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Revision of the Milliped Subfamily Desmoninae (Polydesmida: Sphaeriodesmidae)

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ABSTRACT

The milliped subfamily Desmoninae comprises two tribes – the Desmonini, with *Desmonus* Cook, in southern and southcentral United States and Nuevo León, Mexico, and *Cyphodesmus* Peters, in Morelos and Veracruz, Mexico; and the monobasic Hybocestini, with *Hybocestus* Hoffman, in central Guatemala. *Desmonus* comprises two species, *D. earlei* Cook, the type species, occurring from central Kentucky to eastern Mississippi, northcentral Georgia, and the Florida panhandle, and *D. pudicus* (Bollman), which occupies two areas, one extending from southwestern Missouri to southcentral Oklahoma, northeastern Texas, and northcentral Louisiana, and the other extending from central Texas to central Nuevo León. *Cyphodesmus* contains three species, and *Hybocestus* includes four, three here diagnosed. The following new synonymies are proposed: *Tetraporosoma* Loomis, under *Desmonus*; *Taphrodesmus* Silvestri under *Cyphodesmus*; *D. e. mancus* Causey under *D. earlei*; *Ethocyclus atophus* Chamberlin & Mulaik, *D. inordinatus* and *D. austrus*, both by Causey, and *D. conjunctus*, *D. distinctus*, *D. crassus*, *Desmoniella curta*, *Stilbopagus acclivus*, and *Tetraporosoma seriata*, all by Loomis, under *D. pudicus*; *Peridysoodesmus bifidus* Silvestri under *Cyphodesmus vestitus* (Silvestri), n. comb.; and *Hybocestus plagiodon* Hoffman under *H. octonodus* Hoffman.

Among the more intriguing millipeds in the southern United States are the representatives of *Desmonus* Cook. These heavily sclerotized, tuberculate polydesmoids (Fig. 1) inhabit moist litter in the southeastern states and typically occur

under rocks and dung on the eastern periphery of the Central Plains. The northernmost component of the family Sphaeriodesmidae, which ranges southward to Costa Rica and occurs on Jamaica and Hispaniola (Hoffman 1980), forms of *Desmonus* are often encountered in clusters of small, tightly curled spirals encrusted with soil. They have been reported to volvate, as do glomerids, and characterized as "oniscoid" (Cook 1898, Loomis 1966); Causey (1958) referred to them as "pill millipeds." However, desmonines actually coil into small spirals or disks, with the head in the center and the caudal segments overlapping the third or fourth tergites; they are laterally flattened and typically lie on their sides in the resting position.

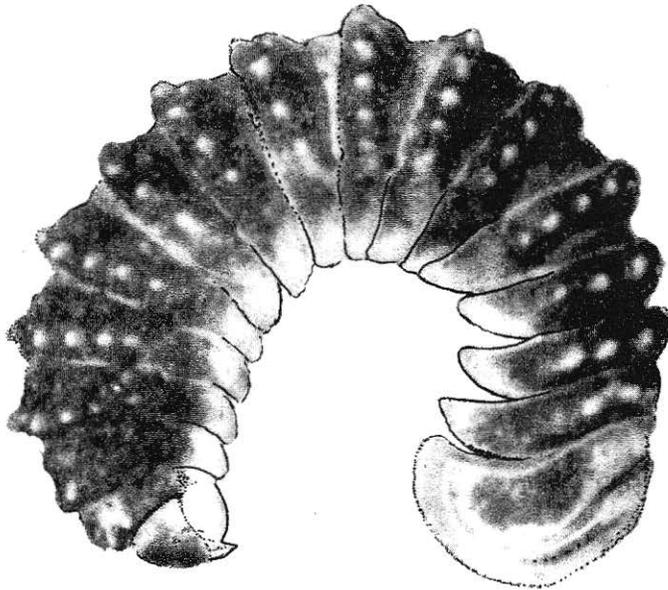


Fig. 1. Lateral view of right side of 19-segmented female of *Desmonus pudicus* from Clark County, Arkansas. Scale line = 1.00.

As with most unrevised American millipede genera, the literature on *Desmonus* is confusing, because five nominal genera, ten species, and one subspecies have been proposed for a fauna that, in my view, comprises only one genus and two species. Males of *D. pudicus* (Bollman) occasionally develop fully-formed gonopods at the penultimate molt, and the synonyms *Desmoniella curta* Loomis (1943) and *Desmonus inordinatus* Causey (1958) were proposed for gonopodal males with 19, rather than 20, segments; likewise, *Hybocestus octonodus* Hoffman (1959), in Guatemala,

was assigned to a subadult, gonopodal, desmonine male. I believe these individuals represent developmental accidents, mistakes in timing, and do not warrant taxonomic recognition. Just as gonopods can develop at the wrong position without representing new taxa (see Shelley [1977] for examples in the Xystodesmidae), they should likewise be able to develop at the wrong time or developmental stage; such males do not differ somatically from other 19-segmented individuals, and their gonopods are identical to those of 20-segmented males. Aberrant males of *D. pudicus* occur sporadically and intermingle with normal individuals in Arkansas, Oklahoma, and Texas, so if one anomalous specimen is recognized taxonomically, for consistency, a new taxon is required for those from each locality. For such males to represent distinct taxa, there should be differences other than the number of segments, particularly in the structure of the gonopods, so the logical resolution is to assign them to *D. pudicus* as developmental anomalies. The question arises as to whether these 19-segmented, gonopodal males can molt or whether development is arrested at this stage, and evidently, genetic control over the timing of gonopod development is not as rigid in desmonines as in other sphaeriodesmids or most polydesmoids.

This contribution addresses the only unstudied family of the polydesmid suborder Chelodesmidea in North America and completes alpha-level studies of the latter taxon except for the xystodesmid genera *Apheloria* and *Nannaria*, both authored by Chamberlin. The Chelodesmidea is represented on this continent by the Xystodesmidae, of which all other genera have either been revised or subjected to comprehensive study; the Eurymerodesmidae, revised by Shelley (1989); and the family Euryuridae, whose principal genera were revised by Hoffman (1978) and Shelley (1982). For completion, I expand this study to include the Mexican desmonine species described by Silvestri (1910) – *Taphrodesmus vestitus*, *Peridyso-desmus bifidus*, and *P. trifidus* – and the Guatemalan species of *Hybocestus* described by Hoffman (1959). I also diagnose three new species of *Hybocestus*, so this contribution revises the entire subfamily, although the literature review only covers *Desmonus*. Acronyms of sources of preserved study material are as follows:

AMNH - American Museum of Natural History, New York, New York.

BMNH - The Natural History Museum, London, United Kingdom.

CAS - California Academy of Sciences, San Francisco.

DEP - Dipartimento di Entomologia e Zoologia Agraria, Portici, Italy.

FSCA - Florida State Collection of Arthropods, Gainesville.

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

NCSM - North Carolina State Museum of Natural Sciences, Raleigh.

NMNH - National Museum of Natural History, Smithsonian Institution,
Washington, D. C.

TMM - Texas Memorial Museum, University of Texas, Austin.

VMNH - Virginia Museum of Natural History, Martinsville.

WAS - Private collection of W. A. Shear, Hampden-Sydney, Virginia.

LITERATURE REVIEW

The history of *Desmonus* begins with the proposal of *Sphaeriodesmus pudicus* by Bollman (1888) for specimens from Little Rock, Pulaski County, and Okolona, Clark County, Arkansas; in a subsequent catalog of North American myriapods, Bollman (1893) cited *S. pudicus* from Arkansas in general. Believing that different species were involved, Causey (1958) subsequently assigned *pudicus* to the specimen from Little Rock and placed that from Okolona in her new species, *D. inordinatus*. In the other relevant work of the 19th century, Cook (1898) erected *Desmonus* and the family Desmonidae, transferred *S. pudicus* into the genus, and proposed *D. earlei*, the type species, for a form from Auburn, Alabama.

The first references to these taxa in the 20th century were by Attems (1914, 1940), who reduced the Desmonidae to subfamilial status in the Sphaeriodesmidae and provided accounts of the genus and both species. Chamberlin and Mulaik (1941) proposed *Ethocyclus* and *E. atophus* for a form from Kerr County, Texas, which they assigned to the Cyclodesmidae. Loomis (1943) erected *Desmoniella* and *Desmoniella curta* for a 19-segmented, gonopodal male from Pontotoc County, Oklahoma. Chamberlin and Hoffman (1958) summarized all the taxa then available and added eastern Tennessee and central Kentucky to the distribution of *D. earlei*. Later that year, Causey (1958) proposed *D. inordinatus* for a 19-segmented, gonopodal male from Okolona, Arkansas, and cited specimens from ten other Arkansas counties and Barry County, Missouri. Causey also described *D. austrus*, from Columbia County, Arkansas, northern Louisiana, and eastern Texas; reported an unidentified species from the Great Smoky Mountains National Park, Tennessee; and divided *D. earlei* into two geographic races - *D. e. mancus*, from Jackson County, Florida, and Polk County, Georgia, and the nominate subspecies, from eastern Kentucky, northern Tennessee, and Atlanta, Georgia. Loomis (1959) placed *Ethocyclus* in synonymy under *Desmonus* and described *D. conjunctus*, *D. crassus*, and *D. distinctus*, all from Texas. In the last work of this decade, Hoffman (1959) concluded that the Desmonidae did not warrant recognition at either the familial or subfamilial levels, and 14 years later, Shear (1973) also reached this conclusion.

