DOCUMENTATION OF ANNUAL GROWTH LINES IN OCEAN QUAHOGS, *ARCTICA ISLANDICA* LINNÉ

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ABSTRACT

About 42,000 ocean quahogs, *Arctica islandica* Linné, were marked and released at a deep (53 m) oceanic site off Long Island, New York, in 1978. Shells of live specimens recovered 1 and 2 years later were radially sectioned, polished, and etched for preparation of acetate peels and examination by optical microscopy or microprojection; selected specimens were similarly prepared for examination by scanning electron microscopy. Specific growth line and growth increment microstructures are described and photographed. An annual periodicity of microstructure is documented, providing a basis for accurate age analyses of this commercially important species.

Numerous bivalve species form periodic growth lines in their shells (Rhoads and Lutz 1980). Internal growth lines found in the shells of ocean quahogs, *Arctica islandica* Linné, have stimulated interest in using these markings to determine age and growth (Thompson et al. 1980a, b), since fishery exploitation has increased significantly within the past decade (Serchuk and Murawski 1980[3]).

Documentation of age and growth of ocean quahogs has been incomplete. Some studies included no account of aging methodologies (Thorson *in* Turner 1949; Jaeckel 1952; Loosanoff 1953; Skuladottir 1967); in others, concentric "rings" or "bands" formed in the periostracum of small quahogs (<ca. 60 mm in shell length) were considered annuli, but validation of the annual periodicity of these markings was not provided (Lovén 1929; Chandler 1965; Caddy et al. 1974; Chéné 1970[4]; Meagher and Medcof 1972[5]). Microstructure of ocean quahog shells has been studied, but the analyses did not specifically distinguish growth lines from growth increments (Sorby 1879; Bøggild 1930; Taylor et al. 1969, 1973; Lutz and Rhoads 1977, 1980). A means of clearly separating such shell features was needed.

Recent investigators of age phenomena in ocean quahogs have microscopically examined the shells and acetate peel images produced from sectioned, polished, and etched shells. This method greatly aided separating the many crowded growth layers in the hinge plate and near the ventral valve margin of large, old specimens. Lutz and Rhoads (1977) found alternating bands of aragonitic prisms and complex-crossed lamellar microstructures in the inner shell layer of ocean quahog shells that they believed were related to periods of aerobic and anaerobic respiration. Thompson et al. (1980a, b) reported that internal growth bands corresponded to external checks on the valves and that the internal growth bands were formed by successive deposition of two repeating growth layers or increments. Jones (1980) labelled the growth increments (GI) as GI I and GI II, since each was microstructurally distinct, had thickness, and was formed within a time frame of several months. For these reasons, he considered the GI I layer to be unlike minute "growth lines" or "striations" appearing as subdaily deposits in the shells of other bivalves (Gordan and Carriker 1978); the GI II layer became thinner and ill-defined from the GI I layer with ontogeny.

Since growth bands in ocean quahog shells seem to lack microstructures of possible subannual periodicities, the definitions of a growth line and growth increment formulated by Clark (1974a, b) have general application. Clark (1974b:1) defined the former as "abrupt or repetitive changes in the character of an accreting tissue" and the latter as "the thick-

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[3]Serchuk, F.M. and S.A. Murawski. 1980. Evaluation and status of ocean quahog, *Arctica islandica* (Linnaeus) populations off the Middle Atlantic Coast of the United States. U.S. Dep. Commer., NOAA, NMFS, Woods Hole Lab. Doc. 80-32, 4 p.
[4]Chéné, P.L. 1970. Growth, PSP accumulation, and other features of ocean quahog (*Arctica islandica*). Fish Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1104, 34 p.
[5]Meagher, J.J., and J.C. Medcof. 1972. Shell rings and growth rate of ocean clams (*Arctica islandica*). Fish Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1105, 26 p.

Manuscript accepted July 1983.
FISHERY BULLETIN: VOL. 82, NO. 1, 1984.

ness or volume of tissue formed by accretionary growth between successive growth lines." In fact, Jones (1980:333) identified the layers as a "consistently thin, dark gray, translucent increment" of prismatic microstructures which was "easily distinguished from" homogeneous and crossed microstructural layers.

Assessment research on ages of ocean quahogs requires accurate counts and measurements of growth increments. Age observations are customarily made of acetate peel images under optical microscopes with transmitted light. An important assessment requirement is that an annual increment has a distinct beginning and end. The concept of a growth line forming between successive growth increments fulfills that requirement.

Counts of supposed annual growth bands seen in the shells of ocean quahogs by Thompson et al. (1980a, b) resulted in slow growth rates and an extreme longevity estimate of 150 yr. Slow growth rate and suspiciously long life for a bivalve seemed to invalidate the thesis of only a single growth line and growth increment being formed annually. Supportive evidence included finding similar bands in surf clams; finding a low number of bands formed during the onset of sexual maturity that were not explained by less than an annual frequency; finding an expected number of bands in small specimens of known age; finding an expected number of bands formed sequentially in samples taken frequently during 2 yr that had only an annual periodicity; finding a line deposited during the fall-winter, a period coinciding with spawning; and finding ages determined by radiometric analyses that were comparable with band counting. The latter three types of investigation have been expanded by Jones (1980) and Turekian et al. (1982) with the same results. As part of the study, I. Thompson (pers. comm.) marked and released ocean quahogs in the natural environment, but none was recovered. Direct and readily comprehended observations of shell growth after marking were considered to be important additional evidence in support of the thesis of an annual periodicity of growth line and growth increment deposition.

In 1978, the National Marine Fisheries Service marked large numbers of ocean quahogs for release and recovery at a site 53 m deep and 48 km south-southeast of Shinnecock Inlet, Long Island, N.Y., (lat. 40°21'N, long. 72°24'W). Details of this project have been reported in Murawski et al. (1982). Periodicity of growth line formation and shell accretion after notching of recovered ocean quahogs and the microstructure of unmarked and marked shells are described herein with photographic documentation.

METHODS

A commercial clam dredge vessel, the MV *Diane Maria*, was chartered for the marking operation during 25 July to 5 August 1978. The knife of the hydraulic dredge was 2.54 m wide, and the cage was lined with 12.7 mm square-mesh hardware cloth to retain small clams. Ocean quahogs for marking were collected within 9 km of the planting site and released during a 10-d period (ca. 17,000 on 26 July, 3,000 on 2 August, and 21,000 on 4 August 1978). Two 0.7 mm thick carborundum discs, spaced 2 mm apart and mounted in the mandrel of an electric grinder, produced distinctive parallel, shallow grooves from the ventral margin up onto the valve surface (Ropes and Merrill 1970). Four operators of grinders marked about 1,600 clams/h. Groups (ca. 3,000-8,000) of marked clams were released at loran-C coordinates within a rectangular area of about 3 by 6 μs.

Marked clam recoveries were made in conjunction with annual clam resource surveys. During recovery operations, a Northstar 6000[6] loran-C unit and Epsco loran-C plotter aided in a systematic search of the planting site. Marked clam recoveries were highly variable. On 20 and 21 August 1979 and about 387 d after the marking operation, 43 hydraulic dredge tows at the planting site captured 14,043 ocean quahogs and 74 (0.5%) were marked; on 9 September 1980 and 773 d after the marking operation, 1,899 ocean quahogs were captured in 2 dredge tows and 249 (13.1%) were marked. Some marked specimens were damaged, but 67 recovered in 1979 and 200 recovered in 1980 were alive and had intact paired valves.

Recaptured specimens were frozen to prevent periostracum loss from drying and to facilitate opening without shell damage. Microscopic examination of 267 notched shells was made to assess the effects of marking and to obtain growth measurements. Shell measurements were made to the nearest 0.1 mm by calipers; growth after marking was measured to the nearest 0.01 mm by an ocular micrometer in a dissecting microscope. Acetate peels of all marked ocean quahogs were prepared by the procedures described by Ropes (1982[7]). Briefly, radial sections from the umbo to ventral margin were produced on left valves, oriented to include the broadest surface of the single prominent tooth in the hinge. This exposed the internal growth lines in the valve and hinge tooth for later treatment. The paired notch marks in a valve

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Ropes, J. W. 1982. Procedures for preparing acetate peels of embedded valves of *Arctica islandica* for aging. U.S. Dep. Commer., NOAA, NMFS, Woods Hole Lab., Doc. 82-18, 8 p.

were not usually oriented in the above plane of radial sections, so additional radial cuts were made to expose growth lines in the notch area. Subsequently, shells were embedded in an epoxy resin, and the cut shell edge ground on wetable carborundum paper and polished. Acetate peels were produced after etching the shell cut surfaces in a 1% HCl solution for 1 min, followed by microscopic examination of the peels that were sandwiched between slides.

Preparation of polished and etched radial sections of marked and unmarked ocean quahog valves were further examined by scanning electron microscopy (SEM)[8]. These examinations included vertical transects from the periostracum to the shell's interior and specific sites affected by the marking operation. Shell microstructure was diagnosed by using the classification scheme of Carter (1980), wherein shell microstructures are elucidated on the basis of their major (i.e., first-order) structural arrangement, independent of genetic or optical crystallographic criteria.

RESULTS

Whole Shells

Notch marks showed clearly on wet shells but periostracum obscured the ventralmost ends extending well beyond the ventral valve margin on all specimens (Figs. 1-4). Cuts made in the shell-free periostracum beyond the ventral margin of some large quahogs had not been repaired after 2 yr (Fig. 4a); small individuals, however, had completely formed yellowish-brown periostracum (grayish white in the photographs) over new shell growth, which contrasted sharply with darker, earlier deposition (Fig. 3a).

