AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

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.

CONTENTS

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
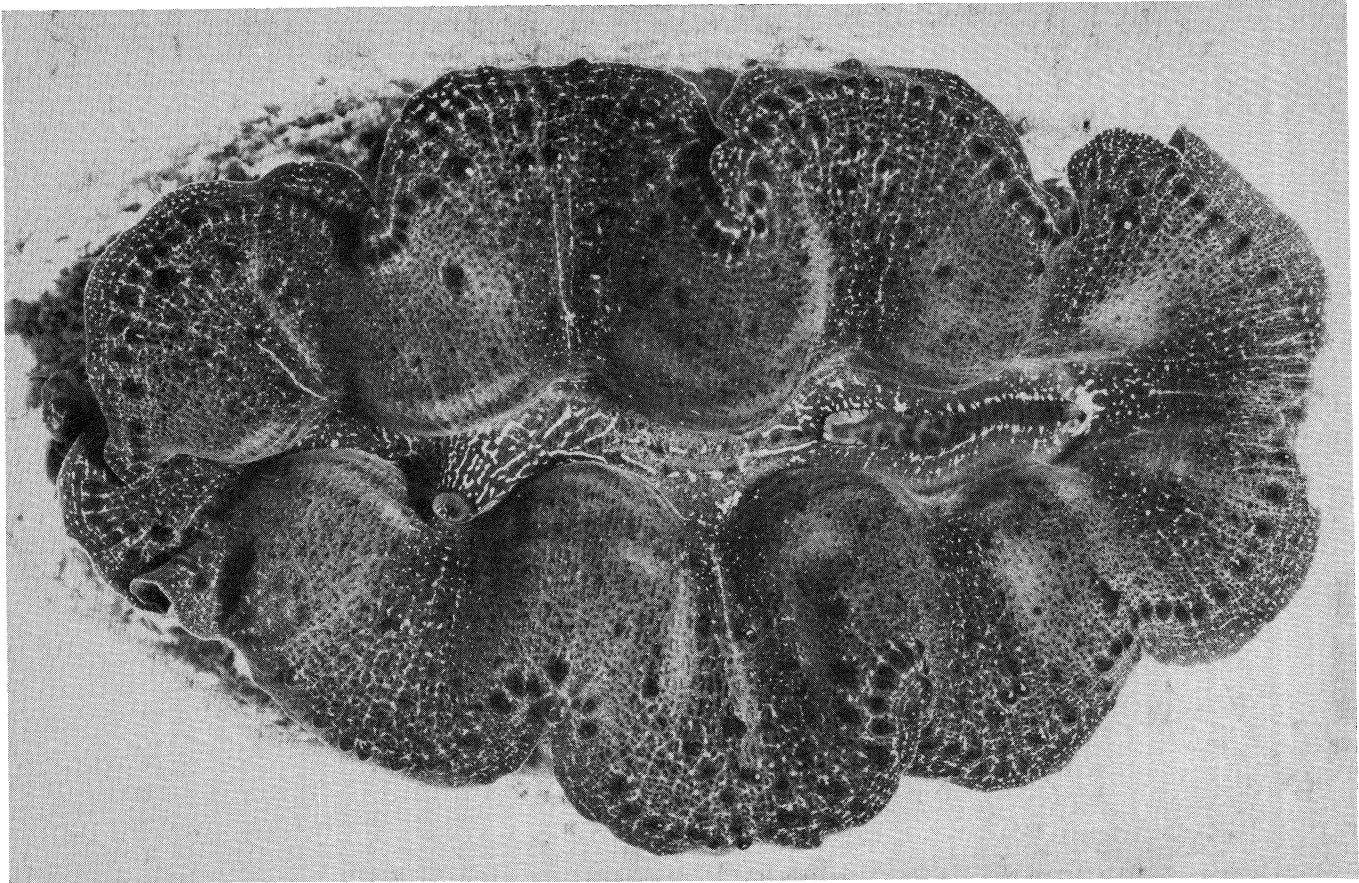
Figure 1. *Tridacna crocea.* Specimen contained in cavity within perspex viewed when siphons fully extended, elongate fully open inhalant aperture on right, tubular exhalant aperture on left, area between composed of fused inner marginal fold, peripheral areas of inner fold extensions overlapping valve margins; dark areas eyes. (Photo T. F. Goreau).
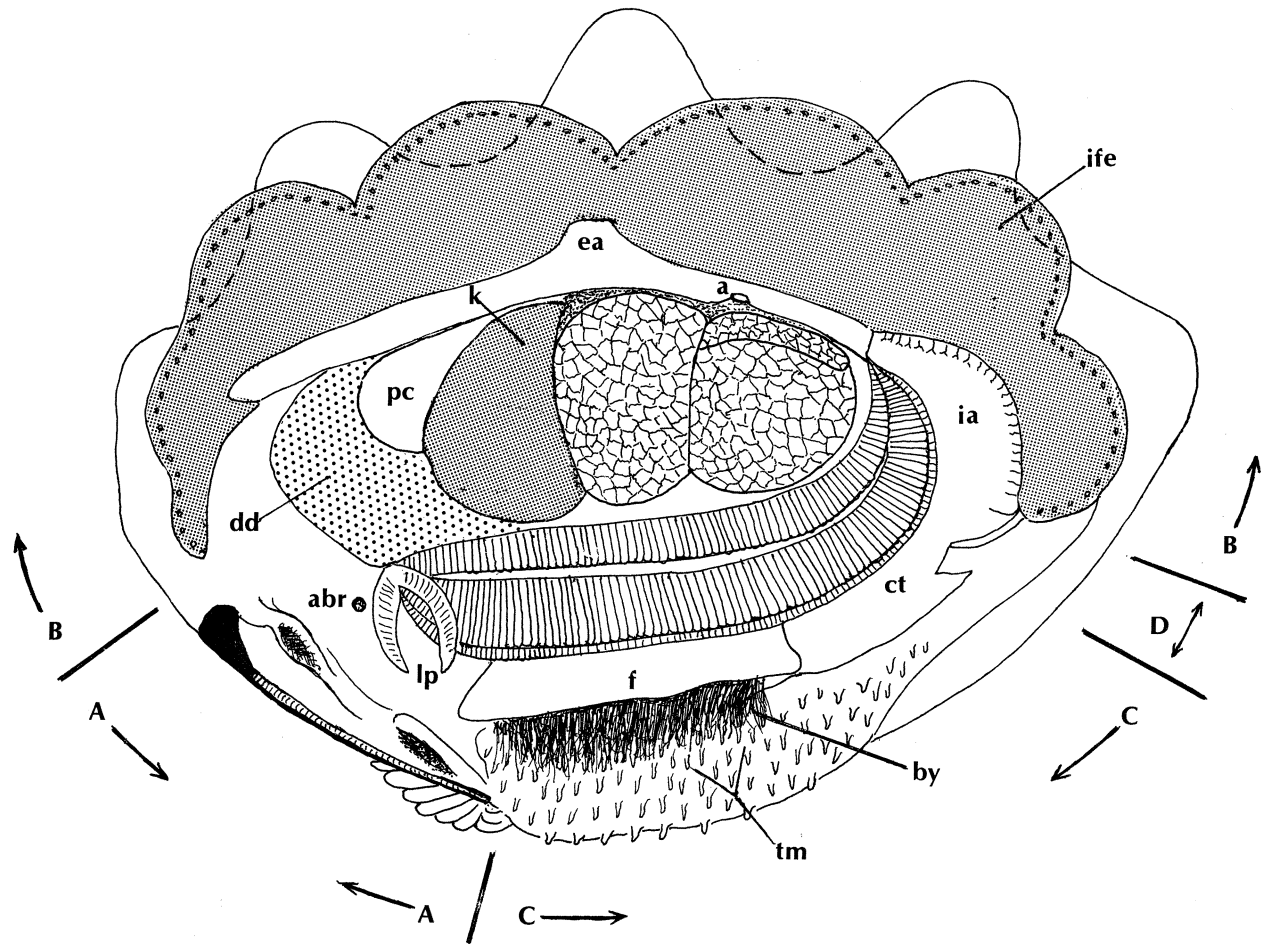
Figure 2. *T. maxima,* viewed from left after removal of valve and mantle lobe showing major organs in the mantle cavity and major peripheral areas, A—A, ligamental (cardinal) area; B—B, siphonal area; C—C, byssal gape; D, region of mantle fusion posterior to byssal gape. (Explanation of abbreviations see page 777.).

each side of the mouth, centrally placed pedal ganglia and a large fused visceral ganglion on the posterior side of the adductor. The only change from other bivalves is the anterior instead of the posterior course of the two more dorsal siphonal nerves (Fig. 3), again due to the anterior displacement of the siphons (Yonge, 1953a).

The major changes are pallial involving the orbital and adductor muscles and the shell. Forward extension of the siphons has involved corresponding movement and enlargement of the siphonal muscles (a localized region of the orbital muscles), from immediately ventral to the posterior adductor in the Cardiidae, to stretch broadly forward above the adductor along the entire upper surface of the valves (Fig. 4).

In relation to difference in habit, the shell is more elongate than in the Cardiidae while the hinge region is inevitably modified. Dentition in the Cardiidae, e.g. the common cockle, Cerastoderma edule, consists of central cardinal teeth below the umbones with very symmetrically sited anterior and posterior laterals. On the right valve the cardinal area consists of a deep socket with teeth on either side, in lateral areas teeth are situated above and below the sockets. The mirror image prevails in the left valve, major teeth being flanked by sockets. The ligament possesses well developed inner (fibrillar) and posterior outer (lamellar) layers with a very short anterior outer layer extending back under the inner layer — a typical opisthodetic condition.[1]

Due to rotation of the mantle/shell, in the Tridacnidae the originally anterior (now, in relation to the viscero-pedal mass, posterior) end of the hinge region at the umbones forms the anterior boundary of the byssal gape (Figs. 2, 5). The anterior lateral teeth are lost while the cardinal area is displaced ("posteriorly" in relation to the mantle/shell but "anteriorly" in respect of the viscero-pedal mass). The cardinal teeth (cth) are reduced to a single very similar tooth and socket in each valve, the tooth on the right fitting into a deep socket below that on the left. All three ligamental layers are long; the posterior outer (Fig. 15, pol) widening out and then stretching anteriorly (in relation to the mantle/shell) and topographically below the thick inner layer (il) secreted by the mantle isthmus. The anterior outer layer (aol) is much longer than in C. edule. The entire hinge region has moved posteriorly in relation to the umbones but the ligament is long and powerful.

The extent of the various pallial regions after rotation is shown in Fig. 2. Of the total periphery about 14% is occupied by (A) the ligamental region (mantle isthmus with epithelia secreting outer ligament layers), the remainder, consisting of the mantle lobes, being made up (B) of siphons 60% (compared with only 13% in C. edule), (C) byssal gape some 20% with the short extent of pallial fusion (D) between this and the siphons accounting for the remaining 6%.

As in all Bivalvia, the lobes are bordered by three folds (a fourth in a few superfamilies is concerned with directing the pseudofaecal stream). They are supremely important. The outer, as in all shelled Mollusca, is secretory forming the outer calcareous layer of the valves on its outer surface and the superficial periostracal layer in a groove usually at the base of the inner surface. The other folds are largely confined to the Bivalvia. The inner one is muscular and controls inflow and outflow of the water current created by the hypertrophied ctenidia. The middle fold is largely sensory with tentacles and sometimes eyes; this region is now in closest contact with the environment, it functionally replaces the enclosed and so atrophied head region.

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1. A more detailed description of these ligaments will be given in a projected survey of the superfamily Cardiacea.
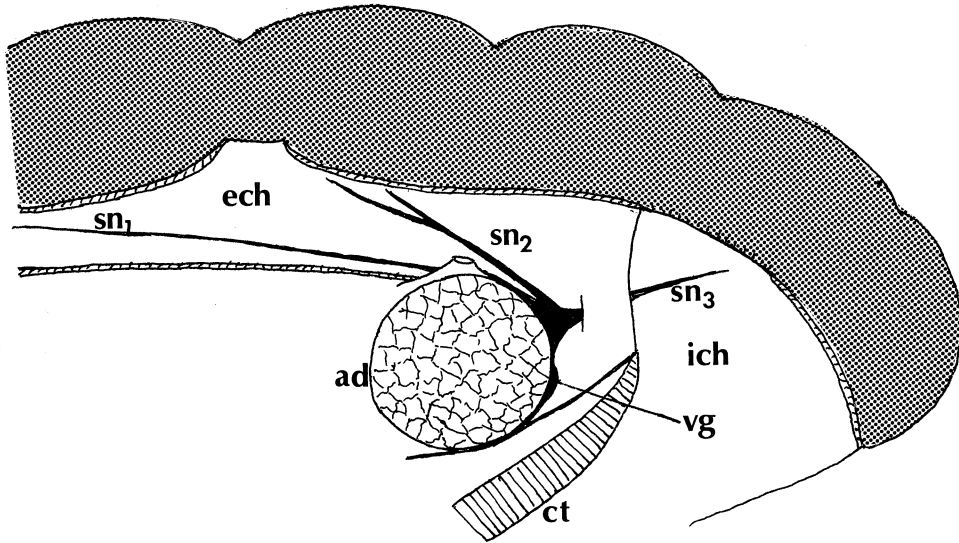
Figure 3. Modification in direction of siphonal nerves (sn₁₋₃) in Tridacnidae due to hypertrophy and anterior extension of siphons. (after Yonge, 1953a).
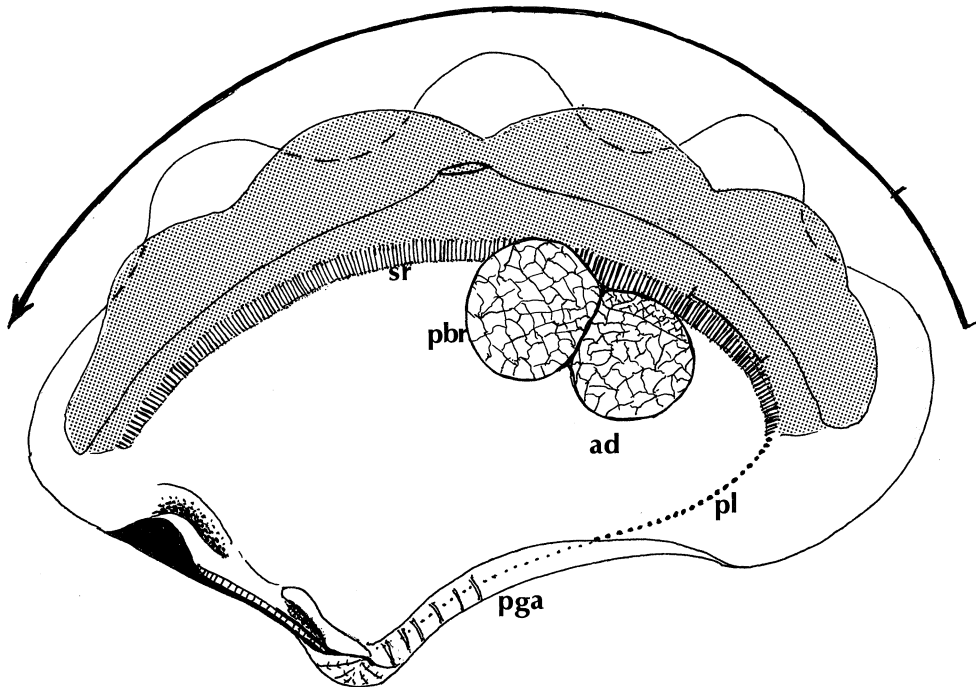

Figure 4. Anterior extension of siphonal retractors, dorsal to adductor and posterior byssal retractor, associated with anterior extension of siphons from AB to AC in the Tridacnidae.

