Nebalia gerkenae, a new species of leptostracan (Crustacea: Malacostraca: Phyllocarida) from the Bennett Slough region of Monterey Bay, California

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Abstract.—A new species of leptostracan crustacean, Nebalia gerkenae, is described from Bennett Slough, Monterey County, California. The species is similar to N. hessleri from deeper waters off La Jolla, California. It differs from N. hessleri in the shape and color of the pigmented region of the eyes, armature of the antennule and antenna, the degree that the carapace covers the abdominal somites, dentition of the protopod of the fourth pleopod, and details of the pleonite border spination. Variation in this spination is discussed, and guidelines are suggested for future descriptions of leptostracan species.

The Leptostraca are malacostracan crustaceans characterized in part by a hinged rostrum, bivalved carapace, phyllopodous thoracopods, and the presence of seven abdominal segments (Kaestner 1980, Schram 1986). In the marine environment, these animals are ubiquitous. They have been recorded from a wide range of habitats, including intertidal mudflats, mangrove lagoons, caves, submarine canyons, the bathypelagic zone, and hydrothermal vents. The order Leptostraca includes 32 nominal species in nine genera. However, the true diversity of the group far exceeds this number; the literature includes many references to collections of undescribed species (Dahl 1985, Vetter 1996b, Olesen 1999).

Historically, the leptostracan Crustacea of the Pacific Coast of the United States have all been identified as *Nebalia pugettensis* (Clark, 1932). Although sometimes present in large numbers (Vetter 1994, Gerken 1995), the leptostracan fauna of California is poorly known. Ecological studies on Leptostraca of southern California (Vet-

ter 1994, 1996a) led to the recognition of three taxa, two of which have been described. Nebalia daytoni Vetter, 1996a, was recorded from oligotrophic sands off the coast of San Diego. Nebalia hessleri Martin et al., 1996, was described from enriched sediments and detrital mats at the head of Scripps Canyon off La Jolla, California. Because Clark's (1932) description was inadequate and type material was not available, Martin et al. (1996) declared Nebalia pugettensis (Clark, 1932) a nomen nudum. Actually, the name Nebalia pugettensis is available, but a neotype must be established in order to avoid taxonomic confusion. Thus, in addition to N. pugettensis, two valid nominal taxa and one undescribed species have been reported from the coast of California. In addition, the identity of populations formerly referred to as N. pugettensis is uncertain. New collections of leptostracans from Monterey Bay represent a fourth species of Nebalia from the coast of California, described herein.

Materials and Methods

The leptostracans were collected from intertidal algal mats of *Chaetomorpha* sp. and *Gracilaria* sp. Salinity, recorded with a hand refractometer, was 33-34%c. Most specimens were placed directly into 75% ethyl alcohol, but five specimens were preserved frozen using dry ice and later transferred to a freezer held at -80° C.

Written descriptions and illustrations are of the mature females. Additionally, sexually dimorphic features are described. Illustrations were made with the aid of a camera lucida attached to a Wild M5APO dissecting microscope and a Nikon Labophot. Specimens were prepared for scanning electron microscopy according to the method of Martin et al. (1996) and examined with a Cambridge Stereoscan 360. 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 ramus but excluding the setation (total length). The carapace also was measured in the lateral aspect from the anterior to posterior margin (lateral carapace length) and from the dorsal to ventral margin (carapace height). The female holotype, male allotype, and 60 paratype specimens were deposited in the Crustacea collections of the Natural History Museum of Los Angeles County (LACM). Additionally, 54 paratype specimens (34 of which are juveniles) have been deposited in the National Museum of Natural History, Washington, D.C. (USNM).

Systematics

Order Leptostraca Claus, 1880 Family Nebaliidae Samouelle, 1819 Genus Nebalia Leach, 1814 Nebalia gerkenae, new species Figs. 1–12

Type locality.—United States, California, Monterey County, Bennett Slough, off Jetty Road, north side of bridge before entrance to Moss Landing State Beach, from mudflat at low tide from surface of fine sediment beneath algal mat consisting of *Gracilaria* sp. and *Chaetomorpha* sp.

