

# AN INTRODUCTION TO THE BIOLOGY OF BRITISH LITTORAL BARNACLES

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## ABSTRACT

This paper provides an introduction to the biology of barnacles that might be encountered on a low spring tide on a British rocky shore. The first part covers features of barnacle biology, system by system. The second part is an account of the biology of the most important British sessile barnacles. The zonation of British barnacles is discussed, identifying the physical and biological factors limiting barnacle distributions and summarising the ecological relationships of the barnacles. Finally the biology of the specialist parasitic barnacles, the Rhizocephalans *Sacculina* and *Peltogaster*, is briefly outlined.

## INTRODUCTION

Barnacles are dominant intertidal organisms of temperate rocky shores and play a prominent part in any zonation scheme (see Ballantine, 1961; Lewis, 1964). Generations of students attending field courses on British shores have learnt to recognise barnacles and perhaps make ambitious attempts at specific identifications. In spite of spending long periods counting on the shore, students often come away with only the barest knowledge of the biology of these unlikely-looking crustaceans.

This paper therefore introduces the main features of barnacle biology for sixth formers and undergraduates, concentrating on those species that might be encountered on a spring low tide on British rocky shores. Some of these are better described as sublittoral than intertidal, and it must be remembered that many other sublittoral species that never occur on the shore receive no mention here.

Throughout this paper I have remained aware of the nature of my audience and, although quoting many original references, I have referred to secondary sources (such as reviews) as much as possible to allow easier access to further reading.

### *What is a barnacle?*

In spite of their superficial similarity to molluscs caused by the presence of a calcareous shell, barnacles are crustaceans and have been accepted as such since 1829 when Vaughan Thompson recognised the unmistakably crustacean nature of the barnacle nauplius larva (Thompson, 1830). Some of the more familiar sessile (or acorn) barnacles of British shores are amongst the most advanced species. To make such statements it is necessary to consider the fossil record and comparative anatomy, not only of adult forms but also of developmental stages. Haeckel's Law of Recapitulation "Ontogeny recapitulates phylogeny" is no longer accepted at face value but, if interpreted with caution, features of embryological and larval development may throw light on the nature of possible evolutionary ancestors. The structure of sessile barnacles can be correlated with that of the more primitive stalked barnacles (Fig. 1). Using evidence from comparative crustacean anatomy it is possible to extrapolate back further and to suggest a pathway for the evolution of barnacles from a more typical (perhaps ostracod-like) crustacean (Fig. 1).

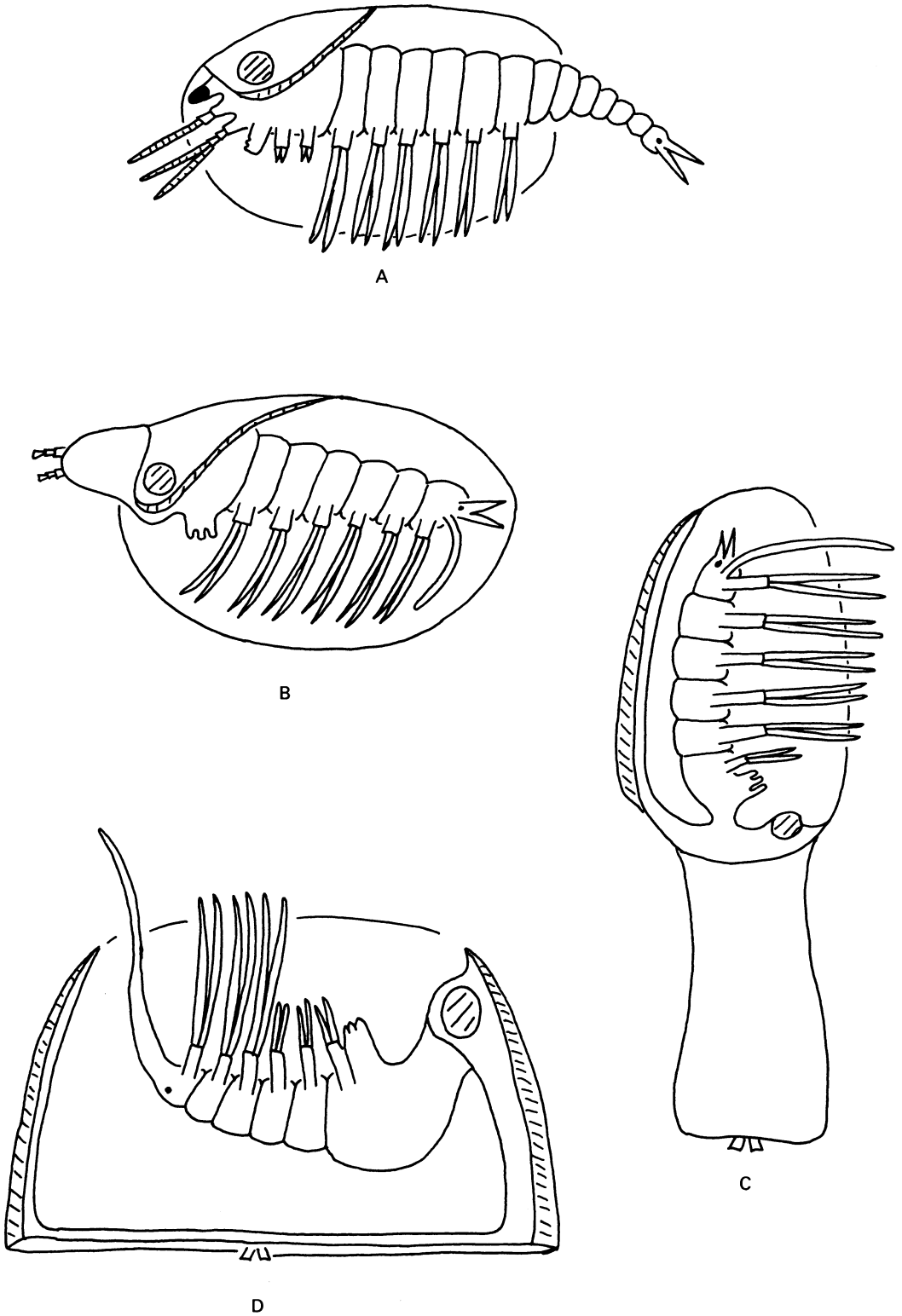


FIG. 1.

A hypothetical pathway for the evolution of barnacles from a typical crustacean (A) via a hypothetical intermediate (B) to a stalked (C) and then a sessile (D) stage. In A and B the left side of the bivalved carapace has been cut away to reveal the body, as has the side of the shell in C and D.

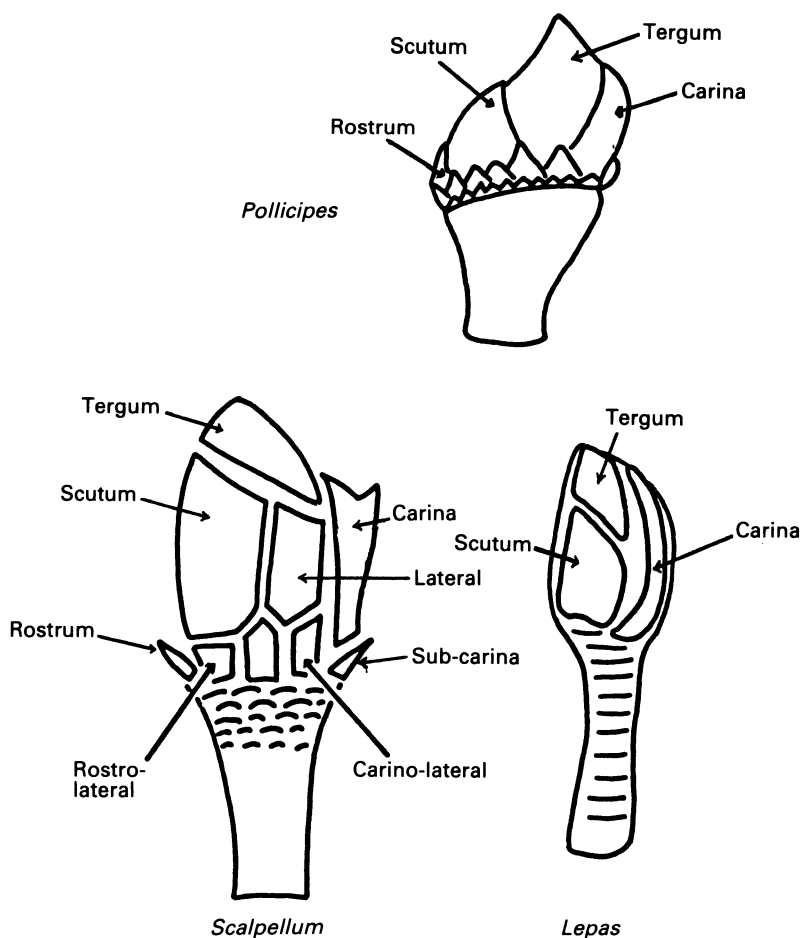


FIG. 2.

Three stalked barnacle genera *Pollicipes*, *Scalpellum* and *Lepas* showing the arrangement of shell plates.

Modern examples of basic crustaceans are microphagous filter feeders, using thoracic limbs both as locomotory appendages and to create feeding currents. Barnacles are attached to the substrate head downwards; the evolution of part of the head into a stalk being associated with the adoption of a sedentary habit. A flexible stalk has the selective advantages of carrying the remainder of the body (with the thoracic legs now specialised as feeding appendages) into the food-bearing water away from competitors, and of allowing increased opportunities for cross-breeding. The abdomen of barnacles is very reduced at the posterior end of the thorax and calcareous shell plates protect the enclosed body from predators.

Stalked or pedunculate barnacles usually live fully immersed in the sea and species of *Lepas* (Goose Barnacles) are found in oceans around the world attached to floating objects, such as logs of wood. The stalk of a pedunculate barnacle is, however, of limited advantage in the intertidal zone. Barnacles, like all other crustaceans, are covered in a chitinous exoskeleton of varying thickness and degrees of sclerotinisation and calcification. The stalk must be flexible, which necessitates that its cuticular covering be thin and therefore not sclerotinised or calcified to a great degree. This thin cuticle offers little barrier to the exit of water and would be an important route of dehydration if emerged on the shore. The barnacles that dominate

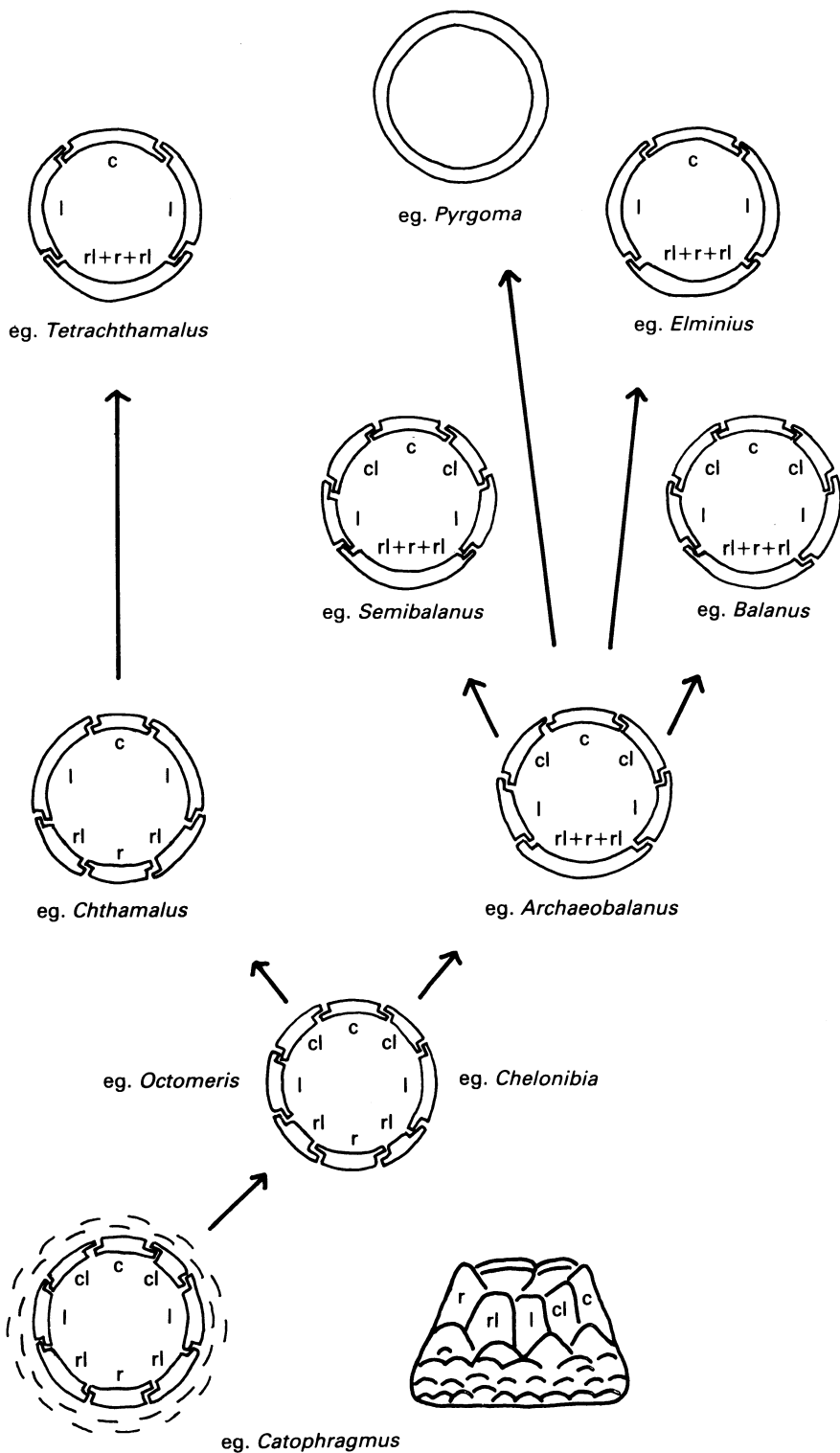


FIG. 3.

Examples of selected stages in the possible evolution of shell plate arrangements in sessile barnacles from an early stage with eight parietal shell plates (see text). c=carina, cl=carinolateral, l=lateral, rl=rostrolateral, r=rostrum.

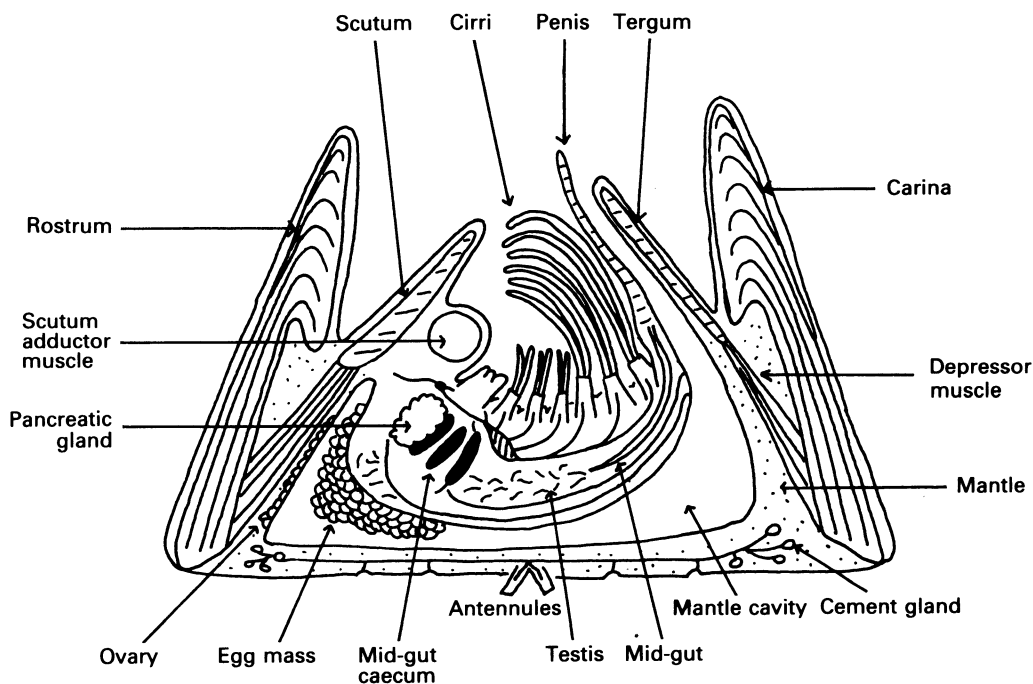


FIG. 4.

The anatomy of *Balanus*, a sessile barnacle.

the intertidal zone, therefore, are those that have lost the stalk and abut closer to the substratum—the sessile barnacles. There are a few intertidal pedunculate species, particularly in the tropics, but these are restricted to wet, wave-splashed shores (e.g. *Pollicipes* with a short, contractile, tough stalk), or are to be found in fissures (e.g. *Ibla*) or even burrows of their own making (e.g. *Lithotrya*) with humid microclimates.

The stalks of many pedunculate barnacles are covered in calcareous scales and large plates, particularly in rings below the major shell plates enclosing the body (see *Scalpellum*, Fig. 2). Amongst the calcareous plates of stalked barnacles can be recognised homologues of the eight parietal shell plates making up the walls of the earliest sessile barnacles, as well as the moveable paired scuta and terga (opercular plates). Primitive living sessile genera, like *Catophragmus* from the West Indies, still show the presence of further rings of small shell plates below the eight major parietal shell plates (Fig. 3). During the evolution of the sessile barnacles there have been different lines of reduction in the number of these eight plates by loss or fusion in various combinations (Fig. 3). Such fusions may reduce the loss of water during emersion (Newman, 1967) and the number of favoured penetration routes available for boring predatory gastropods (Palmer, 1982).

The body of a sessile barnacle is situated in the mantle cavity of the shell (Fig. 4) (the terminology being derived from the anatomy of molluscs). The paired scuta and terga act like trapdoors, opening and closing by muscle action. The remaining shell plates (six in *Chthamalus*, *Semibalanus* and *Balanus* (Figs. 3, 5 and 6)) surround the body and mantle cavity. The base may be membranous or calcareous. The separate parietal shell plates are clearly discernible in newly metamorphosed barnacles but the sutures usually become obliterated with growth.

The origin and evolution of barnacles is discussed in detail by Newman (1982).

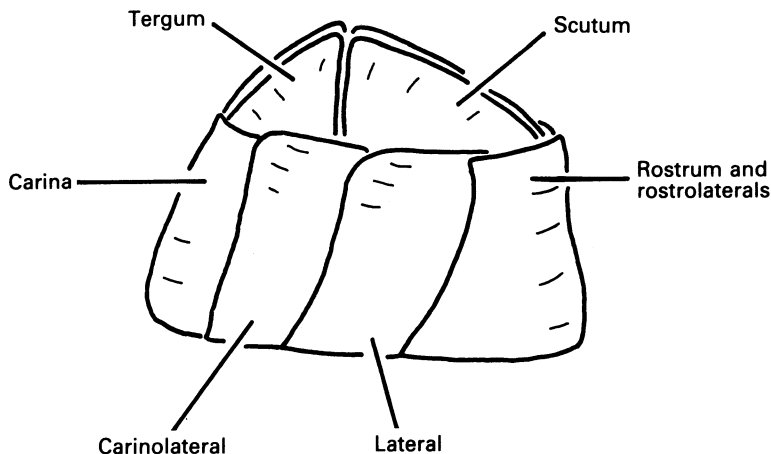


FIG. 5.

