Article

A millipede missing link: Dobrodesmidae, a remarkable new polydesmidan millipede family from Brazil with supernumerary rings (Diplopoda, Polydesmida), and the establishment of a new suborder Dobrodesmidea

WILLIAM A. SHEAR[1,4], RODRIGO LOPES FERREIRA[2],
LUIZ FELIPE MORETTI INIESTA[2] & PAUL MAREK[3]

[1]*1950 Price Drive, Farmville, VA 23901; Emeritus Professor, Department of Biology, Hampden-Sydney College*
[2]*Centro de Estudos em Biologia Subterrânea, Setor de Zoologia Geral, Departamento de Biologia, Universidade Federal de Lavras, Minas Gerais, BRAZIL*
[3]*Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA USA*
[4]*Corresponding author. E-mail: wshear@hsc.edu*

Abstract

Dobrodesmus mirabilis **n. gen.**, **n. sp.** is described from a limestone cave in the state of Bahia, Brazil. The new species is unique among millipedes of the order Polydesmida in having 39+t rings in adult males, two rather than four spinnerets, and in its highly plesiomorphic gonopods, which resemble those of basal members of the orders Callipodida and Stemmiulida. The presence of 39 rings is notable because members of the Polydesmida, the most species rich order of millipedes (>5000 spp.) normally stop development at 19+t rings. Because of these characters, *D. mirabilis* is the basis for the proposal of a new family (Dobrodesmidae) and a new suborder (Dobrodesmidea) of polydesmidans.

Key words: Neotropics, Brazil, limestone caves, conservation, anamorphosis, postembryonic development

Introduction

Polydesmida is the largest and most diverse ordinal taxon in the class Diplopoda (>5000 nominal species), and polydesmidan millipedes are frequently the most obvious and abundant millipedes in both tropical and temperate habitats. Among millipede orders, Polydesmida is perhaps also the most distinctive: Simonsen (1990) provided 13 autapomorphic characters, and Enghoff *et al.* (2015) provide an even longer list in the context of a complete diagnosis. The diplosegments consist of entirely fused rings[1] incorporating the tergites, pleura and sternites of two pedal segments (based on leg numbers); no remnant sutures can be detected between these diplosegmental elements. Additional evidence of the apomorphic nature of the taxon includes the absence of ocelli, trichobothria and Tömösváry organs, all of which are found in more basal millipede orders. Furthermore, polydesmidan development exhibits teloanamorphosis (Enghoff *et al.* 1993): the number of rings at adulthood is fixed for nearly all species at 19+t (19 rings including the legless collum and a subterminal legless ring, plus the telson; thus the total number of rings is often given in the taxonomic literature as 20), with many fewer having 18+t, and only a handful of species exhibiting 17+t, 20+t or 21+t rings. For a very small number of species, still higher numbers of rings (up to 28) have been recorded (Enghoff *et al.* 1993; David & Geoffroy 2011).

We report below on a new genus and species of polydesmidan millipede from a limestone cave in Bahia State, Brazil, which is evidently characterized by a record number of supernumerary rings—a total complement of 39+t (40) in the two adult males available. We argue that this increased ring number is characteristic of the species and not a property of anomalous individuals, since some of the juveniles collected at the same time already have more

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1. We use here the term "rings," following Enghoff, as opposed to "segments" since the trunk divisions are not true segments, and at least two of what have been traditionally called trunk "segments" are not diplosegments (collum and telson). In Polydesmida, the term "rings" is highly appropriate because of the fusion of segmental elements.

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than 23+t (24) rings, and ring numbers at adulthood are species-characteristic in polydesmidans. In addition to this startling observation, we have found that the gonopods of the male, of crucial importance in not only differentiating species but in assigning them to higher taxa, incorporate unique, plesiomorphic features never before observed in any other polydesmidan, and have a basic plan similar to the most basal members of the orders Callipodida and Stemmiulida. The internal phylogenetics and classification of the Polydesmida is largely unexamined and highly unstable (Golovatch 2013), but the extraordinary characters of our new species lead us to establish not only a new family but a new suborder to receive it.

Systematics

Order Polydesmida

Suborder Dobrodesmidea, Shear, Ferreira & Iniesta, new suborder

Diagnosis. As for the family Dobrodesmidae, see below. Differing from Leptodesmidea, Polydesmidea, Dalodesmidea and Strongylosomatidea in the reduced telopodites of the gonopods, lack of a coxal cannula and a seminal (or prostatic) groove, and in the presence of a long coxal flagellum (Figs 16, 18–20). All other polydesmidans surveyed so far have four epiproctal spinnerets, while the only known dobrodesmidean has two (Figs 11, 14). The pair of setae on each paraproct, characteristic of all other polydesmidans, is absent and instead the paraprocts bear small, scattered setae and are divided into two sclerites (Fig 11), while the paraprocts of other polydesmidans are entire. Includes only the family Dobrodesmidae, diagnosed below.

Family Dobrodesmidae Shear, Ferreira & Iniesta, new family

Type genus: *Dobrodesmus,* new genus, described below. Monobasic.

Diagnosis. Differs from all other families in the order Polydesmida in that the only known species has 39 + t trunk rings in adult males (Figs 1, 21). The gonopods of the males (Figs 16, 18–20) are fully articulated with a complete sternum and have no coxal cannula and no seminal (or prostatic) groove as found in almost all other members of the order; members of the family Rhachodesmidae lack a cannula but have an obvious prefemoral fossa and seminal groove. The gonopods are further characterized by a coxal flagellum sheathed in a more distal coxal process, bearing a strong resemblance to the gonopods of species of the basal callipodidan genus *Sinocallipus* Zhang (Fig 17)*,* and the basal stemmiulidan genus *Eostemmiulus* Mauriès, Golovatch & Geoffroy (Fig 22)*.*

***Dobrodesmus* Shear, Ferreira & Iniesta, n. gen.**

Type species: *Dobrodesmus mirabilis* Shear, Ferreira & Iniesta, n. sp., described below.

Etymology. The genus name comes from the Portuguese word for "double" with the combining stem "-*desmus*," meaning band, commonly used in generic names in this order of millipedes, and refers to the doubled number of trunk rings in the type species.
　　Diagnosis. As for the family, see above.
　　Description. Species with 39+t trunk rings in adult males.
　　Head, gnathochilarium and antennae typical of order. Antennae with accessory sensillae on antennomere six (Fig 3).
　　Collum (Fig 2) with short, roughly triangular paranota. Trunk rings with prominent paranota (Figs 4–7), nearly horizontal, angular; metazonites appearing broadly rectangular.
　　Epiproct not concealed by penultimate ring, with two spinnerets; epiproct process with deep indentation between spinnerets (Fig 11). Paraprocts obliquely divided into small dorsal and larger ventral sclerite, with many scattered setae.

Dorsal surfaces of trunk rings finely setose, with scattered longer setae.

Spiracles displaced anteriorly, greatly reduced.

Gonopods (Figs 16, 18–20) with complete sternum, coxae protruding from aperture, basally constricted by aperture; coxa with flagellum; flagellum distally with multiple hastate teeth; telopodite reduced, with few setae, distal acuminate process, not divided into prefemur and acropodite, not modified to sheath coxal flagellum.

Distribution. Mangabeira Cave in Ituaçu Municipality, Bahia State, Brazil.

Dobrodesmus mirabilis **Shear, Ferreira & Iniesta, n. sp.**
Figs 1–14, 16, 18–21

Types. Male holotype (ISLA 3637) male paratype, and numerous juvenile paratypes from Gruta de Mangabeira, Ituaçu Municipality, Bahia State, Brazil (Figs 23–28), collected by R. Ferreira, 30 December 2006, deposited in the Zoology Collection, Seção de Invertebrados Subterrâneos (ISLA) at the Universidade Federal de Lavras, Campus Universitário de Lavras, Minas Gerais, Brazil. The male paratype remains mounted on a scanning electron microscope stub.

Etymology. The species epithet "mirabilis" means amazing in Latin and refers to the characteristics observed in the species.

Diagnosis. As for the genus, see above.

Description. Male (Fig 1; now fragmentary) about 21–22 mm long, 1.0 mm wide.

Head subglobular, setose. Antennae 1.6–1.7 mm long, if extended posteriad, reaching to posterior margin of fifth ring. Penultimate antennal segment with cluster of club-shaped setae lining outer apex (Fig 3).

With troglobiotic character states; colorless, cuticle thin, poorly sclerotized, brittle, legs long and thin.

Collum (Fig 2) densely setose, subelliptical, anteriorly rounded, posterior margin nearly straight, posteriolateral corners rounded.

Typical ring (Figs 4, 5) with dense coat of fine, short setae, 12 longer, stouter setae with prominent apertures in two transverse rows on each metazonite. Midbody rings 1.0 mm wide across paranota, paranota level, projecting directly laterad, squarish, anteriolateral corners (Fig 6) strongly angular, with numerous stout triangular teeth, posteriorlateral corners (Fig 7) acutely produced, lateral edges finely and irregularly serrate in anterior half.

Metazonite cuticle with numerous intercalary microscutes, (Figs 9, 10) limbus unmodified, completely smooth. Prozonite sculpture regular rows of polygonal cells.

Ozopores (Fig 8) on rings 5, 7, 9, 10, 12, 13, 15–38, located on produced posteriolateral corner of paranotum.

Epiproct (Fig 11) twice as long as wide, densely setose, terminal process appears set off by groove, deeply divided into two subtriangular processes, each bearing spinneret for complement of two spinnerets. Paraprocts strongly margined, with oblique transverse sulcus dividing paraprocts into smaller dorsal and larger ventral portions (Fig 11). Paraprocts densely setose, without evident marginal or submarginal macrosetae, but with large, distinct depression or pore at distal angle. Hypoproct entire, semicircular.

Ventral surfaces of rings with transverse depression between insertions of legpairs (Fig 5).

Spiracles small (Fig 13), strongly reduced, advanced directly anterior of each leg coxa (Fig 12).