In some specimens, the mark formed U-shaped notches at the marginal edge of the old shell. New shell deposition was obviously disrupted for quahogs with deep U-notches, since the marginal shell between the notches was outlined in relief over new shell (Fig. 3b, c). Faint paired bulges were also found on the ventral inner surface of the notched valve of a few shells and occasionally the notches extended part way onto the opposite valve. An occasional live quahog was found with a cracked valve caused from handling during the marking operation. The blackened margins of the cracks, suggestive of reducing conditions, indicated that the cracks were old. There was no evidence of repair by shell covering the cracks in quahogs recovered 2 yr after marking.

Sectioned Shells

An interruption of shell deposition from notching in some sectioned shells was visible without magnification in the cut surfaces. Microscopic examination revealed a depression that curved dorsally back into the shell from the external surface and became increasingly attenuated until it was unrecognizable from the usual shell features along the inner margin. This type of interruption was greatest in shells of small quahogs, probably due to some mantle tissue incision. Periostracum penetrated into the interruption to a depth of about 1 mm. The thicker and tougher periostracum of large clams was less easily incised during marking and probably served to minimize incision of mantle tissue.

Acetate Peels of Sectioned Shells

Acetate peels enhanced detection of interruptions in shell deposition due to notching (Figs. 1d, 2d, 3d, 4d). In small clams (<80 mm shell length), the interruption was immediately followed by a line similar to a succession of lines formed throughout the valve before marking. No additional lines were evident thereafter to the marginal tip in shells examined from the late August 1979 recovery, but in 34 shells of small clams recovered in early September 1980, a second line occurred about midway to the tip in all shells and a third line had formed very near the marginal valve tip and along the inner margin in 47% (Fig. 3d). These were all considered to be annual growth lines for reasons dicussed later. Shell deposition between growth lines in the outer layer had a granular appearance, which was sometimes broken by a faint line of uncertain origin (Figs. 1d, 3d). The interruption of shell deposition from marking was also evident in large ocean quahogs (Figs. 2d, 4d), although an infiltration of the depression with periostracum was not clearly evident. The separation of shell deposits was more definite and extended deeper into the shell of large clams, sometimes to a depth of 2 mm (Figs. 2d, 4d). Growth lines were very closely spaced (ca. 100 μm) and the shell depositional texture in between lines appeared similar to that seen in smaller clams. In large ocean quahogs, new shell was formed laterally beyond the notch mark and was an indication that the notching operation had little effect on shell deposition and growth (Figs. 5a, 6a).

None of the marked quahogs had as severe an

[8]SEM work was performed on an ETEC Autoscan instrument at the Dental Research Center, University of North Carolina, Chapel Hill, N.C.; on the JEOLJSM-35 of the Biology Department, Princeton University, Princeton, N.J.; and on the ISI 1200 of the Department of Geology, University of Florida, Gainesville, Fla.

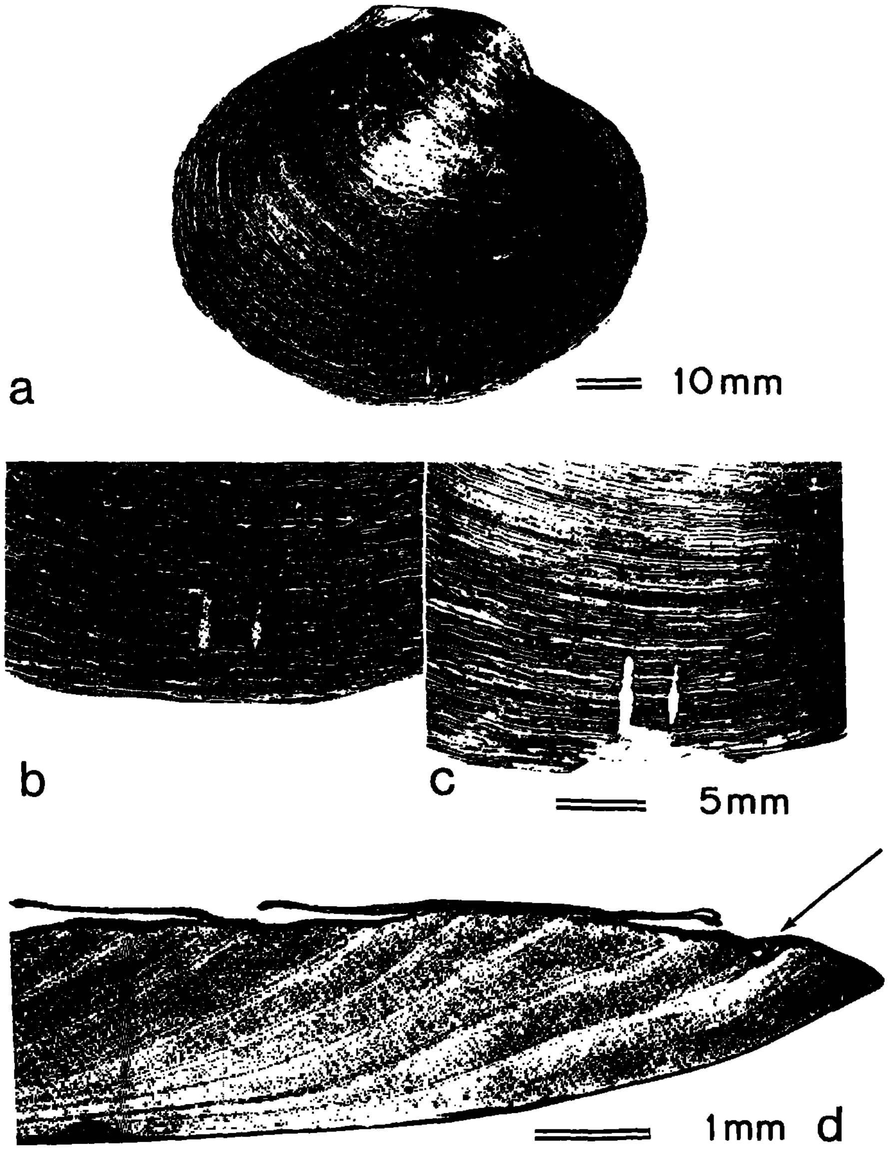
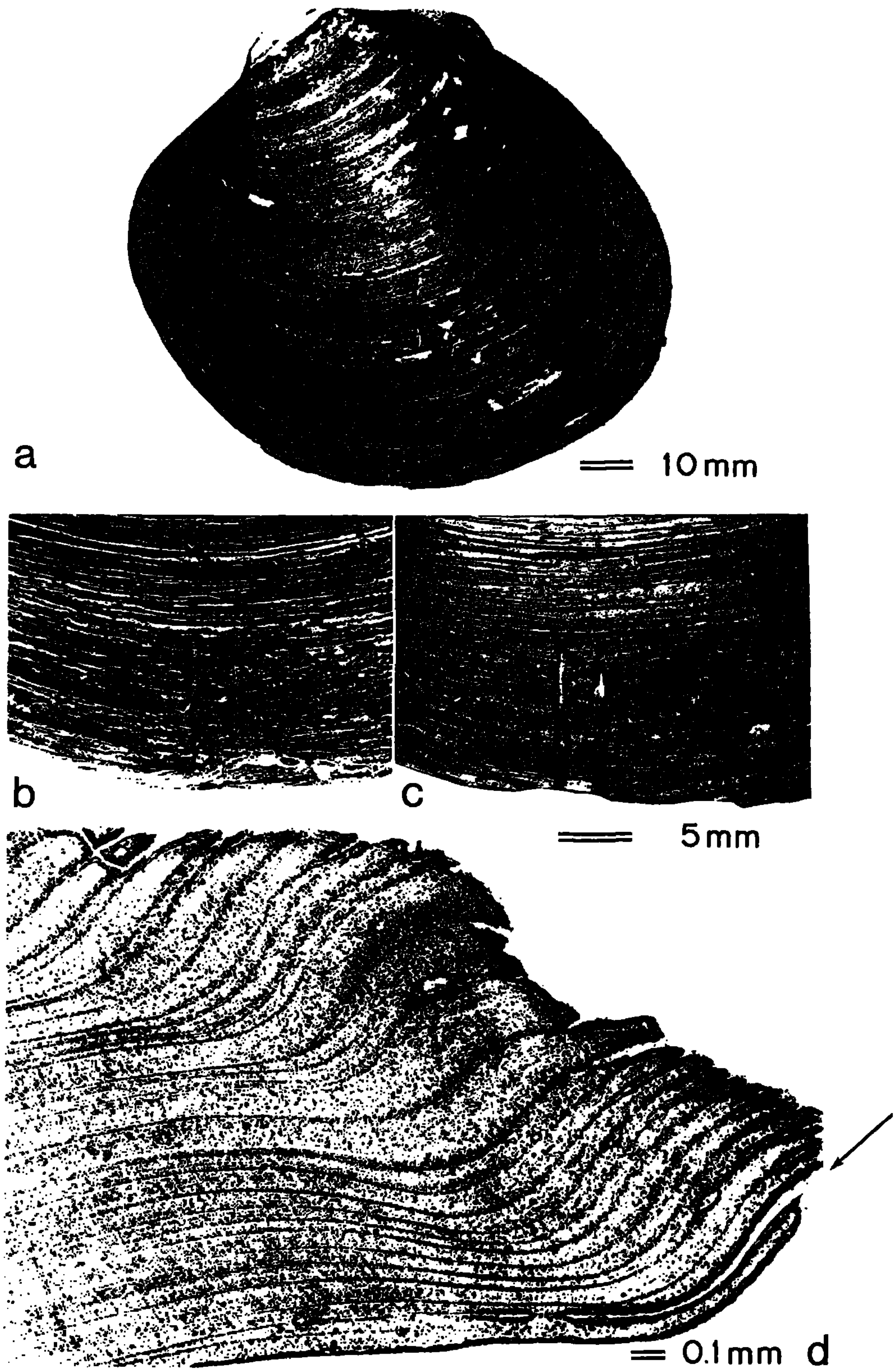


FIGURE 1.—(a) Right valve of an 18-yr-old ocean quahog, *Arctica islandica*, 71.4 mm in shell length recovered on 21 August 1979. Estimated annual growth was 1.3 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (microprojector) of seven repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam in 1978. An internal line is evident between the mark-induced line and the valve edge. This line is the normally occurring age mark probably formed in late autumn-early winter. Scale bars of magnification are included.

