SHELL MICROSCULPTURE IN *STRIATURA, PUNCTUM, RADIODISCUS,* AND *PLANOGYRA* (PULMONATA)

Alan Solem

Department of Zoology
Field Museum of Natural History
Chicago, Illinois 60605

ABSTRACT

Previous anatomical studies have placed Striatura *(Zonitidae),* Punctum *(Punctidae),* Radiodiscus *(Charopidae), and* Planogyra *(Valloniidae) in unrelated families. Their minute size, similar shell shapes, and the sharp differentiation between spiral sculpture on the nuclear whorls and the post-nuclear sculpture of major and minor radial elements, have led to confusion between these genera. Scanning electron microscope photographs of shell microsculpture show that the apparent sculptural similarities are convergent. The same gross result is achieved in quite different ways.*

In many parts of the world, land snails that are 1 to 2 mm in diameter have a complex microsculpture on the shell. When this sculpture is viewed under high optical magnifications, 50 to 100×, a distinction can be made between "major radial ribs" that number 15 to 250 on the last whorl of the shell, and "micro-ribbing" that lies between the "major ribs". Traditionally such species were described as, or subsequently associated with, "endodontid" land snails but anatomical investigations of the past six decades have split many taxa off into a wide variety of families. The many differences in pallial structure, genitalia, radulae, free muscle and nervous systems revealed by the anatomical studies strongly suggest that the similarities in shell form and sculpture are the result of convergent evolution.

Unfortunately, adequate studies of the sculptural elements and their method of formation have not been possible until very recently because of inherent limitations in magnifications, resolution, and depth of field with optical equipment. The scanning electron microscope (hereafter SEM) overcomes these problems and permits investigations of sculpture components and method of formation. As a byproduct of investigations on the Pacific Basin endodontoid land snails, data on shell sculpture in several Nearctic taxa have been accumulated. They illustrate basic differences in mode of sculpture formation and suggest possible major differences between higher groupings in terms of shell structure.

The genera illustrated here, and the anatomical studies that enabled definitely assigning them to family units, are *Striatura (Pseudohyalina)* (Zonitidae, H. B. Baker, 1928a), *Punctum* (Punctidae, H. B. Baker, 1927), *Radiodiscus* (Charopidae, H. B. Baker, 1927), and *Planogyra* (Valloniidae, H. B. Baker, 1928b, 1935). Illustrations of two species belonging to *Striatura, s. s.* were presented in the preceding paper, Solem (1977) and are referred to below. The Valloniidae belongs to the Order Orthurethra and the other three families to the Order Sigmuretha. Both the Punctidae and the Charopidae currently (Solem, In Press) are placed in the Superfamily Arionacea of the Suborder Aulacopoda, while the Zonitidae belongs to the Superfamily Limacacea of the same Suborder. None of these families appear to be related in a direct descendant-ancestor manner.

The families also differ greatly in their basic distribution patterns. The Charopidae (Solem, unpublished) is a "Gondwanaland" taxon with high diversity in South Africa, Australia, New Zealand, New Caledonia, some parts of Polynesia, Juan Fernandez and southern South America. A few taxa reach Indonesia, New Guinea, Central America, and the Western United States. The

Punctidae are primarily Australia and New Zealand in distribution, with scattered occurrences in Africa, South America, Tahiti, Hawaii, and the Holarctic region. The Zonitidae is most diverse in the Holarctic, but has extensive Central American, Polynesian, and some South American taxa. The Valloniidae is strictly a Holarctic family with a fossil record extending back to the Paleocene of Europe. North America is thus on the fringe of the charopid radiation, but central to the zonitid and valloniid distribution patterns. The punctids have their center of diversity elsewhere, but North America is the main secondary center of diversity.

