Convergence in Pulmonate Radulae

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(4 Plates)

Optical observations of pulmonate radulae have revealed numerous similarities in cusp outlines, but the depth of field limitations inherent to optical study have limited the amount of data obtainable. Pilsbry (1893–1895: xiii–xiv) summarized the basic patterns of variation in cusp structure, focusing on departures from a primitive tricuspid pattern either to the broad, gouge-like cusps found in arboreal snails or a reduction to bicuspid or unicuspid structures. Despite numerous drawings of radular cusps published subsequently, our knowledge concerning the trends and patterns of radular evolution remains essentially at the level of Pilsbry's summary.

The scanning electron microscope is a tool that will revolutionize our knowledge of radular structure. Summaries of the initial uses of this instrument in malacology and a report on radular preparation and viewing techniques recently have been published (Solem, 1970, 1972). The latter paper reported the existence of an interlock system between the rows of teeth during feeding. Sympatric species of Australian Camaenidae were figured to show varying patterns of interlock.

This paper traces the evolution of very similar support mechanisms in the endodontoid family Charopidae, surveys stages in the evolution of algae-scraping cusps in the Enidae, and demonstrates the functionally identical, but structurally different, pattern of cusp structure in the Partulidae.

ACKNOWLEDGMENTS

Illustrations for this paper were made at the Electron Optics Laboratory of the American Dental Association during cooperative research on the feeding mechanisms of mollusks. I am indebted to Dr. Harvey Lyon, Mr. John Lenke, and Mr. George Najarian of the ADA for invaluable technical assistance in SEM operation, and to Miss Barbara Walden, Mrs. Nancy Kozlowski, and Mrs. Dorothy Karall for assistance with specimen and manuscript preparation. The quality of the SEM photographs in Solem (1970, 1972) and this paper owe much to the skill and dedication of Mr. Fred Huysmans, photographer at Field Museum of Natural History. Work on the Charopidae was done under sponsorship of National Science Foundation Grant GB-6779. Their support is gratefully acknowledged.

MATERIALS AND METHODS

Specimens from the alcohol collections at Field Museum of Natural History were prepared for SEM observation according to the techniques outlined in Solem (1972). After initial orientation and viewing of the radula at 100× to 500× magnification, detailed observations were made from a variety of angles at 1 000× to 6 000×. The illustrations published here are selected from more extensive sets of photographs and were chosen to demonstrate the particular points under discussion rather than to show the overall tooth patterns and intergroup changes in cusp structure.

SYSTEMS OF SUPPORT

Snails feed by a complex set of movements involving protrusion of the radula and its supporting cartilages, moving the cartilages in relation to the substrate, and pulling the rows of teeth forward, up and around the tip of the cartilages, and then back into the mouth. The teeth are arranged in horizontal rows with the cutting edges (cusps) pointing towards the posterior of the radula. Complex folds and rotational movements mean that at times the cusps point towards the anterior end of the animal, at the moment of rounding the odontophoral tip they point towards the top of the animal, and after rounding the tip they point towards the posterior. Tooth orientation in terms of the body axis shifts with the stage in the feeding stroke. As a result the use of "anterior-posterior" terminology is best limited to ends of the radula and should not refer to body axis orientation.

When teeth in one row are brought into contact with a food source and cut or slice into the object, resistance pressure on the cusp is transmitted to the anterior portion of the basal plate (since the cusp points backward). In genera such as *Papuina* (SOLEM, 1972: figs. 12–16) there is a long anterior extension of the basal plate. Resistance encountered by the cusp is buttressed by this extension pressing against the underlying odontophoral cartilage.

The Australian Camaenidae were shown (SOLEM, 1972: figs. 21–29) to have very different patterns of support, with the anterior end of the tooth encountering resistance being forced down into contact with the posterior portion of the basal plate belonging to the tooth in the next anterior row. The three rather closely related Australian genera showed quite different systems of interlocking for the lateral teeth, although the pattern of interlocking for the marginals was virtually identical. Many other families show similar adaptations.

