others (Torigoe 1981; Harry 1985).

Comments. Small (up to 7 cm high, Torigoe 1981). Extends to greater depths than any other recent oyster: 27 to 2,100 m. Populations are localized throughout its range: eastern Atlantic from Mediterranean to Atlantic coasts of France, western Atlantic from Bermuda, North Carolina, and east coast of Florida, off Texas; in Indo-West Pacific from Red Sea to Madagascar, Philippines, China Sea, Japan, and Hawaii (Harry 1985).

nippona, Crassostrea. See *Crassostrea nippona.*

nippona, Ostrea. Now in genus *Crassostrea.*

nomades, Ostrea. See *Ostrea nomades.*

numisma, Parahyotissa. See *Parahyotissa numisma.*

O

ochracea, Crassostrea. Synonym: *Crassostrea columbiensis.*

***Ostrea crynusi* Payraudeau, 1826.** Corcega oyster. Synonym: A variety of *O. edulis* (Lamy 1929-30; Parenzan 1974).

Comments. Medium (up to 14 cm, Parenzan 1974). Eastern Atlantic and Mediterranean. Edible oyster, harvested in the wild.

Ostrea denselamellosa* Lischke, 1869. Itabogaki. Synonyms: *Ostrea auriculata, O. multicostata.*

Comments. Large (up to 13 cm high, Torigoe 1981). Along main islands of Japan, adjacent shore of Asia (Imai 1977; Harry 1985; Cai and Li 1990), and all along the Chinese coast (Tchang and Tse-Kong 1956). In intertidal zone to 20 m depth. A palatable oyster, difficult to gather, usually dredged. Culture attempted unsuccessfully (Cahn 1950; Torigoe 1981).

Ostrea edulis* Linné, 1758. Edible oyster, European flat oyster. Synonyms: *Ostrea taurica, O. adriatica* (Parenzan 1974), and several others.

Comments. Large (up to 11 cm and more, Tebble 1976; Hidu and Lavoie 1991). Eastern Atlantic from Norway and British Isles to Morocco and the Mediterranean and Black Seas (Harry 1985; Hidu and Lavoie 1991), Aegean and Marble Seas (Mozdyhai-Boltovskoi 1972; Krakatitsa 1973). Common, a main commercial species in Western Europe and the Mediterranean (Quayle and Newkirk 1989). Cultivated since ancient Roman times; cultivation flourishes today in France, Netherlands, United Kingdom, Spain, and other areas (Héral and Deslous-Paoli 1991). Experimentally introduced in Maine, eastern Canada, and in Japan where commercial cultivation has developed (Arakawa 1990). At present natural beds of *O. edulis* are providing the beginnings of a new natural fishery in Maine (Hidu and Lavoie 1991). Has been introduced and is being raised commercially at several west American locations from Boundary Bay, British Columbia to Santa Barbara, California (Coan et al. In prep.). Is the only commercial oyster in Turkey.

***Ostrea lamellosa* Brocchi, 1814.** Synonyms: *Ostrea taurica* var. *karkinitica, O. sublamellosa.* Probably a synonym or variety of *O. edulis* (Lamy 1929-30; Mozdyhai-Boltovskoi 1972; Parenzan 1974).

Comments. Coasts of Portugal, Mediterranean, and Black Sea.

***Ostrea lurida* Carpenter, 1864.** Olympia oyster. Synonym: *Ostreola conchophila*

***Ostrea nomades* Iredale, 1939.** Green oyster. Synonym: *Ostrea crenulifera.*

Comments. Small (up to 5 cm, Thomson 1954). South Pacific, northern Australia (Thomson 1954; Angell 1986). Moderately common? Commercial potential unknown (Angell 1986).

Ostrea puelchana* Orbigny, 1841. Chilean flat oyster, mud oyster, ostra, Port Lincoln oyster, Stewart Island oyster, New Zealand dredge oyster. Has also been placed in *Anodontostrea, Crassostrea,* and *Tiostrea.* Synonyms: Species *angasi, algoensis, chilensis, lutaria* (Lamy 1929-30; Chanley and Dinamani 1980).

Comments. Large (up to 18 cm, MacPherson and Gabriel 1962). Circumglobal between 35° and 50° S latitude, including coasts of east and west South America, southern New Zealand, southern Australia and South Africa (Thomson 1954; Harry 1985). Common, low tide to 15 m, edible, important commercial species, widely cultivated in New Zealand and west coast of South America (De Castellanos 1957; Chanley and Dinamani 1980; Quayle 1980; Castillo-Rodríguez and García-Cubas 1986; Chanley and Chanley 1991; Hernández 1991). Forms beds in estuaries (Arakawa 1990). Artificial production of young in Chile is well advanced, but there is a shortage of seed; in Argentina cultivation is mostly on a pilot scale; in Brazil primarily natural populations are harvested (Hernández 1990). The Chilean [*Tiostrea chilensis* (Phillippi, 1845)] and New Zealand [*Tiostrea lutaria* (Hutton 1873)] oysters are different populations of the same species, the genetic similarity between the two populations being 0.991 (Buroker et al. 1983). Castro and Lucas (1987) report the occurrence of male neoteny in populations of presumably this species from the Atlantic coast of Brazil and Argentina. "Small" individuals function exclusively as males, living about one year attached to the anterior edge of the left valve in the inhalant cavity of females. Whether male neoteny occurs in populations of this species in other parts of the world has not been determined.

Ostrea sandvicensis **Sowerby, 1871.** The species name also has been spelled *sandwichensis* (Galtsoff 1964). Synonyms: *O. rosacea, O. kupua* (Kay 1979).

Comments. Small (5 cm, Kay 1979). Hawaiian Islands. Grows in clusters on rocks and pilings at Pearl Harbor and is a dominant element on reefs in Kaneohe Bay and Ala Moana, Oahu. Also common in brackish water habitats on Hawaii. Non-commercial.

Ostrea spreta **Orbigny, 1841.**

Comments. Small (up to 5 cm, De Castellanos 1957). Antilles, Brazil, Uruguay, and Argentina (De Castellanos 1957). Of limited commercial importance (Hernández 1990). Can be confused with *O. puelchana*, but *O. spreta* lives in shallower water (Boffi 1979).

Ostrea tarentina **Issel, 1882.** Synonym: According to Lamy (1929-30) this is a variety of *Ostrea edulis.*

Comments. Medium. Western and southern Europe, Mediterranean (Parenzan 1974; Cifuentes-Lemus and Juan-Luis 1986). Edible oyster harvested in the wild.

Ostrea trapezina **Lamarck, 1819.** Saddle oyster. Synonym: Probably same as *Parahyotissa imbricata.*

Comments. Large (up to 13 cm, Thomson 1954). Northern Australia and Great Barrier Reef (Thomson 1954; Angell 1986). Commercial potential unknown (Angell 1986).

Ostreola conchaphila **(Carpenter, 1857).*** Native Pacific oyster, Olympia oyster, shell-loving oyster. Has also been placed in *Ostrea.* Synonyms: Species *expansa, laticaudata, lurida, rufoides* (Lamy 1929-30; Abbott 1974).

Comments. Medium (5 to 8 cm, Quayle 1988; Arakawa 1990). Eastern Pacific from Alaska to Panama (Harry 1985). Chiefly in estuaries and salt water lagoons, in numerous places but nowhere in abundance (Quayle 1988). A main commercial species in western North America (Quayle and Newkirk 1989). The form named *O. conchaphila* is usually solitary, attached to living molluscs; the form named *O. lurida* is attached to dead shells or rocks and may form extensive reefs. The species is highly variable, depending on situation and habitat, but there are no discernible consistent differences for recognition of more than one taxon (Coan et al. 1995).

Ostreola equestris **(Say, 1834).*** Crested oyster. Has also been placed in *Ostrea.* Synonyms: *O. spreta, O. gundata, O. cristata.*

Comments. Medium (up to 8 cm, García-Cubas 1981). Western Atlantic from North Carolina to Argentina (Harry 1985). Common in high salinity inlets and bays, subtidal to few meters depth, tropical and temperate seas (García-Cubas 1981; Harry 1985; García-Cubas et al. 1987). Dominant in offshore waters in northwestern Gulf of Mexico, also on oil platforms in the Gulf; unable to withstand brackish water; culture might be possible in high salinity water (Angell 1986; Harry 1986).

Ostreola stentina **(Payraudeau, 1826).*** Has also been placed in *Ostrea.* Synonyms: Many (Lamy 1929-30).

Comments. Small (Angell 1986). Eastern Atlantic from Mediterranean southward possibly to South Africa (Harry 1985; Angell 1986). In tropical and temperate seas, chiefly in shallow subtidal waters to few meters in depth (Harry 1985). Oyster is too small to justify commercial cultivation (Angell 1986).

P

palmipes, Crassostrea. Synonym: *Planostrea pestigris.*

palmipes, Ostrea. Synonym: *Planostrea pestigris.*

palmipes, Saccostrea. Synonym: *Planostrea pestigris.*

palmula, Crassostrea. Now in genus *Saccostrea.*

palmula, Ostrea. Now in genus *Saccostrea.*

palmula, Saccostrea. See *Saccostrea palmula.*

panamensis, Ostrea. Synonym: *Saccostrea palmula.*

Parahyotissa imbricata* (Lamarck, 1819). Kakitsubata. Has also been placed in *Dendostrea, Hyotissa, Ostrea, Pretostrea, Pycnodonta* (Torigoe 1981).

Comments. Medium (up to 13 cm high, Torigoe 1981). Central part of Indo-West Pacific tropics, Australia to Ryukyu Islands (Harry 1985).

Parahyotissa mcgintyi* Harry, 1941. McGinty oyster.

Comments. Tropical eastern and western Atlantic, extending slightly into subtropical areas to North Carolina and Texas (Harry 1985). Common, subtidal to 98 m depth or slightly more. One of most abundant oysters on offshore oil platforms, chiefly off Louisiana (Harry 1985, 1986b).

Parahyotissa numisma* (Lamarck, 1819). Has also been placed in *Ostrea.* Synonyms: *O. thaanumi,* and others (Lamy 1929-30).

Comments. Widely distributed in tropics of Indo-Pacific from East Africa to Hawaii and Tuamoto Islands (Harry 1985).

Parahyotissa quercinus* (Sowerby, 1871). Has also been placed in *Ostrea.*

Comments. Eastern Pacific particularly along east coast of Baja California (Harry 1985).

paraibanensis, Crassostrea. See *Crassostrea paraibanensis.*

paulucciae, Ostrea. Now in genus *Planostrea,* synonym of *Planostrea pestigris.*

permollis, Cryptostrea. See *Cryptostrea permollis.*

permollis, Ostrea. See *Cryptostrea permollis.*

pestigris, Ostrea. Now in genus *Planostrea.*

Planostrea pestigris* (Hanley, 1846). Palm-rooted oyster, talabang pulid-pulid. Has also been placed in *Ostrea* and *Crassostrea.* Synonyms: Species *rivularis, paulucciae, palmipes* (Harry 1985). Harry (1985) proposed the new genus *Planostrea* for *Ostrea pestigris*; however, Coan (pers. comm.) suggests this genus might better be regarded as a subgenus.

Comments. Medium (up to 7.5 cm high, Harry 1985 — in contrast to *Crassostrea ariakensis* which is up to 20 to 24 cm high, Cahn 1950; Torigoe 1981). From Philippines, Taiwan to Formosa, Thailand, and North Borneo. An occasional specimen may occur at low tide, but most seem to have been dredged from few to 100 m. Harry (1985) also noted that the genus *Planostrea* in many ways is the tropical counterpart of *Ostrea* in the Indo-Western Pacific.

plicata, Ostrea. Synonym: *Alectryonella plicatula.*

plicatula, Alectryonella. See *Alectryonella plicatula.*

plicatula, Ostrea. Now in genus *Alectryonella.*

posjectica, Crassostrea. Synonym: *Crassostrea gigas.*

prismatica, Striostrea. See *Striostrea prismatica.*

procella, Ostrea. Synonym: *Ostreola conchaphila.*

puelchana, Ostrea. See *Ostrea puelchana.*

Pustulostrea tuberculata* (Lamarck, 1804). Crenulate oyster, coral oyster, northwest rock oyster, pink oyster, ohagurogaki. Has also been placed in *Ostrea* and *Saccostrea.* Synonyms: Species *amasa, australis, crenulifera, mordax, rufa* (Lamy 1929-30, Harry 1985).

Comments. Medium (up to 9 cm, Torigoe, 1981). Islands off west coast of Malay Peninsula to Singapore, throughout Indonesia and eastward to New Hebrides (Thomson 1954; Torigoe 1981; Harry 1985). Evidently rare and local, in shallow water of high salinity and probably usually associated with coral reefs (Harry 1985).

Pycnodonte, see *Hyotissa hyotis.*

Q

quercinus, Parahyotissa. See *Parahyotissa quercinus.*

R

rhizophorae, Crassostrea. See *Crassostrea rhizophorae.*

rivularis, Crassostrea. Synonym: *Planostrea pestigris.* See also p. 2.

rivularis, Ostrea. Synonym: *Planostrea pestigris.*

rosacea, Ostrea. Synonym: *Ostrea sandvicensis.*

rubella, Ostrea. Synonym: *Dendostrea frons.*

rufoides, Ostrea. Synonym: *Ostrea conchaphila.*

S

***Saccostrea commercialis* (Iredale and Roughley, 1933).** Commercial oyster, mangrove oyster, rock oyster, Sydney rock oyster. Has also been placed in *Ostrea.* Synonym: *Saccostrea commercialis* could be a synonym (Angell 1986) or a subspecies (Buroker et al. 1979a, b) of *S. glomerata*; the two taxa are closely similar (Gaffney and Allen 1993). Anderson and Adlard (1994) support the synonymy of *S. commercialis* and *S. glomerata.*

Comments. Large (up to 25 cm when cultivated, Thomson 1954; Ahmed 1977). East coast of Australia, New Zealand, and north to Thailand (Angell 1986). In intertidal zone attached to rocks and shell, mainly in estuaries (Thomson 1954; Ahmed 1975). Important commercial species, widely cultivated in eastern Australia and New Zealand (Quayle 1980). Introduced to Hawaii (Arakawa 1990).

Saccostrea cucullata* (Born, 1778). Bombay oyster, curly oyster, Indian Rock oyster, Red Sea oyster, talabang kulot. Has also been placed in *Crassostrea* and *Ostrea.* Synonyms: *Saccostrea forskalli, Ostrea cornucopia,* and many others (Lamy 1929-30). See also Nie (1991).

Comments. Tropical coast of West Africa and offshore islands, around Cape of Good Hope, into Indo-West Pacific to southern Japan, southeastern and western Australia, northern New Zealand, and possibly somewhat eastward (Harry 1985), all along the Chinese coast (Tchang and Tse-kong 1956), and Philippines (Rosell 1991). Most widely distributed of the species of *Saccostrea* (Angell 1986). Limited to tropics or slightly beyond. Common on intertidal and shallow subtidal rocky or firm substrata. An important commercial species in the Indian Ocean and southeast Asia, Philippines, Africa, Australia, New Zealand; harvested from the wild and widely cultivated in many regions of its range (Awati and Rai 1931; Ahmed 1975; Quayle 1980; Angell 1986; Mahadevan 1987; Rao 1987; Quayle and Newkirk 1989; Arakawa 1990). Ahmed (1975) states that *Saccostrea cucullata* (on the western coast of Australia) and *S. commercialis* (eastern coast of Australia) are separate species, and Buroker et al. (1979a, b) confirmed their distinctness on the basis of allozyme electrophoresis.

***Saccostrea echinata* (Quoy and Gaimard, 1834).** Black-bordered oyster, black-edged oyster, black-lipped oyster, nisemagaki. Synonym: *Ostrea spinosa.*

Comments. Large (up to 18 cm high, Torigoe 1981). Southeast Asia, Japan, Australia, East Indies, Indian Ocean, Philippines, Western Pacific islands (Thomson 1954; Imai 1977; Angell 1986; Quayle and Newkirk 1989; Cai and Li 1990). Common, attached to intertidal and shallow subtidal rocks and other hard surfaces. Widely cultivated in Indian Ocean and southeastern Asia, is harvested from wild populations. Could have a potential for experimental culture in high salinity seawater (Cahn 1950; Thomson 1954; Angell 1986; Quayle and Newkirk 1989). *Saccostrea echinata* could be an allospecies on the northern coast of Australia (Buroker et al. 1971b).

***Saccostrea glomerata* (Gould, 1850).** New Zealand rock oyster. Has also been placed in *Ostrea, Crassostrea,* and *Saccostrea.* Synonyms: Species *amasa* and *glomerata* called subspecies of *Saccostrea commercialis* by Buroker et al. (1979a). Anderson and Adlard (1994) support the synonymy of *S. commercialis* and *S. glomerata.*

Comments. Medium (up to 10 cm, Ahmed 1971; Torigoe 1981; Dinamani 1991a). New Zealand, Hong Kong, Pakistan, Arabian Sea (Buroker et al. 1979a). Distributed along high water mark in backwaters and creeks, characteristically on breakwater rocks. Forms thick clusters. Smallest of oyster species on coast of West Pakistan. At one time the main commercial species in New Zealand (Ahmed 1971; Quayle and Newkirk 198; Dinamani 1991a).

Saccostrea lugubris **(Conrad, 1857).** Has also been placed in *Crassostrea.*

Comments. South China Sea eastward to Papua New Guinea (Angell 1986). A main commercial species in Thailand and South China Sea (Quayle and Newkirk 1989). Commercially farmed in Thailand and harvested from wild populations in the Philippines (Angell 1986).

Saccostrea malabonensis **(Faustino, 1932).** Subtrigonal oblong oyster, talabang kukong kabayo. Synonym: Possibly *Saccostrea manilai.*

Comments. Medium (up to 8 cm high, Torigoe 1981). Japan, Philippines (Torigoe 1981; Angell 1986). A highly prized edible oyster (Torigoe 1981), cultured commercially in the Philippines (Angell 1986; Rosell 1991). *Saccostrea manilai* has the same characteristics as, and overlaps the home range of, *S. malabonensis,* but is reproductively isolated (Angell 1986; Buroker et al. 1979b). More study is needed to substantiate whether *S. manilai* is a new species (Torigoe 1981).

Saccostrea mordax **(Gould).** Synonym: *Pustulostrea tuberculata.*

Saccostrea palmula **(Carpenter, 1857).*** Palmate oyster. Has also been placed in *Crassostrea* and *Ostrea.* Synonyms: Species *amara, dalli, panamensis, serra, tubulifera* (Abbott 1974).

Comments. Medium (up to 8 cm high, Keen 1971). Eastern Pacific from west coast of Baja California to Panama, Ecuador, and Galapagos Islands (Harry 1985). Common, attached to mangrove roots or rocks in intertidal and shallow subtidal areas of estuaries and mangrove forests. One of the most variably shaped of Panamic Province oysters. Of commercial importance, cultured commercially on west coast of Mexico and cultivated experimentally in Panama (Keen 1971; Angell 1986; Hernández 1990).

sandvicensis, Ostrea. See *Ostrea sandvicensis*.

sedea, Crassostrea. See *Crassostrea sedea.*

serra, Ostrea. Synonym: *Saccostrea palmula.*

sikamea, Crassostrea. Could be a nonsibling species of *C. gigas* (Buroker et al. 1979a). See *Crassostrea gigas.*

sinensis, Hyotissa. Synonym: *Hyotissa hyotis.*

solida, Ostrea. Synonym: *Alectryonella plicatula.*

spathulata, Ostrea. Synonym: *Ostrea iridescens.*

spinosa, Ostrea. Synonym: *Saccostrea echinata.*

spreta, Ostrea. See *Ostrea spreta.*

stentina, Ostrea. Now in genus *Ostreola.*

stentina, Ostreola. See *Ostreola stentina.*

Striostrea circumpicta **(Pilsbry, 1904).*** Kokegoromo oyster. Has also been placed in *Ostrea.*

Comments. Large (up to 20 cm or more). Southern Japan (Torigoe 1981; Harry 1985).

Striostrea margaritacea **(Lamarck, 1819).*** Has also been placed in *Crassostrea.*

Comments. Large (up to 20 cm or more). Coast of tropical Africa to South Africa (Harry 1985). A main commercial species in South Africa (Quayle and Newkirk 1989).

Striostrea mytiloides **(Lamarck, 1819).***

Comments. Large (up to 12 cm high). Samoa to Philippines, Indonesia, northwest Australia, India, and Zanzibar. Generally attached to red mangrove roots (Harry 1985).

Striostrea prismatica **(Gray, 1825).*** Has also been placed in *Crassostrea* and *Ostrea.* Synonyms: Species *iridescens, lucasiana, spathulata, turturina.*

Comments. Large (up to 25 cm or more; Harry 1985; Angell 1986). Common subtidally and on rocks exposed to open ocean (Castillo-Rodríguez and García-Cubas 1986). Of commercial importance in Mexico (Angell 1986). Cultured experimentally on Pacific coast of Colombia (Hernández 1990).

T

talienwhanensis, Crassostrea. Synonym: *Crassostrea gigas.*

talienwhanensis, Ostrea. Synonym: *Crassostrea gigas.*

tarentina, Ostrea. See *Ostrea tarentina.*

taurica, Ostrea. Synonym: *Ostrea edulis,* see *Ostrea lamellosa.*

taylori, Ostrea. Synonym: *Undulostrea megadon.*

thomasi, Ostrea. Synonym: *Hyotissa hyotis.*

***Tiostrea chilensis* (Philippi, 1845).** Chilean oyster, dredge oyster (see Chanley and Chanley 1991). Synonym: *Ostrea puelchana; Tiostrea chilensis* from the Chilean coast and *T. lutaria* from New Zealand are different geographical populations of one species (Buroker 1983; Harry 1985).

townsendi, Ostrea. Synonym: *Lopha cristagalli.*

trapezina, Ostrea. See *Ostrea trapezina.*

tuberculata, Crassostrea. Now in genus *Pustulostrea.*

tuberculata, Ostrea. Now in genus *Pustulostrea.*

tuberculata, Pustulostrea. See *Pustulostrea tuberculata.*

tubulifera, Ostrea. Synonym: *Saccostrea palmula.*

tulipa, Crassostrea. Synonym: *Crassostrea gasar.*

turbinata, Ostrea. Synonym: *Hyotissa hyotis.*

turturina, Ostrea. Synonym: *Striostrea prismatica.*

U

Undulostrea megadon* (Hanley, 1846). Megadon oyster. Has also been placed in *Ostrea.* Synonyms: Species *cerrosensis, gallus, taylori, veatchi* (Lamy 1929-30).

Comments. Medium (up to 8 cm, Keen 1971). Gulf of California and Baja California to Peru. Moderately common, offshore to about 10 m. Unimportant commercially (Abbott 1974; Harry 1985).

V

veatchi, Ostrea. Synonym: *Undulostrea megadon.*

virginica, Crassostrea. See *Crassostrea virginica.*

W

weberi, Cryptostrea. Synonym: *Cryptostrea permollis.*

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REFERENCES

Abbott, R.T. 1974. American Seashells. The Marine Mollusca of the Atlantic and Pacific Coasts of North America, 2nd edition. Van Nostrand Reinhold, New York. 663 pp.

Ahmed, M. 1971. Oyster species of West Pakistan. Pakistan J. Zool. 3:229-236.

Ahmed, M. 1975. Speciation in living oysters. Adv. Mar. Biol. 13:357-397.

Ajana, A.M. 1980. Fishery of the mangrove oyster, *Crassostrea gasar* Adanson (1757) in the Lagos area, Nigeria. Aquaculture 21:129-137.

Allen, S.K., Jr. and P.M. Gaffney. 1993. Genetic confirmation of hybridization between *Crassostrea gigas* (Thunberg) and *Crassostrea rivularis* (Gould). Aquaculture 113:291-300.

Anderson, T.J. and R.D. Adlard. 1994. Nucleotide sequence of a rDNA internal transcribed spacer supports synonymy of *Saccostrea commercialis* and *S. glomerata.* J. Molluscan Studies 60:196-197.

Andrews, J.D. 1991. The oyster fishery of eastern North America based on *Crassostrea virginica.* Pages 11-23 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Angell, C.L. 1986. The biology and culture of tropical oysters. International Center for Living Aquatic Resources Management, Studies and Reviews 13, 42 pp. Manila, Philippines.

Arakawa, K.Y. 1990. Commercially important species of oysters in the world. Mar. Behav. Physiol. 17:1-3.

Awati, P.R. and H.S. Rai. 1931. *Ostrea cucullata* (the Bombay oyster). Indian Zool. Mem., Indian Animal Types, III, 107 pp. Methodist Publishing House, Lucknow, India.

Baqueiro, C.E. 1991. Culture of *Crassostrea corteziensis* in Mexico. Pages 113-116 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Bernard, F.R. 1983. Catalogue of the living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Special Publication of Fisheries and Aquatic Sciences 61, 102 pp.

Boffi, A.V. 1979. Moluscos brasileiros de interesse médico e econômico. Fundacão de Amparo Pesquisa do Estado de São Paulo, Editora Hucitec, São Paulo, [Simbolo S.A. Industrias Graficas, São Paulo, Brasil]. 182 pp.

Buroker, N.E. 1982. Allozyme variation in three nonsibling *Ostrea* species. J. Shellfish Res. 2:157-163.

Buroker, N.E. 1983. Population genetics of the American oyster *Crassostrea virginica* along the Atlantic coast and the Gulf of Mexico. Mar. Biol. 75:99-112.

Buroker, N.E., P. Chanley, H.J. Cranfield, and P. Dinamani. 1983. Systematic status of two oyster populations of the genus *Tiostrea* from New Zealand and Chile. Mar. Biol. 77:191-200.

Buroker, N.E., W.K. Hershberger, and K.K. Chew. 1979a. Population genetics of the family Ostreidae. 1. Instraspecific studies of *Crassostrea gigas* and *Saccostrea commercialis.* Mar. Biol. 54:157-169.

Buroker, N.E., W.K. Hershberger, and K.K. Chew. 1979b. Population genetics of the family Ostreidae. 2. Interspecific studies of the genera *Crassostrea* and *Saccostrea.* Mar. Biol. 54:171-184.

Cahn, A.R. 1950. Oyster culture in Japan. U.S. Department of Commerce, Office of Technical Services, Report 134, 80 pp.

Cai, Y. and X. Li. 1990. Oyster culture in the People's Republic of China. World Aquaculture 21(4):67-72.

Carreon, J.A. 1969. The malacology of Philippine oysters of the genus *Crassostrea* and a review of their shell characters. Proc. Natl. Shellfish. Assoc. 59:104-115.

Carriker, M.R. 1976. The crucial role of systematics in assessing pollution effects on the biological utilization of estuaries. In Estuarine Pollution Control and Assessment, Proc. Conf., vol. 1, 2, U.S. Environmental Protection Agency, Officer of Water Planning and Standards, U.S. Govt. Office, pp. 487-506.

Castillo-Rodríguez, A.G. and A. García-Cubas. 1986. Taxonomía y anatomía comparada de las ostras en las costas de México. An. Inst. Cienc. Mar. Limnol., Univ. Natl. Auton. México 13:249-314.

Castro, N.F. and A. Lucas. 1987. Variability of the frequency of male neoteny in *Ostrea puelchana* (Mollusca: Bivalvia). Mar. Biol. 96:359-365.

Cham, M. 1991. The traditional oyster fishery of the Gambia. Out of the shell, Mollusc Culture Network Newsletter, Internat. Develop. Res. Centre, Halifax, Canada 1(4):13-18, 20.

Chanley, M.H. and P. Chanley. 1991. Cultivation of the Chilean oyster, *Tiostrea chilensis* (Phillipi, 1845). Pages 145-151 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Chanley, P. and P. Dinamani. 1980. Comparative descriptions of some oyster larvae from New Zealand and Chile, and a description of a new genus of oyster, *Tiostrea.* New Zealand J. Mar. Freshw. Res. 14:103-120.

Cifuentes-Lemus, M. and C. Juan-Luis. 1986. Los moluscos como alimento actual y futuro. Memorias II, Reunion Malacología Conquiliología. Soc. Méx. Malacol. Conquil., Univ. Natl. Auton. México, Villahermosa, Tabasco, pp. 123-154.

Coan, E.V., P.H. Scott, and F.R. Bernard. 1995. Bivalve Seashells of Western North America. Marine Bivalve Mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History, Santa Barbara, California.

De Castellanos, Z.J.A. 1957. Contribución al conocimiento de las especies de ostras del literal Argentina (*Ostrea puelchana* y *O. spireta*). Min. Agr. Ganad. Dept. Investig. Pesqueras, Buenos Aires, Argentina, 40 pp.

Dinamani, P. 1991a. The northern rock oyster, *Saccostrea glomerata* (Gould, 1850), in New Zealand. Pages 335-341 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Dinamani, P. 1991b. The Pacific oyster, *Crassostrea gigas* (Thunberg, 1793), in New Zealand. Pages 343-352 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Dix, T.G. 1991. The Pacific oyster, *Crassostrea gigas,* in Australia. Pages 315-318 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Durve, V.S. 1986. On the ancestry and distribution of three species of Indian oysters. Indian J. Mar. Sci. 15:56-58.

Frías, J.A. and R. Rodríguez. 1991. Oyster culture in Cuba: current state, techniques and industry organization. Pages 51-74 in G. F. Newkirk and B. A. Field (eds.). Oyster Culture in the Caribbean. Mollusc Culture Network, Biol. Dept., Dalhousie Univ., Halifax, Nova Scotia, Canada.

Gaffney, P.M. and S.K. Allen, Jr. 1993. Hybridization among *Crassostrea* species: a review. Aquaculture 116:1-13.

Galtsoff, P.S. 1964. Taxonomy. Pages 1-15 in P. S. Galtsoff, The American Oyster *Crassostrea virginica* Gmelin. U.S. Fish. Wildl. Serv. Fish. Bull. 64.

García-Cubas, A. 1981. Moluscos de un sistema lagunar tropical en el sur del Golfo de México (Laguna de Términos, Campeche). Inst. Cienc. Mar. Limnol., Univ. Natl. Auton. México, Publ. Esp. 5:1-182.

García-Cubas, A., Z.G. Castillo-Rodríguez, A. Alvarez-Herrera and R. Muñoz-Chagin. 1987. Moluscos comestibles en las costas de México. Memorias III, Reunion Malacología Conquiliología. Soc. Méx. Malacol. Conquil., Univ. Natl. Auton. México, Monterey, Nuevo Leon, pp. 429-456.

Harry, H.W. 1981. Nominal species of living oysters proposed during the last fifty years. Veliger 24:39-45.

Harry, H.W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). Veliger 28:121-158.

Harry, H.W. 1986a. The relevancy of the generic concept to the geographic distribution of living oysters (Gryphaeidae and Ostreidae). Amer. Malacological Bull. 4:157-162.

Harry, H.W. 1986b. Oysters of the northwestern Gulf of Mexico. Texas Conchologist 23:14-19.

Hedgecock, D., M.A. Banks, and D.J. McGoldrick. 1993. The status of the Kumamoto oyster *Crassostrea sikamea* (Amemiya 1928) in U.S. commercial brood stocks. J. Shellfish Res. 12:215-221.

Hedgecock, D. and N.B. Okazaki. 1984. Genetic diversity within and between populations of American oysters (*Crassostrea*). Malacologia 25:535-549.

Héral, M. and J.M. Deslous-Paoli. 1991. Oyster culture in European countries. Pages 153-190 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Hernández, R.A. 1990. Cultivo de Moluscos en America Latina. RED Regional Entidades Centros Acuicultura America Latina. Centro Internatl. Investig. Desarrollo, Canada. Bogota, Colombia. 405 pp.

Hernández, R.A. 1991. Review of mollusc culture experiences in Latin America. Pages 171-182 in G. F. Newkirk and B. A. Field (eds.). Oyster Culture in the Caribbean. Mollusc Culture Network, Biol. Dept., Dalhousie Univ., Halifax, Nova Scotia, Canada.

Hidu, H. and R. E. Lavoie. 1991. The European oyster, *Ostrea edulis* L., in Maine and Eastern Canada. Pages 35-46 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Imai, T. (ed.). 1977. Aquaculture in shallow seas: progress in shallow sea culture. Koseisha Koseiku Publ., Tokyo. 1971 (Trans. from Japanese, Amerind Publ. Co., New Delhi. pp. 115-204).

Kay, E.A. 1979. Hawaiian Marine Shells. Reef and Shore Fauna of Hawaii. 4. Mollusca. Bernice P. Bishop Museum, Spec. Publ. 64, 653 pp.

Keen, M. with J.H. McLean. 1971. Sea shells of Tropical West America. Marine Mollusks from Baja California to Peru, 2nd edition. Stanford Univ. Press, California. 1064 pp.

Korringa, P. 1952. Recent advances in oyster biology. Quart. Rev. Biol. 27:266-308.

Krakatitsa, T.R. 1973. Size-weight characteristics and the basis of fisheries measurements in the Black Sea oyster *Ostrea taurica* Kryn. (Lamellibranchia, *Ostreidae).* [In Russian]. Biologiya Morya 32:73-87.

Kusuki, Y. 1991. Oyster culture in Japan and adjacent countries: *Crassostrea gigas* (Thunberg). Pages 227-243 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Lamy, E. 1929-30. Révision des *Ostrea* vivants du Muséum National d'Histoire Naturelle de Paris. J. Conchiol. 73(1):1-46, (2):71-108, (3):133-168, (4):233-275.

Littlewood, T.J. 1994. Molecular phylogenetics of cupped oysters based on partial 28S rRNA gene sequences. Molec. Phylog. Evol. 3:221-229.

Littlewood, T.J. and S. K. Donovan. 1988. Variation of recent and fossil *Crassostrea* in Jamaica. Palaeontology 31:1013-1028.

MacPherson, J.H. and C.J. Gabriel. 1962. Marine Molluscs of Victoria. Melbourne Univ. Press, Victoria, Australia. 475 pp.

Mahadevan, S. 1987. Oyster resources of India. In K. N. Nayar and S. Mahadevan (eds.). Oyster Culture: Status and Prospects. Bull. Cent. Mar. Fish. Res. Inst. 38:14-16.

McLean, R.A. 1941. The oysters of the Western Atlantic. Notulae Naturae, Acad. Nat. Sci. Phila. No. 67, 14 pp.

Menzel, R.W. 1974. Portuguese and Japanese oysters are the same species. J. Fish. Res. Bd. Canada 31:453-456.

Menzel, R.W. 1983. Possibilities of molluscan cultivation in the Caribbean. Food and Agricultural Organization, United Nations, Fisheries Report 71(2): 183-200.

Menzel, R.W. 1987. Hybridization of oysters and clams. Pages 47-59 in K. Tiews (ed.). Selection, Hybridization, and Genetic Engineering in Aquaculture. Proc. World Symp., Bordeau, May 27-30, 1986, Vol. II, Berlin.