Material examined.—Holotype female (Fig. 1a), LACM CR19990191, lateral carapace length 3.7 mm, dorsal carapace length 2.4 mm, carapace height 2.4 mm, total length 9.1 mm, collected 17 Oct 1999 by T. A. Haney; collected in type locality. Allotype male (Fig. 1d), total length 8.9 mm, same collection data, LACM CR19990192. Paratype specimens, same collection data, LACM CR19990193 (37 females, 16 males, 7 juveniles) and USNM 306877 (14 females, 6 males, 34 juveniles). Other specimens destroyed in the course of dissecting for illustrations and/or SEM preparation; these and frozen specimens declared non-paratypic. Non-type material: North Pacific Ocean, United States, California, Monterey County, Elkhorn Slough, 22 miles north of Pacific Grove, station 1590-47, sandflats during-1.6 m tide; collected 5 Feb 1947; collected by R/V Velero; LACM CR19470143; 13 specimens (12 females, 1 male) in 4 vials, North Pacific Ocean, United States, California, Monterey County, Elkhorn Slough; collected by E. W. Vetter; no additional data; LACM, unregistered; 8 specimens (4 females, 1 male, 3 juveniles; one female mounted on SEM stub).

Diagnosis.--Average total length of females 5.9 mm (n = 14), of males 5.4 mm (n = 6), average lateral carapace length of females 3.2 mm (n = 52), of males 2.4 mm (n = 23). Eye not lobed or subdivided, oval, widest in center, slightly down-turned and laterally compressed; pigmentation extensive, covering at least distal half of eye. Antennule with 2 heavy spine-like setae on apical face of fourth article. Antennular flagellum well developed, with 10 or more segments. Male antennule sickle-shaped, strongly upturned. Dorsum of fourth pleonite with posterior border bearing acute teeth; tooth of postero-lateral border of fourth pleonite (epimeron of Dahl 1985) slightly longer than others and up-turned. Base (proximal podomere or peduncle) of corresponding pleopod 4 minutely serrated along posterior border, terminating in sharp tooth at postero-lateral corner. Fifth pleopod with 4–6 large spine-like setae on disto-lateral border, with last spine longer than others and located terminally (directed posteriorly). Sixth pleopod with 4–6 spine-like setae along disto-lateral border, 6th seta terminally located terminally, two times as long as others. Rostrum with rectangular keel. Caudal rami in females approximately equal or greater than twice length of telson. Spines along posterior dorsal borders of pleonites acute.

Description of mature female.—Carapace (Fig. 1a): Elliptical laterally, approximately 1.5 to 1.6 times longer than high, with small, u-shaped posterodorsal indentation. Average lateral carapace length in females is 3.2 mm (n = 38). Carapace surface smooth, lacking scales. Posterior margin extending to posterior margin of pleonite three and sometimes extending slightly over anterior portion of pleonite four.

Rostrum (Figs. 1a, 2a–c): Rostrum long, clearly extending beyond eye, distally rounded, length approximately 2.4 to 2.6 times width. Average length of rostrum 1.3 mm (0.35 times lateral carapace length; n= 38 females). Keel rectangular (Fig. 2b), unpaired, with medial depression, depression bearing field of ctenate setae proximally (Fig. 2c).

Compound eye (Figs. 1b, 4c): Large, well developed, elongate-oval. Pigmentation extensive, covering distal half, with pigmented area more or less reflecting shape of eye. Not lobed or subdivided. Base of eyestalk with minute cuticular scales. Disto-ventral portion of eye bearing patch of simple setae (Fig. 4d). Ocular (supraorbital) plate sharply tapering to acute tip, relatively small, length of ocular plate approximately 0.5 times length of eyestalk, and bearing minute setae (visible via SEM) especially along dorsal and dorso-lateral surfaces.

