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REVIEW AND REDESCRIPTION OF THE FRESHWATER ATYID SHRIMP GENUS *SYNCARIS* HOLMES, 1900, IN CALIFORNIA

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ABSTRACT

All known specimens of the presumed extinct freshwater shrimp species *Syncaris pasadenae*, formerly known from the Los Angeles River and other lowland stream sites in southern California, were examined. Existing specimens are housed in the Natural History Museum of Los Angeles County, California Academy of Sciences, or U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. *Syncaris pasadenae* is diagnosed and redescribed and compared to its only congener, *Syncaris pacifica*, an extant species restricted to a few small coastal streams in northern California (Marin, Napa, and Sonoma counties). *Syncaris pacifica* is also redescribed. Salient and consistent differences between the species are the dorsal dentition of the rostrum and the number of pereopods bearing exopods, a character often associated with higher-level taxonomic differences in the past. The distribution of the species and the position of the genus within the family Atyidae are discussed.

In 1895, S. J. Holmes described a new species of freshwater shrimp based on "several specimens from Sonoma County, Cal. (L. E. Ricksecker)." Holmes named the new species *Miersia pacifica*, placing it in a new genus (*Miersia*) and new family (Miersiidae). Holmes was unaware that the name *Miersia* had been used previously by Kingsley (1880) as a replacement name for an alpheid shrimp, and the name *Miersia* has subsequently been placed on the official index of rejected and invalid names in zoology (see discussion in Holthuis, 1993: 33). Although the written description given by Holmes was fairly detailed for the time, the accompanying illustrations were only of the rostrum and second pereopod (his plate xxi, figs. 27 and 28). Two years later, the pioneering naturalist J. S. Kingsley, in a paper devoted mostly to the description of the new genus *Naushonia* and the species *Naushonia crangonoides* (Thalassinidea, family Laomediidae), described a new species of shrimp from freshwater habitats in southern California (Kingsley, 1897). Kingsley named the new species *Caridina pasadenae*, because it had been described by its collector (A. J. McClatchie) as being "common in the streams about Pasadena, California" (Kingsley, 1897: 98). Apparently unaware of Holmes' description of *Miersia pacifica*, Kingsley pointed out several differences between the new California species and other known species of *Caridina*, most notably the length and dentition of the rostrum. Illustrations that accompanied Kingsley's description (1897, plate III, figs. 1–7) were unfortunately somewhat schematic and are not informative by today's standards.

The genus *Syncaris* was established by Holmes (1900) to include two species of freshwater shrimp: (1) the former *Miersia pacifica* described by Holmes from Sonoma County, California, and (2) what he thought was a new species, *Syncaris trewi* (based on four specimens collected "in a small stream near San Gabriel, Los Angeles County, Calif., by Mr. N. C. Trew." Holmes indicated that these specimens were in the "Collection University of California." Apparently it was Bouvier (1925) who first recognized that *Syncaris trewi* Holmes was a junior synonym of *Caridina pasadenae* Kingsley, with the result that the genus *Syncaris* has subsequently contained two species: *Syncaris pacifica* in northern California and *Syncaris pasadenae* to the south.

It is apparent that the southern species, *Syncaris pasadenae*, is now extinct. Extensive efforts to locate the species by Hedgpeth (1968) and colleagues (C. Hand, J. C. Yaldwyn, and others), collecting in streams from the Mexican border north to Santa Barbara, resulted in no

new collections. The most recently collected specimens known to Hedgpeth (1968) were collected in 1933, and this lot remains the most recent material of the species. Hedgpeth (1968) observed that "the type locality appears to have been about where the Rose Bowl now stands." How he determined this is unclear, as Kingsley (1897) did not give a specific type locality.

No detailed descriptions of either species of *Syncaris* exist. Mouthparts of *S. pacifica* were illustrated by Bouvier (1925), but the mandible was not treated. Ironically, the mandible was the only mouthpart that was illustrated by Kingsley (1897) for *S. pasadenae*. However, as noted by Holmes (1900: 215), the mandible drawn by Kingsley and attributed by him to *S. pasadenae* (as *Caridina pasadenae*) cannot possibly belong to that species, as it bears a mandibular palp, which is never present in any member of the family Atyidae. The figure in question undoubtedly belongs to the species of *Naushonia* that Kingsley described and figured in that same paper.

If further specimens of freshwater shrimp are ever found in southern California, or anywhere south of the currently known range of *S. pacifica*, identification of the specimens would be greatly facilitated by more detailed descriptions and a comparison of these two species. Below we redescribe both species of *Syncaris*.

Syncaris Holmes, 1900

Diagnosis.—Atyid shrimp with first and second pereopods chelate and modified (distally setose) for feeding on small particles. Carpus of first cheliped excavated (concave) on anterior surface to receive posterior "heel" of chela, carpus of second cheliped not excavated. Rostrum long and slender, with at least one (usually more) ventral teeth (= dentiform spines), with or without dorsal teeth (depending on species), and terminally appearing minutely bifid. Carapace lacking carinae but with well-developed supraorbital spine, antennal spine, and pterygostomial spine. Exopods present on maxillipeds 2 and 3, variable on pereopods 1–4, always absent on pereopod 5. Epipods always present on pereopods 1–4, never on pereopod 5; where present, epipods well developed and extending posteriorly over coxa of adjacent pereopod. Carpus and merus of pereopods 3–5 each with pair of strong spines on ventral or ventrolateral border. Telson with 2 pairs of marginal spines on distal half, terminally broadly rounded or truncate with distal setae flanked by 2 pairs of short terminal spines. Outer uropod with diaresis weakly developed, not extending full width of uropod, and terminating laterally in one short, movable spine and one immovable lateral point. Second maxilliped with dactylus and propodus fused, resulting in terminal article that appears strongly notched or "indented" medially at approximately one-third its length.

Remarks.—The generic description of Holmes (1900) must be modified in part because of his belief that in this genus one finds "two or more pairs of pereopods furnished with exopods." Whereas this is true for *Syncaris pacifica*, the situation is quite variable in *S. pasadenae*, and occasionally in that species none of the pereopods bears an exopod (see Discussion).

Syncaris pasadenae (Kingsley, 1897)
Figs. 1–4, 5a–c

Caridina pasadenae Kingsley, 1897: 98, plate 3, figs. 1–5, 7, and 8 (not fig. 6, erroneously attributed to this species in the caption to plate 3, but belonging instead to *Naushonia crangonoides*).—Holmes, 1900: 214.

Syncaris Trewi Holmes, 1900: 213, fig. 63.—Bouvier, 1905: 64.

Syncaris Pasadenae Kingsley.—Bouvier, 1925: 70, figs. 110, 111.

Syncaris pasadenae Kingsley.—Hedgpeth, 1968: 516.—Holthuis, 1993: 63, fig. 50 (fig. after Bouvier).

Material Examined.—CAS 4154: *Syncaris pasadenae* (Kingsley), small creek 100 yards from entrance into Santa Anna River, Riverside, California, T. Craig, 27 Feb. 1927, 15 specimens.

LACM CR 1925-001.2: 1 vial, misspelled (as *Syncarius*), with old label bearing Museum of History, Science, and Art, Los Angeles, Calif., and with the following information on the label: "Ac. No. A 1207, 3-31-25, *Syncarius pasadenae* (Kingsley), Fresh Water Shrimp, L. A. River, California, Coll. H. R. Hill, Alc. 75%." Number of specimens in vial: 50, including 5 ovigerous. One female from this large collection stored separately as LACM CR 1925-001.1, carapace and rostrum length 16.3 mm, total length 40.0 mm, Los Angeles River, California, 31 March 1925, H. R. Hill (formerly in lot LACM CR 1925-001.2).

LACM CR 1925-002.1: Second vial, with exact same label type and information (including misspelling of genus), and with the following additional information: "Mus. No. 159 4-13-25" (presumably April 13, 1925), such that collection dates differ. Number of specimens in vial: 6 (one of which illustrated as Fig. 1), including 1 ovigerous.

LACM CR 1912-002.1: Third vial, with different type of label, reading as follows: "Ac. No. A 18, 5-15-12, *Syncaris pasadenae* (Kingsley), Fresh Water Shrimp, San Gabriel River, Coll. N. C. Trew, Alc. 75%." Number of specimens in vial: 3.