In the ensuing decade, Causey (1963) and Loomis (1963) recorded localities of *D. austrus* from Louisiana and Texas, respectively; two years later, Reddell (1965)

reported a Texas cave record of *D. conjunctus*. Loomis (1966) proposed the monotypic genera *Stilbopagus* and *Tetraporosoma* for females from Chipinque Mesa, Nuevo León, Mexico. Two years later, he (Loomis 1968a) described males of the former, but curiously he omitted both genera from the Mexico/Central America checklist (1968b). Jeekel (1971) summarized the genera established before 1958, and Loomis (1976) added a record of *D. crassus*. Hoffman (1979, 1980) revived the Desmoninae at the subfamily level and divided it into two tribes – Desmonini, including *Desmonus*, *Desmoniella*, and *Cyphodesmus* Peters; and Hybocestini, for *Hybocestus* Hoffman. He (Hoffman 1979) also removed *Cyphodesmus hidalgonus* Chamberlin (1943) from the Desmoninae; placed *Stilbopagus* in synonymy under *Desmonus* and *Peridysodesmus* under *Cyphodesmus*; and left *Taphrodesmus* and *Tetraporosoma* unassigned.

Family Sphaeriodesmidae

Subfamily Desmoninae

Desmonidae Cook, 1898: 463. – Chamberlin & Hoffman, 1958: 15. – Loomis, 1959: 157. – Reddell, 1965: 162; 1970: 399.

Desmoninae: Attems, 1914: 280; 1940: 381. Hoffman, 1979: 4, 8; 1980: 162.

DIAGNOSIS: Small to moderate-size Sphaeriodesmidae with smooth to variably tuberculate metaterga on segments 5-19; paranota strongly declined, extending essentially directly ventrad, those of segments 4-19 demarcated by pits on anterior metatergal margins, those of segment 3 broadly expanded anteriorly in adults, obscuring 2nd paranota and covering sides of head when coiled, narrowly expanded in juveniles and 2nd paranota visible; gonopods usually developing on 20-segmented, adult males, occasionally on 19-segmented subadults; telopodite with or without variable prefemoral process, acropodite flagelliform.

REMARKS: Desmonines are hard, heavily sclerotized diplopods; the softest individuals that I have encountered are early juveniles, but even they are relatively hard. Preserved, coiled specimens will not unroll without breakage, which is necessary to determine sex and dissect the gonopods, so examining a sample quickly reduces it to shards and fragments.

TRIBE DESMONINI

Desmonini: Hoffman, 1979: 8; 1980: 162.

DIAGNOSIS: Small- to large-bodied Desmoninae; gonopodal telopodite comprised of large, prominent prefemoral process, divided near midlength or distad, and flagelliform acropodite running along, and closely appressed to, prefemoral process.

DISTRIBUTION: Southcentral Kentucky, southwestern Missouri, and eastcentral Oklahoma, to the northern Florida panhandle and Morelos and central Veracruz, Mexico (Fig. 17).

COMPONENTS: *Desmonus* Cook, *Cyphodesmus* Peters.

Genus *Desmonus* Cook

Desmonus Cook, 1898: 463. – Attems, 1940: 381. – Chamberlin & Hoffman, 1958: 16. – Causey, 1958: 174. – Loomis, 1959: 157-158; 1963: 119; 1976: 287. – Jeekel, 1971: 259. – Hoffman, 1979: 8; 1980: 162.

Ethocyclus Chamberlin & Mulaik, 1941: 58. – Chamberlin & Hoffman, 1958: 15. – Jeekel, 1971: 261.

Desmoniella Loomis, 1943: 400. – Chamberlin & Hoffman, 1958: 15. – Causey, 1958: 174. – Jeekel, 1971: 259. – Hoffman, 1979: 8; 1980: 162.

Stilhopagus Loomis, 1966: 516; 1968a: 385.

Tetraporosoma Loomis, 1966: 517-518. – Hoffman, 1979: 8; 1980: 162. **New Synonymy!**

TYPE SPECIES: *Desmonus earlei* Cook, 1898, by original designation.

DIAGNOSIS: Small, slender Desmonini; gonopodal prefemoral process divided distad into short anterior and caudal branches, latter redivided apically into medial and lateral subbranches; acropodite terminating near midlength of caudal prefemoral branch.

SPECIES: Two.

DISTRIBUTION: Occupying three segregated regions as follows: from southcentral Kentucky and Tennessee west of the eastern arm of the Tennessee River to eastern Mississippi, northcentral Georgia, and the northern Florida panhandle; from southwestern Missouri to northcentral Louisiana, northeastern Texas, and eastcentral Oklahoma; and from central Texas to central Nuevo León, Mexico (Fig. 17).

REMARKS: Hoffman (1969) considered *Desmonus* to be a "late Coenozoic austral immigrant" into the United States.

The apical division of the caudal branch of the prefemoral process into two subbranches has been overlooked by all previous authors; the separation or overlap of these structures is the only difference between the two species.

Loomis (1966) proposed *Tetraporosoma* for an 18-segmented female from Nuevo León that ostensibly had ozopores on slight elevations on the paranota of segments

4-17, but I saw no such structures when examining this specimen. This female is a typical juvenile of *D. pudicus*, and *Tetraporosoma* falls in the generic synonymy.

Desmonus earlei Cook

Figs. 2-11

Desmonus earlei Cook, 1898: 463-465, pl. 22, figs. 1a-n. Attems, 1940: 381-382, figs. 539, 539a. Chamberlin and Hoffman, 1958:16.

Desmonus earlei earlei: Causey, 1958: 174-175.

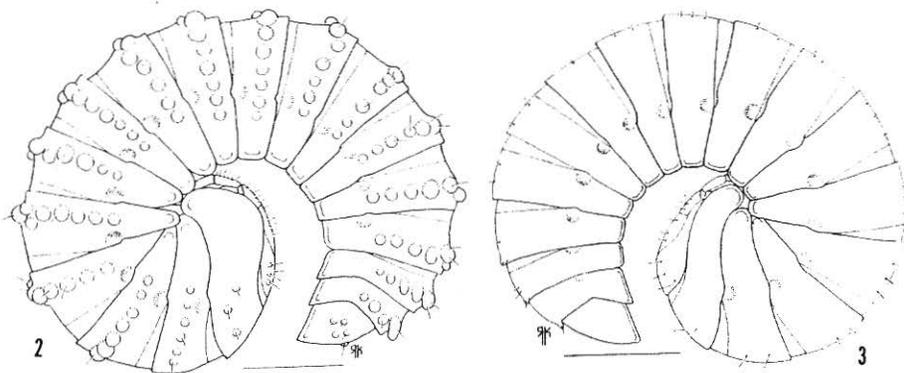
Desmonus earlei mancus Causey, 1958:175. **New Synonymy!**

TYPE SPECIMENS: Four male and two female syntypes (NMNH) taken by O. F. Cook and F. S. Earle in July 1896 at Auburn, Lee County, Alabama.

DIAGNOSIS: Subbranches of caudal branch of gonopodal prefemoral process separated, apex of acropodite visible through gap; 19-segmented, subadult males with gonopod primordia only, never with fully-formed gonopods.

Color in life: Unknown.

DESCRIPTION: Body slender, comprised of head and 20 segments in adults, capable of coiling into compact, laterally flattened spiral of around 4.1 mm diameter with head located centrally and covered laterally by 3rd paranota (Figs. 2-3), epiproct extending over 3rd-4th tergites, paranota fitting perfectly together so as to completely enclose venter, approximate linear length 6.9 mm, maximum width 2.0 mm, widest at anterior end, tapering smoothly and continuously in caudal half of body.

