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OPERCULA OF TWO GASTROPODS FROM THE LILYDALE LIMESTONE (EARLY DEVONIAN) OF VICTORIA, AUSTRALIA

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Abstract

Specimens of both *Cyclonema lilydalensis* and *Oriostoma northi* are known which show the operculum in life position. Additional loose opercula contribute to knowledge of the geometry of fossil paucispiral and multispiral opercula respectively. Various considerations, including the characters of the opercula, suggest that neither species is correctly assigned to genus; no convenient taxa are available for these forms. The opercula show a number of distinctive features and hold potential for stratigraphic and biologic discrimination.

Introduction

Gastropods have been known to occur in the Lilydale Limestone for more than 75 years (Etheridge 1890, 1891, Cresswell 1893) and opercula for almost the same length of time (Cresswell 1894, Etheridge 1894). These opercula have not been studied in detail in recent times, though several taxa of the gastropod fauna known only from their shells have been redescribed (Philip and Talent 1959). Now through the kindness of Mr Edmund D. Gill, Deputy Director, National Museum of Victoria, we have been able to study a large collection of opercula from the well-known Cave Hill locality in Victoria, Australia. In turn, examination of the specimens necessitated an investigation of the widely scattered literature on Palaeozoic gastropod opercula, and some examples from living forms.

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Prevalence and association of gastropod opercula

It is generally accepted that all living prosobranch gastropods develop opercula (Fretter and Graham, 1962, p. 77; Kumé and Dan, 1968, p. 513). Many of the living forms considered to be more advanced lose this structure in post-larval life, and a few others, which are less advanced but have specialized in a clinging mode of life, also lose the operculum. These exceptions reinforce the reasonable assumption that the presence of an operculum is primitive, and therefore that virtually every known Palaeozoic gastropod had an operculum; it is further likely that almost all the animals retained them throughout life.

When one deals with fossil gastropods, the association of a loose operculum with any given shell is always a matter of uncertainty, even if both are from the same stratigraphic interval

and from the same locality. For some genera, such association has been a matter of controversy which is still not fully resolved, as for example with the Early Ordovician *Ceratopea* (Yochelson and Bridge 1957). Palaeozoic gastropods with opercula in place are among the rarest of fossils. Indeed, the collections of the U.S. National Museum of Natural History contain only one such specimen, an Ordovician *Maclurites*. Thus it is surprising that the Lilydale Limestone has yielded two different forms of opercula, both represented by specimens in which association of shell and operculum is as it was in life. These quite different forms in the Lilydale Limestone extend considerably the knowledge of Palaeozoic opercula *in situ*.

Although the upper part of the Early Ordovician has yielded a large number of opercula, especially of the genus *Ceratopea* (Yochelson and Bridge 1957), the post-Ordovician Palaeozoic record of opercula is exceedingly poor. Each new occurrence adds significantly to a meagre record, and we hope that this paper may bring others to the attention of palaeontologists.

One might assume that shells and opercula will occur in a one-to-one ratio, but Hadfield (1970, pp. 307-308) observed that the vermetid gastropod *Petaloconchus montereyensis* (Dall) (1919) periodically moults its operculum and generates a new one. Because of the highly specialized nature of the Vermetidae, this may well be a unique feature. Post-mortem sorting and differential preservation are sufficient as mechanisms to explain deviation of fossil gastropods from the theoretical one-to-one ratio.

Geometry of opercula

Cox (1960, pp. 1124-1126), in a brief but general review, illustrated a variety of opercular shapes. He noted that although at least 20 types have been distinguished, they may be grouped as spiral, concentric, or lamellar in growth plan. Typically, gastropods grow following a logarithmic spiral pattern in the formation of their shells. This growth pattern is also represented in most spiral opercula. Even opercula which complete only part of one whorl grow logarithmically. Taki (1950) divided recent spiral opercula into the broad groups of subspiral, paucispiral, and multispiral; no clear dividing line distinguishes these groups, and terminology is arbitrary. Two of these three types occur in the Lilydale Limestone. We have called the operculum form of *Cyclonema lilydalensis* paucispiral, but another worker might argue that it should be more properly called multispiral, for the opercular does contain a fair number of volutions.

The essence of the logarithmic spiral is that width increases at an increasing rate. A fundamentally different mode of coiling is that of a spiral of Archimedes. In that mode of expansion, the width of each volution remains constant. Some Holocene opercula appear to follow an Archimedian spiral, but have relatively few volutions. Taki (1950, p. 34) may have emphasized the spiral of Archimedes, but his text is in Japanese, and this point is not mentioned in his English summary. However, his classification of opercula does not take any apparent change away from the logarithmic pattern to an Archimedian pattern into account. Thompson (1942, pp. 772-778) discussed the geometry of opercula in terms of logarithmic growth only.

The multispiral form of the *Oriostoma northi* opercular, the second type found in the Lilydale Limestone, may represent growth following the pattern of a spiral of Archimedes. Although there is some slight variation in the width of individual opercular volutions, this is a relatively minor point, particularly when judged against the impressively large number of volutions. Because the number of volutions is very large, there has been confusion with opercula characterized by concentric growth. No convenient term has been proposed for opercula characterized by so many narrow volutions. 'Multispiral' will continue to be used here purely for convenience, but it may be an inappropriate term.

Multispiral opercula, in which the volutions are not so close that their spiral course is difficult to observe, are well known in the Silurian. Lindström (1884, Pl. 17, figs. 32-47) illustrated a variety of multispiral opercula from Gotland. In some instances the opercula

are in life association within the aperture of various species of *Oriostoma*. The occurrence of generally similar opercula in *Oriostoma* and unrelated genera in the Devonian demonstrates that a large number of volutions forming the operculum is most assuredly not in itself an indication of close phyletic relationships; the number may well be critical, but when the volutions become so numerous that they prevent ready observation, all forms tend to be lumped simply as 'numerously volute'.

