GASTROPOD RADULAE have been used by numerous workers as tools for determining relationships. Acceptance of radulae as keys to relationships and as diagnostic characters has not, however, been unquestioned. GRANT (1933) contended that radulae do not provide reliable characters because they bear the stress of contact with the environment and are, therefore, subject to rapid convergent and divergent evolution. CARRIKER (1943), working with Lymnaea stagnalis appressa Say, and HOWE (1960), working with members of the Pleurocerididae, found sufficient variability in the denticular pattern to cast doubt on the reliability of the radula for specific diagnosis.

A major objective of this study has been an examination of the value of radular structures as an aid to the clarification of intrageneric relationships, using 9 species of Tegula from the west coast of North America.

The history of the taxonomy of Tegula is a tortuous one. The first west coast species described, or sometimes figured and named but not described, were assigned to Trochus. Subgenera were proposed from time to time, two being Omphalus and Chlorostoma. These were later used as genus names under which several species were described. Still later those became subgenera in Tegula. Since Tegula has not been monographed many unresolved contradictions in taxonomy and indicated relationships remain.

OLDROYD (1927) placed Tegula funebralis, T. gallina, T. brunnea, T. montereyi and T. rugosa in the subgenus Chlorostoma; T. pulligo in the subgenus Promartynia (as proposed by DALL, 1909); and T. aureotincta and T. mariana in the subgenus Omphalus.

GRANT & GALE (1931) retained Tegula funebralis and T. gallina in the subgenus Chlorostoma, but they believed that T. brunnea belonged with T. aureotincta in the subgenus Omphalus. They accepted the subgenus, however, as doubtful when based on shell characters alone.

KEEN (1958) placed Tegula rugosa as the only west coast member of the subgenus Omphalus. She contends that an early misinterpretation of the type species lead to the misuse of Omphalus for a series of Tegula species which she places under the subgenus Agathistoma which includes one animal considered in this study, T. mariana.

Only FRITCHMAN (1965) has suggested relationships based on radular structure. He placed together Tegula pulligo, T. aureotincta, T. brunnea and T. montereyi. Tegula gallina and T. funebralis were placed in another group. Four other Tegula were grouped together with T. mariana and T. eiseni considered to be closely related and with T. rugosa and T. regina as less closely related. FRITCHMAN did not consider subgeneric groupings but simply stated that the radulae of certain species were more like each other than those in other groups.

PREPARATION OF RADULAE

Each snail was removed from its shell and placed in a caustic solution. The radula was removed according to the method used by FRITCHMAN (1960). Following extraction, the radulae were stained either with aceto-carmine or fast green and then mounted tooth-side up, either as whole mounts or, following VERD'COURL (1948), some radulae were teased to obtain isolated teeth after being placed in Canada balsam.

The stainability of the teeth changes along the length of the radula as found by RAVEN (1958). Fortuitously, that portion of the radula which stained most distinctly was just anterior to the area of proliferation where the teeth show features which are later worn down in older teeth. This area was the one which was utilized for critical study.
PHOTOMICROGRAPHS

Photomicrographs were prepared from the slides for comparison of radular structures. On comparison of Tegula pulligo (Plate 54, Figure 1) with other Tegula species, the radula was found to be quite dissimilar. The extent of difference would confirm Dall’s erection of a separate subgenus, Promartynia, for this species. Tegula pulligo is primarily found off-shore on kelp while the rest of the Tegula species are chiefly found scraping algal film from rocks (Smith & Gordon, 1948). Consideration of the shell shows that it is not radically different from other Tegula species. This lends support to the expectation that the radula might undergo edaphic evolution resulting in quite distinctive radular structure in an animal whose shell evolved more conservatively.

The great similarity of the laterals, especially the fifth laterals, of Tegula aureotincta and T. brunnea (Plate 54, Figures 2 and 3) would seem to lend credibility to the standing of Omphalus. The position of Chlorostoma would seem to be substantiated by the close similarity between T. funebralis and T. gallina. Both possess a dorso-lateral recurved process on the fifth lateral (Plate 54, Figure 4 and Plate 55, Figure 5). Thus, the subgeneric groupings as understood by Grant & Gale (1931) are supported by this study.

