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A PHYLOGENY OF THE LEPTOSTRACA (CRUSTACEA) WITH KEYS TO FAMILIES AND GENERA

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Abstract

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A phylogenetic analysis of the Leptostraca Claus, 1880 is undertaken using 32 of the 41 known species (including 4 undescribed species). The value of outgroups for deriving a plausible phylogeny in a group whose affinities remain contentious is discussed. A hypothetical ancestor is considered the best solution to the problem and states were scored based on general principles of crustacean evolution as evidenced by a wide variety of taxa. States of the 43 characters used in the analysis are detailed. The new phylogenetic hypothesis is compared with those of Olesen (1999). We conclude that a phylogeny based on species-level taxa and many informative characters is more likely to represent true evolutionary relationships than one based solely on genera and few characters. A new classification based on the phylogeny is derived with a new family, Paranebaliidae, being erected for *Paranebalia* Claus, 1880 and *Levinebalia* Walker-Smith, 2000. Nebaliopsididae Hessler, 1984 is supported for *Nebaliopsis* Sars, 1887. A restricted Nebaliidae Samouelle, 1819 for the remaining genera (*Speonebalia* Bowman, Yager and Iliffe, 1985, *Nebaliella* Thiele, 1904, *Dahlella* Hessler, 1984 and *Nebalia* Leach, 1814). *Sarsinebalia* Dahl, 1985 is synonomised with *Nebalia*. New keys and family and generic diagnoses are presented. All known species are listed with notes on distribution.

Introduction

Leptostracans are marine crustaceans of the malacostracan subclass Phyllocarida. Leptostracans have many derived features that separate them from other malacostracans: the loss of ambulatory function of the thoracic limbs, which now only function in feeding, respiration and brood protection (Hessler and Schram, 1984; Dahl, 1976); a movable rostrum (Schram, 1986; Olesen, 1999); the scale-like ramus of the first antenna (Hessler and Schram, 1984; Olesen, 1999); uniramous antenna 2 (Hessler and Schram, 1984; Olesen, 1999); reduction of pleopods 5 and 6 (Hessler and Schram, 1984; Olesen, 1999); and direct larval development (Manton, 1934; Hessler and Schram, 1984).

The first species of the Order Leptostraca Claus, 1880 was described by Otto Fabricius in 1780, as *Cancer bipes* from east Greenland. Herbst (1796) later relegated this species to subspecific status, *Cancer gamarellus bipes* (cited in Sars, 1896). Leach (1814) introduced the genus *Nebalia* for *Cancer bipes* and a new British species *N. herbstii* Leach, 1814.

The genera of Leptostra are distributed differently. *Nebalia* is cosmopolitan. In contrast, *Levinebalia* Walker-Smith, 2000 has been recorded only in Australia and New Zealand. *Paranebalia* Claus, 1880 is found in central America, Bermuda, New Caledonia and Australia. *Nebaliella* Thiele, 1904 is confined to cold waters, being found in Antarctica, southern Australia and the high latitudes of the Northern Hemisphere. *Speonebalia* Bowman, Yager and Iliffe, 1985 has been recorded from only marine caves in the Turks and Caicos, and *Dahlella* Hessler, 1984 was collected from hydrothermal vents near the Galapagos. *Nebaliopsis* Sars, 1887 is a pelagic genus with a world-wide distribution. Leptostracans have been recorded in waters from 1 m deep (Modlin, 1991) to more than 2000 metres (Fage, 1929). Most species occur in less than 200 metres. Water temperatures influence the length of time taken to reach maturity, the size at maturity and the incubation time of young (Macquart-Moulin and Castlebon, 1983).

Until now three families have been recognised: Nebaliidae Samouelle, 1819; Nebaliopsididae Hessler, 1984; and the Permian Rhabdouraeidae Schram and Malzahn, 1984. Hessler's (1984) original spelling, Nebaliopsidae, is incorrect as family names based on genera ending in "*-opsis*" should end "-opsididae" (e.g. Sivertsen and Holthius, 1980). Seven nominal genera (*Nebalia;*

Paranebalia; Nebaliella; Dahlella; Sarsinebalia Dahl, 1985; *Speonebalia*; and *Levinebalia*) and 36 extant species are contained in the family Nebaliidae. Nebaliopsididae consists of the monotypic genus *Nebaliopsis*. *Rhabdouraea* Malzahn, 1962 is the monotypic fossil genus of Rhabdouraeidae.

Martin et al. (1996) reviewed the morphology and natural history of *Nebalia hessleri* Martin, Vetter and Cash-Clark, 1996 and provided a key to the extant families and genera of Leptostraca then accepted.

Olesen (1999) conducted a phylogenetic analysis of the seven extant leptostracan genera then known and described *Nebalia brucei* Olesen, 1999. Olesen questioned the monophyly of *Nebalia* and stated that as he could not find unique characters for this genus he could not exclude the possibility it is paraphyletic with *Sarsinebalia* and/or *Dahlella*. However, he maintained the status of these three genera.

The present study is a derived from an unpublished BSc(Hons) thesis (Walker-Smith, 1993) and presents a detailed phylogenetic analysis of the Leptostraca using 32 of the 41 known species (including four undescribed species). The monophyly of genera is tested and relationships between the included species deduced as far as possible. The value of certain characters in leptostracan systematics is discussed, as are the results of the phylogenetic analyses. The value of outgroups in deriving plausible phylogenies in a group whose affinities remain contentious is also discussed. A new classification based on phylogenetic principles is derived and new keys and new family and generic diagnoses are offered. All known species are listed with distributional notes.

Growth in Leptostraca

Transformations in the shape of the carapace, both pairs of antennae, pleopods, furca and other features are gradual from moult to moult in immature and subadult males and deviate from the female morphology, which generally remains unchanged except when reproductive (Dahl, 1985).

In species of Nebaliidae the terminal article of the juvenile thoracopod endopod is elliptic with thin marginal setae (Figs 4d, 4e). In sexually mature females carrying eggs or embryos, the entire endopod becomes elongated and the terminal article becomes enlarged, generally sitting at right angles to the thoracopod axis (Fig. 4l). The exterior and terminal edges of the terminal article possess a dense armature of plumose setae that are long, strong and curved, and interlock with those of opposite and neighbouring thoracopods to form the floor of the brood chamber. Embryos develop in the brood pouch and when the juveniles are ready to leave the long setae forming the floor of the chamber drop off, leaving behind a pattern of ridges and furrows that are the scars of setal attachment (Dahl, 1985). At this stage, the terminal article of the endopod differs so markedly from those of males and immature females that they could be presumed to belong to a different species (Dahl, 1985: Figs 6–10). The exopod and epipod do not change shape during this metamorphosis.

The eggs of *Nebaliopsis* are thought to be shed directly into the water (Cannon, 1931, 1960) but Brahm and Geiger (1966) reported *Nebaliopsis* with eggs developing under the carapace. These eggs appeared to be contained in a "basket formed by the large and setose posterior pair of thoracic appendages, that extend anteriad to the area of the mouth parts" (Brahm and Geiger, 1966: 41–42) and were shed when the specimens were placed in fixative.

Taxonomic confusion in Leptostraca

In the past, failure to recognise characters related to the sex and maturity of leptostracans resulted in taxonomic confusion. Thomson (1879) described *Nebalia longicornis* without taking sexual dimorphism into account and thus recognised the elongate flagellum of antenna 2 as a specific character rather than one of sexually mature males. Claus (1888) added to the taxonomic confusion by basing his identification of species on few morphological characters, most of which were growth- or sex-related and could not be used to successfully distinguish between genera or species. Claus's (1888) taxonomic concept of Leptostraca was followed by subsequent taxonomists (e.g., Thiele, 1904, 1905) and resulted in the erroneous assumption that each genus consisted of a few highly variable species. In particular, *Nebalia bipes* (Fabricius, 1780) and *N. longicornis* have been reported as geographically widespread while, in fact, each comprises several species. The subspecies described for each are likely to be separate species. Many records of nominal species in areas remote from their type locality probably refer to undescribed species. Fortunately, Dahl (1985) recognised the conservative nature of leptostracan morphology and redefined many species of *Nebalia* using new diagnostic characters. Dahl's assessment of the European shelf and Southern Hemisphere species incorporated the description of six new species of *Nebalia* (Dahl, 1985, 1990).

Analytical methods

Material for this study is deposited in Museum Victoria, Melbourne and type specimens of *Nebalia capensis* Barnard, 1914 were borrowed from the South African Museum, Cape Town. Museum Victoria collections include representative species of *Nebalia, Nebaliella, Paranebalia, Levinebalia* and *Nebaliopsis.* For most described species information relating to character states was obtained from the literature. Thirty-two species, including four undescribed species from southern Australia, were selected for phylogenetic analysis. Literature relating to six species and three subspecies of Nebaliidae was either not obtainable or provided insufficient diagnostic information; these taxa were omitted from the analysis. *Nebalia gerkenae* Haney and Martin, 2000, published later, was not included nor was the fossil family Rhabdouraeidae.

Cladistic analyses were used to generate trees of monophyletic groups as hypotheses of the relationship between the selected taxa. The relationships between genera were of greatest interest. Forty-three characters (all parsimony-informative) were scored for each taxon (Table 1) resulting in a data matrix of 32 leptostracan taxa plus a hypothetical ancestor described by 43 characters (Table 2). Characters were treated as unordered and unweighted.

The program PAUP* 4.0 (Beta 3 version for Windows) (Swofford, 1998 and updates) was used to establish relationships between taxa and produce a hypothesis from which a classification might be derived. A heuristic search was made using most of the default options in the PAUP block, except for the following commands: OUTROOT=MONOPHYL; ADDSEQ=RANDOM; NREPS=1000; NCHUCK=3; CHUCKSCORE =1; RANDOMIZE=TREES. The two most distant parsimony trees were calculated using the FILTER command and the characters states changes were mapped on one of these trees. A 50% majority-rule consensus tree of all trees was generated. Stability of the clades was assessed by bootstrap analysis (using the default settings) and a 50% majority-rule consensus tree of all bootstrap trees was constructed. Bremer support values were calculated for the two most distant trees using Auto Decay 4.0 (Eriksson, 1998) to assess the stability of the clades. Trees were illustrated using Tree View (Page, 1996).

Outgroups

Selection of an outgroup is the major problem encountered in the phylogenetic study of the Leptostraca. Leptostraca have been considered the most primitive subclass within the Malacostraca because they have a primitive caudal furca and polyramous phyllopodous (flattened, leaf-like) thoracic limbs used in filter feeding (Claus, 1888; Manton, 1934; Dahl, 1987, 1992). Hessler and Newman (1975) believed the relatively high number of segments and full complement of segmental appendages should also be regarded as primitive features. Dahl (1976) supported Hessler and Newman's (1975) view with the fact that while Phyllocarida were represented in the Lower Cambrian, no fossils of the other malacostracan subclass Eumalacostraca are known until the Devonian. However, Walossek (1999) disputed the existence of fossil malacostracans appearing in the Cambrian and stated that the only clear record appears after this time.

Other authors have placed the Leptostraca as a subclass in Phyllopoda with phyllopodous (polyramous and foliaceous) thoracopods thought to unite Branchiopoda, Leptostraca and Cephalocarida (in this class) (Milne Edwards, 1834; Schram, 1986). However Dahl (1987: 722) refuted this, stating that "polyramous thoracopods constitute a basic feature of malcostracan morphology and are therefore not a phyllopod synapomorphy." Dahl (1987) also highlighted the fact that while most genera of Leptostraca have foliaceous thoracopods those of *Paranebalia* are most similar to the stenopodous appendages of caridoid Malacostraca (e.g. Euphausiacea). Martin and Christiansen (1995) also detailed many differences between the fourth thoracopod of *Nebalia* (Leptostraca) and *Leptestheria* sp. (Branchiopoda: Conchostraca) including the size and arrangement of endites and the type and number of setae and their function. They too believed that the phyllopodous limb cannot be used as an indicator of phylogenetic affinity. This view was supported by independant evidence from an 18S rDNA study of Branchiopoda, Cephalocarida and Phyllocarida, seven other crustacean taxa and three arthropod outgroups (Spears and Abele, 1999). They concluded, with little doubt, that the presence of foliacous limbs does not define a monophyletic clade comprising branchiopods, cephalocarids and phyllocarids. They, like Dahl (1987) and Martin and Christiansen (1995), believed that foliaceous limbs have multiple origins.

While leptostracans appear to be the basal malacostracans they differ significantly from all other taxa in this class, making selection of an outgroup difficult. One potential sister taxon — the subclass Hoplocarida (Order Stomatopoda) — are morphologically so highly derived that

Table 1. Character transformations used in phyogenetic analysis of 32 species of Leptostraca. Each character is terminated by a colon and states (0, 1 …) separated by a semicolon. The 17 characters with CI=1 in tree 711 are indicated by #, those where 0.5<CI<1 by *.

