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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

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ABSTRACT

A new and relatively large species of leptostracan crustacean, *Nebalia hessleri*, is described from enriched sediments and detrital mats off southern California. The new species is characterized by its size, possession of "normal" (versus lobed) eyes, rectangular and unpaired subrostral keel, acute dentition of the posterior pleonite borders, and caudal furca approximately twice the length of the telson. Clark's *Nebalia pugettensis* (Clark, 1932) is herein declared a nomen nudum. The new species differs from specimens at Friday Harbor, Puget Sound, Washington, in the form of the epimeron of the fourth pleonite, the dentition along the posterior border of the fifth through seventh pleonites, the relative length of the telson and caudal furca, and size. Coloration may also serve to distinguish *N. hessleri* from other species if egg-bearing females are available; eggs of *N. hessleri* are cream or gold colored. The new species differs from a currently unnamed sympatric species that occurs in adjacent sand flats (Vetter, in press) primarily in the morphology of the first antenna, which is greatly reduced in the sand-flat species, and the eye, which has unique dorsal and ventral corneal protrusions in the sand-flat species.

Selected aspects of the external morphology of the new species are illustrated via scanning electron microscopy, highlighting a previously unappreciated diversity of spines and setal types. Based on these photographs, some limbs are suggested as having sensory functions. Selected features of the Friday Harbor specimens also are illustrated via SEM. Limited notes on feeding behavior and oxygen level tolerances are provided, based on preliminary laboratory observations. Finally, we include a morphology-based key to identification of the currently recognized families and genera of the Leptostraca.

The phyllocarid crustacean order Leptostraca is currently recognized as comprising two extant families: Nebaliopsidae Hessler, 1984, containing only the genus *Nebaliopsis* G. O. Sars, 1887, and Nebaliidae Baird, 1850 (emended by Hessler, 1984), containing the genera *Nebalia* Leach, 1814, *Paranebalia* Claus, 1880, *Nebaliella* Thiele, 1904, *Dahlella* Hessler, 1984, *Sarsinebalia* Dahl, 1985, and *Speonebalia* Bowman, Yager, and Iliffe, 1985 (see Hessler, 1984; Dahl, 1985; Bowman *et al.*, 1985). In California waters, only the genus *Nebalia* has been reported, and it has been assumed until recently that all specimens belong to a single species, *Nebalia pugettensis* (Clark, 1932) (originally described as *Epinebalia pugettensis*, transferred to *Nebalia* by Cannon, 1960). Because of similarities between Clark's description of *N. pugettensis* and the species described in this paper, it may be necessary to revive Clark's original genus, *Epinebalia*, at some later date (see Discussion).

Recent and ongoing ecological work in the area of La Jolla, San Diego, California, by one of us (EWV) (Vetter, 1994, 1995, and in press) has demonstrated that there are at least four leptostracan species found along the coast of western North America, only one of which (*N. pugettensis*) has been previously described (and that one incompletely so), with the description of a second species currently in press (Vetter, in press). In this study, we declare the sole previously described west coast species, *N. pugettensis* (Clark, 1932), to be a nomen nudum, and describe a new species from detrital mats in submarine canyons off the coast of southern California. The average number of individuals in these mats has been estimated to reach 1.5 million/m^2, contributing to the highest density of any macrofaunal assemblage yet reported (Vetter, 1994; see below and Vetter, 1995, for more detailed habitat notes). In addition, we extend what little is known about leptostracan ultrastructural morphology by describing selected morphological features using scanning electron microscopy; compare some of these features to those of specimens collected near Friday Harbor, Washington (the original collecting site of *N. pugettensis*); provide preliminary observations on the natural history (feeding and oxygen level tolerances) of the new species; and provide a key to the extant families and genera of the Leptostraca.

Materials and Methods

Animals were collected during ecological investigations of the benthic community off the coast of La Jolla, California, U.S.A. The habitat consists of detrital mats with low oxygen levels (see Vetter, 1995) in submarine canyons. The habitat is dynamic, with the detrital mats expanding during summer periods of calm and contracting when surge, generated by winter storms, moves some or all of the material deeper into the canyon. The mats are composed primarily of surf grass (*Phyllospadix* spp.) and kelp (*Macrocystis pyrifera* (Linnaeus, 1771), *Egregia menziesii* (Turner, 1808), *Laminaria* spp., *Pterygophora californica* Ruprecht, 1852), though other algae including *Sargassum* spp., *Ulva* sp., *Pelvetia fastigiata* Setchell and Gardner, 1917, and a variety of small red algae are sometimes common. Collections from which the specimens described herein were taken were made on 29 February 1992 using an air-powered suction device on a detrital mat at the head of Scripps Canyon, approximately 1,000 m north of the Scripps Institution of Oceanography pier, at approximately 32°52.5′N, 117°15.5′W, at a depth of 60 feet (19 m).

The detrital mats were sampled at least monthly, as weather permitted. Cores were taken using a large steel cylinder (0.185 m^2), which was used to isolate a portion of the mat. Hedge trimmers (shears) were used to cut the detritus along the inner wall of the cylinder, and then a vacuum lift was used to remove the material from within the cylinder.

Animals were separated from the detritus by flotation and were then skimmed off, the remaining water poured through a 500-μm sieve, and the process repeated. Animals were preserved in 4% Formalin in sea water and later transferred to 70% ethyl alcohol.

Specimens of a second species of *Nebalia* were collected from a mud flat at Argyle Bay, Friday Harbor, San Juan Island, Washington, U.S.A., a site closer to Clark's (1932) collecting locality for *N. pugettensis*. These specimens were collected with a 7.62-cm diameter push core and then sieved on a 500-μm screen. Leptostracans were found in samples associated with 3 patches of decaying wood and patches of the green alga *Ulva*.

Written descriptions and illustrations are of the mature females, as recommended by Dahl (1985), and follow the guidelines and terminology provided by him for leptostracan systematics. However, because we are employing scanning electron microscopy (SEM), we have added additional descriptive comments that may or may not prove to be of taxonomic importance once similar structures in other leptostracans become known. In addition, the second antenna of the male is described because of its potential importance as a taxonomic character. Illustrations were made with the aid of a Wild M5APO dissecting microscope and a Nikon Labophot, both equipped with a camera lucida. Specimens subjected to scanning electron microscopy were gradually dehydrated to 100% ethanol and transferred to hexamethyldisilazane (HMDS) for air drying (see Nation, 1983). Slight sonication was used on some samples to clean the cuticular surface. Specimens to be sonicated were rehydrated to distilled water and subjected to brief (5–10-s) bursts in an ultrasonic cleaner with low amounts of a commercial surfactant added for cleaning; these specimens then underwent ethanol dehydration and HMDS drying. After being mounted on stubs, specimens were sputter-coated with gold and examined using a Cambridge Stereoscan 360 at 10kV. Length measurements were made from the tip of the rostrum to the center of the posterior emargination of the carapace (for carapace length) or to the tip of the caudal furca but excluding the setation (for total length). The female holotype, male allotype, 40 designated female paratypes, and many other (nonparatypic) specimens of the new species are deposited in the Crustacea collections of the Natural History Museum of Los Angeles County (LACM). Additional paratypes have been deposited in the National Museum of Natural History, Washington, D.C. (USNM), the California Academy of Sciences, San Francisco (CAS), and the Scripps Institution of Oceanography collection (SIO).

Cursory observations of feeding behavior were made in the laboratory. To keep animals within the focal range of a vertically and horizontally tracking side-mounted dissecting microscope, narrow aquaria (30 × 30 × 3 cm) were constructed. This arrangement allowed individuals to be followed for extended periods of time over the entire volume of the aquarium.

To determine whether the new species has a greater tolerance to low oxygen and elevated hydrogen sulfide relative to other animals from the same or nearby habitats, a preliminary and somewhat crude experiment was conducted. The new species, the amphipod *Orchomene limodes* Meador and Present, 1985 (also from the detrital mats), and several other species from the mats and from the adjacent sandy plain environment were placed individually in 300-ml flasks of anoxic sea water with either 1.23 mmol or 2.08 mmol of hydrogen sulfide. Virtually all oxygen was removed from the sea water by bubbling nitrogen gas through it for 30 min (verified with an oxygen meter), after which time the animals were introduced and the container was sealed while small nitrogen bubbles were still present in the water. The flasks were then maintained in a constant 18°C water bath, and the condition of the animals was checked every 30 min.

Results

Systematics

Nebalia pugettensis (Clark, 1932)

This species was originally described as a new species of a new genus, *Epinebalia*, by Clark (1932). The original description is vague, not only as to the collecting locality (given only as "from Puget Sound"), but also as to the features that would differentiate this species from others in the genus (e.g., see Dahl, 1985). There were few illustrations provided (2 plates) other than micrographs, which were of rather low resolution. Furthermore, and most unfortunately, we have been unable to locate any type specimens in searching the following institutions: The Natural History Museum of Los Angeles County, the California Academy of Sciences, the Canadian Museum of Nature, the U.S. National Museum of Natural History, the Royal British Columbia Museum, the invertebrate teaching collections at Friday Harbor Laboratory, Friday Harbor, Washington, U.S.A., and the Redpath Museum of McGill University in Montreal, Canada (where Clark was employed at the time the description was published). Regrettably, because this is a post-1930 description that fails to conform to Article 13 of the International Code of Zoological Nomenclature (ICZN, 1985), we are forced to declare *Nebalia pugettensis* (Clark, 1932) a nomen nudum (see ICZN, 1985: 260).

Nebalia hessleri, new species

(Figs. 1–13, 16)

Material Examined.—Holotype ♀, LACM 92-169.1, carapace length (CL) 5.1 mm, total length (TL) 10.1 mm, collected 29 February 1992, Scripps Canyon, La Jolla, California, 19 m depth (see Materials and Methods). Paratype ♀♀, same collection data, LACM 92-169.3 (40 specimens), USNM 280090 (10 specimens), CASSIZ 104580 (10 specimens), SIO C 9812 (10 specimens). Allotype ♂, same collection data, LACM 92-169.2. Selected other specimens destroyed in the course of dissecting for illustrations and/or SEM preparation.

Diagnosis of Mature Female.—Total length (excluding setation) up to 15 mm, average total length (of a series of $N = 20$ of the largest individuals) 9.8 mm (total length measurements difficult to make because of strong upward curvature of abdomen); carapace length (CL) up to 6.8 mm. Eye normal (not lobed or subdivided), oval, widest in center, slightly downturned and slightly laterally compressed; pigmentation extensive, covering approximately distal two-thirds of eye. Antennular flagellum well developed, with 14 or more segments. Dorsum of fourth pleonite with posterior border bearing acute teeth; tooth of posterolateral border of pleonite (the epimeron, following terminology in Dahl, 1985) slightly longer than others and slightly upturned. Base (proximal podomere or peduncle) of corresponding limb (pleopod 4) minutely serrulate along posterior border, terminating in sharp tooth at posterolateral corner. Fifth pleopod with 6 large spines on distolateral border, with last spine slightly longer than others and located terminally (directed posteriorly). Sixth pleopod also with 6 spines along distolateral border, with sixth located terminally but much longer than (nearly twice as long as) any other spine. Rostrum with ventral projection or "keel" more or less rectangular, unpaired, but with slight medial depression gently sloping upward toward ventral surface of rostrum and with slightly protruding anterolateral corners. Caudal furcae approximately twice length of telson and sometimes greater than twice its length. Acute spines along posterior dorsal borders of pleonites.

Description of Mature Female.—Carapace (Figs. 1, 2*a*): Approximately 1.5 times longer than deep, unsculptured, with usual posterodorsal indentation.

