

***Nebalia kensleyi*, a new species of leptostracan
(Crustacea: Phyllocarida) from Tomales Bay, California**

Todd A. Haney and Joel W. Martin

(TAH) Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007 U.S.A. and Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, California 90095 U.S.A., e-mail: haney@ucla.edu
(JWM) Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007 U.S.A., e-mail: jmartin@nhm.org

Abstract.—A new species of leptostracan, *Nebalia kensleyi*, is described from the coast of central California. It differs from other species of *Nebalia* most notably in the shape and color of the pigmented region of the eyes, armature of the antennule and antenna, extent that the carapace covers the abdominal somites, epimeron of pereonite 4, dentition of the protopod of the third and fourth pleopod, details of the pleonite border spination, and length of the terminal seta of the caudal furca.

The leptostracan Crustacea can be identified as such by the presence of a movable rostrum, a folded carapace that conceals the thoracic somites, eight phyllopodous thoracic limbs, seven abdominal somites, and conspicuous uropods (Kaestner 1980, Schram 1986). As currently understood, the order Leptostraca includes 39 valid species that have been classified among 10 genera and 3 families (Haney & Martin 2004). Collectively, these animals are found throughout the world ocean and across a wide variety of marine environments. To date, they have been recorded from the intertidal zone to depths exceeding 6000 m. Nine of the ten leptostracan genera erected to date are either monotypic or include relatively few described species. *Speonebalia cannoni* Bowman, Yager & Illiffe, 1985, the only species of the genus, is endemic to caves; the monotypic genus *Dahlella caldariensis* Hessler, 1984 is endemic to hydrothermal vents of the East Pacific Rise; *Nebaliopsis typica* Sars, 1887 is known only from the pelagic zone; and so on. The genus *Nebalia*, on the other hand, contains 21 of the 39 valid species that range from estuarine mudflats and rocky shores to coral

reefs to the bathyal zone. The actual diversity of the order Leptostraca well exceeds that which has been recorded, and the gap in our knowledge of these animals clearly is the result of both taxonomic and sampling bias.

Most of the leptostracan taxa are known from the Atlantic Ocean (see Clark 1932; Kensley 1976; Dahl 1985, 1990; Haney et al. 2001; Haney & Martin 2004). Only six species have been described from the entire Pacific Ocean basin. In this region, populations of leptostracans known from the waters of California have received the most attention because many carcinologists with an interest in the group (Gerken, Haney, Hessler, Martin, Vetter) have resided there. Nevertheless, leptostracans are known to occur throughout the Pacific; recent finds include new collections from Australia, Canada, Chile, China, Fiji, Japan, Mexico, New Zealand, and the United States (TAH, unpublished data). Authors often have referred to undescribed species (e.g., Thiele 1904, Wakabara 1965, Johnson 1970, Dahl 1985, Vetter 1996b, Olesen 1999), and indeed many of the aforementioned collections include species new to science.

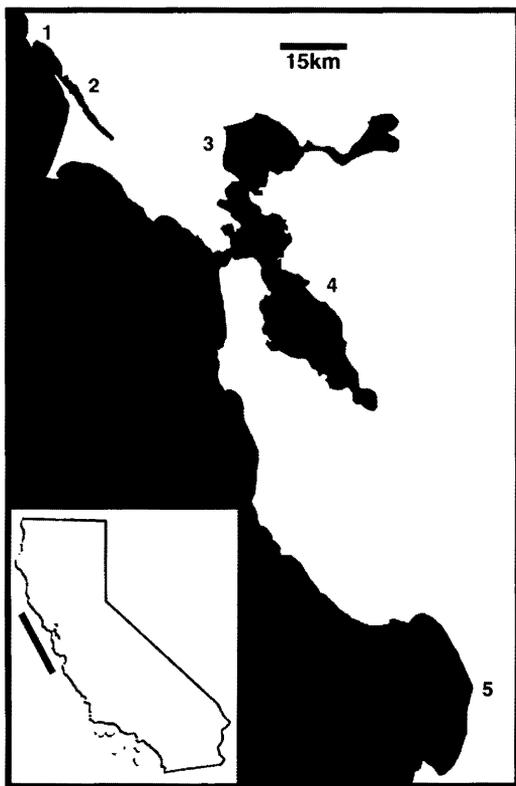


Fig. 1. Map of the central coast of California: 1, Bodega Bay; 2, Tomales Bay; 3, San Pablo Bay; 4, San Francisco Bay; 5, Monterey Bay. Black bar on inset shows position relative to the rest of the California coast.

Of those described from the Pacific, three species are known only from the coast of California: *Nebalia daytoni* Vetter, 1996a, *N. hessleri* Martin, Vetter, & Cash-Clark, 1996, and *N. gerkenae* Haney & Martin, 2000. A fourth species from the West Coast is *Nebalia pugettensis* (Clark, 1932), originally collected from Friday Harbor, Washington; currently, *N. pugettensis* is considered a nomen nudum (see Martin et al. 1996). Another species, *N. longicornis* Thomson, 1879, was originally described from Otago Harbor, South Island, New Zealand. Finally, *Dahlrella caldariensis* is restricted to hydrothermal vent fields of the East Pacific Rise. Herein, we describe the new species *N. kensleyi* from Tomales Bay, on the central coast of California (Fig. 1).

Materials and Methods

Leptostracans were collected by hand from estuarine mudflats of Tomales Bay, Marin County, California. The animals were found associated with an intertidal algal mat consisting primarily of the alga *Ulva*. Initially, specimens were placed directly into a solution of 95% ethyl alcohol; later, all specimens were transferred to 70% ethyl alcohol for long-term storage.

The external anatomy of female and male specimens is described. Illustrations were made with the aid of a camera lucida attached to a Wild M5APO dissecting microscope and a Nikon Labophot-2 compound microscope. Specimens were prepared for electron microscopy according to the method of Martin et al. (1996) and examined using Cambridge Stereoscan 360 and Hitachi S-3000N scanning electron microscopes. Length measurements were made from the base of the rostrum to the center of the posterior emargination of the carapace (dorsal carapace length) or to the tip of the caudal furca but excluding the setation (total length). The carapace was also measured in the lateral aspect from (1) the anteriormost to posteriormost extent of the margin (lateral carapace length) and (2) the dorsalmost to ventralmost extent of the margin (carapace height). The female holotype, male allotype, and 60 paratype specimens of the new species are deposited in the Crustacea collections of the Natural History Museum of Los Angeles County (LACM) and the National Museum of Natural History (USNM) (see Material Examined).

Systematic Account

Order Leptostraca Claus, 1880
 Family Nebaliidae Samouelle, 1819
 Genus *Nebalia* Leach, 1814
Nebalia kensleyi, new species
 Figs. 2–11

Type locality.—North Pacific Ocean, United States, California, Marin County,

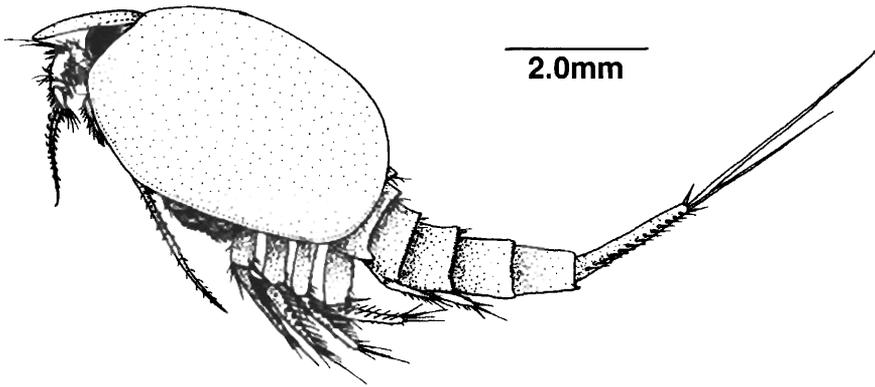


Fig. 2. *Nebalia kensleyi*, holotype female, LACM CR2004-003.1, left side.

Tomales Bay, White Gulch, collected from mudflat at low tide from surface of fine sediment beneath algal mat of *Ulva* sp.

Material examined.—Holotype female (Fig. 2), lateral carapace length 3.70 mm, dorsal carapace length 2.41 mm, carapace height 2.38 mm, total length 9.07 mm, type locality, collected 28 March 2004; collected by C. Winchell and A. Poopatanapong, LACM CR2004-003.1. Allotype male (Fig. 3A), total length 8.89 mm, same collection data, LACM CR2004-003.2. Paratype specimens, same collection data, LACM CR2004-003.3 (22 females, 11 males, 20 juveniles) and USNM 1072635 (10 females, 10 males, 10 juveniles).—North Pacific Ocean, United States, California, Marin County, Tomales Bay, White Gulch, station 1590-47, sandflats during -1.6 m tide; LACM CR1996-167.1 (19 specimens).—North Pacific Ocean, United States, California, Marin County, Tomales Bay; collected by L. Harris; no additional data; LACM CR2004-005.1 (5 specimens). Other selected paratype specimens were destroyed in the course of dissecting for illustrations and/or SEM preparation (2 females, 2 males, 2 juveniles).