USNM 7599: *Syncaris pasadenae* (Kingsley), 1 male, 9 females, San Diego, Calif., C. R. Orcutt, Id. F. A. Chace, 1952, No. 14530. (Locality of these specimens doubted by Hedgpeth, 1968, who suggested that "San Diego" might

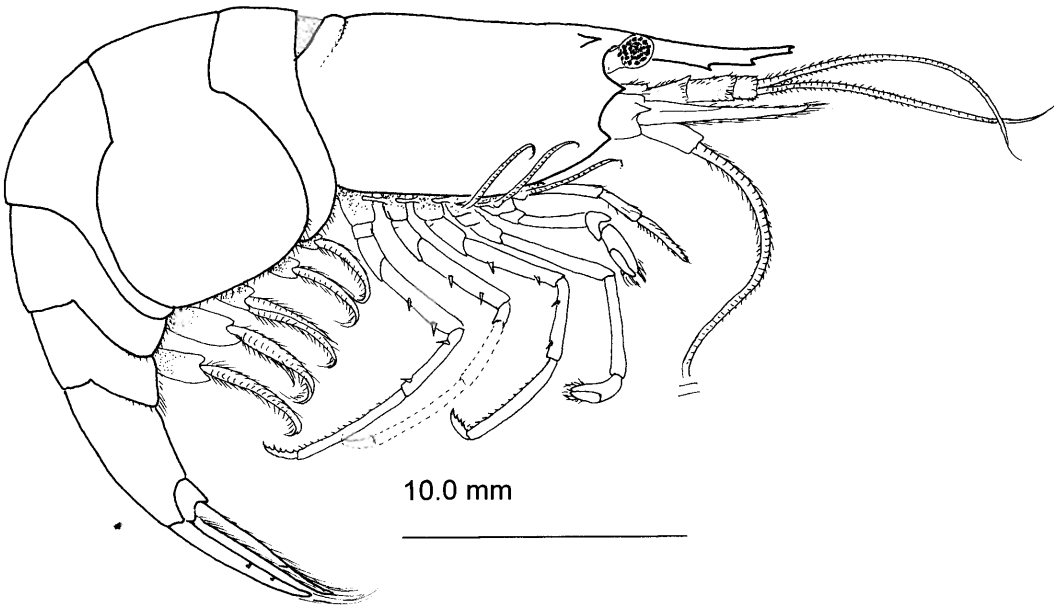

Fig. 1. *Syncaris pasadenae* (Kingsley), lateral view of 16.45 mm CL female from Los Angeles River collected in 1925, one of six specimens in vial (LACM CR 1925-002.1). Scale bar = 10.0 mm.

refer to the address of the collector [Orcutt] instead of to the collecting locality).

USNM 67644: *Syncaris pasadenae* (Kingsley), Warm Creek, San Bernardino, Calif., coll. A. E. Berghduff, don. P. R. Needham, Feb. 6, 1933, Id. W. L. Schmitt, Acc. No. 123282. Another label in this jar states: "*Syncaris pasadenae* (Kingsley) 32 (1 ovig.)," and another smaller label bears the numbers 123/282 without further explanation. 32 specimens, one ovigerous.

USNM 78196: *Syncaris pasadenae* (Kingsley), Los Angeles R., California, K. & M. (coll.), G. S. Myers (don), April 11, 1929, Id. W. L. Schmitt, Acc. No. 140670. (one specimen, carapace of which is illustrated as Fig. 4b).

USNM 86807: *Syncaris trewi* Holmes, San Gabriel, California, Mr. M. C. Trew (coll.), co-types, Id. S. J. Holmes, Acc. No. 180084 (four specimens, all in poor condition).

USNM 59494: *Syncaris pasadenae* (Kingsley), 17 males, 15 females, Los Angeles River, Los Angeles, California, March 13 and June (date not given), 1925, coll. H. R. Hill, identified by F. A. Chace, 1952, Acc. No. 87142. (Label states 17 males and 15 females, however lot contains only 22 specimens, 4 of which are ovigerous females.)

USNM 20323: *Caridina pasadenae* Kingsley, coll. J. S. Kingsley, Id. J. S. Kingsley, Pasadena, California, one ovigerous female, CL = 12.2 mm (Fig. 4d), one male, CL = 13.4 mm (Fig. 4c), and one juvenile, CL = 8.6 mm, listed as "co-types" on the label. These are apparently syntypes collected and identified by J. S. Kingsley.

Diagnosis.—*Syncaris* lacking any dorsal teeth (= dentiform spines) on rostrum and with variable number of pereopods bearing an exopod.

Description.—Rostrum (Fig. 1, 2a–c, 4) without dorsal teeth (= dentiform spines) and with one to five ventral teeth; apex bifid. Carapace with supraorbital, antennal, and pterygostomial spines; posterior dorsal margin slightly raised. First abdominal somite broadly rounded; second somite with margins broadly rounded and greatly overlapping first and third somites; third, fourth, and fifth somites with posterolateral margins obtuse, without spines; sixth somite with blunt margins. Eye large, globular and pigmented. Total length 32–50 mm; more typically 35–45 mm.

Antennae: Antennular peduncle (Fig. 5a, b) shorter than rostrum or scaphocerite. Stylocerite reaching to approximately middle of second segment. All segments setose; first segment longest. Flagella slender, with few scattered small setae. Basicerite of antenna stout, with lateral spine. Carpocerite reaching less than half length of scaphocerite; scaphocerite (Fig. 5c) about as long as rostrum, with well-developed blade exceeding spine.

Mouthparts: Mandibles (Fig. 3a–c) asymmetrical, without palp. Left mandible with 4 strong teeth, with gap between distalmost tooth and 3 lower (proximal) teeth and with tuft of strong setae and well-developed molar process. Right mandible with 4 teeth without gap but with tuft of setae and strong molar process. First maxilla (Fig. 3d) with broad distal endite bearing row of setae on medial margin; proximal endite also

