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A pinhead millipede astray: a new polyzoniidan millipede from New Zealand in Great Britain and the genus *Siphonethus* Chamberlin, 1920 in New Zealand (Polyzoniida: Siphonotidae)

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ABSTRACT

Millipedes are slow-moving soil organisms, which do not easily disperse to new habitats. However, species can be transported by humans across large distances and be found in anthropogenic habitats like botanical gardens and glasshouses. Thus, several millipede species have been introduced from around the world to Europe. Here we describe three new species of pinhead millipedes (Polyzoniida): *Siphonethus dudleycookeorum* sp. nov. from Great Britain with close affinities to specimens from New Zealand, and *Siphonethus coxaespinosus* sp. nov. and *Siphonethus obtusus* sp. nov. from Tawhiti Rahi (Poor Knights Islands) from New Zealand. *Siphonethus dudleycookeorum* sp. nov. was initially discovered in Lamorran House Gardens (Cornwall) in Great Britain and could be traced back to New Zealand with DNA-barcoding and comparison to specimens from the New Zealand Arthropod Collection (NZAC). As generic as well as species characters of the Siphonotidae Cook, 1895 are only poorly worked out, the placement of the new species in the only New Zealand genus *Siphonethus* Chamberlin, 1920 is provisional. Based on the available material and photographs of the holotypes of *S. bellus* Chamberlin, 1920 and *S. enotatus* Chamberlin, 1920, we suggest that the species currently classified as *Siphonethus* belong to at least two separate genera. It can be expected that New Zealand harbours a great diversity of undescribed polyzoniidan millipedes, as a lot of unsorted specimens are present in various collections and already material from the relatively small island Tawhiti Rahi has yielded two species new to science.

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:6D3FF76F-16A2-43ED-B9CC-F34B4EBE7525>



<http://www.zoobank.org/urn:lsid:zoobank.org:act:F59D9647-6F25-448F-AD36-DE9F86F187D6>

<http://www.zoobank.org/urn:lsid:zoobank.org:act:A0718515-C5AE-4BE1-B32A-312FB66E9B5C>

<http://www.zoobank.org/urn:lsid:zoobank.org:act:3D4D8C0C-F30E-42B9-8CBD-E394C635FD87>

KEYWORDS

Alien; Colobognatha; endemism; gonopods; neozoa; Poor Knights Islands

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Introduction

Millipedes (Diplopoda) are relatively small and slow-moving animals, which are often burrowing, and restricted to the leaf litter or upper soil layers (Golovatch & Kime 2009). Therefore, they do not easily disperse to new localities. However, some species are known to be transported by human activity across the world and can be found in anthropogenic habitats. Several introduced tropical species are reported from European botanical gardens (Read 2007; Stoev et al. 2010; Decker et al. 2014; Gregory & Lugg 2020), such as the tramp species *Rhinotus purpureus* (Pocock, 1894), a representative of the taxonomically rather small millipede taxon Polyzoziida, which probably originated from the Neotropics (Shelley 2000) and is now distributed throughout the world (Sierwald & Bond 2007; Wesener 2014). The wide distribution of *Rhinotus purpureus* has led to the description of at least four genus- and several species-level synonyms (Millibase). Besides *R. purpureus*, the only other polyzoziidan millipede of the well-studied British millipede fauna is the native *Polyzozium germanicum* Brandt, 1837 (Blower 1985).

Polyzoziida (and Siphonocryptida) are distinct from other millipedes by their minute, conical heads, which bear only a few ommatidia, large antennae and reduced mouthparts (Moritz et al. 2022). As in all Colobognatha the 9th and 10th legs are modified in males for sperm transfer (gonopods). With less than 80 described species the Polyzoziida is one of the least diverse taxon within millipedes (Diplopoda), which comprise more than 12,000 described species (Enghoff et al. 2015). While the Polyzoziida is species poor in Europe (12 species, Kime & Enghoff 2011), the group seems to be more diverse but largely understudied in other parts of the world, such as Oceania, which holds various undescribed species. An unpublished dissertation lists for example 42 potential species in 8 genera for Australia alone (Marek et al. 2021). New Zealand is home to several endemic and introduced millipede species as summarized by Johns (1962) with 39 described species (Johns 1962; Korsós & Johns 2009). However, only two polyzoziidan millipedes of the family Siphonotidae Cook, 1895, *Siphonethus bellus* Chamberlin, 1920 and *Siphonethus enotatus* Chamberlin, 1920, are described from the North Island of New Zealand, but unsorted material from museum collections suggest that the group is quite diverse in New Zealand.

