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The Spinicaudatan Clam Shrimp Genus *Leptestheria* Sars, 1898 (Crustacea, Branchiopoda) in California

Joel W. Martin and Cora E. Cash-Clark

Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007

Abstract.—The spinicaudatan clam shrimp genus *Leptestheria,* the only genus of the family Leptestheriidae known from North America, is reported for the first time from California. *Leptestheria compleximanus* (Packard, 1877), which earlier had been erroneously reported from California (based on specimens collected in Baja California, Mexico), was found in two locations in the western Mojave Desert of California, where it occurs sympatrically with notostracans and anostracans. Some brief notes on natural history of the species, and a taxonomic synonymy, are provided.

The branchiopod crustacean orders Spinicaudata and Laevicaudata (formerly united as the order Conchostraca; see Fryer 1987; Martin and Belk 1988; Martin 1992) currently include five extant families commonly called clam shrimp. The Laevicaudata contains only the family Lynceidae, with three known genera, two of which are known from North America (see Martin and Belk 1988). The Spinicaudata contains four families (Cyclestheriidae, Cyzicidae, Leptestheriidae, and Limnadiidae), all of which contain at least some species known from North America.

In California, only two spinicaudatan families have previously been reported. The Limnadiidae is represented by several species in the diverse genus *Eulimnadia* (Belk 1989; Sassaman 1989). The taxonomically confusing family Cyzicidae is also relatively common (Mattox 1957a; Wootton and Mattox 1958), although species and genera in this family are badly in need of systematic reevaluation (e.g., see Straškraba 1965).

The family Leptestheriidae, of which the only species known from North America is *Leptestheria compleximanus* (Packard, 1877), has not been previously reported from ephemeral ponds in California. However, because of the following set of circumstances, the species has often been listed as occurring in this state. In two similar publications that appeared in 1895, Jules Richard (1895a, b) listed "Basse-Californie" (Lower California), Mexico, for one collection of *L. compleximanus.* Richard (1895a) stated that his material came from "l'arroyo de la Purissima (Basse-Californie)." Although there is a similarly spelled locality of Purisima Creek, California, on the San Francisco peninsula, it is not in an optimal habitat for ephemeral pond species. In contrast, Richard's Arroyo Purissima [sic] in Baja California ("La Purisima creek" of Maeda-Martinez 1991), site of a former mission, is located in an area of abundant ephemeral ponds (Clay Sassaman, pers. comm.). Furthermore, Richard (1895a: 107) stated that the species was collected along with *Eocyzicus digueti,* a spinicaudatan species known at that time only

from Baja California,[1] strongly suggesting that Richard's specimens of *Leptestheria compleximanus* were from Baja California, and not California. (*Eocyzicus digueti* has since been reported from Kansas and Nevada (Wootton and Mattox 1958), the Sonoran and Chihuahuan deserts of northern Mexico (Maeda-Martinez 1991), Arizona (Belk 1992), and San Diego County, California (Simovitch and Fugate, in press)).

Richard's (1895a, b) Baja California record of *Leptestheria compleximanus* was based on collections made by "M. Diguet." Part of this collection found its way to the Paris Museum, where it was later studied by the great Hungarian limnologist Eugene Daday (Daday 1923), as evidenced by his mentioning specimens collected by Diguet from the "Mares de l'Arroyo de la Puressima" [sic] in "California" in his monograph on the family Leptestheriidae (Daday 1923: 319). These are undoubtedly the specimens listed by Forró and Brtek (1984: 99), in their account of the Hungarian Natural History Museum's collection of Anostraca and Conchostraca taxa described by Daday, as *Leptestheria complexímana* [sic] (the same incorrect spelling used by Daday) from "California." Prior to Daday's (1923) monograph, Dodds (1915) and Pearse (1918: 674) (in the first edition of Ward and Whipple's "Fresh-Water Biology") had correctly listed Richard's record of the species from "Lower" California. However, probably based on Daday's monograph, both Creaser (1935) and Mattox (1959), in two popular texts on freshwater biology, omitted the word "Baja," thereby mistakenly crediting the collecting site to California, and several subsequent compilations (e.g., Pennak 1978, 1989; Moore 1965; Fitzpatrick 1983; Saunders and Wu 1984) have perpetuated this error.

