Observations on the Shells of Some Fresh-Water Neritid Gastropods from Hawaii and Guam[1]

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Abstract

Observations on the fresh-water neritid prosobranch gastropods *Neritina vespertina* Sowerby 1849 and *N. granosa* Sowerby 1825 from Hawaii, and *N. pulligera conglobata* von Martens 1879 and *Septaria porcellana* (Linnaeus 1758) from Guam, have yielded a qualitative correlation between clinging ability of the animal and the degree of development of limpet-like shell characters. The hypothesis is put forth that the granular ornamentation on the shell of *N. granosa,* and possibly the presence of egg capsules on the shells of many fluviatile neritids (notably *N. pulligera conglobata* and *S. porcellana*) may create turbulence and minimize the effects of the strong current in which the animals live.

Methods

Shell dimensions were measured to the nearest tenth millimeter with Vernier calipers. Length was taken as the greatest distance from the apex to a point on the outer lip and usually coincides with the greatest linear dimension of the shell. Width is the greatest distance parallel to the outer edge of the parietal septum. Height is the greatest distance from a point on the dorsal surface to the plane of the opening of the shell measured perpendicular to the length and width dimensions.

Attempts at quantitatively measuring the force by which the animal clings to the substratum and the resistance against shear were not successful, but the qualitative differences in these properties between the various species are striking.

Names for the species discussed in this paper have been taken from Baker (1923), Kira (1962), and Habe (1964), and have been confirmed and augmented by Drs. E. A. Kay of the University of Hawaii and H. K. Mienis of the Zoologisch Museum in Amsterdam.

Observations

1. *Neritina vespertina* Sowerby 1849. The shell of this species is superficially

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much like that of the slipper limpet *Crepidula*, but the apical portion of the shell is produced into anterior and posterior wing-like extensions. Ornamentation consists of inconspicuous growth lines, but corrosion often causes the shell to be deeply pitted in the apical region. The shelf or parietal septum covers somewhat more than half the shell opening. Its outer margin is convex and smooth anteriorly and posteriorly, but concave and slightly serrated in the middle. The operculum is more or less typical of other Neritidae, but its abapical margin is uncalcified and membranous.

Data presented in Table 1 indicate that the width to length (w/l) and height to length (h/l) ratios may increase with length.

Table 1. Measurements of *Neritina vespertina* from Wainiha River, Kauai

l	w	h	w/l	h/l
19.5	17.1	6.2	0.877	0.318
20.7	18.2	6.7	.831	.324
22.9	21.0	7.3	.917	.318
24.2	22.2	8.8	.917	.364
26.5	27.4	9.2	1.04	.347
26.6	26.6	9.2	1.00	.347
28.0	27.1	9.4	0.968	0.336

Specimens of *N. vespertina* were collected on the upper surfaces of large basalt boulders in a fairly gentle current just above the mouth of the Wainiha River on Kauai, Hawaii, with no other gastropods present. The clinging ability of the animal is considerable, but resistance to a shearing force is not great. Upon being removed from the substratum, the snail retracts slowly into its shell, the abapical margin of the operculum jutting out beyond the plane of the opening of the shell in the process. When the animal is fully retracted, the plane of the operculum is flush with that of the adjacent portion of the parietal septum.

2. *Neritina granosa* Sowerby 1825. The shell is rather like that of *N. vespertina*, but the apex is more prominent and located more posteriorly. The most striking feature of the shell is the surface ornamentation, which consists of closely set, rather low granules or pustules and irregularly placed concentric riblets. Small individuals and the older portions of larger specimens have rather ill-defined granules and a smooth outer margin, but the concentric riblets are well developed. In older individuals granules and riblets are prominent, especially near the growing margin. In these specimens the outer margin of the shell, particularly the anterior and posterior edges, are distinctly crenulated. Most specimens have the concentric riblets worn away on the dorsal surface just abapical of the outer margin of the septum and in areas near the apex.

The septum is similar to that of *N. vespertina* except that the outer margin is smooth throughout. The operculum of *N. granosa* has a wider abapical membranous portion than in *N. vespertina*.

Data presented in Table 2 indicate that the width to length ratio decreases with increasing length ($p = 0.003$ by the U-test when comparing shells greater than 27.0 mm in length with smaller ones), but no trend can be observed in the height to length ratio ($p = 0.223$).

