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Revision of the genus *Pseudopolydesmus Attems, 1898* and its relationships to the North American genera of the family Polydesmidae Leach, 1815

Withrow, Charles Phillip, Ph.D.

The Ohio State University, 1988
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REVISION OF THE GENUS *PSEUDOPOLYDESMUS* ATTEMS, 1898
AND ITS RELATIONSHIPS TO THE NORTH
AMERICAN GENERA OF THE FAMILY
*POLYDESMIDAE* LEACH, 1815

Presented in partial fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By
Charles Phillip Withrow, B.S., M.S.

* * * * *

The Ohio State University
1988

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To My Parents
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PUBLICATIONS


FIELDS OF STUDY

Major Field: Diplopoda Systematics and Biogeography
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INTRODUCTION

The family Polydesmidae is a moderately large milliped taxon of the Superfamily Polydesmoidea in the Order Polydesmida. The family has a Holarctic distribution encompassing 24 genera and approximately 220 species. The systematics of the family is presently in a state of disorder, primarily because of a lack of investigators; this is especially true of the Palearctic fauna which will not be addressed in this study. One Palearctic genus, *Polydesmus* Latreille, 1802, which has a wide distribution west of central Asia, is presently composed of 26 subgenera, and hundreds of taxa, including many subspecies and forms. In several cases, taxa are distinguished only by the number of segments. Only in western Europe is there any degree of comprehension in the classification.

The North American fauna is only moderately better understood, chiefly due to fewer taxa. The first modern listing of the North American taxa by Chamberlin and Hoffman (1958) had 11 genera and 50 species. According to Hoffman's revised classification (1979), this has decreased to 6 genera and 35 species. This decrease was
primarily caused by the reevaluation of the works of Richard V. Chamberlin who, through the 1930's and 40's, described a large number of taxa, over half of which are now known to be synonyms. The genera of Polydesmidae listed by Chamberlin and Hoffman are:


Hoffman (1979) made the following changes: *Chaetaspis* and *Tidesmus* were placed in the superfamily Trichopolydesmoidea; *Chaetaspis* in the family Macrosternodesmidae, and *Tidesmus* in the family Trichopolydesmidae. He also suggested the following new synonyms: *Chaetaspis* (=*Antriadesmus*), *Pseudopolydesmus* (=*Dixidesmus*), and *Polydesmus* (=*Brachydesmus*). Also the genus *Bidentogon* (Buckett & Gardner, 1968), which was originally placed in the family Fuhrmannodesmidae, was included.

As of this study, the North American genera of the family Polydesmidae are: *Pseudopolydesmus*, with 9 species; *Scytonotus*, with 11 species; *Speodesmus* with 7 species; *Speorthus*, with 1 species; *Utadesmus*, with 2 species; *Bidentogon*, with 2 species; *Coronodesmus* new genus, with 2 species; and *Idahodesmus* new genus, with 1 species. Also, the Old World genus *Polydesmus* is now well established in the Nearctic, with 7 species.

This paper deals with the taxonomic problems present in the dominant eastern North American genus *Pseudopolydesmus*, and with the
interrelations of all the Holarctic genera. In the past, haphazard definitions of taxa at higher levels and the multiplication of taxonomic species has led to many misidentified forms.

The family Polydesmidae was erected by Leach in 1815. Prior to 1898, when the generic name Pseudopolydesmus was erected by Attems, all North American polydesmids were placed in the externally similar Palearctic genus Polydesmus. The generotype for Pseudopolydesmus is Polydesmus canadensis Newport, 1844, by monotypy. From this early beginning the taxonomic position of Pseudopolydesmus underwent few major changes, although generic associations came and went with increased understanding of millipede systematics.

Chamberlin and Hoffman (1958) list 28 names in the genus Pseudopolydesmus; there are now over 30. Despite this accumulation, no revisional study has been attempted. The names are: canadensis (Newport, 1844); pensylvanicus [sic] and glaucescens (Koch, 1847); branneri and nitidus (Bollman, 1887); minor and pinetorum (Bollman, 1888); euthetus, parvicus, planicolens, scopus, neoterus, echinogon, and natchitoches (Chamberlin, 1942); hubrichti, sylvicolens, penicillus, modocus, humilidens, conlatus, and tallulanus, (Chamberlin, 1943); erasus (Loomis, 1943); christianus (Chamberlin, 1946); catskillus (Chamberlin, 1947); caddo Chamberlin, 1949; paludicolus [sic] Hoffman, 1950; phanus (Chamberlin, 1951); gausadicrorhachus (Johnson, 1954); bidens, Loomis, 1959; and collinus Hoffman, 1973. Much suspected synonymy can be blamed on Chamberlin. The general opinion is that he rarely if ever examined types. A second problem, shared by almost all milliped taxa below
the generic level, is the lack of distinctive morphological characters with the exception of the male gonopods. A third more technical problem deals with labelling and relative positioning of the gonopodal processes. Depending on the orientation of the drawing, processes are hidden or appear to change location. Hoffman (1973) addressed the latter problem by setting up a gonopodal formula for the naming and identification of the processes. In the same paper he stated, without further elaboration, that in <i>Pseudopolydesmus</i> many species could be synonymized.

Very little has been done with the ecology of these millipeds. The only Nearctic polydesmoid millipeds studied are a species of <i>Euryurus</i>, of the family Xystodesmidae by Miley (1927), and the life history and ecology of <i>Orthomorpha gracilis</i> (Koch), of the family Strongylosomatidae by Causey (1943). Other ecological studies only include species in habitat lists (Bailey, 1919, Branson & Batch, 1971; Shelley, 1978; Withrow, 1978; etc.). In eastern North America, the genus <i>Pseudopolydesmus</i> is the most common native polydesmid. Individuals are usually found under decaying leaves and loose bark throughout the year, but are common during spring and fall. They can easily be obtained by hand collecting, sifting, or using a Berlese funnel. This is because millipeds are rarely seen by the typical nature observer, they are economically unimportant, difficult to work with, and (to many) just plain unexciting. They are however very important ecologically in breaking down detritus, thereby returning nutrients to the ecosystem. A habitat study (O'Neill, 1967) dealt with preferences of millipeds in different maple-oak
microhabitats in central Illinois. He states that 66.7% of his sample size *Pseudopolydesmus serratus* occurs under superficial wood of logs and 20.8% on the outer surface of logs under the bark. Based on my observations, O'Neill's data are not typical over the wide geographical range of the genus. Individuals are found in most niches although dependent on temperature and humidity. Mass migrations of *Pseudopolydesmus serratus* have been observed (Ramsey, 1966). Essentially nothing is known about growth, behavior, and metabolism of North American taxa. There is information on the secretions of *Pseudopolydesmus* species by many workers, summarized by Blum (1981). *Pseudopolydesmus* species have been found to produce the typical, polydesmoid products such as formic, isovaleric, acetic, and benzoic acids, mandelonitrile benzoate and hydrogen cyanide.

Because of the phylogenetic closeness of *Pseudopolydesmus* to *Polydesmus*, studies of European taxa may be informative; for example, Blower (1970) looked at growth rates, Kime and Wauthy (1984) examined habitat preference based on soil composition, and Baker (1978) investigated population dynamics.
MATERIALS AND METHODS

MATERIALS

This study was based on the examination of over 8,000 specimens borrowed from the following institutions and individuals. The abbreviations used in the text are also included. The listing of specimens can be found in Appendix D.

AMNH American Museum of Natural History, New York, Dr. Norman Platnick.

ANSP Academy of Natural Sciences, Philadelphia, Mr. Donald Azuma.

BMNH British Museum of Natural History, London, Dr. Paul Hillyard.

CPWC author, personal collection.

DMNH Dayton Museum of Natural History, Ohio, Mr. Gary A. Coevert.

FMNH Field Museum of Natural History, Chicago, Dr. John Kethley.

FSCA Florida State Collection of Arthropods, Gainesville, Dr. G. B. Edwards.
McZc Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, Dr. H. W. Levi.

Mhng Museum d'Histoire naturelle, Geneve, Switzerland, Dr. Hauser.

Muic Marshall University Invertebrate Collection, Huntington, West Virginia, Dr. Donald Tarter.

Ncmh North Carolina Museum of Natural History, Raleigh, Dr. Roland M. Shelley.

Osem Ohio State University Collection of Insects and Spiders, Columbus, Dr. Charles Triplehorn.

Oszm Ohio State University Museum of Zoology, Columbus, Dr. Carol Stein.

Rlhc Dr. Richard L. Hoffman, Radford University, personal collection.

Tmmc Texas Memorial Museum, University of Texas, Austin, Dr. James Reddell.


Wasc Dr. William A. Shear, Hampton-Sydney College, personal collection.

In addition, I have drawn heavily on the literature, especially for familial characters.

Generalized Methods

Several morphological structures need to be defined. The paranotum(a) is the lateral projection of a tergite or diplosegment. The gnathochilarium is the fused labium and maxillae. The most diagnostic tool in millipede systematics is gonopod morphology. The
gonopods are specially modified legs (in polydesmids, the anterior pair of the seventh diplosegment) used for the transfer of sperm from male to female. They are large, easily removable, species specific, and provide numerous characters (Fig. 70). The gonopod components are the gonocoxae, prefemur, femur, and tibiotarsus. The last is probably the fused tibia and tarsus of the original leg. The term telopodite refers to the prefemur, femur, and tibiotarsus, while the acropodite is the terminal, non-grooved structure. On the medial surface of the femur, a femoral groove extends anteriorly from under the endomerite. The endomerite is a hirsute projection distal to the external opening of the seminal groove on the posterior surface. Within the femur there is a seminal groove which may be enlarged into a seminal vesicle. The tibiotarsus may have various spines or processes.

In females, the cyphopods (Fig. 67) are the corresponding sperm receiving structures, located between the second and third segments. These paired structures were examined although they are usually internal, small, and not as diagnostic as the gonopods. In the polydesmids, the cyphopods are composed of a pair of large valves margined with macrosetae. Lateral and medial setae are also present. A small sperm receptacle is located on the posterior edge. The venter of the second segment excluding its single pair of legs, is referred to as the syncoxosternum (Fig. 63).

Specimens were examined in 70% isopropyl alcohol using an AO Spencer binocular microscope with 15X to 90X magnification and incident light. Gonopods were positioned on obsidian sand for easier
observation. Whole body measurements were determined by mechanical calipers (accurate to 0.1mm), while smaller measurements (such as antennomeric and podomeric lengths) were obtained with an ocular micrometer at 90X (accurate to 0.01mm). Individual components (ex. gnathochilarium) were sometimes cleared with 10% KOH or typsin, temporarily slide mounted, and examined with an Olympus compound microscope using transmitted light. Surface sculpturing and setae were examined with specimens temporarily removed from alcohol and allowed to air dry. Specimens for scanning electron microscopy were dissected and ultrasonically cleaned, mounted on stubs, allowed to air dry, and then coated with gold and pallidium. Specimens were examined with a Hitachi S-500 SEM.

A gonopod, usually the right one, was dissected from the seventh segment with watchmakers forceps and hooked minuten pins. Cyphopods were usually studied by first breaking the specimens between the 2nd and 3rd segments, which also permitted examination of the syncoxosternum and sternum III.

Gonopodal measurements proved especially difficult because of the highly variable nature of telopodite curvature. Total length was measured in lateral view along the curve from the tip of the acropodite to the distal tip of the prefemur. A series of chordal measurements was taken from the base of one process to the next proximally. These were used to determine the distance of each process from the tip and combined to obtain total telopodite length. Three or four repetitions of each gonopod measurement were recorded and averaged for each of 10 specimens. The process lengths were
measured from midpoint on the telopodite to the distal tip, in lateral or medial view; depending on visibility. The lateral view was more accurate for process $E_2$ because of process orientation. When possible, specimens from all areas and geographic extremes were used. These measurements are moderately reliable and provide an idea of relative location and degree of variability. Table 11 gives sizes and lengths based on percentage of telopodite length. The process formula follows Hoffman (1974).

Figures were drawn with the binocular microscope fitted with a 10 X 10 ocular reticle.

PHYLOGENETIC AND CLASSIFICATION METHODS

Except when dealing with asexual organisms, a species can be defined as a population of interbreeding individuals which gives rise to viable offspring while maintaining their similarity and relatedness. Therefore breeding and reproductive data are the best and most conclusive types of information for determining speciation. Since this information is rarely available, most modern systematics is based on morphological similarities and differences between species.

This study is based on the principles of cladistics and phylogenetic systematics developed by Hennig (e.g. 1966). Wiley (1981) goes into great detail on phylogenetic theory and application. Cladistic studies are virtually unknown in millipede systematics. Investigations by Enghoff (1981, 1984) represent the
only major works employing cladistic techniques. Most millipede systematists (e.g. Hoffman, 1979) still employ the evolutionary systematics of Simpson and Mayr (e.g. Mayr, 1969).

Phylogenetic systematics is based on the theory of monophyly. A monophyletic taxon is defined as a group of Recent species, which includes all descendants and only the descendants of a single ancestral species. These taxa are indicated by autapomorphies (uniquely derived similarities) shared by their members. Also, there is a decreased importance placed on convergences and parallelism (or homoplasies), which are independently derived similarities. Synaplesiomorphy is a state where similarities inherited from a single ancestral species occur in more than one taxon.

The major problem of phylogenetic systematics is the determination of the polarity of character states between the plesiomorphic or primitive state and apomorphic or derived state. Characters consist of a group of states considered variants of the same thing, usually morphological structures. Character states are the observed conditions in a taxon or group of taxa. Jong (1980) details how to determine character polarity. The most frequently used method is by outgroup comparison. The polarity of a character which is shared with the outgroup (the believed closest relative) is considered plesiomorphic. Another way of stating this is that the single shared ancestor possessed the same character state observed in the primitive members of each taxon. Each taxon is then examined to determine the plesiomorphic or apomorphic status of each character. By convention, the data sets utilize 0 to define the
plesiomorphic state while a 1 designates the apomorphic state. Data sets for the taxa and their states are set up for use in computer analysis for obtaining phylogenetic trees. These dichotomous branching trees, commonly referred to as cladograms, are manufactured using parsimonious methods to develop the simplest and most conservative patterns. This reduces the number of observed homoplasies. These trees are then used to set up a classification scheme.

The Superfamily Polydesmoidea includes five families, Polydesmidae, Haplodesmidae, Doratodesmidae, Opisotretidae, and Cryptodesmidae, with the latter being the most distantly related to the others. Hoffman (1979) stated that the Family Doratodesmidae was the closest relative to the Family Polydesmidae, based on overall gonopodal similarities. I have accepted this opinion and have used the Family Doratodesmidae as the outgroup for the Family Polydesmidae when determining plesiomorphic states. The outgroup for Pseudopolydesmus was determined to be the genus Polydesmus. The characters examined and their states are listed on Tables 1 & 2. Data sets in this study are listed in Appendix A and the actual cladograms are given in Appendix B.

The trees generated in this study were obtained by PAUP (Phylogenetic Analysis Using Parsimony) version 2.4, developed by David L. Swofford. This study employs Wagner parsimony. The assumptions of Wagner parsimony are: 1, ancestral states are unknown; 2, independent evolution of characters; 3, independent evolution of different lineages; 4, changes 0→1 are as probable as
1) 0; 5, both types of changes are a priori improbable over time; 6, evolutionary events such as retention of polymorphism are less probable than 0>1; 7, that evolution rates are slow enough that two changes over a long period of time are less probable than one change over a short period of time (Felsenstein, 1981).

In determining the most parsimonious tree a number of analysis tests were performed through PAUP, the most important measurement being tree length. The calculation of tree length is the summation of all OTUs (operational taxonomic units) or taxa differences between each node of the generated tree. The generation of the trees was by the use of closest selection procedure. Each currently unplaced OTU was added, in turn, to every possible position on a tree, and the length required for each of these new trees computed. The OTU whose connection added the least to the additive length of the existing tree is then chosen for the next addition. The parameters used in obtaining tree length were: the use of Farris optimization (Farris, 1970); the root was set as the outgroup, localized branch swapping with the generation of 50 individual trees; and no character state weighting.

The remaining calculations were derived from the numbers generated for three matrices. The first was the Manhattan distance matrix.

The second matrix was the patristic or path-length distance matrix. The patristic distance is the sum of the internodal distance connection between two pairwised endpoints (OTUs) divided by the number of characters examined. Missing data were calculated as the
mean distance. This matrix was used for the computation of the two f-values. The f-value of Farris (1972) is the sum of all deviations of the path-length across distant pairs of taxa. When there are no missing data this number is equal to the homoplasy of Farris' 78 program. A normalized f-value (f(n)) was also calculated. It was derived by the division of the f-value (Farris) by the sum of pairwise Manhattan distances. This is the same as the deviation ratio of Wagner 78. The f-values give comparative values as to the degree of parsimony in the tree. The lower the value the higher the degree of parsimony. Values tend to be lower in larger trees due to the 'usual' increase of homoplasy. These measurements can help to identify modified or miscoded characters, and also identify highly variable or missing OTUs.

The third matrix deals with homoplasy. For each pair of taxa, homoplasy is equal to the patristic distance minus the character difference (Manhattan distance). Missing data are replaced by the mean patristic distance. The lower each value, the lower the degree of homoplasy.

A final calculation is the generation of the Consistency Index (CI), defined by Kluge and Farris (1969). The consistency index is the sum over all characters of the 'range' of each character (equivalent to the minimum tree length computed for that character only) divided by the total tree length for all characters. This is a measurement of the deviation of the tree from a perfect fit to the data. The range of CI is between 0 and 1, with 1 having no
convergencies. Therefore, the higher the index the more parsimonious the tree.

Two additional tests were examined. These dealt with a variation of the Wagner parsimony. The first was DELTRAN or delayed transformation optimization. The running does not change the tree length, endpoints, or the consistency index, it can change the makeup of the internodal placement of characters. The test optimizes the ratio of parallelism to reversal, it favors two 0\rightarrow 1 changes over 0\rightarrow 1 change followed by a 1\rightarrow 0 change. This tends to reduce the f-value and increase the number of convergences and parallelisms.

The second test is the reverse of DELTRAN, or ACCTRAN, accelerated transformation optimization. Here the ratio of reversal is maximized.

The programs were run on an IBM PC portable.
RESULTS

To understand the North American polydesmid fauna, an analysis of the family was needed to determine relationships of the major taxonomic units. Due to the inadequate descriptions, which are prevalent in millipede systematics, an effort was made to describe those taxa not being revised. These descriptions at the family and subfamily levels were based on literature and specimens examined. Because this represents the first revision of the genus *Pseudopolydesmus*, full morphological descriptions were included.

**FAMILY DORATODESMIDAE** Cook, 1896

(Figs. 1, 13; Map 1)


**DIAGNOSIS:** Small to medium (4 to 25mm). Segments numbering 19 or 20. Capable of involution. Length to width ratio 15-32%. Tergal
width to height ratio 1.3-1.45. Body width to height ratio 1.1-1.25. Brown, yellow or white. Head mostly smooth with microsetae, usually with large tubercles dorsal to antennal sockets. Frons flat and glabrous. Mandible quadrate laterally. Gnathochilarium quadrate. Antennae short and very clavate. Interantennal distance small. Metazonites with regular pattern of small tubercles. Body massive and triangular in cross section. Metaterga (usually 5 through 19) with conspicuous upright, median projections, and laterally trilobed, large medial lobe with ozopore. Anterior terga directed cephalad. Tergites 1-4 with three irregular rows of 6-8 usually very large tubercles, which may be setaceous. Second tergite flabellately enlarged, covering head laterally. Collum oval and small, narrower than head. Paranota poorly developed or extensive and directed ventrad. Peritremata non-existent. Poriferous arrangement normal. Ozopores moderately large, usually located medially and away from lateral edge on anterior and medial segments, becoming more posteriolateral on caudal segments. Dorsal setae absent. Milliped able to involute. Sterna narrow and unmodified. Vasa deferentia open flush on surface of second coxae. Legs slender and long without modifications in male. Leg length to body length 10.9%. Length relationships of podomeres usually 4<7<1<5<2<3<6. Claws short. Sphaerotrichomes absent. Hypoproct small, transverse, smooth, and not produced medially. Paraprocts normal with 2 pairs of marginal setae set fairly close to dorsal end. Epiproct tuberculate, non-hirsute, and may be expanded caudad in males.
Gonopod aperture large, slightly transversely oval, lateral edges elevated. Gonopod (Fig. 13) simple, moderately thin, arcuate, capable of moving parallel to body, and attached to aperture by membrane. Gonocoxae large, in contact medially, and subtriangular with prominent ventral depression to accommodate telopodite reflexion. Depression usually with large dorsolateral field of macrosetae. Prefemur small, thin, and hirsute with a prominent spiniform process covering site of cannular attachment. Femur long with caudal process and posterior row of macrosetae. Cingulum distal on femur, may be very large, forming a hirsute shelf. Seminal groove running distally on medial surface to cingulum, then crossing laterad to small setal pad or setose knob (=endomerite), or may continue to distal tip. Endomerite moderate to non-existent and flush with femur. Seminal vesicle absent. Tibiotarsus regular with large expanded or spiniform processes and attached ventrally to gonocoxae.

Cyphopod elongate with large operculum with few lateral setae and few marginal macrosetae.

The type species in this family was *Doratonotus armatus* Pocock (1894). The genus *Doratodesmus* was subsequently proposed by Cook (1896) to replace *Doratonotus* which was preoccupied in fishes.

Cook proposed the family but without diagnosis. Because of its ability to involute, Verhoeff (1941) placed this family along with the Families Sphaeriodesmidae, Cyrtodesmidae, and Oniscodesmidae into a new Suborder Sphaerosomita. This was immediately rejected by the serious workers in the field.

**DISTRIBUTION:** Southeast Asia (Map 1). Presently known from Malaysia, Sumatra, Java, Japan, and New Guinea. Several genera are confined to caves, and although troglobytic modifications have not been reported, this may be due to insufficient collecting.

**FAMILY POLYDESMIDAE** Leach, 1815

(Map 1)


**DIAGNOSIS:** Small to large (4–36mm). Segments numbering 19 or 20. L/W ratio 8–22. Tergal width to height ratio approximately 1.1–1.3. Body width to height ratio 1.0–1.1. Usually brown, rarely red, white, or black. Head smooth, either covered with microsetae or with
few moderate filiform setae. Frons smooth, flat or bulging. Mandible angled laterally. Gnathochilarium either quadrate or elongate. Antennae usually long and slender but may be short and clavate. Interantennal distance large. Metazonite with regular pattern of small pits. Terga either with small tubercles or transverse rows of flattened polygonal bosses, these sometimes with setae. Anterior terga simple, directed either laterad or cephalad. Collum large, usually wider than head although smaller in some taxa. Paranota variable, may be ventrally, or laterally directed. Peritremata either thin or thickened. Paranotal edge usually serrate. Poriferous arrangement for 19-segmented millipeds 5, 7, 9, 10, 12, 13, 15, 16, 17, and 18, for 20-segmented millipeds 5, 7, 9, 10, 12, 13, 15, 16, 17, 18, and 19. Ozopores small, opening dorsally or dorsolaterally and either flush with peritremata or elevated. Sterna wide and unmodified. Vasa deferentia large, quadrate, and well separated. Legs usually slender and long. Leg length to body length 14-23%. Length relationships of podomeres usually 1=7<4<5<2=3<6. Male legs sometimes more robust than females, usually unmodified, and with ventral spheerotrichomes on various podomeres. Female legs unmodified and without spheerotrichomes. Hypoproct small and oval. Paraprocts with 2 pairs of setae with margin thickened. Epiproct truncated and projecting slightly.

Gonopod aperture large, subcordate, lateral edge slightly elevated with transverse internal shelf on posterior margin. Gonopod usually single, hinged, capable of moving only parallel with body. Gonocoxae large, subtriangular, with prominent ventral depression to
accommodate telopodite reflexion. Seminal groove originates mesally, runs dorsally, then laterally into an internal distal vesicle, usually opening onto a setaceous pad (endomerite). Prefemur moderately hirsute. Femur long with caudally directed distal processes. Tibiotarsus elongate with caudal projections. Syncoxosternum large, smooth, curving posteriolaterally, and sometimes lobed ventrally. Sternum III may be modified. Cyphopod usually oval but may be elongate, valves large, with long, stout, marginal macrosetae. Operculum small. Receptacle absent.

CONTENT: Twenty-four genera including approximately 374 species and subspecies. The Palearctic Region has 16 genera and approximately 345 species and subspecies; the Nearctic Region has 9 genera and 29 species. The genera are arranged into 4 subfamilies, Mastigonodesminae, Scytonotinae, Epanerchodinae, and Polydesminae.

DISTRIBUTION: Holarctic (Map 1), including the extreme northwestern tip of Africa. Introduced species have been established in the southern Hemisphere. Species are concentrated in the Appalachian Mountains, Alps-Balkan Region, and Japan.

Subfamily Mastigonodesminae Attems, 1914
(Figs. 2, 14; Map 1)

DIAGNOSIS: Small (less than 10mm). Body with 19 or 20 segments. L/W ratio 10.0-11.5%. IW between 6.5 and 28.3 mm². Tergal width to height ratio approximately 1.33. Body width to height ratio approximately 1.00. Brown or depigmented. Head subglobose, covered with microsetae. Frons smooth and bulging. Mandible rounded laterally. Labrum projecting very slightly ventrad. Gnathochilarium quadrate. Antennae short and very clavate, with small dorsal tubercle on 7th antennomere. Length relationships of antennomeres 1<7=4<5=2<3<6. Antennomeric shapes: 1 quadrate, 2-3 cylindrical, 4-6 variously clavate, 7 subconical. Interantennal distance small. Metazonites with small pits. Anterior terga laterad. Terga (Fig. 2) arched, with 3 rows of seta-bearing tubercles, the setae long and filiform. Anterior terga directed laterad. Collum small, narrower than head. Paranota poorly developed, dentate laterally, and ventrally with posterior margin wider than anterior margin. Peritremata absent. Poriferous arrangement normal. Ozopores small, opening posteriorly, not elevated. Sterna unmodified. Vasa deferentia small. Legs short (14-18% of body length). Length relationship of podomeres 1<7=4<5=2<3<6. Legs unmodified, although more robust in male than female. Claws thin, long, and tapered. Trochanter and prefemur with sphaerotrichomes, tarsus with long filiform setae. Hypoproct oval. Paraprocts typical, hirsute, and with thin margins. Epiproct slightly truncate with few long setae. Aperture transversely oval with a sternal remnant. Gonopods (Fig. 14) large, massive and arcuate, but not extending over 6th
segment. Gonocoxae large with small distal modifications, extending laterad over edge of aperture. Prefemur small, hirsute, and may have small lateral processes. Femur non-existent. Endomerite long, thin, ending subterminally on the tibiotarsus, and convoluted (=pseudoflagella of Strasser, 1974) with small terminal vesicle. Tibiotarsus simple, massive, long with bend, or curved, attached laterally to the gonocoxae, and may have several terminal caudal processes. Syncoxosternum not narrowed, thickened. Sternum III unmodified. Cyphopod oval without anterior plate.

**CONTENT:** Two genera, *Mastigonodesmus* Silvestri, 1898 (=*Eumastigonodesmus* Brolemann, 1916; =*Schedoleiodesmus* Silvestri, 1898), with 11 species and 2 subspecies, and *Heterocookia* Silvestri, 1898 (=*Cookia* Attems, 1898, =*Haplocookia* Brolemann, 1916) with 4 species are known.

The placement of the mastigonodesmines in the family Polydesmidae was originally by Hoffman (1979). Previously they were usually listed as a separate family. Hoffman listed the genera individually and stated that the genus *Mastigonodesmus* probably deserved subfamilial classification.

**DISTRIBUTION:** Palearctic (Map 1). The subfamily *Mastigonodesminae* is distributed around the western rim of the Mediterranean Sea with *Mastigonodesmus* in Italy, Sardinia, Sicily, and the Pyrenees, and *Heterocookia* in Tunisia and Algeria. Some species are troglobytic with some modification for cave habitation.
The two remaining subfamilies of Polydesmidae include Nearctic representatives and are treated here in more detail. They and their included genera can distinguished as follows:

**Key to North American Genera of Polydesmidae**

<table>
<thead>
<tr>
<th>1a. Dorsum without tubercles; paranota horizontal; ozopores not elevated; male legs unmodified; seminal groove looped with large terminal vesicle; tibiotarsus with caudally directed processes</th>
<th>Subfamily Polydesminae</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1b. Dorsum with tubercles; paranota ventrally directed; ozopores usually elevated; male legs variously modified; seminal groove straight without terminal vesicle; tibiotarsus simple</td>
<td>Subfamily Scytonotinae</td>
<td>3</td>
</tr>
<tr>
<td>2a. Posterior row of quadrate bosses on tergites enlarged; body with 19 or 20 segments; endomerite flush with femur and sometimes with processes</td>
<td>Polydesmus</td>
<td></td>
</tr>
<tr>
<td>2b. Posterior row of quadrate bosses not enlarged, body with only 20 segments; endomerite projecting from femur and without processes</td>
<td>Pseudopolydesmus</td>
<td></td>
</tr>
<tr>
<td>3a. Gonopod highly dendritic with large lateral process</td>
<td>Idahodesmus</td>
<td></td>
</tr>
<tr>
<td>3b. Gonopod not highly branched, simple or with small regular processes</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>4a. Gonopod branched; dorsal setae hooked; leg sphaerotrichomes large; femoral processes absent</td>
<td>Scytonotus</td>
<td></td>
</tr>
<tr>
<td>4b. Gonopod not branched; dorsal setae not hooked; leg sphaerotrichomes small; femoral processes present</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>5a. Endomerite without processes; anterior denticles on gonopods present; legs unmodified; tibiotarsus branched</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>5b. Endomerite with processes; anterior denticles absent; legs variously modified; tibiotarsus unbranched</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>
6a. Antennae long (18-25% of total body length); gonopod with basally directed lateral spine....................Speodesmus

6b. Antennae short (15-18%); gonopod without basally directed lateral spine; tibiotarsus with numerous terminal processes..................Coronodesmus

7a. Endomerite flattened, with numerous setae; without femoral setae................................Utadesmus

7b. Endomerite elongate, without numerous setae; femoral setae present.................................Bidentogon
Subfamily Scytonotinae NEW STATUS

(Map 2)


DIAGNOSIS: Small to medium (4-20mm). Body with 19 segments. W/L ratio 8-18%. LW between 8.6 and 58.5mm². Tergal width to height ratio approximately 1.0-1.1. Body width to height ratio approximately 1.0. Usually brown but may be depigmented. Head usually smooth and covered with numerous microsetae. Mandible usually rounded laterally. Gnathochilarium rectangular. Interantennal distance large. Antennae usually long and may be either filiform or clavate. Length relationship of antennomeres 7<1=4<2<5<3=6. Metazonite with small pits. Terga well arched, never flattened, with seta-bearing tubercles instead of quadrate bosses. Dorsal and lateral setae usually clavate. Anterior terga directed cephalad. Collum transversely oval and small, narrower than head. Paranota poorly developed, directed ventrad, either rectangular or trapezoidal, and dentate laterally. Peritremata usually thick. Poriferous arrangement normal. Ozopores large, opening dorsolaterally or dorsoposteriorly, and may be elevated. Sterna unmodified although wider in female. Vasa deferentia small. Anterior pair of legs slightly separated from posterior pair. Legs short and variously modified. Claws, short, thickened at base, and constricted distally. Various podomeres with sphaerotrichomes. Hypoproct small and non-hirsute. Paraprocts with at least 4-6 setae and thin margin.
Epiproct rugose, sometimes deflexed, setae short and usually with numerous setae.