Menzel, R.W. 1991. Cultural practices and production of the American oyster, with emphasis on the south Atlantic and Gulf of Mexico. Pages 25-34 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Morris, S. 1985. Preliminary guide to the oysters of Hong Kong. Asian Mar. Biol. 2:119-138.

Mozdyhai-Boltovskoi, F.W. (ed.). 1972. Guidebook to the fauna of Black and Azov Seas. Vol. 3, pp. 194-195. Kiev, 'Naukova Dumka.' 340 pp.

Nagabhushanam, R. and U.H. Mane. 1991. Oysters in India. Pages 201-209 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Nascimento, I.A. 1991. *Crassostrea rhizophorae* (Guilding) and *C. brasiliana* (Lamarck) in South and Central America. Pages 125-134 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Newball, S. and M.R. Carriker. 1983. Systematic relationship of the oysters *Crassostrea rhizophorae* and *C. virginica*: a comparative ultrastructural study of the valves. Amer. Malacol. Bull. 1:35-42.

Newkirk, G.F. 1980. Review of the genetics and the potential for selective breeding of commercially important bivalves. Aquaculture 19:209-228.

Newkirk, G.F. and B.A. Field (eds.). 1991. Oyster Culture in the Caribbean. Mollusc Culture Network, Biol. Dept., Dalhousie Univ., Halifax, Nova Scotia, Canada. 244 pp.

Nie, Z.-Q. 1991. The culture of marine bivalve mollusks in China. Pages 261-276 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Nikiforov, S.M. 1979. Systematics of oysters from the Southern Maritime Territory. Biologiya Morya 1: 25-33 (Soviet J. Mar. Biol. 5:18-24, translation).

Parenzan, P. 1974. Carta d'identità delle conchiglie del Mediterraneo. Vol. II, Bivalvi, Prima Parte. Ed. Bios Taras, Taranto. pp. 132-142.

Quayle, D.B. 1980. Tropical oysters: culture and methods. Internat. Develop. Res. Centre, Ottawa, Canada, IDRC-TS17e, 80 pp.

Quayle, D.B. 1988. Pacific oyster culture in British Columbia. Can. Bull. Fish. Aquatic Sci. 218:1-241.

Quayle, D.B. and G.F. Newkirk. 1989. Farming bivalve molluscs: methods for study and development. Adv. World Aquaculture 1:1-294.

Rao, K.S. 1987. Taxonomy of Indian oysters. Bull. Cent. Mar. Fish. Res. Inst. 38:1-6.

Robinson, A.M. and C.J. Langdon. 1992. Development of the commercial aquaculture of the suminoe oyster (*Crassostrea rivularis*). J. Shellfish Res. 11:556.

Rosell, N.C. 1991. The slipper-shaped oyster (*Crassostrea iredalei*) in the Philippines. Pages 307-313 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boston.

Singarajah, K.V. 1980. On the taxonomy, ecology and physiology of a giant oyster, *Crassostrea paraibanensis*, new species. Bull. Mar. Sci. 30:833-847.

Skoglund, C. 1991. Additions to the Panamic Province Bivalve (Mollusca) literature 1971 to 1990. Festivus (San Diego Shell Club) 22, suppl. 2 to 1990: 74 pp.

Stenzel, H.B. 1971. Oysters. Treatise on Invertebrate Paleontology. Part N, Bivalvia 3:953-1224.

Tchang, S. and L. Tse-kong. 1956. A study on Chinese oysters. Acta Zool. Sinica 8:65-93.

Tebble, N. 1976. British Bivalve Seashells. A Handbook for Identification. 2nd Edition. Her Majesty's Stationery Office, Edinburgh, 212 pp.

Thomson, J.M. 1954. The genera of oysters and the Australian species. Australian J. Mar. Freshw. Res. 5:132-168.

Torigoe, K. 1981. Oysters in Japan. J. Sci. Hiroshima Univ., Ser. B, Div. 1 (Zool.) 29:291-319.

Vélez, A. 1991. Biology and culture of the Caribbean or mangrove oyster, *Crassostrea rhizophorae* Guilding, in the Caribbean and South America. Pages 117-124 in W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture, CRC Press, Boston.

Chapter 2

General Anatomy

ALBERT F. EBLE AND ROBERT SCRO

INTRODUCTION

The eastern oyster *Crassostrea virginica* is a monomyarian lamellibranch with a pronounced bilateral asymmetry and a restricted coelom typical of the class (Seed 1983). "With the loss of the head, the most convenient anteroposterior axis (Fig.1) in a bivalve is represented by a line running from the mouth through the middle of the posterior adductor (near the anus)" (Morton and Yonge 1964). The primitive position of the isomyarian bivalve dorso-ventral axis was a line running from the hinge (mid-dorsal) through the foot (mid-ventral). Those bivalves that retained the postlarval byssus complex, however, showed a gradual reduction (anisomyaria) and eventual loss (monomyaria) of the anterior adductor (Seed 1983). As a consequence, the hinge began to migrate towards the anterior end of the animal. This resulted in a more advantageous mechanical advantage with respect to the enlarging posterior adductor. The anteroposterior axis of the eastern oyster is located by a line running through the mouth and adductor muscle to the posterior margin of the shell (Fig. 1). The dorsoventral axis can best be represented by a line perpendicular to the anteroposterior axis running from the dorsal surface to the ventral surface (ancestral position of the foot).

There are several works that describe eastern oyster anatomy and histology in varying degrees of detail: Moore (1898), Brooks (1905), Churchill (1920), with the most comprehensive being Galtsoff (1964). Techniques to demonstrate oyster anatomy, including the circulatory system (Eble 1960; Shuster and Eble 1961), are available. Throughout the text, I refer to my own unpublished observations to supplement literature reports. Unless otherwise indicated, I used Alcian blue, pH 2.6 - periodic acid Schiff stain during my histological studies.

THE SHELL

Details of shell formation, composition and growth are discussed by Carriker in Chapter 3; only the general appearance and axes of symmetry will be mentioned here. The shell of the oyster consists of two calcareous valves joined by a resilient hinge ligament. Valves are asymmetrical, the left being larger and more deeply cupped than the right. Because the oyster invariably settles on its left valve, the right valve is always uppermost (Fig. 2)

THE MANTLE

Anatomy

Internal organs are covered with a fleshy fold of tissue called the mantle or pallium. Left and right lobes of the mantle are joined at their posterior margins in the region of the cloacal chamber and at the so-called "oral hood" (the anterior end of the mantle forms a cap and covers the mouth and labial palps); elsewhere the lobes are unattached and follow the curvature of the valves. The mantle is always in contact with the valves but is not attached to them. The large central cavity bounded by the mantle lobes is the pallial cavity and contains the palps and gills on the ventral side and the rectum on the dorsal side; specifically, the rectum opens dorsally to a special portion of the dorsal pallial cavity known as the cloacal chamber (Figs.1, 2). The right lobe of the mantle is separated from the visceral mass to form the promyal chamber (Fig. 2); the left lobe is fused to the visceral mass.

The pallial cavity is subdivided into two cavities. The cavity formed by the fusion of the mantle dorsally with the visceral mass and ventrally with the bases of the gills is known as the epibranchial chamber and continues posteriorly as the cloacal chamber. The large cavity containing the gills and bounded by the two mantle lobes is the hypobranchial chamber.

Radial muscles originate in the visceral mass, course through the mantle, and insert by fan-like enlargements in the margin at the base of the sensory tentacles that form the distal margin of the mantle (Fig. 3). Most of the radial muscles are accompanied along their length by blood vessels and nerves. Slen-

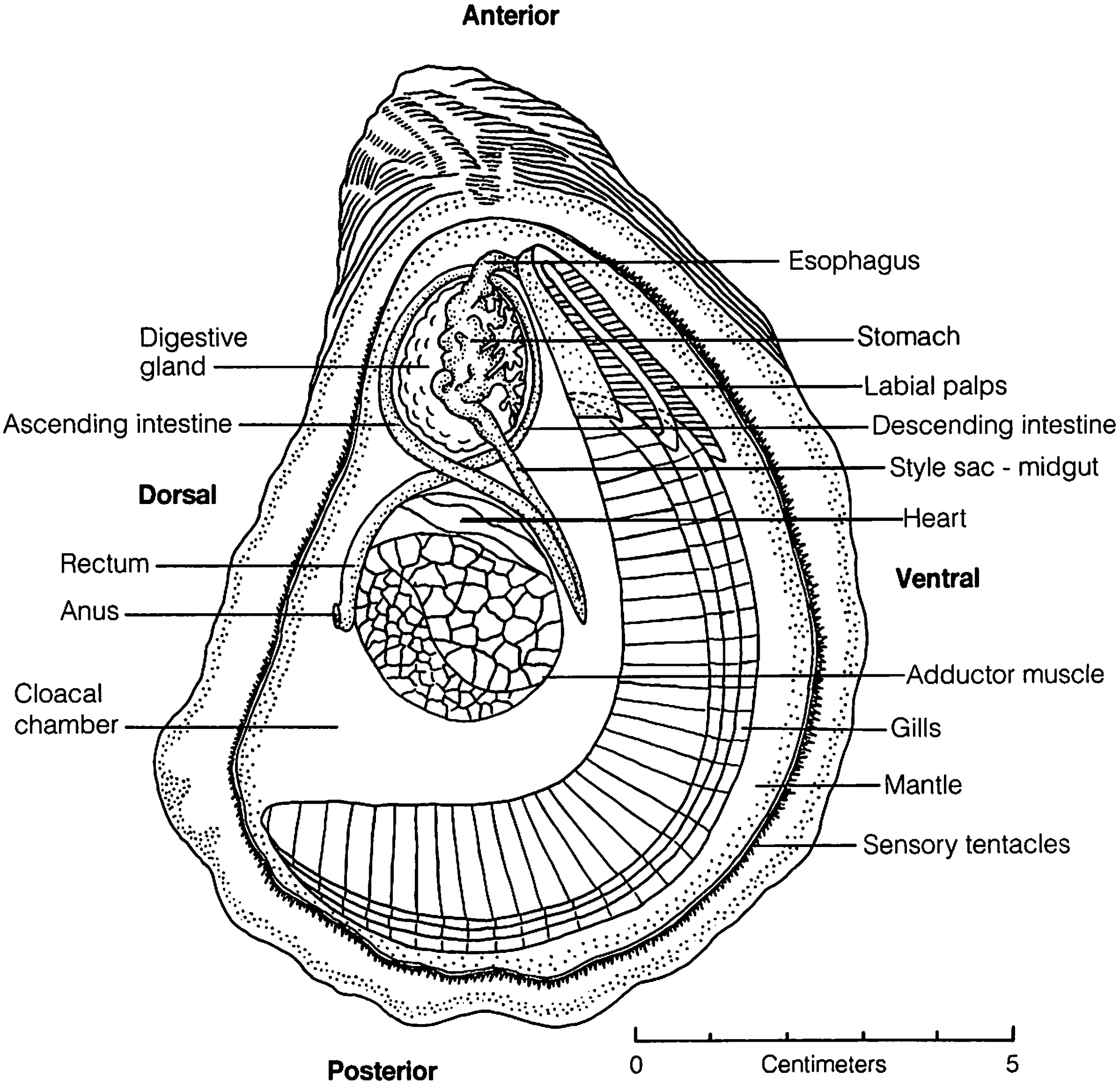

Figure 1. Oyster in left valve showing cardinal axes and digestive system including labial palps and gills. Redrawn from Galtsoff (1964).

der, concentrically arranged muscle bands parallel the free edge of the mantle and intersect the radial muscles at right angles (Galtsoff 1964; Morrison 1993). The prominent circumpallial artery (Fig. 3) runs in the margin of the mantle a few millimeters central to the fringing tentacles (Figs. 3, 4); this artery gives off many fine branches to the tentacles as well as larger branches to the broad face of the mantle. The circumpallial nerve (Figs. 3, 4) lies just peripheral to the circumpallial artery; it receives many fine branches from the tentacles and relays them either to the cerebral or visceral ganglia (it is not known which) via the radial nerves (Galtsoff 1964).

The border of the mantle is divided into three projecting lobes (Galtsoff 1964). The outer or shell lobe (Figs. 3, 4) is narrow and lies in contact with the margin of the shell; it is visualized best in rapidly growing oysters where it can be seen protruding beyond the edge of the valves. The middle lobe bears short and long sensory tentacles. The former are slender and numerous, the latter are thick and occur in a ratio of about 5 short to 1 long. The middle lobe is separated from the shell lobe by a deep cleft, the periostracal groove (Fig. 4). The inner lobe or pallial curtain (Nelson 1938) bears long, thick tentacles. When muscles of the inner lobes contract, the pallial curtain projects inward approximately at right angles to the mantle surface; the mantle lobes of both sides are brought into juxtaposition and the long tentacles of both sides of the pallial curtain interlock, effectively sealing the entrance to the mantle cavity. The valves can be open but no exchange of water can take place where the pallial curtain is sealed; by selectively opening only certain areas of the pallial curtain and then contracting the adductor muscle, the oyster can direct strong jets of water from the mantle cavity for such activities as spawning eggs or removing rejecta (pseudofeces).

Histology

The microscopic anatomy of the mantle consists of two epithelia, shell-side and pallial cavity-side, with connective tissues in between. The shell-side epithelium is composed of non-ciliated cells with microvilli that vary from tall columnar to cuboidal; because cell height is so variable, the basement membrane presents a wavy appearance because all cells are in contact with the valves. Unicellular glands are frequently located in zones of tall columnar cells where the body of the gland is situated near the basement membrane and a short neck connects to the free surface. I found that the surface in contact with the shell is coated with acid glycosaminoglycans (mucopolysaccharides). Unicellular gland cells are present, with one type containing neutral glycoproteins and another type containing a mixture of acid glycoproteins

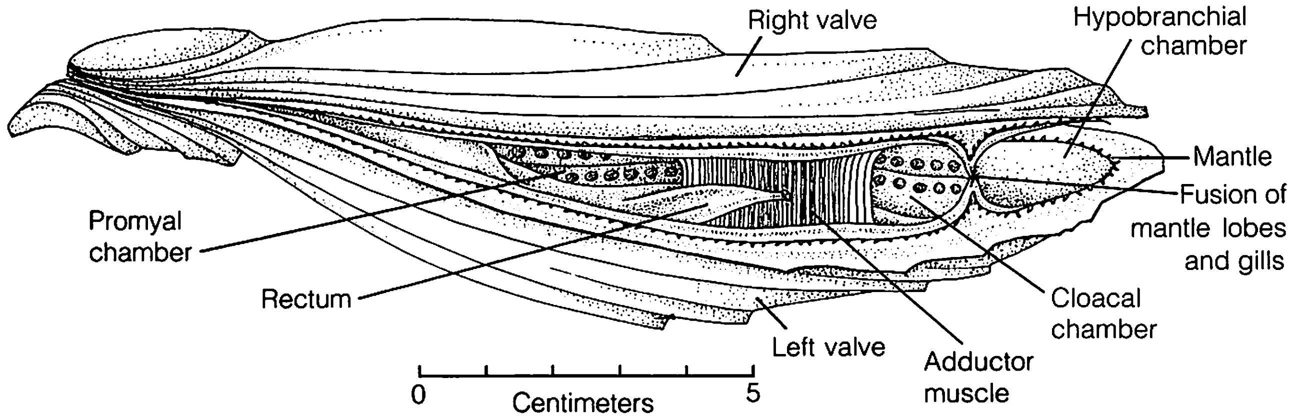

Figure 2. Diagram of dorsoposterior fusion of mantle lobes; the posterior extremity of the gills is found at this point. Openings to the two exhalant regions, the promyal chamber and the cloacal chamber, are clearly seen. From Galtsoff (1964).

rich in carboxyl groups and neutral polysaccharides; the latter outnumber the former by about a 3:1 ratio.

My histological sections show that the pallial cavity-side epithelium is simple, ciliated cuboidal in the dorsal area of the pallial cavity. In the ventral region, however, cilia are restricted to "ciliary tracts": groups of 8 to 10 cuboidal or columnar cells that have long cilia (Fig. 5) and unicellular glands (Morrison 1993). One type of gland cell contains neutral glycoproteins and another has acid glycosaminoglycans rich in carboxyl groups; the latter outnumber the former by about a 4:1 ratio. The cuboidal epithelium on either side of ciliary tracts lacks both cilia and unicellular glands. A subepithelial blood sinus is associated with both epithelia. Connective tissue consists chiefly of vesiculated cells (Leydig cells) that function as storage parenchyma as well as connective tissues; Leydig cells are omnipresent.

Mantle margin epithelia in my sections vary among the three lobes: (1) *pallial curtain (inner lobe)* — the inner surface is lined with an epithelium identical to pallial cavity-side mantle epithelium with which it is contiguous. The outer surface is covered with a simple, cuboidal epithelium; (2) *sensory lobe (middle lobe)* — the inner surface is highly folded simple cuboidal epithelium with many unicellular glands,

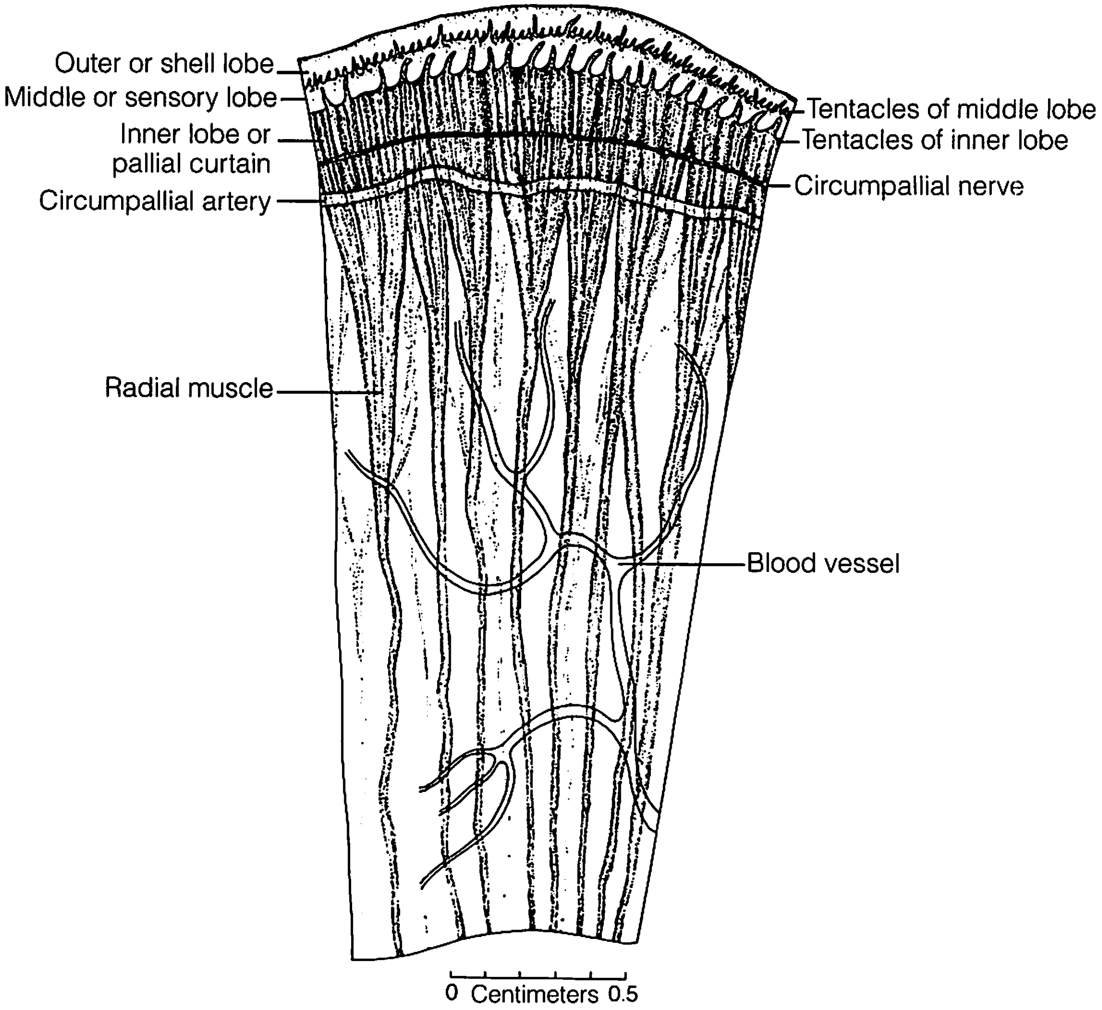

Figure 3. Whole mount of a portion of the mantle from about the middle to the margin. Most connective tissue was removed by maceration. From Galtsoff (1964).

some containing neutral glycoproteins and others acid glycoproteins rich in carboxyl groups; epithelial cells usually contain a dark-brown pigment. The outer surface has a simple, ciliated cuboidal epithelium lacking unicellular glands; (3) shell lobe (outer lobe) — the inner surface has a simple, ciliated cuboidal epithelium; many unicellular glands are present near the tip of the lobe and contain glycosaminoglycans rich in carboxyl groups. The outer surface has an epithelium continuous and identical to the shellside epithelium of the mantle; unicellular glands rich in carboxyl glycosaminoglycans are present deep in folds of the basement membrane. An in-depth discussion of the histology, scanning, and transmission electron microscopy of the mantle, including mantle lobes, is given by Morrison (1993).

ADDUCTOR MUSCLE

Anatomy

The adductor muscle, a prominent organ situated in the posterior region of the body, consists of an anterior translucent larger part and a smaller, white, crescent-shaped region. The adductor muscle func-

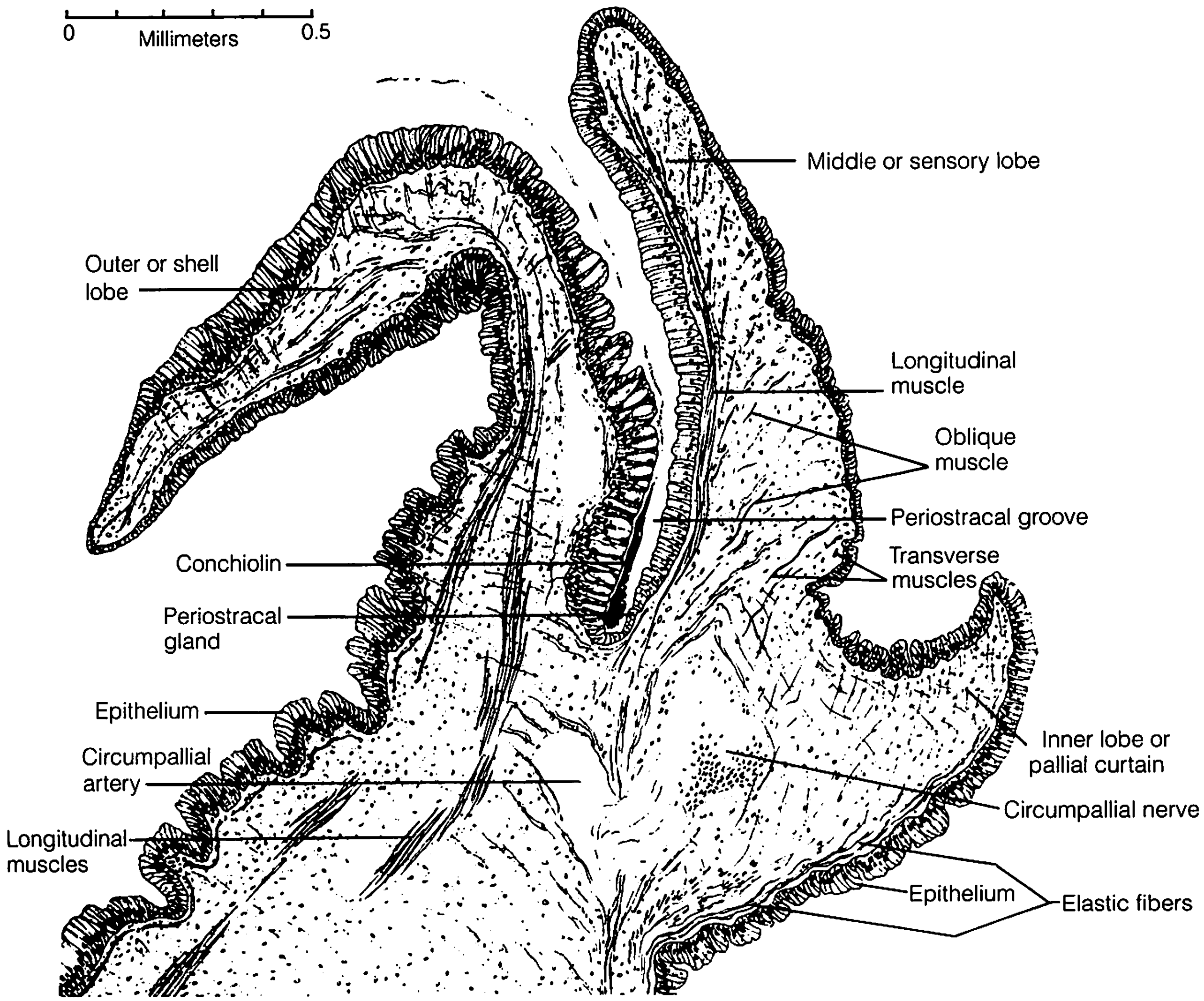

Figure 4. Transverse section of mantle margin to illustrate the three lobes of the mantle margin. The outer or shell lobe is bent as a result of fixation. From Galtsoff (1964).

tions to close the shell. Relaxation of the adductor muscle allows the valves to gape because of the resiliency of the hinge ligament. The rectum passes over its dorsal surface and the kidney is located near the anterior ventral portion. The posterior aorta runs along the anteriomedial face of the adductor muscle before entering the tissues approximately at midpoint to supply muscle fibers.

Histology

Muscle fibers of the translucent part of the adductor muscle have a unique oblique or double-oblique striation (Galtsoff 1964) with nuclei elongated and oriented in the long axis of the fibers. Widest diameter of the fibers is 3 µm (Morrison and Odense 1974). Filaments of the translucent muscle are not obviously aligned. Dense bodies are present but there is no Z membrane (the structure to which actin filaments are anchored); occasionally, dense bodies are obliquely aligned (Morrison and Odense 1974). Hemolymph sinuses are extensive and can be seen easily in well relaxed muscle (Fig. 6); delicate strands of connective tissue envelop each muscle fiber and extend across hemolymph sinuses imparting to the latter a cobweb-like appearance (Fig. 6). Arteries are composed of highly organized connective tissue and feed directly into muscle sinuses.

Muscle fibers of the white, opaque portion of the adductor muscle are smooth and much wider (8 µm) than those of the translucent part. Opaque muscle has wide, thick filaments (110 nm) that vary in diameter in transverse section. Arrangement of thin filaments (actin) around the thick filaments (myosin) is irregular (Morrison and Odense 1974). Construction of arteries and sinuses is similar to that described

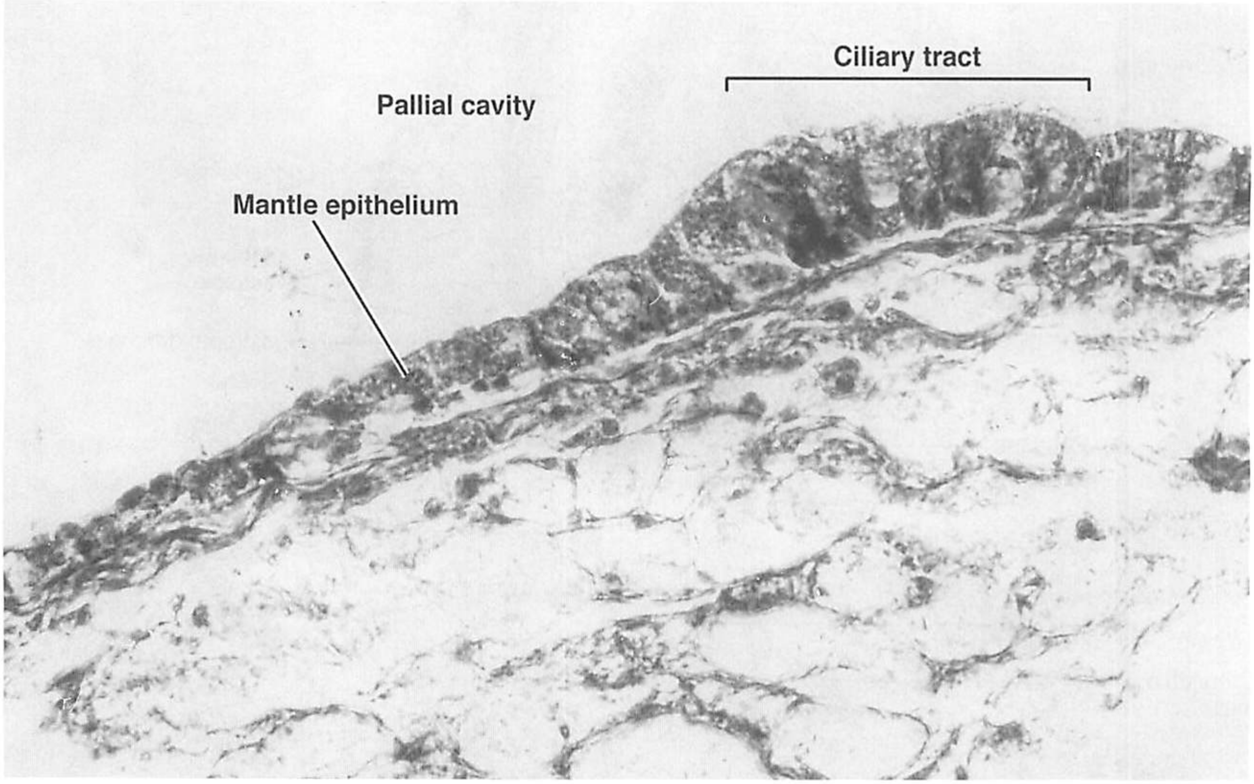

Figure 5. Section of ciliary tract in pallial cavity side of ventral mantle epithelium. Note clusters of 5 to 8 eosinophilic granule cells with cilia that constitute a ciliary tract. Adjacent low cuboidal cells lack cilia. Horizontal Field Width (HFW) = 87.5 µm.

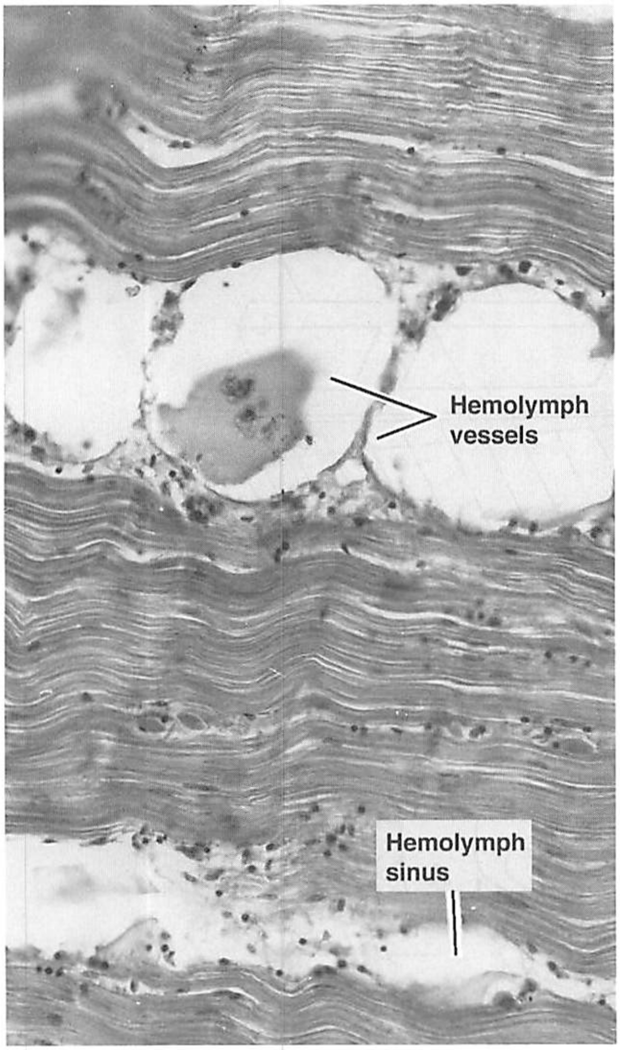

Figure 6. Transverse section of relaxed adductor muscle showing extensive vascular system consisting of delicate hemolymph vessels and broad sinuses. HFW = 190 µm.

for the translucent part. Hemolymph sinuses in the ventral part of the adductor muscle open directly into renal sinuses containing kidney tubules. The morphology and fine structure of the adductor muscle is discussed by Morrison in Chapter 4.

HEART AND CIRCULATION

Details of the heart and circulatory system are discussed by Eble in Chapter 7.

GILLS

Gills of the eastern oyster consist of four folds (demibranchs) of tissue suspended from the visceral mass and occupy much of the ventral and ventroposterior portions of the mantle cavity (Fig. 1). Together with the mantle, they are the chief organs of respiration. They create water currents, collect food particles, and move food particles to the labial palps for further sorting (see Newell and Langdon, Chapter 5, for details). Gills also serve to separate masses of eggs released from the ovary during spawning into individual ova for efficient fertilization.

Anatomy

Gills in each eastern oyster in cross section take the shape of four V's, a double V on the right, and another on the left side of the oyster (Fig. 7); each V is known as a demibranch and each arm of the V is called a lamella, with an inner descending lamella and an outer ascending lamella. Each lamella is composed of vertical filaments that, in turn, are clustered in vertical folds or plicae. Two marginally joined lamellae constitute a demibranch and two joined demibranchs are a gill. Each gill is organically attached to the body of the oyster at the open end of the VV known as the gill base; the pointed end of each V is called the gill margin and projects into the mantle cavity (Galtsoff 1964).

The gill is illustrated from its dorsolateral aspect in Fig. 7 and shows the broad face of a lamella which, as mentioned above, is composed of parallel arrays of filaments. In a eulamellibranch such as the eastern oyster, filaments are joined to each other at regular intervals by tissue connections called interfilamentar junctions; these junctions contain hemolymph vessels. The space between each of these junctions contains an ostium which is the approximately 60 µm long by 20 µm wide opening (Figs. 7, 8) through which water passes into the plical water chamber when the animal is filtering. Both lamellae of a demibranch are connected to one another by interlamellar junctions composed of tissue that contains hemolymph vessels, occurring at regular intervals from base to margin of the gill (Figs. 7, 8).