Evolution of Interrow Support Systems in the Charopidae

The Charopidae are the largest endodontoid family, with an extensive and complex radiation in Australia, New Zealand, New Caledonia, Lord Howe Island, Melanesia, Micronesia and part of Polynesia. Some species are known from South Africa and South America. This is the group variously referred to or fragmented into the Flammulinidae, Phenacohelicidae, Charopidae, and Pseudocharopidae by most workers. Data concerning its differentiation from the Punctidae and Endodontidae is presented elsewhere (SOLEM, in preparation). Here it is sufficient to note that the basic radular pattern is for tricuspid central and lateral teeth, with the marginals variously altered.

The commonest form of the teeth is found in such diverse areas as St. Helena, South Africa, Australia, New Zealand, Tonga, and South America. A good example of this type is *Pseudocharopa pinicola* (Pfeiffer, 1854) from Lord Howe Island (Figures *1*, *2*). The central tooth (middle row in Figure *1*) is tricuspid and slightly but distinctly smaller than the adjacent laterals. Ectoconal and endo-

Explanation of Figures *1* to *6*

Pseudocharopa pinicola (Pfeiffer, 1854)

Figures *1* - *2*: Station 2, Max Nichol's Memorial, north end, Lord Howe Island. Field Museum of Natural History number 127872.
Figure *1*: central and first lateral teeth from posterior end of radula × 2320
Figure *2*: early marginal teeth × 2330

Maoriconcha oconnori (Powell, 1941)

Figures *3* - *4*: Bock Peak, near Mt. Stevens, Wakamarama Range, Collingwood, West Nelson, South Island, New Zealand (*ca.* 172°27′ E, 40°48′ S). Auckland Institute and Museum.
Figure *3*: early lateral teeth × 1545
Figure *4*: mid-marginal teeth × 1570

Suteria ide (Gray, 1850)

Figure *5*: Waiwera-Pohoi Road, north of Auckland, North Island, New Zealand. Field Museum of Natural History number 135430. Two lateral teeth with right tooth pulled partly loose from the basal plate × 2935

Mystivagor mastersi (Brazier, 1876)

Figure *6*: Station 17, near Goathouse, northeast slope of Mt. Lidgbird at 1200 feet elevation, south end of Lord Howe Island. Field Museum of Natural History number 127963. Early to mid-lateral teeth showing flared anterior basal plate with teeth in both elevated and resting position × 1315

Explanation of Figures 7 to *12*

Draparnaudia michaudi (Montrouzier, 1859)

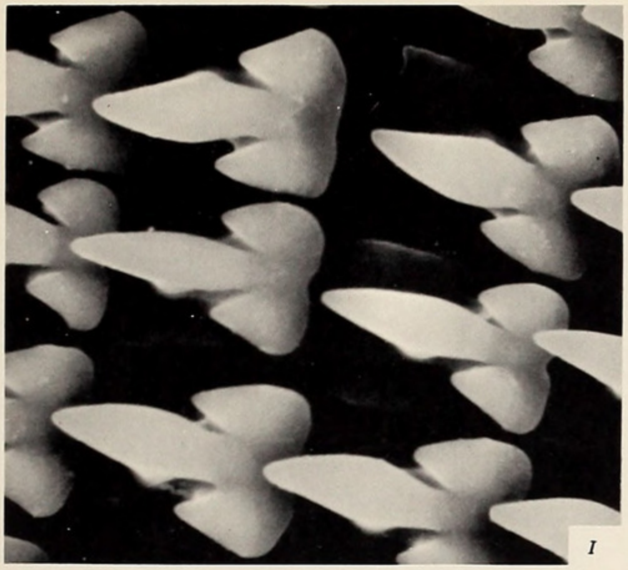
Figures *7* - *8*: Station NC-13, Heinghene, northeast coast of New Caledonia. Field Museum of Natural History number 159299.
Figure *7*: central and early lateral teeth × 1480
Figure *8*: mid-marginal teeth from right side of radula at posterior end × 1470