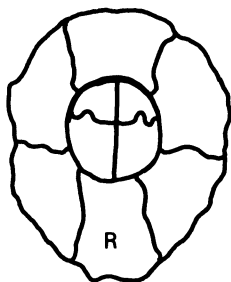
The external appearance of *Balanus* identifying the parietal plates (of which the carinolateral and lateral are duplicated on the other side) and the opercular plates (the paired scuta and terga).

### Feeding

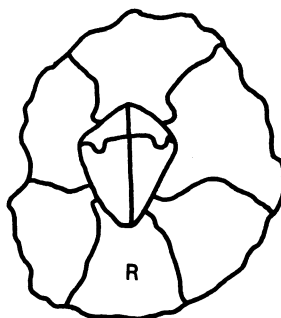
There are two basic patterns of feeding in barnacles (Crisp and Southward, 1961; Anderson, 1980, 1981) involving the six pairs of thoracic limbs or cirri (Fig. 4). The more primitive method is that of "captorial feeding" and involves the prolonged extension of cirri, by an increase in blood pressure, to capture live prey. The cirri are refurled by contraction of their internal muscles. Captorial feeding is characteristic of stalked barnacles and of the more primitive sessile barnacles such as *Verruca* and *Chthamalus* (Anderson, 1981). More advanced sessile barnacles like *Elminius*, *Semibalanus* and *Balanus* characteristically show rhythmic beating of the cirri. Rhythmic beating has been subdivided into "normal beat" accompanied by a flow of water through the mantle cavity, and "fast beat" with little or no passage of water through the mantle cavity (Crisp and Southward, 1961). Feeding using fast beat is a form of captorial feeding directly equivalent to that seen in more primitive barnacles. The ventilation of the mantle cavity during normal beat is probably of respiratory significance but does additionally allow microfeeding (feeding on microscopic particles like phytoplankton) by the filtration of the mantle current by the more anterior cirri (maxillipeds) (Fig. 7). The original role of these anterior cirri was the transfer of prey anteriorly to the oral cone after capture by the more posterior cirri (Fig. 8) using captorial feeding. The evolutionary change from reliance on cirral extension and captorial feeding to rhythmic beating and microfeeding is accompanied by a progressive change in the structure of the more anterior cirri so that in advanced sessile barnacles (balanoids) only the three posterior pairs are used for captorial feeding. In these barnacles each of the posterior cirri wipes off food particles onto the third cirri; these in turn are wiped by the second cirri which themselves are brushed by the first cirri before final transfer of the food particles to the mouth (Crisp and Southward, 1961).

Studies of the details of the mechanisms of rhythmic feeding in several species indicate that it has evolved independently several times from extension feeding and that the classical normal and fast beats described by Crisp and Southward (1961) need not always be present (Anderson, 1981).

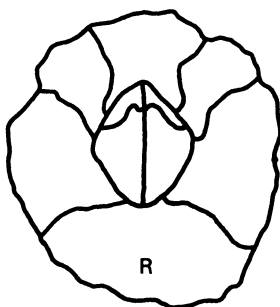
Southward and Crisp (1965) found no evidence for endogenous diurnal or tidal rhythms in barnacles nor any exogenous rhythms in response to light and dark. Barnacles show an



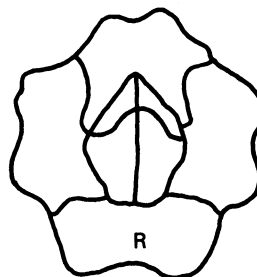
*Chthamalus stellatus*



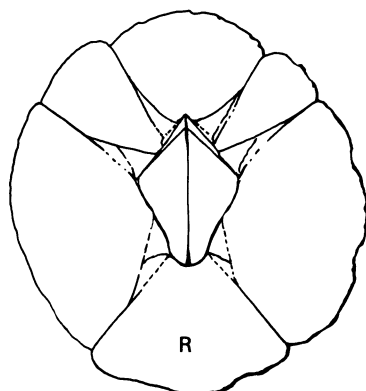
*Chthamalus montagui*



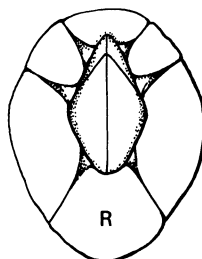
*Semibalanus balanoides*



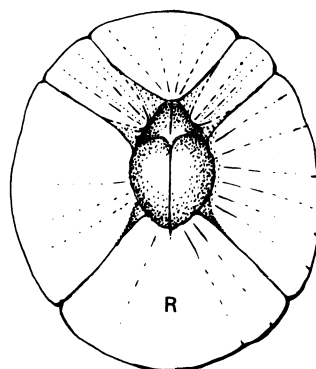
*Elminius modestus*



*Balanus crenatus*



*Balanus improvisus*



*Balanus perforatus*

FIG. 6.

The external appearance of the four British intertidal barnacles with membranous bases (after Southward, 1976) and the three most common *Balanus* species found on the shore. R is the rostral plate which is made up of the fused rostrum and rostrolaterals in *Balanus*, *Semibalanus* and *Elminius* but only the rostrum in *Chthamalus* (see Fig. 3).

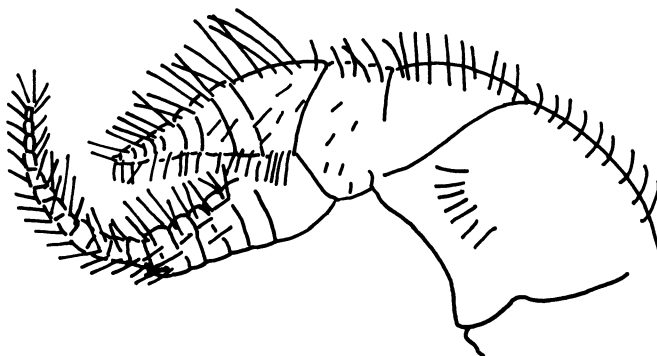


FIG. 7.

The 1st cirrus of a barnacle (after Stubbings, 1975).

almost immediate response to wetting which allows them to feed whenever immersed, irrespective of their position on the shore. Any inherited tendency to synchronise to a particular rhythm suited to one shore level would be unsuitable at another. Since barnacles are widely dispersed as larvae there is no selective advantage to evolve inherited rhythms (Southward and Crisp, 1965). The rate of intake of food is a prime factor influencing the growth of barnacles and so specimens lower on the shore (immersed for a longer period) grow faster than those above them (Barnes and Powell, 1953).

Captorial feeding allows the capture of large prey, including fish, by stalked barnacles, the lower limit to size of prey being dictated by the minimum width of the spaces in the expanded cirral net. In *Balanus perforatus* the minimum width was measured as  $33\text{ }\mu\text{m}$  (Southward, 1955) restricting the prey so captured to zooplankton, particularly crustaceans, and to larger phytoplankton species such as large diatoms. Microfeeding on the other hand allows the filtration of smaller items of food and accounts for the presence of small phytoplankton cells and even bacteria in the guts of balanoid barnacles (Southward, 1955; Barnes, 1959). *Balanus perforatus*, for example, has first and second cirri with groups of fine setae only  $1\text{ }\mu\text{m}$  apart (Southward, 1955). Barnacles also use active selection processes, rejecting particles at or near the mouth and on the cirral net (Crisp and Southward, 1961). They show evidence of chemoreception, feeding activity being stimulated particularly strongly by amino acids and related compounds (Crisp, 1967).

#### *Alimentary tract and associated tissues*

Food particles passed forward by the anterior pairs of cirri are entangled in secretions from the suboesophageal salivary glands at the base of the oral cone and first cirri, and are transferred to the paired labial palps (second maxillae). Food then comes into contact with further salivary secretions from glands in the labial palps before it is masticated by the first maxillae and mandibles (Fig. 9) which act against a thickened region of cuticle lining the pharynx (Rainbow and Walker, 1977a). The food passes from the cuticle-lined pharynx and oesophagus into the wide anterior midgut (expanded into midgut caeca) and receives digestive enzymes secreted from the paired pancreatic glands (Fig. 4) (Rainbow and Walker, 1977a). Absorption occurs in the anterior midgut, caeca and posterior midgut which also produces a peritrophic membrane surrounding the gut contents (Rainbow and Walker, 1977a, 1978). Faecal pellets



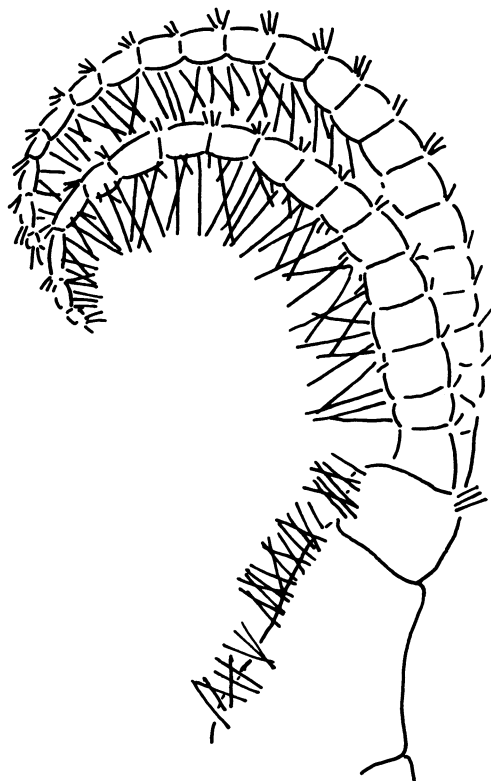


FIG. 8.  
The 4th cirrus of a barnacle (after Stubbings, 1975).

pass through the cuticle-lined hindgut before expulsion from the anus, posterior to the sixth pair of cirri. Beneath the midgut is a layer of cells, the *stratum perintestinale*, which translocates absorbed materials and may play a hepatic role. Body cells beyond the *stratum perintestinale* seasonally accumulate glycoprotein and lipid droplets which are transported to the ovaries in the tissue lining the mantle cavity to form the yolk (a glycolipovitellin) of the developing eggs (Rainbow and Walker, 1977a). The body cells also store glycogen seasonally as an energy reserve (Rainbow and Walker, 1977a).

The body cells of barnacles contain granules of zinc phosphate in amounts in apparent proportion to levels in the surrounding seawater (Walker *et al.*, 1975a, b). Since barnacles appear to have limited powers of zinc excretion the granules may be a result of a detoxification mechanism (Walker *et al.*, 1975a, b; Walker and Foster, 1979; Rainbow *et al.*, 1980). Barnacles from Dulas Bay, Anglesey, receiving copper-rich effluent from Afon Goch, similarly accumulate copper-containing deposits (Walker, 1977a) and barnacles in general accumulate copper and cadmium in addition to zinc (Rainbow *et al.*, 1980).

### *Moulting*

Having an exoskeleton, barnacles need to moult in order to grow and they shed the cuticle lining the body and the mantle cavity at intervals. Increased feeding and temperature raise the frequency of moulting whilst barnacles of temperate regions may cease moulting for long

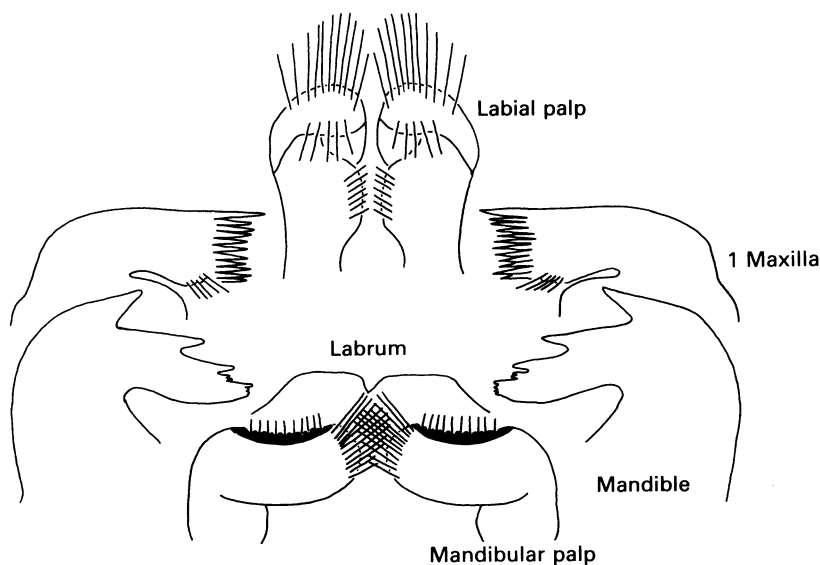


FIG. 9.  
The mouthparts of *Balanus*.

periods (anecdyses) during the winter when planktonic food levels and temperatures are low (Crisp and Patel, 1960). Neither the lunar cycle nor the tidal level influence the moulting rhythm, at least in the case of *Semibalanus balanoides* (Crisp and Patel, 1960), so the moulting cycle is probably under endogenous control (Crisp and Patel, 1969; Barnes and Stone, 1974). Crustacean moulting hormones of the ecdysone type have been identified in barnacles (Bebbington and Morgan, 1977). Barnacles accumulate crystals of tyrosine and this tyrosine, or a derivative, may be involved in the sclerotisation of selected regions of the cuticle (Walker, 1980a).

#### *Nervous system*

Typically the crustacean nervous system is a ladder-like arrangement of a double ventral nerve cord with a circumoral ring and segmental ganglia. Primitive stalked barnacles have a nervous system not unlike this. The sessile barnacles have a more concentrated nervous system of two main ganglia—the supraoesophageal and the suboesophageal in front of and behind the oesophagus respectively (Darwin, 1851, 1854; Cornwall, 1953). The supraoesophageal is made up of two connected ganglia whilst the suboesophageal has been formed by the fusion of all ganglia posterior to the oesophagus. From the supraoesophageal ganglion nerves equivalent to the antennular nerves of other crustaceans supply the body surface. Others run to the scutum adductor muscles and to the photoreceptor organs, two of which are located in the tissue between the scutum and the junction of the rostrum and the lateral shell plates. Paired nerves from the suboesophageal ganglion run to the six pairs of cirri and the viscera of the body (Darwin, 1851, 1854; Cornwall, 1953; see Stubbings, 1975).

#### *Respiration*

Sessile barnacles have a pair of gills, or branchiae, which arise as simple folds from the wall

of the mantle (the tissue lining the mantle cavity) and lie nearly vertically in the mantle cavity obliquely across the front of the carino-lateral shell plates (Stubbings, 1975). The gills are thrown into a series of pleats which are particularly well developed near the attachment of the gill to the mantle. They are lined by very thin cuticle and are well supplied with blood, as befits a respiratory surface. Sessile barnacles are able to produce a respiratory current through the mantle cavity during normal beat when the cirri are extended rhythmically, and also when "pumping"—moving the body in rhythm without unrolling the large cirri (Crisp and Southward, 1961). The expanded cirri may also play an important role as an accessory respiratory surface.

When emersed at low tide, the intertidal barnacles *Chthamalus montagui*, *Semibalanus balanoides* and *Elminius modestus* are unable to survive on the oxygen dissolved in the small amount of water trapped in the mantle cavity (Barnes *et al.*, 1963; Grainger and Newell, 1965). They expel this water which is replaced by air which in turn is extruded as a bubble on reimmersion. During emersion, contact between the air in the mantle cavity and that outside is maintained through a small opening (micropyle or pneumostome) formed by the folds of tissue around the opercular valves, the diameter of the micropyle being just large enough to allow sufficient oxygen to diffuse into the mantle cavity (Barnes *et al.*, 1963). More continuously submerged species like *Balanus crenatus* do not form a micropyle (Foster, 1970). The intertidal barnacles therefore take up oxygen from the air during emersion but run the risk of desiccation. During a normal period of low tide the micropyle remains open most of the time but on a particularly hot or windy day the rate of desiccation is such that the barnacles eventually close the operculum and respire anaerobically, with an associated lowering of metabolic rate and build-up of lactic acid (Barnes *et al.*, 1963). On reimmersion, and a return to aerobic conditions, only a small part of the lactic acid is reoxidised aerobically (requiring increased oxygen uptake over normal aerobic metabolism) and most is excreted. Although wasteful, such an excretion does not unduly stress the metabolic reserves of the barnacle as anaerobiosis is usually of short duration (Barnes *et al.*, 1963).

### Circulation

As in other crustaceans the coelom of barnacles is much reduced and the expanded haemocoel containing the blood (haemolymph) surrounds the body organs. The haemocoel consists of sinuses without specifically differentiated wall tissue, together with vessels which are elongated with recognisable walls of dense parenchyma (Stubbings, 1975). A circulation system is present and blood passes from a large sinus by the rostrum to the mantle and shell plates and on to the gills; then to a sinus by the scutum adductor muscle and so to the gut or cirri before returning via large sinuses to the rostral sinus (Figs. 4, 5) (Stubbings, 1975; Burnett, 1977). The nature of the blood pump driving this circulation has not been identified for certain (Stubbings, 1975). The muscles around the rostral sinus may contract to pump blood round the body (Cannon, 1947) or contraction of body musculature in general may generate sufficient pressure to move the blood (Gutmann, 1960).

### Excretion

The excretory organs of the adult barnacle are the maxillary glands lying on either side of the foregut and exiting via pores at the base of the second maxillae (White and Walker, 1981a). Each maxillary gland consists of an end sac (a remnant of the coelom) linked to an efferent duct (coelomoduct) via a valve. Haemolymph in a blood sinus adjacent to the end sac is filtered through the end sac epithelium to form the primary urine, which is probably

little further modified during the passage through the short efferent duct (White and Walker, 1981a). The major nitrogenous waste product of barnacles is ammonia (White and Walker, 1981b), the typical product of marine invertebrates, which requires dilution with water to avoid toxicity. It is perhaps surprising that intertidal barnacles running the risk of desiccation when using aerial respiration at low tide have not evolved a less toxic nitrogenous waste product to save water. The rate of nitrogen excretion varies seasonally in relation to food availability, to the utilisation of stored energy reserves and to the gametogenic cycle (White and Walker, 1981b).

### *Osmotic balance*

Intertidal and estuarine barnacles come into contact with water of low salinity. Barnacles will then close the opercular valves, so preventing the entry of low salinity water into the mantle cavity; slight separation of the valves allows the occasional testing of the water (Foster, 1970; Davenport, 1976; Cawthorne, 1979). Most barnacles are osmoconformers, the osmotic pressure of the haemolymph following that of the surrounding water—in this case the water in the mantle cavity (Foster, 1970). Superficially, then, barnacles may appear to be osmoregulators when haemolymph osmotic pressures are compared with osmotic pressures of the seawater beyond the barnacle shell. Barnacles are able to acclimate over a number of days to reduced salinity; their closing response is elicited at a lower salinity (Davenport, 1976) and the tissues exhibit an increased tolerance to reduced osmotic pressures (Foster, 1970).

