



Redescription of the South African millipede *Cylichnogaster lawrencei* Verhoeff, 1937 and notes on the family Siphonotidae (Diplopoda, Polyzoniida)

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Abstract

The unusual millipede *Cylichnogaster lawrencei* Verhoeff, 1937 (Diplopoda, Polyzoniida, Siphonotidae) is redescribed from newly collected specimens. Species of *Cylichnogaster* are the only known colobognathan millipedes capable of volvation, and are also distinguished by their small size and low segment number. Taxonomic notes are provided on the poorly known family Siphonotidae.

Key words: *Cylichnogaster nigricornis*, *Siphonotus*, *Burinia*, *Rhinotus*, volvation, South Africa, Table Mountain

Introduction

The millipede genus *Cylichnogaster* was established by Verhoeff in 1937 for the single species *C. lawrencei*, from the Cape Peninsula, South Africa. A second species, *C. nigricornis*, also South African, was added by Schubart in 1966. These two species are perhaps the most distinctive of all members of the millipede subterclass Colobognatha, since they are capable of more or less complete volvation, or enrollment, with reduced numbers of highly arched trunk segments that allow them to defend themselves by rolling up into a ball. When in this form, the legs, head and antennae of the millipedes are well protected, concealed beneath the tergites. Other members of the Colobognatha can at best curl into a tight spiral in which the head and antennae are in the center, but still exposed. Furthermore, species of *Cylichnogaster* are among the smallest of all colobognathans, rarely exceeding 3 mm in length as adults.

After Schubart's 1966 paper, nothing was published on these interesting animals but for a few natural history notes by Lawrence (1984, pp. 116–119), who presented some drawings of extended and enrolled individuals. He noted that the ability to roll up or volvate in *Cylichnogaster* was not as well developed as in sphaeriotheriidans, but represented an intermediate condition between complete protection and coiling into a spiral. Lawrence also observed that unlike other South African polyzoniidans, *C. lawrencei* is gregarious, clustering in groups of 50–100 individuals under moist, decaying wood.

A small collection of *C. lawrencei* was obtained not far from the type locality in 2001 by Gonzalo Giribet, who forwarded them to me for study, prompting this redescription of the species. I also provide some notes on the family Siphonotidae.

Redescription

The genus *Cylichnogaster*

Verhoeff originally proposed the new genus and species *Cylichnogaster lawrencei* in a paper written in German and published in *Zoologischer Anzeiger* on January 15, 1937 (Verhoeff 1937a). As this was the only species in the genus at the time of the proposal, it formally typifies the genus. Later in 1937, a second paper, this time in English, appeared in the *Annals of the South African Museum* (Verhoeff 1937b). In this paper, essentially an incomplete version of the earlier one, *C. lawrencei* is described as a new species but the genus *Cylichnogaster* is not mentioned

separately and is not typified. Fortunately the earlier publication took care of that detail. In any case the year for both the genus and species remains 1937. The description of *C. lawrencei* was immediately followed in the same journal by a second article in English (Verhoeff 1937c), which included the remainder of the contents of the earlier German one .

Verhoeff also set up a subfamily of Buriniidae (= Bureniidae, Siphonotidae), Cylichnogastrinae, which contained only *Cylichnogaster* (Verhoeff 1937a, 1937c). As will be explained, Buriniidae became a synonym of Siphonotidae when Verhoeff included the genus *Siphonotus* in the family. The comparisons with *Burinia* that are detailed by Verhoeff (1937c) make it plain that these two genera are quite similar in many morphological details. The subfamily Cylichnogastrinae appears to be based almost solely on the ability of *C. lawrencei* to enroll, on its smooth tergites, and on its low number of diplosegments. A lower rank may be more appropriate for this taxon.