Amimopina macleayi (Brazier, 1876)

Figures *9* - *10*: Little Stuart River, Silver Plains, Cape York Peninsula, Queensland, Australia. Australian Museum, Sydney, number C63785
Figure *9*: central and lateral teeth viewed from a moderately high angle looking diagonally anteriorly × 745
Figure *10*: mid-marginal teeth × 728

Rhachistia histrio (Pfeiffer, 1854)

Figures *11* - *12*: La Roche, Mare, Loyalty Islands, New Caledonia. Field Museum of Natural History number 109435.
Figure *11*: central (lower left) and early lateral teeth viewed from almost directly above × 1575
Figure *12*: central and lateral teeth viewed from about a 55° angle looking diagonally forward × 835



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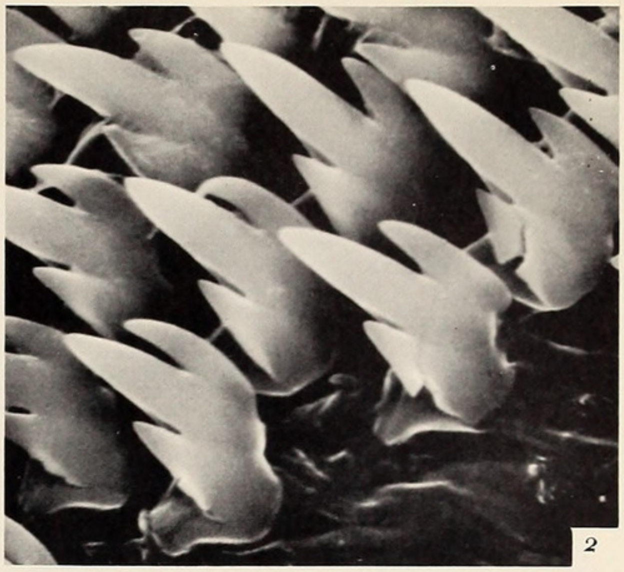

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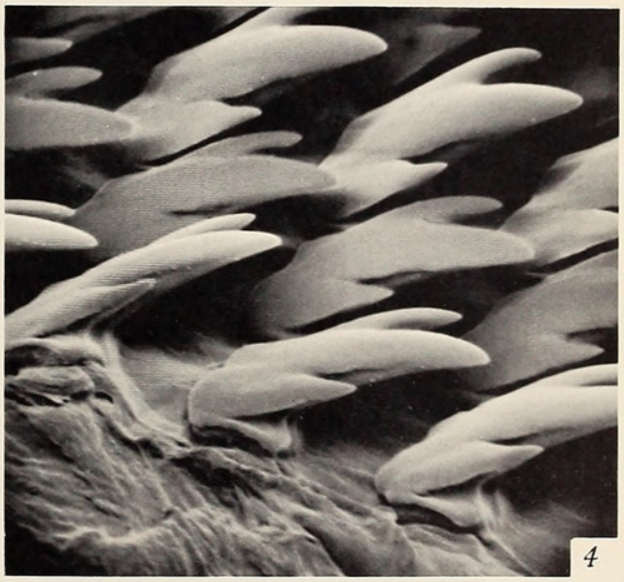