Antennule (Figs. 3a, 5a-c): Peduncle composed of 4 articles. Second article wid-

est at midpoint, with single long, plumose seta arising proximally on anterior margin, cluster of much longer plumose setae arising subterminally, and group of many simple setae at apex. Third article shorter than second, widest distally, with terminal cluster of simple setae on anterior margin and long, simple seta arising from postero-distal margin. Fourth article (Fig. 5a, c) much shorter than third, with conspicuous row of at least 6 long setae increasing in length distally and with 2 robust spines along disto-lateral border; both spines bear minute tubercles along curved outer surface and minute subterminal pore. Antennular scale (Figs. 3a, 5a-c) oval, blade-like, with anterior margin convex and posterior margin straight; scale approximately as long as third peduncular article, bearing marginal rows of several distinct setal types along anterior margin, including long naked setae, stout, curved setae that are proximally smooth but bear large, blunt serrations distally, and longer, thinner setae that bear smaller, sharper teeth along their entire length. Surface of antennal scale bearing many minute pores. Flagellum well developed, at least 4 times length of antennular scale and composed of at least 10 to 15 articles.

Antenna (Figs. 3b, 4c): Peduncle composed of 3 articles, proximal 2 of which bear an acute disto-dorsal process (Fig. 4c, e, f). Process of first article (Fig. 4f) larger than that of second (Fig. 4e), much broader basally, and covered with minute teeth; process of second article (Fig. 4e) with minute tubercles on dorsal border. First article broader than second and third. First and second articles equal in length. Third article longer than first or second, and bearing approximately 8 short, robust spine-like setae along anterior margin, some of which are similar in appearance to those described for article 4 of antennule. Third peduncular article with proximal cluster of simple setae plus single pinnate seta; long, plumose seta arising from posterior margin at midlength, subequal in length to article; group of plu-



Fig. 1. *Nebalia gerkenae*, new species: a, holotype female, LACM CR19990191, left side; b, eye and ocular plate; c, pleonite four and protopod of pleopod one, postero-lateral margins; d, male allotype, LACM CR19990192, anterior part of left side.



Fig. 2. Nebalia gerkenae, new species: a, rostrum, ventral surface, damaged proximally; b, rostral keel; different specimen; c, rostral keel, proximal portion bearing setae.



Fig. 3. Nebalia gerkenae, new species, female: a, antennule, left, article one not drawn; b, antenna.



Fig. 4. *Nebalia gerkenae*, new species: a, male anterior, left side; b, antennal flagella of male, showing ribbon-like setae; c, antennal peduncle of male (morphology of which is similar to that of female); d, ventro-distal surface of left eye; e, distal spine of second article of peduncle; f, distal spine of first article of peduncle.

mose setae among short, robust setae of anterior margin, longer plumose setae distally. Flagellum composed of 10 to 16 articles. Flagellum slightly longer than combined articles of peduncle, each flagellar article with paired terminal and subterminal setae as well as single ventral seta, most of which are unarmed, and covered with minute cuticular scales. Antenna sexually dimorphic; in males, antenna sickle-shaped, strongly



Fig. 5. *Nebalia gerkenae*, new species, female: a, antennule, including distal articles of peduncle, antennular scale and basal articles of flagellum; b, ventral aspect of anterior features; c, distal face of fourth peduncular article of antennule, bearing distal spines and setal rows; d, distal article of right mandibular palp, medial face.

upcurved (Figs. 1d, 4a, b), with articles shorter than those of female, and bearing curved, ribbonlike setae.

Mandible (Figs. 5d, 6a): Molar process $3 \times$ as long as wide, subequal in length to first article of palp. Distal margin forming concave grinding surface, with inner field composed of rows of stout, densely spaced teeth, more widely spaced teeth and long

spines on periphery. Incisor process broad basally, with short sharp teeth along inner (medial) face and acute terminal process. Palp well developed, composed of 3 articles; third article subequal to second; second approximately $2\times$ as long as first, bearing two smooth setae, one at midlength and one subterminally. Setation of distal article complex (Fig. 5d), with short field of very



Fig. 6. Nebalia gerkenae, new species, female: a, mandible and mandibular palp, left side; b, maxilla, right side; c, maxillule, left side.

fine setae and plumose setae extending from proximal quarter to terminus, and with row of more stout setae overlying distal fourth of this row.