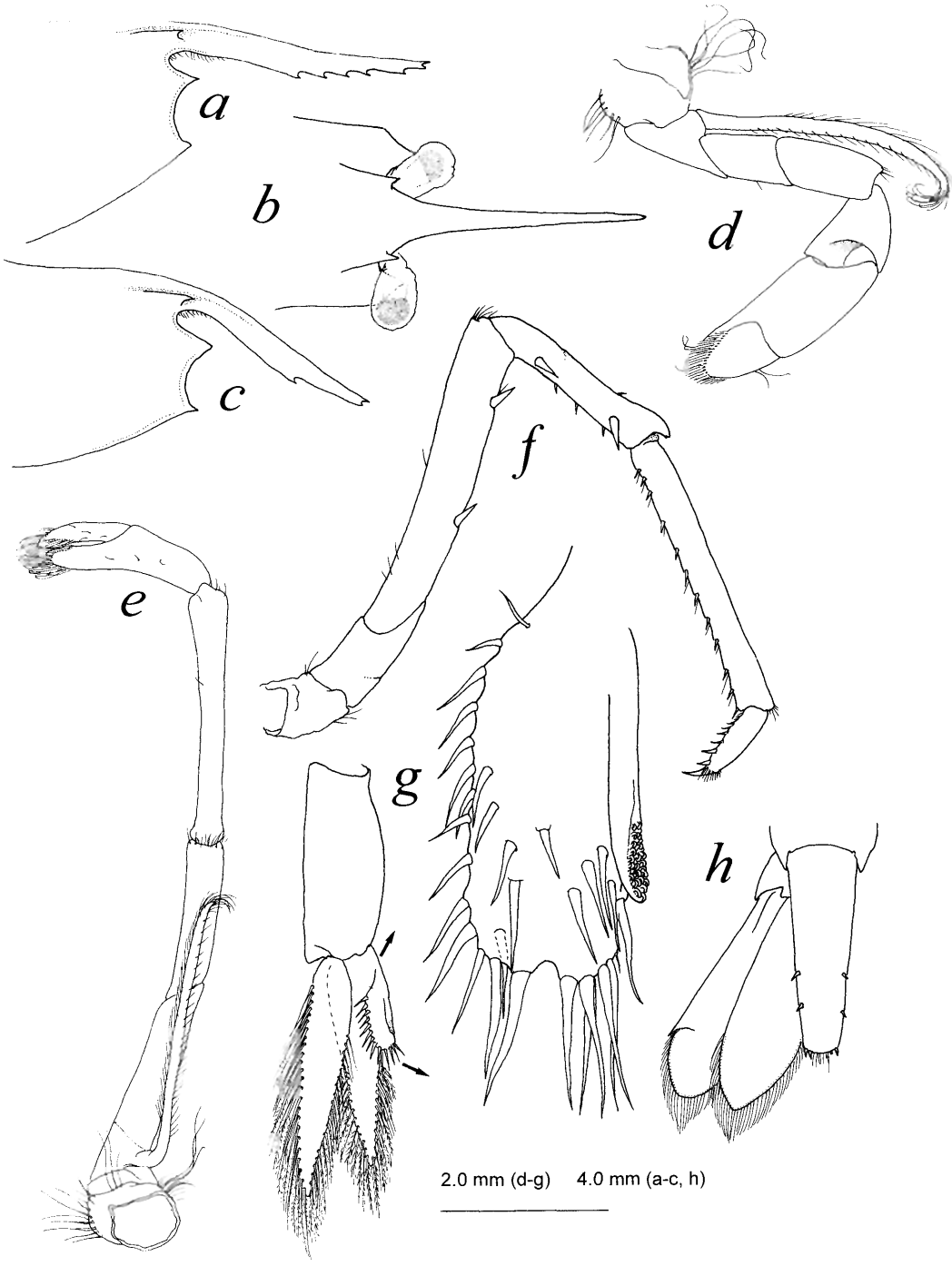

Fig. 2. *Syncaris pasadenae* (Kingsley), carapace and selected appendages from a 40.0 mm (total length, including rostrum) female collected in 1925 from the Los Angeles River (in lot LACM 1925-001.2). *a*, front of carapace in lateral view; *b*, same, dorsal view, showing supraorbital spines; *c*, front of carapace of similar-sized female (one of several in LACM CR 1925-001.2) showing variability in rostrum; *d*, first pereopod (cheliped); *e*, second pereopod; *f*, fourth pereopod (second walking leg), from different female in same lot; *g*, second pleopod of 11.8 mm carapace-length male from same lot, with appendix interna and appendix masculina, both of which are enlarged at right of figure; *h*, telson and left uropods, dorsal view, female. Scale bar = 4.0 mm for *a–c*, *h*; 2.0 mm for *d–g* (except enlargement of *g*).

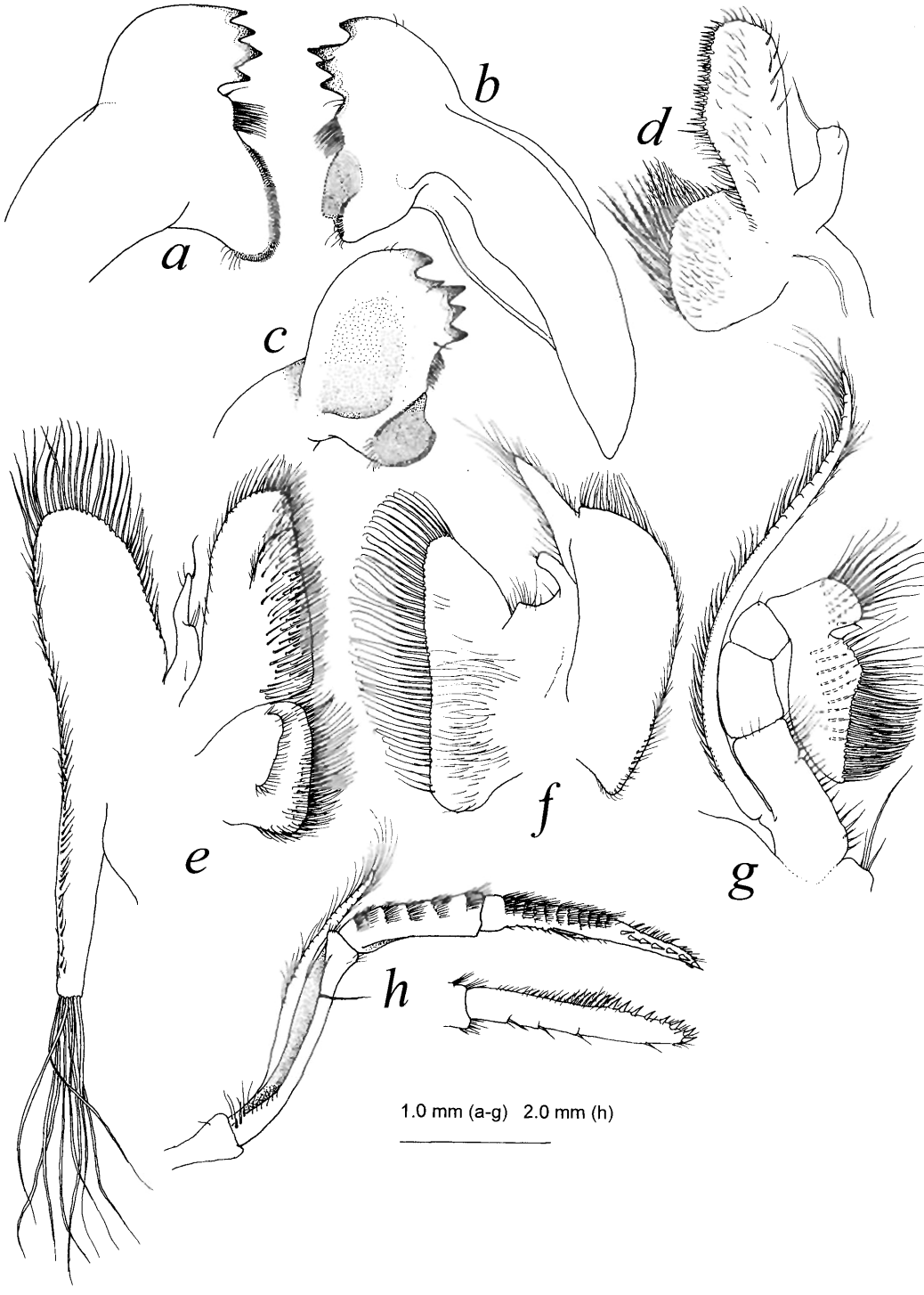

Fig. 3. *Syncaris pasadenae* (Kingsley), mouthparts. *a*, right mandible, outer view; *b*, left mandible, outer view; *c*, left mandible, inner view, showing depressed central region and groove at bottom that accommodates blade-like molar process of right mandible when right and left mandible are approximated; *d*, first maxilla; *e*, second maxilla; *f*, first maxilliped; *g*, second maxilliped; *h*, third maxilliped, with dactylus illustrated from two different angles to show setation and spination. All figures from same female (in lot LACM CR 1925-001.2) except for *b* and *c*, which are from a different female of similar size. Scale bar = 1.0 mm for *a*–*g*, 2.0 mm for *h*.