Rostrum (Figs. 2a, b; 3b): Rostrum long, clearly extending beyond eye, distally rounded, length approximately 2.7 times width. Length of rostrum of holotype 1.5 mm. Ventral projection or "keel" more or less rectangular, unpaired, but with slight medial depression gently sloping upward toward ventral surface of rostrum and with slightly protruding blunt anterolateral corners.

Compound eye (Figs. 2a, c, d; 3a, c): Large, well developed, elongate-oval and slightly downturned distally, slightly compressed laterally resulting in weak dorsal carina (Fig. 2d). Pigmentation (visual surface) extensive, covering at least distal half, with pigmented area longer than high (more or less reflecting shape of eye). Not lobed or subdivided. Base of eyestalk with minute cuticular scales visible in SEM view (Fig. 3c). Ocular (supraorbital) plate (Fig. 2c, d) sharply tapering to acute tip, relatively small, extending to approximately one-third length of eyestalk, and bearing minute setae (visible only via SEM) especially along dorsal and dorsolateral surfaces (Fig. 3c).

Fig. 1. *Nebalia hessleri,* new species, male (upper) and female. Note forward-curving antenna of male and eggs visible beneath cuticle in female. Photograph courtesy of Dale Stokes, Scripps Institution of Oceanography.

Antennule (Fig. 4): Peduncle composed of 4 articles. Second article widest at midpoint, with clusters of terminal and subterminal setae as illustrated (Fig. 4a) and with single dorsal plumose seta. Third article shorter than second, widest distally, with dorsal and ventral terminal setae. Fourth article shorter than third, with conspicuous row of 6–8 long setae and 4 (occasionally 5) stout spines, the latter increasing in size toward distal part of article, along distolateral border; each spine bearing minute tubercles along curved outer surface and minute subterminal pore (Fig. 4b, c). Antennular scale elongate and oval, extending to approximately fifth article of flagellum, bearing marginal rows of several distinct setal types (Fig. 4a, d–g), including long naked setae, stout, curved setae that are proximally smooth but distally bearing large, blunt serrations (Fig. 4e, g), and longer, thinner setae bearing smaller and sharper teeth along their entire length (Fig. 4a, f, g). Flagellum well developed, at least 4 times length of antennular scale and composed of at least 14 articles, each bearing cluster of 4 stout aesthetascs or aesthetasc-like setae and 2 thin unarmed setae at distodorsal border; in SEM view thinner setae curved (possibly artifact of drying) and cluster of thicker aesthetasc-like setae appearing to bear minute annulations at evenly spaced intervals (Fig. 4h).

Antenna (Fig. 5): Peduncle composed of 3 articles, proximal 2 of which with minute distodorsal teeth. Tooth of second article larger than that of first, and covered with minute teeth (visible only via SEM; Fig. 5b). Third article slightly longer than second, and bearing numerous setal types and approximately 15 stout spines (variation likely, and not documented), some of which being similar to those described for article 4 of antennule (i.e., slightly curved, bearing tubercles along outer margin, and having distal pore; Fig. 5c, d). Flagellum distinctly longer than combined articles of peduncle; each flagellar article with terminal and subterminal setae, most of which unarmed, and covered with minute cuticular scales (Fig. 5e, f).

Mandible (Figs. 6a–f; 7): Palp well de-

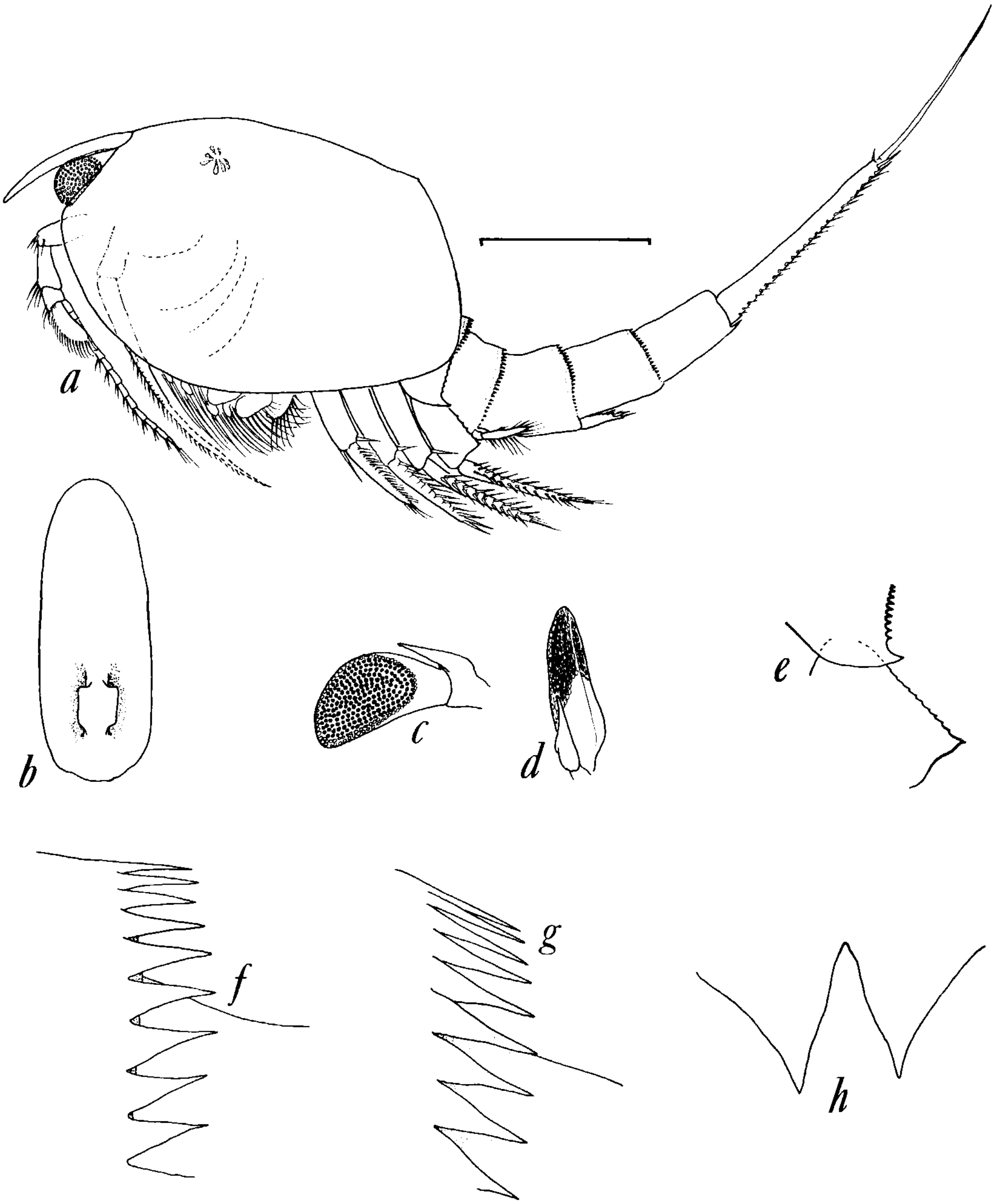

Fig. 2. *Nebalia hessleri*, new species, holotype (*a*) and dissected paratype (*b–h*). *a*, Female holotype, lateral view. Scale = 1.0 mm. *b*, Ventral surface of rostrum showing more or less rectangular subrostral keel. *c*, Left eyestalk and ocular plate, lateral view. *d*, Same eyestalk as in (*c*), dorsal view. *e*, Posteroventral extremity of epimeron of fourth pleonite and posterior border of protopod of fourth pleopod. *f*, Dorsolateral view of teeth along posterior border of fifth pleonite. *g*, Same as (*f*) but for sixth pleonite. *h*, Anal plates in ventral view.

veloped, composed of 3 articles; third article equal to or slightly longer than second; second approximately twice as long as first and with single seta at approximately four-fifths length. Setation of distal article complex, with featherlike setae (i.e., with sinuous shaft bearing small lanceolate setules, each of which with lateral serrations; Figs. 6a, 7c, d) extending from proximal fifth to terminus, and with distal row of stouter se-

Fig. 3. *Nebalia hessleri*, new species, female, selected SEM photographs of taxonomically important features. *a*, Anterior region showing general shape of rostrum and eyestalk. Scale = 500 μm. a1 = antennule, a2 = antenna, c = carapace, e = eye, r = rostrum, s = antennular scale. *b*, Subrostral keel, ventral view, with anterior toward right of figure. Scale = 100 μm. *c*, Anterior region of ocular plates, showing covering of minute setae. Note also the scalloped pattern of cuticular scales on the eyestalks. Scale = 100 μm. *d*, Posterior region, carapace removed, showing pleonites 2–7, telson and base of caudal furca, and pleopods. Scale = 1.0 mm. *e*, Ventral end of epimeron of fourth pleonite and posterior border of fourth pleopod showing acute dentition. Scale = 200 μm. *f*, Posterior border of sixth pleonite. Scale = 100 μm.

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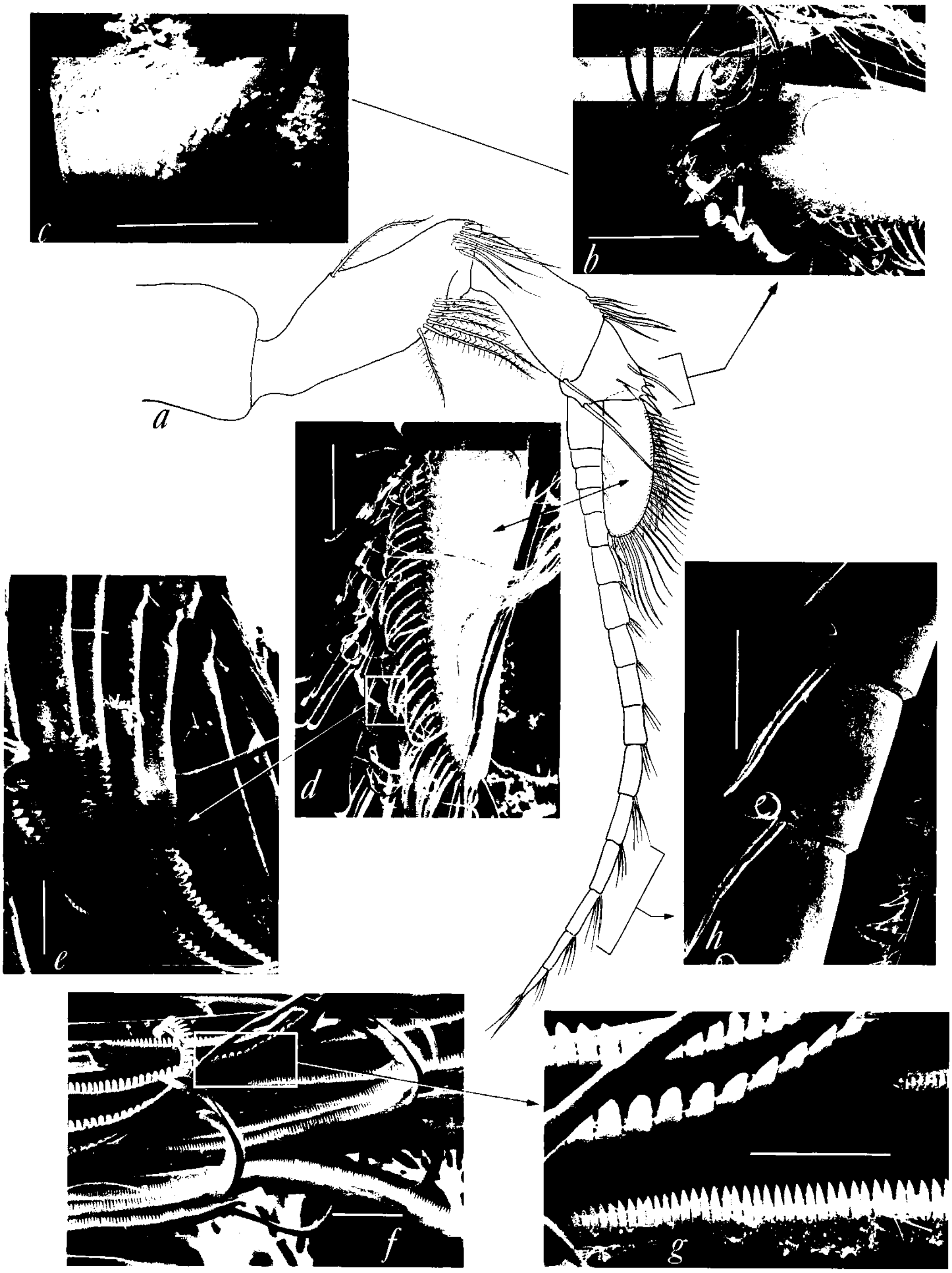
Fig. 4. *Nebalia hessleri*, new species, female, first antenna, lateral view. *a*, Entire appendage, right side, lateral view. *b*, Armature of distal end of fourth article and base of antennular scale (toward right of photograph). Scale = 100 μm. *c*, Higher magnification of distal region of single spine denoted by arrow in (*b*). Note tubercles and



