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PHYLOGENETIC ANALYSIS OF THE FAMILY AMPITHOIDAE STEBBING, 1899 (CRUSTACEA: AMPHIPODA), WITH A SYNOPSIS OF THE GENERA

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ABSTRACT

The Ampithoidae is a speciose family of mostly herbivorous amphipods. Although these amphipods feature heavily in shallow-water community and other ecological studies, their phylogenetic relationships have been little studied. We examined the phylogenetic relationships within Ampithoidae to test the subfamilial and generic classification. Cladistic analysis of 77 morphological characters across 53 terminal taxa representing all recognised genera resulted in five most parsimonious trees, differing only in internal relationships of species of *Perampithoe* Conlan and Bousfield, 1982. The subfamilies Amphitholininae Conlan, 1982, and Exampithoinae Myers and Lowry, 2003, are not recognised. Most genera are recovered as monophyletic, but *Cymadusa* Savigny, 1816, and *Ampithoe* Leach, 1814, are paraphyletic. *Pleonexes* Spence Bate, 1857 is recognised as a valid genus and removed from the synomymy of *Ampithoe*. *Melanesius* Ledoyer, 1984, is synonymised with *Exampithoe* K. H. Barnard, 1925, and *Peramphithoe* is synonymised with *Sunamphitoe* Spence Bate, 1857. A revised generic classification of Ampithoidae is presented, including a key to the 15 valid genera and revised diagnoses for each genus.

KEY WORDS: cladistics, phylogeny, taxonomy

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INTRODUCTION

Amphipods of the family Ampithoidae Stebbing, 1899, constitute a group of herbivorous, algal and seagrass dwellers, common throughout tropical and temperate waters worldwide. The family is the largest family of herbivorous amphipods in terms of number of species, and their ecological importance has stimulated numerous studies examining plant-herbivore interactions, including host impacts (Duffy, 1990; Chess, 1993), dietary preferences (e.g., Duffy and Hay, 1991; Poore and Steinberg, 1999; Cruz-Rivera and Hay, 2001), distributional correlates (Edgar, 1983; Taylor, 1998), responses to secondary metabolites (e.g., Hay et al., 1987), susceptibility to predation (e.g., Hay et al., 1990; Holmlund et al., 1990), and taxonomic and geographic correlates of host use (Poore et al., 2008).

The taxonomy of Ampithoidae has been extensively studied in recent years (e.g., Poore and Lowry, 1997; Peart, 2004, 2007a, b, 2014; Kim et al., 2012), but conflicting subfamilial systems have been proposed. In addition to the nominate subfamily, Conlan (1982) proposed Amphitholininae for *Amphitholina* Ruffo, 1953, whereas Myers and Lowry (2003) proposed Exampithoinae for *Exampithoe* K. H. Barnard, 1925, and *Melanesius* Ledoyer, 1984. At present 206 species are recognised, but there has been considerable flux in the number of recognised genera. *Paradusa* Ruffo, 1969, has been considered to be a synonym of *Cymadusa* Savigny, 1816 (Poore and Lowry, 1997) or as a separate valid genus (Ruffo, 1969; J. L. Barnard and Karaman, 1991). Similarly, *Pleonexes* Spence Bate, 1857, has been usually regarded as a synonym of *Ampithoe* Leach, 1814 (J. L. Barnard, 1970; J. L. Barnard and Karaman, 1991; Peart, 2007b). Others, such as the two genera of the Exampithoinae Myers and Lowry, 2003, have been seen as subgenera (J. L. Barnard and Karaman, 1991; Poore and Lowry, 1997; Just, 2000), separate genera (K. H. Barnard, 1925; Ledoyer, 1984; Lowry and Myers, 2013) or as one genus (Conlan, 1982). The monophyly of larger genera such as *Ampithoe*, *Cymadusa*, and *Paragrubia* Chevreux, 1901, has also been questioned (J. L. Barnard and Karaman, 1991; Peart, 2007a, b; Hughes and Peart, 2013). Despite significant taxonomic attention, phylogenetic relationships among the ampithoids have received little attention. The current generic classification has its basis in the phenetic study of Conlan (1982), and to date, the phylogeny has not been tested by cladistic methods.

Ampithoids belong to a group of amphipods that have an entire and dorsoventrally thickened telson: the infraorder Corophiida Myers and Lowry, 2003. In their major revision of corophiideans, Myers and Lowry (2003) divided Ampithoidae into two subfamilies: Ampithoinae Leach, 1814, and Exampithoinae Myers and Lowry, 2003, largely on the basis of the entire rather than notched lower lip, which was believed to represent a plesiomorphic condition.

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Most ampithoid species fall into three genera, *Ampithoe*, *Cymadusa*, and *Peramphithoe*, each of whose monophyly has been questioned. The remaining genera are either monotypic or contain only a few species. This study, therefore, reassesses the generic and subfamilial classification using phylogenetic analysis and provides a revised synopsis of the genera of Ampithoidae.

Materials and Methods

Terminal Taxa

All currently recognised ampithoid genera were represented by one or more exemplars, minimally including the type species of currently recognised genera (and synonyms if present). For species-rich genera (e.g. *Ampithoe* and *Cymadusa*), multiple exemplars were chosen to represent the morphological diversity within each of these genera and allow testing of their monophyly. Morphological scorings were derived from examination of specimens, supplemented by published accounts. Specimens examined are deposited in the collections of the Australian Museum, Sydney (AM), Museo Civico di Storia Naturale, Verona, Italy (MVR), Museum Victoria, Melbourne (NMV), South African Museum, Capetown (SAMC), South Australian Museum, Adelaide (SAMA), and Western Australian Museum, Perth (WAM). Terminal taxa are listed in Appendix A.

Outgroup Selection

Identification of the sister group to Ampithoidae has been hampered by the paucity of large-scale phylogenetic analyses of Amphipoda. J. L. Barnard and Karaman (1991) noted Ampithoidae to be part of the larger group of corophioids, being possibly closely related to Ischyroceridae. Berge et al. (2000) found Ampithoidae to be closely related to Calliopiidae, but the most recent and most comprehensive analysis of the corophiidean amphipods identified Ampithoidae to be sister to Corophiidae, within which Protomediinae is basal (Myers and Lowry, 2003). Therefore, two species of *Protomedeia* Krøyer, 1842 (*P. articulata* J. L. Barnard, 1962 and *P. crudoliops* Hirayama, 1984) were selected as outgroups.

Analytical Methods

Characters and taxa were scored into an open DELTA (Dallwitz, 2005) database and exported as a nexus file for phylogenetic analysis. The final data matrix included 53 terminals (including 2 outgroups) and 77 characters (Appendix B). All characters were unordered, so the scoring for each state (i.e. 1, 2 etc.) implies nothing about the polarity or order. Polymorphisms were scored as such rather than assuming a plesiomorphic state. All characters were equally weighted and inapplicable data were scored as unknown.

Trees were generated using PAUP* 4.0b10 (Swofford, 2002) under a heuristic search (MULPARS, tree-bisection-reconnection, 500 replicates with random addition sequence). The relative stability of the clades was assessed by jackknifing implemented in PAUP* using 1000 pseudoreplicates and 30% character deletion. Pseudoreplicate bias during jackknifing was reduced by using a tree-space-search of 10 random addition sequence iterations with a maximum of 10 trees saved per iteration. Character state changes were studied in Mesquite Version 3.04 (Maddison and Maddison, 2015).

Character Analysis

Head.—*Mouthparts bundle*. The mouthparts form a bundle on the ventral margin of the head, and its particular conformation and orientation often correlates with the feeding strategies of the amphipod (Watling, 1993). Just (2002) demonstrated this to be reliable character defining *Pseudopleonexes* Conlan, 1982, in which the mouthparts bundle is directed posteriorly at an angle of approximately 45°. In *Amphitholina* Ruffo, 1953, which burrows into the stipes of large kelps, the mouthpart bundle is directed forwards (Myers, 1974). In all other genera the epistome and upper lip are directed approximately straight down, perpendicular to the ventral margin of the head.

Character 1. Epistome and upper lip angle: directed straight down, approximately 90° (1); directed posteriorly at more than 45° (2); directed anteriorly at approximately 45° (3).

Antennae. The length and structure of the antennae, whether antenna 1 is longer than, as long as, or shorter than antenna 2 usually differs between genera. The robustness of the antennae relative to each other also seems to be different between the genera. The relative lengths of the antennae appear to be more consistent between the genera than the robustness, which can sometimes be sexually dimorphic.

The presence or absence of an accessory flagellum is diagnostic among families and genera in many groups of amphipods (J. L. Barnard and Karaman, 1991). The condition of the accessory flagellum is variable among ampithoids. It can be absent (e.g., *Ampithoe*), present as a very small scale-like article (e.g., *Paradusa*), have one elongated article or one elongated and one reduced article (e.g., *Cymadusa*), or have three or more well developed articles, but usually no more than 10 articles (*Paragrubia*).

Conlan (1982) identified two additional antenna 2 characters. These relate to the fusion of flagellum articles and the indentation of the head at the insertion of antenna 2. These characters were not used in the present analysis because they are known in too few taxa. Moreover, these characters appear to have little systematic value based on the species examined.

Character 2. Antenna 1 length relative to antenna 2: shorter than (1); longer than (2), subequal to (3).

Character 3. Antenna 1 accessory flagellum: present (1); absent (2).

Character 4. Antenna 1 accessory flagellum development: absent (1); 1-segmented (2); 2-segmented (3); 3-5-segmented (4); 6-segmented or more (5).

Character 5. Antenna 2: slender, similar to antenna 1 (1); robust, better developed than antenna 1 (2).

Character 6. Antenna 2 ventral setation: long, dense, plumose setae (1); short dense setae (2); minimal setation (3).

Mandible. The molar process and mandibular palp vary in their development, being reduced in some genera. The palp varies in the number of articles and has traditionally been used to separate genera. For example, in *Sunamphitoe* the palp may be absent or 1-articulate, the single distinguishing feature from *Peramphithoe*, in which the palp is 3-articulate. Similarly, in Exampithoinae, the singular difference between *Exampithoe* and *Melanesius* is the number of articles of the mandibular palp. Variability in the condition of the palp within the family and within a number of genera suggests that it may have limited value in generic diagnosis or that some genera as currently defined are not monphyletic. The shape of the third article of the palp has also been used to distinguish genera.

Character 7. Mandible molar process: well developed, triturating (1); reduced (2); absent (3).

Character 8. Mandibular palp development: 3-articulate (1); 2-articulate (2); 1-articulate (3); absent (4).

Character 9. Mandibular palp shape: slender (1), stout (2).

Character 10. Mandibular palp article 3: smooth or rounded distally (1), beak-like, extended to form a point (2).

Lower lip. A diagnostic character of Ampithoidae is a notch in the outer plate of the lower lip (Fig. 1). This varies nevertheless in its expression within in the family. The notch is relatively weak in *Pseudopleonexes* compared to other genera. In Exampithoinae, however, the margin of the outer plate of the lower lip is entire, providing one of the justifications for its putatively basal subfamily status according to Myers and Lowry (2003).

Character 11. Lower lip, outer plate: entire (1), notched (2) (Fig. 1).

Character 12. Lower lip, outer plate, lobe lengths: entire (1), lobes lengths subequal (2), outer lobe longer than inner lobe (3) (Fig. 1).

