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D. T. Anderson

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CIRRAL ACTIVITY AND FEEDING IN THE BARNACLE *BALANUS PERFORATUS* BRUGUIÈRE (BALANIDAE), WITH COMMENTS ON THE EVOLUTION OF FEEDING MECHANISMS IN THORACICAN CIRRIPEDES

By D. T. ANDERSON, F.R.S.
School of Biological Sciences, University of Sydney, N.S.W. 2006, *Australia*

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Earlier studies of rhythmic cirral activity in balanid barnacles have assumed the monophyletic nature of Darwin's Balanidae (*s.l.*) and a similar performance of normal and fast beat among species in this group.

Recent taxonomic revisions of the Balanomorpha have raised the possibility that rhythmic cirral activity evolved polyphyletically at least twice in the Archaeobalanidae (*Elminius modestus* and *Semibalanus balanoides*), as well as in the Balanidae (*s.s.*). Differences in food intake tend to support this hypothesis.

B. perforatus has a mode of cirral beating different from that of other species of *Balanus* (*s.s.*). Instead of normal and fast beat, *B. perforatus* exhibits a characteristic action over the whole range of 2–24 beats per 10 s. At all rates, the operculum is held open and the cirri are extended and withdrawn from the mantle cavity during beating. Cirral extension is less at faster rates than at slower rates. While the cirral action is effective in the capture of small planktonic prey such as nauplii, the major emphasis is on pumping a powerful current of water through the mantle cavity. In contrast to other species of *Balanus*, the volume of water pumped through the mantle cavity increases as the rate of beating increases. An average-sized *B. perforatus* beating at a fast rate passes water through the mantle cavity at a rate greater than 1 l/h.

The action of the maxillipeds and mouthparts in captorial planktivory in *B. perforatus* is similar to that of other extension feeding and rhythmic feeding balanomorphs. A filtratory action of the large, setose maxillipeds is correlated with the production and flow of the mantle current.

At slower rates of beat, up to 9 per 10 s, the main determinant of the rate of beating is the duration of the pause in the withdrawn position. At faster rates of beat, this pause becomes negligible and the main determinant of the rate of beating is the speed of movement of the body during each beat cycle. These two factors, the pause duration and the speed of body movement, appear to be controlled by independent but coordinated neural mechanisms. The evolution of rhythmic cirral beating in balanoids has been mainly of the action of these neural mechanisms in controlling a skeleto-muscular system similar to that of non-rhythmic, extension-feeding balanomorphs. Such an evolution could have occurred more than once.

In the absence of detailed information on the relationship between cirral action, body movements, mantle current production and food capture in other balanoid species, the question of whether the rhythmic cirral activity of balanoids has had a monophyletic or a polyphyletic origin from an extension-feeding ancestry cannot be firmly answered at the present time. Similarities have been emphasized in the past, but clear differences exist. *Elminius modestus* emphasizes fast beat and is a planktivore. *Semibalanus balanoides* performs both normal beat and fast beat and combines planktivory with supplementary filter feeding. Among the Balanidae (*s.s*), *B. perforatus* has a unique rhythmic cirral action and is highly adapted as a current-producing filter feeder. *Balanus nubilus* appears to have independently evolved a similar pumping–filtering action, but has not been studied in detail. Other 'groups' within the genus *Balanus* variously emphasize rhythmic planktivory or a combination of planktivory and filtration. None of these, on present evidence, could have shared an evolution of rhythmic beating with *B. perforatus*. The hypothesis that rhythmic cirral activity has evolved polyphyletically in the Archaeobalanidae and Balanidae can therefore be extended to a polyphyletic origin of rhythmic cirral activity among the various groups of the genus *Balanus* (*s.s.*).

The powerful development of the three pairs of scutal and tergal depressor muscles in *B. perforatus*, shared by other large balanoid species (e.g. *Chirona hameri*, *Balanus nubilus*), is not functionally related to the performance of rhythmic beating or powerful pumping. These muscles function in protective closure of the operculum and in producing a protective rotary action of the closed operculum.

1. INTRODUCTION

(*a*) *Studies of cirripede feeding mechanisms based on the Darwinian classification of the* Thoracica

The classical account of feeding in balanid barnacles is that of Crisp & Southward (1961). Working within the broad Darwinian definition of the family Balanidae, Crisp & Southward established that many species of *Balanus*, as then defined, exhibit four levels of activity, which they called testing, pumping, normal beat and fast beat. In testing, the opercular valves are opened but there is little or no movement of the body or cirri within the mantle cavity. In pumping, the opercular valves are held open and the body performs a characteristic back-and-forth pumping action which drives a current of water through the mantle cavity; but the cirri are protruded only slightly or not at all. In normal beat, the cirri are extended and withdrawn rhythmically, the opercular valves being closed between beats, and a pulse of water passes through the mantle cavity on each beat. In fast beat, the cirri are extended and coiled in a rapid rhythm while remaining exposed outside the mantle cavity, and the opercular valves are held open through the process. Little or no passage of a water current through the mantle cavity accompanies fast beat. The opercular, cirral and pumping mechanisms underlying these actions were described in some detail by Crisp & Southward and were related to the capture of planktonic prey by the rhythmically beating cirri and the filtration of micro-organisms from the mantle current by the maxillipeds during pumping and normal beat.

Much of the analysis presented by Crisp and Southward was based on a study of *Balanus balanoides*, but the same four patterns of activity were described by these authors for *B. amphitrite*, *B. balanus*, *B. crenatus*, *B. eburneus*, *B. improvisus*, *B. perforatus*, and *Elminius modestus*. The latter displays a greater emphasis on fast beat than on normal beat. It was also shown that in a water current the above species tend to exhibit brief periods of continuous extension of the cirri as a captorial net, a mode of activity reminiscent of the prolonged extension of the cirral captorial net previously described in lepadomorph species by Gruvel (1893), Batham (1945), Southward (1957), Barnes & Reese (1959) and Howard & Scott (1959) and reconfirmed by Crisp & Southward (1961) themselves. Crisp & Southward also observed prolonged cirral extension in response to a water current in the verrucomorph *Verruca stroemia*, confirming an earlier observation on *V. recta* by Southward & Southward (1958), and in the balanids (*sensu lato*) *B. hameri*, *Chelonibia patula*, *Pyrgoma anglicum* and *Tetraclita squamosa*, the last observation confirming an account by Mori (1958) of cirral extension as the predominant activity in *T. s. japonica*. In all of these species, testing and pumping also occur, but there is little or no display of normal beat and no expression of fast-beat activity.

The cirral activity of the extension-feeding balanids investigated by Crisp & Southward is not correlated with habitat, which ranges from deep water to epizoic to intertidal, but is shared, as shown by Crisp (1950), Southward (1955*b*) and Crisp & Southward (1961), by the chthamalid balanomorphs *Chthamalus stellatus* and *C. fragilis*. It could be perceived from this cumulative set of observations that the extension feeding characteristic of the Lepadomorpha has been retained, usually with augmentation by a testing and respiratory pumping mechanism, in chthamalid and some balanid balanomorphs, but is replaced in most balanids by a rhythmic cirral action with two levels of activity, normal beat and fast beat. The implication of this perception was that rhythmic cirral activity has evolved only once in balanids (*s.l.*), though how it originated is unclear, and that it takes place in the same way in all species displaying such activity.

Subsequent studies, still adhering to the Darwinian classification, extended the range of species behaving in accordance with this concept. Further descriptions of prolonged cirral extension as the feeding mechanism in lepadomorph species were given by Bieri (1966), Jones (1968) and Lockwood (1968) (see Anderson (1980*a*) for a review). Extension feeding was confirmed for the verrucomorph *V. stroemia* by Stone & Barnes (1973) and was described for additional chthamalids (*Chthamalus depressus*, *Tetrachthamalus oblitteratus*) by Southward (1962, 1967) and Klepal & Barnes (1975), and for another balanid (*B. cariosus*) by Southward & Crisp (1965). The occurrence of normal- and fast-beat rhythmic feeding in the balanids *Elminius modestus*, *Balanus amphitrite*, *B. crenatus*, *B. eburneus* and *B. perforatus* was further confirmed by Southward (1962) and Southward & Crisp (1965). Reference was also made in the last-mentioned paper to the large *Balanus nubilus* of the Pacific Coast of North America, which displays normal beat (though not fast beat) in still water and prolonged cirral extension in a water current, an interesting combination that still awaits elucidation.

(*b*) *The evolution of rhythmic cirral activity in the* Thoracica

All functional morphological and fossil considerations uphold the view that the captorial feeding by prolonged cirral extension displayed in the Lepadomorpha is the basic mode of feeding in thoracican cirripedes (Anderson 1978). Planktonic prey are usually taken, although Colon-Urban *et al.* (1979) have reported that the deepwater epizoic lepadomorph *Octolasmis aymonini geryonophila* captures benthic crawling prey by this means. Either individual cirri or the whole cirral net may be used in prey capture (Barnes & Reese 1959; Crisp & Southward 1961). The only significant modification of this feeding mechanism so far described in a lepadomorph is that displayed by the small neustonic species *Lepas pectinata*, in which rhythmic cirral beating occurs as an adaptation to feeding continuously on microplankton at the surface of the water (Anderson 1980*a*). The cirral beating of *L. pectinata* is in the opposite mode to that of balanids, the cirri being held extended between beats, and has clearly evolved independently as a specialization within the Lepadidae. In this species, the cirri are rarely withdrawn into the mantle cavity and then only momentarily.

Captorial feeding by prolonged cirral extension is also retained in the Verrucomorpha, though the asymmetry of these animals and the associated extension of the cirral net laterally, close to the adjacent substratum, suggest another adaptation to the capture of crawling prey in deep-water habitats (Anderson 1980*b*). The small, shallow-water species *V. stroemia* exhibits rhythmic cirral extension and withdrawal in still water (Stone & Barnes 1973), but this is a specialization, like that of *Lepas pectinata*, for microfeeding (Anderson 1980*b*). The rhythm is similar to that of *L. pectinata*, with the cirri being held extended between beats, but has evolved independently and convergently in the two species.

In view of these independent occurrences of rhythmic cirral activity in lepadomorphs and verrucomorphs, the question arises, whether all instances of rhythmic cirral beating in the Balanomorpha have a common evolutionary origin? This is in addition to questions of how and why rhythmic cirral beating evolved as a feeding mechanism, and the need to explain a random scatter of retention of extension feeding among the balanids (*s.l.*).

A functional interpretation of the mode of origin of rhythmic cirral activity in balanomorphs was developed by Anderson (1978) on the basis of observations on cirral activity in *Boscia* (= *Pyrgoma*) *anglicum*. This will be referred to again below. More importantly, questions about the origin and evolution of rhythmic feeding in balanomorphs were placed in a new context by the major systematic revision of the Balanomorpha presented by Newman & Ross (1976, 1977). Basing their analysis mainly on shell characteristics and fossil evidence, these authors recognized that balanomorph evolution has been much more complex than can be encompassed by Darwin's (1854) recognition of a suborder Balanomorpha divided into two families, Chthamalidae and Balanidae, the latter with subfamilies Coronulinae, Balaninae and Tetraclitinae, and with a large number of species of Balaninae grouped into a single genus, *Balanus*. In the scheme proposed by Newman & Ross, the Balanomorpha comprises three superfamilies, the Chthamaloidea, Coronuloidea and Balanoidea. The first of these, the Chthamaloidea, contains the earliest (Cretaceous–Recent) balanomorphs, the Catophragmidae, generally accepted to have been derived from Mesozoic scalpellid lepadomorphs (Newman & Ross 1976; Anderson 1980*c*), and their direct descendants, the Chthamalidae, now divided into a deep-water group (subfamily Pachylasminae) and an intertidal group (subfamily Euraphiinae and its descendant subfamily Chthamalinae). As far as we have evidence of feeding mechanisms in the Chthamaloidea, all of them retain extension feeding. The intertidal catophragmid *Catomerus polymerus* of south-eastern Australia has a cirral extension and food-capture mechanism identical with that of scalpellids, except for a more obvious specialization of the two pairs of maxillipeds (Anderson 1980*c*). Extension feeding also occurs, as mentioned earlier, in *Euraphia depressa* (= *Chthamalus depressus*) (Southward 1962; Klepal & Barnes 1975), *Chthamalus stellatus*, *C. fragilis* and *C. challengeri* (Sato 1941; Crisp 1950; Southward 1955*b*, 1962, 1967; Crisp & Southward 1961) and *Tetrachthamalus oblitteratus* (Southward 1967). At present there is no evidence of the evolution of rhythmic cirral beating as a mechanism of feeding in chthamaloids. Foster (1978) has attempted to equate this fact with the confinement of modern chthamaloid species to mid- and upper-littoral habitats, but the apparent correlation is probably an over-simplification. The relationship between functional morphology, feeding and habitat is still underexplored for all species of barnacles. Nothing is known, for example, of the feeding mechanisms of the Pachylasminae.

The Coronuloidea of Newman & Ross (1976, 1977) are postulated to be descended from the pachylasmine chthamalids, though the possibility of an independent origin from scalpellids cannot be entirely ruled out. They comprise two divergent lines, the Bathylasmatidae and their descendants the Tetraclitidae, and the Coronulidae. The latter are epizoic on marine crustaceans and vertebrates and, as exemplified by *Chelonibia patula*, retain extension feeding (Crisp & Southward 1961). The feeding mechanisms of the various turtle and whale barnacles have not been described. Similarly, the deep-water *Bathylasma* (*Hexalasma*) *hirsutum* is an extension feeder (Southward 1957; Southward & Southward 1958; Crisp & Southward 1961), and the same mechanism persists in the only tetraclitid whose feeding has so far been described, the intertidal *Tetraclita squamosa* (Mori 1958, 1961; Crisp & Southward 1961; Southward & Crisp 1965).

The Balanoidea of Newman & Ross (1976), in turn, are postulated to be descended from bathylasmatids, though again an independent origin from scalpellid lepadomorphs cannot be entirely discounted. They are based on a family Archaeobalanidae, with two independently descendant families, the Pyrgomatidae or coral-inhabiting barnacles and the Balanidae (*sensu stricto*). The Archaeobalanidae comprises two sub-families, the Archaeobalaninae (a complex group containing, among others, the species *Chirona* (*Balanus*) *hameri* and *Elminius modestus*) and the Semibalaninae (*Semibalanus* (*Balanus*) *balanoides* and *S.* (*B.*) *cariosus*). According to Newman & Ross, the Pyrgomatidae, whose more generalized members include *Boscia*

(*Pyrgoma*) *anglicum*, are descended from the Archaeobalaninae. The Balanidae, on the other hand, appear to have diverged early from the Archaeobalanidae and are not descended directly from either of the extant archaeobalanid subfamilies.

It is within the Balanoidea that rhythmic cirral activity in the form of normal beat and fast beat is known to occur. As mentioned earlier, some balanoid species retain extension feeding. This is the case, for example, in the archaeobalaninid *Chirona hameri* (Crisp & Southward 1961; Southward & Crisp 1965; Allison & Dorsett 1977) and the semibalaninid *S. cariosus* (Southward & Crisp 1965). On the other hand, *S. balanoides* is one of the best known examples of normal- and fast-beat cirral activity (Crisp & Southward 1961), while the archaeobalaninid *Elminius modestus* also shows very active cirral rhythms, with an emphasis on fast beat. If Newman & Ross are correct, these two cases of rhythmic cirral activity have evolved independently in parallel, which might explain why they are somewhat different from one another.

The transition in balanoids from extension feeding to rhythmic feeding is illuminated by the case of *Boscia anglicum*, eludicated by Anderson (1978). While feeding in other pyrgomatids is likely to be specialized in associated with their coral-inhabiting life (the extreme case of *Hoekia monticulariae* is the only one so far described, by Ross & Newman (1969)), *B. anglicum* is a planktivore, basically using prolonged cirral extension, but performing short bursts of rhythmic cirral beating to waft its prey down to prehensile third maxillipeds. A transition to more continuous cirral beating as a prey-capture mechanism is not difficult to envisage from this kind of beginning, with the accompaniment of an advantageous pumping of a respiratory current through the mantle cavity as a result of the body movements underlying the rhythmic cirral extension and coiling. Normal beat and/or fast beat could easily result, the through-mantle current associated with the former also providing a basis for filtratory feeding on micro-organisms by setose maxillipeds. Furthermore, a polyphyletic evolution of rhythmic cirral beating in the Balanoidea is functionally feasible on such an interpretation.

In view of these facts, the question can be asked, has the rhythmic feeding mechanism of the Balanidae (*s.s.*) evolved independently of those exhibited in the Archaeobalanidae? According to the results of Crisp & Southward (1961), Southward (1962) and Southward & Crisp (1965), the cirral activities of *Semibalanus balanoides* and of a number of species of *Balanus* (*s.s.*) (*B. amphitrite*, *balanus*, *crenatus*, *eburneus*, *improvisus* and *perforatus*) are similar. This is suggestive of an origin of the Balanidae from rhythmic feeding semibalaninids. As Newman & Ross (1976) pointed out, however, the genus *Balanus* (*s.s.*) is a complex one, difficult to categorize systematically, and can be provisionally subdivided into six groups of uncertain interrelationships. These are, with the species for which information on feeding is available in parentheses, the groups of:

(1) *B. balanus* (*B. balanus*, *B. crenatus*);
(2) *B. nubilus* (*B. nubilus*, *B. rostratus*);
(3) *B. concavus* (nil);
(4) *B. amphitrite* (*B. amphitrite*, *B. eburneus*, *B. improvisus*);
(5) *B. trigonus* (nil);
(6) *B. perforatus* (*B. perforatus*).

