

THE SUPRAMARGINAL RIDGE IN CERTAIN AMERICAN SNAILS

DAVID T. JONES,

Associate Professor of Zoology, University of Utah
(on leave of absence for one year);
Assistant in Microscopical Anatomy,
Indiana University School of Medicine

INTRODUCTION

It is well known that the periostracum of mussels and clams is secreted in a groove of the mantle margin alongside a roll of high columnar cells (Jones, 1925-27, Figs. 11 and 13). Few persons, however, are aware that the periostracum of the snail shell is secreted from its mantle margin in essentially the same way, from a supramarginal groove in front of a supramarginal ridge (Jones, 1935, Plate I). In the bibliography of a previous article (Jones, 1935) are references which will lead those interested to the literature.

In Europe, Burkhardt, Roth, and others have studied the supramarginal ridge of *Helix pomatia*; Matthes, *Helix pisana*; Eckhardt, *Vitrina pellucida*; Beck, *Buliminus obscurus*; Napela, *Helix arbustorum*; not to mention the works of Longe and Mer, Moynier de Villepoix, Simroth, Zill, Biedermann, Annandale, Prashad, and others. In this same article is described the mantle of the tiger snail, now designated as *Discus alternatus* (Say), one of the very few descriptions of the mantle margin of an American snail. The present article attempts to present the comparative histology of the mantle margins of twenty-one additional species of American snails, as to the ridges and grooves in the periostracum secreting region. While such an article must necessarily be more or less superficial, the comparative view of a wide section of the field cannot but be helpful in promoting later more detailed studies. The former is beyond the immediate reach of the average graduate student, but the latter constitutes a compact, delimited problem.

Before selecting the sections to be drawn, several hundred research slides in the author's private collection were studied. Most of these are on mantles, among which are included several recently prepared serials to help solve doubtful points. European

and Asiatic specimens in this collection were disregarded, as these sections confirm drawings already available in the literature. In most cases sections of from three to eight or ten individuals have been studied. In a few cases, which are noted, sections from one specimen alone have been presented, where these seem to have been cut squarely across. Not only has variation between individuals in the same species made selection of sections difficult, but also variation of ridges and grooves within the same mantle. For example, the phase of a ridge on the columellar lip of the mantle may appear very different from the phase of the same ridge on the outer lip. Personal judgment has had to be used rather arbitrarily in the selection of good sections. In most cases one of the more complex phases was selected, because therein could be demonstrated the most of the more-frequently-occurring structures, which one comes to regard as "characteristics" for that species.

