Shell Character and Habitat of Nonmarine Hawaiian Neritid Snails

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Abstract.—Three species of nonmarine neritid snails in Hawaii range from 4 to 5+ cm in maximum shell size and occur in distinctive habitats. *Neritina granosa* is a diadromous fluviatile species harvested for food, and is now common only in a few, remote, steep-gradient streams. *Theodoxus cariosus* and *T. vespertinus* are euryhaline, occurring in estuaries and brackish coastal ponds. All three snails show considerable intraspecific variation in shell morphology. Shape and surface roughness of *N. granosa* shells varies with altitude. Egg capsules may be attached to shells, apparently when spawning substrata are limited. Shell character of these species does not support earlier hypotheses that roughness has adaptive advantage for life in fast-flowing waters.

Introduction

Among the eight Hawaiian neritid snails recorded by Kay (1978), three are nonmarine in adult life (although their larvae apparently develop in the ocean): the fluviatile *Neritina granosa* Sowerby 1825, and the euryhaline *Theodoxus vespertinus* (Sowerby 1849) and *T. cariosus* (Wood 1828). Probably all are Hawaiian endemics. Two of them, *N. granosa* and *T. vespertinus*, were discussed by Vermeij (1969) along with two Guamanian stream neritids. His observations on the shells of these snails and their habits led him to hypothesize that shell roughness may have adaptive advantage to life in strong currents, and that attachment of egg capsules on shells in some species may be a means of increasing roughness for such adaptation.

My field observations and collections of neritid snails from dozens of Hawaiian locations during the past decade have revealed information that offers alternative explanations to the significance of shell character. The purpose of this paper is to record shell character variations and other information on Hawaiian neritids as contributions to their biology and to an eventual understanding of the evolution of this group. Observations given here should be considered supplementary to those of Kay (1978) and Vermeij (1969).

Observations

Neritina granosa (Fig. 1).

This singular diadromous Hawaiian snail is the largest native neritid; maximum

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shell diameter exceeds 5 cm. The shell is relatively stout and has a thick black periostracum that is rarely eroded. Shape and surface texture of the shell are highly variable, and color pattern differs with size and development. Juveniles less than about 1 cm in diameter have smooth undifferentiated shells patterned with light (buff) spots that become progressively larger with shell growth. Shell forms of large adults vary from smooth and domed to rugose and flaring. Flattened shells with granular surface texture are the more common form. "Wing" development (lateral extension of the palatal lip) often produces shells that are broader than long. Closely spaced granulations, 1–2 mm across and as much as 2 mm high, sometimes coalesce laterally into ridges and result in wrinkled margins. Exterior spotting may persist throughout life in the rough form. The smooth shell form is very dark, without spotting or wings, and therefore is always longer than wide. Egg capsules are not found on smooth shells but commonly are attached to granular shells, always in pits between granules.