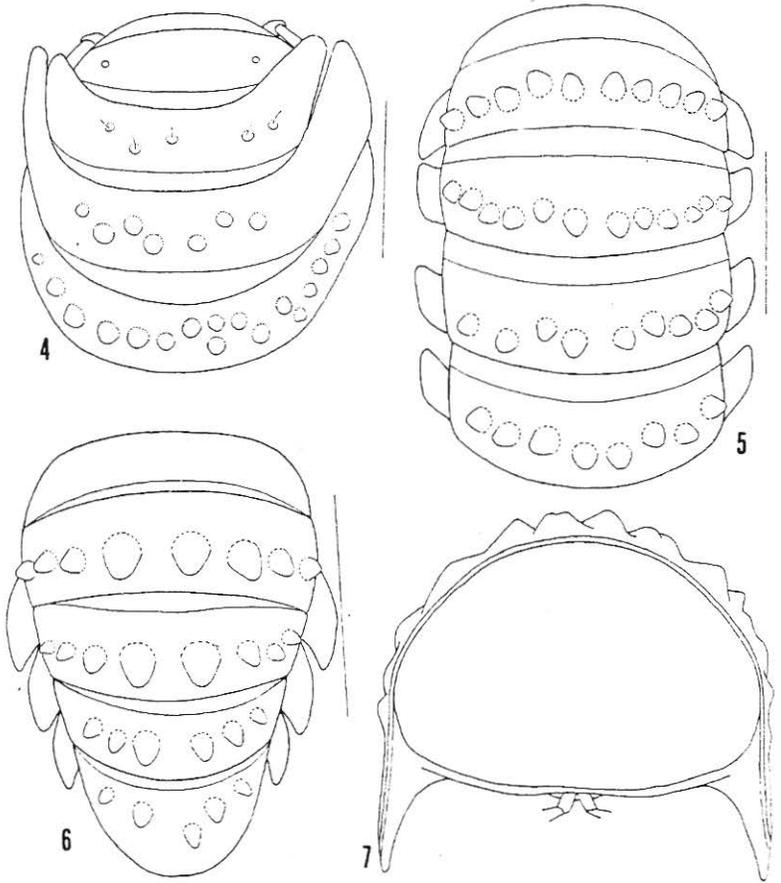


Figs. 2, 3. *Desmonus earlei*, somatic features. 2, lateral view of left side of tuberculate, 20-segmented female from Lee County, Alabama. 3, lateral view of right side of smooth, 19-segmented juvenile from Lee County, Virginia. Scale lines = 1.00 mm for each figure.

Head moderately large, slightly narrower than collum, epicranium lightly hirsute, suture distinct. Antennae relatively short and moderately clavate, reaching backwards to midlength of 2nd tergite, becoming progressively more hirsute distad, relative lengths of antennomeres $6 > 2 > 3 > 4 = 5 > 1 > 7$. Interantennal isthmus broad, subequal to length of 2nd antennomere. Head below interantennal region with moderately dense pubescence.

Collum subtrapezoidal, caudal margin shorter than anterior, surface smooth to subgranular, with or without (if removed by abrasion with substrate) a row of five moderately long setae, two on either side of midline. Proterga smooth; metaterga with or without four setae on each side of midline, arising either from tubercles or smooth surface; paranota steeply declined, extending nearly directly ventrad (Fig. 7). 2nd metatergite smooth to subgranular, caudal margin curving gently anteriorly laterad, anterior margin cupulate, curving strongly anteriorly, paranota slender, extending anteriorly along lateral margins of collum to near level of anterior margin of latter, with or without four setae on either side of midline, one on each paranotum just above base. 3rd metatergite subgranular to moderately tuberculate, caudal margin curving gently anteriorly laterad, anterior margin concave, curving strongly anteriorly laterad, paranota greatly expanded, about twice as wide as those following, obscuring 2nd paranota in lateral view in adults, anterior margin broadly rounded, curving anteriorly then laterad to blunt caudolateral corner, caudal margin shorter and slightly concave (Fig. 2); 3rd paranota with same general configuration but distinctly narrower and less tuberculate in subadults, 2nd paranota visible in lateral perspective (Fig. 3). 4th metatergite variably tuberculate, anterior and caudal margins parallel, curving gently anteriorly, paranota moderately broad, anterior margin demarcated by shallow depression, curving gently anteriorly, caudal margin gently concave, lateral margin short, sublinear (Figs. 1, 4). 5th metatergite similar to 4th but more strongly tuberculate and paranota slightly narrower, anterior margin demarcated by distinct circular pit, curving faintly anteriorly, caudal margin sublinear, meeting anterior margin in subacuminate corner. Metatergites 6-15 subsimilar, anterior margins not curving anteriorly, following general body contours, anterior paranotal margins demarcated by pit, angling caudolaterad, caudal paranotal margins demarcated by notch, angling anteriolaterad and meeting anterior margin at variable corner, subacuminate on 6, becoming progressively broader and more linear caudad, surfaces variably tuberculate with 5-7 rounded to subconical tubercles on either side of midline, strongest segmental tubercles usually 2nd-3rd from midline on each side (Fig. 5). Metatergites 16-18 similar to preceding tergites but tubercles generally stronger and more conical, becoming progressively more so caudad, caudolateral paranotal corners slightly extended. Metatergite 19 similar to 16-18 but the three tubercles on each side of midline often coalesced basally into single, broad elevation with three

small apical lobes. Epiproct broadly rounded, lightly to moderately tuberculate, margin slightly extended in midline (Fig. 6).



Figs. 4-7. *Desmonus earlei*, somatic features of tuberculate, 20-segmented female from Lee County, Alabama. 4, head and first four terga, dorsolateral view. 5, midbody (9-12) terga, dorsal view. 6, caudal (17-20) terga, dorsal view. 7, profile of midbody segment, caudal view. Scale lines = 1.00 mm for each figure.

Pleural and sternal areas glabrous and smooth; strictures faint, indistinct. Pregonopodal sterna narrow, without modifications; postgonopodal sterna narrow, margins straight. Legs generally long and slender, lightly hirsute, pregonopodal legs slightly shorter and heavier, podomeres without lobes, projections, or other modifications, tarsal claws short, gently curved. Gonapophyses long and slender, extending caudad between 3rd coxae. Hypoproct broadly triangular, apically broad; paraprocts with margins slightly thickened.

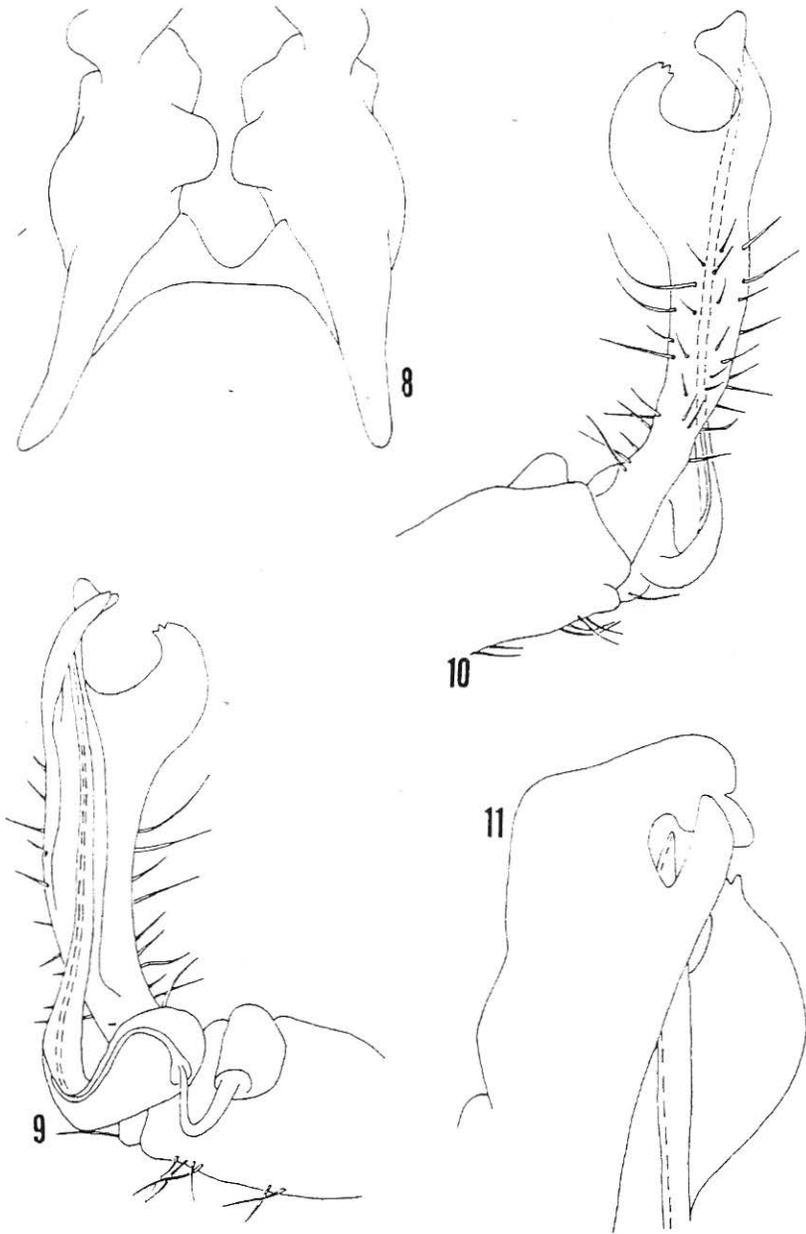
Gonopodal aperture relatively large, subovoid, caudal margin slightly elevated and thickened. Gonopods *in situ* with telopodites well separated, extending over anterior aperture margin in parallel arrangement, slightly overlapping coxae of 6th legs. Gonopod structure as follows (Figs. 8-11): Coxa with broad, truncated apophysis on medial surface, separated from opposite member by lightly sclerotized sternum, latter with broad, triangular, lateral lobes. Prefemoral process much larger than acropodite, relatively narrow basally, widening distal to midlength, divided distad into anterior and caudal branches, with scattered hairs on lateral surface to near level of division point; anterior branch entire, curving gently caudad, with variable number of short, apical teeth; caudal branch subdivided into medial and lateral subbranches, latter extending subventrad, expanding apically, former continuous with fold in stem of prefemoral process, curving antieriad and leaving gap between lateral subbranch. Acropodite arising basally from prefemur, slender and flagelliform, curving anteromedial basally then extending ventrad, running along, and closely appressed to, medial face of prefemoral process, extending along caudal prefemoral branch and terminating at about half length of latter, apically acuminate, tip visible through gap between medial and lateral subbranches of prefemoral process. Prostatic groove running along acropodite to apical opening.

