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Cladistic analysis of the Cirripedia Thoracica

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We present a cladistic analysis of the Cirripedia Thoracica using morphological characters and the Acrothoracica and Ascothoracida as outgroups. The list of characters comprised 32 shell and soft body features. The operational taxonomic units (OTUs) comprised 26 well-studied fossil and extant taxa, principally genera, since uncertainty about monophyly exists for most higher ranking taxonomic units. Parsimony analyses using PAUP 3.1.1 and Hennig86 produced 189 trees of assured minimal length. We also examined character evolution in the consensus trees using MacClade and Clados. The monophyly of the Balanomorpha and the Verrucomorpha *sensu stricto* is confirmed, and all trees featured a sister group relationship between the 'living fossil' *Neoverruca* and the Brachylepdomorpha. In the consensus trees the sequential progression of 'pedunculate' sister groups up to a node containing *Neolepas* also conforms to current views, but certain well-established taxa based solely on plesiomorphies stand out as paraphyletic, such as Pedunculata (=Lepadomorpha), Eolepadinae, Scalpelloomorpha and Chthamaloidea. The 189 trees differed principally in the position of shell-less pedunculates, *Neoverruca*, the scalpelloid *Capitulum*, and the interrelationships within the Balanomorpha, although the 50% majority rule consensus tree almost fully resolved the latter. A monophyletic Sessilia comprising both Verrucomorpha and Balanomorpha appeared among the shortest trees, but not in the consensus. A tree with a monophyletic Verrucomorpha including *Neoverruca* had a tree length two steps longer than the consensus trees. Deletion of all extinct OTUs produced a radically different tree, which highlights the importance of fossils in estimating cirripede phylogeny. Mapping of our character set onto a manually constructed cladogram reflecting the most recent scenario of cirripede evolution resulted in a tree length five steps longer than any of our shortest trees. Our analysis reveals that several key questions in cirripede phylogeny remain unsolved, notably the position of shell-less forms and the transition from 'pedunculate' to 'sessile' barnacles. The inclusion of more fossil species at this point in our understanding of cirripede phylogeny will only result in even greater levels of uncertainty. When constructing the character list we also identified numerous uncertainties in the homology of traits commonly used in discussing cirripede evolution. Our study highlights larval ultrastructure, detailed studies of early ontogeny, and molecular data as the most promising areas for future research.

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ADDITIONAL KEY WORDS:—phylogeny – Crustacea – Thecostraca – barnacle.

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CONTENTS

Introduction	366
Cladistic methods	367
Terms	367
Taxa	367
Choice of outgroup	368
Characters and character scoring	369
Character description	371
Parsimony analysis	380
Methods of parsimony analysis	380
Results of parsimony analysis	381
Discussion	389
Comparison with existing phylogenies	389
Basic thoracican radiation	391
Acquisition of capitular plates	392
Sessilian monophyly and the Balanomorpha	393
The Verrucomorpha	394
Ontogeny and palaeontology	396
New lines of morphological research	398
Conclusions	400
Acknowledgements	401
References	401

INTRODUCTION

The thoracican Cirripedia or barnacles must rank among the most commonly encountered marine crustaceans in the world. They have attracted the attention of many prominent students of the Crustacea, beginning with the seminal monographs of Charles Darwin (1851–1855), whose first concrete experiences in dealing with species stemmed from his study of barnacles. While the literature abounds with scenarios for the evolution of thoracican barnacles, heretofore no-one has attempted to determine their interrelationships using a phylogenetic method of systematics. Even the latest monograph on barnacle biology still describes their phylogeny in terms of ‘balloon diagrams’ replete with paraphyletic assemblages (Anderson, 1994). The lack of a cladistic approach appears as a singular oversight on the part of carcinologists, given the wealth of modern monographs concerning the Cirripedia (e.g. Buckeridge, 1983; Foster, 1978; Klepal, 1985, 1987; Newman, 1980, 1982, 1987; Newman & Ross, 1976; Zevina, 1981, 1982; Zullo, 1992).

In a recent benchmark paper, Spears, Abele & Applegate (1994) employ 18S rDNA sequence data to address the question of cirripede monophyly and estimate the interrelationship of the major subtaxa. However, for practical reasons these authors include only a handful of thoracican species, leaving most key questions concerning intrinsic thoracican phylogeny unanswered. Many taxa considered crucial to thoracican phylogeny are extinct, but fortunately, the thoracican Cirripedia have a well-documented fossil record due to their heavily calcified exoskeleton (Newman, Zullo & Withers, 1969; Newman, 1987; Foster & Buckeridge, 1987; Buckeridge & Newman, 1992). Several ‘living fossils’ recently collected from deep sea habitats provide us with another very important source of information (Newman, 1979; Newman & Hessler, 1989; Yamaguchi & Newman, 1990; Jones, 1993a), but Spears *et al.* (1994) did not study any of these.

In this study we perused the published literature to establish a formal list of morphological characters for thoracican barnacles, scored these for both

extant and fossil taxa, and performed a cladistic analysis on the resulting data matrix using personal computer software for parsimony analysis.

CLADISTIC METHODS

Terms

In accordance with our cladistic approach we have intentionally avoided using terms such as 'lower', 'higher' and 'primitive', which otherwise abound in the literature on barnacle evolution and prefer instead, wherever possible, to talk of specific monophyletic taxa. Any taxon naturally exhibits a mosaic of apomorphic and plesiomorphic characters (Brooks & McLellan, 1991). Taxa may, within a specific character suite, possess a majority of plesiomorphies, but even so we would make a serious mistake in uncritically placing such taxa low down in the cladogram to represent archetypes or ancestors, as has so often been the case in scenarios concerning barnacle evolution. We can only designate *character states* as plesiomorphic in any strict sense and we can only prove this *a posteriori* as the result of a cladistic analysis using the usual criteria for polarizing character transformation series. As an example, instead of speaking of the radiation among 'lower balanomorphs' we prefer the term 'basic balanomorph radiation', which more succinctly confers our meaning.

Taxa

Choice of taxa

We do not present here an exhaustive phylogenetic analysis of all taxa within the Cirripedia Thoracica. We selected as terminal taxa or operational taxonomic units (OTUs) an array of phylogenetically interesting groups, which for the most part have figured prominently in past speculations about the evolution of the Cirripedia. With these choices, we sought to address some key issues in barnacle phylogeny, including the monophyly of the Sessilia, the nature of the basic balanomorph radiation, and the position of the verrucomorphs and brachylepadomorphs. We have excluded several species-rich taxa such as the Poecilasmataidae which, though interesting in themselves, provide little or no information on these questions. We also limited ourselves to a few representative members of the Scalpelloidea, since we could not adequately resolve their internal phylogenetic relationships with the present database.

Monophyly of OTUs

An implicit assumption in a cladistic analysis is that OTUs are monophyletic. However, for many thoracican families only one or a few genera have been analysed for the characters surveyed here. In some cases, e.g. *Lepas*, we have accordingly chosen a well-described genus instead of a larger but less assuredly monophyletic unit (Lepadidae). The genera included in the matrix mostly display little variation relevant to our character set. Naturally, however, we have striven to encode all supraspecific OTUs (e.g. Verrucidae) by the putative character states of the last common ancestor rather than by a single

species that might not represent the ground pattern of the taxon. Concerning balanomorphs, we accept that the Coronuloidea + Balanoidea are most likely to form a monophylum. The diagnosis of the Chthamaloidea seems based principally on symplesiomorphies, so we split this taxon into several more assuredly monophyletic OTUs. We scored our *Catophragmus* so as to also comprise *Catomerus*.

Fossil taxa

Our OTUs include both living and extinct taxa. Preliminary analyses on a larger matrix showed, however, that inclusion of many insufficiently known fossils would serve only to further obscure the basic framework. Thus, we have excluded from the matrix such potentially interesting species as the Cambrian form *Priscansermarinus barnetti* (Collins & Rudkin, 1981) from the Burgess Shale and the epibiont of ammonoids *Blastolepas* (Drushchits & Zevina, 1969). We could have scored these and other fossils for only a minority of the 32 characters, and, including them in the analysis simply increases the possible number of tree topologies in the parsimony analysis. These fossils definitely do not lack phylogenetic interest, since even a very incompletely known fossil may provide important information about the minimum age of a certain character state. We merely believe that at this time the lack of sufficient information about important character states in many fossil taxa confounds attempts to resolve their phylogenetic position.

Throughout this paper † indicates an extinct taxon.

Choice of outgroup

The Thecostraca

Consensus now exists that the taxon Thecostraca is monophyletic (Grygier, 1987a; Newman, 1992). In phylogenetic systematic terms, we define as Thecostraca all descendants from the last common ancestor of the Ascothoracida, the Facetotecta, the Acrothoracica, the Rhizocephala, and our ingroup, the Thoracica. Most authors will unite the last three taxa in a monophyletic Cirripedia (Høeg, 1992). Newman (1992) also includes the Tantulocarida in the Thecostraca.

Among the thecostracan taxa the Facetotecta are known only as larvae, while both the Tantulocarida and Rhizocephala are highly specialized for a parasitic life style. It follows that we can only score these taxa for a minority of the 32 characters used in analysing the Thoracica. We therefore chose the Ascothoracida and the Acrothoracica as outgroups, since they remain the only other thecostracans in which adult features can be reasonably homologized with those in the Thoracica. Furthermore, we consider it a sound principle to have more than a single outgroup in a parsimony analysis. We also emphasize that exclusion of the Tantulocarida, the Facetotecta and the Rhizocephala means that our analysis does not address the current debate concerning the phylogenetic position of these taxa within the Thecostraca (but see: Applegate, Abele & Spears, 1991; Høeg, 1992; Huys, Boxshall & Lincoln, 1993; Newman, 1987, 1992).

Position of the Ascothoracida

Most authorities agree on a close relationship between the Ascothoracida and the Cirripedia. Newman (1979, 1982, 1987) clearly believes that the ascothoracidans and the cirripedes form a monophylum. Schram (1986) supported this position with a cladistic analysis of all crustacean higher taxa. Both of these authors concentrated largely on the classical features of external adult morphology. The analysis by Grygier (1981, 1982) of sperm ultrastructure in some maxillopodans (reviewed by Jamieson, 1991 and extended by Storch & Jamieson, 1992) came to similar conclusions. In addition, Grygier's (1987a, b) studies based on certain features of larval anatomy also placed the ascothoracidans as a sister group to the Cirripedia. Our choice of the Ascothoracida as an outgroup in the present analysis therefore seems well justified.