Creaser (1935) and Mattox (1959), it turns out, were correct in reporting the species from California, albeit for the wrong reason. *Leptestheria compleximanus* (Packard, 1877) does indeed occur in California, and in this paper we report two geographically close areas in the western Mojave Desert of California where the species is found in relatively large numbers.

Materials and Methods

The species first came to our attention in the form of dried mud samples collected on 13 October 1990 from Amboy Crater, Mojave Desert, California (located just southeast of Amboy, California, and approximately 500 m south of Route 66 in San Bernardino County) (Fig. 1A, B) by Dr. Edward Wilson of the Earth Sciences Division of the Natural History Museum of Los Angeles County. Dr. Wilson also reported having seen live conchostracans and notostracans at times when the crater contained water. These dry mud samples were packed with shells of a spinicaudatan clam shrimp, and obviously were collected not long after the population's demise, as the valves were in reasonably good condition (Fig. 1D). In the laboratory, we added dechlorinated water to the samples on 8 November 1990, and soon obtained a series of small conchostracans easily identifiable as *Leptestheria compleximanus* (Packard, 1877). Specimens of these labo-

[1] Although Richard (1895a) suggested that *E. digueti* might be the same as Baird's (1866) *Estheria newcombi*, described from California (and of historical interest as being the first report of any species of conchostracan from California), *E. newcombi* was incompletely described, is possibly synonymous with *Cyzicus californicus* (see Wootton amd Mattox 1958), and is no longer considered a valid species.

