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

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SUMMARY

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

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

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

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

Introduction

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

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

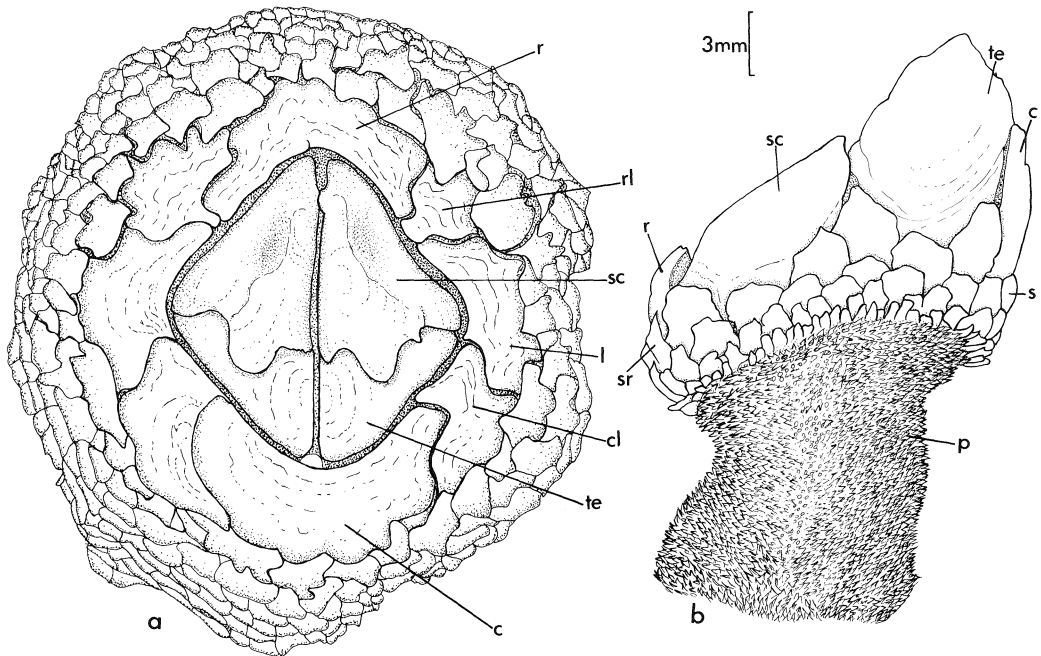


Fig. 1. **a**, *Catomerus polymerus*, apical view. **b**, *Pollicipes polymerus*, right lateral view. *c*, carina; *cl*, carinolateral; *l*, lateral; *p*, peduncle; *r*, rostrum; *rl*, rostromedial; *s*, subcarina; *sc*, scutum; *sr*, subrostrum; *te*, tergum.

Islands in the Western Indian Ocean, as a benthic shelf form at 450–460 m (Stanley and Newman, 1980). *Chionelasmus* is more advanced than *Catophragmus* or *Catomerus* in some features of its carapace. The wall plates are 6 in number, as in most balanomorphs, and there is only a single whorl of supplementary plates outside the primary wall plates. The general anatomy of the body and limbs, however, remains catophragmid.

Catomerus polymerus is therefore a typical representative of the Catophragmidae. Darwin, in a delightful example of his thinking in evolutionary terms, recognised immediately the phylogenetic importance of this animal, which “forms in a very remarkable way the transitional link between” the lepadomorphs and the balanomorphs, “for it is impossible not to be struck with the resemblance of its shell with the capitulum of *Pollicipes*” (see Fig. 1b). “In *Pollicipes*, at least in certain species, the scuta and terga are articulated together—the carina, rostrum and three pairs of latera, making altogether eight inner valves, are considerably larger than those of the outer whorls—the arrangement of the latter, their manner of growth and union,—all are as in *Catophragmus*. If we, in imagination, unite some of the characters found in the different species of *Pollicipes*, and then make the peduncle so short (and it sometimes is very short in *P. mitella*) that the valves of the capitulum should touch the surface of attachment, it would be impossible to point out a single external character by which the two genera in these two distinct families could be distinguished.”

While Darwin went on to recognise that there were some fairly major internal differences, especially in the arrangement of the mantle musculature, that he was unable to explain, he saw *Catomerus* not only as an indicator of a scalpellid ancestry for the balanomorph form, but also as a form ancestral to other balanomorphs. “Considering the whole structure, external and internal, of *Catophragmus*, with the great exception of the exterior whorls of valves, there is hardly a single generic character by which it can be separated from *Octomeris* and *Pachylasma*”; and the generalised position of *Octomeris* and *Pachylasma* at the base of the balanomorph stock continues to be recognised to this day (Newman and Ross, 1976).

Darwin, then, presented a hypothesis of the origin of the Balanomorphs—that they had evolved from a scalpellid ancestry via forms represented today by the catophragmids, which in turn gave origin to the other balanomorphs.

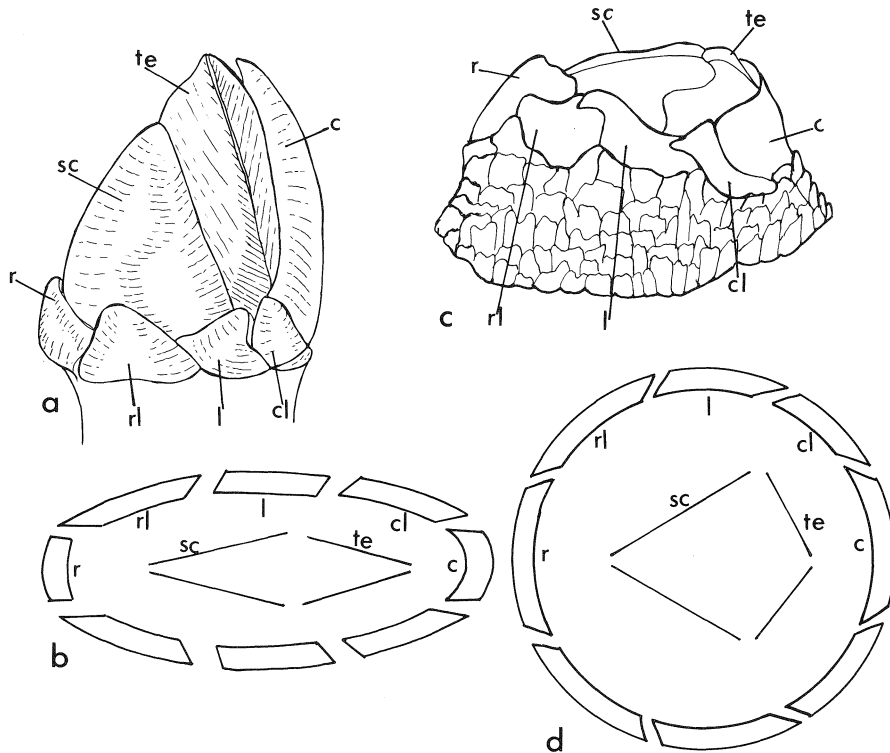


Fig. 2. **a**, *Scillaelepas dorsata*, right lateral view. **b**, *S. dorsata*, plan of capitular plates. **c**, *Catomerus polymerus*, right lateral view. **d**, *C. polymerus*, plan of wall plates. (From Newman, Zullo and Withers, 1969, reproduced with permission, courtesy of the Geological Society of America and University of Kansas.) *c*, carina; *cl*, carinolateral; *l*, lateral; *r*, rostrum; *rl*, rostromlateral; *sc*, scutum; *te*, tergum.