All are credited with the same mechanisms of testing, pumping, normal beat and fast beat as *S. balanoides*, except for *B. nubilus*, which shows normal beat in still water, but no fast beat, and prolonged cirral extension in a water current. Crisp & Southward, however, gave little detailed information on any species other than *S. balanoides*. If we look in more detail, shall we find confirmation of their single interpretation for all balanoid species, or are there distinctive peculiarities in the rhythmic activity of *Balanus* and/or special features characteristic of each *Balanus* group?

(*c*) *The food of thoracican cirripedes*

A final lead into this question can be traced from the information currently available on the food intake of various species of thoracican barnacles, obtained either by experiments on food intake or by direct analysis of gut contents. Once again it is useful to begin with the Lepadomorpha, since all of the available evidence on food intake confirms the utilization of the extended cirri as a zooplankton trap, with some capture of larger food by the larger neustonic *Lepas* species (*L. anatifera*, *L. anserifera*, *L. fascicularis*) and a specialized rhythmic filtration of surface microplankton by the small *L. pectinata* (Batham 1945; Southward 1957; Barnes 1959; Barnes & Reese 1959; Howard & Scott 1959; Patel 1959; Crisp & Southward 1961; Bieri 1966; Jones 1968; Petriconi 1969; Lockwood 1968; Foster 1978; Rainbow & Walker 1978; Anderson 1980*a*). The food captured by the primitive balanomorph *Catomerus polymerus* is similarly a range of small zooplankters, mainly crustaceans (Anderson 1980*c*). Unfortunately, there is at present a dearth of information on food intake in other chthamaloids, or in coronuloids other than *Tetraclita squamosa*. However, this extension feeder is also a planktivore (Barnes 1959), as are the extension-feeding archaeobalaninid *Chirona hameri* (Crisp & Southward 1961; Allison & Dorsett 1977) and semibalaninid *Semibalanus cariosus* (Southward & Crisp 1965). We therefore have limited but consistent evidence that extension feeding is a mechanism for the capture of zooplankton. This also holds for *Boscia anglicum*, with its transitional mode of feeding (Anderson 1978).

In rhythmic feeding balanoids, however, the picture is more complex. *Elminius modestus* and *Semibalanus balanoides* make an interesting contrast. The difference in their rhythmic feeding mechanisms, probably independently evolved, is reflected in their food intake (Barnes 1959; Crisp & Southward 1961; Crisp 1967; Southward & Crisp 1965; Rainbow & Walker 1978). *E. modestus* feeds mainly on nauplius larvae and other zooplankton. *S. balanoides* also takes this prey, but in addition captures numerous diatoms and other microplankton by filtration of the mantle current with the maxillipeds.

The various *Balanus* groups also show interesting differences in food intake, in spite of being said, except for *B. nubilus*, to have a feeding action identical with that of *S. balanoides*. *B. balanus* and *B. crenatus* (group 1) are planktivores (Barnes 1959). The large *B. nubilus* and *B. rostratus* (group 2) feed mainly on large quantities of small particulate matter and capture very few animal prey (Barnes 1959). No information is available for *B. concavus* (group 3) and almost none (surprisingly) for the important estuarine and fouling *B. amphitrite* and its allies *B. eburneus*, *B. improvisus* and *B. variegatus* (group 4). Ota (1957) showed that *B. amphitrite* is a plankton feeder, but whether it is also a filter feeder remains to be determined. *B. trigonus* (group 5) is another species that has not been studied, leaving us without critical information on this group. Finally, in group 6, the relatively large *B. perforatus* is a planktivore, but only on small prey up to 1 mm, and is an efficient feeder on microplankton (Crisp & Southward 1961). There are hints of significant variation in this comparison, in spite of the present poor state of knowledge. The evidence of lack of filter feeding in group 1 is in strong contrast with the evidence that the larger species in group 2 and group 6 (which also includes *Megabalanus*, yet to be studied) are dominantly filter feeders on particular matter. Detailed investigation of the functional morphology of the feeding apparatus, the cirral action in food capture and the composition of the food intake are required on a wide range of species before a proper assessment can be made of the evolution of feeding mechanisms through the Balanomorpha and especially in the Balanidae (*s.s.*).

(*d*) *Cirral activity and feeding in* B. perforatus

The present paper attempts to make a beginning in the further analysis of balanid feeding mechanisms by describing the cirral activity and feeding of *Balanus perforatus* Bruguière, a basic group 6 species in which the food intake, like that of *Semibalanus balanoides*, indicates both captorial planktivory and filtratory microphagy as a result of the cirral rhythm. I would like to point out that it was A. J. Southward, whose work has provided the basis of much of our current knowledge of cirripede cirral mechanisms, who introduced me to the need for further study of *B. perforatus* and provided the advice that made this investigation possible.

2. Materials and methods

Specimens of *B. perforatus* collected from the shores of Plymouth Sound were either maintained in running sea water in the laboratory or preserved in 70 % alcohol. Observations were made on the opercular and cirral activities of living animals in still water, when subjected to a water current, and in the presence of barnacle nauplii as a source of food. Milk was used to display the water currents produced during cirral activity, following the method of Crisp & Southward (1956). Cinephotomacrography was used to record cirral movements and current production, by the method described in Anderson (1978). The films were subjected to frame-by-frame analysis of the recorded events. Anatomical details were obtained from dissections of fresh and preserved animals and drawings were made with the aid of a camera lucida. Thick, handcut sections of preserved specimens, embedded in gelatin after decalcification in 1 M HCl, were found to be useful in elucidating topographic anatomical relationships.

3. Anatomy

(*a*) *General anatomy*

Figure 1 illustrates the general shape and configuration of the shell and operculum, with the operculum in the raised position. As can be seen, the opercular membrane, which joins the operculum to the lower rim of the sheath, is broad and flexible in this species, especially at the carinal end (op.p.). Within this opercular membrane are muscles (r.m., figure 2) running radially from the basal margins of the terga (te.) to the basal margin of the sheath (sh.), supporting the membrane and preventing extension beyond a certain level. The apico-basal and rotational mobility of the operculum resides in the flexibility and width of the opercular membrane. The raising and opening of the opercular valves, as in all balanids, is by hydraulic action, the mechanism of which is still not clear (Crisp & Southward 1961). Closure of the valves is brought about by contraction of the adductor muscle (ad.). Retraction, and the rotational movements of the operculum, result from contractions of the powerful scutal and tergal depressor muscles (r.s.d., l.s.d., t.d.) in the thick mantle underlying the shell (figures 1, 2). These muscles are conspicuously enlarged in *B. perforatus* and form by far the largest organ system in the animal.

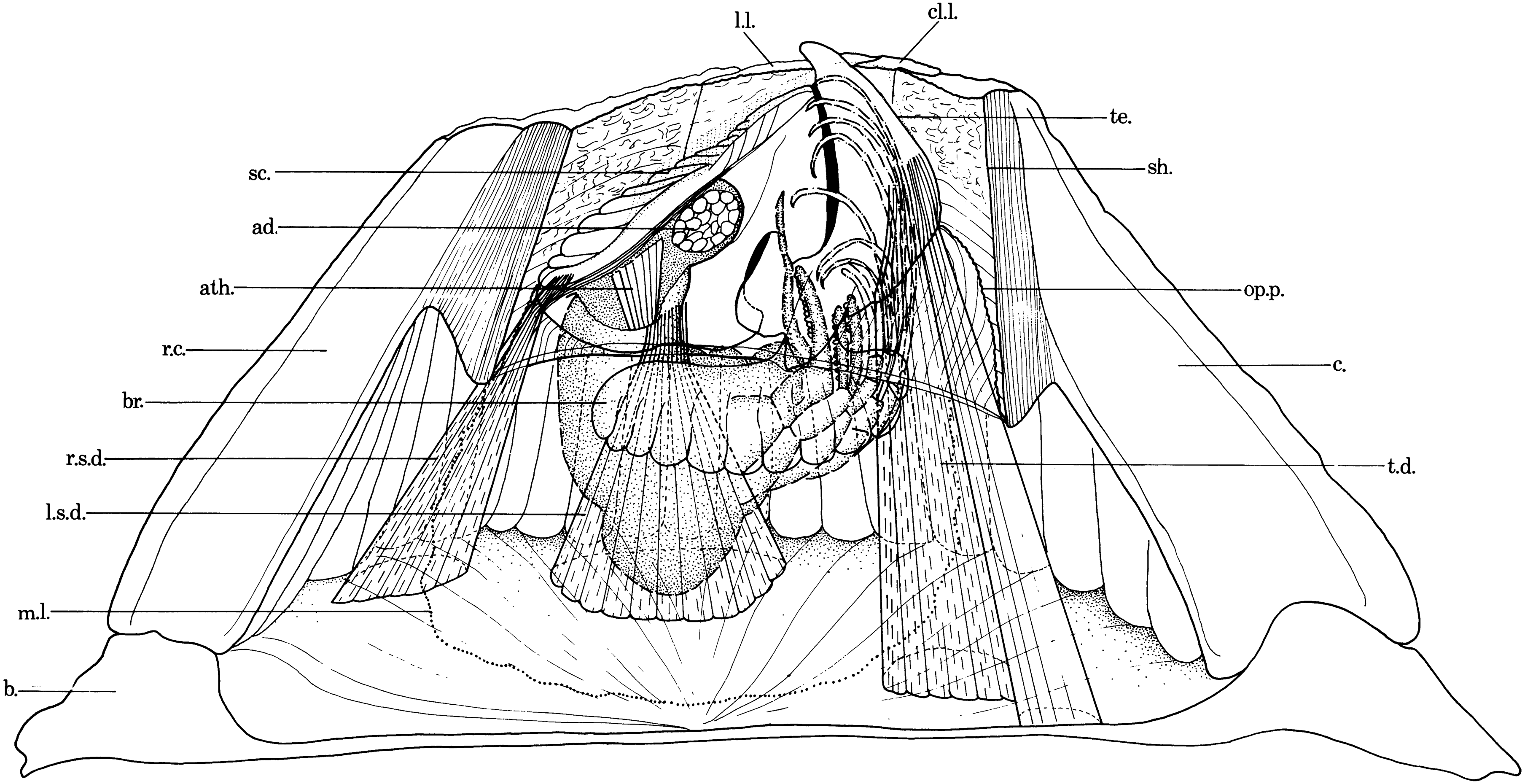

Figure 1. A reconstruction of the general anatomy of *B. perforatus* in right lateral view, showing the relationships between the wall, operculum, depressor muscles, mantle cavity, body and cirri; ad., adductor scutorum; ath., attrahens muscle; b., basis; br., branchia; c., carina; cl.l., left carinolateral; l.l., left lateral; l.s.d., lateral scutal depressor muscle; m.l., lining surface of mantle cavity; op.p., posterior wall of opercular membrane; r.c., compound rostrum; r.s.d., rostral scutal depressor muscle; sc., scutum; sh., sheath; t.d., tergal depressor muscle; te., tergum. Scale bar, 5 mm.

The mantle cavity is also large and is partially occupied by a pair of plicate gills (br.) depended from the tergal spurs of the operculum. The body of the animal is small relative to the shell, mantle and mantle muscles, and has ample space for movement within the mantle cavity. Notable features of the body (figure 3) are the swollen prosoma (pr.) with its protruberant dorsal surface, the large oral cone (co.), the three pairs of large, setose maxillipeds (cirri I–III) and the slim, delicate rami of the three pairs of posterior cirri (IV–VI). These relative proportions of the body, like the size of the body relative to the mantle structures, are all functionally correlated with the activities and mode of life of the animal.

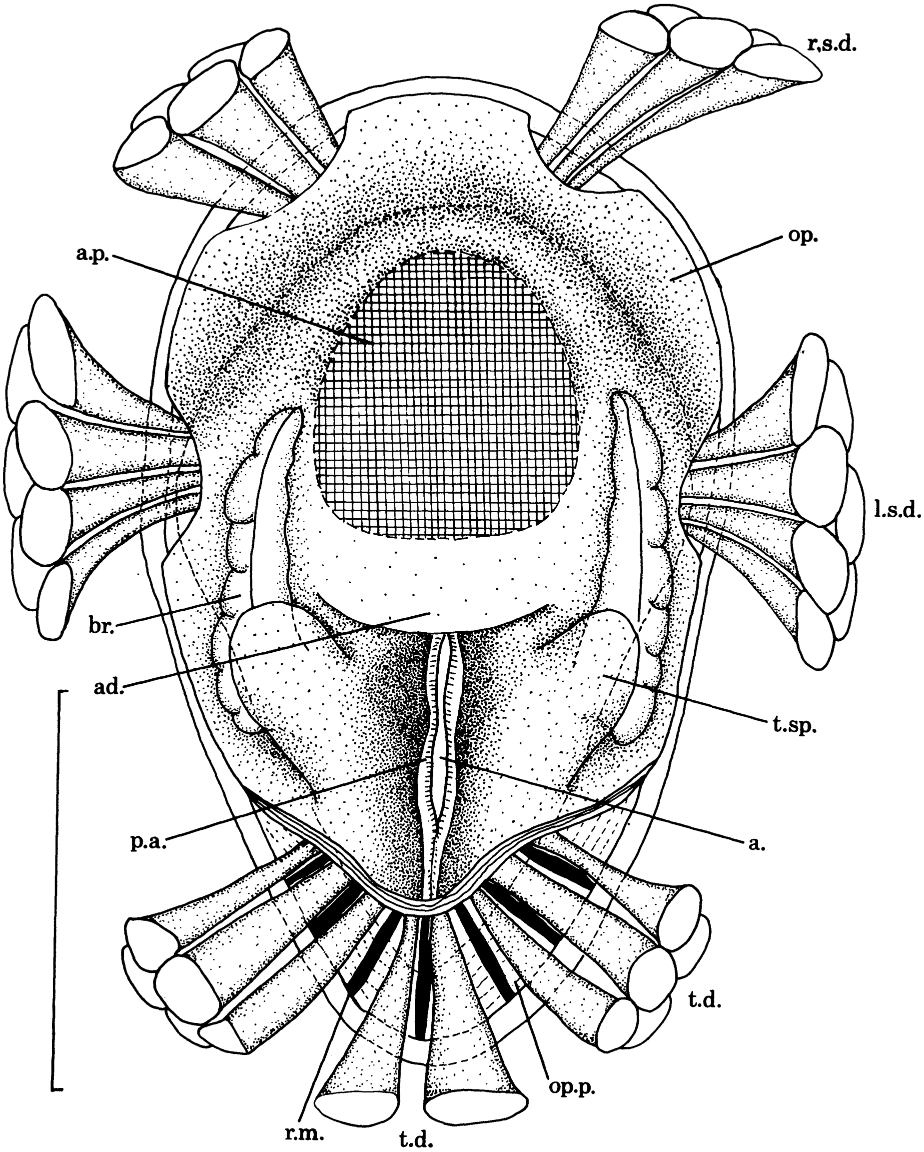

FIGURE 2. *B. perforatus*. An interior view of the operculum and opercular membrane; a., aperture; ad., adductor scutorum; a.p., attachment region of prosoma; br., branchia; l.s.d., lateral scutal depressor muscle; op., opercular membrane; op.p., posterior wall of opercular membrane; p.a., peripheral aperture membrane; r.m., radial muscle; r.s.d., rostral scutal depressor muscle; t.d., tergal depressor muscle; t.sp., tergal spur. Scale bar, 5 mm.