Cyphopod oval. Syncoxosternum thin, small, and spined laterally, with medial hooks.

CONTENT: There are presently 7 genera, Specodesmus, Scytonotus, Utadesmus, Bidentocor, Coronodesmus, Speorthus, and Idahodesmus, and 26 species.

DISTRIBUTION: Nearctic (Map 2). Most genera are from western North America, the exception is Scytonotus, which includes several eastern North American species. Except for Scytonotus, most taxa have limited distribution in pockets of stable and protected environments. This subfamily probably represents primitive taxa with relict populations. Several genera also appear to be troglodytes with various degrees of modification. The presence of troglodytic species in regions unsuitable for epigean populations supports the hypothesis of primitiveness.
Speodesmus Loomis, 1939

(Figs. 4, 16-18, 52; Map 2)

Lapsus.

GENEROTYPE: Speodesmus echinurus Loomis, 1939, by monotypy.


DESCRIPTION: Small to medium (8.5-19mm) polydesmids, 20 segments, not including head. W/L ratio 7.4-12.7% and WL 6.4-40.5mm².

Color in life white or unpigmented, although strongly sclerotized.
Head large, smooth, broader than collum. Genae quadrate.

Cranial suture distinct, extending anteriorly to normal antennal position. Antennae filiform, long, 18-25% of body length, and extending to middle of 4th tergite. Antennomere lengths in increasing sequence 1<7<4<5<6<2<3. First antennomere rectangular, 2nd and 3rd elongate, 4th rounded ventrally with single large distoventral seta, 5th and 6th clavate, 7th typical with 4 terminal sensillae, antennomeres 5, 6, and 7 with dorsodistal patches of bacilliform setae.

Facial setae numerous, fine, and simple.

Mouth components typical except gnathochilarium elongate, L/W approximately 110%.

Metaterga flat, with 4-5 posteriorly curving rows of seta-bearing tubercles, sulcus not distinct, setae not filiform, but peglike (Fig. 52). Collum broadly oval, smaller than head, posterior margin straight, with three rows of setae, lateral denticles absent.

Paranota (Fig. 4) small, curved, anterior margin of tergite narrow, becoming wider posteriorly. T/W ratio approximately 1.4 for paranota and 1.0 for tergites (at midbody). Lateral edges slightly curved, with four or five small denticles, 4 occurring on poriferous segments. Denticles with peglike setae. Ozopores moderate, not elevated, located on posterior margin of paranotum, opening dorsal. Ozopore formula typical.

Epiproct conical with 4-13 pairs of setae. Hypoproct triangular but truncated, with 7-16 pairs of setae. Paraprocts smooth, margin thin, setae absent.
Sterna flat, unmodified. Legs long, slender, 24-30% of total body length. Coxa small, subquadrate; trochanter moderate, slightly barrel-shaped; prefemur slightly curved and clavate; femur and tibia short and subquadrate; tarsus slightly curved and elongate; claw short, simple, and curved. Trochanter, prefemur, and femur usually with large sphaerotrichomes.

Gonopods, in situ, moderately exposed, curving toward body, parallel, orientated along axis of body, capable of independent movement, and extending slightly past anterior margin of 7th sternum.

Gonopod aperture subelliptical with L/W ratio 60-70%. Gonopods large (Figs. 16-18). Gonocoxae large, slightly smaller than telopodite, subglobose, flattened mesially, with small ventral cavity. Prefemur small, moderately setaceous. Femur moderate, straight or slightly curved, with single anterior seta, and posteriolateral patch of small teeth. Tibiotarsus with large, posteriorly directed spine. Endomerite flush with tibiotarsus, with thin elongate curved process. Cannula connected to telopodite under small ledge. Seminal groove straight, not terminating in a vesicle.

Female similar to male except much more slender, legs much shorter and slenderer. Syncoxosternum membranous, narrowed basally and divergent anteriomedially. Sternum III unmodified.

Cyphopods oval, with few valvular macrosetae, and setae absent laterally and medially.
CONTENT: There are 7 species of Speodesmus of which only 3 are described, Speodesmus echinourus Loomis, 1939, S. bicornourus Causey, 1959, and S. aquiliensis Shear, 1984. The remaining four species are tentatively based on the unpublished morphometric study by Elliott (1976).

DISTRIBUTION: The genus is centered in the Karst region of the Balcones Fault Zone of westcentral Texas (Map 2). Elevation of the region is between 450 and 900 meters. The drainage basin includes the Nueces, San Antonio, Guadalupe, and Colorado Rivers. This is primarily a troglodytic genus.

NOTES: Elliott (1976) did an unpublished morphometric study of specimens from central Texas. Although extensive, he didn't examine cyphopods, and he did not give parameters of any of the characters he used in his principal component analyses.

Elliott stated that bicornourus had 3 sister species, all undescribed. These were based on differences of the following characters: body size, segment 3 dентicle number, hypoproct setal number, claw length, setal (bacilliform?) number on sixth antennomere of male and female, height of segment 3, and the following gonopod characters; medial angle of lateral process, tooth number on accessory branch, lateral process length, angle alpha, lateral process width, and number of lateral denticles.

He also determined that echinourus had one sister species, also undescribed. This was based on differences of the following
characters: body size, setal number on sixth antennomere, hypoproct, denticle number on third segment of males and females, second segment width of females, and sphaerotrichome size on male legs. Gonopod characters were angle alpha, lateral process width, lateral process length, medial angle to lateral process, accessory branch tooth number, number of lateral denticles.

Shear (1974b) described a Mexican species, pecki, but in a later paper (Shear, 1975) moved it to the genus Sumidero in the Family Fuhrmannodesmidae.

**Scytonotus** Koch, 1847

(Figs. 5, 20, 21-23, 44, 47, 49, 54, 56 58, 60, 64, 68; Map 2)


DIAGNOSIS: Small to medium, 19 segments, brown or light cream colored. Tergites with seta-bearing tubercles. Setae of adults hooked and filiform; juvenile with clavate setae. Paranota small and curved ventrolaterally. Ozopores usually enlarged, opening dorsolaterally. Male tibia may be modified. Sterna unmodified although wider in males. Gonopods arcuate with flexible tibial arm with processes. Endomerite small, seminal groove sinuous, with small terminal bulb. Female paranota on tergites 5-11 may be reduced. Syncoxosternum base membranous, separated distally, with cephalad lateral spines. Sternum III unmodified. Cyphopod oval, without anterior plate, ventral lobes small and numerous, receptacle small with several large cephalad directed setae.

DESCRIPTION: Small to medium (7 to 20mm) polydesmids, with 19 segments not including head. W/L 10.7-14.6% and WL 18.0-58.5mm². Color in life, either light brown or cream colored. Venter lighter.

Head smooth. Genae quadrate, projecting laterally. Cranial suture distinct. Antennae (Fig. 58) well separated, 20-25% of total head width, slightly clavate, base thicker than in Pseudopolydesmus, approximately 18-24% of total body length, extending to anterior margin of 4th segment. Antennomeric length in increasing sequence 7<1<4<2<5<6<3. Antennomeres 1-4 rectangular, 5 and 6 slightly clavate, and 7 typical with four terminal sensillae present. Antennomeres 5, 6, and small swelling on 7 with small patches of bacilliform setae located dorsodistally.
Mouthparts typical except gnathochilarium elongate, L/W approximately 110%.

Face with numerous moderate filiform setae.

Metaterga (Fig. 5) convex, not quadrate, with 4 or 5 transverse series of seta-bearing tubercles. Each tubercle with long hooked setae. In juveniles setae irregularly clavate. Usually 4 pairs of anterior tubercles located on anterior half of tergum between stricture and transverse sulcus, immediately behind sulcus intermediate set with 5 pairs, and along posterior margin 6 pairs present. Collum small, oval, or with anterolateral edge slightly produced cephalad, with numerous of setiferous tubercles in 3 to 5 rows. Anterior edge of collum flaired. Metazonite with medium sized pits.

Paranota curved ventrally (Fig. 49), W/T ratio 1.46 and tergite ratio 1.0, without serrations but 7-8 lateral projections present, each usually with hooked setae. Paranota quadrate laterally. Ozopores usually elevated with enlarged peritremata (Fig. 47), opening dorsolaterally on posterior half of paranota. Ozopore formula 5, 7, 9, 10, 12, 13, 15, 16, and 17. Paranota of segments 2-4 directed cephalad (Fig. 44), of other segments progressively more caudad; posterior margins with setae and convexities usually less developed than those on anterior segments.

Sterna smooth, penes small. Anterior and posterior sterna (Fig. 60) of male in several species wide but otherwise unmodified. Male legs enlarged (Fig. 54). Leg length to body 17-22%. Coxa clavate; trochanter bowed on both ends; prefemur elongate; femur
short; tibia rectangular or in some species with 1 or 2 irregular projections on legs 13-20; tarsus curved and long; claw moderate, constricted basally (Fig. 56). Sphaerotrichomes on tarsus, small and numerous with small patches on remaining segments except coxa.

Epiproct truncate and rugose, with at least 8 pairs of setae. Hypoproct small, rounded, with a pair of posteriollateral setae on small swellings. Paraprocts smooth, with two pairs of lateral setae, lips thin.

Gonopods, in situ, moderately exposed, usually not inserted, parallel, oriented along medial axis of body, and capable of independent movement, not extending over anterior margin of 7th segment (Figs. 21-23).

Gonopod aperture oval, with L/W ratio between 60 and 76%, posterior shelf large, anterior shelf small, raised laterally. Gonocoxae moderate, smaller than telopodite, with large ventral concavity for retraction of gonopods. Ventrolateral edge with two setae. Prefemur without processes, very hirsute, and long medially. Femur short and either thick (eastern species) or thin (western species), with 1-2 mesial macrosetae, and 1-4 large cephalad directed setae. Telopodite arcuate with two flexible pieces. Based on Hoffman (1962), Scytonotus has up to 2 lateral (x & y) and/or lateral (s & t) and endomerite (a) processes. Cannula connected to prefemur under ledge. Endomerite small and may have a small distal process. Seminal groove sinuous, extending anterior to level of endomerite. Tibiotarsus simple, sometimes with distally directed tooth-like setae.
Female structurally dissimilar depending on species. Paranota 5-11 variously reduced (Fig. 20), the segments appearing almost cylindrical. Antennae shorter and more clavate. Sterna wider than male. Legs short and unmodified but slightly weaker than males, sphaerotrichomes not as distinct. Syncoxosternum membranous, coxae narrowed, separated from sternum, with ventrolateral spine (Fig. 64). Apodemes long. Sternum III rounded but unmodified.

Cyphopods small, axis longitudinal, moderate, with 25-30 small macrosetae (Fig. 68). Flattened ventromedially, receptacle present, small not elongate, with 2-5 very long cephalad directed setae. Lateral and medial surface with few setae.

CONTENT: The eleven described species include seven in the northwest and four in the east. The western species are: amandus Chamberlin, 1910, bergrothi Chamberlin, 1911, columbianus Chamberlin, 1920a, insulanus Attems, 1931, orthodox Chamberlin, 1925, piaer Chamberlin, 1910, and simplex Chamberlin, 1941. The eastern species are: in Group Granulatus: granulatus (Say, 1821) and australis Hoffman, 1962, and in Group Virginicus: virginicus (Loomis, 1943b) and michauxi Hoffman, 1962.

DISTRIBUTION: Nearctic (Map 2). Two separate populations occur, one in the Pacific Northwest, from southern Alaska south to Utah and Idaho, and the other in northeastern North America, New York south to North Carolina, west to Iowa and Missouri. Available data suggest that the disjunction may be real.
NOTES: Type materials of *Polydesmus granulosus* (Say, 1821), and two of its synonyms: *S. scabricollis* (Koch, 1847), and *S. laevicollis* (Koch, 1847) are lost. Say (1821) described the first species of *Scytonotus*. Koch (1847) described the genus but failed to designate a type from the three described species of which *granulosus* was not one. Bollman (1893) (posthumously) states incorrectly (page 146) that Koch designated *granulosus* as the type. On page 151, however, he states that *scabricollis* is the type of the genus.

Cook and Cook's redescription (1894) of *S. granulosus* was very extensive and provides a basis for the modern use of the name.

*Lasiolathus* Loomis (1943) was based on juvenile specimens of *Scytonotus virginicus* and was synonymized into *granulosus* by Hoffman (1947). Hoffman (1962) recognized *S. virginicus* to be a separate species. *Stenonia hispida* was synonymized by Bollman (1893) with *granulatus*.

*Scytonotus cavernarum* Bollman was made a synonym of *S. granulosus* by Chamberlin and Hoffman (1958). The identity of *S. nodulosus* Koch is uncertain because the type is presumed lost and the description is inadequate.

*Utadesmus* Chamberlin and Hoffman, 1950

(Figs. 6, 24-26, 53; Map 2)

GENEROTYPE: *Brachydesmus henriensis* Chamberlin, 1930, by original designation.


DESCRIPTION: Small (5-17mm) polydesmids, 19 segments not including head. W/L 13-19% and WL 12.4-24.6mm². Color in life earth brown, venter and legs lighter. Head smooth and globose. Genae quadrate, projecting laterally. Cranial suture short but distinct, terminating dorsal to antennae. Antennae well separated, set medially on face, antennae short, 12-16% of body length, extending to midline of tergite 3, and very clavate. Antennomeric lengths in increasing size 7<1<5<2=4<3<6. First antennomere small, quadrate, 2-4 elongate, and 5, 6, and 7 markedly clavate, each with patches of bacilliform setae and with 4 terminal sensillae. Head covered with numerous microsetae. Mouthparts typical with slightly elongated gnathochilarium.
Metaterga (Fig. 6) arched, not horizontal, with three transverse rows of tubercles, each with a single peg-like seta. Anterior row with 10 tubercles and separated from medial and posterior rows which have 10 and 8 tubercles respectively. Collum oblong, narrower than head, with 3 rows of seta-bearing tubercles. Collum not flaired.

Paranota curving ventrally, not expanded laterally. W/T ratio 1.5 for paranota and 1.1 for terga. Anterior paranota directed cephalad directed. Lateral edge quadrate. Denticles with peg-like setae, somewhat variable. Non-poriferous segments with 6 lateral denticles which, on the posterior segments, are reduced and directed posteriorly. One to several small non-setaceous teeth may be present anterior to anteriormost denticle. Poriferous segments with 3 denticles anterior and 2 denticles posterior to ozopores, although several very small denticles may be associated with ozopores. Denticles reduced on posterior segments. Ozopores large, elevated, located slightly posterior to midline of tergite, opening dorsally, arrangement typical. Posterior paranota large and posteriorly directed.

Epiproct smooth and truncated with approximately 8 pairs of setae. Hypoproct round with single pair of setae. Paraprocts with thin lips and two lateral pairs of setae.

Sterna flat, unmodified, with few setae. Legs (Fig. 53) short, 10-14% of total body length. Coxae quadrate, trochanter rectangular, femur quadrate, tibia quadrate, tarsus elongate and thin, claw
constricted distally. Sphaerotrichomes large on tarsus, tibia, and femur.

Gonopods (Figs. 24-26), in situ, lying partly out of aperture, gonocoxae exposed, telopodite directed anteriorly, along midline and extending to midway on the sixth segment. Posterior pair of legs on sixth segment only slightly displaced laterally.

Gonopod aperture wide, L/W ratio approximately 60%, kidney-shaped with large medially directed, posterior shelf. Gonocoxae large, globose, and anterior margin quadrate. Prefemur small and hirsute. Femur elongate, very slightly curved, unbranched, without setae, and distally with large flattened endomerite. Seminal groove straight. Tibiotarsus long, spine-like, with small proximolateral spine.

Female similar to male, except legs thinner and without sphaerotrichomes. Syncoxosternum with anteriorly directed lateral spines, a small pair of medial hooks, and anteriomedially, a small lobe between coxae. Coxae slightly expanded medially. Sternum III ventrally lobate.

Cyphopod oval, small, with few diminished macrosetae. Receptacle with several long anteriad directed setae.

CONTENT: Two species, *henriensis* Chamberlin, 1930 and *hoffi* Chamberlin and Hoffman, 1950. Undoubtedly more species will turn up with adequate collecting.
DISTRIBUTION: Central New Mexico and northcentral Utah, on the Colorado Plateau (Map 2). Probably extends into southern Wyoming in the San Juan, Sangre de Cristo, Medicine Bow, and Sawatch mountain ranges.

NOTES: The holotype of U. henriensis has a gonopod missing. The type of U. hoffi also has only one gonopod and lacks the anterior half of the body. The separation between these two species is slight with differences occurring in lateral spine shape and femur curvature. Packard (1877) described Polydesmus caviocola from a northern Utah cave. Because the Packard material has never been located and his description lacks a gonopod description or drawing, its identification will remain in doubt. Chamberlin and Hoffman (1958) placed caviocola in the genus Brachydesmus; however, I expect it to be a Utadesmus.

**Bidentogon** Buckett and Gardner, 1968
(Figs. 7, 27-29, 51; Map 2)


**GENEROTYPE**: **Bidentogon** helferorum Buckett and Gardner, 1968, by monotypy.

DESCRIPTION: Small to medium (<12mm) polydesmids, with 19 segments not including head. W/L 14.1-17.9% and WL 8.6-21.8mm². Color in life, brown, venter and legs lighter.

Head smooth and broad. Genae quadrate, projecting laterally. Mandible laterally rounded. Cranial suture short but distinct, terminating dorsal to antennae. Antennae well separated, set medially on face, antennae short and clavate, 12-18% of body length, extending to anterior edge of 4th tergite. Antennomeric lengths in increasing sequence 7<1<4<2<5<6<3. First antennomere quadrate, 2-4 rectangular, 5 and 6 slightly clavate, and 7 typical with 4 terminal sensillae, antennomeres 5, 6, and small knob on 7 with small patches of bacilliform setae.

Face covered with numerous microsetae.

Mouthparts typical except for elongation of gnathochilarium.

Metazonite (Fig. 7) with small pits. Metaterga convex, with 3 transverse rows of small tubercles, each with a single peg-like seta.
(Fig. 51). Anterior row with 10 tubercles, separated from medial and posterior rows which have 10 and 8 tubercles, respectively. Collum oblong, rounded laterally, smaller than head and remaining tergites, setae-bearing tubercles present, margins not flaired.

Paranota curving ventrally. W/T ratio approximately 1.3 for paranota and 1.0 for tergites. Lateral edges quadrate with 3 or 4 denticles, 4th denticle directed posteriorly, and occurring only on poriferous segments. Anterior paranota anteriorly directed. Ozopores small, elevated, opening dorsolaterally, located on posteriolateral corner, arrangement typical. Posterior paranota progressively more caudally directed.

Epiproct smooth, slightly deflexed, with numerous setae. Hypoproct small, with pair of seta-bearing swellings. Paraprocts smooth, with two pairs of lateral setae, lips small.

Sterna cruciately impressed, otherwise unmodified, with few setae. Posterior 6th sternum with deep depression. Legs short, 15.4% of total body length. Coxa short and globose; trochanter elongate and bowed; prefemur short and rectangular; femur short; tibia moderately short and rectangular; tarsus long and very slightly curved; claw moderate with tip sharply tapered. Male with tibia of third leg twice as large as remaining legs, femur also swollen.

Gonopods, in situ, partly hidden, gonocoaxae moderately exposed, telopodite directed anteriorly and extending to sixth sternum, capable of independent movement. Posterior pair of legs of segment 6 displaced laterally.
Gonopod aperture oval with L/W ratio 67.4%. Gonopods elongate and small (Figs. 27-29). Gonocoxae moderately large, round, with distal edge variously lobed, ventrally large, dorsally small. Prefemur small and hirsute. Femur straight, long, with irregular row of 10-20 elongate, caudally directed setae. Cannula attached to prefemur under small ledge. Seminal groove curved but not looped. Tibiotarsus with two caudal branches: a thin, mesal fork, and a large, lateral fork with seminal groove terminating close to distal tip, with fine setae (vestigial endomerite?).

Female similar to male except legs thinner, unmodified, and without sphaerotrichomes. Syncoxosternum coxae small, separated from sternum; sterna overlap medially and are slightly lobate, with laterally distally directed spines. Sternum III with small, central, anteriorly directed swelling.

Cyphopod oval, small, without anterior plate, but with several long lateral setae. Receptacle small with long setae.

CONTENT: Two species, Bidentogon helferorum Buckett and Gardner, 1968 and B. californicus (Chamberlin, 1918a) are known. More species are expected.

DISTRIBUTION: The genus is limited to the coastal regions of northern and central California.

NOTES: The original description by Buckett and Gardner was well done, although they placed this genus in the family
Vanhoefeniidae (=Fuhrmannodesmidae) which has no North American representatives. This arrangement was continued by Shear (1972) who redescribed and redrew Brachydesmus californicus. Its placement in the family Polydesmidae was corrected by Hoffman (1979).

Coronodesmus NEW GENUS

(Figs. 8, 30-32; Map 2)


GENEROTYPE: Brachydesmus yosemitensis Causey, 1954, by present designation.

DIAGNOSIS: Small, 19 segments, red-brown. Tergites with 3 rows of tubercles, anterior row with filiform setae cephalad and posterior rows with setae caudad. Paranota directed ventrally with anteriorly directed denticle. Ozopores elevated, opening dorsolaterally. Male sterna and third pair of legs modified, hypoproct and paraprocts hirsute. Gonopods straight except tibiotarsus bent anteriorly, with posteriorventrally directed processes and anterior patch of swellings or small teeth. Seminal groove straight, without terminal vesicle. Endomerite small. Female legs thin, unmodified, without sphaerotrichomes. Syncoxosternum membranous with small lateral spines. Sternum III unmodified. Cyphopods oval, with few valvular macrosetae, and a few lateral and medial setae.
DESCRIPTION: Small (5.5-12mm) polydesmids, with 19 segments not including head. W/L 8-18%, and WL 5.9-15.4mm².

Color red-brown. Venter lighter.

Head moderately smooth. Genae quadrate, projecting laterally. Cranial suture faint, not extending to antennae. Antennae well separated, clavate, short, 15-18% of body length, extending to posterior margin of third segment. Antennomeric length in increasing size 1<4<7<2=5<6<3. First antennomere rectangular and short, 2 slightly elongate, 3 elongate and clavate, 4 short and subquadrate, 5 and 6 moderate and slightly clavate, and 7 typical with terminal sensillae; antennomeres 5, 6, and 7 with small patches of bacilliform setae located dorsodistally.

Facial setae short and numerous.

Mouthparts typical, with elongate gnathochilarium, I/W approximately 110%.

Metaterga arched, each with 3 transverse rows of tubercles: anterior row with 8 tubercles each with an anteriorly directed filiform seta, and located on anterior half of tergum between stricture and transverse sulcus; intermediate row immediately behind sulcus with 8 tubercles each with a posteriorly directed filiform seta; posterior margin (row) with 12 tubercles each with a posteriorly directed filiform seta (Fig. 8). Collum large, about equal to head, rounded anteriorly, with 5 uneven rows of tubercles, and posteriolateral angle rounded.

Paranota curved ventrally, W/T ratio 1.4, tergal ratio 1.0, 4 or 5 well defined seta-bearing denticles, 5 occurring on poriferous
segments with anteriorly directed denticle. Paranota 2-5 anteriorly directed. Ozopores moderately large, elevated on posteriolateral corner, opening dorsolaterally on segments 5, 7, 9, 10, 12, 13, 15, 16, 17, and 18. Posterior paranota large, progressively more caudally directed.

Epiproct truncate, with approximately 8 pairs of setae. Hypoproct rounded, with numerous setae. Paraprocts highly setaceous with 20-30 long filiform setae scattered over surface. Lips small.

Sterna flat, unmodified, except 10th segment with anterior sternum with 2 small triangular lobes, posterior sternum with two long conical lobes projecting caudally. Legs short, typically shaped except third pair with tarsus slightly swollen and femur very swollen. Sphaerotrichomes present on tarsus, tibia, and femur.

Gonopods (Figs. 30-32), in situ, moderately exposed, not inserted, parallel, separated, not particularly movable, and not extending past anterior margin of 7th sternum.

Gonopod aperture elliptical with L/W ratio 60-72%. Gonocoxa large, about equal to telopodite, with small ventral concavity. Anterior edge smoothly lobed. Cannula connected to prefemur under small ledge. Prefemur small and hirsute. Femur straight, thin basally, expanding distally, with lateral, distally directed process. Seminal groove straight, terminating in small endomerite without vesicle. Tibiotarsus slightly bent anteriorly, with several large posteriorly directed spines. Anterior surface with a patch of swellings or small simple teeth.
Female similar to male but without sternal and leg modifications. Sphaerotrichomes absent. Syncoxosternum membranous and slightly produced ventromedially, lateral spines small. Sternum III unmodified.

Cyphopods oval, with few macrosetae along valvular edge. Few lateral and medial filiform setae present. Cyphopod plate rounded, with few lateral and medial setae.

CONTENT: Two described species, Coronodesmus yosemitensis (Causey, 1954) and C. bituberculatus (Loomis, 1960), and a third undescribed species.

DISTRIBUTION: Coronodesmus has been collected in central California around San Francisco and in Yosemite National Park.

NOTES: It has been noted by several authors that these species were not in the genus Brachydesmus, but no one has officially made the nomenclatural change.

Speorthus Chamberlin, 1952

(Figs. 9, 33-35; Map 2)


GENEROTYPE: Speorthus tukanbius Chamberlin, 1952, by monotypy.

DESCRIPTION: Small (8.0-9.5mm) polydesmid, with 20 segments not including head. W/L 11-13.5% and WL 8.2-10.8mm^2.

Color in life pale or colorless, although well sclerotized.

Head large. Genae quadrate, projecting laterally. Antennae short and clavate, 11-16% of body length, extending to midline of 4th tergite. Antennomere length in increasing sequence 1<7<2<3=4<5<6. First antennomere short and subquadrate, 2-4 short, rectangular with 3 and 4 rounded ventrally, 5 short and clavate, 6 large and clavate, 7 typical, with 4 terminal sensillae.

Facial setae short and numerous.

Mouthparts typical, gnathochilarium elongate.

Metatergite arched, tuberculate, with 4 or 5 rows each with 10-14 tubercles, each tubercle with a peg-shaped seta (Fig. 9). Collum broadly oval, slightly narrower than head, with 3 irregular rows of setae and two lateral denticles.
Paranota small, curved ventrally, T/W ratio 1.4 and tergal ratio 1.0. Lateral edge with 4 or 5 denticles, each with single seta. Lateral margin quadrate. Ozopores moderately large, elevated, opening dorsolaterally on segments 5, 6, 8, 9, 10, 12, 13, 15, and 16. Posterior margin with large lateral serrations.

Epiproct with approximately 8 pairs of setae. Hypoproct small, non-hirsute, and truncate. Paraprocts with 2 pairs of seta-bearing tubercles, lip slight.

Sterna flat, unmodified. Legs long and enlarged, 17-22% of total body length. Coxae large and globular; trochanter thick and barrel-shaped; prefemur thick and curved; femur short and quadrate, tarsus long and curved, and claw long and constricted. Femur and tibia each with single dorsodistal seta. Only tarsus with sphaerotrichomes.

Gonopods, in situ, exposed, paralleling body axis, extending past anterior margin of 7th sternum.

Gonopod aperture oval with L/W ratio 68-72%. Gonopods long and thin (Figs. 33-35). Gonocoxae moderate, smaller than telopodite, with small, deep ventral concavity, anterior edge monolobed. Prefemur moderate and hirsute. Cannula thin, connected to prefemur beneath ledge. Femur not thin, curved with a single anteriorly directed seta. Seminal groove straight without terminal vesicle. Tibiotarsus simple and elongate. Endomerite large and dendritic, with long lateral process.

Female similar to male; however, more slender, head appearing proportionally larger. Legs shorter, more slender but without
sphaerotrichomes. Syncoxon sternum membranous and thin basally.
Sternum III unmodified.

Cyphopod oval, small, with few valvular macrosetae, and with a very small smooth cyphopod plate.

CONTENT: One species, Speorthus tucanbius Chamberlin.

DISTRIBUTION: Speorthus tucanbius occurs in caves in central and southern New Mexico and the western tip of Texas in the Capitan-Sacramento-Guadalupe mountain systems. The caves are in karst and gypsum plains, elevation 1,800 to 2,450 meters.

