A new species of *Nebalia* (Crustacea, Leptostraca) from Unguja Island (Zanzibar), Tanzania, East Africa, with a phylogenetic analysis of leptostracan genera

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*Nebalia brucei* sp. nov. is described from specimens taken in traps from Unguja Island (Zanzibar), Tanzania, East Africa. The species is characterized by the following unique combination of characters: a short and broad rostrum; a carapace that is large compared to overall body size and that covers pleonite 4; a basally narrow compound eye; and acutely pointed denticles at the dorsal margin of pleon segments 6 and 7. Cladistic analyses of the relationships of the seven recognized leptostracan genera resulted in two hypotheses. One tree has *Nebaliopsis* as sister group to the remaining leptostracans and supports the monophyly of Nebaliidae. The other tree has *Paranebalia* as sister group to the remaining leptostracans and Nebaliidae as paraphyletic with respect to *Nebaliopsis*. Both trees contain a *Nebalia/Dahlella/Sarsinebalia* clade.

**KEYWORDS:** *Nebalia brucei*, systematics, taxonomy, phylogeny.

Introduction

Until a little more than 10 years ago it was believed that the Leptostraca, in particular the genera *Nebalia* Leach, 1814 and *Paranebalia* Claus, 1880, were composed of a small number of highly variable species with almost cosmopolitan distribution. Dahl (1985) revised the European shelf species of *Nebalia* and showed that the distribution of leptostracans, at least in Europe, conforms to patterns found in other small benthic invertebrate species. Dahl (1985) recognized two new European species of *Nebalia* and predicted that continued work would yield similar results in other parts of the world. Since then, a number of species of *Nebalia* and *Paranebalia* have been described from around the world (e.g. Kazmi and Nasima, 1989; Dahl, 1990; Modlin, 1991; Escobar-Briones and Villalobos-Hiriart, 1995; Martin et al., 1996; Vetter, 1996), and more undescribed species are known to exist (Walker-Smith, 1993). The present paper describes a new species of *Nebalia*.

Western Indian Ocean leptostracans remain very poorly studied, essentially with single species known from the northern and southern regions only. It is therefore not surprising to find an undescribed species from Zanzibar, but of interest that limited
collections made in shallow water yielded two additional undescribed species. One of these is another species of *Nebalia* (40 specimens, ZNZ 97/21, Mnemba reef, 5°50.40'S, 39°23.31'E, 9–10 March 1997, reef edge, ca 30–40 m, baited trap, coll. N. L. Bruce and T. Jansen, ZMUC CRU 3464) and the other a species of *Paranebalia* from several localities around Zanzibar (ZMUC CRU 3465). The *Nebalia* species is not described as all specimens were immature males, and the *Paranebalia* species is not described as there were only a few specimens in poor condition. These additional species indicate that the region has a potentially high diversity with at least three species in shallow water habitats around coral reefs and in sea grass beds, and with the probability of further taxa from offshore and deeper water particulate substrata.

There has been no earlier attempt to construct a higher level phylogeny for the seven recognized leptostracan genera. *Nebalia* is by far the most speciose genus with more than 15 described species. *Paranebalia* and *Nebaliella* Thiele, 1904 each have three described species, while *Dahlella* Hessler, 1984, *Sarsinebalia* Dahl, 1985, *Speonebalia* Bowman, Yager and Iliffe, 1985 and *Nebaliopsis* G. O. Sars, 1887 are all monotypic. Hessler (1984) recognized two families: the Nebaliopsidae Hessler, 1984, containing only *Nebaliopsis*, and the Nebaliidae Baird, 1850, containing the remaining extant leptostracan genera. The phylogenetic validity of Nebaliopsidae is indisputable as it includes only one genus with one species, whereas the status of Nebaliidae is more uncertain as most of the defining characters mentioned by Hessler (1984) possibly can be interpreted as ancestral to all leptostracans, but later lost in *Nebaliopsis*. A cladistic analysis of the leptostracan genera is presented here. The purpose is to resolve the phylogeny as far as possible with the present data, and to evaluate various characters in a cladistic frame.

**Material and methods**

Specimens were collected in traps (baited with fish) off Unguja Island (Zanzibar), Tanzania, 1997. Trap design followed instructions of Keable (1995). The species description follows the recommendations of Dahl (1985). As recommended by Martin *et al.* (1996) certain features are illustrated by SEM. Drawings were made with the aid of a Zeiss Axioscope equipped with a camera lucida. Specimens used for SEM were prepared mostly following the procedure of Felgenhauer (1987). Length/width proportions of segments were measured using the greatest length and width on each segment. Whole body measurements are from rostrum tip to the distal end of the furcal rami. Carapace measurements are from rostrum tip to the posterior margin of the carapace.

The phylogenetic analyses were carried out on a Macintosh platform using MacClade 3.04 (Maddison and Maddison, 1993) and PAUP 3.1.1. (Swofford, 1993). The small data matrix allowed for the use of exhaustive search facilities in PAUP. The information in the data matrix has been scored from literature.