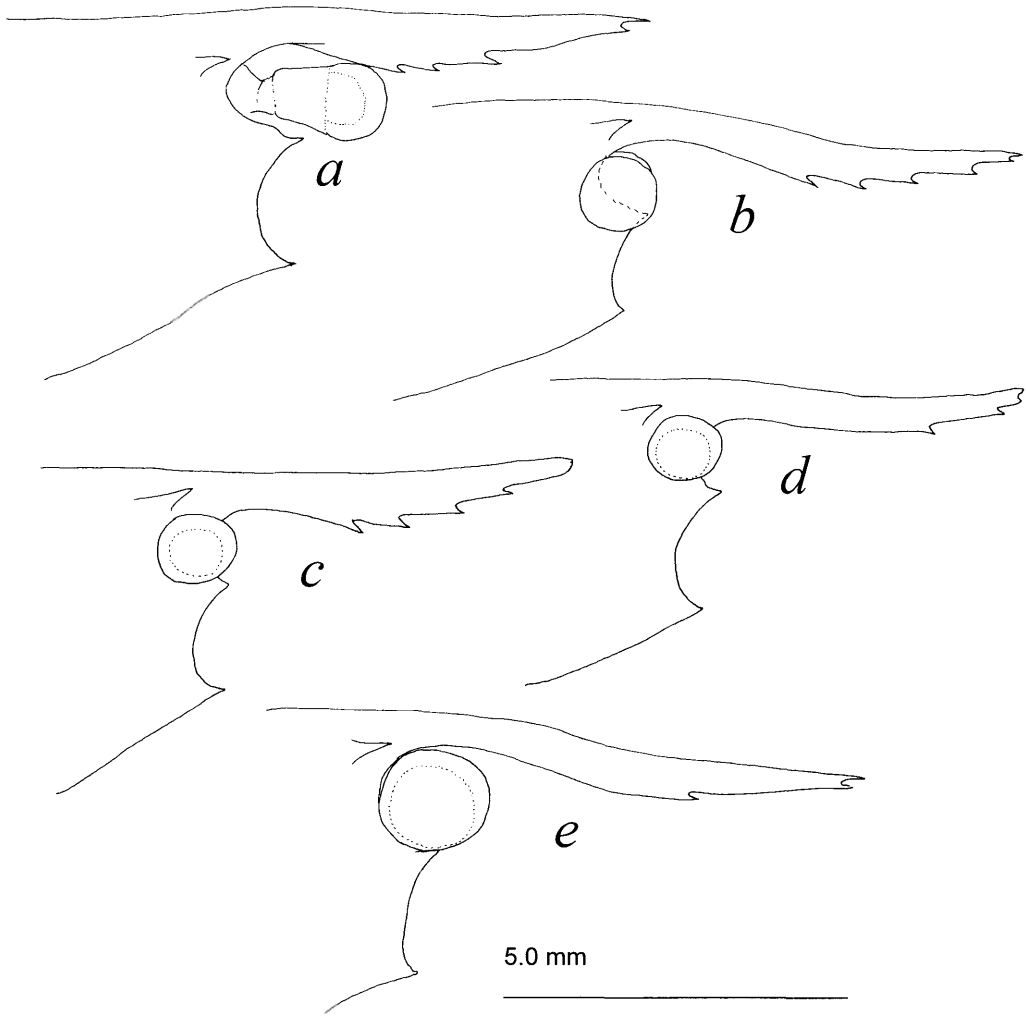

Fig. 4. *Syncaris pasadenae* (Kingsley), variability in rostral morphology. *a*, ovigerous female from a lot of 10 specimens (USNM 7599, San Diego, Calif., C. R. Orcutt, Id. F. A. Chace, 1952); *b*, USNM 78196, coll. "K & M", don. G. S Myers, 11 April 1929; *c*, 13.35 mm CL male "co-type" of *Caridina pasadenae* Kingsley, USNM 20323, coll. J. S. Kingsley, Id. J. S. Kingsley, Pasadena, California; *d*, 12.22 mm CL ovigerous female, another "co-type" of *Caridina pasadenae* Kingsley, USNM 20323, same collection data; *e*, ovigerous female, the only one of 32 specimens (USNM 67644), Warm Creek, San Bernardino, California, coll. A. E. Berghduff, don. P. R. Needham, 6 February 1933. Scale bar = 5.0 mm.

broad, with fringe of feathery setae; palp with 1 long distal seta. Second maxilla (Fig. 3e) with bilobed distal endite, proximal endite broad, both fringed with setae; palp wider in proximal half than distal, with few setae; scaphognathite with upper half broad, lower half very narrow and ending in tuft of long setae. First maxilliped (Fig. 3f) with only one large endite, small palp, short exopod, and very broad caridean lobe. Second maxilliped (Fig. 3g) with small podobranch, long exopod and four-jointed medial branch; ultimate segment of medial branch (fused dactylus and propodus) with distinctive "notch" on mesial surface. Third maxilliped (Fig. 3h) with small exopod reaching to approximate midpoint of middle segment. Proximal segment concave on anterodorsal margin, with few setae. Middle segment with tufts of setae in rows. Distal segment densely setose, with double row of spinules along distal end.

Pereopods: First pereopod (Fig. 2d) with epipod; exopod setose if present, reaching to carpus; merus and ischium smooth and cylindrical, merus slightly longer than basis; carpus triangular and smooth; palm of chela robust, 2× long as wide; fixed finger of chela flat and

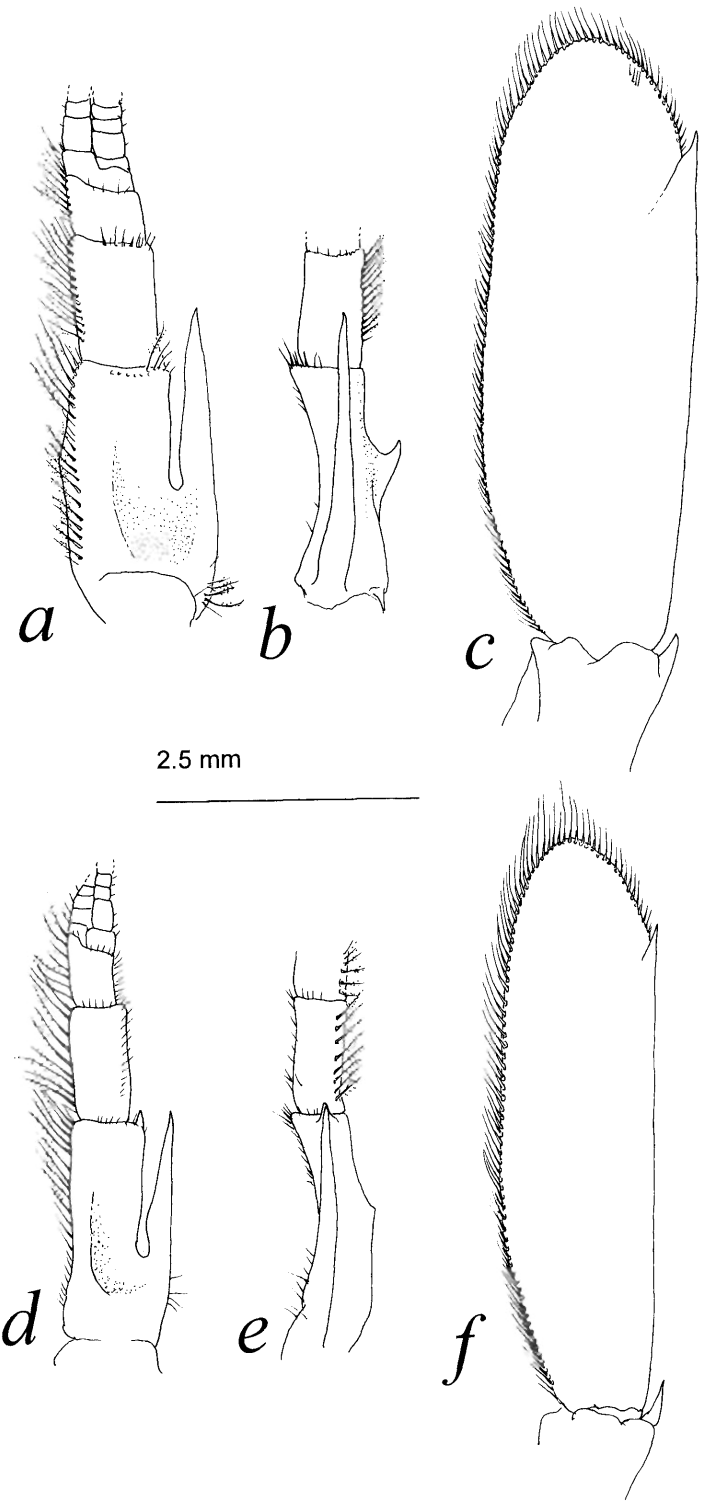

Fig. 5. *Syncaris pasadenae* (Kingsley) (*a–c*) and *S. pacifica* (Holmes) (*d–f*), bases of antennule and antenna. *a*, *Syncaris pasadenae*, base of antennule, dorsal view; *b*, same, lateral view; *c*, same specimen, scaphocerite (antennal scale), dorsal view; *d*, *Syncaris pacifica*, base of antennule, dorsal view; *e*, same, lateral view; *f*, same specimen, scaphocerite (antennal scale), dorsal view. Scale bar = 2.5 mm.

setose; dactylus robust and spatulate, densely fringed with stiff setae. Second pereopod (Fig. 2e) chelate, with epipod; exopod, if present, reaching past middle of merus; basis longer than merus, cylindrical; merus with few setae along distal margin; carpus elongate, 7.5× long as wide and 1.7× longer than merus; palm of chela slender, 1.9× long as wide, with few scattered setae; fixed finger of chela spatulate, ending in dense brush of stiff setae; dactylus curved, ending in brush of stiff setae; fingers of chela gaping. Third pereopod (Fig. 2f) with epipod (not illustrated); lacking exopod; merus longest segment, 6.6× longer than wide, with 2 sharp spines on flexor margin; carpus slender and cylindrical, subequal in length to propodus, with 2 sharp ventrolateral spines; propodus smooth and cylindrical, with numerous small spinules along flexor margin; dactylus simple, with row of spinules along flexor margin. Fourth and fifth pereopods similar to third but shorter; fourth with epipod, fifth without epipod.

Pleopods, uropods, and telson: Pleopods (Fig. 2g) with appendix internae. Second pereopod of male with appendix masculina approximately 0.5× length of appendix interna, with small nodules on mesiodistal surface. Uropods (Fig. 2h) distally rounded to slightly acuminate, setose, longer than telson, with one acute point and one small movable spine at external margin of diaresis on external ramus. Telson with two pairs posterolateral spines, apex round to truncate, with distal setae flanked by 2 pairs of short terminal spines.

Range.—Formerly known from the Los Angeles River drainage, in streams near San Gabriel and Pasadena, Los Angeles County, and Warm Creek, San Bernardino County, California (Hedgpeth, 1968). Hedgpeth (1968: 516) felt that the single record from San Diego was possibly erroneous. A cryptic reference to "freshwater shrimps" in a tributary to the Santa Ana River by George (1927) might also indicate their former presence there. Now believed to be extinct (category EX, IUCN Red List Categories and Criteria, 2001).

Type locality.—"streams near Pasadena" (Kingsley, 1897).

Natural History.—Mostly unknown. Hedgpeth (1968) noted that ovigerous females were present in collections made in February, 1933 (Warm Creek, San Bernardino County), and in "March 13 and June, 1925" (Los Angeles River). Based on this information, Hedgpeth suggested that the species probably had a winter breeding season, as does its northern congener.