Legs long, thin; midbody legs about 1.2 mm long.

Sternum of second legpair not incorporated in second ring, freely articulating; second leg coxae quadrate, with opening of vas deferens mesal on each. No anterior legpairs incrassate.

Gonopods (Figs 16, 18, 19, 20) in tightly constricting oval aperture, coxae entirely exposed, constricted by margin of aperture. Sternum complete, articulated with, rather than partly or entirely fused to, coxae. Coxae large, egg-shaped, closely appressed, perhaps fused in midline, with clusters of 5–7 strong setae on lateral side, mesally with distinct angular flange; mesal coxal surface behind flange either fimbricate or with dense, fine setae. Coxae evidently immovable with respect to one another. Cannula not detected, but long, distally multihastate flagellum articulated with posterior apical coxal lobe sheathed in broad, distally acuminate coxal process. Telopodite single-articled, subglobular with thin, triangular process guiding coxal sheathing process; small, distal, acute process (possibly representing acropodite) subtended by two setae, one of which has many small setulae, mesal group of three stout setae. No seminal (prostatic) groove or channel detected. Telopodite not divided into prefemoral and acropodal regions.

Females not collected.
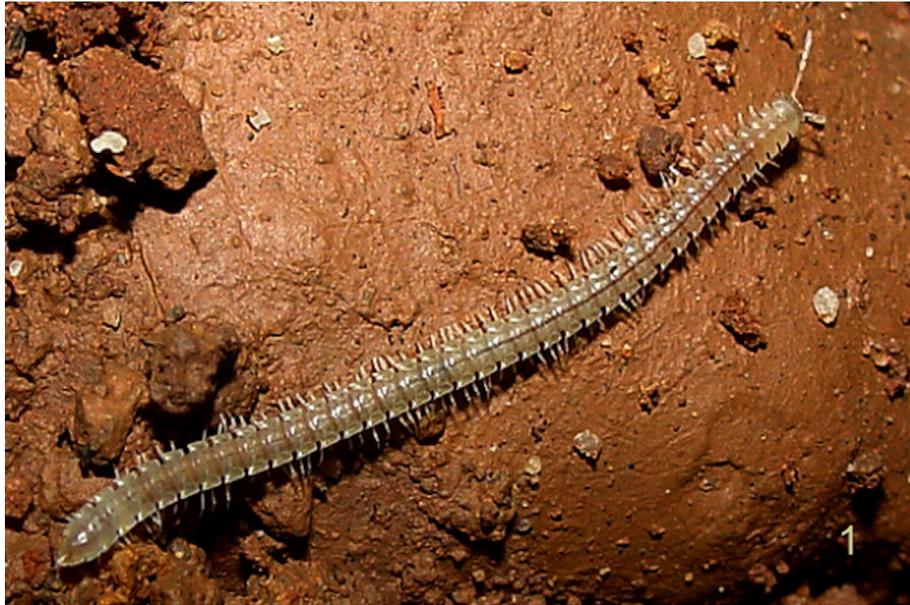
FIGURE 1. *Dobrodesmus mirabilis,* living male in habitat.
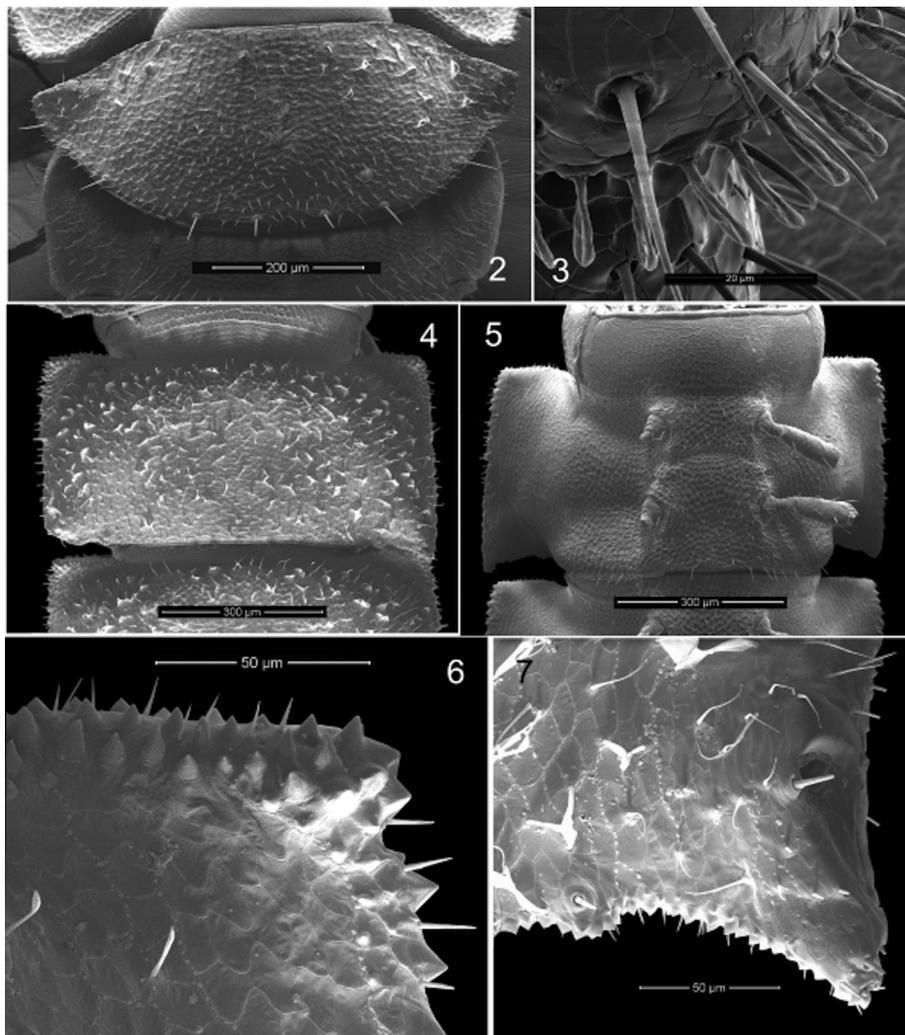
FIGURES 2–7. *Dobrodesmus mirabilis.* **Fig 2**, collum. **Fig 3**, sensilla from sixth antennal article. **Fig 4**, midbody segment, dorsal view. **Fig 5**, midbody segment, ventral view. **Fig 6,** anterior right corner of midbody segment, dorsal view. **Fig 7**, posterior right corner of nonporiferous midbody segment, dorsal view.
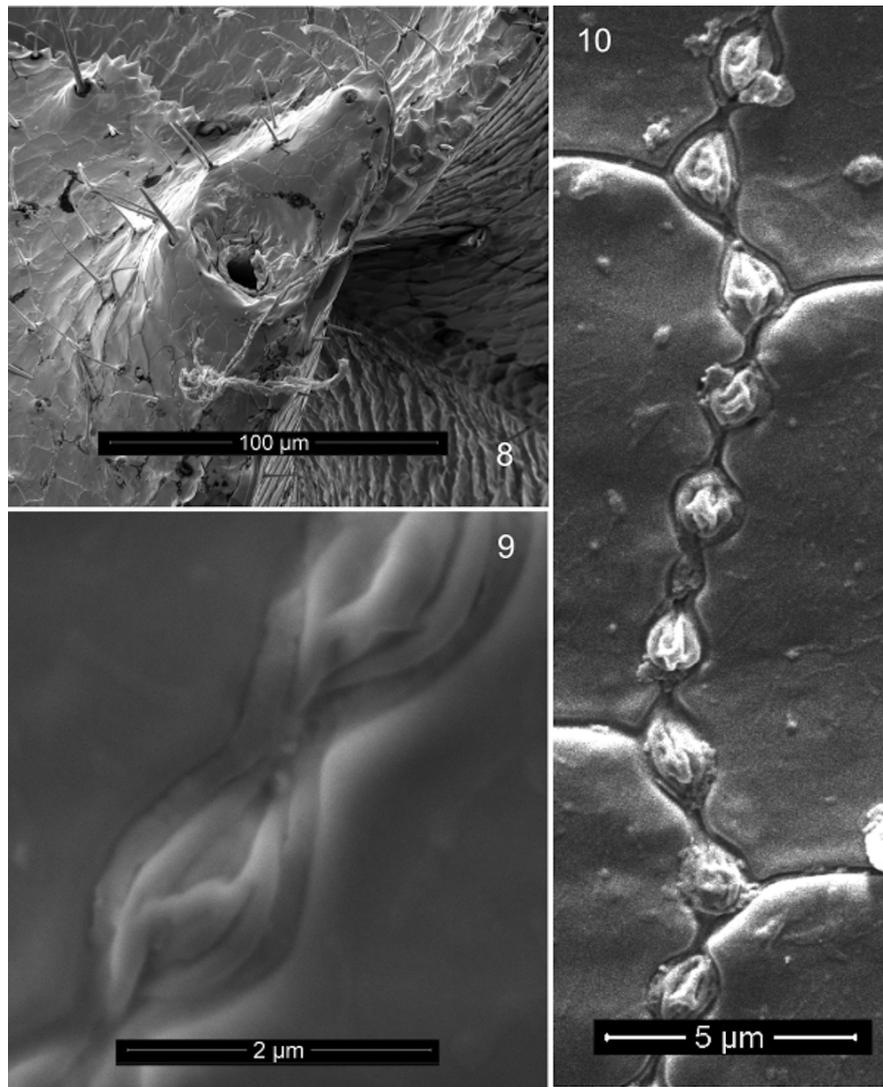
FIGURES 8–10. *Dobrodesmus mirabilis.* **Fig 8**, Ozopore, lateral view. **Fig 9**, intercalary microscutes of metazonital dorsum, dorsal view. **Fig 10**, same.