Diagnosis.—Lateral carapace length up to 3.72 mm, with average lateral carapace length of females 3.36 mm ($n = 11$) and males 2.36 mm ($n = 10$). Eyestalk with pigmentation covering distal two-thirds. Fourth pleonite epimeron forming broad, subtrian-

gular process. Pleopod 4 protopod serrulate along posterior border, terminating in sharp tooth at posterolateral corner. Uropods in females approximately $2\times$ length of telson and sometimes greater than twice its length; terminal seta of furca $1.7\times$ length of furca. Spines along posterior dorsal borders of pleonites distally rounded, blunt.

Description of adult female.—Carapace (Figs. 2, 3B, 8A): Elliptical in lateral aspect, approximately 3.7 mm from anterior-most to posteriormost margin; average lateral carapace length in females is 3.36 mm ($n = 10$). Carapace measures 1.5 times longer than high (range = 1.45 to 1.69, mean = 1.53; $n = 10$). Carapace with small, u-shaped postero-dorsal indentation. Cuticle bearing minute, subtriangular teeth that appear both scattered and arranged in curved rows of 4 to 6 teeth (see Fig. 3B). Carapace bordered by narrow ridge, 12 to 15 μm wide. Posterior margin conceals pleonite three and sometimes extends to posterior margin of pleonite four.

Rostrum (Figs. 2, 3C): Long, clearly extending beyond distal margin of eyestalk, length of rostrum of holotype 1.27 mm. Average length of rostrum 1.20 mm (0.36 times lateral carapace length; $n = 10$ females); length approximately 2.5 times width. Rostrum rounded distally. Ventral projection, or “rostral keel,” more or less rectangular, with medial depression, proxi-

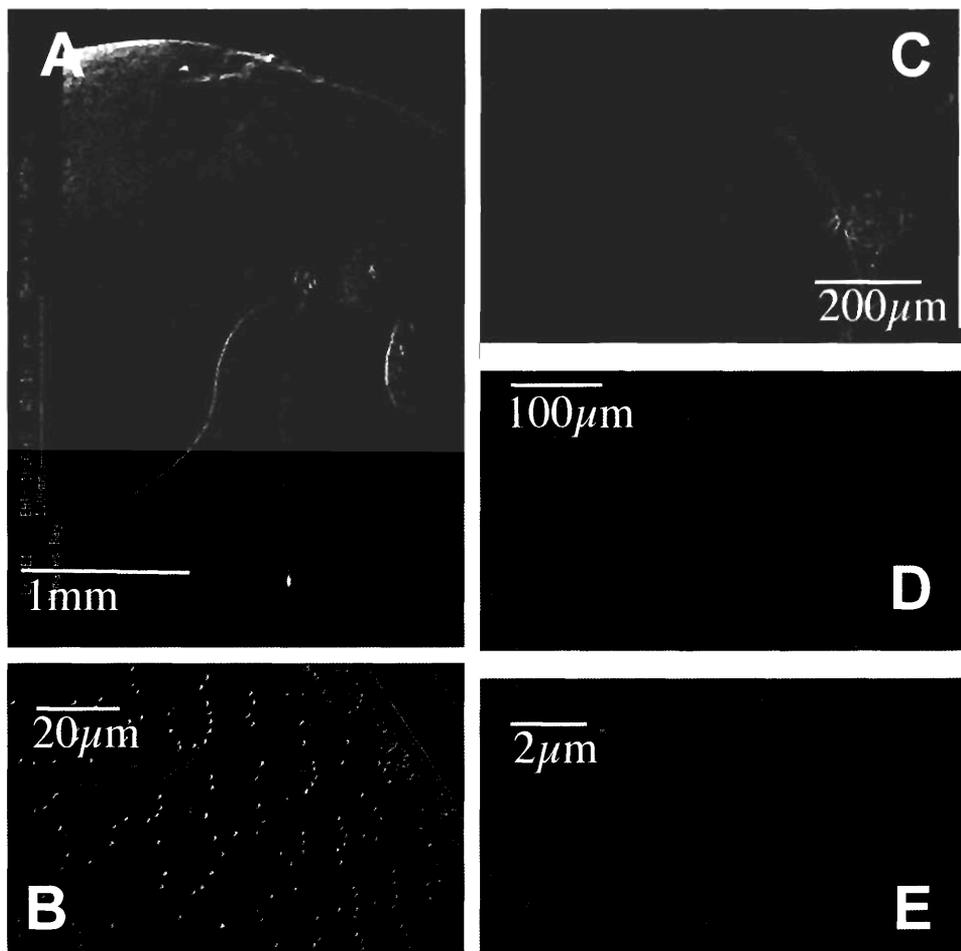


Fig. 3. *Nebalia kensleyi*, paratype male (A) and female (B–E), LACM CR2004-003.3, scanning electron micrographs: A, anterior half of paratype male, showing curvature of antennal flagellum; B, microstructure of cuticular surface of carapace margin; C, rostrum, left eye, and peduncular articles of antennule; D, left eye, with carapace and rostrum removed, with supraocular spine visible; E, microstructure of eye surface.

mal portion of which bears field of ctenate setae.

Compound eye (Figs. 2, 3C–E, 4A): Large, well developed, elongate-oval and slightly downturned distally. Length of eyestalk nearly two-thirds length of rostrum. Ommatidia with pigmentation covering distal two-thirds of eyestalk, where not covered by rostrum; pigmented area more or less reflecting shape of eye. Eyestalk margins relatively even, neither lobed nor subdivided nor tuberculate, with single, long plumose seta on dorsal surface at mid-length. Base of eyestalk with minute cutic-

ular scales, ventrodiscal region bearing patches of simple setae, surface minutely punctate (Fig. 3D). Ocular (supraorbital) scale sharply tapering to acute tip, relatively small, length of ocular scale approximately 0.6 times length of eyestalk; curved ventrally to form groove shaped to accommodate anterior surface of eyestalk, bearing minute setae (visible via SEM) especially along dorsal and dorsolateral surfaces.

Antennule (Figs. 2, 4A, 5B–F): Peduncle composed of 4 articles. First article stout, shorter than eyestalk, with anteroproximal region giving rise to supraocular scale. Sec-

