

Two new species of *Hyalessa* (Crustacea: Amphipoda: Hyalessidae) from Death Valley National Park, California, U.S.A.

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Abstract.—Two new species *Hyalessa* (*Hyalessa*) *muerta* and *Hyalessa* (*Hyalessa*) *sandra* are described from Death Valley National Park, California. *Hyalessa* (*H.*) *muerta*, the first North American hypogean hyalessid, is blind, lacks dorsal mucronations and antenna 1 is longer than antenna 2. *Hyalessa* (*H.*) *sandra* collected from nearby epigean waters, also lacks dorsal mucronations, but has normal eye pigmentation and antenna 1 is shorter than antenna 2. Populations of both species rarely, if ever, coexist together in Death Valley National Park.

Five species in the genus *Hyalessa* occur in the continental United States. These are *Hyalessa* (*Hyalessa*) *azteca* (Saussure, 1858); *Hyalessa* (*Hyalessa*) *inermis* Smith, 1874; *Hyalessa* (*Hyalessa*) *montezuma* Cole & Watkins, 1977; *Hyalessa* (*Hyalessa*) *texana* Stevenson & Peden, 1973; *Hyalessa* (*Hyalessa*) *longicornis* Bousfield, 1996. All are epigean species, have normal eye pigmentation and have antenna 1 shorter than antenna 2. Only *H.* (*H.*) *inermis* and *H.* (*H.*) *longicornis* lack dorsal mucronations.

Examination of recently collected material from Death Valley National Park, California clearly shows the presence of two new species of *Hyalessa*, both of which are newly described in this paper.

In the figures, body parts are marked by the following abbreviations: A, antenna; Gn, gnathopod; LL, lower lip; UL, upper lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; P, pereopod; T, telson; U, uropod; Pl, pleopod; R, right; L, left. Type material is deposited in the Departments of Invertebrate Zoology at the following museums: National Museum of Natural History

(USNM); Museum of Comparative Zoology, Harvard University (MCZ) and California Academy of Sciences (CASIZ).

Hyalessa (*Hyalessa*) *muerta*, new species
Figs. 1–5

Diagnosis.—Eyes absent. Antenna 1 longer than antenna 2. Accessory flagellum absent. Pereon lacking dorsal mucronations or spines. Sternal gills reduced in size and present on pereonites 3–7. Maxilla 1, inner plate narrow with 2 terminal plumose setae. Male gnathopod 2, carpus with strong posterior lobe with 4 submarginal setae; propodus robust and much larger than male gnathopod 1, palm with rectangular tooth near hinge of dactylus. Telson rounded, with 4 distal marginal setae.

Description of male.—Body lacking dorsal mucronations or spines. Eyes absent. Head cuboidal, equal to pereonites 1 and 2 in length. Coxae 1–4 enlarged, subquadrate with distomarginal setae, coxae 5–6 with distinct anterior and posterior lobes. Sternal gills small, present on pereonites 3–7.

Antenna 1, 57% of total body length, peduncular ratio 1:0.7:0.6, flagellum 9 articulate; accessory flagellum absent. Antenna 2 shorter than antenna 1, 49% of body length, peduncle nearly equal in length to head, articles 4 and 5 equal in length, flagellum 8 articulate.

Upper lip rounded, anterior margin with fine setae. Mandibles lacking palp; left incisor and lacina with 4 teeth, molar normal. Right incisor with 5 teeth, outer the largest and bifid, lacina with 3 teeth, spine row with 2 plumose setae, molar normal, with accessory plumose seta. Lower lip large, lacking inner lobes. Maxilla 1, inner plate narrow with 2 terminal plumose setae, inner margin finely setose; outer plate with 8 strong apical serrate spines; palp vestigial, 1 articulate. Maxilla 2, plates subequal in width; inner plate with 1 marginal and 12 apical plumose setae, outer margin with fine setae distally; outer plate with 10 apical plumose setae, both margins with fine setae. Maxilliped, inner plate with 3 strong apical teeth, inner margin with 3 plumose setae distally; outer plate with 7 apical plumose setae, with marginal and submarginal plumose setae; palp 4 articulate, nearly 3× length of outer plate, inner margin of article 2 with distal plumose setae, article 3 with distal setae, dactylus triangular with 3 distal setae.

Gnathopod 1, basis elongate broadening distally, posterior lobe of carpus with 6 marginal setae; propodus rectangular, wider and longer than carpus; palm and hind margin equal in length, palm with marginal and submarginal setae. Gnathopod 2, basis elongate; posterior lobe of carpus strong with 4 submarginal setae; propodus robust and much larger than that of gnathopod 1, distal anterior margin with triangular projection; palm with rectangular tooth near hinge of dactylus, with marginal and submarginal setae. Pereopods 3 and 4 similar in shape and size; carpus of both with distal anterior lobe and 2 setae. Pereopod 5, approximately 70% length of pereopod 6. Pereopod 7 slightly larger than pereopod 6. Pereopods

5–7 bases expanded posteriorly, stronger in pereopod 7; carpus with distal posterior lobe, with 3–4 spines.

Pleopods 1–3 long and slender, peduncles with 2 coupling hooks, rami with plumose setae. Uropod 1, peduncle outer margin with 4 bifurcate spines, inner margin with distal marginal seta; inner ramus with 4 apical spines; outer ramus with 5 apical and 2 marginal spines. Uropod 2, 60% the length of uropod 1, peduncle with 2 marginal spines and 1 marginal seta; inner ramus with 6 apical spines; outer ramus with 5 apical spines. Uropod 3, peduncle with 3 distal marginal spines; ramus with 2 apical spines and 1 apical seta. Telson rounded with 4 distal marginal setae.

Female.—All features same as male except as noted below. Antenna 1, 43% of total body length; flagellum 9 articulate. Antenna 2, 34% of total body length; flagellum 9 articulate. Gnathopod 2 and pereopods 3–5 with oostegites. Gnathopod 1 resembling male, posterior lobe of carpus with 8 marginal setae. Gnathopod 2, basis elongate; posterior lobe of carpus with 6 submarginal setae; propodus longer than wide, palm and hind margin distinct.

Etymology.—The specific epithet is derived from the Spanish *muerta* as a noun in apposition for the word death referring to Death Valley.

Material examined.—Male holotype, 3.28 mm, USNM 230433, Texas Spring, just uphill of the Texas Spring Campground, Death Valley National Park, Inyo County, California, William D. Shepard, 20 Jul 1994. Female (ovigerous) allotype, 3.28 mm, USNM 230434, same data as holotype. Male paratype, 3.28 mm, USNM 230435, same data as holotype. Female (ovigerous) paratype, 3.24 mm, USNM 230436, same data as holotype. 6 males, 8 females (4 ovigerous) paratypes, USNM 230437, same data as holotype. Male (4.00 mm) and female (3.60 mm), paratypes, USNM 230438, Texas Spring tunnel, Death Valley National Park, Inyo County, California, 36°27'27.54"N, 116°50'14.44"W,

