

Review of the Caribbean pyrgodesmid genus *Docodesmus* Cook with notes on potentially related genera (Diplopoda, Polydesmida, Pyrgodesmidae)

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Abstract

The diagnostic characters of the genus *Docodesmus* Cook, 1896 are evaluated. Members of the genus are clearly recognizable by the anterior collum, paranotal and tergite margin lobations. Two different types of gonopods, corresponding to different geographic areas, are found. The potential close affinities of *Docodesmus* with several other pyrgodesmid genera are discussed. This study revealed that *Docodesmus* species carry spinnerets at the epiproct. All 22 species currently assigned to the genus are listed with complete synonymies, citations and diagnoses. *Docodesmus cooki* Loomis, 1969 is a junior subjective synonym of *D. haitiensis* Loomis, 1934 (**syn.n.**) and *Docodesmus griseus* Loomis, 1941 is a junior subjective synonym of *D. angustus* Loomis, 1941 (**syn.n.**).

Key words

Diplopoda, catalogue, West Indies, Antilles, taxonomy, *Coccoelasma*, *Cyphotylus*, *Henicomus*, *Jeekelia*, *Leuritus*, *Lobodesmus*, *Tridesmus*

Introduction

The polydesmidan family Pyrgodesmidae Silvestri, 1896 contains relatively small (3–15 mm) soil-dwelling millipedes with a mostly pantropical distribution, and typically have an enlarged collum (Figure 6a, b) that completely conceals the head in dorsal view (Hoffman 1982, listed as diagnostic feature). Other common characters include lobed paranota and granulated or tuberculated tergites, which provide many of these millipedes with a characteristic ornate dorsal texture. Taxonomically, the family is in dire need of monographic revision. The 371 species (including 17 subspecies) are placed in 169 genera, 116 of which are monotypic. The most species-rich genera are *Lopho-*

desmus Pocock, 1894, *Docodesmus* Cook, 1896, *Myrmecodesmus* Silvestri, 1910, *Calymmodesmus* Carl, 1914, and *Aporodesmus* Porat, 1894, containing 25, 22, 20, 17 and 11 species respectively. All remaining genera contain 8 or fewer species (Fig. 1).

In light of this situation, and considering that the majority of the genera are poorly defined, potentially monophyletic units cannot be delineated without examination of type specimens of all type species. Since a monographic revision of the entire family is beyond feasibility, we decided to select manageable sets of taxa, such as the genus *Docodesmus*, with geography as the main selection criterion until some putative monophyletic units became discernible. We reviewed all relevant literature and examined every available male type specimen of *Docodesmus* species; we confirmed the unavailability of lost types with the respective curators of the collections. We did not examine all female type specimens (Table 1), but base our discussion of these species on the morphological data presented in the first description of the species. The results we found justify this approach. We were able to provide a robust definition for the group and identify potentially related genera. Our research revealed that Pocock's description of the type species was misinterpreted by all subsequent authors, and that diagnostic characters have never been unambiguously identified for the genus. For these reasons we present a review of the genus *Docodesmus* rather than a monographic revision.

Abbreviations

BMNH – The Natural History Museum, London; formerly: British Museum (Natural History)

FMNH – Field Museum of Natural History

FSCA – Florida State Collection of Arthropods

ICZN – International Code of Zoological Nomenclature

INPA – Instituto Nacional de Pesquisas da Amazônia

MACN – Division de Etnomológico, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina

MCZ – Museum of Comparative Zoology, Harvard University

MSNG – Museo Civico di Storia Naturale “Giacomo Doria”, Genova

USNM – National Museum of Natural History, Smithsonian Institution; formerly United States National Museum; types can be searched on-line at: <http://collections.si.edu/search/results.jsp>

ZMB – Museum für Naturkunde, Berlin

ZMUC – Zoological Museum, University of Copenhagen; types can be searched on-line at: <http://www.zmuc.dk/EntoWeb/collections-databaser/diplo-polydesmida.htm>

HT – Holotype

PT – Paratype

LAP – long anterior process of gonopod

SAP – short anterior process of gonopod

Specimen designations follow the established collection codes rather than modified names of their respective museums.

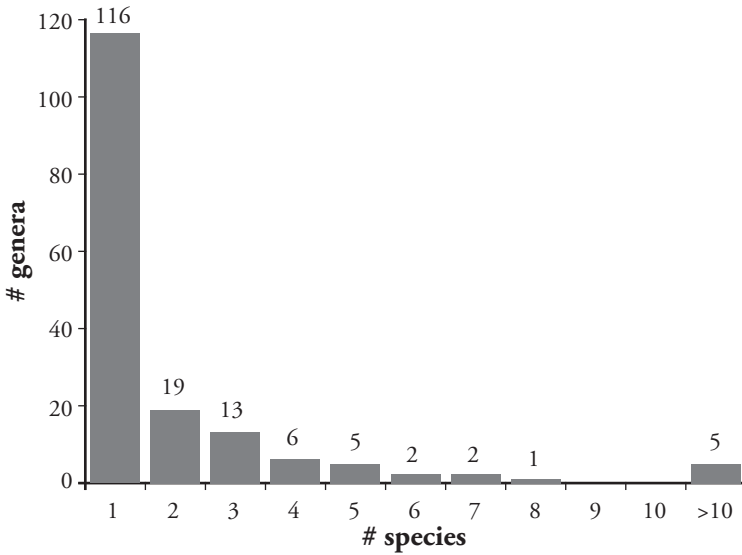


Figure 1. Number of species per genus in the family Pyrgodesmidae. 116 of 169 genera or 69% are monotypic. This suggests that the family is greatly oversplit and requires intense taxonomic revision. Data from global millipede database (Sierwald, unpublished).

Material and methods

We examined the species descriptions for all species assigned to *Docodesmus*, and defined characters and character states. We organized these in a character matrix, which ensured consistent recording of all characters and character states for all taxa and allowed quick capture of missing data. All variable characters found are listed in Table 1.

We examined specimens of the following *Docodesmus* species: *alifer* Loomis, 1941 (HT), *amazonicus* Golovatch, 1997 (HT), *angustus* Loomis, 1941 (HT), *centralis* Silvestri, 1898 (HT), *cooki* Loomis, 1969 (HT, PT), *coxalis* Loomis, 1975 (HT, PT), *cubensis* Loomis, 1937 (HT), *grenadae* Chamberlin, 1918 (HT), *griseus* Loomis, 1941 (HT), *haitiensis* Chamberlin, 1918 (HT), *huridiformis* Golovatch, 1999 (HT, PT), *parvior* Chamberlin, 1918, *robustus* Loomis, 1934 (HT, PT), *sculpturatus* Loomis, 1934 (HT, PT), *semiseptus* Loomis, 1936 (HT), *trinidadensis* Chamberlin, 1918 and *vincentii* Pocock, 1894 (PT). For the species to which we did not have access (*brodzinski* Shear, 1981, *maculatus* Bollman, 1888, *eggletoni* Velez, 1967, *maldonadoi* Velez, 1967, *vidalius* Velez, 1967), we relied on the original descriptions. We also examined specimens of the type species of some of the putatively related genera: *Coccoelasma incisura* Loomis, 1936 (HT), *Henicomus septiporus* Loomis, 1941 (HT) and *Jeekelia granulosa* Loomis, 1950 (HT).

Specimens were examined with a Leica MZ8 dissecting microscope. Digital images were taken with a Microptics®-Imaging-System (based at FMNH). Final images were assembled from 6-10 source images taken at different focal lengths using the software package Helicon Focus. SEM images were taken from gold sputter-coated specimens with a LEO Evo 60 SEM.

Results

Genus *Docodesmus* Cook, 1896

Aporodesmus Pocock 1894b: 789. Type species: *Cryptodesmus vincentii* Pocock, 1894, by original designation. Preoccupied by *Aporodesmus* Porat, 1894.

Docodesmus Cook 1896a: 5. Type species: *Cryptodesmus vincentii* Pocock, 1894, by direct substitution. – Loomis 1937: 224 (key to the 9 then-known species) – Loomis 1941: 67 (key to West Indian Chytodesmidae genera) – Loomis 1969: 249 (key to the 13 then-known species).

Schizodira Loomis 1941: 37. Type species: *Stenonia maculata* Bollman, 1888, by original designation. Synonymized by Loomis 1950: 165.

Currently, the genus *Docodesmus* contains 22 species, 19 from the Caribbean, and three species from mainland South America.

History of *Docodesmus*. Pocock (1894a) described *Cryptodesmus vincentii* from the Caribbean Island St. Vincent. *Cryptodesmus* Peters, 1864 (type species *Polydesmus olfersii* Brandt, 1839) became the type genus of the family Cryptodesmidae Karsch, 1897. Later, Pocock (1894b), designated *vincentii* as the type species for his new genus '*Aporodesmus*' the name of which was preoccupied by *Aporodesmus* Porat, 1894 (type species *Polydesmus gabonensis* Lucas, 1858, from Africa). In a very short note, Cook (1896a) argued that the Caribbean species could not possibly be congeneric with the African species and introduced the new genus *Docodesmus* to accommodate the species *vincentii*.

Earlier, Bollman (1888) had described *Stenonia maculata* from Cuba (*Stenonia* Gray, 1834 is currently placed in the Chelodesmidae). He cited the similarity to *Stenonia fimbriatus* (Peters, 1864, sub *Polydesmus*) as justification for the placement in this genus, despite differences in dorsal tuberculation, crenulation of paranota, anal segment characters and coloration. *Stenonia fimbriatus* became the type species of the genus *Tiodesmus* Cook, 1896 which is currently placed in the Platyrrhacidae. Chamberlin (1918) listed *maculata* under Platyrrhacidae (sic!) as "*Platyrrachus* (?) *maculatus*" without further explanation. Loomis (1941a) recognized that *maculata* did not belong in the Platyrrhacidae and described the genus *Schizodira* to accommodate the species. However later, having examined the paratype female (USNM), Loomis (1950) confidently placed *maculata* in *Docodesmus*, citing Bollman's misleading original description for his 'error' in creating *Schizodira*. His justification for placing *maculata* (corrected to *maculatus*) into *Docodesmus* was the lobation pattern of the paranotal margins.

Silvestri (1898) was the first to describe a new species in *Docodesmus* – *centralis* from La Guaira, Venezuela. The description, however, is brief and contains no justification for placement in the genus. Attems (1899) criticized the introduction of new genera (25 pyrgodesmid and 16 cryptodesmid genera had been described by 1899) and new species supported by sparse descriptions. He assigned *vincentii* to *Aporodesmus* and suggested no placement for *Docodesmus centralis*.

Chamberlin (1918) described four new Caribbean species in the genus *Docodesmus*: *grenadae*, *haitensis*, *trinidadensis* and *parvior*. He provided no justification for their placement in *Docodesmus*, but included a few brief comparisons with *D. vincentii*. Subsequently, Loomis described 9 new species: *robustus* and *sculpturatus* (1934), *semiseptus* (1936), *cubensis* (1937), *alifer*, *angustus* and *griseus* (1941b), *cooki* (1969) and *coxalis* (1975). Loomis (1937) was the first to address all *Docodesmus* species collectively in a key to 9 of the 10 then recognized species (*centralis* was omitted, as Loomis was concerned with only West Indian species). His most recent species key (1969) addressed 13 species, again omitting *centralis* and, oddly enough, *maculatus* (see above). Additionally, Loomis (1941b) was the first to define generic characters of *Docodesmus* in a key to West Indian Chytodesmidae genera. These included a normal pore formula (5,7,9-10,12-13,15-19); anterior margin of collum rounded, posterior margin angled and simple or indistinctly scalloped; low, often indistinct dorsal tubercles; body slightly arched, paranota (termed keels by Loomis) nearly horizontal; outer and posterior margin of paranota with small scallop-like lobes without deep incisions separating them; and paranota of body rings 7, 9, 10, 12 and 13 with four lobes on the outer margin.

Velez (1967) described three species (*eggletoni*, *maldonadoi* and *vidalius*) in the genus, but provided no justification for their placement. Shear (1981) described the fossil species *D. brodzinskyi* in the genus, citing its general similarity to Loomis's (1936) *Docodesmus* descriptions as evidence for the placement. Most recently, Golovatch described two South American species in the genus, *D. amazonicus* (1997) and *D. hirudiformis* (1999). He (1997: 328) summarized the generic characters of *Docodesmus*, referring mainly to *vincentii*, most of which are not shared with his two new species, nor with most other species assigned to *Docodesmus* at that time. These discrepancies are apparently due to a misreading of some of Pocock's original descriptions of *vincentii*. *Docodesmus vincentii* has 12, not 10, lobations of the anterior collum margin ("eleven abbreviated grooves radiate from [the border of the first tergite] towards the centre of the plate" Pocock 1894a). The paramedian pair of setiferous tubercles on the anterior sternum and the similar structures on the adjacent coxae of males (Figs 6e,f), assumed by later authors to occur on the 8th body ring and 10th leg pair, occur in fact on the 5th body ring and the 4th leg pair. Apparently, Pocock's use of the term '8th somite' referred to the 5th body ring (assuming diplosegments and defining somites as individual segments) and not to the 8th body ring. Golovatch (1997) also provided an up to date listing of *Docodesmus* species where he commented on the "shaky" status of *D. maculatus*, citing an unexplained transfer by de la Torre (1974). Apparently, de la Torre was unaware of the previously mentioned work by Loomis (1941a, 1950) and claimed to transfer *maculatus* from *Platyrrachus* to *Docodesmus*. However, Loomis (1950) had already placed *maculatus* in *Docodesmus* twenty-four years prior and provided justification for the transfer (see above).

Characters of the genus *Docodesmus*. All members of the genus share a common pattern of tergite lobation (see diagnosis below and Figures 2, 6). These lobes are formed by indentations in the tergal margins, which can be apparent or indistinct. On occasion, individuals were observed with certain body rings deviating from the general pattern,

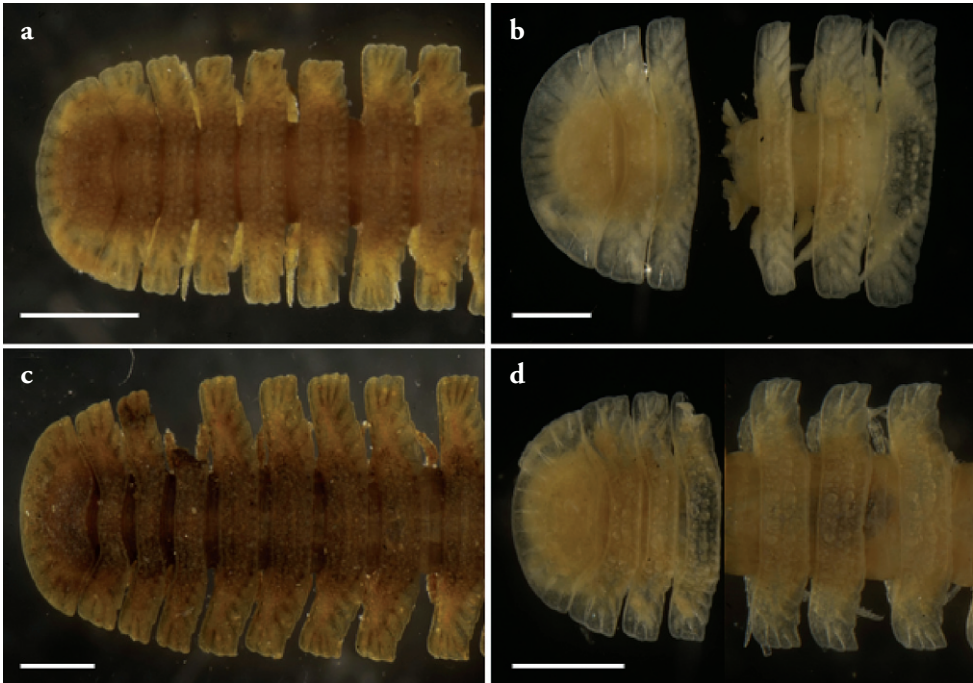


Figure 2. Digital Microptics® images of four *Docodesmus* species. Variation in dorsal granulation and tuberculation is difficult to capture due to their small size, differing degrees of translucence and encrusting of soil particulates. Lobation pattern, however, is clearer and shared by all *Docodesmus* species. a) *D. trinidadensis* male specimen, b) *D. haitiensis* male holotype, c) *D. robustus* female paratype, d) *D. cubensis* female holotype. Scale bars 1 mm.

likely due to developmental defect or injury; for example, the type specimen of *D. griseus* has asymmetrical lateral lobation on several body rings. The genus *Docodesmus*, as other members of the Pyrgodesmidae, is currently defined by somatic features only, no putative apomorphic characters from the male gonopods have been identified to date.

Gonopod description first requires a clarification of terminology. Polydesmidan gonopods consist of a basal coxite and a distal telopodite. Telopodites are highly modified among different taxa usually resulting in several distinct processes or branches. No universally accepted set of terms exists for these structures throughout the order, or within the family Pyrgodesmidae, resulting in the use of multiple terms for the same structure, and use of the same term for different structures (see table 2 in Rowe & Sierwald 2006). Sections of the telopodite have been labeled variously as the podomeres of walking legs (e.g. prefemur, pre-femoral process, tibiotarsus), yet primary homology hypotheses for these sections with the podomeres have not been established. It must also be noted that usage of the terms pre-femur and femur to denote proximal and more distal telopodite sections changed over time; earlier authors (e.g., Attems and Brölemann) used the term femorite for the proximal section, which is currently denoted as prefemur, which typically carries setae, whereas the more distal sections of

the telopodite are smooth. This shift in terminology is confusing and hinders the use of gonopods in phylogenetic analyses. The problem is compounded in the Pyrgodesmidae by the overall complexity of the gonopods and by the lack of any revisionary studies in the group. While we offer no solution to this problem, we avoid implying homology by employing descriptive terms for some gonopod structures.

The gonopods of *Docodesmus* (Figs 3-5) consist of large, bulbous coxae and much smaller, mesally oriented telopodites. Each telopodite has a basal setiferous prefemur (*pf* in Figs 3-4) and three distal processes. The posterior-most distal process is comparably larger, blunt and cylindrical (termed here, 'cylinder', *cyl* in Figs 3-5). The two anterior processes, LAP (long anterior process) and SAP (short anterior process), are long and spear-like (Figs 3-5). The prostatic groove is carried on the LAP. The association between the cylinder and anterior processes divides *Docodesmus* species into two groups, which corresponds to a geographic pattern (Fig. 5). In the group found on the South American mainland, several of the Lesser Antilles, and on Hispaniola, the cylinder is separated from the anterior processes ('type L' – Lesser Antilles, Fig. 5). In the other group, found in the Bahamas, Cuba, Jamaica and Hispaniola, the base of the larger anterior process is continuous with the margin of the cylinder ('type G' – Greater Antilles, Figs 3-5).

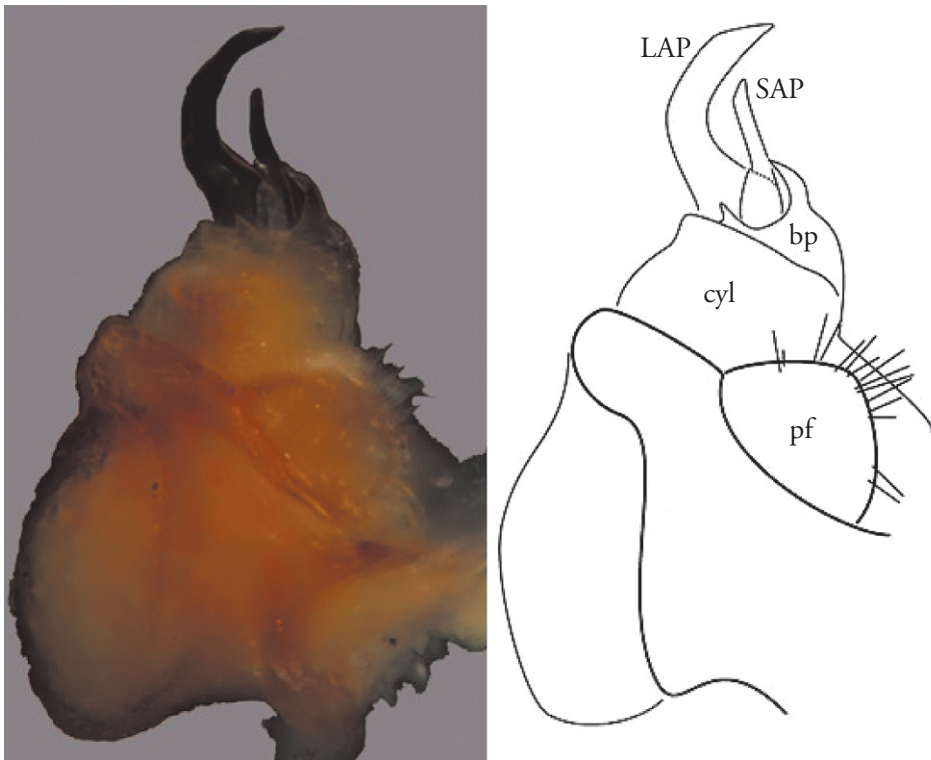


Figure 3. Digital Microoptics® image of *D. coxalis* gonopod used as template for Adobe Illustrator drawing on right, gonopod type G. LAP – long anterior process, SAP – short anterior process, cyl – “cylinder”, pf – prefemur, bp – bifid process formed at margin of cylinder (found only in *D. coxalis* and *D. cubensis*).

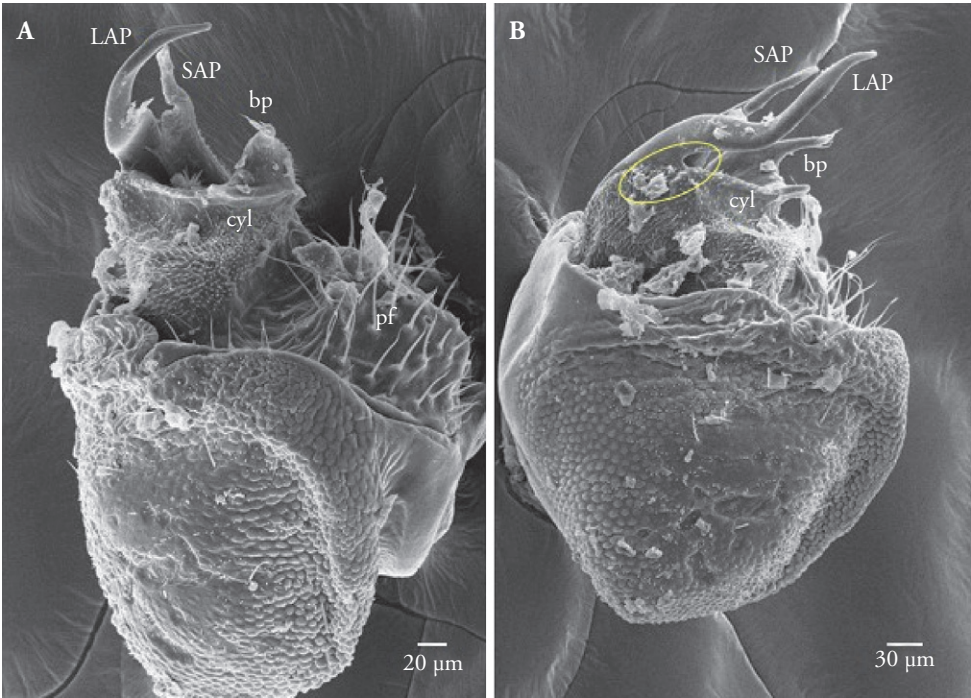


Figure 4. SEM images of *D. coxalis* right gonopod A) ventro-anterior view, B) ventral view. Anterior processes are oriented mesad *in situ*. Abbreviations same as Figure 3. Ellipse highlights area where LAP is continuous with cylinder (type G).

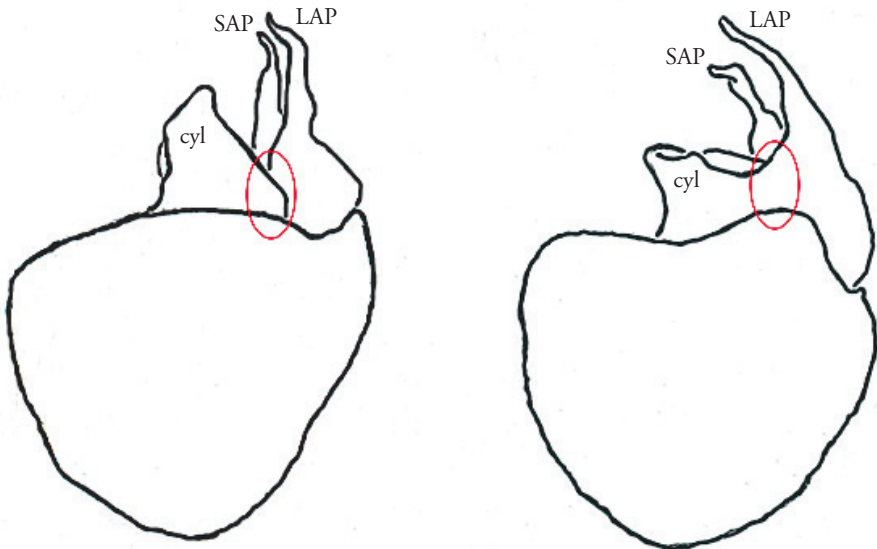


Figure 5. Left gonopods of *D. haitiensis* (left) and *D. angustus*, ventral view, illustrating the difference between type L and type G gonopods. The cylinder (cyl) of Type L species like *D. haitiensis* is separated from the LAP. In Type G species like *D. angustus*, the cylinder and LAP are continuous.

Three species from Puerto Rico – *eggletoni*, *maldonadoi* and *vidalius*, likely fall into these categories; unfortunately the type specimens are unavailable (Agnarsson in litt.) and the original work lacks detailed gonopod descriptions and clear drawings (Velez 1967).

The scanning electron microscope study revealed that *Docodesmus coxalis* possesses four spinneret-like structures on the epiproct (Fig. 6d). Shear (2008) reviewed the occurrence of spinnerets in millipedes, with a focus on Polydesmida, and confirmed that spinnerets are common in many families of Polydesmida. He observed that families with comparatively larger body sizes tend to have putatively vestigial spinnerets that appear to be ordinary setae. Families with smaller individuals (including Pyrgodesmidae) appear to have functioning spinnerets with each seta set in a depression and nested within a short sleeve, as is shown in Fig. 6d.

Most *Docodesmus* males have distinct setiferous tubercles on the anterior face of the 4th coxae (Fig. 6e-f). A similar structure is also found on the adjacent sternum in some species. These structures vary among species in size and pilosity (Table 1).

Table 1. Summary of all *Docodesmus* species recognized at the beginning of this study: the material observed, gonopod type and description of tubercles on 5th body ring. Dashes (–) unknown due to species being known from females only. Question marks (?) unknown due to unavailability of material. ¹ Inferred from figure 25 of Loomis, 1938. ² Unknown due to retraction of anterior processes.

SPECIES	Specimen examined	Gonopod type	Tubercles of 4 th coxa	Tubercles of 4 th sternum
<i>D. alifer</i>	HT (female)	–	–	–
<i>D. amazonicus</i>	HT	type L	reduced	none
<i>D. angustus</i>	HT	type G	present	small swelling
<i>D. brodzinskyi</i>	none	–	–	–
<i>D. centralis</i>	HT	? (missing)	none	none
<i>D. cooki</i>	HT	type L	present	none
<i>D. coxalis</i>	HT	type G	reduced	small swelling
<i>D. cubensis</i>	HT (female)	type G ¹	?	?
<i>D. eggletoni</i>	none	?	?	?
<i>D. grenadae</i>	HT	type L	present	present
<i>D. griseus</i>	HT	type G	present	none
<i>D. haitiensis</i>	HT	type L	present	small swelling
<i>D. hirudiformis</i>	HT	type L	none	small swelling
<i>D. maculatus</i>	none	?	?	?
<i>D. maldonadoi</i>	none	?	?	?
<i>D. parvior</i>	male	type ? ²	reduced	none
<i>D. robustus</i>	HT	type L	present	present
<i>D. sculpturatus</i>	HT	type G	present	present
<i>D. semiseptus</i>	HT	type G	present	none
<i>D. trinidadensis</i>	male	type L	present	none
<i>D. vidalius</i>	none	?	?	?
<i>D. vincentii</i>	male	type L	present	present

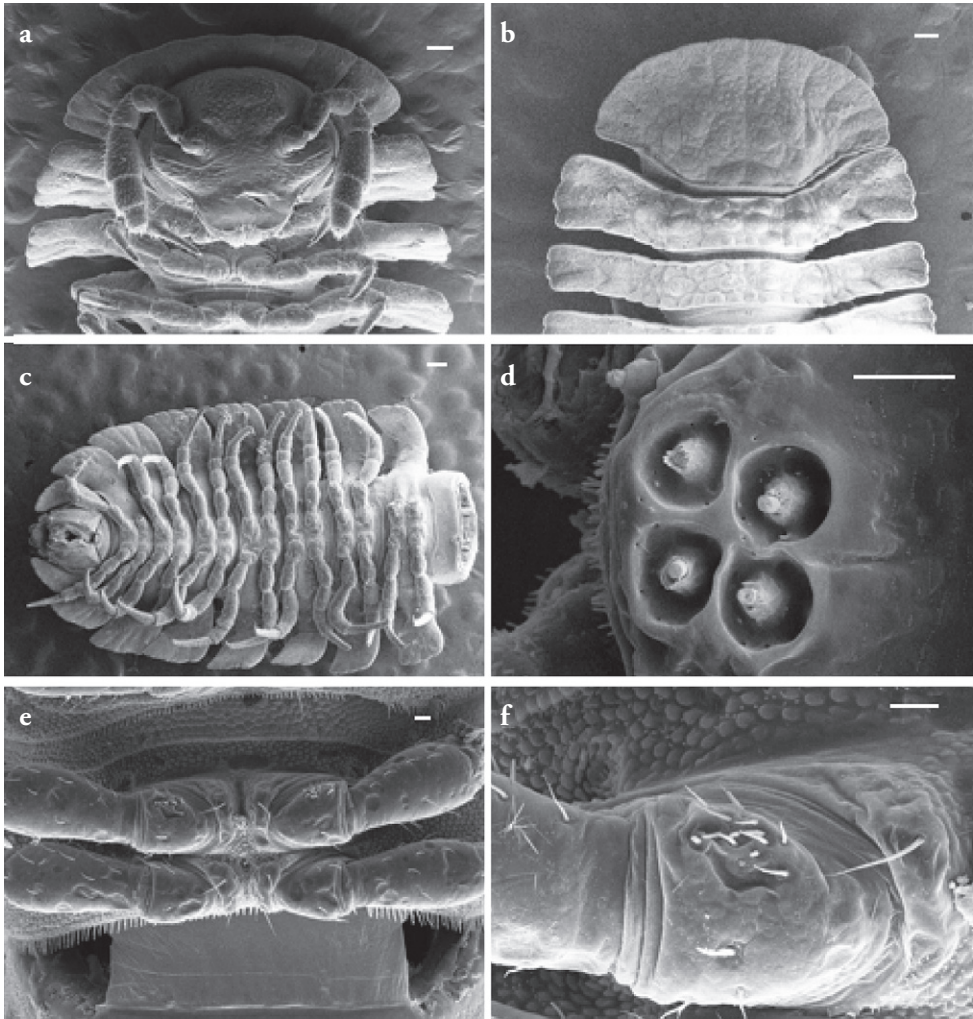


Figure 6. SEM images of *D. coxalis* male. a) ventral and b) dorsal views of anterior end. c) ventral view of posterior end. d) 'spinnerets' on tip of epiproct. e) ventral view of 4th and 5th leg pair and f) close up of tubercles of 4th leg pair coxa (up=anterior). Males of most *Docodesmus* species have such structures, varying in size and pilosity. Scale bars: a-c 100 μ m, d-f 20 μ m.

Species differences within the genus are chiefly associated with size, tergite form and gonopod structure.

Intraspecific variation and species delimiting characters. Original descriptions of *Docodesmus* species rely in their diagnoses on comparisons with other, previously described species assumed to be congeneric. A survey of approximately 50 paratype specimens of *D. coxalis* revealed a significant amount of intraspecific variation in some of the characters used in these comparisons. These specimens were collected at the same time and location as the holotype, and all males can be confidently identified as conspecific due to the presence of the bifid process of the cylinder (Figs 3-4). The

color of the specimens varies from yellow to reddish to brown, the distinctness of the marginal lobes and dorsal tubercles varies from well defined to barely noticeable, and the paranota vary from being nearly flat to dipping acutely ventrad. Therefore, these characters were not included in any of our diagnoses.

Diagnosis. The anterior margin of the first tergite (collum) is semi-circular and has 12 lobes (Figs 6a, b). The posterior margin of this segment is straight and unlobed. The ensuing tergites have an unlobed anterior margin and 16 strictly posterior lobes, quite distinct on the paranota, less so toward the body midline. Paranota have 3 lateral lobes on the non-poriferous body rings plus ring 5 (2-6, 8, 11, 14). The remaining body rings (7, 9-10, 12-13, 15-19) have 4 lateral lobes (Fig. 7). Gonopods with large, bulbous coxites and mesally oriented telopodites consisting of one posterior 'cylindrical' process and two anterior spear-like processes.

Affinities of *Docodesmus*. Golovatch (1997) suggested, without citing characters that the genera *Leuritus* Chamberlin, 1923, *Coccoelasma* Loomis, 1936, *Cyphotylus* Loomis, 1936 and *Lobodesmus* Loomis, 1936 might be close relatives of *Docodesmus* when he discussed placement for his new species *Docodesmus amazonicus*. Three other Caribbean pyrgodesmid genera were cited by other authors as having a close affinity with *Docodesmus*: *Henicomus* Loomis, 1941, *Jeekelia* Loomis, 1950 and *Tridesmus* Cook, 1896. Currently, the delineation of *Docodesmus* rests on the lobe patterns of the collum, the paranota and the posterior tergal margins. Due to insufficient descriptions and figures of potentially closely related taxa, no gonopodal apomorphies for *Doco-*



Figure 7. Comparison of lobation patterns of five Caribbean pyrgodesmid genera. Small numbers = ring number; large numbers = number of lobes, stars indicate difference from *Docodesmus*; ovals represent posterior notches.

desmus can be defined at this point. Furthermore, mature male specimens have been identified for only three of the above genera: *Tridesmus* (one single male), *Lobodesmus* and *Leuritus*. After examination of the characters described, the illustrations of the type species, and examination of type material, we conclude that at this time none of the seven genera listed above can be unequivocally synonymized with *Docodesmus*. Except for *Tridesmus*, the other six genera are currently monotypic. Four genera, *Henicomus*, *Jeekelia*, *Tridesmus* and *Coccoelasma*, may have close affinity with *Docodesmus* based on their lobation pattern as illustrated in Fig. 7.

***Tridesmus* Cook, 1896**

The history of the genus name *Tridesmus* Cook, 1896 exemplifies the nomenclatorial confusion hindering the systematic treatment of many millipede taxa, especially in, but certainly not restricted to the Pyrgodesmidae. The genus *Tridesmus* can essentially be considered a phantom genus. It was described by Cook (1896b: 21), including the type species *Tridesmus* 'sectilis'. However, as Silvestri correctly noted (1908: 577), Cook did not actually describe the type species; he merely listed the name, a specimen of unspecified gender from Puerto Rico deposited in the Berlin Museum. According to ICZN, Article 12.3, the species is not validly described and thus the species name 'sectilis' is not available. Nevertheless, subsequent authors cited 'sectilis' as a valid species and placed other species into *Tridesmus*, without ever designating a type species for the genus. Currently, *Tridesmus* consists of two species from Puerto Rico: *T. portoricensis* Silvestri, 1908, and *T. guilarteus* Chamberlin, 1950, plus the Berlin specimen Cook mentioned as 'sectilis', and four species from South America: *T. serratus* Silvestri, 1898, *T. cognatus* Silvestri, 1898, *T. ortonedae* Silvestri, 1898, and *T. perucola* Chamberlin, 1955. The type specimens of *portoricensis* and *guilarteus* are female; the genders of the type specimens for *T. cognatus*, *T. perucola* and *T. serratus* were not specified in the descriptions, no figures of gonopods were given, nor were males mentioned in the descriptions. Silvestri mentions a male specimen for *T. ortonedae*. According to ICZN Article 67.2.2 the three species placed into *Tridesmus* by Silvestri in 1898 "are deemed to be the only originally included species." A type species by subsequent designation should be selected from these three. *Tridesmus ortonedae*, being one of the first validly described species included in the genus *Tridesmus*, would qualify as the type species. However, it is questionable whether the South American and Puerto Rican species are congeneric. We postpone the designation of the type species until all available specimens assigned to *Tridesmus* have been re-examined.

The somatic features are best described in *T. portoricensis*, which has a 12-lobed collum and 16 lobes at the posterior margin of the tergites. The lateral lobation pattern is similar to *Docodesmus*, differing by poriferous paranota having one less lobe, but with the addition of a distinct structure, likely pore bearing, at the posterior tip of each paranotum. Cook (1896) noted the similarity of *Tridesmus* to *Docodesmus* in size and shape and the differences in dorsal sculpture and poriferous paranota. Thus, the data

that can be gleaned from the published literature, listed completely below, does not provide sufficient evidence to evaluate the possible relationship of any species placed into *Tridesmus* to *Docodesmus*.

Genus ***Tridesmus*** Cook, 1896

Tridesmus Cook, 1896b: 21. Type species: listed as *Tridesmus* *sectilis* Cook, 1896b from Puerto Rico, name not available. Silvestri (1908: 577) noted that the proposed type species of the genus was still undescribed.

Tridesmus cognatus Silvestri

Tridesmus cognatus Silvestri 1898: 63, no figures. HT (ZMUC) of unspecified gender from Venezuela. Type specimen listed as available at: <http://www.zmuc.dk/EntoWeb/collections-databaser/diplo-polydesmida.htm>

Cryptodesmus? *cognatus*: Attems 1899: 368. Placed into *Cryptodesmus* by Attems without reference to characters nor examination of specimens.

Tridesmus guilarteus Chamberlin

Tridesmus guilarteus Chamberlin 1950: 148, no figures. Female HT from Puerto Rico in Coll. Chamberlin, type specimen available in USNM

Tridesmus guilarteus: Hoffman 1999: 499. – Shelley 2004: 1161.

Tridesmus ortonadae Silvestri

Tridesmus ortonadae Silvestri 1898: 63, no figures. Male HT from Guayaquil, Ecuador in Coll. Silvestri, possibly deposited in MFS (Portici) or at MACN.

Cryptodesmus ortonadae: Attems 1899: 368. Placed in *Cryptodesmus* by Attems without reference to characters nor examination of specimens.

The gonopod is described as: organum copulativum articulo ultimo integro apice non attenuato, rotundato, et unco parvo, laterali aucto.

Tridesmus perucola Chamberlin

Tridesmus perucola Chamberlin 1955: 42, no figures. Female HT from Peru deposited in Coll. Chamberlin, type specimen available at USNM.

Tridesmus portoricensis Silvestri

Tridesmus portoricensis Silvestri 1908: 577, figures X, XI. Female HT from Puerto Rico deposited possibly at AMNH.

Tridesmus portoricensis: Chamberlin 1918: 220. – Hoffman 1999: 500. Holotype cited as male. – Shelley 2004: 1161.

Tridesmus sectilis Cook, name not available

Tridesmus *sectilis* Cook 1896b: 21, no figures, no description, gender of specimen not recorded; locality: Puerto Rico, deposited at ZMB (listed as male syntype in Moritz & Fischer 1978).

Cryptodesmus? *sectilis*: Attems 1899: 367. Placed into *Cryptodesmus* by Attems without reference to characters nor examination of specimens, cited as an available name.

Tridesmus *sectilis*: Silvestri 1908: 577, notes that the species has not yet been described.

– Chamberlin 1918: 219. (cited as an available name). – Hoffman 1999: 500. (cited as an available name; holotype cited as male).

Tridesmus *sectile* [sic]: Shelley 2004: 1161. (cited as available name).

***Tridesmus serratus* Silvestri**

Tridesmus serratus Silvestri 1898: 63, no figures. HT (ZMUC) of unspecified gender from Puerto Rico. Type specimen listed as available at: <http://www.zmuc.dk/EntoWeb/collections-databaser/diplo-polydesmida.htm>

Cryptodesmus? *serratus*: Attems 1899: 368. Placed in *Cryptodesmus* by Attems without reference to characters nor examination of specimens.

***Coccoelasma* Loomis, 1936**

Coccoelasma has the same number of lateral and posterior lobes as *Docodesmus*, but only ten on the collum. Loomis (1936) remarked on the association of *Coccoelasma* with *Docodesmus* when he created the genus and described its sole species, *C. incisura* of Hispaniola. He offered proportions of body and antennae, location of pores, squamate areas of dorsum, and gonopod structure as evidence of this association. Contrasting the genera, he described *Coccoelasma* as having a more convex dorsum covered with fine granules, first segment narrower than second and with a narrow anterior margin, ensuing body rings with 3 instead of 2 areas in the longitudinal rows, and a deep incision in the posterior margin of each paranotum. The gonopods were neither described nor figured, but merely mentioned ‘as in *Docodesmus*,’ from which Attems (1940: 237) infers that there are two telopodite branches. Since the delineation of the genus *Docodesmus* currently rests on somatic features, such as the 12-lobed collum, genera such as *Coccoelasma* with a 10-lobed collum cannot be synonymized until gonopodal or other apomorphies have been defined.

***Coccoelasma incisura* Loomis**

Coccoelasma incisura Loomis 1936: 170, figure 71, and plate 3, figure 4. Male HT (USNM) and female PT (MCZ) from Haiti, *vidi*.

Coccoelasma incisura: Attems 1940: 237, figures and description after Loomis. – Hoffman 1999: 478.

***Cyphotylus* Loomis, 1936**

Golovatch (1997) suggested a close relationship with *Docodesmus* without discussion of characters. Loomis placed the genus close to *Coccoelasma*, most likely based on the 10-lobed collum. The pronounced dorsal tuberculation of the specimen’s tergites, as illustrated by Loomis in figure 72, is strikingly different from the tuberculation in any *Docodesmus* species. Since the holotype is an immature male, gonopodal characters cannot be assessed.

***Cyphotylus prolatus* Loomis**

Cyphotylus prolatus Loomis 1936: 172, figure 72. Immature male HT (USNM) from Haiti.

Cyphotylus prolatus: Attems 1940: 253, figures and descriptions after Loomis.

***Leuritus* Chamberlin, 1923**

Leuritus displays several unique, most likely autapomorphic features, which do not support affinities with *Docodesmus*. The type species is densely setose, the epiproct is broad, the gonopodal prefemur has a small process, the telopodite has two long slender branches.

***Leuritus termitophilus* Chamberlin**

Leuritus termitophilus Chamberlin 1923: 413, plate 25, figures 1-7 (plate is incorrectly labeled). Male HT from Guyana, in Coll. Chamberlin, not listed in USNM millipede type collection.

Leuritus termitophilus: Attems 1940: 238, figures and descriptions after Chamberlin. – Silvestri 1947: 16, figure VIII.

***Jeekelia* Loomis, 1950**

The genus *Jeekelia* contains the single species *J. granulosa* from the Dominican Republic. The original genus name for this species was *Melanodesmus*, however this name is preoccupied by the Colombian chelodesmid genus *Melanodesmus* Carl, 1914. Loomis later (1950) established *Jeekelia* to accommodate *granulosa*. This species also shares the anterior collum and lateral paranotal lobe patterns of *Docodesmus* but has fewer posterior lobes with two pronounced posterior notches on each side. Again, Loomis mentioned a possible close relationship to *Docodesmus*, noting the similar shape and proportions. The major differences noted by Loomis are the dorsal texture and the posterior tergite notches. Gonopod characters cannot be assessed as the type of *J. granulosa* is female.

***Jeekelia granulosa* (Loomis)**

Melanodesmus granulosa Loomis 1941b: 74, no figures. Female HT (MCZ) from Puerto Rico, *vidi*.

Jeekelia granulosa: Loomis 1950: 166.

***Lobodesmus* Loomis, 1936**

Loomis placed *Lobodesmus* in close relationship with *Tridesmus*, citing the trilobed non-poriferous paranota. The original description and figures provide no evidence of a close affinity with *Docodesmus*; the posterior edge of the collum features 8 lobes, and the posterior edge of the tergites is marked by 4 large lobes. The gonopod illustration does not show resemblance with gonopods in *Docodesmus*.

***Lobodesmus granosus* Loomis**

Lobodesmus granosus Loomis 1936: 165, figure 70. Male HT (MCZ) from Morne La Hotte, Haiti.

Lobodesmus granosus: Attems 1940: 249, figures and description after Loomis. – Hoffman 1999: 488.

***Henicomus* Loomis 1941**

Henicomus is another monotypic genus described by Loomis (1941b) from the Dominican Republic, containing *H. septiporus*. This species has a 12-lobed collum and a comparable lateral paranotal lobe pattern. Paranota of rings 5, 10, 13 and 16-17 have one less lateral lobe than the respective rings in *Docodesmus*, however the posterior-most of these lobes are quite large and consist of a circular structure containing the ozopore. The posterior margin of each tergite has 14 lobes instead of 16, in addition to a slight posterior notch on each paranotum. Loomis remarked on the similarity of *Henicomus* to *Docodesmus* in general form and sculpture, but noted the more convex dorsum, descending paranota, and uneven sterna of each body ring as distinct differences. The most “outstanding feature” of *Henicomus* according to Loomis, is the unique pore formula (5, 10, 13, 16-19), however, ozopores of pyrgodesmids can be quite cryptic. Additionally, the type specimen for *H. septiporus* is female, thus no comparison of gonopod structure is possible.

***Henicomus septiporus* Loomis**

Henicomus septiporus Loomis 1941b: 79, figure 33. Female HT (MCZ) from Dominican Republic, *vidi*.

Henicomus septiporus: Hoffman 1999: 485.

The species of *Docodesmus*

***Docodesmus alifer* Loomis**

Docodesmus alifer Loomis 1941b: 68, figures. 26a-c. Female HT, *vidi* and female PT, *vidi* (MCZ) from Pico del Yaque, Loma Rucilla, Dominican Republic.

Docodesmus alifer: Loomis 1969: 249. – Golovatch 1997: 328. – Hoffman 1999: 482.

Diagnosis: The prominently elevated paranota distinguish this species from all other congeners. Gonopod structure is unknown, as this species is known from only two female specimens. It is not unreasonable to suspect that these are aberrant specimens of one of the other four Hispaniola species. Length 15 mm, width 3 mm.

Specimens examined: Two fragmented females including holotype (MCZ).

***Docodesmus amazonicus* Golovatch**

Docodesmus amazonicus Golovatch 1997: 327, figures. 17-21. Male HT, *vidi* (INPA) from Rio Tarumã Mirím, Manaus, Brazil.

Diagnosis: Gonopod (Golovatch 1997: figures 20-21) is type L, with LAP significantly longer and more robust than in all island species. SAP is absent or fused with LAP. LAP splits into two branches at the distal third, with the solenomere being the shorter branch. Longer branch distally flat and retrorse. This single, flat tip distinguishes this species from the other Amazonian species *D. hirudiformis*, the tip of which terminates in two flat processes. Length 7 mm, width 1.5 mm.

Specimen examined: Male holotype.

***Docodesmus angustus* Loomis**

Docodesmus angustus Loomis 1941b: 71, figures. 29a-d. Male HT, *vidi* (MCZ) from Valle Nuevo, southeast of Constanza, Dominican Republic.

Docodesmus angustus: Loomis 1969: 250. – Golovatch 1997: 328. – Hoffman 1999: 482.

Docodesmus griseus Loomis 1941b: 69, figure 27. Male HT, *vidi* (MCZ) from Sanchez, Dominican Republic (**syn.n.**). Loomis 1969: 249. – Golovatch 1997: 328. – Hoffman 1999: 483.

Diagnosis: Gonopods (Loomis 1941b: figure 29d) are type G. Cylinder is very distinct without additional processes. LAP with distal 90° bend and single acute tip. SAP with slight bend and single acute tip. Distinguished from other *Docodesmus* species of Hispaniola by the cylinder of the gonopod being continuous with LAP and having no additional processes (opposed to *D. haitiensis*), and by its larger size (compared to *D. parvior* and *D. semiseptus*). HT Length 14mm, width 3mm. From original description: largest male length 15 mm; largest female length 18 mm. *D. griseus* HT length 14 mm, width 2.5 mm.

Docodesmus griseus is a junior subjective synonym of *D. angustus*. In the original description, figure 27 gives a rather inaccurate illustration of the *D. griseus* gonopod. The cylinder appears detached from the LAP in this illustration, which is not the case. The illustration of *D. angustus* in figure 29d is more accurate. The holotype of *D. griseus* appears to be an aberrant specimen in which certain body rings have different numbers of lobes on each paranotum. As first revisors, and to avoid having an aberrant holotype for this species, we have selected *angustus* as the senior synonym despite *griseus* having a two-page priority.

Specimens examined: Male holotypes of *D. angustus* and *D. griseus*.

***Docodesmus brodzinskyi* Shear**

Docodesmus brodzinskyi Shear 1981: 53, figures 1, 2. Female HT, *non vidi* (collection of J. Brodzinsky, Santo Domingo, D.R.) from an uncertain locality in the Dominican Republic.

Docodesmus brodzinskyi: Golovatch 1997: 330. – Hoffman 1999: 482.

This is a fossil specimen in amber, thought to be of Oligocene age (30-35 mya). The two figures from the original description suggest that the lobes of the collum and the lateral lobes of tergites 2, 3 and 11 are consistent with our diagnosis of *Docodesmus*. Length 9.5 mm, width 1.25 mm.

***Docodesmus centralis* Silvestri**

Docodesmus centralis Silvestri 1898: 62. Male HT, *vidi* (deposited in MSNG) from La Guaira, Venezuela.

Docodesmus centralis: Attems 1899: 373. – Golovatch 1997: 328.

The holotype male (the only known specimen for this species) has a lobation pattern inconsistent with all other *Docodesmus* species. The collum has 10 lobes and all paranota have 3 lateral lobes. The ozopore bearing paranota also have a porostele on the caudal lobe. The gonopods are missing from the specimen's vial. The original gonopod description is vague and contains nothing that suggests *Docodesmus*. Length 5 mm, width 1 mm. We conclude that *centralis* does not belong in genus *Docodesmus*, but have no suggestion for placement at this time and leave it *incertae sedis*.

Specimen examined: Holotype (fragmented, gonopods missing). Listed in the original description as being deposited in ZMUC.

***Docodesmus coxalis* Loomis**

Docodesmus coxalis Loomis 1975: 170, figure 4. Male HT, *vidi* (FSCA) from one mile south of Claremont, St. Ann Parish, Jamaica.

Docodesmus coxalis: Golovatch 1997: 328. – Hoffman 1999: 483.

Diagnosis: Gonopods are type G. Cylinder is very distinct with a small additional bifid process on the margin opposite the LAP. LAP with distal 90° bend and single acute tip. SAP with variable bends and curves and single acute tip. Distinguished from other type G *Docodesmus* species by the presence of the additional bifid process on the cylinder. Males assigned to *D. cubensis* have a similar process, as illustrated by Loomis (1938: figure 25). However, *D. cubensis* individuals are much larger. HT length 7 mm, width 1.8 mm. PT males range in length from 7-7.5 mm, in width from 1.5-2 mm. PT females range in length from 7-8 mm, in width from 1.8-2 mm.

Specimens examined: Male holotype, ca. 50 paratypes, all from type locality (all FSCA).

***Docodesmus cubensis* Loomis**

Docodesmus cubensis Loomis 1937: 225, figures 13, 14. Female HT, *vidi* (MCZ) from Soledad, Prov. Cienfuegos, Cuba.

Docodesmus cubensis: Loomis 1938: 473, figure 25. – Loomis 1950: 166. – Loomis 1969: 250. – de la Torre 1974: 8. – Loomis 1975: 170, 172. – Golovatch 1997: 328. – Hoffman 1999: 483.

Diagnosis: The type is female and no male specimens were available to us. Loomis's drawing (1938, figure 25) of a male gonopod assigned to *cubensis* shows a gonopod nearly identical to that of *D. coxalis*. Distinguished from other *Docodesmus* species except *D. coxalis* by the presence of the additional bifid process on the cylinder, however *D. coxalis* individuals are much smaller. Length 11 mm, width 2.5 mm.

Specimen examined: Female holotype (fragmented).

***Docodesmus eggletoni* Velez**

Docodesmus eggletoni Velez 1967: 28, figures 7-9, map II, tbl. III. Male HT, *non vidi* (USNM) from Hy. 119, nine km north of San German, Puerto Rico.

Docodesmus eggletoni: Golovatch 1997: 328. – Hoffman 1999: 483.

The type specimens of *Docodesmus eggletoni*, *D. maldonadoi* and *D. vidalius* were not available for this study. The holotypes (USNM) and paratypes (University of Puerto Rico, Rio Piedras) are apparently missing from their respective depositories (De Roche, in litt., Agnarsson, in litt.). The only literature treatment is the original description (all Velez 1967). The descriptions and illustrations do not provide enough information for diagnoses or comparisons with congeners. The presence of a cylinder, LAP and SAP is apparent, but whether they are type G, type L or something else cannot be discerned. In spite of this, the descriptions clearly show that these three species have a lobe pattern consistent with our diagnosis for *Docodesmus*.

***Docodesmus grenadae* Chamberlin**

Docodesmus grenadae Chamberlin 1918: 218, 259. Male HT, *vidi* (MCZ) from Grand Etang, Grenada, Lesser Antilles.

Docodesmus grenadae: Loomis 1937: 226, figures 15, 16. – Loomis 1969: 250. – Golovatch 1997: 328. – Hoffman 1999: 483.

Diagnosis: Gonopods are type L. The cylinder is reduced to a rounded knob. The LAP is long, flattened and distally bent 90°. The SAP is straight and needle-like and in complete or near-complete contact with the LAP along its entire length. Distinguished from other type L *Docodesmus* species by the complete contact of LAP and SAP. This character is shared only with *D. trinidadensis*, but the two species are distinguished by the tip of the LAP (needle-like in *trinidadensis*). Length 13 mm, width 3 mm.

Specimen examined: Male holotype (fragmented), male specimen from Grenada (BMNH).

***Docodesmus haitiensis* Chamberlin**

Docodesmus haitiensis Chamberlin 1918: 216, 259. Male HT, *vidi* (MCZ) from Diquinini, Haiti.

Docodesmus haitiensis: Loomis 1934: 45, plate 3, figures 1, 2. – Loomis 1936: 162. – Loomis 1937: 225. – Loomis 1941b: 71, figures 28a, b. – Loomis 1969: 250. – Loomis 1975: 170 – Golovatch 1997: 328. – Hoffman 1999: 483.

Docodesmus cooki Loomis 1969: 248, figures 8-10. Male HT, *vidi* (USNM) labeled Etowah, Tennessee (**syn.n.**). – Golovatch 1997: 328. – Hoffman 1999: 482. – Shelley 2004: 1161.

Diagnosis: Gonopod is type L. Cylinder very prominent with a short, flat and blunt extension at the posterior-most margin. LAP with distal 90° bend or slight curve. SAP slightly shorter with bends and curves varying among specimens. Distinguished from other *Docodesmus* of Hispaniola by the cylinder being discontinuous with the LAP (type L). All other Hispaniola species are type G. HT length 14 mm, width 3.5 mm. Other specimens range in length 14-18 mm and width 3.5-4 mm in both sexes.

Docodesmus cooki is a junior subjective synonym of *D. haitiensis* based on our examination of the type specimens. The mystery still remains, as discussed by Loomis (1969) and Shelley (2004), of how two *Docodesmus* specimens turned up in a jar of Tennessee millipedes.

Specimens examined: Male holotype (fragmented), ca. 7 fragmented topotypes (MCZ); 1 male and 1 female from Cape Haitien, Haiti, det. Loomis (USNM); 1 male and 1 female from Pétienville, Haiti, det. Loomis (FSCA); *D. cooki* HT and PT (USNM). Also known from Dominican Republic (Loomis 1941b: 71).

***Docodesmus hirudiformis* Golovatch**

Docodesmus hirudiformis Golovatch 1999: 224. Male HT, *vidi* (INPA) from the environs of Manaus, Brazil.

Diagnosis: Gonopod is type L, with LAP significantly longer and more robust than in all island species. SAP is absent or fused with LAP. Solenomere branches from LAP at distal third. Remaining branch splits into two flattened processes. These two processes distinguish this species from the other Amazonian species, *D. amazonicus*. HT length 6.5 mm, width 2 mm. Male PT length 8 mm, width 2 mm. Female PT length 6-7 mm, width 1.5 mm.

Specimens examined: Male holotype. One male, 2 female paratypes (INPA).

Docodesmus maculatus (Bollman)

Stenonia maculata Bollman 1888: 336. Male HT, *non vidi* (USNM, lost, De Roche, in litt.), from Cuba, without further locality data.

Platyrrhachus maculatus: Pocock 1894a: 511.

Platyrrachus? *maculatus*: Chamberlin 1918: 216, 259.

Schizodira maculata: Loomis 1941a: 37.

Docodesmus maculatus: Loomis 1950: 165. – de la Torre 1974: 9 (cited again as a new combination without mentioning Loomis's placement). – Golovatch 1997: 328. – Hoffman 1999: 483.

Known only from male HT and female PT specimens, which are apparently lost (De Roche, in litt.). No description of the gonopod structure has been published. This may be the same species as *D. cubensis*, but was assigned to Platyrrhacidae at the time of *cubensis*' description. Hence, we designate *Docodesmus maculatus* a *nomen dubium*.

Docodesmus maldonadoi Velez

Docodesmus maldonadoi Velez 1967: 27, figure 6, map II. Male HT, *non vidi* (USNM, not located in collection) from Km 4.4 on the Sabana Road at 1,850 ft, near El Yunque, Puerto Rico.

Docodesmus maldonadoi: Golovatch 1997: 328. – Hoffman 1999: 484.

See treatment of *D. eggletoni* above.

Docodesmus parvior Chamberlin

Docodesmus parvior Chamberlin 1918: 218, 259. Female HT, *non vidi* (MCZ) from Furcy, Haiti.

Docodesmus parvior: Loomis 1936: 162, plate 3, figure 3. – Loomis 1937: 224. – Loomis 1941b: 73. – Loomis 1941c: 194. – Loomis 1969: 250. – Loomis 1975: 170. – Golovatch 1997: 328. – Hoffman 1999: 484.

Diagnosis: Gonopods with telopodite apparently retracted into the coxae, resulting in anterior processes appearing shorter than in other species. Cylinder with a short, flat and blunt extension on posterior end. LAP is flattened and slightly longer than SAP. HT length 8.5 mm, width 2 mm. Other specimens: Female length 8 mm, width 1.5 mm. Male length 8.5 mm, width 2 mm. Length can reach 10 mm (Loomis 1936).

Specimens examined: One male, 2 females from Petionville, Haiti, det. Loomis (FSCA).

The male examined for this diagnosis and several others were identified by Loomis (1936, 1941), but no explanation was given as to how they were identified as such. The

similarity of gonopods with *haitiensis* suggests synonymy, but there is a considerable difference in size between the two species.

***Docodesmus robustus* Loomis**

Docodesmus robustus Loomis 1934:47, figure 24, plate 4, figure 3. Male HT, *vidi* (USNM) from King's Bay, Tobago Island.

Docodesmus robustus: Loomis 1937: 224. – Loomis 1969: 249. – Golovatch 1997: 328.

Diagnosis: Gonopods are type L. The LAP is flat and broadens at the midpoint where it then abruptly narrows and bends 90°. A small process is present near the tip. SAP is considerably shorter than the LAP, needle-like with a slight bend. Known from two specimens. Distinguished from other type L *Docodesmus* species by the broad basal half of the LAP. The other species known from Tobago, *trinidadensis*, has a needle-like LAP tip, and has the LAP and SAP in total contact along their lengths. Length 13 mm, width 3.7 mm.

Specimen examined: Male holotype and female paratype (USNM).

***Docodesmus sculpturatus* Loomis**

Docodesmus sculpturatus Loomis 1934: 45, figure 22, plate 4, figure 1. Male HT, *vidi* (USNM) from a “banana hole” three or four miles from Nassau, New Providence, Bahama Islands.

Docodesmus sculpturatus: Loomis 1937: 225, 227. – Velez 1967: 29, map II. – Loomis 1969: 250. – Golovatch 1997: 328. – Hoffman 1999: 484.

Diagnosis: Gonopods are type G. Cylinder is reduced but still apparent. LAP is flattened, distally bent and promptly tapers to a point. SAP is straight and nearly equal in length as LAP. Distinguished from other type G *Docodesmus* species by the combination of a reduced cylinder and a flattened LAP. Length 5-8 mm, width 1-1.5 mm.

Specimens examined: Male holotype (USNM), 3 male paratypes (FSCA).

Also known from Puerto Rico (Velez 1967, map II).

***Docodesmus semiseptus* Loomis**

Docodesmus semiseptus Loomis 1936: 163, figure 69. Male HT, *vidi* (USNM) from Morne Pilboreau, above Ennery, Haiti.

Docodesmus semiseptus: Loomis 1937: 224. – Loomis 1969: 249. – Golovatch 1997: 328. – Hoffman 1999: 484.

Diagnosis: Gonopods are type G with short, flat extension of posterior margin of cylinder. LAP wide at the base with a slight distal curve. SAP with a slight bend. Distinguished from other type G Hispaniola species by the flat extension on the posterior margin of the cylinder. Length 8 mm, width 1.7 mm.

Specimen examined: Male holotype.

***Docodesmus trinidadensis* Chamberlin**

Docodesmus trinidadensis Chamberlin 1918: 219. Female HT, *non vidi* (MCZ) from Port of Spain, Trinidad.

Docodesmus trinidadensis: Loomis 1934: 46, figure 23, plate 4 figure 2. – Loomis 1937: 224–227. – Loomis 1969: 250. – Golovatch 1997: 328.

Diagnosis: Gonopods are type L. LAP long, straight and wide for most of its length, then abruptly narrowing to a needle-like point. A small knob present on side of needle. SAP is straight and in complete contact with the LAP along its entire length. Distinguished from all other *Docodesmus* species by the abrupt needle-like tip of the LAP. HT length 13.2 mm. Other specimens: 2 males length 9 mm, width 2 mm; 2 females length 10 mm, width 2 mm.

Specimens examined: Two males and 2 females from Arena Forest, Trinidad, det. Loomis (FSCA).

Also found on Tobago (Loomis 1934).

***Docodesmus vidalius* Velez**

Docodesmus vidalius Velez 1967: 24, figures 2–5, map II, tbl. II. Male HT, *non vidi* (USNM, not located in collection) from Km 10.7 on Hy. 146, about 10 km southwest of Ciales, Puerto Rico.

Docodesmus vidalius: Golovatch 1997: 328. – Hoffman 1999: 484.

See treatment of *D. eggletoni* above.

***Docodesmus vincentii* (Pocock)**

Cryptodesmus vincentii Pocock 1894a: 510, plate 39, figures 2–2d. HT, *non vidi* (BMNH) from St. Vincent, Lesser Antilles.

Aporodesmus vincentii: Pocock 1894b. – Attems 1899: 372.

Docodesmus vincenti [sic!]: Chamberlin 1918: 216, 259.

Docodesmus vincentii: Cook 1896: 5, 20. – Loomis 1936: 161. – Loomis 1937: 225. – Velez 1967: 26. – Loomis 1969: 250. – Golovatch 1997: 328. – Hoffman 1999: 484.

Diagnosis: Gonopods are type L and very similar to *D. grenadae*. They differ from *grenadae* by having a 90° torsion at the distal bend of the LAP. Short, rounded process present at bend.

Type material listed as deposited BMNH. We received on loan from BMNH 8 vials identified on the loan invoice as paratypes. Although all specimens are conspecific, no vial contained any information on type status. Two vials had label information similar to that found in the original description ("Forest below 1500 ft., under rotting leaves; pretty common."): one vial with one adult female, one adult male (gonopods missing), 2 juveniles, plus additional pieces; one vial with 3 small juveniles and 3 immature females.

Specimens examined: 5 males, 11 females from St. Vincent (BMNH).

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References

- Attems, C.M.T. Graf von (1899) System der Polydesmiden II. – Denkschriften der Akademie der Wissenschaften Wien, mathematisch-naturwissenschaftliche Klasse 68: 251-435.
- Attems, C.M.T. Graf von (1940) Myriapoda 3. Polydesmoidea III. – Das Tierreich 70: 577 pp.
- Bollman, C.H. (1888) Notes on a collection of Myriapoda from Cuba. – Proceedings of the United States National Museum 11: 335-338.
- Chamberlin, R.V. (1918) The Chilopoda and Diplopoda of the West Indies. – Bulletin of the Museum of Comparative Zoology 62: 149-262.
- Chamberlin, R.V. (1923) On four termitophilous millipeds from British Guiana. – Zoologica: New York Zoological Society 3: 141-421.
- Chamberlin, R.V. (1950) Some diplopods from Puerto Rico. – Proceedings of the Biological Institute of Washington 63: 147-154.
- Chamberlin, R.V. (1955) New millipeds from Peru and adjacent parts. – University of Utah Biological Series 11: 1-47.

- Cook, O.F. (1896a) On recent diplopod names. – *Brandtia* 2: 5-8.
- Cook, O.F. (1896b) *Cryptodesmus* and its allies. – *Brandtia* 5: 19-28.
- de la Torre, S.L. (1974) Lista Preliminar de los Diplopodos (Miriapoda, Diplopoda) de Cuba. – *Ciencias (Serie 4- Ciencias Biologicas)* 42: 1-16.
- Golovatch, S.I. (1997) One some further Neotropical Pyrgodesmidae, partly from the environs of Manaus, Central Amazonia, Brazil (Diplopoda, Polydesmida). – *Amazoniana* 14: 323-334.
- Golovatch, S.I. (1999) On six new and some older Pyrgodesmidae from the environs of Manaus, Central Amazonia, Brazil (Diplopoda, Polydesmida). – *Amazoniana* 15: 221-238.
- Hoffman, R.L. (1982) Diplopoda. – In: Parker, S. (ed), *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York, pp. 689-724.
- Hoffman, R.L. (1999) Checklist of the Millipeds of North and Middle America. Virginia Museum of Natural History Special Publication Number 8: 581 pp.
- Loomis, H.F. (1934) Millipeds of the West Indies and Guiana collected by the Allison V. Armour expedition in 1932. – *Smithsonian Miscellaneous Collections* 89: 1-69.
- Loomis, H.F. (1936) The millipeds of Hispaniola, with descriptions of a new family, new genera, and new species. – *Bulletin of the Museum of Comparative Zoology* 80: 1-191.
- Loomis, H.F. (1937) New Jamaican and Cuban millipeds, with notes on several other species. – *Bulletin of the Museum of Comparative Zoology* 80: 215-228.
- Loomis, H.F. (1938) New and noteworthy millipeds from Cuba collected by Dr. P. J. Darlington in 1936. – *Bulletin of the Museum of Comparative Zoology* 82: 427-480.
- Loomis, H.F. (1941a) A new Cuban milliped, with notes and drawings of other West Indian species. – *Psyche* 48: 35-39.
- Loomis, H.F. (1941b) Millipeds collected in Puerto Rico and the Dominican Republic by Dr. P. J. Darlington in 1938. – *Bulletin of the Museum of Comparative Zoology* 88: 17-80.
- Loomis, H.F. (1941c) New genera and species of millipeds from the southern peninsula of Haiti. – *Journal of the Washington Academy of Sciences* 31: 188-195.
- Loomis, H.F. (1950) Synonymy of some native American and introduced millipeds. – *Journal of the Washington Academy of Sciences* 40: 164-166.
- Loomis, H.F. (1969) New and known millipeds from four southern states. – *The Florida Entomologist* 52: 245-251.
- Loomis, H.F. (1975) New millipeds in a noteworthy collection from Jamaica. – *The Florida Entomologist* 58: 167-185.
- Moritz, M. and Fischer, S-C. (1978) Die Typen der Myriapoden-Sammlung des Zoologischen Museums Berlin. Diplopoda. Teil 4: Polydesmida. – *Mitteilungen aus dem Zoologischen Museum in Berlin* 54: 99-152.
- Pocock, R.I. (1894a) Contributions to our knowledge of the arthropod fauna of the West Indies – Part III. Diplopoda and Malacopoda, with a supplement on the Arachnida of the Class Pedipalpi. – *The Journal of the Linnean Society* 24: 473-544.
- Pocock, R.I. (1894b) The Myriopoda of Burma, Pt. IV. Report upon the Polydesmoidea collected by Sig. L. Fea, Mr. E. W. Oates and others. – *Annali del Museo Civico di Storia Naturale di Genova* 14: 787-836.

- Rowe, M. & Sierwald, P. (2006) Morphological and systematic study of the tribe Australiosomatini (Diplopoda: Polydesmida: Paradoxosomatidea: Paradoxosomatidae) and a revision of the genus *Australiosoma* Brölemann. – *Invertebrate Systematics* 20: 527-556.
- Shear, W.A. (1981) Two fossil millipeds from the Dominican amber (Diplopoda: Chytodesmidae, Siphonophoridae). – *Myriapodologica* 1: 51-54.
- Shear, W.A. (2008) Spinnerets in the milliped order Polydesmida, and the phylogenetic significance of spinnerets in millipeds (Diplopoda). – *International Journal of Myriapodology* 2: 123-146.
- Shelley, R. M. (2004) The milliped family Pyrgodesmidae in the continental USA, with the first record of *Poratia digitata* (Porat) from the Bahamas (Diplopoda: Polydesmida). – *Journal of Natural History* 38: 1159-1181.
- Silvestri, F. (1898) Diagnosticos de nuevos Diplopodos sudamericanos. – *Anales del Museo Nacional de Buenos Aires* 6: 53-79.
- Silvestri, F. (1908) Myriopoda from Porto Rico and Culebra. – *Bulletin of the American Museum of Natural History* 24: 563-578.
- Velez, M.J. (1967) New species of Diplopoda from Puerto Rico with notes on their geographical distribution and ecology. – *Caribbean Journal of Science* 7: 23-36.