Maxilla 1. The condition of the maxilla 1 palp has traditionally been considered as diagnostic for genera. The palp can be reduced (*Pseudoamphithoides* Ortiz, 1976) or absent (*Amphitholina* Ruffo, 1953). Conlan (1982) also emphasised the size of the palp relative to the outer plate. The apparent differences, however, appear to be an observational artefact resulting from different mounting techniques. Therefore, we regard this character as unreliable. The number of setae present on the inner plate

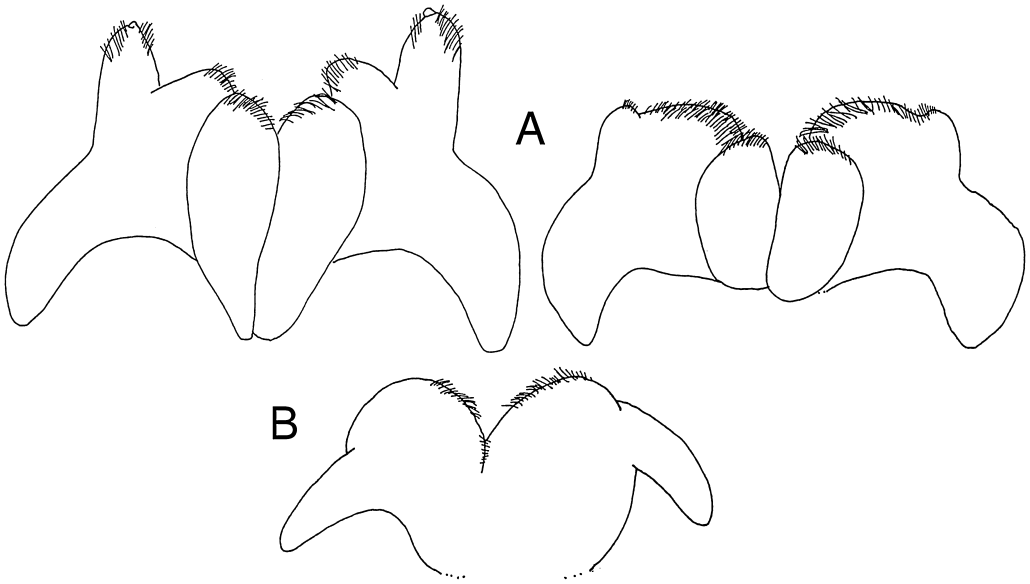

Fig. 1. Lower lip character progression. A, notched lower lip outer plate state (e.g., *Ampithoe* and *Pseudopleonexes*); B, entire lower lip state (e.g., *Exampithoe*).

of maxilla 1 has potential to be a useful taxonomic character, but is not presently known across enough taxa.

Character 13. Maxilla 1 palp size: well developed (1); reduced (2); absent (3).

Maxilla 2. The relative widths of the plates of the maxilla 2 have been traditionally used to separate genera (Conlan, 1982).

Character 14. Maxilla 2: plates similar width (1); outer plate broader than inner (2).

Pereopodal coxae. Species of *Exampithoe* have short coxae (as long as wide to wider than long), whereas those of most other genera have long coxae (longer than wide).

Character 15. Coxae: short (1); long (longer than wide) (2).

Gnathopods 1 and 2. Most ampithoid genera are strongly sexually dimorphic and most diagnostic characters at a species level only vary in the males. Characters associated with gnathopods 1 and 2 are diagnostic for both species and genera. The sculpturing and shape of the propodus of gnathopod 2 especially is useful for species identification. The sexual dimorphism of the gnathopods (especially the second pair) of amphithoids has traditionally been used to distinguish genera.

Character 16. Gnathopod 1 size: larger than gnathopod 2 (1); subequal in size to gnathopod 2 (2); smaller than gnathopod 2 (3).

Character 17. Gnathopod 1 size: robust (1); slender (2).

Character 18. Gnathopod 1 coxa: produced distoventrally (1); not produced distoventrally (2).

Character 19. Gnathopod 1 basis, anterodistal lobe: large and rounded (1); large and subacute (2); absent (3); small and rounded (4); reduced (5).

Character 20. Gnathopod 1 ischium anterodistal lobe: absent (1); present (2).

Character 21. Gnathopod 1 merus lobe: long (1); short (2); absent (3).

Character 22. Gnathopod 1 carpus length to propodus: markedly shorter than propodus (1); slightly shorter than propodus (2); subequal to propodus (3); slightly longer than propodus (4); markedly longer than propodus (5).

Character 23. Gnathopod carpal lobe shape: lobe with straight edge (1); rounded (2); acute (3); subacute (4); absent (5).

Character 24. Gnathopod 1 carpus anterior margin setation: absent (1); 1 robust seta (2); 2 robust setae (3); 3 robust setae (4); 4 or more robust setae (5); slender setae only (6).

Character 25. Gnathopod 1 propodal palm angle: acute (1); transverse or nearly so (2); undefined (3); obtuse (4).

Character 26. Gnathopod 1 propodal palm posterodistal tooth: present (1); absent (2).

Character 27. Gnathopod 1 propodal palm defining robust setae: absent (1); one (2); two (3); three or more (4).

Character 28. Gnathopod 1 dactylus length to palm: shorter than palm (1); subequal to palm (2); overreaching palm (3).

Character 29. Gnathopod 2 form: robust (1); slender (2).

Character 30. Gnathopod 2 basis, anterodistal lobe: prominent, blunt (1); large, narrowed, subacute (2); absent (3); small and rounded (4); reduced (5).

Character 31. Gnathopod 2 ischium anterodistal lobe: absent (1), present (2).

Character 32. Gnathopod 2 merus lobe: long (1); short (2); absent (3).

Character 33. Gnathopod 2 carpal lobe: absent (1); present (2).

Character 34. Gnathopod 2 carpus anterior margin setation: absent (1); 1 robust seta (2); 2 robust setae (3); 3 robust setae (4); 4 or more robust setae (5); slender setae only (6).

Character 35. Gnathopod 2 carpus length to propodus: much shorter than propodus (1); slightly shorter than propodus (2); subequal to propodus (3); longer than propodus (4); much longer than propodus (5).

Character 36. Gnathopod 2 propodal palm angle: transverse or nearly so (1); acute (2); extremely angled, almost in line with posterior margin (3); obtuse (4).

Character 37. Gnathopod 2 propodal palm sculpturing: absent (1); present (2).

Character 38. Gnathopod 2 dactylus length to palm: shorter than palm (1); subequal to palm (2); overreaching palm (3).

Pereopods 3 and 4. Pereopods 3 and 4 are morphologically similar in Ampithoidae. The most important features are the degree of expansion of the basis and the anterior expansion (or its absence) of the merus. This expansion of basis and merus stems from the presence of mucous glands and is most pronounced in specialist nest builders such as the *Pseudoamphithoides*, *Peramphithoe*, *Sunamphithoe*, and *Pseudopleonexes*. The species of these genera tend to construct nests from seaweed or detritus using the mucus as an adhesive to bind together fragments. The mucus is sometimes strong enough to hold blades of the seaweed that are still attached to the plant and also to curl the blades to form a tube. Less host-specific species tend to have a reduced gland and narrow, non-expanded bases and meri on pereopods 3 and 4.

Character 39. Pereopod 3 basis: expanded (1); narrow (2).

Character 40. Pereopod 3 merus: anteriorly expanded (1); narrow (2).

Pereopods 5-7. Pereopods 5-7 show varying degrees of prehensility in ampithoids. Vader (1983) summarised discussions on the value of

prehensile appendages as diagnostic characters. The variety and functional morphology of prehensile pereopods is a complex issue. Several forms of prehensile pereopods are recognized in Ampithoidae. Pereopods 5-7 are either simple, weakly prehensile, strongly prehensile, or nearly subchelate. The expansion of the distal articles of pereopods 5-7 is an important feature in some groups. *Macropisthopous* K. H. Barnard, 1916, has an expanded pereopod 7, but species of *Peramphithoe* and *Sunamphitoe* can also have this character on pereopods 5-7.

Character 41. Prehensility of pereopods 5-7: simple (1); weak (2); strong (nearly subchelate) (3).

Character 42. Length of pereopod 5 to pereopods 6-7: P5-7 equal in length (1); P5 shorter than P6 and P7 (2).

Character 43. Pereopod 5 distal articles size: slender (1); broad (2); strongly broadened (3).

Character 44. Pereopod 5 propodus: slightly expanded distally (1); strongly expanded distally (2); not expanded distally (3).

Character 45. Pereopod 6 distal articles size: slender (1); broad (2); strongly broadened (3).

Character 46. Pereopod 6 propodus: subchelate, heel shaped (1); rectangular, not expanded proximally (2).

Character 47. Pereopod 6 propodus: slightly expanded distally (1); strongly expanded distally (2); not expanded distally (3).

Character 48. Pereopod 7 distal articles size: slender (1); broad (2); strongly broadened (3).

Character 49. Pereopod 7 propodus: subchelate, heel shaped (1); rectangular, not expanded proximally (2).

Epimeral plates. The ornamentation of epimeron 3, and to some extent epimeron 2, is regarded as diagnostic for genera of the Ampithoidae. It is not sexually dimorphic and exhibits little allometric variation. Most members of *Cymadusa* and *Paragrubia* have a small, acute tooth on the posteroventral corner of epimeron 3.

Character 50. Epimeron 2 posteroventral corner: not produced (1); produced (2).

Character 51. Epimeron 3 posteroventral corner: broadly rounded (1); narrowly rounded (2); subquadrate (3); emarginate (4); acute (5).

Uropods. Uropods 1 and 2 are similar in shape. Several characters have diagnostic properties, notably the presence or absence of a distoventral spur on the peduncle of uropod 1. Three groups can be recognised based on the condition of the spur. The spur can be completely absent in both sexes; short and rounded on the peduncle of the male uropod 1 and absent from the peduncle of the female uropod 1; or long and acute on the peduncle of uropod 1. The presence or absence of a laterodistal projection on the peduncle of the male uropod 2, first recognised by Just (2002) is a synapomorphy of *Pseudopleonexes*. Another synapomorphy of *Pseudopleonexes* is the position of uropod 1 relative to uropod 2.

Uropod 3 carries a number of diagnostic characters. The outer ramus of uropod 3 bears two strongly recurved robust, apical setae, diagnostic for the Ampithoidae. Within the family, however, variation exists in the size and shape of these setae. The setation on the peduncle and both rami differs between genera.

Character 52. Uropod 1 in relation to uropod 2: short, reaching to the middle of the peduncle (1); subequal in length, reaching to the rami of uropod 2 (2); long, reaching past the rami of uropod 2 (3).

Character 53. Uropod 1 peduncle armature: unarmed (1); one or two robust setae (2); three to five robust setae (3); six or more robust setae (4).

Character 54. Uropod 1 peduncular setal fringe: absent (1); short (less than half the length of peduncle) (2); long (3).

Character 55. Uropod 1 peduncular distoventral spur in males: small and rounded (1); absent (2); large and acute (3).

Character 56. Uropod 1 inner ramus length: as long as outer (1); shorter than outer (2); longer than outer (3).

Character 57. Uropod 1 inner ramus number of marginal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 58. Uropod 1 outer ramus number of marginal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 59. Uropod 2 laterodistal peduncular projection: absent (1); present (2).

Character 60. Uropod 2 peduncle number of robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 61. Uropod 2 peduncular setal fringe: absent (1); present (2).

Character 62. Uropod 2 inner ramus length: as long as outer (1); shorter than outer (2); longer than outer (3).

Character 63. Uropod 2 inner ramus number of marginal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 64. Uropod 2 outer ramus number of marginal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 65. Uropod 3 peduncle to rami length: short (1); long (2).

Character 66. Uropod 3 peduncle marginal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 67. Uropod 3 peduncle distal robust setae: absent (1); one or two (2); three to five (3); six or more (4).

Character 68. Uropod 3 rami width: broad (1); narrow (2).

Character 69. Uropod 3 outer ramus length to inner ramus: shorter than (1); subequal to (2); longer than (3).

Character 70. Uropod 3 outer ramus setation: 2 large recurved distal robust setae (1); 1 curved plus 1 small or straight robust seta (2); absent (3).

Character 71. Uropod 3 outer ramus lateral denticles: present (1); absent (2).

Character 72. Uropod 3 outer ramus lateral setal fringe: present (1); absent (2).

Character 73. Uropod 3 inner ramus distal robust setae: absent (1); one (2); two or three (3); four or more (4).

Telson. The telson bears diagnostic characters at all taxonomic levels. In ampithoids, the telson is subtriangular in dorsal outline except for the two species of *Austrothoe* Peart, 2014, which have a subrectangular telson bearing patches of conical denticles posterolaterally. Another character distinguishing some genera is the size or presence or absence of the apical cusps. In *Pseudopleonexes* and some species of *Pleonexes*, these cusps are enlarged to form large hooks. In other genera, the cusps are small or absent.

