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Parajulid milliped studies XI: Initial assessment of the tribe Gosiulini (Diplopoda: Julida)

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Parajulid milliped studies XI: Initial assessment of the tribe Gosiulini (Diplopoda: Julida)

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Parajulid milliped studies XI: Initial assessment of the tribe Gosiulini (Diplopoda: Julida)

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Abstract. The parajulid milliped tribe Gosiulini (Diplopoda: Julida) comprises two genera - Gosiulus Chamberlin, with three projections on the posterior gonopod and two species in the southcentral/southwestern United States (US) [Arizona, Colorado, New Mexico, and Texas], and monotypic *Minutissimiulus* Shelley, **n. gen.**, with two projections, in Nuevo León, Mexico. Gosiulus conformatus Chamberlin occupies the plains/flatlands of Texas, while its congener inhabits high elevations to the west in all four US states. Both are anticipated in Mexico (Coahuila, Chihuahua, and Sonora), and G. conformatus is expected in southeastern Colorado, eastern New Mexico, and the Oklahoma panhandle. The eastern boundary of G. conformatus and the genus/tribe conforms to the western border of the Piney Woods biome in eastern Texas. As shown by the posterior gonopod drawing in the original description, Parajulus timpius Chamberlin, previously considered of "uncertain generic position or validity," is unquestionably the oldest name for the western species. The anteriormost posterior gonopod projection, absent from Minutissimiulus, is considered the "prefemoral process," while the "solenomere" and a third branch arise from a common base. Because of positional homology with "process 'C" in Nesoressini, the last projection is accorded this name, which may also apply to the "prefemoral process" in Aniulini. Minutissimiulus biramus Shelley, n. sp., is proposed along with the following new subjective synonymies: Apacheiulus Loomis under Gosiulus; Ziniulus aethes and Z. medicolens, both by Chamberlin, and Z. ambiguus and Z. nati, both by Loomis, under G. conformatus; and A. pinalensis and A. guadelupensis, both by Loomis, under G. timpius, new combination. Ziniulus navajo Chamberlin becomes an **objective synonym** of P. timpius because its holotype is designated neotype of the latter. Minutissimiulus biramus Shelley is the first Mexican gosiuline and "mainland" Mexican parajulid not in the tribe Parajulini.

Key Words. *Apacheiulus*, Arizona, Colorado, *Gosiulus*, *Minutissimiulus*, New Mexico, Nuevo León, objective synonymy, Texas, *Ziniulus*.

Introduction

Referring to the necessary compromises and concessions, a United States (US) senator once stated, "Legislation is the art of the possible." So, we contend, is taxonomy, particularly when groups, like the milliped/diplopod family Parajulidae (order Julida), are diverse and speciose, essentially unknown, and actuarial life expectancies of the few researchers drop into single digits. In these circumstances, something is better than nothing, and the need to publish basic alpha-level knowledge to establish a foundation for future investigations supersedes that of producing perfect, all-inclusive tomes that some diplopodologists in the US and northern Europe demand. RMS and the late N. B. Causey (1910–1979) are the only persons in human history who have held in depth knowledge of this taxon, the dominant Nearctic diplopod family, a precarious situation that compels publication of some level of insight lest all knowledge become extinct with another student having to develop it *de novo*. This, in turn, is unlikely given economic factors, trends in modern biology, and emergency global crises like climate change. Restricted to the Nearctic and northern Neotropics excepting *Karteroiulus niger* Attems in east Asia, Parajulidae's New World distribution is depicted by Shelley (2008, fig. 1), who updated maps by Hoffman (1969) and Enghoff (1993). In its predominant area, Parajulidae is either known or expected in the Alaskan panhandle, every county in each of the lower 48 states, all Canadian provinces bordering

the latter, every state in Mexico possibly excepting those in the Yucatan Peninsula, and Guatemala, Belize, Honduras, and El Salvador. Since Julida is absent from South America and other indigenous Nearctic representatives – *Virgoiulus* Enghoff (Blaniulidae), three species of *Orinisobates* Lohmandeer (Nemasomatidae), *Okeanobates americanus* Enghoff (Okeanobatidae), and the families Aprosphylosomatidae, Chelojulidae, Paeromopodidae, Telsonemasomatidae, and Zosteractinidae – occur within Parajulidae's range. Consequently, this is also the entire, indigenous, ordinal New World distribution (Shelley and Golovatch 2011, fig. 26).

RMS' prior contributions on Parajulidae include a treatment of the Mexican/northern Central American tribe Parajulini (Shelley 2008), proposal of Nesoressini for a new genus and species in New Mexico (Shelley and Medrano 2006), and eight works on Aniulini (Shelley 2000a, b, 2001, 2002, 2004, 2007a, b; McAllister et al. 2009). A summary work on Aniulini, in progress for years, has been delayed because new forms continue to appear in preserved holdings. The alpha-level objective of the present contribution and future ones on Ptyoiulini, Uroblaniulini, Bollmaniulini, and other west-Nearctic tribes sensu Causey (1974) mandates abbreviated treatments focusing on gonopod structure, typification, nomenclature, male diagnostic anatomy, and distributions, to render these taxa available to the biological community. Gosiulini is undoubtedly a soundly based taxon, and we accept Causey's (1974) higher parajulid taxonomy, not being competent to alter it with so many unstudied tribes.

Materials and Methods

Missing data in locality listings were not provided on vial labels, and "MM, FF," and/or "juvs." indicate too many individuals to count. Repository acronyms are **AMNH**, American Museum of Natural History, New York, New York; **FSCA**, Florida State Collection of Arthropods, Gainesville; **LACM**, Los Angeles County Museum of Natural History, Los Angeles, California; **MSB**, Museum of Southwestern Biology, University of New Mexico, Albuquerque; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh; **NMNH**, National Museum of Natural History, Smithsonian Institution, Washington, DC; **UCM**, Museum of Natural History University of Colorado, Boulder; **UTIC**, University of Texas Insect Collection, Austin; **VMNH**, Virginia Museum of Natural History, Martinsville; **WTAM**, West Texas A & M University, Canyon.

Taxonomy

Order Julida Brandt 1833 Family Parajulidae Bollman 1893 Subfamily Parajulinae Bollman 1893 Tribe Gosiulini Causey 1974

Gosiulini Causey 1974: 31. Shelley et al. 2000: 46.

Diagnosis. Small-bodied to minute Parajulinae, adult lengths ranging from 9–20 mm; epiproct short, barely overhanging and extending beyond paraproctal margins; 8th rings of males without sternal lobes. Anterior gonopod lateral syncoxal process long, extending beyond level of distal extremity of telopodite, apically rounded or uncinate. Posterior gonopod telopodite with either two (process "C", solenomere) or three (these plus a prefemoral process) ventrally-directed, vertical projections; process "C" variable in length and configuration, arising (sub)basally from solenomere branch; solenomere filamentous, attenuated for most of length and appearing flagellate, curvilinear or sigmoid, extending ventrad well beyond distal extremities of other projections. Prostatic groove running along inner surface of solenomere for most of its length, opening apically.