FIGURE 2.—(a) Left valve of an ocean quahog, *Arctica islandica*, about 110 yr old and 100.5 mm in shell length recovered on 20 August 1979. Estimated annual growth in 1 yr was 0.1 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (compound microscope) of many repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Scale bars of magnification are included.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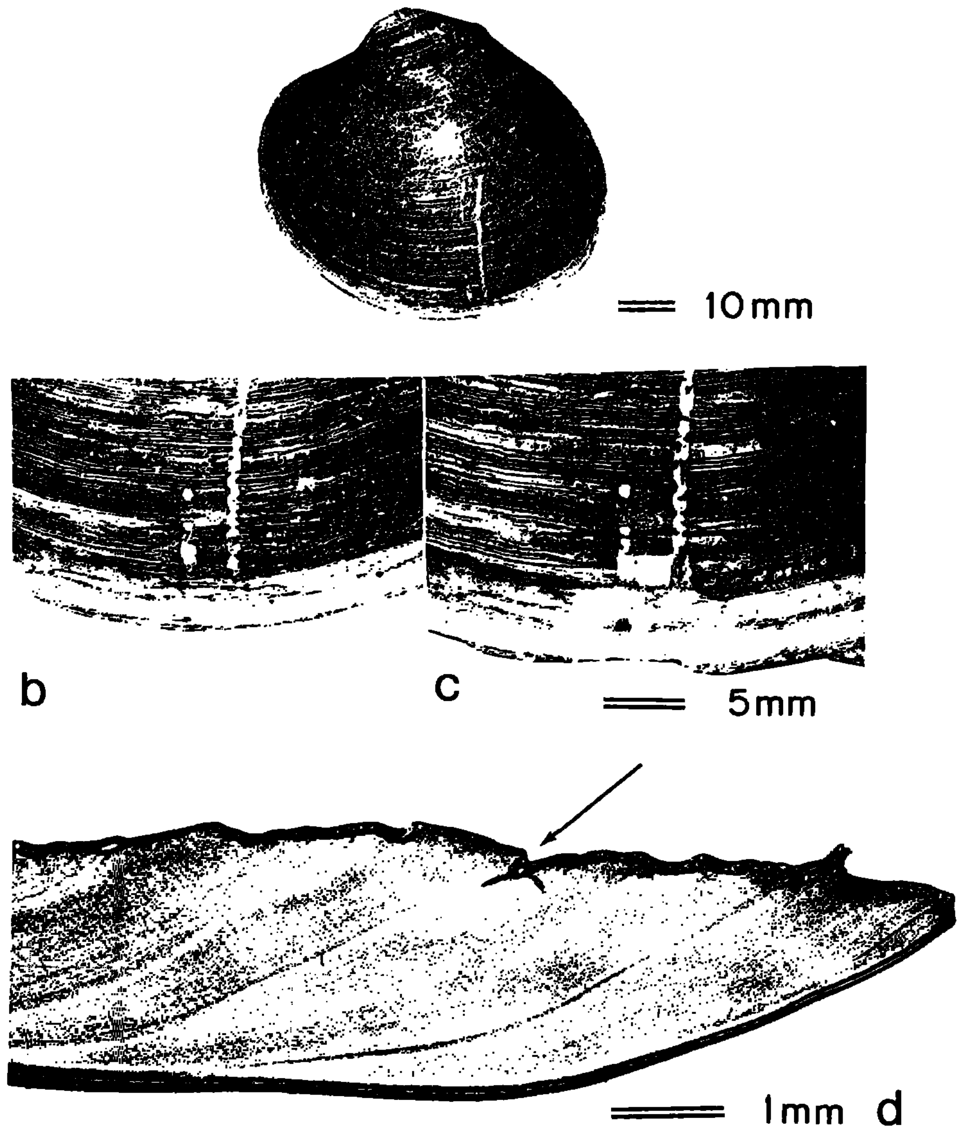
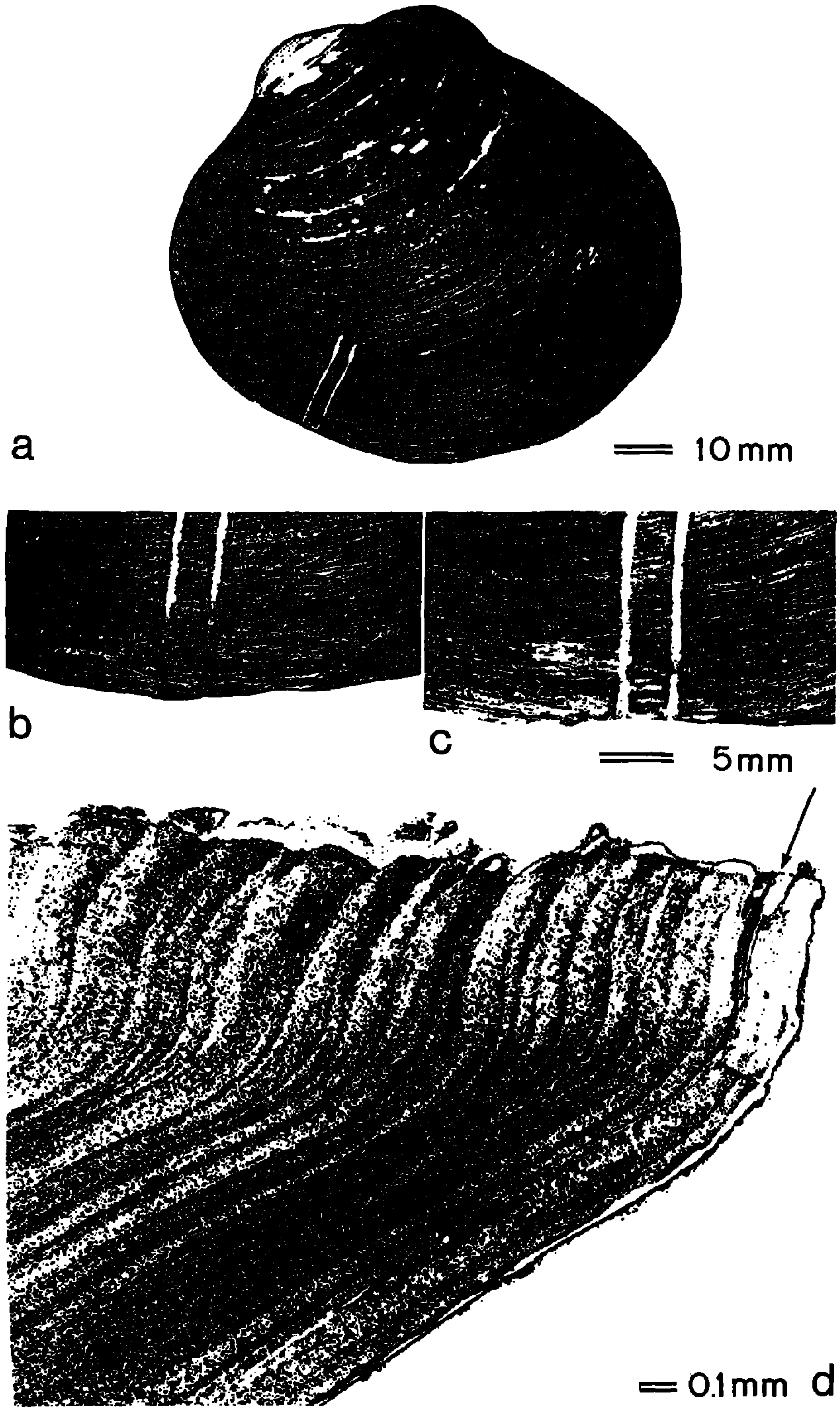


FIGURE 3.—(a) Left valve of a 15-yr-old ocean quahog, *Arctica islandica*, 61.7 mm in shell length recovered on 9 September 1980. Estimated 2-yr growth increment was 3.2 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (microprojector) of five repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Two additional lines, one midway to the valve tip and one near the valve tip, were formed after marking the quahog. Scale bars of magnification are included.