Table 2. Measuremtns of *Neritina granosa* from Kaluanui River, Oahu

l	w	h	w/l	h/l
22.9	21.0	8.7	0.917	0.380
25.1	22.8	10.0	.908	.398
26.7	22.8	9.1	.854	.341
26.7	25.2	9.6	.954	.359
26.9	22.8	9.3	.845	.346
26.9	24.0	9.5	.892	.353
27.8	23.0	10.1	.827	.363
27.9	24.5	10.4	.878	.373
28.5	25.2	10.4	.884	.365
29.6	24.6	10.8	.831	.365
30.2	26.5	10.6	.877	.351
30.4	27.1	10.8	.892	.355
30.7	27.6	12.8	0.899	0.417

Specimens of *N. granosa* were collected below Sacred Falls in the Kaluanui River on Oahu, Hawaii; no other gastropods were present. The species appears to be markedly rheophile, for all specimens seen clung to surfaces of basalt boulders directly exposed to the full force of the swift current, and not to surfaces where even a slight degree of shelter was available. About 80% of the more than 40 snails observed *in situ* were oriented with the posterior margin pointed toward the streambed. The force with which *N. granosa* clings to the substratum and the resistance to shearing are qualitatively much greater than in *N. vespertina*. Opercular movements and positions during and after retraction of the animal into its shell are similar in the two species.

3. *Neritina pulligera* (Linnaeus 1767) f. *conglobata* von Martens 1879. The shell of this species is less limpet-like than in the foregoing two species, being proportionately higher (Tables 3 and 4) and having a somewhat more restricted aperture. The plane of the parietal septum lies at a greater angle to the plane of the opening of the shell than in the other species discussed here, and its juncture with the main portion of the shell is more rounded.

The external surface of the shell is smooth except for the presence of irregular growth lines. All specimens observed, however, were covered with egg cases of their own species, particularly on areas of the dorsal surface closest to the substratum to which the animals cling. The presence of these capsules imparts a granular texture to the external surface of the shell.

The outer edge of the septum is weakly serrated throughout and bears a shallow depression in the middle. The operculum functions as in *N. vespertina*, but it is essentially calcified throughout.

Table 3. Measurements of *Neritina pulligera conglobata* from swift current, Tarzan River, Guam.

l	w	h	w/l	h/l
13.3	11.1	7.5	0.835	0.564
13.4	11.2	7.4	.836	.545
14.6	12.0	7.5	.822	.513
16.8	13.1	8.5	.774	.506
17.1	13.4	8.5	.784	.497
17.6	12.8	9.4	.727	.540
18.6	14.6	9.8	.785	.527
19.3	13.7	9.5	.710	.492
19.7	14.8	10.0	.752	.513
20.0	14.0	9.4	.700	.470
20.0	14.9	10.3	.741	.511
21.1	15.0	10.1	.711	.479
21.2	14.9	10.1	.703	.476
21.6	15.3	10.3	.709	.477
22.0	16.7	10.8	.764	.491
22.3	15.6	11.0	.700	.493
22.6	16.0	10.8	.708	.478
23.6	17.6	12.6	.746	.534
23.7	17.1	11.1	.722	.468
24.0	17.2	12.6	.717	.525
24.4	18.3	12.8	.750	.525
24.4	18.6	12.6	.762	.516
25.3	18.3	12.4	.723	.491
25.9	17.7	13.0	.683	.502
26.7	19.1	12.8	.715	.479
26.7	19.4	13.6	.727	.509
27.7	19.6	13.6	.708	.455
28.6	20.4	14.2	.713	.496
30.2	21.6	14.6	0.715	0.483

The data in Table 3 indicate that shells greater than 16.0 mm in length are relatively lower and less circular than smaller individuals.

Specimens of *N. pulligera conglobata* were collected together with two unidentified thiarid gastropods from two locations several meters apart below Tarzan Falls in the Tarzan River, Guam. The first habitat is the very swiftly flowing river, the snails being very abundant on large basalt boulders. Orientation of the spire with respect to the streambed or current was not constant, and individuals were either fully exposed to or somewhat sheltered from the current. Specimens from the second habitat, a rockpool with basalt boulders separated from the main part of the river by rocks and vegetation, are higher on the average than river shells ($p = 0.060$ by the U-test when comparing height to length ratios in Tables 3 and 4 of shells greater than 25.0 mm in length).