SHELL SCULPTURE AND FORMATION

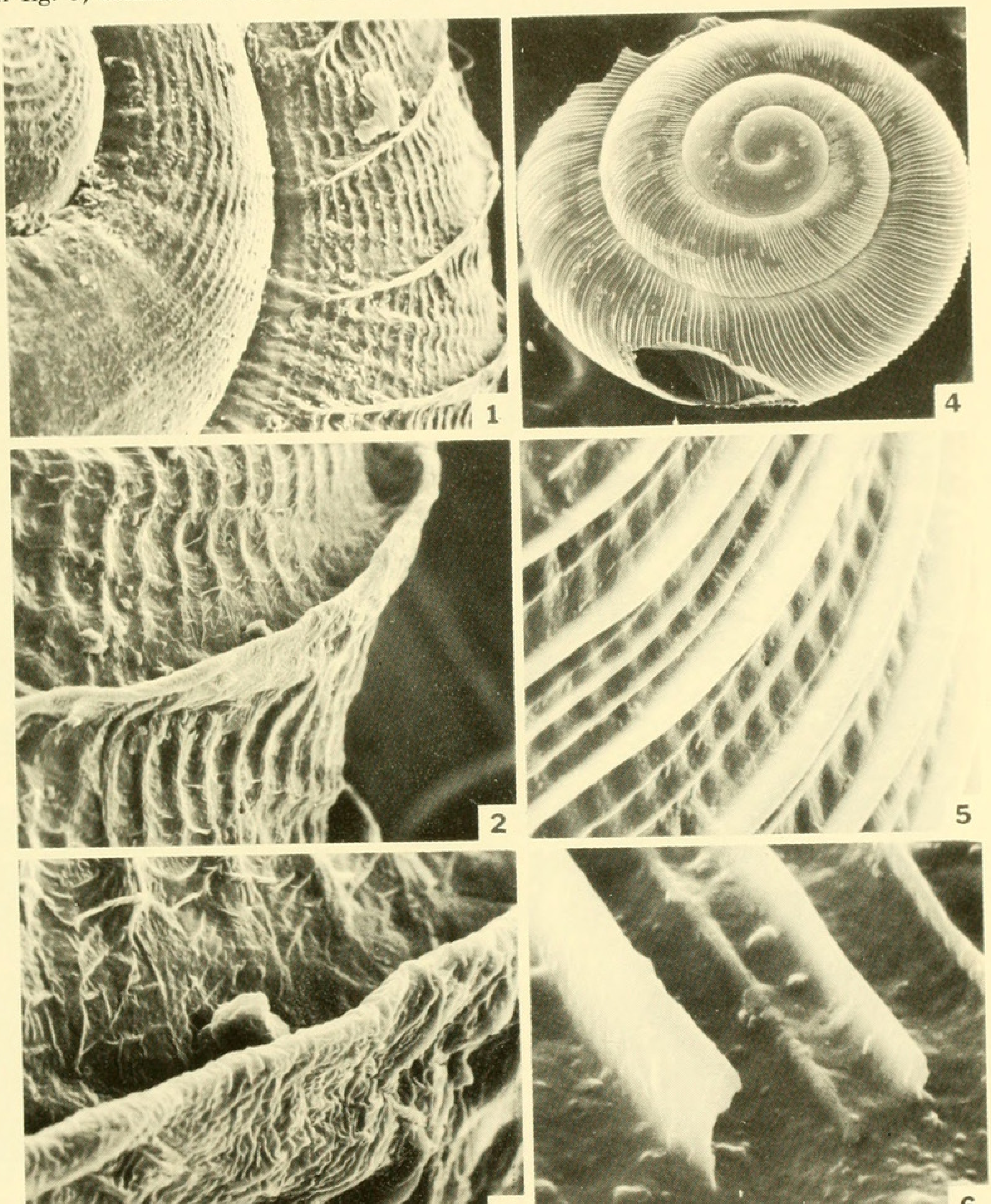
Although Baker (1928a: 33) pointed out that the three dissected species he grouped as *Striatura* could perhaps be placed better as monotypic genera, subsequent workers such as Pilsbry (1946) preferred to use a more broadly defined genus. Certainly the shell sculpture in *S. pugetensis* (Dall, 1895) (see Solem, 1977: figs. 1-3), *S. milium* (Morse, 1859) (see Solem, 1977: figs. 4-7), and *S. (Pseudohyalina) exigua* (Stimpson, 1850) (figs. 1-3) is consistent with a monophyletic derivation. The species differ obviously in their major ribbing. *S. exigua* has widely spaced, narrow, high major ribs (figs. 2, 3) that terminate short of the suture (fig. 1). *S. pugetensis* (Solem, 1977: figs. 5, 6) has much lower, more crowded, narrow ribs. These ribs clearly are periostracal in origin, since (*loc. cit.*, left center of fig. 6) broken rib edges show no underlying calcareous support. *S. milium* (Solem, 1977: figs. 2, 3) gives the appearance of having radial ribs under optical examination, but the SEM shows that a series of short diagonal ridges are lined up in a radially transverse row and hence there are no continuous radial ribs. *S. exigua* (figs. 2, 3) has a clear micro-spiral sculptural element that could be derived from the diagonal ridges of *S. millium* (Solem, 1977: fig. 2).