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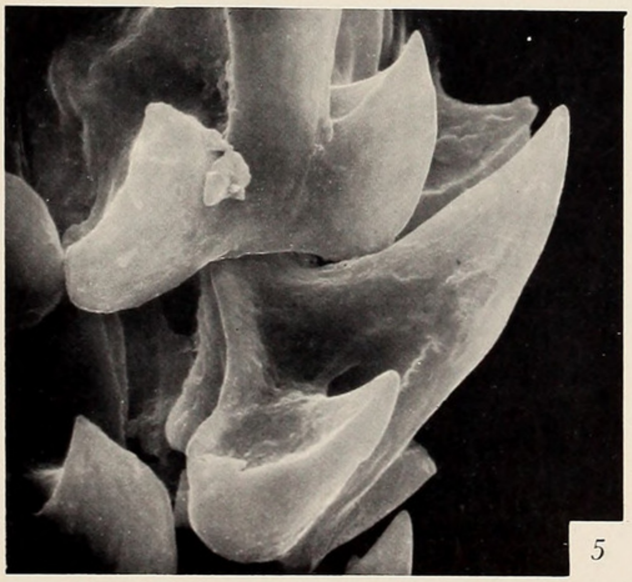

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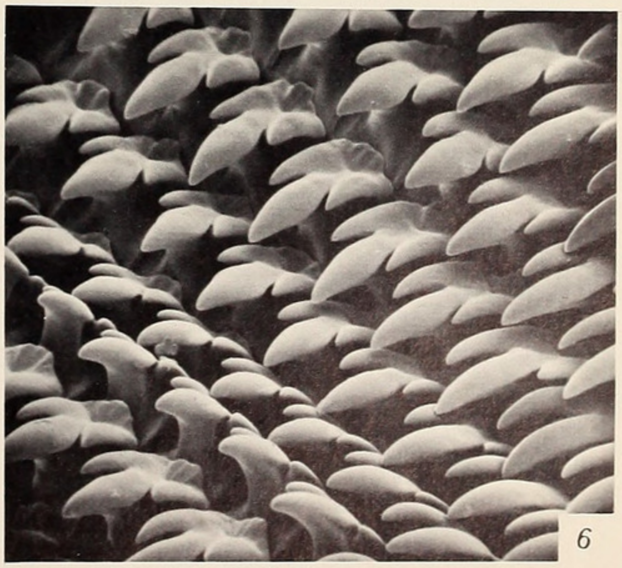

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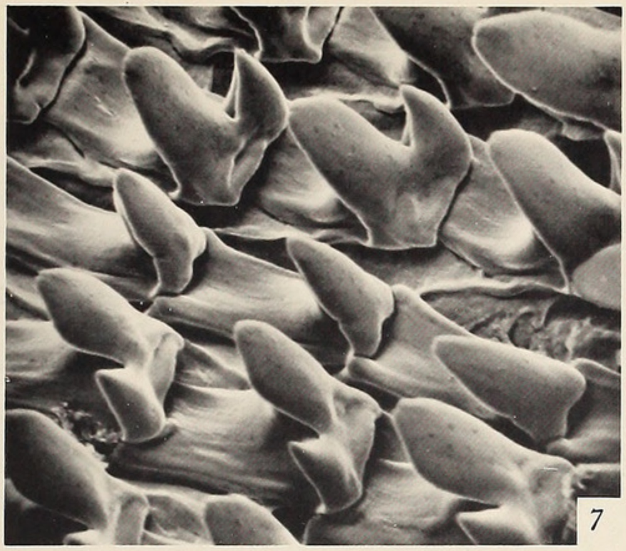

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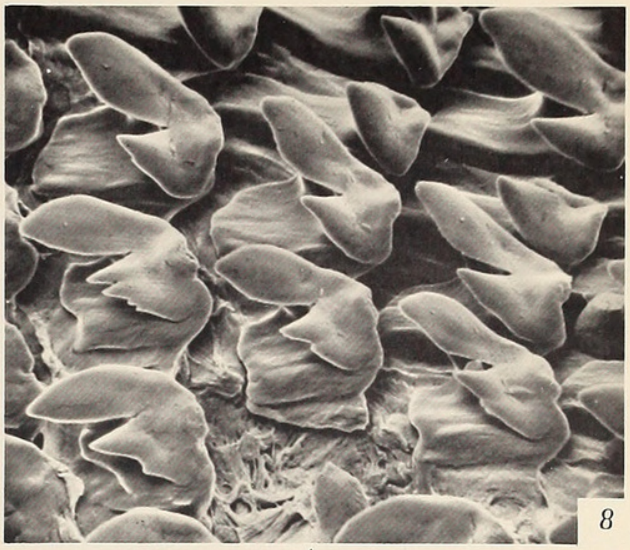