4. *Septaria porcellana* (Linnaeus 1758). The shell of *Septaria* is more limpet-like than in the other species considered here. The aperture is very broad, the shell

Table 4. Measurements of *Neritina pulligera conglobata* from quiet pool, Tarzan River, Guam

l	w	h	w/l	h/l
18.6	13.8	9.5	0.742	0.511
18.6	14.9	9.5	.801	.511
19.6	14.1	10.3	.719	.526
19.6	14.4	9.5	.735	.485
20.1	14.4	10.6	.716	.527
20.1	14.6	10.0	.726	.497
20.2	16.9	10.1	.837	.500
20.8	14.9	10.6	.716	.510
21.0	15.3	10.0	.729	.475
21.0	16.0	10.8	.762	.514
23.0	17.0	10.6	.739	.465
23.4	17.5	12.0	.748	.513
23.4	17.9	13.1	.764	.566
24.3	17.7	12.1	.728	.498
24.5	17.6	12.4	.718	.518
24.5	17.7	12.8	.722	.522
25.0	18.1	13.1	.724	.524
26.0	19.7	13.5	.758	.519
26.5	19.0	13.0	.717	.491
26.9	19.0	13.6	.706	.506
27.2	19.8	13.3	.728	.489
27.9	20.5	14.3	.735	.516
29.5	20.5	14.7	.695	.497
29.5	21.1	14.5	0.715	0.491

is nearly symmetrical about a line from the apex to the midpoint of the abapical margin, and the septum, bearing a smooth margin, has been reduced to a narrow remnant near the apex. The external surface of the shell is smooth except for weakly defined growth lines, but large individuals are covered with egg cases and young of their own species, creating a granular surface on the exterior of the shell. Table 5 indicates that specimens longer than 20 mm are relatively higher and less circular than smaller individuals.

The operculum is a small squarish plate with a wide membranous margin and a straight apical projection. This projection is the only visible portion of the operculum in the living animal when the latter is removed from its shell. It is evident that, since the animal cannot retract into its shell, the essentially internal operculum has lost its primary function of protectively sealing the aperture.

S. porcellana was taken at three localities in Guam:

A. About 100 feet above the mouth of the Tatgua River, on sides and bottoms of large limestone boulders in a swift current. The animal was less abundant than at other localities described here, and specimens were generally flat. Most specimens were oriented with the posterior margin pointing toward the streambed. An unidentified thiarid and a lymnaeid gastropod were found with *Septaria.*

Table 5. Measurements of *Septaria porcellana* from Toguan River, Guam

l	w	h	w/l	h/l
9.4	8.3	3.1	0.883	0.320
9.8	8.0	3.0	.816	.306
10.8	9.4	3.2	.870	.296
11.4	9.8	3.8	.860	.333
12.3	10.5	4.1	.854	.333
12.5	10.6	4.3	.848	.344
13.3	11.9	4.6	.895	.345
13.5	12.0	4.1	.889	.304
13.6	11.1	4.3	.816	.316
13.7	10.6	4.4	.774	.321
14.1	11.4	5.2	.809	.369
14.2	11.8	4.8	.831	.337
14.5	12.4	5.0	.855	.345
14.8	12.5	5.3	.845	.357
15.2	12.9	5.3	.848	.349
15.4	12.9	4.9	.838	.318
15.7	13.0	5.0	.828	.319
16.1	12.8	5.0	.795	.310
16.7	13.7	5.4	.820	.324
18.6	14.6	6.3	.785	.339
19.2	14.8	6.7	.771	.349
19.5	16.3	6.5	.837	.333
19.6	15.2	6.5	.776	.332
20.0	16.2	7.0	.810	.350
20.2	16.2	7.3	.802	.361
21.5	17.9	7.5	.833	.349
23.2	19.2	8.7	.828	.375
25.3	19.4	9.6	.767	.379
25.3	20.1	9.9	.794	.391
25.6	19.7	9.7	.769	.378
25.8	19.3	10.0	.748	.388
27.3	20.2	10.1	.740	.370
27.9	21.5	11.6	.771	.394
28.5	21.4	11.0	.751	.386
32.2	24.0	13.1	0.745	0.407

B. At the mouth of the Toguan River, on limestone and basalt boulders, either directly exposed to or somewhat sheltered from the very swift current. Orientation relative to the streambed or current appeared to be random. The snails were very abundant and grew to a large size. Associated gastropods were *Clithon brevispina* (Lamarck), a globular neritid found sheltered from the current, and two unidentified thiarids.