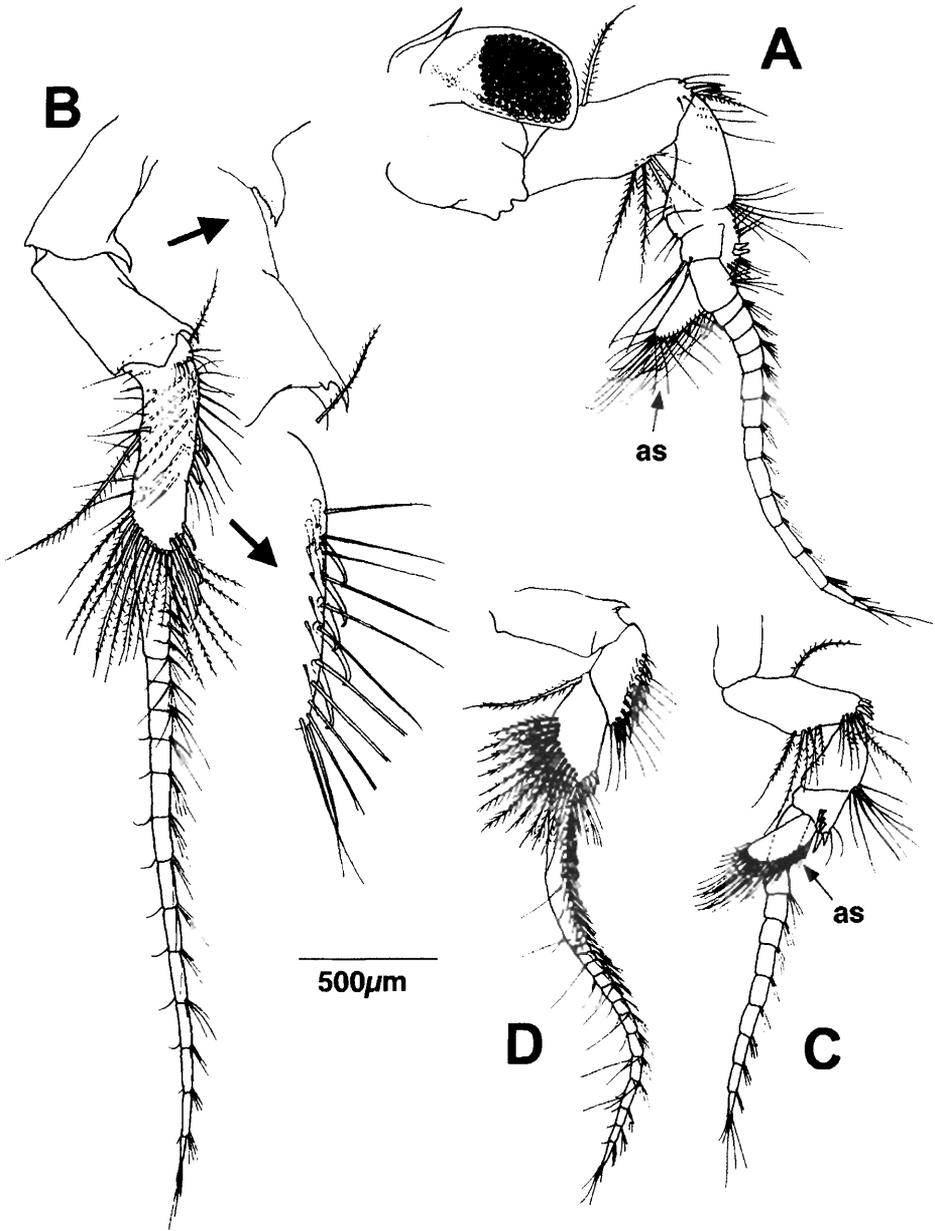


Fig. 4. *Nebalia kensleyi*, paratype female (A–B) and male (C–D), LACM CR2004-003.3: A, eystalk and antennule, right; B, antenna, arrows indicate expanded view of superior margin of peduncular articles; C, antennule, right; D, antenna, right, article one not drawn; as, antennular scale.

ond article widest at midpoint, with (1) single long, plumose seta arising proximally on anterior margin, (2) cluster of plumose setae arising from posterodorsal surface, several of which are as long or longer than the article itself, (3) group of 15 to 20 sim-

ple setae subterminally, and (4) 4 shorter, more robust setae and a single, long plumose seta arising from anterodistal surface. Third article shorter than second, widest distally, with terminal cluster of simple setae on anterior margin and long, simple seta

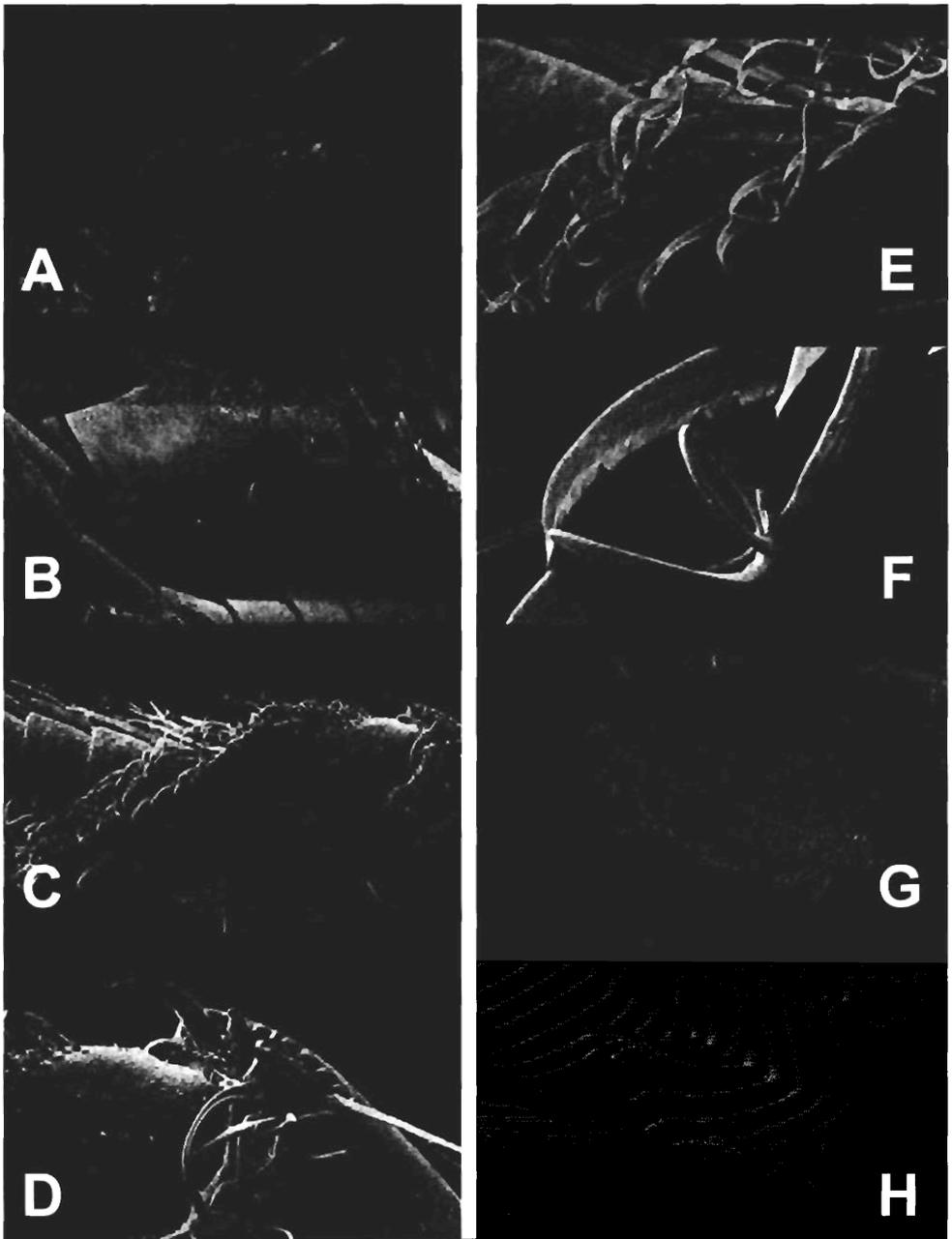


Fig. 5. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3, scanning electron micrographs: A, anterodistal spine of antennal article 1; B, antennal article 3 and articles of antennular flagellum; C, antennular scale, lateral face; D, articulation between antennular scale and peduncular article 4, showing anterodistal setae; E, setae of antennular scale, anterior margin; F, microstructure of same setae from antennular scale; G, mandibular palp, terminal article (article 3); H, microstructure of setal row of mandibular palp at 1000 \times magnification.

arising from posterodistal margin. Fourth article (Figs. 2, 4A, 5D) much shorter than third, with conspicuous row of 7 long simple setae and with 2, sometimes 3, robust spine-like setae along anterodistal border, distalmost of which is larger; both spines bear minute tubercles along curved outer surface and minute subterminal pore; with second row of 6 to 7 simple setae parallel to insertion of antennular scale; posterodistal surface bearing single simple seta, adjacent to and longer than antennular scale. Antennular scale (Figs. 2, 4A, 5C–F) elongate and nearly oval, approximately 0.35 mm long and 0.18 wide (average length to width ratio is 2.3; $n = 10$); posterior margin straight; anterior margin convex, bearing marginal rows of two distinct setal types, including (1) long simple setae, with fold or joint at mid-length (2) 19 to 24 setae that bear teeth along their length; cuticular surface of antennal scale bearing many minute pores. Flagellum well developed, at least 3.5 times length of antennular scale and composed of 11 to 14 articles, each of which bears a cluster of 5 to 6 stout aesthetascs or aesthetasc-like setae and 2 simple setae at anterodistal margin, one of the latter being much thinner and oriented at a 45- to 90-degree angle relative to the other setae.

Antenna (Figs. 2, 4B, 5A–B): Peduncle composed of 3 articles. First article subequal in length to second, and slightly broader than second and third article; bearing a broad-based anterodistal process that tapers sharply to form acute distal spine, this process in turn bearing still smaller spines (see Figs. 4B, 5A). Second article bearing a well defined anterodistal spine with minute tubercles on dorsal surface (Figs. 4B). Third article slightly longer than first or second; article bears multiple groupings of setae: (1) a small row of approximately 6 simple and 1 plumose setae proximally, (2) approximately 8 short, robust spine-like setae along proximal two-thirds of anterior margin, each associated with two longer simple setae, (3) a long plumose

seta arising from posterior margin, (4) a subterminal row of elongate, plumose setae, and (5) a terminal row of 5 robust simple setae, increasing in length from proximal to distalmost of these. Flagellum slightly longer than combined articles of peduncle, composed of 11 to 16 articles; each article with anterodistal group of 4 setae, one being quite small, as well as a single equally small subterminal seta along posterior (inferior) margin. See description of male antennule for discussion of sexual dimorphism.