Variation.: All 20-segmented adults exhibit dorsal tubercles that are always larger on the caudal metaterga, but the degree of sculpturation varies widely. Some display strong tubercles that are rounded on the anterior tergites and subconical caudad (Fig. 2), whereas others are less tuberculate, with smooth anterior metatergites, low, rounded tubercles on midbody segments, and only slightly to moderately subconical tubercles caudad. The tubercles generally arise on tergites 3-5 and either end abruptly on the 19th segment or continue as low to moderate tubercles onto the epiproct. These are considerable differences, but they represent only intraspecific variation and are shown by specimens throughout the range. Causey (1958) erected the subspecies, *D. e. mancus*, for a variant with "degenerate tubercles and shorter setae," which does not warrant taxonomic recognition and is placed in synonymy. Subadults and younger juveniles are usually relatively smooth, exhibiting at most only slight, indistinct tubercles on the caudalmost metaterga (Fig. 3), so the tubercles develop primarily at the final molt.

The breadth of the 3rd paranota also varies. In adults, the structures are broadly expanded and obscure the 2nd paranota in lateral view (Fig. 2). However, in subadults and younger juveniles they are narrower, although exhibiting the same general configuration, and the 2nd paranota are visible in lateral view (Fig. 3); fig. 1 shows the same condition in *D. pudicus*.

The degree of dorsal setation also varies greatly, as many setae are removed by abrasion from the substrate. Some individuals are practically glabrous.

There are no records of 19-segmented, gonopodal males of *D. earlei*, and I did



Figs. 8-11. *Desmonus earlei*, gonopodal characters. 8, sternum and coxae of male from Liberty County, Florida, caudodorsal view. 9, right gonopod of the same specimen, medial view. 10, the same, lateral view. 11, distal extremity of telopodite of the same specimen.

not find any during this study; all subadults have gonopod primordia.

Aside from minor differences in the irregularity of the margins of the prefemoral process, the gonopods of *D. earlei* are uniform throughout the range.

ECOLOGY: *Desmonus earlei* occurs under logs, leaves and other debris, and in upper layers of the substrate; individuals are typically heavily encrusted with soil, which especially adheres to the depressions between the tubercles. Specimens from Lee County, Virginia, were encountered in pine, oak, and sassafras litter. Samples from Liberty County, Florida, were taken in moist leaf litter and under rotten logs in mixed mesophytic forests.

DISTRIBUTION: The easternmost generic area (Fig. 17), which covers parts of the Coastal Plain, Piedmont Plateau, Appalachian Plateaus, and Interior Low Plateaus Physiographic Provinces: Approximate maximal dimensions are 470 mi (752 km), north-south, and 300 mi (480 km), east-west; the present records are the first for the species and all higher taxa from Mississippi and Virginia. I delete Causey's record (1958) of juveniles from the Great Smoky Mountains National Park, Sevier County, Tennessee, as there are no such specimens in the FSCA, where her collection was transferred after her death in 1979, nor are there specimens in any collection from east of the eastern arm of the Tennessee River. I have collected extensively in the "Smokies" without finding a single individual of *Desmonus* and believe this report probably refers to glomerids, as *Onomeris* Cook (Glomeridae) does occur in these mountains. In addition to the types, the following specimens were examined:

KENTUCKY: *Edmonson Co.*, Mammoth Cave Nat. Pk., M, 2F, 4 juvs., 25 August 1961, N. B. Causey (FSCA).

VIRGINIA: *Lee Co.*, Cumberland Gap National Historical Park, Wilderness Road, 2 juvs., 6 September 1970, W. A. Shear (WAS) and trail to Skylight Cv., M, 7F, 10 July 1971, W. A. Shear (WAS).

TENNESSEE: *Anderson Co.*, Norris, Norris Park, M, 18 June 1940, N. B. Causey (FSCA). *Fentress Co.*, Jamestown, Jordan Motel, juv., 13 April 1963, H. R. Steeves (FSCA). *Wilson Co.*, Cedars of Lebanon St. Pk., M, 2F, 16 June 1976, R. M. Shelley (NCSM).

GEORGIA: *Baldwin Co.*, nr. Browns, 4F, 11 June 1960, L. Hubricht (VMNH). *Clarke Co.*, Athens, M, F, 15 September 1959, W. Suter (FSCA). *DeKalb Co.*, Stone Mtn., F, 4 juvs., 14 September 1954, N. B. Causey (FSCA). *Fulton Co.*, Atlanta, along US hwy. 41 nr. Chattahoochee R., M, F, 30 April 1961, L. Hubricht (VMNH). *Monroe Co.*, 1.5 mi (2.4 km) N Culloden, M, F, 4 March 1961, L. Hubricht (VMNH). *Polk Co.*, 9 mi (14.4 km) W Centerton, F, 17 September 1958, N. B. Causey (FSCA).

ALABAMA: *Lee Co.*, Auburn, 2M, 3F, July 1896, collector unknown (NMNH) and F, 14 June 1959, collector unknown (FSCA) TYPE LOCALITY; and Wright's Mill nr. Auburn, MM, FF, July 1896, collector unknown (NMNH); *Madison Co.*, Monte Sano St. Pk., M, 17 May 1972, S. B. Peck (WAS). *Pike Co.*, "The Pocosin," exact location unknown, 3 juvs., 19 August 1962, H. R. Steeves (FSCA). *Talladega Co.*, Sylacauga, 2 juvs., 18 September

1959, W. Suter (FSCA). *Tuscaloosa Co.*, along Hurricane Cr., nr. Peterson, 2F, 1-3 March 1951, B. D. Valentine (VMNH).

FLORIDA: *Jackson Co.*, Florida Caverns St. Pk., F, 27 May 1958, N. B. Causey (AMNH) and F, 13 August 1965, S. B. Peck (FSCA). *Jefferson Co.*, Monticello, Big Bend Hort. Lab, juv., 9 June 1969, collector unknown (FSCA). *Leon Co.*, Tall Timbers Res. Sta. N Tallahassee, F, 14 June 1968, W. H. Whitcomb, W. W. Baker (FSCA). *Liberty Co.*, Torreya St. Pk., juv., 14 May 1964, H. A. Denmark (FSCA), MM, FF, juvs., 24-25 January 1965, N. B. Causey, H. V. Weems (FSCA), F, 8-14 June 1968, W. W. Baker (FSCA), and juv., 21 October 1978, R. Franz (NCSM).

MISSISSIPPI: *Wayne Co.*, along Buckatura R., F, 19 July 1959, N. B. Causey (FSCA).

The following additional literature records are deemed valid:

KENTUCKY: *Bell Co.*, Pine Mountain St. Pk. *Whitley Co.*, Cumberland Falls St. Pk. (Causey 1958).

GEORGIA: *Fulton Co.*, Bankhead Lake (Causey 1958).

Desmonus pudicus (Bollman)

Figs. 1, 12-14

Sphaeriodesmus pudicus Bollman, 1888:3-4; 1893:124.

