CHAPTER VIII

THE ADDUCTOR MUSCLE

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ANATOMY

The adductor muscle of the oyster is a massive organ that controls the opening and closing of the valves. It occupies a slightly asymmetrical position at the ventroposterior part of the body and is surrounded by the following internal organs: the visceral mass, pericardium, epibranchial chamber of the gills, and cloaca (fig. 72). The rectum adheres to the posterior side of the muscle. The protrusion of the visceral mass, containing the crystalline style sac and the lowermost part of the gonad, covers the anterior side of the muscle. A wedge-shaped visceral ganglion located inside the epibranchial chamber rests in a slight depression on the side of the muscle under the visceral protrusion. The ganglion can be exposed by cutting through the wall of the epibranchial chamber and lifting the tip of the visceral mass.

The adductor muscle of the monomyarian mollusks, i.e., those which have only one muscle (such as edible oysters, pearl oysters, scallops, and *Spondylus*), corresponds to the posterior adductor of other bivalves. The anterior adductor, present in larvae, disappears during metamorphosis shortly after the attachment of the larva.

Shortly after the metamorphosis of the larva the posterior adductor muscle develops into the most conspicuous and the heaviest organ of the oyster. In valves of *C. virginica* and in some other species of edible oysters the muscle scar where the adductor is attached to the shell is darkly pigmented. The shape and dimensions of this area are variable (see p. 30 ch. II).

The weight of the muscle of *C. virginica* accounts for 20 to 40 percent of the total weight of the tissues. After spawning, when other parts of the body are watery and poor in solids, the relative weight of the adductor increases. Examples of this condition, usually encountered after the discharge of a large number of sex cells and before the accumulation of the reserve materials (glycogen) in the connective tissue, are given in table 18. It may be deduced from these data that the weight of the adductor muscle is not affected by the changes in the chemical composition which take place in other organs. For further discussion of this problem the reader is referred to chapter XVII of this book.

The adductor is comprised of two distinct parts. About two-thirds of the total bulk of the muscle is translucent, oval-shaped, and slightly concave at

TABLE 18.—*Relative weight of the adductor muscle of six adult* C. virginica *(4 to 5 inches in height) during the spawning season (August) in Woods Hole, Mass. (fresh basis), 1951*

Oyster	Weight		Adductor muscle (total weight)
	Meat	Adductor muscle	
	Grams	*Grams*	*Percent*
Ripe male	17.8	3.5	19.7
Ripe male	15.0	3.7	21.8
Ripe female	18.7	4.4	23.5
Ripe female	6.5	2.1	32.3
Partially spawned female	6.5	2.3	35.3
Spawned out, sex undetermined	5.2	2.2	42.3

