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Complex morphological novelties on a simple basis: an example of transformation of the female structures of reproductive system into an aberrant copulative apparatus in opisthobranch molluscs

A. V. MARTYNOV

Zoological Museum of Moscow State University, Bolshaya Nikitskaya Str., 6, 103009 Moscow, RUSSIA; sasha_martynov@inbox.ru

ABSTRACT. Copulative apparatus of opisthobranch molluscs is characterized by the high complexity and frequent presence of hard chitinous structures. The latter can be roughly classified into solid hooks and hollow apical stylets. The paper is devoted to additional study of aberrant copulative apparatus in nudibranchs molluscs of the group Dunginini (Eubranchidae). This apparatus does not fit into the above-mentioned scheme and represents a special type of copulative apparatus within opisthobranchs molluscs. This should be taken into consideration in phylogenetic studies. The origin of the aberrant copulative apparatus is discussed.

The nudibranch family Eubranchidae is a good example of uniformity in both external and internal morphology with one exception: the taxon Dunginini, which consists of three genera *Aenigmastyletus*, *Leostyletus* and *Dunga,* possesses a very unusual copulative apparatus [Martynov, 1998].

The elaborated distal male part of copulative apparatus of opisthobranchs molluscs quite often contains various sets of chitinous hard structures. It can be roughly divided into two main types. First, there are solid hooks or scales (quite common in Cephalaspidea s.l., Anaspidea and Pteropoda), sometimes forming very complex constructions with several hooks different in size, like in dorids from the genus *Gargamella*, or within taxa of the order Acochlidiida. Second, there is a single apical hollow stylet, more characteristic of species of aeolidacean families Eubranchidae and Tergipedidae and for species of the order Sacoglossa. All these structures are clearly associated with male part of reproductive system, and appeared as a complication of penis. The aberrant pattern in the copulative apparatus of the genus *Dunga* from aeolidacean family Eubranchidae, in spite of being superficially similar to the first type of male genitalia with numerous hard hooks, actually does not fit these two types. Moreover, it demonstrates a more intricate relation to male and female parts of the reproductive system. Edmunds [1969] thoroughly reinvestigated *Dunga nodulosa* Eliot, 1902 and discovered a very unusual set of about 32 accessory glands in the copulative apparatus, together with the total absence of any seminal receptacles in female part of the reproductive system. A short time later, Baba [1971] described a similar but sufficiently simpler construction (containing only two glands in the copulative apparatus) in *Leostyletus misakiensis* (Baba, 1960) from Inland Sea of Seto, Japan, and confirmed absence of a seminal receptacle. In the early 1990s, the new material allowed to reveal that these "glands" are actually only sheaths for very complex and fragile hard structures, for which the term macrostylets was suggested [Martynov, 1998], and to describe two new genera.

The main aim of the present paper is to clarify the position of the aberrant copulative apparatus within opisthobranch molluscs. Besides, since there is no new information on the morphology of copulative apparatus of Dunginini, it is important to present additional data on this unusual case, which may help further researches.

Abbreviations on figures: ca — copulative apparatus; fm — female gland mass; rp — penis rudiment; rs — receptaculum seminis; p — penis; sg — supplementary gland; vd — vas deferens.

Copulative apparatus of *Aenigmastyletus* and *Leostyletus* has two types of hard structures, which are clearly differentiated by size, shape and position (Fig. 1). The first type, macrostylets, are 600-1200 μm in length, waved or helicoidal, elaborated in form, within sheaths. The second, microstylets, are more like a simple hook, 150-270 μm in length, within copulative atrium. The general shape of the copulative apparatus of *Aenigmastyletus alexeii* Martynov, 1998 is cap-shaped, with integrated stylet sheath (Fig. 1 B), whereas in *Leostyletus pseudomisakiensis* Martynov, 1998 it is discoid, with two prominent sheaths of stylets (Fig. 1 G,I). Macrostylets of the genus *Aenigmastyletus* are extremely different and united in one complicated structure of two stylets inserted to each other (Fig. 1 B, D).