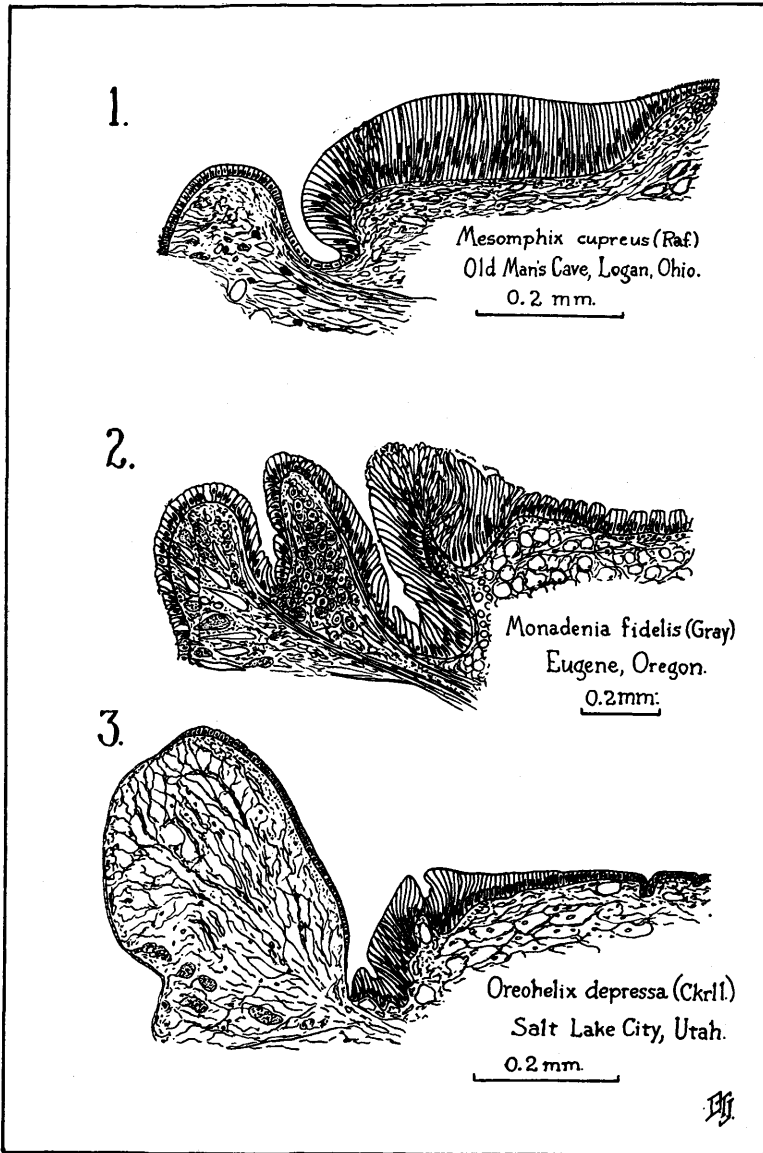
As to nomenclature, in Figure 2 the supramarginal ridge is shown as the heightened epithelium continuous with the low epithelium on the reader's right. To the left of this is the supramarginal groove, to the left of which is an "intermediate ridge," to the left of which in turn is a "secondary groove," to the left of which again is the "frontal ridge," the left margin of which is continuous with the front of the mantle. The terms in quotation marks are purely arbitrary, assigned for convenience in the following descriptions.

DESCRIPTIONS AND DISCUSSIONS OF FIGURES

Figures 1, 2 and 3 are introductory, representing the mantle edge of a large land snail from each of the three great snail regions of America respectively. Figure 1, of *Mesomphix cupreus* is of a snail commonly occurring in southern Ohio and West Virginia. It has a fragile shell covered with smooth shining periostracum. These mantles tend to show a flattened supramarginal ridge at least on the outer lip of the mantle, often extending on to the columellar lip also. Some individuals show the ridge divided into two, three, or more flaps, similar to that of another species shown in figure 14. This condition, when present, is usually more pronounced on the outer lip of the mantle.

Monadenia fidelis, the beautifully colored, heavy shelled snail of the Oregon region, has a shining periostracum. The outer edge of its mantle (fig. 2) has a double groove which usually extends over to the columellar side. Usually the secondary groove is non-secretory, but here it appears to be secretory. It is not known whether the two grooves function simultaneously. The intermediate ridge between the two grooves is of variable height. Flaps of clear epithelial cells, similar to the one shown, tend to project into the supramarginal groove

from its floor. The crest of the supramarginal ridge is often formed of sinuously curved cells, which shatter when cut.



