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COMPLEMENTAL MALES IN THE BARNACLE *BATHYLASMA ALEARUM* (CIRRIPIEDIA: PACHYLASMIDAE)

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SUMMARY

Complemental males are described for the first time in this deepwater family of balanomorph barnacles. The males are usually lodged externally on the tergum, in the angle formed between the articular margin and the articular ridge. Sometimes they occur in the apex angle of the carina. Compared with similar-sized individuals attached to the outside of the parietal shell plates, the body of the male is dominated by testes and seminal vesicles, the latter packed with sperm, and the penis is 4 to 5 times longer. The sexual condition is compared with that in other barnacles, and the mode of sex determination is discussed.

Introduction

Most barnacles (Cirripectida Thoracica) are simultaneous hermaphrodites. A less common sexual condition of some barnacles first fascinated Darwin (1851), who described in the genera *Ibla* and *Scalpellum* (*sensu lato*) little individuals associated with either larger hermaphrodites or, more rarely, females. Darwin ascertained they were males of the same species and called them dwarf and complemental males respectively. Subsequently, such males have been described in two other species of *Ibla*, in numerous scalpellids, and in 4 species of archeobalanid barnacles (McLaughlin and Henry, 1972). This paper describes a new case of complemental males, of a different sort to those in the archeobalanids, and in a different balanomorph family.

Is the more common hermaphrodite condition or the rarer separate-sex condition primitive? Newman (1974, p. 444) was of the opinion that barnacles with separate sexes are primitive, which accords with the views of Broch (1922) that complemental males represent the last vestiges of ancestral dioeciousness prior to the establishment of the more prevalent hermaphrodite condition. However, this may not be so. Independent development of complemental males in diverse families of barnacles, from a more basic hermaphrodite condition, may have arisen to improve reproductive performance in sublittoral barnacles. Whereas a gregarious settling response (Knight-Jones, 1953) must improve the opportunities for cross-fertilisation of hermaphrodites, the advantage of complemental males possibly lies in the speeding up of reproduction of already mature individuals that the little males associate with. The abolishment of the male function of the larger partners in certain scalpellids and species of *Ibla* amounts to a restoration of a precirriped dioecious condition, but with female dominance. This theory is expounded in the discussion.

Material

Thirty-five free-living specimens of *Bathylasma alearum* (Foster), on a boulder collected by "Tangaroa" from New Zealand Oceanographic Institute Stn R6: 42° 29.2'S, 176° 06.3'E, 1568 m, northern Mernoo Slope.

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These mostly disarticulated specimens range in size from 10 mm to about 30 mm basal rostrocarinal diameter. As well, 3 small specimens and two recently metamorphosed spat (Fig. 2a) were attached to the outside of the parietes of larger specimens. A total of 35 males were present on the terga of 21 of the hermaphrodites, the latter all more than 14 mm shell diameter; 8 hermaphrodites had males on both terga. Of the 29 individual terga with males, 24 had one male, 4 carried 2 males, and one had 3 males. In addition, 2 hermaphrodites bore a small male in the internal groove at the apex of the carina.