***Cylichnogaster lawrencei* Verhoeff 1937**

Figs. 1–12

C. lawrencei Verhoeff 1937a, 85; 1937b, 118.

C. lawrencei, Schubart 1966, 200.

C. lawrencei, Lawrence 1984, 116–118.

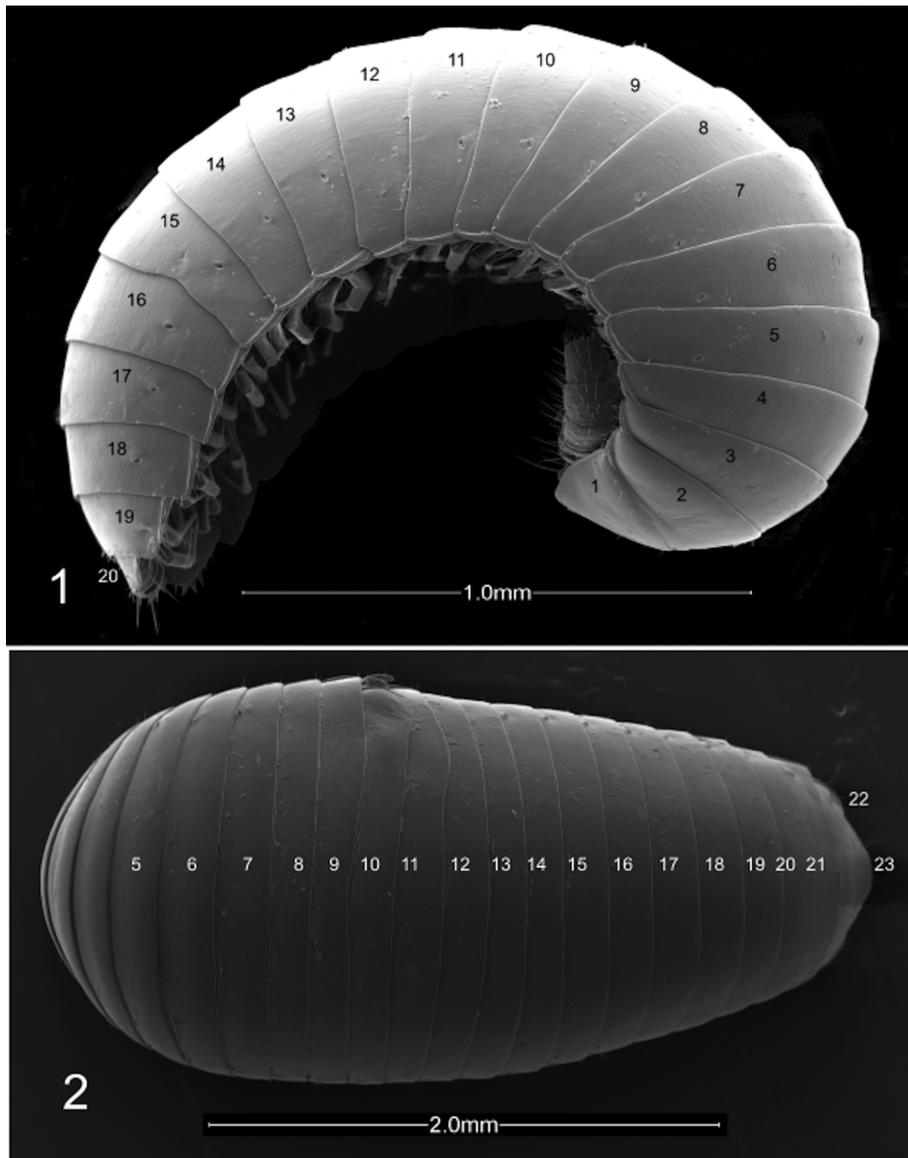
C. lawrencei, Hamer 1998, 21.

Types. Fifty-eight male and female cotypes from Sir Drummond Chaplin's estate, Noordhoek, Western Cape, South Africa (34.1°S, 18.367°E), collected May 1928 by E. L. Gill, deposited in the entomology collection of the Iziko Museum of South Africa (formerly the South African Museum), Cape Town, South Africa; examined 2015.

Verhoeff (1937b) gives the type locality as "...one of the valleys of the mountain slopes near Chapman's Peak, Cape Peninsula." I was not able to exactly locate the Drummond Chaplin estate, but Sir Drummond Chaplin was an important South African and Rhodesian official who owned property called De Goede Hoop near Chapman's Peak; this tallies with latitude and longitude data added at some later date to the locality labels. Verhoeff (1937b) implies that R. F. Lawrence, who transmitted the specimens to him, was the collector, but the labels with the specimens attribute the collection to E. L. Gill. Verhoeff also mentions three males and "numerous" females in the collection, but the cotype collection includes at least a dozen males. Some confusion is introduced in the German version of the species description (Verhoeff 1937a) where the type locality is given as "...am Abhange des Tafelberges...(slope of Table Mountain)." Table Mountain is some 20 km NNE of Chapman's Peak and curiously is closer to the locality of the newly collected specimens. However, the type locality proper should be considered as given on the the labels of the cotypes.

The new specimens (5 males, 9 females and several juveniles) on which the following redescription is based were collected in Kirstenbosch National Botanical Garden at Skeleton Gorge by Gonzalo Giribet on April 9, 2001. Skeleton Gorge is a part of Table Mountain National Park. A trail to the summit of Table Mountain follows the gorge, passing through moist indigenous forest. The specimens were collected by sifting leaf litter near the start of the trail. This site (S 33° 58' 58", E 18° 25' 28", elevation 214 m asl) is only about 13 km from the type locality near Chapman's Peak.

Description of male from Skeleton Gorge, South Africa. Length, about 3 mm, greatest width 1.6 mm (measured dorsally across trunk ring 8). Color light creamy brown, faintly mottled darker; antennae heavily mottled dark purplish brown, eyes prominently black. Body (Fig. 1) fusiform, tapering sharply to width of 0.8 mm at penultimate ring. Head (as in female, Fig. 3) triangular in frontal view, with two prominent, pigmented ocelli obliquely situated on either side, posterior ocellus the larger; two prominent setae between eyerows. Head transversely depressed between antennal sockets. Opening to preoral chamber small, nearly rectangular, between lateral elements of gnathochilarium (Figs, 6, 7). Plate of gnathochilarium truncated-quadrangular, lateral elements meeting anteriorly in midline, each with two prominent setae, numerous peg sensilla (Fig. 7). Antennae about half again as long as head, stout, somewhat clavate; antennomeres 2–5 subequal in length, antennomere 5 widest, with small dorsoapical sensory area bearing two or more sensilla; antennomere 6 about twice as long as 5, also with few accessory sensilla. Antennomeres 7 and 8 much reduced, entirely withdrawn into 6, eighth with usual four sensory cones (Fig. 4).