No data exist on such a fundamental question as whether in the formation of opercula gradation is continuous between the Archimedian and logarithmic spirals. If the two kinds are discontinuous, they may be of use in higher classification; we do not know for certain whether any Holocene opercula are rigidly Archimedian in pattern. It is theoretically possible that true Archimedian growth—within the limits of biological variation—is confined to extinct gastropods. Study of additional Palaeozoic fossil opercula, such as are available in the Silurian, eventually may lead to a more clear-cut distinction between Archimedian and logarithmic growth.

Comparison of the two opercula in the Lilydale fauna is particularly instructive in pointing out the difference between the external shape and internal configuration of a gastropod whorl. Though one might assume from the generally rounded profile of the shell exterior that the Devonian *Cyclonema* might have a nearly circular operculum, it obviously is elongate. On the other hand, the subquadrate external profile of *Oriostoma* belies the circular internal section. Even though there is an apparent lack of fit when viewing the external whorl profile, an inspection of the apertural shape of the two shells shows that the fit of each operculum is very good indeed.

In general, the only shell form which could accept an Archimedian-like spiral or a true multispiral operculum would be one which has an essentially circular aperture. This necessitates a shell with an entire lip and no interference in its outline from preceding whorls. The only shell forms which satisfy this criterion are those with a circular internal whorl profile and whose axis of the generating curve expands outward away from the axis of coiling, or downward along the axis of coiling in pace with the rate of expansion of the generating curve (Raup and Michelson 1965). Among Palaeozoic gastropods, shells like the Euomphalidae or Oriostomatidae primarily possess these characters, and these are the shells known for their calcified multispiral opercula.

In shells where the displacement away from or down the axis of coiling does not keep pace with the rate of expansion of the generating curve, the earlier whorls will interfere with the shape of the aperture. In such cases the shape of the aperture tends to an elongate oval, the parietal lip disrupting the circular shape, The elongated paucispiral operculum is an ideal form to fit within this aperture. The relation between the operculum and the aperture will place theoretical restrictions on opercular form, and obviously many apertural shapes could not be sealed off by spiral growth. In these shells, the opercula characterized by concentric or lamellar growth will be found.

Calcification of opercula

In spite of the large number of opercula which must have been produced in more than 500 million years, remarkably few are preserved as fossils. Typically, the Holocene gastropod operculum is a plate of organic conchiolin (Fleishmann 1932, Kessel 1941), and is unsatisfactory raw material for fossilization. Only in rare instances among the great variety of living gastropods does this organic material serve as a matrix for calcification. Calcified opercula are prominent only in some members of the Trochacea, especially the Turbinidae, and among the Neritacea; these are accepted generally as primitive prosobranchs. Some, though far from all, *Natica* species also have calcified opercula. *Turbo* is a characteristic reef-dweller and is found most commonly on the seaward side. Most members of the family seem to occur in this habitat. *Nerita*, a typical neritacean, lives on both ocean and lagoon sides of reefs, at or above high tide level but most commonly in a rocky intertidal habitat. (For a summary of living reef-dwelling gastropods, see Demond 1947). Species of *Natica*,

some with calcified opercula and some with 'horny' opercula, are primarily sand or mudflat dwellers. Other living gastropods function in all these habitats equally as well without calcification of their opercula. Just why some forms do calcify this structure is not at all clear; at present there is no obvious answer based on physical characteristics of the environment.

No non-calcareous opercula of Palaeozoic age are known to us. One is faced with a record which may be incomplete on two counts. The palaeontologist must accept the normal vagaries of preservation and recovery of fossils. In addition, he must deal with gaps imposed by the paucity of calified opercula, for phylogenetic distribution of calcified opercula was probably as erratic in the past as now. These factors make it most unlikely that a phylogenetic sequence of opercula will ever be recovered.

Functional morphology and evolution of opercula

Among the molluscs, opercula occur in living and fossil gastropods, fossil hyolithids (an extinct group of class rank) and fossil cephalopods. Opercula of living gastropods are used to close the aperture, and in many forms they are also employed as a pad on which to rest the shell during movement. Both functions are important, but the general prevalence of opertural closings among representatives of several mollusc classes suggests that the closure function is the more primitive.

The operculum has been variously modified in different groups and, as noted, even lost in some, but there seems little question that the sealing of the aperture is its prime function (Cox 1960, p. 1125). Adaptations in shape and reduction in size are particularly noteworthy among the more advanced living gastropods. However, opercula of most living snails fit the aperture of the shell closely when retracted. In viewing the Palaeozoic gastropods collectively, the most logical supposition is that the operculum fitted the aperture closely.

In a sense, the operculum is a defence mechanism. The soft parts of the animal must be extended for locomotion and feeding, but if they are retracted and the aperture sealed, the shell is a formidable fortification against predators. A calcareous plug rather than a horny one would increase the strength of the defence. However, it may be even more important to view the operculum as a significant defence against the environment, rather than against predation. Gastropods are not noted for rapid movement such as characterizes coral polyps or tube-dwelling worms, who withdraw almost instantaneously when a shadow falls on them. It would seem *a priori* that a fast-moving carnivore would find a gastropod to be vulnerable. Nevertheless, *Turbo* and *Trochus* may retract at a rapid rate when a shadow passes over them (J. Rosewater oral communcation 1969).

Hedley (1917, p. 98) suggested, and Taki (1950, p. 47) fully supported, the notion 'that the multispiral type of operculum seen in *Pleurotomaria* and Trochidae is the most primitive'. In the scheme of operculum evolution proposed by Taki (1950, fig. 12), calcification is shown occurring at various stages, an overlay, as it were, to changes in shape. He stated (Taki 1950, p. 46) that 'The evolution of operculum types begins with the retardation of its rotation with its growth. The calcification of opercula is of secondary origin, which also slows down its rotation. Thus, a calcified operculum belongs to a more advanced type than the ordinary non-calcified one.'

Speculation on evolution of the operculum cannot be supported from the fossil record, for the earliest known calcified operculum, that of the late Early Ordovician *Ceratopea*, emphasizes growth in the third dimension, the specimens being horn shaped (Yochelson and Bridge 1957). More plate-like opercula, which complete less than one volution, have long been known to occur with shells in the Middle and Late Ordovician *Maclurites*; Salter (1859, pp. 7-10, Pl. 1) gives an excellent description and outstanding illustrations of the shell and operculum. Yochelson (1966a) described a more typically paucispiral operculum from Middle Ordovician which he attributed to *Helicotoma*. Because of the presence of subspiral to paucispiral calcified opercula in these early gastropods, the basic concept that a calcified operculum is an 'advanced type' is a dubious concept and may be spurious.