The estuarine barnacle *Balanus improvisus* may actually be able to osmoregulate at lower salinities although there is confusion and disagreement in the literature (Foster, 1970; Fyhn, 1976). Foster concluded that *B. improvisus* is an osmoconformer with tissues remarkably tolerant of low osmotic pressure but Fyhn (1976) has indicated that the barnacle can osmoregulate in dilute seawater, regulation of cell volume depending on variable concentrations of intracellular amino acids, particularly proline.

The behavioural avoidance of low salinity by isolation from the environment is associated with anaerobiosis and low metabolic activity (Barnes *et al.*, 1963).

Barnacles similarly osmoconform when exposed to salinities greater than that of seawater (Foster, 1970; Fyhn, 1976). *Semibalanus balanoides*, *Elminius modestus* and *Balanus crenatus* cease cirral activity and withdraw below the opercular plates at between 50 and 55‰ salinity but avoidance of outside salinities is apparently less effective in hypersaline than in hyposaline conditions (Foster, 1970).

### *Shell*

The shell of a sessile barnacle consists of a ring of overlapping calcareous plates whose number and arrangement differ between evolutionary lines (Figs. 3, 5). Each of the original eight wall plates of a sessile barnacle consists of a central part, the paries (plural parietes), and overlapping parts called alae or radii (Fig. 10) (Darwin, 1854; see Bourget, 1977), although shell plates of living genera may be formed by the fusion of two or more original plates (see Fig. 3). Each shell plate is in close contact with an underlying epidermis (hypodermis) which secretes it. The shell plates are essentially highly calcified regions of cuticle but, in contrast to a normal crustacean ecdysis, the cuticle making up a shell plate is not cast off at each moult but remains adhered to the outside of the new cuticle (Darwin, 1854). New cuticle is in turn calcified and the shell plates subsequently increase in thickness during growth. An epicuticle covers the outside of the shell plates. The shell wall plates are thickened

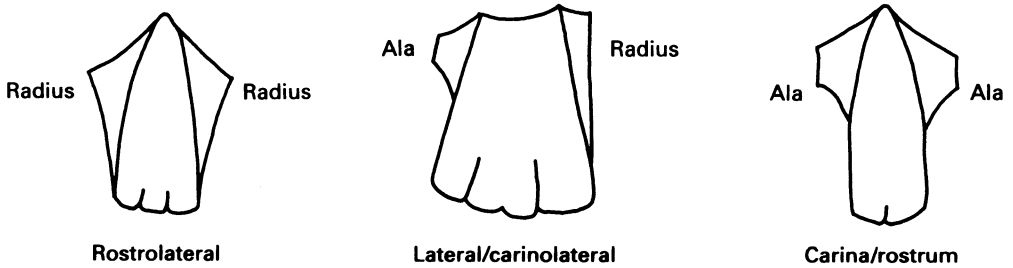


FIG. 10.

The original parietal shell plates of sessile barnacles (after Darwin, 1854). Each consists of a central paries with combinations of alae or radii. Shell plates of living barnacles may be formed by fusion of two or more such plates (see Fig. 3).

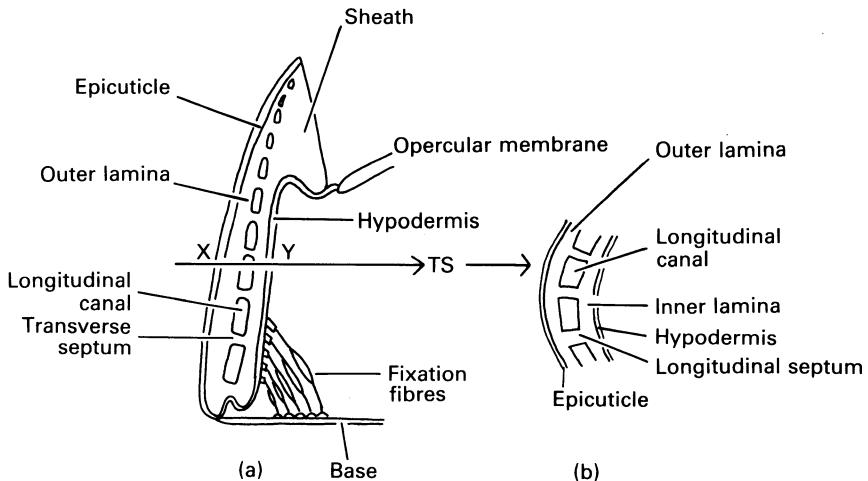


FIG. 11.

The structure of a shell plate of *Semibalanus* (after Bourget, 1977). (a) Vertical section (b) Cross section across XY.

at the top by a calcareous sheath, to which is attached the opercular membrane surrounding the scuta and terga (Fig. 11). The shell walls vary in structure between species and may consist of solid calcite or be porose with empty canals running vertically between an inner and outer lamina (i.e. tubiferous) perhaps with additional transverse septa (Fig. 11) (Bourget, 1977). The canals may even become filled secondarily with calcareous material. Longitudinal sections through the shell plates show that they consist of numerous parallel light and dark growth bands (Bourget and Crisp, 1975a). These bands are formed during periods of tidal immersion, separated by periods of emersion, and indicate where growth has taken place (Bourget, 1977). In some genera, such as *Chthamalus*, growth takes place along the whole internal surface of the plate which is said to be one-layered; but in others, *Semibalanus* for example, growth takes place in specific regions—at the basal margin, resulting in an increase in height and width of the shell plates, and along the upper half, lengthening and thickening the sheath (Fig. 12) (Bourget, 1977). In *S. balanoides* little deposition occurs between these two sites, the intervening region being the site of attachment for the contractile fixation fibres anchoring

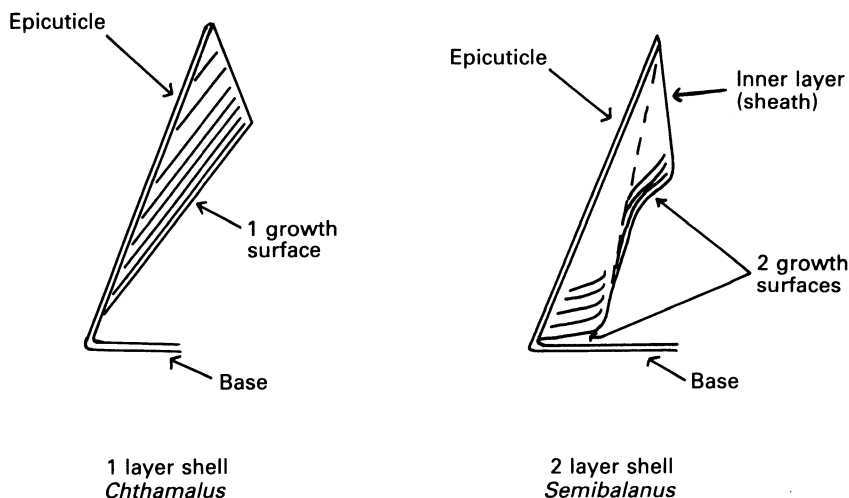


FIG. 12.

Shell plates of *Chthamalus* and *Semibalanus* (after Bourget, 1977) showing the distinction between one and two layered shells (see text).

the shell to the base (Fig. 11). The shell plates cannot be rigidly cemented to the base for this is a region of active growth, new tissue being formed both at the bottom of the shell plate and at the outside of the base. When the fixation fibres are relaxed the secretory hypodermis can be extended by blood pressure out under the edge of the shell to secrete further shell material (Bourget and Crisp, 1975a; Newman, 1982). Many higher balanids have wall plates and calcareous basis intricately locked together, not depending on the presence of fixation fibres: it is not known how shell growth takes place in this case (Newman, 1982).

### *Cement system*

The cement production system of adult sessile barnacles consists of groups of cells lying in the mantle tissue lining the outer region of the base (Figs. 4, 13, 14) (Walker, 1970). The cement cells produce a proteinaceous cement (Walker, 1970; Walker and Youngson, 1975) which passes down a system of ducts to be deposited between the base and the substratum. As the diameter of the base (either membranous or calcareous) increases with barnacle growth, the cement duct system is extended and new cement is added under the outer regions of the base. Cement cells are modified cuticle-forming cells (Thomas, 1944) and the cement contains phenolic amino acids in addition to protein (Walker, 1970, 1978). The newly secreted cement is liquid and spreads between the base and substratum before it may polymerise and set, a process possibly involving quinone tanning (see Walker, 1981). Until (if ever in nature) the cement sets, sessile barnacles may be adhering by Stefan adhesion requiring the cement to be a high viscosity fluid rather than a chemically rigid (set) solid (Crisp, 1973). The possible presence of Stefan adhesion is supported (Walker, 1981) by the observation that barnacles with membranous bases are capable of lateral movement under pressure (Crisp, 1960).

### *Reproduction*

Most barnacles are cross-fertilising hermaphrodites. Spermatozoa are formed in a seasonally-developed pair of testes consisting of many tubes scattered through the connective tissue (Fig.

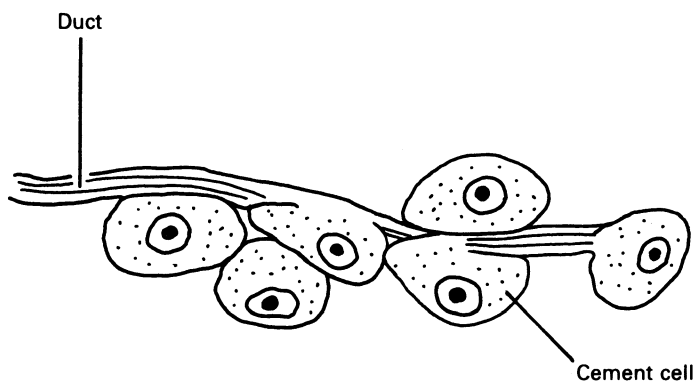


FIG. 13.

A cement gland of an adult barnacle (after Walker, 1973; Stubbings, 1975) showing secretory cement cells leading to a collecting duct.

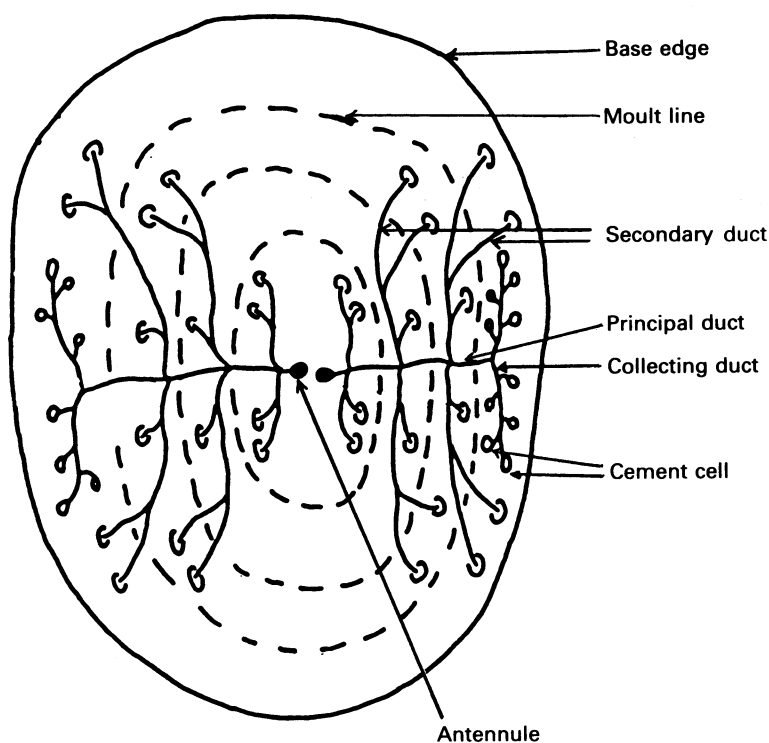


FIG. 14.

The cement system of an adult sessile barnacle (after Walker, 1973).

4). Ducts from the testes lead to the paired seminal vesicles which unite at the base of the penis behind the sixth pair of cirri. The penis is well supplied with blood and is extensible. Paired ovaries are situated in the mantle and an oviduct leads from each to the basal segment of the first cirrus, where it opens to the exterior via an oviducal gland. Each oviducal gland secretes an elastic ovisac into which the eggs are deposited, the sacs expanding into the mantle cavity as more eggs are laid (Walley, 1965; Walker, 1980b).

The greatly-extended penis of a functionally male barnacle makes initially random movements to locate a functional female. The penis is well supplied with chemosensory setae (Munn *et al.*, 1974) and a functional female may be recognised as such chemically—perhaps from secretions of epidermal glands (cirral glands) which develop in a cycle related to the breeding cycle (Walley, 1967). The movements of the penis become more direct once contact with a functional female has been established, and sperm is transferred into the mantle cavity of the “female”. Newly inseminated spermatozoa occur as discrete gelatinous masses and are inactive (Walker, 1977*b*) until stimulated by fluid forced from the oviducal glands into the mantle cavity by the discharge of eggs into the elastic ovisacs during laying (Walley *et al.*, 1971; Walker, 1977*b*). The wall of each ovisac is partially penetrated by regularly-arranged craters, and the activated spermatozoa bore through the relatively thin sac wall at the centre of these craters, the holes so formed then facilitating the entry of other spermatozoa (Walker, 1977*c*; Walker, 1980*b*). The spermatozoa fertilise the newly-laid eggs which form sticky fertilisation membranes, adhering the eggs into cohesive masses, one on each side of the mantle cavity (Walker, 1980*b*).

Most sessile barnacles carry out cross-fertilisation, some, including *Semibalanus balanoides*, *Elminius modestus* and *Balanus crenatus*, apparently obligatorily. In others, including *Balanus perforatus* and species of *Chthamalus*, isolated individuals have been observed with fertilised egg masses so self-fertilisation may occur (Barnes and Crisp, 1956; see Landau, 1976).

The fertilised egg masses are held in the mantle cavity, for several months in some species. The developing eggs rely on yolk reserves for their energy supply and hatch out as free-swimming stage I nauplius larvae. The parent stops feeding during larval emission.

### *Larval development*

*Nauplius larvae.* Barnacles pass through six planktonic nauplius stages (Fig. 15) before moulting into a cypris larva (cyprid) (Fig. 16). The nauplius is the simplest crustacean larva with three pairs of paired appendages—uniramous antennules (first antennae), biramous antennae (second antennae) and mandibles. Barnacle nauplii are characterised by a pair of frontal horns at either front corner of the carapace. Other external features include the labrum covering the mouth between the bases of the limbs, the ventral thoracic process and the caudal spine (Walley, 1969; Rainbow and Walker, 1976). The nauplius stage I is non-feeding with a blocked foregut and survives for a few days on the remnants of glycoprotein and lipid yolk reserves in the anterior midgut (Fig. 17) before moulting to stage II (Rainbow and Walker, 1977*b*). Nauplii are photopositive and swim up into the surface waters thus avoiding benthic filter feeders (including adults of their own species). Nauplius stages II to VI are planktonic, trapping phytoplankton by means of feeding currents set up by the antennae and mandibles (Lochhead, 1936; Rainbow and Walker, 1976). Food particles are drawn to the ventral surface where they are retained by setae, and moved forward by mandibular gnathobases and stout setae along a midline groove to the region of the labrum (Rainbow and Walker, 1976). Here the food comes into contact with secretion from the labral glands (Rainbow and Walker, 1977*b*) and the antennal gnathobases complete the transfer to the mouth. The nauplii increase in size at each moult and also build up lipid (oil) reserves which are needed to support the non-feeding cyprid, first through its planktonic life and then through settlement and metamorphosis to the juvenile barnacle (Rainbow and Walker, 1977*b*). Food ingested by the nauplius is passed into the capacious anterior midgut where it is digested by enzymes secreted by specialised pancreatic constriction cells, absorption being carried out by the anterior midgut cells (Rainbow and Walker, 1977*b*). The ventral thoracic process of the



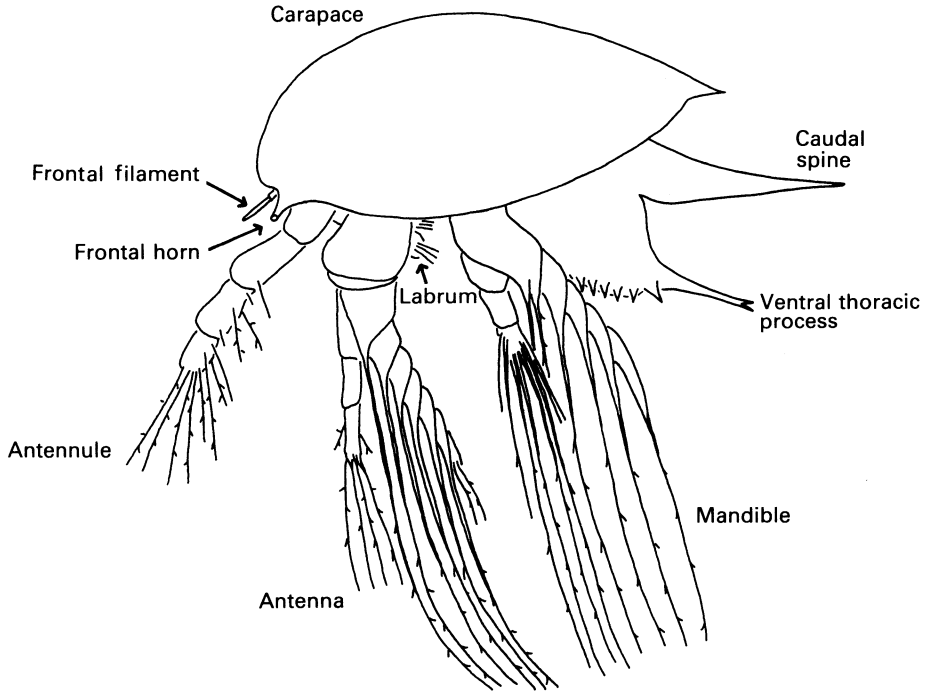


FIG. 15.  
The nauplius larva of a barnacle.

nauplius larva supports six pairs of spines equivalent to the six pairs of locomotory thoracic legs of the cypris larva and the six pairs of cirri of the adult barnacle.