To an extent usually consistent throughout any superfamily, the mantle lobes unite by way of these folds with fusion always beginning, both in phylogeny and ontogeny, by way of the inner folds (Yonge, 1957). Thus where siphons are present, these may be formed by fusion of the inner folds exclusively, the two siphons separate and independently mobile as in the Tellinacea (Type A), by union of inner and middle folds forming fused siphons as in the Veneracea (Type B), or with the further addition of the outer folds and so incorporating the periostracal grooves to produce the periostracally covered siphons of the often deep burrowing Myacea, Mactracea and Saxicavacea (Type C). In the Cardiacea, however, another condition prevails, not recognized when these types were described (Yonge, 1957). Here formation of the siphons involves the inner folds only but, unlike the Tellinacea, the two are united while the inner folds bear the sense organs, particularly eyes, usually carried on the middle folds. These, though present, are greatly reduced in this region. Such siphons, present in all Cardiacea but greatly hypertrophied in the Tridacnidae, are here designated Type A+.

The effect of rotation of the mantle/shell in the Tridacnidae is to separate the originally closely united siphons, the inhalant opening (ia) pulled out to form an elongate slit with the rounded exhalant aperture (ea) situated on the summit of a tubular extension in the middle of the upper surface (Figs. 1, 2). Moreover the function of the marginal folds is widely different on upper and under surfaces[1]. On the former they are modified for housing and exposure to light of the contained zooxanthellae, on the latter, around the margins of the byssal gape, for maintenance of close contact with the usually very irregular surface of the rocky substrate. No other bivalves have taken such advantage of the potentialities latent in the possession of these marginal folds in the course of adaptation to the needs of a new (and here a unique) mode of life. We return to this subject later.

DEVELOPMENT

The Tridacnidae are all protandric hermaphrodites, the process of spawning in *T. crocea*, *T. "serrifera"* *(T. maxima?)* and *H. hippopus* being described by Wada (1952, 1965). The veliger larvae and the pediveligers into which these change on settlement are stated not to contain zooxanthellae (LaBarbera, 1974, 1975). Jameson (1976) reports settlement of *T. crocea*, *T. maxima* and *H. hippopus* as occurring respectively at 12, 11 and 9 days after fertilization, all of them around 200 μm long. He reports the first appearance of zooxanthellae as occurring in settled animals at respectively 19-25, 21-40 and 25-27 days after fertilization. Beyond stating that they appear in the mantle, Jameson gives no account of precisely where they first appear or of how they spread although he did observe a striking increase in the rate of growth beginning at the time of first infection. It is also unknown at what stage in the *algal life history* these infect young tridacnids. This could be by way of the non-motile stages often expelled, apparently intact, by stressed corals (Yonge & Nicholls, 1931; Goreau, 1964) but also probably in the normal process of controlling the algal population, or alternatively by one of the swimming, dinoflagellate, stages never identified in nature but appearing in culture (Taylor, 1969).

There is no information about the manner in which what is apparently (and would be expected to be) a typical bivalve veliger and pediveliger change into the unique tridacnid form with umbo and hinge alongside the byssal gape on the under side. LaBarbera (1975)

1. Reference will now be made exclusively to *upper* and *under* surfaces. This avoids the use of dorsal and ventral and so the conflict between those who regard the umbo and hinge as unalterably dorsal and those (including, as will be apparent, the writer), who consider that throughout the Bivalvia where the foot is retained this, with the byssus, is always mid-ventral, unalterably associated with the substrate whatever the effect this may have on the position of the umbones.

finds evidence of differential growth around the valve margins as claimed by Stasek (1962). This is to be expected, the final form being attained as rapidly as possible just as it is in the even more highly modified Teredinidae where the post-larva begins to bore into wood immediately after metamorphosis (Sigerfoos, 1908; Turner, 1966). There has never been any suggestion by this writer that, as Stasek and LaBarbera appear to think, there is recapitulated in development the course of evolution involving rotation of the mantle/shell in relation to the viscero-pedal mass (as impossible here as the corresponding sequence of events would be in the Teredinidae). The course of post-larval development involving infection by zooxanthellae and their later spread in the siphons and elsewhere requires detailed study. It would also be most illuminating to follow the later course of development should infection by zooxanthellae be prevented as it so easily could be.

Little is known about the growth and habits prior to secure byssal attachment which occurs in all species whether it is maintained throughout life or not. Young *T. crocea* up to 5 mm long were personally observed moving about on rock surfaces by means of the slender foot and attaching byssally from time to time within sheltered areas such as empty barnacle shells (Yonge, 1936). In habit they resembled young *Mytilis edulis,* climbing the sides of glass aquaria in the same manner. The age of these animals was uncertain (in structure apart from the extruded and active foot, they resemble adults) but Hamner and Jones (1977) found small boring individuals of this species in October (in the same region) which they thought had settled early that year and so would be over 6 months old. There is obviously a period of freedom after the adult form is attained and before byssal attachment becomes permanent although with the differing eventual consequences described below. This period of pedal freedom will enable the animal to search the environment for a suitable horizontal surface where it can settle with the siphons facing upward. This is the initial essential need.

However this site of attachment may not be final. Recently attached animals will inevitably be dislodged by heavy seas and possibly some animals may attach and re-attach several times before finding a satisfactory site. McMichael (1974) made most interesting observations on changes over a three year period in the population of *T. maxima* in an area of some 450 square metres on One Tree Island (Capricorn Group, Great Barrier Reef). Initially 359 animals were counted, similar counts yielded 345 animals two years later and 374 the year after that. Losses could largely have been due to natural death or to predation although some small animals might have moved out and some larger ones been dislodged and carried out by water movements. Of the recorded incomers the smallest ones could have settled there directly from the plankton or have crawled in after settlement. This could not have been true of incomers between 80 and 200 mm long (36 in one year and 28 in the other). While a few might have been overlooked in earlier counts, the majority were presumably carried in by heavy seas after these had dislodged them. Numbers are great enough at least to indicate the possibility that up to a considerable size these byssally attached tridacnids may be carried to new sites where, if the substrate is suitable, they can re-attach, although the process must be rapid if predation is to be avoided. As noted later, this passive transport of sizeable animals appears to be the normal state of affairs in *H. hippopus* although the final habitat of this species is often on sand where no byssally attached tridacnid could live.

DISTRIBUTION AND HABITAT

The species of the Tridacnidae, five of *Tridacna* and *Hippopus hippopus* (Linnaeus 1758), inhabit areas of varying extent within the tropical Indo-Pacific (for taxonomic details and maps of distribution see Rosewater, 1965). They invariably occur in

association with coral reefs, requiring much the same range of temperature as do most hermatypic corals. Their need for light is even more demanding, for instance at Palau (Hardy & Hardy, 1969) in the clearest water on the seaward side of reefs tridacnids do not occur below depths of about 20 metres while in more turbid lagoon waters they are confined to areas of only half this depth. The creation, therefore, by coral growth of extensive shallow water areas provides them with their required habitat including wide areas of dead coral which supplies the hard substrate needed for initial settlement and often for permanent colonization. From the living coral possibly also may come the zooxanthellae which, as noted above, are not acquired until after settlement.

All species are initially attached by a massive byssus. This is clearly the primitive tridacnid habit with subsequent immobile "freedom" in certain species a secondary condition. Attachment is retained throughout life in *T. maxima* (Röding 1798), *T. squamosa* Lamarck 1819, and in the boring *T. crocea* Lamarck 1819, these three constituting what Rosewater designates the subgenus *Chametrachea*.

The two first (with the most primitive habit) have the widest distribution extending from the western extremities of the tropical Indian Ocean (to the north including the Red Sea) to the central south Pacific. Presumably they possess the greatest range of breeding temperatures while possibly their larvae spend the longest periods in the plankton. They are also probably the oldest species. In both, the siphons have a bewildering range of colours (see Rosewater, 1965), with hardly two patterns the same[1]. Shell lengths of over 300 mm are attained but *T. squamosa* is broader with more rounded marginal interdigitations of the shell valves and more centrally placed umbones. The projecting scales, present in rows on the ridges on the outer surface of the valves in both, are more pronounced in *T. squamosa* which is usually attached to a firm surface whereas *T. maxima* tends to settle upon, or perhaps make its post-larval way by crawling on to, coral rubble. In both, the broad undersurface is extensively and most firmly attached by byssal threads which appear somewhat more gelatinous in *T. squamosa*. By contractions of the large posterior retractors the shell is pulled firmly down often, particularly in *T. maxima*, penetrating into the substrate especially where this is less coherent. An extreme instance is that of an individual 254 mm long by 190 mm high which was found embedded to a depth of some 130 mm in rubble. The surface of the valves was worn smooth to this height, above this scales protruded. As described below for *T. crocea*, this boring is almost certainly assisted by chemical (probably chelating) action with the certainly accompanying grinding action produced, again as in *T. crocea* (Fig. 18) by alternate contractions of right and left posterior byssal retractors. Where animals are more superficially sited (or the rock surface more impenetrable) protection of the byssal opening is ensured by formation of the byssal "funnels" described below. The final effect in all cases is extremely secure and intimate attachment; it is most difficult to detach well grown specimens of these species and impossible for predators to enter.

T. maxima is the commoner with a somewhat wider distribution. It is the only tridacnid found throughout the Gulf of Eilat at the head of the Red Sea (Goreau, Goreau & Yonge, 1973) and, diagonally across the tropical Indo-Pacific, in the Tuamotus where Salvat (1969, 1971) found it in the closed atolls at densities up to 63 large individuals per square metre with an estimated weight per hectare of 37 tons of shell, with 7 tons of contained tissues. On One Tree Island, McMichael estimated a total population (of *T. maxima* alone) of over 2 million with estimated growth to lengths of around 240 mm in

1. As shown by Kawaguti (1966), pigmentation is due to iridophores. However where tridacnids live in shade, or are subjected to such conditions, the siphons become extremely pale indicating that these structures as well as the zooxanthellae are affected by lack of light.

somewhat over forty years.

The boring habit is developed to the full in the small *T. crocea* which penetrates solid coral rock with the valve margins flush with its surface over which the richly pigmented (usually blue) siphons extend as a conspicuous scalloped sheet of tissue (Fig. 1.) This species is restricted to the central Indo-Pacific but within this still very extensive area it is usually the commonest and certainly the most successful species, this due to the great protection afforded by boring. Hamner and Jones (1976) provide impressive data about its density with numbers "regularly exceeding 100 clams/m$_2$ with notable effects on erosion and sediment production".

In the remaining species, the "giant clams" *T. gigas* (Linnaeus 1758) and *T. derasa* (Röding 1798), attachment is lost after a certain age when the byssal gland atrophies and the gape closes. The animals subsequently maintain themselves in an upright position solely by virtue of their great weight. Large individuals of *T. maximus* were encountered with a reduced byssal opening suggesting that its closure, with reduction and atrophy of foot and byssal gland, would be the consequence of further increase in size and so inevitably occur, after a certain age, in any large species of tridacnid.

Both are restricted to much the same regions in the Central Indo-Pacific from the west coast of Sumatra to Fiji (Rosewater, 1965). *T. gigas* is the largest bivalve ever evolved, the shell reaching recorded lengths of 1370 mm. It has resemblances to *T. squamosa* but has no scales on the valves. *T. derasa* is smaller not exceeding lengths of around 510 mm and easy to distinguish owing to the much lower radial sculpture. Both occur in shallow water and may be partially exposed at low tide. They would seem to settle in relatively sheltered areas where they are unlikely to be displaced while still attached; after this they become too massive to be moved. The two species doubtless have distinct ecological needs but these have never been determined.

The horse-hoof clam, *H. hippopus*, is easily distinguished by its more spherical form, very closely interlocking valves and enclosure of the siphons entirely within the valve margins. It has much the same distribution as those of the two giant tridacnids and like them loses attachment. But it does so at a much earlier age to be then rolled across the reef surface sometimes to remain on this but frequently coming to final rest on sandy substrates in the lee where it may often form the most conspicuous member of the fauna (Fig. 22).

ADAPTATIONS

The major, and unique, adaptation in the Tridacnidae is the modification, with their accompanying great enlargement, of the siphons for housing and exposure to light of the symbiotic zooxanthellae. This involves enormous hypertrophy of the inner mantle fold on the upper surface. But during attachment, i.e. throughout life in permanently attached species, the middle mantle folds are no less significantly modified on the *under* surface. Conditions on both surfaces are shown in Fig. 6. In consequence there is great dissimilarity in the position and width of attachment of the pallial (orbicular) muscles on upper and under surfaces. As shown in Fig. 4, on the former the siphonal retractors (modified and hypertrophied orbicular muscles) are broad and attached well within the margin of the valves whereas on the under side the pallial muscles form only a thin line of attachment just within the rounded margin of the byssal gape.

Description now follows of these adaptations and of their significance in the life of the animals together with that of other adaptations involving boring, increased size and loss of attachment and final freedom in *Hippopus* from dependence on a hard substrate.
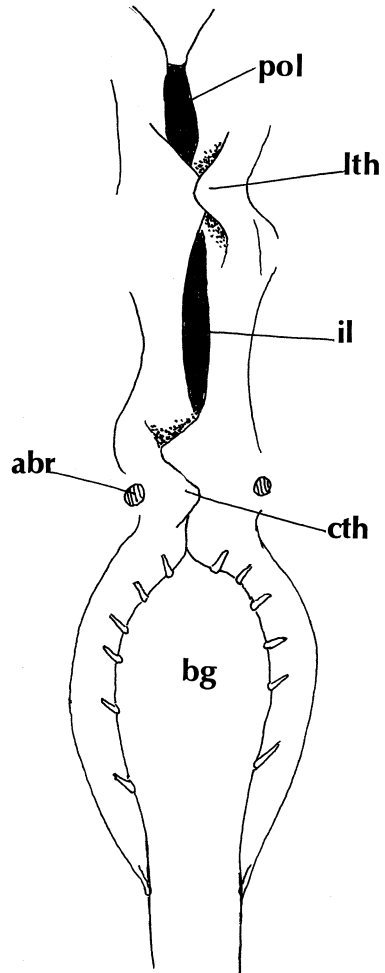
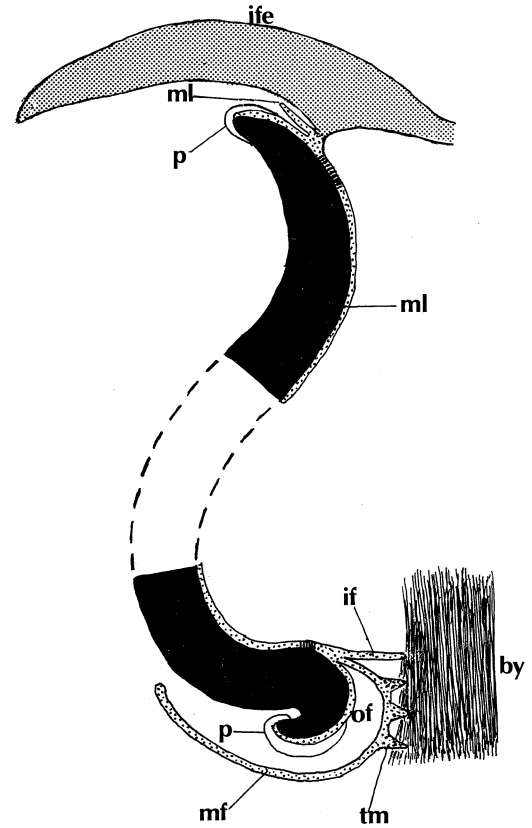Figure 5. *T. squamosa*, byssal gape and hinge region viewed from within.

