



Phylogenetic relationships within the Pylochelidae (Decapoda: Anomura: Paguroidea): A cladistic analysis based on morphological characters

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Abstract

Phylogenetic relationships within the “symmetrical” hermit crab family Pylochelidae were analyzed for 41 of the 45 species and subspecies currently considered valid. In the analyses, 78 morphological characters comprised the data matrix and the outgroup consisted of *Thalassinia anomala*, a member of the Thalassinidae, and *Munida quadrispina*, a member of the Galatheidae. A poorly resolved strict consensus tree was obtained from a heuristic parsimony analysis of unweighted and unordered characters, which showed the family Pylochelidae and the subfamilies Pylochelinae and Pomatochelinae to be monophyletic taxa – the latter two groups had the highest Bremer support values. Additionally, while the subgenus *Pylocheles* (*Pylocheles*) was strongly supported, the subgenera *Xylocheles*, and *Bathycheles* were not. More fully resolved trees were obtained when using implied weighting, which recognized the monotypic subfamilies Parapylochelinae, Cancellochelinae and Mixtopagurinae. The subfamily Trizochelinae was found to have four distinct clades and several ambiguously placed taxa.

Key words: Decapoda, Anomura, Paguroidea, Pylochelidae, phylogenetic relationships

Introduction

Species of the family Pylochelidae Bate, 1888 are known as “symmetrical” hermit crabs because unlike their better known “asymmetrical” counterparts, most have symmetrical chelipeds, a pleon that is most often straight and provided with at least partially calcified, articulated tergites, paired pleopods, and generally symmetrical uropods. They are cryptic in habitat, living in pieces of wood, rocks, sponges, tusk shells, and rarely gastropods. Most of the 45 species and subspecies known from the world are distributed in tropical waters of the Indo-Pacific, with only three known from the western Atlantic; the species range in depth from 30 to 1570 m although they are most frequently found from 200 to 500 m (Forest 1987a, b).

The Pylochelidae were discovered in the late 19th century when the first species, *Pomatocheles jeffreysii* Miers, 1879, was described. Miers placed this unique species in the Paguridea, but noted a mix of characters that led him to believe that *P. jeffreysii* established a “transition from the Paguridea to the Macrura” (Miers 1879: 50). As more “symmetrical” species were discovered (Fig. 1), this evolutionary view was maintained by other carcinologists (e.g., A. Milne-Edwards 1880; Bate 1888; Henderson 1888; Alcock 1905; Bouvier 1940) who allied these hermit crabs with thalassinideans or homarids. It was Bate (1888) who proposed the family Pylochelidae for these unusual hermit crabs, although he placed great importance on their gill structure and classified them in his division Trichobranchiata alongside Macrura with similar gill structure. Despite the evolutionary significance of pylochelids in deciphering hermit crab ancestry or even the Anomura, they were

rarely mentioned in the scientific literature during the most of the 20th century. Hermit crab classifications such as MacDonald *et al.*'s (1957), who considered hermit crabs as polyphyletic (Coenobitoidea and Paguroidea), or McLaughlin's (1983), who viewed hermit crabs as monophyletic (Paguroidea), placed pylochelids as a basal, primitive group. However, inter- and intrageneric relationships have remained poorly understood.

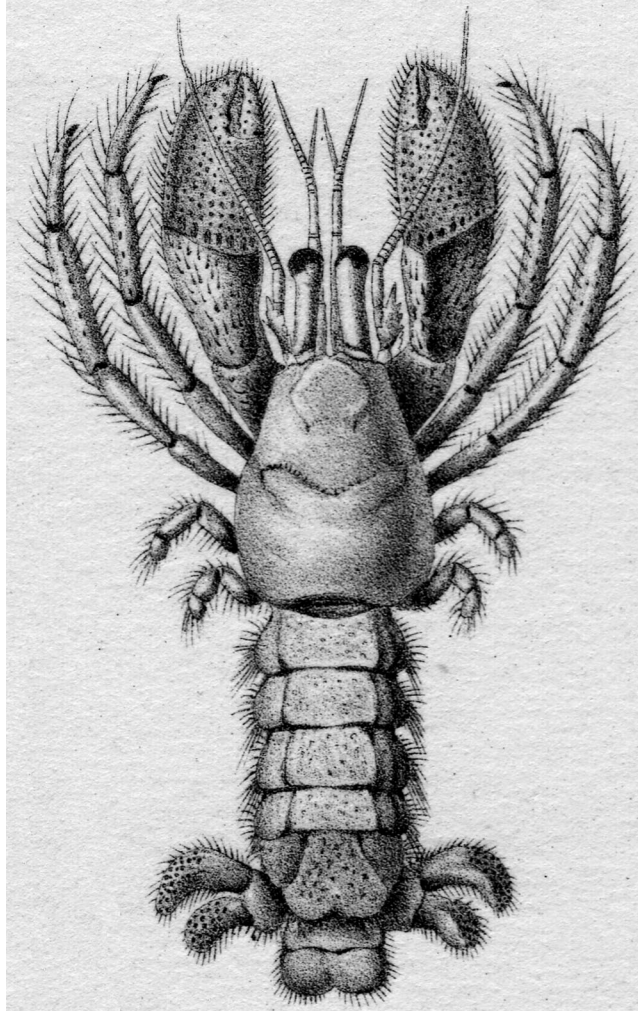


FIGURE 1. *Pylocheles agassizii* A. Milne-Edwards, 1880 (from A. Milne-Edwards & Bouvier, 1893, pl. 1, fig. 1)

Prior to the monographic review of Forest (1987a) only 19 species of the Pylochelidae had been described and several of those were known only from their holotypes or just from their type localities. In addition to placing three of those species in synonymy with other known species, adding 23 new species and one new subspecies, Forest (1987a) redefined the existing five genera, proposed two additional new genera, and provisionally established six subfamilies. Only two species have been added since: *Trizocheles pilgrimi* Forest & McLaughlin, 2000 from New Zealand and *T. vaubanae* McLaughlin & Lemaitre, 2008 from New Caledonia.