**Taxonomy**

**Family NEBALIIDAE** Baird, 1850

**Genus Nebalia** Leach, 1814

*Nebalia brucei*, new species

(figures 1–6)

*Material examined.* **Holotype:** female (4.2 mm), pre-ovigerous. Matemwe, northeastern Unguja, 5°51.21'S, 39°21.96'E, 8–11 March 1997, reef edge on to rubble, 20–25 m, baited trap, coll. N. L. Bruce and T. Jansen (ZMUC CRU 3460).
Fig. 1. *Nebalia brucei*, new species. (A–D) Holotype (ZMUC CRU 3460), (E–G) paratype (ZMUC CRU 3461). (A) Lateral view, scale bar: 500 μm; (B) rostrum; (C) compound eye; (D) pleonite 4; (E) dorsal posterior margin of pleon segment 6; (F) anal scales on ventral part of telson; (G) dorsal side of furcal rami, telson, and pleonite 7.

Paratypes: five pre-ovigerous females, same data as holotype (ZMUC CRU 3461). One pre-ovigerous, dissected, used for figures 2–6, same data as holotype (ZMUC CRU 3462). Two pre-ovigerous females, Mnemba Reef, off northeastern Unguja, 5°50.63'S, 39°23.57'E, 9–10 March 1997, clean sand, 7 m, baited trap, coll. N. L. Bruce and T. Jansen (ZMUC CRU 3466). Two pre-ovigerous females, Stn ZNZ 97/21, Mnemba Reef, 5°50.40'S, 39°23.31'E, 9–10 March 1997, reef edge, ca 30–40 m, baited trap, coll. N. L. Bruce and T. Jansen (ZMUC CRU 3463).
Description of female holotype

*Length* (figure 1A). Total length 4.2 mm. Carapace length 1.8 mm; posterior margin reaching beyond pleonite 4.

*Rostrum* (figure 1B). Short and wide, 1.8 times as long as wide, greatest width 0.6 times length, sides parallel along proximal third, without terminal spine.
Compound eye (figure 1C). Oval and ventrally flexed, about 1.8 times as long as greatest width, narrow at basis; 0.5 times length of rostrum, laterally compressed, with ommatidia, pigmentation covering approximately half of eye, supraocular scale present.
Fig. 4. *Nebalia brucei*, new species. Paratype (ZMUC CRU 3462). (A) Thoracopod 1; (B) thoracopod 4; (C) thoracopod 5; (D) thoracopod 6; (E) thoracopod 7; (F) thoracopod 8.

*Pleon, telson, furca* (figure 1D–G). Posterolateral corner of pleonite 4 ('epimeron', sensu Dahl, 1985) slightly pointed, not upturned; denticles on posterior margin blunt and rounded. Posterior dorsal margins of pleon segments with denticles tapering to acute points. Anal scales acutely pointed with median margin convex, each with a lateral ‘shoulder’. Furcal rami tapering slightly distally, slightly longer than combined lengths of segment 7 and telson, 5.5 times as long as wide, 14 simple setae on lateral margin, 11 simple setae on medial margin, one simple terminal seta, 17 plumose median setae.

*Antennule* (figure 2A). Peduncle with four segments; flagellum with 12 segments: segment 2 is 2.8 times as long as wide, with 13 plumose setae distally, six plumose setae laterally, and one plumose seta proximally; segment 3 is 0.7 times as long as segment 2, with distal cluster of plumose setae; segment 4 with two lateral rows of setae, row one with four simple setae, row 2 with one stout, simple seta and four longer simple setae; antennular scale 2.2 times as long as wide and 2.2 times as long as segment 4; flagellum 1.2 times as long as peduncle.

*Antenna* (figure 2B). Peduncle with three segments (segment 3 and 4 fused):
New species of *Nebalia*.

**Fig. 5.** *Nebalia brucei*, new species. Paratype (ZMUC CRU 3462). (A) Pleopod 1, right side; (B) pleopod 2, right side; (C) pleopod 5, right side; pleopod 6, right side.

Segment 2 is 0.7 times as wide as long, with dorsal spine distally; segment 3 is 0.4 times as wide as long, with four rows of setae anteriorly, first row (lateral-most) with four simple setae, second row with five simple setae, third row with four stout setae, fourth row with six long simple setae, distolateral margin with five long simple setae; distal median margin with five long setulose setae; flagellum 1.4 times as long as peduncle.

**Mandible** (figure 2C). Composed of three segments: segments 2 and 3 of same length; segment 2 with two setae at anterior margin, one subterminal and another approximately midway between proximal and distal margins; segment 3 slightly expanded distally, one row of setae on segment 3 beginning a small distance from proximal margin, with single row of short serrate setae terminally; molar process well developed on first segment.

**Maxilla 1** (figure 3A). Endite 1 with row of nine plumose setae; endite 2 with two long plumose setae and two rows of sculptured setae, anterior row with 11
Fig. 6. *Nebalia brucei*, new species. Paratype. (A) Lateral view, right half of carapace removed, epipod on thoracopods 1–6 broken off; (B) right side pleopods, outer view; (C) exopod of pleopod 1, long row of setae; (D) shape of posterolateral margin of pleonite 4; (E) anal scales. Scale bars: (A) 250 μm; (B) 250 μm; (C) 100 μm; (D) 100 μm; (E) 100 μm. Abbreviations: a1, antenna 1; a2, antenna 2; e, compound eye; ep, epipod; ex, exopod; mx 1, maxilla 1; mx 2, maxilla 2; ro, rostrum; te, telson.

setae, posterior row with 12 setae, endite 2 also with two plumose setae; palp with eight lateral and two terminal setae.

