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The evolutionary diversity of barnacles, with an updated classification of fossil and living forms

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We present a comprehensive revision and synthesis of the higher-level classification of the barnacles (Crustacea: Thecostraca) to the genus level and including both extant and fossils forms. We provide estimates of the number of species in each group. Our classification scheme has been updated based on insights from recent phylogenetic studies and attempts to adjust the higher-level classifications to represent evolutionary lineages better, while documenting the evolutionary diversity of the barnacles. Except where specifically noted, recognized taxa down to family are argued to be monophyletic from molecular analysis and/or morphological data. Our resulting classification divides the Thecostraca into the subclasses Facetotecta, Ascothoracida and Cirripedia. The whole class now contains 14 orders, 65 families and 367 genera. We estimate that barnacles consist of 2116 species. The taxonomy is accompanied by a discussion of major morphological events in barnacle evolution and justifications for the various rearrangements we propose.

ADDITIONAL KEYWORDS: classification – Crustacea – phylogeny – taxonomy – Thecostraca.

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I hate a barnacle as no man ever did before, not even a Sailor in a slow-moving ship.
Charles Darwin, in a letter to W. D. Fox, 24 October 1852.

INTRODUCTION

Barnacles are traditionally known as Cirripedia, which comprise an extremely diverse array of sessile crustaceans that are either acorn, stalked or parasitic (Figs 1–5). From the classical taxonomy summarized by Martin & Davis (2001), Cirripedia forms an important subgroup with Facetoteca (Fig. 1) and Ascothoracida (Fig. 2) under Thecostraca. From molecular phylogenetic analyses (Pérez-Losada *et al.*, 2008, 2012a, b, 2014), Thecostraca forms a monophyletic group, with Facetoteca being the sister group to a clade comprising Ascothoracida and Cirripedia (Figs 3–6). In the present study, we consider the evolutionary history and classification of Thecostraca and treat the group as comprising all barnacles in the widest sense.

Barnacles (Thecostraca) rank among the most biologically diverse, commonly encountered and ecologically important marine crustaceans in the world. However, they deviate from almost all other Crustacea in that only the larval stages (naupliar and cypridoid) are free-living, whereas the adults are permanently sessile as either suspension feeders or parasites (Figs 1–5). Suspension-feeding barnacles normally settle on rocky bottoms (Anderson, 1994), but several epibiotic taxa prefer to grow on mangrove roots (or other marine plants), invertebrates (molluscs, crustaceans, marine sponges or corals) or vertebrates (turtles, sea snakes or whales) (Yamato *et al.*, 1996; Zardus & Hadfield, 2004; Seilacher, 2005; Brickner & Høeg, 2010; Hayashi *et al.*, 2013; Dreyer *et al.*, 2020; Zweifler *et al.*, 2020), and other fouling barnacle species can also attach to man-made objects (Knight-Jones & Crisp, 1953). The numerous species of parasitic barnacles also have a diverse array of hosts, including soft corals, crustaceans, echinoderms and even sharks (Høeg *et al.*, 2015; Ommundsen *et al.*, 2016; Figs 1–5).

Thecostracans display a highly diverse morphology and biology (Ruppert *et al.*, 2003; Høeg & Møller, 2006; Chan & Høeg, 2015), which has made them prime models for studies on intertidal ecology (Dayton, 1971; Carroll, 1996; Miron *et al.*, 1999; Chan & Williams, 2003; Hawkins *et al.*, 2008; Fraser & Chan, 2019; Jung *et al.*, 2019), larval settlement (Høeg, 1985; Clare, 1995; Walker, 1995; Maruzzo *et al.*, 2012), development (Walley, 1969; Turquier, 1972; Glenner, 2001; Glenner *et al.*, 2008; Høeg *et al.*, 2012; Dreyer *et al.*, 2018a), antifouling technology (Aldred & Clare, 2008) and the evolution of morphology, life cycles and reproductive systems (Charnov, 1987; Høeg, 1995a, b; Buhl-Mortensen & Høeg, 2006; Ozaki *et al.*, 2008; Yamaguchi *et al.*, 2008, 2013; Pérez-Losada *et al.*, 2009; Yusa *et al.*, 2012; Lin *et al.*, 2016; Dreyer *et al.*, 2018a, b, c, 2020). Barnacles have attracted the attention of many prominent specialists, most notably Charles Darwin, who devoted several monographs to the study of fossil and extant barnacles (Darwin, 1851, 1852, 1854, 1855). Krüger (1940a, b) provided a comprehensive treatment of both Ascothoracida and Cirripedia, including physiological and ecological issues, and there is still much information to be gleaned from this rarely cited work. Newman *et al.* (1969) provided a basic reference for the taxonomy and morphology of both extinct and extant forms. Chapters in the books edited by Southward (1987) and Schram & Høeg (1995) survey almost all biological issues in the taxon, and the superb book by Anderson (1994) provides the most recent general account.

Cirripede barnacles, with mineralized shell plates, have left an impressive palaeontological record (Withers, 1928, 1935, 1953; Newman *et al.*, 1969; Buckeridge, 1983; Foster & Buckeridge, 1987; Gale, 2019) (Fig. 6), starting with *Praelepas* Chernyshev, 1930 in the middle Carboniferous (320–330 Mya) (Buckeridge & Newman, 2006). As explained below, we choose here not to accept the even earlier fossils, *Priscansermarinus* Collins & Rudkin, 1981 from the Cambrian and *Cyprilepas* Wills, 1962 from the Silurian, as cirripedes. More than 400 fossil species have been described so far, and their study has been linked directly to the study of barnacle evolution, systematics, taxonomy and morphological adaptations and even ancient cetacean migratory pathways from fossils of cetacean-associated barnacles (Buckeridge *et al.*, 2018, 2019; Taylor *et al.*, 2019; Fig. 6).

The class Thecostraca comprises ~65 families, 367 genera and 2116 species distributed in three subclasses: Facetotecta (12 species; Fig. 1), Ascothoracida (114 species; Fig. 2) and Cirripedia (1990 species; Figs 3–6; Supporting Information, Table S1). The Cirripedia includes the Thoracica, the Acrothoracica and the Rhizocephala (Fig. 7). The Thoracica are a highly specialized group of suspension feeders. Their external body armor includes a system of mineralized plates. These shell plates are mineralized parts of the cuticle and are not shed at moults, but increase gradually in both thickness and area. In the variably-sized zones between these plates, the cuticle is moulted regularly. But this occurs in a highly modified fashion that produces a system of parallel growth lines, also called 'cuticular slips' (Anderson, 1994; Blomsterberg *et al.*, 2004). The Acrothoracica, although also suspension feeders, lack mineralized plates (Kolbasov & Høeg, 2000). Instead, they are symbiotic and inhabit self-excavated borings in a wide array of calcareous substrata, including corals, coralline red algae, gastropod shells occupied by hermit crabs, live gastropods, bivalves, limestone and foraminiferal chalk, thoracican barnacles and bryozoans (Kolbasov, 2009; Botha *et al.*, 2020). The Rhizocephala are all highly specialized parasites on crustaceans (mainly Decapoda). The adults lack all organs and structures normally found in Crustacea (Høeg, 1995a; Walker,

Figure 1. Facetotecta. A–F, selected live images of y-nauplii representing some of the morphological diversity: lecitotrophic ones in A, C, D, F; planktotrophic ones in B, E. Note distinct differences in spination and body shapes. G, H, detailed morphology of y-larvae using scanning electron microscopy: G, ventral view; H, dorsal view, showing cuticular facets on the shield. I–K, the drastic metamorphosis from early y-nauplius (I) to last nauplius instar (J) and y-cyprid (K). These three larvae are conspecific. L, higher magnification view of the big rectangular box in K, showing an scanning electron micrograph of the cyprid antennules, with distal hooks (white circles). M, scanning electron micrograph of small square box in K, showing the lateral side of the y-cypris with a spiny labrum. N–P, metamorphosis from y-cypris to free ypsigon. This is most likely to be a larval or juvenile stage of an endoparasitic adult stage in hosts that have yet to be found. The specimens in A, D, F, I–J were sampled in coastal waters in Keelung, Northern Taiwan. The specimens in B, C, E, G, H were sampled on Green Island, Taiwan. The specimens in N–P originate from Sesoko Island, Japan. Abbreviations: a1, antennule; a2, second antennule; ce, compound eye; lb, labrum; mdb, mandible. Specimens J and K provided by Dr. Mark J. Grygier. Specimen J re-photographed from Grygier *et al.*, (2019).

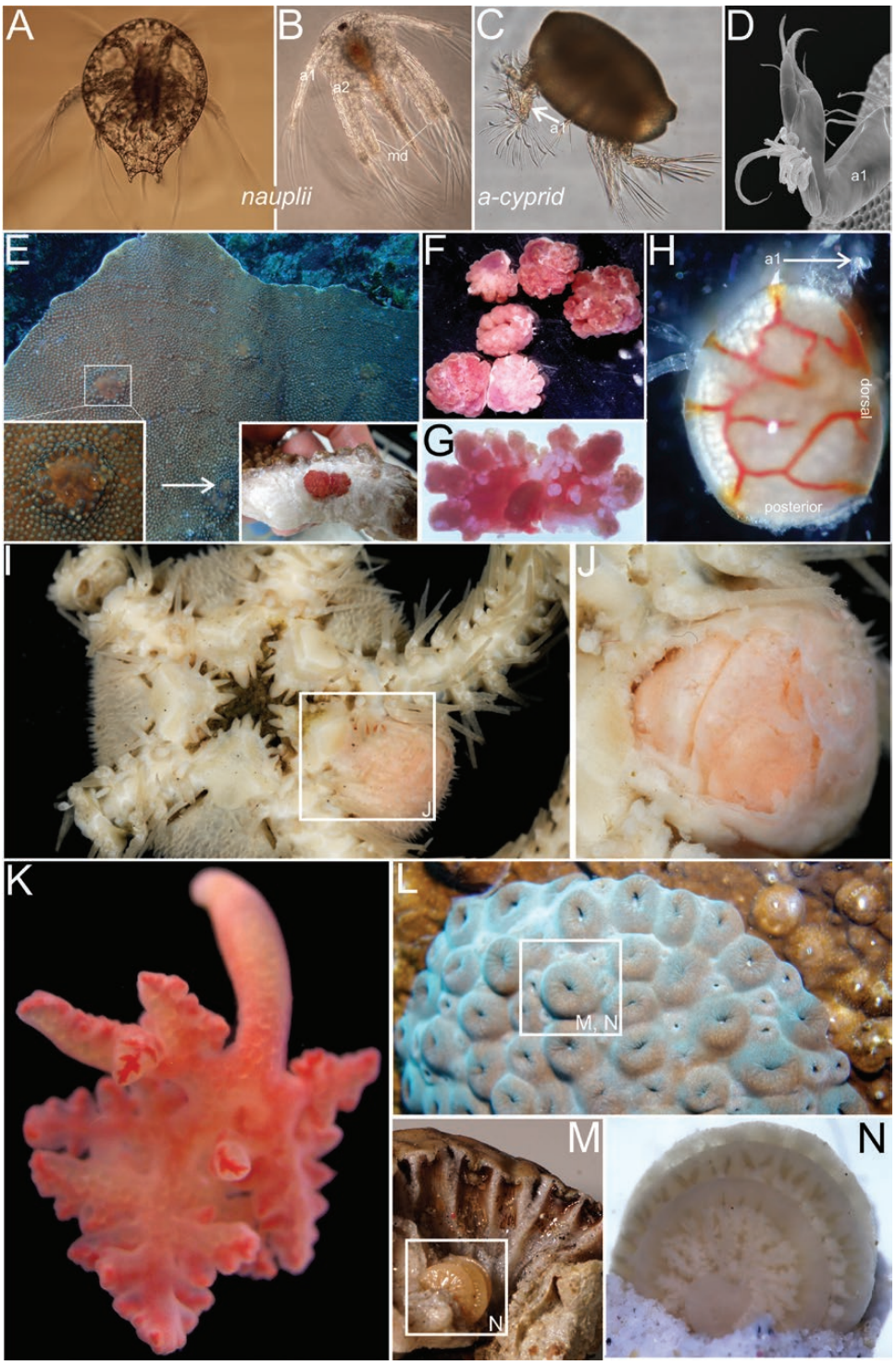

Figure 2. Ascothoracida. A–D, larval diversity of selected Ascothoracida. A, an early, live *Baccalaureus* nauplius larva. B, an early, live *Zibrowia* nauplius larva. C, D, a Tessmann's larva or a-cypris (C), with hooked antennules (D). E–N, adult diversity of selected Ascothoracida. E–G, the coral *Turbinaria*, showing the galls formed by the ascothoracidan *Petrarca*. Insert in E shows the galls in cross-section, with red *Petrarca* inside the coral skeleton. F, *Petrarca*. G, magnified view of *Petrarca*. H, *Synagoga arabesque*, with extended, hooked first antennules. I, J, *Ascothorax rybakovi* on the brittle star *Ophiacantha pacifica*. K, a free *Dengrogaster* sp. L–N, the zoanthid *Palythoa* with *Baccalaureus* sp. inside. Abbreviation: a1, first antennule. Fig 2C photographed by ND and Dr. Jørgen Olesen, Natural History Museum of Denmark.

2001; Høeg *et al.*, 2005) and show a highly complex life cycle, including their mode of infestation (Glenner *et al.*, 2000; Glenner, 2001; Dreyer *et al.*, 2020) (Fig. 4). The subclass Ascothoracida is also parasitic and infests either echinoderms or cnidarians (Fig. 2). The most plesiomorphic ascothoracidans are little modified, but the more derived taxa, such as the Dendrogastridae, can have strongly modified endoparasitic adults, although they always retain body segmentation and appendages (Grygier, 1996a). Finally, the subclass Facetotecta is the most elusive group within the Thecostraca. First recorded > 100 years ago (Hansen, 1899), they occur as y-larvae in the marine plankton throughout the world, but the adult stage has never been found in the wild (Grygier, 1996b). Hormonally stimulated y-cypris larvae metamorphosed *in vitro* into a slug-shaped, highly reduced 'ypsigon' stage, which exhibits many similarities with the rhizocephalan vermigon, such as lacking segments, eyes and a gut (Glenner *et al.*, 2008). This strongly suggests that adult facetotectans might also be endoparasites (Pérez-Losada *et al.*, 2009) (Fig. 1).

Studies on phylogenetic relationships of the Thecostraca started with the benchmark paper by Newman *et al.* (1969). Since then, a number of morphology-based studies have addressed the evolution and phylogeny of larger groups of thecostracan taxa, such as all Cirripedia or all or major parts of the Thoracica, often including both extant and fossil forms (e.g. Newman & Ross, 1976; Newman, 1987, 1996; Pitombo, 2004; Buckeridge & Newman, 2006, and papers cited therein). The concept of cladistic analysis came relatively late to Crustacea; therefore, partly for historical reasons, few of the early studies offered a chacter state matrix amenable for numerical analysis, whether or not this method was the one used. Exceptions were the studies by Glenner *et al.* (1995), Buckeridge (1995), Pitombo (1999, 2004) and Newman & Ross (2001), the last of which was the first study using larval characters across all thoracican barnacles. The last 15–20 years have seen the publication of molecular phylogenetic studies on all Thecostraca (Pérez-Losada *et al.*, 2002, 2009) or major parts of the clade (e.g. Pérez-Losada *et al.*, 2004, 2008, 2014; Glenner & Hebsgaard, 2006; Yusa *et al.*, 2010; Rees *et al.*, 2014; Herrera *et al.*, 2015; Lin *et al.*, 2016; Tsang *et al.*, 2017; Høeg *et al.*, 2019, 2020). These molecularly based phylogenies are in surprising mutual agreement, except for minor but interesting problems (Figs 7, 8). Moreover, they confirm the monophyly of many thecostracan taxa and relationships derived from morphological studies, e.g. the mutual relationship of the subclasses, the monophyly of the Rhizocephala, the the early branching of the Iblidae in Thoracica, the sister-group relationship of the Verrucomorpha and Balanomorpha, and the monophyly and overall relationship of the superfamilies in the latter taxon. Altogether, this yields high confidence that we are approaching a deeper understanding of thecostracan phylogeny (Figs 7, 8). Yet, these molecular studies have also challenged some important concepts, especially in thoracican character evolution and phylogeny, such as the pattern of shell plate acquisition and the relationship of vent- and seep-inhabiting and asymmetrical barnacle forms. Lately, there have appeared several cladistically framed morphological studies, primarily on fossil forms, that again challenge earlier concepts, but in many respects concur with the molecular phylogenies (e.g. Gale, 2014b, 2019; Gale & Sørensen, 2014).

The molecular analyses have demonstrated that all the thecostracan subclasses (as understood here) are monophyletic, but a recent molecular phylogeny by Petrunina *et al.* (2014) suggested that also the Tantulocarida, which are parasites on copepods and other small-sized crustaceans, might be included in the Thecostraca. This analysis used only nuclear 18S ribosomal DNA (rDNA) and is not supported by morphological data; therefore, we choose not to consider tantulocarids as within Thecostraca. Molecularly based trees anchored with fossil and/or geological calibration points have also provided a time frame for barnacle radiations (Pérez-Losada *et al.*, 2008, 2014), allowing for the reconstruction of the evolutionary history of key phenotypic traits (Pérez-Losada *et al.*, 2012a) and generating valuable insights into their diversification at the order and family levels (Pérez-Losada *et al.*, 2012b, 2014).

Most phylogenetic studies have focused on the Thoracica and the Rhizocephala (Ewers-Saucedo *et al.*, 2019). Less attention has been given to the enigmatic Facetotecta, the parasitic Ascothoracida, and the shell- and rock-boring Acrothoracica. Within Thoracica, morphology-based studies have consistently depicted the position and diversification of some assemblages (i.e. the basal split of the Iblomorpha and the diversification of acorn barnacles) but have not concurrently solved the radiation of other groups (e.g. stalked barnacles). Our current understanding of barnacle relationships based on recent molecular phylogenies (Figs 7, 8) has led to some important changes in phylogenetic hypotheses and thus interpretations of character evolution (e.g. Pérez-Losada *et al.*, 2004, 2008; Gale, 2014b; Høeg *et al.*, 2019, 2020). We use these molecular phylogenies as the basis for our revised classification, although we emphasize that there is still much work to be done in order to achieve a fully resolved phylogeny of barnacles as a taxon, because species sampling remains poor in some groups and many polytomies still exist. It will also be interesting to see future studies that use a large morphological character matrix and wide taxon sampling for numerically based phylogenetic analyses that could either support and extend or falsify the

claims based on the molecular data, such as those in the studies by Pitombo (1999, 2004) and Gale (2015b).

In contrast to phylogenetic studies, barnacle taxonomy has not been revised comprehensively since the work of Martin & Davis (2001), and phylogenetic analyses since then have shown that half of the thecostracan families listed are polyphyletic. Central to most barnacle studies is a robust phylogenetically based taxonomic framework for appropriate group comparisons and biological inferences (e.g. Yusa *et al.*, 2012; Tsang *et al.*, 2014, 2015, 2017; Lin *et al.*, 2016). Likewise, a solid taxonomy is pivotal to the arrangement of organismal diversity and genomic information in databases (e.g. National Center for Biotechnology Information (NCBI) and Global Biodiversity Information Facility (GBIF)) (Hinchliff *et al.*, 2015). Unfortunately, there is not yet a single taxonomic summary of the Thecostraca, despite a highly active research community describing barnacle species for > 200 years. A few important and helpful rearrangements have been published recently, involving Rhizocephala (Høeg *et al.*, 2020) and Acrothoracica (Kolbasov, 2009; Lin *et al.*, 2016). But the extensive molecular phylogenetic data now available for Thoracica (stalked and acorn) barnacles have not yet been integrated into a formal phylogenetically based taxonomy (Chan, 2018). Therefore, we are still missing a comprehensive resource that brings together all the barnacle taxonomic information in an evolutionary context.

Here, we attempt to integrate, update and revise barnacle (Thecostraca) taxonomy with insights gained through previous molecular phylogenetic, morphological and taxonomic studies. We identify a number of areas of controversy with previous phylogenetic interpretations, identify what we consider to be promising areas for future study and provide our conclusions in the sections below. We review the fossil record of acorn and stalked barnacles and incorporate all fossil taxa into the new classification. Finally, we present the first comprehensive taxonomic summary for all barnacles, including all recent and extinct forms down to the genus level. We will integrate these results into the World Register of Marine Species (WoRMS) (Horton *et al.*, 2020) for continued update and revision.

MATERIAL AND METHODS

Despite the several molecularly based studies addressing Thecostraca phylogeny (Fig. 8), there is as yet no analysis that investigates this taxon down to at least the family level across all subgroups. To arrive at a phylogenetically based taxonomy, we therefore decided to adopt the approach used by Høeg *et al.* (2020) for the Rhizocephala. Here, the trees from several molecularly based studies were used to arrive at a composite phylogeny for the entire taxon. There is no disagreement about the monophyly of the Thecostraca or of its three principal subgroups, here recognized as subclasses Ascothoracida, Cirripedia and Facetotecta (Figs 7, 8). For the intrinsic phylogeny of these subclasses, we still lack detailed molecular information for the Ascothoracida and Facetotecta, although such data are emerging (Pérez-Losada *et al.*, 2009) (Fig. 7). In the Facetotecta, we have as yet no family- or genus-level taxonomy for what appears to be many but, in most cases, still undescribed species. For the Ascothoracida, we have relied on the morphology-based taxonomy of Grygier (1987a). Unpublished molecular phylogenetic analyses of Ascothoraicda suggest that clades are monophyletic at family levels. Within the Cirripedia, there are now detailed and comprehensive studies on all three infraclasses. For the Rhizocephala, we have relied entirely on the recently published study by Høeg *et al.* (2020). For the Acrothoracica, we use the study by Lin *et al.* (2016). For the Thoracica, there are three studies that address all or most of the taxon (Pérez-Losada *et al.*, 2008; Herrera *et al.*, 2015; Lin *et al.*, 2015). In addition, there are several studies addressing problems within particular parts of the taxon (Pérez-Losada *et al.*, 2014; Rees *et al.*, 2014; Tsang *et al.*, 2017; Chan *et al.*, 2017b). With few, although notable, exceptions, these studies all agree both on the gross structure of thoracican phylogeny and within the major subgroups, but some taxa of great interest vary in position among these studies (Fig. 8). For extant Thoracica, we therefore decided to take a conservative approach and recognize only taxa that were returned in all the molecular analyses. Our final taxonomy is reflected in the composite family-level tree (Fig. 7). It confers confidence in this scheme that most of it is also in agreement with the most recent analyses based on morphology (Gale, 2014a, b, 2015a, b, 2019). This is especially true for our Scalpellidae, Neolepadoidea, Verrucomorpha and Balanomopha.

Our main aim has been to base the new taxonomy on monophyletic groups that are supported by the most recent molecularly based analyses of the Thecostraca. The reason for using primarily molecularly based analyses is that the extreme morphological variation across the Thecostraca makes it virtually impossible to use morphology-based characters alone (Figs 1–5). Taxa with only extinct species (fossil taxa) have been placed using morphological arguments in the taxonomy constructed largely from molecular phylogenies. For some of the fossil-only taxa, paraphyly was the only practical solution. Wherever possible, we also use morphological characters to support our arguments, and this confers the great advantage of integrating the many extinct taxa into the taxonomy to render a comprehensive taxonomy (recent and fossil taxa) based on established evolutionary history.

In naming taxa above the superfamily level, we decided, for reasons of consistency, to use common name suffixes as far as possible. Thus, all ordinal level taxa within the Cirripedia Thoracica now end with '-morpha', but the taxonomic authorities have been retained in cases where there is identity to the same group under a different name suffix. Thus, Buckeridge & Newman (2006) remain the taxonomic authorities for the Iblomorpha, which they called Ibliformes. Applying specific Linnean ranks to taxa identified in a phylogeny is always a compromise. We have generally tried to use groups and names that are already recognized and to use the time of origin, number of species or morphological distinctness as guidelines to absolute rank level, but such decisions must remain an art more than a science (see Kallal *et al.*, 2020). We are generally opposed to erecting empty absolute ranks, where not strictly required by the Zoological Code. Nevertheless, for consistency, we have done this in a few cases, such as the Calanticomorpha and Scalpelloidea, which in our taxonomy contain only the Calanticidae and the Scalpellidae, respectively.

We have made an effort to assure that families are monophyletic, and this has entailed some revisionary steps. Several non-monophyletic families have been abandoned and their species subsumed in other families. Therefore, there are few, if any, cases where monophyly of families is contradicted by any published molecularly based analyses. In several cases, we were also able to abandon some small monogeneric or monotypic families, when the analyses showed that the species concerned were nested within existing families. There are several cases where genera, often small ones or even monotypic, are nested within other genera. This obviously calls for revision, but we have decided not to take any taxonomic steps at generic and species levels here. Below the family level, we recognize subfamilies or even lower categories, where there is either good phylogenetic evidence for their monophyly or where it seems the best conservative approach to retain them until more data are available. This is especially true within the Balanoidea. We emphasize that the few differences between the molecularly based phylogenies of the Thoracica and their general agreement with recent morphological interpretations provide confidence that we are approaching a robust scheme and that interpretations of character evolution will be largely the same, despite the few deviations.

THECOSTRACA TAXONOMY AND LARVAL CHARACTERS

The Facetotecta (Fig. 1) are known only as larvae, and the Rhizocephala (Fig. 4) can be compared with other taxa solely by means of their nauplii and cyprids (Høeg *et al.*, 2009b). It is therefore not surprising that larvae have featured prominently in the history of thecostracan taxonomy (Newman & Ross, 2001; Pérez-Losada *et al.*, 2009). It was larval characters that first allowed the Cirripedia to be recognized as crustaceans, the inclusion of the Rhizocephala in that taxon and, much later, the recognition of the Thecostraca as a monophyletic taxon (see details provided by Grygier, 1987c; Høeg *et al.*, 2009a; Martin *et al.*, 2014). Ultrastructural details of the lattice organs in cypridoid larvae were instrumental in resolving the relationships among both the thecostracan subclasses and the infraclasses of the Cirripedia (Høeg & Kolbasov, 2002). These results were subsequently supported by molecular data (Pérez-Losada *et al.*, 2009). Within Rhizocephala, scanning electron microscopy of cypris larvae could pinpoint family-level relationships (Høeg & Rybakov, 1992). These results were again fully supported by molecularly based phylogenetic studies (Glenner *et al.*, 2010). This bodes well for the use of such morphological data for rhizocephalan taxonomy in the many situations where molecular evidence is lacking.

Cypris characters also seem to be useful in the Ascothoracida and Acrothoracica (Kolbasov & Høeg, 2007; Kolbasov *et al.*, 2008) and will, in the future, be important for a morphology-based taxonomy of the Facetotecta. Høeg *et al.* (2004, 2009a) introduced the use of the 'a-cyprid' for the settlement stage (ascothoracid larva) of the Ascothoracida to emphasize its potential homology with the facetotectan y-cypris and cirripede cyprid (Figs 1K, 2C, D, 3B, 4B, E, 5B). The similarities include a range of structures, such as lattice organs on the carapace, prehensile antennules and frontal filaments. A-cyprids differ markedly in some characters, such as not undergoing a profound metamorphosis and in having more antennular segments.