*Cypris larva* (Cyprid). The cyprid (Fig. 16) is the non-feeding specialist settlement stage of the life cycle, different in structure and behaviour from the preceding nauplius stages (Walley, 1969). During the moult from the sixth stage nauplius to the cyprid, the structure of the body is reorganised (Walley, 1969). The larva now has a bivalved carapace, and looks superficially like an ostracod (from one genus of which its name is derived). The antennules of the cyprid are much altered in structure and function from those of the nauplius stages; the nauplius antennae and mandibles have regressed whilst rudimentary adult mouthparts are incorporated into the non-functional oral cone. All nauplius muscles and the excretory antennary glands histolyse (Walley, 1969). The alimentary canal is reorganised with closed foregut and hindgut (Rainbow and Walker, 1977b). The cyprid drifts or swims in the plankton by means of six pairs of thoracic legs before alighting on a substrate potentially suitable for settlement and metamorphosis.

#### *Settlement behaviour*

The antennules of the cyprid become adapted as walking appendages and are equipped with unicells secreting temporary adhesive (Nott and Foster, 1969). Cyprids walking over a substrate go through an initial phase of broad exploration moving along a relatively straight path with little turning, then a phase of close exploration with frequent changes of direction, and finally a phase of inspection rotating within one body length, closely investigating and perhaps even preparing the area to which they will permanently adhere (Fig. 18) (Crisp,

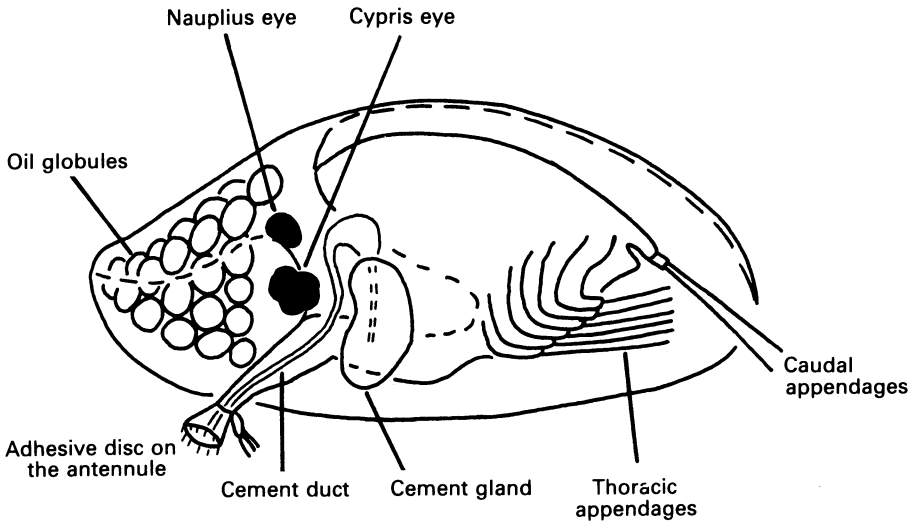


FIG. 16.  
The barnacle cypris (after Walley, 1969).

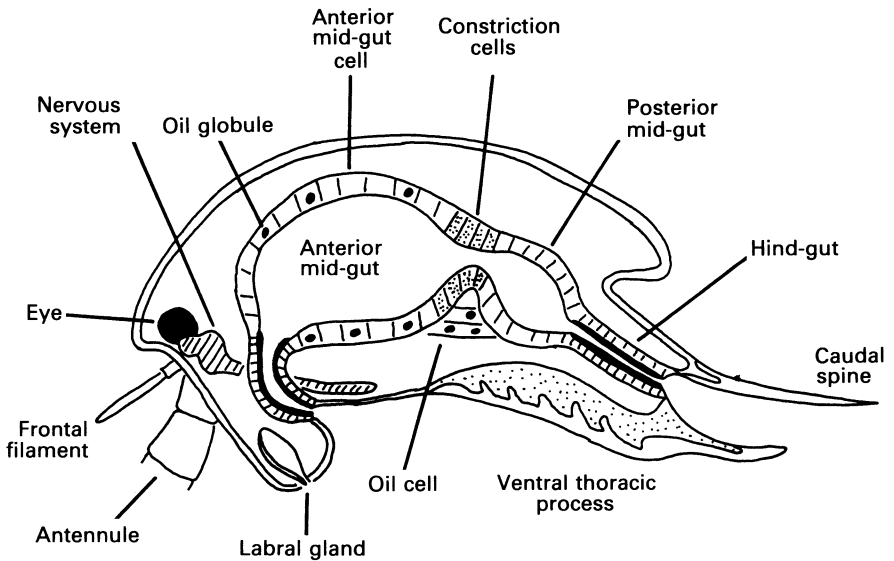


FIG. 17.  
The anatomy of a barnacle nauplius larva (after Walley, 1969; Rainbow and Walker, 1977b).

1974). This pattern may be interrupted and the cypris will swim off to alight elsewhere and begin again. The antennules are well endowed with sense organs (Nott and Foster, 1969) and these, together with others on the caudal appendages and carapace (Walker and Lee, 1976), are believed to play a part in the recognition of features to which the larva responds during settlement.

The settlement behaviour of barnacle cyprids has been reviewed by Barnes (1971), Crisp (1974) and Lewis (1978) and can be generalised as follows, although there are differences in detail between species.

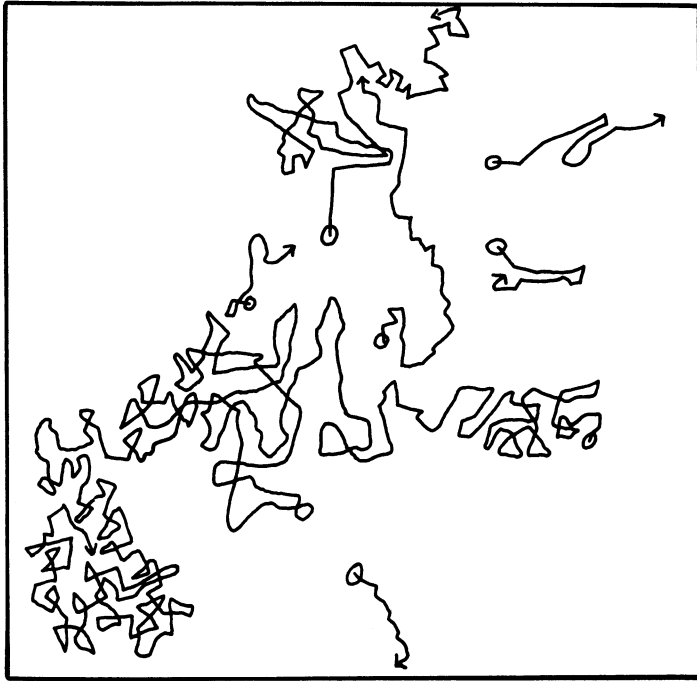


FIG. 18.

Settlement tracks of 7 barnacle cyprids (after Crisp, 1974).

Barnacle cyprids are rugophilic, preferring to settle on roughened rather than smooth surfaces, with the potential advantage of increased adhesive power after metamorphosis (Crisp and Barnes, 1954). They also prefer to settle in depressions and will orientate themselves along grooves (Crisp and Barnes, 1954). They can detect the direction and intensity of light, usually preferring to settle out of strong light and orientated with the anterior end towards it (Barnes *et al.*, 1951). The photoreceptor organs beneath the rostral plate of the metamorphosed barnacle are therefore on the opposite side of the barnacle to the incident light, an advantageous position to increase responsiveness to attack by fish in a sector least likely to receive shading and evoke a subsequent closing response (Forbes *et al.*, 1971). In the laboratory, barnacle cyprids also show a small but significant tendency to settle with the posterior end into the current so that after metamorphosis the cirral net of the adult barnacle opens into the current (Crisp, 1955), although orientation to water current is not normally detectable in the field (Crisp and Stubbings, 1957). When the physical parameters controlling the orientation of the settling larva are in conflict, the cyprid will orientate itself in response to contour, light and current in that order of priority (Crisp and Barnes, 1954; Crisp, 1955). As well as responding to the current direction, cyprids usually settle within a particular range of current velocity gradients (Crisp, 1955), although the upper limit may be that velocity gradient above which a cyprid cannot avoid being swept away before being able to settle. The minimum and maximum current velocity gradients differ between species and thus play a part in their differential habitat selection.

Many marine substrates are covered by a surface film produced by micro-organisms, usually after the initial adsorption of high molecular weight substances to that substrate (Crisp, 1974). Such films are attractive to the settlement of barnacle cyprids as they are to many other invertebrate larvae.

Barnacles also use a chemotactile response to recognise the presence of already-settled barnacles, responding to the presence of arthropodin—the protein constituents of arthropod cuticle (Crisp and Meadows, 1962, 1963; Gabbott and Larman, 1971) and settling nearby in an aggregative, gregarious response (Crisp, 1974). Such a chemotactile response allows a settling cyprid to identify a site with the required parameters for barnacle survival and, by settling gregariously, to increase the chances of successful cross-fertilisation in adult life. The degree of specificity of the chemotactile recognition varies between species, allowing some barnacles to distinguish their own species from others (Crisp, 1974; Larman and Gabbott, 1975) whilst still being able to recognise other barnacle species as indicators of sites suitable for barnacle growth in general. In the laboratory, extracts of animals other than barnacles may elicit settlement behaviour in cyprids if they contain proteins similar to those to which the cyprids normally respond (Larman and Gabbott, 1975). The occurrence of such anomalous settlement inducing activity may be a clue as to how certain barnacles have evolved to be epizootes (e.g. *Conchoderma* on whales, *Chelonibia patula* on crabs) or even parasites (e.g. the Rhizocephalans).

A possible disadvantage of gregarious settlement behaviour is that the barnacles may compete intraspecifically for space to grow or for food suspended in the water. *Semibalanus balanoides* is adapted to overcome this potential disadvantage showing territorial behaviour (Crisp, 1961) within aggregations. Whilst cyprids are attracted to settle next to existing barnacles by the gregarious response, the final settlement process involves a slight movement away from the settled specimen, perhaps via a tactile response on the part of the cyprid to a projection (Crisp, 1961, 1974). This territorial spacing usually provides space for growth (Crisp, 1961) which may involve some further pushing apart of individuals by the pressure of neighbours (Crisp, 1960), and reduces intraspecific competition. At very high settlement densities, competition for space is intense and the barnacles take up a tubular or trumpet-shape with little adhesive area abutting the substrate, with the consequent probability of being dislodged by wave action (Barnes and Powell, 1950).

#### *Attachment of the cyprid*

During exploratory behaviour prior to settlement the cyprid moves by using the paired antennules to walk in a stilt-like fashion. The third segment of the antennule has become adapted both as an adhesive disc and as a sensory probe with the sensory fourth segment arising laterally (Fig. 19) (Walley, 1969; Nott, 1969; Nott and Foster, 1969; Gibson and Nott, 1971). Unicellular glands (Fig. 20) secreting temporary adhesives open onto the disc surface at many points and cuticular villi on the disc may promote more efficient adhesion, with the ultimate proviso that the cyprid does need to detach each antennule again in order to progress (Walker, 1981). It has been observed (Crisp, 1975; Stubbings, 1975) that cyprids test substrate surfaces by placing the disc and then attempting to withdraw it. When the substrate is favourable the disc is less easily detached and the force of adhesion may play a role in the recognition of a suitable settlement site (Crisp, 1975). The settlement behaviour involves the apparent cleaning of the substrate before application of an adhesive disc (Crisp, 1975).

Once a settlement site has been selected, permanent cypris cement is released from each of a pair of cement glands in the body of the larva (Figs. 16, 20). The glands consist of two cell types which produce protein and protein together with phenols and polyphenol oxidase respectively (Walker, 1971). The secretions apparently mix after exudation and the presence of phenols and polyphenol oxidase indicates that some quinone tanning (cross linking of proteins) is occurring to bring about permanent setting of the cement (Walker, 1971, 1981). The cement passes via a muscular sac down a cement duct in the antennule which opens at several

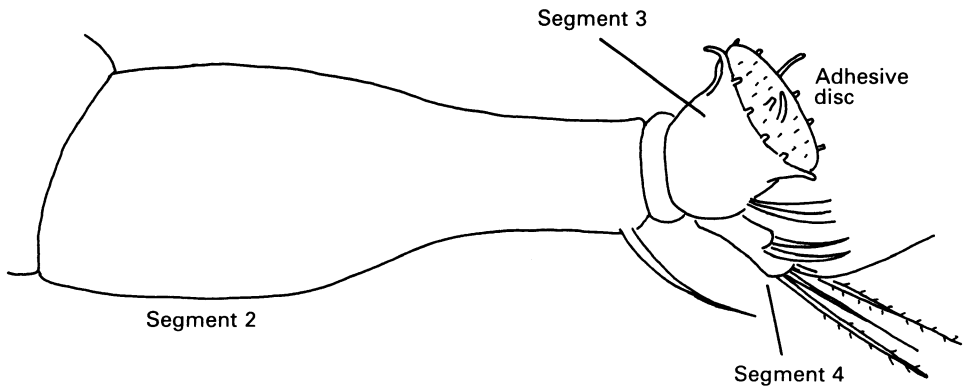


FIG. 19.

Antennule of a barnacle cyprid with adhesive disc and many sensory setae (after Nott and Foster, 1969).

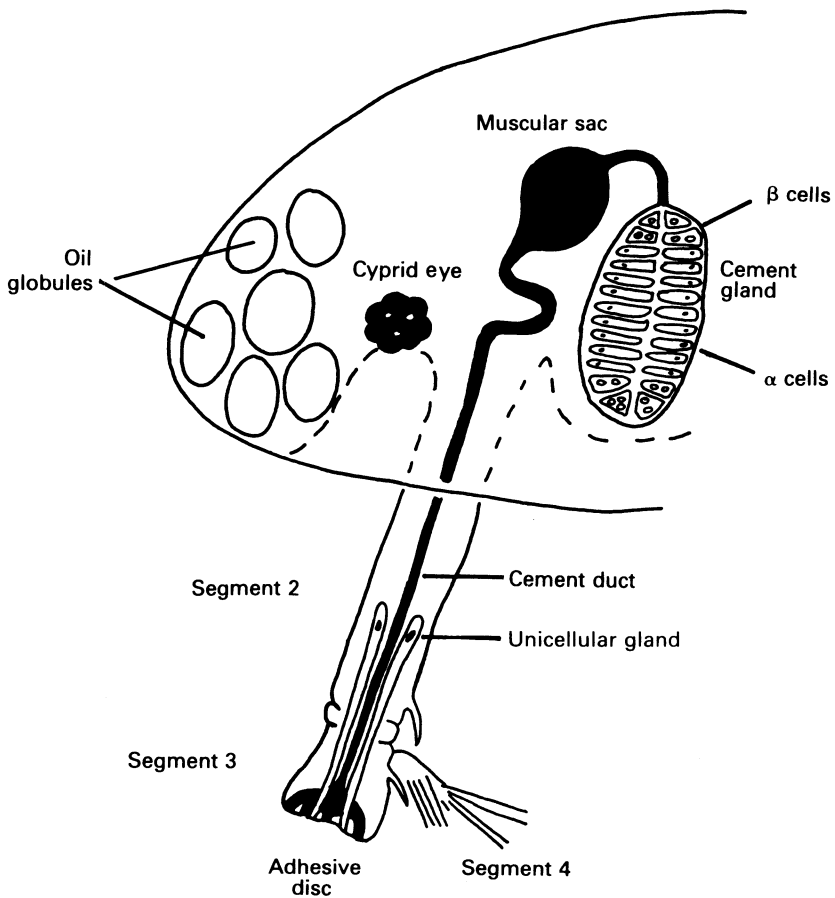


FIG. 20.

The cement system of a barnacle cyprid (after Walker, 1981).

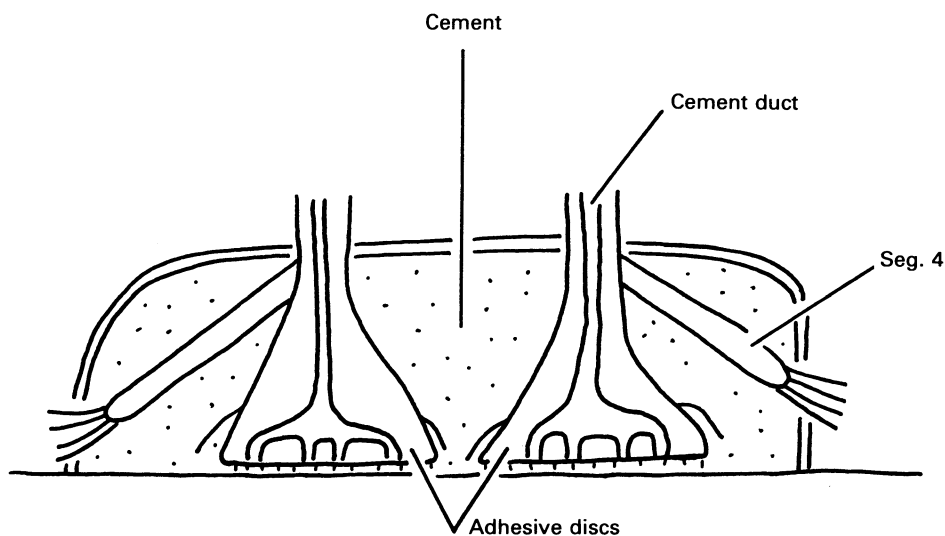


FIG. 21.

Cypris adhesion (after Walker, 1981). The adhesive discs of the antennules are embedded in cement secreted from the cement ducts.

points on the adhesive disc (Walker, 1971, 1981). Enough cement is produced to embed the discs and the adjacent fourth segment of the two antennules together (Fig. 21) (Walker, 1981). Cypris cement may only be exuded once, so defining a permanent settlement site, and serves to maintain the attachment of the metamorphosed barnacle until the adult cement system has developed sufficiently to produce new cement, about 40 days in *Semibalanus balanoides* (Walker, 1973).

Once permanently adhered, the cyprid metamorphoses into the juvenile barnacle. The cypris muscles histolyse and are ingested by phagocytic haemocytes whilst the nervous system and alimentary tract take up their adult form (Walley, 1969). The long axis of the thorax turns 90° in the vertical plane, the cypris carapace is cast off and the shell plates form as the barnacle assumes its adult structure (Walley, 1969).