*Maxilla 2* (figure 3B). With four endites: endite 1 with three rows of plumose setae, anterior row with 16 setae, middle row with 12 setae, posterior row with three
setae; endite 2 half as wide as endite 1, with three rows of plumose setae: anterior row with six setae, middle row with five setae, posterior row with four setae; endite 3 largest; endite 4 small with four long plumose setae; segment 1 of endopod 1.5 times as long as segment 2; exopod slightly longer than segment 1 of endopod.

**Thoracopods** (figure 4). First thoracopod exopod extending to distal end of endopod; epipod reaching to distal two-thirds of exopod. Thoracopods 2–6 similar, all with broad, lobed exopod extending to distal end of endopod; epipod large with distal margin reaching distal margin of exopod. Shape of epipod on thoracopod 7 differs from that of thoracopods 2–6 in being shorter and broader and having the dorsal part concave.

**Pleopod 1** (figure 5A). Peduncle with four simple, stout setae, lateral margin with one short proximal seta and with one long distal seta reaching less than middle of dense setal row of exopod, median margin with two setae close to basis of exopod; exopod 0.8 times as long as peduncle, with comb-row of short trifid setae, row beginning at some distance from basis of exopod, distally with four stout, simple setae.

**Pleopod 2** (figure 5B). Peduncle dorsolateral margin with one proximal stout seta, distally with one larger stout seta, median margin distally with two slender plumose setae near basis of endopod; exopod 0.8 times as long as peduncle, 0.8 times length of endopod, lateral margin with five pairs of simple robust setae, a single plumose seta between setae of each pair, one proximal simple seta, three simple terminal setae, median margin with row of long plumose setae; endopod with long plumose setae on lateral and medial margins, simple robust seta terminally.

**Pleopod 5** (figure 5C). With two segments; length of combined segments 5.4 times width; with five robust simple setae on medial and distal margins.

**Pleopod 6** (figure 5D). One segment; 2.6 times as long as wide; with five robust simple setae on medial and distal margins.

**Remarks.** *Nebalia brucei* can be distinguished from other congeneric species by the unique combination of following characters: rostrum short and broad; carapace large compared to body size and covering pleonite 4; compound eye basally very narrow; denticles on dorsal side of pleonites 6 and 7 acutely pointed.

**Distribution**

Known from Matemwe and Mnemba, Zanzibar, Tanzania.

**Etymology**

The species is named for Niel L. Bruce, collector of the material, and particularly fond of Zanzibar.

**Discussion of the relationship of *Nebalia brucei* to other species of *Nebalia***

*Nebalia brucei* is the first species of Leptostreca to be described from the coast of East Africa. Other species of *Nebalia* known from geographic localities relatively close to Zanzibar are *Nebalia marerubri* Wägele, 1983 from the Red Sea, and *Nebalia capensis* Barnard, 1914, and *Nebalia ilheoensis* Kensley, 1976 from South Africa and south-west Africa. Of these three species *N. brucei* is closest to *N. marerubri*, from which it differs in having a longer carapace, covering more of the body, and a broader rostrum. *Nebalia brucei* differs from *N. capensis* and *N. ilheoensis* in a number of features, including denticles on the dorsal margins of pleon segments 6
and 7 more acutely pointed in \textit{N. brucei} than in \textit{N. capensis} and \textit{N. ilheoensis} (in the latter, the denticles are blunt and rectangular in shape). \textit{N. brucei} also differs from these species in having a relatively broader rostrum and a more narrow basis to the compound eye. In Barnard’s (1914) original description, \textit{Nebalia capensis} is described and figured as having an unsegmented maxilla 2 endopod. If correct, this would be another difference from \textit{N. brucei}, where two segments are present (as in all other known species of \textit{Nebalia}). However, the description of Barnard (1914) is probably incorrect in this respect, as a supplementary description of \textit{N. capensis} by Kensley (1976) shows the maxilla 2 endopod with two segments.

All other species of \textit{Nebalia} described so far are all even more distinct from \textit{N. brucei} than the species just mentioned. \textit{N. brucei} can be distinguished from all the European shelf species, reviewed by Dahl (1985), by having a relatively broader rostrum, and a relatively more narrow basis of the compound eye. Additionally, none of the European shelf species has the dorsal posterior margin of pleon segment 4 serrated in the same way as in \textit{N. brucei}. The Southern Hemisphere species, described by Dahl (1990), and the Californian species (Martin et al., 1996; Vetter, 1996) can be easily distinguished from \textit{N. brucei} by features related to the rostrum shape, thickness of eye basis, serration of postero-lateral margin of pleonite 4, and general serration of the pleonite margins. Of all the species of \textit{Nebalia} described so far, \textit{N. brucei} appears to be most closely related to the Red Sea species \textit{Nebalia marerubri}, from which it can be distinguished by the above-mentioned characters.

\textbf{Phylogenetic analysis of the leptostracan genera}

The results of a phylogenetic analysis of the recent leptostracan genera is presented here, together with a character discussion and various assumptions for the analysis. The character matrix is shown in the Appendix. For outgroups I used the Anostraca (Branchiopoda) and/or the Mysidacea (Malacostraca, Peracarida).

\textbf{Monophyly of the Leptostraca}

The monophyly of the Recent Leptostraca has never been seriously questioned. The following characters can be mentioned as potentially supporting the taxon:

Movable rostrum (character 1); antenna 1 with outer rami as scales (character 8); antenna 2 without exopod (character 11); maxilla 1 with grooming palp (character 15); brood carried between thoracopods (character 19); seven segments in pleon (character 20); pleopods 5 and 6 reduced in size (character 23); larval development direct (character 27).