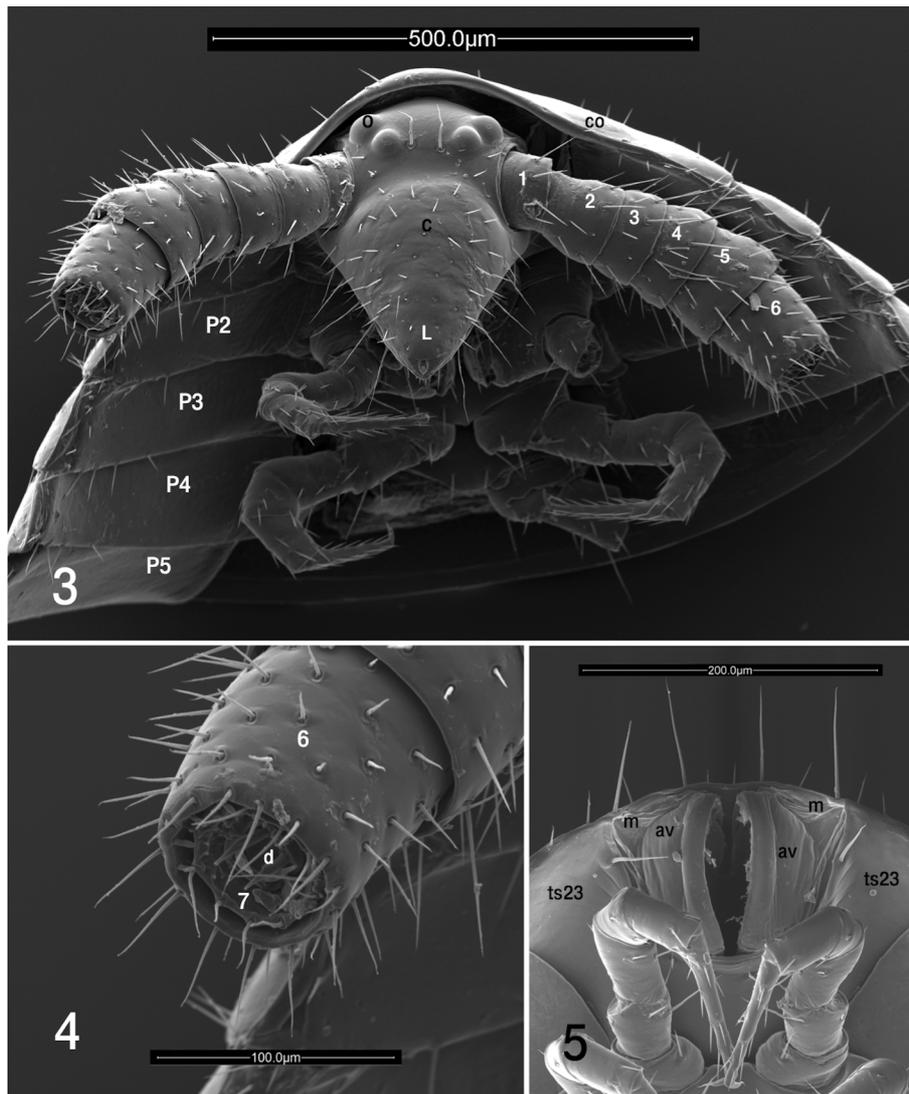


FIGURES 1, 2. *Cylichnogaster lawrencei*. Fig. 1. Partially enrolled male with 20 trunk segments. Fig. 2. Partially extended female with 23 trunk segments.