Attempts at using larval characters for taxonomy have met with much less success within the Thoracica. The Lepadidae is clearly characterized by apomorphies in both nauplii (e.g. exceedingly long spines and frontal horns) and cyprids (many details of the sensory and attachment sturctures; Fig. 5B), and cyprids might also be useful in characterizing groupings within the Scalpellidae. But within Thoracica, larval characters have not yet been used extensively for taxonomic purposes. The attempt by Newman & Ross (2001) to use naupliar appendage setation to resolve thoracican systematics met with little success, possibly because the morphologies are closely associated with swimming and feeding and might well have been subject to extensive convergent evolution. Several recent studies have also highlighted that the morphology of the cypris antennules might also have been the result of convergent evolution (Al-Yahya *et al.*, 2016; Chan *et al.*, 2017b; Dreyer *et al.*, 2020; Yu *et al.*, 2020). Whatever their taxonomic use, the larvae

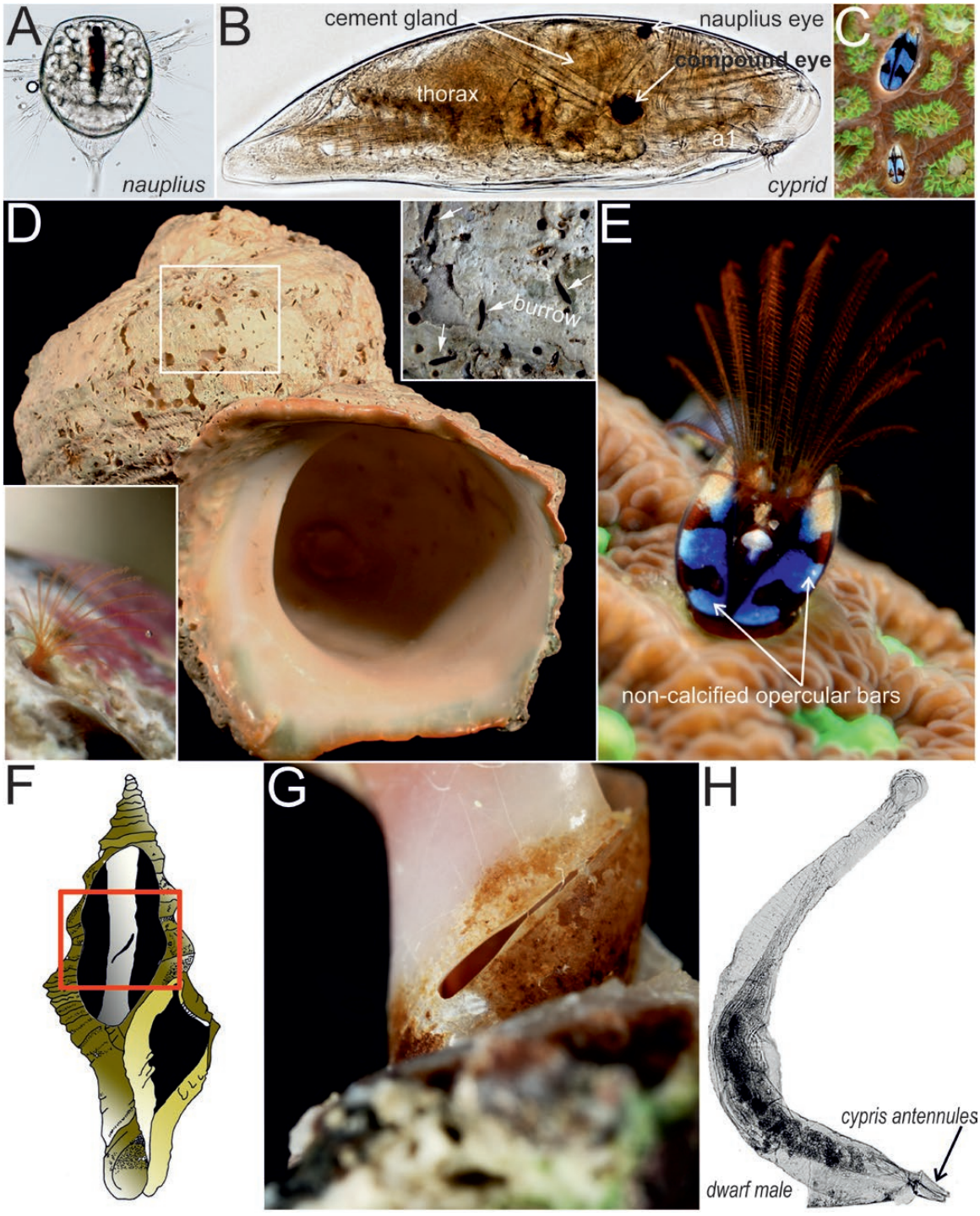

Figure 3. Acrothoracica. A, B, examples of naupliar and cypris larval morphology of Acrothoracica. C, live corals, *Leptatstrea*, with the colour-valved *Berndtia*. D, most acrothoracican species live in gastropod shells, making slit-like burrows. Inserts show the burrows made by the barnacles (upper right) and a specimen in its burrow with extended cirri (lower left). E, *Berndtia purpurea* extending its cirri from the burrow inside the live tissue of the coral *Leptastrea* host. F Schematic diagram showing *Trypetesa* living in the columella of gastropod shells, showing the slit-like burrow opening. G, magnified view of columella of shell, showing the slit-like opening of the *Trypetesa* burrow. H, the dwarf male of *Berndtia utinomii*.

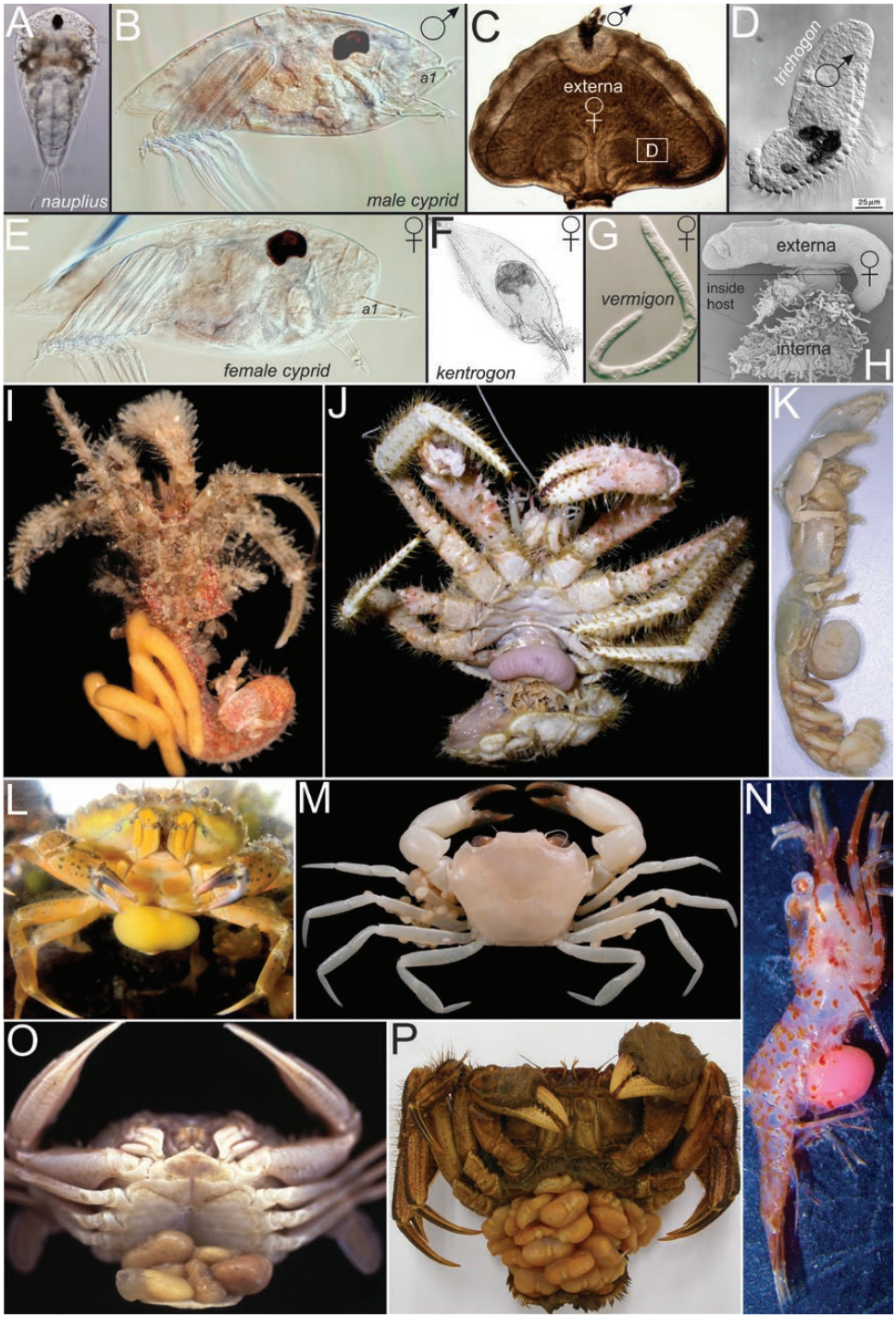

Figure 4. Rhizocephala. A–H, life cycle stages and larval morphology of selected Rhizocephala. A, nauplius larva of *Sacculina carcini*. B, male cyprid of *S. carcini*. C, settled male cyprid of *Lernaeodiscus porcellanae* in the mantle aperture of a virginal female reproductive body (externa). Box D indicates the receptacle holding the trichogon. D, male trichogon of *S. carcini* dissected from the mantle cavity of a virginal female externa. E, female cypris of *S. carcini*. F, kentrogon of *S. carcini*, inside the empty cuticle of the spent female cyprid, in the process of injecting the primordial parasite. G, vermigon of *Loxothylacus panopaei*. H, scanning electron micrograph of *Peltogaster curvata*, showing the reproductive sac (externa) connected to the ramified internal root system. I–P, diversity of selected Rhizocephala externae. I, *Peltogasterella sulcata* on

constitute a crucial part of thecostracan biology during both the free-swimming and the settlement phases. It is therefore an exciting and informative enterprise to map characters associated with this part of the life cycle onto a phylogeny to evaluate how larval morphology evolves in concert with complex biological traits, such as swimming, feeding and reproductive strategies (Ewers-Saucedo & Pappalardo, 2019; Dreyer *et al.*, 2020; Wong *et al.*, 2020).

SYSTEMATIC ADJUSTMENTS AND MORPHOLOGICAL EVOLUTION

Subclass Facetotecta Grygier, 1985

Facetotecta or 'y-larvae' (Fig. 1) were discovered in the North Sea plankton in 1887 by C. A .V. Hensen. Although he assigned them to the copepod family Coryaeidae, H. J. Hansen coined the term 'y-larvae' in 1889 as unidentified larvae of barnacles. There is only a fragmented and scattered literature on y-larvae, and many species have been described based on single, plankton-collected larval specimens. Grygier (1985) erected the superorder Facetotecta.

Y-larvae occur world-wide and have been reported from different parts of the Atlantic Ocean (McMurrich, 1917; Schram, 1972; Grygier, 1987d; Belmonte, 2005), the Arctic Ocean (Mileikovsky, 1968; Kolbasov & Høeg, 2003), the western Pacific (Itô, 1984, 1985, 1986, 1987, 1989; Itô & Ohtsuka, 1984; Grygier *et al.*, 2019) and a few areas of the Indian Ocean (Swathi & Mohan, 2019). Y-larvae are minute, planktonic crustacean larvae ranging from 250 to 700 µm in length (Høeg *et al.*, 2014a). Their nauplii are either lecithotrophic or planktotrophic and terminate development as a non-feeding y-cyprid instar (Fig. 1A–K). Few studies have described both nauplii and cyprids of the same 'type' or species (Itô, 1986; Kolbasov & Høeg, 2003), and there are few accounts of nauplius-to-cyprid metamorphic details (Grygier *et al.*, 2019). The nauplii sport a highly ornamented cephalic shield of complex honeycombed patterns (Fig. 1H), which gave rise to their name. In the y-cyprid, these patterns transform into elongated ridges that run in the anterior–posterior plane (Itô, 1985, 1986; Høeg *et al.*, 2014a) (Fig. 1K). These ridges have been used in species descriptions, although the nomenclature of the naupliar plate regions remains a challenge (Schram, 1972; Itô, 1987). The nauplii occur in a range of transparency levels (Fig. 1A–F). The planktotrophic species are almost entirely transparent, whereas the lecithotrophic forms exhibit a range of colours owing to nutrient-laden cells (Itô, 1985, 1986; Høeg *et al.*, 2014a; Grygier *et al.*, 2019; Fig. 1). The single nauplius eye is pigmented. The naupliar body consists of a cephalic anterior part, covered by the head shield, and a posteriorly projecting hind body, which invariably terminates in one or several conspicuous cuticular spines and, usually, two smaller, ventrally located furcal rami or spines. The larval labra are highly variable in external morphology, and during metamorphosis to the y-cyprid they are transformed into a spinous structure (Høeg *et al.*, 2014a; Grygier *et al.*, 2019). The naupliar limbs resemble those in other crustacean nauplius larvae, with uniramous antennules and biramous antennae and mandibles. These may carry spinous gnathobases in feeding species (Martin *et al.*, 2014).

Bresciani (1965) was the first to describe the cypridoid larva, or y-cyprid, from the Sound in Denmark. The y-cyprid (Fig. 1K) has a univalved carapace, with five pairs of lattice organs. They also have clawed antennules specialized for putative mechanical attachment (Fig. 1L), a spinous labrum (Fig. 1M), so-called paraoccular processes and post-ocular filamentary tufts, and paired compound eyes (Fig. 1J, K). The six pairs of thoracopods are biramous (Fig. 1K). The abdomen consists of two or four segments, including a long telson, which carries pores and sensory setae. It terminates in two unsegmented furcal rami, which hold setae (Høeg *et al.*, 2014a).

Exposure of y-cyprids to a crustacean moulting hormone succeeded in inducing them into a slug-like stage called the ypsigon. This stage lacks eyes, a gut, appendages or any other external structures (Glenner *et al.*, 2008). The ypsigon is unsegmented (Fig. 1N–P), with the body surrounded by a < 5-nm-thick cuticle and an epithelium, enclosing a variety of cells, including a relatively large neuropile (presumed to be derived from the y-cyprid central nervous system) and a series of vesicles, apparently containing stored lipids. The ypsigon therefore resembles the rhizocephalan vermigon, which is the first internally parasitic stage in the parasitic barnacles. The y-cyprid and the ensuing ypsigon, therefore, strongly suggest that juvenile and adult facetotectans are endoparasites in hosts that are yet to be found.

It is already clear from published work (Pérez-Losada *et al.*, 2009) and our own emerging yet unpublished studies that a large number of facetotectan morphological types, representing undescribed species,

its host, *Pagurus cuanensis*. J, *Briarosaccus auratum on* its host, *Lithodes aequispinus*. K, *Parthenopea subterranea* on its host, *Calianassa subterranea*. L, *Sacculina carcini* on its host, *Carcinus manaeas*. M, *Thompsonia* sp. on its host, *Thyraplax truncata*, courtesey of Peter Castro. N, *Sylon hippolytes* on its host, *Spirontocaris lilljeborgi*. O, *Heterosaccus dollfusi* on its host, *Charybdis longicollis*. P, *Polyascus gregarius* on its host, *Eriocheir japonica*.

Figure 5. Thoracica. A, nauplius larva of *Balanus improvisus*. Note the presence of frontal horns. B, cypris larva of *Amphibalanus amphitrite*, showing the pair of extended first antennules and six pairs of thoracopods. C, *Anelasma squalicola*, a parasite of deep-sea lantern sharks (*Etmopterus*). The cirri are rudimentary, and the base of the peduncle has a root-like structure embedded inside the tissue of the shark to absorb nutrients. D, *Fistulobalanus albicostatus*, common on mangrove tree trunks. E, the family Pyrgomatidae are associated with scleratinian corals, and the bases are embedded in the coral skeleton. *Cantellius* sp. extending the cirri. F, *Ibla cumingi*, which is located at the most basal position on the molecular phylogenetic tree of thoracican barnacles. G, *Megabalanus*, *Amphibalanus* and *Lepas* inhabiting the capitulum

can exist even at the same localities (Fig. 1A–I). We recommend that species descriptions in Facetotecta be based on molecular data backed by detailed morphological description of comparable larval instars. For this, we suggest using the last naupliar instar (Fig. 1J), which can be documented *in vivo* and then collected as an exuvium after the metamorphosis to the y-cyprid (Fig. 1J, K). From this, data can potentially be added for prior and succeeding instars from the same individual when available (Fig. 1I). The surprising morphological variation among facetotectans at even a local scale also extends to the ypsigon stages; hence, potentially, to the process of host infection. Glenner *et al.* (2008) depicted both long, slender and short, plump types of ypsigons, and this recalls the variation in the invasive stage (kentrogons and vermigons) found among the rhizocephalan parasitic barnacles (Glenner & Høeg, 1995; Høeg *et al.*, 2012). Future studies must investigate how these variations in morphology of larval and parasitically invasive stages relate to differences in biology among this enigmatic group of thecostracans.

Subclass Ascothoracida Lacaze-Duthiers, 1880

The Ascothoracida (Fig. 2) are exclusively parasitic, ranging from ecto- and mesoparasitic to entirely endoparasitic species, in echinoderms and cnidarians. They sport mostly a dioecious sexual system with females and dwarf males, but the family Petrarcidae and possibly some of Ctenosculidae, which are endo- and mesoparasites in corals and sea stars, have secondarily evolved hermaphroditism (Grygier, 1983, 1987a, b).

Both morphological and molecular data suggest that the Ascothoracida form a monophyletic group, being sister to Cirripedia (Grygier, 1987a, b; Pérez-Losada *et al.*, 2002, 2009; Høeg *et al.*, 2009b; Ewers-Saucedo *et al.*, 2019) (Fig. 7). There are two orders recognized, the Laurida and the Dendrogastrida (Grygier, 1987a; Kolbasov *et al.*, 2008), but their monophyly is yet to be tested by molecular methods.

The larvae and adults of Ascothoracida have been studied extensively since the seminal monograph of Wagin (1976), but there are but few accounts on laboratory rearing of larval series and none on their settlement and metamorphosis into parasites. Important accounts of larval development and features were given by Ito & Grygier (1990). Høeg *et al.* (2014b) summarized the available information on ascothoracidan larval biology, which is highly variable because the larvae can be released as either planktotrophic or lecithotrophic nauplii or directly as the cypridoid stage. The latter should now be called the 'a-cyprid' (Fig. 2C) for comparison with the homologous facetotectan y-cyprid (Fig. 1K) and the cirripede 'true' cyprid (Figs 3B, 4B, E, 5B) and is equivalent to the term 'ascothoracid larva' used until recently. Grygier (1985, 1987a) performed comprehensive taxonomic and morphological reviews of ascothoracidans, the majority of which forms the basis of the following text.

Generally, the body is covered by a laterally compressed, smooth and bivalve-like carapace (Fig. 2E–N), under which the embryos or larvae (= nauplii and a-cyprids) are carried (brooded). Some species have fused valves, sometimes with bizarre extensions. Generally, the females and males have a mid-gut diverticulum, and their gonads are placed in the carapace. They carry four pairs of appendages followed by 11 free trunk somites in total. The prehensile antennules are uniramous, consisting of four to six segments. On the distal segment, they carry a moveable or unmoveable claw, a claw guard and sensory setae, some of which are aesthetascs (Fig. 2C, D). Antennae are absent in adults. The labrum forms a conical oral cone that surrounds piercing mouthparts, which comprise paired mandibles, maxillules and maxillae and unpaired paragnaths, although some of these appendages can be reduced. The penis can be both uni- and biramous and is always located at the seventh trunk somite. The last segment (telson) has moveable, unsegmented furcal rami. The thorax and abdomen can be differentiated or undifferentiated, with three to six pairs of thoracopods of both uniramous and biramous nature. The thoracopods are plesiomorphically setose and biramous, with two-segmented exopods and three-segmented endopods (two-segmented in pairs 1 and 6); advanced forms can have uniramous unsegmented thoracopods. The female gonopores are situated at the base of the first pair of thoracopods, and the coxae of thoracopods 2–5 in females usually carry seminal receptacles for spermatozoa. Compound

of a penduculated barnacle. H, *Capitulum mitella*, a stalked barnacle inhabiting rocky shores. In molecular phylogenetic analyses, it is the sister to *Anelasma* (see C). I, *Conchoderma*, a stalked barnacle with reduced shell plates, epibiotic on many marine taxa, mostly crabs and whales. J, An early dwarf male settled on the surface of an adult *Heteralepas*. K, *Octolasmis cor* lives exclusively on the surface of crab gills. L, *Scalpellum scalpellum*, a stalked barnacle epibiotic with hydroids. The inserts in LM (upper) and SEM (lower) shows the hermaphrodite receptacles, which can house dwarf males. Inserts show a dwarf male with extended penis (upper) and an SEM micrograph of the receptacle structure. M, *Waikalasma* is a deep-sea inhabitant, having a row of imbricating plates on the base of shells. N, *Chthamalus malayensis* is common on intertidal shores. O, *Tetraclita*, with four shell plates, common on rocky and tropical shores.

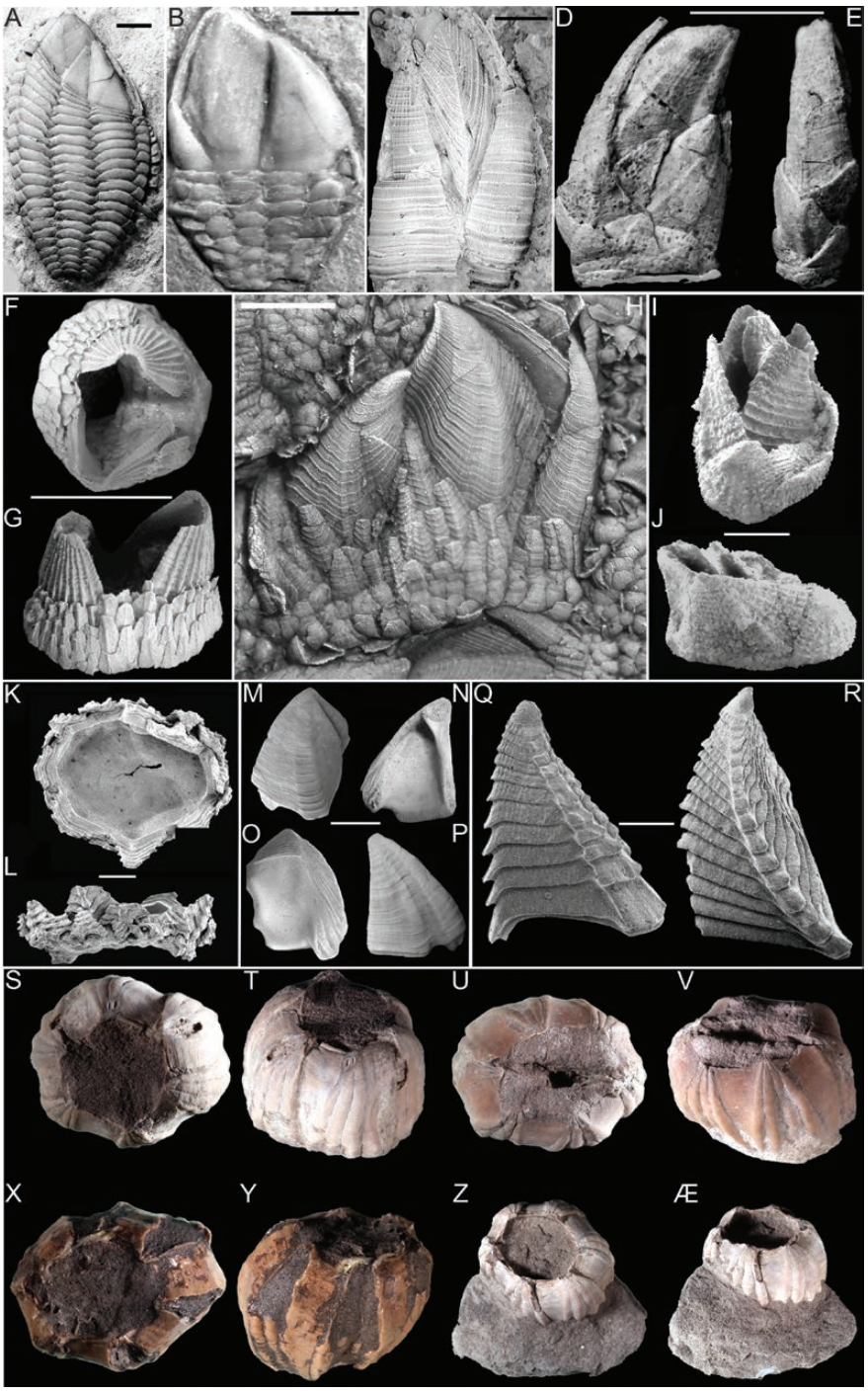

Figure 6. Fossil Thoracica. A, *Stramentum pulchellum*, Stramentidae, Upper Cretaceous, Turonian, UK. B, *Archaeolepas redtenbacheri*, Archaeolepadidae, Upper Jurassic, Tithonian, Germany. C, *Eolepas bathonica*, Eolepadidae, Middle Jurassic, France. D, E, *Witherscalpellum aptiensis*, Cretiscalpellidae, Lower Cretaceous, UK; capitulum, in lateral (D) and dorsal (E) views. F, G, *Brachylepas naissanti*, Brachylepadidae, Upper Cretaceous, UK, in apical (F) and lateral (G) views. H, *Etcheslepas durotrigensis*, Zeugmatolepadidae, Upper Jurassic, UK. I, J, *Proverruca vinculum*, Proverrucidae, Upper Cretaceous, UK, in apical (I) and lateral (J) views. K, L, Q, R, *Eoverruca hewitti*, Eoverrucidae, Upper Cretaceous, UK; K, L, calcified basis with imbricating scales; and Q, R, fixed and moveable scuta. M–P, *Myolepas scanica*, Myolepadidae, Upper Cretaceous, Sweden; external (M) and internal (O) views of tergum; and external (N) and internal (P) views of scutum. S–Æ, fossil whale barnacles, *Coronula*. Scale bars: 5 mm in A–H; 2 mm in M–P; 1 mm in I–L; 0.5 mm in Q, R, Æ.

