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DESERT MILLIPEDES (SPIROSTREPTIDAE, SPIROSTREPTIDA) OF THE SOUTHWESTERN UNITED STATES AND ADJACENT MEXICO

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Large millipedes of the family Spirostreptidae, some of them stretching to a length of seven inches, often are seen during daylight hours in the southwestern United States and northern Mexico. Three species are known with certainty in Arizona, New Mexico, Texas, and Oklahoma, where the northern limit of the family is about 36.5° N latitude. The same three, and a fourth, species occur in the adjacent Mexican border states (Fig. 1). The validity of other species described from this area has not been confirmed by mature male specimens. Complete literature citations for the species mentioned here are in papers by Causey (1954, 1964), Chamberlin (1943), Chamberlin and Hoffman (1958), and Loomis (1963, 1966a, 1966b, 1968).

Notwithstanding their great numbers and conspicuous size and behavior, there is little literature on the natural history of the spirostreptids of North America. Cook (1924) reported that in the deserts of New Mexico, Texas, and Arizona they often emerge from rodent burrows in large numbers in damp weather, though seldom seen at other times. After the spring and summer rains, according to natives of these arid areas, large millipedes abandon their usually secretive daytime habits and many cross highways, move across the desert, climb shrubs, and, later in the day, rest in shadows and under debris. Their movements are omnidirectional. After the rains are over, the millipedes disappear until the following spring. They reputedly retreat as far as 30 inches below the surface of the soil.

Swarms that I have observed or have studied from the collections of others were either diurnal or nocturnal and composed of few or

no mature males, up to 19 times as many gravid females, and numerous immatures of both sexes. Immatures belong to the last one or two stadia immediately preceding the sexual stadium, and, like mature specimens, females greatly outnumber males. Many of the specimens of Orthoporus ornatus that I saw swarming in San Luis Potosí on a bright July day had crawled into shoulder height shrubs. J. F. Quinlan, Jr. (personal communication, 27 June 1961) often saw O. texicolens mating during daytime spring and summer swarming in Karnes County, Texas. R. W. Strandtmann (field note, 14 April 1960) found O. flavior swarming during the day and "apparently feeding on sphagnum moss" in the canyon of the Pecos River near its junction with the Rio Grande. Specimens that he mailed to me packed in sphagnum had the gut well filled with moss. The gut of a male O. texicolens from Tamaulipas was filled with small white seeds. Crawford (1971) found that the dessication resistance of O. ornatus is considerably greater than in millipedes previously studied. Forced coiling reduced transpiration of his specimens at 40°C but not at 30°C. Stewart and Woodring (1973), who studied the water balance of O. texicolens, reported retardation of water loss by coiling and dehydration of fecal pellets. The metabolic waste products are ammonia and uric acid

It is rare to find *O. ornatus* and *O. flavior* in either caves or cave entrances, although there are caves within their ranges that are occupied by other millipedes. No caves exist within the range of *O. texicolens*. The occurrence of *O. mimus* in caves is so frequent during the winter months and so rare during spring and summer months as to suggest that this species sometimes uses such places as hibernacula and even reproduces in them. It is not unusual for immatures of several stadia of *O. mimus* to be collected in caves. Specimens with as few as 29 segments are in a collection from Sótano del Tigre, San Luis Potosí (James Reddell, collector, 24 November 1967).

As seen in Fig. 1, the distributions of these four species are in proximity at several points. However, evidence for range overlap is unavailable because of a lack of precise collection data for many sites. Southern Tamaulipas, where there are at least three species, would be an excellent area for a detailed analysis of distribution. There may be an altitudinal segregation of species there. In Texas the Balcones Fault is a barrier between O. ornatus and O. texicolens.