The family Siphonotidae comprises ca. 30 described species in 12 genera, which are mainly distributed in the tropics and southern hemisphere (South America, South Africa, Madagascar, SE Asia, and Oceania). The only millipede species with more than 1,000 legs belongs to the family (Marek et al. 2021). Siphonotidae are not well defined (see Shear 2016 for a discussion) and diagnostics for the family might be a combination of characters: the position of the male gonopore on the coxa of the 2nd leg, the presence of a long paronychium under the tarsal claw, posterior tergal margins which are not upturned, and a completely fused narrow preanal ring (Hoffman 1977; Enghoff et al. 2015); a character combination which supposedly differentiates them from the two other polyzoziidan families Polyzoziidae Newport, 1844 and Hirudisomatidae Silvestri 1896. The taxonomy and genus-specific characters in this group are only poorly worked out with many rather superficial descriptions (Hoffman 1977) and only few authors give detailed accounts on taxonomically important characters (e.g. Mauriès & Silva 1971; Golovatch 2014; Shear 2016; Marek et al. 2021). This is also true for the only New Zealand genus, *Siphonethus* Chamberlin, 1920, which is seen as problematic by Hoffman (1977) and is in urgent need of revisionary work. As the original description of the genus, based on two female specimens, no other *Siphonethus* species have been proposed, but several specimens assigned to the genus have been reported from New Zealand (Watt 1982; Derraik et al. 2001; Sinclair et al. 2005; Affeld et al. 2009). The original descriptions of *S. enotatus* and *S. bellus* by Chamberlin (1920) lack illustrations and mainly include somatic characters like colouration, setation and the shape of the head, antennae and body-rings. However, the gonopods (legs modified for copulation in males), which are often highly specific and a main character to distinguish millipede species and higher taxa (e.g. Sierwald & Bond 2007), are not described (as both types are female). Therefore, a redescription of material from the type locality is urgently needed, including SEM images of the gonopods and molecular barcoding.

Here we describe three new species, which are provisionally placed in the genus *Siphonethus* for the reasons above: One species from Great Britain with close affinities to siphonotid millipedes from the island Tawhiti Rahi (New Zealand), and two species from the same island.

Material & methods:

Museum acronyms and abbreviations

MCZ - Museum of Comparative Zoology, Harvard, USA

NZAC - New Zealand Arthropod Collections, Manaaki Whenua, Landcare Research, Auckland, New Zealand

SEM - Scanning electron microscopy

ZFMK - Zoological Research Museum A. Koenig, LIB, Bonn, Germany

Material examined

Specimens of *Siphonethus dudleycookeorum* sp. nov. were collected by Steve Gregory in Lamorran House Gardens (Great Britain, Cornwall, St. Mawes, Lamorran House Gardens, SW 843331 / VC2) on 9th September 2020, and on 28th November 2021, fixed in 95% ethanol and are stored in the collection of the Zoological Research Museum A. Koenig (ZFMK, Bonn, Germany). Images of the holotypes of *Siphonethus bellus* Chamberlin, 1920 (MCZ4878) and *Siphonethus enotatus* Chamberlin, 1920 (MCZ4885), which are stored at the Museum of Comparative Zoology (MCZ, Harvard, USA) were provided by Laura Leibensperger; a loan was not possible due to restriction on international loans during the pandemic (COVID-19). Furthermore, we investigated specimens stored in the New Zealand Arthropod Collection (NZAC) from Tawhiti Rahi (Poor Knight Islands, New Zealand; *Siphonethus* aff. *dudleycookeorum*, *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov.) from a previous study by Watt (1982) and specimens from Little Barrier Island (New Zealand; *Siphonethus* sp.) from a study by Drummond et al. (2015).