Mandible (Figs. 5G–H, 6A): Molar process $3\times$ as long as wide, slightly shorter than first article of palp; apex forming concave grinding surface, with inner field composed of 20 to 25 rows of densely spaced teeth, with long spines on periphery. Incisor process much shorter than molar process, broadest basally, with short sharp teeth along inner (medial) face and acute terminal process. Mandibular palp 3-articulate; second article approximately $2\times$ as long as first, bearing two simple setae, one at mid-length on lateral face and one subterminally on anterior margin; second and third articles subequal; inferior margin of third article with (1) row of very fine, short setae on proximal quarter, (2) row of more plumose setae from proximal one-fifth length to terminus, (3) row of approximately 18 to 20 curved, dentate setae along entire distal margin; third article with row of several very fine, short setae on superior margin proximal to midlength (Fig. 6A).

First maxilla (Fig. 6B): Proximal endite with well-rounded medial margin bearing robust simple setae. Distal endite $1.6\times$ as long as proximal and bearing (1) a row of stout, trifid setae, (2) a row of distally broadened, spatulate setae and (3) several long pappose setae (for more detail, see Martin et al. 1996). Maxillipedal palp elongate, approximately $4\times$ longer than combined length of both endites of protopod, bearing proximal cluster of approximately 6 long setae and bearing approximately 13 setae, relatively evenly spaced, along its

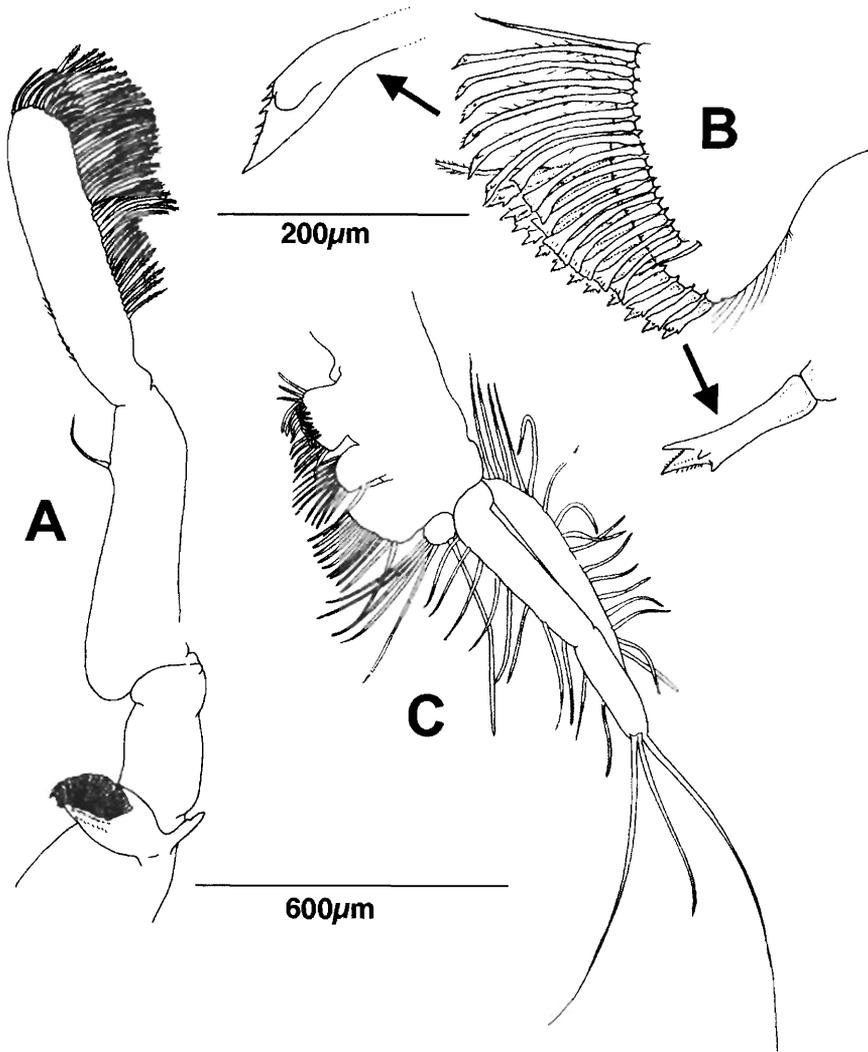


Fig. 6. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3: A, mandible, showing molar process, incisor, and mandibular palp; B, maxillule (maxilla 1), showing only second endite and setal types thereof (see Martin et al. 1996); C, maxilla.

length, the majority of which are approximately 0.25 times length of palp; setae bearing minute setules along their length, apex of seta with several longer setules and strongly recurved to give hook-like appearance (see Martin et al. 1996).

Second maxilla (Fig. 6C): Protopod subdivided into 4 endites. Endites 1 to 3 with rounded medial margin. Endites 1 and 3 approximately subequal and larger than endites 2 and 4; endite 2 approximately 2× size of endite 4. Setal types differ by endite:

endite 1 (basalmost endite) bearing row of simple setae and row of plumose setae; endite 2 with circumplumose setae; endite 3 with row of apically curved, simple setae and row of shorter plumodenticulate setae; endite 4 bearing row of approximately 8 elongate plumose setae. Endopod composed of 2 articles, basalmost of which is longest and subequal in length to exopod. Medial margin of endopod bearing sparse row of pappose setae, distal plumose seta of second article of endopod long, ap-

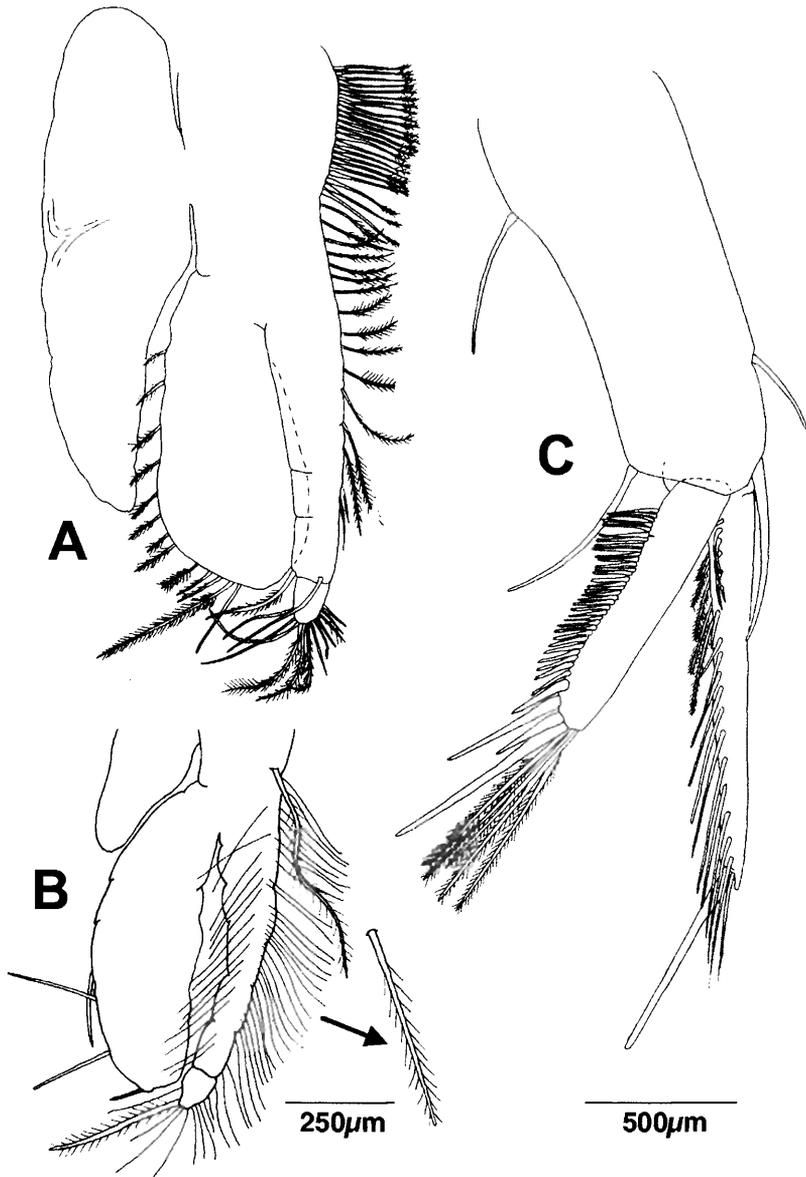


Fig. 7. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3: A, thoracopod 4, right, anterior face; B, thoracopod 8, right, anterior face; C, pleopod 1.

proaching length of entire limb. Lateral margin of exopod lined with plumose setae, distalmost seta of exopod subequal in length to exopod.