Forest (1987a) considered the Pylochelidae a heterogeneous assemblage whose phylogenetically significant characters were difficult to identify. So distinctive were the majority of genera, that only *Pylocheles* A. Milne-Edwards, 1880 and *Cheiroplatea* Bate, 1888 appeared sufficiently closely related as to be grouped together in a single subfamily. That three of the other five subfamilies were monotypic was indicative of the vast array of distinct morphological attributes Forest (1987a) recognized during his detailed and thorough study. Forest suggested that with further investigation, it might be shown that each subfamily warranted full familial rank.

In the 20 years subsequent to Forest's (1987a) monograph, the number of exploratory cruises undertaken by the Muséum national d'Histoire naturelle (MNHN) and the Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), now the Institut de Recherche pour le Développement (IRD) increased dramatically, and with them, the number of specimens of the Pylochelidae. The increased abundance of study material, together with the recent advances in cladistic methodology and computer generated analyses, has made it possible to evaluate the phylogenetic relationships among the genera and species of this family.

Material and methods

Ingroup taxa. This analysis of inter- and intrageneric relationships is based on 78 morphological characters. The ingroup consists of 41 of the 45 species and one subspecies currently recognized as valid taxa in the family. Because of the potential problems encountered by including taxa with missing data (Maddison 1993; Wilkinson 1995; Strong & Lipscomb 1999) four species were omitted from the data matrix. *Cheiroplatea scutata* Ortmann, 1892 and *Pylocheles (Bathycheles) macgilchristi* (Alcock, 1905) are known from one and two specimens, respectively, none of which have been available for personal examination. The holotype and only representative of *Trizocheles balssi* (Stebbing, 1914) has been examined, but the specimen is dry and in poor condition with missing appendages. Although three specimens have been assigned to *Pomatocheles stridulans* Forest, 1987a, one is a megalopa and one a juvenile, both lacking chelipeds and ambulatory legs. The holotype is an adult, ovigerous female, but only the first two pleonal segments are present; thus several important character states are unknown for this taxon.

Despite the large numbers of specimens available for a few species, several species are still known from one or a few individuals. Therefore intraspecific variation has not been factored into the character states; morphological data for the matrix have been taken from the holotypes or lectotypes as often as possible. When species are known from a single specimen or sex, as are the cases for *Cheiroplatea cenobita* Bate, 1888, *C. scutata* and *C. sternus* Forest, 1987a; *Pylocheles (P.) agassizi* A. Milne-Edwards, 1880; *Pomatocheles stridulans*; *Trizocheles albatrossi* Forest, 1987a, *T. balssi*, *T. longicaulis* (Boas, 1926), *T. loquax* Forest, 1987a, *T. manningi* Forest, 1987a, *T. moosai* Forest, 1987a, and *T. mutus* Forest, 1987a, pleonal appendages of the opposite sex have been assumed to be typical of the genus.

Outgroup selection. Selection of outgroup taxa has been difficult because the sister group to the Pylochelidae has not been robustly identified. Faced with a similar problem when considering an outgroup for their phylogenetic appraisal of the Leptostraca, Walker-Smith & Poore (2001) hypothesized an ancestor based on generally accepted crustacean evolutionary character transformations. Unfortunately, the direction of evolutionary transformations within the reptant Decapoda appears to be debatable. The Pylochelidae was considered paraphyletic by Richter & Scholtz (1994), but monophyletic and basal to the rest of the Paguroidea and it in turn basal to the remainder of the Anomura by McLaughlin *et al.* (2007). The Anomura and its sister clade, the Brachyura, were thought to be the most highly evolved of decapod crustaceans by Scholtz & Richter (1995), Schram & Dixon (2003), Dixon *et al.* (2003), and Ahyong & O'Meally (2004) but basal to the rest of the Reptantia by Porter *et al.* (2005). The branch support for the position of the Brachyura was low in the Porter *et al.* study; so we have chosen to polarize our characters using the thalassinid, *Thalassinia anomala* (Herbst, 1804). The debate over the relationship of the Thalassinidea to the Anomura + Brachyura (Meiura of Scholtz & Richter 1995) was succinctly summarized by Ahyong & O'Meally (2004). We accept their conclusion that the homology of the *linea thalassinica* and *linea anomurica* represents a synapomorphy uniting these major taxa.

The accuracy of outgroup rooting is enhanced by including members of the closest group – the sister group. Forest (1987a) was of the opinion that the Diogenidae was most closely related to the Pylochelidae. McLaughlin *et al.*'s (2007) cladogram of anomuran relationships placed the Coenobitidae between the Pylochelidae and Diogenidae; however, because of the specialized adaptations to terrestrial environs exhibited by coenobitids, representatives of this family were not included in the outgroup. Instead, initially we selected

three species as exemplars, representing the theoretically earliest derived genera of the family Diogenidae [*Cancellus panglaoensis* McLaughlin, 2008, *Paguroopsis typica* Henderson, 1888, and *Paguristes acanthomerus* Ortmann, 1892]. However, the analysis done by Ahyong & O’Meally (2004) placed the Pylochelidae, based on *Pylocheles* (*Xylocheles*) *macrops* Forest, 1987a, sister to the Galatheoidea, exclusive of the Aeglidae. For this reason, we also included their exemplar, *Munida quadrispina* Benedict, 1902, in the outgroup. Preliminary analyses explored inclusion of diogenids among the outgroups, but subsequent analyses were rooted to *Munida* and *Thalassinia*.