Position of the Acrothoracica

The phylogenetic position of the Acrothoracica has posed some problems. Newman (1982) originally suggested that acrothoracidans arose from within the scalpelloid pedunculates, specifically from a form similar to *Lithotrya*. Schram's (1986) cladistic analysis had the Acrothoracica and Thoracica as independent OTUs and suggested that they acted as sister groups, a position Newman (1987) eventually came to hold and which Zevina (1991) and Høeg (1992) seconded. Most recently, Spears *et al.* (1994) employed sequencing of 18S rDNA and analyses of its secondary structure to estimate cirripede phylogeny. Their data from one ascothoracidan, two acrothoracidans, one rhizocephalan, and several thoracidans clearly demonstrated that the Thoracica are monophyletic and the sister group to the Rhizocephala, while a monophyletic Acrothoracica appears to have split off very low down in the thecostracan tree. It seems, therefore, that both morphological and molecular data support our choice of the Acrothoracica as one of the outgroups.

Characters and character scoring

We developed a list of 32 characters, which principally concern hard parts in juveniles and adults. The choice of characters grew out of our own collective experiences with barnacles and what has repeatedly proved useful in the literature (e.g. see Newman, 1980, 1987, 1989; Newman & Hessler, 1989; Yamaguchi & Newman, 1990). Based on these papers and discussions between two of us (MJG and JH) and Prof. W.A. Newman at and before the Workshop: 'The Crustacea: Origin and Evolution' held at Kristineberg, Sweden, 1991 (see; Boxshall, Strömberg & Dahl, 1992) we have striven to incorporate the latest theory concerning shell-plate homology within the Thoracica.

Scoring for primary and secondary absence

When constructing the character matrix we wanted to avoid as much as possible preconceived ideas on phylogeny prior to the actual analysis. Therefore, where putative secondary loss cannot be structurally distinguished from primary, plesiomorphic absence, we coded with the same state. The parsimony analysis itself must then clarify whether reversals really took place.

We believe this remains the only valid approach and reflects the current lack of knowledge about the ontogenetic or palaeontological development of some features, and thus uncertainty about homologies. Coding a missing trait as though it still persists because the ancestor supposedly possessed it equates to an unsupported *a priori* assumption about secondary loss.

Scoring fossils

Extending the above policy, we also abstained from coding traits as present in fossils where we cannot or have not observed them, even where supposedly close relatives do exhibit the features in question. Failure to observe these simple but important rules will inevitably result in an evolutionary systematic scenario in cladistic disguise. Even Briggs, Fortey & Wills (1993), in their otherwise scholarly cladistic study of Cambrian and Recent arthropods, lapsed into this trap with their characters 12, 29 and 45.

To exemplify our policy, we scored characters pertaining to soft parts with a (?) for all fossil taxa. Similarly, we scored the shell-less Heteralepadidae with a (?) for all characters concerning shell plate morphology, except, of course, those coding for the observably presence/absence of entire plates. Many researchers would score a taxon for an unobserved character state based on its estimated ancestry; indeed, common practice in some accounts on barnacle evolution comes dangerously close to a circular argument. It is from the character matrix itself that we should aim to estimate phylogenetic relationships.

Uninformative characters

The matrix includes a few characters where we score one of two possible states only for a single OTU. Such characters contribute no information to a parsimony analysis, but we have nevertheless included them. Firstly, other workers habitually consider these features very important in barnacle evolution. Secondly, including them now will facilitate a revision of the matrix when and if new information permits us to replace some of the (?) by positive scorings for the features in question.

State numbers and polarity

In the character state list (Table 1) and in the character matrix, (0)s and (1)s do not signify a polarity decision but simply the neutral principle that the state found in the outgroup is habitually coded (0).

Multistate characters

The 32 characters include five multistate characters (1, 2, 3, 5, 20). The five-state character 3 is an alternative coding of combined characters 1 and 2. In all analyses we inactivated either characters 1+2 or character 3 accordingly. Among the multistate characters, we always kept character 1 unordered (see: Brooks & McLennan, 1991), while we used both ordered and unordered options with characters 3 and 5.

TABLE 1. Character matrix. Extinct OTUs marked by (+); unknown states by (?) and inapplicable states by (-). Codings for *Catophragmus* also include data for *Catomerus*. Character 3 represents an alternative coding of characters 1 & 2; hence we deactivated either characters 1+2 or character 3 in all analyses. The headlines in the OTU column refer to groupings of taxa referred to in the text

OTUs (25)	Characters 1-32
OUTGROUPS	
Ascothoracida	02001000-0-00-0-----0-0010
Acrothoracida	00302000-0-00-0-----0-----000000
<i>Cyprilepas</i> †	101?1000-0-00-0-----0-----?????
Iblidae	10110100-0-00-0-----00--0--011010
Heteralepadidae	10101000-0-00-0-----0-----111010
<i>Praeilepas</i> †	101?1110-0-00-0-----00-000-?????
<i>Lepas</i>	10112110-0-00-0-----00-000-111010
<i>Archaeolepas</i> †	202?211100-00-0---010-0000?????
<i>Neolepas</i>	2021211101-00-0---010-0000111000
SCALPELLOIDEA <i>sensu stricto</i>	
<i>Pollicipes</i>	2021211111011000--02100000110010
<i>Scillaelepas</i>	2021211111?11000--021-100011?010
<i>Scalpellum</i>	2021211111011000--02101000111000
<i>Capitulum</i>	20212111010110000-02100000111000
Brachylepadomorpha	0????211101?00--00-12110000?????
<i>Neoverruca</i>	0031211101100--00-12110111111011
VERRUCOMORPHA <i>sensu stricto</i>	
<i>Eoverruca</i> †	0????21110????10010-130-0111?????
<i>Proverruca</i> †	0????21110????10010-120-0111?????
Verrucidae	0141211100-00-010-130-011-110000
BALANOMORPHA	
<i>Eochioneasmus</i>	0141211100-110011013100000110101
<i>Chioneasmus</i>	0141211100-110011013100000110100
<i>Waikalasma</i> †	0????211100-1101110131?0000?????
<i>Pachylasma</i>	0??0211100-1101110130-0000110100
<i>Catophragmus</i>	0??0211100-110111113100000111100
<i>Octomeris</i>	0????211100-1101111130-0000110101
Chthamalinae	0??0211100-1100111130-0000110100
Balanoidea-Coronuloidea	0140211100-1111111130-0000110101

CHARACTER DESCRIPTION

01. Peduncle in adult

state 0 = Absent.

state 1 = Present but without calcified scales.

state 2 = Present and with calcified scales.

Classical speculations on barnacle phylogeny inevitably treat the presence of a distinct, muscular peduncle in the adult as plesiomorphic, and its absence as apomorphic. The peduncle is considered homologous with the antennules of the cyprid and of forms such as the Ascothoracida, and the developmental link here does seem clear. However, the peduncle remains a unique structure in its own right and includes more than just antennular tissue. One might contemplate a homology between calcified peduncular scales and imbricating plates (character 21), but we do not want to pursue this problem here.

We code sessile barnacles, traditionally assumed to have secondarily lost

a peduncle, with state (0). This is in accordance with our strategy of no *a priori* distinction between primary absence and possible secondary loss. Loss of the peduncle may possibly have occurred convergently, but such a hypothesis must result from an *a posteriori* accumulation of compelling evidence from other characters.

02. Pedunculate stages in ontogeny

state 0 = Present.

state 1 = Only traces present.

state 2 = Absent.

We consider the 'peduncle' seen in ontogeny of the Acrothoracica (Turquier, 1970) as homologous to that in the Thoracica. Zevina (1991) opines that adults of *Weltneria* also have a peduncle, but we do not think that her figures illustrates this convincingly. Darwin (1852, 1854) and Glenner & Høeg (1993) argue that some balanomorphs have a transitory peduncle in early ontogeny (state 1), but among 'sessilian' barnacles only juveniles of *Neoverruca* display a distinct pedunculate stage (Newman, 1989). We code the Brachylepadomorpha with a (?), since no information exists on ontogeny in this taxon, formerly believed to have become extinct. However, the intriguing discovery of an undescribed, living species may soon provide important information (Newman, personal communication). We score as (0) when the peduncle seen in ontogeny appears distinct (i.e. longer than wide) and (1) when not distinct and without a distinct boundary between the capitulum and peduncle.

03. Peduncle (alternative to characters 1 & 2)

state 0 = No peduncle at any stage.

state 1 = Peduncle (in adult) without calcified scales.

state 2 = Peduncle (in adult) with calcified scales.

state 3 = No peduncle in adult, but distinct in juveniles.

state 4 = No peduncle in adult; traces present in early juveniles.

This combines the information from characters 1 and 2 into a single multistate character. In the parsimony analyses we accordingly deactivated either characters 1+2 or character 3. In most analyses we set character 3 to 'ordered' based on evidence from ontogeny and palaeontology. In general, we consider it dubious to split multiple homologous traits into independent binary characters. However, combining all information on the peduncle into a single character results in a problem with taxa whose ontogeny remains unknown, while the adults lack a peduncle altogether. Since we must obviously score such taxa as (?) for character 3, we lose the information that actually exists for the adults.

04. Primordial valves

state 0 = Absent.

state 1 = Present.

This character refers to the cuticular primordia of the scuta, terga, and

where present, the carina (Fig. 1C). The primordial valves develop prior to any mineralization and usually within days or even hours after settlement (Glenner & Høeg, 1993). By the criterion of ontogeny this indicates that we should consider cuticularized plates more plesiomorphic than mineralized plates, and this character therefore also relates to character 5. Darwin (1854) mentions that he observed traces of primordial plates in *Chthamalus*, but Newman (1987) considers this observation as unconfirmed. We therefore scored all balanomorphs except *Chionelasmus* and *Eochionelasmus* with (0).

05. Mantle mineralization

state 0 = Cuticle with phosphatized parts.

state 1 = Cuticle without mineralized parts.

state 2 = Cuticle with calcified parts.