Thoracopods (Figs. 7A–B): Endopod of thoracopod 1 subequal to length of exopod. Endopod of thoracopods 2–8 slightly exceeding length of exopod. Distal article of

endopod of each thoracopod slightly enlarged, typically turned at angle from main axis, and bearing numerous long, plumose setae (Fig. 7A). Plumose setae of distal article of endopod extremely dense, with setules long and overlapping with those of adjacent setae on the same appendage and also with those of opposing (opposite side)

thoracopod, forming floor of brood pouch. Endopod weakly divided into articles, sometimes appearing to have 1, other times 2 or 3, suture lines separating distal articles. Articulation of distalmost segment most obvious in thoracopods 1 and 8. Exopod extending to approximately 0.8 to 0.9 length of endopod, unarmed or with scattered simple setae along margin, distally widest, always exceeding length of epipod. Exopods and epipods of thoracopods 3–6 broadest. Epipod decreasing in size relative to endopod in posterior limbs, such that epipod of thoracopod 8 is smallest.

Pleonites: Surface with scalloped cuticular scales that bear minute teeth along posterior border (Figs. 9C, 10A). Posterior borders of all pleonites bearing evenly spaced teeth (Figs. 2, 9A–D, 10A–B, 11A), with teeth rounded and blunt (Figs. 10A–B). Posterolateral margin of pleonite 4 expanded and forming a broad subtriangular process (Fig. 2, 8A, 9A–B); epimeron having a narrow cuticular ridge along anterior margin that parallels its outline. Pleonites 5 and 6 longer than pleonites 1–4.

Pleopods 1–4 (Figs. 2, 7C, 8A–C, 9A): Pleopod 1–4 stenopodous, consisting of protopod, endopod and exopod; protopod 4× width of endopod, with long, simple setae arising proximally and shorter subterminal seta arising from medial margin; with long, simple seta arising near base of endopod and exopod as shown (Figs. 7C, 8A, 9A). Endopod 10× longer than wide, slightly longer than exopod, 2-segmented; distalmost segment with acute process at apex and bearing long, robust terminal seta, lateral and medial borders of distal (longer) segment each with 17–23 plumose setae. Short basal segment giving rise to appendix interna bearing 3 short, stout, recurved hooks (retinacula) distally for coupling with similar hooks on the appendix interna of the opposing pleopod. Exopod slightly more than two-thirds length of protopod, with row of approximately 30 to 37 (average for females, 33; for males, 28) stout, serrate spines along lateral border, each with tri-

dentate tip (Figs. 2, 7C, 8A–B); 4 stout smooth spines on distolateral border, distalmost of which is longest at approximately 0.60 times length of exopod. Pleopod 2 protopod with proximal region bearing simple seta arising from lateral margin and cluster of 4 or 5 simple seta along medial margin; protopod also with long, stout spine near base of endopod and with long seta at base of exopod; protopod with row of saber-like teeth on anterolateral corner. Endopod lateral and medial borders each with 10–17 long natatory setae. Both endopod and exopod with long heavy seta at distal terminus. Exopod also with three robust setae distally, increasing in size toward apex. Exopod without row of stout serrate setae, instead bearing row of approximately 5–7 spine pairs; spine pair consists of 1 long and 1 short spine; additionally, the exopod bears 2 or 3 unpaired spines along distalmost margin; all paired and unpaired spines covered with minute triangular cuticular scales on all but tip, and with short subterminal, twisted seta of presumed sensory function (see Martin et al. 1996). Third and fourth pleopods similar to second. Pleopod 3 protopod bears 2 or 3 minute spines along posterior margin, sometimes with 1 or 2 still smaller spines between. Pleopod 4 protopod lacks setae and bears 4 or 5 acute serrations (i.e., spines) along posterior margin (Fig. 9A).

Pleopods 5 and 6: Pleopod 5 (Figs. 2, 9C, 11A) 2-segmented, uniramous, with 4–6 large conical setae along the distolateral and terminal border, increasing in size distally, and with approximately 20 to 30 plumose setae lining medial border of distal article; long setae on medial border somewhat “jointed” at approximately mid-length, where corrugations of cuticle appear to confer some flexibility on setal shaft (see Martin et al. 1996). Pleopod 6 (Figs. 2, 9D, 11B) 1-segmented, uniramous, with 4–6 lateral and distal spines, distalmost spine longest, exceeding length of article and extending beyond posterior margin of pleonite 6. Medial border also bearing few simple

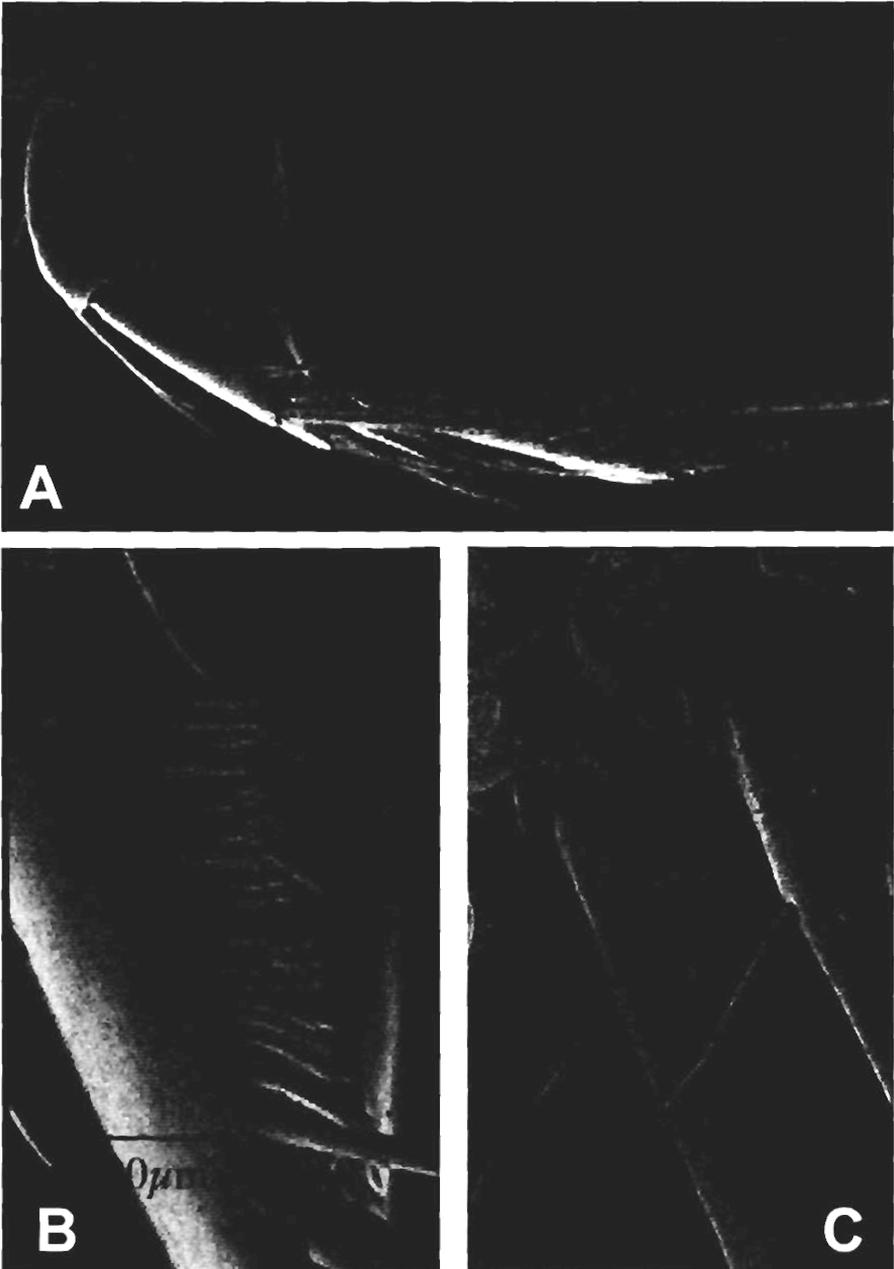


Fig. 8. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3, scanning electron micrographs: A, lateral view of pleopods 1–4, with ventral margin of carapace and pleonite 4 epimeron visible; B, setal row of pleopod 1 exopod; C, protopods of pleopods 2 and 3, showing long seta of posterior margin; with carapace removed, conical spine at base of protopod also visible.

setae. Terminus of pleopod where it gives rise to distalmost spine bearing cirlet of acute teeth. Lateral and distal spines of both pleopods 5 and 6 covered with short triangular scales and bearing short, twisted subterminal seta, as noted for similar setae of pleopods 1–4. Both pleopod pairs with broad triangular ventral process extending posteriorly between bases of rami, more acutely triangular and longer in pleopod 6.

