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# Taxonomic synthesis of the eastern North American millipede genus *Pseudopolydesmus* (Diplopoda: Polydesmida: Polydesmidae), utilizing high-detail ultraviolet fluorescence imaging

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The species of the eastern North American millipede genus *Pseudopolydesmus* are reviewed. Synonyms and comprehensive literature citations are provided for each of the eight recognized species. Diagnostic morphology of the genus, including clarification of male gonopod terminology, is reviewed and defined using scanning electron microscopy and high-quality macrophotographic images, including those in which ultraviolet fluorescence was induced to produce detailed images of morphological structures. Based on the examination of available type material, the following eight species are recognized: (1) *Pseudopolydesmus erasus*; (2) *Pseudopolydesmus canadensis*; (3) *Pseudopolydesmus collinus*; (4) *Pseudopolydesmus pinetorum*; (5) *Pseudopolydesmus minor*; (6) *Pseudopolydesmus caddo*; (7) *Pseudopolydesmus paludicolus*; and (8) *Pseudopolydesmus serratus*. The species names *Polydesmus neoterus* and *Polydesmus euthetus* are here placed as junior subjective synonyms of *Ps. minor* (both **syn. nov.**), and *Polydesmus natchitoches* is placed as a junior subjective synonym of *Ps. pinetorum* (**syn. nov.**).

ADDITIONAL KEYWORDS: anatomy, morphological systematics – ecology – genus revision – taxonomy, biodiversity – taxonomy, genitalia.

## INTRODUCTION

The millipede genus *Polydesmus* Latreille, 1802 is among the first of five described genera of the Diplopoda. It is the name-bearing genus of the family Polydesmidae Leach, 1815, which itself occupies most of the temperate Holarctic region, excluding Central Asia and Mongolia (Golovatch, 1991). Since its first description, the genus has accrued ~480 specific names, of which > 250 remain placed in that genus. The other species have been moved to other genera and families or are of uncertain status (Sierwald, 2018). Polydesmidae continues to need revision despite its 200-year-old usage and the recent acceleration of species description within it, particularly of cave taxa from East Asia (e.g. Golovatch & Geoffroy, 2006; Golovatch, 2013). Although some initial efforts have been made (Withrow, 1988; Djursvoll *et al.*, 2000), a comprehensive phylogenetic analysis addressing genus-level relationships in Polydesmidae remains missing. According to Hoffman (1980): 'The Palearctic fauna of this family is in complete chaos [and] nothing short of an overall revision will bring any kind of order'. Shear (2012) characterizes the family as 'a meaningless wastebasket' in its current state.

This disorder in Polydesmidae makes it difficult to unambiguously define the Nearctic genus *Pseudopolydesmus* Attems, 1898 in reference to its Palaearctic relatives and to the genus *Polydesmus* in particular. The diversity of gonopodal structures (copulatory organs in males) and the lack of a

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standardized terminology based on explicit homology hypotheses among members of Polydesmidae hampers the comparison of taxa in it. For example, the pattern of seta-bearing dorsal blisters and gonopods of *Pseudopolydesmus* strongly resembles those of the Palaearctic species *Polydesmus inconstans* Latzel, 1883 and *Polydesmus complanatus* (Linnaeus, 1761). However, as it is dubious that all nominal members of *Polydesmus* are monophyletic, comparisons with other taxa in the present paper are restricted to these two species.

*Pseudopolydesmus* is one of seven (Shear & Reddell, 2017) currently recognized native North American genera of the family Polydesmidae, occupying most of eastern North America from eastern Texas north to southeastern Ontario and east to the Atlantic coast, excluding the Florida peninsula. They are common in forests throughout the eastern and central USA and are among the widest ranging of the North American millipede genera. These medium-sized millipedes (up to ~35 mm in length) are commonly encountered under leaf litter and detritus in mixed forests. Their coloration varies from pink to brick red to brown, and their shallowly raised dorsal blisters give them the flat-backed appearance typical of other millipedes in the order Polydesmida (Figs 1, 2).

A total of 32 species names have been described in or assigned to *Pseudopolydesmus* at various times over the past century. The genus was revised by Withrow (1988) in an unpublished Ph.D. thesis. Withrow recognized nine species in two species groups and suggested several synonymies. Hoffman (1999), in his checklist of North American millipedes, recognized 12 *Pseudopolydesmus* species and introduced a number of new synonymies, differing partly from those by Withrow. Hoffman emphasized that confirmation of these taxonomic changes was needed. This ubiquitous millipede taxon, widespread in North American forests, is clearly in need of a taxonomic synthesis as a context for the description of biodiversity and as a basis for a biologically informative classification.

Our analysis of gonopodal and somatic characters was enhanced by inducing ultraviolet (UV) fluorescence in the cuticle of specimens. UV fluorescence images can provide additional information about seta distribution and cuticular structures. In particular, the translucent cuticle of *Pseudopolydesmus* gonopods makes some processes and flanges difficult to distinguish using white light. Induced fluorescence of the cuticle or integument has also been documented in numerous orders of centipedes, arachnids, insects and crustaceans (Lawrence, 1954; Rubin *et al.*, 2017; Welch *et al.*, 2012). Therefore, we believe our methods can easily be adapted for imaging a broad range of arthropod taxa.

For the review of the genus we provide here, we examined all available type material and imaged specimens using various macrophotographic techniques, including the use of UV fluorescence of the cuticle to provide false-colour images with enhanced detail. We also used scanning electron microscopy (SEM) to provide high-detail images. Gonopod structures are illustrated and annotated using explicitly defined terminology. We recognize eight species and provide complete literature citations and synonymy lists for the taxa in the genus.


**Figure 1.** Two live examples of *Pseudopolydesmus*. A, *Pseudopolydesmus serratus*, live adult male, dorsal view (VTEC MPE01173). B, *Pseudopolydesmus paludicolus*, live adult female, dorsal view (VTEC MPE01167).

## MATERIAL AND METHODS

### Field-collected material

Material for this study comprised specimens borrowed from natural history museums and individuals that were recently field collected using the methods described by Means *et al.* (2015). The live collected specimens were collected under permit from the Virginia Department of Game and Inland Fisheries (VADGIF), permit no. 056958. Field-collected *Pseudopolydesmus* individuals were typically uncovered in forests with decomposing logs and moist layers of leaf litter covering the soil, although individuals were also found in swamps and dry forests. Leaf litter was turned over with a millipede rake or a small three-pronged garden cultivator, and logs and rocks were flipped to uncover millipedes. *Pseudopolydesmus* were found most often at the soil–leaf litter interface, but were sometimes also found clinging to the bark underneath logs or between matted leaves at the edges of swamps.


**Figure 2.** *Pseudopolydesmus erasus*, adult male habitus, lateral view (FMNH INS3120685).

### LIGHT MICROSCOPY AND ULTRAVIOLET IMAGING

High depth of field (HDOF) photographs of gonopods and somatic characters were obtained using visible and UV light. UV-induced fluorescence photography was adapted for focus-stacking photographic methods and equipment. Owing to the small size and pale, uniform colour of the preserved material, some morphological features were difficult to see in visible light photographs. Under UV light, we found that setae, claws, teeth, gonopods and vulvae emitted a green fluorescence, which provided high contrast to the blue fluorescence of the rest of the animal, thereby highlighting many details not seen in visible light photographs (Marek, 2017).

UV-induced fluorescent imaging of *Pseudopolydesmus paludicolus* (gonopod images) and *Pseudopolydesmus collinus* (gonopod and tergite images) was carried out according to methods already described by Marek (2017). All other HDOF and UV-induced fluorescence imaging was carried out in the Collaborative Invertebrate Laboratories at the Field Museum, using the following techniques. To obtain HDOF photographs, we used a focus-stacking technique with a Microptics system equipped with a Nikon D5100 DSLR camera body, outfitted with an Infinity Photo-Optical K2 Long-Distance Microscope system and a variety of Infinity Photo-Optical objectives: CF2, CF3, CF4, 5× Achrovid and 10× Achrovid (Visionary Digital/Dun, Inc., Ashland, VA, USA; Infinity Photo-Optical, Boulder, CO, USA).

Specimens were secured in a 50 mm glass Petri dish, embedded in a drop of clear hand sanitizer and covered with 70% alcohol. A stage with a magnetic lock (Visionary Digital/Dunn, Inc.) mounted on a steel base plate was used to control vibration and prevent blurring in the images at higher magnifications, particularly under UV lighting. A Pyrex dish (no. 3140) was used as a pedestal on top of the stage. This allowed for some under-lighting of the specimens during visible light photography, which helped to add additional light at high magnification. A black card was used for the background to contrast with the colour of the specimens. CamLift v.2.6.0 (Visionary Digital/Dun, Inc.) was used to control the motorized lift of the system. Control My Nikon v.4.3 was used to control the camera and set shutter, aperture and other settings.

Visible light photographs were taken using a Microptics ML-1000 Flash Fiber Optic Illumination System (Visionary Digital/Dun, Inc.) connected to a Dynalite M2000DR Power Pack (Dynalite, Union, NJ, USA). Dynalite output settings varied from 250 W/s for lower magnification to 1000 W/s for higher magnification. The K2 aperture was set to 4, providing high depth of field, but reducing resolution and increasing vignetting in the images. Cylindrical diffusers were constructed from white copy-machine paper to mitigate glare. The camera was set to ISO 100 with a shutter speed of 1/200 and auto white balance.

UV illumination was from three Convoy S2+ Nichia 365 nm LED flashlights (Shenzhen Convoy Electronics Co., Ltd., China) that contain a Nichia NCSU276A U365 UV LED emitter (Nichia Corporation, Tokushima, Japan), with a peak emission spectrum of 365 nm. The lights were held in place with test-tube clamp laboratory stands and arranged radially around the stage at a distance of ~10 cm from the specimen, shining straight down to ensure that there was no glass between the light source and the specimen. No diffuser was used for UV photography. It is important to note that UV-blocking eye goggles and sun screen should be used, because the UV light will burn the eyes and skin. A hood constructed of heavy black canvas was used to block ambient light. The K2 aperture was set to 6 for UV photography. The camera was set to ISO 100 with a variable shutter speed (from 0.33 to 2 s) and auto white balance. All photographs were saved in TIFF format.

Focal stacks were imported into Adobe Lightroom v.5.7. Each finished composited photograph consisted of between ten (low magnification) and 50 (high magnification) individual photos. Visible light stacks were subjected to a 20-increment addition of luminance to decrease noise. Varying degrees of vignetting compensation and minor exposure compensation were implemented if necessary. The UV stacks were subjected to a temperature adjustment to 10,000 K to render more clarity and detail. If necessary, UV stacks

were subjected to minor exposure compensation and a 20-increment addition of luminance to decrease noise.

Helicon Focus Pro v.6.7.1 was used to create the composite photographs taken at different focal planes. For both UV and visible light photographs, the preferred rendering method was Method C (pyramid) at full resolution [for the images of *Ps. collinus* and *Ps. paludicolus*, Method B (weighted average) was used]. The composited images were saved in uncompressed TIFF format. Adobe Photoshop CS6 was used to despeckle and clean the background. High-pass filters were used to adjust white balance: 2.0–3.0 high pass for visible light and 5.0–6.0 high pass for UV. Scale bars were inserted before cropping and saving the final images.

### Scanning electron microscopy

Scanning electron micrographs were obtained with a Leo SEM (Carl Zeiss SMT, Peabody, MA, USA). Initially, samples were ultrasonically cleaned and dehydrated in an ethanol series (80, 90 and 95% and two times in 100%) and then air-dried overnight. The specimens were mounted on aluminium stubs and coated with gold in a sputter coater for 240 s. Adobe Photoshop CS6 was used to clean image backgrounds, and a 2.0–3.0 high-pass filter was applied to adjust the white balance of the images.

### Institutional abbreviations

ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; BMNH, Natural History Museum (British Museum of Natural History), London; FMNH, Field Museum of Natural History, Chicago, IL, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MHNG, Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; VMNH, Virginia Museum of Natural History, Martinsville, VA, USA; VTEC, Virginia Polytechnic Institute Insect Collection, Blacksburg, VA, USA.

Specimen catalogue numbers are accompanied by institutional and collection abbreviations as follows: FMNH INS, Field Museum Division of Insects; VMNH PSE, Virginia Museum of Natural History *Pseudopolydesmus* specimens; VTEC MPE, Virginia Tech Insect Collection millipede specimens.

## RESULTS

### Taxonomic history of the genus *Pseudopolydesmus*

Beginning with Thomas Say's (1821) description of *Pseudopolydesmus serratus*, 32 species names have been associated with the genus *Pseudopolydesmus*. Described variously in the genera *Polydesmus*, *Pseudopolydesmus* and *Dixidesmus* Chamberlin, 1943, many of these species names have proved redundant. Loomis & Hoffman (1948), Causey (1952) and Shelley (1988) all published species-level synonymies correcting many of the redundancies in their comparisons of various species of *Pseudopolydesmus*. These synonymies often addressed species names originally based on minute variations in gonopod morphology. In some cases, the original author might have viewed a gonopod from different angles, causing them erroneously to designate new species (Withrow, 1988: 4). Chamberlin alone named 18 species between 1942 and 1951, 13 of which have been previously synonymized. Here, we synonymize four of the remaining five.

The first two species of *Pseudopolydesmus* described, incidentally two of the most widespread and commonly collected ones, were placed in the genus *Polydesmus* in the early 1800s. *Pseudopolydesmus serratus* (Say, 1821) was found by the American entomologist Thomas Say while collecting on the eastern shore of Virginia. The second species, *Pseudopolydesmus canadensis* (Newport, 1844), was supposedly collected from the Hudson Bay area in Ontario, Canada, although the type locality has been contested (Hoffman, 1999). There has been some confusion surrounding these two names. Many early authors (as late as Attems, 1940) published descriptions and gonopod illustrations of *Ps. canadensis* that more closely match *Ps. serratus*, leading Bollman (1887b) mistakenly to refer to *Ps. canadensis* as a junior synonym of *Ps. serratus* and create the species name *Polydesmus branneri* for it instead. Consequently, *Ps. canadensis* is instead often referred to as *Po. branneri*, *Pseudopolydesmus branneri* or *Dixidesmus branneri* in late 19th and early 20th century literature.

Attems (1898) established the genus *Pseudopolydesmus* with the type species *Ps. canadensis*, thereby separating the North American species from the Eurasian genus *Polydesmus*. The definition of *Pseudopolydesmus* was erroneously based on Attems' conclusion that the gonopod of *Ps. canadensis* lacks a seminal chamber and a pulvillus ('*Samenblase*' and '*Haarpolster*' respectively, in Attems, 1940: 3), in contrast to the gonopods of the family Polydesmidae as then understood. Attems (1914) then placed *Pseudopolydesmus* in the new family Vanhoeffeniidae, which was also defined by its lack of both a seminal chamber and pulvillus. Neither Brölemann (1916) nor Verhoeff (1929) subsequently recognized Vanhoeffeniidae (see also Jeekel, 1965: 236). Verhoeff (1931) later examined freshly preserved *Pseudopolydesmus* specimens (most

probably *Ps. serratus*), from which he described both an unusually large seminal chamber and a well-developed pulvillus. Verhoeff (1931: 308) thus concluded that poor preservation of Attems' *Pseudopolydesmus* specimens had resulted in the decision to place *Pseudopolydesmus* in the new family.

Later, Chamberlin (1943c) erected the genus *Dixidesmus* for members of *Pseudopolydesmus* whose gonopod telopodites feature an elongate process distal to the pulvillus and a recurved ectal process. *Dixidesmus* roughly corresponds to Withrow's (1988) *Ps. canadensis* species group (see next paragraph). Hoffman (1974) homologized these processes as *e1* and *e2*, respectively, and pointed out that although the telopodite of *Ps. collinus* has a recurved *e2* process like *Dixidesmus*, it lacks an elongate *e1*. He therefore synonymized *Dixidesmus* as a junior synonym of *Pseudopolydesmus*.