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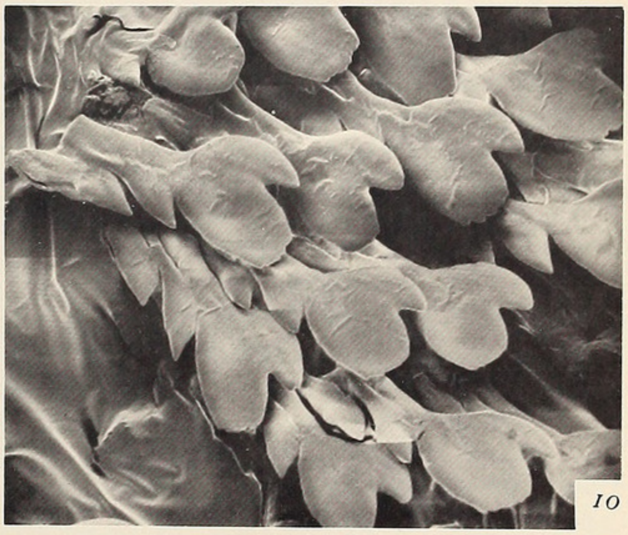

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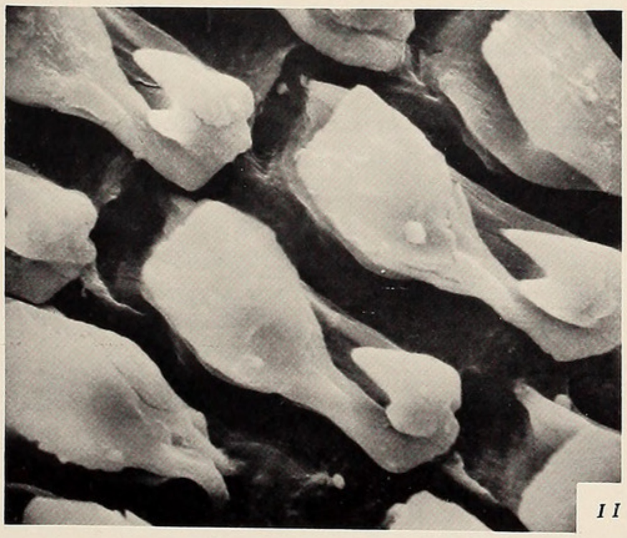

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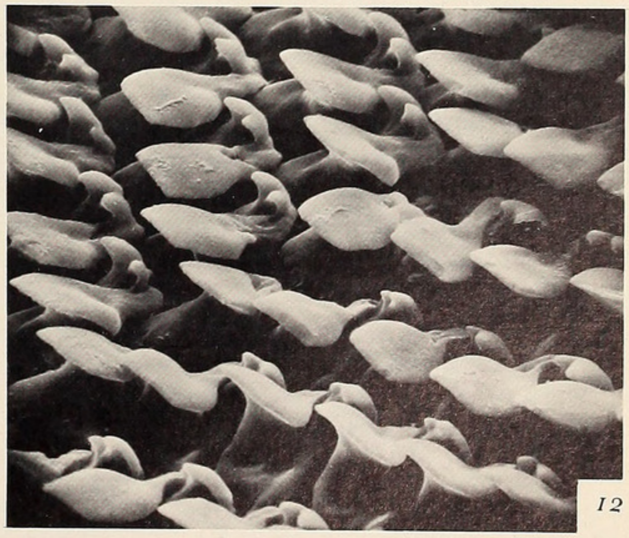

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