small subterminal pore (white arrow). Scale = 10 μm. *d,* Dorsolateral view of antennular scale. Scale = 100 μm. *e,* Higher magnification of stout, upturned serrate setae along dorsal surface of antennular scale border, e.g., as in boxed area of (*d*). Note row of longer, thinner setae arising beneath this row. Scale = 20 μm. *f,* Tips of several stout, serrate setae (toward left) and thinner setae of antennular scale (just distal to view in (*e*)). Scale = 20 μm. *g,* Higher magnification of boxed area in (*f*), showing armature of stout serrate setae (at top) and comblike teeth of thinner, longer setae (bottom of figure). Scale = 10 μm. *h,* Setation of distal segments (3 visible in this photograph) of antennal flagellum. Note curved setae at base of each cluster of stout setae, each of which is subdivided into 3 or 4 regions by slight creases in shaft cuticle. Scale = 100 μm.

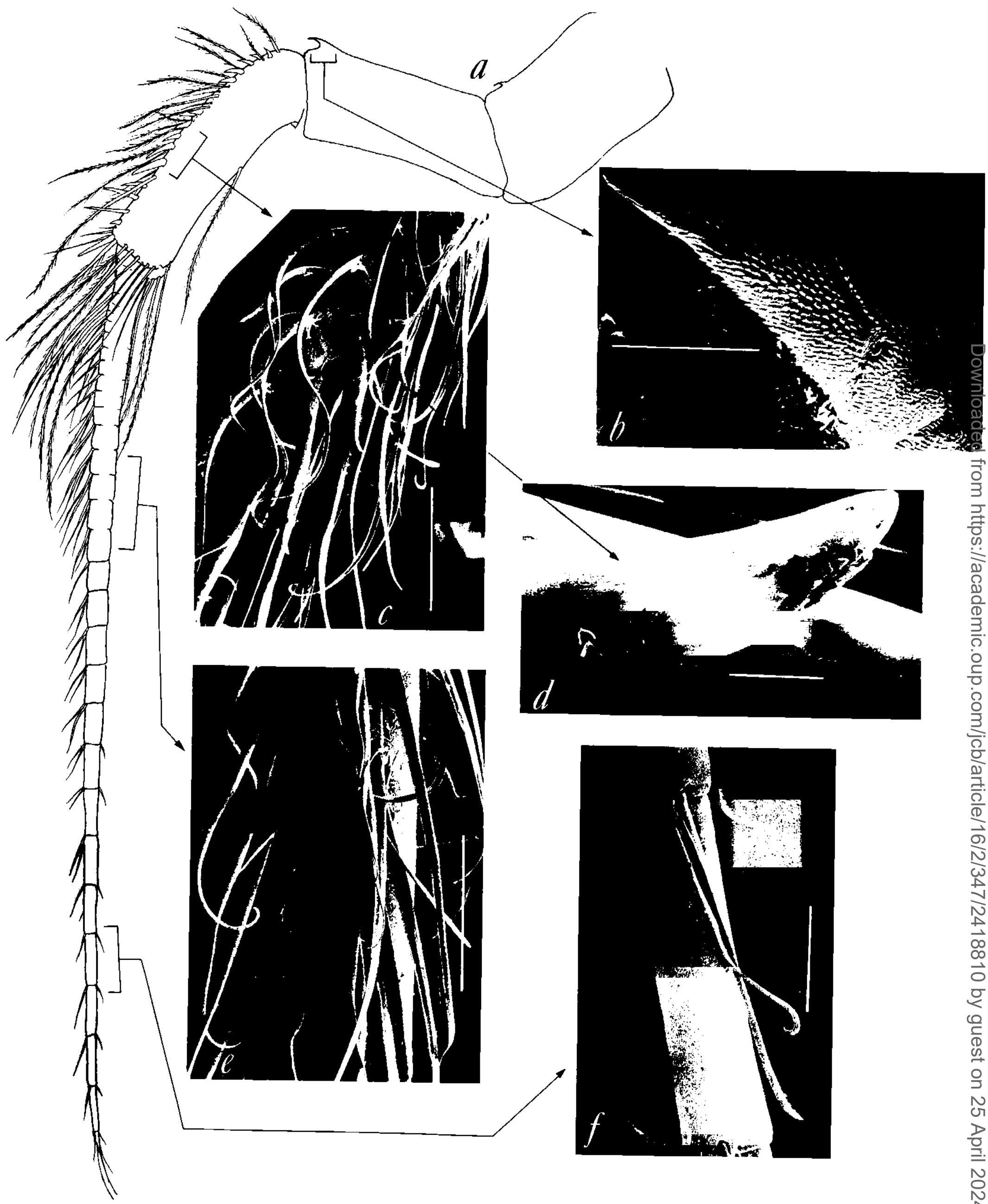


Fig. 5. *Nebalia hessleri*, new species, female, second antenna, lateral view. *a*, Entire appendage, right side. *b*, Dorsal distal spine on second article of peduncle. Scale = 20 μm. *c*, Setation and spination along anterior border of third article (oriented in opposite direction from drawing). Scale = 100 μm. *d*, Tip of isolated spine of the type indicated by arrow in (*c*). Scale = 5.0 μm. *e*, Several articles or "pseudoarticles" (because of incomplete sutures) of flagellum showing arrangement of setae. Scale = 100 μm. *f*, More distal region of flagellum showing setation and minute tubercles covering article. Scale = 50 μm.

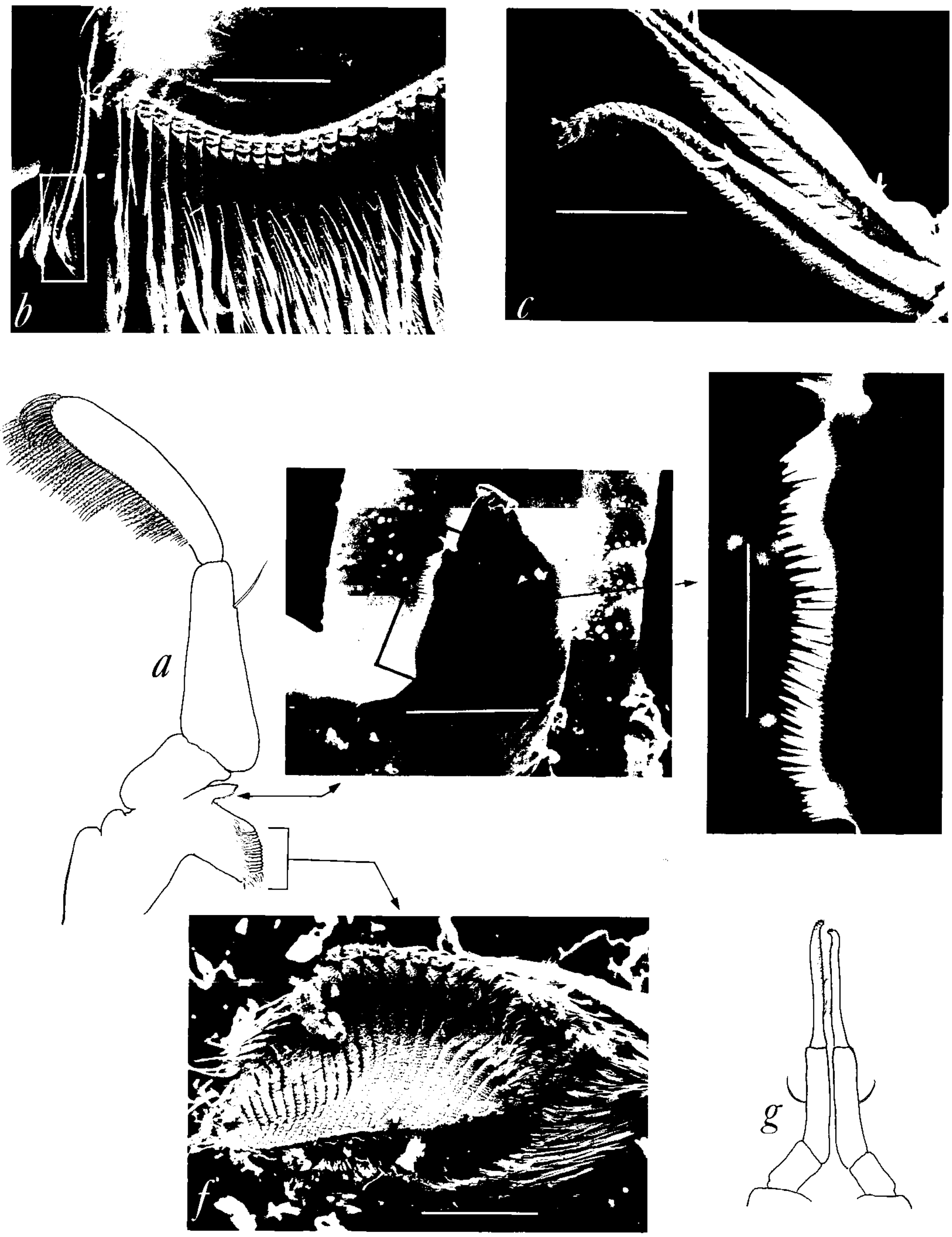


Fig. 6. *Nebalia hessleri*, new species, female, mandible. *a*, Entire appendage, right side. *b*, Distal extremity of palp showing long "sweeping" setae and more distal cluster of stout serrate setae. Scale = 50 μm. *c*, Higher magnification of stout serrate setae. Scale = 20 μm. *d*, Incisor process, lateral view. Scale = 50 μm. *e*, Higher magnification of "comb row" of lower, sinuous blade of incisor process. Scale = 20 μm. *f*, Molar process, distal end-on view (incisor process to the right). Scale = 50 μm. *g*, Tracing of photograph of mandibular palp of *N. pugettensis* in Clark (1932) shown for comparison; differences between this and Fig. 6a are mostly because of orientation of the appendage; see text.