The lipid reserves (Fig. 22) of cyprid are stored anteriorly in oil cells (Walley, 1969), around the midgut and at the bases of the thoracic limbs (Rainbow and Walker, 1977b) and decrease during the life of the cyprid (Holland and Walker, 1975). There is no opportunity to restock energy supplies until the newly metamorphosed barnacle is able to feed again after the completion of metamorphosis (Rainbow and Walker, 1977b) and the finite energy reserves accumulated during naupliar development eventually limit the time that may be spent by the cyprid in seeking a suitable settlement site. Lucas *et al.* (1979) have constructed the energy budget for a *Semibalanus balanoides* cyprid and have broken down the total energy content of the larva into three components (Fig. 23): (i) the energy equivalent of essential structures, (ii) the energy required to fuel metamorphosis into a functional juvenile barnacle from a settled cyprid and (iii) the remaining energy available to support planktonic dispersal and site selection during settlement. As can be seen from Fig. 23 a typical cyprid of *S. balanoides* has sufficient energy reserves to delay metamorphosis whilst seeking a settlement site for about three to four weeks before depleting those reserves too far to allow successful metamorphosis. The barnacle cyprid has a respiratory rate approximately one tenth of that of most marine invertebrate larvae (Crisp, 1976; Lucas *et al.*, 1979)—an adaptation capable of prolonging planktonic life ten fold. It is a feature of marine invertebrate larvae that the longer

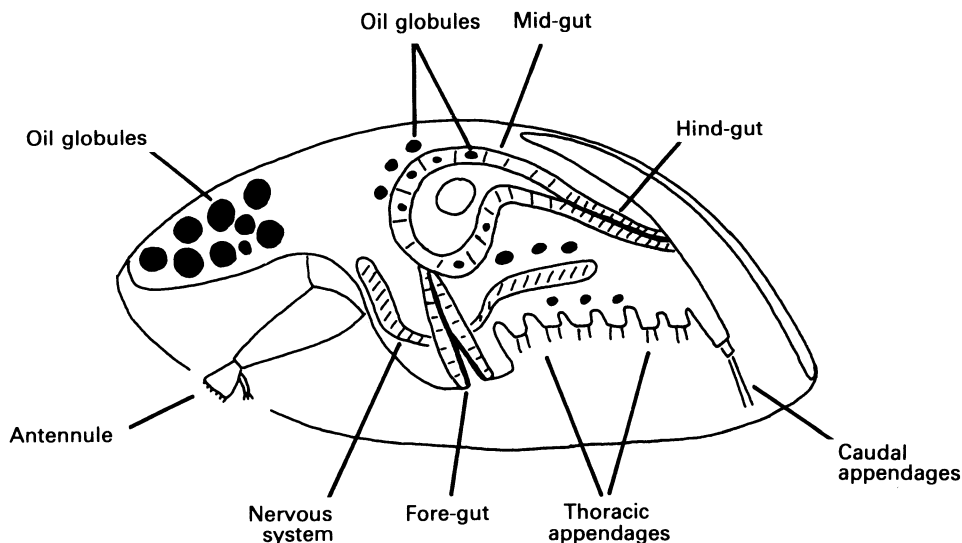


FIG. 22.

Anatomy of a barnacle cyprid (after Rainbow and Walker, 1977b).

that settlement is delayed, the less “choosy” larvae become as regards the preferred physical and chemical characteristics of the settlement site (Crisp, 1974).

#### *Parasites and epizoots*

The cryptoniscid isopod *Hemioniscus balani* is a widespread parasite of barnacles (Buchholz, 1896; Crisp, 1968; Arvy and Nigrelli, 1969). The adult isopod changes from male to female in the mantle cavity of the host and the ensuing female stage feeds firstly on the body fluids of the barnacle before turning to feed on the developing fertilised egg masses, itself changing into a yellow-orange bloated mass as it fills the mantle cavity of the barnacle (Crisp, 1968; Arvy and Nigrelli, 1969). Two genera of gregarine protozoans (Sporozoa) are common in the midguts of barnacles—*Cephaloidophora* and *Pyximioides* (Arvy and Nigrelli, 1969). It is unclear whether the species *C. communis* and *P. balani* are widespread or whether each barnacle host species contains a separate gregarine species. Another protozoan, the peritrich ciliate *Epistylis*, lives on the gills or mantle of barnacles (Arvy and Nigrelli, 1969). Metacercariae of trematode flatworms also occur in or near the gut of barnacles. These have been described as part of the life cycle of *Maritrema* with the sexually mature stages to be found in sea birds like gulls or terns (Hadley and Castle, 1940).

The epizotic lichen *Arthropyrenia sublittoralis* is common, blackening the shells of British midshore barnacles.

### BRITISH LITTORAL BARNACLES

The most common and ecologically important midshore barnacles on British shores are *Chthamalus montagui*, *Chthamalus stellatus*, *Semibalanus balanoides* and *Elminius modestus* (see Fig. 6) the classification of which is shown in Table 1 along with that of the other species. The classification of barnacles has recently been revised (Newman and Ross, 1976), and the enormous genus *Balanus* has been split into several taxa, many of which were previously recognised as natural groupings at the subgeneric level. The British barnacle previously

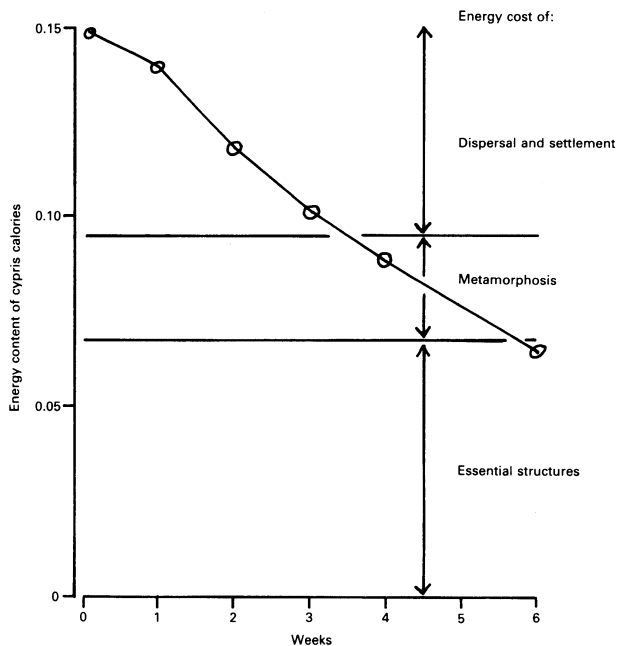


FIG. 23.

Energy budget of the non-feeding barnacle cyprid (after Lucas *et al.*, 1979).

known as *Balanus balanoides* is now named *Semibalanus balanoides* and is in a different family (the Archaeobalanidae) of the Balanoidea from that (the Balanidae) containing the genus *Balanus* itself (Newman and Ross, 1976).

A particularly important reappraisal of the genus *Chthamalus* was made by Southward (1976). *Chthamalus stellatus* was for a long time considered to be the only species of *Chthamalus* on British shores and indeed Darwin (1854) considered it to be distributed world-wide showing wide variation. Many of the barnacles described by Darwin (1854) as varieties of *C. stellatus* have now been recognised as separate species (Pilsbry, 1916; Southward, 1975) and Southward (1976) has shown that there are in fact two morphologically distinct species of *Chthamalus* on British shores, previously considered as environmental variants of *C. stellatus*:- true *Chthamalus stellatus* fitting the original description of Poli in 1791 and a "new" species *Chthamalus montagui*. The separation on morphological grounds has been confirmed by studies of enzyme polymorphisms (Dando *et al.*, 1979).

The ecological importance of the Australasian barnacle *Elminius modestus* is a feature new to British shores since it was first found in Chichester Harbour (near Portsmouth) in 1945 after introduction probably by shipping (Crisp, 1958). It is now widely distributed round the coasts of Britain and settlement has been reported in Shetland (Hiscock *et al.*, 1978).

### ***Chthamalus stellatus* and *Chthamalus montagui***

Much had been published on the ecology (e.g. Lewis, 1964) and other aspects of the biology (see Newman and Ross, 1976) of *C. stellatus* prior to 1976 when Southward showed that two separate species had been confused. Earlier work must therefore be viewed with caution particularly since much of it must have been carried out on what is now known as *Chthamalus montagui* or on mixtures of the two species.



*Chthamalus* species have a membranous base and solid shell plates (see Bourget, 1977). The rostral plate is not fused with the rostrolaterals (see Fig. 3). For this reason it is overlapped by the two plates lateral to it, in contrast to the balanoid arrangement of *Semibalanus* and *Balanus* where the observably distinct rostral plate consists of the rostrum fused with the rostrolaterals which overlap the neighbouring distinct shell plates—the laterals (Figs. 3, 5, 6). Only the first two pairs of cirri differ in structure from the other more posterior pairs and as such play no part in captorial feeding which is by passive extension into a current (Crisp and Southward, 1961).

There are clear morphological differences between *C. montagui* and *C. stellatus* (Southward, 1976) and they can be distinguished in situ with a little practice (see Fig. 6). The operculum of *C. montagui* is kite-shaped whilst that of *C. stellatus* is oval or subcircular; the line indicating the joint between the terga and scuta crosses the centre line less than one third of the way to the rostrum in *C. montagui* but one third or more of the way down in *C. stellatus*; the flaps of tissue around the opercular plates are blue or pale blue with brown and black markings in *C. montagui* but usually bright blue with orange and black markings in *C. stellatus* (Southward, 1976). Both species are up to 1 cm in basal diameter.

There are also ecological differences for, although the two species overlap in their vertical distribution, when they occur together *C. montagui* is usually commoner in the upper barnacle zone (see Lewis, 1964) whilst *C. stellatus* dominates lower down (see Fig. 24) (Southward, 1976; Crisp *et al.*, 1981). The two species overlap extensively in their geographical range but *C. montagui* is more common in more embayed sheltered situations where it seems better adapted to the richly particulate conditions of coastal waters whilst *C. stellatus* favours wave-beaten blue water open coast sites (Southward, 1976; Crisp *et al.*, 1981). Both species of *Chthamalus* are western and southwestern species and their distributions are limited principally by temperature to the coasts of Ireland and the warmer coasts of England, Wales and Scotland (after Lewis, 1964). *C. stellatus* occurs on the west coast of Shetland and on Herma Ness, Shetland's most northerly accessible headland (Crothers, personal communication). Both species are absent east of the Isle of Wight on the south coast and south of Aberdeen in Scotland on the east coast (Crisp *et al.*, 1981). As "southern" species (after Lewis, 1964) both are also found down the west coast of France, on Portuguese, Spanish and north African coasts and in the Mediterranean (Crisp *et al.*, 1981).

Features of the physiology and behaviour of the two species are to be investigated but they appear very similar (Crisp *et al.*, 1981). Specimens of both from south-west Britain are active over the same range of temperatures; differences in pumping activity (see Crisp and Southward, 1961) between the two are within the range of variation of either species and both species will extend their cirri under the stimulation of similar velocities of water flow (Crisp *et al.*, 1981). A slight difference is that *C. stellatus* is more ready than *C. montagui* to open the opercular valves when wetted by splash, the increased wariness of the latter perhaps being associated with its higher position on the shore and greater risk of desiccation (Southward, 1976). Both species breed in the summer in south-west Britain, the presence of ripe egg masses peaking in July and August (Crisp *et al.*, 1981).

When considering the similarities between *C. stellatus* and *C. montagui* in terms of distribution, habitat, physiology and reproductive biology, Crisp *et al.* (1981) have suggested that it is difficult to explain their evolution in Darwinian terms if they are sibling species. The differences in isoenzymes (Dando and Southward, 1980) and morphology (Southward, 1976) indicate, however, that the two species are not immediately related but are separate at the subgeneric level, and that the similarities in ecology and behaviour may be due to convergent evolution in adapting to similar climatic and environmental conditions (Crisp *et al.*, 1981).

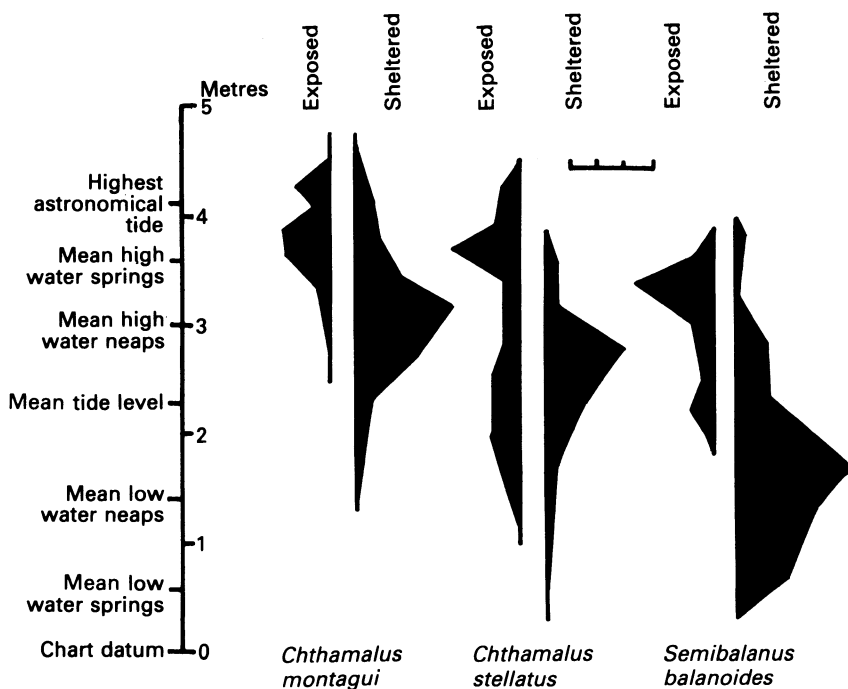


FIG. 24.

The vertical distribution of *Chthamalus montagui*, *Chthamalus stellatus* and *Semibalanus balanoides* at Sherkin Island (Ireland) plotted as height in metres above chart datum (after Crisp *et al.*, 1981). Scale bar shows number per cm<sup>2</sup>.

*C. montagui* may have evolved from a northern temperate ancestor whilst *C. stellatus* may be related to a group of tropical and subtropical species (Crisp *et al.*, 1981).

Moyse and Knight-Jones (1967) have shown that the nauplii of (undistinguished) British *Chthamalus* feed on planktonic flagellates characteristic of nutrient-poor warmer and oceanic waters and common in British waters in the summer, being replaced in spring and autumn by diatoms which are major constituents of algal blooms in more nutrient-rich temperate seas. The season of larval release and the distribution of the *Chthamalus* species on southerly, westerly (oceanic) coasts of Britain correlate then with the feeding biology of the larvae.

Settlement of the cyprids takes place in the autumn, beginning in September (Bassindale, 1964), but shows fluctuation from year to year. No settlement of *C. montagui* was recorded on Anglesey and the north coast of the Lleyn peninsula (north Wales) in 1974 or 1975 although a few settled in the September of each of the next four years, whilst large numbers of the same species settled on the south side of the Lleyn peninsula in most years of this period (Bennell, 1981). No *C. stellatus* settlement was detected at any of several sites in north Wales from 1974 to 1979 (Bennell, 1981). No *C. stellatus* juveniles have been found by the author at Manorbier, Pembrokeshire, in the period 1978–1982 nor at Hurlstone Pt. (Somerset) during 1976–1982 by J. H. Crothers (personal communication) although large specimens are present.

### *Semibalanus balanoides* (formerly *Balanus balanoides*)

*S. balanoides* is the most widespread British intertidal barnacle, being present right round the coasts of the British Isles except on restricted southerly portions of the Irish and Cornish

coasts (Lewis, 1964). It is a boreoarctic (hence northern) species found on both sides of the north Atlantic (genetically separate races, see Flowerdew and Crisp (1975)) and on the northern Pacific coast of north America (Pilsbry, 1916; Barnes, 1958) to which it may have migrated via the Bering Strait (Barnes, 1958; Lewis, 1964). Its northern limits are closely paralleled by the summer limits of pack ice (Barnes, 1957a). The southern-most limits of the distribution of *S. balanoides* in Europe are represented by limited localities in north-west Spain, the major environmental factor limiting the southerly spread of the species in Europe probably being high temperatures which principally prevent final maturation of the gametes but may also affect adult survival in the summer (Barnes, 1958; Lewis, 1964). On American coasts competition from warm temperate *Balanus* species additionally plays an important part in restricting the southward spread of *S. balanoides* (Barnes, 1958).

As in other balanoids (see Table 1) (Fig. 5), *S. balanoides* has a rostral plate which has fused with the rostrolaterals and therefore overlaps the lateral plates (Figs. 3, 6). In both *Semibalanus* and *Balanus* the shell plates are not laid down as a solid wall but are tubiferous with empty spaces (longitudinal canals) running vertically (see Fig. 11), although in *S. balanoides* the spaces are secondarily filled (Darwin, 1854; Pilsbry, 1916). The shell plates are two layered and a sheath is present for the attachment of the flaps of tissue around the operculum (Bourget, 1977). In *S. balanoides* these flaps of tissue are mostly white sometimes tinged with pink (Southward, 1976). The operculum is diamond-shaped and can be used to

Table 1. *Classification of British littoral barnacles (after Newman and Ross, 1976)*

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Subclass Cirripedia
Order Thoracica
Suborder Verrucomorpha
Family Verrucidae
<i>Verruca stroemia</i> (Müller)
Suborder Balanomorpha
Superfamily Chthamaloidea
Family Chthamalidae
Subfamily Chthamalinae
<i>Chthamalus montagui</i> Southward
<i>Chthamalus stellatus</i> (Poli)
Superfamily Balanoidea
Family Archaeobalanidae
Subfamily Archaeobalaninae
<i>Elminius modestus</i> Darwin
Subfamily Semibalaninae
<i>Semibalanus balanoides</i> (L.)
Family Balanidae
<i>Balanus balanus</i> (L.)
<i>Balanus crenatus</i> Bruguière
<i>Balanus improvisus</i> Darwin
<i>Balanus perforatus</i> Bruguière
<i>Balanus amphitrite</i> Darwin
Order Rhizocephala
Suborder Kentrogonida
Family Peltogastridae
<i>Peltogaster paguri</i> Rathke
Family Sacculinidae
<i>Sacculina carcini</i> Thompson

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identify the barnacle on the shore (see Fig. 6) (Southward, 1976). In comparison with *Chthamalus* species, *S. balanoides* is whiter especially in its first year of growth before colonisation by lichens or algae (Lewis, 1964). Unlike *Balanus*, *Semibalanus* has a membranous not a calcareous base (Newman and Ross, 1976), which usually reaches about 12 mm in diameter, when the height of the barnacle is about 8 mm.

*Semibalanus balanoides* is a dominant member of the eulittoral zone of British rocky shores (Lewis, 1964), although it is replaced on sheltered shores by brown (fucoid) seaweeds (Ballantine, 1961). It typically occurs lower on the shore than either *Chthamalus* species, although the distributions do overlap and on very wave-washed shores *C. stellatus* extends below *S. balanoides* (Crisp *et al.*, 1981) (see Fig. 24). It is not possible to generalise the limits of the distribution of any organism with respect to tidal levels over a number of shores for, as Lewis (1964) has shown, any increase in wave exposure between shores will widen the distribution of intertidal organisms thereon.

*Semibalanus balanoides* feeds both by captorial feeding on zooplankton and by microfeeding (Crisp and Southward, 1976), microfeeding being secondary in importance (Anderson, 1981). The first three pairs of cirri of balanoids are alike and differ in structure from the more posterior pairs. When carrying out captorial feeding, *S. balanoides* can beat rhythmically either by normal beat (cirri fully extended and withdrawn into the mantle cavity in rhythm) or by fast beat (fast rhythmical beating of the cirri without full withdrawal of the larger cirri). When stimulated by a current *S. balanoides* will hold its cirri fully extended for varying periods, the time of extension increasing with current velocity (Crisp and Southward, 1961).