Phylogenetic analysis. Parsimony analyses of the morphological data matrix were conducted under equal and implied weights (Goloboff 1993). In the latter approach we used concavity constants (k) ranging from 1 to 16, that is, strong to relatively weak downweighting of homoplastic characters was implemented. The trees that resulted from both the weighted and unweighted procedures were subjected to strict consensus calculations. The weighted consensus tree was based on the topologies obtained from k values ranging from 5 to 10 (and 16). According to Goloboff *et al.* (2008) the preferred approach is to explore the effects of a range of “reasonable” k values (e.g. k=5 to k=16) on the tree structure. All parsimony analyses were run in TNT (Goloboff *et al.* 2003) using the traditional search approach with 2000 replications followed by TBR branch-swapping, swapping 20 trees per replication and collapsing branches with zero length. Bremer support values (Bremer 1988, 1994) for the unweighted consensus trees were also inferred using TNT. TreeView (Page 1996) was used to display the phylogenetic trees. The data matrix (Table 1) originated in MacClade version 3 (Maddison & Maddison 1992) and included 43 taxa, of which two made up the outgroup.

Characters and coding. Eighty-two characters were considered in the initial analysis, and a few of these were appropriate only to the Diogenidae. After exclusion of the diogenid genera from the analysis, the number of characters was reduced to 78, and the states of some of the remaining characters were similarly reduced. Only the characters used with the restricted outgroup are included.

The morphology of pylochelids has been illustrated and described in detail by Forest (1987a), Forest & McLaughlin (2000), and McLaughlin (2003). The list of characters and character states generally are self explanatory; however, clarifications of a few definitions and/or interpretations are necessary. Two terms in particular are herein interpreted differently from those used by Forest (1987a). The post-orbital lobe (“saillie postoculaire”) of Forest is equivalent to the antennular lobe or spine in this analysis, whereas the lateral projection used here is synonymous with Forest’s post-antennal lobe (“saillie postantennaire”).

The shield is defined as the anterior portion of the carapace extending from the tip of the rostrum, midpoint of the rostral lobe, or midpoint of the anterior margin to the midpoint of cervical groove in pylochelids and is equivalent to the anterior carapace (including rostrum) in members of the outgroup. Additionally, we accept the interpretations of Snodgrass (1952) and Powar (1969) that the paguroid ocular peduncle consists of three segments rather than the two segments identified by Forest (1987a: 18). We have used the three types of fourth pereopod termination, subchelate, semichelate and chelate, as defined by Sandberg & McLaughlin (1998), rather than the two, subchelate and chelate, used by Forest (1987a). As previously indicated, intraspecific variation was not considered, therefore the character states represent the attributes observed in the species representatives; no gap coding methods were employed

Dixon *et al.* (2003) “... could see no compelling reasons to differentiate the various types of lineae ...”, scoring them simply absent or present. However, as pointed out by Forest (1987a) one linea, the *linea transversalis* of Boas (1926) and Pilgrim (1973) is an important diagnostic character in the Pylochelidae. This linea seems to be absent in the Thalassinidae. Although it has not been identified in anomurans other than paguroids, it may be equivalent to the accessory groove (t) of A. Milne-Edwards & Bouvier (1894: figs. 10, 12). A linea interpreted herein as homologous is seen in *Munida quadrispina* and may also be identifiable with the lateral extension of the cervical groove depicted by Pike (1947) in his detailed study of *Galathea* Fabricius, 1793 or the continuation of the *linea transversalis* of Forest (1987a). Dixon *et al.* (2003), as well as Ahyong & O’Meally (2004) followed Poore’s (1994) suggestion that the *linea thalassinica* of thalassinoids and the *linea anomurica* of anomurans were synonymous.

McLaughlin *et al.* (2007) considered rudimentary gill structures nonfunctional and excluded them from

gill formulae. The arthrobranches of the third maxillipeds in species of *Pomatocheles* Miers, 1879 and *Parapylocheles scorpio* (Alcock, 1894) are substantially reduced, although the gill number typically is reported as 14 pairs.

TABLE 1. Data matrix.