Variations in somatic and sexual characters have made the taxonomy of *Orthoporus* difficult, and many names have been placed in synonymy. The task has not been completed. Gonopods of five species with type localities within the range covered by this paper have

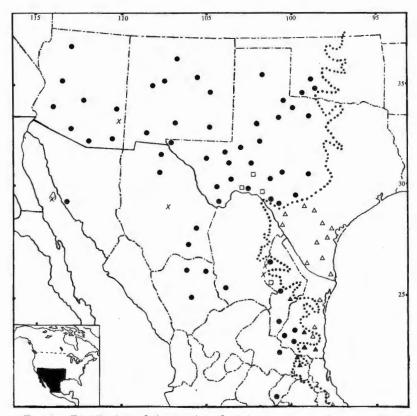


Fig. 1.—Distribution of the species of *Orthoporus* in southwestern United States and northern México: closed circles, *ornatus*; squares, *flavior*; open triangles, *texicolens*; solid triangles, *mimus*; X's type localities of species mentioned in the text that are not known by males; dotted line, the 1000 foot elevation contour, which usually separates the ranges of *ornatus* and *texicolens*.

never been described. These species and their type localities, the latter indicated by x's on the map (Fig. 1), follow: O. chihuanus Chamberlin, 1947, Ciudad Chihuahua, Chihuahua; O. entomacis Chamberlin, 1941, Duncan, Greenlee County, Arizona; O. nesiotes Chamberlin, 1923, south end of Tiburón Island, Gulf of California, Sonora; O. cienegonus Chamberlin, 1952, Ciénega de Flores, Nuevo León; and O. leonicus Chamberlin, 1941, Ojo de Agua, Sabinas Hidalgo, Nuevo León. I suspect that the first three species listed are junior synonyms of O. ornatus and the last two junior synonyms of O. flavior.

O. flavior and O. ornatus are separated easily by the gonopods and collum of the male. Although there is considerable variation in the

lateral coxal spine of the gonopod of *O. ornatus*, it is never in the form of a broad, flattened wedgelike process, as in *O. flavior*. Some of the confusion about these two species has arisen from Chamberlin's use of color as a primary species character. Each species may occur in populations composed of either predominantly brown or predominantly yellow specimens, and wherever their ranges are close the colors are similar. Banding is also common and often striking, especially in immatures and recently molted specimens. The banding may alternate shades of brown, or yellow, or brown and yellow. I have seen *O. flavior* from several sites in West Texas and from two sites near Monterrey, Nuevo León. Its range is nearly surrounded by the much greater range of *O. ornatus* (Fig. 1).

Three of the species of Orthoporus described by Chamberlin (1943), mimus, lenonus, and linares, were regarded by Loomis (1966a) as synonyms of O. ornatus. These three are conspecific but they are much nearer O. texicolens than O. ornatus. They are designated here as O. mimus. The range of O. mimus is east of O. ornatus and O. flavior and south of O. texicolens. O. mimus and O. texicolens belong to the superspecies O. teapensis, which extends from the Gulf Coastal Plain of South Texas into northern and east-central México and is characterized by heavily incised lateral lines on the collum, coarsely pitted body surface, and gonopods of the texicolens type.

The collum is sexually dimorphic in each of the species considered here, but only in *O. ornatus* is the dimorphism conspicuous and the shape of the male collum a good species character. In no species is the number of lines on the collum consistent enough to serve as a reliable species character, but the nature (that is, whether they are incised on one or both surfaces) and the depth of the lateral lines have a limited use as species characters. The surface of the prozonites and metazonites of *O. ornatus* and *O. flavior* is finely pitted and obscurely wrinkled; *O. mimus* and *O. texicolens*, usually, lack wrinkles and have more prominent pits. Males of each species have postfemoral and tibial pads on the legs, and the coxae of legpair 1 are of a somewhat uniform shape. Two tibial spurs, the proximal acute and the distal blunt, are on the gonopods of each species.