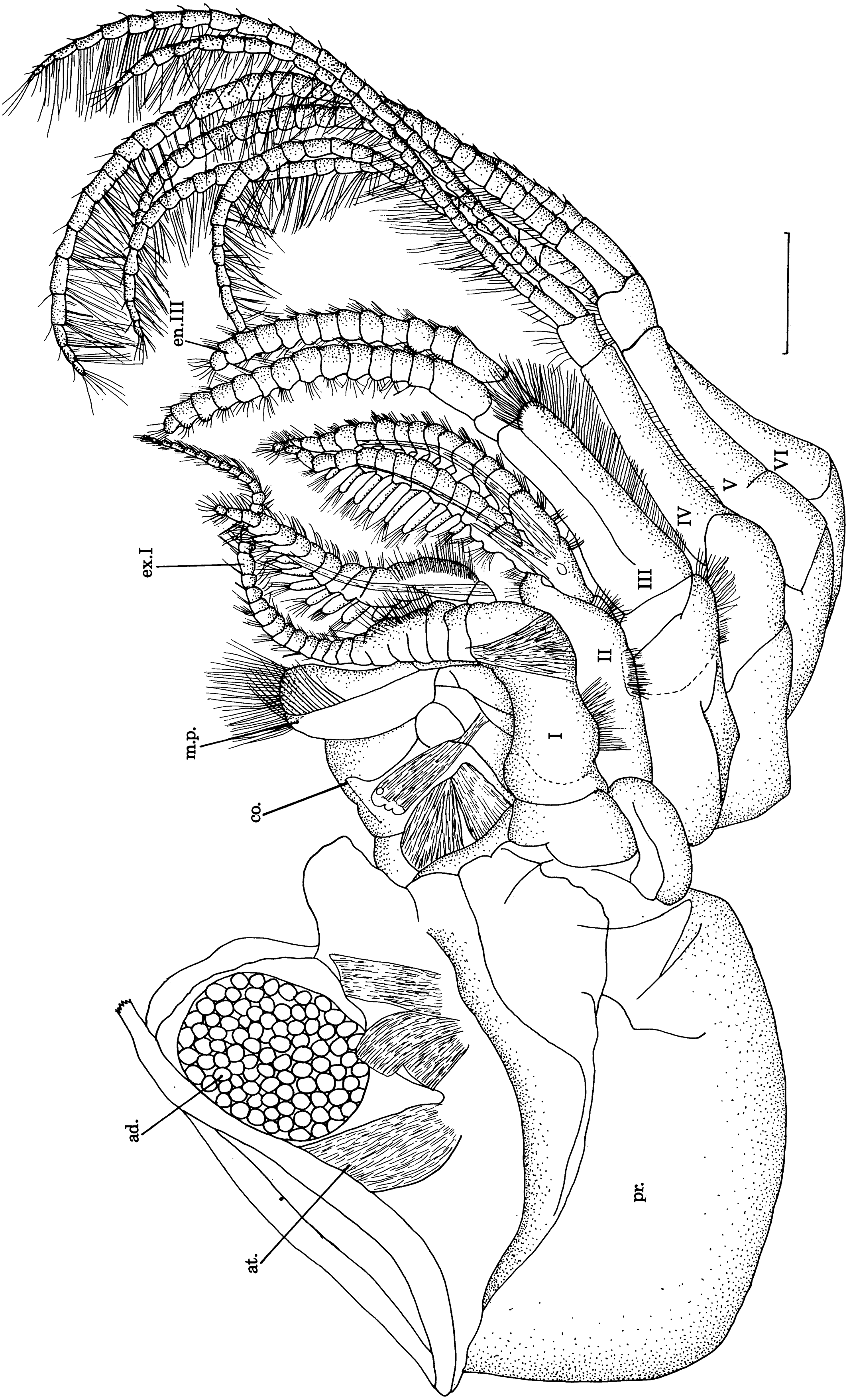

FIGURE 3. The body and limbs of *B. perforatus* in right lateral view; I–VI, cirri I–VI; ad., adductor scutorum; at., attrahens muscle; co., oral cone; en. III, endopod of cirrus III; ex. I, exopod of cirrus I; pr., prosoma. Scale bar, 1 mm.

(*b*) *Cirri*

The interpretation of these activities requires some further consideration of the details of the structure of the cirri, oral cone, and mouthparts of the species. Only details of functional relevance will be emphasized.

The three pairs of maxillipeds are distinctively specialized. Cirrus I (figure 4) has a long, terminally antenniform exopod and a short endopod. Typical podomere numbers are 30 and 17. The numerous podomeres of the exopod bear a dense array of apically directed setae on

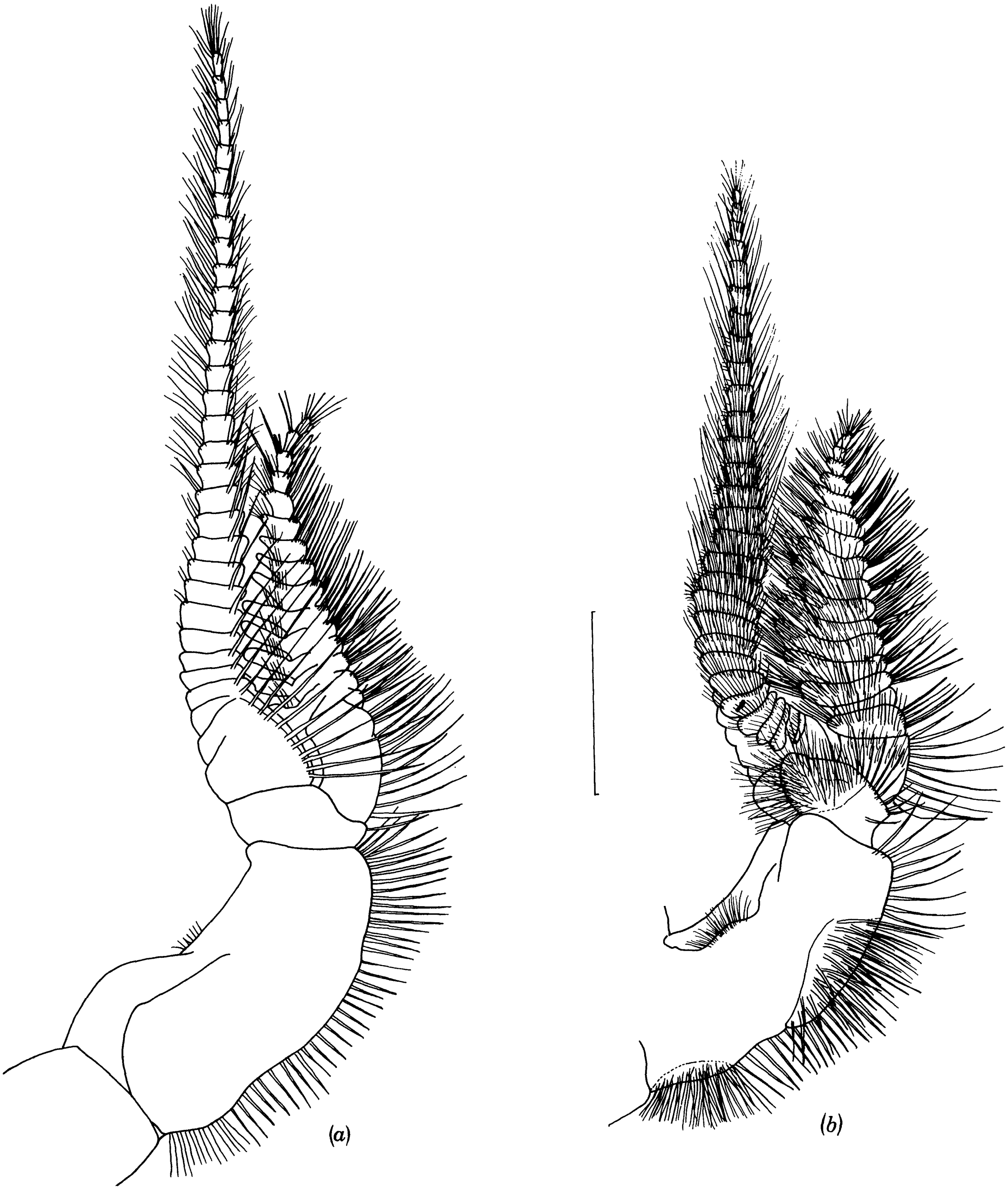

Figure 4. Cirrus I of *B. perforatus*: (*a*) right cirrus in lateral view; (*b*) left cirrus in median view. Scale bar, 1 mm.

their median surfaces. The lateral surface of the exopod is mainly devoid of setae, except for a pallisade of strong, posteriorly directed setae along the proximal posterolateral margin.

The short endopod of cirrus I is also almost devoid of setae laterally, but has a fringe of strong setae along the posterior margin. Medially, each podomere except the terminal few is

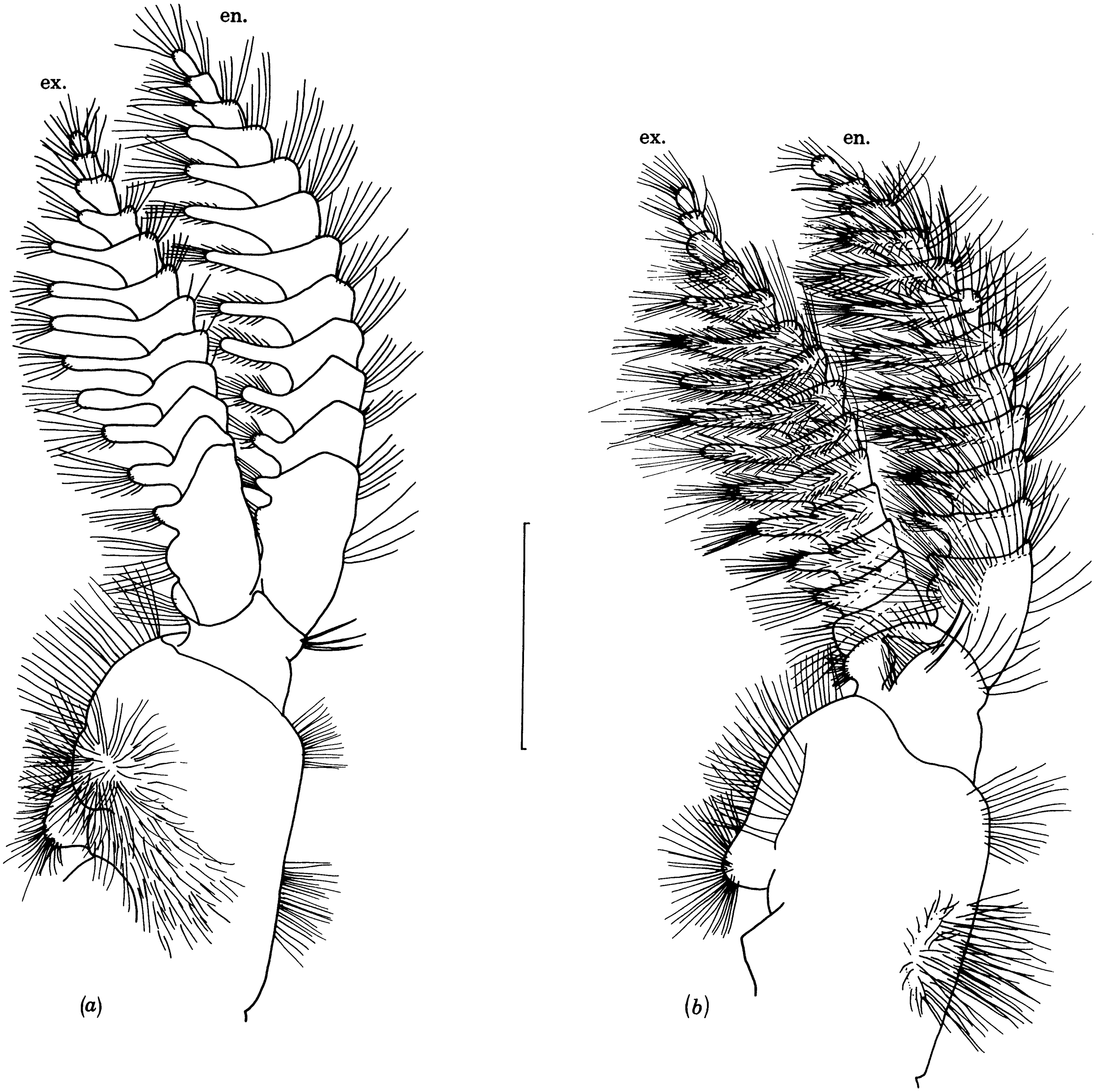

FIGURE 5. Cirrus II of *B. perforatus*: (*a*) right cirrus in lateral view; (*b*) left cirrus in median view; en., endopod; ex., exopod. Scale bar, 1 mm.

enlarged as an anteriorly projecting cushion bearing a dense brush of apically to anteriorly facing setae. Most of these are simple setae, but a number of serrate setae occur among them, especially in the more proximal brushes. The protopod of cirrus I carries two large groups of brush setae posterolaterally. These are presumably cleaning setae.

Cirrus II, in contrast, has two short rami (figure 5), both showing a more extreme modification of the endopod structure of cirrus I. Typical podomere numbers are 14 and 12. The protopod of cirrus II is also short and broad, the limb being tucked close in behind cirrus I on each side of the body (figure 3). The protopod carries bunches of brush setae. The endopod (en.) and exopod (ex.) both have median cushions on the podomeres, extending as forwardly projecting processes and carrying a dense array of apically to forwardly projecting setae. Like cirrus I these are mainly simple setae, but with an intermixture of serrate setae, especially basally.

Cirrus III is less modified as a maxilliped than the two cirri anterior to it, but shows a number of unique features (figure 6). The protopod is large, with a dense mass of brush setae posterolaterally on the coxa and a posterolateral fringe of brush setae on the basis. The exopod and

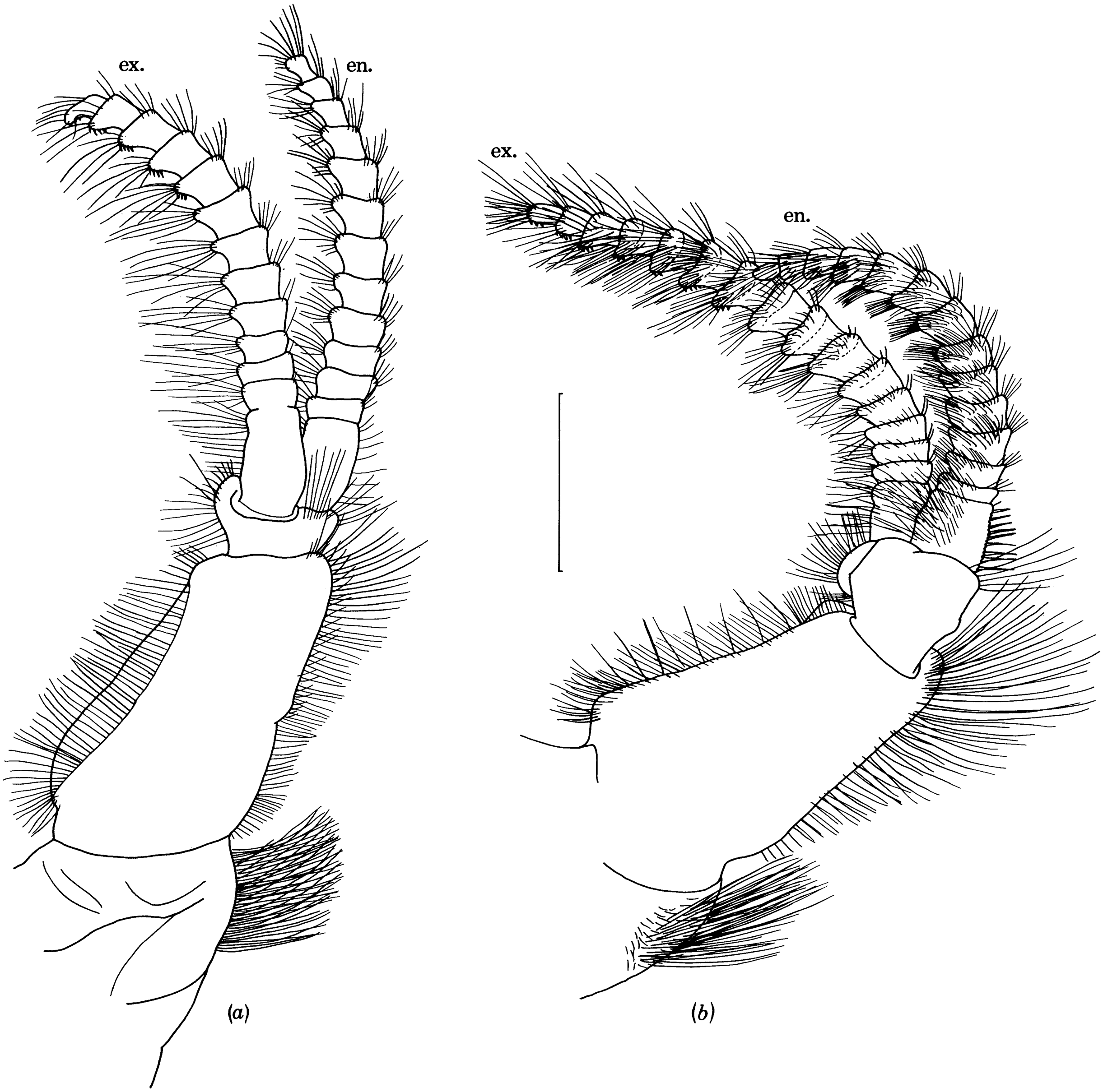

FIGURE 6. Cirrus III of *B. perforatus*: (*a*) right cirrus in lateral view; (*b*) left cirrus in median view; en., endopod; ex., exopod. Scale bar, 1 mm.

endopod are more or less cylindrical, the exopod being of moderate length, the endopod shorter. Typical podomere numbers are 16 and 14. Both rami are almost devoid of setae laterally. The podomeres of the exopod show some development of median forwardly projecting cushions on the apical part of the ramus and a forwardly projecting median setation which is denser on the apical podomeres than on the basal podomeres. In contrast to the two anterior maxillipeds, cirrus III has quite a lot of serrate setae apically on the exopod and a few basally. The