In the years since 1854 this hypothesis, based on comparative anatomy, has gained further support from fossil evidence. Withers (1935) described from the Cretaceous of Sweden a fossil catophragmid, *Pachydiadema cretaceum*, which remains the only known Mesozoic balanomorph. This discovery placed the catophragmids chronologically at the base of balanomorph evolution in the later Mesozoic, a time of abundant and diverse scalpellids (Newman, Zullo and Withers, 1969). *P. cretaceum*, furthermore, shows opercular features more like those of scalpellids than the modern catophragmids, which can now be recognised as relicts of a family of once widespread distribution (Stanley and Newman, 1980). Newman *et al.* (1969) following Aurivillius (1894), developed the idea of a scalpellid ancestry further in a comparison (see Fig. 2) of the plate arrangements of *C. polymerus* and the Eocene calanticine *Scillaelepas dorsata* (Steenstrup). Allowing for only a minor modification of the position of the laterals in relation to the rostromlaterals and carinolaterals, the arrangement of the capitular plates in *C. dorsata* is one which can be easily envisaged, with foreshortening of the stalk, to have become modified to that of the wall plates of *C. polymerus*. Since *Scillaelepas* and *Calantica* are thought to be central and early evolved genera within the calanticine scalpellids, first appearing in the Upper Jurassic (Newman, 1979), Darwin's hypothesis gains further support from this evidence, as it does from the cirral and mouthpart anatomy of the two groups. Pollicipoid scalpellids, including calanticines and pollicipines (Zevina, 1978), show some modification of the first and to a lesser extent the second pair of cirri as maxillipeds (Figs 3a, 3d), and have a characteristic setation of the four posterior pairs of cirri (Fig. 4b). Each cirral segment carries several pairs of long setae anterolaterally and has a bunch of short, forwardly projecting setae between them on the anterior face of the segment. *C. polymerus* shares this feature in the setation of the four posterior pairs of cirri (Fig. 4a), but it exhibits a greater modification of the first two pairs (Figs 3b, 3c) as short maxillipeds (Darwin, 1854; Pope, 1965). A striking similarity also attends the

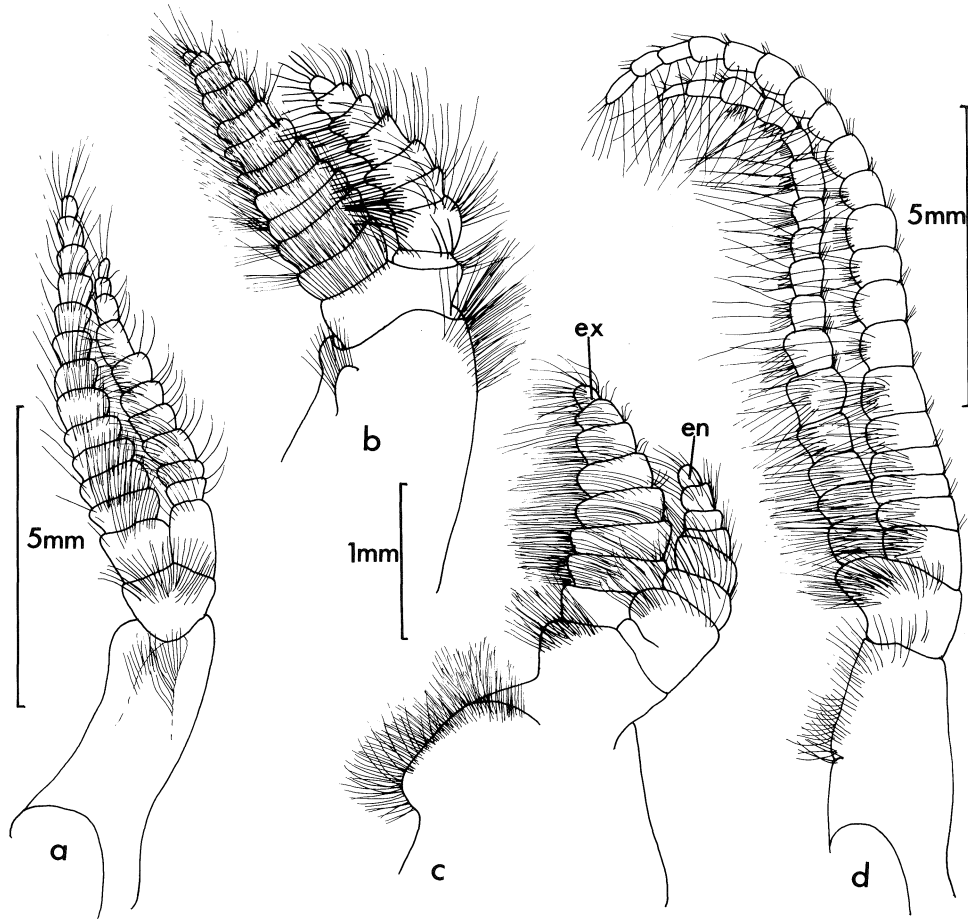


Fig. 3. **a**, Left cirrus I of *Calantica villosa*, median view. **b**, Left cirrus I of *Catomerus polymerus*, median view. **c**, Left cirrus II of *C. polymerus*, median view. **d**, Left cirrus II of *C. villosa*, median view. *en*, endopod; *ex*, exopod.

oral cone and mouthparts (Fig. 5) (Darwin, 1854; Pilsbry, 1916; Nilsson-Cantell, 1926; Pope, 1965; Newman and Ross, 1976; Foster, 1978). The labrum is bullate. The palps are simple, and setose mainly at the tips. The mandibles are tri- or quadridentoid, with a well developed incisor tooth and a strong, setose or pectinated molar process. The maxillules have a large seta on the lateral angle, a fringe of numerous marginal setae, and some development of a double prominence at the median angle. The maxillae are bilaterally flattened, with a fringe of setae around the angulate margin. The mouthparts of *C. polymerus* are more strongly toothed and setose in general than those of *Calantica* or *Scillaelepas*, but the anatomical resemblance between the two types of oral cone is striking and undeniable. Cirral and mouthpart anatomy therefore accord with the idea of a scalpellid ancestry for catophragmids.