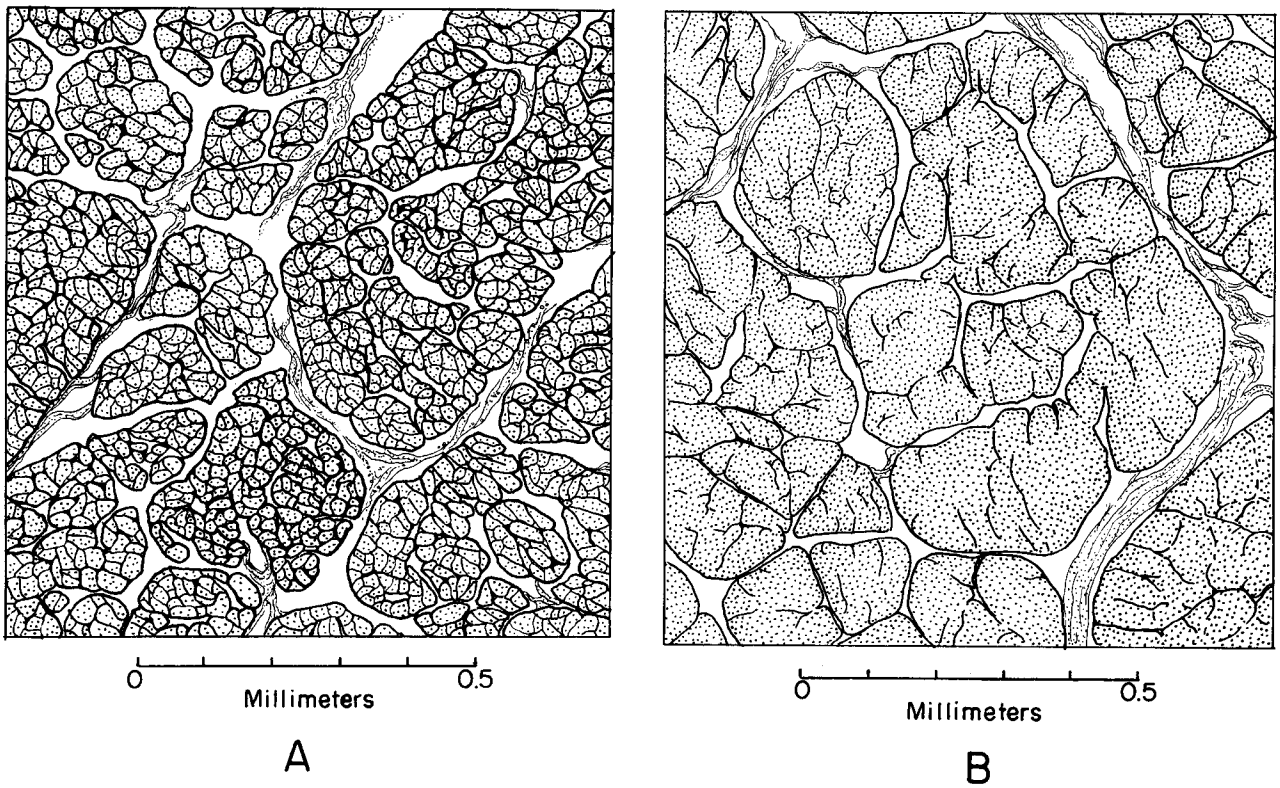

FIGURE 141.—Cross sections of the two portions of the adductor muscle of *C. virginica*. A—white or opaque part. B—translucent part. The muscle bands of the white part are more compact and are surrounded by tougher connective tissue than those of the translucent part (right). Bouin, with formalin hematoxylin-eosin.,

the dorsal side adjacent to the pericardium. This portion is frequently called the vitreous or dark part. The remainder is crescent-shaped and an opaque milky-white. The fibers of this part are tougher than those of the translucent portion; the difference shows clearly when the muscle is being cut or teased.

The fibers of the adductor muscle form dense bands surrounded by connective tissue. In a cross section examined under a low-power microscope (fig. 141) the bands appear as separate units packed more or less parallel to one another. This arrangement is less pronounced in the translucent part (fig. 141, right). The tissue that surrounds the muscle bands is better developed in the opaque section. A layer of connective tissue separates these two major parts of the adductor.

Connective tissue provides a framework for the muscle. Individual fibers do not run the full muscle distance between the two valves; they are anchored at one or both ends in the sheets of tissue which surround the bands. A very thin membrane, called endomysium, invests each muscle cell; the sheathing around the bands of cells is epimysium; the septa which radiate from the latter form perimysium.

The cross-sectional areas and the weight of the two portions vary in different specimens. It was reported by Hopkins (1930) that the ratio of weight of the translucent to the white part of the muscles of oysters growing near Beaufort, N.C., depends on ecological conditions. In the oysters found at the upper limit of their vertical distribution near the high-water level the ratio was 1.26, while in the oysters taken at a level 2.5 feet lower, where they were submerged during about three-quarters of the time, the ratio was 2.51.

The entire adductor muscle is well supplied with blood; wandering leucocytes are usually seen between the fibers and in the connective tissue. Both parts of the adductor muscle are abundantly supplied with nerves. The innervation of the muscle is discussed in Chapter XII.

MICROSCOPIC STRUCTURE

The muscle fibers of the two parts of the adductor differ in both size and structure. The white muscles are smooth and wide, while the dark

(translucent) fibers are thinner and have a peculiar striation which has been described as oblique, double-oblique, helicoidal, and spiral. Some investigators (Kellogg, 1892; Orton, 1935; Hopkins, 1936) and authors of biology textbooks (Borradaile and Potts, 1961) refer to the translucent part as consisting of striated muscles.

Both types of fibers appear under the light microscope as long cylindrical cells, slightly thickened in the middle and tapering toward the ends. An oval-shaped nucleus with one or several nucleoli is near the surface, outside the contracting elements which make up the bulk of the cell. Clear homogenous cytoplasm (sarcoplasm) which can be seen under high magnification forms a very thin surface layer of the cell and around the nucleus. The major part of the cell is made of slender fibrils that differ in their orientation in the two types of muscle cells.

