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Revision of the amphipod (Crustacea) family Stegocephalidae

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The amphipod (Crustacea) family Stegocephalidae Dana, 1852 is revised, and the results of a phylogenetic analysis of the family are presented. The morphological information, obtained mainly through direct examination of the species, has been transformed into 200 characters. 91 stegocephalid species (91% of all recognized species) are included in the analysis, in addition to six outgroup taxa. Based upon this analysis, the family is divided into five subfamilies and 26 genera. Four new subfamilies (Andaniexinae, Andaniopsinae, Bathystegocephalinae & Parandaniinae) and ten new genera (*Alania, Austrocephaloides, Austrophippsia, Bouscephalus, Gordania, Mediterexis, Pseudo, Schellenbergia, Stegonomadia* & *Stegomorphia*) are erected. Five genera are put into synonymy (*Andaniella* with *Andaniopsis*; *Phippsiella* and *Stegocephalopsis* with *Stegocephalus*; *Stegophippsiella* with *Stegocephalina*; *Euandania* with *Parandania*).

ADDITIONAL KEY WORDS: Phylogeny, classification, morphology, analysis.

INTRODUCTION

The present paper is the last in a series of taxonomic papers (Berge & Vader, 1997a–d, 2000,2001, in press a–c; Berge, 2001, a–c; Berge, Boxshall & Vader, 2000; Berge, De Broyer & Vader, 2001; Berge, Vader & Galan, in 2001) on the amphipod family Stegocephalidae Dana, 1852 (Crustacea). In the previous papers, focus has been on providing as much detailed knowledge as possible at the specific level, while relationships at the generic level have been left mostly undiscussed. The main purpose of the present paper is to present a revised classification of the Stegocephalidae, based on the results of a phylogenetic analysis of the family.

The family Stegocephalidae was first described as a subfamily of the Gammaridae by Dana in 1852. Later, the subfamily Stegocephalinae was transferred to the Leucothoidae by Boeck in 1876, until Sars (1883) changed its taxonomic rank to that of a family. The last revision of the family was that by Stebbing (1906); at the time the family consisted of 12 species (of which Stebbing thought two were uncertain) and nine genera. Today, the family consists of 100 species, herein allocated to 26 different genera.

There has, however, never been any thorough discussion of the phylogenetic relationships within the Stegocephalidae, except for the splitting of the family by Barnard & Karaman (1991) into two groups based upon the second maxilla: those possessing an ordinary outer plate and those in which it is gaping and geniculate. A number of character states that earlier authors (e.g. Sars, 1891) thought were 'of generic value' (such as the number of articles on the palp of the first maxilla, the morphology of the basis of pereopods 6 and 7, the form of the telson (cleft or entire), and the number of articles on the outer ramus of U3) have later been found in other closely related genera, thereby blurring the distinctions between them. The classical genera have, until the present, nevertheless been sustained in the classification of the family, thereby resulting in unclear phylogenetic relationships. As an example, the four genera *Phippsiella* Schellenberg, 1925, *Stegocephalus* Krøyer, 1842, *Stegocephalopsis* Schellenberg, 1925, and *Stegocephaloides* Sars, 1891 were all erected based on different combinations of the states of the following three characters: articulation of the palp of mx1, and morphology of the bases of pereopods 6 and 7. Although later new taxa were discovered that variously combined the different states of these characters, the boundaries between the four genera were still retained. This state of affairs, added to the erroneous observation that the palp of mx1 of *S. inflatus* is uni-articulate (see Berge & Vader, 2001) led B & K to conclude that "the classification of genera

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remains cloudy especially in *Phippsiella, Stegocephalus, Stegocephalopsis, Stegocephaloides,* and two anomalous taxa *Stegocephaloides camoti* and *Stegocephalopsis katalia*". Herein, three of the genera discussed above (*Phippsiella, Stegocephalus,* and *Stegocephalopsis*) are considered to be synonymous.

MATERIAL AND METHODS

The analysis presented herein was performed by PAUP* (Swofford, 1998), and is based on a matrix consisting of 97 taxa (91 stegocephalid taxa and six outgroup taxa) and 200 characters. The analysis was carried out by first running 10 000 replicates with a random addition sequence and with 'MulTrees' option in PAUP* turned off. Then, the resulting tree was used as starting tree in a final analysis with 'MulTrees' operational.

The list of characters that were used in the analyses is presented in Appendix 1, and the entire matrix is presented in Appendix 2. The list of apomorphies is presented in Appendix 3.

The choice of outgroup is based mostly on the result of a phylogenetic analysis of the Amphipoda presented elsewhere (Berge, Boxshall & Vader, 2000), which suggests the Lysianassoidea as the most probable outgroup. However, in order to both broaden the outgroup and to 'test' the stability of the ingroup, other outgroups were also selected. Thus, two lysianassid species were selected, in adddition to one species of the four families Amphilochidae, Astyridae, Ochlesidae and Liljeborgiidae, respectively.

Under the discussion (see below) of the different subfamilies and genera, a short morphological description is provided. These descriptions will emphasize the same characters throughout, but characters are usually excluded when they appear in more than one state within the taxon. These short descriptions are meant to be informative about the morphological characteristics of the taxon, but also to provide a set of easily obtained characters by which the taxon in question may be compared to other closely related taxa. Thus, the synapomorphies that define the hypothesized monophyletic taxa may in many cases not be included, and the short descriptions should for this reason not be considered as diagnoses.

Under each genus, the distribution is briefly considered and discussed, but a complete review of the distributional data is presented in Appendix 4. An index of subfamilies, genera and species is included in Appendix 5.

CHARACTERS

One character (#82) is a multistate character (6 states), all others are binary. The character states describing the different arrangements of setae on both maxillae and the maxilliped were discussed and explained by Berge (2001b), and will not be discussed any further herein. Other characters, however, have previously been used in the description of species (e.g. Berge, 2001a–c) without having been the subject of any discussion; these will be discussed briefly below.

Character 4: antenna 1 flagellum articulation between articles one and two.

In most species, article one of the flagellum is conspicuously long compared with the other articles, but the flagellum possesses in addition an equally conspicuously short second article. The articulation appears to be weak compared to the other articulations, but is undoubtedly present in some species.

Character 6: antenna 1 accessory flagellum articulation.

A second article on the accessory flagellum is either absent, or present only as a rudimentary second article on the apex of the first article on the accessory flagellum.

Characters 11, 12: morphology of the epistome (see Appendix 1 and Figs 4 & 5).

The present characters are illustrated in Figures 4 and 5, where the epistome of *Andaniexis lupus* Berge & Vader, 1997c is pictured. In Figure 5, the epistome is produced laterally into two elongated ridges that cover most of the epistome. In other species, these laterally produced ridges may be conspicuously rounded (*vs* rectangular).

Characters 21–24: lacinia mobilis on the left mandible (always absent on the right in the Stegocephalidae).

The morphology of the lacinia mobilis can be divided into two major states: powerful or weakly developed. The powerful lacinia mobilis has a broad toothed cutting edge (usually as broad as the incisor), with the inner margin conspicuously expanded. Conversely, the weakly developed lacinia mobilis is either conical or rectangular to triangular, but both margins are straight (*vs* expanded). Furthermore, the cutting edge is either smooth or only weakly toothed.

Characters 106–110: labrum.

The labrum is considered reduced if its length is shorter than its breadth. The two distal lobes may be symmetrical or asymmetrical, depending upon whether both lobes are reduced or not.

Character 113: distal finger on the labium.

Distally on the outer lobe of the labium (the inner lobe is always absent in the Stegocephalidae), there are usually one or more 'fingers'. These processes are typically pointed and acute, but may also appear distally blunt, crenulated or bifid.

Characters 151, 152: pereopod 6 basis.

In the traditional classification of the Stegocephalidae, many taxa were classified as possessing an unexpanded (i.e. linear) posterior margin of the basis on pereopod 6. However, close examination of the morphology of most stegocephalid species revealed that many taxa that had been described as possessing an unexpanded basis, did in fact have a rudimentarily expanded basis. Such rudimentary expansion can usually only be seen at high magnification.

Character 193: submarginal setae on the apex of each lobe of the telson.

In species that possess a cleft telson, there is usually one submarginal seta on the apex of each lobe. However, in many stegocephalid species the telson is entire (i.e. not cleft), but they may still possess setae located at about 'the same place', i.e. if the telson had been cleft the setae would have been located submarginally on each lobe. However, in those species that possess a short, cleft and rounded telson (e.g. *Andaniotes* spp.), the submarginal setae are not located at the very apex of each lobe, but more laterally on the lobes. The presence of these submarginal setae is therefore considered to be a potentially homologous character state.

RESULTS

The 10 000 initial replicates (random addition sequence and 'MulTrees' turned off) resulted in 23 trees with a length of 1353 steps. The final search (which used this tree as a starting point, with 'MulTrees' turned on) produced 48 trees of the same length as the starting tree. In Figure 1 tree #1 is presented, with a corresponding list of apomorphies in Appendix 3. Character states were optimized using the ACCTRAN option in PAUP*. The strict consensus of these 48 rooted cladograms is shown in Figure 2. In Figure 3, the relationships between the 26 genera are illustrated, with the five junior synonyms indicated after their senior synonym.

According to the topology of the strict consensus tree, the family Stegocephalidae is divided into five major clades, herein treated as subfamilies (Figs 1–3): Andaniexinae, new subfamily; Andaniopsinae, new subfamily; Bathystegocephalinae, new subfamily; Parandaniinae, new subfamily; Stegocephalinae Dana, 1852.

TAXONOMY

FAMILY STEGOCEPHALIDAE DANA, 1852

Subfamilies

Andaniexinae, new subfamily; Andaniopsinae, new subfamily; Bathystegocephalinae, new subfamily; Parandaniinae, new subfamily; Stegocephalinae Dana, 1852.

Remarks

The family Stegocephalidae consists today of 99 valid described species, but this is possibly a significant underestimation of the true number (see also Discussion). Following both the present revision and a number of papers on Stegocephalidae published in recent years, at least five new and undescribed taxa have been reported (e.g. De Broyer & Rauschert, 1999: 286; Berge, 2001a), in addition to three new unpublished species (Berge & Vader, in prep.). In this revision, only one (*Austrocephaloides* nr. *camoti*, see below) of these undescribed taxa has been included.

General morphology

The Stegocephalidae are characterized by their globular body form, partly due to their large and rounded coxae-shield (coxae 1–4). The accessory flagellum on antenna 1 is relatively small and never has more than two articles (the last article is either minute or the articulation between them is lost). The two antennae are subequal in length. The mouthparts are characterized by the absence of both the molar and the palp on the mandible, and the outer plate on the second maxilla is always much narrower than the inner. The basis on pereopod 5 is linear and unexpanded, whereas the basis of pereopod 6 varies between unexpanded and linear to broad and rounded. The telson is flat, but varies between entire and cleft. Gills are generally present on pereopods 2–7, but a few species of the genus *Andaniotes* have lost the gills on the last pair of pereopods. Similarly, oostegites are usually present on pereopods 2–5, but within the genus *Andaniotes* the oostegites are, in some species, absent on pereopods 4 and/or 5.

Sexual dimorphism is generally weak, but the propodus of pereopod 2 is generally larger in males than in females. Furthermore, the males of the genus *Andaniotes* possess a conspicuously enlarged urosome (see below and Berge, 2001a).

Biology

The Stegocephalidae consist predominantly of true deep-sea species, usually recorded from either the bathyal (200–2000 m) or abyssal (2000 +) zones, but three species have also been recorded from the intertidal zone [*Stegocephalina pacis* (Bellan-Santini & Ledoyer, 1974) from the Kerguelen Islands, and *Andaniotes corpulentus* (Thomson, 1882) and *Tetradeion crassum* (Chilton, 1883), from New Zealand]. In general they appear to be micro-predators, and are often recorded in association with benthic sessile invertebrates (e.g.

KEYS TO THE SUBFAMILIES

(A)

1. Maxilla 2 outer plate absent .... Bathystegocephalinae
   Maxilla 2 outer plate present 2
2. Maxilla 2 outer plate gaping and geniculate .... Stegocephalinae
   Maxilla 2 outer plate not gaping and geniculate 3
3. Antenna 2 peduncle article 5 elongate: twice as long as article 4 and conspicuously longer than the entire peduncle on antenna 1 .... Parandaniinae
   This combination not present 4
4. Mandibular incisor and left lacinia mobilis toothed (incisor sometimes only partly), maxilla 1 palp uniarticulate and short (not exceeding outer plate) .... Andaniopsinae
   Mandibular incisor smooth, maxilla 1 palp well developed .... Andaniexinae

(B)

1. Telson entire 2
   Telson cleft 6
2. Telson longer than broad, rounded .... Stegocephalinae
   Telson not longer than broad, triangular and/or weakly pointed 3
3. Antenna 1 flagellum with more than 10 articles; adult specimens larger than 20 mm .... Parandaniinae
   Antenna 1 flagellum with 4 or 5 articles; adult specimens smaller than 20 mm 4
4. Coxa 4 posterior margin concave, pleonites 1–3 usually toothed dorsally .... Andaniexinae
   Coxa 4 posterior margin not concave, pleonites smooth 5
5. Pereopod 6 basis weakly expanded, subrectangular .... Andaniopsinae
   Pereopod 6 basis broad (2 × broader than basis on pereopod 5), rounded .... Andaniexinae
6. Telson longer than broad 7
   Telson not longer than broad 8
7. Mandibular incisor coarsely toothed, epistome smooth .... Stegocephalinae
   Mandibular incisor smooth, epistome produced laterally (see Figs 4 & 5) .... Andaniexinae
8. Pereopod 7 about half the length of pereopod 6; coxae 1–4 conspicuously rounded and deep .... Bathystegocephalinae
   This combination not present 9
9. Antenna 1 flagellum with more than 10 articles .... Parandaniinae
   Antenna 1 flagellum with 4 or 5 articles 10
10. Epistomal plate absent .... Stegocephalinae
    Epistomal plate present 11
11. Mandibular incisor toothed .... Andaniopsinae
    Mandibular incisor smooth .... Andaniexinae

Vader, 1984). In contrast to these general aspects of the biology of the stegocephalid species, Barnard & Karaman (1991: 672) noted that "most Stegocephalidae have strongly parasitic mouthparts and most have the globular body form of pelagic hyperiids". No true (obligate) parasitic stegocephalid species have, however, ever been recorded, although many have been found as associates of marine benthic sessile invertebrates. As for the body form resembling that of the pelagic hyperiids, this is mostly true for the non-pelagic species: most pelagic stegocephalids [except *Parandania gigantea* (Stebbing, 1883) and *P. nonhiata* (Andres, 1985)] are more elongate and have a more reduced coxae-shield, and thus do not look as globular as the non-pelagic taxa.

Apart from these general aspects, the biology of the stegocephalid species has only been examined briefly, although some authors have presented extensive research on the feeding biology of some species (mainly *Andaniexis abyssi*, *A. lupus*, *Andaniopsis nordlandica*, *Parandania boecki* and *Stegocephaloides christianiensis*; see Moore, 1979; Moore & Rainbow, 1984, 1992; Coleman, 1990; Moore *et al.*, 1994). For most of the examined species, examination of stomach contents and the presence of ferritin crystals in the gut caeca led the authors to conclude that they were predominantly micro-predators feeding on cnidarians. As the species examined are representatives from four of the five subfamilies (the monotypic Bathystegocephalinae is the only subfamily that is not represented), it seems natural to conclude that this feeding habit may be characteristic for the entire family. There is, however, one genus, *Andaniotes* (see below), in which the species have regularly been captured in baited traps, and thus

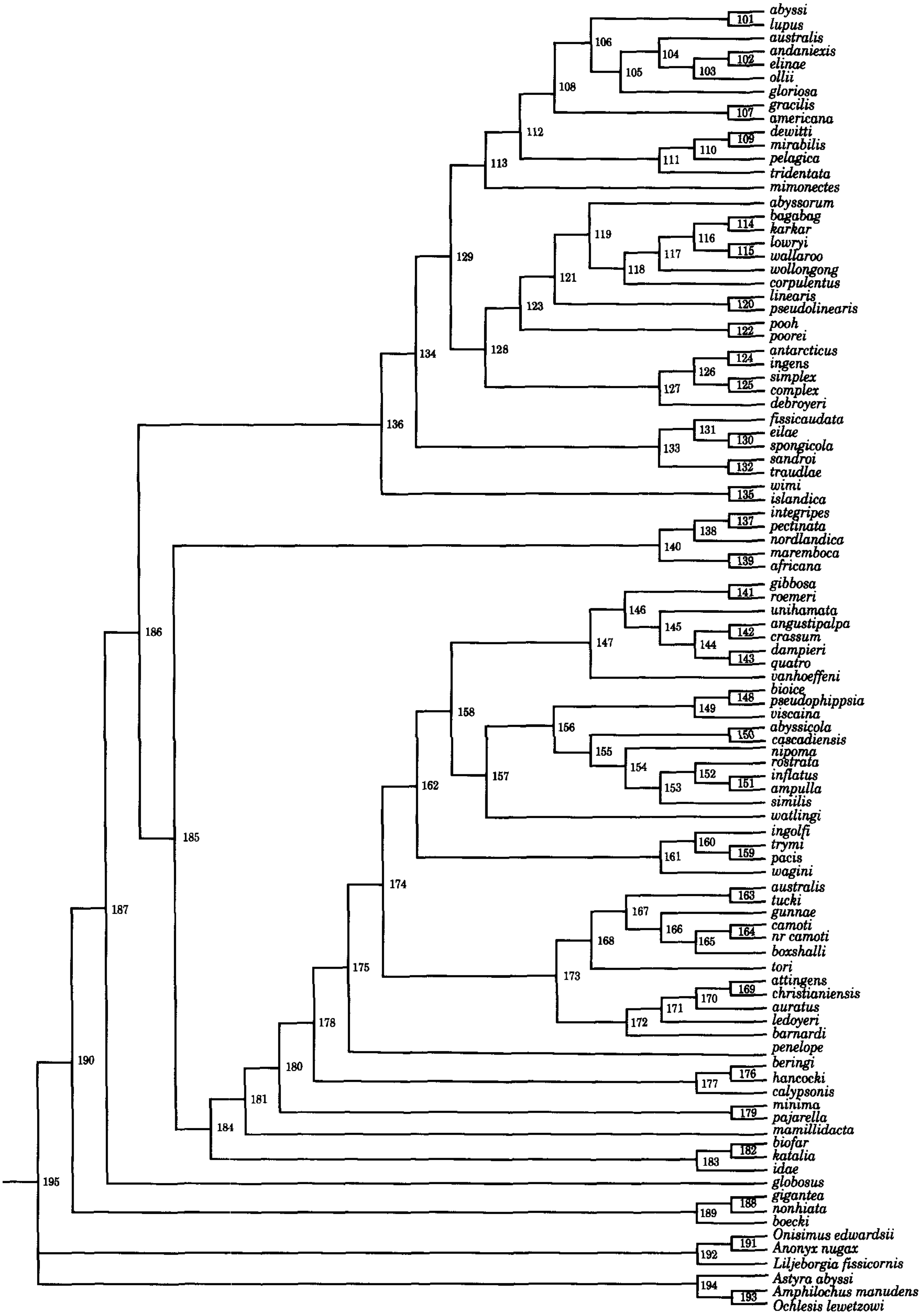


Figure 1. Tree 1 with the internal nodes labelled.

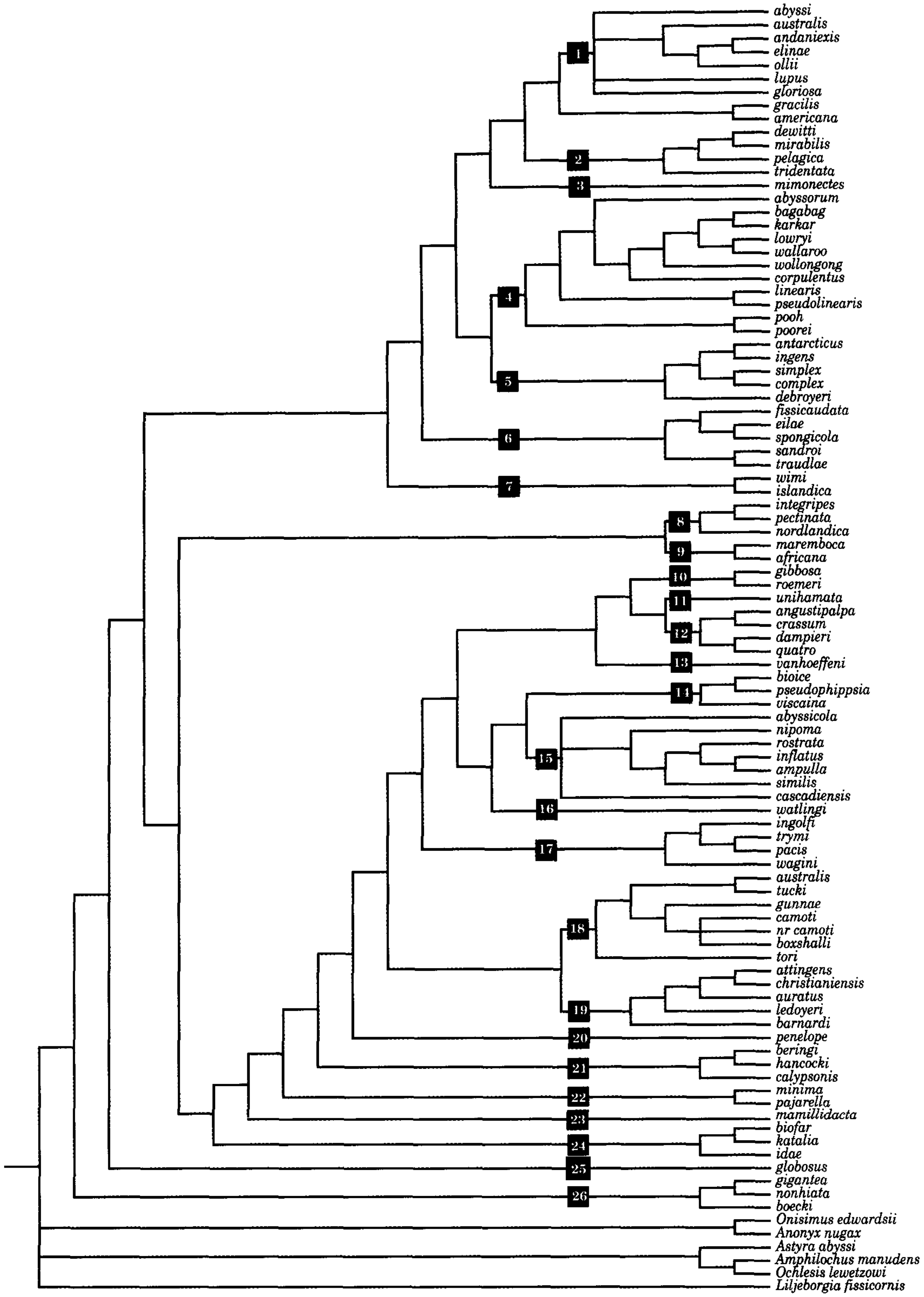


Figure 2. Strict consensus of all 48 most parsimonious trees. Labels on the branches refer to the 26 genera: 1: *Andaniexis*; 2: *Parandaniexis*; 3: *Mediterexis*; 4: *Andaniotes*; 5: *Stegosoladidus*; 6: *Glorandaniotes*; 7: *Metandania*; 8: *Andaniopsis*; 9: *Steleuthera*; 10: *Phippsia*; 11: *Austrophippsia*; 12: *Tetradeion*; 13: *Schellenbergia*; 14: *Pseudo*; 15: *Stegocephalus*; 16: *Stegomorphia*; 17: *Stegocephalina*; 18: *Austrocephaloides*; 19: *Stegocephaloides*; 20: *Stegocephalexia*; 21: *Alania*; 22: *Gordania*; 23: *Bouscephalus*; 24: *Stegonomadia*; 25: *Bathystegocephalus*; 26: *Parandania*.