Components. Gosiulus Chamberlin, 1940; Minutissimiulus Shelley, new genus.

Distribution. Occurring, east-west, from the western fringe of the Piney Woods biome in eastcentral Texas to the mountains of westcentral Arizona, ranging northward through the Texas Panhandle and the Front Ranges of the Rockies about 1/3 of the length of Colorado and southward to the Rio Grande and the Mexican border, continuing southward for most of the length of Nuevo León (Fig. 1, 13). Shelley and Medrano (2006) depicted the range of Gosiulini then known on a map of the "southern clade," but it lacked Colorado, central Arizona, and Nuevo León; however, Causey (1974) had accurately characterized the area as "Arizona and Colorado southeast to northeastern Mexico." Though never describing the genus or species, Causey had samples of *Minutissimiulus biramus*, now housed at the FSCA, and knew of the tribe's occurrence in Nuevo León, the first of a primarily US parajulid taxon south of the Rio Grande and the first occurrence of a tribe other than Parajulini in "mainland" Mexico (Shelley 2008).

Remarks. We label process "C" as such because of positional homology with that projection in Nesoressini (Shelley and Medrano 2006), suggesting affinity between the tribes. Such a relationship is supported by their sympatric occurrence in both western New Mexico (Fig. 1) and likely also eastern Laramidia, Nesoressini occurring near the edge of the former Western Interior Seaway. As the structure in Aniulini that has been termed "prefemoral process" in all prior publications also arises at this position, it also seems homologous and properly labeled as process "C", with the prefemoral process being absent in this tribe.

Key to Genera and Species of Gosiulini

Genus Gosiulus Chamberlin, 1940

Gosiulus Chamberlin 1940: 10. Chamberlin and Hoffman 1958: 138. Jeekel 1971: 159. Hoffman 1980: 108; 1999: 154. Shelley et al. 2000: 46.

Ziniulus Chamberlin 1940: 13. Chamberlin and Hoffman 1958: 149. Jeekel 1971: 180.

Apacheiulus Loomis 1968: 159–160. Hoffman 1980: 108; 1999: 149. Shelley et al. 2000: 43. **New subjective synonymy.**

Type-species. Of Gosiulus, G. conformatus Chamberlin, 1940, by original designation; of Ziniulus, Z. aethes Chamberlin, 1940, by original designation; of Apacheiulus, A. pinalensis Loomis, 1968, by original designation.

Diagnosis. Moderate-sized to large-bodied Gosiulini. Anterior gonopods with or without detectable coxal lobes; telopodite roughly 1/3 as long as lateral syncoxal process; latter leaning mediad, with or without rounded basal lobe. Posterior gonopod with three ventrally directed projections; prefemoral process (anteriormost branch) long, usually blade-like for most of length, (sub)uncinate apically; process "C" either relatively short, extending distad in varying configurations subparallel to basal part of solenomere or twisted and blade-like, curling around and enveloping dorsal, caudal, and ventral surfaces

of solenomere near midlength; latter with basal lobe on outer (caudal) surface, tapering and extending distad, usually sigmoidally, well beyond apices of other projections.

Species. Two that are probably parapatric, with *G. timpius* occurring in mountains and foothills of the western 2/3 of the tribal/generic ranges and *G. conformatus* inhabiting the plains, Edwards Plateau, and flatlands of Texas. The former occupies parts of all four US states – Arizona, Colorado, New Mexico, and Texas - while *G. conformatus* is known only from Texas but projected for eastern New Mexico, southeastern Colorado, and the Oklahoma panhandle.

Distribution. Known only from the tribal range in the US, but the proximity of samples in Arizona, New Mexico, and Texas to the Mexican border suggests occurrence, and eventual discovery, of *G. timpius* in northern Sonora and Chihuahua and *G. conformatus* in Coahuila (red and black arrows in fig. 13). The latter is also projected for adjoining US states. The eastern distributional limit conforms to the western limit of the Piney Woods biome in eastern Texas.

Remarks. Without question, *Parajulus timpius* Chamberlin, 1912, most recently considered of "uncertain generic position or validity" (Hoffman 1999), is the oldest and correct name for the western/mountain species. Chamberlin's illustration of the posterior gonopod (1912, pl. 11, fig. 9) clearly shows process "C" curling partly around the solenomere as in Fig. 17–19 herein. This specific name holds 31 years of priority over *Z. navajo*.

Gosiulus conformatus Chamberlin, 1940

Fig. 2–12

Gosiulus conformatus Chamberlin 1940: 10, pl. 4, fig. 32–35. Chamberlin and Mulaik 1941: 61. Causey 1952: 203. Chamberlin and Hoffman 1958: 138. Loomis 1959: 163; 1968: 160–162, fig. 6–7. Reddell 1965: 162; 1970: 399. Hoffman 1999: 154.

Ziniulus aethes Chamberlin 1940: 13, pl 6, fig. 48–50. Chamberlin and Hoffman 1958: 149. Loomis 1976: 290. New subjective synonymy.

Ziniulus medicolens Chamberlin 1940: 13–14, pl. 6, fig. 51–52. Chamberlin and Mulaik 1941: 61. Chamberlin and Hoffman 1958: 149. Loomis 1959: 163. **New subjective synonymy.**

Ziniulus ambiguus Loomis 1959: 163, fig. 20–23. New subjective synonymy.

Ziniulus nati Loomis 1963: 122, fig. 20–23. New subjective synonymy.

Gosiulus aethes: Reddell 1965: 162; 1970: 399. Hoffman 1999: 154.

Gosiulus ambiguus: Hoffman 1999: 154. Gosiulus medicolens: Hoffman 1999: 154.

Gosiulus nati: Hoffman 1999: 155.

Type specimens. Male Lectotype (NMNH) collected by S. and D. Mulaik on an unknown date in December 1939 south of Three Rivers, Live Oak County (Co.), Texas. Paralectotypes (NMNH), all collected on unknown dates in December 1939 by S. and D. Mulaik, as follows: M, 3F from south of Brady, McCulloch Co.; MM, FF, juvs. from Big Spring, Howard Co.; and M, 3F from 27.2 km (12.0 mi) N Alice, Jim Wells (not Brooks) Co.

