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The shell structure of *Ptychodesma* (Cyrtodontidae; Bivalvia) and its bearing on the evolution of the Pteriomorpha

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[Plates 1–4]

Observations of the hinge structure of the Middle Devonian species *Ptychodesma knappianum* Hall and Whitfield 1872 confirm the cyrtodontid affinities of this once problematic genus.

The shell microstructure of *P. knappianum* supports Douvillé's (1913) hypothesis concerning the ancestral nature of nacreous shell microstructure in the Bivalvia, and suggests further that modern arcoids and pterioids evolved from nacro-prismatic cyrtodontid ancestors. The Arcoida generally retained a rigid sub-periostracal shell margin and consequently evolved rigid crossed microstructure and a strong dentition to effect proper guidance of the shell margins upon closure. In contrast, the early Pterioida evolved a more prominent flexible outer prismatic layer to assist effective closure along the shell margins, and they retained nacreous microstructure as an adaptation for shell durability.

INTRODUCTION

Ptychodesma Hall and Whitfield 1872 is one of the last representatives of a Lower to Middle Palaeozoic superfamily whose early representatives are believed to have given rise to the orders Arcoida and Pterioida of the subclass Pteriomorpha (Douvillé 1913; Newell 1954; Cox 1960; Pojeta 1971, 1975). *Ptychodesma* was allied with the Cyrtodontacea by Newell (1969), but with question since its dentition had not been satisfactorily described. Several unusually well preserved specimens of the Middle Devonian *Ptychodesma knappianum* Hall and Whitfield 1872, the type species of the genus, have provided an opportunity to study both the dentition and shell microstructure of this genus. In addition to resolving the taxonomic status of *Ptychodesma*, these fossils provide new functional insights into the origin and early evolution of the Pteriomorpha.

MATERIALS AND METHODS

Several articulated shells of *Ptychodesma knappianum* were collected from the Middle Devonian Solsville Member of the Marcellus Formation (Hamilton Group) in a small abandoned quarry on the east side of Swamp Road, 1.6 km (1 mile) south of the intersection with Gill Road, Morrisville, New York (locality 3013 of the American Museum of Natural History; see Rollins, Eldredge & Spiller 1971). The specimens came from the upper third level of the outcrop, which is inferred to have been a warm water, delta slope environment. The stratigraphy and gastropod fauna of this and other Solsville Member localities have been described by Rollins *et al.* (1971). The shell microstructure was studied by optical microscopy of acetate peels made from specimens embedded in epoxy resin. Designations of Yale Peabody Museum and American Museum of Natural History catalog numbers are indicated by Y.P.M. and A.M.N.H. respectively.

The shell microstructure of *Ptychodesma knappianum* was compared with over 700 other Recent and fossil species representing most extant bivalve superfamilies. The shell microstructure nomenclature employed in this paper follows that provided by Bøggild (1930), MacClintock (1967), and Taylor, Kennedy & Hall (1969) except for the nacreous and complex crossed lamellar microstructures (see Wise 1970; Carter 1976).

PREVIOUS WORK

Previous descriptions of the external morphology of *Ptychodesma* generally agree with the generic diagnosis provided by Hall & Whitfield (1872, p. 192), i.e. 'Shell modioloid in form; valves equally convex; hinge with a wide ligamental area, the sides of which are sharply grooved in parallel lines, caused by successive growth of the ligament, as in *Pectunculus*. The grooves and ridges are slightly arched beneath the apex of the valves where they take their origin'. Other authors have added that the shell is also characterized by the following features: (1) a strongly reduced anterior portion, (2) weak umbones, (3) an exterior covered with fine concentric lines, (4) a broad anterior lobe, set off from the rest of the shell in some species by a broad sulcus, and (5) a length of generally less than 5 cm (Hall 1885; Nettleroth 1889; Beushausen 1895; Newell 1938, 1969; McAlester 1962; Bailey 1975).

On the other hand, references to the hinge dentition of *Ptychodesma knappianum*, the only species for which a complete dentition has been described, are often vague and contradictory. Hall & Whitfield (1872) did not describe a dentition, but Hall (1885) and Nettleroth (1889) mentioned the presence of two or more cardinal teeth. Kindle (1901) figured the internal shell features of a broken left valve in his pl. 15, fig. 2C, and he referred to 'about three' short cardinal teeth just ventral to the umbones and two long posterior lateral teeth near and parallel to the hinge posterior. However, Kindle's drawing was interpreted by Williams & Breger (1916) as indicating four cardinal teeth and five sockets, so they inferred the presence of five cardinal teeth in the right valve. Williams & Breger noted the Λ -shaped arrangement of what they counted as the second and third cardinal teeth in the left valve, and they commented that Kindle's figure shows that the ligament features noted by Hall & Whitfield (1872) are less constant and therefore taxonomically less important than previously supposed. On this basis, Williams & Breger concluded that *Ptychodesma* Hall and Whitfield 1872 is a synonym of *Cypricardites* Conrad 1841. *Cypricardites* is an Upper Ordovician genus tentatively allied with the Cyrtodontacea, but 'presently unrecognizable from available evidence' (LaRocque 1969). More recently, Bailey (1975) described the left valve of *P. knappianum* as having three cardinal teeth, the middle of which is Λ -shaped. The right valve is described as having only a single cardinal tooth in addition to the Λ -shaped cardinal tooth. Both valves have elongate posterior lateral teeth which are separated from the cardinals by an edentulous gap.

With a single exception, all other descriptions of presumed *Ptychodesma* fail to mention the presence of hinge teeth. Beushausen (1895) described two or more cardinal teeth in a *Ptychodesma* sp. from the Lower Devonian of Germany. Bailey (1975) considered this Lower Devonian form as possibly conspecific with *P. knappianum*. All other reported occurrences of *P. knappianum* are from the Middle Devonian of eastern United States (e.g. Kentucky, Indiana, New York).

A truly edentulous form identified as *Ptychodesma* is *P. nilssoni* (Hisinger) reported from the Silurian of Sweden and England (Angelin & Lindstrom 1880; Williams & Breger 1916). According to Williams & Breger, *P. nilssoni* differs from the North American *Ptychodesma* in its

lack of dentition and possession of an internal ligament pit. In addition, McAlester (1962) has considered *P. neglectum* (Hall) from the Upper Devonian of New York as probably edentulous. Other forms assigned to *Ptychodesma* but lacking descriptions of the hinge dentition include the Middle to Upper Ordovician European *Macrodesma* Isberg 1934 (tentatively placed in synonymy with *Ptychodesma* by Newell (1969), the Upper Devonian (New York) *P. nanum* Hall, and the Devonian (Ghana) *Ptychodesma* sp. described by Saul, Boucot & Finks (1963). In all these cases, the possibility of poor preservation makes it unclear whether these forms were in fact edentulous. *Ptychodesma* has also been reported from Australia (Wyatt & Jell 1967), but without a detailed description.

Other features for *Ptychodesma knappianum* are described by Bailey (1975), who mentioned a small, deeply impressed anterior adductor muscle scar, a larger, moderately impressed posterior adductor scar, and a simple pallial line strongly recessed from the ventral and posterior shell margins.

PRESENT OBSERVATIONS

(a) *Shell morphology*

The most striking external features of *P. knappianum* are its inflated, modioliform shape, reduced umbones and fine concentric sculpture (figure 1*a-c*, plate 1). As noted by Hall & Whitfield (1872) the deeply excavated ligament area shows numerous longitudinal grooves and ridges that are slightly arched just ventral to the umbones. These duplivincular ligament grooves vary in number with the size of the shell, but large specimens commonly show 5–7 grooves (figure 2*a-c*, plate 1).

The right valve possesses three cardinal teeth, including one bifurcated \wedge -shaped tooth located just ventral to the umbo and two oblique teeth located immediately behind the bifurcated cardinal. A socket apparently exists within the bifurcation and additional sockets occur immediately behind and in front of this tooth, between the two oblique cardinals, and possibly immediately behind the posterior-most cardinal (figure 2*b*). Additionally, there are two elongate posterior lateral teeth parallel to the hinge, and these are separated from the cardinals by a wide edentulous gap. One elongate socket is located above the dorsal-most of these two lateral teeth and a second socket lies between the teeth (figure 2*b-c*).