*S. balanoides* is adapted to temperate seas and shows a marked seasonal effect in feeding rate which peaks during spring and autumn (Ritz and Crisp, 1970) when planktonic food levels are high. Little, if any, feeding takes place in the winter when little food is available and the barnacles rely on stored food reserves (Barnes *et al.*, 1963; Ritz and Crisp, 1970; Rainbow and Walker, 1977a). *S. balanoides* similarly shows seasonal variation in moulting rate which is affected by food intake and temperature, falling sharply in November when the barnacles start a period of anecdysis for six to eight weeks before resuming moulting again at a slow rate (Crisp and Patel, 1960). Moulting rate, like feeding rate (Ritz and Crisp, 1970), peaks in the spring, decreases in the summer (June to August) and rises again before November (Crisp and Patel, 1960).

The reproductive biology of *S. balanoides* is similarly adapted to a temperate environment. Lipid droplets and glycoprotein globules are lost from the body during the summer, apparently to the ovaries in the mantle where they form the yolk of developing eggs (Rainbow and Walker, 1977a). After loss of the penis at the first moult of the year in spring a new penis develops during the summer and reaches its maximum length by the onset of the breeding season (Crisp and Patel, 1960). Crossfertilisation is obligatory and copulation occurs in November and early December. In *S. balanoides* more than one functional male may be involved in copulation of a single functional female and multi-insemination is essential to fertilise all the eggs laid (Walker, 1980b).

The fertilised eggs are held in two egg masses in the mantle cavity over winter when the barnacle is in anecdysis, hatching in synchrony with the spring algal bloom (Crisp, 1956; Barnes, 1957b) between February and April, release occurring later in the north and east of Britain (Crisp, 1962), or even as late as midsummer at Spitzbergen (Barnes, 1957a). Hatching is promoted by the secretion into the mantle cavity of a "hatching substance" (a prostaglandin-like compound (Clare *et al.*, 1982) secreted by the tissues of the barnacle following ingestion of food (Crisp, 1956; Crisp and Spencer, 1958)). Synchrony of larval release with the spring algal bloom is an adaptation ensuring that the nauplii grow and develop under

prime conditions of food supply for in temperate and polar seas phytoplankton growth is seasonally discontinuous. Phytoplankton is only available for limited periods in sufficient concentration to repay the high energetic cost of suspension feeding and allow for growth and development. The algal blooms in temperate and polar regions are dominated by diatoms; the planktotrophic nauplius larvae (stages II to VI) of *S. balanoides* which feed on diatoms (Rainbow and Walker, 1976, 1977b), are correspondingly well adapted to planktonic life in boreoarctic conditions. Diatom-filtering larvae hatching before the spring bloom would starve and those hatching late would not have time to build up sufficient lipid reserves to support cyprid dispersal, settlement and metamorphosis (Rainbow and Walker, 1976; Lucas *et al.*, 1979). Stage VI nauplii of *S. balanoides* appear in the plankton about two months after the release of stage I. They moult into cyprids which drift and swim in the plankton for up to two to three weeks before choosing a site for settlement and metamorphosis (Lucas *et al.*, 1979), peak settlement occurring in April to May in the west and in May to June in the east and north of Britain (Crisp, 1962).

Barnes (1957a) concluded that the important factor in determining the northern limits of the distribution of *S. balanoides* is the time period available for naupliar development, cypris settlement and some spat growth. This period is that between the melting of winter ice associated with the diatom bloom and synchronised nauplius hatching, and the reformation of the ice (Barnes, 1957a).

Cypris larvae of *S. balanoides* show both gregarious and territorial behaviour (Crisp, 1961). Settlement of the cypris larvae shows considerable local variation in timing and density, being affected by chance meteorological factors such as wind speed and direction (Bennell, 1981; Hawkins and Hartnoll, 1982). Contrastingly strong onshore winds promoted settlement of *S. balanoides* at Port St. Mary, Isle of Man (Hawkins and Hartnoll, 1982) but along the north coast of Anglesey settlement was heaviest when the wind was offshore and the sea calm (Bennell, 1981).

Many cyprids do not survive initial settlement. The causes of mortality include heavy wave action, limpet grazing, overcrowding and desiccation (Bennell, 1981). The barnacles grow rapidly in the first season after settlement until the winter when little growth occurs. Submerged specimens in the Firth of Clyde, able to feed irrespective of the state of the tide, reached 17.2 mm along the carino-rostral axis after one season, 25.8 mm and 26.3 mm after two and three seasons (Barnes and Powell, 1953). The shell shape in isolated individuals of *S. balanoides* changes considerably during early growth, taking up the adult shape only when 3 mm long (Bourget and Crisp, 1975b). The newly metamorphosed barnacle is very squat and the shape during the earliest growth may maximise adhesion and minimise drag of water currents on the shell whilst directing water flow into the cirral net (Bourget and Crisp, 1975b). The growing barnacle may also gradually reorientate the shell to come into a more favourable filtering position with respect to the current (Crisp and Stubbings, 1957). The animal can also twist its body in the shell to "fish" into the current stream (Stubbings, 1975). Longevity varies with shore position and geographical location. In the Isle of Man *S. balanoides* low on the shore died in their third year whilst those near the mean level of high water neap tides lived for five or six years (Moore, 1934).

### ***Elminius modestus***

Although *Elminius modestus* is now a common inhabitant of the mid and lower shore around the British Isles, it is Australasian in origin and was first noticed in Britain in 1945 in Chichester harbour and in the Thames estuary (Bishop, 1947). It is believed to have been introduced into the Chichester area by shipping during the early years of the second world

war (Stubbings, 1950) and has since spread further through shipping and by natural drift of larvae along the coast (Crisp, 1958; Lewis, 1964).

*Elminius modestus* is easily recognised from the other British intertidal barnacles for it has only four parietal shell plates around the paired opercular plates (Figs. 3, 6), and it is usually a slatey-grey colour. As in the case of *Chthamalus* and *Semibalanus*, *E. modestus* has a membranous base (reaching 1 cm in diameter). The shell plates are two-layered as in *Semibalanus* and *Balanus* but solid and not tubiferous (Bourget, 1977). As in other balanoids, the anterior three pairs of cirri are differentiated from the posterior three and *E. modestus* can carry out both captorial and microfeeding. In fact *E. modestus* mainly feeds captorially on zooplankton showing very active cirral rhythms with emphasis on fast beat (Crisp and Southward, 1961; Anderson, 1981).

*Elminius modestus* is a euryhaline, sheltered coast species able to tolerate salinity fluctuations in the typical manner of intertidal barnacles by closure of the opercular valves at a particular external salinity (Foster, 1970; Davenport, 1976). Specimens from the Menai Strait (North Wales) ceased cirral activity and closed down at a dilution of about 66% seawater reached in a realistic gradual decline, restoring activity at 58% seawater (Davenport, 1976). *E. modestus* also shows non-genetic behavioural adaptations to estuarine conditions, increasing its period of inactivity (Davenport, 1976).

*Elminius modestus* grows very rapidly and may reach maturity at a basal diameter of six to seven millimetres in as little as eight weeks (Crisp, 1958). The feeding rate is about double that of native intertidal species at 20°C (Crisp, 1958), its tolerance of high water temperature presumably being a reflection of its Australasian origin as a temperate to warm-water species (Foster, 1967). It does not show a restricted period of larval production and development, but produces broods of nauplii at regular intervals—about every ten days under optimum conditions (Crisp and Davies, 1955). *E. modestus*, therefore, is able to remove food from suspension and transform it into large numbers of dispersive larvae in a very short time, particularly in the summer (Crisp, 1958), a feature assisting its rapid dispersal round Britain. The main disadvantage of this strategy of larval release (as opposed to that of *S. balanoides*) is that many larvae will not obtain sufficient phytoplankton to fuel larval development, settlement and metamorphosis, particularly in the winter when the phytoplankton levels in temperate seas are especially low.

Larvae of *E. modestus* may therefore be found in the plankton at all times of the year, and are particularly common in the summer, for example in the estuaries of south-east England (Knight-Jones and Waugh, 1949; Crisp, 1958). In the Menai Strait *Elminius* cyprids settle at most times of the year, perhaps in greatest abundance in late summer and early autumn (Bennell, 1981). A peak of *E. modestus* successful settlement on Anglesey took place in July, August and September in 1974, 1976, 1978 and 1979, but in 1975 and 1977 successful settlement was heaviest between October and December (Bennell, 1981). The successful planktotrophic development of *Elminius* larvae, which are produced more or less continuously, is probably directly linked with the presence of suitable food and the absence of competitors. Well adapted boreoarctic marine invertebrates have evolved larval development strategies to exploit the annual spring diatom outburst or the less regular autumn bloom and may outcompete *E. modestus* at these times of year, either in the plankton or post settlement. *E. modestus* larvae gain when temperate planktonic levels unpredictably reach threshold levels at other times of the year or further south, where the discontinuous phytoplankton peaks are less distinctly demarcated in time.

During settlement *E. modestus* cyprids show gregarious behaviour but not territorial behaviour to avoid settling in contact with their own adults (Moyse and Hui, 1981; Hui and Moyse,

1982). In the field then *E. modestus* will settle on top of other established barnacles including their conspecifics. Such substrates are relatively impermanent but *E. modestus* do grow rapidly to maturity and therefore still have a good chance of successful reproduction (Hui and Moyses, 1982).

### ***Balanus perforatus***

*Balanus perforatus* is a massive purple barnacle growing at the bottom of the eulittoral zone and below on shores in south-west England and Wales, reaching its northern and eastern limits in Pembrokeshire and the Isle of Wight respectively (Lewis, 1964). It is common on wave-exposed shores and although its basal diameter reaches 3 cm and its height 2–3 cm (Bassindale, 1964) it may be obscured by the growth of red algae (Lewis, 1964).

*Balanus perforatus* shows the typical features of the genus (Newman and Ross, 1976). It has a calcareous base, tubiferous shell plates (although canals become secondarily filled (Darwin, 1854; Bourget, 1977) and a rostral plate fused with the rostrilaterals, the composite plate therefore overlapping the adjacent lateral plates. Isolated specimens of *B. perforatus* are volcano-shaped, and the terga have beaked points at the top; flaps of tissue round the opercular plates are brightly coloured by patches of purple, blue, pink and white (Southward, 1976).

*Balanus perforatus* is capable of rhythmic captorial feeding and of microfeeding using the first three pairs of cirri to filter the mantle current, but its mode of cirral beating differs from that described for other species in the study of Crisp and Southward (1961) (Anderson, 1981). Although capable of capturing zooplankton, *B. perforatus* is primarily highly adapted as a current-producing filterfeeder; the swinging of the body causing a current to flow through the mantle cavity, entering rostrilaterally, passing over the branchiae and exiting at the carinal end where it is filtered by the three anterior pairs of cirri (Anderson, 1981). *B. perforatus*, therefore, feeds mainly on small food items up to 1 mm and the anterior cirri are elaborately supplied with setae in comparison with those of *Semibalanus balanoides* (Anderson, 1981).

Copulation of *Balanus perforatus* in Britain takes place in the summer beginning in June and continuing until August (Norris and Crisp, 1953). The fertilised egg masses are held in the mantle cavity for less than a month and early stage larvae are present in the plankton from late June until August; settlement of the cypris larvae taking place from late July to September (Norris and Crisp, 1953). *B. perforatus* nauplii can feed on small flagellates (Lochhead, 1936), thanks, perhaps, to a fringe of setae on the antennal expodite—a feature absent from larvae of *S. balanoides* which feed on larger diatoms (Rainbow and Walker, 1976). The larval feeding pattern of *B. perforatus* is therefore similar to that of the two *Chthamalus* species which are similarly restricted to the warmer parts of Britain and extend south into the Mediterranean.

### ***Balanus crenatus***

*Balanus crenatus* is the commonest British sublittoral barnacle, and is also found growing under stones or in crevices at the bottom of the eulittoral zone (Bassindale, 1964; Southward, 1976). It is widely distributed sublittorally throughout the northern hemisphere (Bassindale, 1964) but its southern limit on the shore in the eastern Atlantic is on the coast of France (Lewis, 1964). *B. crenatus* has a white shell, normally conical in shape with a rostro-carinal length reaching about 2.5 cm (Barnes and Powell, 1953). The tops of the shell plates are sharply edged to give a finely notched appearance (hence “crenatus”). The base is calcareous and may remain attached for some time after death of the barnacle and disintegration of the shell. The opercular flaps of tissue are striped yellow (or dirty white) and purple along their length (Southward, 1976).

Nauplii are released from February to September, peaking in spring and late summer (Bassindale, 1964), when phytoplankton levels are highest. Settlement begins at a maximum level in April and continues at a declining rate until late October (Bassindale, 1964). Larval *B. crenatus* do not, therefore, appear to be so keyed into the spring bloom as *S. balanoides* but they are able to utilise the autumn plankton peak and any summer populations of phytoplankton sufficiently concentrated to allow naupliar growth and development. *B. crenatus* in the Firth of Clyde grow rapidly except in winter. The lifespan is about eighteen months, and an April-settled individual may liberate larvae the same July and reach maximum size before their first winter (Barnes and Powell, 1953; Bassindale, 1964). Later settling individuals reach full size by the end of the spring of their second year (Barnes and Powell, 1953).

### ***Balanus improvisus***

*Balanus improvisus* typically occurs low on the shore and sublittorally in estuaries and is similar in appearance to smooth specimens of *B. crenatus*, although it lacks the finely notched appearance at the top of the shell plates, has a somewhat narrower diamond-shaped operculum and the opercular flaps of tissue are speckled white and pink or purple (Southward, 1976). It is normally up to 1.3 cm in basal diameter (Bassindale, 1964).

*B. improvisus* is very widespread around the Atlantic, and has been spread by shipping to the Indo Pacific and Australasia. It is very tolerant of low salinity and is the only barnacle found on the coast of Finland in the Baltic. *B. improvisus* from the Conway estuary, Wales, stayed active in salinities fluctuating as low as 20‰ seawater, only closing the opercular valves if exposed to salinity fluctuations descending to 0‰, perhaps in response to the rate of fall of salinity (Davenport, 1976; Cawthorne, 1979). Specimens of *B. improvisus* from the Swedish Baltic were most active during the low salinity phase of a cycle of salinity fluctuating between 100‰ and 20‰ seawater (Davenport, 1976). It can be concluded that the behaviour of individual *B. improvisus* in low salinity is dependent on the salinity regime to which they have been accustomed (Davenport, 1976), and that the species is impressively tolerant of low salinities (Foster, 1970; Davenport, 1976).

Nauplii of *B. improvisus* are released from May until late September in British estuaries (Jones and Crisp, 1954) and settlement of the cypris larvae occurs over the same period (Bassindale, 1964).

### ***Balanus balanus***

*Balanus balanus* is a large, usually sublittoral, barnacle occasionally found at the bottom of the shore, particularly in Scotland. It is a boreoarctic Atlantic species not found south of the English Channel in the east, but reaching further south to Long Island Sound on the west side of the Atlantic (Bassindale, 1964). The shape of *B. balanus* is steeply conical and the base may exceed 4 cm in diameter with the height almost the same (Bassindale, 1964).

*B. balanus* has a slow rhythm of cirral beating which appears to emphasise captorial planktivory (Crisp and Southward, 1961; Anderson, 1981). Body weight and biochemical composition follow a seasonal cycle closely related to the availability of food (Barnes *et al.*, 1963). Body weight increases rapidly with the spring diatom bloom, doubling in two months, before, in early summer, metabolised food is transferred to the ovaries in the mantle. Body weight then rises rapidly throughout late summer and autumn as the testes develop until copulation takes place in early February with a coincident 50% fall in body weight when the semen is shed (Barnes *et al.*, 1963). The single annual batch of nauplii is liberated in about mid-March (later in the east and north) and the cyprids settle about a month later (Crisp, 1962; Bassindale, 1964). *B. balanus* is therefore, like *S. balanoides*, able to exploit the spring bloom



of temperate waters for larval development and, since the larvae of the two species are similar in appearance and size (Crisp, 1962), it would not be surprising if *B. balanus* nauplii also feed only on diatoms.

### ***Balanus amphitrite***

*Balanus amphitrite* is one of the most widespread fouling barnacles of the world, very common on ships and in harbours in warm temperate and tropical water. *B. amphitrite* occurs at low water and below but in Britain it is restricted to ports and estuaries warmed by heated effluent discharged from power stations as in Shoreham Harbour Canal and Swansea Docks (Crisp and Molesworth, 1951; Bassindale, 1964; Southward, 1976). It has a conical shell up to one centimetre in diameter with regular red or purple stripes on the otherwise white plates, and the opercular flaps of tissue are white crossed by three bands of black or purple (Bassindale, 1964; Southward, 1976).

Copulation in *B. amphitrite* occurs from March to September and cypris settlement between May and August (Crisp and Molesworth, 1951) with larvae released later in the season, presumably being unable to complete development.

### ***Verruca stroemia***

*Verruca stroemia* belongs to a suborder of barnacles (the Verrucomorpha) separate from that (the Balanomorpha) which includes all the sessile barnacles already described. Like the balanomorphs, the verrucomorphs have evolved from the stalked barnacles (the Lepadomorpha) and have lost the stalk. Unlike them, however, the shells of living verrucomorphs are asymmetrical. One scutum and one tergum are incorporated into the shell wall along with the rostrum and carina, leaving the other tergum and scutum to form a moveable lid like a trapdoor. Essentially an eastern North Atlantic species, *V. stroemia* is mainly sublittoral, often attached to mollusc shells, but can be found round Britain at the bottom of the shore usually under stones (Stone and Barnes, 1973). It has a flattened appearance and reaches about 1 cm in diameter (Bassindale, 1964).

*V. stroemia* can carry out rhythmic cirral beating and prolonged cirral extension in a water current, yet still retains the primitive lepadomorph mechanism of prey capture by a single cirral ramus, capturing prey in the 0.25–0.50 mm range (Anderson, 1980). Supplementary to this carnivorous captorial feeding, *V. stroemia* is also capable of microphagous feeding using the first three pairs of cirri (Anderson, 1980) which although distinct from the more posterior cirri also differ from those of the balanoids (Stone and Barnes, 1973; Anderson, 1980). *V. stroemia* is apparently the only verrucomorph barnacle capable of rhythmic cirral beating for its relatives living in the deep sea show only prolonged cirral extension. Since the rhythmic beating is based on a mechanism different to any described in the balanoids, it has probably been independently evolved along with microphagy, perhaps as an adaptation to a shallow water habitat (Anderson, 1980).

Although larvae of *Verruca stroemia* are present in the plankton of the Firth of Clyde (Millport) throughout the year (Pyefinch, 1948) there is a major brood, virtually synchronous throughout the population, released in late February and early March at the time of the spring diatom bloom (Barnes and Stone, 1973). Larval release in lesser amounts continues during the summer (Barnes and Stone, 1973) but the absence of sufficient food prevents breeding in autumn and early winter (Barnes and Barnes, 1975). Isolated individuals of *V. stroemia* are capable of self-fertilisation but cross-fertilisation is normal (Barnes and Crisp, 1956), the major fertilisation period being early January to early February at Millport (Barnes and Stone, 1973). Settlement usually occurs from the end of April to September (Bassindale, 1964).