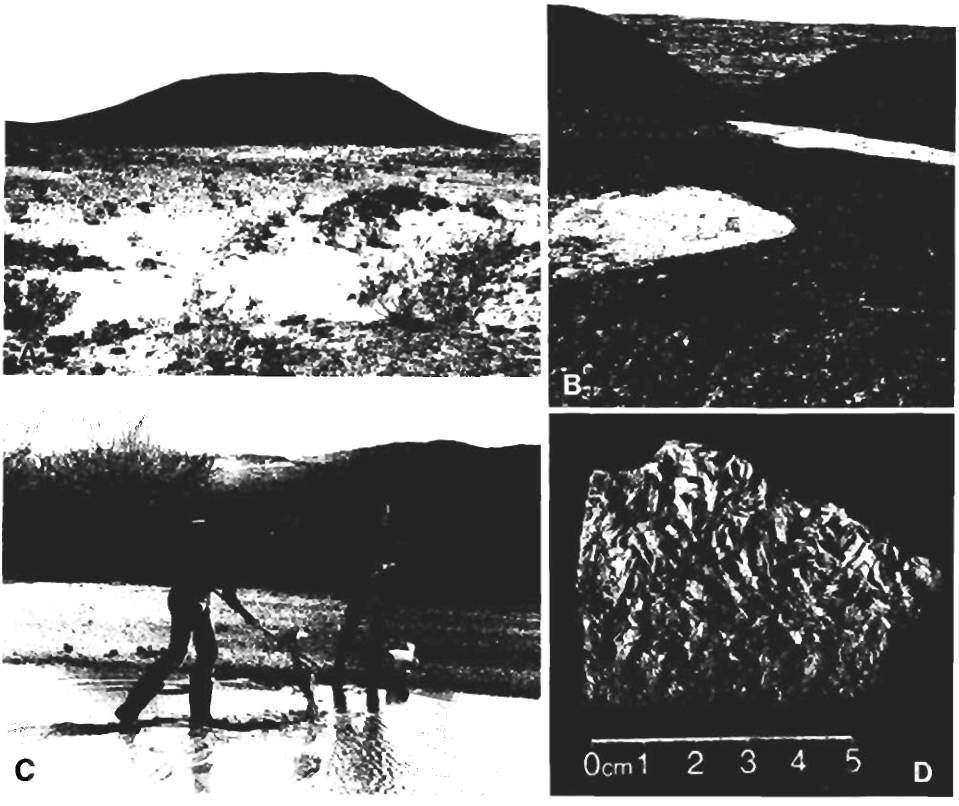

Fig. 1. Collecting localities (Amboy Crater and Troy Dry Lake, western Mojave Desert) for *Leptestheria compleximanus* in California. A, Amboy Crater as seen from state road 66. B, view of crater floor from northeastern rim of crater, showing two small areas (light colored) where temporary pools form. Depression in far crater wall is area of lava outflow to the southwest. C, collecting area at Troy Dry Lake. Road in background is Interstate 40. D, dried mud sample collected from Amboy Crater in 1990, containing numerous valves of *Leptestheria compleximanus*.

ratory-reared samples were preserved on 29 November 1990, when the animals were 21 days old and measured up to 4.70 mm in valve length in both males and females. The animals were not yet mature, as no females were observed with an egg mass visible beneath the shell. In the laboratory this species can reach maturity in only 9 or 10 days (Clay Sassaman, pers. comm.), so it is possible that our rearing conditions were suboptimal.

Live individuals of *Leptestheria compleximanus,* as well as live notostracans (*Triops longicaudatus*) and anostracans (*Branchinecta mackini* and *B. lindahli*), were observed in the field on 18 March 1992 in shallow, very muddy pools (Fig. 1C) on either side of west Interstate 40 at Troy Dry Lake, Mojave Desert, just east of mile marker 26, 1.9 miles east of the Ft. Cady exit to Newberry Spring (which is at mile marker 23.5). These individuals were slightly larger than the laboratory reared specimens from Amboy Crater. Additionally, dry mud from around these pools, and from the easternmost of two small craters within Amboy Crater (Fig. 1B), was returned to the laboratory.

Natural History Observations

The roadside site (Troy Dry Lake) (Fig. 1C) was filled with water so muddy that visibility was minimal; clam shrimp could be seen only as they neared the water surface, which they did often, sometimes to the point that the highest part of the carapace valves extended slightly above the surface. Other branchiopods seen and collected included the anostracans *Branchinecta mackini* and *B. lindahli* and the notostracan *Triops longicaudatus.*

Leptestheriids were active and were observed mating in the field and later in the laboratory, where they lived only about 24 hours. Mating involves clasping of the female's shell by the male's first two pairs of thoracopods so that she is held in front of him in a horizontal plane (with her carapace hinge directed forward while his is directed upward) and is propelled by his motion, adding no appreciable component to movement herself. The female is positioned far toward the front of the male, so that from above the couple resembles a swimming letter T, the horizontally positioned female being the cross of the T (similar to mating in *Cyzicus* as illustrated by Mathias 1937: 44, fig. 3). A photograph of a mating pair of *L. compleximanus* (although referred to only as "clam shrimp" the species is recognizable) appeared in the October 1975 issue of National Geographic magazine (Findley and Sisson 1975: 578–579). Males at Troy Dry Lake were very active in their pursuit of, and attempts to clasp, females. Clasping occurred with egg-less females as well as with females already carrying an extruded egg mass visible beneath the thin shell.

Burrowing is common. This activity was at first thought to be an artifact of the shallow habitat, but even in deeper waters, in the field and in the laboratory, clam shrimp were seen to burrow into the underlying mud, and then to emerge at a point near where they entered. It is possible that they actively ingest mud and derive some nutrition from organic matter contained therein, as it is difficult to envision effective filtering in water so thick with suspended mud and clay. Tasch (1964) did not mention burrowing in a culture of *L. compleximanus* from Mexico, which he maintained in the laboratory for over three and one half months, but commented on their swimming "with ventral valves upward and agape" just below the surface of the very turbid water. We did not see any similar activity in our population.