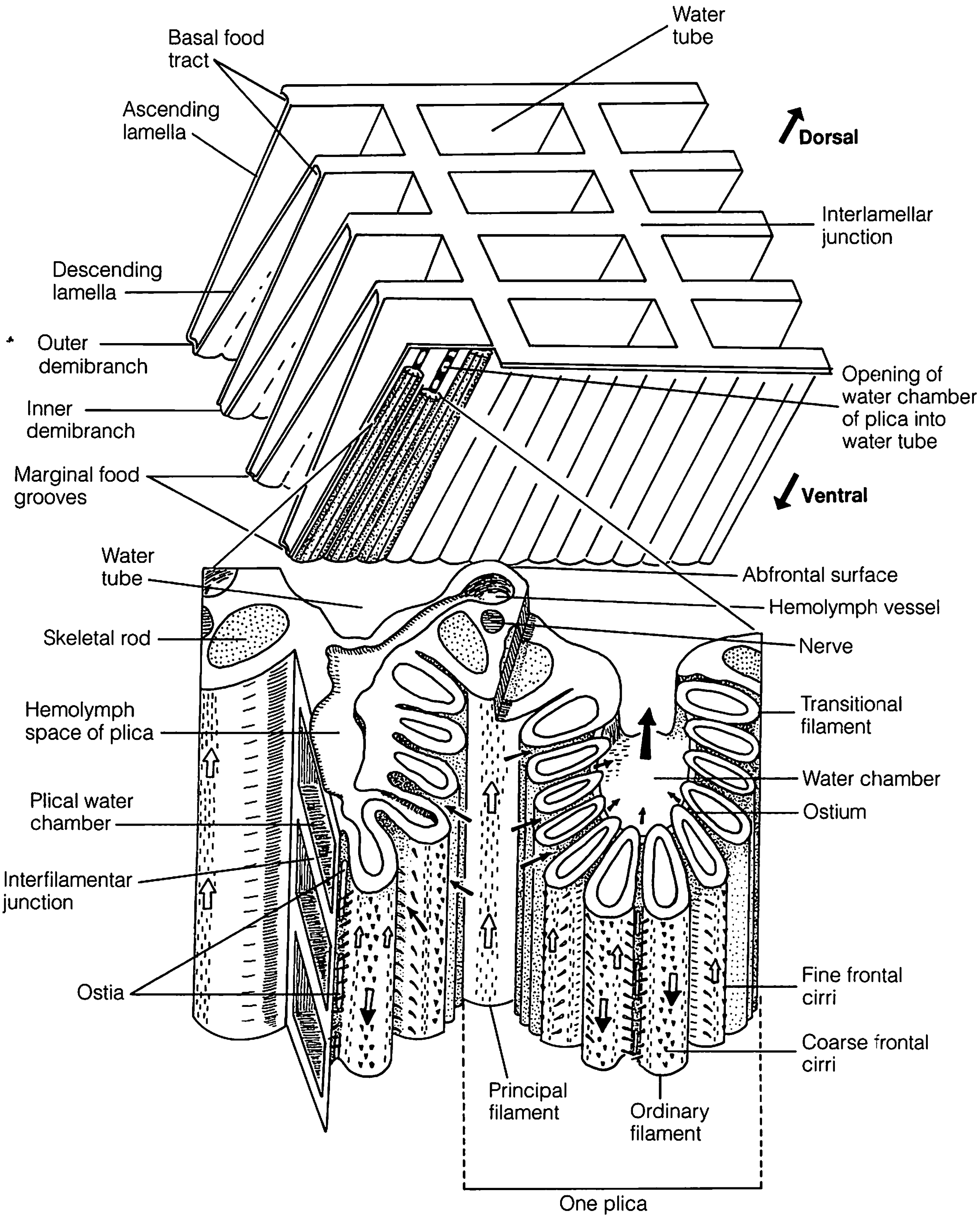

Figure 7. Stereodrawing of part of two gills of *C. virginia* (upper) with expanded detail of a plical fold (lower). The direction of particle movement on the coarse and fine frontal cilia is indicated by the black headed and open arrows, respectively. The direction of water movement between the filaments, through the ostia and into the water tubes is indicated by the solid black arrows. Based on drawings by M.R. Carriker in Nelson (1960).

Filaments of each lamella are arranged in a regular series of folds called plicae. Each plica consists of a large principal filament located at the base of the fold and a series of ordinary filaments; that filament next to the principal filament is termed the transitional filament (Figs. 7,8).

Histology and Fine Structure

Histology

Each gill filament consists of a simple epithelium whose cells on the frontal and lateral surfaces bear cilia of various sizes: contrary to the diagrams in Nelson (1960), my own histological observations indicate that cells on the abfrontal surface lack cilia (Figs. 7, 8, 9).

The marginal food groove is a ciliated trough formed at the apex or margin of each demibranch, the free edge where the ascending and descending lamellae join (Fig. 7). The epithelium varies from a stratified ciliated columnar type, from three to four cells deep near the edges of the groove to only one or two cells thick at the center of the groove. Two types of goblet cells are present usually near the edges of the groove: a more dominant form that secretes acidic glycoproteins and one that secretes neutral glycoproteins (Eble, pers. obs.). Cilia are long in the terminal groove and average 10 to 12 µm, especially

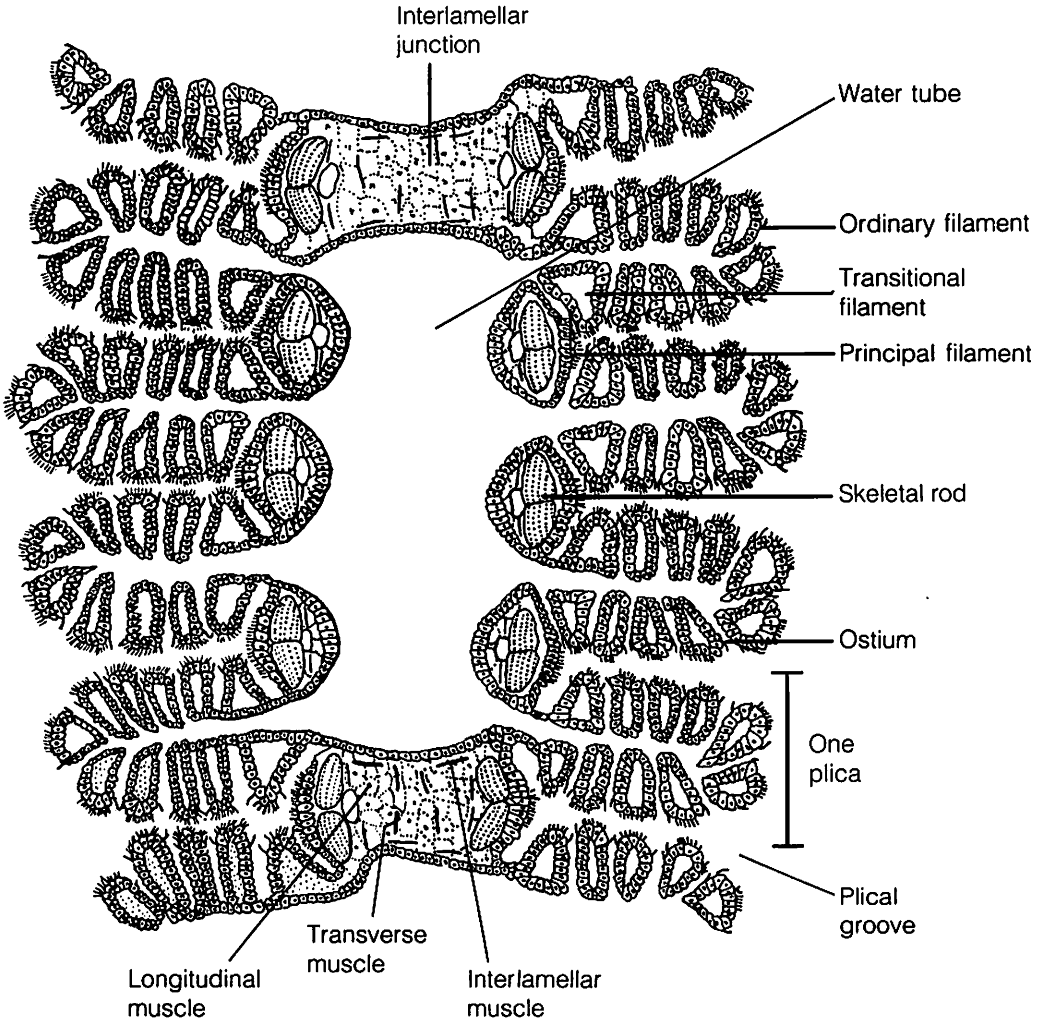

Figure 8. Frontal section through a gill demibranch showing plicae and two interlamellar junctions. × 500. Modified from Galtsoff (1964).

near the edges. The direction of beat is towards the palps.

A pair of skeletal rods is present in all types of filaments; although the older literature refers to them as chitinous, they are composed of a fibrous protein rich in collagen (Brown 1952; Rudall 1955; LePennec et al. 1988). Skeletal rods are found under the epithelium on the frontal and lateral surfaces (Figs. 8, 9); connective tissue can frequently be seen between the rods. The remainder of the interior of the fila-

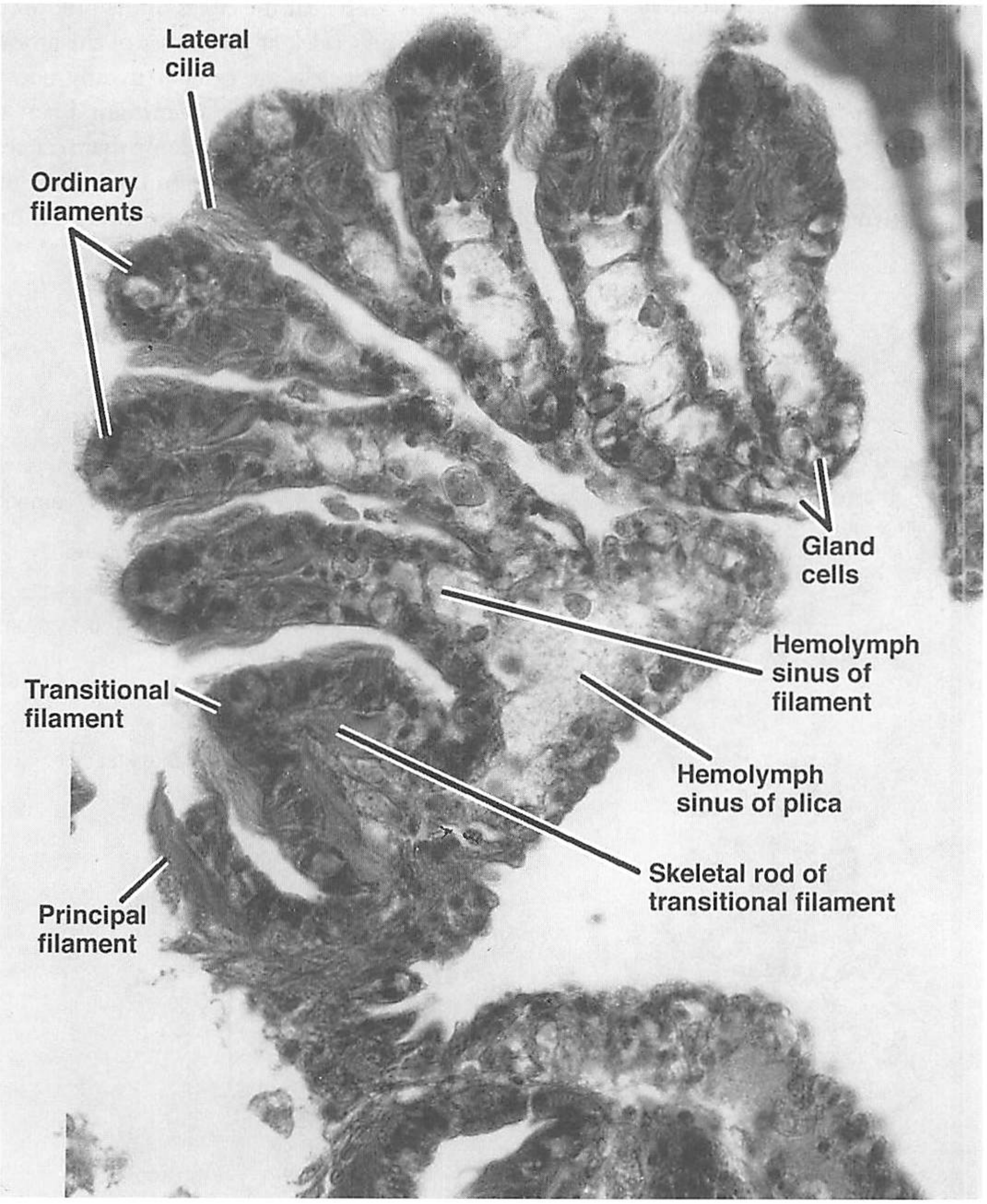

Figure 9. Frontal section through a gill plica to show general structure. Note how blood sinuses of ordinary filaments become contiguous with blood sinus of plica. HFW = 71 µm.

ment is a hemolymph sinus spanned by slender lacunar cells (Figs. 9, 10).

My sections also show two types of goblet cells on gill filaments: a large cell (26 µm) filled with coarse granules composed of acidic glycoproteins located on the frontal surface and smaller cells found near the lateral and abfrontal areas that secrete neutral glycoproteins. According to Bernard (1974), the large, granular mucous cells in *C. gigas* elaborate a zone of mucus about 12 µm thick and 20 µm wide; unicellular glands on the lateral and abfrontal surfaces respond to disturbance (either tactile, temperature, or light stimuli) and form a "rejection" mucous sheet 250 to 400 µm thick (see Newell and Langdon, Chapter 5 for discussion of current theories of particle capture). Atkins (1938) figures two types of mucous glands in European flat oyster *Ostrea edulis* but she does not discuss their histochemistry.

Fine Structure

The epithelium of gill filaments of *C. virginica* consists of two broad categories of cells, those with and those without cilia (Fig. 11). Both cell types possess microvilli and may contain mucus droplets.

Microvilli average 0.7 µm in length and 0.1 µm in diameter; their external surface is covered by a fine filamentous "cell coat" or glycocalyx (Fig. 12). Microvilli are also covered by three to five fine strands of mucus that run parallel to the surface of gill filaments; the thickness of these strands is, on the average, 20 nm. When several microvilli are examined in cross-section, they demonstrate a close contact with

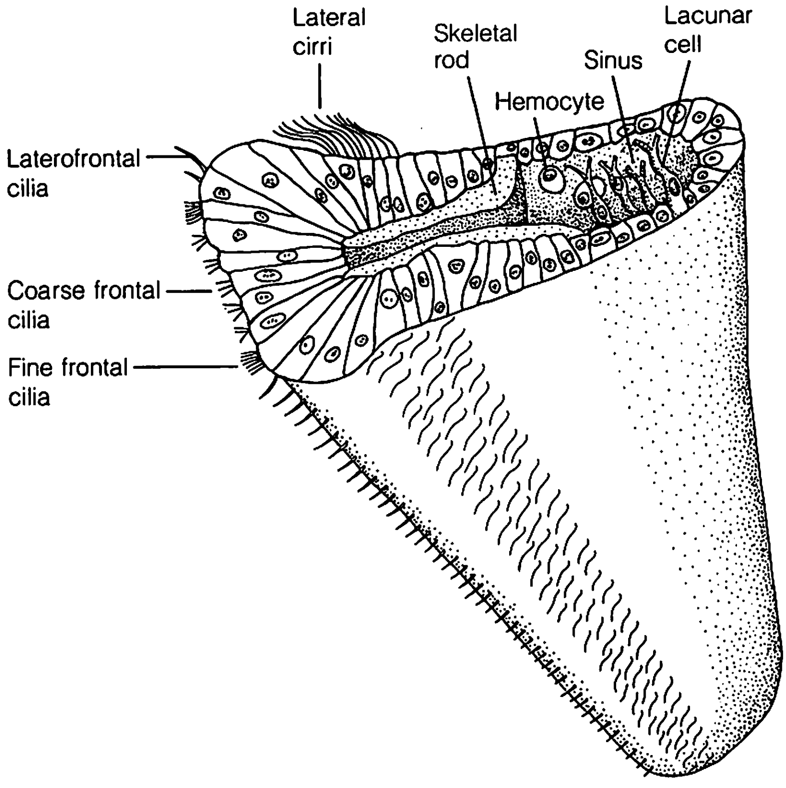

Figure 10. Stereodiagram of an ordinary filament of the gill. Note slender lacunar cells spanning the hemolymph sinus. × 20.

each other (and with adjacent cilia) via the mucus, which imparts a web-like appearance to the microstructure of the gill surface (Fig. 12; pers. obs.).

The cytoplasm of most ciliated epithelial cells contains many round or ovoid mitochondria that are located primarily in the apical portion of cells (Fig. 13); mitochondria are more numerous in ciliated cells than in non-ciliated cells.

The cytoplasm of some non-ciliated epithelial cells is filled with large, round, secretion granules of varying size whose profiles range from 0.70 to 1.30 µm; secretion granules are surrounded by a unit membrane. Based on their ultrastructural difference, these granules can be divided into two morphological types: Type-A granules contain homogeneous electron-dense material and Type-B granules are moderately homogeneous and moderately electron dense (Fig. 13). These two types of granules may represent different maturation stages of a secretion granule or two different types of secretory granules. The

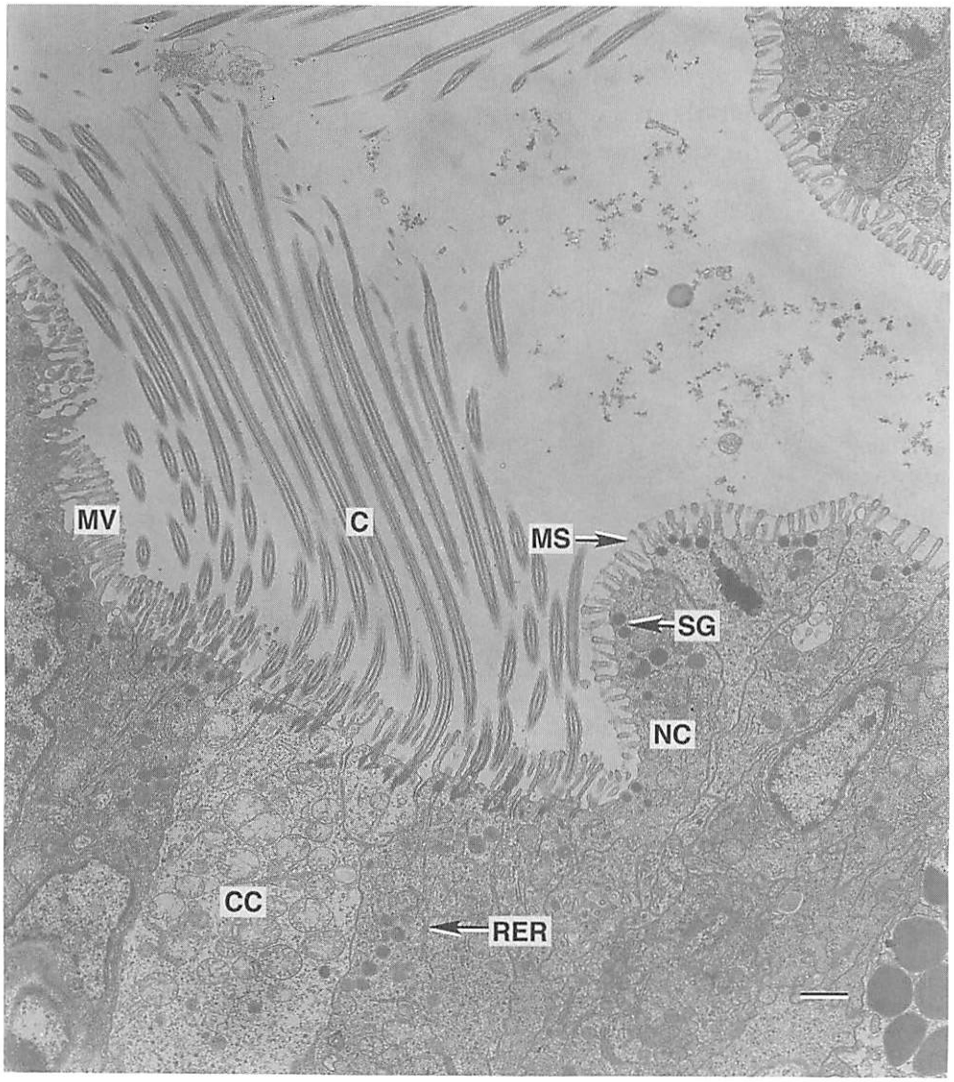

Figure 11. Abrupt transition between lateral ciliated [CC] and non-ciliated [NC] cells in a gill filament. Cilia [C], mucous strands [MS] between microvilli [MV]. Rough endoplasmic reticulum [RER], secretory granule [SG]. × 9,075. Bar = 1 µm.

composition of the secretions and their function remains to be determined.

The cytoplasm of some ciliated epithelial cells contains several morphologically distinct granules, ultrastructurally different from both Type-A and Type-B granules. Based on their fine structural characteristics and location within the cell, these granules are divided into three morphological types: Type-C, Type-D, and Type-E (Fig. 14). Type-C granules are large (average diameter 1 μm), and are surrounded by a unit membrane. Their contents vary considerably in homogeneity and electron density. Type-D granules, grouped near the free surface of the cell, are similar in size (1 μm) to Type-C granules, but are much less homogeneous and electron-dense; the most obvious difference between the two types of granules

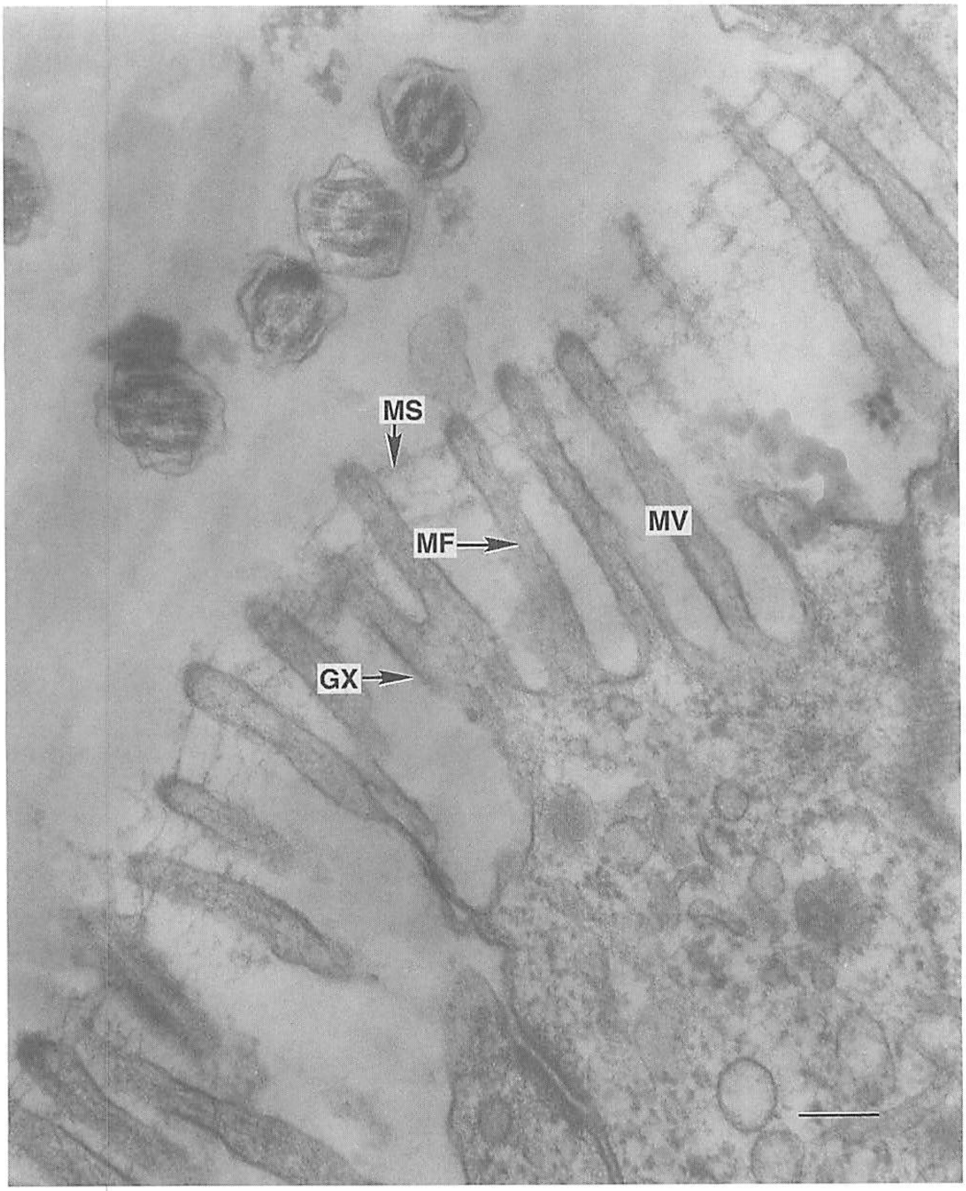

Figure 12. High magnification of microvilli [MV] of ciliated epithelial cell of the gill to show core of microfilaments. Glycocalyx [GX] of microvillus as well as web-like mucous strands [MS] running between microvilli can be seen. × 71,750. Bar = 0.2 μm.

is the lack of a limiting membrane around individual Type-D granules. Type-E granules are usually round or ovoid in shape, electron-dense, and comparatively smaller in size (0.30 μm) than Type-C and Type-D granules (Fig. 14); they are surrounded by a unit membrane and are most often located close to the free cell surface.

Cilia have the typical ultrastructure found in other cilia (Fig. 15): the average length of the axoneme is 13 μm; the width averages 0.30 μm. The basal body is located in the apical cytoplasm beneath the cell surface. A narrow transitional segment, the ciliary plate, is located between the axoneme and basal body. Basal bodies are spaced uniformly and located in parallel rows at the cell surface (Fig. 15; pers. obs.).

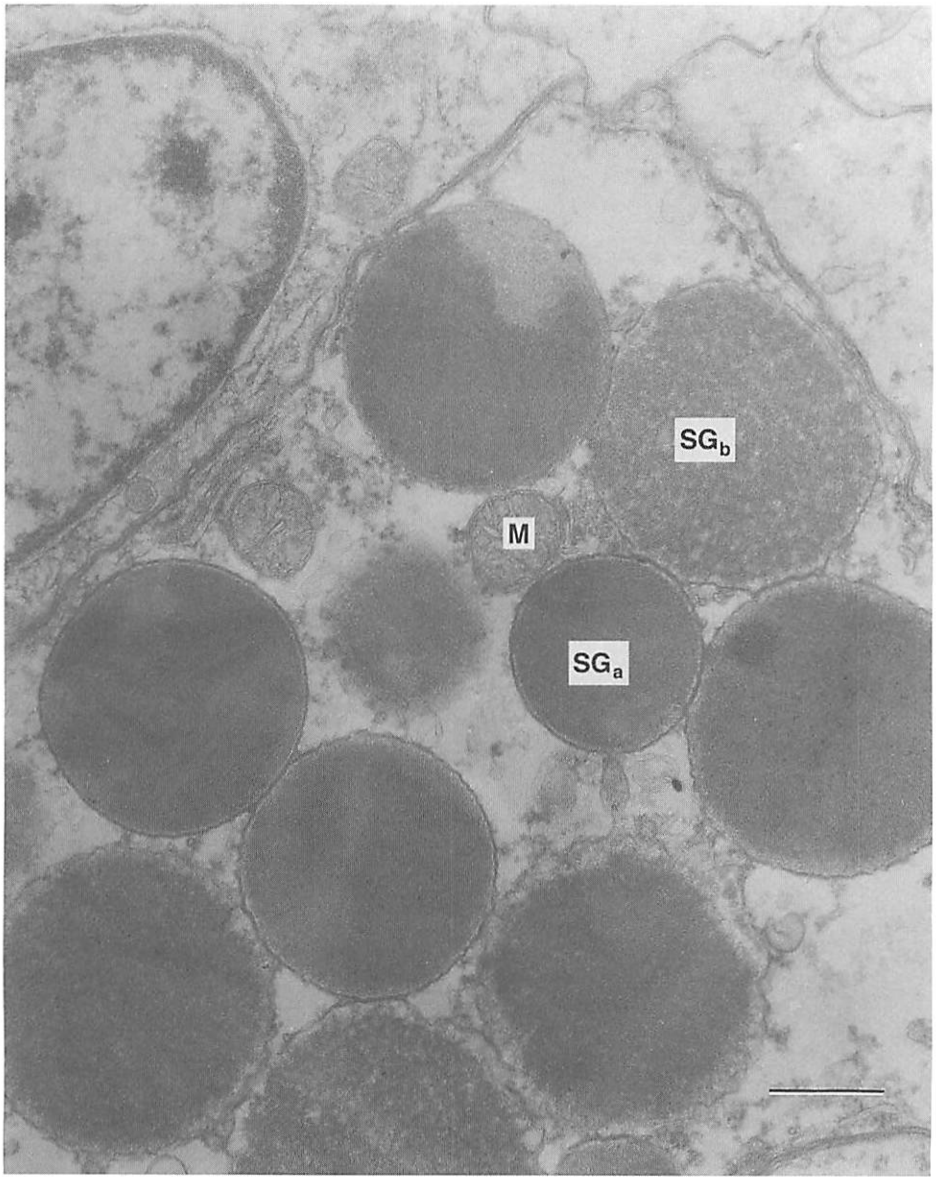

Figure 13. High magnification of Type-A [SG$_a$] and Type-B [SG$_b$] secretory granules in non-ciliated gill epithelial cells. Note connection and common membrane between some granules. Mitochondrion [M]. × 46,750. Bar = 0.5 μm.

At least three ciliary rootlets arise from each basal body and course down the long axis of the cell; as rootlets descend into the cytoplasm, they are frequently in close contact with mitochondria. Branches from several rootlets then converge toward, and end at, one side of the nucleus, where they appear to make contact with the nuclear envelope (Fig. 15).

At high magnification, rootlets are seen to be composed of striated fibrils having a regular cross-banding periodicity of 70 nm; four intraperiodic sub-bands can be observed. This is similar to collagen fibers that have a periodicity of 67 nm.

Cells of gill epithelia possess both adhering junctions (zonula adherens) and septate junctions (impermeable junctions). Adhering junctions encircle the apical portion of cells and extend down an average of

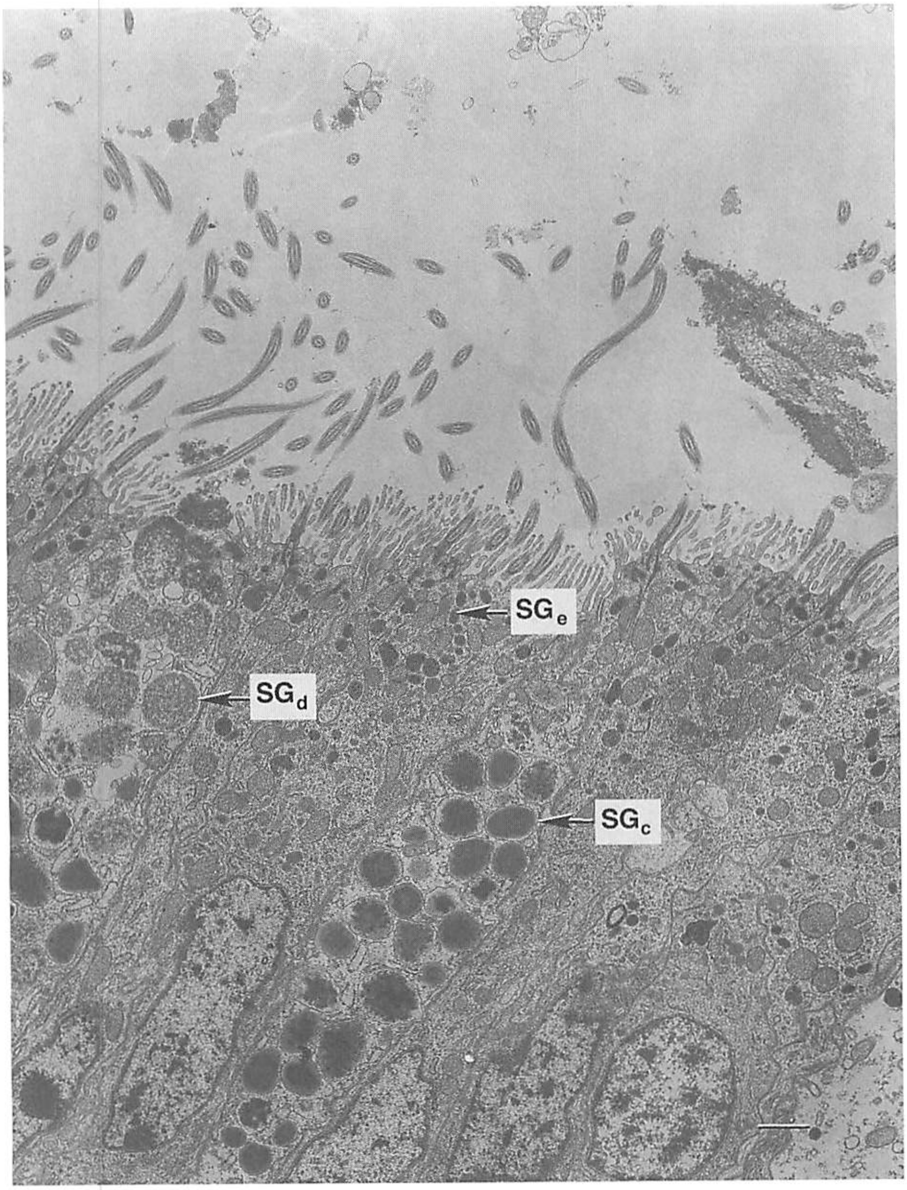

Figure 14. Ciliated epithelial cells of the gill containing Type-C [SG$_c$], Type-D [SG$_d$], and Type-E [SG$_e$] secretory granules. Note the lack of a limiting membrane around Type-D granules, which appear to be in the process of being released from the cell. × 9,075. Bar = 1 µm.

400 nm between adjacent cells; these junctions have an intercellular space averaging 25 nm and contain fine filamentous material (Fig. 16). Septate junctions, which are only present in invertebrate cells (Berridge and Oschman 1972), are commonly found between adjacent cells of the gill, just below the adhering junctions. They have a ladder-like appearance with regularly spaced septa, averaging 30 nm apart; septa are arranged perpendicular to opposing cell membranes (Fig. 16).