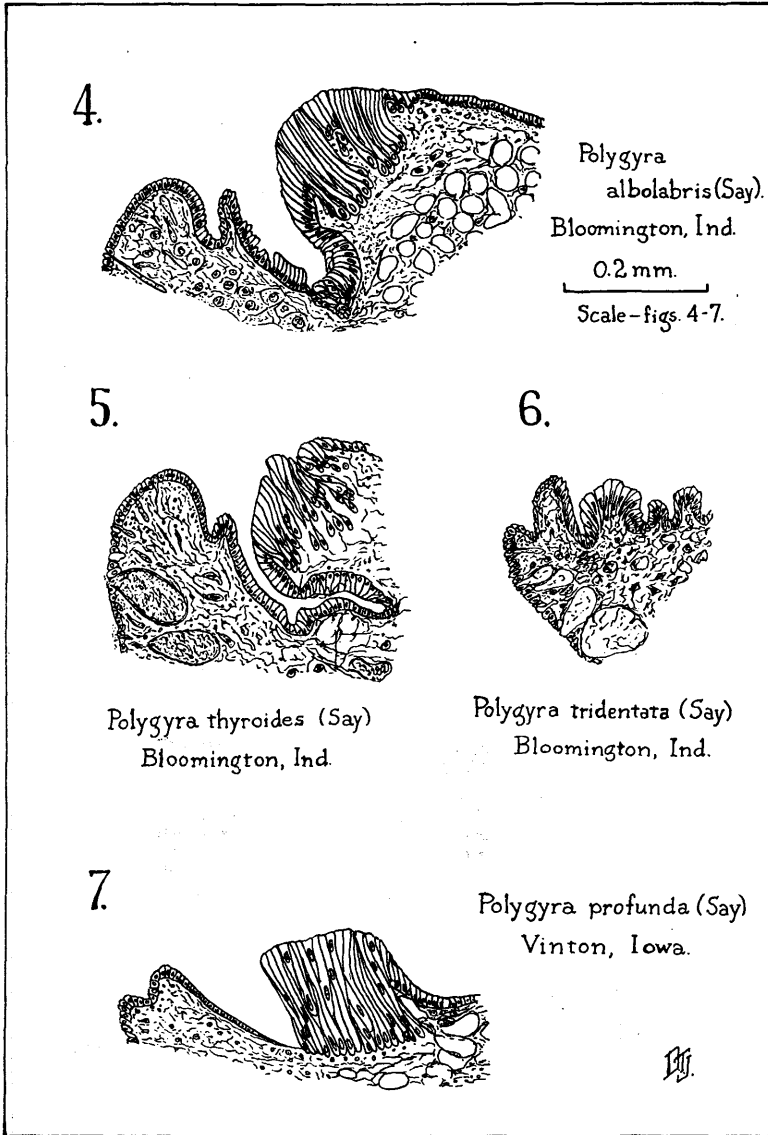
Oreohelix depressa, the widespread land snail of the Great Basin, has a heavy, irregularly-ribbed shell, which has very little periostracum in the mature specimens. The supramarginal ridge and groove are

very variable. On the outer lip of the mantle, the former may be as complex as that shown (fig. 3). An unusual situation is occasionally found, where large unicellular mucous cells empty into the supra-marginal groove. There is a tendency for the supramarginal ridge to be divided into flap-like groups of cells. The mantle margin does not greatly resemble that of most of the groups of large land snails. Some of the above features arouse suspicion that the supramarginal ridge may involute to some degree after shell maturity has been reached, though our present material is insufficient to so conclude.

Many of the *Polygyra* examined (figs. 4 and 5) show a basal grouping of the tall cells of the supramarginal ridge. Such has been reported, not only in European Helices, but also in certain of the Viviparidae (aquatic) by Prashad. It appears as a downgrowth from the ridge of groups of epithelial cells into the connective tissue beneath. The supramarginal ridge (but not the intermediate ridge) is usually obsolete on the columellar side of the mantle. This is a very confusing situation to analyze until the continuity of the ridges can be traced in serials. The supramarginal groove sometimes has a pocket-like cleft, not always continuous in the floor, as shown in figure 5. It is difficult, even with a number of slides, to know whether to interpret these as pockets in the floor of the groove, or as twisted sections of the groove recut. The intermediate ridge, varying in size and shape, is usually present, and with the groove usually continues onto the columellar side of the mantle.