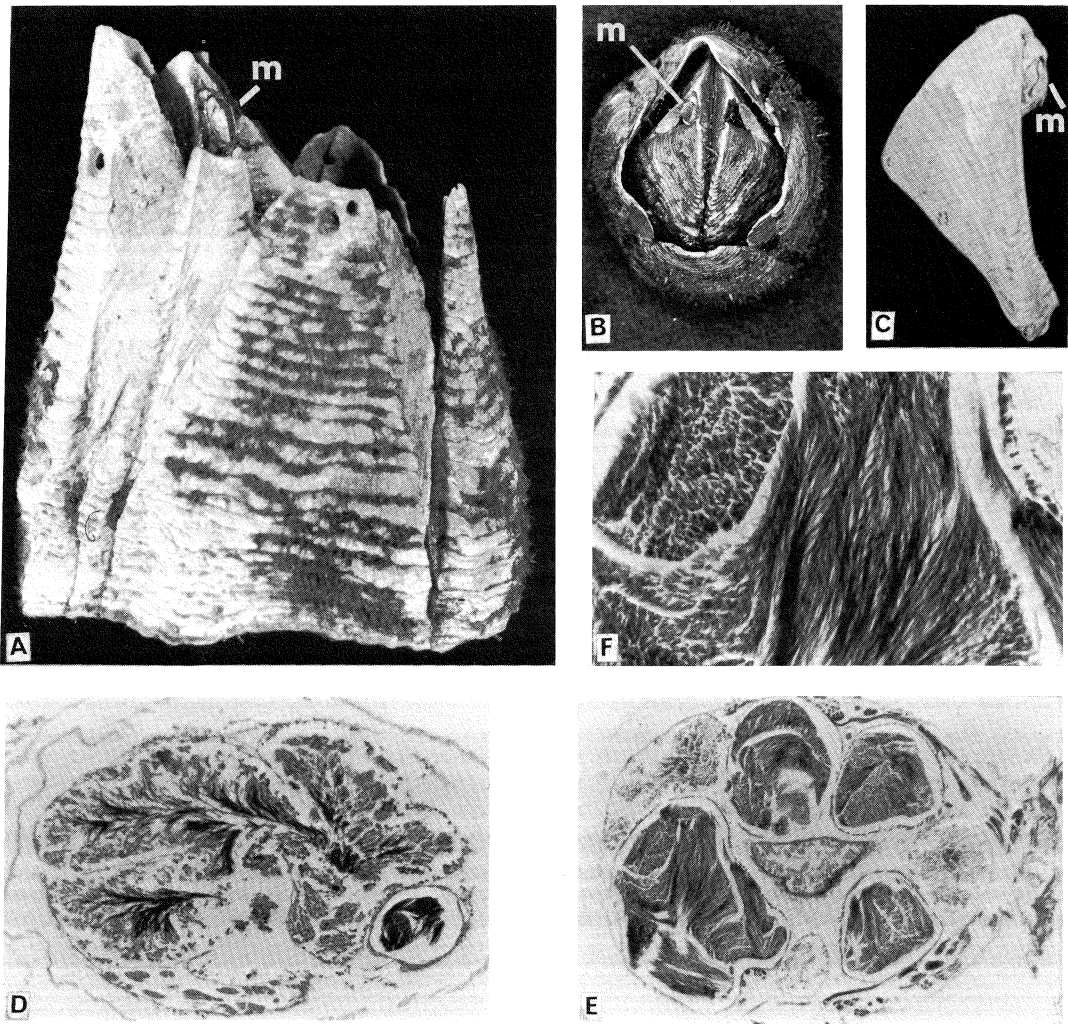


Fig. 1. *Bathylasma alearum*: **A**, lateral view of hermaphrodite showing small male (m) in tergal niche, plus whelk-drilled holes in apical parts of parietes; **B**, apical view of another hermaphrodite with a male (m) on right tergum; **C**, dissected tergum with male (m); **D**, section through prosoma of tergal male, mostly of testis (t) undergoing spermatogenesis and sperm in one seminal vesicle; **E**, section through another male showing distended seminal vesicles with sperm, three marginal testis lobes and centrally the stomach; **F**, aligned sperm in seminal vesicles of specimen E.

The males ranged in size from 1.0 mm (recently metamorphosed) to 4.0 mm rostrocarinal length. The largest males were solitary in their niche, occupying most of the niche.

Note on the taxonomy

Bathylasma alearum was first described as *Hexelasma alearum* by Foster (1978) from two intact specimens and copious shell plates collected on the New Zealand shelf. Since the preparation of my earlier paper, and with extra material, I have reconsidered the taxonomy of the *Bathylasma/Hexelasma/Aptolasma* section of the Pachylasmidae (Foster, 1981) and now uphold *Bathylasma* of Newman & Ross (1971). *Hexelasma* is the senior synonym of *Aptolasma*.

B. alearum (Fig. 1a) is very closely related to the large fossil *B. aucklandicum* (Hector), now known from the Oligocene to the Pliocene of New Zealand (Mr John Buckeridge, pers. comm.). I earlier