Not all of these characters can be considered as unique apomorphies for the Leptostraca. All characters are discussed in further detail in the character discussion section below.

\textbf{Monophyly of the terminal taxa (leptostracan genera)}

The arguments for a monophyletic status are strong for six of the seven recognized leptostracan genera. \textit{Speonebalia}, \textit{Dahlella}, \textit{Sarsinebalia} and \textit{Nebaliopsis} are monotypic and are therefore by definition monophyletic. There is convincing character support for \textit{Paranebalia} and \textit{Nebaliella} (see table 1), whereas the status of \textit{Nebalia} is more uncertain. I have been unable to identify unique characters for \textit{Nebalia} and I cannot exclude the possibility that the genus is paraphyletic with respect to \textit{Sarsinebalia} or \textit{Dahlella} (or both).
Table 1. Ingroup genera included in the analysis.

<table>
<thead>
<tr>
<th>Genera of the Leptostraca</th>
<th>Support for monophyly</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nebalia</em> Leach, 1814</td>
<td>??</td>
</tr>
<tr>
<td><em>Paranebalia</em> Claus, 1880</td>
<td>Subterminal rostral spine; thoracopods extending beyond carapace; denticles on eyes; distal blade with teeth on antenna 1.</td>
</tr>
<tr>
<td><em>Nebaliopsis</em> Sars, 1887*</td>
<td>Molar process reduced; palp on mx1 reduced to small stub; carapace with network; thoracopods well spaced; caudal rami leaf-like.</td>
</tr>
<tr>
<td><em>Nebaliella</em> Thiele, 1904</td>
<td>Rostrum with large keel; eyes curved and elongated.</td>
</tr>
<tr>
<td><em>Dahllella</em> Hessler, 1984*</td>
<td>Eyes large, curved, long, tapering gradually to point, anterior margin denticulate; second maxilla exopod small (Hessler, 1984).</td>
</tr>
<tr>
<td><em>Speonebalia</em> Bowman, Yager and Iliffe, 1985*</td>
<td>Series of marginal organelles (glands?) on maxilla 2 endopod; posterior margin of carapace with a series of close-set obtuse spines (Bowman et al., 1985).</td>
</tr>
<tr>
<td><em>Sarsinebalia</em> Dahl, 1985*</td>
<td>Subterminal rostral spine; eyes with a straight dorsal margin (Dahl, 1985).</td>
</tr>
</tbody>
</table>

*Monospecific genera.

Table 2. Apomorphy table for hypothesis 1, shown in figure 7A. Possible problems with the supporting character changes have been indicated by the following numbering system: 1reversed later; 2paralleled in one or more taxa, in some cases outside the Leptostraca; 3reversal; 4possible plesiomorphy.

<table>
<thead>
<tr>
<th>Clade number</th>
<th>Apomorphies</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Leptostraca</td>
<td>1 Rostrum (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>8 Antenna 1 with exopod as scale (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>11 Antenna 2 with exopod absent (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>15 Maxilla 1 with grooming palp (0→1/2)$^2$</td>
</tr>
<tr>
<td></td>
<td>19 Thoracopods form a brood chamber (0→1)?</td>
</tr>
<tr>
<td></td>
<td>20 Seven pleon segments (0/1/2→2)$^2$</td>
</tr>
<tr>
<td></td>
<td>23 Pleopods 5 and 6 reduced (0→1)$^2$</td>
</tr>
<tr>
<td>2 Nebaliidae</td>
<td>26 Furcal rami taper toward tips (0→1)$^2$</td>
</tr>
<tr>
<td>3</td>
<td>27 Free-living larvae absent (0→1)$^2$</td>
</tr>
<tr>
<td>4</td>
<td>24 Pleopod 5 smaller than pleopod 6 (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>2 Rostrum with subterminal spine (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>10 Antenna 2 with three segments in peduncle (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>22 Pleopod 1 with spine row on exopod (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>25 Pleopod 6 with one segment (0→1)$^2$</td>
</tr>
<tr>
<td>5</td>
<td>6 Eye scale (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>13 Mandible, segment 3 longer than segment 2 (0→1)$^2$</td>
</tr>
<tr>
<td>6</td>
<td>21 Pleonite denticles rounded (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>2 Rostrum with subterminal spine lost (1→0)$^2$</td>
</tr>
<tr>
<td></td>
<td>9 Antenna 2 with dorsal spine on segment 2 (0→1)$^2$</td>
</tr>
<tr>
<td></td>
<td>14 Mandible with segment 3 expanded distally (0→1)$^2$</td>
</tr>
</tbody>
</table>

Character discussion
This section includes a discussion of the *a priori* assumptions concerning homologies of characters. Only characters present in more than one genus (potential synapomorphies) are included; autapomorphies for the respective genera are not included. Potential synapomorphies for the Leptostraca also are included.
Table 3. Apomorphy table for hypothesis 2, shown in figure 7B. Possible problems with the supporting character changes have been indicated by the following numbering system: 1reversed later; 2paralleled in one or more taxa, in some cases outside the Leptostraca; 3reversal; 4a possible plesiomorphy.

