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REVISION OF *MACRELMIS* MOTSCHULSKY, 1860 IN THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO WITH DESCRIPTION OF FOUR NEW SPECIES (COLEOPTERA: ELMIDAE: ELMINAE)

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ABSTRACT

Four new species of *Macrelmis* Motschulsky, 1860 are described from the southwestern United States and northern Mexico: *Macrelmis harleyi* Barr, new species from Arizona, *Macrelmis mexicana* Barr, new species from Mexico, *Macrelmis shepardi* Barr, new species from Arizona, New Mexico, Texas, and Mexico, and *Macrelmis texangusta* Barr, new species from Texas and Mexico. Photographic images illustrate the external morphology and male genitalia of the new species, as well as that of *Macrelmis shoemakei* (Brown, 1971), *Macrelmis moesta* (Horn, 1870), and *Macrelmis texana* (Schaeffer, 1911), which occur in the same geographic region. The genitalia of *M. moesta* and *M. texana* are described and illustrated for the first time. A key to the 14 known species of *Macrelmis* occurring in the southwestern United States and Mexico is provided, accompanied by line illustrations of the genitalia of the remaining seven Mexican species not included in the species treatments. Also included are geographic distribution maps for the seven species that are discussed in this article.

Keywords: riffle beetles, Nearctic, Harley P. Brown, calcium bicarbonate-rich water, tufa

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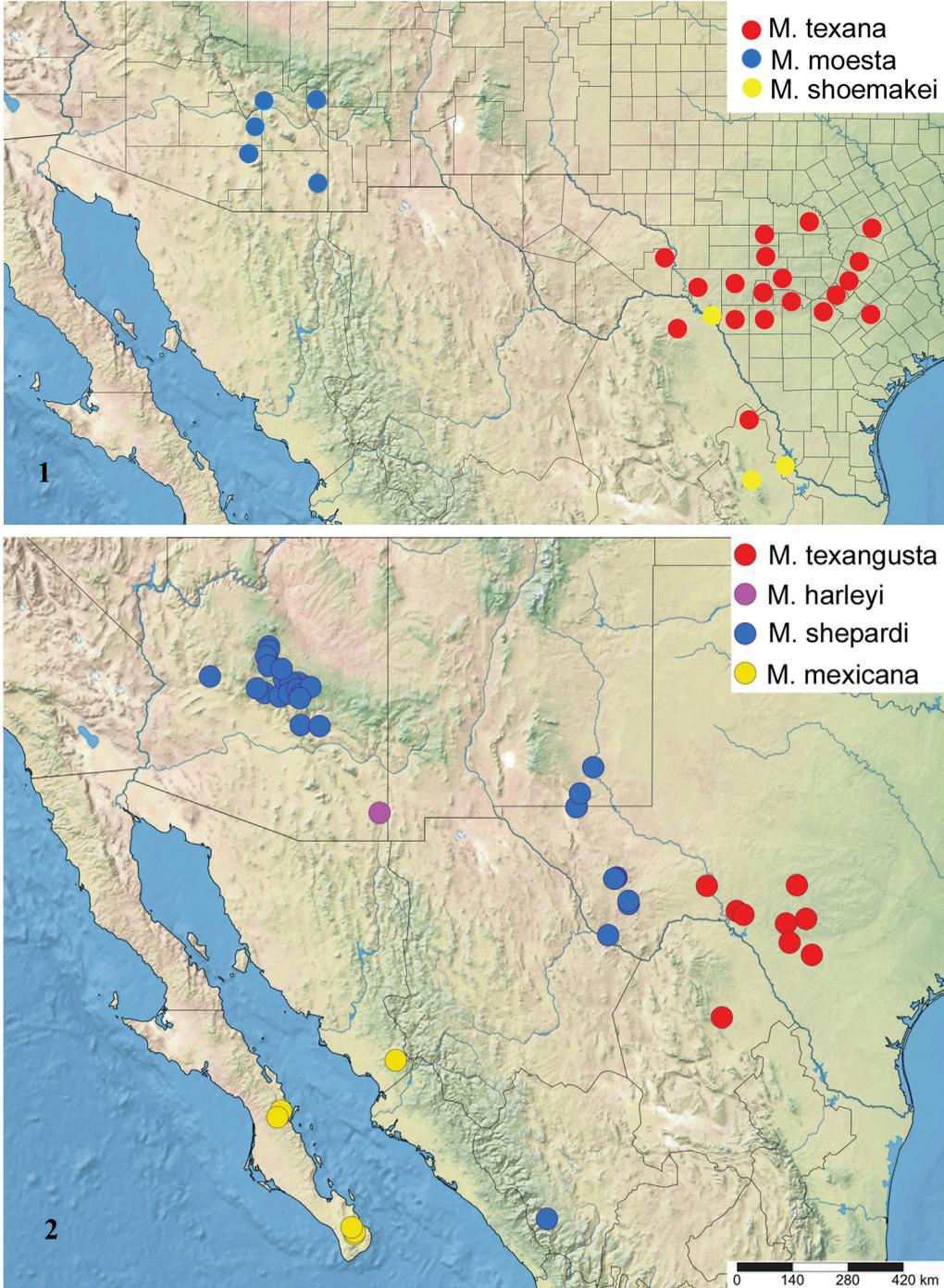
INTRODUCTION

Macrelmis Motschulsky, 1860 is a genus restricted to the Western Hemisphere with 53 species distributed from the southwestern United States to Argentina (Almeida *et al.* 2020; Jäch 2002; Jäch *et al.* 2016; Passos *et al.* 2015). Not only is it one of the most speciose of the elmid genera, but its members are among the largest elmids in terms of general body size.

The taxonomic history of *Macrelmis* and its species is quite convoluted. The generic description was based on a single specimen from Colombia, described as *Macrelmis dentata* Motschulsky, 1860 (Motschulsky 1860) and deposited in the Zoological Museum of Moscow. It was nearly 80 years before additional species were placed in the genus by Hinton and others. In the interim, Sharp (1882) described the genus *Elsianus* Sharp to contain three new Central American species, and other species were added subsequently (Brown 1984). From Motschulsky's description of *M. dentata*, Brown (1984) suspected that species described in *Elsianus* were misplaced. After borrowing and examining the type of *M. dentata*, Brown (1984) transferred to *Macrelmis* the 35 species previously ascribed to *Elsianus*, and relegated *Elsianus* to synonymy. At the same time,

Brown (1984) erected the new genus *Austrelmis* Brown to contain the 14 South American species erroneously placed in *Macrelmis* plus three species originally described in *Elmis* Latreille, 1802. Adults of *Macrelmis* are mainly diagnosed by the presence of a short accessory stria at the base of each elytron between striae 1 and 2; additionally, they possess a fringe of tomentum on the protibia and lack oblique pronotal sculpturing (Brown 1984).

Ten species of *Macrelmis* have been described from the United States and Mexico. Two of these are from the southwestern USA, and one is from the southwestern USA and northern Mexico: *Macrelmis moesta* (Horn, 1870) in Arizona, *Macrelmis texana* (Schaeffer, 1911) in Texas, and *Macrelmis shoemakei* (Brown, 1971) in Texas and Coahuila (Jäch *et al.* 2016). Seven additional described species of *Macrelmis* occur in central and southern Mexico: *Macrelmis grandis* (Hinton, 1934), *Macrelmis graniger* (Sharp, 1882), *Macrelmis leonilae* Spangler and Santiago F., 1986, *Macrelmis sandersoni* (Hinton, 1936), *Macrelmis scutellaris* (Hinton, 1934), *Macrelmis striata* (Sharp, 1882), and *Macrelmis striatoides* (Hinton, 1936). It is surprising that despite the description of *M. moesta* and *M. texana* over a hundred years ago, their male genitalia (which are important and often essential



Figs. 1–2. Maps illustrating the known geographic distributions of *Macrelmis* in the southwestern USA and northern Mexico. **1)** *M. texana*, *M. moesta*, *M. shoemakei* (locality points approximate, not georeferenced); **2)** *M. harleyi*, **new species**, *M. shepardi*, **new species**, *M. texangusta*, **new species**, and *M. mexicana*, **new species**.

diagnostic tools) have not been described and illustrated until now.

At the 1983 meeting of the Entomological Society of America, the late Harley P. Brown (University of Oklahoma, Norman) presented a talk entitled “New Species of *Macrelmis* (formerly *Elsianus*) from Arizona, New Mexico, Texas and Mexico (Coleoptera: Elmidae).” Brown planned to publish his findings, and began a draft manuscript which was never completed. He freely and generously shared his knowledge with me, at the time a rookie riffle beetle worker, and with anyone else who was interested. Over the ensuing years I collected many specimens of *Macrelmis* in the Southwest and Baja California, including Brown’s three undescribed species, and feel that bringing these to light is long overdue. In naming the new species I have retained Brown’s manuscript names and added another new species, unknown to him, which is named in his honor. It is to the memory of my “riffle beetle father”, Harley Brown, that I dedicate this article.

MATERIAL AND METHODS

Loaning institutions and depositories:

ASUHC	Hasbrouck Insect Collection, Arizona State University, Tempe, AZ, USA
EMEC	Essig Museum of Entomology, University of California, Berkeley, CA, USA
OMNH	Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK, USA
TAMU	Texas A&M University Insect Collection, College Station, TX, USA
UMC	Enns Entomology Museum, University of Missouri, Columbia, MO, USA
UNAM	Universidad Nacional Autónoma de México, Mexico City, Mexico
USNM	United States National Museum of Natural History, Washington, DC, USA

The majority of specimens used for this study are from the author’s collection and that of William D. Shepard (University of California, Berkeley), and will ultimately reside in the EMEC. A number of these were obtained from an Arizona Department of Environmental Quality stream survey conducted during 1992–1993 for which the author provided identifications. The remaining specimens were borrowed from the collection of the late Dr. Harley P. Brown which is housed at the OMNH, and a small number belong to UMC. Additional locality records of specimens identified by Brown were obtained from the OMNH Recent Invertebrates Database: samnoblemuseum.ou.edu/collections-and-research/recent-invertebrates/recent-invertebrates-database.

Collections by the author were made by kick-sampling the bottom substrate of the watercourse and capturing dislodged specimens in a D-frame aquatic net. In addition to *Macrelmis*, other riffle beetle taxa were collected and are reported in the species accounts as “Associated Byrrhoid Taxa”. Specimens were placed in vials containing 95% ethanol in the field and examined later in the laboratory. *Macrelmis* specimens are often covered with debris accumulations or encrustations which obscure the external features (Figs. 28–29). In the lab, these coatings were at least partially removed from beetles in ethanol using a fine camel hair brush and insect pin, after which they were dried and card point-mounted. Genitalia dissected from selected specimens were placed in genitalia vials, each containing a drop of glycerin, and affixed to pins below the specimens. A Leica MZ 12.5 stereo microscope fitted with an ocular micrometer was used to examine and measure specimens. Body length measurements consist of the pronotal length plus the elytral length taken at the midline, and do not include the head or the variable space between the pronotum and elytra; body width measurements are of both elytra at their widest point. Identifications of *Macrelmis* and associated byrrhoid taxa were either done or verified by the author.

The habitus images were taken using a Visionary Digital BK Plus Lab System fitted with a Canon EOS 7D camera. A Syncrosopy AutoMontage® system was used for the genitalia images. Images were prepared and assembled using Adobe Photoshop Elements. The line illustrations of the genitalia of Mexican species (Figs. 21–27) were modified and redrawn from those of Hinton (1940) and Spangler and Santiago F. (1986). SimpleMappr, a free internet program (Shorthouse 2010), was used to create the distribution maps (Figs. 1–2).

Label data are reported verbatim. A single slash “/” indicates the end of a line, a double slash “//” indicates the end of a label. Some specimens on loan from OMNH have determination labels with Brown’s manuscript names. These labels were retained in addition to the author’s paratype or determination labels. Abbreviations found in the specimen data, besides those of depositories, include HPB = Harley P. Brown, WDS = William D. Shepard, and TNC = The Nature Conservancy.

SPECIES ACCOUNTS

Macrelmis harleyi Barr, new species

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0727D62C-D264-4906-8857-0330D1C61F2E
(Figs. 2–5)

Type Locality. Cave Creek near Herb Martyr Campground, N 31.872°, W 109.234°, Coronado

National Forest, Cochise County, Arizona, United States.

Diagnosis. *Macrelmis harleyi* (Figs. 3a–b) somewhat resembles *M. shepardi* (Figs. 6a–c) but is generally smaller: 4.6–5.2 mm long and 1.8–2.0 mm wide vs. 5.0–5.9 mm long and 2.0–2.4 mm wide. The two species can be separated by the apicoventral metatarsal setae: *M. harleyi* has dense, short tufts of setae on metatarsomeres 1–4, while *M. shepardi* has much longer setae, with those of tarsomere 1 nearly equaling or exceeding its length (Fig. 6c). *Macrelmis texangusta* (Figs. 9a–b) overlaps in length (3.8–4.8 mm) and but is noticeably more slender (1.4–1.7 mm wide); *M. moesta* (Figs. 15a–b) is considerably shorter (3.4–3.9 mm). In addition, the male genitalia of *M. harleyi* (Figs. 4a–b) are very distinctive and unique, with the parameres and penis in lateral view strongly curved ventrally at the apical 1/4–1/3. *Macrelmis harleyi* keys to *Elsianus striatus* (= *Macrelmis striata*) in Hinton's (1940) key to the Mexican species, but the male genitalia (Fig. 26) are dissimilar.

Description. Holotype male. Cuticle mostly dark brown, shiny; head darker; antennae, palpi, legs lighter; covered with short, pale, recumbent setae; body elongate, about 2.5× as long as wide, widest at posterior 1/4 adjacent to abdominal ventrite 2; size 4.84 mm long, 1.92 mm wide (Figs. 3a–b). **Head:** Black, moderately granulate with sparse, short, recumbent, pale yellow setae; gena with plastron; vertex with broad, U-shaped sulcus, opening anteriorly, extending from above eyes toward occiput, with deeper excavation above eyes and at posterior extent, vertex convex anteriorly and posteriorly to sulcus; frontoclypeal suture nearly straight. Antenna red-brown, mostly glabrous; antennomeres 1–10 cone-shaped, antennomere 11 elongate-ovoid; antennomere 1 longest, finely setose, antennomere 2 shorter, antennomeres 3–5 shortest, subequal, antennomere 6 longer, antennomeres 7–10 longer than 6, subequal, each with tuft of dense setae at ventral apex, antennomere 11 nearly as long as antennomere 1, with apical band of dense setae. Clypeus black; convex; moderately setose; densely granulate; anterior margin emarginate, lateral margins broadly rounded. Labrum black except central anterior margin brown; convex; anterior margin straight; disc with fine, pale yellow, recumbent setae; lateral margins and anterior margin laterad of median 1/3 with longer, dense, pale yellow setae. Maxillary palpus red-brown, palpomere 4 slightly flattened, elongate-ovoid, apex subtruncate. Labial palpus red-brown, palpomere 3 slightly flattened, ovoid. **Pronotum:** Dark brown, convex; length 1.40 mm, width 1.48 mm, widest at 1/3 distance from base; lateral pronotal carinae marginate, granulate with small, crowded granules, each margin bordered medially by a broad sulcus from anterior to posterior angle. Anterior margin

nearly straight; anterior angle acute, sharp; lateral margin straight at apical 1/2, moderately arcuate at basal 1/2, sinuate at acute, sharp posterior angle; posterior margin trisinuate. Disc lightly setose with short, recumbent, pale yellow setae; medially with small, shallow punctures evenly spaced about 1 diameter apart, basal margin with small granules; laterally granulate, marginal sulcus deeply punctate. Disc laterally with two broadly inflated, granulate, sinuate sublateral carinae extending from base to anterior 1/5; each with medial margin acute; each bounded by a sinuate, longitudinal sulcus, basal 2/3 wide, shiny, glabrous, apical 1/3 narrow, less shiny; two small, round prescutellar foveae present. Scutellar shield black, protuberant, subovate, setose, granulate. **Elytron:** Brown; length 3.44 mm, width 0.96 mm. In lateral view, anterior margin depressed, anterior 2/3 flat, posterior 1/3 convex and curved ventrally. Humeral angle obtuse; lateral margin bordered medially by a narrow sulcus; apex produced, posterior margin truncate. Disc striate and punctate; punctures moderately large and deep at anterior 2/3, posteriorly becoming smaller, shallower, more closely spaced; striae deepest at anterior margin, shallowest at posterior 1/3; intervals convex, interval 7 swollen at humerus. Disc with moderately sparse, very short, recumbent, pale yellow setae; granulate at humerus, lateral margin, adjacent sulcus, apex. Epipleuron with plastron; granules mostly round, evenly spaced about 1 diameter apart. **Venter:** Cuticle dark brown, surface covered mostly with a thin layer of silvery plastron; elongate granules emergent from plastron, variably spaced 1–2 diameters apart, aligned in curvilinear patterns; very short, recumbent, pale yellow setae between granules; plastron lacking (possibly abraded) from entire mesoventrite, median 1/4–1/3 of prosternum, metaventrite and abdominal ventrite 1 between and posterior to metacoxae, abdominal ventrite 2 at midline; granules appearing larger, coarser where plastron absent. Prosternum with anterior margin nearly straight; disc with broad, deep, transverse excavation at middle 1/3; prosternal process about 2× as long as wide, nearly parallel-sided, lateral margins elevated and thick, enclosing a broad longitudinal sulcus at anterior 2/3, apex broadly triangular with blunt tip. Mesoventrite with deep mesoventral cavity bounded by two prominent ridges at anterior 1/2; mesepimeron and mesanepisternum each with dense patch of pale yellow setae. Metaventrite with anterior margin sulcate; disc concave. Abdomen with ventrites 1–4 becoming shorter posteriorly, ventrite 5 nearly as long as ventrite 1 at midline; ventrites convex laterad to midline, sutures incised; ventrite 1 with disc deeply excavate at about middle 1/4 for entire length, deepest between metacoxae, posterolateral angles broadly rounded; ventrite 2 with disc moderately depressed at middle, posterolateral angles