Figure 6. Mantle margins in *Tridacna*, semi-diagrammatic representation showing differences in modification on upper and lower surfaces, inner folds hypertrophied on former and middle folds on latter.

746   C. M. YONGE

(a) Permanently Attached Species (*T. maxima, T. squamosa, T. crocea*)

Upper Surface: the richly pigmented siphons extend in a series of deep, slightly overlapping lobes well beyond the margin of the valves to form a flat platform. The *entire exposed surface* (i.e. all shown extended in Fig. 1) consists of the greatly hypertrophied inner marginal folds. These are extended laterally when the valves open, upward when they are closed, to form what are here described as the inner marginal fold extensions (ife) which surround the entire siphonal area (Figs. 1, 2) uniting centrally (fif) between the two openings (i.e. Type A+siphons). This region is shown, following contraction due to fixation, in the transverse section of a very small *T. crocea* (ca. 1 cm long) in Fig. 7.

These folds are everywhere penetrated by branches of the siphonal muscles (sr) responsible for their withdrawal and by the blood sinuses (bs), pressure in which causes their extension when the valves separate. These are also the site of great numbers of zooxanthellae and the means of their eventual transport into the visceral mass. On one side of the figure an eye (ey) has been sectioned. These were earlier described (Yonge, 1936) as "hyaline organs" because although they had a somewhat dumb-bell shaped lens there was no evidence of either retina or nerves. They were regarded as vestigial eyes, the lens retained for better conveyance of light deep into the tissue for the benefit of the zooxanthellae[1]. But more recently, using the electron microscope, Stasek (1966) and in more detail, Kawaguti and Mabuchi (1969) have identified both retinal cells and nerves with Frankboner (1979) finding them totally composed of retinal cells. It appears that these organs, which occur in a more or less regular row near the margins but are also scattered irregularly elsewhere, are responsible for initiating the reflex movements that culminate in sudden expulsions of water through the exhalant siphon. Eyes are certainly present on the tips of the tentacles on the inner fold around the siphons in many, possibly all, species of Cardiidae; on the other hand there are no eyes in *Hippopus*.

The middle folds (Figs. 6, 7, mf) although always present, are never visible on the upper surface. In the section they are greatly contracted following fixation appearing very small both in comparison to the immense inner folds on the one side and the elongated outer folds (of) on the other. When examined in life after removal of the valves in *T. maxima* (Fig. 8) they are revealed as being delicately pigmented with iridescent spots of gold on the inner surface. A few zooxanthellae are contained within the tissues indicating some exposure to light but the sensory functions usually possessed by these folds are absent.

The outer, secretory, fold (Figs. 6, 7, 8, of) is equally obscured in life. It is colourless and without zooxanthellae. The periostracal groove (pg) which in other bivalves is situated between the bases of middle and outer folds, here runs along the inner face of the outer fold some two thirds of the distance from the tip. There can be no question here — as there has been in other bivalves — as to whether the groove is associated with the middle rather than the outer fold. Observed in life the marginal two thirds of the inner surface of this fold is covered with transparent periostracum continuous with the superficial covering of the shell. Within the extrapallial cavity so created the outer, prismatic layer of the valve is secreted by the outer surface of the outer fold.

The secretory activities of the outer fold co-operate with the inner fold extensions to provide the maximum possible surface area for horizontal exposure. The generative curve is thrown into a series of what Rosewater describes as interdigitating projections representing a great increase in length. This is true of all tridacnids. In a shell of *T. gigas* 36.5 cm long, the length of the curved upper surface is about 53 cm but the actual length

1. This may have a measure of truth; zooxanthellae are always particularly numerous immediately around them.
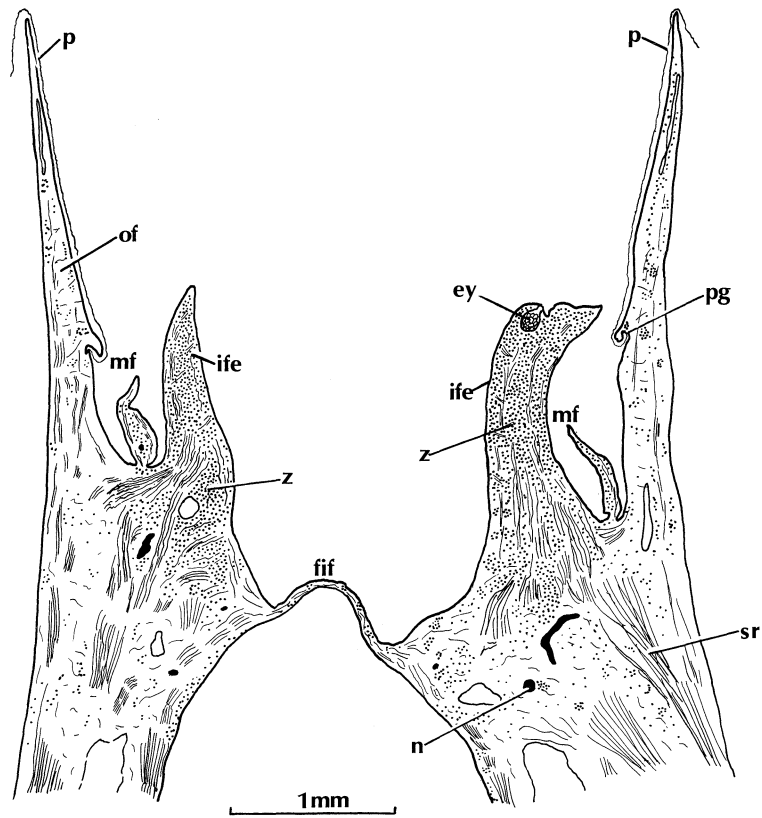
Figure 7. *T. crocea,* transverse section through middle of upper surface showing mantle lobes (much contracted).
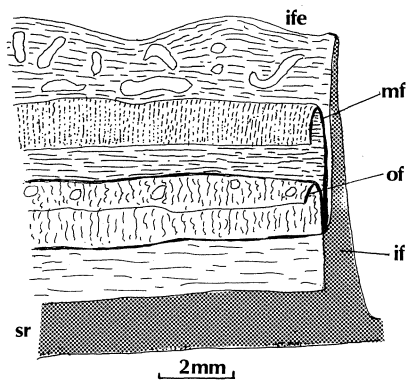

Figure 8. *T. maxima,* drawing, in life, of mantle margins on upper surface viewed from outer side after removal from shell.
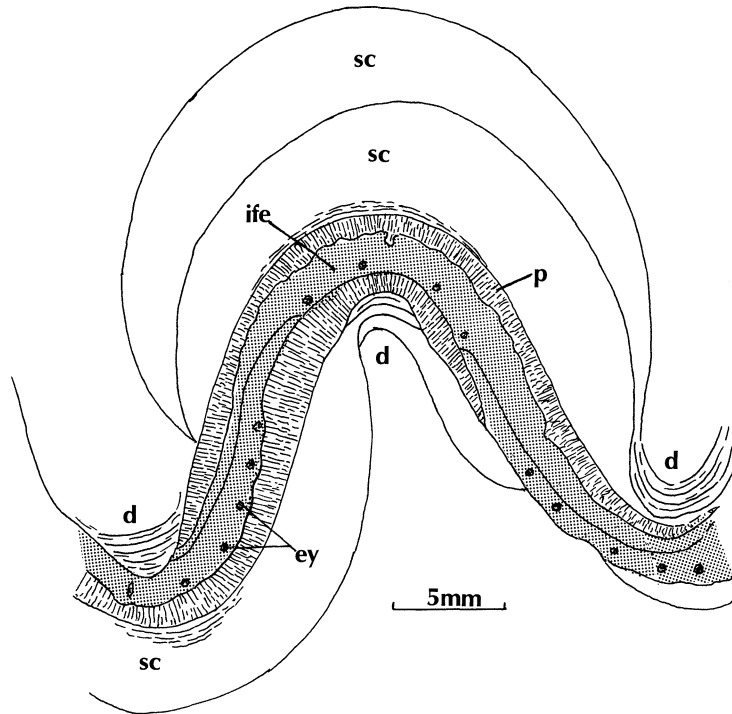
Figure 9. T. squamosa, region of upper surface with valves almost closed and only limited area of siphonal tissues with marginal periostracum visible; shows close interdigitation of valve margins.
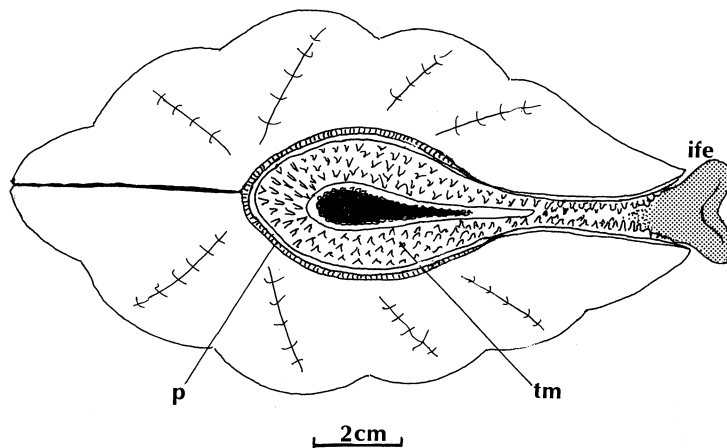

Figure 10. *T. maxima,* intact animal viewed from under surface showing byssal gape with elongate byssal mass surrounded by middle mantle folds with numerous blunt tentacles.

of the undulating margins of the valves is 85 cm. As a result of these undulations, the length of the mantle margins is increased by some 60%. This involves a corresponding increase in the length of the inner mantle folds and so in space for accommodation of additional zooxanthellae.

In these permanently attached species the deep radial grooves in each valve which correspond with the marginal depressions carry a series of projecting scales already noted as being most conspicuously developed in *T. squamosa*. These are added to periodically during growth but worn away basally where the animal grinds into the substrate. Their formation involves a series of extensions by the outer marginal folds beginning, as shown in Fig. 9, by topographically upward growth from the base of the preceding scale (this occurring obscurely beneath the overlying inner folds). Addition to the outer calcareous layer occurs within the periostracal sheet which is attached at progressively higher levels until a further burst of secretory activity produces another scale.

This process has resemblances to the formation of "shoots" in the Ostreacea but reduced growth continues between successive bursts in the Tridacnidae which it does not in these oysters. The final effect is the formation of a broad shell platform on which the expanded siphonal margins are supported.

What has to be said about the siphonal openings covers all species. The extended inhalant aperture (attaining 1/3 the length of the animal) is fringed with very short, usually branched tentacles. These are best developed posteriorly but can only act as strainers when the two sides are very close. The short exhalant tube is extremely mobile folding inward when not open. Through it is directed, with impressive force, the large volume of water that accumulates in an exhalant chamber (Fig. 2) which, due to the anti-clockwise rotation of the siphons stretches to the anterior end of the upper surface (Yonge, 1953a) forming what Stasek (1965) has very suitably termed a "suprabranchial cul-de-sac". Thus, whereas in other bivalves adduction produces the greater outflow through the inhalant opening, so aiding in the disposal of pseudofaeces, the opposite is true of the tridacnids, where pseudofaeces are of minor importance. Stasek (1965) and also McMichael (1974) claim that the water jet is directly aimed against possible predators such as an approaching fish. This is perhaps less certain but the quick muscle of which the adductor is very largely composed certainly reacts to any stimulus reaching it by way of the visual organs on the inner fold extensions. This may often be the shadows of fish which do frequently bite into the exposed siphonal tissues. These can, however, be withdrawn by contraction of the siphonal retractors without involving the adductor.

Under Surface: the structure of the mantle margins along the under surface in *T. maxima* is shown in Fig. 10 with a transverse section through the middle of the byssal gape of *T. crocea* in Fig. 11. The gape is of impressive size in these attached species owing to the exceptional extent of the byssus needed for securing these animals in shallow, well illuminated, but often highly agitated, waters. One example may suffice, that of a specimen of *T. maxima* 205 mm long by 115 mm broad in which the byssal opening was 50 mm long and 34 mm wide. The byssus consisted of a solid central mass about 13 mm in diameter pointing forward and with many attached strands on each side. These were securely cemented to the substrate of irregular coral rock over an area some 30 mm in diameter. Sizes of byssal gape and byssus vary widely but examination of specimens of *T. maxima* ranging in length between 135 and 240 mm revealed byssal openings of between 30 and 60 mm long and 24 and 35 mm wide. In *T. squamosa* of between 200 and 225 mm in length byssal gapes ranged in size from 45 by 15 mm to 55 by 30 mm.

The presence of so large an opening on the under side of a defenceless animal incapable of movement presents major problems. The entrance of any of a host of small
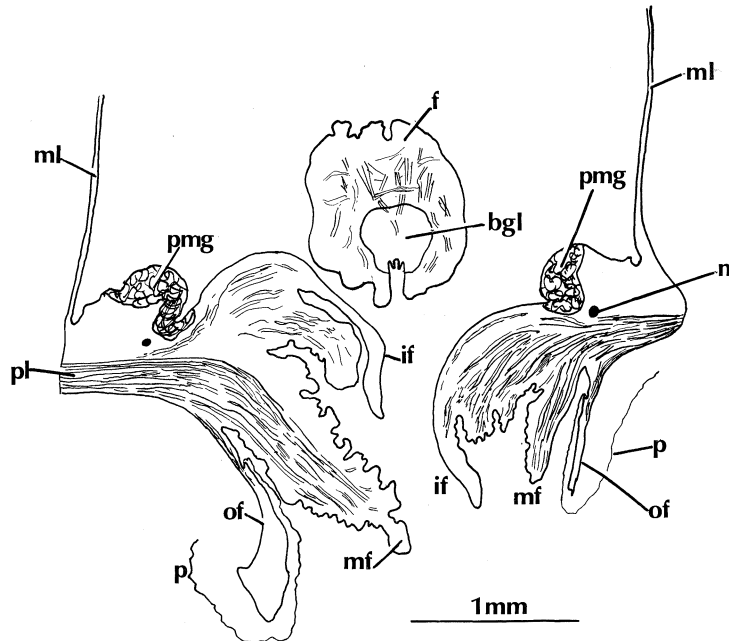
Figure 11. *T. crocea,* transverse section through middle of byssal gape cutting through foot and mantle lobes with pallial mucus glands and marginal folds showing great enlargement of middle folds.
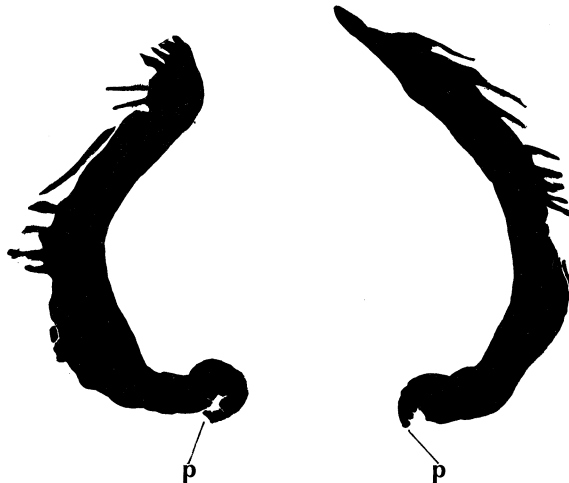
Figure 12. *T. maxima,* shell valves (somewhat separated) embedded in resin and cut transversely in middle of byssal gape, showing scales on outer surface and outward curling of shell margins round gape, due to activities of outer mantle folds.

carnivores — notably errant worms, crustaceans, gastropods and fishes — must be prevented. It is not enough merely to contract the byssal retractors because the coral substrate is usually highly irregular and openings between shell and substrate would usually be left through which such enemies could enter quickly to eat the enclosed animal. That no such spaces normally exist is due to the activities of the marginal folds around the gape.

