CHAPTER III

THE LIGAMENT

APPEARANCE AND STRUCTURE

The significance of the ligament in the phylogeny and classification of bivalves was a favored subject in malacological studies of the past century. Lengthy theoretical speculations about this structure are found in the papers of Bowerbank (1844), Jackson (1890, 1891), Tullberg (1881), Dall (1889, 1895), Reis (1902), Biedermann (1902), Stempell (1900), and others. A review of the literature from the earlier years to 1929 is adequately presented by Haas (1935). These investigations give little information, however, concerning the microscopic structure, origin, chemical composition, and function of the ligament. The latter subjects receive attention in the more recent works of Mitchell (1935) on the ligament of *Cardium corbis*, in a series of detailed studies by Trueman (1942, 1949, 1950a, 1950b, 1951, 1952, 1953a, 1953b) on the ligaments of *Mytilus*, *Pecten*, *Nucula*, *Ostrea edulis*, *Tellina tenuis*, and the Semelidae, and in the paper of Owen, Trueman, and Yonge (1953) on the ligament in the bivalves.

The ligament of the Atlantic oyster is a narrow band of dark, elastic material situated along the edge of the hinge between the two valves. The ligament does not extend deep into the shell, is not visible from the outside, and is called internal or ligamentum internum by Haas (1935) and "alvincular" by Dall (1889). The latter term is no longer used in malacological literature.

The ligament performs a purely mechanical function. Its elastic material, compressed when the contraction of the adductor muscle closes the valves, expands and pushes the valves apart when the tension of the adductor is released. The extent to which the valves may gape depends largely on the shape and size of the beaks. In the specimen shown in figure 17 the large, triangular space beyond the hinge permits wide excursions of the valves and their gaping may consequently be very broad.

On the other hand, the narrow and crooked beaks shown in figure 53 greatly restrict the movement of the valves along the pivotal axis regardless of the degree of relaxation of the muscle. Small pebbles, pieces of broken shell, and other foreign particles often found lodged between the beaks may further limit the opening of the valves. The possibility that such purely mechanical obstructions can impede the movement of the valves should be kept in mind in evaluating the results of physiological tests in which the degree of shell opening is recorded.

The youngest part of the ligament is that which touches the inside of the valves; the oldest portion, which is usually dried, cracked, and nonfunctional, faces the outside. When the

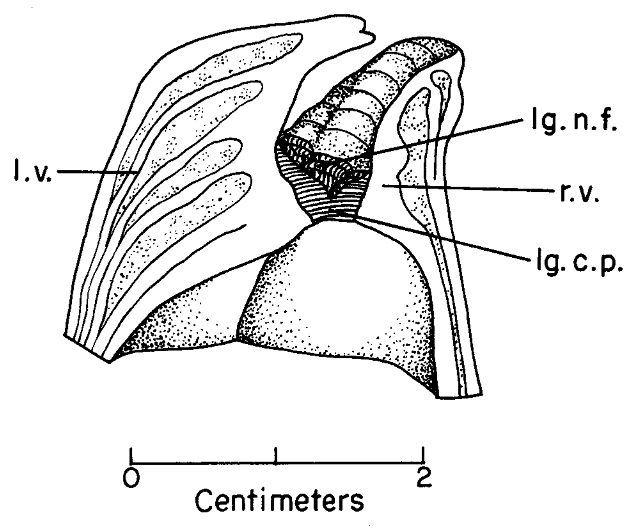

FIGURE 53.—Longitudinal section through the beak and ligament of *C. virginica*. l.v.—left valve; r.v.—right valve; lg.c.p.—functional, compressible part of the ligament; lg.n.f.—nonfunctional, old part of the ligament.

valves are forcibly separated, the ligament breaks approximately along the pivotal axis of the shell (fig. 54, piv. ax.) and the two parts remain attached to the respective valves.

The three parts of the ligament at the edge of the valves differ in color, size, and shape. The usually brownish central (inner) part called resilium forms a bulging ridge marked by fine striations visible to the naked eye or under a low magnification. The resilium is attached to a groove called resilifer or chondrophore (figs. 54, 2, 16). The dark olive anterior and posterior portions of the ligament called by Olsson (1961) tensilia are attached to the edges of the valves (nymphae).

The resilium consists of tightly packed lamellae arranged at about right angles to the longitudinal axis of the ligament; they can be seen on the exposed surface of the central part. These lamellae are intersected by fine striations visible on the side of the resilium after the removal of the adjacent lateral part (fig. 55).