Notes. Observations using optical microscopy on the anatomy of the male holotype were made difficult by the transparency (intra- and inter-ring muscles and digestive tract are clearly visible) and brittleness of the cuticle, so subsequent observations may alter some details. Certain features were clarified using the paratype male for scanning electron microscopy. It was particularly difficult to detect the ozopores and while their distribution appeared to fit the "normal" polydesmidan pattern (except for their continuation beyond ring 19) we are not entirely sure of this; on one specimen of 24 rings, ozopores appeared not to begin until ring seven. It may be that the chemical defense system has been reduced due to relaxed predator pressure in the subterranean environment.

The spiracles are so small as to be undetectable with light microscopy (Fig 13); their position was only determined by careful searching using scanning electron microscopy. The positions of the spiracles on each ring are advanced anteriorly so that the posterior spiracles are between the legpairs of each side, and the anterior spiracles are near the posterior margin of the prozonite (Fig 12). Reduced or apparently absent spiracles occur elsewhere in the Polydesmida. Mesibov (2009) at first thought the Australian haplodesmid *Agathodesmus* Silvestri lacked spiracles, but later examination with scanning electron microscopy revealed them as very reduced (Mesibov 2013).

Spiracles could not be detected in species of the haplodesmid genus *Prosopodesmus* Silvestri (Mesibov 2012), and Golovatch & VandenSpiegel (2014, 2015) failed to find spiracles in *Koponenius* Golovatch & VandenSpiegel species, also haplodesmids. It seems doubtful that openings to the tracheal system could be entirely lacking in a millipede of any size, but their position may be anomalous or they may be so small and misshapen (as in the case of *D. mirabilis*) as to be overlooked even with scanning electron microscopy.
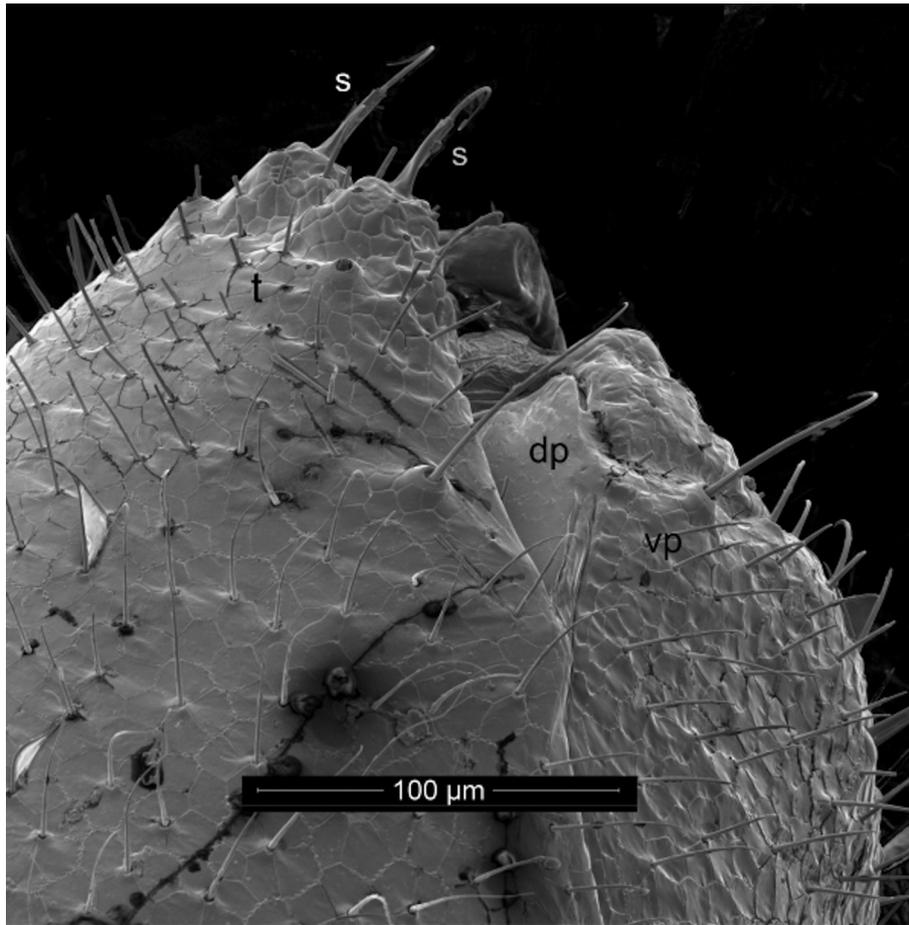
FIGURE 11. *Dobrodesmus mirabilis,* posterior end, dorsolateral view. Abbreviations: s, spinneret; **dp**, dorsal division of paraproct; **vp**, ventral division of paraproct.; **t**, epiproct.

Spinnerets in the Polydesmida are typically four in number, arranged in a quadrangle (Shear 2008). In contrast, two spinnerets are typical of the orders Callipodida and Chordeumatida, and at least one species in the order Stemmiulida (Shear 2008; Mauriès *et al.* 2010). The spinnerets of *D. mirabilis* do not resemble typical polydesmidan spinnerets (Fig 14), but their long basal sleeves and setal shafts are very similar to the spinnerets of callipodidans (Fig 15; further illustrations in Shear 2008). *Eostemmiulus caecus* Mauriès, Golovatch & Geoffroy, arguably the most basal member of the Stemmiulida, also has two spinnerets, in contrast to other members of its order in which the number ranges from four to eight, and those spinnerets resemble polydesmidan spinnerets in having a short, basal sleeve instead of arising from unsocketed mounds as is usual in Stemmiulida.

The dividing ridge on the paraprocts (Fig 11) seems to be unique in the Polydesmida and may represent either an existing division of the paraproct into two sclerites, or a recent fusion of an ancestral two sclerites. The dividing ridge can only be seen in specimens with distended anal regions; in other specimens the ridge is tightly appressed to the margin of the epiproct. In scanning electron micrographs, the ridge appears as a possible suture with flexible cuticle between the sclerites. Divided paraprocts are characteristic of at least some callipodidans. A pair of setae on each of the paraprocts appears to be part of the polydesmidan groundplan, but these setae are absent in *D. mirabilis,* and instead, as in nematophorans, the paraprocts bear numerous fine setae without any regular arrangement.

Akkari & Enghoff (2011) illustrated intercalary microscutes for a number of polydesmidans. The microscutes of *D. mirabilis* differ from those illustrated in their regularly wrinkled surface (Figs 9, 10) rather than being smooth and flat; the wrinkling suggests a thin cuticle or membranous surface. Akkari & Enghoff (2011) found the scutes in members of the families Polydesmidae, Macrosternodesmidae, Trichopolydesmidae, Fuhrmannodesmidae, Opisotretidae, Nearctodesmidae and Dalodesmidae, but not in species of Ammodesmidae, Cryptodesmidae, Cyrtodesmidae, Haplodesmidae, Oniscodesmidae and Pyrgodesmidae. Intercalary microscutes are of no known functional significance, though it is worth noting that many of the members of the families that lack them cover

themselves with debris and soil in life. Reboleira & Enghoff (2015) illustrate, but do not discuss, intercalary microscutes in the pleurotergal cuticle of the dorypetalid callipodidan *Lusitanipus alternans* (Verhoeff). Microscutes have also been detected in two spirostreptidan families (Enghoff 2014, 2016; Enghoff & Fredriksen 2015).
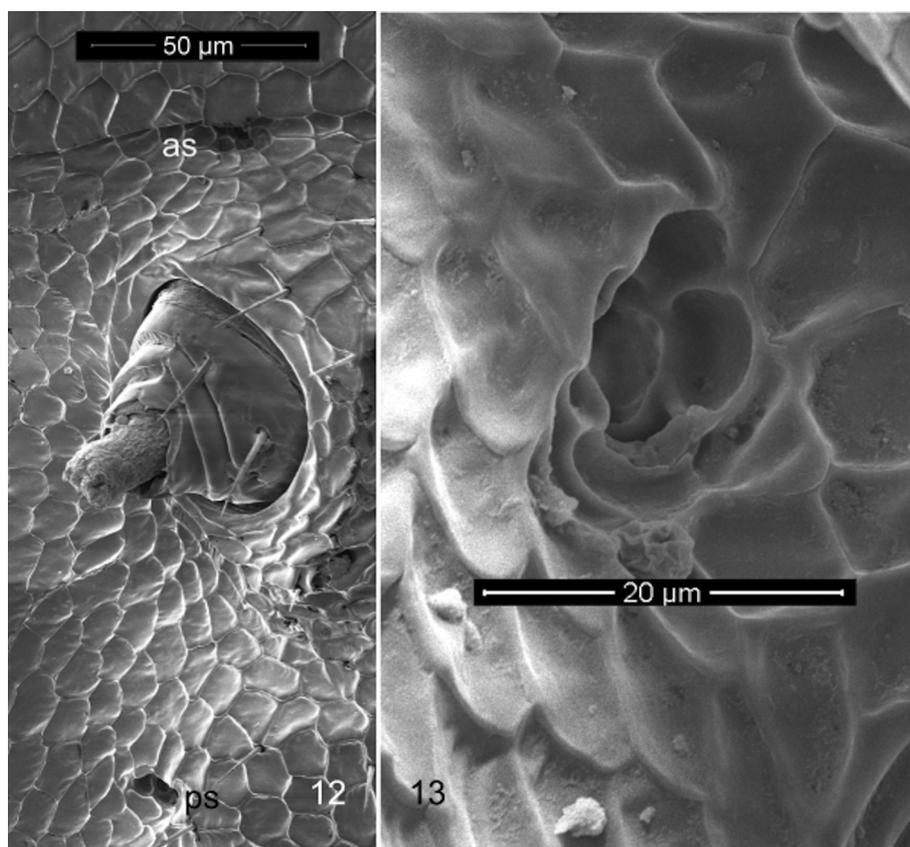
FIGURES 12, 13. *Dobrodesmus mirabilis.* **Fig 12**, ventral view of right lateral part of midbody segment, showing positions of spiracles. Abbreviations: **as**, anterior spiracle; **ps**, posterior spiracle. **Fig 13**. Posterior spiracle.

    Anamorphosis of *D. mirabilis*. Of the 24 specimens of *D. mirabilis* so far collected, only two, the holotype and paratype, are mature, and one other (ISLA 3638) was a juvenile male, with gonopod primordia on ring seven. The other juvenile specimens are either females or are at a stadium too early to show gonopod primordia.

    The weak sclerotization and transparency of the juvenile specimens made it difficult to count rings, and some of our data do not correlate with the anamorphosis tables for other Polydesmida. Nevertheless, since the anamorphosis of *D. mirabilis* is probably atypical in any case, we present our data in the table below as we obtained it. In this table, ring numbers do not include the telson.

    If the anamorphosis of this species proceeds as for *Euryurus leachii* (Gray) (Miley 1927), specimens with eight or nine rings represent stadium II. Specimens with 11 rings are likely to be in stadium III, those with 14–16 rings in either stadium IV or V, and those with 17 rings in stadium VI. Polydesmidans with 19+1 (20) rings mature in stadium VIII, but the presence of juveniles with 24–27 rings indicates that molting continues in *D. mirabilis.*

Discussion

Anamorphosis and ring number: The postembryonic development of millipedes is by means of *anamorphosis*, whereby each molt results in the addition of rings and legpairs. This contrasts with *epimorphosis* (as in insects and scolopendromorph and geophilomorph centipedes), in which the full number of segments is present at hatching, and no new segments are added with later molts. Anamorphosis in millipedes was exhaustively reviewed by Enghoff *et al.* (1993), and much of this discussion is derived from that study.
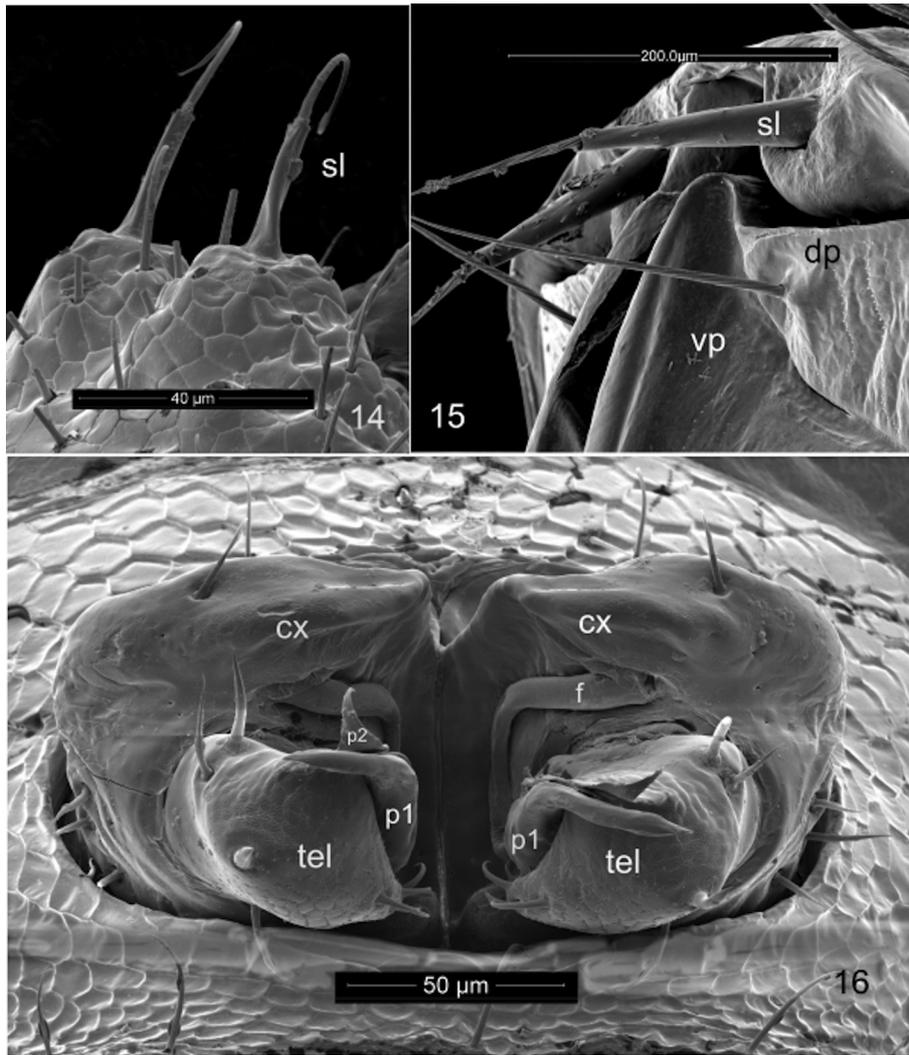
FIGURES 14–16. **Fig 14**, spinnerets of *Dobrodesmus mirabilis.* **Fig 15**, spinnerets of *Tetracion jonesi* Hoffman 1956 (Callipodida, Abacionidae). Abbreviations: **sl**, extended aperture of spinneret; **dp**, dorsal division of paraproct; **vp**, ventral division of paraproct. **Fig 16**, gonopods of *Dobrodesmus mirabilis,* ventral view. Abbreviations: **cx**, gonopod coxa; **f**, flagellum; **p1**, sheathing process of coxa; **p2**, triangular process of telopodite; **tel**, telopodite of gonopo; **a?**, possible acropodite .
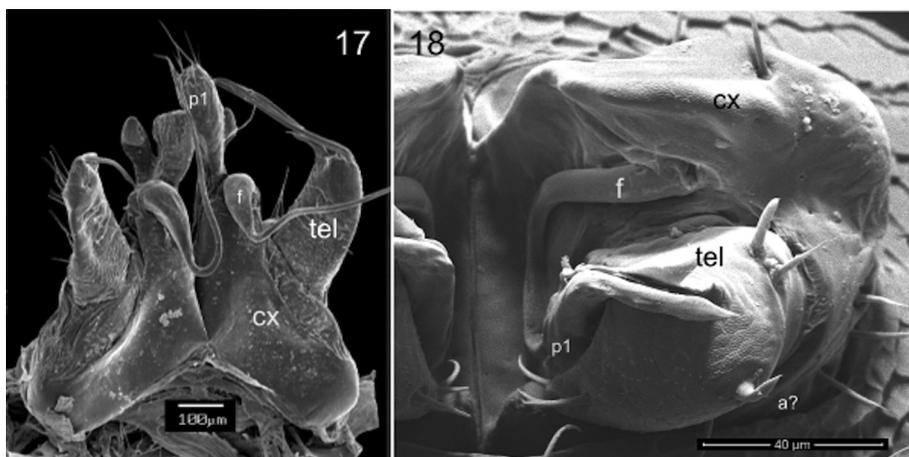
FIGURES 17, 18. **Fig 17**, gonopods of *Sinocallipus simplipodicus* (Callipodida, Sinocallipodidae). **Fig 18**, left gonopod of *Dobrodesmus mirabilis,* ventral view. Abbreviations as for Fig 16.
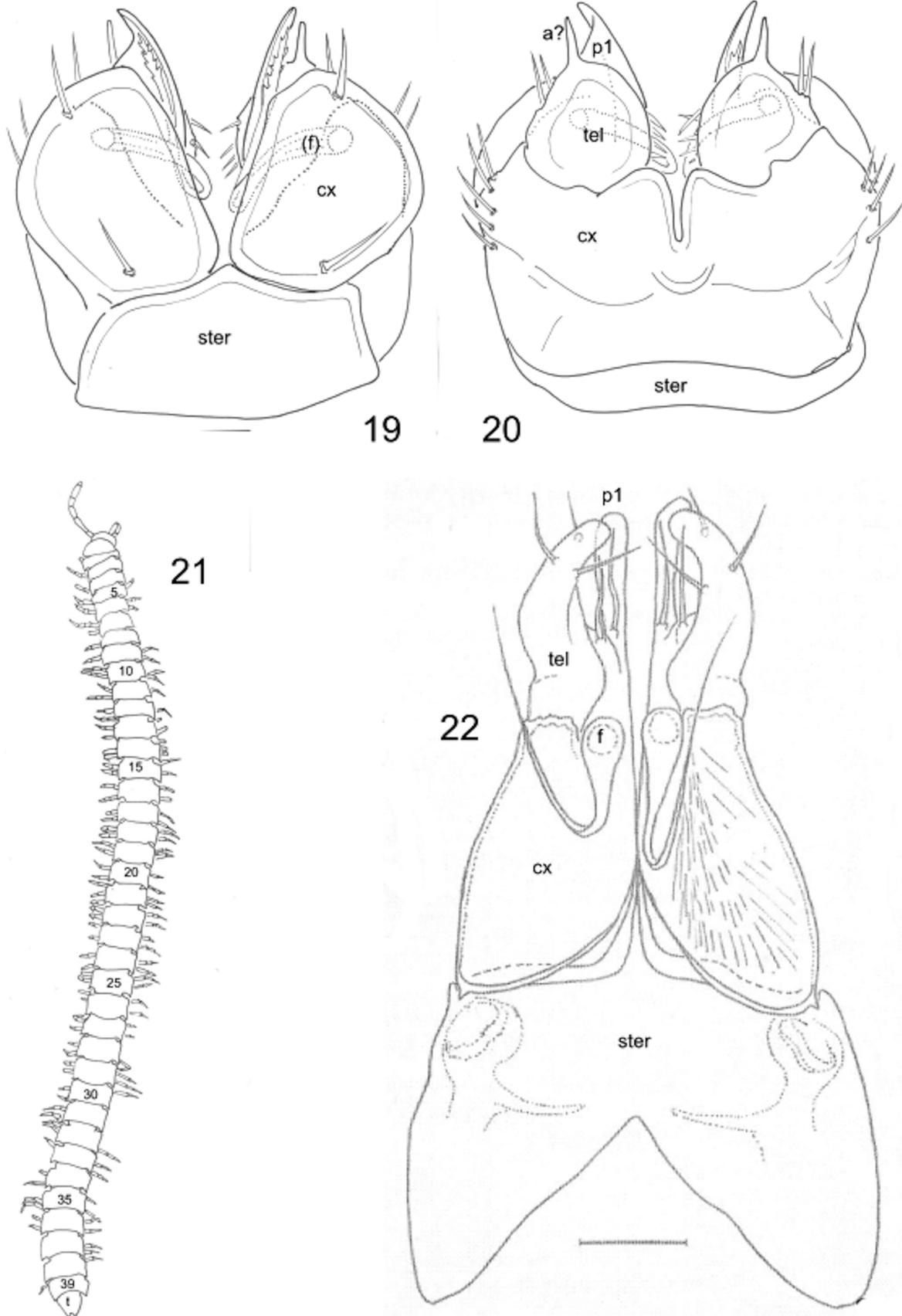
FIGURES 19–22. **Fig 19,** gonopods of *Dobrodesmus mirabilis*, posterior view. **Fig 20**, gonopods of *Dobrodesmus mirabilis*, anterior view. **Fig 21**, male, dorsal view, diplosegments numbered; **t**, telson. **Fig 22**, gonopods of *Eostemmiulus caecus,* (Stemmiulida, Stemmiulidae), posterior view. Abbreviations as for Fig 16; Fig 22 redrawn from Mauriès *et al.* (2010).
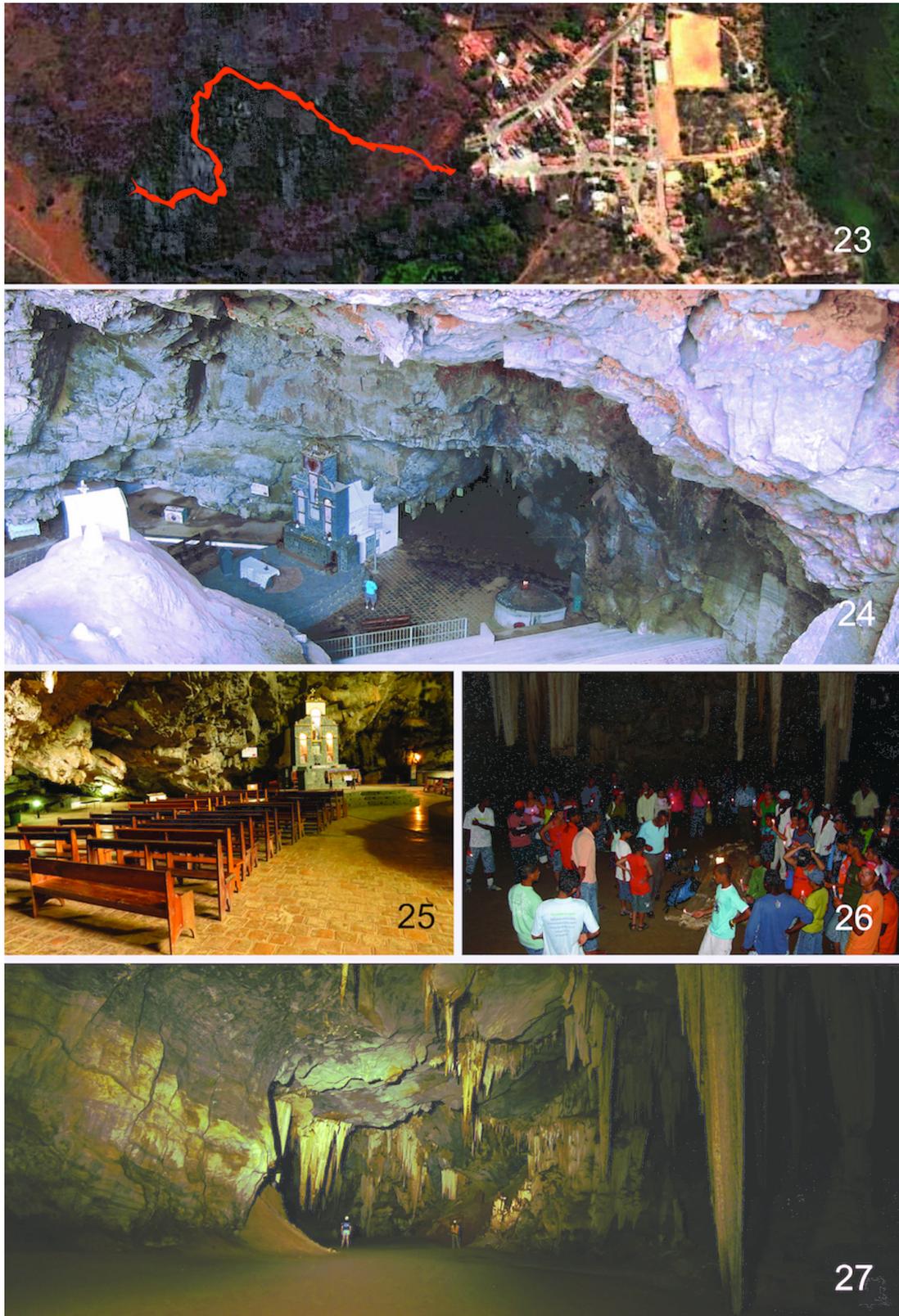
FIGURES 23–27. Habitat of *Dobrodesmus mirabilis* in Mangebeira Cave. **Fig 23**, course of Mangebeira Cave (red) superimposed on aerial view, with part of municipality of Ituaçu. **Fig 24**, sinkhole entrance to the cave showing modifications for religious purposes. **Fig 25**, chapel area inside cave. **Fig 26**, pilgrims visiting the cave. **Fig 27**, deeper interior of the cave, with speleothems, close to collection locality of *D. mirabilis* holotype.

TABLE 1.

Specimen #	Total rings	Podous rings	Apodous rings	Length
ISLA 4066Q	8	5	3	1.10 mm
ISLA 4066A	9	6	3	1.25 mm
ISLA 4066I	9	6	3	1.25 mm
ISLA 4066L	11	8	3	3.50 mm
ISLA 4066K	14	12	2	4.50 mm
ISLA 4066P	14	12	2	4.50 mm
ISLA 4066T	14	12	2	4.50 mm
ISLA 4066N	15	13	2	4.50 mm
ISLA 4066O	15	13	2	4.50 mm
ISLA 4066R	16	15	1	4.75 mm
ISLA 4066B	17	16	1	3.50 mm
ISLA 4066D	17	16	1	3.75 mm
ISLA 4066F	17	16	1	3.75 mm
ISLA 4066M	17	16	1	4.00 mm
ISLA 4066S	17	16	1	3.75 mm
ISLA 4066 H	23	22	1	13.50 mm
ISLA 4066J	23	22	1	13.25 mm
ISLA 3640	23	22	1	12.00 mm
ISLA 4066E	23	22	1	13.00 mm
ISLA 3638	25	24	1	14.25 mm
ISLA 4066C	25	24	1	13.50 mm
ISLA 3639	26	25	1	14.00 mm
ISLA 4066G	26	25	1	13.00 mm
ISLA 3637	38	37	1	19.5 mm

Anamorphosis may be subdivided into three types with regard to millipede development. *Euanamorphosis* is found in some Julida, Cambalidea (Epinannolenidea) and Colobognatha; new segments are added with each molt for as long as the animal lives, even after sexual maturity. In *hemianamorphosis*, the addition of new segments stops at a certain point, though subsequent molts may follow without new segments appearing (epimorphic molts). This type occurs in Polyxenida, Pentazonia, Spirobolida, some Spirostreptida, and possibly other groups that have not been thoroughly studied (Enghoff *et al.* 1993; Miyazawa *et al.* 2014; Minelli 2015). Polydesmida and Chordeumatida are characterized by *teloanamorphosis,* in which the addition of segments stops with the molt to sexual maturity, and this molt is the final one. The number of adult segments in these orders is therefore species-characteristic (Enghoff *et al.* 1993).

The typical number of rings in polydesmidans is 19, which with the addition of the telson gives the characteristic 20 "segments" usually referred to in the systematic literature (19+t). Scattered throughout the order, and evidently arising in parallel, are species with 18+t rings, and in some species males have 18+t rings while females have 19+t. A much smaller number of species, usually quite minute ones, have 17+t rings, but the numbers remain species-characteristic. This reduction in ring number is accomplished by achieving sexual maturity one or two stadia earlier than in the species with 19+t rings (Enghoff *et al.* 1993).

Very rarely, one-ring deviations upwards from these species-characteristic numbers can occur. The best known case is that of the "elongatus" form of *Polydesmus angustus* (Latzel)*,* in which an additional post-adult molt results in one more ring (David & Geoffroy 2011), but this has been observed only twice under laboratory conditions and has never been found in nature. Shelley (2000) reported that mature males with either 19+t or 18+t rings occur sporadically in the sphaeriodesmid species *Desmonus pudicus* (Bollman) and *Hybocestus octonodus* Hoffman*.* Similar phenomena have been recorded for two pyrgodesmids, *Psochodesmus crescentis* Cook (Loomis 1934) and

Poratia obliterata (Kraus) (Adis *et al.* 2000; Adis *et al.* may have been misled by mixed populations of *P. obliterata* and *P. digitata* (Porat) [Henrik Enghoff, pers. comm. to WAS, 2015]).

Additions of more than one ring are even rarer. This condition has up to now been reported only for the Mediterranean polydesmidan genus *Devillea* Brölemann (Xystodesmidae). The anamorphosis of species in this genus has not been studied since they are rare and limited to caves, but it is known that ring numbers are variable within nominal species, and a maximum number of 27+t has been recorded for *Devillea doderoi* Silvestri, 1903 (Silvestri 1903; Enghoff *et al.* 1993). The occurrence of *Devillea* in caves and possession of supernumerary segments, as in *Dobrodesmus*, is notable. However, most cave-dwelling polydesmidans do not possess supernumeration of segments, and an association of the trait with troglomorphism is uncertain.