In my material, *Polygyra albolabris* (fig. 4) shows little difference between individuals. *Polygyra thyroides* (fig. 5) is essentially of the same plan as *albolabris*. However, in *Polygyra tridentata* (fig. 6) the mantle edge exhibits a barely-differentiated supramarginal ridge, though the intermediate ridge is prominent. Scant material of *Polygyra monodon* (Rackett), not figured, shows even less differentiation. Slides of *Polygyra profunda* show considerable individual variation, ranging from the type figured (fig. 7) to one showing an obsolete supramarginal ridge, but with a more pronounced intermediate ridge. European workers have suggested in such cases that the supramarginal ridge may disappear after the shell reaches maturity. (Sexual maturity is attained in most snails long before shell maturity, the latter marking that stage when additions to the shell cease.) Unfigured material of *Polygyra elevata* (Say) shows a condition intermediate between the figures of *P. thyroides* (fig. 5) and *P. profunda* (fig. 7), but with high columnar epithelium on both slopes of the supramarginal groove, also with the supramarginal ridge merging more gradually with the epithelium beneath the shell. *Polygyra palliata* (Say) (mantle figured by Jones, 1937, fig. 5r), is also of special interest, because of the evenly-arranged, hair-like spines of periostracum covering its shell. Where and how these are formed are as yet unexplained. One European malacologist, working with a pilose shell, advanced the hasty conclusion that the "hairs" were pressed into shape as the horny periostracal material was pressed between the two slopes of the supramarginal groove as it was emerging, a semiliquid mass. This explanation, however, could hardly apply, as smooth shells have as pronounced similar mantle structures. In *P. palliata* there is the possibility of

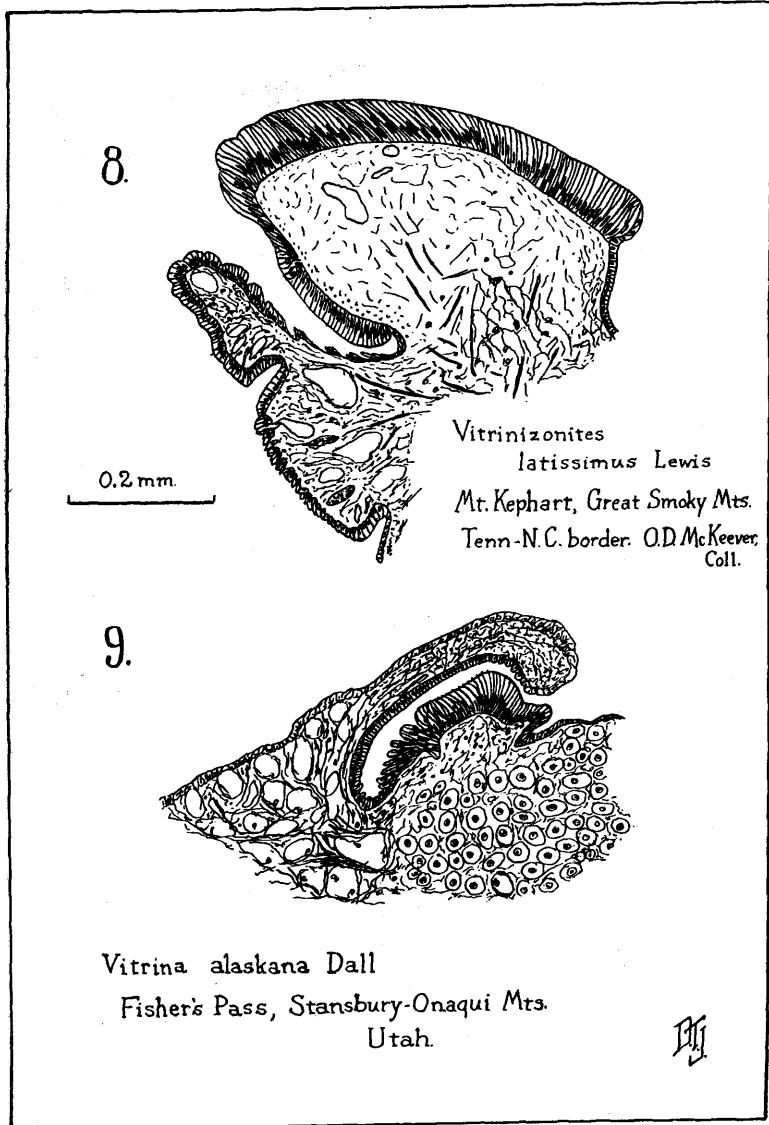
either a groove modification or a deep pocket in the bottom of the groove; my material admits of ambiguous interpretation. Clear



cut sections of *Polygyra appressa* (Say) were not drawn, as they were so nearly like the figure shown for *P. thyroides* (fig. 5).