Chamberlin (1940) did not specifically designate a holotype or paratypes in the original description but merely recorded *G. conformatus* from four Texas localities: south of Three Rivers, Live Oak Co.; south of Brady, McCulloch Co.; 27.2 km (17.0 mi) north of Alice, Jim Wells Co., erroneously placed in Brooks Co.; and Big Spring, Howard Co. In the vials, however, he labeled the male from Live Oak Co., the only individual in the sample, as the holotype and the males, females, and juveniles in the Howard and McCulloch Co. samples. as paratypes, all meaningless without publication. Though not labeled, the specimens from Jim Wells Co. were mentioned simultaneously, so we consider them to be additional syntypes. These samples are from two regions of Texas, McCulloch and Howard Cos. being in the west-center some 563.2 km (325.0 mi) NW of Live Oak Co. in the southeast. Hoffman (1999) erroneously

reported the male from Live Oak Co. as the holotype, so for consistency, we designate it lectotype with the material from McCulloch, Howard, and Jim Wells Cos. becoming paralectotypes.

Diagnosis. Anterior gonopod with or without short, inconspicuous coxal lobes, lateral syncoxal process apically uncinate; posterior gonopod prefemoral process with variable acuminate spine arising from caudal surface around 1/3–2/3 length; process "C" moderately long, erect, extending directly ventrad for 1/3 to 1/2 of solenomere length, configuration variable.

Descriptive notes. Male length ranging from around 20.0–32.4 mm, maximum width 1.3–3.4 mm; 47–57 rings including collum and epiproct. Ventral margin of mandibular stipes with broad, deep, semilunar indentation. Dorsum smooth and glossy with scattered metazonital setae especially on anterior rings, caudal rings glabrous. Paraproctal rims moderately thickened; hypoproct minute. Sterna not modified. 1st legs moderately enlarged and forcipulate, tarsi overlapping in situ. Telopodites of both pairs of gonopods projecting through aperture in situ; anterior gonopod telopodites and lateral syncoxal processes angling caudad and overhanging 8th sternum; posterior gonopods upright, telopodites extending directly ventrad between anterior gonopod structures. Anterior gonopods (Fig. 2-5) with or without short coxal lobes; telopodites leaning mediad and extending ventrad for 2/3 of lengths of lateral syncoxal processes; latter variably uncinate apically. Posterior gonopod prefemoral process (Fig. 6-12) with variable spine on caudal surface at 1/3-2/3 length, with or without small additional spines (Fig. 8), usually distally uncinate/falcate but occasionally rounded and swollen; process "C" (Fig. 6, 9-12) extending ventrad subparallel to solenomere for nearly half its length, configuration varying from filiform (Fig. 6, 12) to boletoid (Fig. 10) and subclavate, solenomere usually variably sigmoid (Fig. 6, 10-12), occasionally curvilinear (Fig. 9), extending substantially farther ventrad than other branches to become ventralmost telopodital projection, tapering smoothly and continuously to finely acuminate tip.

Gonopodal variation. Other than slight differences in their angles, the relative lengths of the telopodites and lateral syncoxal processes, and the degree of the apical uncination, the anterior gonopods are stable and constant. Given the consistent *in situ* arrangement of the two gonopod pairs, the anteriors apparently function as guides to position the posterior ones and/or spermatophores for mating. As guides, the actual structural configuration of the anterior gonopods seems insignificant as long as the posterior ones are properly aligned. This apparent function, as guides for inseminating the female cyphopods, has been postulated for the aniulinine *Aniulus garius* (Chamberlin) [=A. bollmani Causey] (Matthews and Bultman 1993, McAllister et al. 2009). We believe it applies broadly to parajulids and even "bigonopodal" helminthomorph diplopods, particularly representatives of the subterclass Colobognatha, where the posterior gonopods typically project anteriad between the anterior ones *in situ*.

The posterior gonopods, the true reproductive structures, are highly variable. While those of a gonopod pair are virtually indistinguishable, no one pair is structurally identical to another as all three projections vary. Those of the holotype of *Z. aethes*, from Austin, Travis Co. (Fig. 9), are "scrunched together" in less physical space than in other males. Consequently, the branches are in contact, lie over and under each other, and force each other out of position; this is also the only male we examined with a curvilinear, rather than sigmoid, solenomere. We attribute this configuration to distortion caused by the tight, more closely appressed condition of the three projections.

The relative lengths of the branches vary in practically every posterior gonopod pair, but the solenomere is always substantially longer. Its width and degree of sigmoid curvature vary, but the most notable variation is the size of the basal swelling near the origin of process "C"; the male from LaSalle Co. (Fig. 11) lacks this swelling. The solenomere is the least variable projection, but process "C" is highly so. Its length, width, and configuration vary, and it may be apically acuminate or boletoid and sublinear or curve gently anteriad distally.

The prefemoral process consistently displays the diagnostic caudal spine, but its length and position on the process vary (Fig. 6, 9, 10–12, sp) as does practically every other aspect of the projection including overall length. One to three additional short spines may arise distad but proximal to the distal curve/bend of the branch. The distal curve/hook is directed anteriad, opposite to the spined margin, and may be broad or narrow with variable apices; it is an abrupt, sharp bend in the male from Lubbock Co. (Fig. 12).

Chamberlin authored all five available names, two in *Ziniulus* (aethes and nati) and three in *Gosiulus* (conformatus, ambiguus, and medicolens). The posterior gonopods of the type of each differ, so he apparently concluded that each represented a separate species. Assessing these five variants in the context of all lowland Texas gosiulinines reveals them to be variants of one highly variable species for which conformatus is the oldest name. By Chamberlin's standards, we would have as many nominal species as samples with males, but clearly this is not the case. The only name that plausibly could represent a true species is aethes because of its closely appressed posterior gonopod branches and the curvilinear solenomere, but we interpret these as anomalies exhibited by this individual. More sampling in Travis Co. will reveal whether sufficient individuals show this condition to warrant taxonomic recognition, so we assign it to conformatus. An example of a localized milliped species that is surrounded by a wide-spread congener is *Xystocheir prolixorama* Shelley (Polydesmida: Xystodesmidae), occurring inside the range of *X. d. dissecta* (Wood) in northern California (Shelley 1996).

Ecology. Gosiulus conformatus inhabits a variety of low elevation, flatland biotopes and seemingly may be expected virtually any place within its known and projected areas (Fig. 13). Published habitat notations include "bottom of 90' entrance drop, apparently washed into the cave" and "bottom of sink entrance" (both by Reddell 1965) and "leaf litter on a ledge 20 feet below the entrance" (Reddell 1970). Comments on labels with newly examined material include "on the ground under rocks," "cotton field," "berlese of leaf litter," "sandy soil, logs, pipes," "under bags put on concrete floor" (inside an office building), and "slight preference for clay soil."