Character 74. Telson shape: subtriangular (1); subrectangular (2).

Character 75. Telson apical cusps: small (1); expanded into large hooks (2); absent (3).

Character 76. Telson setation: oblique rows (1); apical (2); lateral slender (3); absent (4); lateral robust (5).

Character 77. Telson denticles: absent (1); present (2).

RESULTS

The heuristic search produced five most parsimonious trees of length 610 steps, consistency index (CI) 0.2323, and retention index (RI) 0.5675. Although nodal support is generally low, all trees are congruent except among five species of *Peramphithoe* that form a clade with *Sunamphitoe kanaka* (clade 44). Thus, results are effectively fully resolved. One of the five most parsimonious trees is shown in Fig. 2 with jackknife support and serves as the exemplar for character-state reconstructions. Unambiguous character state changes are listed in Appendix C and correspond to clade numbers marked in Fig. 2.

Monophyly of Ampithoidae is supported by 10 unambiguous changes (clade 1) of which the presence of two robust setae on the outer ramus of uropod 3 is never reversed (character 70). Other unambiguous changes supporting the ingroup node are either reversed or further derived high in the tree. *Amphithoides* Kossmann, 1880, is sister to the remaining amphithoids followed by a monophyletic *Paragrubia* and paraphyletic *Cymadusa* and *Ampithoe*. The remaining ampithoid genera are recovered as monophyletic except for *Sunamphitoe* and *Peramphithoe*, whose species are intermingled within a single clade, and *Melanesius*, which is paraphyletic as a result of an internally nested *Exampithoe*. Like *Peramphithoe* and *Sunamphitoe*, the species of *Exampithoe* and *Melanesius* together form a clade, but neither genus is monophyletic. Moreover, the *Exampithoe* + *Melanesius* clade, comprising Myers and Lowry's (2003)

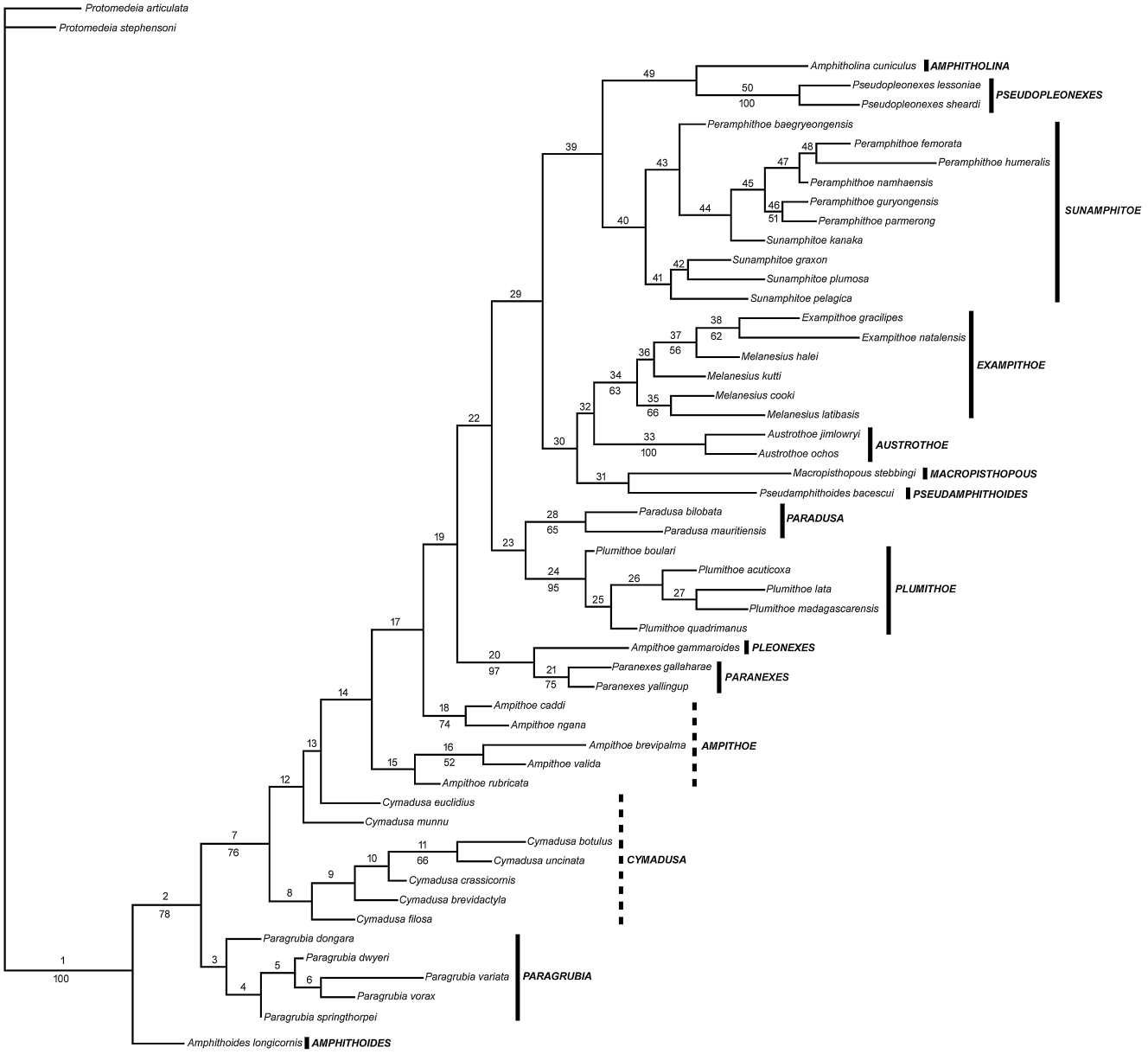

Fig. 2. One of the five most parsimonious trees (length 610 steps, consistency index 0.2323, retention index 0.5675). Clade number indicated above branch, corresponding to character state reconstructions listed in Appendix C. Jackknife support indicated below branch.

Exampithoinae, is deeply nested among the remaining ampithoid genera.

Of the three largest ampithoid genera (*Ampithoe*, *Cymadusa* and *Paragrubia*), only *Paragrubia* is recovered as monophyletic. *Ampithoe* and *Cymadusa* form a paraphyletic series between *Paradusa* and the remaining ampithoid genera higher in the tree. Species of *Ampithoe* are grouped into three separate clades of which one includes the type species of the genus, and another corresponds to the previously synonymised genus, *Pleonexes*. The majority of *Cymadusa* exemplars, however, group with the type species of the genus, *C. filosa*.

Paradusa, *Plumithoe*, *Paranexes* + *Pleonexes* are in clearly defined clades. The monotypic or very small genera of *Macropisthopous*, *Pseudamphithoides*, *Amphitholina* and *Pseudopleonexes* are strongly defined and not nested within other groups of species.

Discussion

Not surprisingly, our cladistic results differ significantly from those of Conlan's (1982) phenetic analysis. Whereas Conlan (1982) interpreted *Amphitholina* as basal in the family and justifying subfamilial status (Amphitholininae), present results indicate that *Ampithoides* is sister to the remaining ampithoids with *Amphitholina* occupying a 'high' position in the tree. As such, Amphitholininae cannot be maintained. Our results, however, corroborate Conlan's (1982), contention of a phylogenetic trend in the palmar angle of gnathopod 1 from oblique to transverse.

J. L. Barnard (1970) noted in his discussion of Hawaiian biodiversity and amphipod morphology that changes in morphology such as loss of mandibular palp articles and reversal of dominance in gnathopods have lower value in diagnosing genera than previously thought. This seems evident throughout the ampithoid genera as well, in which much emphasis has previously been placed on the condition of the mandibular palp and the size of the male gnathopods.

Ampithoidae has usually been defined by two main characters, namely the notched outer plate of the lower lip and the presence of distal recurved robust setae on the outer ramus of the third uropod. The condition of the lower lip (whether notched or entire) is of particular significance in ampithoid taxonomy as a primary feature driving the subfamilial classification: entire in Exampithoinae, notched in Ampithoinae (Myers and Lowry, 2003). Although the entire lower lip unites the two nominal exampithoine genera, *Exampithoe* and *Melanesius*, our results show they form a clade deeply nested among the ampithoine genera as sister to *Austrothoe*. Recognition of Exampithoinae would render Ampithoinae paraphyletic. Therefore, we do not recognise the validity of Exampithoinae and as such abandon the subfamilial classification. The entire lower lip shared by *Exampithoe* and *Melanesius* is a synapomorphy derived from the notched condition of all other ampithoids. Although species of *Exampithoe* and *Melanesius* form a single clade, the former is paraphyletic with respect to the latter. The single feature distinguishing *Exampithoe* and *Melanesius* is the presence or absence of the mandibular palp. Our results, however, show that the condition of the palp does not support two reciprocally monophyletic clades corresponding to *Exampithoe* and *Melanesius*, but that the latter is nested within the former. We therefore synonymise the two nominal genera and recognise only *Exampithoe*.

Paradusa is sister to *Plumithoe*. The status of *Paradusa* and whether it is a synonym of *Cymadusa* has been controversial (Poore and Lowry, 1997). Present results, however, suggest that these taxa are not closely related and thus should be maintained as separate genera.

Although present results suggest that *Cymadusa* is not monophyletic, it would be premature to further divide the genus until more extensive phylogenetic analyses can be undertaken to identify natural groupings that could form separate genera. *Cymadusa* presently includes two genera in its synonymy (*Grubia* and *Acanthogrubia*) both of whose respective type species (*Grubia taurica* Czerniavsky, 1868 = *C. crassicornis* Costa, 1853; *Acanthogrubia uncinata* Stout, 1912) align with the type species of *Cymadusa*, meaning any future division of *Cymadusa* will likely result in new genera. At present, we recognise *Cymadusa* as paraphyletic, requiring further phylogenetic study.

Ampithoe is a difficult genus to assess. Consisting of 72 worldwide species, significant morphological diversity occurs within the group and many of its constituent species remain to be revised. Like *Cymadusa*, most junior generic synonyms of *Ampithoe* align with *A. rubricata* (type species of the genus), so future divisions of the genus will likely result in new genera, rather than resurrection of older names. One clade, however, corresponds to *Pleonexes*, which J. L. Barnard (1970) synonymised with *Ampithoe*. Our results show that the clade containing the type species of *Ampithoe* (clade 15) is phylogenetically distant from that of *Pleonexes* indicating that both genera should be recognised. We refrain from further subdivision of *Ampithoe* until more detailed analyses of its composition can be conducted. It remains possible that some poorly known species of *Ampithoe*, when revised, will prove to be better placed in *Pleonexes* than *Ampithoe*.

The status of *Macropisthopous* K. H. Barnard, 1916, has been a source of controversy (Poore and Lowry, 1997). In erecting *Macropisthopous*, Barnard (1916) provided an inadequate description and figures, particularly with respect to the presence or absence of a spur on the peduncle of uropod 1, important for distinguishing *Sunamphitoe* and *Peramphithoe*. This led to the confusion over whether *Macropisthopous* represented a derived *Sunamphitoe* or *Peramphithoe* or was actually a separate valid genus. Examination of the type material (holotype and slide: SAM 18971, Cat. No. A2917, A3287, A3035) of *M. stebbingi* K. H. Barnard, 1916, indicates that the spur on the peduncle of uropod 1 is absent, distinguishing *Macropisthopous* from *Sunampithoe*. Moreover, present results find *Macropisthopous* to be more closely related to *Pseudoamphithoides*, *Exampithoe* and *Austrothoe* than *Sunamphitoe*. *Macropisthopous* is thus recognised here as a valid genus.