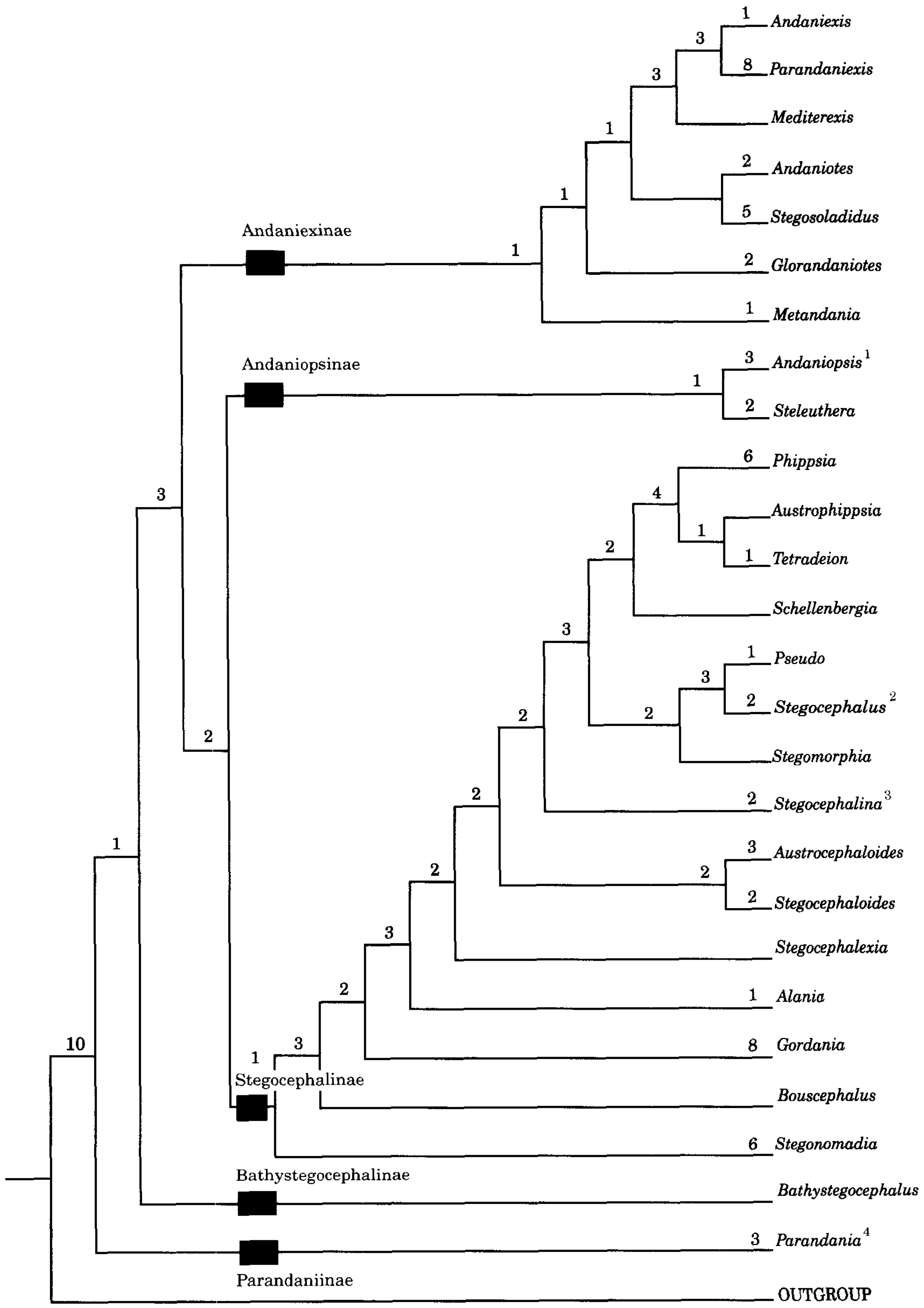


Figure 3. Cladogram describing the relationship between all 26 stegocephalid genera. The five subfamilies are indicated with boxes on the cladogram, and genera considered as junior synonymies are shown as footnotes. On each branch, the Bremer support (decay index) is indicated (branches without a Bremer support number are monotypic genera).

ANDANIEXINAE: KEY TO THE GENERA

1.	Telson entire	2
	Telson cleft	4
2.	Coxa 4 posteriorly concave (e.g. Watling & Holman, 1980: 650, fig. 26)	*Parandaniexis*
	Coxa 4 not posteriorly concave	3
3.	Uropod 3 outer ramus 1-articulate, antenna 1 flagellum 4-articulate	*Mediterexis*
	Uropod 3 outer ramus 2-articulate, antenna 1 flagellum 5-articulate	*Andaniexis*
4.	Epistomal plate large, conspicuous (Fig 5)	5
	Epistomal plate weakly developed	6
5.	Antenna 2 peduncle article 4 clearly shorter than 5	*Metandania*
	Antenna 2 peduncle article 4 about as long as 5	*Glorandaniotes*
6.	Urosome and/or uropods 1 or 2 conspicuously enlarged	*Andaniotes* (males only)
	Neither urosome nor uropods conspicuously enlarged	7
7.	Pereopod 7 similar to pereopod 6 (but usually smaller)	*Andaniotes*
	Pereopod 7 clearly differentiated from pereopod 6	8
8.	Coxae 1–4 overlapping each other or antenna 1 conspicuously longer than antenna 2	*Stegosoladidus*
	Coxae 1–4 contiguous and antennae subequal	9
9.	Epimeral plate 3 posterior margin straight	*Andaniotes*
	Epimeral plate 3 posterior margin medially curved	*Glorandaniotes*

seem to be (or at least be facultatively able to function as) necrophagous species.

ANDANIEXINAE SUBFAM. NOV.

Type genus. Andaniexis Stebbing, 1906.

Genera

Andaniexis Stebbing, 1906; *Andaniotes* Stebbing, 1897; *Glorandaniotes* Ledoyer, 1986; *Mediterexis* n.gen; *Metandania* Stephensen, 1925; *Parandaniexis* Schellenberg, 1929; *Stegosoladidus* Barnard & Karaman, 1987.

Morphological characteristics

Antennae 1 with 4 or 5 (type) articles. Epistomal plate present, small or large. Epistome laterally produced (type) or smooth. Mandible left lacinia mobilis not distally expanded, incisor transverse and smooth. Maxilla 1 palp powerful. Maxilla 2 not gaping and geniculate, setae on outer plate simple. Labium broad. Pereopod 6 basis posteriorly conspicuously expanded. Telson not longer than broad.

Remarks

The present subfamily is one of the two major clades within the Stegocephalidae, and constitutes most genera with an ordinary maxilla 2. The group is defined by 10 synapomorphies (see Appendix 3, nodes 186 to 156). One of the morphologically most characteristic features of the subfamily is the laterally expanded epistome which is not found anywhere outside the Andaniexinae (but see Remarks under *Stegocephalina*). Furthermore, the combination of a transverse and smooth incisor is not found in any of the other subfamilies (*Andaniopsis* has a transverse but toothed incisor). The laterally produced epistome, however, is not present in the genus *Metandania* (the sister taxon to the remaining subfamily), and is thus only a synapomorphy for the remaining part of the subfamily (genera *Andaniexis, Andaniotes, Glorandaniotes, Mediterexis* and *Stegosoladidus,* and presumably secondarily absent in *Parandaniexis*).

Andaniexinae is, as defined herein, a morphologically very unified group, although some taxa appear to be more derived than others. This is first of all the case for the two pelagic genera *Metandania* and *Parandaniexis,* which have, according to Figure 2, shifted from a hyperbenthic to a pelagic habitat (see also Remarks under the respective genera) independently on two occasions. Secondly, within the genus *Stegosoladidus*, two species (*S. complex* and *S. simplex*) are highly derived, but it is unknown whether this is also correlated with a shift in habitat as for the two pelagic genera mentioned above.

ANDANIEXIS STEBBING

Andania Boeck, 1871: 128 [homonym, Lepidoptera]
Andaniexis Stebbing, 1906: 94 [new name]
Andaniexis Barnard & Karaman, 1991: 675
Andaniexis Berge & Vader, 1997c: 1430 and in press a
Andaniexis Berge, Vader & Galan, 2001 (part)

Type species. Andania abyssi Boeck, 1871 (selected by Boeck, 1876).

Species

Andaniexis abyssi (Boeck, 1871); *A. americana* Berge, Vader & Galan, 2001; *A. andaniexis* Berge & Vader, in press; *A. australis* K.H. Barnard, 1932; *A. elinae* Berge & Vader, in press a; *A. gloriosa* Berge, Vader & Galan, 2001; *A. gracilis* Berge & Vader, 1997; *A. lupus* Berge & Vader, 1997; *A. oculata* Birstein & Vinogradov, 1970; *A. ollii* Berge, De Broyer & Vader, 2000; *A. stylifer* Birstein & Vingradov, 1960; *A. subabyssi* Birstein & Vinogradov, 1955. [12 species.]

Short description of the genus

Antenna 1 flagellum 5-articulate. Epistomal plate present but small, epistome produced laterally, with a long ridge on each side covering the entire epistome. Mandibular incisor transverse, smooth; left lacinia mobilis not powerful. Maxilla 1 palp 2-articulate, powerful, distally with short robust setae; outer plate with ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Uropod 3 outer ramus 2-articulate. Telson short, entire.

Remarks

The present genus is defined by only two synapomorphies (see Fig. 1 and Appendix 3, nodes 112 to 108), a consequence of the close phylogenetic and morphological relationships between this and the two genera *Mediterexis* and *Parandaniexis* (see below). *Andaniexis* is one of the most speciose genera in the Stegocephalidae, with 12 described species, but it is still a morphologically highly unified group. Some taxa that have previously been associated with this genus are here transferred to other genera: *A. pelagica*, *A. spinescens* and *A. tridentata* to *Parandaniexis*, *A. eilae* and *A. spongicola* to *Glorandaniotes*, and *A. mimonectes* to *Mediterexis* (see Remarks under the respective genera). With the exception of *A. australis* (see Berge *et al.*, 2001), the present genus, as defined herein, is identical to what Berge & Vader (1997c: 1453) called "the *abyssi*-group".

Three species were not included in the analysis, due to lack of detailed information about the morphology of the mouthparts: *A. oculatus*, *A. stylifer* and *A. subabyssi*. However, their general morphology leaves no doubt that the three species do belong in the present genus (they were all considered part of the "*abyssi*-group" by Berge & Vader (1997c: 1453)).

Andaniexis is a widely distributed genus, represented in all geographical zones (Appendix 4) except one: the Mediterranean.

ANDANIOTES STEBBING

Andaniotes Stebbing, 1897: 30
Andaniotes Stebbing, 1906: 96
Andaniotes Hurley, 1955: 196
Andaniotes Watling & Holman, 1981: 219
Andaniotes Barnard & Karaman, 1991: 678
Andaniotes Lowry & Stoddart, 1995:
Andaniotes Berge, 2001a: 788
Not *Metandania* Stephensen, 1925: 136
Not *Glorandaniotes* Ledoyer, 1986: 957

Type species. Anonyx corpulentus Thomson, 1882.

Species

Andaniotes abyssorum (Stebbing, 1888); *A. bagabag* Lowry & Stoddart, 1995; *A. corpulentus* (Thomson, 1882); *A. karkar* Lowry & Stoddart, 1995; *A. linearis* K.H.Barnard, 1930; *A. lowryi* Berge, 2001a; *A. pooh* Berge, 2001a; *A. poorei* Berge, 2001a; *A. pseudolinearis* Berge, 2001a; *A. wallaroo* Barnard, 1972; *A. wollongong* Berge, 2001a. [11 species.]

Short description of the genus

Antenna 1 flagellum 4-articulate. Epistomal plate present, usually small, epistome produced laterally, with a long ridge on each side covering the entire epistome. Mandibular incisor transverse, smooth; left lacinia mobilis not powerful. Maxilla 1 palp 1-articulate, powerful, distally with long or short robust setae; outer plate with ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Uropod 3 outer ramus 2-articulate. Telson short, cleft.

Remarks

Andaniotes was recently revised by Berge (2001a), and its composition of species is herein left totally unchanged.

The present genus is defined by six synapomorphies (see Fig. 1 and Appendix 3, nodes 128 to 123). The males of the species of this genus possess a conspicuously enlarged urosome, together with an enlarged outer ramus on uropods 2 and/or 3, character states only found within the genus *Andaniotes*. For a further discussion on the genus, see Berge (2001a).

Andaniotes is a strictly southern taxon, found only in the Southern Hemisphere (mainly in the South Pacific, see Appendix 4).

GLORANDANIOTES LEDOYER

Glorandaniotes Ledoyer, 1986: 957
Glorandaniotes Barnard & Karaman, 1991: 679
Glorandaniotes Berge & Vader, in press a
Andaniexis Berge & Vader, 1997: 1448 (part)

Type species. Glorandaniotes fissicaudata Ledoyer, 1986: 958.

Species

Glorandaniotes eilae (Berge & Vader, 1997c); *G. fissicaudata* Ledoyer, 1986; *G. spongicola* (Pirlot, 1933); *G. sandroi* Berge & Vader, in press a; *G. traudlae* Berge & Vader, in press a. [5 species.]

Short description of the genus

Antenna 1 flagellum 4-articulate. Epistomal plate present, large or small; epistome not produced laterally. Maxilla 1 palp 1 or 2-articulate, powerful, distally with short robust setae; outer plate with ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Uropod 3 outer ramus 2-articulate. Telson short, cleft.

Remarks

Berge & Vader (1997a: 1453) discussed reasons for considering the three species *G. eilae*, *G. fissicaudata* and *G. spongicola* as one group ("*spongicola*-group"), but did not then transfer them into the same genus, mainly due to the general confusion that surrounded the genera *Andaniotes*, *Glorandaniotes*, and *Metandania* at the time: Barnard & Karaman (1991: 678–679) considered the three genera as one group, but did not synonymize *Glorandaniotes* with the other two although they did "not know how to distinguish this [*Glorandaniotes*] from *Andaniotes*" (Barnard & Karaman, 1991b: 679). Contrary to Barnard & Karaman's (1991b) concept, Berge & Vader (1997c) hypothesized that, based on the striking similarities in the mouthparts, the *spongicola*-group was closely related to *Andaniexis*. Neither hypothesis is confirmed by the present analysis, as *Glorandaniotes* appears as the sister group to the clade consisting of the five genera *Andaniexis*, *Andaniotes*, *Parandaniexis*, *Mediterexis* and *Stegosoladidus*. *Glorandaniotes* is defined by five synapomorphies (see Fig. 1 and Appendix 3, nodes 134 to 133).

Glorandaniotes appears to have a rather unusual distributional pattern (see Appendix 4); four of the five species are distributed in either the South Pacific or in the Indian Ocean, whereas the fifth (*G. eilae*) is only recorded from the North Atlantic (Iceland).

MEDITEREXIS GEN. NOV.

Andaniexis Ruffo, 1975: 449
Andaniexis Ruffo, 1993: 685
Andaniexis Berge & Vader, 1997c: 1430 (part)

Type species. Andaniexis mimonectes Ruffo, 1975. Monotypic.

Short description of the genus

Antenna 1 flagellum 4-articulate. Epistomal plate present but small, epistome produced laterally, with a long ridge on each side covering the entire epistome. Mandibular incisor transverse, smooth; left lacinia mobilis reduced, conical. Maxilla 1 palp 2-articulate, powerful, distally with short robust setae; outer plate with ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Uropod 3 outer ramus 1-articulate. Telson short, entire.

Etymology

Mediterexis mimonectes is one of only four stegocephalid species (*M. mimonectes*, *Pseudo pseudophippsia*, *Stegocephaloides barnardi* and *S. christianiensis*) that have been recorded from the Mediterranean, hence the name of the genus.

Remarks

Mediterexis is herein erected as a monotypic genus for *M. mimonectes* (Ruffo, 1975), a species that has until present been assigned to the closely related genus *Andaniexis*. As discussed above, *Mediterexis* is part of a monophyletic group consisting of *Andaniexis*, *Mediterexis* and *Parandaniexis* (see above), and is morphologically closely related to *Andaniexis*. These two genera are mainly separated on the absence, in *Mediterexis*, of an articulation on both the outer ramus on uropod 3 and between articles 1 and 2 on the flagellum of antenna 1. For a further discussion of the genus, see Remarks under *Andaniexis* and *Parandaniexis*.

Mediterexis is recorded from the Mediterranean and the North Atlantic (Bay of Biscay only).

METANDANIA STEPHENSEN

Metandania Stephensen, 1925
Metandania Schellenberg, 1953: 187
Metandania Berge, 2001a: 825
Metandania Berge, 2001c: 213
Andaniotes Barnard, 1969: 441 (part)
Andaniotes Barnard & Karaman, 1991: 678 (part)

Type species. Metandania islandica Stephensen, 1925: 136.

Species.

Metandania islandica Stephensen, 1925; *M. wimi* Berge, 2001c. [2 species.]

Short description of the genus

Epistomal plate large, epistome not produced laterally. Mandibular incisor transverse, smooth; left lacinia mobilis not powerful. Maxilla palp uni-articulate, distally with short robust setae; outer plate ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Telson short, cleft.

Remarks

Metandania was put into synonymy with *Andaniotes* by Barnard (1969: 441), but re-established as a valid taxon by Berge (2001a). Later, a second species, *M. wimi* Berge, 2001c, was described in the genus. However, as discussed by Berge (2001a), there are reasons to suspect that Stephensen's and Schellenberg's material, both identified as *M. islandica,* should be considered as representing two different species.

As the genus is defined herein, it consists of two species that, despite their similar morphology, appear to be inhabiting two very different habitats. *Metandania wimi* is only known from its type locality off Iceland, and was collected, as most other stegocephalid species, in a hyperbenthic sledge (at a depth of 680 m). The other species, *M. islandica,* appears to be a bathypelagic species, collected down to 7900 m.

Metandania is defined by eight synapomorphies (see Fig. 1 and Appendix 3, nodes 136 to 135), and is the sister taxon to the remaining subfamily. In contrast to the other genera within the Andaniexinae, *Metandania* does not possess a laterally produced epistome. For a further discussion of the genus, see Berge (2001a,c).

Metandania is not recorded from outside the North Atlantic.

PARANDANIEXIS SCHELLENBERG

Parandaniexis Schellenberg, 1929: 197
Parandaniexis Barnard, 1967: 141
Parandaniexis Watling & Holman, 1980: 651
Parandaniexis Ledoyer, 1986: 958
Parandaniexis Andres, 1977: 64
Andaniexis Ledoyer, 1986: 953 (part)
Andaniexis Berge *et al.*, 2001: 113 (part)

Type species. Parandaniexis mirabilis Schellenberg, 1929.

Species

Parandaniexis dewitti Watling & Holman, 1980; *P. inermis* Ledoyer, 1986; *P. mirabilis* Schellenberg, 1929; *P. pelagica* (Berge *et al.*, 2001); *P. spinescens* (Alcock, 1894); *P. tridentata* (Ledoyer, 1986). [6 species.]

Short description of the genus

Antenna 1 flagellum 5-articulate. Epistomal plate absent; epistome smooth. Maxilla 1 palp 2-articulate, powerful, distally with short robust setae; outer plate with ST arranged in two parallel rows. Maxilla 2 ordinary. Coxa 4 distally concave, pereopod 4 subchelate or simple. Pereopod 6 basis posteriorly expanded. Pleonites 1–3 dorsally smooth or produced. Uropod 3 outer ramus 2-articulate. Telson short, entire.

Remarks

Parandaniexis was erected for *A. mirabilis* by Schellenberg in 1929, based on its subchelate pereopod 4, short and distally concave coxa 4, elongate pereopods 5 & 6, and dorsal teeth on pleonites 1–3. All of these character states are, within the Stegocephalidae, unique for the genus, although all states are not present in all species simultaneously. Three species are herein transferred from *Andaniexis* to *Parandaniexis* (*P. pelagica, P. spinescens* and *P. tridentata*). The three species that are transferred from *Andaniexis* are identical to the three species that Berge & Vader (1997c: 1453) named the "*tridentata*-group".

Parandaniexis is defined by 14 synapomorphies (see Fig. 1 and Appendix 3, nodes 112 to 111), but is closely related to *Andaniexis*. Three genera (*Andaniexis, Mediterexis* and *Parandaniexis*) together constitute a monophyletic group defined by eight synapomorphies (see Fig. 1 and Appendix 3, nodes 129 to 113). They all share some striking similarities in the mouthparts (e.g. maxilla 1 and 2), but *Parandaniexis* is easily separated from the other two due to the highly derived 'external' morphology (e.g. pereopods 4, 5 and 6).

The fact that *Parandaniexis* is highly derived compared to the closely related genera *Andaniexis* and *Mediterexis* may be a consequence of adaptations to the pelagic habitat that these species occupy, in contrast to the hyperbenthic habitat of the other two genera. One other related genus within the subfamily Andaniexinae (*Metandania*) also contains pelagic species (only *M. islandica*), but according to the cladograms (Fig. 2), the shift from a hyperbenthic to a pelagic habitat has occurred independently. In both these taxa, however, the epistome is smooth (*vs* laterally produced), in contrast to all other members of the subfamily.

Two other taxa within the family, i.e. the two new subfamilies Bathystegocephalinae and Parandaniinae (see below), also consist entirely of pelagic species, but also their shift to a pelagic habitat seems independent to that of *Parandaniexis*. This hypothesis of independent shifts is supported by the fact that their adaptations are very different: *Parandaniexis* has basically lost the globular body form that is typical for most stegocephalid species, and shows a reduced coxaeshield and elongated pereopods 5 and 6 (possibly together with dorsal teeth on the pleonites which can be thought to have a function in stabilizing the direction of movement). The pelagic adaptations found in *Parandania* and *Bathystegocephalus* include the retention of the globular body shape and short pereopods

5 and 6, while the body size has increased and they have elongated antennae. However, the globular body shape of these last two groups could be further divided into two different categories: the Parandaniinae seem to resemble more closely the typical stegocephalid species in that the body itself has a conspicuously globular shape. The Bathystegocephalinae, on the other hand, have a relatively slender body, but it is the elongate and conspicuously rounded coxae-shield that accounts for the globular body shape [in contrast, *Parandania gigantea* (Stebbing, 1883) has actually very short and reduced coxae].

Parandaniexis is a strictly southern taxon (see Appendix 4), with three of the six species distributed in the Indian Ocean (*P. inermis*, *P. spinescens* and *P. tridentata*), one in the South Pacific (*P. mirabilis*), one in the Antarctic region (*P. dewitti*) and one in the South Atlantic (*P. pelagica*).

STEGOSOLADIDUS BARNARD & KARAMAN

Stegosoladidus Barnard & Karaman, 1987: 869
Stegosoladidus Barnard & Karaman, 1991: 683
Stegosoladidus Berge, 2001b: 596

Type species. *Andaniotes simplex* K.H. Barnard, 1930.

Species

Stegosoladidus antarcticus Berge, 2001b; *S. complex* Berge, 2001b; *S. debroyeri* Berge, 2001b; *S. ingens* (Chevreux, 1906); *S. simplex* (K.H. Barnard, 1930). [5 species.]

Short description of the genus

Antenna 1 flagellum 4-articulate. Epistomal plate present, usually small, epistome produced laterally, with a long ridge on each side covering the entire epistome. Maxilla 1 palp 1-articulate, powerful, distally with long or short robust setae; outer plate with ST arranged in a pseudocrown. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Uropod 3 outer ramus 2-articulate. Telson short, cleft.

Remarks

Stegosoladidus appears as a well defined clade, with 13 synapomorphies (see Fig. 1 and Appendix 3, nodes 128 to 127). The genus was recently revised by Berge (2001b), and its composition of species is herein left totally unchanged. For a further discussion on the genus, see Berge (2001b).

Stegosoladidus is a strictly southern taxon (see Appendix 4), found only in the Antarctic (*S. antarcticus*, *S. debroyeri* and *S. ingens*) or the South Pacific (*S. complex* and *S. simplex*).

ANDANIOPSINAE, SUBFAM. NOV.

