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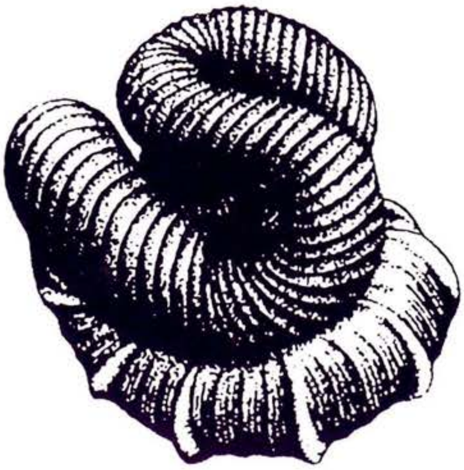

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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Morphological approaches in paleobiology

This special issue is partly based on the workshop of the Palaeontological Society of Japan on "Fossils and Morphology" held at the Misaki Marine Biological Station, University of Tokyo, in Miura City, Japan, from April 21 to 24, 2000. The workshop particularly focused on morphological approaches to paleobiological studies, from both fundamental and practical points of view. Most of the 34 participants of the workshop were young paleontologists interested in morphology.

Research on organic evolution over the Earth's history necessarily depends on the morphology of hard tissues preserved as fossils. Many paleontologists have developed and refined various methodologies for handling the raw morphological data presented by fossils and related extant organisms. However, there has been little reciprocal interaction or feedback in this process. For instance, the skills of an expert in comparative anatomy and the complicated methods handled by a specialist in mathematical morphology are still too far apart from each other. It would seem to be an important goal to make a wide variety of morphological methods accessible to all paleontologists, particularly younger ones.

The workshop setting made it possible to examine the morphological aspects of fossils from a number of viewpoints and provided an opportunity for young paleontologists to learn various methods in morphology. Most major topics concerning morphology, such as functional morphology, constructional morphology, morphometrics, biometry, theoretical morphology, developmental constraints, developmental genetics, heterochrony, cladistics, comparative anatomy, histology, biomineralization, etc., were covered. Topics included current research on various zoophyla, such as molluscs, arthropods, echinoderms and vertebrates, but there were also abstract discussions of methodology or principle that did not deal with particular groups of organisms. We did not attempt to construct a synthesis of those diverse topics. However, the workshop seems to have succeeded in addressing why so many morphological methods are valuable for paleobiology.

In consequence, the workshop was also a good occasion on which to plan a special issue of Paleontological Research on the use of morphology in paleobiology. The present issue partly reflects the activities at the workshop but does not aspire to represent the complete proceedings. The six contributions offered herein cover only a part of the topics presented at Miura. Among the senior authors of this issue, Enrico Savazzi, Takenori Sasaki and Takao Ubukata presented their papers in the workshop, and Richard Reyment and Kazushige Tanabe were welcome additions to the contributors to this special issue. All contributions in this issue underwent the regular review and editing process of the journal. In addition, several papers which were prepared for this special issue but did not complete the review process in time will be treated as regular submissions.

This collection is diverse, to the extent that perhaps there is no coherent theme. It covers specialized topics such as the morphometrics of ammonites, morphodynamics of an endolithic gastropod, macrosymbiosis in bivalves, early shell morphology of ammonoids, comparative anatomy of gastropods, and the theoretical morphology of bivalve shell structure. Although the papers contained in this issue differ in scope, each touches on the phylogenetic, functional and/or morphogenetic aspects of an organic form. These three aspects may be conceived of as the parameters of a Seilacher's triangle of constructional morphology, in which organic form is postulated to result from the interplay of the three factors. An integrated approach focusing on several aspects of organic form is becoming more and more important as paleobiological researches broaden out to include subjects of evolutionary biology. This issue will serve as a benchmark of the present state of this field and indicate lines of inquiry for future research to follow.

It should be noted that most of the approaches in the papers contained in this special issue were based on handy, "low-tech" methods such as observation or mathematical analysis, and required neither cutting-edge high technology nor the supporting framework of a large project. This collection indicates that morphology based on simple and economical techniques remains an exciting and creative field of science. This fact should encourage the young paleontologist who might feel that his or her work is mere handicraft in comparison to what colleagues who participate in large-scale projects in fashionable high-tech fields are doing. I hope that the topics presented here will be of interest to all paleontologists, and that this special issue will awaken the interest of many students in the field of morphology. I believe that new approaches to morphological studies will play a key role in paleontology in the 21st century.

I thank Tomoki Kase and Kazushige Tanabe, co-editors of Paleontological Research, for their help in the course of the editorial process of this issue. Thanks are also due to Rihito Morita for his cooperation in organizing the workshop, to the staff of Misaki Marine Biological Station for their kind hospitality during the workshop, to all participants in the workshop for their active and valuable discussions, and to all of the authors for their thoughtful contributions to this special issue. Although this is only the first time that Paleontological Research has collected papers on a specialized theme, I hope it will not be an isolated instance but the first of many to come.

—TAKAO UBUKATA
JANUARY 15, 2001

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Morphodynamics of an endolithic vermetid gastropod

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Abstract. In coiled mollusc shells, the apex typically is located near the centre of a whorl spiral and the aperture at its outer perimeter (exceptions do occur in molluscs with determinate or periodic growth, but they do not invalidate this general principle). This geometry satisfies simple growth and functional requirements. The Recent vermetid *Dendropoma* sp. defies these requirements with its inside-out shell geometry, in which the aperture is located along the axis of the spiral and earlier whorls coil around it. In addition, this species is unique among the Vermetidae in being fully endolithic in the adult, and is one of very few endolithic molluscs with the shell cemented to the substrate during growth. While *Dendropoma* is typically semi-endolithic, several species appear to have secondarily returned to epifaunal coiling as a response to crowding of the substrate. In *D.* sp., this was prevented by the immediate environment, subjected to a high rate of erosion. This is likely the factor that triggered the onset of endolithic coiling *into* the substrate. The change from a semi-endolithic to a fully endolithic life habit in this form was probably sudden, since the preadaptations of *Dendropoma* prevent a functioning intermediate stage.

Key words: endolithic, evolution, functional morphology, Gastropoda, Mollusca, Vermetidae.

Introduction

In the adult stage, almost all vermetid gastropods are cemented by the shell to a solid substrate (Morton, 1955, 1965; Keen and Morton, 1960; Keen, 1961; Savazzi, 1996, 1999a, and references therein). As a consequence of this habit, vermetid shells are irregularly coiled or lose all traces of coiling in the adult stage (above references, and below). Most vermetids remove a small amount of material from calcareous substrates before cementing the growing shell margin to it (Savazzi, 1996, and therein). This has the apparent adaptive value of removing superficial layers weakened by encrusting organisms and microborers, and of improving the adhesion between shell and substrate. Observation on free-living gastropods with regularly coiled shells shows that a comparable phenomenon, consisting of a secondary removal of periostracum and a thin outermost layer of shell material, is common at the junction between adjacent whorls. In the latter case, this phenomenon likely enhances adhesion between successive shell whorls. It is reasonable to suppose that removal of the superficial layer of substrate in vermetids may have evolved from the latter, widespread feature (Savazzi, 1996). It is not known in detail how this process is carried out by vermetids, but, as in most instances of secondary shell resorption in molluscs, the process is likely of a chemical, rather than mechanical nature.

A few vermetids remove a larger amount of substrate, and excavate a trench sunk into the surface of the substrate, into which subsequently they secrete their shells. This trait is particularly developed in the genus *Dendropoma*, which can be characterised as semi-endolithic because a substantial portion of the shell lies below the original surface of the substrate (Keen and Morton, 1960; Keen, 1961; Savazzi, 1996, 1999a; references therein, and below). In several species of this genus, the shell cavity is covered by a thickened "roof" of shell material, level with or slightly projecting from the surface of the substrate (Figures 1A, 2, and below).

This paper discusses the adaptations and evolution of a Recent species -or ecomorph -of *Dendropoma* with a unique combination of morphologic and ontogenetic characters. The taxonomic position of this form, and whether or not its adaptations and morphology warrant the introduction of a new supraspecific taxon, are discussed summarily, but a decision on these matters is not taken. This organism is hereby referred to as *Dendropoma* sp. because its closest affinities are clearly with this genus. This form differs from typical species of *Dendropoma* in that its adult shell is completely embedded in the substrate, except for the shell opening (see below). This habit can be characterised as fully endolithic, as opposed to the semi-endolithic habit typical of this genus (see above, and below). It is unique among vermetids.

In order to appreciate the unique character of the shell geometry in *Dendropoma* sp., it is useful to review the principal geometric properties of shells that grow by marginal accretion. Coiled mollusc shells typically have the apex located on the axis of a planispiral or helicospiral formed by later whorls. The aperture, on the other hand, is located at the

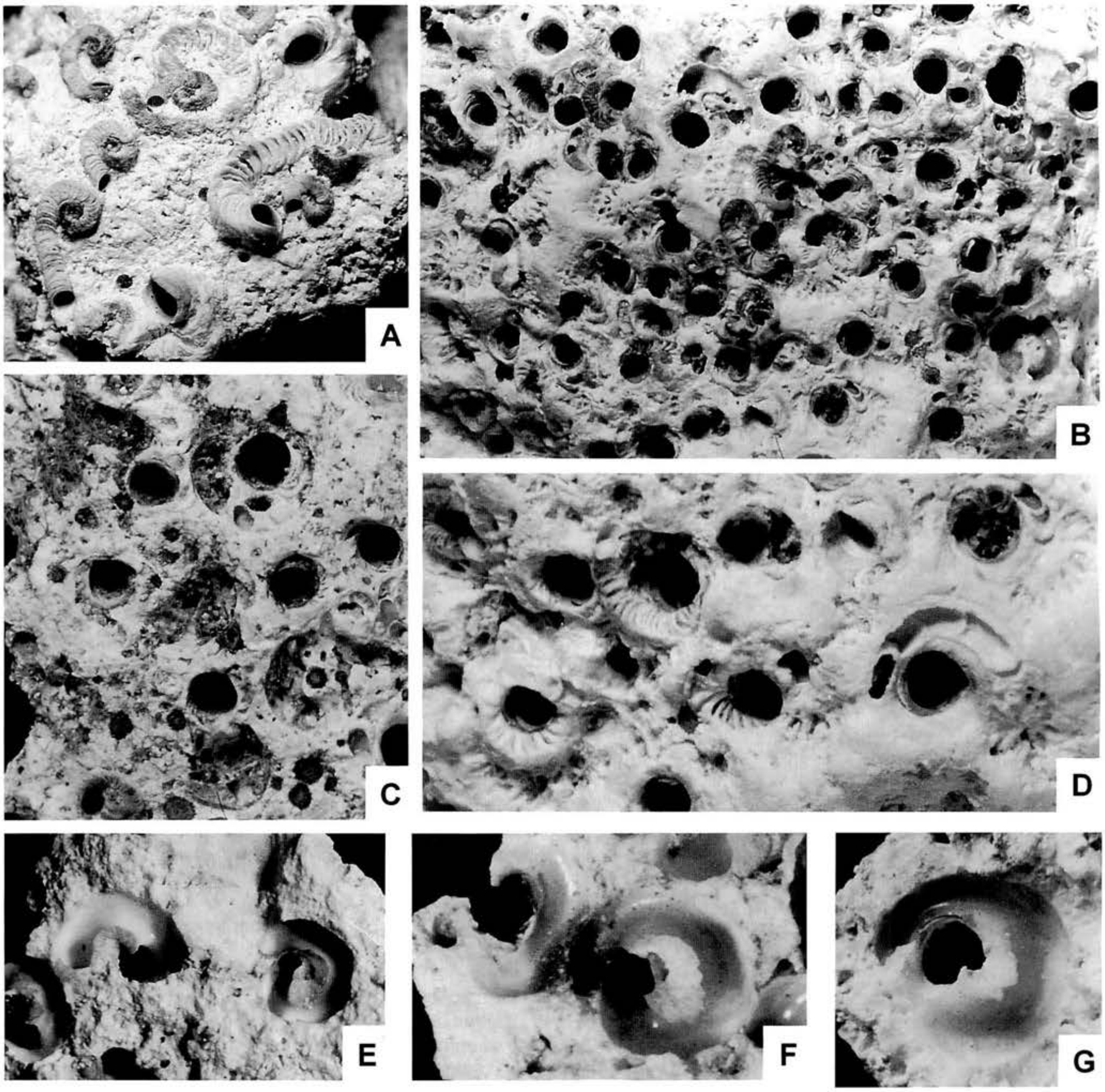

Figure 1. **A.** *Dendropoma annulatum*, Harrington Sound, Bermuda, x 2. **B–G.** *Dendropoma* sp., Hilotongan Island, the Philippines. Exterior view of substrate (**B–D**) and view of aperture and internal shell cavity seen from below the surface of the substrate (**E–G**). B: x 2; C, E: x 4; D, G: x 6.

outer periphery of the spiral. This geometry satisfies simple functional and ontogenetic requirements: it allows continued growth, since earlier shell portions are not in the way of further growth, and yields a relatively compact shell geometry (compatibly with accretionary shell growth). Exceptions to this rule are known, but they do not invalidate the general principle. These exceptions are typically associated with a "count-down" growth process (Seilacher and Gunji, 1993), in which further shell growth is impossible. This growth process is characterised by "preparatory" morphological changes that precede the attainment of the adult size and the cessation of further growth. For instance, several land snails bring the adult aperture close to the coiling axis in the adult stage, and a few bend the aperture back toward the apex, or

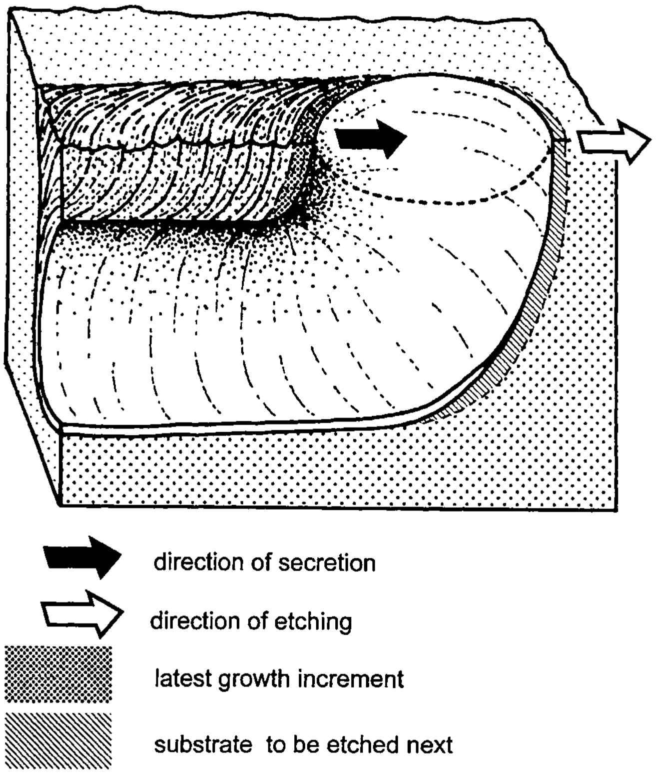

Figure 2. Schematic section through apertural region of typical semi-endolithic *Dendropoma*. The surface of the substrate is at the top. The shell cavity has been cut longitudinally through a plane perpendicular to the surface of the substrate and bisecting the shell aperture (the original outline of the aperture is indicated by a dashed line). Note the growth lines on the surface of the shell "roof" and within its structure. Arrows indicate the direction of migration of the aperture along the surface of the substrate during growth, caused by the twin processes of substrate etching (stippled area) and shell secretion (cross-hatched area).

away from it (e.g., Paul, 1999, and references therein). The same principle applies to several heteromorphic ammonoids with count-down shell geometries. A few gastropods (e.g., *Distorsio*), avoid this problem by returning periodically to a more conventional geometry of the last shell whorl, thus allowing the repetition of the count-down process. *Dendropoma* sp., instead, seems to defy the laws of shell geometry and growth by keeping the apertural region of the shell located at the centre of the whorl spiral, and earlier whorls coiled around it (see below) throughout its adult stage, while at the same time extending the length of its shell and increasing its depth within the substrate.

Material and methods

The species described in this paper is abundant (Figure 1B) in a band extending from high water mark to about 1 m below it on a rocky shore on the east coast of Hilotongan Island, the Philippines (123° 59′ 10′′E, 10° 12′ 50′′N, as measured on Philippine government maps). Population density exceeds 30,000 adult individuals per m^2 in the densest patches. The surface of the substrate is inclined to the vertical and relatively even. The substrate is a Quaternary, coarse-grained, poorly sorted and somewhat recrystallised biogenic calcirudite, containing occasional large bioclasts (mostly fossil scleractinians). Other areas of this island, as well as most of the nearby islands, were visited repeatedly by the writer, but this species was not observed elsewhere.

Samples of the substrate containing the endolithic vermetid were fixed in dilute buffered formaldehyde and subsequently kept in 5% ethanol. The substrate was bathed in dilute chlorine and mechanically scrubbed to remove adherent algae prior to drying for observation and photography.

Morphology and development of *Dendropoma*

In order to appreciate the affinities of *Dendropoma* sp. with other representatives of this genus, as well as the unique characters of this form, it is necessary to discuss the life habits and morphology of typical *Dendropoma* species.

Sexes are separate. Female individuals of *Dendropoma* house a small number of large embryos within the mantle cavity (Keen, 1960; Hughes, 1978). A veliger stage is absent, and the juvenile passes through a crawling stage before cementing to the substrate. Dispersion of juveniles may be facilitated by wave or current action, aided by the secretion of a mucus thread that retards sinking. However, the sinking rate of juveniles is too high to regard passively transported juveniles as planktonic (Hughes, 1978). Typically, the unattached juvenile shell is trochospiral, brown in colour, and consists of about two whorls.

As in other vermetids (above references), the juvenile shell initially becomes cemented to the substrate by its outer lip. Subsequent shell growth continues along a regular helicospiral trajectory, and lifts the aperture away from the substrate. At this point, the aperture bends toward the apex and reattaches to the substrate by its dorsal region. Shortly afterwards, the mollusc starts partially to sink the shell within the substrate, by eroding the substrate in the region adjacent to the aperture (Savazzi, 1996, 1999a, and references therein).

In adult *Dendropoma* (except for the form in question), two shell geometries and modes of growth are represented. In the first, which is exclusive to this genus, the shell follows an irregular path on the substrate, partly sunk within its surface (Figure 1A; Keen and Morton, 1960; Keen, 1961; Hadfield *et. al.*, 1972; Savazzi, 1996). Because of the recessed position of the shell within the substrate, the body whorl is bent outward at an angle of roughly 90° in the region near the aperture, so the plane of the aperture is parallel to the surface of the substrate and perpendicular to the growth direction of the shell (Figures 1A, 2). As a consequence, the aperture moves sideways during growth. Shell secretion takes place along half of the perimeter of the aperture, while erosion of the substrate takes place simultaneously along the other half (Figure 2). The exposed portion of the shell constitutes a "roof" flush with or slightly projecting from the surrounding substrate. Earlier positions of the aperture remain visible as coarse, falcate growth rugae on this roof (Figures 1A, 1C, 3A). The morphology of this relief-pattern is used as a taxo-

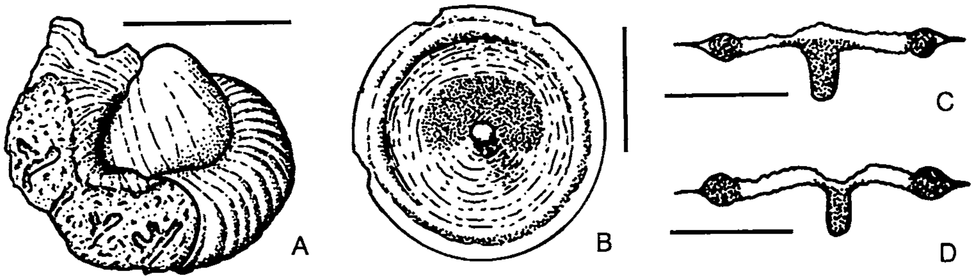

Figure 3. Juvenile shell showing initial cementation scar (**A**) and adult operculum in interior view (**B**) and schematic cross-section (**C**–**D**) of *Dendropoma* sp. Scale bars represent .5 mm.

nomic character at the species level. This mode of growth is common among immature individuals of most species of *Dendropoma*, and in the adult stage of solitary species and morphs.

The second mode of growth in this genus consists of piling successive whorls on top of each other, forming an irregularly coiled helicospiral shell. This mode of growth is well represented in other vermetid genera, such as *Serpulorbis*, *Tripsycha* and *Petaloconchus* (e.g., Keen, 1961; Savazzi, 1996, 1999a). In *Dendropoma*, this morphology is frequent in gregarious species and on crowded substrates.

In the adult stage, vermetids exhibit dextral coiling, or no coiling at all (above references). Since the adult shell portion is cemented to the substrate, or to earlier whorls, by its dorsal surface (see above), the whorls coil in the counterclockwise direction when viewed from above. Sharp bends of the shell in a sinistral (i.e., clockwise) direction are uncommon, and vermetids generally do not exhibit the meandering in alternate directions which is frequently seen in cemented serpulid polychaetes. As discussed by Savazzi (1996), sinistral bending in the Vermetidae is probably prevented by the laterally asymmetrical placement of the columellar muscle.

Dendropoma possesses a corneous operculum, the morphology of which is used as a species-level taxonomic character (Keen and Morton, 1960; Keen, 1961; Morton, 1965; Hadfield *et al.*, 1972). Common to all species of *Dendropoma* is a secondarily thickened central portion of the operculum, forming an inward projecting boss or elongated "handle" (above references, and below).

Several species of *Dendropoma*, as other vermetids, are gregarious and form exclusive or olygotypic associations in the intertidal and shallow subtidal zones, sometimes building small reefs (Keen and Morton, 1960; Keen, 1961; Kempf and Laborel, 1968; Hadfield *et al.*, 1972; Hughes, 1978, and personal observations).

Morphology and growth of *Dendropoma* sp.

Larval and juvenile development

Females incubate few (from 6 to 12) large eggs within the mantle cavity. Mature embryos contain a well developed protoconch consisting of approximately 2 whorls. This shell is translucent, smooth when observed under a dissection microscope, and brown-coloured.

Samples of the substrate inhabited by adults of this species were found to harbour numerous juvenile specimens, usually nested in small crevices. As typical of vermetids (above references), juveniles first cement to the substrate by the outer shell lip. Immediately afterwards, the shell bends in the apical direction, usually lifting free of the substrate, and subsequently reattaches to the substrate by the (homologically) adapical surface of the whorl.

The size of the shell in the smallest attached juveniles is comparable to that of the largest larval shells. Therefore, a veliger stage is apparently lacking. This agrees with observations on other species of *Dendropoma* (see above references).

Immature shell

At this stage, the shell is light brown to white with occasional brown patches (especially on its interior surface), carries coarse falcate ridges on its exposed surface, and is slightly sunk within the substrate. Except for the rather small size of *D.* sp., young specimens (central portion of Figure 1B) are essentially identical, in general appearance, to the adult stages of several other species of *Dendropoma* (e.g., Figure 1A).

Some of the individuals of *D.* sp. afterwards continue to wander in an apparently random fashion during growth, perhaps as a response to a crowded or irregular substrate. Most of the individuals, however, after an irregular early stage build an evenly curved, counterclockwise arch (surrounding the adult shell aperture of several individuals in Figure 1D). The radius of this arch, which gradually extends to one full whorl, is rather constant in length among different individuals, and the free space enclosed within the arch has a diameter comparable to that of the adult shell aperture. While building this arch, the apertural region of the shell becomes gradually embedded deeper within the substrate, thanks to a gradual increase in etching activity. Earlier portions of the body whorl do not change their position relative to the substrate.

Adult shell

Upon reaching one whole, broadly umbilicate whorl, the apertural portion of the shell, instead of rising onto and overlapping the earlier portion of the whorl as in other vermetids (see above), dips beneath it and into the substrate. At the same time, the shell aperture bends toward the umbilicus, thus avoiding the erosion of earlier portions of the arch. It is convenient to characterise these events as the beginning of the adult growth stage of the shell, although they may have no connection with reproductive maturity.

From this moment onward, the shell aperture opens within the umbilicus (Figure 1D–G). Further growth continues in the same fashion, with subsequent whorls becoming embedded deeper within the substrate, and the aperture located at the bottom of an umbilical well surrounded by earlier whorls (Figures 1C–G, 5). As a result, the shell is coiled in an apparently sinistral fashion. However, since the shell initially attaches to the substrate by the adapical side of the whorl, this coiling geometry is not sinistral, but hyperstrophic dextral.

Substrate-etching continues to take place within the aperture, which revolves around its axis and moves deeper within the umbilical well. This results in the formation of a pattern of spiralling ridges on the walls of the umbilical well (Figure 1D, bottom of Figure 1C, centre of Figure 5A). These ridges are homologous to the falcate ridges on the exposed surface of the shell in semi-endolithic species of *Dendropoma*. The largest individuals of *D.* sp. display an internal shell cavity consisting of about two whorls. The earliest, most superficial of the preserved shell whorls are commonly eroded (Figure 1C), with the shell cavity exposed and closed off by internal septa (rightmost portion of Figure 1D). Thus, this portion of the shell is gradually vacated and sealed off by the mollusc. In some specimens, judging from the diameter of the shell cavity, at least one or two additional whorls were originally present, and were destroyed by rapid erosion of the substrate. This is further supported by the frequent occurrence of radular scratch marks on the surface of the substrate (probably caused by chitons and archaeogastropods, which are both frequent in crevices and sheltered areas), and by a general lack of cemented epifauna.

Operculum

The operculum (Figure 3B–D) is corneous, white with reddish-brown periphery and nucleus. It is variable in general shape, with the outer surface slightly concave to highly domed (Figure 3C–D), carrying irregular concentric ridges but no visible spiral ornamentation. The perimeter consists of a thin lamina surrounding a thickened and bulging ring (Figure 3B–D), which, unlike the rest of the outer surface, is smooth and shiny. The inner surface of the operculum is smoother and carries an elongated axial "handle" (Figure 3C–D) and a semicircular or horseshoe-shaped dark patch near the basis of the handle (Figure 3B).

Soft parts

The general appearance of the body (Figure 4) is consistent with that of other species of *Dendropoma* (above references). The body is rather short, with a well developed columellar muscle. The mantle is slitted in the female, whole in the male. The pedal and cephalic tentacles appear to be rather short. A detailed anatomical investigation was not carried out.

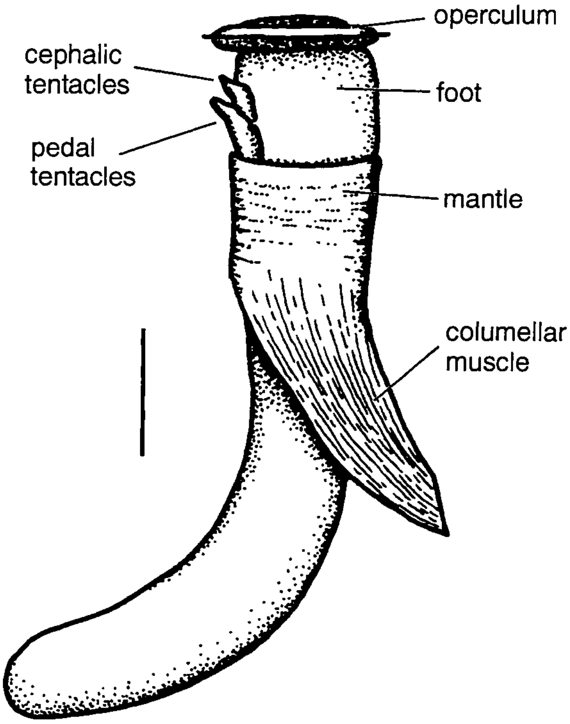

Figure 4. Soft parts and operculum of male *Dendropoma* sp., in lateral view. Scale bar represents 5 mm.

Affinities

The anatomy of the soft parts, morphology of the operculum and general shell characteristics (above, and Figures 1, 3–5) show this species to be a member of the vermetid genus *Dendropoma* Mörch, 1861 (see also Keen, 1961). The gregarious habits and morphology of the operculum are consistent with placement in the subgenus *Novastoa* Finlay, 1927. However, as noted by Keen (1961) this subgenus may be artificial. Furthermore, *D.* sp. is conspicuously different from all other *Dendropoma* in its shell geometry, mode of growth and endolithic habit. These differences are at least as important as those on which the existing subgenera of *Dendropoma* (i.e., *Dendropoma* s.s., *Novastoa* and *Elliptovermetus* Cossmann and Peyrot, 1922) are based. If future observations show that the shell morphology and life habits of *D.* sp. as described in this paper are a constant feature of this species, rather than an ecotypic response to a particular environment, it might be justified to erect a new subgenus to accommodate its unique character. However, a review of *Dendropoma* from the Philippines would be necessary to settle the problems connected with the specific and subgeneric placement of this genus, and such a study lies outside the scope of the present paper.

Evolution

The evolution of the endolithic habit in *D.* sp. cannot be explained as a process characterised by a gradual increase

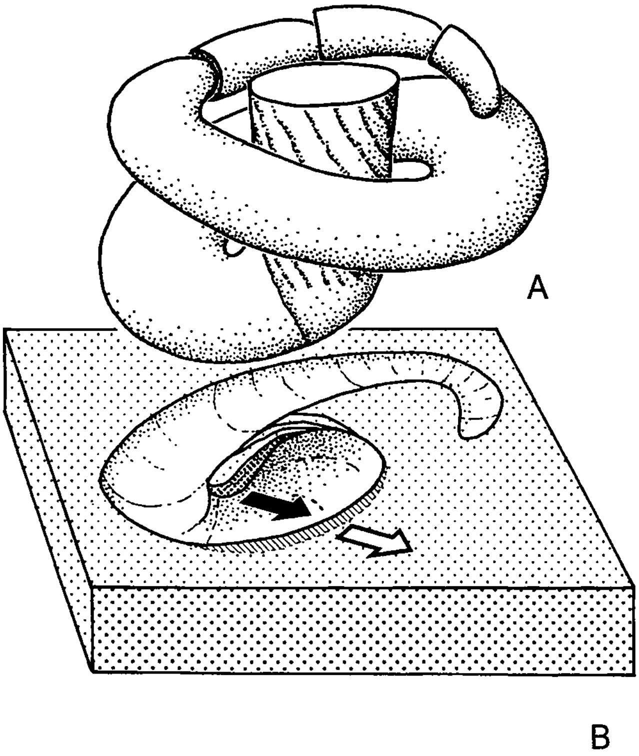

Figure 5. Internal mould of shell cavity (**A**) and cross-section through the deepest portion of the shell cavity (**B**), cut through a plane parallel to the surface of the substrate, in *Dendropoma* sp. In **A**, the early portion of the shell cavity is closed off by septa. A sculpture of coarse oblique rugae is visible on the walls of the apertural well (vertical portion of shell cavity located at the centre of the spiral). The shell aperture proper is located at the bottom of the apertural well.

in depth of the trench excavated by *Dendropoma*. This simple mechanism would produce an external roof above the whorls, which is absent in *D.* sp.

As an alternative, one could envision a growth process in which earlier portions of the shell gradually migrate deeper within the substrate during growth, by eroding substrate along one side of the shell cavity and secondarily depositing shell material on the opposite side (i.e., in a manner analogous to the sideways ontogenetic migration of the aperture). However, this process would leave telltale growth lines in the shell structure indicating earlier positions of the whorls within the substrate. This situation can be compared with the backwards and/or sideways boring process displayed by endolithic lithophaginid bivalves when they move away from their original position within the substrate. This process leaves meniscus-shaped layers of calcareous material filling the vacated region of the borehole (e.g., see Savazzi, 1999b, fig. 17.2B). Such structures, instead, are absent in *D.* sp., thus ruling out the above process and showing that the position of earlier shell portions within the substrate does not change.

A more unconventional growth mechanism (Figures 5B, 6) explains the observed features. The apertural portion of the shell, which is located at the bottom of the apertural well, grows in the manner typical of *Dendropoma*, i.e., by etching substrate along half of its circumference, and depositing shell material along the opposite half. However, in *D.* sp. the shell aperture, instead of migrating along a path parallel to the surface of the substrate, revolves around the bottom of the apertural well. As a result, the aperture rotates and progressively deepens within the substrate, leaving on the walls of the apertural well a set of spiralling, curved ridges homologous to those on the roof of semi-endolithic species (albeit arranged in a different geometric pattern because of the different trajectory of the aperture). At the same time, the rest of the shell cavity becomes coiled around the

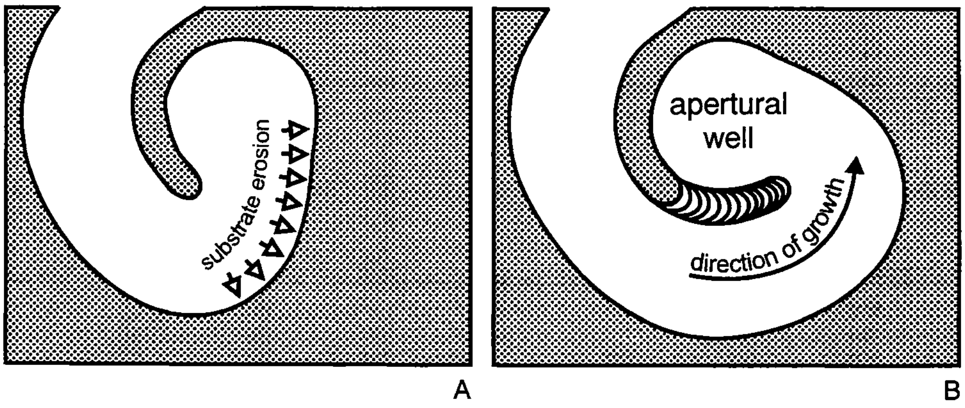

Figure 6. Schematic section through the bottom portion of the shell cavity of *Dendropoma* sp. along a plane parallel to the surface of the substrate (which is located above the plane of the figure), showing the shell growth process. Substrate erosion takes place along a portion of shell cavity in proximity with the apertural well (**A**). The direction of growth follows a circular trajectory (arrow in **B**) around the apertural well, gradually moving deeper within the substrate at the same time. This process is recorded by growth lines in the shell wall that surrounds the apertural well (**B**). Note that, with the exception of the gradual deepening of the apertural well, neither the apertural well nor earlier coiled portions of the shell cavity change their position relative to the substrate during growth.

apertural region because it is connected to the revolving aperture by a short bent portion (Figures 5A, 6). As a result, successive whorls are located progressively deeper within the substrate, trailing behind the aperture like a spiral staircase. Instead of coiling outwards from the surface of the substrate, like regular vermetids, *D.* sp. coils into the substrate. The direction of coiling, however, remains dextral as in epifaunal vermetids. Since in all vermetids the adapical shell surface is cemented to the substrate, the different direction of translation of the whorls along the coiling axis in *D.* sp. results in an inverted direction of translation of the helicospiral. Therefore, the coiling of *D.* sp. is not sinistral as could appear from a superficial observation, but hyperstrophic dextral (see above). Early portions of the shell cavity are vacated and closed off by septa, and thus the soft parts effectively migrate deeper within the substrate, in spite of the shell being cemented to it.

This growth process achieves the combined results of deepening the apertural portion of the shell (which is the only growing shell portion, since earlier shell portions remain immobile with respect to the surrounding substrate) without moving it laterally along the surface of the substrate. In addition, it makes a fully endolithic habit possible without increasing substantially the volume of substrate that must be eroded, compared to a semi-endolithic habit. Finally, it achieves these results without requiring substantial changes in the nature of the mechanisms involved in the shell construction and growth of *Dendropoma*.

Morphodynamics

The evolutionary process that led to this peculiar morphology and ontogeny remains to be explained. Biological morphodynamics (Seilacher, 1991) is a conceptual framework stating that the morphology and evolution of an organism can be understood as the interplay of four factors: function (i.e., all aspects of morphology with a direct adaptive significance), construction (including morphogenesis, structural materials and building principles), phylogenetic tradition (the evolutionary history, preadaptations and *Bauplan*; see below) and immediate environment (the characteristics of the environment in close proximity with the organism). The *Bauplan* is a set of constructional "building blocks" and morphologic characters that constitute the shared features of a lineage or taxonomic group (although they may not be expressed in all its members).

Morphodynamics is a recent extension of constructional morphology (*sensu* Seilacher, 1970; an alternative definition of the latter exists, but is not discussed here), which includes only the first three of the above factors. Both morphodynamics and constructional morphology were meant as practical frameworks to guide and summarise one's reasoning while carrying out an analysis of morphology, not as abstract philosophical generalisations. Therefore, the merits of these frameworks should be judged in the context of specific instances of functional analysis, like the present one.

In both conceptual frameworks, lateral migration of the shell aperture in typical *Dendropoma* is the preadaptation that allowed the evolution of the unique ontogenetic mechanism of *D.* sp. The spiral coiling of this species likewise originates from the generic gastropod *Bauplan*. While adult *Dendropoma* is facultatively not coiled, its larval shell is obligatorily coiled, just as the adult shell in noncemented ancestors of the Vermetidae was regularly coiled. Spiral shell coiling is still visible in the facultative or obligatory (albeit somewhat irregular) adult coiling of several vermetid genera (Keen, 1961; Savazzi, 1996, 1999a, and therein). Dextral shell coiling is also related to the laterally asymmetric placement of the columellar muscle in the Vermetidae (including those that are noncoiled in the adult stage). Thus, it is legitimate to state that spiral coiling is part of the vermetid *Bauplan*.