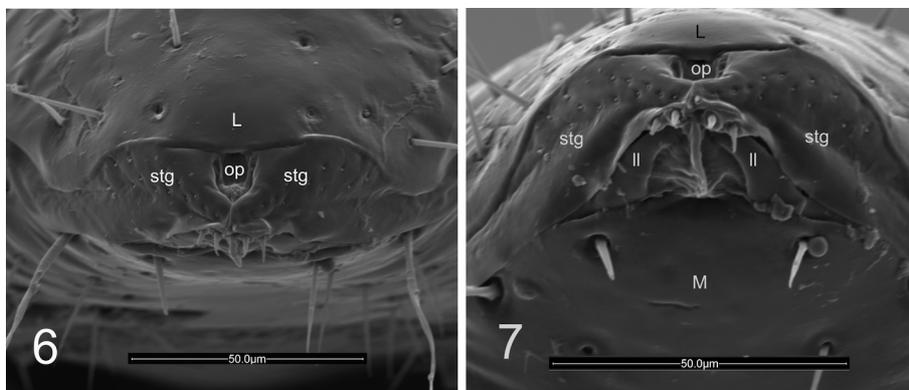
Trunk (Fig. 1) with 20 segments, including collum, and terminal segments (all 5 males in collection with 20 trunk segments). Collum hood-like, completely covering head in dorsal view of partially enrolled animal; head probably partially exposed in fully extended animal. Diplotergites increasing in width and length to tergite 8, then decreasing in width, but not length, to terminal segment (epiproct). Diplotergites with distinct lateral marginations, smoothly overlapping, posterior edges not raised. Ozopores beginning on tergite 5, distinctly rimmed, directed slightly posteriorly, distant from lateral margins of tergites. Terminal segment broadly rounded posteriorly, with four prominent long setae on posterior margin; forming complete ring around strongly margined, hemispherical anal valves (Fig. 5). Sternites narrow, pair of long setae between coxae, coxae nearly touching in midline. Spiracles prominently rimmed, slightly raised. Pleurites 3–5 times wider than long, four prominent setae on laterodistal margin of each. Legs short, stout, prefemora and femora subequal, tarsus abruptly narrower than tibia, about equal to tibia in length. Claw prominent, curved, subtended by slightly sigmoid accessory claw 2–3 times its length. Eversible coxal glands begin on legpair 3.

Second legpair with coxae drawn out into long apophyses, *vas deferentia* open at their tips. Anterior gonopods (Figs. 8, 9) with 7 podomeres, seventh podomere drawn out into long, sigmoidally curved spine, hollow with pore at tip (Fig. 9). Posterior gonopods (Figs. 8–10) with 7 podomeres; coxae separated by slightly more than their width; gonopods curve first mesally, then posteriorly. Seventh (terminal) podomere modified as tarsungulum,

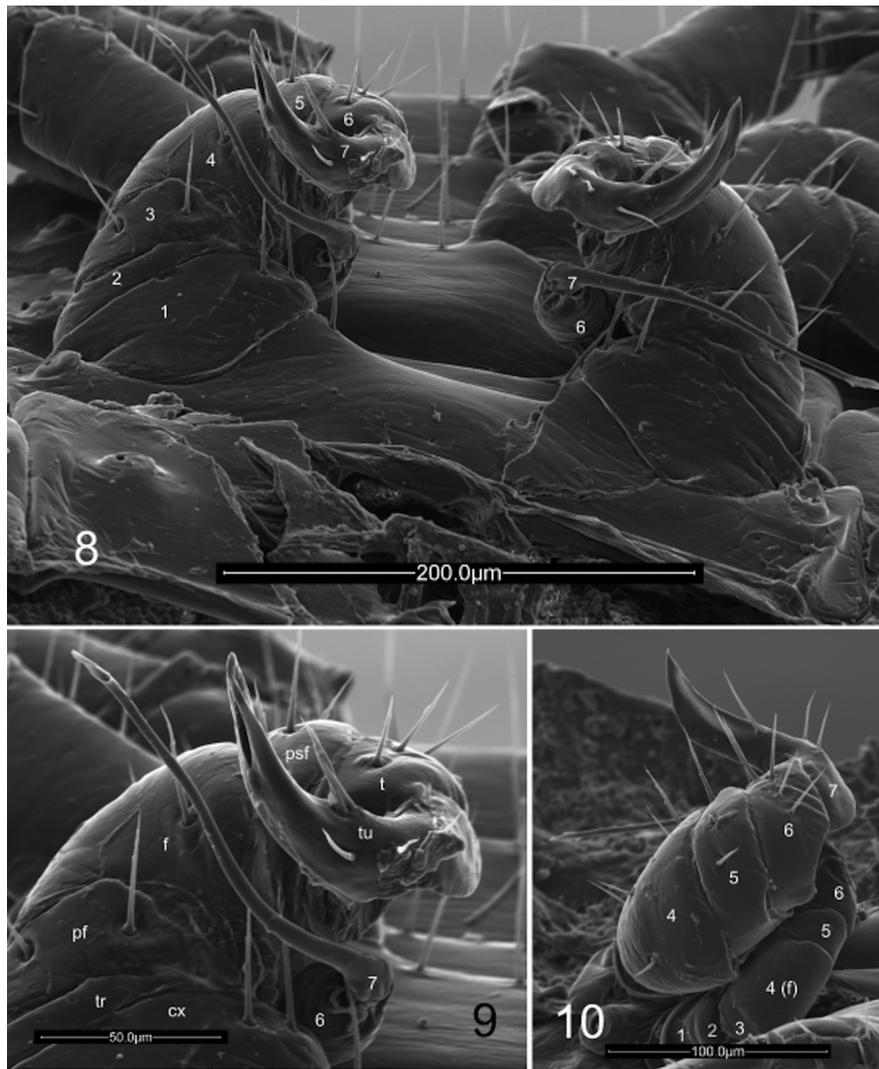
sharply curved ventrally, two or three setae on ventral surface with bases close together in large sockets. Ventrolaterally, seventh podomere with deep groove which receives terminal podomere of anterior gonopod.