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</tr>
<tr>
<td></td>
<td>23 Pleopods 5 and 6 reduced (0 \rightarrow 1)</td>
</tr>
<tr>
<td>2</td>
<td>17 Thoracopods foliaceous ((0 \rightarrow 1))^2</td>
</tr>
<tr>
<td></td>
<td>18 Thoracopods with exopod distally rounded ((1 \rightarrow 0))</td>
</tr>
<tr>
<td>3</td>
<td>25 Pleopod 6 with two segments ((1 \rightarrow 0)^1)</td>
</tr>
<tr>
<td>4</td>
<td>24 Pleopod 5 larger than pleopod 6 ((0 \rightarrow 1))</td>
</tr>
<tr>
<td>5</td>
<td>6 Eye scale ((0 \rightarrow 1))</td>
</tr>
<tr>
<td></td>
<td>10 Antenna 2 with three segments in peduncle ((0 \rightarrow 1)^2)</td>
</tr>
<tr>
<td></td>
<td>13 Mandible with segment 3 longer than segment 2 ((0 \rightarrow 1))</td>
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<tr>
<td></td>
<td>21 Pleonite denticles rounded ((0 \rightarrow 1)^1)</td>
</tr>
<tr>
<td>6</td>
<td>9 Antenna 2 with dorsal spine on segment 2 ((0 \rightarrow 1)^2)</td>
</tr>
<tr>
<td></td>
<td>14 Mandible with segment 3 expanding distally ((0 \rightarrow 1))</td>
</tr>
<tr>
<td></td>
<td>22 Pleopod 1 with spine row on exopod long ((0 \rightarrow 1)^2)</td>
</tr>
</tbody>
</table>

**Character 1:** movable rostrum

0 = absent; 1 = present

A small movable rostrum covers the eyes to varying degrees in different taxa. It is present in all Recent leptostracans and is therefore a possible synapomorphy for the taxon. A similar structure is found in the Hoplocarida and in the fossil phyllocarids *Nahecaris stuertzii* Jaekel, 1921 and *Ceratiocaris papilio* Salter (see Rolfe, 1962; Bergström et al., 1987), but it is believed to be less movable in *Nahecaris* than in recent leptostracans (Bergström et al., 1987). The rostrum therefore may constitute a plesiomorphy for the Leptostraca.

**Character 2:** rostrum with subterminal spine

0 = absent; 1 = present

In *Sarsinebalia* and *Paranebalia* there is a subterminal spine on the rostrum. This is shown for *Sarsinebalia* by Dahl (1985, figures 98, 100), Vader (1973, figure 1e) and Hessler and Sanders (1965, figure 1a, c) and for *Paranebalia* by Wakabara (1976, figure 1b) and Modlin (1991, figure 1b).

**Character 3:** rostrum with keel

0 = absent; 1 = present

In *Sarsinebalia*, *Nebaliella* and in some species of *Nebalia* the rostrum has a keel. In *Nebaliella* the keel is significantly longer than the rostrum (Clark, 1932, figure 1; Hessler and Sanders, 1965, figure 2a, b; Walker-Smith, 1998) whereas, when present, it is shorter than the rostrum in all other species. As this structure is illustrated in varying quality in the literature, I have made no attempt to distinguish different types of keels even though, based on available information in the literature, some variation appears to be present.
Character 4: carapace shape
0 = triangular; 1 = not triangular
In Nebaliopsis the carapace has a triangular appearance which is in contrast to all other leptostracan genera.

Character 5: carapace sculpturing
0 = not sculptured; 1 = sculptured
In Nebaliopsis the carapace is sculptured (Sars, 1887); in other leptostracan genera it is unsculptured.

Character 6: eye scale
0 = scale absent; 1 = scale present
In Nebalia, Sarsinebalia and Dahlella there is a scale associated with the compound eye (supraorbital plate, sensu Dahl, 1985). Such a scale is absent in the remaining genera.

Character 7: antenna 1, distal blade
0 = distal blade absent; 1 = present
Paranebalia has a serrated distal blade at segment 4 at approximately half the length of the antennular scale. (e.g. Sars, 1887). A similar structure is found in Nebaliopsis (Thiele, 1904, figure 41).

Character 8: antenna 1, outer rami
0 = flagellate; 1 = scale
All leptostracans have the outer ramus modified to a scale at segment 4 of the first antennae. To my knowledge, this is unknown in other Crustacea, and constitutes therefore a synapomorphy for the leptostracan genera.

Character 9: antenna 2, spine on segment 2
0 = segment 2 without dorsal spine; 1 = dorsal spine present
In Nebalia, Dahlella and Nebaliella there is a dorsal spine at the distal margin of segment 2. Such a spine is not present in the other described leptostracan genera.

Character 10: antenna 2, number of segments in peduncle
0 = with 4 segments; 1 = with 3 segments
In Nebalia, Dahlella, Sarsinebalia and Paranebalia there are only three peduncular segments, compared to four in the remaining leptostracan genera. Traditionally it is believed that a fusion of two segments has taken place from a four-segmented condition to the three-segmented condition (Cannon, 1960). A study of the limb ontogeny of Nebalia supports this hypothesis as late juveniles of Nebalia have remnants of four segments in the peduncle (Olesen, unpublished). In other malacostracans (outgroups) all possibilities between one and five segments in the peduncle exist.

Character 11: antenna 2 exopod
0 = present; 1 = absent
All leptostracans lack the antenna 2 exopod, which therefore is a putative
A synapomorphy for this taxon. An exopod is also absent in various peracarid malacostracans, but this is probably convergent as a second antenna with two rami has been retained in several other malacostracans.

**Character 12: mandible, molar process**

0 = well developed; 1 = reduced in size

*Nebaliopsis* has a reduced molar process, whereas it is well developed in all other leptostracans.