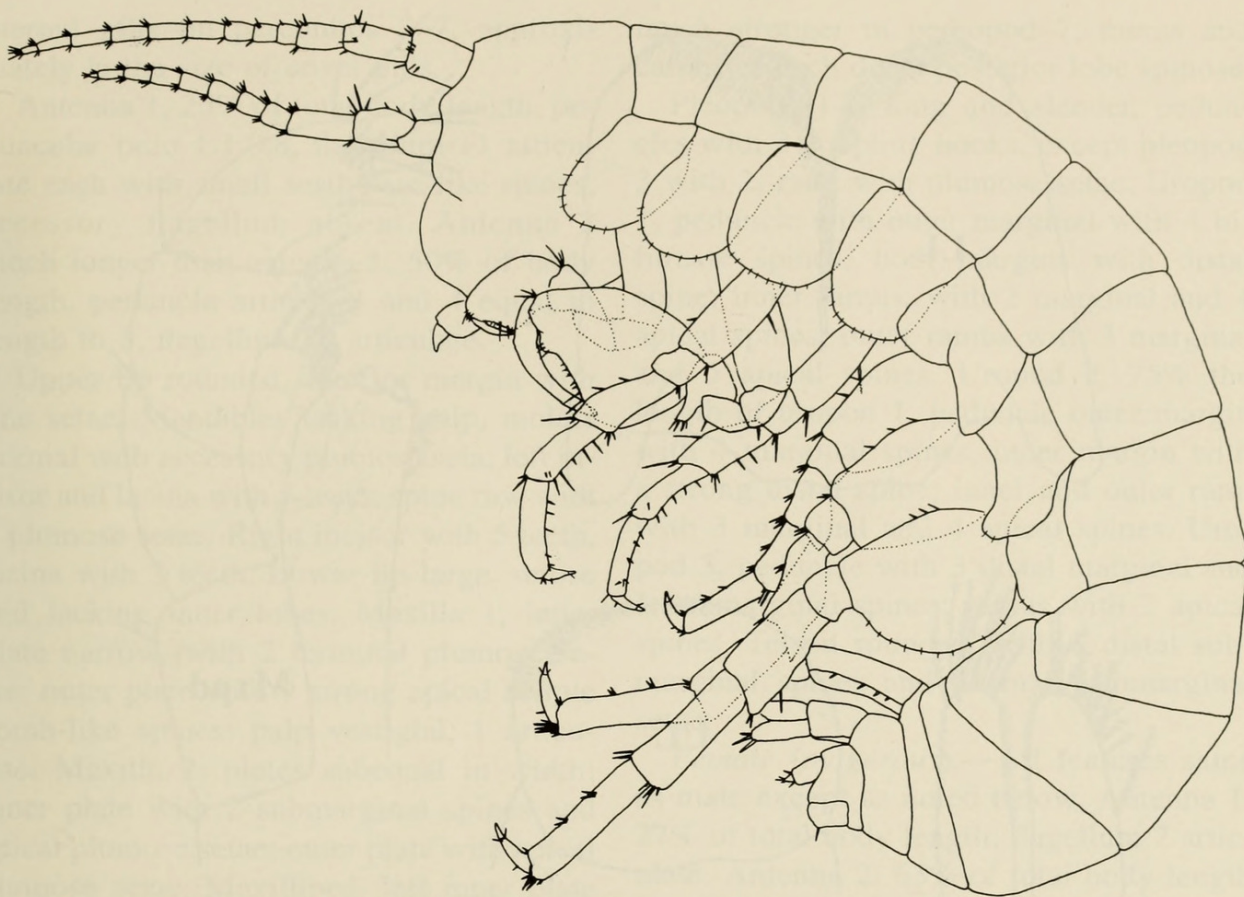


Fig. 1. *Hyalella (Hyalella) muerta*, male, 3.28 mm, USNM 230435.

Doug L. Threlhoff, 19 Dec 1997. Paratypes, MCZ 25390, CASIZ 121603, Texas Spring tunnel, Death Valley National Park, Inyo County, California, 36°27'27.54"N, 116°50'14.44"W, D. L. Threlhoff, 7 Dec 1997. Paratypes, MCZ 25391, CASIZ 121604, Texas Spring tunnel, at discharge point, Death Valley National Park, Inyo County, California, 36°27'26.18"N, 116°50'16.93"W, D. L. Threlhoff, 19 Dec 1997.

Remarks.—*Hyalella (H.) muerta* is morphologically similar to *Hyalella (Mesohyalella) anophthalma* Ruffo, 1957 and *Hyalella (Mesohyalella?) caeca* Pereira, 1989; the former is known from a cave in Venezuela and the latter from Brazil. Both species have sternal gills on pereonites 2–7 and antenna 2 is longer than antenna 1. In contrast, *H. (H.) muerta* has sternal gills on pereonites 3–7 and antenna 1 is longer than antenna 2.

Hyalella (Hyalella) sandra, new species
Figs. 6–10

Diagnosis.—Eyes present. Antenna 1 shorter than 2, flagellum 10–11 articulate; accessory flagellum absent. Antenna 2 elongate, flagellum 20–24 articulate. Pereon lacking dorsal mucronations or spines. Sternal gills on pereonites 3–7, approximately $\frac{1}{3}$ the size of coxal gills. Maxilla 1, inner plate narrow with 2 terminal plumose setae. Male gnathopod 2, carpus with strong posterior conical lobe with marginal setae. Uropod 3, ramus with 7 distal spines. Telson, rounded with 2 distal submarginal spines.

Description of male.—Body lacking dorsal mucronations or spines. Eyes pigmented. Head cuboidal, subequal to pereonites 1 and 2 in length. Coxae 1–3 enlarged, quadrate with distomarginal setae, coxae 5–6 with distinct anterior and posterior lobes.