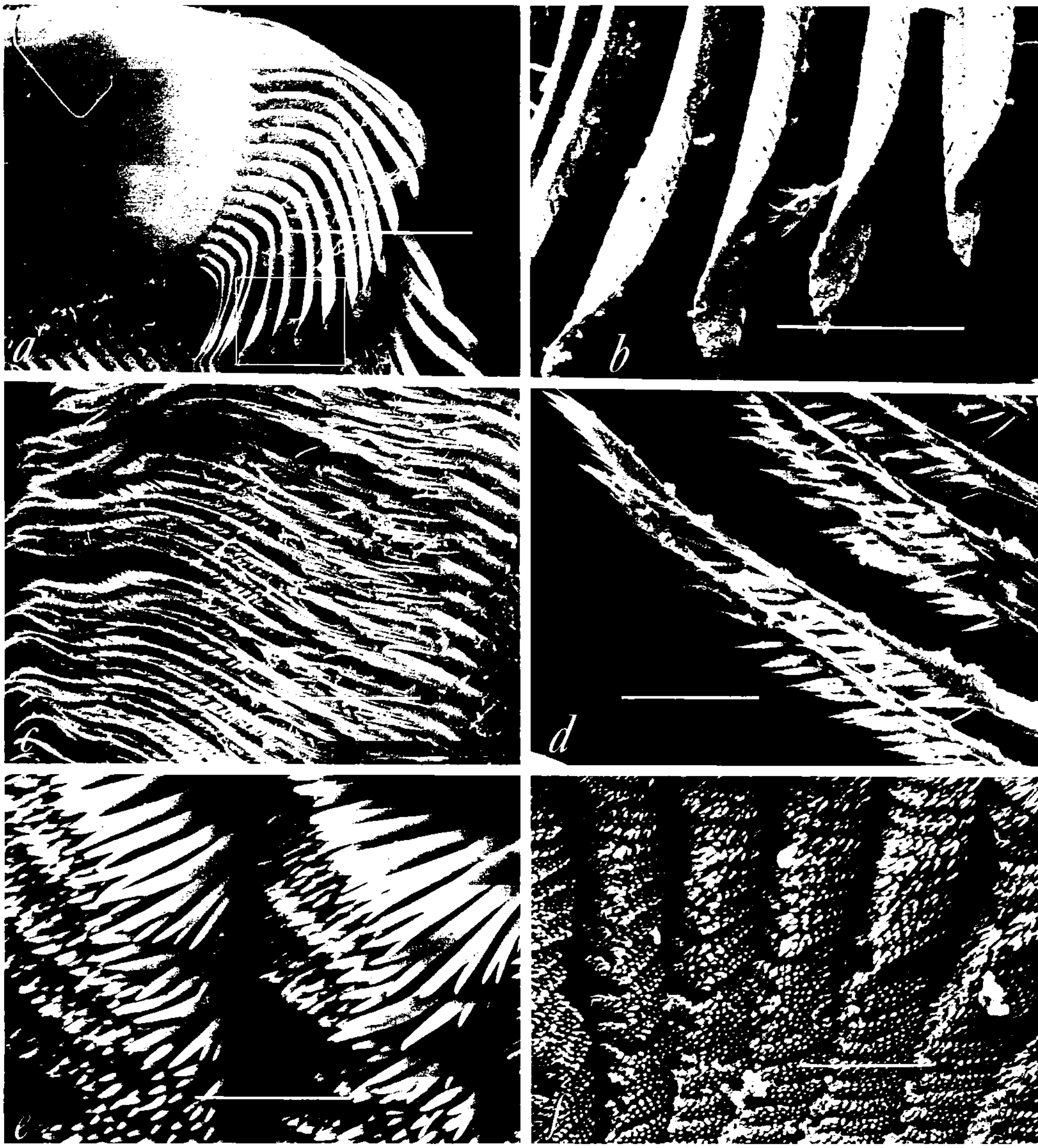


Fig. 7. *Nebalia hessleri*, new species, female, selected SEM photographs of mandible. *a*, Posterior surface of distal region of palp, showing extension of row of stout, serrate setae. Note curvature of each seta at approximately one-third distance from base. Scale = 100 μm. *b*, Tips of stout serrate setae in box in (*a*) showing distal "twist" and rectangular nature of lateral setules. Scale = 20 μm. *c*, Feathery sweeping setae found along upper half of palp. Scale = 50 μm. *d*, Higher magnification of sweeping setae showing serrated, lanceolate setules. Scale = 20 μm. *e*, *f*, Details of grinding surface of molar process. Scale = 5 μm for (*e*), 10 μm for (*f*).

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Fig. 8. *Nebalia hessleri*, new species, female, first and second maxillae. *a*, First maxilla, left side, lateral view, with several setal types found on dorsal endite illustrated below. *b*, SEM of tridentate setae characteristic of dorsal endite, with white arrow indicating centrally located pore. Scale = 10 μm. *c*, Long "grooming" setae of elongate palp. Scale = 20 μm. *d*, Second maxilla, right side, lateral view.


a
b
c
d

tae overlying this row. Distal stout setae curved and bearing heavy almost rectangular serrulations, appearing as unit to be effective scraping device (Figs. 6a–c; 7a, b). Incisor process (Fig. 6d, e) long and thin, with short sharp teeth along inner (medial) face. Molar process (Figs. 6a, f; 7e, f) slightly concave, with inner field composed of rows of stout, densely spaced teeth, giving rise to more widely spaced teeth and long spines toward periphery.

First maxilla (Fig. 8a–c): Distal endite twice as long as proximal and carrying row of stout, distally widened and trifid setae on outer margin. Other setal types including long setose or simple setae restricted to distal part of endite, and row of spatulate setae just distal to row of trifid setae (Fig. 8a). Trifid setae nearly smooth basally, giving rise to smooth setules toward distal tip, and with central of 3 terminal teeth slightly longer than flanking teeth and bearing small pore (white arrow, Fig. 8b). Palp approximately 5 times longer than combined length of both endites of protopod and bearing evenly spaced, long setae, each appearing naked under light microscopy, but bearing minute lateral setulations visible under SEM; each seta strongly recurved and bearing longer setules at extremity (Fig. 8c)

Second maxilla (Fig. 8d): Protopod subdivided into 4 endites, with endites 1 and 3 approximately equal in size and larger than either endite 2 or 4. Endopod longer than exopod, composed of 2 articles, basal one longest and slightly shorter than exopod. All endites, endopod, and exopod bearing plumose setae; distal plumose setae of second article of endopod very long, approaching length of entire limb.

Thoracopods (Fig. 9): Endopod always exceeding length of exopod. Distal article of endopod of each thoracopod slightly enlarged, turned rather sharply at angle from main axis, and bearing numerous long, plumose setae (Fig. 9d–f), thereby indicating mature females (following categorization of Dahl, 1985: 140; figs. 6–10). 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. 9e, f). Endopod weakly divided into articles, sometimes appearing to have 1, other times 2 or 3, suture lines separating distal articles. 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. Epipod more or less bilobed, with lobes divided by thin band of presumed connective tissue; epipod becoming less obviously bilobed and decreasing in size relative to endopod in posterior limbs (e.g., compare thoracopods 1 and 4 (Fig. 9a, b) with thoracopod 8 (Fig. 9c)).

Pleonites: Posterior borders of all pleonites bearing sharp, widely spaced teeth (Figs. 2a, f, g; 3f) and with slightly scalloped cuticular scales bearing minute teeth along posterior border (visible only under SEM; Fig. 3f).

Pleopods 1–4: First pleopod (Fig. 10a–d) exopod approximately two-thirds as long as protopod. Exopod with approximately 36 stout, serrate spines along lateral border (Fig. 10b, d), 4 stout smooth spines on distolateral border increasing in size toward apex, with terminal spine by far largest, and approximately 20 plumose natatory setae along medial margin. Under SEM, stout serrate spines of the lateral border distally tridentate, with stout central projection flanked on either side by sinuous, acutely tipped shorter projection. Endopod slightly longer than exopod, 2-segmented, with plumose setae on lateral and medial borders of distal (longer) segment and with basal segment giving rise to short appendix interna. Appendix interna bearing 3 short, stout, distally recurved hooks (retinacula) for coupling with similar hooks on appendix interna of opposing first pleopod of other side. Protopod with stout, smooth spines arising near base of endopod and exopod as shown (Fig. 10a–c). Second pleopod (Figs. 10e, 11) exopod without row of stout serrate setae, instead with row of spine pairs; spine pair consisting of 1 long and 1 short spine, both covered with minute triangular cuticular scales on all but tip, and both with subterminal, twisted seta of presumed sensory function (Fig. 11c, d). Endopod with long natatory setae on lateral and medial borders. Both endopod and exopod with long heavy spine at distal terminus. Appendix interna with 3 stout recurved hooks (retinacula, Fig. 11f) as described for pleopod 1;

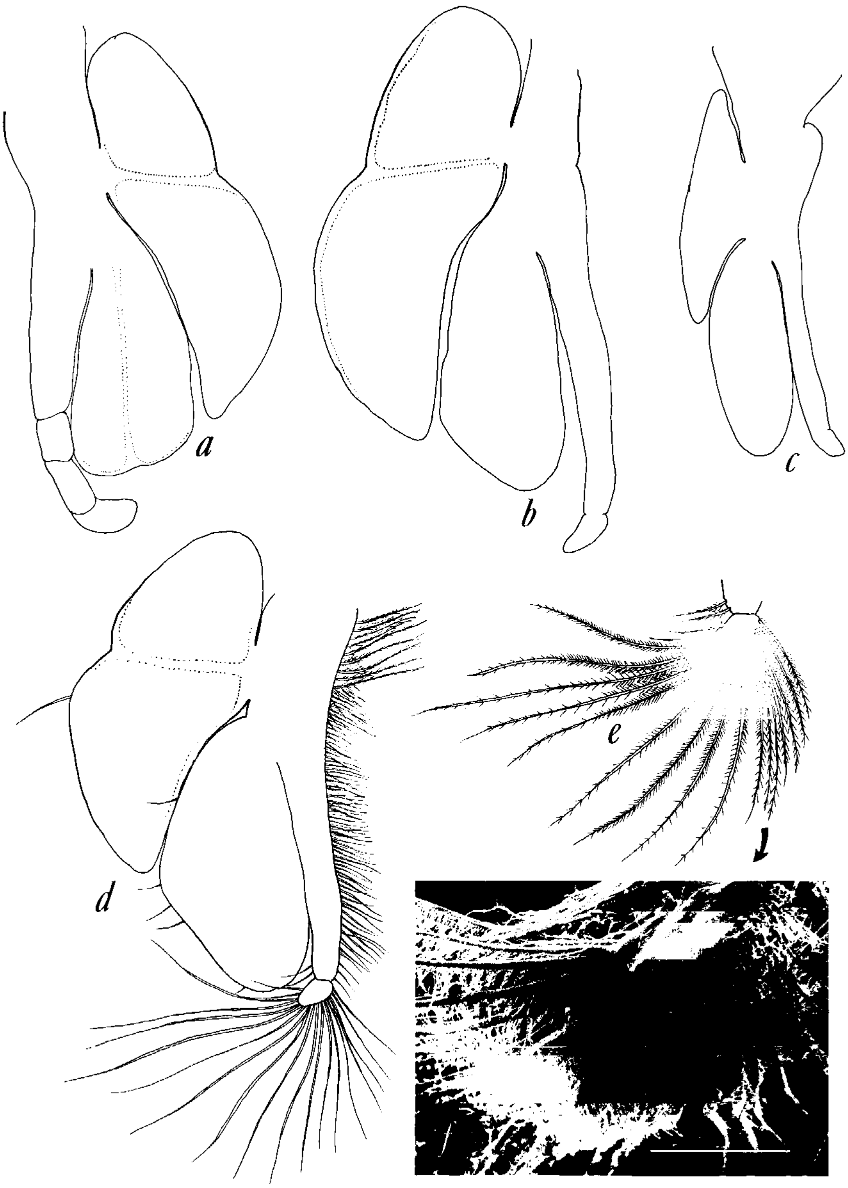

Fig. 9. *Nebalia hessleri*, new species, female, selected thoracopods. *a*, Thoracopod 1, left side, anterior view. *b*, Thoracopod 4, right side, anterior view. *c*, Thoracopod 8, right side, anterior view. *d*, Thoracopod 7 (different animal) to show approximate setation. *e*, Detail of tip of endopod of same thoracopod shown in (*d*) to illustrate density of setules. *f*, SEM of same region. Scale = 200 μm.

these hooks protected ventrally by setose papillae extending ventrally and medially to cover them, not visible in ventral view with opposing pleopods (right and left) coupled (Fig. 11e). Protopod with long, stout spines near bases of endopod and exopod, and with row of sabrelike teeth on anterolateral corner (Figs. 10b, 11a, b). Third and fourth pleopods presumed similar to second, not examined in detail (see Figs. 2a, 3d for low magnification views).