The principal structural elements appear in unstained, isolated fibers examined with phase contrast oil immersion lens under high magnification. Whole mounts can be made after pieces of muscle are macerated in 20 percent nitric acid and then placed in glycerol. Treatment with nitric acid apparently does not affect the visible structure of the fibers. Preparations should be made from fibers which have been taken from both a fully relaxed and a completely contracted adductor. The desirable state of relaxation is obtained by narcotizing the oyster in 5 to 10 percent magnesium sulfate solution for 48 hours; treating the mantle with a strong solution of hydrochloric acid causes long-lasting contraction. In opening the oyster, care should be exercised not to damage the visceral ganglion, since injury to this nerve center may cause relaxation of the adductor.

WHITE MUSCLE FIBERS

White muscle fibers isolated from a completely relaxed adductor of a fully narcotized *C. virginica* are from 2 to 3 mm. long and about 10 μ in diameter. The fibers are too short to stretch from one valve to the other and, with the exception of those attached to the shell, end in connective tissue. Occasionally they bifurcate but do not anastomose. The body of the fiber consists of many fibrils of variable length and a diameter of only a fraction of a micron. The fibrils are oriented parallel to the long axis of the cell and those close to the surface appear to be darker. The arrangement of the fibrils changes somewhat, depending on the state of contraction. Figure 142, A–D, represents four camera lucida drawings made of a white muscle fiber; (A) the fiber is in a completely relaxed state, (B) it is strongly contracted, (C) it is partially contracted, and (D) a noncontracted fiber is folded by the contraction of the surrounding fibers. All drawings were made from glycerin-mounted preparations examined with phase contrast lens. The difference between the relaxed and contracted fiber is primarily in the thickness of the fiber, which in B is about three times greater than in A. In both cases the orientation of fibrils is the same. In a partially contracted and slightly twisted fiber, C, some of the fibrils are at an angle to the long axis of the cell while others retain their original orientation. The fiber D, found in the same preparation with C, is folded but not contracted. Its surface layer of transparent cytoplasm was wider than in the others and the fibrils followed the zig-zag outlines of the fiber. Although the sample was isolated from a contracted adductor, only a few fibers were found in highly contracted state B. The fiber A was separated from a completely relaxed muscle.

DARK MUSCLE FIBERS

The fibers of the dark (translucent) part of the adductor are from 1 to 2 mm. long and in a relaxed state are about 5μ in diameter. When isolated in teased preparations, the fibers have a tendency to twist and coil. The connective tissue around them is less tenacious than in the white muscle, and the fibers can be separated easily by fine needles. As early as 1869 Schwalbe showed that the fast adductor muscle of *Ostrea* is composed of fibers which exhibit a clearly defined diamond lattice pattern. Marceau (1909) maintained that double obliquely striated muscles are widely distributed in the fast parts of the shell closing muscles of bivalves, and Anthony (1918) advanced a theory that oblique striations are a stage in the evolutionary development of transverse striation. The fact that true cross striation occurs in the muscles of *Pecten, Lima, Teredo, Spondylus,* and other bivalves leads to a widely accepted belief that the dark portion of the adductor muscle, also described by some authors as yellow, grey, or tinted (Kawaguti and Ikemoto, 1959), consists of cross striated fibers and that quick movements of these animals are brought about by their contraction.

From their study of the translucent fibers of the adductor of *C. angulata,* Hanson and Lowy (1961)