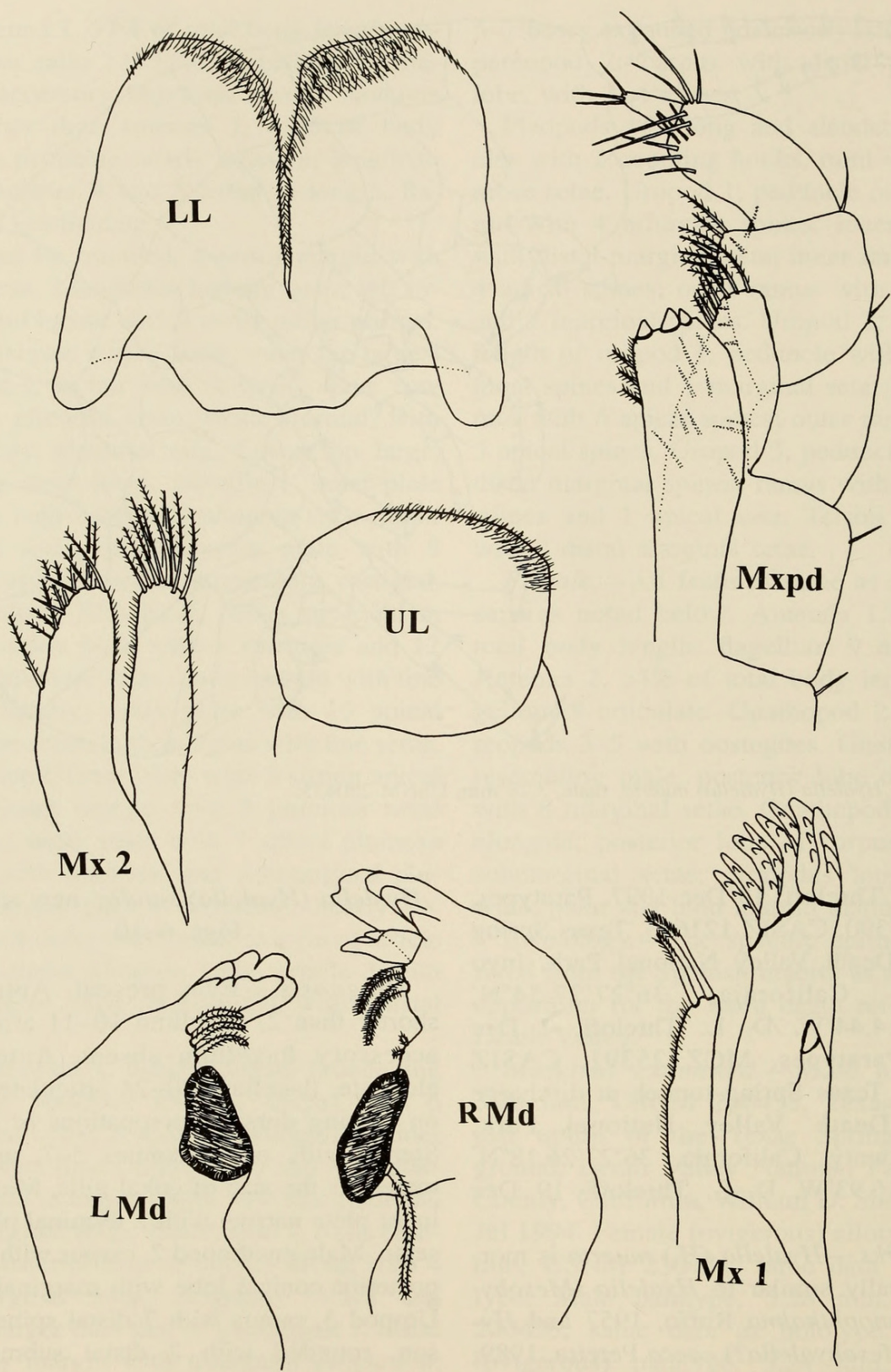


Fig. 2. *Hyalella (Hyalella) muerta*, male, 3.28 mm, USNM 230435.

Sternal gills on pereonites 3–7, approximately $\frac{1}{3}$ the size of coxal gills.

Antenna 1, 25% of total body length, peduncular ratio 1:1:0.8, flagellum 11 articulate each with small aesthetasc-like spines; accessory flagellum absent. Antenna 2 much longer than antenna 1, 50% of body length, peduncle articles 3 and 4 equal in length to 5, flagellum 20 articulate.

Upper lip rounded, anterior margin with fine setae. Mandibles lacking palp, molars normal with accessory plumose seta; left incisor and lacina with 5 teeth, spine row with 3 plumose setae. Right incisor with 5 teeth, lacina with 3 teeth. Lower lip large, setose and lacking inner lobes. Maxilla 1, inner plate narrow, with 2 terminal plumose setae; outer plate with 9 strong apical serrate comb-like spines; palp vestigial, 1 articulate. Maxilla 2, plates subequal in width; inner plate with 2 submarginal spines and apical plumose setae; outer plate with apical plumose setae. Maxilliped, left inner plate with 2 strong apical teeth, right plate with 3; left outer plate with submarginal and apical plumose setae; palp 4 articulate, dactylus with two apical spines.

Gnathopod 1, basis elongate; posterior lobe of carpus with 8 marginal setae; propodus equal in length to carpus; palm with submarginal setae, proximoposterior corner with distinct spine. Gnathopod 2, basis elongate; carpus with strong posterior conical lobe with marginal setae; propodus robust and much larger than that of gnathopod 1; palm with marginal spines and setae, proximoposterior corner with tooth like spine. Pereopods 3 and 4 similar in shape and size; coxal plate of pereopod 4 subquadrate and much larger than that of pereopod 3; merus on both with distal anterior lobe with 3 and 2 spines respectively. Pereopod 5, approximately 75% the length of pereopod 6; basis expanded posteriorly with marginal and submarginal setae. Pereopod 7 slightly smaller than pereopod 6. Pereopods 5–7 bases, anterior margins spinose, posterior margins expanded posteriorly,

much stronger in pereopod 7; merus and carpus of each distal posterior lobe spinose.

Pleopods 1–3 long and slender, peduncles with 3 coupling hooks, except pleopod 3 with 2, rami with plumose setae. Uropod 1, peduncle with outer marginal with 4 bifurcate spines, both margins with distal spine; inner ramus, with 2 marginal and 4 apical spines; outer ramus with 3 marginal and 5 apical spines. Uropod 2, 75% the length of uropod 1, peduncle outer margin with 4 marginal spines, inner margin with a strong distal spine; inner and outer rami with 3 marginal and 4 apical spines. Uropod 3, peduncle with 3 distal marginal and 1 submarginal spines; ramus with 7 apical spines. Telson rounded, with 2 distal submarginal spines and 5 small submarginal setae.

Female (ovigerous).—All features same as male except as noted below. Antenna 1, 27% of total body length; flagellum 7 articulate. Antenna 2, 63% of total body length flagellum 14 articulate. Gnathopod 2 and pereopods 3–5 with oostegites. Gnathopod 2, basis elongate; carpus longer than wide, lacking posterior conical lobe and with 9 submarginal setae; palm and hind margin distinct.

Etymology.—The specific epithet is a name in apposition in reference to the first author's wife Sandra, for her support and encouragement towards his research endeavors.

Material examined.—Male holotype, 4.80 mm, MCZ 25392, Travertine Spring, approximately 1.9 km southeast of Texas Spring, Death Valley National Park, Inyo County, California, 36°26'28.40"N, 116°49'57.01"W, D. L. Threlhoff, 21 Dec 1997. Female (ovigerous) allotype, 3.36 mm, MCZ 25393, same data as holotype. Male paratype, MCZ 25394, same data as holotype, 4.88 mm. Female (ovigerous) paratype, 3.36 mm, MCZ 25395, same data as holotype. Male paratype, 4.80 mm, MCZ 25435, same data as holotype. Male paratype, 4.72 mm, MCZ 25396, Texas Spring outflow, 34 m downstream of discharge