Morphological investigation

Specimens were investigated using a Zeiss Discovery V12 stereo microscope.

For scanning electron microscopy specimens fixed in 95% or 75% ethanol were dehydrated in an ascending ethanol series and critical point dried using a Leica EM CPD 300. The specimens were mounted to SEM-stubs using conductive tape and sputtered with gold using the Cressington Sputter Coater 108auto. SEM images were obtained with a Zeiss Sigma 300 VP scanning electron microscope at the ZFMK.

Genetic analysis

A DNA barcode (Hebert et al. 2003) of the cytochrome *c* oxidase subunit 1 (CO1) gene was obtained for one female specimen of *Siphonethus dudleycookeorum* sp. nov. (ZFMK MYR10095; GenBank: ON023662) from Great Britain and two specimens of *Rhinotus purpureus* (the only member of the family known from Europe) from the Botanical Garden Bonn, Germany, using the COI JJ primer (Astrin & Stüben 2008). For DNA extraction muscle tissue from legs and body-rings was used. DNA extraction, amplification, and sequencing were done as outlined in previous studies (e.g. Wesener 2015). A BLAST search (Altschul et al. 1997) was performed for the DNA COI fragment. The BLAST search led to the discovery of two closely related specimens (<15% p-distance) from New Zealand, labeled as 'Pancrustacea sp.' and 'Mandibulata sp.' (Genbank accession numbers KP421754.1 and KP421302.1). All additional 18 Polyzoniida COI sequences from Genbank (12.2021) were downloaded and added to our dataset. These additional sequences only contained three species determined to genus- or species-level, *Eumillipes persephone*,

Table 1. CO1 sequences used in this study.

Species	GenBank	Voucher
<i>Siphonethus dudleycookeorum</i> sp. nov.	ON023662	ZFMK MYR10095
<i>Rhinotus purpureus</i>	ON023660	ZFMK MYR10127
<i>Rhinotus purpureus</i>	ON023661	
<i>Siphonethus</i> sp.	KP421754.1	NZAC03012795
<i>Siphonethus</i> sp.	KP421302.1	NZAC03011232
<i>Eumillipes persephone</i>	OK602741.1	T147101-MPE5068
Hirudisomatidae sp.	MG320829.1	BIOUG32546-G09
Hirudisomatidae sp.	MG321144.1	BIOUG32547-D08
Hirudisomatidae sp.	MG313136.1	BIOUG24236-C02
Hirudisomatidae sp.	MG310535.1	BIOUG24236-C01
Hirudisomatidae sp.	MF748655.1	BIOUG08056-C03
Hirudisomatidae sp.	MF748591.1	BIOUG08056-C07
<i>Polyzonium germanicum</i>	KJ408479.1	ZFMK:MYR 1351
<i>Polyzonium germanicum</i>	KJ408478.1	ZFMK:MYR 1351
<i>Polyzonium germanicum</i>	JQ350463.1	BC ZSM MYR 00428
<i>Angarozonium aduncum</i>	MN232230.1	MPE03458
Polyzoniidae sp.	MG313496.1	BIOUG16675-B07
Polyzoniidae sp.	MF747336.1	BIOUG20657-F12
Polyzoniidae sp.	MF748857.1	BIOUG08056-A01
Polyzoniidae sp.	MF748772.1	BIOUG08056-A02
Polyzoniidae sp.	MF749827.1	BIOUG12147-H08
Polyzoniidae sp.	MF749315.1	BIOUG20666-C09
Polyzoniidae sp.	MF747063.1	BIOUG12147-H09

Polyzonium germanicum and *Angarozonium aduncum*, as well as several sequences determined to the family-level as Hirudisomatidae and Polyzoniidae.