First maxilla (Fig. 6c): Proximal endite with rounded medial margin, bearing robust simple setae. Distal endite 1.6 times as long as proximal and carrying row of stout, spatulate setae just distal to row of trifid setae on outer margin. Several long plumose setae also present on distal part of endite. Trifid setae are nearly smooth basally, giving rise to smooth setules toward distal tip, and with three terminal teeth slightly longer than flanking teeth and bearing small pore (Martin et al. 1996). Palp elongate, approximately 6 times longer than combined length of both endites of protopod, bearing proximal cluster of approximately 6 long setae and 13 widely spaced setae along its length.

Second maxilla (Fig. 6b): Protopod subdivided into 4 endites, with endites 1 and 3 approximately equal in size and larger than endite 2 or 4. Endite 2 approximately $2\times$ as large as endite 4, well-rounded. Endopod more than 1.5 times longer than exopod, composed of 2 articles, proximal longest and subequal in length to exopod. All endites, endopod, and exopod bearing plumose setae; distal plumose setae of second article about length of entire limb. Distal seta of exopod subequal in length to exopod.

Thoracopods (Fig. 7a–f): Endopod of thoracopod 1 subequal to length of exopod. Endopod of thoracopods 2–8 longer than exopod. Distal article of endopod of each thoracopod slightly enlarged, typically turned at angle from main axis, and bearing numerous long, plumose setae (Figs. 5b, 7c). 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 (Fig. 5b). Endopod articulate, sometimes appearing to have 1, other times 2 or 3, suture lines separating distal articles. Articulation of distal segment obvious in thoracopods 1 and 8. Exopod extending to approximately 0.8 to 0.9 length of endopod, except in thoracopod 1 which is subequal to endopod, unarmed, with only scattered simple setae along margin.

Pleonites: Cuticle textured with denticular scales (Fig. 8e). Posterior borders of all pleonites dentate (Fig. 8b–d). Posterolateral margin of pleonite 4 expanded (Fig. 8a), with narrow cuticular ridge paralleling outline of the epimeron. Pleonites 5 and 6 longer than pleonites 1 to 4.

Pleopods 1-4: First pleopod (Figs. 9a, 10a, b) protopod 3.5 times width of endopod, with long, simple setae arising proximally and shorter subterminal seta medially; long, simple seta near base of endopod and exopod. Endopod slightly longer than exopod, 2-segmented; distal segment with acute process at apex bearing long, robust terminal seta, lateral and medial borders of distal (longer) segment each with 17-23 plumose setae. Appendix interna bearing 3 short, stout retinaculae distally. Exopod approximately two-thirds as long as protopod. Exopod with row of approximately 26-36 stout, serrate spines along lateral border (Fig. 10b-d), 4 stout smooth spine-like setae on distolateral border, distal longest, approximately $0.6 \times$ length of exopod, 18 plumose setae along medial margin. Pleopod 2 protopod proximal region bearing simple seta laterally, cluster of 4 to 5 simple setae medially, long, stout spine and long seta distally, row of minute, sabre-like teeth on anterolateral corner (not figured). Endopod lateral and medial borders each with 10-17 long natatory setae; long, stout seta distally; appendix interna with 3 retinaculae. Exopod with three robust setae distally, increasing in size toward apex, row of approximately 5 to 7 spine pairs consisting of long and short spine, 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). Ple-



Fig. 7. Nebalia gerkenae, new species, female thoracopods of right side (setation shown only for thoracopod three): a, thoracopod one; b, thoracopod two; c, thoracopod three; d, thoracopod six; e, thoracopod seven; f, thoracopod eight.

opod 4 protopod with 4-5 acute serrations along posterior margin (Figs. 1c, 10a, 11b), third and fourth pleopods otherwise similar to second.

Pleopods 5 and 6: Pleopod 5 (Fig. 11a) 2-segmented, uniramous, with 3 to 5 well developed spine-like setae along the distolateral and terminal borders, increasing in size distally, approximately 17 to 30 plumose setae lining medial border of distal article; long setae on medial border are somewhat "jointed" at approximately midlength, where corrugations of cuticle appear to confer some flexibility on setal shaft (see Martin et al. 1996). Pleopod 6 (Fig. 11c) 1segmented, uniramous, 4 to 6 robust lateral and distal setae, terminal seta longest, extending beyond posterior margin of pleonite



Fig. 8. *Nebalia gerkenae*, new species, female: a, pleonite four, lateral margin; b, pleonite five, dentition of distal margin (with surface of pleonite six visible to the right); c, pleonite five, tooth on distal margin; d, pleonite six, distal margin, showing variation in form of dentition; e, dorsolateral surface of pleonite six (area shown on righthand side of Fig. 8b), showing texture of cuticle.