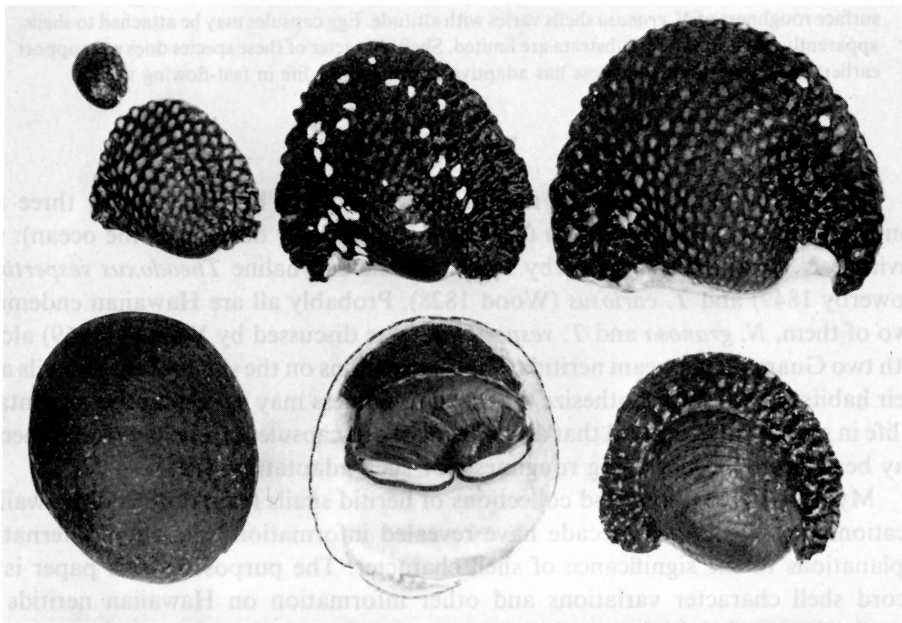

Fig. 1. *Neritina granosa.* Top row: juvenile with undifferentiated shell; small adult of downstream form with moderate roughness and wing development; wrinkled downstream adult with attached egg capsules (white spots); and large adult (45 mm shell width) with strong wing development and attached egg capsules. Bottom row: smooth, wingless upstream adult; ventral view of similar specimen; and shell having early growth as smooth form and terminal growth as rugose form. The species lives only in streams after larval development in the ocean.

This species is found characteristically in clear, bouldery, steep-gradient streams on geologically newer land masses such as windward Mauna Kea (Hawaii Is.) and East Maui. It is uncommon in or absent from modified, degraded, and readily accessible streams. Juvenile and mature stages occur only in freshwater from sea level to

elevations of at least 400 m. Rough-shelled forms are typical of lower stream reaches and smooth forms occur at higher elevations. In some streams, there is an altitudinal gradation of shell types; in others, shell extremes may be separated abruptly by a single large waterfall (e.g., Akaka Falls, Kolekole Stream, Hawaii Is.). Individuals in sparse populations are seclusive, remaining beneath rocks diurnally, feeding nocturnally, and sometimes inhabiting only areas of strong current. The snails are abundant in all habitable areas of a few remote, relatively pristine streams. The greatest density of mature snails recorded, about $50/m^2$, was observed from above-surface vantage in a low elevation riffle on the Lumahai River, Kauai. Individuals in such populations also may be observed mating and browsing in calm pools at midday.

Substantial numbers of *N. granosa* occur in a few streams on major islands except Oahu, where it is rare. Depletion of the species apparently has resulted from habitat degradation and exploitation. This neritid has been sought for food since early Hawaiian time and is currently harvested commercially, bringing a retail market price of about $3 per pound (ca. 10 cents apiece). Predation by waterbirds (Black-crowned Night Heron, *Nycticorax nycticorax*, and possibly the Wandering Tattler, *Heteroscelus incanus*) has been observed at three locations.

Theodoxus vespertinus (Fig.2).

This is the smallest (<4.0 cm shell diameter) and least variable of the neritids described here. The shell and periostracum are relatively thin and smooth. Color varies from light to dark olive brown without spotting. Shell erosion, a frequent condition, may be localized as pits near the apex or generalized over the outer surface; if generalized, the shell may become extremely fragile. It is a comparatively flat snail with a smooth margin. Shell variation is found in the degree of wing (palatal lip) development. Most individuals have slight wing development and are longer than wide. In some, lateral expansion near the apex widens the shell considerably. No egg capsules have been found on the shells of this species.

Stream mouths on all the major islands are the principal habitats of *T. vespertinus*. It is common in estuaries, particularly where salinity is low and water calm. It occurs in some mixohaline coastal ponds, including those diluted by fresh groundwater (Maciolek and Brock, 1974). When present at stream mouths, this snail may be exposed to stream currents and wave action but does not occur upstream from a point influenced by either high tide or occasional large waves. Although it is a euryhaline species that does not inhabit streams per se, specimens have been maintained for more than 2 years in freshwater aquaria. It is less seclusive than *Neritina granosa*, at least in locations where water depth exceeds a few decimeters. *T. vespertinus* is not now harvested for food.

Theodoxus cariosus (Fig. 3).

This euryhaline neritid has a stout domed shell with a thin black periostracum that may be flecked with small white spots or patterned black and white. In size, shape, and texture, it is intermediate between *Neritina granosa* and *T. vespertinus*. Shell erosion is common and sometimes thins the shell severely. Shape extremes are the elongate wingless shell which may have a length: width ratio greater than 1.5, and the strongly