Desmonus pudicus: Cook, 1898:465-466, pl. 22, figs. 2a-b. Attems, 1940:382, fig. 540. Chamberlin and Hoffman, 1958:16. Causey, 1958:175-176, fig. 1.

Ethocyclus atophus Chamberlin & Mulaik, 1941:58-59. Chamberlin & Hoffman, 1958:15. **New Synonymy!**

Desmoniella curta Loomis, 1943:401, figs. 14a-c, pl. 1, fig. 3. Chamberlin and Hoffman, 1958:16. **New Synonymy!**

Desmonus inordinatus Causey, 1958:176-177, fig. 2. **New Synonymy!**

Desmonus austrus Causey, 1958:178, fig. 3; 1963:76. Loomis, 1963:119. **New Synonymy!**

Desmonus conjunctus Loomis, 1959:158, figs. 1-3. Reddell, 1965:162. **New Synonymy!**

Desmonus crassus Loomis, 1959:158, fig. 4; 1976:287. **New Synonymy!**

Desmonus distinctus Loomis, 1959:158, 160, fig. 5. **New Synonymy!**

Desmonus atophus: Loomis, 1959:160.

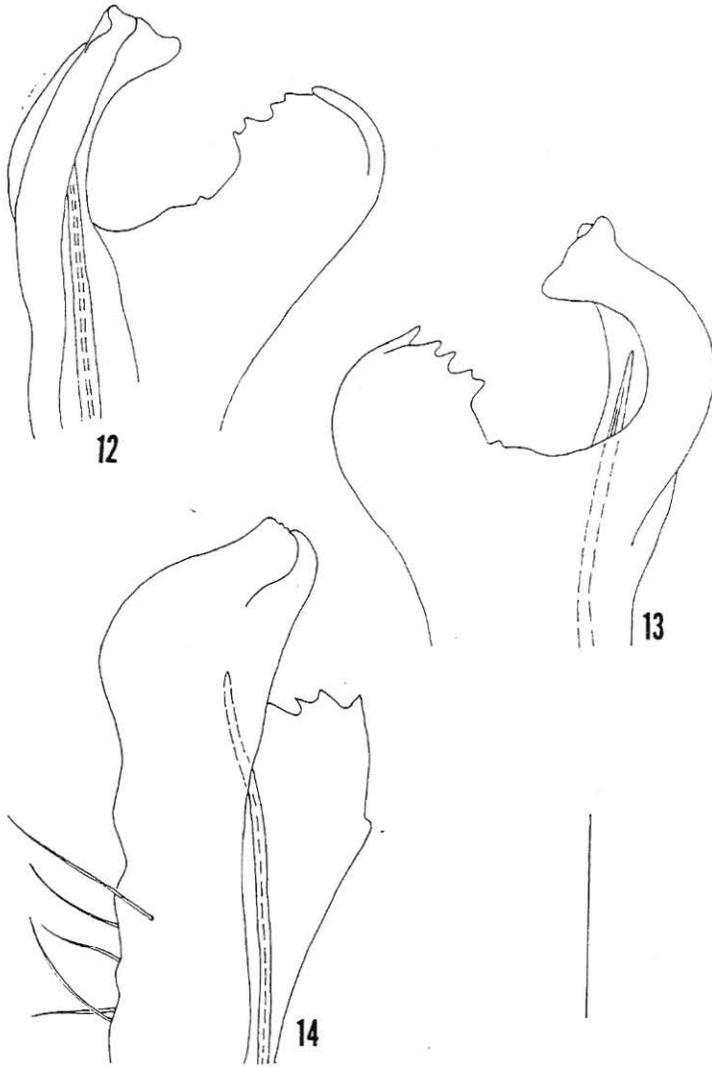
Stilbopagus acclivus Loomis, 1966:516-517; 1968a:385, figs. 2-3. **New Synonymy!**

Tetraporosoma seriata Loomis, 1966:518-519, figs. 3-5. **New Synonymy!**

TYPE SPECIMEN: Male lectotype (NMNH) taken by an unknown collector on an unknown date at Little Rock, Pulaski County, Arkansas. The original type series also

contained a female from Okolona, Clark County, Arkansas, and on 2 September 1959, N. B. Causey labeled the Little Rock male as the lectotype. I now formalize this action.

DIAGNOSIS: Subbranches of caudal branch of gonopodal prefemoral process overlapping, obscuring tip of acropodite (Figs. 12-14); 19-segmented subadult males usually with gonopod primordia, occasionally with fully-formed gonopods.



Figs. 12-14. *Desmonus pudicus*, gonopodal characters. 12, distal extremity of telopodite of male from San Patricio County, Texas, medial view. 13, the same gonopod, lateral view. 14, the same gonopod, caudoventral view. Scale line = 1.00 mm for all figures.

COLOR IN LIFE: The specimens that I collected in San Patricio County, Texas, displayed a pinkish base color with apically white tubercles.

VARIATION: Variation in *D. pudicus* is the same as in *D. earlei* regarding the tubercles, setation, and 3rd paranota. The 19-segmented female in fig. 1 is an exception to the general condition that juveniles exhibit at most only slight, indistinct tubercles on the caudalmost metatergites. Aside from differences in the irregularity of the margins of the prefemoral process, the gonopods of *D. pudicus* are uniform throughout the range.

ECOLOGY: Individuals from the Welder Wildlife Refuge, San Patricio County, Texas, were found under dung, oak leaf litter, and small broken branches. The millipede was extremely abundant at this site in February 1986, and I could have collected hundreds of specimens.

DISTRIBUTION: The two western areas of the genus (Fig. 17). Approximate maximal dimensions are as follows: that from Missouri to Louisiana, 265 mi (424 km), east/west, and 285 mi (456 km), north/south; that from Texas to Nuevo León, 140 mi (224 km), east/west, and 370 mi (592 km), north/south. The sample from Spanish Wells, Travis County, Texas, cited as *Desmonus* sp. by Reddell (1970), is a juvenile male with gonopod primordia of *D. pudicus*. Specimens were examined as follows; the asterisks following juveniles from Clark and Conway counties, Arkansas, Pontotoc County, Oklahoma, and Travis County, Texas, indicate the presence of at least one 19-segmented, gonopodal male.

USA:

MISSOURI: *Barry Co.*, Roaring River St. Pk., M, 18 May 1964, N. B. Causey (NCSM).

OKLAHOMA: *Pontotoc Co.*, Arbuckle Mts. 2.3 mi (3.7 km) S Pittstown, 6F, 2 juvs.*, 22 May 1940, L. Hubricht (FSCA, MCZ, NMNH).

ARKANSAS: *Clark Co.*, Okolona, F, date and collector unknown (NMNH) and M, juv.*, 9 September 1950, N. B. Causey (FSCA); and Arkadelphia, M, 10 October 1950, N. B. Causey (AMNH). *Columbia Co.*, Magnolia, M, 6F, 24 December 1949, N. B. Causey (AMNH, FSCA). *Conway Co.*, Petit Jean St. Pk., F, juvs.*, date and collector unknown (FSCA). *Pulaski Co.*, locality unknown, M, juvs., 22 December 1949, N. B. Causey (FSCA); and Little Rock, M, date and collector unknown (NMNH) LECTOTYPE LOCALITY. *Washington Co.*, Devil's Den St. Pk., M, 2F, 25 September 1949, and 3M, F, 29 May 1964, N. B. Causey (FSCA); and West Fork, 2M, 30 October 1951, collector unknown (FSCA).

LOUISIANA: *Caddo Par.*, Shreveport, M, F, juv., 24 March 1967, N. B. Causey (FSCA).