The left valve cardinal teeth were poorly preserved on most specimens examined, but one specimen showed an oblique cardinal tooth flanked by a prominent posterior and a faint anterior socket. A second, smaller, cardinal tooth is located anterior of this tooth and is flanked anteriorly by a pronounced socket. This smaller cardinal tooth does not appear to be bifurcated, although this is currently not known for certain. The left valve also shows two posterior lateral teeth and two elongate sockets, both separated from the cardinals by a wide edentulous gap (figure 2*a*).

(b) *Comparative shell microstructure*

The shell of *Ptychodesma knappianum* consists of three structurally distinct major shell layers, i.e. outer prismatic, middle nacreous and inner complex crossed lamellar. The reader is referred to MacClintock (1967), Taylor *et al.* (1969), Wise (1970) and Carter (1976) for descriptions and illustrations of these and other shell microstructures discussed below.

The inner shell layer of *P. knappianum* shows a complex crossed lamellar (c.c.l.) structure that varies locally from cone c.c.l. to irregular and fine c.c.l. (figure 4, plate 3). This combination

of c.c.l. varieties is not uncommon in the Bivalvia, and is known to occur in the modern Arcoidea (e.g. *Glycymeris*), Mytilacea (e.g. *Crenella*) and in a few Veneroidea (i.e. certain Carditacea, Arcticea, Mastracea, Tellinacea and Veneracea; see Carter 1976). The predominance of cone c.c.l. and more irregular varieties of c.c.l. structure in the Arcoidea appears to be a function of shell shape. Most elongate arcooids (e.g. *Anadara*) show irregular c.c.l. structure, while most rounded arcooids show a combination of irregular c.c.l. and cone-type c.c.l. structures.

The middle shell layer of *P. knappianum* is nacreous, with stacked nacre predominating in the outer part (figure 3, plate 2) and simple nacre predominating in the middle and inner parts (figure 4). Although simple nacre is widespread in the Bivalvia, stacked nacre is more taxonomically restricted. According to Wise (1970), stacked nacre is associated with relatively rapid shell layer accretion. As in certain Trigoniacea, the semi-reflected shell margin in *Ptychodesma* requires that the outer part of the nacreous layer accrete at a faster rate than the inner part (see Wise 1970). Thus, in both *Neotrigonia* and *Ptychodesma* the outer part of the nacreous layer shows the stacked variety. Both the nacreous and c.c.l. shell layers locally grade into a disordered structure with a granular appearance. In so far as this is most common near the surfaces of the shell, this phenomenon probably represents diagenetic alteration of the original shell fabric (figure 5c, plate 4).

The outer shell layer of *P. knappianum* consists of irregular prisms reclined slightly toward the shell margin (figure 5b). In some individuals the outer prismatic layer is missing, and is apparently replaced by a clear, featureless layer as seen in acetate peels (figure 3a, b). This layer appears honey-brown in thin sections and under reflected light. The thickness and colour of this honey-brown layer are reminiscent of the exterior shell layer noted by Kříž (1972) for the extinct superfamily Cardiolacea. If this layer in *Ptychodesma* does not represent an altered outer prismatic layer, then it is probably a relict periostracum. In the latter case, *Ptychodesma* would resemble the recent arcoid superfamilies in showing a thick periostracum, but would differ in this respect from most living Pterioidea.

The exterior reclined prismatic shell layer in *Ptychodesma* differs structurally from the aragonitic reclined composite prismatic structure rarely developed in the modern Arcacea (e.g. in *Anadara broughtonii*; see Kobayashi & Kamiya 1968), and from the common calcitic simple prismatic structure of many Pterioidea (e.g. in *Pteria* and *Pinna*) (see Taylor *et al.* 1969). Aragonitic irregular prisms superficially like those in *Ptychodesma* are developed in certain Lucinacea (e.g. in *Lucina pennsylvanica*).

Although original aragonite is not preserved in the present material for *Ptychodesma*, the original mineralogy of some of its structures can be inferred through comparisons with modern species. The structural arrangements referred to in *Ptychodesma* as nacreous and c.c.l. were almost certainly originally aragonitic. These structures are almost always aragonitic in the

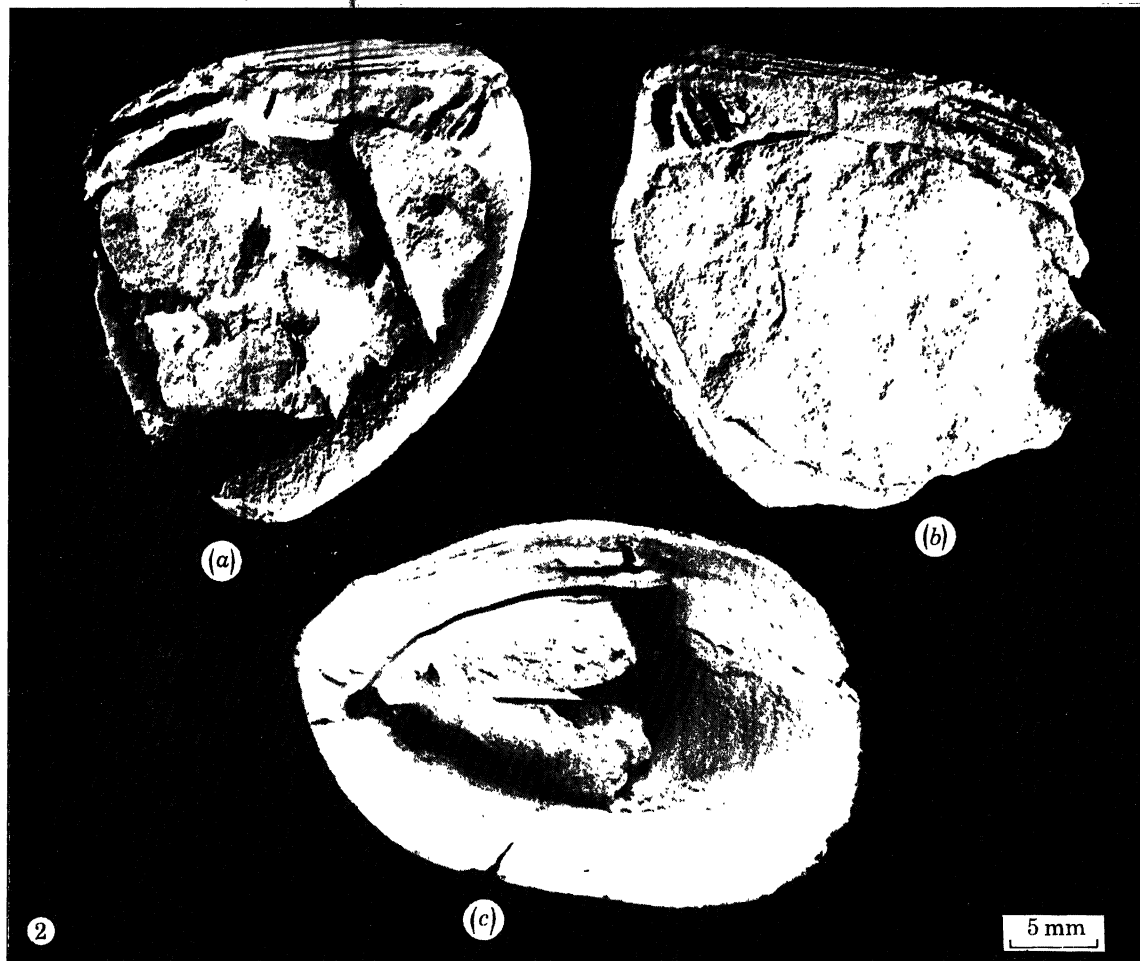
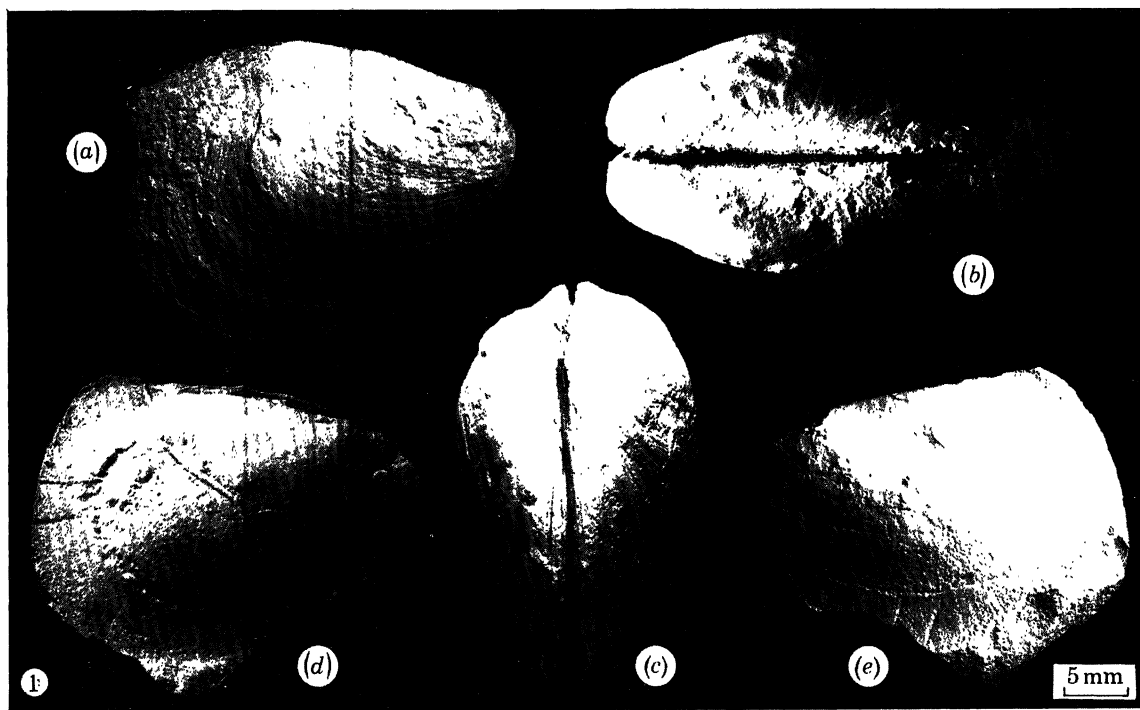
DESCRIPTION OF PLATE 1