Anal somite, anal plates, and uropods: Anal somite (pleonite 8) short, approximately as long as wide, averaging length of 0.75 mm ($n = 10$ females), rectangular or with sides slightly diverging posteriorly (Figs. 2, 11C). Anal plates sharply tapering from broad base to acute extremity, producing Y-shaped medial invagination (Figs. 10C, 11C). Uropod (Figs. 2, 11C) elongate, averaging length of 1.4 mm and ranging from slightly less than 1.4–2.5 times length of telson. Uropod with 12 or 13 robust setae along inner margin and with up to 22 robust setae along lateral margin, gradually increasing in length posteriorly with the distalmost setae $1.7\times$ length of uropod. Inner margins of each uropod also bear at least 15 fine, palmate setae.

Coloration.—In life, specimens appear mostly transparent except for the eyes, which are dark red. The eyes appear black in preserved specimens. Overall, the body appears off white to tan in both living and preserved specimens.

Description of the male.—The gonopores of males and females are located adjacent to the coxae of the fifth and sixth thoracopods, respectively. However, the gonopores can be difficult to observe. The most notable sexual dimorphisms in leptostracans include body size, shape of the carapace, and antennal morphology. The size of female specimens is generally greater than that of males; this holds true for *N. kensleyi*, for which the average carapace length is 2.36 mm and 3.36 mm in males and females, respectively. The average height of the carapace, as measured in lateral aspect, is 1.48 mm and 2.21 mm for males and females,

respectively. Whereas the ratio of length to height for the carapace differs little between the sexes, these measurements alone do not capture the differences observed in the shape of the carapace. Male specimens tend to have a carapace that is less ovate than that of females; this is in part because the ventral margin of the carapace is relatively straight in males whereas it is expanded and well rounded in female specimens. Certainly, the most conspicuous difference between male and female specimens is the morphology of the antenna. This feature was used by Clark (1932) to erect her new genus *Epinebalia*, now considered a junior synonym of *Nebalia*. Clark stated “the males represented a hitherto undescribed type characterized by forwardly directed, sickle-shaped antennae . . .” Sexual dimorphism of the antennae is common throughout the order Leptostraca; for instance, this feature appears notably different in males and females of *Paranebalia* Claus, 1880 (see Modlin 1991). In *Nebalia*, including *N. kensleyi*, the basal articles of the antennal flagellum of the adult male are largely fused, and the proximal half of the flagellum is curved, or sickle-shaped. The flagellum of the female, however, is straight and more posteriorly directed. Also, the antennal flagellum of the adult male is composed of more articles than that of the female; in *N. kensleyi*, the average is 26 and 16 for males and females, respectively.

Morphological variation.—Many aspects of leptostracan anatomy are remarkably conservative. One such example is the ultrastructure of the setae in the setal row present on the exopod of the first pleopod in many leptostracans. However, several features show considerable variation. The appearance of the eyestalk, for instance, varies markedly among leptostracan taxa; hence, the eye is one of the more taxonomically informative features. Attention should be paid to intraspecific anatomical differences as well. Such differences represent sexual dimorphism, as noted above, and ontogeny. The most notable variation is that in setal

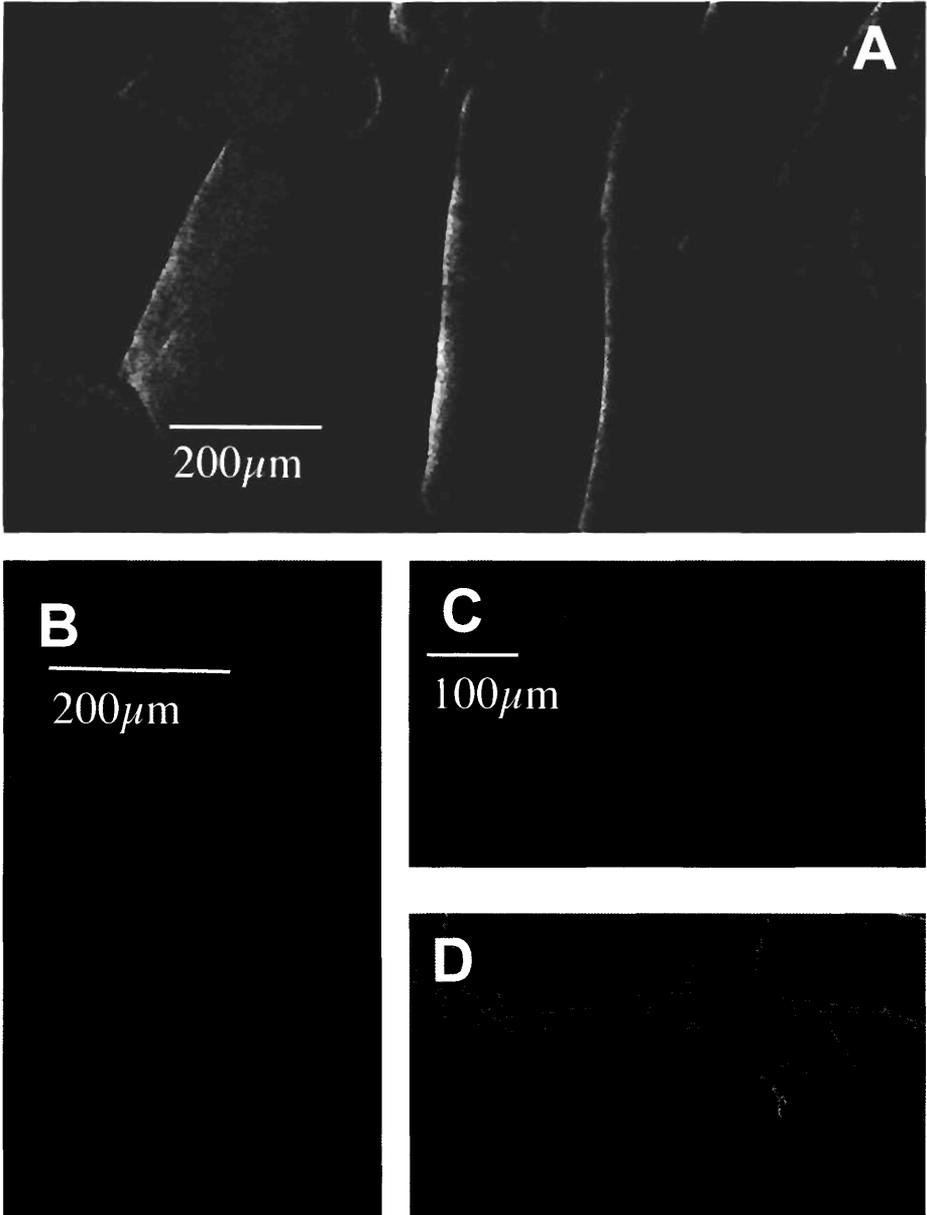


Fig. 9. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3, scanning electron micrographs: A, lateral view, with carapace removed, showing epipods of posteriormost thoracopods overlapping pleopod 1, protopods of pleopods 2–4, and ventrolateral margins of the respective pleonites; B, posterior margin dentition of pleonites 3 and 4; C, posterior margin pleopod 5, with exopod of pleopod 4 at bottom of field of view; D, pleopod 6.

characters. Dahl (1985) compared the size of specimens with several setal characters for two species: *Nebalia bipes* (O. Fabricius, 1780) and *N. pugettensis* (Clark, 1932); he concluded that the number of se-

tae was growth-related and recommended that setal characters not be considered important. Dahl (1985:137) reported variation in the arrangement of setae on the fourth article of the antennule for specimens he