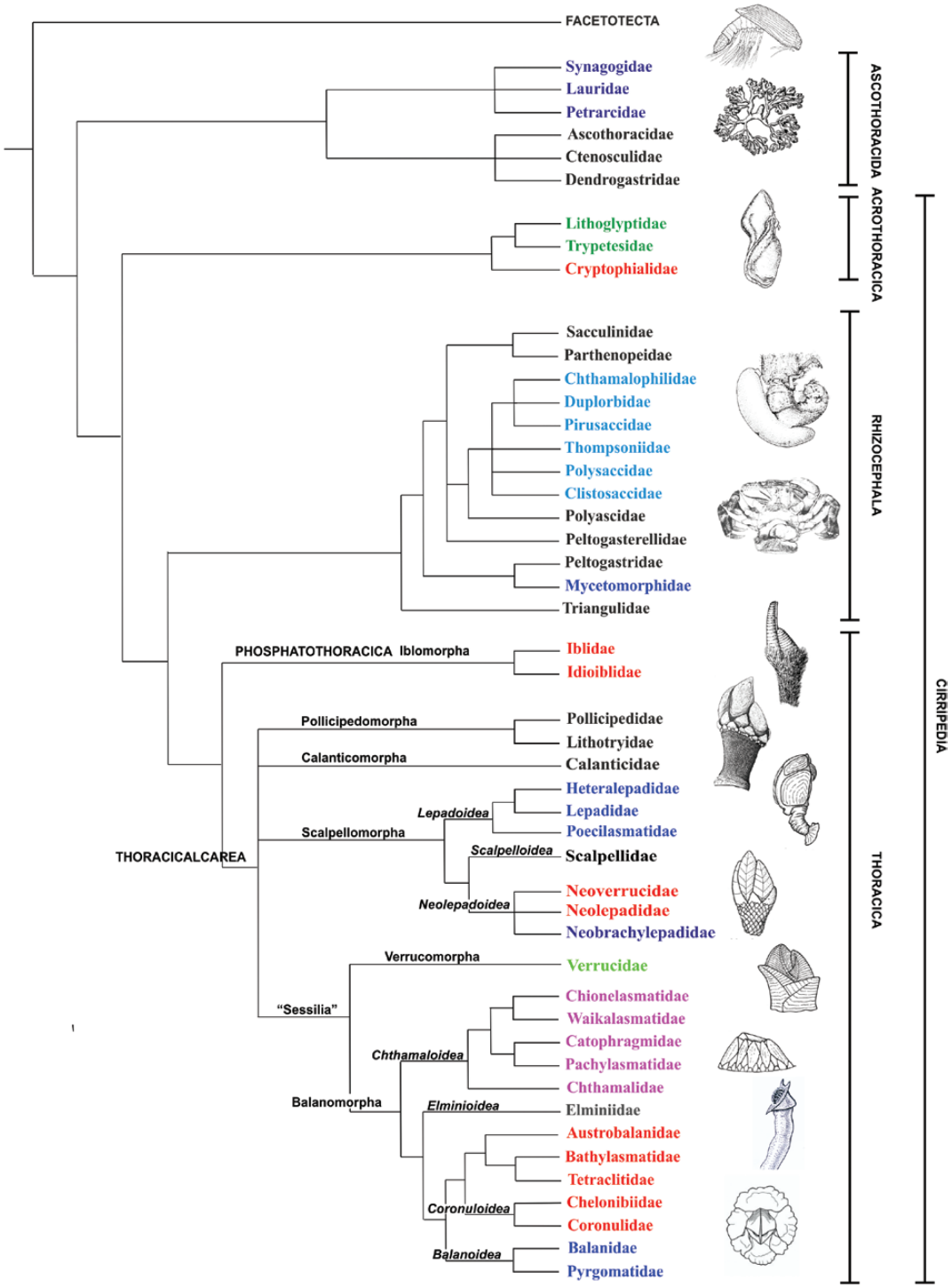

Figure 7. Phylogeny. A summary of the phylogenetic relationships amongst the Thecostraca families, with major groups labelled on the right and on the branches within the Thoracica. All families are considered monophyletic, except where specifically noted in the text. In Rhizocephala, families with an akentrogonid type of host invasion are coloured blue. Drawings representing the different groups are, from the top: *Facetotectan* y-cyprid; *Dendrogaster*; *Trypetesa*; *Clistosaccus*; *Sacculina*; *Ibla*; *Pollicipes*; *Lepas*; *Neolepas*; *Verruca*; *Catophragmus*; *Xenobalanus*; *Balanus*.

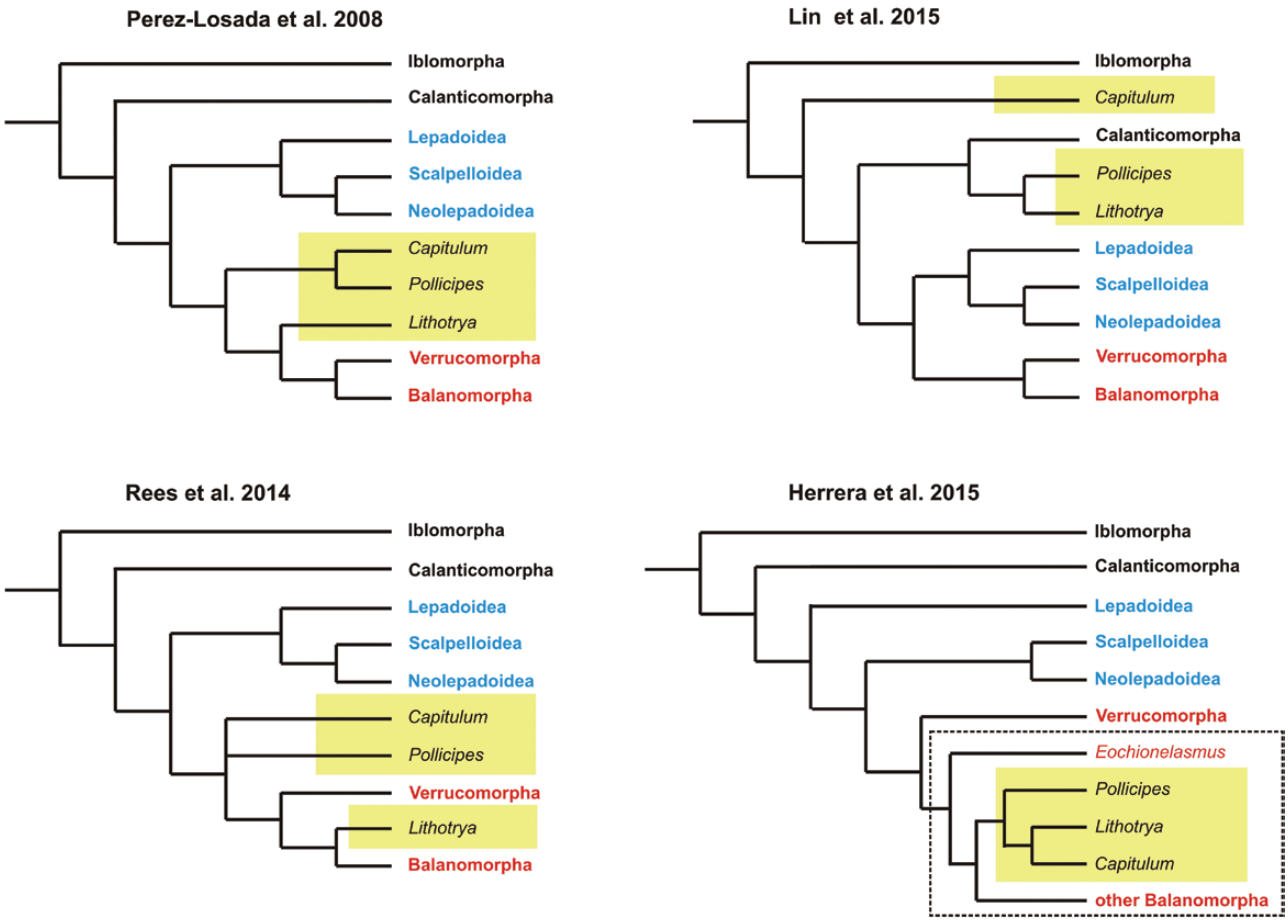

Figure 8. Thoracica phylogenetic hypotheses. Comparison of four recent hypotheses on the phylogenetic relationships among recent Thoracica. Note the overall similarity in topology. Major discordances are highlighted by colour. Note especially the difference in the precise position of the genera *Capitulum*, *Lithotrya* and *Pollicipes*, but also that these taxa always appear 'close together' (highlighted in yellow) in the trees. In the analysis by Herrera *et al.* (2015), these genera are nested inside the Balanomorpha (dotted square). See detailed explanation in the main text.

eyes are present only in larval stages, although their rudiments are fused with the frontal filaments into a sensory organ.

There are few molecular analyses of the Ascothoracida, and there is no detailed study of the molecular systematics of the group. The systematics based on anatomical characters have been studied in detail (Wagin, 1976; Grygier, 1983, 1987a, b). We follow the taxonomy of Grygier (1987a), which recognizes two orders (here ranked suborders), each with three families. Although not formally based on apomorphies, this taxonomy nevertheless attempted to recognize monophyletic groups, and our molecular data seem to confirm the monophyly of most of the six families. Members of the order Laurida clearly exhibit many plesiomorphies, whereas those of the Dendrogastrida are mostly more advanced.

Subclass Cirripedia Burmeister, 1834

The Cirripedia comprise the infraclasses Acrothoracica (burrowing barnacles), Rhizocephala (parasitic barnacles) and Thoracica (stalked and acorn barnacles). Owing to the morphological divergence among these taxa, the only characters that can be compared are those that concern the larvae (Figs 3–5). Thompson (1830, 1836) was the first to recognize that all cirripedes are united by the apomorphy of having nauplii equipped with so-called frontolateral horns (Høeg *et al.*, 2009b; Martin *et al.*, 2014) (Figs 3A, 4A, 5A). To this has since been added the possession of a cypris larva. The cyprid possesses a host of apomorphic traits that are adaptations to its role of locating a settlement site and cementing itself before initiation of metamorphosis (Høeg *et al.*, 2004; Høeg & Møller, 2006). Molecular analyses all agree that each of the three infraclasses is monophyletic, with

the Acrothoracica diverging first (Pérez-Losada *et al.*, 2009; Lin *et al.*, 2016), being sister group to a clade comprising Rhizocephala and Thoracica (Fig. 7). The reduced morphology of rhizocephalans entails that only a few morphological apomorphies in the cypris larvae are shared between these parasites and thoracican barnacles (Høeg *et al.*, 2009b). Moreover, for the same reason it cannot be assured whether early fossils with a thoracican-type morphology should be situated above or below the split between these two taxa. For this reason, there is little purpose in creating a new name and rank for the Rhizocephala–Thoracica clade.

Infraclass Acrothoracica Gruvel, 1905

The Acrothoracica (Fig. 3) comprise barnacles that burrow into calcareous rocks, such as limestone, or calcareous structures of various invertebrate animals, such as gastropod, bivalve and thoracican shells, corals and bryozoans, but some also burrow into the live tissue of *Leptastrea* and *Psammocora* corals. Burrows of extinct species has also been found in echinoids, brachiopods, belemnites and ammonites (Kolbasov, 2009; Chan *et al.*, 2014a, b; Kolbasov *et al.*, 2014; Lin *et al.*, 2016). A recent study also reports that acrothoracicans live in coralline algae in South African waters (Botha *et al.*, 2020). The Acrothoracica was first discovered at relatively high latitudes (Hancock, 1849; Darwin, 1854), but the greatest diversity is now found in the tropical seas (Tomlinson, 1969; Kolbasov, 2009; Kolbasov *et al.*, 2014; Lin *et al.*, 2016). All molecular and morphological analyses find that the Acrothoracica is monophyletic (Pérez-Losada *et al.*, 2002, 2004, 2008, 2009; Kolbasov, 2009; Lin *et al.*, 2016), and their molecular phylogenetic pattern (Lin *et al.*, 2016) supports the recent morphological classification by Kolbasov, Høeg and Newman (Kolbasov, 2009).

The Acrothoracica differ from the stalked and acorn barnacles (Thoracica) in lacking calcareous capitular and opercular shell plates altogether (Chan *et al.*, 2014a) (Fig. 3). A calcified element exists in some species of *Lithoglyptida*, but it is highly debatable whether this structure has any homology with thoracican elements (putatively with thoracican calcareous basis). Such homology is also dubious because stem cirripedes would undoubtedly have had phosphatized shell plates when the Acrothoracica diverged (Newman, 1971, 1974; Grygier & Newman, 1985; Kolbasov, 2009). During the voyage of HMS Beagle, Darwin discovered his first barnacle, an acrothoracican in a gastropod shell from Chile (Tomlinson, 1987). He had such difficulty in assigning this species to a taxonomic group that he named it 'Mr. Arthrobalanus' and only later described it as *Cryptophialus minutus*.

Acrothoracican barnacles are dioecious, with large-sized, suspension-feeding females and dwarf males attached on the exterior of the female mantle sac (Kolbasov, 2009; Chan *et al.*, 2014a). The aperture of the female mantle sac is surrounded by a pair of chitinous opercular bars at the upper part and a comb collar around the posterior margin of the aperture, which is reduced in a few specialized species. The basal (morphologically anterior) part of the mantle forms an attachment disc, serving the purpose of fixing the animal to the burrow. The boring apparatus comprises ctenoid multifid scales, with several spines and papillae. The adult females retain the larval post-oral adductor muscle. The thorax is highly elongate and is equipped with four to six pairs of segmented and generally biramous cirri, of which three to five terminal pairs form a tuft or basket for food capture. The terminal cirri are widely separated from a pair of mouth cirri, situated adjacent to the oral cone. Unlike the situation in Thoracica, the acrothoracican mandibles retain the plesiomorphic connection with the mandibular palps. The dwarf males range from being pear shaped to being elongated sometimes with lateral projections; Fig. 3H) and they are attached on the mantle sac of the females or on the burrow wall close to the opening. The males are non-feeding, and their morphology varies considerably among the different taxa. Some morphological features are undoubtedly autapomorphies for the Acrothoracica (opercular bars, orificial knob, the entire burrowing apparatus with multifid ctenoid scales and the separation of mouth cirri from the terminal feeding basket). In contrast, the post-oral position of the adductor muscle, exactly as in cypris larvae, is clearly a plesiomorphic character, because the same condition is found in the Ascothoracica.

Based on combined morphological and larval characters, Kolbasov (2009) divided the Acrothoracica into two orders, Lithoglyptida and Cryptophialida, and three families, Lithoglyptidae, Trypetesidae and Cryptophialidae. Before this, Berndt (1907) had originally divided the burrowing barnacles into two orders, the Pygophora and the Apygophora, based on the morphology of terminal cirri and the presence or absence of an anus. This division was based on few morphological characters, with some now understood as being symplesiomorphies, e.g. biramous terminal cirri and presence of an anus in Pygophora. In contrast, Apygophora have three pairs of uniramous terminal cirri, and they lack an anus (Berndt, 1907; Tomlinson, 1969). The Pygophora were divided into two families, the Lithoglyptidae and Crytophialidae, whereas Apygophora comprised only the Trypetesidae. Grygier & Newman (1985) considered the Lithoglyptidae as being paraphyletic owing to their several symplesiomorphies, and this view also gains some support from molecular analyses (Lin *et al.*, 2016).

Kolbasov (2002) found that dwarf males of Cryptophialida and Lithoglyptida differ in both cuticular structure and body form, and Kolbasov & Høeg (2007) described significant differences in cypris ultrastructure among the three families. The detailed study by Kolbasov (2009) offered the most comprehensive study of the Acrothoracica and presented a revision of the taxon that contradicts the systematics of Berndt (1907). Based on all this information from larvae and adults, Kolbasov (2009) erected two new orders, the Lithoglyptida (with families Lithoglyptidae and Trypetesidae) and the Cryptophialida (with only the Cryptophialidae). Thus, two former orders, Pygophora and Apygophora, were here considered as the families Lithoglyptidae and Trypetesidae under Lithoglyptida.

Several characters of the Lithoglyptida are *de facto* symplesiomorphies, such as bag-shaped mantle sacs, the presence of well-developed mouth cirri in females, the saddle-shaped labrum, elongated opercular bars, biramous natatory thoracopods in the cypris larvae and the presence of terminal pores in cyprid lattice organs. Several autapomorphies characterize the Trypetesidae, e.g. the reduced, uniramous terminal cirri, the absence of a comb collar, reduced mouthparts, the absence of an anus in females, and a complex external morphology of the dwarf males. The Lithoglyptidae and Trypetesidae share several characters not found in the Cryptophialidae, such as the orificial knob in females, lateral 'wings', a long attachment stalk in the dwarf males, and more setulated and externally complex setae on the fourth antennular segment in cyprids. The cryptophialid females have flask-like mantle sacs with an elongated neck area and lateral bars, crown-like opercular bars, an elongated labrum, reduced mouth cirri and a gastric mill; furthermore, the cryptophialid cyprids are characterized by the union of the subterminal and terminal setae on the fourth segment antennular segment and thoracopods reduced to the extent whereby they cannot swim but move only by walking on their antennules.

Here, we follow Kolbasov (2009) and Lin *et al.* (2016) in dividing the Acrothoracica into Lithoglyptida and Cryptophialida. This is at present the best available scheme, although Lithoglyptidae has an unresolved relationship with the Trypetesidae, whence the monophyly of the Lithoglyptida is not assured. Cryptophialida is monophyletic.

Order Lithoglyptida Kolbasov, Newman & Høeg, 2009

Females have a big, sac-like mantle, a wide aperture, an operculum without a neck, long opercular bars and a big labrum. The mouth cirri are well developed. The thorax lacks long dorsal processes, and gastric mill is absent. The dwarf males have numerous cuticular projections and lack mantle teeth. The burrow aperture is elongated and slit-like (Fig. 3F). The cyprids have developed natatory thoracopods and an unperforated, smooth carapace with frontolateral pores. The five pairs of lattice organs, situated on the dorsal part of the carapace, are narrow and elongated. The terminal pores are sited in an anterior position in lattice organ pair 2, but posterior in pairs 1, 3–5. The surface of each organ is perforated by small, round pores. On the antennules, the setae of the fourth segment are clearly separated into subterminal and terminal clusters. Several of the lattice organ details are plesiomorphic compared with the Rhizocephala and Thoracica and therefore support the molecular evidence for a basal divergence of the Acrothoracica.

The Lithoglyptidae is distinguished by the number of terminal cirri in females. Kolbasov & Newman (2005) revised the largest and perhaps most plesiomorphic genus, *Lithoglyptes* Aurivillius, 1892 *s.l.*, and divided it into three genera. One (Kolbasov & Newman, 2005) turned out to be a junior synonym; therefore, the correct generic names are now *Lithoglyptes* (*s.s.*), *Auritoglyptes* Kolbasov & Newman, 2005 and *Balanodytes* Utinomi, 1950 (Chan *et al.*, 2013). Lithoglyptid females have opercular bars and comb collars. The operculum carries rows of multifid scales, which are often associated with pores and papillae. The protopod of the mouth cirri are two-segmented and the mouth appendages are well developed. The terminal cirri are multisegmented, biramous and widely separated from the mouth cirri. Caudal appendages can be present or absent depending on species. Thoracic lappets and an anus are present. Several species have an anterior (functionally basal) calcareous plate, which is covered by the cuticle of the attachment disc. Dwarf males lack lateral lobes at the base of their attachment antennules or stalk, and their posterior end has an apertural slit, which may be covered by a semicircular fold.

The species from the Trypetesidae live in the columella of gastropod shells occupied by hermit crabs. The females have thin opercular bars, and the comb collar is reduced. The operculum lacks pores, papillae and multifid ctenoid scales. The mouth appendages are reduced in size, and the protopod of the mouth cirri is unisegmented. There are three pairs of four-segmented, uniramous terminal cirri but no caudal appendages. Thoracic lappets are reduced in number and size, and there is no anus. Trypetesid dwarf males have a complex shape and form, with a pair of lateral lobes at the base of the attachment stalk, but they have no apertural slit. A recent study provided new data on reproduction and the relationship to the hermit crab host in *Trypetesa lampas* (Hancock, 1849) (Larsen *et al.*, 2016).

Order Cryptophialida Kolbasov, Newman & Høeg, 2009

The species of the Cryptophialida live on the surface of gastropod shells, corals and calcareous rocks. The females have a flask-like mantle. The neck of the operculum is elongated, with well-developed rod-like lateral bars. The aperture is small, with crown-like opercular bars along its total length. The labrum elongated and tongue-like, but the mouth cirri are rudimentary. The thorax has one or two whip-like, long dorsal processes and thoracic lappets with a clear cuticular border. Internally, the intestine has a gastric mill or gizzard. Caudal appendages are lacking. The dwarf males lack external cuticular, papilliform projections, but their posterior end has circular ribs and often also conspicuous mantle teeth. The cyprid carapace has a perforated sculpture, but there are no frontolateral pores. Frontolateral pores are almost universally present in cirripede cypris larvae, but they are also absent in some specialized species within the Rhizocephala. The elongated lattice organs have no large terminal pores, but numerous small pores.

Infraclass Rhizocephala Müller, 1862

A new taxonomy of the Rhizocephala (Fig. 4) based on molecular data was recently published (Høeg *et al.*, 2020) and is followed here. That study and Høeg *et al.* (2019) also provided an in-depth account of rhizocephalan morphology and biology across the several families, whence we only summarize the main points. Owing to the highly reduced morphology of the rhizocephalan parasites, the taxa recognized here are defined by means of molecular characters. Høeg *et al.* (2020) also offer morphologically based diagnoses, but they are only rarely based on apomorphies for the taxa concerned.

General biology and life cycle: Rhizocephalans are highly advanced parasites on other crustaceans, principally decapods, and the adult stages are so reduced that they offer virtually no clue to the phylogenetic position as crustaceans or even as arthropods (Høeg, 1995a; Høeg & Lützen, 1995; Walker, 2001; Høeg *et al.*, 2015, 2019, 2020). The free-swimming larval stages are, in contrasts, similar to those of other cirripedes, with which they share several apomorphies. Therefore, since Thompson's (1836) benchmark study of the larvae, the relegation of these parasites to the Cirripedia has remained virtually unchallenged. In contrast, their position within the Cirripedia, whether or not they constitute a monophyletic taxon and their intrinsic relationships had largely to wait for results from molecularly based studies (Glenner & Hebsgaard, 2006). The reason is that the parasitic stages have an extremely simplified gross morphology, lacking segmentation, appendages and most other structures apart from the reproductive organs (Fig. 4I–N). Therefore, systematics of Rhizocephala had to be based on simple similarities in the few characters available, such as the shape of the external parasite (externa) or the gross structure of the reproductive organs (Øksnebjerg, 2000).

The parasitic phase is initiated after a cypris larva settles on the potential host. This occurs either by means of a so-called kentrogon stage that can follow the settled cyprid (Fig. 4E, F) or by action of the cyprid itself (Høeg, 1995). Then follows an entirely endoparasitic phase until the parasite emerges on the surface of the host as an external reproductive sac (externa), connected to an internal and nutrient-absorbing root system by a stalk (Glenner, 2001) (Fig. 4F–H). All rhizocephalans have separate sexes, with extremely reduced dwarf males hosted within the female externa (Fig. 4C, D). The males can either reside in special organs within the female (receptacles or spermatogenic islets) or be situated directly in the female tissues (Yanagimachi, 1961; Høeg, 1987, 1991; Høeg & Lützen, 1995). Owing to this specialized morphology, there is no option for an outgroup comparison with other cirripedes, whence any morphological character matrix will be virtually impossible to polarize. In contrast, characters in the larvae can be compared directly with other cirripedes and are therefore useful in the few cases where they are available in detail (Glenner *et al.*, 2010).

Phylogeny and taxonomy: The molecular phylogenies have now shown that Rhizocephala is a monophyletic taxon and is placed consistently as sister to Thoracica (Fig. 7). A number of detailed studies on species from across the taxa provided the basis for the complete family-level revision by Høeg *et al.* (2020), and this resulted in a taxonomy with 13 monophyletic families that could be placed in a fairly well-resolved phylogeny.

The new taxonomy entailed several important revisionary steps. One was the division of the largest family into two, a revised Sacculinidae and the new family Polyascidae. Species within these two families are impossible to separate by morphology, but the molecular data clearly indicate that they form two taxa that are not closely related. The revision also entailed splitting off two new families from a re-diagnosed Peltogastridae. Finally, a major change was the abandonment of the former taxonomic subdivision into the suborders Kentrogonida and Akentrogonida (Høeg & Rybakov, 1992). These suborders were based on the host invasion proceeding either by a kentrogon stage (Fig. 4F) following the cyprid ('Kentrogonida') or by the cyprid itself using one of its antennules to penetrate the host integument ('Akentrogonida'). The molecular data showed that the kentrogonid type

represents a plesiomorphy and that the akentrogonid type of metamorphosis has evolved at least twice homoplastically. The position of the 'akentronid' Mycetomorphidae close to the Peltogastridae and separate from the remaining 'akentrogonid' families (Fig. 4) argues for the lack of utility or the absence of a kentrogon as a unique synapomorphy to characterize a taxon. In contrast, the molecular data also suggest that the remaining 'akentrogonid families', other than the Mycetomorphidae, form a monophyletic unit (Fig. 4). Moreover, this taxon can also be characterized by morphological apomorphies, such as the absence of paired receptacles exiting through a cuticular duct (Høeg, 1991) and a reduced pattern of setae on the cypris antennules (Glenner *et al.*, 2010). Therefore, we might in the future again recognize these taxa as a monophyletic group with a formal rank and new name. At present, however, there are no taxonomic ranks above the family level within the Rhizocephala, although the 13 families can be placed in a fairly well-resolved phylogeny.

Character evolution: It is now clear that it is plesiomorphic to infest the host by means of a kentrogon and for the female externa to have paired male receptacles communicating with the mantle cavity through a cuticular duct. These receptacles serve to receive the trichogon larva (Fig. 4C, D) that follows settlement of male cyprids (Fig. 4B, C) on the virginal parasite and to host and nourish the resulting dwarf male through several reproductive cycles (Ritchie & Høeg, 1981; Høeg, 1987, 1991). The original host taxon was Anomura, such as in the families Triangulidae, Peltogastridae and Peltogasterellidae (Fig. 4I). Evolution onto Brachyura and other hosts occurred in other lineages (e.g. Sacculinidae and Polyascidae), and in some this was accompanied by both loss of the kentrogon stage in host infection (e.g. Clistosaccidae and Thompsoniidae) and advanced modes of implanting and hosting the males in the female body without trichogons or receptacles (Høeg, 1991; Høeg & Lützen, 1995). A unique parasitic host specialization was reached in species of the Chthamalophilidae, which infest balanomorphan barnacles and where males are hosted in so-called spermatogenic islets that float freely in the mantle cavity of the female (Høeg, 1991; Yabuta *et al.*, 2020). Uniquely among all cirripedes, except the Acrothoracica Cryptophialidae, the chthamalophilid cyprids lack thoracic appendages and can therefore disperse only by walking on the substratum using their two antennules. An evolutionary bridge to this advanced family may be seen in the Duplorbidae, which have a similar sexual system and infest various Peracarida, but where the cyprids retain a more plesiomorphic morphology, with thoracopods for swimming.