Remarks.—From USNM 7599, one ovigerous female was illustrated (Fig. 4a). All specimens in this lot were examined, and we found that placement of the exopods varied. Some of the specimens had an exopod only on the third maxilliped, whereas others had it on mxpd 3 and P1. However, none of the specimens in this lot (USNM 7599) examined by us had an exopod on P2 (and of course none of them had one on any of the more posterior pereopods either). In USNM 67644, there were indeed 32 specimens, as indicated on the label. One of us (JM) selected 20 of these at random to examine for presence and position of exopods. Exopods were distributed as follows: Present on third maxilliped only: 12 (including a large ovigerous female). Present on both third maxilliped and first pereopod: 6 specimens. Present on third maxilliped, first pereopod, and second pereopod: 2 specimens. The rostrum of the ovigerous female is also illustrated (Fig. 4e). Lot USNM 59494 contained only 22 specimens, not the 32 (17 females and 15 males) indicated on the label. Specimens from the large lot in Los Angeles (LACM CR 1925-001.2) were also found to vary, but as with all other specimens examined, none had an exopod on the third or fourth pereopod. In the three specimens constituting the syntype collection (USNM 20323), all have an exopod on the third maxilliped but not on any pereopod.

Syncaris pacifica (Holmes, 1895)
Figs. 5d–f, 6–10

Miersia pacifica Holmes, 1895: 577, pl. 21, figs. 27, 28.
Syncaris pacifica.—Holmes, 1900: 213.—Bouvier, 1905: 64.—Bouvier, 1925: 68, figs. 98–109.—Hedgpeth, 1968: 512; 1975: 5, figs. 1, 2.—Born, 1968 (physiology).—Eng, 1981: 2, fig. 1; 1984.—Li, 1981 (distribution).—Serpa, 1986; 1991; 1992a, 1992b; 1996 (distribution).—U.S. Fish and Wildlife Service, 1988 (endangered species listing)—Messer and Brumbaugh, 1989.

Material Examined.—LACM CR 1961-180.1 (Acc. No. 1961): Salmon Creek, Bodega Bay, Sonoma County, California, 13 April 1961, Joel Hedgpeth and party. 5 specimens.

USNM 5495: Brook, California, W. H. Smith, Sebastopol, California, Acc. no. 13469, Sept. 5, 1883, M. J. R. det., 54 specs. There is a single label inside that says "Fig'd" (probably meaning figured, but by whom is unknown). One individual from this large lot illustrated (our Fig. 6); it is now in a small glass vial within the original lot.

USNM 78198: 2 specimens, Napa Creek, Calistoga Co., California, C. H. Gilbert (coll.), W. P. Hay (don.), May 31,

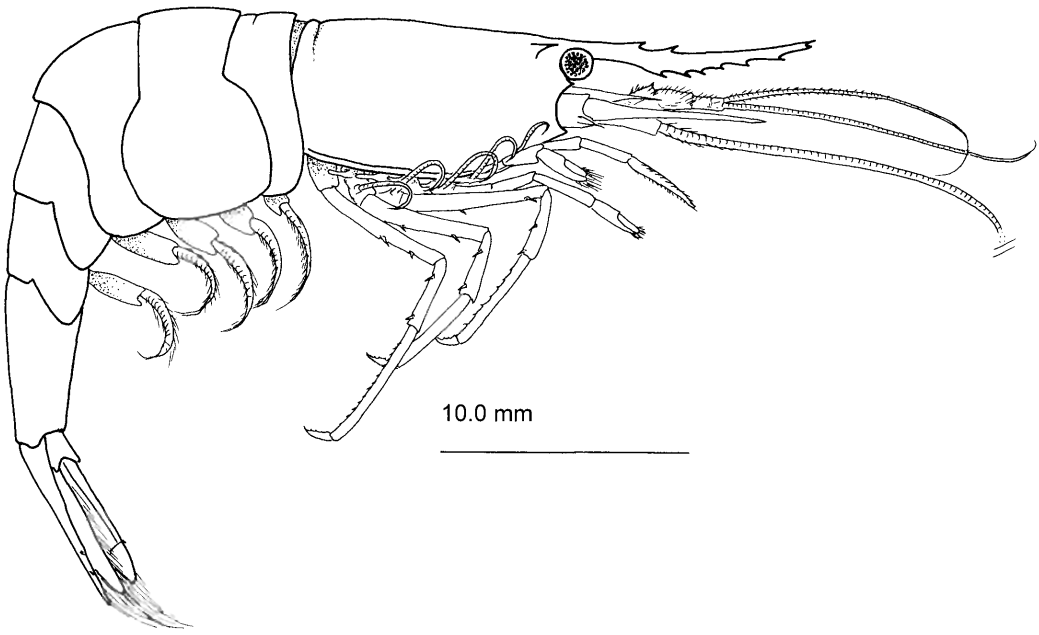

Fig. 6. *Syncaris pacifica* (Holmes), lateral view, USNM 5495, 18.95 mm CL (tip of rostrum to posterior margin of carapace). Scale bar = 10.0 mm.

1897, Id. W. L. Schmitt. Another label in the jar, pre-printed on a "Collection W. P. Hay" label, states: "Type, Napa Creek, Calistoga Co., Cal., Coll. C. H. Gilbert, May 31, 1897."

USNM 6235: Lagonistas [probably a misspelling of Lagunitas] Creek, Cal., 75+ specimens, coll. Gustav Eisen, July, 1877, M. J. R. det.

USNM 6257: Lagonistas [probably a misspelling of Lagunitas] Creek, Cal., 75+ specimens, coll. Gustav Eisen, July, 1877, M. J. R. det.

Diagnosis.—*Syncaris* with 1–2 dorsal teeth on rostrum and with exopods on first four pereopods.

Description.—Rostrum (Figs. 6, 7a) slender, about as long as carapace, with 1–2 dorsal and 5–9 ventral teeth (dentiform spines). Carapace with supraorbital, antennal, and pterygostomian spines. First abdominal somite with anterior border abruptly slanted downward in male, regularly convex in female. Second and third somites with pleura rounded, fourth and fifth somites with subangular borders, sixth with posterolateral margin quadrate. Eyes large, pigmented. Total length up to 50 mm; more typically 30–40 mm.

Antennae: Antennular peduncle (Fig. 5d, e) with stylocerite just exceeding first segment. First segment longest, second shorter, third shortest. Antennular flagella subequal, inner flagellum with short setae. Basicerite with lateral spine. Carpocerite about 0.5× length of scaphocerite. Scaphocerite (Fig. 5f) about equal to rostrum, blade length exceeding lateral spine.

Mouthparts: Mandibles (Fig. 8a) unequal, without palp; right with 4 teeth, few small setae and well-developed molar process; left with 5 teeth, gap between distalmost tooth and lower 4, few setae and well-developed molar process. First maxilla (Fig. 8b) with broad distal endite, proximal endite rounded, palp with 1 long seta. Second maxilla (Fig. 8c) with bilobed distal endite, broad and rounded proximal endite; small palp, elongate scaphognathite, broader at distal end than at proximal end, proximal end with tuft of long setae. First maxilliped (Fig. 8d) with broad distal obtuse endite, small curved palp, broad caridean lobe, and short exopod. Second maxilliped (Fig. 8e) with podobranch, elongate exopod, and 4-segmented medial branch; ultimate segment of medial branch (fused dactylus and propodus) with "notch" on mesial surface. Third maxilliped (Fig. 8f) with arthrobranch, exopod reaching second segment; second segment with 5 rows of stiff setae; terminal segment setose and ending in spines.