1*. Rostrum, subterminal spine: absent (Fig. 1a) (0); present (Fig. 1b) (1).
2#. Rostral keel: absent (0); shorter than rostral flange (Figs 1a, d) (1); longer than rostral flange (Figs 1c, e) (2).
3*. Eye length: shorter than rostrum (0); longer than rostrum (1).
4#. Eye, supraocular scale: absent (0); longer or equal to length of eye (1); shorter than eye (Fig. 1f) (2).
5*. Eye surface: smooth (0); denticulate (Figs 1h, m) (1).
6. Eye dorsal papilla: absent (0); present (Fig. 1f) (1).
7*. Eye, ventral margin: not extremely curved (Fig. 1f) (0); extremely curved (Fig. 1k) (1).
8. Eye, dorsal margin: not dorsally convex (Fig. 1i) (0); dorsally convex (Fig. 1j) (1).
9#. Eye: not bilobed (Figs 1f, g) (0); bilobed (Fig. 1n) (1).
10. Eye: with ommatidia (Fig. 1g) (0); without ommatidia (Fig. 1i) (1).
11*. Antenna 1 anterodenticulate fourth article: absent (0); present (Fig. 1q) (1).
12#. Antenna 1 article 4: without robust setae (0); with 1 or more robust setae (Fig. 1p) (1).
13*. Antenna 1 of male: not swollen or a callynophore (0); a swollen callynophore (Figs 1c, 1d) (1); with dense field of aesthetases but not swollen (Fig. 2f) (2).
14*. Antenna 2 peduncle articles 3 and 4: not fused (Fig. 2a) (0); fused (Fig. 2b) (1).
15#. Antenna 2 peduncle articles 3 and 4: without two large cuticular outgrowths (0); with two large cuticular outgrowths (Figs 1r, 5a, b) (1).
16#. Antenna 2 peduncle surface: without denticles or minute cuticular outgrowths (0); with minute denticles or cuticular outgrowths (Figs 5a, b) (1).
17#. Antenna 2 of male: greatly elongate, reaching to the caudal furca (0); not greatly elongate, only half length of specimen (1).
18*. Antenna 2 peduncle article 2, dorsal surface: without spine (0); with spine (Fig. 2b) (1).
19. Mandible, article 2 of palp: with more than 2 setae (0); with 2 setae (1); with 1 seta (2).
20. Mandible palp, relative lengths of articles 2 and 3: 2 longer than 3 (0); 2 equal to 3 (1); 2 shorter than 3 (2).
21. Mandible, article 3 of palp: tapering distally (0); with parallel margins (1); expanded distally (2).
22. Mandible incisor teeth: 2 (Fig. 2h) (0); 1 (Fig. 2e) (1); absent (2).
23#. Molar accessory tooth/spine: absent (0); present (Fig. 2i) (1).
24#. Molar large accessory process: absent (0); present (Fig. 2e) (1).
25#. Molar process, setal brush: absent (0); present (Fig. 2e) (1).
26#. Maxilla 1 second endite: complex (Fig. 3a) (0); bilobed (Figs 3b, d) (1); elongate (Fig. 3g) (2); simple (Fig. 3c) (3); reduced (4).
27. Maxilla 2 endopod: biarticulate (0); uniarticulate (1).
28*. Maxilla 2 exopod: greater than or equal to half length of endopod (0); less than half length of endopod (1); absent (2).
29#. Thoracopod length: short, not extending well beyond the ventral margin of the carapace (Fig. 4a) (0); long, extending well beyond ventral margin of carapace (Fig. 1l) (1).
30*. Thoracopod exopod: heavily setose (Figs 4b, 4c) (0); with few setae (Fig. 4d) (1); with no setae (Fig. 4e) (2).
31#. Thoracopod exopod: without proximal lobe (Figs 4b–d) (0); with proximal lobe (Fig. 4e) (1).
32#. Thoracopod 2–5: epipod longer than exopod (Fig. 4d) (0); epipod shorter than exopod (Fig. 4b) (1); epipod absent (Fig. 4e) (2).
33#. Pleonite 4 posterior margin: smooth (0); crenate (saw-tooth) (Fig. 4a) (1).
34#. Pleonite 5 posterior margin: smooth (0); crenate (Fig. 4a) (1).
35#. Crenations on pleonites 6 and 7: absent (0); only on dorsal margin (Fig. 1l) (1); over entire margin (Fig. 4a) (2).
36. Pleonite crenation: absent (0); pointed (1); blunt (2).
37*. Pleonite size: pleonite 6 and pleonite 7, each equal in length to pleonite 5 (0); pleonite 6 and pleonite 7, each longer than pleonite 5 (1).
38. Pleopods 1–4 peduncles margins: smooth (0); crenate (Fig. 3i) (1).

Table 1. — continued.

39. Pleopod 1, ratio of lengths of comb-row to exopod: comb-row absent (0); less than or equal to half length of exopod (1); greater than half length of exopod (Fig. 4k) (2).
40*. Pleopod 2–4 exopod lateral margin: with smooth setae not in pairs (Fig. 4i) (0); with smooth setae in pairs (Fig. 4h) (1).
41*. Pleopod 5: shorter than pleopod 6 (0); longer than pleopod 6 (1).
42*. Pleopod 6: biarticulate (0); uniarticulate (1).
43*. Carapace with: posterodorsal marginal spines (Fig. 3e) (0); without posterodorsal marginal spines (1).

Table 2. Character matrix used in phylogenetic analysis of the Leptostraca

Character numbers	1234567891	1234567892	1234567893	1234567894	123
Hypothetical ancestor	0000000000	00?000000?	?0??0?00?0	00????0000	00?
Nebaliopsis typica	0000000000	10?000?000	0200041202	0000000000	101
Levinebalia fortunata	1000000100	1011111020	?100021010	0100000001	011
Levinebalia maria	1000000100	1011111021	0100021010	0100000011	011
Paranebalia belizensis	1000100100	1011101020	010?120010	01??11?121	011
Paranebalia longipes	1000100100	1011101000	0101120010	0100111121	011
Paranebalia sp. A	1000100100	1011101021	0101121010	0100111121	011
Speonebalia cannoni	0010000101	000000?02?	?200031101	0011210101	000
Nebaliella antarctica	0210001101	0000000101	2010011000	1211211120	100
Nebaliella brevicarinata	0210001101	0000000121	0010010000	12112?11?0	100
Nebaliella caboti	0210001101	000000011?	?010011000	12112?1?20	100
Nebaliella declivatas	0210001101	0000000112	0010011000	1211211010	100
Dahlella caldariensis	0012101001	00?100?1?2	2000000101	00112?1121	011
Nebalia antarctica	0102010100	0101000112	2000000001	001121??21	011
Nebalia bipes bipes	0102000100	0101000122	2000000001	001122??21	011
Nebalia borealis	0102000100	0101000121	1000000001	001121??21	011
Nebalia brucei	0102000100	0101000110	2000000001	0011211021	011
Nebalia cannoni	0102010100	0101000102	2000000001	001122??21	011
Nebalia capensis	0102000100	0101000111	2000000001	0011221021	011
Nebalia clausi	0102000100	0101000121	2000000001	001122??21	011
Nebalia daytoni	0101000110	0121000011	2000000001	0011211?21	011
Nebalia falklandensis	0102010100	0101000110	2000000001	001122??21	011
Nebalia herbstii	0102000100	0101000122	2000000001	001122??21	011
Nebalia hessleri	0102000100	0101000121	2000000001	0011211121	011
Nebalia lagartensis	010?000100	0101000 1?0	1000000001	001121??21	011
Nebalia longicornis	0?02010100	0101000112	1000000001	001122??21	011
Nebalia marerubri	0102000100	0101000112	1000000001	0011211121	011
Nebalia patagonica	0?02010100	0101000112	2000000001	001122??21	011
Nebalia strausi	0102000100	0101000?2?	0000000001	001121??21	011
Nebalia sp. A	0101000110	0121000012	1000000001	0011211001	011
Nebalia sp. B	1102000000	0121000112	2000000001	0011211001	011
Nebalia sp. C	0102010100	0101000122	2000000001	0011211121	011
Sarsinebalia typhlops	1102000001	0101000?12	0000000101	00??22??01	011

sufficient characters relevant to generic differentiation in Leptostraca do not exist. Similarly, resorting to the fossil orders of Phyllocarida (e.g. Archaeostraca) provide few characters of value.

Olesen's (1999) phylogenetic anaylsis of seven leptostracan genera resulted in two hypotheses. In one, he used Anostraca (Branchiopoda) and Mysidacea (Malacostraca) as outgroups without justifying these choices. In the other, he used Mysidacea alone. Specific outgroups such as these pose real problems. The presumed shared similarities may not be homologous so it is doubtful whether the same characters are being scored for the in- and outgroups. Besides, they often do not possess relevant characters.

Olesen's (1999) use of Mysidacea as an outgroup was based on Cannon's (1927) view that the thoracopods of *Paranebalia* link malacostracans, such as mysids, with *Nebalia*. Numerous authors have viewed phyllocarids as malacostracans (27 papers cited by Spears and Abele, 1999). Mysidaceans themselves are a problematic group of two distinct clades. Although mysidaceans have until recently been treated as members of Peracarida there is now increasing morphological and molecular evidence that while one clade, Lophogastrida, is a member of Peracarida the other, Mysida, is a member of Eucarida (Watling, 1999; Jarman et al., 2000). Olesen did not differentiate the two.

Curiously, Sars (1887) suggested that body divisions, antennules, antennae, mouthparts, pleopods, caudal limbs, and development of *Nebalia* and Copepoda, especially Harpacticoida Sars, 1903 were homologues. Sars's similarities could be further evidence of the high level of convergence within the Crustacea or symplesiomorphies shared by these and possibly other groups.

Faced with the conditions that the closest relatives of leptostracans do not have similar morphologies, and that similarities between leptostracans and other less related taxa are most likely due to convergences, we were disinclined to chose any one or set of outgroups. The best alternative for polarising character states seemed to be to use a hypothetical ancestor. We used general principles of crustacean evolution as evidenced by a wide variety of taxa and were able to score 31 of 43 characters for the hypothetical ancestor. These included characters where the presence of a structure is confined to some leptostracans, characters involving fusion or loss of articles from a multiarticulate state, characters involving loss of teeth or setae which are generally numerous in the other Crustacea, and characters involving reduction in size or complexity.

Character descriptions

The 43 characters are examined in turn with its reasoned state of the hypothetical ancestor. All characters are unordered and of equal weight (Tables 1, 2). Character descriptions and figures are for females except where male characters are individually specified.

Although Dahl (1985) defined many new characters for *Nebalia*, most of these have not been used. Dahl's (1985) ratio characters (e.g. length/width characters) could only be scored from literature descriptions, generally of a single specimen. The ratios varied continously across all taxa and it was not possible to assign taxa to a few distinct classes.

Setal characters. Dahl (1985) stated that characters related to numbers of spines (= robust setae) and setae are not of primary importance as they are related to growth of the individual. He used rearing experiments to show growth related variation in the moults of six females and five males of *Nebalia pugettensis* (Clark, 1932). While his experiments show a correlation between the carapace length and the number of spines and setae on four appendages (antenna 1, pleopod 1 exopod, pleopod 5 and furca) (Dahl, 1985: Table 1), we believe that for phylogenetic purposes setae may be useful if comparisons were made between ovigerous or brooding females but none is used here.

Rostrum. Dahl (1985) recognised the presence or absence of a ventral subterminal rostral spine (character 1) as taxonomically informative. We hypothesise the possesion of a rostral spine is apomorphic as it appears to be a character unique to the Leptostraca. All species of *Paranebalia* and *Levinebalia* and *Sarsinebalia typhlops* (Dahl, 1985) and *Nebalia* sp. B possess a rostral spine (state 1: Figs 1b, d).

The presence of a keel on the ventral face of the rostrum (the rostrum minus the keel is sometimes referred to as the rostral flange; Fig. 1c arrow pointing to flange) is a character unique to leptostracans (character 2) and so is considered apomorphic. The keel is absent in *Nebaliopsis, Paranebalia, Levinebalia, Speonebalia* and *Dahlella* (state 0). Dahl (1985, 1990) did not draw the rostral keel for any of the species he described but as all other species of *Nebalia* have a keel, we assume this was an oversight. We have scored all *Nebalia* as having a keel shorter than the rostrum (state 1: Figs 1a, 1d). The possession of a keel longer than the rostrum is an autapomorphy of the genus *Nebaliella* (state 2: Figs 1c, e).

Eye. Speonebalia, Nebaliella and *Dahlella* have eyes longer than the rostrum (character 3, state 1: Fig. 1e).

The length of the supraocular scale was considered diagnostic by Dahl (1985) (character 4). *Nebaliopsis, Paranebalia, Levinebalia, Speonebalia* and *Nebaliella* all lack supraocular scales (state 0). *Dahlella* and almost all species of

Nebalia have a supraocular scale shorter than the eye (state 2: Figs 1f, i). *Nebalia daytoni* Vetter, 1996 and *Nebalia* sp. A have supraocular scales longer than the eye (state 1: Fig. 1n). Following the ontogenetic precedence criterion, the absence of the supraocular scale in juveniles of *Dahlella caldariensis* Hessler, 1984 suggests its presence is apomorphic.

Small teeth or denticles over the surface of the eye appear in *Paranebalia* (Fig. 1h) and *Dahlella* (character 5, state 1: Fig. 1m). Hessler (1984) suggested the teeth may be used by *Dahlella caldariensis* to scrape for food such as bacterial encrustations. The teeth on the surface of the eye may not be homologous in *Dahlella* and *Paranebalia*. As the teeth do not appear in the juveniles of *Dahlella* they are thought to be apomorphic.