When the valves are closed the resilium is compressed because of its considerable thickness while both lateral parts (tensilia) are slightly stretched. It can be seen in a series of cross sections of the hinge made at right angles to its pivotal axis (fig. 56) that the curved lines of the compressed resilium (2) are deeply arched, while those in the lateral parts are almost straight. This observation agrees with the description of the operation of the ligament of *O. edulis* by Trueman (1951). Since the beaks of the oyster illustrated are asymmetrical, the distance between the two valves is greater at the anterior than at the posterior end (fig. 56, 3, and 1) and, consequently, the anterior portion

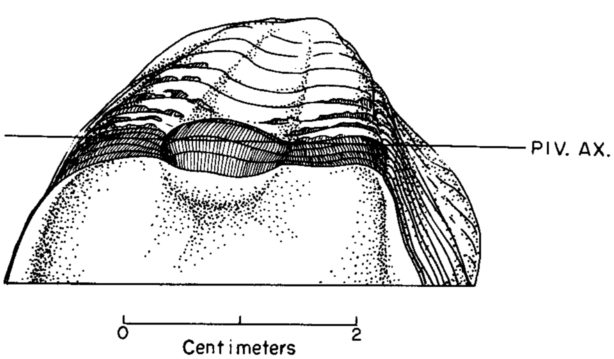

FIGURE 54.—Ligament of large *C. virginica* attached to the right valve. View from the inside. piv. ax.—pivotal axis. The resilium occupies the central position and on both sides is flanked by tensilium. Slightly magnified.

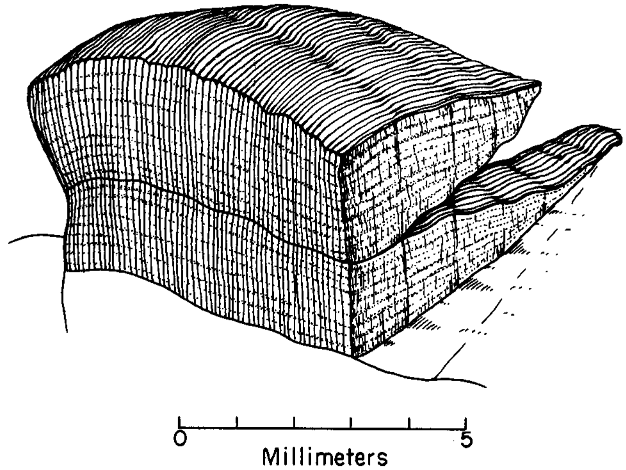

FIGURE 55.—Central portion of the ligament (resilium) attached to the groove (bottom) of a valve. Note the lamellar structure and fine striations visible on the right side of the figure. *C. virginica.*

of the ligament stretches more than its posterior part.

The ligament effectively seals the space between the dorsal edges of the valves and forms an elastic, watertight joint that prevents the entry of water and organisms which otherwise could easily invade the mantle cavity.

The spring-like action of the ligament is a function of the elasticity of its component parts. Examination of transverse and longitudinal sections of fresh ligament under low power discloses its amazingly complex structure. A cross section made with a razor blade at a right angle to the pivotal axis of the valves shows a series of well-defined curved lines extending from the right to the left valve, and a complex system of lamellae arranged perpendicularly to the curves. Both systems are clearly seen in unstained preparations mounted in glycerin jelly or in balsam (fig. 57). The pivotal axis of the ligament lies in the center of the drawing, perpendicular to the plane of the paper; the valves (not shown in the figure) are on the right and left sides, and the newly deposited portion of the ligament lies at the bottom of the drawing. The most conspicuous arches extend almost without interruption from one side to another; the lighter ones can be traced only for short distances over the cross-sectional area. The structure of the resilium resembles a leaf plate of an old-fashioned automobile spring, suggesting that the arches are the lines of stresses corresponding to the deformation of the ligament under compression. Within the mass of the ligamental ma-