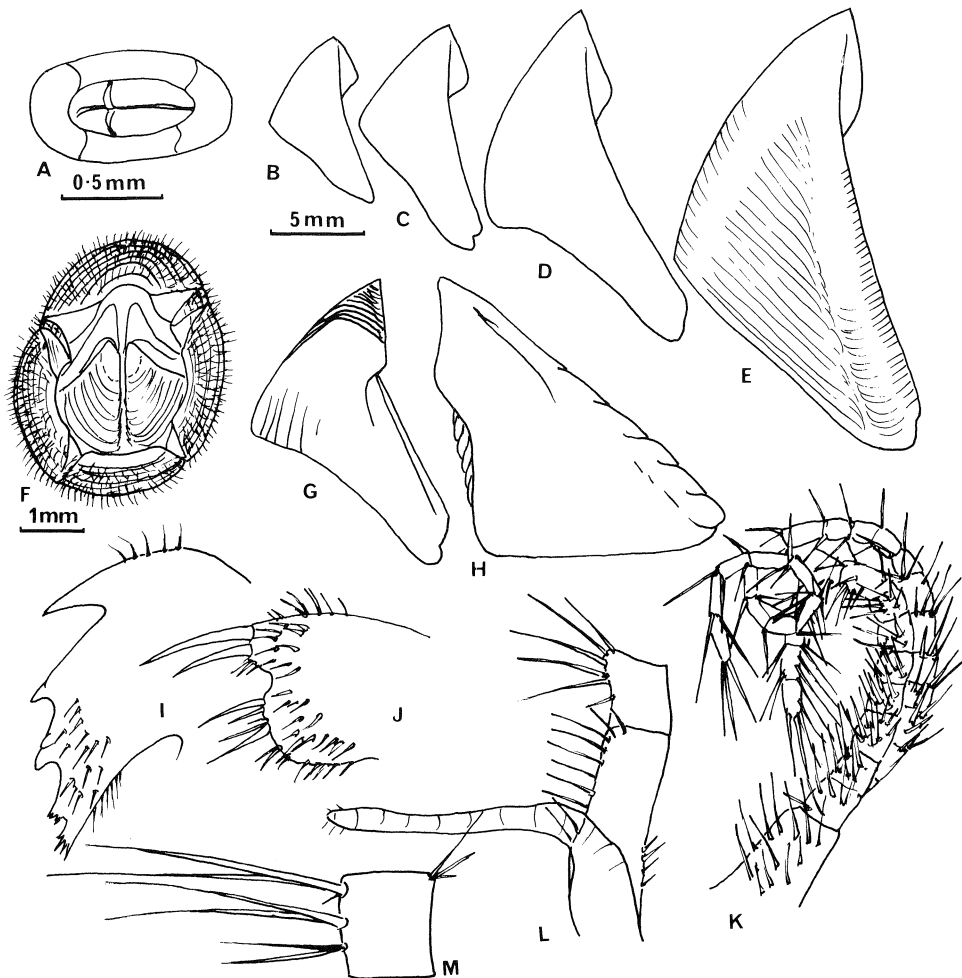


Fig. 2. *Bathylasma alearum*: A, apical view of spat; B-E, external views of terga of range of specimens to show appearance of articular ridge, to same scale; F, apical view of juvenile; G-M, details of this juvenile; G, tergum; H, scutum; I, mandible; J, maxillule, K, cirrus III with antenniform posterior ramus; L, penis and pedicel of cirrus VI; M, intermediate segment of cirrus VI.

distinguished the two species by the shape of the tergal articular ridge, but it is clear from the present material that the triangular articular ridge of *B. alearum* becomes truncated in larger specimens (Fig. 2b-e), as it is in the relatively massive tergum of *B. aucklandicum* (see Foster, 1978, plate 10D). *B. alearum* is conceivably descended from the fossil species with a concomitant reduction of the maximum size attainable.

Description of males

Males laterally compressed with the rostracarinal axis aligned with either the articulation between the tergum and scutum of the 'host' (Fig. 1a-c) or the longitudinal groove of the carina for those seated on a carina. Parietes often cracked and deformed. Opercula embryonic, often deformed. Internal appendage series complete. Mouthparts and appendages as shown in Fig. 3, with cirral segment counts in Table 1. Penis longer than cirrus VI. Prosomata of 1 carinal and 2 tergal males were sectioned; found to be mostly occupied with seminal vesicles containing sperm masses (Fig. 1e-f) and testes undergoing spermatogenesis (Fig. 1d); gut with food remains.