FIGURE 1. *Ptychodesma knappianum* Hall and Whitfield 1872.

(a) Exterior view; broken right valve (Y.P.M. 10057-8); (b) dorsal view; shell anterior is toward the left (Y.P.M. 10057-7); (c) anterior view; dorsal side up; (d) right side; natural internal cast, showing the pallial and adductor muscle impressions (Y.P.M. 10057-9); (e) left side; natural internal cast.

FIGURE 2. *Ptychodesma knappianum* Hall and Whitfield 1872.

(a) Interior view; broken left valve (AMNH); (b) interior view; broken right valve (Y.P.M. 10057-7); (c) interior view; dorsoventrally compressed right valve (Y.P.M. 10057-10). The cardinal teeth are obscured.



FIGURES 1 AND 2. For description see opposite.

(Facing p. 370)



FIGURE 3. For description see opposite.

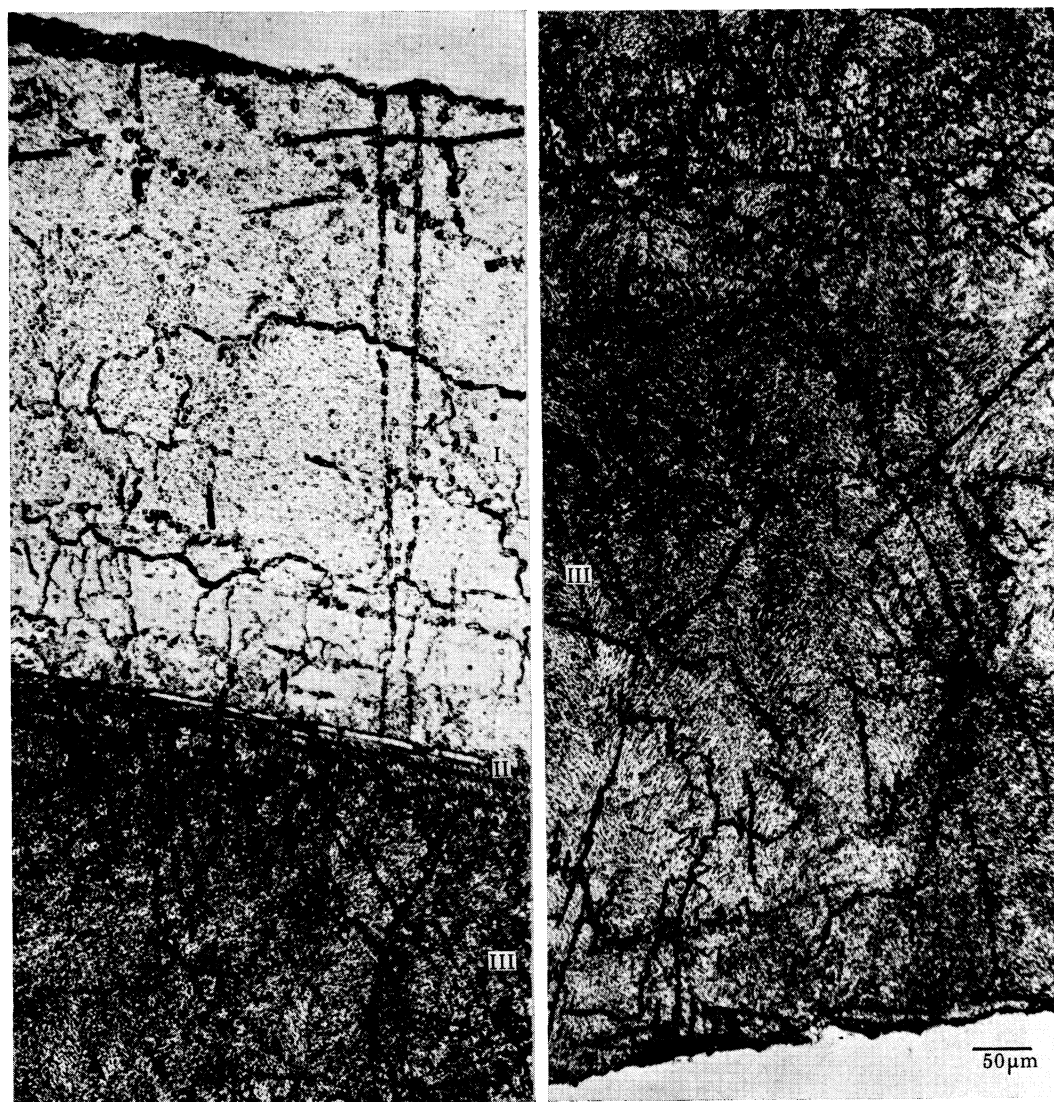


FIGURE 4. Nacreous (I) and cone c.c.l. (III) structures in *P. knappianum* (Y.P.M. 10057-1). Acetate peel; radial, vertical section in the left valve posterior. The shell exterior is up; the shell posterior is toward the left. The left and right photographs form a complete transect when juxtaposed at A. The nacreous layer appears lighter than the inner cone c.c.l. layer. These two layers are separated by a pallial myostracum hardly visible at this magnification (II).

DESCRIPTION OF PLATE 2

FIGURE 3. 'Periostracal' and nacreous structures in *P. knappianum* (Y.P.M. 10057-3). Acetate peel; radial, vertical section in the left valve posterior. The shell exterior is up and the shell posterior is toward the right in all three photographs. (a) Relict 'periostracum' (I), and underlying stacked nacreous layer (II); (b) enlargement of part of (a); (c) inner part of stacked nacreous layer.