The status of *Peramphithoe* and *Sunamphitoe* requires reconsideration given present results. Although exemplars of both *Peramphithoe* and *Sunamphitoe* are united within the same clade, they do not form reciprocally monophyletic units corresponding to their assigned genera. The two putative genera are distinguished by the presence or absence of the mandibular palp. The mandibular palp, however, is lost independently multiple times in not only *Peramphithoe* and *Sunamphitoe*, but also throughout the genera of Ampithoidae, indicating that it has little value in tracing phylogenetic relationships at generic level. Aside from the condition of the mandibular palp, *Peramphithoe* and *Sunamphitoe* are indistinguishable. Given that the species of *Peramphithoe* and *Sunamphitoe* are nested together, we herein synonymise *Peramphithoe* with *Sunamphitoe*.

Based on the results of cladistic analysis, we herein recognise 15 genera as valid. *Perampithoe* is synonymised with *Sunamphitoe*, *Melanesius* is synonymised with *Exampithoe* and Exampithoinae is abandoned. *Pleonexes* is removed from the synonymy of *Ampithoe* and recognised as a valid genus most closely related to *Paranexes*. Although *Cymadusa* and *Ampithoe* are not monophyletic, we defer revising their compositions until more detailed analyses can be completed. The revised generic classification of Ampithoidae is presented below including diagnoses and composition of the genera, and a key to the genera.

SYSTEMATICS

Order Amphipoda Latreille, 1816
Suborder Senticaudata Lowry and Myers, 2013
Superfamily Corophioidea Leach, 1814
Family Ampithoidae Stebbing, 1899

Diagnosis.—Lower lip notched (sometimes entire). Maxilla 1 outer plate broad (occasionally narrowed). Coxae long

(sometimes reduced in length). Uropod 3 outer ramus with distal, strongly recurved robust setae or weakly recurved or straight distal robust setae. Telson with cusps.

Key to the Genera of Ampithoidae

1. Uropod 1 (male) peduncular distoventral spur reduced or absent 2
– Uropod 1 (male) peduncular distoventral spur large and acute 10
2. Coxae 1-4 shorter than wide or as wide as long 3
– Coxae 1-4 longer than wide 5
3. Telson triangular, denticles absent. Pereopods 6-7 propodus subrectangular 4
– Telson rectangular, denticles present. Pereopods 6-7 propodus produced proximally to form a heel . . . . . *Austrothoe* Peart, 2014
4. Lower lip outer plate entire. Maxilla 1 palp well developed. Gnathopod 1 palm acute . . . . . *Exampithoe* K. H. Barnard, 1925
– Lower lip outer plate notched. Maxilla 1 palp reduced. Gnathopod 1 palm transverse . . . . . *Pseudoamphithoides* Ortiz, 1976
5. Uropod 2 (male) peduncle with broad rounded laterodistal projection . . . . . *Pseudopleonexes* Conlan, 1982
– Uropod 2 (male) peduncle without laterodistal projection 6
6. Telsonic cusps reduced 7
– Telsonic cusps expanded to form large hooks 8
7. Gnathopod 1 palm acute . . . . . *Ampithoe* Leach, 1814
– Gnathopod 1 palm transverse . . . . . *Macropisthopous* K. H. Barnard, 1916
8. Mandibular molar and palp absent, maxilla 1 palp absent . . . . . *Amphitholina* Ruffo, 1953
– Mandibular molar and palp present, maxilla 1 palp present 9
9. Uropod 1 peduncular distoventral spur (male) absent . . . . . *Paranexes* Peart, 2014
– Uropod 1 peduncular distoventral spur (male) rounded and reduced . . . . . *Pleonexes* Spence Bate, 1857
10. Antenna 1 accessory flagellum present 11
– Accessory flagellum absent 14
11. Accessory flagellum with 1-2 articles 12
– Accessory flagellum with 3 or more articles . . . . . *Paragrubia* Chevreux, 1901
12. Uropod 3 rami narrow; outer ramus with reduced distal robust setae . . . . . *Amphithoides* Kossmann, 1880
– Uropod 3 rami broad; outer ramus with strongly recurved distal robust setae 13
13. Mandibular palp stout. Maxilla 2 outer plate much broader than inner plate . . . . . *Cymadusa* Savigny, 1816
– Mandibular palp slender. Maxilla 2 outer plate equal width to inner plate . . . . . *Paradusa* Ruffo, 1969
14. Pereopods 3 and 4 bases and meri narrow, antenna 2 with long, dense plumose setae on ventral margin of peduncle . . . . . *Plumithoe* J. L. Barnard and Karaman, 1991
– Pereopods 3 and 4 with expanded bases and meri, antenna 2 with sparse or dense setae on all margins . . . . . *Sunamphitoe* Spence Bate, 1857

Amphithoides Kossmann, 1880

Amphithoides Kossmann, 1880: 135. – J. L. Barnard and Karaman, 1991: 100. – Poore and Lowry, 1997: 898. – Peart, 2014: 886. (Type species: *Amphithoides longicornis* Kossmann, 1880, by original designation)

Diagnosis.—Epistome and upper lip angle directed ventrally, approximately 90° to ventral margin of head. Antenna 1 accessory flagellum present, 2-articulate. Mandibular molar present, well developed, palp with 3 articles, slender, article 3 smooth distally. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 2 palp present, well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 subequal in size to gnathopod 2. Gnathopod 1 coxae produced anteroventrally; palm acute. Pereopods 3, 4 basis narrow; merus not anteriorly expanded. Pereopods 5-7 simple. Pereopods 6-7 propodus subrectangular; distal articles slender. Epimeron 3 with small acute distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; peduncle with long, acute distoventral spur, lateral setal fringe absent. Uropod 2 peduncle without laterodistal projection, lateral setal fringe absent. Uropod 3 rami narrow; outer ramus with 1 reduced recurved, 1 straight robust seta; denticles, lateral setal fringe absent. Telson subtriangular; cusps, denticles absent, apical setae.

Remarks.—*Amphithoides* is sister to the remaining ampithoids and is closest to *Paragrubia*. *Amphithoides* is similar to *Paragrubia* by the structure of uropod 3 rami and the distal setae on the outer ramus of uropod 3. In *Paragrubia* and *Amphithoides* the uropod 3 rami are narrow and the outer rami have reduced non-curved distal robust setae, whereas other ampithoids have broad uropod 3 rami and strongly recurved distal robust setae on the outer ramus of uropod 3. *Amphithoides* and *Paragrubia* are also similar to *Cymadusa*, and the distantly related genus *Paradusa*. These four groups all have an accessory flagellum on antenna 1 and *Paragrubia*, *Amphithoides* and some species of *Cymadusa* have a tooth on the posteroventral corner of epimeron 3.

Species Included.—*Amphithoides longicornis* Kossmann, 1880; *A. mahafalensis* Ledoyer, 1967; *A. patrizii* Maccagno, 1936.

Amphitholina Ruffo, 1953
Fig. 3A

Amphitholina Ruffo, 1953: 5. – Myers, 1974: 463-469. – J. L. Barnard and Karaman, 1991: 101. – Poore and Lowry, 1997: 898. – Peart, 2014: 886. (Type species: *Amphithoe cuniculus* (Stebbing, 1874), by original designation)

Diagnosis.—Epistome and upper lip angle directed anteriorly. Antenna 1 accessory flagellum absent. Mandible molar absent; palp absent. Lower lip outer plate entire. Maxilla 1 palp absent. Maxilla 2 outer plate broader than inner plate. Coxae short. Gnathopod 1 smaller than gnathopod 2, coxae not produced anterodistally, palm obtuse. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 weakly prehensile. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 length in situ reaching halfway along

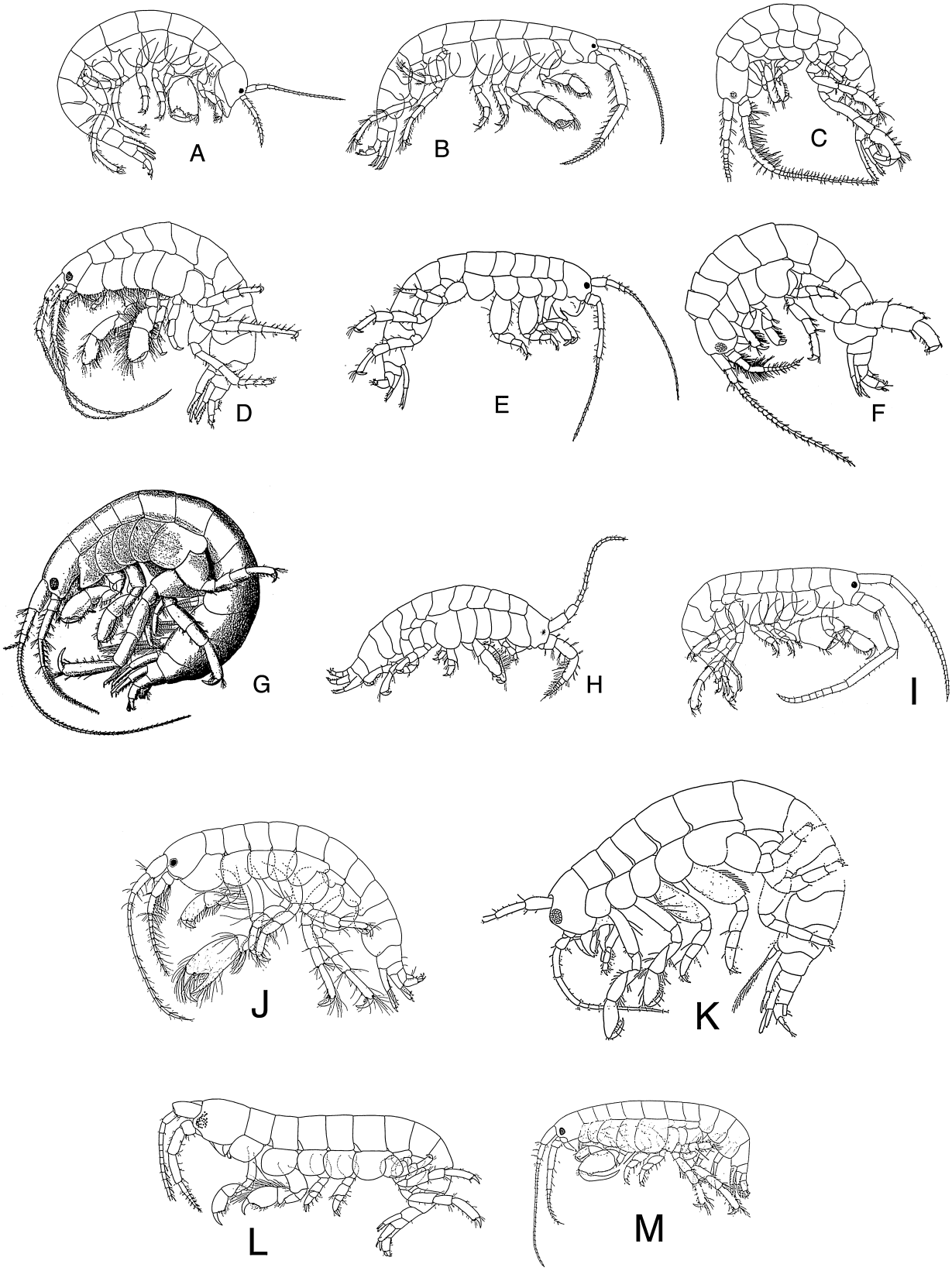

Fig. 3. Habitus of the ampithoid genera (generally type species). A, *Amphitholina cuniculus* (after Lincoln, 1979); B, *Ampithoe rubricata* (after Lincoln, 1979); C, *Austrothoe jimlowryi* (after Peart, 2014); D, *Cymadusa filosa* (after Peart, 2004); E, *Exampithoe kutti* (after Poore and Lowry, 1997); F, *Macropisthopous stebbingi*; G, *Paragrubia vorax* (after Chevreux, 1901); H, *Paranexes yallingup* (after Peart, 2014); I, *Pleonexes gammaroides* (after Lincoln, 1976); J, *Plumithoe hirsuta* (after Myers, 1985); K, *Pseudoamphithoides incurvaria* (after Just, 1977); L, *Pseudopleonexes sheardi* (after Just, 2002); M, *Sunamphitoe pelagica* (after Bousfield, 1973); *Amphithoides* and *Paradusa* are not represented due to the lack of whole animal illustrations.

peduncle of uropod 2; peduncle distoventral spur absent, lateral setal fringe present extending length of peduncle. Uropod 2 peduncle laterodistal projection absent, lateral setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved robust setae, lateral denticles present, lateral setal fringe absent. Telson subtriangular; cusps expanded to form large hooks; denticles, setae absent.