The inner folds (Figs. 6, 10, 11) are here reduced to their customary size providing no more than a border round the opening through which the byssus emerges. It is the middle fold that is modified being greatly enlarged and extending outwards between reduced inner and attached outer folds.

As shown in Fig. 10, on the under side the middle folds emerge from below the hypertrophied inner folds, under which, on the upper surface, they are completely obscured. They lose pigmentation and enlarge greatly with the appearance of increasing numbers of conical tentacles set in irregular rows. These do not appear to be sensory but do form an elaborate meshwork through which the byssal threads pass and which possibly assist in their suitably wide planting. They also secrete mucus which may repel small invaders. Certainly the large byssal gape is occupied by byssal threads surrounded by, and marginally intermingled with, these rather fleshy tentacles (Fig. 19). As shown in Figs. 6 and 18, the distal regions of this fold do not carry tentacles but extend as a smooth sheet for some distance outside the byssal gape. This region, as we shall see, is more extensive in T. crocea than in T. maxima and T. squamosa, and there is clear evidence that in that species it assists, chemically, in excavating the boring. To the variable extent to which the substrate is excavated in T. maxima and T. squamosa, the distal region of the middle fold may be capable of the same activity in these species.

Starting somewhat posterior to the gape, the outer folds begin to curl outwards to secrete, around the gape, a rounded margin (Figs. 5, 6, 12) composed of many closely applied layers within the line of periostracal attachment (p). Anteriorly, i.e. in the umbonal region, periostracal attachment extends across from one valve to the other. The sides of the gape bear a series of transverse ridges (Fig. 4) increasingly widely separated posteriorly.

Such is the condition when animals are attached to a more or less flat and continuous surface. But where this is irregular, and so more frequently in T. maxima, adventitious shell usually consisting of alternate layers of periostracum and calcareous valve, secreted respectively by inner and outer surfaces of the outer folds, is laid down particularly around the umbonal end of the gape. The result is the formation of what may be termed a "byssal funnel" which can be of considerable size, that shown in Fig. 13 being some 20 mm high anteriorly and gradually diminishing behind. Everywhere the irregular margins conform with the irregularities of the substrate against which they are firmly pressed.

A more detailed examination of the nature of these adventitious additions to the margins of the byssal gape — so far as can be determined unique among the many, largely unrelated, byssally attached bivalves — is provided in Fig. 15 showing longitudinal median sections of a resin embedded shell of T. maxima. There are obviously irregularities in the formation of the funnel which involves roughly alternate layers of calcareous and periostracal secretion. As shown in Fig. 13, the overall appearance may be like that of a human lower dentition but with small molars, no canines and greatly enlarged, barely separated, incisors of varying sizes.

Although not so frequently developed, byssal funnels are also formed in T. squamosa (Fig. 14). In both species the funnel widens basally; thus in one specimen of T.
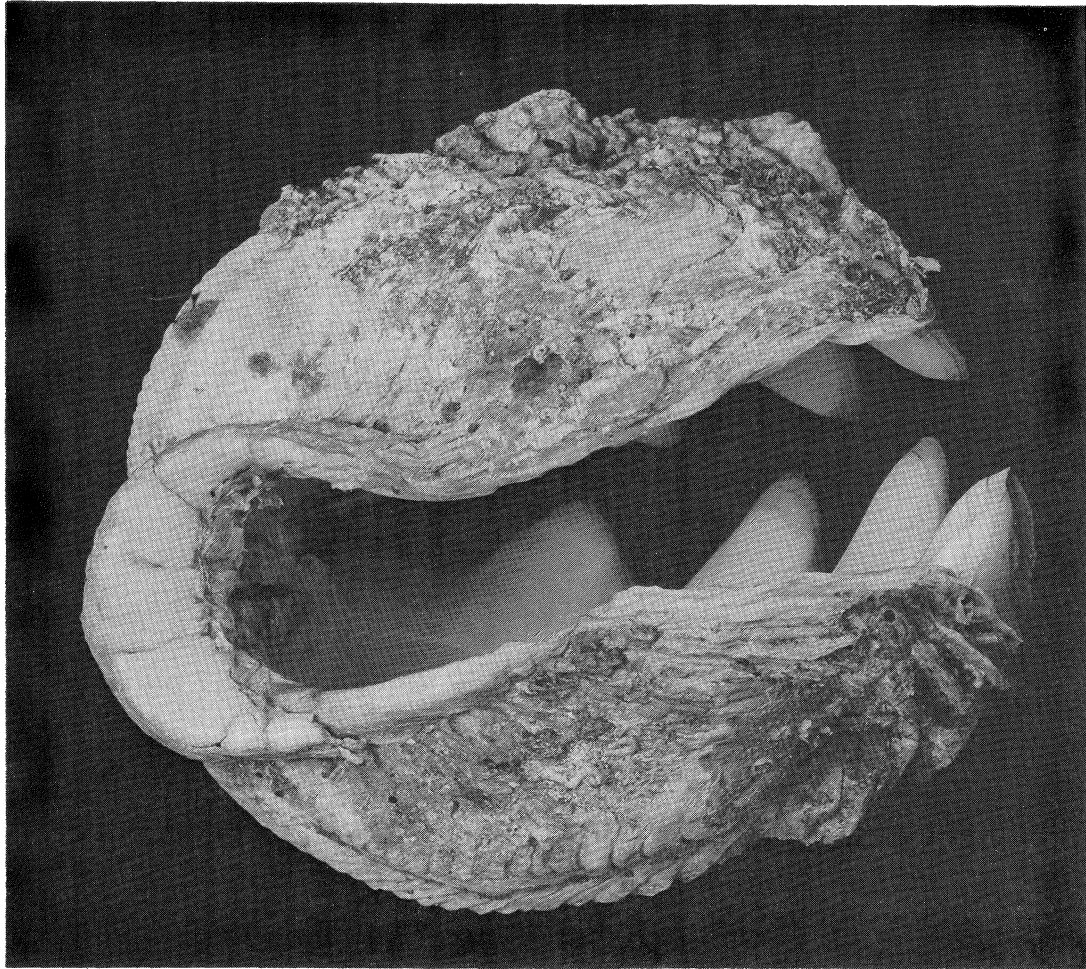
Figure 13. *T. maxima,* under view of shell valves showing byssal gape with very well developed byssal funnel around the umbonal end. (Photo A.I.M.S.)
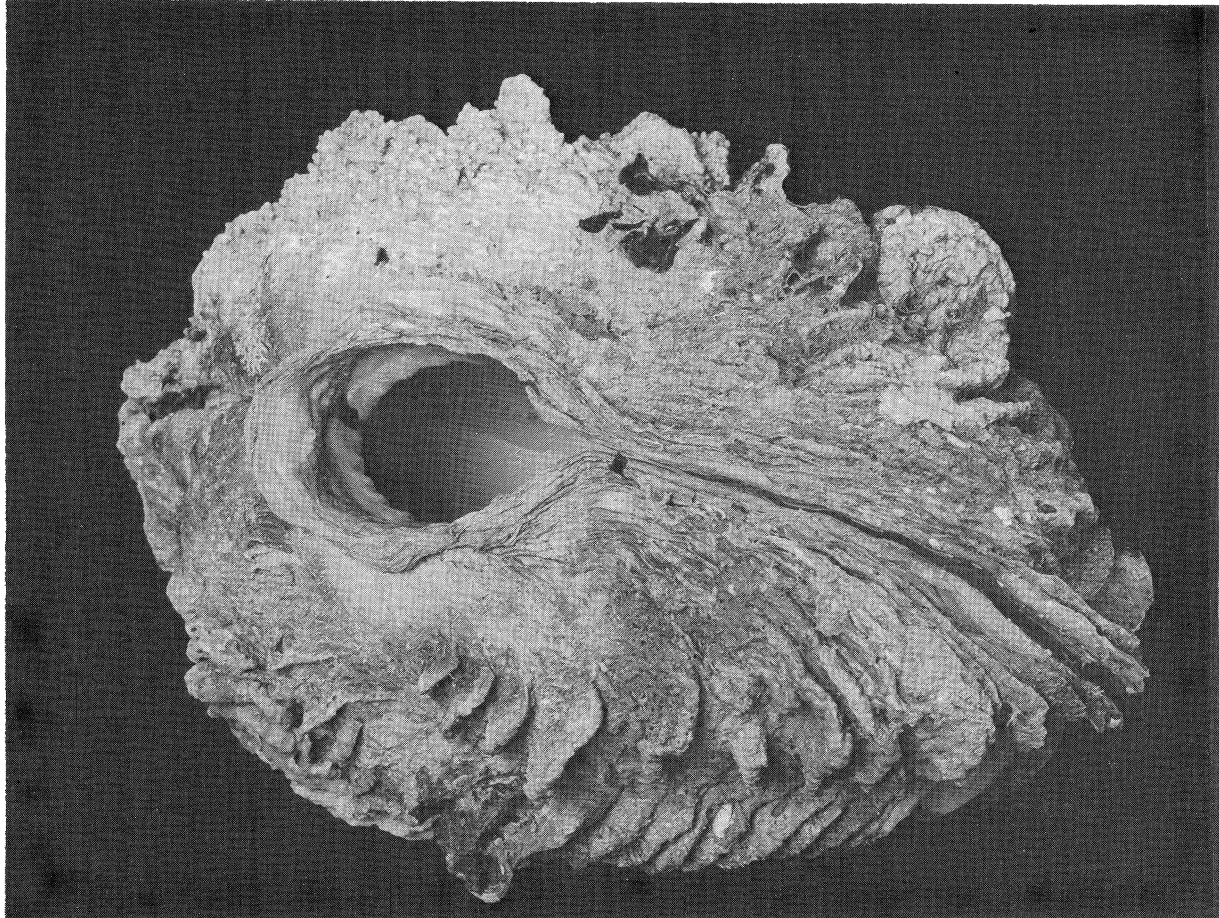
Figure 14. *T. squamosa*, similar view showing byssal gape and funnel, also prominent scales characteristc of this species. (Photo A.I.M.S.)
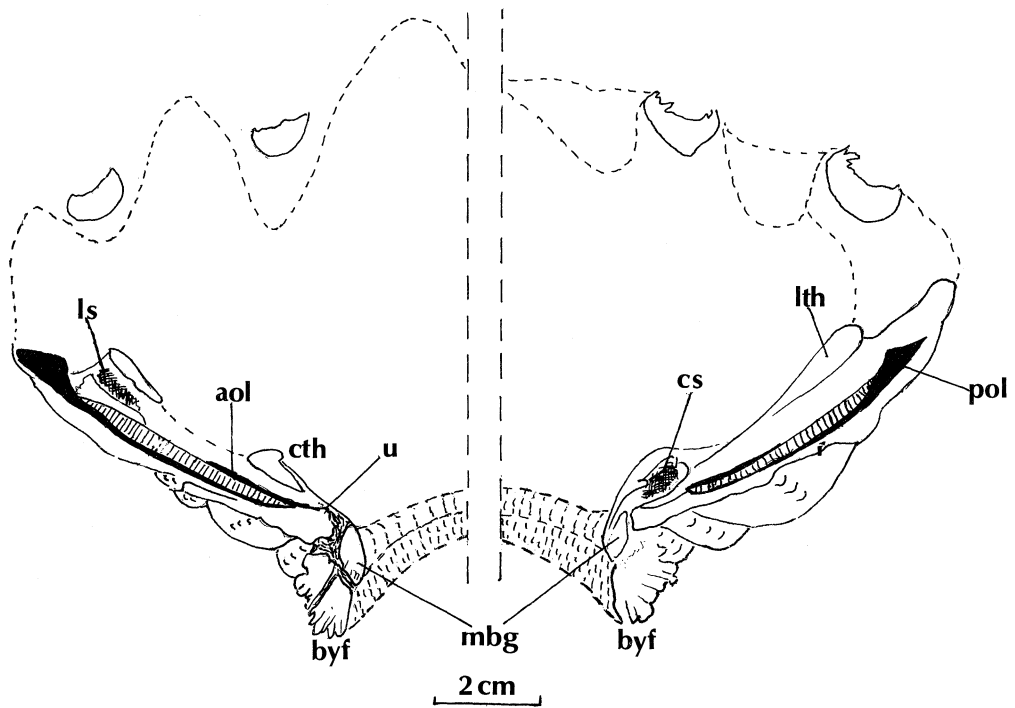
Figure 15. *T. maxima,* resin-embedded shell with large byssal funnel cut along mid-line longitudinally with halves turned to face forward, i.e. left valve on right, right valve on left. Ligament and dentition shown with large byssal funnel cut at right angles at umbonal end and seen diminishing posteriorly within resin (see broken lines). Note distinction between upper regions (mbg) formed by outward curling of margins of the byssal gape and adventitious secretion below (byf).
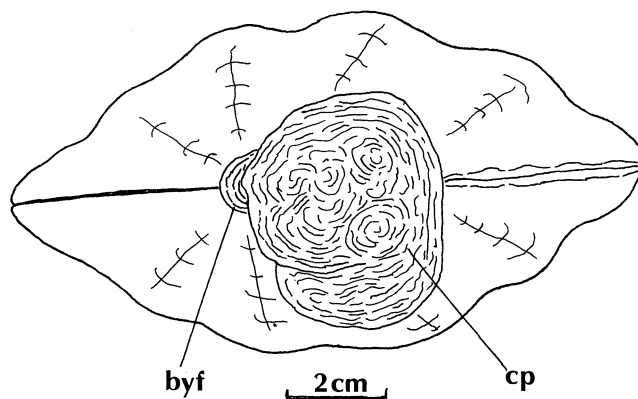

Figure 16. *T. maxima,* under view of a specimen with byssus attached to a free piece of calcareous matter forming a plug to the byssal gape.

squamosa the outer (lower) dimensions of the opening were 60 by 40 mm and the inner (upper) ones 35 by 28 mm. In other byssally attached bivalves (e.g. *Pinna, Pinctada, Mytilus)* the gape is extremely narrow; there is no danger of predators entering. Owing to the much greater size of the byssal mass and the irregularity of the substrate, conditions are totally different in the Tridacnidae.

The gape may, however, be closed in another manner. During 1967, when on the *De Moor* Expedition, a specimen of *T. maxima* was found which had been lying on the left side (Fig. 16). The marginal scallopings on that side were enlarged, those on the other side reduced so that the siphons were more or less horizontally extended. Survival had been possible because, as shown in Fig. 16, the gape had been closed effectively by a "plug" of some calcareous material held in place by the byssus. At the umbonal end the opening was further blocked by local secretion of a reduced byssal funnel fused to the upper surface of the plug.