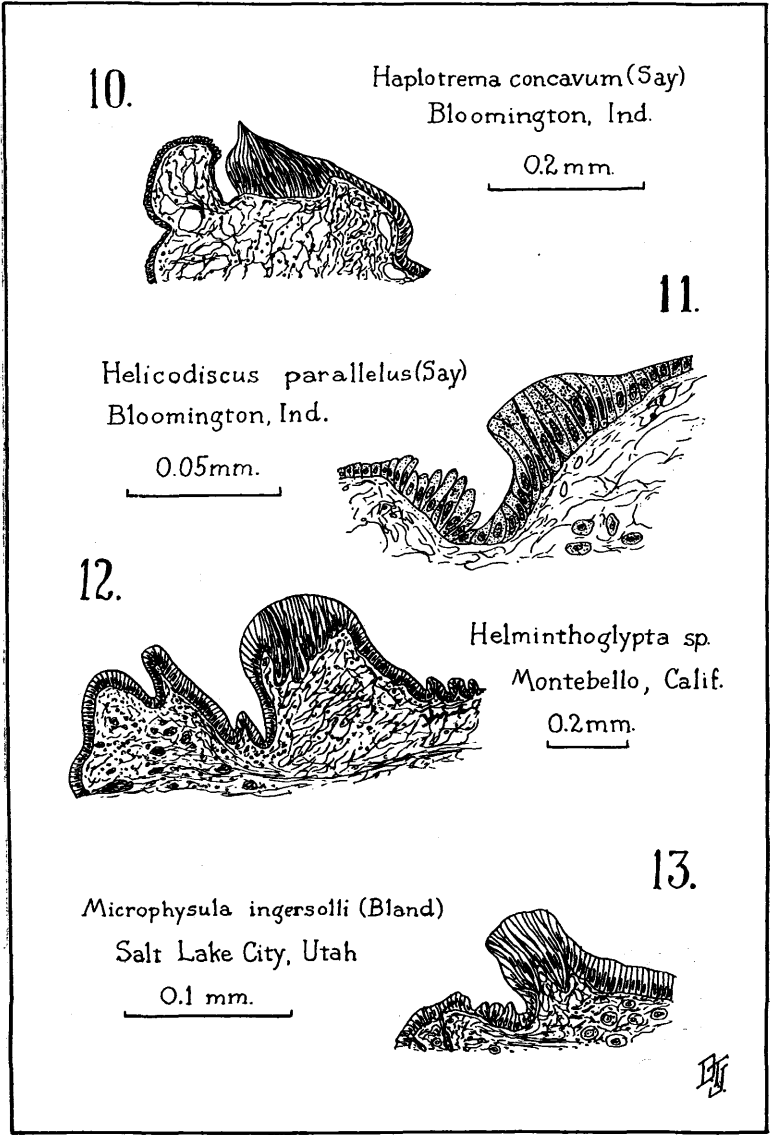
Eckhardt's bizarre figures of the mantle of *Vitrina pellucida* from the Alps, aroused curiosity as to our species of *Vitrina*. I have been

unable to secure live specimens of our eastern *Vitrina*, but the western *alaskana* shows equally as bizarre patterns, one of which is drawn (fig. 9). Here the frontal ridge sometimes arches over the much-



lobulated supramarginal ridge, in a way such as to suggest the manipulating or shaping of the fragile membranous shell, which often has so little calcareous backing that it collapses when touched. On