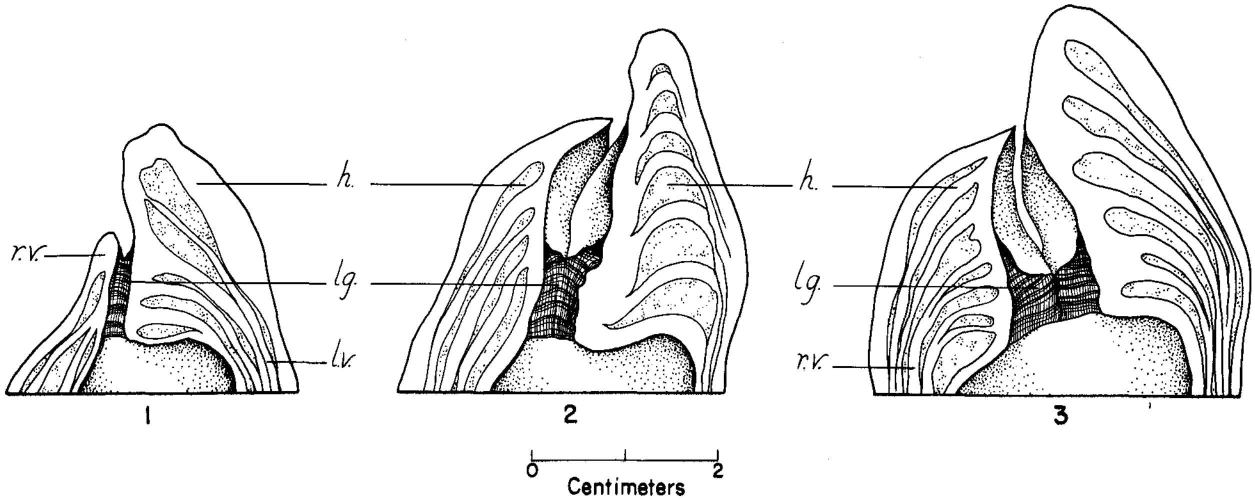

FIGURE 56.—Three longitudinal sections through hinge and ligament of the shell of *C. virginica*. (1) posterior portion; (2) central portion or resilium; (3) anterior portion, h.—beaks, lg.—ligament, l.v.—left valve, r.v.—right valve. Note the arched lines of the resilium (lg.) in the central drawing (2). Slightly magnified.

terial they are the visual evidence of these stresses. Since the "springs" of the resilium do not consist of separate structure parts joined together into a complex unit, the comparison is only superficial.

The ligament is a nonliving structure secreted at a varying rate by the highly specialized epithelium of the subligamental ridge of the mantle (see p. 89). Structurally, the arches, visible at low magnification, represent stages of growth; functionally and in accentuated form, they reflect compressional deformation in the operating structure of the ligament.

Under a binocular microscope the lamellae of the resilium, when separated with fine needles, appear slightly bent and zigzagged. A small piece of the resilium cut in the dorsoventral plane and magnified about 250 times (fig. 58) can be seen to consist of fibrillar material and of dark bands of variable width composed of tightly packed, oval, birefringent globules. Pressure over the cover slip does not change the shape of the globules, which appear to be firmly embedded in the ground substance. The globules contain no acid-soluble material since they are not affected by strong hydrochloric acid, nor are they soluble in alcohol or xylol. Preparations mounted in balsam present the same appearance as nondehydrated sections mounted in glycerin jelly. Besides the globules concentrated in the dark bands within a delicately fibrillar ground substance, some of them are arranged in longitudinal lines at right angles to the dark bands. Some of the horizontal bands (upper part of figure 58) are of much greater complexity than the others; they consist of oval-shaped light areas surrounded by globules. The two structural elements, namely, the bands of fibrils and the rows of globules, repeat themselves with regularity, the successive layers varying only in width and in the concentration and size of globules. The fibrils intersect the arches either perpendicularly or at about 45° (lower part of figure 58) and probably exert additional elastic force under compression.

The anterior and posterior parts of the ligament, the tensilium of Olsson (1961) or outer layer of Trueman (1951), are made of tenacious material which withstands considerable stretching without breaking. This can be easily ascertained by trying to tease or to pull apart the dissected parts of the tensilium. In this respect the material of the tensilium differs from that of the resilium, which is weak under tension but strong under compression. The color of the tensilium differs from that of the resilium. In New England oysters it is usually dark green on the surface, while the resilium is light brown. The tensilium is made of tough lamellae which in a transverse section appear as slender, transparent cylinders of slightly yellowish substance (fig. 59). Both resilium and tensilia are secreted by highly specialized epithelial cells which underly the ligament. The thickness of each lamella corresponds to the width of a ruffle at the edge of the secreting epithelium (See chapter V, p. 89). At low magnification the material of the tensilium appears to be non-