Since catophragmids show so much evidence of being foreshortened descendants of calanticoid scalpellids, originating during the Mesozoic, what is the adaptive significance of the foreshortened form? Commonsense would suggest an adaptation to rocky, exposed, intertidal habitats and this view has been maintained from Darwin to the present day. The catophragmid facies, according to Newman and Ross (1976), was apparently an adaptation to high energy conditions along the shore. In terms of the protective modification of the closable carapace, this interpretation is appropriately functional. It is also supported by the fact that balanomorphs have become extraordinarily diverse and successful in the littoral environment, in a Tertiary radiation that has its zenith in the present day, whereas the lepadomorphs

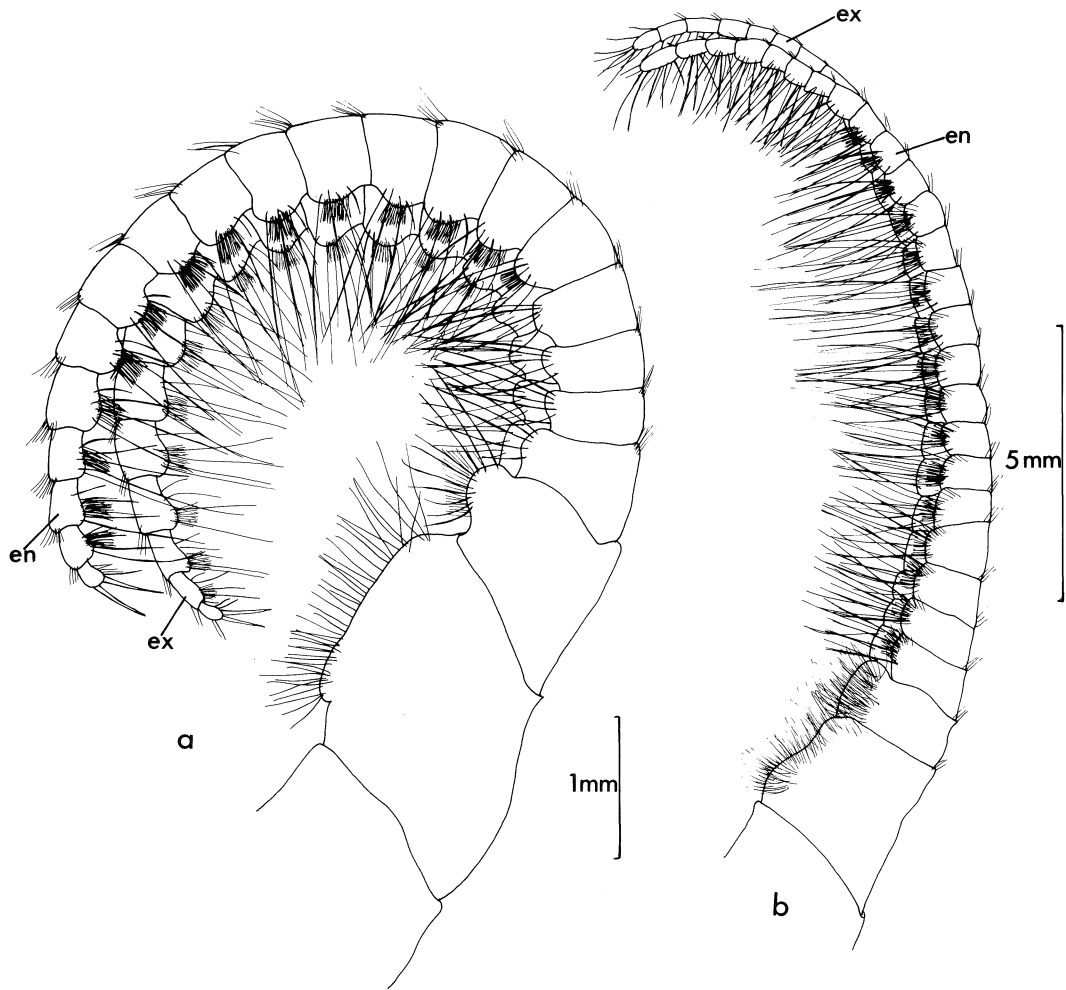


Fig. 4. **a**, Right cirrus IV of *Catomerus polymerus*, lateral view. **b**, Left cirrus IV of *Calantica villosa*, median view. *en*, endopod; *ex*, exopod.

have penetrated this environment only sporadically. Intertidal lepadomorphs are either cryptic, like *Ibla quadrivalvis* Cuvier (Fig. 6a) and *I. cumingi* Darwin, or armour-plated in shaded habitats, like *Pollicipes polymerus* J.B. Sowerby (Fig. 1b) and *Calantica villosa* (Leach) (Fig. 6b), or functionally convergent with balanomorphs, like *Calantica spinosa* (Quoy and Gaimard). The latter species, occurring mid-tidally on exposed rocks in New Zealand, is short and squat, with a reduced capitulum and an exceptionally thick and tough integument on the pedicel (Fig. 6c).

Accepting the assumption that the balanomorph form originated as an intertidal adaptation, and recognising that the anatomical modifications of catophragmids as compared with scalpellids are post-settlement modifications (basically, the form in adult barnacles is established through developmental events which begin *after* settlement of the cyprid larva has occurred), the calanticoid-catophragmid evolutionary hypothesis raises a number of questions. First, what is the major thrust of the adaptation, functionally? Is it trophic, or protective, or both? Protection in this context encompasses resistance both to high energy water movements and to the desiccation resulting from aerial exposure. Secondly, if this question can be resolved satisfactorily, what functional modifications of structure were involved