TEXAS: *Bandera Co.*, locality unknown, F, December 1939, S. & D. Mulaik (NMNH). *Bandera/Bexar cos.*, between Bandera & Helotes, M, F, 26 December 1958, E. M., J. C., & H. F. Loomis (NMNH). *Bastrop Co.*, Bastrop St. Pk., M, 2F, 2-3 April 1960, J. C. Loomis (NCSM). *Bexar Co.*, "Mattke Cave (Cv.)," Helotes, F, juv., 10 June 1993, J. R. Reddell, M. Reyes (TMM); "40 mm Cv.," ca. 1 mi (1.6 km) NE Camp Bullis, F, 29 November 1993, J. Ivy, J. R. Reddell, M. Reyes (TMM); and "Up the Creek Cv.," Camp Bullis, F, 30 March

1995, J. R. Reddell, M. Reyes (TMM). *Blanco Co.*, Flat Cr. Ranch, ca. 12 mi (19.2 km) E Johnson City, F, 28 May 1995, A. G. Grubbs (TMM). *Burnet Co.*, Marble Falls, 2M, F, 15 February 1975, J. C. Loomis (FSCA); "Wagon Trail Cv.," 10 mi (16 km) W Liberty Hill, 4 juvs., 20 October 1990, J. R. Reddell, M. Reyes (TMM); "Twin Digs Pit," 10 mi (16 km) W Liberty Hill, juv., 11 December 1990, J. R. Reddell, M. Reyes (TMM); and "Big Bad Wolf Cv.," 5 mi (8 km) NW Spicewood, M, 13 May 1993, A. G. Grubbs, S. Brossard, T. Whitfield (TMM). *Cameron Co.*, Brownsville, F, December 1905, O. F. Cook (NMNH). *Cass Co.*, Linden, 2M, 9 April 1950, P. Smith, J. Berger (FSCA). *Comal Co.*, Spring Branch, M, 14 July 1941, S. & D. Mulaik (NMNH); New Braunfels, M, 3F, 29 December 1958, E. M. & H. F. Loomis (FSCA); "Kappleman Cv.," 5 mi (8 km) E Bulverde, M, 15 March 1964, J. R. Reddell, B. Russell (FSCA); and 2.5 mi (4 km) S Sattler, MM, FF, juvs., 12 October 1964, J. R. Reddell (FSCA). *Karnes Co.*, Karnes City, MM, FF, 14 November 1959, N. B. Causey (NCSM). *Kendall Co.*, 7.5 mi (12 km) N Boerne, M, F, 15 March 1969, J. R. Reddell (NCSM); 5 mi (8 km) SSW Boerne, 4M, 4F, 31 January 1959, E. M., J. C., & H. F. Loomis (NMNH); and 8 mi (12.8 km) SSW Boerne, M, F, 28 March 1964, H. F. Loomis (FSCA). *Kerr Co.*, 8 mi (12.8 km) N Kerrville, 2M, F, 3 August 1940, S. & D. Mulaik (NMNH); Kerrville, 2F, July 1940, S. & D. Mulaik (NMNH); and Raven Ranch, ca. 12 mi (19.2 km) S Kerrville, 3F, August and December 1939, and F, juv., June 1941, S. Mulaik (NMNH). *San Patricio Co.*, Welder Wildlife Ref., ca. 7 mi (11.2 km) N Sinton, M, 5F, 1 February 1961, 3F, 23 December 1961, M, F, 5 December 1965, and MM, FF, 21 November 1970, R. O. Albert (FSCA) and MM, FF, juvs., 21 February 1986, R. M. Shelley (NCSM). *Travis Co.*, "Little Black Hole," Austin, F, 9 June 1994, W. Elliott, P. Sprouse (TMM); Spanish Wells, juv., 26 June 1965, B. Russell (FSCA); 3 mi (4.8 km) E Oak Hill, M, 31 January 1995, A. G. Grubbs (TMM); and "Tooth Cv.," 12 mi (9.2 km) NW Austin, F, 6 June 1992, J. R. Reddell (TMM). *Victoria Co.*, locality unknown, MM, FF, December 1905 and August 1906, O. F. Cook (MCZ, NMNH). *Williamson Co.*, "Godwin's Goat Grave Cv.," ca. 4 mi (6.4 km) NW Georgetown, 2F, 7 April 1997, P. Sprouse (TMM); "Joint Effort Cv.," on TX hwy. 620, ca. 4 mi (6.4 km) W I-35, F, 25 June 1997, J. Reddell, M. Reyes (TMM); "Lobo's Lair," 2 mi (3.2 km) W Georgetown, M, juv., 11-13 September 1991, J. R. Reddell, M. Reyes (TMM); "Bluewater Cv. #2," Cedar Park, 2M, 21 April 1992, M. Wharton (TMM); "Water Tower Cv.," 3 mi (4.8 km) NNW Round Rock, F, 15 May 1993, J. R. Reddell, M. Reyes (TMM); "Short Stack Cv.," 1 mi (1.6 km) W Round Rock, F, April 1994, M. Warton (TMM); "Wild Card Cv.," 3 mi (4.8 km) W Round Rock, M, April 1994, M. Warton (TMM); "Scoot Over Cv.," 3 mi (4.8 km) W Round Rock, 2M, May 1994, M. Warton (TMM); and "Cedar Elm Sink," Cedar Park, F, 7 May 1989, M. Wharton (TMM).

MEXICO:

NUEVO LEÓN, Chipinque Mesa, 2F, 8 June 1965, H. F. Loomis (NMNH); *Horsetail Falls*, 2M, 3F, 8 June 1967, H. F. Loomis (NMNH), and 1/3 way up rd. to Horsetail Falls, 2F, 2 juvs., 8 June 1967, H. F. Loomis (FSCA).

The following additional literature records are deemed valid:

MISSOURI: *Barry Co.*, Mark Twain Nat. For. (Causey 1958).

ARKANSAS (all by Causey 1958): *Benton Co.*, Monte Ne. *Carroll Co.*, Lake Leatherwood. *Clark Co.*, 4 mi (6.4 km) E Arkadelphia and 15 mi (24 km) E Okolona. *Columbia*

Co., Lumber and 4 mi (6.4 km) E Magnolia. *Johnson Co.*, locality unspecified. *Newton Co.*, Compton. *Pike Co.*, Antoine. *Polk Co.*, Rich Mountain. *Pulaski Co.*, Sweet Home. *Sebastian Co.*, 3 mi (4.8 km) N Hackett. *Sevier Co.*, Wilton. *Washington Co.*, Farmington, Goshen, Mt. Sequoyah, and Spring Valley.

LOUISIANA (all by Causey 1958): *Claiborne Par.*, 5 mi (8 km) S Junction City. *Lincoln* and *Winn Pars.*, localities unspecified.

TEXAS: *Guadalupe Co.*, Lake Placid, between New Braunfels and Seguin (Loomis 1959).

REMARKS. The new synonymies were determined by directly comparing the types of these names with the lectotype and other specimens of *D. pudicus* from central Arkansas.

In the diagnosis of *D. inordinatus*, Causey (1958) stipulated that the species has 19 rather than 20 segments. She cited samples from 11 other counties, with males from Carroll, Clark, Conway, Pike, and Polk counties, Arkansas, and Barry County, Missouri. The only sample available to me besides the holotype, is the one from Conway County, which does include a 19-segmented, gonopodal male. The only other anomalous males that I examined were the types of *Desmoniella curta* and one from Travis County, Texas.

Genus *Cyphodesmus* Peters

Cyphodesmus Peters, 1864: 530. Pocock, 1909: 118. Attems, 1940: 377. Loomis, 1968b: 43. Jeekel, 1971: 257. Hoffman, 1979: 4-5; 1980: 162.

Taphrodesmus Silvestri, 1910: 357. Attems, 1940: 382. Loomis, 1968b: 46. Jeekel, 1971: 289. Hoffman, 1979: 8; 1980: 162. **New Synonymy!**

Peridysodesmus Silvestri, 1910: 357-358. Attems, 1940: 378-379. Loomis, 1968b: 44. Jeekel, 1971: 345.

TYPE SPECIES. *Oniscodesmus mexicanus* Saussure, 1859, by monotypy.

DIAGNOSIS. Large, broad Desmonini; gonopodal prefemoral process divided near midlength into two or three relatively long, and one or two short, undivided branches; acropodite terminating at varying positions along major prefemoral branches.

DISTRIBUTION. Known only from Morelos and Veracruz, Mexico (Fig. 17).

SPECIES. Three.

Cyphodesmus mexicanus (Saussure)

Oniscodesmus mexicanus Saussure, 1859: 328; 1860: 278, pl. 1, fig. 2.

Cyphodesmus mexicanus: Peters, 1864: 530. Cook, 1898: 466. Pocock, 1909: 118. Attems, 1940: 377, fig. 535. Loomis, 1968b: 43. Hoffman, 1979: 5-7, figs. 1-8.

TYPE SPECIMENS. Male lectotype and female paralectotype (Museum d'Histoire Naturelle, Geneva, Switzerland) collected by H. De Saussure on an unknown date at Cordoba, Veracruz, Mexico.

DISTRIBUTION. Known definitely from two sites in Veracruz, the type locality and Fortin de las Flores (Hoffman 1979) (Fig. 17), which are only a few km apart in the interior of the state. A juvenile male (19 segments with gonopod primordia) from the following locality, some 120 mi (192 km) SE Cordoba, is tentatively assigned to *C. mexicanus*.

MEXICO: VERACRUZ: Lago Catemaco, 18°26'N, 95°06'W, juv., 12 February 1964, V. & B. Roth (CAS).

REMARKS. Hoffman's illustrations (1979) show the characters of this species.

Cyphodesmus vestitus (Silvestri), new combination

Taphrodesmus vestitus Silvestri, 1910: 357, fig. 1. Attems, 1940: 383, fig. 541.