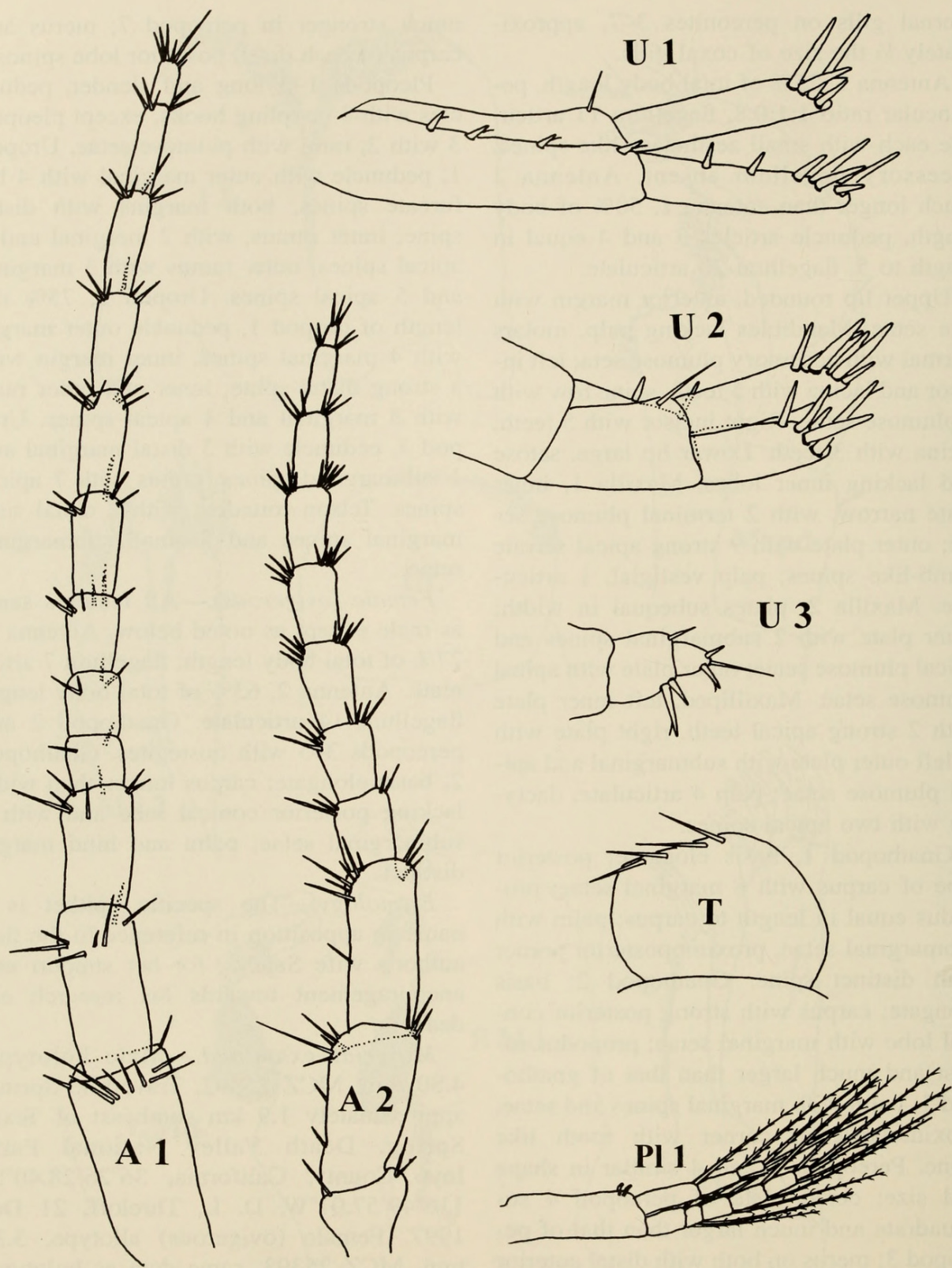


Fig. 3. *Hyalella (Hyalella) muerta*, male, 3.28 mm, USNM 230435.

point, Death Valley National Park, Inyo County, California, 36°27'25.44"N, 116°50'18.01"W, D. L. Threlhoff, 19 Dec 1997. Male paratype, 5.20 mm, MCZ

25397, Texas Spring outflow, 13 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27'25.86"N, 116°50'17.20"W, D. L.

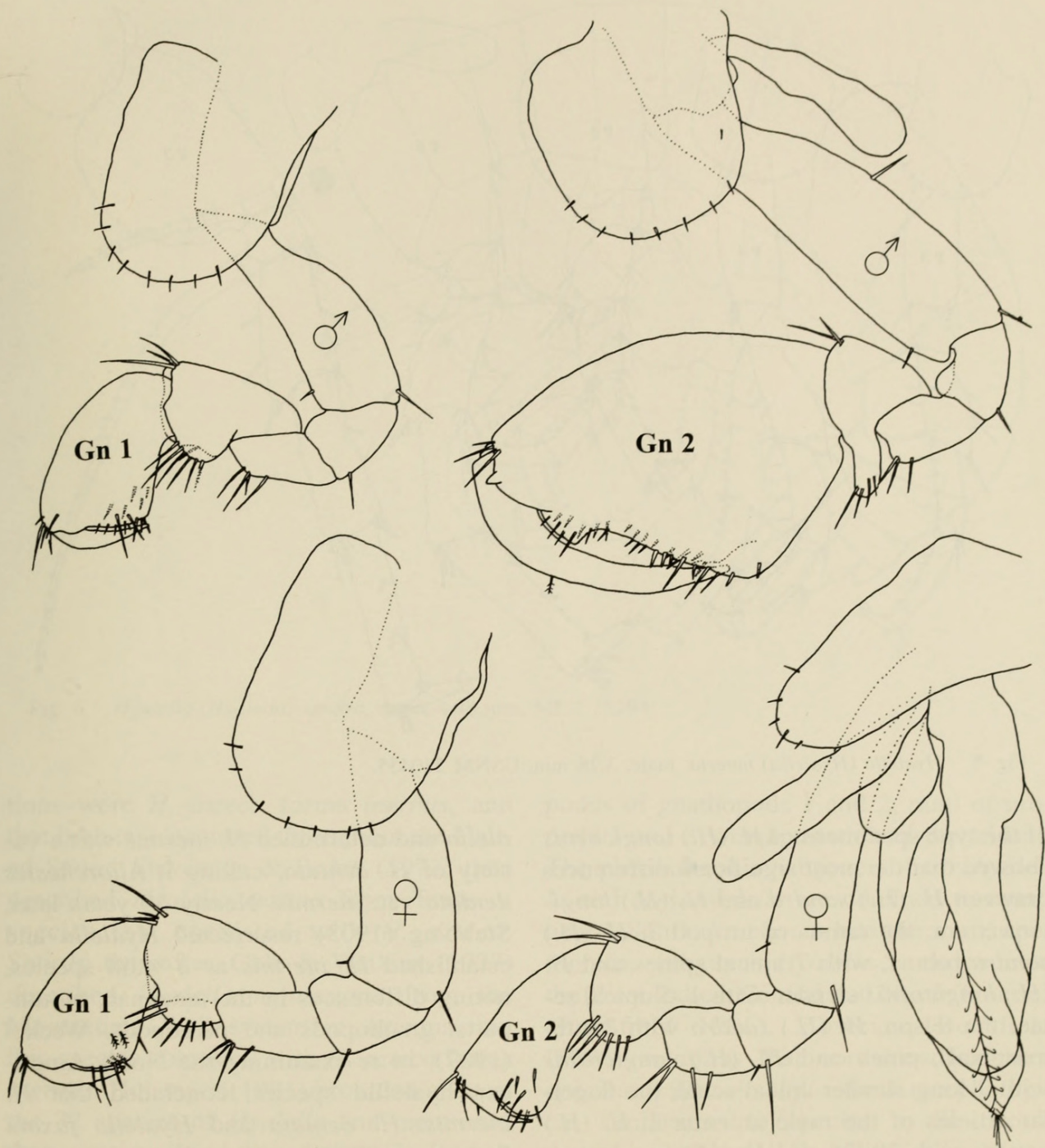


Fig. 4. *Hyalella (Hyalella) muerta*, male, 3.28 mm, USNM 230435: Gn1, Gn2. Female, 3.24 mm, USNM 230436: Gn1, Gn2.

Threloff, 21 Dec 1997. Paratypes, USNM 230439, CASIZ 121605, same data as holotype. Paratypes, MCZ 25398, USNM 230411, CASIZ 121606, Texas Spring outflow, 34 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27'25.44"N, 116°50'18.01"W, D. L. Threloff, 19 Dec 1997. Paratypes, MCZ 25399, USNM 230440, CASIZ

121607, Texas Spring outflow, 13 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27'25.86"N, 116°50'17.20"W, D. L. Threloff, 21 Dec 1997.

Remarks.—*Hyalella (H.) sandra* is morphologically similar to *H. (H.) longicornis*, which is larger in size and is known from only the type locality in Utah. Examination