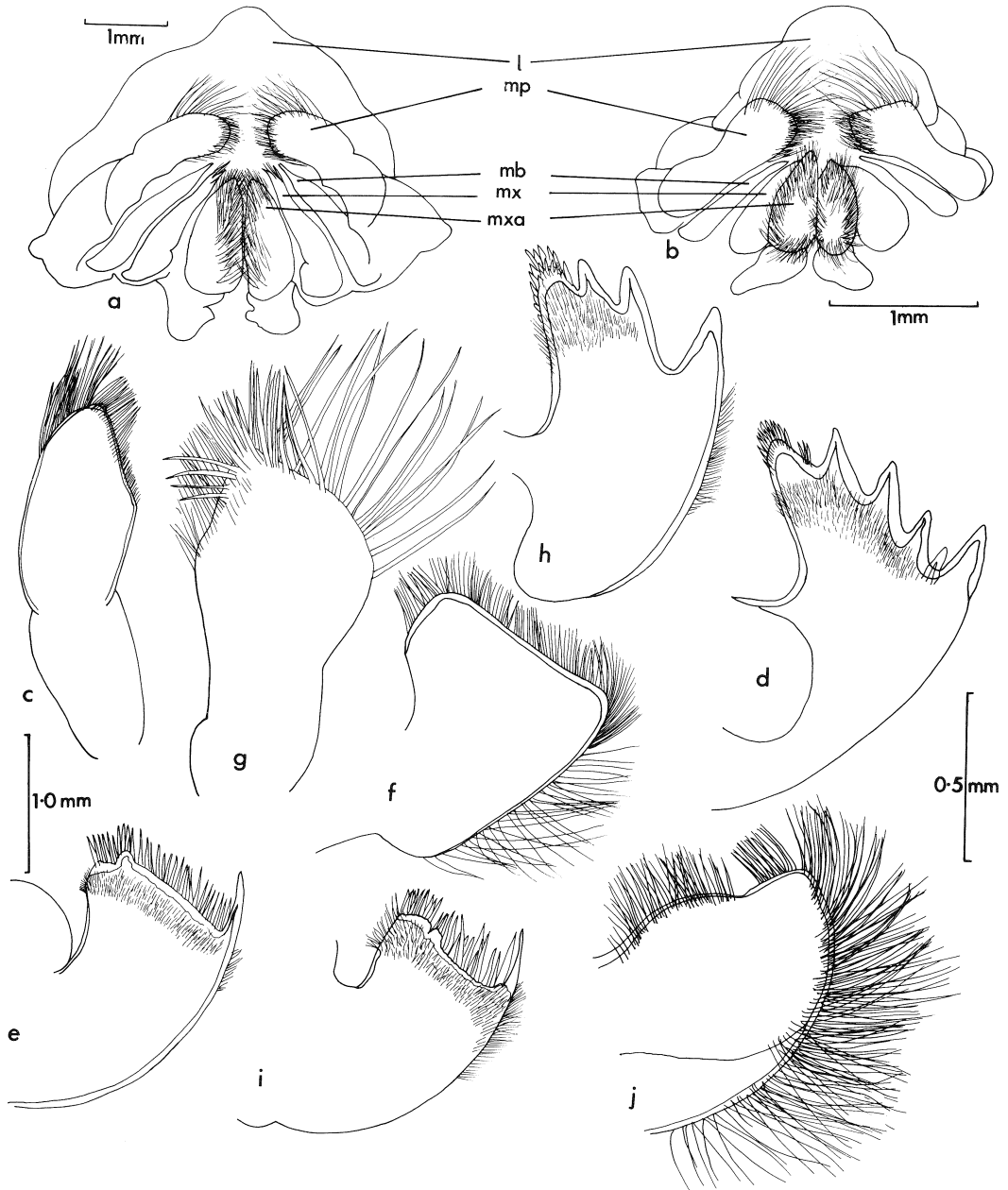


Fig. 5. **a**, Oral cone of *Calantica villosa*, posterior view. **b**, Oral cone of *Catomerus polymerus*, posterior view. **c-f**, the mouthparts of *C. villosa*, right side, lateral view (**c**, mandibular palp; **d**, mandible; **e**, maxillule; **f**, maxilla. The scale of these diagrams is indicated on the left of the figure). **g-j**, The mouthparts of *C. polymerus*, left side, median view (**g**, mandibular palp; **h**, mandible; **i**, maxillule; **j**, maxilla. The scale of these diagrams is indicated on the right of the figure). *l*, labrum; *mb*, mandible; *mp*, mandibular palp; *mx*, maxillule; *mxa*, maxilla.

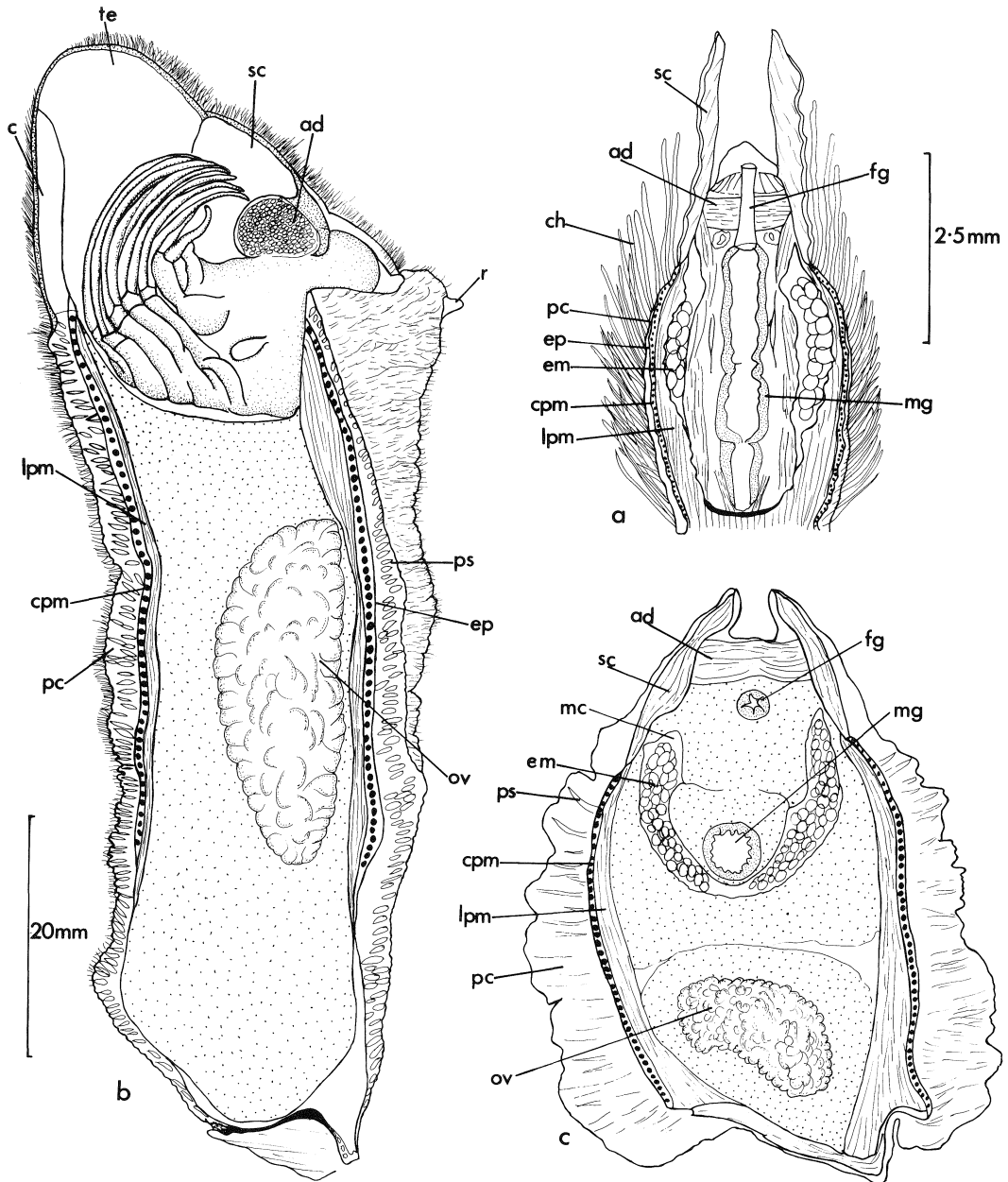


Fig. 6. **a**, Longitudinal frontal section through the apical half of *Ibla quadrivalvis*. **b**, Longitudinal sagittal section through *Calantica villosa*. **c**, Longitudinal frontal section through *Calantica spinosa*. *ad*, adductor scutorum; *c*, carina; *ch*, cuticular hair; *cpm*, circular peduncular muscle; *em*, embryos; *ep*, surface epithelium; *fg*, foregut; *lpm*, longitudinal peduncular muscle; *mg*, midgut; *ov*, ovary; *pc*, peduncular cuticle; *ps*, peduncular spine; *r*, rostrum; *sc*, scutum; *te*, tergum.

