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**Notes on the unique structure of the spiracles and legs
in *Pandirodesmus disparipes* SILVESTRI, 1932
(*Diplopoda*, *Polydesmida*, *Chelodesmidae*), with some possible
implications concerning its mode of life**

Abstract: *Pandirodesmus disparipes* SILVESTRI, 1932, a remarkable diplopod from Guyana taken from an unknown habitat, was restudied from type material. Based on some rare traits (erect metatergal spines; swollen distal parts of most tibiae plus the basal parts of the tarsi; apical part of most tarsi with numerous long but stiff setae instead of a claw) and unique (extruding tubiform spiracles; extremely long legs, with the posterior pair per segment being considerably longer than the anterior one; legs and sternites beset with ramose, tree-like setae) as well as some circumstantial evidence derived from fossils and a few Recent taxa, the mode of life and the environment in this species are presumed as climbing on humid vegetation and/or swimming/gliding on the water surface in floodplains or savannahs, by all means in very close if not direct contact with water.

Key words: *Diplopoda*, *Pandirodesmus*, plastron, structure, ecology, Neotropics.

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INTRODUCTION

The remarkable diplopod *Pandirodesmus disparipes* SILVESTRI, 1932 was originally described as a new genus and species based on an adult female holotype (20 body segments) and a subadult female paratype (19 segments), both taken from an unknown habitat at Kamakusa, British Guiana (now preserved in the collection of the American Museum of Natural History, Nos.

6482 and 6483, respectively). Even though admittedly highly conservative in assigning this millipede to the family *Polydesmidae*, SILVESTRI (1932), due to the creature's very bizarre looks (Fig. 1) and several very rare and unique characters, proposed a separate subfamily, *Pandirodesminae*, to incorporate *Pandirodesmus*. Since then, neither this species nor anything at least slightly resembling *Pandirodesmus* has ever been recorded.

In the currently accepted classification, *Pandirodesmus*, monobasic, is the sole constituent genus of the tribe *Pandirodesmini*, family *Chelodesmidae* (HOFFMAN 1980). In support of SILVESTRI's (1932) perception of the affinities of *Pandirodesmus*, and based on a few peripheral characters alone (reduced claws and enlarged basitarsal region) as well as a similar distribution pattern, HOFFMAN (1975) believes this genus displays particularly close relationships with the disjunct North Andean chelodesmid tribe *Trachelodesmini*. The family *Chelodesmidae* is one of the largest in the *Diplopoda* (more than 150 recognized genera) and is widely dispersed throughout the Neotropical and Afrotropical regions (HOFFMAN et al. 1996). However, as gonopod structure of *Pandirodesmus*, a trait decisive in modern diplopod taxonomy, remains completely unknown, the true relations of this genus within the *Chelodesmidae* are still somewhat ambiguous.