Figs. 3–5. *Macrelmis harleyi*, new species. **3)** Habitus, holotype, size 4.84 mm long, 1.92 mm wide, a) Dorsal view, b) Ventral view; **4)** Male genitalia, a) Dorsal view, b) Lateral view; **5)** Type locality: Cave Creek, Cochise Co., Arizona, USA (photo courtesy of Rebekah Karsch, USDA Forest Service, Coronado National Forest, Arizona).

broadly rounded; ventrites 3–5 with posterolateral angles bearing dorsally curved lobes which clasp epipleural margin; ventrite 5 deeply depressed along anterior margin, weakly convex posteriorly; posterior

margin densely setose, arcuate at middle 1/2, bordered on each side by a wide, deep notch (about 1/4 length of ventrite) forming a lateral, large, subtriangular lobe with dorsally curved tip clasp-

epipleural margin. **Legs:** Fore leg shortest, hind leg longest; each leg with femur slightly shorter than tibia, tarsus shortest. Coxae granulate. Femora and tibiae covered with thin layer of silvery plastron; femora with sparse, short, pale yellow setae and flat, slightly elongate granules, variably spaced 1.0–1.5 diameters apart; tibiae with numerous, short, pale yellow setae and protuberant, round to elongate granules spaced 1.0–1.5 diameters apart, cleaning fringe formula 1-2-1. Tarsi red-brown, without plastron. Procoxa lacking plastron, lateral surface with dense patch of long, golden-yellow setae; profemur with longitudinal band of moderately long, dense, adpressed, golden-yellow setae on anterior surface from base to apical 3/4; protibia moderately arcuate, with longitudinal band of long, dense, golden-yellow setae (cleaning fringe) on anterior surface from near base to apex, apicoventral margin with pair of tibial spurs; protarsus with tarsomeres 1–4 of similar shape and size except tarsomere 1 shorter, each with dense cluster of short, stout setae at apicoventral margin, tarsomere 5 distinctly longer than 1–4 combined, sparsely setose, ventral apex produced between claws; protarsal claws simple. Mesocoxa similar to procoxa; mesofemur with wide band of adpressed, golden-yellow setae on posterior surface from base to apical 2/3; mesotibia straight, with two cleaning fringes, on anterior surface at apical 1/2–2/3 and on posterior surface from base to apex, apicoventral margin with pair of tibial spurs; mesotarsus similar to protarsus; mesotarsal claws simple. Metacoxa with plastron laterally, dense, pale yellow setae on posterior surface; metafemur without band of long setae on posterior surface; metatibia weakly arcuate in dorsal view, with cleaning fringe on posterior surface from near base to apex, apicoventral margin with pair of tibial spurs; metatarsus similar to protarsus and mesotarsus; metatarsal claws simple. **Genitalia:** Elongate, about 3× as long as wide; moderately sclerotized (Figs. 4a–b). Phallobase much longer than parameres; parameres and penis of nearly equal length. In dorsal view (Fig. 4a), parameres with lateral margins subparallel to apical 1/3 then curved inward, inner margins sinuate, apices broadly rounded; penis bottle-shaped, lateral margins subparallel at basal 2/3, apical 1/3 abruptly narrowed, apex truncate; penis at base about as wide as paramere base, at apical 1/3 narrower than paramere apical 1/3. In lateral view (Fig. 4b), phallobase ventral margin strongly arcuate; paramere with ventral margin strongly arcuate, apical 1/4 abruptly narrowed and bent ventrally, apex narrowly rounded; penis strongly curved ventrally beneath paramere at apical 1/3, apex rounded.

Variation. The pronotum varies in that it may be black or brown, slightly wider than long or considerably wider, and the lateral margin varies in the degree of sinuation. The shallow U-shaped impression on the

vertex of the head may be faint or obscured by adhered debris. Males and females are of similar size: males 4.60–4.88 mm long, 1.80–1.92 mm wide ($n = 6$); females 4.52–5.16 mm long, 1.84–2.00 mm wide ($n = 6$). No external sexual differences were noted.

Type Material. Holotype male. ARIZONA. AZ: Cochise County / Chiricahua Mtns. / Coronado NF, Cave / Cr. at Herb Martyr / 8-VI-1993, C.B. Barr // HOLOTYPE / *Macrelmis / harleyi* / Barr [red label, handwritten] // EMEC49610 (EMEC). **Paratypes (42). ARIZONA.** ARIZONA: Cochise Co. / Coronado N.F., Chiri- / cahua Mtns., Cave / Cr. at Herb Martyr / 9-VIII-1987, C.B. Barr (1 EMEC); AZ: Cochise County / Chiricahua Mtns. / Coronado NF, Cave / Cr. at Herb Martyr / 8-VI-1993, C.B. Barr (6 EMEC); AZ: Cochise Co. / Chiricahua Mts. / 8 VI 1993 5780' / Cave Creek // William D. / Shepard, leg. (11 EMEC); AZ: Cochise Co. / 6 mi SW Portal / 25 VI 2007 5820' / Cave Creek (WDS-A-1750, on reverse) // William D. / Shepard, leg. (12 EMEC, 4 ASUHC, 4 OMNH, 4 USNM). All paratypes also have the following final label: "PARATYPE / *Macrelmis / harleyi* Barr" [yellow label, printed].

Etymology. This species is named in honor of the late Professor Harley P. Brown, University of Oklahoma, Norman, who had a profound and lasting effect on the study of riffle beetles in the Western Hemisphere. A personal tribute to his life and research is found in Shepard (2009).

Distribution. *Macrelmis harleyi* is currently known only from Cave Creek in the vicinity of Herb Martyr Campground (Coronado National Forest) in the Chiricahua Mountains of Cochise County, Arizona, USA (Figs. 2, 5).

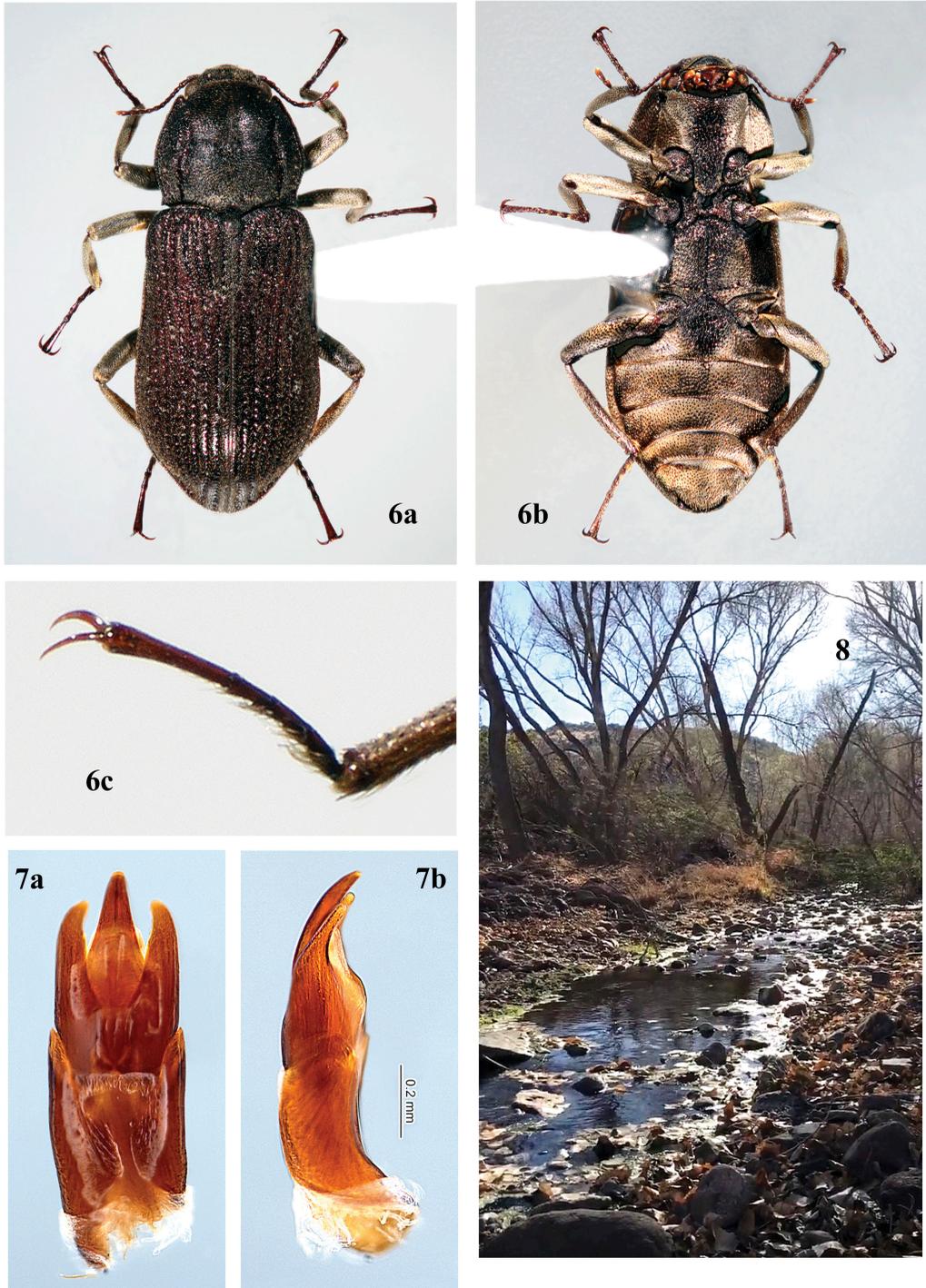
Habitat. At the type locality at an elevation of about 1,770 m, Cave Creek (Fig. 5) is a small (~3 m wide) mountain stream in a canyon. The water is clear and cool, and flows over a substrate of mostly gravel and cobbles. Specimens of *M. harleyi* were collected both above and below a small dam.

Associated Byrrhoid Taxa. *Heterelmis* sp., *Macrelmis moesta*, *Microcylopeus* sp., *Zaitzevia parvula* (Horn, 1870) (Elmidae); *Helichus suturalis* LeConte, 1852, *Helichus triangularis* Musgrave, 1935, *Postelichus immisi* (Hinton, 1935) (Dryopidae); *Psephenus arizonensis* Brown and Murovosh, 1974 (Psephenidae). Cave Creek is also the type locality of *P. arizonensis*, and nearby Pinery Canyon is the type locality of *H. triangularis*.

***Macrelmis shepardi* Barr, new species**

zoobank.org/urn:lsid:zoobank.org:act:
640F120E-BFAC-49B5-84A5-637FE4023632
(Figs. 2, 6–8, 28–29)

Type Locality. Limpia Creek north of Fort Davis, N 30.621°, W 103.867°, Jeff Davis County, Texas, United States.



Figs. 6–8. *Macrelmis shepardi*, new species. **6)** Habitus and metatarsus; size 5.84 mm long, 2.28 mm wide, a) Dorsal view, b) Ventral view, c) Metatarsus, left, inner surface; **7)** Male genitalia, a) Dorsal view, b) Lateral view; **8)** Type locality: Limpia Creek, Jeff Davis Co., Texas, USA (photo courtesy of Tyler Priest, Texas Parks & Wildlife Dept., Fort Davis, Texas).

Diagnosis. *Macrelmis shepardi* (Figs. 6a–c) somewhat resembles *M. harleyi* (Figs. 3a–b) but is generally larger: 5.0–5.9 mm long and 2.0–2.4 mm wide vs. 4.2–5.2 mm long and 1.8–2.0 mm wide. *Macrelmis shepardi* also has characteristic dense tufts of long metatarsal setae on the ventral apices of tarsomeres 1–4, with the setae of tarsomere 1 nearly equaling or exceeding its length (Fig. 6c). This setal character is also present in males of *M. sandersoni* and *M. striatoides* from central Mexico, but it does not appear in species other than *M. shepardi* that occur in northern Mexico and the USA. The robust male genitalia (Figs. 7a–b) are unlike those of other species, with the penis conspicuously longer than the parameres which are strongly curved inward near the apices. In Hinton's (1940) key to the Mexican species, larger specimens of *M. shepardi* (5.5 mm or longer) key to *Elsianus* (= *Macrelmis*) *grandis* and smaller specimens key to *E. striatoides*. However, both species have male genitalia (Figs. 21, 27) unlike those of *M. shepardi*, and *M. grandis* also lacks long metatarsal setae.