In *Dobrodesmus mirabilis,* the previous record for the number of rings in a polydesmidan millipede is exceeded: this species has 39+t rings in the male holotype.
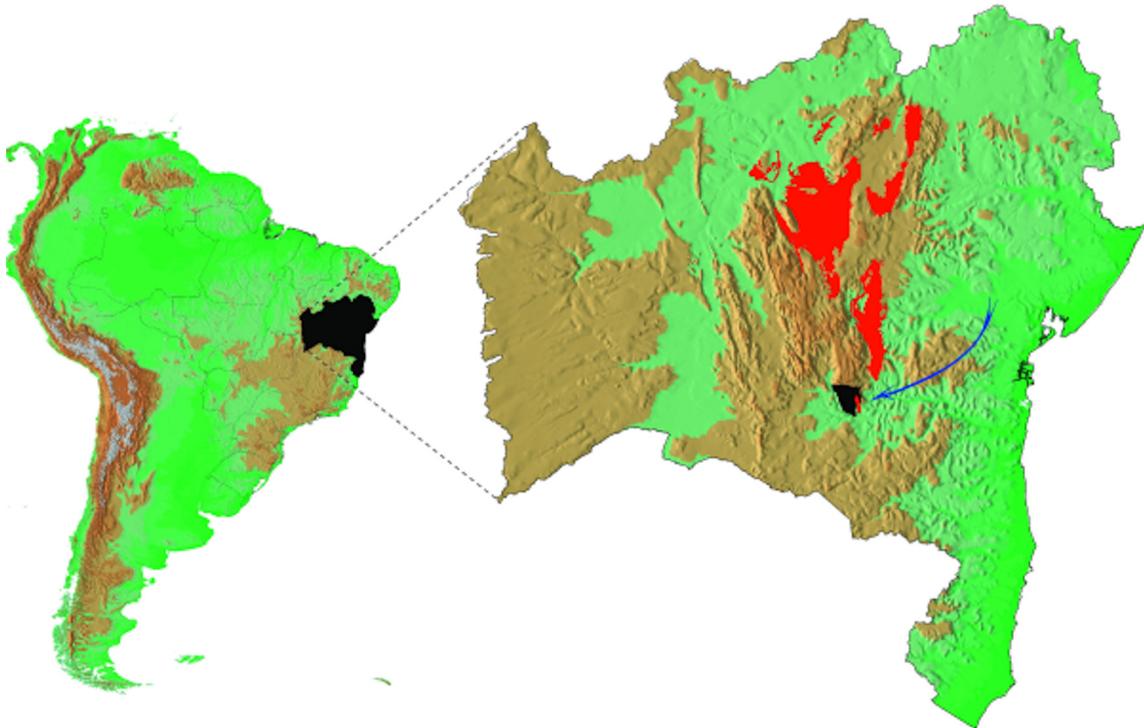
FIGURE 28. Map showing location of type locality of *Dobrodesmus mirabilis.* Expansion is of Bahia State; red is known extent of formations of the Una Group, black is Ituaçu Municipality. Arrow indicates location of Mangebeira Cave.

Recently, reports have been published of segment-number anomalies in the Brazilian centipede genus *Scolopendropsis* Brandt. Schileyko (2006) found that populations of *Scolopendropsis bahiensis* (Brandt) with either 21 or 23 pairs of legs existed in different parts of the species' range in Brazil. Shortly thereafter, Chagas-Junior *et al.* (2008) described a new species, *S. duplicata* Chagas-Junior, Edgecombe & Minelli, with either 39 or 43 pairs of legs, also from Brazil (Tocantins State), and at the margins of the range of *S. bahiensis*. These discoveries overturned the previous conclusion that epimorphic scolopendromorph centipedes had either 21 or 23 pairs of legs, and that the number was constant within species. Minelli *et al.* (2009) described this latter case as "saltational evolution" in segment number and proposed hypothetical patterning mechanisms that might explain it.

The mechanisms of segment development in millipedes have hardly been studied (but see Akkari *et al.* 2014), in contrast to the epimorphic orders of centipedes, in which a good deal of attention has been devoted to the embryological patterning of segmentation (Minelli and Bortoletto 1988; Kettle *et al.* 2003; Chipman *et al.* 2004; Chipman & Akam 2008). The developmental and genetic pathways that control anamorphosis in millipedes therefore remain largely unknown, although certain "rules" have emerged from perceived regularities in the addition of rings with each molt (Enghoff *et al.* 1993). Therefore, although we see in *D. mirabilis* a comparable doubling of the ring number, the mechanism cannot be the same as in *S. duplicata* because in that chilopod order and family, development is epimorphic, and in *D. mirabilis* development is anamorphic.

In anamorphic development, the new rings are added from a proliferation zone just anterior to the telson. In most millipedes, the new rings actually appear in relatively undifferentiated form (they are legless) in the preceding molt. Teloanamorphosis, in which the addition of rings stops at a species-characteristic terminal molt, may reflect the "exhaustion" of the proliferation zone. However, the case of the 'elongatus' form of *P. complanatus,* in which a single added ring rarely appears in a postmaturity molt, may suggest that this is not so. Similarly, the added multiple rings in *Devillea* and *Dobrodesmus* species reinforce the idea that the proliferation zone retains the potential to produce more rings. Undoubtedly this is under genetic control, and the cessation of segment production could conceivably be due to a single gene. If that gene were disabled by mutation or some other factor, the proliferation zone could hypothetically continue to produce new rings. In the case of *Devillea*, since all the species in the genus produce supernumerary rings, the mutation (if that is the explanation) must have occurred in the common ancestor of the genus since no other Xystodesmidae possess the trait. There is no indication from morphological characters that *Dobrodesmus* and *Devillea,* the latter belonging to the apomorphic family Xystodesmidae, are in any way related, and indeed both biogeography and gonopod characters argue strongly against it.

In Polydesmida, the terminal stadium in males is marked by the sudden appearance, from primordia (undifferentiated leg stubs), of functional gonopods. The eighth legpair regresses to primordia in an earlier stadium (usually IV). The gonopods are often highly complex structures that have lost all resemblance to legs. David and Geoffroy (2011) found that one of the 'elongatus' males of *P. complanatus* they produced in the laboratory had normally functional gonopods (at least judging by their anatomy), while another regressed to nonfunctional ones. Aside from this anomalous laboratory situation, the appearance of functional gonopods seems to mark the end of anamorphosis for male polydesmidans. Therefore it would seem that at least for *Dobrodesmus mirabilis*, the delayed inactivation of the proliferation zone is not indefinite, but that a new limit has been set for teloanamorphosis. That would imply a more complex mechanism than the simple deactivation of a single gene that set the original limit. Because we have so far seen only two complete males, we do not know if the number of rings is species-characteristic in *D. mirabilis,* but we assume that this is so. *Devillea* species*,* on the other hand, reportedly have variable adult ring numbers within species (this claim requires examination, particularly as to the species identities), so for those species the proliferation zone may retain an ability to produce new rings without a specific limit as is the case in the euanamorphic Colobognatha. Of course this discussion assumes the possession of supernumerary rings to be an apomorphy, but since teloanamorphosis itself is apomorphic, it is also possible (see below) that "extra" rings in *Dobrodesmus* are a plesiomorphic character.

Another unanswered question regards the number of molts (or stadia, to use the terminology of Enghoff *et al.* [1993]) undergone by *D. mirabilis.* In the case of *Euryurus leachii,* studied by Miley (1927) and used as a standard example for 19-ring species by Enghoff *et al.* (1993), males and females pass through eight stadia. Beginning with the transition from stadium I (with six rings) to stadium II, animals add two, two, three, three, two, one and one ring. Stadium I, II and V individuals have two apodous rings, stadia III and IV have three, and stadia VI–VIII have one. Thus the number of 19 rings is achieved in seven postembryonic molts after stadium I, and more than one ring may be added at each molt. Does *Dobrodesmus mirabilis* achieve its elevated number of rings by undergoing additional molts, or by adding more rings at each of the standard number of molts? In the case of *P. complanatus* 'elongatus,' the additional ring is the result of one additional molt, but this observation on a small number of laboratory-raised animals hardly answers the question. According to Enghoff *et al.* (1993), the addition of rings in *Devillea* species is achieved by additional molts, up to nine in *D. doderoi.* In each of these stadia, only a single apodous ring is present and only one ring is added with each molt. If we apply the same reasoning to *Dobrodesmus mirabilis,* there are 19 additional stadia, with maturity occurring in stadium XXVII. We do not see any indication in the scanty data we have on anamorphosis in this species (Table 1) for the addition of any more than one ring per molt past stadium V, as is usual in polydesmidans (Enghoff *et al.* 1993). This is supported by the fact that we know of at least three concurrent stadia in which only a single ring is added (Table 1). However, in the series collected from Mangabeira Cave, there are three distinct size classes demarcated by a gap in segment number: (1) individuals with 8–17 segments, (2) 23–26 segments, and (3) 38 segments.

Both of the genera of Polydesmida with large numbers of supernumerary rings are cave-dwellers, with well-developed troglobiotic adaptations, but no other examples of supernumerary rings are known from among many species of polydesmidans limited to caves. It is possible that some of the conditions in caves, such as food limitation, constant environmental conditions and relaxed predator pressure, have influenced changes in

anamorphosis in these animals. Studies of the life histories of troglobionts have shown that many have extended lifespans (Culver & Pipan 2009, p. 116), and one way of achieving this in a polydesmidan millipede would be relaxed control over teloanamorphosis.

It is well known that many cave-adapted animals have delayed reproduction, usually associated with longevity (Culver & Pipan 2009; Huppop 2012). This probably evolves as a response to food scarcity, which is a prevalent condition in caves. Accordingly, the longevity would be a result of a low metabolic rate, and the delayed reproduction could be adaptive, since the animals would have more time to gather resources to invest in reproduction. Considering that *Dobrodesmus* is teloanamorphic, one would expect that, during a long life cycle (including delayed reproduction), it would undergo many molts, continuously adding rings, until achieving sexual maturity. Since the Mangabeira Cave is a highly oligotrophic system, this hypothesis is quite plausible. The only other genus with many supernumerary rings within Polydesmida (*Devillea*) also comprises troglobiotic species, for which the same selective forces could have acted. Furthermore, this situation is exactly the opposite from the species with 17+t rings, in which the number of rings is determined by achieving sexual maturity one or two stadia earlier than in the species with 19+t rings, as previously mentioned.