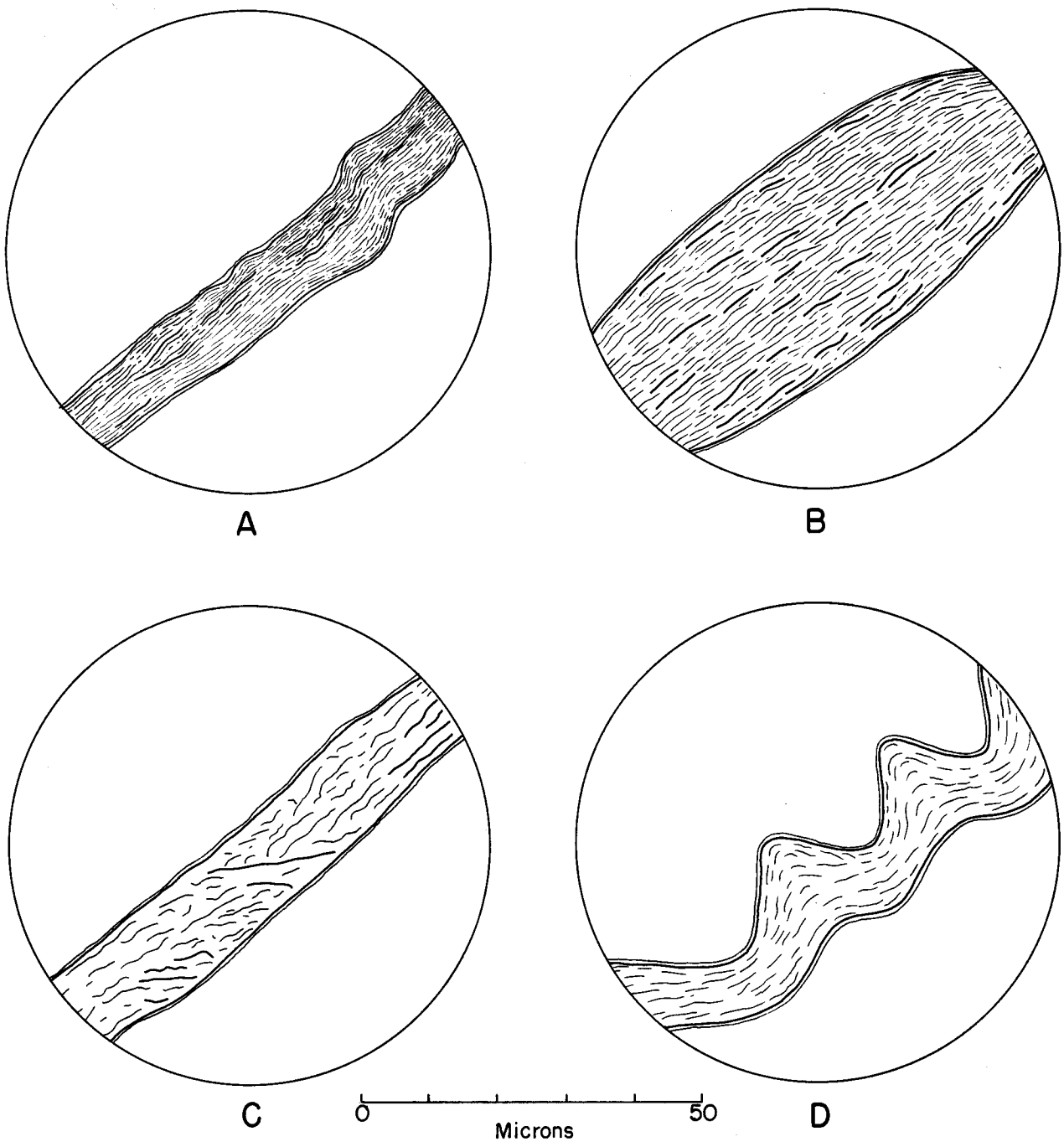

FIGURE 142.—Small pieces of four white fibers of the adductor of *C. virginica* seen under phase contrast lens. Whole mounts of a preparation teased after treatment with nitric acid. Glycerol. A—completely relaxed fiber from narcotized oyster; B—strongly contracted fiber; C—slightly contracted fiber; D—folded but not contracted fiber. Figures B and D are from one preparation of a highly contracted adductor.

concluded that the fibers of that part of the muscle differ from true cross striated muscles in that the bands (A and I) lie at about a 10-degree angle to the fiber axis and are arranged helically around the outer part of the fiber; this produces the double oblique striation visible in the light microscope. Hanson and Lowy's observations were based on electron microscopy, and the bands they refer to as A and I are not visible under the light microscope.

