THE SYSTEMATICS AND ECOLOGY

OF THE MANGROVE-DWELLING *LITTORARIA* SPECIES

(GASTROPODA: LITTORINIDAE)

IN THE INDO-PACIFIC

VOLUME I

Thesis submitted by

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David G. Reid

May 1984

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FRONTISPIECE

Shell colour polymorphism of *Littoraria* species. From top:

Row 1: *L. filosa*, Cockle Bay, Magnetic Island, Queensland; colour forms: Y0, Y2, B4, P0.

Row 2: *L. philippiana*, Cockle Bay, Magnetic Island, Queensland; colour forms: Y0, Y2, B5, P0.

Row 3: *L. pallescens*, Ao Nam-Bor, Phuket Island, Thailand; colour forms: Y0, Y3, B5, P0.

Row 4: *L. luteola*, Kurnell, Botany Bay, New South Wales; colour forms: Y1, Y3, B4, P0.

Row 5: *L. albicans*, Santubong, Sarawak; colour forms: Y0, Y2, Y3, P0.

ABSTRACT

The supposed species '*Littorina scabra* (L.)' has been noted for its extreme variability in shell form and colouration. The project was undertaken with the aim of investigating this variability and its possible adaptive significance.

Recent taxonomic treatments of the '*scabra* group' (comprising the members of the family Littorinidae associated with mangroves in the Indo-Pacific) have recognized three species. Using material personally collected and specimens from fourteen museums, the taxonomy of the *scabra* group was revised, demonstrating the existence of 20 species and one subspecies. Initially, species were defined by the diagnostic morphology of the penis and sperm nurse cells. The form of the pallial oviduct is described in detail, demonstrating that some species are ovoviviparous while others produce egg capsules. In addition, the radula, alimentary system, pallial complex and colouration of the head-foot are described, although less useful for taxonomic purposes than the reproductive anatomy. Once species were defined by anatomical criteria, characters of the shell such as shape, sculpture, columella and protoconch were shown to be rather uniform and adequate for the identification of species in most cases. Systematic descriptions and full synonymies are given for each species.

For comparative purposes, the anatomy of 42 other littorinid species was examined. Employing the method of cladistic analysis, the anatomical data were used to construct a tentative phylogeny of the family Littorinidae. The *scabra* group is classified in the genus *Littoraria*, which is shown to be the sister group of *Nodilittorina*. A cladogram of the 36 Recent species of *Littoraria* is presented, and four subgenera are recognized.

Distribution maps are given for each species in the *scabra* group, and were compiled from a total of 1900 museum collections. The biogeography of the group is discussed. The species can be divided into two classes, characteristic of continental and oceanic habitats respectively, and the members of the latter group show the greatest geographical ranges. The form of the protoconch and data in the literature suggest that both oviparous and ovoviviparous species are widely dispersed as planktotrophic veligers. It is suggested that speciation may be occurring in the peripheral regions of the Indo-Pacific, and that species have accumulated in the central region of highest diversity.

The zonation and abundance of *Littoraria* species were quantified on transects through mangrove forests at 14 localities in Australia, South-east Asia and Hawaii. Species were found to show characteristic patterns of vertical and horizontal zonation, although the degree of overlap between sympatric species was considerable. There was a clear distinction between species dwelling on bark and those on foliage. Densities of *Littoraria* species were very low, except on the trees at the outermost edge of the forest. It is suggested that landward limits of horizontal zonation may be determined by physiological tolerance, and vertical distribution by behavioural responses.

Detailed ecological investigations were carried out at Cockle Bay, Magnetic Island, Queensland. Here five *Littoraria* species were common. From lowest to highest, the order of vertical zonation of these species on *Rhizophora* trees was: *L. articulata* and *L. intermedia*, *L. scabra*, *L. philippiana*, and on *Avicennia* trees: *L. articulata*, *L. filosa*, *L. philippiana*.

The snails were highly mobile, those from the lower levels (*L. articulata*, *L. intermedia*, *L. scabra*) migrating vertically with each tidal cycle, to avoid submersion. Those from the higher levels (*L. filosa*, *L. philippiana*) periodically moved down to the water surface at high tide, and were active during the night, early morning and during light rain. All species occupied higher tidal levels during

spring tides, and those from higher levels occurred further up the trees during rain. All species showed a vertical size gradient, with smaller individuals at the lower levels. Intense predation pressure at low levels during high tides is believed to have been the selective force responsible for the vertical migration behaviour.