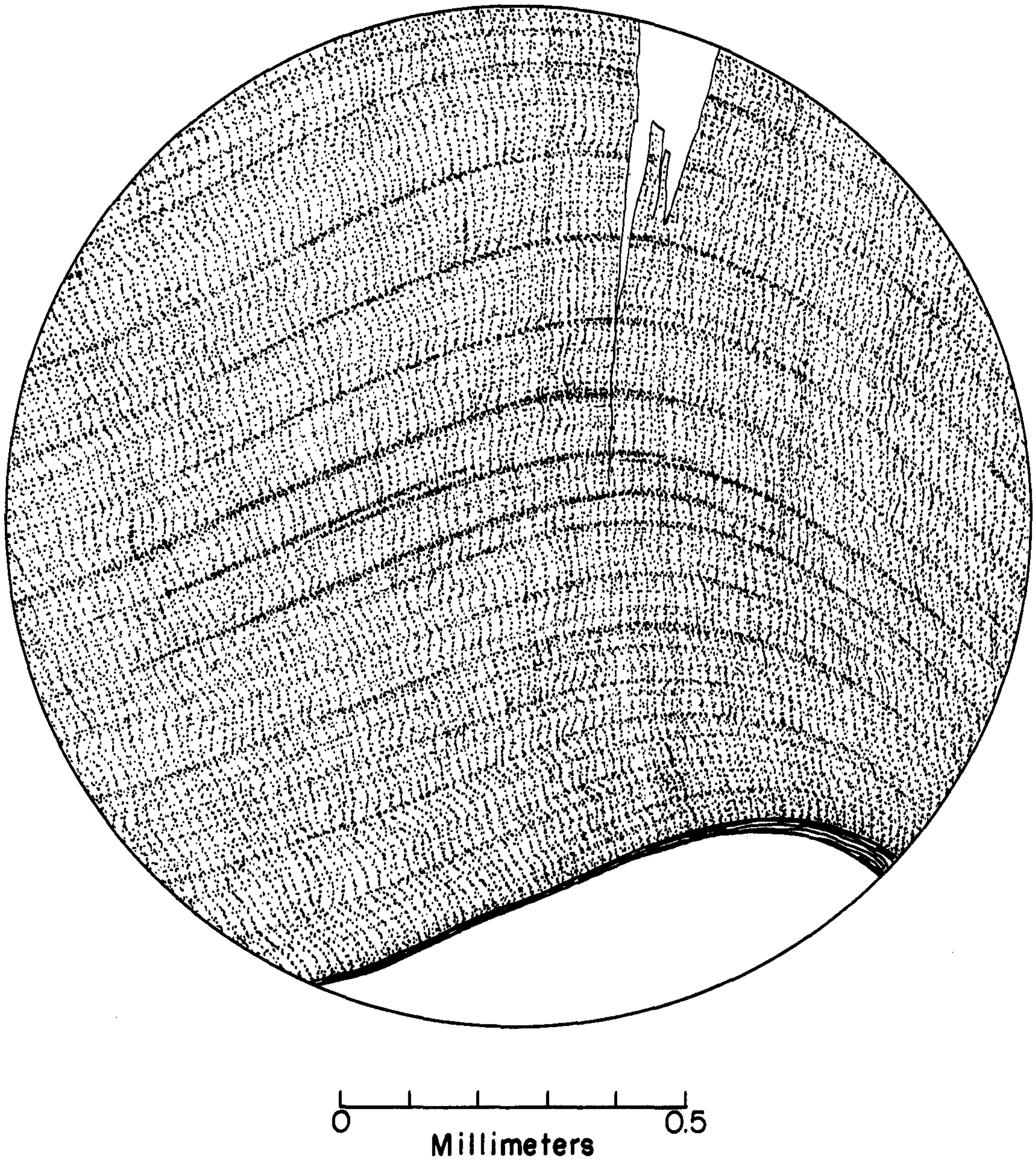

FIGURE 57.—Cross section of the central portion of the ligament of *C. virginica* made perpendicular to the pivotal axis of the valve. Arches (curved lines of dense material) extend from left to right; the valves are not shown in the drawing.

fibrillar, but at higher magnification the fibrillar structure becomes clearly visible. Two types of fibrils can be distinguished on the photomicrograph of tensilium shown in figure 60. Heavy and well-defined bundles of fibers originated along the vertical plane of the lamellae (up and down bundles in fig. 60) and short and slender fibrils in places at right angles to the large bundles (the lower half of fig. 60). Large oval-shaped bodies on the upper right and lower left part of the figure are the accumulation of calcium carbonate crystals. Single minute crystals are scattered over the body of the lamella. The outer dark layer is very thin, its color is due to densely packed narrow fibrils. Large and small globules which are conspicuous in the architecture of the resilium are absent in the tensilium, and the structure of the latter lacks the complex arrangement of globules and fibrils found in the former.