	11111111112222222222333333333344444444445555555555666666666777777777
Taxon\character no.	12345678901234567890123456789012345678901234567890123456789012345678
<i>Thalassina anomala</i>	0101000000000000000110000000000000100001000001220223000300000100000001000000
<i>Munida quadrispina</i>	0002220100000010121012110010000100222023001000222120000120011011202120202211
<i>agassizii</i>	002201311000020001100121110120101112221230110000000101210111000002201001210211
<i>mortensenii</i>	002201311000020101100121110120101112221230110000000101210111000002201001211211
<i>miersi</i>	002201310000020101100121110120201000221120110000000111110111000012201001211210
<i>macrops</i>	000201310000020101000121110120201000221121110000000111120111000012301001210210
<i>cubensis</i>	002201311100120000000121110120201000111120110000000121110111000002201001?11210
<i>incisus</i>	002201311100120000100121110120201000111121110000000221110111000012201001211210
<i>integer</i>	002201311100120000100121110120201000111120110000000121110111000012201001211210
<i>profundus</i>	002201311100120000100121110120201000111120110000000121110111000012201001211210
<i>crosnieri</i>	002201310100120100100121110120201000111121110000000211110111000012201001212210
n. sp A	002101311100120000101121110120201000111121110000000221110111000012201001211210
<i>laticauda</i>	002201200100110100001120110120101112111121110013201221211121000002201011212200
<i>cenobita</i>	002201201100110100000120110120101112111230110010100121111121000012201011210200
<i>mitoi</i>	002201201100110100000120200110101112121230110011101021110121000002201011211201
<i>stenurus</i>	002201201100110100000120110120101112111230110013200121111121000012201011211200
<i>pumicicola</i>	002201201100110100000120110120101112111231110013211221111121000002201011212200
<i>jeffreysii</i>	10020220100002011100010120110110110011012001000020211220121001012101011110111
<i>gaillardi</i>	101202201000020111200101200101101100110120110000101111210121001012001011110111
<i>scorpio</i>	100002201011120200201021100000211000110101010100000221232111011102212021210110
<i>sculptipes</i>	002212100000120200001000001001111120220201010113201201230121010212001001011000
n. sp C	002212201000031201000120200000211022110201001011200211220121000112001001210111
<i>s. spinosus</i>	002222201000031201000120200000211022110200001003222211220121000112001001210111
<i>s. bathamae</i>	002222201000031201000120200000211022110200001003222211220121000112001001210111
n. sp B	001222201000031201000120200000211002110200001013200111220121000112001001210111
<i>pulcher</i>	002222201000032201000120200000211022110200001013200211220121000112001001210111
<i>pilgrimi</i>	002222201000031201000120200000211022110200001013210211220121000112201001210111
<i>longicaulis</i>	000222201000032201300120200000211022110201001003222211220121000112001001211111
<i>vaubanae</i>	002222201000031201000120100000211022110201001103222211220121001112201001210111
<i>loquax</i>	002212201000030201000120200000211020110201001013200211220121000112201001210111
<i>caledonicus</i>	002222201000030200000120200000211000110201001010200211220121000112001001210111
<i>albatrossi</i>	002222201000031201000120200000211022110200001110200211220121000112001001210111
<i>boasi</i>	001212201000031201000120200000211002110200001011200111220121000112201001210111
<i>gracilis</i>	001212201000031201000120200000211002110200001011200111220121000112201001210111
<i>moosai</i>	002222201000030200000120200000211002110200001010200211220121000112101001210111
<i>laurentae</i>	002222201000030201000120200000211002110200001010200211220121000112201001210121
<i>brachyops</i>	001222201000030200000120200000211022110201001012202211220121000112001002212111
<i>sakaii</i>	002212201000031201000120200000211022110200001012200211220121000112201001210111
<i>brevicaulis</i>	001222201000031201000120200000211002110201001112200111220121000112201001210111
<i>manningi</i>	002222201000031201000120200000211020110201000110200211220121001112001001210111
<i>mutus</i>	002222201000031201000120200000211002020201000013200211220121000112201001210111
<i>perplexus</i>	001212201000031201000121000000001020110201000010200111220121000112001001112001
<i>paradoxus</i>	001222201000031201000110200000011022110201010113200201220111101211101002012121

While pleurobranchs are lacking in *Thalassina anomala*, the presence of pleurobranchs has been considered the ancestral condition by most carcinologists (e.g., Calman 1909; Martin & Abele 1986; McLaughlin & Lemaitre 1997; McLaughlin *et al.* 2007), and was viewed as a reversal in the Thalassinidea by Poore (1994). Pleurobranch loss is considered the advanced state.

Although in the majority of paguroids the termination of the fifth pereopods is chelate, this termination is frequently subchelate in pylochelids; however, in certain taxa sexual dimorphism occurs. The states for this character are specifically for males because when dimorphism occurs, it is exhibited principally by males.

1. Arthrobranchs of third maxillipeds: well developed (0); reduced or absent (1).
2. Pleurobranch above fifth pereopod: present (0); absent (1).
3. Shield width: longer than broad (0); width approximately equal to length (1); broader than long (2).
4. Shield length: shorter than posterior carapace (0); approximately equal to posterior carapace (1); longer than posterior carapace (2).
5. Shield lateral margins: entire (0); with unarmed indentation (1); with armed indentation (2).
6. Linea transversalis: not apparent (0); apparent, not contiguous with cervical groove (1); apparent, contiguous with cervical groove at least centrally (2).
7. Rostrum: well developed, without subrostral spine (0); well developed, with subrostral spine (1); somewhat to moderately well developed (2); reduced or absent (3).
8. Post-antennular lobe or spine: absent (0); present (1).
9. Lateral projections: reduced, obsolete or absent (0); well developed (1).
10. Ocular peduncles: well developed (0); reduced (1).
11. Ocular segmental bases: widely separated (0); contiguous or nearly so (1).
12. Ocular peduncle armament: unarmed (0); armed with spines (1).
13. Corneas: normal (0); reduced or absent (1).
14. Ocular acicles: not developed (0); not apparent or present as plate of second segment fused with ultimate segment (1); present as plate-like on free penultimate segment (2); present with spine(s) on free penultimate segment (3).
15. Antennular peduncle length: elongate, overreaching distal margins of corneas by at least length of ultimate peduncular segment (0); overreaching but by less than length of ultimate segment (1); short, not overreaching distal margins of corneas (2).
16. Basal antennular segment: elongate, without spines (0); elongate, with 1 or more spines (1); short, usually with 1 or more spines (2).
17. Second antennular segment: unarmed (0); armed with 1 or more spines (1).
18. Antennal peduncle lengths: overreaching distal margins of corneas (0); not reaching to distal margins of corneas (1).
19. First antennal segment armature: 1 spine to dorsal row of small spines (0); dorsal row of small spines plus more elongate dorsodistal spine (1); no dorsal row of small spines, but prominently produced or spinose dorsodistal margin (2); unarmed (3).
20. Antennal acicle (scaphocerite): moderate to short (0); markedly reduced, vestigial or lost (1).
21. Epistome: unarmed (0); armed with 1 or more spines (1).
22. Mandibular cutting edge: chitinous (0); calcified (1).
23. Maxillary endopod: external lobe articulated, recurved (0); external lobe articulated, not recurved (1); external lobe reduced or obsolete (2).
24. Maxillary scaphognathite: with 1 or more exceptionally long setae proximally on posterior lobe (0); without 1 or more exceptionally long setae proximally on posterior lobe (1).
25. First maxilliped: without exopodal flagellum (0); with non-articulated exopodal flagellum (1) with multiarticulated exopodal flagellum (2).
26. Second maxilliped endopod termination: simple (0) sub- semi- or completely chelate (1).
27. Second maxilliped exopod: unarmed (0); armed with one to several spines (1).
28. Second maxilliped epipod: present (0), absent (1).