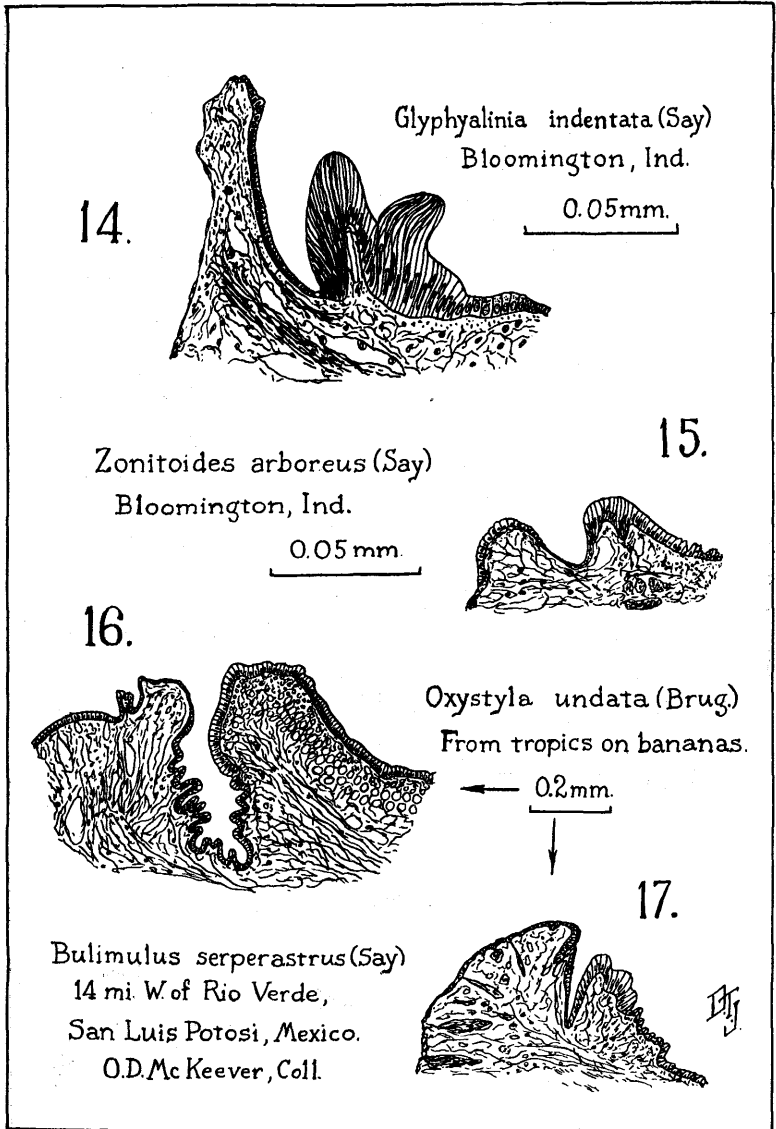
this side of the Atlantic, we are fortunate in having a queer giant vitrinoid, *Vitrinizonites latissimus*, supposedly a mutant glacial relict, now isolated in the Great Smoky Mountains. Of those which O. D.



McKeever attempted to send me, only one came through alive. From sections of this, I have drawn the queer mantle margin shown in figure 9, which shows many *Vitrina* modifications. When investigated more