A simple, unmineralized cuticle exists in the outgroup Ascothoracida and in several of the ingroup OTUs e.g. the Heteralepadidae. With some hesitation we follow Grygier & Newman (1985) and score the Acrothoracica with (2), although the chemical nature of the mineralized element in this taxon needs reinvestigation. We set this triple-state character to ordered (additive) in most analyses, since we consider it highly unlikely that a calcified cuticle could change directly into a phosphatized one as seen in the Iblidae (Whyte, 1988; Löwenstam & Weiner 1992). Running the character unordered, however, did not change any of the resulting trees.

06. Scuta and terga

state 0 = Absent.

state 1 = Present.

These plates always appear in pairs and are apparently the only plates present in *Ibla*. We refrained from scoring the scuta and terga as separate characters because no taxon exemplifies a state possessing one pair but missing the other. Newman (1987) considers the Silurian fossil *Cyprilepas holmi* to have two uncalcified plates, but this is hardly a correct interpretation. In a settled and metamorphosing cypris, all five primordial valves (character 4) develop beneath the cypris carapace, so the carapace corresponds to the entire mantle and hence to all shell plates in the adult. Most likely the same argument applies to the valves in *Cyprilepas*, since they seem to be homologous with the cypris carapace. We score the Heteralepadidae as they appear, i.e. without a trace of either the terga or the scuta. Some would argue that this taxon has secondarily lost shell plates, but the lack of primordial valves (character 4) in *Heteralepas* speaks against this interpretation.

07. Carina (C)

state 0 = Absent.

state 1 = Present.

Presence implies a state with at least five shell plates, since no known cirripede possesses a carina but no scuta and terga. The carina resides between the two terga.

Figure 1. Morphological traits used in parsimony analysis. A–C, *Pollicipes pollicipes*. A, External morphology. B, Mantle cavity exposed. C, Stage from early ontogeny showing primordial valves. Peripheral figures illustrate some selected OTUs to highlight important character states. *Ibla* and *Verruca* represent the OTUs Iblidae and Verrucidae. All figures oriented with carinal side facing left. Numbers refer to those in the character description (see text) and the character matrix (Table 1). Note that *Pollicipes* (B) lacks both branchiae and ovigerous frena (characters 29, 30). A–C, original; peripheral figures redrawn from Newman *et al.* (1969), Yamaguchi & Newman (1990), Buckeridge & Newman (1992), and Anderson (1994).

08. Rostrum (R)

state 0 = Absent.

state 1 = Present.

Presence of an unpaired rostrum situated between the two scuta always represents a stage with at least six plates (rostrum, carina, scuta, terga). A possible exception is the so-called calcareous rostrum of some species of the acrothoracican genera *Weltneria* and *Lithoglyptes*, discussed at length by Newman (1971, 1974) and Grygier & Newman (1985). When present, it is the only calcareous plate found in acrothoracicans. With some hesitation, we nonetheless score the Acrothoracica with a (0) for character 8, because Newman (1987) listed several reasons against a homology with the scalpelloid rostrum, as assumed in the earlier papers cited above.

*09. Size of rostrum*state 0 = Rostrum length $\geq$ carina length.

state 1 = Rostrum length < carina length.

In adults, the rostrum varies much in size relative to its counterpart, the carina, among the six principal plates.

10. Median latus (L)

state 0 = Absent.

state 1 = Present.

We mean a true latus (capital L) in the sense of Newman (1987, 1989) and Yamaguchi & Newman (1990). We score as present (1) only when that latus is actually present. We coded it (0) for *Eoverruca* †, *Proverruca* †, *Verruca*, and for all balanomorphs in accordance with our introductory note on not distinguishing *a priori* between 'primitive absence' and 'secondary loss' for missing structures. We scored *Neoverruca* with a (1), although, uniquely among all OTUs, it has a latus (L) on one side only. This remarkable asymmetry appears as a state of (1) of character 26. See also the notes to character 13.

11. Heterochrony of the median latus (L)

state 0 = L arises before 1.

state 1 = By heterochrony L arises after 1.

Cirripedologists habitually designate as '1' the imbricating plate immediately below L. State (1) has till now only been demonstrated in *Neoverruca darwini* by Newman (1989), so it provided no information to the present analysis. We have nonetheless included this character in the matrix to highlight its possible value in a revised matrix incorporating new, undescribed species from hot vent habitats in the deep sea (Newman, personal communication).

12. Carinolatus (CL)

state 0 = Absent.

state 1 = Present.

Occurrence of carinolaterals in the wall of shell plates. See notes for character 13.

13. *Rostrolatus* (RL)

state 0 = Absent.

state 1 = Present.

Occurrence of rostrolaterals in the wall of shell plates. We must express considerable doubt regarding the traditional homology scheme when comparing lateral plates in scalpelloids and verrucomorphs with those in balanomorphs. Cirripedologists generally agree that a scalpelloid such as *Pollicipes* possess both CL, L, and RL (characters 10, 12, 13). However, our Figure 1A clearly illustrates that the plates bearing these names may often deviate little, if at all, in special morphology and size from the remaining and largely anonymous imbricating plates. Thus the homology seems based principally on the criterion of position, although assisted by some evidence from ontogeny and comparison to OTUs such as *Neolepas*.

Proverruca† and *Eoverruca*† possess two large plates in a lateral position, which the traditional interpretation (Newman *et al.*, 1969) considers as CL and RL. However, this has come to seem doubtful since the putatively more plesiomorphic member of the verrucomorph clade, *Neoverruca*, has a median latus (L) but no dedicated carinolatera (CL) or rostrolatera (RL). We do not want to build our interpretations on preconceived ideas of phylogeny, so we examined the possible homologies between the lateral plates in *Proverruca*† and *Eoverruca*† and those in either balanomorphs or scalpelloids. This reveals that we cannot reject the possibility that the plate overlapping the rostrum (R) in *Proverruca*† and *Eoverruca*† may, positionally, be an RL, but it cannot be an L. We therefore code these two OTUs as 13(1). The other plate, however, overlapped by the one just mentioned and itself overlapping the carina, could either be an L or a CL. We therefore code *Proverruca*† and *Eoverruca*† as 12(?); (see Fig. 1).

14. *RL relation with R*

state 0 = RL not fused with R.

state 1 = RL fused with R.

This character pertains to the intricate patterns of wall plates in balanomorphs.

15. *Presence of CL2*

state 0 = Absent.

state 1 = Present.

Sorting out the identity and homologies of the various lateral plates in thoracicans has recently revealed a series of surprises. Cirripedologists have long doubted the homology between the latus (L) in scalpelloids and the plate traditionally called by the same name in balanomorphs. Recently, Yamaguchi & Newman (1990) took a firm stand based on new evidence and argued that the balanomorph 'median latus' represents an apomorphy, which originated *de novo* by a subdivision of the carinolatus (CL).

16. *Wall of shell plates*

state 0 = Not in contact with substratum.

state 1 = In contact with substratum.

This feature applies to the basic balanomorph radiation, where the principle plates rest on the substratum but some taxa retain imbricating plates.

17. Sheath

state 0 = Absent.

state 1 = Present.

The development of an internal sheath, involving most or all of the wall plates, and the associated pattern of shell growth, is of principal importance in attaining the 'Bauplan' seen in most balanomorphs (Newman & Ross, 1976). We conservatively consider all sheaths as homologous, although Anderson (1994) separates three, substantially different varieties.

18. Sheath and RL

state 0 = RL does not enter into sheath.

state 1 = RL enters into sheath.

This concerns whether the rostrolatus (RL) forms part of the wall's internal sheath. We scored this feature only in OTUs coded with state (1) for character 12.

19. Separation of opercular plates from wall plates

state 0 = No operculum.

state 1 = Operculum present.

A distinct operculum is present whenever the tergum and scutum on at least one side are set off as a moveable lid against the wall plates, and it constitutes an integral part of the 'Bauplan' of sessile barnacles. We have scored inapplicable (-), when the wall does not at least comprise a carina and a rostrum.

20. Articulation between scutum and tergum

state 0 = Opercular plates articulated, but not interlocking.

state 1 = Hinge-like structures, but not interlocking.

state 2 = Hinges movably interlocked.

state 3 = Highly complex hinge.

This character concerns the degree to which the scuta and terga articulate with each other, and state (3) denotes the highly complex state seen in higher Verrucomorpha and Balanomorpha. However, we may express some doubt concerning the homology between the opercula in balanomorphs and verrucomorphs (character 19), and the same goes for the states of character 20. Lacking decisive information, we have hesitantly accepted these homologies.

21. Imbricating whorls

state 0 = Absent.

state 1 = Present.

Whorls of smaller plates can encircle the capitulum beneath the wall plates (carina, latera, rostrum). The OTUs differ in the number of these whorls, but preliminary analysis showed that it was not practical to distinguish between these states. As an example, the single whorl in *Eochionelasmus* and *Capitulum* probably arose convergently from the fusion of several whorls. *Scillaelepas* also portrays an enigmatic condition, and in one interpretation

only the subrostrum and subcarina belong to the imbricating plates. When we know more about the ontogeny of problematic species, both this character and those pertaining to the ontogeny of imbricating plates will need revising. We have scored (–) for the Ascothoracida, because this taxon shows no evidence of ever having had a stalk.

22. Addition of imbricating whorls

state 0 = Added at outer or bottom end.

state 1 = Added at inner or upper end.

This character concerns only those OTUs having the capitulum encircled by complete whorls of imbricating plates. Newman (1989) demonstrated state (1) in the ontogeny of *Neoverruca*. By inference from wear of the plates he also (personal communication) concludes state (1) for an extant and still undescribed brachylepadomorph.

23. Small, isolated plates below carina-rostrum tier

state 0 = Absent.

state 1 = Present.

A homology between these plates and those of complete, imbricating whorls (character 20) probably exists. Furthermore, the lateral plates (RL, CL, CL2, and L) in all likelihood also evolved from imbricating plates and in some OTUs deviate little if at all from these except by their position higher up on the capitulum. We therefore attempted to incorporate all information from characters 10, 12, 13, 21 and 23 into a single multistate character. However, numerous uncertainties compelled us to treat these traits as separate characters with the inherent danger of obscuring some important homologies.

