significant. The intrasite differences could be caused by either environmental factors (Brantwood, 1985 ; Sundberg, 1988) causing the difference in shell morphology, or to differences in the genetic make up of the two populations (Janson, 1983). Unfortunately none of these factors was quantified at the collecting sites, but will be investigated in the attempt to further elucidate the results of the present study.

The study found there is significant microgeographical variation in *L. saxatilis*, even over a distance of a few metres. Most of the sites confirmed previous assumption for more distant samples that the shells on a boulder beach are actually stronger under compressive load than those on a rockface, and not just thicker ; shell thickness does not, however, correlate directly to shell strength under compressive load. One site, Three Cliffs Bay, had reversed results, *ie* the rockface sample is the stronger. However, this pair of samples were widely separated and, because of the configuration of the Bay, each sample could have been exposed to quite different environmental factors. This site will be one of the first to be reexamined.

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Species and speciation in Littorinidae

D.G. Reid
Department of Zoology, The Natural History Museum, London SW 7 5BD, UK

Among Littorinidae, species are usually clearly defined by morphological criteria, especially when details of the reproductive anatomy are considered. Although only a few species have been investigated genetically, where this has been done the results are in agreement with morphological species concepts. So far, no truly cryptic (morphologically indistinguishable) species have been clearly demonstrated.

The systematics and geographical distributions of the Littorinidae are now well known, and they have been the subject of several phylogenetic studies using cladistic analyses of morphology, genetic and molecular data. It has thus been possible to identify 34 pairs of likely sister species out of the total of 180 species in the family. Analysis of the geographical distribution of these pairs shows that in 52 % of cases the two members of the pair are entirely allopatric, and in 29 % of cases largely sympatric. Island endemics account for only a small proportion of the allopatric cases, and the pattern shows no correlation with type of larval development. Evidence for speciation processes can also be sought in the patterns of intraspecific geographical variation in morphology ; here, it is found that large-scale variation predominates, with gradual clines between geographical varieties, while there are few cases of recognisable peripheral isolates. Unfortunately, the fossil record of littorinids is too poor to provide insights into speciation. This combination of evidence suggests that the prevailing mode of speciation in Littorinidae has been allopatric, and probably mainly of the vicariant (large-subdivision) type. This contrasts with the peripheral isolation mode, widely believed to predominate on land. Most littorinids have planktotrophic larvae and are presumably widely dispersed, perhaps explaining why peripheral isolation is relatively rare. Island endemics are found only on the most isolated islands, such as Hawaii, Easter and Juan Fernandez.

There is no clear evidence for parapatric speciation ; stepped clines which may precede this process have not been described in littorinids, and sister species are rarely distributed parapatrically. Sympatric speciation remains a possibility, particularly in direct-developing species. Two theoretical models of sympatric speciation along an exposure gradient have been produced, but have only suggested that stable polymorphisms can be achieved (Boulding, 1990 ; Johannesson & Sundberg, 1992). In fact, sympatric sister species do not generally show the habitat differentiation that this mechanism is expected to produce. The high frequency of sympatry among sister-species pairs may be the result of dispersal following speciation in allopatry.

The only well-documented cases of speciation in Littorinidae concern the trans-Arctic migration of *Littorina* species from the Pacific to the Atlantic following the opening of the Bering Strait 3.5-4 My ago (see Rumbak, Reid & Thomas, this volume).

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The contribution of mating behaviour to the reproductive isolation : the example of the Galician *L. saxatilis* populations

E. Rolán-Alvarez[1], K. Johannesson[2] and A. Ekendahl[2]
1) Departamento de Biología Fundamental, Facultad de Biología, Universidad de Santiago de Compostela, Santiago (Spain),
2) Tjärnö Marine Biological Laboratory, S-452 96 Strömstad (Sweden)

Mating is usually one of the main behaviours capable of producing prezygotic reproductive isolation between incipient species. Mating behaviour mechanisms which may contribute to productive isolation can be partitioned in three additive and independent components : mating success for males (male sexual selection), mating success for females (female sexual selection), and assortative mating (sexual isolation) (Spieth & Ringo, 1983). These three components can present different contributions and can be caused by different biological mechanisms.

Two different morphs of *L. saxatilis* coexist in different vertical habitats of Galician exposed shores. However, both pure morphs overlap with hybridization in midshore areas. Disruptive selection acting on the original population has probably caused the distribution of these two pure morphs (Johannesson *et al.*, in press).

The mating behaviour of *L. saxatilis* was studied in natural populations of upper, mid and lower shore areas (Johannesson *et al.*, in preparation). Copulating mating pairs and non-copulating snails surrounding the former were sampled in order to estimate the three different mating behavioural components. A conspicuous assortative mating between both