Type genus. *Andaniopsis* Sars, 1891.

Genera. *Andaniopsis* Sars, 1891; *Steleuthera* Barnard, 1964.

Morphological characteristics

Antenna 1 flagellum with 4 articles. Epistomal plate present, usually large. Epistome laterally smooth. Mandible incisor transverse, toothed; left lacinia mobilis broad (distally produced), toothed. Maxilla 1 palp short, uni-articulate, distal setae short and simple; outer plate setae arranged in two parallel rows. Maxilla 2 outer plate not gaping and geniculate, setae distally simple. Pereopod 6 basis posteriorly weakly expanded.

Remarks

The Andaniopsinae appear as an intermediate clade between the derived Stegocephalinae and the more plesiomorphic Andaniexinae: the second maxilla is not gaping and geniculate, but the outer plate is considerably more elongate and narrow than in Andaniexinae. Furthermore, the mandibular incisors are toothed, but the orientation of the incisor is transverse. The Andaniopsinae resemble the Stegocephalinae in the broad and toothed lacinia mobilis and in the laterally unproduced epistome, but the outer plate of the first maxilla (setal-teeth arranged in two parallel rows) and the outer plate of the second maxilla (setae distally without hooks) resemble the character states found in Andaniexinae.

Andaniopsinae are defined by five synapomorphies (see Fig. 1 and Appendix 3, nodes 185 to 140).

ANDANIOPSIS SARS

Andania Boeck, 1871: 128
Andaniopsis Sars, 1891: 208
Andaniopsis Stebbing, 1906: 92
Andaniopsis Barnard & Karaman, 1991: 676
Andaniopsis Berge & Vader, 1997d: 349
Andaniella Sars, 1891: 210 (new synonymy)
Andaniella Stebbing, 1906: 93
Andaniella Barnard & Karaman, 1991: 675
Andaniella Berge & Vader, 1997d: 348

Type species. *Andania nordlandica* Boeck, 1871.

Species

Andaniopsis integripes (Bellan-Santini & Ledoyer, 1986); *A. nordlandica* (Boeck, 1871); *A. pectinata* (Sars, 1883). [3 species.]

ANDANIOPSINAE: KEY TO THE GENERA

1.	Telson entire	*Andaniopsis*
	Telson cleft	*Steleuthera*

Short description of the genus

Epistomal plate large, epistome laterally smooth. Mandible incisor transverse, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp short, uni-articulate, distally with short simple setae. Maxilla 2 not gaping and geniculate; outer plate setae distally simple. Maxilliped palp slender, weakly setose; inner plate with 2 nodular setae. Pereopod 6 basis slender to weakly expanded. Uropod 3 outer ramus two-articulate. Telson short, entire.

Remarks

Andaniella is herein synonymized with *Andaniopsis*, in order to avoid oversplitting of the clade. The type species of both *Andaniella* and *Andaniopsis* were both originally described in *Andania*, but Sars (1891) erected new genera for both, based primarily on the differences between these two species and the type species of *Andania*. *Andaniopsis pectinata* and *A. nordlandica* resemble each other in the mouthparts, but *A. pectinata* has the dactyli on pereopods 1 and 2 pectinate, the character upon which Sars based his description of *Andaniella*. Later, Bellan-Santini & Ledoyer (1986) described *Andaniella integripes* that does not possess any pectination on the dactyli on pereopods 1 & 2. *Andaniopsis* is defined by four synapomorphies (see Fig. 1 and Appendix 3, nodes 140 to 138).

Recently, Berge *et al.* (2001) described a new species assigned to the present genus: *Andaniopsis africana*. In accordance with the herein proposed phylogeny (Figs 1–3) of the Stegocephalidae, this species is transferred to *Steleuthera*.

One species (*A. integripes*) is restricted to the South Atlantic (see Appendix 4), whereas the other two species within the genus are widely distributed in both the Arctic and the North Atlantic.

STELEUTHERA BARNARD

Steleuthera Barnard, 1964: 15
Steleuthera Barnard & Karaman, 1991: 683
Andaniopsis Berge *et al.*, 2001: 117
? 'Unknown genus and species' Barnard, 1967: 150

Type species. Steleuthera maremboca Barnard, 1964.

Species

Steleuthera africana (Berge *et al.*, 2001); *S. maremboca* Barnard, 1964. [2 species.]

Short description of the genus

Epistomal plate large and conspicuous, epistome not produced laterally (convex). Mandible incisor transverse, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp short, uni-articulate, distally with short simple setae. Maxilla 2 ordinary; outer plate setae distally simple. Maxilliped palp slender, weakly setose; inner plate with 1 nodular seta. Pereopod 6 basis rudimentarily expanded. Uropod 3 outer ramus 1 or 2-articulate. Telson short, cleft.

Remarks

The present genus was erected by Barnard in 1964 for *S. maremboca*, mostly due to the (at the time) supposedly unique combination of the ordinary maxilla 2 (i.e. not gaping and geniculate), the toothed incisor of the mandible, the short and uni-articulate palp of the first maxilla, and the cleft telson. According to the present analysis, *S. maremboca* should be considered as the sister species to *S. africana*, which is herein transferred to *Steleuthera* from *Andaniopsis*.

Steleuthera maremboca is restricted to the South Pacific (see Appendix 4), whereas *S. africana* is recorded from the South Atlantic (see Appendix 4), possibly also from the North Pacific ('Unknown genus and species'; Barnard; 1967: 150).

BATHYSTEGOCEPHALINAE SUBFAM. NOV.

Type genus. Bathystegocephalus Schellenberg, 1926. Monotypic.

Morphological characteristics and remarks: see under the genus.

BATHYSTEGOCEPHALUS SCHELLENBERG

Bathystegocephalus Schellenberg, 1926a: 221
Bathystegocephalus Barnard & Karaman, 1991: 678
Bathystegocephalus Berge *et al.*, 2001: 119

Type species. Stegocephalus globosus Walker, 1909: 329. Monotypic.

Short description of the genus

Antennae elongate. Epistomal plate present. Mandible incisor triangular, toothed; left lacinia mobilis broad and toothed. Maxilla 1 palp uni-articulate, outer plate ST in two parallel rows. Maxilla 2 outer plate absent. Pereopod 6 elongate, basis rudimentarily expanded.

Uropod 3 outer ramus uni-articulate. Telson short and cleft.

Remarks

The present genus should, according to the strict consensus (Fig. 2), be considered as the type genus of a monotypic new subfamily, and is the sister taxon to the clade consisting of the three subfamilies Andaniexinae, Andaniopsinae and Stegocephalinae. Furthermore, the subfamily consists of only one highly derived species, defined by no less than 15 autapomorphies (see Appendix 3); it is the only species within the family in which the outer plate of maxilla 2 is lacking. As a result, it was difficult to assign the genus to either the "ordinary" or "gaping and geniculate" group as discussed by Barnard & Karaman (1991b) based on the morphology of the second maxilla. *Bathystegocephalus globosus* is a pelagic species that appears to be restricted to the Indian Ocean, but, as discussed above, it shows some very different adaptations to the pelagic habitat than those found in any of the other pelagic taxa in the family.

Bathystegocephalus is only recorded from the Indian Ocean.

PARANDANIINAE SUBFAM. NOV.

Type genus. Parandania Stebbing, 1899. Monotypic.

Morphological characteristics and remarks. See under the genus.

PARANDANIA STEBBING

Parandania Stebbing, 1899: 206
Parandania Stebbing, 1906: 95
Parandania Barnard & Karaman, 1991: 679
Parandania Berge, De Broyer & Vader, 2000: 223
Euandania Stebbing, 1899: 206 (new synonymy)
Euandania Stebbing, 1906: 97
Euandania Barnard & Karaman, 1991: 678
Euandania Berge, De Broyer & Vader, 2000: 223

Type species. Andania boecki Stebbing, 1888: 735.

Species

Parandania boecki (Stebbing, 1888); *P. gigantea* (Stebbing, 1883); *P. nonhiata* (Andres, 1985). [3 species.]

Short description of the genus

Epistomal plate present, epistome not produced laterally. Mandibular incisor transverse, smooth; left lacinia mobilis absent or reduced. Maxilla palp uni-articulate, distally with long setae; outer plate ST arranged in two parallel rows. Maxilla 2 ordinary. Pereopod 6 basis posteriorly expanded. Telson short, cleft (varies from cleft to entire in two species).

Remarks

The present genus consists of three species, two of which had been designated the type species of different genera (*Euandania* and *Parandania*), and is the sister taxon to the remaining family. To avoid 'over-splitting' of clades within the family, *Euandania* is herein synonymized with *Parandania*.

Parandania is a morphologically homogeneous genus, defined by ten synapomorphies (see Fig. 1 and Appendix 3, nodes 190 to 189). Its species are all very large (compared to other stegocephalid species) and pelagic, with morphological adaptations discussed above (see Remarks under *Parandaniexis*). In general, the mouthpart morphology is very similar to that of the Andaniexinae, but in contrast to that subfamily, the Parandaniinae do not possess a laterally produced epistome (see Figs 4, 5).

Two of the three species, *Parandania boecki* and *P. gigantea*, appear to be cosmopolitan (see Appendix 4), whereas the last species (*P. nonhiata*) seems to be restricted to the Antarctic. It should be noted, however, that the latter species was separated from its sister-species *P. gigantea* mainly on two characters, both of which must be considered at best as weak: telson broadly cleft with and absence of a lacinia mobilis on the right mandible. The former has previously been shown to be a highly variable (Watling & Holman, 1981; Berge & Vader, 1997b) character in both its congeners, ranging from entire to deeply cleft, whereas the latter is a synapomorphy for the entire family. At present, the only character that seems to separate *P. gigantea* and *P. nonhiata* seems to be the highly asymmetrical labrum in the latter. However, also this distinction may prove to be more apparent than real, as examination of the types of *P. gigantea* show that also this taxon does in fact possess an asymmetrical labrum, although not as conspicuous as in *P. nonhiata*. Until more material has become available for examination that can shed light on the status of these two taxa, *P. nonhiata* is herein retained as a valid species (see also Berge *et al.*, 2000).

STEGOCEPHALINAE DANA, 1852

Type genus. Stegocephalus Krøyer, 1842.

Genera

Alania gen. nov.; *Austrocephaloides* gen. nov.; *Austrophippsia* gen. nov.; *Bouscephalus* gen. nov.; *Gordania* gen. nov.; *Phippsia* Stebbing, 1906; *Pseudo* gen. nov.; *Schellenbergia* gen. nov.; *Stegocephalexia* Moore,

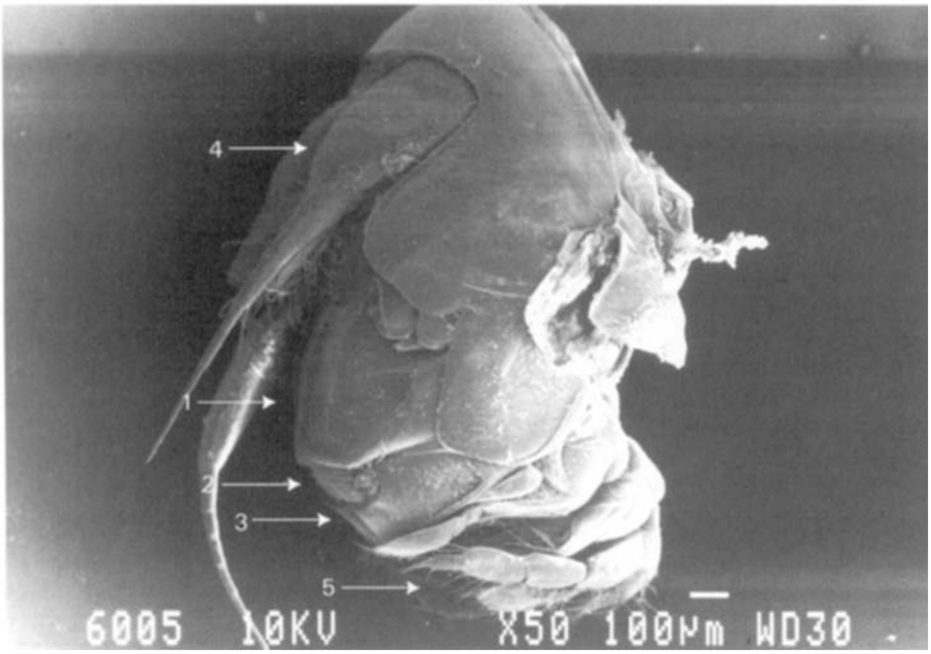


Figure 4. SEM photograph of the head of *Andaniexis lupus* Berge & Vader, 1997. Arrows: 1, epistome; 2, labrum; 3, mandibles; 4, antenna 1; 5, maxilliped.

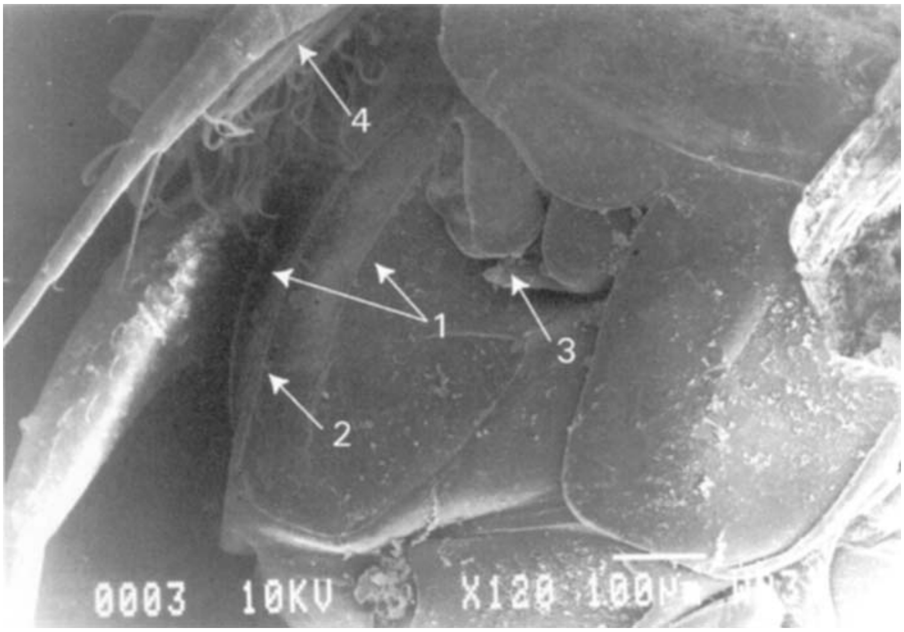


Figure 5. SEM photograph of the epistome of *Andaniexis lupus* Berge & Vader, 1997. Arrows: 1, laterally produced epistome; 2, epistomal plate (weakly developed); 3, peduncle (articles 1–3) antenna 2; 4, flagellum antenna 1.

1992; *Stegocephalina* Stephensen, 1925; *Stegocephaloides* Sars, 1891; *Stegocephalus* Krøyer, 1842; *Stegomorphia* gen. nov.; *Stegonomadia* gen. nov.; *Tetradeion* Stebbing, 1899.

Morphological characteristics

Epistomal plate variable, epistome usually not produced laterally. Mandible incisor lateral, toothed; left lacinia mobilis broad (distally produced), toothed. Max-

STEGOCEPHALINAE: KEY TO THE GENERA

1.	Telson entire	1
	Telson cleft	3
2.	Telson longer than broad	*Tetradeion*
	Telson not longer than broad	*Stegonomadia*
3.	Maxilliped palp dactylus bifid, with one pointed and one heavily setose part	*Austrocephaloides*
	Maxilliped palp dactylus simple and pointed	5
4.	Coxa 1 anteriorly concave	*Stegomorphia*
	Coxa 1 anteriorly convex	4
5.	Epistomal plate large and conspicuous	6
	Epistomal plate absent or rudimentary	8
6.	Antenna 2 peduncle articles 3–5 long, geniculate	*Austrophippsia*
	Antenna 2 peduncle article 3 short, not geniculate	7
7.	Coxa 4 very large: anteriorly concave and reaching beyond pereonite 7 posteriorly, epimeral plate 3 posteriorly pointed or conspicuously serrate	*Phippsia*
	Coxa 4 not reaching pereonite 7 posteriorly, epimeral plate 3 rounded, without serrations	*Austrocephaloides*
8.	Rostrum well developed and/or antenna 2 flagellum with more than 10 articles	*Stegocephalus*
	Rostrum absent or rudimentary, antenna 2 flagellum with no more than 10 articles	9
9.	Uropod 3 outer ramus 2-articulate	10
	Uropod 3 outer ramus 1-articulate	14
10.	Pereopods 3–6 merus, carpus and propodus anteriorly lacking setae	*Stegonomadia*
	Pereopos 3–6 merus, carpus and propodus anteriorly with setae	11
11.	Pereopod 6 basis posteriorly broad and rounded	12
	Pereopod 6 basis posteriorly unexpanded and linear	13
12.	Antenna 1 flagellum article about as long as peduncle	*Stegocephalus*
	Antenna 1 flagellum article 1 clearly shorter than peduncle	*Stegocephalexia*
13.	Antenna 1 flagellum with six or more articles	*Alania*
	Antenna 1 flagellum with four or five articles	*Austrocephaloides*
14.	Pereopod 6 basis posteriorly broad (broader than 1.5 times basis on pereopod 5), rounded	15
	Pereopod 6 basis posteriorly unexpanded (or rudimentarily expanded), linear	20
15.	Labrum about twice as long as broad, triangular	*Stegocephalina*
	Labrum about as long as broad, rounded	16
16.	Pereopod 2 ischium elongate (longer than 1.5 times the length of pereopod 1 ischium)	17
	Pereopod 2 ischium not elongate	18
17.	Maxilla 1 palp two-articulate	*Stegocephalus*
	Maxilla 1 palp uni-articulate	*Alania*
18.	Both antennae conspicuously longer than the depth of coxa 4	*Stegocephalus*
	Antennae not elongate	19
19.	Maxilla 2 inner plate setae rows widely separated	*Pseudo*
	Maxilla 2 inner plate setae rows appressed	*Gordania*
20.	Uropods 1 and 2 rami about half length of peduncle	*Bouscephalus*
	Uropods 1 and 2 rami clearly longer than half length of peduncle	21
21.	Epimeral plate 3 posteriorly serrate	22
	Epimeral plate 3 posteriorly not serrate	23
22.	Labrum twice as long as broad, triangular and pointed	*Stegocephalina*
	Labrum about as long as broad, not triangular	*Schellenbergia*
23.	Pereopod 7 basis distal margin pointed, basis exceeding merus distally	*Stegocephaloides*
	Pereopod 7 different from above	24
24.	Antenna 1 flagellum article 1 longer than peduncle	*Stegocephalina*
	Antenna 1 flagellum article 1 not longer than peduncle	*Stegocephalus*

illa 1 palp well developed, distal setae long; outer plate setae usually arranged in a pseudocrown. Maxilla 2 gaping and geniculate, outer plate setae distally with hooks (reduced in some taxa). Pereopod 6 basis posteriorly variable. Telson elongate.

Remarks

The present subfamily is the largest of the five stegocephalid subfamilies, both in number of species and genera. Furthermore, it does also appear to be the morphologically most variable and heterogeneous, although it is defined by 12 synapomorphies (see Appendix 3). Of these 12 synapomorphies, six are retained unchanged throughout the entire clade: (a) character #21, mandibular incisor with a lateral orientation; (b) character #34, setae on palp of the first maxilla with setules; (c) character #52, maxilla 2 gaping and geniculate; (d) characters 114/115, labium distally pointed and with distal finger present; and (e) character 194, telson elongate.

ALANIA GEN. NOV.

Stegocephaloides Berge *et al.*, 2001: 129 (part)
Stegocephalus Hurley, 1956: 28 (part)
Stegocephalus Berge & Vader, 2001b: 995

Type species. Stegocephaloides calypsonis Berge *et al.*, 2001.

Species

Alania beringi (Berge & Vader, 2001b); *A. calypsonis* (Berge *et al.*, 2001); *A. hancocki* (Hurley, 1956). [3 species.]

Etymology

The present genus is named after Prof. Alan Myers (Cork, Ireland), in honour of his valuable and significant contribution to the knowledge of the Amphipoda in general.

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp short, uni-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally unproduced, dactylus simple; inner plate with 1 (or without) nodular setae. Pereopod 2 ischium elongate. Pereopod 6 basis slender to broadly expanded. Telson elongate and cleft.

Remarks

The present genus appears as a morphologically diverse group, although the genus only consists of three species. The type species, *A. calypsonis*, was first described as belonging to the genus *Stegocephaloides*, although the morphology of especially the mouthparts differed from those typically found within that genus. Together with its two congeners, both originally described in *Stegocephalus*, *Alania* is defined by nine synapomorphies (Fig. 2, nodes 178→177; Appendix 3).

Alania is characterized by a relatively short, but powerful, uni-articulate palp on the first maxilla, an elongate inner plate (together with a reduced number of nodular setae) on the maxilliped, and a coxa 4 very similar to *Stegocephalus similis* (see below).

The genus is a widely distributed taxon, found in the Arctic (*A. beringi*), South Atlantic (*A. calypsonis*) and the North Pacific (*A. hancocki*).

AUSTROCEPHALOIDES GEN. NOV.

Stegocephaloides K.H. Barnard, 1916: 129
Stegocephaloides Barnard, 1967: 148
Stegocephaloides Berge & Vader, in press a (part)
Stegocephaloides Berge *et al.*, 2001 (part)

Type species. Stegocephaloides australis K.H. Barnard, 1916.

Species

Austrocephaloides australis (K.H. Barnard, 1916); *A. boxshalli* (Berge, Vader & Galan, 2001); *A. camoti* (Barnard, 1967); *A.* nr. *camoti* (Berge & Vader, in press a); *A. gunnae* (Berge & Vader, in press a); *A. tori* (Berge & Vader, in press a); *A. tucki* (Berge & Vader, in press a). [7 species.]

Short description of the genus

Epistomal plate absent or present, epistome convex (smooth). Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, 1-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally weakly produced, inner plate short, distally concave. Pereopod 6 basis weakly to broadly expanded. Uropod 3 outer ramus uni- or two-articulate. Telson elongate, cleft.

Etymology

The name of the genus is in analogy to its strictly southern distribution and to the close relationship between this genus and *Stegocephaloides*.

Remarks

All species within *Austrocephaloides* have previously been assigned to its sister taxon *Stegocephaloides* (see also Remarks under that genus), which is herein split into two clades. In addition to the 12 species that are allocated to either of these two genera, two additional species, *Alania calypsonis* and *Stegocephalina wagini* (see also Remarks under their respective genera), have also been, until now, assigned to *Stegocephaloides*. Thus, what appeared as a large and diverse group, which was difficult to isolate from other related genera (see e.g. Barnard & Karaman, 1991: 681), is streamlined by first removing the two most derived species

(*Stegocephalina wagini* and *Alania calypsonis*). Furthermore, the clade is divided into two different genera; for *Stegocephaloides s.s.* this seems adequate, as the five species within the genus are morphologically very similar. However, for the present genus, the clade could easily be divided into three genera (see below), but to avoid over-splitting, only two genera are identified.

One taxon is included in the list of species (see above) which has not yet been given any formal scientific name: *Austrocephaloides* nr. *camoti*. This species is known by only one specimen, but did show some significant differences from Barnard's description of the species (1967). However, as both these apparently different species are only known from one single specimen each, and since it was not possible to examine Barnard's material, *A.* nr. *camoti* was not erected as a valid species (Berg & Vader, in press).

Austrocephaloides is defined by only two synapomorphies (Fig. 2, nodes 173→168; Appendix 3), but the two genera together do constitute a morphologically highly unified group. However, within this genus, the species are more diverse, and easily separated into minor clades. Two of its species, *A. australis* and *A. tucki*, possess a conspicuous palp on the maxilliped (see description of e.g. *A. tucki* in Berge & Vader, in press), whereas two other species, *A. gunnae* and *A. tori* both possess a large and conspicuous epistomal plate. This character does, however, appear to have evolved independently, as the two taxa do not constitute a monophyletic clade.