Loomis, 1968b: 46.

Peridysodesmus bifidus Silvestri, 1910: 358, fig. 2. Attems, 1940: 379, fig. 537.

Loomis, 1968b: 44. **New Synonymy!**

Cyphodesmus bifidus: Hoffman, 1979: 5.

TYPE SPECIMENS. One female and two juvenile syntypes (DEP) collected by F. Silvestri in October 1908 at Jalapa, Veracruz state, Mexico.

DISTRIBUTION. Known only from Jalapa (Fig. 17).

REMARKS. Only one male has been taken of this species, a syntype of *P. bifidus*, which also has two female and two juvenile syntypes. The gonopods are mounted on a slide with a coverslip and are now mashed flat after nearly 90 years in this condition, so I cannot improve on Silvestri's illustration (1910, fig. 2). The specific name, *bifidus*, apparently was chosen to reflect the two long, major branches of the prefemoral process, but there are actually four branches, the others being a short, uncinuate one, directed laterad at the base of the division point, and a short, setose lobe, directed laterad at the base of the prefemoral process. As Jalapa is the type locality for both *T. vestitus* and *P. bifidus* and there are no known instances of sympatry in the subfamily, I combine these names. The former appeared first in Silvestri's paper and hence has priority.

Cyphodesmus trifidus (Silvestri)

Figs. 15-16

Peridysodesmus trifidus Silvestri, 1910: 358, fig. 3. Attems, 1940: 379. Loomis, 1968b: 44.

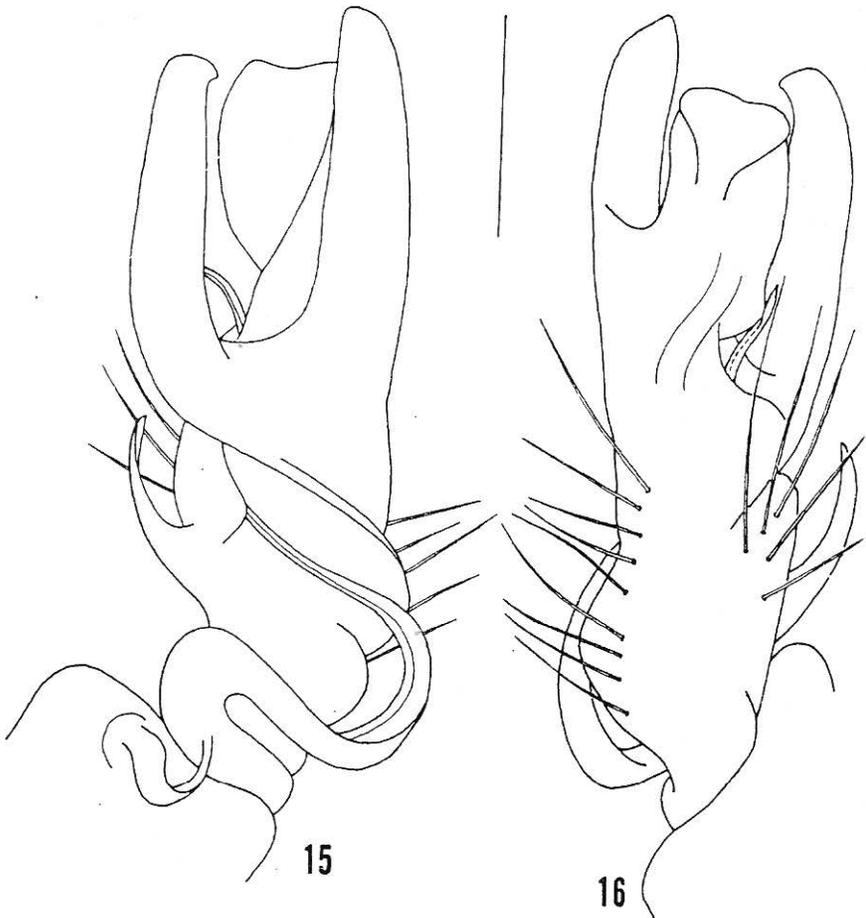
Cyphodesmus trifidus: Hoffman, 1979: 5.

TYPE SPECIMENS: Three male and three female syntypes (DEP) collected by F. Silvestri in October 1908 at Cuernavaca, Morelos state, Mexico; one female syntype (BMNH) taken at same locality in 1901.

DISTRIBUTION: Known from the type locality and the following additional site, some 140 mi (224 km) to the east (Fig. 17):

MEXICO: VERACRUZ: 1.2 mi (3.4 km) S Huatusco, cloud forest, MM, FF, S. & J. Peck (VMNH).

REMARKS: As with *P. bifidus*, Silvestri also mounted the gonopods of a syntype of *P. trifidus* on a slide with a coverslip, so I dissected the gonopods of another male to provide illustrations. The specific name apparently was chosen to reflect the three long, major branches of the prefemoral process, but there are actually four branches, the other being the short, falcate, basal branch, directed anteriorly (Figs. 15-16).



Figs. 15-16. *Cyphodesmus trifidus*, gonopod characters. 15, telopodite of left gonopod of male syntype, medial view. 16, the same, lateral view. Scale-line = 0.50 mm for both figures.

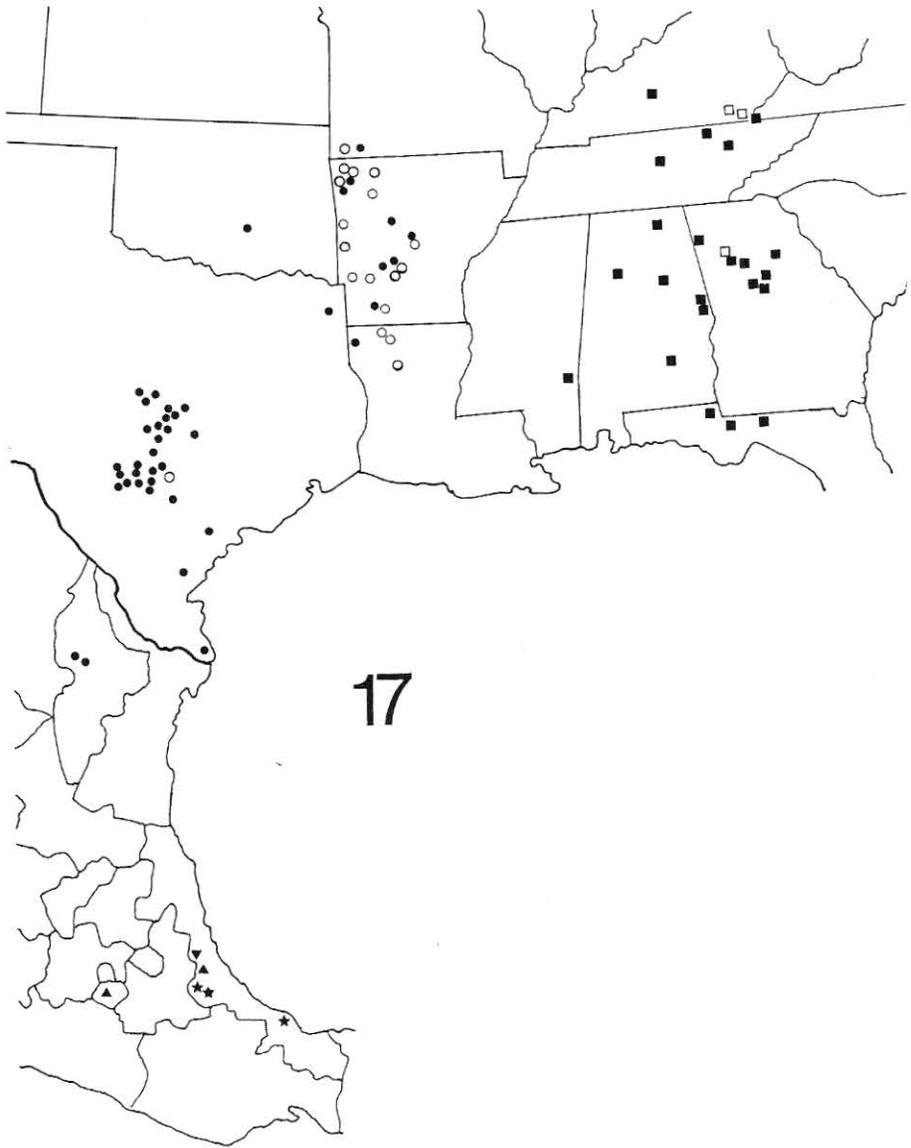


Fig. 17. Distribution of the Desmonini. Dots, *Desmonus pudicus*; squares, *D. earlei*; stars, *Cyphodesmus mexicanus*; inverted triangle, *C. vestitus*; upright triangles, *C. trifidus*. Open symbols denote literature records deemed valid.

