

A revision of the Iblidae and the stalked barnacles (Crustacea: Cirripedia: Thoracica), including new ordinal, familial and generic taxa, and two new species from New Zealand and Tasmanian waters

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Abstract

The discovery of two diminutive and very distinct ibliform barnacles from shallow waters off northern New Zealand and northeastern Tasmania provides an opportunity to re-evaluate the Iblidae, the most primitive of the living thoracicans. These are retained within the Superorder Thoracica, but are distinguished at ordinal level from the remainder of the Pedunculata *s.l.* The resultant new order, the Ibliformes *nov.*, comprises barnacles with predominantly chitinous rather than calcareous capitular plates; two families are recognized, the Iblidae *s.s.*, comprising two subfamilies, the Iblinae (*Ibla s.s.*) and the Neoiblinae *nov.* (*Neoibla gen. nov.*), and the Idioiblidae *nov.* comprising the Idioiblinae *nov.* (*Idioibla gen. nov.*) and the Chaetolepadinae *nov.* (*Chaetolepas Studer, 1889* and *Chitinolepas gen. nov.*). The monotypic *Chitinolepas* further highlights the high endemism and relict nature of the New Zealand marine fauna in particular and the southern hemisphere in general. On the basis of morphology and, where possible, genetic and larval work, it is recommended that the remainder of the stalked thoracicans be divided between three new orders, the †Cyprilepadiformes, Ibliformes, Lepadiformes and Scalpelliformes.

Key words: Cirripedia; Thoracica; †Cyprilepadiformes *ord. nov.*; Ibliformes *ord. nov.*; Lepadiformes *ord. nov.*; Scalpelliformes *ord. nov.*; Iblidae; Idioiblidae *fam. nov.*; †*Illilepas incertae sedis*; *Chaetolepas*; *Chitinolepas gen. nov.*; *Ibla*; *Idioibla gen. nov.*; *Neoibla gen. nov.*; apatite-calcite mineralization; naupliar setation, cyprid lattice organs; molecular clock calibration

Introduction

The Iblidae has been interpreted as an ancient clade of thoracican barnacles having roots in the early Palaeozoic (Newman, *et al.*, 1969: Table 3), and molecular genetics has borne this out (Pérez-Losada, *et al.*, 2004). The uniqueness of this group has been known since Darwin (1852), who noted the relatively undifferentiated cirri, the largely chitinous capitular and peduncular armament and the post-oral placement of the carapace adductor muscle, as in what became Acrothoracica and the then yet to be discovered Ascothoracida.

The first iblomorph was described as *Anatifa quadrivalvis* by Cuvier in 1817 from Kangaroo Island, South Australia. Cuvier gave it to Leach (1825) who recognized its uniqueness and proposed the family Iblidae, as well as the genus *Ibla*, to accommodate it. But it was not until Darwin (1852) dissected and described his new species, *Ibla cumingi* from the Philippines (= *I. sibogae* Hoek, 1907 from Malayan waters), that the remarkable sexuality of the genus became known to science. Darwin not only discovered his new species was a female accompanied by a much smaller and somewhat reduced ‘dwarf’

male, but that the hermaphrodite, *Ibla quadrivalvis* (Cuvier, 1817) was accompanied by a comparable 'complemental' male. These discoveries stimulated much research by other workers on the sexuality of barnacles and other organisms (cf. Ghiselin, 1974).

In 1889, Studer described a miniscule new genus and species, *Chaetolepas segmentata*, from deeper water off of New Zealand, which Broch (1922) subsequently decided was a senior synonym of his *Ibla pygmaea* from comparable depths off Tasmania. This was followed by the discovery of *Ibla idiotica* Batham, 1945, generally from the intertidal in New Zealand, which was not only miniscule, but had a unique dwarf male. These discoveries were followed by *Ibla atlantica* Stubbings, 1967, found by Alan Longhurst in relatively deep water off West Africa.

At this point the Iblidae included five species, *Ibla quadrivalvis*, *I. cumingi* (= *I. sibogae*), *I. segmentata* (= *I. pygmaea*), *I. idiotica*, and *I. atlantica*, but in his review Foster (1978) placed the *I. segmentata* of Studer, which he had not seen, as a questionable synonym of *I. idiotica* and noted that the *I. pygmaea* of Broch, (which he dissected and described), was not *I. idiotica*. Thus, as currently known, the taxonomy of the living species of *Ibla* is, in part, in a state of confusion. The present paper addresses and clarifies these issues, describes new genera and species, and adjusts the higher taxonomy of the stalked Thoracica to reflect current findings concerning their relationships.

Systematics

Subclass CIRRIPEDIA Burmeister, 1834

Superorder THORACICA Darwin, 1854

Remarks: With this revision, it is recommended that the Pedunculata Lamarck, 1818 be divided into four orders whereby the Thoracica is envisaged as comprising five orders; the Ibliformes *nov.*, Cyprilepadiformes *nov.*, Lepadiformes *nov.*, Scalpelliformes *nov.* and Sessilia Lamarck, 1818 (Table 1). The bivalved Cyprilepadiformes, restricted to the Silurian (Wills, 1963), are certainly very distinct. Anderson (1994) recognized *Ibla* as distinct from the Thoracica (i.e. that it was not a true stalked barnacle), and proposed a new superorder, the Prothoracica, to accommodate the sole genus, *Ibla*, with the inference (Fig. 10.18) that the Thoracica arose from them. However, *Ibla* appears to be a thoracican cirripede, perhaps related to *Eolepas* and separated from the rest of the living Thoracica by fossil forms such as *Praeolepas* (Newman *et al.* 1969, Høeg *et al.*, 1999) and hence until now it remained a member of the Pedunculata. Furthermore, the genetic work of Pérez-Losada, *et al.*, (2004), using both "MLhc and 50% majority rule trees", places *Ibla* as sister group to the other thoracicans, a result concordant with our morphological assessment. As

such, this recognition requires a new order, for which the Ibliformes is proposed (cf. Table 1).

Order CYPRILEPADIFORMES *nov.*

Diagnosis: Capitulum comprising two chitinous plates (scuta); peduncle naked.

Type: *Cyprilepas holmi* Wills, 1962: 567.

Etymology: *Cyprilepas* + modifying adjective.

Remarks: This order is known only from the Silurian, attached to a eurypterid (Wills, 1963).

Order IBLIFORMES *nov.*

Diagnosis: Capitulum comprising four generally chitinous plates often containing or largely replaced by carbonate hydroxylapatite; terga with apical umbones; scuta with umbones apical or subapical; peduncle clothed with chitinous spines or scales; carapace adductor muscle post-esophageal; nauplius with dorso-thoracic (= caudal) spine until at least stage four.

Etymology: *Ibla* + modifying adjective.

Distribution: Tropical West Africa, Red Sea, Persian Gulf, Madagascar, Indo-West Pacific (Figure 1).

Included taxa: Two families are currently assigned to this order, the Iblidae Leach, 1825 (*sensu stricto*) and the Idioiblididae *fam. nov.* (Table 1, Figure 2). Neither family currently possesses a fossil record. We also include the Carboniferous *Illilepas* Schram, 1975, as *incertae sedis*.

Remarks: The Ibliformes is distinguished from the Cyprilepadiformes by the presence of terga, and from the Lepadiformes, Scalpelliformes and Sessilia by the absence of a carina.

Recent Ibliformes are readily distinguished from all other Thoracica by the possession of a post- rather than pre-esophageal adductor muscle (Darwin, 1852), a characteristic shared with the Ascothoracica, Acrothoracica, and most other Crustacea possessing a bivalved carapace. In other Thoracica, the carapace adductor of the cyprid disappears during metamorphosis, and a new one replaces it anterior to the esophagus (Darwin, 1852; Anderson, 1965, 1987). A comprehensive review of dwarf and complemental males is provided in Klepal (1987).

A re-examination of Studer's types of *C. segmentata* has revealed the presence of a comb collar, a border of fine setae positioned within the aperture to the mantle cavity guarded by the tergum and scutum. Its presence was also detected in *I. quadrivalvis* (from New South Wales), *I. idiotica* (from Cook Strait), *C. calcitergum* (from Bass Strait) and *C. spiritsensis* (from Spirits Bay). A survey of other primitive stalked barnacles revealed a

pubescence in the upper part of the aperture in *Heteralepas microstoma* (Gruvel, 1901) from the Azores; there was however, no evidence of anything resembling a comb collar in *Heteralepas* cf. *quadrata* (Aurivillius, 1894) from Hawaii and Baja California. Initially, it was considered that this characteristic could be a diagnostic feature of the Ibliformes, and amongst the Thoracica it appears to be, and it is instructive to note that in Schram's (1986: 503) diagnosis of *Illielepas*, it is suggested it may have possessed one (see section below on phylogeny).

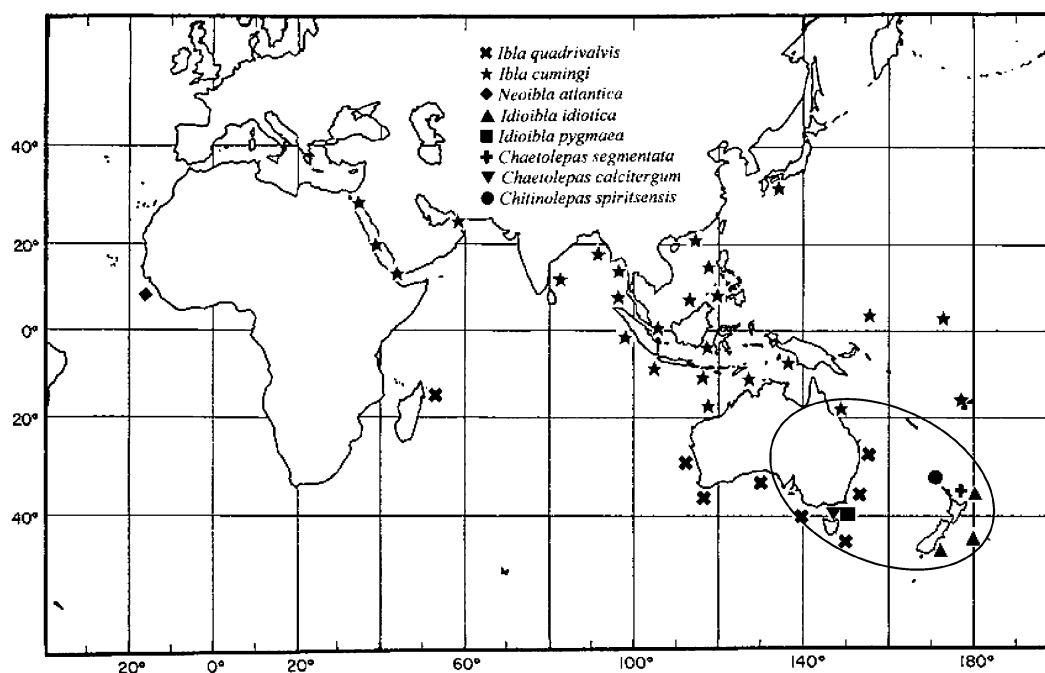


FIGURE 1. Distribution of the extant Ibliformes. Data from various sources, including Hiro (1936), Klepal (1987), supplemented by data from Foster (1974, 1978), Jones *et al.* (1990), Newman (1960), Por (1972), Stubbings (1967), and *pers. obs.* (Hiro's records of *Ibla quadrivalvis* for New Zealand, Fiji, the Red Sea and Persian Gulf are apparently erroneous).

In addition to the post-esophageal positioning of the adductor muscle, which is considered primitive within the Thoracica, many Ibliformes are hermaphrodites, which is also considered basic to thoracicans in general. We envisage a progression from hermaphrodites, which gave rise to complementary males via protandry, to hermaphrodites with complementary males, some of which apparently independently gave rise to females with dwarf males. There is the basic assumption that transformation of a hermaphrodite to a female requires fewer complicated mutations than the other way around, and because complementary males have appeared independently in lower sessilians as well as in other stalked barnacles, and there are ecological principles involved (Charnov, 1987), it follows that hermaphroditism was not only basic to the thoracicans but to the Ibliformes as well.

The distinctive non-skeletal characters of eight living species currently assigned to the Ibliformes are given in Table 2 and a key to the genera and species is provided below.

TABLE 1. Systematics of the early Thoracica: Relevant parts of existing classification (left hand column) and proposed revision (right) for the Thoracica, the latter including four new orders: the †Cyprilepadiformes *ord.*; the Ibliformes *ord.*; the Lepadiformes *ord.*; and the Scalpelliformes *ord.* The Eolepadidae and Praelepadomorpha have the earliest fossil record of what was considered the Pedunculata. The Ibliformes may be distinguished from these taxa by the lack of a carina. Schram (1986) removed *Praelepas damrowi* Schram 1972 from the praelepadomorphs as it lacks a carina. He placed it in a new genus *Illilepas*, within the Ibliformes. However, the nature of the capitular arrangement of *Illilepas* is still unresolved; here it is assigned, with the caveat *incertae sedis*, within the Iblidae (see text for fuller explanations). *Eolepas*, potentially assignable to the Ibliformes (Høeg *et al.*, 1999), has been retained *incertae sedis* in the Scalpelliformes († indicates extinct taxa).