Austrocephaloides is restricted to the southern hemisphere, found only in either the South Atlantic or the South Pacific (see Appendix 4).

AUSTROPHIPPSIA GEN. NOV.

Phippsia Berge & Vader, 2000 (part)

Type species. Phippsia unihamata Berge & Vader, 2000. Monotypic.

Etymology

The name of the genus refers to the strictly Antarctic distribution of this monotypic genus.

Short description of the genus

Antenna 1 accessory flagellum rudimentary. Epistomal plate present, large and conspicuous. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, two-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks (single). Maxilliped palp article 2 inner margin distally conspicuously produced, inner plate with 4 nodular setae. Pereopod 6 basis weakly expanded. Uropod 3 outer ramus two-articulate. Telson elongate, rounded and cleft.

Remarks

The present genus is part of a monophyletic clade, consisting of the four genera *Austrophippsia*, *Phippsia*, *Schellenbergia* and *Tetradeion*. In addition to the eight species represented in the cladograms (Figs 1–3), this clade also consists of two additional species *Schellenbergia pacifica* and *Tetradeion latus* (see Remarks under their respective genera).

Recently, Berge and Vader (2000) published a revision of the two genera *Phippsia* and *Tetradeion*, mainly on the basis of new extensive material from the Southern Hemisphere. In that paper, they argued that the ten species (herein found in the four above mentioned genera), should be considered as closely related, but did not, pending this family revision, erect any new genera.

Austrophippsia is erected as a monotypic genus to encompass *P. unihamata*, due to its position 'between' the genera *Phippsia* and *Tetradeion*. *Austrophippsia* possesses a cleft telson and oval labrum, characters that are shared with both *Phippsia* and *Schellenbergia*. However, the rudimentary accessory flagellum on the first antenna, and the long and geniculate peduncle on the second antenna, are characters shared with the more derived *Tetradeion*. Thus, both in terms of morphology and phylogeny, the present genus appears as a 'transition' clade between the derived *Tetradeion* and the more plesiomorphic genera *Phippsia* and *Schellenbergia*.

Austrophippsia is a strictly Antarctic genus.

BOUSCEPHALUS GEN. NOV.

Stegocephalopsis Moore, 1992: 930 (part)
Stegocephalopsis Berge and Vader, 2001: 994 (part)

Type species. Stegocephalopsis mamillidacta Moore, 1992. Monotypic.

Short description of the genus

Epistomal plate present, inconspicuous. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp short but powerful, uni-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally not produced, slender, inner plate with 2 nodular setae. Pereopod 6 basis unexpanded, rectangular. Telson elongate, cleft.

Etymology

To acknowledge both the quality and quantity of the taxonomic work on amphipods that Dr Ed Bousfield has carried out, especially in the North Pacific, this North Pacific genus is named after him.

Remarks

Bouscephalus mamillidacta (Moore, 1992) was originally described in the genus *Stegocephalopsis*, but both Moore (1992) and Berge and Vader (2001) noted that its morphology did not suggest any close phylogenetic relationships with the type species of *Stegocephalopsis*, *S. ampulla* (Phipps, 1774). In general, *B. mamillidacta* appears to be a rather derived species (17 autapomorphies, see Appendix 3). Thus, the allocation of the species to the genus *Stegocephalopsis* followed the general pattern, as identified by Barnard & Karaman (1991: 681), of treating *Stegocephalopsis* as a catch-all genus. The mouthparts of *B. mamillidacta* show some striking similarities to the relatively closely related genus *Stegonomadia*, but coxae 1–4 suggests that it is more closely related to *Phippsia*.

The genus is restricted to the North Pacific.

GORDANIA GEN. NOV.

Phippsiella Stephensen, 1925: 131 (part)
Phippsiella Barnard, 1967: 144 (part)
Phippsiella Berge & Vader, 1997d (part)

Type species .Phippsiella minima Stephensen, 1925.

Species.

Gordania minima (Stephensen, 1925); *G. pajarella* (Barnard, 1967). [2 species.]

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, two-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with or without hooks. Maxilliped palp article 2 inner margin distally unproduced, dactylus simple; inner plate with 2 nodular setae. Pereopod 2 ischium not elongate. Pereopod 6 basis broadly expanded. Uropod 3 outer ramus uni-articulate. Telson short to elongate, pointed and cleft.

Etymology

The genus is named after Dr Gordan Karaman, who during many years has poured out his numerous 'Contributions to the study of the Amphipoda'.

Remarks

The present genus is defined by nine synapomorphies (Fig. 2, nodes 180→179; Appendix 3), and consists of two minute species (<2.5 mm). Both species in the genus, *G. minima* and *G. pajarella*, were originally described in the genus *Phippsiella*. However, Steele (1967a) pointed out that immature specimens of *Stegocephalus inflatus* were very similar to *G. minima*, and that erroneous identifications of this kind had previously been published (Shoemaker, 1931). Although their general morphology, for example, is very close to *Stegocephalus inflatus*, the two congeners are best characterized by their unique arrangement of ST on the outer plate of the first maxilla. The ST are arranged in two parallel rows containing only six ST, as both ST A & B are absent, in addition to the absence of one ST in the first row.

Gordania is restricted to the Northern Hemisphere, with one species found in the North Atlantic (*G. minima*) and the other in the North Pacific.

PHIPPSIA STEBBING

Aspidopleurus Sars, 1891: 203 (homonym, Pisces)
Phippsia Stebbing, 1906: 89 (new name)
Phippsia Schellenberg, 1925: 197
Phippsia Stephensen, 1925: 133
Phippsia Berge & Vader, 2000 (part)
Phippsia Berge, Vader & Galan, 2001: 120

Type species. Stegocephalus gibbosus Sars, 1883.

Species.

Phippsia gibbosa (Sars, 1883); *P. roemeri* Schellenberg, 1925. [2 species.]

Short description of the genus

Antenna 1 accessory flagellum well developed. Epistomal plate present, large and conspicuous. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, two-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with double hooks. Maxilliped palp article 2 inner margin distally conspicuously produced, inner plate with 2 or 4 nodular setae. Pereopod 6 basis not expanded. Uropod 3 outer ramus two-articulate. Telson elongate, rounded and cleft.

Remarks

Based on the phylogeny as proposed herein, the present genus should only include the two species *P. gibbosa* and *P. roemeri*. Recently Berge & Vader (2000) revised the two sister taxa *Phippsia* and *Tetradeion*, and included four other species in the genus *Phippsia*: *Tetradeion angustipalpa*, *Tetradeion dampieri* (Berge & Vader, 2000), *Austrophippsia unihamata* (Berge &

Vader, 2000) and *Schellenbergia vanhoeffeni* (Schellenberg, 1926b). All are herein transferred to the three closely related genera *Austrophippsia*, *Schellenbergia* and *Tetradeion* (see below). These four genera (*Phippsia, Austrophippsia, Schellenbergia* and *Tetradeion*) constitute a monophyletic group, defined by eight synapomorphies (Fig. 1, nodes 158→147; Appendix 3), whereas the genus *Phippsia* is defined by seven synapomorphies (Fig. 1, nodes 146→141; Appendix 3).

As defined herein, *Phippsia* is a small and morphologically unified clade, although both species are easily separated on the shape of coxa 4: *P. gibbosa* has a very elongate posterior lobe, and with the distal (ventral) margin straight, whereas *P. roemeri* does not possess an equally elongate posterior lobe, and, more importantly, has the entire distal margin of the coxal plate curved (and thus with a coxae-shield similar to that of *Bathystegocephalus globosus*).

The genus is restricted to the Northern Hemisphere, with *P. gibbosa* and *P. roemeri* found only in the Arctic and the North Atlantic (not south of Norway).

PSEUDO GEN. NOV.

Phippsiella Barnard, 1967: 146 (part)
Phippsiella Bellan-Santini, 1985: 296 (part)
Phippsiella Ruffo, 1993: 687 (part)
Phippsiella Berge & Vader, 1997d (part)

Type species. Phippsiella pseudophippsia Bellan-Santini, 1985.

Species

Pseudo bioice (Berge & Vader, 1997d); *P. pseudophippsia* (Bellan-Santini, 1985); *P. viscaina* (Barnard, 1967). [3 species.]

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, 1- or 2-articulate. Maxilla 2 gaping and geniculate, outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally weakly produced. Pereopod 6 basis conspicuously expanded. Uropod 3 outer ramus uni-articulate. Telson elongate, cleft.

Etymology

The name refers to the impression that the morphology of the genus seems, at least for the mouthparts of its type species, as if designed by a committee; inner plate of the maxilliped similar to *Stegocephalus similis*, palp similar to *Phippsia*, second maxilla similar to *Stegocephaloides* and the first maxilla similar to *Stegocephalus inflatus*. In addition, the name of *P. pseudophippsia* was assigned by analogy of the close resemblance of the maxilliped palp between this species and the genus *Phippsia*.

Remarks

All the three species that are assigned to *Pseudo* have initially been assigned to *Phippsiella* (herein put in synonymy with *Stegocephalus*), but constitute a monophyletic group of their own (defined by four synapomorphies, see Fig. 2, nodes 156→149; Appendix 3).

Pseudo is a strictly northern taxon (see Appendix 4), with one species recorded from the North Atlantic (*P. bioice*), one from the Mediterranean (*P. pseudophippsia*) and one from the North Pacific (*P. viscaina*).

SCHELLENBERGIA GEN. NOV.

Stegocephaloides Schellenberg, 1926b: 299 (part)
Stegocephaloides K.H. Barnard, 1930: 328
Stegocephalopsis Barnard & Karaman, 1991: 681 (part)
Phippsia Gurjanova, 1951: 295 (part)
Phippsia Berge & Vader, 2000

Type species. Stegocephaloides vanhoeffeni Schellenberg, 1926b: 299.

Species.

Schellenbergia pacifica (Bulycheva, 1952); *S. vanhoeffeni* (Schellenberg, 1926b). [2 species.]

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, uni-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally weakly produced, inner plate with 2 nodular setae. Pereopod 6 basis weakly expanded. Epimeral plate 3 posteroventral corner strongly serrate. Uropod 3 outer ramus uni-articulate. Telson elongate, cleft.

Etymology

The present genus is named after the late Prof. A. Schellenberg, who described its type species.

Remarks

The type species of the present genus, *S. vanhoeffeni*, has previously been assigned to three other genera: *Stegocephaloides*, *Stegocephalopsis* and *Phippsia*. This flux in generic status can best be explained by the lack of a detailed description, especially of the mouthparts, of this taxon, until Berge & Vader (in press a,b) recently published a redescription, and could thereby argue for its close relationship to *Phippsia* and *Tetradeion*. However, pending the revision of the family presented herein, they provisionally assigned *S. vanhoeffeni* to *Phippsia*.

Schellenbergia is the sister taxon to the three genera *Austrophippsia*, *Phippsia* and *Tetradeion*, and consists of two species: *S. pacifica* and *S. vanhoeffeni*. Due to the limited descriptions that are available of *S. pacifica*, this species was omitted from the matrix. However, based on the morphology of the maxilliped (which is, according to the cladograms, a reliable indicator of phylogenetic relationships within this clade of four related genera), labrum and telson, it is assigned as the sister taxon to *S. vanhoeffeni*. In addition to these characters, both species within this genus possess a large and well developed pereopod 7. In the other three closely related genera, pereopod 7 is considerably smaller than the preceding pereopods (in the most derived genus, *Tetradeion*, two of its species have a reduced number of articles on pereopod 7). Secondly, and possibly equally important, is the fact that the genus *Stegocephalopsis*, as defined by Barnard & Karaman (1991b: 681) with six species, has through the present analysis become totally redundant. None of the five species (two species were synonymized by Berge & Vader, in press b) are even thought to belong to the same genus, thereby creating the need to find a suitable genus also for this relatively poorly known species. However, as the present species is far from sufficiently described, and as no material has been available, the allocation of *S. pacifica* to *Schellenbergia* must be regarded at best as a qualified guess.

Schellenbergia is restricted to the Southern Hemisphere; both species are found in the South Pacific, whereas *S. vanhoeffeni* has also been recorded from the Antarctic (see Appendix 4).

STEGOCEPHALEXIA MOORE

Stegocephalexia Moore, 1992: 927
Stegocephalexia Berge & Vader, 2001: 989

Type species. Stegocephalexia penelope Moore, 1992. Monotypic.

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, uni-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally without hooks. Maxilliped palp article 2 inner margin distally weakly produced, inner plate with nodular setae. Pereopod 6 basis conspicuously expanded. Uropod 3 outer ramus two-articulate. Telson elongate, pointed cleft.

Remarks

Moore (1992) assigned *S. penelope* as type species for the monotypic genus *Stegocephalexia*, but without any thorough discussion of its relationship to other stegocephalid genera. Recently, Berge & Vader (in press b), in their survey of North Pacific stegocephalid species, discussed the relationships between *S. penelope* and *Alania hancocki*. However, the present analysis does not support the hypothesis of a close phylogenetic relationship between these two species, although their respective genera (*Stegocephalexia* and *Alania*) appear to be relatively closely related (see also Berge & Vader, in press b).

Stegocephalexia is a strictly northern taxon (see Appendix 4), with its single species recorded only from the North Pacific.

STEGOCEPHALINA STEPHENSEN

Stegocephalina Stephensen, 1925: 134
Stegocephalina Berge & Vader, 1997b: 350 (part)
Stegocephalina Berge, 2001c
Stegophippsiella Bellan-Santini & Ledoyer, 1974: 694 (new synonymy)
Stegocephaloides Berge & Vader, 1997a: 326 (part)

Type species. Stegocephalina ingolfi Stephensen, 1925.

Species

Stegocephalina ingolfi Stephensen, 1925; *S. pacis* (Bellan-Santini & Ledoyer, 1974); *S. trymi* Berge, 2001c; *S. wagini* (Gurjanova, 1936). [4 species].

Short description of the genus

Epistomal plate absent, epistome laterally produced. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, 1- or 2-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally without (type) or with hooks. Maxilliped palp article 2 inner margin distally unproduced, inner plate long and rectangular. Pereopod 6 basis expanded. Uropod 3 outer ramus uniarticulate. Telson elongate, cleft.

Remarks

The composition of *Stegocephalina* has changed dramatically during the last few years: Stephensen first erected the genus to include only its type species, but Berge & Vader (1997b) assigned three other species (*S. biofar*, *S. idae* and *S. katalia*) to the genus, although they all showed some significant differences from the type species. Later, a fifth species (*S. trymi*) was assigned to the genus by Berge (2001c). Herein, the three species first added to the genus are transferred to a new genus (*Stegonomadia*, see below), while two other species (*Stegocephaloides wagini* and *Stegophippsiella pacis*) are transferred into *Stegocephalina*; this leaves the number of species in the genus at four. Berge (2001c) considered that *S. wagini* was closely related to both *S. ingolfi* and *S. trymi*, but did not then transfer it into the same genus pending the present revision.

The present genus is characterized by its elongate mouthparts, although these are only weakly developed in *S. wagini*. Still more characteristic is the laterally produced epistome, which is clearly different from the produced epistome found in the subfamily Andaniexinae. The epistome of the present genus is triangular and short, and can thus be seen to support the hypothesis indirectly presented in Figures 1–3; i.e. that the laterally produced epistome has evolved independently more than once. *Stegocephalina* is defined by ten synapomorphies (Fig. 1, nodes 162→161; Appendix 3).

One species is recorded only from the Antarctic region (*S. pacis*), whereas the other three species are distributed in the North or South Atlantic (see Appendix 4).

STEGOCEPHALOIDES SARS

Stegocephaloides Sars, 1891: 201
Stegocephaloides Stebbing, 1906: 91
Stegocephaloides K.H. Barnard, 1916: 128 (part)
Stegocephaloides Stephensen, 1925: 133 (part)
Stegocephaloides Schellenberg, 1925: 200 (part)
Stegocephaloides Gurjanova, 1951: 300
Stegocephaloides Barnard & Karaman, 1991: 681 (part)
Stegocephaloides Berge & Vader, 1997a: 326 (part)
Stegocephaloides Berge & Vader, in press a (part)
Stegocephaloides Berge *et al.*, 2001 (part)

Type species. Stegocephalus christianiensis Boeck, 1871.

Species.

Stegocephaloides attingens K.H.Barnard, 1916; *S. auratus* (Sars, 1883); *S. barnardi* Berge & Vader, 1997; *S. christianiensis* (Boeck, 1871); *S. ledoyeri* Berge *et al.*, 2001. [5 species.]

Short description of the genus

Epistomal plate absent, epistome convex (smooth). Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, 1-articulate. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally weakly produced, inner plate short, distally concave. Pereopod 6 basis weakly to rudimentarily expanded. Uropod 3 outer ramus uni-articulate. Telson elongate, cleft.

Remarks

Stegocephaloides was previously one of the most speciose genera within the family Stegocephalidae, but is herein split up into two different genera, see Remarks under *Austrocephaloides*. As treated herein, *Stegocephaloides* consists of five morphologically unified species, but the genus is defined by only four synapomorphies (Fig. 2, nodes 173→172; Appendix 3). Like all four genera within this clade (see above), *Stegocephaloides* is mainly characterized by the morphology of the maxilliped, coxa 4 and pereopods 6 and 7. Due to the close relationships, both in terms of morphology and phylogeny, between these four genera, there are only a few synapomorphies that separate them from each other.

Stegocephaloides is a widely distributed genus, but is not recorded in the Pacific and the Antarctic region (see Appendix 4).

STEGOCEPHALUS KRØYER

Stegocephalus Krøyer, 1842: 150
Stegocephalus Boeck, 1872: 420
Stegocephalus Sars, 1891: 197
Stegocephalus Stebbing, 1906: 90
Stegocephalus Brüggen, 1909: 14
Stegocephalus Stephensen, 1925: 128
Stegocephalus Barnard & Karaman, 1991: 682 (part)
Phippsia Stebbing, 1906: 89 (part)
Phippsiella Schellenberg, 1925: 200 (new synonymy)
Phippsiella Stephensen, 1925: 130
Phippsiella Barnard & Karaman, 1991: 680
Phippsiella Berge & Vader, 1997d: 1502
Phippsiella Berge, De Broyer & Vader, 2000: 226
Phippsiella Berge, Vader & Galan, 2001: 121
Stegocephalopsis Schellenberg, 1925: 200 (new synonymy)
Stegocephalopsis Stephensen, 1925: 132
Stegocephalopsis Barnard & Karaman, 1991: 681
Stegocephalopsis Berge & Vader, 1997b: 361

Type species. Stegocephalus inflatus Krøyer, 1842 [Boeck (1872: 421) named *Cancer ampulla* Phipps, 1774 as type species of the genus, as he synonymized *S.inflatus* with *S. ampulla*].

Species

Stegocephalus abyssicola (Oldevig, 1959); *S. ampulla* (Phipps, 1774); *S. cascadiensis* (Moore, 1992); *S. inflatus* Krøyer, 1842; *S. kergueleni* (Schellenberg,

Table 1. Generic status of species that have traditionally been considered as belonging to the three genera *Phippsiella*, *Stegocephalopsis* and *Stegocephalus*; a comparison between the herein presented classification, their original generic position and the classification in Barnard & Karaman (1991)

Species	Original generic placement	Classification according to Barnard & Karaman (1991)
Bouscephalus mamillidacta	*Stegocephalopsis*	–
Calypso beringi	*Stegocephalus*	–
Calypso hancocki	*Stegocephalus*	*Stegocephalus*
Gordania minima	*Phippsiella*	*Phippsiella*
Gordania pajarella	*Phippsiella*	*Phippsiella*
Pseudo bioice	*Phippsiella*	*Phippsiella*
Pseudo pseudophippsia	*Phippsiella*	*Phippsiella*
Pseudo viscaina	*Phippsiella*	*Phippsiella*
Schellenbergia vanhoeffeni	*Stegocephaloides*	*Stegocephalopsis*
Stegocephalus abyssicola	*Phippsiella*	*Phippsiella*
Stegocephalus ampulla	*Cancer*	*Stegocephalopsis*
Stegocephalus cascadiensis	*Phippsiella*	–
Stegocephalus inflatus	*Stegocephalus*	*Stegocephalus*
Stegocephalus kergueleni	*Phippsiella*	*Phippsiella*
Stegocephalus longicornis	*Phippsiella*	*Phippsiella*
Stegocephalus nipoma	*Phippsiella*	*Phippsiella*
Stegocephalus rostrata	*Phippsiella*	*Phippsiella*
Stegocephalus similis	*Stegocephalus*	*Phippsiella*
Stegomorphia watlingi	*Phippsiella*	–

1926b); *S. longicornis* (Gurjanova, 1962); *S. nipoma* (Barnard, 1961); *S. rostrata* (K.H. Barnard, 1932); *S. similis* (Sars, 1891). [9 species.]

Short description of the genus

Epistomal plate absent. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks (absent in S. ampulla). Pereopod 6 basis conspicuously expanded. Telson elongate, cleft.

Remarks

Two genera, *Phippsiella* Schellenberg, 1925 and *Stegocephalopsis* Schellenberg, 1925, are herein put into synonymy with the older *Stegocephalus*. However, some species that have usually been treated, e.g. by Barnard & Karaman (1991b: 680–682), as belonging to either *Phippsiella, Stegocephalopsis* or *Stegocephalus* are herein reallocated to six different (in addition to the present genus) genera: *Bouscephalus, Alania, Gordania, Pseudo, Schellenbergia* and *Stegomorphia* (see Table 1).

As treated herein, *Stegocephalus* includes nine species, and is defined by five synapomorphies (Fig. 1, nodes 156→155; Appendix 3), but the genus is partly unresolved internally. Due to their highly similar morphology, and to the difficulties of assigning the insufficiently described species (*Phippsiella kergueleni* and *P. longicornis*) that were deleted from the analysis to either of the clades, all nine species are herein treated as belonging to the same genus.

As discussed above, the classification within the subfamily Stegocephalinae has been both in a state of flux and highly uncertain. One reason for this may be, as is evident from the cladograms, that the three species that have been assigned as types of the three oldest genera (*Phippsiella, Stegocephalus* and *Stegocephalopsis*), are in fact very closely related: *S. ampulla* and *S. inflatus* (type species of *Stegocephalus* and *Stegocephalopsis*, respectively) are herein considered as sister taxa). Hence, as the traditional classification of the Stegocephalidae has always been sought to be preserved, artificial generic differences have been created, with the natural consequence of a highly cloudy and uncertain classification. The two most important characters that have been used to separate these and closely related genera are (1) number of articles on the maxilla 1 palp, and (2) shape of basis on pereopod 6. Both these characters have, through the present analysis and through close examination of most stegocephalid species, proved to be inappropriate: the basis on the sixth pereopod is usually rudimentarily expanded, also in taxa that have been characterized as possessing an unexpanded basis, and the articulation of the palp of the first maxilla shows a very high level of homoplasy.

One of the main characteristics of the species in the present genus, compared with most other stegocephalid genera, is their large body size. *Stegocephalus ampulla* is, together with *Parandania gigantea* (see above), the largest known stegocephalid species, growing up to 60 mm. Furthermore, Steele (1967a,b) showed that the type species of the genus is a protandric hermaphrodite. As this particular life-history trait has not been examined for any of its congeners, it is possible that this character may be present also in other closely related taxa.

Stegocephalus is a widely distributed genus (see Appendix 4), but its distribution appears to be biased towards the Northern Hemisphere: six of the nine species are found in the Arctic or the northern regions of either the Atlantic or the Pacific. Two species are restricted to the Antarctic, and one species is not recorded from outside the South Atlantic.

STEGOMORPHIA GEN. NOV.

Phippsiella Berge *et al.*, 2000; 226 (part)

Type species. Phippsiella watlingi Berge *et al.*, 2000. Monotypic.

Short description of the genus

Antenna 2 peduncle article 4 curved. Epistomal plate absent, epistome convex (smooth). Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed, uni-articulate. Maxilla 2 gaping and geniculate, outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally unproduced, inner plate with 2 nodular setae. Coxa 1 anteriorly concave. Pereopod 6 basis conspicuously expanded. Uropod 3 outer ramus uni-articulate. Telson elongate, cleft.