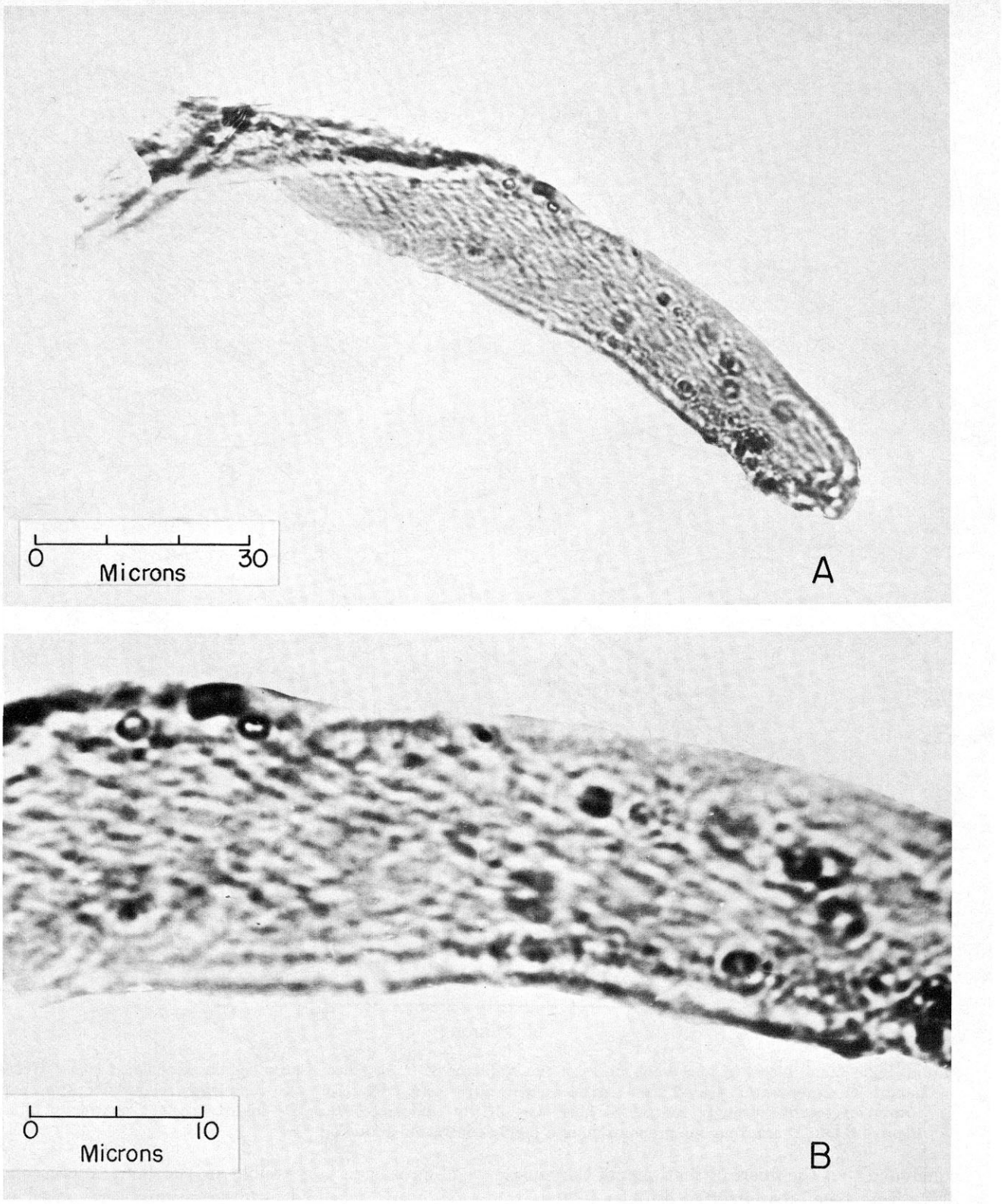

FIGURE 143.—Small piece of dark muscle fiber from the contracted adductor muscle of *C. virginica*. A—Whole mount in glycerol after nitric acid treatment. B—Small portion of the same negative magnified. Round globules are artifacts. Phase contrast lens.

Examination of relaxed fibers of *C. virginica* with phase contrast lenses shows the existence of a distinct diamond lattice pattern shown in figure 143. In the relaxed dark fibers this double oblique striation is absent and the fibrils are oriented parallel to the axis of the cell. My observations confirm the description made by Hanson and Lowy (1957), who found that in helical configuration of myofibrils of the "yellow" part of the adductors of oysters and *Ensis ensis* the angles between the helix and the axis of the fiber increased as the muscle relaxed. The so-called diamond lattice pattern of striation is not a permanent feature of the translucent fiber. It becomes visible in a contracted muscle and is usually confined to the cut ends of the fiber. This observation made by Bowden (1958) for *Ostrea edulis* and *C. angulata* is in accordance with my observations on *C. virginica.*

Considerable advance in the understanding of fine structure of bivalve muscle cells was made by Philpott, Kahlbrock, and Szent-Györgyi (1960), in the work on *C. virginica, Mya arenaria, Mercenaria mercenaria,* and *Spisula solidissima.* Similar studies of *C. angulata* were made by Hanson and Lowy (1961).