Connective tissue and associated cells underlying epithelia of gill filaments consist of (1) basal supporting structures for gill filaments, (2) fibroblast-like cells, and connective tissue fibers resembling collagen, (3) muscle tissue, (4) nerve tissue, and (5) hemolymph spaces containing hemocytes. Epithelial cells

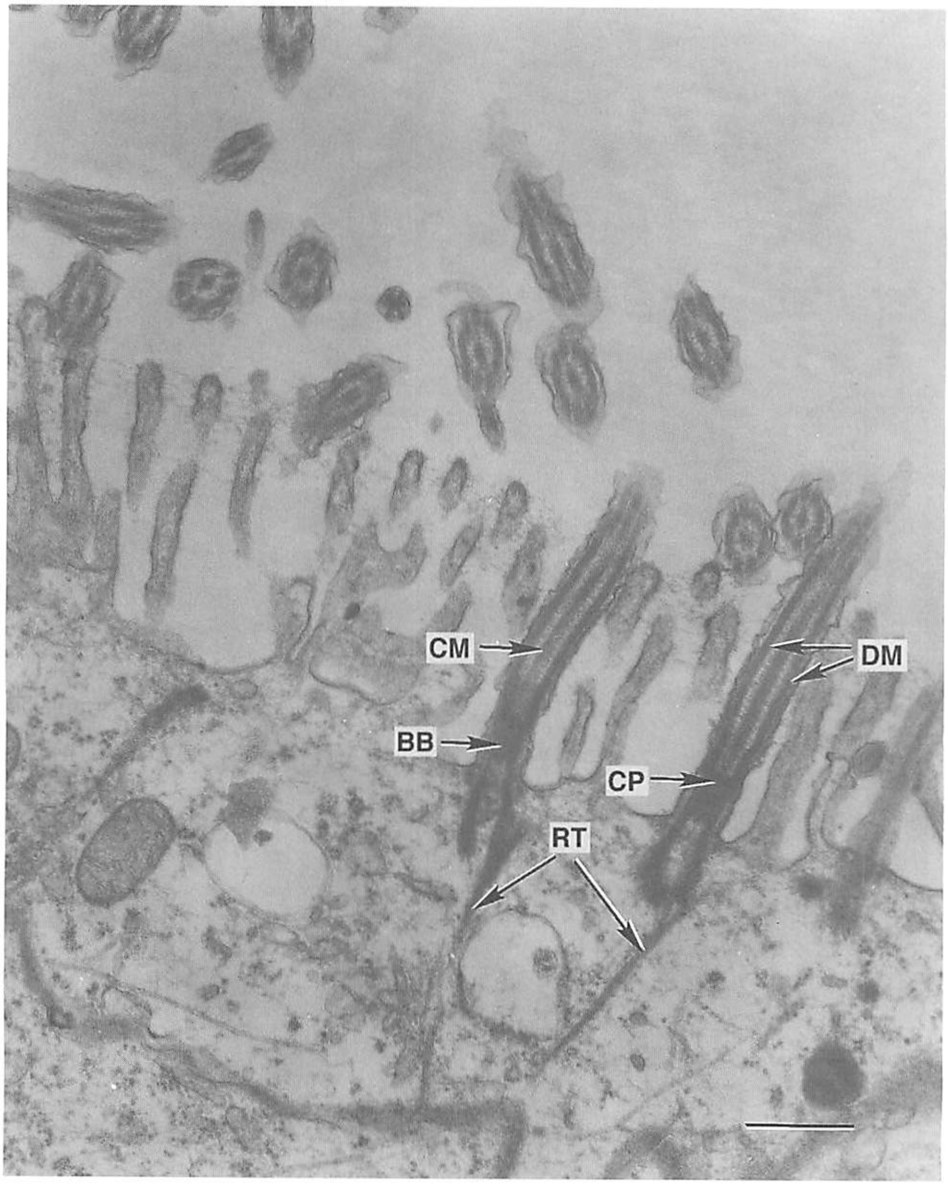

Figure 15. Ciliated epithelial cell of the gill showing longitudinal arrangement of central microtubules [CM] and doublet microtubules [DM]; [BB] basal body, [CP] ciliary plate, [RT] ciliary rootlet. × 26,400. Bar = 1 μm.

rest upon a thin basal lamina of irregular thickness that contains a network of collagen-like fibrils, each about 50 nm in diameter. The basal lamina is continuous with the collagenous rods of gill filaments; the continuity between the basal lamina and collagenous rods physically separates the surface epithelium from the underlying connective tissues and hemolymph sinuses.

Gill filaments are supported by large collagenous rods that contain tightly packed collagen-like fibers (Fig. 17). Where rods taper, they are continuous with the basal lamina. Hemolymph spaces are located adjacent to the rods. Fibroblast-like cells with fusiform nuclei are often in close contact with collagenous rods.

Spindle-shaped smooth muscle fibers, with peripherally oriented mitochondria, are commonly found

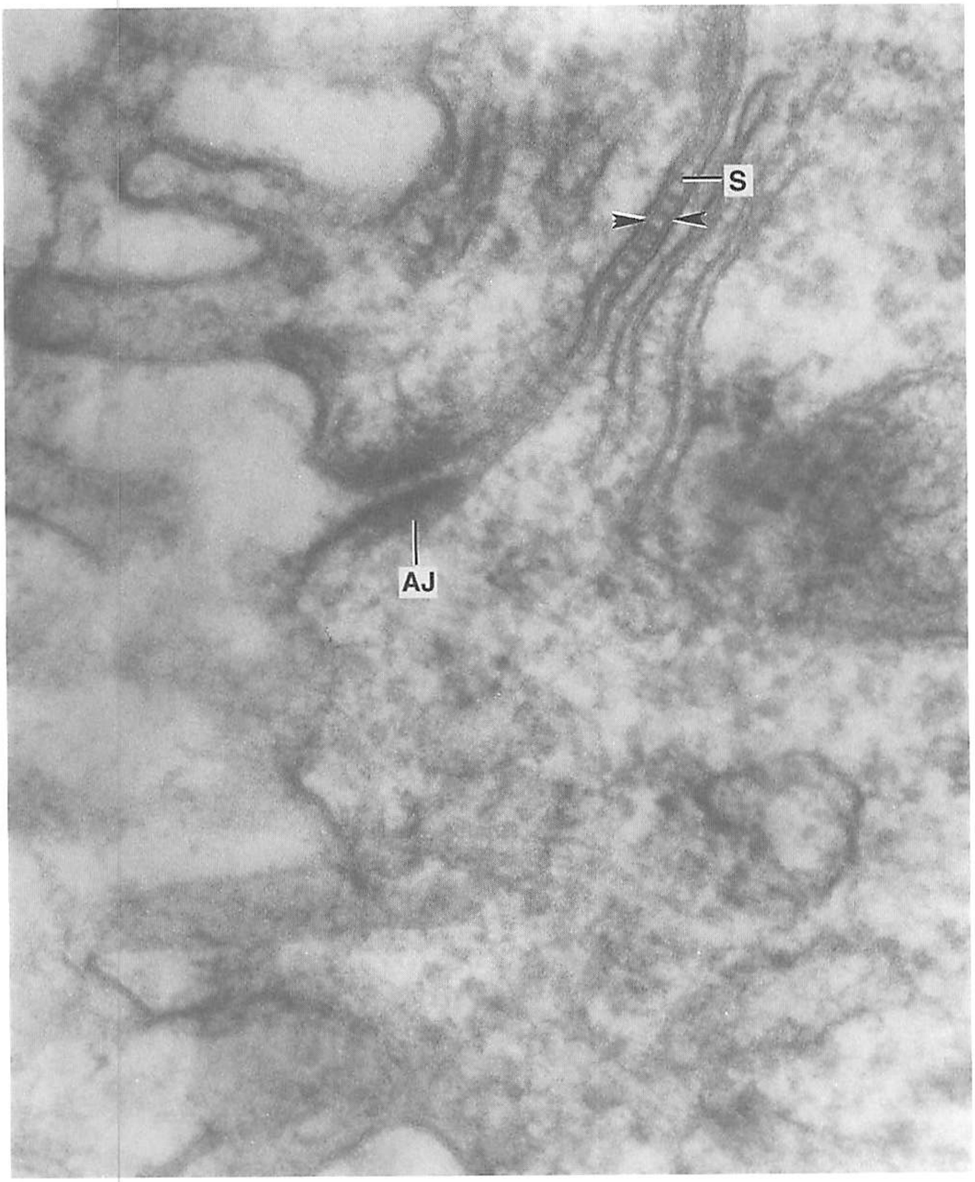

Figure 16. High magnification of septate junction [S] in a gill epithelial cell; note trilaminar structure of apposing cell membranes [arrow heads]. An adhering junction [AJ] is also seen. × 167,750.

in the connective tissue. Nerve fibers are occasionally in direct contact with muscle fibers.

Bundles of nerve axons are frequently seen in connective tissues close to collagenous rods and adjacent to muscle tissue. In some cases, nerve fibers are seen to be in contact with the basal portion of ciliated epithelial cells (Fig. 17). Nerve processes typically contain microtubules aligned longitudinally. In addition to mitochondria, most neurons within a nerve bundle ordinarily contain either of the following organelles:

1. round, membrane-limited granules with an average diameter of 180 nm and having an electron-dense core, suggestive of neurosecretory granules, or

2. round, moderately electron-dense, membrane-limited vesicles with an average diameter of 350 nm, similar to synaptic vesicles (Fig. 17).

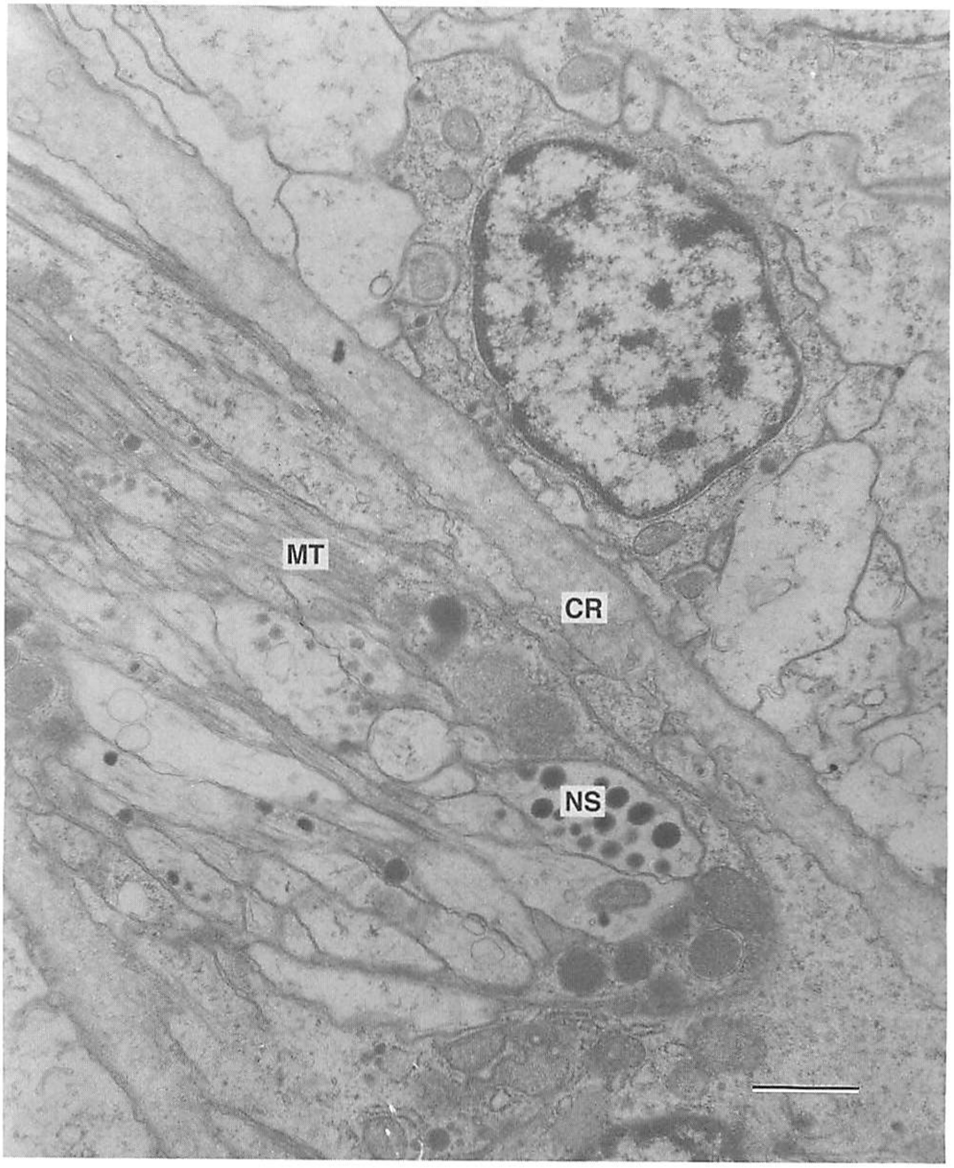

Figure 17. Nerve processes in connective tissue of gill showing neurosecretory-like [NS] dense core granules and microtubules [MT] oriented longitudinally. [CR] Skeletal rod (collagenous rod). × 21,725. Bar = 1 μm.

LABIAL PALPS

Anatomy

Labial palps lie at the extreme anteroventral side of the body just under the oral hood of the mantle (Figs. 1, 18); they consist of two pairs of large, soft flaps that have a roughly triangular shape. The broad bases are attached to the visceral mass dorsally while the slightly curved margins extend posteriorly to the point where they are in juxtaposition to the free edges of the gills. Each pair consists of an outer and an inner palp; each palp has a smooth surface and a ridged surface (Fig. 19), ridged surfaces being in apposition whereas smooth surfaces face outside. Galtsoff (1964) writes, "The two external palps join together above the mouth where they form the outer lip; the two internal palps are united below the mouth into an inner lip. As a result of this arrangement the mouth is an irregularly shaped, narrow, curved slit. Both lips are arched; the lower one is shorter, and its edge is thicker than that of the upper lip" (Fig. 18). The groove formed where the external palp meets its internal

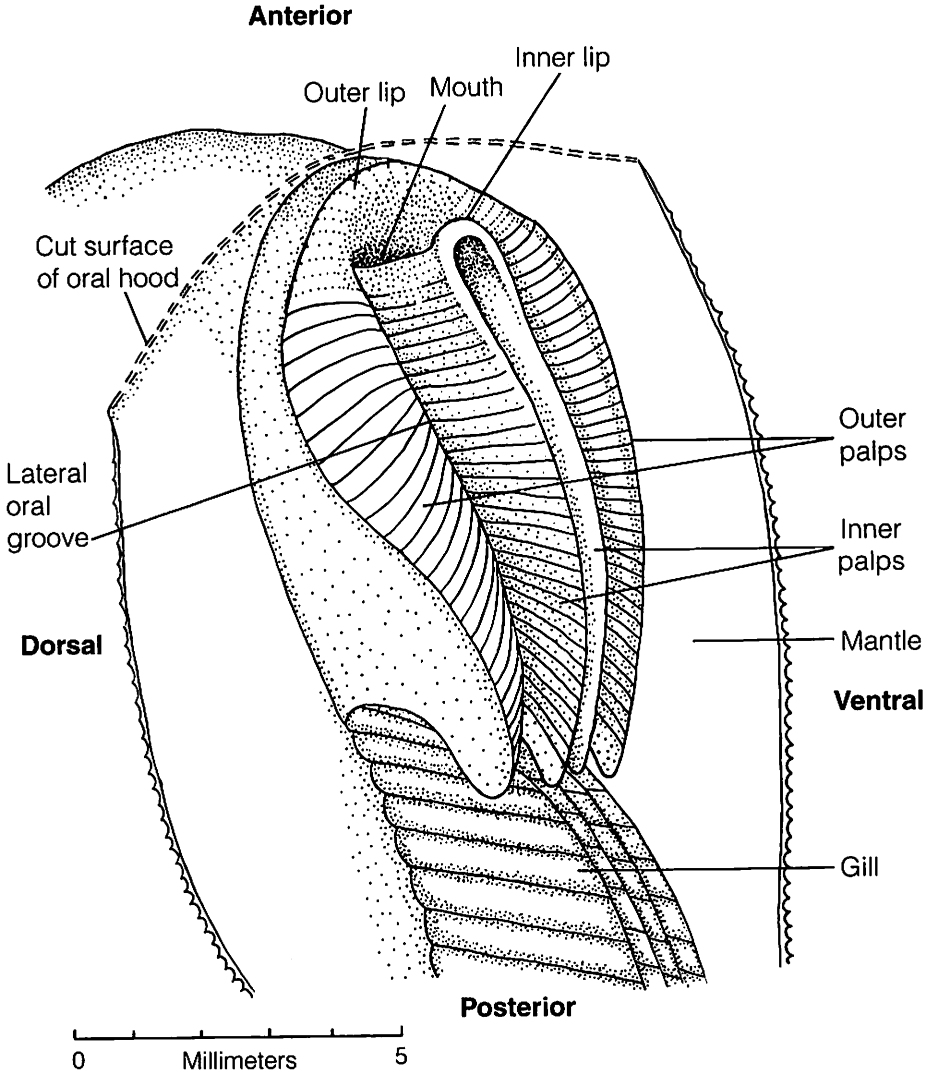

Figure 18. Diagrammatic anatomy of the palp and oral region of *C. virginica*. The mantle hood has been removed along the dashed line and pulled open to reveal the lips and mouth. Modifications to diagram in Galtsoff (1964) based on results from Ward et al. (1994).

member is termed the lateral oral groove; it functions as the major conduit conducting food to the corners of the mouth. In their normal state, the inner, ridged surfaces of the palps are always in juxtaposition (see Newell and Langdon, Chapter 5, for details of palp function).

Histology

Each palp has a core of Leydig cells covered by ciliated epithelia resting on prominent basement membranes; the Leydig-cell connective tissue is permeated by many hemolymph sinuses that give this tissue a spongy appearance (Figs. 19, 20). In addition, bands of prominent longitudinal muscles fibers are present in juxtaposition to basement membranes while transverse muscle fibers crisscross the connective tissue core (Fig. 20).

The simple ciliated columnar epithelium of the smooth surface averages 6 to 9 µm in height and possesses large, spherical nuclei. Cilia are sparse and small (1 to 2 µm), although tufts of long, dense cilia are widely scattered; cilia in these tufts range from 5 to 32 µm. Awati and Rai (1931) concluded that in the Bombay oyster, *Ostrea* (*Saccostrea*) *cucullata*, only some of the epithelial cells on the smooth surface of the palp were ciliated, and this seems to be the case with *C. virginica*. In order to see cilia clearly in fixed sections on this surface, phase-contrast optics must be employed. Interspersed with epithelial cells are many mucous cells whose height is about the same as epithelial cells. I found two types of mucous cells (using Alcian blue, pH 2.6 - PAS stain combination): a cell filled with neutral glycoprotein granules and a goblet-like cell that reacts positively for acidic glycoprotein. Both cell types have low cilia. The neutral glycoprotein granule cell is much more numerous than the acidic glycoprotein cell and in a linear stretch of 400 µm there were 19 of the former as opposed to only two of the latter; repeated counts gave this approximate ratio.

Bernard (1974) mentions two kinds of mucus on the palps, one with a serous consistency with which the palps are normally covered and a rejectory mucus; I assume the former is produced by the granular cells whereas the latter emanates from the goblet-like cells. Bernard (1974) stated, "the subepidermal goblet cells secrete copious quantities of rejectory mucus when stimulated." Galtsoff (1964) stated, "In the subepithelial layer [of the smooth surface of the palps] large eosinophilic cells and mucous cells are very abundant." I could find no evidence of subepithelial goblet cells in my sections and subepithelial eosinophilic cells were well scattered and not numerous.

A prominent band of longitudinal muscle runs just under the smooth epithelium the entire length of the palp. The smooth epithelium is copiously supplied with hemolymph by an extensive network of hemolymph sinuses (Fig. 19).

My sections show that the structure of the epithelium on the ridged surface varies depending upon location. Cells on ridges are simple tall columnar with prominent cilia and ciliary rootlets; cells range in height from 20 to 33 µm and possess cilia averaging 10 µm (Figs. 19, 20). Cells between ridges, the interridge epithelium, are simple, ciliated cuboidal in type and average 9 µm in height; cilia are dense but much shorter than those on the ridges and average 4.5 µm. Mucous cells of the granular neutral glycoprotein type are concentrated in the interridge epithelium; mucous cells reacting positively for acidic glycoproteins are located on the ridges. A longitudinal band of muscle runs under the ridged epithelium sending out slips of muscle to each ridge. A network of hemolymph sinuses supplies the ridged epithelium, especially in areas immediately under each ridge (Fig. 20).

I also found that many large mucous cells are located at the interface between palps and outer and inner lips of the mouth; near the palps these cells are chiefly of the acidic glycoprotein type but quickly grade into cell types with neutral glycoprotein granules. The latter are almost exclusively located on the main portion of outer and inner lips of the mouth.

The core of each palp consists chiefly of strands of Leydig cells separated by an extensive network of hemolymph sinuses (Figs. 19, 20); even from casual inspection of palp histology, it is obvious that their turgidity and shape is dependent upon the large volume of hemolymph they contain.

DIGESTIVE SYSTEM

Mouth

The mouth is an inverted U-shaped slit between outer and inner lips (Fig. 18); it is lined with a stratified, tall, ciliated columnar epithelium (Fig. 21A). In eastern oysters averaging 50 to 60 mm, the outer lip averages 42 µm in height, with long cilia (30 µm); the epithelium of the inner lip is somewhat lower in height (36 µm) with correspondingly shorter cilia

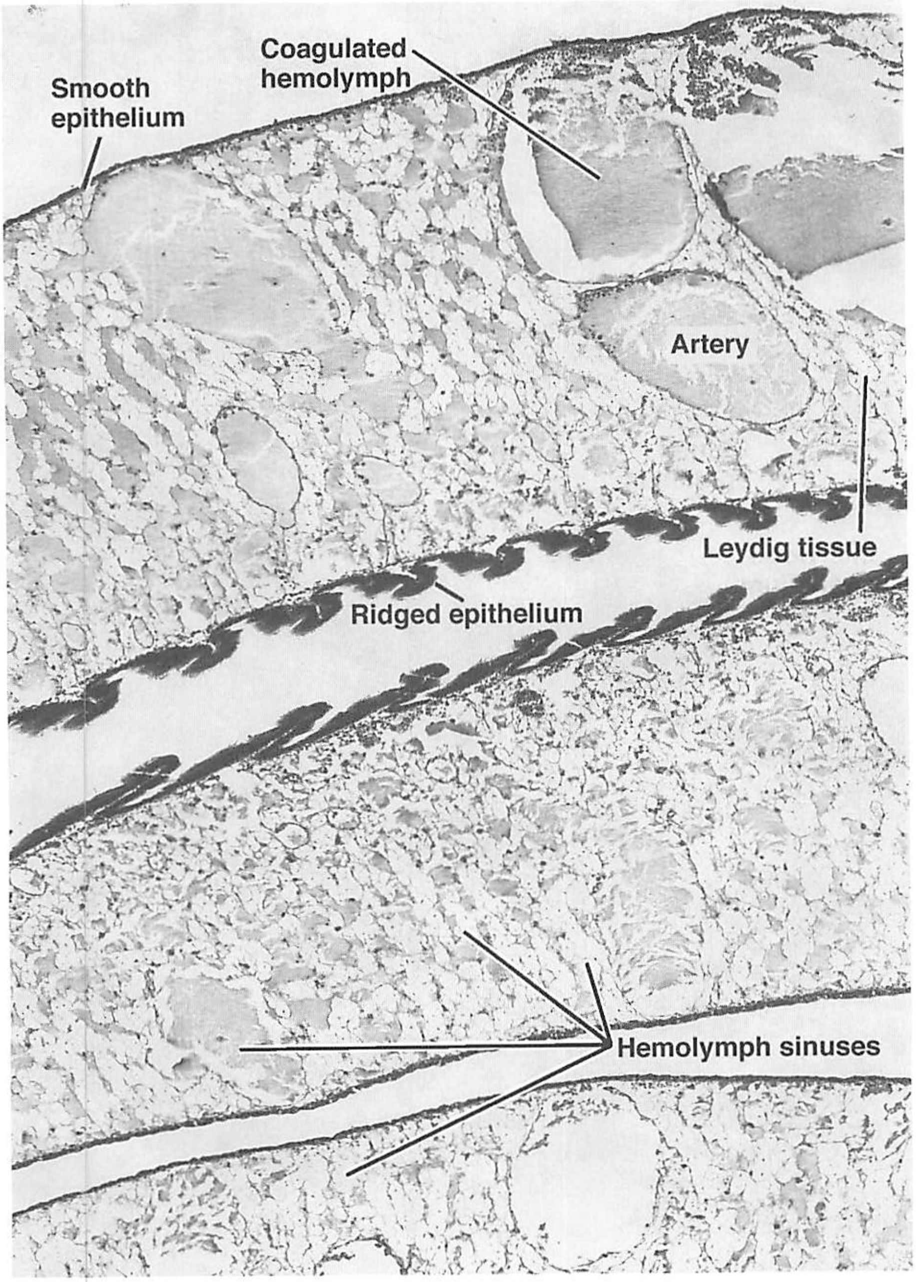

Figure 19. Longitudinal section of labial palps to show ridged epithelium and smooth epithelium. HFW = 1.5 mm.

(24 µm; Fig. 21B). Unicellular glands that stain positively for neutral glycoproteins are more abundant in the outer lip than in the inner. These glands have a flask-shaped portion close to the basement membrane and a long narrow neck that connects to the surface. Secretion droplets from these glands are evident on both outer and inner lip epithelia.

Connective tissues supporting the lips are com-

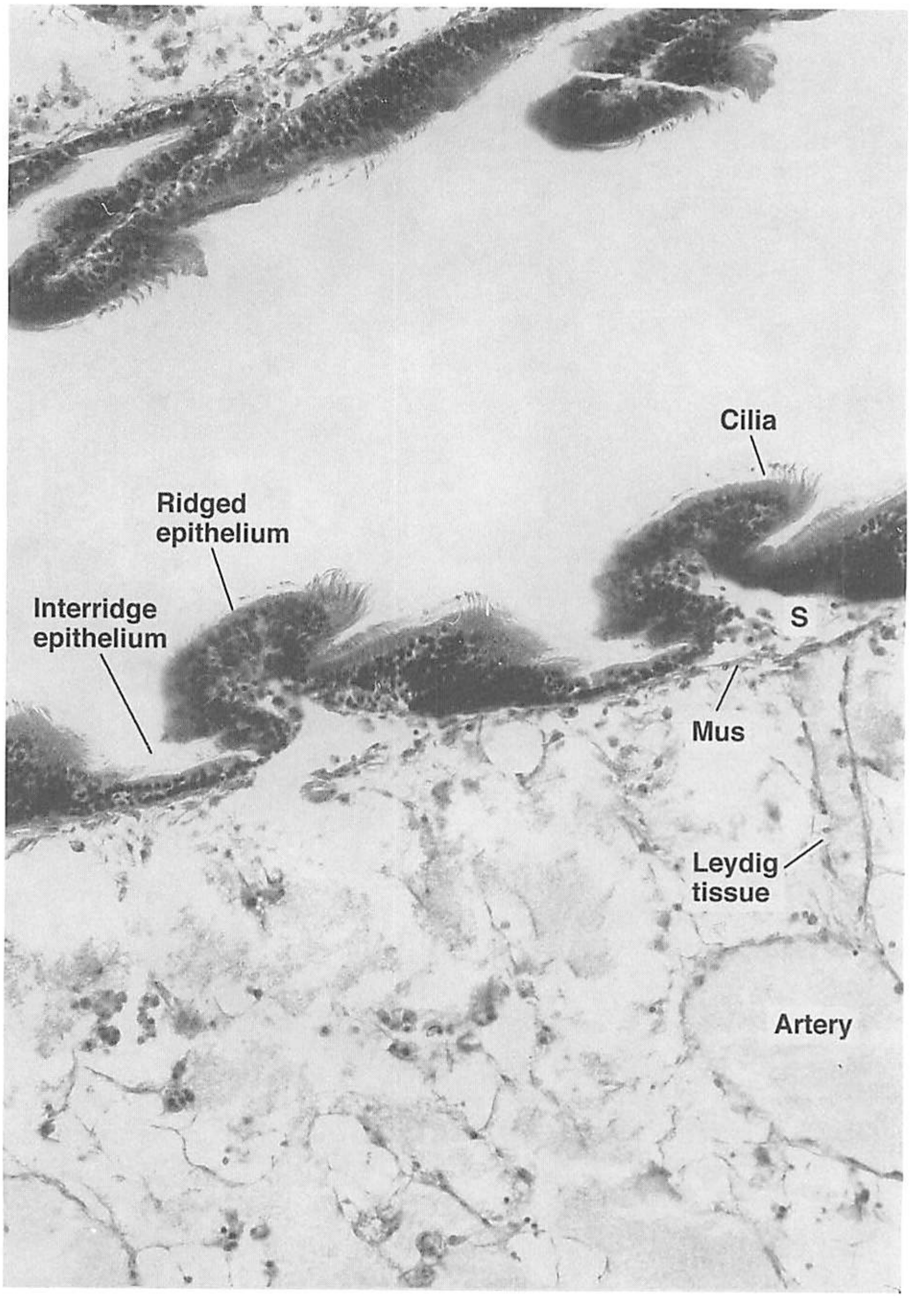

Figure 20. Longitudinal section of ridged epithelium of labial palps showing details of tall ciliated cells that constitute ridges and non-ciliated, low cuboidal cells that make up the interridges. Prominent subepithelial hemolymph sinuses [S] are present under each ridge. Longitudinal muscle [Mus] is seen under the epithelium. HFW = 305 µm.

posed of collagenous fibers interspersed among many Leydig cells. Smooth muscle fibers are present usually in juxtaposition to basement membranes.

Esophagus

The esophagus leads directly from the mouth (Fig. 1) and its epithelium is continuous and of the same type as that of the lips (Fig. 22). The esophagus is a dorsoventrally compressed tube that enters the anterior chamber of the stomach at the junction of the latter with the caecum (Shaw and Battle 1957; Figs. 23, 24).

My stained sections showed that the prominent basement membrane is composed chiefly of acid glycoproteins. Unicellular glands are numerous in the esophageal epithelium with a terminal bulb containing neutral glycoproteins situated close to the basement membrane. Beninger et al. (1991) reported that these glands are few and contain acid and neutral mucopolysaccharides (glycosaminoglycans). These authors also observed a thin layer of smooth muscle under the basement membrane.

Stomach

The stomach is a large sac-like organ that is divided into anterior and posterior chambers. The anterior chamber, an enlargement at the base of the esophagus, gives rise to the anterior and posterior caeca as well as to two primary ducts that lead to the digestive diverticula. The anterior caecum projects dorsally

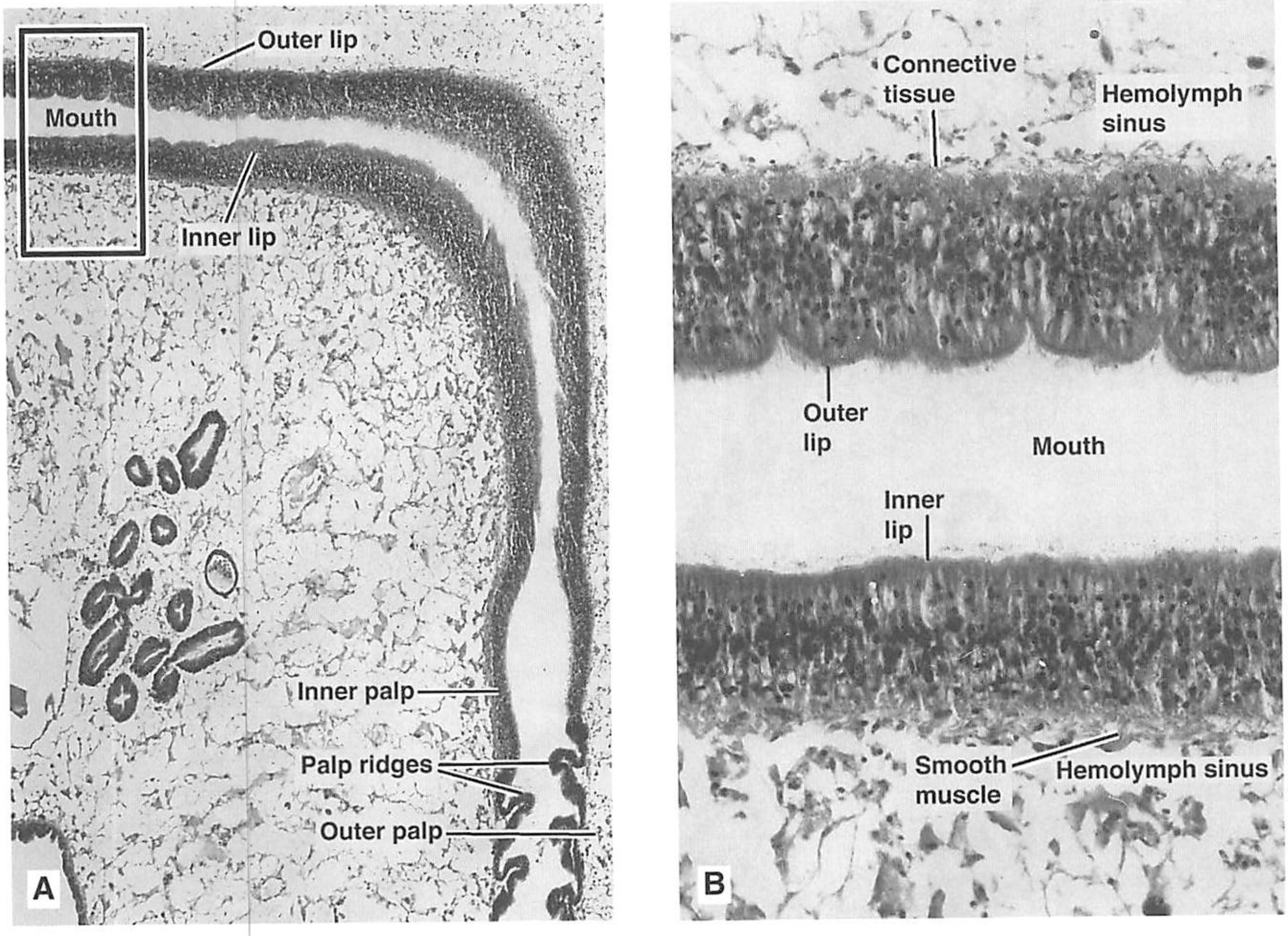

Figure 21. (A) Section of mouth area to show formation of outer and inner lips of mouth from fusion of labial palps. Note the transition from the ridged epithelium of the palps to the non-ridged ciliated epithelium of the inner and outer lips. (B) Details of rectangular area in A. HFW = 206 μm.

along the base of the esophagus whereas the posterior caecum is directed ventrally toward the right of the stomach; both caeca have spiral shapes (Figs. 23, 24).