24. Symmetry of scutum and tergum

state 0 = Free and identical on both sides.

state 1 = Fixed on one side; movable on the other.

Together with character 25 this acts as the ‘classic’ synapomorphy for the Verrucomorpha, whereby the opercular plates on one side have become fixed and form part of the wall, while those on the opposing side form the movable operculum.

25. Symmetry of carina and rostrum

state 0 = Both symmetrical.

state 1 = Asymmetrical and meeting on one side.

(1) denotes a state where the carina and rostrum have asymmetrical shapes and meet on the side of the movable operculum that forms the lateral part of the wall. In OTUs without a rostrum, character 24 applies only to the shape of the carina.

26. Symmetry of latera

state 0 = Latera symmetrically present on both sides.

state 1 = Present on one side only.

Putative early offshoots from the Verrucomorpha possess lateral plates on the side of the movable tergum and scutum, but none on the fixed side.

Neoverruca possesses a single asymmetrical lateral plate, which, following Newman & Hessler (1989), we consider as a true median latus (L). The two asymmetrically positioned latera seen in *Proverruca*† and *Eoverruca*† may represent apomorphies in their own right or they may be homologous to CL and RL in other cirripedes (see: characters 12 and 13). However, all latera, whatever their specific homologies, were most likely recruited from the uppermost tier of imbricating plates, so a homology at this level seems certain.

27. *Position of musculus adductor scutorum (MAS)*

state 0 = Post-oesophageal.

state 1 = Pre-oesophageal.

Cirripedologists generally assume a pre-oesophageal position for the MAS in all Thoracica except *Ibla* (see: Darwin, 1852; Krüger, 1940; Klepal, 1985; Anderson, 1994). We are indebted to W. A. Newman (personal communication) for reports on the state of this character in some of our OTUs. To analyse the state in the Heteralepadidae we embedded three specimens of *Paralepas japonica* in epoxy resin and serially sectioned them at 2 µm. However, some of the other shell-less thoracican taxa, notably the Microlepadidae, should also be checked for this character. Some doubt exists concerning the homology of pre- and post-oesophageal MASs (Klepal, 1985), but we consider them as homologous states of the same structure.

28. *Mandibular palp*

state 0 = Located on the mandible.

state 1 = Located on the labrum.

Much discussion has concerned the nature of the 'labral palp' in thoracican barnacles. Superficially, the palps look like an independent pair of appendages. However, a homology obviously exists between this 'labral' palp in thoracicans and the conventionally positioned mandibular palp in the outgroup Acrothoracica (Klepal, 1985). However, since we code the Ascothoracida as (?), the character remains uninformative in the analysis. Comparison with more distant outgroups such as Copepoda might settle the plesiomorphic state at (0).

29. *Ovigerous frena*

state 0 = Absent.

state 1 = Present.

These structures are lacking in *Pollicipes*, the Verrucidae, and in balanomorphs except for *Catomerus* (Walker, 1983). Frena were previously considered homologous to 'branchiae'. However, Walker (1983) found both types in *Catomerus* so we must consider them as separate characters.

30. *Branchiae*

state 0 = Absent.

state 1 = Present.

We score these structures on the mantle as present in all 'balanomorphs' including *Catophragmus*, *Chionelasmus*, and *Eochionelasmus* (Walker, 1983; Yamaguchi & Newman, 1990).

31. Filamentary appendages

state 0 = Absent.

state 1 = Present.

These represent unarticulated extensions of the prosoma. Their homology throughout the taxa analysed here remains in doubt. At least in *Pollicipes* (Fig. 1B) they contain extensions of the testis, but their nature in other taxa remains unknown.

32. Caudal filaments

state 0 = Present.

state 1 = Absent.

If we assume a homology to caudal rami, the outgroup Ascothoracida also has caudal filaments. Most OTUs have retained these filaments, but they do not occur in *Neoverruca*, *Eochionelasmus*, *Octomeris*, and the Balanoidea-Coronuloidea (Newman & Ross, 1976; Newman & Foster, 1987), and we predict some convergent losses have taken place.

PARSIMONY ANALYSIS

Methods of parsimony analysis

We performed a parsimony analysis in search of shortest trees on two platforms: a Macintosh IIvx running system 7 and using the software package PAUP 3.1.1. (Swofford, 1993) and an Intel 80486-based personal computer running MS-DOS 6.0 and the software package Hennig86 ver. 1.5 (Farris, 1988). In PAUP all options appear in the menu driven interface. For Hennig86 we list the commands employed whenever appropriate.

The parsimony analyses used the Ascothoracida and Acrothoracica as a composite outgroup. In Hennig86 this was effected with the command 'outgroup' and with the option '/[taxon number]' to set the Ascothoracida as the primary outgroup. We obtained identical results, however, when choosing only the Ascothoracida as outgroup and with the Acrothoracica as part of the ingroup.

Tree searches with PAUP 3.1.1 took place on the same matrix used as input to Hennig86. We edited it for appropriate commands and transferred it on disk to the Macintosh in order to eliminate errors that might arise by a manual recoding.

In all our variant analyses, we employed algorithms to find all shortest trees: in Hennig86, the command 'ie*' (implicit enumeration), and in PAUP 3.1.1, the option 'branch and bound'. We always obtained identical results with Hennig86 and PAUP 3.1.1 whenever comparable options were chosen for the tree searches.

We exercised alternate character coding schemes by activating and deactivating character (1+2 or 3 respectively), and by setting multistate characters to ordered (additive) or unordered (Brooks & McLennan, 1991). In Hennig86 this was achieved by using the command 'ccode' with appropriate switches. We always had all character weights set to 1 except when exercising the scheme for successive weighting (see below).

In Hennig86 we saved the trees resulting from variant parsimony analyses

to disk using the command 'tsave'. This allowed us to read the trees into memory again at a later stage for further investigation without having to rerun the time-consuming parsimony analysis. The command 'tchoose' allowed us to select subsets of trees for further analysis. We employed the Hennig86 and PAUP options for successive weighting of characters (Farris, 1969; Carpenter, 1988). In Hennig86 this was achieved by first setting all characters to unordered; hereafter, we alternately used the commands 'ie*' (exhaustive search for shortest trees) and 'xsteps w' (which sets character weights from 0 to 10 according to fit) until no changes occurred in the weights assigned. The PAUP 3.1.1 'constrain' option, unavailable in Hennig86, allowed us to keep sets of terminal taxa as monophyletic during tree searches.

In Hennig86 we used the tree editor 'Dos Equis' for preliminary inspection of character evolution, but generally we exited Hennig86 and read the matrix and appropriate trees into the program CLADOS (Nixon, 1992), designed specifically to interface with Hennig86. Similarly, we transferred trees obtained by PAUP 3.1.1 to MacClade 3.0 (Maddison & Maddison, 1993) for further investigation; the latter program offers more powerful options than the PC-based software. We compared our results to an existing phylogeny by constructing a tree in parenthetical notation and reading it into Hennig86 or by constructing the appropriate tree with MacClade. Character optimization on trees derives from analysis in CLADOS/MacClade.

In Hennig86 we calculated the strict (Nelson) consensus trees with the command 'nelsen'. In PAUP 3.1.1 we calculated the strict, semistrict, Adams, and 50% majority rule consensus trees by using the appropriate menu options.

Values for tree length (L), consistency index (CI), and retention index (RI) provided in text and tables concern individual trees, and, where comparison could be made, Hennig86 returned identical tree diagnostics.

Results of parsimony analysis

Analyses of parsimony with variant assumptions resulted in the trees illustrated in Figures 2–9. In the figures, we have renumbered the nodes from those returned by the software so they can be more easily compared between the different trees. Thus, nodes containing the same cluster of OTUs generally keep their number throughout. If polytomies in the strict consensus tree (Fig. 2) become wholly or partially resolved in variant analyses, the resulting nodes keep their Arabic number with a letter added. Thus node 7 in Figure 2 becomes nodes 7, 7A, and 7B in Figure 3.

To facilitate the discussion of trees we apply the following terms to groupings of OTUs: Scalpelloidea (*Neolepas*, *Capitulum*, *Pollicipes*, *Scillaelepas*, *Scalpellum*); Scalpelloidea *sensu stricto* (*Capitulum*, *Pollicipes*, *Scillaelepas*, *Scalpellum*); Verrucomorpha (*Neoverruca*, *Eoverruca*†, *Proverruca*†, *Verrucidae*); Verrucomorpha *sensu stricto* (*Eoverruca*†, *Proverruca*†, *Verrucidae*); Balanomorpha (*Chionelasmus*, *Eochionelasmus*, *Waikalasma*†, *Catophragmus*, *Pachylasma*, *Chthamalinae*, *Octomeris*, *Balanoidea-Coronuloidea*); Sessilia (Balanomorpha, Verrucomorpha *sensu stricto*, *Neoverruca*, *Brachylepadomorpha*).

Default analysis

In this analysis we activated characters 1+2 (concerning the peduncle) while keeping the alternative character 3 deactivated. We set all characters

Figure 2. Default analysis. Strict consensus from 189 trees resulting from a computerized parsimony analysis on the character matrix in Table 1 and with minimum assumptions about character evolution. The outgroup comprised both the Ascothoracida and the Acrothoracida. Character 3 was deactivated (see text). Character 5 was set to ordered (additive). (†) indicates extinct taxa.

except 5 (type of mantle mineralization) to 'unordered'. The analysis resulted in 189 shortest trees of 61 steps. We obtained exactly the same trees if we also set character 5 to unordered. The strict consensus tree (Fig. 2) has fairly good resolution and shows that all 189 trees exhibit the same sequence of 'pedunculate' taxa between the Iblidae (node 2) and *Neolepas* (node 6). The consensus also contains additional monophyletic groups, notably the Balanomorph, the Verrucomorph *sensu stricto*, a clade comprising Brachylepadomorpha and *Neoverruca*, and a *Pollicipes-Scillaelepas-Scalpellum* clade. It is not surprising that the consensus tree contains several polytomies, considering that our matrix contains a small number of characters compared to the number of OTUs. Notable polytomies appear at node 1 (concerning shell-less forms) and at node 7 (concerning scalpelloids and sessilians).