Pleopods 5 and 6: Pleopod 5 (Fig. 12a–c) 2-segmented, uniramous, with 6 well-developed spines along distal lateral and terminal border, increasing in size distally, and with numerous setae lining medial border; these long setae on medial border being somewhat "jointed" at approximately mid-

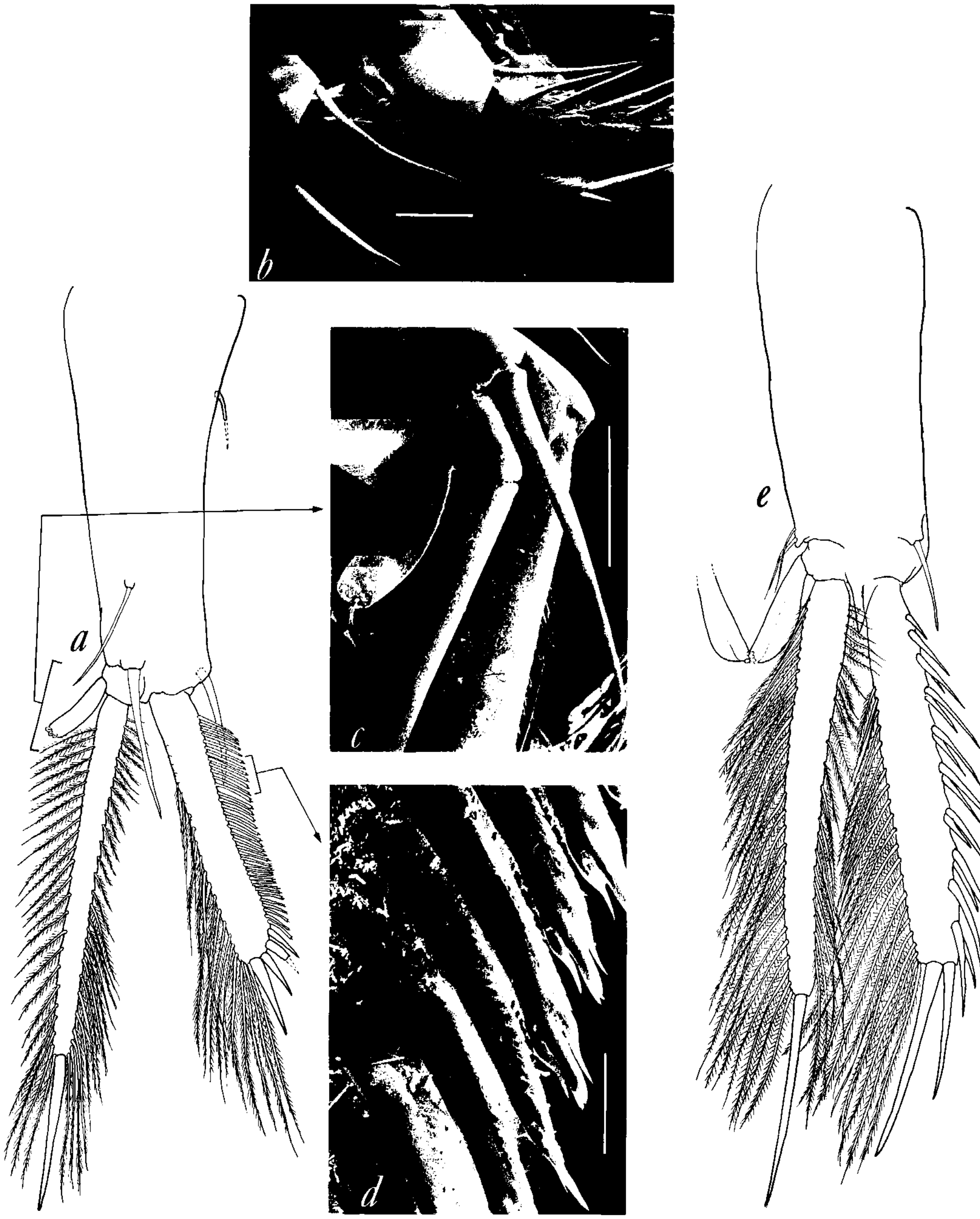

Fig. 10. *Nebalia hessleri*, new species, female, first and second pleopods. *a*, First pleopod, left side, anterior view. *b*, SEM photograph of pleopods 1–3 (partial) in situ. Note row of stout tridentate spines along lateral border of exopod of pleopod 1. Scale = 200 μm. *c*, SEM photograph of pleopod 1, anterior view showing basal region of endopod and exopod and appendix interna. Scale = 200 μm. *d*, SEM photograph of characteristic stout serrate setae from lateral border of exopod, pleopod 1. Scale = 20 μm. *e*, pleopod 2, left side, anterior view, and part of appendix interna of opposite side (pleopod 2, right side).

Fig. 11. *Nebalia hessleri*, new species, female, SEM photographs of pleopods 1 and 2. *a*, Pleopod 2, distal region of protopod and base of exopod, and pleopod 1, comb row of stout serrate setae (at lower left). Note knifelike serrations of anterolateral corner of pleopod 2 protopod (white box) where it contacts comb row of pleopod 1. Scale = 100 μm. *b*, Higher magnification of knife-like serrations indicated in (*a*). Scale = 5.0 μm. c, Pairs of stout spinelike setae, lateral border of exopod of pleopod 2. Scale = 50 μm. *d*, Detail of tip of spinelike seta indicated by box in (*c*). Note covering of triangular scales directed distally, smooth terminus, and twisted subterminal seta. Scale = 10 μm. *e*, Appendix interna of pleopod 2 (right and left sides coupled), ventral view, showing setose fleshy papillae covering interlocking coupling hooks (retinacula). Scale = 50 μm. *f*, Appendix interna, pleopod 2, hooklike coupling setae (uncoupled from corresponding pleopod). Scale = 20 μm.

length; there corrugations of cuticle appearing to confer some flexibility on setal shaft (Fig. 12b, c). Pleopod 6 1-segmented, uniramous, with 6 lateral and distal spines increasing in size distally and with scattered simple setae among these spines and along medial border. Terminus of pleopod at origin of distalmost spine bearing circlet of sharp teeth (Fig. 12f). Lateral and distal spines of both pleopods 5 and 6 covered with short triangular scales and bearing short, twisted subterminal seta of presumed sensory function (Fig. 12g). Both pleopod pairs with broad triangular ventral process

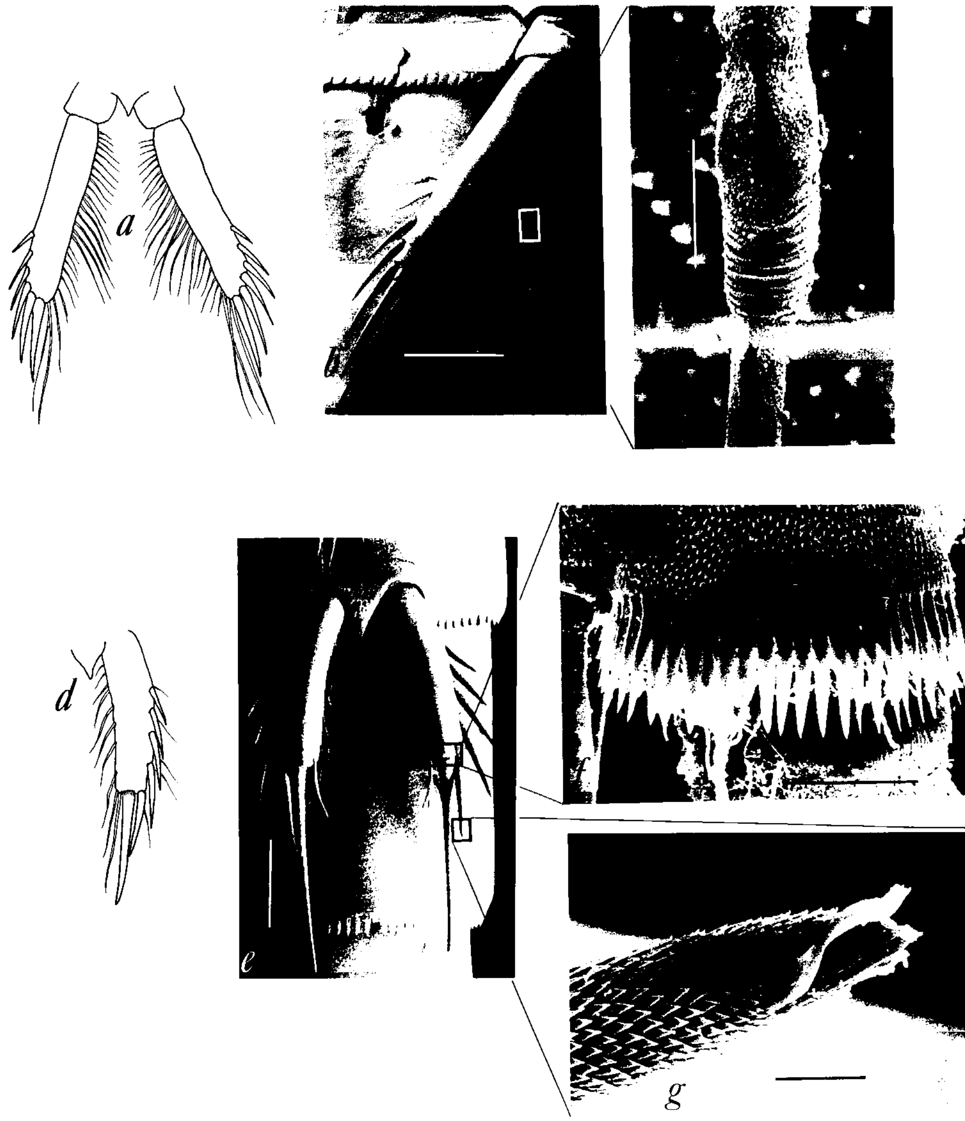

Fig. 12. *Nebalia hessleri*, new species, female, pleopods 5 and 6. *a*, Pleopod 5, right and left, ventral view. *b*, SEM photograph of right pleopod 5, ventral view. Scale = 200 μm. *c*, Higher magnification of box shown in (*b*), showing annulations presumed to confer flexibility on setal shaft. Scale = 5.0 μm. *d*, Pleopod 6, left side, ventral view. *e*, SEM photograph of right and left pleopod 6, ventral view. Scale = 200 μm. *f*, Higher magnification of box shown in (*e*), showing circlet of sharp teeth surrounding base of distalmost spine of pleopod. Note also cuticular microscales. Scale = 20 μm. *g*, Tip of penultimate spine, indicated by box in (*e*). Note covering of triangular scales, terminal area lacking scales, and twisted subterminal seta, as described for anterior pleopods (Fig. 11d). Scale = 5.0 μm.

extending posteriorly between bases of rami, more acutely triangular and longer in pleopod 6 (Fig. 12a, d, e).