29. Third maxilliped termination: simple (0); semichelate (1); chelate (2).
30. Third maxilliped exopod: unarmed (0); with one or more spines (1).
31. Third maxilliped epipod: well developed (0); rudiment or scar (1); lost (2).
32. Crista dentata of third maxilliped: without accessory tooth (0); with accessory tooth (teeth) (1).
33. Pereopod 1: subchelate (0); chelate (1).
34. Chelae: not forming operculum (0); forming operculum (1).
35. Chela shape: subrectangular (0); subovate to ovate (1); subtriangular (2).
36. Chela dorsal surface: generally flattened or smoothly convex (0); with ridge(s) or crests (1); with granules, tubercles or spines (2).
37. Chela/carpal articulation: articulating in same plane (0); rotated approximately 30–45° (1); articulating vertically (2).
38. Cheliped dactyl and fixed finger opening: vertical (0); oblique (1); horizontal (2).
39. Dactyl and fixed finger termination: corneous claws (0); calcified claws (1).
40. Palms of chelae with dorsomesial or upper margins: with elevated entire or scutellated ridges (0); with row(s) of tubercles (1); row(s) of spines (2).
41. Chela dorsolateral or lower margin: not delimited (0); with elevated entire or scutellated ridge(s) or lobes (1); with row(s) of tubercles (2); row(s) of spines (3).
42. Chela setation: with sparse setae (0); with moderate to abundant setae (1).
43. Carpal anterodorsal surface and margin: not prominently elevated (0); prominently elevated (1).
44. Carpal anterodorsal (dorsodistal) margin: unarmed (0); armed with granules, tubercles, spinules or spines (1).
45. Carpal stridulatory apparatus: absent (0); present (1).
46. Setation of carpi: with sparse setae (0); with moderate to dense setae (1).
47. Pereopod symmetry: second and third pereopods similar in shape and/or armature [exclusive of stridulatory apparatus] (0); second and third pereopods dissimilar in shape and/or armature [exclusive of stridulatory apparatus] (1).
48. Propodi of second pereopods: unarmed (0); with few to numerous protuberances, granules, tubercles or spinules (1); with 1 prominent dorsodistal spine (2); with row of few to numerous spines (3).
49. Carpi of second pereopods: unarmed or with only dorsodistal spine (0); with few numerous granules, tubercles or spinules (1); with few to numerous spines (2).
50. Propodi of third pereopods: unarmed or with small spine only at dorsodistal margin (0) with few to numerous protuberances, granules, tubercles or spinules (1); with few to numerous spines (2).
51. Carpi of third pereopods: unarmed or with spine only at dorsodistal margin (0); with few to numerous protuberances, granules, tubercles or spinules (1); with few to numerous spines (2).
52. Dactyl and propodal pereopod setation: lacking setae (0); with sparse setae (1); with moderate to abundant setae (2).
53. Sternite of male seventh thoracic segment (fourth pereopods): straight and undivided (0); straight and divided by transverse suture (1); compactly triangular (2); triangular, drawn out anteriorly to elongate median tip (3).
54. Fourth pereopod development: normal walking leg (0); reduced (1).
55. Fourth pereopod termination: simple (0); subchelate (1); semichelate (2); chelate (3).
56. Propodal rasp of fourth pereopod: not developed (0); consisting of single row of scales (1); consisting of 2 to several rows of scales (2); scales covering approximately half or more of lateral surface (3).
57. Sternite of male eighth thoracic segment (fifth pereopods): simple and plate-like (0); straight and rod-like (1); with prominent tubercle(s) (2); grooved (3).
58. Fifth pereopod development: normal walking leg (0); reduced (1).
59. Fifth pereopod termination in males: simple (0); subchelate (1); chelate (2).
60. Fifth pereopodal rasp: absent (0); present (1).
61. Pleon symmetry: pleomeres symmetrical (0); pleomeres asymmetrical (1).