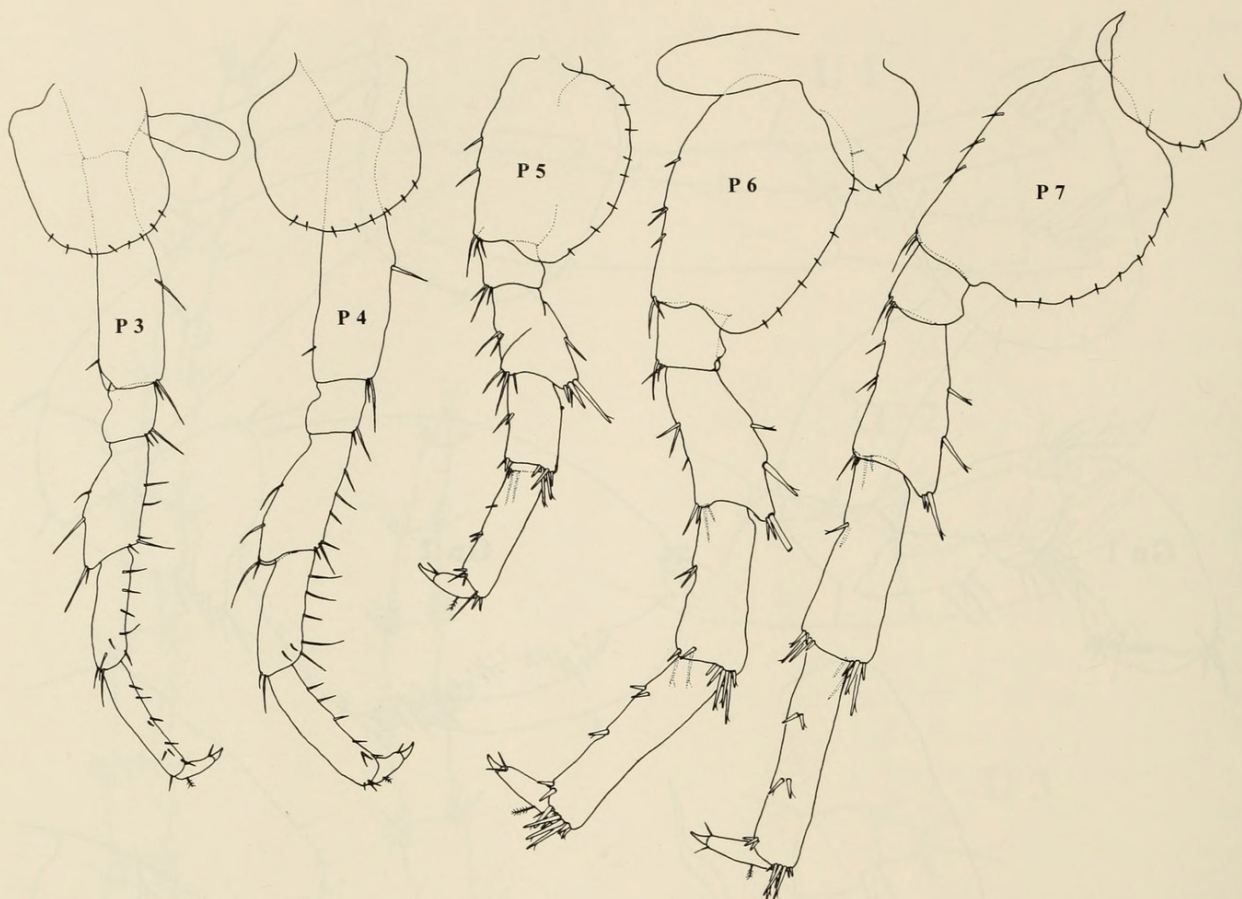


Fig. 5. *Hyalella (Hyaella) muerta*, male, 3.28 mm, USNM 230435.

of the type specimens of *H. (H.) longicornis* showed that the most significant differences between *H. (H.) sandra* and *H. (H.) longicornis* are: the ramus of uropod 3, *H. (H.) sandra* robust, with 7 apical spines and *H. (H.) longicornis* slender, with 4–5 apical setae; the telson, *H. (H.) sandra* with 2 submarginal spines and *H. (H.) longicornis* with 2 long slender apical setae; the flagellar articles of the male antenna 2, *H. (H.) sandra* with 20–24 and *H. (H.) longicornis* with 16; the palp of maxilla 1, *H. (H.) sandra* vestigial, 1 articulate and *H. (H.) longicornis* tall, length $>2\times$ the width; basis of gnathopod 2 posterior margin, *H. (H.) sandra* with 1–3 marginal setae and *H. (H.) longicornis* with 9 marginal setae.

Discussion.—In 1874, Smith established the genus *Hyalella*, describing *Hyalella dentata* and *Hyalella inermis*, both from Colorado. Faxon (1876), working on South American hyalellids, regarded the genus *Allorchestes* as the senior synonym of *Hy-*

alella and determined *H. inermis* was a variety of *H. dentata*, calling it *Allorchestes dentata* var. *inermis*. Nearly 30 years later, Stebbing (1903) resurrected *Hyalella* and established *H. inermis* as a valid species, noting differences in the antennae, mouthparts, gnathopods and pereopods. Weckel (1907), in re-examining the North American hyalellid species, concluded that *H. inermis*, *H. dentata* and *Hyalella faxoni* Stebbing, 1903 were all junior synonyms of *Hyalella knickerbockeri* Bate, 1862 and mentioned that only *H. azteca* var. *inermis* lacked dorsal mucronations. Later, Barnard (1958) provided a list of the *Hyalella* species and listed *H. faxoni* and *H. knickerbockeri* as junior synonyms of *H. azteca* and considered *H. inermis* a valid species. However, Bousfield (1958, 1973) concluded that *H. azteca* is a single morphologically variable species with the number of dorsal mucronations varying from 1–3, that specimens totally lacking dorsal mycrona-

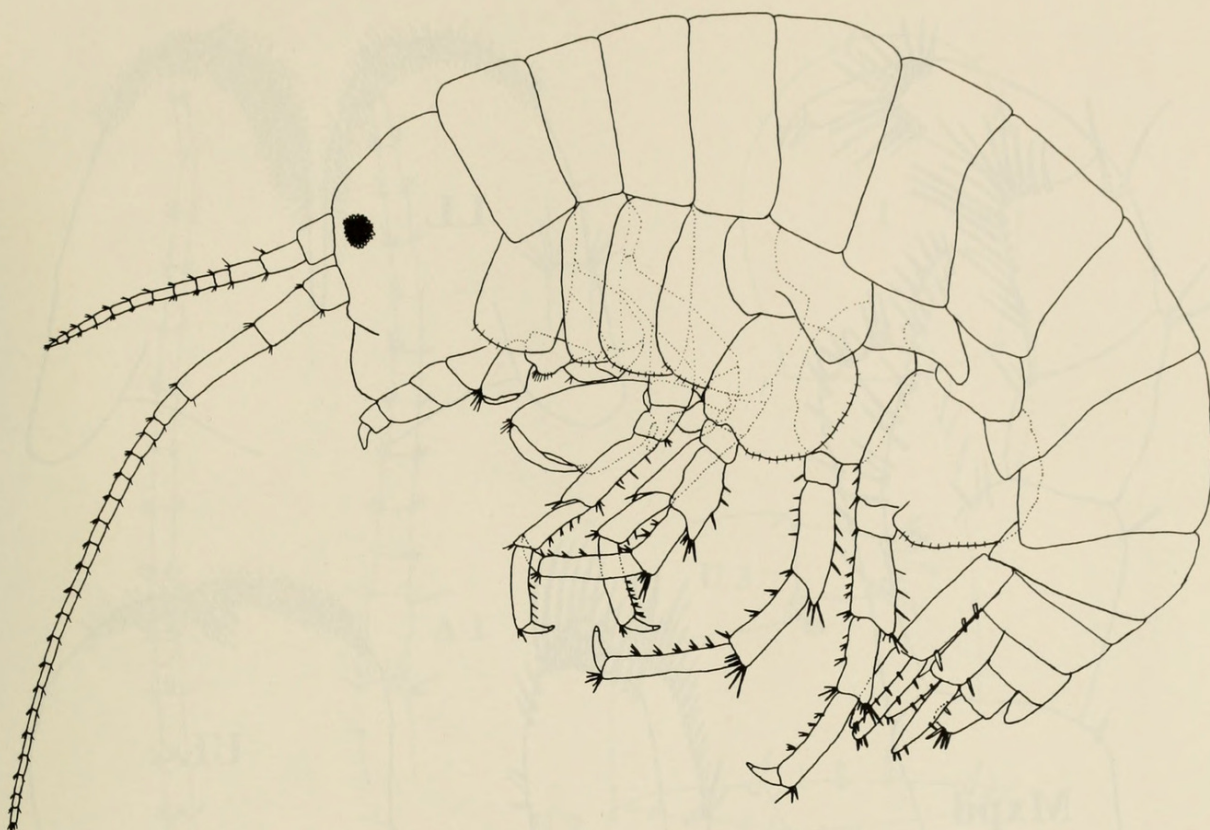


Fig. 6. *Hyalella (Hyalella) sandra*, male, 4.88 mm, MCZ 25394.