In the present case, morphodynamics may display a practical advantage over constructional morphology. The latter provides an explanation for the morphology of *D.* sp. in an adaptive context, but does not explain clearly the cause of its evolution. Morphodynamics, instead, offers a better framework for explaining both. The rock substrate inhabited by *D.* sp. is characterised by a high rate of erosion (as evidenced by grazing tracks and by the fact that early portions of the shell of this species are often eroded away; Figure 1E–F). Significantly, the only other sessile invertebrate common in the same substrate is a rock-boring foraminiferan that lives in a shallow pit (dark grey patches in Figure 1F) and continuously deepens it in order to remain protected against erosion (J. Whittaker and E. Savazzi, unpublished). It can be noticed also that the substrate is crowded (Figure 1B, E–F). These are the key environmental factors to explain the evolution of *D.* sp.

Fast erosion of the substrate encouraged a switch from a semi-endolithic to an endolithic habit, because the latter offers a better protection against erosion, and thereby an enhanced probability of survival. Most endolithic gastropods and bivalves fight erosion of the substrate by boring deeper within the substrate during growth (e.g., Savazzi, 1999a, 1999b, and references therein). This requires mainly behavioural modifications, rather than morphologic ones, since these molluscs are not cemented to the substrate, can move within their boreholes, and already bore deeper into the substrate during growth, in order to accommodate their ontogenetic increase in size. *Dendropoma*, instead, is constrained by shell cementation to the substrate in its possible evolutionary "choices".

Excavation of a deeper trench with a thicker roof (cf. Figure 2) would seem to be a straightforward route into the endolithic habit. However, this solution is not feasible because it involves a substantial increase in the volume of substrate that must be removed, and of shell material that must be secreted (i.e., the "roof" of shell material covering the trench). Alternatively, faster horizontal growth along the surface of the substrate, resulting in an increased length of the shell, would also help to fight off erosion by continually moving the organism to fresh areas of the substrate, but likewise involves an increase in the energy spent boring and secreting shell material, besides being unfeasible in crowded substrates. In *D.* sp., a secondary return to coiling avoided these problems, and provided a working solution to seemingly contrasting necessities: cementing the organism to the substrate, allowing it to move deeper into the substrate during growth, not increasing the used surface area of substrate, and not increasing the volume of removed substrate substantially, compared with a semi-endolithic habit.

The secondary return to coiling in *D.* sp. confronted this species with a "choice" between two mutually exclusive life habits: epifaunal coiling above the surface of the substrate, or endolithic coiling beneath its surface. No working intermediate choices are possible (short of abandoning coiling and reverting to an uncoiled semi-endolithic habit), because this would cause the mollusc to bore into earlier portions of its own shell, still occupied by the soft parts. Thus, the onset of coiling and of fully endolithic habits must have been a sudden evolutionary event, made possible by the facts that coiling was already available in the vermetid Bauplan, and that the accompanying coadaptations did not require the evolution of substantially new morphological or behavioural traits.

Alternatively, an intermediate paedomorphic stage, adaptive in lessening the negative effects of erosion by reducing the life span, may have been involved. Such a stage likely had a life habit comparable to that of juvenile vermetids, and therefore displayed no substantial morphologic innovation. The subsequent return to a larger size forced a switch from epifaunal to endolithic habits and hyperstrophic coiling. Thus, also this alternative process involves a sudden evolutionary change.

The facts that several species of *Dendropoma* display facultative or obligatory epifaunal coiling (see above), while all *Dendropoma* are capable of semi-endolithic boring, suggest an evolutionary scenario in which epifaunal coiling was initially lost in *Dendropoma*, and subsequently reappeared secondarily multiple times during the evolution of this genus, rather than representing the uninterrupted maintenance of this character from epifaunal ancestors. The factor that "tipped the scales" in favour of endolithic boring in *D.* sp., instead of resulting in yet another instance of parallel evolution of epifaunal coiling, is likely the substrate being subjected to a high rate of wave erosion and/or bioerosion, which makes epifaunally coiled individuals excessively vulnerable. Thus, the immediate environment appears to be the trigger of the evolutionary processes that led to the unique shell morphology and growth mechanism in *D.* sp. In turn, the presence of a solid substrate surrounding the organism, which characterises the endolithic environment, allowed the evolution of a growth mechanism that would be impossible in an epifaunal organism.

To the knowledge of the writer, the clavagellid bivalve *Bryopa* is the only other boring mollusc that permanently cements the shell (in particular, the left valve) to the substrate without losing the capability of migrating deeper within the substrate during growth (Savazzi, 2000). *Bryopa* does so by continuously elongating the shell and shifting the position of the soft parts within the left valve, abandoning its early portions. Thus, its adaptations are partly convergent with those of *D.* sp.

Conclusions

Dendropoma sp. is unique among vermetids in being fully endolithic in the adult stage. During the juvenile, semi-endolithic stage, it builds a broadly umbilicated whorl partly embedded in the substrate. Subsequently, instead of building successive whorls upward and elevating its shell above the substrate, as in several epifaunal vermetids, it places new whorls deeper within the substrate and underneath earlier ones, like a descending spiral staircase. The aperture moves into the shell umbilicus and does not migrate further along the surface of the substrate during growth. Instead, it gradually deepens within an umbilical apertural well. This process results in the formation of a characteristic spiralling pattern of ridges on the walls of the well.

While the shell morphology of *D.* sp., at first sight, appears to violate the fundamental laws of gastropod shell geometry, the adaptiveness and evolution of this morphology can be successfully explained within the framework of biological morphodynamics. The demands posed by a substrate subjected to rapid erosion appear to be the factor that triggered the evolution of this form. Its growth mechanism and most of its unique adaptations are related to the sudden change in immediate environment caused by an evolutionary switch from a semi-endolithic to a fully endolithic life habit. This switch was a sudden event, because the preadaptations of *Dendropoma* allow no feasible intermediate stage between a semi-endolithic and a fully endolithic life habit.

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External features of embryonic and early postembryonic shells of a Carboniferous goniatite *Vidrioceras* from Kansas

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Abstract. The ornamentation and dorsal wall structure of *Vidrioceras* (Cycloloboidea, Goniatitina) in the early ontogenetic stage are described on the basis of specimens from the Upper Pennsylvanian in Kansas, USA. The exposed surface of the embryonic shell is smooth, without any trace of ornamentation or growth lines. Regularly spaced lirae abruptly appear on the early postembryonic shell just adoral of the primary constriction. The inner surface of the dorsal wall in the embryonic and early postembryonic stages exhibits a distinct ornament consisting of evenly spaced, longitudinal ridges, which are replaced adorally by the typical wrinkled ornament in the subsequent stage. Our observations are in accord with those of goniatites from the Upper Carboniferous Buckhorn Asphalt of Oklahoma, suggesting that in the Goniatitina, the outer surface of the embryonic shell is smooth. Comparison with the embryonic shell formation of extant *Nautilus* suggests that in the Goniatitina, the embryonic shell was uniformly secreted by the shell gland on the posterior side of the embryo.

Key words: Ammonoidea, Carboniferous, development, embryonic shell, Goniatitina, Kansas, *Vidrioceras*

Introduction

The embryonic shell of ammonoids (termed the ammonitella by Druschits and Khiami, 1970) consists of a spherical initial chamber and approximately one subsequent whorl with a thick nacreous swelling (primary varix) at the aperture (for references see Landman *et al.*, 1996). The boundary between embryonic and postembryonic stages is marked by the primary constriction. Most previous studies on the external morphology and microstructure of embryonic shells of the Ammonoidea have been based on Mesozoic material with aragonitic preservation (Druschits and Doguzhaeva, 1981; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman, 1982, 1985, 1987; Landman and Bandel, 1985; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press, among others). In Paleozoic ammonoids, the microstructure of the embryonic shell is rarely preserved in most fossils due to diagenesis, except for aragonitic goniatites studied by Kulicki *et al.* (in press) from the Carboniferous Buckhorn Asphalt in Oklahoma, USA. Previous authors have indicated that the embryonic shells of Paleozoic ammonoids display ornamentation and features of several internal shell characters different from those of Mesozoic ammonoids (Beecher, 1890; Miller, 1938; House, 1965; Mapes, 1979; Tanabe *et al.*, 1993, 1994; Doguzhaeva, 1996; Landman *et al.*, 1996; Landman *et al.*, 1999; Klofak *et al.*, 1999; Kulicki *et al.*, in press). These studies have revealed a variety in the embryonic shell features in the Ammonoidea that can be used for higher-level phylogenetic analysis.

In this paper, we describe the ornamentation and the dorsal wall structure of goniatites at the embryonic and early postembryonic stages based on specimens from the Upper Pennsylvanian of Kansas, USA. Furthermore, the result of our observations is compared with data on other ammonoids and extant *Nautilus* and discussed for its implications for systematics and embryonic shell formation. Some of the specimens utilized have been studied by Tanabe *et al.* (1993), but those observations are partly reevaluated in this paper.

Material and methods

Tanabe *et al.* (1993) discovered an embryonic ammonoid assemblage in a carbonate concretion recovered from the Virgilian (Upper Pennsylvanian) offshore shale in Pomona, Kansas, USA. These authors classified the embryonic ammonoids into two morphotypes by the difference in the size and shape of their initial chambers, namely into a large and globular and a small and ellipsoidal one. They further assigned these large and small morphotypes to *Vidrioceras* (Vidrioceratidae, Cycloloboidea) and *Aristoceras* (Thalassoceratidae, Thalassoceratoidea) respectively, on the basis of comparison with their initial chambers with those of larger specimens of these two genera from the same concretion.

About one hundred well preserved specimens of the two genera at embryonic and early postembryonic stages were removed without etching from the weathered portion of the concretion by the wet-sieving method. They were coated with platinum and observed by scanning electron microscopy. Although the embryonic shells of *Aristoceras* occur more abundantly than those of *Vidrioceras*, we did not observe early shell features of the former genus because of poor preservation of the dorsal wall sculpture in the available specimens. As already pointed out by Tanabe *et al.* (1993), the goniatite specimens from Pomona preserve calcified shell material, and the recrystalized condition of their shell wall prevents study of the shell ultrastructure. Our observations are, therefore, mainly restricted to the external features of these specimens. All of the specimens utilized are housed in the University Museum, the University of Tokyo (UMUT).

Observations

Embryonic shells

General morphology and ornamentation.— The embryonic shells of *Vidrioceras* examined are all globular in overall shape and consist of a spindle-shaped initial chamber and approximately one subsequent planispiral whorl (Figure 1). In median section, a thick nacreous swelling (primary varix) appears on the inner side of the prismatic layer in the apertural region (see Tanabe *et al.*, 1995, figure 2A). The first whorl is much broader than high, covering the greater portion of the initial chamber (Figures 1, 2). The spiral length of the embryonic shell (=ammonitella angle of Landman *et al.*, 1996) is relatively long, measuring about 360° in median section. The embryonic shell diameter in the specimens examined ranges from approximately 720 μm (UMUT PM19872-1; Figure 1.1) to 780 μm (UMUT PM19872-3; Figure 1.3a). The exposed surface of the shell at the embryonic stage is smooth without any trace of ornamentation or growth lines (Figure 1).

Dorsal wall of the first whorl.— In several embryonic and early postembryonic specimens, part of the first whorl has been lost due to mechanical destruction during the taphonomic process or due to the wet-sieving procedure. In those specimens, evenly spaced longitudinal ridges are visible on the dorsal side of the missing whorl portion (Figures 2.1-2.3, 3.1, 3.2). They never occur on the lateral flanks of the initial chamber that are free from the first whorl. This fact indicates that the longitudinal ridges represent the sculpture on the inside surface of the dorsal wall of the first whorl. A weaker ridge is occasionally intercalated between the longitudinal ridges (Figure 2.3b).

Remarks.— Tanabe *et al.* (1993, fig. 3A) described evenly spaced longitudinal ridges on the ventrolateral side of several embryonic shells of *Vidrioceras* from the same locality and interpreted them as the surface ornamentation. However, our reexamination of these and additional specimens reveals that the longitudinal ridges are not the surface ornamentation but the microornamentation on the inner side of the dorsal wall, and that the exposed surface of the embryonic shell of *Vidrioceras* is in fact smooth.

Early postembryonic shells

The embryonic shell margin is easily visible from outside by the presence of the slightly depressed primary constriction followed by the sharp apertural edge (see arrows, Figure 1.1, 1.3a). Fine transverse lirae abruptly appear on the adoral side of the primary constriction. They are initially rectiradiate in the early postembryonic stage (Figure 1.1, 1.3a, b), but become prorsiradiate and gently convex at the venter in a later stage. Each lira is asymmetric in cross section with a steep edge on the adoral side and is gently inclined adapically (Figure 1.3b).

The change of the inner surface sculpture of the dorsal wall is visible in several early postembryonic shells whose body whorl is partly lost secondarily (Figure 2.1-2.3). In one of these specimens, shown in Figure 2.2, the longitudinally ridged ornament disappears on the dorsal side of the embryonic shell aperture and a wrinkled ornament similar to a human fingerprint pattern begins to appear on the adoral side of the primary constriction. In the embryonic or early embryonic specimen shown in Figure 2.4, the wrinkled ornament already exists on the dorsal side near the shell margin. In another two specimens, shown in Figure 2.1 and 2.3, the longitudinally ridged ornament extends for a half whorl beyond the primary constriction. These observations clearly indicate that *Vidrioceras* exhibits some variation in the ontogenetic change of the dorsal wall ornament.

Comparison with other ammonoids

On the basis of observations on excellently preserved material from the Pennsylvanian (Desmoinesean) Buckhorn Asphalt in Oklahoma, Kulicki *et al.* (in press) reported that the outer surface of the embryonic shells of goniatites is smooth without any trace of ornamentation or growth lines, as is the case of *Vidrioceras* described herein. These observations strongly suggest that in the Goniatitina the embryonic shell is smooth.

Ornamentation on embryonic shells of the Goniatitina differs from those of other ammonoid suborders. In the Devonian Agoniatitina, Anarcestina and Tornoceratina, the

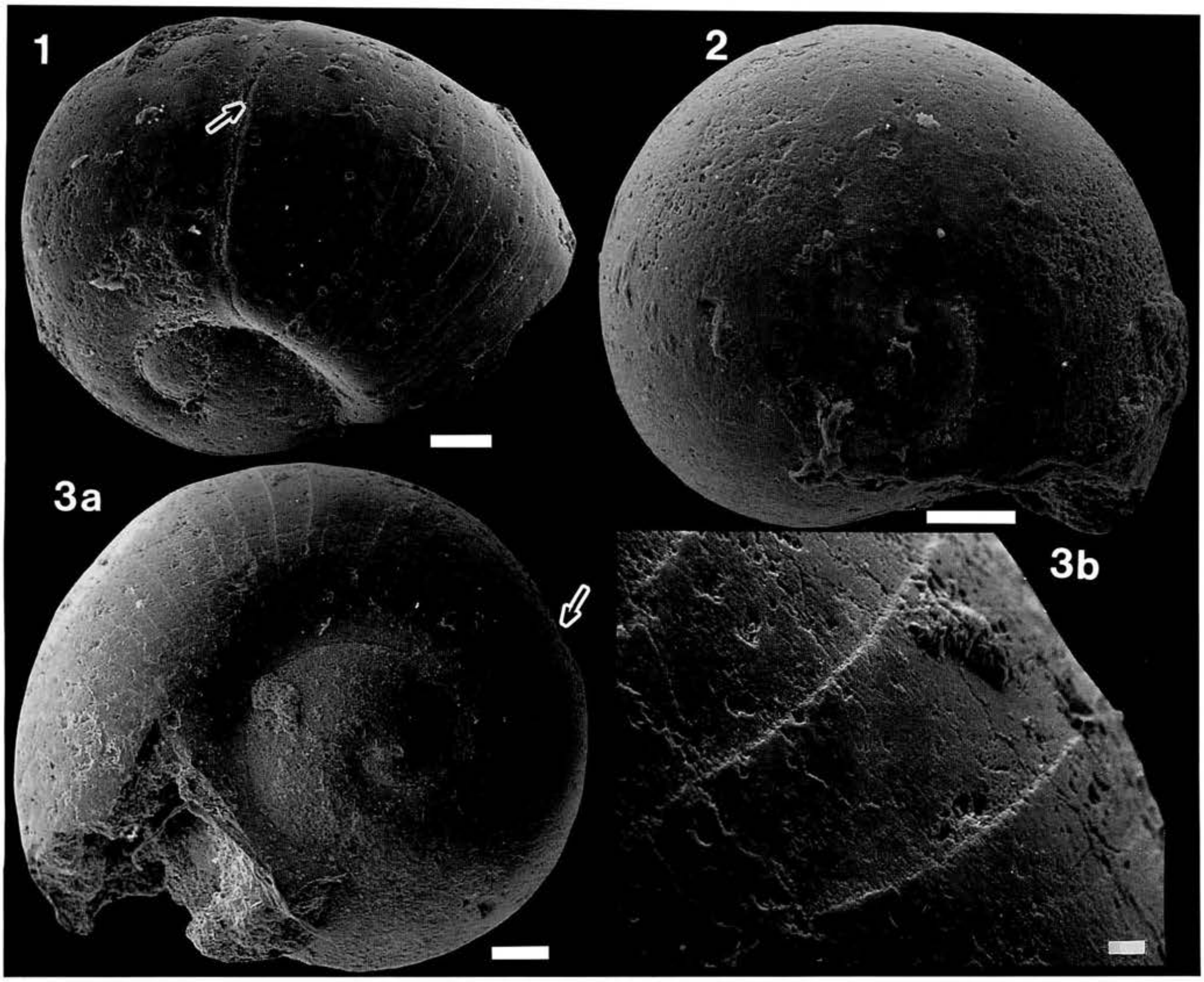

Figure 1. *Vidrioceras* sp. **1**. Oblique view of early postembryonic specimen showing slightly depressed primary constriction and adjacent embryonic shell edge (pointed by an arrow). The embryonic shell is smooth, while the postembryonic shell is sculptured by fine transverse lirae. UMUT PM19872-1. **2**. Lateral view of embryonic shell with smooth surface. UMUT PM19872-2. **3a, b.** UMUT PM19872-3. Lateral view of early postemebryonic shell showing abrupt appearance of fine transverse lirae after primary constriction (pointed out by an arrow) (**3a**) and close-up of lirae (**3b**). Scale bars: 100 μm (1, 2, 3a) and 10 μm (3b)

embryonic shells are characterized by fine transverse lirae parallel to the aperture (Beecher, 1890; Miller, 1938; House, 1965; Landman *et al.*, 1996; Klofak *et al.*, 1999). In the uncoiled Late Silurian and Devonian Bactritina and partly coiled Devonian ammonoids, the straight whorl after the initial chamber is also covered with transverse lirae (Erben, 1964). Mapes (1979) reported both smooth and longitudinal ornament on the initial subspherical chamber and early shaft of "bactritids" from the Carboniferous, and Mapes (1979) and Doguzhaeva (1996) reported a reticulate ornamentation on the earlier embryonic shaft portion of "bactritids" from the Carboniferous and Permian, respectively. However, Doguzhaeva *et al.* (1999) suggested that some of these specimens may eventually be reassigned to the Coleoidea. In the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, the embryonic shell lacks lirae and instead is covered with minute tubercles (Kulicki, 1974, 1979; Bandel, 1982, 1986; Bandel *et al.*, 1982; Landman and Waage, 1982; Landman, 1985, 1987; Tanabe, 1989; Kulicki and Doguzhaeva, 1994; Landman *et al.*, in press). To sum up these previous descriptions, at least three kinds of embryonic shell ornamentation have been recognized in the Ammonoidea excluding Upper Paleozoic "bactritids". Each ammonoid suborder, excluding the doubtful taxon Bactritina, appears to have its own characteristic pattern of ornamentation.

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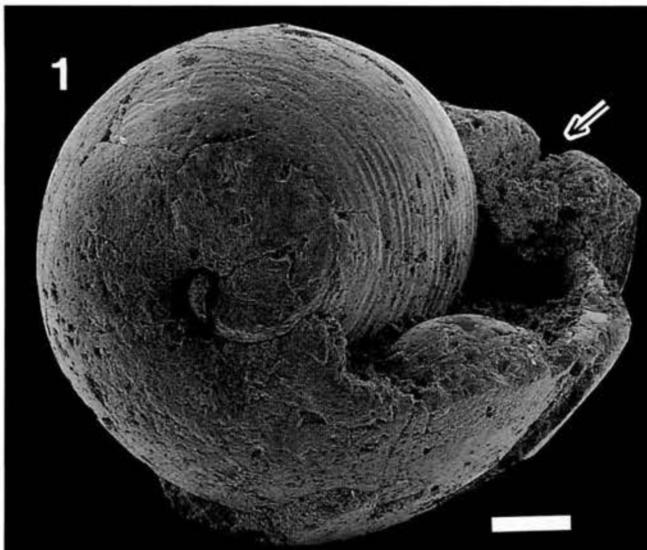

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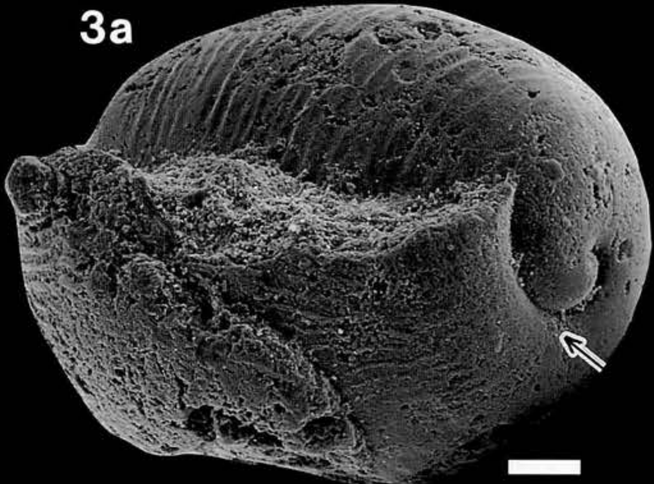

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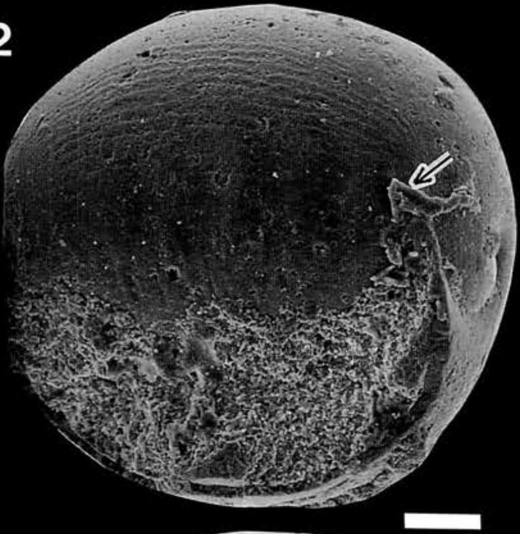

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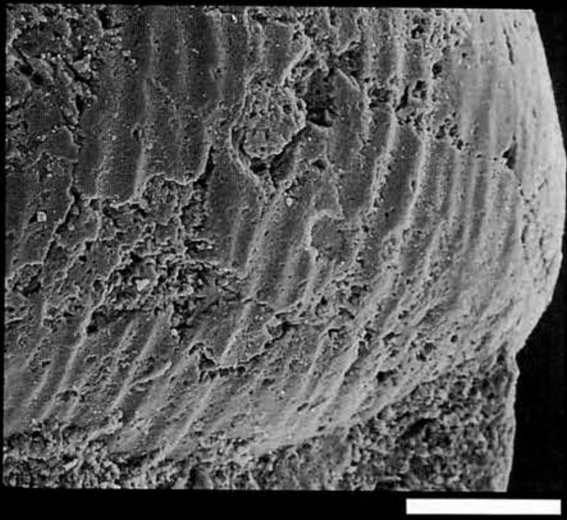

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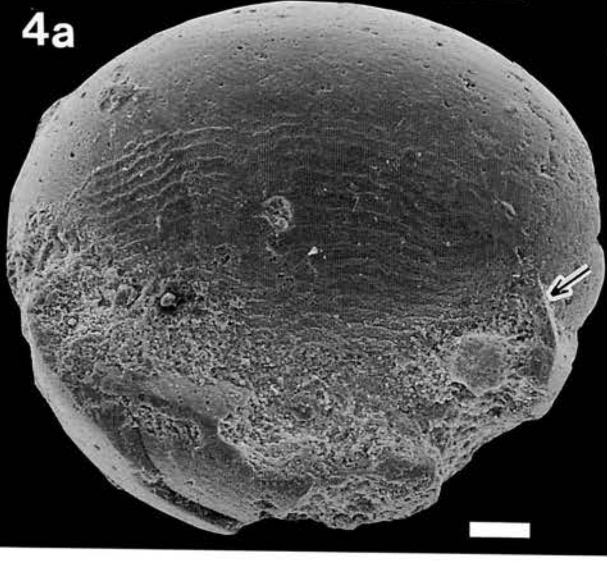

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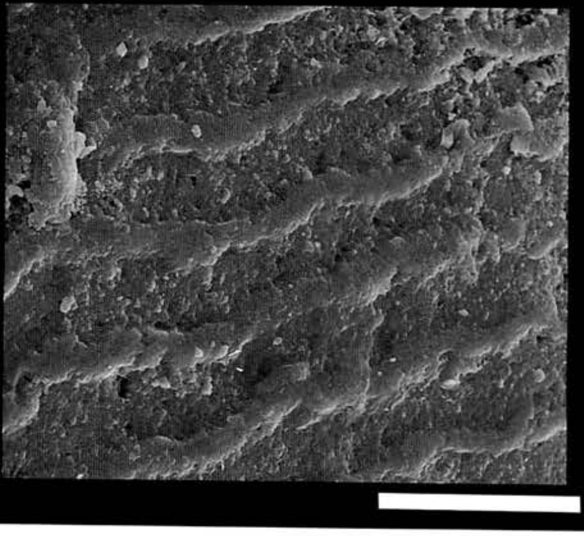

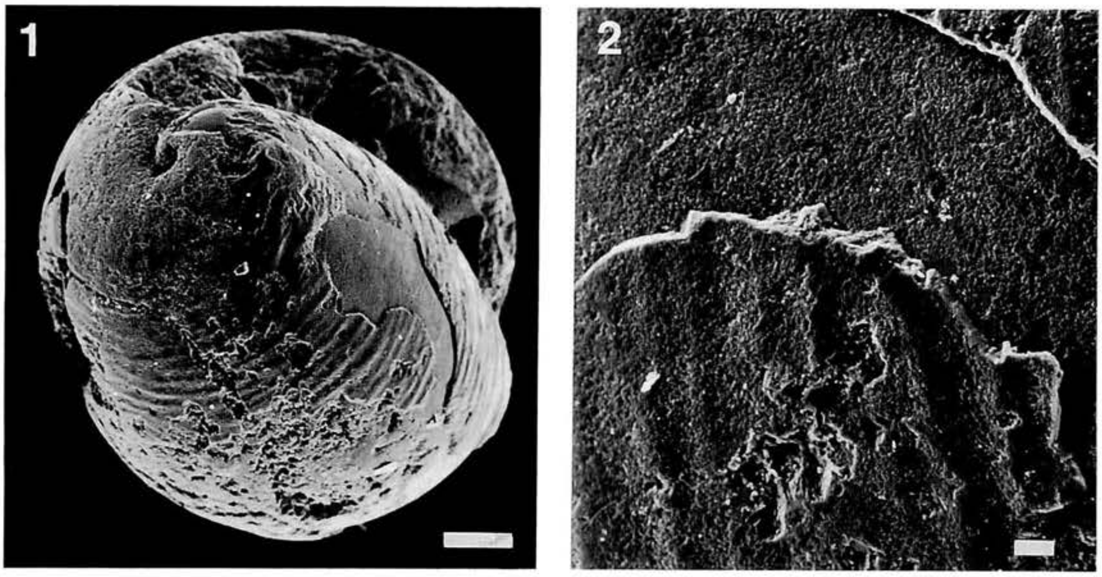

Figure 3. *Vidrioceras* sp. **3a.** Oblique view of embryonic shell with preserving interior dorsal wall sculpture of the first whorl with longitudinal ridges. **3b.** Close-up of longitudinal ridges on interior side of dorsal wall. Note that the boundary between ventral and dorsal shell walls is discernible in this specimen. UMUT MM19872-8.

Discussion

Observations of the early embryonic shells of extant *Nautilus* provide a reference point for discussions about the embryonic development of ammonoids. According to Arnold and Landman (1993) and Tanabe and Uchiyama (1997), the early embryonic shell development of *Nautilus* can be divided into two stages with different shell microstructure and ornamentation. In the first stage (=early organogenetic stage), a low cap-shaped shell with a distinct median depression (called cicatrix) is secreted in the sequence of outer conchiolin and inner prismatic layers. The cicatrix lacks growth lines, indicating uniform shell secretion by the mantle primordium (shell gland) on the posterior side of the embryonic body (see Tanabe and Uchiyama, 1997, fig. 1A). In the second stage (=middle organogenetic stage), a new shell consisting of outermost conchiolin, outer prismatic, middle nacreous, and inner prismatic layers appears at the outer margin of the cicatrix, leaving a discontinuity in the shell structure at the boundary. It is sculptured by transverse growth lines and radial undulations. At this stage of development, the anterior mantle margin is well differentiated and possesses three folds, where shell secretion occurs (Tanabe *et al.*, 1991).

The absence of transverse lirae on the embryonic shells of the Goniatitina strongly suggests that the walls of the initial chamber and the first whorl were secreted synchronously by the undifferentiated shell gland. Bandel (1982) and Kulicki and Doguzhaeva (1994) hypothesized this kind of embryonic shell development in Mesozoic ammonoids, relying upon observations about the biomineralization of embryonic shells of modern "archaeogastropods". The longitudinal dorsal layer was probably secreted at a late stage of embryogenesis and occasionally at an early postembryonic stage. The appearance of transverse lirae on the postembryonic shell indicates an accretionary mode of growth. This event does not occur synchronously with the development of the dorsal wall with wrinkled ornamentation (Figure 2.1-2.4; Kulicki *et al.*, in press, pl. 2, fig. 3). Such a wrinkled dorsal wall has been extensively recognized in Paleozoic ammonoids in the postembryonic stage (House, 1971; Walliser, 1970). Kulicki (1979, 1996) and Kulicki *et al.* (2001) have pointed out that the dorsal wall of ammonoids consists of two components, namely, the outer component consisting of organo-prismatic material, sometimes with a wrinkled texture on the outside, and the inner prismatic component that covers the outer

← **Figure 2.** *Vidrioceras* sp. **1**. Lateral view of incomplete postembryonic shell, part of whose body whorl is lost. Dorsal wall of the first-second whorls exhibits longitudinally ridged ornament on the inner side. UMUT MM19872-4. **2.** Ventral view of early postembryonic shell showing change of interior dorsal wall sculpture from longitudinally ridged pattern to wrinkled pattern at embryonic shell/postembryonic shell boundary. UMUT MM19872-5. **3a, b.** UMUT MM19872-6. **3a.** Oblique view of incomplete postemebryonic shell, showing change of interior dorsal wall sculpture from longitudinally ridged pattern in embryonic stage to wrinkled pattern in postembryonic stage. **3b.** Close-up of longitudinally ridged dorsal wall structure in early postembryonic stage of same specimen. **4a, b.** UMUT MM19872-7. **4a.** Ventral view of embryonic (or early postembryonic) shell showing interior feature of dorsal wall with wrinkled ornamentation. **4b.** Close-up of wrinkled ornamentation in same specimen. Scale bars: 100 μm (1-4a) and 40 μm (4b). Arrows in 1, 2, 3a, and 4a point to the approximate position of primary constriction.

component on the adapical side of the body chamber. Our observations indicate that the inner dorsal wall component is absent in the embryonic shells of *Vidrioceras*. It presumably begins to appear in the postembryonic stage.

In view of the absence of transverse lirae, the mode of embryonic shell formation in the Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina may also be explained by the "archaeogastropod model" of Bandel (1982) and Kulicki and Doguzhaeva (1994). The presence of fine transverse lirae on the relatively large embryonic shells of the Devonian suborders Agoniatitina, Anarcestina and Tornoceratina and on their postembryonic shells (see Landman *et al.*, 1996, appendix I) is, however, problematic. One possibility is that in the embryonic stage the mantle already was differentiated in the embryonic stage to secrete a shell with growth lines at its anterior margin. This type of embryonic shell development would be described as accretionary growth. A second possibility is that the embryonic shell was rapidly mineralised and an accretionary mode of growth characterized only the postembryonic shell (Klofak *et al.*, 1999). Future research utilizing well preserved material will resolve this problem.

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Macro- and microstructure of shell and operculum in two Recent gastropod species, *Nerita* (*Theliostyla*) *albicilla* and *Cinnalepeta pulchella* (Neritopsina: Neritoidea)

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Abstract. The shell and opercular structures of *Nerita* (*Theliostyla*) *albicilla* and *Cinnalepeta pulchella* were described and compared with those of other extant members of Neritopsina. The shell of *N.* (*T.*) *albicilla* is composed of four layers: the outermost prismatic layer, followed by the simple crossed-lamellar layer, the myostracum, and the inner complex crossed-lamellar layers. The operculum consists of three prismatic layers deposited on both sides of an organic layer. *C. pulchella* also has a four-layered shell, but lacks an operculum. The outer layer is a homologous structure. The shells of Recent neritopsine families can be categorized into a four-layered group (Neritiliidae, Neritidae, and Phenacolepadidae) and a three-layered group (other families). In contrast, opercular structure is markedly variable in the Neritopsina, and little correlation can be established in the light of phylogenetic evolution or adaptation.

Key words: Neritidae, Neritopsina, operculum, Phenacolepadidae, shell structure

Introduction

Neritopsina is a phylogenetically distinct gastropod clade which originated in the Ordovician (Bandel and Frýda, 1999). The Recent members share characteristic apomorphies of odontophoral cartilages and muscles, anterior digestive tract, reproductive organs, and nervous system (Haszprunar, 1988; Ponder and Lindberg, 1997; Sasaki, 1998) and exhibit successful adaptive radiation in a wide range of habitats in deep-sea hydrothermal vent or hydrocarbon seep, submarine cave, intertidal rocky shore, and nonmarine aquatic and terrestrial environments (Ponder, 1998; Sasaki, 1988). It is also particularly interesting that neritopsines have rich fossil records since the early Paleozoic (Bandel, 1992; Bandel and Frýda, 1999), and that ancient taxa like *Neritopsis* have survived as relics in cryptic habitats (Kase and Hayami, 1992).

Among hard-part characters, shell structure, along with larval shell morphology, is of primarily taxonomic importance for studies uniting fossil and Recent taxa of Gastropoda (Bandel, 1982; 1988; 1991; Bandel and Geldmacher, 1996). In Gastropoda, Patellogastropoda are known to exhibit remarkable diversification of the shell microstructure (MacClintock, 1967; Lindberg, 1988, 1998). Grouping by shell structure corresponds well to the anatomical division of supraspecific taxa, and therefore enables paleontologists to allocate fossilized taxa within an anatomy-based systematic scheme (Kase, 1994; Kase and Shigeta, 1996; Lindberg and Hedegaard, 1996; Hedegaard *et al.*, 1997). As for other gastropod higher taxa, Vetigastropoda are typically characterized by the apomorphic occurrence of columnar nacreous structure, although some taxa have supposedly lost it secondarily (Hedegaard, 1997). In the Apogastropoda, which is a huge clade including Caenogastropoda and Heterobranchia, the shells are composed primarily of several layers of crossed-lamellar structure and differences between distantly related subclades within it are in general minor (Bøggild, 1930; Bandel, 1979; Togo and Suzuki, 1988). At relatively lower rank, however, some striking differences can be revealed by detailed comparison, as was shown in littorinid genera by Taylor and Reid (1990).

Despite its unique phylogenetic status among gastropods, little discussion has been devoted to exoskeletal evolution of Neritopsina as compared to other major taxa of molluscs. The current knowledge of neritopsine hard-part structures is derived from only a limited amount of literature, and in addition, most data have been documented in simple format with a few or no illustrations. To increase data quality and quantity on neritopsine hard parts, this study aims to describe the shell and opercular structures of two Recent species in detail from the macro- to microscopic level. The results of the observations were compared with the published data of other neritopsines in the literature, and their similarities and dissimilarities were discussed from phylogenetic and adaptational viewpoints.