Telson, anal plates, and caudal furca: Telson (Figs. 2a, 3d, 13a, b) short, approximately as long as wide, rectangular, or with sides slightly diverging posteriorly. Anal plates (Figs. 2h, 13c) sharply tapering from broad base to acute extremity, with outer (lateral) borders smoothly curved and with medial borders slightly bulging along mid-length; overall appearance more acute than typical for genus. Caudal furca elongate, ranging from slightly less than 2 times to more than 2.3 times length of telson, approximately equal to length of telson plus

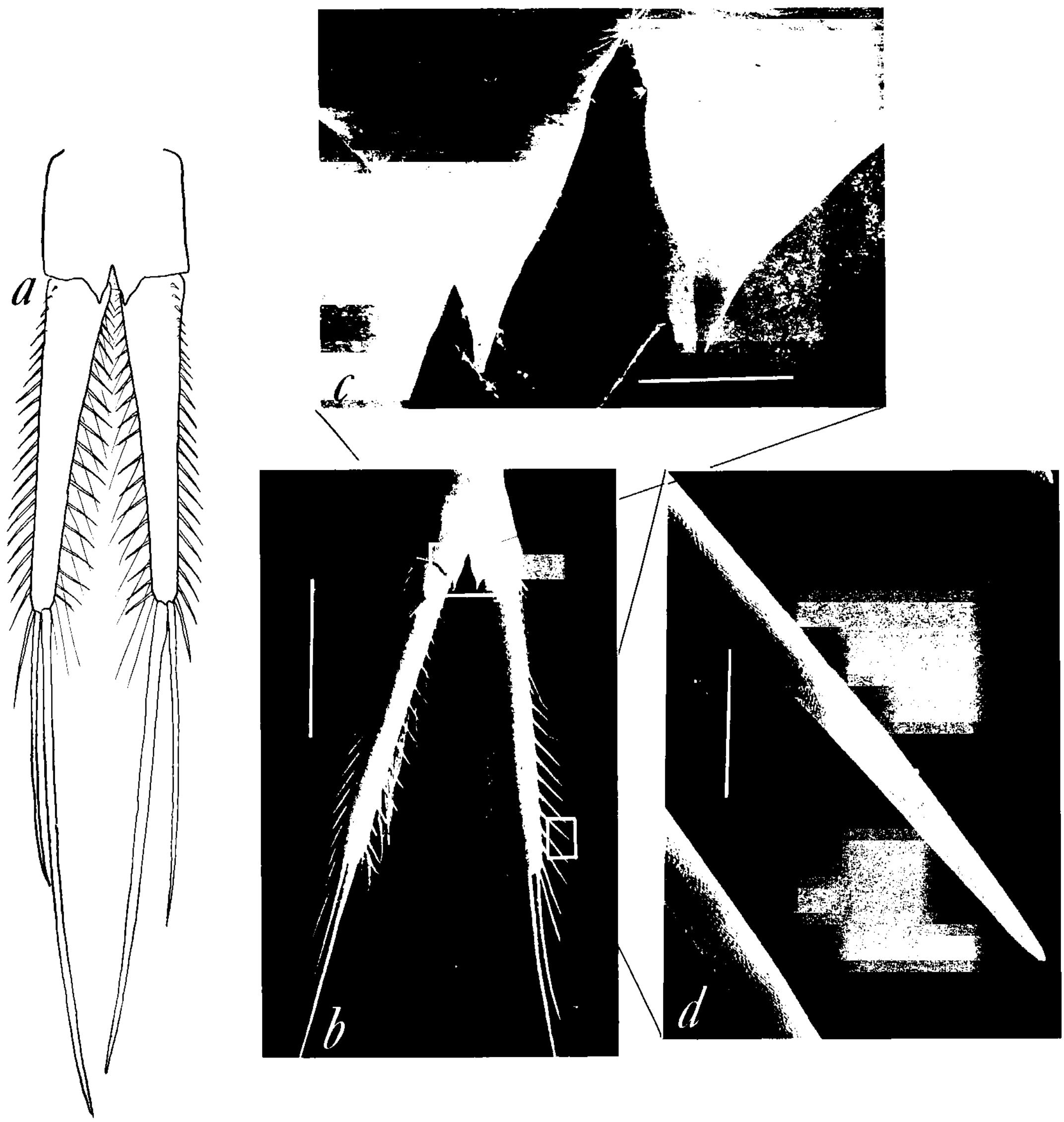

Fig. 13. *Nebalia hessleri*, new species, female, telson, anal plates, and caudal rami. *a*, Telson and caudal rami, ventral view. *b*, SEM photograph of same region. Suture line connecting telson with anterior somite occurs just at upper edge of photograph. Scale = 1.0 mm. *c*, Anal plates (upper box in (*b*)), ventral view. Scale = 100 μm. *d*, Lateral spines of caudal ramus (lower box in (*b*)). Note covering of minute microscales. Scale = 50 μm.

pleon segment 7. Furcal rami each with 16–20 spines along inner margin and with up to 24 spines along lateral margin; these spines gradually increasing in length posteriorly with last two much longer than any of anterior spines; of these last two spines terminal being longer, almost twice length of penultimate spine. Inner margins of each branch also bearing short setae.

Coloration: In life, specimens appeared mostly transparent except for bright red eyes. When viewed with naked eye thoracic region appearing almost white. Some males with slightly ruddy hue, especially in thoracic region. Eggs (barely visible in Fig. 1, lower photograph) are gold or cream colored.

Distribution.—To date known only from the type locality. Our prediction is that the known range will increase with heightened efforts at collecting and identifying leptostracans throughout California and other localities in the eastern Pacific.

Etymology.—We are pleased to name this species after our friend and colleague, Robert R. Hessler, in honor of his many excellent contributions to crustacean morphology and systematics.

Remarks.—The new species shares some features with specimens collected from Friday Harbor, Washington. These characters include common eye morphology, with both species possessing "normal" leptostracan eyes, and the shape of the male second antenna. It can be differentiated from that species by the shape of the teeth along the posterior borders of the pleonites, the shape and dentition of the epimeron of the fourth pleonite, the relative lengths of the caudal furca and telson, and by overall size (see Discussion).

The new species differs from all other described species of *Nebalia* in having 14 or more segments on the antennal flagellum of mature females and a rostrum that is approximately 2.7 times longer than wide (see Discussion). A smaller cooccuring species of *Nebalia,* occupying a different microhabitat (adjacent sand flats), is easily distinguished by the greatly reduced antennular flagellum and by the presence of unusual lobes on the eye of the sand-flat species (Vetter, in press).

Natural History

Preliminary Observations on Feeding

In the laboratory, leptostracans fed on large pieces of meat (e.g., fish, shrimp, fish-containing cat food, and squid) by scraping off chunks, using the peduncle of the first antenna, which bears a row of strong spines (e.g., Fig. 4b). The animals remained in contact with the meat often for five minutes or more, and produced a continuous fecal strand that sometimes rivaled the length of the animal. In such cases, the fecal strand was the same color as the food and thus possibly was poorly processed. If sufficient numbers of individuals were present, they completely covered the meat, apparently using their antennules both to brace themselves against the food and to hold on to it. With tough pieces of meat, such as squid, *N. hessleri* tore off a piece of meat and laid on its back while processing it with its mouthparts. The meat was rapidly tumbled and turned in front of the mouth until it was either entirely consumed or was ejected by a current of water that shot out from the region of the mouth in a line normal to the long axis of the animal. When large pieces of food were not present, the animals fed by lying on their backs and using their antennules to cast sediment into the space between their thoracopods. This material was then moved toward the mouth and tumbled around the mouthparts. Some particles were rejected immediately via the stream of water flowing out from the mouth region, whereas other particles were tumbled for variable periods before being ejected. Animals fed only field-collected, organically enriched sediments grew and reproduced normally. Within the detritus mat habitat of these animals, vertebrate and invertebrate carcasses are frequently seen and are exploited by *N. hessleri* and the lysianassoid amphipod *Orchomene limodes* Meador and Present, 1985, which is also extremely abundant in this habitat (Vetter, 1994). Indeed, these two species, *N. hessleri* and *O. limodes,* are the dominant crustaceans in this rich habitat and are the primary contributors to what is now known as the highest density of any macrofaunal assemblage yet reported, with an estimated 2 million individuals/m^2 (Vetter, 1994). Cannibalism was observed on several occasions. When live, but apparently distressed, adults (a slightly opaque white, rather than clear, appearance was taken to indicate some type of distress) were attacked, the aggressor inserted its head into the victim's thoracic cavity and, apparently with some difficulty, partially ate the victim's thoracopods. Once the victim was dead, the back of the head was also eaten. When dead conspecifics were provided, *N. hessleri* similarly consumed the thoracopods and the head.

Preliminary Observations on Oxygen Level Tolerance

Nebalia hessleri lives in thick detritus mats with low oxygen levels (Vetter, 1995) and, judging by the odor, elevated sulfide. In the laboratory, when not swimming or burrowing, the animals typically rested on their backs or sides. The thoracic appendages rarely stopped moving. Occasionally, when the animals were neither swimming nor feeding, the thoracopods would be motionless, but rarely for more than a few minutes. When placed in anoxic or hypoxic water, the animals swam to the surface and rested on the side of the aquarium with their heads in the surface film, using their thoracopods to draw water from the very surface of the aquarium over their respiratory appendages. Placed in a stoppered flask of anoxic water, they behaved normally for 8–12 h, after which they sought out the surface. With no air-water interface available they eventually settled to the bottom and continued to beat their thoracopods. They then occasionally swam to the top of the flask and then swam around the flask, presumably searching for more favorable conditions. Most animals perished after 14 h in anoxic conditions (Vetter, 1995), but revived completely if removed to aerated water just prior to death (i.e., at around 13 h).

When exposed to both anoxic conditions and high sulfide levels, animals behaved similarly but died sooner (6–7 h; Fig. 15). The results were roughly similar for the amphipod *Orchomene limodes,* which occurs with *N. hessleri* in the detrital mats. Survival for both *N. hessleri* and *O. limodes* was far greater than it was for another amphipod (*Aorides spinosus* Conlan and Bousfield, 1982) that occurs in both the detritus mats and the adjacent sand flat. As might be expected, crustaceans and one pycnogonid known only from the relatively well-oxygenated sand-flat area died relatively quickly under these conditions (Fig. 15).

Discussion

Comparison to Other Descriptions of Leptostracans from the West Coast of North America

One of the factors hindering leptostracan taxonomy along the west coast of North America has been the rather incomplete original description of *Nebalia pugettensis* (as *Epinebalia*) by Clark (1932). Clark illustrated few of what are now considered taxonomically important features of leptostracans (see Dahl, 1985), and unfortunately did not deposit any type material, according to our search of United States and Canadian natural history museums. Without type material or a detailed description for comparison, subsequent workers have had to assume that any *Nebalia* encountered on the west coast must belong to that species, and thus virtually all guidebooks and keys (e.g., Reish, 1972; Haderlie *et al.,* 1980; Rickets *et al.,* 1985; Smith and Carlton, 1980; Kozloff, 1987) list this species as the sole west coast representative of the Nebaliacea (although Kozloff, 1987: 320, was aware of an undescribed species in the intertidal and subtidal of the Pacific Northwest). Because of this uncertainty, we were forced to declare *N. pugettensis* a nomen nudum.