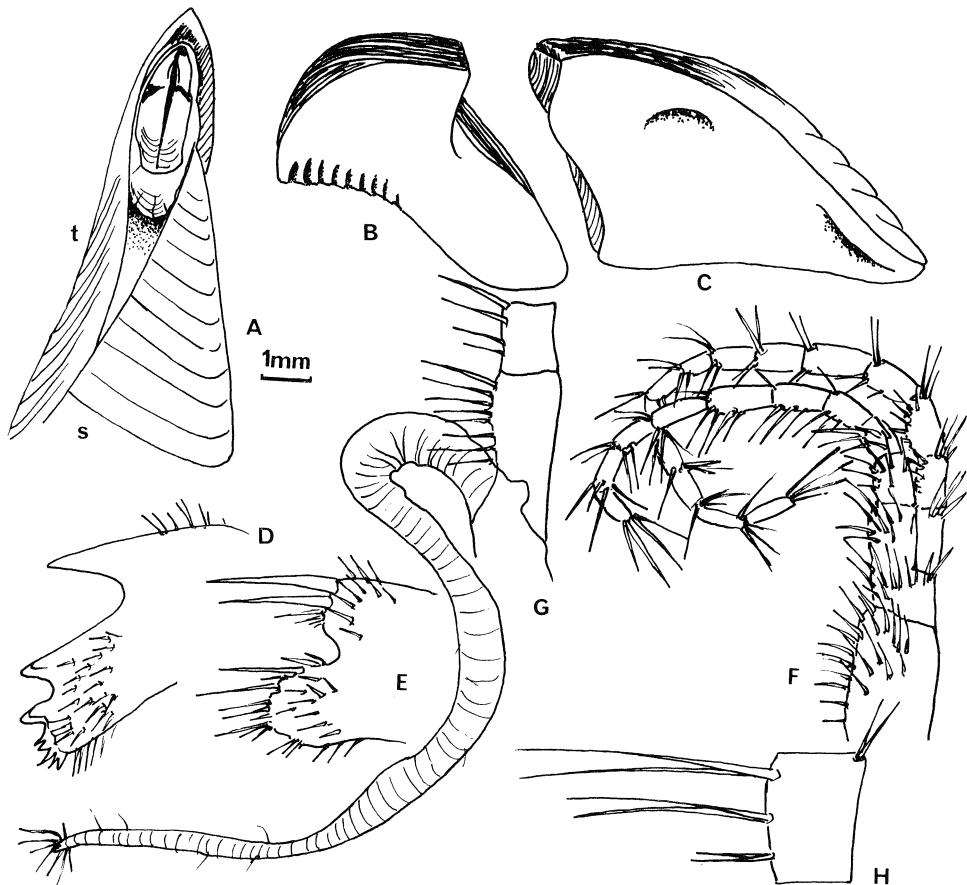


Fig. 3. *Bathylasma alearum*: **A**, apical view of male in tergal niche of a larger specimen, t-tergum, s-scutum; **B-H**, details of male; **B**, tergum; **C**, scutum; **D**, mandible; **E**, maxillule; **F**, cirrus III; **G**, penis and pedicel of cirrus VI; **H**, intermediate segment of cirrus VI.

Comparison with juveniles and hermaphrodites

Shell and appendages of a similar-sized specimen attached on the outside of parietes are shown in Fig. 2f-m, with cirral counts included in Table 1. Penis $\frac{1}{3}$ length of cirrus VI. Testes primordia present, but insignificant in comparison with size of gut. Seminal vesicles small, without sperm.

In larger specimens, the number of segments in the cirri increases (Table 1). In the present material, the posterior ramus of cirrus III is antenniform, with numerous distal elongate segments such that the ramus is as long or longer than cirrus IV. (In the type material there was no evidence of antenniformity). In large specimens the penis is shorter than cirrus VI, sometimes stout and $0.7 \times$ the length of cirrus VI, sometimes degenerate and $<0.1 \times$ cirrus VI.

Table 1. Numbers of segments in the rami of cirri of specimens of *Bathylasma alearum*, anterior ramus first.

	rostro-carinal length	NZOI Stn	Cirrus					
			I	II	III	IV	V	VI
male	0.4 mm	R6	5,5	5,7	9,14	13,14	15,19	16,19
juv.	0.4 mm	R6	8,6	7,12	11,22	16,17	21,19	19,21
herm.	9 mm	F132	8,8	11,18	19,19	18,22	21,22	21,26
herm.*	16 mm	F132	12,11	18,22	24,24	33,27	31,34	35,33
herm.	22 mm	R6	15,14	23,23	29,49	37,35	39,39	34,41

*holotype (Foster, 1978).

DISCUSSION

None of the specimens of the present suite possessed any embryos or larvae in the mantle cavity; many had well developed ovarian tissue. It is suspected that free-swimming nauplius and normal cypris stages are involved in the life cycle of *B. alearum*, because planktotrophic nauplii are known for *B. corolliforme* from Antarctic seas (W. Newman, pers. comm.).

It is postulated that the larvae are potentially sexually hermaphrodite, but the cyprids that settle in the carinal and tergal apical niche of conspecific adults metamorphose there to feed and grow to about 4 mm length, and become precocious males. Cyprids that settle elsewhere within the orifice could be in danger of destruction by the rocking movements of the opercula, known to keep the orifice clear of encroaching organisms (Tait & Emmons, 1925; Crisp & Southward, 1961). Cyprids that settle beyond the orifice, whether on conspecific adults or not, develop to hermaphrodites if they escape the attentions of predatory whelks.

An alternative theory is that the larvae are incipient males or hermaphrodites and the former kind are compelled to find a niche in the orifice for their subsequent functioning.