Material and methods

The shells of *Nerita* (*Theliostyla*) *albicilla* were collected alive from an intertidal zone at Banda, Tateyama, Chiba Prefecture, central Japan, and living specimens of *Cinnalepeta pulchella* from Tosashimizu, Kochi Prefecture, southwest Japan were provided by Dr. Shigeo Hori. In the laboratory, the macroscopic morphology and the distribution of shell layers based on texture were first observed under a binocular microscope. Then, the shell was crushed with a hammer, and the original position of fragments was labeled before cleansing in bleach for 12 hours and later in running water for 30 minutes. The fresh fracture of shell fragments was observed with a scanning electron microscope (SEM).

The description of microstructure was made on layer distribution, boundary between layers, form of crystal aggregation, and orientation and morphology of first- to third-order units (major to minor structural arrangement). The descriptive terminology of microstructure follows Carter and Clark (1985) and Kano and Kase (2000b). The two terms, "crossed lamellar" and "complex crossed lamellar," are abbreviated as "CL" and "CCL."

Terms for orientation were based on the following criteria: (1) "anterior-posterior" direction was determined by body axis of the animal, and (2) "adaxial-abaxial" distinction relative to coiling axis of whorls was used to indicate relative position along inner-outer lips of the aperture.

The samples used in this study are preserved in the University Museum, the University of Tokyo (UMUT).

Description

Order Neritopsina Cox and Knight, 1960
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Nerita* (*Theliostyla*) *albicilla Linnaeus, 1758

Figures 1-5

Shell.—The shell is elongate along the anterior-posterior axis of the animal. The spire is completely depressed as a part of rounded whorls, and the external part of the shell is mostly occupied by a large body whorl and an extended aperture.

The outer lip of the aperture is thickened and indented with elongate denticles, being arranged parallel to the apertural margin. The inner lip spreads widely over the body whorl to form a robust inductura.

The shell wall near the outer lip consists of three layers;

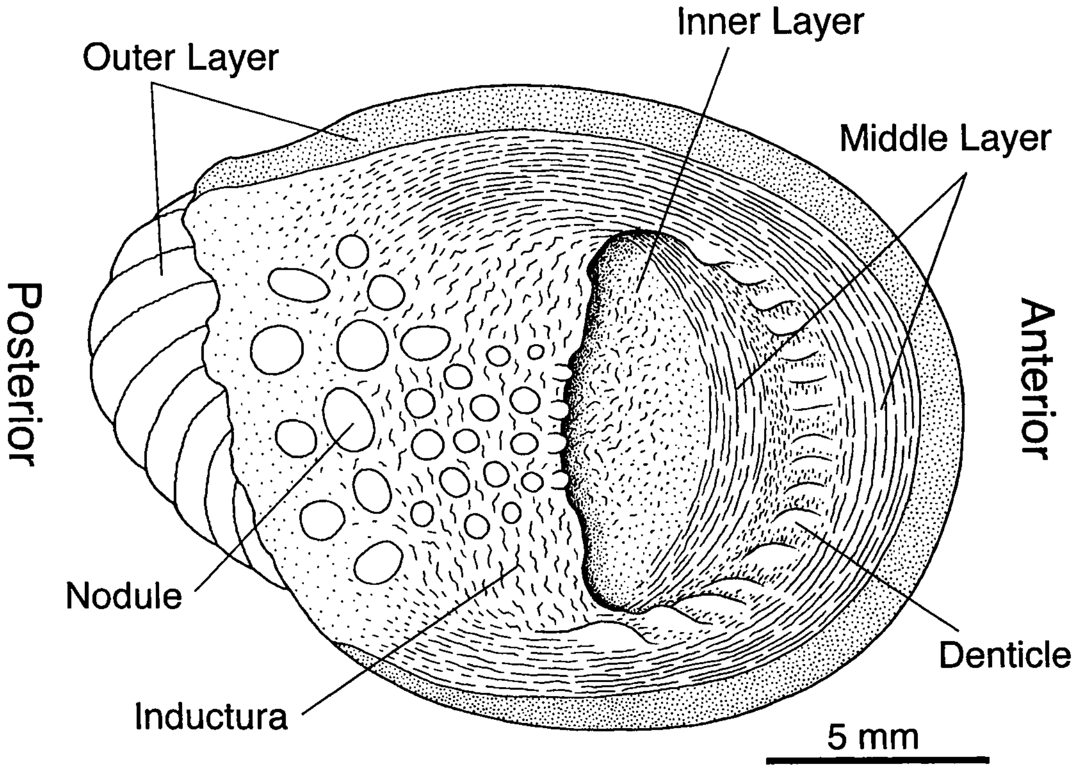


Figure 1. Apertural view of the shell of *Nerita* (*Theliostyla*) *albicilla*. The sculpture and texture of the surface are depicted slightly schematically. The dark outer layer is distinguished by fine-grained smooth surface, the middle layer exhibits dense linear pattern of CL structure, and most of the inner layer is visible as irregularly oriented lines.

i.e. outer and middle layers and a distinct denticular zone (Figure 1). The outer layer contains black pigments, encircles the apertural margin, and makes a clear contrast with the pale inner layer. Microstructurally this layer is formed of a thick aggregate of short prisms (Figure 3A), which can be identified as blocky prismatic structure. The prisms attain less than 4 μm in length and 1 μm in width. The middle layer is composed of comarginal simple CL structure (Figure 3B–E). The linear lines of the first-order units are clearly visible on the inside of the aperture even at low magnification (Figures 1, 2). The denticular zone is built up of a thin layer of irregularly crossed fine crystals (CCL structure). The denticles do not continue spirally toward the inside of the aperture but remain in the identical position due to resorption.

The inner lip margin is shallowly curved with two to four small nodules (Figure 1). The surface of the inductura is roughened with nodules of various size, and their number and distribution are considerably variable intraspecifically. The inductura, especially near the inner lip, shows an irregular texture reflecting the first-order arrangement (Figure 1). There is no sharp boundary between the CL structure of the middle layer and the CCL structure of the inductura. The linear patterns of the middle layer gradually merge into the irregular patterns of the inductura (Figure 1).

Shell muscle scars are separated into a disjunct pair corresponding to right and left shell muscles (see Sasaki, 1998: fig. 73a). The left scar is located on the basal side near the inner lip (Figure 2), while the right one lies on the opposite, apical side. The scars are deeply impressed on the interior shell surface and reflect the form of muscles which are divided into bundles (Figure 2). The myostracum from the left scar is formed as a vertical stack of irregular prisms (Figure 3F), and its thickness exceeds 80 μm in an adult shell. The myostracum from the right scar is immediately resorbed and not traceable in most sections.

The inside of the visceral part of the shell is extensively resorbed and reorganized as a hollow space without a true columella. A platy septum connecting the inner lip and apical wall of the shell is secreted and inserted into the narrow space between head-foot and uncoiled visceral mass of the animal (Figure 2; see also Sasaki, 1998: fig. 73a). The septum, inner lip, inductura, and the interior of whorls are all constructed as a continuity of the inner layer (Figure 2). The layer has CCL structure: lathy third-order units are set radially to form fan-shaped second-order units, which in turn are vertically stacked to form wedgelike first-order units which are irregularly oriented and interdigitate with one another (Figure 3G, H). The structure appears as spinous crossing prisms at the initial stage of formation near its growth front. Several very thin prismatic sublayers are inserted in a thick CCL layer of the inductura (Figure 2).

Operculum.—The operculum is heavily calcified with a distinct apophysis (Figure 4A, B). The exterior surface is

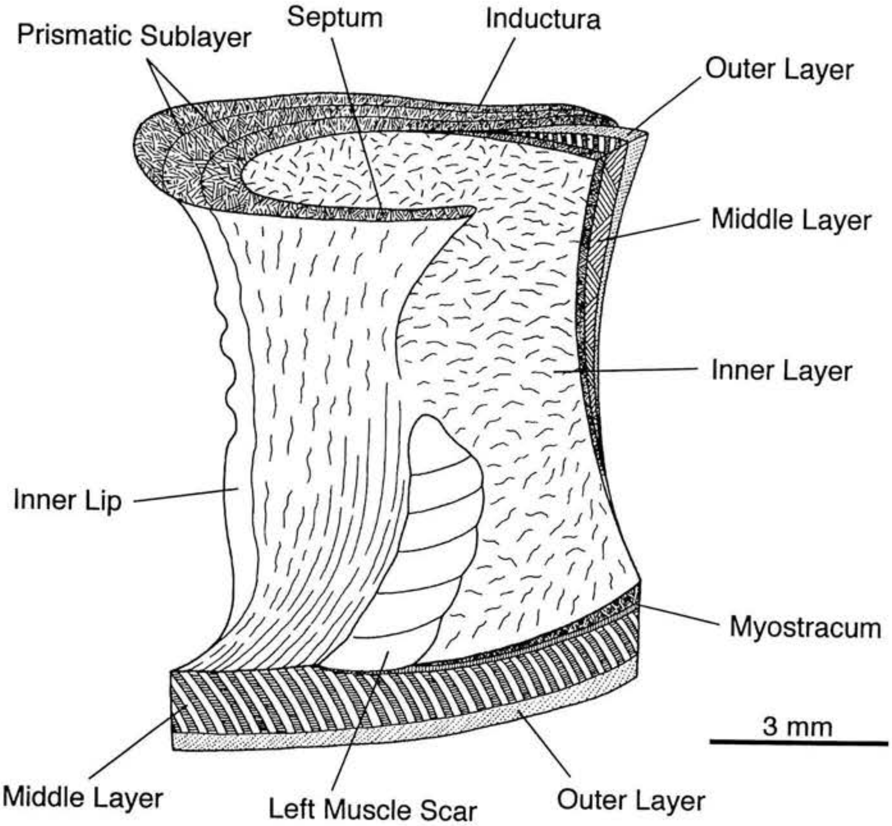
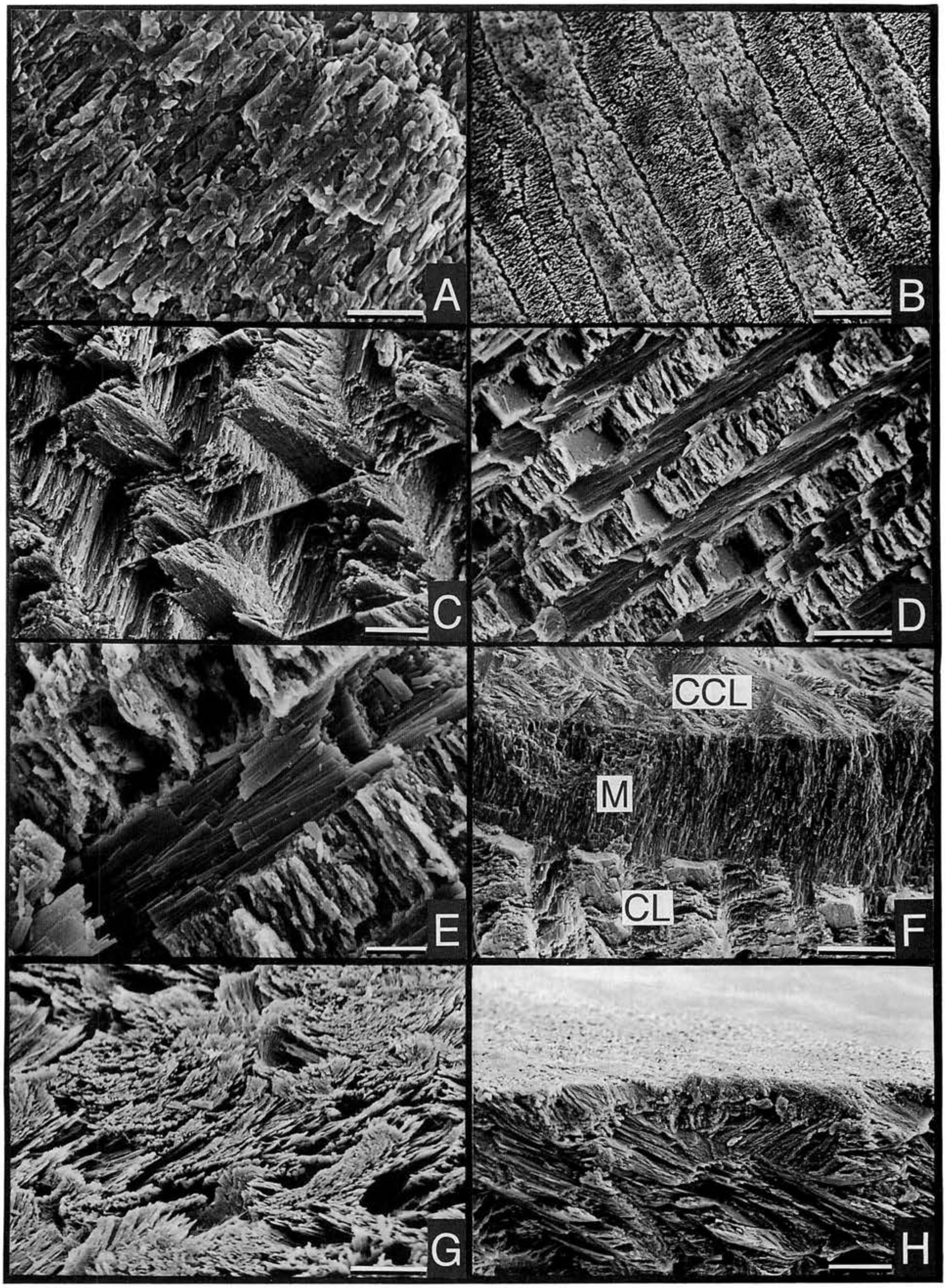


Figure 2. Schematic representation of inner part of whorls of *Nerita* (*Theliostyla*) *albicilla*, seen from the outer lip of the aperture. Shell layers on cut planes are illustrated based on the results of observations with SEM.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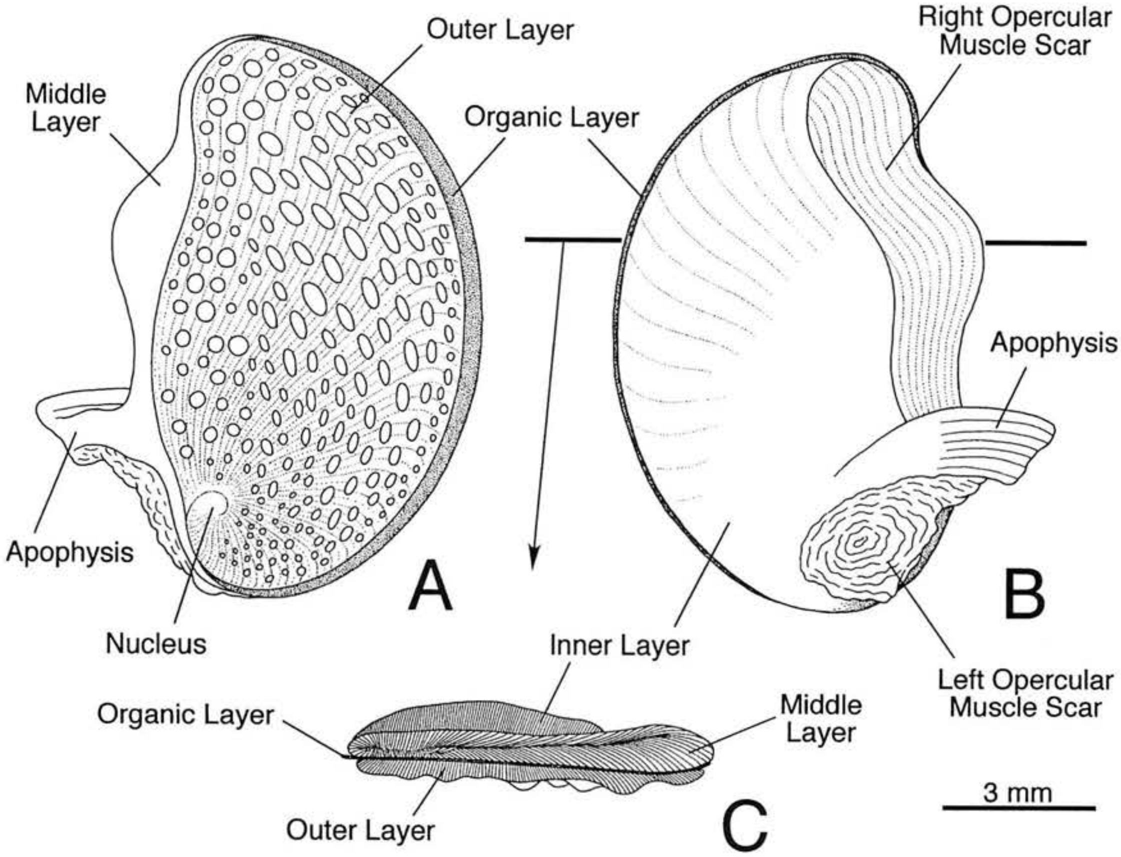

Figure 4. Operculum of *Nerita* (*Theliostyla*) *albicilla*. **A.** Exterior view. **B.** Interior view. **C.** Vertical section showing the growth direction of prisms in three calcified layers. Cut position is shown in Figure B with solid lines.

covered with small nodules which tend to be arranged spirally (Figure 4A). The nucleus lies on the adaxial basal side at the origin of the spiral growth line.

The calcified part of the operculum can be divided into three layers (Figure 4C). The outer and inner layers are both composed of slightly inclined, nearly vertically ordered prisms (Figure 5B, D). In the middle layer, prismatic crystals are arranged in a spherulitic form (Figure 5C). A very thin organic layer, the homologue of the noncalcified operculum of other gastropods, is mostly concealed between the outer and middle layers and appears only along the abaxial margin (Figure 4A, B).

The adaxial side of the operculum is partially embedded in the pedal musculature of the animal and marks clear depressions of muscle scars (Figure 4B). The left scar is small and very irregular with nearly concentric lines (Figure 5A). The right scar is elongated along the abaxial margin and smoothened.

Family Phenacolepadidae Rafinesque, 1815
Cinnalepeta pulchella (Lischke, 1871)

Figures 6, 7

Shell.—The shell is completely limpet-shaped and elongated along the anterior-posterior axis (Figure 6). The apex is situated at the posterior end of the shell. The larval shell in the original position of the apex is involved between whorls and inner lip during growth and no longer visible in a fully matured adult shell. The inside of the apex is slightly remoulded by resorption, but a septumlike structure is not constructed in this species.

The shell consists of four layers, including the myostracum. The outer layer is composed of fine homogeneous crystals (homogeneous structure) (Figure 7A, B). The middle layer is of commarginal simple CL structure. It is somewhat transparent, and clearly demarcated from the

← **Figure 3.** SEM micrographs of shell microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27950). **A.** Blocky prismatic structure of outer layer. Scale = 5 μm. **B.** Outcrop pattern of simple CL structure near outer lip of aperture. Scale = 20 μm. **C.** Oblique view of the fracture of simple CL structure in the middle layer. Scale = 20 μm. **D.** Horizontal view of the fracture of the same layer. Scale = 20 μm. **E.** Enlarged view of the same layer, showing the arrangement of the third-order units of CL structure. Scale = 5 μm. **F.** Vertical fracture of the myostracum inserted between inner (above) and middle (below) layers. M = myostracum. Scale = 40 μm. **G.** Outcrop pattern of CCL structure on interior surface of the whorls. Scale = 20 μm. **H.** Vertical fracture of the same structure in inner layer. Scale = 20 μm.

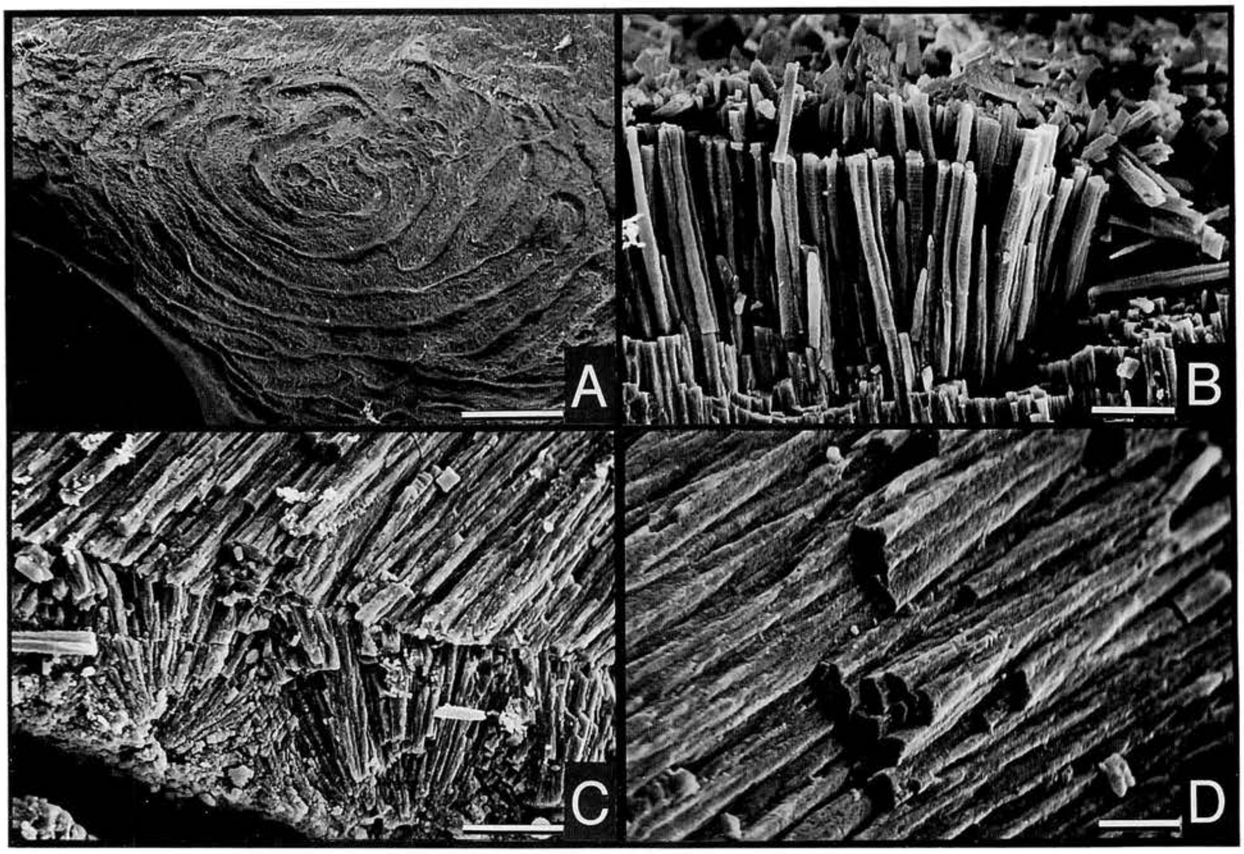

Figure 5. SEM micrographs of opercular microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27951). **A.** Surface of left opercular muscle scar with irregularly concentric lines. Scale = 250 μm. **B.** Vertical fracture of outer prismatic layer. Scale = 10 μm. **C.** Vertical fracture of the middle layer, showing spherulitic arrangement of prisms. Scale = 10 μm. **D.** Oblique view of a section of inner prismatic layer. Scale = 5 μm.

brown outer layer. Linear patterns of the first-order units of the middle layer are parallel near the shell margin and increase in irregularity toward the center (Figure 6). In the typical regular simple CL structure near the apertural margin, the crossing angle of the second-order lamellae is approximately 125 degrees. The inner layer consists of a CCL structure with fan-shaped second-order and lath-type third-order units (Figure 7D, E).

The inner lip projects inside along the posterior apertural margin and is formed as an extension of the CL structure of the middle layer (Figure 6). It lies between the ventral posterior of the visceral mass and the dorsal posterior of the foot of the animal.

The muscles scars are distributed in an elliptical form, keeping an almost constant distance from shell margin (Figure 6). They are inserted by two kinds of muscles of the animal: the thicker horseshoe-shaped part is the attachment of pedal retractor muscles (including head retractors in part), and the thinner anterior part is that of pallial muscle hanging the mantle onto the interior of the shell. The myostracum from these muscle scars is a thin layer of vertically oriented columnar prisms (Figure 7C). The surface of the pedal muscle scar is deeply impressed and exhibits a ridgelike rough sculpture (Figure 7F).

Operculum.—The operculum is completely absent and was not found in any section of pedal musculature as already described by Sasaki (1998: 120).

Discussion

Recent forms of neritopsine gastropods comprise nearly 120 genera and subgenera (Vought, 1989). Although different opinions exist regarding suprageneric systematics, the Recent forms can be grouped into at least seven families, namely Neritopsidae, Hydrocenidae, Helicinidae [this family may be divided into Ceresidae, Proserpinidae, and Helicinidae (Thompson, 1980)], Titiscaniidae, Neritiliidae, Neritidae, and Phenacolepadidae ["Shinkailepadidae" is probably included here] (Ponder, 1998; Sasaki, 1998; Bandel and Frýda, 1999; Kano and Kase, 2000a, b; see also Sasaki, 1998 for their anatomical basis). Information on their shell and opercular structure can be summarized as follows.

Shell structure of Recent Neritopsina

Shells of only ten genera belonging to six families have

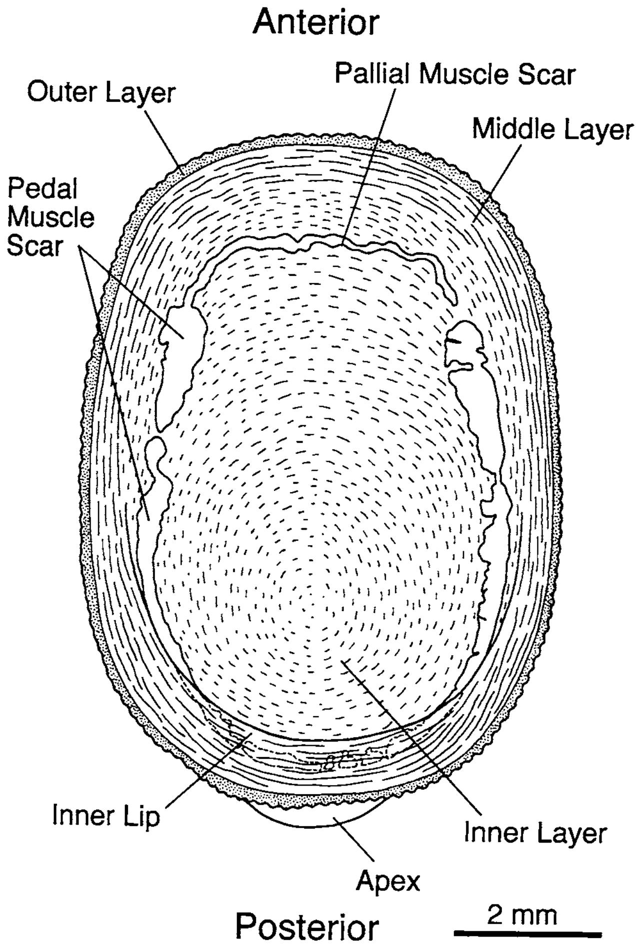

Figure 6. Apertural view of *Cinnalepeta pulchella*. The sculpture texture of the surface is illustrated slightly schematically. The outer layer is separated from other parts by deep brown color, the middle layer is represented by concentric lines of CL structure, and the inner layer is visible as fine irregular lines of CCL structure.

been investigated at the microstructural level (Table 1). Major differences among suprageneric taxa are found mainly in the number of shell layers, the microstructure of each layer, and the crystal forms of carbonate calcium (aragonite-calcite).

(1) Neritopsidae: This family is characterized by intact inner upper whorls in contrast to other families with resorbed, hollow whorls inside (Bandel and Frýda, 1999). The shell wall of *Neritopsis radula* was described as "having two crossed-lamellar layers" by Batten (1979), but according to Suzuki *et al.* (1991), it is composed of an aragonitic outer layer of CL structure and an aragonitic inner layer of "protocrossed lamellar, irregular prismatic, homogeneous, and complex crossed lamellar structures." The mixture of four microstructures in the inner layer of *N. radula* is, therefore, a unique feature among Neritopsina.

(2) Hydrocenidae: The shell of *Georissa japonica* has three layers including the myostracum: the thicker aragonitic outer layer is of CL structure, and the thinner inner aragonitic layer is primarily of irregular prismatic structure and subsidiarily of "protocrossed-lamellar" structure (Suzuki *et al.*, 1991).

(3) Helicinidae: The shell of *Waldemaria japonica* (Helicininae) has almost the same structural design as that of *Georissa japonica*, but the inner layer is mainly occupied by "protocrossed-lamellar" structure (Suzuki *et al.*, 1991). Microstructural data have not been provided for any other member of these families.

(4) Titiscanidae: This family totally lacks the shell at least at the adult stage (Bergh, 1890; Taki, 1955).

(5) Neritiliidae: This group had been extremely poorly known taxonomically but was redefined by Kano and Kase (2000a, b) as small neritiform gastropods with (i) spiral ridges on the protoconch, (ii) the inclination of the protoconch against the teleoconch, and (iii) perpendicular, not inclined, prisms in the outer shell layer. The shell of *Pisulina* species consists of four layers: an outer layer of simple irregular prisms, middle layer of simple CL structure, myostracum, and inner layer of CCL structure with prismatic sublayers (Kano and Kase, 2000b; figs. 6, 7).

(6) Neritidae: All neritid taxa so far investigated share a four-layered shell consisting of an outer layer of calcitic prismatic structure, middle layer of aragonitic CL structure, myostracum, and inner layer of aragonitic CCL structure (Table 1). Their shells can be further classified into two types based on relative thickness of shell layers: marine species have a thicker outer layer with a thinner periostracum, while nonmarine species have a reduced outer layer with a well developed periostracum (Suzuki *et al.*, 1991). This difference is, however, considered to be induced by environmental factors, because thin shells protected by a thick periostracum occur in various distantly related brackish and freshwater mollusks.

(7) Phenacolepadidae: The only description for this family was given for *Cinnalepeta pulchella* in this study, and the difference from other families lies in the homogeneous structure of the outer layer.

Operculum of Recent Neritopsina

Neritopsine operculum exhibits a great diversification in the number of calcified layers, the coverage of the organic layer, the position of calcareous layer(s) on one or both sides of the organic layer, the presence or absence of apophysis, and the morphology of muscle scars.

(1) Neritopsidae: The exterior surface of the operculum of *Neritopsis radula* is covered with a thick callus without a nucleus and spiral lines; the interior is divided into a smooth semilunar zone at the abaxial side and a large projection with a radial striation at the adaxial side (Thiele, 1929: fig. 55; Wenz, 1938: fig. 1001; Knight *et al.*, 1960: fig. 182; Ponder, 1998: fig. 15.71C, D). This projection may be the hypertrophied homologue of the apophysis of other neritopsines, with its origin shifted toward the center. The absence of a spiral line on both surfaces and a large projection from the interior center is quite unique among Gastropoda. However, no microstructural data for this family have been published to date.

(2) Hydrocenidae: The operculum of *Georissa japonica* is calcified with an apophysis and three-layered: the organic

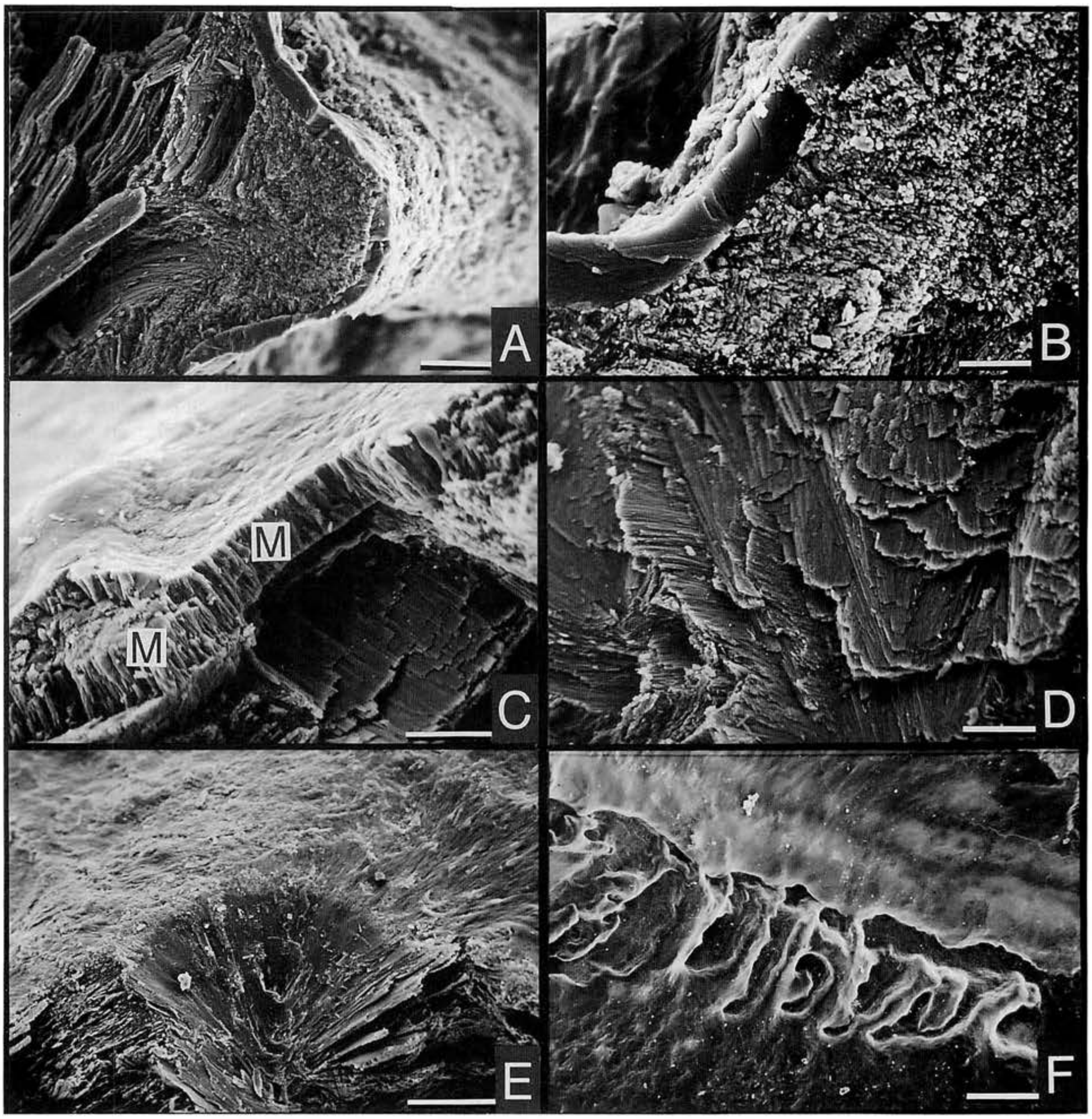

Figure 7. SEM micrographs of shell microstructure of *Cinnalepeta pulchella* (UMUT RM27952). **A.** Vertical fracture of the outer layer. Scale = 20 µm. **B.** Enlarged view of homogeneous structure. Scale = 5 µm. **C.** Vertical fracture of pedal muscle scar showing the myostracum overlying the middle layer. M = myostracum. Scale = 10 µm. **D.** Vertical fracture of CCL structure near the center of the shell. Scale = 10 µm. **E.** Oblique fracture (below) and outcrop surface (above) of CCL structure. Scale = 50 µm. **F.** Oblique view of pedal muscle scar near inner lip, showing irregular rough surface. Scale = 200 µm.

layer on the outermost surface is underlain by two aragonitic layers of irregular prismatic structure (Suzuki, *et al.*, 1991: fig. 5).

(3) Helicinidae: This family is highly specialized for Neritopsina in that Ceresinae and Proserpininae completely lack an operculum, while Helinicinae have a calcified operculum without an apophysis (Thompson, 1980). The operculum of *Waldemaria japonica* has a single layer of calcitic blocky structure on an organic layer (Suzuki, *et al.*, 1991). Helicinids are strikingly different form other neritopsines in that calcification occurs only on the exterior surface, not interior of the organic layer.

(4) Titiscanidae: This shell-less taxon also lacks an operculum and is completely sluglike (Bergh, 1890; Taki,

Table 1. Published data on shell microstructure of the Recent Neritopsina. BL = blocky, CCL = complex crossed lamellar, CL = simple crossed lamellar, HO = homogeneous, IPR = irregular prismatic, PCL = protocrossed lamellar, PR = prismatic.

		Shell microstructure			
Family	Genus	Outer layer(s)		Inner layer	Reference
Neritopsidae	*Neritopsis*	CL		CL	Batten (1979)
	Neritopsis	CL		PCL, IPR, HO, CCL	Suzuki *et al.* (1991)
Hydrocenidae	*Georissa*	CL		PCL, IPR	Suzuki *et al.* (1991)
Helicinidae	*Waldemaria*	CL		PCL, IPR	Suzuki *et al.* (1991)
Neritiliidae	*Pisulina*	PR	CL	CCL	Kano and Kase (2000b)
Neritidae	*Nerita*	PR	CL	CCL	Bøggild (1930); Gainey and Wise (1980);This study
	Nerita	BL	CL	PCL	Suzuki *et al.* (1991)
	Neritina	PR	CL	CCL	Bøggild (1930)
	Neritina	BL	CL	PCL	Suzuki *et al.* (1991)
	Clithon	BL	CL	PCL	Suzuki *et al.* (1991)
	Neripteron	BL	CL	PCL	Suzuki *et al.* (1991)
	Septaria	BL	CL	PCL	Suzuki *et al.* (1991)
Phenacolepadidae	*Cinnalepeta*	HO	CL	CCL	This study

1955).