Remarks.—*Amphitholina* is defined by a suite of apomorphies. These include: epistome and upper lip directed forward instead of straight down, mandibular molar absent, mandibular palp absent, an entire lower lip, maxilla 1 palp absent, and an obtuse gnathopod 1 propodal palm. *Amphitholina* is most closely related to *Pseudopleonexes*.

Species Included.—*Amphitholina cuniculus* (Stebbing, 1874).

Ampithoe Leach, 1814
Fig. 3B

Ampithoe Leach, 1814: 403. – J. L. Barnard and Karaman, 1991: 102. – Poore and Lowry, 1997: 898. – Peart, 2007a: 1-95. – Peart, 2014: 886. (Type species: *Cancer* (*Gammarus*) *rubricatus* Montagu, 1808, by monotypy)

Anisopus Templeton, 1836: 185. (Preoccupied *Anisopus* Meigen, 1803) (Diptera). (Type species: *Anisopus dubius* Templeton, 1836)

Amphitho (*sic*) – Dana, 1852: 213.

Diagnosis.—Epistome, upper lip angle directed ventrally, approximately 90° to head ventral margin. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp 3-articulate, stout, article 3 smooth distally. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 smaller than gnathopod 2, coxa produced forward anteroventrally, palm acute. Pereopods 3, 4 basis narrow; merus anteriorly narrow. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 in situ reaching apices of uropod 2 rami; peduncle distoventral spur absent, setal fringe present (usually) or absent. Uropod 2 peduncle laterodistal projection absent, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles, setal fringe present or absent. Telson subtriangular; cusps small; denticles absent.

Remarks.—*Ampithoe* is a complex genus. Originally the largest ampithoid genus, this analysis suggests that *Ampithoe* is paraphyletic. *Pleonexes*, formerly considered a junior synonym of *Ampithoe*, is removed from synonymy and regarded here as a valid genus.

Species Included.—*Ampithoe africana* K. H. Barnard, 1925; *A. akuolaka* J. L. Barnard, 1970; *A. alluaudi* Chevreux, 1901; *A. aptos* (J. L. Barnard, 1969); *A. atauro* Hughes, 2015; *A. australiensis* Spence Bate, 1862; *A. bizseli* Özaydinli and Coleman, 2012; *A. boecki* Della Valle, 1893; *A. boiana* Peart, 2007; *A. brevipalma* Kim and Kim, 1988; *A. caddi* Poore and Lowry, 1997; *A. cinerea* Haswell, 1879; *A. cookana* Peart, 2007; *A. dalli* Shoemaker, 1938; *A. dentimana* Mateus and Mateus, 1986; *A. djakonovi* Gurjanova, 1938; *A. eremitis* Peart, 2007; *A. fastidiosa* Mateus and Mateus, 1991; *A. ferox* (Chevreux, 1901); *A. geographe* Peart, 2007; *A. grubiformis* Reid, 1951; *A. guaspare* J. L. Barnard, 1979; *A. hiana* Peart, 2007; *A. hinatore* J. L. Barnard, 1972; *A. hirsutamanus* Ortiz and Lemaitre, 1997; *A. hyalos* Peart, 2007; *A. katae* Peart, 2007; *A. kuala* Myers, 1985; *A. kussakini* Gurjanova, 1955; *A. lacertosa* Spence Bate, 1858; *A. lafkui* Appadoo and Myers, 2004; *A. longimana* Smith, 1873; *A. macrocornutus* (Kensley, 1971); *A. mantissa* Hughes and Peart, 2013; *A. marcuzzii* Ruffo, 1954; *A. mascarenensis* Appadoo and Myers, 2004; *A. megaloprotopus* Stebbing, 1895; *A. merimbula* Peart, 2007; *A. ngana* Poore and Lowry, 1997; *A. ningaloo* Peart, 2007; *A. nobrei* Mateus and Mateus, 1986; *A. peronana* Peart, 2007; *A. platycera* Sivaprakasam, 1970; *A. plumulosa* Shoemaker, 1938; *A. plumulosa tepahue* J. L. Barnard, 1979; *A. pollex* Kunkel, 1910; *A. pomboi* Mateus and Afonso, 1974; *A. prolata* Hughes and Peart, 2013; *A. pseudongana* Peart, 2007; *A. rachanoi* Peart, 2002; *A. ramondi* Audouin, 1826; *A. ricaudyana* Peart and Hughes, 2014; *A. riedli* Krapp-Schickel, 1968; *A. roly* Peart, 2007; *A. rosema* Peart, 2007; *A. rubricata* (Montagu, 1808); *A. rubricatoides* Shoemaker, 1938; *A. sectimana* Conlan and Bousfield, 1982; *A. senegalensis* Schellenberg, 1925; *A. serraticauda* Rabindranath, 1972; *A. simulans* Alderman, 1936; *A. tahue* J. L. Barnard, 1979; *A. takeuchii* Peart and Hughes, 2014; *A. tarasovi* Bulycheva, 1952; *A. ulladulla* Peart, 2007; *A. vacoregue* J. L. Barnard, 1979; *A. valida* Smith, 1873; *A. valida shimizuensis* Kim and Kim, 1988; *A. volki* Gurjanova, 1938; *A. waialua* J. L. Barnard, 1970; *A. youngsanensis* Kim and Kim, 1988; *A. zachsi* Gurjanova, 1938.

Austrothoe Peart, 2014
Fig. 3C

Austrothoe Peart, 2014: 887. (Type Species: *Austrothoe jimlowryi* Peart, 2014, by original designation)

Diagnosis.—Epistome, upper lip directed ventrally, 90° to ventral margin of head. Antenna 1 accessory flagellum with 1 article, vestigial. Mandible molar well developed; palp with 3-articulate, stout, article 3 distally smooth. Lower lip outer plate notched, inner lobes shorter than outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae short. Gnathopod 1 subequal in size to gnathopod 2, gnathopod 1 coxa not produced forward anteroventrally, palm acute. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 strongly prehensile. Pereopods 6, 7 propodus produced proximally to form a heel; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; peduncle distoventral spur absent, setal fringe present. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, lateral denticles absent, setal fringe absent or reduced. Telson rectangular; cusps small; denticles present.

Remarks.—*Austrothoe* is closely related to *Exampithoe. Austrothoe*, and *Exampithoe* share a uropod 1 without a distoventral spur and short coxae (wider than long or as wide as long). *Austrothoe* differs from *Exampithoe* in that *Austrothoe* has a notched lower lip (entire in *Exampithoe*); a subrectangular telson (subtriangular telson in *Exampitho*); a vestigial accessory flagellum on antenna 1 (absent in *Exampithoe*); and the mandibular molar and palp are always

well developed (often reduced mandibular molar and palp in *Exampithoe*). Other synapomorphies of this genus are the expansion of the proximal end of the propodi of pereopods 6 and 7 to form a palm-like heel and the presence of denticles on the dorsal surface of the telson.

Species Included.—*Austrothoe jimlowryi* Peart, 2014; *A. ochos* Peart, 2014.

Cymadusa Savigny, 1816
Fig. 3D

Cymadusa Savigny, 1816: 51, 109. – J. L. Barnard and Karaman, 1991: 104. – Poore and Lowry, 1997: 900. – Peart, 2007b: 1-53; 2014: 886. (Type species: *Cymadusa filosa* Savigny, 1816, by monotypy)

Grubia Czerniavsky, 1868: 103. (Type species: *Grubia taurica* Czerniavsky, 1868 = *Cymadusa crassicornis* Costa, 1853)

Acanthogrubia Stout, 1912: 143. (Type species: *Acanthogrubia uncinata* Stout, 1912)

Diagnosis.—Epistome, upper lip directed ventrally, 90° to ventral margin of head. Antenna 1 accessory flagellum present, with 3 articles. Mandible molar well developed; palp 3-articulate, stout, article 3 smooth. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plater broader than inner plate. Coxae long. Gnathopod 1 smaller than gnathopod 2, gnathopod 1 coxa produced forward anteroventrally, palm acute. Pereopods 3, 4 basis narrow; merus not anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 with or without distoventral tooth. Uropod 1 position in situ reaching to apices of uropod 2 rami; peduncle with long, acute distoventral spur, setal fringe of varying lengths generally present. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved, robust distal setae, denticles mostly absent, setal fringe mostly present. Telson subtriangular; cusps small; denticles absent.

Remarks.—*Cymadusa* is a paraphyletic genus, closely related to *Paragrubia* and *Amphithoe*, but also superficially similar to *Ampithoides* and *Paradusa*. *Cymadusa* differs from *Paragrubia* by the length of the accessory flagellum of antenna 1 and the shape of uropod 3 rami. *Cymadusa* differs from *Amphithoides* by the shape of the third uropod rami, being broad and short (compared to the peduncle) in *Cymadusa*, and long (compared to the peduncle) and narrow in *Ampithoides*, and differs from *Paradusa* by the shape of the mandibular palp (narrow in *Paradusa*, stout in *Cymadusa*) and the uropod 3 rami (narrow in *Paradusa*) and short and broad in *Cymadusa*.

In their account of brackish water amphipods of the Parangipettai coast, India, Lyla et al. (1998) validated names for a genus and eight species of amphipods including a species of *Cymadusa*, *C. pathyi*. Lyla et al. (1998) attributed the names to the late K. Peethambaran Asari by placing "Peethambaran" after each species name, but without any type of further clarification or explanation of their intentions. Following a strict interpretation of Article 51 of the International Code of Zoological Nomenclature (ICZN, 1985, 1999) (see also Ng, 1994), however, the correct authorship of *Cymadusa pathyi* is Lyla, Velvizhi and Ajmal Khan, 1998, rather than Peethambaran. Similarly, for the other amphipod species and a genus name listed in the paper against Peethambaran, the authorship should also be attributed to Lyla, Velvizhi and Ajmal Khan, 1998, as follows: Natarajphotis Lyla, Velvizhi and Ajmal Khan, 1998; *Urothoe serrudactyla* Lyla, Velvizhi and Ajmal Khan, 1998; *Urothoe spinidactyla* Lyla, Velvizhi and Ajmal Khan, 1998; *Urothoe viswanthi* Lyla, Velvizhi and Ajmal Khan, 1998; *Eriopisa abhilashi* Lyla, Velvizhi and Ajmal Khan, 1998; *Gitanopsis gouriae* Lyla, Velvizhi and Ajmal Khan, 1998; *Parorchestia morini* Lyla, Velvizhi and Ajmal Khan, 1998; *Gammaropsis esturinus* Lyla, Velvizhi and Ajmal Khan, 1998; and *Natarajphotis manieni* Lyla, Velvizhi and Ajmal Khan, 1998.