The possession of a papilla or dorsal outgrowth on the eyestalk is a feature found in approximately one-third of species of *Nebalia* (character 6, state 1: Figs 1f, 1j) and is thought to be apomorphic.

Dahl (1985) recognised eye shape as a valuable diagnostic feature (characters 7, 8 and 9). The eyes of *Nebaliella* and *Dahlella* have an extremely curved ventral margin (character 7, state 1: Figs 1k, 1m). The eye of the first instar larva of *Dahlella* is almost square, thus the ontogenetic evidence suggests the elongate, curved eye of *Dahlella* and *Nebaliella* is the derived state.

The eyes of *Sarsinebalia typhlops*, *Nebalia* sp. B, *Dahlella* and *Nebaliopsis* are not dorsally convex like those of all other Leptostraca (character 8, state 0). The eyes of *Sarsinebalia typhlops* are almost square (Fig. 1i) (but have also been described as almost circular [Dahl, 1985]), and the eyes of *Nebalia* sp. B are triangular (Fig. 1g). The eyes of *Dahlella* are dorsally angular (Fig. 1m), while the eyes of *Nebaliopsis* are square to rectangular. The eyes of *Nebaliopsis* are very similar in shape to that of the first instar larva of *Dahlella*. *Nebalia daytoni* and *Nebalia* sp. A have an unusual bilobed eye (character 9, state 1: Fig. 1n) shared with no other species.

The presence of ommatidia in the eye is common to most species of Leptostraca (character 10, state 0). *Speonebalia*, *Nebaliella*, *Dahlella* and *Sarsinebalia typhlops* all lack ommatidia (state 1). Embryos of the genus *Nebalia* possess dark eye pigment (Sars, 1896; Manton, 1934) thus, following the ontogenetic precedence criterion, the presence of ommatidia is considered primitive.

Antenna 1. Modlin (1991) referred to the anterodenticulate fourth article of antenna 1 as a lateral flange but our observations reveal the flange lies mesially (character 11, state 1: Fig. 1q). This mesiodistal flange is found in *Levinebalia*, *Paranebalia* and *Nebaliopsis* (state 1). The flange is lacking in all other Leptostraca and assumed so for the hypothetical ancestor (state 0: Fig. 1p).

The first four articles are referred to as the peduncle. The last peduncle article (article 4) bears the scale and flagellum The arrangement of setae on the fourth peduncle article is usually linear with 1–4 simple robust setae in the anterodistal corner and a variable number of thin plumose setae (Fig. 1p). In some species and the hypothetical ancestor robust setae are absent (character 12, state 0: Fig. 1q). Rearing experiments (Dahl, 1985) showed that change in setal formula is growth related but the presence or absence of robust setae, not their number, is a valid character. Only *Nebalia* has robust setae on antenna 1 (state 1).

Mature males of *Levinebalia* and *Paranebalia* possess numerous aesthetases on a swollen flagellum of the first antenna (character 13, state 1: Fig. 2d), this chemoreceptive callynophore is found on many eucarid and peracarid Crustacea (Lowry, 1986). Immature males of *Levinebalia* and *Paranebalia* have a swollen flagellum with few aesthetases (Fig. 2c). Abundant aesthetases on a non-swollen flagellum (state 2: Fig. 2f) occur in *Nebalia daytoni*, *Nebalia* spp. A and B. This is similar to that found in *Nebalia pugettensis* (originally described as *Epinebalia pugettensis*) but this species was excluded from the analysis.

Because the callynophore is so widespread in Crustacea we were unable to score the hypothetical ancestor; the structure may be independently derived in many taxa.

Antenna 2. The peduncle of antenna 2 bears the flagellum. The peduncle has a maximum of four articles but fusion of articles does occur. The fusion of articles 3 and 4 peduncle is an apomorphic state found in *Nebalia*, *Paranebalia*, *Levinebalia* and *Dahlella* (character 14, state 1: Fig. 2b). In *Nebaliopsis*, *Nebaliella* and *Speonebalia* the articles are not fused (state 0: Fig. 2a).

Fused articles 3 and 4 of antenna 2 peduncle of *Paranebalia* possess protuberances or elongate outgrowths (usually one or two) on the anterior surface (character 15, state 1: Figs 1r, 5a and 5b; arrows point to protuberances).

Minute denticles or cuticular outgrowths appear over the surface of fused peduncle articles 3 and 4 and the flagellum in *Levinebalia* (character 16, state 1: Fig. 5a). The flagellum of male *Nebalia* and *Nebaliella* is greatly elongated, often extending past the caudal furca (character 17, state 0). The flagellum length of male *Speonebalia, Dahlella caldariensis* and *Nebaliopsis* is unknown as mature males have not been identified. The length of the flagellum does not differ between males and females in species of *Paranebalia* and *Levinebalia*. The presence of a dorsal spine on article 2 (character 18: Fig. 2b) is recorded for most species of *Nebalia* and *Nebaliella*.The hypothetical ancestor is assumed to have a simple peduncle of 4 articles, without cuticular outgrowths or a dorsal spine.

Mandible. The number of setae on article 2 of the mandibular palp (character 19: Fig. 2g) can be diagnostic (Hessler, 1984). However, Dahl (1985) suggested that there is a growth-related increase in the number of spines (robust setae) and setae throughout the Leptostraea. Therefore, although setal characters may be useful for supplementing other morphological features, leptostracan "chaetotaxonomy" can never be of primary importance. *Levinebalia*, most species of *Paranebalia, Speonebalia, Dahlella, Nebaliella brevicarinata* Kikuchi and Gamô, 1992 and half of the species of *Nebalia* have one seta on article 2 of the mandible palp. Half of the species of *Nebalia* have two setae as does *Nebaliella caboti* Clark, 1932 and *N. declivatas* Walker-Smith, 1998. *Paranebalia longipes* (Willemöes-Suhm, 1875) has more than two setae, as does *Nebaliella antarctica* Thiele, 1904 and *Nebalia cannoni* Dahl, 1990.

The length of article 2 of mandibular palp relative to article 3 was recognised by Dahl (1985) as a diagnositic character (character 20). The plesiomorphic state is unknown.

The shape of article 3 of the mandibular palp was considered by Dahl (1985) to be a diagnostic feature of leptostracans (character 21: Fig. 2g). This is a variable character within *Nebalia*, which displays all three states. *Nebaliopsis, Levinebalia, Paranebalia, Speonebalia* and most species of *Nebaliella* have palps that taper distally (state 0: e.g., Fig. 2g). The palp of *Nebaliella antarctica* and *Dahlella* is expanded distally (state 2).

The mandible incisor of *Nebaliella* has two teeth (character 22, state 0: Fig. 2i). Dahl (1985, 1990) did not draw or mention the mandible incisor in his descriptions of *Nebalia*. However, as all other described species and the undescribed species of *Nebalia* from Australia have two teeth, We have scored all species described by Dahl as having two teeth (state 0: Fig. 2h). *Levinebalia, Paranebalia* and *Dahlella* have one tooth (state 1: Fig. 2c). The incisor is absent in *Speonebalia* and *Nebaliopsis* (state 2).

The molar of *Nebaliella* has an accessory tooth or spine (character 23, state 1: Fig. 2i; see arrow). No other leptostraean has this character state. The molar of *Paranebalia* alone has a large accessory process (character 24, state 1: Fig. 2e; see arrow). The presence of a setal brush on the molar process (character 25, state 1: Fig. 2c) is recorded only for *Paranebalia*. The hypothetical ancestor is assumed to have a setose mandibular palp, well-developed molar and toothed incisor.

Maxilla 1. In all species of Nebaliidae, including *Paranebalia* and *Levinebalia*, the palp of maxilla 1 is long and well-developed as in the hypothetical ancestor. In Nebaliopsididae it is reduced to a small stub.

There are four different types of second endites found on maxilla 1 (character 26); complex (state 0: Fig. 3a) found in *Nebalia* and *Dahlella*; bilobed (state 1: Figs 3b, d) in *Nebaliella*; elongate (state 2: Fig. 3g) in *Paranebalia* and *Levinebalia*; simple (state 3: Fig. 3c) only in *Speonebalia*. The second endite is reduced in *Nebaliopsis* (state 4). The state in the hypothetical ancestor could not be determined.

Maxilla 2. The maxilla 2 endopod is uniarticulate (character 27; state 1) in *Nebaliopsis, Nebaliella* (except *N. brevicarinata*), *Paranebalia* sp. A, *Levinebalia* and *Speonebalia*. This is thought to represent the derived state.

The length of the exopod of maxilla 2 relative to the endopod is informative (character 28). For *Speonebalia, Dahlella* and *Sarsinebalia typhlops* the maxilla 2 exopod is less than half the length of the endopod (state 1). *Nebaliopsis* does not have an exopod (state 2). All other genera have an exopod more than half the length of the endopod (state 0).

Thoracopods. The length of the thoracopods is the most obvious feature diagnosing genera of leptostracans (character 29). All genera except *Paranebalia* and *Levinebalia* have foliaceous thoracopods that do not extend well beyond the ventral margin of the carapace (state 0: Fig. 4a). The thoracopods of *Paranebalia* and *Levinebalia* extend well beyond the ventral margin of the carapace (state 1: Fig. 1l).

Thoracopod exopods are densely setose (character 30) in *Paranebalia, Levinebalia* and *Nebaliella* (state 0: Figs 4b, 4c). The exopods have few setae in *Nebalia* (state 1: Fig. 4d), *Dahlella* and *Speonebalia* and no setae in *Nebaliopsis* (state 2: Fig. 4e).

Thoracopod exopods of *Nebaliella* have a proximal lobe (character 31, state 1: Fig. 4e) not seen in other Leptostraca.

All genera except *Nebaliella* possess thoracopodal epipods (character 32, state 2) whose length relative to that of the exopod is informative. *Paranebalia* and *Levinebalia* have relatively small epipods (state 1: Fig. 4b) compared to those of *Nebaliopsis, Speonebalia, Dahlella* and *Nebalia* which are longer than the thoracopodal exopod (state 0: e.g. Fig. 4d).

Pleonites. All species of *Nebaliella, Speonebalia, Dahlella* and *Nebalia* have a crenate posterior margin on pleonites 4 and 5 (characters 33 and 34: Fig. 4a). In his descriptions of *Nebalia* species Dahl (1985, 1990) did not mention the form of pleonites 4 and 5 but as these pleonites are crenate in all other *Nebalia* species we have assumed this is also the case in Dahl's species. The posterior margins of all pleonites of *Nebaliopsis* are smooth.

Pleonites 6 and 7 of *Paranebalia* are crenate only along the dorsal margin (character 35, state 1: Fig 1l). The pleonite margins of *Nebaliopsis* and *Levinebalia* are smooth (state 0). Pleonites 6 and 7 of *Nebaliella, Speonenbalia, Dahlella* and *Nebalia* are crenate along the entire margin (state 2).

The shape of pleonite crenations is a useful species-level character (character 36). Species of *Nebalia* may have either crenations that are pointed or blunt. *Nebalia* sp. A has both blunt and pointed crenations along the same pleonite margin (Fig. 3f), but as this is an autapomorphy for the purpose of the analysis it has been scored as having only pointed crenations.

For most Leptostraca pleonites 6 and 7 are much longer than pleonite 5 (character 37, state 1). However for *Levinebalia, Speonebalia* and *Nebaliopsis* pleonite 5 is approximately the same length as pleonites 6 and 7 (state 0).

Pleopods. The posterior margin of pleopods 1–4 of *Paranebalia, Speonebalia* and some species of *Nebalia* are crenate (character 38, state 1: Fig. 3i).

The comb-row or "spine-row", considered by Dahl (1985: pp. 142, 163) to be a generic character, consists of a row of short, pinnate setae along the exterior margin of the exopod of pleopod 1 (Figs 4k, 6a and 6b). As Dahl (1985) created a new genus for *Sarsinebalia typhlops* which does not possess a comb-row on its first pleopod. The length of the comb-row relative to the exopod is diagnostic (character 39). For all species of *Nebalia* except *Nebalia* spp. A and B the comb-row is greater than half the length of the exopod (state 2). *Nebalia* spp. A and B do not possess a comb-row (state 0: Fig. 4i). The comb-row of *Levinebalia* Walker-Smith, 2000 and *Nebaliella declivatas* is less than half the length of the exopod (state 1: Fig. 4j).

All genera except *Nebaliella* and *Nebaliopsis* have pairs of smooth setae along the exterior margin of the exopod of pleopods 2–4 (character 40, state 0 (not in pairs): Fig. 4g. state 1: Figs 3i, 4h).

For all genera except *Nebaliella* and *Nebaliopsis* the ramus of pleopod 5 is longer than the ramus of pleopod 6, measured along the midline (character 41, state 0). We have scored pleopod 5 longer than 6 as the plesiomorphic state

Pleopod 6 may be uni- or biarticulate, a character first used by Olesen (1999). *Nebaliopsis, Speonebalia* and *Nebaliella* all have a biarticulate pleopod 6 (character 42, state 0: Fig. 4l). All other Leptostraca have a uniarticulate pleopod 6 (state 1). The biarticulate condition is thought to be plesiomorphic.