(5) Neritiliidae: In the species of *Pisulina,* the operculum is secreted with exterior corneous and interior calcareous layers (Kano and Kase, 2000b: figs. 8, 9, 11). The small initial part containing the nucleus on the corneous layer is demarcated from the remaining part. The muscle scars are divided into three areas: two elongate zones along the adaxial and basal margins, and a central one extending between the nuclear zone and apophysis. The inner calcareous layers are formed of spherulitic prisms (Kano and Kase, 2000b: fig. 6F).

(6) Neritidae: The gross morphology of the neritid operculum is classified into two distinct types (see e.g. Starmühlner, 1993; Komatsu, 1986): (i) The operculum of *Septaria* (subfamily Septariinae) is embedded in the dorsal part of the foot. The anterior left corner has a sharp projection which is supposedly homologous to the apophysis of other neritopsines on the left side. (ii) The rest of the neritids (subfamilies Neritinae and Smaragdiinae) have a semilunar external operculum with a prominent apophysis.

The opercular microstructure of neritids is known to be variable, depending on habitats. The marine neritids have a common opercular plan with a single exterior aragonitic prismatic layer, an organic layer, and two interior aragonitic prismatic layers (Suzuki *et al.*, 1991: fig. 5; this study: Figs. 4, 5). The opercula of nonmarine species (*Neritina* and *Clithon*) have only two aragonitic prismatic layers covered by a well developed organic layer (Suzuki *et al.*, 1991).

The operculum of *Bathynerita naticoidea* (tentatively treated as a neritid here) dwelling exclusively in deep-sea hydrocarbon seeps is "partly calcified with a thicker calcareous layer where it is attached to the foot" (Warén and Bouchet, 1993), and the apophysis is absent. Its operculum with only partial calcification is greatly different from those of shallow-water neritids.

(7) Phenacolepadidae: The opercular morphology of phenacolepadids can be divided into three distinct states. (i) The presence of a vestigial internal operculum with interior calcification and rudimentary apophysis was documented by Fretter (1984) in *Phenacolepas omanensis* and observed with SEM for the first time by Kimura and Kimura (1999: fig. 7C, D) in *Phenacolepas* sp. (ii) The opercula of so-called "Shinkailepedidae" has double structure of calcified anterior and noncalcified posterior parts as described in *Shinkailepas* by Okutani *et al.* (1989: fig. 12) and Beck (1992: pl. 1, fig. 4) and in *Olgasolaris* by Beck (1992: pl. 5, fig. 4). Double-layered nail-shaped operculum is strikingly convergent with that of the neritid genus *Septaria.* (iii) The operculum is absent in *Cinnalepeta*, as described above.

Implication of neritopsine hard-part microstructures

It has been generally accepted that microstructural characters of the shells are useful for the understanding of molluscan higher taxonomy. It is, however, necessary to check the correlation between taxonomic distribution of structural morphotype and phylogenetic relationships in the Recent taxa before comparing extant and extinct forms directly.

(1) Shell structure: As reviewed above, the patterns of shell structure of the Recent Neritopsina can be categorized into two major types: (i) Genera of three families, Neritidae, Phenacolepadidae, and Neritiliidae, all have four-layered shells in which inner CCL and middle CL layers are overlaid by a prismatic (in Neritidae and Neritiliidae) or homogeneous (in Phenacolepadidae) shell layer. (ii) By contrast, other families such as Neritopsidae, Helicinidae, and Hydrocenidae secrete three-layered shells which consist mostly of CL/CCL structures and lack an additional outer layer. This apparent difference between the two groups may be viewed as expressing the distinctness of their relationship, but it is still premature to present phylogenetic implication because of the lack of a reliable phylogenetic hypothesis. The phylogenetic analysis has been conducted only in a part of Neritopsina by Holthuis (1995) and Sasaki (1998), and the phylogenetic status of Neritopsidae, Helicinidae, and Hydrocenidae is totally unknown. The scarceness of struc-

tural data relative to the number of existing genera is also problematic so far as testing the stability of character states within each family.

Another unresolved problem is whether all of the taxa with a four-layered shell share a calcitic outer layer or not. Suzuki *et al.* (1991) revealed that at least the shell of neritids is constructed from a calcitic outer layer and otherwise aragonitic layers in contract to the entirely aragonitic shell of other families. They argued that this bimineralic composition is attributable to adaptation to a shallow aquatic environment, probably as a means of reinforcing the mechanical strength of the shell. Thus, it should be tested as a next step whether non-neritid four-layered shells are also made of two crystal forms of calcium carbonate. Concerning the outermost shell layer, Taylor and Reid (1990) revealed the parallel homoplastic addition of a calcitic outer layer in some genera within littorinid gastropods. This means that the convergence in conchological characters should necessarily be considered also at the microstructural level in other groups of molluscs.

(2) Opercular structure: The opercular structure can be divided into several types as a result of the above comparison: (i) three (single exterior and two interior) aragonitic layers in marine neritids, (ii) two interior aragonitic layers in Hydrocenidae and nonmarine neritids, (iii) single calcitic exterior layer without interior calcification in Helicininae, (iv) interiorly calcified operculum with unknown layer distribution in Neritiliidae and a part of Phenacolepadidae, and (v) absence of an operculum in Titiscaniidae and in part in the Phenacolepadidae and Helicinidae. Thus, a single similar state often occurs across several different families, and also several different states can coexist within the same family. At the family level the similarity and dissimilarity in opercular structure are very difficult to explain in the phylogenetic context.

In connection with nonphylogenetic factors, the less calcified opercula in nonmarine neritids as compare with marine confamilial members may be explained as a consequence of adaptation to low-salinity environments (Suzuki *et al.*, 1991). However, in other taxa, there is no clear correlation between opercular structure and habitat selection. The marked differences in neritopsine opercular structure is difficult to understand also in terms of adaptation. The possession of apophysis is presumably under phylogenetic control within Neritopsina, and at the same time, it is a convergent state also found in caenogastropod rissoideans. The peglike structure has possibly arisen to increase the area of muscular attachment in this case.

Because of the insufficient resolution of neritopsine phylogeny and the lack of mineralogical data in part, the evolutionary scenario of neritopsine hard parts remains largely speculative at present. For further studies, exoskeletal structure including mineralogical characters should be investigated more comprehensively in whole extant and extinct neritopsines together with the comparative anatomy and molecular phylogeny of the Recent species.

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Geometric pattern and growth rate of prismatic shell structures in Bivalvia

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Abstract. The distribution patterns, sizes and nucleation sites of aggregated prisms on the outer shell surface were examined in 16 species of Bivalvia and modeled theoretically. Biometric analysis shows a negative correlation between the median size and variation of sizes of calcitic simple prisms. In species with aragonitic vertical composite prisms, instead, the density of prisms tends to decrease when their nucleation sites are randomly distributed. Comparison of the results of computer simulations with those of biometric analyses reveals the following: 1) a positive correlation between growth rate of prisms and the probability of nucleation for simple prisms, and 2) a limit of the number of nucleations per unit time in vertical composite prisms. Prism size correlates with the growth rate of the entire shell or prisms, and increases as the shell grows faster or prisms grow slower.

Key words: biomineralization, bivalves, prismatic structure, shell growth rate, theoretical morphology

Introduction

The microscopic features of a molluscan shell record certain physiological conditions of the organism at the time the shell is formed. Carbonate minerals within a molluscan shell crystallize and grow under physicochemical conditions controlled by the physiology of the organism. Wada (1972, 1985) reported a seasonal change of shape and size of aragonite crystals in the nacreous layer of such bivalves as *Pinctada fucata*, *Pinna attenuata* and *Hyriopsis schlegeli.* He suggested that the topography of growing crystals may reflect the rate of crystal growth or the degree of supersaturation of the extrapallial fluid. Quantitative analysis of the relationship between size and/or shape of crystals and the rate of crystal growth within a shell provides a reliable basis to understand the 'paleophysiology' of fossil organisms.

The goal of this study is to clarify the relationship between the geometry of bivalve shell microstructure and the relative growth rate of crystals or of the entire shell. For this purpose, the present study focuses on the geometry of the outer shell surface of a simple or vertical composite prismatic shell layer. Although they differ in the ultrastructure of prisms, those two prismatic structures both consist of many parallel-arrayed columnar units (Carter and Clark, 1985; Carter *et al.*, 1990). Each prism is surrounded and bounded by an organic matrix showing a honeycomb-like appearance on the outer shell surface.

For understanding the rule or algorithm forming the geometric pattern of shell microstructure, theoretical morphology is particularly useful (Ubukata, 1997a, b, 2000). In the present study, a biometric analysis of size and nucleation sites of prisms in actual shells was carried out in 16 species. Furthermore, a theoretical morphological modeling of growth kinematics of aggregated prisms was attempted, and the computer simulations of that model were compared with the results of the biometric analyses.

Biometric analyses

Material and methods

The outer shell surface of a simple prismatic or vertical composite prismatic outer shell layer was examined in 16 extant species of Bivalvia (Table 1). Each species was represented by a single specimen, except *Anodonta woodiana.* Most of them were collected at various localities around the Japanese Islands and the Philippines. All the specimens examined are stored at Shizuoka University (SUM).

In order to remove the periostracum from the shell completely, the shells examined were bleached for one day. Pieces of them were washed, dried in air, coated with gold using a JEOL JFC-1500 ion coater, and examined with a JEOL JSM-5800LV scanning electron microscope operated at 15kV and interfaced to a computer (Dell Optiplex Gxa EM).

In order to analyze size-frequency distribution of prisms,

Table 1. List of material examined. All specimens have the prefix SUM.

Family	species	locality	specimens
Pteriidae	*Pteria penguin* (Roding)	San Luice, Bathangas, Philippines	HM-B-0014
	Pinctada maculata (Gould)	Iriomote Is., Okinawa, southwest Japan	HM-B-0015
Isognomonidae	*Isognomon perna* (Linnaeus)	Iriomote Is., Okinawa, southwest Japan	HM-B-0016
	I. ephippium (Linnaeus)	San Luice, Bathangas, Philippines	HM-B-0017
Malleidae	*Malleus regula* (Forskål)	Iriomote Is., Okinawa, southwest Japan	HM-B-0018
Pinnidae	*Atrina pectinata* (Linnaeus)	Ariake, Saga, western Japan	HM-B-0019
	A. vexillum (Born)	Honda Bay, Palawan, Philippines	HM-B-0020
Ostreidae	*Crassostrea gigas* (Thunberg)	Misaki, Kanagawa, Central Japan	HM-B-0021
Margaritiferidae	*Margaritifera laevis* (Haas)	Nakagawa, Hokkaido, northern Japan	HM-B-0022
Unionidae	*Inversidens reiniana* (Kobelt)	Lake Biwa, Shiga, Central Japan	HM-B-0023
	Unio biwae Kobelt	Lake Biwa, Shiga, Central Japan	HM-B-0024
	Lanceolaria oxyrhyncha (Martens)	Lake Biwa, Shiga, Central Japan	HM-B-0025
	Anodonta woodiana (Lea)	Lake Biwa, Shiga, Central Japan	HM-B-0026, -0027
	A. calypygos Kobelt	Lake Biwa, Shiga, Central Japan	HM-B-0028
	Cristaria plicata (Leach)	Lake Biwa, Shiga, Central Japan	HM-B-0029
Trigoniidae	*Neotrigonia margaritacea* (Lamarck)	French Is., Australia	HM-B-0030

areas of prisms on the outer shell surface were measured at 6–12 positions along a growth increment on the shell surface. An SEM image of the measured portion was saved as a computer bitmap file (Figure 1A). Next, the boundaries between prisms were traced on a NEC PC-9821 V166 personal computer using Microsoft PowerPoint 7.0, and then each prism was colored differently using Justsystem Hanako PhotoRetouch (Figure 1B). Subsequently, the area of each prism was measured by counting pixels. For this counting, a program written in VISUAL BASIC was used on a personal computer.

Since the size-frequency distribution of the areas of prisms is generally right-skewed, the mean and standard deviation are not suitable for representing the distribution of the areas of prisms. Therefore, the "average" area of prisms on a shell is represented by the median of the areas ($\tilde{S}$), and the variation of the areas is expressed as a standardized hinge spread (Q_s), which is defined as follows:

$$Q_s \equiv \frac{Q_t - Q_f}{\tilde{S}}, \tag{1}$$

where Q_f and Q_t are the first and third quartiles of the areas of prisms, respectively (Hoel, 1976). $\tilde{S}$ and Q_s were both estimated in all shell portions examined.

On the outer surface of a vertical composite prismatic shell layer, microgrowth increments are clearly visible within a bleached prism (Figure 2A). In a simple prismatic shell layer, growth increments within a prism are faintly observed on the bleached shell surface (Figure 2B). In either case,

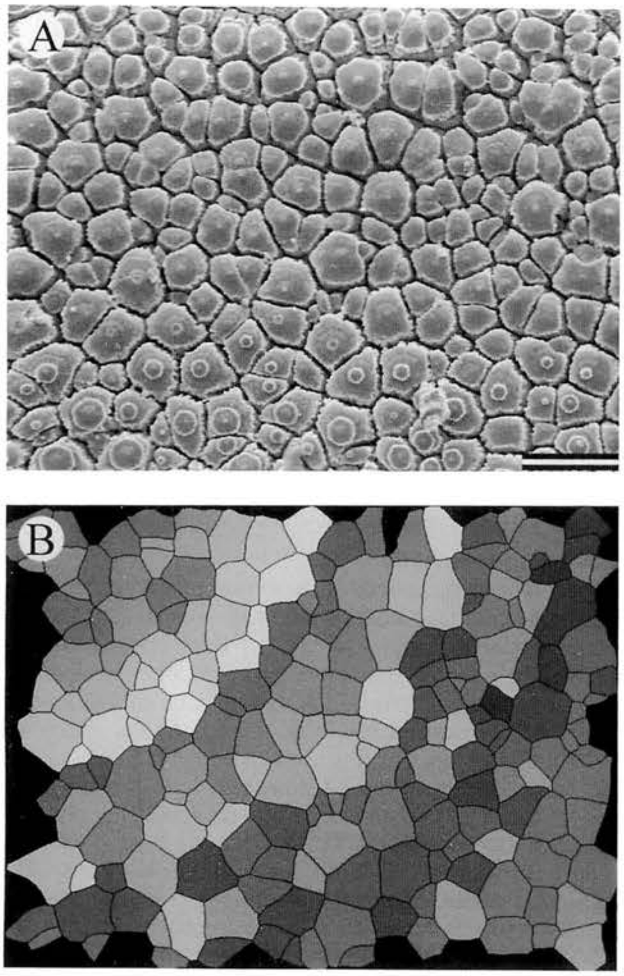


Figure 1. **A**. SEM photograph of the outer shell surface of the vertical composite prismatic layer in *Anodonta woodiana* (SUM-HM-B0027), scale: 50 µm. **B**. Trace of the outlines of prisms on the SEM image of **A**.

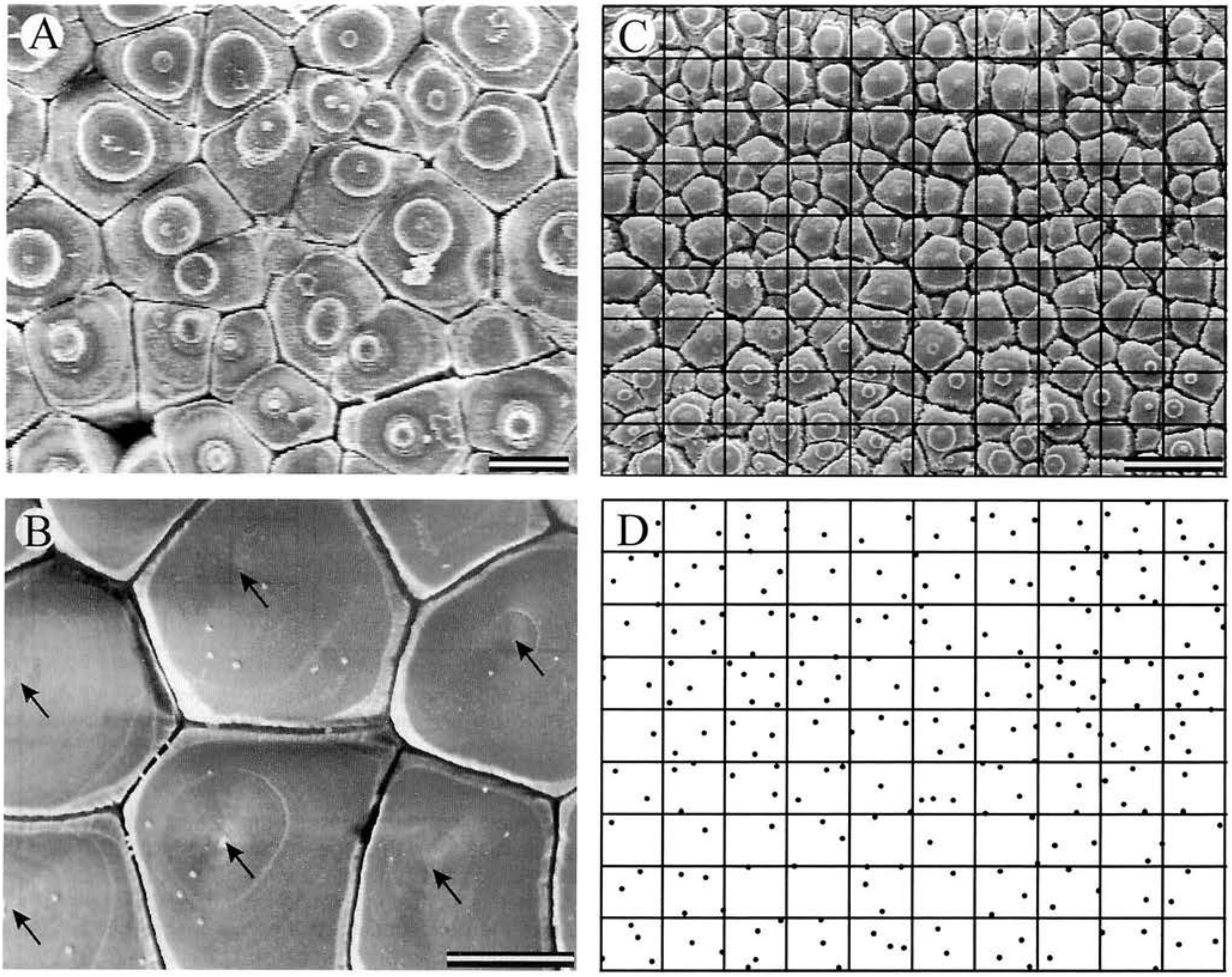


Figure 2. **A**. SEM photograph of the outer shell surface of the vertical composite prismatic shell layer in *A. woodiana* (SUM-HM-B0027) showing clear growth increments within individual prisms, scale: 20 μm. **B**. The simple prismatic layer in *Pinctada maculata* (SUM-HM-B0015). Arrows indicate nucleation sites, scale: 20 μm. **C**. The SEM image of *A. woodiana* subdivided into squares, scale: 50 μm. **D**. Distribution of nucleation sites of prisms in **C**.

the center of the circular growth increments is regarded as the nucleation site of the prism.

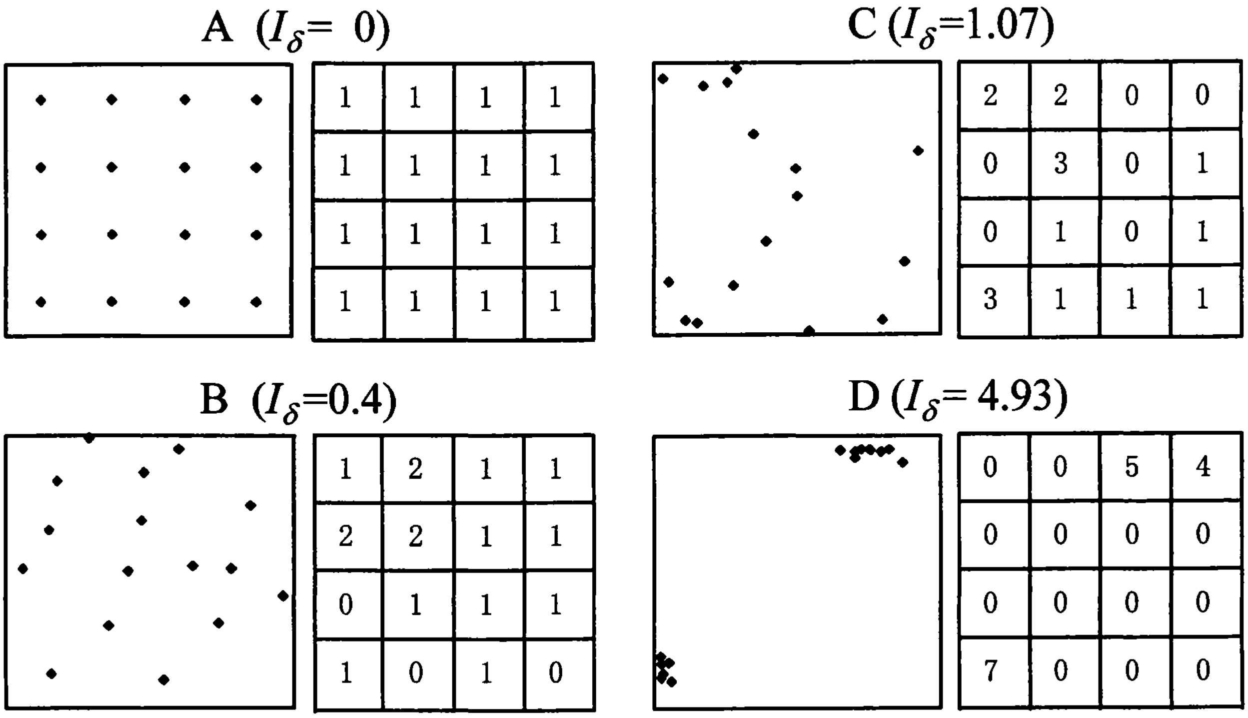
The distribution of nucleation sites of prisms was analyzed in all shell portions in which the areas of prisms were measured. An SEM image was divided into a squared grid of appropriate size for each square to include an average of two nucleation sites (Figure 2C). Next, the number of nucleation sites was counted in each square (Figure 2D). The numbers of squares and nucleation sites in each square both define the I_δ index of Morisita (1959), which represents the nonuniformity of a distribution independent of the size of the quadrates. The I_δ index is defined as:

$$I_\delta = \frac{n\sum_{i=1}^{n} x_i(x_i - 1)}{\sum_{i=1}^{n} x_i\left(\sum_{i=1}^{n} x_i - 1\right)}, \qquad (2)$$

where n is the number of squares, x_i is the number of sites in the square i. The value of I_δ is zero when the distribution is perfectly uniform (Figure 3A). I_δ increases as the distribution becomes nonuniform (Figure 3B), and it is expected to be one when sites are distributed randomly (Figure 3C). When the distribution of sites is biased considerably, I_δ has a large value (Figure 3D). The value of I_δ was estimated in every shell position examined, and the nonuniformity of the distribution of nucleation sites was represented by I_δ.

Results

The biometric analyses revealed a negative correlation between $\tilde{S}$ and Q_s in a single specimen of *Isognomon perna*, and a positive correlation in a single specimen of *Malleus regula* (Figure 4B). In another species, no correlation was observed, though the number of measured portions



A (I_δ= 0)

1	1	1	1
1	1	1	1
1	1	1	1
1	1	1	1

C (I_δ=1.07)

2	2	0	0
0	3	0	1
0	1	0	1
3	1	1	1

B (I_δ=0.4)

1	2	1	1
2	2	1	1
0	1	1	1
1	0	1	0

D (I_δ= 4.93)

0	0	5	4
0	0	0	0
0	0	0	0
7	0	0	0

Figure 3. Effect of the spatial distribution pattern on the value of I_δ. In this figure, the area is divided into 16 contiguous squares each including a number of or no dots. **A.** Perfectly uniform distribution. **B.** Nearly uniform distribution. **C.** Random distribution. **D.** Considerably concentrated distribution.

within a single valve was not large enough to be significant. On the other hand, when the data from all species are combined, Q_s is negatively correlated with $\tilde{S}$ at the 0.01 level of significance, both for simple prismatic and vertical composite prismatic shells (Figure 4A–B). This shows that variation in the size of prisms tends to decrease as prism size increases. The negative correlation between Q_s and $\tilde{S}$ is clear especially in species with a simple prisms (Figure 4B), while the correlation is more or less obscure in species with vertical composite prisms (Figure 4A).

A positive correlation between I_δ and Q_s is found only in each specimen of *Unio biwae*, *Anodonta woodiana* and *Malleus regula* (Figure 4C, D). However, when all the data are combined, a positive correlation clearly emerges between I_δ and Q_s in species with vertical composite prisms (Figure 4C). In the case of species with simple prisms, Q_s is positively correlated with I_δ at the 0.05 level of significance, though the correlation is graphically unclear (Figure 4D). The positive relationship between I_δ and Q_s indicates that variation of the size of prisms tends to increase with increasing randomness of the distribution of nucleation sites.

Theoretical morphology

Growing circles model

To better understand the relationships between geometric features of prisms and the growth rate of each prism and/or of the net growth rate of the entire shell, the growth of aggregated prisms was modeled theoretically.

For modeling the process of microscopic growth, observing the initial growth stage of prisms helps understand the nature of crystal growth. Formerly, I reported that many small hemispherical incipient prisms occur on the inner surface of the periostracum at the growing margin in species possessing simple and vertical composite prisms (Ubukata, 1994, pl. 2, figs. 1–3). Consequently, a growing-circles model, which represents the growth of aggregated prisms, is introduced here.

Growth of a prismatic shell layer consists of three elements, namely, nucleation of prisms, growth of prisms, and accretionary growth of the entire shell. During a single short growth step, the mantle secretes calcium carbonate and nucleation of prisms occurs within the nucleation zone on the inner surface of a periostracum (Figure 5A). The periostracum subsequently secreted by the mantle edge pushes the earlier produced periostracum and its incipient prisms into a more proximal part of the shell (Saleuddin and Petit, 1983). After the prisms pass through the nucleation zone, prisms gradually grow and elongate, forming a columnar structure.

Let us consider hypothetical shell growth (Figure 5B). The accretionary growth of the entire shell during a short period of time is reflected in a shift of the nucleation zone. Growth of a prism is represented by the kinematics of an enlarging circle. Potential nucleation sites are distributed uniformly within a nucleation zone of width *h*. The distance between the potential nucleation sites can be expressed by *d*, which represents the size of a unit cell. Growth compo-

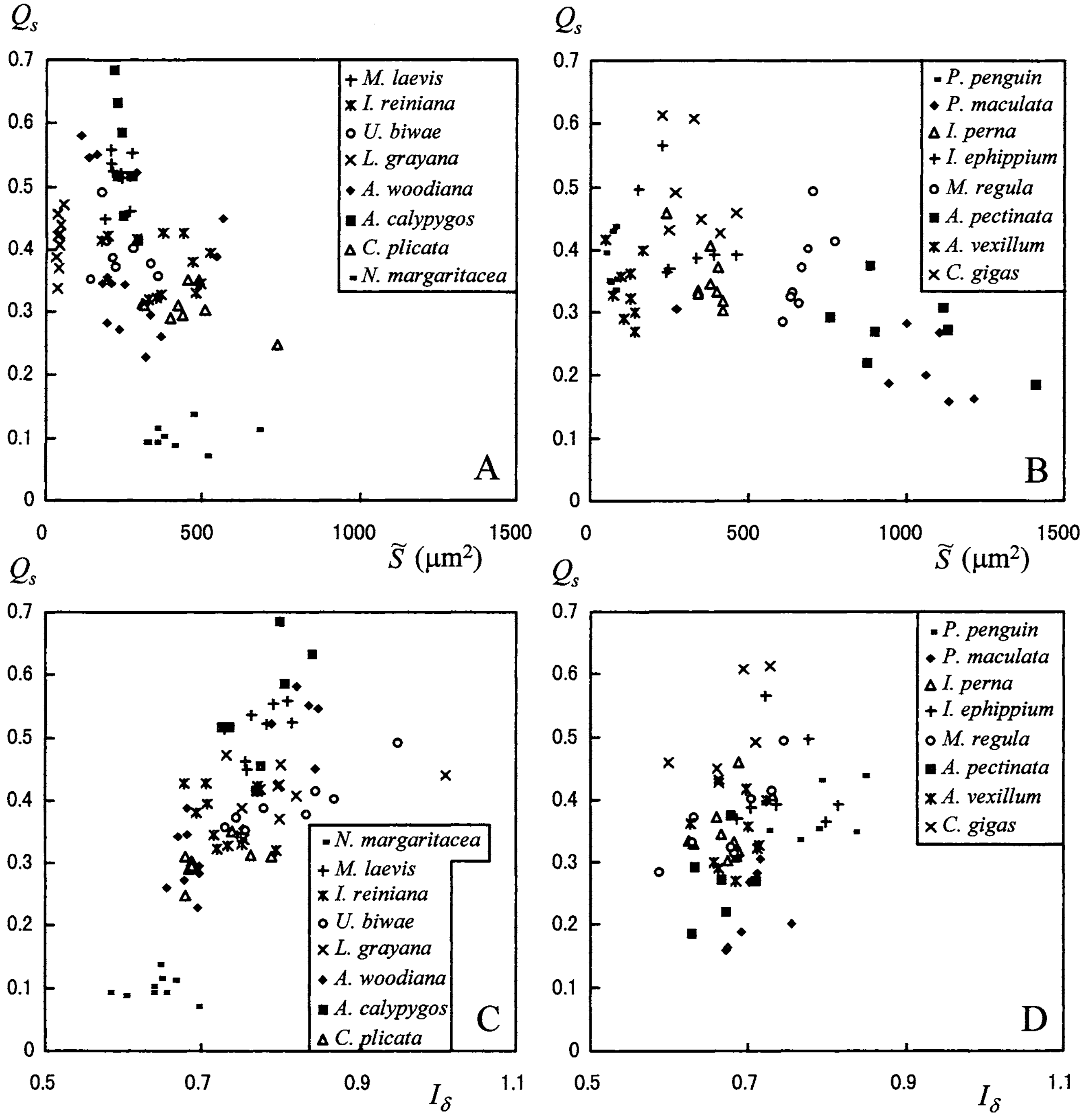


Figure 4. **A-B**. Relationship between $\tilde{S}$ and Q_s in actual shells. **A**. Data from species with vertical composite prisms. **B**. Data from species with simple prisms. **C-D**. Relationship between I_δ and Q_s for species with vertical composite prisms (**C**) and simple prisms (**D**).

nents are expressed as functions of growth stage *s*, rather than as functions of time, since the time scale of the growth process is difficult to ascertain in many cases. Over a period of one growth step, the mantle secretes a periostracum at the shell margin, giving rise to the stippled area in Figure 5B. If the growing margin of the shell shifts downward by *d* during the step, the growth step is regarded to be a unit interval of the growth. Then, the growth step Δs is generally defined as:

$$\Delta S \equiv \frac{\Delta l}{d}, \qquad (3)$$

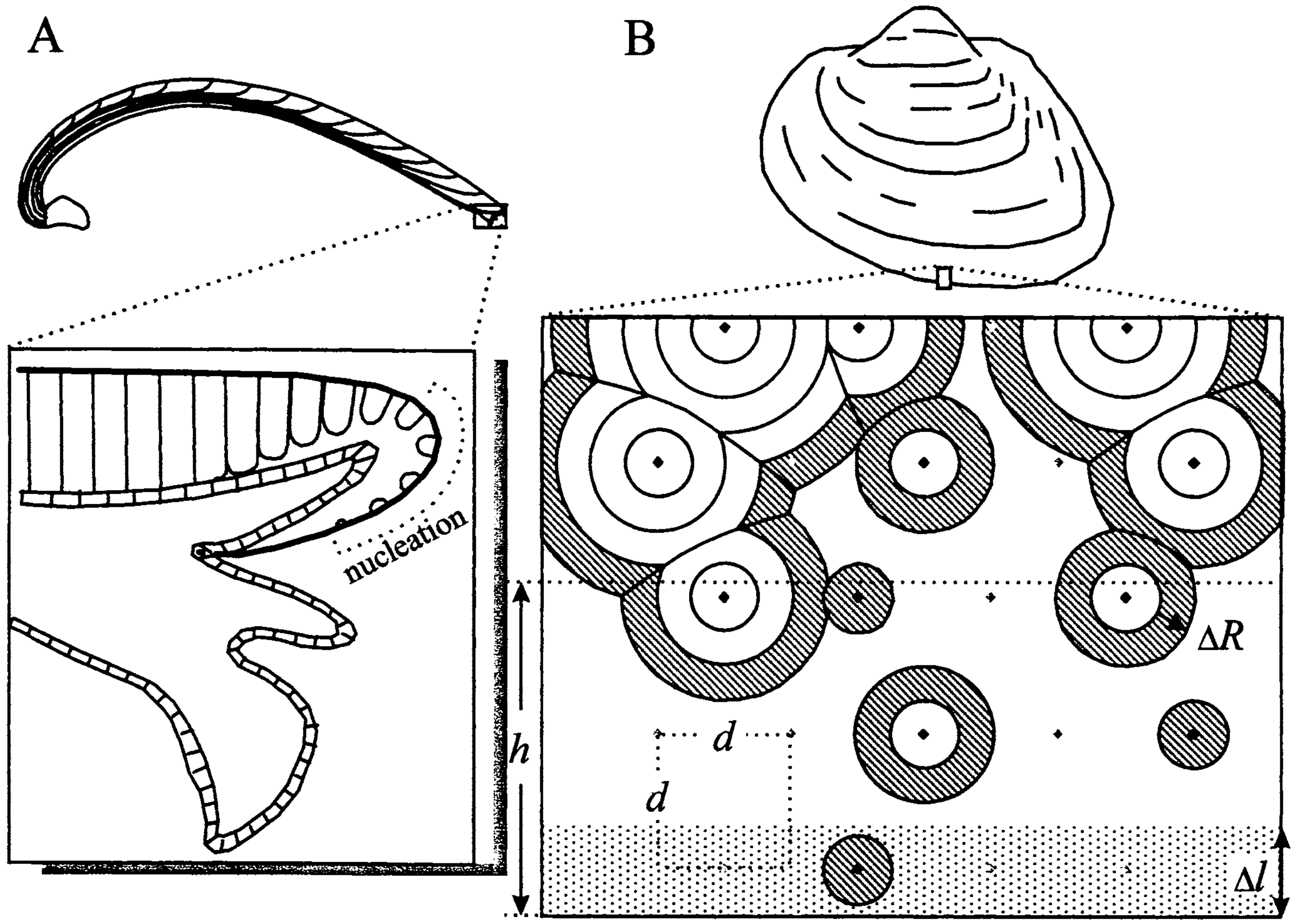


Figure 5. **A**. Schematic diagram of the radial section of the shell and mantle margin of a bivalve showing the position where nucleation of prisms occurs. **B**. The growing circles model. Black bold points indicate initiation sites of produced prisms, and gray ones potential nucleation sites of unborn prisms. During a given growth step Δs, the shell margin shifts by Δl (stippled area) and the radius of prisms increases by ΔR (shaded area). The dotted line indicates the dorsal limit of the nucleation zone.

where the growing margin of the shell shifts by Δl during the growth step.

Meanwhile, nucleation of a prism occurs at a potential nucleation site within the nucleation zone with a probability of q. Each prism is approximated by a circle which enlarges at a steady rate. During a growth step Δs, calcium carbonate precipitates along the circumference of each prism giving rise to a new additional rim shown by the shaded portion in Figure 5B, and the radius of each circle increases by ΔR. As the prisms grow, neighboring prisms come closer and finally in contact with one another, as a result forming a boundary between two prisms. Nucleation of prisms occurs randomly during each growth step, as a result of irregularity of the settling time among prisms. Consequently, a growing circle often occupies the space of nucleation and/or growth of a neighboring 'unborn' prism. A newborn prism sometimes loses in competition for space between neighboring prisms, and is geometrically terminated (Grigor'ev, 1965).

In the growing-circles model, growth of a shell and prisms is generally expressed by the following three parameters: C: the standardized growth rate of prisms, defined as the increase of the radius of a prism per growth step, normalized by size of a unit cell (d), P: probability of nucleation per growth step in each potential site, and L: the extent of the nucleation zone standardized by d. Probability of 'failure' of nucleation at each site per growth step is expressed as $1-P$, and the probability of failure of nucleation during a growth step Δs ($=1-q$) is obtained by raising $1-P$ to Δs^{th} power. Then, three growth parameters C, P and L are given by:

$$C \equiv \frac{\Delta R}{\Delta l},\quad P \equiv 1-(1-q)^{\frac{1}{\Delta s}},\quad L \equiv \frac{h}{d}. \tag{4}$$

Now, we can generally define a growth increment during an arbitrary growth step if three parameters C, P and L are given.