Withrow (1988) recognized nine species in two groups: the *Ps. canadensis* group comprising *Pseudopolydesmus pinetorum*, *Pseudopolydesmus tallulanus*, *Pseudopolydesmus erasus*, *Ps. canadensis* and *Ps. collinus*; and the *Ps. serratus* group comprising *Ps. serratus*, *Pseudopolydesmus minor*, *Pseudopolydesmus caddo* and *Pseudopolydesmus paludicola* [sic]. Withrow also suggested 17 new synonymies. Hoffman, in his checklist (Hoffman, 1999), recognized 12 *Pseudopolydesmus* species and implemented 15 new synonymies. Hoffman emphasized that he did not examine type specimens, basing his classification solely on material conserved in the Virginia Museum of Natural History. Some of his accepted species names differ from those of Withrow (1988), who did examine type material. However, Withrow's dissertation is not considered published under the International Code of Zoological Nomenclature (ICZN, 1999: Article 9.12), because it is a facsimile printed on demand (see discussion by Shelley, 1996). Therefore, those of Withrow's subjective species name synonymies that we affirm are considered new synonymies as of this publication. In our taxonomic section, we use square brackets to indicate Withrow's invalid taxonomic assignments.

## Gonopod terminology in *Pseudopolydesmus*

In the order Polydesmida, the anterior leg pair of the seventh body ring (eighth leg pair) in males is modified into a pair of sperm transfer organs called gonopods. The ninth leg pair remains as normal walking legs. Attems (1894) was the first to define separate sections in the gonopods and discussed possible homologies with leg podomeres. The putative associations of leg podomeres with parts of the male gonopod have shifted over time owing to the difficulty in assigning homology to the podomeres distal from the coxa, resulting in several terms that have multiple precise definitions.

Moreover, gonopod terminology varies in the family Polydesmidae between genera and among different authors (as discussed by Hoffman, 1974). Eurasian polydesmids often have comparably more complex gonopods, with additional processes and branches in comparison to American representatives. These branches and processes have often been assigned names across various genera without discussing hypotheses of homology. As a result, the names for these structures have proliferated wildly, and the existing nomenclature for the gonopods is unwieldy. Various schemes of alphanumerical labelling of gonopod processes have been adopted more-or-less de novo for each newly discovered form. This has made descriptions of similar taxa difficult to compare and discerning homology between genera challenging (e.g. Djursvoll *et al.*, 2000; Djursvoll, 2008; Golovatch, 2013).

Regarding the North American Polydesmidae, the presence of fewer species and simpler gonopod morphology have resulted in a more uniform set of terms, but there are still cases in which identical terms refer to different structures. For example, Shelley (1993: figs 5, 6) used the term endomerite for the entire caudal branch carrying the pulvillus (see Fig. 3) in *Scytonotus*, whereas Hoffman (1950: fig. 4; Hoffman, 1974: 349) used the term for only the pulvillus in *Pseudopolydesmus*. Djursvoll *et al.* (2000) used the descriptive term pulvillus ('*Haarpolster*' of Attems, 1940) instead of endomerite.

The *Pseudopolydesmus* gonopod consists of a moveable telopodite with a single distal branch (acropodite) subtended by a large coxa and cannula typical of Polydesmida. Verhoeff (1931) recognized three sections of the telopodite: the basal prefemoral region carrying setae, the femoral region lacking setae and the terminal region that he called the tibiotarsus. We emphasize caution when using these terms, because they imply false homologies with podomeres of the walking legs (Petit, 1976). The sperm groove (or seminal canal) originates at the medial insertion of the cannula in the basal 'prefemur', then runs distad while twisting around cephalically to the ectal (lateral) side of the 'femoral' section, then curving caudad before opening at the base of the pulvillus ('*Haarpolster*' of Attems, 1940, and Verhoeff, 1931; 'endomerite' of Hoffman, 1974, and others). The functional morphology of the 'large seminal chamber' and its relationship, if any, with the sperm groove is uncertain and deserves further anatomical study (see Verhoeff, 1928, 1931; Carl, 1941).

In his paper describing *Ps. collinus*, Hoffman (1974) introduced a standardized system for denoting the processes along the distal region of the acropodite,

accompanied by a detailed drawing (see Fig. 3, after Hoffman, 1974). He designated processes on the ectal side of the gonopod *e1–e4*, and those on the medial (mesal) side *m1–m4*, enabling comparison between species. Shelley & Snyder (2012: figs 2, 3) and Withrow (1988) adopted Hoffman's system, which currently provides a standardized method for denoting the processes and to differentiate species of *Pseudopolydesmus*.

Withrow (1988) applied Hoffman's system to each of his recognized species. However, he applied it inconsistently in his re-descriptions, key to *Pseudopolydesmus* species, and character matrix for phylogenetic analysis. For example, in step 1a of his key to species, Withrow identified the *Ps. canadensis* group by the presence of process *e3* and the absence of *m2*. However, in contradiction, step 3a identified *Ps. erasus* and *Ps. tallulanus* (both members of the *Ps. canadensis* group according to Withrow) by the presence of *m2*, whereas step 4a identified *Ps. erasus* by the absence of *e3*. Furthermore, his illustrations of gonopods did not show the characters cited for species identification unambiguously, nor are the structures labelled.

Under Hoffman's (1974) system, hypotheses of homology for acropodite processes are based on: (1) position, and (2) to a lesser degree, on special similarity (Remane, 1952). For example, a medial process between *m2* and *m4* must be labelled *m3* based on position, whereas *m4* is recognized by a tuft of special bristles that do not arise from sockets as setae, but project continuously from the cuticle. Such bristles are also located at the apical tip of the telopodite. Uncertainty concerning homology arises for processes *m2*, *m3*, *e2* and *e3* in species where one or more of these acropodite processes are absent. Owing to its unique position, offset ectad from the edge of the telopodite, we hypothesize that *m3* is present only in *Ps. canadensis* and that the intermediate medial process in *Ps. caddo* and *Ps. serratus* is homologous with *m2*. We describe position and special similarity of each process in Table 1, and in Table 2 we summarize which processes occur in each species of *Pseudopolydesmus*.

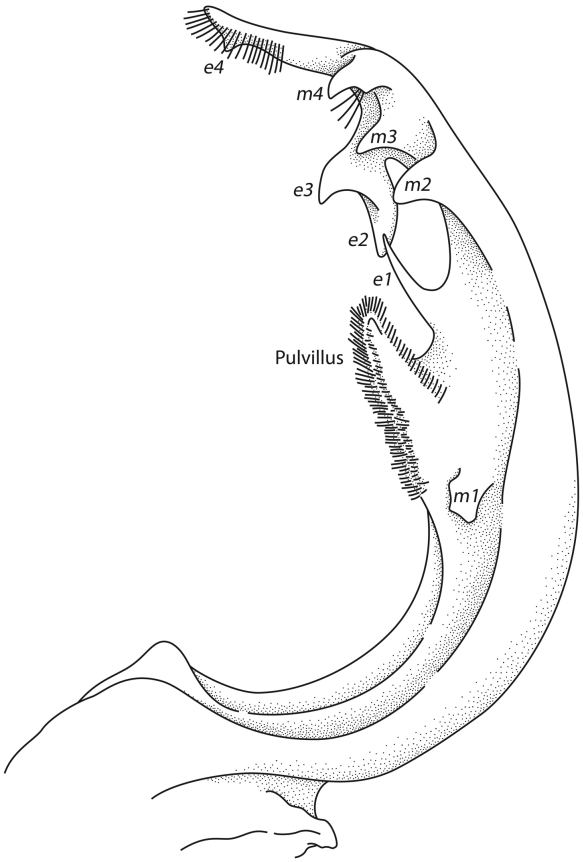


**Figure 3.** Schematic diagram of right gonopod telopodite of *Pseudopolydesmus canadensis*, medial view. Ectal processes labelled *e1, e2, e3,* and *e4.* Medial processes labelled *m1, m2, m3,* and *m4*. After R.L. Hoffman, 1974 (fig. 3).

### Tergal sculpture pattern

Members of the family Polydesmidae possess groups of elevated tergal blisters of differing sizes and shapes. The descriptive terminology for these features has varied over time: '*Beule*' and '*Buckel*' (Attems, 1940), 'convex areas' (Hoffman, 1974) and 'convex bosses' (Withrow, 1988) or 'boss' (Nguyen, 2009: fig. 2). We opt for the term 'blisters'. Verhoeff noted the close similarity of the tergal sculpture pattern ('*Rückenskulptur*', Verhoeff, 1931: 308) between *Polydesmus* and *Pseudopolydesmus*. The blisters are arranged in transverse rows and are slightly to moderately inflated, appearing like a cobblestone road. The blisters are reasonably well circumscribed, and each typically carries a short seta on its most elevated surface or, in the posterior blister row, directed caudad from the posterior apex of the blister. In *Pseudopolydesmus*, these setae are very small and often difficult to distinguish even under SEM, except in posterior body rings or in small-bodied species, such as *Ps. paludicolus*.

In all *Pseudopolydesmus* species, the blisters are arranged in an identical pattern: three transverse rows of blisters on the metazonite, with a central and lateral blister on each paranotum (Fig. 4). The anterior row consists of two large, rectangular blisters (AB) that each bear two setae. The median row consists of four subquadrate blisters (MB1 and MB2) and the posterior row of six (PB1, PB2 and PB3). Blisters are numbered incrementally from medial to lateral. The posterior blister row is wider across the tergite than the median row, although the PB3 blisters may be very slight and not immediately obvious. Each paranotum has two blisters: one large, round, central blister (CB) bearing two setae and one longitudinally

**Table 1.** Summary of telopodite processes in *Pseudopolydesmus*

| | |
|---|---|
| *e1* | Thin spine arising on distal flange of pulvillus, present in *Ps. erasus* and *Ps. canadensis*, present but reduced in *Ps. collinus* |
| *e2* | Rather large, recurved spine, arising on combined stalk with *e3* in *Ps. canadensis* and *Ps. collinus*; forms transverse ridge to *m2* in *Ps. caddo* and *Ps. serratus* |
| *e3* | Medium-sized spine, arising at or close to base of *e2*, usually opposite to *m2* |
| *e4* | Small, most apical spine, usually hidden within tuft of terminal bristles |
| *m1* | Flat spine with broad base, spade to claw shaped, arising at or near proximal flange of pulvillus |
| *m2* | Medium to large spine, usually opposite to *e2* and *e3* |
| *m3* | Small to medium spine, in *Ps. canadensis* offset laterad from the medial edge towards the centre line of acropodite, in *Ps. paludicolus* pointed slightly medially |
| *m4* | Medium-sized spine, positioned proximal to *e4*, with a tuft comprising only a few bristles located at the proximal side of its base |

**Table 2.** Telopodite processes of *Pseudopolydesmus* species in key order

| Key ID | Species | *e1* | *e2* | *e3* | *e4* | *m1* | *m2* | *m3* | *m4* |
|---|---|---|---|---|---|---|---|---|---|
| 2a. | *Ps. erasus* | Yes | Yes | Yes* | Yes | Yes | Yes | – | Yes |
| 3a. | *Ps. canadensis* | Yes | Yes | Yes | Yes | Yes | Yes | Yes | Yes |
| 3b. | *Ps. collinus* | Yes† | Yes | Yes | Yes | Yes | Yes | – | Yes |
| 4a. | *Ps. pinetorum* | – | Yes | Yes | Yes | Yes | Yes | – | Yes |
| 6a. | *Ps. minor* | – | Yes† | –‡ | Yes | Yes | Yes | – | Yes |
| 6b. | *Ps. caddo* | – | – | Yes | – | Yes | Yes | – | Yes |
| 7a. | *Ps. paludicolus* | – | Yes | – | Yes | Yes | Yes | Yes | – |
| 7b. | *Ps. serratus* | – | Yes | – | Yes | Yes | Yes | – | – |

*Process *e3* was present in all specimens observed by the authors (*Ps. tallulanus* morphotype), but varies in size and may be absent in some specimens (*Ps. erasus* morphotype).
†Process is present, but owing to its small size may not be visible under dissecting microscope.
‡An ectal flange is present and might be homologous to process *e3*.

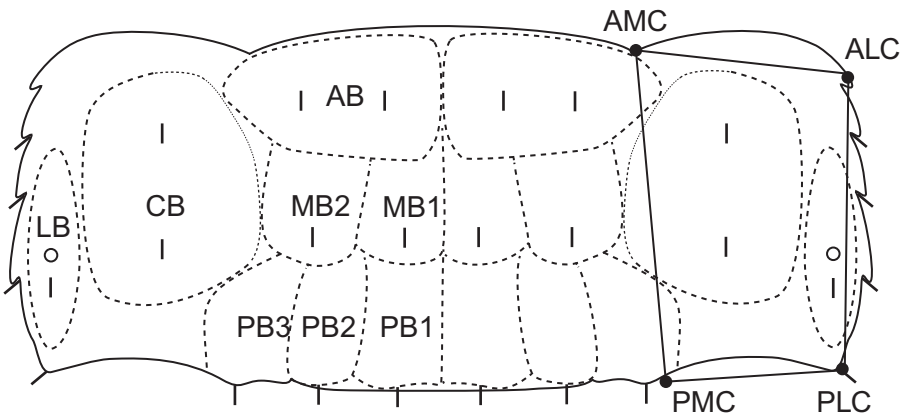


**Figure 4.** Schematic diagram of metatergite and ozopore bearing paranota of *Pseudopolydesmus*, dorsal view. **Blisters:** Anterior Blister (AB); Median Blister Row (MB1, MB2); Posterior Blister Row (PB1, PB2, PB3); Central Blister (CB); and Lateral Blister (LB). **Paranota Corners:** Anterior Medial Corner (AMC), at the medial terminus of the Paranota Leading Edge; Anterior Lateral Corner (ALC), at the anteriormost denticle; Posterior Lateral Corner (PLC), usually forms a natural point; Posterior Medial Corner (PMC), at the caudal apex of PB3. Short vertical and oblique lines represent positions of tergal setae and the small circles in each LB represent the ozopores.

elongated lateral blister (LB) carrying one seta near its posterior end. The paired LBs additionally bear the ozopores on ozoporous body rings.

In general, each blister carries one seta, although the ABs and CBs each carry two. However, a slight longitudinal furrow may sometimes be visible

separating the setae of each AB, suggesting that the ABs each represent two subquadrate blisters that have merged. Likewise, a very slight transverse furrow may sometimes separate the two setae of the CB, suggesting that the CBs represent a merging of blisters from the anterior and median rows.

### Paranota morphology

Several *Pseudopolydesmus* species can be distinguished easily by the shape and size of the paranota. This is especially useful in diagnosing adult females. We therefore introduce four landmarks in order to reduce paranota shape complexity to a simple quadrilateral (Fig. 4; described in Table 3). The anterior medial (AMC) and posterior medial (PMC) corners define the connection point of the paranota to the tergite, while the anterior lateral (ALC) and posterior lateral (PLC) corners delimit the outer edge of the paranota. Connecting these four points allows overall paranota dimensions to be described as a square, rectangular, trapezoidal, parallelogram shaped or rhomboid. The four edges of this quadrilateral are referred to in this paper as the anterior edge (between AMC and ALC), posterior edge (PMC to PLC), medial edge (AMC to PMC) and lateral edge (ALC to PLC).

Furthermore, to describe the silhouette of the paranota in addition to their overall dimensions, we use the terms leading margin, trailing margin and distal margin. Like the quadrilateral edges, the paranota margins connect two corners, but follow the shape of the real paranotum margin rather than using a straight-line path. In *Pseudopolydesmus*, the leading margin (AMC to ALC) and distal margin (ALC to PLC) are usually convex and the trailing margin (PLC to PMC) is concave.

The distal margin bears serrated denticles that occur in a predictable pattern. All non-ozoporous body rings bear three denticles along each paranotum, whereas ozoporous segments bear four denticles. In either case, all denticles bear one seta except the anteriormost denticle (ALC), which bears none. The posterior lateral corner (PLC) also bears a seta. Although the authors have occasionally observed specimens with, for example, an ozoporous paranotum that bears only three apparent denticles, or even one that bears five, these are infrequent exceptions to the rule.

**Table 3.** Definitions of paranotal landmarks

| | |
|---|---|
| AMC | Point of inflection between paranotum and tergite |
| ALC | Tip of anteriormost denticle |
| PLC | Acute caudal corner of paranotum |
| PMC | Caudal tip of posterior blister 3 (PB3) |

## TAXONOMY

### Order Polydesmida Leach, 1815

### Family Polydesmidae Leach, 1815

### Genus *Pseudopolydesmus* Attems, 1898

(Figs 1–8)

*Pseudopolydesmus* Attems, 1898: 270, 479. – Attems, 1914: 161. – Brölemann, 1916: 569. – Attems, 1926: 139. – Verhoeff, 1929: 619. – 1931: 305, figs 1–7. – Attems, 1940: 139, figs 201, 202. – Carl, 1941: 291, figs 1, 2. – Chamberlin, 1943c: 17. – Hoffman, 1950: 222, fig. 4. – 1974: 346 (= *Dixidesmus*). – [Withrow, 1988: 64.] – Hoffman, 1999: 442. – Djursvoll *et al.*, 2000: 40.