KEY TO SPECIES (MALES)

1. Lateral spine of knee of gonopods broad at base, wedge shaped, straight, and directed laterad; anterior angle of ventral margin of collum not prolonged ventrad in either sex (Fig. 3a, b). O. flavior

Lateral spine of knee of gonopods spinous, constricted at base, and 2. Knee of gonopods asymmetrically rounded; lateral spine of knee long, either straight or slightly sinuous, and directed more or less laterad; lateral lines of collum incised along one surface; anterior angle of collum of male prolonged below posterior angle (Fig. Knee of gonopods symmetrically rounded; lateral spine of knee shorter and curved moderately or strongly ventrad; lateral lines of collum incised along both surfaces; anterior angle of collum of 3. Lateral spine of gonopods thin, short, and strongly curved ventrad; O. texicolens Lateral spine of gonopods thicker, longer, and moderately curved either ventrad or obliquely laterad; lateral lines of collum fewer and more heavily incised (Fig. 5a-c) O. mimus

ACCOUNTS OF SPECIES

Orthoporus ornatus (Girard)

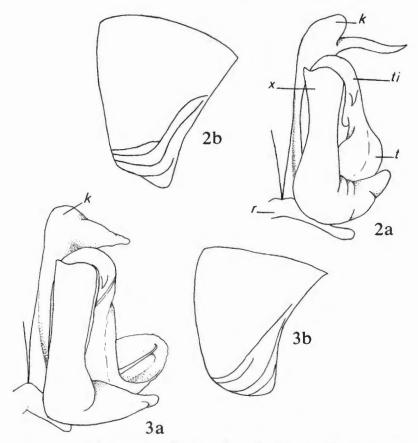
Fig. 2a, b

1853. Julus ornatus Girard, in Marcy, Report on the Exploration of the Red River of Louisiana... in 1852, Appendix F, p. 274.

Description.—Width 5 to 11 millimeters. Segments 63 to 73. Color brown or yellow, either fairly uniformly distributed or banded in one or both colors.

Male. Collum with anterior angle of ventral margin prolonged ventrad in a rounded lobe, and lateral lines incised along one surface and their exact number and position variable. Gonopods characterized by asymmetrical knee of telopodite, rounded margin of tarsus, and especially by knee spine of telopodite (spine long, either slightly sinuous or straight, and usually directed laterad). Minute variations in gonopods common, for example, apex of knee spine may be black, brown, or without special color, either straight or minutely hooked, either acute or blunt, and directed obliquely up or down rather than laterad. Also, mesoventral angle of anterior coxal shield varies between blunt and acute.

Female. Collum with anterior angle no lower than posterior angle, and both angles usually narrowly rounded about equally.



Figs. 2-3.—Left gonopod and right surface of collum: 2a, O. ornatus, generalized figure of gonopod; r, sternum; x, coxal shield; k, knee of telopodite; ti, tibia; t, tarsus; distal margin of tarsus, which is not shown in this view, is evenly rounded as in Fig. 3a; 2b, O. ornatus, collum of male; 3a, O. flavior from Langtry, Val Verde Co., Texas, gonopod; 3b, O. flavior, collum of male.

Type locality.—Restricted (Causey, 1954) to Palo Duro Canyon State Park, Randall County, Texas. Neotype (Causey, 1967) d, National Museum of Natural History.

Distribution.—North-south limits are 36.5° N latitude and 20.3° N latitude. The species range extends from western Arizona and the eastern shore of the Gulf of California eastward to the edge of the Balcones Fault in Texas and similar faults in northeastern México; it does not occur on the Gulf Coastal Plain. Margins of the known

range pass through San Pedro Bay, Sonora; Buckhorn, Tanks, Tule Mountains, Yuma County, Arizona; Grand Canyon, Coconino County, Arizona; Randall County, Texas; Greer and Comanche counties, Oklahoma; Kendall, Kinney, and Zavala counties, Texas; Jaumave, Tamaulipas; Huizaches, San Luis Potosí; San Juan del Río, Querétero, and Ciudad Durango.

New records.—Arizona: Coconino Co., floor of the Grand Canyon; Chihuahua: 15 mi. N Jiménez. Cd. Camargo. New Mexico: Bernillo Co., Albuquerque; Sandoval Co., Rio Grande River bridge between Santa Fe and Los Alamos, 9. Nuevo Leon: 35 mi. N Sabinas Hidalgo, 500 ft. Queretero: 10 mi. N Vizarrón, 5300 ft., ocotillo-cresote desert; nr. Jalpan; San Juan del Río. Tamaulipas: 5 mi. N Jaumaye; Tula. Texas: Ector Co., nr. Odessa.