Females are slightly smaller than males. Size of the Troy Lake specimens, measured from the maximum length and height of the valves, ranged from 6.10 mm long and 3.18 mm high in females (N = 15) to 6.48 mm long and 3.68 mm high in males (N = 15). This is larger than specimens reared from dried mud in 1990 from Amboy Crater, but is smaller than reported lengths of the species (e.g., up to 9.3 mm long in males from Colorado (Saunders and Wu 1984) and up to 11 mm long in Kansas specimens (Packard 1883)). Richard's (1895a) specimens from Baja California are significantly smaller; he lists a carapace length of only 6.5 mm, yet all 36 females in that collection were ovigerous. The Troy Dry Lake specimens are also smaller than those in an unlabeled lot housed at the Natural History Museum of Los Angeles County. That lot, the collecting locality of which is unknown, contains males up to 12.93 mm long and 7.41 mm high. Of the 92 animals we collected at Troy Dry Lake, males (N = 77) outnumbered females (N = 15) in a ratio of approximately 5:1. This is opposite to what Richard (1895a) reported from Baja California (37 females and 6 males). The skewed ratio in both

Richard's and our collections may indicate differential survival or differential susceptibility to capture, because in laboratory rearings the sex ratio in this species invariably approaches 1:1 (Clay Sassaman, pers. comm.) as is the case with many (but not all) other spinicaudatans (e.g., see Sassaman 1989; Sassaman and Weeks, in press) including members of the Leptestheriidae (Scanabissi Sabelli and Tommasini 1992). No females were seen to be carrying eggs within the thoracopodal epipods as has been described for another species in this genus (*Leptestheria dahalacensis*; Tommasini and Scanabissi Sabelli 1989, 1992).

Belk (1992) noted that in Arizona, where this species is the most common conchostracan, the species can be found from mid-June through October at pool temperatures of 19.5 to 27°C. The species is also common in Mexico, where it has the widest distribution of any known conchostracan (Maeda-Martinez 1991). Horne (1967) considered *L. compleximanus* a eurythermal species, as he found it in Wyoming in pools ranging from 1 to 32°C. Additional habitat notes are given by Sublette and Sublette (1967) for populations in playa lakes in Texas and New Mexico. Co-occurrence with other large branchiopod species is common. As one example, in a temporary pond just north of Jimenez, Chihuahua, Mexico, *Leptestheria compleximanus* was found to co-occur with the anostracan species *Streptocephalus moorei, S. mackini,* and *Thamnocephalus platyurus,* the notostracan *Triops longicaudatus,* and the spinicaudatan *Eocyzicus digueti* (Belk 1973).

Descriptive Notes

Specimens from the Troy Dry Lake site (Fig. 2) and those reared from mud from Amboy Crater agreed in almost all morphological respects with each other and with previous descriptions of *L. compleximanus* (e.g., figures in Packard 1883, figs. 8, 9 and plate 5 (Kansas); Daday 1923, fig. 94 (Baja California); Mattox 1957a, figs. 5, 14 (Texas); Saunders and Wu 1984, figs. 10–14 (Colorado); Martin 1989, fig. 1C (Arizona); Dodson and Frey 1991, fig. 20.74B, Mexico (?)). The paired rows of spines along the posterior margins of the telson (Fig. 2C, D) are smaller than those illustrated by Saunders and Wu (1984) for Colorado specimens, but this may be a factor of size, as their specimens were larger than ours.