*Dixidesmus* Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 65.

*Type species: Polydesmus canadensis* Newport, 1844. By monotypy.

#### *Diagnosis*

*Body form:* Adult members of the genus *Pseudopolydesmus* always with 20 body rings including telson (never 19). Lateral corners of collum equal or exceed maximal width of mandibular stipites (narrower in *Polydesmus* and *Brachydesmus*, e.g. Djursvoll *et al.*, 2000: 43, fig. 2a), except in *Ps. paludicolus*. Colour of adults in life ranging from dark brick red (Fig. 1A) to light chestnut brown (Fig. 1B).

*Paranota and tergal sculpture:* Paranota mostly level, extending horizontally (Fig. 2). Leading margin flexed anterodorsad, forming a narrow rim. Tergal sculpture pattern (described above; Fig. 4) very similar to other members of Polydesmidae, such as *Po. inconstans* and *Po. complanatus*, the latter of which is the type species of *Polydesmus*. Tergal blister pattern in *Pseudopolydesmus* less distinct than the strongly impressed pattern of *Polydesmus*. Unlike *Po. inconstans* and *Po. complanatus*, tergal setae not usually visible under dissecting microscope except in *Ps. paludicolus*, but may be visible with UV enhancement.

*Gonopod:* Gonocoxae large, with two long setae at the ventromedial margin. Posterior margin of gonocoxa divided into ventral and dorsal plate-like lobes that partly surround the telopodite basally. Ventral lobe with one or two gonocoxal plates stacked dorsoventrally. Telopodite falcate. Seminal

KEY TO SPECIES OF *PSEUDOPOLYDESMUS* MALES

| | | | |
|---|---|---|---|
| 1 | a. | Large recurved *e2* process or fused recurved *e2*+*e3* process | 2 |
| | b. | *e2* not recurved | 4 |
| 2(1) | a. | Large recurved *e2* not fused with *e3* (Figs 10–12) | *Ps. erasus* |
| | b. | Fused *e2*+*e3* process (Fig. 7) | 3 |
| 3(2) | a. | *m3* process distolaterad of *m2*; *e1* elongate (Fig. 14) | *Ps. canadensis* |
| | b. | *m3* absent; *e1* absent or severely reduced (Fig. 16) | *Ps. collinus* |
| 4(1) | a. | *e3* large, spike-shaped; pulvillus large, rounded (Figs 18–20) | *Ps. pinetorum* |
| | b. | Ectal processes subtriangular or flanged; pulvillus pointed | 5 |
| 5(4) | a. | Ectal surface strongly flanged, *m4* process present | 6 |
| | b. | Ectal surface not flanged, with or without strongly flanged medial surface | 7 |
| 6(5) | a. | Ectal flange smooth; large triangular *m2* between flange and pulvillus (Figs 23–25) | *Ps. minor* |
| | b. | Ectal flange bearing *e3*; no process between flange and pulvillus (Figs 27–28) | *Ps. caddo* |
| 7(5) | a. | Strongly flanged medial surface bearing *m2* and *m3* (Figs 30–31) | *Ps. paludicolus* |
| | b. | Not flanged, with pronounced transverse ridge connecting *e2* and *m2* (Figs 8, 33) | *Ps. serratus* |

canal originating medially before looping laterad, debouching at ectal base of pulvillus. Pulvillus entirely covered in bristles (Fig. 3). Seminal chamber large, with an associated duct (duct of the telopodite gland according to Verhoeff, 1931). Acropodite bearing between four and eight dentate to laminar processes along its ectal and medial surfaces; subterminally bearing from about ten to 60 terminal bristles (Fig. 5A, not socketed like true setae) similar in appearance to a toothbrush; terminally bifurcating into small ectal and medial processes or laminae too small to distinguish under dissecting microscope (Fig. 5B).

*Somatic male characters:* Prefemora of all walking legs beginning with leg pair 3 (body ring 4) strongly swollen dorsad in *Pseudopolydesmus* males (Fig. 6A), much more than in *Polydesmus* males (Fig. 6C). Male sterna with prominent paired lobes or tubercles of various shapes between leg pairs of body rings 5, 6, 7 and 8 (Fig. 7), which carry stiff, peg-like setae, differing from the unmodified setae of the walking legs. Leg pair 3 (body ring 4) with a pair of low lobes in some species; leg pairs 4 and 5 (body ring 5) with prominent lobes; leg pair 6 (anterior legs of body ring 6) with strongly elongated tubercles; leg pair 7 with small tuft of peg-like setae; leg pair 9 (directly posterior to gonopods) with tubercles flattened into longitudinal ridges (Fig. 8); leg pair 10 (anterior leg pair of body ring 8) with prominent ventrad-directed tubercles. This is unlike male *Polydesmus*, in which tubercles of leg pairs 9 and 10 (the first two leg pairs directly posterior of the gonopods) are absent or very slight. In some species (e.g. in *Ps. erasus*) there is an additional pair of lobes at the base of leg pair 11.

The species entries that form the remainder of the taxonomic section are presented in the order they appear in the above key to species. Each species name is given a comprehensive bibliography of published literature, including its junior synonyms and instances in which the name was misapplied. Notes are provided on the disposition of type material for each nominal species. Type abbreviations are as follows: HT, holotype; PT, paratype(s); ST, syntype(s). Names of states in the USA and provinces of Canada are shortened to their standard two-letter postal abbreviations. Specimen numbers of millipedes pictured in this paper that are not part of a type series are notated in bold with an asterisk, e.g. **FMNH INS312685***.

### ***PSEUDOPOLYDESMUS ERASUS*** (LOOMIS, 1943)

(FIGS 9–12)

*Polydesmus erasus* Loomis, 1943: 406, fig. 17, pl. 1: fig. 5, ♂ HT (MCZ, non vidi).

*Dixidesmus erasus* – Chamberlin, 1943c: 18. – Causey, 1952: 7 (= *D. humilidens*). – Chamberlin & Hoffman, 1958: 66.

*Pseudopolydesmus erasus* – [Withrow, 1988: 84, figs 19, 84, 88, 92, 108, 113, 122–126, map 5, tables 9–11.] – Hoffman, 1999: 444 (= *D. tallulanus*; *D. penicillus*).

*Dixidesmus tallulanus* Chamberlin, 1943c: 19, fig. 34, ♂ HT (USNM, vidi). – Chamberlin & Hoffman, 1958: 67.

[*Pseudopolydesmus tallulanus* – Withrow, 1988: 79, figs 75, 83, 87, 91, 107, 112, 122–128, map 5, tables 9–11.]

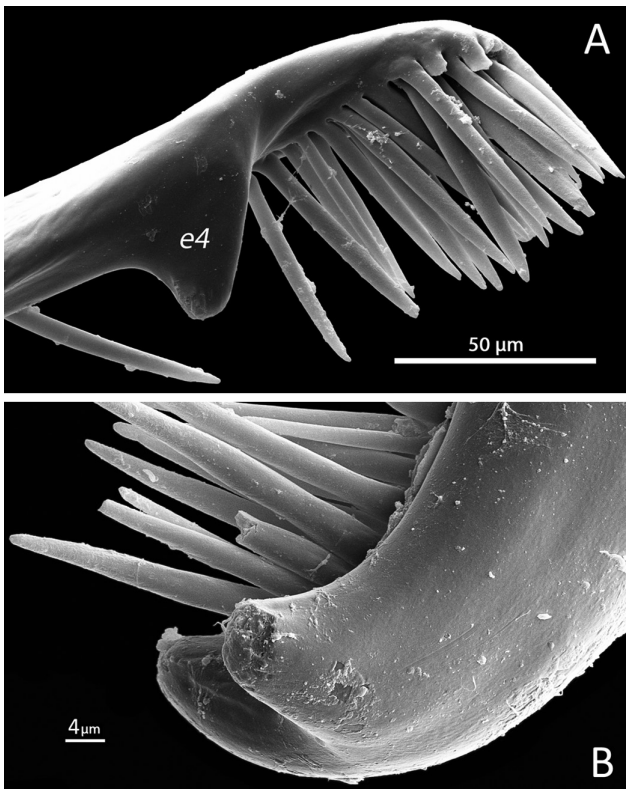


**Figure 5.** Features of the telopodite terminus in *Pseudopolydesmus* (scanning electron micrograph). A, terminal bristles in *Pseudopolydesmus canadensis* right gonopod, ectal view (FMNH INS6934). Unlike true setae, these bristles are not socketed at the base; instead, they project continuously from the cuticle of the telopodite. B, terminal bifurcation in *Pseudopolydesmus serratus* left gonopod, medial view (FMNH INS2819).

*Dixidesmus penicillus* Chamberlin, 1943c: 19, fig. 35, ♂/♀ ST (USNM, vidi). – Chamberlin & Hoffman, 1958: 67.
*Dixidesmus humilidens* Chamberlin, 1943c: 20, fig. 36, ♂/♀ ST (USNM, vidi).

### *Diagnosis*

*Size:* Large to medium-large, with length ranging from 15.8 to 31.8 mm and an average body length of 21.4 mm (*N* = 143; Withrow, 1988: 83, 88, 199). Size variable, comparable to *Ps. canadensis*, *Ps. collinus* and *Ps. serratus*. Usually larger than *Ps. pinetorum*.

*Paranota and tergal sculpture* (Fig. 9): Corners of paranota forming a trapezoid, with the anterior (AMC to ALC) edge longer than the posterior (PMC to PLC) edge. Ratio of anterior to posterior edge length smaller than in *Ps. serratus*. Leading and distal margins moderately curved, similar to *Ps. serratus* but less curved than *Ps. canadensis* and *Ps. collinus*. Denticles weak to obliterated. Trailing margin only slightly concave, nearly straight. Anterior blister row medially much thicker than median blister row, narrowing laterally to become much narrower than median blister row. Median blister 2 much larger in area than MB1. Median blister row thicker than posterior blister row. Central paranotal blisters occupying medial two-thirds of paranota. Lateral blisters anteriorly extending mediad.

*Gonopod* (Figs 10–12): Gonocoxa ventral lobe with single gonocoxal plate. Telopodite basally curved, more-or-less straight between pulvillus and process *m4*, terminally curved, basal half of acropodite distinctly thickened. Pulvillus large and pointed, midway between base and terminus of acropodite. Process *m3* absent. Process *e1* elongate and straight, arising from thickened area; *e2* large and recurved, originating close to base of *e3*; *e3* subtriangular, varies from large to miniscule; *e4* nearly identical to *m4* in size and shape (Figs 10A, 11A, 12A). Process *m1* conspicuous, medial of pulvillus; *m2* large, subtriangular; *m4* typically shaped, well separated from larger *m2* (Figs 10B, 11B, 12B).

### *Type notes*

*Polydesmus erasus (♂ HT and three ♀ PT, MCZ, non vidi):* From Monte Sano State Park, Madison Co., AL, USA, collected 22 July 1939. According to the description by Loomis (1943), the *e3* process is completely absent in *Ps. erasus*. No such specimen has been seen by the authors; it is more likely that Loomis overlooked the process or his specimen was damaged.

*Dixidesmus tallulanus (♂ HT and one ♂ PT, USNM, vidi):* ♂ HT from between Clayton and Tallulah Falls, Rabun Co., GA, USA, collected 28 April 1943; ♂ PT from Tallulah Falls, Habersham Co., GA, USA, collected 27 April 1943; both collected by W. Ivie. We found two type lots. Type lot 1: labelled 'HT', contains one fragmented male, with dissected gonopods in genitalia vial. Type lot 2: labelled 'PT', contains one intact male.

*Dixidesmus penicillus (11 ♂ and five ♀ ST, USNM, vidi):* Chamberlin (1943c) described an unspecified number of male and female specimens from north and northwest of Clarkesville, Habersham Co., GA, USA, collected 27 April 1943 by W. Ivie. We found two type lots. Type lot 1: labelled 'Types', contains two intact males, two fragmented females, and two small vials;

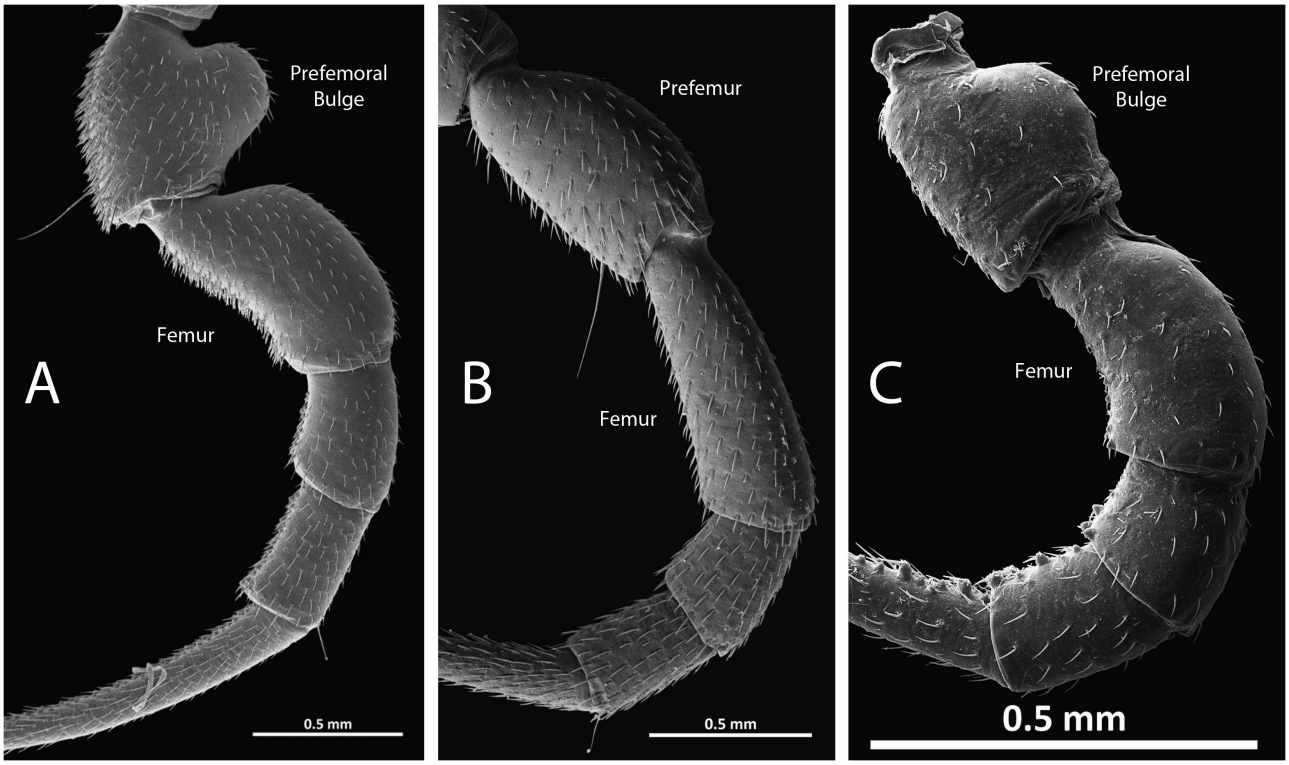


**Figure 6.** The characteristic prefemoral bulge in males of *Pseudopolydesmus*, and comparison of walking legs in *Pseudopolydesmus* and *Polydesmus* (scanning electron micrograph). A, adult male *Pseudopolydesmus erasus*, left leg 9, with characteristically large prefemoral bulge and thickened femur (FMNH INS3120685). B, adult female *Ps. erasus*, right leg 12, without prefemoral bulge (FMNH INS3120685). C, adult male *Polydesmus inconstans*, right leg 14, with slight prefemoral bulge and thickened femur (FMNH INS4265).

first small vial labelled 'HT' (by Withrow?), contains fragmented male, with dissected gonopods in genitalia vial; second small vial labelled 'Lectoallotype' (by Withrow?), contains fragmented female. Type lot 2: labelled 'Paratypes', contains two females and eight males, some males with gonopods damaged.

*Dixidesmus humilidens (two ♂ and two ♀ ST, USNM, vidi):* From Gainesville, Hall Co., GA, USA collected 24 April 1943 by W. Ivie. Type lot labelled '*erasus*' by Withrow. Contains one female, one fragment and two small vials; first small vial labelled 'Holotype' by Withrow, contains fragmented male, with dissected gonopods in genitalia vial; second small vial labelled 'Lectoallotype' by Withrow, contains intact female with everted vulvae.