The complexity of the microscopic structure

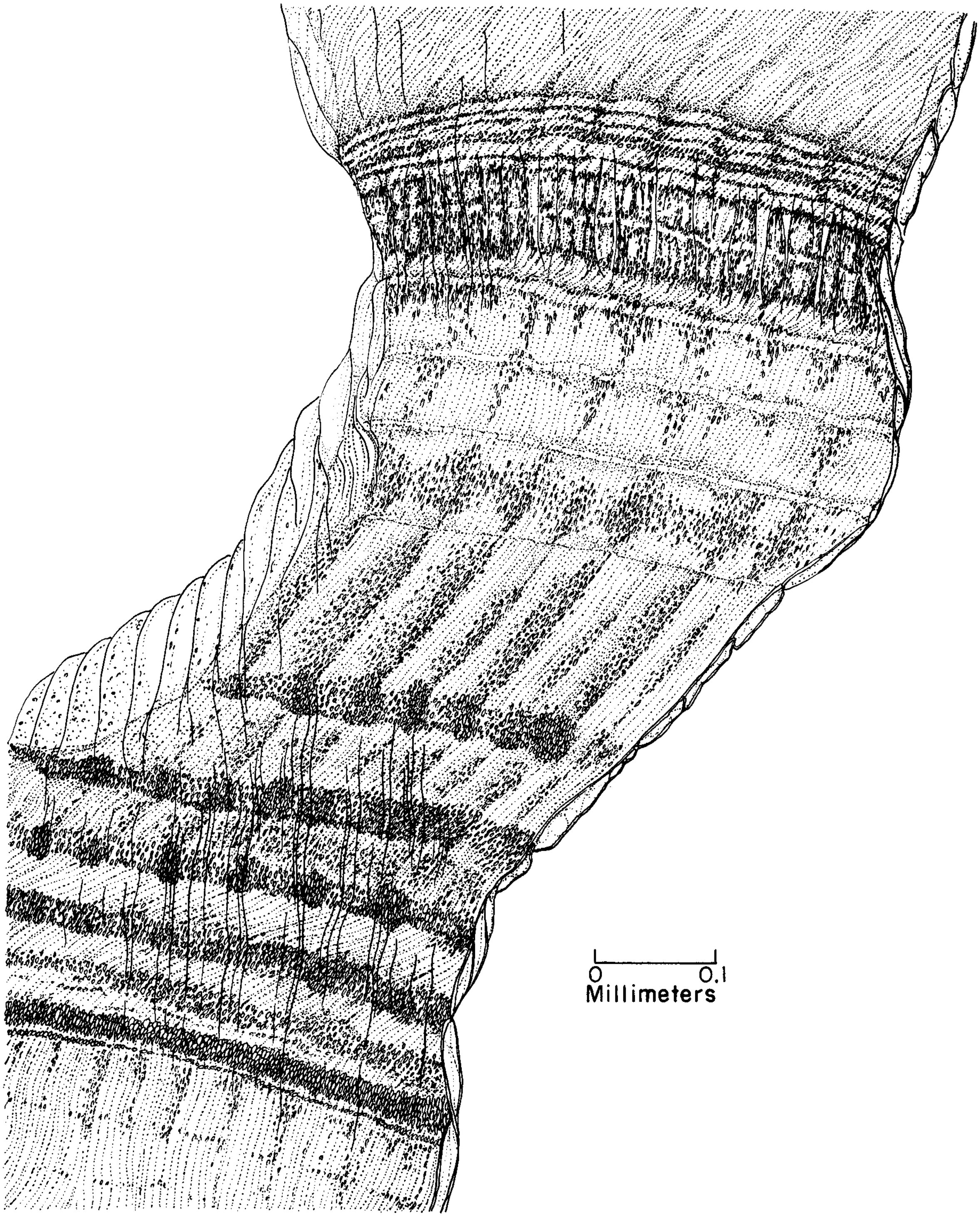

FIGURE 58.—Longitudinal (dorsoventral) section of the resilium of *C. virginica*. Two structural elements are seen: Band of fibrillae extending in vertical direction in the plane of the picture, and horizontal bands of various thicknesses consisting of numerous globules.