Infraclass Thoracica Darwin, 1854

The Thoracica (Fig. 5) comprises the pedunculated (with a stalk) and sessile (no stalk) barnacles. In the ground pattern (Anderson, 1994), the body of thoracicans consists of a flexible peduncle and a capitulum, the latter being armed with a number of mineralized plates. Secondary loss of the peduncle has occurred convergently at least twice, viz. in the Neoverrucidae and in the 'sessilian' lineage leading to the Verrucomorpha and Balanomorpha (Fig. 5). The original number of shell plates was four; the paired scuta–terga that guards the opening into the mantle cavity. Later forms acquired increasing numbers of plates, but reductions and even complete loss of plates also occurred in several lineages (Chan *et al.*, 2009) (Figs 5I–K, 9, 10). Closing of the mantle cavity is by the scutal adductor muscles, the position of which has phylogenetic value. Inside the capitulum, the soma is suspended in the mantle cavity. The soma carries the mouth cone composed of the labrum, with mandibles, maxilla and maxillules (these appendages are often called trophi) (Chan *et al.*, 2009). Unlike the Acrothoracica, the mandibular palp has separated from the mandible itself. The trophi are followed by six pairs of biramous cirri (Fig. 5E) and sometimes paired caudal appendages. The specialization of anterior cirri into mouth appendages is important in both classification and feeding biology. The soma represents both parts of the cephalon and the thorax, and an abdomen is lacking. It is uncertain which, if any, of these characters constitute autapomorphies for the Thoracica, especially compared with the Rhizocephala, for which these characters cannot be scored (Høeg *et al.*, 2009b). It is likely that stem-line cirripedes below the Thoracica–Rhizocephala node also had a thoracican-like morphology, sporting both a peduncle and shell plates. Nevertheless, this does not change the monophyly of the extant forms, which is supported by all molecular analyses published until now (Pérez-Losada *et al.*, 2002, 2004, 2008; Rees *et al.*, 2014; Lin *et al.*, 2015).

Shell plates and growth: Within the mantle cavity, moulting occurs by complete shedding of the old cuticle, as in any other crustacean, but on the external surface the process is highly modified (Fig. 11). The shell plates are mineralized parts of the original cuticle, and their presence has profoundly changed the mode of growth in thoracicans (Bourget & Crisp, 1975; Bourget, 1987; Blomsterberg *et al.*, 2004). The plates themselves increase in area by progressive mineralization around their edges. Regular moulting occurs in the variably sized cuticle areas between the shell plates, and here new cuticle is produced in infolded areas of the epidermis that form a system of growth zones between the plates. At moulting, the old cuticle is shed only as narrow band above the new

cuticle and splits apart on either side (Mahmoud, 1959, 1960). The two edges of the old cuticle therefore form a pair of 'growth lines' running in parallel on either side of the growth zone area. In balanomorphans, these lines have also been called 'cuticular slips' and are often hard to see (Bourget & Crisp, 1975), but in species with broad cuticle areas between smaller sized plates, e.g. *Octolasmis* Gray, 1825 and some scalpellids, the bands of multiple, parallel growth lines form characteristic patterns on the external surface that testify to the number of moulting events experienced by the specimen (Figs 5M, 9) (Dreyer *et al.*, 2018c).

Completely separate from the cuticular slips or growth lines, the shell plates also show a pattern of semiconcentric lines resulting from their progressive increase in size by stepwise mineralization along the edges. Importantly, these lines do not correspond in number to the cuticular growth lines that result from moulting. On increasing in size, the older organic cuticle areas, including the growth lines, come to lie on the surface of the plates, where they are gradually abraded. Such a system of retaining the old cuticle and producing growth lines is known also from the Branchiopoda 'Conchostraca' (Bourget & Crisp, 1975; Bourget, 1987; Blomsterberg *et al.*, 2004). Multiple times, especially in the Lepadoidea, shell plates have been secondarily reduced to rudiments or disappeared altogether. The plates are obviously secreted by the epidermis and are thus part of the body cuticle. Unfortunately, little attention has been given to the plate microstructure and the process by which the mineralization proceeds, but recently, state-of-the-art techniques offer hope for renewed insight (Checa *et al.*, 2019; Mitchell *et al.*, 2019). It is clear that the presence of mineralized shell plates in the integument involves multiple interrelated apomorphies with no parallel elsewhere in the Arthropoda. It complicates the issue that the shell plates were originally phosphatic and only later changed to calcitic mineralization. Unfortunately, we cannot decide precisely where in the phylogeny shell plates and their mineralization first appeared, because it is open to speculation whether the ancestors to the Rhizocephala and Acrothoracica were completely unmineralized or whether they evolved from a cirripede with some form of armature that was secondarily lost. The only solution to this important question would be a detailed analysis that places crucial fossils within the part of the cirripede tree below the last common ancestor to all recent Thoracica, but no such species has been identified with any certainty (Høeg *et al.*, 2009b). In contrast, as detailed below, the change from phosphatic to calcitic plates and their gradual increase in number can be followed in the fossil record (Figs 9, 10).

Plate numbers in thoracican evolution: The number of plates and their disposition have always featured prominently in studies on thoracican evolution. The traditional hypothesis suggested that, commencing with four plates (paired scuta and terga) in the Iblomorpha, the number of capitular plates increased progressively to five (*Lepas* Linnaeus, 1758 and *Praelepas*), six (*Eolepas* Withers, 1928) and then to eight with the addition of paired upper latera (*Neolepas* Newman, 1979) (Fig. 9). Subsequent evolution led to an increase in the number of lateral plates, resulting in a multi-plated condition (Broch, 1922; Newman, 1987; Anderson, 1994; Buckeridge & Newman, 2006). This interpretation was based on the ontogeny of the juvenile barnacles, especially in pollicipedids (Broch, 1922), calanticids and scalpellids, where growth starts with a near-simultaneous development of five primordial chitinous plates, followed by increase in a 6–8–12+ pattern (Fig. 9). The interpretation is also supported, in part, by the fossil evidence, because in phosphate-shelled forms there was a progressive increase in plates through a five-plated *Praelepas* (with carina added; Carboniferous) to a six-plated *Eolepas* (also with a rostrum; Triassic–Jurassic). It is nevertheless important to state that none of the extant forms with five plates (Lepadoidea) or eight plates (Neolepadomorpha) has retained an ancestral condition but that they owe the number of their plates to secondary loss from multi-plated ancestors (Figs 7, 9). Both the molecularly based phylogenies and new interpretations of fossil data agree that such numbers of plates resulted from several separate plate-loss events from multi-plated ancestors (Pérez-Losada *et al.*, 2008, 2012a; Gale, 2015a, 2019; Gale & Schweigert, 2015). In fact, the supposedly 'primitive' *Neolepas* and *Lepas* (Newman, 1987; Glenner *et al.*, 1995) did not appear until the Eocene and have calcite shells (Ullman *et al.*, 2018; Gale *et al.*, 2020).

The mineral transition to calcite took place in a shell that had all six primary plates present, followed by a gradual addition of lateral plates and the addition of peduncular scales. The Jurassic Archaeolepadomorpha (Archaeolepadidae, Myolepadidae and Stramentidae) started with few or no lateral plates, but had large, robust and imbricating peduncular plates arranged in ten vertical columns. The Stramentidae had two pairs of laterals, and a multi-plated situation was reached in the Jurassic Zeugmatolepadidae, which have eight or more laterals in addition to the six primary plates (Gale, 2019).

A few extant thoracicalcareans, such as *Capitulum* Gray, 1825, are still armed with numerous plates, and fossil evidence points to this as a plesiomorphic condition for the more derived thoracicalcareans (Gale, 2019). Calanticids can carry a highly variable

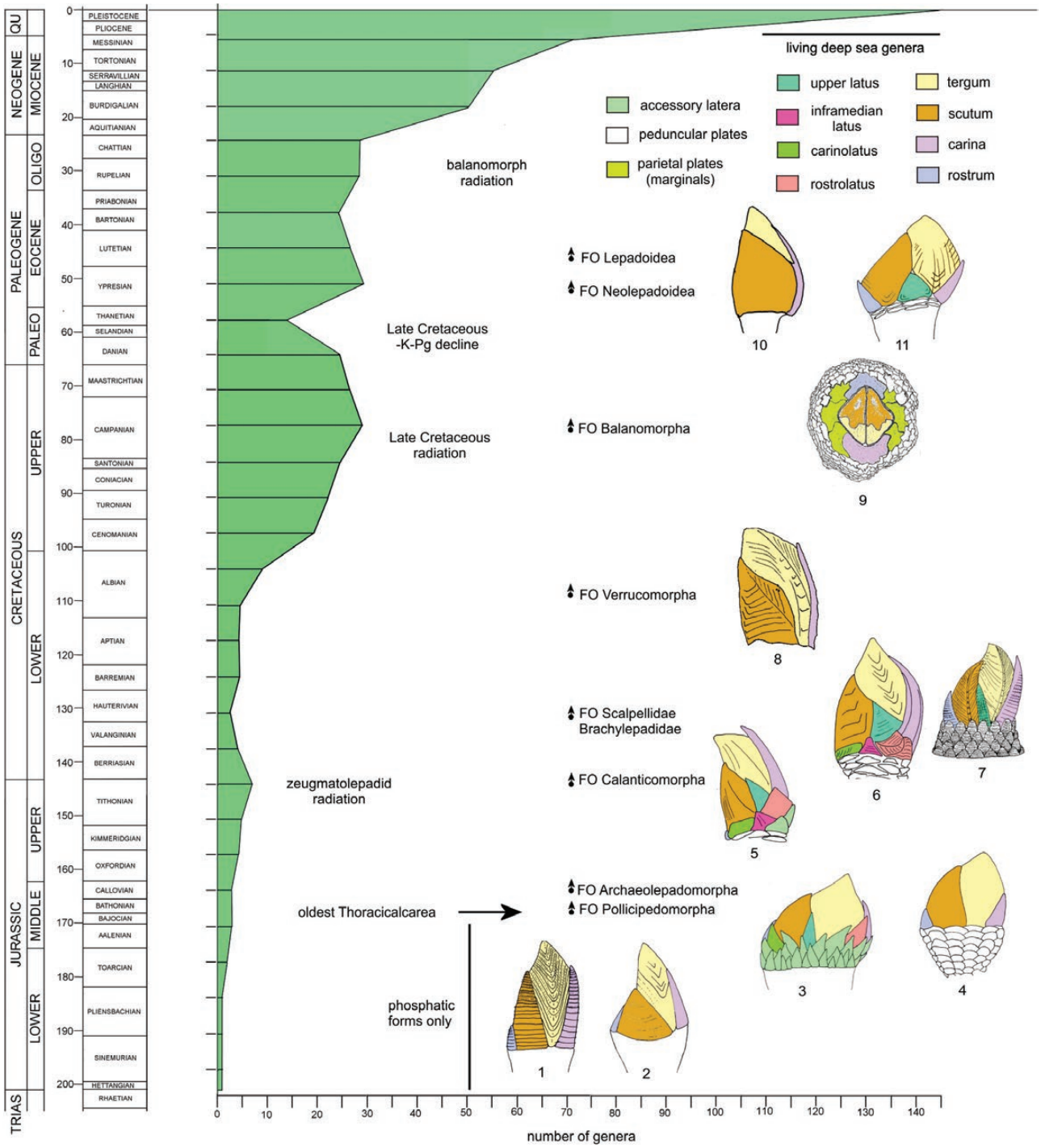

Figure 9. Timeline of Thoracican evolution. Generic diversity of the Thoracica from the latest Triassic to the present. Early forms are entirely phosphatic, followed by calcitic pedunculated forms. Balanomorphans (acorn barnacles) appeared in the Cretaceous, but they radiated only after a low-diversity period following the Cretaceous–Palaeogene (K–Pg) extinction. The diversification starting in the Neogene is still ongoing. Living genera shown include only forms with shell plates, in order to compare with the fossil record. Further explanation is given in the main text. (1) Eolepadomorpha, Eolepadidae, *Eolepas*; (2) Eolepadomorpha, Eolepadidae, *Toarcolepas*; (3) Pollicipedomorpha, Zeugmatolepadidae, *Concinnalepas*; (4) Archaeolepadomorpha, Archaeolepadidae, *Archaeolepas*;

number of numerous, small lateral plates (Jones & Hosie, 2009), whereas in the Scalpellidae the maximum is reduced to 14, and in various fossil taxa it is reduced even further, down to six plates in some members of the Titanolepadidae, Virgiscalpellinae and Zeugmatolepadidae (Gale, 2020a; Gale *et al.*, 2020). In Neolepadidae and some Brachylepadidae, only eight plates are present, again owing to secondary loss (Fig. 9).

All this shows that the armature of shell plates has been subject to complicated patterns of gain and loss throughout thoracicalcarean evolution. The reason for the five-plated condition in extant Lepadoidea might be that they simply arrest development at what corresponds to the earliest ontogenetic stage in multi-plated forms. Most lepadoid species are adapted either to an epibiotic life, where protection is less important, or to living on ephemeral substrata, where rapid attainment of sexual maturity is at a premium. The apex of this trend is seen in lepadoideans that have lost all plates, such as all members of the Heteralepadidae and some species of the Poecilasmatidae (Anderson, 1994; Yusa *et al.*, 2001; Hosie, 2014; Buhl-Mortensen & Mifsud, 2017).

Phylogeny and taxonomy: Traditionally, Thoracica were often divided into the 'Pedunculata' and the 'Sessilia'. The diagnosis of Pedunculata (stalked barnacles) was the possession of a body divided into a peduncle (stalk) and a capitulum, but this is clearly a plesiomorphic condition, and the taxon is accordingly not monophyletic. In the study by Buckeridge & Newman (2006), the Thoracica were divided into the orders Cyprilepadiformes (fossil only), Ibliformes, Lepadiformes, Scalpelliformes and Sessilia (non-stalked barnacles), but they did not base this division on morphological apomorphies, and molecular data were not yet available. Here, we also recognize some of these taxa, although sometimes with different names, definitions and composition of species.

As already mentioned, we do not recognize *Priscancermarinus* and *Cyprilepas* as cirripedes. *Priscancermarinus* from the Burgess Shale formation (Collins & Rudkin, 1981) does not possess any convincing cirripede features, and the dating of lineages provided by Pérez-Losada *et al.* (2004) would probably have been different if this fossil had been omitted. *Cyprilepas* is a small, bi-valved, organically walled fossil found attached to Silurian eurypterids (Wills, 1963) and with limited clear morphological features revealed (without any signs of the presence of appendages). Although having some similarity with a newly settled barnacle, the validity of *Cyprilepas* as a cirripede is still controversial. Even the conclusion by Wills (1963) suggests that *Cyprilepas* might also be an adult entomostracan, and we might add that it could even be a giant shelled ciliate. To decide on this will require re-analysis by modern analytical methods that can reveal internal structures, as was done for another alleged cirripede, *Rhamphoverritor* Briggs *et al.*, 2005, from the Silurian. This was claimed to be a crown group cirripede, but the presence of a distinct and segmented abdomen puts it at best as a stem-line representative of that taxon (Høeg *et al.*, 2009b). Therefore, we consider the oldest certain record of a thoracican cirripede to be *Praelepas* from the Carboniferous (320–330 Mya) (Figs 9, 10).

Initially, plates covering the body might have consisted of cuticle only, and all palaeontological evidence indicates that the original mineralization was by phosphatization, with calcification being apomorphic (Fig. 9). Based on this, we follow Gale (2015a, 2019) and Gale & Schweigert (2015) in dividing the Thoracica into Phosphatothoracica and Thoracicalcarea (Figs 7, 9). The Phosphatothoracica is clearly paraphyletic when extinct taxa are included, but it is a convenient concept to host phosphatic thoracicans, many of which cannot easily be put into a resolved phylogeny. The Thoracicalcarea comprise all extant Thoracica except the Iblomorpha (Fig. 7) and is monophyletic in all molecularly based analyses.

Among extant species, the morphological difference between Phosphatothoracica and Thoracicalcarea is extensive, but this largely disappears when fossil forms are included. In the hard parts, the difference involves the transition from a plesiomorphic condition with only four phosphatic plates (paired scuta and terga; Iblidae), with the addition of a carina (Praelepadidae), a rostrum (Eolepadidae) and through to forms with a calcitic plate armature with numerous plates, such as in extant *Capitulum* and *Pollicipes* Leach, 1817. In soft body anatomy, there are numerous additional differences between the two groups (Anderson, 1994), a spectacular one being the plesiomorphic retention in Phosphatothoracica of post-oral scutal adductor muscles as opposed to the pre-oral position in Thoracicalcarea. A post-oral position is also found in the Acrothoracica, the Ascothoracica and the cypris larva of all cirripedes. The two adductor muscles are clearly not homologous, because ontogenetic studies have shown that both can exist at the same time during the metamorphosis from cyprid to juvenile, and probably also did so during evolution from *Ibla* Leach, 1825 to the extant Thoracicalcarea (Glenner

(5) Calanticomorpha, Cretiscalpellidae, *Witherscalpellum*; (6) Scalpelloidea, Scalpellidae, *Arcoscalpellum*; (7) Brachylepadomorpha, Brachylepadidae, *Pycnolepas*; (8) Verrucomorpha, Verrucidae, *Altiverruca*; (9) Balanomorpha, Catophragmidae, *Catomerus*; (10) Lepadoidea, Lepadidae, *Lepas*; (11) Neolepadomorpha, Neolepadidae, *Stipilepas*.

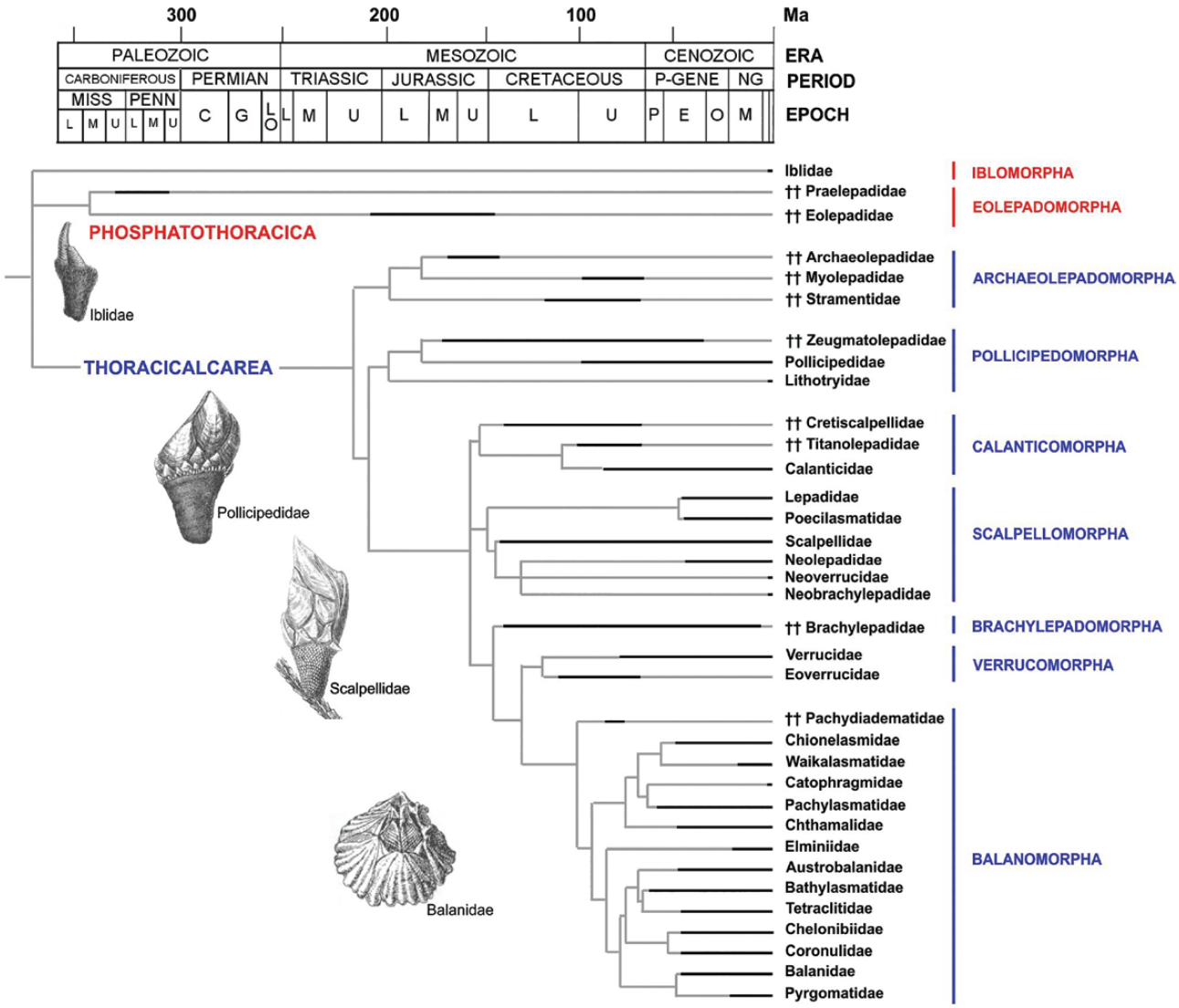

Figure 10. Phylogram of thoracican phylogeny, based on a combination of morphology (fossils and extant taxa) and guided by molecular data. The successively later first appearance of more crownward (derived) taxa supports the overall story, although there are some 'ghost' ranges within individual clades, in which fossil taxa appear anonymously late in the record. Note that based on the morphological interpretation, the Pollicipedomorpha are here placed basalmost among extant Thoracicalcarea. Compare with the tree derived from molecular analysis of extant forms (Fig. 7) and thoracican diversity through time (Fig. 9). Abbreviations: C, Cisuralian; E, Eocene; G, Guadulupian; LO, Lopingian; MISS, Mississippian; M, Miocene; NG, Neogene; O, Oligocene; P, Paleocene; PENN, Pennsylvanian; P-GENE, Paleogene. L, M, U (MISS, PENN, TRIASSIC, JURASSIC) and L, U (Cretaceous) refer to Lower, Middle and Upper.

& Høeg, 1998). This shows that the accumulation of shell plates towards extant Thoracicalcarea must also have been related intimately to changes in soft body characters, such as muscles.

Superorder Phosphatothoracica Gale, 2019

The Phosphatothoracica is a paraphyletic taxon that comprises all extinct and extant thoracicans with phosphatized shell plates. Among extant forms, it comprises only the Iblomorpha, which is probably monophyletic. Iblomorphans have only four shell plates (Fig. 5F), viz. the paired scuta and terga, and all evidence points to this as an original condition.

Order Iblomorpha (*sensu* Ibliformes Buckeridge & Newman, 2006)

Until now, only two species (of the Iblidae) have been analysed molecularly (Pérez-Losada *et al.*, 2008; Lin

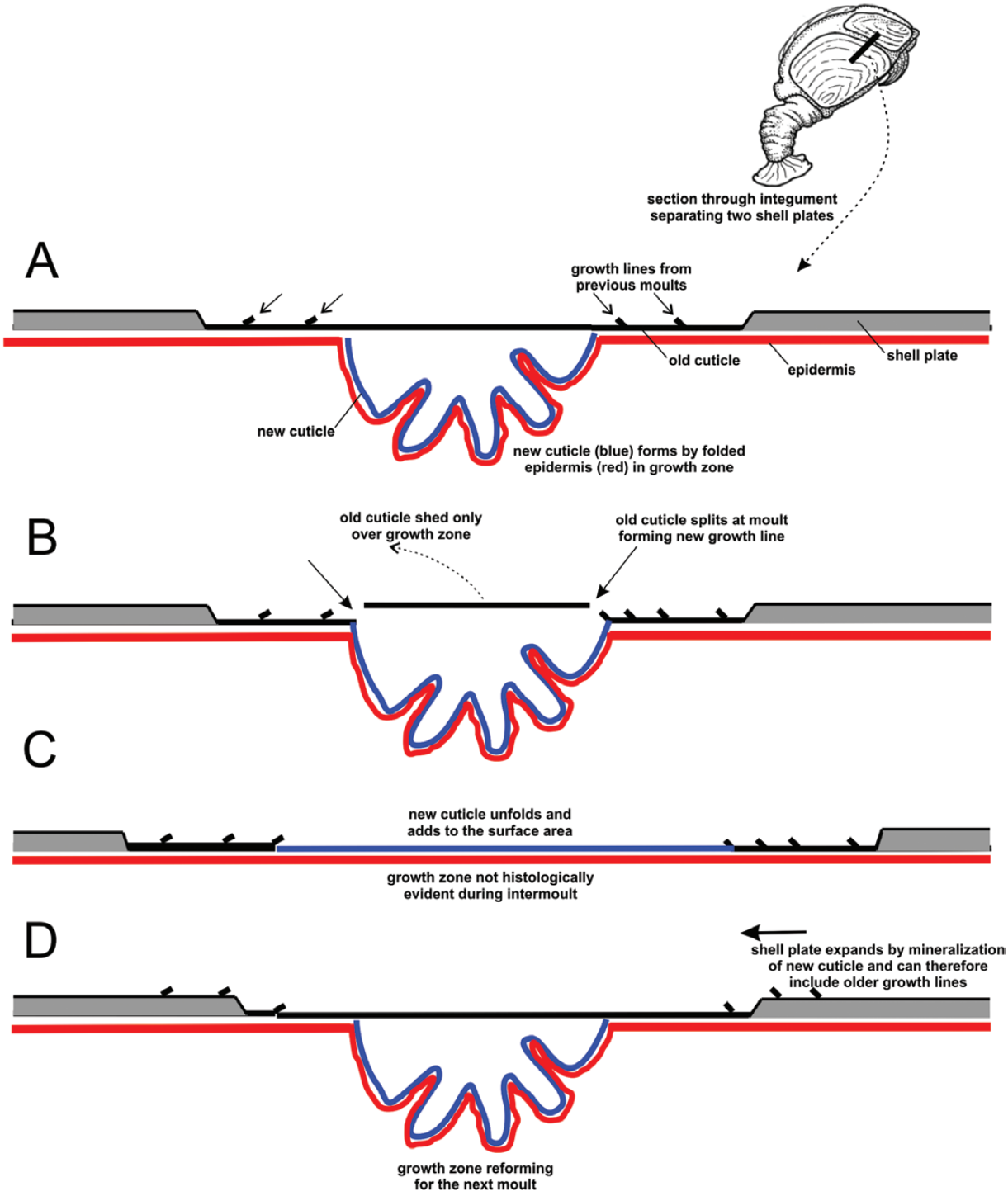

Figure 11. Moulting and growth in Thoracica. Moulting occurs in the cuticular zones separating shell plates. A, new cuticle is formed by infolded epidermis in a narrow growth zone between two adjacent shell plates. B, old cuticle is shed only above the growth zone. The broken-off cuticle leaves distinct growth lines on either side of the growth zone. C, the new cuticle expands by outfolding; the growth zone is not distinct during intermoults. D, a new growth zone forms for the next moult; the shell plate can now expand laterally under the cuticle; older growth lines can thereby be included on top of the plate. Constructed from descriptions by Mahmoud (1959, 1960), Bourget & Crisp (1975) and Blomsterberg *et al.* (2004).

et al., 2015), and they form the sister group to the Thoracicalcera, i.e. all remaining extant thoracicans (Fig. 7). This agrees with morphology, because most, if not all, morphological characters distinguishing extant iblomorphans from other Thoracica are putative plesiomorphies (Glenner *et al.*, 1995; Buckeridge & Newman, 2006). These characters include the position of the adductor muscle, chitinous spines on the peduncle, the so-called comb collar around the mantle aperture, and some characteristics in the nauplii. Buckeridge & Newman (2006) offered a review of the only eight described species of Iblomorpha and divided them into the families Iblidae and Idioiblidae. Although not based on a cladistic analysis, we retain these families and the subfamilies contained in them.

Order Eolepadomorpha ord. nov.