### *Distribution*

Southern Appalachian Mountains, west through Tennessee and Kentucky into southern Illinois and south through Alabama to the coast of the Gulf of Mexico.

### *Additional specimens examined*

**FMNH INS**1554, 1556, 3120684, **3120685***.

## ***PSEUDOPOLYDESMUS CANADENSIS*** (NEWPORT, 1844)

(FIGS 7, 13–14)

*Polydesmus canadensis* Newport, 1844: 265, immature ♀ HT (BMNH, non vidi). – Gervais, 1847: 106. – de Saussure & Humbert, 1870: 52.

*Pseudopolydesmus canadensis* – [Withrow, 1988: 89, figs 55, 61, 70–73, 76, 109, 114, 122–126, map 6, tables 9–11.] – Hoffman, 1999: 443 (= *Po. glaucescens*; *Po. nitidus*; *Po. branneri*; *Po. echinogon*; *Po. conlatus*; *D. sylvicolens*; *D. christianus*; *D. catskillus*; *D. phanus*; *D. gausodicrorhachus*). – Shelley, 2000: 246.

*Polydesmus glaucescens* C. L. Koch, 1847: 133, types unknown. – Koch, 1863a: 59, pl. 26: fig. 51.

*Pseudopolydesmus glaucescens* – Attems, 1940: 141, uncertain placement.

*Polydesmus nitidus* Bollman, 1887a: 45, ♂/♀ ST (not located at USNM, non vidi).

*Dixidesmus nitidus* – Chamberlin & Hoffman, 1958: 67.


**Figure 7.** Sternal tubercles in male *Pseudopolydesmus canadensis*, ventral view, body rings 4–8 (FMNH INS6934, ultraviolet enhancement). Visible body rings (BR4–8) and their corresponding leg pairs (LP3–11) and gonopods (GPs) are labelled. Also note the characteristic silhouette of the gonopods of *Ps. canadensis*, with processes *e2* and *e3* sharing a narrow stalk.

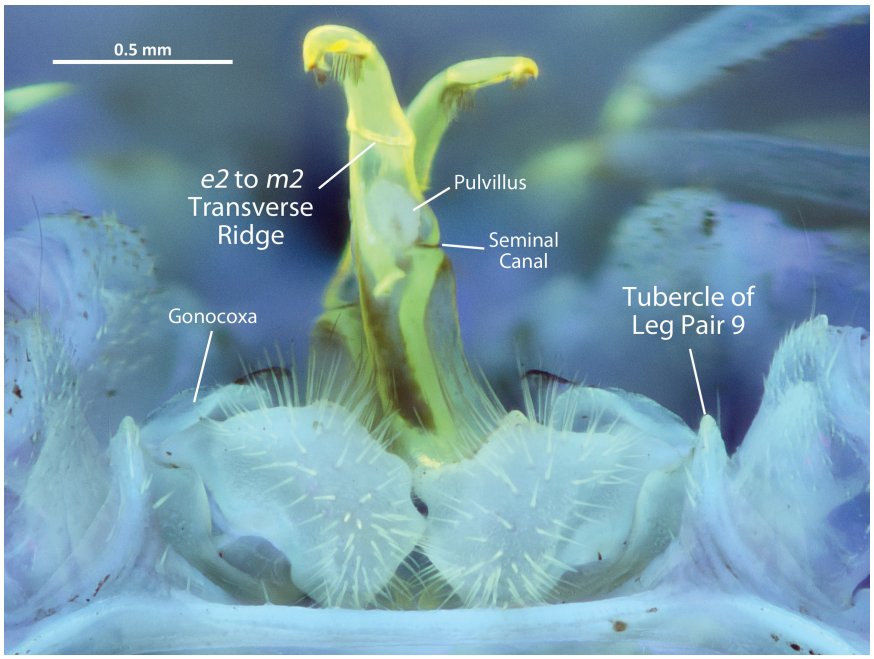


**Figure 8.** Body ring 7 in adult male *Pseudopolydesmus serratus*, posterior view, showing gonopods and sternal tubercles of leg pair 9 (FMNH INS8238, ultraviolet enhancement). Note the prominent transverse ridge between processes *e2* and *m2* in the gonopods of *Ps. serratus*.

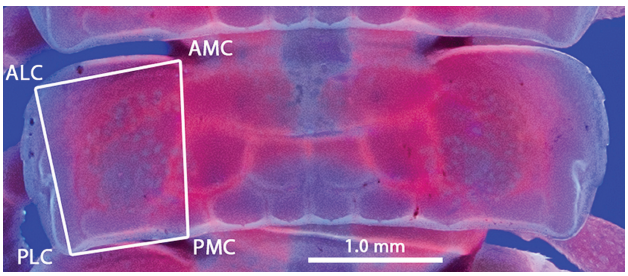


**Figure 9.** *Pseudopolydesmus erasus*, metatergite and paranota of body ring 9. Adult male (FMNH INS3120685, ultraviolet enhancement).

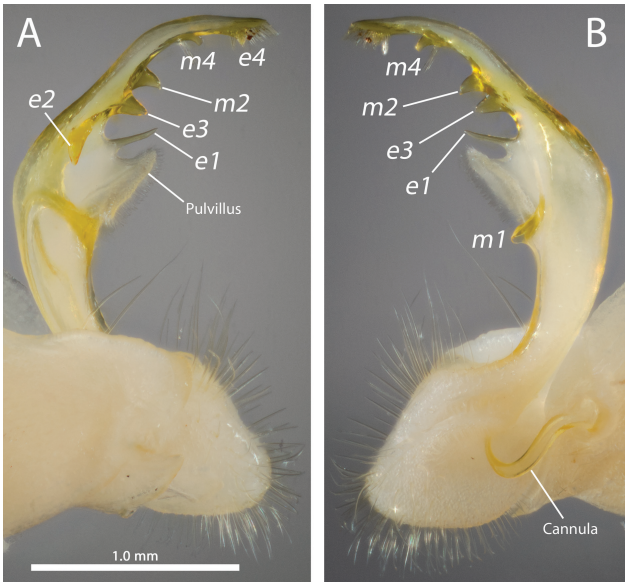


**Figure 10.** Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

*Polydesmus branneri* Bollman, 1887b: 620, ♂ HT (USNM, vidi). – Loomis, 1943: 405, fig. 16, pl. 1: fig. 4.
*Dixidesmus branneri* – Loomis & Hoffman, 1948: 54 (= *Polydesmus conlatus*; *Dixidesmus christianus*). – Hoffman, 1950: 223. – Causey, 1952: 7. – Chamberlin & Hoffman, 1958: 65.
*Pseudopolydesmus branneri* – Hoffman, 1974: 346, fig. 3. – Shelley, 1988: 1651, figs 27, 31 (= *Dixidesmus catskillus*; *D. gausodicrorhacus* [sic]).
*Polydesmus echinogon* Chamberlin, 1942b: 10, fig. 33, ♂/♀ ST (USNM, vidi).
*Dixidesmus echinogon* – Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 66.
*Polydesmus conlatus* Chamberlin, 1943b: 36, fig. 5, ♂ HT (FMNH INS977, vidi). – Sierwald *et al.*, 2005: 40.

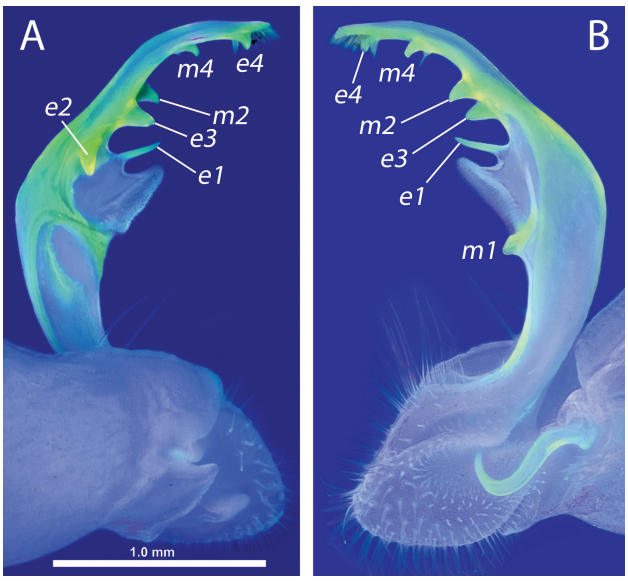


**Figure 11.** Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685, ultraviolet enhancement). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

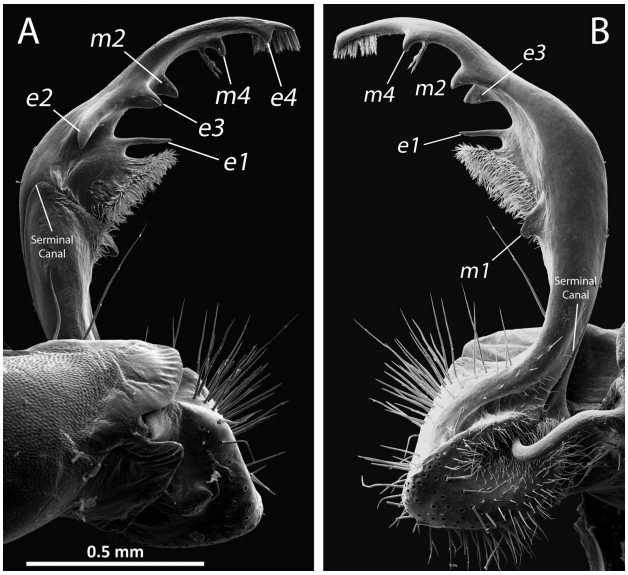


**Figure 12.** Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685, scanning electron micrograph). A, right gonopod, ectal view. B, right gonopod, medial view.

*Dixidesmus conlatus* – Chamberlin, 1943c: 18.
*Dixidesmus sylvicolens* Chamberlin, 1943c: 20, figs 37, 38, ♂/♀ ST (USNM, vidi). – Chamberlin & Hoffman, 1958: 67.
*Dixidesmus christianus* Chamberlin, 1946: 140, fig. 4, ♂ HT (USNM, vidi). – Chamberlin & Hoffman, 1958: 66.

*Dixidesmus catskillus* Chamberlin, 1947: 24, fig. 2, ♂ HT (ANSP, non vidi). – Chamberlin & Hoffman, 1958: 66.
*Dixidesmus phanus* Chamberlin, 1951: 27, fig. 1, ♂ HT (USNM, vidi). – Chamberlin & Hoffman, 1958: 67.
*Dixidesmus gausodicrorhachus* Johnson, 1954: 1, fig. 1, ♂ HT (USNM, vidi). – Chamberlin & Hoffman, 1958: 66.

### *Diagnosis*

*Size:* Usually large, with length ranging from 11.8 to 28.6 mm (Withrow, 1988: 199) and an average body length of 22.2 mm ($N$ = 162; Withrow, 1988: 94). Comparable in size or slightly larger than *Ps. erasus* and *Ps. serratus*. Often larger than *Ps. collinus*. Usually larger than *Ps. pinetorum*.

*Paranota and tergal sculpture* (Fig. 13): Corners of paranota forming a roughly rhomboid quadrilateral, with ALC posterior to AMC and lateral to PLC. Edges meeting at ALC and PMC forming right angles, with posterior edge shorter than in *Ps. collinus*. Leading and distal margins very rounded, denticles weak to obliterated. Angle of curve along distal margin and lateral portion of leading margin uniform from PLC past ALC. Trailing margin moderately concave, less so than *Ps. serratus*. Anterior, median and posterior blister rows subequal in thickness. Anterior blister row narrowing only slightly at lateral ends. Individual MBs and PBs subequal in area. Central paranotal blisters large, occupying more than two-thirds of paranotal breadth, as wide as long. Lateral blisters anteriorly widening laterad.

*Gonopod* (Figs 7, 14): Gonocoxa ventral lobe with single gonocoxal plate. Telopodite shallowly curved except at thickened section basal to pulvillus, with subterminal kink followed by straight terminal section. Pulvillus medium-sized, midway between base and terminus of acropodite. Process *e1* elongate and kinked; processes *e2+e3* large, joined at base into elongate stalk (Fig. 7), sometimes connected by a lamina; *e4* small (Fig. 14A). Process *m1* small, medial of pulvillus; *m2*, *m3* and *m4* large, subtriangular, equidistant from each other; *m3* offset laterad from *m2* and *m4* (Fig. 14B).

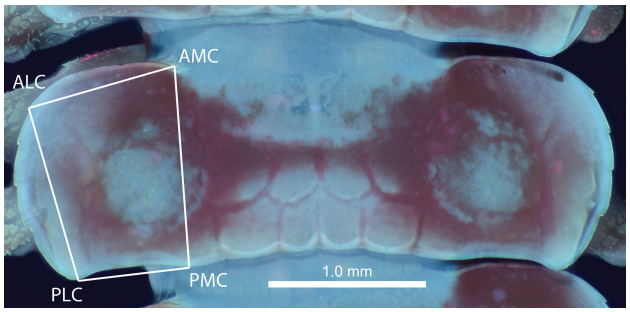


**Figure 13.** *Pseudopolydesmus canadensis*, metatergite and paranota of body ring 10. Adult male (FMNH INS3120683, ultraviolet enhancement).

### *Type notes*

*Polydesmus canadensis (immature ♀ HT, BMNH, non vidi):* Type presumed extant. Collected from Albany River, Hudson Bay, ON, Canada.

*Polydesmus glaucescens:* Location of types, if extant, unknown. Koch (1847) described the type locality only as 'Nordamerika'.

*Polydesmus nitidus (15 ♂/♀ ST, non vidi):* Location of type material unknown (not located at USNM). Bollman (1887a) described 15 specimens from Pensacola, Escambia Co., FL, USA.

*Polydesmus branneri (♂ HT, USNM, vidi):* From Mossy Creek (now Jefferson City), Jefferson Co., TN, USA. Vial contains one male and one dissected gonopod, tip of gonopod damaged.

*Polydesmus echinogon (three ♂ and nine ♀ ST, USNM, vidi):* Chamberlin (1942b) described four specimens from Shawanese, Harveys Lake, Luzerne Co., PA, USA, collected 23 September 1905 by F. C. Paulmier. We found two type lots, both labelled 'Types' by Chamberlin and

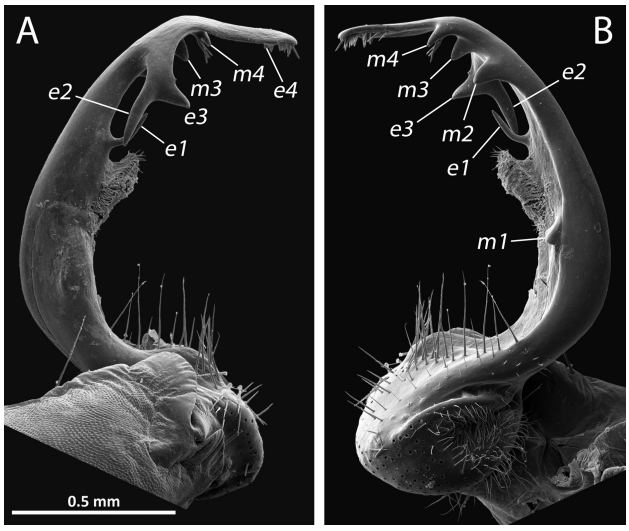


**Figure 14.** Gonopod of *Pseudopolydesmus canadensis* (FMNH INS6934, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod. Cannula removed.

with older labels erroneously identifying the specimens as *Ps. serratus*. Type lot 1 (probably the four specimens described by Chamberlin): contains one male with a single gonopod in situ, one intact female, and two small vials; first small vial labelled 'MALE HT' by Withrow, contains one male with a single gonopod in situ and two dissected gonopods (one damaged); second vial labelled 'Lectoallotype' by Withrow, contains one fragmented female. Type lot 2: contains five intact females, fragments of two females, one male with a single gonopod in situ, one genitalia vial with a single gonopod. We found two *Ps. serratus* males with gonopods in situ in Type lot 2 and separated them into a third vial.