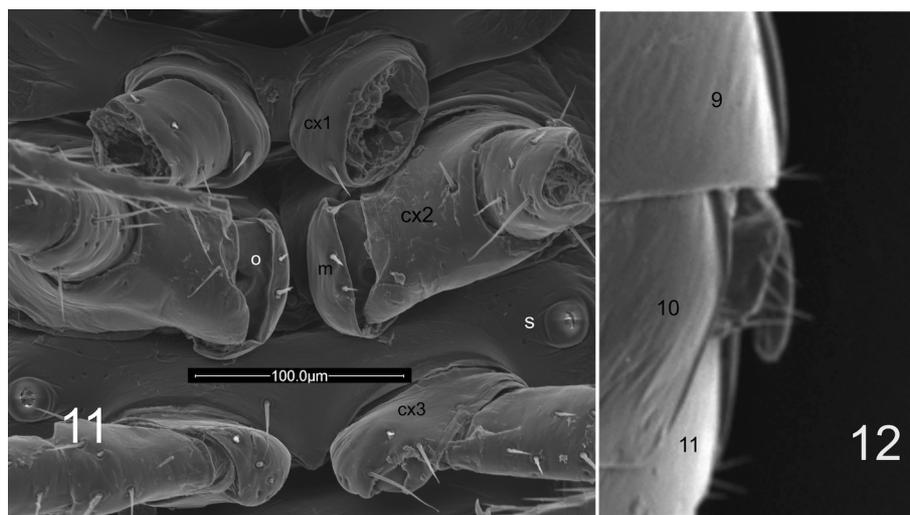
FIGURES 3–5. *Cylichnogaster lawrencei*. Fig. 3. Head of female, frontoventral view. **C**, clypeus; **co**, collum; **L**, labrum; **o**, ocellus; **P2–P5**, pleurites 1–5; numerals indicate antennal segments. Fig. 4. Tip of right antenna of the same specimen. **6**, antennal segment 6; **7**, antennal segment 7; **d**, antennal disc (segment 8) with sensory cones. Fig. 5. Terminal segment and anal valves of the same specimen, ventral view. **av**, anal valves; **m**, membranous region; **ts23**, terminal segment (23).



FIGURES 6, 7. *Cylichnogaster lawrencei*. Fig. 6. Rostrum and gnathochilarium of female, frontal view. **L**, labrum; **op**, opening to preoral chamber; **stg**, stipes of gnathochilarium. Fig. 7. The same, ventral view. **L**, labrum; **ll**, laminae linguae; **M**, mentum; **op**, opening to preoral chamber; **stg**, stipes of gnathochilarium.



FIGURES 8–10. *Cylichnogaster lawrencei*, gonopods. Fig. 8. Posterior view. Fig. 9. Right gonopods, posterior view. Fig. 10. Same as Fig. 9, lateral view. Numerals indicate gonopodomere numbers; **cx**, coxa; **tr**, trochanter; **pf**, prefemur; **f**, femur; **psf**, postfemur; **t**, tibia; **tu**, tarsungulum.



FIGURES 11, 12. *Cylichnogaster lawrencei*. Fig. 11. Second leg coxae and female genitalia; **cx1**, first coxa; **cx2**, second coxa; **cx3**, third coxa; **m**, mesal valve; **o**, opening of oviduct; **s**, spiracle. Fig. 12. Possible arthropod parasite on female shown in Fig. 2, numerals indicate trunk segment numbers.

Description of female from Skeleton Gorge, South Africa. Length, 3.3 mm, greatest width, 1.65 mm. Trunk (Fig. 2) with 23 segments (all other females in collection with 21 or 22 segments). Other nonsexual characters as in male. Coxae of second legpair enlarged, extended posteriomesally. Cyphopods mesal to coxae, evidently with mesal valves only, lacking lateral valves and opercula; mesal valves with pair of setae (Fig. 11).

Distribution. Now known from two localities in the Western Cape, about 13 km apart.

Notes. Comparisons with original description and cotypes. Verhoeff's (1937b) English description of *C. lawrencei* was prepared with optical microscopes, while the description above is based on both optical and scanning electron micrography.

Presumably, Verhoeff (1937b) studied the 58 cotype specimens and gives the trunk segment numbers of both sexes as 20–26, with males from 3.75–5.0 mm in length, and females 3.75–5.25 mm. I was able to confirm those counts. The largest females in the cotype collection have 26 trunk segments; all the males, however, have 20. In the Giribet collection, all 4 males had 20 trunk segments and were close to 3.0 mm long, while 9 females were somewhat longer, but none more than 4.0 mm, with 21–23 trunk segments. I found it difficult to accurately count segments under a dissecting microscope at 60X, but with SEM the figures of 20 and 23 were verified for the specimens used. The length differences are due to the fact that the cotypes are inflated and extended by whatever manner of original preservation was used, while the new specimens have retained their live appearance. Verhoeff described the color as “dark brown,” in contrast to the light pigmentation of the new specimens, but the cotypes are now pale creamy white and largely transparent. Verhoeff counted 7 podomeres in both the anterior and posterior gonopods, as did I. Schubart (1966) clearly illustrates 6 podomeres in the anterior gonopods of *C. nigricornis*, but seems unclear about the posterior gonopods; 7 podomeres are illustrated on the right posterior gonopod and only 6 on the left. In very small animals, this character is hard to observe without at least removing the gonopods and mounting them on a slide for examination at high magnification with a compound microscope. The number of podomeres in the gonopods has been a contentious issue as regards its taxonomic significance in polyzoniidans. While Attems (1928) reported 7 podomeres in both pairs of gonopods of *Burinia*, Mauriès & Silva (1971) show no more than 5 in their detailed illustrations of Chilean species of *Siphonotus*. Yet Hoffman (1977) and Golovatch (2014) considered the Chilean species to belong to *Burinia*.