The posterior chamber of the stomach is separated from the anterior chamber by a broad ridge that projects into the lumen from the mid-ventral wall; this chamber is complex and, in addition to having the gastric shield, it gives rise to several ducts:

1. a primary duct that leads to the digestive diverticula emanates from the left ventral side (Figs. 23, 24);

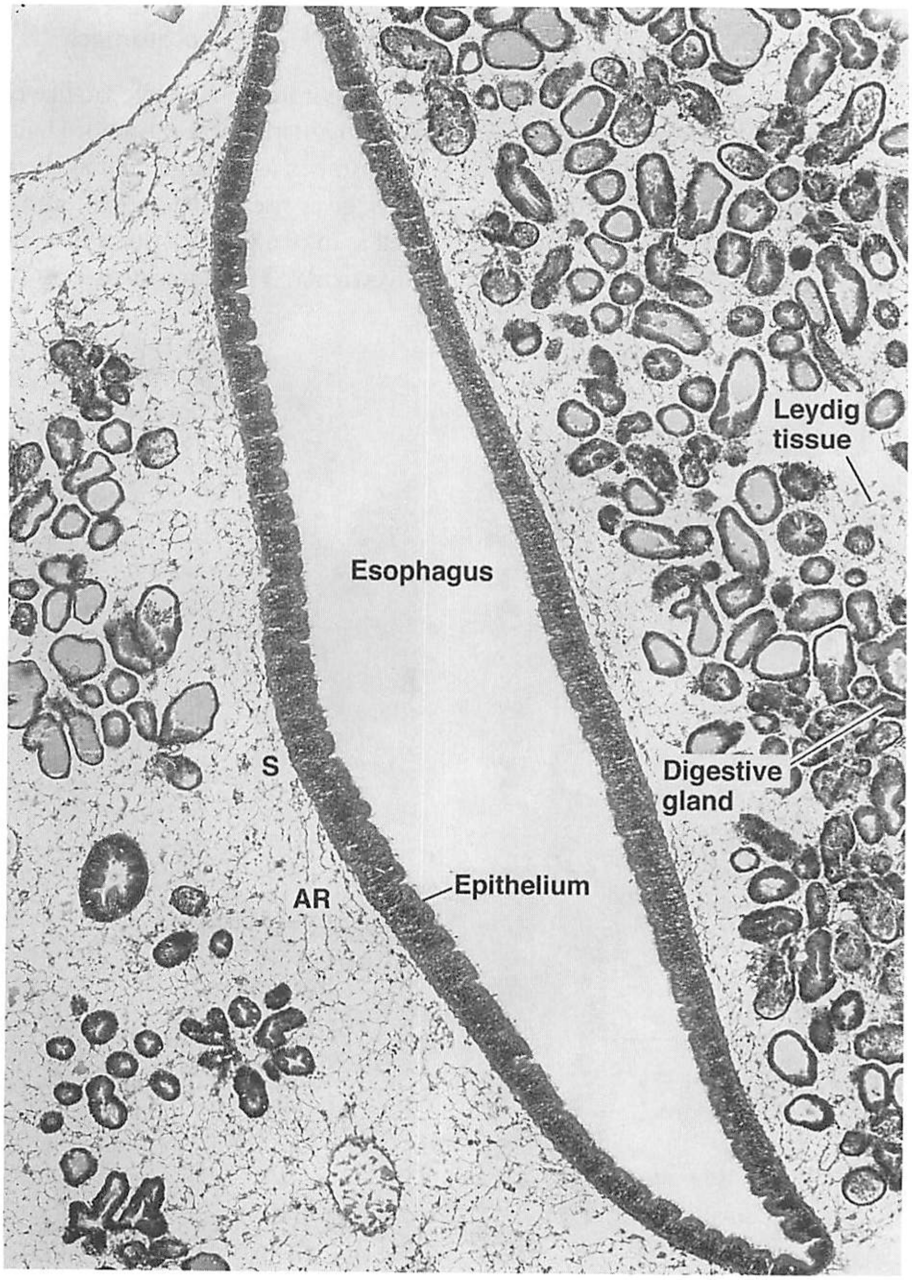

Figure 22. Transverse section of esophagus to show esophageal epithelium. [AR] longitudinal section of small artery terminating in peri-esophageal hemolymph sinus [S]. HFW = 1.5 mm.

2. just posterior to the gastric shield, the posterior stomach leads into an elongated outpouching called the style sac-midgut (Figs. 1, 23, 24); the style sac produces the crystalline style and rotates it against the gastric shield releasing the contained carbohydrases into the lumen of the posterior stomach; the midgut is separated from the style sac by the greater and lesser typhlosoles (Shaw and Battle 1957; Galtsoff 1964). Langdon and Newell in Chapter 6 provide a detailed discussion of digestive enzymes.

The gastric shield, a plate-like, translucent structure is embedded in the left ventral wall (Figs. 25A, 25B, 30); it consists of two main lobes joined by a narrow neck and receives the anterior end of the crystalline style (Nelson 1918; Shaw and Battle 1957).

The epithelium of the stomach is pseudostratified, tall, ciliated, and columnar. Many unicellular glands are present that contain acid glycoproteins rich in carboxyl groups. I have found that the prominent basement membrane is composed of carboxylated and sulfated glycoproteins.

The epithelium underlying the gastric shield is similar in type to the general gastric epithelium but taller with cells averaging 130 µm; cilia are scarce and appear degenerate. The gastric shield appears laminated and has strands of material clinging to its epithelial-side border (Figs. 25A, B, 30); this has been

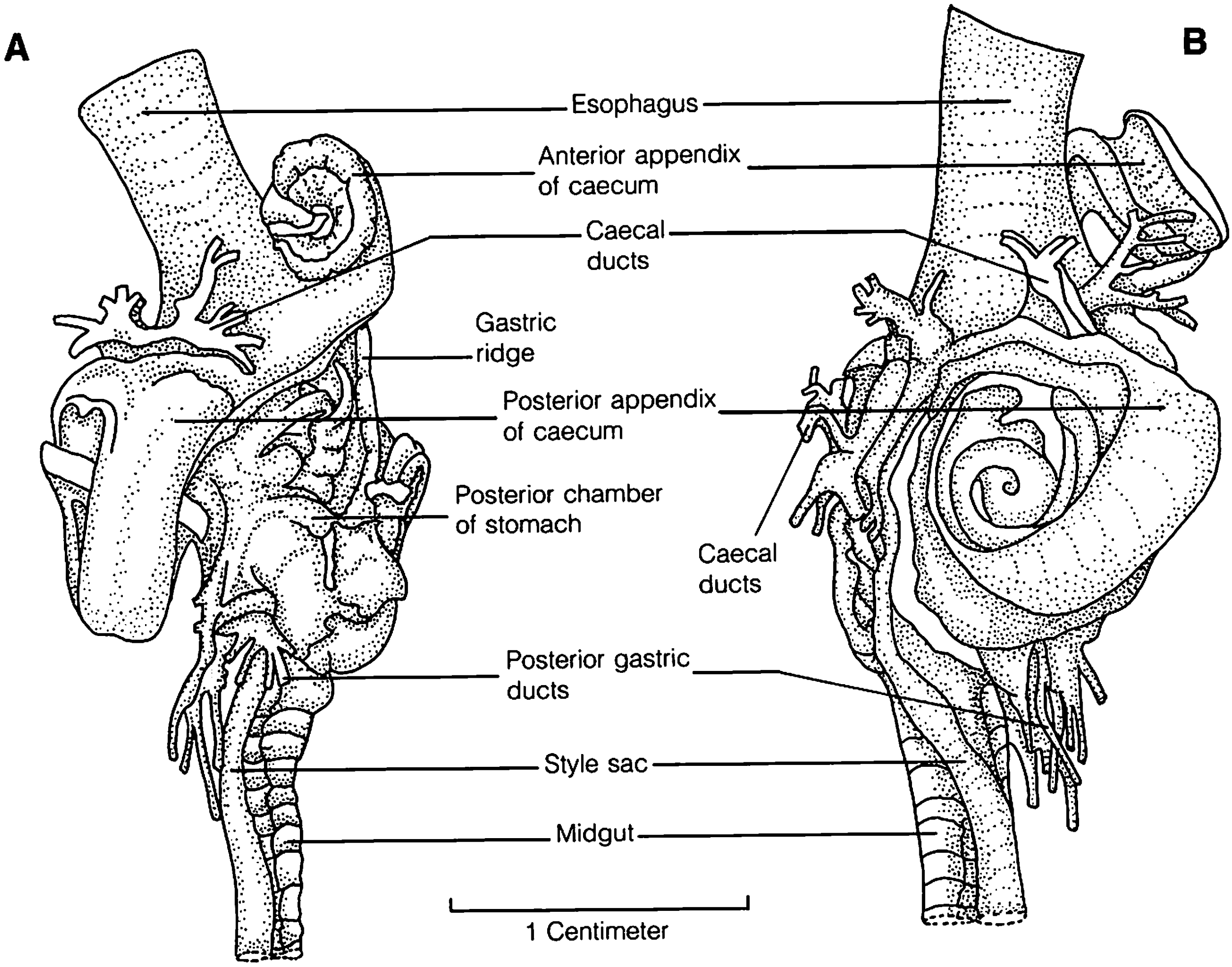

Figure 23. Latex mold of esophagus and stomach viewed from the (A) left lateral aspect and (B) left ventral aspect. Redrawn from Shaw and Battle (1957).

described in detail by Shaw and Battle (1957). Galtsoff's (1964) statement that the origin of the gastric shield has not been fully explained is still true. Yonge (1926a) thought the shield was formed by the fusion of cilia whereas Leenhardt (1926) described torch-bearing cells (cells whose apical surface connects with strands of connective tissue that flare out in many directions) near the edges of the area occupied by the shield in the Portuguese oyster *C. angulata.* Galtsoff (1964) could find no evidence of such cells in *C. virginica,* but my sections show cells very similar to those described by Leenhardt (1926).

McQuiston (1970) showed that the gastric shield of the erycinid bivalve, *Lasaea rubra,* is composed largely of microvilli that originate from cells of the underlying epithelium. Microvilli taper distally in *L. rubra* and are more widely spaced in the distal portion of the shield near the lumen of the stomach. Spaces between microvilli are occupied by a matrix that is composed of fine granular and fibrous elements; a gradation of matrix material exists from the base of the microvilli, where matrix material is scarce, to the luminal area where matrix is compact and dense. Fine filaments run the length of microvilli; these are presumably actin filaments, although McQuiston (1970) did not identify them as to chemical type. Elston (1980a) showed clearly that the gastric shield in larval *C. virginica,* similar to adult *Lasaea rubra,* is composed of a dense mat of intertwined microvilli. In all probability, the gastric shield in adult *C. virginica* is also derived from microvilli.

Style Sac-Midgut

Just posterior to the gastric shield, the stomach leads into an elongated outpouching that extends along most of the ventro-posterior section of the visceral mass (Fig.1). Two lateral folds project into the lumen of the outpouching and continue posteriorly as the lesser, or right, and the greater, or left typhlosoles, which incompletely divide the lumen into two parallel channels (Fig. 26), the ventral midgut and the dorsal style sac. The cross section of the style sac's lumen usually appears larger than the midgut's, and irregularly circular to oval compared to the laterally compressed midgut (Fig. 26) (Shaw and Battle 1957).

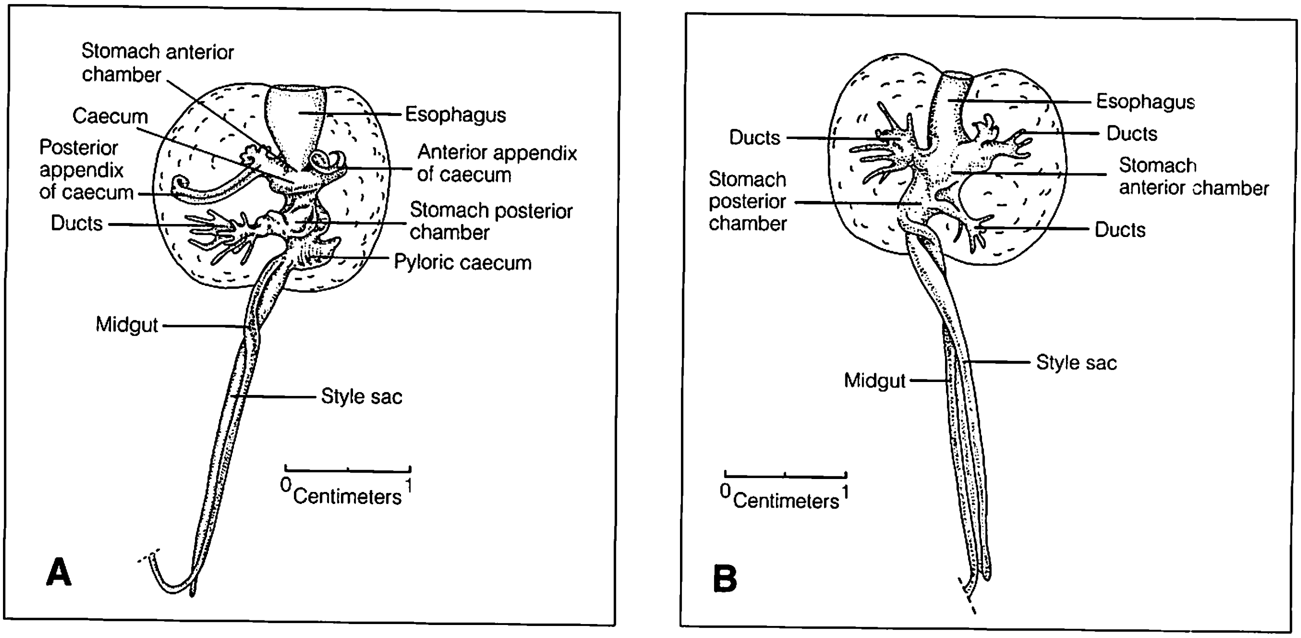

Figure 24. Latex cast of stomach, crystalline style sac and esophagus viewed from the (A) left side and (B) right side. Esophagus is slightly distended by latex injection process. Redrawn from Galtsoff (1964).

The style-sac epithelium is characterized by the density, uniformity, and large size of the cilia (average length 15 µm) that are larger than other cilia within the digestive tract (Figs. 26, 27). The epithelium is simple columnar with no mucous or eosinophilic granular cells. This epithelium has been termed the "A" cell layer in other bivalves (Kato and Kubomura 1954; Mathers 1973).

The midgut is separated from the style sac by the greater and lesser typhlosoles. The transition from the epithelium of the style sac to that of the typhlosoles is especially abrupt on the lesser typhlosole. Here, a cleft marks the point where the densely ciliated, simple columnar, non-glandular style sac epithelium ends and the less densely ciliated, pseudostratified, columnar epithelium of the lesser typhlosole begins (Fig. 27). The latter has many eosinophilic granular cells, with a prominent cell body located basally in the epithelium and a long neck that ends in a swollen apical sac containing the granules. I found that the cell body consists of mixtures of acidic and neutral glycoproteins whereas granules in the apical sac are chiefly acidic glycoproteins. Further, marked differences in concentrations of selected enzymes (alkaline and acid phosphatases and nonspecific esterase) as revealed by enzyme histochemistry can be seen on either side of the cleft separating the style sac from the typhlosoles (Eble 1965). The typhlosole epithelium has been termed the "B" cell layer in other bivalves.

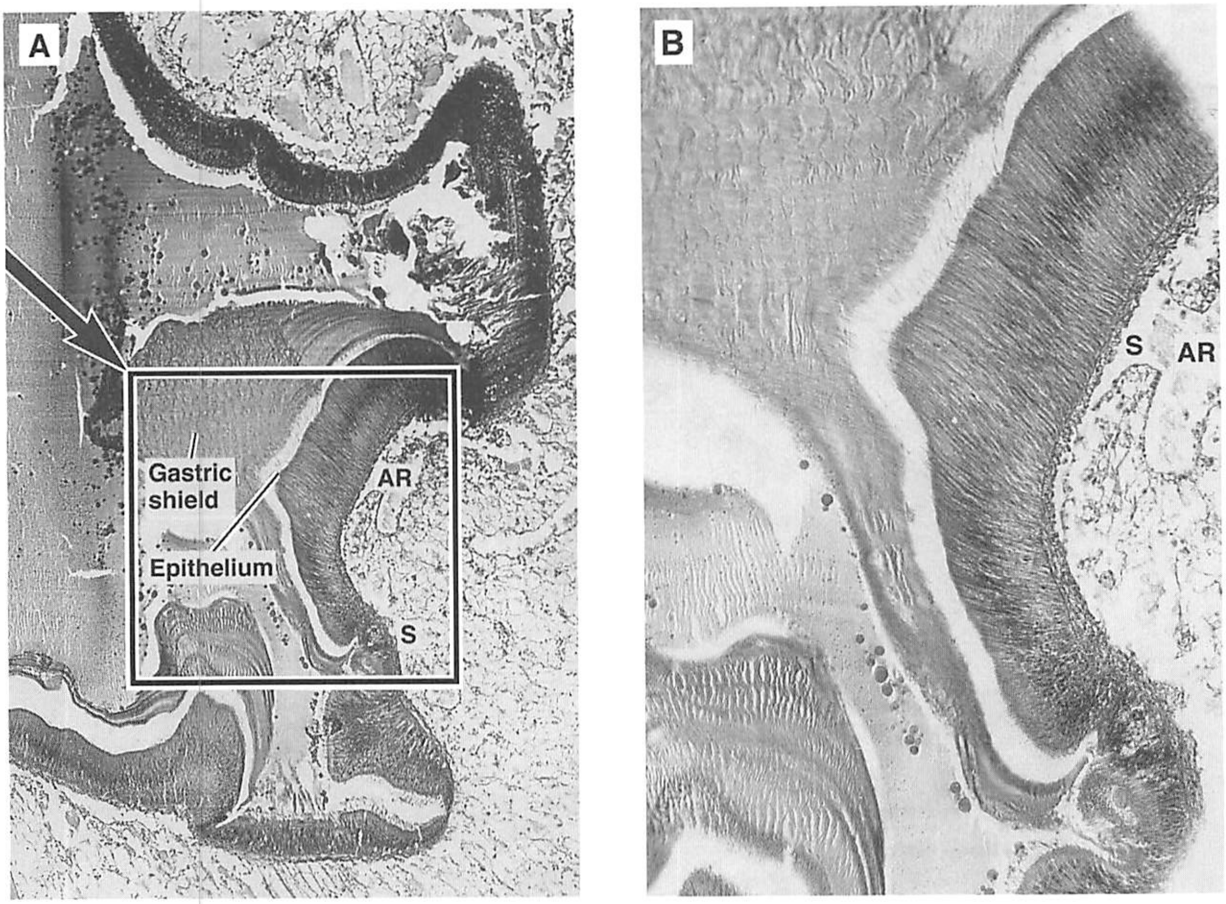

Figure 25. (A) Section through stomach in area of gastric shield. Arrow indicates direction from which style impinges upon gastric shield. (B) An enlargement of rectangular area in A. [AR] artery grading into the peri-gastric sinus [S]. HFW in A = 1 mm; HFW in B = 430 µm.

The midgut epithelium is not as tall as that of the typhlosoles and has been termed the "C" cell layer in other bivalves. I have found many unicellular glands rich in carboxylate glycoproteins in this epithelium; these glands are vase-shaped with the sac-like swollen part near the basement membrane and the long, narrow neck in the apical portion of the epithelium. The midgut epithelium is enveloped by a prominent layer of connective tissue consisting chiefly of acidic glycoproteins whereas the style sac has a poorly developed connective tissue. Both style sac and midgut are supplied by prominent hemolymph sinuses (Figs. 26, 27). The histology of the midgut-style sac area is described by Shaw and Battle (1957).

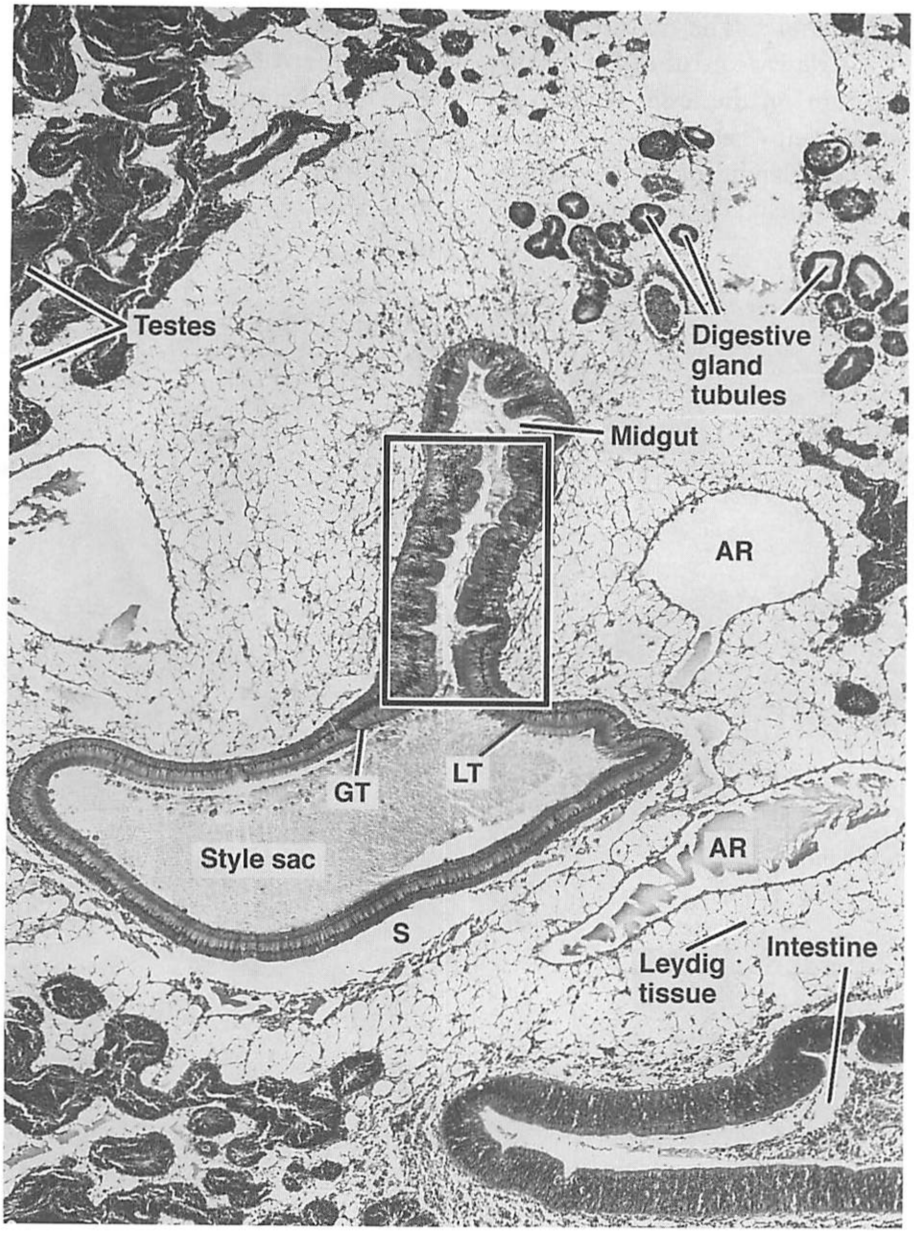

Figure 26. Section of style sac-midgut complex; area within rectangle is shown as an enlargement in Figure 27. [AR] arteries sending branches to peri-style sac-midgut hemolymph sinus [S], [GT] greater typhlosole, [LT] lesser typhlosole. HFW = 1.5 mm.

Intestine — Ascending, Median, and Descending Portions

The ascending limb of the intestine arises at the common posterior chamber of the style sac and midgut and runs by an abrupt flexure anteriorly and dorsally in the visceral mass (Fig. 1). Near the anterior extremity of the visceral mass, the ascending limb descends ventrally to form the median limb. The descending intestine runs posteriorly in the ventral portion of the visceral mass, then crosses obliquely to the left and runs along the dorsal margin of the pericardial sac before opening into the rectum (Fig. 1).

The intestine has a prominent typhlosole con-

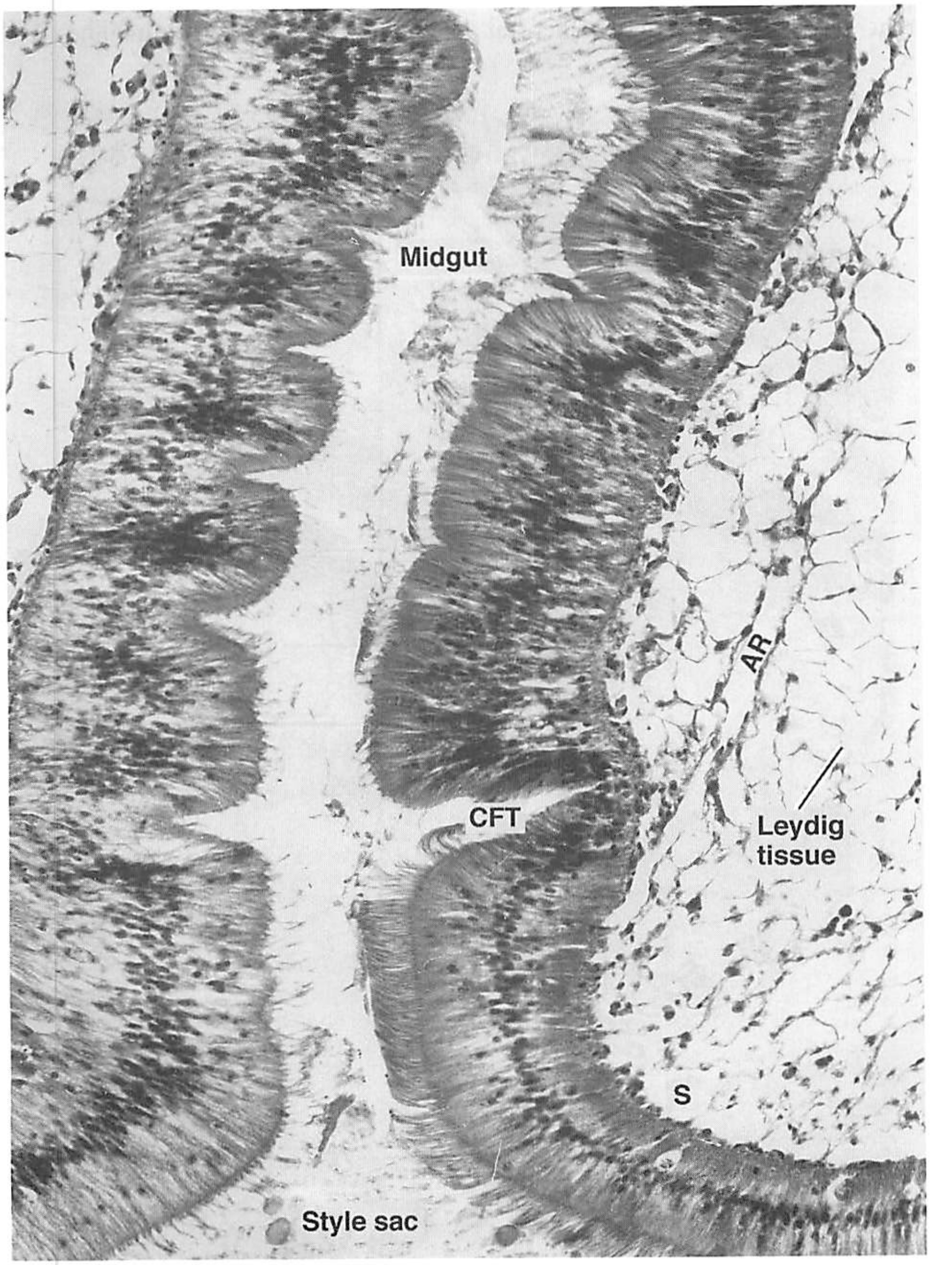

Figure 27. Enlargement of rectangular area in Fig. 26. Cleft in lesser typhlosole [CFT] that separates style sac from midgut. [AR] small artery opening into peri-style sac hemolymph sinus [S]. HFW = 305 µm.

sisting of a core of Leydig cells covered with a ciliated epithelium with a prominent median groove; the narrow lumen takes the shape of a double crescent when seen in transverse section (Fig. 28). My sections show that the ciliated, pseudostratified epithelium rests on a prominent basement membrane that is composed of glycoproteins rich in both carboxyl and sulfate groups. The non-typhlosole epithelium has granular unicellular glands that are rich in neutral glycoproteins; these gland cells increase in number from anterior to posterior and are particularly dense in the descending (posterior) intestine. Shaw and Battle (1957) refer to these gland cells as eosinophilic cells and list them as more numerous in the ascending (anterior) intestine of *C. virginica*, but my observations indicate just the reverse; presumably, these gland cells lubricate intestinal contents, thus facilitating passage to the rectum. The typhlosole epithelium

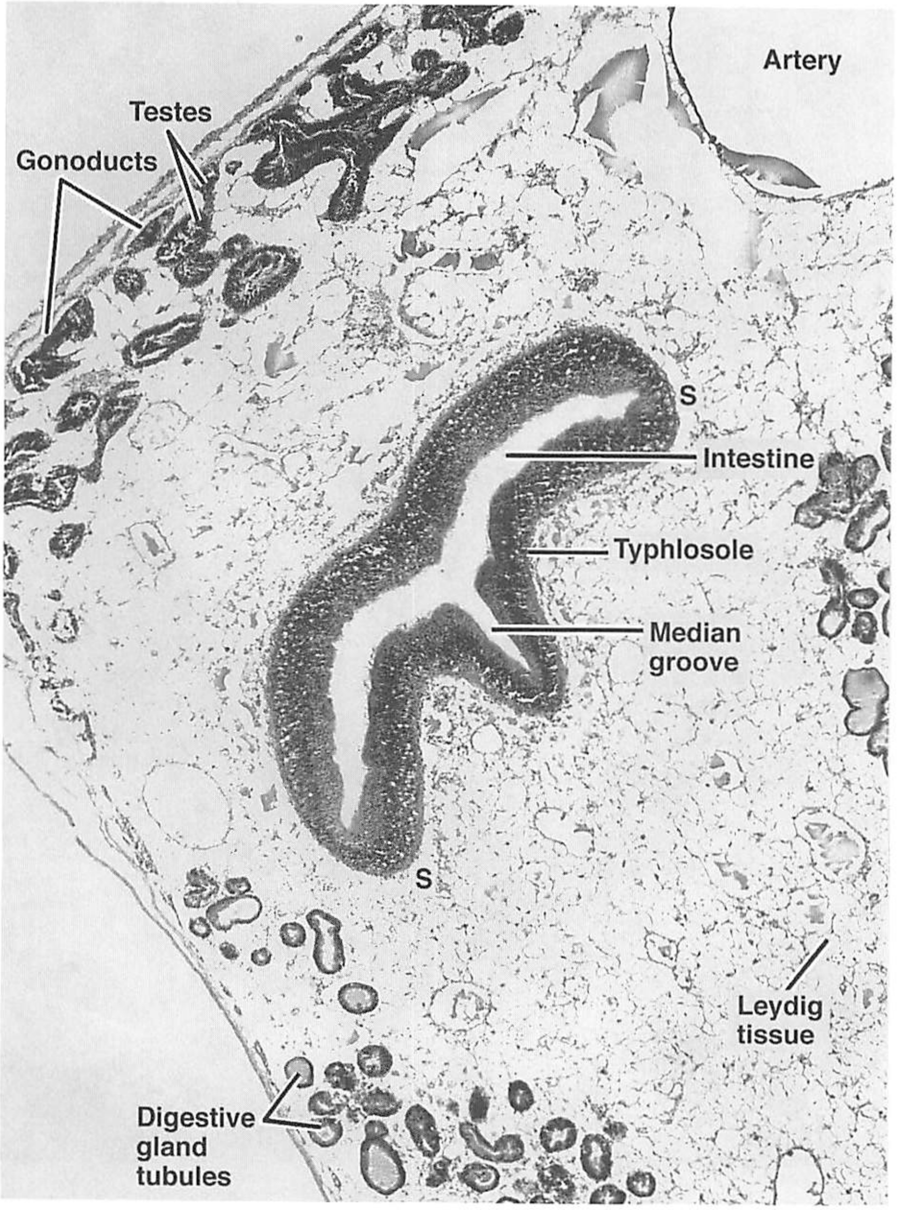

Figure 28. Transverse section of intestine; note prominent typhlosole. [S] peri-intestinal hemolymph sinus. HFW = 1.5 mm.

has large, flask-shaped unicellular glands situated near the basement membrane; the narrow neck of the gland conducts the neutral glycoprotein secretions to the free edge of the epithelium. The glands increase in density from ascending to descending limbs of the intestine and are numerous in the latter. This agrees well with Shaw and Battle (1957) who refer to these cells as mucous cells.

The entire digestive system is bathed by prominent peri-intestinal hemolymph sinuses (Fig. 28), similar to the scallop, *Pecten maximus* (Le Pennec et al. 1991). Strands of connective tissues run from the collagen that supports basement membranes across hemolymph sinuses to the surrounding Leydig tissue. These "peri-gut" sinuses not only provide a rich supply of hemolymph for the alimentary canal, but also create fluid-filled cavities that may allow for some gut motility (Shaw and Battle [1957] and Galtsoff [1964] report some smooth muscle associated with all branches of the digestive tract).

Rectum

The rectum is a continuation of the descending intestine; it runs dorsally over the adductor muscle and ends in the anus that is located in the cloacal chamber (Figs. 1, 29).

I found that, as with the intestine, the rectum has a ciliated pseudostratified columnar epithelium that rests on a prominent basement membrane composed chiefly of sulfated glycoproteins. A peri-rectal hemolymph sinus bathes the entire length of the rectum (Fig. 29). A well-defined typhlosole on the ventral surface of the rectum has a deep groove; tall cells bordering the groove average 103 µm in height. Many granular unicellular glands rich in neutral glycoproteins are present in the superficial portions of the epithelium with the exception of the notch of the typhlosole.

Digestive Gland

The digestive gland is a compound, tubular gland. Three primary ducts leave the stomach, two from the anterior chamber and one from the posterior chamber (Figs. 23, 24); they divide into many secondary ducts (Fig. 30) which, in turn, ultimately branch into pretubular ducts that lead directly to digestive tubules (Fig. 31). Digestive tubules are always bathed by hemolymph sinuses.

Primary ducts have an epithelium that resembles that of the stomach (Fig. 30). Secondary ducts have two types of cells: cell Type I is short and broad and has a heavy cuticle with long, dense cilia; cell Type II is approximately double in height with apical ends of cells pinching off vesicles via apocrine secretion (Fig. 32) — this is the so-called "bubbling epithelium" of Owen (1955). Battle and Shaw (1957) report that Type II duct cells have short cilia but my sections show they do not. This histological construction is consistent with the two-way direction of particle movement in bivalve digestive-gland ducts postulated by Owen (1955): the ciliated region (cell Type I) directs material after intracellular digestion away from the tubules back towards the stomach while countercurrent flow along the cell Type II brings partially digested food from the stomach to the tubules. Apocrine secretion by cells of Type II release acid phosphatases and non-specific esterases into the duct lumen (Fig. 32; Eble 1965). These hydrolytic enzymes undoubtedly aid in extracellular digestion before final intracellular digestion in the tubules.

Pretubular ducts are densely ciliated over two-thirds of the epithelium; the remaining epithelium lacks cilia and shows evidence of apocrine secretion similar to cell Type II of secondary ducts discussed above (Fig. 31).