**Character 13: mandible, length ratio between segments 2 and 3**

0 = segment 3 shorter than or as long as segment 2; 1 = segment 3 longer than segment 2

In *Nebalia, Dahlella* and *Sarsinebalia* segment 3 (the distal segment) is longer than segment 2. In the remaining genera segment 3 is shorter than segment 2 or the same length as this. The latter is also so for various other malacostracans (e.g. mysidaceans).

**Character 14: mandible, shape of segment 3**

0 = tapering distally or sides parallel; 1 = segment expanded distally

In *Nebalia* and *Dahlella* segment 3 is expanded distally. In the remaining genera the segment is either tapering or the sides are parallel.

**Character 15: maxilla 1, grooming palp**

0 = absent; 1 = with a short palp; 2 = with a long grooming palp

All leptostracans except *Nebaliopsis* have an elongated grooming palp on maxilla 1. *Nebaliopsis* has a small lobe in the position of the palp of other leptostracans, which is often interpreted as the vestiges of a grooming palp (e.g. Thiele, 1904, figures 47, 48). However, there is no morphological evidence available in support of this interpretation. There is no similar grooming palp found in any other Recent crustaceans. Bergström *et al.* (1987) found a structure in *Nahecaris stuertzii* that could be the palp of maxilla 1, but its origin proximally was not discernible.

**Character 16: maxilla 2, size**

0 = about the same size as thoracopod 1; 1 = much smaller than thoracopod 1

In *Nebaliopsis* maxilla 2 is subequal in size to thoracopod 1, whereas in other leptostracans it is much smaller (Cannon, 1931).

**Character 17: thoracopods, type**

0 = stenopodous, tapering distally; 1 = foliaceous

In all leptostracans the thoracopods are broad and foliaceous except in *Paranebalia*, where they are long, slender and somewhat stenopodous, bearing some resemblance to those of mysids (see Cannon, 1927).

**Character 18: thoracopods, exopods**

0 = distally tapering; 1 = distally rounded; 2 = strongly reduced

In *Paranebalia* the thoracopod exopods are long, slender and taper distally, as in many other malacostracans (e.g. mysids); in other leptostracans the thoracopod exopod is a broad, lobed structure.
Character 19: thoracopods forming a brood chamber

0 = thoracopods not forming a brood chamber; 1 = thoracopods forming a brood chamber

The thoracopods form a brood chamber in ovigerous females of *Nebalia*, *Paranebalia*, *Nebaliella* and *Sarsinebalia*, whereas the situation is unknown in *Speonebalia* and *Dahlella*. Cannon (1931, 1960) described the brood chamber in *Nebalia*, *Paranebalia* and *Nebaliella* as being formed by the tips of the endopods of the trunk limbs, which curve inwards and form a basket under the trunk. The transformation in shape of the distal part of a trunk limb is described for *Nebalia puttegensis* (A. E. Clark) by Dahl (1985), who mentions that the same type of transformation is found in *Sarsinebalia typhlops* (G. O. Sars). Linder (1943) believed that a brood chamber is formed by the trunk limbs in *Nebaliopsis*, but in a different way from that of other leptostracans; he hypothesized that the elongated first and eighth trunk limbs, present only in the most developed specimens, together form a brood chamber by bending towards each other to form the chamber floor. As this function of the trunk limbs has never been observed and is purely hypothetical, the character is scored as ‘?’ in the matrix. A further complication is that since then (Linder, 1943), free-living larvae of what is presumably *Nebaliopsis* have been found in plankton, indicating that brooding probably does not take place (Cannon, 1960).

Character 20: number of pleon segments in adult

0 = pleon tagma absent; 1 = six; 2 = seven

Only malacostracans have a pleon tagma. In all leptostracans there are seven segments in the pleon of the adult, in most other malacostracans there are six.

Character 21: pleonite denticles

0 = pointed; 1 = rounded

All leptostracans have marginal pleonite denticles. In *Dahlella*, *Sarsinebalia* and partly in *Nebalia* these are rounded, while they are acute in other leptostracans. A more detailed coding of this character can be made when the shape of the pleonite denticles become known in more detail in various species.

Character 22: pleopod 1, spine row on exopod

0 = absent; 1 = present

In *Nebalia*, *Dahlella* and *Paranebalia* there is a dense row of stout setae at the exopod of pleopod 1. In *Nebalia* and *Dahlella* (e.g. see Hessler, 1984; Dahl, 1985) the row is of almost the same length as the exopod, whereas it is slightly shorter in *Paranebalia* (Sars, 1887; Modlin, 1991).

Character 23: pleopods 5 and 6, size compared to pleopods 1–4

0 = not smaller than pleopods 1–4; 1 = smaller than pleopods 1–4

In all leptostracans, pleopods 5 and 6 are significantly smaller than pleopods 1–4. They are uniramous and never consist of more than two segments. This is not seen in any other malacostracans. It differs also from that in various fossil phyllocarids, where only five pleopods are present, decreasing gradually in size posteriorly (e.g. *Nahecaris stuertzi* and *Ceraticarisc papilio*, see Rolfe, 1962; Bergström *et al.*, 1987).
Character 24: pleopods 5 and 6, size, compared to each other

0 = pleopod 5 larger than pleopod 6; 1 = pleopod 5 smaller than pleopod 6

In Nebaliopsis and Nebaliella pleopod 5 is smaller than pleopod 6 (only slightly smaller in Nebaliopsis, see Thiele, 1904 for both genera), whereas the opposite occurs in other leptostracans.