Daday's illustrations indicate minute spinules along the length of the furcal rami, whereas these are absent in the figures of Packard (1883) and Dodson and Frey (1991). The discrepancy is probably accounted for by the fact that the furcal rami are slightly rotated inward, with the result that the row of minute spinules often seen along the dorsal border in other species is, in this species, nearly hidden from lateral view and more visible only in dorsal view (Fig. 2C, D). Packard's (1883) illustration (his plate 5, fig. 1) of the entire animal is slightly misleading, in that the male claspers are obviously very stylized in that drawing. The basal protrusion of the clasper "hand" and the spine-covered pad that opposes the movable finger (Fig. 2E) are not as stalked or as distant from the clasper as depicted by Packard's illustrator. Other minor discrepancies were noted between our Troy Dry Lake specimens and previous descriptions of this species, but they seem to fall within the range of acceptable variation in this morphologically rather plastic family (Straškraba 1966).

The species is easy to identify and distinguish from all other clam shrimp species (orders Laevicaudata and Spinicaudata) in North America by its possession of an acute angle on the extremity of the "head" region just cephalad to the occipital

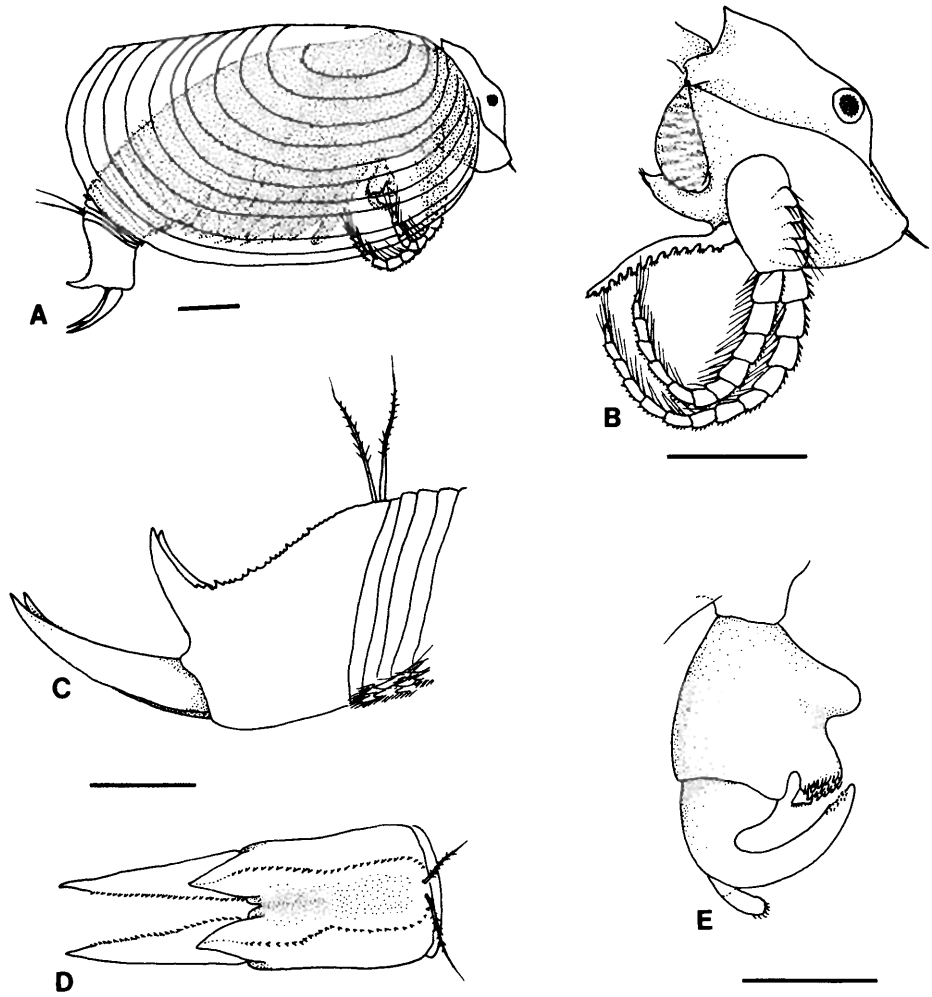

Fig. 2. Selected diagnostic features of a 6.1 mm long male *L. compleximanus* (Packard) from the Troy Dry Lake site. A, entire animal, lateral view. B, higher magnification of head region; note frontal seta projecting from apex of rostrum. C and D, lateral (C) and dorsal (D) views of the telson and furcal rami. E, lateral view of right first thoracopod (first clasper). Scale bars = 1.0 mm for A, B; 0.5 mm for C–E.