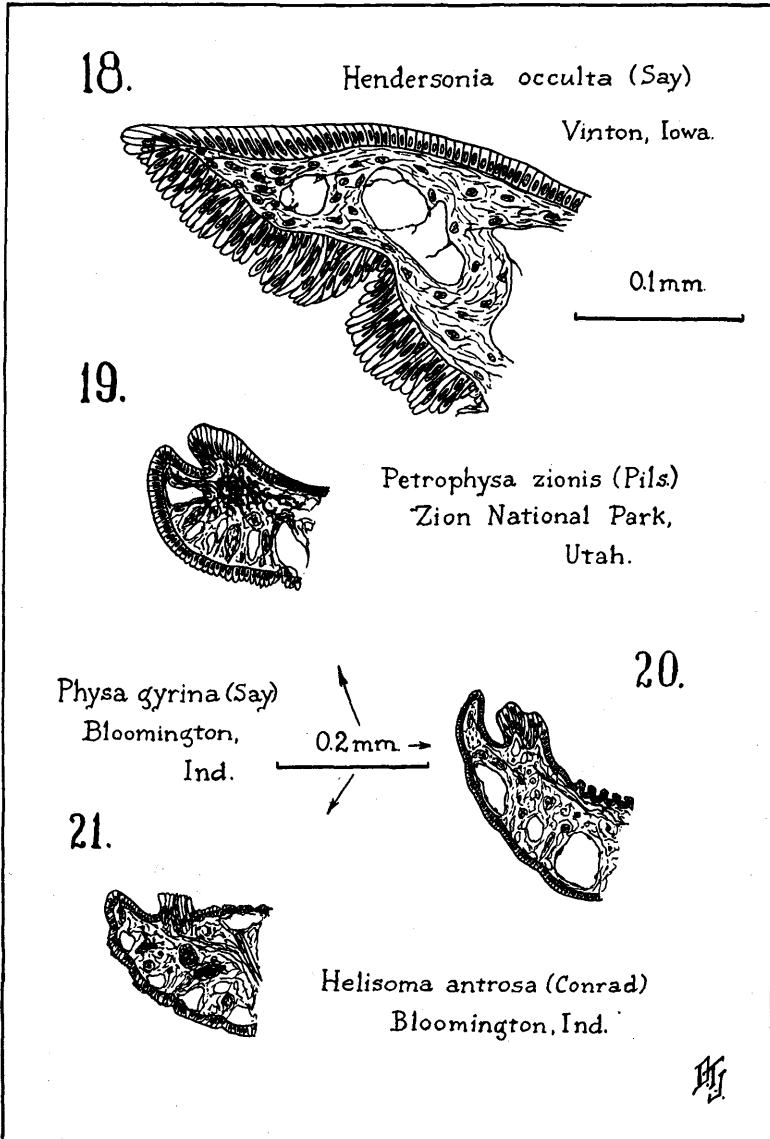
thoroughly, it may show as much variation within one mantle as is shown by the western *Vitrina*.

Haplotrema concavum, the only eastern representative of this green-



shelled, carnivorous genus, exhibits a pattern (fig. 10) quite its own. The ridge is usually sharp-pointed, and is composed of long cells twisted out of one plane, which generally causes the ridge to break when sec-

tioned. *Helminthoglypta*, probably *tudicatula* (Binney), is the only one of that genus of large California land snails examined (fig. 12). Note its similarity to *Polygyra* (figures 4 and 5), also to *Monadenia*



(fig. 2). In other specimens this *Helminthoglypta* shows a more prominent intermediate ridge than the one figured, which separates off a distinct secondary groove that may be secretory as in *Monadenia*.

In some specimens both grooves are present on both inner (columellar) and outer lips of the mantle.

Among the small snails the endodont, *Helicodiscus parallelus* (fig. 11) exhibits a clear-cut, but extremely simple supramarginal ridge and groove, usually only on the outer lip of its mantle. *Microphysula ingersolli* (fig. 13), a small Utah helicid, shows more complex tendencies toward the helicid structure of *Polygyra*. Sections of only one specimen of pupillid, *Gastrocoptera armifera* (Say), unfigured, show a short supra-marginal ridge approximately five cells in length. The ridge is less sharply defined than in *Microphysula*, and the groove is barely differentiated. The mantle of *Zonitoides arboreus* (fig. 15) shows a structure simpler than that of the helicids, tending, with great variation, as much perhaps in that direction, as toward the glassy snails, with which it is commonly allied systematically. As has been mentioned, another large zonitoid, *Mesophix cupreus* (fig. 1) tends even more strongly toward *Vitrea* than the figure shows. The only one of the ordinary glassy snails (*Vitrea*) examined was *Glyphyalinia indentata*. It shows a very variable supramarginal ridge, which may be split as shown (fig. 14). Cells just back of the supramarginal ridge show golden granules in the Golgi region. Of course, *Vitrina* (fig. 9) and *Vitrinizonites* (fig. 8) are considered closely allied to *Vitrea*, but as shown their mantle margins are much more highly differentiated.