Tubules in healthy, actively feeding oysters have either X- or Y-shaped lumina (Fig. 32). Light microscopy reveals two cell types in tubules of the digestive gland: (1) a digestive cell or secretory-absorbtive cell and (2) a basiphil cell (Fig. 32); Owen (1955) discusses and illustrates both cell types including the flagellum associated with basiphil cells. Transmission electron microscopy reveals three types of cells in digestive-gland tubules: (1) a digestive cell or secretory-absorbtive cell; (2) a non-flagellated basiphil cell, and (3) a flagellated basiphil cell.

Digestive or secretory-absorbtive cells have long, well-developed microvilli and the apical plasma membrane exhibits much pinocytic activity. The most characteristic feature of this cell is the presence of three types of macrovesicles (Sugawara 1969; Weinstein 1995) which corresponds to the lysosomal-vacuolar system of other bivalves (Owen 1972; Pal et al. 1990).

Non-flagellated basiphil cells possess microvilli, a prominent rough endoplasmic reticulum (RER), an extensive Golgi apparatus lying just above the basally situated nucleus, and many secretory vesicles lying just under the apical plasma membrane. This cell appears to be specialized for the production of extracellular enzymes, but exocytosis of secretory vesicles has not been reported (Weinstein 1995). High concentrations of alkaline phosphatase have been reported in these cells (Eble 1965) and Mathers (1973) described secretion of arylamidase and esterase in two closely related species (*Ostrea edulis* and *Crassostrea angulata*). Weinstein (1995) concludes that non-flagellated cells secrete some enzymes into the lumen of tubules that are used for extracellular digestion.

Flagellated basiphil cells have a single, long flagellum in addition to microvilli; RER, Golgi apparatus, and secretory vesicles are lacking in this cell (Weinstein 1995). This cell has been considered to serve as a stem cell, giving rise to all cell types in the tubule (Yonge 1926b; Galtsoff 1964; Sumner 1966; Owen 1970); indeed, Shaw and Battle (1957) termed basiphil cells, "generative cells." Pal et al. (1990) did not find mitotic figures in basiphil cells of the clam *Meretrix meretrix* and concluded that basiphil cells did not act as stem cells. Weinstein (1995) did not observe mitoses in basiphil cells of *C. virginica* and supports Pal et al. (1990) in their conclusions. Clear-

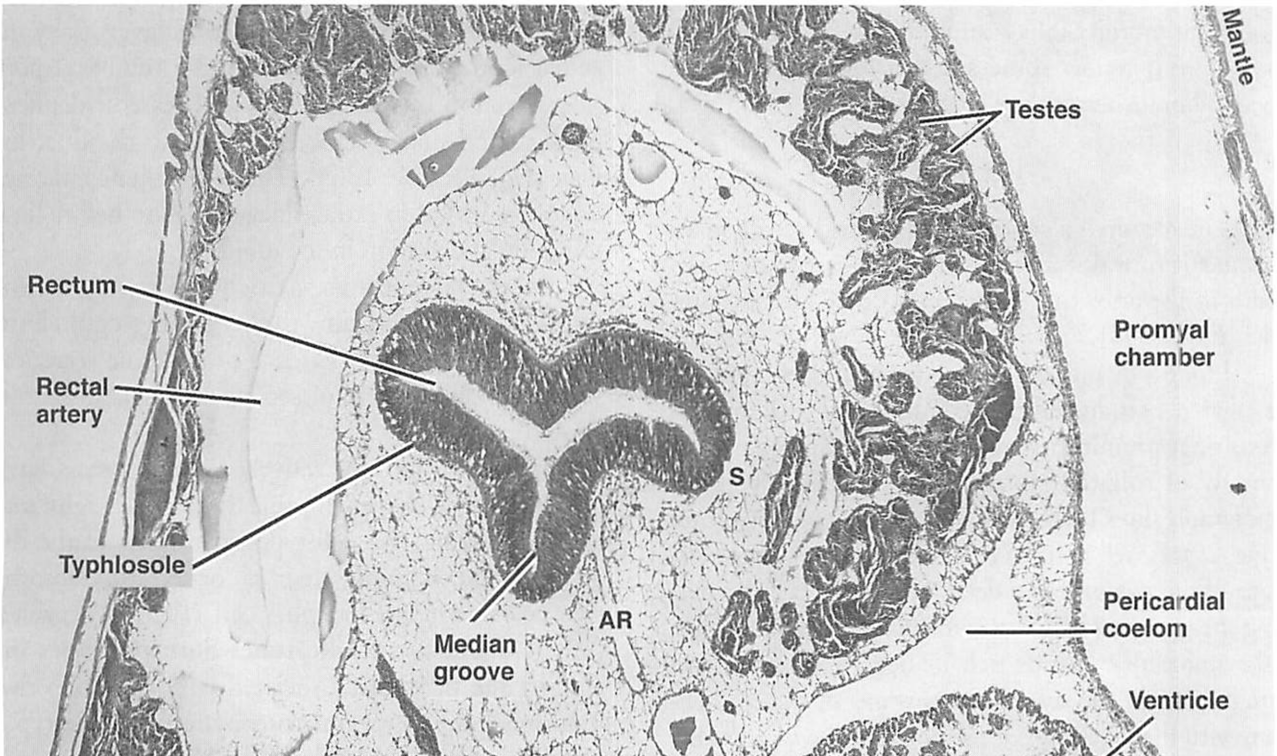

Figure 29. Transverse section through rectum; note prominent typhlosole. [AR] small artery terminating in peri-rectal hemolymph sinus [S]. HFW = 1.5 mm.

ly, much work remains to be done on the cytology and physiology of the digestive gland of bivalves.

Diseased, stressed, or non-feeding eastern oysters during cold torpor possess digestive-gland tubules that have simple, low cuboidal epithelia and a large circular lumen (Fig. 31). Such abnormal histology of digestive gland tubules can be used as an indicator of the general physiological condition of bivalves (Lowe et al. 1981; Winstead 1995). After winter hibernation or recovery from the stressed state, eastern oysters regenerate secretory-absorptive cells and the digestive gland resumes its normal physiology.

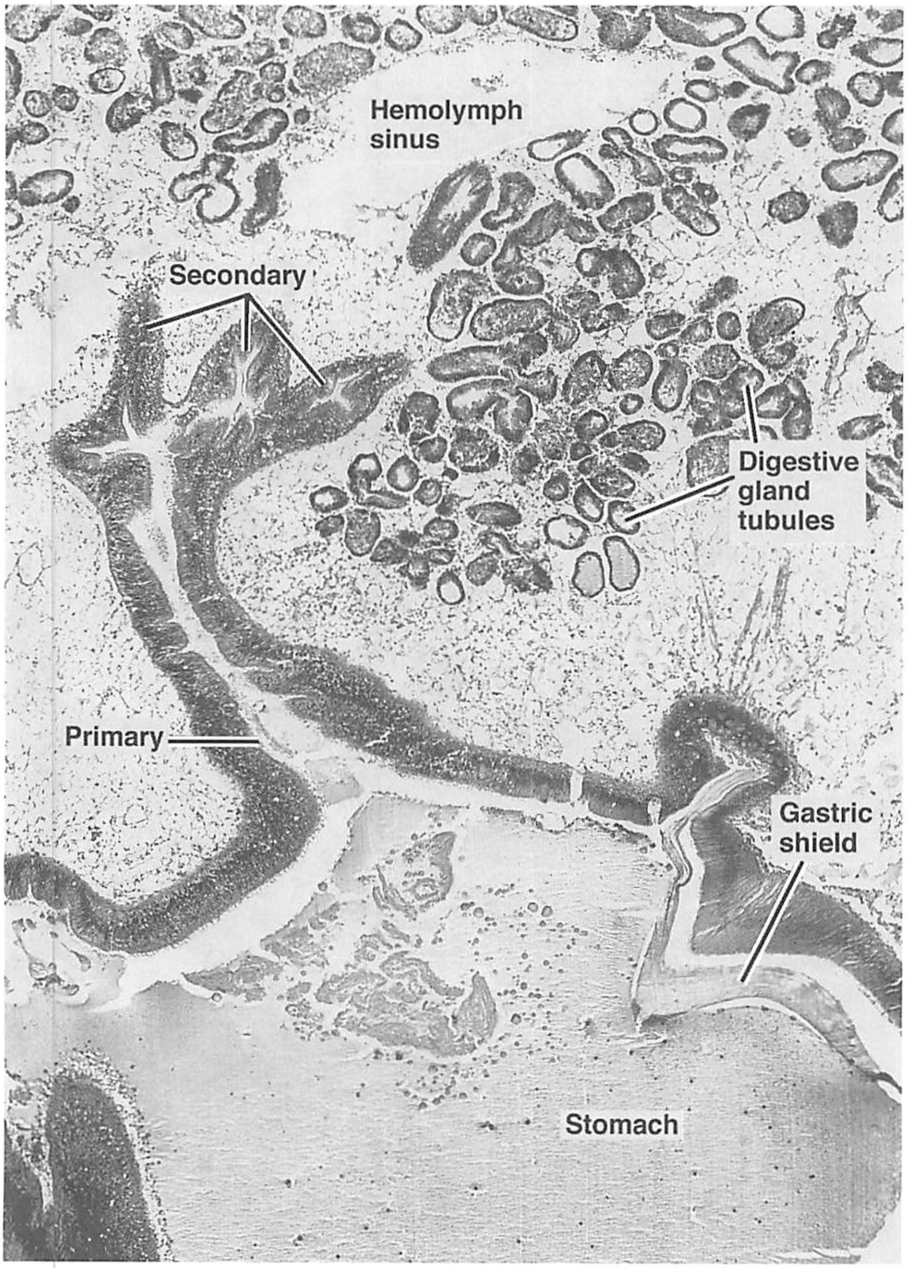

Figure 30. Section through stomach and gastric shield showing origin of a primary duct branching into secondary ducts supplying the digestive gland. HFW = 1.5 mm.

EXCRETORY SYSTEM

The kidney of the eastern oyster, as in all bivalves, is derived from mesodermal coelomoducts. Physiologically, renal filtration occurs in the atria and podocytes have been reported from the atria (Hawkins et al. 1980). The pericardial gland, part of the bivalve excretory system, is reduced in the eastern oyster to mesothelial granular cells that line the pericardial coelom; heaviest concentrations of these cells are located along the anterior face of the adductor muscle and over the roots of the atria. Cell types vary according to location: ventral — cells are similar to and contiguous with the kidney; lateral — cells contain many large granules (diameter 1 µm) that stain yellow to brown with hematoxylin and eosin; dorsal — cells are usually

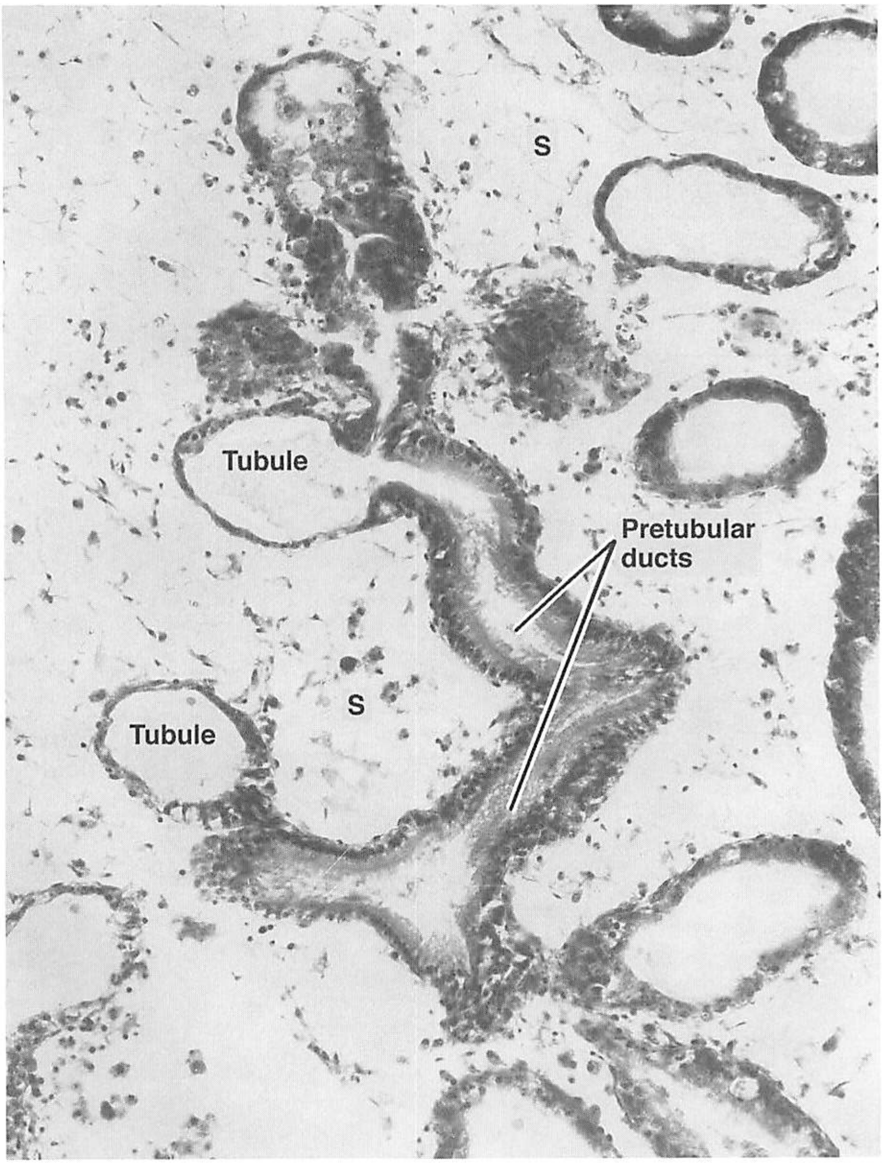

Figure 31. Section of pretubular duct branching and terminating in tubules of digestive gland. There is dense ciliation in the pretubular duct and absence of cilia in the tubule. Tissue from winter-collected oyster in which digestive tubules are in non-feeding condition (compare with Fig. 32). [S] hemolymph sinus of digestive gland. HFW = 300 µm.

grouped around hemolymph sinuses, penetrate into hemolymph sinuses of the adductor muscle, and are filled with small (diameter 0.3 µm), yellowish granules. The pericardial gland is also present as so-called "brown cells" associated with the atria. Brown cells are found throughout the oyster body but are concentrated in the atria. The structure and function of brown cells as well as renal filtration and physiology are discussed by Eble in Chapter 7.

The pericardial coelom is connected to the kidney (that lies in another part of the coelom, the renocoel), via the renopericardial canal (Figs. 33, 34). The

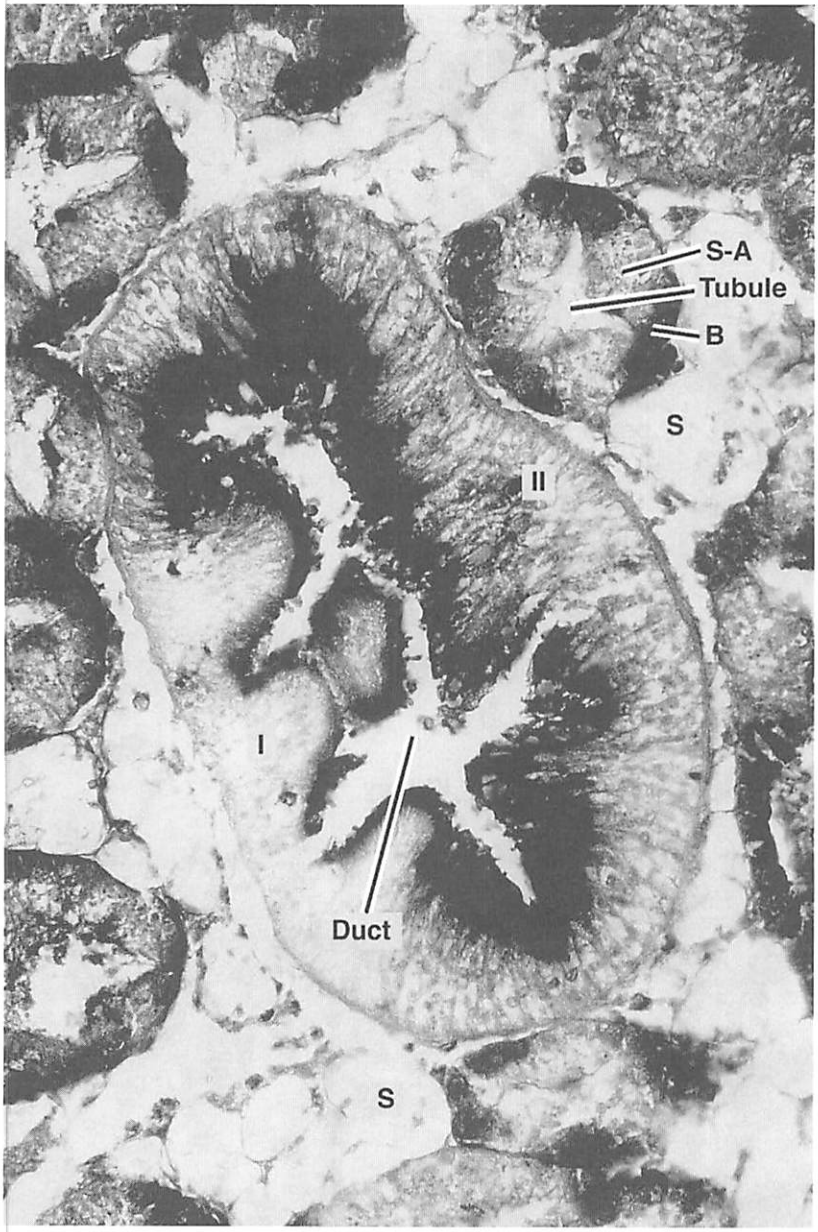

Figure 32. Transverse section of large secondary duct of digestive gland showing distribution of alkaline phosphatase. There is greater activity of enzyme in Type II cells [II] than in Type I cells [I]. Note intense enzyme activity in basiphil cells [B] of digestive gland tubule and absence of activity in tubule secretory-absorptive cells [S-A]. Tissue from actively feeding oyster (compare with Fig. 31). [S] hemolymph sinus of digestive gland. HFW = 70 µm.

kidney lies ventral to the heart and adductor muscle and empties into the epibranchial chamber by means of the renopore (Fig. 35).

Renopericardial Canal

The renopericardial canal originates as a wide funnel or nephrostome, in the ventral floor of the pericardium; the epithelium of the nephrostome is simple, tall columnar with long cilia, in striking contrast to the pericardium with which it is contiguous (Fig. 33).

My sections show that the renopericardial canal is lined with a simple, low columnar ciliated epithelium; each cell has about 7 to 10 long cilia (30 to 32 µm) (Figs. 33, 34). Cells of the renopericardial canal

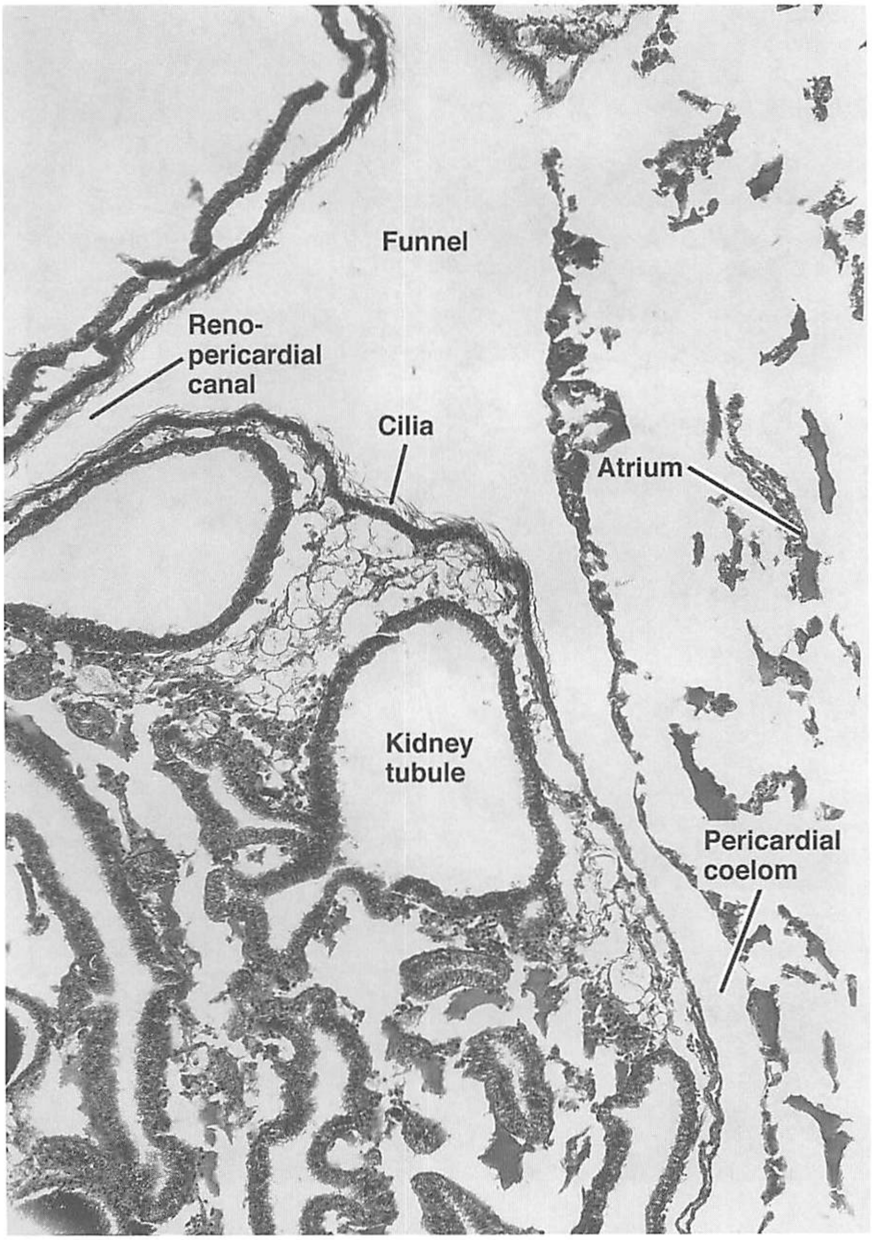

Figure 33. Section through pericardial coelom to show origin of the funnel or nephrostome leading to the renopericardial canal. HFW = 290 µm.

are filled with an assortment of granules and are bathed by prominent hemolymph sinuses (Figs. 33, 34). The renopericardial canal ends at the renal pore (Fig. 35) and does not connect to the main body of the kidney. Many eosinophilic granular cells are located in distal regions of the renopericardial canal near its connection with the renopore; further, cilia in this region become progressively shorter as the canal approaches the renopore (Fig. 34).

Kidney

The kidney is a compound, tubular gland that lies in a large hemolymph sinus, the renal sinus. The anterior limbs of the kidney lie anterior to the heart,

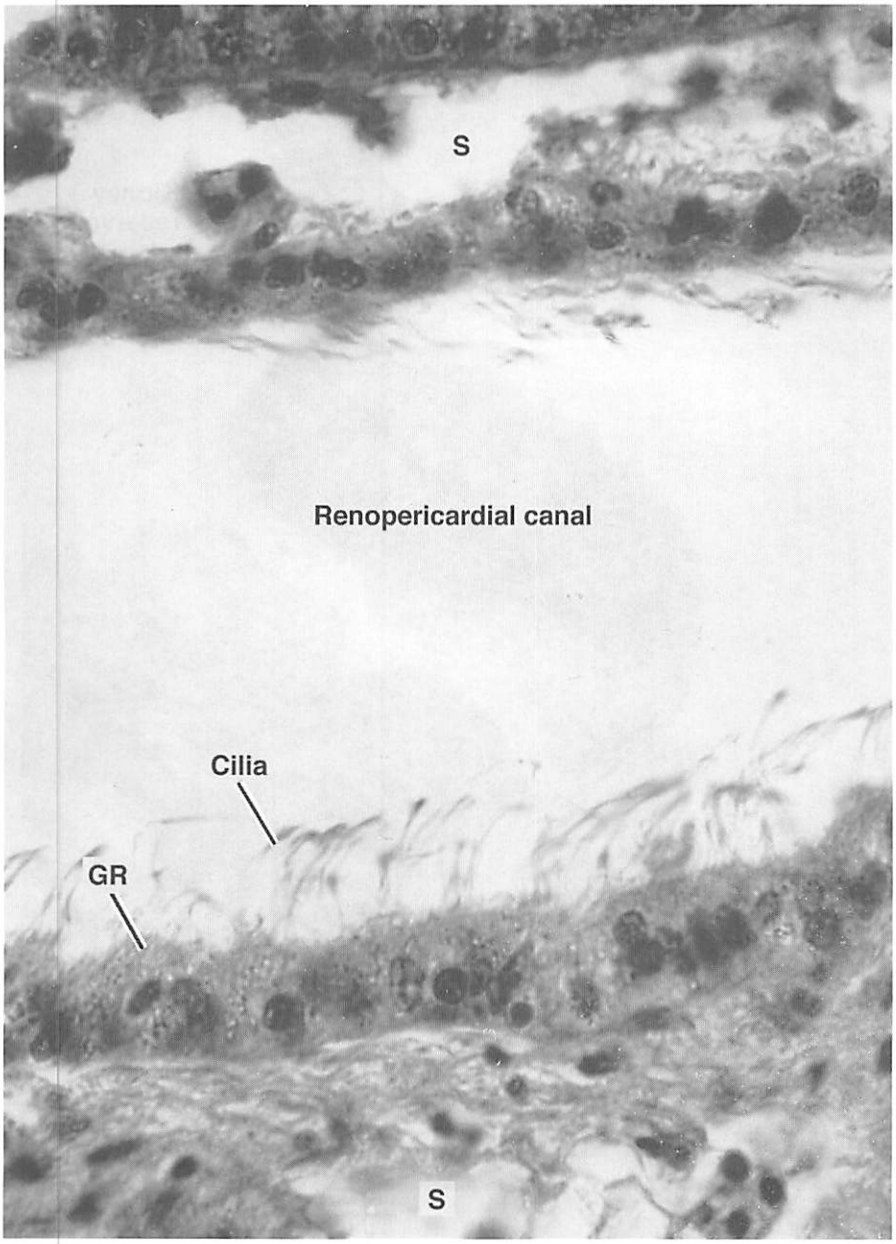

Figure 34. Longitudinal section through renopericardial canal. Long cilia and granular cytoplasm of epithelial cells [GR] of the canal are visible. [S] prominent subepithelial hemolymph sinuses of the renopericardial canal. HFW = 79 µm.

embedded in Leydig cell connective tissue just under the mantle; the main part of the kidney lies under the heart and adductor muscle (Fig. 36), extending the entire width of the animal. I found that the renal tubular epithelium is simple and columnar with cells vesiculated at the luminal surface (Fig. 37; this agrees with Fig. 251 in Galtsoff 1964); possibly, cellular secretions are discharged into the lumen by means of exocytosis or apocrine secretion. Cells are about 20 to 25 µm long by 5.5 µm wide; slightly smaller cells

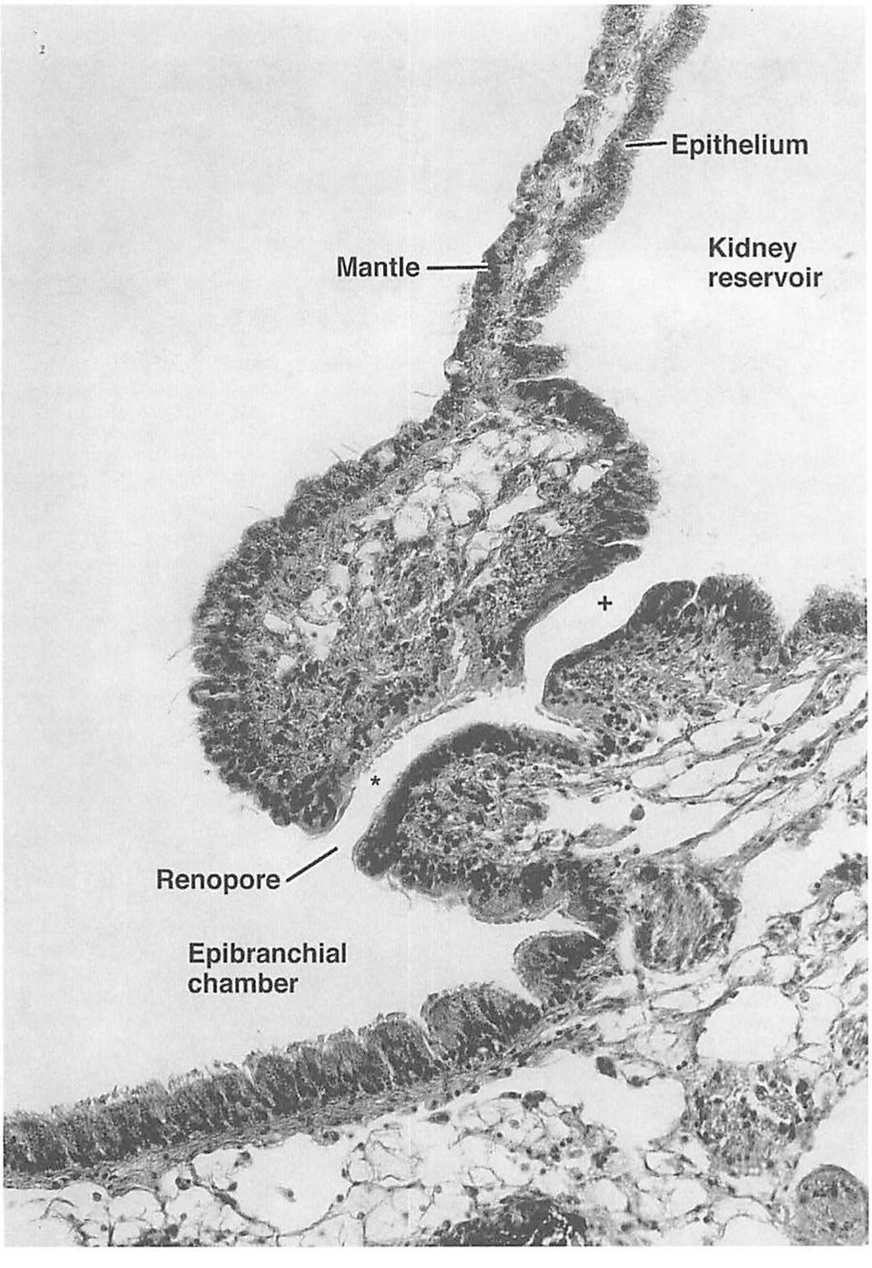

Figure 35. Section through the renopore. Epithelium of outer half of the pore [*] is contiguous with the epibranchial chamber and is ciliated whereas the inner half of the renal pore [+] contiguous with the kidney reservoir is not. HFW = 149 µm.

are found in the anterior kidney. Nuclei average 4.5 µm in diameter and are located from the middle of the cell to an area just under the apical vesicle (Fig. 37); nuclei possess a prominent eccentric nucleolus, and chromatin is restricted to two or three small masses. Scanning electron microscopy reveals long strands of what appear to be cilia intertwined about the vesiculated portions of the renal cells (Fig. 38). Apical vesicles of many renal tubule cells appear collapsed (Fig. 38); this may reflect their state during discharge of vesicle contents or may be a fixation artifact. Renal tubules are suspended from the adductor muscle and connected to each other by slender strands of connective tissue (Figs. 36, 39); renal tubules are bathed by the large renal hemolymph sinus. Because the renal sinus is contiguous with the hemolymph sinus of the adductor muscle, it allows many of the renal tubules to extend dorsally into hemolymph sinuses within the adductor muscle.

Large kidney reservoirs, translucent swellings on each side of the pyloric process, are located bilaterally just under the anterior part of the adductor muscle. My sections show that epithelial cells of the kidney reservoir are simple columnar and average 14 to 16 µm in height by 7 µm wide; cells are vesiculated at their luminal surface. Nuclei are spherical and displaced towards the base of the cell and are filled with large, irregular clumps of chromatin; no nucleoli can

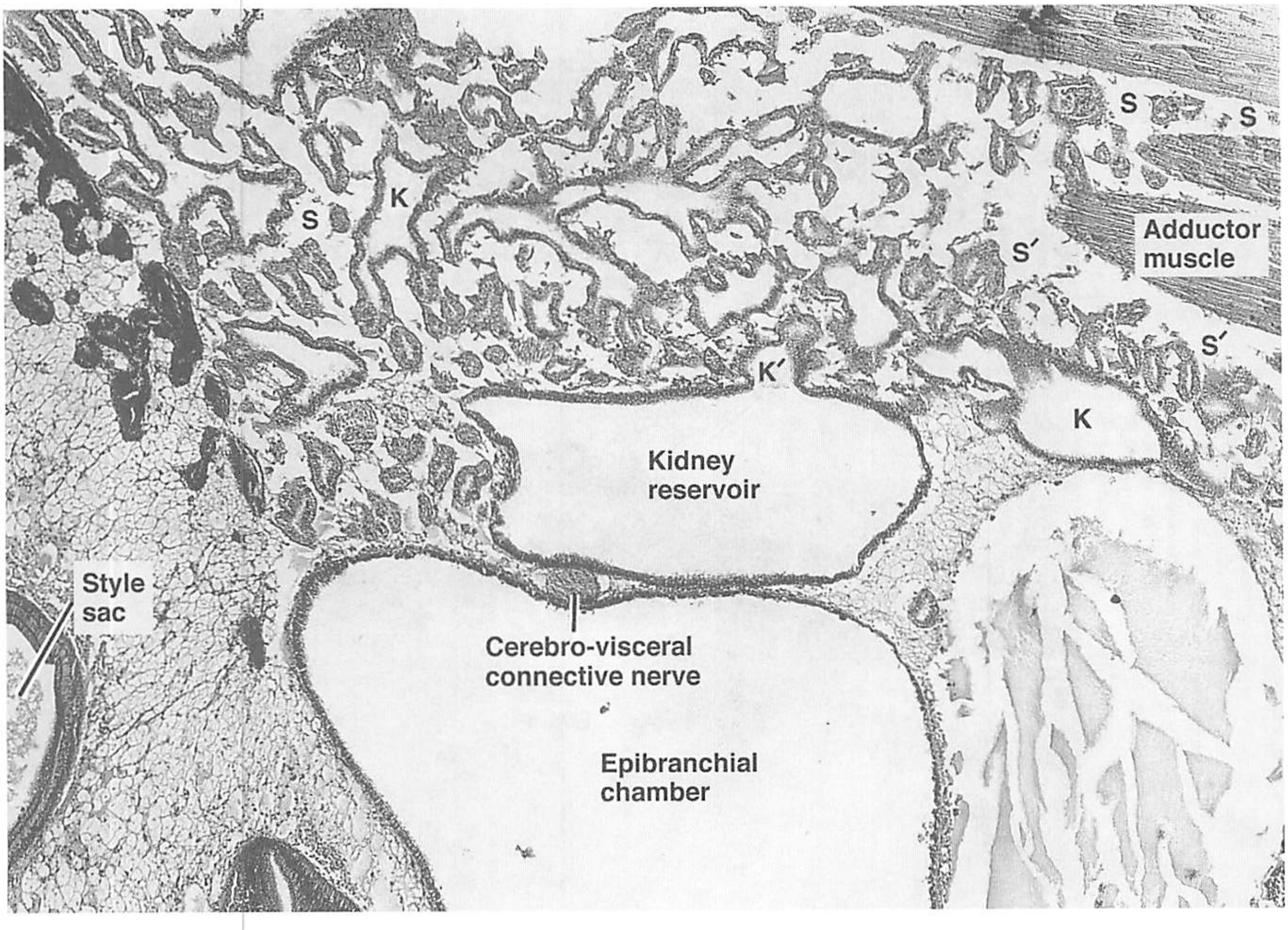

Figure 36. Section through kidney [K] at level of adductor muscle. One kidney tubule [K′] can be observed emptying directly into the kidney reservoir. Note that hemolymph sinuses of the adductor muscle [S] are contiguous with renal hemolymph sinuses [S′]. HFW = 1.5 mm.

be discerned. The cytoplasm is filled with large eosinophilic granules (diameter 1 µm). Cells of the kidney reservoir resemble renal tubular cells but the difference in nuclear cytology (no nucleoli) makes them a distinct cell type. Galtsoff (1964) does not mention this difference but figures it correctly (his Fig. 252). A prominent layer of smooth muscle is located just under the basement membrane of the reservoir (Galtsoff 1964).