62. Pleonal tergal surfaces: weakly to well calcified, smooth (0); partially to completely calcified, sculptured (1); chitinous or membranous (2).
63. Pleonal pleura 2–5: moderately to well developed, at least covering bases of pleopods (0); poorly developed, not covering bases of pleopods (1); not developed (2).
64. Pleonal tergite 1: broad, subrectangular (0); triangular (1); reduced (2).
65. Pleomere 6 tergal shape: subrectangular (0); subquadrate to subcircular (1).
66. Pleomere 6 lateral margins: entire (0); with transverse incisions, sutures or indentations (1); with oblique incisions (2).
67. Pleomere 6 terminal margin: entire, unarmed (0); entire, with spines or spinules (1); with median incisions or concavity (2); with median area produced (3).
68. Male paired first pleopods: terminally spatulate (0); simple (1).
69. Male pleopods 3–5: paired, equally or subequally biramous (0); paired, endopods reduced or absent (1); paired, exopods reduced or absent (2).
70. Female first pleopods: present (0); absent (1).
71. Egg-bearing pleopods: both rami well developed (0); endopod reduced or absent (1); exopod reduced or absent (2).
72. Uropod symmetry: symmetrical, forming tailfan (0); symmetrical, not forming tailfan (1); asymmetrical (2).
73. Protopods of uropods: neither produced nor armed (0); produced posteriorly, unarmed (1); produced, with prominent posterior spine (2).
74. Uropodal endopods and exopods: without rasps (0); with rasps (1).
75. Telson shape: longer than broad (0); length approximately equal to width (1); broader than long (2).
76. Telson lateral margins: entire (0); with transverse indentations (1); with transverse sutures (2).
77. Telson posterior lobes: not delimited (0); delimited, symmetrical or nearly so (1); delimited, asymmetrical (2).
78. Telson terminal margin: entire or with slight median depression (0); with median concavity or cleft (1).

Results

The unweighted analysis (Bremer support values on the resolved nodes) with the diogenids excluded from the outgroup gave rise to 445 most parsimonious trees that were 311 steps long (CI = 0.40; RI = 0.74; RC = 0.30). The best fit (and homoplasy) score and the number of optimal trees for each k value implemented under implied weighting are shown in Table 2. As may be seen in Figure 2, the tree obtained from analyzing the characters as unweighted gave poor resolution. When the analysis was repeated with weighting against homoplasy (Goloboff *et al.* 2008), the results were significantly improved. Either the unweighted or the weighted tree (Figs. 2, 3) have three primary evolutionary branches in the Pylochelidae. The first includes the taxa of the subfamily Pylochelinae, the second is restricted to the Pomatochelinae, and the third contains the remaining taxa. Forest's (1987a) suggestion that each of the present subfamilies should be elevated to familial rank was not supported.

Discussion

A recent study by Goloboff *et al.* (2008) compared the performance of parsimony analyses of morphological characters under implied and equal weights, and found that the former outperformed the latter regardless of concavity constant used. This result, however, does not alleviate the need to explore the effects of different concavity values on the clade structure in trees obtained under implied weighting. Drawing firm conclusions about the existence of a taxonomic group that is only present for a given k value (Goloboff *et al.* 2008) is

unwarranted. In our present study, we inferred trees for concavity constants ranging from 1 to 16 (Table 2 and Fig. 3). The consensus tree based on optimal phylogenies derived from k values between 5 and 16 was the same as that obtained from the best topologies inferred based on k constants ranging from 5 to 10, suggesting that the clades shown in the strict consensus tree (Fig. 3) are robust to a wide degree range of downweighting strengths of homoplastic characters. However, in the strict consensus tree (not shown), based on all the implemented concavity constants (i.e. $k=1$ through $k=16$), two clades within *Trizocheles* collapsed into a polytomy and the structure of another group changed within the same clade.

TABLE 2. Summary of results obtained from the implied weighting analyses. Trees obtained with concavities 5–10 and 5–16 were the same, and were used to generate strict consensus trees. See Fig. 4.

K –values	No. of Trees	Fit scores	Homoplasy scores
1	167	29.71	40.29
2	2	38.05	31.95
3	2	43.25	26.75
4	46	46.88	23.12
5	46	49.60	20.40
6	46	51.71	18.28
7	45	53.41	16.58
8	46	54.82	15.18
9	1	56.00	14.00
10	1	57.01	12.99
11	1	57.88	12.12
12	1	58.63	11.36
13	1	59.30	10.70
14	1	59.90	10.10
15	1	60.42	9.58
16	1	60.90	9.10

From these analyses, the monophyly of the Pylochelidae is not clearly confirmed. However, the three major branches that are recognized herein, strongly indicate evolutionary transformations. The Pylochelinae is sister to the remaining taxa, the latter sharing the synapomorphy of a continuous *linea transversalis*. Forest's (1987a) assessment of the Pylochelinae is corroborated to the extent that the subfamily contains the two genera *Pylocheles* and *Cheiroplatea* that share the synapomorphy, chelate termination of the third maxilliped. But the subdivision of *Pylocheles* into three subgenera is not as substantiated. In the Contree5K10(16) cladogram, only the subgenus *Pylocheles* (*Pylocheles*), i.e., *P. (P.) agassizii* and *P. (P.) mortensenii*, is clearly defined.

The Pomatochelinae is sister to Parapylochelinae + Canellochelinae, and defined by the apomorphy, spinose second antennal segments. The monotypic Parapylochelinae and Canellochelinae are, as indicated, sister taxa, sharing several synapomorphies. However, the distinctiveness of the Parapylochelinae is substantiated by four unique apomorphies: the spinose and basally approximate ocular peduncles, the prominent tubercle on the sternite of the fifth pereopod, terminally simple male first pleopods, and the markedly reduced exopods of the female egg-bearing pleopods. Two apomorphies define the Canellochelinae, the subrostral spine and the operculate chelae. While it is true that chelipeds forming an operculum is characteristic of species of *Pylocheles* (*Pylocheles*) and *Cheiroplatea*, the opercula formed are not homologous with the operculum of *Canellocheles*. In these Pylochelinae, it is only the chelipeds that contribute to the opercula. In *Canellocheles sculptipes* (Miyake, 1978) the operculum is formed in

conjunction with the second pereopods. *Mixtopagurus paradoxus* A. Milne-Edwards, 1880, representing the monophyletic Mixtopagurinae, is unique within the family because of the asymmetry of its pleon, uropods and telson. Relationships among the taxa of the subfamily Trizochelinae primarily are unresolved in the strict consensus cladogram of unweighted characters (Fig. 2). However, when *Trizocheles manningi* Forest, 1987a and *T. perplexus* Forest, 1987a are excluded, the strict consensus tree based on optimal phylogenies derived from k values between 5 and 16 is the same as that obtained from the best topologies inferred based on k constants ranging from 5 to 10, suggesting that the clades shown in Figure 3 are robust to a wide range of downweighting strengths of homoplastic characters. Nonetheless, the relationships among the species *T. pulcher* Forest, 1987a, *T. mutus* Forest, 1987a, *T. albatrossi* Forest, 1987a and *T. pilgrimi* are unresolved. The remaining species assigned to the genus *Trizocheles* represent four distinct clades.