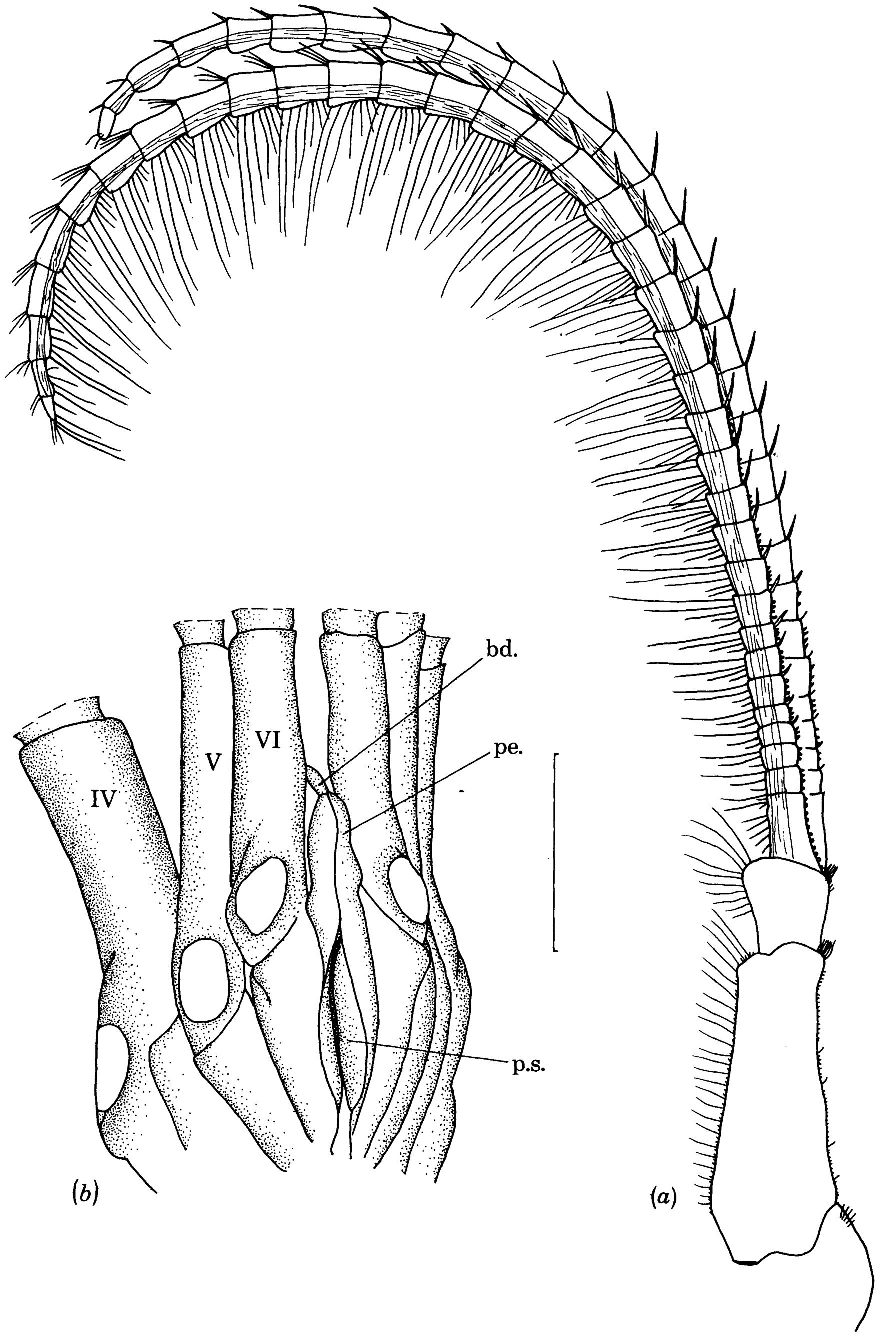

FIGURE 7. *B. perforatus*: (*a*) right cirrus V in lateral view; (*b*) bases of cirri IV–VI in posterodorsal view; IV–VI, cirri IV–VI; bd., basidorsal point of penis; pe., penis; p.s., pulsatile sac. Scale bar, 1 mm.

terminal seven podomeres of the exopod also bear chitinous teeth on the anterior apical surface. The short endopod is devoid of these teeth or of the median cushions present on the exopod. It has a less dense median setation, though the setae again point anteriorly on each podomere.

In contrast to the well developed maxillipeds, the last three pairs of cirri (IV–VI) of *B. perforatus* are long and slender (figure 7*a*), with more or less equal, cylindrical rami and narrow, close-set protopods. Typical podomere numbers are 32/32, 36/29 and 30/30 for the exopod and endopod of the three cirri. Each podomere carries a row of paired anterolateral setae, the distal pairs being long, the proximal pairs progressively shorter. In the middle region of the ramus there are seven pairs of setae per podomere, with smaller numbers proximally and distally. Short setae also arise from the distal posterior margins of the podomeres, in groups distally and as single spines proximally. Over the posterior third of the exopod and quarter of the endopod of cirrus IV and V, but not VI, the podomeres also carry a row of chitinous teeth. These presumably function in cleaning the carinal end of the aperture.

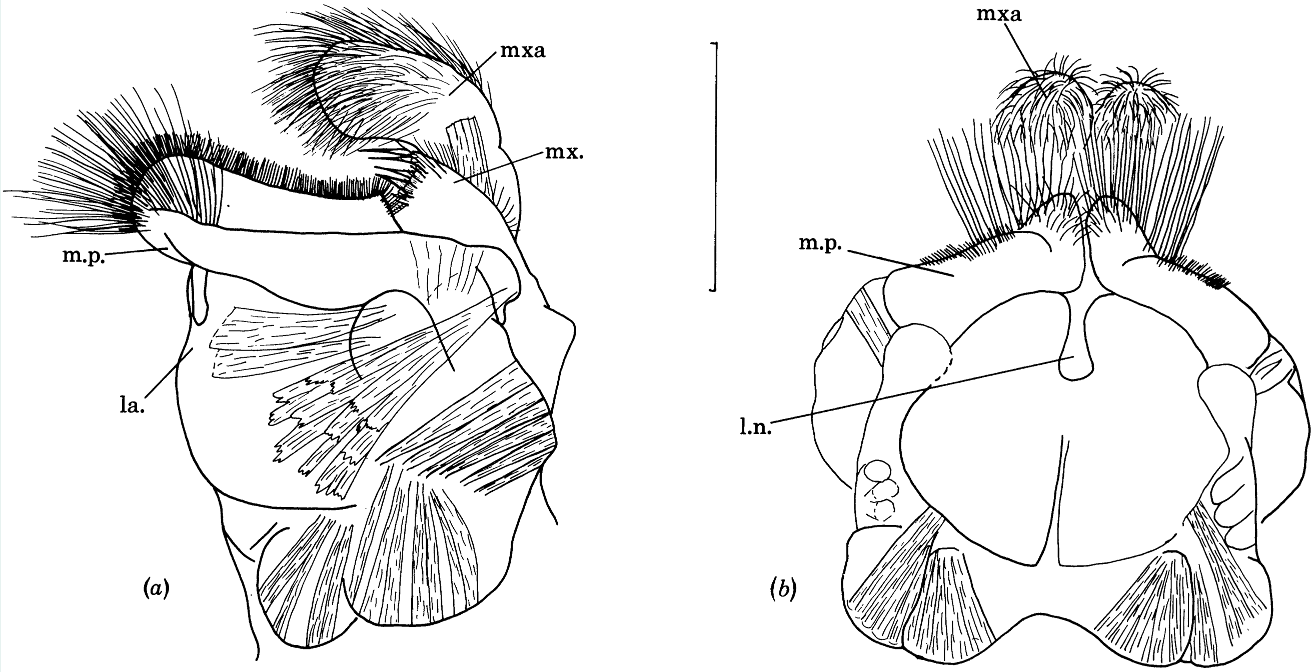

FIGURE 8. Oral cone of *B. perforatus*: (*a*) right lateral view; (*b*) ventral view; la., labrum; l.n., labral notch; m.p., mandibular palp; mx., maxillule; mxa, maxilla. Scale bar, 1 mm.

At the base of the penis, between the bases of the last pair of cirri, is an elongate, double swelling, the pulsatile sac (figure 7*b*). This sac enlarges and diminishes in association with each rhythmic extension and withdrawal of the long cirri. As the cirri are curled and withdrawn the pulsatile sac swells and enlarges. As the next cirral extension proceeds, the swelling disappears and the sac becomes a concavity at the surface of the body. This pulsatile sac therefore acts as a reservoir of fluid involved in the hydraulic extension of the cirri, though whether it has any contractile function in this action has yet to be determined.

(*c*) *Mouthparts*

The oral cone of *B. perforatus* (figure 8) is large, with a flattish labrum bearing a typical balanoid labral notch (l.n.). The most conspicuous features of the intact oral cone are the setose mandibular palps (m.p.) flanking the labrum and the highly setose and elongate lobes of the maxillae (mxa).

A dense, fine setation is characteristic of all the mouthparts. The mandibular palps have long, posteriorly directed setae apically, on either side of the labral notch, and a fringe of short

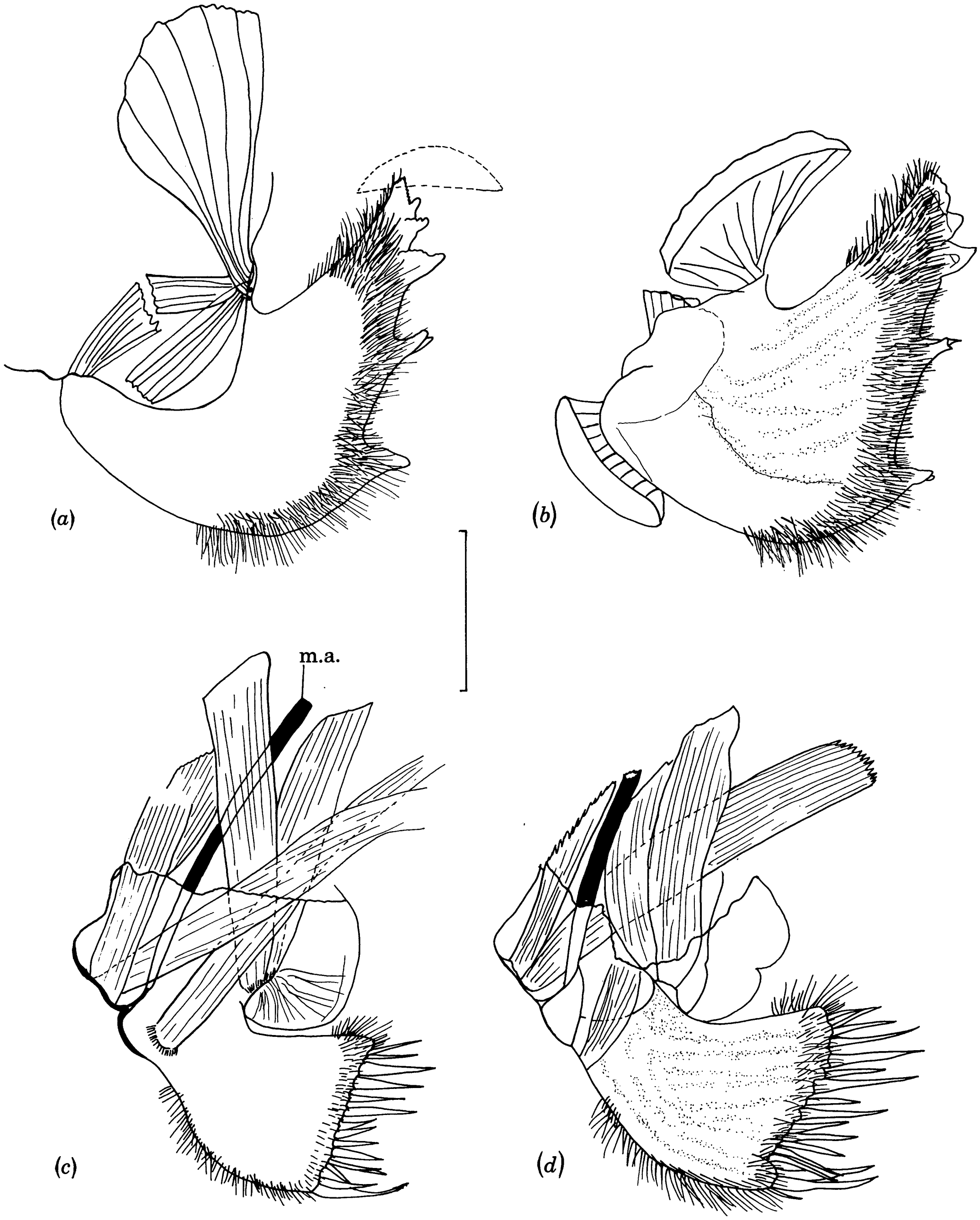

FIGURE 9. *B. perforatus*: (*a*) right mandible, lateral view; (*b*) left mandible, median view; (*c*) right maxillule, lateral view; (*d*) left maxillule, median view; m.a., maxillulary apodeme. Scale bar, 0.5 mm.

setae along the posterior edge. These fringed edges form the lateral margins of the entrance of the preoral cavity. The mandibles (figure 9*a*, *b*) are setose along the cutting margin, both laterally and medially. In contrast, the incisor tooth and the three intermediate teeth of the mandibular edge are low and blunt and the molar process is only weakly rugose. The maxillule (figure 9*c*, *d*) has fine setation along the lateral and cutting margins. The cutting margin is also more or less straight, bearing spines of moderate size along its length, with little differentiation of larger spines at the lateral angle. The maxillae (figure 10) are elongate, soft lobes, reflexed towards the labrum, with an apical covering of long, soft setae. Proximal to the terminal lobe, the maxilla of each side bears a smaller lobe, also directed towards the labrum. Between these smaller lobes, the maxillae are conjoined to form the slightly convex roof of the preoral cavity, the surface of which is beset with very short setae. As will be discussed below, the setose nature of the mouthparts and walls of the preoral cavity is functionally correlated with a capacity for particulate feeding.

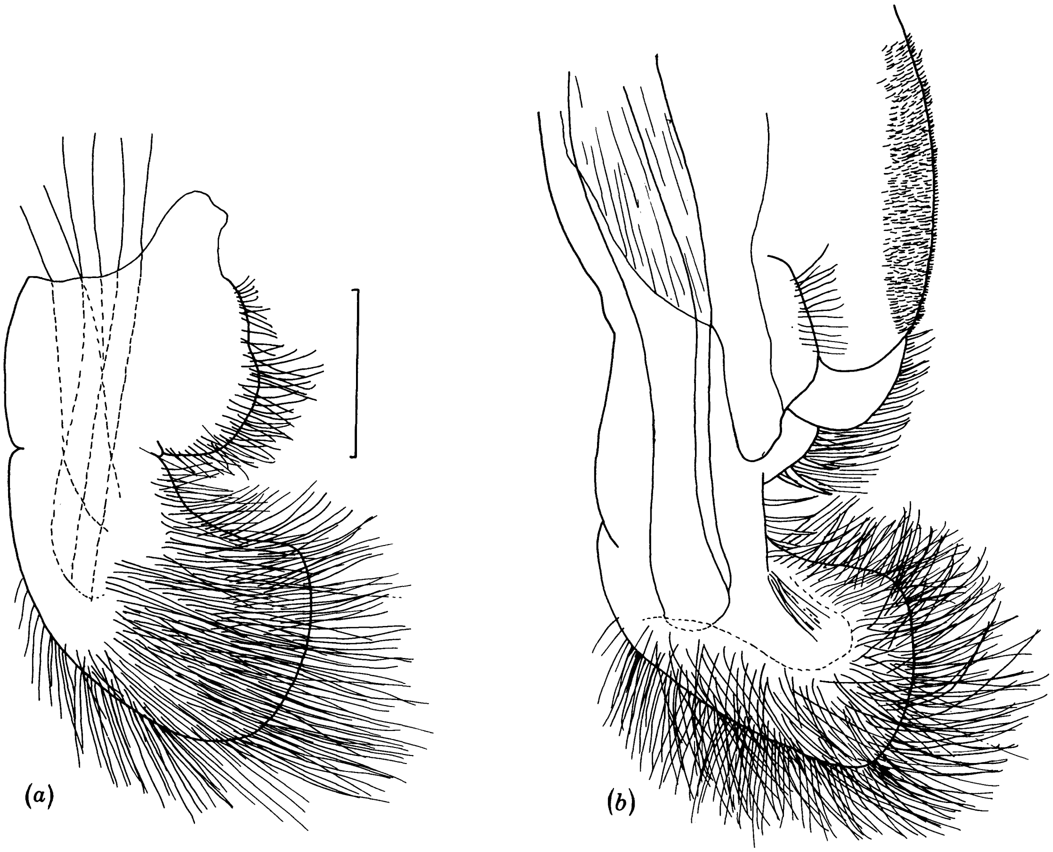

FIGURE 10. *B. perforatus*: (*a*) right maxilla, lateral view; (*b*) left maxilla, median view. Scale bar, 0.5 mm.