6. Medial border also bearing few simple setae. Terminus of pleopod where it gives rise to distalmost spine bearing circlet 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 to 4. Both pleopod pairs with broad triangular ventral process extending posteriorly between bases of rami (Fig. 11a), more acutely triangular and longer in pleopod 6.

Telson, anal plates, and caudal rami: Telson short, approximately as long as wide, averaging length of 0.8 mm (n = 38 females), rectangular, sides slightly diverging posteriorly (Fig. 12a, b). Anal plates sharply tapering from broad base to acute extremity, producing Y-shaped medial invagination (Fig. 12a). Caudal rami (Fig. 12b,



Fig. 9. Nebalia gerkenae, new species, female: a, pleopod one, right; b, pleopod two, right.

c) elongate, averaging length of 1.0 mm $(1.4 \times -2.5 \times \text{ length of telson})$. Rami each with 12 to 13 robust setae along inner margin, about 22 robust setae along lateral margin, gradually increasing in length posteriorly with length of two distal setae more than two-thirds length of ramus. Inner margins of each ramus also bear at least 15 fine, pinnate setae.

Sexual dimorphism.—Dahl (1985) recommended that male specimens not be used in species descriptions. While not in disagreement with Dahl's focus on the morphology of the female leptostracan, we suggest that any sexual dimorphism also be noted in descriptions of new taxa. Gerken (1995) found males to constitute a relatively small proportion of the individuals in a given sample, typically representing less than 15% of the specimens collected. However, Gerken (1995) noted that many of the individuals in each sample were unidenti-



Fig. 10. *Nebalia gerkenae*, new species, female: a, pleopods one-four, right side; b, exopod of pleopod one; c, distal portion of setal row of pleopod one exopod; d, microstructure of setae in setal row of pleopod one exopod.



Fig. 11. Nebalia gerkenae, new species, female: a, pleopod five, right and left; b, pleopod four, right side; c, pleopod six, left side.







Fig. 12. Nebalia gerkenae, new species, female: a, anal plates; b, caudal rami, same individual; c, detail of caudal ramus, right side.

fied, so it could have been the case that many of the unidentified specimens were in fact males. Males were more common in our collections of N. gerkenae, constituting 30% of those individuals for which sex could be determined. As also noted for males of N. hessleri and Clark's (1932) "Nebalia pugettensis," the second antenna of the male of the new species is strongly recurved toward the anterior. Although the curvature of the male's antennular flagellum varies among individuals (see Martin et al. 1996), it differs considerably from the relatively straight and posteriorly directed antennular flagellum of the female. The articles of the flagellum of the male are also notably shorter than those of the female, and the setation of the flagellar articles differs greatly. In males, each flagellar article bears a simple seta and a curved, ribbonlike setae, as described earlier (Fig. 4a, b). The male is typically smaller than the female, with an average lateral carapace length of 2.6 mm (n = 17).

Color.—In life, specimens are mostly transparent except for the eyes, which are dark red. The eyes are black in preserved specimens. Overall, the body appears cream-colored in both living and preserved specimens.

Distribution.—To date, the new species is known only from the region of the type locality to the mouth of Elkhorn Slough, Monterey County. The extent to which populations of these animals occur in the upper reaches of Elkhorn Slough is unknown.

Etymology.—We are pleased to name the species for Sarah Anne Gerken, whose MS thesis on the biology of this species (Gerken 1995, as *Nebalia pugettensis*) provided a wealth of information on the animal's natural history.