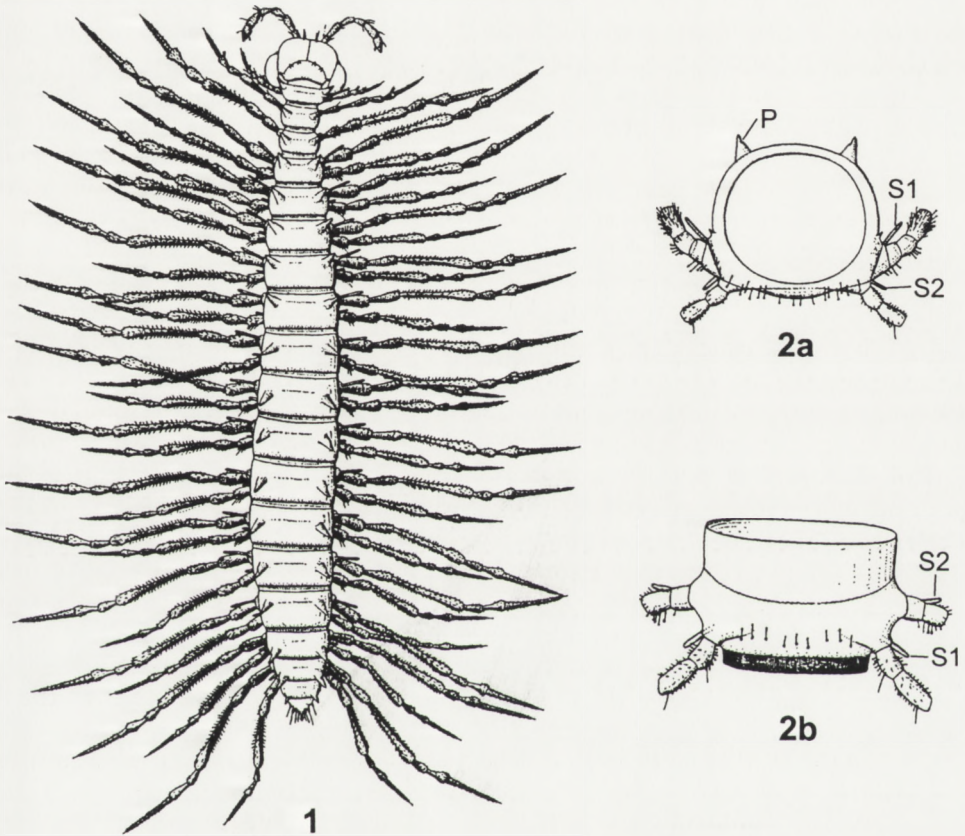
The paratype was received for restudy, with a permission to use some pieces for taking SEM micrographs (courtesy of N. Platnick). The animal looks so unusual indeed, and agrees completely with the original description, that, based on our own re-examination of the spiracles and legs, it has inspired us to make some further insights/speculations concerning its presumed ecology and behaviour.

RESULTS AND DISCUSSION

This polydesmidan is rather medium-sized, the adult reaching 13 mm in length. In other respects, however, it does look bizarre (Figs 1 & 2)! The metaterga are supplied with 1+1 distinct, erect spines (P in Fig. 2a), a character only very seldom present in modern diplopods, e.g., the "dragon millipede" genus *Desmoxytes* Chamberlin, 1923 (*Paradoxosomatidae*, *Polydesmida*) (cf. GOLOVATCH & ENGHOFF 1994) but most common in Palaeozoic *Diplopoda*, representing at least two extinct orders, which are known to have been conspicuously spinose (HOFFMAN 1969, KRAUS 1974, SHEARR, 1997). Whether this trait in *Pandirodesmus* can be related to a particularly ancient ancestry remains a pure guesswork but, as it seems to be very readily adaptive, it looks like the result of parallel evolution in many various diplopod lineages in response to some particular habits and habitats (see below). In other words, there is hardly any room for plesiomorphy of the "spiny character". The same can generally be said about any other outstanding feature of *P. disparipes*.

Another modern group of particularly strongly spinose diplopods is represented by the small Central American family *Tridontomidae* (*Polydesmida*),

with three conspicuous, upwards projecting metatergal spines on each side of the body. Even though gonopods are sometimes totally absent in the male sex in this group, which is a bizarre trait of course, the whole sum of morphological evidence seems to indicate that *Tridontomidae* are perhaps better downgraded to a subfamily of *Rhachodesmidae* (cf. LOOMIS & HOFFMAN 1962; HOFFMAN et al. 1996), hence they are not particularly closely related to *Pandirodesmus*.



Figs 1 & 2. *Pandirodesmus disparipes* Silvestri, 1932, habitus, dorsal view (1) and body segment 12, anterior (2a) and ventral (2b) views (after SILVESTRI 1932). S1 = anterior spiracle, S2 = posterior spiracle, P = metatergal spines (with subterminal ozopores on pore-bearing segments, pore formula normal).