Tribe Hybocestini

Hybocestini Hoffman, 1979:8; 1980:162.

DIAGNOSIS: Moderate-size Desmoninae; gonopodal telopodite with or without narrow, undivided prefemoral process, acropodite flagelliform, clearly segregated from latter, configuration variable but with one or more distal loops.

DISTRIBUTION: Known only from Alta Verapaz and Baja Verapaz Departments, Guatemala (Fig. 22).

Genus *Hybocestus* Hoffman

Hybocestus Hoffman, 1959: 173-174; 1980: 162. Loomis, 1968b:43.

TYPE SPECIES: *H. octonodus* Hoffman, 1959, by original designation.

DIAGNOSIS: With the characters of the tribe.

DISTRIBUTION: Same as that of the tribe (Fig. 22).

SPECIES. Four are known. The discovery of the three new species among unsorted material at the NMNH suggests that *Hybocestus* could be extremely diverse, with numerous species in poorly sampled parts of Guatemala.

Hybocestus octonodus Hoffman

Fig. 18

Hybocestus octonodus Hoffman, 1959: 174-177, figs. 1-4. Loomis, 1968b:44.

Hybocestus plagiodon Hoffman, 1959: 177-178, fig. 5. Loomis, 1968b: 44. **New Synonymy!**

TYPE SPECIMEN. Male holotype and female paratypes (NMNH) collected by O. F. Cook in May 1904 at Cobán, Alta Verapaz Dept., Guatemala.

DIAGNOSIS. Telopodite without prefemoral process; acropodite curving symmetrically anteriorly, in form of broad, simple loop (Fig. 18).

DISTRIBUTION. The vicinity of Cobán, Alta Verapaz Department, not Baja Verapaz. Trece Aguas, the type locality of *H. plagiodon*, is a small community about 3.1 mi (5 km) south of Cobán; its coordinates are 15°24'N, 89°45'W. The following additional (non-typical) samples from these localities are in the NMNH:

GUATEMALA: ALTA VERAPAZ, Cobán, in coffee plantation, 6M, 12F, 9 juvs., May 1904, O. F. Cook; Cobán, juv. M, May 1904; and Trece Aguas, F, 6 June 1907, O. F. Cook.

REMARKS. Hoffman (1959) noted that the holotypes of *H. octonodus* and *H. plagiodon* differ primarily in the fact that the former has 19 segments and the latter 20. I directly compared these specimens and found no other differences; the gonopods are virtually identical. As in *Desmonus*, I interpret the occurrence of gonopods on a subadult as an accident in genetic timing that does not warrant taxonomic recognition.

I draw this gonopod from a slightly more caudal angle than did Hoffman (1959), to be able to present comparable views of the other species that show all aspects of the distal acropodal loops. Parts of these loops would be hidden behind each other, or overlie the stem of the acropodite, in Hoffman's more anterior perspective, particularly in *H. spiralis*.

Hybocestus clavulus, new species

Fig. 19

TYPE SPECIMENS. Male holotype and three male and four female paratypes (NMNH) collected by O. F. Cook in May 1904 at Santa Rosa (ca. 9 mi (14.4 km) S Cobán), Tactic Mun., Alta Verapaz Dept., Guatemala. Tactic is a municipality or subdivision of Alta Verapaz.

DIAGNOSIS. Telopodite with short, spiniform prefemoral process extending directly anteriorly; acropodite with broad, flattened middle section extending anteriorly into broad, distal loop (Fig. 19).

DISTRIBUTION. Known only from the type locality.

REMARKS. The specific name is a latin word meaning "nail," and refers to the appearance of the prefemoral process.

Hybocestus bacrionis, new species

Fig. 20

TYPE SPECIMENS. Male holotype and three female paratypes (NMNH) collected by O. F. Cook in June 1904 at Seamay (15°23'N, 89°47'W), Alta Verapaz Dept., Guatemala.

DIAGNOSIS. Telopodite with long, subspatulate prefemoral process, leaning caudad and extending to near midlength of acropodite; latter linear and leaning caudad basally, curving broadly anteriorly distal to midlength and continuing into narrow distal loop (Fig. 20).

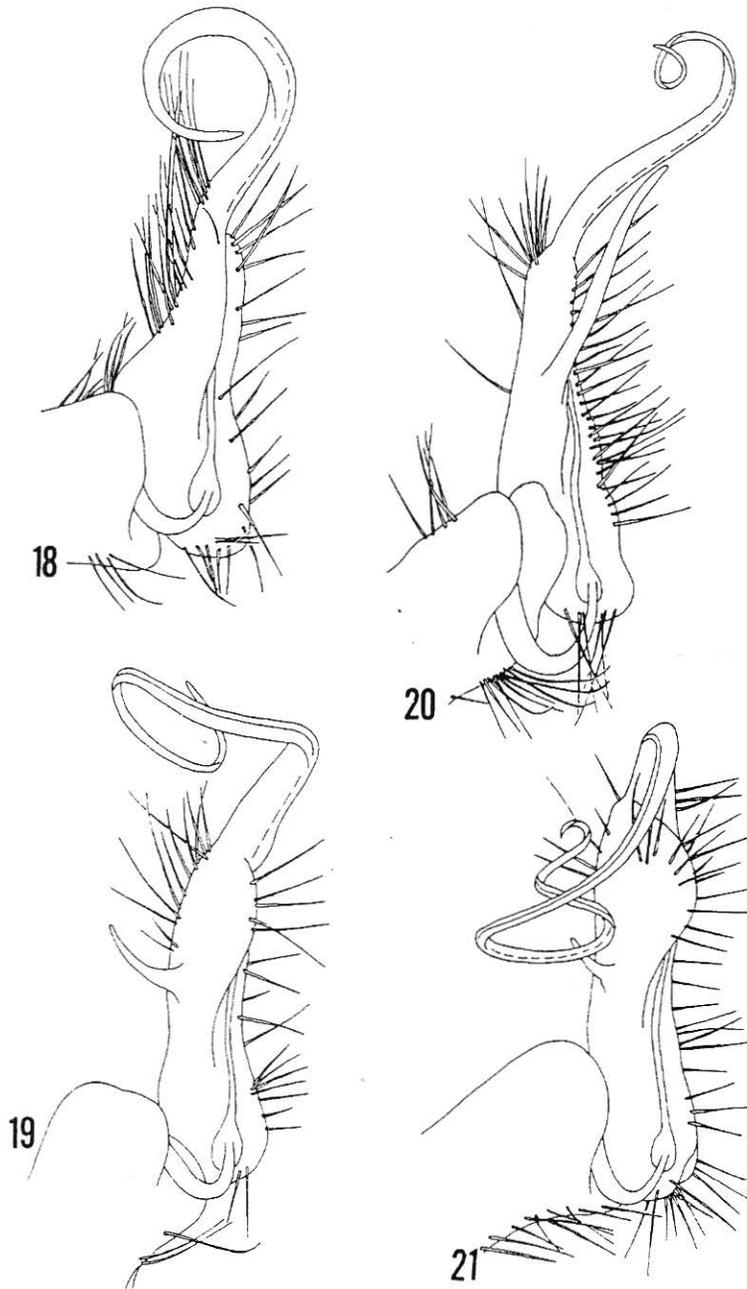
DISTRIBUTION. Known only from the type locality.

REMARKS. The specific name is a latin word meaning a "vessel with a long handle," referring to the length of the prefemoral process.

Hybocestus spiralis, new species

Fig. 21

TYPE SPECIMEN. Male holotype (NMNH) collected by O. F. Cook in June 1904 at Purulha, Baja Verapaz Dept., Guatemala. Purulha is a small community just inside the border with Alta Verapaz Dept., ca. 12 mi (19.2 km) NNW Salama; coordinates are 15°16'N, 90°12'W.



Figs. 18-21. Left gonopods of four species of *Hybocestus* species. 18, *H. octonodus*, topotype, medial view. 19, *H. clavulus*, holotype, medial view. 20, *H. bacrionis*, holotype, medial view. 21, *H. spiralis*, holotype, medial view.

DIAGNOSIS. Telopodite with short, spiniform prefemoral process extending directly anteriad; acropodite curving mediad basally and extending anteriad, curving caudad distal to midlength then anteriad, caudad, and anteriad again to form spiral configuration (Fig. 21).

DISTRIBUTION. Known only from the type locality.

REMARKS. The specific name refers to the distal configuration of the acropodite.



Fig. 22. Distributions of *Hybocestus* and the Hybocestini in Guatemala. Dots, *H. octonodus*; star in dot, *H. clavulus*; star, *H. bacrionis*; asterisk, *H. spiralis*.

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