FIGURE 4.—(a) Left valve of an ocean quahog, *Arctica islandica*, about 95 yr old and 91.7 mm in shell length recovered on 9 September 1980. Estimated 2-yr growth increment was 0.3 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (compound microscope) of many repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Scale bars of magnification are included.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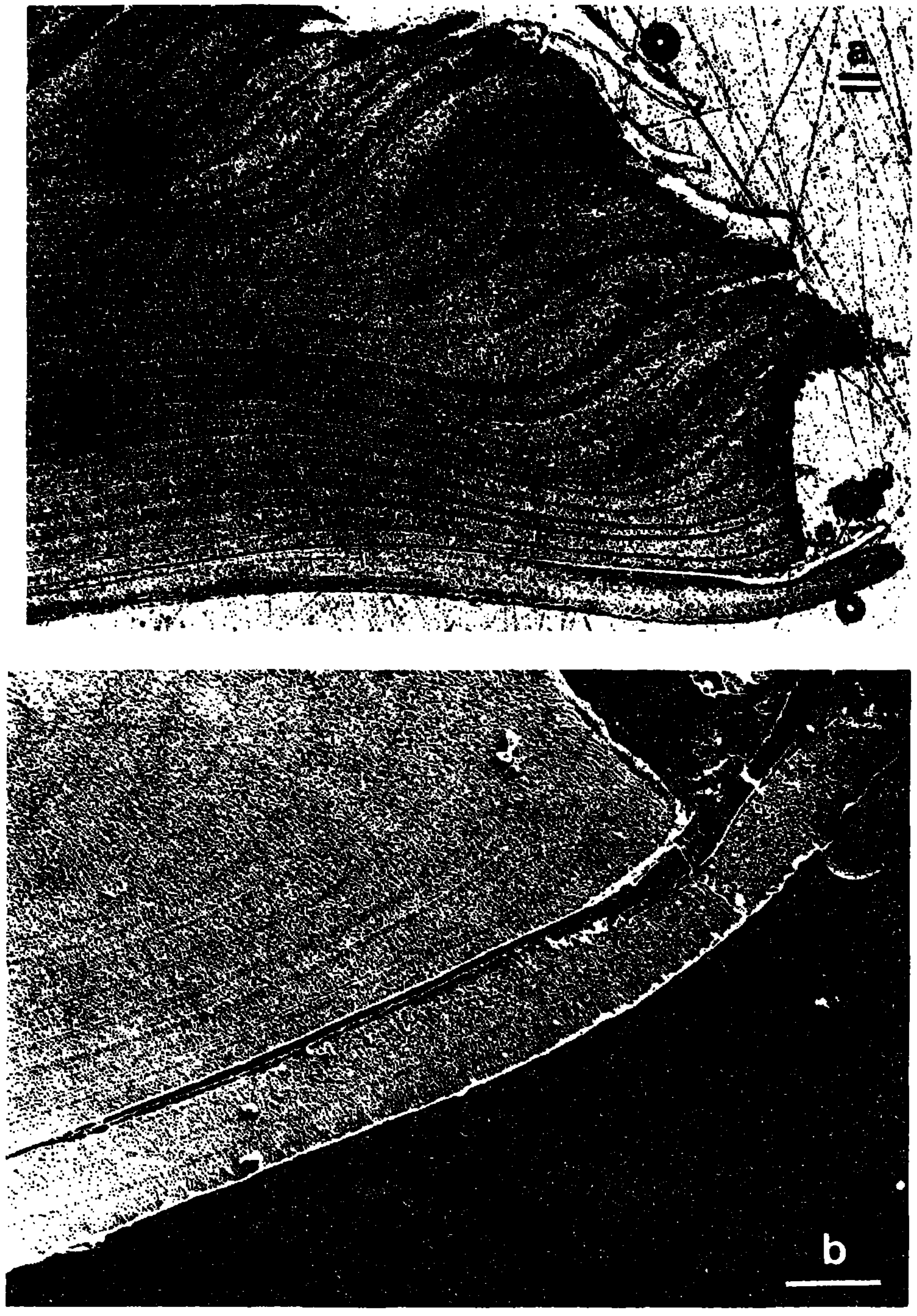
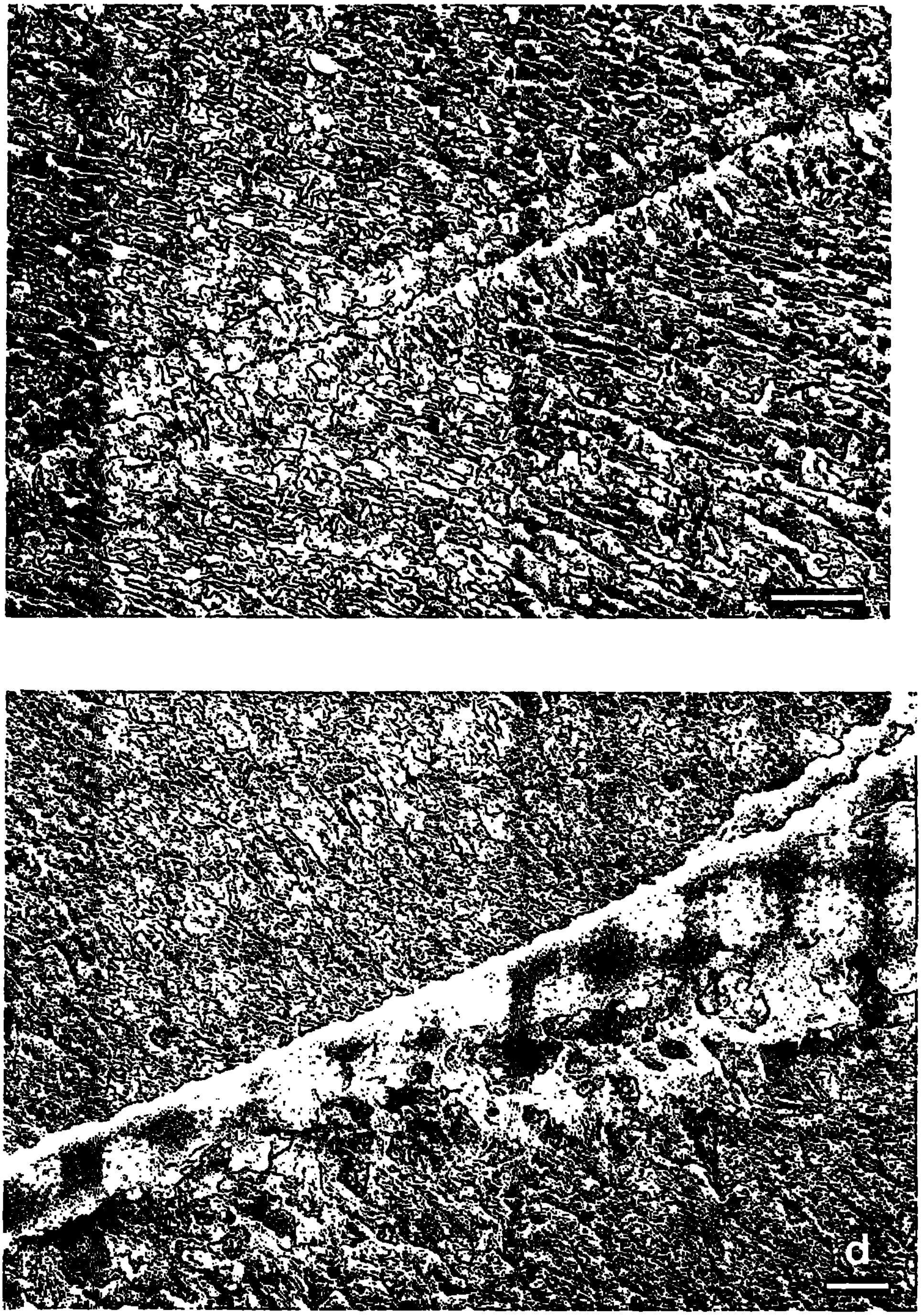


FIGURE 5.—(a) Optical photomicrograph (compound microscope) of an acetate peel at a notch-mark in the ocean quahog, *Arctica islandica*, shown in Figure 2 (scale bar = 100 μm). Note the single annual increment of growth formed laterally beyond the notch-mark. (b) SEM photomicrograph of the same shell specimen (scale bar = 100 μm). Abbreviatons of shell microstructural terms in this and subsequent figures are expalined in this text. (c) Transitional CA-CL microstruc-



ture interrupted by an ISP band that extends from the notch-line seen in (b) (scale bar = 10 μm). This photomicrograph was taken beyond the field of view of (b), to the lower left and beyond the zone of epoxy penetration. (d) Enlargement of epoxy penetration zone from (b) interrupts normal shell microstructure followed by a zone of cavernous, poorly organized, disrupted shell growth (scale bar = 10 μm).