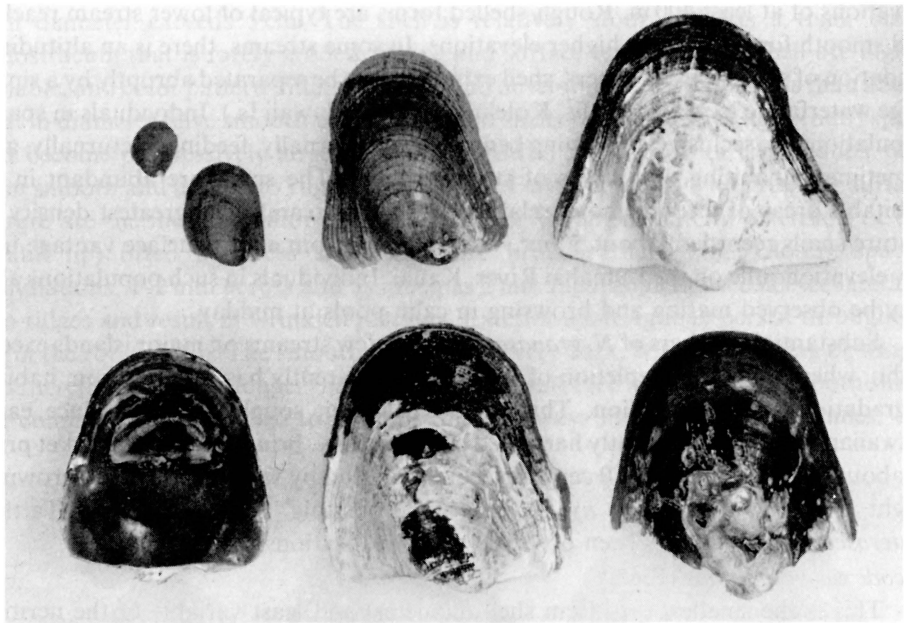

Fig. 2. *Theodoxus vespertinus*. Top row: juvenile with undifferentiated shell; subadult with slight wing development; typical adult with intact periostracum; and eroded adult with strong wing development (35 mm shell width). Bottom row: ventral view of adult; adult with slight wing development and severe erosion that weakened the shell so much that it broke (center) in handling; and shell strongly pitted in apical region. This euryhaline olive brown species inhabits stream mouths at ocean and low-salinity portions of estuaries.

winged shell which may have a ratio less than 0.7. Winged shells are largest and rarely may exceed 4 cm in width. Although *T. cariosus* has no shell granulations, growth ridges may be prominent in old specimens, especially toward the flaring edges of winged forms. Such individuals have wavy margins. Egg capsules have been found on shells at two locations where the rock substratum was coated with a crustose algal community.

T. cariosus is found in estuaries and brackish shoreline ponds on all islands. It is a common and often abundant inhabitant of mixohaline ponds in recent lavas of Maui and Hawaii Islands. Maciolek and Brock (1974) reported it from 56 of 318 ponds inventoried along the leeward coast of Hawaii. It is broadly euryhaline, occurring in waters with salinities ranging from 0.5 to 30‰, but has not survived long in freshwater aquaria. Occasionally, *T. cariosus* is found coexisting with *T. vespertinus*. In esturies, this snail seems to prefer the more saline seaward end. It is a quiet-water species that is less seclusive than either of the foregoing species. Large numbers are sometimes seen foraging diurnally on submerged rock in the clear waters of lava-bound ponds. Bird predation similar to than noted for *Neritina granosa* has been observed at a few locations. Although *T. cariosus* probably was eaten in historic times, apparently it is no longer harvested.