Our sequences and those of the Polyzoniida from GenBank (Table 1) were aligned by hand in Bioedit (Hall 1999). Our total dataset contained 23 Polyzoniida sequences (Table 1) with 657 base pairs. The dataset was translated into amino-acids using the ‘invertebrate’ code in MEGA6 (Tamura et al. 2013) to rule out pseudogenes. All three new sequences were deposited in GenBank (see Table 1).

The number of base differences per site between sequences was calculated. The analysis involved 23 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All ambiguous positions were removed for each sequence pair. There were a total of 657 positions in the final dataset. Evolutionary analyses were conducted in MEGA6 (Tamura et al. 2013).

The best fitting substitution model for a maximum likelihood analysis was calculated with Modeltest (Tamura & Nei 1993) as implemented in MEGA6. Models with the lowest BIC scores (Bayesian Information Criterion) are considered to describe the substitution pattern the best (Nei & Kumar 2000). The best fitting model was the Hasegawa, Kinshino, Yano Model (Hasegawa et al. 1985) with gamma distribution and invariant sites (lnL = -3682.469, Invariant = 0.37586, Gamma = 0.82789, R = 3.158; Freq A: 0.28, T: 0.317, C: 0.24, G: 0.16). Phylogenetic analyses were performed in MEGA6 based on the Hasegawa, Kinshino, Yano Model (HKY + G+I). A species tree was constructed using maximum likelihood method with gamma distribution of five categories. The tree with the highest log likelihood (-3682.4690) is shown. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbour-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.8279)). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 37.5869% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 23 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All positions with less than 5% site coverage were eliminated. That is, fewer than 95% alignment gaps, missing data, and ambiguous bases were allowed at any position. There were a total of 657 positions in the final dataset. The bootstrap consensus tree was calculated

from 1000 replicates (Felsenstein 1985) in MEGA6 (Tamura et al. 2013). The obtained tree was edited in Adobe Illustrator CS2.

Results

Order Polyzoniida Newport, 1844

Family Siphonotidae Cook, 1895

Remarks: All investigated specimens can be placed in the family Siphonotidae based on the following character combination: Tarsus with paronychium, preanal ring narrow and forming a complete ring around paraprocts, male gonopore positioned on coxa of leg two, tergal margins not upturned.

Genus *Siphonethus* Chamberlin, 1920

Chamberlin, 1920: 99 (first description); Jeekel 1971: 44 (list).

Type species: *Siphonethus enotatus* Chamberlin, 1920

Other species included:

Siphonethus bellus Chamberlin, 1920

Siphonethus dudleycookeorum sp. nov.

Siphonethus coxaepinosus sp. nov.

Siphonethus obtusus sp. nov.

Remarks: The placement of the three new species in the genus *Siphonethus* is provisional. A re-description of *S. enotatus* (Figure 1) and *S. bellus* (Figure 2), based on fresh material from the type localities is urgently needed, including detailed descriptions of the gonopods and molecular analyses.