*Polydesmus conlatus (♂ HT and two ♀ PT, FMNH, vidi; ♂/♀ PT, USNM, vidi; additional ♂/♀ PT, non vidi):* Chamberlin (1943b) nominated ♂ HT and described several male and female specimens from Gatlinburg, Sevier Co., TN, USA, collected 13–19 June 1942 by H. Dybas, and one male and one female from Thomasville, Thomas Co., GA, USA, collected 2 April 1940 by F. Field. The FMNH type lot is from the Gatlinburg locality: contains ♂ HT with gonopods in situ and two ♀ PT, images are available online at https://collections-zoology.fieldmuseum.org/catalogue/956102, last accessed 25/3/2019 (FMNH INS977). At USNM, we found an additional type lot from Greenbrier Cove, Sevier Co., TN, USA: labelled 'Paratype', contains at least one female, several males, one dissected gonopod in genitalia vial and one small vial labelled 'Lectoallotype'; the small vial contains one female with one dislodged vulva. The location of the one ♂ and one ♀ PT from GA is unknown.

*Dixidesmus sylvicolens (♂/♀ ST, USNM, vidi):* Chamberlin (1943c) described 'many specimens' from 7 miles north of Sylvania, Screven Co., GA, USA, collected by W. Ivie, 12 April 1943. We found one type lot: labelled '*branneri*' by Withrow, contains several specimens including males with gonopods.

*Dixidesmus christianus (♂ HT, three ♂ PT and five immature PT, USNM, vidi):* Chamberlin (1946) nominated ♂ HT and described three ♀ and five immature PT, all from Pass Christian, Harrison Co., MS, USA, collected 15 February 1946 by J. Rapp and W. Rapp. We found one type lot: labelled '*branneri*' by Withrow, contains two intact males, one male with gonopods missing, five immature specimens and one small vial; small vial labelled 'HT', contains fragmented male with one gonopod missing. The three ♂ PT we found might represent the three ♀ PT described by Chamberlin.

*Dixidesmus catskillus (♂ HT, ANSP, non vidi):* From Catskill, Greene Co., NY, USA, collected by Knight.

*Dixidesmus phanus (♂ HT and four PT, USNM, vidi):* From Suwanee River, FL, USA, without further locality, collected 15 April 1950 by D.E. Beck. We found two type lots. Type lot 1: labelled 'Male HT' and labelled '*branneri*' by Withrow, contains one male with gonopods. Type lot 2: contains several female specimens, one with vulvae everted.

*Dixidesmus gausodicrorhachus (♂ HT, one ♂ and two ♀ PT, USNM, vidi):* From west side of Garnet Lake, Mackinaw Co., MI, USA, collected 31 July 1949. There are two type lots. Type lot 1: contains ♂ PT with gonopods in situ and one ♀ PT with vulvae everted, nominated by Johnson (1954) as the allotype. Type lot 2: contains ♂ HT with single gonopod and one ♀ PT.

### *Distribution*

Northern Wisconsin east through southeastern Ontario and southern Quebec to the Atlantic Coast, south through the Appalachian Mountains to the Gulf Coast as far west as southern Mississippi.

### *Additional specimens examined*

**FMNH INS**1421, 1455, 1461, 1465, 1552, 1569, 3574, **6934***, 7632, 7699, 14219, **3120683***.

## ***PSEUDOPOLYDESMUS COLLINUS*** HOFFMAN, 1974 (FIGS 15, 16)

*Pseudopolydesmus collinus* Hoffman, 1974: 346, figs 1, 2, ♂ HT (VMNH, non vidi but see type notes). – [Withrow, 1988: 98, figs 85, 89, 93, 110, 115, 122–126, map 7, tables 9–11.] – Hoffman, 1999: 444.

*?Polydesmus moniliaris* – Williams & Hefner, 1928: 112, fig. 13a. Mistaken identification!

### *Diagnosis*

*Size:* Medium-large, with length ranging from 12.9 to 25.3 mm (Withrow, 1988: 199) with an average length of 19 mm ($N$ = 40; Withrow, 1988: 101). Often smaller than *Ps. canadensis* and *Ps. serratus*. Comparable in size or slightly smaller than *Ps. erasus*. Usually larger than *Ps. pinetorum*.

*Paranota and tergal sculpture* (Fig. 15): Corners of paranota forming a roughly rhomboid quadrilateral, with ALC posterior to AMC and lateral to PLC. Edges meeting at ALC and PMC forming right angles, with posterior edge longer than in *Ps. canadensis*. Leading and distal margins very rounded, denticles weak. Angle of curve along distal margin and lateral portion of leading margin uniform from PLC past

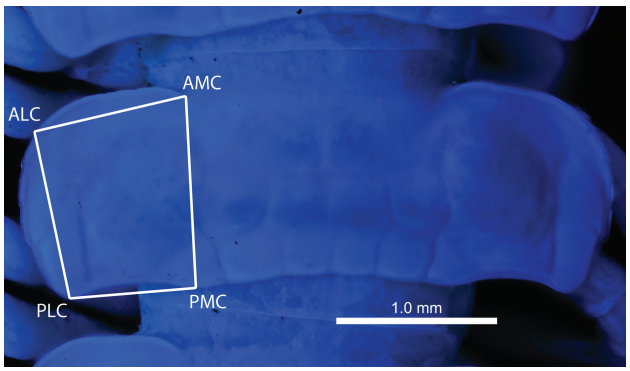


**Figure 15.** *Pseudopolydesmus collinus*, metatergite and paranota of body ring 9. Paratype, adult male (VMNH PSE00202, ultraviolet enhancement).

ALC. Trailing margin moderately concave, less so than *Ps. serratus*. Anterior blister row medially thicker than median blister row, narrowing only slightly at lateral ends. Median blister row thicker than posterior blister row. Central paranotal blisters large, occupying more than two-thirds of paranotal breadth, as wide as long. Lateral blisters anteriorly widening laterad.

*Gonopod* (Fig. 16): Gonocoxa ventral lobe with single gonocoxal plate. Telopodite curved and slightly thickened basal to pulvillus, nearly straight beyond pulvillus, with a subterminal kink followed by straight terminal section. Pulvillus medium-sized, midway between base and terminus of acropodite. Process *m3* absent. Process *e1* reduced to near absence; *e2* large, recurved, combined on short, thick stalk with large, subtriangular *e3* (Fig. 16C); *e4* small (Fig. 16A). Process *m1* small, medial of pulvillus; *m2* large, subtriangular; *m4* typically shaped, well separated from *m2* of a similar size (Fig. 16B).

### *Type notes*

*(♂ HT, non vidi; five ♂ PT and eight ♀ PT, VMNH, vidi):* From Pinnacles of Dan, ~4 miles southwest of Vesta, Patrick Co., VA, USA, collected 22 April 1972. We found one jar at VMNH labelled 'PARATYPE', containing two vials. One vial contained five ♂ PT (VMNH PSE00044); the other vial contained eight ♀ PT (VMNH PSE00043). The ♂ HT might be included in the vial of ♂ PT without a label. Two male paratype specimens from VMNH PSE00044 were individually relabelled and imaged (**VMNH PSE00202***  and **VMNH PSE00203***).

### *Distribution*

Southern Indiana east to West Virginia, south to central Virginia and north-central South Carolina. Williams &

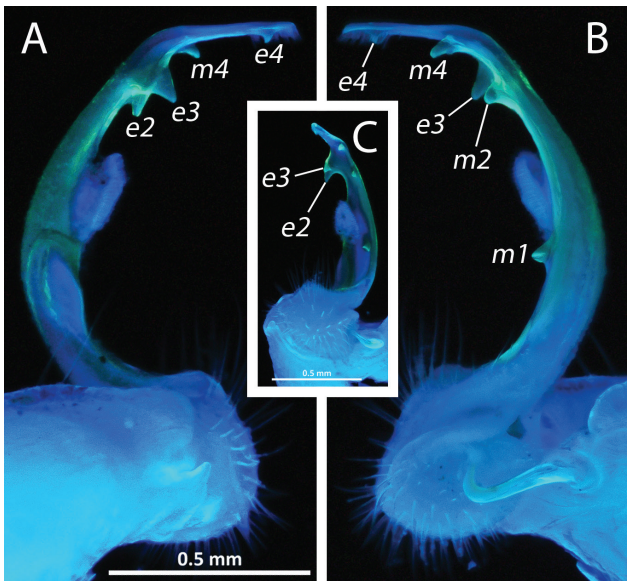


**Figure 16.** Gonopod of *Pseudopolydesmus collinus*. Paratype (VMNH PSE00203, ulatraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. C, left gonopod, posterior oblique view, showing fusion of *e2* and *e3* processes onto a short, thick stalk. All images mirrored to appear as right gonopod.

Hefner (1928) reported *Polydesmus moniliaris* C. L. Koch, 1847 as common and abundant throughout the state of Ohio. Based on their figure (fig. 13), Withrow (1988) suggested that this was a misidentification of *Ps. collinus*, although the figure lacks detail and most probably depicts *Ps. canadensis*, which also occurs in Ohio.

## ***PSEUDOPOLYDESMUS PINETORUM*** (BOLLMAN, 1888) (FIGS 17–20)

*Polydesmus pinetorum* Bollman, 1888: 3, ♂ HT (USNM, non vidi, type lost).

*Pseudopolydesmus pinetorum* – Causey, 1952: 6, fig. 5 (= *Po. americanus*; *Po. paroicus*; *Po. hubricthi*; *Po. modocus*). – Chamberlin & Hoffman, 1958: 70. – [Withrow, 1988: 72, figs 74, 80, 82, 86, 90, 106, 111, 122–128, map 4, tables 9–11.] – Hoffman, 1999: 445.

*Polydesmus americanus* Carl, 1902: 611, pl. 11: fig. 37, two ♂ ST (MHNG, non vidi).

*Pseudopolydesmus americanus* – Attems, 1940: 140, fig. 202. – Carl, 1941: 292, figs 1–2.

*Polydesmus natchitoches* Chamberlin, 1942b: 10, figs 34, 35, ♂ HT (USNM, vidi), synon. nov.

*Pseudopolydesmus natchitoches* – Chamberlin & Hoffman, 1958: 70. – Hoffman, 1999: 445.

*Polydesmus paroicus* Chamberlin, 1942b: 11, figs 37, 38, five ♂/♀ ST (USNM, vidi).

*Pseudopolydesmus paroicus* – Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 70. – Hoffman, 1999; 445.
*Polydesmus hubrichti* Chamberlin, 1943a: 15, figs 1, 2, ♂ HT (USNM, vidi).
*Pseudopolydesmus hubrichti* – Chamberlin, 1943c: 18.
*Polydesmus modocus* Chamberlin, 1943b: 36, fig. 6, ♂ HT (FMNH INS927, *vidi*). – Sierwald *et al.*, 2005: 40.
*Pseudopolydesmus modocus* – Chamberlin, 1943c: 18.

### *Diagnosis*

*Size:* Medium, with body length ranging from 13.6 to 25.6 mm and an average body length of 18.6 mm ($N = 212$; Withrow, 1988: 76, 199). Usually smaller than *Ps. canadensis*, *Ps. collinus*, *Ps. erasus* and *Ps. serratus*. Clearly larger than its small sympatric congeners *Ps. minor* and *Ps. caddo*.

*Paranota and tergal sculpture* (Fig. 17): Corners of paranota forming a broad rectangle, nearer to a square than any other *Pseudopolydesmus* species. Leading and distal margins weakly curved compared with *Ps. erasus* and *Ps. serratus*, denticles always distinct. Trailing margin concave, strongly curved. Anterior blister row much thicker than median and posterior blister rows, which are subequal in thickness. Median blister 2 and PB2 subequal in area and much larger than MB1 and PB1. Central paranotal blisters large, occupying over two-thirds of paranotal breadth, as wide as long. Lateral blisters anteriorly widening laterad.

*Gonopod* (Figs 18–20): Gonocoxa ventral lobe with single gonocoxal plate. Telopodite entirely arcuate and fishhook-shaped, section distal of pulvillus tightly curved. Pulvillus large, rounded, closer to terminus of acropodite than base. Processes *e1*, *m3* absent. Process *e2* lobe-like, recurved, separate from *e3*; process *e3* very large, subtriangular to spike-shaped; process *e4* small and laminate, proximal to terminal tuft of bristles (Figs 18A, 19A, 20A). Process *m1* small, hidden at base of pulvillus; *m2* small, subtriangular; *m4* medium-sized, subtriangular, close to *m2* (Figs 18B, 19B, 20B).

### *Type notes*

*Polydesmus pinetorum (♂ HT, USNM, non vidi, type lost):* From Little Rock, Pulaski Co., AR, USA. Bollman (1888) mentions additional specimens from Clark, Pike and Sevier Cos in Arkansas. Apparently, Withrow examined the ♂ HT at USNM; no type material was found there (Sierwald, November 2015).

*Polydesmus americanus: (two ♂ ST, MHNG, non vidi):* From Texas, without further locality.

*Polydesmus natchitoches (four ♂/♀ ST, USNM, vidi; one ♂ ST, USNM, non vidi):* Chamberlin (1942b) described four ST from two miles south of Saline, collected 12 April 1936, and one ♂ ST from four miles north of Chestnut, collected 14 April 1936. All collected by L. Hubricht. Both localities are in Natchitoches Par., LA, USA. One type lot found, from the Saline locality: labelled '= *pinetorum*' by Withrow, contains genitalia vial with two intact male gonopods and three or four fragmented male and female specimens, including one female with vulvae everted. Specimens sorted

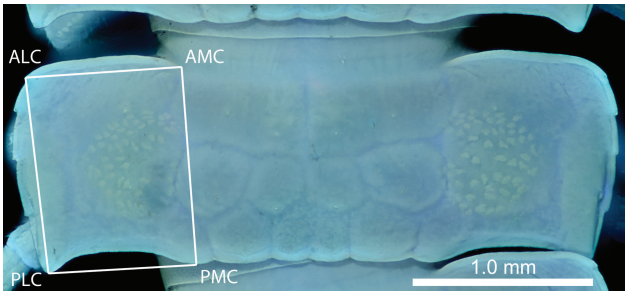


**Figure 17.** *Pseudopolydesmus pinetorum*, metatergite and paranota of body ring 10. Paratype, *Polydesmus hubrichti* type series vial from Glencoe Station, MO, USA, adult female (USNM, ultraviolet enhancement).

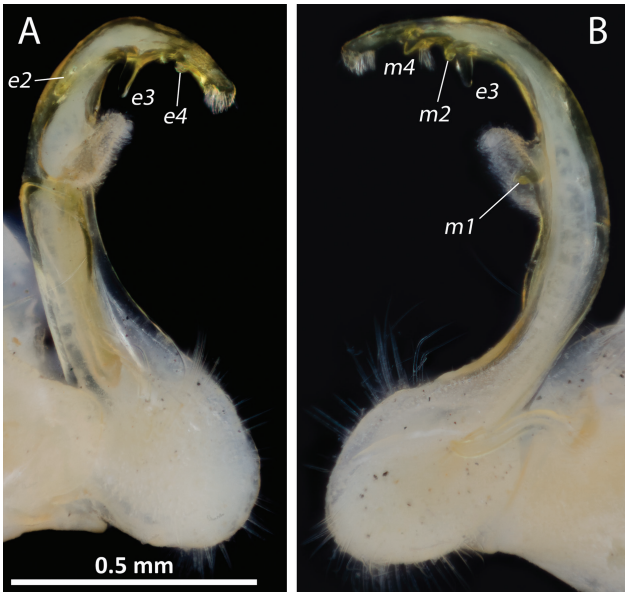


**Figure 18.** Gonopod of *Pseudopolydesmus pinetorum*. Holotype, *Polydesmus natchitoches*, from genitalia vial (USNM). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

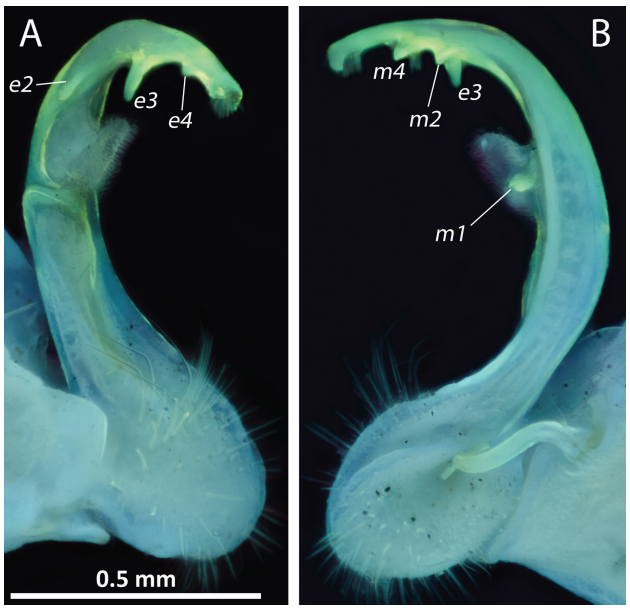


**Figure 19.** Gonopod of *Pseudopolydesmus pinetorum*. Holotype, *Polydesmus natchitoches*, from genitalia vial (USNM, ultraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

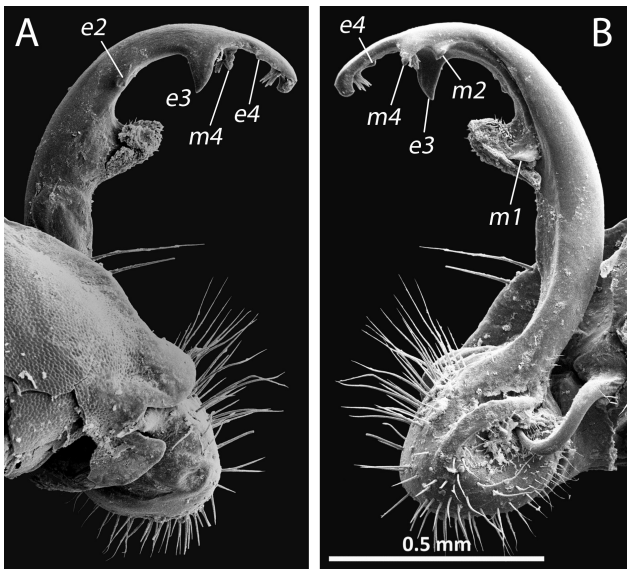


**Figure 20.** Gonopod of *Pseudopolydesmus pinetorum* (FMNH INS1445, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

into three vials. Vial 1 contains one fragmented male with gonopods missing and genitalia vial containing two gonopods (most probably not from the same male). Vial 2 contains two fragmented females, one with everted vulvae. Vial 3 contains several specimen fragments. ♂ ST from Chestnut locality not found.