notch, a long and somewhat quadrate shell with a more or less flattened dorsal line (Fig. 2A), possession of a well developed fornix (which leptestheriids share with the cyzicids), distinctive male first claspers with proximal protuberance (Fig. 2E), and a diagnostic frontal seta on both males and females (Fig. 2B). The frontal seta, often considered an apomorphy of the family Leptestheriidae, also has been reported in developing juveniles of the family Cyzicidae and in a reduced state in adult female cyzicids (e.g., Barnard 1929), again underlining the close phylogenetic relationship of these two families.

When first proposing the new genus *Maghrebestheria,* Thiery (1987) mentioned the similarity between the only known species of that genus (*M. maroccana*) and *L. compleximanus,* but no mention was made of this in his formal erection of the genus (Thiery 1988).

Taxonomic History

The taxonomic history of this species, like that of so many other species of the Branchiopoda, is convoluted and confusing. The species was first described as a member of the genus *Eulimnadia* (which today is in the family Limnadiidae), and later assigned to *Estheria,* a name that had to be dropped as it had been previously employed for a group of parasitic dipterans. The history of the genus was discussed by Mattox (1957a, b). In the synonymy that follows, we list the major publications that treat this species, while acknowledging that this probably is not an exhaustive list.

Leptestheria compleximanus (Packard, 1877)

Eulimnadia compleximanus Packard, 1877, p. 174, fig. 13a, b (Kansas).—Packard 1879, 1880, Zoology for Colleges and High Schools, 1st and 2nd editions (no description), fig. on p. 302 (not seen)[2].

Estheria compleximanus Packard, 1883, p. 305, figs. 8a, 8b, 9, plate V figs. 1–7, plate XXIV figs. 8, 10, plate XXV fig. 6 (Kansas) (described as a "new species" in this work, although citing his previous mention of it above).—Richard 1895a, p. 104; 1895b, p. 107 (Baja California, Mexico).—Cockerell 1912, p. 43 (Colorado).—Pearse 1918, p. 674, fig. 1046.—Dodds 1915, p. 275 (key), fig. 16 (Colorado).—Dodds 1917, p. 73 (Colorado).—Dodds 1920, p. 96 (Colorado).

Estheria complexímana.—Simon 1886, p. 453 (list).

Leptestheria complexímana.—Sars 1898, p. 10.—Daday 1923, p. 391, fig. 94a–s.—Wootton and Mattox 1958, p. 122 (Mexico).—Forró and Brtek 1984, p. 99 (in reference to Daday's collections).—Thiery 1987, p. 192.