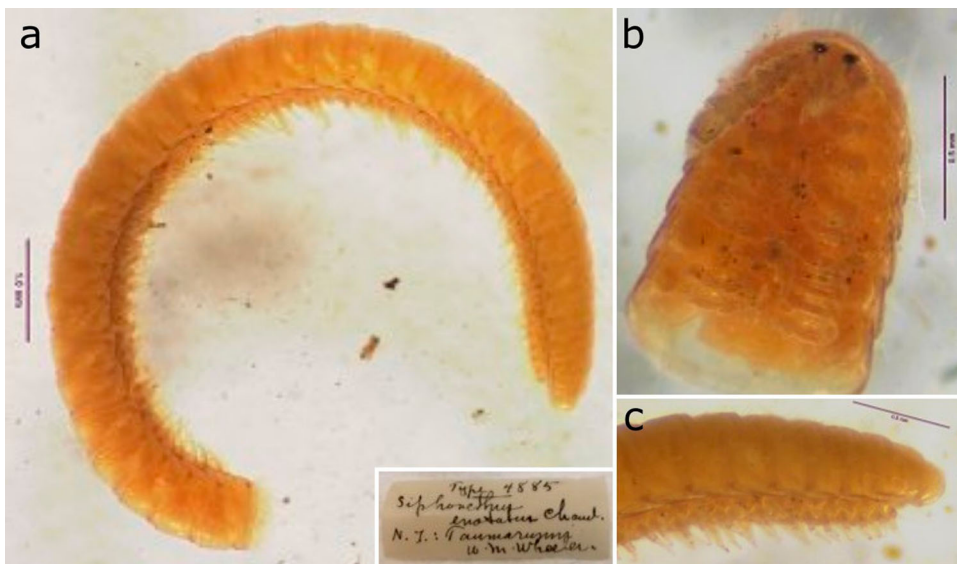


Figure 1. Holotype of *Siphonethus enotatus* Chamberlin, 1920 (MCZ4885), photographs by Laura Leibensperger (MCZ). (a) Habitus, lateral view. (b) Head and anterior body-rings, ventral view. (c) Preanal ring and posterior body-rings, lateral view.



Figure 2. Holotype of *Siphonethus bellus* Chamberlin, 1920 (MCZ4878), photographs by Laura Leibensperger (MCZ). (a) Habitus, lateral view. (b) Head and anterior body-rings, lateral view. (c) Preanal ring and posterior body-rings, lateral view.

We place the newly described species in the genus *Siphonethus* because this is the only Polyzoniida genus known from New Zealand, and based on the blast results of the specimens from Great Britain (with close morphological affinities to specimens from New Zealand), showing the best match for the specimens with unidentified ‘Mandibulata sp.’ (Sequence ID: KP421302.1; Voucher: NZAC 03011232) with 13.9% p-distances and ‘Pancrustacea sp.’ (Sequence ID: KP421754.1; Voucher: NZAC 03012785) with 14.3% p-distance. The latter two specimens are from Little Barrier Island (New Zealand) from a study by Drummond et al. (2015) and show a p-distance of 0.2% to one another. The short description of the genus by Chamberlin (1920: 99) does not allow an in-depth comparison of morphological characters. Chamberlin (1920: 99) states as diagnosis for the genus: ‘Distinguished from *Siphonotus* by having two ocelli on each side instead of one, and by having the head excavated on each side above for the reception of the antennae.’ We suggest to provisionally include all species from New Zealand in the genus *Siphonethus* until a detailed examination of the type material is possible.

Siphonethus dudleycookeorum sp. nov. shows distinct morphological differences to *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov., which might justify placing the species in two different genera (Table 2), but at the moment we hesitate to create a new genus, without revision of the holotypes and topotypic material of *S. enotatus* and *S. bellus* (which might not be congeneric either), to avoid creating further chaos in the group. As outlined below *S. dudleycookeorum* sp. nov. shows closer morphological similarities to *S. enotatus*, while *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov. show closer affinities to *S. bellus*.

Siphonethus enotatus Chamberlin, 1920

Chamberlin, 1920: 99 (first description). Jeekel 1971: 44 (list);

Original description (Chamberlin, 1920: 99): ‘Color uniform fulvoferruginous, or rather more ferruginous at anterior end, with collum, head and antennae somewhat dusky. Face below level of eyes

Table 2. Comparison of *Siphonethus* species. Information for *S. enotatus* and *S. bellus* taken from the original description (Chamberlin 1920) and inferred from photographs of types. *might be an artefacts due to preservation. Inverted commas ('...') indicate text directly quoted from Chamberlin (1920: 99). Question marks (?) indicate unknown character states.