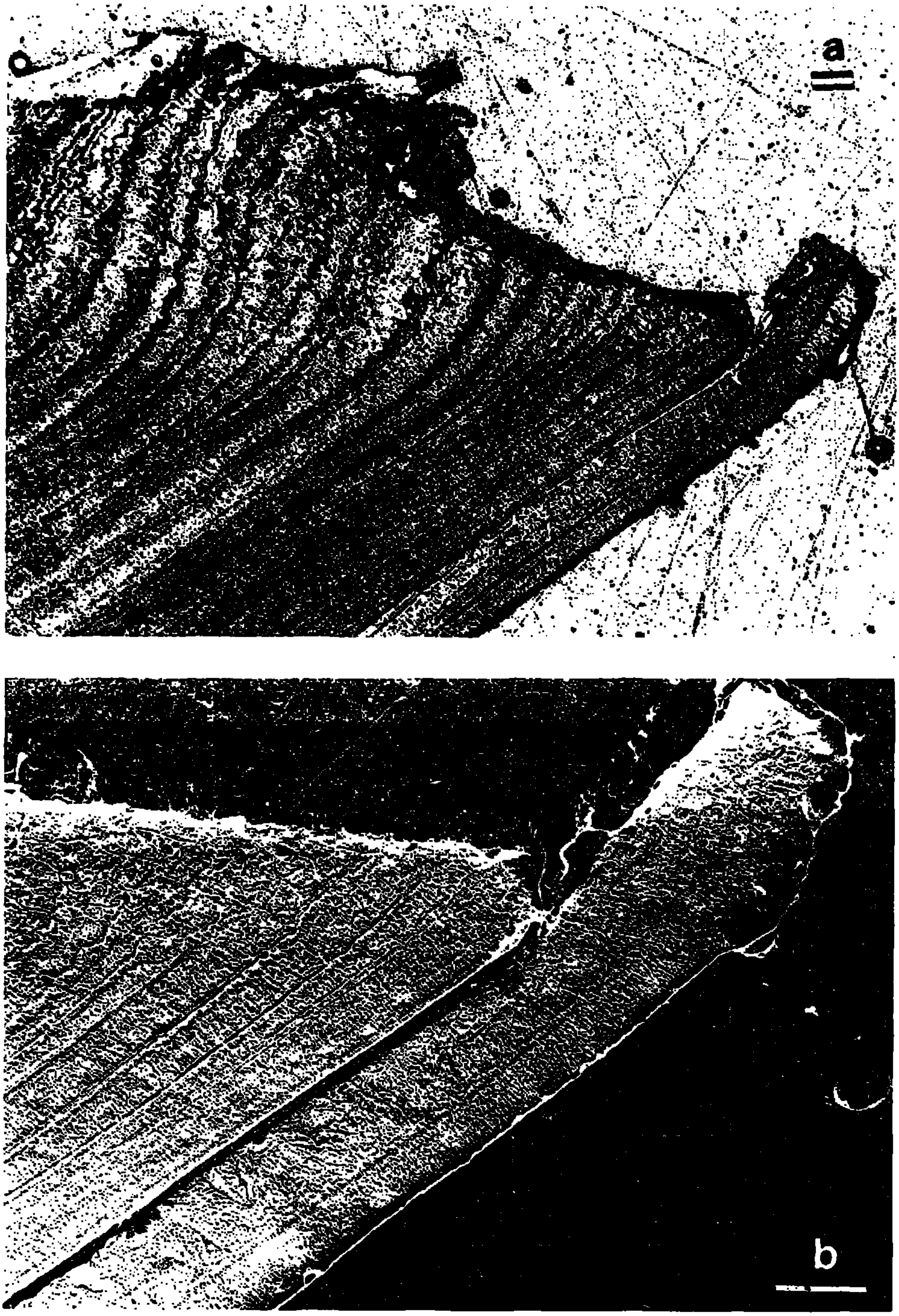
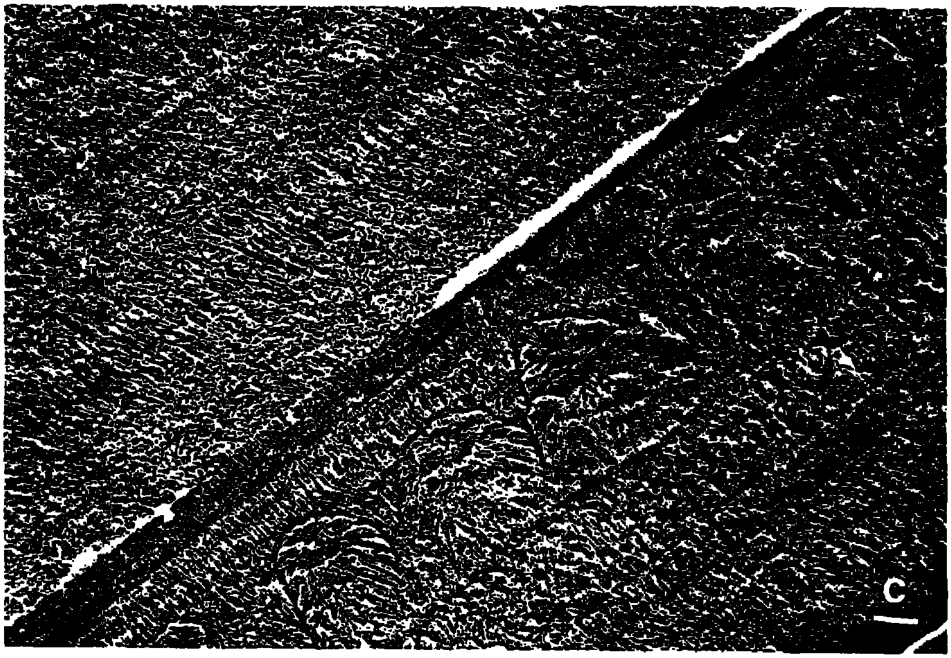
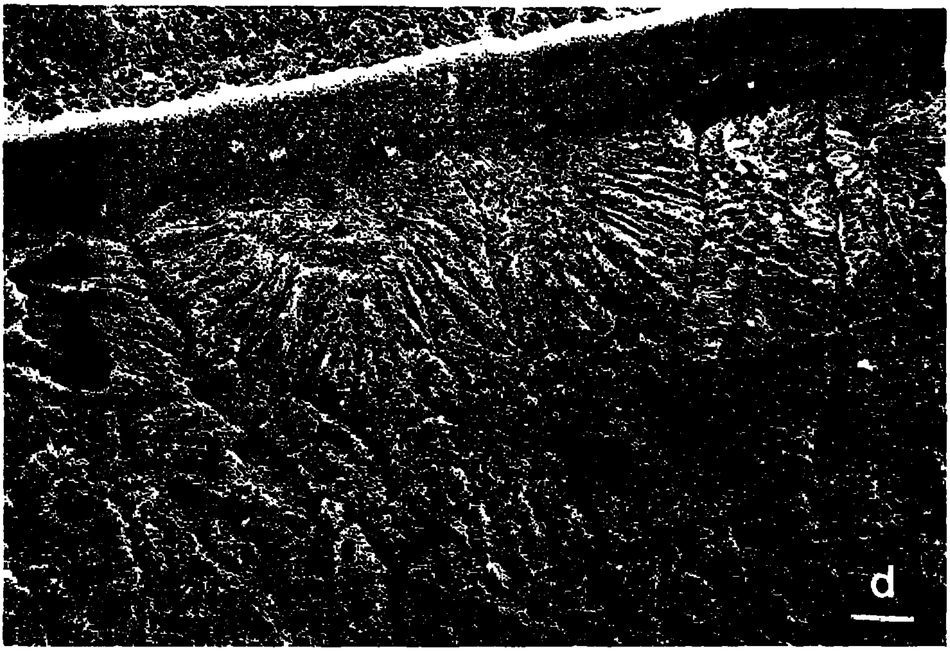


FIGURE 6.—(a) Optical photomicrograph (compound microscope) of an acetate peel at a notch-mark in a 100.3 mm long ocean quahog, *Arctica islandica*, about 110 yr old recovered on 9 September 1980. Note two annual increments of growth formed laterally beyond the notch-mark, estimated to be 0.1 mm (scale bar = 100 μm). (b) SEM photomicrograph of the same specimen (scale bar = 100 μm). The penetration of epoxy medium corresponds to the marking event. (c) Tran-





sitional CA-CL microstructure in the upper left interrupted by the penetration of epoxy into the shell along the line corresponding with the notching event (scale bar = 10 μm). Beyond the zone of epoxy penetration this line is recognized as an ISP band. Following this line is a zone of SphP disruption growth which gradually gives way to transitional CA-CL. This photomicrograph was taken off the field of view of (b), to the lower left. (d) Disruption growth of SphP microstructure following the line which corresponds to marking of the clam (scale bar = 50 μm).

interruption in shell deposition as did a 66.4 mm shell-length specimen collected during a 1980 winter clam survey (Fig. 7 a, b). A depression outlined the entire shape of the clam at the time of its formation and at 25.9 mm shell length. The shell formed before the depression was raised laterally above that formed afterwards in a shinglelike fashion. Both valves of the clam showed the interruption. The smaller shell shape was only slightly atypical for ocean quahogs, and no irregularity was found as an indication that an injury had occurred. The ratio between the greatest shell height (21.4 mm) and shell length (25.9 mm) of the smaller shell was 0.826, and for the entire shell (50.2 mm shell height; 66.4 mm shell length) was 0.756. These values suggest that growth after the depression departed from the more typical, isomet-

