Systematics, Biogeography and Functional Morphology of the Box Crabs (Family Calappidae)

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ABSTRACT

The box crabs (family Calappidae, H. Milne Edwards 1837) are a morphologically and ecologically distinctive group of marine crabs found in tropical and subtropical regions of the world. Traditionally placed in the section Oxystomata because of their characteristic triangular buccal frame (the 'oxystomatous' condition), they are one of the few brachyuran families capable of burying completely in soft substrata. This study aims to review the systematics of the family and to examine the phylogenetic and functional implications of the oxystomatous condition in an evolutionary and biogeographic framework.

The systematic status of the family Calappidae and the phylogenetic relationships of its four component subfamilies were re-evaluated based on a cladistic analysis of 78 adult morphological characters. A single tree was produced (CI = 0.654, RCI= 0.403). The monophyly of the Calappidae *sensu lato* is rejected. Yet the monophyly of each subfamily is supported, with the Calappinae clearly defined by 13 autapomorphies and the Matutinae and Orithyiinae well-defined by 6 and 5 autoapomorphies, respectively. Only the Hepatinae appears to be a relatively weakly-defined taxon supported by 1 autapomorphy. The data also suggest that the Calappinae and Hepatinae form a single lineage which is closer to some xanthids than to the Matutinae or Orithyiinae. A close link between the Matutinae and some leucosiids and between the Orithyiinae and some dorippids is also apparent, with a suggestion that these four taxa all belong to a single lineage. A revised classification of the Oxystomata *emend.* and Calappidae *sensu stricto* is proposed.

The phylogenetic relationships of 8 genera within the Calappidae *sensu stricto* were further examined based on a cladistic analysis of 55 adult morphological characters. A single tree was produced (CI=0.833, RCI=0.717). The data revealed two major lineages within the Calappidae: the 'calappine' clade consisting of *Calappa*, *Cryptosoma*, *Cycloes*, *Paracyclois* and *Cyclozodion*, and the 'mursiine' clade consisting of *Acanthocarpus*, *Mursia* and *Platymera*. Analyses of the fossil record and biogeographic patterns point to vicariance events associated with Gondwanan fragmentation. The earliest fossil record of the group suggest that present-day genera were already established by the Oligocene. Optimization of depth distributions on the cladogram indicates that the family initially diversified in deep water. Of the 10 genera, only three have a significant proportion of species recorded in waters less than 50 m: *Calappa*, *Cycloes* and *Cryptosoma*. All three genera comprise a single crown-group clade. The remaining genera are largely restricted to water between 100 and 300m deep. This suggests that the family had deep-water origins with only a single, derived, lineage moving into shallow waters.

An evaluation of existing evidence reveals two distinct means of concealment within the substratum in Brachyura: burrowing and burying. There are fundamental differences between the two types of behaviour, both in terms of ecological, mechanical and physiological implications. The oxystomatous condition was found to be primarily associated with burying crabs. The functional basis of the oxystomatous condition and its role in the burying habit was evaluated, based on two distinct forms within the Calappidae *sensu lato*: *Calappa* and *Matuta*. Although the morphology of the respiratory system of both taxa follow the typical brachyuran pattern, *Calappa* and *Matuta* both possess two unusual modifications which appear to be associated with their

burying habit: accessory inhalant channels and elongate exhalant channels. Video analyses demonstrated that both taxa enter the substratum backwards, within seconds, at relatively steep angles. Both taxa are capable of burying completely within the substratum for extended periods of time while maintaining contact with overlaying water at the surface. *Matuta* is unusual in that it is also capable of complete deep burial. Dye tracer studies show that ventilation patterns in both taxa are broadly similar and confirm the function of the accessory inhalant channels as the primary inhalant pathway. Both *Calappa* and *Matuta* ventilate their branchial chambers in the normal forward pattern and do not rely on prolonged reversed ventilation even when buried under the sediment. This is unique within Brachyura and is found only in one other family, the Leucosiidae, another oxystomatous group also characterized by accessory inhalant channels. It is hypothesized that the role of the oxystomatous configuration of the exhalant channels enhances the efficiency of the accessory inhalant channels. It serves to separate the inhalant and exhalant currents by dispersing the exhalant stream with sufficient force so as to prevent re-mixing, as well as creating a suction effect via the Bernoulli principle which facilitates the movement of fresh oxygenated water into the vicinity of the inhalant openings.

In summary, this study demonstrates that the Calappidae *sensu lato* is not a monophyletic, natural, group and that component taxa exhibit a clear evidence of convergent evolution. The oxystomatous condition, on which traditional groupings have long been based, has no phylogenetic basis and appears to have arisen independently in a number of lineages. In most lineages, however, the evolution of the oxystomatous condition appears to be closely associated with respiration whilst buried in soft substrata. The oxystomatous condition therefore is a functional not a systematic characteristic.

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