A review of the Genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea)

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ABSTRACT. The family Rissoidae is defined, and a detailed diagnosis of the family is given. The characters of the shell (and protoconch), radula, operculum, head-foot and anatomy are described and discussed for the family and for each genus (where they are known). The Rissoidae is contrasted with other Rissoacea, and the relevance of genital characters in higher classification is discussed. The genera are reviewed in the light of new information on the anatomical, radular, opercular and head-foot characters as well as shell microsculpture and other aspects of shell morphology. Thirty one genera and 24 subgenera are recognized in the family. Four of the subgenera are described as new, and one new genus and species are also described. A further 106 genus-group taxa are listed as synonyms. Eleven family-group taxa are included in the synonymy of the Rissoidae, and two subfamilies (Rissoinae and Rissoininae) are recognized. Of the remaining 119 genus-group taxa referred to the Rissoidae by previous reviewers, four Jurassic genera are tentatively included in the family and the remaining 115 are included in other families. A phenetic classification of the genera is developed using a summary of unweighted characters. The Falsicingulidae is diagnosed and it is suggested that it is closely allied to the Pomatiopsidae. A new family is created for *Epigrus* Hedley.

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The rissoids are a group of small to minute epifaunal prosobranchs that are abundant in seas throughout the world. Almost all are marine although a few species live in brackish water. Some closely related families are adapted to live in fresh and brackish water, and four of these are, at least in part, terrestrial.

Rissoids occur in considerable numbers in the northeastern Atlantic and the Mediterranean Sea, and some species achieve a high biomass in intertidal and shallow sublittoral habitats (Fretter & Graham, 1962). The larvae of some have been shown (Lebour, 1934) to be important as food for larval herrings.

The Rissoidae have proved to be very difficult to classify at all levels because of their small size, diverse form and the confusion caused by convergence, especially in shell characters. Although there have been attempts to revise the genera and subfamilies contained within the Rissoidae (sensu lato) no previous author has had access to the quantity of material examined during this revision. The reviews of Thiele (1929) and Wenz (1939) were but small parts of major treatises and were based, in the main, on the general similarity of shells, as was the compilation of generic units by Coan (1964). I revised the subfamilial classification of the Rissoidae, and some of the genera it contains, on the basis of observations and anatomical work on New Zealand species (Ponder, 1967). This work refined the fundamentally sound work of Thiele (1929), and substantially modified Coan's (1964) listing of subfamilies and genera, but was limited because of lack of specimens of many genera. Nordsieck (1972) revised the European species and introduced many changes, especially at the generic level. The classification of prosobranchs by Golikov & Starobogatov (1975) placed members of what I considered (1967) a single family in ten families assigned to five superfamilies. Slavoshevskaya (1975a) recognized seven families amongst the rissoids (sensu lato) on the basis of differences in their genitalia, and later (1983) raised the Rissoacea to the level of suborder. I (Ponder, 1967) recognized four subfamilies of which two are now included in a separate family, Barleeidae (Ponder, 1983a), and several genera that were previously included in the Rissoidae have now been placed in the Iravadiidae (Ponder, 1984) and Cingulopsidae (Ponder & Yoo, 1980).

This paper assesses the taxonomic position of genera previously assigned to the Rissoidae, and reviews genera now included in the family. Type-species of genera have been examined whenever possible. The classification adopted is based on a combination of characters found in the shell, radula, operculum and, where possible,

from the details of the head-foot and internal anatomy of living specimens. The assessment of the significance of these characters and the relationships of the genera is primarily subjective. A large number of characters are tabulated to facilitate comparison and these are analysed using data processing methods (Appendix 3) to give a somewhat more objective assessment of intergeneric relationships.

The classification presented is still at a somewhat tentative stage, largely because of lack of information regarding living animals and anatomical features of some type-species of genera. It is, however, unlikely that even with further delay in publication, the amount of information available will alter substantially.

Biology

Ecology and habits. Rissoids are found generally in the shallow seas of the world and in the mid to lower littoral zone. A few species live on the continental slopes and in abyssal depths. The greatest diversity of species is found in the lowest littoral and shallow sublittoral where the majority occur on algae, beneath stones, slabs of coral or other objects that provide shelter. Habitat may be associated with presence or absence of pigmentation and a posterior pedal mucous gland. In general the species living on algae are highly mobile, usually have a well developed posterior pedal mucous gland and are often pigmented. Species living beneath stones usually lack a posterior pedal gland and have a translucent-white head-foot. Species with a posterior mucous gland generally have the ability to secrete threads of mucus and suspend themselves from the surface film. The usual mode of locomotion is by the action of pedal cilia in a mucous film. The behaviour and locomotion of Rissoa parva (Da Costa) has been described by Delphy & Magne (1938).

It is assumed that most rissoids are annuals (Fretter & Graham, 1978) but there is very little data available to support this view. Wigham (1975) has shown that *Rissoa parva* has a life span of 8–9 months or only 3–4 months depending on the time of settlement.

Feeding. Most algal-living species appear to feed on the diatomaceous or micro-algal film covering the macro-algae they inhabit, rather than the macro-alga itself. Some species that shelter beneath stones or in crevices, feed on Foraminifera (e.g. *Rissoina*: Kosuge, 1965; Ponder, 1968) but these species have particles of other food in their stomachs. Presumably some deepsea species, and possibly some shallow-water forms, are selective deposit feeders. *Alvania jeffreysi* (Waller), and *Cingula* (= *Setia (Pseudosetia)) turgida* (Jeffreys) are