

Book Review

David G. REID, 1996. Systematics and evolution of *Littorina*. The Ray Society Publication, 164. London. i-x, 1-463, 2 colour plates, 63 black-and-white plates of shells and radulae, 24 pages of anatomical drawings and 19 distribution maps. Price £ 89.

Periwinkles are snails belonging to the genus *Littorina*, common on rocky sea shores of Western Europe, Scandinavia, North America, Siberia and Japan. *Littorina* is one of the most thoroughly studied of all marine gastropod genera. Reid lists almost 1500 references at the end of his book, of which 1300 are concerning *Littorina* species. This work is unique among *Littorina* literature, and even among marine molluscs in general, since it compiles all known information about all known fossil and living species of a single genus, including taxonomy, shell variation, morphology, reproductive anatomy, habitat, distribution, biology, ecology, allozyme frequencies as well as DNA sequences. Information is based on both original research and the above mentioned bibliography.

The book is clearly structured. The introduction provides a historic perspective of research on *Littorina*. The chapter 'Material and Methods' is exceptionally thorough as all morphological characters from both the soft parts and the shell (teleoconch) that are most useful for taxonomic discrimination and phylogenetic analysis of *Littorina* species are described and evaluated at length. Since the comparatively stable anatomical features are most important to identify unequivocally the various (sibling) species, and the extreme variability in shell features provide excellent possibilities for micro-evolutionary research; the comments on the causes of variation are also of great importance. The main part of Reid's magnificent work is formed by the systematic descriptions. All available knowledge is presented consistently. A typical treatment of a species (here *L. littorea*) consists of synonymy, taxonomic history, a diagnosis, the anatomical description (head-foot, penis, sperm, oviduct, spawn and development, radula and foregut), shell variation (geographical variation, ecotypic variation, sculptural variation, sexual dimorphism, recent monstrosities, Norwich Crag monstrosities, colour variation), distribution (habitat, range, spread in North America, fossil record), discussion (intraspecific variation, spread in North America, phylogenetic relationships, similar species). This occupies 25 pages. *Littorina saxatilis* needs 62 pages, of which 9 are used for synonymy only. Whenever confusion between species is most likely, the description of the most discriminative characters is tabulated.

The bewildering diversity of the shells in this genus inspired former authors to introduce 329 names of specific, subspecific and infraspecific rank. Reid resolved this chaos into 19 living species with repeated patterns of geographical, ecotypic, ontogenetic, sexual and colour variation and explains them in terms of life history and geneflow, adaptation to selection by predators and the physical environment, and ecophenotypic influences. In addition 10 fossil species are evaluated.

Using information from the cladistic analysis of morphological characters, from the fossil record, and from published work on allozyme frequencies and DNA sequences, a detailed species-level phylogeny has been reconstructed. It could be demonstrated that the 19 species of *Littorina* presented here, form a monophyletic group. A pragmatic approach using both monophyletic and paraphyletic groups of species results in a formal classification in which four subgenera are accepted: the monotypic *Liralittorina*, *Planilittorina* with only one living species, *Littorina* with seven living species and *Neritrema* with 10 living species.

In combination with distributional data, the phylogeny is used to discuss speciation mechanisms and historical biogeography in the final chapter of macroevolutionary history. Contrasting modes of speciation predominate in planktotrophic and nonplanktotrophic lineages, and the likelihood of sympatric speciation is suggested by recent microevolutionary studies. Although dominant on the shores of the northern Atlantic Ocean today, the genus only invaded from the Pacific during the late Pliocene, when it took part in the trans-Arctic biotic interchange. These patterns of speciation and migration are related to both ecological shifts and morphological adaptations.

With this 'Systematics and evolution of *Littorina*', Reid contributed enormously to a better understanding of this popular but highly complex genus. This work will be a great help for both shell collectors and professional malacologists in general. They both can finally get rid of the *Littorina*-chaos in their collections and in the

meanwhile have a superb and up to date introduction in the theories of many major disciplines related to modern evolutionary biology. Reid's treatise is a fine example of how modern revisions should be set up. It is a very readable book which is also pleasantly designed, an absolute must for marine malacologists, for a very reasonable price.

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