C. At the mouth of the Umatac River, on surfaces of basalt boulders exposed to the fairly weak current. Individuals were abundant but generally small. No particular orientation was observed with respect to the current or streambed.

Associated gastropods were *C. brevispina, Neritina squamipicta* Recluz, and two unidentified thiarids.

The ability of *Septaria* to cling to the substratum and to resist shearing forces appears qualitatively superior to that in the three other species under consideration.

Discussion

The shells of fresh-water neritids exhibit certain features which would appear to be adaptations to life in a swift current. The most evident of these is the assumption of the flattened limpet-like or crepiduliform habit. There is a strict correlation between the degree of development of limpet-like shell characters and the clinging ability of the animal. In the least limpet-like species studied (*N. pulligera conglobata*) clinging ability and resistance to shear are weakest, while in *Septaria porcellana* (the most limpet-like form studied) cling and resistance to shear are greatest. In the two Hawaiian species, in which development of limpet characters is intermediate with respect to the two Guamanian forms, the adhesive capacity of the animal is also intermediate.

In *S. porcellana* and *N. vespertina*, where large specimens are relatively higher than small ones, the adhesive force of the animal is apparently in excess of the shearing forces generally precent in its environment. This is probably not the case with *N. pulligera conglobata*, in which large individuals are flatter than small ones and river shells are flatter than those from a quiet pool nearby. No correlation could be made between relative height and length in *N. granosa*.

From the above considerations one might infer that it pays to be as flat as possible, if the maximum clinging force of the snail is of the same order of magnitude as the environmental shearing forces encountered. By becoming more limpet-like, that is, by increasing the area of the opening of the shell relative to volume, the adhesive ability will be greatly increased. In this connection it is noteworthy that a number of basommatophoran pulmonate stocks have given rise to fresh-water limpets (Hubendick, 1962), some of which (*e.g. Ancylus fluviatilis*) live in flowing fresh water.

The limpet form achieved by the fresh-water neritids can be considered as a culmination of trends initiated in marine members of the group. All neritids are characterized by a shell in which the inner whorls have been resorbed; that is, the internal cavity of the shell lacks the spiral structure typical of most other gastropods. In some marine forms such as the Indo-Pacific *Nerita polita* Linnaeus 1758, the shell is more less flattened and lacks ornamentation other than growth lines, the aperture is rather broad and bounded by weakly developed teeth on the inner and outer lips, and the septum is large and at an angle to the opening of the shell not unlike that in *Neritina pulligera conglobata*. A form with comparable shell characteristics may well have been the ancestral stock of at least some fresh-water neritids.

The major modifications in shell architecture necessary to transform a marine species in the *Nerita polita* stage into a fresh-water species in the *Neritina pulligera conglobata* stage would be as follows: (1) Broadening the aperture and flattening the shell by increasing the rate of whorl expansion; (2) Reduction in thickness of the septum and simplification of the internal cavity of the shell; and (3) Loss of teeth on the outer lip and reduction of teeth on the inner lip to serrations. Further accentuation of the limpet form would involve: (1) Further broadening of the aperture and flattening of the shell; (2) Reduction in the relative size of the septum and loss of serrations on its outer edge; and (3) Reduction and internalization of the operculum.

The granular surface ornamentation on the shell of *Neritina granosa* may also be of considerable adaptive significance. A granular surface in a current differs from a smooth one as follows: (1) The strong force of the incident current is scattered into a large number of deflected smaller components by the granules due to turbulence, thereby decreasing the effect of the initial force; (2) The shell bearing the granular surface would be strengthened, especially at the crenulated margins; and (3) The surface area would be increased. It might thus be supposed that the overall effect of a granular surface as opposed to a smooth one is beneficial in environments dominated by strong shearing forces, even though surface area is greater. It is most interesting in this connection to recall that *N. granosa* was found only on surfaces fully exposed to the current.

One might further speculate that the presence of egg capsules on the shells of *N. pulligera conglobata* and *Septaria porcellana* has the same physical effects as the granules on the shell of *N. granosa*. Most, if not all neritids may cover their shell with their own egg cases (Andrews, 1935). If the irregularities caused by the presence of these capsules on the shell do indeed serve to scatter the shearing force of the current, then the behavior of gluing egg capsules to the shell could be considered as an "ingenious" preadaptation of marine neritids to life in swift freshwater currents.