We have examined specimens from Friday Harbor, Washington, a site much closer to the original collecting site for *N. pugettensis* (Puget Sound, Washington) than is our collecting site off La Jolla, California. There is no guarantee that these specimens belong to the species described by Clark, since there may be several species found in that area. We point out here the following features (some of which are shown in Fig. 14) that serve to differentiate between these Friday Harbor specimens and *N. hessleri.* (1) In the Friday Harbor specimens the epimeron of the fourth pleonite bears shorter, broader, and blunter teeth along its posterior border, and the posterolateral corner tapers more gradually toward a blunt tip (Fig. 14a). The basal article of the corresponding fourth pleopod does not bear sharp teeth along its posterior border (compare Figs. 14a, 2e, 3e). (2) The posterior borders of pleonites 5 and 6 (Fig. 14b), and indeed of all pleonites, bear short, closely spaced teeth that are markedly truncated distally, appearing nearly rectangular, in the Friday Harbor specimens (Fig. 14c). (3) The caudal furcae in the Friday Harbor specimens are relatively short, exceeding the length of the telson, but clearly less than twice its length (Fig. 14d), whereas in *N. hessleri* the caudal furcae are sometimes more than twice the length of the telson (Fig. 13a, b). (4) Overall size differs significantly, with the new species attaining lengths of up to 15 mm in adult females (although 9–11 mm is more common), versus 7 mm in our Friday Harbor specimens and reported by Clark (1932: 226) for *N. pugettensis.* Dahl (1985: 136) also described specimens of *Nebalia* from this area (which he referred to as *N. pugettensis*) as small, with "carapace lengths only rarely exceeding 3.5 mm" (versus up to 6.8 mm in *N. hessleri*).

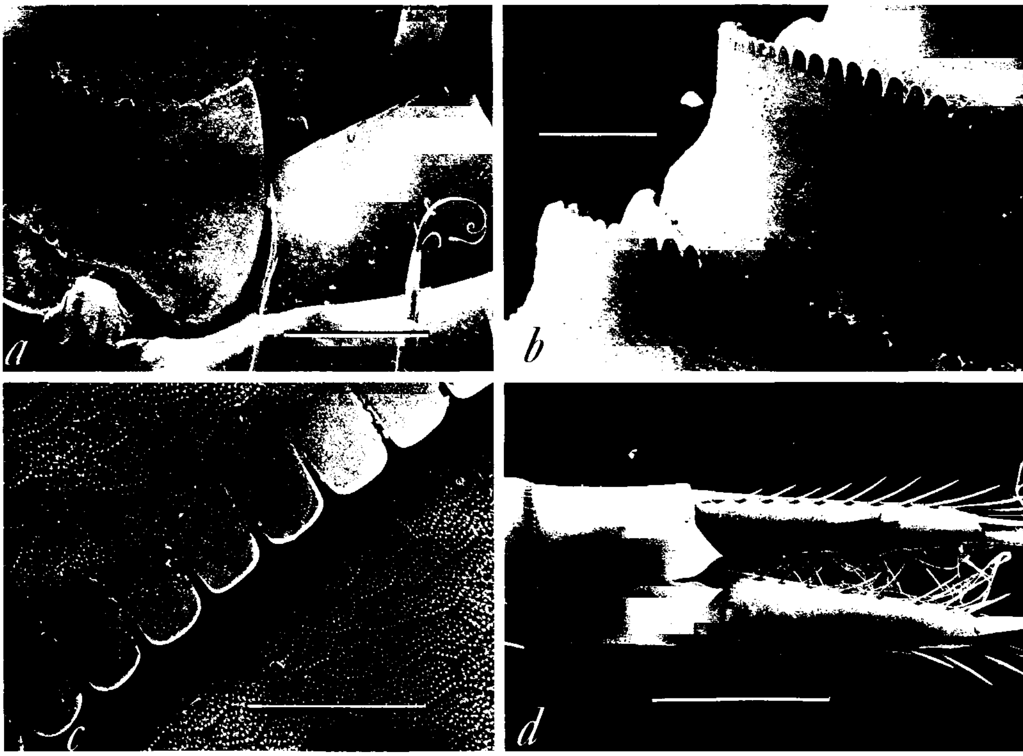

Fig. 14. Selected features of specimens (female) of an undescribed species of *Nebalia* collected at Friday Harbor, Washington. *a*, Posterolateral border of fourth pleon and base of corresponding limb (fourth pleopod). Note size and shape of teeth as compared to Fig. 1*e*, 2*e*. Scale = 200 μm. *b*, Dorsolateral region of pleon 5 and 6. Scale = 100 μm. *c*, Higher magnification of teeth along posterior border of pleon 6. Note truncate terminus as compared to similar teeth in Figs. 1*f*, *g*, 2*f*. Scale = 50 μm. *d*, Ventral view of telson, anal plates, and caudal furca. Compare relative size of furcal rami to telson with what is seen in Figs. 1*a*, 12*a*, *b*. Scale = 500 μm.

(5) In addition, although not shown here, the coloration of the eggs may differ between these species. In *N. hessleri*, eggs are cream or gold colored, whereas eggs are apparently pink in at least one species of *Nebalia* from Moss Landing, California (personal communication, Cathy LeFaye, Moss Landing, California). In light of our declaring *N. pugettensis* a nomen nudum and the uncertainty of identifications of west coast leptostracans, there is at this time no certainty as to the identity of the Moss Landing species. Those specimens came from a similar intertidal mud-flat habitat as did our Friday Harbor specimens.

Although the figure of the mandibular palp of *N. pugettensis* in Clark (1932) is very different from that in the present study (Figs. 6a–f, 7), this should not be considered a diagnostic character. Clark's figure (reproduced here as Fig. 6g for comparison) is a photograph taken from a posterior angle, in such a way that the palp is oriented with its flat blade parallel to the body axis. In other words, the distal article was photographed on edge, resulting in the thin, elongate appearance seen in Fig. 6g (traced from Clark's photograph). The curving, "rasping" setae described by Clark (1932) are part of the row of curved stout setae on the external (outer) face of the distal article of the palp (Figs. 6b, c, 7a, b); turning the mandible of *N. hessleri* on edge yields a profile similar to that shown by Clark.

Dahl (1985), in his revision of the European shelf species of *Nebalia*, included some valuable ontogenetic data for reared specimens of what he called *N. pugettensis* (see Dahl, 1985: 137, table 1). His specimens came from "near the Marine Biological Station at Friday Harbor, Washington," and were apparently from a mud environ-

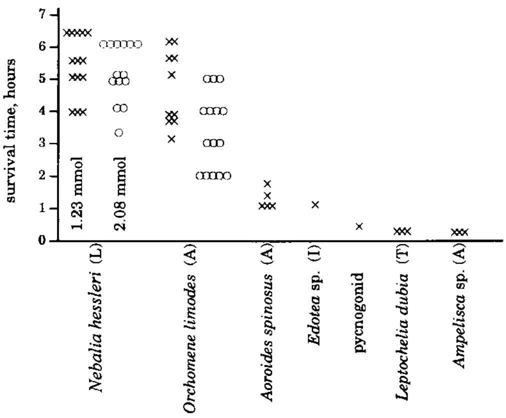

Fig. 15. Comparison of survival time (in hours) under conditions of anoxia and elevated sulfide levels for arthropod species known only from the detrital mats (*Nebalia hessleri, Orchomene limodes*) versus a species that occupies both the detrital mats and adjacent, better oxygenated sand flats (*Aoroides spinosus*) versus several species known only from sand flats. L = leptostracan, A = amphipod, I = isopod, T = tanaidacean. Circles represent higher concentrations (2.08 mmol) of hydrogen sulfide.

ment, since he stated that "sifted mud from the collecting site" was pipetted into the dishes from time to time to renew their food supply (Dahl, 1985: 136). Thus, our Friday Harbor specimens (Fig. 14) and Dahl's specimens may belong to the same species, although there is also the strong likelihood that such areas contain more than one species of leptostracan, as we are finding to be the case in southern California. The habitat of Clark's specimens was not listed by her; she stated only that they came "from Puget Sound" via the Pacific Biological Laboratories in Pacific Grove, California. Packard (1883) mentioned a species that he felt was similar to the European *N. bipes* (O. Fabricius, 1780) collected from "just below low-water mark among fucoids" (as cited by Clark, 1932: 225; Packard's monograph not seen by us). Our specimens were collected from a mudflat, as apparently were those of Dahl (1985). Packard also mentioned having collected "what is probably a fifth species" between tide marks at Victoria, Vancouver Island, British Columbia. According to Clark (1932), that specimen was lost. This lost specimen might be what Kozloff (1987: 320) was referring to when he mentioned an undescribed species in the Pacific Northwest. Thus, whereas there is little doubt that the two species described in our paper are distinct, there are almost certainly other undescribed species along the Pacific Northwest, and there is no guarantee that our Friday Harbor, Washington, specimens are the same as, or even morphologically close to, whatever Clark (1932) described as *N. pugettensis*.

Comparison to Other Species of *Nebalia* Leach, 1814

The possibility that *N. hessleri* is an introduced species was considered in light of the increasing problem of exotic species being introduced into California via shipping (e.g., see Carlton and Geller, 1993). However, several features serve to separate *N. hessleri* from any other previously described member of the genus. First, the antennular flagellum of the mature female bears 14 or more segments (Figs. 2a, 4a). No other species is known to have more than 11; this number of segments is seen only in females of *N. falklandensis* Dahl, 1990, *N. antarctica* Dahl, 1990, *N. strausi* Risso, 1826, *N. herbstii* Leach, 1814, and the male of the species that occupies sand flats adjacent to the habitat of *N. hessleri* (Vetter, in press). In addition, the rostrum of *N. hessleri* is approximately 2.7 times its width. *Nebalia longicornis* Thomson, 1879, and the undescribed sand-flat *Nebalia* have long, thin rostrums as well, but neither exceeds a length of 2.6 times the width. This combination of features distinguishes *N. hessleri* from all other species in the genus.

Note on Males of *N. hessleri*

Because of the rarity of males in most populations (and therefore in most collections) of leptostracans, Dahl (1985) recommended that they not be used in species descriptions. However, males in our collections are relatively common. Although not counted, we estimate that males constituted perhaps 20% to 40% of our collections. Additionally, we found it interesting that, although there can be little doubt as to the distinctness of our new species, males of *N. hessleri* are similar to males of Clark's (1932) "*Nebalia pugettensis,*" in at least one character. Males of *N. hessleri* have a second antenna that is curved rather sharply in an anterior direction. Most often this condition appears as in the male allotype of

N. hessleri (Fig. 16a), but considerable variation exists, with the antenna sometimes extending almost directly anteriorly (Fig. 16b) and at other times curved medially so that the two opposing rami are crossed (Fig. 16c) or even appearing slightly corkscrewed (Fig. 16d). Clark (1932: 225) described this as "forwardly directed, sickle-shaped antennae, bearing a strong resemblance to the antennules of male cyclopoids," and based her new genus *Epinebalia* on this one character of the males.

Functional Morphology

Another factor that currently hinders comparisons of *N. hessleri* with other species of *Nebalia* along the west coast is that very few species have been examined via SEM. Thus, it is difficult to know whether some of the unusual ultrastructural features described herein, such as the twisted distal subterminal seta on the pleopodal spines, or the minute pore on the tip of the spines found on the antennular fourth article, are unique to this species versus shared by some or all members of the genus or perhaps shared by all leptostracans. The only previous electron microscope studies of leptostracans of which we are aware are the survey of European shelf species by Dahl (1985), which included only two SEM plates, a brief note on epipods by Itô (1988), and the study of spermiogenesis (coincidentally also using "*N. pugettensis*") by Jesperson (1979), in which only transmission electron microscopy was employed. Dahl's SEM photographs included only the dorsolateral teeth of the sixth and seventh pleonite borders in four species (his figs. 107–114) and one view of the setae of the first pleopod of *N. borealis* (his fig. 115). The acutely toothed pleonite borders of *N. hessleri* (Figs. 2f, g, 3f) are most similar to those of *N. borealis* (see Dahl, 1985: figs. 109, 110). The rich diversity of spine and setal types and the cuticular scales suggest that SEM may prove to be a valuable tool in leptostracan systematics, as has certainly been the case for other small crustacean taxa.