Gratacap (1907) has pointed out both the

utility of opercula in classifying some Holocene gastropods and some of the dangers inherent in placing too great a weight on them. These mid-Palaeozoic Lilydale opercula, when compared with other opercula, show that different opercular forms may often converge. However, the opercula offer a new line of evidence on classification. This must be treated with extreme caution, but data on distribution of operecula form could be significant in corroborating new concepts of gastropod arrangement at the familial level.

Stratigraphic and ecologic setting of Lilydale Limestone

The Lilydale Limestone constitutes the third youngest of four formations forming the Yering Group (Gill 1965). Although classically this group was considered to be Silurian in its entirety, now only the basal Christmas Hills Sandstone is judged to be Siluro-Devonian. The overlying Ruddock Siltstone and Lilydale Limestone are generally accepted as Lower Devonian. Talent (in Talent and Banks 1967, p. 151) considered the Lilydale Limestone to be Emsian, and possibly lower Emsian. Philip (1967, p. 918), following Gill (1965), considered the unit to be Siegenian; Edmund D. Gill (written communication 1969) judges that the formation is most likely of upper Siegenian age. This is actually only a minor difference in age, and is not surprising that workers considering a richly fossiliferous thick unit should have minor differences in interpretation. The opercula contribute no data to the question of the age of the Lilydale Limestone, but the fact that the Lilydale is Devonian rather than Silurian is highly significant for better understanding of the record of opercula.

The Lilydale Limestone is about 700 feet thick. Regarding its general character, Edmund D. Gill (written communication 1969) notes:

'Proximity to a large city of a deposit of good limestone has led to the extensive working of the Lilydale Limestone and so the opportunity for its study. It is a lenticle of recrystallized limestone well stratified and dipping 60°E. with beds mostly 6 in. to 3 ft thick. The formation is richly fossiliferous, with corals and stromatoporoids predominating. Mollusca are represented chiefly by gastropods, which are common, but pelecypods and cephalopods are comparatively rare. Brachiopods and trilobites are very rare. Foraminifera, Ostracoda and *Girvanella* are present. No fish have been discovered.

'The sediment types vary from low energy lime muds (grading into noncalcareous silts in places) to high energy conglomerates of waterworn pebbles of coral, stromatoporoids, and such. No reefs or organisms in position of growth have been recognized. The formation as exposed is a coral-stromatoporoid biostrome. In some places, the gastropod shells are worn while in others they are excellently preserved. The gastropod with the operculum appears to have come from such a low energy environment.'

Except for the opercula assigned to the early Ordovician *Ceratopea*, the most abundant Ordovician calcareous operculum is that of *Maclurites*. In the Silurian, the *Oriostoma-Poleumita* generic complex is noteworthy for the abundance and variety of calcified opercula. Although no palaeoecologic studies *per se* have been done of these three genera, they are readily interpreted as having lived in a near-reef, shallow-water, and possibly high-energy environment. It may be more than coincidence that both kinds of operculate Lilydale snails lived in a similar environment.

Operculum of *Cyclonema lilydalensis* and similar paucispiral forms

The Australian literature during 1893 and 1894 contains several references to gastropod opercula from the Lilydale Limestone. However, the only description and illustration of an operculum is that of Etheridge (1894) for *Oriostoma* which is discussed below. Sufficient vagueness surrounds the discussion of a paper given at the Royal Society of Victoria (Hall and Pritchard, in Anonymous 1893, p. 260) to suggest that one person may have been commenting on the operculum of *Cyclonema* while another commented on that of *Oriostoma*. On the other hand, Etheridge (1894, p. 154) indicated that only one specimen was in question.

The description below is based on twelve free opercula of *Cyclonema lilydalensis* ranging from 9 to 23 mm in greatest length. These specimens supplement one shell with the operculum in life position within the aperture.

The operculum of *Cyclonema lilydalensis* is paucispiral, expanding in the characteristic counter-clockwise direction, with all volutions observable on the external surface. Its overall general shape is that of a wide oval disc. Growth is accomplished by adding increments which are essentially tangent to the rim; the increments are inclined at an oblique angle to the plane of the operculum. Were it not for the one specimen in place it would be difficult to assign this operculum to a shell, for the whorl profile of *C. lilydalensis* follows essentially the arc of a circle. The similarity of apertural shape and opercular shape are not at all obvious, and the confusion in the literature as to which shell this operculum should be assigned is perfectly understandable.

The first four observed volutions on most specimens lie in essentially one plane, though one specimen suggests that the first two observed are slightly depressed (Pl. 1, fig. 2a); the nucleus of the operculum is unknown. The individual volutions have a flattened exterior surface (Pl. 1, figs. 1a, 2a). With increasing size, perhaps beyond six volutions, the axis of the volutions is displaced toward the inner surface of the operculum, so that large opercula are very slightly convex in cross-section (Pl. 1, fig. 3c). In spite of this gradual slight inclination, the individual segments remain flattened, rather than convex. The suture on the outer face is distinct, but not deep.

As seen from the side, the operculum is a moderately thin plate, the thickness seemingly increasing in direct proportion to increasing diameter. In the early growth stages, the periphery is close to the outer surface and may protrude as a very narrow flange so that the profile is step-like. In larger specimens the periphery is near the middle, and the profile is well rounded (Pl. 1, fig. 3c).

The inner face also shows volutions, but as they are approximately twice as wide as those on the exterior surface, much of the surface area of the earlier whorls is covered (Pl. 1, figs. 1b, 2b, 3b). The inner surface of each volution is as flat as the exterior, the only exception being near the rim at the zone of growth; this growth edge thins toward the periphery so that it is blade-like (Pl. 1, fig. 3b). The zone of growth occupies roughly one-eighth of the circumference of the operculum.