These extinct phosphatothoracicans include the Carboniferous Praelepadidae (*Praelepas* and *Illilepas* Schram, 1986), with a carinal plate, and the Triassic–early Cretaceous Eolepadidae (*Eolepas*), which also had a rostrum, thus showing a progression in the number of plates towards the Thoracicalcarea (Figs 9, 10). The Eolepadidae Buckeridge, 1983 was redefined by Gale *et al.* (2020) to house *Eolepas* and *Toarcolepas* Gale & Schweigert, 2015, while excluding the calcified eight-plated members in the Neolepadinae, which were raised to family status and are presently placed much higher in the phylogeny within the Thoracicalcarea.

Superorder Thoracicalcarea Gale, 2015

All molecular and morphological analyses agree that the Thoracicalcarea is a monophyletic unit (Fig. 7). There is also general agreement among the molecular studies about the monophyly of the major lineages within the group, and again, this largely agrees with the recent morphological study by Gale (2019). Nevertheless, the precise relationships of these major lineages differ somewhat between studies (Fig. 8). There is general agreement among the molecular studies on the monophyly of our Balanomorpha, Calanticomorpha, Scalpellomorpha and Verrucomorpha (Fig. 8). The sister relationship between our Lepadoidea and Scalpelloidea (= Scalpellomorpha) is also favoured by morphology, but Herrera *et al.* (2015) put the scalpellomorphs closer to the Sessilia (Fig. 8). The molecular studies always show the Calanticomorpha diverging below the Lepadoidea and Scalpelloidea (= our Scalpellomorpha), but Gale *et al.* (2019) argues by morphology that these three taxa together might form a monophyletic clade. Most uncertainty revolves around the position of our Pollicipedomorpha, comprising *Capitulum*, *Lithotrya* Gruvel, 1905 and *Pollicipes* (highlighted in yellow in Fig. 8). The position of these three genera is discussed in detail below. In our taxonomy, we have chosen to reflect the uncertainties by having the orders Balanomorpha, Calanticomorpha, Pollicipedomorpha, Scalpellomorpha and Verrucomorpha put as equally ranked taxa (orders) within the Thoracicalcarea. The remaining nodes in our composite family tree (Fig. 7) remain unnamed and unranked. A more resolved phylogenetic hypothesis based on morphology is available in the study by Gale (2019).

Order Pollicipedomorpha ord. nov.

Capitulum, *Lithotrya* and *Pollicipes* are pedunculated barnacles from the rocky intertidal zone, and by molecular evidence these three genera move around in different phylogenetic analyses (highlighted in yellow rectangular areas in Fig. 8). Only Herrera *et al.* (2015) recovered these genera as a monophyletic group. Recent mitochondrial genome-based phylogenetic analyses showed that *Pollicipes* and *Capitulum* are sister to each other (Tsang *et al.*, 2017; Kim *et al.*, 2018, 2019). Pending future analyses, we have chosen to unite the three genera into a single and, most probably, paraphyletic taxon, the Pollicipedomorpha. Most studies have placed them close to the Balanomorpha. In the studies by Pérez-Losada *et al.* (2008) and Rees *et al.* (2014), they diverged immediately below a node uniting the Balanomorpha and Verrucomorpha. Herrera *et al.* (2015) have them situated within the balanomorphan tree, but morphology argues strongly against this position. A recent full mitochondrial genome analysis placed *Pollicipes* + *Capitulum* as sister to the Balanomorpha, with the Verrucomorpha diverging from this node, but that study did not include *Lithotrya* (Kim *et al.*, 2018). In contrast, Lin *et al.* (2015) placed *Capitulum* as sister to the remaining Thoracicalcarea (Fig. 8), with *Pollicipes* + *Lithotrya* being sisters to the Calanticomorpha as a poorly supported clade; in our Figure 10, based on fossil data, we suggest the same position. Such a basal position of pollicipedomorphs is in agreement with morphological data, where a multi-plated condition with several latera is seen as ancestral within all extant thoracican orders listed here (Gale, 2019).

Both *Capitulum* and *Pollicipes* have been recorded from the Cretaceous; *Capitulum* and *Pollicipes* from the Late Cretaceous (Campanian, 80 Mya) in rocky shoreline deposits of Sweden (Gale & Sørensen, 2015); and *Capitulum* also from similar (94 Mya) deposits in the Czech Republic (Kocova Veselska *et al.*, 2015).

In the study by Pérez-Losada *et al.* (2008), *Capitulum* and *Pollicipes* are sister groups, although without high support, and we maintain these two genera within the Pollicipedidae. Based on mitogenome phylogenetic analyses, *Capitulum* and *Pollicipes* are sister groups (Tian *et al.*, 2020). Rees *et al.* (2014) showed with high confidence that *Anelasma squalicola* (Lovén, 1844), a parasite of lantern sharks, is a sister group

to *Capitulum*; therefore, we also place this parasite in the Pollicipedidae and abandon the former Anelasmatidae. Keeping these diverse genera in the same family will serve exactly to emphasize extreme divergence within monophyletic lineages, something that would be obscured if *Anelasma* Darwin, 1852 was kept at the family rank. This surprising relationship shows that a pedunculated and suspension-feeding barnacle evolved into a parasite that gains nutrition through a system of roots penetrating into the host, as also hypothesized for the origin of the Rhizocephala (Glenner & Høeg, 2002). The divergence between *Anelasma* and extant *Capitulum* might have taken place late in the Cretaceous, although its origin of parasitism could have been much later. *Lithotrya* has only eight plates and is morphologically specialized for boring into calcareous substrata. At present, its uncertain position argues for maintaining the monogeneric family Lithotryida.

Order Calanticomorpha ord. nov.

Both Lin *et al.* (2015) and Pérez-Losada *et al.* (2008) agree that the Calanticidae is a monophyletic assemblage and that it diverged before the Lepadoidea + Scalpelloidea (= our Scalpellomorpha), with the two studies disagreeing only in the position of the Pollicipedomorpha (see above). Gale (2019) and Gale *et al.* (2019) argued, from fossil and morphological evidence, that the Calanticidae diverged before the Scalpellomorpha (Fig. 9) but that calanticids are the first branch on a monophyletic lineage comprising also our Lepadoidea and Scalpelloidea. There is, in fact, substantial morphological similarity between calanaticids and scalpellids, but this could be a plesiomorphy at this level in the phylogeny. Calanticids can have numerous lateral plates, and the number is highly variable (Jones & Hosie, 2009). Following the molecular analyses, we have chosen to keep the Calanticidae within a separate order, situated at present in a polytomy that also comprises the Pollicipedomorpha, Scalpellomorpha and Sessilia (Fig. 7). The Calanticomorpha have dwarf males, in which the body consists of a peduncle and a capitulum with shell plates. These males can be situated in different positions on their female or hermaphrodite partner (inside the capitulum, on the scutal edge, on the subrostrum or on the stalk).

Order Scalpellomorpha Buckeridge & Newman, 2006

Most molecular analyses agree on the monophyly of the superfamilies Lepadoidea, Neolepadoidea and Scalpelloidea, as comprised here, and that together they form a larger monophyletic clade, our Scalpellomorpha, that diverges between the Calanticomorpha and Sessilia (Figs 6, 7). Both the Neolepadoidea (eight plates) and Lepadoidea (five plates) are believed to have secondarily reduced the number of shell plates from the 14 found in the Scalpellidae. In slight disagreement, Herrera *et al.* (2015) have the Scalpelloidea + Neolepadoidea situated closer to the Sessilia than the Lepadoidea (Fig. 8). Within Scalpellomorpha, the Scalpelloidea and Neolepadoidea are sister groups in all molecular studies, but we do not provide a formal rank or name for that taxon. It is difficult to give a diagnosis that conforms to all members of the Scalpellomorpha, because most species have 12 plates but other forms are wholly or virtually naked (Fig. 5). Thus, the recognition of the Scalpellomorpha clade is based on it being returned in all recent molecular phylogenetic analyses (e.g. Perez-Losada *et al.*, 2008; Rees *et al.*, 2014; Lin *et al.*, 2015). This does not mean that morphological apomorphies did not originally exist in the stem-line of the taxon, but they have been secondarily lost or obscured in the Lepadoidea clade and even in some Scalpellidae.

A purely morphological analysis yields a slightly different phylogeny (Gale, 2019). Here, the Neolepadoidea are placed as sister to the two sessilian lineages under the name Unilatera, the apomorphy being the loss of all lateral plates except the paired upper latera. The advantage of this scenario is that the plate reduction to only a single pair of latera occurred once, viz. in the stem-line to the Unilatera, rather than convergently in lines leading to the neolepadoideans and sessilians. Topologically, the difference really concerns only a single node in the tree.

In our taxonomy, we follow the molecular studies, but we also emphasize that these disagree slightly among themselves and that every hypothetical cladogram presents its own problems in explaining character evolution. Dwarf males of Scalpellomopha are sac like, with much reduced plates, and are located in receptacles on the inner surface of the female or hermaphrodite scuta (Klepal, 1987; Buhl-Mortensen & Høeg, 2006, 2013; Spremberg *et al.*, 2012; Dreyer *et al.*, 2018a, b, c).

Superfamily Lepadoidea superfam. nov.

The monophyly of this taxon is supported by all molecular and morphological analyses. All members either sport five shell plates or display an even further reduced armament, with some species being completely naked (Figs 5, 7, 8, 9). A number of lepadoid species are minute in size, specialized to epibiosis on a variety of organisms (Fig. 5G, I, K), and some were, until now, contained in families with only one or two species. *Rhizolepas* Day, 1939 (two species) are poorly known parasites of polychaetes. They have highly reduced

cirri, a non-functional alimentary canal and have a branching root system inside the host that emanates from the peduncle. *Pagurolepas* Stubbings, 1940 (two species) is symbiotic with sea anemones that sit on gastropod shells inhabited by hermit crabs (Keeley & Newman, 1974). *Koleolepas* Stebbing, 1900 (three species) is epibiotic on sea anemones, whence they feed and may therefore be considered a true parasite (Yusa & Yamamoto, 1999; Hosie, 2014). *Malacolepas* Hiro, 1933 (one species) lives symbiotically with bivalves. *Microlepas* Hoek, 1907 and *Rugilepas* Grygier & Newman, 1991 are two similar genera, which live on the test of diadametid sea urchins, where they induce gall formation (Yamamori & Kato, 2020). Their nutrition was recently shown to be particulate organic matter and not, as previously believed, tissue from the host. Molecular evidence now enables us to abandon the Koleolepadidae and Microlepadidae because their species are nested within other genera in existing families (Yamamori & Kato, 2020). *Pagurolepas* and members of the Rhizolepadidae and Malacolepadidae have not been analysed molecularly, and morphology offers virtually no clue to their position other than being naked or near naked. We therefore provisionally let *Paguroplepas* remain within the Poecilasmatidae and retain the two monogeneric families as *incertae* within the Lepadoidea. The recently demonstrated sister relationship between *Anelasma* and *Capitulum* (Figs 6, 7) hints that such specialized forms might be situated almost anywhere within pedunculated thoracicans.

Family Lepadidae: This taxon comprises both five-plated species and naked or near-naked ones. *Dosima* Gray, 1825 and *Lepas* are five-plated forms that are highly specialized to a life floating at the surface of oceanic waters, and they form a well-supported group together with the naked or near-naked species of *Conchoderma* von Olfers, 1814, all of which are epibiotic (Fig. 5I). The taxonomy within the genus *Lepas* is not well understood, and there is a need for a molecularly based study of all the species.

Family Heteralepadidae: The members of this large family either lack any armament of shell plates completely or retain only traces of them (Fig. 5J). This is not a unique situation, because 'naked' forms are also found elsewhere in the thoracican phylogeny. Until this study, the Heteralepadidae comprised *Heteralepas* Pilsbry, 1907 (42 species), *Paralepas* Pilsbry, 1907 (30 species) and *Alepas* Rang, 1829 (five species), all of which are epibiotic forms on a variety of host animals. The analysis by Chan *et al.* (2009) shows a close relationship between *Paralepas* and *Heteralepas*, giving support to this family. In addition, Yamamori & Kato (2020) found that *Koleolepas* is, in fact, nested within *Paralepas* and therefore also belongs in the Heteralepadidae. We therefore abandon the former monogeneric Koleolepadidae, and our redefined Heteralepadidae now comprises *Paralepas*, *Heteralepas*, *Alepas* and *Koleolepas*, and we place it as sister to Lepadidae (Fig. 7). Some uncertainty concerns *Alepas*, which is epibiotic and likely to be parasitic on jellyfish (Yusa & Yamamoto, 1999), because no species have yet been analysed by molecular methods. Numerous taxonomic changes have previously taken place with the position of the multiple species of *Heteralepas* and *Paralepas*, probably because these naked forms offer few useful morphological characters. Although the monophyly of the Heteralepadidae is well supported, we might yet see some rearrangements as molecular evidence accumulates.

Family Poecilasmatidae: This family comprises both five-plated species and some with fewer plates or none at all. All species are epibiotic on a wide array of substrata, including the branchial chamber of crabs, such as in some *Octolasmis* species (Fig. 5K), and surfaces of decapods or sea snakes. The former Microlepadidae comprised two similar genera, *Rugilepas* (one species) and *Microlepas* (one species), both epibiotic on spines of diadematid sea urchins. Yamamori & Kato (2020) used molecular characters to place *Rugilepas* among species of *Octolasmis*. We therefore abandon the Microlepadidae and place both *Microlepas* and *Rugilepas* in the Poecilasmatidae. The family includes several genera, but species from only a few of these genera have been analysed molecularly. We therefore see no reason at present to uphold a subfamilial subdivision, especially given that the former Oxynaspinae contains only the genus *Oxynaspis* Darwin, 1852. Both mitochondrial and nuclear DNA sequences place Poecilamatidae as sister to Lepadidae (Pérez-Losada *et al.*, 2008; Kim *et al.*, 2019). At present, there is no molecular information on a special group of naked, stalked barnacles living in the inner shell surface of bivalves, *Arcalepas* Jones & Morton, 2009 and *Malacolepas*. We retain the family Malacolepadidae in the present study until further molecular phylogenetic studies can examine the phylogenetic position of this family.

SUPERFAMILY SCALPELLOIDEA SUPERFAM. NOV.

Our Scalpelloidea is a convenience to host only the Scalpellidae. All molecular analyses agree that the Scalpellidae (*s.s.*, i.e. excluding the Pollicipedidae and Lithotryidae) is a monophyletic entity, and this is supported by the detailed morphological cladistic analysis of Gale (2015b), which also included fossil forms.

Family Scalpellidae: With 250+ species, the Scalpellidae is the largest family within both

Thoracica and Cirripedia in general, and the taxon is well delimited by both molecular and morphological characters. In addition to the extant species diversity, the family also holds a wealth of extinct forms (Fig. 6). The number of shell plates is a maximum of 14, but secondary loss has occurred in *Scalpellopsis* Broch, 1921. The family is of particular interest for the study of the evolution of sexual systems (Yusa *et al.*, 2012; Lin *et al.*, 2015; Høeg *et al.*, 2016; Dreyer *et al.*, 2018a, b, c), and this calls for a detailed study of its intrinsic phylogeny-based taxonomy. The revision by Zevina (1981) included many changes, but in our opinion the diagnoses for generic and species-level taxa suffers from lack of detail. We recommend that future morphological analyses should use scanning electron microscopy of shell plates, which provide a host of details (Gale, 2015b). Until now, only a minority of the species have been subjected to analyses, but both molecular (Lin *et al.*, 2015) and morphological (Gale, 2015b) studies agree on the existence of two species clusters within the family. We recognize these as the subfamilies Scalpellinae and Amigdoscalpellinae. In the study by Lin *et al.* (2015) both clusters are monophyletic, but Gale (2015b) included species not analysed molecularly, and his Scalpellinae is a paraphyletic 'ladder'.

Sexual systems in Calanticomorpha and Scalpellomorpha: One interesting similarity between the Calanticidae and Scalpellidae is that all or almost all species have a sexual system in which dwarf males are associated with either a hermaphrodite (androdioecy) or a female (dioecy) partner (Klepal, 1987; Yusa *et al.*, 2012; Lin *et al.*, 2015; Dreyer *et al.*, 2018a). Dwarf males are also found in many species of Heteralepadidae and Poecilasmatidae within the Lepadoidea, where morphologically they are simply hermaphrodites arrested in development and might be able to mature into the latter condition (Yusa *et al.*, 2010, 2012). In contrast, males of the calanticids and scalpellids have a reduced morphology not seen in hermaphrodite or female development (Klepal, 1987; Dreyer *et al.*, 2018a). Dwarf males of calanticids are covered by shell plates, and in some species they retain cirri and seem to be able to feed (Klepal, 1987). The males of scalpellids are always much further specialized (Klepal, 1987; Buhl-Mortensen & Høeg, 2006, 2013; Spremberg *et al.*, 2012; Dreyer *et al.*, 2018a). They are either naked or have only four minute opercular plates and no cirri, whence they are non-feeding and persist only by the resources provided by the egg. Locations of dwarf males in calanticids range from outside of the capitulum to alongside the mantle cavity. In the Scalpellidae, the dwarf males are always small (Fig. 5L) and situated in shell-plate receptacle areas at or inside the edge of the mantle, and in many species the site is morphologically preformed as a pocket, the size of which controls the number of resident males (Dreyer *et al.*, 2018c) (Fig. 5L).

Aside from calanticids, scalpellids and lepadoids, sexual systems with dwarf males are omnipresent in the Acrothoracica (Fig. 3H), Rhizocephala (Fig. 4D) and Iblomorpha. This highlights the entire Cirripedia and especially the Scalpellomorpha for studying the evolution of reproductive systems and therefore the need to obtain an even more precise understanding of their relationship (Høeg, 1991, 1995b; Kelly & Sanford, 2010; Lin *et al.*, 2016; Yamaguchi *et al.*, 2012, 2013).

Superfamily Neolepadoidea superfam. nov.

One of the most consistent results from the molecular phylogenetic analyses of Thoracica is the grouping of several barnacles from hydrothermal vents and seeps deep within the Thoracicalcarea as sister to the Scalpellidae (Figs 7, 8). The genera in our Neolepadoidea were previously assigned to two different positions on thoracican phylogeny, also when using a more extensive character analysis (Glenner *et al.*, 1995). More recent morphological analysis by Gale *et al.* (2020) using character analysis supports the molecular phylogeny. Formerly, the Neolepadidae had subfamily status, in a different composition, within the Eolepadidae, but, as explained above, that taxonomy must be rejected. *Eolepas* is a six-plated phosphatothoracican with absolutely no close relationship to the eight-plated *Neolepas* and other neolepadids. The Eolepadidae *sensu* Gale *et al.* (2020) is an exclusively fossil (Triassic–early Cretaceous), phosphate-shelled taxon situated on the stem-line towards the Thoracicalcarea. Neolepadidae did not appear until the Eocene (Gale *et al.*, 2020).

Family Neolepadidae: This comprises the genera *Ashinkailepas* Yamaguchi, Newman & Hashimoto, 2004, *Leucolepas* Southward & Jones, 2003, *Neolepas*, *Stipilepas* Carriol, 2016 and *Vulcanolepas* Southward & Jones, 2003, all of which have a similar morphology, being pedunculated and armed with eight plates (six primary plates and paired upper latera).

Family Neoverrucidae: This comprises *Imbricaverruca* Newman, 2000 and *Neoverruca* Newman, 1989, which have an asymmetric plate arrangement paralleling that developed in Verrucomorpha (Gale, 2014b). Where studied (in *Neoverruca*), a distinct peduncle is present in the early juveniles, but it disappears during later growth (Newman, 1989).

In support of our taxonomy, the ontogenetic stages of neoverrucids and neolepadids are similar, underlining their close phylogenetic affinity within the Neolepadoidea (Gale, 2014b, 2019). The neoverrucid asymmetry involves only the upper latus, with this

plate being either small or absent on one side of the body. The remaining plates are symmetrically placed, or at best placed in a slightly asymmetrical manner, and the whole is surrounded by a whorl of imbricating plates. The asymmetry is therefore much less pronounced and fundamentally different from the one characterizing the Verrucidae (Verrucomorpha), where it involves a morphological and functional asymmetry of the scuta–terga, with latera being absent in the extant species. Until recently, the neoverrucids were claimed to be relatively plesiomorphic relatives to the Verrucidae within the previous concept of the Verrucomorpha (e.g. Buckeridge & Newman, 2006). All molecular analyses contradict this view (Pérez-Losada *et al.*, 2008; Rees *et al.*, 2014; Herrera *et al.*, 2015). Furthermore, the morphological cladistic study of Glenner *et al.* (1995) found no putative synapomorphies between the Neoverrucidae and the Verrucidae, whence they were unable to confirm any close relationship. Gale (2014b) has given a new account on verrucomorphan evolution that does not involve *Neoverruca* or any such morphological stage.

Family Neobrachylepadidae: The family formerly had subfamily status in the Brachylepadomorpha but is here elevated to family and transferred to the Neolepadoidea. It contains only the monotypic genus *Neobrachylepas* Newman & Yamaguchi, 1995, which resembles the extinct Brachylepadomorpha. *Neobrachylepas* is symmetrically shaped, with basal imbricating scales and without a peduncle, but it exhibits an opercular plate morphology similar to that of *Neoverruca*. In full agreement, the molecular analysis of Herrera *et al.* (2015) places *Neobrachylepas relica* Newman & Yamaguchi, 1995 as intercalated between a monophyletic Neoverrucidae and a monophyletic Neolepadidae. Its morphology and phylogenetic position both argue for a separate monotypic family.

Evolution of vent and seep barnacles: All living species of the Neolepadoidea inhabit vent or cold seep habitats, but originally their ancestors might have had a different mode of life. Carriol *et al.* (2016) recently described the extinct species *Stipilepas molerensis* Carriol, 2016, from the Danish Eocene Moler formation, which has a clear morphological affinity to the Neolepadoidea but was attached to tree logs, perhaps much like extant *Lepas*. At present, the most parsimonious interpretation is that some common adaptations enabled the ancestor of extant Neolepadoidea to invade the vent and seep habitats, which might have acted as a refuge that prevented extinction of the clade. The adaptations concern not only the adults but also the larvae, which must disperse over long distances in search of their rare and patchy habitats (Yorisue *et al.*, 2012). In the Thoracica, evolution into these specialized habitats happened convergently in only one other lineage, viz. in the balanomorphan species *Eochionelasmus* Yamaguchi, 1990, which is situated among the Chthamaloidea.

'Sessilian' thoracicans

The name Sessilia is used for the monophyletic taxon comprising the Verrucomorpha and the Balanomorpha. In most analyses, these two orders are sister groups with high support (Figs 7, 8). We recognize this relationship but decided to leave the Sessilia clade without a formal rank, because we can then conveniently have the Verrucomorpha and Balanomorpha as orders. The Sessilia name refers to the lack of a peduncle but is misleading because such loss also occurred convergently in the Neolepadoidea (Neoverrucidae). The verrucomorphans and balanomorphans are otherwise morphologically and biologically distinct. The Verrucomorpha has a strongly asymmetrical disposition of the wall plates and an opercular lid formed by a moveable scutum and tergum (Darwin, 1851; Gale, 2014b). The Balanomorpha, often called acorn barnacles, are perfectly symmetrical, with an operculum that evolved convergently with the verrucomorphans and a wall that includes so-called marginal plates unique to that lineage (Gale & Sørensen, 2014). The 'sessilian' forms lack a peduncle, both as adults and during ontogeny, and this can be seen as a synapomorphy that evolved in their brachylepadid ancestors, such as *Pycnolepas* Withers, 1914 (Gale, 2014b). The two extant lineages have independently lost the upper latus and imbricating peduncular plates.

Order Brachylepadomorpha Withers, 1923

This extinct order contains only the extinct Brachylepadidae, because we place the extant *Neobrachylepas* in the Neolepadoidea (see above). It is a paraphyletic taxon that was abundant and diverse in the Upper Cretaceous (Gale & Sørensen, 2014) and forms a stem group to both the Verrucomorpha and the Balanomorpha (Fig. 10). The Brachylepadomorpha includes basal sessile barnacles, which have lost the peduncle, but they do not show the full suite of derived character states of either the Balanomorpha (new wall plates, orifice and sheath) or the Verrucomorpha (box-like asymmetric shell made up of four plates, plus opercular lid). In all Brachylepadomorpha, the carina and rostrum are large and concavo-convex, and an upper latus is present between the tergum and scutum; whorls of imbricating plates surround the capitulum.

Order Verrucomorpha Pilsbry, 1916

The monophyly of Verrucomorpha is strongly supported by the presence of their characteristic asymmetry. Being mostly found in deeper and deep-sea habitats, only a handful of verrucid species from four genera have been analysed molecularly, but these studies suggest the monophyly of the family. In extant verrucomorphans, the number of shell plates is limited to carina, rostrum, terga and scuta, all of which are arranged asymmetrically. The wall plates consist of the carina and rostrum that meet and articulate on one side and one set of tergum and scutum that are fixed to the substratum. The remaining scutum–tergum form a moveable and asymmetrically oriented operculum. Basal fossil forms (Eoverrucidae) possessed additional imbricating peduncular plates surrounding the wall, and Gale (2014b) recently gave an account of how the Verrucomorpha evolved in the Cretaceous from pedunculate, multi-plated and symmetrical ancestors to the highly derived condition in extant forms. The distinct asymmetry of the Verrucomorpha was displayed by extinct relatives, such as *Faxelepas* Gale, 2014, and the late Cretaceous *Eoverruca* Withers, 1935 is considered the most basal member of the Verrucomorpha. The extant fauna includes both shallow-water and deep-sea forms. Gale (2014b) suggests that the asymmetry might have evolved as an adaptation to catch crawling benthic prey in nutrient-poor deep-sea habitats, but this is speculative because extant species, such as *Verruca stroemia* (O.F.Müller, 1776), use the cirri for normal suspension feeding. The Cretaceous and asymmetric *Proverruca* Withers, 1914 is not closely related to the Verrucomorpha as defined here, but is now seen as a separate, convergent evolution of asymmetry. Thus, asymmetry evolved at least three times in the Thoracica and in morphologically different ways, viz. in the Neoverrucidae, in the Verrucomorpha and in the *Proverruca* lineages (Gale, 2014b).

Order Balanomorpha Pilsbry, 1916

The Balanomorpha are morphologically distinct and appear to be monophyletic in almost all molecular analyses. The only exception is the unusual position of the pollicipedomorphan genera basal within balanomorphans in the analysis of Herrera *et al.* (2015) (Fig. 8). Morphology disagrees with this result, and we have discussed (see above) the uncertain position of pollicipedomorphans across the available molecular analyses (Fig. 8). All balanomorphan species share a common morphology, where a peduncle is lacking and the body is, in all species except the whale barnacle, *Xenobalanus* Steenstrup, 1852, encased by a wall of articulating shell plates and covered by a distinct operculum (lid) of paired scuta and terga (Newman & Ross, 1976). The operculum articulates with a so-called sheath on the inside of the wall plates and altogether this offers a watertight closure of the mantle cavity. This special morphology enables balanomorphans to inhabit the upper intertidal zone and thus endure long periods (up to weeks) of exposure to air. Undoubtedly, this was the main reason for the immense success of this taxon from the late Cretaceous and, in support of this, almost all members of the plesiomorphic Chthamaloidea inhabit the intertidal habitat, whereas deeper water and epizoic forms began to evolve only later in the phylogeny. Another biologically important innovation is the clear separation of the anterior two or three pairs of thoracic appendages into specialized mouth cirri. This seems to be accompanied by an ability to catch much smaller food items from the plankton in comparison to other cirripedes (Anderson, 1994). The loss of the flexible peduncle also necessitated that the soma is suspended flexibly in the mantle cavity in order that it can be turned to face the current when extended for feeding and can even reverse orientation rapidly with shifting waves (Trager *et al.*, 1994).