Description. Holotype male. Cuticle mostly dark brown, shiny; head darker; antennae, palpi, legs lighter; covered with short, pale, recumbent setae; body elongate, about 2.5× as long as wide, widest at posterior 1/4 adjacent to abdominal ventrite 2 (Figs. 6a–c); size 5.76 mm long, 2.24 mm wide. **Head:** Black, rugose, coarsely granulate with sparse, short, recumbent, pale yellow setae; gena with plastron; vertex with broad, U-shaped sulcus, opening anteriorly, extending from above eyes toward occiput, with deeper excavation above eyes and at posterior extent, vertex convex anteriorly and posteriorly to sulcus; frontoclypeal suture barely emarginate. Antenna light red-brown, mostly glabrous; antennomeres 1–10 cone-shaped, antennomere 11 elongate-ovoid; antennomeres 1 and 11 longest, subequal, antennomere 1 finely setose, antennomere 2 shorter, antennomeres 3–5 shortest, subequal, antennomere 6 longer, antennomeres 7–10 longer than 6, each with tuft of dense setae at ventral apex, antennomere 11 with apical band of dense setae. Clypeus black; convex; moderately setose; densely granulate; anterior margin emarginate, lateral margins broadly rounded. Labrum black except central anterior margin brown; convex; anterior margin straight; disc with fine, pale yellow, recumbent setae; lateral margins and anterior margin laterad of median 1/3 with longer, dense, pale yellow setae. Maxillary palpus light red-brown; palpomere 4 slightly flattened, subquadrate, apex subtruncate. Labial palpus light red-brown; palpomere 3 slightly flattened, ovoid. **Pronotum:** Dark brown, moderately convex; length 1.68 mm, width 1.84 mm, widest at 1/3 distance from base; lateral pronotal carinae marginate, granulate with small, crowded granules, each margin bordered medially

by a shallow sulcus from anterior to posterior angle. Anterior margin arcuate; anterior angle acute, blunt; lateral margin straight at apical 1/2, strongly arcuate at basal 1/2, weakly sinuate at acute, sharp posterior angle; posterior margin trisinate. Disc with faint, median longitudinal sulcus; moderately setose with short, recumbent, pale yellow setae; anterior 1/2 with small, fine, dense punctures spaced about 1 diameter apart; posterior 1/2 with low, variably spaced granules; lateral margins coarsely granulate. Disc laterally with two broadly inflated, granulate, strongly sinuate sublateral carinae extending from near base almost to anterior margin; each with medial margin acute; each bounded by sinuate, longitudinal sulcus, basal 2/3 wide, shiny, glabrous, apical 1/3 narrow, less shiny; two small, round prescutellar foveae present. Scutellar shield dark brown, protuberant, subcircular, very setose, granulate. **Elytron:** Brown; length 4.08 mm, width 1.12 mm. In lateral view, anterior margin depressed, anterior 2/3 flat and slightly constricted at about 1/3, posterior 1/3 convex and curved ventrally. Humeral angle nearly round; lateral margin bordered medially by a narrow sulcus; apex produced, posterior margin slightly oblique. Disc striate and punctate; punctures large and deep at anterior 2/3, posteriorly becoming smaller, shallower, more closely spaced, less distinct; striae deepest at anterior margin, shallowest at posterior 1/3; intervals convex, interval 7 swollen at humerus. Disc with moderately sparse, very short, recumbent, pale yellow setae; granulate at anterior margin, humerus, lateral margin, adjacent sulcus, apex. Epipleuron with plastron; granules round, evenly spaced about 1 diameter apart. **Venter:** Cuticle dark brown, surface mostly covered with a thin layer of silvery plastron; elongate to round granules emergent from plastron, variably spaced 1–2 diameters apart, aligned in curvilinear patterns; very short, recumbent, pale yellow setae between granules; plastron lacking (possibly abraded) from entire mesoventrite, median 1/4–1/3 of prosternum, metaventrite and abdominal ventrite 1 between and posterior to metacoxae, abdominal ventrite 2 from small area at midline; granules appearing larger, coarser where plastron absent. Prosternum with anterior margin straight; disc with shallow transverse depression at middle; prosternal process irregularly sculptured, about 2× as long as wide, nearly parallel-sided, apex broadly rounded. Mesoventrite with deep mesoventral cavity bounded by two prominent ridges at anterior 1/2; mesepimeron and mesanepisternum each with dense patch of pale yellow setae. Metaventrite with anterior margin sulcate; disc concave. Abdomen with ventrites 1–4 becoming shorter posteriorly, ventrite 5 nearly as long as ventrite 1 at midline; ventrites convex laterad to midline, sutures incised; ventrite 1 with disc deeply excavate at about

middle 1/4 for entire length, deepest between metacoxae, posterolateral angles broadly rounded; ventrite 2 moderately depressed at middle of anterior margin and disc, posterolateral angles broadly rounded; ventrites 3–5 with posterolateral angles bearing dorsally curved lobes which clasp epipleural margin; ventrite 5 deeply depressed along anterior margin, weakly convex posteriorly; posterior margin densely setose, arcuate at middle 1/2, bordered on each side by a wide, deep notch (about 1/4 length of ventrite) forming a lateral, large, subtriangular lobe with dorsally curved tip clasping epipleural margin. **Legs:** Fore leg shortest, hind leg longest; each leg with femur distinctly shorter than tibia, tarsus shortest. Coxae granulate. Femora and tibiae covered with thin layer of silvery plastron and round to elongate granules spaced 1.0–1.5 diameters apart; femora with sparse, short, pale yellow setae; tibiae with setae more numerous, cleaning fringe formula 1-2-1. Tarsi red-brown, without plastron. Procoxa without plastron, lateral surface with dense patch of long, golden-yellow setae; profemur with longitudinal band of long, dense, adpressed, golden-yellow setae on anterior surface from near base to apical 1/3; protibia weakly arcuate, with longitudinal band of long, dense, golden-yellow setae (cleaning fringe) on anterior surface from near base to apex, apicoventral margin with pair of tibial spurs; protarsus with tarsomeres 1–4 of similar shape and size except tarsomere 1 shorter, each with cluster of short, stout setae at apicoventral margin, tarsomere 5 longer than 1–4 combined, sparsely setose, ventral apex produced between claws; protarsal claws simple. Mesocoxa similar to procoxa; mesofemur with wide band of adpressed, golden-yellow setae on posterior surface from base to apical 2/3; mesotibia weakly sinuate in dorsal view, with two cleaning fringes, on anterior surface at apical 2/3 and on posterior surface from base to apex, apicoventral margin with pair of tibial spurs; mesotarsus similar to protarsus except tarsomeres 1–4 with apicoventral setae slightly longer; mesotarsal claws simple. Metacoxa with plastron laterally, dense, pale yellow setae on posterior surface; metafemur without band of long setae on posterior surface; metatibia moderately arcuate in dorsal view, with cleaning fringe on posterior surface from near base to apex, apicoventral margin with pair of tibial spurs; metatarsus similar to mesotarsus except tarsomeres 1–4 with apicoventral setae much longer and denser, setae of tarsomere 1 as long or nearly as long as tarsomere; metatarsal claws simple. **Genitalia:** Elongate, about 3× as long as wide; heavily sclerotized (Figs. 7a–b). Phallobase much longer than parameres; parameres shorter than penis. In dorsal view (Fig. 7a), parameres with lateral margins subparallel to apical 1/4 then curved inward, inner margins weakly sinuate, apices

rounded; penis slightly bulbous at basal 2/3, narrowed, tapered, more strongly sclerotized at apical 1/3, apex rounded, dorsal surface with a shallow, median sulcus bounded by two longitudinal carinae; penis at base wider than paramere base, at apical 1/3 about as wide as paramere apical 1/3. In lateral view (Fig. 7b), phallobase ventral margin strongly arcuate; paramere with ventral margin slightly sinuate at basal 2/3, apical 1/3 digitate, abruptly narrowed and curved ventrally, apex rounded; penis bulbous at basal 2/3, apical 1/3 projecting dorsally above and beyond paramere, apex narrowly rounded.

Variation. In some individuals the pronotal disc has a shallow depression rather than a shallow sulcus; the pronotal lateral margins are less than strongly arcuate; and the prosternal process has lateral margins slightly elevated and shallowly sulcate between, rather than flat. Many specimens from Roundtree Creek/Canyon (Yavapai Co., AZ), in particular, are darker in color than those from elsewhere, with black elytra and dark brown antennae and palpi, and dark male genitalia; also, their heads are less rugose and the U-shaped sulci are barely evident. The male genitalia of specimens from Arizona, in comparison with those from Texas, are slightly smaller overall, proportionally narrower, and have the apical, digitate part of the parameres not quite as long and narrow (the relative penis length is not variable, however, being consistently longer than the parameres). Males and females are of similar size: males 5.04–5.80 mm long, 2.12–2.24 mm wide ($n = 9$); females 5.16–5.88 mm long, 2.04–2.40 mm wide ($n = 9$); and both have characteristic long apicoventral setae on metatarsomeres 1–4.

Type Material. Holotype male. TEXAS. TEXAS: Jeff Davis Co. / Limpia Cr. at Hwy. 17 / 2.7 mi. N Fort Davis / 23-XII-1989, C.B. Barr // HOLOTYPE / Macrelmis / shepard / Barr [red label, handwritten] // EMEC49611 (EMEC). **Paratypes (230). ARIZONA (110). AZ:** Coconino Co. / Oak Creek / 85/6/14 H. Brown // Catalog No. / OMNH-112611 (1 OMNH); ARIZONA: Coconino Co. / Coconino N.F., Chavez / Crossing Cgd. S Sedona / Oak Creek, 20-VIII- / 1987, C.B. & J.E. Barr (1 EMEC); AZ: Coconino Co. / Sedona-Chavez / Crossing 8 VI 88 / Oak Creek (WDS-A-556, on reverse) // William D. / Shepard, leg. (3 EMEC); AZ: Coconino Co. / 6 mi N Sedona / 29 VI 2007 4866' / Oak Creek (WDS-A-1752, on reverse) // William D. / Shepard, leg. (1 EMEC); AZ: Coconino Co. / Pine Flat Cmpgd. / 19 IX 2017 1684 m / Oak Creek / N35°00.73' W111°44.33' (WDS-A-2064, on reverse) // William D. / Shepard, leg. (1 EMEC); US: AZ: Coconino Co. / West Fork Oak Creek / above 4th trail crossing / 34°59'54"N, 111°5'12"W / elev. 5310 ft., 13-V-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey,

- 1992-93 (1 EMEC); as above, 30-IX-1992 (2 EMEC); US: AZ: Coconino Co. / East Clear Creek above / Kinder Crossing / 34°34'00"N, 111°08'48"W / elev. 6450 ft., 22-VI-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); US: AZ: Coconino Co. / upper West Clear Creek / at Maxwell Trail / 34°33'20"N, 111°24'32"W / elev. 5985 ft., 6-V-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); US: AZ: Gila County / Salome Creek below / Little Turkey Creek / 33°54'30"N, 111°02'14"W / elev. 4820 ft., 5-V-1993 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (4 EMEC); US: AZ: Gila County / Pine Creek above / E. Verde R. confluence / 34°13'30"N, 111°29'12"W / elev. 3360 ft., 8-X-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); US: AZ: Gila County / Reynolds Creek / below McFadden Cr. / 33°52'32"N, 110°59'17"W / elev. 5065 ft., 11-V-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); AZ: Gila County / Tonto Cr., Bear Flat / C. Gnd. Aug. 6, 1982 / M. W. Sanderson (2 OMNH); AZ: Gila Co., Tonto / Cr., H 260 e. Payson / July 14, 1985 / M. W. Sanderson (3 OMNH); US: AZ: Gila County / Tonto Creek below / Haigler Cr. confluence / at Hellsgate, 28-V-1993 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); US: AZ: Gila County / Haigler Creek ca. 1.5 mi. / blw. Alderwood Rec. Site / 34°12'12"N, 111°00'28"W / elev. 4870 ft., 15-VI-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (2 EMEC); as above, 24-V-1993 (1 EMEC); US: AZ: Gila County / upper Canyon Creek / above Valentine / Canyon, 16-VI-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (10 EMEC); US: AZ: Gila County / Spring Creek above / Bryant Canyon / 34°04'50"N, 111°04'32"W / elev. 4260 ft., 15-VI-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (5 EMEC); ARIZONA: E. Verde / River 4.6mi. NNW. / Payson Gila Co. / 4500' X-6-1973 / Charlene Stauffer // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105888 (1 OMNH); E. Verde R. N. of Payson / Gila Co., AZ. 24-V-78 / C. Olson // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105906 (1 OMNH); [as above] // Catalog No. / OMNH- 105907 (1 OMNH); East Verde R. 5 mi. / NW Payson, AZ / Gila Co., 24-V-78 / Olson // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105898 (1 OMNH); AZ: Gila Co. / n. Payson / 80-8-7 WDS // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105905 (1 OMNH); AZ: Gila Co., E. / Verde R. n. Payson / VII 14 1985 / M. W. Sanderson // Catalog No. / OMNH- 112582 (1 OMNH); AZ: Gila Co., 10 mi N / Payson, 7-VIII-1980 / trib. East Verde River / William D. Shepard / WDS-A-24A // Macrelmis / shepardi / det. HPB (3 OMNH); AZ: Gila Co. / Christopher Cr. / 74-6-13 B. Stark // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105900 (1 OMNH); AZ: Gila County / Christopher Cr. / H 260 e. Payson / VII 18 1985 / M. W. Sanderson // Catalog No. / OMNH- 112583 (1 OMNH); AZ: Yavapai Co. / Beaver Creek / 87-V-21 / M. W. Sanderson // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 112575 (1 OMNH); US: AZ: Yavapai County / Wet Beaver Creek / above USGS gauge / 34°40'26"N, 111°40'12"W / elev. 4025 ft., 6-V-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (3 EMEC); US: AZ: Yavapai County / Little Ash Creek / near Estler Peak / 34°23'01"N, 112°01'30"W / elev. 3840 ft., 29-IV-1993 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); US: AZ: Yavapai County / Conger Creek near / Conger Spring / 34°45'39"N, 113°07'50"W / elev. 4360 ft., 29-V-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (1 EMEC); as above, 21-IV-1993 (1 EMEC); Bloody Basin / Yavapai Co., Ariz. / 69/4/18 H.P. Brown // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105899 (1 OMNH); ARIZ: YAVAPAI CO. / Roundtree Canyon / nr Bloody Basin / VI-18-74 H.P.B. // Catalog No. / OMNH- 105909 (1 OMNH); [as above; series of 4 with sequential catalog numbers] // Catalog No. / OMNH- 105010-10513] (4 OMNH); [as above] PARATYPE [deep pink label] // OMNH- 105914 (1 OMNH); AZ: Yavapai Co., Tonto / Natl. For., Roundtree Cyn. / creek E of F.S. Rd. 24, 18- / VIII-1987, C.B. & J.E. Barr (6 ASUHC, 10 EMEC, 4 USNM); US: AZ: Yavapai County / Roundtree Cr. ca. 3 mi. / above Tangle Cr. confl. / 34°08'08"N, 111°50'53"W / elev. 3300 ft., 2-X-1992 // AZ Dept. Environmental / Quality Reference / Stream Survey, 1992-93 (11 EMEC); AZ: Yavapai Co. / Montezuma Well / 80-8-8, HPB & WDS // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105902 (1 OMNH); [as above] // Catalog No. / OMNH- 105903 (1 OMNH); [as above] PARATYPE [deep pink label] // Catalog No. / OMNH- 105904 (1 OMNH); AZ: Yavapai Co. 14 mi / S Sedona, 8-VIII-1980 / William D. Shepard / Montezuma Well / overflow, WDS-A-26 // Macrelmis / shepardi / det. HPB // (5 OMNH); AZ: Yav. Co. / Oak Creek / 71-8-21 E. May // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105892 (1 OMNH); AZ: Yavapai Co. / Red Rock / 8 VI 1988 / Oak Creek (WDS-A-553, on reverse) // William D. / Shepard, leg. (3 EMEC). **NEW MEXICO (6)**. NM: Eddy Co. / Sitting Bull Falls / 65-8-6 C.W. Beasley // Macrelmis / shepardi / det. HPB // Catalog No. / OMNH- 105915 (1 OMNH); NEW MEXICO: Eddy Co. / Lincoln N.F., Sitting / Bull Falls creek /

6-VIII-1987, C.B.Barr (2 EMEC); S of Artesia / New Mexico / 71/7/4 H. Brown // Catalog No. / OMNH- 105916 (1 OMNH); [as above; series of 2 with sequential catalog numbers] // Catalog No. / OMNH- 105917–105918] (2 OMNH). **TEXAS (110)**. TX: Brewster Co. / 20 mi S Alpine / 25 VI 1978 / Calamity Creek // William D. / Shepard, leg. (9 EMEC); USA, TX: Brewster Co. / Woodward Ranch / VII-26-1987 / D. J. Heffern coll (1 EMEC); TEXAS: Culberson Co. / Guadalupe Mtns. Natl. / Pk., McKittrick Creek / 4-VIII-1987, C. B. Barr (1 EMEC); N. McKittrick / Canyon TX / Guadalupe N. P. / 11 VIII 1976 // D. D. Ralston / Coll. // Catalog No. / OMNH-105889 (1 OMNH); [as above] // Catalog No. / OMNH- 105890 (1 OMNH); TX: Jeff Davis Co. / 2 mi N Ft. Davis / 4 I 1983 / Limpia Creek (WDS-A-154, on reverse) // William D. / Shepard, leg. (18 EMEC, 1 TAMU, 2 USNM); TEXAS: Jeff Davis Co. / Limpia Creek just W / jct. Hwy. 17 & 118 / 2-VI-1983 C.B. Barr (8 EMEC); TEXAS: Jeff Davis Co. / Davis Mountains St. Pk. / Limpia Cr. N of Hwy. 118 / 1.8 mi. W jct. Hwy. 17 / 23-VIII-1987, C.B.Barr (11 EMEC); TEXAS: Jeff Davis Co. / Limpia Cr. at Hwy. 17 / 2.7 mi. N Fort Davis / 23-XII-1989, C.B. Barr (13 EMEC); TX: Jeff Davis Co. / 2.7 mi N Ft. Davis / 23 XII 1989 4750' / Limpia Creek (WDS-A-676, on reverse) // William D. / Shepard, leg. (43 EMEC, 5 TAMU, 2 USNM); USA, TEXAS / Presidio County / Big Bend Ranch St. Pk. / Ojito Adentro // 16 March 1994 / D. E. Bowles (3 UMC); as above, 29 April 1994 (1 EMEC, 3 UMC); USA, TEXAS / Presidio County / Big Bend Ranch St. Pk. / Fresno Canyon // small spring nr. mine / 30 December 1995 / D. E. Bowles (1 EMEC; 2 UMC). **MEXICO (4)**. La Lecheria / Durango, Mex. / 8.70 H P Brown // Catalog No. / OMNH-105894 (1 OMNH); [as above; series of 3 with sequential catalog numbers] // Catalog No. / OMNH- 105895–105897 (3 OMNH). All paratypes also have the following final label: "PARATYPE / *Macrelmis* / *shepardi* Barr" [yellow label, printed].