Distribution (Fig. 13). Known only from lowland regions of Texas, extending from the western periphery of the Piney Woods biome in eastcentral Texas, approximately 280.0 km (175.0 mi) west of the Louisiana border, west- and northward to the eastern Trans Pecos and High Plains biomes, respectively, and southward to approximately 160.0 km (100.0 mi) north of the Rio Grande in Jim Wells Co. Gosiulus conformatus has not been taken south of the Rio Grande in Mexico (Tamaulipas, Nuevo León, or Coahuila states), but it occurs approximately 22.4 km (14.0 mi) from the River in Webb Co. (Loomis 1963) and up to the watercourse itself in Maverick and Val Verde Cos.; it should be expected directly across the Rio Grande in Coahuila (Fig. 13, short black arrows) and perhaps even farther south. As the lowlands of westcentral Texas and the Panhandle spread west- and northward into eastern New Mexico, southeastern Colorado, and the Oklahoma Panhandle (Fig. 13, long black arrows); it also plausibly occurs north of the Red River in southern Oklahoma (Fig. 13) and conceivably even western Kansas. We doubt that the milliped inhabits southernmost Texas and the well-sampled Rio Grande Valley because it seemingly would have been found by now.

Published records. Texas: Bexar Co. (Loomis 1968, Hoffman 1999); and Bullis Hole (Reddell 1970). Bexar/Comal/Guadalupe Cos., Schertz, J. O. Vaughan Ranch (Loomis 1959). Burnet Co. 6.0 km (5.0 mi) SE Marble Falls (Loomis 1976, Hoffman 1999). Edwards Co., 12.8 km (8.0 mi) NE Rock Springs, Devil's Sinkhole (Reddell 1965). Goliad Co., Berclair (Causey 1952). Howard Co., Big Spring (Chamberlin and Mulaik 1941, Loomis 1968). Jim Wells Co. (Hoffman 1999); 80.0 km (30.0 mi) N Alice (Chamberlin 1940, Chamberlin and Mulaik 1941). Kendall Co., 8.0 and 17.6 km (5.0 and 11.0 mi) SSW Boerne (Chamberlin and Mulaik 1941, Loomis 1959, Hoffman 1999). Kerr Co., Raven Ranch, 19.2 km (12.0 mi) S Kerrville (Chamberlin 1940, Chamberlin and Mulaik 1941, Chamberlin and Hoffman 1958, Hoffman 1999). LaSalle Co., 2.7 km (1.7 mi) N Artesia Wells (Loomis 1963, Hoffman 1999). Live Oak Co. (Hoffman 1999); and S of Three Rivers (Chamberlin 1940, Chamberlin and Mulaik 1941, Chamberlin and Hoffman 1958, Loomis 1968, Hoffman 1999). McCulloch Co. (Hoffman 1999); and S of Brady (Chamberlin 1940, Chamberlin and Mulaik 1941). Medina Co., Valdina Farms Sinkhole 30.0 km (18.8 mi) NW Rondo (Reddell 1965). Travis Co., Austin (Chamberlin 1940, Chamberlin and Hoffman 1958, Hoffman 1999). Webb Co., 22.4 km (14.0 mi) N Laredo (Loomis 1963). Williamson Co., Cobb Cavern, 8.0 km (5.0 mi) N Sun City; Georgetown (Reddell 1965).

Material examined. Texas: *Bandera Co.*, Bandera, Shaw Ranch, M, F, 2 February 1962, G. Marion (FSCA). *Bee Co.*, Beeville, M, 10 October 1895, E. Swain (NMNH). *Bell Co.*, 19.2 km (12.0 mi) N Temple, 2M, 3 November 1927, O. F. Cook (FSCA); and SW Belton, 3M, January 1931, O. F. Cook (FSCA). *Bexar*