4. CIRRAL ACTIVITY

Figure 11 illustrates the sequence of cirral extension and withdrawal in *B. perforatus* during a single beat. Cirri IV–VI emerge from the aperture, uncurling to stand upright as a forwardly curved fan at the carinal end of the aperture. Cirrus III on either side is included in this extension, the short rami of this cirrus being situated carinolaterally at the sides of the main cirral fan in the extended position.

As the long cirri emerge and uncurl at the carinal end of the aperture the antenniform exopods of cirrus I emerge and project upwards at the rostral end of the aperture as a parallel pair. At the onset of the withdrawal process, these rami are quickly withdrawn. The short endopods of cirrus I and the short rami of cirrus II do not protrude from the aperture at any stage during cirral extension and withdrawal. In the extended position, these short rami can be seen within the aperture, grouped over the maxillae and labrum at the tip of the oral cone. The endopods of the first maxillipeds are just posterolateral to the maxillae. The second maxillipeds are in a more posterior position, projecting obliquely forwards towards the maxillae.

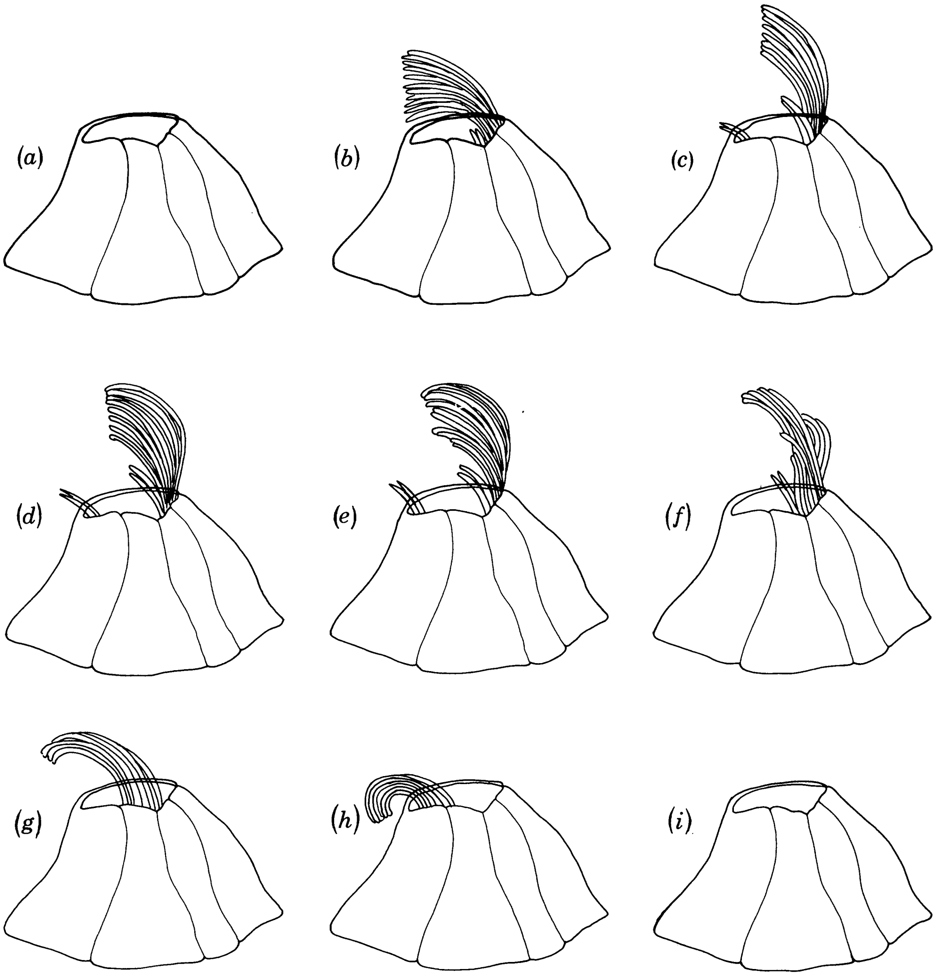

FIGURE 11. *B. perforatus*. A single sequence of extension and withdrawal of the cirri in an animal beating at an average rate of 7 per 10 s. (*a*)–(*i*) From successive frames of a film taken at 18 frames per second.

In the withdrawal sequence, as the exopods of cirrus I are retracted within the mantle cavity, the long cirri begin to swing forwards towards the rostral end of the aperture. At the same time, cirrus III on either side stands upright before curling down into the mantle cavity. The long cirri bend forwards and downwards over the edge of the rostrum before being finally withdrawn into the interior, preparatory to the next extension. The body movements under-

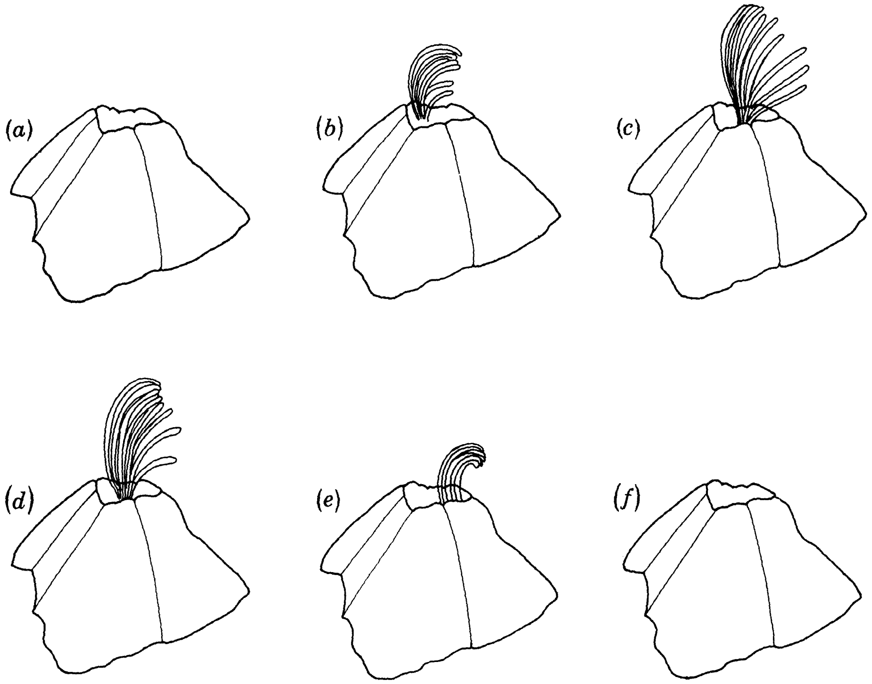

Figure 12. *B. perforatus*. A single sequence of extension and withdrawal of the cirri in an animal beating at an average rate of 24 per 10 s. (*a*)–(*f*) From successive frames of a film taken at 18 frames per second.

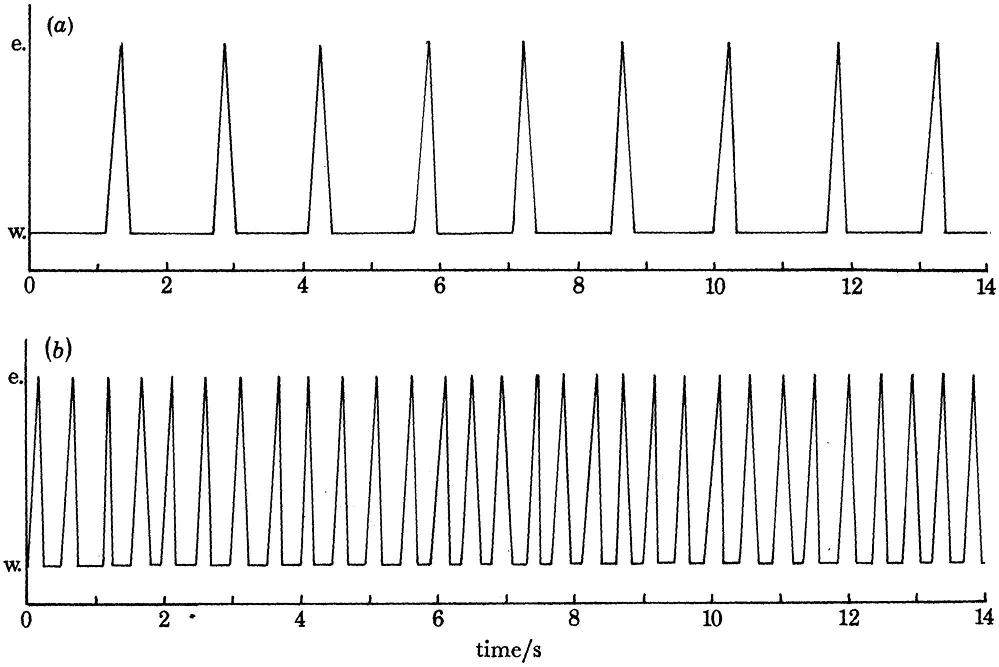

Figure 13. *B. perforatus*. Timing of cirral beating, based on cinematographic data; e., cirri extended; w., cirri withdrawn. Number of beats per 10 s: (*a*) 7; (*b*) 21.

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lying this sequence of cirral extension and withdrawal, and the position and actions of the limbs in the withdrawn position, will be discussed in § 5.

The above sequence of events is displayed by animals performing cirral beating at slow to moderate rates. At faster rates of beat, some simplification of this sequence is evident (figure 12). The long cirri are less fully extended, begin their forward and downward swing as extension is completed, and curl less far over the rostral margin during their withdrawal into the mantle cavity. The rami of the third and first maxillipeds (cirrus III and I) do not protrude through the aperture during the beat. In general, as well as being faster, the cirral stroke is lower and shorter at faster rates of beat.

TABLE 1. THE TIMING OF EVENTS DURING BEATING IN *B. PERFORATUS*

number of beats per 10 s	mean time for cirral extension/s	mean time for cirral withdrawal/s	mean interval between withdrawal and next extension/s	total mean duration of beat cycle/s
2.8	0.17	0.09	3.28	3.54
7	0.20	0.13	1.11	1.44
9	0.22	0.11	0.85	1.18
10	0.23	0.11	0.58	0.92
12.6	0.21	0.14	0.31	0.66
17.6	0.10	0.06	0.40	0.56
21	0.17	0.08	0.22	0.47
23	0.17	0.06	0.20	0.43
24	0.17	0.06	0.18	0.41

The timing of the externally visible events of cirral beating is illustrated in figure 13 for two individuals beating at rates of 7 and 21 per 10 s respectively. Each beat cycle is measured from the onset of one cirral extension to the onset of the next. The rates of cirral extension and withdrawal are almost constant from beat to beat and are only slightly higher at the faster rate of beat. As expected from the functional mechanisms involved, hydraulic extension is the slower and muscular withdrawal the faster process.

Table 1 compares the timing of events of the beat cycle for a range of rates of beat. The rates of extension and withdrawal of the cirri vary little throughout this range. A much greater variation is seen in the duration of the interval between each cirral withdrawal and the next extension. For example, as figure 13 shows, this interval averages 1.1 s at 7 beats per 10 s and 0.22 s at 21 beats per 10 s. Thus, to a large extent, the rate of beating in *B. perforatus* is governed by the duration of the withdrawn portion of the beat cycle rather than by changes in cirral action (figure 14). The slower the rate, the longer is the duration of the period in the withdrawn position. Conversely, the faster the rate, the shorter this interval becomes, up to an asymptotic minimum of 0.18 s at 23° in the present study (rates at higher temperatures were not observed). At this interval duration, the rate of beating is maximal, at 24 per 10 s. For reasons that will be explained below, it seems unlikely that *B. perforatus* can exeed this performance.

Figure 14 also implies another feature of cirral beating in *B. perforatus*, confirmed from direct observation, that there is no sharp distinction between mechanisms of normal and fast beat in this species. The rate of beating is continuously variable over a range from 2 to 24 per 10 s, without any significant change in the pattern of cirral extension and withdrawal other than a tendency towards less full protrusion at faster rates.

B. perforatus also holds the opercular valves raised and open continuously when beating, at all rates, and each beat cycle is accompanied by a pumped flow of water through the mantle cavity. The faster rates, which have a lesser emphasis on cirral extension and spread, simultaneously increase the flow of water through the mantle cavity. This is the opposite of the fast-beat activity described by Crisp & Southward (1961). The functional significance of this feature of *B. perforatus* compared with the previously analysed balanid rhythmic actions is examined in § 5.

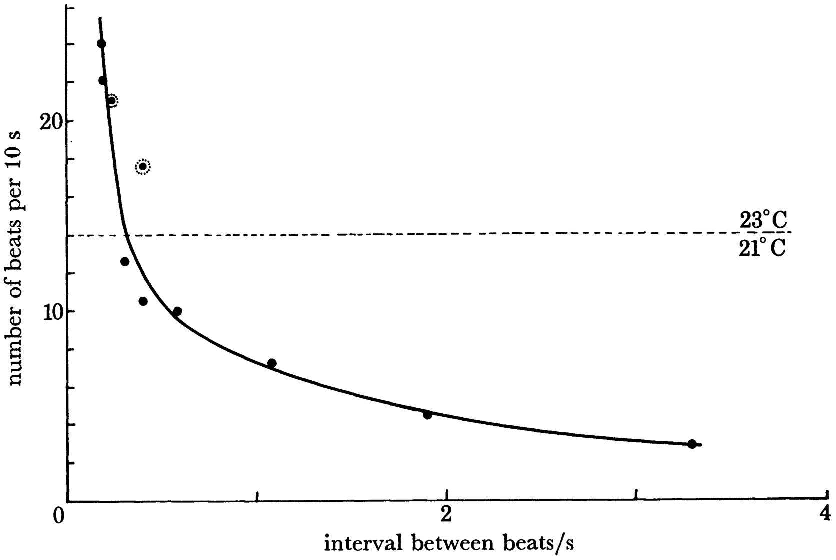

FIGURE 14. *B. perforatus*. Relation between rate of beating (successive cirral exposures) and duration of interval between successive beats. Each point represents an average for a different animal, obtained by analysis of cinematographic records (see table 1 for details). The observations were made on animals in still water containing nauplii of the same species. In two cases, indicated by rings, a milk stream was also applied to the animal to display water currents.

Factors governing the rate of beating in *B. perforatus* were little explored in the present work. At temperatures ranging from 15 to 21 °C, different individuals were simultaneously observed beating at rates varying from 2 to 12.5 per 10 s, in still water containing balanid nauplii as a source of food. A variety of devices was used to produce a flow of water over the animals, but none resulted in any striking changes in their range of rates of activity. An increase in the temperature to 23 °C, however, caused the rate of beating in some individuals to tend towards maximal, while other individuals closed the operculum and ceased activity. Apart from this observation, there appears to be much individual variation in the activity of *B. perforatus* at its normal temperature range, with activity being little influenced by water movement or the presence of zooplanktonic prey. The whole question of activity rates in this species needs further study.

5. PUMPING ACTIVITY

(*a*) *The water current*

Crisp & Southward (1961) used the term ‘pumping’ for the level of rhythmic activity in which the cirri are not extended through the aperture. Since the pumping of a current of water through the mantle cavity also accompanies the process described by these authors as normal beat, it would seem more appropriate to restrict the term pumping to the flow generated on a single beat, and to redefine the 'pumping' of Crisp & Southward as pumping beat.

In *B. perforatus*, pumping beat is not an important activity. Animals that are open and active usually show rhythmic cirral extension. At all rates of cirral activity the pumping action association with cirral beating is vigorous and consists of a sequence of pulses of water drawn in and forced out by the body movements underlying the cirral movements. The purpose of the present section is to describe this water flow and to analyse the mechanism of the pumping action.