NOTES: Loomis (1960) suggested that Speorthus and Speodesmus may be related. Shear (1974a) placed Speorthus with Speodesmus and placed Speodesmus in the family Fuhrmannodesmidae, based on gonopod characteristics. Buckett and Gardner (1968) mentioned that a number of similarities are shared with Bidentogon.

Idahodesmus NEW GENUS

GENEROTYPE: Idahodesmus dentatus new species.

DIAGNOSIS & DESCRIPTION: See below under I. dentatus.

DISTRIBUTION: Northern Idaho.
Idahodesmus dentatus NEW SPECIES
(Figs. 10, 36-39; Map 2)


TYPES: Holotype and allotype deposited in USNM; 2 male and 1 female paratypes deposited in North Carolina Museum of Natural History; all collected from the U. S. Forest Service campground, 1.5mi. E. of Harvard, Latah Co., Idaho, IX-17-1978 by A. K. Johnson.

DESCRIPTION: Small (5-9mm) polydesmids, with 20 segments not including head. W/L 11.2-13.4% and WL 4.9-8.2mm². Color in life, probably white.
Head small, globose. Mandible quadrate laterally. Cranial suture indistinguishable. Interantennal distance small. Antennae set medially on face, long, slightly clavate, 18-26% of body length, and extending to posterior margin of 3rd tergite. Length relationship of antennomeres 7<1=4<2<5<3<6. First antennomere small and quadrate, 2 globose, 3 elongate and slightly clavate, 4 rounded ventrally, 5 short and clavate, 6 long and enlarged, and 7 typical with 4 terminal sensillae. Small patches of bacilliform setae located dorsolaterally on antennomeres 5, 6, and small knob on 7.

Head covered with numerous microsetae.

Mouthparts normal except gnathochilarium elongate.

Metaterga arched, not horizontal, with 3 transverse rows of small tubercles, each with single filiform seta. Anterior row with 10 tubercles, separated from remaining rows which have 10 and 8 tubercles respectively (Fig. 10). All dorsal setae directed caudad. Collum semicircular, with 3 rows of setae, not flaired, and with small lateral denticles.

Paranota curving ventrally, not expanded laterally. W/T ratio approximately 1.3 for paranota and 1.0 for tergites. Anterior paranota 2-4 directed cephalad. Lateral edges rounded, with six denticles on poriferous segments and five on non-poriferous segments. Small teeth or serrations present anterior to anterior denticle. Ozopores small, opening dorsolaterally and elevated. Poriferous arrangement typical. Posterior paranota progressively reduced and directed posteriorly.
Hypoproct small with single pair of seta-bearing swellings. Paraprocts with 4-6 pairs of setae, lips thin. Epiproct rugose, slightly deflexed, with numerous setae.

Sterna unmodified, with many short setae. Posterior half of 6th sternum slightly displaced laterally and moderately deep. Legs unmodified and short, 16.2% of total body length. Coxae, short and quadrate; trochanter, moderately long and quadrate; prefemur, elongate and subquadrate; femur, enlarged and rounded dorsally; tibia, moderately short and quadrate; tarsus, long and slightly curved; claw, short and constricted. Legs with numerous setae and sphaerotrichomes.

Gonopod, in situ, lying out of aperture, gonocoxae exposed, telopodite directed anteriodorsally, and extending to anterior margin of 6th sternum.

Gonopod aperture oval and wide, with L/W ratio 52.5%. Gonopod large (Figs. 36-38). Gonocoxae large, globose, with large anteriorly directed spine. Cannula attached under base of coxal spine. Prefemur large, hirsute. Femur with medial band of small, posteriorly directed, dendritic teeth, laterally with three major processes, proximally with small, simple dendritic process, the central process large with medially scimitar-shaped branch with small teeth on outer edge and two smaller laterally directed branches, one with two spines and 4 dendritic branches, and distal process spine-like with two smaller spines. Endomerite inserted distally on femur, elongate,
with short medial bifurcated process and large terminal process. Seminal groove straight. Tibiotarsus simple, curving laterally.

Female similar to male, except sternum wider, legs thinner, and without sphaerotrichomes. Syncoxosternum rough and hirsute, lateral spines present. Sternum III (Fig. 39) modified.

Cyphopods elongate with few marginal macrosetae, although with 20-25 large lateral and medial setae, anterior plate absent.

**DISTRIBUTION:** Known only from the vicinity of the type locality. Idaho: Latah Co., 1.5mi. E. of Harvard, USFS campground, (NCMH). Approximate elevation between 450 and 900 meters.

**Subfamily Polydesminae Leach, 1815, NEW STATUS**

(Table 1)


**DIAGNOSIS:** Small to large (7-36mm). Body usually with 20 segments, sometimes with 19. W/L ratio between 8-22%. IW between 10 and 165 mm². Tergal width to height ratio approximately 1.3. Body width to height ratio approximately 1.0. Usually brown with occasional red, white, and black. Head smooth with few filiform setae. Frons flat or slightly globose. Mandible quadrate laterally. Gnathochilarium quadrate. Antennae long and filiform, rarely clavate. Length relationship of antennomeres $7<1<2<6=5<4<3$. Antennal shape usually long and filiform. Interantennal distance

Gonopods simple, arcuate, with caudally projecting processes. Gonopodal aperture transversely oval. Gonocoxae large, triangular, variously lobed anteriorly, with ventral depression. Prefemur large, hirsute, and unmodified. Femur long, curved, with small distal cingulum. Seminal vesicle looped, ending in large terminal bulb. Endomerite midway up tibiotarsus, large, and may have processes. Tibiotarsus unbranched, attached ventrally to gonocoxae, and with various caudad projecting processes.

Syncoxosternum unspined, thickened, and massive. Sternum III may be modified. Cyphopods may oval or kidney-shaped with moderately large anterior plate.
CONTENT: Presently includes 11 genera (Table 1) and 220 species. The status of many Central Asia genera is uncertain. The subfamilial designation by Attems (1898) included Polydesmus, Brachydesmus, Archipolydesmus, and Pseudopolydesmus.


*Polydesmus* Latreille, 1802

(Figs. 11, 40-42, 65)

*Polydesmus* Latreille, 1802, Histoire naturelle.....des crustacés et des insectes. 3:44.—Attems, 1940, Das Tierreich 70:3.

GENEROTYPE: *Julus complanatus* Linnaeus, 1761, by monotypy.

DIAGNOSIS: Small to large, 19 or 20 body segments, brown, sometimes dull white, red, or black. Antennae usually filiform but may be slightly clavate. Tergites quadrate, each with polygonal bosses including a pair of lateral bosses, four medial bosses, and three rows of internal bosses. Paranota large and horizontal. Ozopores not elevated, opening dorsally. Male sterna and legs unmodified. Female legs unmodified, thin, without sphaerotrichomes. Gonopods arcuate with enlarged endomerite usually with at least one process, seminal groove looped with large terminal vesicle.
Syncoxosternum ventromedially modified but not enlarged, base not expanded laterally. Sternum III variously lobed. Cyphopod elongate, short macrosetae only on posterior edge of valves, anterior plate variable, usually small. Lateral and medial setae present.

DESCRIPTION: Small to large (7-36mm) polydesmids, with 19 or 20 segments not including head. W/L approximately 11-18% and W L 10-180mm².

Dull colors prevalent, usually brown, although white, brown, and black may occur. Venter, legs, and genae usually lighter. Antennomeres darker distally with terminal antennomere darkest.

Head smooth. Genae slightly triangular, projecting laterally. Cranial suture distinct, not extending to antennal insertion. Antennae well separated, set medially on face, short, slightly clavate, reported to be filiform in some species, approximately 12-18% of total body length, extending to midpoint of third segment. Length relationship of antennomeres 7<1<2=3<4<5<6. First antennomere short and rectangular, antennomeres 2-4 short and subquadrate, antennomeres 5 and 6 clavate with 6 elongate, and 7 typical short, with 4 terminal sensillae, antennomeres 5 and 6 and small knob on 7 with small distinct patches of bacilliform setae dorsally.

Facial setae numerous, filiform, and small.

Mouthparts typical, with quadrate gnathochilarium.

Metaterga essentially flat, not tuberculate, each with three well defined transverse internal rows of quadrate convex bosses, anterior row usually with two bosses located on anterior half of
tergum between stricture and transverse sulcus, immediately behind sulcus intermediate row with 4 small bosses, posterior margin with 6 toothed projections (Fig. 11). Medially to the three internal rows are an anterior and posterior boss. Also a single lateral boss is present. Setae, usually filiform, may be associated with bosses. Collum wider than head, rounded, unflared, and may have denticles and setae.

Paranota flat, expanded laterally, dorsally with one large medial boss and two elongated lateral bosses. Paranotal W/T ratio 1.6-1.9 and tergal ratio 1.0-1.2. Lateral edge straight with 3 or 4 minute denticles, 4 occurring on poriferous segments. Denticles may each have a single filiform seta. Ozopores small, not elevated, located on posterior half of paranota, opening dorsally on small rounded convex bosses, in 20-segmented species, on segments 5, 7, 9, 10, 12, 13, 15, 16, 17, and 18 and in 19-segmented species on segments 5, 7, 9, 10, 12, 13, 15, 16, and 17. Posterior paranota progressively more caudally directed.

Epiproct smooth, truncate, with 8 pairs of setae, sometimes deflexed. Hypoproct small, moderately rounded, with a pair of small posteriolateral seta-bearing knobs. Paraprocts smooth with moderately thick lips.

Sterna cruciately impressed, but otherwise unmodified, each quadrant usually without setae. Sterna between leg pairs 3, 4, 5, and 6 slightly produced into small, blunt, paramedial lobes. Legs long, approximately 17-24% of total body length. Coxae small and subquadrate; trochanter moderate with dorsal bulge; prefemur long
and curved ventrally; femur subquadrate; tibia elongate; tarsus very long and curved slightly ventrally; claws short, curved, and regularly tapered. Sphaerotrichomes on femur, tibia, and tarsus.

Gonopods, in situ, moderately exposed, partly retractile, caudally directed, parallel to each other, oriented along median axis of body, and capable of independent movement although connected by a thin membrane. Prefemur and gonocoxae extend over sternum between posterior legs of sternum 7, causing legs to be displaced laterally. Tibiotarsus and femur curving ventrally, extending anterior to midpoint of sternum 6.

Gonopod aperture subelliptical to circular, I/W ratio between 50 and 90%. Gonopod arcuate (Figs. 40-42). Gonocoxae large, slightly smaller than telopodite, with large, open, ventral concavity for gonopod retraction. Ventrolateral edge without setae. Anterior edge variously lobed. Prefemur hirsute and posteriorly directed. Seminal groove looped, extending to endomerite, terminating in a large terminal vesicle. Tibiotarsus usually single but may be extensively modified. Caudal surface with at least one processes. Acropodite generally scythe-shaped, variously bent. Endomerite usually small, flush with femur, and a small lateral process may be present.

Female similar to male. Sterna flat without lobes. Legs less robust, shorter. Tarsus usually shorter, femur smaller, prefemur not curved nor as massive, and trochanter not expanded. Sphaerotrichomes may be absent. Syncoxosternum fused, massive, posteriorly flattened, enlarged ventromedially, not expanded laterally, and curved slightly
posteriolaterally to protect cyphopods. Sternum III with median lobe (Fig. 65).

Cyphopods usually withdrawn internally behind second pair of legs, large, oval, and with posteriolateral projecting macrosetae on ventral edges of valves, flattened medially with membranous connection, lateral and medial surfaces with various numbers of elongate filiform setae. Receptacle small, closely associated with posterior edge of valves.

CONTENT: The number of species in the genus *Polydesmus* may approach 200. It is probable that a revisional study will reduce this number. These "species" are presently divided into 26 subgenera mostly confined to the Old World. In the United States the following introduced species have been reported: *Polydesmus* (*Rubrachydesmus*) *anguistus* Latzel, *P. (Polydesmus) complanatus* (Linnaeus), *P. (Nomarchus) denticulus* Koch, *P. (Polydesmus) inconstans* Latzel, *P. (Hormobrachium) racovitzai* Brolemann, *P. (Rubrachydesmus) superus* Latzel.

DISTRIBUTION: Native to the Palearctic region. The Nearctic representatives are introduced, with several now established throughout many areas of primarily urban North America. Several species have also been introduced into other temperate and semitropical regions throughout the world.
NOTES: Several new species have been described from the New World, all of which have subsequently been determined to be synonyms or placed in other genera.

Those in other genera are: Brachydesmus californicus Chamberlin, 1918 (= Bidentogon), B. hastingsus Chamberlin, 1941 (= Pheatodesmus), B. yosemitensis Causey, 1954, and B. bituberculatus Loomis, 1960 (both = Coronodesmus).

The following species have previously been synonymized with Polydesmus inconstans Latzel, 1884: Polydesmus testi Bollman, 1888, from Indianapolis, Indiana, P. socarnius Chamberlin, 1910, from Salt Lake City, Utah, P. hortus Williams and Hefner, 1928, from Athens Co., Ohio, P. pronomeutes Chamberlin, 1942b, from Fort Collins, Colorado, and P. wheeleri Causey, 1950, from Grand Forks, North Dakota.

The following species have previously been synonymized with Brachydesmus superus Latzel: P. dux Chamberlin, 1940, from Durham, North Carolina, P. pallidus Loomis, 1939, from Charleston, West Virginia, and P. gladiolus Williams and Hefner 1928, from Allen Co., Ohio. Brachydesmus has recently been defined as a subgenus of Polydesmus (Hoffman, 1979).

One species name has had a varied and troubled history. Polydesmus moniliaris Koch (1847) has been used for different species in eastern North America by several authors because of a poor description, lack of a locality, and the loss of the type. Pseudopolydesmus serratus, P. collinus, and Polydesmus inconstans have at one time or another been identified as moniliaris as have
several unrecognizable taxa. The positive identification of moniliaris is still in doubt.

The Palearctic genera of the subfamily included:
Archiopolydesmus, Attems, 1898; Polydesmus, Latreille, 1802; Jaxartes, Verhoeff, 1930; Kirgisodesmus, Lohmander, 1933; Schizoturanus, Verhoeff, 1931; Schizomeritius, Verhoeff, 1931; Turanodesmus, Lohmander, 1933; Ubekekodesmus, Lohmander, 1933; Cretodesmus, Strasser, 1974; and Serradium, Strasser, 1974. The dominant genus is Polydesmus with over 200 species recorded; the relationships of the remaining genera which total 25 species is uncertain. They may very well be synonymized with Polydesmus.

The most recent revision of Polydesmus was by Attems (1898), prior to the description of many of the species. Verhoeff (1941), reorganized the superfamily and in the process violated virtually every principle of logical systematic procedure. For example, he invalidly proposed most of the 26 subgenera. His higher classification was based on various misconceptions and errors which was swiftly disregarded by other workers. However, his lower classification, at generic and specific levels, was blindly accepted, despite the fact that Attems did not designate types; this is a major stumbling block to the understanding of the genus.

Attems' (1940) massive work on the complex was impressive in his determination but also lead to much confusion. In most cases, his descriptions and figures were just reediting of earlier or the original works. He took little or no time to understand or examine the specimens in detail. Many of the earlier genera, subgenera under
Attems, were and still are based principally on differences in segment number.

The first major step in cleaning up the genus Polydesmus will be the simplification and standardization of gonopod terminology. A list of gonopod processes from Attems' (1940) revision includes:

- terminal: s
- medial: p, q, i, lo, f, l, a, F, Z₁, Z₂
- prefemur: a
- lateral: T, l₂, k, z, n, A, ha, b, u, d, c, Q, r, h

The proliferation of medial and lateral processes is due to the recognition of many minor variations.

Since 1940, other authors have described new species and have added more new names for these processes. A system similar to that in Pseudopolydesmus needs to be set up to handle this problem. A complete, modern revision of this genus will take many years.

**Pseudopolydesmus** Attems, 1898

(Figs. 12, 19, 45, 46, 48, 50, 55, 57, 59, 63, 66, 67; Map 3)

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**Polydesmus** of American authors prior to 1943 (not Latreille, 1802).


(Type species: *D. tallulanus* Chamberlin, by original designation.) Synonymy by Hoffman, 1974.
GENOTYPE: *Polydesmus canadensis* Newport, 1844, by monotypy.


CONTENT: Two groups totaling nine species can be distinguished by gonopodal differences: Group Serratus, consists of *serratus*, *paludicola*, *caddo*, and *minor*, and Group Canadensis consists of *pinetorum*, *tallulanus*, *erasus*, *canadensis*, and *collinus*.

DESCRIPTION: Small to large (9-32mm) polydesmids, with 20
segments not including head (Fig. 19). W/L 12.2-22.0% and WL 38.0-
164.8mm².

Color in life usually brown or black metaterga although paranota may be red. Venter, legs, and genae usually light brown. Antennomeres darker distally, with 7th darkest.

Head smooth. Epicranial suture distinct, not extending to antennae. Vertex and frons equally large. Gena with large lateral projection. Parietal sclerite small, adjacent to Organ of Tomosvary. Mandible with large cardo and stipes, triangular, projecting laterally, with incomplete suture dorsally. Antennae well separated, set medially on face, usually filiform, 10-25% of body length, and extending to posterior edge of 4th tergite (Fig. 57). Antennomeric lengths in increasing sequence 7<1<6<4=2<3<5. First antennomere rectangular, 2-5 moderately long, subquadrate, and usually very slightly clavate, 6 elongate, and 7 quadrate with 4 terminal sensillae. Antennomeres 5, 6, and 7 normal, each with a small dorsodistal patch of bacilliform setae.

Facial setae few, long, and filiform. Distribution as follows: subantennal, several; frontal numerous and evenly spaced; clypeal 3 pairs; labral 3 pairs; genal 9-13 pairs; postantennal none.

Labrum with 3 small, blunt teeth, medial tooth largest. Mandible with one external, broadly-rounded, single-cusped tooth; 6 round, flat, single-cusped internal teeth, 6 single-toothed pectinate lamellae, and molar plate with several deep furrows with anteriorly curved monocusped fringe teeth. Epipharynx with large, medial, teardrop-shaped keel without teeth. Lateral keels very


Metaterga (Fig. 12) essentially flat, not tuberculate, each with three transverse rows of medial quadrate convex bosses, anterior row usually with two bosses located on anterior half of tergum between stricture and transverse sulcus intermediate row posterior to sulcus, with 4 bosses, and posterior margin with 6 bosses, with a single elongate lateral boss. On caudal segments posterior row projects slightly caudally beyond margin. Filiform setae (Fig. 50) may be associated with these quadrate areas. Prozonite completely covered in small pits. Collum moderately large, wider than head, rounded, not flared, and sometimes with several lateral denticles and setae.

Paranota expanded laterally and horizontally, T/W ratio approximately 1.6 for paranota and 1.0 for tergites. Lateral edges curved, with 3 or 4 minute denticles, 4 occurring on poriferous segments. Denticles may have one or two filiform setae. Ozopores small, not elevated, located on posterior half of paranotum, opening dorsally, on segments 5, 7, 9, 10, 12, 13, 15, 16, 17, and 18.
Peritremata thicker on poriferous segments. Posterior paranota progressively more caudally directed.

Epiproct smooth, truncated, with 8 pairs of setae, and may be deflexed. Hypoproct small, rounded, with single pair of small seta-bearing posteriolateral swellings. Paraprocts smooth, with two pairs of lateral setae; lips thin to moderate.

Sterna cruciately impressed, each quadrant usually moderately setose (Fig. 59). Sterna between legs 3, 4, 5, 6, 9, 11, and 13, produced into paired prominent, angular, blunt, paramedial lobes.

Legs long, 14–25% of total body length. Coxa small and subquadrate; trochanter moderate and clavate; prefemur curved and massive; femur long and curving; tibia subquadrate; tarsus elongate; claw (Fig. 55) moderately long, simple, and tapered gradually. Tarsus, tibia, and femur of males with sphaerotrichomes, and large ventral mammulations, each with a single proximally directed seta.

Gonopods, in situ, moderately exposed, partly retractile, directed caudad, parallel, and oriented along median axis of body, capable of moving independently, although attached medially by thin membrane. Prefemur and gonocoxa extend over sternum between posterior legs of segment 7, causing legs to be displaced laterally. Tibiotarsus directed anteroventrally, extending over anterior margin of segment 6.

Gonopod aperture subelliptical with L/W ratio of 55–70%. Gonocoxa large, slightly smaller than telopodite, with large, open, ventral concavity for retraction of gonopod, ventrolateral edge with two setae, anterior edge variously lobed. Prefemur very hirsute and
squared posteriorly. Cannula connected to telopodite under small ledge. Femur curved and long. Seminal groove looped, extending to endomerite where it terminates in a large internal vesicle. Tibiotarsus single, not divided. Caudal surface with various processes, mesal (M1-4) and ectal (E1-4). Process M1 located proximal to endomerite. All processes directed caudad except E2 which is directed laterad. Process M4 usually adjacent to small distal setal series. Tip may be bent or straight, with small linear series of flattened setae. Telopodite scythe-shaped or variously bent: from subevenly curved to bent with one or two proximal or distal angulations. Many variations occur. If a proximal bend is present, the angle usually measures between 118° and 137°, while a distal bend, if present, measures between 111° and 140°. The telopodite tip is usually sharply hooked, or occasionally slightly curved. The terminal setal tuft appears highly variable, primarily due to breakage. Endomerite large, sloping away from telopodite.

Female very similar to male, except sterna flat without lobes. Legs not as robust as in males, tarsus usually shorter, femur smaller, prefemur not curved or as massive, and trochanter not expanded. Sphaerotrichomes absent. Syncoxosternum (Fig. 63) fused, massive, posteriorly flattened and curved slightly posteriolaterally. Sternum III (Fig. 66) slightly lobed ventrally.

Cyphopods (Fig. 67) large, kidney-shaped, and usually withdrawn internally behind second pair of legs. Valves large, flattened medially, lateral and medial surfaces with various numbers of elongate setae, with 10–18 caudad macrosetae on dorsal edge.
Dorsal surface expanded into irregular plate. Operculum small, closely associated with ventral surface of valves. Receptacle absent.

DISTRIBUTION: Nearctic region (Map 3). Southeastern Canada west to Minnesota, south to northern Florida and eastern Texas. Usually found in leaf duff of deciduous forests.

Key to males of the species of *Pseudopolydesmus*

1a. Process $M_2$ absent; process $E_3$ present; cyphopodal plate large and with long ventral setae; body with small posterior sternal lobes on 7th segment......

...............Group Canadensis.............2

1b. Process $M_2$ present; process $E_3$ absent; gonocoxae multi-lobed. Process $M_1$ & $E_2$ connected by ventral ridge and with large posterior sternal lobes on 7th segment..............Group Serratus.............6

2a. Process $E_1$ present; denticles large; epiproct downturned slightly..................pinetorum

2b. Process $E_1$ absent; denticles small; epiproct normal..3

3a. Processes $E_2$ and $E_3$ joined on single stalk ($E_{2+3}$); process $M_2$ present; telopodite thickened longitudinally..............................4

3b. Processes $E_2$ and $E_3$ not joined; process $M_2$ absent; telopodite thickened longitudinally......................5

4a. Process $E_2$ absent; found on Cumberland Plateau..erasus

4b. Process $E_3$ present; found in southern Appalachians..........................tallulanus

5a. Process $M_3$ present; process $M_1$ distal to base of endomerite; usually with red paranota; gonocoxae monolobed..........................canadensis
5b. Process $M_3$ absent; process $M_1$ next to endomerite; brown paranota; gonocoxae multi-lobed...........collinus

6a. Process $M_4$ present; large, greater than 20mm; cyphopod elongate; sometimes with red paranota; dorsal setae absent; habitat generalized.....serratus

6b. Process $M_4$ absent; small less than 20mm; cyphopod oval; dorsal setae present; brown paranota; habitat lowlands.................................7

7a. Process $E_2$ absent; $M_1$ and $E_2$ connected by posterior ridge.................................paludicola

7b. Process $E_2$ present; $M_1$ and $E_2$ not connected...........8

8a. Process $M_3$ present; process $M_4$ absent; body flattened, $W/L$ ratio greater than 70%; sternum II of female modified.......................minor

8b. Process $M_3$ absent; process $M_4$ present; body much flattened, $W/L$ ratio less than 80%; sternum II unmodified.........................caddo

Group Canadensis

The Group Canadensis consists of five species, Pseudopolydesmus pinetorum, tallulanus, erasus, canadensis, and collinus. Apomorphies for the group are: $M_1$ not connected to $E_2$, posterior sternal lobe on 7th segment small, cyphopodal plate small, long sternal setae, paranota with small denticles, and process $E_1$ usually present. These are medium to large millipedes of the genus. They have paranota slightly rounded laterally and posteriolateral corner slightly produced caudally, simple gonocoxae, cyphopod elongate with laterally expanded plate, legs longer than in Group Serratus, with longer trochanters and smaller coxae. The Appalachian
Mountains region has *canadensis*, *collinus*, *erasus*, and *tallulanus*, while *pinetorum* occurs to the south and west.

**Pseudopolydesmus pinetorum** (Bollman, 1888)
(Figs. 74, 80, 82, 86, 90, 106, 111, 122-126)

Map 4; Tables 9-11)

**Polydesmus pinetorum** Bollman, 1888, Ent. Amer. 4:3 (type locality: Arkansas, Pulaski Co., Little Rock; type: USNM).
**Polydesmus americanus** Carl, 1902, Rev. Suisse Zool., 10:611, fig. 37 (type locality: "Texas"; type: GZH).
**Polydesmus natchitoches** Chamberlin, 1942, Bull. Univ. Utah, biol. ser., 6(8):10, figs. 34, 35 (type locality: Louisiana, Natchitoches Par., 2mi. S. Saline; type: USNM). NEW SYNONYMY.
**Polydesmus paroicus** Chamberlin, 1942, Bull. Univ. Utah, biol. ser., 6(8):11, figs. 37, 38 (type locality: Louisiana, Jackson Par., 1.5mi. N. Clay; type: USNM).
**Polydesmus hubrichti** Chamberlin, 1943, Ent. News, 54:15, figs. 1, 2 (type locality: Missouri, St. Louis Co., St. Louis; type: ANSP).

**DIAGNOSIS:** Medium to large (11-28mm). Metaterga and paranota brown. Dorsal and paranotal setae absent. Dorsal sculpture medium. Antennae short. Posterior sternum of 7th segment small. Gonocoxae monolobed. Gonopodal process $M_1$ small, on base of endomerite, $M_3$ small to medium, $M_4$ small to medium, $E_1$ small, if present on lateral edge, $E_2$ medium, $E_3$ small, $E_4$ small. Cyphopods not expanded
dorsally. Cyphopod plate mediolateral lobe rounded, lateral edge with several small teeth.

DESCRIPTION: (Based on adult male and female from Missouri, Barry Co., Roaring River State Park, VI-21-1983, C. P. Withrow, (CPWC)). Adult male, 16.6mm long, maximum width (7th segment), 2.6mm, W/L 15.7%, and WL 43.2mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Segment</th>
<th>Width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collum</td>
<td>1.8</td>
</tr>
<tr>
<td>2</td>
<td>2.1</td>
</tr>
<tr>
<td>3-4</td>
<td>2.2</td>
</tr>
<tr>
<td>5</td>
<td>2.3</td>
</tr>
<tr>
<td>6</td>
<td>2.5</td>
</tr>
<tr>
<td>7</td>
<td>2.6</td>
</tr>
<tr>
<td>8</td>
<td>2.5</td>
</tr>
<tr>
<td>9-13</td>
<td>2.4</td>
</tr>
<tr>
<td>14-15</td>
<td>2.3</td>
</tr>
<tr>
<td>16</td>
<td>2.2</td>
</tr>
<tr>
<td>17</td>
<td>2.0</td>
</tr>
<tr>
<td>18</td>
<td>1.6</td>
</tr>
<tr>
<td>19</td>
<td>1.0</td>
</tr>
<tr>
<td>20</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Color in life brown, paranota lighter.

Head typical for genus. Head width 1.06mm, interantennal distance 0.32, 30.2% of total head width. Antennae moderate (2.49mm), 15.0% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere, 0.24mm (9.8%); 2nd, 0.42mm (16.8%); 3rd, 0.62mm (24.8%); 4th, 0.34mm (13.6%); 5th, 0.41mm (16.6%); 6th, 0.44mm (17.5%); 7th, 0.13mm (5.0%).

Dorsal sculpture moderately defined. Collum moderate, with acute posteriolateral angle and anteriomedial bulge. Paranota with
anterior, lateral, and posterior edges straight, anterior corner slightly cephalad. Medial boss large, anterior bosses slightly separated (Fig. 74). Lateral denticles normal, located from anteriolateral corner (% of total length of 8th segment): 1st denticle, 0.04mm (6.6%); 2nd, 0.13mm (21.3%); 3rd, 0.25mm (41.0%); 4th, 0.46mm (75.4%). Posteriomedial teeth distinct on segments 15-19. Ventrolateral surface of paranota rough and irregular.

Sterna cruciately impressed, each quadrant moderately setose. Sternum 2 edge sharply indented anteriomedially, posteriomedial margin also indented, with small medial cross-ridge. Sternum 3 posterior heavy margined, anterior edge moderately inflated, moderately rough without setae posteriomedially between penes, small, truncated anteriomedial swelling, posterior plate field moderate, and penes typical although margined laterally. Sternum 4 with 5-6 long setae and numerous short stubby setae. Sternum 5 similar to 4 but sternal lobes more defined. Sternum 6 typically shaped except posterior legs moderately displaced laterally, median depression striated, broad, and moderately deep. Posterior sternum of 7th segment with small pointed lobe. Leg shape typical and short. Length of right posterior leg of 8th segment 3.07mm, 18.5% of total body length. Length of podomeres (% of total leg length): coxae, 0.27mm (8.9%); trochanter, 0.47mm (15.3%); prefemur, 0.63mm (20.4%); femur, 0.37mm (12.1%); tibia, 0.31mm (10.2%); tarsus, 0.84mm (27.4%); claw, 0.17mm (5.7%). Sphaerotrichomes typical.
Epiproct straight (Fig. 80). Hypoproct and paraprocts normal.