Protection of the wide byssal gape by the basal tentacles on the enlarged middle mantle folds with the distal region of these folds probably assisting penetration into the substrate, together with the formation of byssal funnels by the outer folds, all represent basic adaptations. Only by such means could the Tridacnidae have successfully established themselves on the irregular — but essential, because *illuminated* — upper surface of reefs and eventually have achieved the size made potentially possible by the additional source of nutrition provided by the zooxanthellae. In *T. maxima* and *T. squamosa* this protection of the byssal gape continues to be as important as the hypertrophy of the siphons on the upper surface. In the further course of evolution it ceases to be important after a certain age in the giant species and in *H. hippopus* while in the boring *T. crocea,* now to be considered, no funnel is needed while the middle folds on the under side are further developed in connection with the boring process.

(b) Boring Species *(T. crocea).*

This is the smallest species, rarely reaching its maximum length of 150 mm. It differs in no way from *T. maxima* and *T. squamosa* on its upper surface and is even more firmly attached but needs to be considered separately because of its different mode of life with associated adaptations. It has joined company with a wide assortment of unrelated bivalves (species of Mytilacea, Myacea, Veneracea, and Saxicavacea with all species of Pholadacea and Gastrochaenacea) in the ability to bore into rock, here always of coral origin. *T. crocea,* however, is unique in penetrating by way of the under, umbonal, instead of the anterior, surface. This is a consequence of the basic tridacnid habit of extensive byssal attachment and is foreshadowed by the limited extent of downward penetration noted particularly in *T. maxima.* It involves further modification of the middle marginal folds on this side and results in a highly successful mode of life. The animals penetrate to their full depth with the broad inner fold extensions spreading widely over the rock surface and completely obliterating valves and boring below (Fig. 1). Thus from a boring with an opening 90 mm long and 15 mm wide there emerges a sheet of intense blue tissue some 105 by 55 mm in extent to provide an area of about 5775 sq.mm in which zooxanthellae are exposed to light.

The only previous, and inadequate, account of the boring process has been given by this author (Yonge, 1936), although Hamner and Jones (1976) have recently presented a wealth of data about the ubiquity of the species in shallow waters on the inner reefs of the Great Barrier and of the impressive effect its activities have on erosion. *T. crocea* probably demands relatively sheltered water for initial settlement but once established within a boring no tridacnid is so secure.
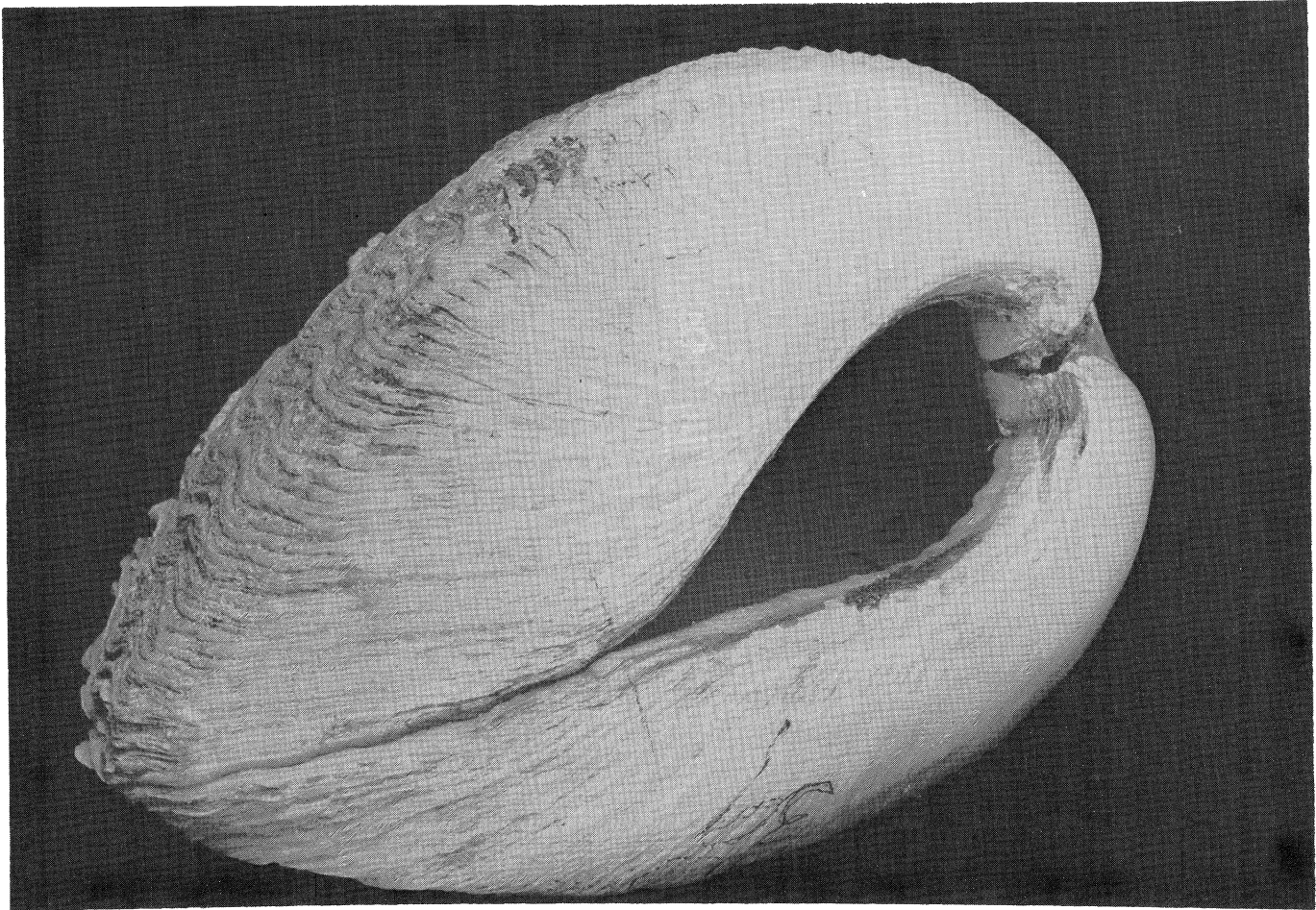
Figure 17. *T. crocea*, under view of shell valves showing large byssal gape with extremely smooth surrounding area probably due to chemical activity, in more peripheral areas scales worn down by mechanical action; no byssal funnel.

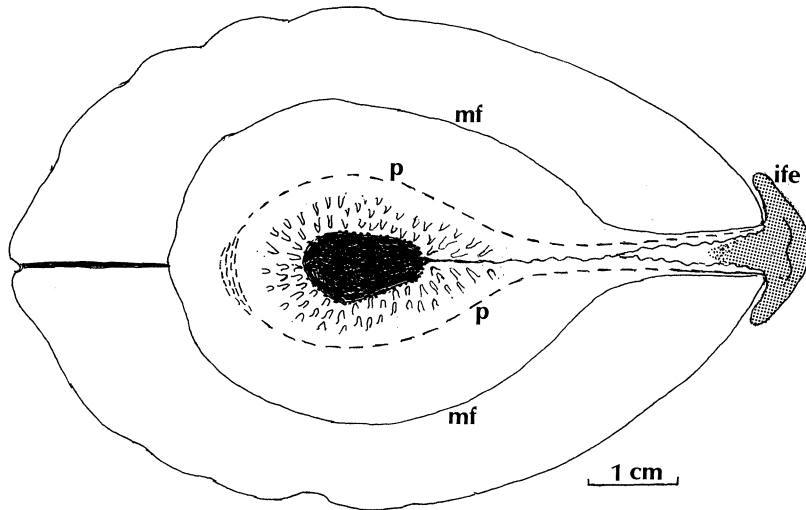Figure 18. *T. crocea*, under view showing more condensed byssal mass (cf Fig. 10) with wide extension of peripheral regions of the middle mantle fold (mf) reaching far beyond the region of periostracal attachment (broken line).
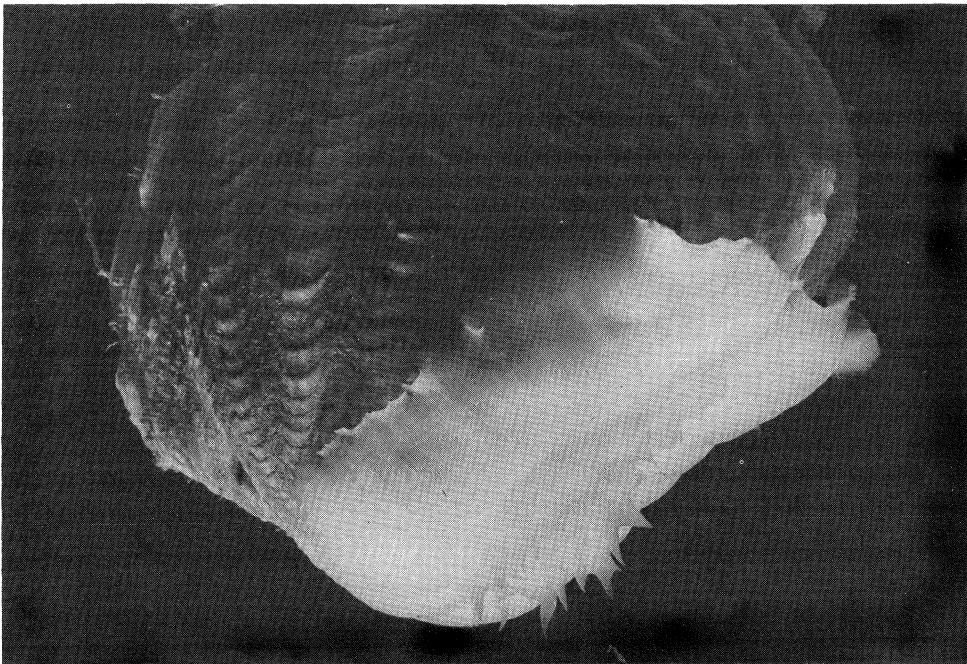

Figure 19. *T. crocea*, under view of living animal showing extended middle mantle folds (white on dark shell) with tentacles on proximal area, i.e. *in situ* around byssal mass. (Photo Martin Jones).

The shell is somewhat longer and also wider than the opening into the boring which has to be enlarged before the animal can be withdrawn. The byssal gape (Fig. 17) is relatively both longer and broader than in other tridacnids allowing egress for a larger and more concentrated accumulation of byssus threads (Fig. 18). There is occasionally some adventitious shell secretion but only at the extreme umbonal end (Fig. 17) and below the level of the gape; there is here no danger from intruding predators. The boring conforms in shape with that of the shell, a ridge along its under surface corresponding to the depression between the valves in the umbonal region. This ridge may culminate, below the gape, in a pillar to which the byssus is attached. This identity of shape between shell and boring is true of all cases where the bivalve does *not* rotate as it bores (e.g. *Platyodon* and *Botula*; Yonge, 1951, 1955).

Scales are formed on the valves only to be worn flush with its surface except near the upper margins. There is no trace of them in the umbonal regions where the surface is completely smooth (Fig. 17). Boring was earlier regarded (Yonge, 1936) as entirely mechanical but this now appears to be untrue. When borings are opened along one side, so as to expose the under surface of the animal without disturbing attachment, considerable extrusion of the middle mantle folds from the byssal gape is often observed and this may also occur after removal from the boring as shown in Fig. 19. The proximal regions of these middle folds carry tentacles as in the other species but the here more extensive distal regions are smooth. Because extended far beyond the line of periostracal attachment, these folds have inner and outer surfaces applied respectively to the umbonal surface of the valves and to the surface of the boring in that region. This great extension of the middle mantle folds supplies the explanation for the description (with a somewhat imaginary figure) of a "mushroom-shaped foot" by Hedley (1921).

These extensive tissues applied to the extremely smooth (umbonal) area of the shell obviously present the possibility of chemical activity affecting both the shell and the wall of the boring. The original protective covering of periostracum will soon have been removed by abrasion of the shell. Indeed conditions resemble those in *Lithophaga,* all species of which bore almost invariably into calcareous rocks and many of which are extremely common on coral reefs. These also are byssally attached with middle marginal fold tissues extending beyond the valve margins at the anterior, here the boring, end (Yonge, 1955). There is evidence of softening of the rock which would assist the undoubted mechanical action of the valves. No secretion of acid has been detected by any worker but that of a chelating mucus from abundant glands in the middle fold has been suggested, most recently by Jaccarini, Bannister & Micallef (1968).

Similar action in *T. crocea* would explain the complete smoothness in the umbonal region. There must, however, be alternate periods of mechanical and chemical activity. During the former the adductors will be relaxed and the opened valves ground against the wall of the boring by the probably alternate contractions of the left and right retractors which are shown, attached to valves and byssus, in Fig. 20. During such mechanical activity no tissues could be extruded through the pedal gape; this would occur when the adductor contracted leaving space between shell and boring. Chemical activity could then proceed over the limited area of initial (i.e. deepest) penetration (precisely as in *Lithophaga).* Such alternation of chemical and mechanical action has been extensively demonstrated in gastropods such as *Urosalpinx* which bore through the calcareous shell of their prey (Carriker, 1969). That bivalves can bore into calcareous rock exclusively by chemical means is shown in *Fungiacava eilatensis,* a mytilid which penetrates through the skeleton of living fungid corals exclusively by means of a "pallial envelope" composed of the middle marginal folds which *completely enclose* the excessively delicate valves (Goreau, Goreau, Soot-Ryen & Yonge, 1969). This undoubted

chemical boring is probably the best evidence that similar, probably chelating, activity occurs in *Lithophaga* and *T. crocea*.

In the original description of boring (Yonge, 1936), it was suggested that this took place diagonally, the pillar to which the byssus is attached needing to be continuously undercut. Later Purchon (1955) considered that the attachment area did not change position, byssal threads being worn away during growth and replaced by others. However the problem is changed if the pillar is subject to continuous chelating action; indeed examination of a large series of borings shows wide variation in the size of the pillar in some cases reduced to an irregular spine in the middle of the byssal threads. It is now thought that *T. crocea* bores straight down, the pillar largely eroded by chemical means and new byssal threads attached.

(c) "Giant" Species *(T. gigas, T. derasa)*.

Starting with the structure and mode of life in *T. maxima* and *T. squamosa*, further adaptations within the genus lead either to the appearance of the smaller boring *T. crocea* or else to that of much larger species which lose attachment. Judging by the partial closure of the byssal gape already mentioned in the large specimen of *T. maxima*, such increase in size is possibly *inevitably* accompanied by reduction and closure of the gape with atrophy of the byssal apparatus and retractors and reduction of the marginal folds on the under side. It is uncertain precisely at what size these giant species lose attachment but Rosewater (1965) in his plates 278 and 281 shows shells of *T. gigas* and *T. derasa* respectively 123 and 258 mm long both with an apparently functional byssal gape. Owing to the breadth of the under surface in these enlarging animals a stage must come when no predator can make its way into the now increasingly reduced byssal gape. Certainly the mantle margins on the under side will cease to have any but the primitive function of shell secretion. This, however, is now most actively taking place throughout the general surface of the mantle which secretes what eventually must become enormous thicknesses of the porcellaneous inner calcareous layer (Taylor, Kennedy & Hall, 1969). It is the thickness and so weight of the under (umbonal) areas of the valves which maintains the adult posture in these species.