Co., San Antonio, 7M, 26 November 1912 (FSCA), 2M, 9 December 1930, O. F. Cook (FSCA), and M, 27 December 1965, T. Stewart (FSCA); and 28.8 km (18 mi) N San Antonio, 2 January 1943, W. S. Ross (FSCA). Brown Co., Lake Brownwood St. Pk., MM, FF, juvs., 27 November 2002, C. T. McAllister (FSCA, UTIC). Burnet Co., Marble Falls, 2M, F, 15 February 1975, J. C. Loomis (FSCA); rest area W side Marble Falls, M, 13 March 1982, J. C. Cokendolpher (FSCA); Eckhardt Root Cave, 11.0 km (6.9 mi) S Bertram, M, F, 17 April 1990, M. Reyes (UTIC); and Simon Says Sink, 10.0 km (6.3 mi) S Bertram, M, 12 November 1990, J. R. Reddell, M. Reyes (UTIC). Caldwell Co., Maxwell, M, 1 March 1963, R. O. Albert (FSCA). Comal Co., New Braunfels, FF, 18 December 1954, L. Hubricht (FSCA); Hendricks Cave nr. New Braunfels, F, 19 March 1960, W. J. Gertsch (FSCA); 6.4 km (4.0 mi) E Bulverde, Kappelman Cave, M, F, 15 March 1964, J. R. Reddell, W. Russell (FSCA); 32.0 km (20.0 mi) W San Marcos, Espinajo Diablo, 2M, 8-14 March 1995, W. E. Steiner, J. M. Swearingen (NMNH); and Barely Cave, Camp Bullis, M, 12 January 2000, P. Sprouse (UTIC). Dallas Co., Dallas, MM, FF, May-June 1955 (FSCA). Duval Co., 6.4 km (4.0 mi) NW San Diego, FF, 8 January 1961, R. O. Albert (FSCA); and NE corner, 0.8 km (0.5 mi) W Jim Wells Co. line, along Parrits Cr., MM, FF, 4 April 1962, R. O. Albert (FSCA). Goliad Co., Goliad, M, 2 January 1952, (FSCA). Grimes Co., Navasota, M, 2 November 1961, S. Hopkins (FSCA). Hays Co., 27.2 km (17.0 mi) W San Marcos, F, 2 March 1995 and 6.4 km (4.0 mi) NW Kimberley, Twin Sister Peaks, 3M, 3F, 9 March 1995, W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine (NMNH). Howard Co., Big Spring St. Pk., MM, FF, 24 December 2003, C. T. McAllister (FSCA). Hunt Co., Greenville, F, 8 February 1932 (FSCA). Irion Co., 9.6 km (6.0 mi) SSE Mertjon, M, F, 18 November 2005, C. T. McAllister (FSCA). Jim Wells Co., 1.6 km (1.0 mi) N Brooks Co. line, 2M, 24 April 1961, J. F. Quinlan (FSCA); Alice, MM, FF, November 1961 and M, FF, 22 January 1967, R. O. Albert (FSCA); and 27.1 km (17.0 mi) N Alice, M, 3F, S. and D. Mulaik (NMNH). Johnson Co., along county road 1434, M, 27 March 2010, C. T. McAllister (FSCA). Karnes Co., 1.6 km (1.0 mi) N Falls City, 2M, F, 3 April 1961, J. F. Quinlan (FSCA); and Falls City, 2M, F, 17-19 April 1961, J. F. Quinlan (FSCA). Lavaca Co., Hallettsville, M, 19 January 1962, M. E. Key (FSCA). Live Oak Co., George West, M, F, 4 December 1960, R. O. Albert (FSCA); and 24.0 km (15.0 mi) N Sandia, M, juvs., 18 February 1961, R. O. Albert (FSCA). Lubbock Co., Yellow House Canyon, MM, FF, juvs., 30 March and 26 April 1973, T. R. Mollhagen (FSCA). Mason Co., 8.0 km (5.0 mi) SW Mason, M, F, 8 November 1964, J. R. Reddell (FSCA). Maverick Co., Eagle Pass, MM, FF, 19 October 1932, O. F. Cook (FSCA). Nolan Co., Sweetwater, M, F, 2 November 1932, H. C. McNamara (FSCA). Randall Co., Palo Duro Canyon St. Pk., 24.0 km (15.0 mi) E Canyon, MM, FF, juvs., 28 April 1962, R. O. Albert (FSCA); and Canyon, M, 1 November 1993, W. D. Sissom (NCSM). Reagan Co., 13.6 km (8.5 mi) NW Barnhart, along US hwy. 67, M, F, 11 November 2005. C. T. McAllister (FSCA). Real Co., Prade Ranch on Frio R., F, 21 April 1962, R. O. Albert (FSCA). Runnels Co., Miles, along US hwy. 67, M, 2F, juv., 23 December 2006, C. T. McAllister (FSCA). San Patricio Co., Sinton, 2M, F, 11 December 1960, F, juv. (FSCA). Shackleford Co., between Albany and Lueders, M, F, 8 November 1927, O. F. Cook (FSCA). Stonewall Co., between Swenson and Peacock, 8 November 1927, O. F. Cook (FSCA). Sutton Co., Caverns of Sonora headquarters, 7M, 8F. 3 juvs., 18 November 2005, C. T. McAllister (FSCA). Taylor Co., 16.0, 24.0, and 40 km (10.0, 15.0, and 25.0 mi) SW Abilene, MM, FF, juvs., 1 March 1944, H. S. Dybas (FSCA). Terrell Co., 16.0 km (10.0 mi) SE Sanderson, 2M, F, 30 October 1943, W. S. Ross (FSCA). Tom Green Co., 56.0 km (35.0 mi) NW San Angelo, March Ranch, M, 22 November 1970, D. L. Rambo (FSCA). Travis Co., S of Austin on TX hwy. 135, along Onion Cr., M, 23 January 1976, J. Richter (UTIC); and 2.8 km (1.75 mi) S Longhorn Dam, M, 2 March 1973, J. T. Moore (UTIC). Uvalde Co., Uvalde, M, F, 10 October 1927, O. F. Cook (FSCA); Laguna, 5M, 2F, 25 December (AMNH); 4.2 km (2.6 mi) W Uvalde, M, F, 12 April 1940, S. and D. Mulaik (NMNH); 32.0 km (20.0 mi) NW Rondo, Valdina Farms Sinkhole, M, F, 12 January 1964, J. R. Reddell (FSCA); and 35.2 km (22.0 mi) NW Uvalde, Mason Ranch, M, F, 1 February 1967, Miles, R. Tandy, R. Ballinger (FSCA). Val Verde Co., Del Rio, 2M, 19 October 1932, O. F. Cook (FSCA); 8.0 km (5.0 mi) E Shumba, near Comstock, M, 8F, 4 juvs., S. and D. Mulaik (NMNH); and 16.0 km (10.0 mi) SE Del Rio, M, F, 22 March 1978, O. F. Franke, T. B. Hall, J. V. Moody (UTIC). Williamson Co., TWAS A Cave, Cedar Park, 2M, 2F, 16 April 1989, W. Elliott, J. R. Reddell, M. Reyes (UTIC); Garden of Sinks Cave, Cedar Park, 2M, F, 13 February 1990, J. R. Reddell, M. Reyes (UTIC) and M, 16 February 1990, J. R. Reddell (UTIC); Chaos Cave, 3.0 km (1.9 mi) N McNeil, 2M, F, 14 April 2000. J. R. Reddell, M. Reyes (UTIC); and Ranch at Deer Cr., Cedar Park, Jumbled Rocks Cave, M, 2F, 10 April 2001, M. Warton (UTIC). Wilson Co., 19.2 km (12.0 mi) W Falls City, M, F, 2 May 1961, J. F. Quinlan (FSCA); and 3.2 km (2.0 mi) NW Falls City, juv., 25 February 1961, J. F. Quinlan (FSCA).

Remarks. The holotype of the synonym, Ziniulus medicolens, is an unusually large-bodied gosiulinine. Comparing Fig. 1 and 13 reveals that the entire distribution of G. conformatus was submerged at the height of the Western Interior Seaway in the Cretaceous/Paleocene periods (65–100 mya) while the western part of the range of G. timpius (El Paso, western New Mexico, and Arizona) was land in eastern Laramidia as was at least most of the distribution of Nesoressini. Consequently, G. conformatus appears substantially younger than its more anatomically stable congener, and its greater variability may reflect insufficient time to stabilize.

Gosiulus timpius (Chamberlin 1912), new combination Fig. 14–19.

Paraiulus timpius Chamberlin 1912: 165, pl. 11, fig. 8-9.

Ziniulus navajo Chamberlin 1943: 146–147, fig. 6. Chamberlin and Hoffman 1958: 149. New objective synonymy.

Apacheiulus pinalensis Loomis, 1968: 160, fig. 1–5. Hoffman, 1999: 149. New subjective synonymy. Apacheiulus guadelupensis Loomis 1975: 217–218, fig. 1–4. Hoffman, 1999: 149. New subjective synonymy.

Parajulus timpius: Hoffman, 1999: 171.

Type specimens. The male and female syntypes (Chamberlin 1912, Hoffman 1999) are lost. They were collected by T. D. A. Cockerell on an unknown date prior to 1912 at Los (misspelled as "Las") Valles, New Mexico, an unknown location that modern computer programs place in San Miguel Co., ca. 16.0 km (10.0 mi) SE of Las Vegas (elevation 5,900'), in the Gallinas River Valley near the community of San Augustin (35°27'13.77"N, 105°09'3.39"W). The habitat was probably the predominant pinyon pinejuniper grassland. As no new male-containing samples are available from this county, we exercise the right of first reviser and designate the individuals in the type-sample of *Z. navajo*, the second oldest name (omitted by Hoffman (1999)), as the neo-/paraneotypes of *P. timpius*; *Z. navajo* thus becomes an objective synonym of the latter. Male neotype and one M and one F paraneotypes (NMNH, the holotype, paratype, and allotype, respectively, of *Z. navajo*) collected by S. and D. Mulaik, 31 May 1941, 9.6 km (6.0 mi) south of Mountainair, Torrance Co., New Mexico, some 154.0 km (96.0 mi) southwest of Los Valles/San Augustin. We do not so designate the two female paratypes of *Z. navajo* from other New Mexico localities - south of Ft. Stanton, Lincoln Co., and Lamy (=Santa Fe Station), Santa Fe Co.