Gonopod aperture subelliptical (0.84mm long, 1.17mm wide), with L/W ratio of 71.8%. Gonocoxae large (0.81mm high, 1.03mm long), posterioventral edge monolobed, blunt, extending outward twice its width, sides parallel, smooth, and rounded. Telopodite (Figs. 82, 86, 90) moderate (1.10mm long). Prefemur normal. Femur thin with rounded femoral ledge. Tibiotarsus typically shaped, M\(_1\) small (0.05mm), irregular, located 0.45mm (40.9%) from tip, on base of endomerite; M\(_3\) small (0.05mm), finned, 0.23mm (20.9%) from tip; M\(_4\) medium (0.06mm), having a second smaller lobe for setal tuft, 0.14mm (12.7%) from tip; E\(_1\) very small (0.005mm), 0.40mm (36.4%) from tip; E\(_2\) medium (0.06mm), hooked, 0.27mm (24.8%) from tip; E\(_3\) small (0.01mm) and hooked, 0.17mm (16.3%) from tip; E\(_4\) small (0.02mm), triangular, 0.08mm (7.3%) from tip. Tip slightly lobate. Telopodite with distal and proximal curves. Seminal groove typical. Telopodite thickness measured at femoral ledge perpendicular to body axis, 0.09mm, parallel to axis, 0.20mm. Tibiotarsus thickened proximal to seminal groove. Endomerite blunt, 0.42mm (26.2%) from tip, extending 0.23mm on telopodite, projecting 0.13mm high and 0.21mm long.

Female 20.15mm long, maximum width 2.96mm, W/L 14.7%, and WL 59.6mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>2.2 mm</th>
<th>9-11</th>
<th>2.9 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>2.5 mm</td>
<td>12-15</td>
<td>2.8 mm</td>
</tr>
<tr>
<td>3</td>
<td>2.6 mm</td>
<td>16</td>
<td>2.6 mm</td>
</tr>
<tr>
<td>4</td>
<td>2.7 mm</td>
<td>17</td>
<td>2.5 mm</td>
</tr>
</tbody>
</table>
Color and structure similar to male. Sterna and legs unmodified. Syncoxosternum straight laterally, quadrate and rough distally. Sternum III rounded distally, notched, and curved gently laterally, and rough medially.

Cyphopods (Figs. 106, 111) compact (0.53mm long, 0.24mm high). Valves with 9 long macrosetae projecting from lateral half over intervalvular opening, and dorsal edge not flattened. Cyphopod plate with distomedial lobe rounded, smooth, lateral edge with small notch containing 2-3 small teeth. Operculum small (0.11mm long, 0.18mm high) and thin.

VARIATION: Based on 715 specimens, Pseudopolydesmus pinetorum although wide-ranging, showed slight size variation with little or no geographic significance. Based on 212 specimens (112 males, 100 females) measured, the means of the body measurements for males and females, respectively, were: length 18.60mm, 18.70mm; width 3.1mm, 3.1mm; W/L 16.45%, 16.60%; IW 57.65mm², 59.37mm². The ranges and standard deviations are given in Tables 9, 10, and Figures 122-125. Females are slightly longer than males. Females also have a higher W/L ratio and dorsal area.

Based on ten specimens, the gonopodal processes varied little in their relative position on the tibiotarsus (Fig. 126). The
positions of the processes relative to telopodite length are: M₁ 56.15%, M₂ 22.0%, M₄ 13.6%, E₂ 27.55%, E₃ 16.3%. For actual ranges see Table 11.

Gonopod processes of *Pseudopolydesmus pinetorum* varied slightly in size and location. In several specimens the E₁ process was absent. In a number of specimens a process distal to E₁ (designated E₁⁺) was present. This condition being more prevalent in the northern and eastern parts of the range. Process E₃ tended to be smaller in the northeastern segment of the range, and varied from a single process with a lateral setal tuft to a double process with the tuft on the proximal prong. Process M₁ was irregularly shaped. Processes were generally shark-fin or hook-shaped.

**Distribution:** The range of *Pseudopolydesmus pinetorum* covers the lower and middle Mississippi River drainages from southern Illinois and Iowa south through eastern Kansas, Oklahoma, and Texas; eastward to central Alabama, and sporadically in central Tennessee and eastern Kentucky (Map 4). The distribution east of the Mississippi River is not clear, due inadequate collecting. Records from central Kentucky and eastern Tennessee are very suspect. Although those specimens from eastern Tennessee were examined and verified as *pinetorum*, I believe that the locality labels were somehow mixed up. *Pseudopolydesmus pinetorum* is the dominant species west of the Mississippi River and is most prevalent in the Ozark Mountain region. The habitat is typical for the genus.
NOTES: *Polydesmus americanus* Carl, holotype examined, was synonymized by Causey (1952a). Carl's description was atypical in that it was done well. All telopoditic processes were visible in his drawing.

In the original description, *Polydesmus natchitoches* Chamberlin, holotype examined, was illustrated in medial view with an enlargement of the telopodite tip, endomerite without setae, M₁ absent, and M₃ absent, and in distal view, M₃ was present as well as a small E₂. The last structure is not present on the type!

*Polydesmus paroicus* Chamberlin, holotype examined, was synonymized by Causey (1952a). The gonopod figures in the description were again misdrawn. In the mesal view, M₁ was absent, with process E₂ absent from the distal view.

*Polydesmus modocus* Chamberlin, holotype examined, was also synonymized with *pinetorum* by Causey (1952a). The Chamberlin (1943a) figure shows M₁ missing. In his paper Chamberlin also drew two figures clearly representative of *pinetorum* but with no statement or identification in the text or key. While examining types from the Chamberlin collection at the U.S. National Museum, a manuscript holotype identified as "*Polydesmus scholasticus*" was found. It was collected from St. Louis, Missouri but a description was never published. This specimen may be the source of those figures. Although a type exists, the name *scholasticus* has not been validly published, and my mention of it here is not to be construed as validation.
Polydesmus hubrichti Chamberlin, holotype examined, was synonymized by Causey (1952a). The gonopod drawings showed process M₁ absent in medial view but present in distal view.

Pseudopolydesmus tallulanus (Chamberlin, 1943) NEW COMB.

(Figs. 75, 83, 87, 91, 107, 112, 122–126; Map 5; Tables 9–11)


Dixidesmus penicillus Chamberlin, 1943, Bull. Univ. Utah, biol. ser. 8(2):19, fig. 35 (type locality: Georgia, Habersham Co., Clarkesville; type: USNM). NEW SYNONYMY.


DIAGNOSIS: Medium to large (18–26mm). Metaterga brown with paranota red or brown. Dorsal sculpture light. Small dorsal and paranotal setae present. Denticles small. Antennae long. Gonocoxae monolobed, ventrodorsally large, smooth, and pointed. Telopodite thick longitudinally. Gonopodal process M₁ medium, next to endomerite; M₃ medium; M₄ small with small setal pad; E₁ size variable distal to endomerite; E₂ large, projecting posteriorly; E₃ medium; E₄ small, subterminal. Cyphopod elongate, with slight lateral twist and small lateral projection.

DESCRIPTION: (Based on adult male and female from North Carolina, Transylvania Co., 12.1mi. WSW. of Rosman, County Route
Adult male 25.7 mm long, maximum width (7th segment), 4.7 mm, and maximum thickness, 3.0 mm. W/L 18.3% and WL 120.8 mm^2. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>2.9 mm</th>
<th>11-12</th>
<th>4.4 mm</th>
</tr>
</thead>
<tbody>
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<td>8</td>
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<td>19</td>
<td>1.6 mm</td>
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<tr>
<td>9-10</td>
<td>4.5 mm</td>
<td>20</td>
<td>1.0 mm</td>
</tr>
</tbody>
</table>

Color in life, brown.

Head typical for genus. Head width 0.92 mm, interantennal distance 0.23 mm, 25.3% of total head width. Antennae long (4.44 mm), 17.3% of total body length. Antennomeric lengths (% of total antennae length): 1st antennomere, 0.22 mm (5.0%); 2nd, 0.55 mm (12.4%); 3rd, 1.07 mm (24.1%); 4th, 0.84 mm (18.9%); 5th, 0.85 mm (19.1%); 6th, 0.68 mm (15.3%); 7th, 0.23 mm (5.2%).

Dorsal sculpture slight. Lateral boss of paranotum elongate, angling anteriomedially, anteriomedial bosses well separated, medial boss large, equidistant from anterior and posterior edges (Fig. 75). Collum moderate with rounded posteriolateral angle, medial anterior
bulge, and indented posteriomedially with single pair of denticles. Paranota with anterior edge straight, posterior margin indented. Denticles small, usually distinct, located from anteriolateral corner (% of total length of paranotum, 8th segment): 1st dentine, 0.10mm (7.2%); 2nd, 0.28mm (20.2%); 3rd, 0.67mm (47.6%); 4th, 0.95mm (67.9%). Ventrolateral surface of paranota rough and irregular.

Sterna cruciately impressed, each quadrant heavily setose. Sternum 2 sharply indented anteriorly, smoothly indented posteriorly, with wide rough border. Sternum 3 with small medial swellings, not as rough medially, penes normal, one posteriomedial seta and two anteriomedial setae. Sterna 4 and 5 similar, with many lateral setae. Sternum 6 anterior lobes widely separated, with short and long setae; posterior sternal lobes slightly displaced anteriorly, with numerous short setae, longitudinal groove inverted V-shaped, deep, with distinct contour ridges. Remaining sterna hirsute. Posterior sternum of 7th segment elongate, extending ventrally close to coxae. Leg shape typical and short. Length of right posterior leg of 8th segment 5.10mm, 19.8% of total body length. Length of leg segments (% of total leg length): coxa, 0.44mm (8.6%); trochanter, 0.96mm (18.8%); prefemur, 0.93mm (18.4%); femur, 0.50mm (9.8%); tibia, 0.55mm (10.6%); tarsus, 1.38mm (27.5%); claw, 0.32mm (6.3%), slightly curved. Sphaerotrichomes typical.

Epiproct slightly downturned. Hypoproct and paraprocts typical for genus.

Gonopod aperture subelliptical (1.27mm long, 1.89mm wide) with L/W ratio of 67.3%. Gonocoxae large (0.92mm high, 1.57mm long),
triangular, slightly trilobed. Telopodite (Figs. 83, 87, 91) large (1.68mm long). Prefemur irregular with small mound 1.35mm from distal tip. Femur thickened, femoral ledge round. Tibiotarsus typically shaped, $M_1$ medium (0.08mm), located 0.84mm (53.6%) from tip; $M_3$ medium (0.09mm), 0.36mm (22.9%) from tip; $M_4$ small (0.04mm), 0.21mm (13.4%) from tip; $E_3$ medium (0.08mm), 0.61mm (38.9%) from tip, distally on base of endomerite; $E_2$ large (0.14mm), 0.44mm (28.0%) from tip; $E_3$ medium (0.08mm), 0.52mm (33.1%) from tip; $E_4$ small (0.03mm), 0.13mm (8.3%) from tip. Tip slightly bent.

Telopodite with distal bend 0.36mm from tip. Tibiotarsal thickness measured at femoral ledge, perpendicular to body axis, 0.03mm, and parallel to axis, 0.03mm. Seminal groove normal. Endomerite typical, 0.72mm (46.1%) from tip, extending 0.28mm on telopodite, projecting 0.12mm high and 0.41mm long.

Female 23.3mm long, maximum width 4.5mm, W/L 19.3%, and WL 104.9mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum/Segment</th>
<th>Width</th>
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<th>Width</th>
<th>14</th>
<th>Width</th>
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<th>18</th>
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<th>19</th>
<th>Width</th>
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<tbody>
<tr>
<td>2</td>
<td>3.7</td>
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<td>3.8</td>
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<td>4.5</td>
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<td>0.8</td>
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</table>
Color and structure similar to male. Sterna and legs unmodified. Syncoxosternum wide medially, ventrolateral shelf small, straight laterally, rough anteriorly. Sternum III flattened, projecting slightly ventrolaterally, and posteriorly smooth with small medial ridge.

Cyphopods (Figs. 107, 112) large (0.90mm long, 0.42mm high). Valves not expanded, lateral setae moderate. Cyphopodal plate twisted laterally, projecting slightly laterally, sloping medially, not curving. Operculum small with numerous long anterior curving setae.

VARIATION: Based on approximately 250 specimens, *Pseudopolydesmus tallulanus*, showed slight size variation with little or no geographical significance. Based on 55 (33 males, 22 females) specimens measured, the means of the body measurements for males and females, respectively, were: length 23.27mm, 23.25mm; width 4.28mm, 3.95mm; W/L 18.39%, 16.99%; IW 99.60m², 91.82mm². The ranges and standard deviations can be seen in Tables 9, 10, and Figures 122-125.

Based on ten specimens, the gonopodal processes varied little in their relative position on the telopodite (Fig. 126). The positions of the processes relative to telopodite length are: M₁ 52.6%, M₂ 22.45%, M₃ 10.9%, E₁ 42.35%, E₂ 32.8%, E₃ 22.9%, E₄ 8.65%. For actual ranges see Table 11. The most notable variation observed is the length of process E₁ which ranges from a small tooth to an elongate spine.
DISTRIBUTION: The range of *Pseudopolydesmus tallulanus* covers the eastern slopes of the southern Appalachians from southwest North Carolina and extreme eastern Tennessee into northwestern South Carolina and northern Georgia (Map 5). The western limit of this species borders its sister species *Pseudopolydesmus erasus*. Based on the localities recorded for both species, they appear to be allopatric, although this may be a collecting artifact.

NOTES: *Dixidesmus penicillus* Chamberlin, holotype examined. Chamberlin's drawing of the gonopod shows sharper bends in the tibiotarsus and a smaller process E₃ than actually present in *tallulanus* and his holotype.

*Dixidesmus humilidens* Chamberlin, holotype examined. Chamberlin's figure shows a smooth curvature of the tibiotarsus, also E₃ smaller than that of *tallulanus*. The species was said to be smaller than *tallulanus* although sympatric.

*Pseudopolydesmus erasus* (Loomis, 1943) NEW COMB.  
(Figs. 84, 88, 92, 108, 113, 122-126; Map 5; Tables 9-11)

DIAGNOSIS: Medium (15.8-24.0mm). Metaterga brown with reddish paranota. Dorsal sculpture weak, similar to tallulanus. Denticles small. Dorsal and paranotal setae small. Antennae moderately long. Gonocoxae monolobed, sharp and thickened anteriorly. Gonopodal process $M_1$ medium, regular, close to base of endomerite; $M_3$ large, distal to $E_3$; $M_4$ medium; $E_1$ large, on distal side of endomerite, $E_2$ large, basally directed; $E_4$ small, subterminal. Telopodite thick longitudinally. Endomerite typical. Cyphopods large, elongate, with many lateral setae. Valves with marginal macrosetae. Cyphopodal plate with slight lateral twist, and small lateral projection.

DESCRIPTION: (Based on adult male and female from Tennessee, Bradley Co., US Rt. 75, 25mi. S. of Cleveland, IV-14-1978, C. P. Withrow, (CFWC)). Adult male, 19.8mm long, maximum width (8th segment), 3.2mm. W/L 16.2%, and WL 63.4 mm$^2$. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Segment</th>
<th>Width (mm)</th>
<th>Width (mm)</th>
</tr>
</thead>
<tbody>
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<td>Collum</td>
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<td>3.0</td>
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<tr>
<td>5</td>
<td>3.1</td>
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<tr>
<td>6-10</td>
<td>3.2</td>
<td>19</td>
</tr>
<tr>
<td>11</td>
<td>3.1</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>2.0</td>
<td>0.6</td>
</tr>
</tbody>
</table>
Color in life, typically light brown with reddish paranota.

Head typical for genus. Head width 1.72mm, interantennal distance 0.45mm, 26.1% of total head width. Antennae robust, moderately long (3.61mm), 18.2% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere, 0.29mm (8.0%); 2nd, 0.39mm (10.8%); 3rd, 0.82mm (22.7%); 4th, 0.67mm (18.6%); 5th, 0.64mm (17.7%); 6th, 0.55mm (15.2%); 7th, 0.25mm (6.9%).

Dorsal sculpture weak, similar to tallulanus. Collum moderate, with acute posteriolateral angle, longer medially, and indented posteriomedially. Paranotal anterior edge straight, with posteriolateral angle acute. Dorsal and paranotal setae small. Denticles small, located from anteriolateral corner (% of total paranotal length, 8th segment): 1st denticle, 0.17mm (12.8%); 2nd, 0.39mm (28.9%); 3rd, 0.63mm (47.4%); and 4th, 0.99mm (75.0%).

Ventrolateral surface of paranota rough and irregular.

Sterna similar to tallulanus. Leg shape normal and long. Length of right posterior leg of 8th segment 4.17mm, 21.1% of total body length. Length of leg segments (% of total leg length): coxae, 0.37mm (8.9%); trochanter, 0.77mm (18.5%); prefemur, 0.78mm (18.7%); femur, 0.45mm (10.8%); tibia, 0.48mm (11.5%); tarsus, 1.12mm (26.9%); claw, 0.20mm (4.8%).

Epiproct slightly down-turned. Hypoproct and paraprocts normal.

Gonopod aperture subelliptical (0.98mm long, 1.26mm wide), with L/W ratio of 77.8%. Gonocoxae large (0.92mm high, 1.37mm long),
posteroventral edge monolobed, smooth, sharp, and thickened.

Telopodite (Figs. 84, 88, 92) large (1.94 mm long). Prefemur irregular with small posteroventral knob, 1.49 mm (76.8%) from distal tip. Femur thickened, femoral ledge round. Tibiotarsus typically shaped, \( M_1 \) medium (0.08 mm), located 0.96 mm (49.9%) from tip, next to endomerite; \( M_3 \) large (0.10 mm), 0.54 mm (28.3%) from tip; \( M_4 \) medium (0.06 mm), 0.37 mm (19.2%) from tip; \( E_1 \) large (0.13 mm), 0.94 mm (48.3%) from tip, located distally on base of endomerite; \( E_2 \) large (0.14 mm), 0.83 mm (42.7%) from tip; \( E_4 \) small (0.05 mm), 0.16 mm (8.4%) from tip. Tip curved dorsally. Telopodite with proximal bend 28.6% from tip. Seminal groove typical. Tibiotarsal thickness measured at femoral ledge, perpendicular to body axis, 0.03 mm, and parallel to axis, 0.02 mm. Endomerite sharp, 0.87 mm (44.6%) from tip, extending 0.35 mm on telopodite, projecting 0.13 mm high and 0.39 mm long.

Female 20.05 mm long, maximum width, 3.25 mm, W/L 16.2%, and WL 65.2 mm². Segmental widths across paranota as follows:

<table>
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<th>Collum</th>
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<td>6-8</td>
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<td>1.4 mm</td>
</tr>
<tr>
<td>10-11</td>
<td>3.1 mm</td>
<td>20</td>
<td>0.6 mm</td>
</tr>
<tr>
<td>12-13</td>
<td>3.0 mm</td>
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</tbody>
</table>
Color and structure similar to male. Sterna and legs unmodified. Syncoxosternum similar to *tallulanus*, lateral angle gradually sloping, medial lobe bulbous. Sternum III flattened, projecting slightly ventrolaterally, and posteriorly smooth, with small medial ridge.

Cyphopods (Figs. 108, 113) elongate (1.24mm long, distally 0.77mm high, proximally 0.65mm high), lateral setae abundant. Dorsal plate twisted laterally, projecting slightly laterally, sloping medially, not curving. Operculum small with many long setae.

VARIATION: Based on approximately 200 specimens of *Pseudopolydesmus erasus* examined, little variation was observed. Based on 88 (77 males, and 11 females) specimens measured, the means of the body measurements for males and females, respectively, were: length 20.38mm, 19.57mm; width 3.6 mm, 3.20mm; W/L 17.66%, 16.35%; LW 73.37mm$^2$, 62.62mm$^2$. The ranges and standard deviations can be seen on Tables 9, 10, and Figures 122-125.

Normal variation in location and size of processes was present. Based on ten specimens, the gonopodal processes varied little in their relative position on the tibiotarsus (Fig. 126). The positions of the processes relative to telopodite length are: $M_1$ 55.45%, $M_2$ 19.5%, $M_3$ 11.45%, $E_1$ 40.5%, $E_2$ 30.2%, $E_4$ 8.0%. For actual ranges see Table 11.

On several specimens a small shoulder spine was located on $E_2$, however this spine is not the same as the $E_2$ process seen in
Pseudopolydesmus tallulanus. In several specimens the posterior margin of the collum had two large convex extensions.

**DISTRIBUTION:** The range of *Pseudopolydesmus erasus* covers the western slopes of the middle Appalachians from the southern tip of Illinois, south to eastern Mississippi, southern Alabama, and western Georgia (Map 5). This species is allopatric with *Pseudopolydesmus tallulanus*, which occurs to the southeast at essentially higher elevations. *Pseudopolydesmus erasus* appears to be limited to the Cumberland Plateau below 450 meters.

**Pseudopolydesmus canadensis** (Newport, 1844) NEW COMB.

(Figs. 55, 61, 70, 71, 72, 73, 76, 109, 114, 122-126; Map 6; Tables 9-11)

*Polydesmus serratus* of many authors, not Say, 1821.

(type locality: CANADA; Ontario, Hudson's Bay, Albany River; type: BMNH). [hereby designated as holotype]

(type locality: Tennessee, Jefferson Co., Jefferson City, Mossy Creek; type: USNM). NEW SYNONYMY.

*Polydesmus nitidus* Bollman, 1887, Ent. Amer. 3(1):45 (type locality: Florida, Escambia Co., Pensacola; type: USNM). NEW SYNONYMY.


Washington, 59:140, pl. XII, fig. 4 (type locality: Mississippi, Harrison Co., Pass Christian; type: USNM). NEW SYNONYMY.  


**DIAGNOSIS:** Medium to large (11-29mm). Metaterga vary from dark brown to black with red, pink, or brown paranota. Dorsal sculpture light. Dorsal and paranotal setae absent. Antennae long. Gonocoxae monolobed. Gonopodal process $M_1$ small, on edge, shark-fin shaped; $M_2$ medium, on edge across from $E_{2+3}$; $M_3$ medium, caudomedial; $M_4$ small with proximal setal patch; $E_1$ long, thin, caudomedial; $E_{2+3}$ large, stalked, forked; $E_2$ prong large, extending proximad along side of tibiotarsus; $E_3$ prong large, extending away from tibiotarsus; $E_3$ usually smaller than $E_2$; $E_4$ small. Cyphopod projecting caudally, not flattened. Cyphopod plate with straight distal edge, not sloping.  

**DESCRIPTION:** (Based on adult male and female from Tennessee, Campbell Co., on US Rt. 75, 19.7mi. S. of Jellico, VII-14-1982, C. P. Withrow, (CFWC)). Adult male, 21.5mm long, maximum width (7th segment), 4.3mm, W/L 18.3%, and WL 84.9mm². Segmental widths across paranota as follows:
Color in life, dark brown with red paranota.

Head typical for genus. Head width 2.08mm, interantennal distance 0.58mm, 27.8% of total head width. Antennae long (4.06mm), 18.8% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere, 0.35mm (8.9%); 2nd, 0.38mm (9.7%); 3rd, 0.95mm (24.2%); 4th, 0.67mm (17.0%); 5th, 0.73mm (18.6%); 6th, 0.57mm (14.5%); 7th, 0.28mm (7.1%).

Dorsal sculpture light. Collum moderate, subquadrate, slightly rounded along posterior edge. Anterior paranota rounded anteriorly and slightly cephalad, becoming straight on posterior segments, slightly sloping medially, lateral edge curved, posterior corner projecting caudalad only slightly. Lateral boss of paranotum elongate, anteriomedial bosses well separated (Fig. 76). Lateral denticles small, barely visible, distance from anteriolateral corner (% of total length of 8th segment): 1st denticle, 0.10mm (7.7%); 2nd, 0.28mm (21.5%); 3rd, 0.60mm (46.2%); 4th, 0.90mm (69.2%).

<table>
<thead>
<tr>
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<th>11-13</th>
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<td>8-10</td>
<td>4.2 mm</td>
<td>20</td>
<td>0.4 mm</td>
</tr>
</tbody>
</table>

Sterna cruciately impressed, each quadrant heavily setose. Sternum 2 sharply indented anteriorly, smoothly indented posteriorly, with wide rough border. Sternum 3 with small medial swellings, not as rough medially, penes normal, one posteriomedial seta and two anteriomedial setae. Sterna 4 and 5 similar, with many long setae. Sternum 6 anterior lobes with short and long setae; posteriorly, gonopodal groove wide with many slender lateral setae, posterior sternal lobes slightly displaced anteriorly, longitudinal groove inverted V-shaped, deep, apices extending to coxae. Posterior coxae of 7th segment projecting only slightly (Fig. 61). Leg shape typical and long. Length of right posterior leg of 8th segment 4.16mm, 19.3% of total body length. Length of podomerteres (% of total leg length): coxae, 0.37mm (9.9%); trochanter, 0.80mm (19.2%); prefemur, 0.84mm (20.2%); femur, 0.45mm (10.8%); tibia, 0.52mm (12.5%); tarsus, 0.95mm (22.8%); claw (Fig. 55), 0.23mm (5.5%). Sphaerotrichomes typical.

Epiproct slightly downturned. Hypoproct and paraprocts normal.

Gonopod aperture subelliptical (0.98mm long, 1.70mm wide) with L/W ratio of 57.6%. Gonocoxae large (0.84mm high, 1.10mm long), posterioventral edge monolobed, smooth, and subquadrate. Telopodite (Fig. 70-73) large (2.50mm long). Prefemur normal. Femur thin with femoral ledge rounded. Tibiotarsus typically shaped, M₁ small (0.02mm), blunt, on edge proximal to endomerite, 0.88mm (35.2%) from tip; M₂ medium (0.08mm), sharp, 0.44mm (17.7%) from tip; M₃ medium
(0.08mm), sharp, 0.36mm (13.2%) from tip; M$_4$ small (0.03mm), with proximal setal patch, 0.15mm (6.0%) from tip; E$_1$ large (0.13mm), blunt, 0.68mm (27.7%) from tip; E$_{2+3}$ bifurcate, stalk 0.61mm (24.4%) from tip, prong E$_2$ large (0.28mm), hooked, extending proximally on tibiotarsus; prong E$_3$ large (0.17mm), 0.87mm (34.8%) from tip, beside endomerite; E$_4$ small (0.03mm) and hooked, 0.09mm (3.6%) from tip. Tip slightly bent dorsally. Telopodite proximally curved, bent distally. Seminal groove typical. Tibiotarsus thickness measured at femoral ledge, perpendicular to body axis, 0.03mm, and parallel to axis, 0.02mm. Endomerite sharp and thin, 0.78mm (31.2%) from tip, extending 0.28mm on telopodite, projecting 0.15mm high and 0.24mm long.

Female 21.7mm long, maximum width 3.63mm, W/L 16.7%, and WL 78.7mm$^2$. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>2.6 mm</th>
<th>14-15</th>
<th>3.5 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>3.0 mm</td>
<td>16</td>
<td>3.3 mm</td>
</tr>
<tr>
<td>3</td>
<td>3.2 mm</td>
<td>17</td>
<td>3.0 mm</td>
</tr>
<tr>
<td>4</td>
<td>3.3 mm</td>
<td>18</td>
<td>2.4 mm</td>
</tr>
<tr>
<td>5</td>
<td>3.4 mm</td>
<td>19</td>
<td>1.5 mm</td>
</tr>
<tr>
<td>6-7</td>
<td>3.5 mm</td>
<td>20</td>
<td>0.4 mm</td>
</tr>
<tr>
<td>8-13</td>
<td>3.6 mm</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Color and structure similar to male. Sterna and legs unmodified. Syncoxonosternum flat posteriorly and slightly curved
posteriolaterally to protect cyphopods. Sternum III with raised anterior margin.

Cyphopods (Figs. 109, 114) large and elongate (1.18mm long, 0.61mm high). Valves with numerous small macrosetae, posterior half with long setae laterally. Cyphopod plate large, edge straight, not sloping.

VARIATION: Based on 1000 specimens, *Pseudopolydesmus canadensis* appears to be the most variable species of the genus, thereby explaining the proliferation of specific names. The variability is probably correlated with the wide geographical range and high telopoditic complexity.

Based on 162 (100 males, 62 females) specimens measured, the mean body measurements for males and females, respectively, were: length 22.79mm, 21.15mm; width 4.03mm, 3.74mm; W/L 17.76%, 17.60%; LW 93.77mm², 80.89mm². The ranges and standard deviations can be seen on Tables 9, 10, and Figures 122-125. The length, width, W/L, and WL were higher in the males than females.

Based on ten specimens, the gonopodal processes varied little in their relative location on the tibiotarsus (Fig. 126). The average positions of the processes relative to telopodite length are: M₁ 52.8%, M₂ 30.5%, M₃ 13.4%, M₄ 4.0%, E₁ 37.8%, E₂+3 23.7%, E₄ 4.0%. For actual ranges see Table 11. Specimens from the southern part of the range tended to be smaller, with a more compact telopodite. Process E₂+3 showed variation in the relative lengths and direction of the two components. Prong E₂ tended to be longer in
the northern and southern parts of the range while both were equal in Michigan. The tibiotarsus was more robust and the red paranota seem to be most consistent in the Appalachian Mountains. In some cases, small secondary spines were found associated with normal spines, although no geographical continuity was observed. The tip which is usually straight, may either be sharply hooked or slightly curved. Terminal setae, previously used as a diagnostic characteristic, primarily by Chamberlin and Causey, vary greatly, but most variation was due to breakage.