At Cockle Bay the three species from lower levels were found to be reproductively mature throughout the year, and spawning probably occurred each month. The two species from higher levels were reproductively mature only during the wet summer months. There was no correlation between the method of development (release of either pelagic egg capsules or planktotrophic veligers) and the habitats of the species. Phylogenetic patterns of method of development and of breeding season in the Littorinidae are discussed.

Population dynamics of *L. intermedia*, *L. scabra*, *L. philippiana* and *L. filosa* were investigated by a multiple mark and recapture technique. Despite probably continuous spawning, recruitment of *L. intermedia* and *L. scabra* was only significant following the peak spawning period in January and February. In contrast, recruitment of *L. filosa* was highly successful, perhaps because this species settled on foliage, out of reach of predatory crabs. The subsequent survivorship of *L. filosa*, under more rigorous microclimatic conditions, was relatively low. Survivorships of all species were lowest in the smallest size classes and in the summer months, and all showed a marked drop in survivorship during three weeks of monsoonal rain.

Growth rates, as measured on the individually numbered snails, are the highest recorded for the family. Values of the instantaneous size-specific growth rate (k in the von Bertalanffy growth equation) ranged from 0.05 to 0.25 per month. *L. intermedia* and *L. scabra* attained a size of 6 mm in the first month of growth following settlement, and reached the minimum size for sexual maturity in 3 to 4 and 6 to 8 months respectively. Growth rates were highest during the summer months, with the exception of *L. filosa*, in which the season of maximum growth followed that of spawning. These patterns are related to the zonation and feeding behaviour of the species. Few individuals survived to reach 2 years of age, but maximum longevity may be 6 years.

The major predators of the post-larval stages of *Littoraria* species at Cockle Bay were crabs of the genus *Metopograpsus* and the species *Thalamita crenata*. Direct estimates of the causes of death of snails were obtained for artificial populations of *L. filosa* in exclusion cages. Crabs caused 57% of the total loss, or 86% of the total mortality, of *L. filosa* in the size range 7 to 12 mm, accounting for the loss of 19% of the population per month. Bird predation appeared to be insignificant. The severity of crab predation on *Littoraria* species was supported by an analysis of the repaired breakages of the shell, which indicated sublethal damage by crabs. The average numbers of repairs per adult shell were between 0.7 and 3.5 in the five species at Cockle Bay. The rate of sublethal damage (repairs per whorl per month) was highest in 2 to 5 mm shells of *L. intermedia*, *L. scabra* and *L. philippiana*, although in *L. filosa* the rate was highest in adult shells (23 mm). This pattern is explained by the much lower resistance of the thin-shelled *L. filosa* to attack, as demonstrated in laboratory predation trials. The distribution of crabs on the trees at Cockle Bay suggested a gradient of increasing intensity of predation at lower tidal levels. A corresponding interspecific gradient of increasing shell thickness in the species typical of lower tidal levels was shown at nine out of ten of the localities where zonation was recorded on transects, and this is interpreted as an adaptive trend. Interspecific trends of increasing shell size, stronger sculpture and narrower shells at higher tidal levels are interpreted as adaptations to the more rigorous microclimatic conditions at higher levels.

Within the *scabra* group, nine species show a phenotypically similar colour polymorphism, with yellow, pink or brown shells, while the remaining species are merely variable in the degree of shell pigmentation. The degree of colour variation was greatest in

Littoraria species typically found on foliage at the higher tidal levels, while species from bark substrates at lower levels were brown. In some species there was a suggestion of a direct influence of the substrate upon shell colour. This was not the case in *L. filosa*; in this species the polymorphism was presumed to have a genetic basis, and the mechanisms maintaining the polymorphism were investigated. Evidence is presented for the action of visual selection on *L. filosa* on backgrounds of different colour, although the predators involved were not identified. Climatic selection did not appear to be operating. The shell colour forms did not show significant behavioural differences. Manipulation of the colour proportions of *L. filosa* on isolated trees showed that disappearance of colour forms was frequency-dependent. On the basis of this evidence and the persistent rarity of the conspicuous pink colour form, it is concluded that the polymorphism is maintained by apostatic selection.

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