The apical sculpture of *S. milium* (Solem, 1977: fig. 1) consists of broad, flat ridges separated by narrower grooves, with faint traces of a radial element. In both *S. pugetensis* (Solem, 1977: fig. 5) and *S. exigua* (fig. 1) the apex has very narrow spiral ridges, with their interstices wider than the ribs.

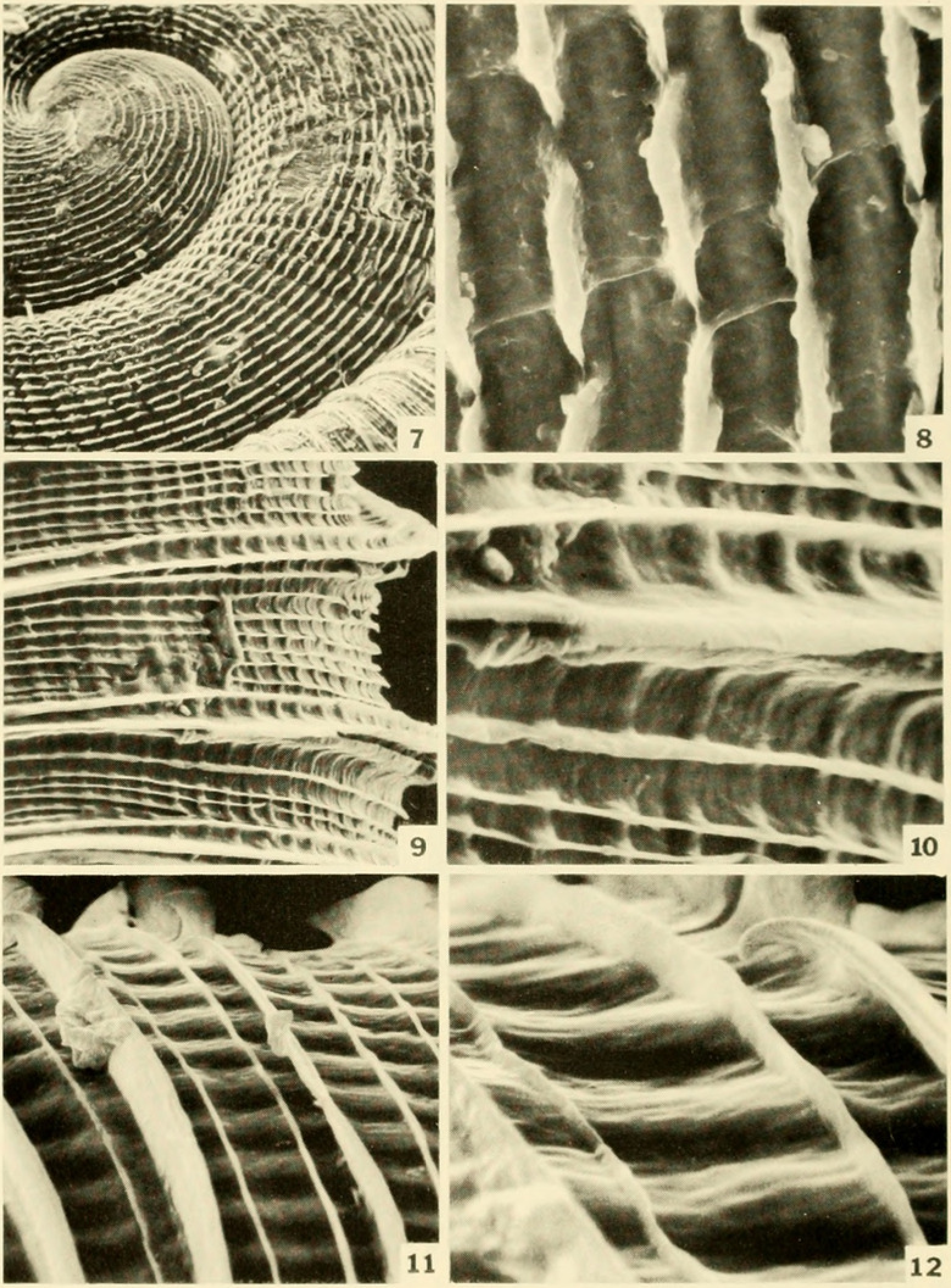
The most characteristic feature of *Striatura* is the very peculiar micro-folding pattern (Solem, 1977: figs. 3, 7). This is particularly clear on the major rib surface in *S. exigua* (fig. 3). Similar stress marks in dried films of paint or plastic are familiar to physical chemists. I interpret this folding pattern as the result of shrinkage drying by an outer periostracal layer.