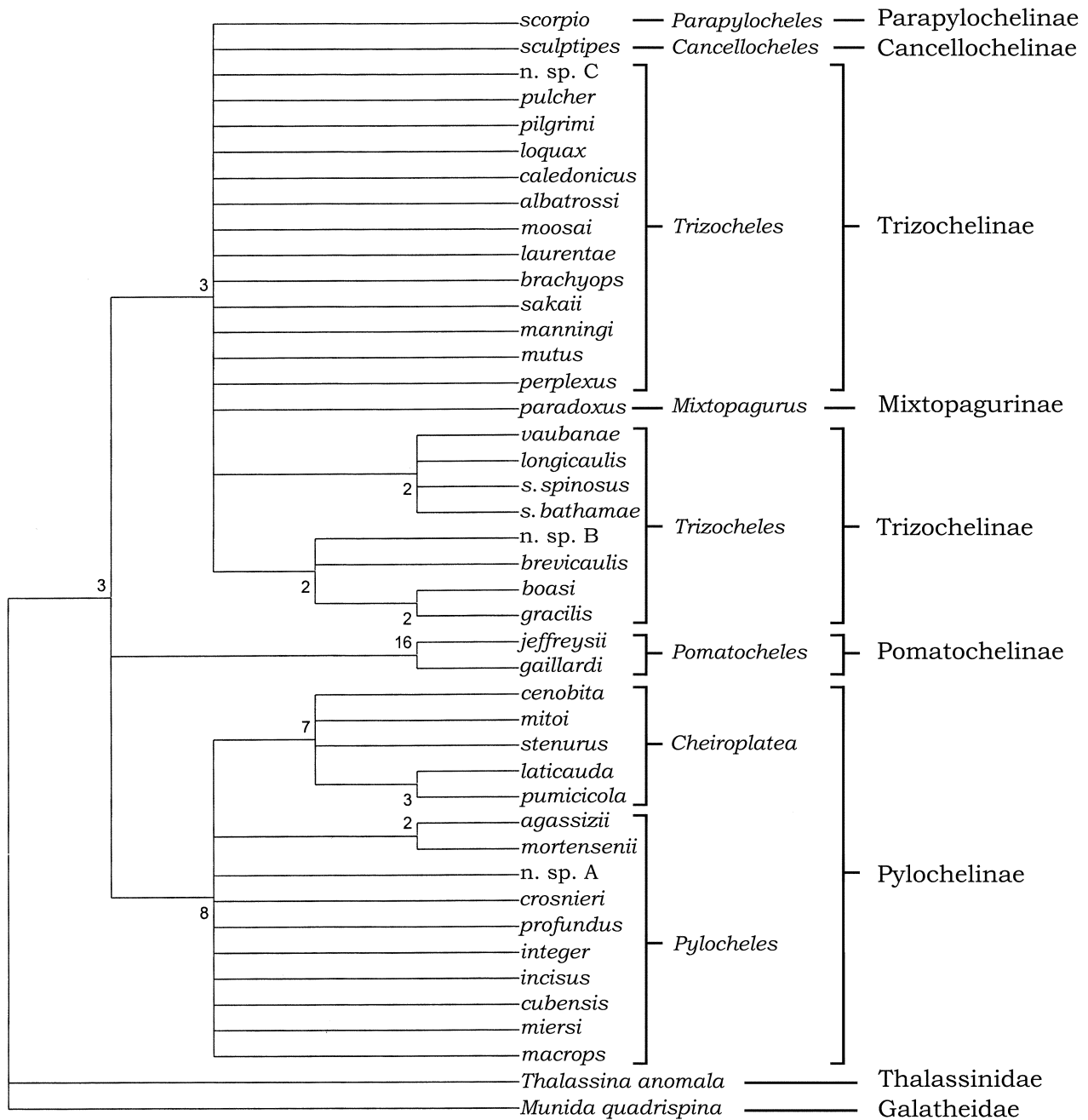


FIGURE 2. Strict consensus cladogram of 445 most parsimonious trees (length=311 CI = 0.40; RI = 0.74; RC = 0.30) obtained from heuristic parsimony analyses of unweighted and unordered characters. Subfamily names as proposed by Forest (1987a) are indicated. Two taxa (Thalassinidae: *Thalassinina anomala*, Galatheidae: *Munida quadrispina*) were used as the outgroup. Bremer support values are shown for the resolved nodes.