Table 1

Relevant higher classification and genera:

SUPERORDER THORACICA Darwin, 1854
 ORDER PEDUNCULATA Lamarck, 1818
 SUBORDER †Cyprilepadomorpha Newman, 1987
 (= Cyprilepadoidea Newman *et al.*, 1969; = Archithoracica Anderson, 1994)
 SUBORDER Iblomorpha Newman, 1987
 (=Prothoracica, Anderson, 1994)
 Family Iblidae Leach, 1825
Ibla Leach, 1825
 ?†*Illilepas* Schram, 1986
 SUBORDER Heteralepadomorpha Newman, 1987
 Families Heteralepadiade Nilsson-Cantell, 1921 (= Lepadoidea Zevina, 1980 in part), etc.
 SUBORDER †Praelepadomorpha Newman, 1987
 Family †Praelepadidae Chernyshev, 1930
 SUBORDER Lepadomorpha Pilsbry, 1916
 (Lepadoidea Zevina, 1980 in part)
Lepas Linnaeus, 1758
Dosima Gray, 1825
 SUBORDER Scalpellomorpha Newman, 1987
 (Scalpellloidea Zevina, 1980)
Scalpellum Leach, 1817
Ornatoscalpellum Zevina, 1978
 Family Eolepadidae *nom. trans* Buckridge, 1983
 Subfamily †Eolepadinae Buckridge, 1983
 †*Eolepas* Withers, 1928
 †*Archaeolepas* Zittel, 1884
 Subfamily Neolepadinae Yamaguchi, Newman & Hashimoto, 2004
 etc.
 ORDER SESSILIA Lamarck, 1818
 (= Sessiles Bellermann, 1816).
 SUBORDER Brachylepadomorpha Woodward, 1901
 SUBORDER Verrucomorpha Pilsbry, 1916
Verruca Schumacher, 1817
 SUBORDER Balanomorpha Pilsbry, 1916
 Superfamily Chthamaloidea Darwin, 1854
 Superfamily Balanoidea Leach, 1817

Proposed relevant classification:

SUPERORDER THORACICA Darwin, 1854
 ORDER †CYPRILEPADIFORMES *nov.*
 ORDER IBLIFORMES *nov.*
 Family Iblidae Leach, 1825
 †*Illilepas* Schram, 1986:503 (*incertae sedis*)
 Subfamily Iblinae Leach, 1825 *nom. trans.*
Ibla Leach, 1825
 Subfamily Neoiblinae *nov.*
Neoibla *nov.*
 Family Idioiblididae *nov.*
 Subfamily Idioiblinae *nov.*
Idioibla *nov.*
 Subfamily Chaetolepadinae *nov.*
Chaetolepas Studer, 1889.
Chitinolepas *nov.*
 ORDER LEPADIFORMES *nov.*
 SUBORDER Lepadomorpha Pilsbry, 1916
 Families Lepadidae etc.
 SUBORDER Heteralepadomorpha Newman, 1987
 Families Heteralepadiidae, etc.
 SUBORDER †Praelepadomorpha Newman, 1987
 ORDER SCALPELLIFORMES *nov.*
 Family Eolepadidae Buckridge, 1983
 Subfamily †Eolepadinae Buckridge, 1983
 †*Eolepas* Withers, 1928 (*incertae sedis*)
 †*Archaeolepas* Zittel, 1884
 Subfamily Neolepadinae Yamaguchi, Newman & Hashimoto, 2004
 etc.
 ORDER SESSILIA Lamarck, 1818
 etc.

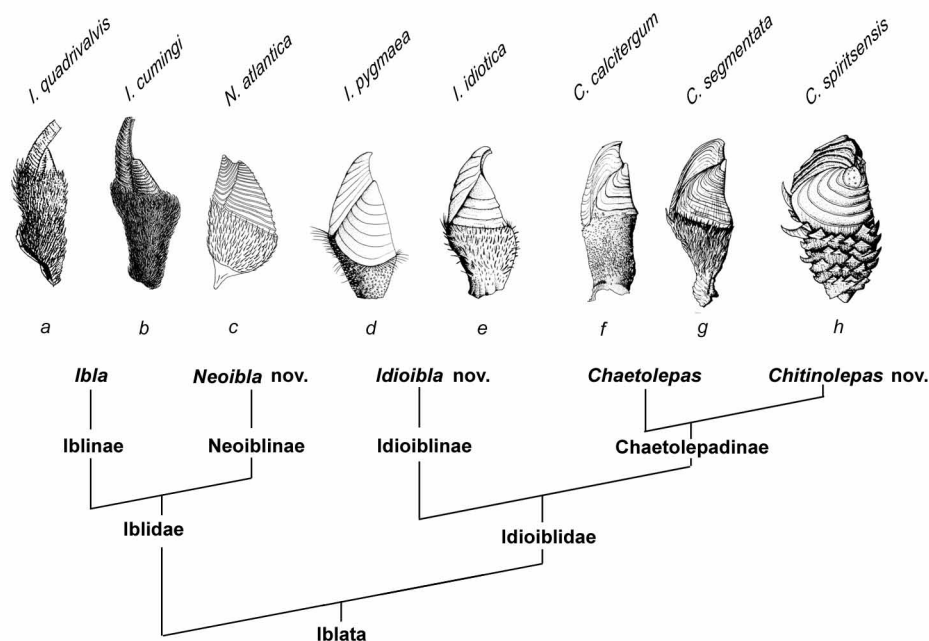


FIGURE 2. The Ibliformes: A phylogeny. Hermaphroditism has been interpreted as basic to thoracicans in general, is possessed by taxa on the left hand side of each clade, and progresses to separate sexes, along with increasing complexity of plate structure, from left to right (cf. Table 2). **a**, *Ibla quadrivalvis* (Cuvier, 1817); **b**, *Ibla cumingi* Darwin, 1852; **c**, *Neoibla atlantica* (Stubbings, 1967); **d**, *Idioibla pygmaea* (Broch, 1922); **e** *Idioibla idiotica* (Batham, 1945); **f**, *Chaetolepas segmentata* Studer, 1889; **g**, *Chaetolepas calcitergum* sp. nov.; **h**, *Chitinolepas spiritsensis* sp. nov. (**a**, after Gruvel, 1905; **b**, after Darwin, 1852; **c**, after Stubbings, 1967; **d**, after Batham, 1945; **e**, after Broch, 1922; and **f–h**, herein).

Family IBLIDAE Leach, 1825

Diagnosis: Large Ibliformes having basal margin of tergum relatively broad (40–75% width of scutum); peduncle armoured with long, chitinous strap-like or simple spines; dwarf and complementary males reduced but still capable of feeding, found cemented to wall of mantle cavity by cyprid antennules; and where known, with plankto- or lecithotrophic nauplii.

Type: *Ibla* Leach, 1825: 209.

Distribution: Recent, tropical eastern Atlantic, Red Sea, Persian Gulf, Madagascar, Indo-West Pacific to the Republic of the Marshall Islands.

Remarks: Two subfamilies, the Iblinae Leach, 1825 and the Neoiblinae nov. are included in the Iblidae.

TABLE 2. Principal non-skeletal characters of the species of the Ibliformes: Cirri ctenopod = setae along the lesser curvature of each article like a comb, or lasiopod = setae grouped at distal end of each article like brushes; males attached = planktrophic males attached by antennules to lining of mantle cavity; or free = lecithotrophic males found free amongst eggs and cyprids in the mantle cavity. The question marks under “sexuality” and under “males” indicate males have not been observed. Only *Ibla* is known to possess nauplius larvae and they are lecithotrophic or planktrophic in *I. quadrivalvis* and *I. cumingi* respectively (Yan *et al.*, in press). The hermaphroditic condition is considered primary for thoracicans and is therefore depicted in boldface here.

Species	sexuality	males	larvae	Int. segment cirrus VI	Caudal appendages
<i>Ibla quadrivalvis</i>	♀+♂	attached	lecithotrophic nauplii + cyprid	ctenopod	32
<i>Ibla cumingi</i>	♀+♂	attached	planktotrophic nauplii + cyprid	ctenopod	10-19
<i>Neoibla atlantica</i>	♀+♂	attached	cyprid	lasiopod	uniarticulate
<i>Idioibla pygmaea</i>	♀+?	see ¹	cyprid	lasiopod	10
<i>Idioibla idiotica</i>	♀+♂	free	cyprid	lasiopod	uniarticulate
<i>Chaetolepas calcitergum</i>	♀+?	see ²	cyprid	lasiopod	10
<i>Chaetolepas segmentata</i>	♀+♂	see ³	?cyprid	ctenopod	none ⁴
<i>Chitinolepas spiritsensis</i>	♀+♂	free	cyprid	ctenopod	uniarticulate

¹Broch (1922: 265) initially reported cyprids as complementary males in *I. pygmaea*, but he subsequently sectioned some and found no sperm whereby he retracted the claim (Broch 1922: 559); Foster (1978) made no mention of larvae or males in this species. Since *I. pygmaea* is a hermaphrodite with a well-developed penis it need not necessarily have males.

²A well-developed penis and embryos but no complementary males were observed in *C. calcitergum*, and since it too is a hermaphrodite it need not have males.

³Studer (1889) did not illustrate a penis in the holotype of *C. segmentata*, nor did we see one in the paratype. Therefore it is evidently a female, but no dwarf males were found and hence the question mark. However, while parthenogenesis cannot be ruled out, it is likely that it at least occasionally acquires males.

⁴The terminal segment supporting a pair of two-segment rami in Studer's (1896: fig. 16) illustration of *C. segmentata* was apparently what remained of the left sixth cirrus rather than a caudal furca. No caudal appendages, uniramous or even lobular, could be seen, and if none *C. segmentata* is the only known ibliform lacking them.

Subfamily Iblinae Leach, 1825 *nom. trans.* Herein

Diagnosis: As for the genus.

Type: *Ibla* Leach, 1825: 209.

Distribution: Recent, Red Sea, Persian Gulf, Madagascar, Indo-West Pacific to the Republic of the Marshall Islands.

Remarks: Two intertidal species are currently assigned to this subfamily: *Ibla cumingi* Darwin, 1852 (type by subsequent designation), Indo-West Pacific, Red Sea to the Republic of the Marshall Islands; *Ibla quadrivalvis* (Cuvier, 1817), Indo-West Pacific, Madagascar; southern Indian Ocean to New South Wales.

Genus *Ibla* Leach, 1825

Diagnosis: Capitulum with tergum extending well beyond scutum, generally delaminating terminally with age so as to end more or less bluntly; peduncle armoured with densely distributed, flexible, strap-like spines; cirri ctenopod; caudal appendages multiarticulate.

Type species: *Ibla cumingi* Darwin, 1852: 183. Intertidal, Indo-West Pacific. Recent.

Subfamily Neoiblinae *nov.*

Diagnosis: As for the genus

Type: *Neoibla atlantica* (Stubbings, 1967).

Distribution: Recent, 800 metres, Tropical West Africa.

Remarks: One species, *Neoibla atlantica* (Stubbings, 1967), is currently assigned to this subfamily.

Genus *Neoibla nov.*

Diagnosis: Capitulum with scuta and terga sub-equal in height, tergal growth lines upturned along articular margin; peduncle armoured with sparsely distributed spines; cirri lasiopod; caudal appendages lobate, uniarticulate; sexes separate, nauplius passed in the egg, embryo hatches as a cyprid.

Type species: *Ibla atlantica* Stubbings, 1967; 800 metres, Sierra Leone, West Africa. Recent.

Etymology: *Neo* (new) + *Ibla*.

Incertae sedis

Genus *Illilepas* Schram, 1986: 928 pro *Praeilepas damrowi* Schram, 1975: 928.

Diagnosis: Scuta sub-rectangular, scutal growth lines nearly surrounding apical umbones;

terga with growth lines upturned along scutal margin, umbones apical; peduncle unarmoured.

Distribution: Illinois, United States of America (Middle Pennsylvanian).

Remarks: The nature of the capitular armament of *Illilepas* is unresolved. Schram (1975) indicated that it possessed a carina, with paired terga and scuta. This placed it within the Praelepadidae (see Table 1). Upon further consideration, Schram (1982) decided it may be an iblomorph and in 1986 proposed the genus *Illilepas* to accommodate it. He also decided that what was previously thought to be the carina was a tergum, and that a small triangular projection was not a tergum but an enlarged spine amongst a row of fine spines along the margin of the aperture (which are perhaps comparable to comb collar ibliforms described herein).