To consider these alternatives, it is profitable to recapitulate the types of complementary males amongst barnacles, which can be classified as follows:

- Those that have trophi and are essentially minute forms of their associate hermaphrodites:
 - males attached among the rostral plates of *Scillaelepas* (Newman, 1980);
 - males attached to the integument between the terga below the orifice of species of *Calantica*, *Smilium* and *Euscalpellum* (see Foster, 1978);
 - males of *Bathylasma alearum*.
- Those with degenerate trophi and occurring in special pouches near the orifice of their 'host':
 - sac-like males of scalpellids, in pouches on the inside near the umbo of the scuta of scalpellids with hermaphrodites in some species (e.g. *Graviscalpellum pedunculatum*), but mostly with females in most species of arcoscalpellids (Foster, 1980);
 - small degenerate males in pouches on the inside of the rostrum of three species of *Solidobalanus* and one of *Conopea* (McLaughlin & Henry, 1972).
- Those of *Ibla* spp. that reside inside the mantle cavity, with degenerate trophi or without trophi and then either attached or lying loosely respectively (Darwin, 1815; Batham, 1945).

Within the family Scalpellidae, the most primitive genera like *Lithotrya*, *Capitulum* and *Pollicipes* (Foster, 1978; Newman, 1979) do not have males and are hermaphrodites. Somewhat more advanced genera like *Calantica*, *Scillaelepas* and *Smilium* have males of types 1a and 1b. Finally, the scalpellids that lack subcarinae and subrostra (226 species assigned to 29 genera by Zevina, 1978 a, b), and probably variously evolved from a calanticid ancestor, are of type 2a. The phylogenetic trend shown in the scalpellids is towards an association with complementary males, perhaps facultative in calanticids (see Foster, 1978) but obligatory for cross-fertilisation in the 'higher' arcoscalpellids where the larger and more normal partner lacks a male reproductive system. If this is the correct sequence of evolution, and the phylogeny is compelling, then it follows that instances of complementary males in other families have been independently evolved.

Looking beyond the barnacles (Thoracica) to the semi-parasitic and morphologically more primitive Ascothoracica, it is noteworthy that the most generalised genus, *Synagoga*, exists as sequential protandric hermaphrodites (Newman, 1974), giving a superficial impression of there being two similar sexes. The Cirripedia may be fundamentally hermaphroditic, even though they may have originally derived from the isomorphic dioecious condition of other Maxillopoda. The advent of hermaphroditism may have been associated with a parasitic life of the first cirripeds, but subsequent radiation has involved changing the protandric hermaphroditism to simultaneous hermaphroditism or, at various times, to a complementary partnering arrangement. But what are the selective advantages in the latter option?

An ability of cyprids of parasitic species to detect hosts could, with a shift in the chemical basis of that response, have changed to the gregarious response that has been demonstrated to operate in some barnacle species (Knight-Jones, 1953). The gregarious response enhances opportunities for cross-fertilisation. If an already established hermaphrodite not only attracts a conspecific neighbour but also controls its sexual identity so that it becomes sexually functional very quickly after settlement, then cross-fertilisation can be effected much more quickly. The second-comer is forced to be precocious and protandric. Otherwise the hermaphrodite would have to wait for the new-comer to grow and mature with increased chance of predation. Judging from the number of drill holes in the plates of pachylasmid barnacles (see e.g. in Fig. 1a) whelks are predators as much for sublittoral barnacles as for shore barnacles, and in sublittoral environments there can be no respite during low tides. Many shallow water fouling barnacles increase the onset of reproduction by growing rapidly and maturing at small size. In the deepsea, low food levels would not favour fast growth; the precocious complementary male possibly enhances reproduction in slow-growing species in low food environments.

If the development of complementary males is viewed as the influence of an existing barnacle over a cyprid that settles on it, the mechanism may involve a sex pheromone that operates only on cyprids that settle in close proximity to the orifice, or crawl inside the mantle as in *Ibla*. This environmental influence is what was concluded by Callan (1941) for the situation in *Scalpellum scalpellum*. There is, nevertheless, growing opinion that sex in barnacles is genotypically determined in so far as larvae exist in two types: those that will develop into males only, and those that are destined to be normal-form hermaphrodites or females (Veillet, 1956; Gomez, 1973). These latter conclusions have been based on studies of species of type 2 above, where the degree of degeneration of the male is more advanced than in *B. aleorum*, or in others of type 1. Where complementary males have become obligatory for reproduction it could well be that there is an underlying early sex-determining mechanism of a different nature to the conventional chromosome one. However, because complementary males have arisen separately on at least 7 occasions in the Cirripedia, there may be as many mechanisms.

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