Some of the features illustrated herein are possibly indicative of sensory roles. This is true for the spines of the fourth article of the antennule, which bear a pore on the distal outer surface (Fig. 4b, c). A similar condition is seen in the spines bordering the distal article of the antennal peduncle (Fig. 5a, c, d). Although it is certainly possible for setae and spines lacking such pores to be chemosensory devices, with chemical mediators being transported across the thin cuticle of the appendage instead of via a pore (Laverack and Barrientos, 1985), it is unlikely that such pores would be present on a seta or spine with no such function. An alternative explanation, that these depressions are "molting pores," is easily dismissed by comparing the presumed chemosensory setae to surrounding spines and setae, none of which bear a similar terminal depression. Pores are also seen on the central spike of the tridentate spines of the first maxilla (Fig. 8a, b). Although these spines and setae have been illustrated accurately by previous workers (in this genus and in other leptostracan genera), the pores are a new finding, and suggest a sensory role in addition to the mechanical function of this limb. Also suggestive of a sensory function are the thin, twisted setae found on the subterminal undersurface of the rather heavy spines of the pleopods (Figs. 11c, d, 12e, g). Although we did not obtain sufficient resolution to determine whether these thin, straplike setae have distal openings, the impression given is that they do (especially see Figs. 11d, 12g).

Although SEM has not been widely applied to leptostracans for taxonomic purposes, some authors have illustrated spine and setal types that appear very similar to those we have shown in *N. hessleri*. For example, the characteristic spines along the lateral border of the first pleopod have been illustrated in nearly all descriptions of leptostracan species, and the better illustrated accounts (e.g., Wägele, 1983; Hessler, 1984) even include figures of the array of setal types on the maxillae, pleopods, etc. The emerging picture is one of great uniformity of setal and spine types in this order. Even in those species occupying disparate and unusual habitats (e.g., *Dahlella* at deep-sea hydrothermal vents, *Speonebalia* in caves), the setal types and their locations appear similar. Despite the fact that we have revealed previously unknown ultrastructural details of setae and spines in one leptostracan, overall it appears that di-

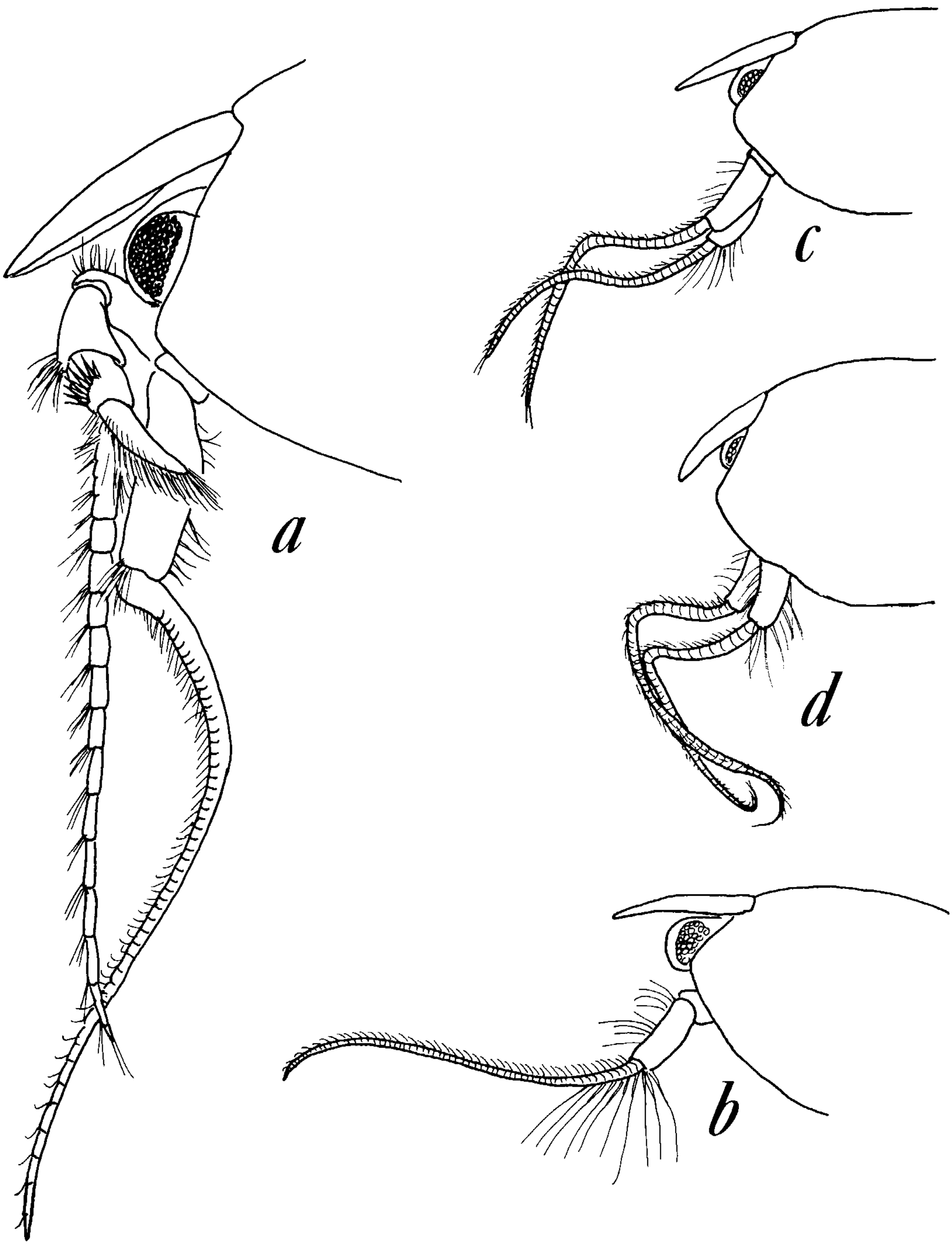

Fig. 16. *Nebalia hessleri*, new species, figures of the male second antenna. *a*, Allotype male, CL 2.8 mm excluding rostrum, same collection data as for female types, with first and second antenna illustrated. *b–d*, Variations in the shape and curvature of the flagellum of the second antenna (both right and left sides shown in (*c*) and (*d*)) in similar-sized males in the collection.

versity of these structures within the Leptostraca is not great. Thus, although ultrastructural details may provide species-specific characters, we are in agreement with Dahl's (1985: 138) statement that among leptostracan species and genera "basic armature pattern is remarkably uniform." This also leads us to suspect that structures newly described here as being sensory in nature, such as the subterminal twisted seta on the pleopodal spines, are probably to be found in other leptostracans as well.

Finally, this work supports and underscores the comments of Dahl (1987) concerning the morphology of leptostracans as compared to other "phyllopodous" crustaceans (particularly the Branchiopoda). The SEM photographs highlight the fact that even at an ultrastructural level, the thoracopodal appendages of nebaliaceans are grossly different from those of branchiopods, possessing a suite of spines and setae such as is seen in no living or extinct branchiopod (e.g., see Martin *et al.*, 1986; Martin, 1992; Martin and Christiansen, in press).

Because so few SEM studies exist for other species of *Nebalia* or other leptostracan genera, for purposes of identification at present we recommend reliance on previously recognized morphological (versus ultrastructural) characters, and suggest the following key to leptostracan families and genera (mostly compiled from information in Hessler, 1984; Dahl, 1985; Bowman *et al.*, 1985; and Modlin, 1991).

Key to the Extant Families and Genera of the Leptostraca

1. Thoracic region appearing inflated. Carapace and body cuticle thin, membranous. Carapace lacking posterior medial indentation and with slight sculpturing. Mandible lacking incisor process and with reduced molar process. First maxilla with palp reduced to small stub. Second maxilla nearly as large as thoracopod 1; endopod 1-segmented and reduced to small, blunt, distal lobe; exopod absent; proximal endite enormously enlarged. Pleopods 2–4 with exopods paddle-like, less than 3 times longer than wide. Caudal rami leaflike, broadest at midpoint . . . . Family Nebaliopsidae Hessler, 1984 (*Nebaliopsis* G. O. Sars, 1887)

– Thoracic region not inflated. Carapace and body cuticle more or less firm. Carapace strongly emarginate (indented) posteromesially and lacking sculpturing. Mandible with well-developed incisor (*Paranebalia* is an exception to this) and molar process. First maxilla with palp long, well developed. Second maxilla much smaller than thoracopod 1; endopod 1- or 2-segmented; endopod and exopod well developed, each longer than wide; first three endites similarly developed (proximal endite not enormously enlarged, although slightly larger than other endites). Pleopods 2–4 with exopods slender, more than 4 times longer than wide. Caudal rami tapering evenly from base to tip . . .2 (Family Nebaliidae Baird, 1850; emend. Hessler, 1984)

2. Eyestalk long, clearly exceeding rostrum in mature individuals, gently curved or abruptly angled ventrally, tapering distally, lacking any visual pigment 3

– Eyestalk short, not exceeding length of rostrum in mature individuals (or, if exceeding length of rostrum, then not deflected ventrally [*Speonebalia*]), widest at midpoint (not tapering), with or without visual pigment 4

3. Eyestalk with abrupt angle on anterodorsal surface, and with anterior margin flattened and bearing minute lobes. Second maxilla with exopod reduced, less than half length of proximal article of endopod. Posterior emargination of carapace lacking minute spines along either side of midpoint. Thoracopods with well-developed epipods . . . . *Dahlella* Hessler, 1984

– Eyestalk smoothly curving on anterodorsal surface, banana- or sausage-shaped, not flattened on anterior margin, lacking minute lobes. Second maxilla with exopod more than half length of proximal article of endopod (usually exceeding length of proximal article of endopod). Posterior emargination of carapace minutely spinulose along either side of midpoint. Thoracopods lacking epipods . . . . *Nebaliella* Thiele, 1904

4. Pleopod 1 with row of stout, equally sized, complex serrate spines along outer (lateral) margin of exopod. Eyes with at least some visual pigment 6

– Pleopod 1 lacking row of stout, equally sized, complex serrate spines along outer (lateral) margin of exopod. Eyes lacking visual pigment . . 5

5. Carapace long, extending posteriorly to just beyond level of fifth pleonite, sometimes as far as sixth pleonite. Eyestalks narrow, tapering distally, slightly exceeding length of reduced rostrum. Maxilla 2 endopod 1-segmented, with series of oval organelles (glands). Rostrum lacking distal spine. Caudal rami very short, length approximately equal to width of telson, with densely spaced long setae. . . . . *Speonebalia* Bowman *et al.*, 1985

– Carapace short, not extending posteriorly beyond fifth pleonite. Eyestalks laterally compressed, disc-shaped or subrectangular, never exceeding length of rostrum. Maxilla 2 endopod 2-segmented, lacking glands. Rostrum with minute distal spine articulating with rostral cuticle. Caudal rami slender, length more than twice length of telson, with widely spaced setae . . . . *Sarsinebalia* Dahl, 1985

6. Antenna 1 peduncle distal (fourth) segment with distolateral, toothed processes, but not with armature of spines (as, e.g., in *Nebalia*). Mandibular incisor weakly developed. Thoracopods nar-

row and long, almost flagelliform. Epipods of thoracopods present but reduced in size, with surface area less than half that of endopod. Eyes often bearing spines that increase in size distally . . . . *Paranebalia* Claus, 1880

– Antenna 1 peduncle distal (fourth) segment without distolateral, toothed process, instead with stout spines. Mandibular incisor well developed. Thoracopods expanded, leaflike. Epipods of thoracopods well developed, surface area clearly one-half or more that of endopod. Eyes sometimes with blunt lobes but never with numerous spines . . . . *Nebalia* Leach, 1814

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