Punctum (figs. 4-6, 11, 12) superficially looks very similar to *Striatura* in sculpture, having spiral apicals (Giusti, 1973: pl. 5, fig. 1) and narrow, crowded radial ribs when viewed at optical range magnification (fig. 4). At higher magnification (figs. 5, 6), the presence of two or three micro-riblets between each pair of major ribs is obvious. By inspecting an area where the ribs are broken (fig. 6), the very thin, lamellar nature of the ribs, the occasional sudden termination of a micro-riblet, and the fact that the major ribs surmount a low radial swelling on the shell surface can be detected. When the sculpture is viewed from a very low angle (figs. 11, 12), the presence of spiral swellings, with the radial sculpture essentially unaffected by these elements, is evident. In addition, there is a vague pattern of corrugations on the surface of the spiral ridges.

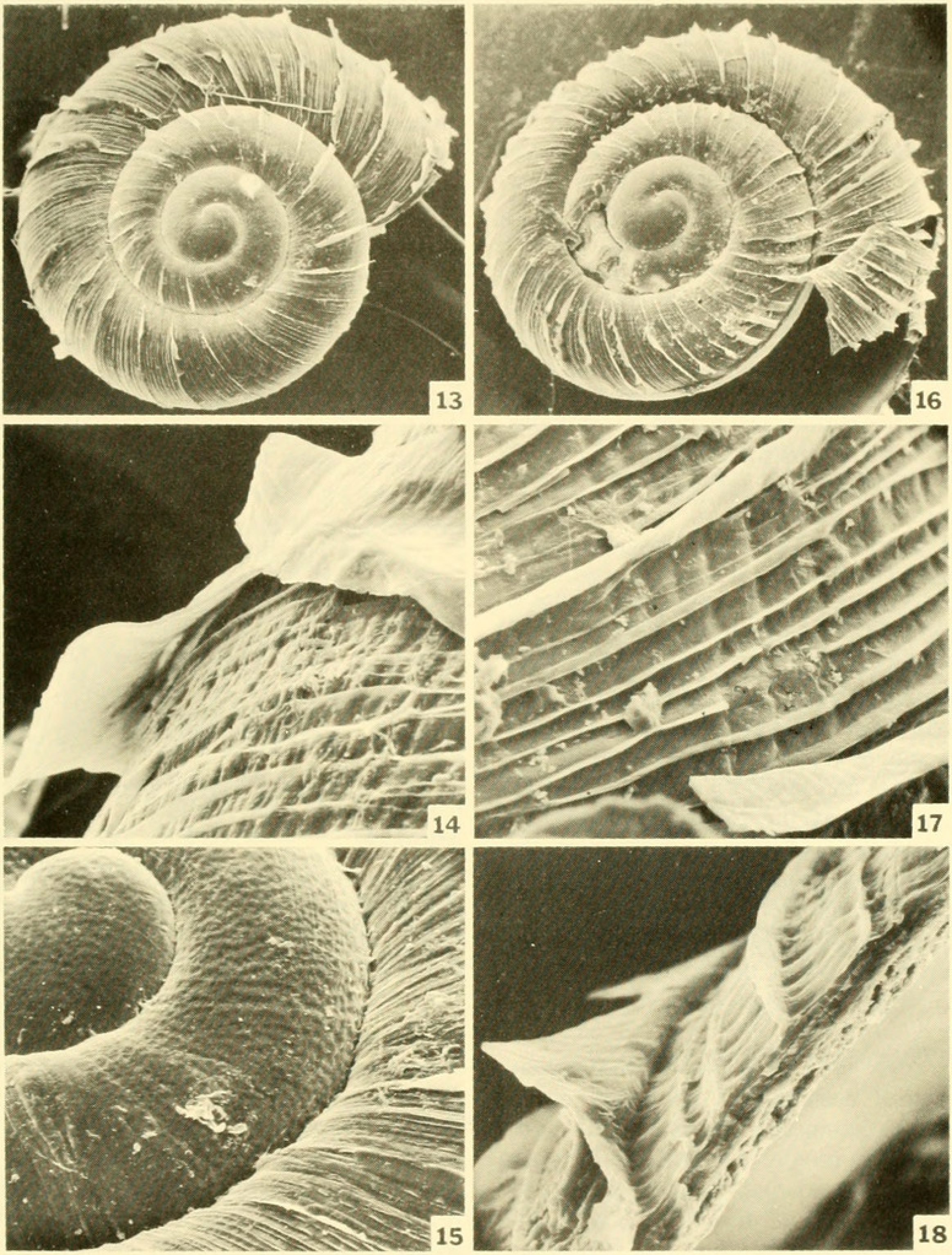
Previous reports on the shell sculpture of *Radiodiscus* (summarized by Pilsbry, 1948: 654-655) characterize the apex as "minutely engraved spirally" and the "rest of the shell densely radially costate". While the apex does start out (fig. 7) with continuous spiral cords, very shortly these become interrupted by narrow radial lines. At very high magnification (fig. 8), the apical sculpture can be seen to consist of short, slightly sinuated segments that line up spirally. The post-nuclear sculpture (figs. 9, 10) is complex, and compares in all essentials with that found in such Pacific charopids as the New Zealand *Ptychodon microundulata* (Suter, 1890) (see Solem, 1970: pl. 59) and a still undescribed Tongan species (Solem, 1974: 199, figs. 8a, b). The major radial ribs in all these taxa are periostracal extensions above a calcareous swelling (Solem, 1974: 199, fig. 8b). There are a few to many micro-riblets, again formed by the periostracum, between the major ribs (fig. 9; Solem, 1970: pl. 59, figs. 8, 9; Solem, 1974: 199, figs. 8a, b). In addition, there is a complex spiral microsculpture (fig. 10). Larger spiral elements (also visible in fig. 9) connect two microradials, tending to buttress the apical side of the microradial. This is particularly evident in *Ptychodon microundulata* (Solem, 1970: pl. 59, fig. 10), but is much less developed in *Radiodiscus* (figs. 9, 10). Be-