The flat inner surface of each volution uniformly occupies about one-half of the total width at every growth stage. The inner edge of each volution abruptly bends downward to an eccentric depression in which the more central portions of the earlier whorls are seen. This inner edge of the inner surface—that is, the area of the operculum that would be analagous to the umbilicus of a widely phaneromphalous gastropod shell—has the sides of the depression perpendicular in the early stages of growth. However as the operculum increases in size, the inner edge of the inner surface becomes more and more rounded and protruding as an overhang, thus producing below it an 'umbilical suture' of increasing depth (Pl. 1, fig. 3d). This suture would enlarge the area of opercular surface available for attachment of the retractor muscle. There is no indication of any central boss or shell thickening within the central depression. The outer surface of the operculum irregularly shows growth lines which are tangent to the preceding whorl, following the shape of the growing edge (Pl. 1, figs. 1a, 3a), but these growth lines are not visible on the inner surface because the layers are deposited parallel to the plane of the operculum.

The operculum in place (Pl. 1, figs. 4a-c) rests tightly within the shell only just behind the apertural opening and is not retracted, its outer edge and surface being just within the outer lip. The growth edge of the operculum is at the upper part of the opening, the farthest point being below the suture, that is, at the juncture of the parietal and the upper part of the outer lips. The straight growing edge itself lies parallel to the parietal lip.

When the shell is held with the columellar axis perpendicular, the plane of the operculum is inclined at an angle of 50° to the columellar axis. Our interpretation is that the operculum of this gastropod is held in place only by force of the retractor muscle. Although there may be

development of grooves, teeth or ridges on the columellar margin of the aperture, as occurs in more advanced forms such as the Neritacea, it seems most unlikely. The only specimen in our possession is that illustrated with the operculum in place.

Most of the opercula are broken or fragmentary; the thin inner whorls are particularly an area of weakness. The opercula are relatively soft, and more difficult to clean than the shell. Essentially no preparation was possible. The free specimens may be weathered or they may be softer because calcium carbonate was more porous in the operculum than in the shell.

The type specimen of *Cyclonema lilydalensis* Etheridge (1891, p. 128, Pl. 19, fig. 3), at the Australian Museum, has not been studied and compared by us. However, because of its globose profile and numerous, evenly-spaced, uniformly-rounded spiral cords (Pl. 1, fig. 4a) the operculate specimen is probably conspecific with this species rather than with *Cyclonema australis* Etheridge, 1890 (p. 63-64, Pl. 9, figs. 4-5), the type specimen of which is also at the Australian Museum. That species has fewer spiral elements and a less globose whorl profile. The illustration of *C. australis* given at the time *C. lilydalensis* was described, indicates more clear-cut differences between the two taxa than does the 1890 drawing. When these two species were described, their opercula were unknown. This report appears to be the first presenting the operculum of either form.

Like all other Devonian species which have been assigned to the genus *Cyclonema*, both species of the genus described from the Lilydale Limestone probably are not members of that genus. True *Cyclonema* has a calcitic shell, as well as imperfections in its spiral ornament as a consequence of sedentary life habit at maturity. The operculate Lilydale specimen is recrystallized, and its soft, powdery texture suggests to us that it may have been aragonite originally. The mid-Palaeozoic assemblage of spirally ornamented globose gastropods, into which the Lilydale taxa fall, have not been critically studied. Correct assessment of the taxonomic position of both species would be premature at this time, and beyond the scope of this paper. The operculated form is referred to as *Cyclonema lilydalensis* purely in quotational sense.

It cannot be assumed that a paucispiral operculum is confined to the Devonian or restricted to a particular shape of shell. In addition to Yochelson's (1966a) report of a paucispiral operculum with *Helicotoma*, Teller (1910) illustrated a Silurian shell from the Racine Dolomite (Niagaran) of Wisconsin with a paucispiral operculum in place; this is probably the same as the form described by Whiteaves (1891; 1895, p. 96) from the Guelph Formation, but we have not compared specimens from the two units. Though this Silurian operculum is paucispiral, it expands at a more rapid rate than that of the Australian Devonian *Cyclonema*. Teller's form has a gently concave outer surface rather than convex and perhaps it is relatively thinner. Still, the similarity to the Australian form is interesting.

What is perhaps even more interesting is that this operculum occurs within the aperture of a moderately high-spired pleurotomariacean gastropod. Teller (1910) incorrectly assigned his shell to *Murchisonia conradi* Hall, but the operculate form has a more prominent upper shoulder than true *Murchisonia*. This may be another example of convergence in opercular form, such that lower-spired shells (*Helicotoma*) and moderately high-spired shells with striking differences in external forms (*Murchisonia* and *Cyclonema*) all have similar opercula. No other examples of paucispiral opercula in the Palaeozoic are known to us.

Lindström (1884) assigned several Silurian opercula to *Cyclonema*. So far as it can be determined from his illustrations, none were actually found in life position. These opercula are multispiral and are relatively thick. Apparently they are more similar to Silurian opercula of *Oriostoma* illustrated by him than to either of the Devonian forms described herein. At least some of the Silurian shells which Lindström described originally as *Cyclonema* might better be transferred to *Oriostoma* or to *Polennita*. Should study of his specimens support this suggestion, evidence on classification from the shape of the shell and the operculum would tend to reinforce one another rather than be at variance.

Operculum of *Oristoma northi* and its distribution

Two specimens identified as *Oriostoma northi* Etheridge (1890, p. 64-65, Pl. 9, figs. 6-7), which have the operculum within the aperture, are available for study. One is only a fragment of the final conch whorl, and the outer surface of the operculum is badly weathered. This specimen from the Pritchard collection could be the one mentioned, but apparently not seen by Etheridge (1894, p. 154). Etheridge also noted a large operculated specimen in the collection of Rev A. W. Cresswell (National Museum of Victoria no. P1107). We have also examined 21 isolated opercula, one of which was donated by Cresswell. It is a minor footnote to history that two of the specimens figured herein (a large operculum, and a fine specimen with the operculum in place) were donated to the National Museum of Victoria by him in 1902.