*Polydesmus paroicus (three ♂ and two ♀ ST, USNM, vidi):* From 1.5 miles north of Clay, boundary of Lincoln and Jackson Parishes, LA, USA, collected 12 April 1936 by L. Hubricht. One type lot: contains two fragmented females, two fragmented males with gonopods in situ, one male with dissected gonopods but intact body ring 7, and one genitalia vial with fragments of body ring 7 and at least one gonopod, most probably not belonging to the male in this vial.

*Polydesmus hubrichti (♂ HT and 13 ♂ PT, USNM, vidi):* Chamberlin (1943a) described ♂ HT, ♀ allotype, and approximately ten additional ♂/♀ PT from University City, St. Louis Co., MO, USA, collected 29 March 1936 by L. Hubricht. We found one type lot and two additional lots; all labelled with the nomenclaturally invalid manuscript name '*Polydesmus scholasticus*' by Chamberlin, labelled '*P. serratus*' by Hubricht. Type lot: labelled 'Types', contains ≥ 14 specimens: male labelled 'Lectotype' with one dissected gonopod in a genitalia vial and 13 adult males, most with intact gonopods in situ. Non-type lot 1: labelled 'Paratype', contains a single female collected March 1936 under logs, from 4.3 miles northwest of Glencoe Station, St. Louis Co., MO, USA. Non-type lot 2: labelled 'Paratypes', collected 8 March 1936, from Creve Coeur Lake Park, St. Louis Co., MO, USA, containing seven specimens belonging to three species: two males of *Ps. pinetorum* (both with gonopods in situ, one with a single intact gonopod), two females of *Ps. pinetorum*, two males of *Ps. minor* (gonopods intact in situ) and one female *Ps. serratus* (with everted vulva). Despite labelling three lots as types (for *Po. scholasticus*), Chamberlin (1943a) explicitly designated only the material from University City (vial labelled 'Types') in the *Po. hubrichti* type series.

*Polydesmus modocus (♂ HT, FMNH, vidi):* From between Modoc and Roots, Randolph Co., IL, USA, collected 14 April 1936 by K. P. Schmidt. ♂ HT in fragments, single gonopod in genitalia vial, images are available online at https://collections-zoology.fieldmuseum.org/catalogue/955981, last accessed 25/3/2019 (FMNH INS927).

### *Distribution*

Louisiana north to southern Iowa, east through Alabama and Tennessee. Most commonly collected west of the Mississippi River.

*Additional specimens examined*

**FMNH INS**1435, 1438, **1445***.

### ***PSEUDOPOLYDESMUS MINOR*** (BOLLMAN, 1888) (FIGS 21–25)

*Polydesmus minor* Bollman, 1888: 2, ♂ ST (USNM, non vidi, type lost). – Chamberlin, 1942b: 19, fig. 32.
*Pseudopolydesmus minor* – Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 70. – Loomis, 1959: 161, fig. 9. – [Withrow, 1988: 120, figs 62, 79, 97, 101, 105, 117, 119, 122–126, map 9, tables 9–11.] – Hoffman, 1999: 444.
*Polydesmus neoterus* Chamberlin, 1942b: 10, figs 30, 31, ♂ HT (USNM, vidi), synon. nov.
*Pseudopolydesmus neoterus* – Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 70.—Hoffman, 1999: 445.
*Polydesmus euthetus* Chamberlin, 1942b: 11, fig. 36, two ♂/♀ ST (USNM, vidi), synon. nov.
*Pseudopolydesmus euthetus* – Chamberlin, 1943c: 18. – Chamberlin & Hoffman, 1958: 70.—Hoffman, 1999: 444.

*Diagnosis*

*Size:* Small, with body length ranging from 8.8 to 12.7 mm and an average body length of 10.5 mm ($N$ = 31; Withrow, 1988: 124, 199). Comparable in size to *Ps. caddo* and *Ps. paludicolus*. Clearly smaller than all other congeneric species.

*Paranota and tergal sculpture* (Figs 21, 22): Corners of paranota forming a narrow parallelogram, with medial and lateral edges roughly twice as long as anterior and posterior edges. Anterior lateral and posterior lateral corners posterior to AMC and PMC, respectively, giving characteristic swept-back appearance. Leading and distal margins highly variable, ranging from moderately to weakly curved. Anterior lateral corners and denticles ranging from moderate to obliterated. Trailing margin concave, strongly curved. Anterior blister row as thick as MB and PB rows combined. Individual MBs and PBs subequal in area. Central paranotal blisters occupying two-thirds of paranotal breadth. Lateral blisters unusually distinct, extending anteriorly past all setiferous denticles, aligned with longitudinal axis.

*Gonopod* (Figs 23–25): Gonocoxa ventral lobe with two gonocoxal plates stacked dorsoventrally (Fig. 25A). Telopodite uniformly curved. Pulvillus elongate, pointed, much closer to base of acropodite than terminus. Processes *e1*, *e3* and *m3* absent. Process *e2* very small, lobe-like (Fig. 25A); *e4* medium-sized, unusually prominent, basal to terminal bristles. Ectal surface also with large flange (possibly homologous to *e3*) between processes *m2* and *m4* (Figs 23A, 24A, 25A). Process *m1* unusually large, subtriangular, proximal to pulvillus; *m2* large, subtriangular, midway between base and terminus of acropodite; *m4* small (Figs 23B, 24B, 25B).

*Type notes*

*Polydesmus minor (♂ ST, USNM, non vidi, type lost):* Bollman (1888) described an unspecified number of specimens from Little Rock, Pulaski Co., AR, USA. He made no mention of female specimens. No type specimens of *Ps. minor* were located in the USNM collection (Sierwald, November 2015).

*Polydesmus neoterus (♂ HT and two ♂ PT, USNM, vidi):* From New Orleans, LA, USA, collected 17 April 1936 by L. Hubricht. Type lot: contains two ♂ PT, ♂ HT with gonopods removed, distal extremities of one broken gonopod (without pulvillus). The gonopod remains do not allow unequivocal identification of the specimen. However, paranota shape and tergal sculpture is distinct from that in the types of *Ps. caddo*

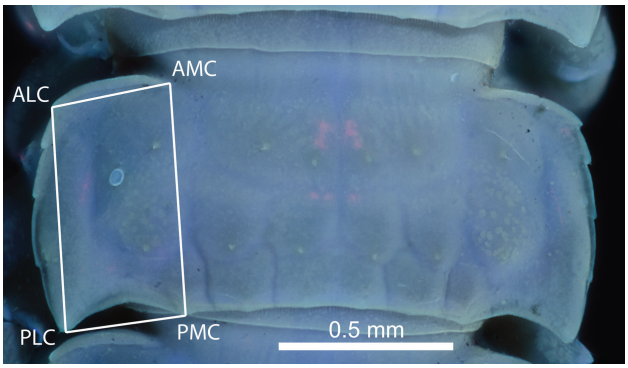


**Figure 21.** *Pseudopolydesmus minor*, metatergite and paranota of body ring 10. Holotype, *Polydesmus euthetus* (USNM, ultraviolet enhancement).

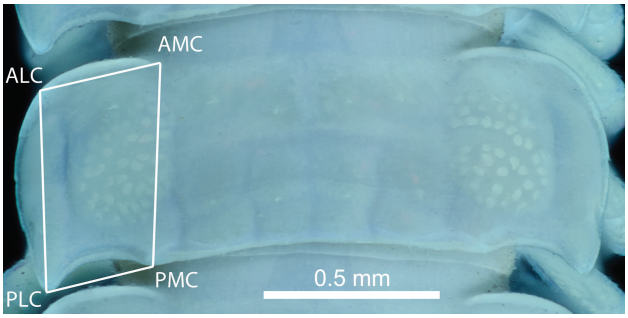


**Figure 22.** *Pseudopolydesmus minor*, metatergite and paranota of body ring 9. Paratype, *Polydesmus neoterus* type series, adult female (USNM, ultraviolet enhancement).

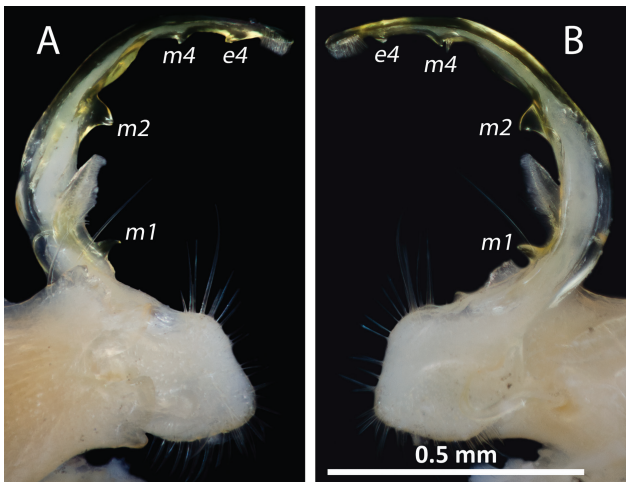


**Figure 23.** Gonopod of *Pseudopolydesmus minor*. Holotype, *Polydesmus euthetus* (USNM). A, right gonopod, ectal view. B, right gonopod, medial view.

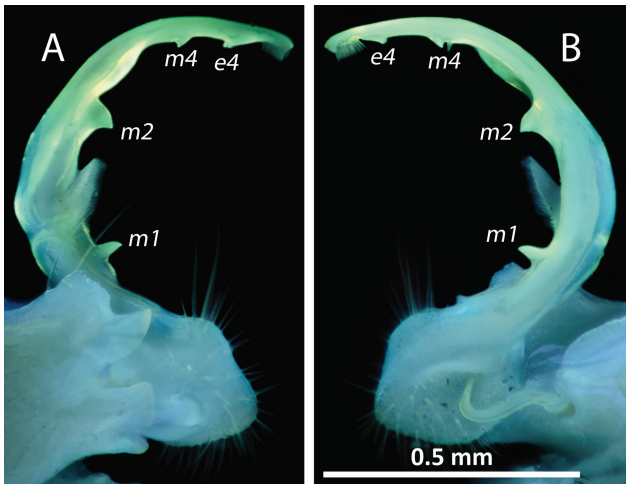


**Figure 24.** Gonopod of *Pseudopolydesmus minor*. Holotype, *Polydesmus euthetus* (USNM, ultraviolet enhancement). A, right gonopod, ectal view. B, right gonopod, medial view.

(= *Ps. bidens*), the only small-bodied congener that occurs in Louisiana.

*Polydesmus euthetus (one ♂ and one ♀ ST, USNM, vidi):* From Buder Park, Fenton, St. Louis Co., MO, USA collected 15 March 1936 by L. Hubricht. Type lot contains ♂ ST erroneously labelled 'HT' with a single dissected gonopod and ♀ ST labelled 'Lectoallotype'.

### *Distribution*

Southern Arkansas northward through Missouri and Illinois to Lake Michigan. Most commonly collected near the Mississippi River and its tributaries.

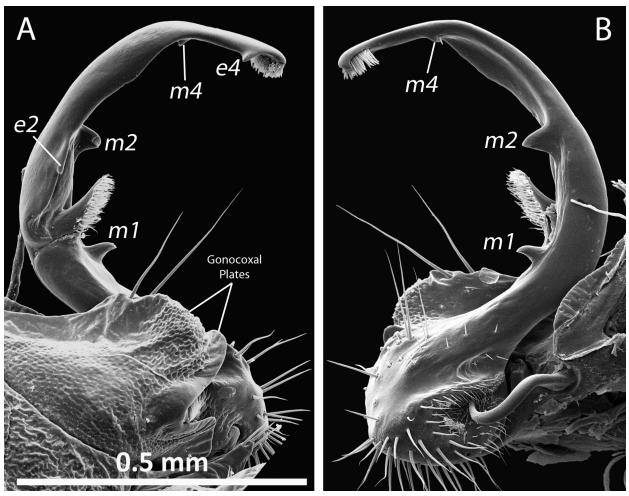


**Figure 25.** Gonopod of *Pseudopolydesmus minor* (FMNH INS7107, scanning electron micrograph). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

### *Additional specimens examined*

**FMNH INS7107***.

## ***PSEUDOPOLYDESMUS CADDO*** CHAMBERLIN, 1949 (FIGS 26–28)

*Pseudopolydesmus caddo* Chamberlin, 1949: 97, fig. 11, ♂/♀ ST (USNM, vidi). – Chamberlin & Hoffman, 1958: 69. – [Withrow, 1988: 115, figs 50, 77, 96, 100, 104, 116, 118, 122–126, map 9, tables 9–11.] – Hoffman, 1999: 442 (= *Ps. bidens*).

*Pseudopolydesmus bidens* Loomis, 1959: 161, fig. 8, ♂ HT (USNM, vidi).

### *Diagnosis*

*Size:* Small, with body length ranging from 7.5 to 13.3 mm and an average body length of 10.0 mm ($N$ = 28; Withrow, 1988: 119). Comparable in size to *Ps. minor* and *Ps. paludicolus*, clearly smaller than all other congeneric species.

*Paranota and tergal sculpture* (Fig. 26): Corners of paranota forming a roughly trapezoidal quadrilateral, with lateral edge longer than medial edge, giving the paranota a characteristic flared-out appearance. Leading margin moderately curved, distal margin nearly straight, trailing margin strongly concave. Anterior lateral corner and denticles always strongly distinct. Anterior blister row thicker medially than MB row, MB row thicker than PB row. Median blister 2 much larger in area than MB1. Tergal blisters poorly

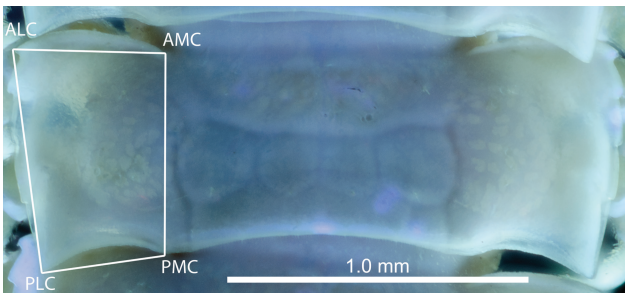


**Figure 26.** *Pseudopolydesmus caddo*, metatergite and paranota of body ring 10. Paratype, adult male (USNM, ultraviolet enhancement).