To investigate the pattern of water flow, small amounts of milk diluted with sea water were supplied by pipette to the vicinity of the aperture of actively beating animals (Crisp & South-

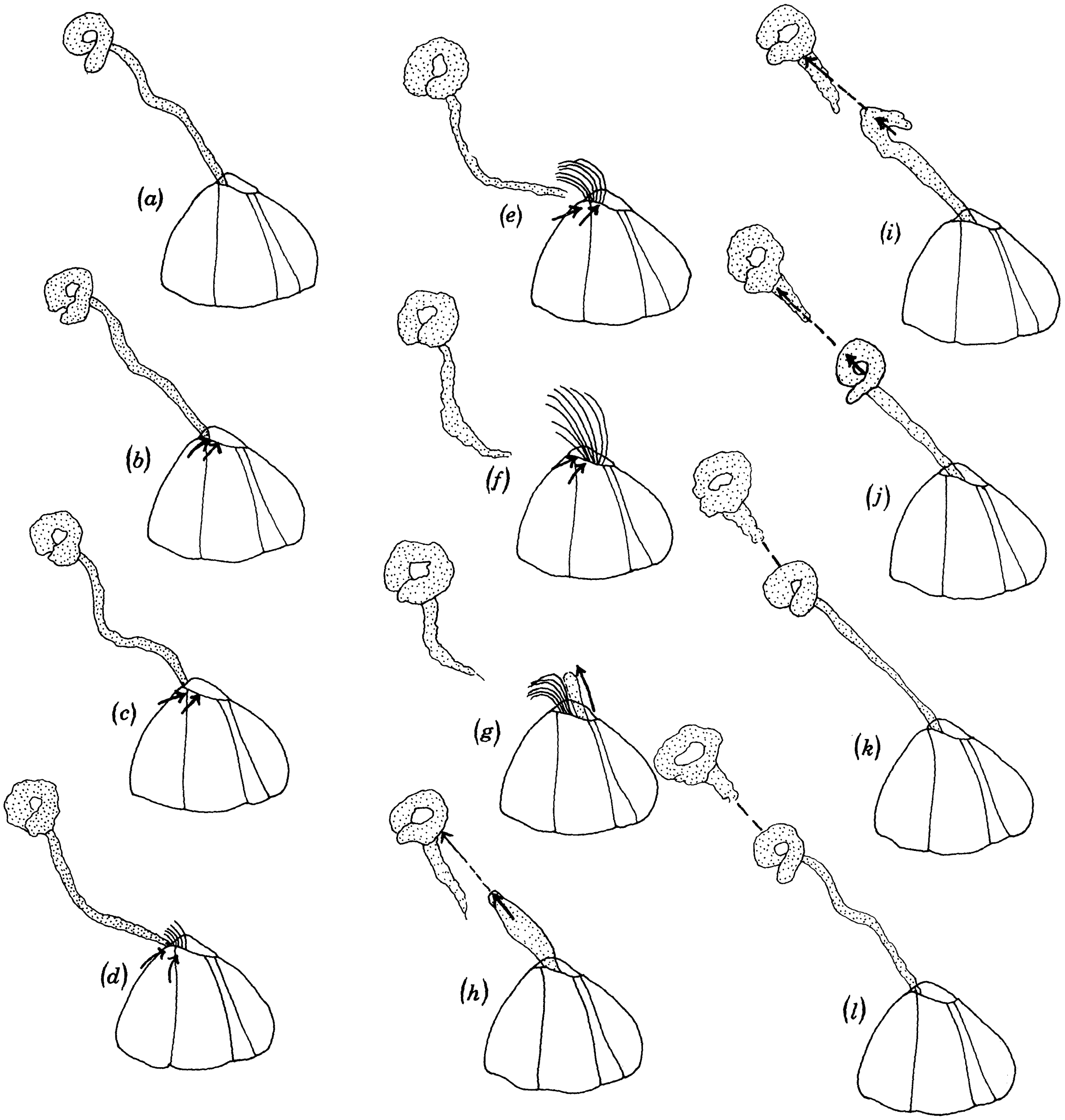

FIGURE 15. *B. perforatus*. The production of a water current in an animal beating at an average rate of 23 per 10 s, with milk used to display the current. Diagrams (*a*)–(*l*) are of successive frames of a film taken at 18 frames per second.

ward 1956). Cinematographic records were then made of the resulting milk trails produced by the pumping action and subjected to frame-by-frame analysis. Figure 15 shows the current flow associated with a single beat by an animal treated in this way when beating at 23 beats per 10 s, a rate close to the maximum for the species. The rostral end of the animal is on the left. As can be seen, the beginning of the sequence (*a*) shows the milk trace of the water expelled from the mantle cavity by the pump of the preceding sequence. The outflow is directed rostrally and upwards from the orifice, travelling about 50 mm before losing momentum and beginning to eddy into the surrounding water. Before the tips of the cirri begin to emerge through the aperture at the onset of the next phase of cirral extension (*b*, *c*), water begins to flow into the mantle cavity around the rostral margin of the orifice. This inflow continues (*d*, *e*, *f*) as the cirri extend and swing back to stand upright at the carinal end of the aperture. Meanwhile, the previously expelled pulse of water remains in the water above and rostral to the animal, slowly aggregating and eddying.

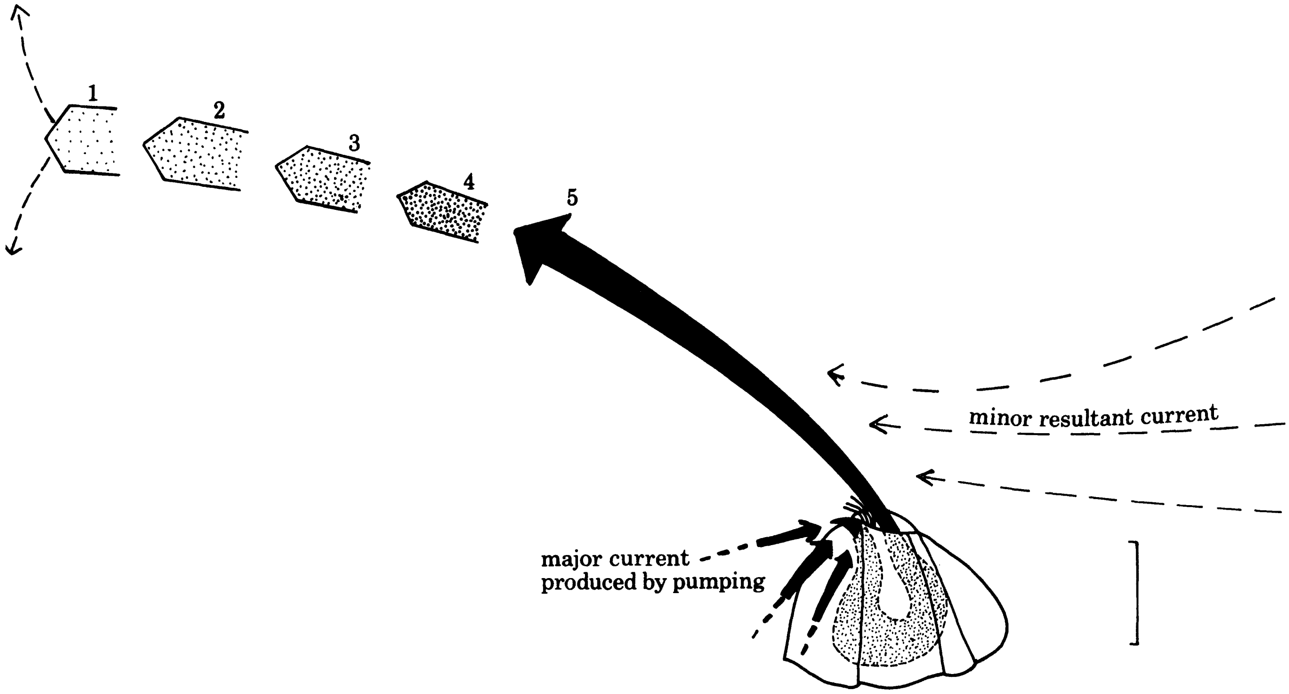

Figure 16. *B. perforatus*. Major and minor water currents associated with cirral beating. (1)–(5) Outflow from mantle cavity, on successive beats, at 23 beats per 10 s. Scale bar, 10 mm.

As soon as the extended cirri swing rostrally and down at the next withdrawal movement, the rostral inflow into the mantle cavity ceases and a powerful outflow begins (*g*). This outflow emerges as a jet from the carinal end of the orifice, flowing rostrally and upwards behind the withdrawing cirri. The outflow continues as a powerful, narrow stream after cirral withdrawal is complete (*h*, *i*, *j*), gradually slowing and eddying terminally (*k*, *l*). As it flows, the jet pushes ahead of it the pulse of water moved by the preceding pumping action.

The repeated pumping which accompanies rhythmic cirral protrusion and withdrawal in *B. perforatus* thus results in a pulsed inflow of water into the mantle cavity and its expulsion as a strong current flowing rostrally and upwards away from the animal (figure 16). For an individual of some 12 mm shell height, the outflow can be traced for about 100 mm into the water above and in front of the animal before it disperses. This, together with the direction of inflow, indicates that little or no recirculation of the same water through the mantle cavity occurs as pumping proceeds. The emergent cirri sweep the water close to the orifice between each pulsed outflow. The powerful, rostrally directed jet causes the resultant flow of a minor current of water towards the orifice from a carinal direction, which may play a part in bringing particles into the vicinity of the sweeping cirri.

While it is difficult to establish precise figures, some estimate of the rate and volume of flow of the mantle current can be attempted from the film records, the dimensions of the animal and the distance travelled by the outflow being known. For the specimen illustrated in figure 16, beating at 23 beats per 20 s, each pulsed outflow has an average diameter of 2 mm and length of 45 mm. The pulse of water ejected at each beat, therefore, has an approximate volume of 0.14 ml. On this basis, the amount of water flowing through the mantle cavity of a 12 mm high *B. perforatus* pumping at close to maximum performance is approximately 3.25 ml per 10 s or about 1.2 l/h. While this figure can only be proposed as a rough estimate, it is indicative of the order of magnitude of the water flow through the mantle cavity in this species. For slower rates of beating the volume of the water pulse produced with each beat remains similar, so that a proportionately smaller volume of water is passed per unit time. The significance of this through current will be discussed in § 6*b*.

(*b*) *The pumping action*

The point that emerges most clearly from the observation of the pumping activity of *B. perforatus* is that each intake and expulsion of water from the mantle cavity in this species occupies a much longer time than the associated extension and withdrawal of the cirri through the aperture. During the course of the present investigation an opportunity presented itself to examine in detail the body movements underlying the intake and expulsion of water during pumping. An individual was obtained, fortuitously, in which a naturally occurring hole in the basis permitted the simultaneous observations of body movements within the mantle cavity and the extension and withdrawal of the cirri through the aperture. This animal maintained normal activity for two days in the laboratory, beating at a rate of 9 beats per 10 s for long periods. Film records were obtained of the body and cirral movements and subjected to frame-by-frame analysis. Direct observation also allowed the position of the body within the mantle cavity to be ascertained for various stages in the beat cycle. Figure 17*a*, *b* represents the sum of these observations, with the animal fully withdrawn in figure 17*a* and fully extended in figure 17*b*. In the fully withdrawn position, the dorsal surface of the prosoma is pressed against the inner rostral surface of the wall and basis. In the fully extended position, the prosoma has swung carinally and upwards on the axis of the adductor scutorum and the cirral bases block the aperture carinally. As described by Crisp & Southward (1961), the intake and expulsion of water from the mantle cavity is a natural corollary of these movements, in which the prosoma acts as a force pump. As the body swing carinally, culminating in cirral extension, a space is created at the rostral end of the mantle cavity, into which water flows via the rostro-lateral regions of the aperture. As the body then swings rostrally, accompanied by cirral coiling, the additional water in the space is forced carinally and deflected, via the inner surface of the mantle, out through the carinal end of the aperture. Due to this channelling effect, the exhalent pulse emerges from the aperture as a narrow, rostrally directed jet. Figure 17*c* illustrates the

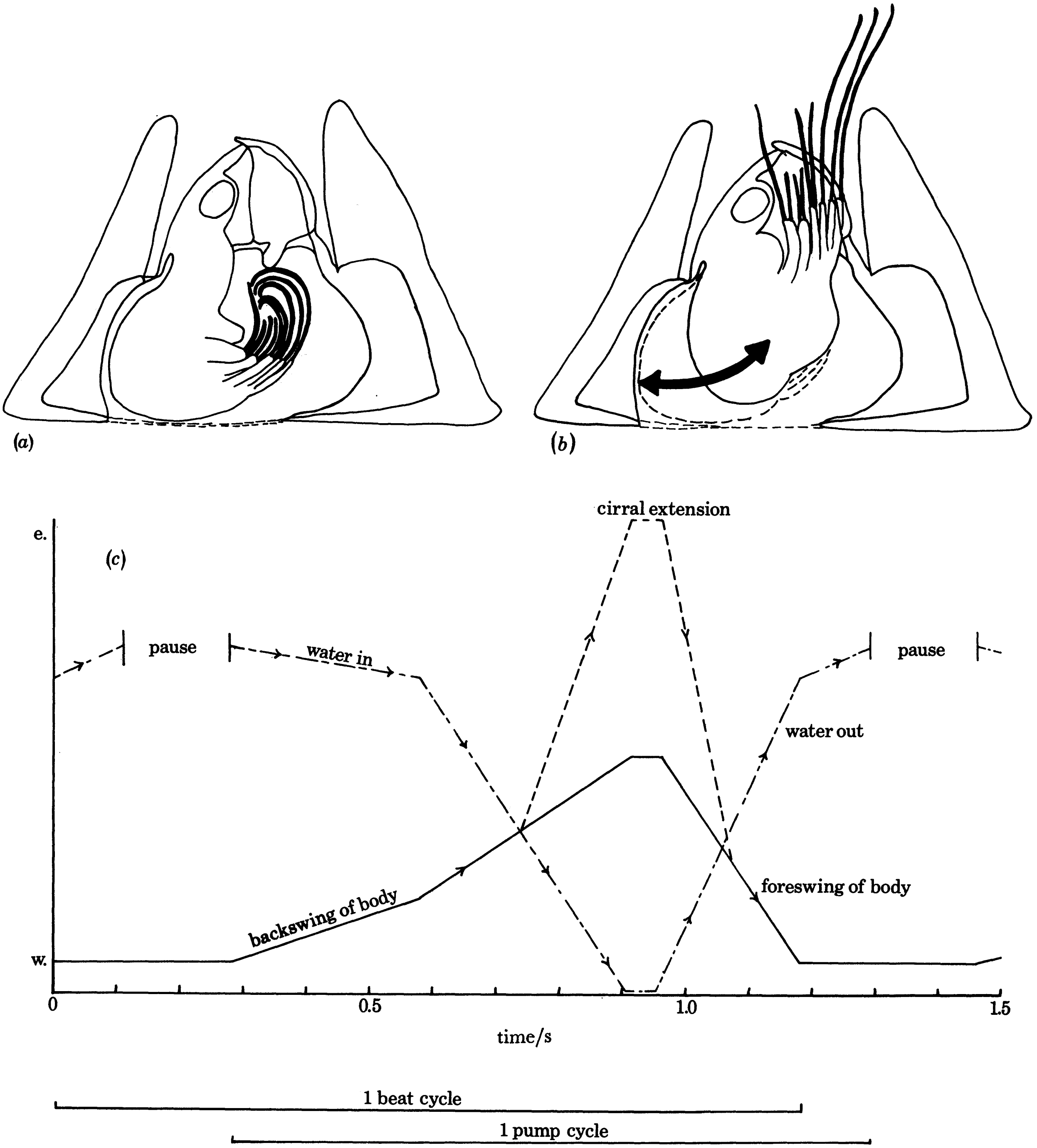

FIGURE 17. *B. perforatus*: (*a*), (*b*) body movements underlying cirral extension and withdrawal; (*a*) animal in the withdrawn position; (*b*) animal in the extended position; (*c*) the temporal relation between the beat cycle and the pump cycle in an animal beating at an average rate of 9 per 10 s (for explanation, see text); e., cirri extended; w., cirri withdrawn.

temporal relationship between body movement, cirral extension and water flow, based on the average timing of events during a sequence of 25 beats at 9 per 10 s. The representation of body movement is derived from direct analysis of the film records. Between body movements, the body pauses in the withdrawn position for 0.28 s. When the back swing commences, it proceeds slowly for the first 0.30 s, then faster for 0.33 s, to completion at 0.63 s from the onset of the movement. The body is then held briefly in the raised position, for 0.05 s, before commencement of the downward and forward swing. This movement proceeds at a constant rate, more rapid than the backswing, and is completed in 0.22 s.

The extension and withdrawal of the cirri, measured as emergence from and retreat within the aperture, occupies only a brief period embracing the peak of the underlying body movement. Cirral extension begins 0.46 s after the onset of the backswing and is completed in 0.17 s, coincident with the completion of backswing. The cirri remain extended for 0.05 s, while the body holds its raised position, and are then rapidly curled down and withdrawn as the body commences its forward and downward swing. Cirral withdrawal takes 0.11 s. Thus cirral extension occurs during the last quarter of the backswing of the body and cirral withdrawal during the first half of the forward swing. Relating this information to that presented in figure 13*a*, the intervals between cirral beats in the latter figure include the time when the body is moving within the mantle cavity as well as the time when the body is stationary in the withdrawn position.

When observations on beating are made in external view, the beat cycle is most conveniently measured from the onset of each cirral extension (table 1). When the underlying body movements are appreciated, however, it becomes obvious that cirral extension and withdrawal occur during a sequence of events that begins and ends with the body in the fully withdrawn position, shortly after the completion of cirral withdrawal. In this definition, at average rates of beat, the beat cycle begins with a pause in the withdrawn position, followed by a backswing of the body, accompanied by cirral extension, then culminates in a forward swing of the body, accompanied initially by cirral withdrawal. Of these events, only cirral extension and withdrawal can normally be observed, but a definition of the beat cycle based on body movements has marked advantages over one based on cirral extension when different rates of beating and the mechanism of pumping are being considered.