Computer simulation

In order to evaluate the effects of parameters C, P and L on the geometric pattern of prismatic structure, computer simulations were performed for growth of prisms based on

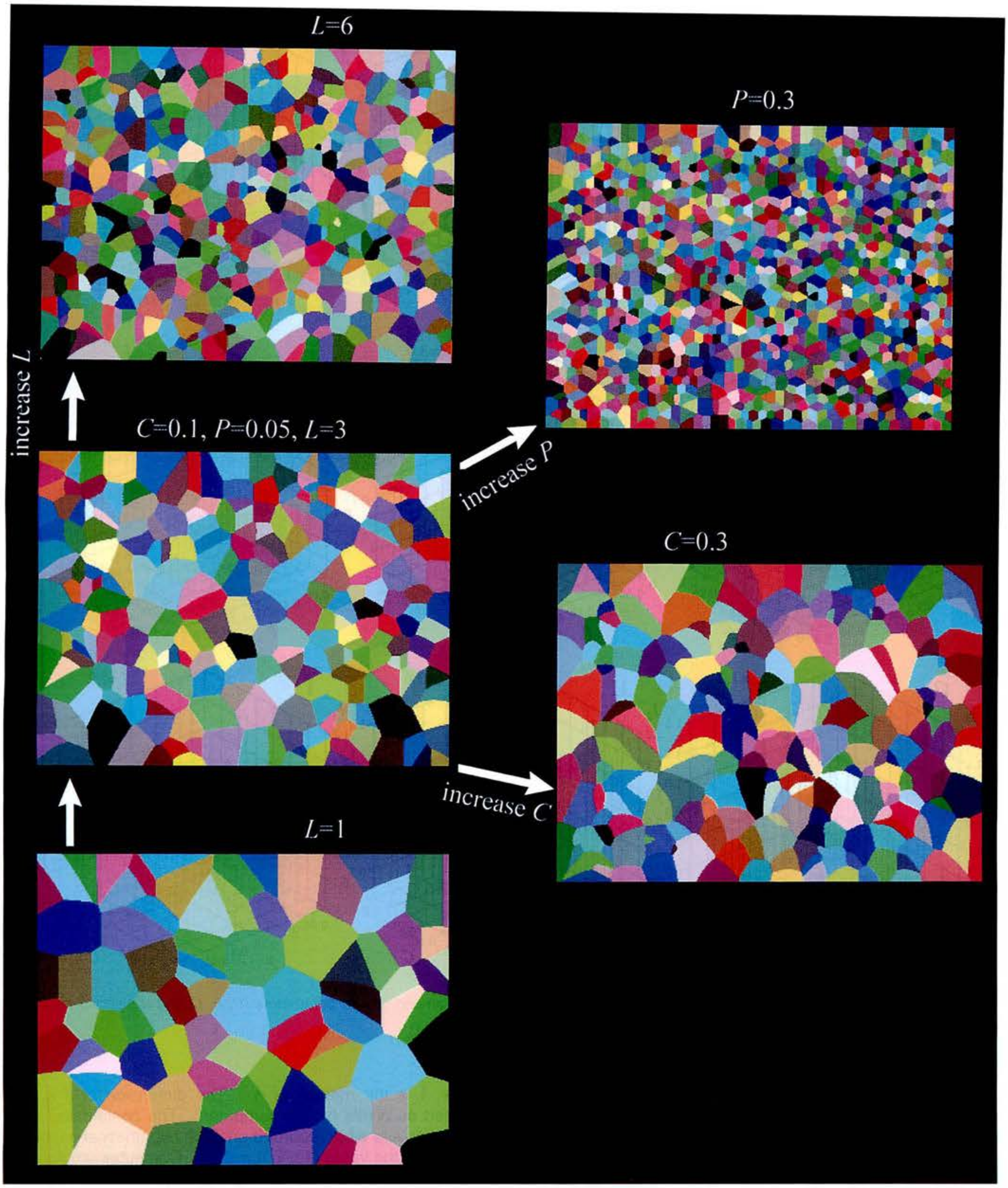


Figure 6. Color display of the growing circles model. Each prism is identified by its color. As C increases, size variation of the prisms also increases. As P or L increases, the median size of prisms tends to decrease.

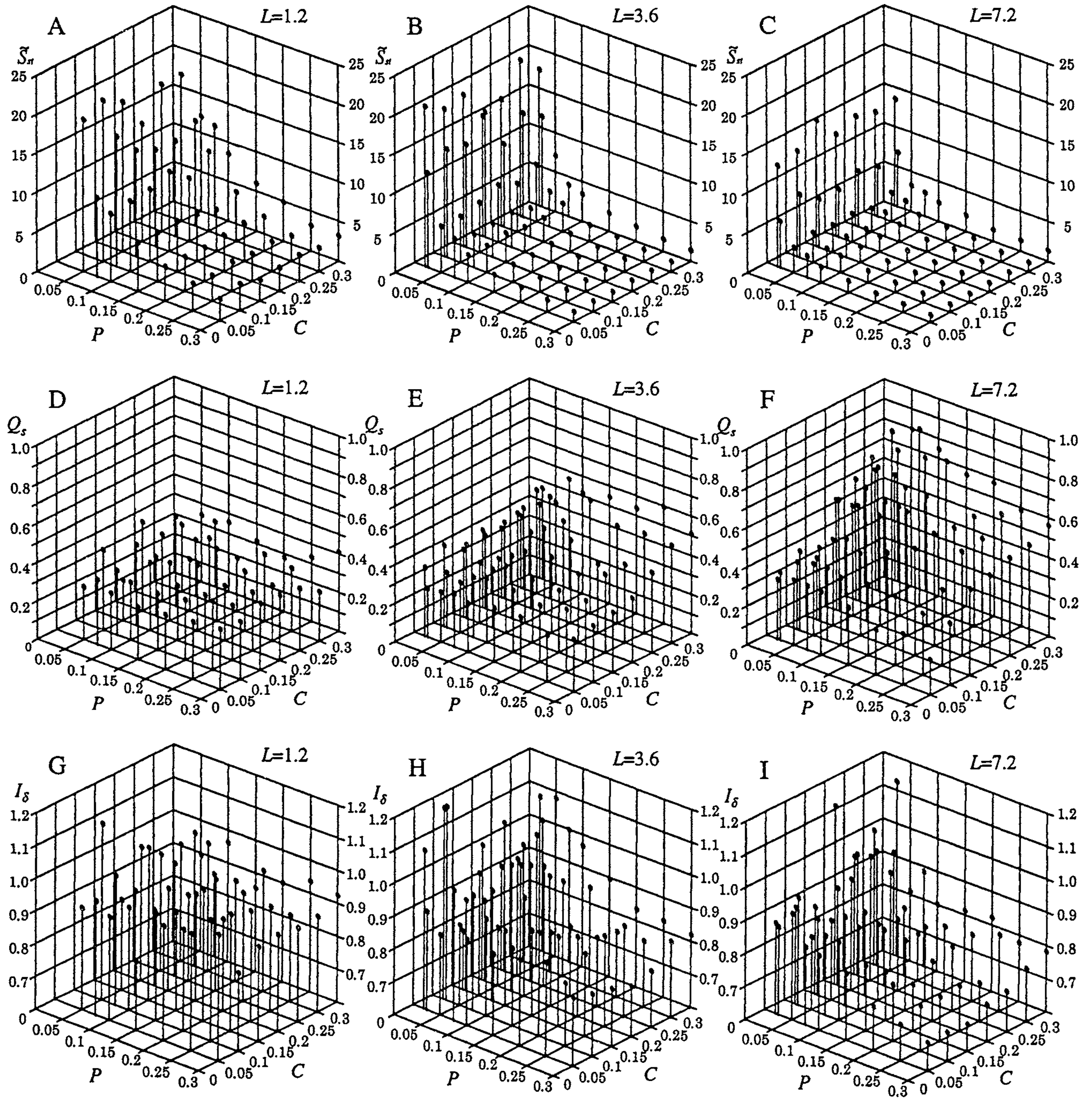


Figure 7. Three-dimensional block diagrams showing the relationships among growth parameters (C, P, L) and statistics $\tilde{S}$ (**A–C**), Q_s (**D–F**) or I_δ (**G–I**) on a C-P diagram at L values of 1.2, 3.6 and 7.2.

the growing-circles model. In the theoretical model, the area of a hypothetical prism was measured as the number of pixels (A) on the display surface, and both the standardized hinge spread (Q_s) and the median of a standardized area of hypothetical prisms ($\tilde{S}_{st}$) defined below were estimated in each model:

$$\tilde{S}_{st} \equiv \frac{\tilde{A}}{d^2}, \qquad (5)$$

where $\tilde{A}$ is the median of A. The dimension of d is expressed as pixels on the computer. The coordinates of a nucleation site were recorded on each hypothetical prism for calculating the value of I_δ in a model. Computer simulations were carried out with a program written in VISUAL BASIC by means of a 64-bit workstation computer (Visual Technology VT-Alpha 600) interfaced with a CRT (Iiyama A702H).

Figure 6 shows a spectrum of geometric patterns of hypothetical prisms that were made by the growing circles model.

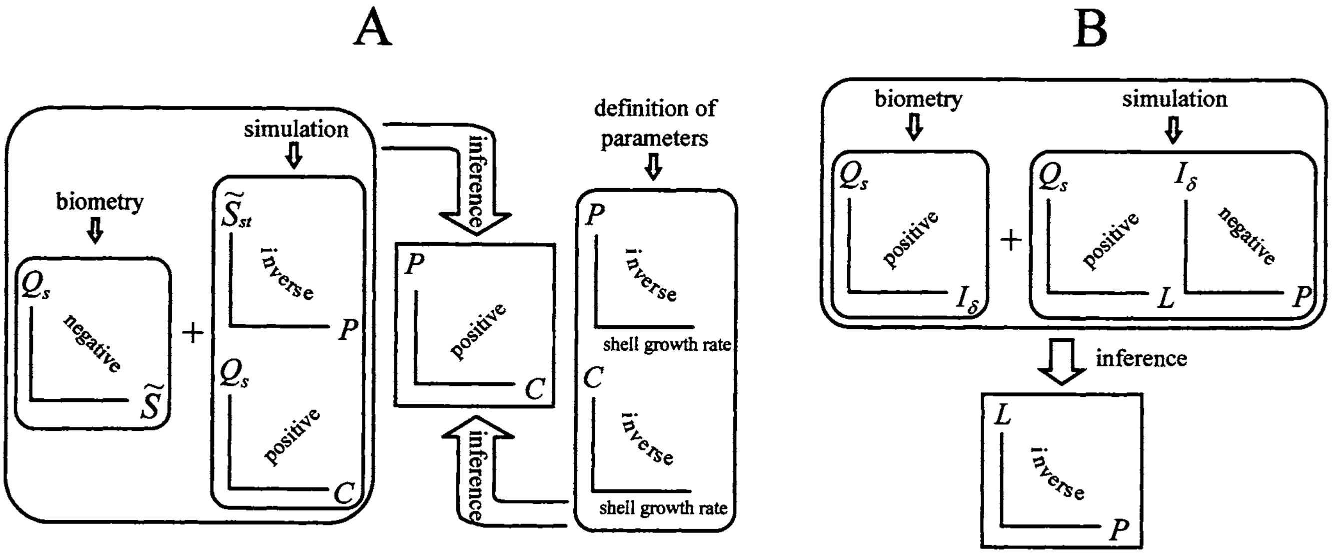


Figure 8. Summary of the biometric analyses and computer simulation. From coupling their results with the consequences from definition of the parameters, a relationship between growth parameters is inferred either in simple prisms (**A**) or composite prisms (**B**).

Each prism is identified by its color in a theoretical prismatic structure. If C is large, each prism grows considerably while it passes through the nucleation zone, as a result of the great irregularity of the birth time among prisms. Then, as C increases, the variation of prism size also increases. As P or L increases, the number of prisms increases while their size decreases.

Three-dimensional scatter diagrams illustrating the values of $\tilde{S}_{st}$ in relation to C and P, at L=1.2, 3.6 and 7.2 are given in Figure 7A-C, respectively. $\tilde{S}_{st}$, which means an 'average' prism size, seems to be inversely proportional to P, which represents the probability of nucleation. In addition, at the same combination of C and P, $\tilde{S}_{st}$ tends to increase as L decreases. This fact indicates that the size of hypothetical prisms increases as the nucleation zone becomes narrow.

Figure 7D-F is a series of diagrams showing the relationship among four parameters C, P, Q_s and L. When L is large enough, Q_s is positively correlated with C (Figure 7E, F). This fact suggests that variation of prism size tends to increase with increasing growth rate of prisms (ΔR in Eq.1) or with decreasing the accretion rate of the entire shell (Δl in Eq.1). When L is small, no clear relationship exists between pairs of C, P and Q_s (Figure 7D). In a high C condition, Q_s at a given P also tends to increase with increasing L (Figure 7D-F).

Figure 7G-I shows the variation of I_δ in relation to C, P and L. When L is large, I_δ gradually decreases with increasing P. Since I_δ represents the degree of nonuniformity, this result indicates that the nucleation sites tend to be distributed uniformly as the probability of nucleation increases. In the high P region, I_δ at a given C decreases as L increases. This fact indicates that nucleation sites tend to be distributed randomly as the nucleation zone becomes narrower, when the probability of nucleation is high enough.

Geometric pattern and growth rate of prismatic shell

As mentioned above, the biometric analyses indicated a negative correlation between $\tilde{S}$ and Q_s especially in the species with simple prisms (Figure 4B), and the computer simulation predicted an inverse relationship between P and $\tilde{S}_{st}$ (Figure 7A-C) and also a positive correlation between C and Q_s (Figure 7E, F). To sum up these results, it can be predicted that P increases as C increases for those species with simple prisms (Figure 8A). That is also inferred from the definition of parameters. Since both P and C are inversely proportional to the growth rate of the entire shell, a positive correlation between C and P is quite reasonable (Figure 8A) if the size-frequency distribution of prisms is controlled mainly by the growth rate of the entire shell. Furthermore, even if both the growth rate of prisms and the probability of nucleation reflect the activity of mantle secretion, and if the size of prisms is controlled mainly by the activity of mantle secretion, the positive correlation between C and P is also expected.

Coupling of the biometrics and the simulation also suggests to us a relationship between the parameters P and L. The biometric analyses demonstrated a positive correlation between I_δ and Q_s, especially for species with vertical composite prisms as shown in Figure 4C. In addition, the computer simulation predicted a positive relationship between L and Q_s, and a negative correlation between P and I_δ as shown in Figure 7G-I. These two results suggest that P possibly decreases as L increases in species with vertical composite prisms (Figure 8B). Actually, an inverse relationship between L and P is expected if we assume that the frequency of nucleation per unit time interval is fixed.

To ascertain this prediction, relationships among simulated values of $\tilde{S}_{st}$, I_δ and Q_s were analyzed for each combina-

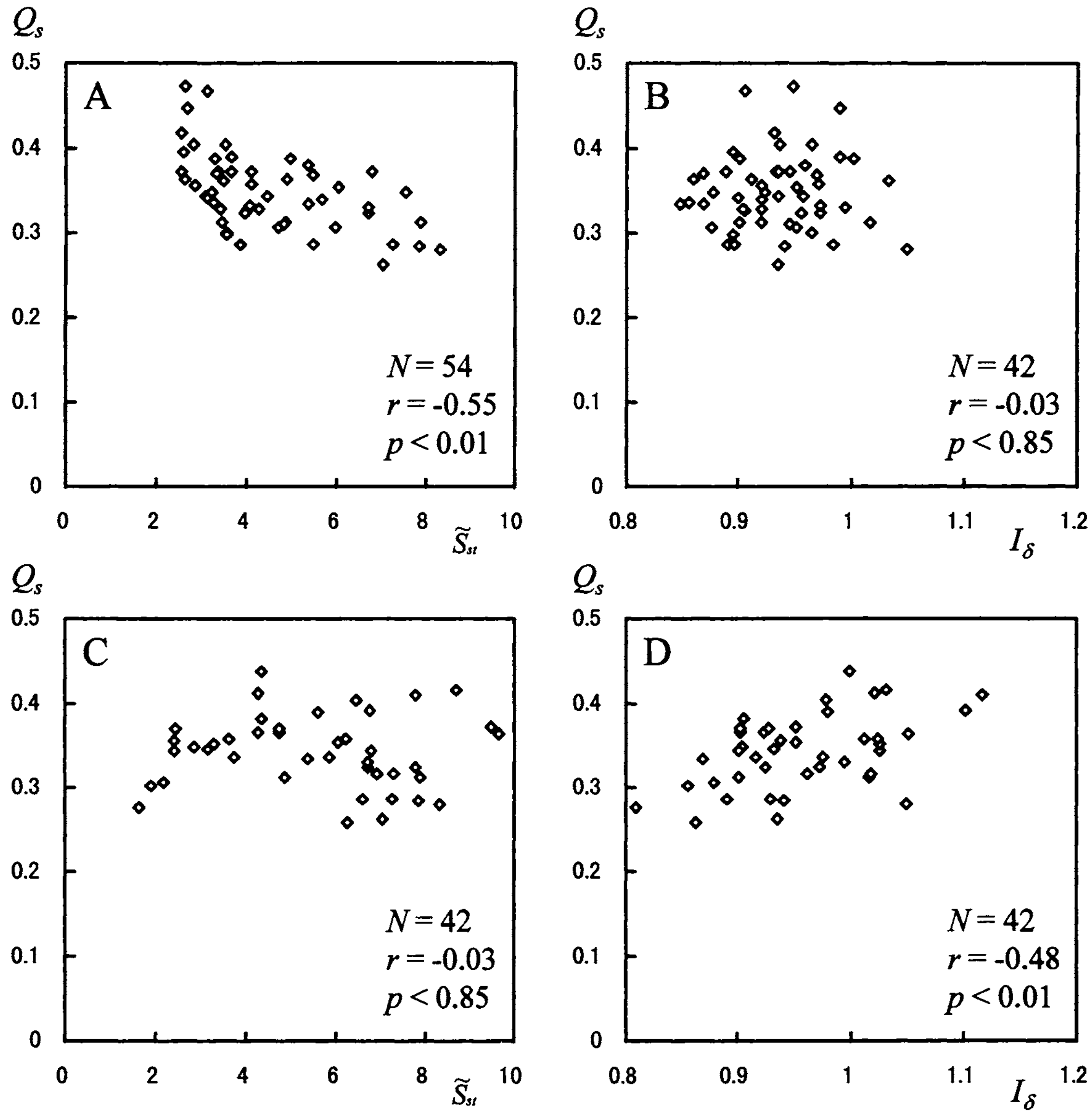


Figure 9. Relationships between $\tilde{S}_{st}$ and Q_s and between I_δ and Q_s when three parameters satisfy equations as follows: $C=aP$, $P=b/L$, where a and b are coefficients. N represents the total number of samples examined, r exhibits the correlation coefficient, and p is the significance level of the correlation. **A-B.** a=3, $0.05 \leq b \leq 0.175$. **C-D.** $1 \leq a \leq 3$, b=0.05.

tion of C, P and L, when a positive correlation between C and P and an inverse relationship between L and P are assumed, as in the following relations:

$$C = aP,\ P = \frac{b}{L}, \qquad (6)$$

where a and b are coefficients. Computer simulations were performed under the following conditions: 1) a is fixed to 3, and b varies between 0.05 and 0.175, 2) a varies between 1 and 3, and b is fixed to 0.05. Figure 9 is a diagram showing the relationships between $\tilde{S}_{st}$ and Q_s and between $I_\delta$and Q_s.

The results of the simulations under a fixed value of a (=3) and various values of b show a negative correlation between $\tilde{S}_{st}$ and Q_s (p<0.01, Figure 9A), but do not indicate any linear relationship between I_δ and Q_s (Figure 9B). Under even this condition, a negative correlation between $\tilde{S}_{st}$ and Q_s and a positive correlation between I_δ and Q_s were approached by a multiple regression analysis, which shows a significant trend for Q_s to increase as a function of - $\tilde{S}_{st}$ and I_δ:

$$Q_s^* = -0.573\tilde{S}_{st}^* + 0.128\, I_\delta^* \ (r=0.565,\ F=11.94,\ p<0.01),$$

where Q_s^*, S_{st}^* and I_δ^* are standardized variables of Q_s, $\tilde{S}_{st}$ and I_δ, respectively. In this case, a negative relationship between $\tilde{S}_{st}$ and Q_s is especially prominent. This relationship, concordant with that of the biometric analyses as shown in Figure 4B, D, strongly supports conspicuous positive correlation between C and P assumed as in the Eq. 6, particularly for simple prisms. As stated above, a positive correlation between C and P suggests that both prism size and its variation are mainly controlled either by the growth rate of the entire shell, or by the activity of mantle secretion. If the former is the case, simple prisms must tend to be uniformly large as the entire shell grows faster. On the other hand, if the latter is the case, density of nucleation and growth rate of prisms both must decrease as the secretive activity of the mantle decreases, and a negative relationship is expected between size and the growth rate of simple prisms.

On the other hand, the results of computer simulations with various values of the coefficient *a* and the fixed coefficient b (=0.05) show a positive correlation between I_δ and Q_s ($p<0.01$, Figure 9D), but no significant relationship between $\tilde{S}_{st}$ and Q_s (Figure 9C). A multiple regression analysis for Q_s on $\tilde{S}_{st}$ and I_δ provides a significant trend to increasing Q_s as a function of $\tilde{S}_{st}$ and I_δ:

$$Q_s^* = -0.393\tilde{S}_{st}^* + 0.686\, I_\delta^* \quad (r=0.582,\ F=9.99,\ p<0.01).$$

In this equation, a positive relationship between I_δ and Q_s is more striking than a negative relationship between $\tilde{S}_{st}$ and Q_s. This is concordant with the results of the biometric analyses in species with vertical composite prisms shown in Figure 4A, C. This fact supports the assumption that P has an inverse relationship with L as defined in Eq. 6, particularly in vertical composite prisms. This assumption implies that the number of nucleations per unit time interval is fixed to a constant value. In the species having a large nucleation zone, in which the value of L is large, maintenance of the probability of nucleation inevitably causes a large number of nuclei. If we assume an upper limit of the total number of nuclei per unit time interval, the probability of nucleation will vary inversely with the width of the nucleation zone. If the total number of nuclei per unit time interval is fixed, the density of nucleation is expected to decrease as the total shell grows faster. In this case, the median size of prisms is controlled mainly by the growth rate of the entire shell. This fact suggests that, in the case of vertical composite prisms, prism size tends to increase as the entire shell grows faster.

Discussion and conclusion

Wada (1961) studied the size of crystals in a nacreous shell layer of *Pinctada martensii* in relation to the rate of calcium carbonate deposition. He demonstrated that when the rate of shell deposition is at a maximum, a large number of small crystals occurs on all the nacreous surfaces, while larger crystals occur as the rate of deposition decreases. In addition, Wada (1972, 1985) also reported an inverse relationship between them for such bivalves as *Pinctada fucata*, *Pinna attenuata* and *Hyriopsis schlegeli*. Wada assumed that the primary factor determining size of crystals was the degree of calcium carbonate concentration in the extrapallial fluid. He regarded the rate of calcium carbonate deposition as the rate of crystal growth, and thought that larger crystals tend to grow slowly at a low degree of supersaturation of the fluid, at which the frequency of nucleation diminishes. The results of the present study may partly support those of Wada, since the negative correlation between size and growth rate of crystals is also expected in this study if the size of prisms is assumed to be controlled by the activity of mantle secretion.

Unlike prismatic structure, nacreous structure does not form the outermost shell layer in bivalves. In the nacreous layer, deposition corresponds to thickening of the shell or growth of crystals, rather than growth of the entire shell. Therefore, the size of crystals in the nacreous layer correlates with the rate of crystal growth rather than with the growth rate of the entire shell. On the contrary, the net growth rate of the entire shell, which reflects the growth rate of the soft parts, seems to be significant for the size of crystals which constitute the outermost shell layer.

Ubukata (1994) claimed that relatively rapid growth of prisms produces prisms prominently inclined to the outer shell surface, because of retardation of the initiation of their forward growth relative to the radial direction. Although such inclined prisms are commonly found in species belonging to Unionidae and Ostreidae (Ubukata, 1994), their prisms also characteristically fell in low (small size) and high Q_s (irregular in size) regions in Figure 4A, B (refer to Table 1 for higher taxonomy). The present study suggests that such a pattern is produced under the condition of either rapid growth of prisms or slow growth of the entire shell. Ubukata (1994) demonstrated that the relative growth rate of prisms to that of the entire shell determines the orientation of elongation of the prisms.

This study suggests that the sizes of prisms and their size variability correlate with the growth rate of the shell in bivalves. It is well known that internal microgrowth increments often provide a high-resolution record of growth rate and physiological condition of a bivalve (Lutz and Rhoads, 1980), particularly in species with crossed lamellar and horizontal composite prismatic shells. In simple prismatic and vertical composite prismatic shells, however, it is hard to estimate the growth rate of the shell from an analysis of internal microgrowth increments, because periodic growth increments tend to be obscure. The size-frequency distribution of prisms may be a promising index for estimating the growth rate of a fossil bivalve shell.

This study indirectly estimates the relationship between the size of prisms and the growth rate of the shell or prisms from computer simulations, but the direct observation of the growth rate of the shell or prisms remains to be performed. An experimental study on growth of a shell and/or crystals may be required for clarifying the relationship between the crystal size and the growth rate more clearly, and for obtaining a regression equation to predict the growth rate from prism size. The growth rate of the shell and/or crystals is clearly related to the physiological condition of a fossil organism, and has the potential to in spire a research field of 'paleophysiology'.

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Evolution in morphometric traits in North American Collignoniceratinae (Ammonoidea, Cephalopoda)

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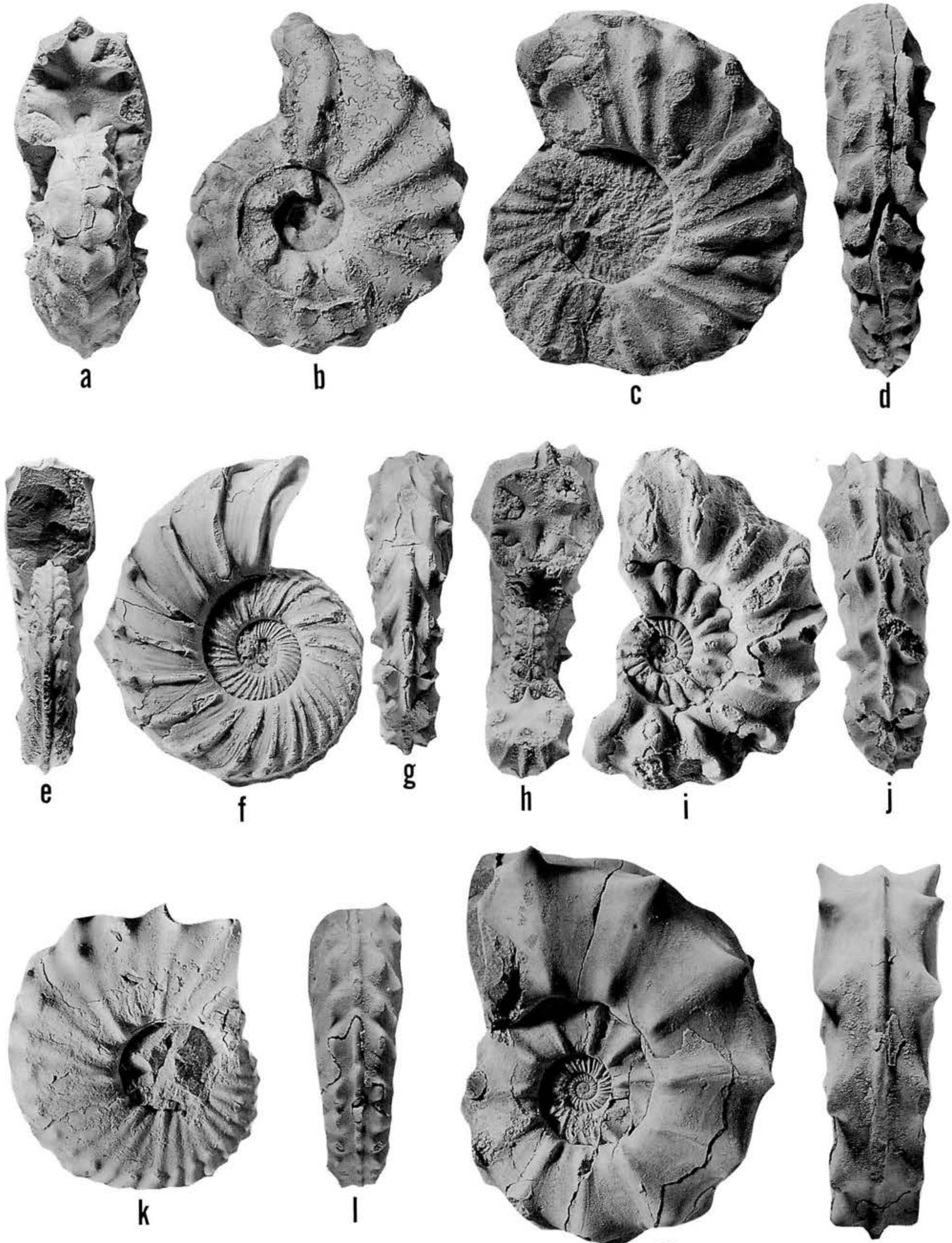
Abstract. Eight species and one subspecies of two genera of Collignoniceratinae, *Collignoniceras* and *Prionocyclus*, are analysed with respect to standard morphological distance measures and rib-frequencies, methods of multivariate statistical analysis, including canonical variate ordination, principal components and generalized distances. It was found that the biostratigraphically inferred evolutionary sequence, as currently perceived, is upheld in detail for the *Collignoniceras* data. The 'nearest -neighbour' relationships between the *Prionocyclus* part of the sequence is less complete, although links in main branches are supported. The other aspect given consideration, that of "gracile" and "robust" shells (based on visual inspection of the conch), yielded the result that the subjective assignation of shells to gross morphological type is largely, though not unequivocally, upheld by the statistical analysis. Illustrations of typical representatives of the species analysed are provided.

Key words: Ammonites, Collignoniceratinae, compositional analysis, Cretaceous of U.S.A., evolution, morphometrics

Introduction

Ammonite taxonomy is perforce largely based on external morphology — mode of coiling, tuberculation, ribbing and carination. The diagnostic significance of the suture line seems to have been recognized as being of secondary importance for many groups of Jurassic and Cretaceous ammonites (cf. Pérez Claros, 1999). Reyment and Kennedy (1998) and Reyment and Minaka (2000) recorded and described polymorphism in ornamental properties of Cretaceous ammonites of the genus *Neogastroplites*. However, it is by no means a trivial matter to distinguish between true polymorphism, in the classical genetic sense of the property (Falconer, 1981, p. 42; Manly, 1985, p. 402; Roughgarden, 1979, p. 259), and the merging of ornamental types in response to ecophenotypic variation of the kind that seems to occur in the present material with respect to the categories referred to as being 'gracile' and 'robust'. The functional significance of such differentiation, if any, remains obscure. A palaeobiological treatment of the problems involved, and methods for their analysis, are given in Reyment (1991), chapters 5, 6 and 8.

The primary aim of the present study is directed towards ascertaining to what degree the stratigraphically supported phylogeny within a subfamily of ammonites arrived at by the traditional methods can be recognized by the quantitative analysis of external morphological characteristics (excluding sutures); that is, mainly distance measures on the shape of the shell, but also ribbing density. With such information available, it should become possible to extrapolate to other groups and to work towards stabilizing phylogenetic relationships on less subjective grounds than are yielded by purely descriptive procedures. As far as is known to us, there have been no studies devoted to ascertaining to what extent, if any, wholly distance-related variables are correlated with evolutionary status in ammonites (and, by extension, whether such differentiation can represent a relationship between form and function). The work accounted for in this note shows, with reasonable clarity, that such is indeed the case, at least in the evolution of the Collignoniceratinae. There is, moreover, a more far-reaching consequence to our project. Gross morphology, such as is expressed in coiling and whorl shape, has not been attributed importance of the first order in many evolutionary and taxonomical studies known to us. As we demonstrate in this note, there is information of evolutionary significance in characters of this kind, but it can only be effectively extracted by means of appropriate quantitative procedures in a multidimensional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perspective. The detailed classical taxonomy of the material considered here is scheduled to appear in a separate monograph (Kennedy *et al.*, in press). In order to avoid eventual misunderstanding, we are not concerned with the cladistics/phenetics confrontation; our analysis is solely multivariate morphometric in nature as defined by Blackith and Reyment (1971).

The material analysed

Members of the subfamily Collignoniceratinae that inhabited the Cretaceous Western Interior seaway of the United States first appeared in the Lower Turonian and ranged into the Upper Turonian. On a mondial scale, the subfamily arose in the uppermost Cenomanian and died out in the Coniacian. The analysis reported here is based on data being presented elsewhere in Kennedy *et al.* (in press), to which monograph reference is made for details of taxonomy, provenance and stratigraphy. Owing to the scarcity of available specimens of some of the species concerned, the phylogenetic study is somewhat less complete than we should have liked it to be. Hence, the conclusions put forward here are necessarily of a preliminary nature.

The earliest Collignoniceratinae of the preserved sequence considered here is the monospecific genus *Cibolaites* Cobban and Hook 1983, of which neither its whence nor its whither seem to be known with any certainty. The genus is distinguished throughout most of its ontogeny by the presence of umbilical, ventrolateral and siphonal tubercles. Its mature body chamber is flat-sided, with progressively weakening tubercles and ribs (Cobban and Hook, 1983, p. 16-18, pl. 2, figs. 1-9; pl. 3, figs 3-8; pl. 8, figs 6-8; pl. 13, figs 1-5; pl. 14, fig. 14).

Collignoniceras woollgari (Mantell, 1822) is believed to have descended from *Cibolaites*. It is thought to have given rise to several contemporaneous species in western Europe (Kennedy *et al.*, 1980). In the region under consideration, four successive species seem to have derived from it (presumably via its subspecies *C. w. regulare* Haas, 1946, although the ensuing multivariate study leaves this undecided with respect to the actual route that may have been followed), of which one is considered in the present analysis, to wit, *C. praecox* Haas, 1946; the other three are not available in sufficient numbers for study. *C. praecox* differs from *C. woollgari woollgari* and *C. woollgari regulare* by the persistence of long and short ribs with ventrolateral tubercles outnumbering the umbilical, and a near-continuous siphonal keel. As shown by the results of the morphoevolutionary analysis, the inferred biostratigraphical relationships between successive species may be a simplification of the actual evolutionary sequence of events.

The later Turonian history of the Collignoniceratinae in the U. S. Western Interior is considered to be marked by the evolution from *Collignoniceras praecox* of species of *Prionocyclus*. Juveniles of species of the two genera can be distinguished in that the keel of *Collignoniceras* has siphonal clavi equal in number to the ventrolateral tubercles, whereas in *Prionocyclus* Meek, 1872, the serrations outnumber the ribs. It is significant that *Prionocyclus hyatti* Stanton, 1894, an early representative of the genus, is morphometrically closely allied to *Collignoniceras woollgari regulare* and somewhat less so with its putative ancestor, *C. praecox*. In general terms, there is semiquantitatively manifested intraspecific variation in the strength of the ornament of most of the species of the Western Interior Collignoniceratinae, a 'gracile' category and a 'robust' one. These are not discrete morphological categories such as are recorded by Reyment (1971) for the genus *Benueites*. Testing the soundness of this interpretation of morphological variability forms an integral part of the analysis presented in the following. Figures 1-3 provide illustrations of typical representatives of the species considered, including examples of shells determined as being robust or gracile.

Methods

Photographs of the specimens passing muster for statistical study were scanned and the coordinates of seven sites (Figure 4) considered diagnostic were recorded, using the digitization program *TpsDig* written by F. James Rohlf (SUNY at Stony Brook, USA). Only complete specimens were selected for analysis; the numbers of each of the samples of the species are recorded in Table 1. The required distances were computed from these coordinates by simple geometry. This is freely admitted to be an arbitrary manoeuvre and we have desisted from confusing the issue by not calling the coordinate pairs thus obtained "landmarks". In any event, they cannot be equated to the landmarks used by Johnston *et al.* (1991) in their analysis of spiral growth in gastropods. The approach utilized in that study is clearly one that should prove eminently useful in future studies of growth and shape-variation in ammonites, not

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← **Figure 1.** **a, b.** *Cibolaites molenaari* Cobban and Hook, 1983. USNM 498205, a robust form from USGS Mesozoic locality D8429, sec. 1 and NE¼ sec. 12, T. 4N., R. 19W., Cibola County, New Mexico. Mancos Shale, from limestone concretions 24-30 m below the top of the Rio Salado Tongue. **c, d.** *Collignoniceras woollgari woollgari* (Mantell, 1822). USNM 356903, a gracile form from USGS Mesozoic locality D 10243, E½ NE¼ sec. 9, T. 5S., R. 2E., Socorro County, New Mexico, Rio Salado Tongue of the Mancos Shale. **e-j.** *Collignoniceras woollgari regulare* (Haas, 1946). **e-g**, USNM 498237, a gracile form from USGS Mesozoic locality 21792, west of Newcastle, in the NE¼ sec. 31, T. 45N, R. 61W., Weston County, Wyoming, limestone concretions in the Carlile Shale, 18.3 m below the base of the Turner Sandy Member. **h-j,** USNM 498244, a robust form from USGS Mesozoic locality D9896, NE¼ sec. 35, T. 46M, R. 63W., Weston County Wyoming, limestone concretions in the Carlile Shale, 18.3 m below the base of the Turner Sandy Member. **k-n.** *Collignoniceras praecox* (Haas, 1946). **k, l**, USNM 498272, a gracile form from USGS Mesozoic locality D 13832, sec. 35, T. 8S., R. 1E., Fall River County, South Dakota, from limestone concretions in the lower part of the Carlile Shale. **m, n**, USNM 498266, a robust variant from USGS Mesozoic locality D 10697, S E¼ SE¼ sec. 18, T. 9S., R. 2E., Fall River County, South Dakota, limestone concretions in the Carlile Shale 6 m below the base of the Turner Sandy Member. USGS: United States Geological Survey; USNM: U.S. National Museum of Natural History, Washington D.C. All figures are × 0.9.