If an ibliform, *Illilepas* will be the only fossil representative, and while it may differ from all modern forms by the absence of peduncular spines or setae, it seems closest to the Iblidae and therefore we have placed it, *incertae sedis*, there. Nonetheless, until more material has been studied, the systematic position of this most unusual taxon cannot be finalised.

Family IDIOIBLIDAE *nov.*

Diagnosis: Minute Ibliformes with basal margin of tergum acute; tergum triangular to broadly rounded; peduncle armoured with slender spines or broad imbricating scales; non-feeding males free within mantle cavity; larvae brooded to the cyprid stage.

Type: *Idioibla idiotica* (Batham, 1945).

Distribution: Recent, Southeastern Australia, New Zealand. Low intertidal to between 423 and 1500 m.

Remarks: The Idioiblidae comprises five species representing the three genera currently assigned to this family:

Idioibla idiotica (Batham, 1945), New Zealand. (intertidal to 1500 metres). Foster (1978: 21) stated that three specimens were found attached to a gastropod occupied by a hermit crab retrieved from 423–920m Saunders Canyon, New Zealand, and Alan Longhurst recovered numerous specimens from 800 fms (1500 m) in the Cook Strait area (British Museum of Natural History cat. no. 1958.9.29.1). On the basis of these deepwater finds, we concur with Foster's proposal that specimens from the intertidal represent the upper fringe of an otherwise subtidal distribution.

Idioibla pygmaea (Broch, 1922), southeastern Australia. (from between 184 and 294 metres).

Chaetolepas segmentata Studer, 1889, northern New Zealand. (1100 metres).

Chaetolepas calcitergum *sp. nov.*, southeastern Australia. (from between 120 and 140 metres).

Chitinolepas spiritsensis *gen. et sp. nov.*, northern New Zealand. (from between 30 and 50 metres).

Species in this family may be readily distinguished from the Iblidae by the tergum, which has as an acute rather than a broad basal margin. Furthermore, the Idioiblididae differ by the possession of an actual diastema between the first and second cirri. Darwin (1852) had noted the first pair of cirri is situated at “an extraordinary” distance from the second in *Ibla cumingi*, but as can be seen in his figure (Pl. IV 8a’) there is no diastema: the first pair is displaced down onto the base of the oral cone rather than the second being displaced backwards from it.

Subfamily Idioiblinae nov.

Type: *Idioibla idiotica* (Batham, 1945: 347).

Diagnosis: Scuta with growth lines not upwardly reflected along tergal margin; terga with growth lines parallel or slightly oblique to scuta margin; scuta without tergal notch; cirral setation lasiopod.

Distribution: New Zealand and southeastern Australia.

Remarks: The distribution of the two species in this subfamily is poorly known, indeed, both species may be under threat. *I. pygmaea* has not been recorded since Broch’s original description (Broch, 1922) and *I. idiotica* although once relatively common in New Zealand’s low intertidal, has not been collected from this habitat for at least a decade. However a single specimen of *I. idiotica*, was collected by RV *Kaharoa* on 5 May, 1998 from Spirits Bay, NZOI stn. Z9677: 34°22.14’S, 172°49.5’E, from 55m, where it was attached to the cosmopolitan hydroid *Hydrodendron mirabile* (Hincks, 1866).

Subfamily Chaetolepadinae nov.

Type: *Chaetolepas segmentata* Studer, 1889: 270.

Diagnosis: As for the genus.

Distribution: Southeastern Australia and northern New Zealand.

Genus *Chaetolepas* Studer, 1889

Diagnosis: Scuta with growth lines reflected upwardly along tergal margin; terga with growth lines sub-parallel to scutal margin; scutum with tergal notch; peduncle armoured with sparse to moderately dense spines.

Type species: *Chaetolepas segmentata* Studer, 1889. ca.1100 metres, about 55 kilometres east of the Poor Knights Island, New Zealand.

Remarks: *Chaetolepas* is represented by two species and both may have very restricted geographical distributions: *C. calcitergum* sp. nov., from off Flinders Island, Bass Strait, Tasmania, and *C. segmentata* Studer, 1889, from the Hauraki Gulf, New Zealand.

Note: Foster (1978) dissected one of Broch's type specimens of *Ibla pygmaea* from off Tasmania, which Broch (1922: 559), after seeing specimens of *Chaetolepas segmentata* Studer, 1889 from New Zealand in the Berlin Museum, declared were synonyms, a decision seconded by Stubbings (1967: 136) and Klepal (1984: 48). But while Foster had demonstrated that Broch's *Ibla pygmaea* (and therefore presumably Studer's *segmentata*), represented a very distinct species, for some reason he included *segmentata* from New Zealand as a possible senior synonym of *I. idiotica* – also from New Zealand. This may have been because Broch had said *pygmaea* and *segmentata* were superficially identical, and since *pygmaea* does resemble *idiotica* superficially we might have followed suite. However it was possible to borrow and examine Studer's specimens of *segmentata* from the Berlin Museum, and it is clear that although *pygmaea* is externally in some respects more like *idiotica* than *segmentata*, they are in fact readily assignable to different genera.

***Chaetolepas segmentata* Studer, 1889**

(Figure 3A–F, 6B)

Chaetolepas segmentata Studer, 1889: 270

Ibla pygmaea Broch; Broch 1922: 559; Batham 1945: 355; Stubbings 1967: 236

not *I. pygmaea*; Foster 1978: 21

?*I. idiotica* Batham, Foster 1978: 21

I. idiotica, Zevina 1982: 104

I. pygmaea as in Klepal 1985: 48

Diagnosis: Tergum not conspicuously mineralised, setation of posterior cirri ctenopod; sexes separate.

Material examined: Collection 7846, comprising two specimens from *Gazelle* Stn. 64, 35°21'S, 175°40'E, 1092.5 metres, 12 November, 1875, Berlin Museum.

Notes: No further specimens of *C. segmentata* have been collected. Although the capitular plates appeared uncalcified, the nature and length of time of preservation do not permit us to state conclusively that there is no visibly detectable mineralization of the terga as in its sibling species.

Type specimens: As Studer (1889) did not designate types, his figured specimen is here designated the lectotype, the second specimen the paratype: 7846/A ("Figure 18" in Studer 1889: 270) and 7846/B, (Figure 3A–F), respectively; Museum Naturkunde, Berlin, Germany.

Description: Peduncle covered in long, flexible, chitinous spines, spines densest near capitulum; tergum not visually mineralised, with growth lines well formed, inflected upwards along scutal margin until near apex of scutum where they curve downwards to a tergal extension that notches into inner surface of scutum; interior of occludent margin of tergum with well formed comb collar of short setae (Figure 3F); scutum triangular,

primordial valve apical, apical notch for receiving basal extension of tergum, basi-occludent angle slightly less than 90 degrees, growth lines strongly inflected apically at tergal margin; and there is a very minor extension of peduncle between scutum and tergum.

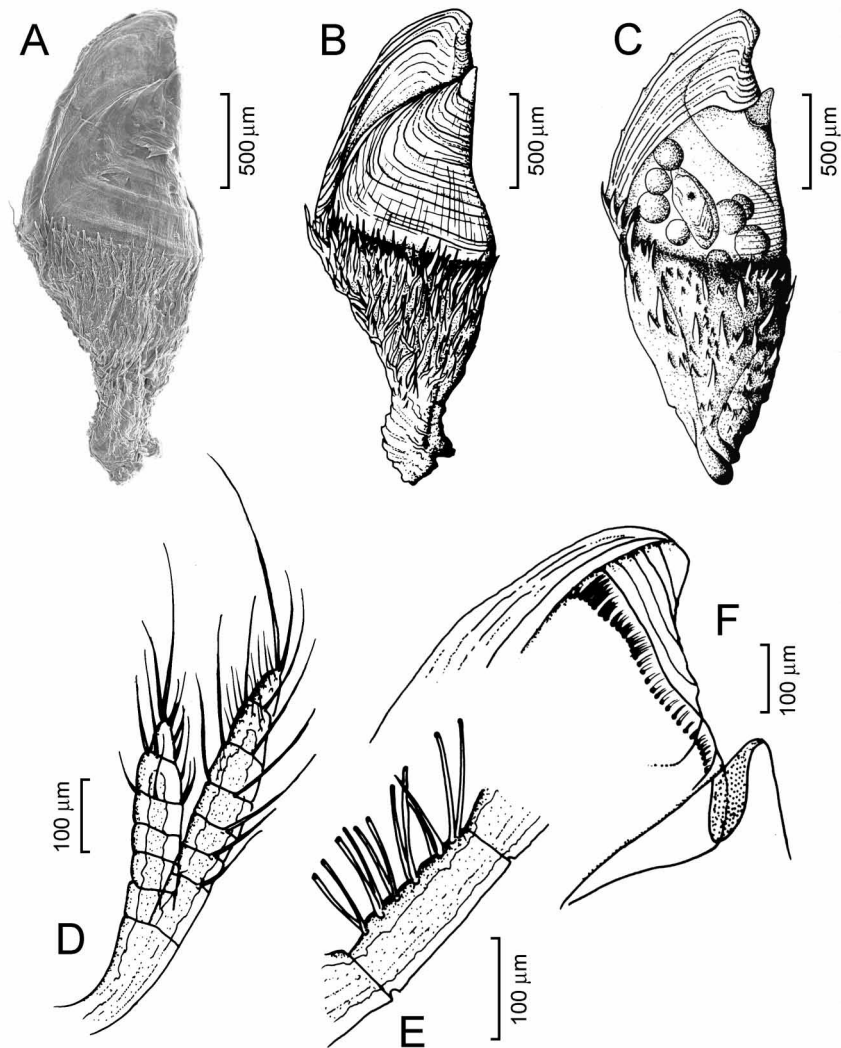


FIGURE 3. *Chaetolepas segmentata* Studer, 1889. A, Scanning electron micrograph, lateral view (left side); B, Line drawing of A (note that peduncle has shrunk due to desiccation in preparation for the SEM); C, Line drawing with scutum transparent, showing cyprid and eggs within mantle; D, First cirrus; E, Intermediate segment of sixth cirrus, showing ctenopod setation; F, Aperture between the occludent margin of the left tergum and the apex of the left scutum, with left side removed so as to expose comb collar. From paratype, specimen 7846B, Berlin Museum.

Mandible with four teeth plus pectinate lower angle; Cirrus I with inner ramus of six segments and outer ramus of seven segments; intermediate segments of VI cirrus ctenopod, that is, with six pairs of setae on inner curvature of each segment; no caudal appendages could be detected.

Remarks: Studer's (1889) description of this species was most brief, and his drawing does not help much with the diagnosis, as the mouthparts are barely visible, and the cirri are depicted as arising sequentially from a segmented thorax. Having re-examined this specimen, we note that although it appears damaged, the cirral disposition is not distinctive. As noted, *C. segmentata* is distinguished from *C. calcitergum* by the ctenopod setation, the lack of conspicuously mineralised terga, and the apparent absence of caudal appendages and penis. (While Studer noted embryos and cyprids in the mantle cavity, from his illustration there were apparently no males, and this was our observation on the paratype). *C. segmentata* has been confused with *I. pygmaea* (Batham, 1945; Foster, 1978) but they can be readily distinguished as noted above. In addition, *C. segmentata* is not a hermaphrodite, and *I. pygmaea* has lasiopod setation.

***Chaetolepas calcitergum* sp. nov.**

(Figure 4A–L)

Diagnosis: Tergum conspicuously mineralised, setation of intermediate segment of sixth cirrus lasiopod, caudal appendages multiarticulate; hermaphroditic, males unknown.

Material examined: Stn BSS 167 S, 39°44.48'S, 148°40.36'E, 124.0 metres, collected by R.S. Wilson, Eastern Bass Strait, 63 km E of North Point, Flinders Island, three specimens; Stn BSS 169 S, 39°02.24'S, 148°30.36'E, 120 metres, collected by R.S. Wilson, Eastern Bass Strait, 85 km NE of North Point, Flinders Island, one specimen; Stn BSS 170 G, 38°51.48'S, 148°26.30'E, 130 metres, collected by R.S. Wilson, Eastern Bass Strait, 100 km NE of North Point, Flinders Island, one specimen; Stn BSS 170 S, 38°52.36'S, 148°25.12'E, 140 metres, collected by R.S. Wilson, Eastern Bass Strait, 100 km NE of North Point, Flinders Island, one specimen.

Type specimens: **Holotype** J53102: A specimen from stn BSS 167 S. (NB this specimen was removed from collection J14655).