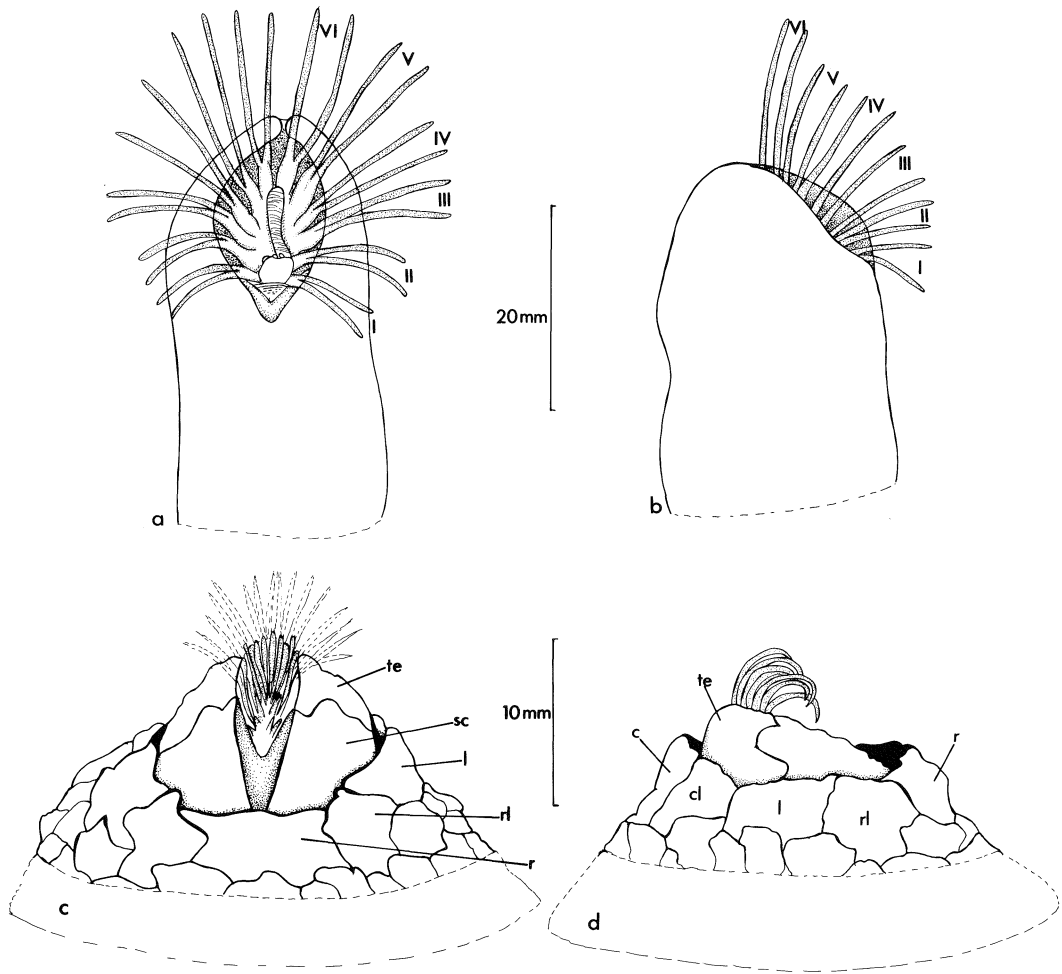


Fig. 7. **a** and **b**, Rostral and left lateral views of *Calantica villosa* during cirral extension. **c** and **d**, Rostral and left lateral views of *Catomerus polymerus* during cirral extension. I-VI, cirri I-VI; c, carina; cl, carinolateral; l, lateral; r, rostrum; rl, rostromlateral; sc, scutum; te, tergum.

in the transformation, through time, of stalked barnacles into sessile barnacles? In order to answer these questions, it is necessary to have some understanding of the functional morphology of both types of animal.

Functional morphology of *Catomerus polymerus*

Structure and function have been explored to some extent in the Scalpellidae, though very little in the calanticoids until now, but the catophragmids have never been examined in a functional way. The results reported in the following lines were obtained through an investigation of specimens of *C. polymerus* collected from the rock platform at Harbord, N.S.W. during 1978 and 1979 and examined by the methods reported in previous papers (Anderson, 1978, 1980a, b, 1981). Similar observations on specimens of *Calantica villosa* collected at Warrington, Otago, New Zealand in January 1979 provided a supplement to previous knowledge of the functional morphology of pollicipoid scalpellids and a basis for comparison with *C. polymerus*.