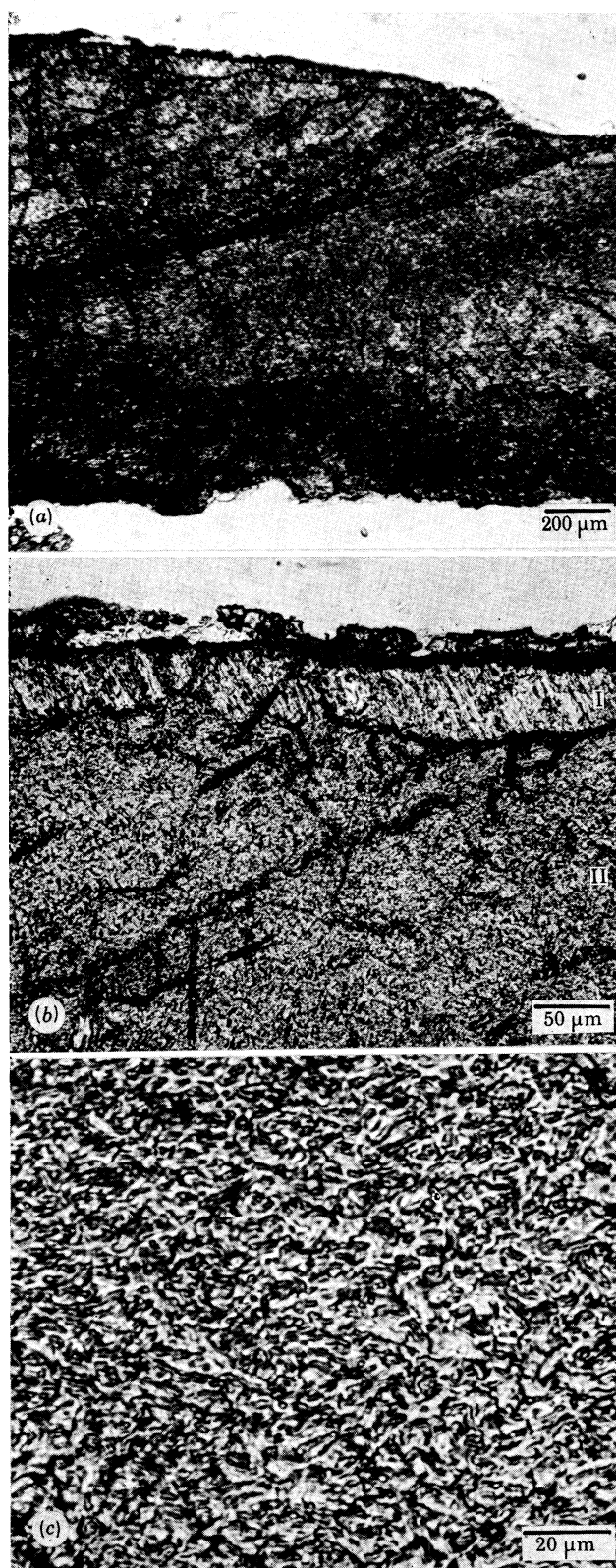


FIGURE 5. Prismatic and irregularly nacreous (altered) structures in *P. knappianum* (Y.P.M. 10057-2). Acetate peel; radial, vertical section in the left valve posterior. The shell exterior is up and the shell posterior is toward the right in all three photographs.

modern Arcoida and Pterioida (Taylor *et al.* 1969; Carter 1976). Irregular, reclined prisms similar to those in *Ptychodesma* are aragonitic in the modern *Lucina pensylvanica*, but extremely thin calcitic prismatic layers in some Pterioida may appear structurally similar.

DISCUSSION

The present data for *P. knappianum* confirm the presence of strong dentition in this once problematic genus, and clearly ally this taxon with the Cyrtodontidae (cf. Newell 1969; Bailey 1975). The presence of cardinal teeth and a prominent, chevron-grooved ligament in *P. knappianum* indicates that *Ptychodesma* should not be considered in synonymy with the problematic *Cypricardites*, as suggested by Williams & Breger (1916). In so far as *P. knappianum* is the type species of *Ptychodesma*, all truly edentulous bivalves previously identified as *Ptychodesma* should be reassigned elsewhere.

The apparent variability of tooth number in *Ptychodesma* reinforces other shell morphological evidence indicating a phylogenetic tie between the Cyrtodontacea and the higher Arcoida (see Newell 1954). Even allowing for the fact that different workers have counted the bifurcated cardinal tooth as one or two teeth, comparison of the present hinge data with data from the literature indicates a variable number of cardinal teeth per valve in *Ptychodesma*. This intra-specific variation in tooth number recalls the characteristic ontogenetic variation in many higher Arcoida, in which hinge teeth are added as the animal matures (Bernard 1896), but where tooth number is also reduced in older individuals through interumbonal shell growth (Thomas 1976). Furthermore, the general pattern of radially arrayed cardinal teeth and elongate lateral teeth in *Ptychodesma* supports Douvillé's (1913) suggestion that the arcacean family Paralleodontidae evolved from post-Ordovician cyrtodontids. Ordovician Cyrtodontacea were more distinct in their hinge dentition from the Paralleodontidae than are the Devonian forms (see Pojeta 1971).

The occurrence of nacreous and cone c.c.l. structure in *Ptychodesma* provides a previously unknown microstructural tie between the Arcoida and the more primitive superfamilies in the Pterioida. Since the Cyrtodontidae may be a common ancestor to the Arcacea and the early Pterioida, this mixture of nacreous and c.c.l. structures may be evolutionarily significant. It is possible to interpret the phylogenetic significance of the nacreous/c.c.l. shell microstructure of *Ptychodesma* in two ways. First, the earliest Cyrtodontacea may have been nacro-prismatic. In this case, the Pterioida would have differentiated from this stock while it was characterized by a nacro-prismatic structure grade. The Arcacea would evolve later from the Cyrtodontidae after the latter had evolved a nacreous/c.c.l. structure grade. This possibility is illustrated in figure 6. Alternatively, the Cyrtodontacea may have been nacreous/c.c.l. throughout their history. The Arcacea and early Pterioida would then have evolved microstructurally through their general loss of nacreous or c.c.l. structures, respectively. The first scheme is simpler and is also compatible with general considerations of the primitiveness of nacreous structure in the Mollusca (Taylor 1973), so it is regarded as the more likely interpretation.

Further evidence from well preserved cyrtodontids is required to verify whether the prismatic shell layer in *Ptychodesma* was originally aragonitic or calcitic. The hypothesis of an original aragonitic mineralogy in the exterior shell layer of *Ptychodesma* is certainly compatible with the suggestion by Carter & Aller (1975) that the earliest molluscs were entirely aragonitic, and is in keeping with the lack of calcite in the modern Arcoida. If this layer is found to be originally

aragonitic then the appearance of calcitic mineralogy in the Pterioida probably constituted a major evolutionary innovation.

In addition to clarifying the structural evolution of the early Pteriomorphia, *Ptychodesma* provides new insight into the early functional-structural evolution of the orders Arcoida and Pterioida. Data of shell structure and functional morphology suggest that the presence of a prominent outer prismatic shell layer is functionally related to shell form and hinge dentition

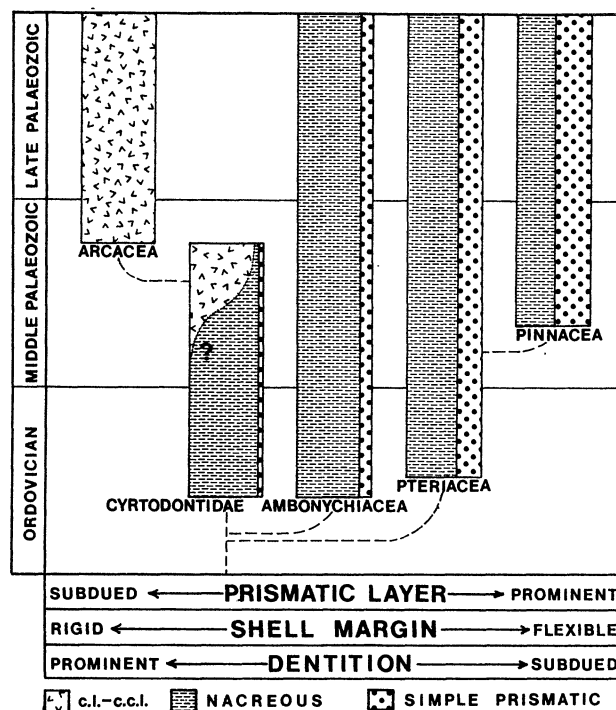


FIGURE 6. Characteristic shell microstructures of the early Pteriomorphia. The predominant shell microstructure in each group is indicated by the fields representing c.l.-c.c.l., nacreous, and simple prismatic structure. Myostracal structures are not shown here. The width of the structure field in each vertical bar represents its relative area of deposition on the inner shell surface. The times of appearance of the taxa and their evolutionary arrangement follow data from Pojeta (1971, 1975). The shell microstructure data come from the present paper and numerous references in the literature (e.g. Bøggild 1930; Taylor *et al.* 1969; Taylor, Kennedy & Hall 1973; Kauffman & Runnegar 1975).