Most of the legs in *P. disparipes* possess tibiae that are conspicuously swollen distally to support a basally swollen tarsus (Figs 11 & 15). This condition vividly resembles that met with in numerous *Arachnida* and, in the *Diplopoda*, only shared with several genera constituting the tribe *Trachelodesmini* (*Chelodesmidae*, *Polydesmida*) (HOFFMAN 1975). This trait is deemed an adaptation to climbing, at least as much as walking on the ground (SILVESTRI 1932). Perhaps the same can be postulated as regards the claws strongly reduced

and replaced by numerous long but stiff setae, a feature that *Pandirodesmus* also appears to share with some *Trachelodesmini* only (HOFFMAN 1975).

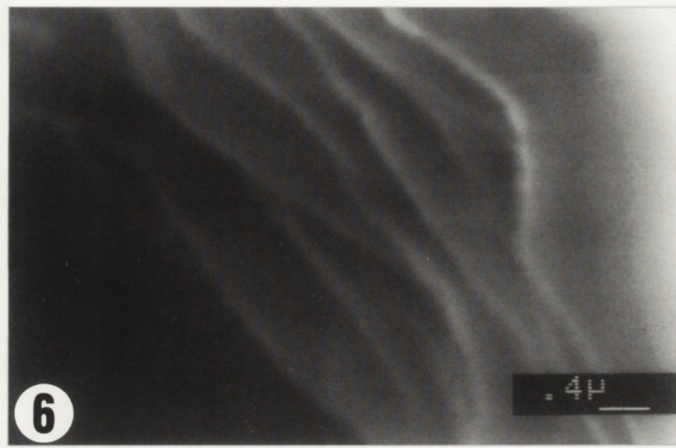
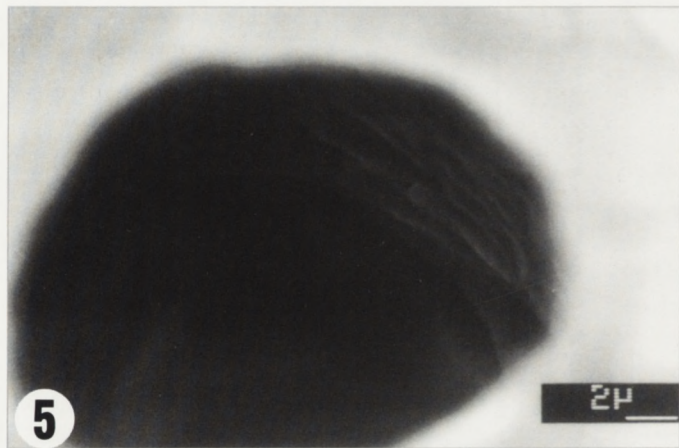
While the metatergal spines, the reduced claws and the swollen distal parts of most tibiae plus the basal parts of the tarsi in *Pandirodesmus* are features that occur in common with a few Recent polydesmidan taxa, several traits appear truly unique among the *Diplopoda*. All of these are expressed from the fourth body segment on: (1) extruding tubiform spiracles (Figs 1, 2a, b); (2) extremely long legs, with the posterior pair per segment being considerably (by ca. 1/4) longer than the anterior one (Fig. 1); (3) the legs and sternites beset with ramose, tree-like setae (Fig. 13).

In *Diplopoda*, 'dendroid' setae similar to those in *P. disparipes* have hitherto been noted on metaterga only, i.e., for cementing the dirt crust on the body of the Mexican *Bonetesmus ojo* Shear, 1973 (*Sphaeriodesmididae*, *Polydesmida*) (SHEAR 1977). Yet, as such remarkable setae are on the legs and sterna of *Pandirodesmus disparipes*, it is indeed unique in this respect.