Pereopods: Pereopods 1–4 with exopods and epipods. First pereopod (Fig. 7b) with merus approximately equal to carpus; carpus short,

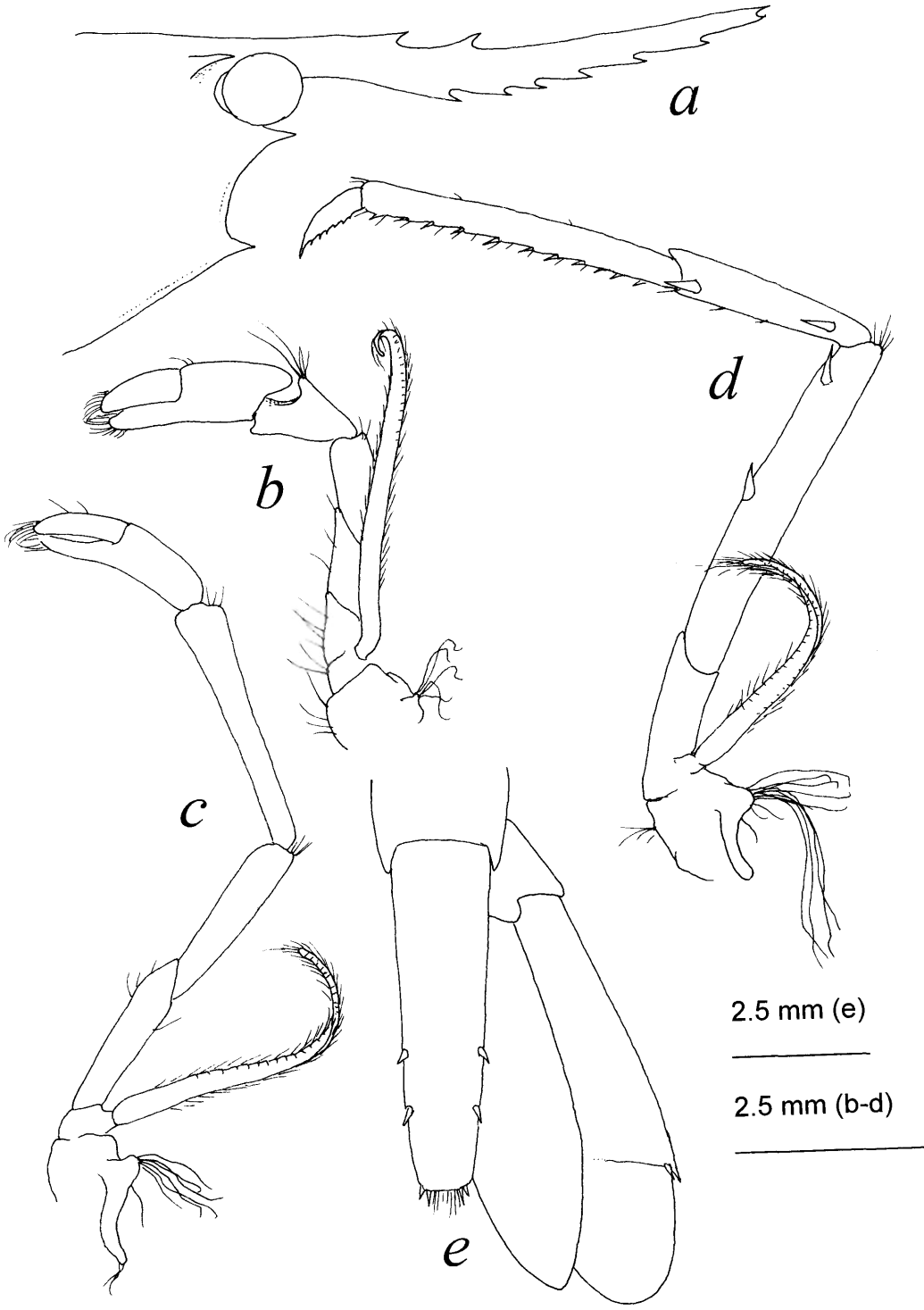

Fig. 7. *Syncaris pacifica* (Holmes), rostrum, left side pereopods, telson, and uropods, same individual illustrated in Fig. 6. *a*, rostrum and front of carapace; *b*, first pereopod (cheliped); *c*, second pereopod (cheliped); *d*, third pereopod; *e*, telson and right uropods, dorsal view. Scale bar = 2.5 mm for *e* (upper bar); 2.5 mm for *b–d* (lower bar).

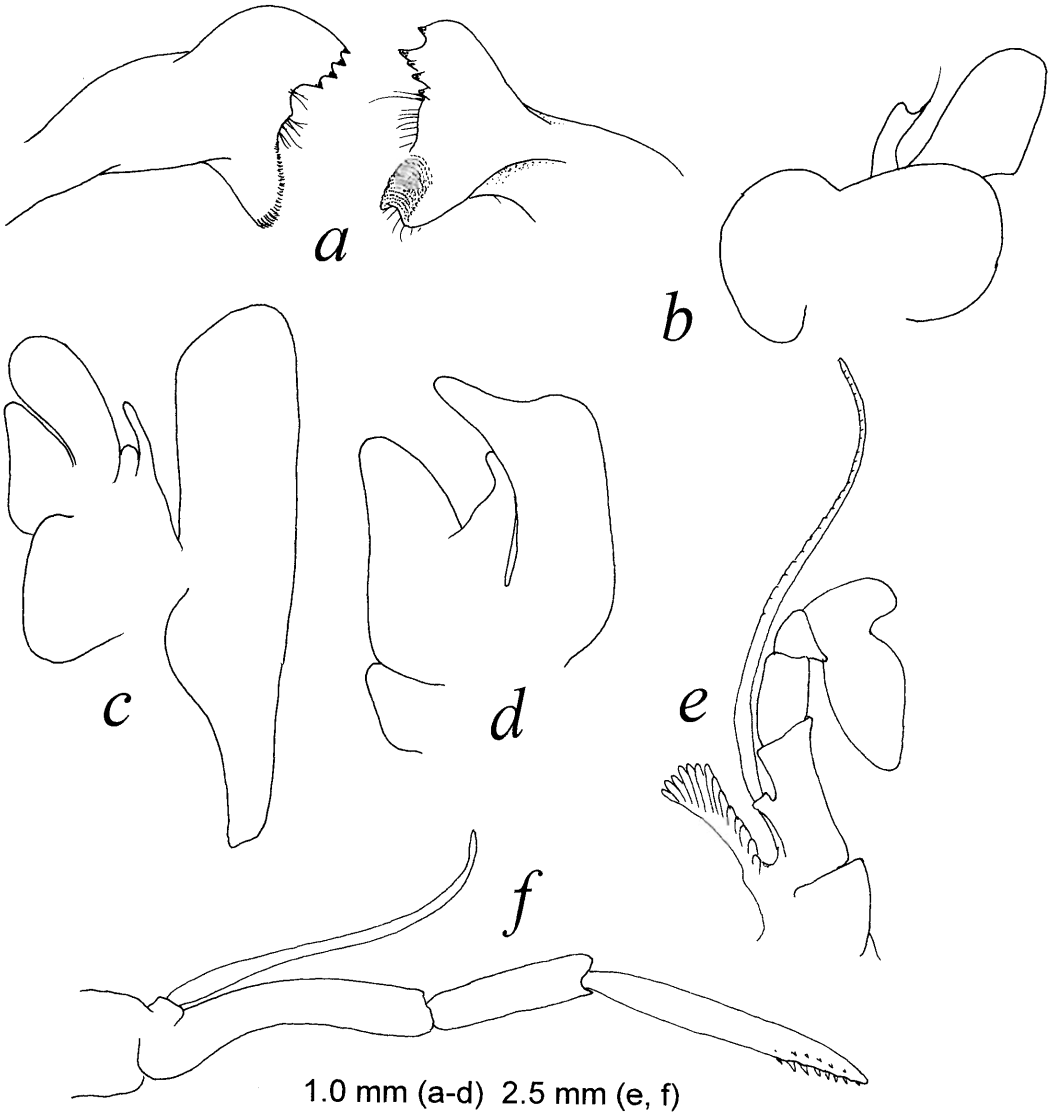

Fig. 8. *Syncaris pacifica* (Holmes), mouthparts, same individual illustrated in Fig. 6. *a*, mandibles in outer view (right mandible therefore on left side of figure; left mandible on right side of figure); *b*, left first maxilla (maxillule), outer view; *c*, left second maxilla, inner view; *d*, left first maxilliped, inner view; *e*, left second maxilliped, outer view; *f*, left third maxilliped, outer view. Setation omitted for clarity. Scale bar = 1.0 mm for *a–d*; 2.5 mm for *e*, *f*.

excavate at junction with chela; fingers of chela spatulate and ending in brush-like setae. Second pereopod (Fig. 7c) with merus shorter than carpus; carpus 4× longer than wide and not excavate; palm longer than fingers of chela; fingers of chela gaping, spatulate and ending in stiff brush-like setae. Third pereopod (Fig. 7d) with merus having 2 spines on flexor side, carpus with two ventrolateral spines, about 0.5× length of merus; propodus about 2× carpus, with row of spinules along flexor margin; dactylus simple, with 6 spinules along flexor margin. Fourth and fifth pereopods similar to third, but shorter; fifth without exopod or epipod.