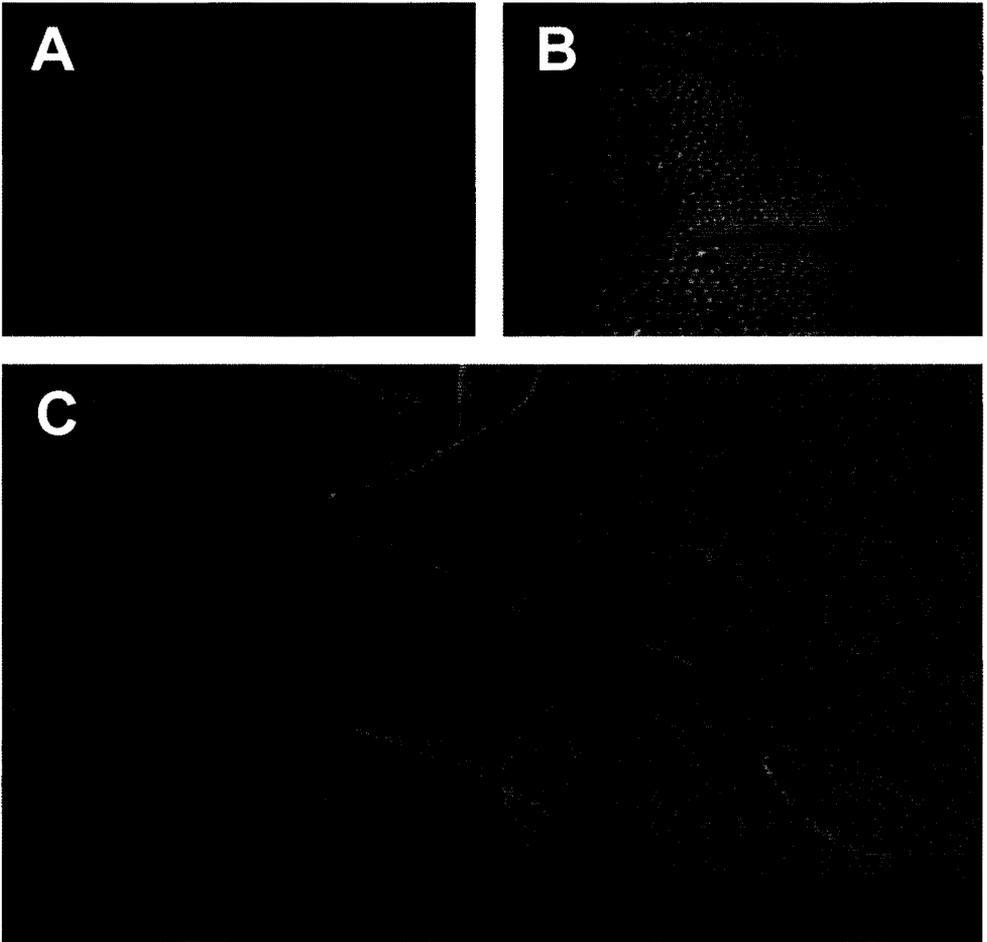


Fig. 10. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3, scanning electron micrographs: A, pleonite 6 posterior margin dentition; B, microstructure of same teeth; C, anal plates, ventral surface.

referred to *N. pugettensis*, and Wakabara (1965) illustrated variation in the same feature among specimens of *Nebalia* from Brazil. Study of *Nebalia kensleyi* and other species indicates that the number of articles of the antennular and antennal flagella also varies with size.

Distribution.—To date, the new species is known only from the region of the type locality, near the mouth of Tomales Bay, Marin County, California. Populations of *Nebalia* are known also from Bodega Bay, just to the north of the mouth of Tomales Bay, as well as from San Francisco Bay to the south. While it is possible that specimens from Bodega Bay could be attributed

to *N. kensleyi*, we have recognized fine-scale differences (e.g., patterns of cuticular ornamentation) among specimens from these collections. For this reason, we have chosen to await the analysis of molecular evidence from these and other populations. Comparisons of a fragment of the cytochrome oxidase subunit I (COI) gene reveal the following uncorrected sequence divergences from *N. kensleyi*: Bodega Bay, 0.2–0.4%; *N. gerkenae*, 0.4–1.1%, and Friday Harbor, 1.5–2.2% (Haney, unpublished data).

Etymology.—We are pleased to name the species for our departed friend and colleague Brian Kensley. Despite spending the

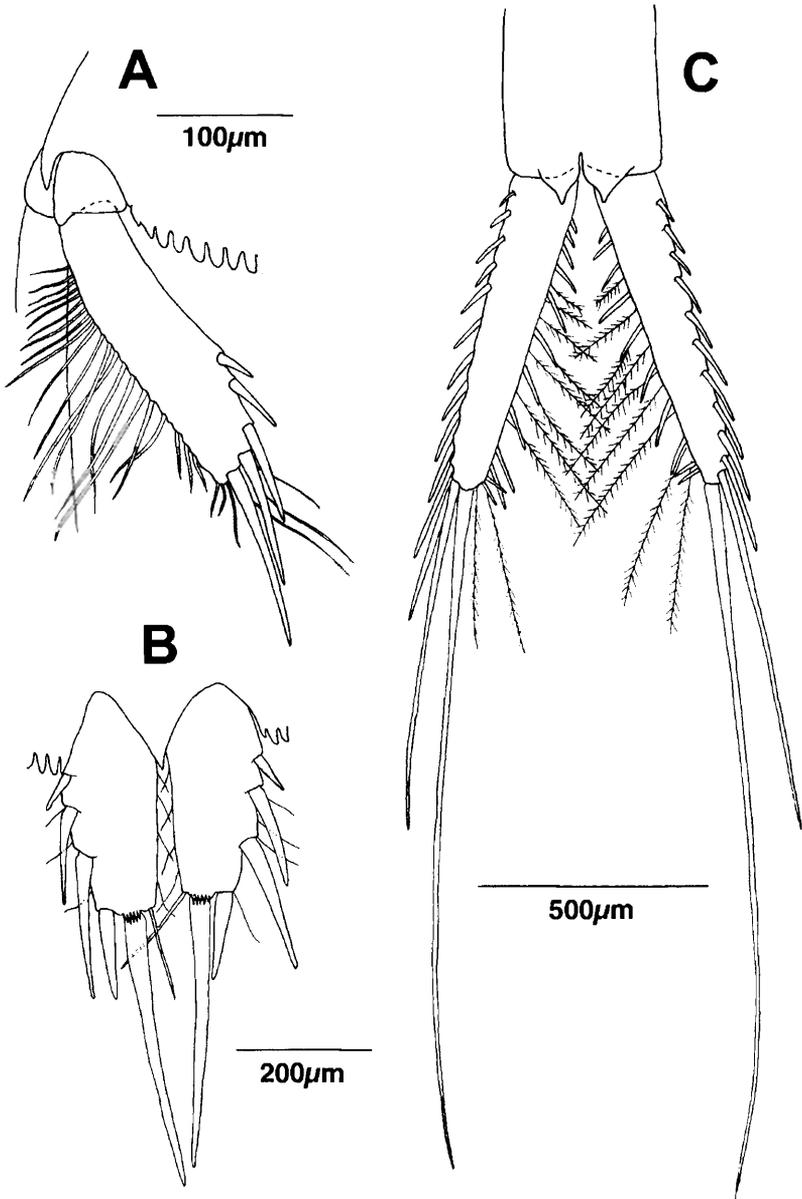


Fig. 11. *Nebalia kensleyi*, paratype female, LACM CR2004-003.3: A, pleopod 5, left; B, pleopod 6, left and right; C, anal somite, with anal plates, and uropods.

majority of his career working on isopod and decapod crustaceans, he also published on the discovery of a new leptostracan, *Nebalia ilheoensis* Kensley, 1976, from his home country of South Africa.

Remarks.—Understanding of leptostracan diversity along the western coast of North America has improved dramatically

in the last eight years. Prior to 1996, the literature included only scattered records of leptostracans from the west coast of the United States (see Packard 1883, La Follette 1914, Clark 1932, Menzies & Mohr 1952, Kozloff 1987). La Follette (1914) identified specimens from Laguna Beach, California, as *Nebalia bipes* Fabricius,

1780; we doubt the accuracy of this identification because La Follette (1914) offered no evidence for it and because all material of true *N. bipes* that is available for study is from the North Atlantic. All other collections from the region were either listed as unidentified or assigned to *N. pugettensis*. The description of *N. pugettensis* (as *Epinebalia*) was remarkably detailed for its time; however, the lack of suitable illustrations and loss of the original specimens now prevent reliable identification of this species. As Martin et al. (1996) declared *Nebalia pugettensis* a nomen nudum, four valid nominal species are now known from the West Coast. *Nebalia daytoni* and *N. hessleri* are both known from La Jolla, in southern California. *Nebalia gerkenae* occurs in Elkhorn Slough, Monterey Bay. *Nebalia kensleyi*, described herein, occurs in Tomales Bay (see Fig. 1). Although these are the only named taxa from the region, populations of *Nebalia* are now known to occur in numerous localities ranging from Alaska to southern Mexico. Collections from Alaska known to the authors include material from the holdings of the National Museum of Natural History (Washington, D.C.) and the Canadian Museum of Nature (Ottawa). Specimens of *Nebalia* have been noted from sites along the coast of Oregon (John Chapman, pers. comm.), including Coos Bay (Richard Fox, pers. comm.). We are not aware of collections available for study from the neritic zone of Oregon's coast. However, an undescribed leptostracan species has been collected from submerged wood both on the continental slope off Oregon and the Endeavor Segment of the Juan de Fuca Ridge at 2200 m. To date, only three species of the genus have been described from all of Latin America; these include *Nebalia lagartensis* Escobar-Briónes & Villalobos-Hiriart, 1995 from eastern Mexico, *N. patagonica* Dahl, 1990 from Tierra del Fuego in southern Argentina, and *N. falklandensis* Dahl, 1990 from the nearby Falkland Islands. The specimens of *Nebalia* reported from southern Brazil by

Wakabara (1965) remain unidentified. Many collections of *Nebalia* and *Paranebalia* have been made from Brazilian waters and are housed at the Museu Nacional (Rio de Janeiro) and Instituto Oceanográfico (São Paulo).