## ZONATION OF BRITISH INTERTIDAL BARNACLES

*A. Introduction*

Although the cypris larvae of intertidal barnacles respond to many subtle factors in choosing a settlement site for metamorphosis and subsequent adult growth, the larvae still settle over a wider area of the shore than that occupied by the adults. The upper limits of the intertidal distribution shown by organisms of marine origin (like barnacles) are set by their degree of tolerance to physical parameters experienced during emersion. These include the rate of desiccation and the wider range of temperature. Variations in one physical parameter may have more than one effect. An increase in air temperature for example will also increase desiccation rate. Physical factors like temperature, humidity and windspeed all interact to affect the emersed barnacle, and their effects will be modified by local topographical features such as shore aspect, rock type, surface contour, surface roughness and the other determinants of microclimate (see Lewis (1964) for more details). The upper limit to the distribution of the various barnacle species will therefore vary between shores according to the local characteristics. A major factor controlling this limit is the degree of wave exposure (Lewis, 1964). An increase in the exposure will raise the upper limits of intertidal organisms relative to tidal height and datum levels, as increased spray and wash moderate the influence of the terrestrial environment (Lewis, 1964). This exposure effect is inversely related to tidal range, waves of a given size having a more significant effect in areas of small ranges.

The lower limits of the distribution of intertidal organisms including barnacles are set by biological not physical factors. These factors include competition for space (for attachment and growth) and predation. On sheltered shores and at the bottom of most shores brown and red algae grow rapidly and smother the barnacles.

*B. Tolerance of British intertidal barnacles to variable physical parameters*

1. *Desiccation*: Table 2 provides data extracted from Foster (1971a) on the desiccation of several British intertidal barnacles. *Chthamalus* is clearly the most resistant to desiccation as befits its high position on the shore, *Elminius modestus* and *Semibalanus balanoides* are remarkably similar in their permeability and survival time whilst *Balanus crenatus*, found at the bottom of the shore and not forming a micropyle, loses water most rapidly and dies soonest. It is noticeable that small barnacles, especially newly metamorphosed spat, are at particular risk of desiccation. Spat of all the barnacles except *Chthamalus* may even come close to severe desiccation problems in a single period of tidal emersion under good drying conditions. *Chthamalus* tolerates long periods of desiccation because of the low permeability of its shell plates and at the point of death had not dried out any more (with concomitant increase in the osmotic pressure of body fluids) than the other barnacle species (Table 2). *Chthamalus* in this case may have been killed by toxic metabolic waste accumulated in the mantle cavity as a result of anaerobiosis after closing of the micropyle to reduce desiccation after aerial respiration (Barnes *et al.*, 1963; Barnes and Barnes, 1964).

Foster (1971b) has reported observations on the distribution, water content and survival of barnacles in the field in an attempt to evaluate the ecological significance of the results of relevant laboratory experiments. He concluded that death as a result of desiccation at high shore levels can and does occur in the cases of *Elminius modestus* and *Semibalanus balanoides*, but that *Chthamalus* is not so affected.

2. *High temperature*: The most commonly used measure of tolerance to high temperatures in barnacles has been the "upper lethal temperature" (ULT)—the water temperature at which 50% of the population are killed when the temperature is raised at a defined rate

Table 2. *Desiccation in British intertidal barnacles (after Foster, 1971a). MLT=Median Lethal Time. For derivation of relative permeability see Foster (1971a).*

(a)			
Species	Spat at 18°C	Adults at 19°C	
	MLT (hr)	Diameter (mm)	MLT (hr)
<i>Chthamalus</i> sp.	48	6	165
<i>Elminius modestus</i>	7	6	46
<i>Semibalanus balanoides</i>	6	5	45
		11	92
<i>Balanus crenatus</i>	3.5	6	17
		11	40
(b)			
Species	Relative	% water lost	% water lost
	permeability	from blood at MLT	from body at MLT
<i>Chthamalus</i> sp.	0.0012	49	40
<i>Elminius modestus</i>	0.0070	65	53
<i>Semibalanus balanoides</i>	0.0069	80	64
<i>Balanus crenatus</i>	0.0122	60	49

(Foster, 1969). Such a measure is useful for comparative purposes but is too high to have any direct ecological significance (Foster, 1969). From Table 3 it can be seen that *Chthamalus* is most tolerant to high temperature, then *E. modestus* and *B. perforatus* with the more northerly species *S. balanoides*, *B. crenatus* and *B. balanus* following. These results correlate not only with height on the shore but also with geographical distribution, *E. modestus* being mid-shore and temperate to warm-water in origin (Foster, 1967), *Chthamalus* and *B. perforatus* being restricted to warmer coasts with *Chthamalus* able to extend the furthest up the shore. Of the northern species *S. balanoides* extends much the furthest into the intertidal zone. The higher ULT apparent at the more rapid heating rate (Table 3) may be an effect of a temperature lag between barnacles and water at high heating rates and/or the cumulative effect of longer exposure to sublethal but stressful temperatures when heated more slowly (Foster, 1969).

In a more ecologically significant comparison, temperatures of 36° and 38°C, if held for a full six hours as during low tide at midtide level, would cause 50% mortality in *S. balanoides* and *E. modestus* respectively (Foster, 1969). Such temperatures may not be exceptional on intertidal substrates during emersion on fine days in the British Isles (Foster, 1969).

In *Elminius modestus* and *Balanus crenatus* temperature tolerances were the same in summer and winter but in the case of *S. balanoides*, although the upper lethal temperature did not vary seasonally, the barnacles were more susceptible in winter to prolonged exposure to high temperatures a little lower than the ULT (Foster, 1969).

3. *Low temperature*: Data on tolerance of low temperatures are available for only one British intertidal barnacle—*Semibalanus balanoides*. The lower median lethal temperature, defined as the temperature at which 50% of the population were killed after an 18 hour exposure in air, of *S. balanoides* varied from -17.6°C in January to -6.0°C in June (Crisp and Ritz, 1967). Therefore, tolerance to low temperature like tolerance to high temperature

Table 3. *Immersed upper lethal temperature (ULT see text) of British barnacles (after Foster, 1969). Sources: (1) Southward, 1958 (2) Crisp and Ritz, 1967 (3) Foster, 1969.*

Species	Stage	ULT for 50% mortality heated at:	
		1°C min <sup>-1</sup>	0.2°C min <sup>-1</sup>
<i>Chthamalus</i> sp.	adults	52.5 (1)	49.7 (3)
<i>Elminius modestus</i>	adults	48.3 (1)	44.2 (3)
<i>Balanus perforatus</i>	adults	45.5 (1)	
<i>Semibalanus balanoides</i>	adults	44.3 (1)	43.6 (2)
			42.2 (3)
	spat	44.2 (3)	42.3 (3)
		43.8 (2)	
<i>Balanus crenatus</i>	adults		36.8 (3)
<i>Balanus balanus</i>	adults		36.5 (3)

(Foster, 1969) shows seasonal variation in this barnacle and increased tolerance to low temperature in winter coincides with the period of physiological hibernation (Crisp and Ritz, 1967). Cold tolerance is due to frost resistance rather than the avoidance of ice formation (for example by glycerol) for more than 80% of the body water in the barnacles was frozen at the winter lower median lethal temperature (Crisp *et al.*, 1977).

4. *Freshwater runoff during emersion*: Intertidal barnacles avoid the osmotic effects of temporary immersion in freshwater during rain at low tide by closing their opercular valves before their blood reaches intolerable dilutions (Foster, 1971b).

### *C. Biological factors affecting the zonation of British intertidal barnacles*

1. *Spatial competition*: In a classic study at Millport (Firth of Clyde), Connell (1961a, b) showed that, by spatial crowding, *Semibalanus balanoides* is able to exclude *Chthamalus montagui* from all but the highest portion of the intertidal zone of British rocky shores (Connell actually used the name *Chthamalus stellatus* but only *C. montagui* occurs at Millport—personal observations; P. G. Moore: personal communication). *C. montagui* cyprids settled on the upper middle shore, down to midtide level. When surrounding *S. balanoides* were removed, the *Chthamalus* grew and survived well; when, on the other hand, *C. montagui* spat were left intermingled with *S. balanoides*, the latter grew over, crushed or uplifted the *Chthamalus* (see Fig. 25) by more rapid growth (Connell, 1961a, b). *Chthamalus montagui* is therefore only dominant in the physiological refuge higher on the shore than the upper limits of *S. balanoides* distribution.

Stanley and Newman (1980) and Newman and Stanley (1981) have extended this specific example to propose that, worldwide, the more recently evolved and still adaptively radiating balanoid barnacles have caused by competitive exclusion the ecological restriction and decline of the chthamaloids which were formerly more ecologically widespread. Balanoid barnacles have more advanced feeding mechanisms than chthamaloids with the development of the third pair of maxillipeds, an adapted labrum and improved microfeeding, but according to Stanley and Newman (1980) their most significant adaptive advance has been the evolution of tubiferous shell wall plates. The presence of the tubiferous shell allows balanoids to grow at a faster rate than chthamaloids with solid shell plates and outcompete them spatially. Balanoids pay a price for rapid growth for during emersion water may be lost through the shell

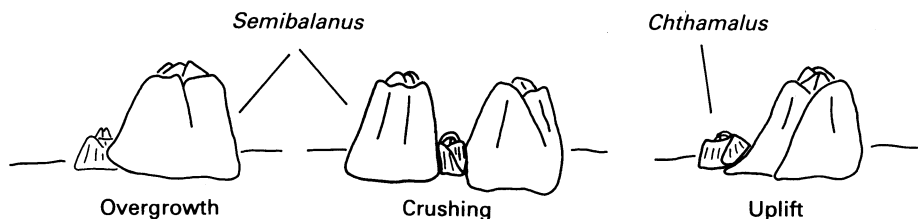


FIG. 25.

Interspecific competition for space between dominant *Semibalanus balanoides* and *Chthamalus montagui* (after Connell, 1961b).

(Newman, 1967) and the porous condition of the shell plates may contribute to the increased desiccation rate of *Semibalanus* in comparison to *Chthamalus* (Foster, 1971a). It is relevant that the highest intertidal balanoid barnacles like *Semibalanus balanoides* (and *Balanus glandula* from the Pacific coast of N. America) secondarily fill in the shell walls (Darwin, 1854; Pilsbry, 1916), presumably reducing desiccation (Stanley and Newman, 1980).

Individual balanoid barnacles do not only compete with chthamaloids; intraspecific spatial competition may reduce the lifespan of *Semibalanus balanoides* at low shore levels at Millport (Connell, 1961a) although such competition is reduced by the territorial settlement behaviour of the cyprids (Crisp, 1961). Interspecific spatial competition with larger *Balanus* species (particularly *B. perforatus* in southwest Britain) is also an important determinant of the lower limit of the distribution of *S. balanoides*.

On sheltered shores and towards the bottom of most shores macrophytic algae such as the fucoids, laminarians, *Gigartina*, *Himanthalia* and *Alaria* are strong competitors for space. Seaweeds grow relatively quickly to smother growing barnacles and will sweep settling cyprids and new spat off the rock as they are moved back and forth by the tide. Silt deposition on sheltered shores covers potential settlement sites and inhibits the growth of settled barnacles by clogging the filtering apparatus.

**2. Predation:** Muricean gastropods are major predators of barnacles and the dogwhelk *Nucella lapillus* plays an important role in determining the lower limits of the distribution of *Semibalanus balanoides* at Millport, Firth of Clyde (Connell, 1961a). Of other muriceans *Ocenebra erinacea* is a significant predator of lower shore barnacles (Crothers, personal communication) and the American Oyster Drill *Urosalpinx cinerea* also preys on barnacles (Wood, 1968) although it is of limited ecological significance in Europe being restricted to oyster beds at low water spring tide and below on the Essex coast (Graham, 1971). Muriceans have a proboscis armed with a radula and an accessory boring organ is present (usually on the mid-anterior ventral part of the foot) which produces acid, enzymes and chelating agents to dissolve calcite and assist the physical boring of the radula through the shells of their prey (Carricker, 1981). *N. lapillus* attempt to narcotise barnacles directly between the opercular plates but if necessary will bore through the shell plates of barnacles to inject the narcotic before feeding (Carricker, 1981).

The distribution of *Nucella lapillus* at Millport is limited by its physical tolerance limits to the midshore and, consequently, dogwhelk predation does not here affect the distribution of *Chthamalus montagui* to any great extent for where *C. montagui* might grow within range of *Nucella* it is already losing out to strong interspecific spatial competition from *S. balanoides* (Connell, 1961b). Furthermore, *N. lapillus* shows a size preference amongst *S. balanoides* for larger barnacles (Connell, 1961a) and this size preference results in a prey species preference at Millport for *S. balanoides* over the smaller *C. montagui* (Connell, 1961b). *N. lapillus* will also feed on *Elminius modestus* which is, however, a less preferred prey than *S. bala-*

*noides*, and such prey selection by the dogwhelk will not only affect the ecology of both species but also aid *E. modestus* to become established on a shore already occupied by *S. balanoides* (Barnett, 1979). Indeed species of *Nucella* in both the Atlantic and Pacific favour *Semibalanus* over *Balanus* over *Elminius* over *Chthamalus* when prey of the correct size is available (Crothers, personal communication). The distribution of *N. lapillus* on the shore varies geographically in Britain from mostly below mean tide level in southern England to the top of the barnacle zone in Shetland and so different barnacle species are available for selection as prey in different areas (Crothers, personal communication). *Urosalpinx cinerea* also shows prey selection between intertidal barnacles on British shores (Wood, 1968) as does another gastropod predator, the nudibranch *Onchidoris bilamellata* (Potts, 1970, as *O. fusca*).

Palmer (1982) has suggested that predation by muricacean gastropods has been of such ecological significance that it offers an explanation as to why balanomorph barnacles show repeated parallel evolutionary reduction from eight to six to four parietal plates in many lineages. Many muricacean predators selectively attack barnacles by boring at plate margins where access is easier and it is suggested that barnacles with fewest interplate sutures have a selective advantage (Palmer, 1982). Strong external ribbing on the shell may similarly be favoured in opposition to muricacean attack, as may indeed the evolution of tubiferous walls which increase the distance necessary to be penetrated by the accessory boring organ on the gastropod foot and of limited extensibility (Palmer, 1982). Higher balanids also have an altered articulation between the tergum and scutum possibly as an adaptation against predatory attack (Newman, 1982).

Other predators of British littoral barnacles include indiscriminate grazers such as the sea-urchin *Echinus esculentus* and limpets. *Blennius pholis*, the shanny, will bite off barnacle cirri under water and the ballan wrasse *Labrus bergylta* and the swimming crab *Liocarcinus puber* are also known to eat barnacles (Bassindale, 1964). The shore centipede *Scoliopterus maritimus* will attack barnacles as will the common polychaete worm *Eulalia viridis* (Bassindale, 1964), although the latter lacks any well developed proboscis armature and is more likely to be a scavenger on moribund barnacles (Crothers, personal communication). Turbellarian worms have also been shown to be predators of barnacles elsewhere in the world (Skerman, 1960; Hurley, 1975). Shore birds and temporary visitors like rats probably use barnacles as a source of food (Bassindale, 1964) and even insects like the larvae of the dipteran *Aphrosylus celtiper* prey upon barnacles intertidally.

#### *D. Ecological relationships of British intertidal barnacles*

The geographical distribution of the two *Chthamalus* species is limited by temperature to the warmer west coasts of the British Isles and, when present, they both extend higher up the shore than the balanoid barnacles (Fig. 24) as a result of their increased tolerances to desiccation. There is a great deal of overlap in their distribution but *C. montagui* is the more common in relatively sheltered coastal conditions whilst *C. stellatus* favours exposed open oceanic coasts. When both are present, *C. montagui* extends the further upshore (Fig. 24) (Southward, 1976; Crisp *et al.*, 1981). The lower limit of their distribution is determined by spatial competition with the faster growing balanoids (Connell, 1961b; Stanley and Newman, 1980). Such competition is reduced on more exposed shores where *S. balanoides* is less abundant (Ballantine, 1961) either as a result of the decreased ability of the cyprids to settle or of a weaker resistance of the tubiferous shell to the mechanical damage of heavy wave action. In correspondence with their different geographical distributions, the relative abundance of the *Chthamalus* species and of *S. balanoides* is affected by long term temperature fluctuations and shows yearly variations (Southward and Crisp, 1954).

In the mid and lower shore, particularly in more sheltered and estuarine locations, *S. balanoides* has met severe ecological competition from the immigrant barnacle *Elminius modestus* (Crisp, 1958). *E. modestus* is more tolerant of low salinity and of silt in the water and has replaced *S. balanoides* in many southern estuaries (Crisp, 1958). Barnacles are able to acclimate to local conditions in their closing response to decreasing salinity yet *S. balanoides* and *E. modestus* taken from the same habitat in the Menai Strait ceased cirral beating and closed the opercular plates to avoid osmotic problems at about 72% and 66% seawater respectively (Davenport, 1976). The cyprids of the two species prefer to settle under the influence of slightly different currents. *S. balanoides* cyprids preferentially settle at velocity gradients\* between 60 and 80  $\text{sec}^{-1}$  whilst *E. modestus* cyprids prefer to settle at velocity gradients below 50  $\text{sec}^{-1}$  (Crisp, 1955). *E. modestus* therefore settles preferentially in more sheltered conditions than *S. balanoides*, although the *E. modestus* cyprids are physically capable of attaching at higher velocity gradients than their *S. balanoides* counterparts (Crisp, 1955).

As in other barnacles the cyprids of both species settle over a wider range of the intertidal zone than that occupied by the growing adults. The physical and biological limits to distribution come into effect later—perhaps immediately after settlement in the case of desiccation of high shore spat. *E. modestus* adults reach slightly higher levels than those of *S. balanoides* (Crisp, 1958; Foster, 1971b) in spite of almost identical desiccation properties (Foster, 1971a). A probable reason lies in the different settlement periods of the barnacles. The settlement of *S. balanoides* only occurs in late spring whereas *E. modestus* settles throughout most of the year and it is the newly metamorphosed spat that are most in danger from desiccation (Foster, 1971a, b). Those *E. modestus* spat that settle in the more inclement periods like autumn and winter may therefore avoid desiccation and become established at shore levels at which newly metamorphosed *S. balanoides* spat are desiccated under the weather conditions of late spring (Foster, 1971b).