In marked contrast to the operculum of *Cyclonema lilydalensis*, this operculum is virtually circular in plan and is of the multispiral type with extremely narrow volutions. The statements and drawings given by Etheridge (1894) suggested incorrectly that it is made of concentric increments. The individual volutions may be seen only on the exterior surface (Pl. 2, figs. 1a, 2a, 3a, 5a). All specimens are somewhat weathered, and the spiral course of the volutions cannot be traced readily; no doubt this misled Etheridge in his interpretation. Forty volutions were counted on a specimen 1·8 cm in diameter, but the actual number is probably closer to 60. The whorls are not of constant width, nor is increase in width completely uniform, for several specimens have volutions of very slightly greater width between the central portion and the rim. In the large specimens there appears to be a narrowing of the volutions near the mature rim. This can be seen fairly well in thin section (Pl. 1, figs. 6a-d). The slight variation or ontogenetic change is far less significant than the very large number of volutions.

The overall shape of the operculum is such that, as Cresswell (1894, p. 157) remarked, originally there was controversy as to the origin of the fossil, 'some taking for a nummulite, and some for the lid of a coral, others for the vertebrae of a fish'. Most specimens are concave on the outer surface and so resemble fish vertebrae. Although all specimens have the central area sunken relative to the rim, individual variation is considerable. Among specimens of similar diameter, some individuals will be twice as thick as others (Pl. 2, figs. 1c, 2c, 3c, 5b). However, on all specimens the inclination of the outward-facing surface appears uniform throughout growth, though this may be masked by differential erosion of the central area. Chapman (1916, p. 90) indicated that the exterior of the operculum is concave; Cresswell (1894, p. 158) stated the operculum to be 'plano-concave', an accurate description of the form.

Both the outer and inner edges of the rim are relatively sharp. The rim is straight in profile but inclined slightly inward, the inner opercular surface being a bit narrower than the outer. No ontogenetic change in the profile has been observed, and there does appear to be a difference in inclination of the rim between the thinner and the thicker opercula.

The inner surface is smooth, being built of laminae deposited at almost right angles to the rim, each lamina completely covering the one previously laid down (Pl. 2, figs. 1b, 2d, 3d, 5c). The surface varies from almost horizontal to distinctly inclined inward. The thicker opercula may be more strongly inclined, but the inclination of this surface varies considerably with individuals. There is no indication that this is an ontogenetic change.

Approximately one-third of the inner surface is occupied by the central depression, presumably the point of attachment of a retractor muscle. Each lamina bends down gently to form this concavity. However, in weathered specimens, the depression appears to a flat-based pit, the walls of which are nearly vertical except at the uppermost rounded edge. Such a configuration would impose impossible mechanical problems in increasing the size of the depression as each succeeding lamina was deposited. Thin sectioning (Pl. 1, fig. 6d) shows the central depression to be shallow.

One large specimen has a mound within

the central depression (Pl. 2, fig. 5c). It is not possible to determine whether this is a gerontic feature or whether it is a result of weathering and subsequent preparation by another worker of the soft material forming the laminae. A thin section of another specimen suggests that this feature may be spurious (Pl. 1, fig. 6c), but it cannot be entirely ruled out, for comparable thickening of the attachment area has been observed in unusually large Pennsylvanian neritacean opercula.

Although these opercula are generally thick, they are also as soft as those of *Cyclonema lilydalensis*; a number has been modified in details by weathering. Specimens vary in diameter from the smallest 1·2 cm, to the largest just over 3 cm (Pl. 2, fig. 5). The ratio of width to thickness means little because of the likelihood of modification of the inner surface, in particular by weathering. Variation in the slope of the outer surface cannot be attributed to weathering.

The operculum fits tightly into the shell aperture. The well-preserved shell which has a portion of the aperture unbroken, shows that the operculum is essentially not retracted for more than two millimetres at the inner lip (Pl. 2, figs. 4 b-c). It may be withdrawn a slight distance more at the outer lip (Pl. 2, fig. 4a), but even here this cannot be more than a few millimetres. The interior of the aperture of several specimens examined shows no indication of any sort of groove or teeth to assist in holding the retracted operculum. However, the thinning of the shell toward the aperture is a perfect match for the inclination of the opercular rim.

Oriostoma northi Etheridge (1890, p. 64-65, Pl. 9, figs. 6-7) is a common species in the Lilydale gastropod fauna; the type specimen is housed in the Australian Museum. This species was redescribed by Philip and Talent (1959) who assigned it to *Straparollus* (*Euomphalus*); we prefer to use the original generic name in a quotational sense, for reasons noted below. They not only discussed the general external form and ornament of the shell in considerable detail but also demonstrated the spurious nature of the genus *Liomphalus* Chapman (1916, p. 90), which had been based on steinkerns of this species. They figured a number of shells, but no opercula. As noted by Philip and Talent (1959) both Hall and Pritchard (in Anonymous 1893, p. 260), when commenting on a paper by Cresswell (1893), discussed the occurrence of operecula *in situ* at Lilydale, though Cresswell (1894, pp. 157-158) was the first to exhibit such a specimen at a public meeting. It remained for Etheridge (1894) to describe the operculum itself, which he illustrated by line drawings of isolated examples. So far as we have been able to determine, in spite of the report by Cresswell (1894) of a specimen showing the operculum in place, none has been figured.

Spitz (1907, Pl. 14, fig. 1a-c) recovered one operculum from the Lower Devonian of Austria which is remarkably similar to that of *O. northi*. Comparison of an Austrian specimen with the Australian specimens reveals no obvious difference, and were the opercula presented without locality data they would immediately be judged to be conspecific. Part of this Early Devonian gastropod fauna has recently been redescribed (Jhaveri 1969), while other parts and opercula are still under investigation. It seems highly probable that *Straparollus* (*Euomphalus*) *carnicus* (Frech) is the host shell for this operculum. The similarity in both shell and operculum between this species, as illustrated by Jhaveri (1969, Pl. 21, fig. 8), and *Oriostoma* [*Straparollus* (*Euomphalus*)] *northi* (Etheridge), as illustrated by Philip and Talent, is striking.