Additional Material Examined (10). ARIZONA. ARIZ. YAVAPAI CO. / Roundtree Canyon / nr Bloody Basin / VI-18-74 H.P.B. // PARATYPE [deep pink label] // *Macrelmis* / *shepardi* / det. HPB // OMNH- 105908 (1 OMNH); AZ: Yavapai Co. / Montezuma Well / 80-8-8, HPB & WDS / *Macrelmis* / *shepardi* / det. HPB // Catalog No. / OMNH- 105901 (1 OMNH). **NEW MEXICO.** S of Artesia / New Mexico / 71/7/4 H. Brown // *Macrelmis* / *shepardi* / det. HPB // Catalog No. / OMNH- 105919 (1 OMNH). **TEXAS.** N. McKittrick / Canyon TX / Guadalupe N. P. / 1 VI 1977 // D. D. Ralston / Coll. // *Macrelmis* / *shepardi* / det. HPB // Catalog No. / OMNH-105891 (1 OMNH) [M genitalia missing]; USA, TEXAS / Presidio County / Big Bend Ranch St. Pk. / Cienega Creek @

house // 29 April 1996 / D. E. Bowles (5 UMC). **MEXICO.** La Lecheria, Dur., Mex. / 70/8/7 Harley P. Brown // *Macrelmis* / *shepardi* / det. HPB // Catalog No. / OMNH-105893 (1 OMNH).

Etymology. This species is named in honor of William D. Shepard, aquatic Byrrhoidea specialist and last doctoral student (1974–1980) of Harley P. Brown at the University of Oklahoma, Norman.

Distribution. *Macrelmis shepardi* has been collected in the southwestern United States in Arizona, New Mexico, and west Texas, and in northern Mexico (Fig. 2). Currently the only Mexican record is from the state of Durango, although the species should be expected to occur in the bordering states of Sonora, Chihuahua, and Coahuila.

Habitat. *Macrelmis shepardi* has been collected at elevations ranging from 1,000–2,550 m in a wide variety of lotic habitats—small rivers, streams, springs and spring runs—which often have calcium bicarbonate-rich water and exhibit varying amounts of tufa (calcium carbonate) deposition on submerged objects, including elmids (Figs. 28–29). In these watercourses, the beetles inhabit cobble and gravel substrates in the faster flow of riffles and runs. The type locality, Limpia Creek (Jeff Davis Co., TX), at an elevation about 1,450 m, is a largely intermittent stream with perennial stretches inhabited by *M. shepardi* and other elmids (Fig. 8). This stream apparently does not have high levels of carbonates, unlike many others where the species occurs.

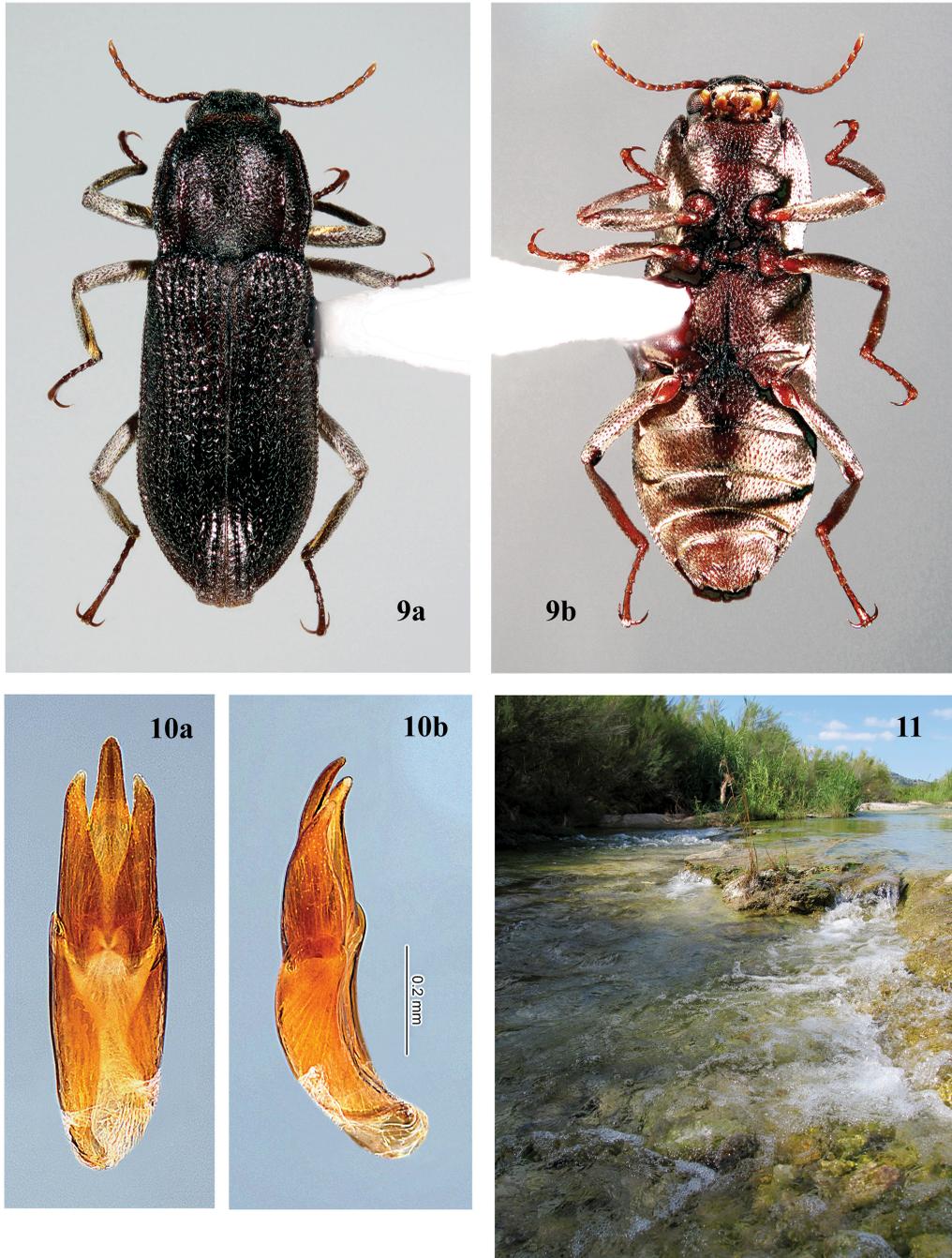
Associated Byrrhoid Taxa. *Cylloepus abnormis* (Horn, 1870), *Cylloepus parkeri* Sanderson, 1953, *Dubiraphia* sp., *Heterelmis glabra* (Horn, 1870), *Heterelmis obesa* Sharp, 1882, *Huleechius marroni* Brown, 1981, *Microcylloepus similis* (Horn, 1870), *Microcylloepus* spp., *Narpus arizonicus* (Brown, 1930), *Neocylloepus* sp., *Neoelmis caesa* (LeConte, 1874), *Neoelmis* sp., *Optioservus divergens* (LeConte, 1874), *Xenelmis sandersoni* Brown, 1985, *Zaitzevia parvula* (Elmidae); *Helichus suturalis*, *H. triangularis*, *Postelichus confluentus* (Hinton, 1935), *Postelichus immsi* (Dryopidae); *Lutrochus arizonicus* Brown and Murvosh, 1970 (Lutrochidae); *Psephenus murvoshi* Brown, 1970 (Psephenidae).

Comments. This widespread species has long been mistaken for *M. moesta*, the only *Macrelmis* previously known from Arizona (H. P. Brown, unpublished data). *Macrelmis moesta* has thus far been found only in southeastern Arizona. The two species have not been reported from the same streams.

***Macrelmis texangusta* Barr, new species**

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9830A298-D0EC-47FC-93BD-38F93D787381
(Figs. 2, 9–11)

Type Locality. Independence Creek at Independence Creek Preserve (The Nature Conservancy), N



Figs. 9–11. *Macrelmis texangusta*, new species. **9)** Habitus, size 4.32 mm long, 1.48 mm wide, a) Dorsal view, b) Ventral view; **10)** Male genitalia, a) Dorsal view, b) Lateral view; **11)** Type locality: Independence Creek at Independence Creek Preserve, Terrell Co., Texas, USA.

30.462°, W 101.771°, Terrell County, Texas, United States.

Diagnosis. The body form of *M. texangusta* (Figs. 9a–b) is distinctively slender (1.7 mm wide or less) and elongate (nearly 3× as long as wide), with legs also appearing long and slender. *Macrelmis texana* (Figs. 19a–b), which often co-occurs, is less slender (2.5× as long as wide) and has a very protuberant scutellar shield, whereas that of *M. texangusta* is barely so. *Macrelmis harleyi* (Figs. 3a–b) and *M. shepardi* (Figs. 6a–c) are likewise more robust (1.8–2.4 mm wide) and about 2.5× as long as wide, and have pronotal lateral margins moderately to strongly arcuate; *M. texangusta* has pronotal lateral margins which vary from weakly arcuate to nearly parallel-sided. *Macrelmis mexicana* (Figs. 12a–b) has pronotal sublateral carinae that can be either very weak or not present, whereas those of *M. texangusta* are prominent. The male genitalia of *M. texangusta* (Figs. 10a–b) are distinctive, with the penis gradually narrowed at the apical 1/3; in *M. moesta* (Figs. 16a–b) the penis is abruptly narrowed at the apical 1/3; *M. shoemakei* (Figs. 18a–b) has a narrowly spatulate penis; *M. texana* (Figs. 20a–b) has a broad penis nearly subparallel at the apical 1/3. *Macrelmis texangusta* keys to *Elsianus striatus* (= *Macrelmis striata*) in Hinton's (1940) key to the Mexican species, but the body form and male genitalia (Fig. 26) differ.

Description. Holotype male. Cuticle mostly red-brown, shiny; head darker; antennae, palpi, legs lighter; covered with short, pale, recumbent setae; body elongate, slender, nearly 3× as long as wide, nearly parallel-sided, widest at posterior 1/3 adjacent to abdominal ventrite 2 (Figs. 9a–b); size 4.04 mm long, 1.44 mm wide. **Head:** Mostly black, moderately granulate with sparse, short, recumbent, pale yellow setae; gena with plastron; vertex with very shallow U-shaped impression, opening anteriorly, extending from above eyes toward occiput, vertex convex anteriorly and posteriorly to impression; frontoclypeal suture weakly emarginate. Antenna yellow-brown, mostly glabrous; antennomeres 1–10 cone-shaped, antennomere 11 elongate-ovoid; antennomeres 1 and 11 longest, subequal, antennomere 1 finely setose, antennomere 2 shorter, antennomeres 3–4 shortest, subequal, antennomeres 5–6 longer, antennomeres 7–10 longer than 6, subequal; antennomeres 6–10 each with tuft of dense setae at ventral apex, antennomere 11 with apical band of dense setae. Clypeus black; convex; moderately setose; granulate at lateral 1/4; anterior margin emarginate, lateral margins weakly rounded. Labrum black except central anterior margin red-brown; convex; anterior margin barely emarginate; disc with fine, pale yellow, recumbent setae; lateral margins and anterior margin laterad of median 1/3 with longer, dense, pale yellow setae.

Maxillary palpus yellow; palpomere 4 slightly flattened, elongate-ovoid, apex rounded. Labial palpus yellow, palpomere 3 slightly flattened, broadly ovoid. **Pronotum:** Red-brown, moderately flat; length 1.12 mm, width 1.20 mm, widest between 1/3–1/2 distance from base; lateral pronotal carinae narrowly marginate, granulate with a single row of granules, each margin bordered medially by a shallow sulcus from anterior to posterior angle. Anterior margin weakly arcuate; anterior angle acute, sharp; lateral margin weakly arcuate; posterior angle nearly obtuse, sharp; posterior margin trisinate. Disc moderately setose with short, recumbent, pale yellow setae; anterior 1/2 with shallow, faint punctures; posterior 1/2 indistinctly punctate and granulate, basal area just anterior to scutellar shield with cluster of large, prominent granules; lateral margins with medium-sized granules spaced about 1 diameter apart. Disc medially with weak transverse impression; laterally with two low, broadly rounded, granulate, weakly sinuate sublateral carinae extending from base to anterior 1/5; each with medial margin acute, each bounded by weakly sinuate, shiny, glabrous, longitudinal sulcus, basal 1/2 wide, apical 1/2 narrower; two small, round, shallow prescutellar depressions present; band of minute, plastron-like setae extending anteriorly from between prescutellar depressions to transverse impression. Scutellar shield red-brown, barely protuberant, subovate, granulate, setose with typical setae and minute plastron-like setae. **Elytron:** Red-brown; length 2.92 mm, width 0.72 mm. In lateral view, anterior margin weakly depressed, anterior 2/3 flat, posterior 1/3 angled ventrally, flat to apex. Humeral angle obtuse; lateral margin narrow, bordered medially by a narrow sulcus; apex produced, posterior margin slightly oblique. Disc striate and punctate; punctures moderately large and deep; striae distinct but shallow; intervals weakly convex, nearly flat near apex, interval 7 swollen at humerus. Disc with moderately sparse, short, recumbent, pale yellow setae; granulate at humerus, lateral margin (single row), adjacent sulcus. Epipleuron with plastron; granules elongate, variably spaced. **Venter:** Cuticle red-brown, surface mostly covered with a thin layer of silvery plastron; elongate granules emergent from plastron, variably spaced, aligned in curvilinear patterns; very short, recumbent, pale yellow setae between granules; plastron lacking (possibly abraded) from entire mesoventrite, median 1/4–1/3 of prosternum, metaventrite and abdominal ventrite 1 between and posterior to metacoxae, abdominal ventrite 2 at midline; granules appearing larger, coarser where plastron absent. Prosternum with anterior margin barely arcuate, disc with shallow transverse depression at middle; prosternal process less than 2× as long as wide, slightly narrowed