**DISTRIBUTION:** The range of *Pseudopolydesmus canadensis* covers most of eastern North America from Hudson Bay, Canada, south into northern Alabama along the Appalachian Mountains with scattered localities in northern Florida and southern Mississippi (Map 6). The species is most common in colder microclimates such as the higher elevations of the Appalachian Mountains. Discontinuous populations of *Pseudopolydesmus canadensis* can be seen; 1) New England and southeast Canada, 2) Appalachian Mountains, 3) Michigan, and 4) the extreme southern populations. Little collecting has been recorded in Pennsylvania so this gap is probably due to inadequate data. This is probably also true across southern Canada thereby linking the Michigan and eastern populations. However, there does appear to be a well-defined break between the Michigan and Appalachian populations. Personal collecting in northern Ohio failed to turn up any *canadensis* specimens. Since *canadensis* appears to reside in cooler habitats, the southern populations from central Florida and southern
Mississippi are atypical. These may represent relic populations from the last period of glaciation. I expect these populations are truly disjunct from the remaining range.

A specimen of *canadensis* has a Hawaii label and is either introduced or mislabelled. It would be interesting to know if the species has become established, because of the depauperate native millipede fauna of the islands.

**NOTES:** Examination of Newport's single dried female holotype of *Polydesmus canadensis* shows it to be distinct from *Pseudopolydesmus serratus* with which it had long been synonymized. I hereby designate the male type of *causodirochacus* as the neo-allotype of *canadensis*, due to its close proximity to the holotype locality and the need for a male type. The synonyms of *canadensis* are discussed below. As is the case with most Chamberlin species, all descriptions were based on 1 or 2 paragraphs of text.

*Polydesmus branneri* Bollman, holotype examined. In the original description, Bollman states that the gonopods were different from *serratus*, although he did not explain how, and that they would be drawn in a later paper which was never published.

*Polydesmus nitidus* Bollman, holotype examined, is hereby synonymized with *canadensis*.

*Polydesmus echinogon* Chamberlin, holotype examined. The species was based on a specimen from Pennsylvania. In his gonopod drawing, *M₂* was slightly more proximal than normal and the *E₂+3*
stalk has a small tertiary point between E₂ and E₃. These conditions have been observed throughout the range of canadensis.

**Polydesmus conlatus** Chamberlin, holotype examined. The species had previously been synonymized with **branneri** by Loomis and Hoffman, 1948. In the gonopod description, E₄ was omitted.

**Dixidesmus sylvicolens** Chamberlin, holotype examined. The gonopods were misdrawn by placing a small secondary process adjacent to M₃ and omitting E₄.

**Dixidesmus christianus** Chamberlin, holotype examined. The species had been previously been synonymized (Loomis and Hoffman, 1948) with **branneri**. In the description, the gonopod figure was misdrawn with all the gonopodal processes slightly displaced distally.

**Dixidesmus catskillus** Chamberlin, holotype examined. The gonopod was misdrawn with M₂ missing and the tibiotarsus bent caudally.

**Dixidesmus phanus** Chamberlin, holotype examined. The gonopod was misdrawn with M₁ absent and either M₂ or M₃ absent.

Upon examination of the holotype, **Dixidesmus gausodicerhachus** Johnson, was also determined to be a synonym of **canadensis**, the only difference being that E₁ was shorter than normal. In Johnson's description, E₁ was short, E₄ was placed next to E₂+3, and E₂ was short or at least equal to E₃. The first two conditions were observed in the paratype, but not in the holotype. Apparently the gonopods of the holotype were not removed and examined. The short length of E₂ has been seen in other specimens throughout the range.
An effort was made to find and obtain part of Johnson's apparently large Michigan collection but neither he nor his collection could be found.

The species names, *branneri*, *nitidus*, *echinogon*, *sylvicolens*, *catskillus*, *phanus*, and *quasodicrorhachus* are here synonymized for the first time.

Packard (1886) described the "larval" form of *canadensis* although it may be *serratus* due to similarities seen in juvenile forms.

**Pseudopolydesmus collinus** Hoffman, 1974

(Figs. 85, 89, 93, 110, 115, 122-126; Map 7; Tables 9-11)


**DIAGNOSIS:** Medium (12.8-25.3mm). Metaterga and paranota brown. Dorsal and paranotal setae very small. Dorsal sculpture moderate. Antennae long. Gonocoxae trilobed. Gonopodal process $M_1$ small, on edge, close to endomerite; $M_2$ medium; $M_4$ medium with small setal pad; $E_1$ very small to large, distal to endomerite; $E_2$ medium; $E_3$ medium; $E_4$ small. Cyphopod elongate, similar to *canadensis*.

**DESCRIPTION:** (Based on adult male and female from West Virginia, Mason Co., Mud Run, 0.75mi. off State Route 2, IV-27-1977,
C. P. Withrow, (CEWC)). Adult male 20.7mm long, maximum width (7th segment), 3.6mm, W/L 17.6%, and WL 75.7mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Paranota</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collum</td>
<td>2.1 mm</td>
</tr>
<tr>
<td>2</td>
<td>2.6 mm</td>
</tr>
<tr>
<td>3</td>
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<td>8</td>
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<tr>
<td>9-11</td>
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<tr>
<td>19</td>
<td>1.1 mm</td>
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<tr>
<td>20</td>
<td>0.6 mm</td>
</tr>
</tbody>
</table>

Color in life, brown.

Head typical for genus. Head width 2.2mm, interantennal distance 0.42mm, 19.1% of total head width. Antennae long (3.66mm), 17.7% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere, 0.19mm (5.2%); 2nd, 0.46mm (12.6%); 3rd, 0.87mm (23.8%); 4th, 0.60mm (16.4%); 5th, 0.65mm (17.8%); 6th, 0.64mm (17.5%); 7th, 0.25mm (6.8%).

Dorsal sculpture weak, similar to canadensis. Collum moderate, gradually sloping posteriorly, posterior margin rounded. Paranota subquadrate with anterior edge perpendicular to body. Lateral denticles distinct, located from anteriolateral corner (% of total length of paranotum, 8th segment): 1st denticle, 0.10mm (8.8%); 2nd,
0.32 mm (28.1%); 3rd, 0.58 mm (50.9%); and 4th, 0.80 mm (70.2%). Posteriomedial teeth located on segments 15-19. Ventrolateral surface of paranota rough and irregular.

Sterna cruciately impressed, each quadrant heavily setose. Sternum 2 and 3 typical. Posterior sternum of 6th segment deep, inverted U-shaped, not cephalad; coxae produced ventrally. Posterior sternal lobes of 7th segment only slightly elongate. Leg shape normal and long. Length of right posterior leg of 8th segment 3.70 mm, 17.8% of total body length. Length of podomeres (% of total leg length): coxae 0.40 mm (10.8%); trochanter 0.67 mm (18.1%); prefemur 0.63 mm (17.0%); femur 0.33 mm (8.9%); tibia 0.42 mm (11.4%); tarsus 1.05 mm (28.4%); claw 0.20 mm (5.4%).

Epiproct slightly downturned. Paraprocts and hypoproct normal. Gonopod aperture subelliptical (0.75 mm long, 1.44 mm wide) with L/W ratio of 52.1%. Gonocoxae moderate, (0.62 mm high, 1.17 mm long), triangular, slightly trilobed. Telopodite (Figs. 85, 89, 93) large (1.75 mm long). Prefemur normal with small swelling situated 1.35 mm from distal tip. Femur thin with straight femoral ledge. Tibiotarsus typically shaped, M₁ small (0.04 mm), 0.99 mm (56.6%) from tip; M₂ medium (0.06 mm), 0.50 mm (28.8%) from tip; M₄ medium (0.07 mm), curved anteriorly similar to canadensis, 0.17 mm (9.7%) from tip; E₁ medium (0.06 mm), 0.67 mm (38.3%) from tip; E₂ + 3 on combined stalk, 0.40 mm (22.9%) from tip; E₂ medium (0.08 mm), stubby; E₃ medium (0.08 mm), stubby; E₄ small (0.02 mm), 0.12 mm (6.9%) from tip. Tip slightly bent. Seminal groove typical. Telopodite with distal bend. Tibiotarsus thickness measured at femoral ledge, perpendicular to
body axis, 0.27mm and parallel to axis, 0.15mm. Seminal groove rounded. Endomerite moderately long and rounded distally, 0.72mm (41.1%) from tip, extending 0.26mm on telopodite, projecting 0.13mm high and 0.23mm long.

Female 22.1mm long, maximum width 3.7mm, W/L 16.8%, and WL 81.6mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Segment</th>
<th>Width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collum</td>
<td>2.6</td>
</tr>
<tr>
<td>2</td>
<td>3.1</td>
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<td>3</td>
<td>3.2</td>
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<td>4</td>
<td>3.3</td>
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<tr>
<td>5-6</td>
<td>3.6</td>
</tr>
<tr>
<td>7-12</td>
<td>3.7</td>
</tr>
<tr>
<td>13</td>
<td>3.6</td>
</tr>
</tbody>
</table>

Color and structure similar to male, sterna and legs unmodified. Syncoxosternum wide medially, ventrolateral shelf small, laterally straight, rough anteriorly. Sternum III smooth but lightly punctate, with small round median lobe.

Cyphopods (Figs. 110, 115) elongate (0.90mm long, 0.42mm high). Valves not as extended as canadensis, lateral setae moderate. Operculum small with large anterior curving setae. Cyphopod plate similar to canadensis.

VARIATION: Based on 40 (22 males, 18 females) specimens measured, the means of the body measurements for males and females,
respectively, were: length 19.73mm, 19.43mm; width 3.92mm, 3.60mm; W/L 16.95%, 17.15%; and LW 78.45mm², 68.75mm². The ranges and standard deviations can be seen on Tables 9, 10, and Figures 122-125.

Based on ten specimens, the gonopodal processes varied little in their relative position on the tibiotarsus (Fig. 126). The average positions of the processes relative to telopodite length are: $M_1$ 57.9%, $M_2$ 26.6%, $M_4$ 5.6%, $E_1$ 40.4%, $E_{2+3}$ 22.0%, $E_4$ 6.3%. For actual ranges see Table 11. Process $E_1$ variation in size and shape was most notable, ranging from a small swelling to a long slender process similar to canadensis.

Several specimens of collinus possess dorsal setae. The setae were very short compared to those species that normally have dorsal setae.

DISTRIBUTION: The range of Pseudopolydesmus collinus covers eastcentral North America, from the Atlantic coast of Maryland and northern South Carolina to western Ohio and eastern Tennessee (Map 7). The species is uncommon and sporadically found. The habitat is variable. Specimens have been collected from Ohio River mud-clay floodplains, above 3000 ft in the Appalachians, and the sandy soils along the Atlantic coast.

NOTES: Chamberlin and Hoffman (1958) state that even though the name, moniliaris has been used by several authors in reporting northeastern polydesmids, the exact identity, because of the absence
of specimens, has never been conclusively settled. They also state that the specimens were probably the introduced species *Polydesmus inconstans* or some other synanthropic species. This, however, does not appear to be the case with Williams and Hefner's usage of the name. Even though the specimens were missing from the Hefner collection, based on their description and illustration I believe their *P. moniliaris* is *collinus*. This argument is strengthened by a collection of *collinus* from westcentral Ohio, very close to the area in which Williams and Hefner worked. There are still other records of *moniliaris* in the literature which remain unidentified.

The Group Serratus consists of four species, *serratus*, *paludicola*, *caddo*, and *minor*. The characteristics of the group are: posterior sternum of 7th segment with long sternal lobes, $E_1$ absent, gonocoxae multiple, and cyphopod slightly elongate, with plate compressed laterally. The range of the group is middle eastern North America, extending into the lower Mississippi River Valley and eastern Texas.

*Pseudopolydesmus* *serratus* (Say, 1821)  
(Figs. 12, 44, 46, 48, 57, 59, 63, 66, 68, 65, 78, 94, 98, 102, 122-126; Map 8; Tables 9-11)

*Polydesmus* *serratus* Say, 1821, *J. Acad. Nat. Sci. Philadelphia,*
2:106 (type locality: "Eastern shore of Virginia"; type: unknown, presumed lost; Neotype designated below).

**Polypdesmus pensylvanicus** [sic] Koch, 1847, in Krit. Rev. Insect. Deutschlands, 3:133.—1863, Die Myriapoden, 1:18, pl. 69, fig. 142 (type locality: Pennsylvania; type: unknown, presumed lost; Neotype designated below). NEW SYNONYMY.

**Polypdesmus glaucescens** Koch, 1847, in Krit. Rev. Insect. Deutschlands, 3:133.—1863, Die Myriapoden, 1:59, pl. 26, fig. 51 (type locality: North America; type: unknown, presumed lost; Neotype designated below). NEW SYNONYMY.

**Polypdesmus scopus** Chamberlin, 1942, Canadian Ent., 74:16, fig. 1 (type locality: Iowa, Boone Co., 6 miles south of Boone; type: USNM). NEW SYNONYMY.

**Polypdesmus planicolens** Chamberlin, 1942, Canadian Ent., 74:16, fig. 2 (type locality: Iowa, Story Co., Ames; type: USNM). NEW SYNONYMY.


**DESCRIPTION:** (Based on adult male and female from West Virginia, Cabell Co., SR 10, 1 mi. S of jct. Alternate State Route 10, V-20-1983, C. P. Withrow, [CPWC]). Adult male, 23.3mm long, maximum width (8th segment), 3.9mm, W/L 16.7%, and WL 90.40mm². Segmental widths across paranota as follows:
Color in life, brown.

Head typical for genus. Head width 2.5 mm, interantennal distance 0.54 mm, 21.6% of total head width. Antennae moderately robust (Fig. 57) long (4.89 mm), extending to posterior edge of 4th segment, 18.9% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere 0.22 mm (4.5%); 2nd 0.77 mm (15.8%); 3rd 1.19 mm (24.4%); 4th 0.85 mm (17.5%); 5th 0.94 mm (19.3%); 6th 0.64 mm (13.1%); 7th 0.26 mm (5.3%).

Dorsal sculpture moderate. Lateral and medial bosses of paranotum small, medial boss almost round (Fig. 12). Anterior bosses of dorsum well separated. Collum large with acute posterolateral angle, anteriomedial bulge. Anterior terga projecting laterally (Fig. 44). Dorsal and paranotal setae absent. Paranota with straight anterior edge, posterior corner directed caudally, lateral edge curved. Lateral denticles distinct, located from anteriolateral corner (% of total length of paranotum, 8th segment): 1st denticle, 0.08 mm (6.7%); 2nd, 0.08 mm (13.4%); 3rd, 0.48 mm (38.3%); and 4th,
0.83mm (66.0%). Posteriomedial teeth distinct on segments 14-19. Ventrolateral surface of paranota rough and irregular. Laterally diplopodegments as in figure 46.

Sterna cruciately impressed, each quadrant moderately setose (Fig. 59). Sternum 2 very irregular, short, anterior and posterior plate fields flat, small, and regular, with medial ridge irregularly asperate. Sternum 3 posteriomedially between large penes, slightly depressed ventrally, anterior edge pointed slightly with lateral and posterior margins raised, surface depressed, smooth, with about 12 long, thin setae; interpenial distance small, with a pair of longitudinal parallel ridges on sternum. Sterna 4 and 5 large, with many long, thin setae, however gap between sternum lobes shallow and steep. Lobes of sternum 6 blunt distally, each with one medial and one lateral pair of setae and with two pairs of posterior setae between them. Sternal setae short and stubby with a small patch of similar setae posteriolaterally. Medial longitudinal depression on posterior of sternum 6 narrow and deep. Coxae covered with short, stubby setae and single, large, thin, ventrad seta. Posterior sternum 7 with long, thin, coxal lobes. Legs long (Fig. 69). Length of right posterior leg of 8th segment 3.87mm, 16.1% of total body length. Length of podomeres (% of total leg length): coxa 0.41mm (10.7%); trochanter with large dorsal protuberance which is slightly wider distally, 0.64mm (16.5%); prefemur 0.79mm (20.5%); femur 0.37mm (9.5%); tibia 0.41mm (10.7%); tarsus 1.04mm (26.9%); claw 0.20mm (5.2%). Sphaerotrichomes normal. Cross section as in figure 48.
Epiproct straight (Fig. 81). Hypoproct trilobed, medial lobe small with single lateral pair of setae. Paraprocts typical.

Gonopod aperture subelliptical (1.6mm long, 1.05mm wide) with L/W ratio of 65.6%. Gonocoxae large (0.80mm high, 1.13mm long), posterioventral edge bilobed, ventral lobe blunt, extending outward twice its width, sides parallel, smooth, rounded, and directed ventrally; dorsal lobe irregular, flattened with edges. Telopodite (Figs. 94, 98, 102) large (1.56mm high). Prefemur normal. Femur thin with straight femoral ledge. Tibiotarsus typically shaped, process $M_1$ small to medium (0.05mm), 0.60mm (57.0%) from tip, close to base of endomerite; $M_2$ small (0.04mm), regular, 0.42mm (40.3%) from tip; $M_4$ small (0.04mm), 0.18mm (17.0%) from tip; $E_2$ medium (0.07mm), connected to $M_2$ by small ridge, 0.38mm (36.4%) from tip; $E_4$ medium (0.06mm), 0.18mm (17.7%) from tip. Tip hooked dorsally. Seminal groove typical. Tibiotarsus with distal and proximal curves. Tibiotarsal thickness measured at femoral ledge, perpendicular to body axis, 0.19mm, and parallel to axis, 0.21mm. Endomerite thin and sharp, 0.63mm (46.9%) from tip, extending 0.24mm on telopodite, projecting 0.11mm high and 0.15mm long, with acute tip.

Female 22.9mm long, maximum width 3.9mm, W/L 16.9%, and WL 88.9mm². Segmental widths across paranota as follows:

<table>
<thead>
<tr>
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<th>2.8 mm</th>
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<th>3.9 mm</th>
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<tr>
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<td>3.4 mm</td>
<td>16</td>
<td>3.5 mm</td>
</tr>
<tr>
<td>4</td>
<td>3.5 mm</td>
<td>17</td>
<td>3.3 mm</td>
</tr>
</tbody>
</table>
Color and structure similar to male. Sterna and legs unmodified. Syncoxosternum quadrate distally, mesal surface very rough, and posterior surface smooth with small grooves (Fig. 63). Sternum III slightly enlarged with lateral projection moderate, ventral surface very rough and irregular (Fig. 66).

Cyphopods (Fig. 67) elongate (1.2mm long, 0.87mm high), valves with large number of short, macrosetae along valvular lips. Lateral surface with numerous setae on ventral 1/3 grading to none dorsal, anterior edge rounded and flattened laterally with edge slightly thickened. Operculum small with several long setae. Dorsal plate (Fig. 120) distinct and slightly sloped medially.

VARIATION: Based on approximately 4500 specimens, *Pseudopolydesmus serratus*, although wide-ranging, has slight size variation with little or no geographic significance. Based on 500 (250 males, 250 females) specimens measured, the means of body measurements for males and females, respectively, were: length 23.86mm, 21.50mm; width 4.14mm, 3.72mm; W/L 17.31%, 17.90%; and LW 99.42mm², 86.99mm². The ranges and standard deviations can be seen on Tables 9, 10, and Figures 122-125. Males are only slightly longer and wider than females (23.9mm by 4.1mm to 21.5mm by 3.7mm, respectively). The females had a slightly higher W/L ratio. Because
males were longer and wider than females, dorsal area was also
greater, 99.4 mm$^2$ to 87.0 mm$^2$. Specimens from the Appalachians also
appear slightly larger. When *serratus* and other species, usually *canadensis*, were sympatric, *serratus* was consistently the larger.

Denticles tended to be smaller on extreme northern populations
(Ontario).

Coloration was usually brown, however paranota may be reddish
in some specimens.

The hypoproct was usually bilobed although a trilobed
condition had been observed on several specimens.

The gonopods of *Pseudopolydesmus serratus* showed extensive
non-geographic variation in the size, shape, and location of the
processes, the latter varying from spined, triangular, to finned.
The relative location of processes of the tibiotarsus varied little
(Fig. 126). The positions of the processes relative to telopodite
length are: $M_1$ 56.1%; $M_2$ 37.8%; $M_4$ 13.0%; $E_3$ 37.1%; and $E_4$ 8.1%. For
actual ranges and standard deviation see Table 11. The inner ridge
between $M_2$ and $E_3$ may be toothed.

The cyphopods varied very little, although the plates of
southern populations (ex. Louisiana) tend to be more rounded.

DISTRIBUTION: The range of *Pseudopolydesmus serratus* covers
eastern North America from southern Quebec, Canada and Iowa, south
to Georgia, the Gulf Coast and eastern Texas (Map 8). *P. serratus* is
the most common species east of the Mississippi River and is only
sporadically found farther west. Generally, it occurs in deciduous
hardwoods in non-urbanized environments. Even in many disturbed areas, *Pseudopolydesmus serratus* is common although *Polydesmus inconstans* and *Oxidus gracilis* often appear to displace it. Mass migrations have been recorded from Ohio (Ramsey, 1966).

Due to incomplete records, the exact western extension of the species in Canada is unknown.

NOTES: *Polydesmus canadensis*, based on a female, has been considered a synonym of *serratus* by all authors since Attems (1898), but is instead the senior synonym of *branneri*.


It appears that character displacement may be occurring. This deals with the case of red and brown tergite color between *Pseudopolydesmus serratus* and *canadensis*. Under normal conditions both have brown paranota, however when both species are sympatric, *canadensis* usually has red paranota and *serratus* has brown. However, many specimens of *serratus* collected from Ohio, where no *canadensis* occurs, have definite red paranota.
Both *Polydesmus scopus* Chamberlin, holotype examined, and *P. planicolens* Chamberlin, holotype examined, were based on five-line descriptions with poorly drawn gonopod figures. In describing *P. scopus*, Chamberlin presented an inaccurately drawn figure of the gonopods, while giving no verbal description of them. Examination of the type shows that the gonopod figure was misleading in the following ways: processes $M_1$, $M_2$, or $E_3$, and $E_4$ were not shown but are present and the elongation of the femur of the telopodite is exaggerated. From the same article, similar problems occur with the figure of *P. planicolens*: the inner ridge between $M_2$ and $E_3$ is spined, $E_4$ is present but not shown, and the shape is exaggerated. All other characters match *serratus* and fit within the limits of variation. Chamberlin described the two species from single males collected within 12 miles of each other. A trip was made to both type localities but no additional specimens were found.

**Pseudopolydesmus paludicola** Hoffman, 1950

(Figs. 95, 99, 103, 126; Map 9; Table 11)


DIAGNOSIS: Small (11-13mm). Metaterga and paranota brown. Dorsal sculpture well defined. Dorsal and paranotal setae present. Lateral denticles very small or absent, caudolateral corner produced
caudally. Antennae short. Gonocoxae monolobed. Gonopodal process $M_1$ medium, hooked, and at base of endomerite; $M_2$ medium and reduced to a low swelling; $M_3$ small and triangular; inner ridge with median elongated process extending proximally connecting $E_4$ and $M_2$; $E_4$ medium. No females have been recorded.

DESCRIPTION: (Based on adult male from Virginia, Princess Anne Co., Norfolk, east side of Norfolk Reservoir, V-18-1963, P. Hall, (RLHC)). Adult male 12.4mm long, 1.83mm maximum width (8th segment), W/L ratio 14.8%, and WL 22.7mm$^2$. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Segment</th>
<th>Width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collum</td>
<td>1.2</td>
</tr>
<tr>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td>3-4</td>
<td>1.5</td>
</tr>
<tr>
<td>5-6</td>
<td>1.7</td>
</tr>
<tr>
<td>7-8</td>
<td>1.8</td>
</tr>
<tr>
<td>9-14</td>
<td>1.7</td>
</tr>
<tr>
<td>15</td>
<td>1.6</td>
</tr>
<tr>
<td>16</td>
<td>1.5</td>
</tr>
<tr>
<td>17</td>
<td>1.4</td>
</tr>
<tr>
<td>18</td>
<td>1.1</td>
</tr>
<tr>
<td>19</td>
<td>0.8</td>
</tr>
<tr>
<td>20</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Color in life, brown, as described by Hoffman (1950), preserved specimens white.

Head typical for genus. Head width (1.0mm), interantennal distance 0.33mm, 33.3% of total head width. Antennae short (1.29mm), 10.4% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere, 0.11mm (13.7%); 2nd, 0.19mm
Dorsal sculpture well defined, similar to *serratus*. Collum small, without denticles, wider along posterior margin, straight anteriorly but rounded laterally. Lateral denticles very small or absent. Dorsal setae present. Paranota rounded anteriorly and pointed posteriolaterally with lateral edge curved. Lateral surface ventral to paranota smooth, without denticles.

Sterna cruciately impressed. Each quadrant moderately setaceous. Sternum 3 with penes normal, with anteriomedial and posteriomedial pairs of setae. Sterna 4-5 narrow, unmodified, with numerous long setae. Sternum 6 with large anterior lobes, posterior sternal lobes displaced slightly anteriolaterally; medial V-shaped indentation wide and shallow. Sternum 7 with posterior sternal lobes long and thin. Sterna 8-20 typical with numerous short setae. Legs short but typical. Length of right posterior leg of 8th segment, (1.14mm), 9.1% of total body length. Length of podomeres (% of total leg length): coxae 0.18mm (12.8%); trochanter with dorsal extension larger proximally 0.28mm (19.6%); prefemur 0.22mm (15.7%); femur 0.14mm (9.8%); tibia 0.11mm (7.8%); tarsus 0.40mm (28.5%); claw 0.08mm (5.9%). Sphaerotrichomes on prefemur, femur, and tarsus.

Hypoproct slightly deflexed. Epiproct and paraprocts typical for genus.

Gonopod aperture subelliptical (0.71mm long, 1.04mm wide) with L/W ratio of 69.2%. Gonocoxae large (0.19mm high, 0.47mm long), long, and posterioventrally bilobed. Telopodite (Figs. 95, 99, 103)
small (0.98mm high). Prefemur small and hirsute. Femur thin with femoral ledge straight. Tibiotarsus typical with process M1 medium (0.07mm), pointed, located 0.51mm (52.8%) from tip, at base of endomerite; M2 medium (0.07mm), sharp, connected distally to small, medial, secondary spine, 0.28mm (28.9%) from tip; M3 small (0.02mm), with barely visible medial ridge to secondary spine of E4, 0.20mm (20.1%) from tip; E4 medium (0.08mm), 0.5mm (5.0%) from tip. Tip thick with slight dorsal bend. Telopodite with slight curve. Seminal groove typical. Tibiotarsus thick at femoral ledge, measured perpendicular to body axis, 0.08mm, parallel to axis, 0.06mm. Endomerite thin and sharp, 0.57mm (58.6%) from tip, extending 0.20mm on telopodite, projecting 0.03mm high and 0.13mm long.

No females have been positively identified.

VARIATION: Almost nothing can be said about variation because only two males are known. The positions of the processes relative to telopodite length (Fig. 126) are: M1 55.75%, M2 30.55%, M3 21.15%, E4 5.55%. For actual ranges of the percentages see Table 11.

DISTRIBUTION: The range of Pseudopolydesmus paludicola is limited to two localities in southeastern Virginia, south of Chesapeake Bay (Map 9). Shelley (1978) stated that paludicola can be expected in the Piedmont of the Carolinas. This was based on a personal statement by Hoffman that a specimen was collected from Orangeburg, Orangeburg Co., South Carolina. However, this specimen could not be located in any collection. I expect paludicola to be
present throughout the Mid-Atlantic Coastal Plain and possibly to extend into the Piedmont.

**NOTES:** According to Hoffman (1950b) the holotype was found under a board on the inner dunes, several hundred feet from the ocean (generally an atypical locality for millipeds). The recorded vegetation was grass and sedge, a few pines, and *Myrica* thickets.

The specific name is Latin for swamp-inhabitant; although not found in a swamp it probability refers to the close proximity to the Dismal Swamp. The name does not take the masculine gender suffix of the genus. A female specimen from Greene Co., North Carolina (NMNH) was tentatively identified by Shelley to be *paludicola*, but was not included here until males can be collected from the site.

**Pseudopolydesmus caddo** Chamberlin, 1949

(Figs. 50, 77, 96, 100, 104, 116, 118, 122-126; Map 9; Tables 9-11)

**Pseudopolydesmus caddo** Chamberlin, 1949, J. Washington Acad. Sci., 39:97, fig. 11 (type locality: Louisiana, Caddo Par., 5mi. NW. Shreveport; type: USNM).

**Pseudopolydesmus bidens** Loomis, 1959, J. Washington Acad. Sci., 49(5):163, fig. 8 (type locality: Louisiana, Leblanc Par., Kinder, US Rt. 190; type: USNM). NEw SYNONYM.

**DIAGNOSIS:** Small (9-14mm). Metaterga and paranota light brown. Dorsum slightly arched and well defined. Small dorsal and paranotal setae present. Collum subquadrate. Paranota extending slightly anteriorly and squared laterally, flatter than anyother species.
Antennae short. Gonocoxal margin trilobed. Gonopodal process $M_1$ small, at base of endomerite, $M_2$ small to medium, across from $E_2$, $M_4$ small, $E_2$ small, elongate, usually with small distal tooth, $E_4$ small. Cyphopod compact, edge with setae evenly spaced along length of valve, lateral setae long. Cyphopod plate elongate and loping medially.

**DESCRIPTION:** (Based on adult male and female from Louisiana, Iberville Par., Maringouin Levee, 13.3mi. N. of Bayou Sorrel, X-30-1965, R. E. Tandy, (FSAC)). Adult male, 12.6mm long, 2.1mm maximum width (8th segment), maximum thickness 1.4mm, W/L 16.0%, WL 27.0mm^2, and thickness/width ratio of 70.0%. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>1.5 mm</th>
<th>11-15</th>
<th>2.0 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.7 mm</td>
<td>16</td>
<td>1.9 mm</td>
</tr>
<tr>
<td>3</td>
<td>1.8 mm</td>
<td>17</td>
<td>1.8 mm</td>
</tr>
<tr>
<td>4</td>
<td>1.9 mm</td>
<td>18</td>
<td>1.4 mm</td>
</tr>
<tr>
<td>5-6</td>
<td>2.0 mm</td>
<td>19</td>
<td>0.9 mm</td>
</tr>
<tr>
<td>7-10</td>
<td>2.1 mm</td>
<td>20</td>
<td>0.3 mm</td>
</tr>
</tbody>
</table>

Color in life, brown.