Etymology

The name of the genus refers to its highly derived morphology.

Remarks

Stegomorphia is a monotypic genus, characterized mainly by the conspicuous morphology of antenna 2, coxa 1, and merus on pereopods 3 and 4, all characters that separate it from all other known stegocephalid taxa. The genus is characterized by 13 autapomorphies (Fig. 1, nodes 157→*watlingi*; Appendix 3), and is the sister taxon to the large genus *Stegocephalus*.

Stegomorphia is only recorded from the Antarctic region.

STEGONOMADIA GEN. NOV.

Stegocephaloides Barnard, 1962: 40
Stegocephalopsis Barnard & Karaman, 1991: 681 (part)
Stegocephalina Berge & Vader, 1997b: 350 (part)

Type species. Stegocephalina biofar Berge & Vader, 1997b.

Species

S. biofar (Berge & Vader, 1997b); *S. idae* (Berge & Vader, 1997b); *S. katalia* (Barnard, 1962). [3 species.]

Short description of the genus

Epistomal plate present, epistome not produced laterally. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp short, uni-articulate, distally with short simple setae. Maxilla 2 gaping and geniculate; outer plate setae distally simple or cleft. Maxilliped palp slender, weakly setose; inner plate with 2 nodular setae. Pereopod 6 basis weakly expanded. Uropod 3 outer ramus 2-articulate. Telson long or short, cleft.

Etymology

The name refers to the unstable classification of the genus' species; *Stegonomadia katalia* (Barnard, 1962) has been assigned to four different genera since it was described in 1962 by J.L. Barnard.

Remarks

According to the cladogram presented herein (Fig. 2), *Stegonomadia* is the sister taxon to the remaining subfamily. The species of this genus do, in contrast to the remaining subfamily, possess setae on the outer plate of the second maxilla that are neither hooked nor distally bent (but see also Discussion below), although the outer plate itself is truly gaping and geniculate.

All three species of the present genus were provisionally placed in the genus *Stegocephalina* by Berge & Vader (1997b), despite the fact that they are all "morphologically very distinct from the type species of this genus [i.e. of *Stegocephalina*]" (Berge & Vader 1997b: 354). *Stegonomadia* is defined by ten synapomorphies (see Fig. 1 and Appendix 3, nodes 184→183), and is, compared with the other species within the subfamily, highly derived. This can first of all be seen in the mouthparts, where many of the different setae-groups (as identified by Berge, 2001b) are totally absent. As a consequence, the phylogenetic position of the present genus could be somewhat misleading, as many characters necessarily had to be scored as 'inapplicable' for the three species.

One species (*S. katalia*) is restricted to the South Atlantic (see Appendix 4), whereas the other two species are distributed in the Arctic and the North Atlantic.

TETRADEION STEBBING

Tetradeion Stebbing, 1899: 207
Tetradeion Chilton, 1924
Tetradeion K.H. Barnard, 1930: 329
Tetradeion Hurley, 1955: 197
Tetradeion Barnard, 1972: 155
Tetradeion Barnard & Karaman, 1991: 683
Tetradeion Berge & Vader, 2000
Phippsia Berge & Vader, 2000 (part)

Type species. Cyproidea crassa Chilton, 1883.

Species

Tetradeion angustipalpa (Berge & Vader, 2000); *T. crassum* (Chilton, 1883); *T. dampieri* (Berge & Vader, 2000); *T. quatro* Berge & Vader, 2000; *T. latum* (Haswell, 1879). [5 species.]

Short description of the genus

Epistomal plate present, usually conspicuous. Mandible incisor lateral, toothed; left lacinia mobilis powerful, toothed, distally produced. Maxilla 1 palp well developed. Maxilla 2 gaping and geniculate; outer plate setae distally with hooks. Maxilliped palp article 2 inner margin distally produced. Pereopod 6 basis slender to weakly expanded. Telson elongate, rounded and entire.

Remarks

The present genus was erected by Stebbing (1899: 207) to encompass *T. crassum* based primarily on its strongly reduced seventh pereopod (only two articles present). The genus remained monotypic until Berge & Vader (2000) assigned a second species to the genus: *T. quatro*, which also has a strongly reduced seventh pereopod, but with four articles present. Berge & Vader (2000) acknowledged the obvious and close relationship to *Phippsia*, but, pending the present revision, retained *Tetradeion* to encompass only those species with a reduced pereopod 7.

Herein, three other species are transferred to *Tetradeion*: *Phippsia angustipalpa*, *P. dampieri* and *Stegocephalopsis latus*. The last of these species was not included in the analysis, due to insufficient morphological knowledge of the species. *Tetradeion latum* was originally described as *Stegocephalus latus*, but was later transferred to *Stegocephalopsis* by Barnard & Karaman (1991b: 682). The reasons for doing so were not given, but *Stegocephalopsis* was treated as a 'catch all' genus, encompassing six highly diverse and generally insufficiently known species. Based on the following characters: (1) eyes present (small, round and conspicuous), (2) morphology of coxa 1–4, and (3) the reduced pereopod 7, the species is transferred to *Tetradeion*. However, the species remains one of the poorest known stegocephalid species, and its allocation to the present genus may prove to be erroneous in the future.

Tetradeion is defined by ten synapomorphies (Fig. 1, nodes 145→144; Appendix 3), and is part of a clade consisting of three other genera: *Austrophippsia*, *Phippsia* and *Schellenbergia* (see also above). In contrast to these three genera, the species of *Tetradeion* all possess an entire telson, in addition to a long and geniculate peduncle on the second antenna.

Tetradeion is a strictly southern genus (see Appendix 4), recorded only from either the Antarctic (*T. crassum*), the South Pacific (*T. angustipalpa*, *T. crassum*, *T. latum* and *T. quatro*) or the Indian Ocean (*T. dampieri*).

DISCUSSION

Nine species were excluded from the analysis of the ingroup (family Stegocephalidae) due to lack of suitable knowledge about their morphology, especially their mouthparts: *Andaniexis oculatus* Birstein & Vinogradov, 1970, *A. spinescens* (Alcock, 1894), *A. stylifer* Birstein & Vinogradov, 1960, *A. subabyssi* Birstein & Vinogradov, 1955, *Parandaniexis inermis* Ledoyer, 1986, *P. kergueleni* Schellenberg, 1926b, *P. longicornis* Gurjanova, 1962, *Stegocephalopsis latus* (Haswell, 1879), and *S. pacifica* (Bulycheva, 1952). The generic status of some of the species listed above seems rather obvious: *Andaniexis oculatus*, *A. stylifer* and *A. subabyssi* all belong to the genus *Andaniexis*, *Andaniexis spinescens* and *Parandaniexis inermis* belong to *Parandaniexis*, whereas *Phippsiella kergueleni* and *P. longicornis* are transferred to *Stegocephalus* (see also Remarks under the respective genera). The generic status of the remaining two is, unfortunately, not so easy to assess, but they are here transferred to *Tetradeion* and *Austrophippsia*, respectively (see Remarks under these genera for a further discussion).

The present revision aims at providing a revised classification based entirely upon the presented phylogenetic analysis, which follows a thorough morphological examination of most of the species within the family. The phylogenetic relations and morphological features have been discussed under each genus (see above), and will thus not be discussed here. The general pattern, however, needs to be examined more closely. Until now, the Stegocephalidae have been divided into two major groups: with or without a gaping and geniculate second maxilla. At the generic level, the number of articles on the palp of the first maxilla and the shape of the basis of pereopod 6 were significant characters. According to the results presented herein, the separation of the family into two major groups is only partially supported. One group, the Andaniexinae, consists of most taxa possessing an ordinary outer plate of maxilla 2, and the Stegocephalinae consist of all taxa from the gaping and geniculate group.

The three remaining smaller subfamilies, the Andaniopsinae, Bathystegocephalinae and Parandaniinae, consist of taxa from the 'ordinary' group, although the absence of an outer plate on the second maxilla in the Bathystegocephalinae makes it difficult to assign its only species, *Bathystegocephalus globosus*, to either of the two groups (i.e. 'ordinary' or 'gaping and geniculate'). According to the cladograms, the gaping and geniculate maxilla 2 is thus a global synapomorphy for the Stegocephalinae, as this character state is not found in any other taxa, either within or outside the Stegocephalidae. The species in the genus *Stegonomadia* all possess a gaping and geniculate maxilla 2, but none of the species shows the distal hooks that are characteristic of most of the members of the Stegocephalinae. It is suggested here that a transition state between distally unhooked and hooked setae can be identified within the genus *Stegonomadia*, as *S. idae* (the sister taxon to the rest of the genus, and thus possibly with most plesiomorphic characters) possesses setae on the outer plate that are deeply and conspicuously cleft distally (see Berge & Vader, 1997b: 375 fig. 4). By imagining that these setae were subsequently curved distally, it is possible to envisage a transformation from straight and unhooked setae to setae with distal hooks. Some species within this subfamily appear secondarily to have lost these hooks, but all those species have their setae sharply curved distally into what could be interpreted as the remains of the distal hooks.

There is, however, one other appendage that, according to the strict consensus, appears to be equally important for higher level classification, viz. the left mandible. In both the Andaniopsinae and Stegocephalinae, all taxa possess a distally expanded and toothed lacinia mobilis, in addition to the lateral orientation of the incisor. In the Andaniexinae, on the other hand, the taxa are characterized by a transverse incisor, and a rectangular or conical lacinia mobilis that is either smooth or only weakly toothed. As in the second maxilla, there is also one exception to the general rule for the mandible: *Bathystegocephalus globosus* has a toothed and triangular incisor, which is thus not similar to any of the other stegocephalid subfamilies, but it possesses a lacinia mobilis very similar to that of the two subfamilies Andaniopsinae and Stegocephalinae. In *Parandania*, the lacinia mobilis is clearly different from those in the remaining subfamilies: *P. boecki* has lost the lacinia mobilis, whereas in the other two species the lacinia mobilis appears to be longer and more powerful than in most other species within the Andaniexinae. Furthermore it is slightly curved distally, and this could, in light of the phylogenetic evidence presented herein, be interpreted as a secondary reduction from the distally expanded and toothed state.

In Figure 3, the Bremer support values are plotted on each of the branches (not on branches of monotypic genera). According to these values, there is substantial support in the data for the monophyletic status of the ingroup (Bremer support of 10 steps). Also at the generic level, there seems to be substantial support (in terms of Bremer support values) for most genera, with values varying between 1 and 8. However, the five subfamilies do not appear as well supported as many of the genera, as Andaniexinae, Andaniopsinae and Stegocephalinae all have a Bremer support of only 1. These low indices are probably the result of the instability of three genera: *Bathystegocephalus*, *Parandania* and *Stegonomadia*. Although all these genera themselves are well supported, they are all morphologically highly derived, and thus difficult to relate to other groups. *Bathystegocephalus* has lost the outer plate on its second maxilla (see also Remarks under the genus), whereas *Stegonomadia* has lost many of the different setae-groups used in the matrix, in addition to the unique morphology of the setae on the outer plate of the second maxilla. By saving sub-optimal trees (of e.g. 2 steps longer than the most parsimonious), their phylogenetic positions are readily altered, whereas most other arrangements are retained. *Stegonomadia* shares some similarities with the Andaniopsinae, and in many of the sub-optimal trees appears as closely related to this group. Nevertheless, it seems adequate to assume that the *Stegonomadia* is, as is indicated on the cladograms in Figures 1–3, in fact more closely related to the remaining Stegocephalinae than to any of the Andaniopsinae genera. Although *Stegonomadia* has, as do the Andaniopsinae, a strongly reduced palp of the first maxilla, both the outer and inner plates indicate closer relationships towards the Stegocephalinae. Similarly, although the setae on the outer plate of the second maxillae are simple (*vs* hooked in the remaining Stegocephalinae), the outer plate is conspicuously gaping and geniculate and the setation of the inner plate suggest a closer relationship towards the Stegocephalinae.

The two subfamilies Bathystegocephalinae and Parandaniinae share many morphological features with the Andaniexinae, and appear within this clade in many of the sub-optimal trees. However, although these two subfamilies both have a relatively low

Bremer support (Fig. 3), neither possesses the conspicuous laterally produced epistome of the Andaniexinae.

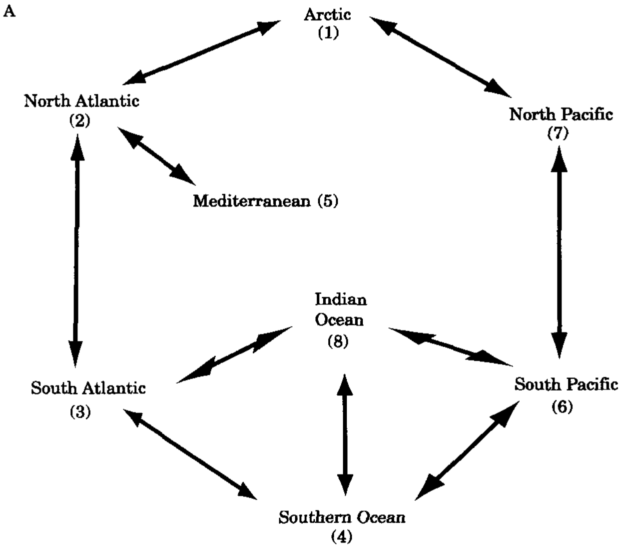
As discussed above, the selection of outgroups was made predominantly on the basis of the results of a phylogenetic analysis of the Amphipoda (Berge *et al.*, 2000), which suggested that the Stegocephalidae are the sister taxon to the Lysianassidae. As for the Stegocephalidae, the Lysianassidae predominantly consist of hyperbenthic species, but several pelagic taxa can also be found within the group. According to the cladograms presented from this analysis (Figs 1–3), it would seem most parsimonious to consider the common ancestor of the Stegocephalidae as a pelagic species, with subsequent shifts to the hyperbenthic habitat. However, as discussed above (see Remarks under *Parandaniexis*), the adaptations found in the four pelagic stegocephalid taxa (*Bathystegocephalus*, *Metandania*, *Parandania* and *Parandaniexis*) are all very different. Furthermore, the hyperbenthic genera, which by far outnumber the pelagic genera, seem to be much more similar and possibly more conservative in morphology. Thus, it seems appropriate to suggest that the ancestor of the Stegocephalidae was a hyperbenthic species, and that, during evolution, there have been four independent shifts to a pelagic habitat.

The Stegocephalidae are a widely distributed family, represented in all the eight geographical zones defined in Appendix 4. The area that is least well represented is the Mediterranean where only four stegocephalid species have been recorded (see Appendix 4), whereas in the North Atlantic and the South Pacific, 26 and 31 species have been recorded, respectively. Of all the one hundred stegocephalid species listed in Appendix 4, 77% appear to be endemic to one of the geographical zones. However, a very high percentage of these species is known only from (or in close vicinity to) their type locality, which makes it difficult to define their distribution: stegocephalids are mostly deep-sea species, and the distribution of both species and genera appears to correlate very well with how extensively the different deep-sea areas have been explored. Thus, the distributional pattern as known today is most probably not a suitable subject for any biological or geographical explanations. As a geographical example of the distributional patterns of the Stegocephalidae, the Antarctic was, until 1980 (see Berge *et al.*, 2001), represented by five species belonging to four genera. Today, after the area has been subject to extensive sampling, there are 19 species (belonging to 11 genera) reported from the area. This close link between number of taxa reported from an area, and the number of sampling projects carried out in the area, makes it difficult to use the distributional data in any further analysis of the origin of the Stegocephalidae. Over the last 10 years, the number of described (and valid) species has increased from 55 (counted from Barnard & Karaman, 1991b) to the 100 species treated herein. In addition to these 100 species, De Broyer & Rauschert (1999) have recently indicated four new species and two new genera in their report. Based on these experiences, it seems prudent to expect further significant increases in the number of stegocephalid taxa as new, and previously poorly sampled, regions become the subject of thorough studies. As a consequence, the following discussion on the distributional patterns, and the hypothesized origin of the Stegocephalidae, must be regarded as being based on a probably far from complete data set.

If the Indian Ocean is interpreted as mainly belonging to the southern Hemisphere (as the Stegocephalidae are predominantly a group of deep-sea species, there are significantly more barriers towards the northern Hemisphere, than from the southern to the Indian Ocean), there is a total of 68 southern species, whereas the corresponding number of species recorded from the northern Hemisphere is 54. At the generic level, eight genera are endemic to the northern Hemisphere, whereas the corresponding number for the southern Hemisphere is 10. None of the species are endemic to the Arctic, whereas in the Southern Ocean 12 out of a total of 19 recorded species are endemic to the region. In general, 55 species are restricted to the southern Hemisphere, whereas only 22 species are restricted to the northern. In the Atlantic Ocean, there are recorded 39 species, of which 22 are endemic to the Atlantic. Similarly, in the Pacific, there are recorded 43 species of which 36 appears as endemic to that region. It is however, evident that as many as 16 of the species found to be restricted to the southern Hemisphere, are all found within two genera: *Andaniotes* and *Stegosoladidus*. Thus, the relatively high number of species endemic to the southern Hemisphere, compared to that of the northern, seems to be more apparent than real.

The fossil record in the Amphipoda is sparse (Schram, 1986), but the group has nevertheless been assumed to be relatively old (e.g. Bousfield, 1982). For the Stegocephalidae, however, there are no fossil records, and, in addition, according to the cladograms presented by Berge *et al.* (2000), the Stegocephalidae belong to a rather derived group; it seems very difficult to make any assumptions about the relative age of the family. However, as the family in general consists of deep-sea species, there would probably have been pronounced barriers limiting the distribution of stegocephalid taxa already before the break-up of the continental plates. Thus, although the model may seem simplistic, Figure 6A represents a general way of illustrating the relationship between different major marine geographical zones, which in turn could be used to analyse the present day distribution of the

A



B

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
1		1	2	3	2	2	1	3
2	1		1	2	1	3	2	2
3	2	1		1	2	2	3	1
4	3	2	1		3	1	2	1
5	2	1	2	3		4	3	3
6	2	3	2	1	4		1	1
7	1	2	3	2	3	1		2
8	3	2	1	1	3	1	2	

Figure 6. (A) General scheme for present-day connections between the different areas. Each arrow accounts for one evolutionary step, hence two steps are required for a taxon to invade the South Atlantic (area 3) from the Arctic (area 1). (B) Stepmatrix for a multistate character (8 states) as inferred from (A).

Stegocephalidae. Based upon these relationships, a stepmatrix can be constructed (Fig. 6B) that describes the number of steps (i.e. each transition equals one step) that are required to explain the present-day distribution of the Stegocephalidae among the different geographical areas.

Thus, the distribution of the species is scored as a multistate character (not scored for the outgroups) with eight states, with each state corresponding to zones 1 through 8 in Appendix 4. This stepmatrix can then be assigned as a user defined character type in PAUP*, and subsequently be used to infer the most parsimonious state (and hence the hypothesized geographical origin) for the common ancestor of the family.

When this method is applied, and the character is plotted on tree 1, the result unequivocally suggests that the family has its origin in the South Atlantic (area 3, Fig. 6A and node 190, Fig. 1). However, it also suggests that it is most parsimonious to assign state '2' (i.e. North Atlantic) to node 186 (see Fig. 1), which thus means that the three subfamilies Andaniexinae, Andaniopsinae and Stegocephalinae all have their origin in the North Atlantic. All four species allocated to the remaining two subfamilies (Bathystegocephalinae and Parandaniinae) are strictly pelagic, and, in addition, two of them appear as cosmopolitan taxa. Furthermore, the phylogenetic position of Bathystegocephalinae, as discussed above, is somewhat uncertain, as its only species does not possess an outer plate of the second maxilla. Although the cladograms specifically suggest an origin in the southern parts of the Atlantic, there are thus reasons to treat this result with some caution. Therefore, it seems reasonable to suggest only that the family has its origin within the Atlantic Ocean.

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APPENDIX 1

CHARACTER LIST FOR THE ANALYSIS OF THE STEGOCEPHALIDAE

The character list was initially written in TAXASOFT, which labels the character states in a binary character '1' and '2', hence state label '0' is not used. The order of the states does not reflect any assumptions about which state is plesiomorphic and apomorphic, respectively.

1. Head
1. not retractable under pereonite 1
2. retractable under pereonite 1

2. Rostrum reduction
1. short, inconspicuous
2. well developed

3. Antennae reduction
1. present
2. absent

4. Antenna 1 flagellum articulation
1. present
2. absent

5. Antenna 1 accessory flagellum
1. normal
2. vestigial

6. Antenna 1 accessory flagellum articulation
1. absent
2. present

7. Antenna 1 accessory flagellum elongation [in relation to flag.art.1]
1. absent
2. present, longer than flagellum article 1

8. Antenna 2 peduncle article 3
1. short, about as long as broad
2. elongate, article 3 and 4 geniculate

9. Antenna 2 peduncle article 4 reduction
1. absent
2. present

10. Antenna 2 peduncle article 5 reduction
1. absent
2. present

11. Epistome laterally
1. curved (convex) and smooth
2. produced

12. Epistome
1. rectangular, with a long ridge on each side
2. broad and round

13. Epistomal plate (medial keel)
1. produced
2. not produced

14. Epistomal plate
1. small elongate medial ridge covering the entire epistome
2. large conspicuous medial keel

15. Mouthparts
1. ordinary
2. elongate; pointed and narrow

16. Mandible palp (ingroup)
1. present
2. absent

17. Mandible molar (ingroup)
1. present
2. absent

18. Mandible raker setae (ingroup)
1. present
2. absent

19. Mandible incisor orientation
1. lateral
2. transverse

20. Mandible incisor
1. smooth
2. toothed

21. Mandible left lacinia mobilis
1. present
2. absent

22. Mandible left lacinia mobilis
1. powerful
2. reduced

23. Mandible left lacinia mobilis distally
1. straight
2. expanded

24. Mandible left lacinia mobilis
1. not conical
2. conical

25. Maxilla 1 palp articulation
1. absent
2. present

26. Maxilla 1 palp
1. rectangular
2. oval

27. Maxilla 1 palp length
1. apex not reaching above the apex of outer plate
2. apex reaching above the apex of outer plate

28. Maxilla 1 palp setae on outer margin
1. absent
2. present

29. Maxilla 1 palp with short simple setae
1. absent
2. present

30. Maxilla 1 palp short robust setae
1. present
2. absent

31. Maxilla 1 palp long setae
1. present
2. absent

32. Maxilla 1 palp setae with setules
1. present
2. absent

33. Maxilla 1 palp long distal setae distally
1. pappose
2. pectinate

34. Maxilla 1 outer plate distally
1. rounded
2. rectangular

35. Maxilla 1 outer plate ST arranged as
1. two parallel rows, first marginal and second submarginal
2. a pseudocrown

36. Maxilla 1 outer plate ST 1
1. ordinary (similar to ST 2–4)
2. conspicuously enlarged

37. Maxilla 1 outer plate ST 1–5
1. all present
2. reduced, 4 setae present

38. Maxilla 1 outer plate ST 6
1. present
2. absent

continued

APPENDIX 1 – *continued*

39. *Maxilla 1 outer plate gap between ST 5 and ST 7*
  1. present
  2. absent

40. *Maxilla 1 outer plate ST first row [expanded]*
  1. with 6 setae (ST 1–5, ST 7)
  2. with more than 6 setae (ST 1–5 expanded, ST 7)

41. *Maxilla 1 outer plate ST A*
  1. present
  2. absent

42. *Maxilla 1 outer plate ST A*
  1. part of second row
  2. relocated, part of first row

43. *Maxilla 1 outer plate ST B*
  1. present
  2. absent

44. *Maxilla 1 outer plate ST B*
  1. part of second row
  2. relocated, part of first row

45. *Maxilla 1 outer plate ST C*
  1. present
  2. absent

46. *Maxilla 1 outer plate ST D*
  1. present
  2. absent

47. *Maxilla 1 inner plate shoulder*
  1. well developed
  2. weakly developed

48. *Maxilla 1 inner plate, setae*
  1. pappose
  2. pappopectinate

49. *Maxilla 2 outer plate (ingroup)*
  1. broad
  2. narrow, much less than 1/2 of inner plate