between procoxae, lateral margins elevated and thick, enclosing a longitudinal, broad sulcus, apex broadly triangular with blunt tip. Mesoventrite with deep mesoventral cavity bounded by two low ridges at anterior 1/2; posterior margin raised; mesepimeron and mesanepisternum each with dense patch of pale yellow setae. Metaventrite with anterior margin sulcate; disc nearly flat. Abdomen with ventrites 1–4 becoming shorter posteriorly, ventrite 5 nearly as long as ventrite 1 at midline; ventrites nearly flat, sutures shallowly incised; ventrite 1 with disc shallowly excavate at about middle 1/5 for entire length, deepest between metacoxae, posterolateral angles broadly rounded; ventrite 2 weakly depressed at middle of anterior margin, posterolateral angles broadly rounded; ventrites 3–5 with posterolateral angles bearing dorsally curved lobes which clasp epipleural margin; ventrite 5 deeply depressed along anterior margin, weakly convex posteriorly; posterior margin densely setose, arcuate at middle 1/2, bordered on each side by a wide, deep notch (about 1/4 length of ventrite) forming a lateral, large, subtriangular lobe with dorsally curved tip clasping epipleural margin. **Legs:** All very slender and long; fore leg shortest, hind leg longest; each leg with femur distinctly shorter than tibia, tarsus shortest. Coxae granulate. Femora and tibiae covered with thin layer of silvery plastron; elongate granules spaced 1.0–1.5 diameters apart; femora with sparse, short, pale yellow setae; tibiae with numerous, short, pale yellow setae, cleaning fringe formula 1-2-1. Tarsi red-brown, without plastron. Procoxa lacking plastron, lateral surface with dense patch of long, golden-yellow setae; profemur with longitudinal band of long, dense, adpressed, golden-yellow setae on anterior surface from base to apical 3/4; protibia with longitudinal band of long, dense, golden-yellow setae (cleaning fringe) on anterior surface from near base to apex, apicoventral margin with pair of tibial spurs; protarsus with tarsomeres 1–4 of similar shape and size except tarsomere 1 shorter, each with several short, stout setae at apicoventral margin, tarsomere 5 distinctly longer than 1–4 combined, sparsely setose, ventral apex produced between claws; protarsal claws simple. Mesocoxa similar to procoxa; mesofemur with wide band of adpressed, golden-yellow setae on posterior surface from base to apical 1/2; mesotibia straight, with two cleaning fringes, on anterior surface at apical 1/2–2/3 and on posterior surface from base to apex, apicoventral margin with pair of tibial spurs; mesotarsus similar to protarsus; mesotarsal claws simple. Metacoxa with plastron laterally, dense, pale yellow setae on posterior surface; metafemur without band of long setae on posterior surface; metatibia weakly arcuate in dorsal view, with cleaning fringe on posterior surface from near base

to apex, apicoventral margin with pair of tibial spurs; metatarsus similar to protarsus and mesotarsus; metatarsal claws simple. **Genitalia:** Elongate, about 4× as long as wide; moderately sclerotized (Figs. 10a–b). Phallobase much longer than parameres; parameres shorter than penis. In dorsal view (Fig. 10a), parameres with lateral margins subparallel then preapically angulate, inner margins at apical 2/3 nearly straight, apices barely acute; penis with lateral margins subparallel at basal 2/3 except for a small constriction at 1/3, then tapered to rounded apex, apical 1/3 more strongly sclerotized than basal 2/3; penis at base slightly wider than paramere base, at apex slightly wider than paramere apex. In lateral view (Fig. 10b), phallobase ventral margin strongly arcuate; paramere narrowly triangular with ventral margin sinuate, apical 1/4 narrowed and weakly bent ventrally, apex rounded; penis slender at apical 1/3, projecting above and beyond paramere, apex narrowly rounded.

Variation. The cuticle color varies between individuals from black to dark brown on the head, and from dark brown to red-brown on the pronotum and elytra. The pronotum is usually wider than long but in some it is almost quadrate; the lateral margins can be either evenly arcuate or arcuate posteriorly and nearly straight at the anterior 1/2–1/3. The tarsal claws are unusually variable, particularly in specimens from the Devils River, ranging from very small and thick to moderately large and slender. In most cases it is the front claws that are reduced in size, while the other two pairs are of more normal size. Males and females are of similar size: males 3.80–4.76 mm long, 1.40–1.72 mm wide ($n = 14$); females 3.84–4.52 mm long, 1.36–1.68 mm wide ($n = 16$). No external sexual differences were noted.

Type Material. Holotype male. TEXAS. TEXAS: Terrell County / Independence Creek at / Independence Creek / Preserve (TNC) / 5-XI-2013, C. B. Barr // HOLOTYPE / Macrelmis / texangusta / Barr [red label, handwritten] // EMEC49612 (EMEC). **Paratypes (64). TEXAS.** TEXAS: Bandera Co. / Lost Maples St. Nat. / Area, Sabinal River / 2-VIII-1987, C. B. Barr (1 EMEC); TEXAS: Kimble Co. / Junction, TTUC, S Llano / River, 4-6 July 1986 / R. S. Zack, collector (1 OMNH); TEXAS: Kimble Co. / South Llano River / Junction-TTU Cntr / 10 April 1988 / coll: R. W. Sites (1 UMC); TEXAS: Kimble Co. / TTU Ctr- Junction / South Llano Riv. / 14 June 1988 / coll: R. W. Sites (1 UMC); as above, 5 August 1988 (3 UMC); TEXAS: Kimble Co. / Junction-TTU Ctr / South Llano Riv. / 13 November 1988 / coll: R. W. Sites (1 UMC); TX: Real/Edwards Co. / Nueces River at Hwy. / 55 S of Barksdale / 1-VI-1983 C.B.Barr (1 EMEC); TEXAS: Terrell County / Independence Creek / Preserve / Springs, 19-V-2007, 616m / 30.4690°, 101.8035°, / J. R. Gibson &

J. Denton (2 EMEC, 1 TAMU, 1 USNM); TEXAS: Terrell County / Independence Creek / Preserve (TNC), Caroline / Springs, elev. 616m / 30.4690°, 101.8035°, / 22-VI-2007, J. R. Gibson (2 EMEC); Texas: Terrell County / Independence Creek / Preserve (TNC), Caroline / Springs, 616m / 30.4690°, 101.8035° / 26-X-2007, C. B. Barr (2 EMEC); TEXAS: Terrell County / Independence Creek / Preserve (TNC) / Independence Creek / 22-X-2007, C. B. Barr (2 EMEC); TEXAS: Terrell County / Independence Creek at / Independence Creek / Preserve (TNC) / 5-XI-2013, C. B. Barr (2 EMEC); TEXAS: Terrell County / Independence Creek / below Hwy. 349 bridge / 5-XI-2013, C. B. Barr (5 EMEC, 1 TAMU); TX: Uvalde Co. / 12 mi S Sabinal / 26 April 2001 / Frio River // Gil L. / Challet, leg. (2 EMEC); TEXAS: Uvalde Co. / Nueces River / 16 miles S Montell / 8 December 1989 (4 UMC); TX: Val Verde Co. / 21 mi N Comstock / 24 VI 1978 / Devil's River // William D. / Shepard, leg. (2 EMEC, 1 USNM); TX: Val Verde Co. / 20 mi N Comstock / 3 I 1983 / Devil's River (WDS-A-152, on reverse) // William D. / Shepard, leg. (1 EMEC); TEXAS: Val Verde Co. / Devils R. at Hwy. 163 / 21 mi. N of Comstock / 31-III-1985, C. B. Barr (2 EMEC, 2 TAMU); TEXAS: Val Verde Co. / 18 mi. S. Juno / Devil's River / 6 August 1988 / coll: R. W. Sites (5 UMC); TEXAS: Val Verde Co. / Devils River at Bakers / Crossing, Hwy. 163 / 21 mi. N Comstock / 23-VIII-1992, C. B. Barr (6 EMEC); Devil's River / Comstock, Texas / 72/3/21 HPBrown // Catalog No. / OMNH- 105962 (1 OMNH); [as above; series of 7 with sequential catalog numbers] // Catalog No. / OMNH- 105963–105969 (7 OMNH); as above, 72/3/22, OMNH-105971 (1 OMNH); TEXAS: Val Verde Co. / Dolan Falls Preserve / (TNC), Devils River / Blue Spring outflow / 11-IX-2008, J.R. Gibson (1 EMEC). **MEXICO.** El Carino / Coah. Mex. / 70/8/ 17 HPB // Catalog No. / OMNH- 105960 (1 OMNH); El Carino / Coah. Mex. / 8.70 H P Brown // Catalog No. / OMNH- 105959 (1 OMNH). All paratypes also have the following final label: "PARATYPE / *Macrelmis* / *texangusta* Barr" [yellow label, printed].

Etymology. The specific name, "*texangusta*", is a combination of "*tex*" from "Texas" plus "*angustus*" from the Latin word meaning "narrow, slender, thin", an apt descriptor of the body form.

Distribution. *Macrelmis texangusta* is known only from a moderately small area of southwestern Texas, USA, including the counties of Bandera, Edwards, Kimble, Real, Terrell, Uvalde, and Val Verde, and from the adjacent state of Coahuila, Mexico (Fig. 2).

Habitat. *Macrelmis texangusta* has been collected from various-sized waterbodies, small streams to small rivers, with shallow cobble/gravel riffles. Many, if not most, of these have waters rich in calcium bicarbonate resulting in deposition of

tufa on the bottom substrate and submerged objects. Elevations at these localities range from about 200–650 m. At the type locality of Independence Creek at Independence Creek Preserve (Fig. 11), a large stream with a wide, exposed floodplain at about 600 m elevation, *M. texangusta* inhabits shallow riffles of limestone cobbles, gravel and tufa deposits along with *M. texana*. Nearby Caroline Springs is a small group of perennial, artesian springs fed by a deep groundwater upwelling with a discharge of 227–379 L/s (3,000–5,000 gal/min). *Macrelmis texangusta* is common in the spring headwaters under rocks (J. R. Gibson, *in litt.*). The discharge from the springs comprises about 25% of the flow of Independence Creek.

Associated Byrrhoid Taxa. *Hexacyclopeus ferrugineus* (Horn, 1870), *Macrelmis texana*, *Microcyclopeus* spp., *Neocyclopeus boeseli* Brown, 1970, *Stenelmis cheryl* Brown, 1987 (Elmidae); *Lutrochus luteus* LeConte, 1852 (Lutrochidae); *Psephenus texanus* Brown and Arrington, 1967 (Psephenidae).

***Macrelmis mexicana* Barr, new species**

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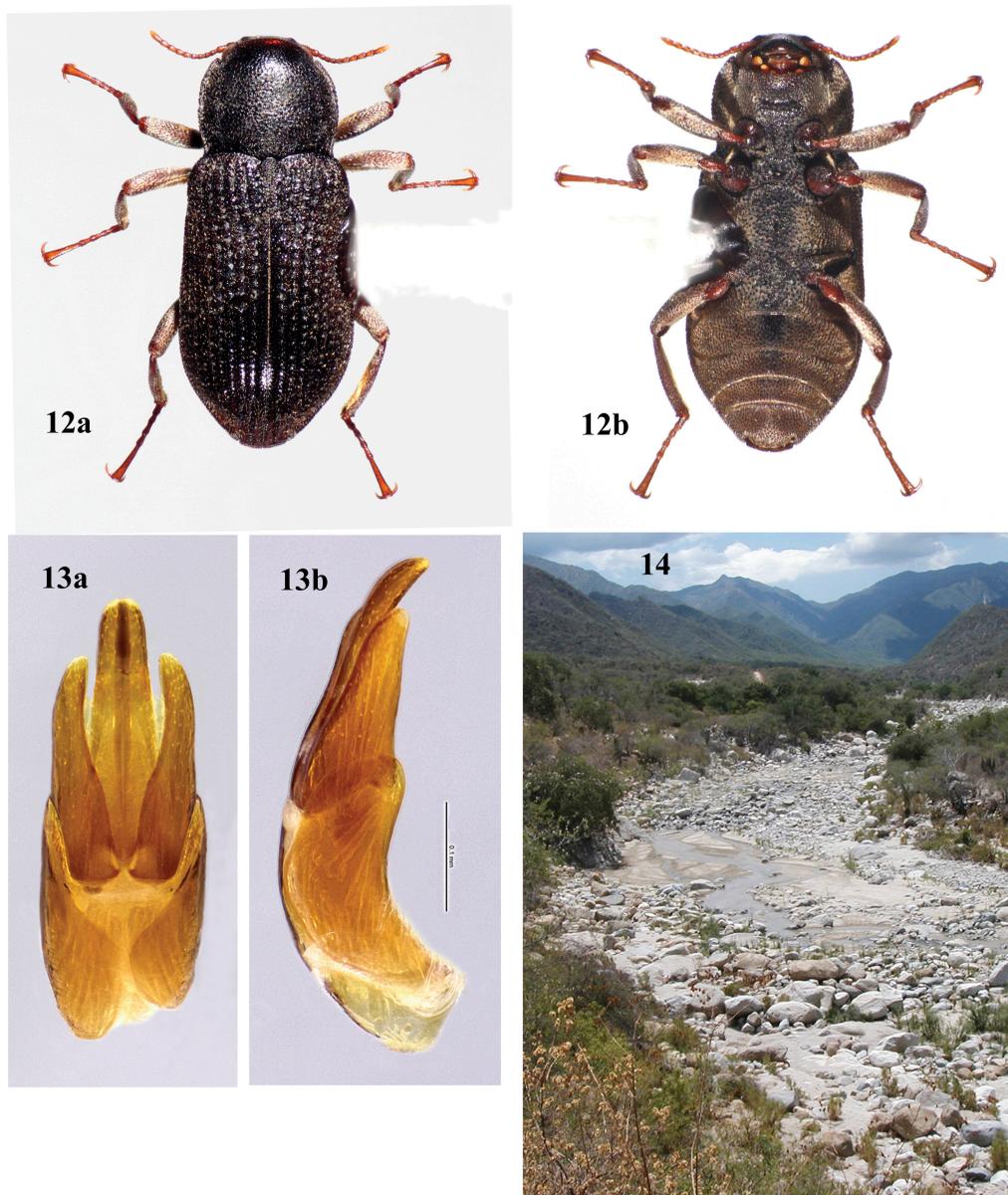
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(Figs. 2, 12–14)

Type Locality. Arroyo San Dionisio SW of Santiago, N 23.579°, W 109.866°, Sierra de la Laguna, Baja California Sur, Mexico.

Diagnosis. *Macrelmis mexicana* (Figs. 12a–b) can be distinguished from all but one of the currently known species occurring in Mexico and the United States by having pronotal sublateral carinae that are obscure or lacking. *Macrelmis leonilae* from southern Mexico and Central America also lacks pronotal sublateral carinae, but the two species differ in the morphology of the male genitalia: in *M. leonilae* (Fig. 23) the parameres are curved inward at the tips, which are about as wide as the apex of the penis; in *M. mexicana* (Figs. 13a–b) the parameres are straight at the tips, which are narrower than the apex of the penis. *Macrelmis mexicana* keys to *Elsianus striatus* (= *Macrelmis striata*) in Hinton's (1940) key to the Mexican species, but the male genitalia (Fig. 26) are dissimilar and the latter species has distinct pronotal carinae.

Description. Holotype male. Cuticle black, shiny; antennae, palpi, legs lighter; covered with short, pale, recumbent setae; body elongate, about 2.5× as long as wide, nearly parallel-sided, widest at posterior 1/3 adjacent to abdominal ventrite 2 (Figs. 12a–b); size 3.68 mm long, 1.48 mm wide. **Head:** Black, moderately granulate with sparse, short, recumbent, pale yellow setae; gena with plastron; frontoclypeal suture emarginate. Antenna yellow-brown, mostly glabrous; antennomeres 1–10 cone-shaped, antennomere 11 elongate-ovoid; antennomeres 1 and



Figs. 12–14. *Macrelmis mexicana*, new species. **12)** Habitus, size 3.68 mm long, 1.48 mm wide, a) Dorsal view, b) Ventral view; **13)** Male genitalia, a) Dorsal view, b) Lateral view; **14)** Type locality: Arroyo San Dionisio, Sierra de la Laguna Baja California Sur, Mexico.