Plate evolution in the Balanomorpha: The number of plates in the wall was originally eight, but in most groups the number has been reduced to six or four by secondary losses or plate fusions. Much discussion has taken place concerning the homology of the plates between balanomorphans and pedunculated thoracicalcareans, such as the Pollicipedomorpha and Scalpellidae (e.g. Newman, 1996). Here, we focus on a novel interpretation based on detailed examination of extant and extinct forms, including extensive new fossil material (Gale & Sørensen, 2014). In the view of Gale & Sørensen (2014), the only balanomorphan plates with a homology in pedunculated forms are the scuta–terga, the rostrum and the carina, whereas all lateral plates known from pedunculated forms have been lost. The key to understanding balanomorphan plate evolution lies in the Brachylepadomorpha. Among these stem-line forms (see above), the peduncle was lost, but they had the capitulum still raised above the substratum on an inflexible body part encircled in numerous imbricating scales. The only lateral plates were the pair corresponding to the upper latera in scalpellids, and these had become small, integrated into the operculum, and were also subsequently lost altogether. In the crucial fossil, *Brachylepas* Woodward, 1901, this left a large gap between the rostrum and carina, filled only in part with small imbricating scales. During later evolution, this gap gradually became filled with entirely new wall plates that probably originated from the said scales and thus have no homology whatsoever among other pedunculated cirripedes. These barnacles first developed a pair of marginal plates, to be followed by two additional

pairs, the carino- and rostromarginals. This resulted in the wall of eight plates that is now held to be plesiomorphic for extant (crown) balanomorphans and is found among some extant chthamaloid forms, such as *Octomeris* Sowerby, 1825 (see Fig. 9). Some chthamaloid species also retain one or several rows of imbricating scales around the base of the wall plates, as in their brachylepadomorphan ancestors.

It is noteworthy that ontogeny of extant balanomorphans reflects the evolutionary addition of the novel median plates. The juvenile barnacle first lays down a wall of the rostrum, carina and two medians, to be followed only later by the other median plates (Broch, 1922; Glenner & Høeg, 1993). From the original eight-plated wall, later evolution among crown balanomorphans implicated either losses or fusions of plates to, for example, four walled forms (e.g. *Tetraclita* Schumacher, 1817) or fusion of all wall plates into a solid ring, such as seen in the Pyrgomatidae. All these later processes were lucidly analysed by Newman & Ross (1976), with the only necessary change being that the 'laterals' of former descriptions should now be called 'marginals' (Gale & Sørensen, 2014). The operculum also underwent gradual but significant changes in the brachylepadomorphan stem lineage, enabling it to act as a watertight lid, as explained above.

Taxonomy of the Balanomopha: The morphological characters offer a wealth of largely unharvested data for taxonomic purposes. The mineralization of the hard parts has begun to be studied by modern techniques only recently (but see Mitchell *et al.*, 2019). There are also numerous specializations of the hard parts. The base can be membranous or calcified. Both the base and the wall plates can be furnished with tubes, and these can be partly or wholly filled with cuticle. Additional hard part characters concern details of the sheath, which is a structure on the inside of the wall plates that supports the operculum. In the soft body, the Balanomorpha have both the first and the second pair of thoracic cirri specialized into mouth cirri (maxillipeds), as opposed to non-balanomorphan thoracicalcareans, in which only the first pair is specialized in this way. There are probably many additional soft body apomorphies for the Balanomorpha, such as at the ultrastructural level relating to the setation of the mouthparts (Høeg *et al.*, 1994) and the morphology of the cirri (Chan *et al.*, 2017b). Some of these hard and soft part characters have been used to characterize subsets of the Balanomorpha, but there has never been an analysis that studies these hard and soft body characters across the entire order. Such an analysis is needed to assess the extent to which these characters are phylogenetically conservative or subject to ad hoc adaptive evolution.

Until now, only a small number of balanomorphan species have been analysed molecularly, but the available studies nevertheless include good coverage of all presently recognized families, thus enabling a thorough revision. Newman & Ross (1976) gave the classic taxonomic account, and most major lineages recognized in their study are largely recovered by the molecular analyses as monophyletic groups (Pérez-Losada *et al.*, 2012b, 2014; Chan *et al.*, 2017a; Tsang *et al.*, 2017). We presently recognize four superfamilies, with the Chthamaloidea diverging first, then the Elminoidea (new superfamily) and, finally, the Coronuloidea and Balanoidea as sister groups (Fig. 4). These superfamilies and the families we recognize are all monophyletic according to the recent molecular analyses. We accept many of the previous families, but a few poly- or paraphyletic ones are subsumed in others, and there are also some movements of genera between taxa. We do not make any changes at the genus level, but it is clear from the published analyses that much revisionary work will need to be done to arrive at genera that are monophyletic. Therefore, the present affiliation to genus, not least within the Balanidae, should not be taken per se as signifying phylogenetic relationship.

Superfamily Chthamaloidea Darwin, 1854

This superfamily is generally agreed to display the most plesiomorphic morphology within balanomorphans, but nevertheless to form a monophyletic taxon (Pérez-Losada *et al.*, 2014; Chan *et al.*, 2017a). They have eight, six or four wall plates. The three other superfamilies have a maximum of four wall plates. In soft body anatomy, chthamaloids also have only two pairs of mouth cirri, whereas coronuloids and balanoids have three pairs, leaving only the posterior three cirri for the feeding basket (Southward, 2008). Epibiosis, a mode of life common in coronuloids and balanoids, is rarely found among the chthamaloids, where most species occupy an intertidal habitat on hard substrata (Fig. 5N). A spectacular exception is the hydrothermal vent-inhabiting *Eochionelasmus*. An interesting character in several chthamaloids is the presence of one or several whorls of scales, or 'imbricating plates' around the base of the wall plates, e.g. *Catomerus* Pilsbry, 1916, *Catophragmus* Sowerby, 1826, *Chionelasmus* Pilsbry, 1911, *Eochionelasmus* and *Waikalasma* Buckeridge, 1983 (Buckeridge & Newman, 1992; Ross & Newman, 2001; Chan *et al.*, 2020a). Such whorls were found in the extinct Brachylepadomorpha, and their presence is therefore considered to be plesiomorphic. Accordingly, it might have been expected that extant forms with such whorls would be clustered at the base of the balanomorphan tree, but their positions indicate that loss of whorls occurred independently several times (Pérez-Losada *et al.*, 2012b; Chan *et al.*, 2017a). We recognize five

families within the superfamily (Chthamalidae, Pachylasmatidae, Catophragmidae, Chionelasmatidae and Waikalasmatidae), all of which are monophyletic in our definition. The fossil form *Archaeochionelasmus* Kočí, Newman & Buckeridge, 2017 does not appear in our taxonomy, because it is not a cirripede but a fragment of a rudist bivalve (see Gale & Skelton, 2018).

Superfamily Elminoidea superfam. nov.

This superfamily contains only the Elminiidae, which is here elevated from subfamily to family level. The molecular analyses all agree in putting it as an independent branch, diverging between the Chthamaloidea and the large clade consisting of the Corunuloidea + Balanoidea (Fig. 7). Erection of a new superfamily is therefore warranted for consistency. The elminid species are all rocky intertidal forms.

Superfamily Coronuloidea Leach, 1817

The Cornuloidea comprises the monophyletic Tetraclitidae, Bathylasmatidae, Austrobalanidae, Chelonibiidae and Coronulidae from molecular evidence (Chan *et al.*, 2017a) (Fig. 7). Owing to the topology of the molecularly derived trees, we abandon the former Tetraclitoidea (Martin & Davis, 2001), because all six families form a single monophyletic clade, and the members of the former Platylepadidae are here subsumed into the Coronulidae (Hayashi *et al.*, 2013). Members of the Tetraclitidae and Austrobalanidae are found on hard substrata and mostly inhabit the rocky intertidal zone, whereas Bathylasmatidae are deep-sea inhabitants. Members of the Chelonibiidae and Coronulidae are all epibiotic on a wide array of invertebrates and vertebrates, including, for example, whales, sea cows, sea snakes, marine turtles and various crustaceans. Some species are even relaxed in their host preferences and can be found on crabs, turtles and horseshoe crabs (Ewers-Saucedo *et al.*, 2016). Species of the Chelonibiidae are little modified in their morphology compared with their intertidal relatives, whereas the Coronulidae show perhaps the most extensive morphological specialization among balanomorphans; for example, the whale barnacles *Tubicinella* Lamarck, 1802 and *Xenobalanus*, where the body is only little covered by shell plates and superficially resembles a pedunculated form (Seilacher, 2005; Dreyer *et al.*, 2020).

Superfamily Balanoidea Leach, 1817

Traditionally, this superfamily consists of three families, Balanidae, Archaeobalanidae and Pyrgomatidae. The major morphological difference between Balanidae and Archaeobalanidae is that Balanidae has tubiferous wall plates, whereas most of Archaeobalanidae have solid, non-tubiferous shells representing a plesiomorphic condition. Pyrgomatidae is composed of species living in corals and a few in sponges, and they have either four wall plates or the wall plates are fused into a solid ring. Molecular analyses suggest that the multiple species of the Balanoidea fall into two large clades, the Balanidae + Archaeobalanidae clade and the Pyrgomatidae clade. Given that the balanid and archaeobalanid species are mixed, we recognize only two families, the Balanidae and the Pyrgomatidae. At present, an increasing number of species within these two families are being subjected to molecular analysis, and it is already clear that serious taxonomic changes can be expected at all levels below the family.

Family Balanidae: This large family now combines the former Archaeobalanidae and Balanidae because molecular evidence has confirmed that neither of these was monophyletic in their former composition. It includes free-living species, sponge-associated species and fire coral-associated species. The last half-century has seen many taxonomic rearrangements, but from the emerging molecularly based analyses it seems clear that many additional rearrangements are needed to arrive at monophyletic units also down to genus level. Several of the balanid species are used as 'models' in many contexts, not least larval settlement and antifouling studies. This highlights the need to strive for a robust and phylogenetically based taxonomy in the future, because generalizations from models can depend crucially on phylogeny. *Wanella* Anderson, 1993, found on fire corals, does not group with the remaining coral barnacles in the Pyrgomatidae but is the sister to all remaining species of the Balanidae. This argues for recognizing *Wanella* as its own subfamily (Tsang *et al.*, 2014; Yu *et al.*, 2020). At present, we keep all the existing species in Archaeobalanidae and Balanidae under the Balanidae but extensive further molecular studies should be conducted to examine the phylogenetic relationships of these subfamilies. But note that at least the Acastinae is not monophyletic by molecular anlaysis (Yu *et al.*, 2020).

Family Pyrgomatidae: All members of this family are highly specialized to epibiosis in either corals or marine sponges (Anderson, 1992; Chan *et al.*, 2013, 2020b). Interestingly, it seems that evolution onto such hosts presents interesting patterns of homoplasy. Molecular phylogenetic studies (Simon-Blecher *et al.*, 2007; Malay & Michonneau, 2014; Tsang *et al.*, 2014) showed that Pyrgomatidae is composed of three monophyletic clades, accepted here as subfamilies. Recent phylogenetic analysis of sponge and coral barnacles (Yu *et al.*, 2020) showed that *Conopea* Say, 1822, which live on gorgonian corals, is situated in

the pyrgomatid clade, suggesting that *Conopea* should be considered a genus within the pyrgomatids. The molecular position of *Conopea* will therefore require further molecular analyses. Kolbasov *et al.* (2016) conducted a morphological revision of *Conopea*.

Subfamily Ceratoconchinae: The first clade houses *Ceratoconcha* Kramberger-Gorjanovic, 1889 in the subfamily Ceratoconchinae (Newman & Ross, 1976). Certatoconchinae contain two genera, the exclusively fossil genus *Eocertatoconcha* Newman & Ladd, 1974 (three species; Ross & Newman, 2000) and Ceratoconcha (27 species: 23 extinct species and four living species) (Ross & Newman, 2000). It is believed that Ceratoconchinae originated in Caribbean waters. At present, there are at least four living species of *Ceratoconcha*, all recorded in the west Atlantic, including Brazil, Belize, Trinidad, Dominican Republic–Haiti, Jamaica, Barbados, Texas, Florida and Bermuda.

Subfamily Megatrematinae: The second monophyletic clade is the Megatrematinae (Malay & Michonneau, 2014), sister group to the Ceratoconchinae. Megatrematines have almost world-wide distribution, being absent from the eastern Pacific, and have low diversity (seven living and six extinct species) (Ross & Pitombo, 2002).

Subfamily Pyrgomatinae: This is the third clade and the most species-rich subfamily of Pyrgomatidae (> 20 genera and > 80 species), being present in the Indo-West Pacific, including the Red Sea, but absent from the Atlantic and Mediterranean. Pyrgomatinae comprise three tribes. The Pyrgosellini contains *Pyrgopsella* Zullo, 1967, inhabiting corals, and *Pyrgospongia* Achituv & Simon-Blecher, 2006, inhabiting sponges. *Pyrgospongia* has been recorded from the Philippines, Andaman Islands and Hong Kong. The Hoekiini include coral-eating barnacles in the coral genus *Hydnophora* Fischer von Waldheim, 1807 only. This tribe is presently recorded from the Great Barrier Reef and Japan. The third tribe, Pyrgomatini, is composed of 20 genera and > 80 species and has great diversity in shell forms and opercular plate structures (Ross & Newman, 1995, 2000). Fossil records of Pyrgomatini are fragmented, being recorded only in *Nobia* Sowerby, 1839 and *Savignium* Leach, 1825 in the Miocene of Fiji and Pleistocene of the Marshall Islands (Ross & Newman, 2000). *Cantellius* Ross & Newman, 1973, *Darwiniella* Anderson, 1992 and *Galkinius* Perreault, 2014 are found in the Holocene terraces in Japan (Asami & Yamaguchi, 1997; Ross & Newman, 2000). Although Malay & Michonneau (2014) included these three tribes in the molecular phylogenetic analysis, the phylogenetic relationships for these three tribes appear not to be supported by molecular evidence but confirm that each genus in the Pyrgomatidae is monophyletic.

TIMELINE AND PATTERNS OF THORACICAN EVOLUTION

The generic diversity of the Thoracica since the latest Triassic is depicted in Figure 9. Late Triassic to Early Jurassic forms are exclusively phosphatic (Phosphatothoracica). The first Thoracicalcarea (calcite-shelled) forms appear in the Bathonian at ~170 Mya. The Zeugmatolepadidae underwent a minor radiation, peaking in the Tithonian (latest Jurassic). A major radiation in the Cretaceous was caused both by the diversification of Archaeolepadomorpha, Pollicipedomorpha and Calcanticomorpha and by the first appearance of extant families, including Scalpellidae and Verrucidae. The Balanomorpha appeared in the Cretaceous, but are represented by only a single extinct family, the Pachydiadematidae. Late Cretaceous and Cretaceous–Palaeogene boundary extinction (Stramentidae, Myolepadidae, Archaeolepadidae, Cretiscalpellidae and Titanolepadidae) resulted in low diversity through the Palaeocene, but there was a marked diversification of the balanomorphs in the Eocene, which also saw the first appearance of Lepadoidea and Neolepadoidea. Diversification continued through the Oligocene to the Pliocene, largely as a result of the appearance of new balanomorph genera. Living genera shown in Figure 9 include only forms with shell plates, for comparison with the fossil record. The 35+ extant genera from the deep sea are unlikely to be represented in the fossil record; therefore, the large present-day diversity is, in part, an artefact of this fact. However, the rapid increase in diversity through the Neogene indicates that the present-day diversity continues a long trend. As Charles Darwin said, we live in the 'Age of Barnacles'.

SUMMARY AND FUTURE RESEARCH

Our study has led to several fundamental changes in taxonomy of the barnacles (Thecostraca) owing to the evidence from molecular phylogenetic studies published over the last 20 years. These were significant in the Rhizocephala (Høeg *et al.*, 2020), and this is hardly surprising because there were few phylogenetic studies of this taxon. Our analysis also resulted in major changes within the Thoracica, but we could, in contrast, also demonstrate the validity of some existing phylogenetic hypotheses and confirm the monophyly of a substantial number of existing families and superfamilies. The interpretation of morphological

evolution within the thoracicans has recently been revised substantially (Gale, 2014a, b, 2015a, b, 2019, 2020a; Gale & Sørensen, 2014; Gale & Schweigert, 2015). It is satisfying that these new interpretations of morphology are, in most respects, in agreement with the molecularly based systematic arrangements. This opens the door for a 'total evidence' approach to barnacle phylogeny and is of particular importance owing to the wealth of fossil information available for this taxon. Many taxa still require further study before we can arrive at monophyletic units down to generic and species levels. Such studies are especially needed in species-rich but phylogenetically poorly understood groups, such as the Scalpellidae, Balanidae and Pyrgomatidae. Each of these families is species rich and biologically diverse and presents many problems of general biological interest, such as the evolution of reproductive systems (Scalpellidae), larval settlement studies (Balanidae) and adaptation to epibiotic life on a wide variety of organisms (Pyrgomatidae). A full evolutionarily based analysis of such problems can be undertaken only when many species have been analysed and their relationship is known in a phylogenetic context. Recent studies, such as those by Yusa *et al.* (2012), Lin *et al.* (2015) and Yu *et al.* (2020), effectively demonstrate the power of such analyses.

CLASSIFICATION

Class Thecostraca Gruvel, 1905

Diagnosis: Adapted from Høeg *et al.* (2009b). The taxon is monophyletic by molecular analyses, but see Petrunina, *et al.* (2014) on the possible inclusion of the Tantulocarida. No post-maxilular limb buds in nauplii; the larval development terminates with a cypridoid larva; the cypridoid with prehensile antennules is used in attachment; well-developed frontal filaments and compound eyes, whenever present, with three crystalline cones; the cypridoid larval carapace with five pairs of lattice organs.

Comment: Owing to the morphological diversity among the adults, the taxon can be diagnosed morphologically only by larval characters; those listed here are synapomorphic for the class; the adult stages are permanently sessile in the most of Ascothoracida and in all Cirripedia and are suspected to be so in Facetotecta.

Subclass Facetotecta Grygier, 1985

Diagnosis: Dorsal side of naupliar head shield and carapace of y-cyprid with reticulated external cuticular ridges, forming semi-symmetrical patterns of polygonal plates. Knob-shaped dorsocaudal organ on posterior part of naupliar hindbody. Carapace of y-cyprid univalved, partly covers larval body; antennules often with hook on segment 2; labrum unarmed or with 3-5 or more spines; six pairs of biramous swimming thoracopods; abdomen two- or four-segmented; elongated, plated telson with short, unsegmented furcal rami and multiple setae and pore-openings. Slug-like, unsegmented larval stage (ypsigon). Adults unknown.

Comment: Many additional potential species are becoming known as morphological 'types' (Fig. 1A–K) and are presently also being characterized by molecular methods. A future taxonomy will therefore need new genera and probably also new families (Grygier *et al.*, 2019).

Hansenocaris Îto, 1985 (12 species)

Subclass Ascothoracida Lacaze-Duthiers, 1880

Diagnosis: Bivalved crustaceans, with diverticula of midgut and gonads in carapace. Body generally with 11 free trunk segments, first six with biramous thoracopods, seventh with biramous or uniramous penis in both sexes (vestigial in females), last with moveable unsegmented furcal rami. Antennules four- to six-segmented, with claw guard and claw on terminal segment. Conical labrum surrounds piercing mouthparts. Parasites of echinoderms and anthozoans.

Comment: Grygier (1987a) provided a comprehensive review on the taxonomy of the Ascothoracida.

Order Dendrogastrida Grygier, 1987

Diagnosis: Soft-walled carapace partly fused and enlarged in females; females vary from plesiomorphic morphology to being extremely reduced; antennules with four or five segments, subchelate either present at some stage of development or reduced to vestigial; proximal sensory process of terminal antennular segment reduced to separate aesthetasc and seta. Mandibles and maxillules, if present, with reduced armament. Thoracopods leaf-like, biramous or uniramous, without distinct ramal segments, or absent. Meso- or endoparasites of echinoderms.

Family Ascothoracidae Grygier, 1987

Diagnosis: Parasites of ophiuroids living in cysts within genital bursae. Females with bivalved, swollen, usually rounded carapace, with dorsal brood chamber. Antennules five-segmented, fourth segment usually with bifid preaxial chin, fifth segment with moveable

or fixed claw or fused with claw completely. Long, setiform mandibles ending in brush of distal setules. Anterior thoracomeres with various dorsal processes or ridges. Six or five pairs of thoracopods; first thoracopod reduced in size, uniramous or absent. Abdomen five-segmented, furcal rami elongated. Cypridiform males accompanying females with oval, bivalved carapace; thorax without dorsal processes; antennules and mouthparts resembling those of females; six or five pairs of thoracopods, uniramous or with reduced endopods on pairs 2–5. Carapace with four pairs of lattice organs.

Comment: Kolbasov & Petrunina (2019) concluded that there are no diagnostic differences between the monotypic *Parascothorax* Wagin, 1964 and *Ascothorax* Djakonov, 1914 and proposed that *Parascothorox* is an invalid genus. *Parascothorax synagogoides* Wagin, 1964 was reassigned to *Ascothorax*.

Ascothorax Djakonov, 1914 (ten species)

Cardiosaccus Kolbasov & Petrunina, 2019 (one species)

Family Ctenosculidae Thiele, 1925

Diagnosis: Mesoparasites of sea stars, forming cysts. Ovoid or subspherical carapace, with short posteroventral or ventral aperture. Antennules minute or absent. Labrum with short frontal side; mandibles absent; maxillae bifid, non-hooked. Thorax big, elongated, with dorsal projections or long horns. Six pairs of large, leaf-like, simplified thoracopods, mostly biramous, sometimes uniramous. Abdomen four-segmented. Penis vestigial or absent. Adult males unknown.

Ctenosculum Heath, 1910 (one species)

Endaster Grygier, 1985 (one species)

Gongylophysema Grygier, 1987 (one species)

Family Dendrogastridae Gruvel, 1905

Diagnosis: Endoparasitic in sea stars or sea urchins. Carapace of females with large, soft-walled lobes or branches, often with bizzare extensions. Antennules four-segmented, subchelate. Mandibles and maxillules absent or morphologically reduced. Five pairs of short and uniramous thoracopods, absent in advanced forms. Abdomen to- to three-segmented or absent in advanced forms. Furcal rami present as unarmed lobes or entirely absent. Dwarf males found in advanced forms.

Bifurgaster Stone & Moyse, 1985 (three species)

Dendrogaster Knipovich, 1890 (35 species)

Ulophysema Brattström, 1936 (two species)

Order Laurida Grygier, 1987

Diagnosis: Adult morphology highly variable (see detailed diagnoses below); parasites of anthozoans.

Family Lauridae Gruvel, 1905

Diagnosis: Meso- or endoparasites of zoanthids. Univalved, enlarged, often coiled carapace in females; dwarf males bivalved. Antennules with reduced segmentation; claw rudimentary or absent in females. Oral cone developed. Cypridiform males with generalized antennules and oral cone. Four to six uniramous thoracopods with short, spine-like setae in females; six pairs in males, some biramous. Abdomen four-segmented. Penis uniramous in both sexes (i.e. penis vestigial in females); often long in males. Telson and furcal rami usually with spines and dense ctenoid scales. Furcal rami with up to four terminal setae.

Baccalaureus Broch, 1929 (12 species)

Laura Lacaze-Duthiers, 1865 (three species)

Polymarsypus Grygier, 1985 (one species)

Zoanthoecus Grygier, 1985 (two species)

Family Petrarcidae Gruvel, 1905

Diagnosis: Endoparasitic in scleratinian corals. Carapace with two thick valves covered by spines and/or papillae, without brood chamber. Antennules five-segmented, not subchelate, with developed armament on distal segment. Mandibles and maxillules rarely unarmed and with short, cutting edge; distal parts of maxillae reduced. Thoracopods uniramous, with few or no setae; first pair absent or reduced. Enlarged abdominal segment 1. Simultaneous hermaphrodites.

Introcornia Grygier, 1983 (two species)

Petrarca Fowler, 1889 (eight species)

Zibrowia Grygier, 1985 (one species)

Family Synagogidae Gruvel, 1905

Diagnosis: Ecto-, meso- or endoparasites of alcyonaceans, antipatharians and stalked crinoids. Carapace and main body have generalized morphology. Females with bivalved or dorsally fused carapace. Antennules six-segmented; terminal segment with claw and proximal sensory process. Lanceolate mandibles with one or more longitudinal setal rows and complex or simple teeth. Hypopharynx modified to long languette (absent in *Waginella* Grygier, 1983). Six pairs of setose, biramous thoracopods. Large epaulets on thoracomere 6 (absent in *Synagoga* Norman, 1888).

Cardomanica Lowry, 1985 (three species)

Flatsia Grygier, 1991 (one species)
Gorgonolaureus Utinomi, 1962 (seven species)
Isidascus Moyse, 1983 (one species)
Sessilogoga Grygier, 1990 (two species)
Synagoga Norman, 1888 (seven species)
Thalassomembracis Grygier, 1984 (seven species)
Waginella Grygier, 1983 (three species)

Subclass Cirripedia Burmeister, 1834

Diagnosis: Following Høeg *et al.* (2009b). Permanently sessile crustacean; nauplii fitted with frontolateral horns of complex morphology; settlement by means of adhesive cement; the cypris larvae are without an abdomen or the abdomen is reduced to a tiny rudiment; four-segmented antennules, with the first segment divided into two articulating sclerites (Lagersson & Høeg, 2002); multicellular cement gland with muscular sac and terminating on attachment surface of the third antennular segment; the second pair of lattice organs in the cypris carapace with large terminal pore located anteriorly (this character is shared with other ascothoracidans).

Comment: Owing to the reduced morphology in the parasitic Rhizocephala, the taxon can be diagnosed morphologically only by means of larval characters. All those mentioned are synapomorphic for the three cirripede infraclasses.

Infraclass Acrothoracica, Gruvel, 1905

Diagnosis: Monophyletic by molecular analyses. Minute, burrowing females found primarily in calcareous substrates (corals, molluscs, barnacle shells, bryozoans etc.), with soft carapace, accompanied by dwarf males. All female and male calcareous shell plates are a single pair of largely chitinous plates (opercular bars) guarding the aperture, three to five pairs of terminal cirri, gathering in the posterior elongated portion of the thorax, single pair of developed or reduced cirri located at the side of the mouth, caudal appendages present or absent, abdomen reduced in adults. Borings probably made by acrothoracicans are known as far back as the Lower Devonian, but do not provide morphological information; these are trace fossils and have no taxonomic validity.

Order Cryptophialida Kolbasov, Newman & Høeg, 2009

Diagnosis: Monophyletic group in molecular analyses. Females with bottle-like mantle; operculum with elongated neck; aperture small, crown-shaped opercular bars occupy the complete apertural length, lateral and reinforcing bars developed, long and thin; labrum elongated, tongue-like; mouth cirri rudimentary; thorax with one or two whip-like, long dorsal processes, sets of thoracic lappets with cuticular border; intestine with gizzard (gastric mill); caudal appendages absent. Dwarf males with elongated posterior end having circular cuticular ribs. Cypris larvae with rudimentary thorax and thoracopods. Boring aperture rounded.