FIGS. 1-3. Striatura (Pseudohyalina) exigua *(Stimpson, 1850). Ohio. FMNH 11020.* FIG. 1. *Apical (left) and postnuclear (right) sculpture. 185X.* FIG. 2. *Sculpture on body whorl showing one major radial rib. 620X.* FIG. 3. *Detail of periostracal surface on major rib. 1,850X.* FIGS. 4-6. Punctum minutissimum *(Lea, 1841). Cedar bog on Woodburn Road, 4 miles southwest of Urbana, Champaign Co., Ohio. October 20, 1969. E. Keferl! FMNH 151102.* FIG. 4. *Entire shell (lip broken). 63X* FIG. 5. *Sculpture on body whorl. 1,560X. Broken ends of major radial (left) and two microradials (center and right). 5,400X.*



FIGS. 7-10. Radiodiscus (R.) millecostatus *Pilsbry & Ferriss, 1906. Wickersham Gulch, Huachuca Mts., Cochise Co., Arizona. James Ferriss! FMNH 146619.* FIG. 7. *Apical sculpture. 195X.* FIG. 8. *Detail of late apical sculpture. 1,900X.* FIG. 9. *Two major ribs on body whorl. 630X.* FIG. 10. *Detail of a major rib and microriblets on body whorl. 2,000X.* FIGS. 11-12. Punctum minutissimum *(Lea, 1841). FMNH 151102.* FIG. 11. *Sculpture on body whorl. 2,000X.* FIG. 12. *Detail of microsculpture on body whorl. 6,700X.*