Species Included.—*Cymadusa alyxis* Hughes and Lowry, 2009; *C. aungtonyae* Peart, 2002; *C. botulus* Hughes and Peart, 2013; *C. brevidactyla* (Chevreux, 1907); *C. cavimana* (Sivaprakasam, 1970); *C. chalongana* Peart, 2002; *C. chuawe* Peart, 2007; *C. compta* (Smith, 1873); *C. crassicornis* (Costa, 1857); *C. drummondae* Hughes and Peart, 2013; *C. elegantis* Peart, 2007; *C. euclidius* Hughes and Peart, 2013; *C. excavata* Dang and Le, 2012; *C. filosa* Savigny, 1816; *C. grossimana* Ledoyer, 1984; *C. hadros* Hughes and Peart, 2013; *C. hallex* Hughes and Peart, 2013; *C. hawaiensis* (Schellenberg, 1938); *C. hentyana* Hughes and Peart, 2013; *C. heronensis* Peart, 2007; *C. herrerae* Ortiz and Winfield, 2015; *C. hoeyae* Hughes and Lowry, 2009; *C. imbroglio* Rabindranath, 1972; *C. jiigurru* Peart, 2007; *C. jubata* Hughes and Peart, 2013; *C. khbarnardi* Hughes and Lowry, 2009; *C. ledoyeri* Peart, 2004; *C. lituus* Peart and Hughes, 2014; *C. lumanus* Hughes and Peart, 2013; *C. lunata* Myers, 1985; *C. mariabyrneae* Hughes and Lowry, 2009; *C. microphthalma* (Chevreux, 1901); *C. munnu* Poore and Lowry, 1997; *C. oceanica* J. L. Barnard, 1955; *C. panwa* Peart, 2002; *C. paradisaea* Peart and Hughes, 2014; *C. pathyi* Lyla, Velvizhi and Ajmal Khan, 1998; *C. peartae* Andrade and Senna, 2013; *C. pemptos* Peart, 2007; *C. platys* Hughes and Peart, 2013; *C. priscileo* Hughes and Peart, 2013; *C. sardenta* (Oliveira, 1953); *C. setosa* (Haswell, 1879); *C. tattersalli* Peart, 2004; *C. thagaay* Peart, 2007; *C. tishana* Peart, 2007; *C. vadosa* Imbach, 1967; *C. wistari* Peart, 2007.

Exampithoe K. H. Barnard, 1925
Fig. 3E

Exampithoe (*Exampithoe*) K. H. Barnard, 1925: 363. – Ledoyer, 1984: 23. – J. L. Barnard and Karaman, 1991: 105. – Poore and Lowry, 1997: 901. (Type species: *Exampithoe natalensis* K. H. Barnard, 1925)

Exampithoe (*Melanesius*) Ledoyer, 1984: 23. – J. L. Barnard and Karaman, 1991: 105. – Poore and Lowry, 1997: 901. (Type species: *Exampithoe* (*Melanesius*) *cooki* Ledoyer, 1984)

Exampithoe – Myers and Lowry, 2003: 467.

Melanesius – Myers and Lowry, 2003: 467.

Diagnosis.—Epistome, upper lip angle directed ventrally at 90° to ventral margin of head. Antenna 1 accessory flagellum absent. Mandible molar reduced or absent. Mandibular palp 2- or 3-articulate or absent; when present slender, article 3 distally smooth. Lower lip outer plate entire. Maxilla 1 palp well developed. Maxilla 2 outer plate either broader than or subequal to inner plate. Coxae short. Gnathopod 1 subequal to or smaller than gnathopod 2, gnathopod 1 coxa sometimes produced forward, palm acute. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal

articles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; distoventral spur absent, setal fringe usually absent. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles present, setal fringe absent. Telson subtriangular; cusps small; denticles absent, lateral setae.

Remarks.—Ledoyer (1984) originally proposed *Melanesius* as a subgenus of *Exampithoe* on the basis of the absence of the mandibular palp; it was subsequently given separate generic status (Myers and Lowry, 2003). Present cladistic results, however, demonstrate that *Exampithoe* is nested within *Melanesius*, justifying neither separate generic nor subgeneric status. *Melanesius* is therefore treated as a junior synonym of *Exampithoe*. *Exampithoe* is closely related to the recently established genus, *Austrothoe*; distinctions between the two genera are discussed under the account of the latter.

Species Included.—*Exampithoe burrowwo* Hughes and Peart, 2015; *E. compressa* Just, 2000; *E. cooki* Ledoyer, 1984; *E. gracilipes* Ledoyer, 1984; *E. halei* Just, 2000; *E. kutti* Poore and Lowry, 1997; *E. latibasis* (Appadoo and Myers, 2004); *E. natalensis* K. H. Barnard, 1925; *E. taylori* Hughes and Peart, 2015; *E. waratah*, Hughes and Peart, 2015.

Macropisthopous K. H. Barnard, 1916
Fig. 3F

Macropisthopous K. H. Barnard, 1916: 260. – J. L. Barnard and Karaman, 1991: 106. – Poore and Lowry, 1997: 901. (Type Species: *Macropisthopous stebbingi* K. H. Barnard, 1916, by monotypy)

Diagnosis.—Epistome and upper lip angle directed ventrally at 90° to ventral margin of head. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp with 3-articulate, slender, article 3 smooth. Lower lip outer plate notched, lobes subequal height. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 subequal in size to gnathopod 2, coxa not produced forward anteroventrally; palm obtuse. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 prehensile. Pereopods 6, 7 propodus subrectangular; distal articles broad. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; distoventral spur absent, setal fringe absent. Uropod 2 peduncle without laterodistal projection; setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, lateral denticles present, lateral setal fringe absent. Telson subtriangular; cusps absent; denticles absent.

Remarks.—*Macropisthopous* is closely related to *Pseudoamphithoides* but is morphologically close also to *Sunamphitoe*. It differs from *Pseudoamphithoides* by the presence of a well-developed maxilla 1 palp, broad uropod 3 rami and strongly recurved robust setae on the outer ramus of uropod 1. *Macropisthopous* differs from *Sunamphitoe* in the absence of the uropod 1 distoventral peduncular spur, the slender mandibular palp, the obtuse palms on both gnathopods 1 and 2.

Species Included.—*Macropisthopous stebbingi* K. H. Barnard, 1916.

Paradusa Ruffo, 1969

Paradusa Ruffo, 1969: 63. – J. L. Barnard and Karaman, 1991: 106. – Poore and Lowry, 1997: 902. – Appadoo and Myers, 2004: 332. (Type species: *Paradusa bilobata* Ruffo, 1969, by monotypy)

Diagnosis.—Epistome and upper lip angle directed ventrally at 90° to ventral margin of head. Antenna 1 accessory flagellum with 1 small article. Mandible molar well developed; palp with 3-articulate, slender, article 3 smooth. Lower lip outer plate notched, inner lobes shorter than outer lobes. Maxilla 1 palp well developed. Maxilla 2 plates subequal in width. Coxae long. Gnathopod 1 subequal in size to gnathopod 2, coxa produced forward anteroventrally; palm acute. Pereopods 3, 4 basis narrow; merus not anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; distoventral spur large, acute, setal fringe reduced or absent. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, lateral denticles absent, lateral setal fringe absent. Telson subtriangular; cusps small; denticles absent.

Remarks.—Poore and Lowry (1997) synonymised *Paradusa* with *Cymadusa* on the basis of their presumed close relationship. Appadoo and Myers (2004), however, treated it as a separate genus. Present results support the latter classification and suggest *Paradusa* is more closely related to *Plumithoe* than *Cymadusa*.

Species Included.—*Paradusa bilobata* Ruffo, 1969; *P. mauritiensis* Ledoyer, 1978.

Paragrubia Chevreux, 1901
Fig. 3G

Paragrubia Chevreux, 1901: 426. – J. L. Barnard and Karaman, 1991: 107. – Poore and Lowry, 1997: 902. – Hughes and Peart, 2013: 70. – Peart, 2014: 886. (Type species: *Paragrubia vorax* Chevreux, 1901, by monotypy)

Diagnosis.—Epistome and upper lip angle directed ventrally, approximately 90° to head ventral margin. Antenna 1 accessory flagellum present, with 3 or more articles. Mandible palp 3-articulate, slender, article 3 smooth distally. Lower lip outer plate notched, inner lobe is subequal in height to outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than the inner plate. Coxae long. Gnathopod 1 subequal to or larger than gnathopod 2; gnathopod 1 coxa is produced forward anteroventrally, palm acute. Pereopods 3, 4 basis narrow; merus not anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 with small acute distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; peduncle with long, acute distoventral spur, setal fringe absent. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami narrow; outer ramus with 1 recurved and 1 straight robust seta; lateral denticles absent, lateral setal fringe present. Telson subtriangular, cusps small, denticles absent, setae always in medial oblique rows.

Remarks.—*Paragrubia* is closely related to *Cymadusa* and *Amphithoides*. These three genera are "basal" or near "basal" ampithoids. Originally, one of the main characters that distinguished *Paragrubia* from *Cymadusa* was the larger size of gnathopod 1 relative to gnathopod 2. However, the majority of the species placed in the genus have the gnathopod 1 subequal to or larger than gnathopod 2; they are placed in *Paragrubia* because of the multi-articulate accessory flagellum and reduced curvature of the uropod 3 outer rami setae (similar to *Amphithoides* but different from *Cymadusa*) and the shape and setation of the rami of uropod 3 and the lower lip notched outer plate lobes are always of equal height.

Species Included.—*Paragrubia apoorei* Hughes and Peart, 2013; *P. cassini* Hughes and Peart, 2013; *P. dongara* Hughes and Peart, 2013; *P. dwyeri* Hughes and Peart, 2013; *P. edgari* Peart in Hughes and Lowry, 2009; *P. latipoda* Ren, 2001; *P. pilipes* (Ledoyer, 1984); *P. springthorpei* Hughes and Peart, 2013; *P. variata* (Sheard, 1936); *P. vorax* Chevreux, 1901.

Paranexes Peart, 2014
Fig. 3H

Paranexes Peart, 2014: 897. (Type species: *Paranexes yallingup* Peart, 2014, by original designation)

Diagnosis.—Epistome and upper lip angle directed ventrally at 90°. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp 3-articulate, stout, article 3 smooth distally. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 smaller than or subequal to gnathopod 2, coxa produced forward anteroventrally, palm acute. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 strongly prehensile. Pereopods 6, 7 propodus subrectangular; distal articles broad. Uropod 1 position in situ reaching apices of uropod 2 rami; male, female peduncle without distoventral spur, setal fringe long reaching entire length of peduncle. Uropod 1 outer ramus much narrower than inner ramus. Uropod 2 peduncle without laterodistal projection, no setal fringe. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles present, setal fringe absent. Telson subtriangular, with cusps produced to form 2 large hooks; denticles absent, apical and lateral setae.

Remarks.—*Paranexes* is most closely related to *Pleonexes* but is also morphologically similar to *Pseudopleonexes* and *Ampithoe*. It resembles *Pseudopleonexes* and *Pleonexes* in the expansion of pereopods 3 and 4 bases and meri and strongly prehensile pereopods 5-7 and the strong hooked cusps on the telsons. *Paranexes* differs from *Pseudopleonexes* by the well-developed maxilla 1 palp, the palmar angle of gnathopod 1 propodus, the position of uropod 1 in relation to uropod 2, and the absence of the peduncular projection on male uropod 2. *Paranexes* and *Ampithoe* share an acute gnathopod 1 palm and lack the posterodistal peduncular spur on uropod 1. The two genera differ by the angle of the epistome and upper lip, and the expansion of pereopods 3 and 4 bases and meri, and the strongly prehensile pereopods 5-7.

Species Included.—*Paranexes yallingup* Peart, 2014; *P. gallaharae* Peart, 2014.

Pleonexes Spence Bate, 1857
Fig. 3I

Pleonexes Spence Bate, 1856: 59 (*nomen nudum*); 1857: 147 (Type species: *Pleonexes gammaroides* Spence Bate, 1857)

Diagnosis.—Epistome and upper lip angle directed ventrally, approximately 90° to head ventral margin. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp 3-articulate, stout, article 3 distally smooth. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 smaller than gnathopod 2, coxa produced forward anteroventrally, palm acute. Pereopods 3, 4 basis slightly expanded; merus slightly anteriorly expanded. Pereopods 5-7 prehensile. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of uropod 2 rami; peduncle distoventral spur reduced, rounded in males, absent in females, setal fringe long, reaching entire length of peduncle; rami of similar length, inner only slightly longer than outer. Uropod 2 peduncle laterodistal projection absent, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles present, setal fringe absent. Telson subtriangular; cusps small; denticles absent.

Remarks.—*Pleonexes*, formerly considered a junior synonym of *Ampithoe*, is herein resurrected. It is separated from *Ampithoe* by the presence of a rounded, reduced uropod 1 peduncular spur, sometimes large telsonic cusps, expanded bases and meri of pereopods 3, 4, and prehensile pereopods 5-7.