All four types of consensus tree (strict, semistrict, Adams, and majority rule) have an identical topology below the *Neolepas* node. The semistrict

Figure 3. The 50% majority rule consensus tree from the analysis in Figure 2. Percentages at nodes denote their frequency of occurrence among the 189 shortest trees.

consensus tree (not illustrated) differs from the strict consensus only in the Balanomorph, where it features a sister group relationship between the Chthamalinae and the Balanoidea-Coronuloidea-*Octomeris* clade. The majority rule consensus tree (Fig. 3) fully resolves node 7 and all higher nodes except for the trichotomy between *Chionelasmus*, *Eochionelasmus* and the remaining Balanomorph. This tree also features both a monophyletic Scalpelloidea *sensu stricto* (node 7A) and a monophyletic Sessilia (node 7B). The Adam's consensus tree (not illustrated) had an identical topology except that it failed to resolve node 9 in the Scalpelloidea and collapsed nodes 13A and B in the Balanomorph. Both the strict and the semistrict consensus trees had *Capitulum* as part of the polytomy at node 7.

A screening of all 189 trees revealed two gross topologies above the *Neolepas* node, which differed in the position of *Capitulum* and the Brachylepadomorpha-*Neoverruca* clade. With the 'tchoose' command in Hennig86 we selected the relevant subsets of trees and computed their strict consensus separately (Figs 4, 5). The first topology (i) occurs in 126 trees and features a monophyletic Scalpelloidea *sensu stricto* (= *Capitulum*, *Pollicipes*, *Scalpellum* and *Scillaelepas*) as sister group to a monophyletic Sessilia (= Brachylepadomorpha-*Neoverruca*, Verrucomorpha *sensu stricto* and Balanomorph). However, a monophyletic Scalpelloidea *sensu stricto* finds support only in the appearance of a carinolatus (character 12) at node 7A, an event which in this topology also occurred convergently at node 12 in the balanomorphan lineage.

The second topology (ii) occurs in a third of the trees and contains neither a monophyletic Scalpelloidea *sensu stricto* nor a monophyletic Sessilia. Instead, the Brachylepadomorpha-*Neoverruca* clade diverges lower on the tree (node 7) between *Neolepas* and a clade comprising only *Pollicipes*, *Scillaelepas* and

Figure 4. Topology (i). Strict consensus from the subset of 126 trees in the default analysis conforming to topology (i). The cladogram contains a monophyletic Scalpelloidea *sensu stricto* at node 7A.

Scalpellum. *Capitulum* appears as sister group to a clade consisting of the Verrucomorpha *sensu stricto* and the Balanomorpha. However, also in topology (ii) only a single apomorphy supports the position of *Capitulum* (node 7D); in this case the loss of filamentary appendages (character 31), which among the ingroup OTUs were also lost convergently in *Neolepas* and *Scalpellum*.

Figure 5. Topology (ii). Strict consensus from the subset of 63 trees in the default analysis conforming to topology (ii). This cladogram features a sistergroup relationship between *Capitulum* and a lineage (node 10) containing the Verrucidae *sensu stricto* and the Balanomorpha.

Figure 6. Outgroups and character options. Strict consensus trees from variant analyses estimating the effects of different outgroups and character options. The trees differ from Figure 2 (default analysis) in the basic radiation only. A, Default options on full matrix but the Iblidae as outgroup. B, Default options on reduced matrix (shell-less forms excluded) and the Iblidae as outgroup. C, Default options on full matrix but the Heteralepadidae as outgroup. D, Outgroups as in Figure 2, but characters 1 + 2 inactivated, character 3 activated and set to ordered.

Topology (i) occurs in the PAUP majority rule consensus tree simply because the trichotomy in the consensus tree within the Scalpelloidea (Fig. 4: node 9) leads to more variant trees than does topology (ii), which has the

Figure 7. Verrucomorpha monophyletic. Strict consensus from 1392 trees resulting from a heuristic search in PAUP with the Verrucomorpha (= OTUs above node 16) constrained to remain monophyletic. Note the position of the Brachylepadomorpha just below *Neoverruca*.

comparable *Pollicipes*, *Scillaelepas*, *Scalpellum* clade fully resolved in the consensus (Fig. 5: nodes 9, 9A). Therefore, Figure 3 does not signify that topology (i) is better supported and exemplifies the inherent danger in relying blindly on majority rule consensus trees without inspecting how they arise from individual trees. In our case, a more reasonable choice between the two topologies would rely on the characters supporting either of them. However, having identified the problem, we are not inclined to make such a decision based on the present database.

Effect of outgroup

Most of our characters concern the morphology of shell plates. One may therefore question the soundness of designating the Ascothoracida and Acrothoracica as outgroups, since both taxa lack shell plates altogether and therefore code inapplicable (-) for many traits. To investigate this we performed an analysis with the default options but designating the Iblidae as outgroup. We justify this based on the general consensus among cirripedologists that this taxon branches off very low on the cirripede tree (Klepal, 1985; Newman, 1987). Reassuringly, the analysis resulted in 189 trees of 61 steps, just as in the default analysis, and the strict consensus had the same topology above the *Praelepas*† node (Fig. 6A). The only difference from the default consensus tree exists at the base, where we see a clade consisting of all the shell-less forms. Evidently, this depends on whether some or all of these taxa have a primary absence of shell plates or have secondarily lost them. To circumvent this issue altogether, we also constructed a modified matrix from which we excluded the four shell-less OTUs (Ascothoracida, Acrothoracica, *Cyprilepas*†, Heteralepadidae) and once again designated the Iblidae as the outgroup in an analysis with default options.

Figure 8. Successive weighting. Strict consensus from 26 trees resulting from applying a scheme of successive weighting to the 189 trees from the default analysis (see text). The cladogram shows much resemblance to those illustrated in Figures 3 and 4.

Figure 9. Extinct OTUs excluded. Strict consensus tree from parsimony analysis on matrix comprising only extant OTUs. It differs from all our other cladograms, notably in the positions of *Neolepas* and the *Neoverruca*+*Brachylepdomorpha* clade, and also in the intrinsic branching of the Balanomorpha.

Again we obtained a strict consensus tree identical to the default tree above the Iblidae node (Fig. 6B). Some authors have argued that the Heteralepadidae diverged very low on the cirripede tree, but once again designating this taxon as the outgroup in the full matrix changed neither tree length nor the topology above the Iblidae node (Fig. 6C). With this background, we felt confident in using the Ascothoracida and Acrothoracica as outgroups in all the variant analyses reported below.

Including character 3

In this scheme we deactivated characters 1 and 2 and activated character 3, which combines characters 1 and 2 (concerning the peduncle) into a single and ordered, five-state character. We obtained 315 trees of 62 steps. Character 3 probably represents the most preferable coding scheme in terms of homology, but it also entails several (?)s for OTUs where the ontogeny remains unknown (see character list). Nevertheless, this variant analysis yielded a strict consensus tree very similar to the strict consensus of the default analysis (Fig. 6D). The trees differ only at the base, where the activation of character 3 causes the loss of all resolution among the shell-less forms below the Iblidae node. This results from the added effect of the 'stalk' in juvenile Acrothoracica when including the ordered, five-state character.

We specifically designed character 3 as 'ordered' based on evidence from ontogeny and the fossil data. For the record, however, we also performed the analysis with character 3 set to 'unordered'. This resulted in 105 trees of 60 steps, whose strict consensus tree exhibits the type (ii) topology from the default analysis.

Keeping a monophyletic Verrucomorpha

The composition of the Verrucomorpha remains ambiguous. *Eoverruca*†, *Proverruca*†, and the Verrucidae consistently form a monophylum, and the trichotomy joining these OTUs obviously results from an insufficient number of characters to resolve the intrinsic relationships within this clade. Surprisingly, however, none of our analyses featured a monophyletic Verrucomorpha that includes the deep-sea genus *Neoverruca*. To investigate the cost of forcing a monophyletic Verrucomorpha, we ordered PAUP to implement a heuristic search using our default options but constrained the Verrucomorpha *sensu stricto* and *Neoverruca* to remain monophyletic. This resulted in 1392 trees of 63 steps, i.e. two steps longer than the default analysis. The strict consensus resembles the one from the default analysis but has the Brachylepadomorpha as a sister group to the Verrucomorpha (Fig. 7). Moreover, all scalpelloids were part of a large polytomy (node 7). We obtained an identical strict consensus tree with 1128 trees of 63 steps when instead we constrained PAUP to keep the Brachylepadomorpha + Verrucomorpha as monophyletic.

Quite obviously, our data matrix cannot unequivocally demonstrate any close relationship between *Neoverruca* and the Verrucomorpha *sensu stricto* and leaves open the question of whether the asymmetrical body form could have evolved convergently.

Successive weighting

When applying the scheme for successive weighting to the result from the default analysis, character weights stabilized after two repetitions. Figure 8 illustrates the strict consensus tree from the resulting 27 trees. When we reset the character weights to 1 and recalculated the tree statistics with the 'xx' command, the tree length (of the 27 trees) remained at 61 as in the 189 original trees from the default analysis, a criterion that must be met. Manual comparison also verified that all of the 27 trees resulting from the successive weighing scheme existed among the 189 original trees.

The strict consensus trees from successive weighting and from the default analysis have identical topologies in the basal stem. Above the *Neolepas* node, moreover, the tree from successive weighting agrees in most respects with topology (i) among the 189 trees from the default analysis, i.e. it contains a Scalpelloidea *sensu stricto* clade including *Capitulum*. This grouping gains support in a change from state (0) to (1) in character 12 (presence of carinolatus), which represents a convergence with the appearance of CL in the Balanomorpha. The consensus tree from successive weighting differs from the default analysis in having only a slightly better resolution of both the Balanomorpha and the Scalpelloidea.