FIGS. 13-15. Planogyra asteriscus *(Morse, 1857). Fraserdale, Cochrane Dist., Ontario, Canada. S. D. Downing! June 1938. FMNH 46783.* FIG. 13. *Apical view of subadult specimen. 36X.* FIG. 14. *Major rib and microsculpture on body whorl. 355X.* FIG. 15. *Apical sculpture and early post-nuclear sculpture. 285X.* FIGS. 16-18. Planogyra clappi *(Pilsbry, 1898). Quamicham, Vancouver Id., British Columbia. FMNH 140588 ex W. J. Eyerdam.* FIG. 16. *Apical view of subadult specimen. 37.3X* FIG. 17. *Sculpture on body whorl. 373X.* FIG. 18. *Broken edge of body whorl showing major rib and details of microsculpture. 792X.*

tween these "major" spiral elements are vague sprial corrugations (fig. 10; Solem, 1970, pl. 59, figs. 10, 11) that resemble those found on the spiral ridges in *Punctum* (fig. 12).

Planogyra asteriscus (Morse, 1857) (figs. 13-15) from the boreal areas of Eastern North America and *P. clappi* (Pilsbry, 1898) (figs. 16-18) from Oregon to British Columbia differ from each other in major rib spacing (compare figs. 13 and 16) and umbilical width. They both have very high, lamellar periostracal ribs that stand erect when the live animal is in the moist litter, but warp and twist (fig. 14) in the dry museum cabinets (H. B. Baker, 1928a: 122). Seen at a broken edge (fig. 18), the periostracal nature and thinness of the ribs is obvious. Similarly, the microradial riblets are formed by the periostracum (fig. 17) and are fewer in number in *P. clappi* (fig. 17) than in *P. asteriscus* (fig. 14). Both species have a weak microspiral sculpture that shows most clearly in figs. 14 and 18 because of the oblique angle of view. The microspirals blend into the raised radial ribs, but do not buttress them as in many Charopids. The apical sculpture in *Planogyra* usually is eroded, but in unworn examples (fig. 15) it can be seen to form a series of corrugated wrinkles and pits with a vague diagonally radial pattern. At the highest magnification (fig. 18) there are evident irregularities on the periostracal surface. These appear homologous to the structures on the spiral microribs of *Radiodiscus* (fig. 10) and *Punctum* (fig. 12), and quite different from the stress drying marks in *Striatura* (fig. 3; Solem, 1977: figs. 3, 7).

COMPARATIVE REMARKS

Under optical examination, the spiral apical sculpture and post-nuclear sculpture with both major radials and usually microradials found in the four genera appear quite similar, but at the higher magnifications of the SEM, major differences appear. In both *Striatura* and *Planogyra*, the shell sculpture appears to be totally periostracal in nature. The raised major ribs are simple lamellar protrusions from the surface. They are scarcely wider at their base than at their midsection (figs. 2, 18). In *Punctum* and *Radiodiscus*, the microradial riblets are purely periostracal, but the major radial ribs are underlaid and partly formed by a swelling in the calcium layer. *Punctum* (fig. 6) differs in that the periostracal ribs are simple lamellae, while in the Charopidae (Solem, 1974: 199, fig. 8b) the basal portions of the periostracal ribs are distinctly wider than the middle sections, with tapering continuing to the top of the ribs.

Microspiral sculpture is present, but differs greatly. In *Striatura* (fig. 2; Solem, 1977: figs. 2, 3, 6, 7) the spiral elements initially are short diagonals, becoming coalesced into wavy spiral cords only in *S. exigua* (fig. 2). In both *Planogyra* (fig. 18) and *Punctum* (figs. 11, 12) the microspirals are basically independent of the radial ribs and riblets, but in *Radiodiscus* (figs. 9, 10) they serve to buttress the apical edge of each riblet. In *Punctum* and *Radiodiscus*, weak spiral corrugations are associated with the sprial ridges.

All four genera have spiral sculpture on the nuclear whorls. In *Radiodiscus* (figs. 7, 8) this consists of short interrupted threads arranged serially in spiral rows, although other charopids (Solem, 1970: pl. 58, fig. 1) normally have prominent, narrow spiral cords, such as are seen in both *Punctum* (Giusti, 1973: pl. 5, fig. 1) and *Striatura* (fig. 1). *Planogyra* (fig. 15), in contrast, has a less well defined, almost punctate sculpture.