Body movements were observed in the present study for only one rate of beat, but certain inferences can be drawn from a comparison of figures 13 and 17*c* and table 1. These inferences are expressed graphically in figure 18. At 9 beats per 10 s, the total duration of the beat cycle is 1.18 s, of which the body movement, back and forth, occupies 0.90 s and the pause in the withdrawn position 0.28 s. At 21 beats per 10 s, the total duration of the beat cycle is 0.47 s. Even if, as seems likely, there is no pause in the withdrawn position at this rate of beat (pause duration 0 s), it is obvious that the body movement must be about twice as fast at 21 beats per 10 s than at 9 beats per 10 s.

At the slower end of the range, in contrast, observations on beating at 2.8 beats per 10 s show that the total duration of the beat cycle is 3.54 s, but cirral extension and withdrawal occur at the same rate as in faster beating (table 1). The body movement underlying cirral extension and withdrawal, therefore, is not likely to be much slower at 2.8 beats per 10 s than at 9 beats per 10 s. If this assumption is correct, the pause in the withdrawn position lasts about 2.5 s of each beat cycle at the slow rate of beat. As figure 18 shows, at rates of beat faster than 9 per 10 s, reduction in duration of the pause in the withdrawn position soon becomes an insignificant factor in increasing the rate of beating. Speeding up the rate of body movement is the dominant change that occurs. At rates less than 9 beats per 10 s, in contrast, the rate of body movement probably remains more or less constant and the dominant factor in slowing the rate of beat is a marked increase in the duration of the pause in the withdrawn position at the beginning of each beat cycle.

In relating water flow to pumping movements in figure 17*c*, information on water flow has been drawn from the results obtained by using milk as a tracer (compare figures 15 and 16) for animals beating at a similar rate, 9 beats per 10 s. Water begins to flow into the mantle cavity coincident with the onset of the backswing of the body. The inflow is slow for the first 0.3 s, then more rapid for the next 0.33 s, being completed when the cirri are fully extended. Outflow begins coincident with the onset of cirral withdrawal and proceeds rapidly over 0.22 s as a jet, then as a trickle during a further 0.11 s. A pause of 0.17 s supervenes before the next inflow commences. The total time of each pump cycle is 1.01 s and is coincident with the body movement of the causal beat cycle, except for the final trickle of exhaled water at the end of the pump cycle. At this stage the animal is already resting preparatory to the next pump. Cirral extension and withdrawal occur in the second half of the pump cycle, during the final intake and first expulsion of the water. At fast rates of beat, when the pause between beats is negligible (figure 18), the pump cycle and the beat cycle are coincident.

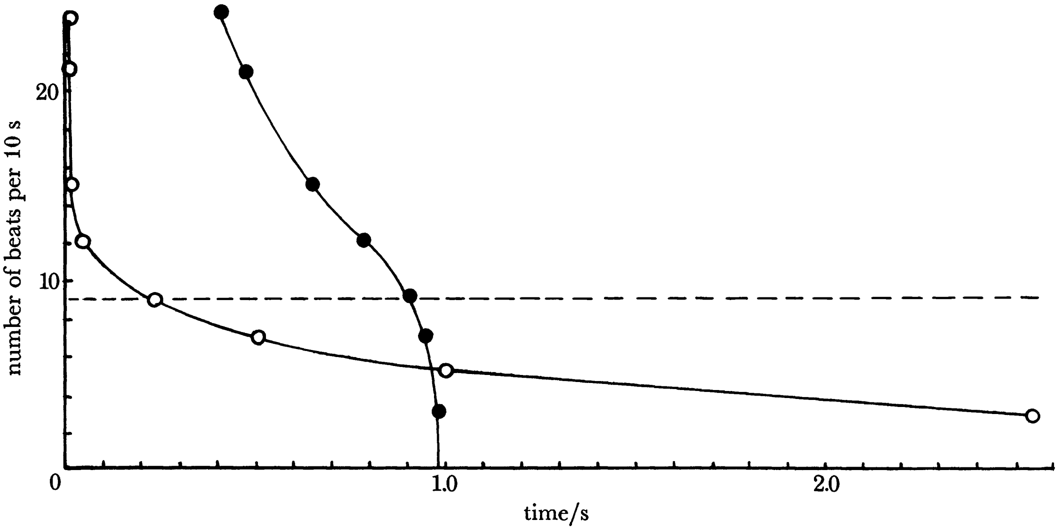

FIGURE 18. *B. perforatus*. Relation between rate of beat and events in the beat cycle; ○, duration of pause in the withdrawn position; ●, duration of body movement; broken line, 9 beats per 10 s.

Since each extension and withdrawal of the cirri is indicative of one underlying pump cycle, an animal beating at 21 per 10 s (figure 13*b*) pumps three times as much water per unit time as an animal beating at 7 per 10 s (figure 13*a*). At a rough approximation, the volume pumped per hour at the two rates is 1.2 l (see § 5*a*) as compared with 0.4 l. In contrast, the time spent by the long cirri in captorial sweeping per 10 s is 0.91 s at the slower rate and 1.68 s at the faster rate, a less than twofold increase. Since the cirri are extended less fully at faster rates, it seems unlikely that captorial efficiency per stroke is greater at the faster rate in *B. perforatus*.

The present evidence therefore indicates that, in *B. perforatus*, an increase in the rate of beating increases the pumping activity to a greater extent than it increases captorial cirral activity. This, together with the fact that pumping is a major activity at all rates of beating, suggests that filter feeding is more important than captorial feeding in this species. Observations on the cirral and mouthpart movements of *B. perforatus* add to those of cirral and mouthpart morphology in lending weight to this suggestion.

6. FEEDING

(*a*) *Captorial feeding*

B. perforatus is well known to feed on zooplankton and on microorganisms (Southward 1955; Crisp & Southward 1961). During the present observations, the capture of nauplius larvae during cirral beating was observed, but it was also seen that the powerful exhalant jet from the mantle cavity tends to sweep zooplanktonic animals away from the vicinity of the beating cirri. Prolonged cirral extension in response to a water current could be elicited in this species only with difficulty and then only for about 1 s before resumption of beating.

Capture of zooplankton is effected as the long cirri sweep rostrally at the onset of each withdrawal stroke. As the cirri curl down into the mantle cavity, they also bunch together, with their long setae folded forwards, bringing all captured material towards the midline.

During the forward coiling and descent of the long cirri, the third maxillipeds also sink down within the aperture but remain in an upright position. The long cirri thus roll down over the upright rami of the third maxillipeds. At the end of the withdrawal movement, the long cirri in the coiled position exhibit a series of short back and forth shuffling movements. It appears that their anterior faces are being cleaned by the third maxillipeds at this time. As the long cirri then begin to uncurl and extend, the rami of the third maxillipeds hook down and forwards, thrusting the collected material between the short rami of the first and second maxillipeds. As extension of the long cirri continues, the third maxillipeds normally rise up to follow them out of the aperture. Occasionally they remain thrust down between the rami of the first and second maxillipeds for a few seconds while long cirri effect one or two further rhythmic withdrawals and extensions.

The long exopods of the first maxillipeds, protruding vertically at the rostral end of the aperture on each extension, also play a part in food transfer to the deeper placed, shorter maxilliped rami. During the downward curling of the long cirri, material swept down in the water towards the rostral end of the aperture is captured between the upright exopods. The exopods may then, by bending as they are withdrawn, transfer this material to the shorter maxillipeds. Alternatively the tips of the contracting third maxillipeds may brush the captured material down onto the short maxillipeds.

Small zooplankters captured by the long cirri and the exopods of cirrus I are thus thrust by the action of the third maxillipeds (cirrus III) between the short maxilliped rami (endopod of cirrus I, exopod and endopod of cirrus II). This thrust occurs at the onset of each extension stroke of the long cirri. At this stage of the process, the short maxilliped rami are spread around the tip of the oral cone. During the continuing extension of the long cirri, the short maxilliped rami can be seen to press against the labrum and maxillae in a series of rapid alternating jerks. This action presumably transfers the food material to the mouthparts. At the commencement of the next withdrawal stroke, the short maxilliped rami lift away from the maxillae in preparation for receipt of the next contribution from the third maxillipeds.

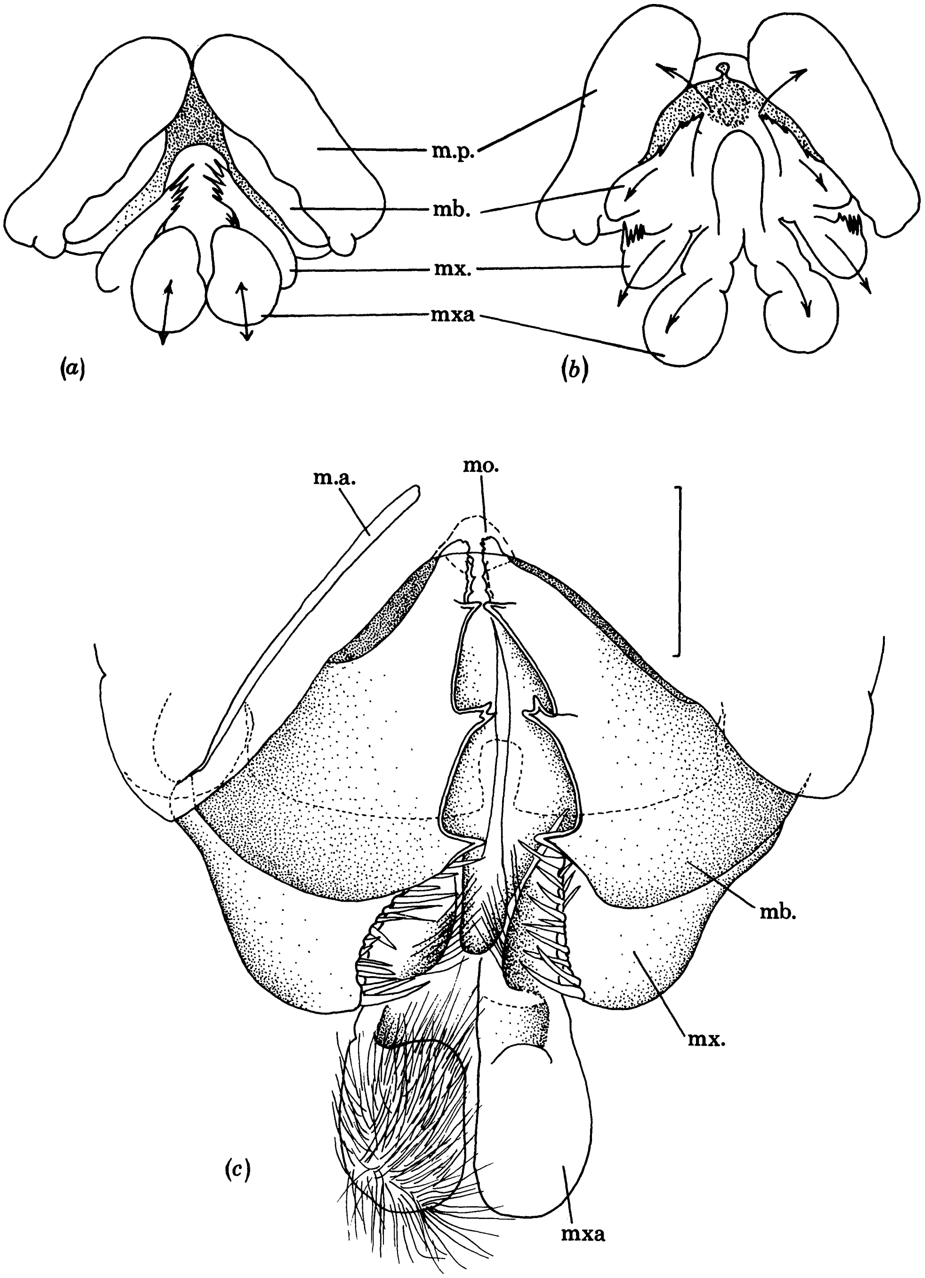

FIGURE 19. (*a*), (*b*) Mouthpart movements of *B. perforatus* as seen in a posterior view of the oral cone (for explanation, see text); (*c*) mouthparts of *B. perforatus* in ventral view after removal of the labrum and mandibular palps; m.a., maxillulary apodeme; mb., mandible; mo., mouth; m.p., mandibular palp; mx., maxillule; mxa, maxilla. Scale bar, 0.5 mm.

(*b*) *Filter feeding*

The positions and movements of the short maxilliped rami must also be considered in relation to the powerful pumping action which drives the current of water through the mantle cavity. As discussed in § 5 *b*, this current flows into the mantle cavity rostrolaterally, beginning while the cirri are in the withdrawn position and continuing until the cirri are fully extended. The current then flows across the branchiae and out through the carinal end of the aperture during the curling down and withdrawal of the long cirri and for a short time thereafter. During the intake of water into the mantle cavity, the body is swinging carinally and upwards towards the aperture. During the outflow of water, the body is swinging rostrally and down.

The short maxilliped rami with their dense brushes of anteromedian setae are spread on either side of the oral cone throughout most of this action. They take up the spread position as the body begins its downward and forward swing, and thus sweep through the base of the exhalent jet. They remain spread while the body pauses and then enters into its upward and backward swing, thus filtering the first part of the inhalent flow. Only during the final part of this swing, as the next extension of the cirri takes place and the inflow of water comes to completion, do the short maxilliped rami perform the action that transfers collected material to the mouthparts.

(*c*) *Mouthpart movements*

The action of the mouthparts of *B. perforatus* cannot be observed in the intact animal, but is displayed in specimens in which the body has been dissected carefully from the mantle cavity and pinned out in sea water under a dissecting microscope. While, due to damage to the hydraulic system of the haemocoel, the long cirri perform only weak and irregular movements in specimens prepared in this way, the maxillipeds and mouthparts remain active for several hours. The muscular movements of the maxillipeds follow a rhythmic pattern similar to that seen in the intact animal, indicating that neuromuscular coordination is maintained in the preparation. The correlated movements of the mouthparts are likely, therefore, to mimic those of the intact animal. The most regular mouthpart movements are those of the maxillae (mxa), which perform an alternating series of hammer-like blows towards the preoral cavity (figure 19*a*). The setae of the maxillae brush the setae of the maxillipeds as a result of this action and gather particulate material from them.

At intervals, as this material accumulates, the maxillipeds are held away from the oral cone and the preoral cavity is enlarged by a simultaneous abduction of the maxillae posterolaterally and the mandibular palps (m.p.) anterolaterally (figure 19*b*). The maxillules (mx.) are then abducted, and adduct as the maxillae close together again. As a result the maxillules scrape the maxillae and push the scraped material into the preoral cavity. The mandibles (mb.) abduct and adduct slightly later than do the maxillules, further pushing the material in the preoral cavity to the level of the mouth (mo., figure 19*c*), where ingestion occurs.

(*d*) *Rejection and cleaning*

Not all of the material gathered on the maxillipeds is transferred to the mouthparts for ingestion. Rejection is another possibility, though the basis of discrimination is at present not clear. The rejection process is a second function of the long exopods of cirrus I. When extended through the rostral end of the aperture, at a time when the short rami of the maxillipeds are transferring the material to the mouthparts, these exopods may rub together with an up and down action. Material from the vicinity of the limb bases is worked distally by the setae as a result of this rubbing action and cast off into the water.

A third function is also performed by these exopods as a cleaning activity. When the rolled rami of the long cirri are uncurled during the next extension stroke, the first maxilliped exopods are sometimes pressed against the external (posterior) surfaces of the uncurling rami, brushing them clean.

7. Discussion

(*a*) *General balanoid structure in relation to cirral activity*

Aspects of structural organization shared between extension feeding and rhythmically feeding balanoids are plainly features that preceded the evolution of rhythmic feeding. Much of the structural and functional organization of balanoids falls into this category, as shown, for example, by a comparison between *B. perforatus* and *Boscia anglicum* (Anderson 1978; this account). *B. anglicum*, although using short bursts of rhythmic cirral contraction in prey capture, is essentially an extension feeder, yet shares with *B. perforatus* the following features: well developed sheath; mobile helmet-shaped operculum on a flexible opercular membrane, broad and pleated at the carinal end; three pairs of well developed opercular depressor muscles; prominent tergal spurs bearing dependent branchiae; three pairs of maxillipeds, of which the first pair has elongate exopods functioning as a rejection mechanism; short endopods on the first maxillipeds and short rami on the second; somewhat longer rami on the third maxillipeds, the exopod being longer than the endopod, with anterior denticulation distally on the rami; three pairs of long, captorial cirri (IV–VI); and mouthparts of a generally similar configuration.

There are differences in the proportions of these components in the two species. They are functionally related to the differences in their mode of cirral activity and feeding, but it is clear than rhythmic cirral activity has evolved in balanoid barnacles mainly through modifications of activity patterns in an existing organization, rather than as an associate or consequence of striking structural innovation.

The general features listed above are also shared by other species of *Balanus* (see, for example: Darwin 1854; Crisp & Southward 1961; Newman & Ross 1976; Foster 1978), though again there are differences in the proportions of the various components in different species. Except for a less prominent sheath and the absence of tergal spurs, the same features are also found in the Archaeobalanidae, both in extension feeders and in rhythmic feeders. If, as the phylogenetic system of Newman & Ross (1976) implies, rhythmic feeding has evolved more than once in the Balanoidea (see § 1 *b*), it has been based in every case on the same ancestral type of organization, the one shared among extension-feeding archaeobalanids. It would be exceptional, however, if a detailed examination of the way in which rhythmic cirral activity occurs in the different instances of this apparent polyphyletic evolution did not reveal some basic differences between them. If all appear to be identical, as suggested by Crisp & Southward (1961), the polyphyletic argument is greatly weakened and its classificatory basis would require reconsideration.