Each reservoir empties into the epibranchial chamber via the renopore (Fig. 35). The epithelium of the renopore is derived from two cell types: the reservoir epithelium lines the inside of the pore whereas the outside and middle are lined with a simple, cil-

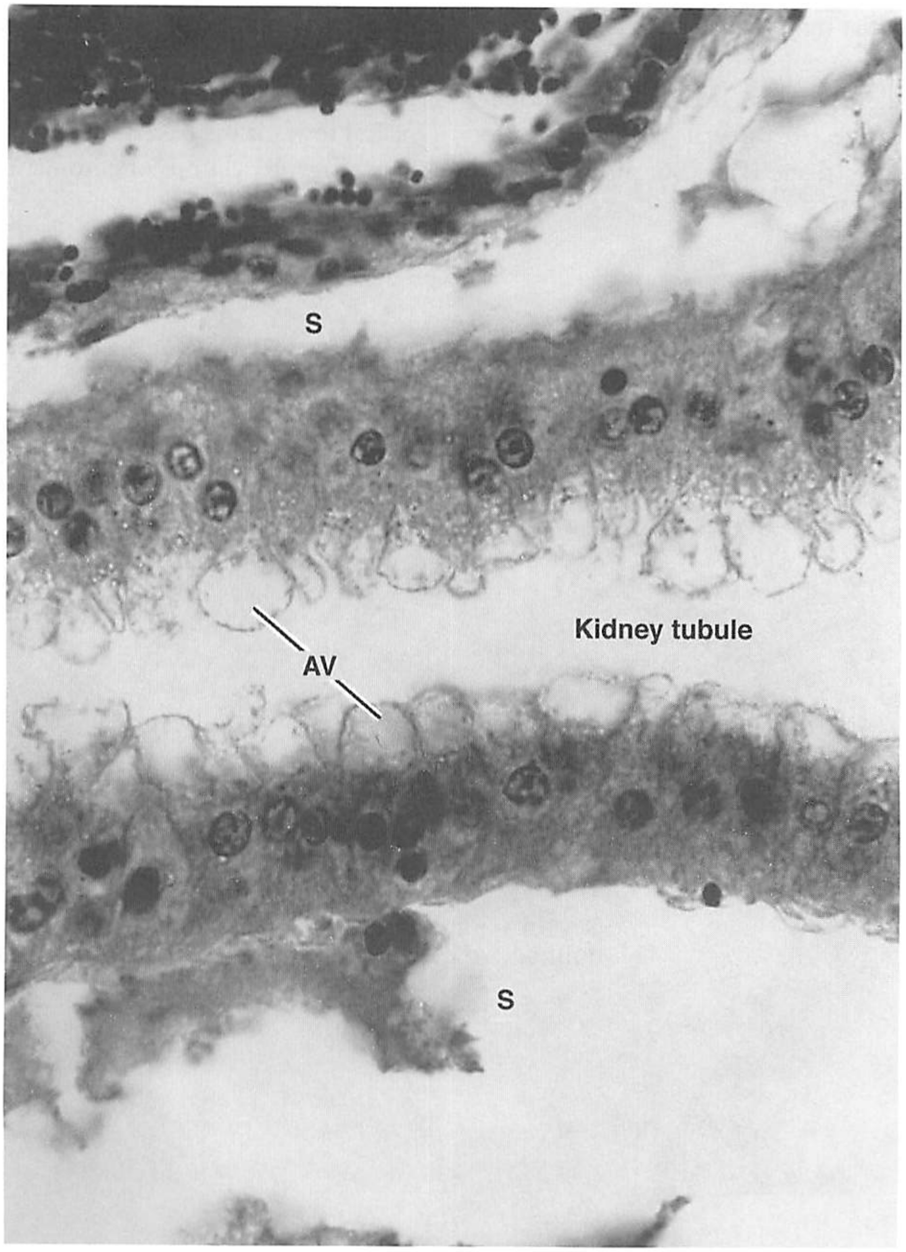

Figure 37. Longitudinal section of kidney tubule; note large apical vesicles [AV] of renal epithelial cells; [S] prominent renal hemolymph sinuses bathe kidney tubules. HFW = 78 µm.

iated columnar epithelium contiguous with the epithelium of the epibranchial chamber (Fig. 35). Morse (1987) presents a comprehensive discussion of the structure and function of the bivalve pericardial gland and kidney.

REPRODUCTIVE SYSTEM

Anatomy

The gonad is situated in the visceral mass between the digestive gland and the mantle. It originates at the region of the esophagus, extending the length of the visceral mass to the pericardial area where it bifurcates into a dorsal lobe that extends towards the rectum and a ventral lobe that extends to the posterior extension of the visceral mass. During the dormant phase the gonad cannot be distinguished grossly from the surrounding vesicular connective tissue. Leydig cells in the tissues surrounding the gonad serve as the site of storage of glycogen that is then mobilized to provide energy for gametogenesis (see Thompson et al., Chapter 9). As the eastern oyster begins to develop sexually, however, the gonad increases in size until it reaches a maximum in the ripe phase that precedes spawning. The primordial germ cells of the eastern oyster larva originate in paired mesodermal bands but all traces of this bilateral condition are lost when gonadal cells proliferate on both sides of the body and meet and fuse in the dorsal area.

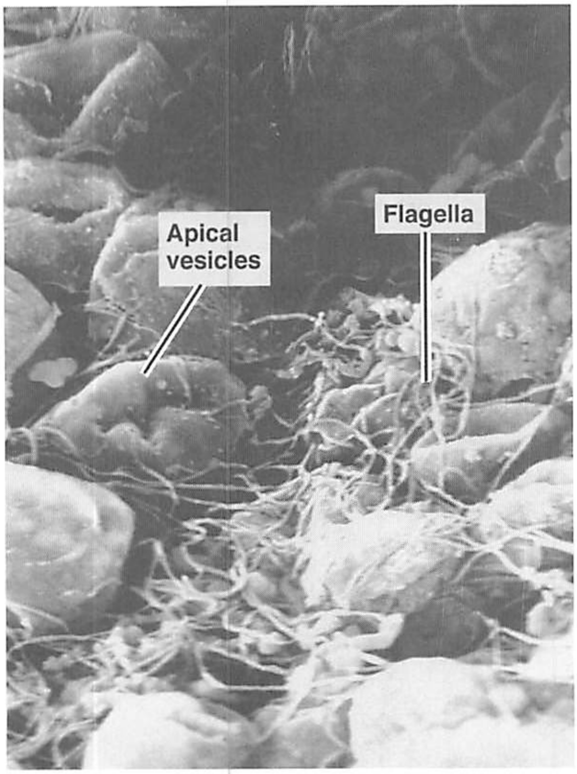

Figure 38. Scanning electron micrograph of kidney. Note collapsed condition of apical vesicles of renal tubule cells and structures that resemble flagella between renal cells. × 4000.

Histology

In most eastern oysters, primordial gonadal tissues, consisting of branching tubules, develop 8 to 12 weeks after settlement of the spat. The germinal epithelium consists initially of undifferentiated cells that will develop into oocytes and spermatocytes by the end of the first year (Galtsoff 1964). *Crassostrea virginica* is protandric and, as such, usually spawns as a male the first year. There seems to be, however, an influence of water temperature and other environmental factors in determining sex during the first spawning season; Coe (1936) reported that the proportion of *C. virginica* females to 100 males varied at different locations along the U.S. east coast: Apalachicola, FL–7.1; Beaufort, NC–37.1 to 48.8; Delaware Bay, NJ–41.9; West Sayville, NY–31.2; New Haven Harbor, CT–3.3 to 12.5 and at Milford, CT–5.6 to 24 (see Thompson et al., Chapter 9).

Indifferent Stage

After completion of spawning and resorption of undischarged eggs and sperm, the gonad enters the indifferent phase. Follicles become very small and widely separated and contain only indifferent cells; sex cannot be distinguished at this time.

Winter Inactive Stage

Gonadal follicles are reduced in size and number and grouped near genital ducts; follicles are bordered by and connected to each other by slender strands of connective tissue consisting of collagenous and reticular fibers which, in turn, are supported by Leydig cells.

Oogonia develop from indifferent cells and are easily distinguished by their large nuclei and granular cytoplasm; these, plus remaining indifferent cells, constitute the female germinal epithelium at this stage. Males may be recognized by their developing spermatogonia nested among indifferent cells; occasionally, a few oogonia may be found in the germinal epithelium, an indicator of the potential bisexual nature of the oyster gonad.

Genital ducts are evenly distributed around the periphery of the entire gonadal area. Their convex, ciliated, epithelial margins are bound to collagenous

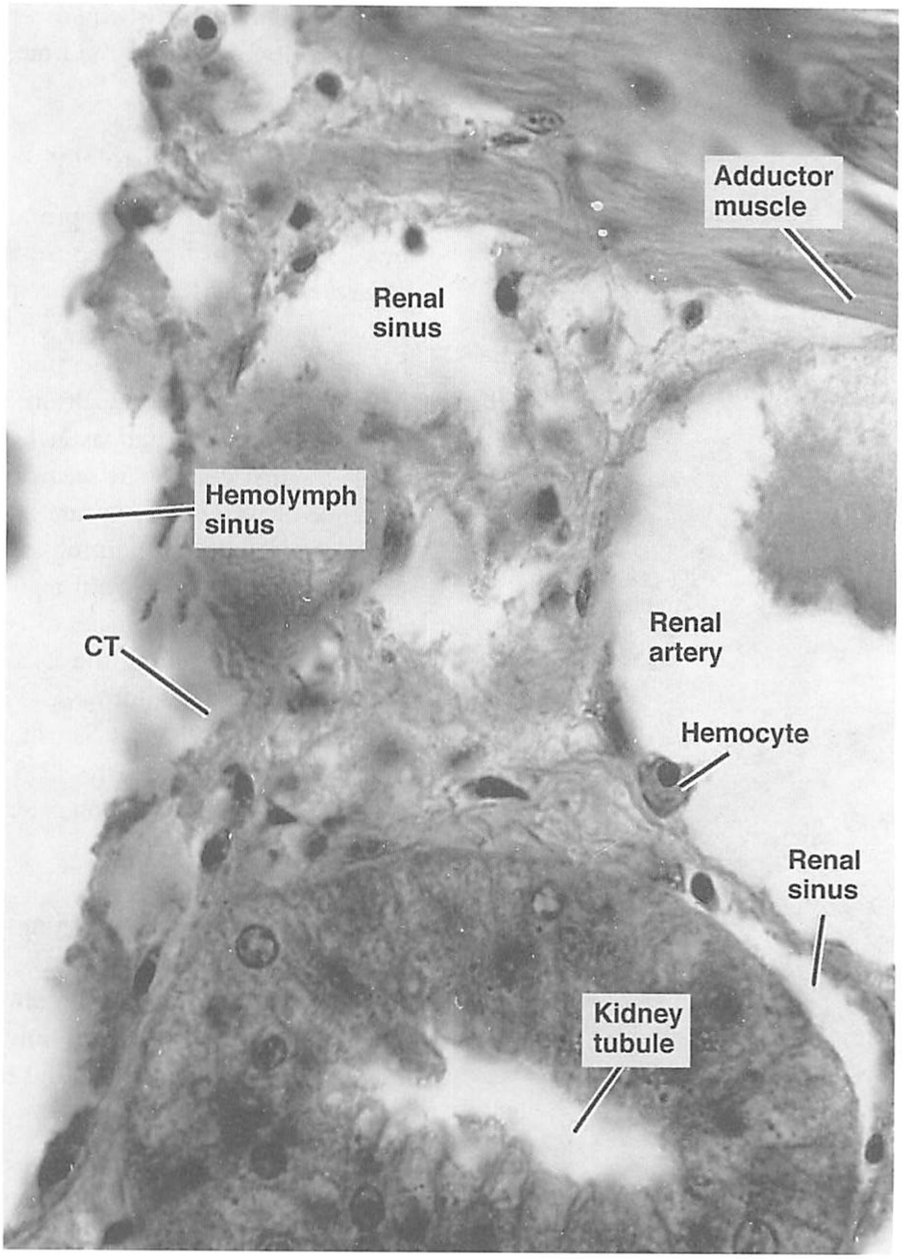

Figure 39. Collagenous connective tissue [CT] suspends kidney tubules from adductor muscle and binds together all kidney tubules. HFW = 78 µm.

connective tissue that separates the mantle from the visceral mass. Epithelia of genital ducts consist of (1) simple, ciliated cuboidal cells interspersed with mucous cells lining the peripheral portion of the duct and (2) germinal epithelium lining the medial portion (Kennedy and Battle 1964; Fig. 40).

Sexual Differentiation Stage

Ovarian follicles enlarge, anastomose, and extensively invade the surrounding vesicular connective tissue (Fig. 40). Oogonia that comprise the female germinal epithelium begin to divide actively; these cells may be recognized by their compact, densely staining, ovoid nucleus and narrow rim of finely granular, basiphilic cytoplasm (Fig. 40). As oogonia differentiate into primary oocytes, the nucleus enlarges into a spherical, vesicular type with chromosomes usually in the leptotene stage of early prophase. As the volume of the primary oocyte increases, the cytoplasm becomes more coarsely granular and less basiphilic, even slightly acidophilic (Fig. 40) indicative of yolk deposition. Kennedy and Battle (1964) discuss and figure two types of nucleoli in growing primary oocytes: type K (karyosome), so designated by Kobayashi (1954) for *Ostrea laperousii*, takes the form of a crescent and stains black with Heidenhain's iron hematoxylin and slightly pink with Feulgen; type P (plasmasome) is spherical and stains diffuse grey with Heidenhain's iron hematoxylin and is negative with Feulgen. In young primary oocytes, the two types of nucleoli are separated in the nucleus but become closely applied in mature primary oocytes.

During the sexual differentiation stage in males, follicles enlarge, anastomose, and invade the interfollicular connective tissue consisting of Leydig cells (Fig. 28). Spermatogonia divide rapidly and constitute the chief cell type of the germinal epithelium in early sexual differentiation stages (Fig. 41). Another cell type can be found in the germinal epithelium of the male follicle: it has a hyaline cytoplasm and ranges in diameter from 9 to 12 µm; nuclei of these cells are usually interphasic and measure 4.5 to 6.3 µm in diameter. It has been postulated that these cells are potential oogonia (Loosanoff 1942; Kennedy and Battle 1964).

Nuclei of spermatogonia measure 3.2 to 4.1 µm but cytoplasmic boundaries are difficult to ascertain (Coe 1932). As spermatogonia differentiate into primary spermatocytes, the nucleus decreases slightly in size (2.5 to 2.9 µm) and usually is seen in leptotene stage of prophase I (Fig. 41). Kennedy and Battle (1964) noticed this and postulated that metaphase I, anaphase I, and telophase I stages were, in all probability, of short duration.

Nuclei of secondary spermatocytes are smaller than primary spermatocytes (1.6 to 2.0 µm) and stain more densely with basic stains. Spermatids stain more densely than either of the two preceding stages and have a range of 1.5 to 1.7 µm in diameter (Fig. 41). Heads of sperm are located in juxtaposition to spermatids and stain most intensely of all stages with basic stains; heads are ovoid to triangular, with a range of 1.3 to 1.5 µm; sperm tails are acidophilic and project into the lumen of follicles and ducts (Fig. 41; Coe 1932).

Spawning and Post-Spawning Stages

Female follicles from which some of the eggs have been discharged begin to shrink. Oocytes still attached to germinal epithelia appear normal in all respects; oocytes free in lumina of follicles show breakdown of germinal vesicles (nuclei) and appearance of spindles preparatory to the first meiotic division (Fig. 42). Kennedy and Battle (1964) induced spawning in *C. virginica* and fixed oysters 5 min after first ejection of eggs; they found that most primary oocytes free in lumina of follicles as well as those in the epibranchial chamber were in various phases of meiosis I. They concluded that meiosis is triggered by rupture of the primary oocyte from the germinal epithelium of the follicle.

After completion of the spawning season, follicles shrink markedly and contain few oocytes, some still attached to germinal epithelia. Invasion of hemolymph sinuses contiguous to follicles by masses of hemocytes is obvious; subsequently, hemocytes invade atretic follicles and resorb unspawned oocytes. Leydig cells proliferate within the interfollicular area and then serve as glycogen-storage cells (Fig. 43).

Central portions of male follicles are usually empty during spawning due to discharge of sperm; germinal epithelia still show all stages of spermatogenesis and spermiogenesis. After completion of the spawning season, follicles begin to shrink and become atretic. As with females, hemocytes accumulate in hemolymph sinuses supplying follicles before invading follicles and resorbing residual sperm and spermatocytes. Leydig-cell connective tissue proliferates within interfollicular areas and becomes the principal cell type during this phase.

Fine Structure

Sperm of *C. virginica* are about 40 μm long with the head and middle piece together measuring about 2 μm. The head, middle piece, and tail are enclosed

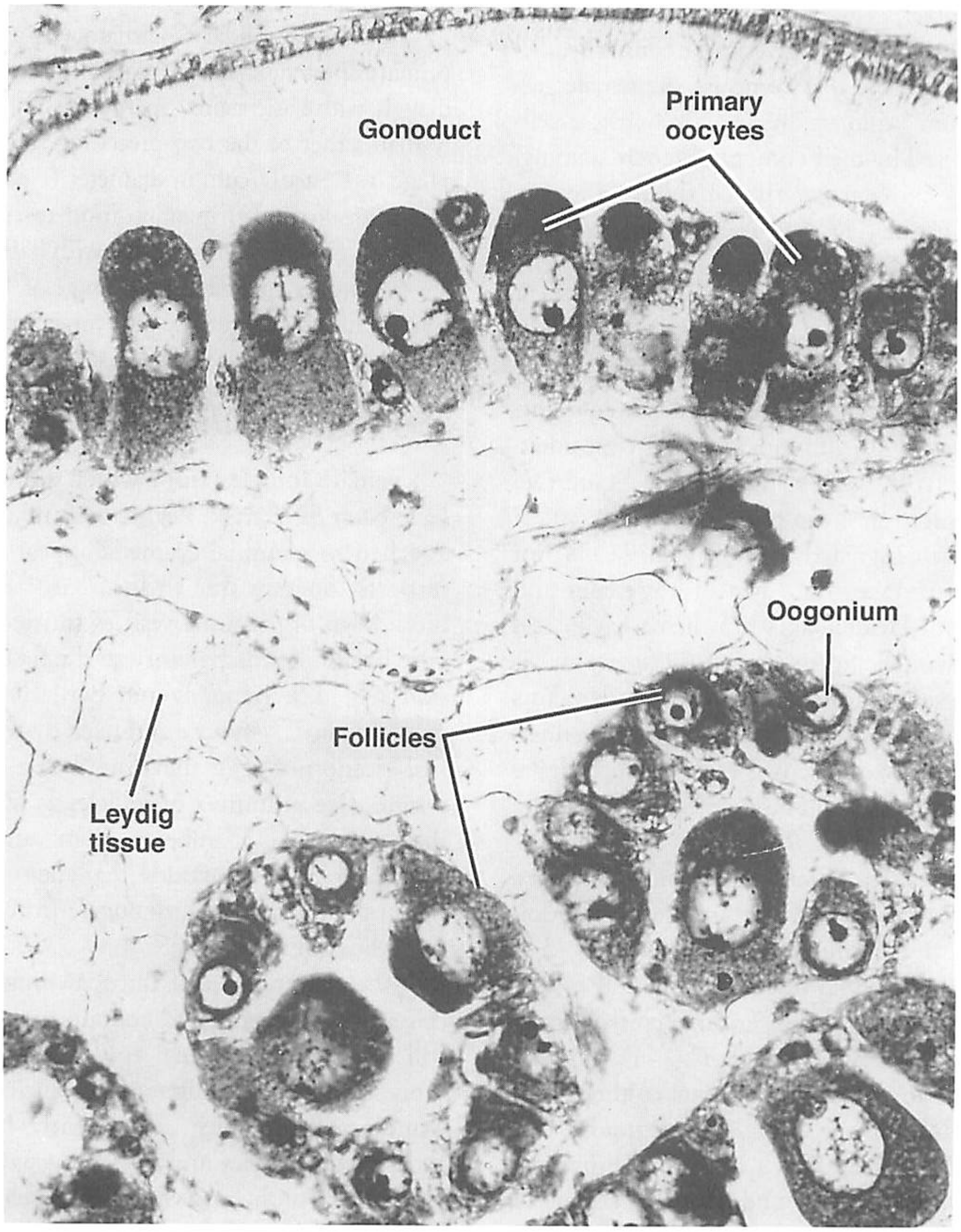

Figure 40. Developing primary oocytes in growing follicles in the ovary. Oocytes at top of figure protrude into the gonoduct. HFW = 215 μm.

by a plasma membrane. The head consists of the nucleus, the axial body, the axial rod, and the acrosome. The nucleus consists of thin filaments of DNA and occupies most of the roughly triangular head. It is invaginated at its anterior extremity to accommodate the axial body in the middle of which is the axial rod (Galtsoff 1964); the axial body extends from the base of the nuclear invagination to the inner surface of the apex of the acrosome (Fig. 44). Tilney (1976) reported large quantities of G-actin stored in a cup-shaped organelle just posterior to the acrosome of the sea cucumber, *Thyone briareus*. G-actin units are mobilized from this organelle and rapidly added to the plus ends of actin microfilaments of the acrosome process. The axial body of eastern oyster sperm may be similar in function to the cup-shaped organelle of *T. briareus*, i.e., a repository of G-actin molecules to supply materials for the acrosomal process during the initial attachment of sperm to eggs. The nucleus of eastern oyster sperm is capped by the acrosome whose posterior rim slightly depresses the anterior portion of the nucleus (Fig. 44). The anterior extremity of the acrosome ends in a peak formed by the sperm plasma membrane; a single apical vesicle has been observed between the plasmalemma and the acrosome (Daniels et al. 1971).

The middle piece of each sperm consists of four laterally arranged mitochondia enclosing two centrioles. Mitochondria are almost as long as the nucleus and contain many convoluted cristae (Fig. 44). The proximal and distal centrioles each measure 250 nm in length by 250 nm in width and are positioned at right angles to each other. Each centriole contains nine sets of three microtubules embedded in an electron-opaque material. A small centriolar satellite, when present, is located between the subnuclear fossa, an invagination in the posterior medial surface of the nuclear envelope, and the proximal centriole. The proximal centriole is positioned at right angles to the longitudinally oriented distal centriole; the latter is continuous with the microtubules of the flagellum (Daniels et al. 1971).

The basal plate of the sperm tail connects to the distal centriole in the middle piece (Galtsoff 1964).

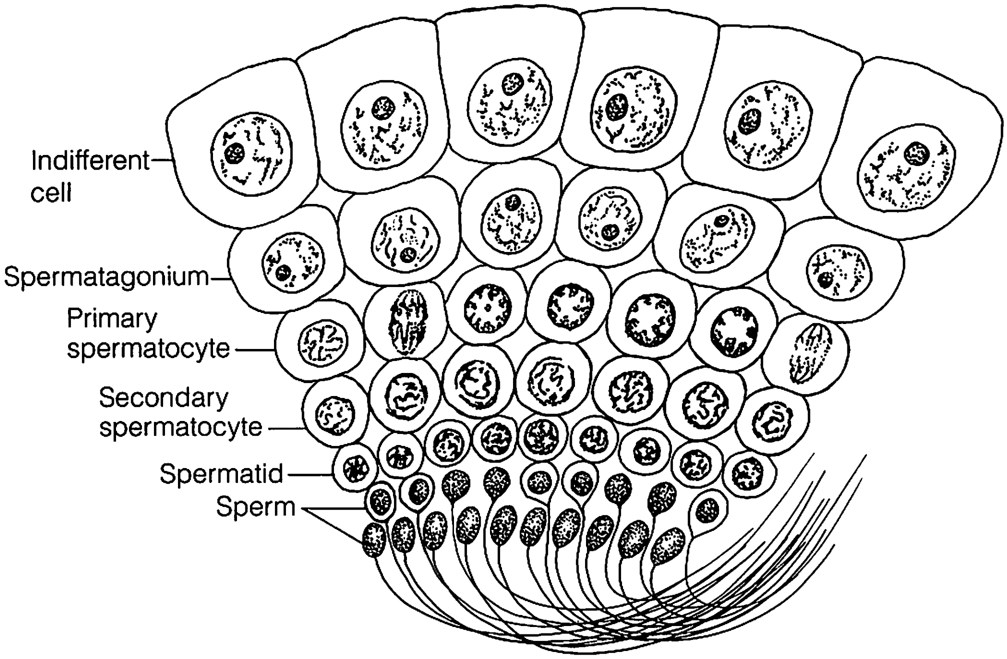

Figure 41. Sketch of mature testes showing indifferent cells with prominent nucleolus, spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and sperm. HFW = 70 µm. Based on Coe (1932) and Galtsoff (1964).

The fine structure of the basal plate consists of nine peripheral electron-opaque masses, each connecting to a doublet set of microtubules by an electron-opaque strand. Doublet microtubules are situated just peripheral to an inner ring or sleeve; the latter extends down to the level of the origin of the central doublets in the ampulla (Daniels et al. 1971).

The tail of the sperm consists of a long flagellum that tapers to a narrow end piece. The fine structure of the body of the flagellum is typical of all flagella:

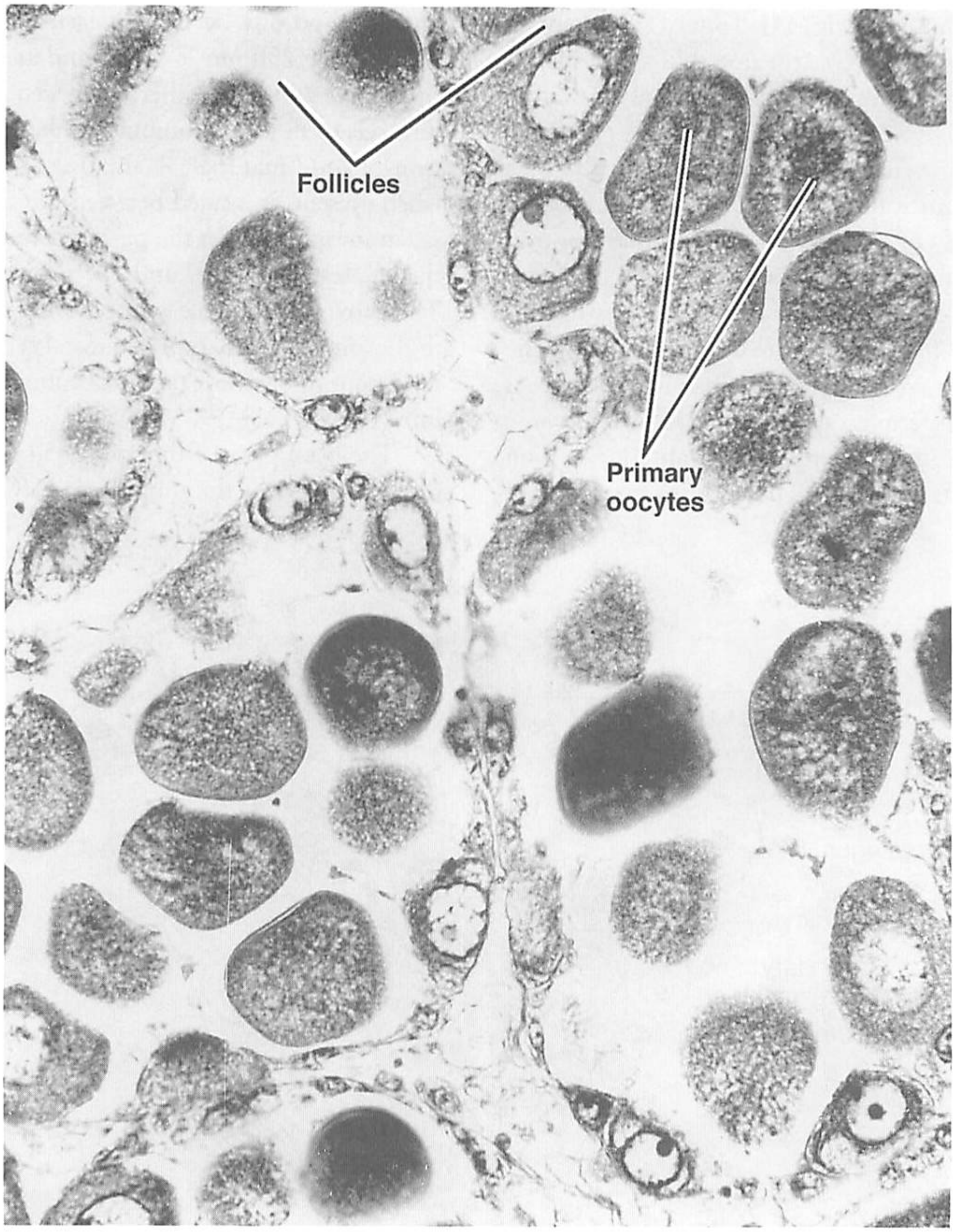

Figure 42. Partially spawned female. Note that most primary oocytes free in lumina of follicles show breakdown of germinal vesicles (nuclei) before entering meiosis I. HFW = 215 µm.

nine pairs of doublet microtubules surround and are connected to a central axial pair of microtubules by radial spokes. Each peripheral pair of microtubules has two dynein arms extending from the A microtubule of one pair to the B microtubule of the adjacent pair. The fine structure of the tail end piece has only nine peripheral A microtubules that connect to the central pair by radial spokes. Dynein arms in this region extend between A microtubules only (Daniels et al. 1971).

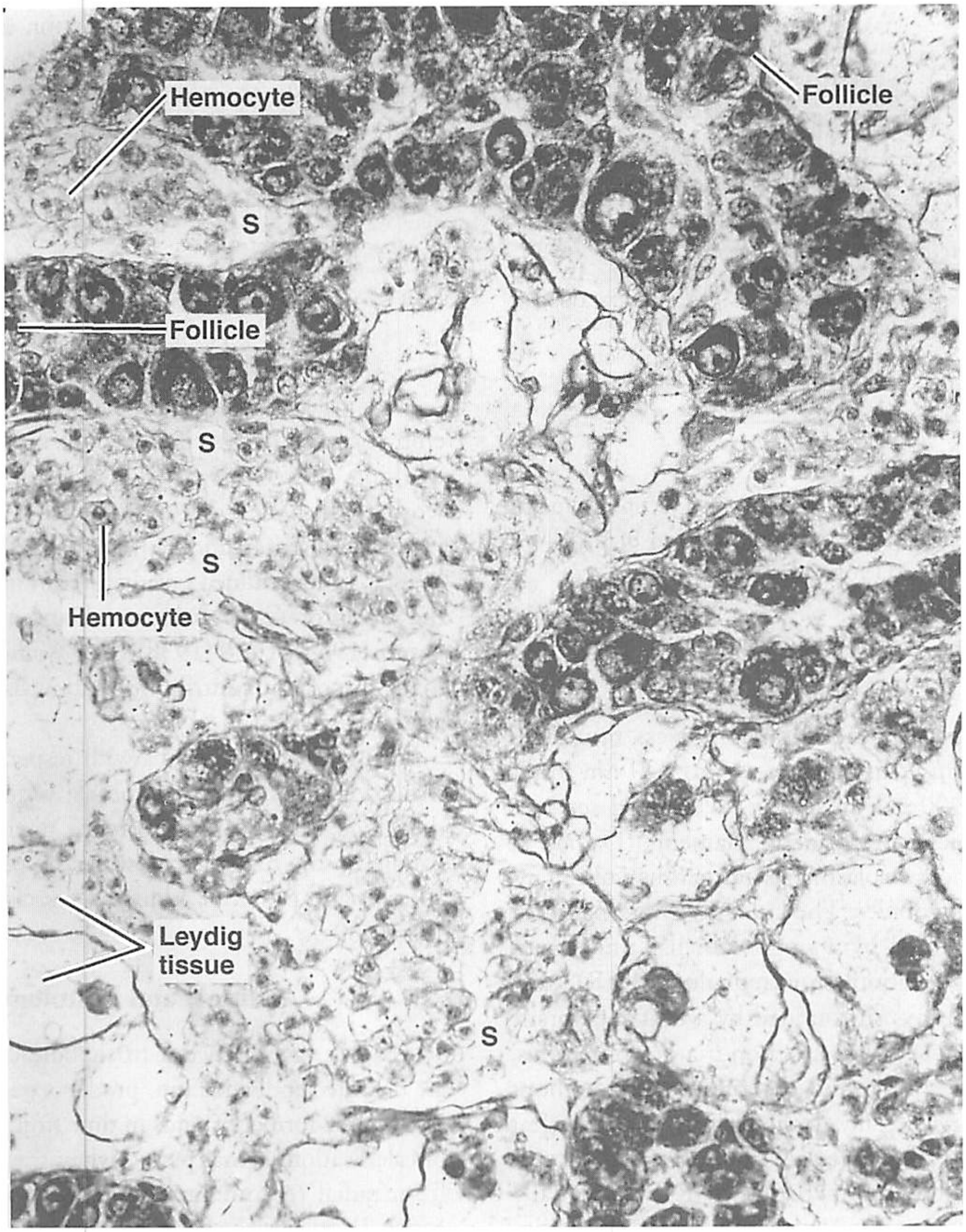

Figure 43. Appearance of ovary after completion of spawning. Vesicular Leydig connective tissue begins to proliferate within interfollicular areas as follicles shrink. Hemocytes mass in follicular hemolymph sinuses [S] before invading follicles and resorbing residual oocytes. HFW = 215 µm.