Remarks.—The new species is most similar in appearance to *Nebalia hessleri* Martin et al., 1996, described from detrital mats at the head of the Scripps submarine canyon. The similarity in the morphology of appendages is striking. However, *Nebalia gerkenae* can be easily differentiated from N. hessleri by body size, features of the antennule and antenna, length of the carapace relative to the body, and the dentition of the posterior margins of the pleonites. The average total length (excluding setation) of female and male specimens of N. gerkenae is 5.9 mm and 5.4 mm, respectively, whereas the average total length of N. hessleri was reported as 9.8 mm. The apical face of the fourth article of the antennular peduncle bears a row of four to five robust spines in N. hessleri (see Martin et al. 1996: fig. 4b), whereas only two such spines are present in N. gerkenae (Figs. 3a, 5c); this number did not vary among the specimens for which it was examined (n = 20). Also, the antennular scale arising from the fourth peduncular article of N. hessleri is posteriorly directed and crosses the flagellum at an angle. In N. gerkenae, however, the antennular scale is typically parallel to the flagellum. The first two articles of the antennal peduncle of N. hessleri each bear an acute process distally, and that of the first (proximal) article is considerably smaller; in N. gerkenae, the process of the first article is much larger than that of the second article (Fig. 4c). Males possess a sickle-shaped antennule in both taxa. The shape of the endopod of the first pleopod differs somewhat between the two species; the endopod tapers more sharply in N. gerkenae and bears a longer spine at its apex. The dentition of the posterior border of each pleonite varies considerably with position along the border; i.e., the apex of the dorsal teeth is acute, whereas that of the teeth occurring on the ventral margin is blunt. Thus, in descriptions of leptostracan taxa, reference should be given to the exact position as well as the shape of the teeth along the posterior margin of the pleonites. In N. hessleri, the teeth of the posterior margin of pleonites four through seven taper sharply, producing a fine point distally. The teeth along the dorsal and dorsolateral pleonite margins of N. gerkenae taper less strongly; the lateral margins of each tooth are parallel until midlength, at which point they converge to form a subtriangular apex. The dentition of the posterior margin of the fourth pleopod also differs between these two taxa, with the protopod of N. *hessleri* bearing approximately eight acute serrations and that of N. *gerkenae* bearing only four or five serrations (Figs. 1c, 11b).

Undoubtedly, close study of leptostracan populations along the western coast of the United States will result in the discovery of additional leptostracan species that will be new to science. Populations of unidentified leptostracans are known, for instance, from intertidal mudflats of Marina del Rey and Long Beach, California. Specimens received from Friday Harbor, Washington, also appear to represent multiple undescribed taxa (one of which is likely the species described as N. pugettensis by Clark). Extensive collections of southern Californian leptostracans were made during the cruises of the R/V Velero IV, comprising 135 lots and a total of 443 specimens; however, only four of these lots, including material collected near the type locality of N. gerkenae, have been examined.

Perhaps more surprising to us than the similarity of N. gerkenae to N. hessleri is the similarity of N. gerkenae to species of Leptostraca from eastern Africa (i.e., N. brucei Olesen, 1999) and the Red Sea (i.e., N. marerubri Wägele, 1983). Even when examined at high magnification, some characters in this group continue to exhibit considerable morphological similarity across large geographic scales. For example, features such as the setal row of pleopod one, mouthparts, and dentition of the pleonite margins of N. gerkenae are nearly indistinguishable among these species (see Wägele 1983: figs. 9-11, 13; Olesen 1999: fig. 6c, e). However, other morphological differences clearly rule out the possibility that the new species is conspecific with either of these taxa. This great morphological similarity, at least as pertains to some features, in part necessitates our use of electron microscopy and detailed figures in the description of new species of Leptostraca.

We recommend that future reports of new leptostracan species include detailed descriptions and SEM and line illustrations of the following features: antennular peduncle, antennular scale, antennal peduncle, antennal flagellum of male, rostrum and rostral keel, eye and ocular spine, carapace, setal row of exopod of pleopod one, posterior margins of protopods of pleopods, dentition of the postero-dorsal margin of pleonites 5-7, and the anal plate. Consideration should also be given to the considerable intraspecific variability exhibited for some features; such is the case, for instance, with the number of articles of the flagella of the antennule and antenna in N. gerkenae.

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