In general shape and ornament, the shell of *Oriostoma northi* is also similar to species of *Omphalocirrus* from the Middle Devonian of Germany (see Yochelson 1966b). This raises yet another interesting point. In connection with redescription of *Omphalocirrus manitobensis* (Whiteaves 1890) from the Middle Devonian Winnepegosan of Manitoba, Canada (Geological Survey of Canada No. 4174), Whiteaves (1890, Pl. 6, figs. 3-3a) figured an apparently free convex operculum. The operculum actually is in a shell some distance within the aperture. Considerable uncertainty has surrounded this material, for the operculum has appeared to be exceptionally thin and in an unusual orientation. In the light of the Lilydale specimens, it is now readily interpreted as the impression

of the concave external surface of a multispiral operculum slightly out of life position and pushed or retracted a short distance into the aperture. Additional closely similar opercula have been found in *Omphalocirrus*-like shells in the Middle Devonian Rogers City Limestone of Michigan (R. M. Linsley, unpublished).

The shell of *Omphalocirrus manitobensis* has slightly less prominent collabral ornamentation on the basal surface but is still impressively similar to that of *Oriostoma northi* and *Straparollus* (*Euomphalus*) *carnicus*. All three probably form a closely allied group almost certainly within the same subfamily. Similarity in opercular type thus has led to reinterpretation of phyletic relationships which were not suspected earlier because of the scattered nature of the literature. So far as we can determine, no operculum has yet been reported for the type species of *Omphalocirrus*. The currently accepted classification of Euomphalacea (Knight, Batten and Yochelson 1960, pp. 1189-1196), does not include *Omphalocirrus*. However, to engage in a major reorganization of the Euomphalacea at this time would greatly exceed the scope of this discussion of opercula.

When one considers the paucity of mid-Palaeozoic opercula, it is remarkable that specimens have been found from Australia and Canada, let alone within shells. This geographic range rivals that of the late Early Ordovician *Teiichispira* opercula known from Malaya and the United States (Yochelson and Jones 1968); none of them has been found in life position. The Austrian and Australian occurrences constitute a remarkable range.

Allied genus *Cyclospongia*

In his description of the operculum of *Oriostoma northi* Etheridge (1894) noted its similarity to *Cyclospongia discus* Miller (1891) described from Indiana. The observation that the taxon described by Miller is based on a gastropod operculum rather than a sponge has only recently been documented by Solem and Nitecki (1968); Miller's work appeared in a more formal format in 1892 (Solem and Nitecki 1968, p. 1007), which would have allowed a full year for it to come to Etheridge's attention before his paper on the Australian fossil. Solem and Nitecki demonstrated that *C. discus* was characterized by narrow, closely spaced, multispiral volutions, rather than concentric growth. In a sense, this indicates the perception shown by Etheridge, but it is a case of arriving at the right answer for the wrong reason, for Etheridge believed that the operculum was formed by concentric growth.

Although these two forms are generally similar, as was observed by Etheridge, the differences certainly warrant retention of *Cyclospongia* as a distinct gastropod genus, which was known originally only from its operculum. Opercula of that genus differ from those of *Oriostoma* in being relatively thinner, having relatively fewer whorls, having a rounded rim, and having a convex outer surface.

Tyler (1965) recently described a multispiral operculum in the gastropod fauna from the Middle Devonian Four Mile Dam Limestone of Michigan; a thin section of one of his specimens is figured for comparison (Pl. 1, fig. 5) to *O. northi*. He assigned this operculum to his species *Turbinilopsis anacarina* (Tyler 1965, p. 348, Pl. 48, figs. 19-25). The shell is moderately low spired with a well-rounded whorl profile. Examination of shells and opercula of this species indicates that the presumed association morphologically is likely; the geologic evidence further supports the inference of a life association. However, comparison of Tyler's holotype with a cast of *T. inconspicua* De Koninck, the type species, suggests that the taxa are not congeneric.

This operculum of *Turbinilopsis anacarina* and *Cyclospongia discus* are impressively similar in terms of general shape, number of volutions, and details of the rim and attachment pit. This similarity in overall form reinforces the suggestion of Solem and Nitecki (1968) that the poorly documented *Cyclospongia discus* occurs in rocks of Middle Devonian age rather than Silurian.

Further, if generic characters can be inferred from these opercula, it would suggest that *Turbinilopsis anacarina* be transferred to *Cyclospongia* Miller. Some may judge this to be too large a step to contemplate seriously at the present stage of our knowledge, but careful comparison of opercula of both species has

convineed us that at least a questioned transfer of Tyler's speeies is warranted.

From horizon 11 of the Dalhousie beds in Gaspé, Clarke (1909, p. 25, Pl. 1, figs. 10-12) briefly described and figured several speeimens of opereula. One speeimen in the collections of the U.S. National Museum (USNM 56745) indieates that these opereula are elose to *Cyclospongia*; the material is not well enough preserved to demonstrate that they are congeneric. Although they are questionably ascribed to *Euomphalus*, it seems more likely that these opereula are to be associated with one or more of the speeies in the fauna placed by Clarke under *Holopea*. *Holopea* as used by Clarke and *Turbinilopsis* as used by Tyler are simple shells of similar form.

In addition to an opereulum referred to *Oriostoma*, Spitz (1907, p. 139) recovered at least two other different isolated opereula. An impression of the inner surface (Pl. 13, fig. 9) of one speeimen is at least suggestive of *Cyclospongia*. Another form (Pl. 13, figs. 22a-e, 23) is similar to that of *O. northi* in shape but may have fewer whorls.

Koken (1889, Pl. 12, figs. 11-12) illustrated two speeimens which appear to be external views of *O. northi* opereula, *Cyclospongia*, or closely similar forms. Unfortunately, these figures are neither mentioned on the plate description nor noted in the text. Their souree and significance remain an enigma.

Finally, Wright (1915, p. 71) lists an 'opereulum' from the Lower Devonian of Alaska. The speeimens are distinet from both those of *Oriostoma northi* and *Cyclospongia*. It is evident from the seattered literature that a variety of generally similar multispiral opereula oeeur in the Devonian. Considerable eare will have to be taken in the future to differentiate them.