Species Included.—*Pleonexes auriculata* (Rabindranath, 1972); *P. gammaroides* Spence Bate, 1856; *P. helleri* (Karaman, 1975); *P. kaneohe* (J. L. Barnard, 1970); *P. kaneohe navosa* (Myers, 1985); *P. kava* (Myers, 1985); *P. koreana* (Kim and Kim, 1988); *P. kulafi* (J. L. Barnard, 1970); *P. maxillissius* (Ledoyer, 1984); *P. meganae* (Peart, 2007); *P. parakava* (Peart, 2007); *P. poipu* (J. L. Barnard, 1970); *P. rotunda* (Peart, 2007).

Plumithoe J. L. Barnard and Karaman, 1991
Fig. 3J

Plumithoe J. L. Barnard and Karaman, 1991: 109. – Poore and Lowry, 1997: 903. (Type species: *Amphithoe plumicornis* Ledoyer, 1979, by original designation)

Diagnosis.—Epistome and upper lip angle directed ventrally at 90° to ventral margin of head. Antenna 1 accessory flagellum absent. Antenna 2 peduncle with long, dense, plumose setae along ventral margin of the peduncle only. Mandible molar well developed; palp 3-articulate, slender, article 3 distally smooth. Lower lip outer plate notched, inner lobes shorter than outer lobes. Maxilla 1 palp well developed. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 smaller than gnathopod 2; gnathopod 1 coxa produced anteroventrally, palm acute. Pereopods 3, 4 basis narrow; merus anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal arti-

cles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching midlength of uropod 2 peduncle; distoventral spur large, acute, setal fringe sometimes present. Uropod 2 peduncle without laterodistal projection, setal fringe present. Uropod 3 rami narrow; outer ramus with 2 large recurved distal robust setae, denticles absent, setal fringe absent. Telson subtriangular; cusps small; denticles absent.

Remarks.—*Plumithoe* is morphologically similar to both *Cymadusa* and *Ampithoe*. The main differences between *Plumithoe* and *Cymadusa* are that *Plumithoe* lacks an accessory flagellum on antenna 1, and has large tufts of long, plumose setae on the ventral margins of articles 3-5 of antenna 2. Some species of both *Cymadusa* and *Ampithoe* have setose antennae 2, but the arrangement of the setal tufts is totally different in species of *Plumithoe*. *Plumithoe* differs from *Ampithoe* by the presence of an acute distoventral spur on the peduncle of uropod 1, which is absent in *Ampithoe*. *Plumithoe* differs from both *Cymadusa* by having a long setal fringe on the uropod 2 peduncle.

Species Included.—*Plumithoe acuticoxa* Myers, 2012; *P. boulari* Peart and Hughes, 2014; *P. hirsutus* (Ledoyer, 1978); *P. lata* Myers, 2012; *P. madagascariensis* Myers, 2012; *P. plumicornis* (Ledoyer, 1979); *P. quadrimana* (Haswell, 1879).

Pseudoamphithoides Ortiz, 1976
Fig. 3K

Pseudoamphithoides Ortiz, 1976: 12. – J. L. Barnard and Karaman, 1991: 109-110. – Poore and Lowry, 1997: 903. (Type species: *Pseudoamphithoides bacescui* Ortiz, 1976, by original designation and monotypy)
Amphyllodomus Just, 1977: 229. (Type species: *Amphyllodomus incurvaria* Just, 1977, by original designation and monotypy)

Diagnosis.—Epistome and upper lip angle directed ventrally at 90° to ventral margin of head. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp 3-articulate, slender, article 3 beaked. Lower lip outer plate notched, inner lobe shorter than outer lobe. Maxilla 1 palp reduced. Maxilla 2 outer plate broader than inner plate. Coxae long. Gnathopod 1 subequal to gnathopod 2; coxa not produced forward anteroventrally, palm acute. Pereopods 3, 4 basis expanded; merus anteriorly narrow. Pereopods 5-7 prehensile. Pereopods 6, 7 propodus subrectangular; distal articles slender. Epimeron 3 without distoventral tooth. Uropod 1 position in situ short, reaching midlength of uropod 2 peduncle; distoventral spur absent, setal fringe long. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami narrow; outer ramus with large straight distal robust seta and weak smaller robust seta, denticles, lateral fringe absent. Telson subtriangular; cusps absent; denticles absent, lateral setae.

Remarks.—*Pseudoamphithoides* is closely related to *Macropisthopous*, and can be distinguished by having a reduced maxilla 1 palp, the narrow rami of uropod 3, and the reduced curvature of the robust setae on the uropod 3 outer ramus.

Species Included.—*Pseudoamphithoides bacescui* Ortiz, 1976; *P. incurvaria* (Just, 1977).

Pseudopleonexes Conlan, 1982
Fig. 3L

Pseudopleonexes Conlan, 1982: 2020. – J. L. Barnard and Karaman, 1991: 110. – Poore and Lowry, 1997: 903-904. – Peart, 2006: 1-22. (Type species: *Pleonexes lessoniae* Hurley, 1954, by original designation)

Diagnosis.—Epistome and upper lip angle directed posteriorly at more than 45°. Antenna 1 accessory flagellum absent. Mandible molar well developed; palp 3-articulate, slender, article 3 strongly beaked. Lower lip outer plate weakly notched, lobes of equal size. Maxilla 1 palp reduced. Maxilla 2 outer plate broader than inner plate. Coxae short. Gnathopod 1 smaller than gnathopod 2, gnathopod 1 coxa not produced anteroventrally, palm transverse. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 strongly prehensile. Pereopods 6, 7 propodus subrectangular; distal articles occasionally broad. Epimeron 3 without distoventral tooth. Uropod 1 position in situ short, reaching midlength of uropod 2 peduncle; peduncle distoventral spur absent, setal fringe sometimes present. Uropod 2 peduncle with laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles present, setal fringe absent. Telson subtriangular; cusps expanded to form large hooks; denticles absent.

Remarks.—*Pseudopleonexes* is closely related to *Amphitholina* but differs by the angle of the epistome and upper lip, the development of the mandibular molar and palp, weakly notched instead of entire lower lip, presence of the peduncular projection on uropod 2.

Species Included.—*Pseudopleonexes burney* Peart, 2006; *P. justi* Peart, 2006; *P. lessoniae* (Hurley, 1954); *P. nexis* Peart, 2006; *P. sheardi* (Just, 2002).

Sunamphitoe Spence Bate, 1857
Fig. 3M

Sunamphitoe Spence Bate, 1857: 147. – J. L. Barnard and Karaman, 1991: 111. – Poore and Lowry, 1997: 904. (Type species: *Amphithoe pelagica* H. Milne Edwards, 1830, by subsequent designation (Chevreux and Fage, 1925))
Peramphithoe Conlan and Bousfield, 1982: 60. – J. L. Barnard and Karaman, 1991: 108. – Poore and Lowry, 1997: 902. (Type species: *Ampithoe femorata* Krøyer, 1845, by original designation)

Diagnosis.—Epistome and upper lip directed ventrally, almost 90° to ventral margin of head. Antenna 1 accessory flagellum absent. Mandible molar well developed. Mandibular palp absent or 3-articulate; when present stout, article 3 smooth distally. Lower lip outer plate notched, inner and outer lobes subequal in height. Maxilla 1 palp well developed. Maxilla 2 outer plate similar or broader than inner plate. Coxae long. Gnathopod 1 smaller than gnathopod 2, gnathopod 1 coxa not produced anterodistally, palm transverse. Pereopods 3, 4 basis expanded; merus anteriorly expanded. Pereopods 5-7 simple. Pereopods 6, 7 propodus subrectangular; distal articles slender to very broad. Epimeron 3 without distoventral tooth. Uropod 1 position in situ reaching apices of rami of uropod 2; peduncle with long, acute distoventral spur, setal fringe present or absent. Uropod 2 peduncle without laterodistal projection, setal fringe absent. Uropod 3 rami broad; outer ramus with 2 large recurved distal robust setae, denticles, setal fringe present or absent. Tel-

son subtriangular; cusps small; denticles absent, setae lateral.

Remarks.—*Sunamphitoe* is morphologically similar to *Macropisthopous* and *Ampithoe*. *Sunamphitoe* differs from *Macropisthopous* by having simple (as opposed to prehensile) pereopods 5-7 and the presence of a long, acute spur on the peduncle of uropod 1. *Sunamphitoe* differs from *Ampithoe* in the transverse palm of gnathopod 1, the expansion of pereopods 3, 4 bases and meri, and a long, acute spur on the peduncle of uropod 1. Within *Sunamphitoe*, the mandibular palp varies from absent to having 3 articles. The presence or absence of the mandibular palp was originally used to separate *Sunamphitoe* from *Peramphithoe*. Given that the palp is independently gained and lost within the *Sunampithoe* + *Perampithoe* clade, and that putative species of *Sunampithoe* and *Perampithoe* are nested together, the two genera are nevertheless herein synonymised.

Species Included.—*Sunamphitoe africana* (Milne and Griffiths, 2013); *S. annenkovae* (Gurjanova, 1938); *S. aorangi* (J. L. Barnard, 1972); *S. baegryeongensis* (Kim and Kim, 1988); *S. bungareei* Hughes and Peart, 2013; *S. chujaensis* Kim, Hong, Conlan and Lee, 2012; *S. eoa* (Brüggen, 1907); *S. falsa* (K. H. Barnard, 1932); *S. fantome* Peart in Hughes and Lowry, 2009; *S. femorata* (Krøyer, 1845); *S. graxon* Freewater and Lowry, 1994; *S. guryongensis* Shin et al., 2015; *S. humeralis* (Stimpson, 1864); *S. kanaka* Peart and Hughes, 2014; *S. lessoniophila* (Conlan and Bousfield, 1982); *S. lindbergi* (Gurjanova, 1938); *S. mea* (Gurjanova, 1938); *S. namhaensis* (Kim and Kim, 1988); *S. orientalis* (Dana, 1853); *S. parmerong* (Poore and Lowry, 1997); *S. pelagica* (H. Milne Edwards, 1830); *S. plea* (J. L. Barnard, 1965); *S. plumosa* Stephensen, 1944; *S. sineplumosa* Kim and Kim, 1991; *S. spuria* (Krapp-Schickel, 1978); *S. stypotrupetes* (Conlan and Chess, 1992); *S. tea* (J. L. Barnard, 1965); *S. tjibaoui* Peart and Hughes, 2014.

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Appendix A. Terminal taxa used in phylogenetic analysis and sources of character-state scorings.