Head typical for genus except genae bulge only slightly. Head width 0.83mm, interantennal distance 0.25mm, 30.1% of total head width. Antennae short 1.87mm, 14.8% of total body length. Antennomeric lengths (% of total antennal length): 1st antennomere,
Dorsal sculpture distinct. Anteromedian bosses not well separated, lateral boss extending entire length of each paranotum (Fig. 77). Tergites directed slightly ventrolaterally. Collum small, bulging slightly posteriomedially, rounded anteriolaterally, and with 3 transverse rows of setae. Dorsal and paranotal setae small and filiform (Fig. 50). Paranota quadrate, extending slightly cephalad, anterior edge straight. Lateral denticles distinct, located from anteriolateral corner (% of total length of 8th paranotum): 1st denticle, 0.17mm (22.7%); 2nd, 0.23mm (31.8%); 3rd, 0.40mm (54.5%); 4th, 0.60mm (81.8%). Posteriomedial teeth not visible. Ventrolateral surface of paranota smooth.

Sterna cruciately impressed, each quadrant moderately setose. Sterna 2-5 typical for group. Lobes of sternum 6 large, blunt, displaced anteriorly, with short sternal setae; deep, inverted, U-shaped longitudinal groove, with contour ridges. Posterior sternum of 7th segment long and thin, coxae with short, stubby setae, and each with a single, long, filiform macroseta. Legs short, prefemur slightly curved ventrally, femur and tibia with small, distal, dorsal process. Leg shape typical but short. Length of right posterior leg of 8th segment, 1.80mm, 14.3% of total body length. Length of podomeres (% of total leg length): coxae 0.28mm (15.7%); trochanter 0.38mm (21.0%); prefemur 0.32mm (17.9%); femur 0.20mm
(10.8%); tibia 0.20mm (11.2%); tarsus 0.47mm (26.0%); claw 0.14mm (7.6%). Sphaerotrichomes normal.

Hypoproct straight. Epiproct and paraprocts normal.

Gonopodal aperture subelliptical (0.67mm long, 0.99mm wide) with L/W ratio of 67.7%. Gonocoxae small (0.50mm high, 1.00mm long), triangular. Telopodite (Figs. 96, 100, 104) small (0.94mm high). Prefemur normal. Femur thin with femoral ledge slight and straight. Tibiotarsus typical, process M\(_2\) small (0.03mm), triangular, at base of endomerite, 0.52mm (55.3%) from tip; M\(_2\) small (0.03mm), hooked, 0.26mm (27.7%) from tip; M\(_4\) small (0.03mm), triangular, 0.08mm (8.5%) from tip; E\(_2\) small (0.02mm), long and thin, extending from 0.34-0.46mm (36.1-48.9%) from tip, E\(_4\) small (0.02mm), triangular, 0.8.0mm from tip. Tip with small, dorsally directed tooth.

Telopodite evenly and gently curved. Seminal groove normal. Telopodite width measured at femoral ledge, perpendicular to body axis, 0.14mm, and parallel to axis, 0.08mm. Endomerite sharp, base 0.50mm (0.53.2%) from tip, extending 0.20mm on telopodite, projecting 0.03mm high and 0.14mm long.

Female 13.2mm long, maximum width 1.8mm, W/L 16.3%, and WL 22.7mm\(^2\). Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>1.3 mm</th>
<th>17</th>
<th>1.6 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.6 mm</td>
<td>18</td>
<td>1.3 mm</td>
</tr>
<tr>
<td>3</td>
<td>1.7 mm</td>
<td>19</td>
<td>0.9 mm</td>
</tr>
<tr>
<td>4-15</td>
<td>1.8 mm</td>
<td>20</td>
<td>0.2 mm</td>
</tr>
<tr>
<td>16</td>
<td>1.7 mm</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Color and structure similar to male, with sterna and legs unmodified. Syncoxosternum quadrate distally, straight laterally, and very rough mesally and distally. Sternum III posterior edge ridged.

Cyphopods (Figs. 116, 118) small (0.61mm long, 0.42mm high), compact. Valves with 14-15 overlapping macrosetae, dorsal edge thickened, deeply marginated dorsally, and lateral setae extending dorsally. Operculum normal. Cyphopod plate elongate, sloping medially.

VARIATION: Based on 28 (17M, 11F) specimens, the means of the body measurements for males and females, respectively were: length 10.21mm, 9.75mm; width 1.42mm, 1.37mm; W/L 13.04%, 12.87%; and LW 15.22mm², 14.37mm². Ranges and standard deviations can be seen in Tables 9, 10, and Figures 122-125. Females were only slightly smaller than males. Thickness ranged from 0.84 to 1.02mm and the thickness/width ratio ranged between 72.7 and 87.2%.

Based on ten specimens, the gonopodal processes varied little in their relative position on the telopodite (Fig. 126). The positions of the processes relative to telopodite length are: M₁ 53.6%; M₂ 29.6%; M₃ 9.7%; and E₂ 38.5%. For actual percentages see Table 11.

DISTRIBUTION: The known range of Pseudopolydesmus caddo is along the Gulf Coast, from eastern Texas, through Louisiana. Pseudopolydesmus caddo appears to be associated with wet low areas
along the Lower Mississippi and Red Rivers, and along the Texas Coastal Plain. Because of habitat similarities caddo probably extends into western Mississippi (Map 9).

NOTES: The holotype of Pseudopolydesmus bidens Loomis, examined, was misdrawn. Loomis only showed M$_2$ and M$_4$ on the telopodite. Like Chamberlin, Loomis gave no written description of the gonopods.

**Pseudopolydesmus minor** (Bollman, 1888)

(Figs. 62, 79, 97, 101, 105, 117, 119, 122-126; Map 9; Tables 9-11)

**Polydesmus minor** Bollman, 1888, Ent. Amer. 4:2 (type locality: Arkansas, Pulaski Co., Little Rock; type: USNM).

**Polydesmus neoterus** Chamberlin, 1942, Bull. Univ. Utah, biol. ser. 6(8):10, fig. 30 (type locality: Louisiana, Orleans Par., New Orleans; type: USNM). NEW SYNONYMY.

**Polydesmus euthetus** Chamberlin, 1942, Bull. Univ. Utah, biol. ser., 6(8):11, fig. 36 (type locality: Missouri, St. Louis Co., Buder Park, 1mi. SE. of Valley Park; type: USNM). NEW SYNONYMY.


**DIAGNOSIS:** Small (9-14mm). Metaterga and paranota light brown. Dorsum slightly arched and well sculptured. Small dorsal and paranotal setae present. Antennae short. Gonocoxae bilobed, not as flat as Pseudopolydesmus caddo. Gonopodal process M$_1$ medium, separate from base of endomerite; M$_2$ medium, distal to endomerite; M$_3$ small, medial; E$_2$ small, elongate, usually with distal process;
E₄ small, subterminal. Endomerite small and sharp. Sterna 2 and 3 of female with irregular ventral swellings. Cyphopods small, compact, few small lateral setae present, flattened dorsally, with a dorsal clump of macrosetae overlapping the valves, with small medially sloping dorsal plate.

DESCRIPTION: (Based on adult male and female from Arkansas, Desha Co., McGhee, I-7-1954, N. B. Causey, (FSAC)). Adult male 10.1mm long, maximum width (8th segment) 1.5mm, thickness 1.2mm, W/L 16.8%, WL 14.9mm², and thickness/width 80.0%. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>0.8 mm</th>
<th></th>
<th>15</th>
<th>1.3 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.2 mm</td>
<td>16</td>
<td>1.2 mm</td>
<td></td>
</tr>
<tr>
<td>3-4</td>
<td>1.3 mm</td>
<td>17</td>
<td>1.0 mm</td>
<td></td>
</tr>
<tr>
<td>5-7</td>
<td>1.4 mm</td>
<td>18</td>
<td>0.9 mm</td>
<td></td>
</tr>
<tr>
<td>8-9</td>
<td>1.5 mm</td>
<td>19</td>
<td>0.7 mm</td>
<td></td>
</tr>
<tr>
<td>10-14</td>
<td>1.4 mm</td>
<td>20</td>
<td>0.2 mm</td>
<td></td>
</tr>
</tbody>
</table>

Color in life, light brown.

Head typical for genus. Mandible with slight lateral bulge. Head wide 0.83mm, interantennal distance 0.25mm, 30.1% of total head width. Antennae short (1.22mm), 12.1% of total body length. Antennomorphic lengths (% of total antennal length): 1st antennomere, 0.13mm (10.6%); 2nd, 0.17mm (14.3%); 3rd, 0.26mm (21.2%); 4th,
Dorsal sculpture well defined. Collum moderate with single lateral denticle, three transverse rows of dorsal setae, and posteriomedial edge indented. Tergites are directed ventrolaterally slightly. Paranota quadrate, not extending cephalad, anterior edge straight, posterior corner pointed, lateral edge straight. Anteriomedial bosses not well separated, lateral boss extending entire length of paranota. Lateral denticles distinct, located from anteriolateral corner (% of total length of 8th paranotum) 1st denticle, 0.07mm (13.6%); 2nd, 0.15mm (30.5%); 3rd, 0.26mm (52.5%); 4th, 0.40mm (61.4%). Denticles usually with one or sometimes two short, blunt, setae. Posteriomedial teeth not distinct, only visible on segments 18-19. Surface ventrolateral to paranota rough and irregular.

Sterna cruciately impressed, each quadrant heavily setose. Sternum 2 with normal penes, with anteriomedial and posteriomedial pair of setae. Sternum 3 with 2 anteriomedial setae on small swelling, and one posteriomedial seta. Sterna 4-6 typical, with numerous long setae. Sternal lobes on 6th segment largest. Posterior sternal lobes of 6th segment slightly displaced anteriorly, medial indentation of sternum deep from coxa to coxa. Posterior sternal lobes of 7th segment long and thin (Fig. 62). Contour ridges of groove longer than minor. Leg shape typical although short. Length of right posterior leg of 8th segment, 1.43mm, 14.3% of total body length. Length of podomeres (% of total length): coxae 0.21mm
(12.9%); trochanter 0.34mm (21.1%); prefemur 0.26mm (16.0%); femur 0.13mm (8.2%); tibia 0.19mm (11.4%); tarsus 0.40mm (24.3%); claw 0.10mm (6.2%). Sphaerotrichomes normal.

Hypoproct straight. Epiproct and paraprocts normal.

Gonopod aperture subelliptical (0.62mm long, 0.80mm width), with L/W ratio of 70.7%. Gonocoxae small (0.47mm high, 0.50mm long), similar to serratus, with large ventral and small dorsal lobes, ventral setae absent. Telopodite (Figs. 97, 101, 105) short (0.96mm). Prefemur rounded and elongate. Femur thin with straight femoral ledge. Tibiotarsus typically shaped, process M₁ medium (0.06mm), located 0.54mm (56.3%) from tip, away from base of endomerite; M₂ medium (0.05mm), finned, and 0.38mm (39.6%) from tip; M₃ small (0.03mm), located 0.17mm (17.7%) from tip; E₂ small (0.02mm), elongate, 0.34-0.28mm (35.5-29.2%) from tip; E₄ small (0.02mm), 0.07mm (7.3%) from tip. Tip hooked dorsally. Telopodite with distal and proximal curves. Seminal groove typical. Tibiotarsus thickness, measured at femoral ledge, perpendicular to body axis, 0.08mm and parallel to axis, 0.11mm. Endomerite thin, sharp, 0.43mm (44.8%) from distal tip, extending 0.21mm on telopodite, projecting 0.02mm high and 0.14mm long.

Female 13.4mm long, maximum width 2.2mm, maximum thickness 0.18mm, W/L 16.4%, WL 29.5mm², and thickness/width 83.5%. Segmental widths across paranota as follows:

<table>
<thead>
<tr>
<th>Collum</th>
<th>1.5 mm</th>
<th>12-13</th>
<th>2.0 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.7 mm</td>
<td>14</td>
<td>1.9 mm</td>
</tr>
</tbody>
</table>
Color and structure similar to male, however legs and sterna unmodified except for sterna 2 and 3 with small irregular swellings (Fig. 79). Syncoxosternum rounded distally, lateral edge projecting caudally with posterior margin turned medially, and very irregular mesally. Sternum III slightly enlarged with lateral projection moderate, and ventral surface rough.

Cyphopods (Figs. 117, 119) small (0.56mm long, 0.40mm high), large dorsally, and similar to caddo. Valves with many short macrosetae along margin. Dorsal plate compressed laterally, not elongated, but sloping medially. Cyphopods with several setae on posterior 1/2 grading to none dorsally, dorsal edge rounded, flattened laterally and slightly marginate.

VARIATION: Based on 31 (17M, 14F) specimens, the means of the body measurements for males and females, respectively, were: length, 10.34mm, 10.78mm; width, 1.34mm, 1.34mm; W/L 12.95%, 12.45%; and LW, 13.92mm², 14.59mm². The ranges and standard deviations can be seen in Tables 9, 10, and Figures 122-125. No significant difference was
observed between males and females. Thickness ranged between 0.97 and 1.25 mm. The thickness/width ratio ranged from 83.2 to 112.2%.

Based on ten specimens, the gonopodal processes varied little in their relative position on the telopodite (Fig. 126). The positions of the processes relative to telopodite length are: $M_1$ 57.2%, $M_2$ 37.8%, $M_3$ 19.8%, $E_2$ 32.3%, and $E_4$ 7.8%. These percentages were derived as described in the methods section. For actual ranges of the percentages see Table 11.

**DISTRIBUTION:** The range of *Pseudopolydesmus minor* is centered in the middle Mississippi River drainage. Specimens were collected from northern Illinois, Missouri, and Arkansas, east through Kentucky and Tennessee (Map 9). The New Orleans locality was probably due to flood transport or mislabeling. All localities for *minor* appear to be associated with flood plains of major rivers, including the Illinois, Wasbash, Lower Missouri, and Lower Arkansas River systems.

**NOTES:** The holotype of *Polydesmus euthetus* Chamberlin, examined, was misdrawn in the original description. Chamberlin drew the $M_1$ process too close to the endomerite.

The holotype of *Polydesmus neoterus* Chamberlin, examined, was typical except that the apical tip of the gonopod was bent laterally, and the apical row of setae was absent.

In both descriptions, as is the case with many of Chamberlin's
works, the gonopods were not described verbally, and only poorly
drawn figures were given.

Subfamily Epanerchidae, NEW SUBFAMILY

(Figs. 3, 15; Map 1)

Epanerchodus Attems, 1901. Mitt. Mus. Hamburg 18:102. (subgenus of
Polycetesmus).

DIAGNOSIS: Small to large (6-29mm), one species smaller than
13mm. Body with 20 segments. L/W ratio 8.8-19.5%. IW between 4.3 and
59.9mm². Tergal width to height 1.3. Body width to height 1.00.
Brown or depigmented. Head subglobose or slightly quadrate with
Antennae long and either filiform or slightly clavate. Length
relationships of antenonemeres 7<1<2<6<5<4<3. Antennomeres 2-4
cylindrical, 5 & 6 slightly clavate, and 7 subconical, with typical
dorsal knob and also small dorsoproximal knob. Interantennal
distance large. Metazonite with small pits. Terga (Fig. 3)
horizontal with polygonal bosses, not tuberculate. Setae may be
associated with bosses. Anterior terga directed anteriad or laterad.
Collum semiovate or ovate and usually large, wider than head.
Paranota directed ventrally or horizontally, may be large or small.
Lateral edge usually dentate with dorsal filiform or clavate setae.
Peritremata thick. Poriferous arrangement normal. Ozopores small,
marginal, opening dorsolaterally, and not elevated. Sterna

Gonopods (Fig. 15) moderate, bent at right angle and not extending over anterior edge of 7th segment. Aperture large, transversely oval, extending laterad beyond ends of coxal sockets of 7th pair of legs, lower edge of posterior side slightly concave and upper edge markedly extending forward to form a broad shelf. Sternum 7 broadly depressed between 8th coxae. Seminal groove typical, extending subterminally on the tibiotarsus, usually with seminal vesicle, and terminating near the endomerite which opens on surface, near an enlargement (=clivus of Attems, 1901) or proximal to it. Cannula distinctly attached to prefemur under large ledge. Gonocoxae triangular, small, and hirsute. Prefemur large, irregular, hirsute, and may have patches of elongate setae. Femur short, unbranched, with small proximal cingulum, and usually with large caudal process. Clivus variable, from a large inflated sac to a small, hirsute mound. Tibiotarsus attached ventrally to gonocoxae, highly variable, bent 90° to the femur, and with caudally projecting processes.

Syncoxosternum thickened, not projecting. Sternum III may be modified. Cyphopods oval, without anterior plate.
CONTENT: This subfamily presently contains one large heteromorphid genus, *Epanerchodus*, with 8 subgenera containing approximately 98 species. This genus can probably be divided into several genera.

The species were placed in the genus *Polydesmus* prior to 1901, when Attems erected a new subgenus. In 1914, he raised it to generic level. In the early 1940's Verhoeff in a series of publications erected 6 subgenera. Two additional subgenera were later added by Chamberlin and Wang (1953) and Miyosi (1954). Little work except for species description has been done on this taxon.

DISTRIBUTION: Palearctic (Map 1). Restricted to East Asia, primarily Japan, with several species in Siberia and Korea. Many species are known from lava caves around Mt. Fuji, these caves are known to be less than 10,000 years old, yet many contain unique species.
In the Phylogenetic and Classification Methods section of this study, some of my cladistic ideas and techniques were outlined. What follows is an analysis of taxonomic relationships based on those ideas. The relationships are based on the sequences and patterns of branching, which in turn are based on shared apomorphic character states. This analysis includes listing of monophylies, characters, character states, polarities, and analysis of phylogenetic trees.

CHARACTER STATES

This section presents the characters, their relative states, and the polarities that were used in formulating the phylogenetic hypotheses. This is basic for further study at family and superfamily levels. The arrangement of characters and character states is based on the clade level to which that character belongs.
The Superfamily Polydesmoidea is a large, almost entirely Holarctic taxon; dealing with it except in a generalized sense is beyond this study. The characteristics of each of the five families, except for the Polydesmidae and its sister group, Doratodesmidae, have not been studied. Because this study deals with the North American polydesmid fauna, which contains only two subfamilies, exotic taxa are not covered in depth.

**Monophyly of the Family Doratodesmidae**

There has been no in depth study of this small southeast Asian family. It is not the author's intention to rectify this problem in this study. However, there was a need to obtain some understanding of this taxon beyond Hoffman's (1977) family description, in which he also suggested that Doratodesmidae is the closest relative to the Polydesmidae. In Hoffman's 1979 classification, 9 genera, mostly monotypic were listed. The systematics of the family has two major problems: one is the lack of any previous revision and the other is the lack of specimens due to incomplete collecting or scarcity of individuals.

Based on the few specimens I have examined, I agree with Hoffman (1977) that Doratodesmidae is the sister group of the Polydesmidae and that at least two subfamilies can be recognized.

The following list of apomorphies is probably not complete. It is based on the several specimens examined (Appendix D) and the literature. The 5 autapomorphies for the Family Doratodesmidae are:
Character 1: Paranota of 2nd Segment Flabellately Enlarged

In the plesiomorphic state, the paranota of an individual are essentially all the same relative size. The flabellate enlargement of the second paranotum is present in the doratodesmids, therefore autapomorphic (Fig. 1). This enlargement gives added protection to the head and legs when the milliped is curled. There is also a corresponding reduction in the collum.

Character 2: Ability to Involute

Most millipeds lack the ability to curl into a tight ball and is considered the plesiomorphic condition. Those in several unrelated taxa, however do curl up and are completely protected by dorsal and paranotal (character 1) modifications. In the Order Polydesmida, this ability is shared by several families, Doratodesmidae, Sphaeriodesmidae, Cyrtodesmidae, and Oniscodesmidae. This ability is not present in any other taxon of the Superfamily Polydesmoidea. This condition is considered by me to be autapomorphic for the doratodesmids within the superfamily and to have arisen independently in all four families. In each family different tergal modifications are employed.

Character 3: Gonocoxae with Ventral Macrosetae

The plesiomorphic condition is the absence of ventral macrosetae in the excavation. The presence of a patch of numerous macrosetae in the ventral excavation is autapomorphic in doratodesmids (Fig. 13). Although most polydesmids have a pair of
elongate setae on the ventrolateral edge, all lack setae within the ventral excavation.

Character 4: Sternal Width Narrow

This autapomorphy appears to be related to character 2. The doratodesmids have very narrow or contiguous sterna permitting tighter involution. In the polydesmids the sterna are generally very wide.

Character 5: Body Length/Width Ratio High

In the doratodesmids the paranota are very wide, extending relatively far from the body. For this reason the width is relatively large compared to total body length. In the autapomorphic state, seen in the doratodesmids, this ratio ranges from 18 to 30%. In the plesiomorphic state, seen in the remaining polydesmoids, this ratio ranges from 8 to 22%.

Monophyly of the Family Polydesmidae

The monophyly of the Family Polydesmidae is not definitively established; this problem can only be alleviated by a total ordinal revision. Although some progress has been made in the last decade (e. g., Hoffman, 1979), problems remain, especially how the trichopolydesmids, macrosternodesmids, and fuhrmannodesmids fit into the overall picture. In the past 20 years, all three taxa have been placed in the family at one time or another; and at the other
extreme, Hoffman (1979) placed each in a separate family within 2 other superfamilies! Most of the problems are due to inadequate descriptions of taxa by past workers. In most cases the original and only generic description covers at most one or two paragraphs. Hoffman, whose works and studies are based primarily on gonopods, states that the apomorphic characters for Polydesmidae are development of a terminal chamber of the seminal groove, and the cordate or subcordate shape of the gonopod aperture, with the posterior margin projecting inward forming a transverse shelf. Only recently (e.g. Enghoff, 1981) has the study of millipede systematics progressed beyond the almost pragmatic use of gonopods to the utilization of other structures.

Presently I agree with Hoffman (1979) on the monophyly of the family Polydesmidae. An indepth study of the Polydesmoidea may uncover more apomorphic characters for the Polydesmidae. Characters which are apomorphic in the family also include 18 and 64 which are plesiomorphic in several taxa and will be discussed later. The family has the following 5 apomorphies (characters 6-10):

Character 6: Interantennal Distance Wide

This autapomorphy is characteristic of the family Polydesmidae. The antennae are well separated, by approximately 25% of the total head width. In the doratodesmids and several other taxa in the superfamily the antennal bases are or almost are contiguous.

Character 7: Antennae Long
This autapomorphy is characterized by the elongation of the antennae relative to body length. As in character 4, several families as well as the doratodesmids have short, very clavate antennae. There is shortening of the relative length in some of the smaller-sized taxa (ex. mastigonodesmines and *Pseudopolydesmus minor*) but this appears to be secondarily derived.

**Character 8: Seminal Groove Subterminal**

The opening of the seminal groove, located subterminally on the tibiotarsus, is apomorphic for the Polydesmidae. In the polydesmines, it is about midway up the tibiotarsus near the endomerite. In the epanerchodines, it is near the clivus. The plesiomorphic condition, where the opening is terminal, is seen in many taxa of the superfamily. In several genera of doratodesmids the plesiomorphic condition is observed, however, in these cases I believed that the subterminal condition is independently derived.

**Character 9: Cyphopod Elongate**

The elongation of the cyphopod is apomorphic for the polydesmids. The plesiomorphic condition of an ovate cyphopod is seen in the doratodesmids and several polydesmines and epanerchodines but the state in the latter two taxa is believed to be secondarily derived due to small body size.

**Character 10: Metazonal Tubercles**
The absence of metazonal tubercles is autapomorphic in the polydesmids. The metazonal surface is usually covered by small regular pits.

The following apomorphies are present for the subfamilies Mastigonodesminae and Scytonotinae. The placement of these two subfamilies into a major separate clade was not expected, due to distance between the two subfamilies. I expect this clade to represent relict taxa. This clade has the following 6 apomorphies (characters 11-16):

**Character 11: Mandible Round**

The apomorphic state, where the mandible is rounded laterally contrasts to the plesiomorphic state, where it is quadrate. This character is easily observed in dorsal view. The plesiomorphic condition is seen in Doratodesmidae, the subfamily Mastigonodesminae, and the genus Bidentogon in the subfamily Scytonotinae. This condition in these latter cases was probably derived independently, but the strength of rounded mandible as an autapomorphy is diminished.

**Character 12: Ozopore Marginal**

The plesiomorphic condition is the location of the ozopore medial to the margin of the paranotum. The autapomorphic condition, seen in the Polydesmidae, has the ozopore located on the lateral or posterior margin, in contact with the edge (Fig. 12).
Character 13: Ozopore Posteriorly Located

The posterior placement of the ozopore is apomorphic for several taxa, the subfamily Mastigonodesminae and in the subfamily Scytonotinae, the genera *Speodesmus*, *Coronodesmus*, and *Idahodesmus*. The plesiomorphic condition is the placement of the ozopore laterally on the paranotum.

Character 14: Terga Trapezoidal

The plesiomorphic character is the normal rectangular shape with lateral paranota. However in two taxa, Mastigonodesminae (Fig. 2) and the genus *Speodesmus* (Fig. 4), the apomorphic state in which the paranota are equilaterally trapezoidal is present. The anterior edge is narrower transversely than the posterior edge.

Character 15: No Individuals Over 20mm

For the purpose of this study size was divided into three ranges; small, those individuals under 10mm; medium, between 10-20mm and large, over 20mm. The absence of large individuals is considered apomorphic. Large body size appears to be the plesiomorphic condition; however, a number of taxa have evolved various degrees of smallness. This is probably due to habitat constraints.

Character 16: Tibiotarsus Attachment Lateral

The apomorphic characteristic is the lateral origin of the tibiotarsus on the gonocoxae. It appears that this attachment is
less secure than the plesiomorphic or ventral condition. The apomorphic condition is present in the Scytonotinae and some elements of the Polydesminae.

Monophyly of the Subfamily Mastigonodesminae

In most classifications, this taxon is placed at the familial level (e.g., Strasser, 1974). The latest examination, by Hoffman (1979), placed it in the Family Polydesmidae. He speculated that this complex of 3 genera deserved subfamilial designation. Specimens and literature examined suggest that Hoffman was correct. The following 5 apomorphies (characters 17-21) are present for the subfamily Mastigonodesminae:

Character 17: Unpigmented

The apomorphic condition is the loss of body pigmentation. This state is seen in the subfamily Mastigonodesminae, Speodesmus, Speorthus, Idahoesmus, and some species in the Epanerchodinae. This characteristic is common in troglodytic species and in various small-sized non-troglodytic taxa.

Character 18: Leg Modifications Present

This apomorphic state includes various modifications of either the third pair of legs or of multiple legs in the males, which have probably been derived independently. The first type is present in the subfamily Mastigonodesminae, Bidentogon, and Coronodesmus where there is an enlargement of the tibial podomere (Fig. 53). The second
case, several species of *Scytotonotus*, involves various knobs and projections on the tibial podomeres of leg pairs 5-11 (Fig. 54).

Character 19: Legs with Elongate Setae

The apomorphic condition is the presence of a number of long, dorsodistal, sensory setae, on at least the tibial and tarsal podomeres. These are not present in the plesiomorphic condition. The Mastigonodesminae and the genera *Speorthus* and *Idahodesmus* exhibit the apomorphic condition. These three taxa include the smallest individuals studied and may be related to size. In *Speodesmus* the legs possess a large number of moderately long setae which may be a troglodytic modification.

Character 20: Paraprocts Hirsute

The presence of hirsute paraprocts is apomorphic. The plesiomorphic condition is the presence of only two pairs of setae. The apomorphic condition which varies from 7 to 18 pairs, is present in four taxa, Mastigonodesminae, and the genera *Bidentogon*, *Speorthus*, and *Idahodesmus*.

Character 21: Sternum III Modified

The modification of the third sternum in males is apomorphic in the Mastigonodesminae and the genus *Idahodesmus* (Fig. 39). Although similar in both taxa, these bifurcated Y-shaped projections may have arisen independently.
Monophyly of the Subfamily Scytonotinae

The monophyly of the subfamily is well documented. The following 11 apomorphies (characters 22-32) are present in this subfamily:

Character 22: Syncoxosternal Hooks Present

The presence of lateral syncoxosternal hooks is autapomorphic for the Scytonotinae (Fig. 64). These small ventrocaudal hooks have no known function. The plesiomorphic condition is the absence of these hooks.

Character 23: Claws Long

The plesiomorphic condition is the presence of short claws, less than 4% of total leg length. Taxa with the autapomorphic condition have longer claws, usually over 5.5% of leg length. The apomorphic condition is seen in the scytonotines, the polydesmines, and a few epanerchodines.

Character 24: Biogeography

Biogeographical information is usually used to substantiate the generated tree. Here a possible series was set up with Southeast Asia the most plesiomorphic as represented by the Family Doratodesmidae; the Holarctic region as intermediate, and the Nearctic as apomorphic. The subfamilies Mastigonodesminae, Polydesminae, and Epanerchodinae are intermediate, while the apomorphic condition is exhibited by the scytonotines.
Character 25: Only 19 Segments Present

The plesiomorphic condition is where 20-segmented or 19- and 20-segmented species are present. The apomorphic state of only 19-segmented individuals is present in two subfamilies, the Mastigonodesminae and the Scytonotinae. Some individuals in the Polydesminae have 19 segments and are believed to be independently derived. Character 65 also deals with segment number.