The extended settlement period of *E. modestus* also allows this barnacle to rapidly occupy temporary spaces on the midshore, which may for example have been created by the grazing of *S. balanoides* cyprids by limpets (Barnes and Barnes, 1960) or by selective predation of *S. balanoides* by *Nucella lapillus* (Barnett, 1979). Once settled, particularly in the summer in the south, *E. modestus* has a particularly rapid feeding rate, tolerates high temperatures better than *S. balanoides* and may produce successive broods as often as every ten days within only two months of initial settlement (Crisp and Davies, 1955; Crisp, 1958). Larvae are, therefore, readily available to colonise temporary spaces and block these for the following year's settlement of *S. balanoides* cyprids. Eventually, large individuals of *S. balanoides* remain standing out amongst the smaller *E. modestus*, growing well in the absence of intraspecific competition for space and fishing for food beyond the reach of *Elminius* (Crisp, 1958). Few new *S. balanoides* cyprids have space to settle and eventually *E. modestus* replaces the original *S. balanoides* population. *E. modestus* cyprids do not suffer to the same extent from the apparent lack of settling space if occupied by other barnacles for *E. modestus* is much more ready to settle on top of existing barnacles including those of their own species (Hui and Moyses, 1982).

On less sheltered shores *S. balanoides* is more successful, *E. modestus* becoming less common as wave action increases perhaps because its shell plates may be less resistant to wave

\*A current moving over a substratum is affected by frictional drag such that water molecules directly adjacent to the substratum may be effectively motionless. There therefore exists a gradient of velocities of water movement decreasing towards the substratum. A current of 100  $\text{cm sec}^{-1}$  measured 1 cm from a substratum will therefore set up a velocity gradient of 100  $\text{cm sec}^{-1}$  per cm i.e. 100  $\text{sec}^{-1}$ .

action (Crisp, 1958; Foster, 1971*b*). Although *E. modestus* has spread to the Shetlands (Hiscock *et al.*, 1978) it is a temperate to warm-water species (Foster, 1967) and is a less successful competitor to the boreoarctic *S. balanoides* in the north of Britain as a fall in temperature reduces its fecundity and as minimum phytoplankton levels for planktotrophic larval development become more seasonal. Indeed, after settlement in the hot summer of 1976, populations of *E. modestus* in Shetland subsequently declined possibly as a result of a return to normal cold sea temperatures causing reproductive failure (Crothers, personal communication).

The lower distribution limits of both *S. balanoides* and *E. modestus* are controlled by the biological factors of spatial competition (particularly by macrophytic algae) and predation, *E. modestus* spreading the further downshore into the sublittoral zone. Low on the more exposed shores of southwest Britain, *S. balanoides* is outcompeted for space by *B. perforatus*. Elsewhere *B. crenatus* replaces *S. balanoides* at the bottom of shores receiving relatively undiluted seawater, being found under stones and in crevices not suitable for algal growth. The sublittoral *Balanus balanus* may be found similarly spreading onto the bottom of the shore in the north.

In areas of decreased salinity the euryhaline barnacle *Balanus improvisus* is of ecological significance. *B. crenatus* and *S. balanoides* show similar closing responses to diluted seawater, closing down before *E. modestus*, but *B. improvisus* is active at even greater dilution (Davenport, 1976). In estuaries, therefore, *B. improvisus* directly replaces *B. crenatus* and used to limit the estuarine penetration of *S. balanoides*. *E. modestus* has however competed for space with *B. improvisus* since its introduction and due to similar competitive advantages as those which are effective against *S. balanoides* (see above), it has very much reduced the range of *B. improvisus*, particularly in the warmer south of Britain. *B. improvisus* is still common in the north and in inner estuaries, but *E. modestus* has replaced it over wide stretches of southern English estuaries such as that of the Thames (Crisp, 1958). *Balanus amphitrite* requires warmer waters for successful growth and breeding than indigenous British barnacles but is tolerant of low salinities and is established on the low shore and below in some sites receiving heated effluents.

### RHIZOCEPHALAN BARNACLES

Most rhizocephalans are parasites of decapod crustaceans and are not readily recognisable as barnacles without study of their typically cirripede nauplii with characteristic frontal horns. Rhizocephalan means root-headed, reflecting the structure of the female parasite which spreads in the form of an absorptive network through the host. The female barnacle develops an external brood sac (the externa) with ovaries and mantle cavity, the site of settlement of male cyprids which bring about the fertilisation of the eggs of the female to be incubated in the mantle cavity.

Two common British rhizocephalan barnacles that are found intertidally are *Sacculina carcini*, parasitic on crabs (see Fig. 26), especially the shore crab *Carcinus maenas*, and *Peltogaster paguri*, parasitic on hermit crabs, especially *Pagurus bernhardus* (see Table 1 for classification).

The rhizocephalans may be a polyphyletic order with evolutionary lines arising from different stocks (Newman *et al.*, 1969; Newman, 1982) and indeed morphological intermediates between stalked barnacles and rhizocephalans exist today. *Anelasma squalicola* (Fig. 27) is parasitic on the deep-sea shark *Etmopterus spinax* (Broch, 1919; Johnstone and Frost, 1927). Johnstone and Frost (1927) concluded that *Anelasma* feeds holozoically like a free-living barnacle on suspended food, whilst at the same time being able to absorb material from its



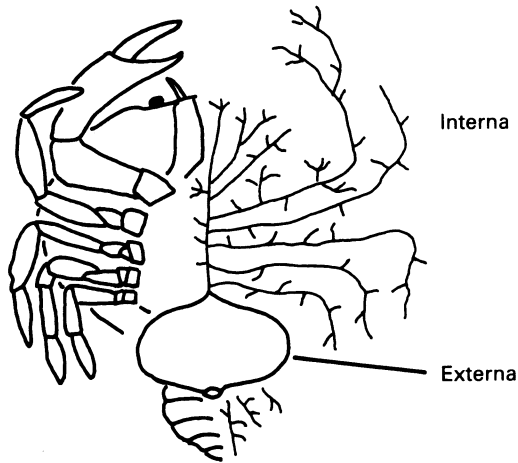


FIG. 26.

The rhizocephalan barnacle *Sacculina*, parasitic on crabs, exists as a network (interna) penetrating the body of the crab with an externa emerging at the base of the crab's abdomen.

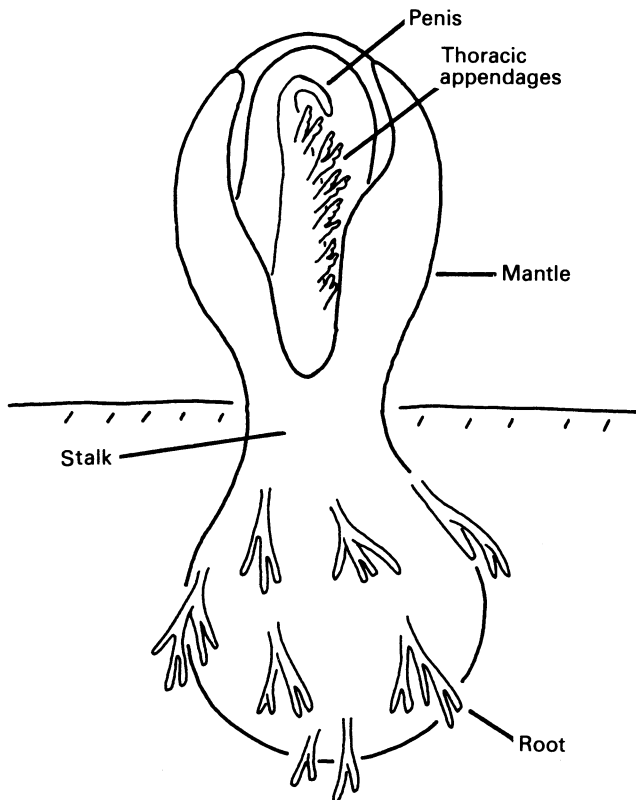


FIG. 27.

The structure of *Anelasma* (after Johnstone and Frost, 1927).

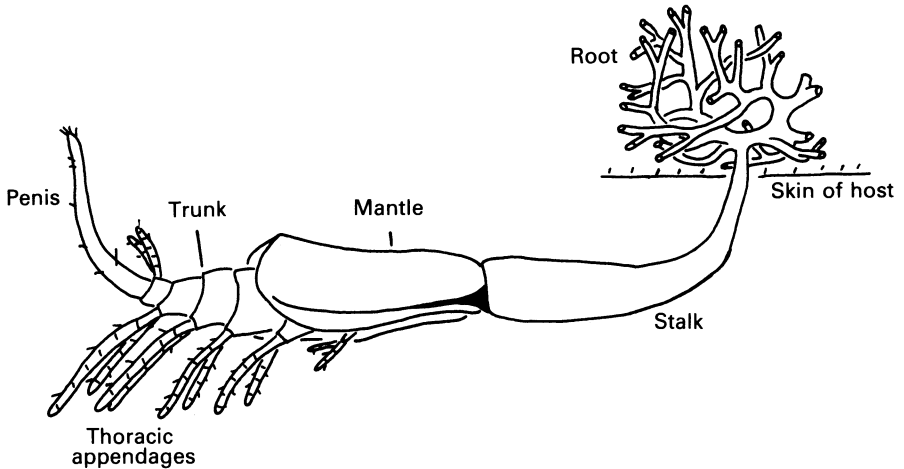


FIG. 28.  
The structure of *Rhizolepas* (after Day, 1939).

host as in the rhizocephalans; but Hickling (1963) was in no doubt that *Anelasma* gains its nourishment totally from the host. *Rhizolepas annelidicola* (Fig. 28), a parasite of the polychaete *Laetmonice producta* off Mozambique, clearly obtains all its food from the host via a very extensive root system (Day, 1939). It is by no means certain that rhizocephalans arose from thoracicans and Newman (1982) discusses possible evolutionary pathways by which rhizocephalans might be related to other barnacles.

Both *Sacculina* and *Peltogaster* belong to the larger of the suborders of the Rhizocephala—the Kentrogonida, which is characterised by the presence of a specialist infection stage, the kentrogon, in the life cycle. Early workers were confused as to whether or not the parasites were hermaphrodite but the work of Ichikawa and Yanagimachi (1958, 1960), Yanagimachi (1961*a*, *b*), Yanagimachi and Fujimaki (1967) and Ritchie and Høeg (1981) has shown that visible kentrogonid rhizocephalan barnacles are in fact females with modified hyperparasitic larval males.

Full details of the life cycle are lacking for most rhizocephalans but a typical kentrogonid life cycle (Yanagimachi, 1961*b*; Ritchie and Høeg, 1981) is shown in Fig. 29 and is probably correct in the most part for *Sacculina* and *Peltogaster*. Male and female nauplius larvae of different size are produced from separate male- or female-bearing females. The larvae develop through several nauplius stages in the plankton without feeding by utilising their own yolk reserves and moult (after five or six days in *S. carcini* (Day, 1935)) to give rise to the cyprids. Three days later, the female cyprid settles at the base of a seta on the decapod crustacean host (Day, 1935) and attaches by means of the antennules (Delage, 1884). Settlement usually takes place towards the end of the year in British waters (Foxon, 1940). The female cyprid then metamorphoses into the remarkable infection stage—the kentrogon, a process taking twenty-four hours in *S. carcini* (Delage, 1884). In *Sacculina* the kentrogon consists of a sac of undifferentiated cells together with the antennules; a new cuticle is secreted round the sac and the kentrogon separates from the old cypris cuticle, limbs and remaining body (Delage, 1884). A hollow spine (kentron) develops at the base of the antennules and is pushed into the base of the seta of the crab, whereupon the mass of undifferentiated cells migrates into the crab as if through a hyperdermic syringe. (Ritchie and Høeg (1981) have suggested

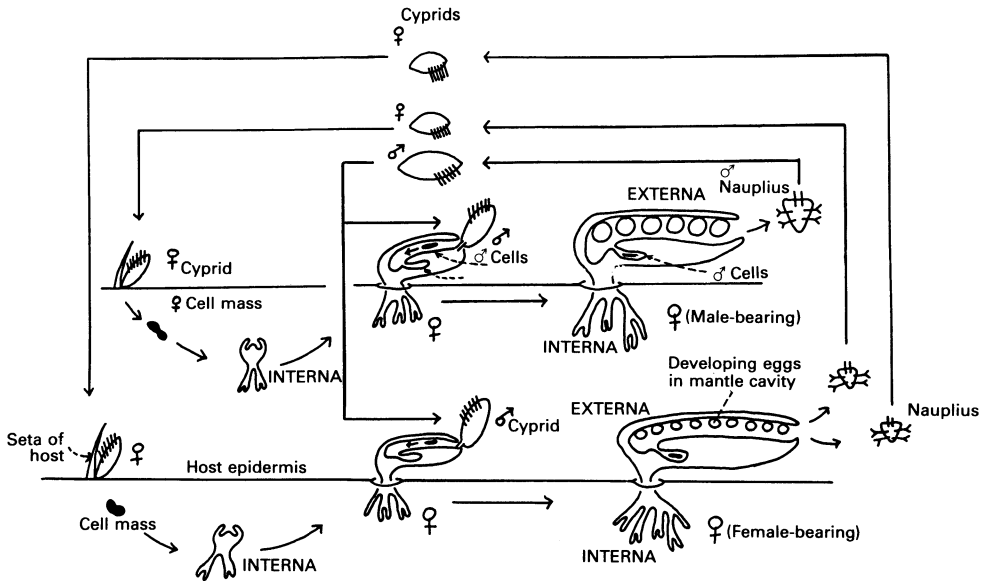


FIG. 29.

Typical life cycle of a kentrogonid rhizocephalan (see text) (after Yanagimachi, 1961*b*).

that rhizocephalans may have originally evolved as external parasites (as in the Akentrogonida) but evolved a flattened external kentrogon stage (as in the kentrogonid rhizocephalan, *Lernaeodiscus*) as an adaptation to resist grooming by the host, before becoming endoparasitic as a final counter-defensive measure). The cells differentiate into a system of root-like processes (the interna) spreading over the surfaces of the organs of the host, taking up nutrients from the haemolymph. In the case of *S. carcini* in *Carcinus maenas*, about nine months or so after infection (Foxon, 1940), a tube grows posteriorly and exits through the host's cuticle to end in a sac—a process commonly occurring in August and September (Foxon, 1940). Within days the external brood sac has reached 4 mm in diameter and is ready to receive a male cyprid (Delage, 1884; Foxon, 1940; Ichikawa and Yanagimachi, 1960). The male cyprid attaches to the mantle opening and injects its cellular mass into the mantle cavity; the cell mass migrates into one of two cypris-cell receptacles (often misidentified as testes) and the cells multiply rapidly and differentiate into spermatozoa (Yanagimachi, 1961*b*). The externa now develops quickly, the much branched ovary produces eggs (Fig. 30) to be fertilised by the sperm from the cypris cell receptacles. The fertilised eggs are incubated in the mantle cavity. Usually in late summer, *Sacculina carcini* in *Carcinus maenas* releases the first of many batches of nauplii, six weeks after settlement of the male cyprid and when the externa is about 12 mm wide; eleven months or so after initial infection of the crab (Day, 1935; Foxon, 1940). In those kentrogonids so far examined in detail (Yanagimachi, 1961*b*; Ritchie and Høeg, 1981) females either produce male or female offspring and this may well be the case in *Sacculina* and *Peltogaster*.

Rhizocephalans are the classic perpetrators of parasitic castration (see Reinhard, 1956). Male crabs infested with rhizocephalans develop female secondary sexual characteristics with respect to the shape of abdomen, pleopods and claws whilst the testes more or less atrophy. The abdomen of the "sacculinised" male crab for example becomes broader with more setae round the margin; the third, fourth and fifth abdominal segments, usually coalesced in the

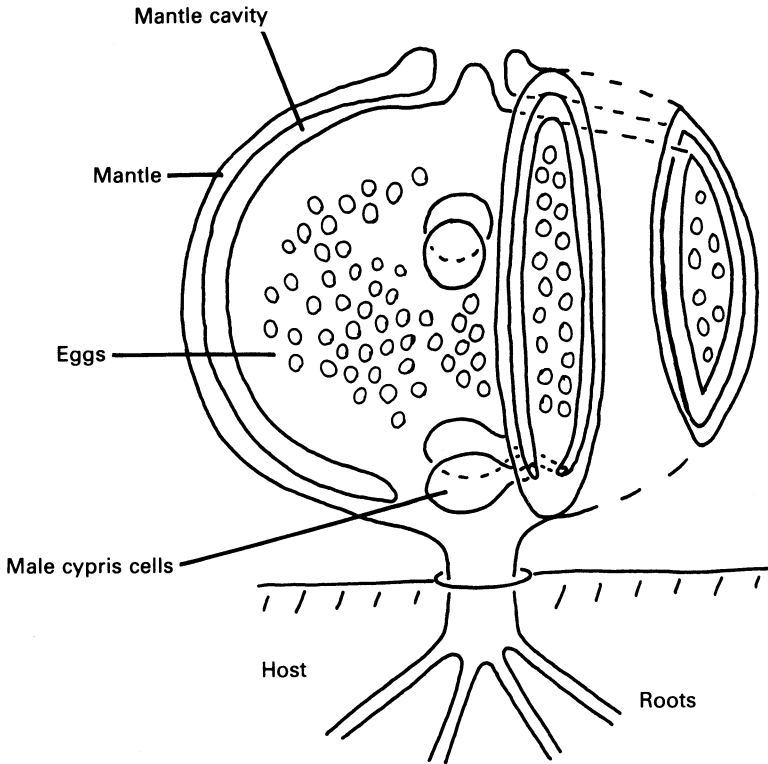


FIG. 30.

The structure of the externa of *Sacculina* (after Ichikawa and Yanagimachi, 1960).

male, become distinct and the number and shape of the pleopods change (Reinhard, 1956). Such morphological changes occur at moults of the crab with an internal parasite, and since brachyuran crabs with rhizocephalan externae usually do not moult, the degree of modification of the host crab is related to the number of moults prior to the emergence of the externa. Sacculinisation of female crabs may bring about hyperfeminisation of the abdomen to make it even wider (Reinhard, 1956). The mechanism by which rhizocephalans upset the sexual characteristics of the host has not been clarified (Reinhard, 1956), but it might be surmised that the parasite receives a selective advantage in mimicking in turn the developing eggs and then the fertilised egg mass of the crab. By interfering with the metabolism of the host perhaps via the production of its own crustacean hormones, the parasite may set up metabolic conditions by which it stimulates the host to produce energy-rich metabolites like yolk usually destined for developing eggs from which the parasite would benefit. The usual location of the parasite externa on crabs or hermit crabs bearing *Sacculina carcini* or *Peltogaster paguri* respectively is that of the fertilised egg mass and morphological modifications caused to the abdomen of the host are probably to the advantage of the parasite with respect to services provided by the host such as aeration and grooming which may come into effect as if for an incubated egg mass.

Sacculinised *Carcinus maenas* with more than one externa are less common than would be expected by chance, as if the presence of an established parasite has inhibited the development of others (Rainbow *et al.*, 1979). Established parasites may directly inhibit the growth of

further parasites by secreting a toxin (Levy, 1923; see Rainbow *et al.*, 1979) or it may be that the host has developed an immune response counteracting the successful growth of later arrivals.

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