FUNCTIONAL MORPHOLOGY AND EVOLUTION IN THE TRIDACNIDAE (MOLLUSCA: BIVALVIA: CARDIACEA)

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SUMMARY

The Tridacnidae are a family of the Cardiacea in which the byssal apparatus has been retained and hypertrophied in connection with obligate life on the surface of Indo-West Pacific coral reefs. The greatly enlarged siphons occupy the entire upper surface, their inner marginal folds housing enormous populations of dinoflagellate symbionts (*Symbiodinium microadriaticum* Freudenthal) exposing them to high light intensities. The umbones are displaced on to the under side alongside the byssal gape.

The least specialized species (*T. maxima* and *T. squamosa*) retain byssal attachment throughout life. On the under side intimate contact is maintained with the irregular substrate by adventitious secretion of shell around the byssal gape and by a grinding action probably assisted by chemical activity by way of the enlarged middle folds of the mantle margins. This penetration is further developed in the smaller *T. crocea* which bores into coral rock, umbonal side foremost, by this probable combination of mechanical and chemical means.

In the "giant" species, *T. gigas* and *T. derasa*, the byssal apparatus atrophies after a certain size is attained, the byssal gape closing with reduction of the mantle folds. Subsequently the unattached animals maintain themselves solely by their great weight. Adaptation here involves increase in size with the much greater number of algae that can be maintained.

Hippopus differs in the more globular and smoother adult shell and by retention of the siphons within the valve margins. The final habitat is on the lee of reefs, frequently on sand, with initial attachment probably on the seaward side, then early freedom and subsequent rolling over the reef surface. The globular shell represents a self righting mechanism.

Knowledge about the significance of the zooxanthellae — certainly the major food source — is reviewed and the probable course of evolution in the Tridacnidae with acquisition of the symbionts, possibly from hermatypic corals, surveyed. The Tridacnidae appear to have separated from the other Cardiacea about the beginning of the Caenozoic, possibly filling the niche left vacant when the bivalve rudists (Hippuritacea) became extinct.

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INTRODUCTION

Apart from the corals, the bivalve Tridacnidae are the most characteristic, as they are frequently the most striking, members of the fauna of Indo-West Pacific coral reefs. To look down upon their opened valves is to view the upward directed and vastly hypertrophied siphons which, richly pigmented, are continually exposed even to the strongest light (Fig. 1). Retaining their original function, the siphons have altered in size and in position so as to house and expose vast populations of the dinoflagellate symbionts or zooxanthellae which have become a major if not *the* major source of nutrition. Unique in this respect the Tridacnidae are yet related to the superficially burrowing Cardiidae and are included with that family and the Hemidonacidae in the superfamily Cardiacea. The possible course of their evolution, involving intimate association with hermatypic corals, is discussed later. After early post-larval freedom, the modern species, five species of *Tridacna* and *Hippopus hippopus,* become immobile to be invariably byssally attached in early life. Later the two "giant" species, *T. derasa* and *T. gigas,* and *H. hippopus* lose attachment although remaining immobile.

TRIDACNID FORM

As already personally described (Yonge, 1936, 1953a, 1974, 1975) and as indicated in Figs. 2 and 29, the enlargement and consequent extension of the siphons along the entire upper surface involves (in phylogeny but *not* in ontogeny) an anti-clockwise rotation in the sagittal plane of the mantle/shell in relation to the viscero-pedal mass. The latter is effectively unaltered, foot and byssal apparatus mid-ventrally situated, in necessary contact with the substrate, throughout the long period of evolutionary change. The dorsal region of the mantle, with the umbones and hinge secreted by it, moves to the underside eventually to become situated at the anterior end of the large byssal gape. In the course of this 180° rotation, the anterior adductor is lost and the anterior byssal (pedal) retractors (abr) very much reduced. The Tridacnidae thus become monomyarian in a unique manner (Yonge, 1953b) and with the greatly hypertrophied posterior byssal retractors (pbr) in close association with the single greatly enlarged adductor (ad). The visceral organs are little affected. The anus (a) moves from its customary position on the hind surface of the adductor to the upper surface so maintaining its relationship with the anteriorly displaced exhalant aperture. The line of the ctenidial axes is little changed while the visceral organs — gut, heart, gonads and greatly enlarged kidneys — and the foot, all retain their original positions (Figs. 2, 29). The nervous system, originally figured and described by Lacaze-Duthiers (1902), is typical with a cerebro-visceral ganglion on