With respect to the ultrastructure of the fibers of the adductor muscles of these species, the results of the two investigations are in agreement although they present different theories of the so-called catch mechanism of the adductor, which is discussed later. In both parts of the muscle the fibrils consist of two types of filamentous structures that can be clearly seen on the electron micrograph of the transverse section of the fibril (fig. 144). The thick filaments form the largest part of the fibril; their diameter varies from 250 to 1,500 Å. The thin filaments which occupy the space around the thick ones are about 50 Å. in diameter. The thick filaments have the 145 Å. periodicity associated with paramyosin. The authors surmise that actomyosin is localized in the thin filaments. Hanson and Lowy (1961), in confirming the presence of two kinds of filaments in the fibrils of *C. angulata,* assume that the thinner filaments contain mainly actin. Accord-

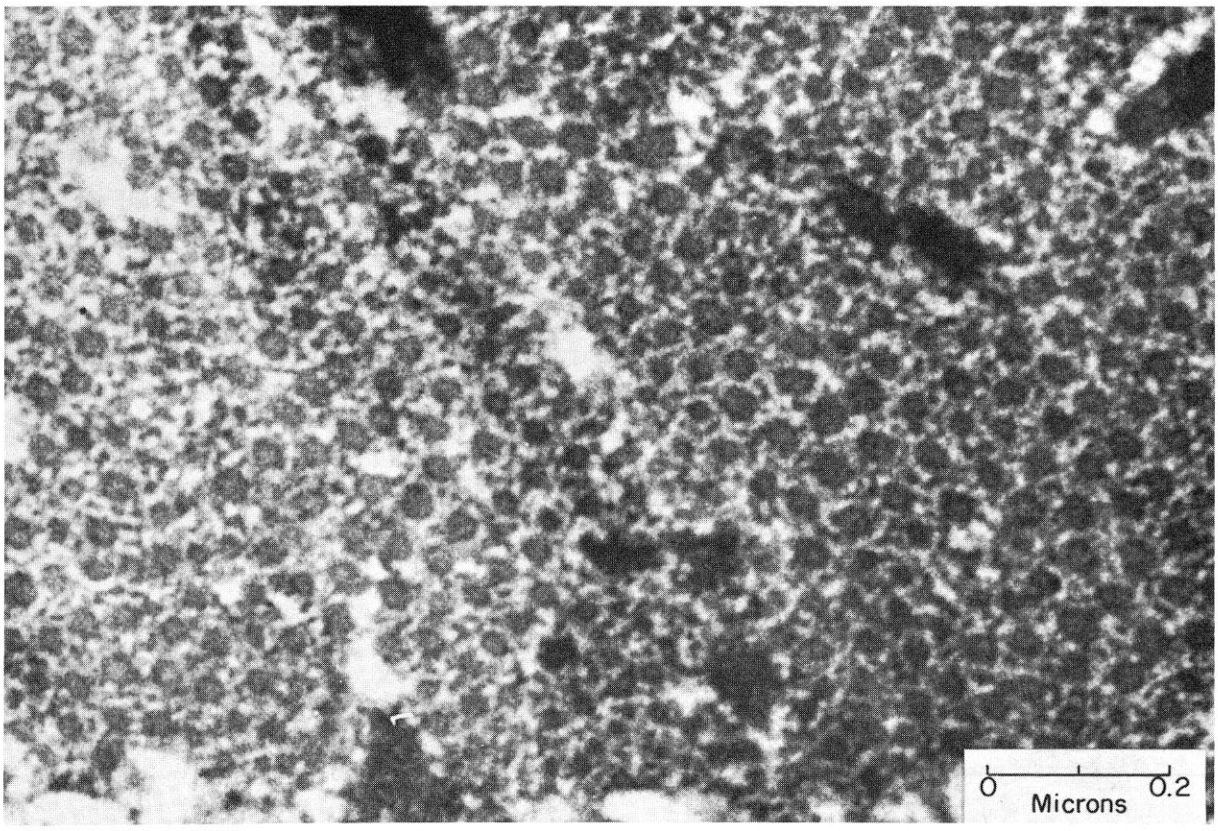

FIGURE 144.—Electron micrograph of a small portion of a muscle fiber of the translucent part of the adductor of *C. virginica.* Courtesy of Philpott and Szent-Györgyi.

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