in the Arcoida and early Pterioida. As summarized in figures 6 and 7, this prismatic shell layer increases in prominence from the Arcacea to the Cyrtodontidae, Ambonychiacea, Pteriacea and Pinnacea. This trend generally correlates with decreasing prominence of the hinge dentition and with greater lateral compression of the shell. By the present hypothesis, these features are functionally related because of the increasing rôle of the outer prismatic shell layer in assisting effective closure at the shell margins. A prominent outer prismatic shell layer provides for a wide band of margin-to-margin contact during shell closure, thereby reducing the necessity of valve guidance afforded by a strong hinge dentition (figure 7). Lateral compression of the shell decreases the degree of flexing necessary to provide a wide margin of shell valve contact. Therefore, a prominent prismatic shell layer, reduced hinge dentition, and lateral compression constitute an integrated functional-structural adaptation. A flexible shell closure mechanism may be adaptive for excluding predators that may chip at the shell margins, for superior water retention

in intertidal species, and for permitting effective valve closure about small obstacles incidentally caught between the valves.

The rôle of flexing by the outer prismatic shell layer in shell closure is strikingly apparent in the modern Pteriacea. But this flexible shell closure mechanism is developed to an even higher degree in the Pinnacea. Apparently taking advantage of the greater flexibility of the prismatic shell layer, the Pinnacea have increased its width in the shell posterior at the expense of the

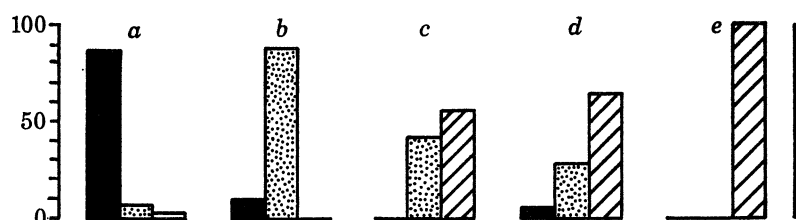


FIGURE 7. Prominence of dentition in the Pteriomorpha. The data are based on generic and subgeneric diagnoses in Cox *et al.* (1969). Adult characters are tabulated for (a) 75 taxa in the Arcacea, (b) 9 in the Cyrtodontidae, (c) 42 in the Ambonychiacea, (d) 85 in the Pteriacea, and (e) 9 in the Pinnacea. Data judged as indeterminate are not represented in the histograms for 5 taxa in the Arcacea, 2 in the Cyrtodontidae, 20 in the Ambonychiacea, and 10 in the Pteriacea. The histograms represent percentages of the total population sampled for each superfamily or family. Black: strong dentition (teeth extending over 90% of the hinge area); stippled: intermediate (teeth extending over less than 90% of the hinge area; in most cases less than 50%). Hatched: dentition absent in adults.

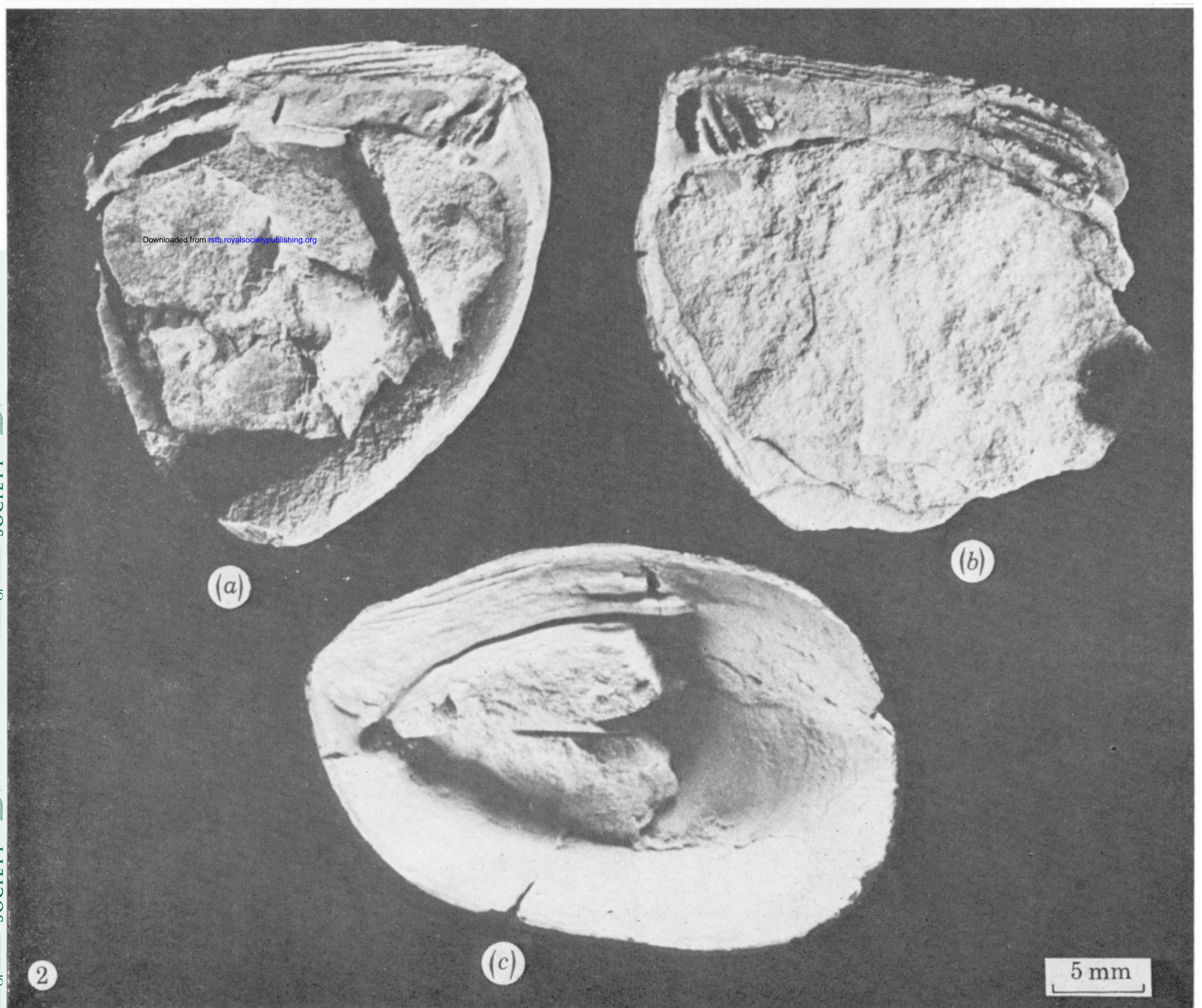
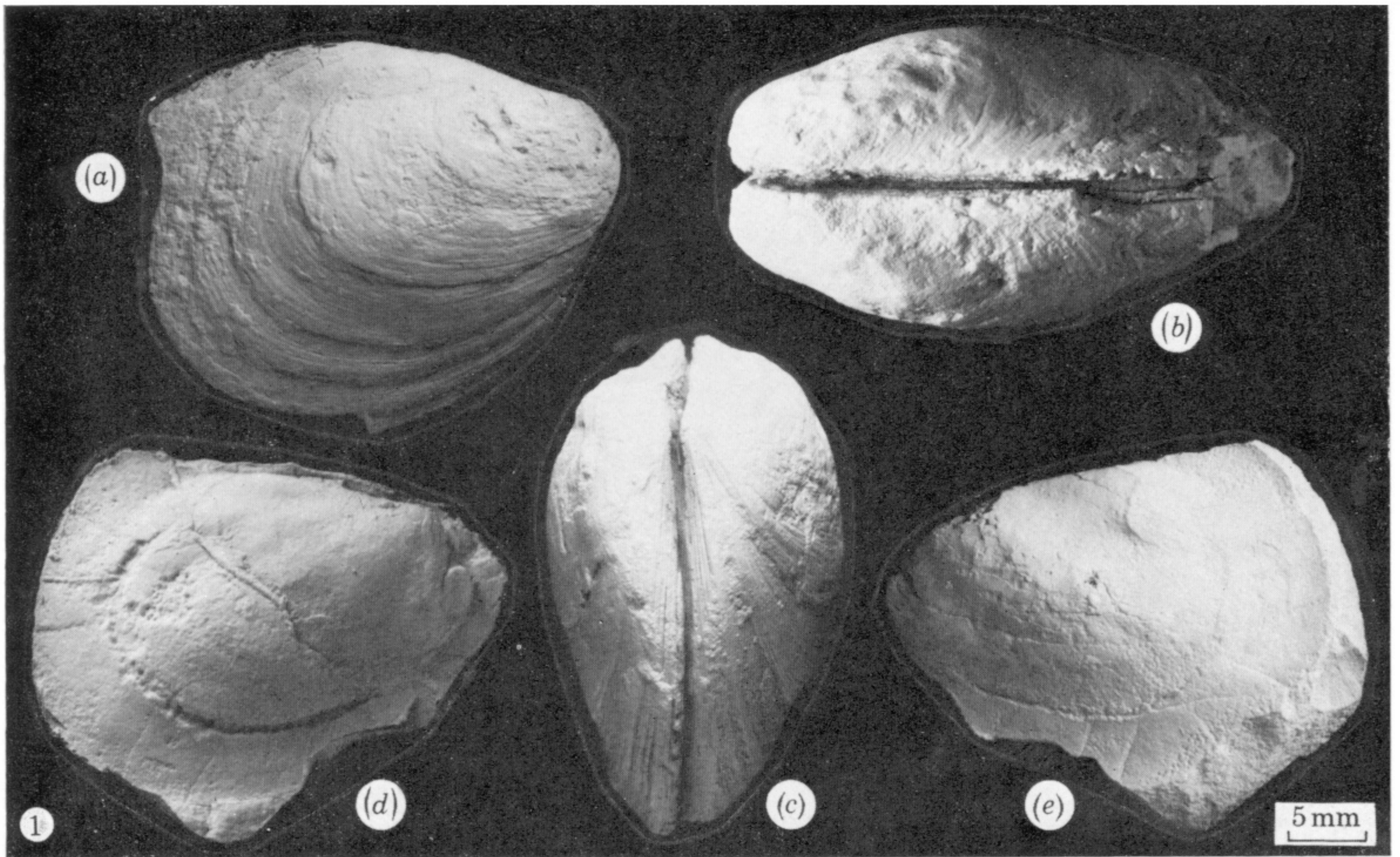
nacreous layer (Carter 1976). In *Pinna* and *Atrina* the ventral shell margins are more or less permanently closed, and closure along the shell posterior occurs entirely through bending the outer prismatic shell layer (Yonge 1953). The more rigid nacreous layer is absent from the shell posterior in both genera, and in *Pinna* it is also absent along the longitudinal axis of each shell valve. The nacreous layer in *Pinna* also differs from *Atrina* in showing a peculiar row stacking (Wise 1969) in which elongate nacre tablets are arranged in parallel rows. The nacre row stacks in *Pinna* are generally uniformly orientated relative to the centre of the shell posterior. In this orientation the nacre row stacking may complement the flexibility of the shell posterior. Directional flexibility may be expected in the row stack nacre because of the more numerous interstack organic partitions and the reduced interlocking of nacre tablets toward the shell posterior. The retention of row stack nacre in *Pinna* and simple nacre in *Atrina* may be adaptive for improving the shell's resistance to breakage upon impact. Taylor & Layman (1972) have shown that nacre is apparently superior to simple prismatic structure in this regard.