11 longest, subequal, antennomere 1 setose, antennomere 2 shorter, antennomeres 3–6 shortest, subequal, antennomeres 7–10 longer, each with tuft of dense setae at ventral apex, antennomere 11 with apical band of dense setae. Clypeus black; convex; moderately setose and granulate; anterior margin emarginate, lateral margins broadly rounded. Labrum black except central anterior margin brown; convex;

anterior margin slightly emarginate; disc with sparse, fine, pale yellow, recumbent setae; lateral margins with longer, dense, pale yellow setae. Maxillary palpus yellow, palpomere 4 slightly flattened, elongate-ovoid, apex subtruncate. Labial palpus yellow, palpomere 3 slightly flattened, ovoid, apex subtruncate. **Pronotum:** Black, convex; length 1.08 mm, width 1.16 mm, widest at middle; lateral

pronotal carinae marginate, granulate with small, crowded granules, each margin bordered medially by a broad sulcus. Anterior margin weakly arcuate; anterior angle acute, sharp; lateral margin arcuate; posterior angle nearly right-angled; posterior margin trisinate. Disc sparsely setose with short, recumbent, pale yellow setae; densely granulate with large granules spaced about 1 diameter apart. Disc laterally with a pair of nearly obscure, narrow, low, straight sublateral carinae at basal 1/3; two faint, shallow prescutellar foveae present. Scutellar shield black, barely protuberant, oval, granulate. **Elytron:** Black; length 2.60 mm, width 0.74 mm. In lateral view, anterior 2/3 flat, posterior 1/3 convex and curved ventrally. Humeral angle obtuse, almost rounded; lateral margin bordered medially by a shallow sulcus, wider anteriorly; apex produced, posterior margin arcuate. Disc striate and punctate; punctures large and deep at anterior 2/3, at posterior 1/3 becoming smaller, shallower, more closely spaced, especially medially; intervals slightly convex. Disc with moderately sparse, short, recumbent, pale yellow setae; with large granules at basal 1/3, lateral margin, adjacent sulcus. Epipleuron with plastron; granules round or elongate, spaced about 0.5–1.0 diameter apart. **Venter:** Cuticle black, surface mostly covered with a thin layer of silvery plastron; variably spaced, elongate granules emergent from plastron, aligned in curvilinear patterns; sparse, short, recumbent, pale yellow setae between granules; plastron mostly lacking (possibly abraded) from entire mesoventrite, median 1/4–1/3 of prosternum, metaventrite and abdominal ventrite 1 between and posterior to metacoxae, midline of abdominal ventrites 2–3; granules appearing larger, coarser where plastron absent. Prosternum with anterior margin slightly emarginate; disc with broad, moderately deep, transverse sulcus at middle; prosternal process about 1.5× as long as wide, nearly parallel-sided, lateral margins elevated and thick, enclosing a longitudinal, broad sulcus, apex broadly rounded. Mesoventrite with deep mesoventral cavity bounded by two prominent ridges at anterior 1/2; mesepimeron and mesanepisternum each with dense patch of pale yellow setae. Meta-ventrite with anterior margin deeply sulcate; disc shallowly concave. Abdomen with ventrites 1–4 becoming shorter posteriorly, ventrite 5 shorter than ventrite 1 at midline; ventrites convex laterad to midline, sutures incised; ventrite 1 with disc deeply excavate at about middle 1/5 for entire length, deepest between metacoxae, posterolateral angles broadly rounded; ventrite 2 with disc slightly depressed at middle of anterior margin, posterolateral angles broadly rounded; ventrites 3–5 with posterolateral angles bearing dorsally curved lobes which clasp epipleural margin; ventrite 5 deeply depressed along anterior margin, weakly convex posteriorly; posterior margin with short, dense setae,

arcuate at middle 1/2, bordered on each side by a wide, deep notch (about 1/4 length of ventrite) forming a lateral, large, subtriangular lobe with dorsally curved tip clasping epipleural margin. **Legs:** Fore leg shortest, hind leg longest; each leg with femur shorter than tibia, tarsus shortest. Coxae granulate. Femora and tibiae covered with thin layer of silvery plastron over red-brown cuticle; femora with sparse, short, pale yellow setae and flat, round to slightly elongate granules, variably spaced <1.0–1.5 diameters apart; tibiae with numerous, short, pale yellow setae and slightly protuberant, round to elongate granules spaced 1.0–1.5 diameters apart, cleaning fringe formula 1-2-1. Tarsi yellow-brown, without plastron. Procoxa lacking plastron, lateral surface with dense patch of long, golden-yellow setae; profemur with longitudinal band of moderately long, dense, adpressed golden-yellow setae on anterior surface from base to apical 1/4; protibia slightly arcuate, with longitudinal band of long, dense, golden-yellow setae (cleaning fringe) on anterior surface from near base to near apex, apicoventral margin with pair of tibial spurs; protarsus with tarsomeres 1–4 of similar size and shape, each with a few short, stout setae at apicoventral margin, tarsomere 5 distinctly longer than 1–4 combined, sparsely setose, ventral apex produced between claws; protarsal claws simple. Mesocoxa similar to procoxa; mesofemur with wide band of adpressed, golden-yellow setae on posterior surface from base to apical 1/2–2/3; mesotibia weakly arcuate, with two cleaning fringes, on anterior surface at apical 1/2 and on posterior surface from base to near apex, apicoventral margin with pair of tibial spurs; mesotarsus similar to protarsus; mesotarsal claws simple. Metacoxa with plastron laterally, dense, pale yellow setae on posterior surface; metafemur without band of long setae on posterior surface; metatibia weakly arcuate in dorsal view, with cleaning fringe on posterior surface from near base to near apex, apicoventral margin with pair of tibial spurs; metatarsus similar to protarsus and mesotarsus; metatarsal claws simple. **Genitalia:** Elongate, about 3× as long as wide; moderately sclerotized (Figs. 13a–b). Phallobase much longer than parameres; parameres distinctly shorter than penis. In dorsal view (Fig. 13a), parameres with lateral margins subparallel to apical 1/3 then curved inward, inner margins sinuate, apices rounded; penis with lateral margins subparallel except at base, wider than paramere width at apical 1/2, apex bluntly rounded, apical 1/3 more strongly sclerotized than basal 2/3. In lateral view (Fig. 13b), phallobase ventral margin strongly arcuate; paramere evenly tapered to broadly rounded apex, dorsal and ventral margins barely sinuate; penis flattened, with apex narrowly rounded and slightly curved ventrally.

Variation. Most noteworthy is the presence of very low pronotal sublateral carinae in some individuals, whereas others have barely discernible carinae or apparently none at all. Some of the

specimens examined are lighter-colored, red-brown, and very clean, indicating that they were perhaps teneral and had not been in the water long. On these specimens some cuticular features were more visible (*i.e.*, pronotal sublateral carinae) and less worn (*i.e.*, elytral granulation). Only one of the specimens from Sonora was a male with undamaged genitalia. The penis of that specimen was noticeably longer and slightly more slender than those of specimens from Baja California. It was otherwise quite similar, but nonetheless it was not designated as a paratype. Males are a little smaller than females: males 3.32–4.00 mm long, 1.44–1.68 mm wide ($n = 15$); females 3.60–4.20 mm long, 1.36–1.72 mm wide ($n = 11$). No external sexual differences were noted.

Type Material. Holotype male. MEXICO: Baja California / Sur, Arroyo San Dionisio / ca. 12 mi. SW Santiago / 17-VII-2004, C. B. Barr // Sierra de la Laguna / Rancho San Dionisio / 23°34.75' N / 109°52.00' W / elevation 1400 ft. // HOLOTYPE / *Macrelmis / mexicana* / Barr [red label, handwritten] (UNAM). **Paratypes (97).** MEXICO: BAJA CALIF. [SUR] / Agua Caliente / Rio Chorro / 73/7/29 H.P. Brown (3 OMNH); MEX: BAJA CALIF. [SUR] / w. Santiago / VI-8-74 H. Brown (3 OMNH); MEX: BAJA CALIF. [SUR] / 7 mi s Santiago / VI-9-74 H.P. Brown (3 OMNH); MEX: BAJA CALIF. SUR / Arroyo Agua Caliente / 3 mi. e Ejido Agua / Caliente 1978/VI/4 / C. Murvosh & R.K. Allen (6 OMNH); MX: B.C. Sur / Agua Caliente / 78-VI-4 CM & RA (1 OMNH); MEXICO: Baja Cal Sur / 3 mi W Agua Caliente / 22 VI 1997 / Rio Agua Caliente (WDS-A-1259, on reverse) // William D. / Shepard, leg. (5 EMEC, 1 UNAM); MEXICO: Baja California / Sur, Arroyo Agua Caliente / ca. 8 mi. SW Santiago / 2 mi. W Agua Caliente / 12-VII-2004, C. B. Barr // Sierra de la Laguna / 23°26.38' N / 109°48.51' W / elevation 660 ft. (3 EMEC, 1 UNAM); MEXICO: Baja Calif. Sur / 8 mi SW Santiago / 12 VII 2004 / Rio Agua Caliente (WDS-A-1595, on reverse) // William D. / Shepard, leg. (2 EMEC); MEXICO: Baja California / Sur, Arroyo San Dionisio / ca. 12 mi. SW Santiago / 17-VII-2004, C. B. Barr // Sierra de la Laguna / Rancho San Dionisio / 23°34.75' N / 109°52.00' W / elevation 1400 ft. (6 EMEC, 2 UNAM, 2 USNM); MEXICO: Baja Calif. Sur / 12 mi WSW Santiago / 17 VII 2004 1400 ft / Arroyo San Dionisio (WDS-A-1596, on reverse) // William D. / Shepard, leg. (4 EMEC, 2 UNAM, 2 USNM); MEX: BAJA CALIF. [SUR] / w. of Santiago / Presa San Jorge / 73/7/29 H.P. Brown (5 OMNH); MEXICO: Baja California / Sur, Arroyo San Jorge / 1.3 mi. W San Jorge / ca. 7.5 mi. W Santiago / 17-VII-2004, C. B. Barr // Sierra de la Laguna / Rancho Santa Rita / 23°28.90' N / 109°47.81' W / elevation 900 ft. (6 EMEC, 2 UNAM, 2 USNM); MEXICO: Baja Calif. Sur / 7 mi W Santiago / 17 VII 2004 900 ft / Arroyo San Jorge

(WDS-A-1597, on reverse) // William D. / Shepard, leg. (4 EMEC, 2 UNAM, 2 USNM); MEXICO: Baja California / Sur, Arroyo Las Parras / at Cuevas Pintas Area / ca. 9 rd. mi. W of Loreto / 10-VII-2004, C. B. Barr // Sierra de la Giganta / 25°58.49' N / 111°27.97' W / elevation 750 ft. (8 EMEC, 2 UNAM); as above, 20-VII-2004 (5 EMEC); MEXICO: Baja Calif. Sur / 9 mi WSW Loreto / 10 VII 2004 680 ft / Arroyo Las Parras (WDS-A-1594, on reverse) // William D. / Shepard, leg. (6 EMEC); as above, 20 VII 2004 (WDS-A-1601, on reverse) (2 EMEC, 2 UNAM); MEXICO: Baja Calif. Sur / 1.6 mi S San Javier / 20 VII 2004 1180 ft / Arroyo San Javier (WDS-A-1598, on reverse) // William D. / Shepard, leg. (2 EMEC, 1 UNAM). All paratypes also have the following final label: "PARATYPE / *Macrelmis / mexicana* Barr" [yellow label, printed].

Additional Material Examined (8). MEX: BAJA CALIF. [SUR] / Presa Agua Caliente / 7 mi. s. Santiago / VI-9-74 H.P. Brown (2 OMNH); MEXICO: SONORA / Rio Chucujaqui / 5 mi. e Alamos / VI-11-74 HPB (6 OMNH).

Etymology. This species is named for its country of origin, Mexico.

Distribution. Northwestern Mexico, in particular, the states of Baja California Sur and Sonora bordering the Gulf of California (Sea of Cortez) (Fig. 2).

Habitat. *Macrelmis mexicana* has been collected by the author and William D. Shepard in the Sierra de la Giganta and the Sierra de la Laguna, Baja California Sur (Fig. 2) at elevations ranging from 200–430 m, where it was found in riffles and runs amid sandy gravel and cobbles. The streams are similar in that they are all located in canyons of variable size and are mostly exposed and unshaded. The water has high levels of calcium bicarbonate as evidenced by a white, powdery coating on the rocks. The specimens were collected from riffles, between pools, with substrate compositions of bedrock, boulders, cobbles, gravel and sand. In July the water was clear and very warm at all of the sites. Arroyo San Dionisio (Fig. 14), the type locality, is situated in a wide canyon in the Sierra de la Laguna. Although rather low gradient, it had moderate flow over a mostly sandy substrate with some gravel and cobbles in the riffles and scattered boulders in the streambed.

Associated Byrrhoid Taxa. *Cylloepus abnormis*, *Heterelmis obscura* Sharp, 1882, *Huleechius marroni*, *Microcylloepus inaequalis* (Sharp, 1882), *Neelmis* sp. (Elmidae); *Helichus suturalis*, *Postelichus propinquus* (Hinton, 1935) (Dryopidae); *Psephenus haldemani* Horn, 1870 (Psephenidae).

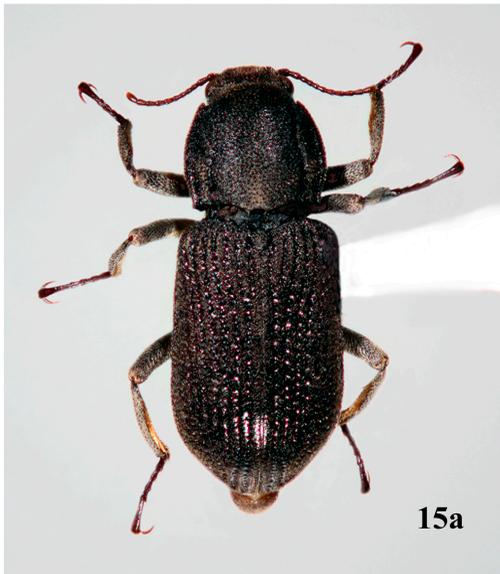
Comments. Sampling of the streams in Baja California to the north of the Desierto de Vizcaíno,

including in the Sierra de San Pedro Mártir, has failed to yield *M. mexicana*.

***Macrelmis moesta* (Horn, 1870)**
(Figs. 1, 15–16)

Macrelmis moesta was described as *Elsianus moestus* by Horn (1870) from a unique female specimen (H. P. Brown, unpublished data) from the San Pedro River, Cochise County, Arizona. The

male genitalia of the species are described and illustrated (Figs. 16a–b) herein for the first time. For the past 150 years *M. moesta* has been the only species recorded for Arizona, and the more widespread, formerly undescribed species *M. shepardi* has been confused with it (H. P. Brown, unpublished data). Arizona records from Gila and Yavapai counties attributed to *M. moesta* by Brown (1971) are actually of *M. shepardi*. *Macrelmis moesta* is known only from a few localities in far southeastern Arizona



Figs. 15–16. *Macrelmis moesta*. 15) Habitus, size 3.96 mm long, 1.52 mm wide, a) Dorsal view, b) Ventral view; 16) Male genitalia, a) Dorsal view, b) Lateral view.

(Gila/Graham counties, San Carlos River; Greenlee County, Blue River and tributary Pigeon Creek; Pinal County, Aravaipa Canyon; Pima County, Sabino Canyon; Cochise County, Cave Creek), but it likely also occurs in the adjacent state of Sonora, Mexico. *Macrelmis moesta* has not been found to occur in the same streams as *M. shepardi*, but one specimen has been examined from the type locality of *M. harleyi* in Cochise County (Fig. 5).