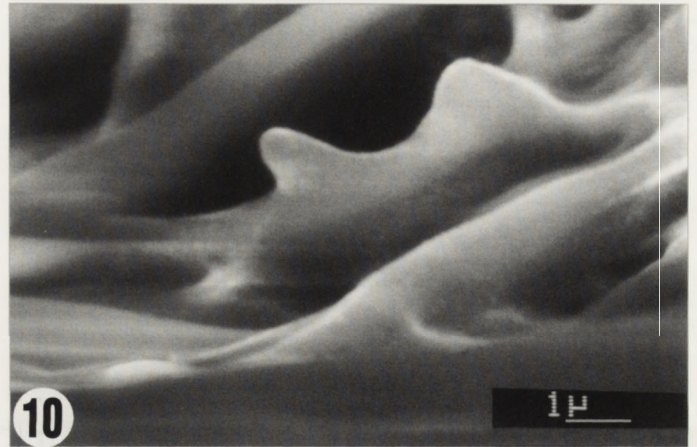
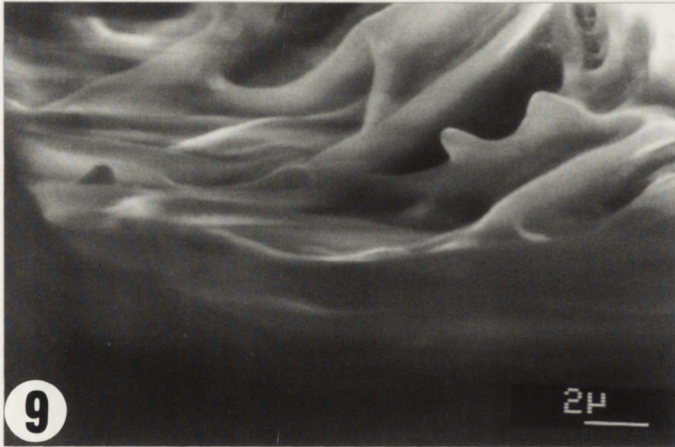
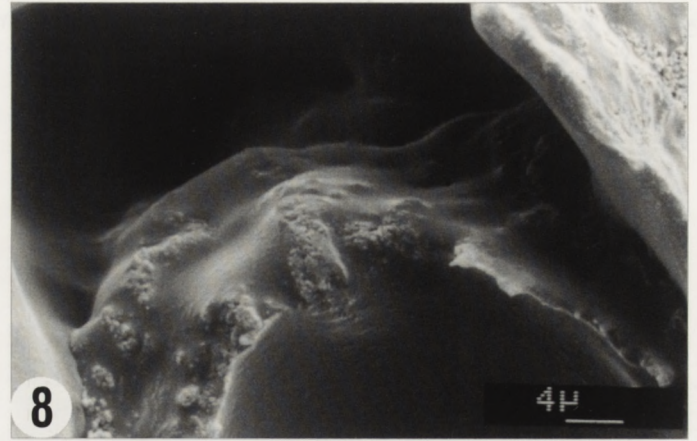
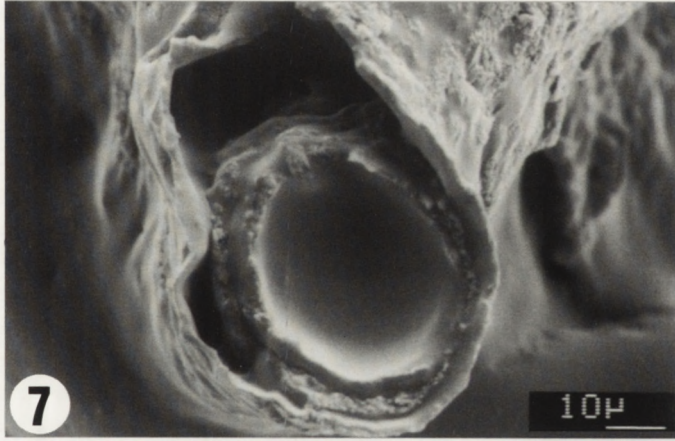
Although the habitat of *P. disparipes* is unknown, its habitus suggests that it might live in moist places (cf. SILVESTRI 1932) where the upright tubiform spiracles could facilitate respiration on/near water surfaces and/or even underwater. In some polydesmidans that populate wetlands of different climatic zones, including Amazonian inundation forests, spiracles have been found to have cuticular microtrichia or the cuticular surface is covered by a hydrophobic secretion layer (cerotegument), both enabling plastron respiration. A relationship between these types of cuticular structures and water tolerance has been observed (ADIS & MESSNER 1997, ADIS et al. 1997, 1998).