Orthoporus flavior Chamberlin and Mulaik Fig. 3a, b

1941. Orthoporus flavior Chamberlin and Mulaik, J. New York Ent. Soc., 49:63.

Description.—Width 5 to 9.5 millimeters. Segments 67 to 74. Color brown or yellow, either fairly uniformly distributed or banded in one or both colors.

Male. Collum with posterior angle of ventral margin more broadly rounded than anterior angle. As in *O. ornatus*, collum with lateral lines incised along one surface, their exact number and position variable. Gonopods characterized by wedge-shaped, laterally directed process (a spine in other species) on knee, and by rounded margin of tarsus. Knee process sometimes shorter but never longer than in Fig. 3a.

Female. Collum with both angles of ventral margin broadly and about equally rounded.

Type locality.—4 mi. E Dryden, Terrell County, Texas. Holotype, immature 3, National Museum of Natural History.

Distribution.—From Crockett, Terrell, and Val Verde counties in West Texas south to the vicinity of Monterrey in western Nuevo León. I have females suspected of being this species from additional sites in Nuevo León and Coahuila. Although O. flavior and O. ornatus occur in proximity, I have never seen them in the same collection or found evidence that they intergrade.

New record.—Nuevo Leon: Cuesto Los Muertos, halfway between Monterrey and Saltillo. This possibly is the species that Loomis (1966a), on the basis of a female and immatures from Horsetail Falls near Monterrey, reported as Orthoporus sp.

Orthoporus texicolens Chamberlin

Fig. 4a-c

1938. Orthoporus texicolens Chamberlin, Proc. Biol. Soc. Washington, 51:207.

Description.—Closely related to O. mimus, differing in larger size and details of collum and gonopods. Width 6 to 9 millimeters. Segments 67 to 79. Color brown, either fairly uniformly distributed or banded inconspicuously. Collum with lateral lines embossed, but not as heavily as in O. mimus; lines tend to be more numerous and more variable in northern than in southern populations.

Male. Gonopods characterized by short, spinous, strongly hooked knee process, acute mesoventral angle of coxal shield, and incised margin of tarsus. Southern populations have knee spine up to one-third longer but no less strongly hooked and no thicker than in northern populations.

Female. Collum with both ventral angles broadly rounded, lateral lines usually four or five in number.

Type locality.—Edinburg, Hidalgo County, Texas. Holotype, d, National Museum of Natural History.

Distribution.—Gulf Coastal Plain of South Texas, where it is sometimes very abundant, and Tamaulipas, where it is scarce. The northern margin of the range passes through Bexar and San Patricio counties and the southern margin is a few miles north of El Mante. All except the southernmost collections are from elevations below 1000 feet. In southern Tamaulipas this species is replaced by O. mimus. West of O. mimus and always at a greater elevation are O. ornatus and O. texicolens.

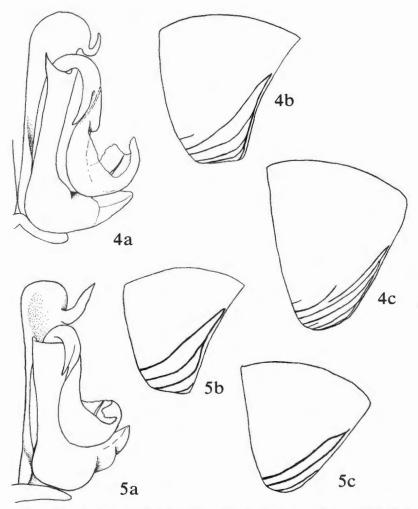
Remarks.—North-south gradients in body size and length of the coxal spine of the gonopods suggest that O. texicolens has formerly intergraded with the much more abundant O. mimus in southern Tamaulipas. A collection from Km. 7, hwy. to Gómez Farías, Tamaulipas, appears to be a hybrid swarm of texicolens-mimus and is the southernmost record of texicolens.

New record.—TAMAULIPAS: San Francisco: 15.3 mi. S Cd. Victoria.