At the present stage of knowledge, a serious problem is presented by the inadequacy of the evidence. The present study of *B. perforatus* has given some indication of the level of functional information required to give a reasonable understanding of the processes underlying rhythmic cirral activity in a balanoid. Evidence at a similar level is not presently available for other species. For the polyphyletic argument to be properly tested, we need as a minimum to be able to make comparisons at this level of detail between *Semibalanus balanoides*, *Elminius modestus* and representatives of the various 'groups' of the genus *Balanus*. As mentioned in § 1 *b*, *c*, some tantalizing indications can be found, in the work of Crisp & Southward (1961), Southward (1962) and Southward & Crisp (1965), of differences in the rhythmic activity of different species. There also appear to be correlated differences in the food intake of species that have been studied from this point of view, and in the functional anatomy of the feeding apparatus. The following discussion examines these differences and draws, where possible, tentative conclusions from them.

(*b*) *Cirral activity and captorial feeding in balanoids*

All balanoid species in which rhythmic cirral activity has been described are said to perform normal beat or fast beat as defined by Crisp & Southward (1961) (see § 1 *a*). *B. perforatus*, as the present account shows, displays neither of these modes and maintains a characteristic pattern of action at rates of beating ranging from 2 to 24 per 10 s. Extension and withdrawal of the long, posterior cirri occur in basically the same way at all rates of beating, with extension taking 0.10–0.23 s and withdrawal 0.06–0.14 s. The operculum remains open as long as beating continues and is not closed between beats. At the faster rates of beating, the long cirri extend less far than at slower rates; the other cirral components, which emerge from the mantle cavity at slower rates (exopods of cirrus I, rami of cirrus III), do not emerge at the faster rates.

Since each extension–withdrawal of the cirri in *B. perforatus* takes only 0.23–0.35 s, the duration of the beat cycle as observed in external view is determined mainly by the time spent inside the mantle cavity between each cirral withdrawal and the next extension. This time varies from 3.28 s at 2.8 beats per 10 s to 0.18 s at 24 beats per 10 s. At slow rates of beat, the body pauses in the withdrawn position. Up to 9 beats per 10 s, the duration of this pause is the main factor determining the rate of beating. At rates faster than 9 beats per 10 s, the pause becomes negligible and the main determinant of the rate of beating is the speed of body movement in the mantle cavity. This relationship, between the rate of cirral extension and withdrawal, the rate of the body movement underlying this action and the time spent in the withdrawn position during beating, has not been described previously for any species of thoracican barnacle. Separate control systems must govern the pause duration and the speed of body movement in these animals and must themselves be under the control of a coordinating system. The neurological basis of these control systems is not known, but their existence provides a key to the evolution of cirral action in the Thoracica. Extension feeding thoracicans have the same basic skeleto-muscular apparatus of the body as rhythmic feeders. Furthermore, the extension feeders exhibit the same independent control of the withdrawn position and the speed of the body movements which underlie cirral extension and withdrawal, and show coordination between these controls. The evolution of rhythmic feeding in thoracicans, therefore, is essentially a result of modifications of these neurological control systems, though skeleto-muscular changes which permit faster movements using the same basic apparatus must also have played a part. Such an evolution could easily have occurred polyphyletically.

According to present information, no other rhythmically feeding balanoid has as wide a range of rates of cirral beating as *B. perforatus* (table 2).

The figures available for other species, however, have obvious limitations. Except for *B. balanus* and *B. nubilus*, all of the species listed in table 2 are said to perform fast beat as well as normal beat. Since fast beat involves rates of cirral beating greater than 10 per 10 s, more information is required on beating rates in *S. balanoides*, *B. crenatus* and *B. improvisus*. Information is also required on species in group 3 (*B. concavus*) and group 5 (*B. trigonus*). No useful comparisons between species can be made at present.

Similarly, information on rates of cirral extension and withdrawal during beating is also limited, only average figures for a few species being available (table 3). In *E. modestus* and *S. balanoides*, the occurrence of cirral extension and withdrawal at the same rate was observed during fast beat. Normally, extension is slower than withdrawal. *E. modestus* has a faster cirral action than *S. balanoides*. Of the *Balanus* species, *B. balanus* has a slow cirral action, *B. amphitrite* a moderate rate of cirral action and *B. perforatus* an unusually fast rate of cirral extension and withdrawal. The explanation of the latter in an animal that is large among the listed species lies partly in the fact that the cirri are not fully extended at any rate of beating in *B. perforatus* in the manner in which they are in other species. This in turn is correlated with the emphasis in *B. perforatus* on pumping filtratory feeding at the expense of cirral captorial feeding. Like the information on rates of beating, the present figures on cirral extension and withdrawal rates are too meagre to suggest conclusions, merely pointing to the existence of marked differences between species.

A firmer statement of differences can be made on more general grounds. *Elminius modestus* emphasizes fast beat much more than normal beat. *Semibalanus balanoides* shows the reverse, as does *Balanus balanus* (Crisp & Southward 1961). *B. nubilus* shows only normal beat (Southward & Crisp 1965). *B. crenatus*, however, a group 1 species associated with *B. balanus*, performs normal and fast beat with equal facility, as do the group 4 species *B. amphitrite*, *B. eburneus* and *B. improvisus*. The mode of cirral beating in the group 6 species *B. perforatus* is uniquely different

TABLE 2. RATES OF CIRRAL BEATING IN BALANOIDS

species	number of beats per 10 s	reference
Archaeobalanidae		
Archaeobalaninae		
Elminius modestus	6–26	Crisp & Southward (1961)
Semibalaninae		
Semibalanus balanoides	4–6	Southward (1956*b*) Crisp & Southward (1961)
Balanidae		
group 1		
Balanus balanus	2–5	Southward (1957) Crisp & Southward (1961)
B. crenatus	5–10.5	Crisp & Southward (1961)
group 2		
B. nubilus	2	Southward & Crisp (1965)
group 3		
nil	—	
group 4		
B. amphitrite	2.7–16.5	Southward (1957, 1962)
B. eburneus	3–13	Southward (1962)
B. improvisus	11	Southward (1957)
group 5		
nil	—	
group 6		
B. perforatus	2.8–24	this account

TABLE 3. TIMES FOR CIRRAL EXTENSION AND WITHDRAWAL IN BALANOIDS

species	extension time/s	withdrawal time/s	references
Elminius modestus	0.12–0.16	0.12–0.16	Crisp & Southward (1961)
Semibalanus balanoides	0.25–0.31	0.25–0.31	Southward (1956*b*) Crisp & Southward (1961)
Balanus balanus	0.75–1.25	0.5–1.0	Southward (1957) Crisp & Southward (1961)
B. amphitrite	0·31–0.43	0.18–0.31	Southward (1957) Crisp & Southward (1961)
B. perforatus	0.10–0.23	0.06–0.14	this account

from any of these. These differences are not correlated with size or environment and seem more likely to be related to the independent evolution of different patterns of rhythmic feeding activity. A consideration of filter-feeding activities in balanoids also tends to support this view.

(*c*) *Pumping activity and filter feeding in balanoids*

A general carino-rostral drift of water over the apex, such as occurs in *B. perforatus*, is a normal accompaniment to cirral beating in balanoids. This drift is emphasized during fast beat, when it assists in both food gathering and respiration, usually in still water (for, e.g., *Elminius modestus*; Crisp & Southward 1961).

A pumped water flow through the mantle cavity is also an accompaniment of normal beat where this occurs. This mantle current was first demonstrated by Crisp & Southward (1956) and described in more detail for a number of species by Crisp & Southward (1961). It follows the general route described in the present paper, entering the mantle cavity rostrolaterally as the body is raised and the cirri are extended, and being exhaled as a carinal jet when the cirri are coiled and the body is lowered. The mantle current has been demonstrated in *E. modestus*, *S. balanoides*, *B. balanus*, *B. crenatus*, *B. nubilus* and *B. improvisus* (Crisp & Southward 1956, 1961; Southward & Crisp 1965), in *B. perforatus* (Crisp & Southward 1956, 1961; this account) and in *Megabalanus nigrescens* (Anderson, unpublished). As a result of the present work, the causal body movements that underlie the water flow are now clear for *B. perforatus*. It seems likely that other species perform pumping in a generally similar manner, the action being a modification of the respiratory pumping movements of the body, without extension of the cirri, performed alike by many lepadomorph and balanomorph barnacles. The capability of producing a through-mantle current accompanying rhythmic cirral protrusion and withdrawal, like the rhythmic cirral action itself, could therefore have evolved independently several times.

At present, the only case that can be compared in any detail with that of *B. perforatus* is that of *Balanus balanus*, from data of Crisp & Southward (1961). The pumping action of the body shows some interesting similarities and differences in the two species. The similarities are general ones. There is a pause of the body in the withdrawn position between pumps. The inhalent backswing of the body is of longer duration than the exhalent forward swing. A brief pause occurs while the long cirri are held extended between the backswing and the forward swing. The differences concern the rate of action of the pump. For reasons discussed in §5, there is little difference in the rates of backward swing and forward swing of the body in *B. perforatus* at any rate of beat. Taking 3.5 beats per 10 s as an example, the backswing takes 0.63 s, the forward swing 0.22 s, and the pause in the withdrawn position lasts 1.85 s. In *B. balanus* beating at the same rate, the body movement is much more ponderous. The backswing takes 1.15 s and the forward swing 0.30 s. The pause in the withdrawn position is correspondingly less, 1.13 s The pumping action is therefore different in the two species. The volume of water pumped is also different. At comparable rates of beat, 5 and 7 per 10 s respectively, in animals of comparable size, *B. balanus* appears to pump water through the mantle cavity at a rate of about 0.1 l/h, and *B. perforatus* at about 0.4 l/h. *B. perforatus* can also ‘crank up’ to much faster rates than this, which *B. balanus* cannot do. The pumping activity of *B. perforatus*, as the present work shows, is correlated with an emphasis on filter feeding using the maxillipeds. The feeding activity of *B. balanus* appears to emphasize captorial planktivory, though precise information on this point is not available.

(*d*) *Maxillipeds and mouthparts in balanoids*

One role of the three pairs of maxillipeds in balanoids is in the forward transfer of food captured by the long cirri. The description of this process given by Crisp and Southward (1961) for *Semibalanus balanoides* and *Balanus balanus* has been confirmed in the present study of *B. perforatus*, indicating a common mode of action in all rhythmically feeding balanoids. In *B. perforatus*, however, this action is subsidiary to a specialized filter feeding role in which the first and second maxillipeds filter particulate food from the mantle current. Experimental evidence of filter feeding as the major feeding mode in *B. perforatus* was provided by Southward (1955*a*) and Crisp & Southward (1961). The enlargement of the maxilliped region, the numerous setose processes on the short maxilliped rami and the capacity of *B. perforatus* to produce and filter a voluminous mantle current all confirm this finding.

Among other rhythmic feeding balanoids, a similar emphasis on filter feeding is evident in some species, but not in all. *Elminius modestus*, for example, is a planktivore and does not appear to filter feed. In *Semibalanus balanoides* filter feeding by setose maxillipeds occurs as a secondary feeding activity and the maxillipeds are much less elaborate than those of *B. perforatus* (Crisp & Southward 1961; Stubbings 1975). There is no evidence at present for filter feeding in *Balanus balanus* or other group 1 *Balanus* species, but the studies of gut contents carried out by Barnes (1959) show that the group 2 species *B. nubilus* and *B. rostratus* are primarily particulate feeders. The circumstantial evidence of maxilliped setation also indicates a role for maxilliped filter feeding in *B. amphitrite* and *B. variegatus* (group 4; Foster 1978) but the matter has still to be investigated. Group 3 and group 5 species (*B. concavus*; *B. trigonus*), on the other hand, have spinose maxillipeds indicative of planktivory. Lastly *B. perforatus* shares with the other group 6 species of the genus *Megabalanus* the elaboration of setose processes on the short rami of maxillipeds 1 and 2, together with a powerful and voluminous through-mantle current (Foster 1978; Anderson, unpublished). Further investigation may reveal that feeding by filtration of the mantle current by the maxillipeds has evolved several times in the Balanoidea and has become a dominant mode of feeding in several of the larger balanoid species.

Whatever the mode of feeding and type of food, the action of the mouthparts in forward food transfer from the maxillipeds appears to be uniform throughout the balanoids. The present study of *B. perforatus* confirms and amplifies previous descriptions by Barnes & Reese (1959) of *B. nubilus*, and Crisp & Southward (1961) on other species. The maxillae perform alternating hammer blows which transfer food from the maxillipeds to the pre-oral cavity. The maxillules and mandibules perform scraping actions that work the food forward towards the mouth for ingestion.

(*e*) *Shell, operculum, mantle muscles and mantle cavity in balanoids*

Associated with the emphasis on rhythmic pumping and filter feeding in *B. perforatus*, the shell is tall and conical, with a large mantle cavity and a deep sheath. The helmet-shaped operculum on its pleated opercular membrane has an extensive range of apicobasal movement within the sheath. When the operculum is raised, by hydraulic inflation of the underlying mantle, the working volume of the mantle cavity is substantially increased. When the operculum is withdrawn to the base of the sheath, it clamps down in a deeply placed, protective position. In this position, the operculum can also perform a powerful, protective, rotary action.

The depressor muscles of the operculum of *B. perforatus* are notably enlarged and powerful, all three pairs being well developed. These muscles function in controlling the position of the operculum when raised, by antagonizing the hydraulic raising mechanism, and in opening the aperture, an action antagonized by the adductor scutorum; but neither of these actions requires muscle of such massive dimensions. There is also no indication in the activities of *B. perforatus* that the depressor muscles play any part in pumping water through the mantle cavity. It follows that in *B. perforatus*, and probably in other large species of the *B. perforatus* group, the basic functional significance of the massive depressor muscles is in the performance of two simple defensive actions, a rapid protective clamp down of the operculum and a powerful rotary action of the operculum within the sheath. Both are defences against penetration by predators through the large orifice and broad, flexible opercular membrane associated with the functional organization of the pumping feeding mechanism.

Other large balanoids with massive depressor muscles perform either one or both of these defensive actions. Such muscles occur in *Chirona hameri*, an extension feeder, and serve to clamp down the operculum (Crisp & Southward 1961). *Balanus nubilus* is also a well known possessor of large depressor muscles, much used in physiological experimentation on muscle contraction. Rotation of the closed operculum was first described in this species, by Tait & Emmons (1925). This rotary action also occurs in *B. balanus* (Crisp & Southward 1961), as well as in *B. perforatus* (this account) and *Megabalanus nigrescens* (Anderson, unpublished). The link between large size, large depressor muscles, protective opercular clamp down and opercular rotation, irrespective of mode of feeding, support the view that large depressor muscles are a functional correlate of aperture protection in large balanoids and are not related functionally to the feeding or other muscular activities of these animals.

(*f*) *The evolution of rhythmic cirral activity in the* Balanoidea

B. perforatus can now be recognized as a balanoid, typifying group 6 of the genus *Balanus* as defined by Newman & Ross (1976), specialized as a filter feeder. The organization and activities of *B. perforatus* clearly had their ancestry among balanids that used their long cirri in rhythmic, captorial planktivory, pumped a respiratory current through the mantle cavity while feeding and used their maxillipeds in subsidiary filter feeding. There is no evidence that these ancestors performed normal beat in the manner described by Crisp & Southward (1961) or that they had any capacity for fast beat. Archaeobalanid rhythmic beating patterns as exemplified by *Elminius modestus* or *Semibalanus balanoides* can therefore be ruled out as ancestral to the specializations seen in *B. perforatus* and its group 6 relatives. Similarly, the rhythmic cirral actions so far described among *Balanus* species of other groups cannot share an ancestry with that of *B. perforatus*. It seems likely that the unique structural–functional configuration of *B. perforatus* as a pumping filter feeder evolved directly from early species of Balanidae, which, like many Archaeobalanidae, were extension-feeding planktivores.

Present evidence, although inadequate in many respects, indicates that the independent evolution of mechanisms of rhythmic feeding, basically for captorial planktivory (p.), secondarily in some cases for maxilliped filter feeding (f.), has occurred at least twice in the Archaeobalanidae (*Elminius modestus*, p.; *Semibalanus balanoides*, p.f.) and at least twice in the Balanidae (*Balanus perforatus*, f.p.; other species of *Balanus* variously p., p.f. and f.p.). The possibility also exists of further instances of the independent evolution of rhythmic feeding within the genus *Balanus*, but present information is inadequate on this matter.

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Since becoming aware of the results of this investigation, Dr Southward has re-examined a film, taken in 1959, on cirral activity in *B. perforatus*, which confirms the observations recorded in the present paper.

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