Paratypes J14655, two specimens from stn BSS 167 S; J14656, one specimen from stn BSS 169 S; J14657, one specimen from stn BSS 170 G; J14661, one specimen from stn BSS 170 S.

All type specimens are held in the collections of Museum Victoria, Melbourne, Australia.

Description: Peduncle covered in short, evenly distributed chitinous spines; tergum distinctly mineralised (carbonate hydroxylapatite), growth lines well formed, inflected upwards along scutal margin until near apex of scutum, where they curve downwards to a tergal extension that notches into inner surface of scutum; interior of occludent margin of

tergum with well formed comb collar of short setae; scutum triangular, primordial valve apical, apical notch for receiving basal extension of tergum, basi-occludent angle less than 90 degrees, growth lines strongly inflected apically at tergal margin; portion of peduncle extends up between scutum and tergum for approximately one third length of capitulum; peduncular spines with sharply pointed, often with curled tips (Figure 4C).

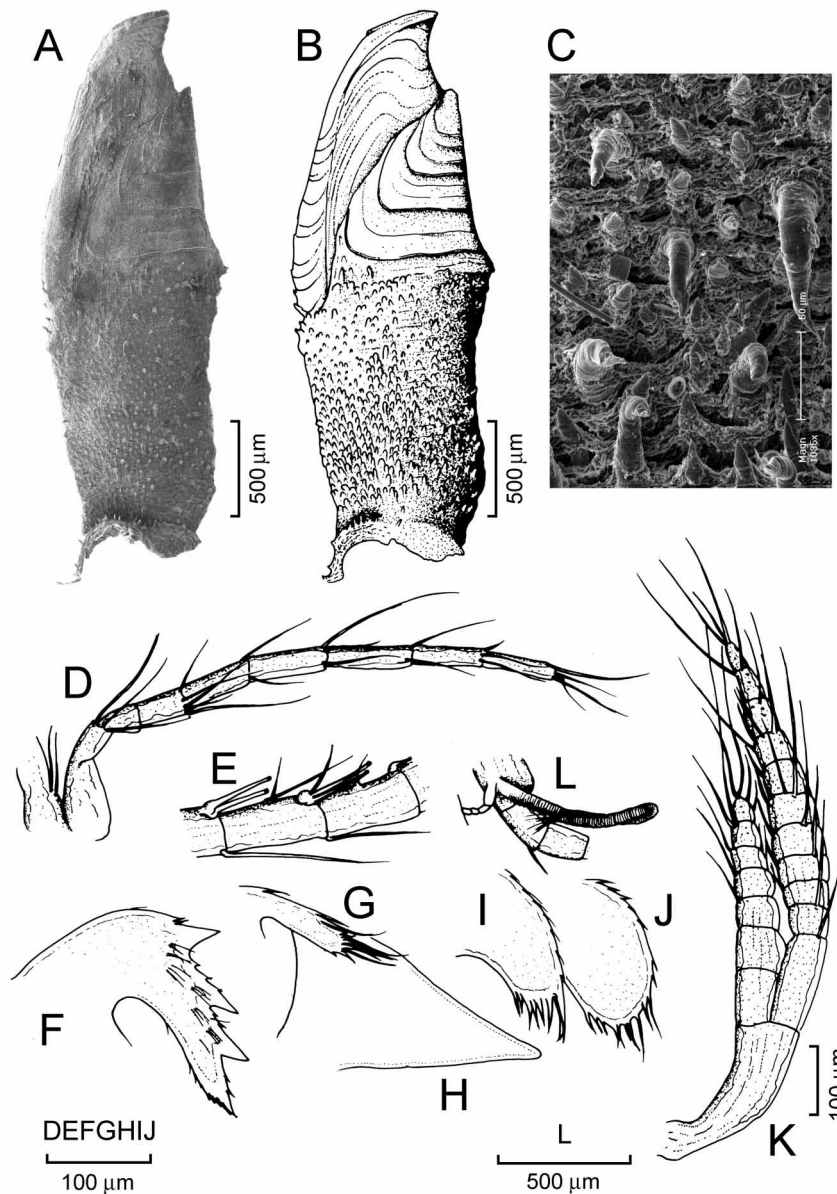


FIGURE 4. *Chaetolepas calcitergum* sp. nov. A, Scanning electron micrograph, lateral view (left side); B, Line drawing of A; C, Scanning electron micrograph showing detail of peduncle; D, Caudal appendage; E, Intermediate segment of sixth cirrus, showing lasiopod setation; F, Mandible; G, Palp; H, Labrum; I, First maxilla; J, Second maxilla; K, First cirrus; L, Base of sixth cirrus, showing caudal appendages (truncated) and penis. A–L from specimen J 14655.

Mandible with four teeth plus pectinate lower angle; first maxilla with two stout teeth at upper angle and four to five smaller teeth at lower; second maxilla larger than first, with several stout teeth on upper surface; labrum anteriorly pointed; penis with numerous terminal setae. Cirrus I with inner ramus of seven segments and outer ramus of 11 segments; cirrus VI with rami of 10 segments each, intermediate segments lasiopod; that is, with two pairs of setae on inner curvature and a pair of large setae on outer curvature of each segment; caudal appendages of 10 segments each.

Remarks: *Chaetolepas calcitergum* sp. nov. was originally identified in the Victoria Museum collections as *I. idiotica* (Figure 6A). It clearly differs from *I. idiotica* by the upturned growth lines along the tergal margin of the scutum, the basal angle of the tergum extending well below the base of the scutum, the nature and disposition of the peduncular spines, and in having multi-segmented caudal appendages. It can be distinguished from *C. segmentata* by the setation, conspicuously mineralised tergum, more clearly defined growth ridges on the capitular plates, the multi-segmented caudal appendages and more spinose peduncle. It is found in the same geographic region as *I. pygmaea* from which it can be distinguished by the same characters as from *I. idiotica*, and from both by the lack of a fringe of setae around the base of the capitulum.

Specimen J 14655 was examined using a scanning electron microscopy and energy dispersive spectrometry. The tergum provided clear spikes for both phosphorus and calcium; by comparison, Ca and P levels in the peduncle were only slightly above background.

Genus *Chitinolepas* gen. nov.

Diagnosis: Capitulum with scuta and terga with elevated growth ridges; scutal growth lines nearly encircling the apical umbone, tergal growth lines down-turned as they approach the scutal umbo; peduncle armoured with large imbricating scales.

Type species: *Chitinolepas spiritsensis* sp. nov., 30–50 metres, Spirits Bay and Tom Bowling Bay, New Zealand. Recent.

Etymology: *Chitin* (in reference to the pronounced chitinous exoskeleton) + *Lepas*.

Remarks: This genus is presently monotypic. Criteria such as sexuality are not considered to be generic characteristics since species of both *Ibla* s.s. and *Chaetolepas* have sexes separate or combined.

Chitinolepas spiritsensis sp. nov.

(Figure 5A–M; 6D)

“Iblomorph barnacle”, Buckeridge and Gordon, 1998: 8.
Ibla sp. Buckeridge, *in press*.

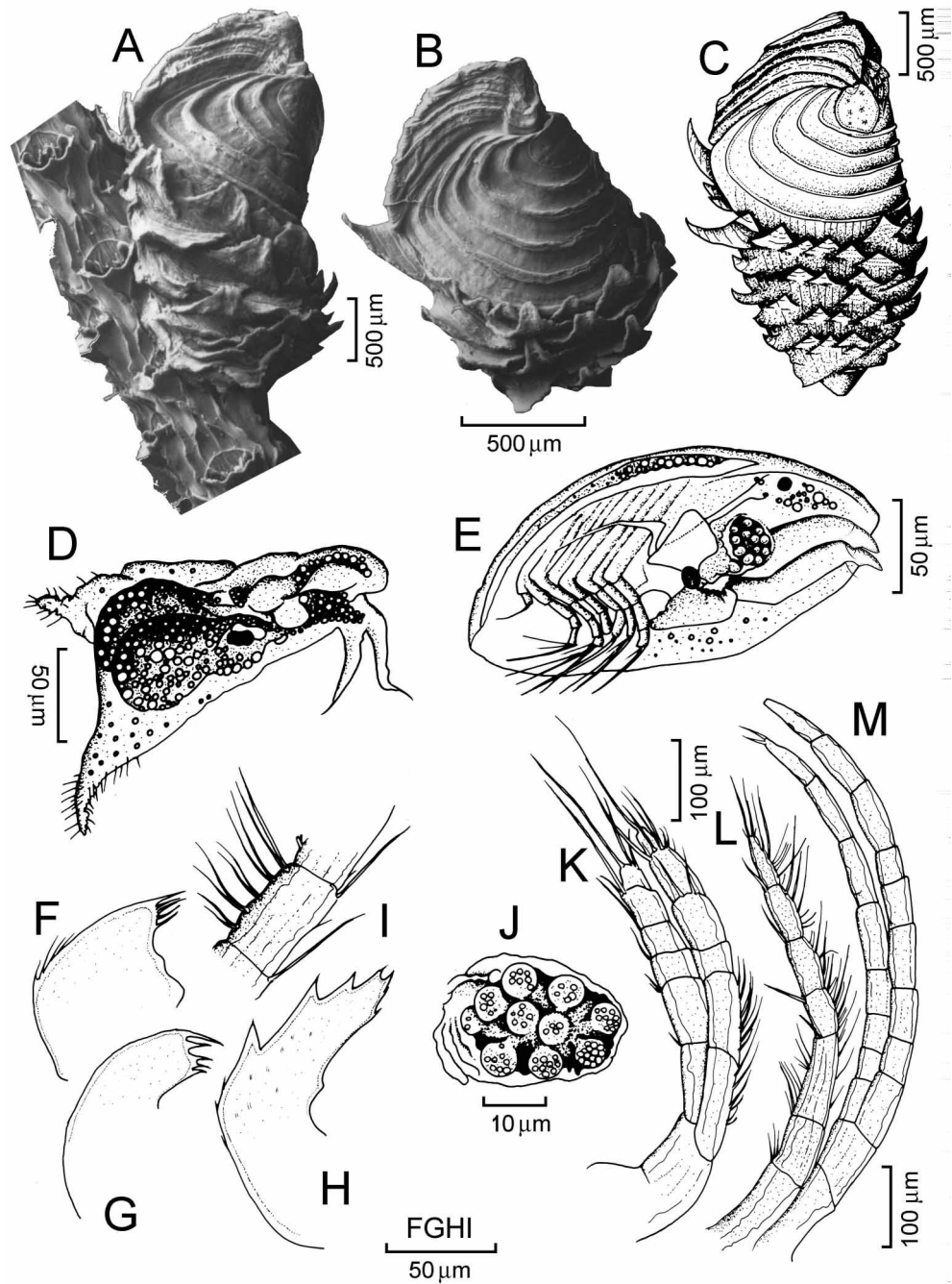


FIGURE 5. *Chitinolepas spiritsensis* gen. et sp. nov. A, Scanning electron micrograph, left-lateral view slightly canted to right side, attached to the hydroid *Crateritheca novaezelandiae* (Thompson, 1879); B, scanning electron micrograph (left side); C, Line drawing including detail of scutal primordial valve seen in A & B; D, Dwarf male and E, cyprid from mantle cavity of C; F, Second maxilla; G, First maxilla; H, Mandible; I, Intermediate segment of sixth cirrus, showing ctenopod setation J, Detail of cyprid eye; K, First cirrus; L, Single ramus of second cirrus; M, Third cirrus. A from NZIO stn Z8641, B–K from NZIO stn Z9105.

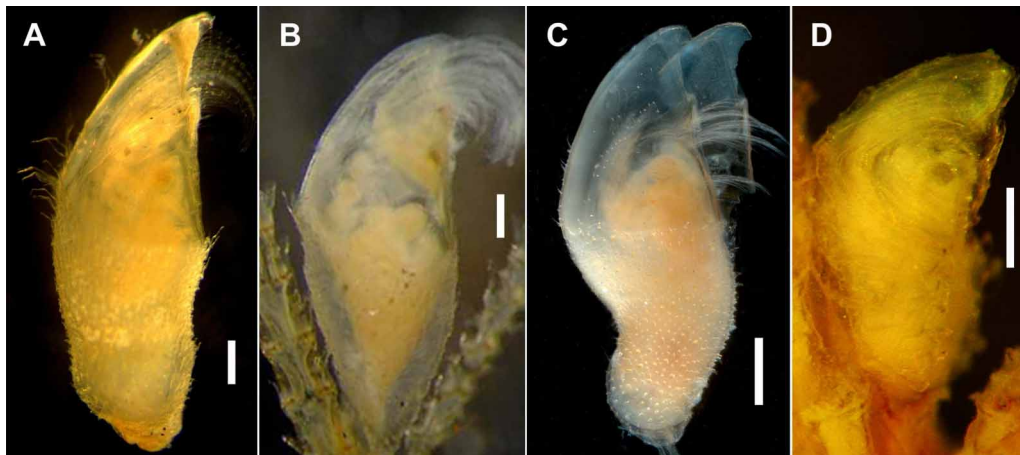


FIGURE 6. Idioiblidae: A, *Idioibla idiotica* (Batham, 1945), from Cook Strait, New Zealand (SIO C-10815, from a fish gut); B, *Chaetolepas segmentata* Studer, 1889, from Gazelle stn 64, off Coromandel Coast, New Zealand (7846/B); C, *Chaetolepas calcitegum* sp. nov. from Eastern Bass Strait, Australia (J14655); D, *Chitinolepas spiritsensis* gen. et sp. nov. from Spirits Bay, New Zealand (NZOI stn Z8641). Station details listed under each taxon in systematics. Scale bars 400 μ m.