tions were *H. azteca* forma *inermis*, and that both taxa occurred throughout the United States. Stevenson & Peden (1973) then described *Hyalella texana* from Texas, a species that coexisted with *H. azteca*. Shortly thereafter, Cole & Watkins (1977) described *Hyalella montezuma* from the Montezuma Well system in Arizona, but this species coexisted with *H. azteca* forma *inermis*. Holsinger (1981) provided a list of the 32 species of *Hyalella* and mentioned that most workers agreed that *H. dentata*, *H. inermis* and *H. knickerbockeri* are synonyms of *H. azteca*. Lastly, Bousfield (1996) described *Hyalella (Hyalella) longicornis* that lacked dorsal mucronations and was known only from Utah [although table 1 of Bousfield (1996) gives distribution as "Texas"].

Bousfield (1996) divided *Hyalella* into three subgeneric groups (*Hyalella*, *Austrohyalella*, and *Mesohyalella*) based on geographical distributions and morphological characters (i.e., body mucronations, the pro-

podus of gnathopods 1 and 2, rami of uropods 1 and 3, ornamentation of the telson). The plesiomorphic subgenera *Austrohyalella* and *Mesohyalella* are confined to continental South America while the more apomorphic subgenus *Hyalella* is endemic to the West Indies, Central and North America (Bousfield 1996). However, Bousfield (1996) mentions that northern distributed species of *Mesohyalella* show morphological similarities to species in the North American subgenus *Hyalella*.

Both species described here exhibit some morphological characters similar to species in the subgenus *Mesohyalella* [*H. (H.) muerta*, smooth body, 1 plumose seta on the inner plate of maxilla 2; *H. (H.) sandra*, smooth body, 1 submarginal spine on the inner plate of maxilla 2, spines on the telson]. However, the presence of 5 sternal gills, the morphology of male gnathopod 1 [*H. (H.) muerta*, propodus with 5 weak and short facial setae, palm margin convex and short; *H. (H.) sandra* propodus with 5 weak

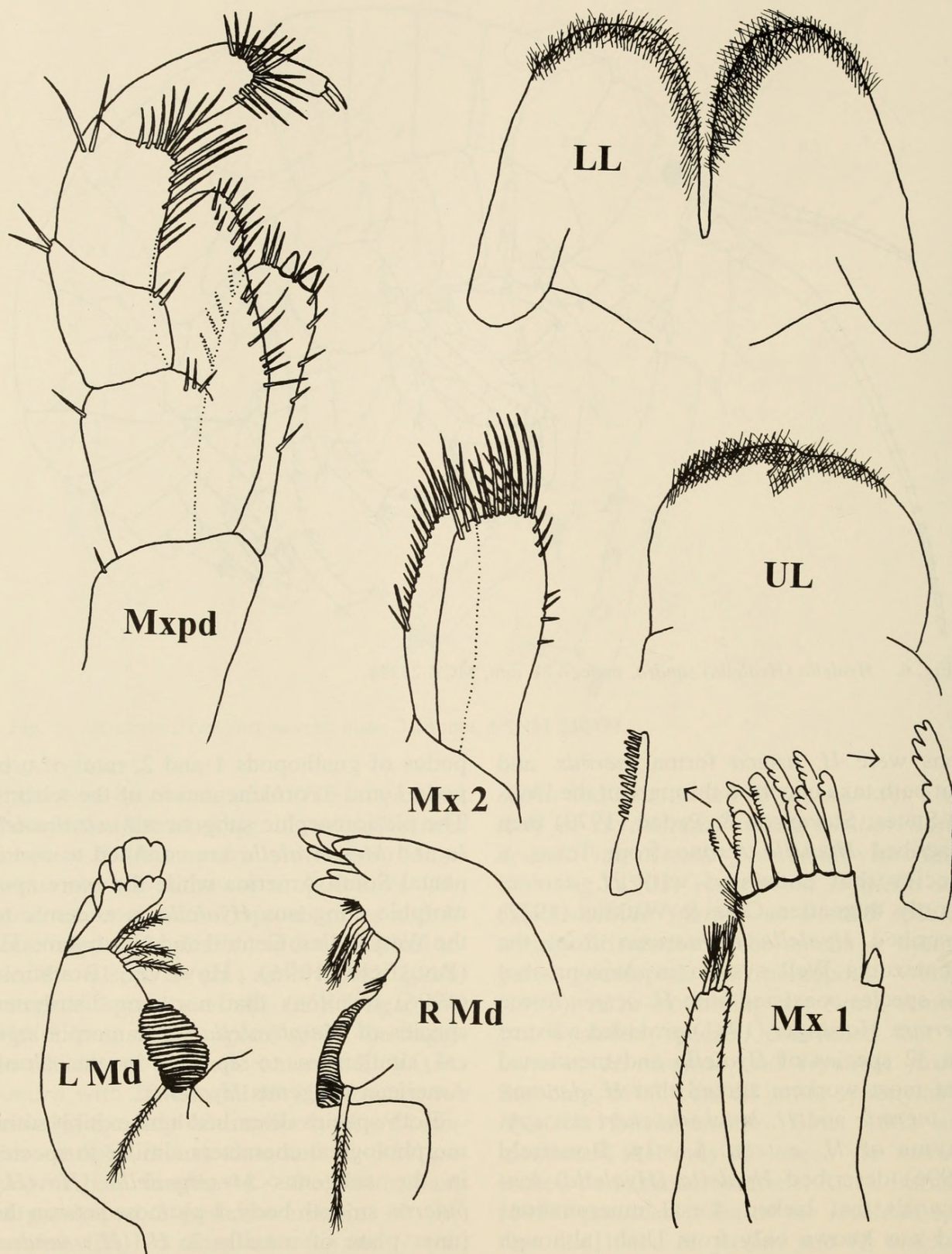


Fig. 7. *Hyalella (Hyalella) sandra*, male, 4.88 mm, MCZ 25394.

and short facial setae, palm margin convex and short, palmer angle with 1 short spine] and the morphology of the female gnathopod 2 of both species (propodus long and

slender) would place them in the subgenus *Hyalella*. In addition, as both new species lack copulatory spines on uropod 1, have a peduncle and ramus of uropod 3 subequal