Diagnosis. Anterior gonopod coxal lobe long, distinct; lateral syncoxal process apically rounded. Posterior gonopod prefemoral process unspined; process "C" long, blade-like, curling around and enveloping dorsal, caudal, and ventral surfaces of solenomere near midlength.

Descriptive notes. Body dimensions, somatic features, and gonopods *in situ* agreeing closely with those of *G. conformatus*. Anterior gonopod (Fig. 14–16) with relatively long coxal lobe; telopodite nearly upright, lateral syncoxal process leaning strongly mediad, apically rounded with strong basal lobe on outer surface. Posterior gonopod prefemoral process without spines, long and blade-like for most of length, narrowing distad and apically uncinate; process "C" long, twisted, and blade-like, curling over and enveloping dorsal, caudal, and ventral surfaces of solenomere around midlength; basal bulge of solenomere small, inconspicuous, stem angling anterioventrad, curvilinear or sigmoid.

Variation. Body size and somatic features vary as in *G. conformatus*, but the anterior is the more variable gonopod. It possesses a distinct coxal lobe that ranges from short and rounded to moderately long and dactyliform, and the basal lobe on the lateral syncoxal process varies from short, globular, and broadly rounded to long, narrow, and subdactyliform. The posterior gonopod is more anatomically stable than that of the type species, the most variable aspects being the relative length of the prefemoral process,

the size of the apical hook, and the sigmoid or curvilinear configuration of the solenomere. Process "C" is constant, but the degree of overhang of the solenomere varies from complete and extending beyond its inner margin to half of its width.

Ecology. The mountain/upland species, *G. timpius* occurs in all four US states occupied by the tribe/genus. Habitat notations on sample labels include "below igneous outcropping," "limestone cliff," "in west draining canyon," "sifting pinyon litter in a Pinyon Pine/Juniper association with a little yellow pine," "under rocks in pinyon pine/juniper zone," "sweeping fir at night," "cantrap in pinyon pine, juniper, and *Nolina*," "litter beneath *Dasylirion wheeleri*" (Desert Spoon or Sotol), and "under rocks and leaves in ravine."

Distribution (Fig. 13). The distribution of *G. timpius* extends from the mountains of west Texas (Guadalupe, Davis, Chisos, and Franklin) through those in central New Mexico (Organ, Sacramento, Capitan, Sierra Blanca, Manzano, Sandia, and Sangre de Cristo) and the Front Ranges of the Rockies to one-third of the north-south dimension of Colorado and the mountains in westcentral Arizona. The southernmost localities are about 16.0 km (10.0 mi) from the International Border in Cochise and Pima Cos., Arizona, Luna Co., New Mexico, and El Paso and Brewster Cos., Texas, so we anticipate discovery in northern Sonora and Chihuahua, Mexico. The Texas sites are separated from Mexico by the Rio Grande, but those in New Mexico and Arizona are only separated by a line in the sand. The southernmost record, in Brewster Co., Texas, is based on females and less certain than those vouchered by males, so it is denoted by the red question mark.

Published records. Arizona: *Pinal Co.*, Pinal Mts. between Miami and Superior (Loomis 1968, Hoffman 1999, Shelley et al. 2000). New Mexico: *Lincoln Co.* (Chamberlin and Hoffman 1958), 9.6 km (6.0 mi) S Mountainair, 8.0 km (5.0 mi) S Tijeras, S of Ft. Stanton, and N of Glencoe (Chamberlin 1943). *San Miguel Co.*, "Las Valles," probably a misspelling of "Los Valles," 16.0 km (10.0 mi) SE Las Vegas (Chamberlin 1912, Hoffman 1999). *Santa Fe Co.*, "Santa Fe Station" (Chamberlin 1943), apparently referring to Lamy, the Amtrak passenger train stop for Santa Fe (city) that was served in the 1930s-40s by the AT&SF railroad. *Torrance Co.* (Chamberlin and Hoffman 1958). Texas: *Culberson Co.*, Guadalupe Mountains National Park, Bush Mountain (Loomis 1968, Hoffman 1999).

Material examined. USA. Arizona: Cochise Co., Dragoon Mts. nr. Dragoon, MM, FF, 3 January 1928, H. F. Loomis (FSCA). Gila Co., Seneca, Tonto Nat. For., 2M, 2F, 30 December 1970, D. Thomas (LACM). Pima Co., Molino Basin, Santa Catalina Mts., Coronado Nat. For., 4,300', M, F, 22 November 1959, J. A. Beatty (FSCA). Pinal Co., Oracle, Cherry Valley Ranch, Santa Catalina Mts., 4,650', F, 3 April 1960, J. A. Beatty (FSCA). Yavapai Co., 40.0 km (25.0 mi) NW Phoenix, Hells Canyon, Hieroglyphic Mts., M, FF, 2 November 1932, A. V. Willis (FSCA).

Colorado: Fremont Co., 16.0 km (10.0 mi) N Cañon City, along Oil Cr., 6M, 6F, 23 September 1961, B. Vogel (UCM, NCSM, UTIC); and Royal Gorge Rim, 5M, FF, juvs., 16 September 1940, S. and D. Mulaik (NMNH).

New Mexico: Bernalillo Co., Sandia Mts. Cibola Nat. For., Sulphur Springs, 7,200', MM, FF, July 1948 (FSCA), Lower Canyon Estates USFS Trail, M, F, 17 November 1990, north of South Peak, 2M, 16 August 1991, and ca. 1.6 km (1.0 mi) S jct. Pino and Sandia Creek Trails, M, 22 September 1991, C. S. Crawford (NCSM); and 17.6 km (11.0 mi) S Tijeras, M, 30 May 1941, S. and D. Mulaik (NMNH). Catron Co., Gila Nat. For, along USFS 41, ca. 16.0 km (10.0 mi) E jct. NM hwy 435, F, 20 July 2004, R. M. Shelley, M. F. Medrano (FSCA). Cibola Co., El Malpais Nat. Mon., 3M, 3F, 11 July 1991 – 11 January 1992, D. C. Lightfoot (NCSM) and Rattlesnake Canyon, 2M, 5F, 11 June 1991 – 15 March 1992, D. C. Lightfoot (MSB); rd. from Grants to La Mosca lookout on Mt. Taylor, 7,950', 2M, 22 July 1953, C. C. Hoff, Gorham, Joseph (AMNH); and Grants, M, 2F, 18 September 1993, W. D. Sissom (WTAM). Doña Aña Co., Organ Mts., Dripping Springs, 2F, 19 April 1888, T. D. A. Cockerell (FSCA) and MM, FF, juvs., 13 January 1927, H. F. Loomis (FSCA), near Organ, 10M, F, 27 December 1927, H. F. Loomis (AMNH, FSCA), and E side Organ Mts., 5,800-6,500', MM, FF, juvs., 29 January 1980, A. K. Johnson, R. Casteller (FSCA); and 11.2 km (7.9 mi) NW Las Cruces, NW side Picacho Mt., 1,340', 3M, 4F, 14 February 1996, R. D. Worthington (VMNH). Grant Co., 9.6 km (6.0 mi) N Piños Altos, 2M, 2F, 16