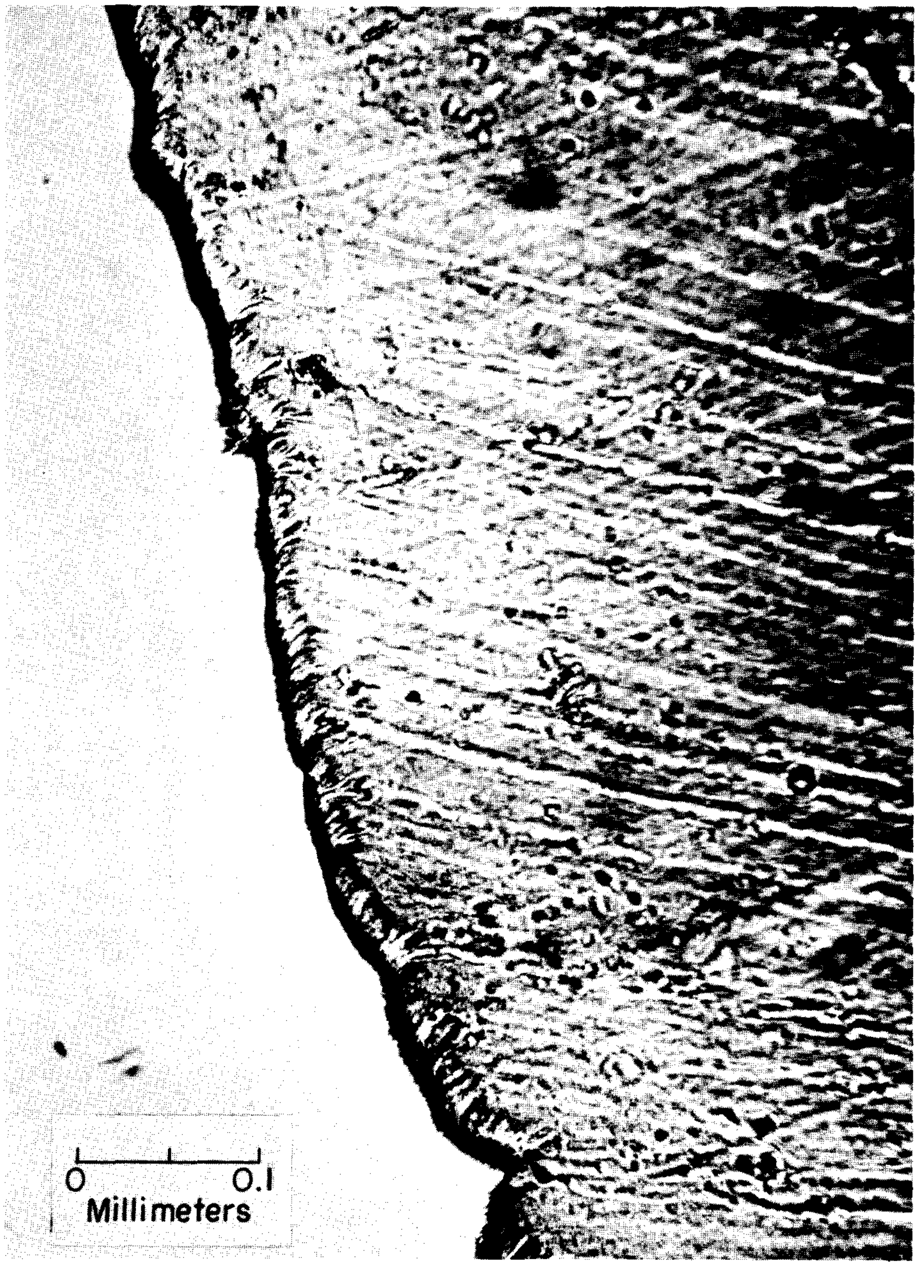

FIGURE 59.—Transverse section of tensilium showing lamellar structure and darkly pigmented surface, *C. virginica*. Photomicrograph of unstained and nondecalcified preparation.

suggested that electron microscopy might reveal some interesting details. Small pieces of the resilium fixed in 1 percent osmic acid were embedded in plastic and sectioned. Although the material is very hard, it was possible to obtain sections from 0.3 to 0.5μ in thickness. The electron micrograph (fig. 61) shows bands of fibrils varying in diameter from 370 to 500 Å.

A section made across the plane of the arches (fig. 62) shows a membrane honeycombed by holes about 500 Å in diameter. Two interpretations seem possible: (1) that the fibrils are tubular, the light areas corresponding to the centers of the tubes, or (2) that the empty circles represent spaces between the fibrils. The first interpretation is more plausible because of the gradation