Character 25: pleopod 6, number of segments

0 = with two segments; 1 = with one segment

Pleopod 6 is one-segmented in Paranebalia (see Sars, 1887), Sarsinebalia (see Dahl, 1985), Dahlella (see Hessler, 1984) and Nebalia (e.g. see Dahl, 1985; Martin et al., 1996), whereas it is two-segmented in the remaining three leptostracan genera (for Nebaliopsis, see Thiele, 1904; for Nebaliella, see Walker-Smith, 1998; for Speonebalia, see Bowman et al., 1985).

Character 26: furcal rami

0 = leaflike, broadest in the middle; 1 = tapering evenly distally

In Nebaliopsis the furcal rami are leaf-like, broadest in the middle (see Linder, 1943), whereas they taper evenly distally in other leptostracans.

Character 27: free-living larvae

0 = present; 1 = absent

Parental care of the offspring (epimorphic or direct development) is seen in Nebalia, Paranebalia, Nebaliella (e.g. see Cannon, 1960), whereas the developmental mode is unknown for Speonebalia and Dahlella. The situation in Nebaliopsis is unclear. Specimens of Nebaliopsis with brood-chamber-like modifications of the trunk limbs were reported by Linder (1943) (see character 19), which could indicate that brooding occurs. However, free-living larvae of Nebaliopsis have been caught in the plankton. There is little information available about this larva, only a simple line drawing given by Cannon (1960). This larva does not look like any other free-living crustacean larva, but basically looks like a swimming embryo.

Results of phylogenetic analysis

Description and comparison of two shortest trees

An analysis with both outgroups included yielded one shortest tree with 44 steps with CI 0.80 and RI 0.70 (figure 7A). Another analysis with Mysidacea as outgroup yielded one shortest tree of 37 steps with CI 0.84 and RI 0.71 (figure 7B). Both trees have the clade (Sarsinebalia (Dahlella, Nebalia)), but differ with respect to the position of the remaining four genera. The first tree (figure 7A) has Nebaliopsis as sister group to the remaining leptostracans with Nebaliella, Speonebalia and Paranebalia derived in a sequence before the Sarsinebalia/Dahlella/Nebalia clade. The other tree (figure 7B) has Paranebalia as sister group to the rest of the leptostracans and has a Speonebalia/Nebaliella/Nebaliopsis clade as sister group to the Sarsinebalia/Dahlella/Nebalia clade. In other words, the most significant difference between the two trees is the position of Nebaliopsis and Paranebalia.

Position of Nebaliopsis and the validity of Nebaliidae

The two single characters that give Nebaliopsis sister-group status to the rest of the leptostracans in the tree shown in figure 7A are the ‘appearance of slender furcal
New species of Nebalia

Fig. 7. Two phylogenetic hypotheses for the Leptostraca. (A) Inclusion of two outgroups (Anostraca and Mysidacea) gave one shortest tree with Nebaliopsis as sister group to a monophyletic Nebaliidae; (B) Inclusion of one outgroup (Mysidacea) gave one shortest tree with Paranebalia as sister group to the remaining leptostracans. In this tree Nebaliidae is not monophyletic.

rami' (character 26) and perhaps also 'loss of free-living larvae' (direct development) in the remaining leptostracans (character 27) (Clade 2, figure 7A). One problem with this character support is that the free-living larva of Nebaliopsis is possibly a secondary larva as it basically looks like a 'swimming embryo' (see figure 46 in Cannon, 1960), which suggests that it has been derived from an ancestor exhibiting parental care (as present in other Recent leptostracans). The hypothesis in figure 7A
agrees with the existing classification, which divides Recent leptostracans into two families, Nebaliopsidae and Nebaliidae (Hessler, 1984). It is surprising, however, that the Nebaliidae is supported by only one weak character. Several characters potentially supporting Nebaliidae were included in the analysis, but did not provide support for this taxon, as they either could not be polarized with certainty or appear to be plesiomorphies shared with other crustaceans and therefore are unacceptable as supporting characters for that clade/family. The plesiomorphies probably include the ‘unsculptured carapace’ (character 5), the ‘well-developed molar process’ in Nebaliidae (character 12), the small size of the second maxillae as compared to the first trunk limb (character 16), and possibly also the ‘long maxilla grooming palp’ (character 15). The same can be said about some of the diagnostic characters for Nebaliidae listed by Hessler (1984), and not included in this analysis. Among these probably are ‘the large endopod, with some segmentation indicated’, and ‘thoracopod 1 differing only slightly from thoracopods 2–8’. Furthermore, other previously used characters could not be placed with certainty to support the monophyly of the Nebaliidae due to a reduced or uncertain status of the feature in Nebaliopsis. For instance, the presence of a brood chamber formed by the thoracopods is not necessarily a synapomorphy for Nebaliidae as it is uncertain whether a brood chamber is present in Nebaliopsis (character 19, see character discussion). If the modification of the thoracopods in Nebaliopsis is interpreted as a type of brood chamber (different from that in Nebaliidae), there is no information available to polarize this character, and it appears equally likely that the structures in Nebaliopsis have been derived from a ‘normal’ leptostracan type of brood chamber as vice versa. The same argument can be applied to the large and rounded exopods seen in Nebaliidae (character 18). The thoracopod exopod in Nebaliopsis is small and it cannot be excluded from consideration that this has been modified from a type seen in the Nebaliidae as this character cannot be polarized with certainty.