December 1954, K. W. Haller, and Burro Mts., M, 2F, 29 April and 15 May 1973, M. H. Muma (FSCA). Lincoln Co., Carrizozo Malpais ca. 16.0 km (10.0 mi) W Carrizozo, S. Riechert (UTIC). Luna Co., 8.6 km (6.0 mi) NNW Columbus, Tres Hermanas Mts., N side Middle Sister Mt., 2M, 4F, 25 November 1995, R. D. Worthington (VMNH). Otero Co., campground in Lincoln Nat. For., M, 22 July 1964, W. A. Shear (VMNH); and Cloudcroft, 2F, 22 August 1962, P. Weems (FSCA). Sandoval Co., summit of Cabezon Peak, M, 2F, 24 March 1990, C. S. Crawford (NCSM). San Miguel Co., Las Vegas, 2F, 9 August, Barber and Schwarz (FSCA). Santa Fe Co., Lamy (=Santa Fe Station), F, 31 May 1941, S. and D. Mulaik (NMNH). Socorro Co., Sevilleta Nat. Wildlife Ref., Ladrone watershed, 3M, F, 11 May 1989, Cerro Montoso, M, 2F, 10 April and 11 May 1989, and eastern base of Ladrone Mt., M, F, April-June 1989, C. S. Crawford (NCSM). Taos Co., 9.6 km (6.0 mi) S Questa, 7,800', M, 2F, 20 July 1953, C. C. Hoff, Joseph (AMNH); Columbine Camp W of Red River, 8,000', M, 19 August 1953, C. C. Hoff, Joseph (AMNH); and 6.4 km (4.0 mi) N Arroyo Hondo, M, 20 August 1953, C. C. Hoff, Joseph (FSCA). Torrance Co., 9.6 km (6.0 mi) S Mountainair, 2M, F, 31 May 1941, S. and D. Mulaik (NMNH); and Manzano Mts., campground ca. 3.2 km (2.0 mi) W Tajique, M, 19 May 1993, K. J. McWest (NCSM).

Texas: Brewster Co., Alpine, M, 2 juvs., 20 October 1932, O. F. Cook (FSCA); 16.0 km (10.0 mi) W Alpine, M, F, 28 November 1946, E. S. Ross (FSCA); and Big Bend Nat. Pk., Chisos Mts., foot of Pulliam Ridge, 5,400', 2F, 5 September 1961, H. F. Loomis (FSCA). Culbertson Co., Guadalupe Pass, Guadalupe Mts., 2F, 25 September 1950, W. J. Gertsch (FSCA). El Paso Co., Hueco Mt., Hueco Tanks State Historic Park, M, 15 October 1995, J. Bohuslavek, R. D. Worthington (VMNH); and El Paso, Franklin Mts., 0.6 km (0.4 mi) WNW summit of Anthony's Nose in west draining canyon, 5,700', 3F, 12 November 1995, and NE slope 1.9 km (1.2 mi) SE summit of South Franklin Mt., 2F, 22 November 1998, R. D. Worthington (VMNH). Hudspeth Co., Guadalupe Mountains Nat. Pk., M, 2F, April-May 1973, J. C. Loomis (VMNH). Jeff Davis Co., Mt. Locke, juv., 23 January 1973, T. R. Mollhaven (FSCA).

Remarks. The correct spelling of the mountain range and national park is "Guadalupe," but Loomis (1975) spelled the specific name as "guadelupensis" in both the original description and figure caption; this (mis)spelling was repeated by Hoffman (1999). As the name falls in synonymy under timpius, emendation is moot. In the descriptive and subsequent accounts (Loomis 1975, Hoffman 1999), Bush Mtn. is reported as being in the Hudspeth Co. section of Guadalupe Mountains National Park, but it is actually in the Culberson Co. sector.

The posterior gonopods of the holotype of *A. pinalensis* are lost. They were not in the vial with the anterior pair and the fragmented body, nor was the female paratype that was collected with the holotype.

Minutissimiulus Shelley, new genus

Type- and only component species. M. biramus Shelley, new species.

Diagnosis. Minute to small-bodied Gosiulini. Posterior gonopod with two projections, prefemoral process absent; process "C" short, closely appressed to solenomere and extending for around half its length; latter curvilinear for most of length, bending abruptly subapically, tip short, simple, and acuminate, overhanging process "C."

Distribution (Fig. 13). Nuevo León, Mexico.

Etymology. The generic name references the minute size of the lone component species.

Remarks. As a representative of Gosiulini, *Minutissimiulus* is the first parajulid genus recorded from "mainland" Mexico in a tribe other than Parajulini.

Minutissimiulus biramus Shelley, new species Fig. 20–21.

Type specimens. 3 M and 6 F syntypes (VMNH) collected by G. E. Ball and D. R. Whitehead, 18 October 1965, 19.2 km (12.0 mi) N Linares, 1,200', Nuevo León, Mexico.

Diagnosis. With the characters of the genus.

Descriptive notes. Male syntype 15.1 mm long, maximal width 1.1 mm, 46 rings including epiproct; female syntype 13.7 mm long,, maximal width 1.1 mm, 45 rings. Anterior gonopod (Fig. 20) coxal lobe minute, telopodite and lateral syncoxal process subupright, former 2/3 as long as latter; latter apically uncinate. Posterior gonopod with two ventrally directed projections; prefemoral process absent; process "C" short, closely appressed to solenomere, expanding into ovoid bulge at midlength, narrowing abruptly thereafter with tip overlapping solenomere; latter curvilinear, bending abruptly subapically, tip short, overhanging process "C".

Variation. The midlength swelling of process "C" varies, and the projection's length ranges from 1/2 to 2/3 of that of the solenomere; its tip may slightly overlap the latter or extend beyond its outer margin. The solenomere stem is slightly bisinuate in males from west of Linares.

Ecology. Unknown. Habitat notes are not provided with any sample.

Distribution (Fig. 13). Same as that of the genus, the entire known range in Mexico. In addition to the types, the following specimens were examined:

Mexico, Nuevo León, 32.0 km (20.0 mi) W Linares, 3M, F, 2 juvs., September 1956, S. and D. Mulaik (AMNH); E of Cadereyta Jiménez, M, 4F, 3 January 1950, S. Mulaik (NMNH); 17.6 km (11.0 mi) S Monterrey, M, F, juv., 5 January 1950, S. Mulaik, R. V. Chamberlin (NMNH); 3.2 km (2.0 mi) S Bustamente, M, 31 December 1963, W. Russell (FSCA); 8.0, 6.4, and 4.8 km (5.0, 4.0, and 3.0 mi) W Bustamente, MM, FF, 9 September 1946, 26 September and 30 December 1964, W. S. Ross, D. McKenzie. J. R. Reddell (FSCA); 2.1 km (1.3 mi) E Iturbide, 4,800', M, F, 18 October 1965, G. E. Ball, D. R. Whitehead (VMNH); along route 85, 52.6 km (32.9 mi) N Montemoralos, 1,700', 26 October 1965, G. E. Ball, D. R. Whitehead (VMNH); and Lampazos de Naranjo, 10.0 km (6.0 mi) E Rancho Cerro Colorado, M, 24 January 1998, P. Sprouse (FSCA).