Family Cryptophialidae Gerstaecker, 1866–1879

Diagnosis: As for the Order.
Australophialus Tomlinson, 1969 (five species)
Cryptophialus Darwin, 1854 (16 species)

Order Lithoglyptida Kolbasov, Newman & Høeg 2009

Diagnosis: Monophyletic in molecular analyses. Females with sac-like mantle; operculum without neck, with wide aperture, opercular bar less than aperture length; labrum big, saddle-like; mouth cirri developed; thorax without long dorsal processes, sets of thoracic lappets without cuticular border; gastric mill absent. Cypris larvae with developed thorax and thoracopods. Burrow aperture elongated, slit-like.

Family Lithoglyptidae Aurivillius, 1892

Diagnosis: Monophyletic in molecular analysis. Females with developed opercular bars and comb collar, operculum with rows of massive multifid scales, often associated with opercular pores and papillae; protopod of mouth cirri two-segmented, mouth appendages developed, terminal cirri multisegmented, biramous; caudal appendages present or absent; thoracic lappets developed; intestine with anus. Dwarf males without a pair of lobes at the base of attachment antennules; posterior end with apertural slit.

Subfamily Berndtiinae Utinomi, 1950

Berndtia Utinomi, 1950 (six species)
Weltneria Berndt, 1907 (12 species)

Subfamily Kochlorininae Gruvel, 1905

Kochlorine Noll, 1872 (seven species)
Kochlorinopsis Stubbings, 1967 (one species)

SUBFAMILY LITHOGLYPTINAE AURIVILLIUS, 1892

Auritoglyptes Kolbasov & Newman, 2005 (one species)
Balanodytes Utinomi, 1950 (11 species)
Lithoglyptes Aurivillius, 1892 (four species)

FAMILY TRYPETESIDAE STEBBING, 1910

Diagnosis: Monophyletic in molecular analyses. Females with thin, unclear opercular bars, comb collar reduced, operculum without rows of massive multifid scales; protopod of mouth cirri unsegmented, mouth appendages reduced in size; three pairs of uniramous terminal cirri; caudal appendages absent; thoracic lappets reduced; intestine without anus. Dwarf males with a pair of lobes at the base of attachment process; posterior end without apertural slit. Inhabit columella of gastropod shells occupied by hermit crabs.
Tomlinsonia Turquier, 1985 (two species)
Trypetsa Norman, 1903 (five species)

INFRACLASS RHIZOCEPHALA MÜLLER, 1862

Diagnosis: Here given in abbreviated form after Høeg *et al.* (2020). Monophyletic by molecular analyses. All parasitic stages without segmentation, appendages and alimentary canal. Specialized cypris antennules; parasites on Crustacea; with parasitic phase starting with an initial internal phase. The adult parasite consists of an internal ramifying and nutrient-absorbing root system and an external reproductive sac (externa). Separate sexes, with the female externa hosting and nourishing one or several dwarf males reduced to sperm-producing tissue and a few somatic cells.

Comment: Høeg *et al.* (2020) provided diagnoses of all the families; these can only exceptionally be characterized as monophyletic by morphology alone, but the molecular analyses support the monophyly of all almost presently recognized families.

FAMILY CHTHAMALOPHILIDAE BOCQUET-VEDRINE, 1961

Diagnosis: As provided by Høeg *et al.* (2020).

Host: Balanomorpha.
Bocquetia Pawlik, 1987 (one species)
Boschmaella Bocquet-Védrine, 1967 (two species)
Chthamalophilus Bocquet-Vedrine, 1957 (one species)

FAMILY CLISTOSACCIDAE BOSCHMA, 1929

Diagnosis: As provided by Høeg *et al.* (2020).

Host: Paguroidea and Caridea.
Clistosaccus Lilljeborg, 1861 (one species)
Sylon Kröyer, 1855 (one species)

FAMILY DUPLORBIDAE HØEG & RYBAKOV, 1992

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: Monophyly rests on morphology alone because no species has been sampled for molecular analyses. The family shares several potential apomorphies with the Chthamalophilidae.

Host: Isopoda (including Epicaridea) and Cumacea.
Arcturosaccus Rybakov & Høeg, 1992 (one species)
Cryptogaster Bocquet-Védrine & Bourdon, 1984 (one species)
Duplorbis Smith, 1907 (three species)

FAMILY MYCETOMORPHIDAE HØEG & RYBAKOV, 1992

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: Originally hosted in the now abandoned 'Akentrogonida'; molecular analyss now places *Mycetomorpha* within or as sister group to the Peltogastridae, and thus widely separated from the other akentrogonid-type rhizocephalans.

Host: Caridea.
Mycetomorpha Potts, 1912 (two species)

FAMILY PARTHENOPEIDAE RYBAKOV & HØEG, 2013

Diagnosis: As provided by Høeg *et al.* (2020).

Host: Calianassidae.
Parthenopea Kossmann, 1874 (three species)

FAMILY PELTOGASTRIDAE LILLJEBORG, 1861

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: The family includes most members of the former Lernaeodiscidae, except *Triangulus galatheae* (Norman & Scott, 1906), which is now in the Triangulidae.

Host: Anomura Galatheoidea and Paguroidea; Gebiidea; Caridea.
Briarosaccus Boschma, 1930 (four species)
Dipterosaccus van Kampen & Boschma, 1925 (two species)

Galatheascus Boschma, 1929 (two species)
Lernaeodiscus Müller, 1862 (eight species)
Ommatogaster Yoshida & Osawa, 2011 (one species)
Paratriangulus Høeg & Glenner, 2019 (one species)
Peltogaster Rathke, 1842 (16 species)
Pterogaster Van Baal, 1937 (two species)
Septodiscus Van Baal, 1937 (one species)
Septosaccus Duboscq, 1912 (four species)
Temnascus Boschma, 1951 (one species)
Tortugaster Reinhard, 1948 (three species)
Trachelosaccus Boschma, 1928 (one species)
Triangulopsis Guerin-Ganivèt, 1911 (one species)

Family Peltogasterellidae Høeg & Glenner, 2019

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: All species have multiple (colonial) externae attached to the same root system. The externae are lost after one reproductive event and then replaced by a new generation of externae.

Host: Paguroidea.
Angulosaccus Reinhard, 1944 (one species)
Boschmaia Reinhard, 1958 (one species)
Cyphosaccus Reinhard, 1958 (four species)
Peltogasterella Krüger, 1912 (four species)

Family Pirusaccidae Høeg & Glenner, 2019

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: Monophyly rests on morphology alone because no species has been sampled for molecular analyses. The structure hosting the males (spermatogenic islet) might be homologous with those in Duplorbidae and Chthamalophilidae.

Host: On the galatheoid species *Galacantha* (syn. *Munidopsis*) *rostrata* A. Milne Edwards, 1880.
Pirusaccus Lützen, 1985 (one species)

Family Polyascidae Høeg & Glenner, 2019

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: This family was recently separated from the Sacculinidae by molecular evidence. Future analyses might well see the transfer of additional species from the Sacculinidae to the Polyascidae.

Host: Brachyura and Gebiidea.
Parasacculina Høeg & Glenner, 2019 (five species)
Polyascus Glenner, Lützen & Takahashi, 2003 (three species)

Family Polysaccidae Lützen & Takahashi, 1996

Diagnosis: As provided by Høeg *et al.* (2020).

Host: Callianassoidea.
Polysaccus Høeg & Lützen, 1993 (two species)

Family Sacculinidae Lilljeborg 1861

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: This large family is in need of a generic- and species-level revision based on molecular data. Future transfer of species to the Polyascidae is likely.

Host: Brachyura and Callianassidae.
Drepanorchis Boschma, 1927 (five species)
Heterosaccus Smith, 1906 (15 species)
Loxothylacus Boschma, 1928 (28 species)
Ptychascus Boschma, 1933 (two species)
Sacculina Thompson, 1836 (125 species)
Sesarmaxenos Annandale, 1911 (two species)

Family Thompsoniidae Høeg & Rybakov, 1992

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: As for the Peltogasterellidae, these parasites have obligatory colonial externae that are lost and replaced after a single reproductive cycle.

Host: Brachyura, Anomura, Caridea and Stomatopoda.
Diplothylacus Høeg & Lützen, 1993 (four species)
Jensia Boyko & Williams, 2015 (two species)
Thompsonia Kossmann, 1872 (five species)
Thylacoplethus Coutière, 1902 (13 species)

Family Triangulidae Høeg & Glenner, 2019

Diagnosis: As provided by Høeg *et al.* (2020).

Comment: The family was placed with high confidence as sister to all remaining Rhizocephala.

Host: Anomura, Galatheoidea.
Triangulus Smith, 1906 (four species)

Infraclass Thoracica Darwin, 1854

Diagnosis: Monophyletic in all molecular analyses. Body consists of a capitulum raised on a flexible peduncle, or the peduncle secondarily lost; capitulum armed with at least paired scuta–terga; plates may be lost secondarily.

Comment: None of the morphological characters is necessarily an apomorphy compared with the remaining Cirripedia.

In the subsequent taxonomic ranking, taxa containing both fossils and extant species are indicated with †. Taxa with fossil species alone are indicated with ††.

Superorder Phosphatothoracica Gale, 2019

Diagnosis: Thoracicans with phosphatic shell plates; the number of shell plates formed is between four (paired scuta and terga) and six (rostrum and carina added). The primary mineralogy of living taxa was discussed by Reid *et al.* (2012), and the plates are composed of a hydrogen phosphate-like calcium phosphate biomineral.

Comment: The extant forms possess only four plates (paired scuta and terga).

Order Iblomorpha Buckeridge & Newman, 2006

Diagnosis: As the Ibliformes by Buckeridge & Newman (2006); with paired phosphatic scuta and terga; the scutum adductor muscle is positioned post-orally; a comb collar (Buckeridge & Newman, 2006) surrounds the edge of the mantle opening.

Comment: We change the name only to have thoracican order-level taxa with the same '-morpha' suffix. The morphological characters are likely to be plesiomorphic, but the two species are sister species and form a sister group to all other extant thoracicans based on molecular analyses.

Family Iblidae Leach, 1825

Diagnosis: As provided by Buckeridge & Newman (2006).

Comment: The characters characterizing the family cannot at present be verified as apomorphies.

Subfamily Iblinae Leach, 1825

Ibla Leach, 1825 (two species)

Subfamily Neoiblinae Buckeridge & Newman, 2006

Neoibla Buckeridge & Newman, 2006 (one species)

Family Idioiblidae Buckeridge & Newman, 2006

Diagnosis: As provided by Buckeridge & Newman (2006).

Comment: The characters characterizing the family cannot at present be verified as apomorphies.

Subfamily Idioiblinae Buckeridge & Newman (2006)

Idioibla Buckeridge & Newman, 2006 (two species)

Subfamily Chaetolepadinae Buckeridge & Newman (2006)

Chaetolepas Studer, 1889 (two species)
Chitinolepas Buckeridge & Newman, 2006 (one species)

††Order Eolepadomorpha ord. nov. (Carboniferous–Lower Cretaceous)

Diagnosis: Phosphatothoracica in which a carina is present.

††Family Eolepadidae Buckeridge, 1983 (Triassic–Lower Cretaceous)

Diagnosis: Eolepadomorpha that possess a rostrum.
Eolepas Withers, 1928 (seven species)
Toarcolepas Gale & Schweigert, 2015 (three species)

††Family Praelepadidae Chernyshev, 1930 (Carboniferous)

Diagnosis: Eolepadomorpha that lack a rostrum.
††*Illilepas* Schram, 1986 (one species)
††*Praelepas* Chernyshev, 1930 (one species)

†Superorder Thoracicalcarea Gale, 2015

Diagnosis: As described by Gale (2015a); extant taxa are monophyletic by molecular analyses. Thoracicans with five or more plates composed of calcite, or secondarily lost; living taxa with a pre-orally positioned adductor muscle and no comb collar around mantle aperture; first pair of thoracopods modified into mouth cirri (maxillipeds).

††Order Archaeolepadomorpha ord. nov. (Jurassic–Cretaceous)

Diagnosis: Robust forms, in which the peduncle is armoured with eight to ten columns of broad, strongly imbricating plates.

Comment: The phylogenetic position of calcareous forms with few lateral capitular plates and strongly armoured peduncles was discussed by Gale (2015a), who argued that these are basal to Thoracicalcarea.

††Family Archaeolepadidae Gale, 2019 (Jurassic–Cretaceous)

Diagnosis: Lateral plates absent; peduncle plesiomorphically with ten columns of plates.

††*Archaeolepas* von Zittel, 1884 (Upper Jurassic) (two species)

††*Loriolepas* Gale, 2015 (Jurassic–Lower Cretaceous) (four species)

††Family Myolepadidae Gale in Gale & Sørensen, 2015

Diagnosis: Capitulum robust, constructed of two scuta, two terga, carina, rostrum; no lateral plates; short internal spur at rostrobasal margin of scutum carries ridges and grooves for insertion of large rostroscutal muscle.

††*Myolepas* Gale in Gale & Sørensen, 2015 (Cretaceous) (eight species)

††*Bosquetlepas* Gale in Gale & Sørensen, 2015 (Cretaceous) (two species)

††Family Stramentidae Withers, 1920 (Cretaceous)

Diagnosis: Oval, laterally compressed forms that possess a carinolatus, an upper latus and a peduncle, which is covered by eight columns of strongly imbricating plates.

††Subfamily Loriculinae Gale, 2015

Blastolepas Drushchits & Zevina, 1969 (one species)
Loriculina Dames, 1885 (three species)
Metaloriculina Gale, 2015 (two species)

††Subfamily Stramentinae Withers, 1920

Angulatergum Hauschke, 1994 (three species)
Leweslepas Gale, 2015 (five species)
Parastramentum Gale, 2015 (four species)
Stramentum Logan, 1897 (seven species)

†Order Pollicipomorpha ord. nov. (Jurassic–Recent)

Diagnosis: Capitulum includes a large number (20–40+) of imbricating, secondary lateral plates, which decrease in size towards the basal margin.

Comment: This group was abundant and widespread in the Upper Jurassic and Cretaceous (Zeugmatolepadidae; see Gale, 2014a, 2020a). Extant Pollicipedidae (*Capitulum* and *Pollicipes*) extend back into the Cretaceous and, with Lithotryidae, form a group that always cluster closely together in the molecular analyses.

†Family Pollicipedidae Leach, 1817 (Cretaceous–Recent)

Diagnosis: Small accessory lateral plates present on basal lateral surfaces of capitulum.

Comment: The family is possibly paraphyletic but convenient for housing the genera contained here. The selachian parasite *Anelasma* is by molecular analyses sister taxon to *Capitulum mitella* (Linnaeus, 1758) and placed here, but has secondarily lost all shell plates; the Anelasmatidae Darwin, 1852 is therefore abandoned.

Anelasma Darwin, 1852 (one species)

†*Capitulum* Gray, 1825 (two species) (Cretaceous–Recent)

†*Pollicipes* Leach, 1817 (four species) (Cretaceous–Recent)

Family Lithotryidae Gruvel, 1905

Diagnosis: Eight capitular plates comprising paired scuta–terga, carina, rostrum and paired carinolatera; peduncular scales small.

Comment: The peduncular scales are used to scrape the calcareous substrata and form a boring.

Lithotrya Gruvel, 1905 (four species)

††Family Zeugmatolepadidae Newman, 1996 (Jurassic–Eocene)

Diagnosis: Capitulum plesiomorphically with numerous imbricating lateral plates, which form a wall around the basal margin.

††Subfamily Martillepadinae Gale, 2014

††*Concinnalaepas* Gale, 2014 (Jurassic) (two species)

††*Etcheslepas* Gale, 2014 (Jurassic–Lower Cretaceous) (three species)

††*Icenilepas* Gale, 2014 (Cretaceous) (one species)

††*Litholepas* Nagler, Haug, Glenner & Buckeridge, 2017 (Jurassic) (one species)

††*Martillepas* Gale, 2014 (Jurassic–Cretaceous) (two species)
††*Subsecolepas* Gale, 2020 (Cretaceous) (one species)

††Subfamily Zeugmatolepadinae Newman, 1996

††*Aporolepas* Withers, 1953 (Eocene–Oligocene) (five species)
††*Tetrinus* Hirt, 1992 (Cretaceous) (one species)
††*Zeugmatolepas* Withers, 1913 (Cretaceous) (two species)
††*Texaslepas* Gale, 2020

†Order Calanticomorpha ord. nov.

Diagnosis: Capitulum with three to five pairs of larger lateral plates; subrostrum and subcarina usually present; smaller laterals variably developed, often absent.

Comment: Calanticomorpha are a paraphyletic assemblage of pedunculate forms, which are sister taxa to the Cretaceous–Recent Scalpellidae; only the Calanticidae survive to the present and represent a morphologically diverse group, which is shown to be monophyletic from molecular analyses (Lin *et al.*, 2015).

††Family Cretiscalpellidae Buckeridge, 1983 (Cretaceous)

Diagnosis: Eighteen plates in capitulum (paired scuta, terga, upper latera, rostrolatera, inframedian latera; carinolatera (two pairs), one subcarina.

Comment: Cretiscalpellidae form a sister group to the Scalpellidae, which evolved from them by loss of the subcarina and lower pair of carinolatera (Gale *et al.*, 2019).
††*Cretiscalpellum* Withers, 1922 (nine species)
††*Jagtscalpellum* Gale, 2020 (five species)
††*Striascalpellum* Gale, 2020 (four species)
††*Witherscalpellum* Gale, 2020 (two species)

††Family Titanolepadidae Gale in Gale & Sørensen, 2015 (Cretaceous)

Diagnosis: Twelve plated capitulum (paired scuta, terga, rostrolatera, inframedian latera, carina, subcarina, rostrum and subrostrum). Tergum and scutum possessing interlocking apical processes; scutal umbo subapical to central, all other umbones apical.

††*Ivoelepas* Gale in Gale & Sørensen, 2015 (six species)
††*Levelepas* Gale in Gale & Sørensen, 2015 (one species)
††*Titanolepas* Withers, 1913 (three species)

†Family Calanticidae Zevina, 1978 (Cretaceous–Recent)

Diagnosis: Number of plates highly variable (Jones & Hosie, 2009); usually with three pairs of larger laterals (rostrolatus, upper latus and carinolatus), often with subrostrum and subcarina; inframedian latus probably absent.

Comment: Monophyletic in molecular analyses.
†*Aurivillialepas* Newman, 1980 (Miocene-Recent) (five species)
†*Calantica* Gray, 1825 (Cretaceous–Recent) (17 species)
Crosnieriella Jones, 1998 (one species)
†*Euscalpellum* Hoek, 1907 (Eocene–Recent) (seven species)
†*Gruvelialepas* Newman, 1980 (Pleistocene–Recent) (three species)
Newmanilepas Zevina & Yakhontova, 1987 (one species)
††*Pachyscalpellum* Buckeridge, 1991 (Cretaceous) (three species)
Paracalantica Utinomi, 1958 (one species)
Pisiscalpellum Utinomi, 1958 (one species)
†*Scillaelepas* Seguenza, 1872 (Miocene-Recent) (six species)
†*Smilium* Gray, 1825 (15 species)
Zeascalpellum Buckeridge, 1983 (Eocene) (one species)

†Order Scalpellomorpha Buckeridge & Newman, 2006

Diagnosis: Monophyletic by molecular analyses (except in the study by Herrera *et al.*, 2015). Plesiomorphically, 14 plates present (carina, rostrum, paired scuta, terga, upper latera, carinolatera, inframedian latera and rostrolatera); plates reduced in some taxa, lost in many Lepadoidea.

†Superfamily Lepadoidea superfam. nov.

Diagnosis: Monophyletic by molecular analyses. Plesiomorphically, five plates present (paired scuta, terga and carina); base of carina highly modified for

articulation with scuta. Monophyletic by molecular analyses, including diverse forms that have no plates.

†Family Lepadidae Darwin, 1852, amended

Diagnosis: Monophyletic by molecular analyses. The morphological characterization is as for the superfamily. The subfamily Lepadinae Darwin, 1852 is hereby redefined and elevated to family status.

Comment: Species of *Conchoderma* von Olfers, 1814 are completely naked or near-naked forms and form a clade with a sister relationship to species of *Lepas* and *Dosima*. The monotypic *Dosima* is nested within species of *Lepas*. The plate arrangement of *Hyalolepas* Annandale, 1906 is basically the same as in *Lepas*, with the only difference being the extension of a long fork at the base of the carina, which reaches the basal margin of the scutum. At present, no molecular information is available for *Hyalolepas*; we tentatively allocated it inside Lepadidae owing to its high morphological affinity with *Lepas*.

Conchoderma von Olfers, 1814 (four species)
Dosima Gray, 1825 (two species)
Hyalolepas Annandale, 1906 (two species)
†*Lepas* Linnaeus, 1758 (Eocene–Recent) (17 species)
††*Pristinolepas* Buckeridge, 1983 (Upper Oligocene to Middle Miocene) (four species)

Family Heteralepadidae Nilsson-Cantell, 1921 amended

Diagnosis: Monophyletic by molecular analyses. Capitular plates much reduced and often with large part of uncalcified capitulum exposed.

Comment: All contained species are devoid of shell plates, or (*Koleolepas*) only cuticular rudiments (Hosie, 2014), but such reduction also evolved convergently within some species of the Poecilasmatidae. Based on DNA data provided by Yamamori & Kato (2020), we include the *Koleolepas* from the now abandoned Koleolepadidae Hiro, 1933.

Alepas Rang, 1829 (five species)
Heteralepas Pilsbry, 1907 (25 species)
Koleolepas Stebbing, 1900 (three species)
Paralepas Pilsbry, 1907 (29 species)

†Family Poecilasmatidae Annandale, 1909

Diagnosis: Monophyletic by molecular analyses; five shell plates, but often reduced in size or partly or completely lost. Epibiotic species.

Comment: The family cannot be diagnosed at present by morphological apomorphies. The family includes members of the abandoned Oxynaspitidae Gruvel, 1905 because its members are nested among the Poecilasmatidae. Yamamori & Kato (2020) showed that the former Microlepadidae Hoek, 1907 is nested within species of *Octolasmis*; therefore, this family is abandoned. The monophyly and relationships of most genera remain unanalysed.

††*Archoxynaspis* Van Syoc & Dekelboum, 2011 (one species)
Dianajonesia Koçak & Kemal, 2008 (nine species)
Dichelaspis Darwin, 1852 (five species)
†*Glyptelasma* Pilsbry, 1907 (11 species)
Megalasma Hoek, 1883 (five species)
Microlepas Hoek, 1907 (two species)
Minyaspis Van Syoc & Dekelboum, 2011 (15 species)
Octolasmis Gray, 1825 (30 species)
Oxynaspis Darwin, 1852 (13 species)
Pagurolepas Stubbings, 1940 (two species)
Poecilasma Darwin, 1852 (eight species)
Rugilepas Grygier & Newman, 1991 (one species)
Scleraspis Van Syoc & Dekelboum, 2012 (one species)
Trilasmis Hinds, 1844 (one species)

Family Rhizolepadidae Zevina, 1980

Diagnosis: Parasitic on polychaetes; without shell plates; cirri reduced and non-functional; a gut exists but is non-functional; the peduncle extends as a ramified, nutrient-absorbing root system into the host.

Rhizolepas Day, 1939 (two species)

Family Malacolepadidae Hiro, 1937

Diagnosis: Parasitic inside bivalves; without shell plates; orifice large; first and second cirri short, and mandibles with six or seven teeth.

Comment: Arcalepas and *Malacolepas* are found attached to the inside of the shells of the bivalves *Arca navicularis* Bruguière, 1789 and *Cucullaea labiata*, (Lightfoot, 1786) respectively.

Arcalepas Jones & Morton, 2009 (one species)
Malacolepas Hiro, 1933 (one species)

†Superfamily Scalpelloidea superfam. nov.

Diagnosis: As for the family Scalpellidae.

†Family Scalpellidae Pilsbry, 1907 amended

Diagnosis: Monophyletic by molecular analyses. Fourteen capitular plates, but some have been

secondarily lost in some species. All species have dwarf males, which are attached in special confined receptacle areas along the edge of the mantle opening.

Comment: By the molecular study of Lin *et al.* (2015) and the morphologically based one by Gale (2015b), the species analysed fall into two clusters, which Gale (2015a) erected as the subfamilies Scalpellinae and Amigdoscalpellinae. The remaining extant subfamilies are at best without any clear phylogenetic support.

†Subfamily Amigdoscalpellinae Gale, 2015 (Cretaceous–Recent)

†*Amigdosalpellum* Zevina, 1978 (22 species)
†*Catherinum* Zevina, 1978 (47 species)
Weltnerium Zevina, 1978 (21 species)

Subfamily Brochiinae Zevina, 1978b

Australscalpellum Newman & Ross, 1971 (one species)
Brochia Newman & Ross, 1971 (one species)

Subfamily Meroscalpellinae Zevina, 1978b

Abathescalpellum Newman & Ross, 1971 (two species)
Alcockianum Zevina, 1978b (two species)
Annandaleum Newman & Ross, 1971 (six species)
Gymnoscalpellum Newman & Ross, 1971 (seven species)
Hamatoscalpellum Zevina, 1978 (five species)
Litoscalpellum Newman & Ross, 1971 (24 species)
Meroscalpellum Zevina, 1978 (five species)
Neoscalpellum Pilsbry, 1907 (seven species)

†Subfamily Scalpellinae Pilsbry, 1907 (Cretaceous–Recent)

Comment: Until now, the species analysed molecularly form a monophyletic taxon, but in Gale's (2015b) definition these species form a paraphyletic ladder towards the Amigdoscalpellinae.

†*Arcoscalpellum* Hoek, 1907 (45 species)
††*Arcuatoscalpellum* Gale, 2015 (three species)
†*Diotascalpellum* Gale, 2015 (seven species)
†*Graviscalpellum* Foster, 1980 (four species)
††*Jaegerscalpellum* Gale, 2019 (one species)
†*Regioscalpellum* Gale, 2015 (seven species)
†*Scalpellum* Leach, 1818 (24 species)
Zevinaella Shalaeva & Newman, 2015 (two species)

Subfamily Scalpellopsinae Zevina, 1978a

Scalpellopsis Broch, 1921 (one species)

††Subfamily Virgiscalpellinae Gale, 2020 (Cretaceous)

††*Collinslepas* Gale, 2020 (five species)
††*Virgilepas* Gale, 2020 (three species)
††*Virgiscalpellum* Withers, 1935 (17 species)

Subfamily *incertae sedis*

Anguloscalpellum Zevina, 1978b (five species)
Barbascalpellum Zevina, 1978a (three species)
Compressoscalpellum Zevina, 1978a (four species)
Diceroscalpellum Zevina, 1978b (five species)
Mesoscalpellum Hoek, 1907 (one species)
Pilsbryiscalpellum Zevina, 1978b (four species)
Planoscalpellum Zevina, 1978b (four species)
Pteroscalpellum Zevina, 1978b (two species)
Sinoscalpellum Ren & Sha, 2014 (one species)
Teloscalpellum Zevina, 1978b (20 species)
Trianguloscalpellum Zevina, 1978b (21 species)
Vertebroscalpellum Newman & Ross, 1998 (five species)

††Family Proverrucidae Newman, 1989

Diagnosis: As amended by Gale (2014b).