	<i>S. enotatus</i> Chamberlin, 1920	<i>S. bellus</i> Chamberlin, 1920	<i>S. dudleycookeorum</i> sp. nov.	<i>S. coxaespinosus</i> sp. nov.	<i>S. obtusus</i> sp. nov.
Head (face anterior of antennae)	Acuminate 'sides nearly straight, inferior end acute' 'transversely depressed'	Stout 'sides convex, the lower end acutely rounded'	Acuminate, narrowing anterior of antennae, sides straight, anteriorly pointed	Stout, sides rounded, anteriorly rounded	Stout, sides rounded, anteriorly rounded
Head transverse depression	'Face transversely depressed or furrowed at lower level of antennal notches'	No depression	Distinct depression	No depression	No depression
Labrum	?	?	Sculptured	Not sculptured	Not sculptured
Head (Antennal insertion)	Deeply excavated	?	Deeply excavated	Moderately excavated	Moderately excavated
Ommatidia	2	2	2	2	2
Macrosetae position	?	?	Anterior of ommatidia	Between ommatidia	Between ommatidia
Antennae	'Cylindrical, enlarging distad', long	'Stout, moderately clavate'	Cylindrical, long, enlarging distally	Stout, moderately clavate	Stout, moderately clavate
Hairs on body	'moderately long, sparsely and nearly uniformly distributed'	'nearly glabrous, the hairs few'	Dense, long	Few, short	Dense, long
Rectangular structure on metazonite	?	?	Present	Present	Present
Ozopores	?	?	Not elevated	Not elevated	Elevated
Number of tergites	49	36	35–43	10–41	26–28
Coxal process	?	?	Absent	Present	Absent
Paronychium on anterior legs	?	?	Cylindrical, long	Flat, long	Cylindrical long
Penes*	?	?	Cylindrical	Fanned	Fanned
Anterior gonopod	?	?	6 podomeres	5 podomeres	5 podomeres
Posterior gonopod	?	?	6 podomeres	6 podomeres	6 podomeres
Colour*	Uniform	Longitudinal stripes	Uniform with darker tergite margins	Whitish pale	Whitish pale

broadly triangular, sides nearly straight, inferior end acute. Ocelli on mesodorsal side of antennal socket, two in number on each side of which the upper one is the smaller. Head rather deeply excavated on each side for insertion or reception of antennae. Antennae cylindrical, enlarging distad, the lower end of face reaching to near middle of fourth article. Face transversely depressed or furrowed at lower level of antennal notches.

Collum three times as wide as the head. Body hemicylindrical. Each segment transversely furrowed or constricted. Hairs of body moderately long, sparsely and nearly uniformly distributed. Number of segments, forty-nine. Width, 0.93 mm.'

Material examined (based on photographs, Figure 1): Holotype: Female (MCZ4885), NEW ZEALAND, Taumarunui ('Taumarunni' in Chamberlin (1920: 99)), leg. W.M. Wheeler.

Remarks: The type species of the genus *Siphonethus*, *Siphonethus enotatus* is of uniform orange-brown colouration (Figure 1a) and has a rather pointed head and longer cylindrical antennae (Figure 1b) similar to *S. dudleycookeorum* sp. nov., and is densely covered by long setae (Table 2). Gonopod characters are unknown as the type is a female specimen.

Siphonethus bellus Chamberlin, 1920

Chamberlin, 1920: 99 (first description).

Original description (Chamberlin, 1920: 99): 'Distinguished readily by its colour-pattern. The general color yellow with a median dorsal longitudinal black line and a broader but still narrow submarginal black stripe on each side, a small yellow dot enclosed in the black of the latter on each segment. Collum, face, and antennae dusky. Legs fulvous. Antennae stout, moderately clavate; reaching to caudal edge of second tergite. Face below antennae triangular, the sides convex, the lower end acutely rounded. Each segment constricted across middle, the furrow with longitudinal striae. Body of type nearly glabrous, the hairs few. Number of segments, thirty-six. Width, .92 mm.'

Material examined (based on photographs, Figure 2): Holotype: Female (MCZ4878), NEW ZEALAND, Day's Bay, near Wellington, leg. W.M. Wheeler.



Figure 3. Habitat of *Siphonethus dudleycookeorum* sp. nov. in Lamorran House Gardens (Great Britain, Cornwall), photographs by S. J. Gregory. (a) Path lined by planted tree ferns from New Zealand. (b) *Siphonethus dudleycookeorum* sp. nov.