Character 26: Gonopodal Prefemur Long

The apomorphic condition is an elongated gonopod (Fig. 24). This state is seen in the Subfamily Scytonotinae with the exception of Scytonotus and Speodesmus, the two most primitive taxa. The plesiomorphic condition is a relatively short gonopod with some degree of curvature.

Character 27: Gnathochilarium Rectangular

A rectangular gnathochilarium is autapomorphic for the subfamily Scytonotinae. Taxa with the plesiomorphic condition exhibit a quadrate gnathochilarium.

Character 28: Syncoxosternal Spine Present

Another autapomorphy for the subfamily Scytonotinae, is the presence of lateral spines on the syncoxosternal plate lateral to the hooks (Character 22) (Fig. 64).
Character 29: Claw Constricted

The autapomorphic condition, present only in the Scytonotinae, is a distally constricted claw (Fig. 54). The plesiomorphic state has a gradually tapered claw (Fig. 55).

Character 30: Leg Sphaerotrichomes

In the Scytonotinae, the autapomorphic condition involves sphaerotrichomes present only on the tibia and tarsus. The plesiomorphic state has other podomeres with sphaerotrichomes.

Character 31: Collum Enlarged

The apomorphic state, where the collum is enlarged and equal to or wider than the head is present only in the Scytonotinae. The plesiomorphic state involves a small collum much narrower than the head.

Character 32: Head with Microsetae

The head in the Scytonotinae is covered with numerous short microsetae. This autapomorphy gives the head an almost fuzzy appearance. The plesiomorphic state has a few, long setae present.

The following 24 characters (characters 33-56) deal with the genera in the Subfamily Scytonotinae:
Character 33: Legs Robust

The apomorphic state of relatively robust male legs is characteristic of the subfamilies Polydesminae and Epanerchodinae as well as the genus *Speodesmus* in the scytonotines.

Character 34: Gonopod Prefemur Not Hirsute

The gonopod prefemur is not hirsute in the genus *Speodesmus*. The plesiomorphic state is where the prefemur is hirsute.

Character 35: Anterior Edge of Gonopod With Serrations

This apomorphy in which the anterior edge of the gonopod has a small field of serrations is present in the genera *Speodesmus* (Fig. 16) and *Coronodesmus* (Fig. 30).

Character 36: Gonopodal Femur with Setal Row

This apomorphy, present in the genera *Speodesmus* and *Bidentogon*, is a linear row of long setae on the posterior surface of the femoral region of the gonopod. These setae are not present on any other polydesmids.

Character 37: Tibiotarsus with Caudal Projection

*Speodesmus* is the only taxon with a proximally directed spine on the anterior edge of the tibiotarsus distal to the serrations (Fig. 16). The plesiomorphic condition is spineless.
Character 38: Hypoproct Hirsute

The hirsute hypoproct is apomorphic for *Speodesmus* and *Coronodesmus*. This condition usually involves over 6 pairs of setae, as compared to the plesiomorphic condition with 2 pairs.

Character 39: Epiproct Hirsute

The hirsute epiproct is apomorphic for most of the subfamily Scytonotinae with the exception of some species in the genus *Speodesmus*. The plesiomorphic condition is a single pair of setae.

Character 40: Terga Directed Ventrad

This apomorphic state, limited to the subfamily Scytonotinae, is caused by the paranota being ventrally directed. This is opposed to the laterally projecting paranota of most polydesmoids where the millipede has a definite flat-backed appearance (Fig. 48). This condition is most extreme in males of the genus *Scytonotus* where the body is almost circular in x-section (Fig. 49).

Character 41: Dorsal Setae Hooked

This autapomorphic state is present only in the genus *Scytonotus*. Dorsal setae of adults are filiform and hooked terminally. This condition is not exhibited by juveniles, which have irregular clavate setae. The difference between adult and juvenile setae in other taxa is unknown.
Character 42: Peritremata Large

The apomorphic condition involves large, wide peritremata. This character is found in Scytonotus and Idahodesmus of the Scytonotinae, and in the subfamilies Epanerchodinae and Polydesminae. In the plesiomorphic condition, the peritremata are either absent or very small.

Character 43: Gonopodal Femur Branched

The autapomorphic state of a branched femur is present only in the genus Scytonotus (Fig. 21). Both branches are movable. The primitive state has an unbranched femur although it may have various lobes and processes.

Character 44: Anterior Edge of Collum Flared

This autapomorphy for the genus Scytonotus is not present in any other taxa studied. It allows the collum to over-ride the head giving additional protection to it while the milliped is flat and extended.

Character 45: Ozopores Elevated

This apomorphy is present in the more derived Scytonotinae. The ozopores are elevated on large bulbous mounds (Fig. 9). This state is present in the genera Utadesmus, Bidentogon, Coronodesmus, Speorthus, Idahodesmus, and several species of the genus Scytonotus.
Character 46: Dorsal Tubercle Formula 10, 10, 8

The dorsal tubercle formula, 10, 10, 8, representing the number of tubercles in each transverse row on the dorsum, is apomorphic in three genera, Bidentogon (Fig. 7), Coronodesmus (Fig. 8), and Idahodesmus (Fig. 10). The plesiomorphic condition is of three rows with 8 tubercles.

Character 47: Gonopod Elongate

The apomorphy, present in genera Utadesmus (Fig. 24) and Bidentogon (Fig. 27), is exhibited as an elongated gonopod. The plesiomorphic state is a short arcuate gonopod.

Character 48: Endomerite Flattened

In the genus Utadesmus this autapomorphy is the transverse flattening of the endomerite. In the plesiomorphic condition the endomerite is usually slightly flattened longitudinally as in Pseudopolydesmus.

Character 49: Dorsal Setae Clavate or Peg-Shaped

The apomorphic state present in several genera, Utadesmus, Speorthus, and some Speodesmus, is that the setae of adults are short and either peg-shaped (Fig. 52) or slightly clavate (Fig. 51). The exact relationship between the peg or clavate setae is unknown. The plesiomorphic condition is the presence of typical filiform setae (Fig. 50).
Character 50: Paranota with Cephalad-Directed Denticles

The apomorphic state is distinguished by a large denticle on the anterior edge of each paranotum (Fig. 9). This state is present in Bidentogon, Coronodesmus, Speorthus, and Idahodesmus.

Character 51: Tibiotarsus Branched

The apomorphic state of major branching of the tibiotarsus is present in Bidentogon, Coronodesmus, Speorthus, and Idahodesmus. Although some branching occurs in other taxa, such as Polydesmus and Epanerchodus, these are believed to be derived independently.

Character 52: Anterior Row of Dorsal Setae Directed Cephalad

The apomorphic state, present in Bidentogon (Fig. 7) and Coronodesmus (Fig. 8), is where the setae associated with the anterior of three dorsal rows of tubercles are directed cephalad with the posterior two rows of setae directed posteriorly. The plesiomorphic condition has all three rows of setae directed posteriorly.

Character 53: Sterna Modified

The apomorphic state, exhibited by Coronodesmus, Epanerchodinae, and some Polydesminae, is the modification of the sterna with spines, and plates. It is atypical in Coronodesmus where sternal spines are located only on the tenth sternum. The plesiomorphic state is a flat and unmodified sternum.
Character 54: Dorsum with 4 or 5 Rows of Tubercles

The apomorphic state of 4 or 5 transverse rows of dorsal tubercles is present in Scytonotus (Fig. 5), Speorthus (Fig. 9), and Idahodesmus (Fig. 10). The remaining scytonotines have the plesiomorphic condition of only 3 rows of tubercles. The rows are less regular in 4- or 5-row taxa than in 3-row taxa.

Character 55: Leg Pairs Separate on Sternum

The apomorphic state, observed in the Scytonotinae, is exhibited by the slight separation of the anterior pair of legs from the posterior pair on the midbody sternum (Fig. 60). The plesiomorphic state has the leg pairs contiguous (Fig. 59).

Character 56: Medium-sized Individuals Absent

This character is used in conjunction with character 15 to obtain some usable information dealing with size. The apomorphic condition is the absence of medium-sized individuals (between 10-20mm), all being small (less than 10mm). Speorthus and Idahodesmus are apomorphic.

The placement of the subfamilies Epanerchodinae and Polydesminae in an independent clade is due to similarities observed by previous workers and their overall general appearance. The following 3 apomorphies (characters 57-59) support this clade:
Character 57: Anterior Terga Directed Lateral

This apomorphic condition, present in the epanerchodines and polydesmines, is the presence of laterally-directed paranota on segments 2-4 (Fig. 44). The plesiomorphic condition has paranota 2-4 curving or bending anteriorly (Fig. 45).

Character 58: Seminal Vesicle Present

The presence of the seminal vesicle at the terminal end of the seminal groove has always been a good apomorphy for the epanerchodines and polydesmines as stated by Attems (1914). The plesiomorphic condition is the lack of this terminal seminal vesicle.

Character 59: Dorsum with Smooth Bosses

The apomorphic state, dorsum covered with flat, non-tuberculate bosses, is present in the epanerchodines and polydesmines. In the plesiomorphic condition, the dorsum is covered to various degrees with tubercles.

Character 60: Endomerite Large

The apomorphic state, an enlarged endomerite, is present in the epanerchodines and some polydesmines. The plesiomorphic condition is either the absence or the presence of a small endomerite.
Character 61: Cyphopod Modified Ventrally

The apomorphic condition is the modification of the ventral surface of the cyphopod. This condition is best expressed in the genus *Pseudopolydesmus* where the surface is enlarged into a large irregular flat surface (Fig. 67).

**Monophyly of the Subfamily Epanerchodinae**

As stated in the descriptions, Attems (1901) placed this taxon in *Polydesmus* as a subgenus. He corrected this in 1914. This taxon of approximately 100 species has not been revised although a need is present. An indepth study of this taxon is beyond the scope of this study. From the limited number of specimens examined (Appendix D) and the literature, there are 4 autapomorphies (characters 62-65) for the subfamily Epanerchodinae:

**Character 62: Clivus Present**

The presence of the clivus on the gonopod is an autapomorphy for the epanerchodines (Fig. 15). This usually bulbous structure is located laterally about 1/3 distance up the tibiotarsus. In many cases it is closely associated with the endomerite.

**Character 63: Aperture Triangular**

The apomorphic state, present in the epanerchodines, is the triangular shape of the gonopodal aperture on the posterior sternum
of the 7th segment. The plesiomorphic state is a transversely oval aperture.

Character 64: Secondary Lobe on 7th Antennomere

In the epanerchodines another apomorphy is the presence of a small secondary lobe located proximal to the primary lobe. The plesiomorphic state has only the small primary lobe present.

Character 65: Body with 19 or 20 Segments

In conjunction with character 25, presence of 19 or 20 body segments is apomorphic while the plesiomorphic state is only 20. The apomorphic condition is seen only in the subfamily Epanerchodinae.

The phylogenetic tree generated by the PAUP program for the family Polydesmidae and the genera of the subfamily Scytonotinae is based on the preceding 65 character states (Tables 2a & b). The individual states for each taxon can be seen in Tables 3a & b. The minimum tree length is 92 character steps. The difference between the absolute minimum length of 66 and the determined minimum of 92 is due to reversals and parallelisms.

The cladogram (Fig. 43) shows that there are two major clades in the family Polydesmidae; one including the subfamilies Mastigonodesminae and Scytonotinae, and the second including the subfamilies Polydesminae and Epanerchodinae. In the subfamily Scytonotinae, which includes only North American representatives,
the first genus to separate is Speodesmus, followed by Scytonotus and then Utadesmus. The remaining four genera form two clades, one consisting of the genera Bidentogon and Coronodesmus and the second Speorthus and Idahodesmus.

The polydesmine-epanerchodinae clade is well established. The Polydesmineae includes two large genera, Pseudopolydesmus and Polydesmus, the first Nearctic, the second Palearctic. There are also several small, mostly monotypic genera from central Asia of uncertain positions although based on the literature, they have close affinity to Polydesmus.

The consistency index (CI) is a high 0.717. If the tree contained no reversals or parallelisms, this index would be 1.000. Variation is responsible for this value.

The f-value and normalized f-value were 3.124 and 0.161 respectively.

The Manhattan or character state matrix (Table 4) can be used to show relative distances between taxa on comparable taxonomic levels. The differences would range between 0 and 1 for the value generated. In a combined study, part of that range would be taken up by the second level of taxa (in this case the genera of Scytonotinae). If the second taxonomic level was removed from the calculation, the differences between the taxa would increase proportionally but still be based on a range between 0 and 1. On the subfamily level, the greatest distance is between Epanerchodinae and Doratodesmidae, with a distance of 0.354, while the smallest character distance is between Polydesmineae and Epanerchodinae
In the subfamily Scytonotinae, the greatest distance is between *Idahodesmus* and *Speodesmus* (0.328), while the shortest distance is between *Idahodesmus* and *Speorthus* (0.062).

The patristic distance matrix (Table 5) would show the same proportionality as the character state distances mentioned above. The greatest subfamilial distance is between Epanerchodinae and Doratodesmidae and between Mastigonodesminae and Doratodesmidae (0.354), while the smallest distance is between Polydesminae and Epanerchodinae (0.138). In the subfamily Scytonotinae the greatest distance is between *Idahodesmus* and *Speodesmus* (0.668), while the shortest distance is between *Idahodesmus* and *Speorthus* (0.062).

The homoplasy matrix (Table 6) has the same proportionality as the other two matrices. The greatest amount of homoplasy on the subfamilial level is between Doratodesmidae and Mastigonodesminae and between Epanerchodinae and Mastigonodesminae (0.031) with a single homoplastic character. The other pairwise distances are 0.000.

In the subfamily Scytonotinae the greatest amount of homoplasy is between *Coronodesmus* and *Scytonotus* (0.123), and the lowest degree of homoplasy (0.000) is shared with a number of pairwised taxa.

The Deltran test, which maximizes parallelism to reversal, lists no change in the tree length or consistency index. However, changes in the cladogram, with variations in the corresponding clades, lowered the f-value from 3.124 to 2.200, and the normalized f-value from 0.161 to 0.113. There were four characters listed for
possible change in their character state: in the case of marginal ozodeme location (12), seen in Bidentogon and is probably a reversal of secondarily derive because the change would require the change of state for four taxa, unlikely; in small size (15), seen in the Mastigonodesminae and Speodesmus probably represent secondarily derive size, since both taxa appear to be well established troglodites; in leg modifications (18), are in most cases appear to be independently derived; in strictly asian in range (24), seen in the doratodesmids and the epanerchodines probably represent a primitive stock in the doratodesmid, the sister group for the polydesmids, while the epanerchodines a very recent taxon.

The Acctran test, which maximizes reversals to parallelisms, addressed the same characters mentioned above, but with a reversal of emphasis. The arguments are the same for the stated conditions. Although the cladogram remained the same the variations lowered the F-value from 3.124 to 2.460 and the normalized F-value from 0.161 to 1.117.

**Monophyly of the Genus Pseudopolydesmus**

As is the case with almost all milliped taxa, there have been few systematic studies to determine diagnostic characters in polydesmids. Attems' (1898) original description distinguished Pseudopolydesmus from Polydesmus only in a key without further statement. He used the absence of the "haarpolster" (=endomerite) and "samenblase" (=seminal vesicle), which are present in Polydesmus, to separate the two genera. These two structures are
present in *Pseudopolydesmus* and he corrected this oversight in 1940. The first question which must be answered here is the monophyly of the genus *Pseudopolydesmus*. Characters 1 to 9 below are the suggested autapomorphies for *Pseudopolydesmus*; characters 10-35 are for distinguishing clades or species in *Pseudopolydesmus*.

Character 1: Presence of Process $M_1$

In all *Pseudopolydesmus*, presence of the $M_1$ process on the tibiotarsus is autapomorphic. A comparable process is present on several species of *Polydesmus* but I believe that these are derived states.

Character 2: Connected Medial Bosses

The plesiomorphic condition of two medial bosses (MB) (anterior and posterior) is present in *Polydesmus* (Fig. 11). In *Pseudopolydesmus*, the autapomorphic state is exhibited by the fusion of these two bosses into one (Fig. 12). It appears that the remaining polydesmines are variable, but the majority have two medial bosses. All other members of the family appear to have the plesiomorphic condition.

Character 3: Sternum 3 of Female Unmodified

The third sternum of *Polydesmus* is modified with variously shaped lobes, spines, and processes (ex. Demange, 1968). In the
autapomorphic condition, seen in *Pseudopolydesmus*, the third sternum is flat and unmodified.

**Character 4: Presence of Cyphopod Plate**

The autapomorphic condition is the presence of a distal, flattened, and variously modified plate-like dorsal enlargement of the cyphopod, present in *Pseudopolydesmus* and not present in any other polydesmids. In *Polydesmus* this dorsal area may be somewhat modified but not flattened.

**Character 5: Sternum 7 of Male Modified**

Although the amount of modification is not large, a laterally enlarged 7th sternum is present in all *Pseudopolydesmus* and absent in the genus *Polydesmus*, making it a good autapomorphy.

**Character 6: Anterior Tibiotarsal Attachment**

The attachment of the tibiotarsus to the gonocoxa is more lateral in *Polydesmus*, and more anterior in *Pseudopolydesmus*. This autapomorphy gives *Pseudopolydesmus* the appearance of a more firmly attached tibiotarsus.

**Character 7: Endomerite Enlarged**

The large size of the endomerite, used by Attems (1940), appears to be a good autapomorphy for *Pseudopolydesmus*. The endomerite is also more consistent in size and location than in *Polydesmus*.
Character 8: Cyphopod Elongate

The longitudinal elongation of the cyphopod is autapomorphic. This character is seen in all *Pseudopolydesmus*; in *Polydesmus* the shape is more oval. The cyphopod is secondarily reduced to a slightly oval shape in *minor*, *caddo*, and probably *paludicola* as a result of their small size.

Character 9: Tibiotarsus with Terminal Setae

The presence of a row of setae on the tip of the tibiotarsus is autapomorphic for *Pseudopolydesmus* (Fig. 91). Setae may be absent from specimens due to breakage. The plesiomorphic state has no terminal setae.

Character 10: Presence of Process M3

Process M3 is considered apomorphic because it is always present in the Group Canadensis (Fig. 70). In the remaining species of *Pseudopolydesmus*, the process is absent.

Character 11: Cyphopodal Plate Enlarged

The enlargement of the dorsal surface of the cyphopod is also apomorphic for the Group Canadensis (Fig. 103). The plesiomorphic condition, seen in the Group Serratus, is exhibited by a smaller plate.
Character 12: Numerous Sternal Setae

The number of sternal setae is characteristic. Group Canadensis has the apomorphic condition of numerous setae. In Group Serratus, the number always appears to be less than 10.

Character 13: Presence of Process E₁

Presence of process E₁ is apomorphic in the Group Canadensis. The process is absent in the Group Serratus. Although in Polydesmus there are species with processes in a similar position as process E₁, it is accepted that the plesiomorphic condition is with the process missing. This is because character states have not been determined in Polydesmus and the simplest form is probably plesiomorphic. The variability of all process should increase the probability of homoplasies.

Character 14: Small Paranotal Denticles

The small size of the lateral denticles is apomorphic for the Group Canadensis. In many cases these denticles are almost nonexistent. In Hoffman's description of paludicola he states that denticles are absent, however this not the case. They appear to be reduced; however more specimens are needed to establish variability.

Character 15: Epiproct Downturned

In the species pinetorum the epiproct is downturned (Fig. 77). This condition is not normal in any other Pseudopolydesmus (Fig.
158); however, some specimens of other species showed an uncharacteristic downturned condition.

Character 16: Gonopod Thickened Longitudinally
In the Group Canadensis, the apomorphic condition of the longitudinal thickening of the tibiotarsus around the endomerite characterizes the tallulanus-erasus clade (Figs. 80, 81). The plesiomorphic condition has the typical thin tibiotarsus.

Character 17: Presence of Process \( E_3 \)
The presence of process \( E_3 \) is apomorphic for two groups of taxa, the Group Serratus and the canadensis-collinus complex. This is probably a case of parallelism: the appearance of this process twice in unrelated taxa. I speculate that the low number of genes controlling these processes permits mutations, causing similar phenotypes.

Character 18: Presence of Process \( M_2 \)
The presence of the \( M_2 \) process is autapomorphic for the canadensis-collinus complex.

Character 19: Presence of Process \( E_2 \)
The loss of the \( E_2 \) process is autapomorphic for erasus.

Character 20: Montane Habitat
The use of habitat information is not customary but is included because of its distinctive influence. Here the generalized
habitat is assumed to be plesiomorphic. The mountain or cold-dwelling habitat can be seen in two species. In the erasus-tallulanus complex, tallulanus is found only in the central and southern Appalachians at higher elevations than erasus which is found primarily on the Cumberland Plateau below 450 meters, west of tallulanus. There does not appear to be any overlap of the two species.

In the canadensis-collinus complex, canadensis is found only at higher elevations of the Appalachians and expands beyond them in the northern areas of its range. P. collinus appears to be a generalist of a different type. The species has been found from high elevations (over 2000 meters) to muddy river flood plains, to sandy coastal regions.

Character 21: Presence of Process E$_{2+3}$

The presence of process E$_{2+3}$ is apomorphic in the Group Canadensis except for pinetorum. It is however, attached differently in the erasus-tallulanus and canadensis-collinus complexes. In erasus-tallulanus the process is basally attached to the tibiotarsus (Figs. 88, 89) while in canadensis-collinus the process is elevated on a distinct lateral stalk.

Character 22: Anterior Edge of Gonocoxae Multilobed

This apomorphic condition is present in the Group Serratus, and with the exception of collinus, absent in the Group Canadensis (Fig. 82). Here the apparent parallelism is probably caused by
multiple gene loci, not by a single locus. There appears to be a high degree of variation in the gonocoxae, ranging from monolobed to multilobed.

Character 23: Processes $M_2$ and $E_1$ Connected Ventrally
The connection of these two processes along the posterior face of the tibiotarsus is autapomorphic in the Group Serratus. Both processes may be present in several other species, but the connecting ridge is not present. This ridge is most clearly seen in *Pseudopolydesmus serratus* (Fig. 99). The connecting ridge may also bear a small process; however, the latter appears sporadically throughout the range, without discernable geographic pattern.

Character 24: Sternum 7 Laterally Enlarged
As mentioned in character 5, the modification of the lateral edge of the 7th sternum is apomorphic for *Pseudopolydesmus*. There is further modification of the structure in the Group Serratus into a moderately long, thin spine (Fig. 62). This contrasts with a very weak spine in the Group Canadensis (Fig. 61).

Character 25: Legs Short
Presence of relatively short legs is autapomorphic for the *minor-caddo* complex and *paludicola*. Although all three species are noticeably smaller than the others in the genus, the relative leg length to body length is also smaller. In these species leg length to body length ranges from 9-14% while in the remaining species this ratio is over 16%.
Character 26: Body Length Short

The overall smaller size of individuals in the minor-caddo complex and paludicola is a good autapomorphic character. These species have a length ranging from 9 to 14mm while the remaining species range between 12 and 32mm. The reduction in body size can be seen in many millipede taxa.

Character 27: Dorsal Setae Present

The presence of dorsal setae is apomorphic for the minor-caddo complex and paludicola. These small setae are associated with the bosses and denticles. There are also cases where other species have dorsal setae, for example in collinus, but this is rare. Each boss and denticle will usually have a single seta, however two setae are occasionally present.

Character 28: Antennae Short

The autapomorphic condition of short antennae is present for paludicola and the minor-caddo complex. Again these three species are small (character 25), but the relative length of the antennae is also shorter. In these three species, the relative antennal length ranges from 10 to 12% of the total body length while the plesiomorphic condition ranges between 15 and 21%.

Character 29: Cyphopodal Plate Margin Straight

As mentioned earlier (character 4), the presence of the cyphopodal plate is apomorphic for the genus. However the condition
exhibits two general shapes, quadrate and angular. The straight plate margin is apomorphic, and can be seen in the minor-caddo complex (Figs. 115, 116). The status of paludicola is unknown but I believe that when females of this species have been examined, they will be similar, so this character is used as an apomorphy for all three species. To restrict the trait to minor and caddo would only move the apomorphy one branch distally, and change nothing in the phylogenetic pattern.

Character 30: Lowland Habitat

As in character 19 the use of geographical information may be somewhat suspect due to incomplete collecting. As before, the generalized habitat is considered plesiomorphic. Three species: paludicola, minor, and caddo exhibit apomorphic lowland preferences, inhabiting low, wet, flood-prone areas. Two of these, minor and caddo, are usually found along the margins of major rivers which are prone to flooding. P. paludicola has been found in lowland swamps of eastern Virginia and North Carolina, in very wet localities. These localities are not generally regarded as good millipede habitats. During personal collecting, the caddo type locality had flood debris on overhanging power lines and water marks 9-12 meters up trees. This habitat does not preclude the occasional occurrence of other species, as, for example, serratus in Louisiana.
Character 31: Process $M_4$ Absent

The absence of $M_4$ is apomorphic in two species, *paludicola* and *caddo*, with the plesiomorphic condition present in *minor* (which is a probable case of reversal). The plesiomorphic condition is present in the remaining species of the genus as well as in *Polydesmus* where some type of terminal medial process is usually present.

Character 32: Dorsal Curvature Decreased

In *minor* and *caddo* the body is depressed dorsoventrally. This apomorphic condition may be related to habitat preference (see character 30). The width/thickness ratio of *minor* and *caddo* is less than 80% as compared to over 90% in the remaining species.

Character 33: Bunched Cyphopod Setae

This condition is apomorphic for at least the *minor-caddo* complex but may include *paludicola* (no female *paludicola* have been positively identified). This condition involves a distinct ventral bunching of marginal setae (Fig. 114) on the cyphopod as compared to the regularly spaced setae seen in all other polydesmids (Fig. 107).

Character 34: Process $M_1$ Isolated from Endomerite

The general location of process $M_1$ is near the base of the endomerite. The apomorphic condition is more proximal and separate from the endomerite (Fig. 94). This is an autapomorphy for *minor*. 
Character 35. Sternum II of Female Modified

The presence of small, smooth bumps on the second sternum of females is an autapomorphy for *Pseudopolydesmus caddo* (Fig. 76). The plesiomorphic condition is the absence of any modification on sternum II.

Character 36. Dorsum Flattened

There appears to be a trend in many polydesmid taxa to flatten the body. The extreme case can be seen in *minor* where the body has a relative width/thickness ratio of approximately 70% as compared to 80% in *caddo* and over 90% in the remaining species. This is a further and noticeable step beyond character 32.

The phylogenetic tree generated by the PAUP program for the genus *Pseudopolydesmus* was based on the preceding 36 character states (Table 7). The data set listing the states present in each taxon is in Table 8. The tree (Fig. 118) easily splits *Polydesmus* from *Pseudopolydesmus* based on 9 autapomorphies. From this point the tree is divided for clarity into two Groups, Canadensis and Serratus. The Group Canadensis is composed of five species with *pinetorum* splitting off first. The next major clade sees the remaining four species divided into two-species complexes, *tallulanus-erasus* and *canadensis-collinus*. The Group Serratus is composed of four species. The species *serratus* splits off first. The next derived species is *paludicola* leaving the final clade consisting of the *caddo-minor* complex.
The minimum tree length was 46 character steps. The difference between the absolute minimum of 35 and the determined minimum of 46 is due to reversals and parallelisms.

The consistency index (CI) is a moderate 0.761. If the tree length was 35, without any reversals or parallelisms, this ratio would be 1.000.

The f-value and normal f-value are 3.296 and 0.196 respectively, which is also moderate.

The Manhattan or character state distance matrix (Table 12) is the pairwise distance between two taxa. The greatest distance for Pseudopolydesmus is between the minor-caddo and the tallulanus-erasus and canadensis-collinus complexes (0.629). The shortest distance is between minor and caddo, and tallulanus and erasus (0.114).

The patristic distance matrix (Table 13) shows that the greatest distance is between minor and collinus (0.829) while the shortest distance is between canadensis and collinus (0.086).

The greatest amount of homoplasy as presented in the homoplasy matrix (Table 14) is between minor and collinus (0.286), while a number of taxa showed no homoplasy between them (0.000).

The Deltran test, which maximizes parallelism to reversal, shows no variation in the above calculations. There were five characters listed for possible change in their character state: in the case of cyphopodal shape (8), the parallelism of the oval shape seen in minor and caddo is probably related to size and therefore secondary; in antennal length (27), the same is true; in the M₂-E₁
connection (22), this condition also requires a change in the state of both minor and caddo; the loss of process $M_4$ is seen in caddo; and the multilobed condition seen in collinus and Group Serratus, may be due to gonocoxal variation.

The Acctran test, which maximizes reversals to parallelisms, was the same as the original Farris test.

CLASSIFICATION OF POLYDESMIDAE

My classification of the Polydesmidae is summarized in Table 1 and is expressed as a phyletic sequence scheme (Wheeler, 1979). In the phyletic sequence, each taxon is the sister group of all taxa of equal or lesser rank listed below it. Also included are the tentative subfamilies and genera from the Old World that were not covered in this study; these are marked with an asterisk.

In this classification, I retain the subfamily Mastigonodesminae with 3 genera and propose new subfamily status for Scytonotinae, with a new genus, Idahodesmus, and the new name Coronodesmus, to handle the observed diversity. Also proposed are the subfamilies Polydesminae to include a number of palearctic genera and Pseudopolydesmus, and Epanerchodinae to include from 3 to 8 Asian genera.
ZOOGEOGRAPHY

In a morphological cladistic analysis, insights into relationships among taxa correlate with the areas these taxa occupy. Since a special effort was made to obtain locality information for the genus *Pseudopolydesmus*, a moderately satisfactory picture of distribution of its species was obtained. In the absence of complete locality information, general distribution patterns, especially in the Scytonotinae, can only be surmised.