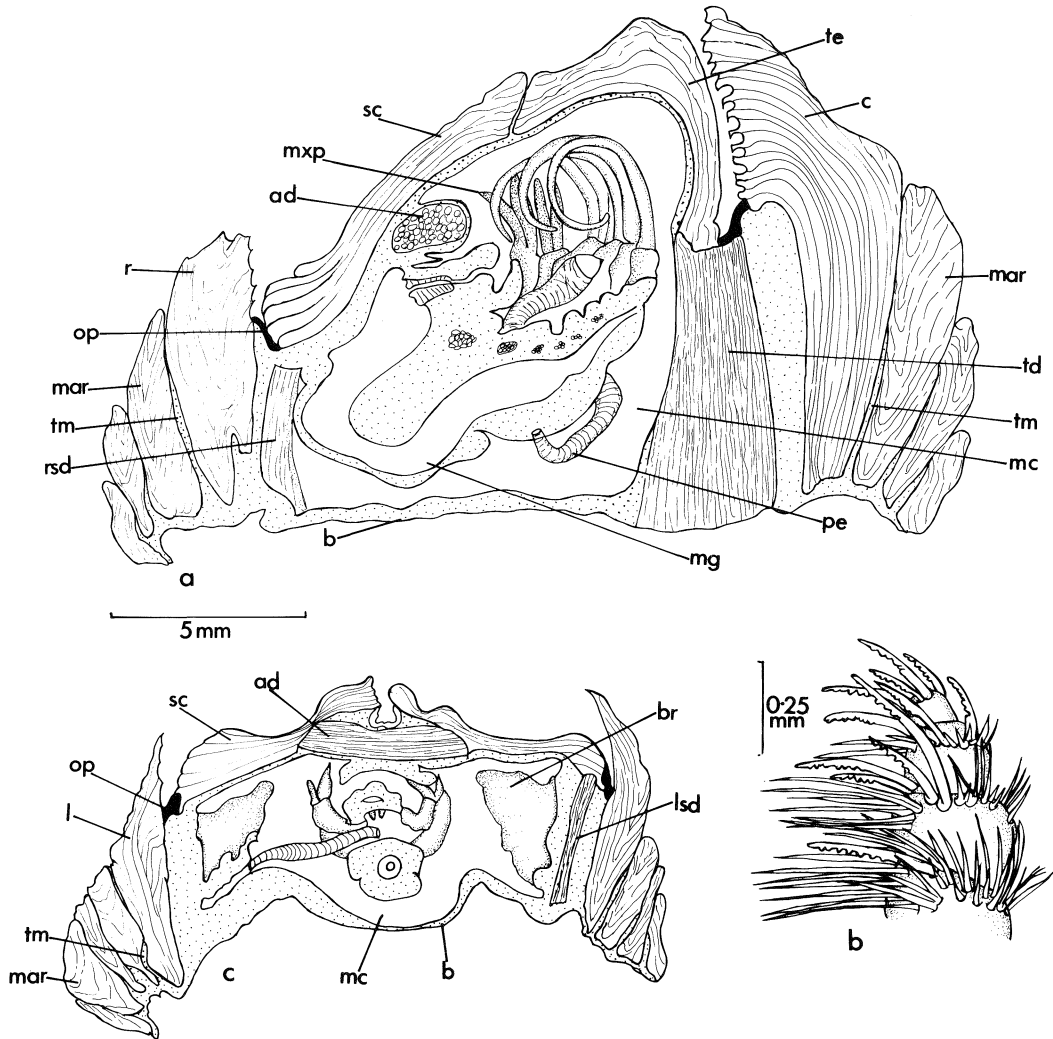


Fig. 8. **a**, Sagittal section through a decalcified specimen of *Catomerus polymerus*. **b**, Specialised setation at the tip of cirrus II of *C. polymerus*. **c**, Transverse section through a decalcified specimen of *C. polymerus* at the level of the adductor scutorum. *ad*, adductor scutorum; *b*, basis; *br*, branchia; *c*, carina; *l*, lateral; *lsd*, lateral scutal depressor muscle; *mar*, marginal wall plate; *mc*, mantle cavity; *mg*, midgut; *mxp*, maxilliped; *op*, opercular membrane; *pe*, penis; *r*, rostrum; *rsd*, rostral scutal depressor muscle; *sc*, scutum; *td*, tergal depressor muscle; *te*, tergum; *tm*, mantle tissue.

(a) Feeding

Feeding in scalpellids was described in detail for *Pollicipes polymerus* by Barnes and Reese (1959). Feeding in *Calantica villosa* is similar and so, judging by the brief comments provided by Batham (1946), is feeding in *C. spinosa*. All three species are extension-feeding planktivores, preying on small to moderate size plankton, mainly crustaceans, the remains of which can be easily identified in the stomach contents. The aperture being on the rostral margin of the capitulum, the long cirri are slowly extended and held as an apico-rostrally projecting fan, with the shorter cirri extending more laterally towards the basal end of the aperture (Figs 7a, 7b). Prey organisms are captured either by individual rami of the long

cirri or, if larger, by the cirral net as a whole. The captorial cirri coil down and are cleaned off by the maxillipeds, which transfer the food to the mouthparts. Cirral extension is maintained for long periods provided there are water currents. In still water, the cirri are usually withdrawn and the aperture closed, as is also the case when the animal is exposed to air. Withdrawal of the cirri is a relatively faster movement than cirral extension, but still occurs quite slowly as compared with the corresponding movement in advanced balanomorph barnacles. For example, in *Calantica villosa* at 15°C, extension of the cirral net in response to a water current takes 4.0 s, withdrawal 0.95 s. In *C. spinosa* at the same temperature the corresponding figures are extension 2.94 s, withdrawal 1.76 s. The advanced balanomorph *Balanus perforatus*, at 21°C, in contrast, extends its cirri in 0.17–0.23 s and withdraws them in 0.06–0.14 s on each beat (Anderson, 1981).

Investigation of *Catomerus polymerus* has now revealed that the scalpellid mode of feeding is also a feature of this species. On immersion in water, the aperture slowly opens and the long cirri are extended to project as a partly curled fan at the carinal end of the aperture (Figs 7c, 7d). When a water current flows over the aperture, the cirri extend to a more upright position, though still maintaining an apico-rostral posture. Food in the form of small planktonic prey such as copepods, cyprid larvae and other crustaceans of similar size is captured, usually by the curling down of a single cirral ramus. Larger prey are occasionally engulfed by contraction of the whole cirral net. The maxillipeds transfer the captured prey from the coiled long cirri to the mouthparts. In association with the horizontal posture of the body relative to the basis and aperture and the more posterior placement of the long cirri (Fig. 8a), the process of forward food transfer by the maxillipeds is more complex than in scalpellids. The long cirri coil down mainly in a position behind the oral cone. The short maxillipeds with their dense setation, including a number of comb-like, stout serrate spines (Fig. 8b) on the distal segments of the second maxillipeds ("grapples" of Pope, 1965; "cards" of Newman, 1967a), are adapted to a forward combing action in the limited space between the coiled long cirri and the apex of the oral cone. Allowing for this functional adaptation related to changed body posture, however, *C. polymerus* has retained the feeding mechanism seen in scalpellids. The rate of cirral extension is comparable, though the withdrawal process is accelerated. At 20°C, extension in *C. polymerus* takes 2.8 s, withdrawal 0.33 s. Since *P. polymerus*, *C. villosa*, *C. spinosa* and *C. polymerus* are all intertidal and all feed in the same way, it can be concluded that the evolution of the balanomorph form in the catophragmids was not a functional correlate of the evolution of a new feeding mechanism. The diversification of feeding mechanisms in balanomorphs (e.g. Crisp and Southward, 1961; Anderson, 1978, 1981) is a result of further evolution after the balanomorph form had been attained.

(b) Protection

It follows, therefore, that the modifications leading from calanticine to catophragmid were functionally associated with a changed role of the peduncle and capitular plates. Some of this is evident from the anatomical considerations set out earlier in this paper. The long peduncle, with its obvious advantages for a subtidal extension feeder, is disadvantageous in exposed intertidal situations and is vulnerable to predators such as crabs. Elimination of the peduncle, resulting in a squat, conical form with a broad circular basis, is clearly advantageous. The extension of the basal capitular plates downwards to meet the basis as an interlocking vertical wall of 8 plates (Fig. 2) is also advantageous in terms of protection from desiccation, predation and mechanical damage, and is only a minor structural change, given a virtual cessation of peduncular growth. The lateral displacement of the pedunculo-capitular scales as concentric whorls of marginal plates is a corollary of this modified growth pattern, the marginals being turned to grow upright and imbricating, rather than lateral (Figs 8a, 8c). The progressive elimination of these marginals, even within the catophragmids, is indicative of their vestigiality of function as well as of structure.