***Cylichnogaster nigricornis*.** *Cylichnogaster nigricornis* Schubart, 1966 is almost certainly a distinct species, based on the gonopod illustrations published with the original description (Schubart 1966). The type locality (Stormsrivierpiek, Eastern Cape) is 505 km east of the known localities for *C. lawrencei*, in quite a different climatic regime. The tarsungulum of the posterior gonopod of *C. lawrencei* has a broad, spatulate terminus, while that of *C. nigricornis* ends in a long, attenuate filament. The anterior gonopods of the two species are essentially the same, though in both anterior and posterior gonopods of *C. nigricornis*, Schubart illustrates fewer distinct podomeres than probably actually exist, likely due to the small size of the appendages and his use of an optical microscope to draw them. *Cylichnogaster nigricornis* is also described as larger (males from 3.5–4.0 mm long, females from 4.0–4.5 mm long) and with more trunk segments (two males with 31 and 34, four females ranging from 29–33).

The smallest colobognathan? *Cylichnogaster lawrencei* might take the title of the smallest known colobognathan; its congener is similar in size, and two recently described species (both polyzoniidans) are challengers. *Nepalozonium trimaculatum* Shelley, 1996 was described from two males collected in Nepal that measured 3.7 and 4.3 mm long, with 22 and 27 trunk segments respectively. *Octoglena claraqua* Shelley, Richart & Bogan, 2010 is known only from the holotype male, taken in Idaho, USA; that specimen is 4.0 mm long with 28 trunk segments. However it must be kept in mind that colobognathans do not have fixed numbers of trunk segments and continue to molt and add segments after maturity at an early instar, thus individuals of *C. nigricornis*, *N. trimaculatum* and *O. claraqua* may represent young males which could have grown larger with time. In particular, all of the other species of *Octoglena* are larger and have more segments in the largest, and presumably oldest, specimens (Shelley 1995).

Volvation. Golovatch (2003) reviewed volvation in the millipede order Polydesmida. As with the Colobognatha, only a small number of species of polydesmidans are capable of volvation. Due to the differences in the adaptations that make polydesmidan volvation possible, and the distribution of volvatory forms in several unrelated families, Golovatch concluded that the habit had evolved in parallel several times among them. The morphological changes allowing volvation were summarized as follows: small, cryptic species with relatively few body segments (a little more than 20 at the most), declined paraterga, at least one much enlarged postcollum tergite

(often the second), reduced collum, relatively short legs with their bases close together, short antennae, and a reduced terminal segment. Golovatch also pointed to a few features that often, but not always, accompany volvation: mimetic coloration, hardened cuticle, and reduced ozopores.

Cylichnogaster lawrencei, while capable of volvation, has few of these adaptations. It is a small, cryptic species with a reduced number of segments. The tergites are highly arched, almost a half-circle in outline, and their lateral parts (similar to paranota in polydesmidans) are nearly vertical. But none of the postcollum tergites is conspicuously enlarged. Instead the trunk behind the collum broadens sharply to the sixth or seventh tergite, which in dorsal view is the widest; behind these tergites the trunk tapers sharply to a width of less than half that of the sixth tergite. The terminal segment is not reduced, but the legs are short and set close together. Compared to confamilial forms (Chilean specimens of *Siphonotus*), the antennae are of the usual length. For the auxiliary features, mimetic coloration does not appear to be present and the ozopores are quite conspicuous.

The trunk segments of *C. lawrencei*, as with those of glomerid millipeds, are much longer dorsally than ventrally, since when volvated much more of the dorsal surface stands to be exposed, while the ventral surface is compressed. Ventrolaterally, the ventrodiscal part of each tergite slides under the same part of the preceding tergite and head and antennae tuck in at about the ventral midpoint of the trunk, while the legs are drawn inward and hidden by the overlapping tergites. Thus, as Lawrence (1984) observed, the defensive behavior of *C. lawrencei* is intermediate between the spiral coil of larger colobognathans and true volvation.

A possible parasite. Unnoticed until the SEM photographs were taken was a segmental anomaly of tergite 10 in one of the newly collected female specimens. The anomaly seems due to an object protruding from between tergites 9 and 10, and possibly between the pleurite and tergite of diplosegment 10. The exact nature of this object (Fig. 12) remains unclear but it appears to have arthropod setae, and may be a parasite.