THE VICARIANCE MODEL

Theories explaining the distribution of most animal groups fall into two categories, dispersal and vicariance. The ideas dealing with dispersal have been championed by Darlington (1957), Brundin (1966), and Hennig (1966). The vicariance model is more recent, first presented in Croizat's *Panbiogeography* (1958) and later modified by Croizat, et al. (1974), Platnick and Nelson (1978), and Rosen (1978). The only difference lies in the type and
degree of isolating barriers. Vicariance is when a widespread population, or species, has its range divided into smaller populations by developing barriers. Dispersal takes place if the barrier is already present, and success in crossing that barrier leads to the founding of a separate and new population. Both models have as their central point, the idea of allopatric speciation (Mayr, 1969), but because of the differences in environmental conditions and genetic make-up, evolution will act differently on each isolated population.

Platnick and Nelson (1978) stated that by inference it is possible to develop a vicariant model based on the cladistic relationships of the areas. If an initial pattern can be established, and can be seen in other organisms, this is representative of a shared "generalized track" (Croizat, et al., 1974). The idea is that if a barrier isolates a geographic region, many taxa, including millipeds, should also be isolated.

It is now apparent to most biogeographers that both dispersal and vicariance are important in understanding the distribution of organisms. However the degree of importance varies with the group. In dealing with flightless soil arthropods which spend their lives in a very controlled and relatively homeostatic environment, dispersal probably plays a minimal role. Temperature, humidity, light, and moisture are critical, so barriers don't have to be large to be efficient. Because of the limited mobility of these organisms and their slow rate of dispersion, soil arthropods hold a great future as indicators of vicariant events.
DISTRIBUTION PATTERNS

Below is a brief discussion of the distributions of the 4 subfamilies and the North American genera of Polydesmidae.

Subfamily Mastigonodesminae. Palearctic: Around the western basin of the Mediterranean Sea, extending into northern Italy and central France. Several species are troglodytic.

Subfamily Scytonotinae. Nearctic: In eastern North America north of Tennessee and south of Canada, and in the west from Texas, Wyoming, and California to southern Alaska (Map 3).

2. Scytonotus. Nearctic: Two populations, one from Iowa and Arkansas east to the Atlantic coast, and the other from Wyoming and Utah northwest into southern Alaska.

Subfamily Polydesminae. Holarctic: Palearctic from Europe to extreme western Siberia (although how extensive in Siberia is
uncertain) and the extreme northwestern tip of Africa (Morocco, Algeria, and Tunisia). In the Nearctic, all except Mexico and the Central Plains. All species are epigean.


Subfamily Epanerchodinae. Palearctic: Japan, Korea, and China. Some species are troglodytic.

The structures and exact relationships of the exotic genera of Polydesmidae are uncertain with the exception of the genus Epanerchodus which is well described in the literature. Although few specimens and inadequate data made clarification of other central Asian and European polydesmids impossible, the genus Epanerchodus, with several associated genera, should be elevated to subfamilial ranking.

Speciation Patterns—An important part of zoogeography is the appraisal of speciation patterns. All distributions are obviously continental. Two patterns can be observed in the Polydesmidae: widespread genera with numerous species (Polydesmus, Pseudopolydesmus, Epanerchodus, and Scytonotus) and genera with a limited distribution and few species.
The species of *Pseudopolydeshmus* fall into three distribution and habitat patterns. *Pseudopolydeshmus minor*, *caddo*, and *paludicola* inhabit lowlands and major river floodplains or areas where inundation by flood waters is highly probable (for example trees at the type locality of *minor* in Louisiana had water marks thirty feet above the ground). The second type involves primarily montane and colder habitats. This is characterized by *canadensis*, *tallulanus*, and possibly *pinetorum* although to a lesser extent. The disjunct populations of *canadensis* in southern Mississippi and central Florida probably represent isolated relicts from the last period of glaciation. The remaining species, *serratus*, *erasus*, and *collinus* appear to be generalists with little elevation preference, with *serratus* wide-spread and *erasus* and *collinus* less so. At least two species pairs are seen, *canadensis-collinus* and *tallulanus-erasus*, with one member northern or montane and the other primarily not. The non-montane species may represent young species dispersing since the last period of glaciation.

In the *Scytonotinae*, with its high species to genus ratio, adequate data for only one genus, *Scytonotus*, are available. The eleven species are divided into eastern and western populations supported by a number of distinct morphological characters. Although disjunct based on present data, it is possible that they are continuous through southern Canada. I expect that the genus was wide-spread across the North but increasing aridity in the Great Plains caused the extirpation of the genus there. It would be
interesting if relict populations occur in the gap between Wyoming and Iowa.

HISTORICAL ZOOGEOGRAPHY

The patterns for the family Polydesmidae indicate a moderately simple model because of the Holarctic distribution. The family in its present form didn't arise until after the breakup of Pangea (180 MYBP). The Holarctic was continuous until late Cretaceous (75 MYBP) when the Palearctic and Nearctic continents separated. The distribution of the family basically conforms to the Arcto-tertiary Nemoral Circumpolar Forest of the Northern Hemisphere (Kornas, 1972). This forest was continuous up to the Miocene and possibly the Pliocene (7 MYBP) and then diminished to its present-day distribution. Only three major areas of this substantial deciduous forest survive: eastern North America, western Europe, and the Far East of Asia including China and Japan, each isolated by seas or intervening drier areas. All three areas are centers where radiation and speciation has taken place, *Polydesmus* in Europe, *Epanerchodus* in the Far East, especially Japan, and to some extent *Pseudopolydesmus* in North America. In west and central Asia and western North America only isolated populations remain with a few relict genera and species.
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seen).
APPENDIX A

TABLES
Table 1. Systematics of the Family Polydesmidae

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<td>Mastigonodesmus</td>
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* Old World Taxa
Table 2. List of generic character states for the Family Polydesmidae.

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<th>Apomorphlic</th>
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<td>1. 2nd Paranotum</td>
<td>normal</td>
<td>flabellately enlarged</td>
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<tr>
<td>2. Involution Ability</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>3. Gonocoxal Ventral Surface</td>
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<td>with microsetae</td>
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<td>4. Sternal Width</td>
<td>narrow</td>
<td>wide</td>
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<td>5. Length/Width Ratio</td>
<td>low (8-23%)</td>
<td>high (15-32%)</td>
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<td>6. Interantennal Width</td>
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<td>7. Antennal Length</td>
<td>short</td>
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<td>8. Seminal Groove on Tibiotarsus</td>
<td>subterminal</td>
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<td>9. Cyphopodal Shape</td>
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<td>10. Metazonite</td>
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<td>16. Tibiotarsal Attachment</td>
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<td>lateral</td>
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<td>17. Coloration</td>
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<td>18. Leg Modifications</td>
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<td>19. Macrosetae on Legs</td>
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</tr>
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<td>20. Paraproct Setation</td>
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<td>21. Sternum III</td>
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<td>22. Syncoxosternal Hooks</td>
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</tr>
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<td>23. Claw Length</td>
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<td>short</td>
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<td>25. Segments Numbers</td>
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<td>19</td>
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<td>27. Gnathochilarium</td>
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<td>29. Claw</td>
<td>evenly</td>
<td>constricted</td>
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<td>30. Leg Sphaerotrichomes</td>
<td>most</td>
<td>only tibia and tarsus</td>
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<td>31. Collum Width</td>
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<td>32. Head Setae</td>
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<td>33. Leg Thickness</td>
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Table 2. (continued),

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</tr>
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<td>36. Gonopodal Femur with Setal Row</td>
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<td>present</td>
</tr>
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<td>37. Tibiotarsus with Caudal Process</td>
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<td>present</td>
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<td>38. Hypoproctal Setae</td>
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<td>39. Epiproct Setae</td>
<td>little</td>
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<td>40. Tergal Size</td>
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<td>small</td>
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<tr>
<td>41. Setae shape</td>
<td>straight</td>
<td>hooked</td>
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<td>42. Peritremata</td>
<td>narrow</td>
<td>wide</td>
</tr>
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<td>43. Femur</td>
<td>simple</td>
<td>branched</td>
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<td>44. Anterior Edge of Collum</td>
<td>unflared</td>
<td>flared</td>
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<td>45. Ozopore Shape</td>
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<td>46. Dorsal Tubercle Formula</td>
<td>variable</td>
<td>10, 10, 8</td>
</tr>
<tr>
<td>47. Gonopod</td>
<td>arcuate</td>
<td>elongate</td>
</tr>
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<td>48. Endomerite X-section</td>
<td>round</td>
<td>flat</td>
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<td>49. Dorsal Setae Shape</td>
<td>filiform</td>
<td>clavate or peg</td>
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<td>50. Paranotal Denticles</td>
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<td>unbranched</td>
</tr>
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<td>52. Anterior Row of Dorsal Setae</td>
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<td>cephalad</td>
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<td>53. Sternal Modifications</td>
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<td>54. Dorsal Row Number</td>
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<td>4 or 5</td>
</tr>
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<td>55. Tibiotarsus Setae Row</td>
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<td>present</td>
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<tr>
<td>56. Medium Sized</td>
<td>cephalad</td>
<td>laterad</td>
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<td>58. Seminal Bulb</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>59. Tergal Texture</td>
<td>tuberculate</td>
<td>smooth</td>
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<td>60. Endomerite Size</td>
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<tr>
<td>61. Aperture Shape</td>
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<td>triangular</td>
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<td>62. Clivus</td>
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<td>present</td>
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<tr>
<td>63. Seventh Antennomere</td>
<td>w/o lobe</td>
<td>w/ secondary lobe</td>
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<td>64. Cyphopodal Plate</td>
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<td>present</td>
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<tr>
<td>65. Segment Number</td>
<td>20</td>
<td>19 or 20</td>
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Table 3, data set for the family Polypeptide and genera of S. polytrichum.
Table 4. Manhattan distance matrix for the Family Polydesmidae.

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<th>Mas</th>
<th>Spe</th>
<th>Scy</th>
<th>Uta</th>
<th>Bid</th>
<th>Cor</th>
<th>Spr</th>
<th>Ida</th>
<th>Pol</th>
<th>Epa</th>
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<td>0.185</td>
<td>0.172</td>
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Table 5. Patristic distance matrix for the Family Polydesmidae.

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<th>Scy</th>
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<th>Bid</th>
<th>Cor</th>
<th>Spr</th>
<th>Ida</th>
<th>Pol</th>
<th>Epa</th>
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Table 6. Homoplasy matrix for the Family Polydesmidae.

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<th>Cor</th>
<th>Spr</th>
<th>Ida</th>
<th>Pol</th>
<th>Epa</th>
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<td>0.123</td>
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Table 7. List of specific character states for the genus *Pseudopolydesmus*.

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<th>Plesiomorphy</th>
<th>Apomorphy</th>
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<td>1. Process M₁</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>2. Medial Boss</td>
<td>split</td>
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</tr>
<tr>
<td>3. Sternum III (Female)</td>
<td>modified</td>
<td>unmodified</td>
</tr>
<tr>
<td>4. Cyphopodal Plate</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>5. Sternum 7 (Male)</td>
<td>unmodified</td>
<td>modified</td>
</tr>
<tr>
<td>6. Tibiotarsal Attachment</td>
<td>lateral</td>
<td>medial</td>
</tr>
<tr>
<td>7. Endomerite</td>
<td>small</td>
<td>expanded</td>
</tr>
<tr>
<td>8. Cyphopod</td>
<td>oval</td>
<td>elongate</td>
</tr>
<tr>
<td>9. Tibiotarsus with Terminal Setae</td>
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<td>present</td>
</tr>
<tr>
<td>10. Process M₃</td>
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<td>present</td>
</tr>
<tr>
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<tr>
<td>13. Process E₁</td>
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<td>present</td>
</tr>
<tr>
<td>14. Paranotal Denticles</td>
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<td>small</td>
</tr>
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<td>15. Epiproct</td>
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<td>18. Process M₂</td>
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</tr>
<tr>
<td>19. Process E₂</td>
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<td>present</td>
</tr>
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<td>montane</td>
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<td>present</td>
</tr>
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<td>22. Ant. Gonocoxae Edge</td>
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</tr>
<tr>
<td>23. M₂-E₁ Connection</td>
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<td>present</td>
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Table 9. Length and Width measurements of *Pseudopolydesmus* species, males and females, with range, mean, standard deviation, and number measured. (pin-pinetorum; tal-tallulanus; era-erasus; can-canadensis; col-collinus; ser-serratus; cad-caddo; min-minor).

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Table 10. W/L (width/length) and WL (width X length) measurements of *Pseudopolydesmus* species, males and females, with range, mean, standard deviation, and number measured. (pin-pinetorum; tal-tallulanus; era-erasus; can-canadensis; col-collinus; ser-serratus; cad-caddo; min-minor).

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Table 11. Distance from telopodite tip to base of mesial ($M_{1-4}$) and ectal ($E_{1-4}$) processes as a percentage of total telopodite length.

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Table 12. Manhattan distance matrix for the species in the genus *Pseudopolydendrom*.

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<td>0.200</td>
<td>0.114</td>
<td>0.171</td>
<td>0.000</td>
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<tr>
<td>collinus</td>
<td>0.429</td>
<td>0.229</td>
<td>0.200</td>
<td>0.200</td>
<td>0.086</td>
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<td>0.543</td>
<td>0.629</td>
<td>0.600</td>
<td>0.486</td>
<td>0.514</td>
<td>0.343</td>
<td>0.216</td>
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<tr>
<td>caddo</td>
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<td>0.543</td>
<td>0.629</td>
<td>0.600</td>
<td>0.486</td>
<td>0.514</td>
<td>0.343</td>
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Table 13. Patristic distance matrix for the species in genus *Pseudopolydromus*.

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</tr>
<tr>
<td><em>pinetorum</em></td>
<td>0.314</td>
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<td></td>
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<tr>
<td><em>tallulanus</em></td>
<td>0.400</td>
<td>0.143</td>
<td>0.000</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>erasus</em></td>
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<td>0.057</td>
<td>0.000</td>
<td></td>
<td></td>
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<tr>
<td><em>canadensis</em></td>
<td>0.457</td>
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<td>0.171</td>
<td>0.171</td>
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<tr>
<td><em>collinus</em></td>
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<tr>
<td><em>serratus</em></td>
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Table 14. Homoplasy matrix for the species in the genus Pseudopolydesmus.

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<td>0.000</td>
<td></td>
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<td></td>
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<tr>
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APPENDIX B

FIGURES
Figures 33-35. Right gonopod of *Speorthus tuguribus*, New Mexico, Eddy Co.; 33. medial view; 34. lateral view; 35. ventral view.
Figures 40-42. Right gonopod of *Polydesmus inconstans*, Ohio, Franklin Co.; 40. medial view; 41. lateral view; 42. ventral view.
Figure 43. Cladogram for the Family Polydesmidae including the subfamilies and the genera of Scytonotinae (Mast-Mastigonodesminae; Epa-Epanerchodinae; Pol-Polydesminae; Spe-Speodesmus; Scy-Scytonotus; Uta-Utadesmus; Ida-Idahodesmus; Spr-Speorthus; Bid-Bidentogon; Cor-Coronodesmus.)
Figures 44-45. Head and tergites 1-4, dorsal view. 44. Scytonotus granulatus, Ohio, Fairfield Co.; 45. Pseudopolydesmus serratus, West Virginia, Cabell Co.
Figure 69. Midbody leg of *Pseudopolydesmus serratus*, West Virginia, Cabell Co., anterior view, male and female, semidiagrammatic, setae omitted. Double-headed arrows indicate length as measured. c-coxa, tr-trochanter, prf-prefemur, f-femur, ti-tibia, ta-tarsus, cl-claw, sp-sphaerotrichomes.
Figures 70-73. Right gonopod of *Pseudopolydesmus canadensis*, Tennessee, Campbell Co., male; 70. mesal view; 71. lateral view; 72. ventral view; 73. in situ.
Figure 121. Cladogram for the genus *Pseudopolydesmus*. (pin-pinetorum; tal-tallulanus; era-erasus; can-canadensis; col-collinus; ser-serratus; pal-paludicola; min-minor; cad-caddo.)
Figure 122. Graph of length measurements of *Pseudopolydesmus* species, male and female. Range—horizontal line, means—vertical line, one standard deviation—rectangle.
Figure 123. Graph of width measurements of Pseudopolydesmus species, male and female. Range-horizonal line, means-vertical line, one standard deviation-rectangle.
Figure 124. Graph of W/L measurements of *Pseudopolydesmus* species, male and female. Range-horizontal line, means-vertical line, one standard deviation-rectangle.
Figure 125. Graph of WL measurements of Pseudopolydesmus species, male and female. Range-horizontal line, means-vertical line, one standard deviation-rectangle.
Figure 126. Graph of distances from telopodite tip to bases of mesial (M₁-₄) and ectal (E₁-₄) processes as a percentage of total telopodite length.
APPENDIX C

MAPS
Map 1. Distribution of families Polydesmidae and Doratodesmidae. Doratodesmidae ( III ); Polydesmidae ( II ).
Map 2. Distribution of Scytonotinae. Scytonotus ( ), Bidentogon ( □ ); Utadesmus ( ▲ ); Speodesmus ( ▼ ); Speorthus ( ▲ ); Coronodesmus ( ▲ ); Idahodesmus ( ⬜ ).
Map 3. Distribution of *Pseudopolydesmus*.
Map 4. Distribution of *Pseudopolydesmus pinetorum*.
Map 5. Distribution of *Pseudopolydesmus tallulanus* (●) and *erasus* (●).
Map 6. Distribution of *Pseudopolydesmus canadensis.*
Map 7. Distribution of *Pseudopolydesmus collinus*.
Map 8. Distribution of *Pseudopolydesmus serratus*.
Map 9. Distribution of *Pseudopolydesmus paludicola* (●), caddo (▲), and minor (■).
APPENDIX D

LOCALITY DATA
This is a list of localities and specimens examined. Those marked with a * are literature sites where the identifications are assumed to be correct. Distances are copied and have not been converted to metric units.

The following abbreviations were used in the list:

Approximately- circa
Between- btwn
County- Co.
County Road- CR.
Creek- Ck.
Female- F
Great Smoky Mountain National Park- GSMNP
Junction- jct
Juvenile- J
Male- M
Mountain- Mt.
Near- nr
Parish- Par.
River- R.
Road- Rd.
State Forest- S. F.
State Park- S. P.
State Route- SR.
United States Forest Service- USFS

All relative directions are abbreviated (ex.: north of Clarkesville as N. Clarkesville).

\textit{Pseudopolydesmus pinetorum}


\textbf{ARKANSAS}: Benton Co., Vough, 1M, X-13-1962, H. M. Bevel, (FSAC); Vough, 1F, XI-4-1960, H. M. Bevel, (FSAC); Logan Cave, 2M, I-27-1958, T. Barr, (FSAC); Siloam Springs, 1F, III-1-1955, (FSAC);
Arkadelphia, (Bollman, 1888). Columbia Co., Magnolia, 2M 3F, XI-26-
1961, R. Rogers, (FSAC). Dallas Co., E. of Princeton, 2M, VII-1-54,
N. B. Causey, (FSAC). Faulkner Co., Conway, 1F, XII-24-1952, M. A.
Jackson, (FSAC); Bridge on Warren Ck., Rt. 64, 1F, XI-18-1966, M.
Hite, (FSAC). Franklin Co., Spirit Ck. Drainage, Sec.7 R28W, T13N,
SM 8F 4J, XI-6-1958, J. R. Preston, (FSAC); Shores Lake Area, 1M 3F,
70, 13.3mi. E. jct US Rt. 70B, 1M 1F, VI-23-1983, C. P. Withrow,
(CFWC). Independence Co., Batesville, 1M 4F 22J, IX-X-1959, O. D.
Brown, (FSAC); 1.3mi. W. Cushman, vicinity Blowing Cave, 1M, III-5-
3-1954, N. B. Causey, (FSAC). Jackson Co., Elmo, 1M, IV-26-1952,
Kirkwood, (FSAC). *Lawrence Co., IM, IV-3-1937, K. P. Schmidt,
Causey, (FSAC); Huntsville, 1F, V-19-1962, C. Caby, (FSAC); Withrow
Co., 10mi. NW. Langley, AR at Albert, 1M 1F, 1979, H. W. Robinson,
(NCMH); 1M, VIII-25-1950, N. B. Causey, (FSAC). Nevada Co., Jackson
Township, 2M 1F, XII-30-1954, R. Delaney, (FSAC). Newton Co., SR.
59, 2.5mi. S. Harrison, 2F 1J, VI-22-1983, C. P. Withrow, (CFWC); US
Rt. 74, 12.0mi. E. jct SR. 21, 1M 1F, VI-22-1983, C. P. Withrow,
(CFWC); Glenwood, 3M, I-8-1954, N. B. Causey, (FSAC); 1M, VIII-25-
1950, N. B. Causey, (FSAC). North Crawford Co., 0.75mi. S. No. 12
Rich Mts., 1F, Redman, (FSAC); Murfreesboro, 1M, IV-15-1953, W. S.
Carter, (FSAC); Bear Ck., IV-13-1953, 1M, N. B. Causey, (FSAC). Polk
Co., SR. 88, 1.0mi. W. Queen Wilhelmina S. P., 2M 1F, VI-20-1983, C.
mi. E. Woldrove, 1J, IV-4-1961, D. Combs, (FSAC). Searcy Co., 1M,
VIII-24-1950, N. B. Causey, (FSAC); *cave, (Youngsteadt &
Causey, (FSAC). Washington Co., Cove Ck. Valley, 4M 4F, IX-1-
1956, M. Hite, (NCMH); 1M 1J, XII-1958, G. Ogden, (FSAC);
Habberton, 3M, IV-4-1953, B. Johnson, (FSAC); Fayetteville, 1M, X-
30-1962, F. Clayton, (FSAC); Fayetteville, Mt. Kessler, 1F, V-4-
1955, (FSAC); Cove Ck. Valley, IM 3J, 1st week II-1955, Mr. & Mrs.
O. Hite, (FSAC); 7M 14F, Spring 1956, (FSAC); 1M 1J, XII-1958, G.
Ogden, (FSAC); Clear Ck., 1F, II-14-1955, Hastings, (FSAC). *Caves,
(McDaniel & Smith, 1976).

ILLINOIS: Champaign Co., SR. 49, 3.8mi. S. Ogden at US Rt.
Randolph Co., btwn Modoc and Roots, 1M, IV-14-1936, K. P. Schmidt,
(USNM), holotype of Polydesmus modocus. Tazewell Co., US Rt. 74,
13.6mi. E. SR. 121, rest area, 1M 1F, VI-14-1983, C. P. Withrow,

IOWA: Appanoose Co., jct SR. T30 & SR. 5, 4M 2F, C. P.
Withrow, (CFWC).


Pseudopolydesmus tallulanus


Pseudopolydesmus erasus

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Pseudopolydesmus canadensis

**CANADA**


ONTARIO: Hudson's Bay, Albany River, 1F, (BMNH), holotype of Polydesmus canadensis; Capreol, 1F, V-10-1964, A. Nimmo, (RLHC).

**UNITED STATES**


Knight, (RIHC); Vesuvius Table Rock, 4M, VIII-13-1954, M. Caskie, (RIHC).

Pseudopolydesmus collinus


**Pseudopolydesmus serratus**

**CANADA**


QUEBEC: *Gaspe Peninsula, 1M, 1883, R. Wells, (Chamberlin, 1920a); *Ottawa, 6 specimens (Chamberlin, 1920a); *Ottawa and Chelsea, 1918, F. Johansen, (Chamberlin, 1920a).

**UNITED STATES**


MASSACHUSETTS: Middlesex Co., MCZ Reserve nr Bedford, 1M 1F, X-6-1968, W. A. Shear, (WASC).

MICHIGAN: *Lake Douglas, University of Michigan Biological Station, VII/VIII-1913, G. F. Sutherland, (Chamberlin, 1914).


MISSOURI: Franklin Co., 3mi. ESE. Sullivan, Camp Cave, 1M, V-


SOUTH CAROLINA: Richland Co., Pocahontas, 2M 1F 1J, Spring 1963, Simpkins, (RIHC).


VIRGINIA: Albemarle Co., Charlottesville, 1M 2F, V-22-1947, R. L. Hoffman (RIHC); 1F, V-3-1960, (FSAC); Sugar Hollow, 1948, 2M, (RIHC); Saddle Hollow, 1M 1F, III-1948, (RIHC); Scottsville, 10M 1F,


*Pseudopolydesmus paludicola*


*Pseudopolydesmus caddo*


*Pseudopolydesmus minor*


No Data: 1M, (FSAC).
OTHER SPECIMENS EXAMINED


Other localities for *Speodesmus echinurus* as determined by Elliott (1976)
Texas: Bandera Co., Station "C" Cave No. 1; Haby Swallow Cave; Fossil Cave; Haby Water Cave; Fog Fissure; Reese Cave; Garrison Hilltop Cave; Sutherland Hollow Cave; Medina Lake Sinkhole. Comal Co., Bad Weather Pit; Pair Hole; Dierk Cave; Honey Creek Cave; Bender's (Bartel's); Rittiman Cave; Voges Cave. Edwards Co., Wyatt Cave; Three Bounce Cave; Deep Cave. Hay Co., Boyett's Cave; Morton's Cave; Donaldson Cave; Boggs Cave; Wonder Cave; Ezell's Cave; Mccarty Cave. Kendall Co., Kohl Ranch Cave No. 1; Behr's Cave; Pfeiffer Crawley Cave; 474 Cave; Victor Phillips Water Cave; Schneider Ranch Cave; Century Caverns (Cave-Without-A-Name); Cricket Cave; Skunk X Water Cave; Cascade Caverns. Kerr Co., Pinto Ranch Cave; Stormers Cave; Mingus Root Cave; Seven Room Cave; Smith Cave. Mason Co., Koethmann Cave. Medina Co., Davenport Cave; Sixty Minute Cave. Sutton Co., Felton Cave; Harrison Cave. Uvalde Co., Tampke Cave; McNair Cave; Dripstone Cave; Story Cave; Cedar Brake Cave. Val Verde Co., Twin Tree Cave. Edwards Co., Jacoby Cave; Devil's Sinkhole; Vance Cave. Manard Co., Powell's Cave; Nell Cave. Real Co., Pape (Bradford Cave); Skeleton Cave; Orell Crevise Cave; Tucker Hollow Cave; Section 6 Cave; Haby Cave (Cave of the Lakes); Emmett Wilson Cave.

*Speodesmus* #1, new species, as determined by Elliott (1976)

Texas: Hays Co., Halifax Bat Cave; Travis Co., Pipelane Cave; Goat Cave; Beckett's Cave; Pennie's Cave; Cave X.


Other localities for *Speodesmus* bicornurus as determined by Elliott (1976)

Texas: Lampasas Co., Jackson One-Bat Cave. Travis Co., Ireland's Cave; Beckett's Cave; Cave X; Aimans' Cave; Cave Y; Lost Gold Cave; Broken Straw Cave; Bee Creek Cave; Bandit Cave; Tooth Cave; McNeil Bat Cave; Dead Dog Cave No. 1; Dead Dog Cave No. 2; Cotterall Cave; Jack's Joint; Kretschmarr Cave; Lunsford Cave; Schulze Cave. Williamson Co., Great Mud Cave; Four Corners Cave; Circle Cave; Man-With-A-Spear Cave; Bone Cave; Steam Cave; Inner Space Cave (laubach Cave); Three Mile Cave; Williams Cave; Bat Well; Cobb Cavern.

*Speodesmus* #2, new species, as determined by Elliott (1976).

Texas: Bexar Co., Government Canyon Bat Cave; Helotes Hilltop Cave; Adam Wilson's Cave. Medina Co., Surprise Cave; Goat Cave.

*Speodesmus* #3, new species, as determined by Elliott (1976).
Specodesmus #4, new species, as determined by Elliott (1976).

Texas: Val Verde Co., Fern Cave.


Utadesmus henriensis (Chamberlin, 1930) Utah: Henry Mountains, Mount Ellen, 1M, holotype, TX-1929, R. V. Chamberlin, (USNM).


The revision of the genus *Pseudopolydesmus* and its relationships to other North American polydesmids first required the examination of the higher taxa in the family. It was determined that the sister group of the Polydesmidae is the family Doratodesmidae from Southeast Asia. A cladistic analysis, based on 65 characters, was performed. Four subfamilies are proposed for the Family Polydesmidae: Mastigonodesminae Attems, 1914, Scytonotinae new status, Polydesminae new status, and Epanerchodinae new status. The Mastigonodesminae consists of 2 genera and is limited to the western rim of the Mediterranean; the Scytonotinae consists of 7 genera and is primarily western Nearctic in distribution; Polydesminae, with approximately 11 genera and Holarctic; and Epanerchodinae with one large heteromorphic genus located in eastern Asia, primarily Japan.

The North American genera of the subfamily Scytonotinae are: *Speodesmus* Loomis, 1939, consisting of 7 troglobitic species located in westcentral Texas; *Scytonotus* Koch, 1847, consisting of 11 species from eastern and northwestern North America; *Utadesmus* Chamberlin and Hoffman, 1950, with 2 species from New Mexico and Utah; *Bidentogen* Buckett & Gardner, 1968, consisting of 2 species from central California; *Coronodesmus* new genus, with 3 species from coastal California; *Speorthus* Chamberlin, 1952, with 1 troglobitic species from western Texas and New Mexico; *Idahodesmus* new genus and new species, *I. dentatus*, from northern Idaho.

The native fauna of the subfamily Polydesminae is represented by the genus *Pseudopolydesmus*. A cladistic analysis based on 36 characters, divided the genus into two groups: *canadensis*, including the species *pinetorum* (Bollman, 1888), and two two-species complexes *tallulanus* (Chamberlin, 1943)–*erasus* (Loomis, 1943) and *canadensis* (Newport, 1844)–*collinus* Hoffman, 1974, group serratus, including *serratus* (Say, 1921), *paludicola* Hoffman, 1950, *minor* (Bollman, 1888), and *caddo* Chamberlin, 1949. Twenty-one new synonyms in the genus *Pseudopolydesmus* are recognized.