Summary

Few mid-Palaeozoie opereula are known, and the literature is seattered. We have exeeeded the limits of deseribing two Australian forms by drawing together these seattered references, but we believe that it is appropriate to use the remarkable Lilydale speeimens as a basis from which to draw more general eonelusions as to the form and funetion of opereula.

If there is one lesson in the subjeet of Palaeozoie opereula, it is that eonvergenee among diverse groups is eonsiderable, for in only a limited number of ways ean an opereulum be eonstrueted. At the same time, we have attempted to demonstrate that when one interprets the opereula in a rigorous fashion, then similarity of opereula may be useful in associating shells. This is particularly evident with the multispiral opereula.

Although there might be some relationship at the superfamily level between the shells of *Oriostoma* and *Omphalocirrus*, the Silurian opereula of *Oriostoma* eollectively show differenees in external profile, rim, and inner surfaee which may be of a greater order of magnitude than those between the Devonian *Cyclospongia* and the Devonian *Oriostoma-Omphalocirrus* eomplex. Etheridge (1894, p. 154) pointed out the differenee between the Silurian and Devonian opereula and questioned the generie plaeement of *Oriostoma northi*. However, the shells of *Oriostoma* and *Omphalocirrus* have more in eommon than either has with the shells of the speeies questionably assigned here to *Cyclospongia*. Classifieation based on shell form and that based on opereular form are still disjunet rather than eoordinate. Finer diserimination within the 'multispiral' group of opereula may resolve this problem. Collectively, these three groups prove that eonvergenee in opereular form has oeeurred in the fossil reeord more than onee. We eertainly eoneur with Etheridge's (1894, p. 154) remark that 'the subjeet is too long and eomplex to be eonsidered now'.

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Explanation of Plates

PLATE 1

Figs. 1-4—Operculum and shell of *Cyclonema lilydalensis* Etheridge Jr., from the Lilydale Limestone quarry, Lilydale, Victoria, Australia.

1. Relatively large operculum × 1·5, NMV P26889, (a) exterior, (b) interior.
2. Smallest available operculum ×3, NMV P26889, (a) exterior, (b) interior.
3. Largest available operculum × 1·5, NMV P26889, (a) exterior, (b) interior, (c) side view to show ontogenetic change in profile, (d) portion of oblique interior view × 4 to

show overhang, and at lower right start of taper toward growing edge.

4. Shell with operculum in place × 1, NMV 26888, (a) side, note that specimen is partially broken and obscured with matrix so that juvenile whorls appear isolated from body whorl, (b) apertural view, (c) view of shell with outer operculum face at right angles to camera.

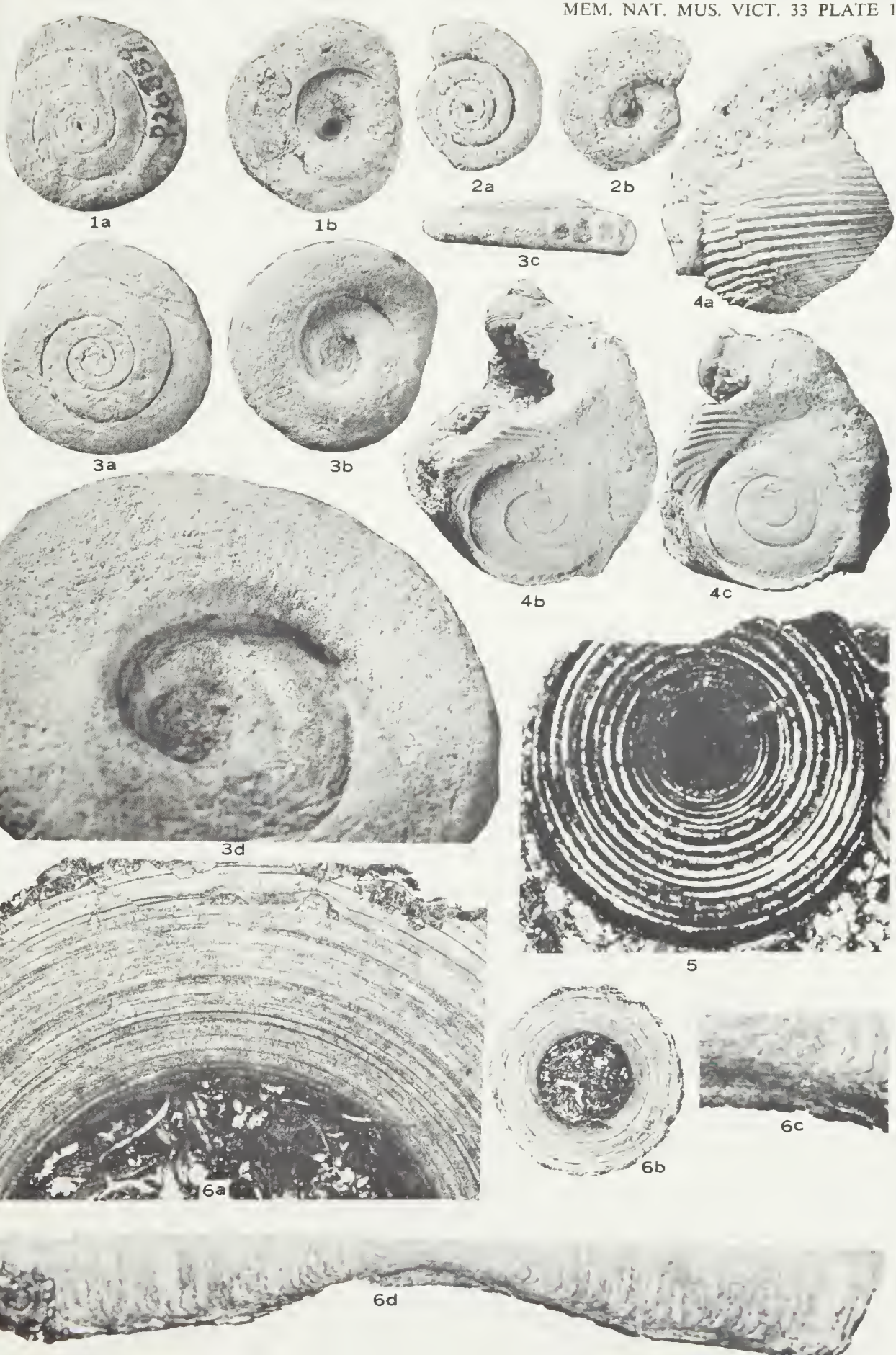
Fig. 5—Thin section of *?Cyclosponiga anacarina* (Tyler) for comparison. Museum of Paleontology, University of Michigan no. 57302d, × 5. Collected by J. M. Tyler from the Four Mile Dam Limestone, at Four Mile Dam on Thunder River, Michigan.