The family Siphonotidae

Hoffman's classification

The order Polyzoziida is comprised of three families: Polyzoziidae Newport 1844, Hirudisomatidae Silvestri 1896, and Siphonotidae Cook 1895. The first two of these three families are well understood thanks to the work of Shelley (*i.e.*, 1995, 1998). New genera and species of polyzoziids and hirudisomatids continue to be described from poorly explored areas (Shelley 1996, Shelley & Shear 2005, Shelley *et al* 2010). Both families are now considered to be limited to the northern hemisphere. In contrast, the family Siphonotidae remains ill defined both in terms of its component taxa and relationships to the other two families. Siphonotids, with the exception of one anthropochoric species, *Rhinotus purpureus* (Pocock, 1894), are found only in the southern hemisphere (Chile/Brazil, southeast Asia, Australia/New Zealand, and South Africa and Madagascar).

Hoffman (1977, 1980) reviewed the classification of the Siphonotidae and brought some clarity to what historically had been a confused taxonomy (see discussion in Hoffman 1977). Wesener (2015), in a taxonomic overview of the Colobognatha, did not attempt to do more than list the genera of Siphonotidae. Hoffman's classification, repeated unchanged in 1980, is as follows:

Family Siphonotidae Cook, 1895 (syn. Buriniidae Verhoeff, 1937)

Subfamily Siphonotinae, Cook 1895 (syn. Buriniinae Verhoeff, 1937)

Tribe Siphonotini Cook, 1895

Siphonotus Brandt, 1837 (Brazil, ?Chile)

Burinia Attems, 1926 (syn. *Burenia*, Attems, 1928, *Megaclia* Attems, 1951, *Pampiconus* Chamberlin, 1957; South Africa, Brazil, ?Chile)

Dawydoffia Attems, 1953 (Vietnam)

Rhynchomecogaster Verhoeff, 1937 (South Africa)

Tribe Rhinotini Hoffman, 1977

Rhinotus Cook, 1896 (syn. *Orsilochus* Attems, 1900 [preoccupied], *Paraburenia* Verhoeff, 1939, *Boninozonium* Takukawa, 1942, *Paraconus* Chamberlin, 1945, *Siphonoconus* [not Attems] Causey, 1965. Nearly pantropical due to distribution by human agency)

Siphonoconus Attems, 1930 (Java, Flores)
Subfamily Cylichnogastrinae Verhoeff, 1937
Cylichnogaster Verhoeff, 1937 (South Africa)
Unplaced siphonotid genera: *Bdellotus* Cook, 1895 (Java), *Metrozonium* Attems, 1951 (Java),
Upsima Chamberlin, 1945 (Prinsen Island, Indonesia), *Siphonethus* Chamberlin, 1920 (New Zealand).

Comments on Hoffman's classification. Hoffman's effort represents a first try at bringing some order out of the chaos introduced into the group by the posthumous publication of Attems (1951). However, even though he examined the type specimen of *Siphonotus brasiliensis* Brandt, 1837, on which the family was based, that specimen is a female and so male characters were not described. He stated that his conclusions were based on "...several better-known species, and some specimens at hand..." but does not detail which species those were, or which species were represented among the "specimens at hand." Many of his synonymies and taxonomic placements are unargued and unsupported by evidence. Therefore future research on the family will need to begin with the examination of male specimens of all of the nominal genera, to confirm or refute Hoffman's generic synonymies.

The spelling of the names Bureniidae and Bureniinae (as in Verhoeff 1937 and Hoffman 1977) must be corrected to Buriniidae and Buriniinae under ICZN Article 35.4.1. *Burinia* is the original and correct spelling of the type genus (Attems 1926), but in 1928 Attems misspelled the name *Burenia*, and it was on this error that Verhoeff (1937) based the family name. See Jeekel (1970, p. 36) for a full discussion. Because Verhoeff included *Siphonotus* in the family, he brought in the name Siphonotidae Cook, 1895, which has precedence over Buriniidae.

The tribe Rhinotini may not deserve separate rank; the gonopods (Wesener 2014) and the densely pilose tergites are similar to those of *Burinia*.

Hoffman's suggestion that the Chilean species described as *Siphonotus* (Mauriès & Silva 1971) actually belong in *Burinia* is supported by the gonopod morphology of the Chilean species compared with South African *Burinia*. The type species of *Siphonotus*, *S. brasiliensis*, is known only from the female holotype, so my preference is to continue to consider these Chilean species as belonging to *Siphonotus*, though Golovatch (2014), following Hoffman, placed them in *Burinia*. *Siphonotus* is the older name, so South African *Burinia* might end up being called *Siphonotus* when the dust settles. Three species of *Siphonotus* have been described from Australia (i.e. Pocock 1903) and evidently the genus is diverse there; an unpublished thesis by Dennis Black describes numerous new species (R. Mesibov, pers. comm. 2015).

I have seen at least three species assignable to *Siphonethus* from New Zealand, and those from a small region of the North Island. This genus may also occur in Australia.

Taxonomic characters in Siphonotidae

The descriptions of many putative siphonotids are sketchy, or dwell on characters of little value for higher classification; several are based on female or juvenile specimens (Hoffman 1977). An exception to this are the excellent papers on Chilean siphonotids by Mauriès and Silva (1971) and by Golovatch (2014), in which new species of *Siphonotus* are described and illustrated in detail.

According to the studies of Shelley (1995, 1997), the major character distinguishing the families Polyzoziidae and Hirudisomatidae is the position of the pseudopenis (opening of the *vasa deferentia*) on the second coxae of males. In hirudisomatids, this is a short cone ventrodorsal on the coxa, while in polyzoziids it is a longer, sometimes flask-shaped tube arising from the posteroventral surface. It may appear to be separate from the coxa in Polyzoziidae. This seems a slender reed on which to suspend a distinction between millipede families (perhaps due to the influence of Richard Hoffman, who considered the position of the pseudopenis or *vasa deferentia* openings to be of great importance in millipede taxonomy), but it appears to be consistent throughout all known genera of both families, though Wesener (2015) found that *Angarozonium*, described as a polyzoziid, has an opening like a hirudisomatid. An additional character that seems to be reliable is the slight elevation of the posterior margins of the metazonites in hirudisomatids; in polyzoziids the margins are tightly appressed against the following tergite. For most of the genera and species in Siphonotidae, the condition of the pseudopenis character is unknown, but as

illustrated by Mauriès and Silva (1971) for Chilean species of *Siphonotus* it differs from either situation in the other two families. The second coxae are drawn out into long apophyses, at the tips of which are the openings of the *vasa deferentia*, without a distinct pseudopenis. As described above, this is also the situation in *Cylichnogaster lawrencei*.

According to Hoffman (1977), the following characters distinguish Siphonotidae: “the *vasa deferentia* open through conical lobes of the 2nd coxae; anal segment forms a complete ring around the paraprocts; ozopores are placed far in from lateral edge of metaterga; and tarsal claws are provided with long, prominent accessory structures.” The “coxal lobes” referred to are the long apophyses illustrated by Mauriès & Silva (1971).

In a key to North American polyzoniidan families, Shelley (1995) stated that siphonotids (he may have been referring just to *Rhinotus purpureus*, the only siphonotid found in North America) have tarsal claws with prominent, overhanging paronychialia. There is ambiguity about the term *paronychium*; to some authors it means a seta-like accessory claw, but to others it means an extension of the tarsus that overhangs the true claw. This may refer to what Hoffman (1977) called “accessory structures.” The claws of siphonotids I examined (*Rhinotus*, *Siphonotus*, *Cylichnogaster*) all have a long, sometimes sigmoid accessory claw situated at the base of the actual claw, and which exceeds the claw in length. The accessory claw is also illustrated by Mauriès & Silva (1971) and Golovatch (2014) for Chilean siphonotids. Further investigation of this character is warranted.

The character referring to the anal segment and the paraprocts (anal valves) may also be confusing, since Verhoeff (1937c) obviously considered only the paraprocts to comprise the “anal segment,” while what Hoffman (1977) and some others call the anal segment is called the “pre-anal segment” by Verhoeff, and his illustrations and discussion must be considered in that light. Parenthetically, the anal segment of Hoffman and other diplopodologists is also often referred to as the telson. In arthropods, the telson is post-anal and the anus is on the preceding segment. Here I refer to the last complete body segment as the “terminal segment” or epiproct, to avoid any confusion regarding its true nature. In *Cylichnogaster lawrencei* this character is hard to interpret because just behind the anal valves is a membranous area that extends to the posterior margin of the tergal part of the terminal segment (Fig. 5). Does the terminal segment “completely surround” the paraprocts or not? I think the question to be answered is whether or not any part of the telson, or “anal segment,” is fused *anterior* to the paraprocts, therefore forming a complete ring, and this appears to be the case in *C. lawrencei*.

It would seem that no further progress will be made on understanding the Siphonotidae until consensus is reached on the characters that can be used to distinguish the family from Polyzoniidae and Hirudisomatidae. This can only be done by examining the type material of the type species of all the genera proposed for inclusion by Hoffman (1977), as well as other material of putative siphonotids in museums. Fresh collections should be made to facilitate genetic studies.

Acknowledgements

Thanks to Gonzalo Giribet (Museum of Comparative Zoology) for sending the specimens on which this paper is based and for collecting notes. I am grateful to Dawn Larsen (Iziko South African Museum) for arranging the loan of the type specimens of *Cylichnogaster lawrencei*. Hans Reip, Thomas Wesener and Sergei Golovatch are thanked for providing important literature resources; thanks to Markus Koch for a discussion of the nature of the millipede terminal segment. The scanning electron micrographs were taken at East Carolina University, through the courtesy of Jason Bond. Comments by two anonymous reviewers markedly improved the manuscript. This research was supported by National Science Foundation Grant # DEB-1256139 to the author, Jason Bond, Petra Sierwald and Paul Marek, and by the Asa Kreevich Foundation.

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