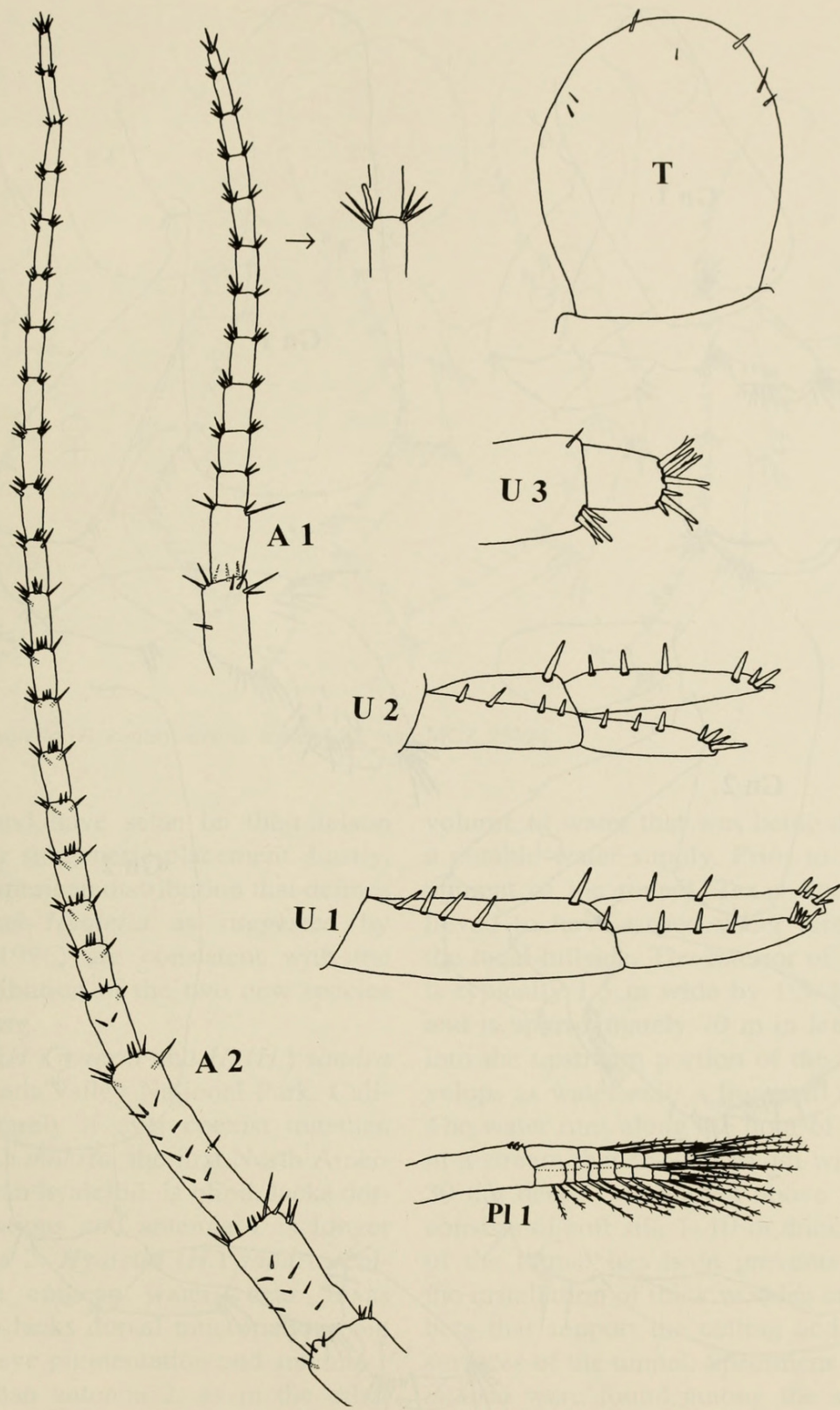


Fig. 8. *Hyalella (Hyalella) sandra*, male, 4.88 mm, MCZ 25394: A1, A2, U3, T, Pl1. Male, 4.80 mm, MCZ 25435: U1, U2.

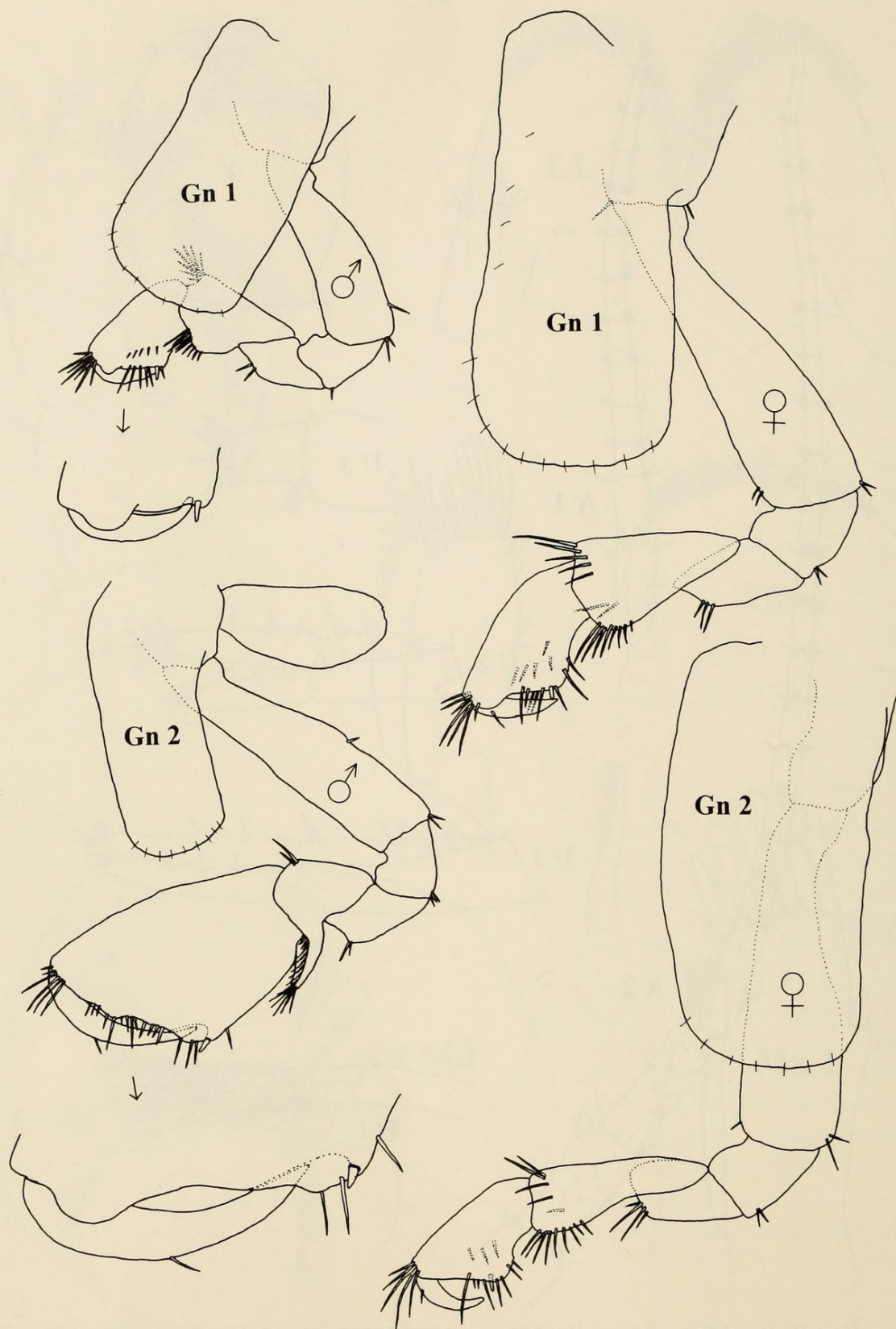


Fig. 9. *Hyalella (Hyalella) sandra*, male, 4.88 mm, MCZ 25394: Gn1, Gn2. Female (ovigerous), 3.36 mm, MCZ 25395: Gn1, Gn2.