The most striking difference is the peculiar micro-folding pattern found in *Striatura* (fig. 3; Solem, 1977: figs. 3, 7). This effect is lacking from the other taxa, although having analogous structures in some other Orthurethra (see Solem, 1977).

The sculpture of these four taxa, although "macroscopically" very similar and functionally probably serving an identical purpose, is composed of quite different elements. On the basis of this and other data available now, primarily a review of Pacific Basin endodontoid taxa, it seems possible that certain of these differences are consistent for at least family units. The total periostracal nature of the shell sculpture in *Striatura* and *Planogyra* contrasts with the combination of calcareous and periostracal sculpture in *Punctum* and *Radiodiscus*. At the other extreme the Endodontidae, as restricted by Solem, has a uniformly thin periostracum, with even the microsculpture on the apical whorls formed mainly by the calcareous layers. Except where the sculpture is secondarily reduced in the Charopidae, the combination of periostracal and calcareous elements is consistent, as is the use of microspiral ridges to buttress the riblets. In the valloniids, species of *Vallonia* with regularly spaced ribs do have calcareous extensions into the ribs, and some of the punctids from Australia and New Zealand lack the calcareous swellings underneath the main ribs.

The tapered and buttressed ribs in the Charopidae are quite unlike the simple lamellar ribs of the other taxa, while the stress folds and "pit and swirl" microsculpture of the zonitid *Striatura* separate it from the other three. A study of the physical chemistry of the periostracum in *Striatura* as compared to the other taxa might yield highly significant information.

In conclusion the grossly similar shell sculpture of these four taxa show several significant differences in mode of formation and composition. Extended studies on the ribbed pupillids, small polygyrids, streptaxids, and helicids might yield equally interesting results.

ACKNOWLEDGMENTS

Figures 1 through 12 were taken during a factory demonstration of a JEOLCO SEM, and figures 13 through 18 were taken on a Cambridge S4-10 provided Field Museum of Natural History by NSF grant BMS72-02149. I am grateful to Mr. Fred Huysmans for the excellent photographic prints, to Dorothy Karall for mounting them into prints, and to Sharon Bacoyanis for help with manuscript preparation.

LITERATURE CITED

Baker, H. B. 1927. Minute Mexican Land Snails. *Proc. Acad. Nat. Sci., Philadelphia*, 1927: 223-246, pls. 15-20.

Baker, H. B. 1928a. *Planogyra asteriscus* (Morse). *The Nautilus*, **41**(4): 122-123.

Baker, H. B. 1928b. Minute American Zonitidae. *Proc. Acad. Nat. Sci., Philadelphia*, 1928: 1-44, pls. 1-8.

Baker, H. B. 1935. Review of the Anatomy of the Pupillidae and Related Groups. *In* Manual of Conchology, (2) **28**: 191-209.

Giusti, F. 1973. Notulae Malacologicae XVIII. I Molluschi terrestri e salmastri delle Isole Eolie. *Lavori Della Soc. Italiana Biogeog., n. s.,* **3**: 113-306, pls. 1-16, 2 tables, 39 text figs.

Pilsbry, H. A. 1946. Land Mollusca of North America (North of Mexico). *Acad. Nat. Sci., Philadelphia*, Monog. 3, **2**(1): i-vi, 1-520, figs. 1-281.

Pilsbry, H. A. 1948. Land Mollusca of North America (North of Mexico). *Acad. Nat. Sci., Philadelphia*, Monog. 3, **2**(2): i-x-lvii, 521-1113, figs. 282-585.

Solem, A. 1970. Malacological Applications of Scanning Electron Microscopy. I. Introduction and Shell Surface Features. *The Veliger* **12**: 394-400, pls. 58-60, 1 table.

Solem, A. 1974. The Shell Makers: Introducing Mollusks. New York: John Wiley. pp. xii, 289.

Solem, A. 1977. *Radiodiscus hubrichti* Branson, 1975, a synonym of *Striatura (S.) pugetensis* (Dall, 1895) Mollusca: Pulmonata: Zonitidae). *The Nautilus* **91**(4) in this issue.

Solem, A. *In Press.* Systematics of non-marine gastropods, other than Basommatophora. *In* Pulmonata, vol. 2, Systematics, Evolution and Ecology. Academic Press.