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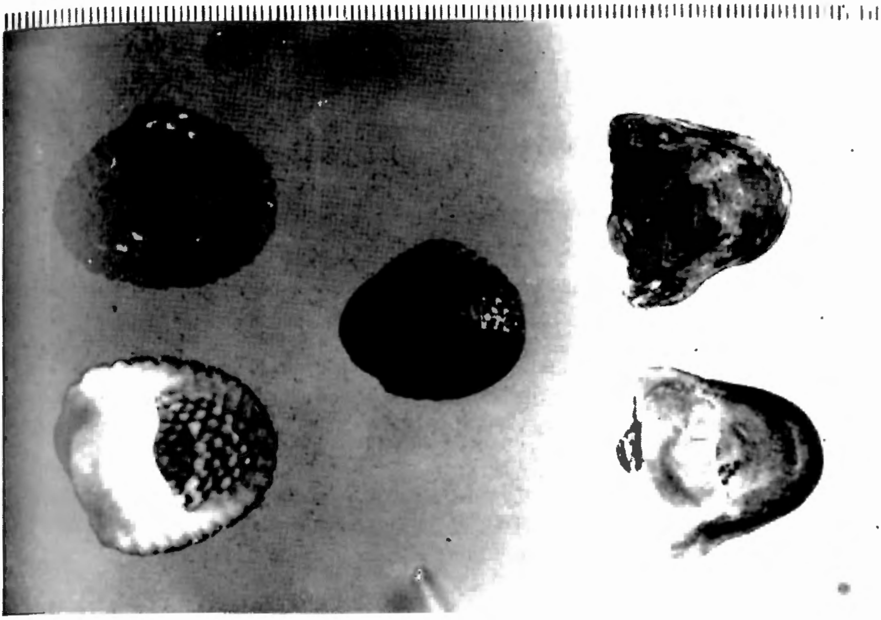

Figure 1

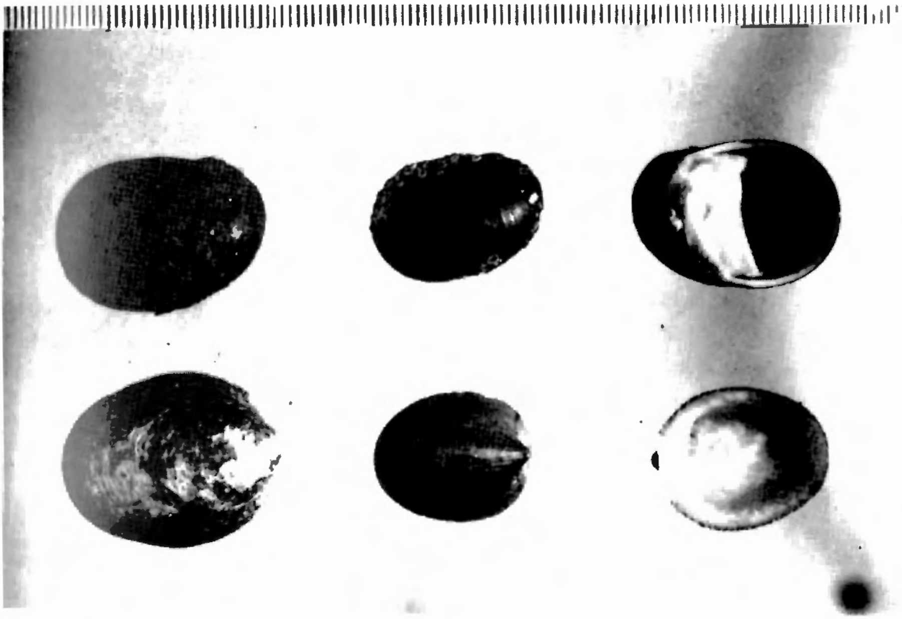

Figure 2

LEGEND TO FIGURES

Fig. 1

Upper left: dorsal view of large *Neritina granosa*
Lower left: Ventral view of *N. granosa*
Center: Dorsal view of small *N. granosa*
Upper right: Dorsal view of *N. vespertina*
Lower right: Ventral view of *N. vespertina*

Fig. 2.

Upper left: Dorsal view of *Nertitina pulligera conglobata* without egg cases
Upper center: Dorsal view of *N. pulligera conglobata* with egg capsules
Upper right: Ventral view of *N. pulligera conglobata*
Lower left: Dorsal view of large *Septaria porcellana* with egg capsules
Lower center: Dorsal view of *S. porcellana* without egg capsules
Lower right: Ventral view of *S. porcellana*