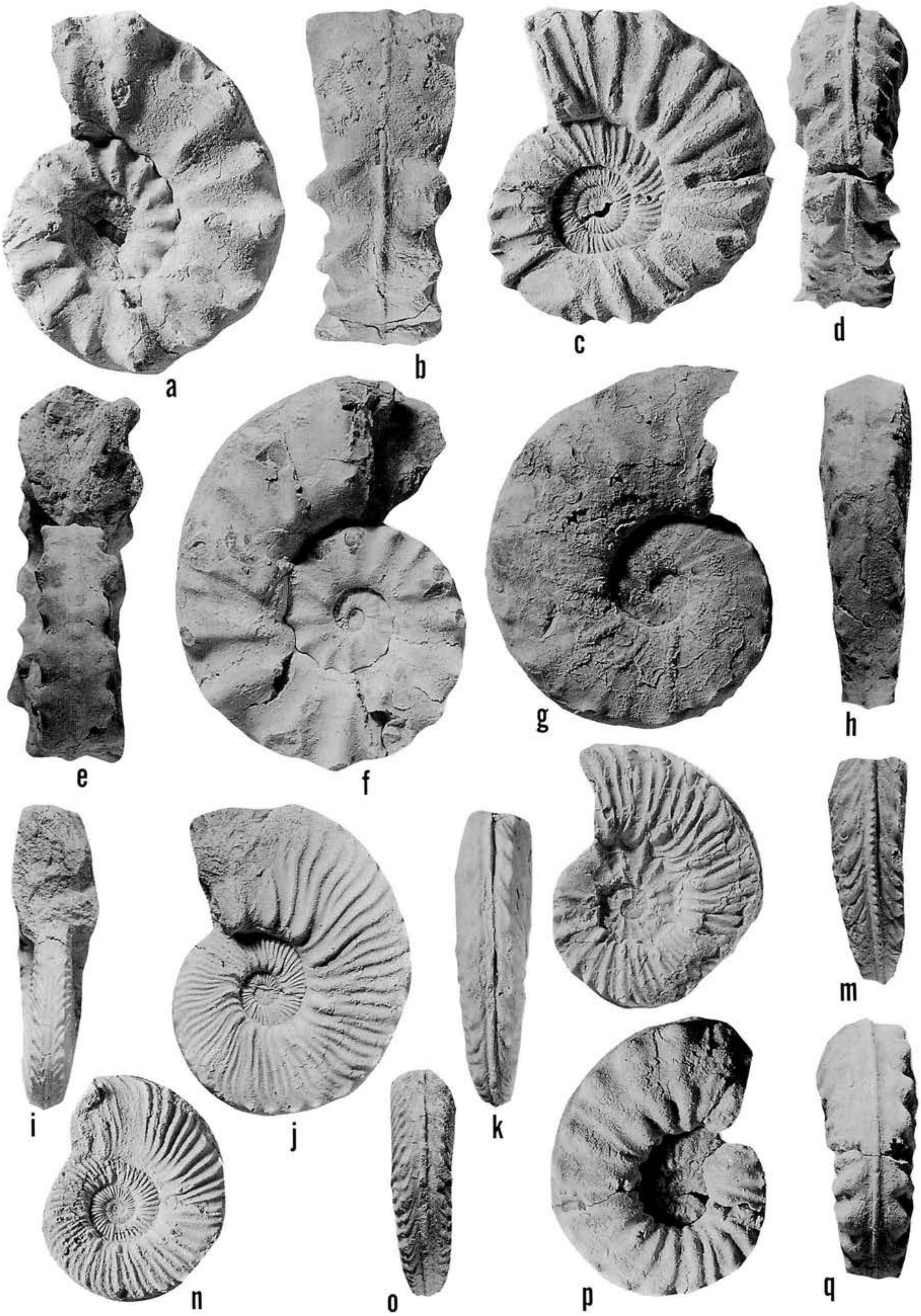
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Figure 3. *Prionocyclus wyomingensis* Meek, 1876. Paralectotype, USNM 7729, a gracile form from the Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. USNM: National Museum of Natural History, Washington D.C. Natural size.

least because of the finding that mean-forms with similar shapes at the same arbitrary growth increment may have achieved that shape in different ways. The resulting data, suitably corrected for slight differences in magnification from specimen to specimen, were studied by standard multivariate analyses made on the distance measures between adjacent sites and the maximum breadth of the last whorl. The factor of ornamental complexity was introduced into the analysis by appending rib counts to the data matrix. This latter addition accounts adequately for the morphological categories gracile/robust.

The multivariate statistical methods most useful for our study were found to be (1) principal component analysis of the distances (six in all) and the breadth, maximum directly

← **Figure 2.** **a–d.** *Prionocyclus hyatti* (Stanton, 1894). **a, b**, USNM 498308, a robust form from USGS Mesozoic locality D3884, Arroyo Lopez, 1 km. north of Holy Ghost Spring, Sandoval County, New Mexico, Mancos Shale, from lower part of Semilla Sandstone Member. **c, d**, USNM 498323, from USGS Mesozoic locality D 11208, NE¼ sec. 36, T. 6N., R. 19W., Cibola County, New Mexico, from the D Cross Member of the Mancos Shale. **e–h,** *Prionocyclus macombi* Meek, 1876. **e, f**, USNM 498341, a robust form from USGS Mesozoic locality D4395, north of Rio Gallina in SE¼ sec. 15, T. 20N., R. 1E., Rio Arriba County, New Mexico, Mancos Shale, from the base of the Juana Lopez Member. **g, h**, USNM 498348, a gracile form from the same locality and horizons as **c, f**. **i–m.** *Prionocyclus novimexicanus* (Marcou, 1858). **i–k,** USNM 498434, a gracile form, from USGS Mesozoic locality D9833, NW¼ NW¼ Sec. 33, T. 40N., R. 82W., Natrona County, Wyoming, from the second ledge forming sandstone below the top of the Frontier Formation. **l, m**, USNM 498446, a robust form from USGS Mesozoic locality D6928, NE¼ SE¼ sec. 31, T. 22N., R. 75W., Albany County, Wyoming, from the Wall Creek Sandstone Member of the Frontier Formation. **n–q,** *Prionocyclus germari* (Reuss, 1845). **n, o**, USNM 498458, a gracile form from USGS Mesozoic locality D9118, NW¼ NE¼ sec. 4, T. 33N., R. 81W., Natrona County, Wyoming, from the uppermost sandstone of the Wall Creek Member of the Frontier Formation. **p, q**, USNM 498483, from the same horizon and locality as **n, o**. USGS: United States Geological Survey; USNM: National Museum of Natural History, Washington D.C. All figures are × 1.

Table 1. The biostratigraphical sequence for the species included in the analysis and sample sizes.The asterisks denote species currently used as zonal indices in the Turonian sequence of the Western Interior USA.

Substage	Species	N
UPPER TURONIAN	*Prionocyclus germari**	24
	Prionocyclus novimexicanus	10
	Prionocyclus wyomingensis	6
	*Prionocyclus macombi**	16
MIDDLE TURONIAN	*Prionocyclus hyatti**	19
	*Collignoniceras praecox**	12
	*Collignoniceras woollgari**	26
LATE LOWER TURONIAN	*Cibolaites molenaari**	7

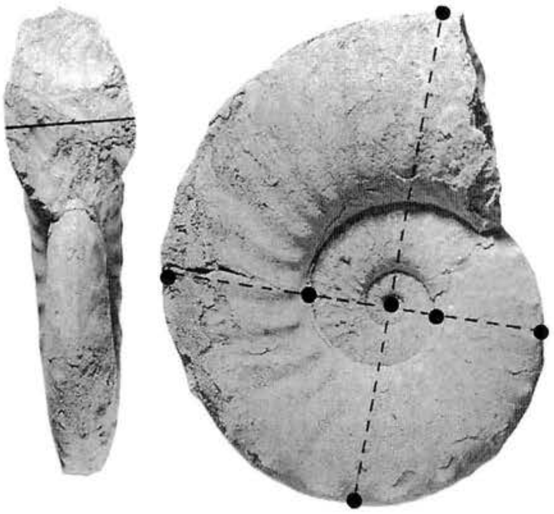

Figure 4. Locations of the points observed on the shells superimposed on a gracile specimen of *Prionocyclus macombi* Meek, 1876.

observed diameter and ribbing density, (2) principal coordinate analysis of the coordinate data, and (3) canonical variate analysis of the distance measures in "ordination mode". Unless otherwise stated, the measures were logarithmically transformed. The use of this transformation tends to stabilize the multivariate distribution of the data and to minimize the effects of size differences. Accounts of these procedures applied in like situations are to be found, for example, in Reyment (1991) and Reyment and Savazzi (1999), including examples of the computational procedures applied here and exemplified by ammonite data. Additionally, comparisons between species were made by standard procedures of generalized statistical distance analysis (for the larger samples), backed up by one-way univariate analysis of variance.

The links indicated by the superimposed minimum spanning tree on the plots are certainly not infallible statements of fact. For this reason, relationships between species have been further illuminated by means of pair-wise contrasts between latent vectors (principal components) of the logarithmic covariance matrices of the individual samples. Almost all multivariate "variability" in samples is located to the first latent root. For the most part, the smallest latent roots are almost zero and hence the associated latent vector may be considered as representing an almost invariant linear relationship between variables, as was suggested by Gower (1967). A somewhat similar approach to the study of variation in the shape of ammonite shells is outlined in Neige and Dommergues (1995).

Findings

Ordination of canonical variate means

A useful morphometric tool is often provided by the minimum spanning tree superimposed on the plot of the canonical variate means (Reyment and Savazzi, 1999). This gives the standard ordination of multivariate means a nearest-neighbour categorization. A partial analogy with stars in the firmament serves to illustrate this—stars that to the unaided eye seem to be close to each other can actually lie at extremely great distances from each other in the third dimension. The analyses accounted for in this section are designed to see how well morphometric and morphological characters can reproduce the inferred phylogeny of the lineage.

The first set of means was obtained from the canonical variate extraction in covariance space of the logarithms of the distances between seven sites and nine samples, augmented by directly measured maximum breadth of the shell and ribbing frequency counts in relation to directly measured diameter. How well then is the inferred evolutionary succession based on traditional procedure mirrored in the coiling and ornamental properties of the species of the lineage? In Figure 5, the canonical variate means are seen to divide into two branches. The sequence shown in Figure 5 indicates implied relationships with respect to form within the collignoniceratinid lineage. The minimum spanning tree for the means is superimposed on both plots. It is seen that *C. molenaari* is markedly distant from all other species, as is reflected in its being a monospecific genus established by traditional criteria. This observation accords with the supposition that the morphological passage from *Cibolaites* to *Collignoniceras* was abrupt ('punctuated' as it were). The ordinated linkage order goes from *C. w. woollgari* to *C. w. regulare* to *P. hyatti*, on one branch, and from *C. w. regulare* to *C. praecox* to *P. macombi* Meek, 1876, to *P. wyomingensis* Meek, 1876, on the second branch. However, we shall see in the following that in some relationships, *P. hyatti* tends to behave as though it were a *Collignoniceras,* a peculiarity it does not share with the other representatives of the genus included in our study, and which may reflect its middle-of-the-road evolutionary and morphological status between *Collignoniceras* and *Prionocyclus.*

A minimum spanning tree cannot be expected to provide a mirror image of an inferred phylogenetic sequence. What

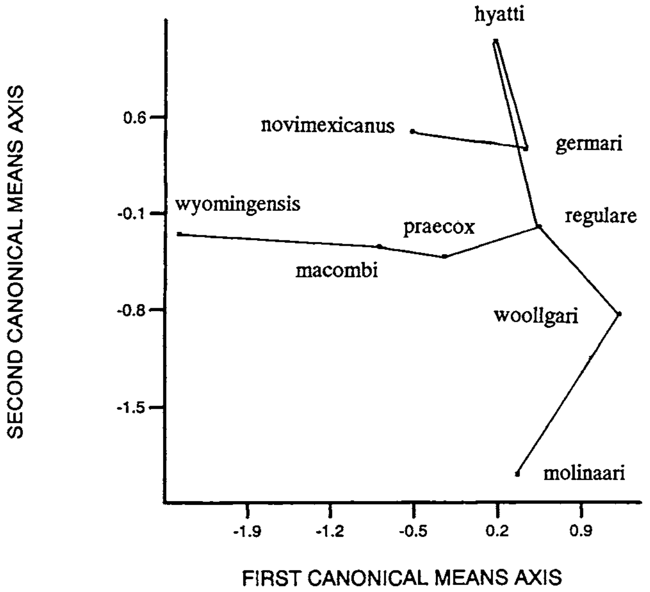

Figure 5. Minimum spanning tree superimposed on the plot of the first two canonical variate means for 7 distance measures (6 coordinate-based and maximum breadth of the conch), one frequency (ribbing) and 9 groups (the species and subspecies). Analysis made on the covariances of the logarithmically transformed data.

it is designed to seek is morphometric nearness relationships free of any obligatory time constraint. It is therefore interesting to be able to record that the multivariate analytically obtained results reflect rather well the phylogenetic indications based in part on biostratigraphical context. Many of the samples are small and it is encouraging that the results yielded by this analysis are so clearly manifested. In general, it seems clear that the observed stratigraphical ordering of the species is upheld, grosso modo, by the morphometric ordination. We note that, excluding the small samples (to wit, *woollgari woollgari, praecox, wyomingensis*), all generalized statistical distances between samples are highly significantly different.

In order to test the reliability of results obtained for such small samples, an alternative canonical variate model was used (Reyment and Savazzi, 1999). Here, all values were reduced to standard size by division of them by the maximum diameter of the shell. This standardization has a subsidiary effect, notably, that it transforms the data into compositions, and, consequently, the variables to parts. (N. B. it is fairly common practice in ammonite "biometry" to make scatter plots of ratios and then to look for meaningful constellations of points—statistically, this is not sound procedure.) This change in statistical properties necessitates a methodology appropriate to (constrained or "closed") simplex space (Aitchison, 1986). The multivariate analysis was therefore made on the log-ratio covariances (which involves the loss of one dimension due to the division by one of them). The ordination illustrated in Figure 6 differs in several respects from the foregoing (full-space) version in that *P. germari* (Reuss, 1845) is quite out of place in relation to the evolutionary succession. The morphoevolutionary passage from *C. molenaari* through the two subspecies of *Co. woollgari* is, however, maintained. We note that *P. hyatti* is now relegated to a branch of its own. Sidestepping the anomalously located *P. germari*, there is a branch that runs from *C. woollgari* s. l. through *C. praecox, P. macombi, P. wyomingensis* and *P. novimexicanus* (Marcou, 1858), the latter being registered as a branchoff from *P. macombi.* Apart from the anomalous location of *P. germari*, the result illustrated in Figure 6 is in many respects more closely compatible with the conventionally established succession of species than Figure 5. The main point to be heeded is, however, that the linkages are essentially the same in both representations, notably the *Cibolaites-Collignoniceras* sequence and the *C. praecox–P. macombi–P. wyomingensis* passage.

Results obtained by the principal component analysis of the distances

For the purposes of this part of the analysis, two latent vectors turned out to be of special interest. The latent root attached to the first latent vector is overwhelmingly large in relation to the other roots. The smallest latent root is virtually zero and hence may be considered to be an expression of an almost invariant linear relationship between the variables (Gower, 1967). Such an invariant relationship is of special taxonomic and hence phylogenetic interest because it represents a linear combination that is intrinsically bound to the form under consideration. The species studied in this connexion are: *C. woollgari woollgari* and subspecies *C. w. regulare, C. praecox, P. hyatti, P. novimexicanus, P. macombi* and *P. germari.* We wish to make it clear that the method of comparison of angles (Blackith and Reyment, 1971) is not a statistical technique, being rather a procedure appropriate to *ad hoc* data-analysis. Nonetheless, it has proven itself to be useful in many taxonometric studies.

The first principal component

This section is concerned with examining how morphometrically divergent succeeding species in the evolutionary succession are from each other. The angles between pairs of first latent vectors and sixth latent vectors, respectively, are listed in Table 2. The angles for the first latent vector for the comparisons of *C. molenaari* and *C. w. woollgari*, respectively *C. w. regulare* are almost identical (21.33°, respectively, 21.88°). This interesting result indicates not only that the ancestral species is separated by a strongly expressed morphological jump from its descendants, but also that the angle between ancestor and descendant subspecies is identical and that the two subspecies of *C. woollgari* are morphologically close to each other. This observation is supported by the small angle between these two subspecies, namely, 2.21°. The species next in the stratigraphical hierarchy is *C. praecox*, the angle between its first latent vector and both subspecies of *C. woollgari* being the same, to wit, 9.56°. The angle between *C. praecox* and *P. hyatti* is quite small, being 4.82°, whereas that between *P. hyatti* and *P. macombi* is 6.24°. The next passage from *P. macombi* to *P. wyomingensis* is connected with a small an-

Table 2. Angles between first and sixth latent vectors (covariance matrix of logarithmically transformed variables) for critical pairings.The asterisk denotes comparisons made on very small sample sizes.Co=*Collignoniceras*, Ci=*Cibolaites*, P.=*Prionocyclus.*

Comparison between	Angle for vector I	Angle for vector VI
*Ci. molenaari/Co. woollgari woollgari**	21.33	87.80
*Ci. molenaari/Co. woollgari regulare**	22.88	38.75
*Co. woollgari woollgari/Co. praecox**	9.56	81.53
Co. woollgari woollgari/Co.regulare	2.21	67.31
Co. woollgari regulare/Co. praecox	9.56	59.54
Co. woollgari regulare/P. hyatti	6.71	20.53
Co. w. regulare/P. germari	3.29	48.23
P. hyatti/P. germari	3.58	33.92
Co. praecox/P. hyatti	4.82	90.00
Co. praecox/P. macombi	5.45	54.06
*P. macombi/P. wyomingensis**	3.18	88.10
P. novimexicanus/P. germari	7.73	46.06

gular difference, notably, 3.18°. There is a notable leap in the angle between the first latent vector of *P. wyomingensis* and its descendant *P. novimexicanus,* namely 11.24°. The final link, from *P. novimexicanus* to *P. germari* is accompanied by an angular divergence of 7.73°. It is significant that the angular divergences between latent vectors of the *Prionocyclus* sequence are mostly of the same order of magnitude.

Comparisons made for the 'smallest' latent vectors are all noticeably greater. This could conceivably indicate that intrinsic morphometric specific differences are to be found in the (almost) invariant principal component, granted that the first latent vectors, which are all connected to more than 98% of the total variability, are so similar. The more interesting of these relationships are:

1. *Cibolaites molenaari-Collignoniceras woollgari* subspecies. The angles for vector I are here almost identical, as reported above. The values for vector VI differ strongly, with the angle between the vectors for *molenaari- C. woollgari woollgari* being almost a right angle, whereas that for the comparison with *regulare* is a relatively low 38.75°.

2. *Collignoniceras praecox-C. woollgari* subspecies. The angular differences for vector VI are large, being essentially greater for the comparison with *C. woollgari woollgari.* The angular differences for the comparisons between first latent vectors are small, and smallest for the latter subspecies.

3. *C. praecox-P. hyatti.* The result yielded here is noteworthy. The first latent vectors are almost collinear, which hardly accords with the linkage in Figure 6 yielded by the minimum spanning tree. However, the value for vector VI places these vectors exactly at right angles to each other. We are inclined to accept this result as indicating support for the view that the invariant latent vector of distances harbours taxonomically relevant information.

4. The plot in Figure 6 shows *C. w. regulare* and *P. germari* to be located near to each other, but the linkage sequence does not indicate these two taxa to be close. Comparison of the smallest latent vectors yields a relatively large angle, namely 48.23°.

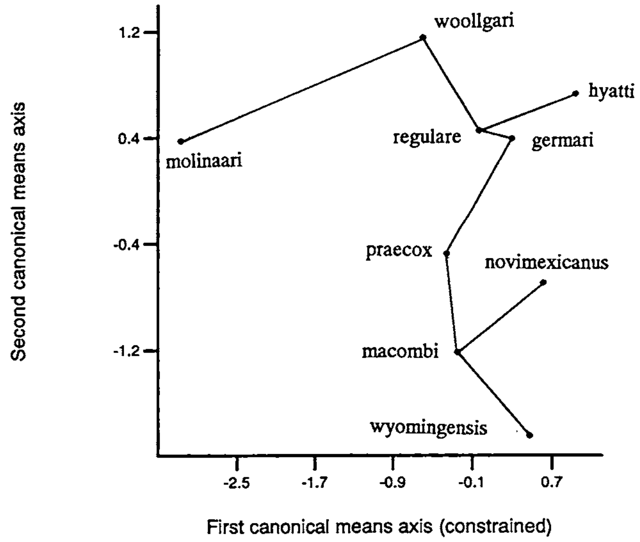

Figure 6. Minimum spanning tree superimposed on the plot of the first two canonical variate means for the same set of data as in Figure 5, but standardized with respect to size (hence in compositional mode). Analysis made on the log-ratio covariances (cf. Aitchison, 1986).

5. *C. w. regulare - P. hyatti.* The biostratigraphical scheme leads one to expect that *C. praecox* would be more like *P. hyatti* than *C. w. regulare,* considering that it has been put forward as the logical ancestor of the former, and this is indeed implied by the angle between the first latent vectors, being among the smallest of the entire set of values reported in Table 2 and, in effect, denoting collinearity. However, the angle between vector VI for these two taxa is by far the smallest of all and it seems that it is this relationship that is reflected in the pattern obtained for the minimum spanning tree (Figure 5).

6. Anomalously large angular differences occur for the pairings *macombi-wyomingensis* and *wyomingensis-novimexicanus,* probably due to the small sample sizes involved. We note that the sample size for *P. wyomingensis* is beneath the level for a resolvable covariance matrix (i.e. more variables than specimens).

Robust vs gracile shells

The routine taxonomic appraisal of the material (Kennedy, 1988) suggested that there are two classes of ornamental categories in the species of the genera considered here, to wit, robustly ornamented shells and finely ornamented shells (the gracile shell-type). These do not appear to be morphs of the kind described by Reyment and Kennedy (1998). Only three species occur in sufficient numbers to permit statistical appraisal of these categories- *P. hyatti, P. macombi* and *P. germari.* The same suite of methods as were used for the full set of observations were applied to the reduced set, noting that there are now 6 groups for 6 distance measures. In Figure 7, the canonical variate means for the two ornamental categories for these three species are plot-

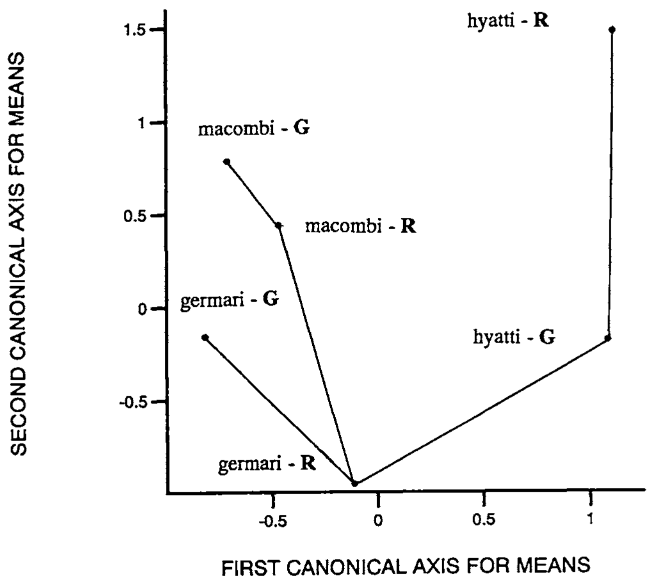

Figure 7. Minimum spanning tree superimposed on the canonical variate means for robust and gracile categories of three species of *Prionocyclus,* based on 6 distance measures and 6 groups (three "robust" classifications and 3 "fragile" classifications).

Table 3. Angles between first and sixth latent vectors for the robust/gracile data for critical pairings of three species of *Prionocyclus*

Comparison between	Angle for vector I	Angle for vector VI
germari G/germari R	1.99	41.07
macombi G/germari R	1.87	85.40
germari G/hyatti G	2.21	55.62
germari G/macombi G	3.35	7.91
hyatti G/macombi G	5.22	56.69

ted and linked by the superimposed minimum spanning tree. The most notable feature of the plot is that robust and gracile shell-types for each species, respectively, are linked, and that their means do not coincide, or almost coincide in location. Hence, differences in multivariate means of the subjectively identified categories are tangible, but not so great as to confuse taxonomic issues. In Figure 7, we show the plot of the individual points in the plane of the first two canonical variate axes (i.e. the canonical variate scores on the first two axes). The points for the six categories group naturally with gracile and robust forms for each species being nearest neighbours. Links between species are the union of robust *germari* to robust *macombi* and robust *germari* to gracile *hyatti.*

Comparisons of the first and sixth principal components lead to interesting consequences (Table 3). All angles between various comparisons of first latent vectors of the logarithmic covariance matrix are low. Note particularly the values for *germari* and *macombi,* 1.99° and 1.87° respectively. The angles for the sixth latent vectors are large and generally of the same order of magnitude as found for the complete data-set, but with one striking exception, notably, the comparison between gracile individuals of *germari* and *macombi,* 7.91°. This would seem to point to a close morphometrical relationship between the two species, which is possibly of taxonomical significance.

Doubtlessly, the gracile/robust subsamples yield a more structured multivariate statistical analysis than do the full samples. Granted that the taxonomic integrity of the subsamples was not infringed upon by the partitioning, it may be suggested that the qualitatively arrived at subdivision into two morphological types is largely justifiable.

The question now arises as to how morphometrically similar are the two categories *robust* and *gracile*? The material is not sufficiently comprehensive to allow categoric assertions. However, the data for *P. germari* may be taken to serve as a guideline. Robust *germari* links to robust *macombi,* thus implying a certain degree of ornamental homogeneity, whereas robust *germari* links to gracile *hyatti.* Figure 7 intimates also that *germari* and *macombi* are morphometrically more alike than either is with *hyatti.* This observation adds further evidence with respect to the transitional evolutionary status of *Prionocyclus hyatti,* which in many features displays morphometrical properties of *Collignoniceras* type.

Conclusions

The multivariate-morphometrical analysis of a sequence of Collignoniceratinae from the Turonian of the U. S. Western Interior has brought to light several features of general interest for the study of evolution in ammonite morphometry with respect to the property of coiling. This result is somewhat unexpected, granted that coiling in shell-bearing cephalopods is under the rigid constraint imposed by the biomechanism determining logarithmic growth. These are:

1. The species of *Collignoniceras* align in accordance with biostratigraphical observations, thus preserving generic integrity and evolutionary status. The passage from *Cibolaites* to *Collignoniceras* is abrupt, a saltation as it were.
2. The passage to *Prionocyclus* is slightly less well manifested in that there is a dichotomy in the relationship implied by the minimum spanning tree with *P.hyatti* occupying, jointly with respect to linkage (but naturally not time), an evolutionary position on a par with *C. praecox.* In this respect, the former species behaves in some cases as though it were a *Collignoniceras.* The dichotomous impression is further strengthened by the passage of *praecox* to *macombi* which in turn, links to *wyomingensis* (in agreement with the biostratigraphical inference—cf. Table 1).
3. The second branch in Figure 5 lets *hyatti* link directly to *germari* and *novimexicanus.* In Figure 6, *hyatti* is located on a separate branch. This result accords with the transitional status of this species, as indicated by the results of the present study.
4. The qualitative observations leading to the recognition of robust and gracile shell forms in all species can be upheld in part, as far as can be judged from those samples compris-

ing sufficient material for statistical calculations. Also here, the ambiguous evolutionary status of *P. hyatti* is manifested. The possible functional significance of the two shell types would seem to be worth detailed study, possibly in relation to foraging aspects (Reyment, 1988).

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A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis

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Abstract. The symbiosis (defined as a strict interspecific association) between bivalves and other organisms is examined. Microsymbiosis (i.e., symbiosis with microorganisms) is frequent among Recent bivalves, and has been proposed to explain the unusual characters of several fossil bivalves. However, a critical review of the morphological criteria used to infer microsymbiosis in fossil bivalves shows that their application is likely to result in a large number of false positive and false negative results. Symbiosis with macroscopic organisms (i.e., macrosymbiosis), on the other hand, has a better chance of being recognised correctly in fossils, although direct preservation of the associated organisms remains the only completely safe criterion. Recent and fossil instances of macrosymbiosis are reviewed, and new evidence is presented to clarify the adaptive significance of some of these associations.

Key words: Bivalvia, chemosymbiosis, commensalisms, functional morphology, Lingulidae, Mollusca, parasitism, photosymbiosis, Porifera, Scleractinia, symbiosis

Introduction

Symbiosis was originally defined as a strict, usually obligatory association of individuals belonging to two or more species (Bary, 1879). This definition does not imply that the association is mutually advantageous to the organisms involved. Only subsequently was the term used with the latter meaning. The present paper follows the original definition of symbiosis, since no other concise term is available to characterise an interspecific association without connotations of usefulness to the involved organisms. Use of the terms commensalism and parasitism, for instance, requires that the life habits and the advantages and/or disadvantages to the species involved are known.

For the purposes of this paper, two categories of symbiosis can be recognised among bivalves. The first involves microscopic endosymbionts living in a bivalve host. This category can be characterised as microsymbiosis. The second category involves macroscopic organisms associated with bivalves, and can be called macrosymbiosis. This paper concentrates on the latter category, but a discussion of microsymbiosis is useful as an introduction, because this subject has received considerable attention by palaeobiologists (see references below). In addition, this theme illustrates several of the problems that characterise the recognition of macrosymbiosis in the fossil record.

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Microsymbiosis

Photosymbiosis

Most of the literature on symbiosis in bivalves deals with microscopic endosymbionts hosted by bivalves. In particular, photosymbiotic zooxanthellae and the associated adaptations of the hosts have been studied in the Recent Tridacnidae (Yonge, 1936; Purchon, 1955; Stasek, 1961, and references therein) and Cardiidae (Kawaguti, 1950, 1968, 1983; Hartman and Pratt, 1976; Jacobs and Jones, 1989; Jones and Jacobs, 1992). The host bivalves show a range of cytological adaptations to the symbionts, as well as microstructural and macroscopic adaptations in shell morphology (e.g., see above references, and Seilacher, 1972, 1973, 1990).

Among these bivalves, the Tridacnidae build extremely large and thick shells thanks to photosymbiosis, and their ventral commissure (uppermost in the life position) is modified to maximise exposure of the mantle tissues to sunlight. In some species, sculpture on the external shell surface further increases the mantle area exposed to light (above references).

The cardiid *Corculum* has an antero-posteriorly flattened, semitransparent shell to optimise the exposure of the mantle to sunlight passing through the shell. The posterior shell slope possesses numerous semitransparent windows, which result from a peculiar type of shell pigmentation rather than from a specialised microstructure (Watson and Signor, 1986).

Other Recent bivalves are known to possess photosynthetic endosymbionts. Among them are the freshwater unionid *Anodonta* (Goetsch and Scheuring, 1926) and the trapeziid *Fluviolanatus subtorta* (Morton, 1982). The significance of these associations has not been studied in detail. Other bivalves are frequently infected by microscopic algae (e.g., the Recent pectinid *Placopecten magellanicus*; Naidu and South, 1970; Naidu, 1971). Although these can be characterised as instances of parasitism by the alga, they are interesting in that they constitute a possible evolutionary stepping-stone toward a mutually advantageous situation.

The adaptive significance of photosymbiosis is not uniform among bivalves. In the Tridacnidae, photosymbionts are an important food-source for the host, and they allow the construction of very large and heavy shells (above references). In all other studied instances, however, the bivalves are relatively small, and their shells thin or only moderately thick. In at least part of these cases, the spectrum of sunlight appears to be selectively filtered by the mantle tissues of the host in order to fine-tune the metabolic products of the photosymbionts (above references).

A few palaeontologists (e.g., Kriz, 1979; Yancey, 1982; Yancey and Boyd, 1983; Seilacher, 1990) have proposed photosymbiosis in a broad range of fossil bivalves, using morphological convergence with *Tridacna* and/or *Corculum* to support their theses. These fossil bivalves range in age from the Palaeozoic to the Caenozoic, belong to several superfamilies, and possess extremely large and/or thick shells, or antero-posteriorly flattened and presumably translucent *Corculum*-like shells.

The reliability of these morphologic criteria to infer photosymbiosis in fossil bivalves, however, is questionable. With the exception of *Corculum* and the Tridacnidae, Recent photosymbiotic bivalves show little or no morphological specialisation of the shell to photosymbiosis. In addition, while photosymbiosis in *Tridacna* is directly related to increased shell secretion and affects its stable-isotope composition (above references), such phenomena are absent in other Recent photosymbiotic bivalves (Jones and Jacobs, 1992). Nonetheless, stable-isotope analysis can be used in fossils when one desires to test whether shell secretion was aided by photosymbiosis, in a manner convergent to the Tridacnidae. Such an analysis led Jones, Williams and Spero (1988) to exclude photosymbiosis (or at least its involvement in shell secretion) in the Pliocene *Mercenaria "tridacnoides"*. This bivalve is a morph of *M. campechiensis*, and differs from the latter in a shell with a wavy or zigzag ventral commissure. Seilacher (1990) had earlier proposed photosymbiosis in this form, based on shell morphology.

Finally, one may test the reliability of the above morphologic criteria by applying them to Recent bivalves. There are several living bivalves which have at least one of the morphologic characters mentioned above. Among these are large and thick-shelled Ostreidae, Spondylidae, Pectinidae and Arcidae. However, none of these bivalves are known to host photosymbionts.

A flattened and translucent shell in an epifaunal bivalve is not a reliable indication of photosymbiosis, either. A very good example is the Recent anomiid (or placunid) *Placuna placenta*. This species possesses a laterally flattened, thin and very translucent shell (Yonge, 1977, regarded this species as the most flattened bivalve), and is a recliner on the surface of soft sediments in shallow water. Incidentally, the shell of this species was commonly used by the human population of the Philippines for the construction of house windows, before glass became broadly available. In a fossil species, such a shell might be regarded as an indication of photosymbiosis. However, *P. placenta* apparently hosts no photosymbionts. Although I am not aware of any explicit statement to this effect in the literature, the soft tissues were studied extensively by Yonge (1977), who most likely would not have failed to observe photosymbionts if they had been present.

Other Recent species of *Placuna*, like *P. ephippium*, are even larger than *P. placenta*. In *P. ephippium*, however, a reddish or brown pigmentation of the internal shell layer reduces shell translucency, and could be adaptive in sheltering the soft tissues from sunlight. Presumably, this pigmentation would be lost in fossilised material, leading an observer to conclude incorrectly that the shell was translucent like the one of *P. placenta*.

A further example is the Recent endolithic pectinid *Pedum*, which exposes a broad surface of ventral mantle tissues to the ambient light, in a fashion not unlike the Tridacnidae. The mantle tissues of *Pedum* are heavily pigmented and resemble the brightly-coloured ones of the Tridacnidae. However, this species hosts no photosymbionts (Savazzi, 1998). The broad expanse of exposed mantle tissues in *Pedum* does not appear to be adaptive by itself, and is rather a consequence of the mode of growth of this bivalve (see also below).

The presence of a prismatic or fibrous shell microstructure in some large fossil bivalves has been advocated in support of the photosymbiosis hypothesis, on the grounds that such a structure could conduct light well, working like a bundle of optical fibres (e.g., Seilacher, 1990). However, this type of light transmission has not been verified in Recent shell material. In particular, it is not known whether the sides of the prisms (which in living bivalves are interfaces between calcite and organic matrix) act as reflectors, or whether the refraction index at the periphery of the fibres is different from the one at its centre. Either condition is indispensable for the fibre to function as a light guide. The fibrous layers of some fossil bivalves do seem to act as optical fibres, but this could be misleading, since the organic shell matrix in this material was likely lost or altered during diagenesis, so that the prism sides are now calcite/air interfaces with optical properties different from the original ones. In addition, the optical properties of fibrous layers could be irrelevant, because sunlight may have been absorbed by additional shell layers with different microstructures (which, in addition, may have disappeared through selective diagenetic solution), or by a pigmented periostracum or organic shell matrix (see also above).