Fig. 6—Thin sections made from one large operculum of *Oriostoma northi* Etheridge Jr., NMV P26890. (a) portion of section parallel to outer face × 5, (b) same × 1, (c) right-central portion of a transverse section × 10, (d) same × 5. Note short recrystallized portion to left.

PLATE 2

Figs. 1-5—Operculum and shell of *Oriostoma northi* Etheridge Jr. from the Lilydale Limestone at Cave Hill quarry, Lilydale, Victoria, Australia.

1. Relatively thick operculum × 1·5, NMV P26890, (a) exterior, (b) oblique exterior, (c) unbroken side.
2. Thin operculum × 1·5, NMV 26890, (a) exterior, (b) oblique exterior, (c) side, (d) interior.
3. Thick operculum, somewhat weathered × 1·5, NMV P26890, views comparable to fig. 2 to illustrate especially differences in width and slope of outer operculum face.
4. Shell with operculum in place × 1, NMV P1107, presented A. W. Cresswell July 1902, (a) view at right angles to operculum, (b) very slightly oblique top view, (c) apertural view.
5. Largest available operculum × 1·5, NMV P26890, (a) exterior, (b) side, (c) interior.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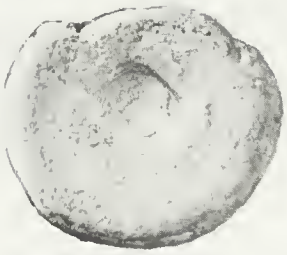
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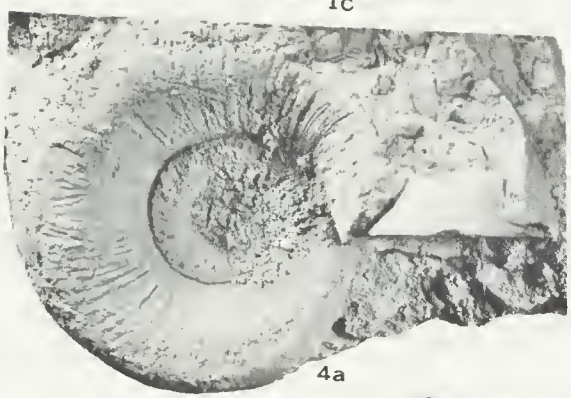
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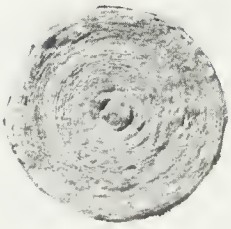
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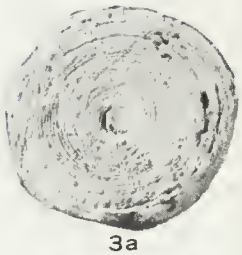
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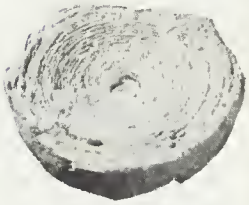
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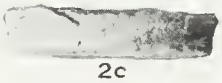
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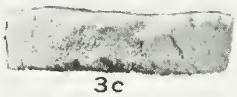
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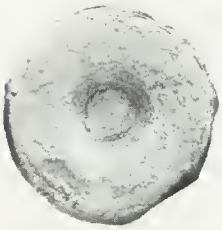
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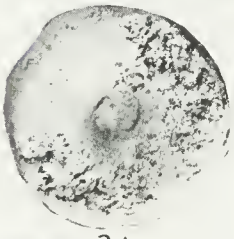
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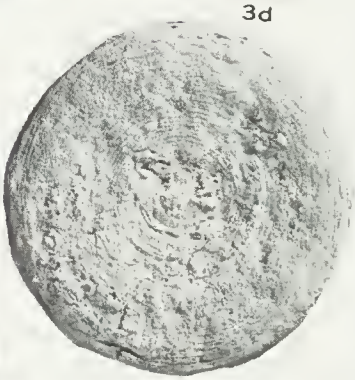
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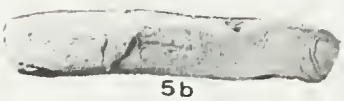
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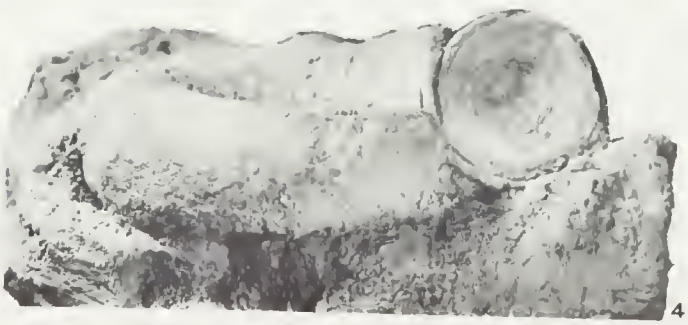
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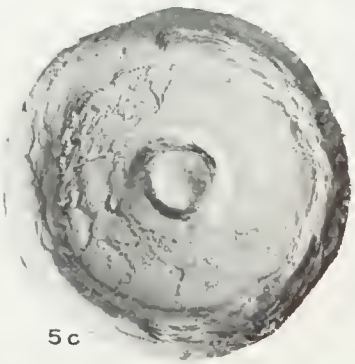
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