For this reason, the structure of one spiracle and of a leg deriving from half of a broken segment of the paratype of *P. disparipes* was studied in detail using Scanning Electron Microscopy (SEM). The opening and base of a tubiform upright spiracle are devoid of plastron-retaining cuticular structures (Figs 3–5). The inner wall of the tube is wrinkled (Figs 5 & 6) and its base occupies most of the entrance to the atrium (Fig. 7). The atrium wall is partly smooth (Fig. 8) or partly weakly denticulate (Figs 9 & 10). The tarsus is covered in part with simple or ramose setae (Figs 11 & 12). The latter predominate on the other leg parts (Figs 12, 13, 15 & 16) and on the sternites (Figs 3, 17 & 18).

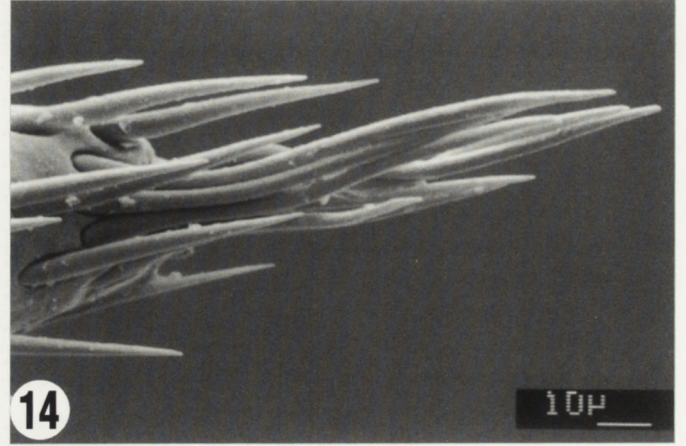
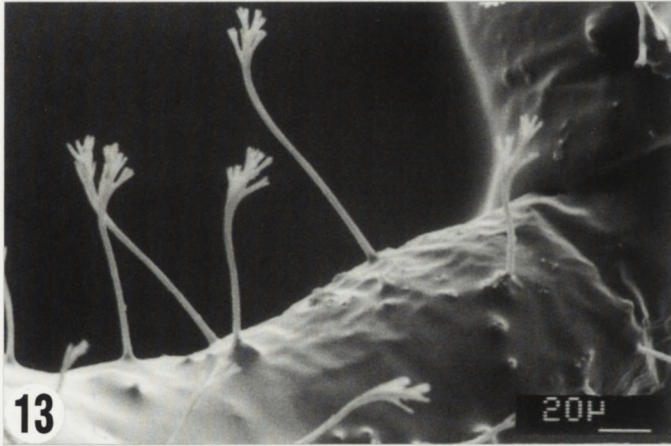
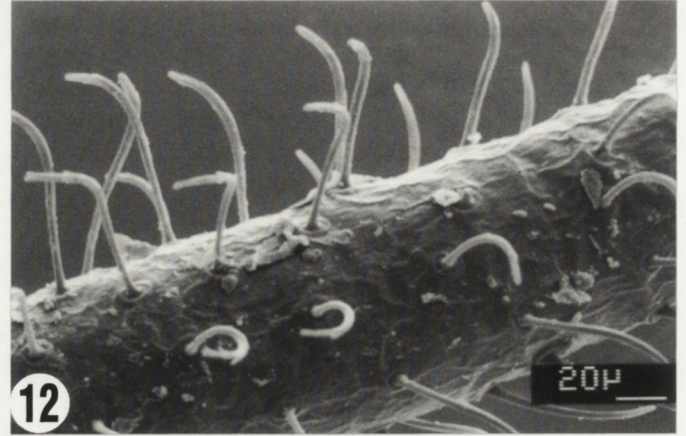
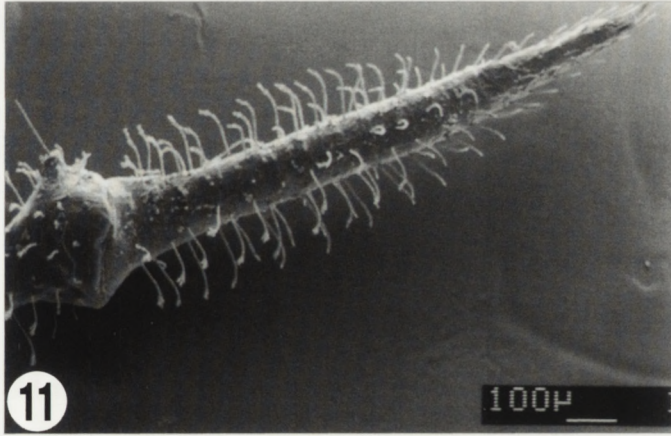
Even though neither cerotegument nor microtrichia have been revealed in *P. disparipes*, based on the unique structure of the spiracle alone, plastron respiration can very readily be presumed for this species. The upright tubular spiracles would enable respiration above the water or even allow for temporal submersion which results in an air casing inside the tube and/or on the cuticula, serving as physical gill in a semiaquatic mode of life (cf. ADIS & MESSNER 1997). Both heteropody and the long and strong uniform setae at the tarsal tip (Fig. 14) could certainly increase the contact area of the creature with the water film, suggesting its swimming/gliding capacity on the water surface.