Diagnosis: As for genus.

Material examined: **Spirits Bay** New Zealand Oceanographic Institute (NZOI) stn Z8641, 34°23.4'S, 172°51.8'E., 49.0 metres, collected by F/V *Ben Gunn* 27 February, 1997, 50+ complete specimens attached to the hydroid *Crateritheca novaezelandiae* (Thompson, 1879); NZOI stn Z9100: 34°22.4'S, 172°46.6'E, 41m, collected 5 May, 1998, 17 specimens; Tom Bowling Bay NZOI Stn Z9105: 34°24.3'S, 172°52.4'E, 32m, collected 4 May, 1998, 60 specimens attached to the hydroid *C. novaezelandiae*.

Type specimens

Holotype H-699: NIWA 3487. A specimen from NZOI stn Z8641, (Figure 5A). Held in the type collections of the National Institute of Water and Atmospheric Research, Wellington, New Zealand.

Paratypes P-1432: NIWA 3488. 19 specimens from NZOI stn Z8641; AUT 132: A specimen, from NZOI stn Z8641; AUT 133: A dissected specimen with cyprid and eggs, from NZOI stn Z9105; AUT 134: A specimen from NZOI stn Z9105; AUT 135: A specimen from NZOI stn Z9105; AUT 136: A specimen, from NZOI stn Z9105. AUT 158: A specimen (juvenile) from NZOI stn Z9105; AUT 159: four specimens from NZIO stn Z9100; C-9943: six specimens from NZOI stn Z9100; C-10406: two specimens plus slide of ones cirri, from NZOI stn Z9100; J53193: one specimen from NZOI stn Z9105. Paratypes with the prefix "P" are held in the type collections of the National Institute of Water and Atmospheric Research, Wellington, New Zealand; "AUT" in the type collection of Auckland University of Technology, Auckland, New Zealand; "C" in the Benthic Invertebrate Collection, Scripps Institution of Oceanography, California and "J" in the collections of Museum Victoria, Melbourne, Australia.

Habitat: All known specimens of *C. spiritsensis sp. nov.* were found attached to stems and branches of the arborescent hydroid, *C. novaezelandiae* (Figure 5A); site of attachment variable, but usually oriented with aperture directed outwards so as to feed in prevailing currents; cryptically coloured to match the hydroid, from which it likely gains physical protection.

Description: Capitulum triangular in lateral view, approximately equal in height to the length of the peduncle; scuta and terga comprised of tough, horny chitin, externally with well defined, well separated, elevated growth ridges; scuta equilateral, with large, rounded, triangular primordial valve apically, occludent margin weakly concave, basal margin broadly convex, tergal margin convex, but with small sub-apical depression to receive tooth on basi-occludent angle of tergum (Figure 5B, 5C); interior of occludent margin of tergum with a well formed comb collar of short setae; insertions of scutal adductor muscle large, pigmented (reddish-brown); tergum acutely triangular, with umbo apical and replaced basally by one or two enlarged scales situated at the “carino-lateral” position (were there carinal and lateral plates), scutal margin concave, sharply curved at basi-occludent angle and notched into the apex of scutum, primordial valve with finely raised margins, surface with irregularly spaced punctae. Peduncle with up to 14 scales in each whorl, scales broader than high, apices curved upward and inwards, exterior surface variable, with or without a median apico-basal ridge. Colour of scuta and peduncle pale yellow-brown, terga translucent cream (Figure 6D).

Mandible with four teeth, lower angle pectinate; first maxilla with two stout teeth at upper angle, and three to four smaller teeth at lower angle; second maxilla larger than first, with marginal indentation and several moderately stout teeth at upper angle; labrum anteriorly pointed. Cirri relatively short, slightly more elongate posteriorly, cirrus I separated from cirri II–VI by a diastema of approximately three pedicel widths, intermediate segments of cirrus VI ctenopod, with five pairs of setae, upper angle of distal edge of articles with single large seta; caudal appendages uniarticulate.

Segment counts for cirri I–VI follow (for specimen AUT 133), anterior ramus first, with capitulum length (cl), peduncle length (pl), and caudal appendages (ca). An incomplete ramus is indicated with the superscript “+”, if damaged beyond recognition as “_”.

cl/pl	side	I	II	III	IV	V	VI	ca
0.9/1.0	left	6/6	5/-	8/9	10/8 ⁺	10/11	9 ⁺ /8 ⁺	1
	right	6/7	-	9/10	-	-	-	1

Dwarf males (Figure 5D): Similar in form to the males of *Idioibla idiotica* described by Batham (1945); reach a maximum length of about 0.35 mm, found amongst the embryos in the spacious mantle cavity extending from the capitulum well into the

peduncle, as in Iblidae. Batham described their ontogeny from the cyprid stage but they remain free rather than attach by cyprid antennules, and they do not differentiate into a capitulum and peduncle. Anteriorly there are two enlarged antennular lobes armed with short spines and a nauplius eye and central ganglion. Posteriorly there is a caudal furca. Most of body occupied by two large, spherical testes leading to the posterior end via a seminal vesicle.

Juveniles: Cyprids (Figure 5E) were found in the mantle cavity of adult specimens from all three stations. Characterised (in unstained state), by two large antennules, and six articulated cyprid limbs posteriorly; lateral eyes compound (Figure 5J), with at least twelve separate ommatidia, eye connected to supra-esophageal ganglion by well defined optic nerve; nauplius eye small, lying dorsal to lateral eyes. Pigmentation lacking except for dark brown nauplius and lateral eyes.

Embryos: Eggs, if present, approximately the same size as cyprids, and slightly larger than the dwarf males; scanning electron microscopy showed a distinct pitted surface pattern (not illustrated). Eggs measured approximately 0.4 mm in diameter.

Remarks: Spirits and Tom Bowling Bays, at the northern tip of New Zealand's North Island, are the only places where *Chitinolepas spiritsensis* has been found; the region is otherwise known for its high faunal endemism (Buckeridge and Gordon, 1998). Dispersal methods are unclear, but the known (and somewhat restricted) distribution of the species suggests that dispersal may be linked to the host, fragments of which may be detached and transported between Tom Bowling and Spirit's Bays. *C. spiritsensis* is not known from any other substrate, and *Crateritheca novaezealandiae* is currently recorded only from a very restricted area to the north of the North Island (i.e. 34°–37.5°S, 172°–179°E, Three Kings Islands region, Spirits Bay, Ranfurly Bank, King Bank, 73–105m depth), (Vervoort and Watson, 2003).

Chitinolepas spiritsensis is an extraordinarily little barnacle, one of the smallest thoracican barnacles known. It has a maximum overall height of about two millimetres, may simultaneously contain as many as three dwarf males and 14 eggs, as well as one or more cyprids within the mantle. The dwarf males are differentiated into gonad sacs and they are somewhat smaller than the eggs. When compared with the other known Ibliformes, it is the only species in which broad peduncular scales are formed.

Knowledge of this barnacle and its allies adds significantly to our understanding of the biogeography of such endemism as well as to the relict nature of the marine fauna of New Zealand in particular and the Southern Hemisphere in general.

Etymology: Geographic (Spirits Bay, Northland, New Zealand).

Key to the Ibliformes

1. Basal margin of tergum broad, approximately a quarter to three quarters the width of the basal margin of the scutum..... 2

- Basal margin of tergum forming a relatively acute angle 3
2. Basal margin of tergum approximately three quarters the width of the basal margin of the scutum, cirral setation ctenopod 4
 Basal margin of tergum approximately one quarter the width of the basal margin of the scutum, cirral setation lasiopod *Neoibla atlantica* (Stubbings)
3. Peduncle armoured with sparse, slender spines 5
 Peduncle armoured with whorls of imbricating scales..... *Chitinolepas spiritsensis* nov.
4. Internal surface of tergum as high as wide, sexes separate *Ibla cumingi* Darwin
 Internal surface of tergum almost twice as high as wide, hermaphroditic plus complementary males..... *Ibla quadrivalvis* (Cuvier)
5. Cirral setation lasiopod 6
 Cirral setation ctenopod, caudal appendages uniarticulate, sexes separate
Chaetolepas segmentata Studer
6. Caudal appendages uniarticulate, sexes separate *Idioibla idiotica* (Batham)
 Caudal appendages multi-articulated (ca. 10 articles) 7
7. Tergum not visually mineralised, peduncle with well-formed setal fringe immediately below capitulum, hermaphroditic..... *Idioibla pygmaea* (Broch)
 Tergum visibly mineralised, peduncle with numerous small, short chitinous spines over entire surface, hermaphroditic..... *Chaetolepas calcitergum* nov.

Order LEPADIFORMES *nov.*

Diagnosis: Capitulum and peduncle distinct, capitulum with five approximate, calcareous plates (carina with basal or sub-basal umbo, plus paired terga and scuta with apical umbones), or five or two reduced, widely separated plates (when terga and carina absent) or no plates; caudal appendages variable; hermaphroditic, sometimes accompanied by complementary males.

Etymology: *Lepas* + modifying adjective.

Remarks: The proposed revision of the Thoracica represents a significant departure from the current barnacle classification, as shown in Table 1. The relatively primitive Lepadidae, Poecilasmataidae and Oxynaspididae were previously restricted to the Lepadomorpha *s.s.* (cf. Newman, 1987). Molecular genetics now places the Lepadomorpha a step above the Ibliformes (Pérez-Losada, *et al.*, 2004). Furthermore, the naupliar setation sequences of lepadids are unique, the reduced setation sequence of a poecilasmataid is similar (Newman and Ross, 2001), and so naupliar setation as well as the lattice organs (Jensen *et al.*, 1998) distinguishes the Lepadomorpha from the remainder of the Thoracica (Figures 7 & 8).

Since Foster (1978), the Heteralepadidae (*Heteralepas* and *Paralepas*) has been considered a primitive family of primarily plate-less stalked barnacles near the base of the thoracican tree. However, the Heteralepadomorpha, which it represents, is to some extent a

convenient catch-all for a diversity of families lacking calcareous plates and, therefore, it is not necessarily monophyletic (Newman, 1987). Since then, molecular genetics has revealed that a single heteralepadid species, *Paralepas palanuri*, resides near the stem of the Lepadomorpha (Pérez-Losada *et al.*, 2004). Thus, the question arises as to “what becomes of the Heteralepadomorpha?” with the proposed transfer of the Lepadomorpha from the Pedunculata to the Lepadiformes? Unfortunately, there is no knowledge of their cyprid lattice organs or of their naupliar setation sequencing. Yet, the molecular genetics suggests that the Lepadomorpha is more closely related to the Heteralepadomorpha than to the remainder of the Thoracica, and the test is relatively robust. Therefore, we propose the two be formally united under the Lepadiformes until advances in our knowledge dictate otherwise.

Order SCALPELLIFORMES *nov.*

Diagnosis: Capitulum comprising the five primary plates of the Lepadiformes (carina and paired terga and scuta) plus a rostrum (C-T-S-R), all umbones basically apical.

Etymology: *Scalpellum* + modifying adjective.

Remarks: Of the morphologically diverse Scalpelliformes only the Eolepadidae has direct relevance to this paper, as the status of *Eolepas* is conjectural (cf. remarks below).

Suborder EOLEPADIDAE Buckeridge, 1983

Diagnosis : Capitulum of six/eight plates; paired scuta and terga, unpaired carina and rostrum in the Eolepadinae (R-S-T-C), with an additional pair of latera in the Neolepadinae (R-S-L-T-C); where peduncular plates known, basic number per whorl is eight for the former, six for the latter. Peduncular whorls include unpaired subrostrum and subcarina, and paired rostrilatera, latera and carinolatera (sr-rl-l-cl-sc) in the former, but with the pair of latera absent in the latter (sr-rl-cl-sc).