Of Neotropical land snails, I have examined only two, the *Oxystyla* that seals itself on bananas and is thus imported to our northern states, and several specimens of *Bulimulus serperastrus* (fig. 17) shipped alive to me by O. D. McKeever. The former (fig. 16), a single specimen, shows no heightening of the epithelium over a connective-tissue ridge. The supramarginal groove is well developed.

In this survey the simplest ridge found was that of *Helicodiscus parallelus* (fig. 11). However, one land snail, *Hendersonia oculata* is reputed to be far more primitive (H. B. Baker, 1925). As it is found only in isolated patches in widely scattered regions, it is not readily accessible. However, I had previously found it in the vicinity of Vinton, Iowa (Jones, 1930, also 1931). From this locality mantles were first secured which showed no supramarginal ridge or groove. Dubious of these observations, some years later, several whole animals were secured and sectioned serially. While some of these sections were not cut in the right direction for the study of these parts, a few were. Careful study of these reveals no ridge or groove, either on the outer mantle (fig. 18) or on the inner strap-like mantle. It is possible that the simplicity in this mantle may not be correlated with its primitiveness, but with the fact that the shell is practically devoid of periostracum when fully developed.

Another primitive mollusk described by Pilsbry (1925), *Petrophysa zionis*, lives on the vertical walls of Zion National Park, where water trickles over the cliff. Last year, Perry Plummer brought several back to Salt Lake City alive, but most did not fix well. However, a few show on the outer lip (fig. 19), and also to some extent on the inner, a ridge and a groove, not much different from that of the eastern pond snail, *Physa gyrina* (fig. 20). The *Physa* mantle has much epithelial

pigment in the region back of the supramarginal ridge. Subepithelial pigment may also be present. The only other mantle of a native aquatic snail observed has been that of the planorbid, *Helisoma antrosa* (fig. 21).

In conclusion, may it be re-emphasized that the limits of variation of mantle ridges and grooves should be intensively studied for each snail, both within single mantles, and between different individuals of the same species. Little is known at present of the correlation between mantle structures and the shell. Mantle ridges and grooves may serve other functions than merely secreting the periostracum, as shaping the drying periostracum, clasping and protecting the recently-formed edges of the shell, stiffening the mantle edge for support of such membranous shells as that of *Vitrina*, or closing the space between the deeper mantle and the shell, not only for protection but also to conserve shell-forming liquids. Most digitations of the mantle arise from the front of the mantle rather than from the mantle margin, where the above-described ridges and grooves are located.

BIBLIOGRAPHY

- Baker, H. Burrington.** 1925. Anatomy of *Hendersonia*: A Primitive Helicid Mollusk. Proc. Acad. Nat. Sci. Phila., Vol. 77, pp. 273-303. Pls. 7-10.
- Jones, David T.** 1925-27. A Study of *Tritogonia tuberculata*, the Pistol Grip Mussel. U. of Iowa Studies in Nat. Hist., Vol. 11, pp. 3-16.
1930. Notes Taken in the Vicinity of Vinton, Iowa. Naut., Vol. 43, pp. 118-119.
1931. Red Cedar River Collections (Iowa). Naut., Vol. 44, pp. 87-91.
1935. The Formation of Shell in the Tiger Snail. J. Morph., Vol. 57, pp. 547-569.
1937. A Comparative Study of Certain Goblet Cells. Bull. U. of Utah, Biol. Series, Vol. 27, pp. 3-15.
- Pilsbry, H. A.** 1925. A Fresh-water Snail, *Physa zionis*, Living under Unusual Conditions. Proc. Acad. Nat. Sci. Phila., Vol. 77, pp. 325-328. Pl. 11.
-