Another possible position of Nebaliopsis is within the Nebaliidae (which then would be paraphyletic), as sister group to Nebaliella based on the fact that in both, pleopod 5 is longer than pleopod 6 (character 24), which is opposite to the condition in all other leptostracans (see figure 7B). The support for the clade containing Nebaliopsis, Nebaliella and Speonebalia is an unconvincing reversal from one segment to two segments in pleopod 6 (character 25).

The position of Paranebalia

Paranebalia is suggested to be the sister group to the rest of the recent Leptostraca (figure 7B) or to the Sarsinebalia/Dahlella/Nebalia clade (figure 7A). The first-mentioned position of Paranebalia (figure 7B) is supported by two characters: (1) the appearance of foliaceous thoracopods as a synapomorphy for the remaining leptostracans (character 17), whereas somewhat stenopodous thoracopods, in this interpretation, are retained from earlier in Paranebalia; and (2) a change in the exopod morphology from a long and slender appearance in Paranebalia to large and broad appearance in the remaining leptostracans (character 18), secondarily reduced in Nebaliopsis.

A perhaps more convincing position of Paranebalia is as sister-group to the Sarsinebalia/Dahlella/Nebalia clade (figure 7A). This is supported by two unique synapomorphies: reduction from four to three segments in the peduncle of antenna 2 (character 10), and reduction from two segments to one in pleopod 6 (character 25). Additional support is a long spine row on the exopod of pleopod 1 (character 22), which then must be assumed secondarily lost in Sarsinebalia. The interpretation
of the subterminal rostral spine (character 2) is uncertain, but is possibly also a synapomorphy for this clade, lost in a common ancestor to *Dahlella* and *Nebalia*. The largest problem with this position of *Paranebalia* is the fact that the limb morphology has to be assumed to have reversed to a stenopodous morphology with long slender exopods in *Paranebalia* (characters 17 and 18).

Comparison with literature

There are no published accounts of the phylogeny within the Leptostraca. Hessler (1984) divided the Leptostraca into two families, Nebaliopsidae and Nebaliidae. This division is in accordance with the hypothesis presented in figure 7A, even though the intrinsic phylogeny of the Nebaliidae was not commented on by Hessler (1984). As mentioned above, the support for the Nebaliidae in this analysis is found to be weak, and many of the characters mentioned in the diagnosis of Hessler (1984) are either plesiomorphies, present also in other crustaceans, or uncertain, as they can be interpreted as having been present in an ancestor to *Nebaliopsis*, and therefore not apomorphies to the Nebaliidae alone.

Cannon (1927) expressed the view that, with respect to the morphology of the thoracopods, *Paranebalia* constitutes a link between malacostracans, such as mysids, and *Nebalia*. Cannon (1927) considered that the trunk limbs of *Paranebalia* are not markedly foliaceous, the endopodites not very flattened, and the exopods closely resemble those of a mysid (see characters 17 and 18 herein). In conclusion he stated that the trunk limb morphology of *Paranebalia* leads to *Nebalia*, where the trunk limbs are much more foliaceous, and hence provide a more efficient filtering mechanism. Furthermore, Cannon (1927) saw *Nebaliopsis* as showing a development beyond *Nebalia*. Cannon’s (1927) view appears only to be compatible with an early derivation of *Paranebalia* within the Leptostraca, and with a derivation of *Nebaliopsis* after *Paranebalia* has branched off, presumably quite close to what is depicted in figure 7B.

A detailed phylogeny of most leptostracans is given by Walker-Smith (1993). That phylogeny differs from the present analysis in some respects, but a comparison is postponed until the work of Walker-Smith (1993) is available.

Summary

*Nebalia brucei*, new species is described from Zanzibar, Tanzania.

The monophyly of the Leptostraca is supported by few unique characters: ‘scale on antenna 1’ (character 8), ‘reduced pleopods 5 and 6’ (character 23) and perhaps by the ‘grooming palp on maxilla 1’ (character 15, reduced to a small stub in *Nebaliopsis*). Many of the characters previously mentioned to support the Leptostraca are either possible plesiomorphies (seven pleon segments, character 20), also found in other malacostracans (rostrum, character 1 and lacking A2 exopod, character 11), or depend on the position of *Nebaliopsis* (brood pouch, character 19 and direct development, character 27) or *Paranebalia* (characters 17 and 18).

The monophyly of *Nebalia*, the largest genus within the Leptostraca, is uncertain.

A cladistic analysis of the seven recognized leptostracan genera yielded two equally parsimonious cladograms, obtained by using different outgroup combinations (figure 7). Both convincingly supported the clade *Sarsinebalia* (*Dahlella*, *Nebalia*). No consensus could be obtained with regard to the relationship of the remaining four leptostracan genera, *Nebaliopsis*, *Nebaliella*, *Speonebalia* and...
**Paranebalia.** One cladogram had *Nebaliopsis* as sister-group to the remaining leptostracans, the other had *Paranebalia* in this position.

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**References**


Leptostraca), from southern California, with a key to the extant families and genera of the Leptostraca, *Journal of Crustacean Biology*, 16(2), 347–372.


### Appendix

| Taxa (7) | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|    |
| Anostraca (Outgr.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mysidacea (Outgr.) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Nebaliopsis | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Speonebalia | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Nebaliella | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| Paranebalia | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| Nebalia | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| Sarsinebalia | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| Dahlella | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |