Taxonomic synthesis of the eastern North American millipede genus *Pseudopolydesmus* Attems, 1898 (Diplopoda: Polydesmida: Polydesmidae), utilizing high-detail ultraviolet fluorescence imaging

Running title: **Genus review of *Pseudopolydesmus***

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INTRODUCTION

The millipede genus *Polydesmus* Latreille, 1802 is among the first 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). Over its history, the genus has accumulated about 480 specific names, of which over 250 remain. The other species have been moved to other genera and families or are of uncertain status (Sierwald, MilliBase 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 within 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 Palearctic relatives, and to the family's name-bearing genus *Polydesmus* in particular. The diversity of gonopodal structures (copulatory organs in males) and the lack of a standardized terminology based on explicit homology hypotheses among members of Polydesmidae hampers the comparison of taxa within it. For example, the pattern of seta-bearing dorsal blisters as well as gonopods of *Pseudopolydesmus* strongly resemble those of the Palearctic species *Polydesmus inconstans* Latzel, 1883 and *Polydesmus complanatus* (Linnaeus, 1761). However, since it is dubious that all nominal members of *Polydesmus* are monophyletic, comparisons with other taxa in this 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 United States and are among the widest-ranging of the North American millipede genera. These medium-sized millipedes (up to about 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 (Fig. 1, Fig. 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, in his checklist of North American millipedes (1999), 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 make 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 be easily adapted for imaging a broad range of arthropod taxa.

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

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 employed 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, though 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.

Light microscopy & ultraviolet imaging

High depth of field (HDOF) photographs of gonopods and somatic characters were obtained using visible and ultraviolet light. Ultraviolet-induced fluorescence photography was adapted for focus-stacking photographic methods and equipment. Because of the small size and pale, uniform color 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).

Ultraviolet-induced fluorescent imaging of *P. paludicolus* (gonopod images) and *P. 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 Field Museum's Collaborative Invertebrate Laboratories, employing the following techniques. To obtain HDOF photographs, we employed a focus stacking technique using 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, 5x Achrovid and 10x Achrovid (Visionary Digital/Dun, Inc., Ashland, VA; Infinity Photo-Optical, Boulder, CO).

Specimens were secured in a 50 mm glass Petri dish embedded in a drop of clear hand sanitizer and then covered with 70% alcohol. A stage with a magnetic lock (Visionary Digital/Dunn, Inc., Ashland, VA) 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 add additional light at high magnification. A black card was used for the background to contrast with the color of the specimens. CamLift version 2.6.0 (Visionary Digital/Dun, Inc., Ashland, VA) was used to control the motorized lift of the system. Control My Nikon version 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., Ashland, VA) connected to a Dynalite M2000DR Power Pack (Dynalite, Union, NJ). Dynalite output settings varied from 250 watts/second for lower magnification to 1000 watts/second 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.

Ultraviolet illumination was from three Convoy S2+ Nichia 365 nm LED flashlights (Shenzhen Convoy Electronics Co., Ltd., China) which 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 lab stands and arranged radially around the stage at a distance of approximately 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, as the UV light from 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 speeds (from one-third second to two seconds) and auto white balance. All photos were saved in TIFF format.

Focal stacks were imported into Adobe Lightroom version 5.7. Each finished composited photograph consisted of between 10 (low magnification) to 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. UV stacks were subjected to a temperature adjustment to 10,000 Kelvin 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 version 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 *P. collinus* and *P. 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 taken with a Leo SEM (Carl Zeiss SMT, Peabody, MA). First, samples were ultrasonically cleaned, and dehydrated in an ethanol series (80%, 90%, 95% and two times in 100%) and then air-dried overnight. The specimens were mounted on aluminum stubs and coated with gold in a sputter coater for 240 seconds. Adobe Photoshop CS6 was used to clean image backgrounds, and a 2.0-3.0 high pass filter was applied to adjust white balance of the images.

Institutional abbreviations

Institutional abbreviations used in this paper are as follows: Academy of Natural Sciences of Drexel University, Philadelphia (ANSP); Natural History Museum [British Museum of Natural History], London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Muséum d'Histoire Naturelle de Genève, Switzerland (MHNG); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Virginia Museum of Natural History, Martinsville, Virginia (VMNH); Virginia Polytechnic Institute Insect Collection, Blacksburg, Virginia (VTEC).

Specimen catalog 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. Type material is abbreviated in literature citations and type notes as follows: Holotype (HT); Syntype (ST); Paratype (PT).

RESULTS

Taxonomic history of the genus *Pseudopolydesmus*

Beginning with Thomas Say's 1821 description of *P. 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 proven redundant. Chamberlin & Loomis (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 may have viewed a gonopod from different angles, causing them to erroneously designate new species (Withrow, 1988: 4). Chamberlin alone named 18 species between 1942-1951, 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—though the actual 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 *P. canadensis* that more closely match *P. serratus*, leading Bollman (1887b) to mistakenly refer to *P. canadensis* as a junior synonym of *P. serratus* and create the species name *Polydesmus branneri* in its stead. Consequently, *P. canadensis* is instead often referred to as *Polydesmus branneri*, *Pseudopolydesmus branneri*, or *Dixidesmus branneri* in late nineteenth and early twentieth century literature.

Attems (1898) established the genus *Pseudopolydesmus* with the type species *Pseudopolydesmus 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 *P. canadensis* lacks a seminal chamber and a pulvillus ('*Samenblase*' and '*Haarpolster*' respectively, in Attems, 1940: 3) in contrast with 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 likely *P. 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 with Withrow's (1988) *canadensis* species group (see below). Hoffman (1974) homologized these processes as *e1* and *e2*, respectively, and pointed out that while the telopodite of *Pseudopolydesmus 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 *canadensis* group comprising *pinetorum, tallulanus, erasus*, *canadensis,* and *collinus*; and the *serratus* group comprising *serratus, minor, caddo,* and *paludicola* [sic]. Withrow also suggested numerous synonymies. Hoffman, in his 1999 checklist, recognized 12 *Pseudopolydesmus* species and introduced a number of new synonymies. Hoffman did not examine type specimens, basing

231 his classification solely on material conserved in the Virginia Museum of Natural History.
232 Some of his accepted species names differ from those of Withrow (1988), who did examine
233 type material. However, Withrow's dissertation was never published in accordance with the
234 International Code of Zoological Nomenclature (ICZN 1999, Article 9.12; see discussion in
235 Shelley, 1996). Therefore, those of Withrow's subjective species name snynonymies that we
236 affirm are considered new synonymies as of this publication. In our taxonomic section, we
237 use square brackets to indicate Withrow's invalid taxonomic assignments.
238
239 **Gonopod Terminology in *Pseudopolydesmus***
240 In the order Polydesmida, the anterior leg pair of the seventh body ring (eighth leg
241 pair) in males is modified into a pair of sperm transfer organs called gonopods. The ninth leg
242 pair remains as normal walking legs. Attems (1894) was the first to define separate sections
243 within the gonopods, and discussed possible homologies with leg podomeres. The putative
244 associations of leg podomeres with parts of the male gonopod have shifted over time due to
245 the difficulty in assigning homology to the podomeres distal from the coxa, resulting in
246 several terms that have multiple precise definitions.
247 Moreover, gonopod terminology varies within the family Polydesmidae between
248 genera and among different authors (as discussed by Hoffman, 1974). Eurasian polydesmids
249 often have comparably more complex gonopods, with additional processes and branches
250 compared to American representatives. These branches and processes have often been
251 assigned names across various genera without discussing homology hypotheses. As a result,
252 the names for these structures have proliferated wildly, and the existing nomenclature for the
253 gonopods is unwieldy. Various schemes of alphanumeric labeling of gonopod processes have
254 been adopted more or less *de novo* for each newly discovered form. This has made

255 descriptions of similar taxa difficult to compare and discerning homology between genera
256 challenging (*e.g.* Djursvoll *et al.*, 2000; Djursvoll, 2008; Golovatch, 2013).

257 Regarding the North American Polydesmidae, the presence of fewer species and
258 simpler gonopod morphology have resulted in a more uniform set of terms, but there are still
259 cases in which identical terms refer to different structures. For example, Shelley (1993, figs
260 5-6) used the term endomerite for the entire caudal branch carrying the pulvillus (see below)
261 in *Scytonotus*, whereas Hoffman (1950: fig. 4; 1974: 349) used the term for only the pulvillus
262 in *Pseudopolydesmus*. Djursvoll *et al.* (2000) used the descriptive term pulvillus
263 (‘*Haarpolster*’ of Attems, 1940) instead of endomerite.

264 The *Pseudopolydesmus* gonopod consists of a moveable telopodite with a single distal
265 branch (acropodite) subtended by a large coxa and cannula typical of Polydesmida. Verhoeff
266 (1931) recognized three sections of the telopodite: the basal prefemoral region carrying setae,
267 the femoral region lacking setae, and the terminal region which he called the tibiotarsus. We
268 emphasize caution when using these terms because they imply false homologies with
269 podomeres of the walking legs (Petit, 1976). The sperm groove (or seminal canal) originates
270 at the medial insertion of the cannula in the basal “prefemur”, then runs distad while twisting
271 around cephalically to the ectal (lateral) side of the femoral section, then curving caudad
272 before opening at the base of the pulvillus (‘*Haarpolster*’ in Attems, 1940 and Verhoeff,
273 1931; ‘endomerite’ in Hoffman, 1974 and others). The functional morphology of the ‘large
274 seminal chamber’ and its relationship, if any, with the sperm groove is uncertain and deserves
275 further anatomical study (see Verhoeff, 1928, 1931; Carl 1941).

276 In his paper describing *Pseudopolydesmus collinus*, Hoffman (1974) introduced a
277 standardized system for denoting the processes along the distal region of the acropodite,
278 accompanied by a detailed drawing (see Fig. 3, after Hoffman, 1974). He designated
279 processes on the ectal side of the gonopod *e1* through *e4*, and those on the medial (mesal)

side *m1* through *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 applied the system to each of his recognized species; however, in his re-descriptions, key to *Pseudopolydesmus* species, and character matrix for phylogenetic analysis, Hoffman's system is not consistently used. For example, in step 1a of his key to species, Withrow identifies the *canadensis* group by the presence of process *e3* and the absence of *m2*. However, in contradiction, step 3a identifies *P. erasus* and *P. tallulanus* (both members of the *canadensis* group according to Withrow) by the presence of *m2*, while step 4a identifies *P. erasus* by the absence of *e3*. Furthermore, his illustrations of gonopods do not unambiguously show the characters cited for species identification, nor are the structures labelled.

Under Hoffman's (1974) system, homology hypotheses for acropodite processes are based on: a) position and b) 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, while *m4* is recognized by a tuft of special bristles which 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. Due to its unique position, offset ectad from the edge of the telopodite, we hypothesize that *m3* is only present in *P. canadensis*, and that the intermediate medial process in *P. caddo* and *P. 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*.

Table 1.
Summary of telopodite processes in *Pseudopolydesmus*

e1	Thin spine arising on distal flange of pulvillus, present in *P. erasus* and *P. canadensis*, present but reduced in *P. collinus*
e2	Rather large, recurved spine, arising on combined stalk with *e3* in *P. canadensis* and *P. collinus*; forms transverse ridge to *m2* in *P. caddo* and *P. serratus*
e3	Medium sized spine, arising at or close to base of *e2* mostly opposite of *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, mostly opposite to *e2* and *e3*
m3	Small to medium spine, in *P. canadensis* offset laterad from the medial edge towards the center line of acropodite, in *P. 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.	*P. erasus*	Y	Y	Y[a]	Y	Y	Y	-	Y
3a.	*P. canadensis*	Y	Y	Y	Y	Y	Y	Y	Y
3b.	*P. collinus*	Y[b]	Y	Y	Y	Y	Y	-	Y
4a.	*P. pinetorum*	-	Y	Y	Y	Y	Y	-	Y
6a.	*P. minor*	-	Y[b]	-[c]	Y	Y	Y	-	Y
6b.	*P. caddo*	-	-	Y	-	Y	Y	-	Y
7a.	*P. paludicolus*	-	Y	-	Y	Y	Y	Y	-
7b.	*P. serratus*	-	Y	-	Y	Y	Y	-	-

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

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 blister's posterior apex. 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 *P. 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, MB2), and the posterior row of six (PB1, PB2, 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 elongated lateral blister (LB) carrying one seta near its posterior end. The paired LB additionally bear the ozopores on ozoporous body rings.

In general, each blister carries one seta, although the AB and CB each carry two. However, a slight longitudinal furrow may sometimes be visible separating the setae of each AB, suggesting that the AB each represent two subquadrate blisters that have merged. Similarly, a very slight transverse furrow may sometimes separate the two setae of the CB, suggesting that the CB represent a merging of blisters from the anterior and median rows.

Paranota Morphology

Several *Pseudopolydesmus* species can be easily distinguished 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).

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)

Furthermore, to describe the silhouette of the paranota in addition to their overall dimensions, we introduce 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 actual 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 which occur in a predictable pattern. All non-ozoporous body rings bear three denticles along each paranotum, while 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. While 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.

373

374 **TAXONOMIC SECTION**

375 Order **Polydesmida** Leach, 1815

376 Family **Polydesmidae** Leach, 1815

377

378 Genus ***Pseudopolydesmus*** Attems, 1898

379 *Pseudopolydesmus* Attems, 1898. *Denkschriften der Kaiserlichen Akademie der*
380 *Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 67: 270, 479. Type
381 species: *Polydesmus canadensis* Newport, 1844, by monotypy; synonymized under
382 *Polydesmus* in a footnote by Carl, 1902: 613; revalidated by Verhoeff, 1931: 305.

383 *Pseudopolydesmus:*-- Attems, 1914. *Archiv für Naturgeschichte, Abteilung A* 80(4): 161.

384 *Pseudopolydesmus:*-- Brölemann, 1916. *Annales de la Société Entomologique de France* 84:
385 569.

386 *Pseudopolydesmus:*-- Attems, 1926. *Handbuch der Zoologie* 4(1): 139.

387 *Pseudopolydesmus:*-- Verhoeff, 1929. *Zoologische Jahrbücher, Abteilung für Systematik,*
388 *Ökologie und Geographie der Tiere* 57: 619.

389 *Pseudopolydesmus:*-- Verhoeff, 1931. *Zoologischer Anzeiger* 94(11-12): 305, figs. 1-7.
390 Definition of genus *Pseudopolydesmus*, detailed examination of *Pseudopolydesmus*
391 *serratus* gonopod.

392 *Pseudopolydesmus:*-- Attems, 1940. *Das Tierreich* 70: 139, figs. 201-202.

393 *Pseudopolydesmus:*-- Carl, 1941. *Zoologischer Anzeiger* 133(11-12): 291-295, figs. 1-2.
394 Detailed examination of *Pseudopolydesmus pinetorum* gonopod.

395 *Pseudopolydesmus:*-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 17.

396 *Pseudopolydesmus:*-- Hoffman, 1950. *The Virginia Journal of Science* 1(3): 222, fig. 4.

Pseudopolydesmus:-- Hoffman, 1974. *Proceedings of the Biological Society of Washington* 87(31): 346.

[*Pseudopolydesmus:*-- Withrow, 1988. Unpublished D. Phil. thesis, Ohio State University: 64. Recognized nine species and proposed 20 species-level synonymies.]

Pseudopolydesmus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 442. Recognized 12 species, established 15 new species-level synonymies.

Pseudopolydesmus:-- Djursvoll *et al.,* 2000. *Fragmenta Faunistica* 43, Supplement: 40.

Dixidesmus Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18. Type species: *D. tallulanus* Chamberlin, by original designation. Synonymized by Hoffman, 1974: 346.

Dixidesmus Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 65.

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 maximum width of mandibular stipites (narrower in *Polydesmus* and *Brachydesmus*, *e.g.* Djursvoll *et al.*, 2000: 43, fig. 2A), except in *Pseudopolydesmus paludicolus*. Color 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 antero-dorsad, forming a narrow rim. Tergal sculpture pattern (described above, Fig. 4) very similar to other members of Polydesmidae, such as *Polydesmus inconstans* and *Polydesmus complanatus*, the latter of which is the type species of *Polydesmus*. Tergal blister pattern in *Pseudopolydesmus* less distinct than the strongly

422 impressed pattern of *Polydesmus*. Unlike *Po. inconstans* and *Po. complanatus*, tergal setae
423 not usually visible under dissecting microscope except in *Ps. paludicolus*, but may be visible
424 with UV enhancement.
425 Gonopod: Gonocoxae large, with two long setae at the ventro-medial margin.
426 Posterior margin of gonocoxa divided into ventral and dorsal plate-like lobes that partially
427 surround the telopodite basally. Ventral lobe with one or two gonocoxal plates stacked
428 dorsoventrally. Telopodite falcate. Seminal canal originating medially before looping laterad,
429 debouching at ectal base of pulvillus. Pulvillus entirely covered in bristles (Fig. 3). Seminal
430 chamber large, with an associated duct (duct of the telopodite gland according to Verhoeff,
431 1931). Acropodite bearing between four and eight dentate to laminar processes along its ectal
432 and medial surfaces; subterminally bearing from about 10 to 60 terminal bristles (Fig. 5, not
433 socketed like true setae) similar in appearance to a toothbrush; terminally bifurcating into
434 small ectal and medial processes or laminae too small to distinguish under dissecting
435 microscope.
436 Somatic male characters: Prefemora of all walking legs beginning with leg pair 3
437 (body ring 4) strongly swollen dorsad in *Pseudopolydesmus* males (Fig. 6), much more than
438 in *Polydesmus* males. Male sterna with prominent paired lobes or tubercles of various shapes
439 between leg pairs of body rings 5, 6, 7, and 8 (Fig. 7), which carry stiff, peg-like setae,
440 differing from the unmodified setae of the walking legs. Leg pair 3 (body ring 4) with a pair
441 of low lobes in some species; leg pairs 4 and 5 (body ring 5) with prominent lobes; leg pair 6
442 (anterior legs of body ring 6) with strongly elongated tubercles; leg pair 7 with small tuft of
443 peg-like setae; leg pair 9 (directly posterior to gonopods) with tubercles flattened into
444 longitudinal ridges (Fig. 8); leg pair 10 (anterior leg pair of body ring 8) with prominent
445 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 *P. erasus*) there is an additional pair of lobes at the base of leg pair 11.

Key to species of *Pseudopolydesmus* males

1. a. Large recurved *e2* process or fused recurved *e2*+*e3* process.....2
   b. Non-recurved *e2* process.....4

2. (1) a. Large recurved *e2* process not fused with *e3* process or *e3* process absent.. *P. erasus*
   b. Fused *e2*+*e3* process 3

3. (2) a. *m3* process disto-laterad of *m2* process; elongate *e1* process ..... *P. canadensis*
   b. *m3* process absent; *e1* process absent or severely reduced..... *P. collinus*

4. (1) a. Large, spike-shaped *e3* process; large rounded pulvillus .....*P. pinetorum*
   b. Ectal processes subtriangular or flanged; pointed pulvillus 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. Large triangular *m2* located proximal to smooth ectal flange..... *P. minor*
   b. No process between *e3*-bearing ectal flange and pulvillus..... *P. caddo*

7. (5) a. Strongly flanged medial surface bearing processes *m2* and *m3*..... *P. paludicolus*

b. Not flanged, with pronounced transverse ridge connecting *e2* and *m2*.....*P. serratus*

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. 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)

Polydesmus erasus Loomis, 1943. *Bulletin of the Museum of Comparative Zoology* 92(7): 406, fig. 17, pl. 1: fig. 5. MALE HT (MCZ, *non vidi*) from Huntsville, Madison Co., Alabama. According to Loomis' description, the *e3* process was completely absent in *P. erasus*. No such specimen has been seen by the authors; more likely Loomis overlooked the process or his specimen was damaged.

Dixidesmus erasus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Dixidesmus erasus:-- Causey, 1952. *The Chicago Academy of Sciences Natural History Miscellanea* 106: 7.

Dixidesmus erasus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 66.

[*Pseudopolydesmus erasus:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 84, figs. 19, 84, 88, 92, 108, 113, 122-126, map 5, tables 9-11.]

Pseudopolydesmus erasus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 444.

Dixidesmus tallulanus Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 19, fig. 34. MALE HT (USNM, *vidi*) and males and females from a site between Clayton and Tallulah Falls, Rabun Co., Georgia, collected by W. Ivie, 28 April, 1943; MALE PT Tallulah Falls, collected by W. Ivie, 27 April 1943. Synonymized by Hoffman, 1999: 444 under *erasus* (listed as *syn. nov.*).

Dixidesmus tallulanus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 67.

[*Pseudopolydesmus tallulanus:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 79, figs. 75, 83, 87, 91, 107, 112, 122-128, map 5, tables 9-11.] Considered a valid, separate species.

Dixidesmus penicillus Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 19, fig. 35. (USNM, *vidi*) from north and northwest of Clarkesville, Habersham Co., Georgia, unspecified number of males and females, collected by W. Ivie, 27 April 1943. Synonymized [under *tallulanus* by Withrow, 1988: 79;] under *erasus* by Hoffman, 1999: 444 (listed as *syn. nov.*).

Dixidesmus penicillus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 67.

Dixidesmus humilidens Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 20, fig. 36. (USNM, *vidi*) two males and two females from Gainesville, Hall Co., Georgia, collected 24 April 1943 by W. Ivie. Synonymized under *Dixidesmus erasus* by Causey, 1952: 7 and by Hoffman & Chamberlin, 1958: 66; [under *Pseudopolydesmus tallulanus* by Withrow, 1988: 79;] listed under *Pseudopolydesmus erasus* by Hoffman, 1999: 444.

Type Notes:

Dixidesmus tallulanus (USNM, *vidi*): Two vials with Chamberlin labels, labelled *Polydesmus tallulanus*. Type Lot 1 labelled HT, contains one male in fragments and gonopods in genitalia vial, identifiable as *erasus*; Type Lot 2 labelled PT, with one intact male identifiable as *erasus*.

Dixidesmus penicillus (USNM, *vidi*): 2 Chamberlin vials. Type Lot 1: vial labelled 'Types' contains small vial with HT label (by Withrow?) with male in fragments, 2 dissected gonopods in genitalia vial, identifiable as *erasus*; small vial with 'Lectoallotype' label (by Withrow?) with female in fragments; and 2 intact males and two females in fragments. Type Lot 2: vial labeled 'Paratypes' with two females and eight males, some males with damaged gonopods, all males identifiable as *erasus*.

Dixidesmus humilidens (USNM, *vidi*): One Chamberlin vial, labelled by Withrow as Holotype and Lectoallotype in two small vials. Withrow label identifies *erasus* Lectoallotype: adult female with everted vulvae. Male holotype in fragments in small vial, gonopods in vial, identifiable as *erasus*, plus one female, one fragment (female most likely in vial).

Diagnosis:

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

moderately curved, similar to *P. serratus* but less curved than *P. canadensis* and *P. collinus*. Denticles weak to obliterated. Trailing margin only slightly concave, nearly straight. Anterior blister (AB) row medially much thicker than median blister row (MB), narrowing laterally to become much narrower than MB. MB2 much larger in area than MB1. MB row thicker than posterior blister row (PB). Central paranotal blisters (CB) occupying medial two-thirds of paranota. Lateral blisters (LB) anteriorly extending mediad.

Gonopod (Figs. 10, 11, 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).

Range: 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 INS1554, 1556, 3120684, **3120685***

Pseudopolydesmus canadensis (Newport, 1844)

Polydesmus canadensis Newport, 1844. *The Annals and Magazine of Natural History* 13: 265. Immature FEMALE HT (BMNH, *non vidi*, type presumed extant) from Albany

River, Hudson Bay, Ontario, Canada. Synonymized under *serratus* by Bollman, 1887b: 620; resurrected by [Withrow, 1988: 89 and] Hoffman, 1999: 443.

Polydesmus canadensis:-- Gervais, 1847. *Histoire naturelle des Insectes. Aptères* 4: 106.

Polydesmus canadensis:-- Saussure & Humbert, 1870. *Mission scientifique au Mexique et dans l'Amérique centrale: Recherches Zoologiques* 6(2): 52.

[*Pseudopolydesmus canadensis:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 89, figs. 55, 61, 70-73, 76, 109, 114, 122-126, map 6, tables 9-11.]

Pseudopolydesmus canadensis:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 443.

Pseudopolydesmus canadensis:-- Shelley, 2000. *Insecta Mundi* 14(4): 246.

Polydesmus glaucescens C.L. Koch, 1847. *Kritische Revision der Insectenfaune Deutschlands* 3: 133. Location of types, if extant, unknown, labeled only 'Nordamerika.' Synonymized under *serratus* in a footnote by Bollman, 1887b: 620; under *canadensis* by Hoffman, 1999: 443.

Polydesmus glaucescens:-- C.L. Koch, 1863. *Die Myriapoden. Getreu nach der Natur abgebildet und beschrieben. Band 1*: 59, pl. 26: fig. 51.

Pseudopolydesmus glaucesens:-- Attems, 1940. *Das Tierreich* 70: 141. Uncertain placement.

Polydesmus branneri Bollman, 1887b. *Proceedings of the United States National Museum* 10: 620. MALE HT (USNM, *vidi*) from Mossy Creek (now Jefferson City), Jefferson Co., Tennessee. Synonymized by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Polydesmus branneri:-- Loomis, 1943. *Bulletin of the Museum of Comparative Zoology* 92(7): 405, fig. 16, pl. 1: fig. 4.

Dixidesmus branneri:-- Loomis & Hoffman, 1948. *Proceedings of the Biological Society of Washington* 61: 54.

Dixidesmus branneri:-- Hoffman, 1950. *The Virginia Journal of Science* 1(3): 223.

Dixidesmus branneri:-- Causey, 1952. *The Chicago Academy of Sciences Natural History Miscellanea* 106: 7.

Dixidesmus branneri:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 65.

Pseudopolydesmus branneri:-- Hoffman, 1974. *Proceedings of the Biological Society of Washington* 87(31): 346, fig. 3.

Pseudopolydesmus branneri:-- Shelley, 1988. *Canadian Journal of Zoology* 66: 1651, figs. 27, 31.

Polydesmus nitidus Bollman, 1887a. *Entomologica Americana* 3(3): 45. Location of type material unknown (not located at USNM), 15 specimens from Pensacola, Escambia Co., Florida. Synonymized by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus nitidus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 67.

Polydesmus echinogon Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 10, fig. 33. MALE HT (USNM, *vidi*) from Shawanese (a village on Harveys Lake), Luzerne Co., Pennsylvania, four specimens collected by F. C. Paulmier, 23 September 1905. Synonymized by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus echinogon:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Dixidesmus echinogon:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 66.

Polydesmus conlatus Chamberlin, 1943b. *Proceedings of the Biological Society of Washington* 56: 36, fig. 5. MALE HT (FMNH INS977, *vidi*) from Gatlingburg, Sevier Co., Tennessee, collected by H. Dybas, 13-19 June 1942. Type images available online. MALE PT (USNM, *vidi*) from Greenbrier Cove, Tennessee. Synonymized under *Dixidesmus branneri* by Loomis & Hoffman, 1948: 54; under *Pseudopolydesmus canadensis* by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus conlatus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Polydesmus conlatus:-- Sierwald *et al.*, 2005. *Zootaxa* 1005: 40.

Dixidesmus sylvicolens Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 20, fig. 37-38. MALE HT (USNM, *vidi*) from seven miles north of Sylvania, Screven Co., Georgia, collected by W. Ivie, 12 April 1943, numerous specimens. Synonymized by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus sylvicolens:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 67.

Dixidesmus christianus Chamberlin, 1946. *Proceedings of the Biological Society of Washington* 59: 140, fig. 4. MALE HT (USNM, *vidi*), three females, and immatures from Pass Christian, Harrison Co., Mississippi, collected by J. Rapp & W. Rapp, 15 Feb 1946. Synonymized under *Dixidesmus branneri* by Loomis & Hoffman, 1948:

54; under *P. canadensis* by [Withrow, 1988: 89 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus christianus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 66.

Dixidesmus catskillus Chamberlin, 1947. *Proceedings of the Academy of Natural Sciences of Philadelphia* 99: 24, fig. 2. MALE HT (ANSP, *non vidi*) from Catskill, Greene Co., New York. Synonymized under *branneri* by Shelley, 1988: 1652; under *canadensis* by [Withrow, 1988: 90 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus catskillus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 66.

Dixidesmus phanus Chamberlin, 1951. *Great Basin Naturalist* 11(1-2): 27, fig. 1. MALE HT (USNM, *vidi*) from Suwanee River, Florida, without further locality, five specimens, collected by D.E. Beck, 15 April 1950. Synonymized by [Withrow, 1988: 90 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus phanus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 67.

Dixidesmus gausodicrorhachus Johnson, 1954. *The Chicago Academy of Sciences Natural History Miscellanea* 137: 1, fig. 1. MALE HT (USNM, *vidi*) from west side of Garnet Lake, Mackinaw Co., Michigan. Synonymized under *branneri* by Shelley, 1988: 1652; under *canadensis* by [Withrow, 1988: 90 and] Hoffman, 1999: 443 (listed as *syn. nov.*).

Dixidesmus gausodicrorhachus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 66.

Type Notes:

Polydesmus branneri MALE HT (USNM, *vidi*): Vial with single male and one dissected gonopod, tip of gonopod damaged.

Polydesmus echinogon (USNM, *vidi*): Two type lots labelled 'Types' by Chamberlin located at USNM. Type lots contain an older label identifying the specimens erroneously as *P. serratus*. Type Lot 1: MALE HT (vial with label by Withrow) with single gonopod *in situ* and two dissected gonopods (one damaged), identifiable as *P. canadensis*. Single male specimen with single gonopod *in situ*, one female and one vial with fragmented female labeled Lectoallotype by Withrow. All male specimens in Type Lot 1 identifiable as *canadensis*. Type Lot 2, same locality: five females and female fragments, single male with single gonopod *in situ* identifiable as *canadensis*, one genitalia vial with single gonopod identifiable as *canadensis*; separated two males with gonopods *in situ* identifiable as *P. serratus* from Type Lot 2.

Polydesmus conlatus MALE HT (FMNH INS977 *vidi*): Adult, intact, gonopods *in situ*; with two adult females. Images available online. MALE PT (USNM, *vidi*): the vial located at the USNM is labeled paratype, and contains several specimens, at least one adult female and one adult male with a single gonopod in a separate genitalia vial. The specimens are from Greenbrier Cove, a locality that is not listed for types of this species in the original description. The male gonopod is identifiable as *canadensis*.

Dixidesmus sylvicolens MALE ST (USNM, *vidi*): One type lot with several specimens, Chamberlin label, Withrow label identifies lot as *branneri*, males clearly identifiable as *canadensis*.

Dixidesmus christianus MALE HT (USNM, *vidi*): One dissected male in fragments with single gonopod, labeled HT, two intact males and five small specimens. Males identifiable as *canadensis*; Withrow label identifies lot as *branneri*.

Dixidesmus phanus MALE HT (USNM, *vidi*): Two type lots with Chamberlin labels. Male HT in Type Lot 1 identifiable as *canadensis*, Withrow label identifies lot as *branneri*. Type Lot 2 with several female specimens.

Dixidesmus gausodicrorhachus MALE HT and PT (USNM, *vidi*): Male HT with single gonopod and male PT identifiable as *canadensis*, one female PT with everted vulva.

Diagnosis:

Size: Usually large, with length ranging from 11.8 mm 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 *P. erasus* and *P. serratus*. Often larger than *P. collinus*. Usually larger than *P. pinetorum*.

Paranota and tergal sculpture (Fig. 13): Corners of paranota forming a roughly rhomboid quadrilateral, with anterior lateral corner (ALC) posterior to anterior medial corner (AMC) and lateral to posterior lateral corner (PLC). Edges meeting at ALC and posterior medial corner (PMC) forming right angles, with posterior edge shorter than in *P. 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 *P. serratus*. Anterior (AB), median (MB), and posterior (PB) blister rows subequal in thickness. AB narrowing only slightly at lateral ends. Individual MB and PB subequal in area. Central paranotal blisters (CB) large, occupying over two-thirds of paranotal breadth, as wide as long. Lateral blisters (LB) 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* all large, subtriangular, equidistant from each other; *m3* offset laterad from *m2* and *m4* (Fig. 14B).

Range: 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 INS1421, 1455, 1461, 1465, 1552, 1569, 3574, **6934*,** 7632, 7699, 14219, **3120683***

Pseudopolydesmus collinus Hoffman, 1974

Pseudopolydesmus collinus Hoffman, 1974. *Proceedings of the Biological Society of Washington* 87(31): 346, figs. 1-2. MALE HT (VMNH, *non vidi* but see type notes) from Pinnacles of Dan, *ca.* four miles southwest of Vesta, Patrick Co., Virginia, collected 22 April 1972.

[*Pseudopolydesmus collinus:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 98, figs. 85, 89, 93, 110, 115, 122-126, map 7, tables 9-11.]

Pseudopolydesmus collinus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 444.

Type Notes: *Pseudopolydesmus collinus* (VMNH, *non vidi*): a jar labeled PARATYPE was found at VMNH. It contained a vial of 5 male paratypes (VMNH PSE00044) and a vial of 8 female paratypes (VMNH PSE00043). The holotype may have been included in the vial of male paratypes without a label. Two male paratype specimens from vial VMNH PSE00044 were individually relabeled and imaged (**VMNH PSE00202***, **VMNH PSE00203***).

Diagnosis:

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

Paranota and tergal sculpture (Fig. 15): Corners of paranota forming a roughly rhomboid quadrilateral, with anterior lateral corner (ALC) posterior to anterior medial corner (AMC) and lateral to posterior lateral corner (PLC). Edges meeting at ALC and posterior medial corner (PMC) forming right angles, with posterior edge longer than in *P. 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 ALC. Trailing margin moderately concave, less so than *P. serratus*. Anterior blister row (AB) medially thicker than median blister row (MB), narrowing only slightly at lateral ends. MB row thicker than posterior blister row (PB). Central paranotal blisters (CB) large, occupying over two-thirds of paranotal breadth, as wide as long. Lateral blisters (LB) 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 similarly sized *m2* (Fig. 16B).

Range: Southern Indiana east to West Virginia, south to central Virginia and north-central South Carolina. Williams & 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 this was a misidentification of *P. collinus*, though the figure lacks detail and most likely depicts *P. canadensis*, which also occurs in Ohio.

Pseudopolydesmus pinetorum (Bollman, 1888)

Polydesmus pinetorum Bollman, 1888. *Entomologica Americana* 4(1): 3. MALE HT (USNM, *non vidi*, type lost) from Little Rock, Pulaski Co., Arkansas.

Pseudopolydesmus pinetorum:-- Causey, 1952. *The Chicago Academy of Sciences Natural History Miscellanea* 106: 6, fig. 5.

Pseudopolydesmus pinetorum:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

[*Pseudopolydesmus pinetorum:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 72, figs 74, 80, 82, 86, 90, 106, 111, 122-128, map 4, tables 9-11.]

Pseudopolydesmus pinetorum:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 445.

Polydesmus americanus Carl, 1902. *Revue Suisse de Zoologie* 10: 611, pl. 11: fig. 37. MALE HT (MHNG, *non vidi*) from Texas without further locality. Synonymized by Causey, 1952: 6.

Pseudopolydesmus americanus:-- Attems, 1940 *Das Tierreich* 70: 140, fig. 202.

Pseudopolydesmus americanus:-- Carl, 1941. *Zoologischer Anzeiger* 133(11-12): 292-293, figs. 1-2.

Polydesmus natchitoches Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 10, figs. 34-35. MALE HT (USNM, *vidi*) with three specimens from two miles south of Saline, Natchitoches Par., Louisiana, 12 April 1936; one male from four miles north of Chestnut, 14 April 1936 (*non vidi*, missing, November 2015); all collected by L. Hubricht. [Synonymized by Withrow, 1988: 72.] **New synonymy!**

Pseudopolydesmus natchitoches:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

Pseudopolydesmus natchitoches:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 445.

Polydesmus paroicus Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 11, figs. 37-38. MALE HT (USNM, *vidi*) from 1.5 miles north of Clay, Jackson Par., Louisiana, five specimens collected by L. Hubricht, 12 April 1936. Synonymized by Causey, 1952: 6; [synonymy accepted by Withrow, 1988: 72;] treated as valid by Chamberlin & Hoffman, 1958: 70 and Hoffman, 1999: 445.

Pseudopolydesmus paroicus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Pseudopolydesmus paroicus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

Pseudopolydesmus paroicus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 445**.**

Polydesmus hubrichti Chamberlin, 1943a. *Entomological News* 54(1): 15, figs. 1-2. MALE HT (USNM, *vidi*) together with 12 specimens from University City, St. Louis Co., Missouri. One female from Creve Coeur Lake Park, 8 March 1936. Three males and one female from Arbuckle Mountains, Murray Co., two miles east of Gowen, Oklahoma, 26 April 1936. All collected by L. Hubricht, some paratype specimens apparently deposited in ANSP. Synonymized by Causey, 1952: 6.

Pseudopolydesmus hubrichti:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Polydesmus modocus Chamberlin, 1943b. *Proceedings of the Biological Society of Washington* 56: 36, fig. 6. MALE HT (FMNH INS927, *vidi*) from a site between Modoc and Roots, Randolph Co., Illinois, collected by K.P. Schmidt 14 April 1936. Type images available online. Synonymized by Causey, 1952: 6.

Pseudopolydesmus modocus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Polydesmus modocus:-- Sierwald *et al.*, 2005. *Zootaxa* 1005: 40.

Type Notes:

Polydesmus pinetorum MALE HT (USNM, *non vidi*, type lost): Apparently, Withrow examined the type of *pinetorum* (USNM); no type material was located in the USNM collection (Sierwald, November 2015).

Polydesmus natchitoches MALE HT (USNM, *vidi*): Type series consists of a single vial with Chamberlin label and damaged locality label, containing numerous male and female fragments. Specimens sorted into three vials. Vial 1: fragmented male, gonopods missing, and a genitalia vial containing two gonopods (most likely not from the same male); Vial 2: two fragmented females, one with everted vulva; Vial 3: several specimen fragments.

Polydesmus paroicus MALE HT (USNM, *vidi*): Single type lot with Chamberlin label and Hubricht locality label, which agrees with published locality data. Contains fragments of two females and two 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 likely not belonging to the male in this vial.

Polydesmus hubrichti (USNM, *vidi*): USNM collection contains three vials labelled by Chamberlin [with the nomenclaturally invalid manuscript name *Polydesmus scholasticus*]. All specimens collected by Hubricht and identified by him as *P. serratus*. Vial labelled ‘Types’ collected March 29, 1936 from University City, Missouri, containing at least 14 specimens: male labelled ‘Lectotype’ with one dissected gonopod in a genitalia vial and 13 adult males, most with intact gonopods *in situ*. Vial labelled ‘Paratype’ contains a single female collected March, 1936 under logs, from 4.3 miles northwest of Glencoe Station, St. Louis Co., Missouri. Vial labelled ‘Paratypes’ collected March 8, 1936, from Creve Coeur Lake Park, St. Louis Co., Missouri, containing seven specimens belonging to three species: two males of *P. pinetorum* (both with gonopods *in situ*, one with a single intact gonopod), two females

of *P. pinetorum*, two males of *P. minor* (gonopods intact *in situ*), and one female *P. serratus* (with everted vulva). Despite labelling three vials as types [for *P. scholasticus*], Chamberlin (1943a) nominated only the material from University City (vial labelled 'Types') in the type series of *P. hubrichti*.

Polydesmus modocus MALE HT (FMNH INS927, *vidi*): Male HT in fragments, single gonopod in genitalia vial, identifiable as *pinetorum*; Withrow label. Images available online.

Diagnosis:

Size: Medium, with body length ranging from 13.6 mm to 25.6 mm, and an average body length of 18.6 mm (n=212, Withrow, 1988: 76, 199). Usually smaller than *P. canadensis*, *P. collinus*, *P. erasus*, and *P. serratus*. Clearly larger than its small sympatric congeners *P. minor* and *P. 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 to *P. erasus* and *P. serratus*, denticles always distinct. Trailing margin concave, strongly curved. Anterior blister row (AB) much thicker than median (MB) and posterior (PB) blister rows, which are subequal in thickness. MB2 and PB2 subequal in area, and much larger than MB1 and PB1. Central paranotal blisters (CB) large, occupying over two-thirds of paranotal breadth, as wide as long. Lateral blisters (LB) anteriorly widening laterad.

Gonopod (Figs. 18, 19, 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* lobelike, 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).

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

Additional specimens examined: FMNH INS1435, 1438, **1445***

Pseudopolydesmus minor (Bollman, 1888)

Polydesmus minor Bollman, 1888. *Entomologica Americana* 4(1): 2. MALE HT (USNM, *non vidi*, type lost) from Little Rock, Pulaski Co., Arkansas.

Polydesmus minor:-- Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 19, fig. 32.

Pseudopolydesmus minor:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Pseudopolydesmus minor:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

Pseudopolydesmus minor:-- Loomis, 1959. *Journal of the Washington Academy of Sciences* 49(5): 161, fig. 9.

[*Pseudopolydesmus minor:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 120, figs 62, 79, 97, 101, 105, 117, 119, 122-126, map 9, tables 9-11.]

Pseudopolydesmus minor:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 444.

Polydesmus neoterus Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 10, figs. 30-31. MALE HT (USNM, *vidi*) from New Orleans, Louisiana, collected with two females by L. Hubricht, 17 April 1936. [Synonymized by Withrow, 1988: 120.] **New Synonymy!**

Pseudopolydesmus neoterus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Pseudopolydesmus neoterus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

Pseudopolydesmus neoterus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 445. Listed as a valid species.

Polydesmus euthetus Chamberlin, 1942b. *Bulletin of the University of Utah* 32(8): 11, fig. 36. MALE HT (USNM, *vidi*) from Buder Park, one mile southeast of Valley Park, St. Louis Co., Missouri, collected with one female by L. Hubricht, 15 March 1956. [Synonymized by Withrow, 1988: 120.] **New Synonymy!**

Pseudopolydesmus euthetus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Pseudopolydesmus euthetus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

Pseudopolydesmus euthetus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: Listed as a valid species.

Type Notes:

Polydesmus minor MALE HT (*non vidi*, type lost): No type specimens of *minor* were located in the USNM collection (Sierwald, November 2015).

Polydesmus neoterus MALE HT (USNM, *vidi*): Type lot contains two female specimens and one male holotype. The gonopods are dissected, a single broken gonopod was found in the vial; the endomerite/pulvillus is missing, only the distal zone of the telopodite was found. The gonopod remains do not allow unequivocal identification of the specimen. However, the body form and sculpture of the *bidens* and *caddo* specimens are distinctive and differ clearly from the *neoterus* specimen; sculpture, body form, and body size of adult male agree with *minor*.

Polydesmus euthetus MALE HT (USNM, *vidi*): Type lot contains one adult male (HT) with a single dissected gonopod and one adult female labelled Lectoallotype.

Diagnosis:

Size: Small, with body length ranging from 8.8 mm to 12.7 mm and an average body length of 10.5 mm (n=31, Withrow, 1988: 124, 199). Comparable in size to *P. caddo* and *P. 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 (ALC) and posterior lateral (PLC) corners posterior to anterior medial (AMC) and posterior medial (PMC) corners, respectively, giving characteristic swept-back appearance. Leading and distal margins highly variable, ranging from moderately to weakly curved. ALC and denticles ranging from moderate to obliterated. Trailing margin concave, strongly curved. Anterior blister row (AB) as thick as median (MB) and posterior (PB) rows combined. Individual MB and PB subequal in area. Central paranotal blisters (CB), occupying two-thirds of paranotal breadth. Lateral blisters (LB) unusually distinct, extending anteriorly past all setiferous denticles, aligned with longitudinal axis.

Gonopod (Figs. 23, 24, 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*, *m3* absent. Process *e2* very small, lobelike (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 (Fig. 23B, 24B, 25B).

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

Additional specimens examined: FMNH INS7107*

Pseudopolydesmus caddo Chamberlin, 1949

Pseudopolydesmus caddo Chamberlin, 1949. *Journal of the Washington Academy of Sciences* 39(3): 97, fig. 11. MALE HT (USNM, *vidi*) from five miles northwest of Shreveport, Caddo Par., Louisiana, collected by L. Hubricht, 13 April 1936. The original description lists two males and one female.

Pseudopolydesmus caddo:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 69.

[*Pseudopolydesmus caddo:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 115, figs. 50, 77, 96, 100, 104, 116, 118, 122-126, map 9, tables 9-11.]

Pseudopolydesmus caddo:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 442.

Pseudopolydesmus bidens Loomis, 1959. *Journal of the Washington Academy of Sciences* 49: 161, fig. 8. MALE HT (USNM, *vidi*) from site beside U.S. Highway 190, between Kinder and Le Blanc, Allen Par., Louisiana, collected by E.M. Loomis & H.F. Loomis, 20 December 1958. Original description lists seven males and five females. Synonymized by [Withrow, 1988: 115 and] Hoffman, 1999: 442 (listed as *syn. nov.*).

Type Notes:

Pseudopolydesmus caddo MALE HT (USNM, *vidi*): *caddo* type lot contains one female specimen, labeled Lectoallotype, and two male specimens as reported by Chamberlin in the original description. In both males, the gonopods are dissected out; they are missing from one male specimen. In the male specimen labeled HT, the gonopods are separated in a small vial; the tip of the telopodite of the left gonopod is broken off.

Pseudopolydesmus bidens MALE HT (USNM, *vidi*): *bidens* type lot consists of one intact female specimen and three males. One male specimen is intact, with both gonopods *in situ*; one male's dissected gonopods are stored in a genitalia vial. One male in a tube labeled Holotype contains a complete specimen and two separated dissected gonopods.

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 *P. minor* and *P. 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 (ALC) and denticles always strongly distinct. Anterior blister row (AB) thicker medially than median blister row (MB), MB thicker than posterior blister row (PB). MB2 much larger in area than MB1. Tergal blisters poorly differentiated, PB row nearly obliterated except lateral sulcus of PB3. Central paranotal blisters (CB), occupying two-thirds of paranotal breadth. Lateral blisters (LB) 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*, *m3* absent. Process *e3* projecting from a flanged ectal lamina (Fig. 28B). Processes *m1*, *m2*, *m4* all medium-sized, subtriangular; *m1* at base of pulvillus; *m2* connected to *e2* via weak transverse ridge (not as distinct as in *P. serratus*); *m4* proximal to terminal bristles. Our process *m4* may actually be homologous to *e4* in other *Pseudopolydesmus*: it is located subterminally on the acropodite and, in both the *bidens* and *caddo* type specimens, does not bear proximal bristles (though the specimens may have been damaged).

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

Pseudopolydesmus paludicolus Hoffman, 1950

Pseudopolydesmus paludicolus Hoffman, 1950. *The Virginia Journal of Science* 1(3): 222, fig. 4. MALE HT (USNM, *vidi*) from Sand Bridge, City of Virginia Beach, Princess Anne Co., Virginia, collected by L.M. Carter, H.I. Kleinpeter & R.L. Hoffman, 8 May 1949.

Pseudopolydesmus paludicolus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 70.

[*Pseudopolydesmus paludicola* [sic]*:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 111, figs. 95, 99, 103, 126, map 9, table 11.]

Pseudopolydesmus paludicolus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 445.

Type Notes: *Pseudopolydesmus paludicolus* MALE HT (USNM, *vidi*): Single intact male in vial, gonopods missing (Sierwald, November 2015).

Diagnosis:

Size: Small, with male body length measured at 11 and 13 mm (n=2, Withrow, 1988: 111). Comparable in size to *P. minor* and *P. caddo*. Clearly smaller than all other congeneric species. May be mistaken *e.g.* for the similarly sized *Polydesmus inconstans* because, unlike in most *Pseudopolydesmus*, the collum is narrower than the mandibles and tergal setae are clearly visible under 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 anterior lateral corner (ALC) indistinct. Trailing margin concave, strongly curved. Anterior blister row (AB) thicker than median blister row (MB) along its entire breadth, MB row thicker than posterior blister row (PB). Individual MB

subequal in area, as are individual PB. Central paranotal blisters (CB), occupying two-thirds of paranotal breadth. Lateral blisters (LB) 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*, *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).

Range: Coastal plain of southeastern Virginia south to South Carolina.

Additional specimens examined: VTEC MPE1167*, 1169*, 1170*

Pseudopolydesmus serratus (Say, 1821)

Polydesmus serratus Say, 1821. *Journal of the Academy of Natural Sciences of Philadelphia* 2(1): 106. 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 this species was found under the bark of *Pinus variabilis*, now a synonym of *Pinus echinata*, shortleaf pine.

Polydesmus serratus:-- Gervais, 1847. *Histoire naturelle des Insectes. Aptères* 4: 105.

Polydesmus serratus:-- Saussure, 1860. *Mémoires de la Société de Physiques et d'Histoire naturelle de Genève* 15(2): 325.

Polydesmus serratus:-- Peters, 1864. *Monatsberichte der Königlich Preußischen Akademie der Wissenschaften zu Berlin* 1864(7): 539.

Polydesmus serratus:-- Bollman, 1887b. *Proceedings of the United States National Museum* 10: 620. Lists *P. canadensis* and *P. glaucescens* as junior synonyms of *P. serratus*.

Polydesmus serratus:-- Williams & Hefner, 1928. *Ohio State University Bulletin* 33(7): 112, fig. 13B.

Pseudopolydesmus serratus:-- Attems, 1940. *Das Tierreich* 70: 141. Uncertain placement.

Pseudopolydesmus serratus:-- Chamberlin, 1943c. *Bulletin of the University of Utah* 34(6): 18.

Pseudopolydesmus serratus:-- Chamberlin, 1951. *Great Basin Naturalist* 11(1-2): 27.

Pseudopolydesmus serratus:-- Causey, 1952. *The Chicago Academy of Sciences Natural History Miscellanea* 106: 6.

Pseudopolydesmus serratus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 71.

Pseudopolydesmus serratus:-- Loomis, 1959. *Journal of the Washington Academy of Sciences* 49(5): 161.

Pseudopolydesmus serratus:-- Ramsey, 1966. *Ohio Journal of Science* 66(3): 339.

[*Pseudopolydesmus serratus:*-- Withrow, 1988. Unpublished D. Phil. Thesis, Ohio State University: 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.]

Pseudopolydesmus serratus:-- Hoffman, 1999. *Virginia Museum of Natural History Special Publication* 8: 446.

Pseudopolydesmus serratus:-- Shelley, 2000. *Insecta Mundi* 14(4): 246. New record for Florida.

Pseudopolydesmus serratus:-- Shelley & Snyder, 2012. *Insecta Mundi* 0239: 6, figs 2-4.

Polydesmus canadensis:-- Wood, 1865. *Transactions of the American Philosophical Society* 13: 216, figs. 43-44. Wood's illustration of a gonopod of *P. canadensis* matches *P. serratus*. Adding to the confusion, his illustration of the gonopods of *P. serratus* (fig. 42) clearly does not agree with either *P. serratus* or *P. canadensis*.

Pseudopolydesmus canadensis:-- Attems, 1898. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 67: 480, fig. 244.

Pseudopolydesmus canadensis:-- Verhoeff, 1931. *Zoologischer Anzeiger* 94(11-12): 305, figs. 1-7. Anatomical examination of the gonopod.

Pseudopolydesmus canadensis:-- Attems, 1940. *Das Tierreich* 70: 140, fig. 201.

?Polydesmus pennsylvanicus C.L. Koch, 1847. *Kritische Revision der Insectenfaune Deutschlands* 3: 133. Type material unknown, from 'Pensylvanien'. Synonymized by Chamberlin & Hoffman, 1958: 71 [and Withrow, 1988: 104]; tentatively synonymized by Bollman, 1887b: 621 and Hoffman, 1999: 446.

Polydesmus pensylvanicus [sic]:-- C.L. Koch 1863. *Die Myriapoden. Getreu nach der Natur abgebildet und beschrieben. Band 2*: 18-19, pl. 69: fig. 142.

Polydesmus scopus Chamberlin, 1942a. *The Canadian Entomologist* 74: 16, fig. 1. MALE HT (USNM, *vidi*) from The Ledges, six miles south of Boone, Boone Co., Iowa, collected by D.T. Jones, 19 May 1941; one female collected close by. Synonymized by [Withrow, 1988: 104 and] Hoffman, 1999: 446 (listed as *syn. nov.*).

Pseudopolydesmus scopus:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 71.

Polydesmus planicolens Chamberlin, 1942a. *The Canadian Entomologist* 74: 16, fig. 2. MALE HT (USNM, *vidi*) from Ames, Story Co., Iowa, collected by D.T Jones, spring 1941. Synonymized by [Withrow, 1988: 104 and] Hoffman, 1999: 446 (listed as *syn. nov.*).

Pseudopolydesmus planicolens:-- Chamberlin & Hoffman, 1958. *Bulletin of the United States National Museum* 212: 71.

Type Notes:

Polydesmus scopus MALE HT (USNM, *vidi*): One Chamberlin vial, identified by Withrow as *serratus*, single male in fragments with one loose gonopod, identifiable as *serratus*.

Polydesmus planicolens MALE HT (USNM, *vidi*): One Chamberlin vial, identified by Withrow as *serratus*, single male in fragments with two gonopods in small vial; gnathochilarium dissected.

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 *P. canadensis* and *P. erasus*. Usually larger than *P. collinus* and *P. 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 *P. erasus*. Leading and distal margins moderately curved, similar to *P. erasus* but less curved than *P. canadensis* and *P. collinus*.

Denticles moderate to obliterated. Trailing margin concave, moderately curved. Anterior (AB) and median (MB) blister rows subequal in thickness, AB and MB rows much thicker than posterior blister row (PB). MB2 only slightly larger in area than MB1, individual PB subequal in area. Central paranotal blisters (CB), occupying two-thirds of paranotal breadth. Lateral blisters (LB) 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*, *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).

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

Additional specimens examined: FMNH INS1413, 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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Conflict of interest: PS and her husband (Rüdiger Bieler) are associate editors of the Zoological Journal of the Linnean Society.

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Figure 1. Two live examples of *Pseudopolydesmus*. A, *Pseudopolydesmus serratus*, live adult male, dorsal view (VTEC MPE1173). B, *Pseudopolydesmus paludicolus*, live adult female, dorsal view (VTEC MPE1167).

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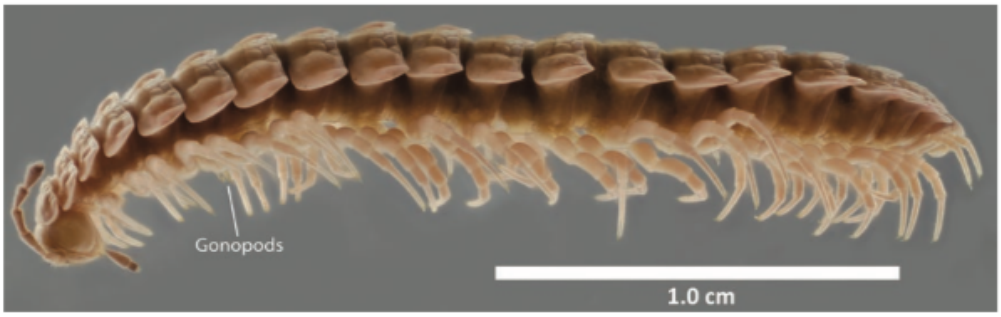

Figure 2. *Pseudopolydesmus erasus*, adult male habitus, lateral view (FMNH INS3120685).

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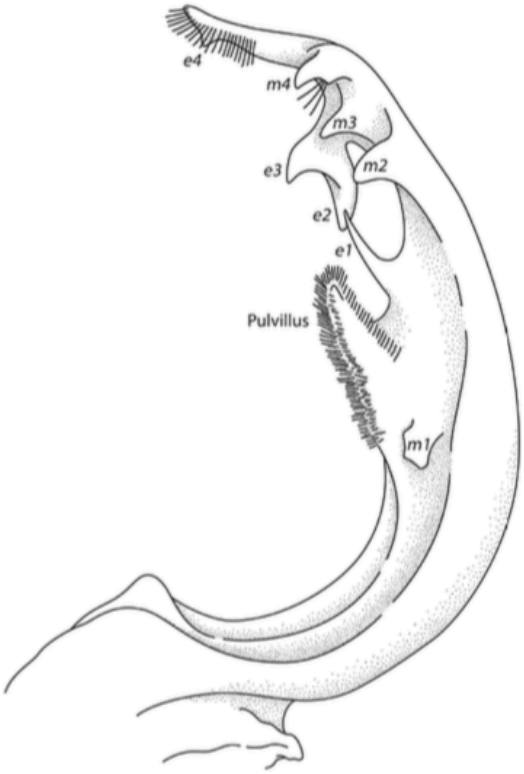

1375 **Figure 3.**

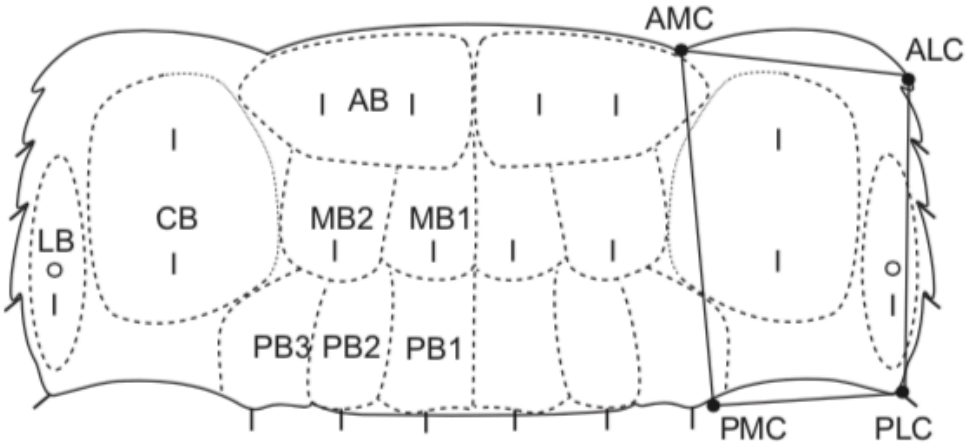

Figure 4.

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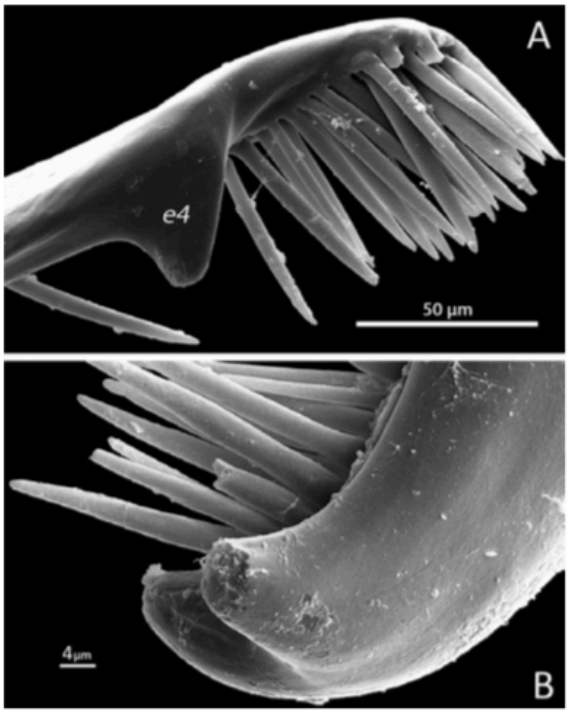

Figure 5. Features of the telopodite terminus in *Pseudopolydesmus* (scanning electron micrograph). A, terminal bristles in *Pseudopolydesmus canadensis* right gonopod, ectal view (FMNH INS6934). Unlike true setae, these bristles are not socketed at the base; instead, they project continuously from the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

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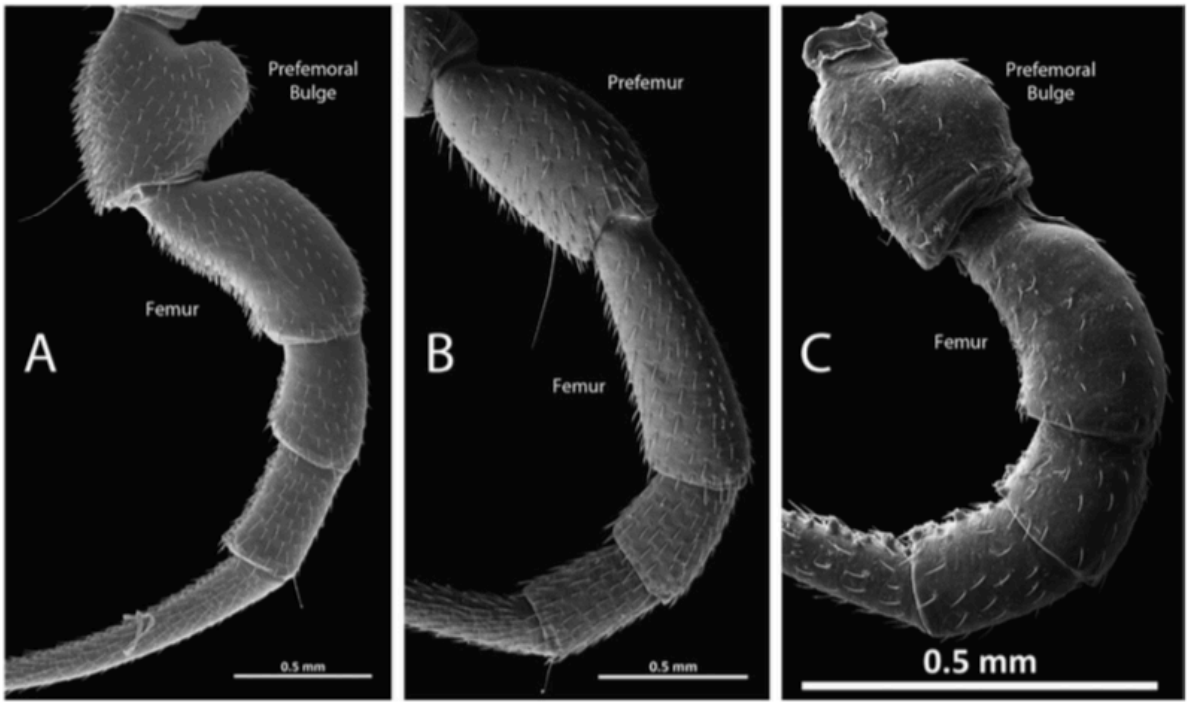

Figure 6. The characteristic prefemoral bulge in males of *Pseudopolydesmus*, and comparison of walking legs in *Pseudopolydesmus* and *Polydesmus* (scanning electron micrograph). A, adult male *Pseudopolydesmus erasus*, left leg 9, with characteristically large prefemoral bulge and thickened femur (FMNH 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).

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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.

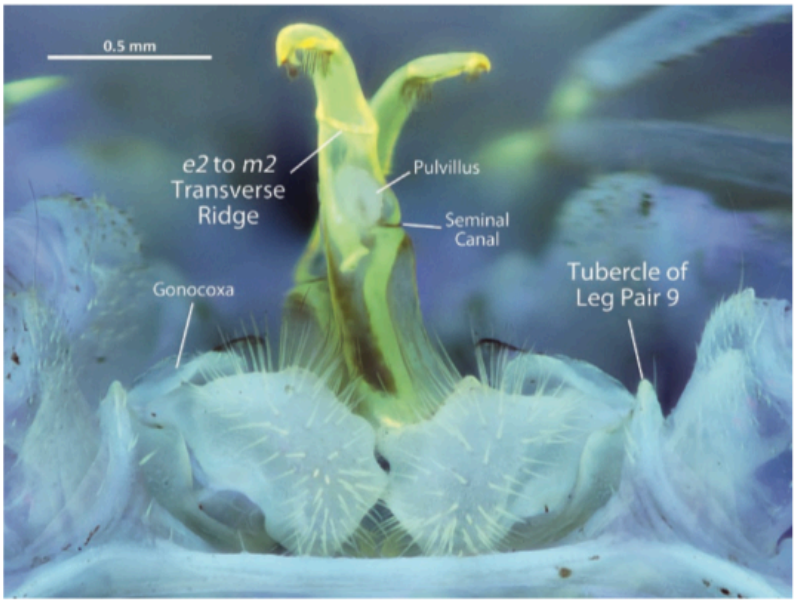

Figure 8. Body ring 7 in adult male *Pseudopolydesmus serratus*, posterior view, showing gonopods and sternal tubercles of leg pair 9 (FMNH INS8238, ultraviolet enhancement). Note the prominent transverse ridge between processes *e2* and *m2* in the gonopods of *Ps. serratus*.

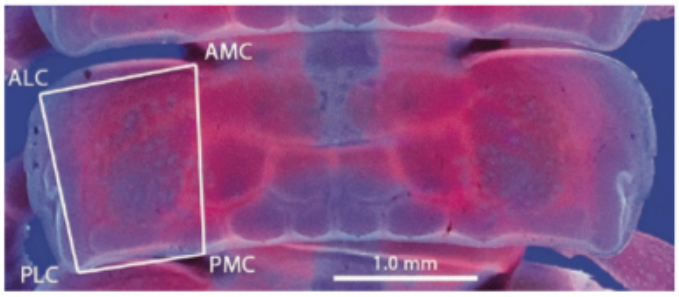

Figure 9. *Pseudopolydesmus erasus*, metatergite and paranota of body ring 9. Adult male (FMNH INS3120685, ultraviolet enhancement).

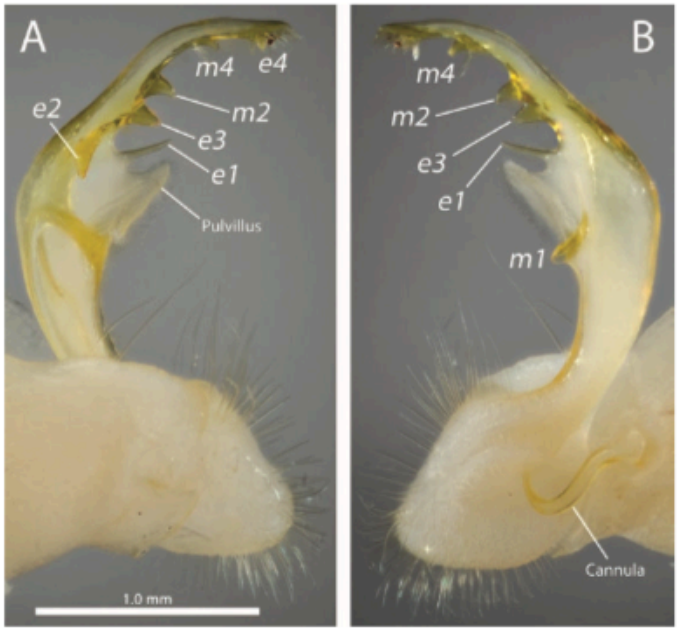

Figure 10. Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

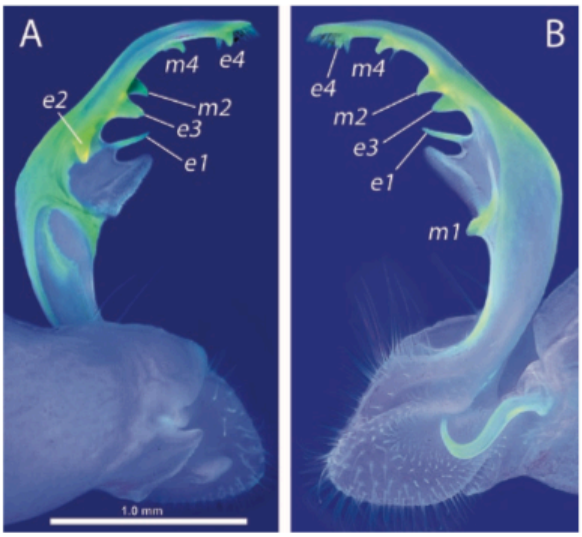

Figure 11. Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685, ultraviolet enhancement). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

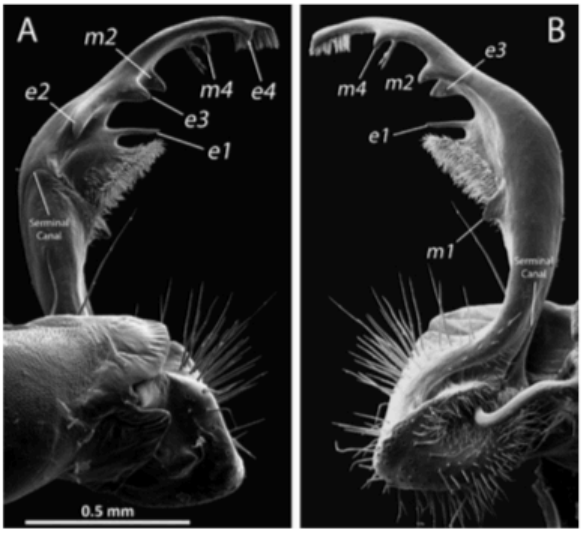

Figure 12. Gonopod of *Pseudopolydesmus erasus* (FMNH INS3120685, scanning electron micrograph). A, right gonopod, ectal view. B, right gonopod, medial view.