As part of the process of evolution of the wall plates as a short upright cylinder, there has been a reduction in height of the ancestral carina. At the same time, the apical margin of the wall has expanded laterally, from the oval shape of the basal capitular region in calanticines to the diamond shape of the orifice in *Catomerus*. Both of these changes are associated with modifications of the opercular valves. In calanticines, as mentioned above, the aperture is rostral (Figs 1b, 2a, 6b). The scuta and terga are tall, arising from that basal part of the capitulum which is bordered by a horizontal row of 7 small plates (rostrum and latera) and the base of the carina. The carina, extending apically from this level, supports the junction between the terga along their carinal margins. The scuta, with their apical umbones and adductor muscle, cover the rostral halves of the valves. The terga, again with apical umbones, are taller and narrower than the scuta and cover the carinal halves of the valves. In some species of *Calantica*,

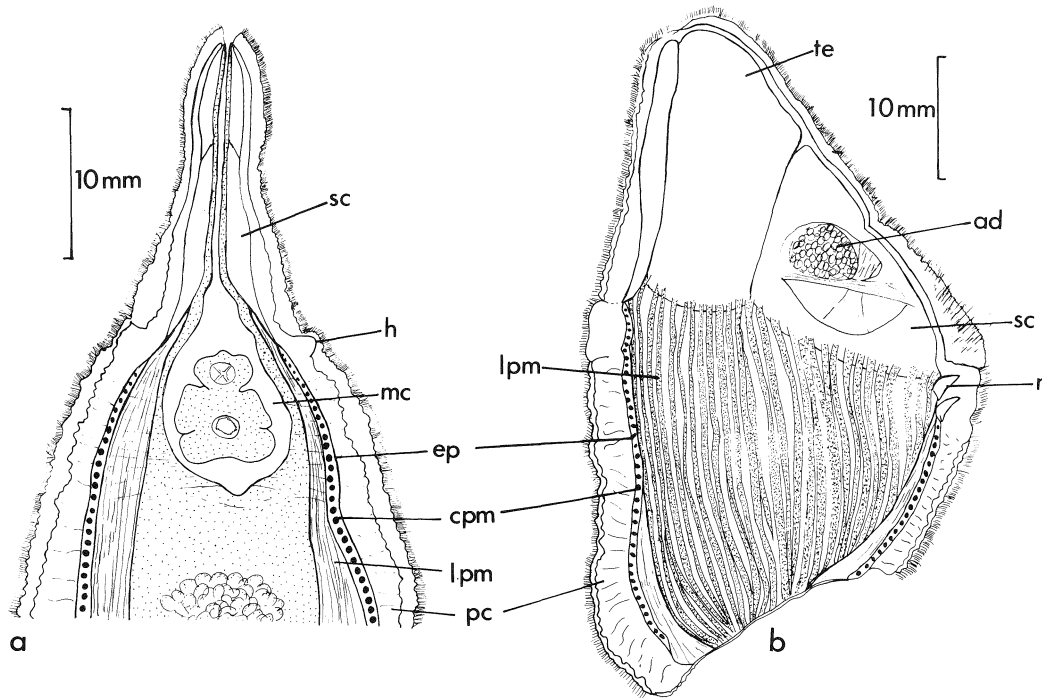


Fig. 9. **a**, Frontal section through the apical half of a decalcified specimen of *Calantica villosa*. **b**, Median view of the left half of a decalcified specimen of *C. villosa*, bisected sagittally and dissected to expose the longitudinal peduncular muscle. *ad*, adductor scutorum; *c*, carina; *cpm*, circular peduncular muscle; *ep*, surface epithelium; *h*, hinge; *lpm*, longitudinal peduncular muscle; *mc*, mantle cavity; *pc*, peduncular cuticle; *r*, rostrum; *sc*, scutum; *te*, tergum.

as noted by Darwin (1854), the scutum and tergum of each side are articulated together along their apposed margins.

In relation to the intertidal habitat, the calanticoid capitular plates have certain functional disadvantages. They project upwards as a bilaterally flattened cone and their mechanism of aperture closure is simple and potentially leaky. In catophragmids, through *P. cretaceum* to *C. polymerus*, a functional transformation of capitular plates to opercular valves has occurred. While retaining the capacity for opening to produce a wide aperture, the valves now have a low profile (Figs 1a, 2c), especially in the closed position, and can clamp tightly shut. It is to be noted, however, that the latter involves no interlocking of the aperture margins. These are still straight, so the tight closure of the aperture is a matter of bringing the aperture margins harder together.

The first consideration in understanding this change is to examine the modifications of the valves themselves. With the foreshortening of the carina, the aperture is rotated from a rostral to an apical position. It is in connection with this change that the body, within the mantle cavity, is also rotated from an oblique to a horizontal position, displacing the long cirri postero-basally and necessitating a functionally correlated modification, shortening of the maxillipeds, as illustrated by Newman (1967b).

At the same time, with a broadening of apical margin of the wall, the valves are canted from an upright to an oblique position, with the establishment of a sharp angle at the junction with the wall. The angled region acts as a hinge for the opening and closure of the opercular valves on the now rigid wall (Fig. 8c). Certain changes in the shape and growth pattern of the scuta and terga are a part of this general modification (Fig. 2). The scutal umbones are displaced carinally, so that the scuto-tergal junctions slope obliquely in a carinal direction and the scuta grow mainly in a rostral direction. The tergal umbones are also displaced carinally, maintaining their position behind the carinal end of the aperture, and the terga themselves are now relatively short and broad.