An alternative hypothesis, that *D. mirabilis* is a plesiomorphic polydesmidan retaining the plesiomorphic condition of >20 rings, is discussed below.

Gonopods: Millipede gonopods are modified legs, but the modifications in an advanced group such as the Polydesmida are so great that similarities to legs are hard to see, and the homology to walking legs is based on position. In all but a few polydesmidans, at least the lateral parts of the gonopod sternum have disappeared or have fused into the basal part of the coxa; in a few scattered families or genera, a relatively small, sclerotized median remnant of the sternum may connect the gonopod coxae. Thus the sternal apodemes appear to arise from the coxae themselves. Early workers named divisions of the telopodite for the podomeres (femorite, tibia, tarsus) from which they were supposedly derived, but developmental studies refute this idea.

Typically the gonopods of polydesmidans consist of two divisions, the coxae and the telopodites. The telopodites are often thought of as consisting of all the postcoxal elements of the leg, fused and modified. The names historically given to the divisions of the telopodite imply derivation from the corresponding leg segments. However, developmental studies by Petit (1976) show that this is probably not the case, with the gonopod developing from the coxae and prefemora alone. Nevertheless, because these anatomical terms are still being widely used in the literature, we apply them, for clarity, in our discussion. The basal, usually very setose portion of the telopodite is considered the prefemur. The more distal portion, which may have a few scattered setae, is called the acropodite, and sometimes this is divided into the femorite and tibiotarsus, but generally such a division cannot be clearly made leaving us with three usually discernible elements: coxa, prefemur and acropodite. Often arising from the prefemur or near the base of the acropodite is a branch called the solenomere, which carries a pore. The pore is the outlet of the seminal (or prostatic) groove (or channel), which runs up the gonopod from the base of the prefemur. The groove originates in a fossa, into which a movable apophysis of the coxa fits, like the needle in a needle valve. This apophysis is the cannula. Below, in boldface, we have highlighted the ways in which the gonopod of *Dobrodesmus* deviates from this basic model.

The gonopods of *Dobrodesmus* are very small (total gonopod complex is about 0.25 x 0.4 mm). The gonopods are tightly set in a small aperture which constricts the coxae basally. **The coxae are almost entirely exposed outside the aperture and independently movable.**

There is a broad, well-sclerotized sternum to which the coxae either articulate or with which they may be at least partially fused. The sternum is obvious in both posterior and anterior views.

A single seta arises near the base of each coxa, and a second single seta is seen apicolaterally. The coxae appear to be heavily sclerotized. **From a posterior lobe of the coxa arises a long, articulated flagellum**; within the coxa the muscles that operate this flagellum can be seen in transmitted light. **No cannula could be detected.**

The small unit articulated with the coxa represents the entire telopodite, and **no separate prefemoral region** can be discerned. Arising from the anterior side of the coxa is a long, triangular process which sheaths the distally multihastate tip of the coxal flagellum. There is **no seminal groove and no solenomere**.

The supposed telopodite in this interpretation is a relatively small globular structure that is separate from and articulated with the coxa. It bears 3 setae mesally and a distal acuminate process, which could be construed as representing the acropodite, and is subtended by two setae similar in size to the process itself. The anteriormost of these setae differs in having fine projections throughout its length.

At this point it is not possible to connect these unique gonopods to those of any other known polydesmidan taxon. In particular, the articulated, muscularized coxal flagellum sliding in a groove on a more distal coxal process is unique. Even at high magnification (400X) in transmitted light, with Nomarski contrast optics, it was not possible to see a prostatic groove.

The gonopod as a whole, if seen in isolation, would be thought by most diplopodologists to be an unusual callipodidan or stemmiulidan gonopod. Both of these orders are possible sister-groups of the polydesmidans and most do not have fixed ring numbers (some callipodidans may have teloanamorphosis [Enghoff *et al.* 1993]); adults generally have many more than 20 rings. Nevertheless *Dobrodesmus mirabilis* has all the usual synapomorphies of the Polydesmida. For comparative purposes, we present illustrations of the gonopods of two species thought to be basal to the orders Callipodida and Stemmiulida. *Sinocallipus simplipodicus* Zhang is one of six species of this genus, the gonopods of which differ strongly from those of other members of the order (Fig 17). *Eostemmiulus caecus* (Stemmiulida) has gonopods which also are much less modified and simpler than those of all other members of the order, and which conform to the *Sinocallipus-Dobrodesmus* plan (Fig 22).

The mode of action of millipede gonopods has not been much studied. However, a feature which recurs in several eugnathan orders (Julida, Callipodida, Chordeumatida) is a long, thin, apparently movable process, called a flagellum, which lies in an open or closed channel; both the flagellum and the sheathing channel are coxal derivatives, at least in the Chordeumatida. Hypothetically, such an arrangement could work by having the flagellum slide in the channel and push a spermatophore or seminal fluid into the seminal receptacles of the female, but this has never been directly observed. This action may also occur in the Colobognatha in which the posterior flagelliform gonopods may slide through the spade-shaped anterior gonopods. In the typical polydesmidan gonopod, the coxal cannula inserts in an open vesicle on the prefemur, from which a groove or closed channel (evidently both occur) runs up the telopodite to open at some point; often the opening is at the tip of a process called a solenomere, although in some species the opening is simply a pore, flat on the surface of the acropodite, frequently subtended by dense cuticular fimbriae. This arrangement suggests that polydesmidans transfer seminal fluid, rather than a spermatophore (spermatophores have been directly observed in millipedes only in the orders Chordeumatida [*e.g.*, Shear 2010] and Julida [Mathews & Bultman 1993]). The hypothesis has been repeatedly raised that the polydesmidan cannula is homologous to the flagellum of other orders. While both are movable outgrowths of the coxae, the cannula inserts into the prefemur, while the flagellum is usually sheathed by a coxal extension.

In *D. mirabilis* we see a morphology that differs strongly from the usual in Polydesmida. A long flagellum arising from the coxa is sheathed in a coxal process and an obvious cannula is absent. There is no indication of separate prefemur, nor of a spermatic groove or channel leading out along the telopodite.

The gonopod with the most striking similarity to that of *D. mirabilis* is found not among the polydesmidans, but in the basal callipodidan genus *Sinocallipus* (Shear *et al.* 2003). In this gonopod, we see a large coxa firmly articulated with a complete sternum; the coxa apically carries a movable, long flagellum. The flagellum does not appear to be sheathed in a coxal process, but the small, articulated, single-articled telopodites bear complex spinose processes apically. The coxal flagellum of *S. simplipodicus* even has a series of teeth distally that resemble the multihastate tip of the *D. mirabilis* flagellum (Fig 17; see also illustrations in Shear *et al.* 2003; Stoev & Enghoff 2011). The same general plan is seen in the gonopod of *Eostemmiulus caecus* (Fig 22). Again, a complete sternum is present, with clearly defined coxae and single-articled telopodites; a long, movable flagellum arises apically from the coxa (see illustrations in Mauriès *et al.* 2010). The genus *Eostemmiulus* is considered basal in the Stemmiulida and has other characters interestingly suggestive of both *Dobrodesmus* and *Sinocallipus,* including a single pair of spinnerets that do not resemble those usually associated with stemmiulidans, but the spinnerets of Chordeumatida, Callipodida and Polydesmida, a chordeumatidan-like gnathochilarium, and dual vas deferens openings rather than the single "penis" found in all other known stemmiulidan species (Mauriès *et al.* 2010).

Other characters: The presence of only two spinnerets is discordant with the situation in all polydesmidans that have been examined, where there are four spinnerets in a rectangular array (Shear 2008), often recessed at the tip of the epiproct. Two spinnerets are characteristic of the orders Callipodida and Chordeumatida, but the presence of complete rings excludes *Dobrodesmus* from these orders, which have free sternites and a middorsal sulcus separating the right and left pleurotergites. However, if dobrodesmids are plesiomorphic polydesmidans it is possible that the presence of four spinnerets is apomorphic for all other members of the order. The spinnerets of *D. mirabilis* themselves are unusual in appearance, with a very long, sleeve-like extension of the aperture not seen in

other polydesmidans, but present in callipodidans (compare Figs 14 and 15; other illustrations in Shear 2008). With regard to *Eostemmiulus,* while only a single pair of spinnerets is present (opposed to variable numbers ranging from four to eight in other stemmiulidan genera), the illustrations by Mauriès *et al.* (2010) suggest, but do not confirm, that the spinnerets have a basal sleeve. In other stemmiulidan genera, the spinnerets have a swollen base, but not a sleeve (illustration in Shear 2008).

The dividing ridge of the paraprocts is suggestive of an affiliation with the Callipodida. Many species of Callipodida have transversely divided paraprocts, so that the paraproct consists of dorsal and ventral sclerites. It is not known if these sclerites are movable with respect to one another, but the suture between them occurs in a position very similar to what we have called the dividing ridge or sulcus in *D. mirabilis* paraprocts. This sulcus may be homologous to the suture in the paraprocts of callipodidans. Callipodidans, chordeumatidans and stemmiulidans have randomly distributed fine setae on the paraprocts, as in *D. mirabilis,* but all other polydesmidans have a single pair of large setae on each paraproct. The large pore or depression in the paraproct immediately distal to the dividing ridge has not been reported before in millipedes.