Leptestheria compleximanus.—Creaser 1930, p. 7 (Utah).—Creaser 1931, p. 267 (Mexico).—Creaser 1935, p. 380, fig. 512.—Moore 1950, p. 655 (Texas).—Moore 1965, p. 41 (Oklahoma).—Mattox 1957a, p. 367, figs. 5, 14A, B (Texas).—Mattox 1959, p. 583, fig. 26.8.—Tasch 1964, p. 128 (Mexico).—Tasch and Shaffer 1964, p. 806 (Mexico).—Horne 1967 p. 474 (Wyoming).—Horne 1974, p. 476 (Texas).—Sublette and Sublette 1967, p. 383 (New Mexico, Texas).—Belk 1973, p. 509 (Mexico).—Belk and Cole 1975, p. 211 (Arizona).—Oldham 1978, p. 50 (Kansas).—Pennak 1978, p. 344 (key), fig. 243C (after Packard).—Pennak 1989, p. 362 (key), fig. 17C (after Packard).—Hartland-Rowe 1982, p. 175.—Fitzpatrick 1983, p. 49.—Saunders and Wu 1984, p. 11, figs. 10–14, 23 (map) (Colorado).—Chengaleth 1987, p. 15 (Manitoba, Canada).—Martin 1989, figs. 1, 2D, 3F, 4A, B, 5C, 6A (Arizona).—Debrey et al. 1991, p. 399 (Wyoming).—Maeda-Martinez 1991, p. 215, fig. 7 (map) (Mexico).—Belk 1992, p. 123 (Arizona).

Leptestheria compleximannus.—Slack 1967, p. 1021 (Lake Winnipeg, Canada) (misspelling).

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[2] Packard (1883) mentioned two other appearances of the name *Eulimnadia compleximanus,* in the first and second editions of "Zoology for Colleges and High Schools" (1879, 1880), subsequent to his original 1877 description of the species. According to Packard (1883), no description was included, although a figure on p. 302 is mentioned. We have not been able to locate these text books and cite them here following Packard (1883: 305).

Unnamed "clam shrimp" in photograph. Findley and Sisson 1975, p. 578–579 (Utah).

Leptisthera complexiimanus.—Dodson and Frey 1991, p. 774, fig. 20.78 (misspelling) (Mexico [?]).

Leptistheria.—Dodson and Frey 1991, p. 772 (key) (misspelling).

Discussion

As currently recognized (Thiery 1988) the family Leptestheriidae consists of five genera: *Eoleptestheria* Daday, 1914, *Leptestheria* Sars, 1898, *Leptestheriella* Daday, 1923, *Maghrebestheria* Thiery, 1988, and *Sewellestheria* Tiwari, 1966. The last two genera are monotypic, but the first three contain a large number of species, over 30 worldwide (unpublished data).

Although the genus *Leptestheria* Sars, 1898, is widely distributed on all continents except Antarctica (Marincek and Petrov 1985), *Leptestheria complexiimanus* (Packard, 1877) is the only species known from North America (i.e., the United States, Canada, and Mexico). The occurrence of this species in southern California is not surprising in light of its known presence in Arizona and in Baja California. Debrey et al. (1991), in a brief and error-filled account of branchiopods in southeastern Wyoming, believed their record of *L. complexiimanus* from Wyoming to be the first; it had previously been reported from that state by Horne (1967). The record of the species in Lake Winnipeg, Canada (Slack 1967) should be verified, as large permanent lakes are not usually the habitat of this species or of many other spinicaudatans. To date, the species has been reported from Canada (above record), from 9 states in Mexico (Baja California Sur, Chihuahua, Coahuila, Distrito Federal, Durango, Estado de Mexico, San Luis Potosi, Sonora, and Zacatecas), and from the following states in the United States: Arizona, California (this study), Colorado, Kansas, New Mexico, Oklahoma, Texas, Utah, and Wyoming. References for the above records are listed in the synonymy.

Intensive sampling of many Mojave Desert ephemeral ponds, and the subsequent laboratory rearing of eggs from dried mud taken from many Mojave sites, has not previously revealed the presence of leptestheriids (Clay Sassaman, pers. comm.). We are unsure as to whether *L. complexiimanus* is confined to a restricted area in California or is abundant only for a short time, or both. A brief population duration might be indicated by its potential for rather rapid development (9 to 10 days from hatching to adulthood) in the laboratory (C. Sassaman, pers. comm.). More sampling to determine the exact extent of the range of the species, and its habitat and physiological requirements, is needed, as is also the case with many other clam shrimp and indeed other branchiopods in North America (e.g., see Martin et al. 1986).

Acknowledgments

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