Pleopods, uropods, and telson: Male with specialized appendix interna on first pleopod. Second pleopod with appendix interna. External uropod (Fig. 7e) with acute point and one

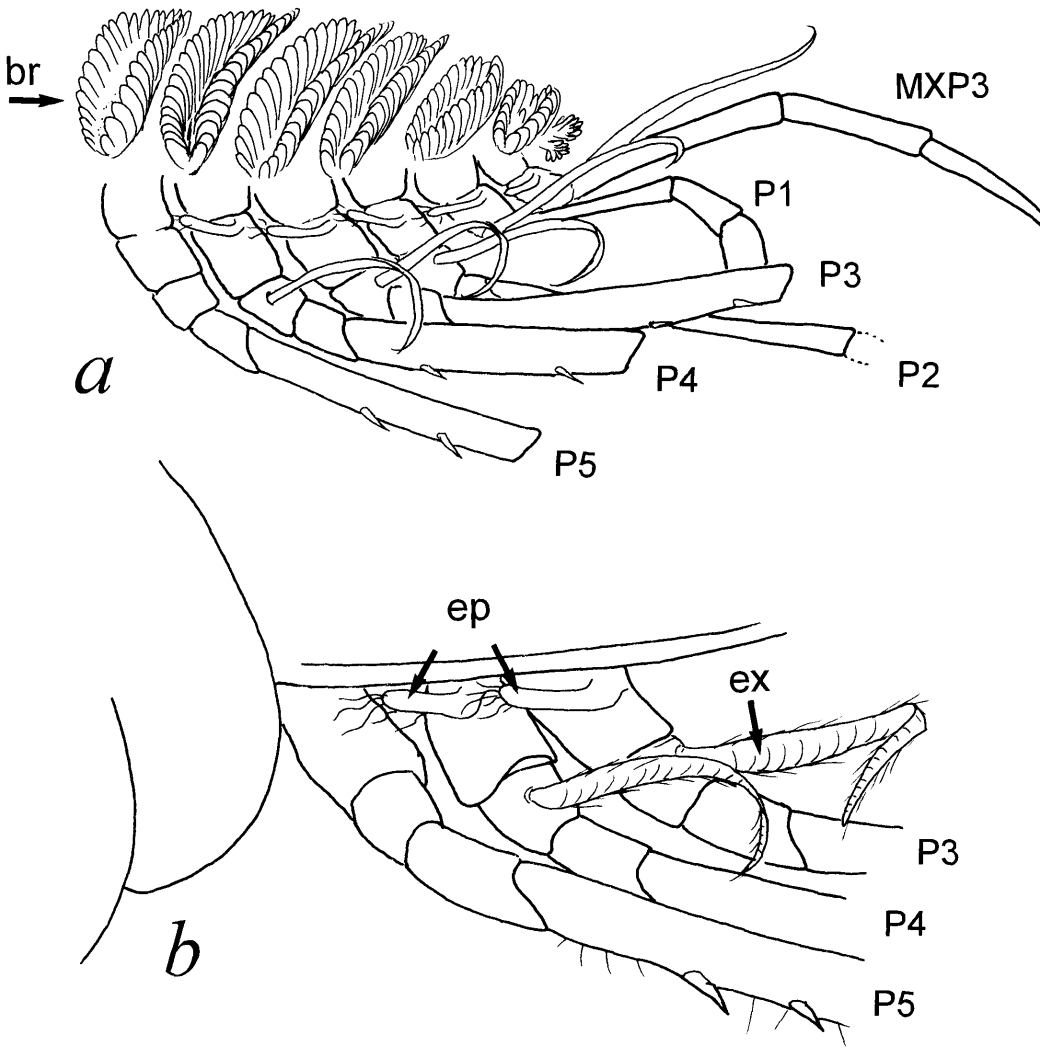

Fig. 9. *Syncaris pacifica* (Holmes), lateral view of gills and limb bases; *a*, carapace removed (same individual illustrated in Fig. 6); *b*, carapace in place, base of posterior 3 pereopods. br = branchiae (arthrobranch gills), ep = epipods, ex = exopods, MXP3 = third maxilliped, P1–5 = pereopods 1 through 5.

movable spine medial to point at diaresis. Telson (Fig. 7e) with 2 pairs of dorsolateral spines, posterior margin straight or slightly rounded, with mesial setae and 2 pairs of small posterolateral spines.

Range.—*Syncaris pacifica* is known only from a few lowland creeks and streams in Sonoma, Marin, and Napa Counties, California (Messer and Brumbaugh, 1989; Serpa, 1996) (Fig. 10). According to Serpa (1996, and on the World-wide Web at http://desfbay.fws.gov/Archives/shrimp/shrimp.htm), the species was known from nine streams by the time biologists began to study them seriously. They were apparently extirpated from Santa Rosa Creek by development in 1964. Serpa (1996), after extensive sampling, reported small populations in other streams, such that at present the species is known from 16 streams in 11 stream systems, as follows (Fig. 10): Sonoma County: Big Austin, East Austin, Green Valley, Jonive, Redwood Creek (a tributary of Jonive), Yulupa, Blucher, Sonoma, and Salmon Creeks. Most recently, *S. pacifica* has been found in Franz Creek, west of Calistoga, a different watershed system in Sonoma County (C. Rogers, personal communication). Marin County: Lagunitas, Stemple,

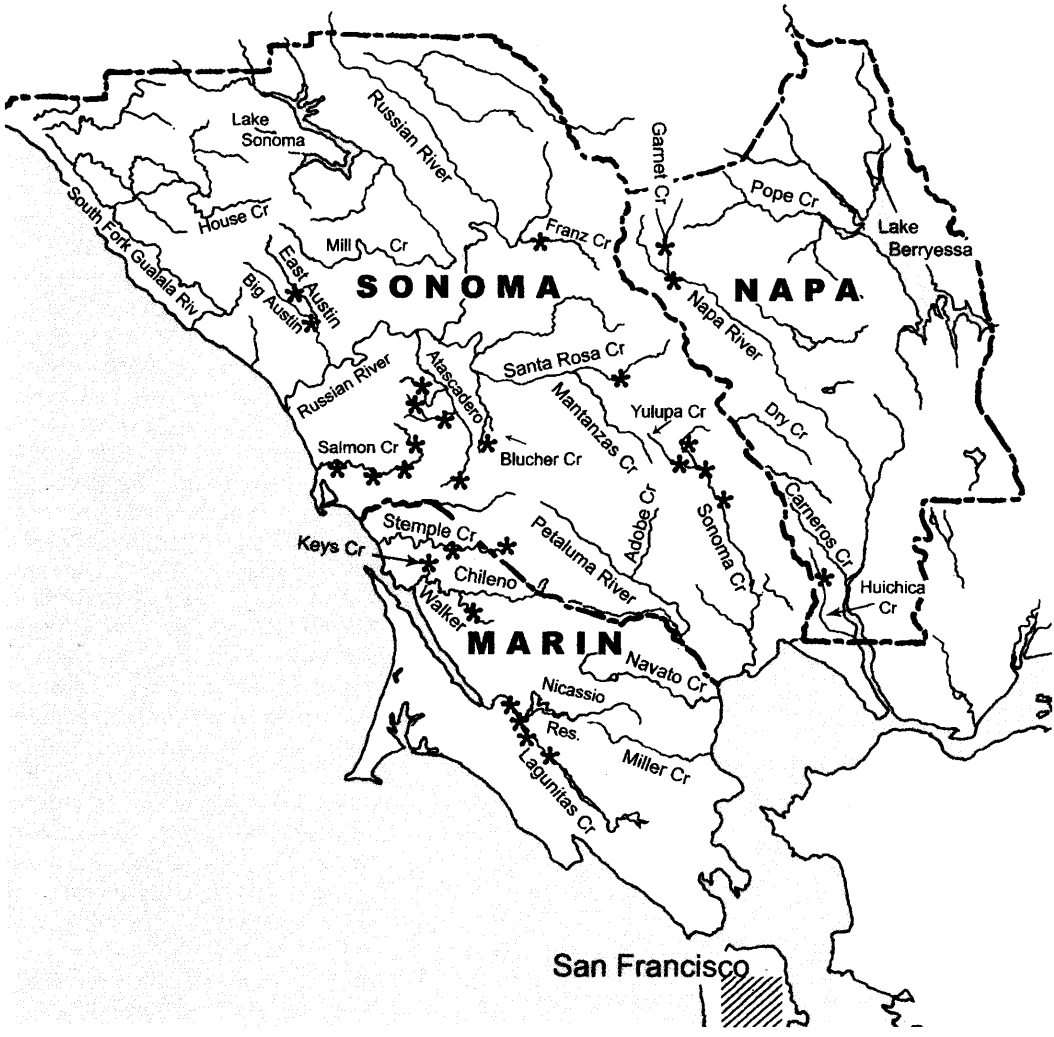

Fig. 10. Known distribution of *Syncaris pacifica* (Holmes). Asterisks (*) indicate streams or rivers where the species has been collected. Three of the smaller creeks (Green Valley, Jonive, and Redwood), all of which flow eventually into Atascadero Creek, are not named because of space restrictions, although asterisks indicate their location.

and Walker Creeks, and Keys Creek (a tributary of Walker). Napa County: Napa River (and its Garnet Creek tributary), Huichica Creek. Evidence suggests that the species was more widespread prior to 1964 (Hedgpeth, 1968; Eng, 1981; Serpa, 1996).