Phylogenetic implications: The most significant unresolved phylogenetic problem in Diplopoda at this time is the position of the Polydesmida. The various hypotheses are most recently reviewed, and alternatives argued, by Blanke & Wesener (2014) and Brewer & Bond (2014). The maximum parsimony phylogeny of Blanke & Wesener (2014) is based on 64 morphological characters of 15 of the 16 orders of millipedes. Strict consensus of the five equally parsimonious trees found that Polydesmida was adelphotaxon to the superorder Nematophora (orders Callipodida, Chordeumatida and Stemmiulida); however, support was relatively low (bootstrap = 59, Bremer = 1, jackknife = 41). This placement of Polydesmida accords with some "classical" views. Brewer & Bond (2014), on the other hand, resolved Polydesmida as adelphotaxon to the orders Stemmiulida and Spirostreptida in a tree arrived at by Bayesian inference. Their data came from RNA transcriptome sequences of single exemplar taxa from 9 of the 16 orders. The position of Polydesmida had lower support than other nodes in the tree; posterior probabilities/maximum likelihood bootstrap values were 0.99/60. No previous phylogenetic studies have arrived at this conclusion; it should be noted that the Brewer and Bond analysis did not include representatives of the important orders Julida and Spirobolida, which in all previous phylogenies have grouped with Spirostreptida. Denser taxon sampling may well alter their result. At this time we favor the tree of Blanke & Wesener (2014) as it minimizes morphological homoplasy. Important characters we see as uniting Polydesmida with Nematophora are: gonopods derived from legpair 8 only, presence of spinnerets on the epiproct, defensive secretions phenolic in composition (in Polydesmida the plesiomorphic phenolic secretion has been supplemented or replaced in most species by cyanogenesis [Shear 2015]). *Dobrodesmus mirabilis* also has some surprising characters shared with Callipodida: two spinnerets with long basal sleeves instead of the usual four with short sleeves, divided paraprocts without paired macrosetae, and a coxal flagellum in the gonopods.

Among the nematophoran orders, Chordeumatida shares development by teloanamorphosis with Polydesmida. In Callipodida, some species exhibit teloanamorphosis and others hemianamorphosis, while stemmiulidans probably develop by hemianamorphosis (Enghoff *et al.* 1993).

One can make a good argument that the gonopod anatomy of *D. mirabilis* is primitive (or plesiomorphic) in that it more closely resembles the anatomy found in basal Callipodida and Stemmiulida (see above and Shear *et al.* 2003; Mauriès *et al.* 2010; Stoev & Enghoff 2011). Since many callipodidans and stemmiulidans do not have fixed numbers of rings at maturity but always have substantially more than 20, the "extra" rings in *D. mirabilis* might represent a plesiomorphic character suggesting that the lower number of rings in all other polydesmidans is evolved and that the number of rings in *D. mirabilis* is not due to some anomaly in the genetic control of ring formation, hypothetically as an adaptation to the cave environment, as discussed above. However, the other case of significant numbers of additional rings, the species of *Devillea,* occurs in a genus of the Xystodesmidae, a cladistically apical family of the order, and is therefore unlikely to be plesiomorphic. The same may be true for *Dobrodesmus* species, and the two spinnerets and the gonopod anatomy may represent symplesiomorphic (shared ancestral) traits that have been modified in newer lineages and not indicative of monophyly. This is a question that could be answered by molecular genetic data, not available at this time. The establishment of a well-supported comprehensive phylogeny of the orders based on genetic data is a prime *desideratum* in millipede studies, no less similar work on Polydesmida itself. Once such a phylogeny has been established, morphological characters can be mapped on the tree and homoplasy unequivocally assessed.

Justification for a new suborder of Polydesmida: At the present time, families of Polydesmida are grouped

into four suborders: Leptodesmidea (sometimes called Chelodesmidea), Dalodesmidea, Strongylosomatidea and Polydesmidea (Shear 2011). These suborders defy simple diagnosis; the most successful attempts are probably those of Hoffman (1980) and Enghoff *et al.* (2015) which are based partly on characters of the gonopod aperture, the form of the gonopod coxae and their means of attachment to the margins of aperture, as well as the manner of articulation of the free sternum of the second pair of legs. For example, leptodesmideans typically have broadly oval gonopod apertures and large, freely movable gonocoxae. In Dalodesmidea the aperture is similarly broad but in many genera the gonocoxae are reduced and bilaterally fused without an obvious suture, and the fusion may even extend to the basal parts of the telopodites. Polydesmideans have smaller, tight gonopod apertures with the gonocoxae attached to the rim; the closely appressed gonocoxae are likely not independently movable (but not fused) and often have an anterior groove or cavity into which the hinged telopodites may be withdrawn. Strongylosomatideans are unique in having a medially constricted gonopod aperture; the gonocoxae are almost entirely outside the aperture. For the most part, however, the formation of the suborders depends on the superfamilies and families that are included and is more the result of a consensus of authorities than anything else; no rigorous analysis has ever been applied and no genetic data is available that would allow a grouping of polydesmidan families on that basis. Thus there is no good evidence that the suborders are monophyletic and they may be no more than categories of convenience. Why add a fifth taxon to this system?

Shear (2000) carefully analyzed the gonopodal and somatic characters of species of the callipodidan genus *Sinocallipus* (Sinocallipodidae), and came to the conclusion, based largely on the obviously plesiomorphic nature of the gonopods of members of this genus that a grouping of the families of the order into three (rather than the previous two) suborders was justified, establishing a new suborder Sinocallipodoidea. This arrangement has been widely accepted (Shear *et al.* 2003; Stoev *et al.* 2007; Stoev *et al.* 2008; Stoev & Enghoff 2011). Our arguments for the establishment of the polydesmidan suborder Dobrodesmidea are essentially parallel, but we believe considerably stronger. Conversely, in describing *Eostemmiulus,* Mauriès *et al.* (2010), while arguing that the genus was basal and disjunct, chose not to recognize its position by describing any new higher taxa, an action we think would have been well-justified.

Not only do the gonopods of *Dobrodesmus mirabilis* display remarkable plesiomorphies, they also bear a strong resemblance to those of the most basal members of two potential adelphotaxa to Polydesmida, Callipodida and Stemmiulida. In addition, *D. mirabilis* is unique in Polydesmida in having only two spinnerets instead of four, a character found in callipodidans, chordeumatidans and the stemmiulidan genus *Eostemmiulus*. Opposed to all other polydesmidans, the paraprocts of *D. mirabilis* have a dividing ridge and lack either marginal or submarginal setae. While the ring number and anamorphosis of this species are also unique in the order, we do not claim unequivocally that this is either a plesiomorphic character or that possible other members of the suborder that may be discovered in future will necessarily have this elevated ring number. Since the apomorphic genus *Devillea* also has unusually high ring numbers it is possible that this character is due to some saltational change in the genetics of development.

Dobrodesmus mirabilis may not be the sole member of its suborder for very long, however. At another locality distant from the limestone caves, RLF and LFMI have collected a single specimen of a distinct species of polydesmidan, smaller than, and with a very different somatic morphology from, *D. mirabilis.* The specimen is fragile and damaged, but we believe it to be a mature female with 33 rings. This species is also troglobiotic.

Natural history and conservation: The Mangabeira Cave (Figs 23–28) is dissolved in limestones from the Una group (Neoproterozoic) with ages from 650 to 850 ma. The cave has two main entrances, both located at the bottoms of dry sinkholes. The cave has a main voluminous conduit, which is sub-meandrine. The entrances are located in the opposite sides of this conduit. Although the cave was probably formed by a river (due to the architecture of the galleries), it has seemingly been dry for the last thousand years. This can be confirmed due to the presence of different levels of carbonate layers in the cave walls or floor, which would not have been deposited in the presence of a river.

The cave is poor in organic resources. There are only few guano piles (which are very old), and some roots growing into few points in the cave. The presence of huge collapsed blocks near the entrances certainly contributed to the low importation of organic resources to the cave. Such blocks act as "filters" retaining organic debris and preventing it from being transported deeper inside the cave. Furthermore, alterations in the cave entrance and in the external area (by human activities—see below) are also preventing the importation of organic matter into the cave system.

The Mangabeira Cave is certainly one of the caves most altered by human activities in Brazil. A herdsman discovered it in the eighteenth century, and since then it has been regularly visited by people from the surrounding region. The cave started to be used especially for religious purposes, and the first religious mass occurred in 1884. In this period the main entrance was disturbed by the construction of an altar and modifications in the external area. Since then a pilgrimage has begun, which usually attracts thousands of people. In 2005, around 100,000 pilgrims visited the cave.

During more than a century, the main conduit of the cave was severely altered by this intense use (which is concentrated in one month of the year). The sediments on the cave floor were trampled, and were turned into a compressed mass. Many microhabitats were certainly altered, and the main pristine organic resources were depleted. Nowadays the main organic resources used by the invertebrates in the cave are remains left by the pilgrims, such as food scraps, paper and especially candles, on which many fungi grow, attracting invertebrates, including crickets (*Endecous* sp.), Isopoda (Platyarthridae), Psocoptera (Psyllipsocidae) and young *Dobrodesmus mirabilis*.

Individuals of *Dobrodesmus mirabilis* are not homogeneously distributed within the cave. Specimens are observed only in moist areas, near drippings from speleothems. Most individuals were found in the median portion of the main conduit (the most inner part of the cave, considering the two entrances in the opposite sides of the conduit). Although the immature specimens are commonly found on the cave floor almost always associated with old candles left by pilgrims or sheltering under rocks or in fissures in the soil, the few older immatures and the adult male holotype were found in upper areas, far from the route used by pilgrims. Such older specimens were always found alone, in some cases walking on speleothems. The population is not large, and during five visits paid to the cave by RLF and LFMI, only 30 specimens were found, most of them young immatures. It is possible that a larger number of individuals, including adults, live in small cavities inaccessible to humans. Leaf litter and soil from the area surrounding the cave has not been surveyed for this, or related, species.

It is difficult to determine the degree of threat to which the species is exposed, especially due to the lack of information on the pristine conditions of the population (density, distribution, etc.). However, it is plausible to assume that the species is threatened, since no special attention is being given to the cave fauna or ecosystem. Accordingly, urgent actions should be taken in order to protect this unique species.

Acknowledgements

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