Taxon	Source
Protomedeia articulata Barnard, 1962	J. L. Barnard (1962)
Protomedeia stephensoni Hirayama, 1984	Hirayama (1984)
Amphithoides longicornis Kossmann, 1880	Kossmann (1880)
Amphitholina cuniculus Stebbing, 1874	Stebbing (1874), Myers (1974)
Ampithoe brevipalma Kim and Kim, 1988	Kim and Kim (1988)
Ampithoe caddi Poore and Lowry, 1997	Type material (AM P45054-45056)
Ampithoe gammaroides Spence Bate, 1857	Spence Bate (1857), Chevreux and Fage (1925)
Ampithoe ngana Poore and Lowry, 1997	Type material (AM P45061-45064)
Ampithoe rubricata Montagu, 1808	Montagu (1808), Bousfield (1973)
Ampithoe valida Smith, 1873	Smith (1873), Kim and Kim (1988)
Austrothoe jimlowryi Peart, 2014	Type material (AM P61903-61904)
Austrothoe ochos Peart, 2014	Type material (WAM C55180; SAMA C7887)
Cymadusa botulus Hughes and Peart, 2013	Type material (WAM C52210-52211)
Cymadusa brevidactyla Chevreux, 1907	Chevreux (1907, 1908)
Cymadusa euclidius Hughes and Peart, 2013	Type material (NMV J64939)
Cymadusa filosa Savigny, 1816	Type material (MVR-Cr.)
Cymadusa uncinata Stout, 1912	Stout (1912)
Cymadusa munnu Poore and Lowry, 1997	Type material (AM P45081-45085)
Cymadusa crassicornis Costa, 1857	Costa (1857), Chevreux and Fage (1925)
Exampithoe gracilipes Ledoyer, 1984	Ledoyer (1984)
Exampithoe natalensis K. H. Barnard, 1925	K. H. Barnard (1925)
Macropisthopous stebbingi K. H. Barnard, 1916	Type material, holotype and slide (SAMC 18971, A2917, A3287, A3035)
Melanesius kutti Poore and Lowry, 1997	Type material (AM P45087-45090)
Melanesius halei Just, 2000	Just (2000)
Melanesius cooki Ledoyer, 1984	Ledoyer (1984)
Melanesius latibasis Appadoo and Myers, 2004	Appadoo and Myers (2004)
Paradusa bilobata Ruffo, 1969	Ruffo (1969)
Paradusa mauritiensis Ledoyer, 1978	Ledoyer (1978)
Paranexes gallaharae Peart, 2014	Type material (WAM C55181-55183, AM P.62555)
Paranexes yallingup Peart, 2014	Type material (AM P.51274-51276)
Paragrubia dongara Hughes and Peart, 2013	Type material (WAM C52215-52216)
Paragrubia dwyeri Hughes and Peart, 2013	Type material (AM P.90117, P.81800)
Paragrubia springthorpei Hughes and Peart, 2013	Type material (WAM C52217-52218)
Paragrubia variata (Sheard, 1936)	Sheard (1936)
Paragrubia vorax Chevreux, 1901	Chevreux (1901)
Peramphithoe baegryeongensis Kim and Kim, 1988	Kim and Kim (1988)
Peramphithoe femorata (Krøyer, 1845)	Krøyer (1845), Conlan and Bousfield (1982)
Peramphithoe guryongensis Shin, Colman, Hong and Kim, 2015	Shin et al. (2015)
Peramphithoe parmerong (Poore and Lowry, 1997)	Type material (AM P50767-50770, AM P45092)
Peramphithoe humeralis Stimpson, 1864	Stimpson (1864), Conlan and Bousfield (1982)
Peramphithoe namhaensis Kim and Kim, 1988	Kim and Kim (1988)
Plumithoe boulari Peart and Hughes (2014)	Peart and Hughes (2014)
Plumithoe acuticoxa Myers, 2012	Myers (2012)
Plumithoe lata Myers, 2012	Myers (2012)
Plumithoe madagascariensis Myers, 2012	Myers (2012)
Plumithoe quadrimana (Haswell, 1879)	Haswell (1879), Poore and Lowry (1997), Hughes and Peart (2013)
Pseudoamphithoides bacescui Ortiz, 1976	Ortiz (1976)
Pseudopleonexes lessoniae Hurley, 1954	Hurley (1954)
Pseudopleonexes sheardi Just, 2002	Just (2002)
Sunamphitoe graxon Freewater and Lowry, 1994	Freewater and Lowry (1994)
Sunamphitoe kanaka Peart and Hughes, 2014	Peart and Hughes (2014)
Sunamphitoe pelagica H. Milne Edwards, 1830	H. Milne Edwards (1830), Chevreux and Fage (1925)
Sunamphitoe plumosa Stephensen, 1944	Stephensen (1944), Kim and Kim (1988)

Appendix B. Data matrix. Inapplicables marked (-). Species are listed under the generic combinations used prior to the present study.

Protomedeia articulata	12151311211111121131334411131312243123221213123122524133331311331132332231321
Protomedeia stephensoni	12151311211111121131232411231312243123221213123121124131441413441132332241311
Amphithoides longicornis	12131311112312221141121112131122243213221213123121524133341313441232222221321
Amphitholina cuniculus	32211334-113213221133244123111224122211222112112122332114131114211121122124l
Ampithoe brevipalma	12211311212312232141224412221122241122212211121152412134141144244121214113l
Ampithoe caddi	12211311212312231111223412121112242212222211121121224223341411441141211241131
Ampithoe gammaroides	11212311212312232141224212221122231211213212212211233133113113221312112212 31
Ampithoe ngana	13212311212312231111123412121112242212222211121121224223341313231141311241131
Ampithoe rubricata	12212311212312231111234412121112212212221213123121324121441311341141112131131
Ampithoe valida	13212311212312231142234412221122241122221213123121524321441413331241212131131
Austrothoe jimlowryi	11121211212312121211222412221113242212113213113111222321231312222211212222112
Austrothoe ochos	13121211212312121211224412221112243212113221111111224223231313232111212122112
Cymadusa botulus	12142311212312231141131412221422211222221213123122224133231313442431112231131
Cymadusa brevidactyla	12121311212312231142141112221412211221221213123121224333441313441241212141111
Cymadusa euclidius	12141311212312231111221412221112232122221213123122224333431313311412111411111
Cymadusa filosa	12131111212312231141142412221411242212221213123122224233441413441341212131111
Cymadusa uncinata	12141311212312321412324122211122113212212213123122224233441313442431112241131
Cymadusa munnu	12131311212312231111233412221112242312211213123121124333441413441141311141111
Cymadusa crassicornis	12131311212312232131241112221412211221221213123121124233441313441331112131111
Exampithoe gracilipes	13211322-111112211124141222211214421211211112112412332131333211212221111
Exampithoe natalensis	13212321111111122111134312222112134212111113123121124121231311222231311221131
Macropisthopous stebbingi	12211111112212222231325141232313112413112211121321121123231213332131311221331
Melanesius kutti	13211324-111212121122241222111224222211321212212122412133131332211131122113l
Melanesius halei	13211334-111112225122241222251214221211211112112112422333131332212131122113l
Melanesius cooki	13211323-111211121122241212211224321211211112112132412322131322212131122111l
Melanesius latibasis	12211334-111111121123141222211314322211221112112222312322121322212131122113l
Paradusa bilobata	13121311112311221111222412121123242212222211121121224132213132211311122311 31
Paradusa mauritiensis	12121311112311221111122412221112242212221223123121224233221211231131112231111
Paranexes gallaharae	12212311212312222211322212221112232212113122122121124323221313131131211231231
Paranexes yallingup	12212311212312232111324312221112222221211312212212112432311131112113121123123l
Paragrubia dongara	12151311112212211111331412121113243212221213123122524133441313441342122141111
Paragrubia dwyeri	12151311112212211112222112121112242212221213123122524133431213341232222141111
Paragrubia springthorpei	12151311112212211111222112121112243212221213123122524133441313341242222141111
Paragrubia variata	12151311112212222111224112122412212222221213123121223131331212331232222131111
Paragrubia vorax	12141311112212221111222112121112212212221213123122524133441313331132222141111
Peramphithoe baegryeongensis	12211311112211232241224222311122113121122111211211243333413134422413122211 31
Peramphithoe femorata	12212311212312232241224222314122113221112131232121224133441313442131211131131
Peramphithoe guryongensis	12211311212212232241232422231412241322112233223121124333341313442131311231131
Peramphithoe parmerong	12211311212212232241232422231412211312111233223221324133341313342131311231131
Peramphithoe humeralis	12212311212212232231231442232312243413111213123121124133441413442111212221131
Peramphithoe namhaensis	12211311212212232241231422231412211322111213123121224333441313442231211231131
Plumithoe boulari	12211111112312232111222112221412242212212211211212233332213232211322121311 31
Plumithoe acuticoxa	12211111112312232141224112231512241322122111211212232331212232111222122211 31
Plumithoe lata	12211111112312232111224112221412211222211113123122223333111223211112212231131
Plumithoe madagascariensis	12211111112312232141222412221112242322211213123121223131221223211132212231131
Plumithoe quadrimanus	12211111112312232141224112221412212212212211211212242332213232111322121311 11
Pseudoamphithoides bascecui	13211311122322222231235412222312243212122111121122214323131313331112122211331
Pseudopleonexes lessoniae	22212311122222132241225422231112242212113222122121214221132412132111311211241
Pseudopleonexes sheardi	23212311122222132231322122221112242212113222122121211122122312122111311211221
Sunamphitoe graxon	12212314-221123224122242213131224131211222112112112413324131324214131113113l
Sunamphitoe kanaka	12211314-221123224123242223141224132211222112112132433333131344213131123113l
Sunamphitoe pelagica	12211314-221123224122212223131221132211222112112122313122131123211121122113l
Sunamphitoe plumosa	12211214-221123225122242223151221131211121112112222413324131334113131213113l

Appendix C. Unambiguous character state changes for 1 of 5 most parsimonious topologies shown in Fig. 2. Clade numbers correspond to those indicated in Fig. 2.

Clade no.	Character state changes
1	11:1→2, 12:1→3, 14:1→2, 15:1→2, 26:1→2, 30:3→1, 36:1→2, 37:2→1, 69:3→2, 70:3→2
2	28:3→2, 38:3→2, 67:3→4, 72:2→1, 75:3→1
3	12:3→2, 50:1→2
4	23:1→2, 24:4→1, 63:4→3
5	35:3→2, 67:4→3
6	16: 1→2, 34:4→1, 64:4→3
7	27:1→2, 35:3→2, 51:5→2, 68:2→1, 70:2→1
8	22:2/3→4, 30:1→4
9	34:4→1, 35:2→1, 37:1→2, 38:2→1
10	67:4→3, 69:2→1
11	4:3→4, 22:4→3, 50:1→2, 65:1→2, 72:1→2, 76:1→3
12	62:3→1, 71:2→1
13	63:4→3
14	3:1→2, 23:1→4, 55:3→2, 76:1→3
15	56: 3→1, 71:1→2
16	19:1→4, 31:1→2, 35:2→1, 36:2→1, 37:1→2, 60:3→4
17	41:1→2, 44:3→1, 47:3→1, 72:1→2
18	23:4→3, 27:2→1, 59:3→2
19	17:1→2, 40:2→1, 64:4→2, 67:4→3
20	24:4→2, 34:4→3, 41:2→3, 44:1→2, 47:1→2, 51:2→1, 58:4→1, 75:1→2
21	21:2→3, 39:2→1, 42:2→1, 43:1→2
22	9:2→1, 23:4→2, 62:1→3
23	55:2→3, 58:4→2, 71:1→2
24	6:3→1, 24:4→1, 30:1→4, 61:1→2, 68:1→2
25	19:1→4, 23:2→4, 64:2→1
26	37:1→2, 60:3→2
27	41:2→1, 44:1→3, 46:1→3
28	3:2→1, 4:1→2, 14:2→1, 16:3→2, 17:2→1, 40:1→2, 69:2→1
29	18:1→2, 39:2→1, 65:1→2, 69:2→3
30	16:3→2, 58:4→3
31	19:1→3, 23:2→5, 30:1→3, 63:2→3, 64:2→3, 75:1→3
32	15:2→1, 17:2→1
33	3:2→1, 4:1→2, 6:3→2, 9:1→2, 41:2→3, 46:2→1, 49:2→1, 69:2→1, 71:1→2, 74:1→2, 76:3→1, 77:1→2
34	7:1→2, 8:1→4, 11:2→1, 12:3→1, 54:3→1
35	16:2→1, 35:2→3, 58:3→2, 67:1→2
36	57:2→3, 63:2→3
37	14:2→1, 17:1→2, 33:2→1, 42:2→1, 51:2→1
38	18:2→1, 35:2→4
39	12:3→2, 25:1→2, 28:2→3
40	14:2→1, 34:4→1, 36:2→3, 55:2→3
41	8:1→4, 30:1→3, 54:3→1
42	72:2→1, 73:2→3
43	57:2→3, 63:2→4
44	22:2→3, 30:1→4, 37:1→2, 73:2→3
45	14:1→2, 44:1→3, 47:1→3
46	45:1→2
47	57:3→4, 69:3→2
48	5:1→2, 54:3→1
49	15:2→1, 56:3→1, 57:2→1, 63:2→1, 75:1→2, 76:3→4
50	5:1→2, 41:2→3, 44:1→2, 47:1→2, 52:2→1, 59:1→2, 73:2→1