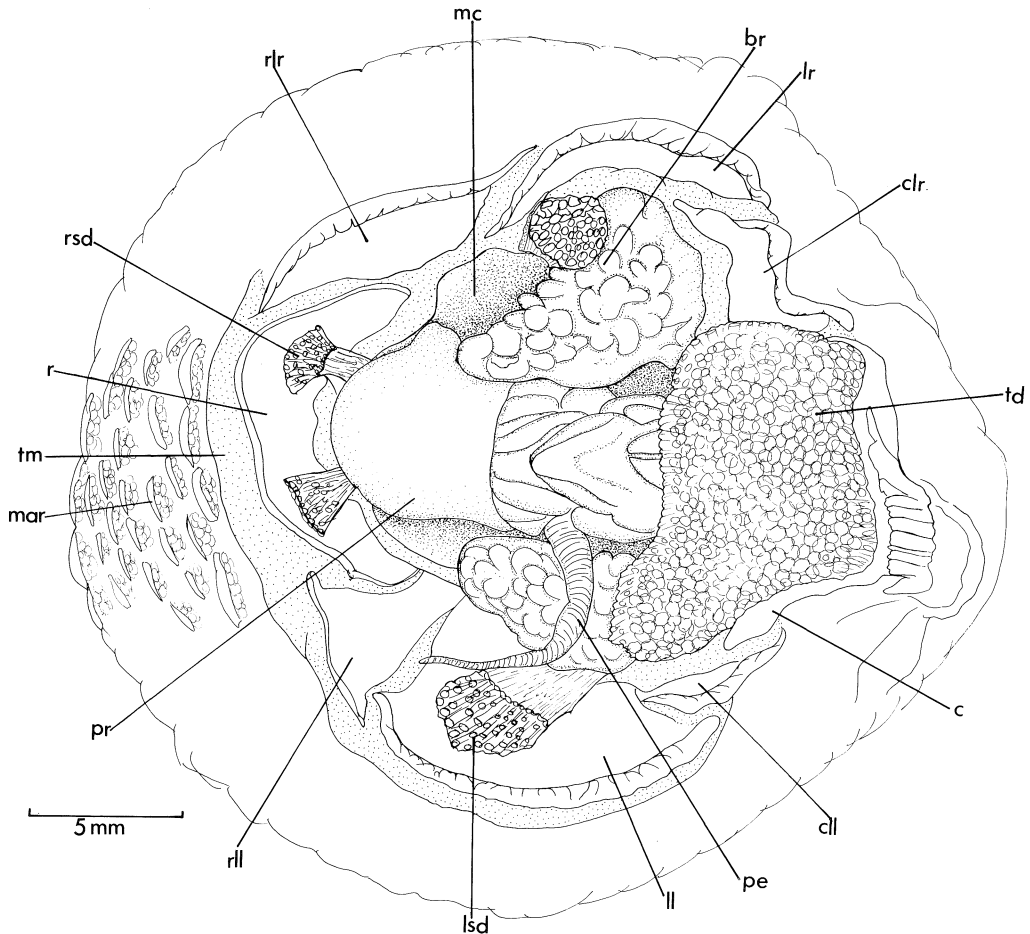


Fig. 10. *Catomerus polymerus*, basal view with basis removed. *br*, branchia; *c*, carina; *cll*, left carinolateral; *clr*, right carinolateral; *ll*, left lateral; *lr*, right lateral; *lsd*, lateral scutal depressor muscle; *mar*, marginal wall plates; *mc*, mantle cavity; *pe*, penis; *pr*, prosoma; *r*, rostrum; *rll*, left rostralateral; *rlr*, right rostralateral; *rsd*, rostral scutal depressor muscle; *td*, tergal depressor muscle; *tm*, mantle tissue.

The changes in growth pattern that transform upright capitular plates into a flattened operculum are readily understandable. The resulting low profile of the valves is functionally sensible. The opening mechanism of the valves, operating through hydraulic inflation of the mantle tissue underlying the scuta and terga (Burnett, 1972, 1977), remains unchanged. Attention needs to be paid, however, to the form and origin of the opercular hinge and the closure mechanism of the balanomorph operculum.

The hinge, as it happens, is not an innovation. A fully developed hinge is present between the basal margins of the scuta and terga and the more basal capitular plates in *Calantica* (Fig. 9a). Thus the hinge mechanism was already present before the balanomorph form evolved.

The closure mechanism, however, is more complex. In calanticines, closure is brought about in part by the scutal adductor muscle, working at good mechanical advantage, but also in part by the strongly developed sheath of longitudinal muscles in the peduncle (Fig. 9b). These muscles, lying within a sheath of connective tissue, are able to effect slow shape changes of the peduncle, but from the present point of view the significant feature is that their apical ends insert on the inner basal margins of the scuta and terga. In this position, contractions of these muscles can assist in closure, though at poor mechanical advantage.

A calanticine–catophragmid evolutionary transition requires that this system of closure should have been functionally transformed into the system present in *C. polymerus*. Previously, no details of the opercular closure mechanism in this species were available. Opercular closure remains a slow process, proceeding at about the same rate as in *Calantica villosa*. The adductor muscle remains an important functional component of valve closure, but in relation to the new position of the valves its efficiency would appear to be diminished (Fig. 8c). Valve closure is more of a downward swing than a bilateral apposition, and yet the adductor muscle retains its transverse orientation. It cannot therefore be as effective in valve closure as it is in scalpellids.

On the other hand, the downward swing of the closing valves in *Catomerus* is an exaggeration of that component of calanticine closure which is brought about by the peduncular longitudinal muscles, namely, a swing on the hinge due to an apicobasal pull of muscles inserted on the inner side of the hinge. The peduncular longitudinal muscles, instead of remaining as a muscle sheath, are transformed in *Catomerus* into a massive block of tergal depressor muscles extending from the terga to the basis (Fig. 8a) and two pairs of much smaller depressor muscles extending from the rostral and tergal corners of the scuta to the basis. The wall of the carapace no longer retains any pliability and these modified longitudinal muscles function solely in clamping down the opercular valves into the closed position. Because of their direction of pull, apicobasal, they play a major role at excellent mechanical advantage in swinging the valves downwards and shut. The same pull also serves to bring the occludent margins hard together in the closed position and hold them tightly shut.

One question remains to be examined. Why is it that the tergal depressor muscles in *C. polymerus* are so large and the two pairs of scutal depressor muscles quite small, when the ancestral form had an equal development of longitudinal muscles all round the peduncle? Functional considerations make it clear that the answer to this lies in the availability of space within the modified external wall (Fig. 10).

Allowing for the foreshortening of the mantle cavity and the rotation of the body to a horizontal position, the rostral half of the mantle cavity is almost entirely taken up by the large prosoma, and the lateral parts by the branchiae. The need for enlarged branchiae is correlated with the reduction in the surface area and exposure of the inner surfaces of the opercular valves as respiratory surfaces (see Burnett, 1972, 1977 for details of vascularisation of these surfaces). In this configuration, the only possibility for the development of large, longitudinal opercular muscles exists at the carinal end of the mantle cavity. A whole series of consequent proportional and functional changes in the prosoma relative to the mantle cavity has been associated with the subsequent evolution of the opercular depressor muscles in balanomorphs as three more or less equally developed pairs (Crisp and Southward, 1961; Anderson, 1978, 1981) but, like the evolution of the feeding mechanisms of balanomorphs, these changes have post-dated the establishment of the basic balanomorph form.

Thus in its opercular mechanism and every other aspect of its functional organisation, the balanomorph form as expressed in *C. polymerus* is a functional modification of the calanticine form, and Darwin's hypothesis withstands the functional test. The balanomorph modification is basically adaptive to enhanced protection in the high energy, stressful and predator-rich environment of the rocky intertidal. Feeding, in the early evolution and establishment of the balanomorph form, remained basically unchanged.

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