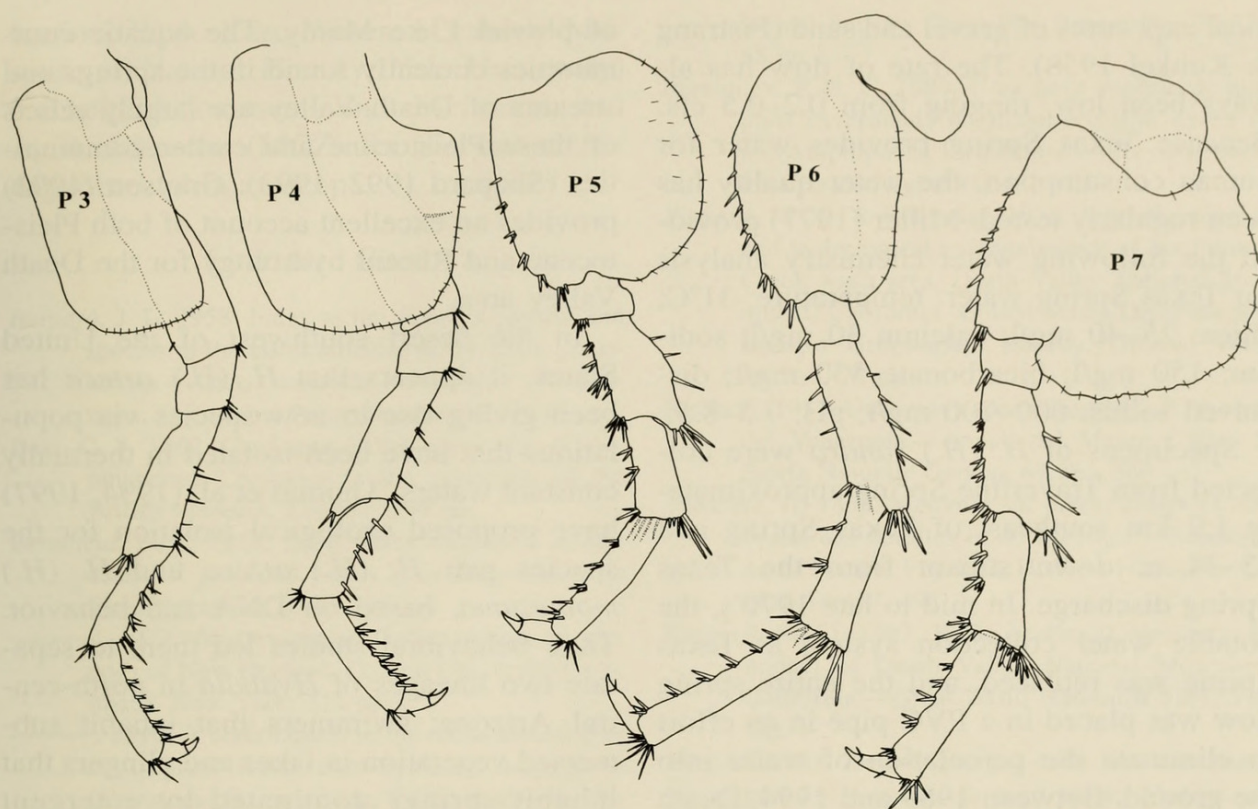


Fig. 10. *Hyalella (H.) sandra*, male, 4.88 mm, MCZ 25394.

in length, and have setae on their telson support their subgeneric placement. Lastly, the North American distribution that defines the subgenus *Hyalella* as suggested by Bousfield (1996) are consistent with the known distribution of the two new species described here.

Hyalella (H.) muerta and *H. (H.) sandra* occur in Death Valley National Park, California but rarely if ever coexist together. *Hyalella (H.) muerta*, the first North American hypogean hyalellid, is blind, lacks dorsal mucronations and antenna 1 is longer than antenna 2. *Hyalella (H.) sandra*, collected from epigean waters near Texas Spring, also lacks dorsal mucronations but has normal eye pigmentation and antenna 1 is shorter than antenna 2, as in the other North American *Hyalella* species. These two new species bring the total number of North American *Hyalella* taxa to seven.

Specimens of *H. (H.) muerta* were collected in an artificial tunnel that was excavated in the 1930's. The tunnel was most likely excavated in an effort to increase the

volume of water that was being diverted as a potable water supply. Prior to the development of the tunnel, Texas Spring is believed to have issued water directly from the local hillside. The interior of the tunnel is typically 1.5 m wide by 1.5–2.0 m high and is approximately 70 m in length. Flow into the upstream portion of the tunnel develops as water exits a fractured rock zone. The water runs along the floor of the tunnel in a stream that is 60–150 cm wide and 3–30 cm deep. Overburden above the tunnel consists of soft silt, 1–10 m thick. Collapse of the tunnel has been prevented through the installation of thick wooden cross members that support the ceiling and side wall surfaces of the tunnel. Specimens of *H. (H.) muerta* were found among the submerged roots originating from surface-inhabiting, riparian plants. In 1995, a one meter portion of the wooden tunnel structure collapsed. It is not known if the concurrent sediment input had any impact on the amphipod population.

At Texas Spring the water emerges from

local exposures of gravel and sand (Pistrang & Kunkel 1958). The rate of flow has always been low, ranging from 0.2–0.5 cfs. Because Texas Spring provides water for human consumption, the water quality has been regularly tested. Miller (1977) provided the following water chemistry analysis for Texas Spring water: temperature: 31°C; silica: 25–40 mg/l; calcium 30 mg/l; sodium: 150 mg/l; bicarbonate 330 mg/l; dissolved solids: 600–700 mg/l; pH: 7.5–8.5.

Specimens of *H. (H.) sandra* were collected from Travertine Spring approximately 1.9 km southeast of Texas Spring and 13–34 m down stream from the Texas Spring discharge. In mid to late 1970's, the potable water collection system at Texas Spring was replaced, and the entire spring flow was placed in a PVC pipe in an effort to eliminate the percolation of water into the ground. Between 1989 and 1994, Death Valley National Park maintenance personnel diverted some of the piped water back onto the ground in an effort to re-establish a stream habitat. Maintenance personnel then transplanted benthic sediment and vegetation from Travertine Spring to an area down stream of Texas Spring tunnel with the intentions of reinoculating the stream with aquatic invertebrates and plants. Presumably, *H. (H.) sandra* was transported with the sediments that established an introduced population. Extensive sampling has revealed one live specimen of *H. (H.) muerta* occurring in the surface stream downstream of Texas Spring tunnel. Preliminary investigations therefore suggest that *H. (H.) muerta* and *H. (H.) sandra* rarely coexist in Death Valley National Park.

Although Death Valley is one of the driest and hottest deserts in the New World, the climate there has not always been so harsh. During the Pleistocene the climate was cooler and wetter, similar to that found today around Lake Mono, 240 km (150 mi) to the north. Numerous large pluvial lakes occupied the many depressions in this area and at that time Texas Spring would have been at or only slightly above the shoreline

of pluvial Lake Manly. The aquatic communities currently found in the springs and streams of Death Valley are largely relicts of these Pleistocene and earlier communities (Shepard 1992, 1993). Grayson (1993) provides an excellent account of both Pleistocene and Recent hydrology for the Death Valley area.

In the desert southwest of the United States, it appears that *H. (H.) azteca* has been giving rise to new species via populations that have been isolated in thermally constant waters. Thomas et al. (1994, 1997) have proposed ecological isolation for the species pair *H. (H.) azteca* and *H. (H.) montezuma*, based on DNA and behavior. Their behavioral studies led them to separate two lineages of *Hyaella* in north-central Arizona; swimmers that inhabit submersed vegetation in lakes and clingers that inhabit springs dominated by emergent macrophytes. Jackson (1912) also noted two distinct locomotion behaviors. *Hyaella* (*H.*) *muerta* and *H. (H.) sandra* both fall into the clinger behavior category and likely have speciated from local epigeal populations of *H. (H.) azteca*.

Another undescribed *Hyaella* (*Hyaella*) species has also been found in Ash Meadows National Wildlife Refuge, 45 km to the east (in prep.). It also occurs in a warm spring. Because of the discovery of a number of new species in such a small area, we suggest that aquatic biologists more carefully collect and identify specimens in the future, particularly when dealing with thermally constant waters.

Acknowledgments

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