

# The Systematics and Phylogeny of Phyllidiid Nudibranchs (Doridoidea)

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**ABSTRACT.** Investigations into the taxonomy, phylogeny, biogeography and ecology of nudibranchs belonging to the family Phyllidiidae Rafinesque are reported. All prior research on the Phyllidiidae is reviewed. There were 74 nominal species as of January, 1992. The literature revealed enormous confusion in the taxonomy of phyllidiids caused primarily from inadequate anatomical study (or none at all) and descriptions of single preserved specimens. Intraspecific variation, particularly its ontogenetic component, is identified as an additional cause of misidentification.

Traditional sources of nudibranch taxonomic characters, such as jaws and radula, are lacking in the Phyllidiidae. Characters used in this study are: general shape and body profile; colour and pattern; morphology of notal tubercles, ridges, and the mantle margin; rhinophoral colour; number of lamellae on each rhinophoral clavus; gills; morphology of foot and foot sole; oral tentacles; anatomy of the alimentary system; anatomy of the reproductive system; penial spine morphology; and sperm ultrastructure.

Six genera are recognised and each is redescribed. Features which clearly demarcate the genera occur principally in the digestive system, and also in the reproductive system and external morphology. A key to genera is provided. A total of 49 valid, Indo-Pacific species is recognised; a full synonymy is given for each species. *Phyllidia* Cuvier remains the largest genus with 15 (including 8 new) species. *Fryeria* Gray is considered a valid genus with six (including 3 new) species. *Phyllidiella* Bergh is reinstated and nine (including 4 new) species are recognised. *Phyllidiopsis* Bergh, the second largest genus, contains 14 (including 6 new) species. *Ceratophyllidia* Eliot appears to contain three (including 2 new) species, however specimens are very rarely collected and further work remains to be done prior to their formal description. The recently described genus *Reticulidia* Brunckhorst contains two species. In all, 22 new species of phyllidiid nudibranchs are described.

Study of anatomy has allowed a phylogenetic hypothesis to be proposed for the first time. *Ceratophyllidia* is the sister group to the remaining genera. *Phyllidia*, *Fryeria* and *Reticulidia* are the most derived genera. The morphology and anatomy of phyllidiids indicates monophyly with dorids. However, the grouping of the Phyllidiidae and Dendrodorididae as Porostomata is

polyphyletic and rejected as homeoplaseous. Differences in foregut anatomy between the two groups support the view that suctorial feeding of sponges has arisen independently in both groups.

Biogeographical distribution of species and ecological observations are reported. As a result of field observations, the sponge foods of several phyllidiid species are reported for the first time. The sponge food and chemical defence compounds of phyllidiid species may also be useful in taxonomic study. *In situ* observations of feeding and study of the functional anatomy of the foregut enabled a description of the method of operation of the feeding apparatus of each genus. The spawn of three species are described for the first time.

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