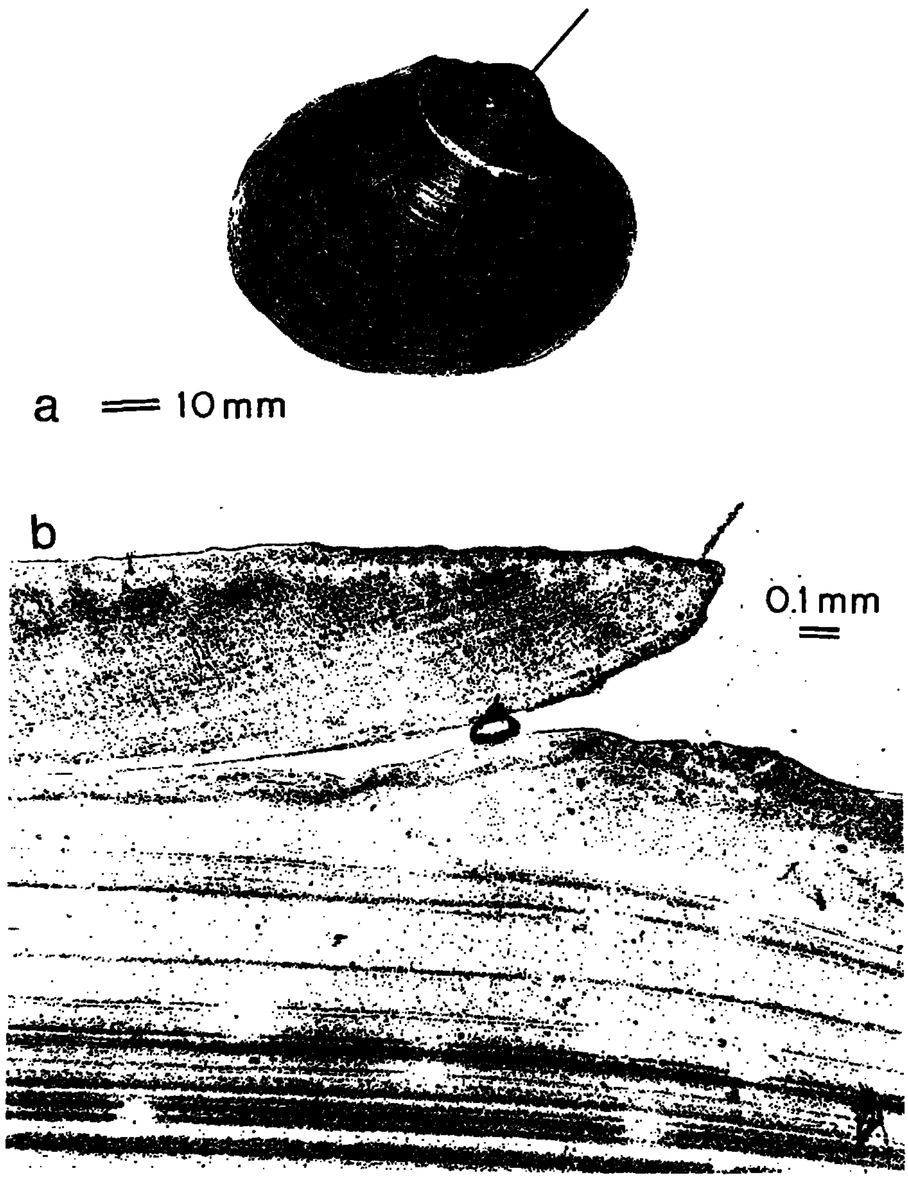


FIGURE 7.—(a) Right valve of an ocean quahog, *Arctica islandica*, 23 yr old and 66.4 mm in shell length collected near the marking site during 1980. An obvious interruption of growth (arrow) and radiating lines in the anterior half of the valve are shown. (b) Optical photomicrograph (compound microscope) of an acetate peel of the sectioned valve at the site of growth interruption. Scale bars of magnification are included.

ric growth reported for ocean quahogs by Murawski et al. (1982). Light radial lines extended from the umbonal area to valve margin in the periostracum of the anterior half of the shell formed after growth had been interrupted, but their significance was not evident.

Microstructure of Unmarked Shells

The ocean quahog shell is entirely aragonitic with an inner and outer layer separated by an extremely thin prismatic pallial myostracum. The latter is composed predominantly of irregular simple prisms (ISP) and occasionally a few fibrous prisms (FP). Both principal shell layers contain two growth sublayers: The thin annual growth line and the wider annual growth increment. Significant variations were found in the microstructure of each during examinations by SEM.

The distribution of microstructures in a typical ocean quahog shell may be seen by considering a transect from the exterior to interior depositional surfaces. The thick, dark brown or black periostracum is an obvious exterior surface covering, but it is intimately associated with the shell. Some aragonitic shell material is invariably removed when peeling off the periostracum and granules of aragonite were found embedded in it during examination of unetched thin sections under the crossed nicols of a polarizing microscope. The aragonite is dissolved by etching the polished surfaces of sectioned shells, leaving cavities, some with angular faces in the periostracum (Fig. 8a).

Important microstructures for aging purposes are found mostly in the outer shell layer. The dominant growth increment sublayer beneath the periostracum exhibits a granular homogeneous (HOM) microstructure which is very cavernous and has bleblike isolated crystal morphotypes (ICM) (Fig. 8b, c). These microstructures typically grade into incipient ISP (Fig. 8d). Below the prisms is a layer of crossed microstructures which appear to be transitional between simple crossed lamellar (CL) and crossed acicular (CA) structures (Fig. 8d). The latter predominates in the middle portion of the outer shell layer with occasional occurrences of fine complex-crossed lamellar (FCCL) microstructure. Transitional CA-CL microstructures are also seen in Figure 8e.

In the thin growth lines of the outer shell layer, FP near the external surface soon give way to very distinctive spherultic prisms (SphP) (Fig. 9a-d). These SphP themselves grade into composite prisms (CompP) which are comprised of first-order prisms with the second-order prisms radiating toward the depositional surface from a central, longitudinal axis. Closer toward the inner shell layer the FP, SphP, and CompP microstructures are gradually replaced by ISP bands.

The inner shell layer is characterized by growth lines composed of ISP which alternate with growth increment bands of FCCL microstructures. The hinge plate and tooth region have microstructures recognizable as distinct sublayers that are important for aging purposes. Here growth lines are constructed of narrow ISP (Fig. 9e). These alternate with growth increment bands that are composed of transitional CA-CL, FCCL, and HOM microstructures (Fig. 9e).

In summary, ocean quahog shells are composed largely of HOM, CA-CL, and minor amounts of FCCL microstructures with prismatic bands of local importance. The latter constitute the growth line layer; the former the growth increment layer. Figure 10 is a diagrammatic sketch of the distribution of microstructures in the two principal layers of the valve of a typical ocean quahog.

Microstructure of Marked Shells

Variations in the shell microstructure associated with notching and subsequent shell growth of ocean quahog specimens were studied by examining the ventral margins of six quahogs. The same basic pattern described for unmarked shells was observed in these specimens. Optical and scanning electron photomicrographs of two shells illustrate the salient features (Figs. 5, 6).

The notching event in both shells was accompanied by a disruption of the normal growth pattern and a resumption of shell growth at a new orientation. This is seen in Figures 5a and 6a as a prominent flattened surface in the exterior shell surface from the marking operation followed by a lateral extension of the shell margin out beyond the notch mark and old shell surface. The extension represents renewed growth at a new orientation. Retraction of the mantle during the marking process and resumption of shell growth at a slightly new orientation resulted in a zone of either loosely calcified or uncalcified shell paralleling the shell margin and extending from the notch inward toward the depositional surface. This zone is filled with epoxy medium during the embedding process and is seen in Figures 5b and 6b, c, and d as the resistant, unetched material penetrating several millimeters into the outer shell layer. The penetration zone disappeared shortly beyond the field of view in Figures 5b and 6b. Where this happened (Fig. 5c), a