Within the Balanomorpha the consensus tree from successive weighting deviates in minor details from all four consensus trees in the default analysis,

TABLE 2. Statistics for the trees resulting from parsimony analyses in PAUP 3.1.1 and Hennig86 and for the manually constructed BNY-tree. L, tree length; CI, consistency index; RI, retention index

Analysis	Figure	Number of trees	L	CI	RI
Default (see text)	Fig. 2	189	61	0.59	0.81
Iblidae as outgroup	Fig. 6A	189	61	0.59	0.81
Character 3 activated and ordered	Fig. 6D	315	62	0.58	0.81
Character 3 activated and unordered		105	60	0.60	0.82
Constraining Verrucomorpha monophyletic	Fig. 7	1392	63	0.57	0.81
Extinct OTUs excluded	Fig. 9	16	57	0.63	0.80
BNY-tree (see text)	Fig. 10	—	66	0.54	0.78

but this hardly warrants discussion, given the insufficient number of characters concerning this part of our matrix.

Effect of fossils

We also assessed the importance of information from extinct OTUs. Figure 9 illustrates the strict consensus trees from an analysis similar to the default analysis in Figure 2, except that the modified matrix contained only extant OTUs. The topology deviates rather significantly from all the other analyses and does not resemble any published tree. It contains a true Scalpelloidea (i.e. including *Neolepas*) supported by apomorphies in character 19 (change from separation to no separation between opercular plates and wall plates) and in character 1 (appearance of peduncular scales on the peduncle). However, the apomorphy in character 19 arose only because we conservatively coded *Lepas* as inapplicable (-), since we can hardly speak of a wall when only represented by a carina. Hennig86 makes no distinction between inapplicable (-) and unknown (?) and so assigned state 19(1) to the hypothetical ancestor. We therefore obtain a curious result, where presence of an operculum represents the plesiomorphic state. Obviously, however, the evolution of an operculum relates to the sessilian 'Bauplan' seen in Verrucomorpha and Balanomorpha. The extinct *Archaeolepas*† had both a carina, a rostrum, and calcified peduncular scales, but no operculum, and exemplifies the importance of fossil OTUs in cirripede phylogeny. We do not argue, however, for the uncritical inclusion of all fossils irrespective of the number of unknown character states.

DISCUSSION

Comparison with existing phylogenies

Not too surprisingly, our analysis reveals the paraphyletic nature of several higher taxa usually recognized in the Thoracica. These include 'Pedunculata', 'Lepadomorpha', Eolepadinae (= *Archaeolepas*† and *Neolepas*), Scalpelloomorpha (*Neolepas*, *Scillaelepas*, *Capitulum*, and *Pollicipes*), and Chthamaloidea *sensu lato* (*Eochionelasmus*, *Chionelasmus*, *Pachylasma*, *Catophragmus*, *Octomeris* and Chthamalinae).

Newman (1979, 1987), Yamaguchi & Newman (1990), Buckeridge & Newman (1992), and Anderson (1994) have provided the most recent set of

Figure 10. The Buckeridge-Newman-Yamaguchi (BNY) tree. Our attempt at constructing a formal cladogram reflecting the evolutionary scenarios in Newman (1979, 1987), Yamaguchi & Newman (1990) and Buckeridge & Newman (1992). Mapping the Table 2 character matrix onto this 'BNY-tree' returns a tree length of 66 steps, i.e. five steps longer than the 189 shortest trees in our default analysis. Nodes 9A and 11A form no part of the BNY-hypothesis. We introduced them here merely to resolve the tree to an extent where we could compare it with our analysis.

hypotheses on thoracican evolution, but comparison with our results meets with several difficulties. First, these papers present their ideas in the form of evolutionary systematic diagrams where some extant taxa sit as direct ancestors to lineages. Second, these papers follow the traditional approach and discuss every step in the 'trees' in terms of a limited set of 'key' characters while leaving aside other potentially important traits. They provide no formal character matrix, whence we cannot explicitly compare the underlying character states for taxa and tree nodes with our results. Finally, the diagrams in these papers do not include all the taxa present in our analysis. This obviously impedes a formal comparison to our phylogenetic hypotheses, but we have nevertheless attempted to construct a tree (Fig. 10) conforming as closely as possible to the ideas put forward by Buckeridge, Newman and Yamaguchi (BNY). A tree directly reflecting the BNY papers would apparently contain trichotomies between members of the Verrucomorpha *sensu stricto* and between *Pollicipes*, *Scillaelepas* and *Scalpellum*. However, unresolved polytomies usually increase tree length, and since each of our 189 trees in the default analysis had both scalpelloids and verrucomorphs fully resolved,

a fair comparison commands that we also resolve these polytomies in the BNY tree. After this manipulation (Fig. 10), the BNY tree still contains 66 steps, i.e. five steps more than our 189 trees. The BNY papers do not explicitly fix the position of *Capitulum*, but, fortunately, tree length remains the same whether this genus pairs with the remaining scalpelloids, as in our topology (i), or with the Sessilia, as in our topology (ii). The main difference between the BNY hypothesis and our analysis concerns the positions of the Brachylepadomorpha and *Neoverruca*. In the BNY tree, the Brachylepadomorpha pairs with a monophyletic Verrucomorpha comprising *Neoverruca* and the Verrucomorpha *sensu stricto*. This contrasts with our analysis, where the Brachylepadomorpha and *Neoverruca* form a monophylum in all 189 trees from the default analysis, but where a monophyletic Verrucomorpha does not emerge in any of them. Among the Balanomorpha our trees agree with the BNY-tree in having *Chionelasmus* and *Eochionelasmus* branching off lowermost and *Waikalasma*† as part of the next node. However, we note differences in the relationships of the remaining balanomorphs.

Basic thoracican radiation

Position of the Iblidae

A node linking the Iblidae and all 5 and 5+ plated taxa, and with the Heteralepadidae as the sister group, appears as a common feature in all our trees with the default outgroups. This stands in contrast to traditional thinking, whereby the Iblidae habitually reside at the base of the thoracican tree based on the supposedly plesiomorphic location of the adductor muscle in a post-oesophageal position. However, tree length increases by only one step if we switch the positions of the Iblidae and the Heteralepadidae. We can easily explain our tree topology by the fact that the total absence of shell plates and their primordia in the Heteralepadidae concerns two different characters (4 & 6), which naturally outweighs the effect of the single character (30) concerning adductor muscle position. We caution, however, that the absence of shell plates in heteralepadids could represent a secondary loss. Moreover, it follows from the lucid review of Kelpal (1985) that we cannot easily dismiss the position of the adductor muscle. In addition to outgroup comparison, ontogenetic evidence also argues that the post-oesophageal position represents a plesiomorphic state. Both ascothoracid larvae and cyprid larvae have a carapace adductor in a post-oesophageal position, but in thoracicans other than the Iblidae the adductor shifts to a pre-oesophageal position during metamorphosis (see: Kelpal, 1985). Because of this, Foster & Buckeridge (1987) questioned whether the iblid scutum is homologous to that found in other barnacles and suggested that the plates of the Iblidae may represent an independent attempt at armoring the carapace. Whyte (1988) and Löwenstam & Weiner (1992) discovered that the iblid shell plates have a rather unique composition. Additional evidence comes from the fossil record, where the probable ibloid fossil form, *Illilepas damrowi*†, from the Carboniferous (Schram, 1975, 1986) appears to have possessed cuticular rather than calcified plates. However, in both the Iblidae and other Thoracica, primordial valves precede the scuta and terga. On this evidence our character list assumes a homology between all thoracican scuta and terga.

Position of the Heteralepadidae

The traditional view (Pilsbry, 1907; Nilsson-Cantell, 1921) interpreted the lack of plates in heteralepadids as a secondary loss from an originally fully-plated condition. Foster (1978), however, first had the idea that these forms never developed plates but arose from their original, bivalved condition. Zevina (1982) treated these forms within the Lepadoidea, but Newman (1987) essentially agreed with Foster (1978) and united all the plate-less families together into a single superfamily Heteralepadoidea, except for *Pagurolepas*, which remains in the Lepadoidea. Newman (1987) also pointed out that the problematic Cambrian form *Priscansermarinus* described by Collins & Rudkin (1981) 'looks' very much like a heteralepadid, but perhaps this is only another way of stating that this fossil resembles a plate-less thoracican. On the other hand, Collins & Rudkin (1981) could not totally dismiss the possibility that this fossil had plates. Newman (1987) further mentioned that the mouthparts in heteralepadids differ from those of lepadids. Høeg, Karnick & Frølander (1994) recently demonstrated the wealth of details in thoracican mouthparts when studied under the SEM, but they included neither iblids nor heteralepadids in their analysis.

Clearly, both the Iblidae and the Heteralepadidae figure as peculiar forms whose phylogenetic position remains enigmatic with a matrix based largely on hard parts. Our analyses with variant outgroups highlight this point. We do not seriously believe in a clade of plate-less forms as in Figure 6A, but the result serves to emphasize that we need new characters independent of the traditional shell plate traits to deal with these taxa. However, we consider it as a strong point in our matrix and analysis that the relationship of plated thoracicans other than iblids did not change at all whether we designated as outgroup the Ascothoracida-Acrothoracica, the Iblidae, or even the Heteralepadidae (Figs 6A-C).

Acquisition of capitular plates

The consistent position of *Praeolepas*†, *Lepas*, *Archaeolepas*† and *Neolepas* in all our variant analyses clearly demonstrate an incremental acquisition of the capitular plates. This 'lepadomorph ladder' dovetails with available information from both ontogeny and palaeontology (Newman, 1979, 1987) and argues against theories claiming that forms with few shell plates represent a reduced state. Newman (1979) initially allied the genus *Neolepas* with the lithotryine scalpellids, and Zevina (1981) followed him in this. However, Buckeridge (1983) recognised a special status for *Eolepas*† and allies, and erected a separate subfamily, the Eolepadinae, including *Eolepas*†, *Archaeolepas*† and *Neolepas*. Newman (1985) and Newman & Hessler (1989) accepted with little or no comment Buckeridge's placement. However, the single diagnostic feature for this subfamily, the possession of six or eight capitular plates insured this subfamily's paraphyletic status in any scheme of barnacle phylogeny, including ours. Reanalysis of the intriguing Cretaceous fossils, *Blastolepas orlovi*†, and associated forms (Drushchits & Zevina, 1969) should help sort out the confusion in relationships between the Stramentidae and Eolepadinae, and the possibility may exist for drawing out a separate clade with some of these genera at a *Neolepas* grade of organization.