Remarks. *Minutissimiulus biramus* is the first "mainland" Mexican parajulid belonging to a predominantly US tribe. Its adults are the shortest/smallest mature parajulids we have seen.

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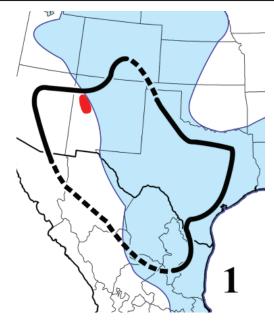
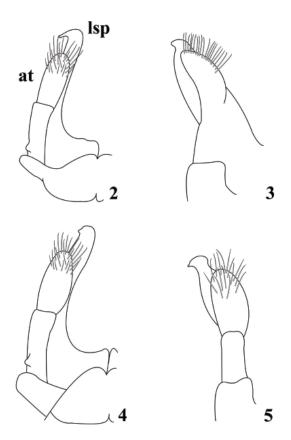
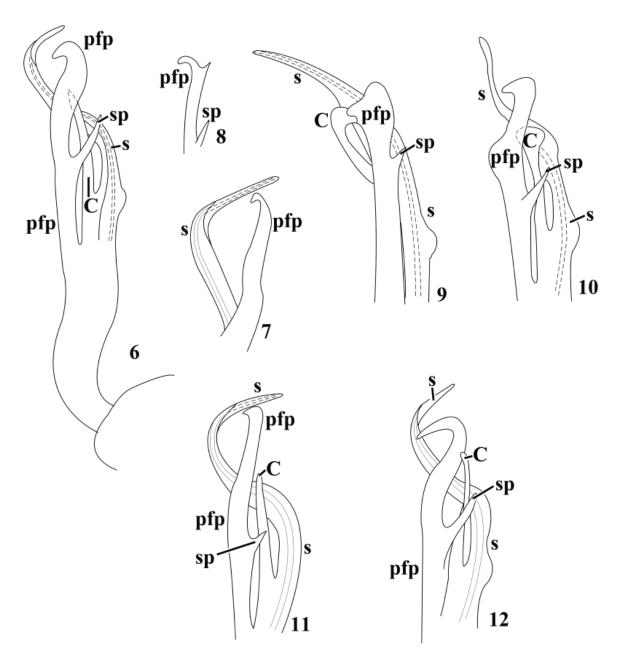


Figure 1. Known (solid lines) and projected (dashed lines) distribution of Gosiulini plotted against the maximal extent of the Western Inland Seaway in the Cretaceous Period, ca. 65–100 mya. The approximate distribution of Nesoressini (Shelley and Medrano 2006) is shaded in red.



Figures 2–5. Gosiulus conformatus, left anterior gonopods. **2)** Holotype, anterior view. **3)** The same, lateral view. **4)** Male from Travis Co., anterior view. **5)** The same, lateral view. at, anterior gonopod telopodite; lsp, lateral syncoxal process.



Figures 6–12. Gosiulus conformatus, left posterior gonopods (sub)medial views, all from Texas. 6) Lectotype, Live Oak Co. 7) Distal halves of prefemoral process and solenomere of paralectotype from McCulloch Co., lateral view. 8) Distal half of prefemoral process of male paralectotype from Jim Wells Co., lateral view. 9) Telopodital projections of male from Travis Co. 10) The same of male from Kerr Co. 11) The same of male from LaSalle Co. 12) The same of male from Lubbock Co. C, process "C"; pfp, prefemoral process; s, solenomere; sp, subbasal prefemoral spine.

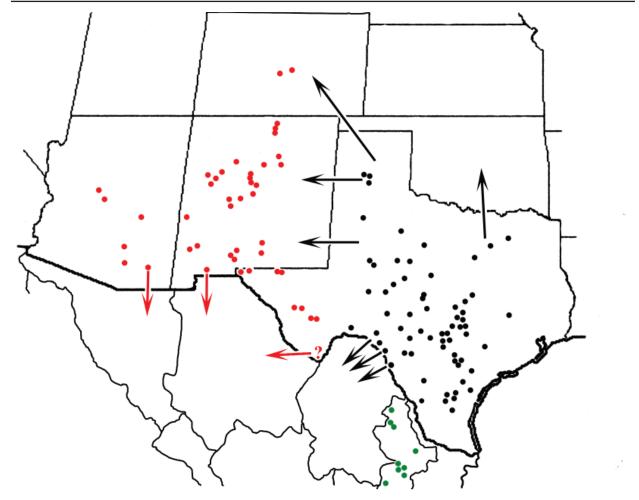
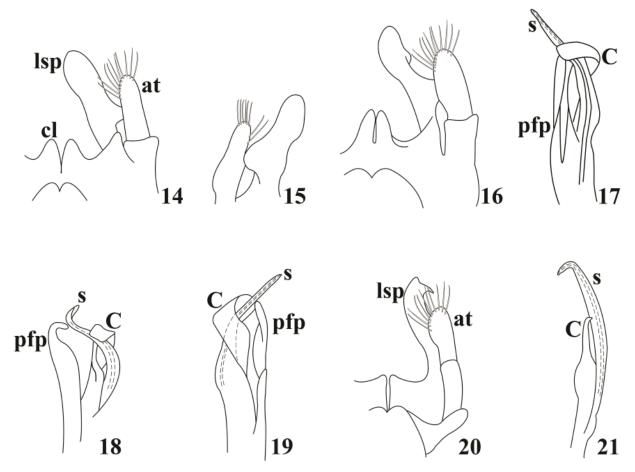


Figure 13. Distributions of species of Gosiulini. Black, G. conformatus. Red, G. timpius. Green, M. biramus.



Figures 14–21. Gosiulini gonopods. **14)** Right anterior gonopod of the neotype of *Gosiulus timpius* (holotype of *Z. navajo*), anterior view. **15)** The same, lateral view. **16)** Right anterior gonopod of male of *G. timpius* from Culberson Co., Texas, anterior view. **17)** Left posterior gonopod of neotype, lateral view. **18)** The same, anterior view. **19)** The same, medial view. **20)** Right anterior gonopod of the holotype of *Minutissimiulus biramus*, anterior view. **21)** Left posterior gonopod of the same, lateral view. cl, coxal lobe; other abbreviations as in Fig. 2–5, 6–12.