50. *Maxilla 2*
  1. ordinary
  2. gaping and geniculate

51. *Maxilla 2 outer plate setae with distal hooks*
  1. absent
  2. present

52. *Maxilla 2 outer plate setae distally*
  1. straight
  2. curved

53. *Maxilla 2 outer plate setae distal cleft*
  1. absent
  2. present

54. *Maxilla 2 inner plate row A, length*
  1. covering the entire margin
  2. reduced, not covering the entire margin

55. *Maxilla 2 inner plate row A*
  1. appressed to row B
  2. clearly separated from row B

56. *Maxilla 2 inner plate row A and D*
  1. separated
  2. continuous

57. *Maxilla 2 inner plate row A with 2–3 first setae*
  1. similar to the other setae
  2. differentiated from the other setae

58. *Maxilla 2 inner plate row A setae proximally with setules*
  1. absent
  2. present (pappose)

59. *Maxilla 2 inner plate row A setae distally with pectinations*
  1. absent
  2. present

60. *Maxilla 2 inner plate row B*
  1. present
  2. absent

61. *Maxilla 2 inner plate row B setae*
  1. thick and distally blunt
  2. similar to A setae

62. *Maxilla 2 inner plate row B setae proximally*
  1. pappose
  2. simple

63. *Maxilla 2 inner plate row B setae distally with cusps*
  1. absent
  2. present

64. *Maxilla 2 inner plate row C*
  1. present
  2. absent

65. *Maxilla 2 inner plate row D*
  1. present
  2. absent

66. *Maxilla 2 inner plate row D, length*
  1. reduced, 1–3 long setae distally
  2. expanded, row covering most of the distal margin of inner plate

67. *Maxilla 2 inner plate row D setae distally with cusps*
  1. absent
  2. present

68. *Maxilla 2 inner plate row D setae proximally with setules*
  1. absent
  2. present (pappose)

69. *Maxilliped palp [number of articles]*
  1. 3-articulate
  2. 4-articulate

70. *Maxilliped palp article 2 distally [produced]*
  1. unproduced
  2. produced

71. *Maxilliped palp article 2 distal inner margin*
  1. weakly produced
  2. greatly produced (at least one third of article 3)

72. *Maxilliped palp dactylus distally*
  1. simple (pointed)
  2. cleft, one pointed and one heavily setose part

73. *Maxilliped palp dactylus distal collar of setae*
  1. present
  2. absent

74. *Maxilliped palp articles 1–3 inner margin plumose setae*
  1. present
  2. absent

75. *Maxilliped inner plate elongation*
  1. absent
  2. present (exceeding palp article 1)

continued

APPENDIX 1 – *continued*

76. *Maxilliped inner plate distal margin*
 1. convex
 2. concave

77. *Maxilliped inner plate distal margin inner corner*
 1. unproduced
 2. produced

78. *Maxilliped inner plate distal margin outer corner*
 1. unproduced
 2. produced

79. *Maxilliped inner plate nodular setae*
 1. absent
 2. present

80. *Maxilliped inner plate, number of nodular setae*

81. *Maxilliped inner plate inner margin distally with nodular setae*
 1. absent
 2. present

82. *Maxilliped inner plate medial setae-row [presence]*
 1. present
 2. absent

83. *Maxilliped inner plate medial setae-row*
 1. not reduced
 2. reduced to one or two setae, but differentiated from distal row

84. *Maxilliped inner plate, medial row*
 1. vertical
 2. transverse (or following the distal margin)

85. *Maxilliped inner plate, medial setae-row*
 1. pectinate
 2. simple

86. *Maxilliped inner plate, distal setae-row [distally on outer corner]*
 1. absent
 2. present

87. *Maxilliped inner plate inner setae-row*
 1. present
 2. absent

88. *Maxilliped inner plate inner setae-row [setae]*
 1. conspicuously large and robust setae
 2. setae not conspicuously large

89. *Maxilliped inner plate inner setae-row [number]*
 1. row not reduced, more than two setae
 2. now reduced to one or two setae

90. *Maxilliped inner plate inner setae-row [location]*
 1. distally
 2. medially

91. *Maxilliped outer plate inner margin outer setae-row*
 1. present
 2. absent

92. *Maxilliped outer plate, outer setae-row [location]*
 1. marginal
 2. submarginal

93. *Maxilliped outer plate outer setae-row, setae attached*
 1. normally
 2. in a deep hollow

94. *Maxilliped outer plate outer setae-row, setae*
 1. long robust
 2. short

95. *Maxilliped outer plate, outer setae-row [curved upwards]*
 1. straight
 2. strongly curved upwards (hooks)

96. *Maxilliped outer plate inner margin inner setae-row [presence]*
 1. present
 2. absent

97. *Maxilliped outer plate inner margin inner setae-row*
 1. well developed
 2. present, but strongly reduced

98. *Maxilliped outer plate, inner setae-row setae*
 1. long robust
 2. short simple

99. *Maxilliped outer plate inner setae-row, setae-type*
 1. slender
 2. pappose

100. *Maxilliped outer plate inner setae-row [adpressed]*
 1. adpressed to outer row
 2. not adpressed to outer row

101. *Maxilliped outer plate inner setae-row [parallel]*
 1. parallel to outer
 2. not parallel to outer

102. *Maxilliped outer plate inner setae-row distally*
 1. transverse
 2. vertical

103. *Maxilliped outer plate distal setae-group [present]*
 1. absent
 2. present

104. *Maxilliped outer plate distal setae-group, setae attached*
 1. normally
 2. in a deep hollow

105. *Maxilliped outer plate distal setae-group, setae [type]*
 1. long robust
 2. short simple

106. *Labrum reduction*
 1. absent
 2. present

107. *Labrum (shape)*
 1. oval
 2. conspicuously triangular and pointed

108. *Labrum lobes [asymm. or symm.]*
 1. symmetrical
 2. asymmetrical

109. *Labrum right lobe*
 1. ordinary
 2. reduced

110. *Labrum left lobe*
 1. ordinary
 2. reduced

111. *Labrum [fused with epistome?]*
 1. separated from the epistome
 2. fused with the epistome

continued

APPENDIX 1 – *continued*

112. Labrum distally
1. narrowing
2. broad, oval

113. Labrum distal finger
1. present
2. absent

114. Labrum number of distal fingers
1. 1
2. 2

115. Labrum finger distally
1. pointed and acute
2. rounded

116. Labrum finger distally crenulation
1. absent
2. present

117. Coxal plates and basis on the pereopods
1. smooth
2. covered with setae

118. Coxal plates and basis, setae
1. very short, setules
2. simple [not very short]

119. Coxae 1–3 [overlapping]
1. contiguous
2. overlapping, coxa broad

120. Pereopod 1 coxa (ingroup)
1. rectangular
2. triangular

121. Pereopod 1 coxal plate
1. not as deep as basis
2. about as deep as basis

122. Pereopod 1 basis [straight or not]
1. straight
2. anterior margin weakly expanded

123. Pereopod 1 [propodus shape]
1. subrectangular
2. subovate

124. Pereopod 1 propodus posterior margin, groups of setae
1. absent, all setae in one single row
2. present

125. Pereopod 1 propodus, submarginal row of setae
1. absent
2. present

126. Pereopod 1 propodus distally, conspic. large cuspidate setae
1. absent
2. present

127. Pereopod 2 length
1. longer and thinner than pereopod 1
2. general appearance like pereopod 1

128. Pereopod 2 ischium elongation
1. absent
2. present [ratio length:breadth exceeding 1.5]

129. Pereopod 2 ischium distal posterior margin plumose setae
1. absent
2. present

130. Pereopod 2 [propodus shape]
1. subrectangular
2. subovate

131. Pereopod 2 palm
1. developed
2. absent

132. Pereopod 2 propodus, posterior submarginal row of robust setae
1. present
2. absent

133. Pereopod 2 propodus posterior margin, groups of robust setae
1. present
2. absent

134. Pereopod 2 propodus distally, conspic. large cuspidate setae
1. absent
2. present

135. Pereopods 3 & 4 merus and carpus posterior margins
1. without setae
2. with setae

136. Pereopods 3 & 4 [groups of setae] propodus posterior margin
1. without setae
2. with setae

137. Pereopods 5–6 [groups of setae] merus and carpus anterior margins
1. without setae
2. with setae

138. Pereopods 5–6 [groups of setae] propodus anterior margin
1. without setae
2. with setae

139. Pereopod 7 [groups of setae] merus and carpus anterior margins
1. without setae
2. with setae

140. Pereopod 7 [groups of setae] propodus anterior margin
1. without setae
2. with setae

141. Pereopod 4 coxa, shape of the lower margin
1. anterior part of the lower margin forming a straight line
2. entire lower margin curved

142. Pereopod 4 coxa, distal margin
1. broad
2. pointed (making coxa heart-shaped)

143. Pereopod 4 coxa posterior margin
1. convex
2. concave

144. Pereopod 4 basis anterior margin long setae
1. absent
2. present

145. Pereopod 4 basis posterior margin long setae
1. absent
2. present

146. Pereopod 4 basis, plumose setae on distal anterior margin
1. absent
2. present

147. Pereopod 4 basis, plumose setae on distal posterior margin
1. absent
2. present

148. Pereopod 4 ischium, plumose setae on posterior distal margin
1. absent
2. present

continued

APPENDIX 1 – *continued*

149. Pereopod 4 propodus and dactylus
1. simple
2. subchelate

150. Pereopod 5 basis (ingroup)
1. expanded
2. rectangular

151. Pereopod 6 basis posteriorly
1. expanded
2. unexpanded

152. Pereopod 6 basis expansion
1. conspicuous
2. rudimentary

153. Pereopod 6 basis expansion
1. rounded posteriorly (approaching linear)
2. concave

154. Pereopod 6 basis with a row of long plumose setae
1. absent
2. present

155. Pereopod 6 basis distal posterior corner
1. rounded
2. acute

156. Pereopod 6 basis, posterior margin of the expansion
1. smooth
2. serrated

157. Pereopod 7
1. differentiated from p6
2. similar to p6

158. Pereopod 7 basis posterior margin
1. smooth
2. serrate

159. Pereopod 7 basis anterior margin
1. straight
2. concave

160. Pereopod 7 basis distally
1. rounded
2. pointed and acute

161. Pereopod 7 basis with posterodistal corner
1. absent
2. present

162. Pereopod 7 basis, medial row of setae
1. present
2. absent

163. Pereopod 7 basis, setae-type in medial row
1. long
2. short and robust

164. Pereopod 7 carpus
1. present
2. absent

165. Pereopod 7 dactylus
1. present
2. absent

166. Oostegites on pereopod 2
1. present
2. absent

167. Oostegites on pereopod 3
1. present
2. absent

168. Gills pereopods 2–3
1. broad (ordinary)
2. long and narrow, similar to oostegites

169. Pleonite 1–3 dorsally
1. smooth
2. with a carina

170. Epimeral plate 3 lower margin, serrations
1. absent
2. present

171. Epimeral plate 3 posterior margin, serrations
1. absent
2. present

172. Epimeral plate 3 posteroventral corner, serrations
1. absent
2. present

173. Epimeral plate 3 posteroventral corner
1. not produced
2. produced

174. Epimeral plate 3 posteroventral corner
1. rounded
2. pointed and acute

175. Epimeral plate posterior margin
1. unproduced
2. broadly produced

176. Urosomites 2 and 3, articulation
1. present
2. absent

177. Uropod 1 outer ramus lateral margin with robust setae
1. absent
2. present

178. Uropod 1 outer ramus medial margin with robust setae
1. absent
2. present

179. Uropod 1 inner ramus outer margin with robust setae
1. absent
2. present

180. Uropod 1 inner ramus inner margin with robust setae
1. absent
2. present

181. Uropod 2 outer ramus outer margin with robust setae
1. absent
2. present

182. Uropod 2 outer ramus inner margin with robust setae
1. absent
2. present

183. Uropod 2 inner ramus outer margin with robust setae
1. absent
2. present

184. Uropod 2 inner ramus inner margin with robust setae
1. absent
2. present

185. Uropod 3 peduncle reduction
1. absent
2. present [shorter than half the length of rami]

186. Uropod 3 peduncle elongation
1. absent
2. present [at least as long as rami]

continued

APPENDIX 1 – *continued*

187. Uropod 3 outer ramus
1. 1-articulate
2. 2-articulate

188. Uropod 3 outer ramus lateral margin with robust setae
1. absent
2. present

189. Uropod 3 outer ramus medial margin with robust setae
1. absent
2. present

190. Uropod 3 inner ramus lateral margin with robust setae
1. absent
2. present

191. Uropod 3 inner ramus medial margin with robust setae
1. absent
2. present

192. Telson elongation
1. absent
2. present [longer than broad]

193. Telson submarginal setae on apex of each lobe
1. absent
2. present

194. Telson
1. cleft
2. entire

195. Telson apically
1. rounded
2. pointed

196. Males: Pereopod 2 propodus
1. larger in males than in females
2. equally sized in males and females

197. Males: Urosome
1. ordinary (similar to females)
2. conspicuously larger than in females

198. Males: Uropod 1 outer ramus
1. ordinary
2. enlarged, curved upwards

199. Males: Uropod 2 outer ramus
1. ordinary
2. enlarged, curved upwards

200. Males: Uropod 3 rami
1. ordinary
2. reduced

APPENDIX 2

TWO HUNDRED CHARACTERS SCORED FOR 91 INGROUP TAXA AND SIX OUTGROUP TAXA

abyssi
2 1 1 1 1 2 2 1 2 1 2 1 1 1 1 2 2 2 2 1 1 2 1 1 2 2 2 2 2 1 2
2 – 1 1 1 1 2 1 1 1 1 1 1 1 2 2 1 2 1 1 1 1 1 2 1 2 2 1 1 1 1
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2 1 1 1 1 1 2 2 2 2 1 1 1 1

australis
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2 1 1 1 1 1 2 2 2 2 1 1 1 1

gracilis
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lupus
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mimonectes
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americana
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andaniexis
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gloriosa
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elinae
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abyssorum
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bagabag
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APPENDIX 2 – *continued*

corpulentus
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karkar
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linearis
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lowryi
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pooh
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poorei
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pseudolinearis
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wallaroo
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wollongong
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antarcticus
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complex
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debroyeri
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continued

APPENDIX 2 – *continued*

ingens
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simplex
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wimi
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islandica
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fissicaudata
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eilae
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spongicola
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sandroi
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traudlae
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trymi
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APPENDIX 2 – *continued*

wagini
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pacis
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attingens
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auratus
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barnardi
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christianiensis
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ledoyeri
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gunnae
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tori
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camoti
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nr camoti
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APPENDIX 2 – *continued*

australis
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calypsonis
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beringi
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hancocki
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mamillidacta
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penelope
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Onisimus edwardsii
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Anonyx nugax
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Astyra abyssi
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Amphilochus manudens
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Ochlesis lewetzowi
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APPENDIX 2 – *continued*

Lilljeborgia fissicornis
1 1 2 1 1 2 2 1 1 1 1 – 2 – 1 1 1 1 1 2 1 1 1 1 2 2 2 2 2 2 1 1
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APPENDIX 3

Apomorphy lists according to tree number 1

Tree length = 1353
Consistency index (CI) = 0.1486
Homoplasy index (HI) = 0.8514
CI excluding uninformative characters = 0.1454
HI excluding uninformative characters = 0.8546
Retention index (RI) = 0.6852
Rescaled consistency index (RC) = 0.1018

Branch	Char#	Steps	CI	Change
node 195→node 190	1	1	0.500	1⇒2
	9	1	0.100	1→2
	16	1	1.000	1⇒2
	17	1	1.000	1⇒2
	18	1	0.500	1⇒2
	25	1	0.091	2⇒1
	30	1	0.250	1⇒2
	32	1	0.143	1→2
	46	1	0.500	1→2
	49	1	0.500	1⇒2
	57	1	0.250	1→2
	68	1	0.250	1→2
	129	1	0.143	1⇒2
	131	1	0.143	1→2
	148	1	0.083	1⇒2
	150	1	1.000	1⇒2
	157	1	0.500	2⇒1
	162	1	0.048	2→1
	174	1	0.067	2→1
	183	1	0.067	2→1
node 190→node 187	23	1	0.250	1→2
	94	1	0.167	1→2
	100	1	0.125	1→2
	178	1	0.077	2⇒1
	182	1	0.091	2⇒1
	188	1	0.077	2⇒1
	189	1	0.200	2⇒1
	190	1	0.167	2⇒1
	191	1	0.167	2⇒1
node 187→node 186	3	1	0.125	2⇒1
	9	1	0.100	2→1
	31	1	0.200	1⇒2
	34	1	0.333	2→1
	97	1	0.111	1⇒2
	98	1	0.083	1⇒2
	106	1	0.333	2→1
	108	1	0.091	1→2
	109	1	0.100	2→1
	123	1	0.077	2→1
	128	1	0.100	1⇒2
	130	1	0.045	2⇒1
	146	1	0.056	1⇒2
	179	1	0.083	2→1
	184	1	0.083	2→1
	187	1	0.083	1⇒2
	193	1	0.043	1→2
node 186→node 136	20	1	0.250	2⇒1
	23	1	0.250	2→1
	30	1	0.250	2⇒1
	55	1	0.111	1⇒2
	61	1	0.250	2⇒1
	68	1	0.250	2→1
	77	1	0.091	1⇒2
	94	1	0.167	2→1
	127	1	0.083	2⇒1
	154	1	0.059	1⇒2
node 136→node 134	11	1	0.333	1⇒2
	14	1	0.125	2→1
	22	1	0.333	1⇒2
	88	1	0.056	1→2
	106	1	0.333	1→2
	108	1	0.091	2→1
	109	1	0.100	1→2
	192	1	0.125	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
node 134→node 129	59	1	0.200	2→1		146	1	0.056	2⇒1
	98	1	0.083	2⇒1		148	1	0.083	2⇒1
	123	1	0.077	1→2		174	1	0.067	1⇒2
	180	1	0.059	2⇒1		192	1	0.125	1⇒2
node 129→node 113	9	1	0.100	1⇒2	node 108→node 107	159	1	0.500	1⇒2
	25	1	0.091	1⇒2		177	1	0.111	2⇒1
	65	1	0.125	2→1	node 107→*gracilis*	78	1	0.125	1⇒2
	88	1	0.056	2→1		129	1	0.143	2⇒1
	97	1	0.111	2⇒1		146	1	0.056	2⇒1
	121	1	0.167	2⇒1		148	1	0.083	2⇒1
	142	1	0.143	1⇒2	node 107→*americana*	9	1	0.100	2⇒1
	194	1	0.200	1⇒2		77	1	0.091	1⇒2
node 113→node 112	4	1	0.200	2⇒1		80	1	0.238	2⇒1
	77	1	0.091	2⇒1		87	1	0.111	1⇒2
	100	1	0.125	2⇒1		178	1	0.077	1⇒2
	145	1	0.067	2⇒1	node 112→node 111	3	1	0.125	1⇒2
	154	1	0.059	2⇒1		11	1	0.333	2⇒1
	186	1	0.125	1⇒2		13	1	0.100	1⇒2
node 112→node 108	7	1	0.077	1⇒2		59	1	0.200	1→2
	92	1	0.250	1⇒2		65	1	0.125	1→2
node 108→node 106	89	1	0.059	1⇒2		78	1	0.125	1⇒2
	141	1	0.083	2→1		85	1	0.083	1→2
	142	1	0.143	2⇒1		143	1	0.500	1⇒2
	195	1	0.056	1⇒2		147	1	0.042	1→2
node 101→*abyssi*	156	1	0.077	1⇒2		152	1	0.111	1⇒2
	170	1	0.500	1⇒2		162	1	0.048	1→2
node 101→*lupus*	144	1	0.071	1⇒2		169	1	0.250	1→2
	145	1	0.067	1⇒2		174	1	0.067	1⇒2
node 106→node 105	80	1	0.238	2⇒1		193	1	0.043	2⇒1
node 105→node 104	6	1	0.045	2⇒1	node 111→node 110	6	1	0.045	2⇒1
node 104→*australis*	130	1	0.045	1⇒2		32	1	0.143	2⇒1
	159	1	0.500	1⇒2		98	1	0.083	1⇒2
node 104→node 103	77	1	0.091	1⇒2		177	1	0.111	2⇒1
	147	1	0.042	1→2		181	1	0.100	2⇒1
node 103→node 102	85	1	0.083	1⇒2		195	1	0.056	1⇒2
	136	1	0.143	2⇒1	node 110→node 109	80	1	0.238	2→4
	144	1	0.071	1⇒2		103	1	0.100	1⇒2
node 102→*andaniexis*	6	1	0.045	1⇒2		149	1	1.000	1⇒2
	123	1	0.077	2⇒1	node 109→*dewitti*	41	1	0.333	1⇒2
	147	1	0.042	2→1	node 109→*mirabilis*	62	1	0.143	1⇒2
	195	1	0.056	2⇒1		145	1	0.067	1⇒2
node 102→*elinae*	89	1	0.059	2⇒1	node 110→*pelagica*	4	1	0.200	1⇒2
	138	1	0.167	2⇒1		89	1	0.059	1⇒2
	145	1	0.067	1⇒2		97	1	0.111	1⇒2
node 103→*ollii*	7	1	0.077	2⇒1		169	1	0.250	2→1
	98	1	0.083	1⇒2		186	1	0.125	2⇒1
	180	1	0.059	1⇒2	node 111→*tridentata*	88	1	0.056	1⇒2
	184	1	0.083	1⇒2		132	1	0.077	2⇒1
	188	1	0.077	1⇒2		183	1	0.067	1⇒2
node 105→*gloriosa*	7	1	0.077	2⇒1		192	1	0.125	1⇒2
	82	1	0.250	1⇒2	node 113→*mimonectes*	6	1	0.045	2⇒1
	141	1	0.083	1→2		47	1	0.100	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	80	1	0.238	2⇒3
	144	1	0.071	1⇒2
	146	1	0.056	2⇒1
	148	1	0.083	2⇒1
	172	1	0.077	1⇒2
	183	1	0.067	1⇒2
	187	1	0.083	2⇒1
node 129→node 128	26	1	0.200	2⇒1
	29	1	0.077	2⇒1
	89	1	0.059	1→2
	122	1	0.059	1⇒2
	136	1	0.143	2⇒1
	138	1	0.167	2⇒1
	173	1	0.042	2⇒1
	176	1	0.063	1→2
	193	1	0.043	2⇒1
node 128→node 123	24	1	0.143	1→2
	59	1	0.200	1→2
	74	1	0.167	2⇒1
	80	1	0.238	2⇒3
	197	1	1.000	1⇒2
	199	1	0.500	1⇒2
node 123→node 121	89	1	0.059	2→1
	98	1	0.083	1⇒2
node 121→node 119	28	1	0.250	2⇒1
	198	1	0.500	1⇒2
	200	1	1.000	1⇒2
node 119→*abyssorum*	12	1	0.250	1⇒2
	14	1	0.125	1⇒2
	89	1	0.059	1→2
	130	1	0.045	1⇒2
	131	1	0.143	2⇒1
	145	1	0.067	2⇒1
	146	1	0.056	2⇒1
	156	1	0.077	1⇒2
	162	1	0.048	1⇒2
	176	1	0.063	2→1
	196	1	0.143	2⇒1
node 119→node 118	27	1	0.143	2→1
	121	1	0.167	2⇒1
	135	1	0.200	2→1
	137	1	0.200	2→1
	199	1	0.500	2⇒1
node 118→node 117	24	1	0.143	2⇒1
	85	1	0.083	1⇒2
	122	1	0.059	2⇒1
	166	1	0.500	1⇒2
	168	1	0.500	1→2
	173	1	0.042	1→2
	193	1	0.043	1⇒2
node 117→node 116	27	1	0.143	1→2
	77	1	0.091	2⇒1
	83	1	0.083	1→2
	98	1	0.083	2⇒1
	135	1	0.200	1→2
	137	1	0.200	1→2
	140	1	0.200	2⇒1
	157	1	0.500	1⇒2
	162	1	0.048	1→2
node 116→node 114	89	1	0.059	1⇒2
	97	1	0.111	2⇒1
	173	1	0.042	2→1
node 114→*karkar*	136	1	0.143	1⇒2
	147	1	0.042	1⇒2
	167	1	1.000	1⇒2
node 116→node 115	12	1	0.250	1⇒2
	88	1	0.056	2⇒1
	131	1	0.143	2⇒1
	161	1	0.250	1⇒2
node 115→*lowryi*	6	1	0.045	2⇒1
	96	1	0.100	1⇒2
	147	1	0.042	1⇒2
	156	1	0.077	1⇒2
node 115→*wallaroo*	24	1	0.143	1⇒2
	83	1	0.083	2→1
	85	1	0.083	2⇒1
	122	1	0.059	1⇒2
	125	1	0.091	1⇒2
	126	1	0.333	1⇒2
	130	1	0.045	1⇒2
	134	1	0.333	1⇒2
	141	1	0.083	2⇒1
	154	1	0.059	2⇒1
	158	1	0.111	2⇒1
	162	1	0.048	2→1
	166	1	0.500	2⇒1
	168	1	0.500	2→1
	174	1	0.067	1⇒2
	195	1	0.056	1⇒2
node 117→*wollongong*	32	1	0.143	2⇒1
	108	1	0.091	1⇒2
	109	1	0.100	2⇒1
node 118→*corpulentus*	88	1	0.056	2⇒1
	147	1	0.042	1⇒2
	154	1	0.059	2⇒1
	180	1	0.059	1⇒2
node 121→node 120	85	1	0.083	1⇒2
	140	1	0.200	2⇒1
	154	1	0.059	2⇒1
	180	1	0.059	1⇒2
	184	1	0.083	1⇒2
node 120→*linearis*	6	1	0.045	2⇒1
	83	1	0.083	1⇒2
	88	1	0.056	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	153	1	0.250	1⇒2
	179	1	0.083	1⇒2
node 120→ *pseudolinearis*	12	1	0.250	1⇒2
	77	1	0.091	2⇒1
	80	1	0.238	3⇒2
	100	1	0.125	2⇒1
	130	1	0.045	1⇒2
	147	1	0.042	1⇒2
	158	1	0.111	2⇒1
	162	1	0.048	1⇒2
	176	1	0.063	2→1
node 123→node 122	125	1	0.091	1⇒2
	132	1	0.077	2⇒1
	153	1	0.250	1⇒2
node 122→*pooh*	80	1	0.238	3⇒4
	180	1	0.059	1⇒2
	198	1	0.500	1⇒2
node 122→*poorei*	6	1	0.045	2⇒1
	24	1	0.143	2→1
	85	1	0.083	1⇒2
	88	1	0.056	2⇒1
	147	1	0.042	1⇒2
	193	1	0.043	1⇒2
node 128→node 127	27	1	0.143	2⇒1
	30	1	0.250	1⇒2
	31	1	0.200	2⇒1
	35	1	0.167	1⇒2
	42	1	0.167	1⇒2
	62	1	0.143	1⇒2
	63	1	0.333	2⇒1
	77	1	0.091	2⇒1
	84	1	0.167	2→1
	90	1	0.111	1→2
	117	1	0.111	1⇒2
	119	1	0.333	1→2
	131	1	0.143	2→1
node 127→node 126	10	1	0.167	1→2
	28	1	0.250	2⇒1
	43	1	0.200	1⇒2
	55	1	0.111	2⇒1
	79	1	0.200	2⇒1
	85	1	0.083	1⇒2
	154	1	0.059	2→1
	176	1	0.063	2→1
	192	1	0.125	1→2
node 126→node 124	84	1	0.167	1→2
	90	1	0.111	2→1
	103	1	0.100	1⇒2
	180	1	0.059	1⇒2
	184	1	0.083	1⇒2
	188	1	0.077	1⇒2