Specimens of *T. gigas* 740 mm long and of *T. derasa* 380 mm long were examined at Lizard Island in 1975. The byssal apparatus was lost in both but a reduced, flaccid foot persisted in the former without trace of retractors although relatively slender muscles persisted in the other. Stasek (1962) revealed interesting differences in the ctenidia, those of *T. gigas* do not significantly differ from those in other species of *Tridacna* but in *T. derasa* unique "plical nodes" occur in rows parallel to the free margin across the face of the lamellae. The ctenidia also extend anterior to the labial palps with which they are connected by way of long distal oral grooves. The significance of these features remains to be determined.

The exceptional size attained by these two tridacnids may reasonably be attributed to their capacity for "farming" algae in the still larger siphons (Fig. 21). This additional source of food, the quantity of which *automatically increases as the animals increase in size*, removes the limitations in size which are imposed by even the most efficient ciliary feeding mechanism. Speed of calcification is also involved. By the aid of radioautography, Bonham (1965) suggests that one specimen of *T. gigas* increased in shell thickness by 10 mm annually. This is sixteen times the increase noted by Wilbur and Jodrey (1952) in the oyster *Crassostrea virginica* which is a rapidly growing bivalve. Observations on a second specimen of *T. gigas* indicated even greater speed of calcification, the animal reaching a length of 550 mm in an estimated period of six years. Although there is very little evidence about growth rates in other bivalves, Bonham
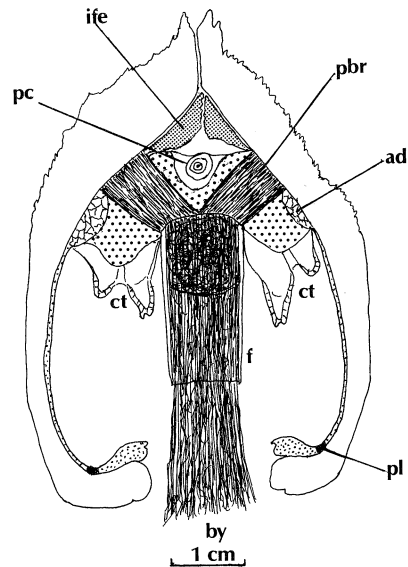
Figure 20. *T. crocea*, preserved specimen frozen and cut transversely, showing mode of byssal attachment with posterior byssal retractors attached to upper region of shell valves, probably contracting alternately when boring, outer surface of under regions of valves worn smooth by boring.
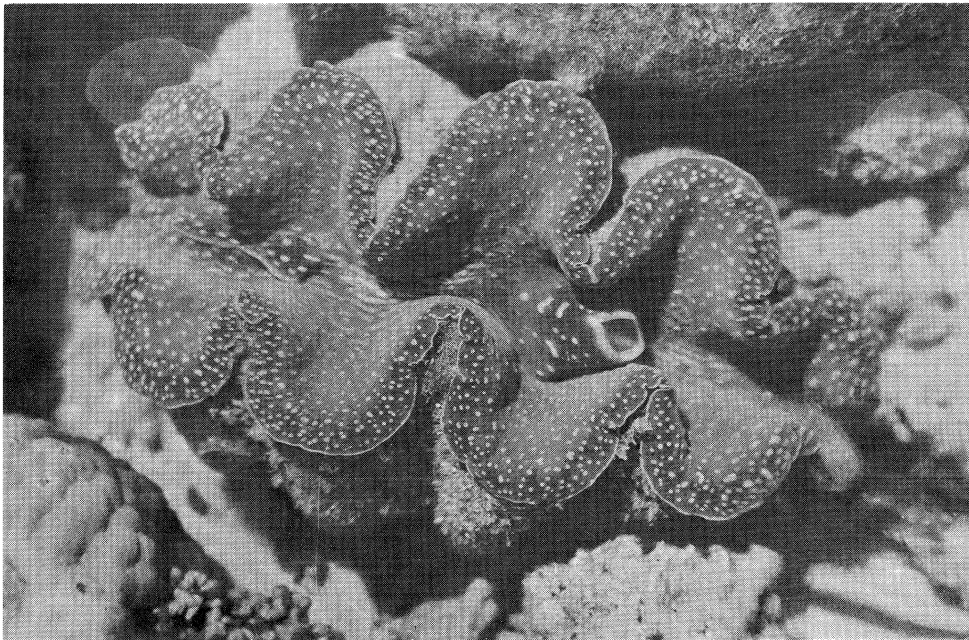

Figure 21. *T. gigas*, fully expanded under minimum depth of water, Low Isles, N. Queensland. (Photo M. J. Yonge).
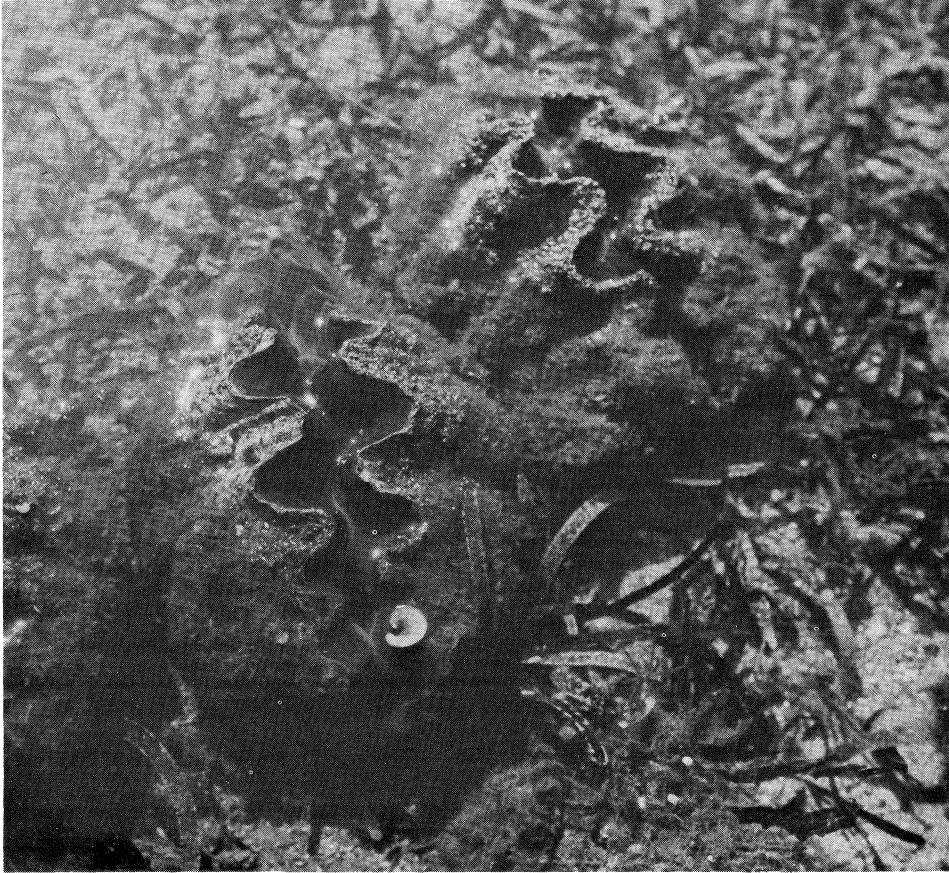
Figure 22. *Hippopus hippopus,* two specimens on sandy area with turtle grass, *Thalassia hemprichii,* on lee of reef flat, Low Isles. (Photo M. J. Yonge).
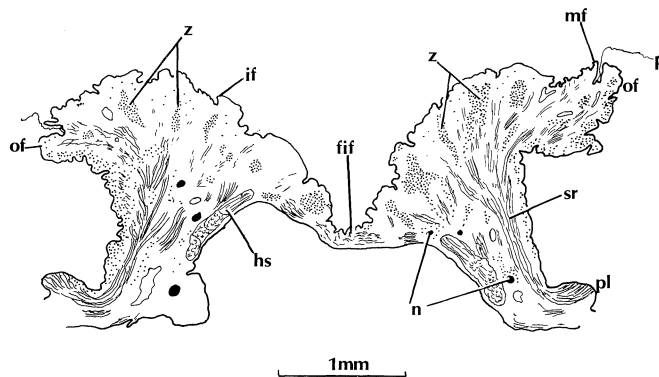

1mm

Figure 23. *H. hippopus,* transverse section through middle of upper surface, between siphonal openings, inner folds hypertrophied but without the extensions present in *Tridacna.*

concludes that tridacnids are the fastest growing of all bivalves. In support, however, may be quoted the estimates of McMichael (1974) that *T. maxima* attains lengths of around 160 mm in eight years although then slowing down to reach an eventual length of some 240 mm after 40 years. In hermatypic corals the zooxanthellae are essential in the necessarily high rate of calcification (if reefs are to be maintained in shallow seas). This may prove to be true also of the Tridacnidae.

Adaptation in these giant species consists essentially of still greater increase in size (*all* Tridacnidae are exceptionally large bivalves). On the upper surface of the animals this results in still further enlarged siphons (Fig. 21) with a greater capacity for housing zooxanthellae and so the increase in nutrition this must represent. On the under side it involves a simplification, the loss of the byssal apparatus and the byssal gape, with only the outer marginal folds of the mantle retaining any function. Greater increase in shell thickness (calcification possibly enhanced by greater algal populations) ensures continued and secure stability with the animal resting on the broad umbonal surface of the enormously thickened shell valves.

(d) Horse-hoof Clam *(Hippopus hippopus)*

Although basic morphology is similar, *Hippopus* differs from *Tridacna* significantly and in ways largely associated with its different mode of life. The siphons are similarly hypertrophied but the inner mantle folds do not extend beyond the margin of the valves (Fig. 22). These invariably separate widely to reveal, stretching between them, a flat expanse of invariably translucent olive green tissue with a superficial pattern of fine, more or less parallel, wavy lines. The elongate inhalant aperture, about a quarter the length of the shell, is usually widely open and edged with a few fine tentacles valueless as strainers. The very mobile exhalant aperture is shorter and points more anteriorly than in *Tridacna*. There is the same immediate reaction to the shadows and other stimuli although there are *no eyes* or other obvious receptors.

In transverse section (Fig. 23) the massive inner folds without extensions are penetrated by numerous strands of muscle and by many blood sinuses. Zooxanthellae are less numerous than in *Tridacna* spp., and both middle and outer folds are still smaller, especially the former which is also pigmented. Unlike *Tridacna,* the periostracal groove occupies the usual position at the base of the somewhat deeper outer fold which is pigmented with iridescent spots. On the under side pigmentation continues along the region of fusion posterior to the byssal gape (Fig. 24). Around this all mantle folds are small, the middle ones bearing only a row of small tentacles, the outer ones, as described below, growing anteriorly *within* (topographically *above*) the (umbonal) region instead of outward and so around this as in the byssally attached species of *Tridacna*.

The general structure of an unattached animal 100 mm long is shown in Fig. 24. Compared with *Tridacna* spp., the adductor is more central while the foot and retractors are reduced. In an attached animal 62 mm long these muscles were 30 mm long by 25 mm broad but here they are reduced to small remnants attached to the anterior sides of the adductors under the kidneys and *not* to the valves. The small anterior retractors (apr) persist. Survey of all available specimens revealed that the byssus has usually been lost in animals 80 mm long although traces persisted in one 120 mm in length. In the largest animal 370 mm long, 300 mm broad and 280 mm high, every trace of the retractors had gone. Other organs in the mantle cavity have the form described by Stasek (1962) although in no specimen personally examined did the outer demibranchs possess the food groove he figures.

The shell, described by Rosewater as having "an elongate triangular outline", demands careful description. Starting with an elongate "tridacnid" form, with growth it
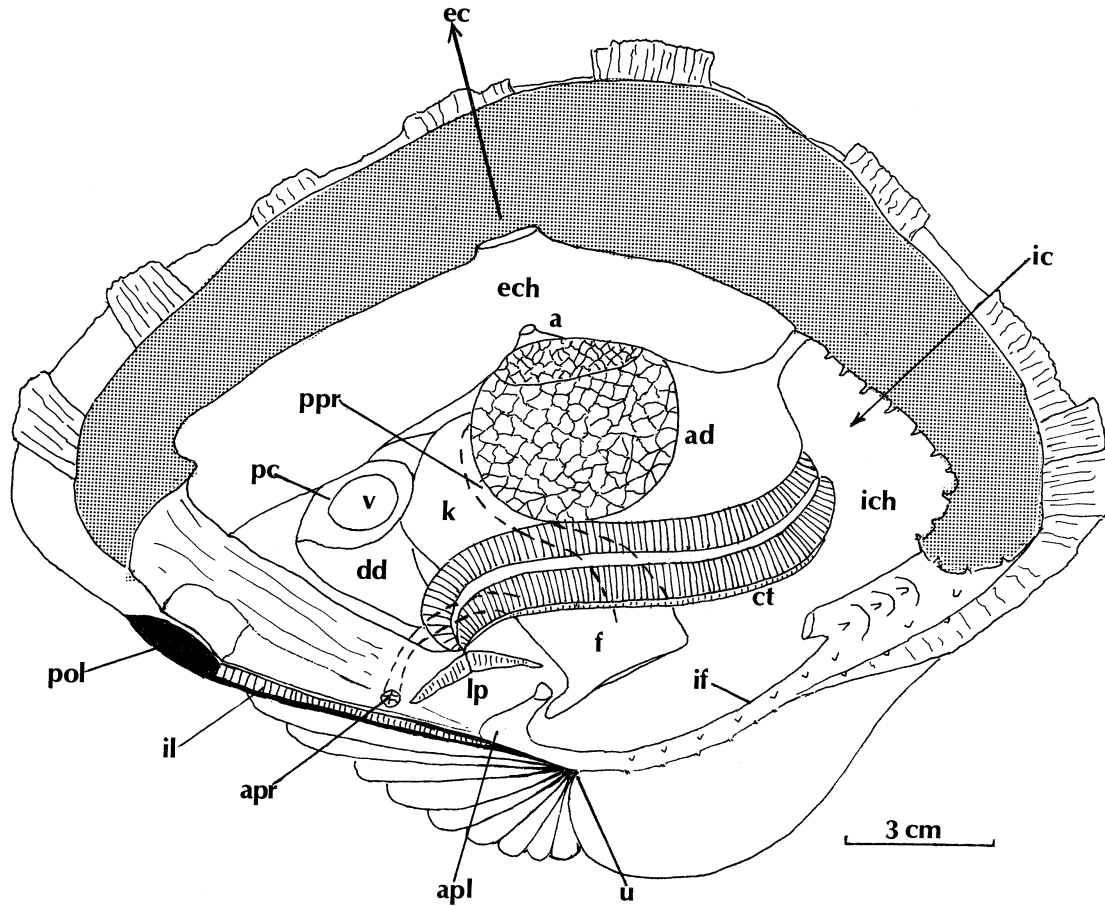
Figure 24. *H. hippopus,* unattached animal viewed from left after removal of valve and mantle lobe. Note details of pedal muscles and anterior extension of pallial tissues (apl) within umbonal region.

becomes broader and higher in relation to length so that large, i.e. unattached, individuals become increasingly globular. On the upper surface the obvious feature is the exact interdigitation of sinuous valve margins. What matters is the precise fit achieved when the adductor contracts. As indicated in Fig. 24, the under surface is sharply differentiated into a posterior region (in relation to the viscero-pedal mass) which is flattened in younger attached individuals (when it includes the byssal gape) but later becomes increasingly concave, the older, unattached animals resting either on this surface or on the more convex but broad anterior (umbonal) region.

