

CATOMERUS POLYMERUS AND THE EVOLUTION OF THE BALANOMORPH FORM IN BARNACLES (CIRRIPEDIA)

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SUMMARY

On the basis of comparative anatomy, Darwin proposed that the catophragmid *C. polymerus*, representing the basic form among balanomorphs, had evolved from a scalpellid lepadomorph ancestry. This hypothesis has since been supported by fossil evidence, but has not been tested by the techniques of comparative functional morphology.

Functional studies of *C. polymerus* and *Calantica villosa* have now shown that an evolution of catophragmid balanomorphs from calanticine scalpellids is functionally feasible, upholding Darwin's proposal. *C. polymerus* retains the scalpellid mode of planktivorous extension feeding, except for further modification of the first two pairs of cirri as short maxillipeds acting in forward food transfer in a limited space. The basic adaptive significance of the foreshortened form and flattened operculum of *C. polymerus* lies in allowing a species with this mode of feeding to inhabit a high energy intertidal environment. Protection against certain kinds of predation may also have been important.

The development of the opercular valves from capitular plates and their changed orientation relative to the wall is accommodated by further modification of a hinge mechanism already present in calanticine scalpellids. The closure mechanism of the operculum involves supplementation of the action of the adductor scutorum by the downward pull of large tergal depressor muscles, evolved as a modification of the peduncular longitudinal muscles of calanticines.

Massive tergal and small scutal depressor muscles, a basic balanomorph condition, are functionally associated with a large prosoma and paired branchiae occupying the rostral part of the limited mantle cavity.

Introduction

Catomerus polymerus (Darwin) is a common balanomorph barnacle on the rocky shores of southeastern Australia (Pope, 1965), easily distinguished by its eight wall plates supplemented by several concentric whorls of marginal plates (Fig. 1a). The recent revision of the Balanomorpha by Newman and Ross (1976) follows Utinomi (1968) and places *C. polymerus* in the family Catophragmidae of the superfamily Chthamaloidea. The species was first described by Darwin (1854) in his monograph on the Balanidae, from specimens collected from Twofold Bay, N.S.W. Darwin placed his specimens in the genus *Catophragmus*, previously erected by Sowerby (1826) for a similar animal, *Catophragmus imbricatus* Sowerby, known as two shells from Antigua in the West Indies in the collections of the British Museum. Pilsbry (1916) with more material of *C. imbricatus* at his disposal from Bermuda, recognised a difference between the two species sufficient to require transfer of *C. polymerus* to another genus, which he named *Catomerus*. A difference already noted by Darwin, is the presence in *C. imbricatus* of a pair of caudal appendages, absent in *C. polymerus*. The distinction between the two is otherwise minor, comprising slight differences in the operculum and basis. In a personal communication, W.A. Newman writes "I have despaired of finding much if any differences in the appendages between the two." At the same time, it has been recognised recently that *C. imbricatus* is now confined to the tropical W. Atlantic (Antigua and Bermuda), while the animals on the other side of the isthmus, in Panama and Costa Rica, are a distinct species, *C. pilsbryi* Broch (Southward and Newman, 1977).

The Catophragmidae also includes another surviving form, *Chionelasmus darwini* (Pilsbry), which apparently has a disjunct distribution, Hawaii and New Zealand in the Pacific Ocean and the Rodriguez