Carapace. The posterodorsal margin of the carapace of *Nebaliella* has small denticles (character 43, state 0: Fig. 3e). This character state is not seen in other Leptostraca and the plesiomorphic condition is unknown.

Results

Cladograms

The phylogenetic program PAUP* 4.0 revealed 1527 equally parsimonious trees of 114 steps. Tree 711 and tree 340 were the two most distant parsimony trees (found using the FILTER command). Their statistics are: consistency index (CI) = 0.52; homoplasy index (HI) = 0.48; retention index (RI) = 0.79; rescaled consistency index (RC) = 0.41.

Bremer support values were calculated for tree 711 (Fig. 6) and tree 340. Branch lengths for tree 711 were calculated in PAUP* 4.0 and are presented diagramatically (Fig. 7). Characters with CI=1 are also plotted on this tree.

A 50% majority-rule with bootstrap values and the percentage of parsimony trees retaining nominal clades is also presented (Fig. 8).

Characters defining the clades of parsimony tree 711.

As trees 711 and 340 retain the same character state changes at the major (generic level) nodes, only tree 711 is discussed in detail (Figs. 6 and 7) with character state changes (Table 3).

Clade 63 contains all Recent Leptostraca and is supported by three synapomorphies from the characters used (plus those characters generally stated to define the taxon).

Table 3. Character transformations at all nodes in tree 711 (one of 1527 parsimonious trees). Character numbers follow each clade labelled in Fig. 6. Character numbers alone indicate a change from state 0 to state 1, – indicates a reversal from state 1 to 0, and superscripts indicate a change from one state (default 0) to another. Characters in bold have CI=1.

Clade number or taxon	Characters changing
Clade 63	11, 22^{2}, 27
Nebaliopsis typica	**26**^{4}, 28^{2}, 302, **41**
clade 62	8, 19^{2}, 36, 38, 40
clade 37 (Paranebaliidae)	1, 13, 14, **15**, **17**, $22^{2>1}$, **26**^{2}, **29**, **32**, 42
clade 34 (*Levinebalia*)	**16**, –36, –38
Levinebalia maria	20, 39
clade 36 (*Paranebalia*)	5, **24**, **25**, **35**, 37, 39^{2}
clade 35	–27
Paranebalia longipes	$19^{2>0}$
Paranebalia sp. A	20
clade 61 (Nebaliidae)	3, 10, –11, 20^{2}, 30, **33**, **34**, **35**^{2}, –43
Speonebalia cannoni	**26**^{3}, 28
clade 60	7, 18, 22, 37, 39^{2}
clade 40 (*Nebaliella*)	**2**^{2}, **23**, **26**, 30, **31**, **32**^{2}, –40, 41
clade 38	$20^{2>1}$
Nebaliella antarctica	$19^{2>0}$, 21^{2}
Nebaliella brevicarinata	–27
clade 39	$19^{2>1}$, –38
Nebaliella declivatas	$39^{2>1}$
clade 59	4^{2}, 14, 21^{2}, –27, 42, 43
Dahlella calderiensis	5, –8, 28
clade 58 (*Nebalia*)	**2**, –3, –7, –10, **12**
clade 51	$19^{2>1}$
clade 43	6
Nebalia sp. C	$19^{1>2}$
clade 41	$36^{1>2}$
Nebalia cannoni	–19
Nebalia longicornis	$21^{2>1}$
Clade 49	–38
clade 45	$20^{2>0}$
clade 44	$36^{1>2}$
Nebalia capensis	20
Nebalia falklandensis	6
clade 48	13^{2}, $39^{2>0}$
clade 46	$4^{2>1}$, 9, –18
Nebalia daytoni	$20^{2>1}$, 39^{2}
Nebalia sp. A	$21^{2>1}$
clade 47	1, –8
Sarsinebalia typhlops	10, $13^{2>0}$, $21^{2>0}$, 28, $36^{1>2}$
Nebalia marerubri	$21^{2>1}$
clade 57	$36^{1>2}$
clade 56	$20^{2>1}$
clade 55	$36^{2>1}$
clade 54	$21^{2>0}$
clade 53	21
Nebalia lagartensis	–20

Nebaliopsis typica Sars, 1887 (Nebaliopsididae) is defined by four apomorphies (from the characters used): maxilla 1 second endite reduced; maxilla 2 exopod absent; thoracopod exopod with no setae; pleopod 6 shorter than pleopod 5. At least 14 more character states define *Nebaliopsis typiea* but these unique states are uninformative and had been excluded a priori: molar process reduced; maxilla 1 palp reduced to a small stub (but may terminate in long seta); maxilla 1, second endite reduced; maxilla 2 with endites 2–4 reduced in size and setation; maxilla 2 nearly as large as thoracopod 1; thoracopod 1 differing greatly from thoracopods 2–7, somewhat maxillipediform; thoracopod endopod not articulate; thoracopods well spaced; pleopods 2–4 exopod paddle-like, outer margin strongly curved with numerous small spinules; carapace not emarginate; carapace with network pattern of sculpturing; body cuticle and carapace thin, membranous; caudal furca leaf-like, broadest midway; entire length of mature female greater than 20 mm.

Clade 62 contains all Leptostraca except Nebaliopsididae. This clade occurs in all shortest trees and has a Bremer support value of 2 and 72% bootstrap support. Five synapomorphies define this clade although none has CI=1.

Clade 37, *Paranebalia* plus *Levinebalia*, occurs in all trees and has a Bremer support value of 3 and 85% bootstrap support. The clade is defined by ten synapomorphies, five with CI=1: antenna 2 articles 3 and 4 with two large cuticular outgrowths; antenna 2 of male not greatly elongate, only half length of specimen; maxilla 1 second endite elongate; thoracopods long, extending well beyond the ventral margin of the carapace; thoracopod 2–5 with epipod shorter than exopod. This clade is also defined by the character state — males with swollen callynophore — but as this character is multistate it has CI=0.67.

Clade 34 (*Levinebalia*), evident in 100% of trees, has Bremer support of 1 and 77% bootstrap support. It is defined by three synapomorphies: antenna 2 peduncle and flagellum surface with minute denticles or cuticular outgrowths (CI=1); pleonite margins smooth (reversal); pleopods 1–4 peduncles with margins smooth (reversal).

Clade 36 (*Paranebalia*), evident in 100% of shortest trees, has Bremer support of 5 and and 99% bootstrap support. Six synapomorphies including three with CI=1 define this clade: molar with large accessory process; molar process with setal brush; and pleonites 6 and 7 with denticles only over dorsal part of margin.

Clade 61 occurs in all trees and has Bremer support of 2 and 67% bootstrap support. This clade, all species of *Speonebalia, Nebaliella, Dahlella* and *Nebalia*, is defined by nine synapomorphies including three with CI=1. Some of the characters defining the clade are: antenna 1 without anterodenticulate fourth article (CI=0.5); thoracopod exopod not heavily setose (CI=0.67) pleonite 4 margin denticulate (CI=1); pleonite 5 margin denticulate (CI=1); with crenations over entire pleonite margin (CI=1).

Speonebalia cannoni Bowman, Yager and Iliffe, 1985 is defined by two apomorphies, one with CI=1; maxilla 1 second endite simple. *Speonebalia cannoni* also has an autapomorphy that was excluded from the analysis: maxilla 2 with marginal organelles.

Clade 60 (*Nebaliella, Dahlella* and *Nebalia*) occurs in all trees and has a Bremer support value of 1 and bootstrap support <50%. It is defined by five synapomorphies. None is unique.

Clade 40 (*Nebaliella*) is supported in all trees with Bremer support value of 6 and 100% bootstrap support. It is defined by eight synapomorphies, five with CI=1: presence of a rostral keel longer than the rostral flange; molar with accessory tooth/spine; maxilla 1 second endite bilobed; thoracopod exopod with proximal lobe; and thoracopods 2–5 without epipod. Pleopod 6 longer than pleopod 5 and pleopod 6 uniarticulate are also characters linking species in this clade.

Clades 38 and 39 relating the species of *Nebaliella* occur in all shortest trees, each clade has Bremer support of 1 and clade 39 has 50% bootstrap support.

Clade 59 (*Dahlella* and *Nebalia*), occurs in all parsimony trees and has a Bremer support value of 2 and 72% bootstrap support. Six synapomorphies define this clade but the presence of a supraocular scale is the only unique character (CI=1). All species in this clade also share: antenna 2 peduncle articles 3 and 4 not fused (CI=0.5); pleopod 6 shorter than pleopod 5 (CI=0.5) and pleopod 6 biarticulate (CI=0.5)

Dahlella has three apomorphies among the characters in this matrix but none is unique.

Clade 58 (*Nebalia*) was evident in all trees with Bremer support of 1 and <50% bootstrap support. It is defined by five synapomorphies. The presence of a rostral keel shorter than the rostral flange and article 4 of antenna 1 with robust setae are characters unique to *Nebalia*. Species in this clade also have eyes shorter than the rostrum and eyes with the ventral margin not extremely curved.

Only four clades, grouping three pairs and one group of four species of *Nebalia* appear in the 50% majority-rule tree (Fig. 8). Clade 46 (*N. daytoni* and *Nebalia* sp. A) was retained in all trees and has a Bremer support of 2 and 69% bootstrap support. Clade 47 (*S. typhlops* and *Nebalia* sp. B), retained in all trees, has a Bremer support value of 1 and <50% bootstrap support. Clade 52 (*N. bipes* and *N. herbstii*) was retained in 62% of parsimony trees but has no Bremer support and <50% bootstrap support. The clade linking *Nebalia cannoni*, Dahl, 1990, *N. falklandensis*, Dahl, 1990, *N. longicornis* and *N. patagonica* Dahl, 1990 did not occur in tree 711 but occurred in 75% of all trees. It has no Bremer support and <50% bootstrap support. The relationships of the remaining species of *Nebalia* could not be resolved.

Systematics and a new classification

Four synapomorphies used in this analysis and at least 14 other character states define *Nebaliopsis typica* (Nebaliopsididae) and differentiate it from all other Leptostraca. The sister group (clade 62) is described by robust synapomorphies so there is support for the existing family Nebaliopsididae.

All shortest trees contain a clade (clade 37), *Paranebalia* plus *Levinebalia*, sister taxon of all other species. We believe that with a Bremer support value of 3, bootstrap value of 85% and five autapomorphies for this clade, a new family can be justified for the two genera.

Clade 61, apparent in all trees, contains the remaining genera of Nebaliidae (*Speonebalia, Dahlella, Nebaliella*, and *Nebalia*). This clade is supported by nine synapomorphies, three autapomorphic for the clade (see above) and has Bremer support of 2 and 67% bootstrap support. This clade defines the restricted family, Nebaliidae.

The monophyly of *Speonebalia, Nebaliella, Dahlella*, and *Nebalia* is supported by the analysis. *Speonebalia* and *Dahlella* are monotypic and their status as genera is confirmed by the synapomorphies of their sister taxa.

Two autapomorphies for clade 58 unite all species of *Nebalia* (including *Sarsinebalia typhlops*): the presence of a rostral keel shorter than the rostrum and the presence of robust setae in the fourth article of antenna 1.

We were unable to find any characters which support separate generic status for the monotypic *Sarsinebalia* and the genus must be synomised with *Nebalia* and its species, *S. typhlops* returns to its original combination.

Table 4 lists all described species with their distribution.

Comparison with Olesen's (1999) trees

Olesen (1999) presented two equally parsimonious hypotheses of the phylogeny of the genera of Leptostraca. He used 27 mostly binary characters. The four monotypic genera are clearly monophyletic and he was convinced a priori of the monophyly of *Paranebalia* and *Nebaliella*. He entertained the possibility that *Nebalia* might be paraphyletic with respect to *Sarsinebalia* or *Dahlella* (or both). Our hypothesis differs from his. Olesen's first tree was rooted against two outgroups, Mysidacea and Anostraca, and placed *Nebaliopsis* as a sister taxon to all other Leptostraca, as in our tree. However, the position of *Nebaliella* and *Paranebalia* was directly transposed compared to our tree and *Sarsinebalia* was placed as a sister to *Dahlella* and *Nebalia*. This 3-taxon clade occurred in both of Olesen's trees (the second tree having only Mysidacea as an outgroup) and he suggested this indicated strong support. However, two of the characters linking *Dahlella* and *Nebalia* in Olesen's tree actually vary within *Nebalia* and thus are not useful (character 9: antenna 2, spine on segment 2; character 14: mandible, shape of segment 3). The third character, character 2 (the absence of a rostral spine) occurs throughout the Leptostraca and was a reversal. Our tree treats *Dahlella* as a sister taxon to *Nebalia* and synonomises *Sarsinebalia* with *Nebalia*.

Olesen's second tree (with only Mysidacea as an outgroup) suggested *Paranebalia* at the base of the Leptostraca, with the remaining taxa split into two clades. *Speonebalia* sits as a sister taxon to *Nebaliella* and *Nebaliopsis* supported by a single character (25: pleopod 6 biarticulate). A single character unites *Nebaliella* and *Nebaliopsis* (character 24: pleopod 6 longer than pleopod 5). These characters are both useful characters but, in our tree appear to have evolved twice. The second clade in Olesen's tree was the *Sarsinebalia-Dahlella-Nebalia* clade, supported by four characters, the three mentioned above and character 10 (antenna 2 with three articles), which occurred twice in this tree but only once in Olesen's other tree.