This change in form is the consequence of two growth processes. The first, due to the growth gradients around the generative curve along the upper surfaces of the valves, produces the very marked increases in convexity shown in the sections through valves of different sizes in Fig. 25, a-d and e-g. At the same time the valves thicken greatly by additions to the inner porcellaneous layer. As in the giant clams, this is a major factor in stability. As appears in Table 1(a), this growth change has the added effect of increasing height in relation to length and so further contributing to the alterations leading to a more globular form.

The other growth change is on the under surface and involves a relative reduction in length. As shown in Fig. 24, the mantle margins (apl) bounding the umbonal end of the "pedal gape" (which persists as a region of *pallial* separation after byssus and foot are respectively lost and reduced) extend anterior to the umbones (u) morphologically beneath (but topographically above) the posterior end of the hinge region. This also causes an increasing separation of the umbones as displayed to maximum extent in the large shell shown in Fig. 26. These differences from conditions in *Tridacna* appear to be due to the local appearance of a tangential component in shell growth which is exhibited to its fullest extent in the Chamacea and Hippuritacea (Yonge, 1967) and in *Cleidothaerus* (Morton, 1974; Yonge & Morton, 1980). In these bivalves the effect of this component dorsally is to split the hinge anteriorly with wide separation of the umbones, and to extend it posteriorly. In *Hippopus* its effects are confined to the anterior (umbonal) end with consequent production of the beginning of a spiral in each valve, new shell being secreted between the increasingly separated umbones (Fig. 26). The overall result is to cause a rotation of the mantle/shell but in a *clockwise* direction and so in opposition to the other movements of the pallial tissues in relation to the viscero-pedal mass. Measurements given in Table 1(b) reveal the increasing extent to which, with growth, the anterior pallial boundary (Fig. 24, apl) advances beyond the line of the umbones, namely from 2.3% of total shell length to 19% with increase in shell length from 43 to 395 mm This represents a significant "telescoping" and a reduction in shell length in relation to other shell dimensions.
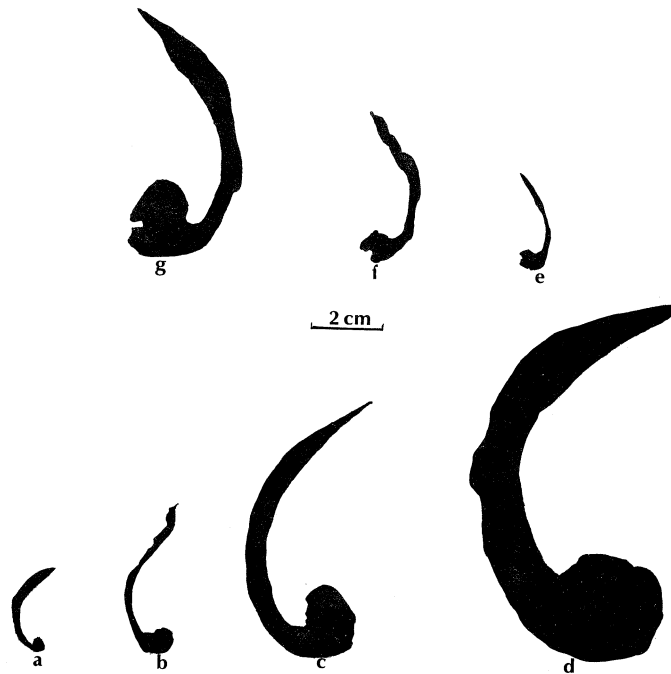
2 cm

Figure 25. *H. hippopus,* sections through resin embedded valves of various sizes showing increase in thickness, especially basally, with age, and accompanying loss of byssal attachment.
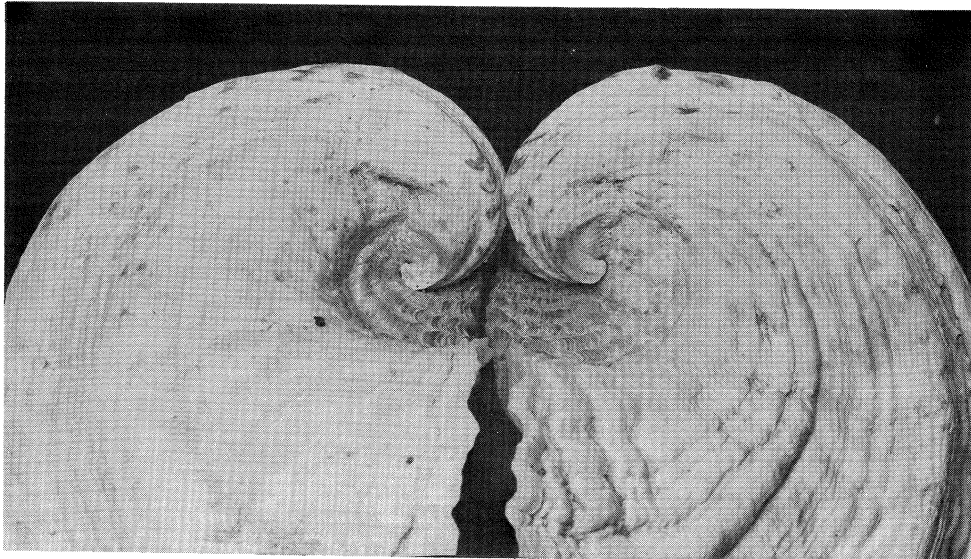

Figure 26. *H. hippopus,* under surface of large shell (395 mm long) showing wide separation of umbones due to effect of tangential component in shell growth. (Photo A.I.M.S.)

TABLE 1. *H. hippopus;* changes in the relations of different regions during growth. (a) Relation of height of shell to length; (b) Relation of anterior end of mantle lobes ("pedal gape") to line of separated umbones.

(a) Length in mm	Height in mm	Ratio H/L	(b) Extension of mantle lobes anterior to umbones in mm (Fig. 24, apl-u)	Relation of this to shell length
43	28	65%	1	2.3%
63	44	70%	2.5	4.0%
90	74	82%	6	6.7%
98	71	73%	6	6.1%
115	81	70%	8.5	7.4%
130	104	80%	15	11.5%
135	100	76%	16	12.0%
145	111	77%	17	12.0%
204	*	—	31	15.2%
395	304	77%	75	19.0%

* irregular

The end result of both growth processes is conversion of an elongate, moderately high although basally always broad, bivalve into one that becomes increasingly globular although with flattened anterior and posterior under surfaces on either of which it can securely rest. Aided by the intimate interlocking of the undulating valve margins, the upper surface is rounded. Projections (not scales) on the outer surface of the valve in small attached individuals are not present on the larger valves of older animals which thus offer no resistance to being turned over and then back. All of these characters, with absence of any overlapping of the valve margins by the siphonal tissues so that valves can close quickly, enable *Hippopus* to be rolled about with impunity.

Available evidence suggests that settlement takes place on seaward surfaces. Later, when attachment is lost young animals will be carried over the surface of the reef where individuals will find temporary or permanent rest in suitable depressions. But the ultimate site of most of the larger animals is on sandy areas in the lee where they may be the most conspicuous member of the fauna as with those shown in Fig. 22 living on sand among growths of turtle grass, *Thalassia hemprichii*. Large numbers of *Hippopus* were viewed on sandy areas to the west of the anchorage at Low Isles during 1928/29 and, despite great deterioration in the fauna generally due to sedimentation, they appeared just as numerous when the same sandy areas were revisited during February 1978, scores of large animals being seen. The only attached animal noted during this brief visit, and actually the smallest one recorded in Table 1, was collected on the exposed southeastern surface of the reef.

Although in constant danger of being rolled over in the surf generated by the trade winds, *Hippopus* is always found upright after it loses attachment. This is due to the great thickness of the umbonal regions of the shell which steadily increases after detachment as shown in Fig. 25. The final enormous thickness in a shell 340 mm long is illustrated in Fankboner (1971a, Fig. 1). This great basal weight represents a self-righting mechanism as noted by Purchon (1977) and by Fankboner. But whereas the former considers that the animals immediately right themselves when rolled over, Fankboner regards righting as a

step-wise process. The animals remain on their sides until the adductors relax when the upper umbone will no longer lie directly above the under one. The unbalanced shell then rolls over with both umbones coming to lie undermost when balance is regained. Personal observations support Fankboner's conclusions.

Hippopus is, therefore, unique among bivalves because adapted, after initial attachment in exposed areas, for being rolled to leeward by prevailing seas, never re-attaching itself as McMichael (1974) has shown may happen with *T. maxima*, but maintaining an essential upright posture. It thus becomes the only tridacnid able to exploit life on the sandy leeward extensions of reefs. It shares this capacity with the similarly specialized hermatypic Fungiidae (also with the Atlantic *Manicina (Maeandra) areolata)*. These corals also start life attached, being later carried to leeward, often on to sandy areas. They are there capable of uncovering themselves when buried under sand during storms (Marshall & Orr, 1931; Yonge, 1935) and also of righting themselves when turned over (Abe, 1939). *Hippopus* is too large to be buried but is beautifully fitted for righting itself when rolled on to one or other side.

ZOOXANTHELLAE

The supreme significance of the zooxanthellae[1] is here taken for granted with the unique tridacnid form the direct consequence of structural changes ensuring their more extensive housing and maximum exposure to light. Further research is for others to whom the electron microscope and facilities for physiological and biochemical investigation are available. Nevertheless some assessment of the present state of knowledge about the interaction of symbiont and host appears necessary, the more comprehensive owing to the recent general review by Dr R. K. Trench (1979) and information kindly supplied by him about the conclusions contained in a joint paper dealing specifically with symbiosis in the Tridacnidae and still in the press (Trench, Wethey & Porter, 1981).

Early personal conclusions about the nature of the association (Yonge, 1936, 1953a) were that the algae present and often observed dividing in superficial tissues were always contained within blood cells. These were regarded as being later responsible for conveyance of senescent algae into the visceral mass where they were digested within these phagocytic amoebocytes. Removal of the waste products of digestive processes carried out in the blood stream was held to explain the uniquely large size of the tridacnid kidney (Fig. 27). No passage of zooxanthellae into the gut was noted, those found there were assumed to have entered following rupture of the tissues prior to examination.

Subsequent research has not supported these views. Using the electron microscope, Kawaguti (1966) found that in *T. crocea* the zooxanthellae are usually free although sometimes they are "accompanied by" or "coated with" blood cells. Fankboner (1971b), also using electron microscopy, concluded that "senescent zooxanthellae are selectively culled from the algal population of the mantle edge" (i.e. of the siphons) "by amoebocytes and are intracellularly digested via amoebocyte lysosomes both in the circulatory system and the interdiverticular spaces of the digestive gland."

Morton (1978) who accepts the view that zooxanthellae may be contained within amoebocytes describes, again in *T. crocea*, a diurnal pattern of activity with clusters of

1. Nomenclature raises problems. When initially cultured and shown to be dino-flagellates, Freudenthal named these organisms *Symbiodinium microadriaticum* the generic placing later changed by Taylor to *Gymnodinium*. With discovery that thecal plates occur in motile stages, Loeblich and Sherley (1979) now place *Symbiodinium* Freudental in the synonymy of *Zooxanthella* Brandt. Trench (1979) retains the generic name *Symbiodinium* and is here followed.
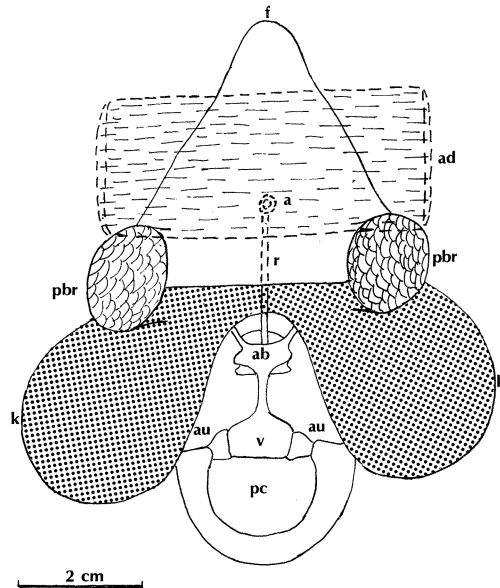
Figure 27. *T. squamosa,* visceral mass viewed from antero-dorsal aspect showing pericardium with contained heart with aortic bulb and hypertrophied kidneys characteristic of the Tridacnidae.
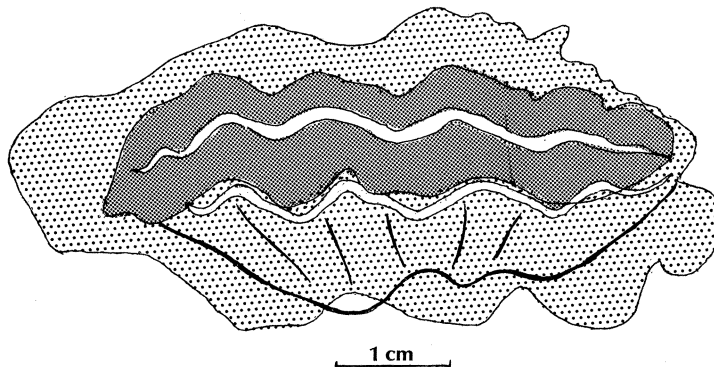

Figure 28. *T. crocea,* result of time/lapse photography over day and night. Coarse stippling indicates full extent of siphonal expansion, as at 1345 hrs. but maintained during daylight; fine stippling, extent of expansion during night, actually as at 0100 hrs. but maintained continuously presumably by partial contraction of siphonal retractors. Sinuous white areas indicate margin of valves exposed during rare contraction of adductor.

zooxanthellae and amoebocytes appearing within the digestive cells of the digestive diverticula around dawn. These appear in great numbers in the lumen some two hours later after the distal two thirds of the digestive cells disintegrate. This he relates to a diurnal pattern of feeding and digestive activity he has described in other bivalves. He also reports some passage of zooxanthellae into the kidneys.

Without attempting to confirm his general results the opportunity was taken of the presence of skilled photographic assistance at the Australian Institute of Marine Science in 1978 to carry out a series of time/lapse photographs of *T. crocea* over periods of around 48 hours. The results are indicated in Fig. 28. Morton had recorded the extent of adduction kymographically and found that during the night the valves gaped slightly with few adductor contractions whereas during the day they gaped widely with frequent adduction. Photographic data only revealed the degree of expansion of the siphons which was at least 50% greater during the period of light than during the night. Sudden withdrawals for which the siphonal retractors must have been solely responsible occurred at all times and would be great enough to expel water from both inhalant and exhalant openings to remove pseudofaeces and faecal pellets respectively. Greater withdrawals involving contractions of the adductor which may be frequent in nature where predators abound were rare in the undisturbed laboratory conditions. They were revealed by the occasional appearance on the film of opposing sinuous white areas (Fig. 28) due to complete withdrawal of the siphons and exposure of the margins of the white shell valves. The consequent back pressure of blood within the siphons would explain the large aortic bulb (Fig. 27, ab) present in all tridacnids. In other bivalves this is associated with the variable pressure of blood within the actively burrowing foot.