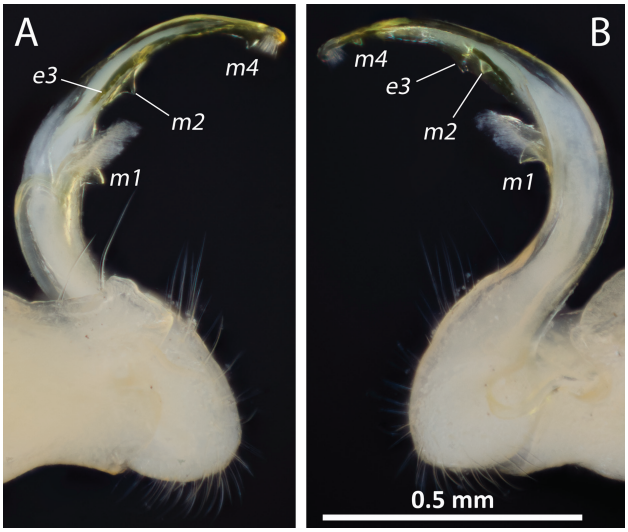


**Figure 27.** Gonopod of *Pseudopolydesmus caddo*. Holotype (USNM). A, right gonopod, ectal view. B, right gonopod, medial view.

differentiated, PB row nearly obliterated except lateral sulcus of PB3. Central paranotal blisters occupying two-thirds of paranotal breadth. Lateral blisters aligned with longitudinal axis.

*Gonopod* (Figs 27, 28): Gonocoxa ventral lobe with single gonocoxal plate. Telopodite uniformly curved. Pulvillus elongate, pointed, midway between base and terminus of acropodite. Processes *e1*, *e2*, *e4* and *m3* absent. Process *e3* projecting from a flanged ectal lamina (Fig. 28B). Processes *m1*, *m2* and *m4* all medium-sized, subtriangular; *m1* at base of pulvillus; *m2* connected to *e2* via weak transverse ridge (not as distinct as in *Ps. serratus*); *m4* proximal to terminal bristles. Our process *m4* might be homologous to *e4* in other *Pseudopolydesmus*: it is located subterminally on the acropodite and, in both the *Ps. bidens* and *Ps. caddo* type specimens, does not bear proximal

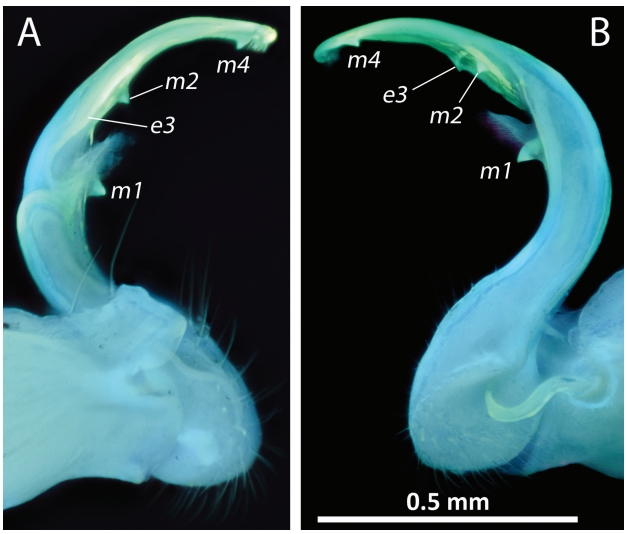


**Figure 28.** Gonopod of *Pseudopolydesmus caddo*. Holotype (USNM, ultraviolet enhancement). A, right gonopod, ectal view. B, right gonopod, medial view.

bristles (although the specimens may have been damaged).

*Type notes*

*Pseudopolydesmus caddo (two ♂ and one ♀ ST, USNM, vidi):* From 5 miles northwest of Shreveport, Caddo Par., LA, USA, collected 13 April 1936 by L. Hubricht. Two ♂ ST both with gonopods removed; one is erroneously labelled 'HT' with gonopods in genitalia vial, left gonopod with tip broken off. ♀ ST labelled 'Lectoallotype'.

*Pseudopolydesmus bidens (♂ HT, six ♂ and five ♀ PT, USNM, vidi):* Loomis, 1959 nominated ♂ HT and described six additional ♂ and five ♀ from site between Kinder and Le Blanc, Allen Par., LA, USA collected 20 December 1958 by E. M. Loomis and H. F. Loomis. We found one type lot containing one small vial labelled 'Holotype', one male with gonopods in situ, one male with gonopods dissected into a genitalia vial and one intact female. Holotype vial contains complete male with both dissected gonopods.

*Distribution*

Coast and coastal plain of the Gulf of Mexico, from eastern Texas to southern Mississippi.

***PSEUDOPOLYDESMUS PALUDICOLUS*** HOFFMAN, 1950 (FIGS 29–31)

*Pseudopolydesmus paludicolus* Hoffman, 1950: 222, fig. 4, ♂ HT (USNM, vidi, gonopods missing).

– Chamberlin & Hoffman, 1958: 70. – Hoffman, 1999: 445.

*Pseudopolydesmus paludicola* [sic] – [Withrow, 1988: 111, figs 95, 99, 103, 126, map 9, table 11.]

### *Diagnosis*

*Size:* Small, with male body length measured at 11 and 13 mm ($N = 2$; Withrow, 1988: 111). Comparable in size to *Ps. minor* and *Ps. caddo*. Clearly smaller than all other congeneric species. May be mistaken, e.g. for the similarly sized *Po. inconstans*, because, unlike in most *Pseudopolydesmus*, the collum is narrower than the mandibles and tergal setae are clearly visible under the dissecting microscope.

*Paranota and tergal sculpture* (Fig. 29): Corners of paranota forming a longitudinally oblong rectangle. Leading and distal margins moderately curved. Denticles strongly distinct with unusually long, easily visible setae, but ALC indistinct. Trailing margin concave, strongly curved. Anterior blister row thicker than median blister row along its entire breadth, and MB row thicker than PB row. Individual MBs subequal in area, as are individual PBs. Central paranotal blisters occupying two-thirds of paranotal breadth. Lateral blisters aligned with longitudinal axis. Tergal and paranotal blisters also with unusually long, easily visible setae.

*Gonopod* (Figs 30, 31): Gonocoxa ventral lobe with two gonocoxal plates stacked dorsoventrally (Fig. 31). Telopodite roughly boomerang-shaped, abruptly kinked distal from pulvillus, curving terminally. Pulvillus very small (comparable in size to process *m1*), pointed, slightly closer to base of acropodite than terminus. Processes *e1*, *e3* and *m4* absent. Process *e2* projecting laterally (Fig. 30C); *e4* unusually large, spike-shaped. Process *m1* unusually large, subtriangular, medial of pulvillus; *m2* and *m3* medium-sized, connected by a shared lamina (Figs 30–31); *m2* offset laterad from *m3* (Fig. 30C).

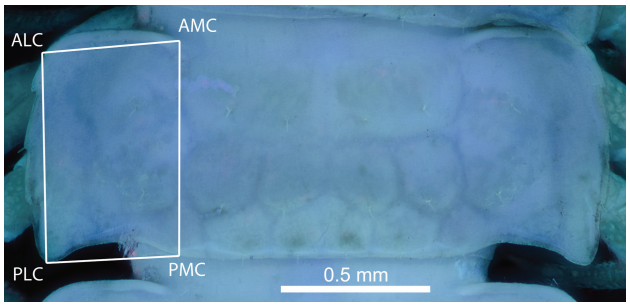


**Figure 29.** *Pseudopolydesmus paludicolus*, metatergite and paranota of body ring 13. Holotype, adult male (USNM, ultraviolet enhancement).

### *Type notes*

*(♂ HT, USNM, vidi):* From Sand Bridge, City of Virginia Beach, Princess Anne Co., VA, USA, collected 8 May 1949 by L. M. Carter, H. I. Kleinpeter and R. L. Hoffman. ♂ HT intact with gonopods removed (gonopods non vidi).

### *Distribution*

Coastal plain of southeastern Virginia south to South Carolina.

### *Additional specimens examined*

**VTEC MPE01167*, 01169*, 01170***.

## ***PSEUDOPOLYDESMUS SERRATUS*** (SAY, 1821)

(FIGS 8, 32, 33)

*Polydesmus serratus* Say, 1821: 106, type material not extant. – Gervais, 1847: 105. – de Saussure, 1860: 325. – Peters, 1864: 539. – Bollman, 1887b: 620 (?= *Po. pennsylvanicus*). – Williams & Hefner, 1928: 112, fig. 13b.

*Pseudopolydesmus serratus* – Attems, 1940: 141, uncertain placement. – Chamberlin, 1943c: 18.

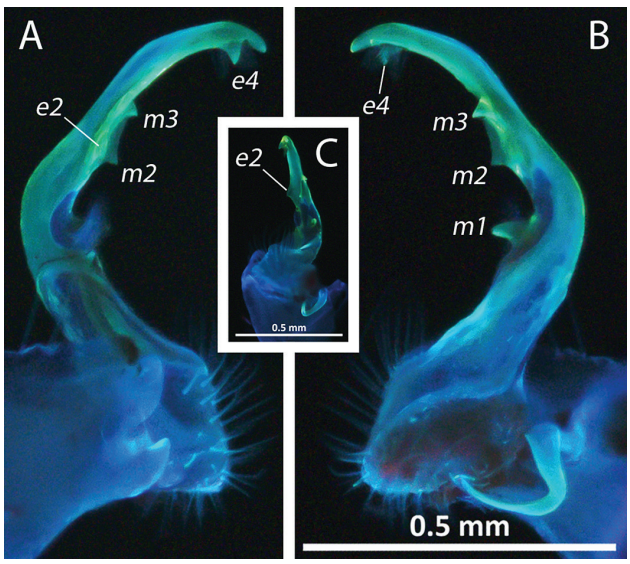


**Figure 30.** Gonopod of *Pseudopolydesmus paludicolus* (VTEC MPE01170, ultraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. C, left gonopod, posterior oblique view, showing process *e2* projecting laterally. All images mirrored to appear as right gonopod.

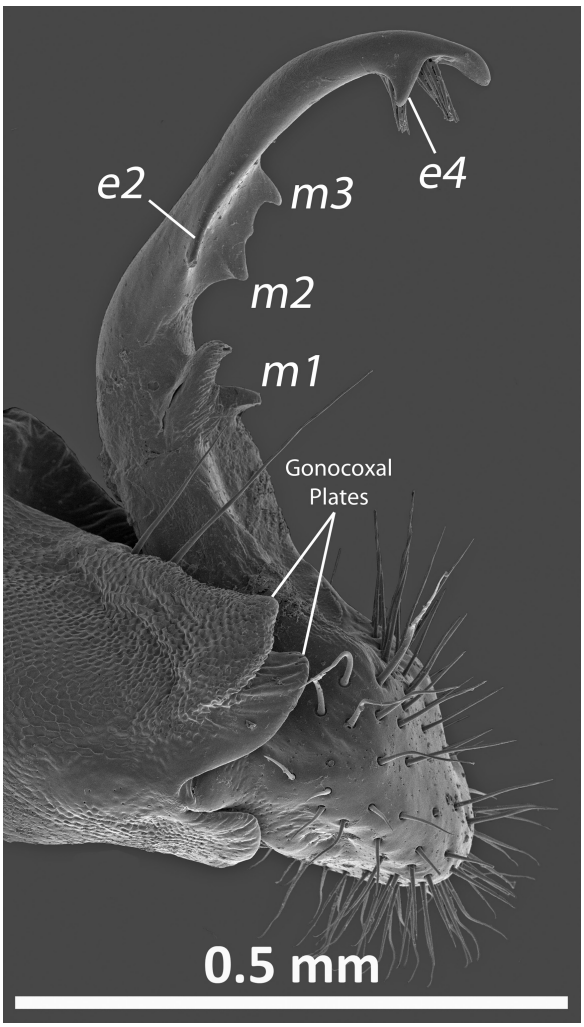


**Figure 31.** Left gonopod of *Pseudopolydesmus paludicolus*, ectal view (VTEC MPE01169, scanning electron micrograph). Image mirrored to appear as right gonopod.

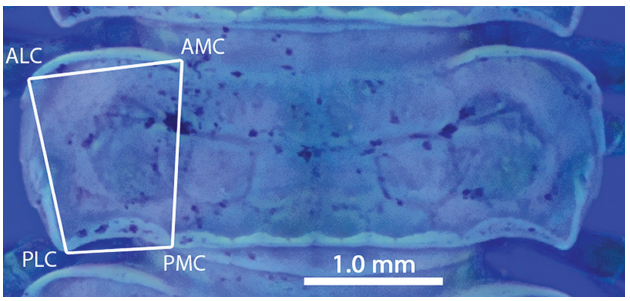


**Figure 32.** *Pseudopolydesmus serratus*, metatergite and paranota of body ring 9. Adult female (FMNH INS2817, ultraviolet enhancement).

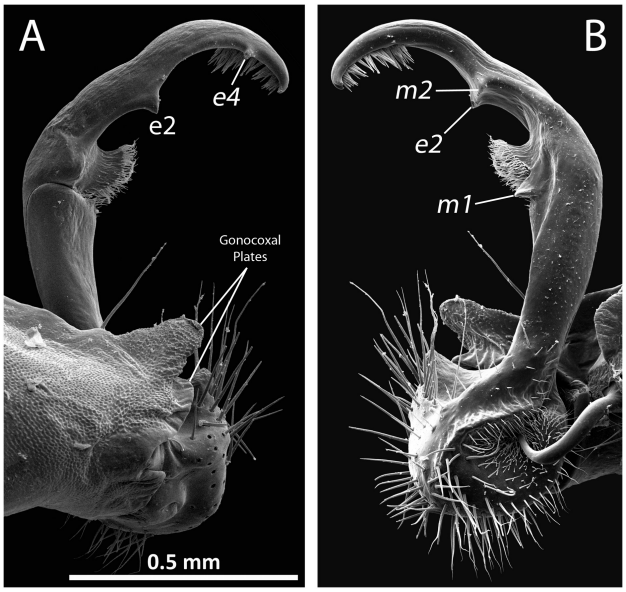


**Figure 33.** Gonopod of *Pseudopolydesmus serratus* (FMNH INS2819, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

– Chamberlin, 1951: 27. – Causey, 1952: 6. – Chamberlin & Hoffman, 1958: 71. – Loomis, 1959: 161. – Ramsey, 1966: 339. – [Withrow, 1988: 103, figs 12, 45, 46, 48, 57, 59, 63, 66, 67, 69, 78, 81, 94, 98, 102, 120, 122–126, map 8, tables 9–11.] – Hoffman, 1999: 446 (= *Po. scopus*; *Po. planicolens*). – Shelley, 2000: 246. – Shelley & Snyder, 2012: 6, figs 2–4.

*Polydesmus canadensis* – Wood, 1865: 216, figs 43, 44. Mistaken identity!

*Pseudopolydesmus canadensis* – Attems, 1898: 480, fig. 244. – Verhoeff, 1931: 305, figs 1–7. – Attems, 1940: 140, fig. 201. Mistaken identity!

*?Polydesmus pennsylvanicus* C. L. Koch, 1847: 133, type material unknown.

*Polydesmus pensylvanicus* [sic] – C. L. Koch 1863b: 18, pl. 69: fig. 142.

*Polydesmus scopus* Chamberlin, 1942a: 16, fig. 1, ♂ HT (USNM, vidi).

*Pseudopolydesmus scopus* – Chamberlin & Hoffman, 1958: 71.

*Polydesmus planicolens* Chamberlin, 1942a: 16, fig. 2, ♂ HT (USNM, vidi).

*Pseudopolydesmus planicolens* – Chamberlin & Hoffman, 1958: 71.

### *Diagnosis*

*Size:* Usually large, with body length ranging from 13.2 to 32 mm and an average body length of 22.7 mm ($N$ = 500; Withrow, 1988: 108, 199). Comparable in size

to *Ps. canadensis* and *Ps. erasus*, usually larger than *Ps. collinus* and *Ps. pinetorum*.

*Paranota and tergal sculpture* (Fig. 32): Corners of paranota forming a trapezoid, with the anterior (AMC to ALC) edge longer than the posterior (PMC to PLC) edge. Ratio of anterior to posterior edge length larger than in *Ps. erasus*. Leading and distal margins moderately curved, similar to *Ps. erasus* but less curved than *Ps. canadensis* and *Ps. collinus*. Denticles moderate to obliterated. Trailing margin concave, moderately curved. Anterior and median blister rows subequal in thickness, AB and MB rows much thicker than PB row. Median blister 2 only slightly larger in area than MB1, individual PBs subequal in area. Central paranotal blisters occupying two-thirds of paranotal breadth. Lateral blisters anteriorly widening laterad.