Topology (ii) in both our default analysis and the result from successive weighting (Fig. 8) indicates that among lepadomorphs with more than 12 shell plates, *Capitulum* may possibly form a monophylum together with the Verrucomorpha *sensu stricto* and the Balanomorpha (but excluding the Brachylepadomorpha-*Neoverruca* clade). We are aware that our matrix includes only a few key scalpelloid taxa, but attempting to include more at this point would bring in all the uncertainty currently associated with the complex relationships within the 'Scalpelloidea' and the Scalpellidae. We cannot address this problem any further because our database excludes important issues such as dwarf males (Klepal, 1985, 1987) and subcarinal and subrostral plates. The inclusion of these features and taxa such as *Calantica* and *Arcoscalpellum* might not only clarify the positions of *Pollicipes*, *Scillaelepas* and *Scalpellum*, but also allow the establishment of a distinct scalpelloid clade immediately above the *Neolepas* node, implicitly recognized by Newman (1980, 1982) and finding support in topology (i) in our default analysis.

A major deficiency in sorting out the relationship between scalpelloids and various sessile barnacles concerns uncertainties in the homology, ontogeny, and evolution of the smaller plates below the carino-rostral tier (characters 1 & 21–23) and their relation to larger, lateral plates in the wall of balanomorphs and some verrucomorphs (characters 10–15). The several tiers of small, imbricating plates (character 21) seen in taxa such as *Pollicipes*, *Neoverruca*, *Brachylepadomorpha* and *Eochionelasmus* look very similar, but we still cannot explain why they apparently arise by two different growth processes (character 22). Similarly, we need to understand the evolutionary relationship between these several tiers and the single consolidated whorl seen in *Capitulum* and *Eochionelasmus*, and our coding scheme admittedly failed to deal with this issue altogether. The greatest problem, however, concerns the nature of dedicated wall plates other than the rostrum and carina. All scenarios of barnacle evolution argue that such lateral plates evolved from the uppermost tier of small, imbricating plates. However, except in the well-defined wall of the Balanomorpha it remains unclear by which criteria imbricating plates of the upper tier deserve recognition by a special name. The situation in the Scalpellidae highlights this question since they lack true tiers of imbricating plates. Instead, they possess beneath the five primary plates a smaller number of plates, including the so-called subcarina and subrostrum. Finally, cirripedologists usually distinguish between tiers of imbricating plates and peduncular scales, but again we doubt that the underlying homologies have been sufficiently analysed. Anderson (1994) provides some insight by suggesting that we look at the growth zone that gives rise to the various small plates as a basic, homologous, fixed point on the body. Most likely, however, we can only solve these problems with new, detailed studies of early shell plate ontogeny and by using modern techniques such as SEM (Glenner & Høeg, 1993) or X-ray micrographs (Jones, 1993b).

Sessilian monophyly and the Balanomorpha

The strict consensus of our default analysis did not contain a monophyletic Sessilia *sensu stricto* Newman (1987), *viz.*, a clade comprising Brachylepadomorpha, *Neoverruca*, Verrucomorpha *sensu stricto* and

Balanomorpha. However, a monophyletic Sessilia appeared as topology (i) among the 189 trees from the default analyses, in the 50% majority rule consensus (Fig. 3), and in the trees resulting from successive weighting of characters (Figs 3, 4 and 8). A monophyletic Sessilia finds support in four synapomorphies concerning characters 1, 2, 11 and 19, but we nevertheless doubt the validity of this clade. The apomorphy in character 11 rests only on inferred states in balanomorphs and the Verrucomorpha *sensu stricto*, since representatives of these groups lack a median latus altogether. Clearly, our matrix allows for the possibility that sessility and the loss of the peduncle evolved convergently, as exemplified by topology (ii), where the Brachylepadomorpha-*Neoverruca* clade diverge immediately above the *Neolepas* node.

Certain groups within the Sessilia consistently appeared as monophyletic, viz., the Verrucomorpha *sensu stricto* (i.e. without *Neoverruca*), and the Balanomorpha. Several characters assure the monophyly of the Balanomorpha, notably the distinctive opercular plate structure and the presence of brachiae. However, problems remain in resolving the intrinsic relationships of that taxon. The tree resulting from successive weighting partially resolved the balanomorphs and almost full resolution emerged in the 50% majority rule consensus, but we would not place too much confidence in this. All the trees agree, however, in having an unresolved trichotomy including *Eochionelasmus*-*Chionelasmus* as the first balanomorph node and having *Waikalasma*† as part of the next node. Not unexpectedly, our analysis also illustrates the paraphyly or even polyphyly of the Chthamaloidea in any of their previous definitions. The balanomorph part of the BNY-tree in Figure 10 rests on information in Buckeridge & Newman (1992) and could well contain much of value, since we did not design our matrix to specifically address problems of intrinsic balanomorph relationships. For example, in our analysis, support for the clade consisting of Balanoidea-Coronuloidea and *Octomeris* comes only from the absence of caudal filaments (Character 29).

Clearly, a detailed analysis of balanomorph relationships would require many more characters, but most of these concern balanomorph apomorphies that we must score as inapplicable (-) in the full Thoracica matrix. This also underlines a crucial weakness of all computerized analyses, i.e. that the basic morphology ('Bauplan' or 'morphotype') may evolve in a lineage to the extent that few meaningful homologies remain when compared with other taxa. Given the obvious monophyly of the Balanomorpha, we are now free to construct a new matrix specifically designed to resolve the intrinsic phylogeny of that taxon. Such an effort is presently being carried out by J. Buckeridge (personal communication).

The Verrucomorpha

Considerable problems remain in trying to understand the evolution of the Sessilia from a pedunculated ancestor and of the verrucomorph morphotype. Our failure to find a monophyletic Verrucomorpha (i.e. including *Neoverruca*) contrasts to Newman & Hessler (1989) and Newman (1989), who put this intriguing 'living fossil' at the base of the verrucomorph lineage. The classic synapomorphies of verrucomorphans concern asymmetry of shell

plates, *viz.*, characters 24–26. For these three characters *Neoverruca* codes as the Verrucomorpha *sensu stricto*, but evidently this does not suffice to enforce a monophyletic Verrucomorpha upon the tree. Instead, *Neoverruca* allied with the Brachylepadomorpha and this clade displayed a surprisingly peripatetic behaviour (cf. Figs 4, 5 and 9). The apparently close relationship to brachylepadomorphs could well be real, considering that a Recent representative of the latter looks almost identical to the fixed side of *Neoverruca* (Newman, personal communication).

The asymmetry of the Verrucomorpha *sensu stricto* (*viz.*, *Eoverruca*†, *Proverruca*† and the Verrucidae) appears identical and complex. The adult verrucomorphs have the tergum and scutum of either the left or right side fixed to the substrate, leaving only one scutum and one tergum movable in the operculum. The side of the fixed opercular plates has reductions of shell plates to a larger degree than the side of the movable opercular plates. This asymmetry makes it possible for the adult verrucomorph to sweep the hard surface with its cirri in the immediate vicinity of the fixed side.

Neoverruca, however, is only weakly asymmetrical and displays many plesiomorphic characters, while some similarities between other verrucomorphs and balanomorphs appear to be convergent losses. The rostrum, the carina, and the opercular plates are only weakly asymmetrical in *Neoverruca*, while the most pronounced asymmetry concerns the unilateral presence of a latus (L) (Newman & Hessler, 1989). However, the Verrucidae do not possess median latera (L) at all at any stage of development (Runnström, 1926). The extinct taxa *Eoverruca*† and *Proverruca*† possess on the fixed side two plates, one of which we hesitantly coded as the rostrolatus (RL) and another that may possibly represent a carinolatus (CL). Compared to extant Verrucidae, however, *Proverruca*† and *Eoverruca*† may possibly also display apomorphic features in the lateral plates, and topologies conforming to this assumption actually appeared among our 189 default trees. This serves to highlight the important, but too often neglected, fact that extinct taxa may well possess traits that are apomorphic relative to those in extant groups.

In our constrained PAUP analysis, it cost two steps to force *Neoverruca* into a monophyletic Verrucomorpha, but coding asymmetry as in the present matrix is likely a gross oversimplification. We predict that future studies will enable us to split asymmetry into more characters and states than in the present matrix, including some from soft parts. One such scheme would grade the degree of asymmetry in characters 24 and 25. This will assist both in pinpointing the phylogenetic position of *Neoverruca* and in resolving the trichotomy between *Eoverruca*†, *Proverruca*† and the Verrucidae. A new species of Verrucomorpha dredged from hot vent habitats may soon afford the means to take important steps in this direction, since it portrays an exciting combination of traits from both *Neoverruca* and the Verrucomorpha *sensu stricto* (Newman, personal communication to JTH and MJG).

The complex issues concerning the origin of sessile barnacles continue to vex, and it is still difficult to choose between various alternatives. The ancestral balanomorph may have resembled some kind of brachylepadomorph, albeit with a reversal in the direction of the addition of imbricating plates to the capitulum from that seen in both *Neoverruca* and the Brachylepadomorpha (character 22). Alternatively, the balanomorphs may never have passed

through a stage resembling *Brachylepas*, but evolved directly from a *Capitulum*-like ancestor as already suggested by Darwin (1852), recently argued by Anderson (1994), and implicit in topology (ii) from our default analysis.

Ontogeny and palaeontology

We credit W.A. Newman with demonstrating through a long series of papers how ontogeny and palaeontology can elucidate thoracican phylogeny. Evidence from studies of the ontogeny of shell plates, especially from lepadid and scalpellid barnacles, support the phylogeny in the 'lepadomorph ladder' part of our analysis (Newman, 1979, 1989). Furthermore, fossil data suggest an increasing shell plate complexity from the Silurian to the late Cretaceous and essentially second the data applied from shell plate ontogeny, thus strengthening the validity of this phylogeny. Not surprisingly, therefore, we got very vexing results when we excluded all extinct OTUs from our analysis (Fig. 9).

The fossil record may allow us to set the events of barnacle evolution in a time frame by providing minimum ages for particular apomorphies, taxa and bifurcations. Such information will in turn serve to guide future carcinologists in their efforts to discover and interpret new material.