Tegula eiseni and T. mariana would seem to be closely related on the basis of commonality in: obtuse blades on the lateral teeth; all round marginal teeth; a “beaked” dorsal horizon line where the cusp joins the stem of the fifth lateral (Plate 55, Figures 6 and 7). This is in agreement with Fritchman’s (1965) suggested grouping.

Tegula rugosa (Plate 55, Figure 8) appears to stand alone in radular features. This would seem to confirm Keen’s (1958) placement of it in a separate subgenus.

Tegula montereyi, in accord with Fritchman (1965), was found to be variable in radular structure. This variability suggests that this organism warrants further study before its systematic placement is determined.

It was concluded that denticular patterns on the radula provide an adequate means for deducing intrageneric relationships for 8 of the 9 Tegula species considered, T. montereyi being the exception.

CRITIQUE OF FRITCHMAN’S METHODS

Fritchman’s (1965) suggested intrageneric relationships were based, in part, on a consideration of the following data and on a numerical treatment of the length/width ratio of the central tooth expressed as a per cent. The slides were examined microscopically and the following information was recorded for each: the character of the lateral teeth (pointed or blunt); the point where the marginal teeth serrations begin; where the serrations become complete; and, the length and width of the central tooth measured in micra.

The range of his ratios was graphed and the range of the ratios obtained in this study was graphed beside his (Text figure 1). It was seen that the addition of as few as 3 samples to his might greatly alter the range of ratios for a given species and that the ranges of data overlap. He also placed emphasis on the average of the ratios. However, a consideration of all the averages proved essentially meaningless.

Still another character used by Fritchman was that of noting the point of conversion of the tip of the marginal teeth from pointed to round. It was quite clear that some teeth were pointed and that others, later in the row, were rounded. The conversion in some species is very gradual and determining what tooth should be termed round was highly subjective. The ranges of these data, which overlap, were also graphed (Text figure 2).

Fritchman utilized two other characters of the marginal teeth: the point where serrations begin and the point where the serrations are complete. The use of these properties poses practical difficulties as the radula has a tendency to curl and in so doing may turn the teeth out of view. The problem is not easily overcome since critical counts may reach 25 teeth before serrations are complete and they may be as small as 3 μ across the base where they join the tooth. Of the 50 Tegula examined, only 28 could be seen well enough to obtain these data. An attempt

Explanation of Plate 54

Figure 1: Tegula pulligo (x 204) – Showing the fringed aspect of the third, fourth and fifth lateral.
Figure 2: Tegula aureotincta (x 204) – Portion of a radular row showing the fifth lateral (arrow).
Figure 3: Tegula brunnea (x 204) – Portion of a radular row showing the fifth lateral (arrow).
Figure 4: Tegula funebralis (x 204) – Portion of a radular row showing the third, fourth and fifth lateral. Note the dorso-lateral recurved process (arrow).
was made to graph them but the result was not subject to interpretation.

A consideration of the graphs and of the other data obtained by measuring and counting techniques lead to the conclusion that these are not valid devices for determining systematic placement of Tegula.

CORRELATION STUDY

Howe (1930) suggested that radula studies include the size of the shell as part of the requisite data. Accordingly, every shell was measured from the upper margin of the lip to the apex and from the upper margin of the lip to the farthest body whorl. A correlation study was made utilizing shell size and central tooth length and width. The simple correlation, \( r \), was found using the formula (Mosteller, 1961):

\[
r = \frac{(x_i - \bar{x})(y_i - \bar{y})}{NS_Sy}
\]

Results involving only 3 specimens were disregarded as being a statistically unreliable sample. According to Frank (1965), the shell width is inherently subject to less measurement error. Therefore, only data for samples larger than 3 and correlations utilizing shell width were considered as meaningful.

Examination of these data showed inconsistencies since three species, Tegula brunnea, T. funebralis, and T. rugosa, showed negative correlations implying an inverse relationship between shell and central tooth dimensions while the balance of the correlations for these and the other species considered were positive, indicating a direct relationship.

Considering that \( r^2 \) = the proportion of variances in Y predictable from or attributable to variations in X, it was possible to determine the relationship between shell size and central tooth measurements for all Tegula specimens studied (50 individuals). The square of the correlation coefficients indicated that 50% and 58% of the time the shell width and tooth size were related while the