Using the electron microscope, Trench, Wethey and Porter (1979) find no evidence that either in superficial or in the deeper regions, i.e. within the visceral mass or in the lumina of any region of the gut, are the algae contained within blood cells. They find that degenerate zooxanthellae occur even in the siphonal regions while intact, and demonstrably living, zooxanthellae are voided with the faeces. Unlike Morton, they find no trace of zooxanthellae within the kidneys, not even indications of algal pigments. But the tridacnid kidney is enormous. For instance in a specimen of *T. derasa* examined at Lizard Island, the total wet weight of the tissues was 1070 grams, with siphons 280, adductor 260, visceral mass 389, foot 40, and kidneys 101 grams. It is difficult not to associate this enormous organ, 1/10th of the total tissue weight with the presence of symbiotic algae.

There is also the problem of the regulation of the numbers of contained symbionts which are continually increasing by division in superficial areas. This affects all cases of plant/animal symbiosis and has recently been reviewed by Muscatine and Pool (1979). In the Tridacnidae control appears to be exercised by the periodic outward passage of excess numbers of algae via the digestive diverticula into the lumen of the gut as demonstrated by Morton. This is essentially similar to what occurs in hermatypic corals where any excess is removed by way of the absorptive/excretory zone of the mesenteries and is dramatically increased when corals are stressed by exposure to sublethal temperatures or very low oxygen tensions (Yonge & Nicholls, 1931) or to greatly lowered salinities (Goreau, 1964).

Earlier views that tridacnids acquire energy from the algae by digesting them appear at best only partially true. Exposure of specimens of *T. maxima* to water containing [14]C (Goreau, Goreau & Yonge, 1973) resulted in the appearance within ten minutes of radioactivity within zooxanthellae in superficial regions and later in more deeply situated algae. This radioactivity passes out of the zooxanthellae as a result of the nutrient movement from symbiont to host of the photosynthate (Muscatine, 1967; Smith, 1979). It

was then identified in all the major centres of metabolic activity, namely in the byssal gland, periostracal groove, pallial and ctenidial mucous glands and, most strikingly, in the cells of the minor typhlosole of the style sac providing evidence that the style can be completely replaced in 73 hours. It was concluded that the Tridacnidae obtained the major benefit from their symbionts by way of these released photosynthates predominantly composed of glycerol and alanine (Smith, 1979; Trench, 1979). While it is impossible at present completely to dismiss the possibility that some energy is obtained by digestion of senescent algae within phagocytic amoebocytes (intact ones are now known to pass unchanged through the cells of the digestive diverticula), this does appear to be of minor significance. Indeed Trench (1979) states that "good evidence for digestion of zooxanthellae by animal hosts is lacking."

What has been stated above roughly covers the present state of knowledge and does at least show the need for more extensive and precise information on the role of the hypertrophied kidneys and the relative importance in nutrition of the "imprisoned" phytoplankton of zooxanthellae and the external supplies of "free" phytoplankton collected and utilized by the unmodified organs of feeding and digestion. The great importance of the former, already stressed as responsible for the large size of the Tridacnidae culminating in the unique dimensions of the giant species, is strikingly indicated by the earlier mentioned observations of Salvat (1969, 1971) in the Tuamotus. The enormous populations of *T. maxima* found in the closed atolls where no phytoplankton from surrounding waters is available is the best present evidence of the overwhelming importance as food to the animal of the contained zooxanthellae. Recently Ricard and Salvat (1977) have shown that *T. maxima* lives as well without as with available phytoplankton; also, from discharged zooxanthellae, much protein is added to the lagoon water.

EVOLUTION

While basic structure, both of mantle/shell and viscero-pedal mass, indicates association with the Cardiidae and Hemidonacidae in the superfamily Cardiacea, the totally distinctive structure of the Tridacnidae indicates long and intimate association with coral reefs. As Rosewater (1965) notes, they "are obligatory inhabitants of the shallower waters of coral reefs." Taking information from the *Treatise on Invertebrate Palaeontology*, the Cardiacea appeared in the Upper Triassic with the earliest tridacnids not until the early Tertiary, possibly the Upper Cretaceous.

The Cardiacea appear always to have been superficial burrowers with very short siphons (absent in the Hemidonacidae) acquiring a characteristically large foot, angulate in the Cardiidae and compressed in the Hemidonacidae, enabling them to move through and, in the former often over, the substrate (Ansell, 1967). In this family a byssus may, although rarely, be retained into adult life as in *Corculum*. Members of both of these families live exclusively on soft substrates. *Corculum*, however, comes eventually to final byssally attached settlement on dead coral rock thinly covered with sand (personal observations). The story is different in the Tridacnidae which are basically adapted for life on hard substrates, i.e. become epifaunal instead of infaunal. The byssal apparatus is retained into adult life, its formation the sole concern of the foot which atrophies when the byssus is lost in the giant species and in *Hippopus*. In virtue of its size, the last named becomes epifaunistic on a soft substrate.

Shallow coral reef seas, largely formed by hermatypic scleratinian corals presumably with the associated symbiotic zooxanthellae needed to ensure an adequate rate of calcification, appear in the middle Jurassic. The environment the tridacnids were later to exploit was thus created. Their appearance, however, was delayed until the end of the

Mesozoic or early Caenozoic during a period of major decline and change when, as pointed out by Newell (1971), reefs decline and the previously dominant, even reef-forming, bivalve rudists disappear. It is indeed possible that this disappearance left settling space and unexploited phytoplankton food for these early tridacnids. These must initially have maintained position by retention and enlargement of the byssal apparatus with loss of other pedal functions while maintaining exclusive dependence on their ciliary feeding mechanism for food. Possibly they settled in cracks or depressions which, with continued enlargement of the byssal apparatus, ensured survival in these often turbulent waters.

At some stage zooxanthellae were acquired and became housed in the siphonal regions. i.e. those areas alone exposed to light. It is reasonable to assume that the tridacnids were initially infected by algae already adapted for symbiotic existence within hermatypic corals or some of the other numerous coelenterates that harbour them in coral reef areas. In the Scleractinia and other "closed" systems, zooxanthellae are passed from generation to generation via the egg and so, always within the same host environment, would not tend to diverge. This is less probable in "open" systems as in the tridacnids but also the rhizostome medusae, *Cassiopeia* and *Mastigias* (Trench, 1979) and in the gorgonid *Pseudopterogorgia bipinnata* (Kinzie, 1974). In all of these the aposymbiotic post-larvae are infected from the ambient environment which must contain motile stages of zooxanthellae from many sources. Schoenberg and Trench (1979) have demonstrated the presence of 12 strains of zooxanthellae distinct on the basis of isoenzyme patterns and so presumably genetically distinct. It does, however, remain to be demonstrated to what extent "open" hosts are restricted to colonization by particular strains.

The post-larvae of the medusae and the gorgonid will be infected via the mouth, i.e. being taken into the tissue through the "absorptive" region of the gastric ridges or mesenteries. A similar mode of infection remains to be proved in the Tridacnidae. Conditions are vey different because corals, and effectively all other coelenterates, are highly specialized carnivores never reacting to, or being capable of digesting, vegetable matter (Yonge, 1930a, b) whereas plant cells are the normal food of all bivalves. Trench (1979) recognizes this problem but, because there is a route whereby excess of algae are removed from the gut, postulates a similar course for infection. While algae already specialized for life within animal cells may be able to resist the action of digestive enzymes while passing through the cells of the digestive diverticula this may not be true of the motile stages while there is the possibility of direct infection through the exposed tissues around the inhalant siphon. Some evidence in favour of this is provided by Goetsh and Scheuring (1926) who found some specimens of the freshwater bivalves *Anodonta cygnaea* and *Unio pictorum* that were infected around the siphonal regions, to the extent that light reaches, by species of *Chlorella* which were most unlikely to have survived passage through the gut. However further speculation about the original mode of infection must await precise knowledge about how this occurs in modern post-larvae.

Certainly initial infection must have been followed by major changes in form as the siphons enlarged to house ever increasing numbers of algae which rendered the animals ever more independent of the restricted phytoplankton of impoverished coral reef seas. Personal views, strengthened over the years of research on the Bivalvia, are that mantle/shell and viscero-pedal mass with their different symmetries have some measure of independence. In the evolution of the Tridacnidae, it is postulated that natural selection favoured the continued enlargement over the entire upper surface of the siphons which, without loss of their original function, came to house and expose to the light ever greater populations of zooxanthellae. This anterior movement of pallial tissues
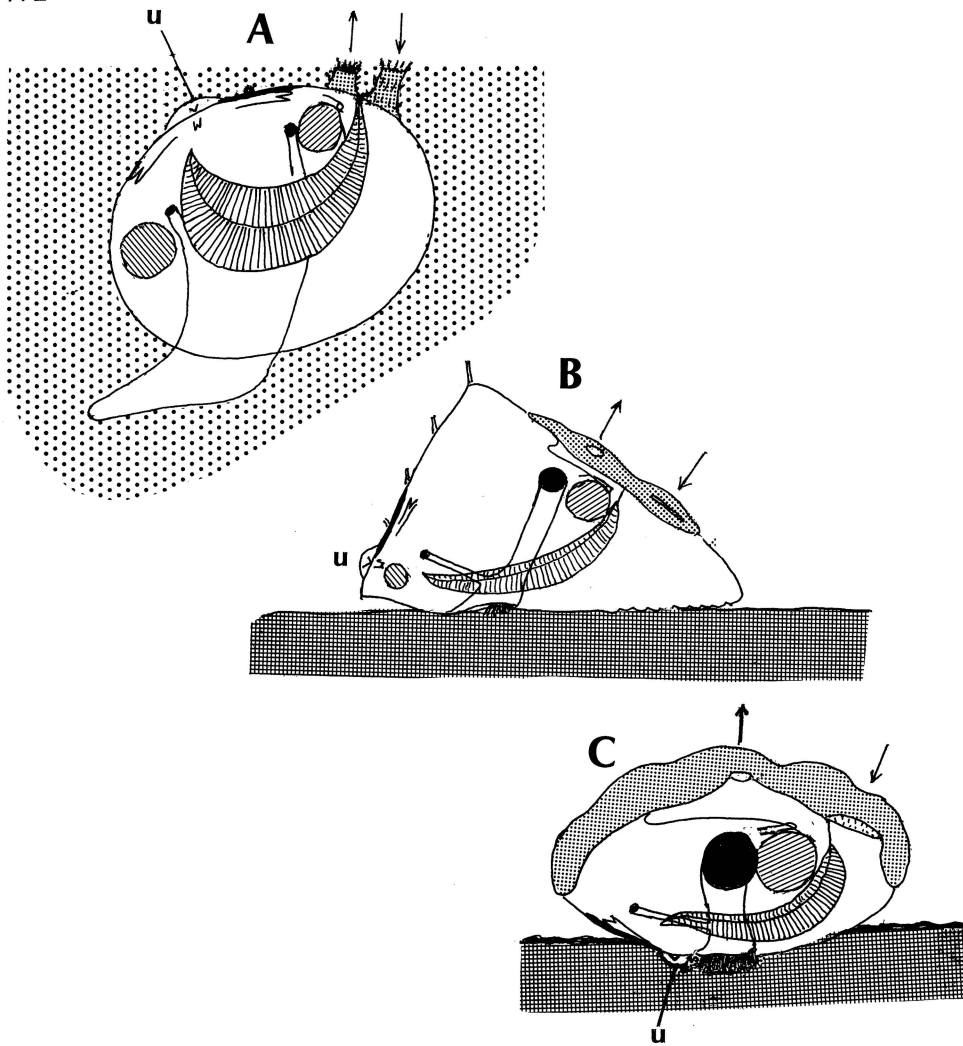
Figure 29. Comparison of basic structure in A, modern cardiid — isomyarian, infaunal; B, Eocene *Lithocardium* — heteromyarian, epifaunal, byssally attached (structure postulated); C. modern tridacnid — monomyarian, epifaunal, byssally attached with some penetration ventrally into hard substrate. Changing position of umbo (u) indicates degree of turning of the mantle/shell in relation to the viscero-pedal mass. Other structures shown:- siphons (stippled), adductors (oblique lines), ligament (black), ctenidia, foot with retractors and (in B, C) byssus, hinge teeth and anus. Arrows indicate inhalant and exhalant currents.

involved that of the shell and only ceased when the anterior end of the ligament came in contact with the byssal mass below. The continued presence of this attachment throughout the entire process held the viscero-pedal mass in position, the foot unalterably ventral. Such views are credible because at no stage do they involve the assumption of structures incompatible with further existence. As noted earlier (Yonge, 1953a), the Eocene *Lithocardium aviculare* (Fig. 29B) with triangular shell, heteromyarian and without anterior lateral teeth and with an assumed byssal attachment is a possible stage in the turning movement of mantle/shell that culminated in the Tridacnidae. This involves extension of the siphonal region with contained zooxanthellae to form an intermediate condition between a cardiid (Fig. 29A) and a tridacnid (Fig. 29C).

Regarding mantle/shell and viscero-pedal mass as an integrated unity, Stasek (1963) has sought to transform the cardiid into the tridacnid form by way of a series of co-ordinates. This, because the two are basically similar, he has succeeded in doing but only as a result of a purely morphological exercise, reminiscent of the "pure morphology" of Geoffrey St. Hilaire. He makes no attempt to follow the structure of the animal during the complex series of changes involved in the "transformation" or to discover whether all stages could have been viable. It seems unnecessary to say more about this, only to repeat what was stated earlier, namely that the course of evolutionary change here postulated is not, and indeed could not, be recapitulated during development.

After the initial appearance of the tridacnid form, *Hippopus* must have separated from *Tridacna* relatively early, presumably before the siphons had begun to extend laterally beyond the margin of the valves. Subsequent evolution, with closure of the byssal gape, must have proceeded independently, the modified shell form in *Hippopus* enabling it to exploit its distinctive habitat on soft substrates.

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ABBREVIATIONS USED IN FIGURES:

a	anus
ab	aortic bulb
abr	anterior byssal retractor
ad	adductor
aol	anterior outer ligament layer
apl	anterior end pallial lobes
apr	anterior pedal retractor
au	auricle
bg	byssal gape
bgl	byssal gland
by	byssus
byf	byssal funnel
cp	calcareous plug
cs	cardinal socket
ct	ctenidia
cth	cardinal tooth
d	marginal end of depression
dd	digestive diverticula
ea	exhalant aperture
ec	exhalant current
ech	exhalant chamber
ey	eye
f	foot
fif	fused inner folds
hs	haemal sinus
ia	inhalant aperture
ic	inhalant current
ich	inhalant chamber
if	inner fold of mantle margin
ife	inner fold extension
il	inner ligament layer
k	kidney
lp	labial palps
ls	lateral socket
lth	lateral tooth
mbg	margin byssal gape
mf	middle fold of mantle margin
ml	mantle lobe
n	nerve
of	outer fold of mantle margin
p	periostracum
pbr	posterior byssal retractor
pc	pericardium
pg	periostracal groove
pga	pedal (byssal) gape
pl	pallial line
pmg	pallial mucus gland
pol	posterior outer ligament layer
ppr	posterior pedal retractor
r	rectum

sc	scales
sn 1-3	siphonal nerves
sr	siphonal retractor muscles
tm	tentacle on middle fold
u	umbo
v	ventricle
vg	visceral ganglion
z	zooxanthellae