Type: *Eolepas* Withers 1928: 65; pro *Pollicipes rhaeticus* Moore 1861: 512, by subsequent designation of Withers (1928: 65). Somerset, England (Upper Triassic).

Remarks: In an article on the phylogeny of the Cirripedia, Høeg *et al.* (1999) comment on a microanalysis of mineralization of the extinct *Eolepas* (Whyte, in prep.) that purportedly demonstrates the plates were basically phosphatic. They follow Glenner *et al.* (1995) who, in their consideration of the affinities of the living iblifforms which also have phosphatic plates (Whyte 1988), argue that direct transformation between phosphatic and calcitic plates is highly unlikely and that on the basis of fossil evidence, such a change must go through an unmineralised phase. If one form of mineralization must cease before another can become established, then both *Eolepas* and the iblifforms, as presently known, apparently constitute evolutionary dead ends. But unfortunately Whyte has neither confirmed that *Eolepas*, which is known only from the Mesozoic (Withers, 1928;

Buckeridge, 1983), is exclusively phosphatic, nor has he provided conclusive evidence demonstrating that where phosphatic, this was primary.

Whyte (1988), Glenner *et al.*, (1995) and Høeg *et al.*, (1999) do not seem to take into account some important observations and considerations related to the mineralisation of iblifirms. To begin with, while Darwin (1852) emphatically believed the plates of *Ibla* were unmineralised, Annandale (1909) noted that older specimens of *Ibla cumingi* contained calcareous salts, and Newman (1960) concluded that since *I. cumingi* plates bubbled in weak acid, they were impregnated with calcium carbonate. Above we noted the visible mineralisation in *C. calcitergum* contained calcium as well as phosphorous, and since it bubbles in acid, a carbonate must be present, but is it a mix of apatite and calcite, the latter being the carbonate mineral of higher barnacles, or is it carbonate hydroxylapatite?

Carbonate hydroxylapatite is a naturally occurring calcium phosphate having a general formula of $\text{Ca}_5[(\text{OH},\text{O})(\text{PO}_4,\text{CO}_3)_3]$, similar in structure to the mineral portions of vertebrate bones and teeth, and mineralogically referred to as dahllite. As it so happens, Lowenstam *et al.* (1992) and Lowenstam and Weiner (1992) show, though x-ray diffraction, dahllite in the plates of both *I. cumingi* and *I. quadrivalvis*, rather than amorphous apatite as the previous authors, apparently unaware of the significance of the bubbling in weak acid, had believed. In light of this, must one assume that, if for some reason natural selection favoured a largely or wholly carbonate exoskeleton over a phosphatic one, a species would have to pass through an unmineralised phase for the transformation to take place? If the transformation from carbonate hydroxylapatite to a carbonate, such as calcite, were biologically possible, and there is extensive literature on such transformations [e.g. Somasundaran *et al.*, (1985), including some *in vivo*, cf. Constantz *et al.*, (1998)], it follows that postulating a non-mineralised intermediary between the iblifirms and the higher thoracicans is an unnecessary complication.

In addition to the question of mineralisation, Høeg *et al.* (1999) re-evaluated the capitular arrangement of *Eolepas* and deduced that the plates originally described by Withers (1928) as rostra are in fact carinae. This interpretation is however somewhat conjectural as no complete capitula of *Eolepas* are known. Nonetheless, Darwin (1851: 51) and Withers (1928: 65) were both confident *Eolepas* possessed a rostrum; Withers (*loc. cit.*) notes that "... there can be no doubt now that *P. ooliticus* (now a species of *Eolepas*) had a large rostrum such as Darwin had figured." The best-preserved *Eolepas* is *E. quenstedti* (von Ammon), which is figured in Withers (1928: plate III. 9), wherein there was no indication of a rostrum, although most of the carina, about two thirds of the tergum and all of the scutum were present. But such negative evidence is less compelling when comparing such plates in other species of *Eolepas*; e.g. *E. rhaetica* (Moore), in which some, as figured by Withers (1928: plate I.6, 7) have infilled apices, as do rostra when they extend away from the capitulum. This infilling is not evident in any of the carinae, and the "rostrum" is proportionately much shorter than any carina figured by Withers (*loc. cit.*).

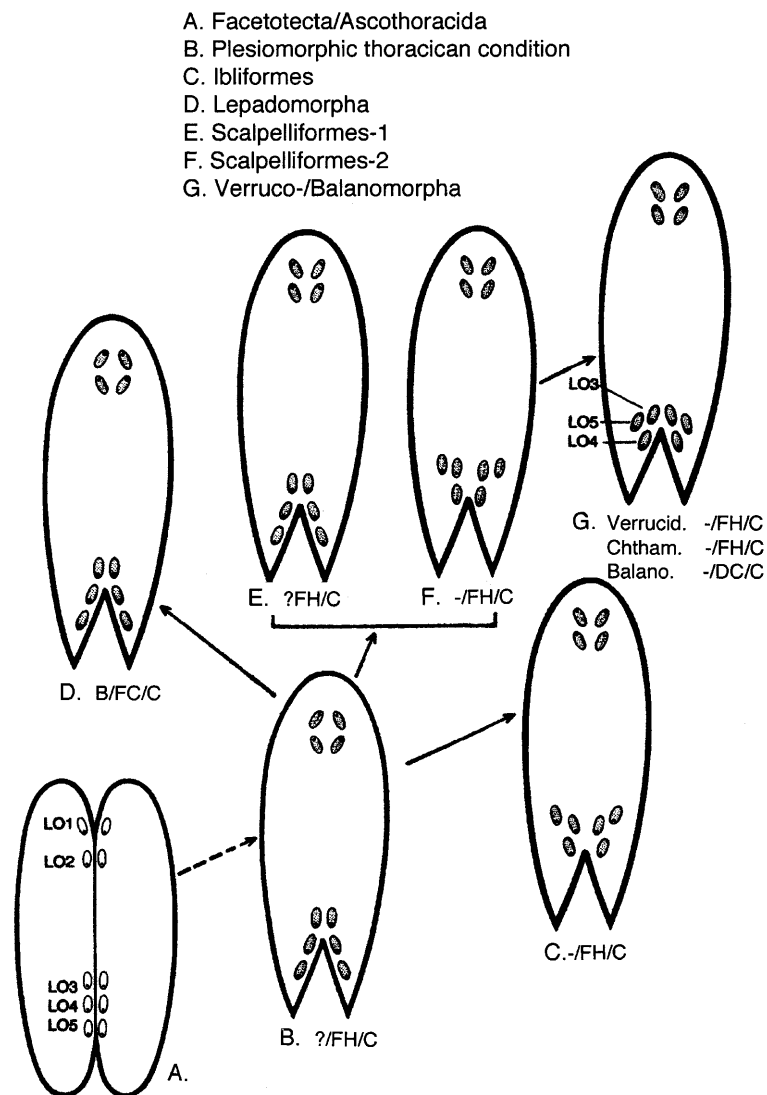


FIGURE 7. Arrangement of cyprid lattice organs (based on Jensen *et al.*, 1994, Høeg *et al.*, 2004 and Yan *et al.*, in press), and the distribution of distinctive naupliar setae based on Newman and Ross (2001), in Facetotecta/Ascothoracida and the principal thoracicans.

A, Lattice organ arrangement in Facetotecta/Ascothoracida combined (after Høeg *et al.*, 2004).

Note linear alignment of two anterior pairs (LO1 and LO2) and three posterior pairs (LO3, LO4, LO5) of lattice organs, all of which have posterior terminal pores (naupliar setation ignored as inadequately unknown).

B, The plesiomorphic arrangement of lattice organs in the Thoracica inferred from the patterns occurring in the Facetotecta/Ascothoracida, Lepadomorpha and Scalpelliformes-1. Note the toe-in/toe-out arrangement of LO1 and LO2, respectively, as in Lepadomorpha, and the linearity of LO3-LO5, as in Facetotecta/Ascothoracida (A), Acrothoracica (not illustrated) and in but one group of thoracicans, the Lepadomorpha (D). The terminal pores of LO2 went from posterior to anterior in the common ancestor of the Acrothoracica and Rhizocephala (not illustrated), and the

Thoracica, and of LO1 from posterior to anterior in the Rhizocephala/Thoracica (Jensen *et al.*, 1994). Therefore both sets of terminal pores were anterior in the stem thoracican cyprid (B). The pattern of distinctive naupliar setae of the plesiomorphic thoracican (B) is inferred to have been -FH/C, as in all thoracicans described so far (C, E, F, G), except Lepadomorpha (D) (Newman and Ross, 2001) (“?” = naupliar setation notation unknown, inferred as written, see text for explanation).

- C, Ibliformes: Represented by *Ibla cumingi*; lattice organ pattern from the SEMs of the cyprid, and setation notation from illustrations of naupliar VI appendages of Yan *et al.*, (in press). Note the lattice organ pattern is similar to, and the setation notation is the same as that of Scalpelliformes-2, and the same and as inferred in Scalpelliformes-1, and as in the lower Balanomorpha (Verrucidae and Chthamaloidea).
- D, Lepadomorpha: Represented by *Lepas* spp. and *Dosima fascicularis*, lattice organ pattern from Jensen *et al.*, (1994), setation notation deduced from Newman and Ross (2001). Note LO1–LO2 pattern and the setation notation distinguish the Lepadomorpha from all other thoracicans except the stem form (B).
- E, Scalpelliformes-1: Represented by *Scalpellum scalpellum* and *Ornatoscalpellum stroemia*, from Jensen *et al.*, (1994), “?” before the setation notation indicates that while unknown, it is probably the same as in Scalpelliformes-2 and Verruco-Balanomorpha (except the Balanoidea as indicated in G).
- F, Scalpelliformes-2: Represented by *Capitulum mitella* and *Pollicipes pollicipes* (also similar to that of chthamaloid, *Chthamalus stellatus*), as deduced from Figures. 5E and 6 (and 7B) in Jensen *et al.*, (1994); setation notation deduced from Newman and Ross (2001).
- G, Verruco-/Balanomorpha: Represented by the verrucid (1) *Verruca stroemia*, the chthamaloids (2) *Chthamalus montagui* and (3) *C. stellatus*, and the balanoids (4) *Balanus improvisus*, (5) *Austrominius modestus*, (6) *Megatrema anglicum*, (7) *Acasta spongites*, and (9) *Semibalanus balanoides*. However, the sketch (Jensen *et al.*, 1994) is generalized, for there is considerable variation in the posterior configuration, e.g. in species 1–3 listed above, LO5 is somewhat forward of LO3 (1994: text and Figure 7B respectively, as it is in Scalpellomorph-2); in species 4 and 7 where LO5 is postero-lateral or lateral to LO4 (1994: Figure 7F and text, respectively); in species 5 and 6 in which LO5 is missing (text); and in species 8, where no lattice organs could be recognized (1994: text). Setation notations determined from Newman and Ross (2001). Abbreviations for naupliar setation include B = bristled, C = cuspidate, D = plumo-denticulate, F = feathery and H = hispid (cf. Newman and Ross 2001); Balano. = Balanoidea, Chtham. = Chthamaloidea, and Verrucid = Verrucidae.

If *Eolepas* is an ibliform, an interpretation that we currently do not support, then it is very distinct from other members of the order. The carina (lacking in the Ibliformes) is scalpelliform as well as praelepadomorphan, and the kite-shaped tergum is certainly unlike any of the Ibliformes, particularly the strong apico-basal ridge that typifies all *Eolepas*, a ridge that forms ontogenetically on the tergum between the base of the scutum and another plate such as the carina in scalpellids. Further, if in *Eolepas* the presence of a rostrum can again be confirmed, then even if its plates were carbonate hydroxylapatite rather than calcitic, the hypothesis of Høeg *et al.* (1999), that *Eolepas* be placed among the Ibliformes would be untenable: it would remain a scalpelliform.