In conclusion, when performing this type of functional reconstruction, it should be remembered that morphologic criteria alone are unreliable, since flattened and/or thickened shells may have several adaptive explanations. Therefore, many instances of photosymbiosis inferred from large and thick shells, translucent shells and/or flattened shell geometries in fossils are likely false positives, while most of the true instances of photosymbiosis in fossils are likely to pass undetected.

A few fossil bivalves with highly specialised morphologic features may have been photosymbiotic. This is the case, for instance, of some rudists (Vogel, 1975; Seilacher, 1998, and references therein). Shell morphology indicates that, in several representatives of this group, a well-developed system of mantle diverticula occupied cavities within the shell, and in some cases was also exposed to the outer environment. However, it must be stressed that, based on palaeoenvironmental reconstructions, as well as on the lack of the above morphological features in most rudists, photosymbiosis must have been restricted to few representatives (see Jablonski, 1996).

Another candidate for symbiosis is represented by the Triassic wallowaconchids (Yancey and Stanley, 1999), in which the wing-like lateral carinae of the large *Corculum*-shaped shells were subdivided into partitions by radially-growing septa and, presumably, occupied at least in part by finger-like extensions of mantle tissues. This morphology is compatible with photosymbiosis (assuming the shell was translucent) as well as chemosymbiosis (assuming that the shell cavities housed chemosymbionts). However, septation of the carinae may be functional as a lightweight mechanical reinforcement, and a critical analysis of the symbiosis hypothesis shows that no septa, or at most a single septum separating the space within the carina from the rest of the shell cavity, are required for both photosymbiosis and chemosymbiosis to take place.

In these and comparable instances, photosymbiosis should be regarded as a reasonable hypothesis only if (1) the observed morphology satisfies all requirements for photosymbiosis, and (2) alternative functions for the observed morphology can be discarded. In the rudists with exposed mantle tissues, for instance, one should try first to eliminate the possibility that the mantle functioned as a ciliated carpet for the collection of food particles. In the case of rudists with shell diverticula, one should exclude alternative functions like brood pouches, cavities for the "farming" of chemosymbionts, structures for discouraging attacks by shell borers, energy-absorbing "bumpers" that would stop impact cracks from propagating to the inner shell layers, and lightweight shell structures like those observed in Recent soft-bottom oysters (e.g., cf. Chinzei, 1995). If these precautions are taken, unusual morphological adaptations like those of the rudists and wallowaconchids may be more reliable in inferring instances of photosymbiosis than general criteria based on large massive shells or antero-posterior shell flattening.

Chemosymbiosis

Chemosymbiosis appears to be more common than photosymbiosis among Recent bivalves. In addition to deep-water forms, like *Calyptogena*, which are associated with hydrothermal vents (e.g., Hashimoto *et al.*, 1989; Horikoshi, 1989) or hydrocarbon seeps (Childress *et al.*, 1986), several deep-infaunal bivalves from shallower water rely on bacterial chemosymbionts. These forms rely on bacteria that oxidise sulphide or methane (above references). In several cases (e.g., the Lucinidae, *Solemya*), the chemicals necessary to feed the symbionts are drawn to the mantle cavity by pumping pore water from deeper, anoxic layers of sediments (Felbeck *et al.*, 1983; Dando *et al.*, 1985, 1986; Reid and Brand, 1986). At least in some of these bivalves, elemental sulphur can be stored within the organism, possibly as a means to store energy (Vetter, 1985).

Solemya and *Lucinidae.—Solemya* builds Y-shaped burrows, and collects water from underlying, oxygen-poor and nutrient-rich sediment through the lowermost branch of its burrow (Stanley, 1970, pl. 3; Seilacher, 1990). Lucinids use the highly extensible foot to build a system of narrow canals with a comparable function (e.g., see Stanley , 1970, pls. 15–18).

Fossil burrows of *Solemya* (or bivalves with similar habits) have been described as ichnotaxa (Seilacher, 1990), and the burrows of lucinids are potentially preservable. These ichnostructures can be used to detect indirectly chemosymbiosis in these and similar bivalves. However, one must keep in mind that several burrowing bivalves build a single siphonal gallery directed downwards (e.g., see Stanley, 1970). This gallery leads the exhalant current deep into the sediment, and therefore cannot be related to chemosymbiosis.

Teredinidae. — Most Teredinidae are wood-borers and host symbiotic cellulose-digesting microorganisms in an enlarged gut (Turner, 1966, and references therein). Thus, these bivalves utilise the substrate as a food source. Chemosymbiosis is not directly reflected in morphological adaptations of the skeletal parts. However, the boreholes of the Teredinidae are uniquely long (up to 2 m) and slender (typically 5–20 mm in diameter), and can "snake" around obstacles and other boreholes, thus allowing these bivalves to utilise the substrate with a higher efficiency than any other wood-borers.

The Caenozoic to Recent teredinid *Kuphus* reaches very large sizes (over 1 m in length, with a diameter of up to 60 mm) and builds a thick calcareous tube. However, this form is not a wood borer but a secondary infaunal soft-bottom dweller (Savazzi, 1982a, 1999b). It is not known whether it utilises the substrate as a food source, and therefore its body volume, which is substantially larger than that of any wood-boring teredinid, remains unexplained.

Fresh-water bivalves.— The unionid *Pleiodon adami* from the African Pleistocene possesses a tube-like structure projecting from the antero-dorsal shell margin and parallel to the elongated hinge line. Seilacher (1990) suggested that this tube functioned like a pipette, in order to funnel pore water from underlying sediment layers into the mantle cavity. This would have avoided direct contact of the soft parts with the anoxic sediment. However, Savazzi and Yao (1992) found that other Recent and Pleistocene fresh-water bivalves of similar overall shell morphology (albeit possessing smaller or no anterior projections) burrow with the commissure plane conspicuously inclined, rather than subvertical as inferred by Seilacher for *P. adami*. In the latter species, a subvertical orientation would seem to be optimal for siphoning pore water from deep within sediment, while a substantially inclined orientation like the one observed in other fresh-water bivalves would place the antero-dorsal pipe in an unfavourable position. Thus, chemosymbiosis would have required *Pleiodon* to assume a shell orientation unusual for these bivalves. Specimens recorded in the life position could help to shed light on this species.

Conclusions

In spite of numerous attempts, the feasibility of detecting reliably photo- and chemosymbiosis in fossil bivalves appears questionable. All the criteria discussed above for inferring photosymbiosis in fossil bivalves are likely to produce a large number of false positive and/or false negative results. Probably, the fossilised burrows of a few chemosymbiotic bivalves are so far the only reliable evidence of such life habits. However, it cannot be excluded that careful analyses and new evidence may reveal probable instances of photo- and chemosymbiosis among fossil bivalves.

Macrosymbiosis

Macrosymbiosis in bivalves has received a lesser attention than microsymbiosis, and it is legitimate to ask whether it has a potential for being recognised in fossil material. Macrosymbiosis can be subdivided into two broad categories. The bivalve may be embedded in a larger organism or attached to its outer surface, or the reverse situation may occur.

Embedded macrosymbiotic bivalves

Lithophaginae.—Several Recent species of the mytilid *Lithophaga* occur constantly within living scleractinian corals (e.g., Kleemann, 1980). This type of association dates at least from the Palaeogene (Krumm and Jones, 1993). Although each of these *Lithophaga* species is recorded from several species of host coral, they are never found in dead corals (which are inhabited by other species of *Lithophaga*, exclusively living in this habitat). The siphonal opening of the borehole is exposed to the external environment, and there is no indication that the bivalve exploits the host as a source of food. Most likely, the living substrate provides better protection (living corals grow, while dead ones are subjected to erosion and/or fouling by encrusters) and possibly a lesser degree of competition by other borers (living corals may be less subjected to bioerosion than dead ones, and the endolithic fauna of living corals is, at any rate, less diverse than that of dead substrates).

Boring in living scleractinians requires the veliger to settle on the epithelium of the host and to pierce it to reach the skeleton. Alternatively, the veliger could be ingested by a coral polyp and subsequently pierce its coelenteron lining. In either case, this appears to require a behavioural and/or biochemical specialisation. It is not known whether *Lithophaga* boring in live coral constitutes a monophyletic or polyphyletic group. These species, at any rate, cannot be distinguished reliably from dead-substrate species on the basis of shell morphology. Several (possibly a majority) of live-coral *Lithophaga* possess a secondary calcareous coating on the outer shell surface. In several cases, this coating forms into structures (aristae, or sets of denticles) that protect the posterior shell commissure against predators (e.g., Savazzi, 1999b, and references therein). Most species of *Lithophaga* that bore in dead substrates are devoid of shell encrustations, but some dead-substrate species possess coatings fully comparable to those of live-coral borers (pers. obs.).

The boreholes of live-coral *Lithophaga* show distinctive morphological characters. The coral surface immediately surrounding the borehole opening is often depressed into a shallow funnel. This feature is absent in dead-substrate *Lithophaga*. In addition, growth of the coral forces the bivalve to move backwards through the substrate, in order to remain close to the external environment. This, in turn, is required by the relatively inefficient filibranch gills of these bivalves (Carter, 1978). The backwards-boring process causes the bivalve to vacate the anterior region of the borehole. This results in a long anterior extension of the borehole, partly filled with meniscus-shaped calcareous septa and/or loose calcareous deposits (Figure 5H). In Quaternary deposits along the coast of Hilotongan Island, the Philippines, the writer observed weathered sections of large coral boulders containing *Lithophaga* backward-boring tracks reaching approximately 1 m in length. Assuming a rate of backward-boring equal to or higher than that of forward-boring (because of the presence of the siphonal opening, backward-boring necessitates the removal of a smaller volume of substrate per unit of length than forward-boring), the observed length of boring tracks is consistent with observations on the Recent rock-boring species *L. lithophaga* by Kleemann (1973, and references therein), who reported a boring rate in limestone of up to 12.9 mm per year and a life span of up to about 80 years.

Lithophaga lessepsiana is a small Recent species that bores either in living reef corals or in solitary free-living scleractinians of the genus *Heteropsammia* (Arnaud and Thomassin, 1976; Kleemann, 1980). *Heteropsammia*, in turn, is symbiotic with a sipunculid housed in a spirally coiled cavity in the basis of the coral. *L. lessepsiana* bores within the basis of *Heteropsammia*, and grows to a shell length comparable to the coral diameter, probably causing the eventual death of the coral (Arnaud and Thomassin, 1976). When boring in *Heteropsammia, L. lessepsiana* lies with the ventral commissure uppermost (Arnaud and Thomassin, 1976). This species is entirely or almost entirely devoid of secondary calcareous deposits of the external shell surface.

The Recent mytilid *Fungiacava* went one step further and evolved into an endoparasite of fungiid corals (Goreau *et al.*, 1976, and references therein). The siphonal opening of this small form communicates with the coelenteron of the host, from which the bivalve draws its food. *Fungiacava* follows the growth of the host by migrating within its borehole to remain near the coelenteron. Like *L. lessepsiana*, it lies with the ventral commissure uppermost. This habit is recognisable in fossils, because of the placement of the siphonal opening of the borehole in a region of the coral skeleton covered by a considerable thickness of soft tissues. In fact, boreholes of *Fungiacava* were described in

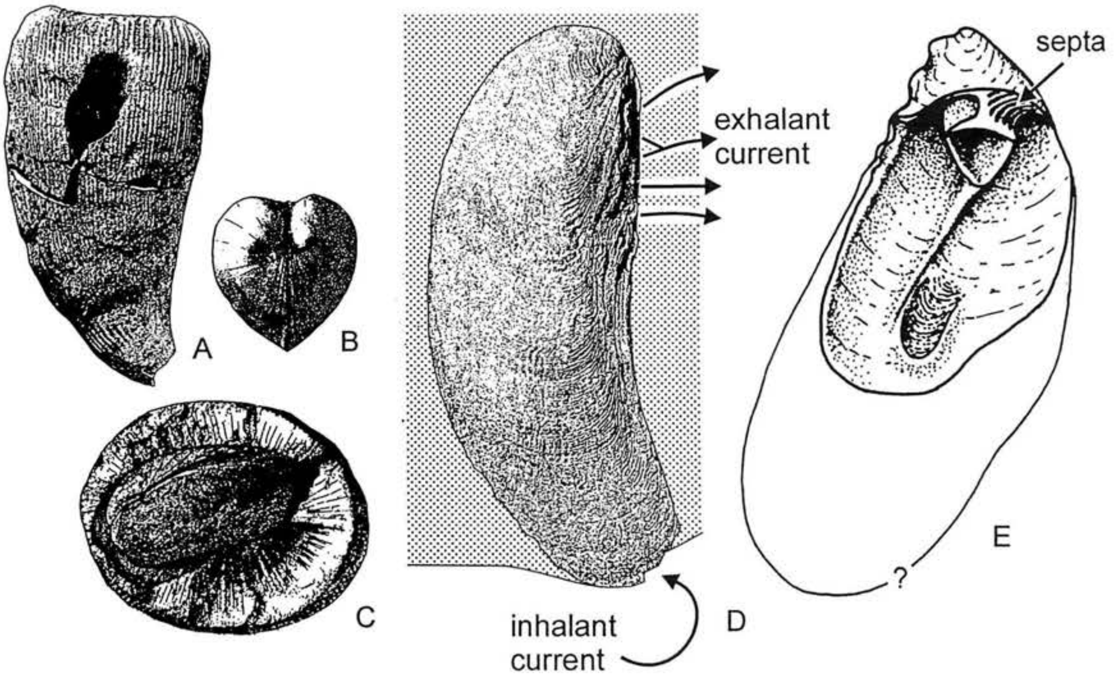

Figure 1. **A–C**. *Botula hortensis* (Lamarck) symbiotic in *Pattalophyllia* sp., Upper Eocene, Possagno, Italy, (Geologisch-Paläontologisches Institut, Tübingen, Germany, GPIT 1571/2–4). Host coral with siphonal opening of borehole (**A**), anterior view of shell (**B**) and shell in place within the borehole (**C**). Shell length is 19 mm. **D**. Schematic drawing of *Vulsella vulsella* (Linnaeus) embedded in host sponge, Recent, Cebu Island, the Philippines. The surface of the sponge is at the bottom. Shell length is 4 mm. **E**. *Stefaniniella colosii* Tavani, Cretaceous, Somalia (modified from Tavani, 1941). Height of the preserved shell portion is 85 mm. The extent of the original shell outline (indicated with a question mark) is reconstructed by analogy with Recent *Vulsella* and other malleids.

Pleistocene fungiids (Goreau *et al.*, 1976).

Botula.—The Eocene mytilid *Botula hortensis* (Figure 1A-C) was a borer obligatorily associated with living solitary corals (Savazzi, 1982b). Unlike other boring bivalves (cf. Savazzi, 1999b, and therein), *B. hortensis* did not secrete a lining onto the walls of the borehole. Instead, the coral host reacted to the presence of the borer by sealing the spaces between adjacent septa with a secondary calcareous secretion in the region surrounding the borehole. This reaction by the host enables one to detect that the coral was alive at the time it was bored. The borehole of *B. hortensis* opens on the side of the coral theca (Figure 1A).

The corals inhabited by *B. hortensis* were soft-bottom forms attached to a substrate only in their juvenile phase and probably capable of active righting. Their theca is horn-shaped, rather than flattened like fungiids. *B. hortensis* had a life orientation with the ventral commissure uppermost (like *Lithophaga* in soft-bottom corals; see above).

Although morphologically similar to other species of *Botula*, *B. hortensis* differs in behaviour and autecology. Recent *Botula* are mechanical borers in soft rocks and packed mud, while *B. hortensis* appears to be a chemical borer, because its shell is thin, has no specialised sculpture, and yet displays no surface wear (Savazzi, 1982b, 1999b).

It is difficult to imagine an evolutionary pathway leading from typical *Botula* to *B. hortensis*. Therefore, it is legitimate to suspect that the morphological similarity of this species with *Botula* is due to convergence rather than phylogenetic affinity (i.e., that *B. hortensis* is not a true *Botula*), or alternatively, that the life habits of *Botula* in the past were substantially more varied than those of Recent species.

Gastrochaenidae.— This family contains rock and dead-coral borers, as well as several taxa that evolved secondarily into tube dwellers in soft sediments (Carter, 1978, Savazzi, 1982a, 1999b; Morton, 1983). The boring representatives secrete a calcareous lining onto the inner walls of the borehole, and can extend this lining into a chimney-like projection when threatened by the overgrowth of encrusting organisms. The lining is also functional in protecting the bivalve when it becomes partly exposed. This lining became a stepping-stone to the evolution of the tube-dwelling habit, in which the bivalves are encased in a calcareous envelope, or crypt (Savazzi, 1982a).

Freneix and Roman (1979) illustrated Tertiary echinoids containing the calcareous linings of gastrochaenids boreholes, and interpreted this as an instance of parasitism by the bivalves. However, an analysis of this instance shows that the echinoids most likely were dead at the time of boring, and that the bivalves utilised the test as a substrate. In fact, none of these echinoids visibly reacted to boring by the bivalves, which often passed through the test and built calcareous canopies on both its internal and external surfaces. This lack of a reaction is highly unlikely in a living echinoid, since its test is a porous dermaskeleton containing abundant living tissues. Savazzi (1982a, fig. 3E) il-

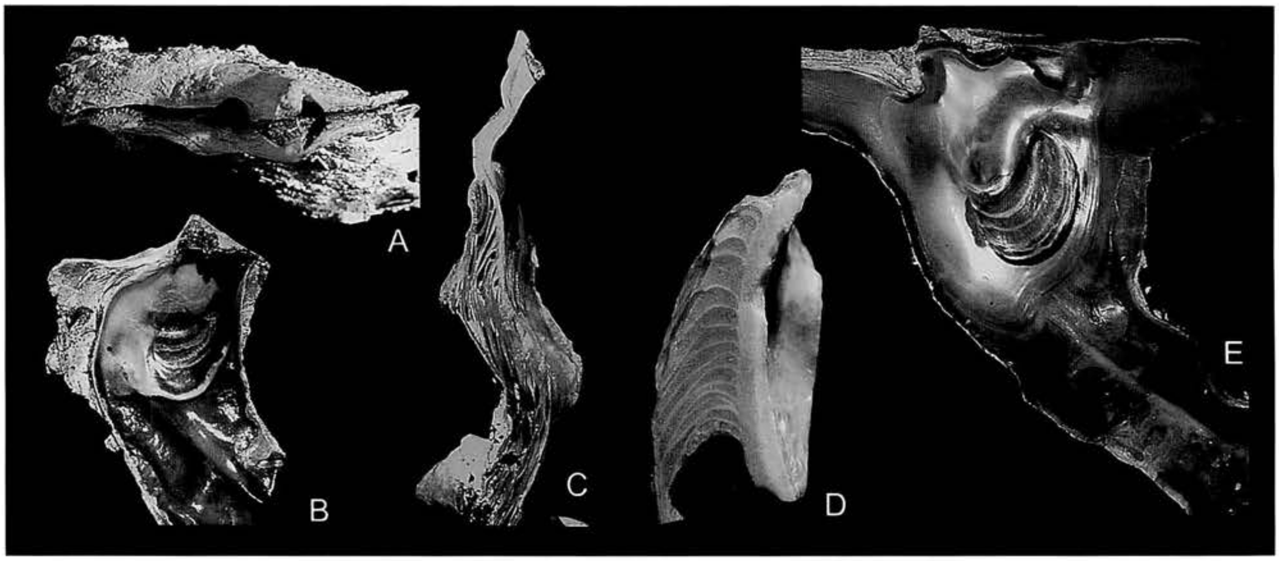

Figure 2. **A–B**. *Malleus anatinus* (Gmelin), Recent, Cebu Island, the Philippines. Dorsal view with byssal gape (**A**, × 1.2) and interior of dorsal portion of right valve (**B**, × 0.7). **C, E**. *Malleus malleus* (Linnaeus), Recent, Cebu Island, the Philippines, × 1. Interior of right valve of subadult specimen, not yet showing the secondary shrinkage of mantle tissues (see the text for details). **D**. Unidentified malleid, Middle Eocene, Verona, Italy, × 4.

lustrated a comparable instance of a gastrochaenid boring in the test of a Recent sand dollar (also dead at the time of boring), and building calcareous canopies on both sides of the thin echinoid test (in the illustrated specimen, the test was subsequently destroyed by erosion, leaving an isolated crypt).

Malleidae.—Typical malleids are epibyssate forms. They are characterised by a monovincular resilium, a byssal notch located close to the umbones (Figure 2A), and in several genera by projections of the shell that function as a stabilising surface in connection with an epibyssate or reclining habit (e.g., Figure 2E; Seilacher, 1984). Yonge (1986) described *Malleus* as a semi-infaunal orthothetic form, but the writer's field observations on living *Malleus* in the Philippines confirm Seilacher's interpretation of this genus as an epifaunal recliner. In malleids, the organism often displays a determinate growth pattern, in which the mantle first grows to the full extent of the shell perimeter in order to build the projections along the edge of the shell, and subsequently shrinks to a substantially smaller area of the inner shell surfaces, leaving behind growth lines on the abandoned inner shell surfaces that allow one to detect the stages of this growth process (leftmost region of Figure 2B).

The genus *Vulsella* (Figures 1D, 3F–N) is a malleid endosymbiont in soft sponges (e.g., see Reid and Porteous, 1978, and references therein). The shell is completely embedded in the sponge tissues, and only a short length of the ventral commissure communicates with the external environment (Figures 1D, 3L–M). This genus does not display the shrinking of the mantle tissues in the adult stage displayed by other malleids. The proportions of the shell and its outline are very variable, as a result of irregular growth of the host sponge. Shell height can reach about 100 mm in the largest specimens, but is usually limited to 30–40 mm.

As verified in living specimens of *V. vulsella* from Cebu Island, the Philippines, the region of exposed commissure is the site of an inhalant water current (Figure 1D). There is, however, no detectable exhalant current along the exposed commissure or the surrounding sponge surface. By letting the bivalve inhale pigment dissolved in sea water, it was found that the sponge tissues facing the posterior commissure of the bivalve (which is deeply embedded within the sponge) absorbed the pigment. Further observation of the sponge in this region showed that it contains numerous openings connecting the postero-dorsal commissure of the bivalve with the canal system of the host. Therefore, *Vulsella* exploits the host sponge as a sink for its exhalant current, and probably takes advantage of the passive flow induced within the sponge canal system by surrounding water currents, in a manner closely similar to that described by Savazzi (1996, 1999a) for the gastropod *Siliquaria*. This flow may reduce the energy expended by the bivalve to strain water. The sponge may gain from the symbiotic association in that the bivalve shells provide a rigid internal framework that allows the sponge to extend in height (Reid and Porteous, 1978). Empty shells of *Vulsella* completely embedded within the sponge are common.

The outer surface of the shell in *Vulsella* bears a sculpture of sharp frills directed obliquely outward (Figure 3N). This sculpture is likely adaptive in greatly increasing the adhesion of the shell to the tissues of the host. It is delicate and always worn away in dead shells found loose on the bottom. Therefore, it is unlikely to be preserved in fossils. The sculpture is prominent in the juvenile stage, and becomes irregular and subdued in the adult stage. This is consistent with the above functional hypothesis, since juveniles are

Figure 3. **A-E**. Unidentified malleid, Middle Eocene, Verona, Italy. Resilifer and double buttress (**A-C**, × 2; **C** is viewed from an oblique left-ventral direction), byssal notch (indicated by arrow, **D**, × 3) and bivalved specimen lacking the hinge region (**E**, × 0.7). **F-N**. *Vulsella vulsella* (Linnaeus), Recent, Cebu Island, the Philippines. Interior and exterior of right valve of juvenile (**F-G**, × 2.5), exterior of adult (**H-J**, × 1.3), interior of hinge region of right valve (**K**, × 2.5), ventral commissure of living specimens in host sponge, probably *Ricinia* sp. (**L-M**, × 2) and detail of sculpture on exterior of juvenile shell (**N**, × 10).

less deeply embedded within the sponge, and more likely to be broken loose.

The biomechanics and geometry of the shell in *Vulsella* suggest criteria applicable to detect comparable life habits in fossil forms. The resilium of *Vulsella* is unusually large (Figure 3F, K), and grows proportionally larger with age. By comparison, much larger epifaunal forms like *Malleus* have proportionately smaller resilia (Figure 2B, E), in spite of their much thicker and heavier shells. In *Vulsella*, the large resilium is probably related to the fact that the valves must open against the pressure exerted on the shell by the tissues of the host sponge. As a consequence, the resilium in adult *Vulsella* is inserted onto a well developed and thick resilifer, which displaces the ligament ventrally to the hinge line (Figure 3K). The resilifer is almost absent in juveniles (Figure 3F), and the resilium at this stage is inserted close to the hinge line. The shell wall near the resilifer in adults is strengthened against flexing by a buttress deposited onto the inner shell surface (Figure 3K). This buttress, which is absent in juveniles, is located near the anterior side rather than in a medial position.

The buttress, together with the strong resilium and a somewhat thickened dorsal shell region, stiffens this part of the shell. As a result, the ventral commissure closes thanks to the thinner central region of the shell flexing under the contraction of the adductor muscle. This results in closure of the exposed ventral shell gape. A permanent gape remains along the anterior shell margin (which is embedded within the sponge, and stiffened by the nearby buttress). Reid and Porteous (1978) reported the presence also of a posterior gape, but this feature is absent or reduced in the material available to the writer, especially when the valves are adducted and the ventral gape closed. Thus, it appears that the main function of the resilium is to open the valves progressively during growth, in order to allow further shell growth along the ventral margin.

Most fossil malleids were undoubtedly epibyssate or recliners (see Hertlein and Cox, 1969; Seilacher, 1984). A few forms, however, are similar in general shell morphology to *Vulsella*. In particular, the African Cretaceous *Stefaniniella* (Figure 1E) is comparable in general shape, but has a zigzag postero-dorsal commissure and a larger size (Tavani, 1941, and references therein; Hertlein and Cox, 1969). The inner shell surface of this genus is characterised by a large resilifer, a roughly medial buttress connecting the resilifer to the shell, and a series of septa spanning the space between resilifer and shell surface in the posterior region (Figure 1E). Tavani (1941) regarded such a chambered structure as absent in the Malleidae, and placed this genus in the separate family Stefaniniellidae, but subsequent authors placed it in the Malleidae.

An imperfectly known, unidentified form from the Middle Eocene of Italy (Figures 2D, 3A–E) is similar to *Stefaniniella* in its relatively large size (estimated to about 150 mm in shell height), large resilifer, and septa connecting the resilifer to the shell (Figure 2D). However, its posterior commissure is apparently straight like *Vulsella*, and unlike *Vulsella* and *Stefaniniella* it possesses two buttresses (Figure 3A–C). The buttresses have a massive internal structure, and surround the central septate region on either side. Unlike both *Vulsella* and *Stefaniniella*, this form also displays what appears to be a well developed byssal notch (arrow in Figure 3D). Unlike in epibyssate malleids (cf. Figure 2A), this notch continues in the ventral direction into an extensive permanent anterior gape, which does not agree well with an epibyssate habit in shallow water. It is possible, instead, that this permanent gape was embedded within a sponge, like *Vulsella*. It may be noted that also in *Vulsella* the anterior gape appears to be delimited dorsally by a vestigial byssal gape. A comparable habit is also possible in *Stefaniniella*, although it is difficult to decide whether this genus possessed a permanent commissural gape. By analogy with *Vulsella*, the exhalant current in *Stefaniniella* would have exited in correspondence with the zigzag portion of commissure. The distinctive zigzag folding of this region of commissure could be an adaptation for increasing stiffness of this shell region.

The Eocene malleid *Euphenax* possesses a lightweight shell with a cavernous outer layer and a chambered inner layer (Hertlein and Cox, 1969). Therefore, a septate or vacuolar structure is not unique to *Stefaniniella* and related genera. Such a structure is also found, for instance, in *Malleus* (Figure 2C). The shell of *Malleus* and related forms displays several constructional elements shared by *Vulsella*, *Stefaniniella* and the Eocene form discussed above. However, these elements are placed in different positions, and their mechanical effects are therefore different. For instance, the adductor muscle in *Malleus* is located close to the hinge (Figure 2B, E), the vacuolar structure is distributed along the height of the shell with the exception of its dorsal region (Figure 2C), and a buttress-like dorso-ventral ridge stiffens the inner side of the shell, but is located ventrally to the adductor muscle, rather than immediately below the resilium (Figure 2B, E). A true resilifer differentiated from the hinge line is also absent in *Malleus*. All these characters are related to an epifaunal life habit, in which the shell is stiff and opens by flexing the resilium, which does not need to be overly large and therefore allows a placement of the adductor muscle not far from the hinge. Finally, the byssal gape in *Malleus* and related forms is well developed, but clearly delimited from the rest of the commissure (Figure 2A), which shows no other permanent gapes.

Pteriidae. — *Crenatula modiolaris* is a Recent pteriid byssally attached to soft sponges and covered by a thin layer of sponge tissues (Figure 4A–F). The writer observed living *C. modiolaris* in Bantayan Island, the Philippines, and preserved specimens of *C. nakayamai* in museum collections. Unlike *Vulsella*, this species is not deeply embedded, and its shell morphology is therefore relatively unspecialised with respect to epibyssate pteriids. Unlike in epibyssate forms, its shell is often irregular and visibly distorted. Epibyssate forms can be of variable morphology, as a result of different current regimes, but their shell geometry is rarely distorted. This difference is potentially useful in detecting similar habits in fossils. Crevice-dwelling pteriids are also irregular, but in a different manner. For instance, in the latter it is often possible to recognise in the shell morphology irregularities of the substrate to which the shell had to conform. In *Crenatula*, instead, the contours and surfaces are smooth and often characteristically bulging outwards in

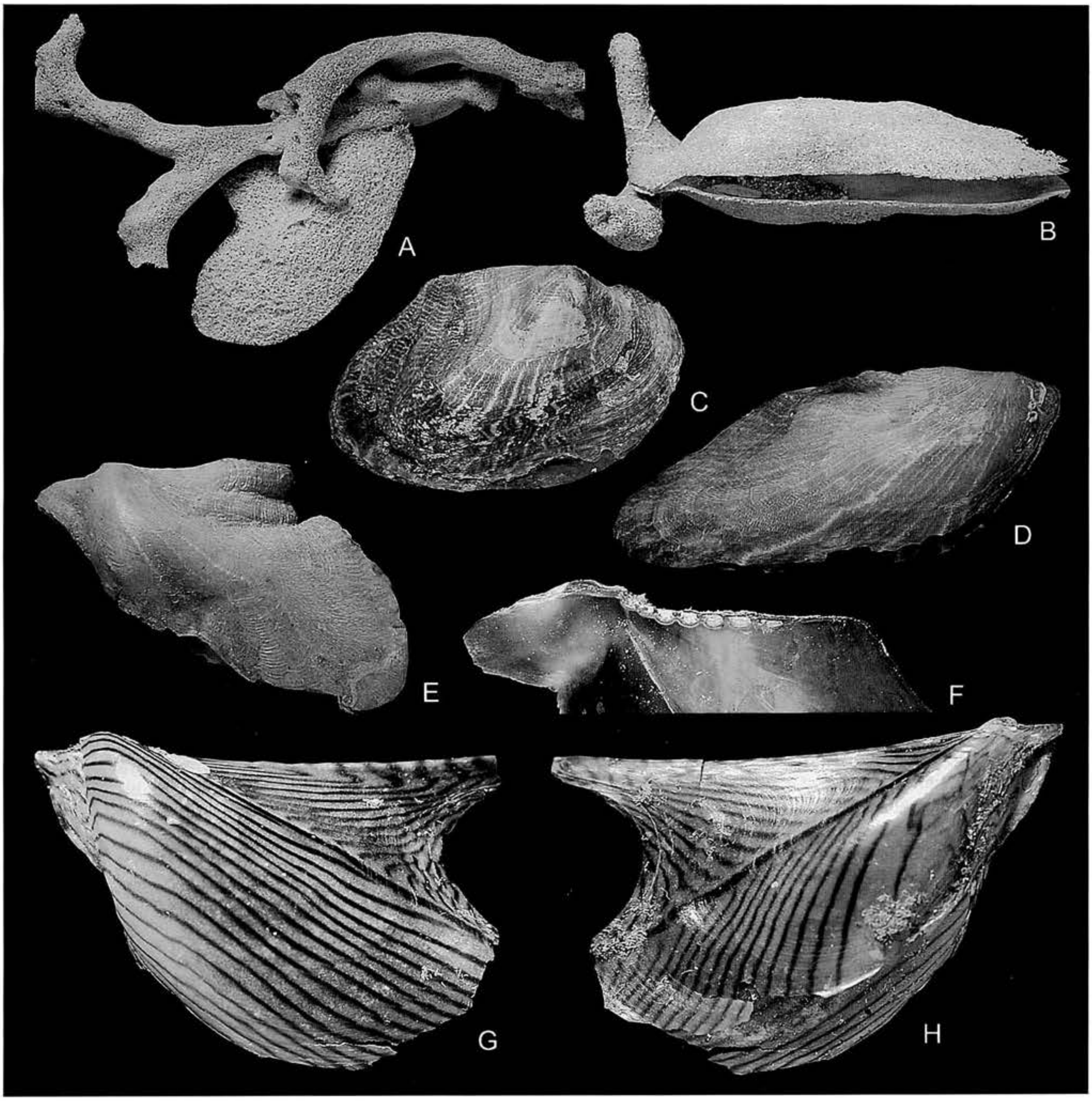

Figure 4. **A–F.** *Crenatula nakayamai* Kuroda & Habe, Recent, Amami-Oshima Island, Kagoshima Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Dried specimens embedded in host sponge, probably *Haliclona* sp. (**A**, approximately × 1.2, **B**, approximately × 2), isolated shells (**C–E**, approximately × 1.6), and interior of right valve showing the curved hinge line (**F**, × 1.8). **G–H.** *Pterelectroma zebra* (Reeve), Recent, Nagai, Kanagawa Prefecture, Japan (Sakurai collection, National Science Museum, Tokyo, Japan). Left (**G**, × 5) and right (**H**, × 5) valve of the same specimen.

a balloon-like fashion (see especially Figure 4E). This irregularity may extend to the ligamental area, which may be bent (Figure 4F). In the long run, this situation is incompatible with further growth, because a bent hinge line prevents the valves from opening gradually during growth, in order to allow the ventral margins to be extended. The thin shell flexes under the contraction of the adductor muscles, and this allows the bivalves to close the ventral commissure even though the hinge line is curved.

The coating of sponge tissues in *Crenatula* may deter some predators. However, Reid and Porteous (1978) reported that *Octopus* often predates on *C. modiolaris*. There seems to be no possibility for the exhalant current of the bivalve to be led into the canal system of the sponge, since the whole commissure of the bivalve is exposed, except for the hinge and byssal gape. It is possible that the encrusting sponge is effective as visual camouflage against other predators, since the shell colour of *C. modiolaris* always matches that of the associated sponge, which ranges from light brown to almost black (pers. obs. in Bantayan Island, the Philippines). There is no apparent advantage for the host sponge.

Several pteriids are epibyssate on soft corals or other organisms. *Pterelectroma zebra* possesses an unusual colour pattern (Figure 4G-H) that mimics the hydrozoan substrate. This pattern appears to constitute a visual camouflage (see also Seilacher, 1972, fig. 7G, 10). The fact that this pattern is different on opposite valves (Figure 4G-H) contributes to this function, since an observer sees the pattern on both valves simultaneously through the highly translucent shell. This further hides the shell outline and makes it merge visually against the hydrozoan substrate. Since this specialised colour pattern would not be effective against a different substrate (e.g., rock), it is of potential usefulness as an indicator of symbiotic habits.

Ostreidae.—The Recent *Ostrea permollis* is embedded within soft sponges, in a manner comparable to *Vulsella* (Forbes, 1964, 1966). This bivalve is smaller than *Vulsella* (up to about 25 mm in shell length), and its mantle margins and conchiolin are bright yellow like the surrounding sponge tissues. The shell displays no attachment scar. *O. permollis* grows normally when raised in the laboratory in the absence of a host sponge, and the stomach contents in field-collected specimens consist of phytoplankton (above references). A large sponge may contain hundreds of symbiotic oysters, often stacked parallel to each other in especially crowded areas. The inhalant region of commissure is exposed, while the exhalant current is funnelled into canals of the sponge interior.

The adaptive significance of this association is probably protection from predators for the oyster, and, for the sponge, achieving a stiffening structure without spending energy for its construction (Forbes, 1964, 1966). However, the above authors reported that empty oyster shells, although frequent in the outermost layers of sponge tissues, are absent from its centre. The oyster may additionally profit from passively induced flow within the canal system of the sponge. Therefore, this case can be regarded as convergent with *Vulsella*.

