size of *L. obtusata* decreased with increasing exposure, while the opposite occurred in *L. mariae*.

In the present study, there was a significant difference between the species in the frequency of the shell colour morphs. On sheltered shores, the dominant morph of *L. obtusata* was olivacea, while that of *L. mariae* was citrina. On more exposed shores, reticulata *L. obtusata* were found to be common but there was not a significant difference in shell colour with exposure for *L. mariae*. Both species were found on *Fucus serratus* and *Fucus vesiculosus*, but *L. obtusata* also occurred on *Ascophyllum nodosum*.

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# Microgeographical differences in the shell morphology and shell strength of *Littorina saxatilis*


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Pettitt (1971) found a highly significant difference in shell thickness between a pair of samples of *Littorina saxatilis* taken from a rockface and a boulder beach very close together at Mumbleshead, South Wales. This finding has now been extended to other sites, using paired rockface and boulder beach samples collected close together at Torteval and Cobo, Guernsey in 1992, and an earlier (1971) pair from Three Cliffs Bay, South Wales ; the Mumbles sample also was re-examined. Linear measurements were taken to the nearest 0.1 mm, and the shells were weighed to the nearest 0,01 mg. Strength was measured using an Instrom 4301 table testing machine ; the following comparisons were used to describe shell morphology and strength : Shell breadth on shell length (Shell Shape) ; Mouth width on mouth height (Aperture Shape) ; Failure load on shell length (Strength/Size) ; Failure load on shell weight (Strength/Mass).

Analysis of variance was performed on the data, and two best-fit lines plotted, one for each microhabitat, and then one for the site as a whole. F values were calculated, testing whether the two separate lines are significantly different from the single line.

*Shell Shape* : Rockface samples had rounder shells at both the Guernsey sites, and boulder shells were more elongated ; there were no intrasite differences in shell shape at the South Wales sites.

*Aperture shape* : Rockface samples had rounder apertures than the boulder samples at all the sites.

*Strength* : All the paired samples had significantly different shell strengths. Shell thickness or volume to weight ratios do not necessarily, as previously assumed, correlate directly to shell strength, for when load against mass was regressed, the resulting F values were still

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

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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