As an example we have in Figure 11 taken the present limited array of taxa and extended our default consensus tree into a time dimension with the addition of stratigraphic ranges for known fossils of our taxa or clearly related forms (derived largely from Newman *et al.*, 1969; Buckeridge, 1983; and Foster & Buckeridge, 1987). *Catophragmus* is only known from Recent material, but the fossil record of both the higher balanomorphs and *Chionelasmus* extends back into the Eocene, while *Pachylasma* occurs back even to the Palaeocene. So the last common ancestor to all balanomorphs must be at least of Palaeocene age. It follows that fossils relevant to the vexing problems of the balanomorph radiation will most likely occur in lower Tertiary strata.

The earliest verrucomorph fossils occur in the Early Cretaceous, so relevant information concerning their evolution must lie somewhere in the Early Cretaceous or Late Jurassic, at least. The range of brachylepadomorphs (*Brachylepas*† and *Pycnolepas*†) extending from the Middle Jurassic serves to further emphasize the middle Mesozoic as a crucial time in the evolution of sessile barnacles. Certainly, fossils related to *Neoverruca* should occur in that time frame.

The radiation of the scalpellomorphs presents another crucial but poorly understood problem in barnacle evolution. Fossil specimens of *Pollicipes* occur back to the Cretaceous, but closely related forms such as fossil *Calantica* and the extinct genus *Zeugmatolepas*† extend the range of that lineage back to late Triassic time. *Scillaelepas* occurs in the Upper Jurassic, but the intriguing and poorly understood species, *Pabulum spathiforme*† [which one of us (FRS) has examined and believes to have a scalpellomorph morphology], occurs in the Carboniferous of Britain. These findings predict that Permo-Triassic material will most likely contain fossils relevant to sorting out the events of the scalpelloid radiation.

It is at this point that the fossil record begins to fail us in helping to set

Figure 11. Time stratigraphic context. The cladogram of Figure 3 (50% majority consensus) placed in a time stratigraphic context given the current knowledge of the fossil record of the barnacle taxa used in our analysis, or their close fossil relatives. The times of occurrence of particular branching points are only approximations of the latest possible horizon that might prove productive in the search for fossils relevant to that event.

times for the events of barnacle history. Material occurs in the Jurassic that may relate to *Neolepas*, and certainly the Cretaceous *Blastolepas*† may help to extend that morphotype into the middle Mesozoic. *Archaeolepas*† occurs in the Jurassic, but the rather similar *Eolepas*† (type genus of the paraphyletic Eolepadinae) extends this lineage into the Triassic. *Lepas*, which in our phylogeny represent a very old lineage, is known back only to the Eocene, but *Praelepas*† comes from the Carboniferous of Russia. So it appears that much material relevant to the early radiation of pedunculated cirripedes yet awaits us in Palaeozoic rocks. This expectation is whetted by the occurrence of what appears to be an early ibloid in the Carboniferous, *Illilepas damrowi*†, and of course the intriguing Silurian form, *Cyprilepas holmi*†, the oldest assured cirripede known (Wills, 1963). Even earlier material might await us, if the affinities of the Middle Cambrian *Priscansermarinus*† indeed lie with the heterolepadids. In that event, the separation of the Acrothoracica, Rhizocephala and Thoracica must have taken place previous to the time

horizon of *Priscansermarinus*†. The known record of the outgroups in our analysis, Devonian for Acrothoracica (Rodriguez & Gutschick, 1977) and possibly Cretaceous for Ascothoracida (Voigt, 1959, 1967; Madsen & Wolff, 1965) contributes little to timing this event. However, a Cambrian origin of the Cirripedia agrees well with the view (Müller & Walossek, 1988; Walossek, 1993) that the Upper Cambrian *Bredocaris*† from the Swedish 'Orsten' possibly belongs to the Thecostraca and represents the sister group to all other members of that monophylum. However, material that may relate to the early diversification of thoracicans will likely involve the delineation of shell plates and the establishment of calcification, so it may prove difficult to find and even more difficult to interpret.

New lines of morphological research

Larval morphology

Except for a few recent papers (Moyse, 1987; Jensen, 1993; Jensen *et al.*, 1994; Grygier, 1994), cirripedologists have largely disregarded larval morphology in tracing intrinsic cirripede phylogeny. We consider this surprising since the monophyly of the Cirripedia itself largely depends on very unique apomorphies in nauplii and cyprids (Høeg, 1992). The universal and autopomorphic presence of fronto-lateral horns in cirripede nauplii should greatly ease identification in phosphatized faunas such as the 'Orsten' (Müller & Walossek, 1986; Walossek & Müller, 1992), and this could well prove the most certain way of estimating a minimum age for the taxon.

Figure 12 illustrates how cirripede nauplii offer a wealth of traits when analysed in sufficient detail, preferably using SEM or TEM techniques and with an eye for functional considerations. A few authors have employed such morphological features to discriminate large taxa and effectively to support existing phylogenies (Egan & Anderson, 1989; Grygier, 1994; Kado, 1982; Korn, 1988). We have gleaned about 25 multistate characters from papers like these. However, only 13 of the 26 OTUs in our study are scorable by having described nauplii: Ascothoracida, Acrothoracica, Iblidae, *Lepas*, *Pollicipes*, *Scalpellum*, *Capitulum*, Verrucidae, *Octomeris*, *Cataphragmus* (i.e. *Catomerus*), Chthamalinae, *Octomeris*, and Balanoidea + Coronuloidea. Because of the excessively high proportion of (?)s, we consider it premature to add these data to the main character matrix. Furthermore, about 10 of these characters represent autopomorphies or convergent apomorphies of the Balanoidea + Coronuloidea, the monophyly of which has already been assumed.

With regard to the cyprid, the lack of a comparative morphological approach most likely stems from the colossal influence of studies on the 'model' barnacle *Semibalanus balanoides*, leaving the impression that all cyprids are morphologically similar. However, when studied with SEM or TEM, cyprids do reveal a host of details that vary in a phylogenetically significant manner (Glennner *et al.*, 1989; Jensen *et al.*, 1994). For cirripedes with no hard parts, such as the Acrothoracica, Rhizocephala, and several Thoracica, larval characters may offer one of the few character suites that we can compare throughout all Cirripedia and where little doubt concerning homology can prevail.

Figure 12. Nauplius of an unidentified lepadid. Shown as it would appear when swimming in the plankton and illustrating the wealth of morphological details available for analysis. This illustration, drawn by the scientific illustrator Mr. Anthony d'Attilio, was most courteously made available to us by Prof. W.A. Newman and Dr A. Ross.

Spermatozoa

No other line of ultrastructural research has been more useful towards sorting out relationships between animal groups than comparative spermatology. Among barnacles and their purported relatives information from spermatology has in several instances proven interesting (Wingstrand, 1972; Jamieson, 1991). Grygier (1981, 1982) and Storch & Jamieson (1992) employed sperm structure to sort out differences between possible lineages of maxillopodans and revealed ascothoracidan sperm as a plesiomorphic relative to cirripede sperm. Within the Cirripedia, Healy & Anderson (1990) have done the most extensive work to date, but they produced data largely relevant only to sorting out balanomorph relationships. The evidence concerning the evolution of pedunculates remains ambiguous right now, largely because most of them appear to retain a basically primitive arrangement of structures.

Ribosomal RNA/DNA has become a stylish molecule to use in trying to sort out phylogenetic relationships within Crustacea (Applegate *et al.*, 1991; Abele *et al.*, 1992; Spears *et al.*, 1994). Some interesting results have come out of this work. However, different molecules give different results or have differing limits to their usefulness. Spears *et al.*, (1994) believe that 18S ribosomal DNA may not reveal much about phylogenetic relationships

within the Balanomorpha, and Abele (personal communication) suggests that mitochondrial DNA may prove to be more effective.

Molecular techniques will take on increasing importance as novel and independent means of estimating phylogenetic relationships, but we should not place our complete trust or effort in test tubes. Phylogenies based on molecular techniques will not assist in filling the great gaps which still exist in our knowledge of palaeontology, larval morphology, and developmental sequences leading to adult morphology. Traditional morphological efforts should not cease because newer techniques such as gene sequencing come into vogue. This especially applies to groups such as barnacles, where an extensive fossil record means that palaeontological evidence is of crucial importance. The variety of new and exciting species to come from the deep sea in the last two decades and the way in which these have effected a revolution in our understanding of barnacle relationships also emphasize that traditional approaches to estimating animal relationships still hold great promise (Newman, 1979, 1989; Newman & Hessler, 1989).

CONCLUSIONS

Although some might argue that the present cladistic analysis contributes little to a 'new' understanding of barnacle evolution, we would strongly disagree. We present for the first time a phylogenetic systematic framework within which future discoveries and discussions of barnacle phylogeny can take place. The elegance of phylogenetic systematics rests perhaps not so much in the production of convincing phylogenies as in providing such a framework whereby one can evaluate and compare hypotheses. As in the present case, a cladistic analysis will always identify problems in the data base and therefore highlight the most promising area for new research projects. In this respect we took inspiration from Briggs and Fortey's (1989) study which for the first time attempted a cladistic analysis of both Recent arthropods and the so-called 'enigmatic' Cambrian fossils. A cladistic analysis cannot by itself solve the many problems that remain in understanding the phylogeny of the Balanomorpha, the origins of the Verrucomorpha, the evolution of a sessile habitus from a pedunculate one, and the various radiations that occurred among the pedunculates. Basically, these riddles result from uncertainties regarding the underlying homologies and must be solved by new investigations. Nonetheless, a phylogenetic systematic approach identifies exactly where such new research effort is needed and we now for the first time have a framework into which we can insert old and new information on barnacles from areas like palaeontology, morphology and biochemistry.

Certainly, if the basic patterns of the phylogeny remain firm, someone will have to propose a new taxonomy of barnacles. Toleration of paraphyletic groups will in our opinion only serve to obscure the underlying events that channeled barnacle evolution. However, we have far to go before a new taxonomy can emerge, and until then we do not hesitate to employ such terms as 'lepadomorphs' or 'pedunculates' as long as it is clearly understood that these names do not identify true systematic groups but only informal classes. Many hypotheses now suggest themselves and many more will

emerge. Only through a programme of sound procedures for testing these models and uncovering information to fill the gaps in our knowledge will understanding of this important and fascinating group of crustaceans ever truly advance beyond the level where Darwin left it almost 140 years ago.

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