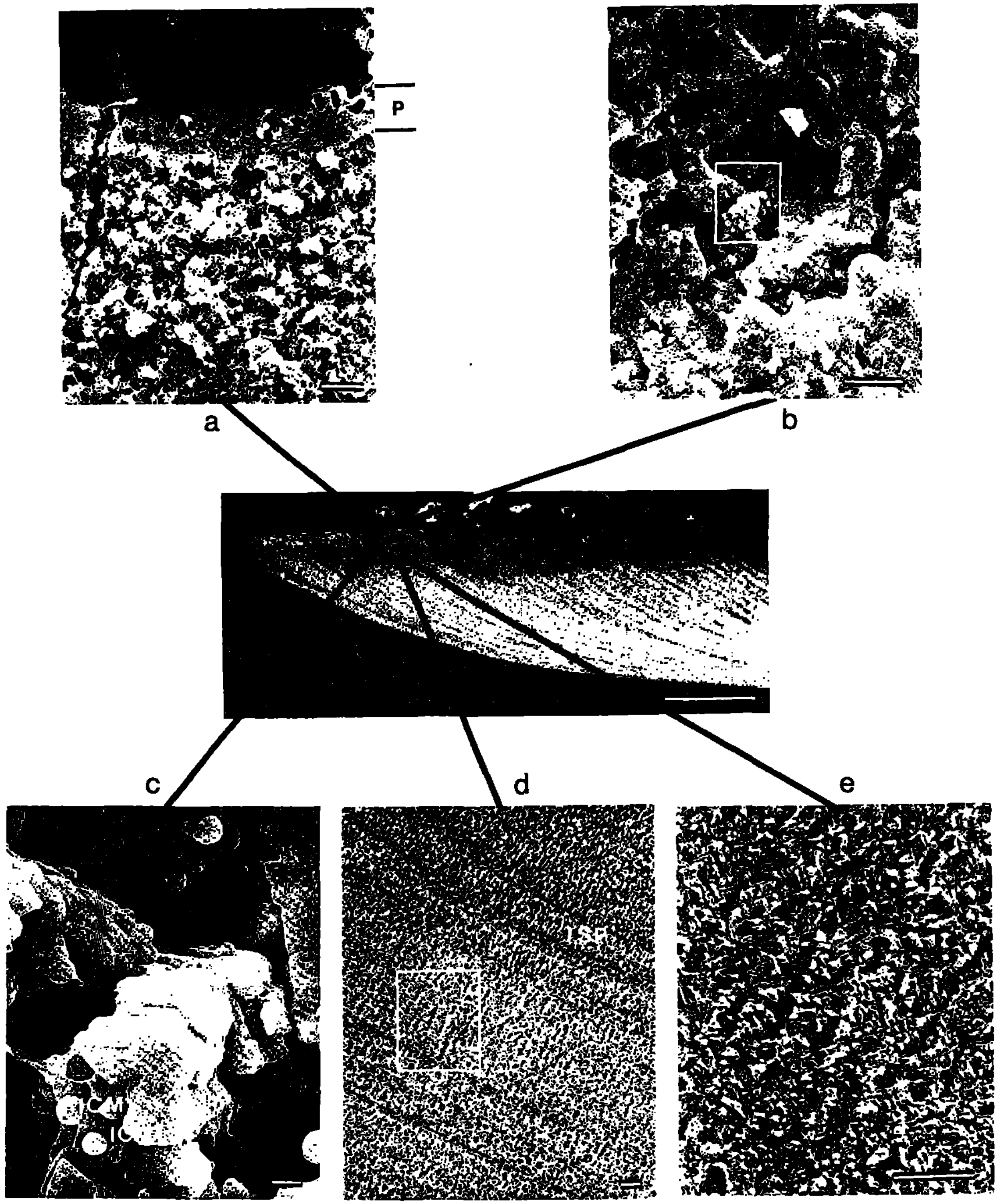


FIGURE 8.—Microstructural variation in the shell of a 97.5 mm long, 92-yr-old ocean quahog, *Arctica islandica*. The central photograph is of an acetate peel from a radial, polished, and etched section through the valve at the ventral margin. Black lines locate SEM photomicrographic enlargements of specific polished and etched areas in the section valve (scale bar = 1 mm). (a) Periostracum ("P") with angular cavities and HOM microstructure (scale bar = 10 μm). (b) Cavities in HOM microstructure of outermost valve surface. White rectangle encloses are enlarged in (c) (scale bar = 10 μm). (c) Cavities showing bleblike ICM structures (scale bar = 1 μm). (d) HOM microstructure at top trending to ISP, then to transitional CA-CL toward the bottom. White rectangle encloses the area enlarged in (e) (scale bar = 10 μm). (e) Transitional CA-CL microstructure at higher magnification (scale bar = 10 μm).

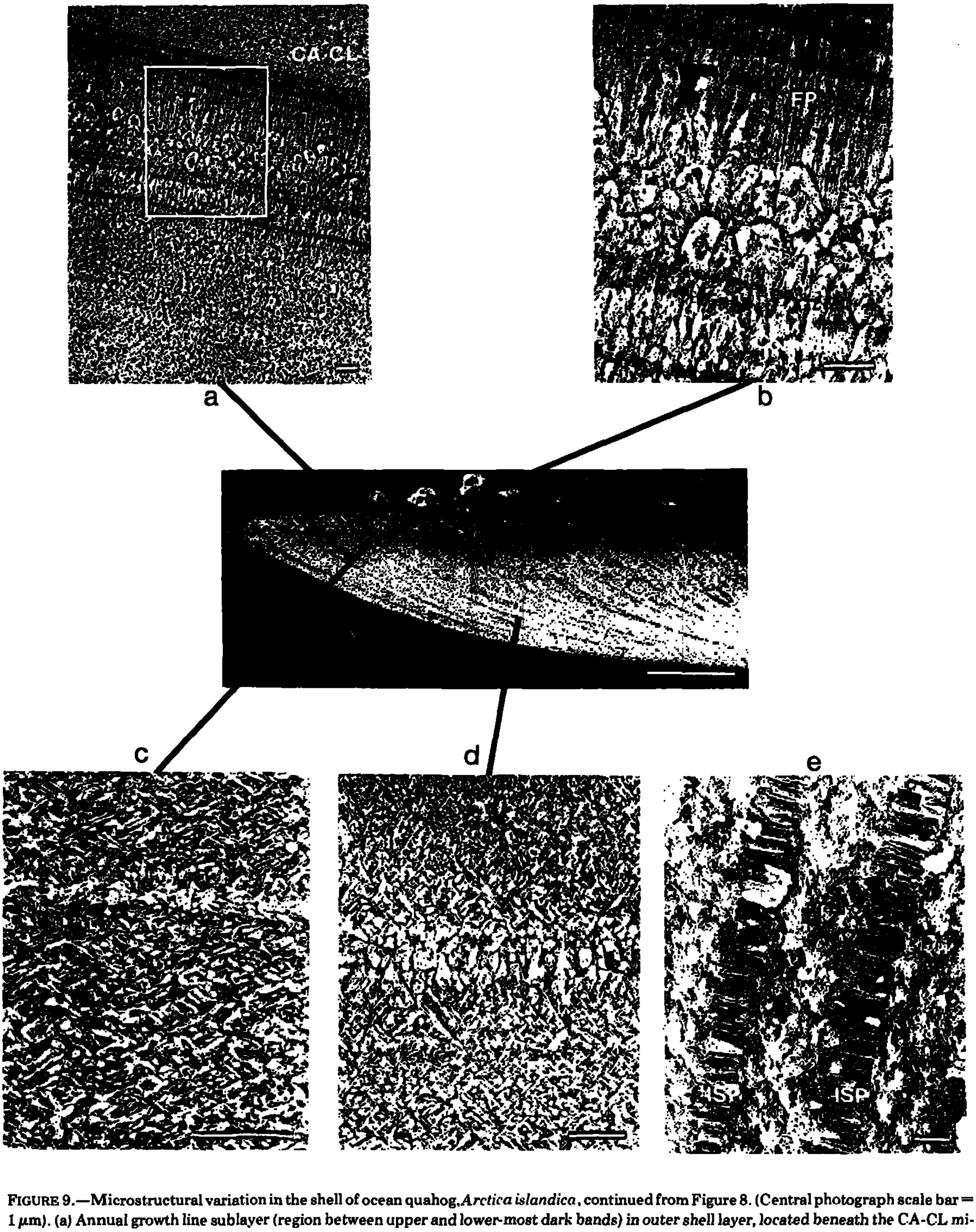


FIGURE 9.—Microstructural variation in the shell of ocean quahog, *Arctica islandica*, continued from Figure 8. (Central photograph scale bar = 1 μm). (a) Annual growth line sublayer (region between upper and lower-most dark bands) in outer shell layer, located beneath the CA-CL microstructure of Figure 8e. White rectangle encloses the area enlarged in (b) (scale bar = 10 μm). (b) The center of the growth line sublayer showing FP, SphP, and CompP microstructures (scale bar = 10 μm). (c) Transitional CA-CL microstructure of the growth increment sublayer below (b) (scale bar = 10 μm). (d) ISP forming growth line sublayer within FCCL microstructure. Photomicrograph from area closer to the depositional surface than previous photos (scale bar = 10 μm). (e) HOM microstructure interrupted by two prominent ISP bands from a section through the hinge plate (scale bar = 10 μm).

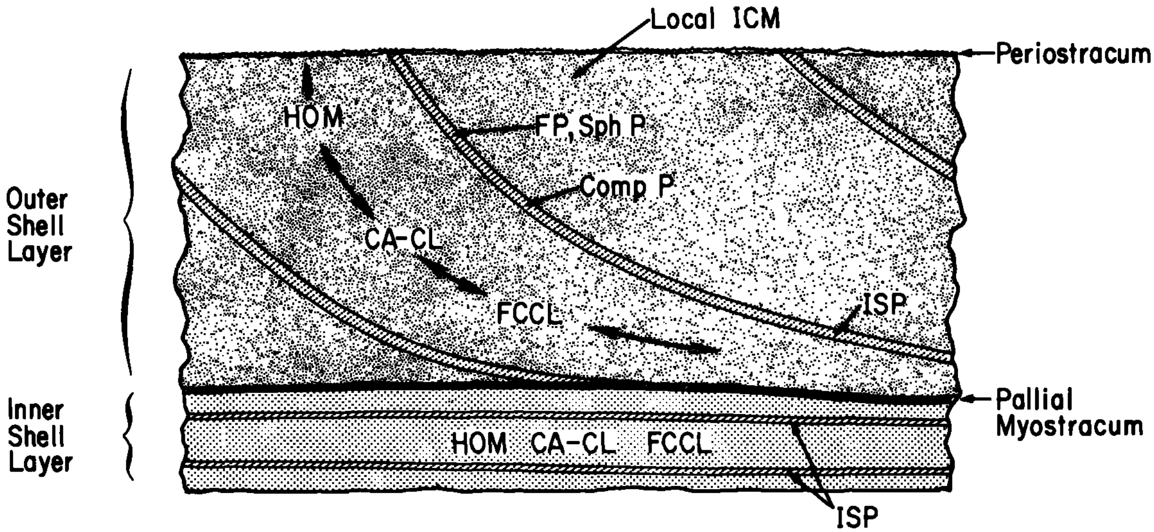


FIGURE 10.—Idealized, partial, radial cross section through the shell of a typical ocean quahog, *Arctica islandica*, showing the distribution of shell microstructures. Ventral margin is toward the left. Section is located inside the pallial line. Legend of acronyms: ICM = isolated crystal morphotypes; FP = fibrous prisms; SphP = spherulitic prisms; CompP = composite prisms; ISP = irregular simple prisms; HOM = granular homogeneous; CA = crossed acicular; CL = crossed lamellar; FCCL = fine complex crossed lamellar.

growth line of ISP continued parallel to the earlier growth lines.