In conclusion, the available evidence of shell structure and inferred functional morphology suggest that the Pteriomorpha evolved two early functional-structural adaptations that relate to their ordinal and superfamily level differentiation. These grades are: (1) a flexible margin/nacro-prismatic grade characterized by progressive increase in the prominence of the outer prismatic shell layer (e.g. from the Ambonychiacea to the Pteriacea and Pinnacea) and (2) a rigid or semi-rigid margin/c.l.-c.c.l. grade characterized by a reduction of the ancestral outer prismatic shell layer.

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FIGURES 1 AND 2. For description see opposite.

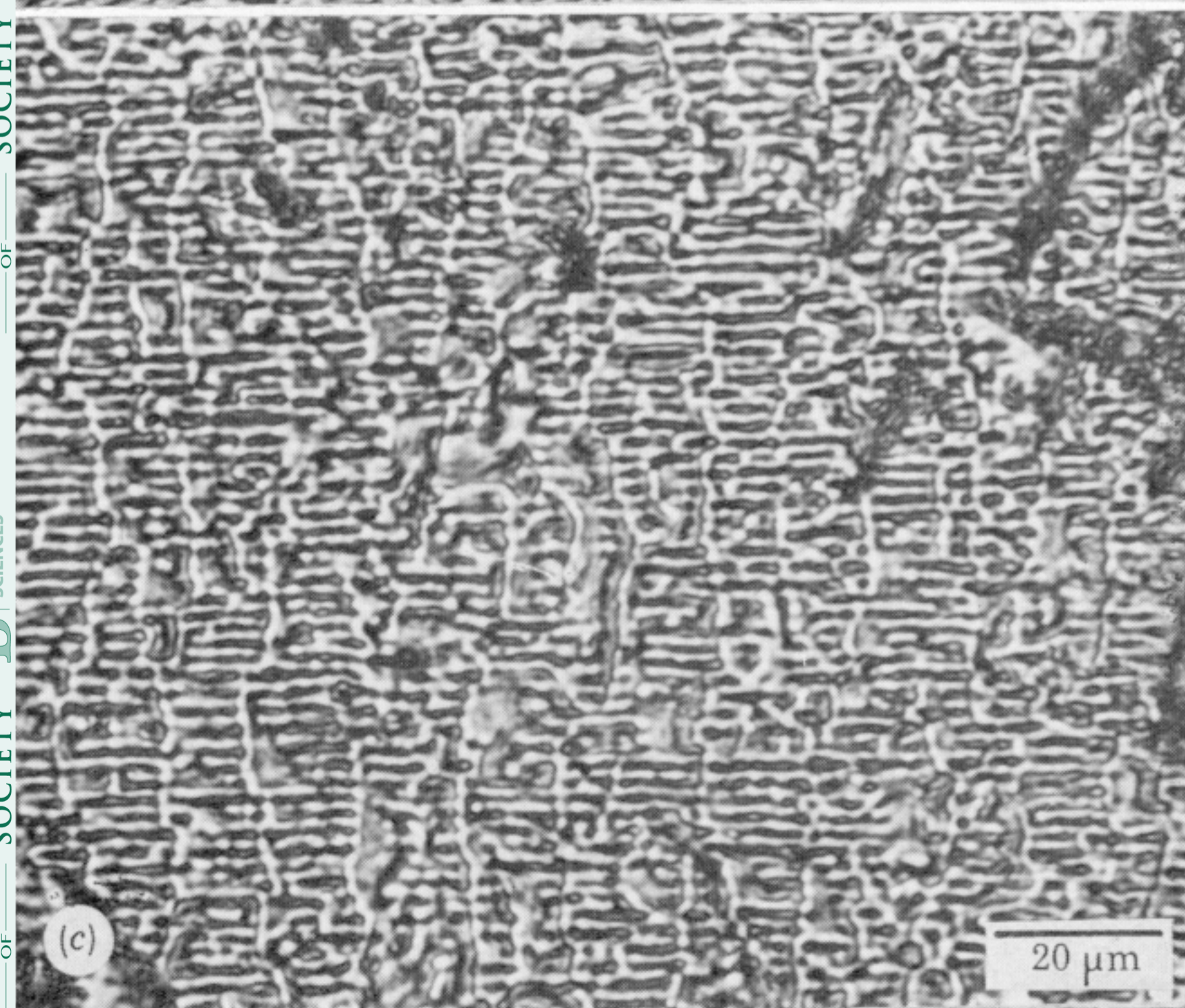
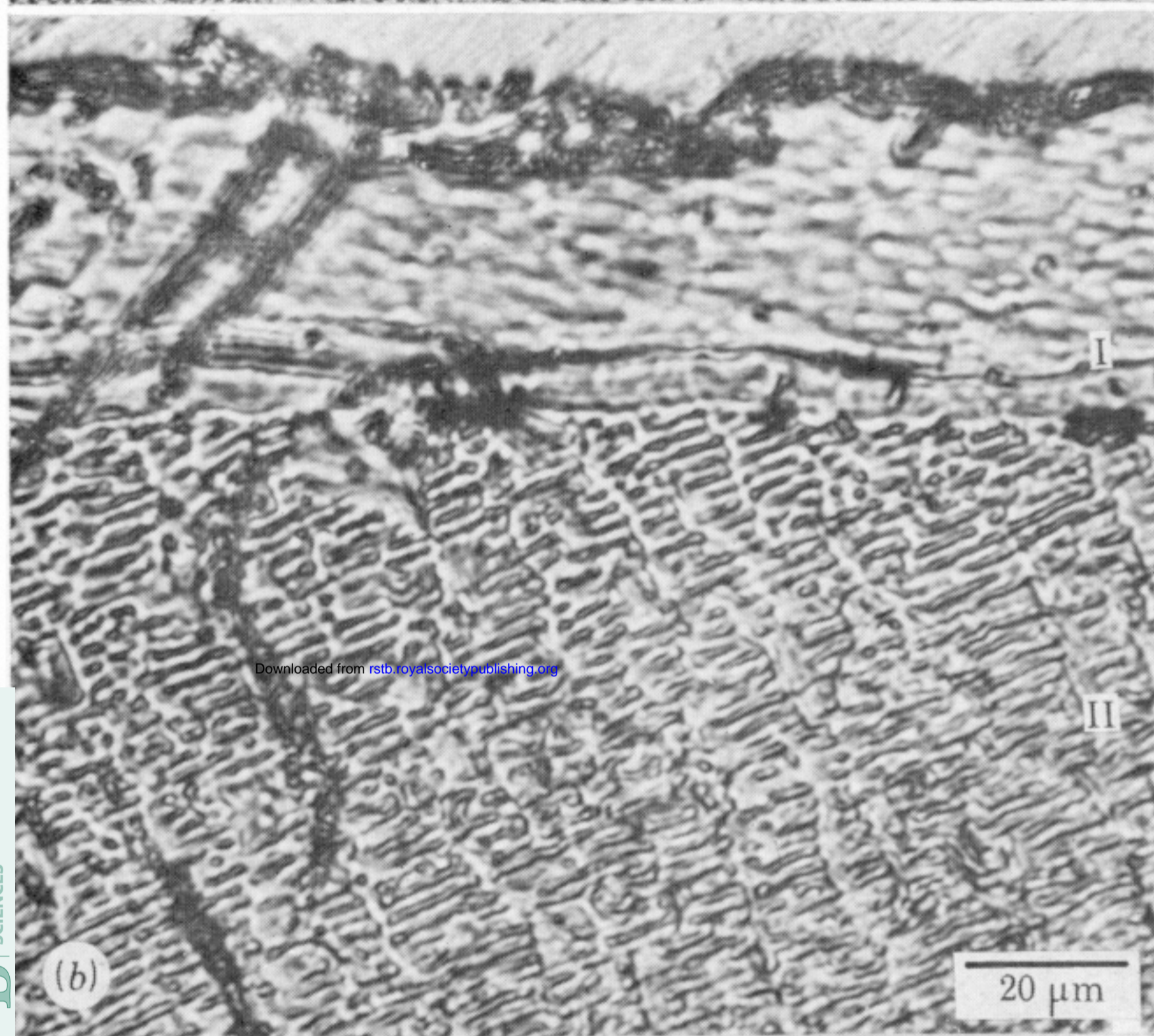
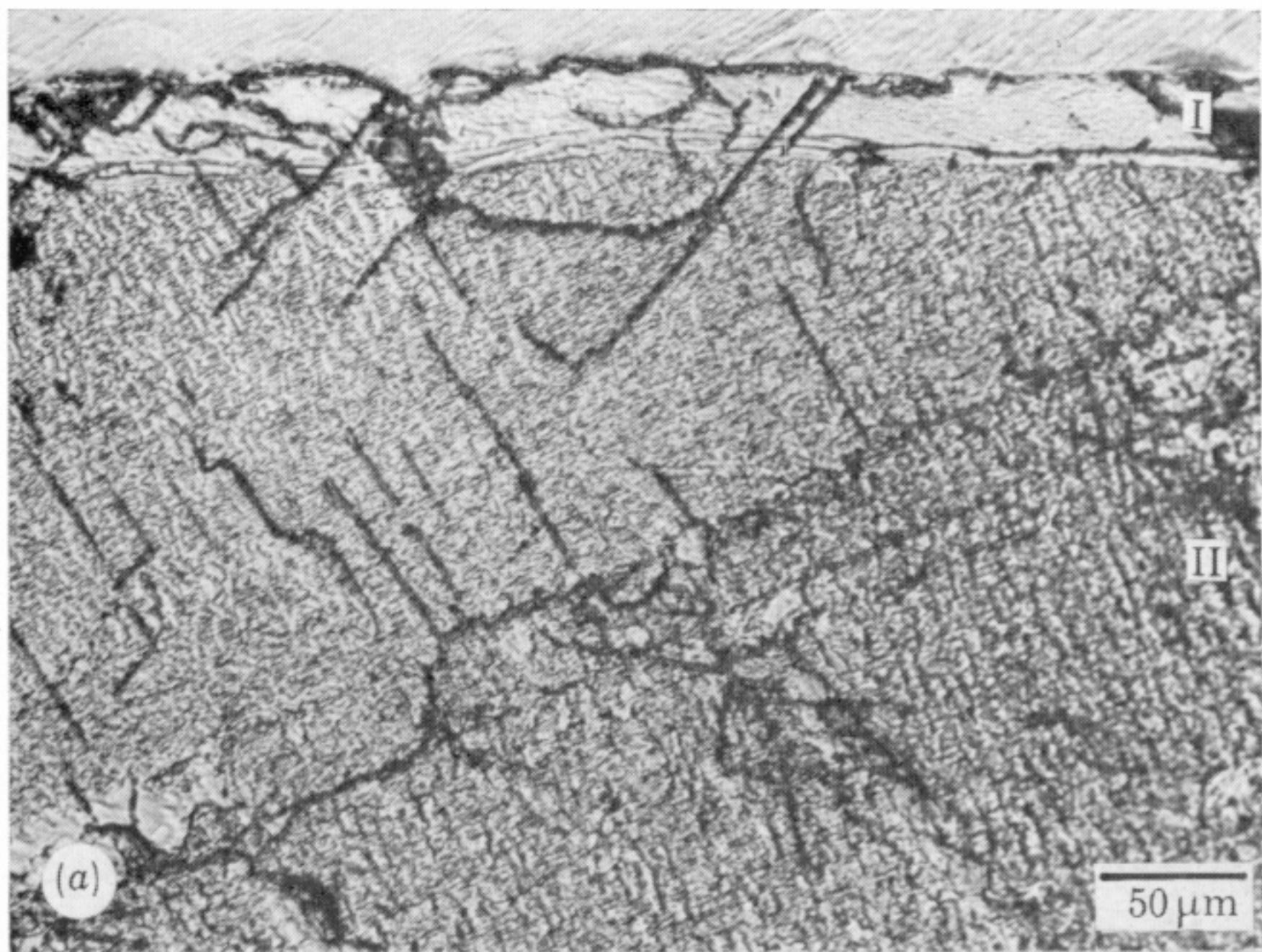
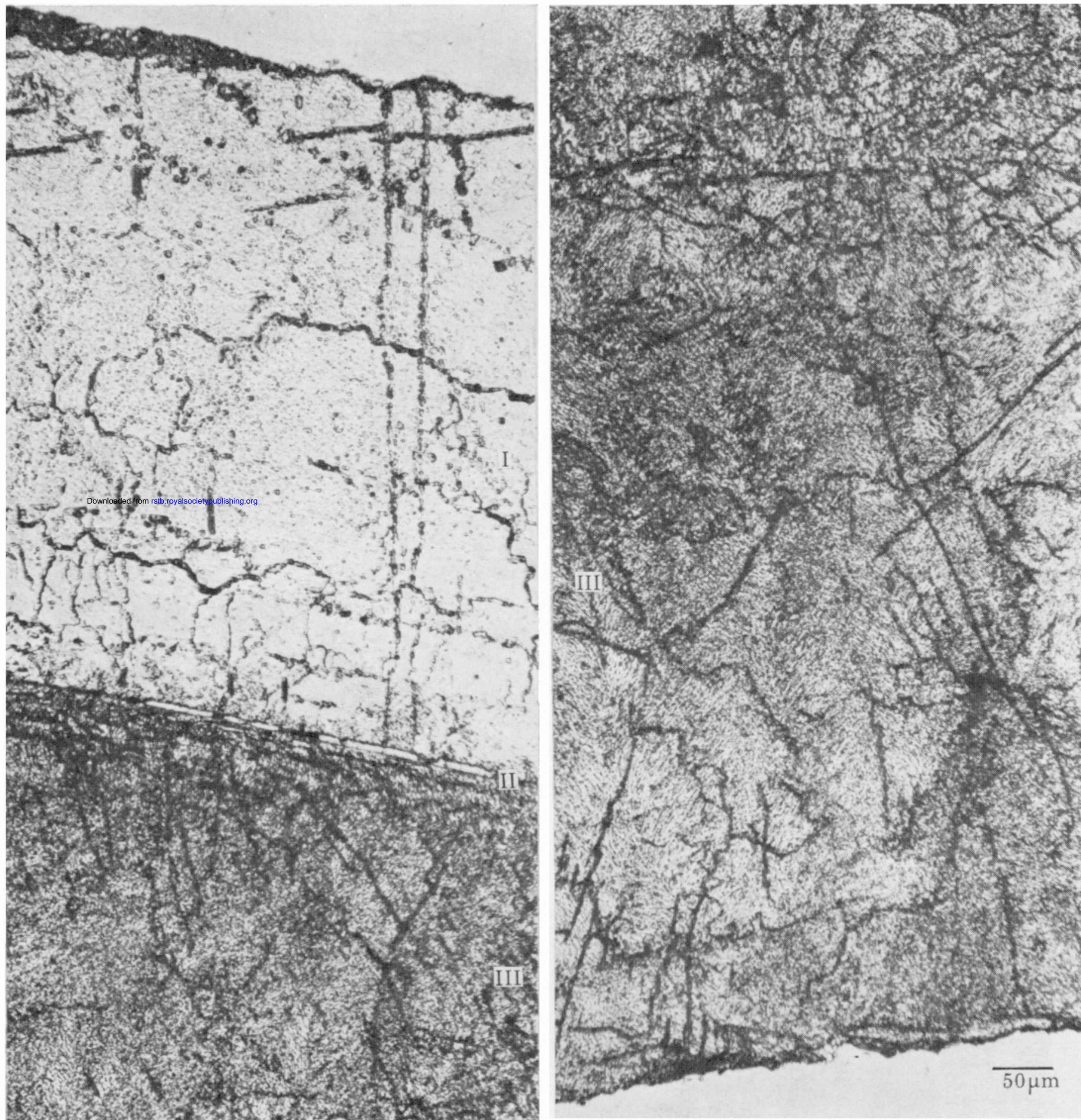
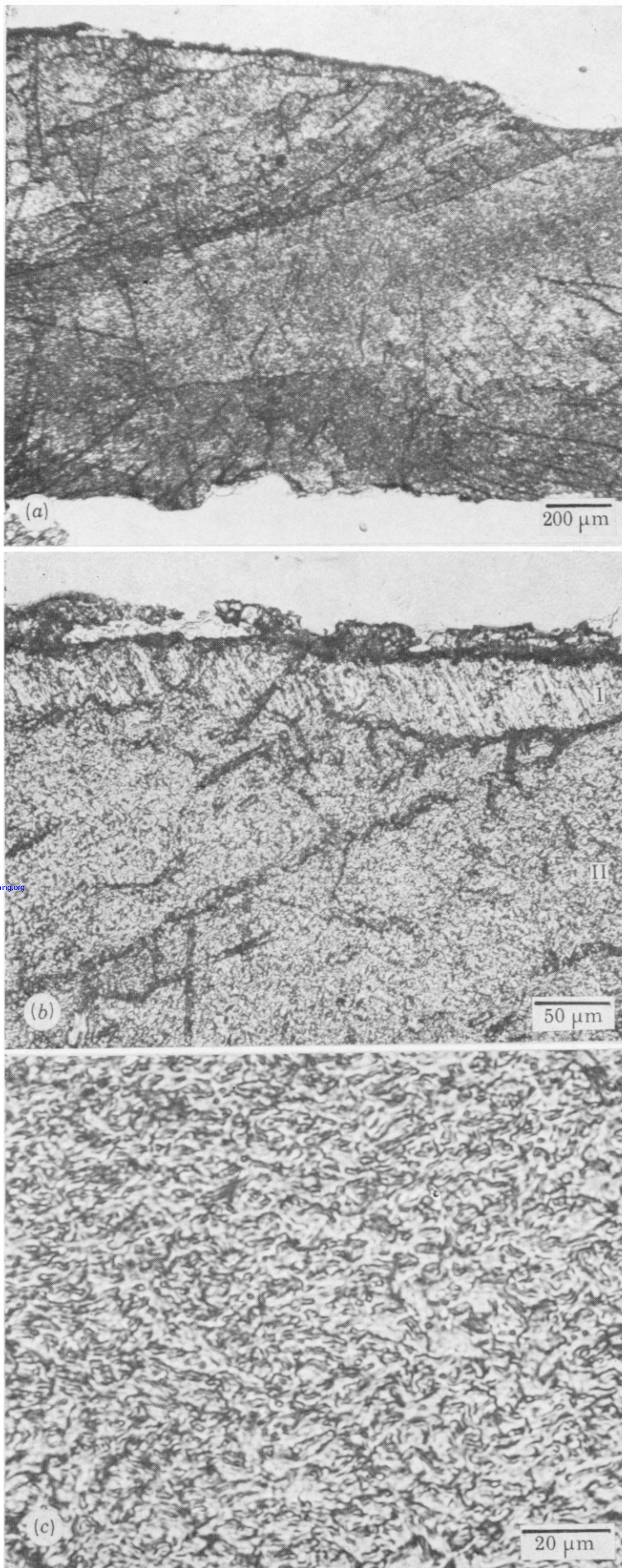


FIGURE 3. For description see opposite.



A

FIGURE 4. Nacreous (I) and cone c.c.l. (III) structures in *P. knappianum* (Y.P.M. 10057-1). Acetate peel; radial, vertical section in the left valve posterior. The shell exterior is up; the shell posterior is toward the left. The left and right photographs form a complete transect when juxtaposed at A. The nacreous layer appears lighter than the inner cone c.c.l. layer. These two layers are separated by a pallial myostracum hardly visible at this magnification (II).



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FIGURE 5. Prismatic and irregularly nacreous (altered) structures in *P. knappianum* (Y.P.M. 10057-2). Acetate peel; radial, vertical section in the left valve posterior. The shell exterior is up and the shell posterior is toward the right in all three photographs.