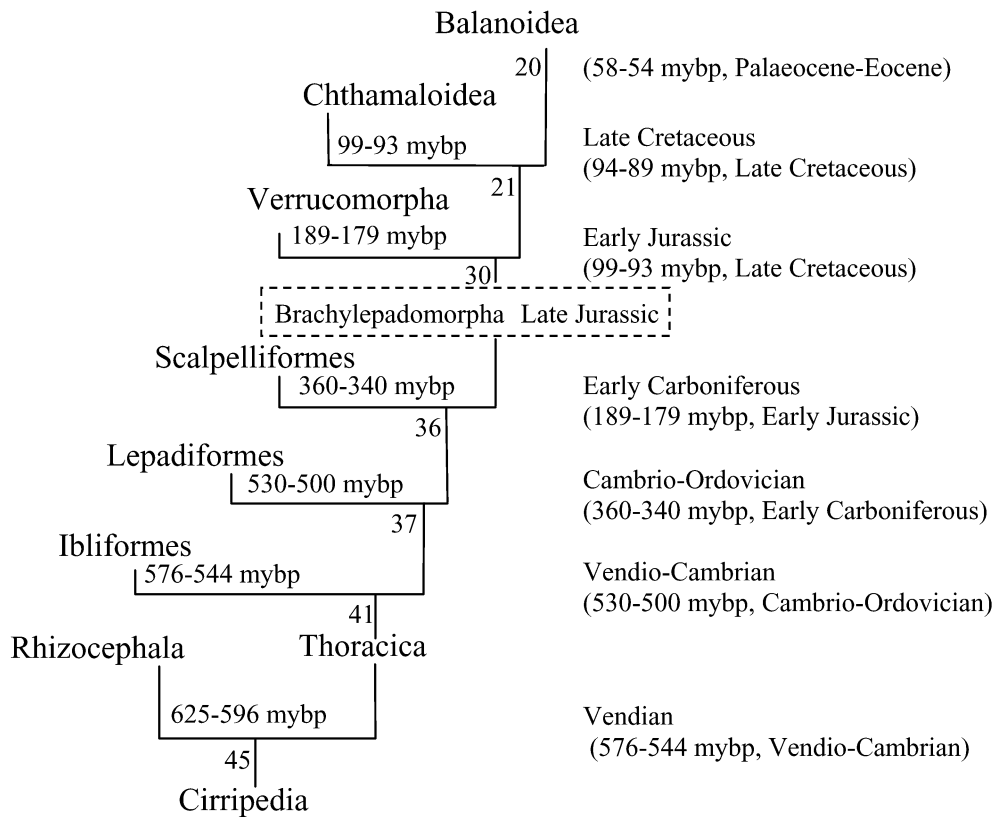


FIGURE 8. Thoracican evolution and geological time: Recalibrated evolutionary tree, derived from the fossil record (Newman *et al.* 1969) and DNA sequencing (Pérez-Losada *et al.*, 2004, Fig. 1). The adjusted ages and corresponding periods for each taxon, are given in parentheses. 1) the rhizocephalan-thoracican (iblifform) divergence (45) is moved up from Vendian to the Vendio-Cambrian, 2) the iblifform-lepadifform divergence (41) moves from the Vendio-Cambrian to the Cambrio-Ordovician, 3) the lepadifform-scalpellifform divergence (37) is moved from the Cambrio-Ordovician to the Early Carboniferous, 4) the scalpellifform-verruciform divergence (36), is moved from the Early Carboniferous to the Early Jurassic, 5) the brachylepadifform (verruciform)-chthamaloid divergence (30) from Jurassic to Late Cretaceous, 6) the chthamaloid-balanoid divergence (21) from the latest Cretaceous to early in the Late Cretaceous, and 7) the first major divergence within the balanoids from Late Cretaceous to Palaeocene-Eocene. See text for discussion (mybp = millions of years before present).

Biogeography

The wide-ranging intertidal form, *Ibla cumingi*, is found as far as 30°N in Japan and 20°S in Australia and its closest relative, *I. quadrivalvis*, is largely restricted to tropical, intertidal waters of the Indo-West Pacific, whereas the distantly related monotypic genus represented by *Neoibla altantica* occurs in moderately deep water at approximately 8°N in

the eastern Atlantic (Fig. 1). Yet, despite representation in the northern hemisphere, iblifform diversity as presently known is largely a southern hemisphere phenomenon, centring on S.E. Australia and New Zealand where 80% of the genera and 87% of the species are represented (Figure 1). Furthermore, the very distinct monotypic genus, represented by *Chitinolepas spiritsensis*, is only known from off northern New Zealand. Thus this group of barnacles complement the seminal work of Fleming (1975) who demonstrated high endemism in the southern hemisphere, particularly in the New Zealand region. Our understanding of this phenomenon was subsequently expanded by Newman (1979) and Buckeridge (1979, 1996) utilizing southern hemisphere barnacles.

The high diversity of iblomorph barnacles within the southern Australasian refugial realm (Figure 1) suggests the group is at least in part Gondwanan in origin, and if that were all there were to it, it would take dispersal along the coasts of New Zealand and Australia to explain present distributions in the Pacific and Indian Oceans, but whether the Atlantic form originated from this centre would remain unclear. However, as just observed, it is a member of the generalized and therefore presumably more primitive iblids, rather than the specialized idioiblids, that are absent from New Zealand. One of them is widely distributed in the Indo-West Pacific, the other in the Atlantic, and both are tropical. Furthermore, the roots of the iblifforms are in the early Palaeozoic (Newman *et al.* 1969) or earlier (Pérez-Losada, *et al.*, 2004) and perhaps informatively, there is the possible iblid (*Illilepas*) from the Upper Carboniferous of Illinois (North America). It, along with the present distribution of the Iblidae, suggests that a Panthalassian origin is likely. However, this does not preclude a more recent, Gondwanan origin for the idioiblids since both families may owe at least their southern hemisphere restriction to extinction of their northern hemisphere counterparts (Newman & Foster 1987; Newman 1991).

While the affinities of *Illilepas* from the Carboniferous of North America are conjectural, Schram (1986) and Høeg, *et al.* (1999) have suggested iblomorph affinities for species of *Eolepas* from the early Mesozoic of Europe. Should either of these genera prove to be iblifforms, then the Ibliformes origins are definitely Panthalassian.

Phylogeny

It has long been considered that *Ibla* is the most primitive of the living Thoracica (cf. Newman *et al.* 1967, Table 3) and recently genetic studies have borne this out (Harris *et al.*, 2000; Pérez-Losada *et al.*, 2004). In light of this, it is not surprising that the Ibliformes share a number of morphological features with the burrowing barnacles (Acrothoracica), a tentative relationship noted by Tomlinson (1969: fig. 42). These include the carapace adductor muscle being posterior rather than anterior to the esophagus, the shift of the first pair of cirri from the thorax onto the back of the mouth field and the appearance of a diastema between this and the posterior cirri, development of a dioecious sexual system

including highly reduced dwarf males, a largely chitinous exoskeleton, and to this list we have added the comb collar. It was such characteristics that led Tomlinson (1969) to suggest that acrothoracicans stemmed from the stalked barnacles. However, Tomlinson (1969) and Newman (1971) had the relationships wrong; that is, according to cyprid characters (Jensen *et al.* 1994) and molecular genetics (Pérez-Losada, *et al.*, 2004), the Acrothoracica not only preceded the Thoracica but also the Rhizocephala, although early in the Palaeozoic rather than Vendian. Thus, while the switch from hermaphroditism to separate sexes, the reduction of males to a mere sac of testes, and the separation of the first pair of cirri from the posterior pairs in iblifforms are likely convergences with the acrothoracicans, the largely chitinous exoskeleton, the number of plates guarding the aperture and the position of the esophagus relative to the carapace adductor are evidently primitive thoracican characters.

The inferred phylogeny of the Ibliformes is provided in Figure 2, where the more primitive taxa are represented to the left. The most generalized clade, *Ibla s.s.*, possess nauplii, have males attached by their antennules and apparently capable of feeding while within the mantle cavity of the hermaphrodite or female, and have a peduncle that is heavily armored with “strap-like” chitinous projections. *Ibla quadrivalvis* is a hermaphrodite, but in possessing dwarf males, it may be more derived than *I. pygmaea* and *C. calcitergum* (Table 2). There is however, rarely an harmonious change of characters in evolutionary phylogeny, and the iblifforms show this mosaic evolution (Mayr, 1963); for example, *I. cumingi* has the more primitive nauplii, in that they are planktotrophic, whereas the nauplii of *I. quadrivalvis* are lecithotrophic. Of the Iblidae, the neoibline condition shows two important trends in iblifform phylogeny: a reduction in size, and a modification in the growth pattern of the capitular plates, beginning with the tergum that shows growth lines inflected upward along the scutal margin. *Neoibla atlantica*, like many of the more derived taxa, is refugial, with an apparently restricted geographic distribution.

In the Idioiblididae there are no nauplii, and it seems that most if not all of its representatives have unattached dwarf males that occupy the mantle cavity. Also, unlike those in *Ibla*, their males do not feed; i.e. they are little more than gonad sacs. The more generalized sister-group of the Idioiblididae, the Idioiblinae, has modified terga and spinous peduncles. Members of its sister group in the Chaetolepadinae, have modified scuta as well, with growth lines inflected upward along the tergal margin. In the most derived form, *Chitinolepas*, further development of this character approaches the *Praelepas* form. *Chitinolepas* also possesses the most modified peduncle, with scale-like, rather spinous armature. Broch (1922) noted there was a carinal extension of the peduncle with spines in *I. pygmaea* that protects the basi-“carinal” area of the capitulum, and in *Chitinolepas* there is an enlarged peduncular scale in the carinal position – an incipient carina, *en route* to the *Praelepas* condition perhaps, and both have similarly configured scuta.

The phylogenetic model proposed here strengthens, as well as supports, the cladistic assessment of the Thoracica by Harris *et al.* (2000) and Pérez-Losada, *et al.*, (2004) based

in good part on molecular genetics, in which the *Ibla* can be seen as distinct from the remainder of the Pedunculata. But their treatment does not include fossil taxa. Of the four cladistic models proposed by Høeg *et al.*, (1999: 108), who do included fossils, this most closely fits the Adams consensus tree where *Ibla*, *Eolepas*, and *Praelepas* are shown as distinct from the other thoracicans. Nonetheless, it is maintained here that *Eolepas*, as presently known, had best remain with the Scalpelliformes, and that *Praelepas* is not an iblifform and should be included with the Lepadiformes.

Thoracican naupliar setation sequences: The larvae of *Ibla cumingi* have been recently described (Yan *et al.*, in press), who demonstrate that the species has the only planktotrophic nauplii known for the Iblifomes. Yan *et al.* utilised a condensed setation formula (their Table 1), a format suggested by Newman (1965), to summarize the ontogeny of the naupliar stages I–VI. The following naupliar stage VI setation sequence for *I. cumingi* is based on the illustrations of Yan *et al.*, (in press: Figs. 2–4):

1 13/14 25/26 44/45 50/51 67
SPPSSSSPPSPS.PPPPPPPPPPP.PSSSSSSSSSPFSSFSH:PPPPPP:SSSSSSPPPCPCP-:

An inspection of the 74 sequences presented by Newman & Ross (2001: Appendix 1) shows there can be as many as 67 setae in a thoracican setal sequence. However, the 67th is commonly absent in lepadomorphs, verrucomorphs, and lower balanomorphs (chthamaloids), and this is the case here. The setal sequence for the first antenna (interval 1–13) is SPPSSSSPPSPS. By further perusal of the previously known sequences, it will be seen that while this particular sequence is unique among thoracicans, it is closest to those of the chthamaloids (species 10–25) whose setation sequences are essentially intermediate between the scalpellomorphs and lower balanoids.

Intervals 14–25, and 45–50 (the exopods or largely swimming portions of the second antenna and mandible, respectively), include only plumose setae (P). This is a departure from the lepadomorphs and verrucomorphs, but it is commonly the case in the remainder of the thoracicans (species 6–8 and the majority of the species between 9–74; i.e. the scalpellomorphs and majority of balanomorphs, respectively). This leaves intervals 26–44, and 51–67 (endopods and bases of the second antenna and mandible, respectively). While the abundance of simple setae (S) in the distal portion of the antennal endopod is uniquely plesiomorphic to *I. cumingi*, the feathery (F) and hispid (H) setae on the proximal portion of the endopod, and the basis and of the second antenna (FSSFSH), are shared with scalpellomorphs, verrucomorphs, and the chthamaloid balanomorphs. The distal portion of the mandibular endopod also has an abundance of simple setae, as is commonly the case in scalpelliforms and lower balanomorphs, but the proximal portion and basis (PCPPCP-), while unique, is most like that in scalpelliforms and lower chthamaloids (species 6–19).

From the foregoing, it is evident that while the setation formula for *I. cumingi* is, with the apparent exception of two species of *Chthamalus*, unique; this is generally the case with setation sequences. Where there are notable similarities between various portions of

the sequence with the those portions in other taxa, it is generally with the lower or plesiomorphic forms, and since musculature of the larvae of *I. quadrivalvis* is apparently the least modified (reduced) of the thoracicans (Anderson 1987), it is not surprising the setation sequence of its sister species, *I. cumingi*, is likewise highly plesiomorphic. It is curious however that its setation sequence compares more favorably with that of the scalpelliforms and higher thoracicans, than with the more primitive lepadiforms. Pérez-Losada, *et al.*, (2004) also demonstrate this (see their fig, 1), where they show that there has been less change between the common ancestor of *Ibla* and the scalpello-verruco-balanomorph clade than the lepado-heteralepadomorph clade.