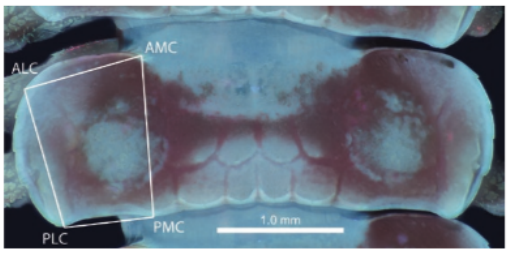

Figure 13. *Pseudopolydesmus canadensis*, metatergite and paranota of body ring 10. Adult male (FMNH INS3120683, ultraviolet enhancement).

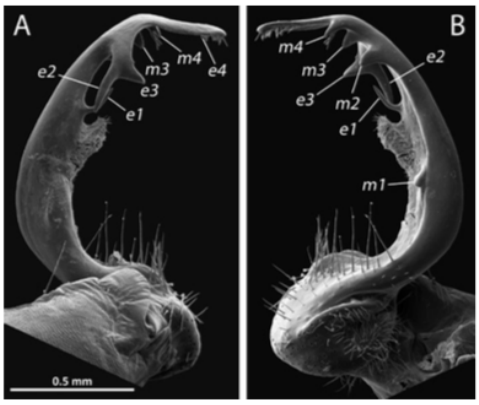

Figure 14. Gonopod of *Pseudopolydesmus canadensis* (FMNH INS6934, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod. Cannula removed.

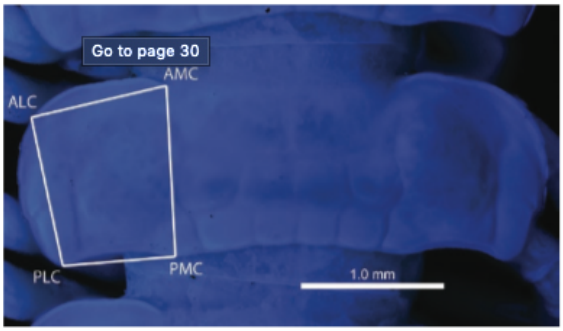

Figure 15. *Pseudopolydesmus collinus*, metatergite and paranota of body ring 9. Paratype, adult male (VMNH PSE00202, ultraviolet enhancement).

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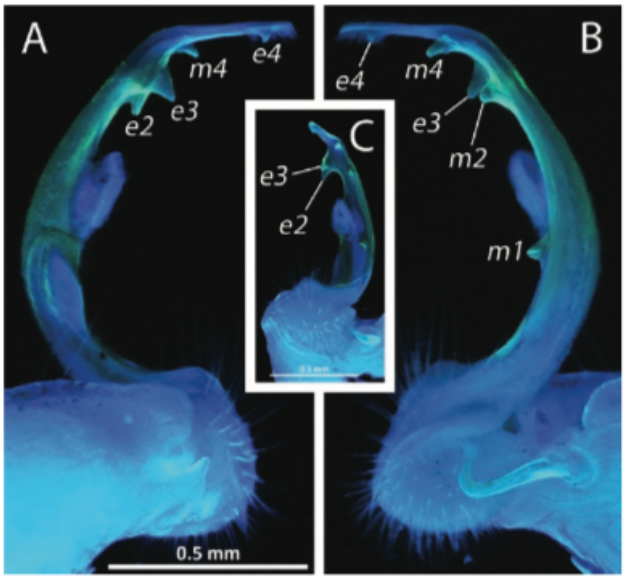

Figure 16. Gonopod of *Pseudopolydesmus collinus*. Paratype (VMNH PSE00203, ulatraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. C, left gonopod, posterior oblique view, showing fusion of *e2* and *e3* processes onto a short, thick stalk. All images mirrored to appear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

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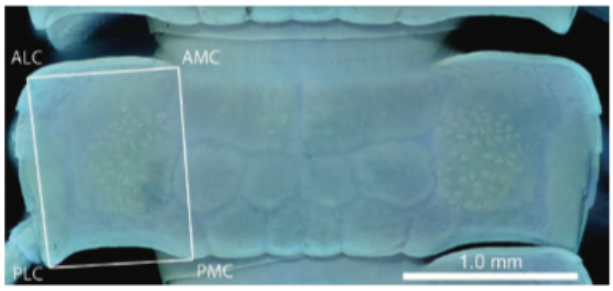

Figure 17. *Pseudopolydesmus pinetorum*, metatergite and paranota of body ring 10. Paratype, *Polydesmus hubrichti* type series vial from Glencoe Station, MO, USA, adult female (USNM, ultraviolet enhancement).

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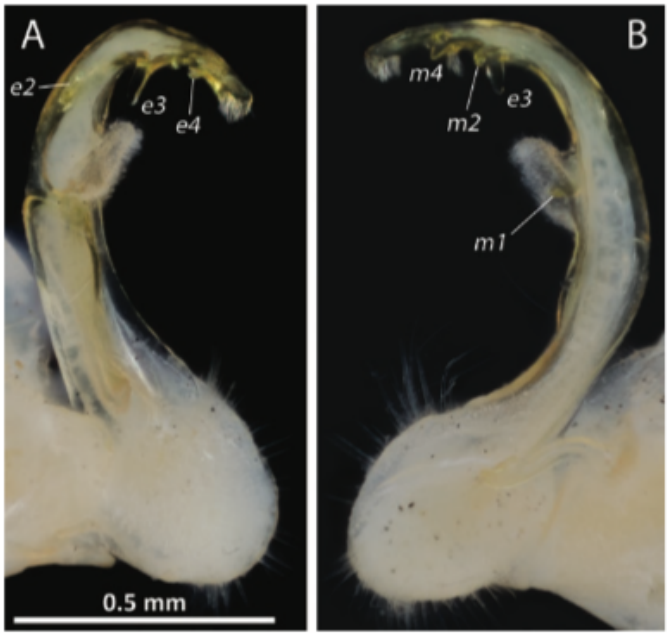

Figure 18. Gonopod of *Pseudopolydesmus pinetorum*. Holotype, *Polydesmus natchitoches*, from genitalia vial (USNM). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

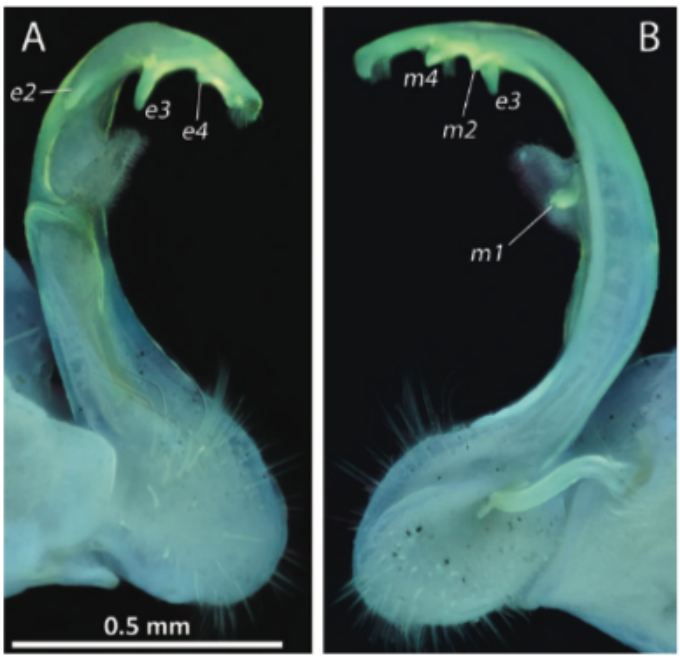

Figure 19. Gonopod of *Pseudopolydesmus pinetorum*. Holotype, *Polydesmus natchitoches*, from genitalia vial (USNM, ultraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

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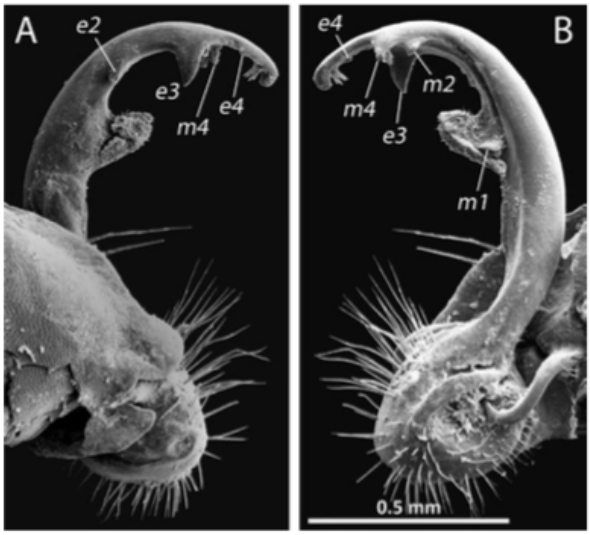

Figure 20. Gonopod of *Pseudopolydesmus pinetorum* (FMNH INS1445, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

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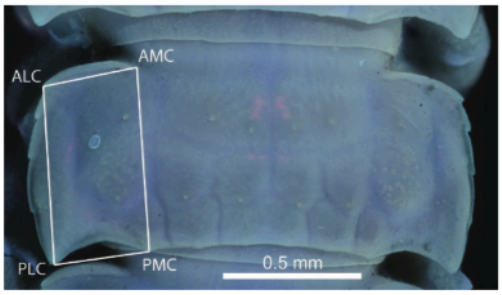

Figure 21. *Pseudopolydesmus minor*, metatergite and paranota of body ring 10. Holotype, *Polydesmus euthetus* (USNM, ultraviolet enhancement).

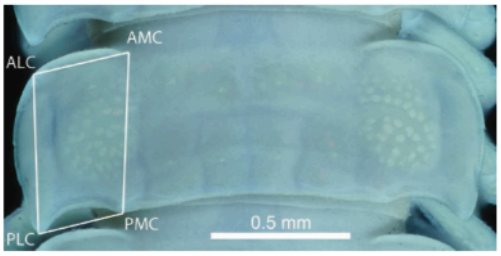

Figure 22. *Pseudopolydesmus minor*, metatergite and paranota of body ring 9. Paratype, *Polydesmus neoterus* type series, adult female (USNM, ultraviolet enhancement).

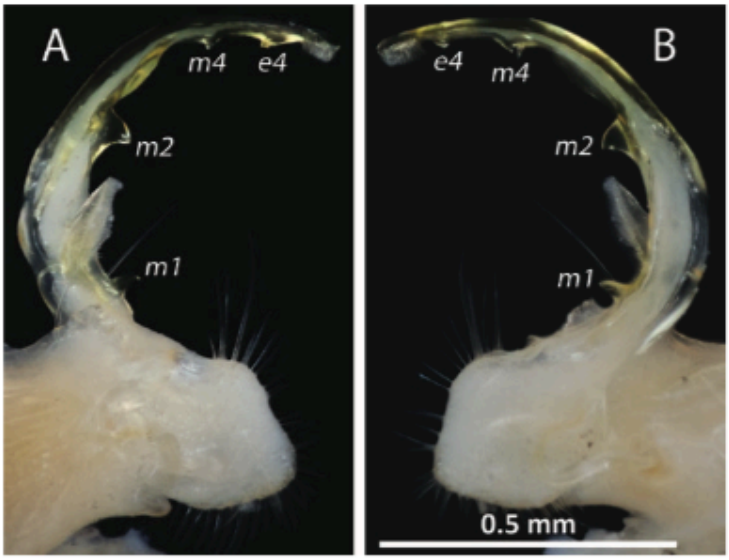

Figure 23. Gonopod of *Pseudopolydesmus minor*. Holotype, *Polydesmus euthetus* (USNM). A, right gonopod, ectal view. B, right gonopod, medial view.