Type Locality.—"Sonoma County, California."

Natural History.—*Syncaris pacifica* occurs only in lowland freshwater streams, in pool areas away from main stream flow, often among roots, branches or undercut banks. They have never been found at elevations higher than 380 feet (125 m). The species apparently can tolerate up to 50% sea water (about 17‰) for at least 13 days, but dies within seven hours at a salinity of 75% sea water (about 24‰; Hedgpeth, 1968). However, Born (1968), who studied osmoregulatory capabilities in *S. pacifica*, noted that in the wild, adults "have not been found in even the most slightly brackish parts of this [Salmon Creek] or other streams." Juveniles and adult males are opaque to nearly transparent and are thus well camouflaged. Adult females in streams are similar in color, but may be dark brown to purple, often with a broad tan dorsal band if living among stems, tree roots and undercut stream banks (Hedgpeth, 1968; Eng, 1981;

Serpa, 1986; Messer and Brumbaugh, 1989). Adult females are capable of changing color. Populations have been lost primarily because of habitat destruction by channelization, construction of dams, removal of streamside vegetation, and pollution, and by introduction of predators such as the green sunfish (*Lepomis cyanellus*) (Eng, 1981; Serpa, 1996). Born (1968) and Eng (1981) provided descriptions of the unusual winter reproductive cycle; reproduction occurs once annually, with females appearing ovigerous in mid- to late September and with nearly all mature females gravid by early November (Born noted that nearly all adult females were ovigerous from early October through mid-April). Eclosion from the eggs occurs from late May to early June.

Remarks.—Although Serpa (1996) found the species in more streams than had been reported previously, he also noted that it is rare in some of those habitats (e.g., a single specimen was found in Walker Creek after wading and sampling several miles of the creek). *Syncaris pacifica* was federally listed as an endangered species by the U.S. Fish and Wildlife Service in 1988 (see also their Worldwide Web site for this species at: http://www.ccfwo.r1.fws.gov/es/inverts/fw_shrimp.html) and by the State of California, and it meets the criteria for endangered species status (category EN, IUCN Red List Categories and Criteria, 2001). Nearly all authors have commented on the vulnerability of the species to development and to introduced species. Among the known threats to the species (from various publications of L. Serpa, e.g., 1986, 1991, 1992a, b, 1996) are introduced fish, deterioration or loss of habitat resulting from water diversion, impoundments, livestock and dairy activities, agricultural activities and developments, flood control activities, gravel mining, timber harvesting, migration barriers, and water pollution. This animal may not be collected or handled without the appropriate State of California and federal permits.

Discussion

Systematics

The most obvious character that serves to separate specimens of the extinct species *Syncaris pasadenae* from those of the extant *S. pacifica* is the presence, in the latter, of dorsal teeth on the rostrum. Additionally, *Syncaris pacifica* is morphologically a more delicate species than its extinct southern congener, as it has an overall more gracile appearance and a (usually) shorter overall length.

Although rostral morphology is often quite variable (see Figs. 2a–c and 4 for variability within *S. pasadenae*), we found no specimens of *S. pasadenae* with dorsal rostral teeth, and no specimens of *S. pacifica* without them. A more fundamental difference is the number of pereopods that bear an exopod. In *S. pacifica*, an exopod is found on all of the maxillipeds and on all pereopods save the last (fifth) (Fig. 9a, b). We saw no variablity in this pattern in the specimens of *S. pacifica* we examined. In contrast, specimens of *S. pasadenae* bear exopods on all three maxillipeds and on a variable number of pereopods. The maximum number of pereopods bearing exopods is two (pereopods 1 and 2, the two chelate pereopods); pereopods 3 and 4 never bear an exopod, and occasionally none of the pereopods bears an exopod. For example, in USNM 67644 (*Syncaris pasadenae*, Warm Creek, San Bernardino, Calif., coll. 6 Feb. 1933, the last known collection of this species) there are 32 specimens. Selecting and examining 20 of these at random, we found that 12 (including a large ovigerous female, the only ovigerous one of the 32 specimens, and the rostrum of which is illustrated in Fig. 4e) bore an exopod on maxilliped 3 (but not on any pereopods). Of the remaining eight specimens, six bore an exopod on maxilliped 3 and pereopod 1, and only two bore an exopod on maxilliped 3, pereopod 1, and pereopod 2.

The presence or absence of pereopodal exopods has traditionally been considered a taxonomic character of some significance in the Caridea. Both Chace (1992) and Holthuis (1993) used the presence of exopods as distinguishing characters to separate genera in several families of caridean shrimp (as recognized by Martin and Davis, 2001). Within the atyid subfamily Paratyinae Holthuis, 1986 (the subfamily to which *Syncaris* currently belongs) (the paratyines were recognized first as a "series" by Bouvier in 1925; the group was elevated to subfamily status by Holthuis, 1986: 104), the genus *Paratya* is distinguished from all other genera on the basis of an exopod on pereopod 5, and *Troglocaris* and *Atyaephyra* are separated on the basis of the numbers of legs bearing exopods (Holthuis, 1993: 59). Indeed, it is clear that when Holmes (1900) established the genus *Syncaris* and described *Syncaris trewi*, he separated it from Kingsley's *Caridina pasadenae* on the basis of the number of pereopods bearing exopods,

believing that this was an important taxonomic character that was not likely to vary within a species. Thus, it would be relatively easy to justify placing *S. pasadenae* and *S. pacifica* in separate genera on this basis alone. However, several lines of evidence prevent us from taking this step. Despite the difference in the number of pereopodal exopods, the two species are otherwise morphologically quite similar, down to detailed morphology of their feeding appendages. Indeed, perhaps the most unusual of the features shared by the two species of *Syncaris* is the fusion of the dactylus and propodus of the second maxilliped, resulting in a strong indentation or notch on the medial border of what is now the distal-most article (see Figs. 3g, 8e). This character occurs in no other genus in the subfamily Paratyinae or family Atyidae to our knowledge, and thus it argues strongly for retention of both species in one genus, in contrast to what the presence of exopods might suggest (above).

Zoogeography

The species of the atyid subfamily Paratyinae (following Holthuis, 1986, 1993) show a disjunct distribution. There are at least 12 species of *Paratya* ranging from eastern Siberia and Korea to the Lesser Sunda Islands, Australia, New Zealand and nearby islands (Chace, 1997). Six species of *Troglocaris* Dormitzer, 1853, live in caverns in southern Europe from France and Italy to the vicinity of the Caspian and Black Seas (Noel, 1992). *Atyaphyra desmaresti* Millet, 1831, has a historic range throughout the Mediterranean region and has spread northward in Europe (Hedgpeth, 1968). The species of *Dugastella* Bouvier, 1912, are known only from Morocco and Spain.

The other members of the subfamily have more restricted distributions. *Palaemonias ganteri* Hay, 1901, lives in the Mammoth-Flint Ridge Cave System, Kentucky, and *P. alabamae* Smalley, 1961, lives in caves near Huntsville, Alabama. These two species, along with the species of *Syncaris* (both restricted to California), are the only species of the family Atyidae native to the continental United States.

Bouvier (1925) suggested that the members of the Paratyinae are remnants of a group having a distribution around the ancient Tethys Sea. The disjunct distribution indicates the fragmentation of a once-widespread subfamily, with remnants today occurring in isolated locations and in refugia such as caves. Bouvier suggested that such fragmentation occurred by the Cretaceous period. Ortmann (1902), in a review of the Atyidae, suggested that members of the family moved from marine to freshwater habitats during Jurassic times. Hobbs and Hart (1982), in a review of the species of *Atya*, concluded that ancestors of the genus could have been recognizable by the early Jurassic. They also noted that similar species occur in Africa and Central America, indicating that species of *Atya* probably had a monophyletic origin that must have preceded the opening of the modern Atlantic Ocean.

The species of *Syncaris* can be regarded as relics of a Mesozoic biota in California (Hedgpeth, 1968, 1975). The shrimp are not the only such relics of ancient ecosystems. The coast redwood, *Sequoia sempervirens*, is related to fossil forms found in many parts of the world, but its only living close relatives are the giant sequoia of the Sierra Nevada in California and the dawn redwood of China. Fossils of large marine animals such as plesiosaurs in California indicate that there were shallow marine areas present during the Mesozoic. The ancestors of *Syncaris* spp. could have dispersed by sea during that time. Hedgpeth (1968: 520–522) discussed in some detail the Pliocene to Pleistocene events that might have led to present day distributions in low-lying coastal streams in northern California.

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