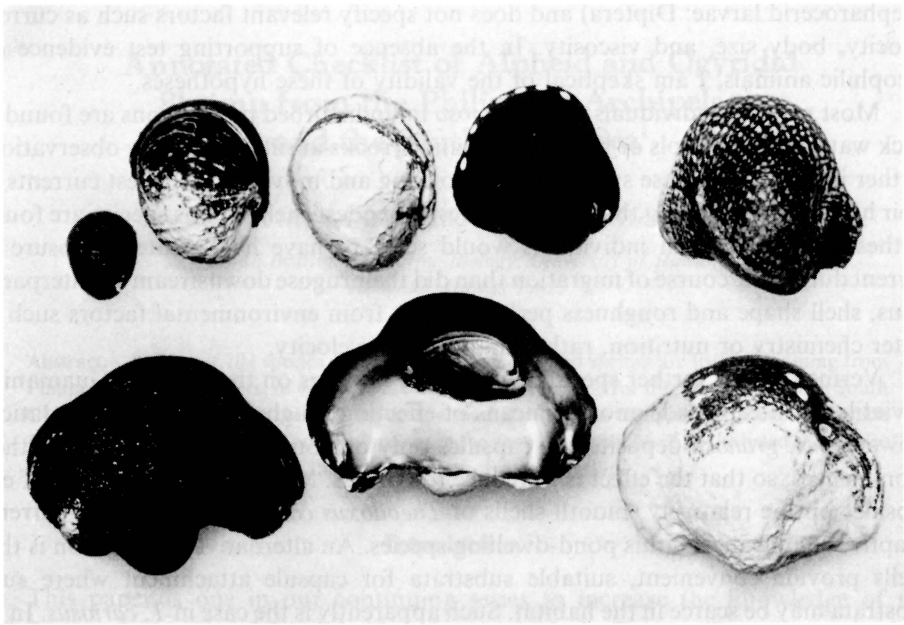

Fig. 3. *Theodoxus cariosus*. Top row: undifferentiated juvenile; wingless adult with eroded apex; wingless, ridged, severely eroded shell; smooth, slightly winged shell with attached egg capsules (on anterior margin and wing near apex); and white-spotted smooth shell with moderate wing development. Bottom row: smooth shell with strong wing development. (36.5 mm wide); ventral view of winged shell; and white-spotted winged shell with egg capsules (white area on apex and wings is a weakly mineralized algal mat). This species is characteristic of mixohaline coastal pools, particularly those in recent lava flows, and is sometimes found in estuaries and other saline areas of stream mouths.

Discussion

It is noteworthy that all types of inland waters with some connection to the ocean are inhabited by at least one of the neritid snails described here. Unlike three similar sympatric neritids reported by Govidan and Natarajan (1972) that coexist at a single stream location in India and have uniform intraspecific shell character, the Hawaiian neritis occur with little spatial overlap and display a great degree of intraspecific shell variation. Spatial isolation in Hawaiian neritids seems to be related to habitat preferences, particularly salinity and current. Reasons for shell variation are less evident.

Neritina granosa displays the greatest variation in shell shape and texture. Vermeij (1969) suggested that roughness of this snail has adaptive advantage for life in strong currents, the roughness creating turbulence which distributes incident shear forces away from the shell. This hypothesis is similar to "Hora's theory" (Hora, 1930: 255) in which roughness presumably reduces resistance to current by creating calm water in the vicinity of the animal's surface. However, Hora cites only one example

(blepharocerid larvae: Diptera) and does not specify relevant factors such as current velocity, body size, and viscosity. In the absence of supporting test evidence on rheophilic animals, I am skeptical of the validity of these hypotheses.

Most resident individuals of *N. granosa* in undisturbed populations are found in slack water, be it in pools or between and under rocks in riffle areas. My observations further indicate that these snails are able to cling and move in the fastest currents of their habitat. Considering that the smoothest, roundest shells of this species are found farthest upstream, such individuals would seem to have had greater exposure to current during the course of migration than did their rugose downstream counterparts. Thus, shell shape and roughness perhaps result from environmental factors such as water chemistry or nutrition, rather than current velocity.

Vermeij (1969) further speculated that egg capsules on the shells of Guamanian fluviatile neritids provide another means of effecting roughness for rheic adaptation. However, *N. granosa* deposits egg capsules only on rough shells and between their prominences, so that the effect is to reduce roughness. Moreover, the presence of egg capsules on the relatively smooth shells of *Theodoxus cariosus* cannot have current-adaptive significance in this pond-dwelling species. An alternative explanation is that shells provide convenient, suitable substrata for capsule attachment where such substrata may be scarce in the habitat. Such apparently is the case in *T. cariosus*. In *N. granosa*, shell-attached capsules occur in downstream areas where epilithic algae are more luxuriant and siltation is more common than in upstream reaches.

Vermeij's (1969) paper indicates considerable perceptiveness of detail. Its shortcoming is the paucity of collection sites and specimens on which the hypotheses are based. Specifically, he collected *Neritina granosa* from only one stream location—that on Oahu, a highly developed island, where probably no native stream animal fully retains its natural ecology. Throughout Hawaii, aquatic species are decreasing in abundances and their habitats deteriorating in natural quality (Maciolek, 1975). It is obvious from the foregoing that increasing environmental attrition in Hawaii and other oceanic archipelagos necessitates an urgent but cautious study of native aquatic species if we are to understand their evolution and natural biology.

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