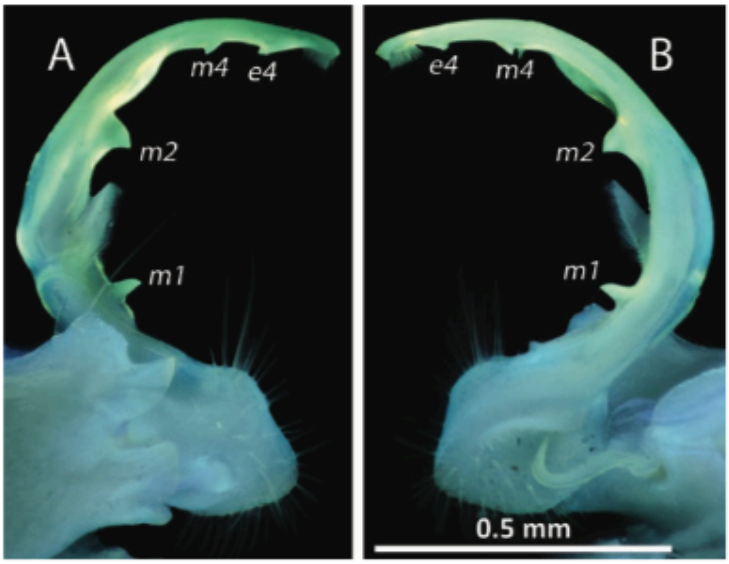

Figure 24. Gonopod of *Pseudopolydesmus minor*. Holotype, *Polydesmus euthetus* (USNM, ultraviolet enhancement). A, right gonopod, ectal view. B, right gonopod, medial view.

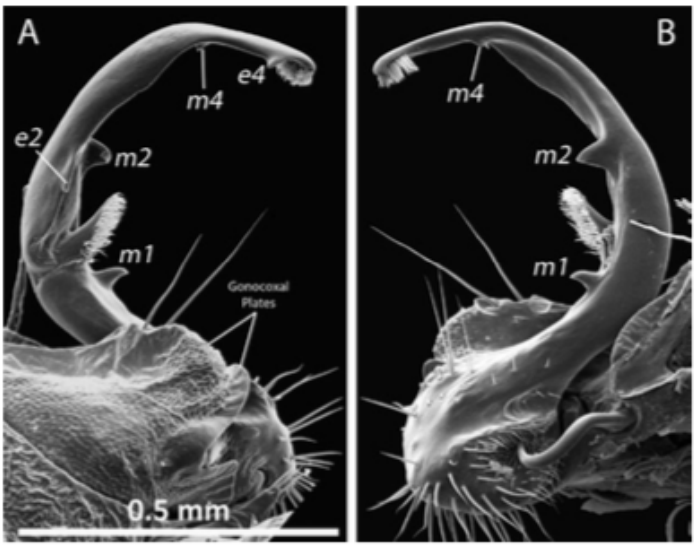

Figure 25. Gonopod of *Pseudopolydesmus minor* (FMNH INS7107, scanning electron micrograph). A, right gonopod, ectal view. B, left gonopod, medial view (image mirrored to match right gonopod).

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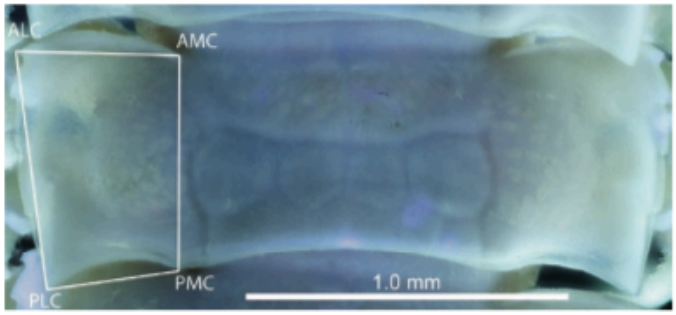

Figure 26. *Pseudopolydesmus caddo*, metatergite and paranota of body ring 10. Paratype, adult male (USNM, ultraviolet enhancement).

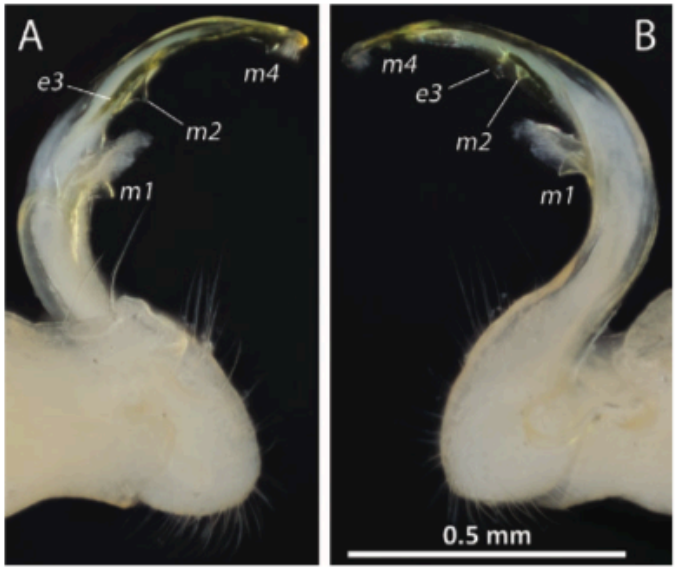

Figure 27. Gonopod of *Pseudopolydesmus caddo*. Holotype (USNM). A, right gonopod, ectal view. B, right gonopod, medial view.

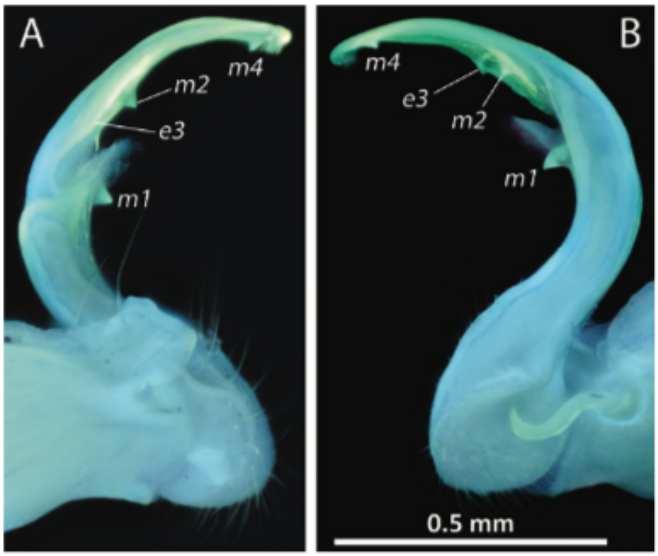

Figure 28. Gonopod of *Pseudopolydesmus caddo*. Holotype (USNM, ultraviolet enhancement). A, right gonopod, ectal view. B, right gonopod, medial view.

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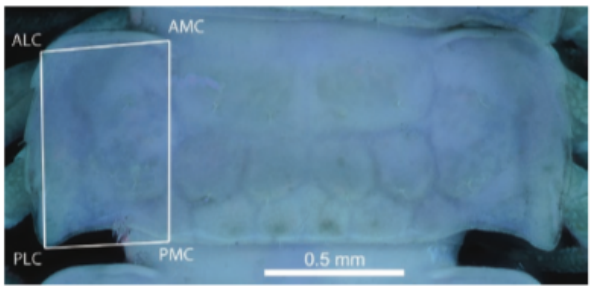

Figure 29. *Pseudopolydesmus paludicolus*, metatergite and paranota of body ring 13. Holotype, adult male (USNM, ultraviolet enhancement).

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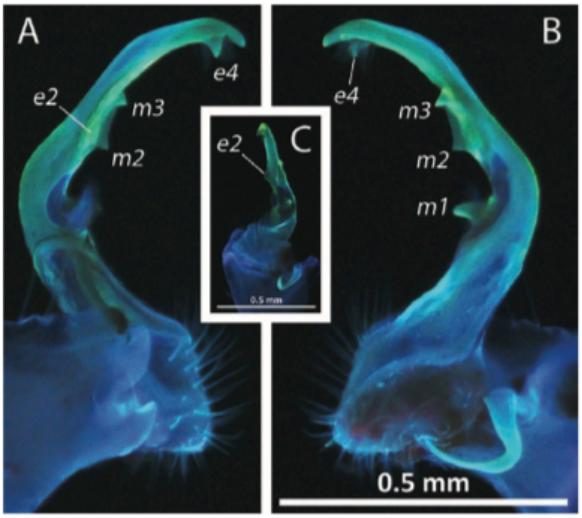

Figure 30. Gonopod of *Pseudopolydesmus paludicolus* (VTEC MPE1170, ultraviolet enhancement). A, left gonopod, ectal view. B, left gonopod, medial view. C, left gonopod, posterior oblique view, showing process *e2* projecting laterally. All images mirrored to appear as right gonopod.

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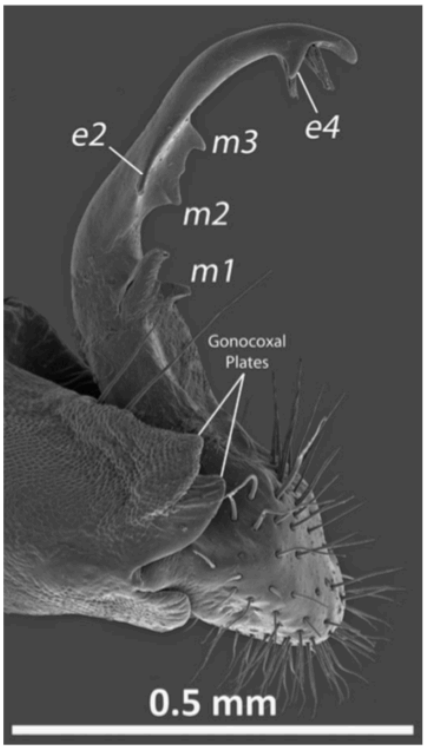

Figure 31. Left gonopod of *Pseudopolydesmus paludicolus*, ectal view (VTEC MPE1169, scanning electron micrograph). Image mirrored to appear as right gonopod.

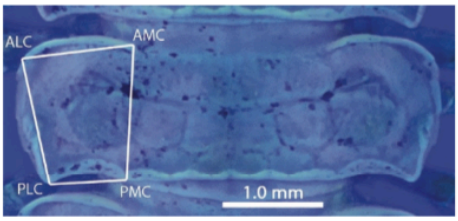

Figure 32. *Pseudopolydesmus serratus*, metatergite and paranota of body ring 9. Adult female (FMNH INS2817, ultraviolet enhancement).

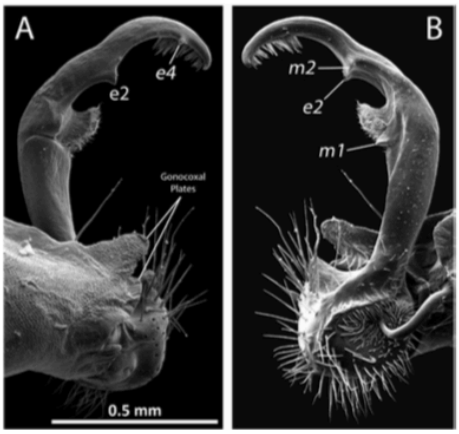

Figure 33. Gonopod of *Pseudopolydesmus serratus* (FMNH INS2819, scanning electron micrograph). A, left gonopod, ectal view. B, left gonopod, medial view. Both images mirrored to appear as right gonopod.

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