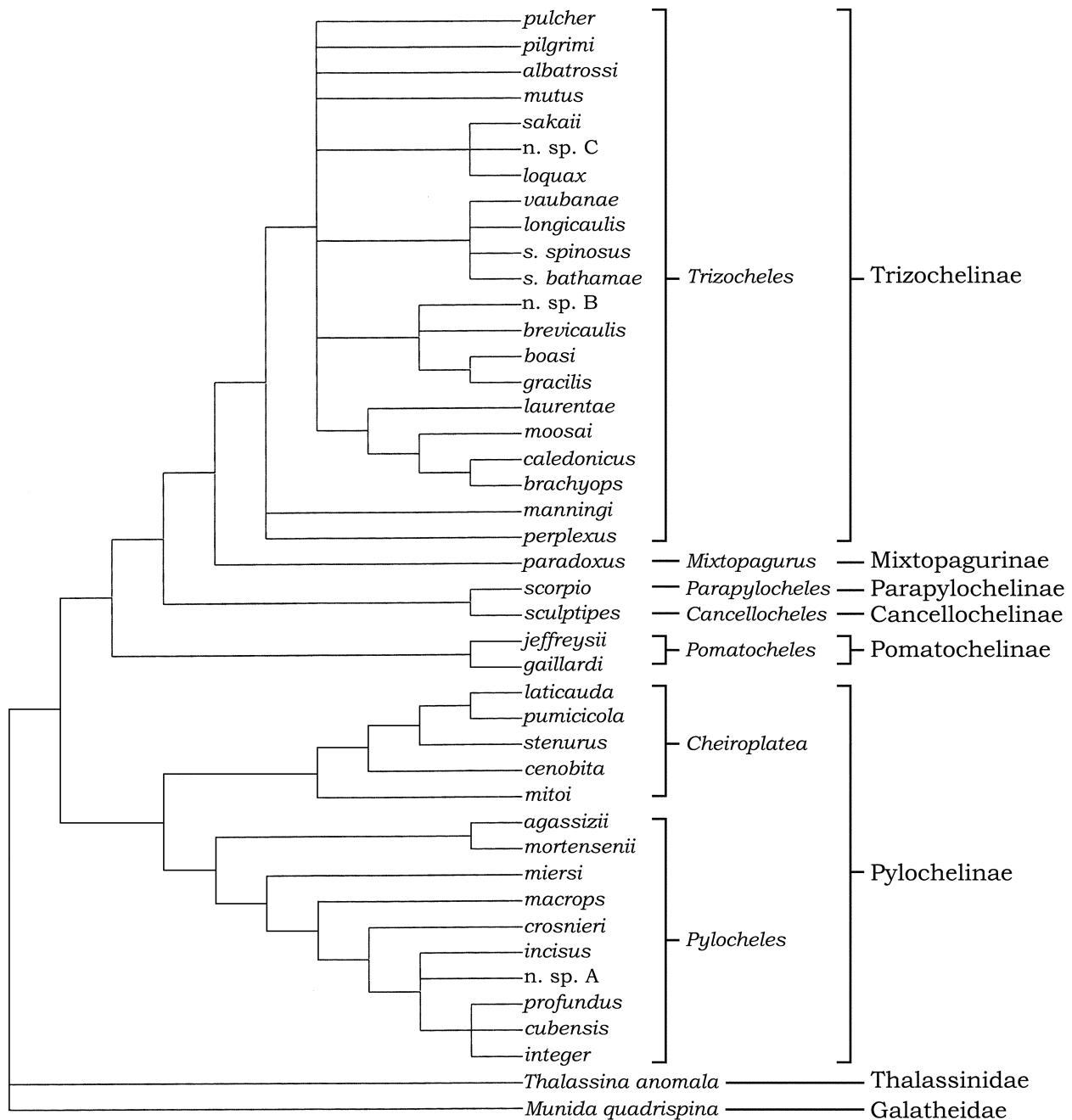


FIGURE 3. Strict consensus cladogram based on the optimal trees obtained under concavity values (i.e., k-values) ranging from 5 to 16. Subfamily names as proposed by Forest (1987a) are indicated. Two taxa (Thalassinidae: *Thalassina anomala*, Galatheidae: *Munida quadrispina*) were used as the outgroup. See Table 2 for fit and homoplasy scores.

Although larval data are very limited, what is available does add strength to the phylogenetic analysis. As discussed by McLaughlin & Lemaitre (2008), the larvae of *Pylocheles* (*Pylocheles*) *mortensenii* Boas, 1926 and *Pomatocheles jeffreysii* differ so dramatically from one another and also from the larvae of *Trizocheles spinosus spinosus* (Henderson, 1888) and *T. vaubanae* that distinct subfamilial classification seems justified. *Trizocheles s. spinosus* and *T. vaubanae* are members of one of the *Trizocheles* clades. Regrettably, comparable data on larval development for either *Canellocheles sculptipes* or *Parapylocheles scorpio* are not available to confirm or deny their apparent sister-group relationship as indicated by the phylogenetic analysis.

As our analyses have demonstrated, the Pylochelidae appears to consist of three distinct and divergent

clades. Whether each should be treated as a taxonomically separate major taxon is beyond the scope of the present study. This question will be addressed in a subsequent investigation. However, our results may provide some insight into the seemingly untenable results of four recent studies of decapod phylogeny (Dixon *et al.* 2003, Schram & Dixon 2003, Ah Yong & O'Meally 2004, Tsang *et al.* 2008). In these studies the Pylochelidae have consistently been aligned with the Galatheaidea (though with low nodal support) rather than the Paguroidea. The single pylochelid exemplar defining the Pylochelidae was identified only as *Pylocheles* sp. in the studies of Dixon *et al.* (2003) and Schram & Dixon (2003), but specifically as *Pylocheles* (*Xylocheles*) *macrops* in the studies of Ah Yong & O'Meally (2004) and Tsang *et al.* (2008). Given the morphological and presumably genetic diversity now recognized in this family, it is perhaps understandable why the use of a single species as representative of all, gave a somewhat erroneous placement of the Pylochelidae among the Anomura.

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