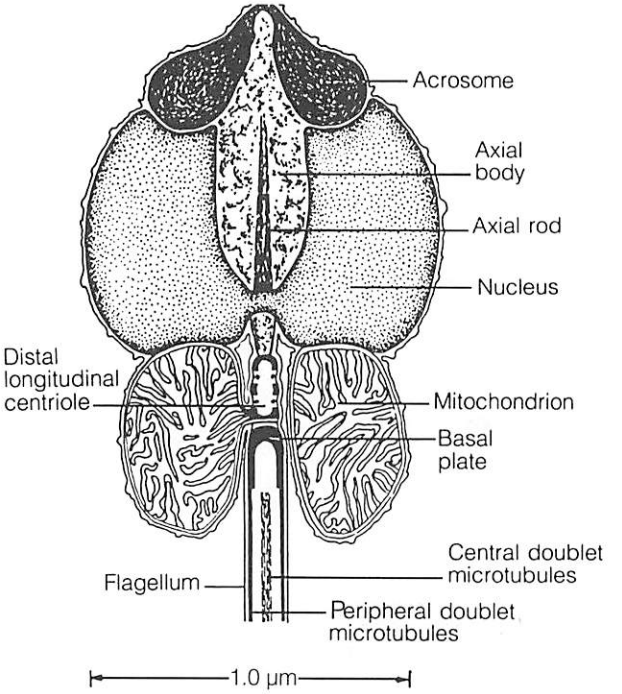

Figure 44. Fine structure of longitudinal section of sperm head, middle piece, and proximal portion of flagellum (tail). From Galtsoff (1964).

Oocytes

Oocyte plasma membranes possess microvilli 200 to 350 nm apart; they are 85 to 120 nm in diameter and 900 nm in length. Well-fixed sections show the typical core of actin filaments (Daniels et al. 1973). The cytoplasm has numerous yolk granules and lipid globules. The latter are either naked or closely surrounded by a single lamellar unit membrane of rough endoplasmic reticulum (RER). Yolk granules are always surrounded by a unit membrane (Daniels et al. 1973). Mitochondria are numerous, possess many cristae, and are scattered throughout the cytoplasm especially in the vicinity of the nuclear envelope. Free ribosomes are abundant and distributed throughout the cytoplasm; RER is usually found in bundles or enveloping lipid globules as single lamellae. Golgi bodies consist of 4 to 5 flattened membranes with enlarged vesicles forming the outer edges; they are not abundant (Daniels et al. 1973).

The nucleus is 25 to 40 µm in diameter and contained by a nuclear envelope with numerous pores; the latter consist of eight subannuli and a central granule, which may simply represent material either entering or leaving the nucleus through the pore. The nucleolus is excentric and ultracentrifugation (85,000 g; 0.5 h) demonstrates that it consists of two parts, a less dense granular portion and a heavier, compact, and more electron opaque part. These two parts probably correspond to the P (plasmasome) and K (karyosome) components of the oocyte nucleolus designated by Kobayashi (1954) and discussed by Kennedy and Battle (1964).

LARVAL STAGES

Development

Complete descriptions of cell lineage and early embryogenesis of oysters were made by Brooks (1880) working with *C. virginica* and Horst (1883-1884) working with *O. edulis.* Prytherch (1934), Galtsoff (1964), Carriker and Palmer (1979), and Elston (1980a, b) have added greatly to our knowledge about the larvae of *C. virginica* and Dantan (1916), Erdmann (1935), Cole (1938), and Waller (1981) have made important contributions about larval histology and development in *O. edulis.*

I use directional terms with respect to the larval shell: dorsal is towards the hinge; ventral away from the hinge; anterior and posterior refer to directions parallel to the hinge and toward the positions of the anterior and posterior adductor muscles (Fig. 45; Elston 1980a).

Anatomy and Histology

Larval stages between trocophore and pediveliger are broadly subdivided into prodissoconch I and II (P-I, P-II); the former extends in time from the beginning of calcification to that period when shell striae change from radial to commarginal (concentric). Prodissoconch II stages are characterized by prominent commarginal shell growth ridges together with the origin of the posterodorsal shell notch and its spiral growth tract (Carriker and Palmer 1979; Waller 1981).

Details of the larval shell (both prodissoconch I and II) including development, morphology, and fine structure are described by Carriker in Chapter 3.

Visceral Cavity

The larval visceral cavity is a fluid-filled chamber bounded laterally and dorsally by the mantle and ventrally by the velum. It contains the digestive organs as well as free cells; bundles of muscle fibers run through the visceral cavity to insert on the velum and foot (Fig. 45). The visceral cavity has many functions: it provides a fluid milieu for free phagocytic cells, provides space for the rapid growth of the organs of the digestive system, allows room for the rapid contraction of the velar and foot retractor muscles, and is responsible for the continuous expansion and contraction of digestive gland lobes by hydrostatic pressures. The visceral cavity is separated from the mantle cavity by the posterior visceral cavity membrane.

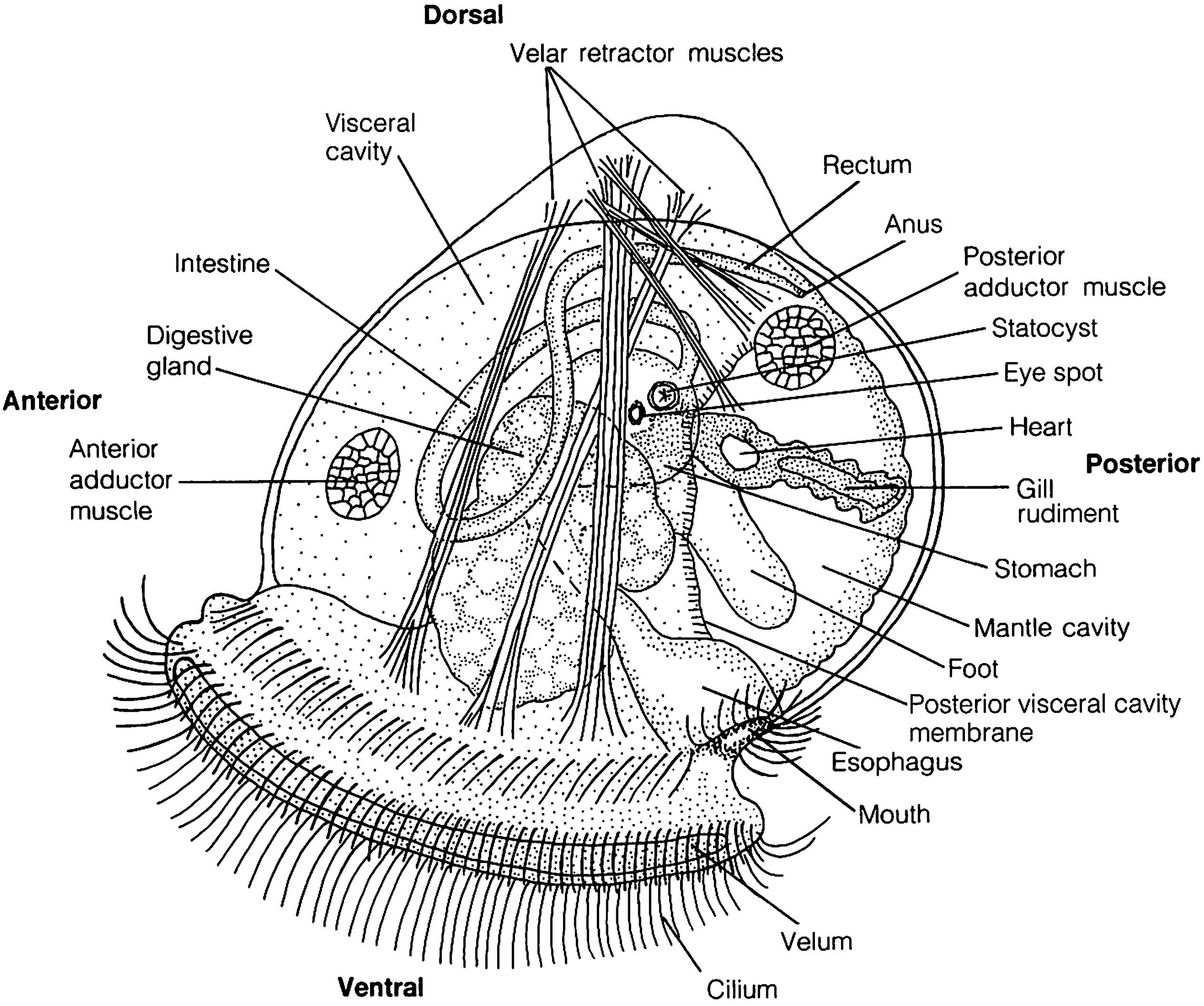

Figure 45. Diagrammatic representation of prodissoconch II larva viewed from the left side. × 380. Redrawn from Galtsoff (1964) and Elston (1980a).

Velum

The velum is the principal swimming and feeding organ of the larva; it consists of outer and inner peripheral lobes (Fig. 46) enclosing a food groove (see Newell and Langdon, Chapter 5, for details of feeding in larvae). The inner peripheral lobe contains densely ciliated columnar cells that form the principal ciliary ring (Elston 1980a); cilia are large with deep cytoplasmic rootlets in the cells. Cells of the inner peripheral lobe form a thin, sparsely ciliated cell layer as they extend medially to form the base of the velar cup; a ring of cilia from these cells forms the inner ciliary ring, and the central cells form the central ciliary tuft (Elston 1980a; Fig. 46).

Mantle

The left and right mantle folds are usually one cell layer thick and each lies in contact with the medial aspect of its corresponding valve (Fig. 45). Cells are usually flattened with dense, granular cytoplasm containing much rough endoplasmic reticulum. Near its peripheral margins, the mantle increases to two to four cells in thickness and consists of two folds between which the periostracum emerges (Elston 1980a).

Foot

The foot, especially in late P-II stages, is a large, ciliated organ whose base lies in the visceral cavity while the bulk of the organ projects into the mantle cavity (Fig. 45). The base is formed by secretory cells of the byssal gland that connect to paired byssal ducts; the latter open into the mantle cavity on the posterior aspect of the foot. Epithelial tissues of the foot bordering the mantle cavity consist of cuboidal cells with large nuclei, apical mitochondria, and a prominent cell coat (Elston 1980a).

Digestive System

The mouth is located near the posterior aspect of the extended velum (Fig. 45); it merges laterally with the outer peripheral lobe of the velum and ventrally with the inner peripheral lobe, and forms a funnel that is continuous with the food groove of the velum (Elston 1980a).

The esophagus is lined with a simple, ciliated columnar epithelium; this cell arrangement can change, however, with the degree of distensibility of the esophagus: the epithelium becomes flatter as the esophagus fills; when contracted, the cross-sectional shape of the lumen is stellate, but changes to round as the esophagus becomes distended (Elston 1980a).

The junction between the esophagus and the stomach is marked by a cellular constriction that separates the dense mucous secretions and food particles in the stomach from the relatively clear esophagus. The stomach is highly distensible and bell shaped (Fig. 45); it connects with several other organs: the esophagus on its ventral apex, the style sac at its dorsal base, and the digestive gland posteriorly near the spiralling extension of the fecal groove (Fig. 45). The stomach is lined with a pseudostratified, ciliated columnar epithelium containing many goblet cells. The gastric shield is located in the anterolateral aspect of the stomach and, as in the adult, consists of long, intertwining microvilli embedded in a dense mucinous matrix (Elston 1980a).

The digestive gland is H-shaped; the central bar connects with the stomach as well as with the two halves of the organ (Fig. 45). In P-II larvae, the larger lobes of the digestive gland extend ventrally around the esophagus. Three types of cells are present: (1) absorptive cells are the most numerous with long, widely spaced microvilli on their luminal border containing electron-dense vacuoles that may be lipid surrounded by glycogen-like granules; (2) secretory cells are basiphilic and contain much rough endoplasmic reticulum, Golgi stacks, and vesicles typical of protein-secreting cells (Elston 1980a); (3) undifferentiated cells with a large nuclear-to-cytoplasmic ratio are found wedged between bases of absorptive and secretory cells (Elston 1980a).

The style sac is a deep cup-shaped organ that protrudes dorsally from the stomach; the epithelium is ciliated and pseudostratified and, consequently, is highly distinctive because of the uniformity of prominent cilia which also characterize this organ in the adult. Cells contain various types of vacuoles ranging from electron lucent to electron dense (Elston 1980a). This epithelium ends at the junction of the style sac with the stomach. Elston (1980a) found no evidence of a crystalline style in any of the sections he examined; this may be due to the loss of the style during sample preparation.

The intestine arises from the fecal groove at the dorsal base of the stomach. It proceeds ventrally and anteriorly until it reaches the ventral tip of the digestive gland lobes near the anterior adductor muscle where it turns 180° towards the anus, located between the posterior adductor muscle and the mantle lobes (Fig. 45). The intestine is lined with a simple,

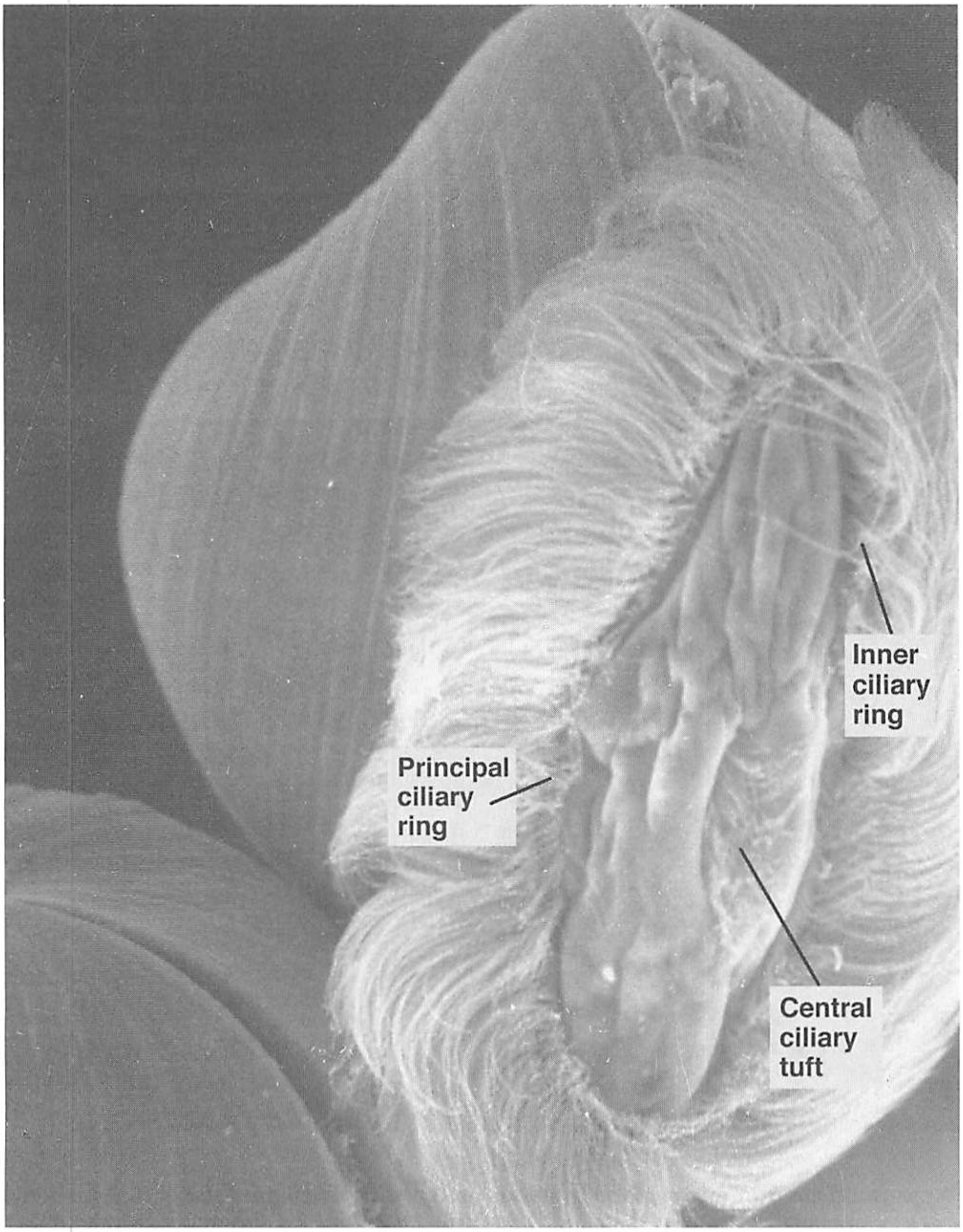

Figure 46. Scanning electron micrograph of extended velum of prodissoconch II larva. × 350. From Elston (1980a).

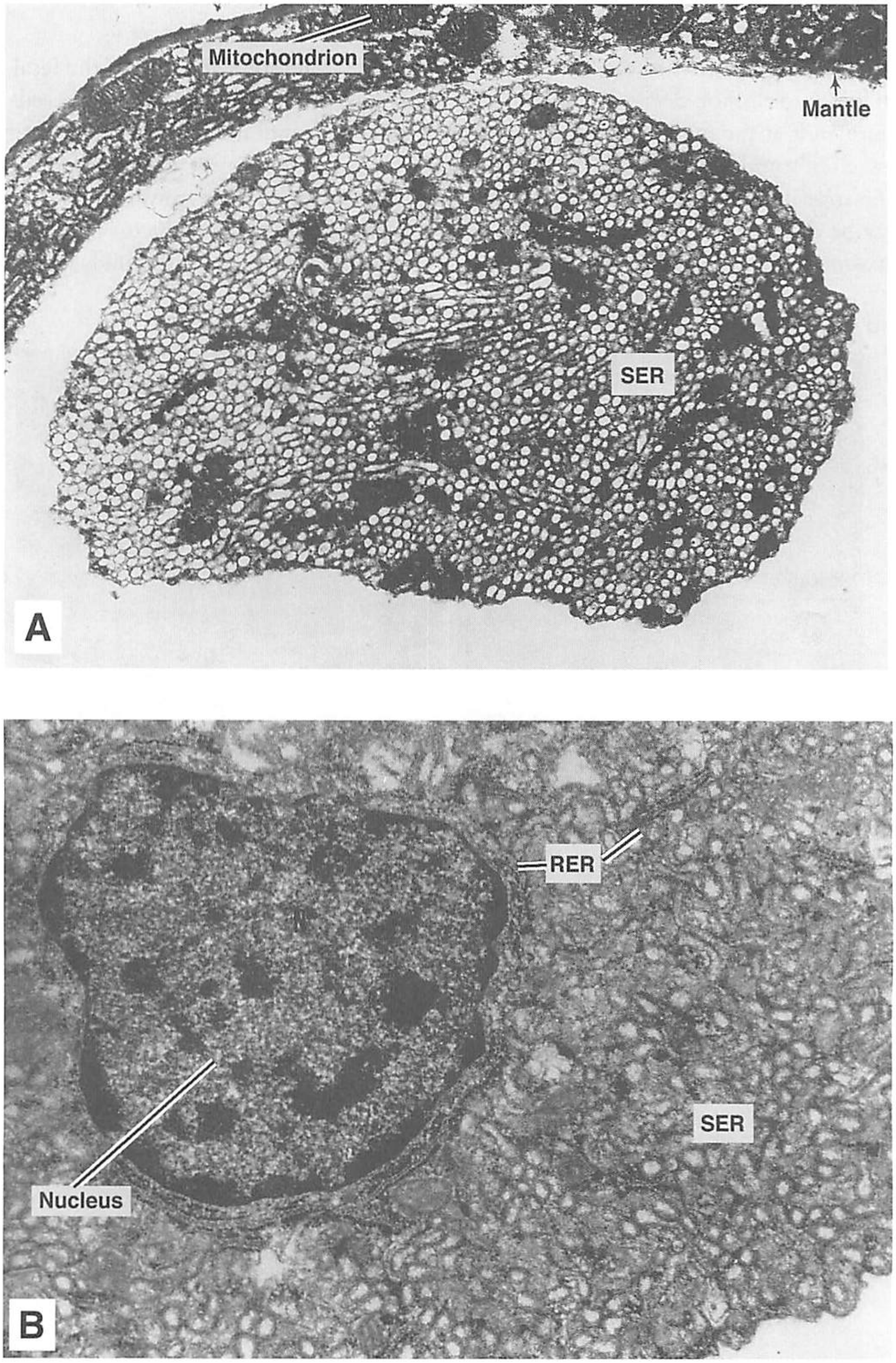

Figure 47. (A) Transmission electron micrograph of smooth endoplasmic reticulum [SER] cell (oval body) adjacent to larval mantle. Note the abundance and general distribution of SER in cell. × 3150. (B) Transmission electron micrograph of nucleus and adjacent cytoplasm of SER cell. Note the large amount of SER and the nucleus-associated rough endoplasmic reticulum [RER]. × 8400. From Elston (1980b).

cuboidal ciliated epithelium whose cells exhibit a variable degree of vacuolation, basal nuclei, and dense granular cytoplasm (Elston 1980a).

Gill plates arise laterally as folds of tissue from each mantle lobe and extend from the mantle margins to an area near the base of the foot (Fig. 45). Rudimentary gill filaments develop in late P-II larvae, but it is doubtful if these are ever fully functional before metamorphosis. Details of gill development including ridge formation and time and appearance of ciliation are not well known in *C. virginica* but have been described for *O. edulis* (Waller 1981).

Four pairs of retractor muscles originate on the dorsal surface of specialized mantle tissue at dense hemidesmosomes and insert on the foot, velum, and mouth areas (Fig. 45); retractor muscles are striated and can rapidly withdraw the foot and velum into the prodissoconch. Further, as the swimming veliger can rapidly change the degree of expansion and position of the velum, striated fibers are required for these functions (Galtsoff 1964).

Larvae have anterior and posterior adductor muscles (Fig. 45); the number of fibers gradually increases to about 40 in larvae measuring 263 µm in shell height (Elston 1980a). Muscle fibers show cytoplasmic interdigitations with adjacent fibers and terminate on modified mantle tissue: myoepithelial cells that have dense bundles of fibrils running between the muscle tissue and shell (Elston 1980a).

Two types of hemocytes in the visceral cavity have been described by Elston (1980b): a phagocytic cell similar to the hemocytic granulocyte of the adult and a large, cuboidal cell containing abundant smooth endoplasmic reticulum (SER), hence designated as the SER cell.

Phagocytic cells attach to all surfaces of the visceral cavity (Elston 1980b). Eosinophilic granules observed with light microscopy within phagocytic cells appear as electron-lucent, membrane-bound vacuoles and have been tentatively identified as unreacted lysosomes (Elston 1980b). Phagocytes also contain mitochondria and a course, dense granular cytoplasm. Many phagocytes contain phagosomes with remains of bacteria or cellular debris; these cells, especially in the velar and mantle epithelia, can wander across epithelial surfaces by diapedesis. Phagocytes appear to act as scavenger and defensive cells, engulfing foreign material as well as cellular debris; ultimately these cells leave the larva by diapedesis across epithelial barriers.

Smooth endoplasmic reticulum cells (Fig. 47A) also contain small amounts of rough endoplasmic reticulum, which occur in juxtaposition to the nuclear envelope (Fig. 47B) (Elston 1980b). The presence of large amounts of SER, coupled with the fact that this cell is markedly basiphilic, particularly with the basic dyes, hematoxylin and carbol fuchsin, led Elston (1980b) to conclude that this cytotype synthesizes much negatively charged material. The greatest abundance of SER cells occurs in the umbonal region near the thickened mantle overlying the valve hinge (Elston, 1980b).

Elston (1980b) concluded that SER cells are involved in the processing, conversion, and resecretion of dissolved nutrient substances in the visceral cavity and, because this cytotype does not exist in the adult, that these functions are unique to the larva.

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REFERENCES

Atkins, D. 1938. On the ciliary mechanisms and interrelationships of lamellibranches. Part VII. Laterofrontal cilia of the gill filaments and their phylogenetic value. Quart. J. Micros. Sci. 80 (319):345-436.

Awati, P.R. and H.S. Rai. 1931. *Ostrea cucullata* (the Bombay oyster). Indian Zool. Mem. on Indian Animal Types, III, Methodist Pub. House, Lucknow, India. 107pp.

Beninger, P.G., M. Le Pennec, and A. Donval. 1991. Mode of particle ingestion in five species of suspension-feeding bivalve molluscs. Mar. Biol. 108: 255-261.

Bernard, F.R. 1974. Particle sorting and labial palp function in the Pacific oyster *Crassostrea gigas* (Thunberg,1795). Biol. Bull. 146:1-10.

Berridge, M.J. and J.L. Oschman. 1972. Transporting Epithelia. Academic Press, San Diego. 91pp.

Brooks, W.K. 1880. The development of the oyster (*Ostrea virginica*) (List). Johns Hopkins Univ., Studies from the Biological Laboratory 4:1-83, 10 plates.

Brooks, W.K. 1905. The Oyster. A Popular Summary of a Scientific Study. Second ed. The Johns Hopkins Univ. Press, Baltimore. 225pp.

Brown, C.H. 1952. Some structural proteins of *Mytilus edulis.* Quart. J. Micros. Sci. 93:487-502.

Carriker, M.R. and R.E. Palmer. 1979. Ultrastructural morphogenesis of prodissoconch and early dissoconch valves of the oyster *Crassostrea virginica.* Proc. Natl. Shellfish. Assoc. 69:103-128.

Churchill, E.P. 1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. US Bureau of Fisheries, Report of the Commissioner of Fisheries for the fiscal year 1919, Appendix 8 (Document 890), pp 1-51.

Coe, W.R. 1932. Sexual phases in the American oyster (*Ostrea virginica*). Biol. Bull. 63:419-441.

Coe, W.R. 1936. Environment and sex in the oviparous oyster *Ostrea virginica.* Biol. Bull. 71:353-359.

Cole. H.A. 1938. The fate of the larval organs in the metamorphosis of *Ostrea edulis.* J. Mar. Biol. Assoc. U. K. 22:469-484.

Daniels, E.W., A.C. Longwell, J.M. McNiff and R.W. Wolfgang. 1971. Ultrastructure of spermatozoa from the American oyster *Crassostrea virginica.* Trans. Amer. Micros. Soc. 90:275-282.

Daniels, E.W., A.C. Longwell, J.M. McNiff and R.W. Wolfgang. 1973. Ultrastructure of oocytes from the American oyster *Crassostrea virginica* Gmelin. Trans. Amer. Micros. Soc. 92:337-349.

Dantan, J.L. 1916. La larve de l'*Ostrea edulis* (L.). Annales de L'Institut Oceanogr. (Foundation Albert I^{er}, Prince de Monaco). 7(6):1-20.

Eble, A.F. 1960. The use of vinyl acetate in studies on the circulatory system of the American oyster, *Crassostrea virginica.* Proc. Natl. Shellfish. Assoc. 51:12-14.

Eble, A.F. 1965. Some observations on the seasonal distribution of selected enzymes in the American oyster as revealed by enzyme histochemistry. Proc. Natl. Shellfish. Assoc. 56:37-42.

Elston, R. 1980a. Functional anatomy, histology and ultrastructure of the soft tissues of the larval American oyster, *Crassostrea virginica.* Proc. Natl. Shellfish. Assoc. 70:65-93.

Elston, R. 1980b. Functional morphology of the coelomocytes of the larval oysters (*Crassostrea virginica and Crassostrea gigas*). J. Mar. Biol. Assoc. U. K. 60:947-957.

Erdmann, W. 1935. Untersuchungen Uber die Lebengeschichte der Auster, 5: Uber die Entwicklung und die Anatomie der "Ansatzreifen" Larvae von *Ostrea edulis* mit Bemerkungen uber die Lebengeschichte der Auster. Wissenschaft. Meeres. Komm. zur Wissenschaft. Untersuch. der Deutschen Meere in Kiel und der Biolog. Anstalt Helgoland, new series, 19(6):25 pp.

Galtsoff, P.S. 1964. The American Oyster *Crassostrea virginica* Gmelin. Fish. Bull. 64:1-480.

Hawkins, W.E., H.D. Howse, and T.G. Sarphie. 1980. Ultrastructure of the heart of the oyster *Crassostrea virginica* Gmelin. J. Submicrosc. Cytol. 12:359-374.

Horst, R. 1883-1884. The development of the oyster (*Ostrea edulis* L.) [Translation from Dutch by Herman Jacobson.] U.S. Comm. Fish and Fisheries, Report of the Commissioner for 1884, Part 12 [1886]:891-910, 2 plates.

Kato, K. and K. Kubomura. 1954. On the origins of the crystalline style of lamellibranchs. Science Rep. Saitama Univ. B3:135-152.

Kennedy, A.V. and H.I. Battle. 1964. Cyclic changes in the gonad of the American oyster, *Crassostrea virginica* (Gmelin). Can. J. Zool. 42:305-321.

Kobayashi, H. 1954. Cyto-chemical study on the nucleolus in the common Japanese oyster (*Ostrea laperousii* Schrenck). II. Nucleic acids and nucleoproteins. J. Sci. Hiroshima Univ. Ser. B., Div. 1, 15:167-181.

Leenhardt, H. 1926. Quelques etudes sur *Gryphea angulata.* Annales de L'institut ocean. N. S. 3:1-93.

LePennec, M. P.G. Beninger and A. Herry. 1988. New observations of the gills of *Placopecten magellanicus* (Mollusca:Bivalvia), and implications for nutrition. II. Internal anatomy and microanatomy. Mar. Biol. 98:229-237.

LePennec, M., P. Gerard, G. Dorange, and Y.-M. Paulet. 1991. Trophic sources and pathways to the developing gametes of *Pecten maximus* (Bivalvia:Pectinidae). J. Mar. Biol. Assoc. U.K. 71:451-463.

Loosanoff, V.L. 1942. Seasonal gonadal changes in the adult oysters, *Ostrea virginica,* of Long Island Sound. Biol. Bull. 83: 195-206.

Lowe, O.M., M.N. Moore and K.R. Clarke. 1981. Effects of oil on digestive cells in mussels. Quantitative alterations in cellular and lysosomal structure. Aquat. Toxicol. 1:213-226.

Mathers, N.F. 1973. A comparative histochemical survey of enzymes associated with the processes of digestion in *Ostrea edulis* and *Crassostrea angulata* (Mollusca: Bivalvia). J. Zool. Lond. 169:169-179.

McQuiston, R.W. 1970. Fine structure of the gastric shield in the lamellibranch bivalve, *Lasaea rubra* (Montagu). Proc. malac. Soc. Lond. 39:69-75.

Moore, H.F. 1898. Oysters and methods of oyster culture with notes on clam culture. U.S. Comm. Fish and Fisheries, Part 23, Report of the Commissioner for 1897:263-340.

Morrison, C.M. 1993. Histology and cell ultrastructure of the mantle and mantle lobes of the eastern oyster, *Crasostrea virginica* (Gmelin): a summary atlas. Amer. Malacol. Bull. 10:1-24.

Morrison, C.M. and P.H. Odense. 1974. Ultrastructure of some pelecypod adductor muscles. J. Ultrastruct. Res. 49:228-251.

Morse, M.P. 1987. Comparative functional morphology of the bivalve excretory system. Amer. Zool. 27:737-746.

Morton, J.E. and C.M. Yonge. 1964. Classification and Structure of the Mollusca. Pages 1-58 in K. Wilbur and C. M. Yonge (eds.). Physiology of Mollusca, Vol. 1. Academic Press, New York.

Nelson, T.C. 1918. On the origin, nature and function of the crystalline style of Lamellibranchs. J. Morph. 31:53-111.

Nelson, T.C. 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica, O. edulis* and *O. angulata* with comparisons with other species of the genus. J. Morph. 63:1-61.

Nelson, T.C. 1960. The feeding mechanism of the oyster. II. On the gills and palps of *Ostrea edulis, Crassostrea virginica* and *C. angulata.* J. Morph. 107:163-191.

Owen, G. 1955. Observations on the stomach and digestive diverticul of the Lamellibrancia. I. The Anisomyaria and Eulamellibranchia. Quart. J. Micros. Sco. 96:517-537.

Owen, G. 1970. The fine structure of the digestive tubules of the marine bivalve, *Cardium edule.* Phil. Trans. Roy. Soc. Lond. Ser. B. 158:245-260.

Owen, G. 1972. Lysosomes, peroxisomes and bivalves. Sci. Prog. Oxford. 60:299-318.

Pal, S.G., B. Ghosh and S. Modak. 1990. Fine structure of the digestive tubules of *Meretrix.* Pages 167-175 in B. Morton (ed.). The Bivalvia — Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986. University Press, Hong Kong.

Prytherch, H.F. 1934. The role of copper in the setting, metamorphosis, and distribution of the American oyster, *Ostrea virginica.* Ecol. Monogr. 4:47-107.

Ruddall, K.M. 1955. The distribution of collagen and chitin. Symp. Soc. Exp. Biol. 9:49-71.

Seed, R. 1983. Structural organization, adaptive radiation, and classification of molluscs. Pages 1-54 in P. Hochachka (ed.). The Mollusca, Vol. 1. Academic Press, San Diego.

Shaw, B.L. and H.I. Battle. 1957. The gross and microscopic anatomy of the digestive tract of the oyster, *Crassostrea virginica* (Gmelin). Can. J. Zool. 35:325-347.

Shuster, C.N. and A.F. Eble. 1961. Techniques in visualization of organ systems in bivalve mollusks. Proc. Natl. Shellfish. Assoc. 52:13-24.

Sugawara, Y. 1969. Electron microscopic observations of the epithelial cell of the digestive diverticulum in the oyster, *Crassostrea gigas* Thunberg. Tohoku J. Agri. Res. 20:48-53.

Sumner, A.T. 1966. The cytology and histochemistry of the digestive gland cells of *Anodonta.* J. Roy. Micros. Soc. 85:417-423.

Tilney, L.G. 1976. The polymerization of actin. II. How nonfilamentous actin becomes nonrandomly distributed in sperm: evidence for the association of this actin with membranes. J. Cell Biol. 69:51-72.

Waller, T.R. 1981. Functional morphology and development of veliger larvae of the European oyster, *Ostrea edulis* Linne. Smithsonian Contrib. Zool. 328:1-70.

Weinstein, J.E. 1995. Fine structure of the digestive tubule of the eastern oyster. J. Shellfish Res. 14:97-103.

Winstead, J.T. 1995. Digestive tubule atrophy in eastern oysters, *Crassostrea virginica* (Gmelin 1791), exposed to salinity and starvation stress. J. Shellfish Res. 14: 105-111.

Yonge, C.M. 1926a. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis.* J. mar. Biol. Assoc. U. K. 14:295-386.

Yonge, C.M. 1926b. The digestive diverticula of the Lamellibranchs. Trans. Roy. Soc. Edinb. 54:703-717.