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The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda)

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Abstract

The Hymenosomatidae is unique among the Brachyura on the basis of spermatozoal ultrastructure and morphological characters of the adults and larvae. The location of the hymenosomatid male gonopore, always a controversial question, is here shown to be sternal, not coxo-sternal. This disposition, analogous to the arrangement of Thoracotremata, contradicts all morphological characters that indicate a heterotreme affiliation, close to the Majoidea and Dorippoidea. Molecular data also support such an assignment. The multiple hymenosomatid plesiomorphies are reviewed. The exceptional male reproductive system, a new scheme for the Eubrachyura, is assumed, at least in part, to be the result of a strong carcinisation in an ancient, deeply rooted group, at present the most ecologically diverse in Brachyura. The presence of the Hymenosomatidae on the former Gondwanan landmasses and its worldwide pattern of distribution are consistent with the hypothesis of a Gondwanan origin of the family.

Key words: Brachyura, Eubrachyura, Thoracotremata, Heterotremata, Hymenosomatidae, Majoidea, Dorippoidea, male reproductive system, male gonopore, spermatozoa, coxo-sternal condition, carcinisation, larval development, megalopa, phylogeny

Introduction

The placement of the Hymenosomatidae MacLeay, 1838, within the Brachyura Latreille, 1802, has been controversial at one time or another, the family being considered heterotreme, close to or within the Majoidea Samouelle, 1819 (e.g., Rathbun 1925; Richer de Forges 1976, 1977; Guinot & Richer de Forges 1997; Guinot & Bouchard 1998; Martin & Davis 2001; Ng *et al.* 2008) or thoracotreme, often close to the Pinnotheroidea De Haan, 1833 (e.g., H. Milne Edwards 1837; Alcock 1900; Garth 1958; McLay 1988). A new step has been achieved when Hymenosomatidae has been found to be unique among the Brachyura on the basis of the spermatozoal ultrastructure so that it was difficult to accommodate the family in the three brachyuran divisions, Podotremata Guinot, 1977, Heterotremata Guinot, 1977, and Thoracotremata Guinot, 1977 (Richer de Forges *et al*. 1997). This discovery conformed to a puzzling situation, the sternal emergence of the male ejaculatory duct and gonopore in Hymenosomatidae. This is a thoracotreme disposition in contradiction with all the morphological characters that indicate a heterotreme affiliation for the family (Guinot & Richer de Forges 1997). The presence in the Hymenosomatidae of seminal receptacles connected to sternal openings of sternite 5, the vulvae (Guinot 1979a: 186), the salient apomorphy of the Eubrachyura Saint Laurent, 1980, supports a eubrachyuran assignment. Nevertheless, the retention in the basal Hymenosomatidae (Odiomarinae Guinot, 2011) of dorsal uropods as in the basal Podotremata (Guinot & Bouchard 1998; Guinot 2011), so far unique among eubrachyurans, merits discussion. In addition, a wide range of other plesiomorphic features is present in hymenosomatids, notably a weak cephalic condensation, with the absence of orbits and proepistome in basal representatives and incomplete orbits even in the more derived taxa. The great number of unique and exceptional traits of Hymenosomatidae, in particular the absence of a megalopal stage in the larval development of all its members, as well as occurrence in marine, brackish and freshwater habitats (Lucas 1980), requires a reappraisal of character evolution in Hymenosomatidae. The basal position of Hymenosomatidae in the heterotreme Eubrachyura as recovered by a wide range of data, including molecular analysis, necessitates a reappraisal of the relationships of the family and has led to a re-evaluation of the phylogeny of Brachyura.

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