Diagnosis. *Macrelmis moesta* (Figs. 15a–b) is rather small, 3.4–4.16 mm long and 1.4–1.6 mm wide. It externally resembles and is close in size to *M. shoemakei* (Figs. 17a–b), but *M. moesta* is more densely granulate and the male genitalia are very different: in *M. moesta* (Figs. 16a–b) the penis is a little bit longer than the parameres and abruptly narrowed at the apical 1/3; in *M. shoemakei* (Figs. 18a–b) the penis is much longer than the parameres and narrowly spatulate. *Macrelmis mexicana* (Figs. 12a–b) is also of similar size, but the pronotal sublateral carinae are obscure or lacking (prominent in *M. moesta*), and in the males, the penis (Figs. 13a–b) is nearly parallel-sided and not abruptly narrowed towards the apex. *Macrelmis harleyi* (Figs. 3a–b) and *M. shepardi* (Figs. 6a–c), which like *M. moesta* also occur in Arizona, are both much larger, over 4.2 mm long and 1.8 mm wide, and the males have different genitalia (Figs. 4a–b, 7a–b). The male genitalia of *M. moesta* (Figs. 16a–b) somewhat resemble those of *M. texangusta* (Figs. 10a–b), but the parameres are narrower and the penis is wider at the tip.

Description. Male genitalia: Elongate, about 3× as long as wide; well sclerotized. Phallobase much longer than parameres; parameres a little shorter than penis (Figs. 16a–b). In dorsal view (Fig. 16a), parameres with lateral margins nearly parallel at basal 2/3, inner margins sinuate, apices rounded and weakly curved inward; penis wide at basal 2/3, abruptly narrowed at apical 1/3 with lateral margins nearly parallel, apex rounded to broadly rounded; penis at base much wider than paramere base, at apical 1/3 wider than paramere apical 1/3. In lateral view (Fig. 16b), phallobase ventral margin strongly arcuate; paramere with ventral margin moderately arcuate, variably narrowed at apical 1/4, apex bluntly rounded; penis with apex narrowly rounded and slightly curved ventrally.

***Macrelmis shoemakei* (Brown, 1971)**

(Figs. 1, 17–18)

Macrelmis shoemakei was described by Brown (1971) as *Elsianus shoemakei* from San Felipe Creek, Val Verde County, Texas, and the adjoining state of Coahuila, Mexico. The OMNH Recent Invertebrates Database contains additional records of specimens determined by Brown (1971) from the Mexican states

of Morelos, Nuevo Leon, San Luis Potosí, and Tamaulipas, and the species has also been reported from the state of Puebla by Curiel and Morrone (2012). In the United States, it is known only from the type locality, where it co-occurs with *M. texana*.

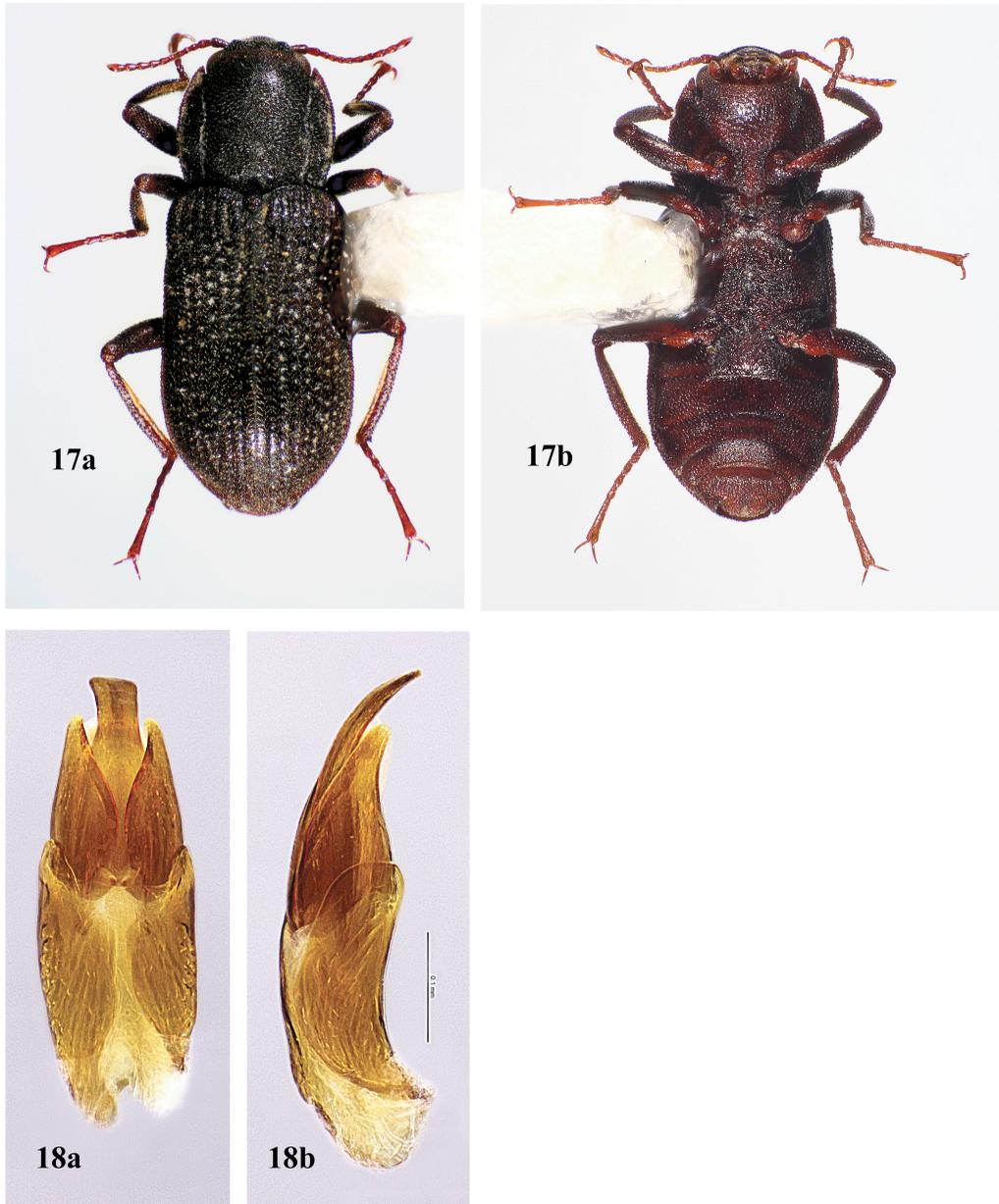
Diagnosis. *Macrelmis shoemakei* (Figs. 17a–b) is a small species, 3.1–3.8 mm long and 1.2–1.5 mm wide (Brown 1971). *Macrelmis moesta* (Figs. 15a–b) overlaps in size (3.4–3.9 mm long, 1.4–1.6 mm wide), but *M. shoemakei* is less densely granulate and the male genitalia are very different: in *M. shoemakei* (Figs. 18a–b) the penis is narrowly spatulate and much longer than the parameres; in *M. moesta* (Figs. 16a–b) the penis is abruptly narrowed at the apical 1/3 and only slightly longer than the parameres. *Macrelmis mexicana* (Figs. 12a–b), which is about the same size or a bit larger, has the pronotal sublateral carinae obscure or lacking; *M. shoemakei* (Figs. 17a–b) has prominent pronotal sublateral carinae. In his diagnosis, Brown (1971) compared his new species with *M. graniger* and *M. striata* and concluded that it appears to be closest to the latter. He also added a couplet containing *M. shoemakei* to Hinton's key to the Mexican species (Hinton 1940).

Comments. *Macrelmis shoemakei* was described by Brown (1971) from a male specimen, and the genitalia were described and illustrated. Although it is not necessary to repeat the description, photographic images of the male genitalia are provided (Figs. 18a–b). Note that because the penis is so strongly curved, the spatulate shape of the apical third does not appear as pronounced in Fig. 18a as it actually is.

***Macrelmis texana* (Schaeffer, 1911)**

(Figs. 1, 19–20)

The common Texas species *M. texana* was described by Schaeffer (1911) as *Elsianus texanus* from a unique female specimen (H. P. Brown, unpublished data) from the Devils River, Texas. The male genitalia of the species are described and illustrated herein for the first time (Figs. 20a–b). There are verified records of the species from central Texas from the following counties: Bandera, Bell, Bexar, Comal, Edwards, Gonzales, Hays, Kerr, Kimble, Kinney, Menard, Real, San Saba, Terrell, Travis, Uvalde, and Val Verde (type locality: Devils River), and it likely occurs throughout the Edwards Plateau. Specimens determined by Brown from the bordering Mexican states of Coahuila and Nuevo Leon are housed in the OMNH Recent Invertebrates Collection with the records appearing in their Recent Invertebrates Database. The New Mexico and Jeff Davis County, Texas, records attributed to *M. texana* by Brown (1971, 1972) are actually of *M. shepardi*, so the species is currently known only from Texas and Mexico. *Macrelmis texana* often occurs with *M.*

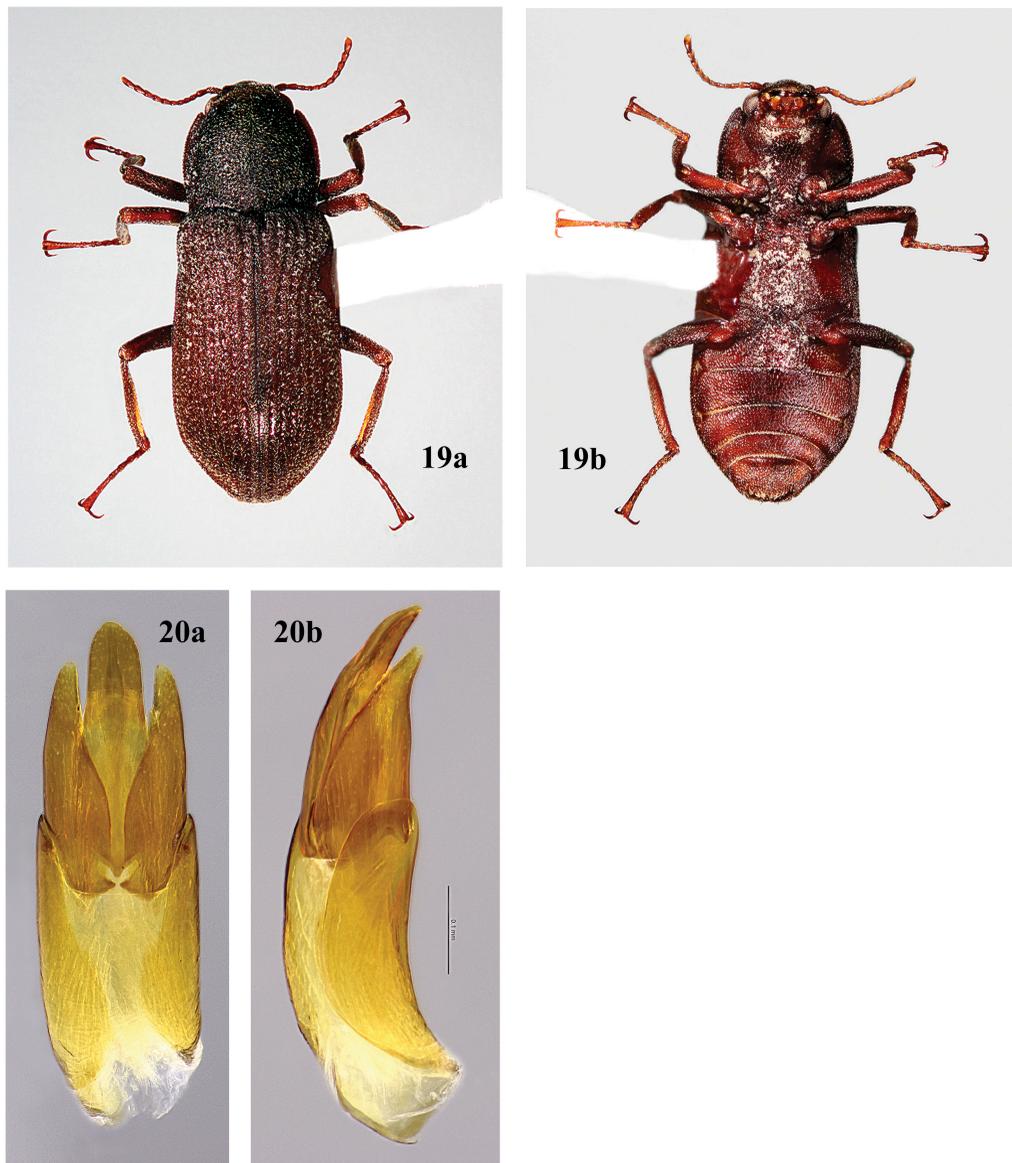


Figs. 17–18. *Macrelmis shoemakei*. **17)** Habitus, size 3.48 mm long, 1.40 mm wide, a) Dorsal view, b) Ventral view; **18)** Male genitalia, a) Dorsal view, b) Lateral view.

texangusta in the same rivers and streams, and also has been collected with *M. shoemakei* in San Felipe Creek, Val Verde County, Texas.

Diagnosis. *Macrelmis texana* (Figs. 19a–b) and *M. texangusta* (Figs. 9a–b) occur together in some streams and historically have been confused with each other. Although the species are of similar length (4.0–4.8 mm long and 3.8–4.8 mm

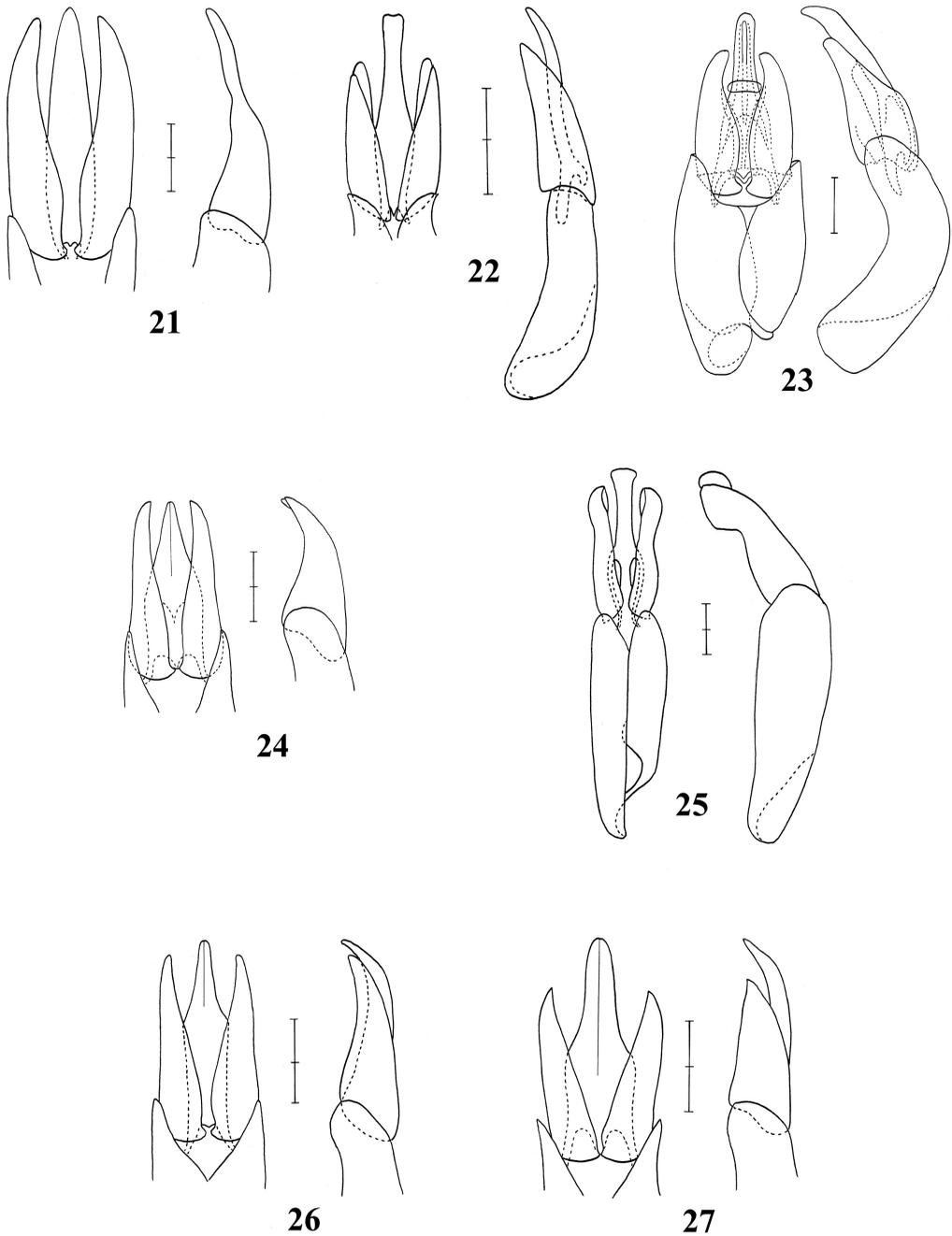
long, respectively), *M. texangusta* is proportionally more slender than *M. texana*, about 3× as long as wide in comparison to 2.5×, respectively, and *M. texana* is more coarsely granulate. The following species are usually distinguishable from *M. texana* on the basis of size: *Macrelmis shepardi* (Figs. 6a–c) is larger, 5.0–5.9 mm long; *M. moesta* (Figs. 15a–b) and *M. shoemakei* (Figs. 17a–b) are both smaller, less



Figs. 19–20. *Macrelmis texana*. **19)** Habitus, size 4.16 mm long, 1.6 mm wide, a) Dorsal view, b) Ventral view; **20)** Male genitalia, a) Dorsal view, b) Lateral view.

than 4 mm long. *Macrelmis texana* (Figs. 19a–b) is most similar to *M. harleyi* (Figs. 3a–b) (4.2–5.2 mm long) and may be difficult to separate on the basis of external morphology alone, although the scutellar shield of the former is noticeably more protuberant. Fortunately, the unique male genitalia (Figs. 20a–b), with a wide penis subparallel at the apical 1/3 and with a broadly rounded tip, serve to easily distinguish *M. texana* from the males of other species.