Pectinidae.—The Recent pectinid *Pedum* (Figure 5A-E) is a nestler in living scleractinian corals (Yonge, 1967; Savazzi, 1998). It settles on the surface of the coral, and it becomes gradually embedded by growth of the host (Figure 5A, B). This genus does not abrade the substrate (except to a very limited extent, see Savazzi, 1998), and both valves are almost flat as viewed in section along the dorso-ventral axis. This is a consequence of the lack of substrate abrasion, because growth of a convex, coiled shell requires the umbones to rotate and move away from each other, thus increasing shell inflation in this area (see Savazzi, 1987). *Pedum* displays also a very limited amount of ontogenetic migration of the shell toward the surface of the substrate (see the space vacated at the bottom of the coral cavity in Figure 5B). These constraints are reflected in a number of peculiar morphological adaptations, such as the anterior auricle of the right valve being located inside the earlier shell cavity and exposed by secondary resorption of the shell wall (Figure 5C). An inequivalve condition is a further consequence of this mode of growth (Figure 5D, E).

The inability to remove any substantial volume of substrate forces the juvenile to gape broadly (Figure 5A), in order to maintain a cavity in the substrate large enough to accommodate the adult hinge region, which, in turn, becomes laterally asymmetric in order to allow the smaller left valve to move ventrally during growth, thus reducing the space needed to allow valve opening. In conclusion, the shell geometry and growth process of this genus are explained by its symbiosis with scleractinian coral and by its inability to abrade the substrate. A more detailed analysis of the biomechanics and growth of *Pedum* was provided by Savazzi (1998).

The Recent *Chlamys acroporicola* (Figure 5F, G) nestles among the branches of living ramose scleractinians like *Acropora*. Its shell is often slightly deformed in the adult, because of space constraints. Such deformations, together with the lack of attachment scars (this species is byssally attached) would be recognisable in fossils. However, in this instance there appears to be no indirect way to infer the association of this species with living coral. This habit may explain how the life habit of *Pedum* evolved (Savazzi, 1998).

Carditidae and other nestlers.—A few other Recent bivalves, like the carditid *Beguina semiorbiculata*, are facultative or obligatory nestlers or borers in scleractinian corals, but their morphology does not seem to be distinctive of these life habits. Several of these forms have been discussed by Savazzi (1999b).

Other embedded bivalves.—Several Recent leptonaceans and galeommataceans live within the digestive tract of echinoderms (especially holothurians) and, less frequently, inside the body of other invertebrates (e.g., Voeltzkow, 1891; Malard, 1903; Anthony, 1916; Bourne, 1906). The shell of these bivalves normally shows no morphological adaptation. *Cycladoconcha*, an endoparasite in holothurians, is an exception. The central portion of its shell bears a large hole as a result of secondary resorption (Spärck, 1931), a character potentially recognisable in fossils.

Ectosymbiotic bivalves

Unionacea.—The glochidium of several Recent freshwater Unionacea is an ectoparasite on fishes. Each valve bears a sharp spear along its ventral margin. The tips of these spears converge toward each other, and allow the valves to grip the host like the tips of tweezers when the adductor muscles are contracted (Kat, 1984). The principal adaptive significance of this adaptation is likely that it provides a means for the molluscs to spread upstream along rivers and streams, which would be problematic for bivalves with a planktonic larval stage and a scarcely mobile adult stage. The fossilisation potential of these larval stages is extremely low, so it is not feasible to ascertain directly when

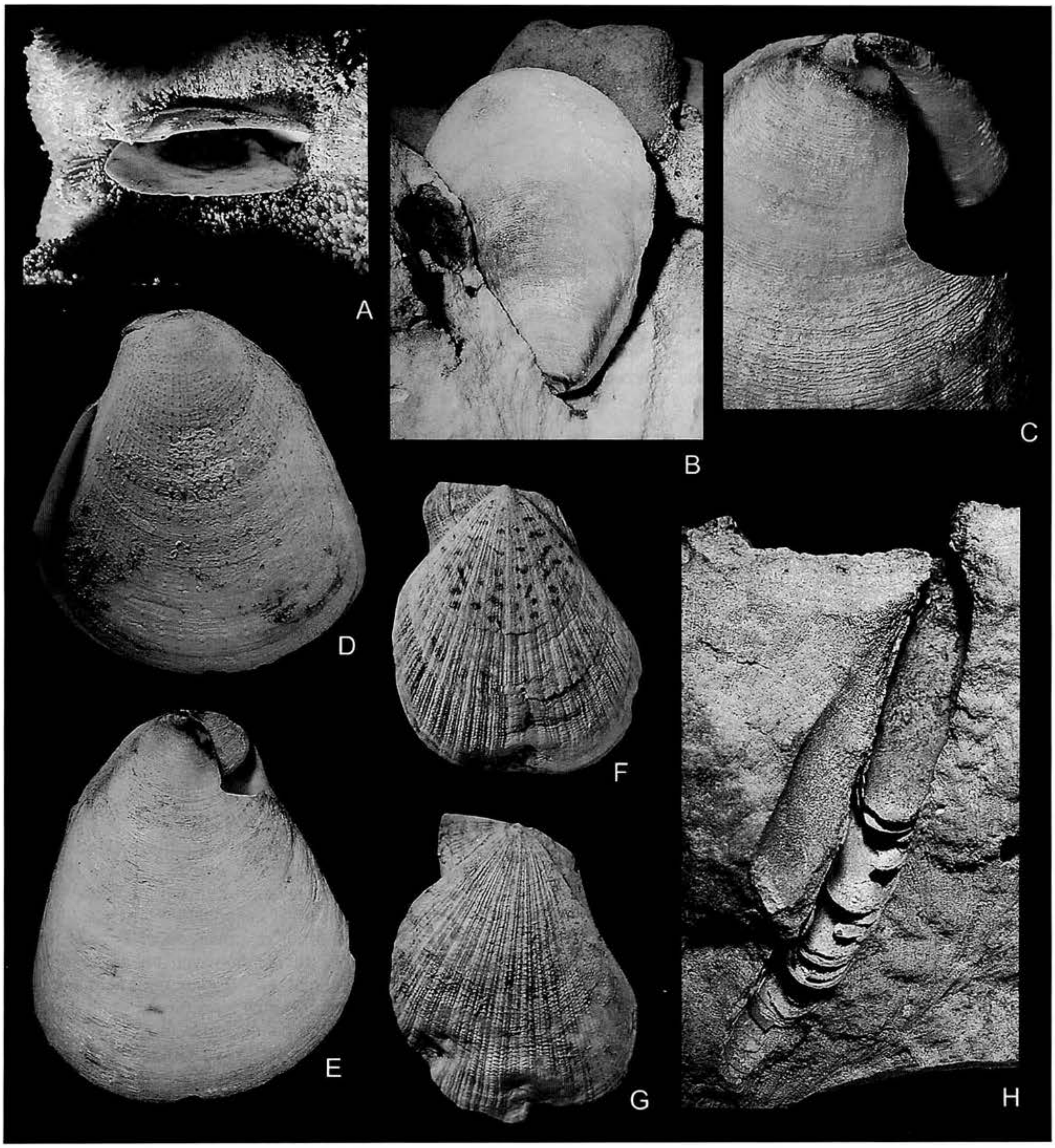

Figure 5. **A**–**E**. *Pedum spondyloideum* (Gmelin), Recent, Cebu Island, the Philippines. Juvenile (**A**, × 2) and adult (**B**, × 1.5) nestling in coral, detail of auricle of right valve (**C**, × 3), left and right sides of adult (**D**–**E**, × 1.4). **F**–**G**. *Chlamys acroporicola* (Iredale), Recent, Cabuyan Island, the Philippines, × 2.5. **H**. Borehole of *Lithophaga* sp. originally in a living *Porites* coral, subfossil, Cebu Island, the Philippines, × 1.3.

this habit evolved within the superfamily.

Leptonacea and Galeommatacea.—These bivalves are typically symbiotic with other organisms. A broad range of hosts has been recorded for Recent representatives. They include crustaceans (especially brachyurans, macrurans, stomatopods and tanaid shrimps), echinoderms (especially holothurians), sipunculids and polychaetes. Association with other organisms (burrowing sea anemones, phoronids)

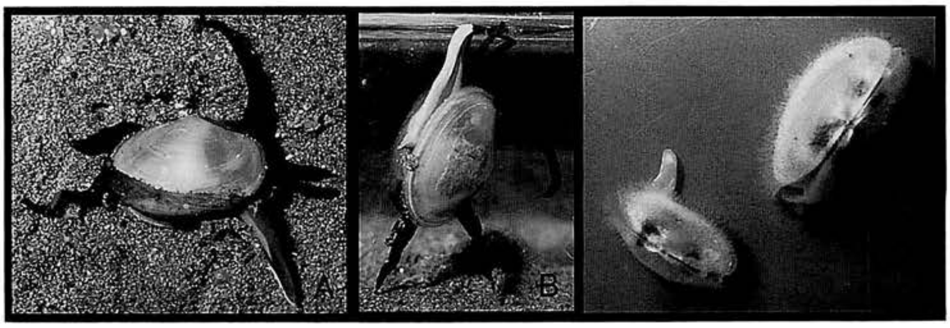

Figure 6. **A–B**. Living *Scintilla* sp., Cebu Island, the Philippines, × 1.4, crawling on sand (**A**, with the foot lowermost) and climbing the glass of an aquarium (**B**, with the white sole of the foot visible). **C**. Two living specimens of *Galeomma* cf. *polita*, Cebu Island, the Philippines, × 3. The foot is visible in the lowermost specimen. The anterior inhalant (with larger gape) and posterior exhalant mantle regions are also visible. The shells appears "fuzzy" because they are covered by villous mantle tissue.

has been described as well (e.g., see Fischer, 1930; Ohshima, 1930; Popham, 1940; Caullery, 1952; Boss, 1965; Rees, 1967; Morton, 1980, 1988; Noble *et al.*, 1989). Many of these bivalves are associated with a specific type of host, but exceptions are known. *Mysella bidentata*, for instance, has been observed on a large variety of invertebrates, including annelids, sipunculids and echinoderms (Boss, 1965). Leptonacean and galeommatacean bivalves may be byssally attached to the host, or live in its burrow. Several species have been found nestling among epifaunal bivalves or rock and coral crevices, and their hosts, if any, are unknown.

Some leptonaceans and galeommataceans are free-living, and can use the adhesive sole of the foot to creep, and even to climb (Figure 6). Additional peculiarities are constituted by the mantle often covering totally or in part the outer shell surface, and by mantle tentacles, ranging in number from a few to hundreds, which may be functional as a defence against predators (above references). In these superfamilies, the inhalant current enters the mantle in correspondence with the anterior shell slope, and the exhalant leaves from the posterior. The taxonomy of these groups is difficult, and several species are highly polymorphic.

The Recent galeommatacean *Curvemysella paula* (Figure 7A–D) possesses a conspicuously concave ventral margin and a twisted commissure plane. This peculiar morphology is adaptive: this species is byssally attached to the columella of a gastropod shell inhabited by a hermit crab (Morton and Scott, 1989; pers. obs.). The bivalve is located well within the shell, and invisible from the aperture. The commissure conforms to the geometry of the columella and inner shell surface of the gastropod.

Shell morphology in this species is rather constant, but it is not known whether it is genetically preprogrammed or ecotypically determined by space constraints. The somewhat irregular shape of the byssal gape suggests a morphogenetic programme at least partly controlled by the topography of the substrate. The Eocene sportellid *Hindsiella*, which possessed a comparably concave ventral margin, may have had a similar life habit. Several other representatives display a concave ventral margin. This feature may be related to byssal attachment to a convex substrate (e.g., exoskeletal surfaces of arthropods). As discussed by Savazzi (1987), this geometry is adaptive in relieving stress on the byssus, and therefore may enhance the adhesion of the organism to the host.

The galeommatid *Ephippodonta* possesses a shell with a straight hinge line and roughly semicircular and almost flat valves. This genus lives within crustacean burrows, and typically keeps the valves spread apart at an angle of about 180° to each other. The valves cannot be closed and, at maximum adduction, form an angle of roughly 90° to each other. The foot is large, with a wide flat sole used for creeping.

Mysella, a symbiont on *Lingula*

A Recent galeommatid (Figure 7E–I), here identified as *Mysella* sp. because of its hinge structure, was observed by Savazzi (1991) byssally attached to the shells of the living inarticulate brachiopod *Lingula anatina* from the Philippines. This seems to be the only literature record of bivalves symbiotic with brachiopods. The constant placement of these bivalves near the anterior commissure of *Lingula* and their apparently obligatory association with the brachiopod suggest a symbiotic association. Subsequent field work by the writer provided the opportunity for a more detailed investigation, and the results are discussed below.

Material. — In November, 1994, 141 specimens of *L. anatina* were collected manually by digging out sediment from an area of approximately 2 m^2 on a tidal flat in front of the Poor Clare Monastery, Tayud, Cebu Island, Philippines (10° 21´ 15´´N, 123° 59´ 15´´E). This is the same locality studied by Savazzi (1991). About 20 specimens carrying attached bivalves were placed in aquaria for observation, while the rest were fixed and dried.

Observations on Lingula.—Savazzi (1991) reported that *L. anatina* collected in 1990 from the same locality sometimes exceeded 50 mm in shell length. However, in 1994 only 5 specimens in the collected sample exceeded 30 mm, with none reaching 40 mm. A search in the surrounding area failed to produce larger specimens. A subsequent visit in the same locality in 1997 yielded specimens of *L. anatina*

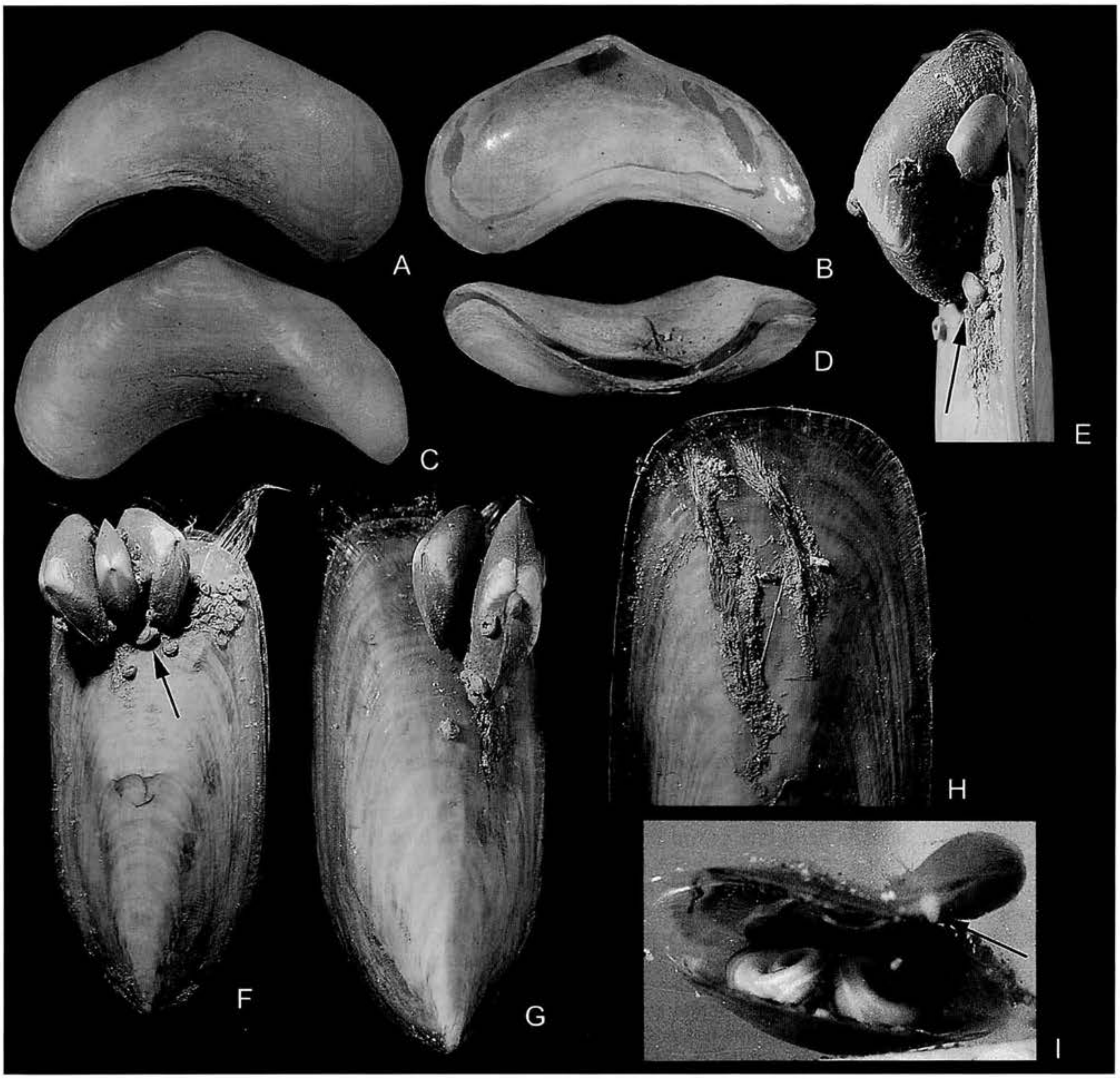

Figure 7. **A–D**. *Curvemysella paula*, Recent, Cebu Island, × 10. **E–I**. *Mysella* sp. on *Lingula anatina*, Recent, Cebu Island, the Philippines. Specimens epibyssate on *Lingula* (**E**, × 8; **F–G**, × 5, arrows indicate juvenile *Mysella*, small round objects are egg capsules), byssal threads on *Lingula* (**H**, × 8) and living specimen probing the edge of the *Lingula* mantle with the extended foot (**I**, × 6, arrow indicates the bivalve foot).

never exceeding 25 mm in shell length. In 1997, *Mysella* sp. was absent from this locality and surrounding areas. The local environment may have become gradually less favourable for *L. anatina* because of the construction of numerous dry piers, which restrict water currents, and an increase in pollution. The gradual decrease in size and abundance of *L. anatina* observed in the test locality may be general in Cebu Island. While this species was available on a daily basis in local fish markets until 1990, it was seldom seen in 1994 and 1997.

Frequency and distribution of epibionts.—Several *Lingula* collected in 1990 and 1994 carried byssally attached *Mysella* sp. These bivalves were exclusively found attached to living *Lingula*. No other epibionts were observed on *L. anatina* with the exception of two specimens of the gastropod *Calyptraea* sp., but several specimens of *Lingula* carried egg capsules, possibly laid by gastropods (e.g., Figure 7E–G).

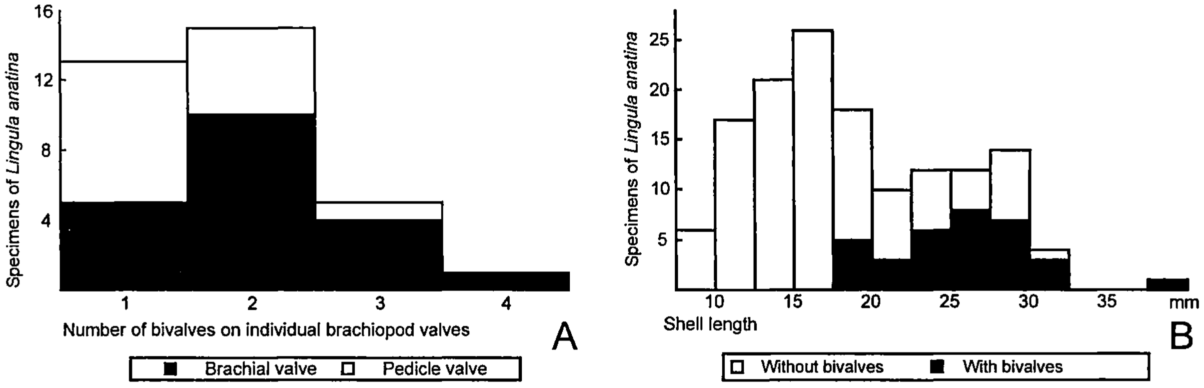

Figure 8. **A**. Distribution and clustering pattern of *Mysella* sp. on right and left valves of *Lingula anatina*. **B**. Size distribution of *Lingula* specimens with and without attached *Mysella*.

Mysella sp. is attached indifferently on either valve of the brachiopod (Figure 8A). However, only one specimen of *L. anatina* carried individuals of *Mysella sp.* on both valves. As shown in Figure 8B, the size-distribution of the sample of *L. anatina* is visibly bimodal, with a single outlier at the extreme right of the histogram suggesting a third peak. These peaks likely correspond to year classes. If so, they indicate a rather high yearly mortality (roughly 50% from year 1 to 2, much higher from year 2 to 3). *Mysella sp.* shows a clear preference for larger hosts: 53% of the specimens of *L. anatina* above 20 mm in shell length carry one or more attached *Mysella sp.*, while only 5.7% of the specimens below 20 mm do. In total, 23.4% of *L. anatina* carry bivalve commensals. 37 specimens of *Mysella sp.* were collected in total.

Most specimens of *L. anatina* carry one or two bivalves, with a single specimen carrying four (of which one is a small juvenile; Figure 7F). When two or more individuals are present, they usually forms tight clusters. This pattern may result from a preference by *Mysella* sp. to attach near an already present individual, as shown by the different sizes of individuals within the same cluster (Figure 7E–G).

In several cases, the bundle of byssal threads by which *Mysella* sp. is attached to the host continues posteriorly into a trail of old, severed byssal threads (Figure 7G, H). This trail is apparently produced by the migration of *Mysella* sp. toward the anterior commissure of its host. Since *Mysella* sp. is invariably located close to the anterior commissure of *L. anatina* (see also below), this migration must be a response to growth of the brachiopod shell. *Mysella* sp. is preferentially attached in correspondence of the inhalant currents of the host, which enter the shell along the lateral regions of the anterior commissure (see Chuang, 1956; Rudwick, 1970; Savazzi, 1991; and references therein), rather than in correspondence with the centrally located exhalant current.

The shell of *Mysella* sp. is antero-posteriorly elongated, with a straight or slightly concave ventral margin. The umbones are slightly opisthocline and opisthogyrate, and located slightly posterior to the midlength of the shell. The anterior shell slope is slightly more developed than the posterior, which is somewhat truncated. The ventral shell margin is straight or slightly concave, with a thickened shell edge. The periostracum on the outer shell surface is thick and dark brown in colour, and forms a thick carpet of short periostracal shingles arranged in radial lines.

The hinge shows a well developed, elongated anterior tooth and a somewhat shorter posterior tooth on the right valve. The left valve shows corresponding sockets, delimited ventrally by anterior and posterior teeth shorter than in the opposite valve. The ligament consists of a resilium located immediately below the umbones and inserted onto the shell within a depressed ligamental pit. The resilium has a roughly circular median section and is arcuate in antero-posterior view, with the convexity on its ventral side. This suggests that some flexing, in addition to compression, is involved in its function. The ventral side of the ligament bears a central calcified patch, white in colour, on its ventral surface. This is not a true ossiculum or lithodesma, because it does not have well defined edges and cannot be isolated from the rest of the ligament by maceration in alkali (when this was attempted, the calcified patch invariably disintegrated into its constituent aragonitic crystals).

The anterior adductor muscle scar is located in a rather dorsal position, while the posterior is displaced ventrally and close to the posterior shell margin. The area of the anterior adductor scar is substantially larger than that of the posterior. The reduced area of the posterior adductor scar, compared to its anterior counterpart, may be related to the fact that the displacement of the posterior adductor in the ventral direction results in an increase in length of the lever-arm acted upon by this muscle, which in turn lessens its strength requirements. The anterior pedal retractor scar is adjacent to the anterior adductor scar, while the posterior pedal retractor scar is well separated from the corresponding adductor scar, and located more dorsally. This separation is likely a consequence of the unusual placement of the posterior adductor (see above).

The ventral displacement of the posterior adductor muscle (see above) is infrequent in bivalves, and reduces substantially the length of posterior commissure available to the respiratory current(s). However, the posterior commissure in

Mysella houses only the exhalant current, thus reducing the need for an extensive length of commissure to keep the inhalant and exhalant currents separate in the lack of siphons.

When *Lingula* is in life position with the anterior region of the commissure uppermost (see Savazzi, 1991, and references therein), the posterior region of *Mysella sp.* does not face upwards, unlike what was reported by Savazzi (1991). Instead, it is directed downwards. Thus, the life orientation of *Mysella* sp. is essentially the opposite of typical infaunal bivalves.

In the laboratory, *Mysella* sp. is inactive for most of the time. At intervals of several minutes, the anterior commissure of *Mysella* sp. gapes, and the foot is extended toward the anterior commissure of the host. The tip of the foot probes several times in quick succession on the basal region of and between the brachiopod setae (Figure 7I), and is subsequently retracted within the shell. The process lasts 1-2 seconds, may be repeated 2-3 times in succession, and is followed by another period of inactivity. The foot was never extended into the mantle cavity of the host, and the probing activity caused no visible reaction by the brachiopod. On the other hand, artificial stimulation of the setae and mantle of the brachiopod with a flexible bristle in the same region touched by *Mysella* sp. caused an immediate valve-adduction by the brachiopod. The setae, mantle tissues and shell margin of *L. anatina* in proximity of attached *Mysella* sp. showed no visible damage or alteration.

After spending a few hours in aquaria, a few specimens of *Mysella* sp. detached from their host and started to move about epifaunally. Locomotion consists of a forward extension of the foot, adhesion of its tip to a solid object, followed by retraction of the foot, which causes the shell to be dragged forward. The tip of the foot readily adheres to smooth glass surfaces. No burrowing activity was observed, and detached individuals did not reattach to any of the brachiopods placed in the aquaria.

Four preserved specimens of *Mysella* sp. were dissected and their guts examined. They were found to be empty or to contain small amounts of matter, the nature of which was not recognisable under an optical transmission microscope or a dissecting microscope.

Significance of association between Mysella *and* Lingula.—*Mysella* sp. likely feeds on mucus and/or on detritus trapped in mucus secreted by *L. anatina*. As described above, the tip of the foot is adhesive, and likely used to collect food particles from the mantle and setae of the host. This feeding activity causes no detectable damage to the host, and might aid in its cleansing. This is apparently the first time the feeding of a galeommatacean on its host was observed.

The preferential placement of *Mysella* sp. near the inhalant currents of *L. anatina* is adaptive in this context. The faeces of *L. anatina* are a potential source of food for a symbiont, but faecal pellets are projected into the water column by quick contractions of the brachiopod valves (above references), and therefore may be difficult or impossible to exploit by an organism attached to the outside of the *Lingula* shell.

The shells of *Mysella* sp. byssally attached on *L. anatina* may hinder or prevent the host from reburrowing when it becomes exposed by sediment erosion. In this situation, it is possible that *Mysella* sp. detaches itself from exposed *Lingula*, as observed in the laboratory, or becomes dislodged by the energetic burrowing movements employed by *Lingula* (see Savazzi, 1991). It is also likely that *Mysella* sp. hinders the vertical movements of *L. anatina* within its burrow (see also below). A few of the specimens of *L. anatina* showed tufts of byssal threads produced by individuals of *Mysella* sp. that subsequently detached (Figure 7H). The distance of some of these tufts from the anterior commissure of *L. anatina* shows that the brachiopod shell grew substantially after the bivalve detached.

The clustering of *Mysella* sp. provides no obvious advantage in feeding, since adjacent bivalves must then share the same region of host commissure. Rather, it is possible that clustering of *Mysella* sp. makes their individual shells less likely to be dislodged by the movements of *Lingula* within its burrow. This may be especially true of small individuals of *Mysella* nestling close to adult ones (arrows in Figure 7E, F).

The morphology of the burrows of *L. anatina* carrying *Mysella* sp. was observed in three instances. These burrows show a larger diameter and an irregular cross-section in correspondence of the epibionts. These irregularities are potentially preserved in fossilised burrows of linguliform brachiopods (e.g., *Lingulichnites*, see Szmuc *et al.*, 1976). The existence of a comparable association between extinct inarticulate brachiopods and external symbionts, therefore, could be detectable from trace fossils.

Bivalves as hosts to macrosymbionts

The internal surfaces of bivalve shells occasionally display teratological characters produced by worm-shaped organisms living within the mantle or between the mantle and the inner shell surface (Figure 9). These endosymbionts are likely parasites, because the bivalve host is visibly damaged, and likely receives no advantage from the association.

In some Triassic localities of NE Italy, most specimens of megalodontid bivalves display a U-shaped furrow within one valve (or, more rarely, one such furrow in each valve), with the bottom of the U in proximity to the apex (pers. obs.). A comparable type of infestation was described in Pliocene *Isognomon* (Figure 9B, C; Savazzi, 1995). In this case, the parasite body, as outlined by secondary shell secretion of the bivalve, often spanned across the hinge and followed a twisted and snaking pathway along one or both valve interiors. In two specimens, this induced the formation of a teratologic lithodesma, a feature which is absent in normal shells of all representatives of this family, but present in taxonomically unrelated bivalves (above reference).

In a specimen of the Pliocene arcid *Barbatia mytiloides*, tens of parasites were inhabiting the space between mantle and shell (Figure 9A; Savazzi, 1995). It is interesting to note that the parasite did not spread to the myostraca, a situation which probably would have resulted in the death of the host, and that all parasites eventually were sealed off by the bivalve. A morphologically identical reaction to a parasite is observed also in Recent *Scapharca* from Japan (pers. obs.).

It is usually infeasible to decide the nature of these symbionts in fossil material, since their traces on the bivalve

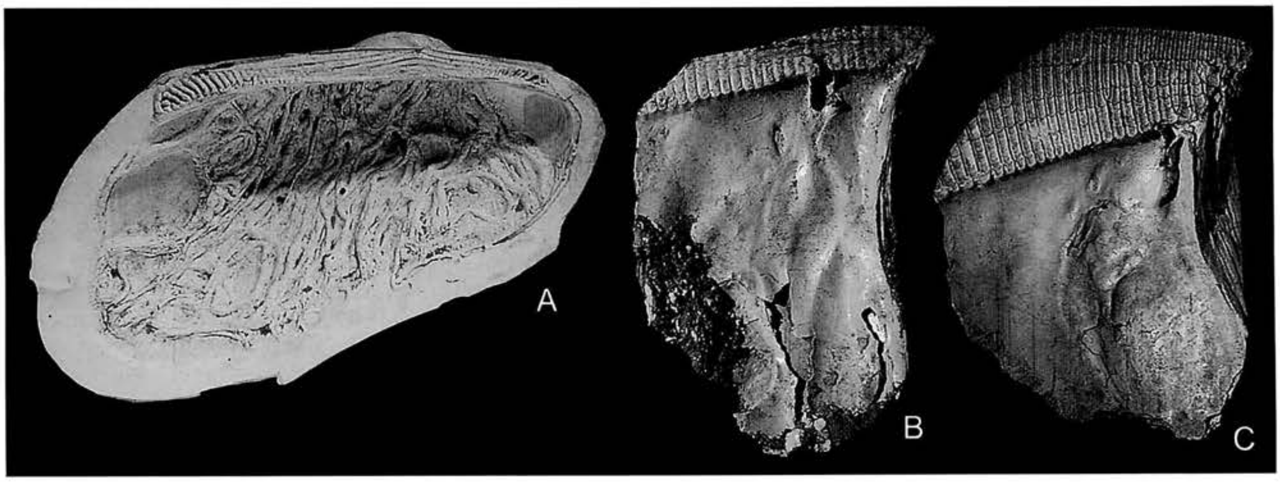

Figure 9. Interior of right valves of bivalves parasitised by worm-like organisms. **A**. *Barbatia mytiloides* (Brocchi), Middle Pliocene, Piacenza, Italy, × 1.2. **B–C**. *Isognomon (Hippochaeta) maxillatus* (Lamarck), Upper Pliocene, Asti, Italy, × 0.4.

shells reveal no morphological features, except the general body shape and size of the symbiont.

Both boring and tube-building polychaetes are frequent on the external surface of bivalve shells, and their distribution provides information on the life orientation and life habits of the hosts. In particular, in semi-infaunal bivalves the presence of polychaetes indicates that the shell region they inhabited was exposed above the surface of the sediment. Usually it is not possible to decide whether these polychaetes are true symbionts (frequently, they may settle on a variety of different substrates and organisms). The preferential settlement of semi-endolithic polychaetes in proximity of the exhalant region of commissure of nonsiphonate bivalves (e.g., Arcidae, pers. obs.), however, suggest that they exploit the faeces and/or pseudofaeces of the bivalve as a food source.

Concluding thoughts

Photosymbiosis has been proposes to explain the large size and/or unusual shell thickness of several fossil bivalves (see above). However, the Tridacnidae are the only Recent bivalves complying with this interpretation. All other documented cases of Recent photosymbiotic bivalves are small forms and, except for *Corculum*, virtually nothing in their shell morphology suggests photosymbiosis.

Stable-isotope analyses could be used to prove photosymbiosis in fossils. This method assumes that the stable-isotope composition of the shells of bivalves housing photosymbionts differs from those of conventional bivalves, since a substantial portion of the carbonate found in the tridacnid shell originates from the photosymbionts. However, with the exception of the Tridacnidae, all Recent photosymbiotic bivalves studied in this respect show isotope profiles similar to those of nonphotosymbiotic forms (above references). In most cases, therefore, proving (or disproving) reliably instances of photosymbiosis in fossil bivalves is not possible at present, unless photosymbiosis is reflected in morphological adaptations that cannot be explained by other adaptive contexts.

Chemosymbiosis in fossils is even more difficult to prove than photosymbiosis. The only reliable method is probably the study of ichnofossils, especially if associated with specimens preserved in the life position. It may be possible to infer chemosymbiosis in bivalves which, like the Recent *Solemya* and Lucinidae, build specialised feeding burrows with canals that reach deep within the anoxic sediment.

Macrosymbiosis has a better potential than microsymbiosis of being recognised in fossil material, especially if the associated organisms are preserved. It is usually possible to decide, for instance, whether scleractinian coral was dead or alive at the time it was inhabited by a boring or nestling bivalve. Bivalves that bore in living coral display a range of distinctive behavioural and morphological adaptations to this life habit.

It is more difficult to recognise whether a bivalve was embedded in a sponge or other organism with a low likelihood of being preserved. Specialised life habits like the deep embedding of *Vulsella* and *Ostrea permollis* within sponges can be suspected from the lack of a byssal gape or cementation surface, coupled with a shell morphology and size unlikely for a sessile soft-bottom dweller. A few forms taxonomically related and morphologically similar to *Vulsella* may have had comparable habits in spite of the presence of a byssal notch, since byssal attachment on the surface of a sponge in the juvenile stage may have preceded the embedded adult stage, and the byssal notch may have constituted the morphogenetic "trigger" for the subsequent formation of a broader respiratory gape in the same region of the commissure. The presence of unusually strong hinge structures in otherwise thin shells and of adductor muscle scars unusually (for malleids) displaced toward the ventral region corroborate this idea.

Shallow-embedded pteriids within sponges display a highly variable shell morphology with distinctively bulging irregularities, also potentially recognisable in fossils. Epibyssate attachment to soft-skeleton coelenterates, on the other hand, does not result in comparable morphological characters.

It is usually difficult to decide from shell morphology alone whether an epibyssate pteriid was attached to a living or dead substrate. The cryptic colour pattern of *Pterelectroma zebra*, which provides camouflage against the background of the branched hydrozoan with which the bivalve is associated, seems to be the only exception.

Symbiotic hosts contained within bivalves sometimes can be recognised from teratological reactions of the bivalve. Worms or worm-like organisms living in the mantle cavity, or between the mantle and the shell, often cause recognisable deformation in the shell. Shell-boring or externally cemented polychaetes are usually placed in correspondence to the exhalant current (especially in nonsiphonate bivalves). In addition to allowing one to detect an association between worms and bivalves, these epibionts are useful in helping one to reconstruct the life position of the bivalve with respect to the substrate.

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Erratum

In the Contents on the back cover of Vol. 4, No. 2 and the Contents (p. 314, line 14 from bottom) of Vol. 4, No. 4, the name of the first author of the paper by Hasegawa and Hatsugai was misspelled. Read Takashi Hasegawa for Takeshi Hasegawa.

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行事予定

◎2001年年会・総会は，2001年６月29日（金），６月30日（土），７月１日（日）に「国立オリンピック記念青少年総合センター」で開催されます．21世紀最初の年会ですので，「21世紀の古生物学」を統一テーマとし，29日に統一シンポジウム，30日と１日に17件の課題別シンポジウムが行われます．

一般講演はポスター講演だけに限って受け付けます．口答発表形式による一般講演はありませんのでご注意下さい．ポスター講演の申し込み締切日は2001年５月９日（水）です．

◎第151回例会は，2002年１月26日（土），１月27日（日）に鹿児島大学理学部で開催されます．１月27日（日）午後に公開講演として「21世紀は自然史の時代　―古生物学・フィールド科学からの提言―：世話人，森　啓・矢島道子」を実施致します．一般講演の申し込み締切は11月30日（金）です．

◎2002年年会・総会（2002年７月上旬開催予定）には福井県立恐竜博物館から開催申し込みがありました．また，第152回例会（2003年１月下旬開催予定）には横浜国立大学教育人間科学部から開催申し込みがありました．

◎古生物学会では，小人数で実施されるワークショップやショートコースを主催しております．学会から金銭を含む援助を行なうことができますので，企画をお持ちの方は行事係までお問い合せ下さい．

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THEME ISSUE

Morphological Approaches in Paleobiology

CONTENTS