Branch	Char#	Steps	CI	Change
node 124→*antarcticus*	8	1	0.167	1⇒2
	145	1	0.067	2⇒1
	146	1	0.056	2⇒1
	173	1	0.042	1⇒2
	192	1	0.125	2→1
	193	1	0.043	1⇒2
node 124→*ingens*	6	1	0.045	2⇒1
	10	1	0.167	2→1
	40	1	0.333	1⇒2
	89	1	0.059	2⇒1
	97	1	0.111	2⇒1
	127	1	0.083	1⇒2
	152	1	0.111	1⇒2
	158	1	0.111	2⇒1
node 126→node 125	24	1	0.143	1⇒2
	64	1	0.143	1⇒2
	83	1	0.083	1→2
	94	1	0.167	1⇒2
	96	1	0.100	1⇒2
	119	1	0.333	2→1
	122	1	0.059	2⇒1
	131	1	0.143	1→2
	135	1	0.200	2⇒1
	137	1	0.200	2⇒1
	141	1	0.083	2⇒1
node 125→*complex*	37	1	0.200	1⇒2
	78	1	0.125	1⇒2
	82	1	0.250	1⇒2
	87	1	0.111	1⇒2
	140	1	0.200	2⇒1
	145	1	0.067	2⇒1
	147	1	0.042	1⇒2
	154	1	0.059	1→2
	173	1	0.042	1⇒2
	193	1	0.043	1⇒2
node 125→*simplex*	69	1	1.000	2⇒1
	92	1	0.250	1⇒2
	130	1	0.045	1⇒2
	176	1	0.063	1→2
	177	1	0.111	2⇒1
	181	1	0.100	2⇒1
node 127→*debroyeri*	8	1	0.167	1⇒2
	12	1	0.250	1⇒2
	153	1	0.250	1⇒2
	162	1	0.048	1⇒2
	195	1	0.056	1⇒2
node 134→node 133	32	1	0.143	2⇒1
	76	1	0.143	1⇒2
	117	1	0.111	1⇒2
	146	1	0.056	2→1
	147	1	0.042	1→2
node 133→node 131	14	1	0.125	1→2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	89	1	0.059	1⇒2		64	1	0.143	1→2
	142	1	0.143	1⇒2		66	1	0.500	1→2
	162	1	0.048	1⇒2		86	1	0.200	2⇒1
	174	1	0.067	1→2		93	1	0.333	1⇒2
node 131→node 130	7	1	0.077	1→2		104	1	1.000	1→2
	25	1	0.091	1⇒2		105	1	0.250	1→2
	108	1	0.091	1→2		135	1	0.200	2→1
	109	1	0.100	2→1		136	1	0.143	2→1
	136	1	0.143	2⇒1		137	1	0.200	2→1
	138	1	0.167	2⇒1		138	1	0.167	2→1
	186	1	0.125	1⇒2		140	1	0.200	2→1
node 130→*eilae*	188	1	0.077	1⇒2		180	1	0.059	2⇒1
node 130→*spongicola*	24	1	0.143	1⇒2	node 185→node 140	124	1	0.250	2→1
	123	1	0.077	1⇒2		181	1	0.100	2⇒1
	147	1	0.042	2→1		186	1	0.125	1→2
	174	1	0.067	2→1		192	1	0.125	2⇒1
	180	1	0.059	2⇒1	node 140→node 138	147	1	0.042	1→2
node 133→node 132	29	1	0.077	2⇒1		152	1	0.111	1⇒2
	127	1	0.083	1⇒2		173	1	0.042	2⇒1
	128	1	0.100	2⇒1		194	1	0.200	1⇒2
node 132→*sandroi*	146	1	0.056	1→2		195	1	0.056	1⇒2
	186	1	0.125	1⇒2	node 138→node 137	48	1	0.077	1⇒2
node 132→*traudlae*	176	1	0.063	1⇒2		86	1	0.200	1⇒2
	188	1	0.077	1⇒2		127	1	0.083	2⇒1
	196	1	0.143	2⇒1	node 137→*integripes*	6	1	0.045	2⇒1
node 136→node 135	48	1	0.077	1→2		9	1	0.100	1⇒2
	121	1	0.167	2⇒1		43	1	0.200	1⇒2
	122	1	0.059	1⇒2		64	1	0.143	2→1
	156	1	0.077	1⇒2		78	1	0.125	1⇒2
	173	1	0.042	2⇒1		147	1	0.042	2→1
	178	1	0.077	1⇒2		148	1	0.083	2⇒1
	179	1	0.083	1→2		162	1	0.048	1⇒2
	184	1	0.083	1→2		171	1	0.167	1⇒2
node 135→*wimi*	142	1	0.143	1⇒2		172	1	0.077	1⇒2
	193	1	0.043	2⇒1	node 137→*pectinata*	62	1	0.143	1⇒2
node 135→*islandica*	6	1	0.045	2⇒1		82	1	0.250	1⇒2
	9	1	0.100	1⇒2		87	1	0.111	1⇒2
	29	1	0.077	2⇒1		142	1	0.143	1⇒2
	74	1	0.167	2⇒1		146	1	0.056	2⇒1
	80	1	0.238	2⇒6		154	1	0.059	1⇒2
	103	1	0.100	1⇒2		181	1	0.100	1⇒2
	123	1	0.077	1→2	node 138→				
	128	1	0.100	2⇒1	nordlandica	77	1	0.091	1⇒2
	144	1	0.071	1⇒2		144	1	0.071	1⇒2
	183	1	0.067	1⇒2	node 140→node 139	61	1	0.250	2⇒1
	187	1	0.083	2⇒1		89	1	0.059	1⇒2
	188	1	0.077	1⇒2		128	1	0.100	2⇒1
	190	1	0.167	1⇒2		139	1	0.500	2⇒1
	191	1	0.167	1⇒2		142	1	0.143	1⇒2
node 186→node 185	26	1	0.200	2⇒1		145	1	0.067	2⇒1
	27	1	0.143	2⇒1		148	1	0.083	2⇒1
	28	1	0.250	2⇒1	node 139→*maremboca*	36	1	0.111	1⇒2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	37	1	0.200	1⇒2
	57	1	0.250	2⇒1
	64	1	0.143	2→1
	80	1	0.238	2⇒1
	83	1	0.083	1⇒2
	96	1	0.100	1⇒2
	121	1	0.167	2⇒1
	124	1	0.250	1→2
	146	1	0.056	2⇒1
	158	1	0.111	2⇒1
	162	1	0.048	1⇒2
	186	1	0.125	2→1
node 139→*africana*	59	1	0.200	2⇒1
	74	1	0.167	2⇒1
	94	1	0.167	2⇒1
	177	1	0.111	2⇒1
	187	1	0.083	2⇒1
node 185→node 184	13	1	0.100	1→2
	14	1	0.125	2→1
	19	1	0.500	2⇒1
	32	1	0.143	2⇒1
	34	1	0.333	1→2
	50	1	1.000	1⇒2
	57	1	0.250	2⇒1
	88	1	0.056	1→2
	90	1	0.111	1⇒2
	112	1	0.500	2⇒1
	113	1	0.333	2⇒1
	162	1	0.048	1→2
	196	1	0.143	2⇒1
node 184→node 181	51	1	0.200	1⇒2
	52	1	0.500	1→2
	64	1	0.143	2→1
	103	1	0.100	1⇒2
	123	1	0.077	1→2
	127	1	0.083	2⇒1
	135	1	0.200	1→2
	136	1	0.143	1→2
	137	1	0.200	1→2
	138	1	0.167	1→2
	140	1	0.200	1→2
	146	1	0.056	2⇒1
	187	1	0.083	2⇒1
node 181→node 180	6	1	0.045	2→1
	31	1	0.200	2⇒1
	42	1	0.167	1→2
	80	1	0.238	2→1
	86	1	0.200	1⇒2
	88	1	0.056	2→1
	95	1	0.143	1⇒2
	101	1	0.167	1⇒2
	122	1	0.059	1→2

Branch	Char#	Steps	CI	Change
node 180→node 178	29	1	0.077	2→1
	35	1	0.167	1→2
	48	1	0.077	1⇒2
	125	1	0.091	1⇒2
	180	1	0.059	1⇒2
	184	1	0.083	1→2
	193	1	0.043	2⇒1
node 178→node 175	70	1	0.143	1⇒2
	80	1	0.238	1→2
	83	1	0.083	1→2
	98	1	0.083	2→1
	128	1	0.100	2⇒1
	195	1	0.056	1⇒2
node 175→node 174	29	1	0.077	1→2
	36	1	0.111	1→2
	54	1	0.200	1⇒2
	55	1	0.111	1⇒2
	65	1	0.125	2⇒1
	97	1	0.111	2⇒1
	117	1	0.111	1⇒2
	146	1	0.056	1⇒2
	154	1	0.059	1⇒2
	162	1	0.048	2→1
node 174→node 162	47	1	0.100	2⇒1
	75	1	0.143	1→2
	83	1	0.083	2→1
	108	1	0.091	2⇒1
	110	1	0.200	2→1
	179	1	0.083	1→2
	193	1	0.043	1⇒2
	196	1	0.143	1→2
node 162→node 158	14	1	0.125	1→2
	90	1	0.111	2⇒1
	99	1	0.167	1⇒2
	147	1	0.042	1⇒2
	162	1	0.048	1→2
node 158→node 147	39	1	0.250	1⇒2
	84	1	0.167	2⇒1
	89	1	0.059	1→2
	93	1	0.333	2⇒1
	102	1	0.200	2⇒1
	111	1	1.000	1⇒2
	152	1	0.111	1⇒2
node 147→node 146	13	1	0.100	2⇒1
	25	1	0.091	1⇒2
	33	1	0.500	2→1
	55	1	0.111	2⇒1
	56	1	0.333	1⇒2
	71	1	1.000	1⇒2
	80	1	0.238	2→4
	92	1	0.250	1⇒2
	94	1	0.167	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	105	1	0.250	2⇒1		81	1	0.333	1⇒2
	110	1	0.200	1→2		179	1	0.083	2⇒1
	122	1	0.059	2→1		182	1	0.091	2→1
	132	1	0.077	2→1		184	1	0.083	2⇒1
	151	1	0.200	1→2		189	1	0.200	2→1
	187	1	0.083	1⇒2	node 142→				
	193	1	0.043	2⇒1	*angustipalpa*	10	1	0.167	1⇒2
	195	1	0.056	2⇒1		14	1	0.125	2⇒1
node 146→node 141	53	1	0.250	1⇒2		25	1	0.091	2⇒1
	108	1	0.091	1⇒2		36	1	0.111	2⇒1
	117	1	0.111	2⇒1		65	1	0.125	1⇒2
	146	1	0.056	2⇒1		70	1	0.143	2⇒1
	147	1	0.042	2⇒1		80	1	0.238	3→2
	184	1	0.083	2⇒1		90	1	0.111	1⇒2
node 141→*gibbosa*	78	1	0.125	1⇒2		96	1	0.100	1⇒2
	80	1	0.238	4→2		107	1	0.333	1⇒2
	114	1	0.333	1⇒2		115	1	0.143	1⇒2
	123	1	0.077	2⇒1		117	1	0.111	2⇒1
	141	1	0.083	2⇒1		122	1	0.059	1→2
	173	1	0.042	2⇒1		132	1	0.077	1→2
	175	1	0.250	1⇒2	node 142→*crassum*	53	1	0.250	1⇒2
	183	1	0.067	1⇒2		54	1	0.200	1→2
node 141→*romeri*	81	1	0.333	1⇒2		62	1	0.143	1⇒2
	90	1	0.111	1⇒2		88	1	0.056	2→1
	122	1	0.059	1→2		89	1	0.059	2⇒1
	180	1	0.059	2⇒1		95	1	0.143	2⇒1
node 146→node 145	5	1	0.333	1⇒2		108	1	0.091	1⇒2
	8	1	0.167	1⇒2		109	1	0.100	2→1
	88	1	0.056	1→2		164	1	0.500	1⇒2
	109	1	0.100	1→2		165	1	0.500	1⇒2
	130	1	0.045	1⇒2		173	1	0.042	2⇒1
	182	1	0.091	1→2		180	1	0.059	2⇒1
	189	1	0.200	1→2		187	1	0.083	2⇒1
node 145→*unihamata*	87	1	0.111	1⇒2	node 144→node 143	178	1	0.077	1⇒2
	125	1	0.091	2⇒1		193	1	0.043	1⇒2
	132	1	0.077	1→2	node 143→*dampieri*	95	1	0.143	2⇒1
	151	1	0.200	2→1		108	1	0.091	1⇒2
	172	1	0.077	1⇒2		109	1	0.100	2→1
	180	1	0.059	2⇒1		122	1	0.059	1→2
	188	1	0.077	1⇒2		155	1	0.333	1⇒2
node 145→node 144	33	1	0.500	1→2		173	1	0.042	2⇒1
	39	1	0.250	2⇒1		183	1	0.067	1⇒2
	54	1	0.200	2→1		188	1	0.077	1⇒2
	80	1	0.238	4→3		196	1	0.143	2⇒1
	100	1	0.125	2⇒1	node 143→*quatro*	66	1	0.500	2⇒1
	101	1	0.167	2⇒1		68	1	0.250	2⇒1
	127	1	0.083	1⇒2		80	1	0.238	3→4
	162	1	0.048	2→1		99	1	0.167	2⇒1
	176	1	0.063	1⇒2		115	1	0.143	1⇒2
	194	1	0.200	1⇒2		146	1	0.056	2⇒1
node 144→node 142	15	1	0.250	1⇒2		164	1	0.500	1⇒2
	56	1	0.333	2→1		165	1	0.500	1⇒2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	174	1	0.067	1⇒2
	177	1	0.111	2⇒1
	181	1	0.100	2⇒1
node 147→*vanhoeffeni*	29	1	0.077	2⇒1
	87	1	0.111	1⇒2
	134	1	0.333	1⇒2
	162	1	0.048	2→1
	171	1	0.167	1⇒2
	172	1	0.077	1⇒2
	176	1	0.063	1⇒2
	179	1	0.083	2→1
node 158→node 157	75	1	0.143	2→1
	78	1	0.125	1⇒2
	125	1	0.091	2⇒1
	156	1	0.077	1→2
node 157→node 156	25	1	0.091	1⇒2
	35	1	0.167	2⇒1
	42	1	0.167	2⇒1
	76	1	0.143	1⇒2
	108	1	0.091	1⇒2
	110	1	0.200	1→2
	154	1	0.059	2→1
	178	1	0.077	1⇒2
	182	1	0.091	1⇒2
	183	1	0.067	1⇒2
node 156→node 149	29	1	0.077	2→1
	75	1	0.143	1→2
	127	1	0.083	1⇒2
	172	1	0.077	1→2
node 149→node 148	130	1	0.045	1⇒2
	147	1	0.042	2⇒1
	156	1	0.077	2→1
node 148→*bioice*	25	1	0.091	2⇒1
	148	1	0.083	2⇒1
	162	1	0.048	2⇒1
node 148→ *pseudophippsia*	129	1	0.143	2⇒1
	158	1	0.111	2⇒1
	172	1	0.077	2→1
	185	1	0.125	1⇒2
node 149→*viscaina*	174	1	0.067	1⇒2
node 156→node 155	3	1	0.125	1⇒2
	47	1	0.100	1⇒2
	99	1	0.167	2→1
	163	1	0.200	2→1
	193	1	0.043	2⇒1
node 155→*abyssicola*	173	1	0.042	2⇒1
	195	1	0.056	2⇒1
node 155→node 154	154	1	0.059	1→2
	156	1	0.077	2→1
node 154→node 153	48	1	0.077	2→1
	188	1	0.077	1⇒2

Branch	Char#	Steps	CI	Change
	189	1	0.200	1⇒2
	190	1	0.167	1⇒2
	191	1	0.167	1⇒2
node 153→*nipoma*	99	1	0.167	1→2
	154	1	0.059	2→1
	193	1	0.043	1⇒2
node 153→node 152	3	1	0.125	2→1
	117	1	0.111	2⇒1
	185	1	0.125	1⇒2
	195	1	0.056	2⇒1
node 152→node 151	2	1	0.500	1⇒2
	6	1	0.045	1→2
	48	1	0.077	1→2
	70	1	0.143	2⇒1
	98	1	0.083	1⇒2
	161	1	0.250	1⇒2
node 151→*rostrata*	3	1	0.125	1→2
	62	1	0.143	1⇒2
	86	1	0.200	2⇒1
	87	1	0.111	1⇒2
	123	1	0.077	2⇒1
	127	1	0.083	1⇒2
	148	1	0.083	2⇒1
	178	1	0.077	2⇒1
	180	1	0.059	2⇒1
	182	1	0.091	2⇒1
	184	1	0.083	2⇒1
	189	1	0.200	2⇒1
	190	1	0.167	2⇒1
	191	1	0.167	2⇒1
node 151→node 150	29	1	0.077	2⇒1
	35	1	0.167	1⇒2
	36	1	0.111	2⇒1
	54	1	0.200	2⇒1
	55	1	0.111	2⇒1
	65	1	0.125	1⇒2
	76	1	0.143	2⇒1
	80	1	0.238	2→1
	101	1	0.167	2→1
node 150→*inflatus*	6	1	0.045	2→1
	7	1	0.077	1⇒2
	9	1	0.100	1⇒2
	25	1	0.091	2⇒1
	42	1	0.167	1⇒2
	122	1	0.059	2⇒1
	132	1	0.077	2⇒1
	155	1	0.333	1⇒2
	156	1	0.077	1⇒2
	162	1	0.048	2⇒1
	170	1	0.500	1⇒2
	174	1	0.067	1⇒2
	185	1	0.125	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	193	1	0.043	1⇒2		70	1	0.143	2⇒1
	195	1	0.056	1⇒2		84	1	0.167	2→1
node 150→*ampulla*	51	1	0.200	2⇒1		95	1	0.143	2⇒1
	57	1	0.250	1⇒2		100	1	0.125	2→1
	80	1	0.238	1→5		101	1	0.167	2→1
	81	1	0.333	1⇒2		103	1	0.100	2→1
	95	1	0.143	2⇒1		107	1	0.333	1⇒2
	96	1	0.100	1⇒2		123	1	0.077	2→1
	103	1	0.100	2⇒1		129	1	0.143	2→1
	130	1	0.045	1⇒2		158	1	0.111	2⇒1
	144	1	0.071	1⇒2	node 160→*ingolfi*	29	1	0.077	2⇒1
	153	1	0.250	1⇒2		51	1	0.200	2⇒1
	171	1	0.167	1⇒2		85	1	0.083	1⇒2
	172	1	0.077	1⇒2		89	1	0.059	1⇒2
	173	1	0.042	2⇒1		90	1	0.111	2⇒1
	175	1	0.250	1⇒2		96	1	0.100	1⇒2
node 152→*similis*	116	1	0.250	1⇒2		114	1	0.333	1⇒2
	144	1	0.071	1⇒2		130	1	0.045	2→1
	162	1	0.048	2⇒1		145	1	0.067	2⇒1
	171	1	0.167	1⇒2		146	1	0.056	2⇒1
	172	1	0.077	1⇒2		173	1	0.042	2⇒1
	173	1	0.042	2⇒1		175	1	0.250	1⇒2
node 154→						193	1	0.043	2⇒1
cascadiensis	27	1	0.143	1⇒2	node 160→node 159	109	1	0.100	1→2
	118	1	0.125	1⇒2		110	1	0.200	1→2
	174	1	0.067	1⇒2		126	1	0.333	1⇒2
	187	1	0.083	1⇒2		134	1	0.333	1⇒2
node 157→*watlingi*	6	1	0.045	1⇒2		144	1	0.071	2→1
	64	1	0.143	1⇒2		147	1	0.042	1→2
	101	1	0.167	2⇒1		183	1	0.067	2→1
	105	1	0.250	2⇒1		195	1	0.056	2⇒1
	118	1	0.125	1⇒2	node 159→*trymi*	48	1	0.077	2⇒1
	128	1	0.100	1⇒2		76	1	0.143	1⇒2
	130	1	0.045	1⇒2		78	1	0.125	1⇒2
	144	1	0.071	1⇒2		79	1	0.200	2⇒1
	145	1	0.067	2⇒1		84	1	0.167	1→2
	173	1	0.042	2⇒1		88	1	0.056	1⇒2
	179	1	0.083	2→1		115	1	0.043	1⇒2
	188	1	0.077	1⇒2		122	1	0.059	2⇒1
node 162→node 161	11	1	0.333	1⇒2		152	1	0.111	1⇒2
	13	1	0.100	2⇒1		172	1	0.077	1⇒2
	36	1	0.111	2→1		176	1	0.063	1⇒2
	52	1	0.500	2→1		178	1	0.077	1⇒2
	127	1	0.083	1⇒2		191	1	0.167	1⇒2
	130	1	0.045	1→2	node 159→*pacis*	5	1	0.333	1⇒2
	144	1	0.071	1→2		10	1	0.167	1⇒2
	163	1	0.200	2⇒1		13	1	0.100	1⇒2
	183	1	0.067	1→2		53	1	0.250	1⇒2
	184	1	0.083	2⇒1		55	1	0.111	2⇒1
node 161→node 160	15	1	0.250	1⇒2		103	1	0.100	1→2
	35	1	0.167	2⇒1		108	1	0.091	1⇒2
	42	1	0.167	2⇒1		123	1	0.077	1→2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	125	1	0.091	2⇒1
	179	1	0.083	2⇒1
	180	1	0.059	2⇒1
	181	1	0.100	2⇒1
	186	1	0.125	1⇒2
node 161→*wagini*	25	1	0.091	1⇒2
	48	1	0.077	2⇒1
	77	1	0.091	1⇒2
	83	1	0.083	1→2
	88	1	0.056	1⇒2
	118	1	0.125	1⇒2
	141	1	0.083	2⇒1
	151	1	0.200	1⇒2
	174	1	0.067	1⇒2
	178	1	0.077	1⇒2
	188	1	0.077	1⇒2
	196	1	0.143	2→1
node 174→node 173	76	1	0.143	1⇒2
	88	1	0.056	1⇒2
	98	1	0.083	1→2
	132	1	0.077	2⇒1
node 173→node 166	7	1	0.077	1→2
	130	1	0.045	1→2
	141	1	0.083	2⇒1
	181	1	0.100	2⇒1
node 166→node 165	152	1	0.111	1⇒2
	172	1	0.077	1⇒2
	178	1	0.077	1⇒2
	182	1	0.091	1⇒2
node 165→node 164	7	1	0.077	2→1
	55	1	0.111	2⇒1
	56	1	0.333	1⇒2
	115	1	0.143	1⇒2
	116	1	0.250	1⇒2
	122	1	0.059	2⇒1
	132	1	0.077	1⇒2
	160	1	0.333	1→2
	193	1	0.043	1⇒2
node 164→node 163	48	1	0.077	2⇒1
	179	1	0.083	1⇒2
	181	1	0.100	1⇒2
	183	1	0.067	1⇒2
node 163→*attingens*	118	1	0.125	1⇒2
	127	1	0.083	1⇒2
	130	1	0.045	2→1
	141	1	0.083	1⇒2
	163	1	0.200	2⇒1
	173	1	0.042	2⇒1
	176	1	0.063	1⇒2
	178	1	0.077	2⇒1
	182	1	0.091	2⇒1
node 163→ *christianiensis*	36	1	0.111	2⇒1