Description. Male genitalia: Elongate, about 3.5× as long as wide; well sclerotized (Figs. 20a–b). Phallobase much longer than parameres; parameres much shorter than penis. In dorsal view (Fig. 20a), parameres with lateral margins weakly arcuate, inner margins sinuate, apices narrowly rounded to acute; penis wide with lateral margins subparallel at basal 2/3, narrower and subparallel at apical 1/3, apex broadly rounded; penis at base wider than paramere base, at apical 1/3 much wider than



Figs. 21–27. *Macrelmis* species of central and southern Mexico, male genitalia, dorsal and lateral views. **21)** *M. grandis*; **22)** *M. graniger*; **23)** *M. leonilae*; **24)** *M. sandersoni*; **25)** *M. scutellaris*; **26)** *M. striata*; **27)** *M. striatoides*. Figs. 21, 22, 24–27, modified and redrawn from Hinton (1940), scale bars = 0.2 mm; Fig. 23 redrawn from Spangler and Santiago F. (1986), scale bar = 0.1 mm.

paramere apical 1/3. In lateral view (Fig. 20b), phallobase ventral margin strongly arcuate; paramere ventral margin strongly sinuate, wide at basal 2/3, slightly curved ventrally and digitate at apical 1/4, apex narrowly rounded; penis with apical 1/3–1/2 dorsoventrally flattened, slightly angled ventrally, apex sharply acute.

**KEY TO THE DESCRIBED SPECIES OF
MACRELMIS OF THE UNITED STATES AND
MEXICO BASED ON MALE GENITALIA**

[partly modified from Hinton (1940) and H. P. Brown (unpublished data)]

1. Pronotum with a basal gibbosity anterior to the scutellum 2
- 1'. Pronotum without a basal gibbosity..... 3
2. Length over 4 mm; prosternal process with apex acute (Fig. 25, male genitalia); central Mexico *M. scutellaris* (Hinton)
- 2'. Length 4 mm or less; prosternal process with apex broadly rounded (Fig. 22, male genitalia); central Mexico *M. graniger* (Sharp)
3. Hind tarsi of males with tufts of long setae on ventral apices of tarsomeres 1–4 (Fig. 6c) .. 4
- 3'. Hind tarsi of males without tufts of long setae on ventral apices of tarsomeres 1–4..... 6
4. Male genitalia with penis not extending beyond apices of parameres (Fig. 24); central Mexico *M. sandersoni* (Hinton)
- 4'. Male genitalia with penis extending beyond apices of parameres 5
5. Size larger, 5.0 mm long × 2.0 mm wide or more; male genitalia with paramere apices rounded and curved inward (Fig. 7a); Texas, New Mexico, Arizona, Durango *M. shepardi* Barr, new species
- 5'. Size smaller, 4.5 mm long × 1.9 mm wide or less; parameres with apices subacute and not curved inward (Fig. 27); central Mexico *M. striatoides* (Hinton)
6. Pronotum without sublateral carinae..... 7
- 6'. Pronotum with sublateral carinae 8
7. Male genitalia with parameres having outer margins rounded, apices abruptly curved inward; each nearly as wide as penis apex (Fig. 23); southern Mexico, Guatemala, Honduras *M. leonilae* Spangler and Santiago F.
- 7'. Male genitalia with parameres nearly parallel-sided, apices slightly curved inward; each narrower than penis apex (Fig. 13a); Baja California Sur, Sonora *M. mexicana* Barr, new species
8. Size larger, more than 5.5 mm long (Fig. 21, male genitalia); central Mexico *M. grandis* (Hinton)
- 8'. Size smaller, less than 5.5 mm long..... 9
9. Male genitalia with penis extending well beyond apices of parameres 10
- 9'. Male genitalia with penis not extending much, if at all, beyond apices of parameres 13
10. Male genitalia with penis narrowly spatulate, widened at apex (Fig. 18a); Texas, Coahuila *M. shoemakeri* (Brown)
- 10'. Male genitalia not as above 11
11. Body elongate and slender; male genitalia with penis tapered at apical third, apex narrowly rounded (Fig. 10a); Texas *M. texangusta* Barr, new species
- 11'. Body not elongate and slender; male genitalia with penis nearly parallel-sided at apical third, apex blunt and broadly rounded 12
12. Pronotum with sublateral carinae prominent; male genitalia with penis broad, abruptly constricted at apical third, paramere tip digitate in lateral view (Fig. 20b); Texas, Coahuila *M. texana* (Schaeffer)
- 12'. Pronotum with sublateral carinae low, narrow; male genitalia with penis gradually narrowed at apical third, paramere tip blunt, not digitate in lateral view (Fig. 13); Baja California Sur, Sonora *M. mexicana* Barr, new species
13. Male genitalia with parameres broader than penis and about the same length, paramere tips digitate and strongly curved in lateral view (Fig. 4); body size usually larger, 4.5 mm long × 1.8 mm wide or more; Arizona *M. harleyi* Barr, new species
- 13'. Male genitalia with parameres narrower, slightly shorter than penis, paramere tips not digitate or strongly curved in lateral view; body size usually smaller, 4.5 mm long × 1.8 mm wide or less 14
14. Male genitalia with penis bulbous at base, wider than paramere base; penis apex broad, much wider than paramere apex (Fig. 16a); Arizona *M. moesta* (Horn)
- 14'. Male genitalia with components slender; penis base subparallel, not bulbous, not wider than paramere base; penis apex narrow, as wide as paramere apex or not much wider (Fig. 26); central Mexico *M. striata* (Sharp)

DISCUSSION

Geographic Distribution. The genus *Macrelmis* is at the northernmost limits of its range in the

southwestern United States (Figs. 1–2) and extends as far south as Argentina. I know of no occurrences north of Coconino County in central Arizona (*M. shepardi*) (Fig. 2), nor east of western Gonzales County in south-central Texas (*M. texana*) (Fig. 1). Four of the six species which occur in the United States (*M. shepardi*, *M. shoemakeri*, *M. texana*, *M. texangusta*) are also recorded from northern Mexico, three of them from bordering Mexican states. The remaining two species, *M. harleyi* and *M. moesta*, occur in southeastern Arizona and should be expected in Mexico as well. *Macrelmis mexicana* is common in the streams of Baja California Sur but has not been found in Baja California north of the Desierto de Vizcaíno (Fig. 2). The species also occurs across the Gulf of California (Sea of Cortez) in the state of Sonora and probably is more widespread on the mainland. This disjunct distribution is not that surprising given that Baja California is a microplate that ruptured from the mainland due to rapid sea floor spreading in the geologic past (Umhoefer 2011).

Similar general distribution patterns seem to be fairly common for species and subspecies that are found only in the southern Nearctic, Mexico, and Central America, with aquatic beetle examples in the Gyrinidae [e.g., *Dineutus solitarius* Aubé, *Dineutus sublineatus* (Chevrolat)] (Gustafson and Miller 2015) and the Dytiscidae (e.g., *Laccophilus horni* Van den Branden, *Laccophilus o. oscillator* Sharp, *Laccophilus m. mexicanus* Aubé, *Laccophilus pictus coccinelloides* Régimbart, *Laccophilus v. vacaensis* Young, *Laccophilus vacaensis chihuahuae* Zimmerman, *Laccophilus vacaensis thermophilus* Zimmerman) (Zimmerman 1970). At the generic level, there are several other elmids that exhibit distributions comparable to *Macrelmis*, with species occurring from the southwestern USA through Neotropical South America, including *Cylloepus* Erichson, *Heterelmis* Sharp, *Hexacylloepus* Hinton, *Huleechius* Brown, *Neocylloepus* Brown, *Neoelmis* Musgrave, and *Phanocerus* Sharp (Jäch *et al.* 2016).

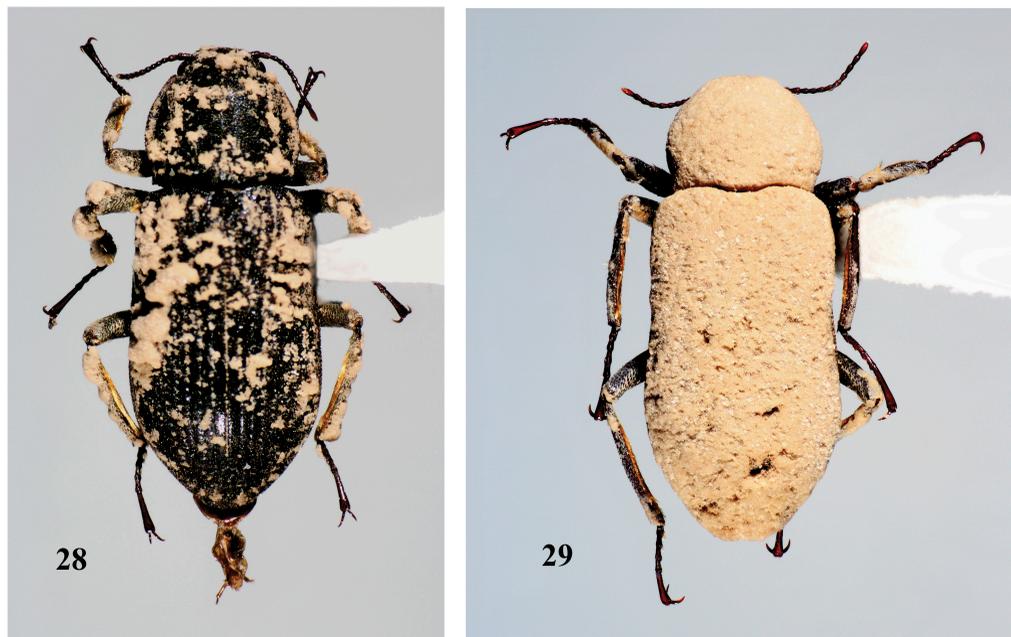
Macrelmis is the key player in a taxonomic mystery involving monotypic *Uralohelmis jureceki* (Roubal, 1940). The species was described from two male specimens from Orenburg Russia in the southern Ural Mountains, and was later discovered to be a species of *Macrelmis* (Jäch 2002). Since the species had never been collected again, and *Macrelmis* is an exclusively New World genus, it is probable that the type locality is incorrect. Jäch (2002) proposed that the specimens had become mixed up during the extensive travels of the collector, Štěpán Jureček, and actually had been collected near San Diego, California, rather than in the Palearctic. After examining the type material, Jäch (2002) synonymized *Uralohelmis* with *Macrelmis*, diagnosed the species noting its similarity to

Macrelmis isus (Hinton, 1946) from Brazil, and described and illustrated the male genitalia. In his paper, Jäch mentioned that Harley Brown had previously examined the specimens and believed them to resemble *Macrelmis tarsalis* (Hinton, 1936) from Costa Rica. Fortunately, Hinton illustrated the male genitalia of both *M. isus* (Hinton 1946: 130) and *M. tarsalis* (Hinton 1936: 419) when he described the species. Comparison of his illustrations with those of *M. jureceki* by Jäch (2002) shows that the genitalia of the three are quite dissimilar. Recently, Passos *et al.* (2015) briefly discussed *Macrelmis jureceki*, created a “*jureceki* new species group” to include that species and *M. leonilae*, and reported its distribution as “USA: California,” citing Jäch (2002). Although it is possible that *Macrelmis* may occur in southern California, I am not aware of any verified records (Shepard 1993) or collections despite extensive sampling in that area. Therefore, I think that the claim that Roubal’s specimens are from California should be regarded as dubious, given that it remains unverified.

Habitats Rich in Calcium Bicarbonate. The seven species of *Macrelmis* occurring in the southwestern United States and northern Mexico are typically, but not exclusively, found in streams and rivers with limestone substrates which are often associated with karst topography and groundwater. Their calcium bicarbonate-rich waters enable chemical deposition of tufa (calcium carbonate), often incorrectly referred to as travertine, on the bottom substrate and submerged objects (Capezuoli *et al.* 2014). Depending on environmental factors, the degree of deposition varies from a whitish powdery coating on the surface of rocks and cobbles (Fig. 14), to the partial or complete cementing of the substrate with porous, calcareous rock (Fig. 11). Because *Macrelmis* adults are most often found among gravel and cobbles and beneath larger stones, consolidation of the substrate makes specimen collection difficult.

Elmid adults are slow-moving and long-lived for insects, and under certain circumstances accumulate external encrustations which may partly or completely cover the cuticle (Brown 1987). In the case of *Macrelmis* beetles inhabiting calcium bicarbonate-rich streams, this occasionally results in a complete suit of calcite armor (Figs. 28–29), or more often, a thin coating on the dorsal surfaces. Sometimes these accumulations must be removed to see diagnostic characters in order to identify the species. Mechanical cleaning, by hand, using pins and fine brushes usually suffices, but severe cases are most easily handled by a brief bath in hydrochloric acid which dissolves away the carbonates.

Species Groups. Based on earlier work by Hinton (1940, 1945, 1946), Spangler (1997) and Sampaio *et al.* (2012), Passos *et al.* (2015)



Figs. 28–29. *Macrelmis shepardi*, **new species**, with cuticular calcite deposits. **28)** Specimen from Gila County, Arizona; **29)** Specimen from Presidio County, Texas.

reformulated six species groups and presented four new groups in order to categorize 33 of the 49 currently known species of *Macrelmis*. Their treatment excluded *M. moesta* and *M. texana* because they: “...have incomplete descriptions and/or lack illustration of their genitalia, making impossible the comparison and discussion based on our current proposal...” (Passos *et al.* 2015: 196), but now it is possible to include them.

Only one of the species treated in this revision was included in Passos *et al.* (2015), *M. shoemakeri*, which was assigned to the *granigera* species group. I attempted to place the remaining six species in the species groups with the following results: *M. shepardi* and *M. texangusta* fall into the *striata* group fairly well; *M. moesta* is closest to the *striata* group although the penis is more parallel-sided rather than tapering proximal to the median constriction; *M. harleyi* has a penis with a truncate apex, but the paramere length is subequal to that of the penis, so it does not quite fit the *granigera* group; the genitalia of *M. mexicana* most resemble those of the *aristea* group, but several external morphological characters exclude it; *M. texana* has elements of the *celsa* group because of its genitalia morphology, but does not lack pronotal carinae. Only three of the seven species treated in this article seem to fit into the classification even somewhat. For this reason, I am not formally assigning them to species groups.

Almeida *et al.* (2020) expressed concern about the arrangement, noting that it is an artificial division rather than a natural grouping based on taxonomic or systematic evidence, and I am in agreement with this observation.

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