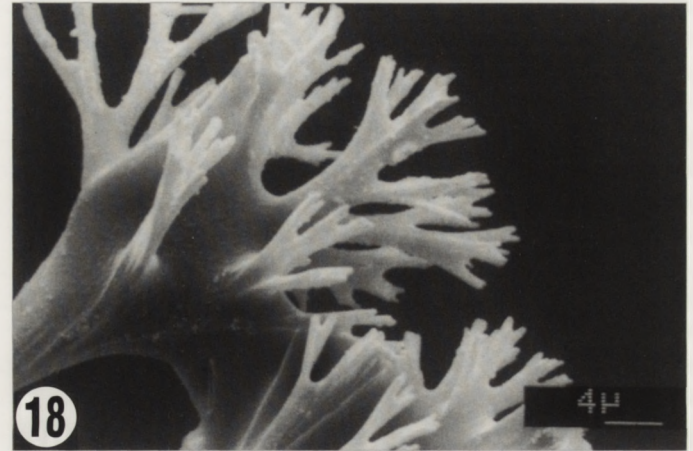
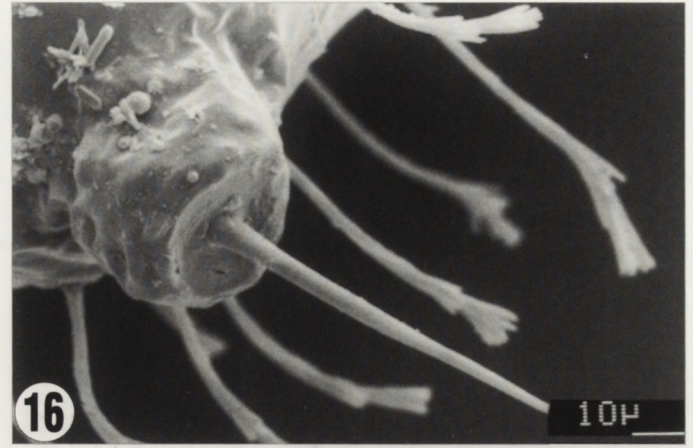
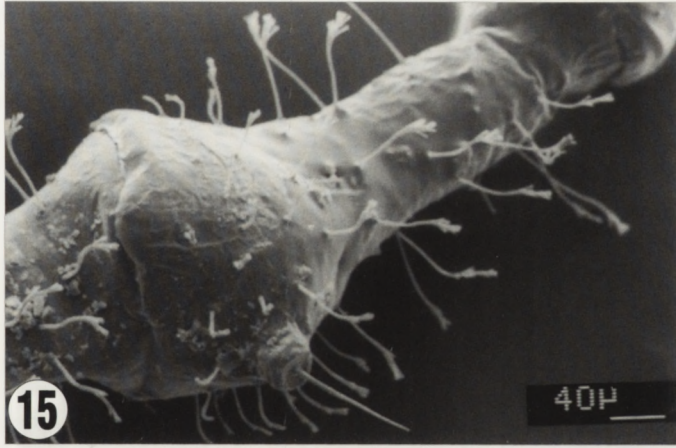
Figs 3-6. Upper part of a spiracle in *Pandirodesmus disparipes* (SEM), dorsal view of tube adjacent to coxal cavity with ramose setae (3), lateral view of tube (4), wrinkled cuticular surface near tube opening (5 & 6); $-4 \mu = 0.4 \mu\text{m}$.