Orthoporus mimus Chamberlin

Fig. 5a-c

- 1943. Orthoporus mimus Chamberlin, Bull. Univ. Utah, Biol. Ser., 8(3):15-16, figs. 13, 14.
- 1943. O. linares Chamberlin, Bull. Univ. Utah, Biol. Ser., 8(3):15, figs. 8, 9. New synonymy.
- 1943. O. lenonus Chamberlin, Bull. Univ. Utah, Biol. Ser., 8(3):14, figs. 11-12. New synonymy.



Figs. 4-5.—Left gonopod and right surface of collum: 4a, O. texicolens from Brownsville, Cameron Co., Texas, gonopod; 4b, O. texicolens, collum of male; 4c, O. texicolens, collum of female from Victoria, Victoria Co., Texas; 5a, O. mimus, from Sótano de la Tinaja, nr. Valles, San Luis Potosí, gonopod; 5b, O. mimus, collum of male; 5c, O. mimus, collum of female.

Description.—Closely related to O. texicolens, differing in smaller size and details of collum and gonopods. Width 4.7 to 7.1 millimeters. Segments 67 to 77. Color brown, either fairly uniformly distributed or banded inconspicuously. Collum with lateral lines embossed more heavily than in O. texicolens.

Male. Gonopods characterized by coxal spine that is longer and thicker than in O. texicolens and typically curved gently and obliquely

ventrad. Coxal spine varies in thickness, length, and curvature (it is almost straight in specimens of *O. asper* from Tuxpan); with mesoventral angle of coxal shield blunt to acute. Margin of tarsus also variable: may bear a tag, as shown in Fig. 5a; may have a short toothed emargination; or, may be even except for one small angle.

Female. Easily distinguished from other female orthoporids in area covered by this paper by collum with three heavily incised lateral lines. Closely resembles *O. teapensis*, which has a more southern range.

Type locality.—O. mimus, 19 mi. N El Limón, Tamaulipas; holotype, &, National Museum of Natural History. O. linares, Linares, Nuevo León; holotype, &, National Museum of Natural History. O. lenonus, 2 mi. N Lenon [El Limón], Tamaulipas; holotype, &, National Museum of Natural History. I have examined no holotypes but have studied topotypes from El Limón, specimens of both sexes of the closely related O. asper from Tampico and Tuxpan, and females tentatively referred to asper from coastal sites farther south in Veracruz. I suspect that Attems' type collection of O. asper came from the vicinity of Tampico.

Distribution.—Southern Tamaulipas, eastern San Luis Potosí, and eastern Nuevo León.

Remarks.—A closely related population tentatively identified as O. asper (Attems, 1950) occurs along the coast of southern Tamaulipas and northern Veracruz. Specimens are smaller (body width, 3.5 to 5.5 millimeters) and have fewer body segments (59 to 68) than O. mimus, but other somatic characters and the gonopods are very close to O. mimus. Because of the differences in their ranges (coastal plain vs. mountains) I have assigned these populations to two semi-species, pending the demonstration of an intergrading population. The spirostreptids of central México occur in many small, closely related, geographically isolated populations, making the taxonomy extremely difficult. In few cases do closely related taxa occupy ranges as unalike as those of mimus and asper.

O. mimus has sometimes been confused with O. ornatus because of the similarity of the coxal spine of the gonopods. If the shape of the collum and the nature of the lateral lines on it are considered, there should be no difficulty in distinguishing between them. I suspect that their ranges, although close, do not overlap. O. ornatus appears to keep to the west and, where they approach, occurs in fewer and smaller populations than O. mimus. The location of most collection sites has not been well documented, unfortunately.

New records.—San Luis Potosi: Sótano del Tigre, 10 mi. NE Valles; Sótano de la Tinaja, 10 mi. NE Valles; El Sótano de Yerbaniz; 8 mi. N Valles. Tamaulipas: Cueva del Virgen del Guadalupe, Sierra de Tamaulipas; pineoak forest 5000-6000 ft., 15-20 km. NNW Gómez Farias, Sierra de Gauatemala; El Sótano de Santa Elena, 25 km. S Cd. Mante. See the note in the section on O. texicolens on a possible hybridization with this species. Collections of females from 13-20 mi. SW Cd. Victoria, 2550-4300 ft., are tentatively referred to this species.

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