*Gonopod* (Figs 8, 33): Gonocoxa ventral lobe with two gonocoxal plates stacked dorsoventrally (Fig. 33A). Telopodite slender, kinked at pulvillus, strongly curved terminally. Pulvillus medium-sized, rounded, midway between base and terminus of acropodite. Processes *e1*, *e3*, *m3* and *m4* absent. Process *e2* large, subtriangular, connected to *m2* via prominent transverse ridge (Fig. 8); *e4* small, surrounded by terminal bristles (Fig. 33A). Process *m1* medium-sized, medial of pulvillus; *m2* large, subtriangular (Fig. 33B).

### *Type notes*

*Polydesmus serratus (non vidi):* Type material no longer extant. According to Hoffman (1999), Say collected millipedes on Assateague and Chincoteague Islands, off the eastern shore of Virginia. New collections from this area could serve as material to designate a neotype. In his description, Say noted that this species was found under the bark of *Pinus variabilis* (Aiton) Lamb., now a synonym of *Pinus echinata* Mill., shortleaf pine (Govaerts, 2019).

*Polydesmus pennsylvanicus (non vidi):* Type material unknown, from 'Pensylvanien'.

*Polydesmus scopus (♂ HT, USNM, vidi):* From Ledges State Park, Boone Co., IA, USA, collected 19 May 1941 by D. T. Jones. ♂ HT in fragments with one loose gonopod. Chamberlin (1942a) mentioned one female collected nearby but expressed doubt in its identity.

*Polydesmus planicolens (♂ HT, USNM, vidi):* From Ames, Story Co., IA, USA, collected spring 1941 by D. T. Jones. ♂ HT fragmented with gonopods in small vial, gnathochilarium dissected.

### *Distribution*

Minnesota east to southern Quebec, south to northern South Carolina, west to east Texas. Absent from Georgia and peninsular Florida.

### *Additional specimens examined*

**FMNH INS**1413, 1416, 1423, 1436, 1441, 1443, 1452, 1453, 1454, 1495, 1513, 1514, 1517, 1559, 1572, 1576, **2817***, 2818, **2819***, 2820, 2821, 2823, 2827, 2828, 2829, 2832, 2833, 2835, 4814, 7103, 7104, 7109, 7185, 7207, 7312, 7316, 7348, 7363, 7366, 7373, 7384, 7390, 7490, **8238***; **VTEC MPE01173***.

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## REFERENCES

**Attems CMT Graf von. 1894.** Die Copulationsfüsse der Polydesmiden. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abteilung I* **103:** 39–54.

**Attems CMT Graf von. 1898.** System der Polydesmiden I. Theil. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* **67:** 221–482.

**Attems CMT Graf von. 1914.** Die indo-australischen Myriopoden. *Archiv für Naturgeschichte, Abteilung A* **80:** 1–398.

**Attems CMT Graf von. 1926.** Progoneata. In: Kükenthal WG, ed. *Handbuch der Zoologie, Vierter Band, Erste Hälfte*. Berlin: De Gruyter, 7–238.

**Attems CMT Graf von. 1940.** Myriapoda 3. Polydesmoidea III. Fam. Polydesmidae, Vanhoeffeniidae, Cryptodesmidae,

Oniscodesmidae, Sphaerotrichopidae, Periodontodesmidae, Rhachidesmidae, Macellolophidae, Pandirodesmidae. *Das Tierreich* **70:** 1–577.

**Bollman CH. 1887a.** New genus and species of Polydesmidae. *Entomologica Americana* **3:** 45–46.

**Bollman CH. 1887b.** Description of fourteen new species of North American myriapods. *Proceedings of the United States National Museum* **10:** 617–627.

**Bollman CH. 1888.** A preliminary list of the Myriapoda of Arkansas, with descriptions of new species. *Entomologica Americana* **4:** 1–8.

**Brölemann HW. 1916.** Essai de classification des Polydesmiens. *Annales de la Société Entomologique de France* **84:** 523–608.

**Carl J. 1902.** Exotische Polydesmiden. *Revue Suisse de Zoologie* **10:** 563–679.

**Carl J. 1941.** Diplopodenstudien V. 3. Die Gonopoden der Gattung *Pseudopolydesmus* Att. *Zoologischer Anzeiger* **133:** 291–295.

**Causey NB. 1952.** Some records and descriptions of polydesmoid millipeds from the United States. *The Chicago Academy of Sciences Natural History Miscellanea* **106:** 1–11.

**Chamberlin RV. 1942a.** On a collection of myriapods from Iowa. *The Canadian Entomologist* **74:** 15–17.

**Chamberlin RV. 1942b.** New southern millipeds. *Bulletin of the University of Utah* **32**(8): 1–19.

**Chamberlin RV. 1943a.** A new *Polydesmus* from Missouri and Oklahoma (Diplopoda). *Entomological News* **54:** 15–16.

**Chamberlin RV. 1943b.** On nine North American polydesmoid millipeds. *Proceedings of the Biological Society of Washington* **56:** 35–40.

**Chamberlin RV. 1943c.** On some genera and species of American millipeds. *Bulletin of the University of Utah* **34**(6): 1–20.

**Chamberlin RV. 1946.** On four millipeds from Georgia and Mississippi. *Proceedings of the Biological Society of Washington* **59:** 139–142.

**Chamberlin RV. 1947.** Some records and descriptions of diplopods chiefly in the collection of the academy. *Proceedings of the Academy of Natural Sciences of Philadelphia* **99:** 21–58.

**Chamberlin RV. 1949.** Some millipeds of the families Polydesmidae and Xystodesmidae. *Journal of the Washington Academy of Sciences* **39:** 94–102.

**Chamberlin RV. 1951.** Records of American millipeds and centipeds collected by Dr. D. Elden Beck in 1950. *Great Basin Naturalist* **11:** 27–35.

**Chamberlin RV**, **Hoffman RL. 1958.** Checklist of the millipeds of North America. *Bulletin of the United States National Museum* **212:** 1–236.

**Djursvoll P. 2008.** Revision of the Iberian millipede genus *Schizomeritus* Verhoeff, 1931 (Diplopoda: Polydesmidae), with the description of three new species. *International Journal of Myriapodology* **1:** 111–122.

**Djursvoll P**, **Golovatch SI**, **Johanson KA**, **Meidell BA. 2000.** Phylogenetic relationships within *Polydesmus sensu lato* (Diplopoda: Polydesmidae). In: Wytwer J, Golovatch SI, eds. *Progress in Studies on Myriapoda and Onychophora, Fragmenta Faunistica 43, Supplement*. Warsaw: Museum and Institute of Zoology, Polish Academy of Sciences, 37–59.

**Gervais P. 1847.** Myriapodes. In: Walckenaer CA, ed. *Histoire Naturelle des Insectes, Aptères, Tome Quatrième*. Paris: Libraire Encyclopédique de Roret, 1–623.

**Golovatch SI. 1991.** The millipede family Polydesmidae in Southeast Asia, with notes on phylogeny (Diplopoda: Polydesmida). *Steenstrupia* **17:** 141–159.

**Golovatch SI. 2013.** Two new and one little-known species of the millipede genus *Epanerchodus* Attems, 1901 from southern China (Diplopoda, Polydesmida, Polydesmidae). *Fragmenta Faunistica* **56:** 157–166.

**Golovatch SI**, **Geoffroy JJ. 2006.** Review of the Southeast Asian millipede genus *Pacidesmus* Golovatch, with the description of a new troglobitic species from southern China (Diplopoda: Polydesmida: Polydesmidae). *Zootaxa* **1325:** 363–368.

**Govaerts R. 2019.** *Pinus variabilis* (Aiton) Lamb., Descr. Pinus 1: 22 (1803). In: Govaerts R, ed. *World Checklist of Selected Plant Families*. Available at: https://wcsp.science.kew.org/namedetail.do?name_id=380053, last accessed 25/3/2019.

**Hoffman RL. 1950.** Notes on some Virginia millipeds of the family Polydesmidae. *The Virginia Journal of Science* **1:** 219–225.

**Hoffman RL. 1974.** A new polydesmid milliped from the southern Appalachians, with remarks on the status of *Dixidesmus* and a proposed terminology for polydesmid gonopods. *Proceedings of the Biological Society of Washington* **87:** 345–350.

**Hoffman RL. 1980.** *Classification of the Diplopoda*. Geneva: Muséum d'Histoire Naturelle de Genève.

**Hoffman RL. 1999.** Checklist of the millipeds of north and middle America. *Virginia Museum of Natural History Special Publication* **8:** 1–584.

**International Commission of Zoological Nomenclature 1999.** *International Code of Zoological Nomenclature, 4th edn*. London: The International Trust for Zoological Nomenclature.

**Jeekel CAW. 1965.** The identity of *Dalodesmus tectus* Cook, 1896, and the status of the family names Dalodesmidae Cook, 1896, Vanhoeffeniidae Attems, 1914, and Sphaerotrichopodidae Attems, 1914 (Diplopoda, Polydesmida). *Entomologische Berichten* **25:** 236–239.

**Johnson BM. 1954.** A new species of milliped, genus *Dixidesmus*, from Michigan. *The Chicago Academy of Sciences Natural History Miscellanea* **137:** 1–5.

**Koch CL. 1847.** System der Myriapoden mit den Verzeichnissen und Berichtigungen zu Deutschlands Crustaceen, Myriapoden und Arachniden. In: Panzer GWF, Herrich-Schäffer A, eds. *Kritische Revision der Insectenfaune Deutschlands* **3:** 1–196.

**Koch CL. 1863a**. *Die Myriapoden, Getreu nach der Natur abgebildet und beschrieben, Erster Band*. Halle: H. W. Schmidt.

**Koch CL. 1863b.** *Die Myriapoden, Getreu nach der Natur abgebildet und beschrieben, Zweiter Band*. Halle: H. W. Schmidt.

**Lawrence RF. 1954.** Fluorescence in Arthropoda. *Journal of the Entomological Society of Southern Africa* **17:** 167–170.

**Loomis HF. 1943.** New cave and epigean millipeds of the United States, with notes on some established species.

*Bulletin of the Museum of Comparative Zoology* **92:** 371–410.

**Loomis HF. 1959.** Millipeds collected en route from Florida to San Antonio, Texas, and vicinity. *Journal of the Washington Academy of Sciences* **49:** 157–163.

**Loomis HF**, **Hoffman RL. 1948.** Synonymy of various diplopods. *Proceedings of the Biological Society of Washington* **61:** 51–54.

**Marek PE 2017.** Ultraviolet-induced fluorescent imaging for millipede taxonomy. *Research Ideas and Outcomes* **3:** e14850.

**Means JC**, **Francis EA**, **Lane AA**, **Marek PE. 2015.** A general methodology for collecting and preserving xystodesmid and other large millipedes for biodiversity research. *Biodiversity Data Journal* **3:** e5665.

**Newport G. 1844.** A list of the species of Myriapoda, order Chilognatha, contained in the cabinets of the British Museum, with description of a new genus and thirty-two new species. *The Annals and Magazine of Natural History* **13:** 263–270.

**Nguyen DA. 2009.** A new species of the family Polydesmidae (Diplopoda: Polydesmida) from Vietnam. *International Journal of Myriapodology* **2:** 63–68.

**Peters WCH. 1864.** Übersicht der im Königl. zoologischen Museum befindlichen Myriopoden aus der Familie der *Polydesmi*, so wie Beschreibungen einer neuen Gattung, *Trachyjulus*, der *Juli* und neuer Arten der Gattung *Siphonophora*. *Monatsberichte der Königlich Preußischen Akademie der Wissenschaften zu Berlin* **1864:** 529–551.

**Petit G. 1976.** Developpements compares des appendices copulateurs (gonopodes) chez *Polydesmus angustus* Latzel et *Brachydesmus superus* Latzel (Diplopodes: Polydesmidae). *International Journal of Insect Morphology and Embryology* **5:** 261–272.

**Ramsey JM. 1966.** Vast migrating armies of the millipede, *Pseudopolydesmus serratus* (Say) in the Dayton region. *Ohio Journal of Science* **66:** 339.

**Remane A. 1952.** *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Leipzig: Geest & Portig.

**Rubin M**, **Lamsdell JC**, **Prendini L**, **Hopkins MJ. 2017.** Exocuticular hyaline layer of sea scorpions and horseshoe crabs suggests cuticular fluorescence is plesiomorphic in chelicerates. *Journal of Zoology* **303:** 245–253.

**Say T. 1821.** Description of the Myriapodae of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* **2:** 102–114.

**de Saussure HLF. 1860.** Faune des Myriapodes du Mexique avec la description de quelques espèces des autres parties de l'Amerique. *Mémoires de la Société de Physiques et d'Histoire Naturelle de Genève* **15:** 259–393.

**de Saussure HLF**, **Humbert A. 1870**. Études sur les Myriapodes. In: Milne-Edwards M, ed. *Mission Scientifique au Mexique et dans l'Amérique Centrale, Recherches Zoologiques, Sixième Partie, 2ème Section*. Paris: Imprimerie Imperiale, 1–211.

**Shear WA. 2012.** *Snoqualmia*, a new polydesmid millipede genus from the northwestern United States, with a description of two new species (Diplopoda, Polydesmida, Polydesmidae). *Insecta Mundi* **238:** 1–13.

**Shear WA**, **Reddell JM. 2017.** Cave millipedes of the United States. XIV. Revalidation of the genus *Speorthus* Chamberlin, 1952 (Diplopoda, Polydesmida, Macrosternodesmidae), with a description of a new species from Texas and remarks on the families Polydesmidae and Macrosternodesmidae in North America. *Insecta Mundi* **529:** 1–13.

**Shelley RM. 1988.** The millipeds of eastern Canada (Arthropoda: Diplopoda). *Canadian Journal of Zoology* **66:** 1638–1663.

**Shelley RM. 1993.** Revision of the milliped genus *Scytonotus* Koch (Polydesmida: Polydesmidae). *Brimleyana* **19:** 1–60.

**Shelley RM. 1996.** The identity of *Alpertia lunatifrons* Loomis (Polydesmida: Polydesmidae), with records of introduced polydesmids from the northwestern states, deletion of *Polydesmus racovitzai* Brölemann, and identification of invalid taxa. *Myriapodologica* **4:** 17–20.

**Shelley RM. 2000.** Annotated checklist of the millipeds of Florida (Arthropoda: Diplopoda). *Insecta Mundi* **14:** 241–251.

**Shelley RM**, **Snyder BA. 2012.** Millipeds from the eastern Dakotas and western Minnesota, USA, with an account of *Pseudopolydesmus serratus* (Say, 1821) (Polydesmida: Polydesmidae); first published records from six states and the District of Columbia. *Insecta Mundi* **239:** 1–17.

**Sierwald P. 2018.** *Polydesmus* Latrellie, 1802. In: Sierwald P, Spelda J, eds. *MilliBase*. Available at: http://millibase.org/aphia.php?p=taxdetails&id=894050, last accessed 25/3/2019.

**Sierwald P**, **Bond JE**, **Gurda GT. 2005.** The millipede type specimens in the collections of the Field Museum of Natural History (Arthropoda: Diplopoda). *Zootaxa* **1005:** 1–64.

**Verhoeff KW. 1928.** Zur Kenntnis der Diplopodenfauna Ungarns. 109. Diplopoden-Aufsatz (Chilopoden). *Állattani Közlemények* **25:** 182–199.

**Verhoeff KW. 1929.** Zur Systematik, vergleichenden Morphologie und Geographie europäischer Diplopoden, zugleich ein zoogeographischer Beitrag. 111. Diplopoden-Aufsatz. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* **57:** 555–659.

**Verhoeff KW. 1931.** *Pseudopolydesmus* "im Wechsel der Zeiten". 122. Diplopoden-Aufsatz. *Zoologischer Anzeiger* **94:** 305–318.

**Welch VL**, **Van Hooijdonk E**, **Intrater N**, **Vigneron JP. 2012.** Fluorescence in insects. In: Liang R, ed. *Conference proceedings of SPIE: nature of light: light in nature IV*. Available at: https://doi.org/10.1117/12.929547, last accessed 25/3/2019.

**Williams SR**, **Hefner RA. 1928.** The millipedes and centipedes of Ohio [Ohio Biological Survey Bulletin 4(3)]. *Ohio State University Bulletin* **33:** 93–146.

**Withrow RP. 1988.** *Revision of the genus Pseudopolydesmus Attems, 1898 and its relationships to the North American genera of the family Polydesmidae Leach, 1815*. Unpublished D.Phil. Thesis, Ohio State University. Available from: University Microfilms, Ann Arbor, order no. 8820372.

**Wood HC. 1865.** On the Myriopoda of North America. *Transactions of the American Philosophical Society* **13:** 137–248.