Nebalia kensleyi differs from the species of *Nebalia* described by Dahl (1990) from the southern hemisphere in that the superior margin of the eyestalk is even, lacking a protuberance or "papilla." A pronounced papilla is present on the eye of *N. antarctica* Dahl, 1990, *N. cannoni* Dahl, 1990, *N. falklandensis*, *N. longicornis* Thomson, 1879, and *N. patagonica*. Another character shared by these five species is the presence of only one robust seta, or "spine," on the fourth article of the antennule (see Dahl 1990). Whereas the latter character has been observed to exhibit intraspecific variation in taxa from the western coast of North America, nearly all specimens seen by us bear at least two robust setae on the fourth antennular article. *Nebalia kensleyi* can be distinguished from species known from the North Atlantic most notably by the (1) shape of the terminal article of the mandibular palp, (2) relative lengths of the endopod and exopod of the thoracic limbs, (3) relative lengths of the endopod and exopod of the pleopods, (4) expansion of the posterolateral margin of the fourth pereonite, (5) shape of the dentition on the posterior margin of the pleonites, and (6) shape of the anal plates. Dahl (1985) presented a taxonomic key to the shallow-water taxa of Europe that continues to be helpful for such comparisons. One of us (TAH) has examined the type series for these taxa, with the exception of type material for *N. bipes*, which is presumably no longer extant. Dahl (1985) stated that the type for *N. bipes* was housed in the collections of the Zoologisk Museum (Copenhagen). However, our survey of that collection and the holdings of Leptostraca at the Natural History Museum (London) revealed that the type is missing.

The new species shares many aspects of its morphology with other species known

from the west coast of the United States. However, *Nebalia kensleyi* differs from *N. daytoni* in such features as the eyestalk, which in the latter species is bilobed, and the antennular and antennal flagellum of the male. *Nebalia hessleri* is a large-bodied animal, with strikingly acute dentition along the posterior margins of its pleonites. The ecology of the new species also appears to differ. *Nebalia kensleyi* was collected from intertidal mudflats, whereas the two species from southern California were described from subtidal waters, *N. daytoni* from sands and *N. hessleri* from accumulations of organic matter at the head of a submarine canyon. Not surprisingly, *N. kensleyi* is quite similar in form to *N. gerkenae*, a species described from Monterey Bay (see Fig. 1). The eyes of *N. kensleyi* appear to be more heavily pigmented; that is, the area of pigmentation appears to cover a larger portion of the eyestalk. The dentition of the posterior margins of the pleonites also differs; in *N. gerkenae*, the teeth have parallel sides that taper distally to form a point (see Haney & Martin 2000: Fig. 8), whereas the teeth of *N. kensleyi* are distally rounded and blunt. Finally, the terminal seta of the caudal furca is considerably longer in *N. kensleyi* than that of other species on the West Coast.

Acknowledgments

Our taxonomic work was supported by an award from the PEET initiative of the Systematic Biology Program of the U.S. National Science Foundation (DEB 9978193 to J. W. Martin and D. Jacobs). We thank Leslie Harris, Chris Winchell and Amy Poopatanapong for collecting specimens from Tomales Bay. We are grateful to Lisa Haney and David Jacobs for their helpful comments and assistance with the collection of specimens from Bodega Bay, and we thank both Sarah Gerken and an anonymous reviewer for comments that improved the manuscript.

Literature Cited

- Bowman, T. E., J. Yager, & T. M. Iliffe. 1985. *Speonebalia cannoni*, n. gen., n. sp., from the Caicos Islands, the first hypogean leptostracan (Nebaliacea: Nebaliidae).—Proceedings of the Biological Society of Washington 98:439–446.
- Clark, A. E. 1932. *Nebalia Caboti*, n. sp., with observations on other Nebaliacea.—Transactions of the Royal Society of Canada 26:217–235.
- Claus, C. 1880. Grundzüge der Zoologie, 4th edition, vol. 1, Marburg, 822 pp.
- Dahl, E. 1985. Crustacea Leptostraca, principles of taxonomy and a revision of European shelf species.—Sarsia 70:135–165.
- . 1990. Records of *Nebalia* (Crustacea Leptostraca) from the Southern Hemisphere—a critical review.—Bulletin of the British Museum of Natural History (Zoology) 56(1):73–91.
- Escobar-Briones, E., & J. L. Villalobos-Hiriart. 1995. *Nebalia lagartensis* (Leptostraca) a new species from the Yucatán peninsula, Mexico.—Crustaceana 68:1–11.
- Fabricius, O. 1780. Fauna Groenlandica. Hafniae et Lipsiae, 452 pp.
- Haney, T. A., R. R. Hessler, & J. W. Martin. 2001. *Nebalia schizophthalma*, a new species of leptostracan (Crustacea, Malacostraca) from deep waters off the east coast of the United States.—Journal of Crustacean Biology 21:192–201.
- , & J. W. Martin. 2000. *Nebalia gerkenae*, a new species of leptostracan (Crustacea: Phyllocarida) from the Bennett Slough region of Monterey Bay, California.—Proceedings of the Biological Society of Washington 113:996–1014.
- , & J. W. Martin. 2004. A new genus and species of leptostracan (Crustacea: Malacostraca: Phyllocarida) from Guana Island, British Virgin Islands, and a review of leptostracan genera.—Journal of Natural History 38:447–469.
- Hessler, R. R. 1984. *Dahlrella caldariensis*, new genus, new species: a leptostracan (Crustacea, Malacostraca) from deep-sea hydrothermal vents.—Journal of Crustacean Biology 4:655–664.
- Johnson, D. S. 1970. Occurrence of the mud-shrimp *Nebalia* (Crustacea Leptostraca) at Singapore.—Journal of the Singapore National Academy of Science 2:50–52.
- Kaestner, A. 1980. Invertebrate Zoology, Crustacea, vol. 3. Robert E. Krieger Publishing Company, New York, 523 pp. (translated from second German edition by H. W. Levi and L. R. Levi)
- Kensley, B. 1976. The genus *Nebalia* in south and south-west Africa (Crustacea: Leptostraca).—Cimbebasia 4:156–162.
- Kozloff, E. N. 1987. Marine invertebrates of the Pacific Northwest. University of Washington Press, Seattle, 511 pp.

- La Follette, R. 1914. A *Nebalia* from Laguna Beach.—*Journal of Entomology and Zoology* 6:204–206.
- Leach, W. L. 1814. The zoological miscellany, being descriptions of new and interesting animals. McMillan, London, 149 pp.
- Martin, J. W., E. W. Vetter, & C. E. Cash-Clark. 1996. Description, external morphology, and natural history observations of *Nebalia hessleri*, new species (Phyllocarida: Leptostraca), from southern California, with a key to the extant families and genera of the Leptostraca.—*Journal of Crustacean Biology* 16:347–372.
- Menzies, R. J., & J. L. Mohr. 1952. The occurrence of the wood-boring crustacean *Limnoria* and of Nebaliacea in Morro Bay, California.—*The Wasmann Journal of Biology* 10:81–86.
- Modlin, R. F. 1991. *Paranebalia belizensis*, a new species from shallow waters off Belize, Central America (Crustacea: Malacostraca: Leptostraca). *Proceedings of the Biological Society of Washington* 104:603–612.
- Olesen, J. 1999. A new species of *Nebalia* (Crustacea, Leptostraca) from Unguja Island (Zanzibar), Tanzania, East Africa, with a phylogenetic analysis of leptostracan genera.—*Journal of Natural History* 33:1789–1809.
- Samouelle, G. 1819. The Entomologist's Useful Compendium; or An Introduction to the Knowledge of British Insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and the modern method of arranging the Classes Crustacea, Myriapoda, Spiders, Mites and Insects, from their affinities and structure, according to the views of Dr. Leach, Also an explanation of the terms used in entomology; a calendar of the times of appearance and usual situations of near 3000 species of British insects; with instructions for collecting and fitting up objects for the microscope. Thomas Boys, London, 496 pp.
- Sars, G. O. 1887. Report on the Phyllocarida collected by H.M.S. Challenger during the years 1873–76.—*Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873–76.*—*Zoology* 19:1–38.
- Schram, F. R. 1986. *Crustacea*. Oxford University Press, New York, 606 pp.
- Thiele, J. 1904. Die Leptostraken.—*Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition* 8: 1–26.
- Vetter, E. W. 1996a. *Nebalia daytoni*, n. sp., a leptostracan from southern California (Phyllocarida).—*Crustaceana* 69:379–386.
- . 1996b. Life-history patterns of two southern California *Nebalia* species (Crustacea: Leptostraca): the failure of form to predict function.—*Marine Biology* 127:131–141.
- Wakabara, Y. 1965. On *Nebalia* from Brazil (Leptostraca).—*Crustaceana* 9(3):245–248.

Associate Editor: Christopher B. Boyko