Olesen's (1999) trees lead him to question the family status of Nebaliopsididae and the monophyly of *Nebalia*. Our tree indicates the validity of the Nebaliopsididae, and more significantly of Nebaliidae and a third family. Our tree suggestes *Nebalia* is monophyletic, *Dahlella* is a separate genus and *Sarsinebalia* is a synonym of *Nebalia*.

Table 4. Taxonomic list of all families, genera and species of Recent Leptostraca with reported distributions. * indicates species omitted from phylogenetic analysis.

Order Leptostraca Claus, 1880

NEBALIOPSIDIDAE Hessler, 1984

Nebaliopsis Sars, 1887

N. typica Sars, 1887. West and south-east coast of South America, near Falkland Is, off coast of Ghana, Ivory Coast, south-west Indian Ocean, South Pacific, Scotia Sea

PARANEBALIIDAE fam. nov.

Paranebalia Claus, 1880

P. belizensis Modlin, 1991. Belize
P. longipes (Willemöes-Suhm, 1875). Bermuda, Virgin Is, southern Florida (USA), Japan, Gulf of Siam, Torres Strait (Australia)
P. sp. A. South Australia (Australia)

Levinebalia Walker-Smith, 2000

L. fortunata (Wakabara, 1976). Otago Peninsula (New Zealand)
L. maria Walker-Smith, 2000. Tasman Sea, off E coast of Tasmania (Australia)

NEBALIIDAE Samouelle, 1819

Nebalia Leach, 1814

N. antarctica Dahl, 1990. Wilhelm II Land, Adelie Land (Antarctica)
**N. bipes abyssicola* Fage, 1929. Monaco
N. bipes bipes (Fabricius, 1780). Greenland, Arctic North America, Svalbard to western Norway
**N. bipes valida* Thiele, 1904. Pribilof Is (Bering Sea)
N. borealis Dahl, 1985. Norway, Sweden, British Isles, Shetland Is, Sleat Sound (Scotland)
N. brucei Olesen, 1999. Unguja I., Zanzibar (Tanzania)
N. cannoni Dahl, 1990. South Georgia
N. capensis Barnard, 1914. South Africa
**N. chilensis* (Claus, 1888) *nomen nudum*. Chile
N. clausi Dahl, 1985. Adriatic Sea (Italy)
**N. dahli* Kazmi and Tirmizi, 1989. Karachi (Pakistan)
N. daytoni Vetter, 1996. San Diego (southern California, USA)
N. falklandensis Dahl, 1990. Falkland Is
**N. gerkenae* Haney and Martin, 2000. Monterey Bay, California (USA)
N. herbstii Leach, 1814. Shetland Is, western Bristish Isles, western France to Spanish border
N. hessleri Martin, Vetter and Cash-Clark, 1996. Southern California (USA)
**N. ilheoensis* Kensley, 1976. South-western Africa
**N. japanensis* (Claus, 1888). Japan
**N. lagartensis* Escobar-Briones, 1995. Rìa Largartos, Yucatán Peninsula (Mexico)
N. longicornis longicornis Thomson, 1879. South Island (New Zealand), New Britain (Papua New Guinea), South Africa, Lifou (New Caledonia), Blanche Bay, Sandal Bay
**N. longicornis soror* Thiele, 1904. Caribbean Sea, Cuba
N. marerubri Wägele, 1983. Red Sea
N. patagonica Dahl, 1990. Magellan region
**N. pugettensis* (Clark, 1932). Friday Harbour (Washington, USA)
N. strausi Risso, 1826. Channel Is, Guernsey, France, Monaco, Italy including Sicily
N. typhlops Sars, 1870. Red Sea, Lofoten Is (Norway), Messina, Bay of Naples (Italy), North America from Davis Strait to New Jersey, Australia
N. sp. A. Eastern Bass Strait (Australia)
N. sp. B. Tasmania and eastern Bass Strait (Australia)
N. sp. C. southern Western Australia (Australia)

Table 4. continued

Nebaliella Thiele, 1904

N. antarctica Thiele, 1904. Kerguelen I., Akaroa Harbour (New Zealand)
N. brevicarinata Kikuchi and Gamô, 1992. Princess Ragnhild Coast (Antarctica), bathyal
N. caboti Clark, 1932. Cabot Strait (between Newfoundland and Cape Breton I.), New Jersey (USA), Rockall Trough
N. declivatas Walker-Smith, 1998. E coast of Victoria, New South Wales, Tasmania (Australia)
**N. extrema* Thiele, 1905. Kaiser Wilhelm II Land, Palmer Archipelago (Antarctica)

Dahlella Hessler, 1984

D. caldariensis Hessler, 1984. Galapagos I., hydrothermal vents

Speonebalia Bowman, Yager and Iliffe, 1985
S. cannoni Bowman, Yager and Iliffe, 1985. Turks and Caicos Is, marine caves

Key to families of Leptostraca

1. Maxilla 2 with endites 2–4 reduced in size and setation (Fig. 2j); thoracopods well spaced (Fig. 3h); pleopods 2–4 exopod paddle-like, outer margin strongly curved, with numerous small spinules (Fig. 4g); caudal furca leaf-like, broadest midway (Fig. 4n)........................Nebaliopsididae (monotypic)
— Maxilla 2 with at least first 3 endites well developed (Fig. 2l); thoracopods closely space (overlapping); pleopods 2–4 exopod slightly expanded midway and/or distally or outer margin parallel (Figs 4b, d, e); caudal furca tapering evenly to tip (Fig. 4m) 2
2. Antenna 1 of mature male with swollen callynophore (Figs 2d, e); thoracopods long, extending well beyond the ventral margin of carapace (Fig. 1l); thoracopods 2–5 epipod shorter than exopod (Fig. 4b)............Paranebaliidae
— Antenna 1 of mature male not swollen or with callynophore, may have a dense field of aesthetases (Fig. 2f); thoracopods short, not extending well beyond ventral margin of carapace (Fig. 4a); thoracopod 2–5 epipod longer than exopod or absent (Figs 4d, e)..Nebaliidae

Nebaliopsididae Hessler

Nebaliopsidae Hessler, 1984: 656.

Type genus. Nebaliopsis Sars, 1887 (original designation).

Diagnosis. Rostrum without spine or keel. Eye shorter than rostrum and with visual elements; without denticles; without dorsal papilla; ventral margin not extremely convex. Supraocular scale absent. Antenna 1 with anterodenticulate fourth article; article 4 without robust setae. Antenna 2, peduncle articles 3 and 4 not fused, without cuticular outgrowths, or minute denticles; without dorsal spine. Mandible without incisor process; molar process reduced, with armature. Maxilla 1 reduced to small stub. Maxilla 2 (Fig. 2j) nearly as long as thoracopod 1; endopod reduced to small, blunt distal lobe, without organelles; exopod absent; proximal endite enormously enlarged, well-armed with marginal setae; endites 2–4 reduced in size and setation. Thoracopods not extending well beyond ventral margin of carpace; well-spaced (Fig. 3h). Thoracopod 1 differentiated from thoracopod 2–8. Thoracopod (Fig. 4c) endopod blunt, featureless lobe, not articulate; exopod strongly reduced, poorly differentiated, without setae; epipod well developed, longer than exopod, somewhat maxillipediform. Posterior margins of pleonites smooth. Pleopod 1 exopod without comb-row. Pleopods 2–4 exopods paddle-like (Fig. 4g), length less than 3 times width. Pleopod 6 longer than pleopod 5 and biarticulate. Caudal rami leaf-like, broadest midway (Fig. 4n). Thorax inflated; body cuticle and carapace thin and membranous. Carapace with a network pattern of sculpturing; not emarginate; extending furthest posteriad midsagittally, without carina on anterolateral lower corner. Entire length of mature female greater than 20 mm.

Composition. Nebaliopsis Sars, 1887.

Nebaliopsis Sars

Nebaliopsis Sars, 1887: 21.

Diagnosis. With the characters of the family.

Remarks. This family, contains only the type species *N. typica* Sars, 1887. Descriptions of *N. typica* may be found in Thiele (1905), Cannon (1931) and Linder (1943). Males have not been reported.

Paranebaliidae fam. nov.

Type genus. Paranebalia Claus, 1880.

Diagnosis. Subterminal rostral spine present (Fig. 1b); keel absent. Eye shorter than rostrum; visual elements present. Eye sometimes with denticles (Fig. 1h); without dorsal papilla; ventral margin not extremely convex. Supraocular scale absent. Antenna 1 with anterodenticulate fourth article (Fig. 1q); article 4 without robust setae; male flagellum modified, either swollen (juveniles) or transformed into callynophore (Figs 2e, 2d). Antenna 2 peduncle articles 3 and 4 fused; peduncle with 2 rounded cuticular outgrowths and sometimes with minute cuticular denticles or spines (Figs 5a, b); without dorsal spine. Antenna 2 of male not greatly elongate, only half body length. Mandible incisor with 1 tooth (Fig. 2e). Molar process well developed (Fig. 2c); with or without setal brush and sometimes with large accessory process. Maxilla 1 palp (Fig. 2g), long, well developed; second endite elongate. Maxilla 2 with at least first 3 endites well developed; much smaller than thoracopod 1; endopod without organelles; exopod greater than half length of endopod. Thoracopods long, extending beyond ventral margin of the carapace; closely spaced (Fig. 1l). Thoracopod 1 differing only slightly from thoracopods 2–7. Thoracopod exopod heavily setose and without proximal lobe (Fig. 4b). Thoracopods 2–5 epipod shorter than exopod; endopods showing a degree of articulation. Pleonites 4 and 5 with smooth margins. Pleonites 6 and 7 dorsal margins sometimes crenate (Fig. 1l). Pleopod 1 exopod comb-row present. Pleopods 2–4 exopod with parallel margins; outer margins with setae in pairs. Pleopod 5 longer than pleopod 6. Pleopod 6 uniarticulate. Caudal rami tapering evenly to tip. Thorax not inflated; body cuticle and carapace firm. Carapace not sculptured; emarginate; without carina on anterolateral lower corner. Entire length of female less than 20 mm.

Composition. Paranebalia Claus, 1880; *Levinebalia* Walker-Smith, 2000.

Remarks. Six unique character states link the genera of Paranebaliidae: antenna 2, articles 3 and 4 with two large cuticular outgrowths; male antenna 1 flagellum with swollen callynophore; males without greatly elongate antenna 2; maxilla 1 second endite elongate; slender thoracopods extending well beyond the ventral margin of the carapace; thoracopods with reduced epipods. The subterminal rostral spine is a synapomorphy of the Paranebaliidae, shared with *Sarsinebalia typhlops* and *Nebalia* sp. B. The presence of an anterodenticulate fourth article on antenna 1 is found in Paranebaliidae and Nebaliopsididae.

Key to genera of Paranebaliidae

1. Eye with denticles (Fig. 1h); mandible molar with setal brush and large accessory process (Fig. 2e); antenna 2, without minute denticles or spine over ther surface of the peduncle and flagellum (Fig. 5b); pleopods 1–4, peduncle margin crenate (Fig. 2i); pleonites 6 and 7 margin dorsally denticulate (Fig. 1l)..*Paranebalia*

— Eyes without denticles; mandible molar without setal brush and accessory process; antenna 2, with minute denticles or spines over the surface of the peduncle and flagellum (Fig. 5a); pleopods 1–4, peduncle margin smooth; pleonites 6 and 7 without clearly defined crenations.....................*Levinebalia*

Paranebalia Claus

Paranebalia Claus, 1880: 576.—Thiele, 1905: 14–19, 24–25.—Verrill, 1923: 206–207.—Wakabara, 1976: 297.

Type species. Nebalia longipes Willemöes-Suhm, 1875 (by monotypy).

Diagnosis. Eyes with denticles or cuticular outgrowths (Fig. 1h). Mandible incisor with setal brush and molar large accessory process (Fig. 2e). Antenna 2 without minute denticles or spines over the surface of the peduncle and flagellum (Fig. 5b). Pleopods 1–4, peduncle margin crenate (Fig. 2i). Pleonites 6 and 7, margin dorsally crenate (Fig. 1l).

Composition. P. longipes, P. belizensis Modlin, 1991.

Remarks. This genus is distinguished most easily from *Levinebalia* by the denticulate eyes, antenna 2 without minute denticles or spines over the surface of the peduncle and flagellum, pleopods 1–4, peduncle margin crenate and pleonite 6 and 7 dorsally crenate. Undescribed species are known from Australia.

Levinebalia Walker-Smith

Levinebalia Walker-Smith, 2000: 138.

Type species. Levinebalia maria Walker-Smith, 2000 (original designation).

Diagnosis. Eyes without denticles or cuticular outgrowths. Mandible incisor without setal brush or accessory molar process. Antenna 2 peduncle and flagella with patches of minute denticles or spines (Fig. 5a). Pleopods 1–4, peduncle margin smooth. Pleonites 6 and 7, margins with ill-defined crenations.

Composition. L. maria, L. fortunata (Wakabara, 1976).

Remarks. This genus is distinguished from *Paranebalia* by smooth eyes, minute denticles or spines over the surface of antenna 2 peduncle and flagella, smooth pleonites margins and smooth pleopod peduncles. Pleonites may sometimes have tiny, ill-defined crenations.

Nebaliidae Samouelle

Nebaliadae Samouelle, 1819: 100.
Nebaliidae Baird, 1850: 31–38.—Sars, 1887: 6–7.—Verrill, 1923: 205–206.—Hessler, 1984: 656.

Type genus. Nebalia Leach, 1814 (by monotypy).

Diagnosis. Subterminal rostral spine rarely present; keel sometimes present (Figs 1a, d). Visual elements present or absent. Supraocular scale sometimes present (Fig. 1f). Antenna 1, antero-denticulate fourth article absent; male, flagellum not swollen, but may have numerous aesthetases (Fig. 2f). Antenna 2, peduncle without cuticular outgrowths or minute denticles; articles 3 and 4 sometimes fused (Fig. 2b); male antenna 2 greatly elongate, reaching to the caudal furca (unknown for *Dahlella*). Mandible incisor, present (except for *Speonebalia*). Molar process well developed (Fig. 2h), without setal brush; without accessory process; sometimes with accessory tooth/spine (Fig. 2i). Maxilla 1 palp long, well developed. Maxilla 2 (Fig. 2l) with at least first 3 endites well developed; much smaller than thoracopod 1. Thoracopods not extending well beyond ventral margin of carapace; closely spaced (Fig. 4a). Thoracopod 1 differing only slightly from thoracopods 2–7. Thoracopods 2–5 epipod longer than exopod (Fig. 4d), or absent (Fig. 4e); endopods showing a degree of articulation. Pleonites 4–7 crenate over entire margin (Fig. 4a). Pleopod 1 exopod generally with comb-row (Fig. 4k). Pleopod 2–4 exopod with parallel margins or slightly expanded medially; outer margins with setae sometimes in pairs. Pleopod 5 longer or shorter than pleopod 6. Pleopod 6 uni- or biarticulate. Caudal rami tapering evenly to tip. Thorax not inflated, body cuticle firm. Carapace strongly emarginate midsagittally. Entire body length less than 20 mm.

Composition. Nebalia Leach, 1814; *Nebaliella* Thiele, 1904; *Dahlella* Hessler, 1984; *Speonebalia* Bowman, Yager and Iliffe, 1985.

Remarks. The diagnosis for Nebaliidae has been modified since Hessler (1984) to include *Speonebalia* and exclude *Paranebalia* and *Levinebalia* (removed to Paranebaliidae). *Sarsinebalia* has been synonymised with *Nebalia*. Authorship of the family name has been attributed to Baird (1850) by other authors but Samouelle's (1819) name has precedence.

Key to genera of Nebaliidae

1. Rostrum with keel shorter than rostral flange (Figs 1a, d) or absent; molar without accessory tooth/spine (Fig. 2h); thoracopod exopod without proximal lobe (Fig. 4d); thoracopods 2–5 epipod longer than exopod (Fig. 4d); pleopods 2–4 outer margins parallel (Figs 4h–k)..2

— Rostrum with keel longer than rostral flange (Figs 1c, e); molar with accessory tooth/spine (Fig. 2i); thoracopod exopod with proximal lobe (Fig. 4e); thoracopods 2–5 epipod absent (Fig. 4e); pleopods 2–4 outer margins slightly expanded midway and/or distally (Fig. 4f)........................*Nebaliella*

2. Rostrum without keel; eye longer than rostrum; antenna 1 article 4 without robust setae 3
— Rostrum with keel shorter than rostral flange (Figs 1a, 1d); eye shorter than rostrum; antenna 1, article 4 with robust setae (Fig. 1p) ....*Nebalia*
3. Eye without denticles, narrow, tapering distally, surface smooth, without visual elements, without supraocular scale; maxilla 1 second endite simple (Fig. 3c), maxilla 2 with marginal organelles (Fig. 2k)................*Speonebalia*
— Eye (Fig. 1m) with denticles, strongly curved (banana shape), surface with denticles, without visual elements, with supraocular scale; maxilla 1 second endite complex (Fig. 3a); maxilla 2, marginal organelles absent.......*Dahlella*

Nebalia Leach

Nebalia Leach, 1814: 99.—Thomson, 1879: 418–419.—Sars, 1896: 7–8.— Thiele, 1904: 10–12.—Thiele, 1905: 61.—Barnard, 1914: 443–446.—Fage, 1929: 41–42.—Cannon, 1931: 221–222.—Clark, 1932: 225–230.—Wägele, 1983: 127–138.— Dahl, 1985: 144–157.—Dahl, 1990: 73–91.

Epinebalia Clark, 1932: 225–230 (type species *Epinebalia pugettensis* Clark, 1932 by monotypy).

Sarsinebalia Dahl, 1985: 160–163 (type species *Nebalia typhlops* Sars, 1870 by original designation) syn. nov.

Type species. Cancer bipes Fabricius, 1780 (by monotypy).

Diagnosis. Rostrum with keel shorter than rostral flange, commonly without subterminal spine (Fig. 1a). Eyes shorter than rostrum, generally dorsally convex, sometimes with papilla (Figs 1f, j); usually with ommatidia or visual elements; surface without denticles, ventral margin not extremely convex. Supraocular scale present (Figs 1f, i). Maxilla 2 exopod at least half length of endopod (except *N. typhlops*). Antenna 1 article 4 with 1 or more robust setae (Fig. 1p). Antenna 2, article 2 with commonly with dorsal spine, articles 3 and 4 fused (Fig. 2b). Mandible palp article 3 tapering distally. with parallel margins; incisor with 2 teeth (Fig. 2h); molar process well developed without accessory tooth/spine. Maxilla 1 second endite complex (Fig. 3a). Thoracopods exopod without proximal lobe; with few setae (Fig. 4d); epipods large, well developed. Pleopod 1, exopod generally with comb-row (Fig. 4k). Pleopod 6 shorter than pleopod 5, uniarticulate.

Remarks. The two characters distinguishing *Nebalia* from other Leptostraca are the presence of a keel shorter than the rostral flange and the presence of one or more robust setae on article 4 of antenna 1. Most species of *Nebalia* are very alike and difficult to distinguish from one another. However, four species are particularly distinctive. *Nebalia daytoni* and *N.* sp. A have an unusual bilobed eye (Fig. 1n). *Nebalia* sp. A also has verticle striations on the anteroventral surface of the carapace. *Nebalia* sp. A and sp. B and *N. typhlops* all lack the comb-row on the exopod of pleopod 1. *Nebalia* sp. B has an unusual triangular shaped eye and *N. typhlops* has a rectangular to circular eye that lacks pigment. The exopod of maxilla 2 of *N. typhlops* is reduced to less than half the length of the endopod.

Sarsinebalia Dahl, 1985 is a new junior synonym.

Nebaliella Thiele

Nebaliella Thiele, 1904: 4-9, 24-25.—Cannon, 1931: 216–221.—Walker-Smith, 1998: 41.

Type species. Nebaliella antarctica Thiele, 1904 (by monotypy).

Diagnosis. Rostrum with keel longer than rostral flange, subterminal spine absent (Fig. 1c). Eyes strongly curved, extending beyond the end of the rostral keel, lacking visual elements (Fig. 1e). Antenna 1 without robust setae on article 4. Antenna 2, peduncle articles 3 and 4 not fused, without cuticular outgrowths (Fig. 2a). Mandible incisor with 2 teeth. Molar with accessory tooth/spine (Fig. 2i), without large accessory process (Fig. 2e). Maxilla 1 second endite bilobed (Figs 3b, 3d). Maxilla 2 exopod greater than half length of endopod, biarticulate, without organelles. Thoracopods without epipods (Fig. 4e). Thoracopod exopod with proximal lobe, heavily setose (Fig. 4e). Pleonites 2–7 posterior margin crenate. Pleopods 2–4 with lateral setae not in pairs (Fig. 4f). Pleopod 6 longer than pleopod 5, biarticulate. Carapace not sculptured, but may have a carina on lower anterolateral surface, posterodorsal margin with tiny denticles.

Remarks. Nebaliella occurs at depths ranging from 3 m to over 100 m. The eyes, like those of *Dahlella* and *Nebalia* typhlops, lack visual pigments; they are strongly curved and extend beyond the end of the rostrum like those of *Dahlella* but, unlike *Dahlella*, lack denticles. The rostrum is unique. Antenna 2 articles 3 and 4 are not fused in *Nebaliella*, *Nebaliopsis* and *Speonebalia*. Thoracopod epipods are absent in

Nebaliella but present in all other leptostracans. The posterior margin of the carapace of *Nebaliella* has a series of close-set spines; similar ornamentation is found in *Speonebalia*.

Dahlella Hessler

Dahlella Hessler, 1984: 656.

Type species. Dahlella caldariensis Hessler, 1984 (original designation).

Diagnosis. Rostrum without keel or subterminal spine. Eyestalks without visual elements, curved, longer than rostrum, tapering gradually to point; anterior margin denticulate (Fig. 1m); supraocular scale present. Antenna 1 without robust setae on article 4. Antenna 2, peduncle articles 3 and 4 fused. Mandible incisor with 2 teeth; molar process well developed, without accessory tooth/spine; mandible palp, distal article with 2 rows of setae. Maxilla 1 second endite complex (Fig. 3a). Maxilla 2 exopod small, less than quarter length of endopod; endopod biarticulate, without organelles. Thoracopod exopod without proximal lobe, with few setae; epipod large, approximately equal in size to exopod; proximal lobe small. Pleonites 2–7 posterior margin crenate. Pleopods 2–4 exopods with pairs of lateral setae. Pleopod 6 shorter than pleopod 5, uniarticulate. Carapace not sculptured.

Remarks. The most pronounced feature of *Dahlella* is the large, blind, toothed eye, seen only in this monotypic genus from deep-sea vent communities. Hessler (1984) suggested the eyes may be used in scraping surfaces to loosen food such as bacterial encrustations. *Dahlella* is most similar to *Nebalia*, differing in the structure of the eye, the lack of rostral keel, the small size of the exopod of maxilla 2 and the shape of the proximal lobe of the thoracic epipod. *Dahlella* shares with *Nebalia* the presence of a supraocular scale.

Speonebalia Bowman, Yager and Iliffe

Speonebalia Bowman et al., 1985: 439.

Type species. Speonebalia cannoni Bowman, Yager and Iliffe, 1985 (original designation).

Diagnosis. Rostrum without keel and subterminal spine. Eyes long and narrow, tapering distally, extending beyond tip of rostrum, without visual elements, surface smooth. Antenna 1 article 4 without robust setae. Antenna 2 peduncle articles 3 and 4 not fused, without large cuticular outgrowths or minute denticles. Mandible without incisor. Maxilla 1 second endite, simple (Fig. 3e). Maxilla 2 endopod, uniarticulate, with series of oval marginal organelles, exopod very small (Fig. 2k). Thoracopods exopod without proximal lobe, with few setae; epipods large, well developed. Pleopod peduncles with crenate lateral margin. Pleopod 1 without comb-row on lateral margin of exopod. Pleopod 2–4 exopod with parallel margins, smooth setae in pairs. Pleopod 6 shorter than pleopod 5, biarticulate. Caudal rami short and broad, tapering distally, margins densely setose, setae on medial margin very long. Carapace strongly compressed laterally, covering pleopods 1–5, more than 8 times length of rostrum, with series of close-set obtuse spines along posterior margin.

Remarks. Visual elements are also absent in *Dahlella, Nebaliella* and *Nebalia typhlops*. The mandibular incisor, absent in *Speonebalia*, is present in all other Nebaliidae. The mandibular palp is unusually large in *Speonebalia*, reaching the distal segment of the peduncle of antenna 2; article 3 is unusual in its slender tapered shape and its armature of three rows of complex setae. The shape of the maxilla 1 second endite (Fig. 3e) of *Speonebalia* is unique. *Speonebalia* is the only leptostracan with glands on maxilla 2. The exopod of maxilla 2 is reduced in *Speonebalia* and *Dahlella*. The posterior margin of the carapace of *Speonebalia* has a series of close-set obtuse spines; species of *Nebaliella* also show similar ornamentation on the carapace margin. The caudal rami of *Speonebalia* has a dense armature of long setae along the medial margin.

The genus is monotypic, its only species recorded from marine caves. It has been suggested the caudal setae prevent the animal from sinking and indicate a pelagic rather than a benthic life (Bowman et al., 1985). All other species of Leptostraca except *Nebaliopsis typica* are thought to be benthic.

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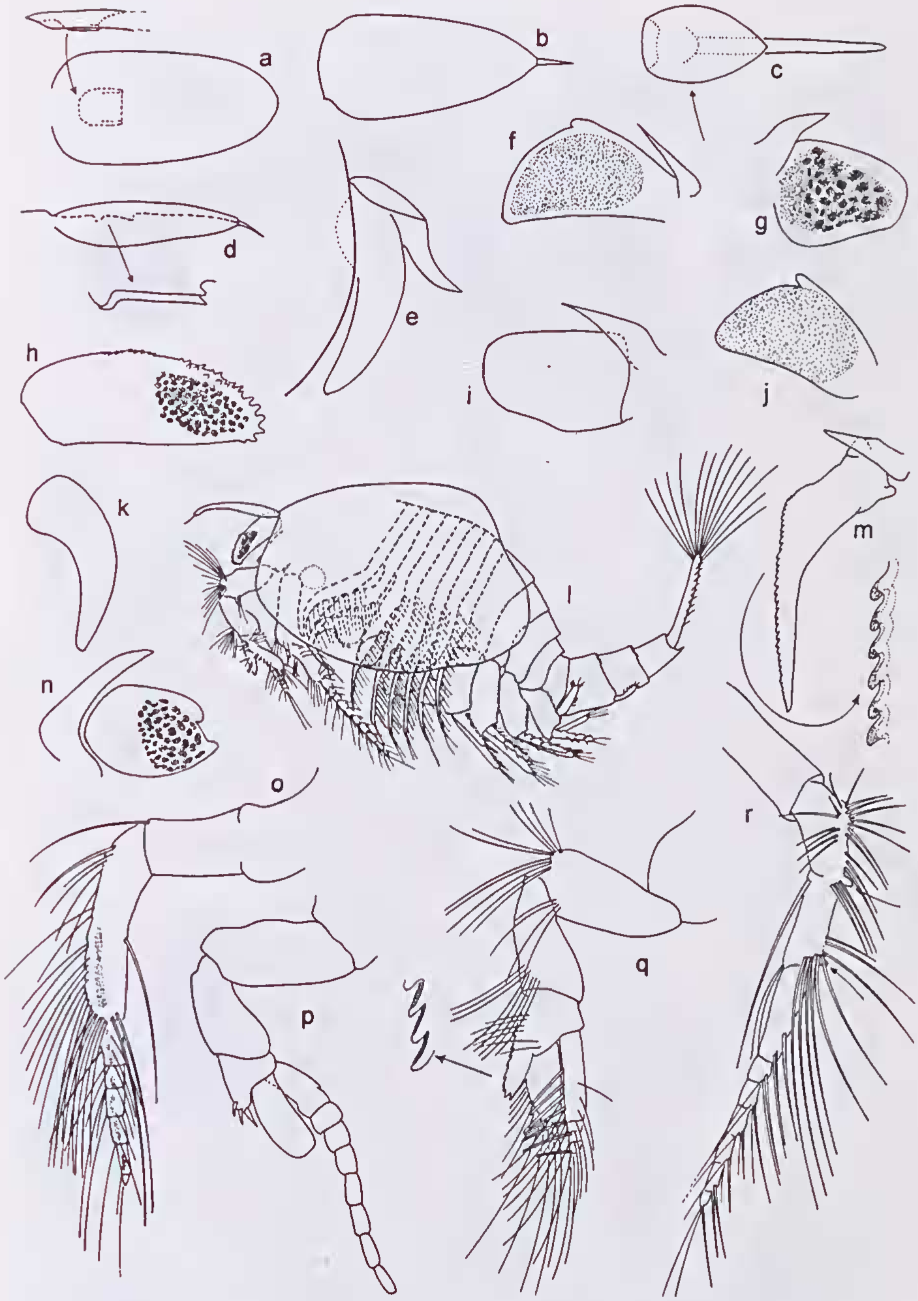

Figure 1. **a**, rostrum, dorsal and part lateral view, *Nebalia* sp. C. **b**, rostrum dorsal view, *Paranebalia* sp. A. **c**, rostrum dorsal view, *Nebaliella extrema*, after Thiele, 1905. **d**, rostrum lateral view, *Nebalia typhlops*, after Dahl, 1985. **e**, eye and rostrum, *Nebaliella extrema*, after Thiele, 1905. **f**, eye and supraocular scale, *Nebalia patagonica*, after Dahl, 1990, **g**, eye and supraocular scale, *Nebalia* sp. B. **h**, eye, *Paranebalia* sp. A. **i**, eye and suproeular scale, *Nebalia typhlops*, after Dahl, 1985. **j**, eye with dorsal papillae, *Nebalia longicornis*, after Dahl, 1990. **k**, eye, *Nebaliella declivatas*. **l**. *Paranebalia* sp. A. **m**, eye and supraocular scale, *Dahlella caldarensis*, after Hessler, 1984. **n**, eye and supraocular scale, *Nebalia* sp. A. **o**, antenna 2, *Levinebalia maria*. **p**, antenna 1, *Nebalia bipes bipes*, after Dahl, 1985. **q**, antenna 1, mesial view, *Paranebalia* sp. A. **r**, antenna 2, *Paranebalia* sp. A.

Figure 2. **a**, antenna 2, *Nebaliella declivatas*. **b**, antenna 2, *Nebalia* sp. C. **c**, immature male, *Paranebalia tippara*. **d**, mature male, *Paranebalia* sp. A. **e**, mandible incisor and molar, *Paranebalia* sp. A. **f**, antenna 2, *Nebalia* sp. A, male. **g**, mandible palp, *Levinebalia maria*. **h**, mandible incisor and molar, *Nebalia* sp. A. **i**, mandible incisor and molar, *Nebaliella declivatas*. **j**, maxilla 2, *Nebaliopsis typica* after Sars, 1887. **k**, maxilla 2, *Speonebalia cannoni*, after Bowman et al. 1985. **l**, maxilla 2, *Nebalia* sp. C.

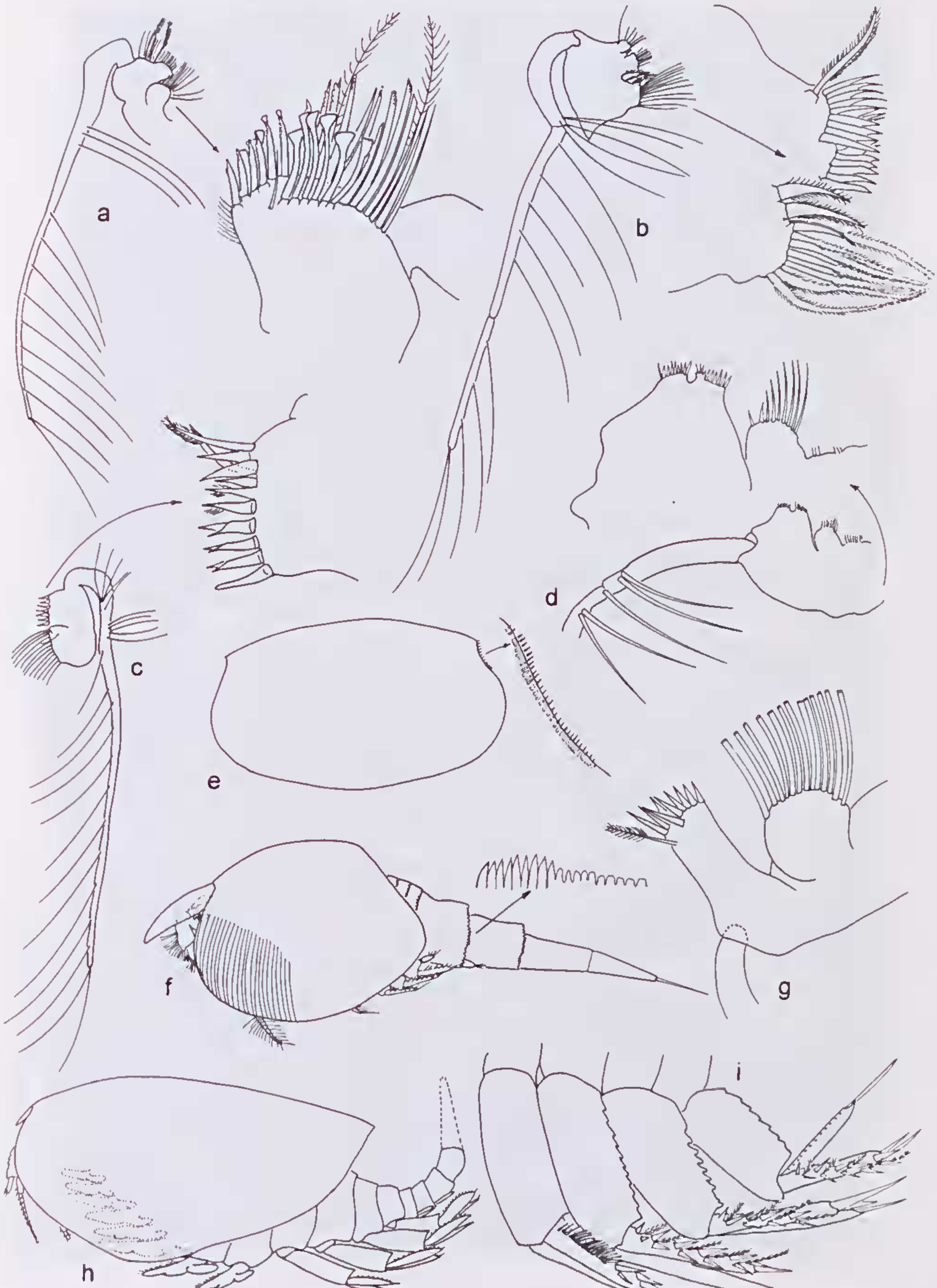

Figure 3. **a**, maxilla 1, *Nebalia* sp. C. **b**, maxilla 1, *Nebaliella declivatas*. **c**, maxilla 1, *Speonebalia cannoni*, after Bowman et al. 1985. **d**, maxilla 1, *Nebaliella declivatas*, male. **e**, carapace, *Nebaliopsis typica*, after Sars, 1887. **f**, *Nebalia* sp. A. **g**, maxilla 1 (without palp), *Paranebalia* sp. A. **h**, *Nebaliopsis typica*, after Linder (1943). **i**, pleopods 1–4, *Paranebalia* sp. A.

Figure 4. **a**, *Nebalia* sp. C. **b**, thoracopod 3, *Levinebalia maria*. **c**, thoracopod 7, *Nebaliopsis typica*, after Sars, 1887. **d**, thoracopod 3, *Nebalia* sp. C. **e**, thoracopod 3, *Nebaliella brevicarinata*, after Kikuchi and Gamô 1992. **f**, pleopod 2, *Nebaliella declivatas*. **g**, pleopod 4, *Nebaliopsis typica*, after Thiele, 1904. **h**, pleopod 2, *Nebalia* sp. C. **i**, pleopod 1, *Nebalia* sp. A. **j**, pleopod 1, *Nebaliella declivatas*. **k**, pleopod 1, *Nebalia* sp. C. **l**, end of thoracopod 3, *Nebalia pugettensis*, after Dahl, 1985. **m**, caudal furca, *Nebaliella declivatas*. **n**, caudal furca, *Nebaliopsis typica*, after Thiele, 1904.

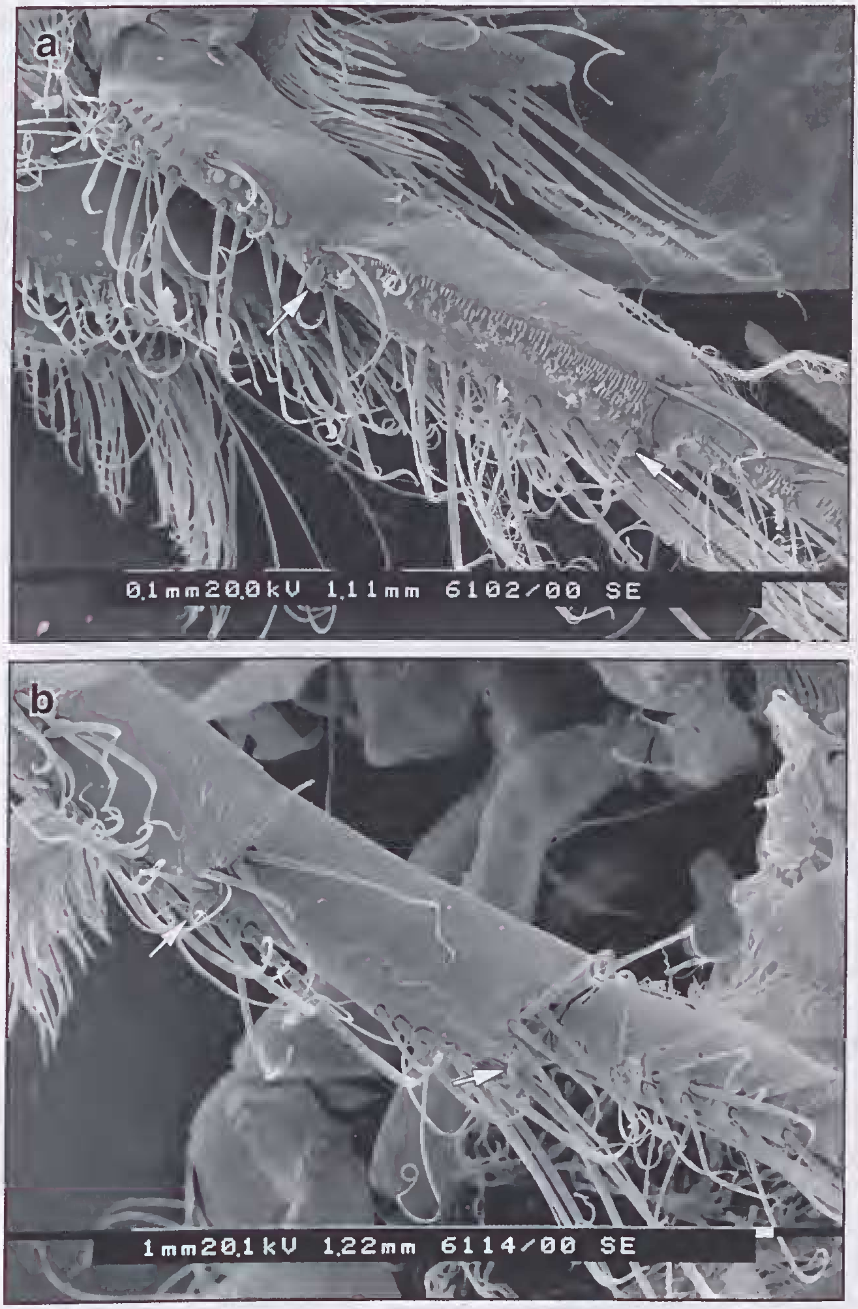

Figure 5. Antenna 2 in situ (left), pedunclc article 3 and 4 (these are fused) and first article of flagellum. **a**, *Levinebalia maria*, note row of small spines. Arrows point to large cuticular outgrowths. **b**, *Paranebalia* sp. A, note absence of small spines. Arrows indicate large cuticular outgrowths.