It would be instructive if it were possible to compare the stage VI nauplius of *I. cumingi* with those of the burrowing barnacles (Acrothoracica), but they are generally passed through in the egg, and where nauplii are known there are but four lecithotrophic stages with reduced setation (Turquier, 1967). Likewise, a comparison with stage VI nauplii of the closest living relatives of the Cirripedia, the Ascothoracida, could be useful. However, the only one known (Grygier, 1993) apparently has specialisations, such as deletions in the antennal endopodal enditic region (most setae being plumose rather than simple), and problems with the first antenna having a "spine" destined to become the antennular hook for which homology with a seta has not been established (Newman & Ross, 2001). Therefore, whether or not these more primitive out-groups had similar or significantly different naupliar setation sequences is unknown. Nevertheless, it can be deduced that while the setation sequence of the stage VI nauplius of *Ibla* differs from that of all other known thoracicans, it is by no means as different as lepadomorph stage VI naupliar sequences are from those of the balanomorphs, or those of the lower balanomorphs with respect to the higher balanomorphs. Therefore, the setation sequence of the stage VI nauplius of *I. cumingi* provides no support for a hypothesis calling for the separation of the iblomorphs from the Thoracica.

Cyprid lattice organs and naupliar setation notations: There are two pairs of anterior and three pairs of posterior lattice organs in the cyprid-like larvae of the Thecostraca. Those of the closest out-groups of the cirripedes, the Facetotecta/Ascothoracida, are arranged linearly along the mid-dorsal or hinge line, and the pairs have been numbered 1 to 5 (LO1–LO5 Jensen *et al.* 1994). Each lattice organ has a terminal pore, which in the Facetotecta/Ascothoracida opens posteriorly. This simple pattern (Figure 7A) becomes variously modified as one ascends the Thoracican tree.

In the Acrothoracica, the most primitive living thoracicans, members of the LO1 & LO2 pairs toed-in and toed-out respectively, and the terminal pores of LO2 are anteriorly rather than posteriorly situated (Jansen *et al.* 1994; not illustrated herein, but see following). This toe-in/toe-out arrangement is also seen in the Lepadomorpha, except that the terminal pores of both LO1 and LO2 are situated anteriorly (Figure 7D), and it is therefore what one would expect in the stem thoracican cyprid (Figure 7 B). In the rest of the thoracicans (Figure 7C, E–G), in addition to the LO1 and LO2 terminal pores being

situated anteriorly, both pairs toe-out (Jensen *et al.* 1998; Høeg *et al.*, 2004; Yan *et al.* in press). Thus, by anterior lattice organs, the Ibliformes (Figure 7C) is more like the Scalpelliformes-Verruco-/Balanomorpha (E–G) than the Lepadomorpha (D), something one would neither have predicted from the current classification (Table 1) nor from molecular genetics (cf. Pérez-Losada, *et al.*, 2004, Fig. 1).

As noted above, in the Facetotecta/Ascothoracida (Figure 7A) the posterior three pairs of lattice organs (LO3, LO4 & LO5) are also arranged linearly. This too is the plesiomorphic condition, and it is also seen in the lepadomorphs (Figure 7D) and Scalpelliformes-1 (Figure 7E), but in both, the posterior two of the three pairs are separated by the postero-dorsal portion of the opening to the bivalved carapace, and this is the condition one would expect in the stem thoracican cyprid (Figure 7B).

In the Acrothoracica the arrangement is different; e.g., while two of the three pairs of posterior lattice organs lie along the midline, a third pair has separated laterally and moved to flank them (an arrangement similar to that in Figure 7G). To explain this Jensen *et al.* (1994) infer that it was LO5 that separated and moved antero-laterally, so as to straddle LO3 & LO4, and this interpretation is tentatively accepted here. Variations in this pattern are found in the Ibliformes (Figure 7C), Scalpelliformes-2 (Figure 7F), and the sessile barnacles (Figure 7G, Verruco-/Balanomorpha). Thus, while in this regard the Ibliformes, as exemplified by *Ibla cumingi* (Figure 7C), is distinct from Scalpelliformes-1 (Figure 7E) as well as the Lepadomorpha (Figure 2D), it is similar to the remainder of the Thoracica (Figure 7F and 7G, the Scalpelliformes-2 and Verruco-Balanomorpha respectively). Indeed, *Pollicipes pollicipes* (Jensen *loc. cit.*, fig. 5E) is intermediate between *Capitulum mitella* (Figure 7E herein, deduced from Jensen *loc. cit.*, Fig. 6E) and the ibliform configuration, and *Chthamalus stellatus* (Jensen *loc. cit.*, Fig. 7B) appears intermediate between all three of these and Verruco-/Balanomorpha (Figure 7F, a consolidation of Figs. 2E, F of Jensen *loc. cit.*). But, considering the ranges of variation included in Scalpelliformes-1 and 2, when they are represented by only two species each, dividing them may be premature. However that works out, judging by lattice organs, the Ibliformes is more like the scalpelliform and verruco-/balanomorph lines than the lepadomorph line.

As noted in the previous section, a similar trend was found in the distribution of distinctive setae in nauplius VI setation sequences of thoracican cirripedes (Newman & Ross, 2001), and it can be summarized as follows. The nauplius has three pairs of limbs; the uniramous antennules (a'), biramous antennae (a'') and biramous mandibles (m). The nauplii of Ascothoracida and Acrothoracica have yet to provide adequate setation sequences, but fortunately we now have that for *Ibla cumingi*, the only ibliform known to have a planktotrophic nauplius (cf. Yan *et al.* in press), and therefore we begin here with it. While its antennule has no distinctive setae (-), the basal portions of its antenna and mandible, portions largely involved in feeding, have feathery (F) and hispid (H), and cuspidate (C) setae, respectively. Thus the ibliform nauplius can be characterized by an a'/a''/m notation of -/FH/C, as indicated to the right of C in Figure 7

While the naupliar setal notation for Scalpelliformes-1 (Figure 7D) is unknown (even though such common forms as *Scalpellum scalpellum* are known to have planktotrophic nauplii), it is likely the same as that for Scalpelliformes-2 (Figure 7F) and the Verruco-Balanomorpha (F), at least up to the balanoids; namely, -FH/C. Curiously, the balanoids change abruptly from -FH/C to -DC/C while their distinctive lattice organ pattern remains the same as that of the lower sessile barnacles (verrucids & chthamaloids, Figure 7G). This is instructive because in the lepadomorphs (Figure 7D), in addition to a distinctly different setal notation, B/FC/-, the arrangement of the anterior two pairs of lattice organs also distinguishes them from all other thoracicans. Thus, the lepadomorphs differ in larval characters from other thoracicans considerably more than the higher balanoids do from lower sessile barnacles, but at the present state of our knowledge such differences do not preclude their being monophyletic (Newman, 1987; Pérez-Losada, *et al.*, 2004). On the other hand, judging from larval characters, the Lepadomorpha (and presumably the genetically closely related Heteralepadomorpha for which no larvae have been described), apparently diverged from the stem thoracican stock, rather than from the Ibliformes as might be inferred from molecular genetics.

As for the Ibliformes, while closer by larval characters to the scalpelliform-verrucobalanomorph line than to the lepadiform line, there are problems; e.g., 1) the apparently advanced arrangement of the posterior three pairs of lattice organs being comparable to those of Scalpelliformes-2 rather than Scalpelliformes-1, and 2) the genetics suggesting they are more closely related to the Lepadomorpha than to the Scalpelliformes. This, in conjunction with unique ibliform adult characteristics, such as the carapace adductor muscle being anterior rather than posterior the esophagus, suggests the Ibliformes also arose independently (paraphyletically) from the stem thoracican stock, and molecular genetics is compatible with such a interpretation. Thus, while larval evidence supports our proposal to abandon the Pedunculata as a monophyletic taxon, it does not support separation of the Ibliformes from the Thoracica. So, in more specific terms, what does molecular genetics illustrate with regard to these relationships?

Molecular genetics

From a comparison between the fossil record (Newman *et al.* 1969: Tab 2) and the phylogram provided by Pérez-Losada *et al.* (2004), it can be observed that age estimates based on molecular evidence are invariably older than those of the fossil record. This suggests that recalibration maybe in order, and for illustrative purposes, we first skeletonised the tree of Pérez-Losada *loc cit.* (Figure 8). Since the offset appears to be systematic, we have simply moved each of the age estimates and their corresponding periods (between nodes 19 and 41), down one node each. This reduces the age and corresponding period for each taxon, as indicated in parentheses, and the results are summarised as follows:

1) The rhizocephalan divergence from earlier cirripedes (node 45) should be adjusted from the Vendian (Precambrian) to no earlier than the Cambrian, as Early Cambrian is given for the crustaceans in general. Thus the systematic adjustment to Vendio-Cambrian is still too early.

2) The ibliform divergence (node 41) has been adjusted from the Vendio-Cambrian to the Cambrio-Ordovician. In light of the previous change, adjustment to no earlier than Early Cambrian is a given. Nonetheless, as seen at the next node, an adjustment to as late as the Ordovician is a possibility.

3) The lepadiform divergence (37) has been adjusted from Cambrio-Ordovician to Early Carboniferous. This would be fine, since the praelepadomorphs appear then, but only if they and the lepadomorphs are closely related. However the lepadomorphs, (upon which that this node was based), do not appear in the fossil record until the Early Eocene, so from the lepadomorphs alone, the adjusted age would still be much too early. On the other hand, the heteralepadomorphs have also been tentatively included in the Lepadiformes, because of their relatively close affinities indicated by molecular genetics, and *Priscansermarinus* from the Middle Cambrian has been tentatively included in the Heteralepadomorpha (Newman, 1996). Furthermore, our larval analysis suggests the Lepadomorpha diverged from an early thoracican stock distinct from the ibliform-scalepliliform line, and this most likely would also have been in the Cambrian. If so, the initial calibration would be more in keeping with the facts than the adjusted one. Appropriate larval as well as additional genetic data for the heteralepadomorphs could help resolve the situation in general as well as within this order.

4) The scalpelliform divergence (36), is adjusted from the Early Carboniferous to the Early Jurassic, which would be about right if the equivocal *Pabulum* (Early Carboniferous) were not acceptable as a scalpelliform, since at least *Archaeolepas* (Early Jurassic) among the eolepadids is an uncontested scalpelliform. If *Eolepas* (Early Triassic) remains a scalpelliform, the adjusted divergence for the scalpelliforms would be a bit too late.

5) While the divergence times of the sessile barnacles are not at issue here, but the fact is, other than for the verrucomorphs, where genetic data is available, divergence time estimates are earlier than expected, even when readjusted. The verrucomorphan divergence (30), adjusted from Early Jurassic to Late Cretaceous, is in keeping with an extensive fossil record. Genetics places the verrucomorphs (with their bilaterally asymmetrical shells) closest to the balanomorphs (chthamaloids and balanoids, which have symmetrical shells). On the other hand, it has been inferred that the brachylepadomorphs (which are also bilaterally symmetrical but for which there is yet no genetic information), gave rise to both of them. Therefore the brachylepadomorphs have been inserted in the phylogram (Figure 8) in a dotted box below the verrucomorphs, and it will be observed that their age, based on the fossil record alone, is in keeping with the general scheme.

6) The chthamaloid divergence (21) moves from the Late Cretaceous to later in the Late Cretaceous. This would be fine if the Cretaceous *Pachydiadema* had not been rejected as a balanomorph (Buckeridge 1996). Nonetheless, as it stands Early Tertiary is no less likely.

7) The balanoid divergence (20) is adjusted from Late Cretaceous to Palaeocene-Eocene, which still may be a little early.

From the forgoing, it can be seen that the initial times of divergence were more or less too early for 6 of the 7 taxa, the exception, 3), being the lepadiforms, especially if *Priscansermarinus* and larval characteristics are also taken into consideration. Thus, the systematic reduction in their ages was a largely a step in the right direction, but how much did it improve things? The adjustments left 1), 6) & 7) with improved but still perhaps somewhat earlier dates than expected and with 5) just right and 4) probably right if *Pabulum* were ignored. That leaves two: 2) likely being a little too late and 3) being complicated by the ancillary considerations just noted. Therefore, in the main, this simple recalibration improved the situation for most of the taxa involved, and therefore we are confident that it was justified.

However the details workout, it is gratifying to see that the order in which these higher taxa appeared, their separation in geologic time, and their diversification in adult and now larval morphological complexity, all falls in a logical sequence. This was first addressed by Darwin in his four monographs on the Cirripedia and it is now being substantiated and elucidated by molecular genetics, without which we could not be so confident that the living iblifforms are relics of the Early Palaeozoic (indeed, the most primitive of the thoracicans known). That they have their greatest diversity in the great refugium offered by the Southwest Pacific is notable.

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