Branch	Char#	Steps	CI	Change
	40	1	0.333	1⇒2
	97	1	0.111	1⇒2
	125	1	0.091	2⇒1
	128	1	0.100	1⇒2
	146	1	0.056	2⇒1
	147	1	0.042	1⇒2
	160	1	0.333	2→1
node 164→*auratus*	47	1	0.100	2⇒1
	148	1	0.083	2⇒1
	151	1	0.200	1⇒2
	154	1	0.059	2⇒1
	177	1	0.111	2⇒1
node 165→*ledoyeri*	6	1	0.045	1⇒2
	9	1	0.100	1⇒2
	39	1	0.250	1⇒2
	130	1	0.045	2→1
	173	1	0.042	2⇒1
	180	1	0.059	2⇒1
node 166→*barnardi*	37	1	0.200	1⇒2
	47	1	0.100	2⇒1
	48	1	0.077	2⇒1
	118	1	0.125	1⇒2
	127	1	0.083	1⇒2
	129	1	0.143	2⇒1
	162	1	0.048	1→2
node 173→node 172	128	1	0.100	1⇒2
	176	1	0.063	1⇒2
node 172→node 171	6	1	0.045	1⇒2
	152	1	0.111	1⇒2
node 171→node 169	146	1	0.056	2⇒1
	184	1	0.083	2⇒1
	185	1	0.125	1⇒2
node 169→*gunnae*	13	1	0.100	2⇒1
	173	1	0.042	2⇒1
	193	1	0.043	1⇒2
node 169→node 168	62	1	0.143	1⇒2
	85	1	0.083	1⇒2
	128	1	0.100	2⇒1
	176	1	0.063	2→1
	180	1	0.059	2⇒1
	187	1	0.083	1⇒2
	195	1	0.056	2⇒1
node 168→node 167	29	1	0.077	2→1
	68	1	0.250	2→1
	70	1	0.143	2⇒1
node 167→*camoti*	87	1	0.111	1⇒2
	101	1	0.167	2⇒1
	115	1	0.143	1⇒2
	116	1	0.250	1⇒2
	174	1	0.067	1⇒2
node 167→*nr camoti*	176	1	0.063	1→2
node 168→*boxshalli*	36	1	0.111	2⇒1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	47	1	0.100	2⇒1		148	1	0.083	2⇒1
	89	1	0.059	1⇒2		151	1	0.200	1⇒2
	130	1	0.045	1⇒2		176	1	0.063	1⇒2
node 171→node 170	47	1	0.100	2⇒1		184	1	0.083	2→1
	72	1	1.000	1⇒2		187	1	0.083	1⇒2
	73	1	1.000	2⇒1	node 177→node 176	47	1	0.100	2⇒1
	88	1	0.056	2⇒1		79	1	0.200	2⇒1
node 170→*australis*	132	1	0.077	1⇒2		102	1	0.200	2→1
	147	1	0.042	1⇒2		115	1	0.143	1⇒2
	172	1	0.077	1⇒2		147	1	0.042	1→2
	177	1	0.111	2⇒1		171	1	0.167	1⇒2
	187	1	0.083	1⇒2	node 176→*beringi*	9	1	0.100	1⇒2
node 170→*tucki*	7	1	0.077	1⇒2		48	1	0.077	2⇒1
	118	1	0.125	1⇒2		85	1	0.083	1⇒2
	173	1	0.042	2⇒1		96	1	0.100	1⇒2
	178	1	0.077	1⇒2		122	1	0.059	1→2
	182	1	0.091	1⇒2		125	1	0.091	2⇒1
node 172→*tori*	13	1	0.100	2⇒1		154	1	0.059	1⇒2
	89	1	0.059	1⇒2		161	1	0.250	1⇒2
	147	1	0.042	1⇒2		173	1	0.042	2⇒1
	180	1	0.059	2⇒1		178	1	0.077	1⇒2
	193	1	0.043	1⇒2		182	1	0.091	1⇒2
node 175→*penelope*	43	1	0.200	1⇒2		183	1	0.067	1⇒2
	51	1	0.200	2⇒1	node 176→*hancocki*	6	1	0.045	2→1
	78	1	0.125	1⇒2		7	1	0.077	2→1
	89	1	0.059	1⇒2		95	1	0.143	2⇒1
	95	1	0.143	2⇒1		116	1	0.250	1⇒2
	102	1	0.200	2⇒1		132	1	0.077	2⇒1
	173	1	0.042	2⇒1		145	1	0.067	2⇒1
	182	1	0.091	1⇒2		172	1	0.077	1⇒2
	183	1	0.067	1⇒2		179	1	0.083	2→1
node 178→node 177	6	1	0.045	1→2		188	1	0.077	1⇒2
	7	1	0.077	1→2		191	1	0.167	1⇒2
	40	1	0.333	1⇒2		193	1	0.043	1⇒2
	75	1	0.143	1⇒2		195	1	0.056	1⇒2
	76	1	0.143	1⇒2	node 180→node 179	25	1	0.091	1⇒2
	77	1	0.091	1⇒2		36	1	0.111	1⇒2
	122	1	0.059	2→1		37	1	0.200	1⇒2
	156	1	0.077	1→2		41	1	0.333	1⇒2
	179	1	0.083	1→2		43	1	0.200	1⇒2
node 177→*calypsonis*	3	1	0.125	1⇒2		90	1	0.111	2⇒1
	35	1	0.167	2→1		97	1	0.111	2⇒1
	39	1	0.250	1⇒2		145	1	0.067	2⇒1
	42	1	0.167	2→1		147	1	0.042	1⇒2
	54	1	0.200	1⇒2	node 179→*minima*	47	1	0.100	2⇒1
	55	1	0.111	1⇒2		130	1	0.045	1⇒2
	65	1	0.125	2⇒1		148	1	0.083	2⇒1
	88	1	0.056	1⇒2		177	1	0.111	2⇒1
	123	1	0.077	2⇒1		181	1	0.100	2⇒1
	136	1	0.143	2⇒1		195	1	0.056	1⇒2
	138	1	0.167	2⇒1	node 179→*pajarella*	51	1	0.200	2⇒1
	141	1	0.083	2⇒1		174	1	0.067	1⇒2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change
	185	1	0.125	1⇒2
node 181→ *mamillidacta*	13	1	0.100	2→1
	15	1	0.250	1⇒2
	75	1	0.143	1⇒2
	130	1	0.045	1⇒2
	148	1	0.083	2⇒1
	152	1	0.111	1⇒2
	158	1	0.111	2⇒1
	162	1	0.048	2→1
	163	1	0.200	2⇒1
	171	1	0.167	1⇒2
	172	1	0.077	1⇒2
	173	1	0.042	2⇒1
	175	1	0.250	1⇒2
	176	1	0.063	1⇒2
node 184→node 183	59	1	0.200	2⇒1
	70	1	0.143	1⇒2
	74	1	0.167	2⇒1
	83	1	0.083	1⇒2
	84	1	0.167	2→1
	98	1	0.083	2→1
	99	1	0.167	1→2
	100	1	0.125	2→1
	139	1	0.500	2⇒1
	177	1	0.111	2⇒1
node 183→node 182	9	1	0.100	1⇒2
	63	1	0.333	2⇒1
	75	1	0.143	1⇒2
	85	1	0.083	1→2
	114	1	0.333	1⇒2
	129	1	0.143	2⇒1
	130	1	0.045	1⇒2
	154	1	0.059	1⇒2
	181	1	0.100	2⇒1
node 182→*biofar*	142	1	0.143	1⇒2
node 183→*idae*	6	1	0.045	2⇒1
	53	1	0.250	1⇒2
	96	1	0.100	1⇒2
	115	1	0.143	1⇒2
	141	1	0.083	2⇒1
	145	1	0.067	2⇒1
	147	1	0.042	1⇒2
	192	1	0.125	2⇒1
	193	1	0.043	2⇒1
node 187→*globosus*	4	1	0.200	2⇒1
	6	1	0.045	2⇒1
	8	1	0.167	1⇒2
	37	1	0.200	1⇒2
	46	1	0.500	2→1
	48	1	0.077	1→2
	79	1	0.200	2⇒1
	83	1	0.083	1⇒2
	117	1	0.111	1⇒2
	124	1	0.250	2⇒1
	125	1	0.091	1⇒2
	152	1	0.111	1⇒2
	163	1	0.200	2⇒1
	173	1	0.042	2⇒1
	176	1	0.063	1⇒2
	185	1	0.125	1⇒2
node 190→node 189	14	1	0.125	2⇒1
	20	1	0.250	2⇒1
	22	1	0.333	1→2
	27	1	0.143	2⇒1
	29	1	0.077	2⇒1
	55	1	0.111	1⇒2
	65	1	0.125	2⇒1
	147	1	0.042	1⇒2
	154	1	0.059	1⇒2
	186	1	0.125	1⇒2
node 189→*boecki*	6	1	0.045	2⇒1
	21	1	1.000	1⇒2
	26	1	0.200	2⇒1
	34	1	0.333	2⇒1
	48	1	0.077	1→2
	61	1	0.250	2⇒1
	76	1	0.143	1⇒2
	87	1	0.111	1⇒2
	99	1	0.167	1⇒2
	103	1	0.100	1⇒2
	122	1	0.059	1⇒2
	125	1	0.091	1⇒2
	132	1	0.077	2⇒1
	174	1	0.067	1→2
	194	1	0.200	1⇒2
node 189→node 188	74	1	0.167	2⇒1
	83	1	0.083	1⇒2
	108	1	0.091	1⇒2
	144	1	0.071	1→2
	146	1	0.056	1⇒2
	156	1	0.077	1→2
	162	1	0.048	1→2
	183	1	0.067	1→2
node 188→*nonhiata*	7	1	0.077	1⇒2
	32	1	0.143	2⇒1
	77	1	0.091	1⇒2
	85	1	0.083	1⇒2
	109	1	0.100	2⇒1
node 195→node 194	26	1	0.200	2⇒1
	28	1	0.250	2⇒1
	31	1	0.200	1⇒2
	80	1	0.238	2→3
	94	1	0.167	1→2

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	98	1	0.083	1→2		32	1	0.143	1→2
	100	1	0.125	1→2		64	1	0.143	1⇒2
	102	1	0.200	2→1		92	1	0.250	1⇒2
	117	1	0.111	1→2		106	1	0.333	2⇒1
	118	1	0.125	1→2		131	1	0.143	1→2
	119	1	0.333	1⇒2		144	1	0.071	1→2
	120	1	0.500	2⇒1		158	1	0.111	2→1
	130	1	0.045	2→1	node 193→*Astyra*				
	145	1	0.067	2→1	*abyssi*	4	1	0.200	2⇒1
node 194→node 191	7	1	0.077	1→2		47	1	0.100	2⇒1
	8	1	0.167	1⇒2		90	1	0.111	1⇒2
	10	1	0.167	1⇒2		98	1	0.083	2→1
	20	1	0.250	2⇒1		100	1	0.125	2→1
	38	1	1.000	2⇒1		102	1	0.200	1→2
	61	1	0.250	2⇒1		154	1	0.059	1⇒2
	93	1	0.333	1⇒2		173	1	0.042	2⇒1
	123	1	0.077	2⇒1		174	1	0.067	2⇒1
	125	1	0.091	1⇒2		185	1	0.125	1⇒2
	126	1	0.333	1⇒2	node 193→node 192	2	1	0.500	1⇒2
	127	1	0.083	2⇒1		3	1	0.125	2⇒1
	128	1	0.100	1⇒2		49	1	0.500	1⇒2
	132	1	0.077	2⇒1		58	1	1.000	2⇒1
	156	1	0.077	1→2		63	1	0.333	2⇒1
	187	1	0.083	1⇒2		70	1	0.143	1→2
	193	1	0.043	1→2		75	1	0.143	1⇒2
node 191→*Onisimus*						80	1	0.238	3→1
edwardsii	3	1	0.125	2⇒1		82	1	0.250	1⇒2
	14	1	0.125	2⇒1		88	1	0.056	1→2
	83	1	0.083	1⇒2		97	1	0.111	1→2
	103	1	0.100	1⇒2		103	1	0.100	1⇒2
	113	1	0.333	2⇒1		112	1	0.500	2⇒1
	141	1	0.083	2⇒1		113	1	0.333	2⇒1
	178	1	0.077	2⇒1		117	1	0.111	2→1
	179	1	0.083	2⇒1		121	1	0.167	2⇒1
	182	1	0.091	2⇒1		133	1	0.500	1⇒2
	183	1	0.067	2⇒1		194	1	0.200	1⇒2
	188	1	0.077	2⇒1	node 192→				
	190	1	0.167	2⇒1	*Amphilochus*				
	192	1	0.125	2⇒1	*manudens*	8	1	0.167	1⇒2
node 191→*Anonyx*	89	1	0.059	1⇒2		10	1	0.167	1⇒2
nugax						26	1	0.200	1⇒2
	96	1	0.100	1⇒2		29	1	0.077	1→2
	118	1	0.125	2→1		62	1	0.143	1⇒2
	129	1	0.143	1⇒2		65	1	0.125	2⇒1
	130	1	0.045	1→2		80	1	0.238	1→2
	145	1	0.067	1→2		87	1	0.111	1⇒2
	185	1	0.125	1⇒2		91	1	1.000	1⇒2
	195	1	0.056	1⇒2		96	1	0.100	1⇒2
node 194→node 193	5	1	0.333	1⇒2		109	1	0.100	2⇒1
	6	1	0.045	2→1		110	1	0.200	2⇒1
	23	1	0.250	1→2		130	1	0.045	1→2
	29	1	0.077	2→1		131	1	0.143	2→1

continued

APPENDIX 3 – *continued*

Branch	Char#	Steps	CI	Change	Branch	Char#	Steps	CI	Change
	156	1	0.077	1→2		123	1	0.077	2⇒1
	158	1	0.111	1→2		132	1	0.077	2⇒1
	183	1	0.067	2⇒1		143	1	0.500	1⇒2
	190	1	0.167	2⇒1		144	1	0.071	2→1
	195	1	0.056	1⇒2		169	1	0.250	1⇒2
node 192→*Ochlesis lewetzowi*	1	1	0.500	1⇒2	node 195→*Lilljeborgia fissicornis*	4	1	0.200	2⇒1
	13	1	0.100	1⇒2		7	1	0.077	1→2
	15	1	0.250	1⇒2		13	1	0.100	1⇒2
	18	1	0.500	1⇒2		19	1	0.500	2⇒1
	20	1	0.250	2⇒1		48	1	0.077	1→2
	22	1	0.333	1⇒2		74	1	0.167	2⇒1
	23	1	0.250	2→1		79	1	0.200	2⇒1
	24	1	0.143	1⇒2		88	1	0.056	1⇒2
	25	1	0.091	2⇒1		121	1	0.167	2⇒1
	27	1	0.143	2⇒1		124	1	0.250	2⇒1
	30	1	0.250	1⇒2		133	1	0.500	1⇒2
	31	1	0.200	2⇒1		141	1	0.083	2⇒1
	36	1	0.111	1⇒2		144	1	0.071	1→2
	41	1	0.333	1⇒2		155	1	0.333	1⇒2
	43	1	0.200	1⇒2		156	1	0.077	1→2
	45	1	1.000	1⇒2		160	1	0.333	1⇒2
	86	1	0.200	2⇒1		161	1	0.250	1⇒2
	105	1	0.250	1⇒2		169	1	0.250	1⇒2
	107	1	0.333	1⇒2		193	1	0.043	1→2
	120	1	0.500	1⇒2		195	1	0.056	1⇒2
	122	1	0.059	1⇒2		196	1	0.143	2⇒1

APPENDIX 4

DISTRIBUTION OF ALL KNOWN STEGOCEPHALID SPECIES

	Species	Area							
		Arctic	North Atlantic	South Atlantic	Southern Ocean	Med.	South Pacific	North Pacific	Indian Ocean
1	*Alania beringi*	x						x	
2	*Alania calypsonis*			x					
3	*Alania hancocki*							x	
4	*Andaniexis abyssi*		x						
5	*Andaniexis americana*						x		
6	*Andaniexis andaniexis*						x		
7	*Andaniexis australis*			x					
8	*Andaniexis elinae*						x		
9	*Andaniexis gloriosa*								x
10	*Andaniexis gracilis*		x						
11	*Andaniexis lupus*	x(?)	x						
12	*Andaniexis oculatus*							x	
13	*Andaniexis olli*				x				
14	*Andaniexis stylifer*						x		
15	*Andaniexis subabyssi*							x	
16	*Andaniopsis integripes*				x		x(?)		x
17	*Andaniopsis nordlandica*	x	x						
18	*Andaniopsis pectinata*	x	x						
19	*Andaniotes abyssorum*						x		
20	*Andaniotes bagabag*						x		
21	*Andaniotes corpulentus*						x		
22	*Andaniotes karkar*						x		
23	*Andaniotes linearis*			x	x				
24	*Andaniotes lowryi*						x		
25	*Andaniotes pooh*				x(56°S)		x(50°)		
26	*Andaniotes poorei*						x		
27	*Andaniotes pseudolinearis*				x				
28	*Andaniotes wallaroo*						x		
29	*Andaniotes wollongong*						x		
30	*Austrocephaloides australia*			x					
31	*Austrocephaloides boxshalli*			x					
32	*Austrocephaloides camoti*						x		
33	*Austrocephaloides gunnae*						x		
34	*Austrocephaloides nr camoti*						x		
35	*Austrocephaloides tori*						x		
36	*Austrocephaloides tucki*						x		
37	*Austrophippsia unihamata*				x				
38	*Bathystegocephalus globosus*								x

continued

APPENDIX 4 – *continued*

	Species	Area							
		Arctic	North Atlantic	South Atlantic	Southern Ocean	Med.	South Pacific	North Pacific	Indian Ocean
39	*Bouscephalus mamillidacta*							x	
40	*Glorandaniotes eilae*		x						
41	*Glorandaniotes fissicaudata*								x
42	*Glorandaniotes sandroi*						x		
43	*Glorandaniotes spongicola*								x
44	*Glorandaniotes traudlae*						x		
45	*Gordania minima*		x						
46	*Gordania pajarella*							x	
47	*Mediterexis mimonectes*		x			x			
48	*Metandania islandica*		x						
49	*Metandania wimi*		x						
50	*Parandania boecki*		x	x	x		x	x	x
51	*Parandania gigantea*		x	x	x		x		x
52	*Parandania nonhiata*				x				
53	*Parandaniexis dewitti*				x(57°)				
54	*Parandaniexis inermis*								x
55	*Parandaniexis mirabilis*						x		
56	*Parandaniexis pelagica*			x					
57	*Parandaniexis spinescens*								x
58	*Parandaniexis tridentata*								x
59	*Phippsia gibbosa*		x						
60	*Phippsia roemeri*		x						
61	*Pseudo bioice*		x						
62	*Pseudo pseudophippsia*					x			
63	*Pseudo viscaina*							x	
64	*Schellenbergia pacifica*							x	
65	*Schellenbergia vanhoeffeni*				x(?)		x		
66	*Stegocephalexia penelope*							x	
67	*Stegocephalina ingolfi*		x						
68	*Stegocephalina pacis*				x				
69	*Stegocephalina trymi*			x					
70	*Stegocephalina wagini*	x	x						
71	*Stegocephaloides attingens*			x					
72	*Stegocephaloides auratus*	x	x						
73	*Stegocephaloides barnardi*		x			x			
74	*Stegocephaloides christianiensis*		x			x			
75	*Stegocephaloides ledoyeri*								x

continued

APPENDIX 4 – *continued*

	Species	Area							
		Arctic	North Atlantic	South Atlantic	Southern Ocean	Med.	South Pacific	North Pacific	Indian Ocean
76	*Stegocephalus abyssicola*	x	x						
77	*Stegocephalus ampulla*	x	x						
78	*Stegocephalus cascadiensis*							x	
79	*Stegocephalus inflatus*	x	x						
80	*Stegocephalus kergueleni*				x				
81	*Stegocephalus longicornis*							x	
82	*Stegocephalus nipoma*			x					
83	*Stegocephalus rostrata*				x				
84	*Stegocephalus similis*	x	x						
85	*Stegomorphia watlingi*				x				
86	*Stegonomadia biofar*	x	x						
87	*Stegonomadia idae*		x						
88	*Stegonomadia katalia*			x					
89	*Stegosoladidus antarcticus*				x				
90	*Stegosoladidus complex*						x		
91	*Stegosoladidus debroyeri*				x				
92	*Stegosoladidus ingens*				x				
93	*Stegosoladidus simplex*						x		
94	*Steleuthera africana*			x				x(?)	
95	*Steleuthera maremboca*						x		
96	*Tetradeion angustipalpa*						x		
97	*Tetradeion crassum*				x		x		
98	*Tetradeion dampieri*								x
99	*Tetradeion latum*						x		
100	*Tetradeion quatro*						x		

APPENDIX 5

INDEX TO SUBFAMILIES, GENERA AND SPECIES