Figs 7-10. Lower part of spiracle in *Pandirodesmus disparipes* (SEM), base of spiracular tube (upper part removed) and entrance to atrium (7 & 8), denticulate surface of atrium near base of spiracular tube (9 & 10).



Figs 11-14. Setae on legs of *Pandirodesmus disparipes* (SEM), normal and ramosae setae on tarsus and distal part of tibia (11 & 12), ramosae setae on tibia (13), strong, uniform setae at end of tarsus (14).



Figs 15-18. Setae on legs and sternum of *Pandirodesmus disparipes* (SEM), ramose setae on tibia and postfemur as well as sensory seta on tibia (15 & 16), ramose setae on sternite near coxal cavity (17 & 18).

The situation concerning the reduced claw replaced by numerous long setae in *Pandirodesmus* is not that straightforward. HOFFMAN (1975) considers this condition as one of the strongest synapomorphies of *P. disparipes* and the *Trachelodesmini*, the latter a tribe composed of small to medium-sized, relatively short-legged, often dirt-encrusted, soil/litter-dwelling creatures apparently showing no particular association with water (cf. SHELLEY 1999). The long terminal setae combined with rudimentary claws on the legs in *P. disparipes* may well be evidence of common ancestry with trachelodesmines rather than an immediate adaptive response of this bizarre millipede to its presumed particular habitat. In *Trachelodesmini* at least, the function of the terminal setae on the legs can very easily be suggested as being tactile/sensory.

In *Pandirodesmus disparipes*, however, every second leg being particularly long, and nearly all tarsi enlarged basally and crowned with numerous long and strong setae, let alone the entire ventral surface of the animal being beset with dendroid setae, would rather suggest an adaptive response towards increasing the area of contact with the water film so as to prevent sinking. Furthermore, heteropody might be advantageous for an easier/swifter gliding on the water surface, also allowing for leg movements free of interference on each side of the body.

Most of the extinct millipede species with long legs and large tergal spines are known from fairly well-preserved remains. These developments were possibly related to the Palaeozoic 'arms race' (SHEAR & KUKALOVÁ-PECK 1990). Their taphonomy suggests that they might have lived near water. As KRAUS (1974: 20) put it, "representatives of genera such as *Euphoberia* or *Acantherpestes* must have lived on the surface, especially on plants". With their strong spines and relatively large size, often accompanied by large ocellaria, those early diplopods must have been unable to burrow in substrates such as rotten wood or soil. So as not to get entangled, they must have lived in/on/among vegetation which was not particularly dense. "Perhaps as insects evolved, they became more and more restricted to what we may call «underground habitats». At the same time this would explain the tendencies... (i) towards the reduction of eyes, and (ii) towards more solid diplosomites" (loc. cit., p. 20).

While this statement might not hold entirely true concerning the necessarily weaker exoskeleton ascribed to the larger fossil species (e.g., SHEAR 1997), the general picture is such that, to avoid being entangled in plants, these ancient diplopods inhabited more open habitats/areas, yet hardly too far away from water. It is noteworthy that none of the presumed Palaeozoic 'climbers' so far known had such conspicuous spiracles and/or claw modifications as those observed in *Pandirodesmus*. Nor has heteropody ever been noted elsewhere.