The typical outer shell layer structure formed by the time of marking is noted in Figures 5b and 6b. These figures clearly show the alternation of the growth line and growth increment sublayers. However, immediately following the marking event all specimens showed a disruption in microstructural development, especially out near the shell surface. This coincided with the presence of loosely organized SphP immediately following the marking event line (see particularly Fig. 6c, d). The disruption zone consisted of cavernous, poorly organized, microstructure (Fig. 5d).

In all six shells examined, the growth line associated with the marking event continued inward toward the shell interior, even beyond the zone of epoxy penetration (Figs. 5b, 6b). When this line was traced inward, it was indistinguishable from the many earlier formed growth lines. Such a view is seen in Figure 5c located well off the field of view Figure 5b, to the bottom left. Here the growth line consisted of a diagonal ISP band bounded on both sides by transitional CA-CL microstructure.

DISCUSSION

The layering and separation between growth lines and growth increments of small ocean quahogs (< ca 60 mm shell length) are often visible macroscopically on the external surfaces of whole valves and in the cut surfaces of radial sections. However, macro- or microscopic examinations of large ocean quahog valves are consistently frustrated by a lack of clear differentiation of the same growth phenomena. Preparation of acetate peels of shell cross sections, as has been described and photographically documented, greatly enhances discrimination of the lines and increments of growth throughout the range of shell sizes.

Past investigators of the microstructure of ocean quahog shells described some of the basic components, but did not clearly elucidate differences between the lines and increments of growth. Sorby (1879: 62) appears to have given the first description of the structure of the *Arctica* (= *Cyprina*) *islandica* shell: "In *Cyprina islandica* we have another extreme case, in which the fibres perpendicular to the plane of growth are so short as to appear like granules, though the optic axes are still definitely oriented in the normal manner." Bøggild (1930:286) reported that he was unable to confirm Sorby's observations. Instead he stated that *Arctica islandica* belongs to a group of species within the Arcticidae (= Cyprinidae) having the least visible structure among all the bivalves. He terms this structure homogeneous but suggests there are small traces of other structures in the shell. Bøggild (1930) goes on to point out that the lower part of the shell (inner layer) is perhaps more "... representative of the common, complex structure ... and ... there are alternating layers of more transparent layers and finely grained ones." More recently Taylor et al. (1969, 1973) examined the shell microstructure of *Arctica islandica*, which they adopted as their "type species" to illustrate homogeneous shell microstructure. Basically, the general picture by Bøggild (1930) agrees with that of Taylor et al. (1969), who used electron microscopy in their investigation. However, they disagreed sharply with Bøggild that the inner shell layer was "representative of the common complex structure." After examining unetched fractured sections and polished and etched sections of both shell layers, Taylor et al. (1969, 1973) concluded that both shell layers in *Arctica islandica* are built of minute, irregular rounded granules, quite variable in size (1.5-3 μm across), having highly irregular contacts with their neighbors and being poorly stacked. Taylor et al. (1969:51) further reported: "In peels and sections of the inner layer, within the pallial line there is a marked colour banding, in greys and browns. The only fine structure that can be resolved is a suggestion of minute grains, which are most conspicuous in the translucent, grey-colourless parts of the shell. These grains are arranged in sheets parallel to the shell interior. In the outer layer grains can also be resolved, but are arranged in sheets parallel to the margin of the shell and growth lines." They also noted that these features are more clearly seen in the umbonal region where the orientation of grains normal to layering is very conspicuous. Taylor et al. (1969) suggested that the layering is a reflection of repeated (?diurnal) deposition of carbonate (a prospect deemed very unlikely by Thompson et al. 1980a). Also in the umbonal region are thin (2-3 μm) prismatic bands which parallel the layering. Outside the pallial line, Taylor et al. (1969) reported the outer shell layer to be very dense and opaque, with the most obvious structural features being fine grains arranged in sheets giving the layer a finely banded appearance.

Analyses under SEM of oriented fractured, and polished and etched sections of ocean quahog shells revealed that microstructural variation is more complex than had been proposed by Bøggild (1930) or Taylor et al. (1969, 1973). Thin sections of isolated periostracal fragments examined under crossed nicols confirmed the presence of embedded aragonite granules in the periostracum of ocean quahogs reported for other recent bivalves (Carter and Aller 1975). These granules probably form a layer like that described for the blue mussel, *Mytilus edulis*, by Carriker (1979). After special treatment of the valves for examination by SEM, he found "a thin discrete calcareous layer continuous over the outer surface of the valves between the periostracum and the outermost shell layer." The layer is called mosaiostracum. The shell microstructure in the growth increment sublayer beneath the periostracum is HOM, as Bøggild (1930) and Taylor et al. (1969, 1973) reported. The "... minute, irregular, rounded granules ... have highly irregular contacts ... " (Taylor et al. 1969:51) that are particularly well exposed in fracture sections. An abundant transitional CA-CL microstructure was found in the middle portion of the outer shell layer and growth increment sublayer. This study confirmed its presence in ocean quahogs as reported by Carter (1980). The growth line sublayer of the outer shell layer had four grades of prismatic structure (FP, SphP, ComP, and ISP). Lutz and Rhoads (1977) examined the inner shell layer near the umbo of ocean quahogs and found bands of simple aragonitic prisms alternating with complex-crossed lamellar and homogeneous structures. We found similar microstructures in the inner shell layer of the valve of ocean quahogs. Our analyses identified distinct microstructures, not unlike those found in the valve for the growth line and growth increment layers in the hinge plate.

Growth line deposition more nearly approximates an annual event than any shorter or longer interval. Marked clams recovered in late August 1979 had formed only one growth line other than the mark-induced check soon after the notching operation in 1978. They had been free about 22 d longer than a calendar year. Those recovered in early September 1980 all had formed the growth line soon after the notching operation, like those recovered in 1979, and a second line appeared midway to the ventral valve edge, which in all probability had been formed after the late August 1979 recovery effort. These clams were free about 33 d more than 2 calendar years since the notching operation. A feature of the specimens recovered in 1980 was that about half had formed a third line very near the ventral valve edge and along the inner margin. All of the narrow growth lines were separated by relatively even, broad areas of growth increment deposits suggestive of no more or less than an annual interval for the deposition of growth lines, even though the time of formation of such lines may not correspond to an exact number of calendar days. These observations confirm similar conclusions of an annual periodicity of growth line formation by Thompson and Jones (1977), Thompson et al. (1980a, b), and Jones (1980).

Radiometric techniques for aging bivalve shells have recently been applied to ocean quahogs.

Thompson et al. (1980a) reported that the predicted radiometric age of an ocean quahog having 22 bands corresponded exactly to 22 yr when aged using ^{228}Ra. Turekian et al. (1982) concluded that age determinations of ocean quahogs from radiometric analyses are compatible with counts of bands formed annually. Thus, radiometric studies support the contention of an annual periodicity of growth lines in ocean quahogs.

Various environmental disturbances have been implicated in the formation of shell abnormalities and atypical growth lines in other bivalve species (Weymouth et al. 1925; Shuster 1957; Merrill et al. 1966; Clark 1968; Palmer 1980). It is therefore, conceivable that the stress imposed by dredging, marking, and returning the ocean quahogs to the ocean floor and their burrowing activities hastened the formation of a growth line in 1978. Thereafter, natural events affecting the metabolism of shell deposition are more likely stimuli. Such events apparently did not occur during the period after the formation of the growth line in 1978 and recovery of clams in late August 1979. Instead a growth line that in all probability had formed in 1979 was found in the shells of clams recovered on 9 September 1980. Its formation may have occurred in late August 1979, but the third line found in half of the clams recovered on 9 September 1980 suggests the possibility of its formation in early September 1980. By inference, then, growth line formation in 1979 and 1980 occurred in September.

The reported life span (150 yr, Thompson et al. 1980a) of ocean quahogs surpasses similar estimates for other bivalves. Age and growth of the far east mussel, *Crenomytilus grayanus*, have been determined from examinations of shell structure, an oxygen-isotope method, and notching experiments (Zolotarev 1974; Zolotarev and Ignat'ev 1977; Zolotarev and Selin 1979). These investigations indicated that longevity of the mussel may exceed 100 yr. Turekian et al. (1975) proposed a longevity of about 100 yr for a deep-sea nucoloid, *Tindaria callistiformis*, after determining ages by radiometric means and counting regularly spaced bands in the shell of one of the largest (8.4 mm in shell length). It seems likely that longevity of ocean quahogs may exceed 150 yr. Murawski and Serchuk (1979) reported a maximum shell length of 131 mm for ocean quahogs in extensive collections taken from the Middle Atlantic Bight. A specimen of this size is half again as large as the 88 mm example of a 149-yr-old ocean quahog reported by Thompson et al. (1980a).

In conclusion, the foregoing description of annual growth line formation in marked ocean quahogs and analyses of growth in the same specimens by Murawski et al. (1982) present significant supporting evidence for the hypothesis of slow growth and a long life span in the species. Ocean quahogs apparently live longer than any other bivalve known to man.

ACKNOWLEDGMENTS

We thank Brenda Figuerido and John Lamont for their assistance in preparing the art work and photographs, and Ida Thompson, University of Edinburgh, Department of Geology, King's Building, Edinburgh EH 9 3JW, Scotland, for encouragement in undertaking the study and helpful comments on the manuscript.

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