Comment: The asymmetry in this family evolved convergently with that seen in the Verrucomorpha and the Neoverrucidae.

††*Proverruca* Withers, 1914 (Upper Cretaceous) (five species)

†Superfamily Neolepadoidea superfam. nov.

Diagnosis: Eight-plated capitulum comprising paired scuta, terga, upper latera, rostrum and carina. Asymmetry commonly involves loss of the upper latus on one side of the capitulum.

Comments: The group forms a well-defined clade based upon molecular analysis. All living species inhabit hydrothermal vent or seep habitats. There is remarkable morphological convergence of some taxa with Brachylepadomorpha (Gale *et al.*, 2020), and the neolepadomorphs were probably derived from a form close to *Pycnolepas*. Gale (2019) included the Balanomorpha, Brachylepadomorpha, Neolepadomorpha and Verrucomorpha in the clade Unilatera, characterized by possession of only two latera (upper latus pair).

†Family Neolepadidae Yamaguchi, Newman & Hashimoto, 2004 (amended)

Diagnosis: Eight-plated capitulum comprising two scuta, two terga, two upper latera, a carina and a

rostrum. The large rostrum articulates with the rostral margin of the scutum, and the carina with the lower carinal margin of the tergum.

Comment: The number of shell plates has evolved secondarily from forms with additional lateral plates. In the amended diagnosis, the family does not include *Neoverruca* and *Imbricaverruca*. Note that we do not here consider ††*Litholepas klausreschi* Nagler, Haug, Glenner & Buckeridge, 2017 as a member of this family.

†*Ashinkailepas* Yamaguchi, Newman & Hashimoto, 2004 (Pleistocene–Recent) (three species)

Leucolepas Southward & Jones, 2003 (one species)

Neolepas Newman, 1979 (three species)

††*Stipilepas* Carriol, 2016 (Eocene) (one species)

Vulcanolepas Southward & Jones, 2003 (five species)

Family Neoverrucidae, Newman, 1989 in Hessler & Newman, 1989

Diagnosis: Asymmetrical Neolepadoidea, in which the upper latus is present, or enlarged, on one side of the capitulum.

Comment: The asymmetry evolved separately from that in Verrucomorpha (Gale, 2014b).

Imbricaverruca Newman, 2000 (one species)

Neoverruca Newman in Hessler & Newman, 1989 (two species)

Family Neobrachylepadidae Newman & Yamaguchi, 1995, amended

Diagnosis: Symmetrical shell, carina and rostrum large, surrounded by imbricating plates. The family superficially resembles Brachylepadidae, but the scuta and terga are similar to those of *Neoverruca*.

Comment: The taxon falls within the Neolepadoidea from molecular analyses (Herrera *et al.*, 2015) and is here raised from subfamily to family level.

Neobrachylepas Newman & Yamaguchi, 1995 (one species)

††Order Brachylepadomorpha Withers, 1923

Diagnosis: Symmetrical, pedunculated and sessile forms, in which the large carina and rostrum are surrounded by alternating rows of imbricating plates.

Comment: The order is paraphyletic and includes species that form a stem group to both the Verrucomorpha and the Balanomorpha.

††Family Brachylepadidae Woodward, 1901 (Cretaceous–Miocene)

Diagnosis: As for Order.

††*Brachylepas* Woodward, 1901 (Upper Cretaceous) (six species)

††*Epibrachylepas* Gale in Gale & Sørensen, 2014 (Upper Cretaceous) (one species)

††*Fallaxlepas* Gale in Gale & Sørensen, 2020 (Palaeocene) (two species)

††*Faxelepas* Gale, 2014 (Palaeocene) (one species)

††*Parabrachylepas* Gale in Gale & Sørensen, 2014 (Upper Cretaceous) (one species)

††*Pedupycnolepas* Gale, 2014 (Lower Cretaceous) (three species)

††*Pycnolepas* Withers, 1914 (lower Cretaceous-Pleistocene) (six species)

†Order Verrucomorpha Pilsbry, 1916

Diagnosis: Body asymmetric; capitulum wall made up of carina, rostrum, fixed scutum and fixed tergum; moveable scutum and tergum form opercular lid.

††Eoverrucidae Gale, 2020 (Cretaceous, Albian–Campanian)

Diagnosis: Basal verrucomorphs, in which the rostrum and carina do not articulate; imbricating plates surround the shell wall, fused with calcified basis (Gale, 2014b, 2020b).

††*Eoverruca* Withers, 1935 (Albian to Campanian) (three species)

†Family Verrucidae Darwin, 1854

Diagnosis: Verrucomorpha, in which the rostrum and carina articulate; monophyletic in molecular analyses.

Comment: The asymmetry evolved separately both from that found in the Neoverrucidae and in the extinct *Proverruca*. Gale (2014b) traced the origin back to the Cretaceous *Eoverruca*.

†*Altiverruca* Pilsbry, 1916 (Pliocene–Recent) (26 species)

Brochiverruca Zevina, 1993 (three species)

Cameraverruca Pilsbry, 1916 (two species)

†*Costatoverruca* Young, 1998 (Pliocene–Recent) (seven species)

†*Cristallinaverruca* Young, 2002 (Pliocene–Recent) (one species)

†*Gibbosaverruca* Young, 2002 (Pliocene–Recent) (five species)

Globuloverruca Young, 2004 (one species)
†*Metaverruca* Pilsbry, 1916 (Pliocene–Recent) (17 species)
†*Newmaniverruca* Young, 1998 (Pliocene–Recent) (four species)
††*Priscoverruca* Gale, 2014 [Cretaceous–Palaeocene (Campanian–Danian)] (four species)
†*Rostratoverruca* Broch, 1922 (Pliocene–Recent) (four species)
Spongoverruca Zevina, 1987 (one species)
†*Verruca* Schumacher, 1817 [Cretaceous (Maastrichtian–Recent)] (two species)
††*Youngiverruca* Gale, 2014 [Cretaceous (Maastrichtian)] (one species)

†Order Balanomorpha Pilsbry, 1916

Diagnosis: Monophyletic in molecular analyses. A peduncle is absent at all stages of development; shell wall made up of four to eight plates, plesiomorphically comprising rostrum, carina, rostromarginals, marginals and carinomarginals. The body is covered by an operculum formed by the paired scuta–terga; the operculum articulates with the wall plates and forms a watertight cover over the mantle cavity. The structure of the wall plates and articulation with the basis is often complex in more derived balanomorphs; the apicobasal (longitudinal) septa are composed of a frond-like array of calcite crystals in cross-section, called an interlaminate figure.

Comment: In some forms, the wall is surrounded by one or more whorls of small-sized imbricating scales, as also seen in the Brachylepadomorpha.

††Superfamily Pachydiadematoidea superfam. nov.

Diagnosis: Large, oval cirripedes, in which the wall is constructed of eight plates surrounded by imbricating whorls of solid smaller plates. All external surfaces of adult lateral plates, and the terga, display flat apical surfaces, where the young stages of the plates have spalled off. The operculum is of low profile, and a small upper latus is present between the scutum and tergum.

††Family Pachydiadematidae fam. nov.

*Zoobank registration: lsid:*urn:lsid:zoobank.org:act:A16DF979-F1B2-4678-87F3-D3753B05F90B
††*Pachydiadema* Withers, 1935 (Type genus) (Cretaceous) (one species)

†Superfamily Chthamaloidea Darwin, 1854

Diagnosis: Monophyletic by molecular analyses; shell plates composed of rostrum, carina and one to three pairs of marginals (eight or six or four wall plates); the wall can be surrounded by one or more whorls of imbricating plates; wall plates and radii solid, internal surface of wall plates lacks uniform ribs; basis often membranous, when calcareous, solid but not forming complex interdigitations with walls; two pairs of mouth cirri; penis without basidorsal point; caudal appendages multi-articulate when present.

Comment: The morphology of this superfamily is the most plesiomorphic within the Balanomorpha. The five families are all monophyletic by molecular analyses in the study by Chan *et al.* (2017a).

†Family Chthamalidae Darwin, 1854

Diagnosis: Wall composed of eight, six or four plates, without any whorls of supplementary plates; mandible tridentoid or quadridentoid.

Comment: Pérez-Losada *et al.* (2012b) conducted a multigene molecular phylogeny in Chthamaloidea and showed that the subfamilies Chthamalinae, Euraphinae and Notochthamalinae are not monophyletic groups. We did not retain these subfamilies and assign all these genera under Chthamalidae. Neither the number of plates nor the number of mandibular, cuticular 'teeth' reflects any phylogenetic pattern in Chthamalidae, as reflected in previous subfamily assignments.
Caudoeuraphia Poltarukha, 1997 (one species)
†*Chamaesipho* Darwin, 1854 (three species)
Chinochthamalus Foster, 1980 (one species)
Chthamalus Ranzani, 1817 (27 species)
Euraphia Conrad, 1837 (three species)
Hexechamaesipho Poltarukha, 1996 (one species)
Jehlius Ross, 1971 (one species)
Microeuraphia Poltarukha, 1997 (seven species)
Nesochthamalus Foster & Newman, 1987 (one species)
†*Notochthamalus* Foster & Newman, 1987 (Eocene–Recent) (one species)
Octomeris Sowerby, 1825 (three species)
Pseudoeuraphia Poltarukha, 2000 (one species)
Rehderella Foster & Newman, 1987 (one species)
Tetrachthamalus Newman, 1967 (two species)

†Family Pachylasmatidae Utinomi, 1968

Diagnosis: Shell wall comprises eight distinct compartmental plates, including rostrum, paired rostromarginals, marginals and carinomarginals, and carina. Shell with or without imbricating plates. Rostrum compound with rostromargin but not

entering sheath, parietes solid and radii absent. Base membranous or solid calcareous, not interdigitated with shell wall.

†Subfamily Eolasmatinae Jones, 2000

††*Eolasma* Buckeridge, 1983 (Palaeocene–Eocene) (two species)

†*Neoeolasma* Gale, 2020 (Pliocene–Recent) (one species)

Subfamily Metalasmatinae Jones, 2000

Metalasma Jones, 2000 (one species)

†Subfamily Pachylasmatinae Utinomi, 1968

Atetralasma Newman & Jones, 2011 (one species)

Eurylasma Jones, 2000 (three species)

Eutomolasma Jones, 2000 (four species)

Microlasma Jones, 2000 (four species)

†*Pachylasma* Darwin, 1854 (Miocene–Recent) (eight species)

Pseudoctomeris Poltarukha, 1996 (one species)

Tetrapachylasma Foster, 1988 (five species)

†Family Waikalasmatidae Ross & Newman, 2001

Diagnosis: Shell symmetrical, with eight solid, weakly articulated plates; single pieces of wide carina and narrow rostrum, paired rostromarginals, marginals and carinomarginals; alae well developed, radii absent; shell with two or more whorls of imbricating plates; basis membranous; caudal appendages absent.

Waikalasma Buckeridge, 1983 (Miocene–Recent) (three species)

Family Catophragmidae Utinomi, 1968

Diagnosis: Shell consisting of eight solid plates fully integrated into sheath (rostrum, rostromarginals, marginals and carinomarginals, and carina); wall encircled by a few to numerous whorls of monomorphic imbricating plates; radii absent; opercular plates thick; mandible tridentoid; first two pairs of cirri as maxillipeds; caudal appendages when present multi-articulate.

Comment: The phylogeny provided by Chan *et al.* (2017a), based on six molecular markers (both mitochondrial and nuclear), showed Catophragmidae as sister to Pachylasmatidae within the Chthamaloidea clade. Chan *et al.* (2018) sequenced the mitogenome of *Catomerus* and found that it is more closely related to Tetraclitodea rather than to Chthmaloidea. The molecular position of Catophragmidae might need further confirmation from additional molecular studies.

Catolasmus Ross & Newman, 2001 (one species)

Catomerus Pilsbry, 1916 (one species)

Catophragmus Sowerby, 1826 (one species)

†Family Chionelasmatidae Buckeridge, 1983

Diagnosis: Shell six plated, with single rostrum, carina, paired carinomarginals and rostromarginals. Shell with up to several rows of imbricating plates at base; imbricating plates including two pairs of dedicated latera. Sheath formed by rostrum, carina and carinomarginals only; rostromarginals do not enter sheath. Basis thin, calcareous.

†*Chionelasmus* Pilsbry, 1911 (Eocene–Recent) (two species)

Eochionelasmus Yamaguchi, 1990 (three species)

†Superfamily Elminoidea superfam. nov. (Oligocene–Recent)

Diagnosis: Six- or four-plated shells with solid parietes, without chitinous laminae or stringers and interlaminate figures; radii solid; basis membranous.

Comment: This superfamily contains only a single family but is created for formal reasons, because the Elminiidae diverge phylogenetically between the Chthamaloidea and the clade consisting of the Coronuloidea + Balanoidea.

†Family Elminidae Foster, 1982

Diagnosis: As for Elminoidea, upgraded from subfamily to family.

†*Austrominius* Buckeridge, 1983 (six species)

Elminius Leach, 1825 (two species)

Hexaminius Foster, 1982 (two species)

††*Matellonius* Buckeridge, 1983 (Miocene) (one species)

††*Protelminius* Buckeridge & Newman, 2010 (one species)

Superfamily Coronuloidea Leach, 1817

Diagnosis: Wall of eight (rostrum discernibly tripartite), six or four plates; plates tubiferous; tubes formed between inner and outer lamina, between internal buttresses or between external ribs; radii solid; basis membranous or weakly calcareous. First three pairs of cirri modified as maxillipeds.

Comment: The presence of three pairs of mouth cirri is synapomorphic with the Balanoidea; the members seem originally to have inhabited the rocky intertidal zone, but many members have been both morphologically and biologically adapted to epibiosis on a wide variety of invertebrate and vertebrates.

†Family Chelonibiidae Pilsbry, 1916

Wall of eight or six plates, without median longitudinal sulcus; opercular plates weakly articulated; terga well developed; one row of confluent wall tubes formed between inner and outer lamina, basis membranous.

Subfamily Chelonibiinae Pilsbry, 1916

†*Chelonibia* Leach, 1817 (Eocene–Recent) (five species)
Stephanolepas Fischer, 1886 (one species)

††Subfamily Protochelonibiinae Harzhauser & Newman, 2011

††*Protochelonibia* Harzhauser & Newman, 2011 (Miocene) (two species)

†Family Coronulidae Leach, 1817

Diagnosis: Wall of six plates, without a median longitudinal sulcus; terga vestigial; opercular plates lacking in *Xenobalanus*; borders of mantle forming a hood over the cirri; single row of wall tubes formed by infoldings of outer lamina against the sheath.

Cetolepas Zullo, 1969 (one species)
Cetopirus Ranzani, 1817 (two species)
Chelolepas Ross & Frick, 2007 (one species)
†*Coronula* Lamarck, 1802 (Miocene–Recent) (eight species)
Cryptolepas Dall, 1872 (two species)
Cylindrolepas Pilsbry, 1916 (two species)
††*Emersonius* Ross, 1967 (Eocene) (one species)
Platylepas Gray, 1825 (nine species)
Stomatolepas Pilsbry, 1910 (six species)
Tubicinella Lamarck, 1802 (two species)
Xenobalanus Steenstrup, 1852 (one species)

†Family Tetraclitidae Gruvel, 1903 (Eocene–Recent)

Diagnosis: Wall of six or four plates; parietes tubiferous or solid, permeated by chitin, or have one or more rows of tubes containing living tissue or secondarily filled with calcareous and chitinous material; radii well developed or obsolete; basis commonly membranous; first three pairs of cirri are modified as maxillipeds.

Comment: Results of both multiple marker phylogenetic analyses by Tsang *et al.* (2014) and Chan *et al.* (2017a) and mitogenome phylogenetic analyses Shen *et al.* (2017) and Cai *et al.* (2018) in Tetraclitidae, showed that the subfamilies Tetraclitinae, Tetraclitellinae, Newmanellinae and *Epopella* Ross, 1970 are clustered in the same clade. The genus *Epopella* (previously identified as Austrobalanidae) and all the three subfamilies above are grouped under Tetraclitidae.

Astroclita Ren & Liu, 1979 (one species)
†*Epopella* Ross, 1970 (Miocene–Recent) (six species)
Lissaclita Gomez-Daglio & Van Syoc, 2006 (one species)
Neonrosella Jones, 2010 (one species)
Newmanella Ross, 1969 (one species)
†*Tesseroplax* Ross, 1969 (one species)
†*Tesseropora* Pilsbry, 1916 (Miocene–Recent) (eight species)
†*Tetraclita* Schumacher, 1817 (Miocene–Recent) (18 species)
†*Tetraclitella* Hiro, 1939 (Miocene–Recent) (16 species)
Yamaguchiella Ross & Perreault, 1999 (one species)

†Family Bathylasmatidae Newman & Ross, 1971 (Palaeocene–Recent)

Diagnosis: Wall of six plates; parietes solid or tubiferous; when tubiferous, tubes uniformly arranged in single row; interlaminate figures simple; basis calcareous or membranous; when membranous, wall solid.

Comment: Jones (2000), based on morphology, classified *Hexelasma* Hoek, 1913 and *Bathylasma* Newman & Ross, 1971 under Pachylasmatoidea. Based on molecular evidence, Chan *et al.* (2017a) showed that the clade containing *Hexelasma* and *Bathylasma* is sister to Tetraclitidae in the same clade. This suggests that Bathylasmatidae should be treated as an individual family and included in Coronuloidea.

†Subfamily Bathylasmatinae Newman & Ross, 1971 (Palaeocene–Recent)

†*Bathylasma* Newman & Ross, 1971 (Palaeocene–Recent) (one species)
†*Mesolasma* Foster, 1981 (Oligocene–Recent) (one species)

††*Tessarelasma* Withers, 1936 (Miocene) (two species)

Tetrachaelasama Newman & Ross, 1971 (two species)

†Subfamily Hexelasmatinae Newman & Ross, 1976 (Eocene–Recent)

†*Hexelasma* Hoek, 1913 (Eocene–Recent) (16 species)

†Family Austrobalanidae Newman & Ross, 1976

Diagnosis: Four-plated shells with thin-walled parietes; paries smooth internally, lacking 'an inflected basal margin'; scutum without adductor ridge, articular ridge moderately prominent, adductor pits for depressor muscles absent; tergum with articular furrow wide, spur confluent with basirostral angle.

Comment: Chan *et al.* (2017a) conducted a molecular analysis of pachylasmatids, bathylasmatids and tetraclitids. *Austrobalanus* formed a basal relationship with the clade containing bathylamatids and tetraclitids. Molecular evidence therefore supports the family status of Austrobalanidae.

†*Austrobalanus* Pilsbry, 1916 (Eocene–Recent) (three species)

Superfamily Balanoidea Leach, 1817

Diagnosis: Wall composed of rostrum, carina and one to two pairs of marginals, or wholly concrescent; parietes solid or tubiferous; radii solid or tubiferous; basis commonly calcareous, solid or permeated by tubes, rarely membranous; when basis calcareous, internal surfaces of compartments commonly with uniform ribs and interdigitations with wall; mandible quadri- or quinquidentate; caudal appendages absent; penis with basidorsal point; first three pairs of cirri are maxillipeds.

Comments: The species at present analysed molecularly form two distinct clades that are here recognized as the Balanidae and Pyrgomatidae. Relationships of the many species within each of these are much less clear and clearly in need of future analysis by molecular methods.

Family Balanidae Leach, 1817

Diagnosis: Monophyletic by molecular analysis. Wall of six or four plates; parietes tubiferous or solid; tubiferous shell, with tubes basically in a single uniform row formed between inner and outer laminate, although supplementary tubes may form basally; interlaminate figures complex, arborescent; radii either solid or tubiferous; basis commonly calcareous and tubiferous or membranous.

Comments: There are no clear morphologically based apomorphies for this family compared with the Pyrgomatidae. The genus *Wanella* is sister group to all remaining species as yet analysed by molecules, and this could argue for a separation within two subfamilies. Many genera are polyphyletic, and more low-level taxonomic revision is therefore needed.

Subfamily Wanellinae subfam. nov.

*Zoobank registration: lsid:*urn:lsid:zoobank.org:act:8EEDFA1B-8E36-4217-8C78-92231F1C84CA

Diagnosis: Shell complete, one-plated, depressed; orifice and shell oval shaped; only inhabit fire corals (*Millepora* spp.).

Comment: From molecular analyses (Malay & Michonneau, 2014; Tsang *et al.*, 2014), *Wanella* formed a separate clade, outside the pyrgomatid clade and inside the balanid clade. This argues for a subfamily-level classification under Balanidae.

Wanella Anderson, 1993 (type genus) (three species)

Subfamily Acastinae Kolbasov, 1993

†*Acasta* Leach, 1817 (59 species) (Oligoscene-Recent)
Archiacasta Kolbasov, 1993 (nine species)
Euacasta Kolbasov, 1993 (ten species)
Neoacasta Kolbasov, 1993 (six species)
Pectinoacasta Kolbasov, 1993 (six species)

Subfamily Amphibalaninae Pitombo, 2004

Amphibalanus Pitombo, 2004 (22 species)
Fistulobalanus Zullo, 1984 (12 species)
Tetrabalanus Cornwall, 1941 (one species)

Subfamily Archaeobalaninae Newman & Ross, 1976

††*Actinobalanus* Moroni, 1967 (Miocene-Pleistocene) (four species)

††*Archaeobalanus* Menesini, 1971 (Eocene–Oligocene) (one species)

†*Armatobalanus* Hoek, 1913 (Oligocene–Recent) (12 species)

Bathybalanus Hoek, 1913 (one species)

†*Chirona* Gray, 1835 (Eocene–Recent) (six species)

†*Conopea* Gray, 1825 (Miocene-Recent) (21 species)

†*Hesperibalanus* Pilsbry, 1916 (Miocene–Recent) (ten species)
††*Kathpalmeria* Ross, 1965 (Eocene) (two species)
†*Membranobalanus* Hoek, 1913 (Pliocene–Recent) (11 species)
†*Notobalanus* Newman & Ross, 1976 (Oligocene–Recent) (two species)
†*Palaeobalanus* Buckeridge, 1983 (Eocene–Oligocene) (three species)
†*Solidobalanus* Hoek, 1913 (Eocene–Recent) (18 species)
†*Striatobalanus* Hoek, 1913 (Eocene–Recent) (nine species)
††*Zullobalanus* Buckeridge, 1989 (Oligocene to Pliocene) (five species)

Subfamily Balaninae

†*Balanus* Costa, 1778 (Oligocene–Recent) (55 species)
††*Tamiosoma* Conrad, 1857 (Miocene–Pliocene) (two species)
††*Zulloa* Ross & Newman, 1996 (Miocene) (one species)

Subfamily Bryozobiinae Ross & Newman, 1996

Bryozobia Ross & Newman, 1996 (two species)
Eoatria Van Syoc & Newman, 2010 (three species)
Microporatria Van Syoc & Newman, 2010 (one species)
Multatria Van Syoc & Newman, 2010 (three species)
Poratria Van Syoc & Newman, 2010 (two species)

Subfamily Concavinae

††*Alessandriella* Carriol & Cahuzac, 2001 (Miocene) (one species)
†*Arossia* Newman, 1982 (Miocene–Recent) (nine species)
††*Chesaconcavus* Zullo, 1992 (Oligocene–Pliocene) (eight species)
††*Concavus* Newman, 1982 (Oligocene–Pleistocene) (two species)
†*Menesiniella* Newman, 1982 (Miocene–Recent) (three species)
†*Paraconcavus* Zullo, 1992 (Miocene–Recent) (six species)
Perforatus Pitombo, 2004 (one species)
††*Zulloconcavus* Carriol, 2000 (Miocene) (one species)

Subfamily Hexacreusiinae Zullo & Newman, 1996

Hexacreusia Zullo, 1961 (two species)
Zulloana Pitombo & Ross, 2002 (one species)

Subfamily Semibalaninae Newman & Ross, 1976

†*Semibalanus* Pilsbry, 1916 (Miocene–Recent) (four species)

Subfamily Megabalaninae

†*Austromegabalanus* Newman, 1979 (Miocene–Recent) (eight species)
††*Fosterella* Buckeridge, 1983 (Pliocene–Pleistocene) (four species)
†*Megabalanus* Hoek, 1913 (Oligocene–Recent) (37 species)
†*Notomegabalanus* Newman, 1979 (Miocene–Recent) (13 species)
Paractinobalanus Carriol, 2008 (Miocene) (one species)
Pseudoacasta Nilsson-Cantell, 1930 (one species)
††*Tasmanobalanus* Buckeridge, 1993 (Oligocene–Pliocene) (one species)

†Family Pyrgomatidae Gray, 1825

Diagnosis: Wall of four or six plates or wholly concrescent; parietes solid or tubiferous; when tubiferous, tubes occur between outer lamina and sheath or between external ribs of wall; interlaminate figures complex, radii solid; basis calcareous, rarely tubiferous, membranous in *Pyrgospongia*.

Comment: All species of this family are highly specialized to symbiosis in corals or sponges (Anderson, 1992). This has affected many extreme morphological specializations in some clades. The existing subdivisions within the family may not always be based on monophyletic groups, but we have decided to retain them anyway. A future revised division is much needed.

†Subfamily Ceratoconchinae Newman & Ross, 1976

Ceratoconcha Kramberger-Gorjanovic, 1889 (27 species)
††*Eoceratoconcha* Newman & Ladd, 1974 (Miocene–Pliocene) (three species)

†Subfamily Megatrematinae Holthuis, 1982

Adna Sowerby, 1823 (one species)
†*Megatrema* Sowerby, 1823 (Pliocene–Recent) (two species)
Memagreta Ross & Pitombo, 2002 (one species)
†*Pyrgomina* Baluk & Radwanski, 1967 (Pliocene–Recent) (six species)

SUBFAMILY PYRGOMATINAE GRAY, 1825
(MIOCENE–RECENT)

Ahoekia Ross & Newman, 1995 (three species)
Arossella Anderson, 1993 (two species)
Australhoekia Ross & Newman, 2000 (one species)
Cantellius Ross & Newman, 1973 (26 species)
Cionophorus Ross & Newman, 2001 (three species)
Creusia Leach, 1817 (one species)
Darwiniella Anderson, 1992 (two species)
Eohoekia Ross & Newman, 1995 (two species)
Galkinius Perreault, 2014 (11 species)
Hiroa Ross & Newman, 1973 (one species)
Hoekia Ross & Newman, 1973 (four species)
Neopyrgoma Ross & Newman, 2002 (one species)
Neotrevathana Ross, 1999 (one species)
Nobia Sowerby, 1839 (four species)
Parahoekia Ross & Newman, 1995 (one species)
Pyrgoma Leach, 1817 (five species)
Pyrgopsella Zullo, 1967 (two species)
Pyrgospongia Achituv & Simon-Blecher, 2006 (one species)
Savignium Leach, 1825 (two species)
Trevathana Anderson, 1992 (11 species)

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Overview of the taxonomy of the Crustacea: Thecostraca, including numbers of genera and species in the families. The table lists both extinct and extant species. See main text for details.