As "nothing suggests that the ecological role of millipeds (*Diplopoda*) has changed in the more than 400 million years since they first may have appeared" (SHEAR & KUKALOVÁ-PECK 1990: 1813), we can assume this group, although presently at a stage of active adaptive radiation, is quite uniform in terms of ecomorphological types (= life-forms) (KIME & GOLOVATCH 2000).

Diplopoda are currently known to be dominated by forest floor-dwellers (= stratiobionts) but they also include a considerable proportion of cavernicoles, fewer geobionts and subcorticoles, and still fewer epiphytobionts/arboricoles. Stratiobionts seem to have prevailed among the Palaeozoic forms as well (KIME & GOLOVATCH 2000).

Both *Pandirodesmus* and *Desmoxytes* may indeed prove to have similar ecology and behaviour, yet with certain reservations. Thus, nearly all *Desmoxytes* specimens, representing several species, taken in nature by the second author (GOLOVATCH & ENGHOFF 1994) occurred on vegetation in humid (sub)tropical rainforest, not necessarily near water. Furthermore, nearly all *Desmoxytes* are brightly coloured, red to variegated, suggesting a warning colouration. This might be advantageous for an arboricolous way of life. Maybe the same holds true for *Tridontomidae* as well but, regrettably, too little is known yet to suggest more at the moment.

Pandirodesmus alcohol material is pale, apparently faded. However, as brightly coloured *Desmoxytes* samples tend to fade very quickly when preserved in alcohol, the fact that the type series of *Pandirodesmus* is pallid is hardly of any importance. Although, like in *Desmoxytes*, the exoskeleton in *Pandirodesmus* is hard and about as strongly sclerotized, the metatergal spines are less conspicuous. The highly peculiar spiracles, heteropody and setae seem to reinforce the impression of *Pandirodesmus* as of a good climber combined with swimming and/or water gliding capacity. Then SILVESTRI's (1932: 11) guess that this remarkable millipede might "live in marshes or on trees among very wet arboreal vegetation" can be accompanied by a still wilder guess of *Pandirodesmus* being the equivalent of a "gerroid water bug" in *Diplopoda*. Of course the function of the unique morphological structures in *P. disparipes* will remain unknown until its habitat (floodplains or savannahs) and mode of life in Guyana are finally revealed. But what is evident already now is, *Pandirodesmus* seems very likely to represent another distinct and disjunct life-form in *Diplopoda* (cf. KIME & GOLOVATCH 2000).

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STRESZCZENIE

[Tytuł: Uwagi o niezwyklej strukturze przetchlinek i odnóży *Pandirodesmus disparipes* SILVESTRI, 1932 (*Diplopoda*, *Polydesmida*, *Chelodesmidae*) i jej możliwych konsekwencjach dla stylu życia krocionoga]

W pracy poddano badaniom materiał typowy *Pandirodesmus disparipes* SILVESTRI, 1932, niezwyklego krocionoga, pochodzącego z nieznanego środowiska w Gujanie. Opisano i zilustrowano rzadko występujące cechy: wyprostowane kolce metatergalne, zgrubienia dystalnej części goleni i basalnej części stopy, wierzchołkowa część stopy z licznymi, długimi i sztywnymi szczecinami

zamiast pazura, czy wręcz unikalne u *Diplopoda*: wystające rurkowształtne przetchlinki, niezwykle długie nogi, z których tylna para każdego segmentu jest wyraźnie dłuższa niż przednia, odnóża i sternity z licznie rozgałęzionymi szczecinami. Cechy te, a także pośrednie dowody kopalne oraz anatomia współczesnych taksonów, dały podstawy koncepcji o stylu życia opisanego gatunku. Przypuszcza się, iż jest to krocionóg biegający po roślinności wodnej, bądź pływający czy ślizgający się po powierzchni wód zalewających obszary dolin lub sawann; jednakże wszystko wskazuje na jego bliski, jeśli nie bezpośredni, kontakt z wodą.