



Taxonomy and anatomy of Amphiboloidea (Gastropoda: Heterobranchia: Archaeopulmonata)

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ABSTRACT

The taxonomy of the pulmonate superfamily Amphiboloidea is investigated with particular reference to Australasian taxa. Anatomical features of the alimentary, reproductive and central nervous systems differ substantially between taxa, and conchological, opercular and radular characters are also described. Four genera are recognised in Amphibolidae; *Amphibola* Schumacher, 1817, *Salinator* Hedley, 1900, *Lactiforis* gen. nov. and *Naranjia* gen. nov.. Two additional genera are assigned to new families; *Phallomedusa* gen. nov. (Phallomedusidae fam. nov.) and *Maningrida* gen. nov. (Maningrididae fam. nov.). Phallomedusidae fam. nov. is characterised by a paucispiral, keeled operculum and syntremous diaulic reproductive system with a complex, spiral penis. Maningrididae fam. nov. has an expanded operculum with a marginal nucleus and a syntremous diaulic reproductive system with two novel copulatory structures at the genital aperture. Taxonomic descriptions and a key are provided for eight Australian species; *Salinator fragilis* (Lamarck, 1822), *Salinator tecta* sp. nov., *Salinator rhamphidia* sp. nov., *Salinator rosacea* sp. nov., *Lactiforis tropicalis* sp. nov., *Phallomedusa solida* (Martens, 1878), *Phallomedusa austrina* sp. nov., and *Maningrida arnhemensis* sp. nov. and three non-Australian taxa; *Amphibola crenata* (Martyn, 1786), *Lactiforis takii* (Kuroda, 1928) and *Naranjia* cf. *swatowensis* (Yen, 1939).

Key words: Basommatophora, Pulmonata, Archaeopulmonata, Amphibolidae, new taxa, morphology

INTRODUCTION

The Amphiboloidea are regarded as a basal superfamily of archaeopulmonate gastropods containing a single small family, the Amphibolidae (Hubendick 1978). The group is characterised by a globose shell and the presence of an operculum in adults. Amphibolids are found in Indo-Pacific intertidal mangrove, saltmarsh and estuarine mudflat habitats. While this habitat is shared with many ellobiids and onchidiids, most other pulmonates are freshwater or terrestrial and all other pulmonates are inoperculate (Hubendick 1978). Despite their assumed basal phylogenetic position, very little is known about amphibolids (Fukuda & Kosuge 2000), with the systematics, anatomy and phylogeny of the family poorly understood. This study provides a comprehensive morphological and taxonomic review of the Amphiboloidea, with a focus on Australasian taxa.

The Amphibolidae currently comprise two genera, namely *Amphibola* Schumacher, 1817 and *Salinator* Hedley, 1900, with nine nominal species occurring from New Zealand to Japan and the Arabian Gulf (Hubendick 1945) (Table 1, Fig. 1). Two species, presently known as *Salinator solida* (Martens, 1878) and *Salinator fragilis* (Lamarck, 1822), are common in mangrove habitat in Australia, but the anatomy and systematics of these taxa have not been examined in detail (Hubendick 1945). In contrast, the New Zealand species *Amphibola crenata* (Martyn, 1786) has been studied in some detail with reports on its anatomy (Hutton 1879, 1881; Farnie 1919; Hubendick 1947; Pilkington *et al.* 1984), ecology (Watters 1964; Juniper 1986) and development (Pilkington & Pilkington 1982). All other amphibolids are known principally from shell descriptions. Descriptions of the anatomy of *A. crenata* have revealed several features uncommon in other pulmonates, including a monaulic (undivided) hermaphroditic reproductive system (Farnie 1919) and opposed ciliary tracts in the mantle cavity (Pilkington *et al.* 1984). Thus, at the time of commencing this study, it was not known whether the anatomy of *A. crenata* is representative of other amphibolids.

Hubendick (1945) carried out the only existing taxonomic review of the Amphibolidae. His review was based on limited morphological data, mainly shell characters. The anatomical information in his generic distinctions was based on previously published reports of *Amphibola crenata* and simple anatomical sketches attributed to *Salinator fragilis* derived from Pelseneer (1894). However, Pelseneer's (1894) original account illustrated the distal reproductive system of '*Amphibola nux avellana*' (a synonym of *A. crenata*), not *S. fragilis* as supposed by Hubendick (1945).

Confusing taxonomy has further complicated the understanding of the family. For example, Lamarck's (1822) original description of *Ampullaria fragilis* tentatively listed the distribution as New Zealand, although