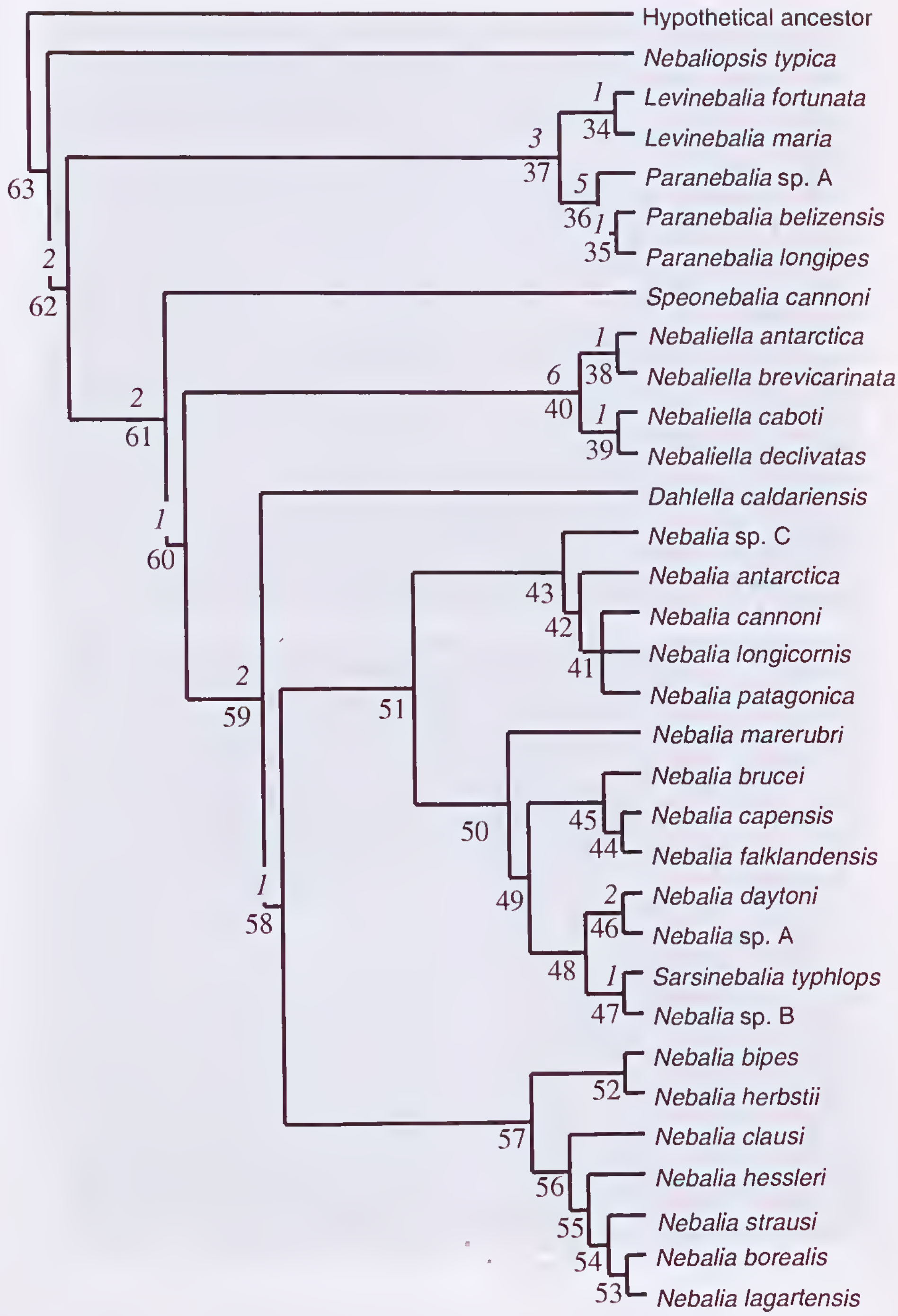

Figure 6. Hypothesis for phylogeny of Leptostraca, tree 711. Numbers above branches are Bremer values; numbers below are node numbers.

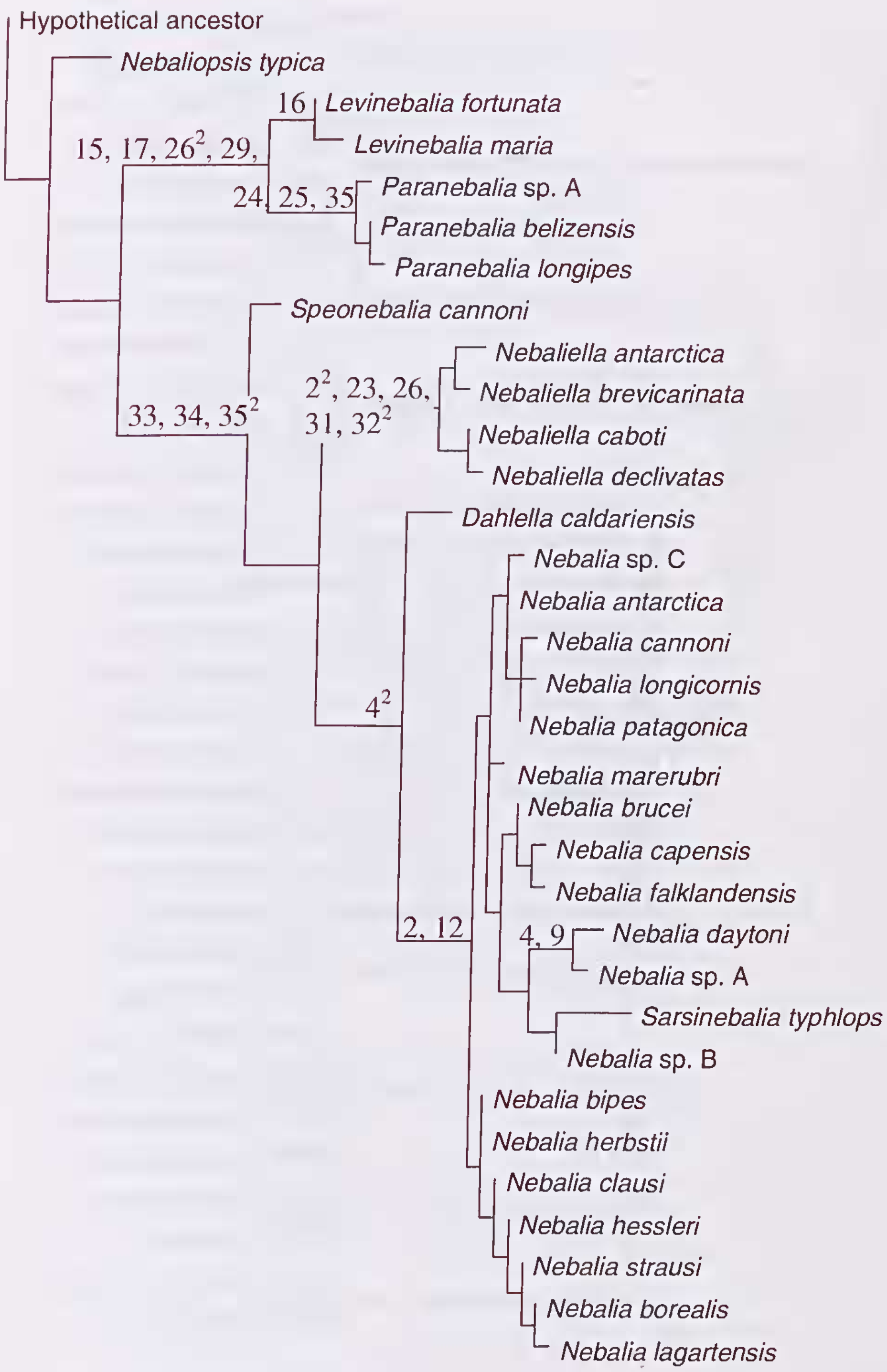

Figure 7. Tree 711 with branch lengths. Numbers are characters with CI=1 and superscripts are state changes from the plesiomorphic condition.

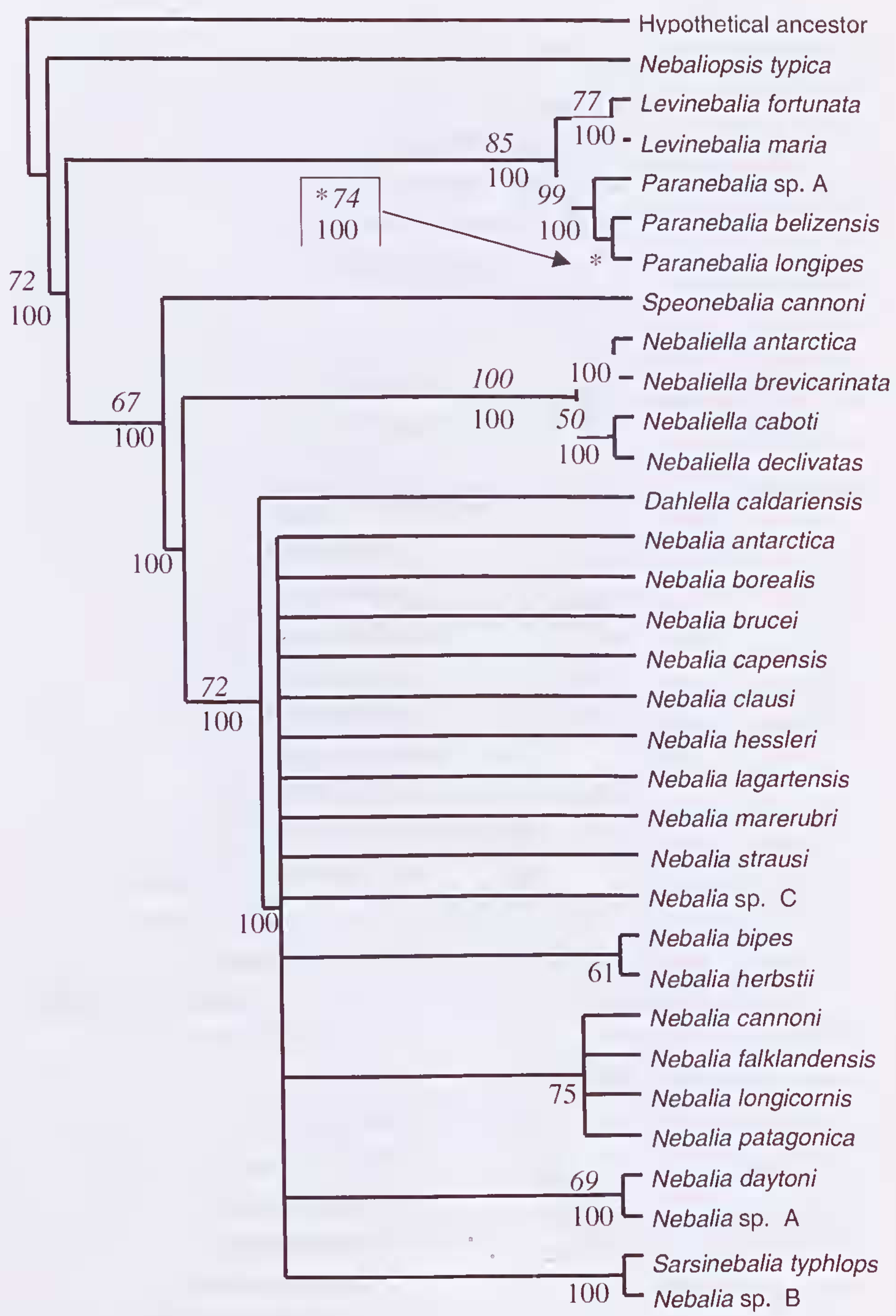

Figure 8. 50% majority-rule tree. Number above branch lines are Bootstrap values; numbers below are percentage of parsimonious trees retaining each clade (only values above 50% are included).