Remarks: The second species currently placed in *Siphonethus*, *S. bellus* shows longitudinal stripes (Figure 2a) similar to *Burinia* Attems, 1926 from South America and South Africa (Golovatch 2014) and several undescribed species from New Zealand. *S. bellus* has an apically rounded and stouter head (Figure 2b) than *S. enotatus*, with stouter clavate antennae similar to *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov., and its body is covered by few shorter setae similar to *S. coxaespinosus* sp. nov. (Table 2). Based on these characters, we suspect that *S. bellus* is not a *Siphonethus* but might represent a second native genus of Siphonotidae present in New Zealand, to which also *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov. may belong. Gonopod characters are unknown as the type is a female specimen.

***Siphonethus dudleycookeorum* sp. nov.**

Figures 3–7

Material examined: Holotype: Male (ZFMK-MYR11376), GREAT BRITAIN, Cornwall, St. Mawes, Lamorran House Gardens, SW 843331/ VC2, Lat 50.158535 Lon -5.0199108, 09.ix.2020, leg. S.J. Gregory; In soil under tree ferns and beneath cut stems lying on the ground of tree ferns from New Zealand (NZ) and Australia (AU) (*Cyathea dealbata* (NZ), *Australis smithii* (AU, introduced to NZ), *Sphaeropteris medullaris* (NZ), *Dicksonia antarctica* (AU), *D. squarrosa* (NZ), *D. fibrosa* (NZ)) (Figure 3a). Paratypes: 3 females (ZFMK-MYR10094, ZFMK-MYR10095, ZFMK-MYR11377) same data as holotype. Paratypes: Male (ZFMK-MYR11433) 14 Females (ZFMK-MYR11419 – ZFMK-MYR11432), same location as holotype, 28.xi.2021.

Etymology: The species name dudleycookeorum honours Robert and Maria-Antoinette Dudley-Cooke, who own and manage Lamorran House Gardens, the type locality of the species, and who allowed Steve J. Gregory to collect there. Noun in apposition.

Diagnosis: Two pairs of ommatidia and mesal rectangular structure on anterior margin of metazonite are present as in *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov.. Differs from



Figure 4. *Siphonethus dudleycookeorum* sp. nov. from Lamorran House Gardens (Great Britain, Cornwall), female. (a) Habitus, lateral view. (b) Anterior body rings, dorsal view. (c) Midbody-rings dorsal view.

S. coxaespinosus sp. nov. and *S. obtusus* sp. nov. by a more pointed head, which tapers strongly anterior of the antennae (as in *S. enotatus*), with a transverse depression, a unique sculptured labrum, and the position of the macrosetae anterior of the ommatidia (opposed to between ommatidia in *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov.). Differs from *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov. by the shape of the apical podomere of the gonopod, which is divided into two lobes of which the outer lobe carries a conspicuous curved spine. Differs from *S. coxaespinosus* sp. nov. by longer setation and the absence of coxal projections.

Description

Colouration of specimens freshly fixed in ethanol: Brownish-orange overall colour (Figures 3b, 4a). Collum with a single median white field and a pair of large lateral white fields (Figure 4b). Tergites anteriorly and posterior margin brownish-orange, purple transverse band in between. Medially the margin of the purple band is incised (v-shape). Tergites laterally with pair of white fields in purple area (Figure 4b, c).

Measurements: Ca. 10 times as long as wide. Length: 9 mm, Width: 0.8-0.9 mm. up to 43 tergites + preanal ring and 78 leg pairs.

Head: Head small, long, conical. The head capsule is slightly excavated and tapers anterior of the antennal base (Figure 5a, b). Labrum split longitudinally, posteriorly delimited by transverse fold resulting in a t-shaped or triangular field. Margin of labrum sculptured with tubercles, which are prominent anteriorly and flatten laterally, mesally two pairs of longer tubercles. On each side dorsally of the labral sculptures lies a single row of up to 12 cones, which are sunken into pits (Figure 5c). Two pairs of ommatidia, one lateral posterior pair and one pair positioned mesal and slightly anterior of the other. One pair of macrosetae mesally of the anterior pair of ommatidia. Head covered by few setae (ca. 30) anterior of ommatidia. Mandibles not visible externally (Figure 5b), except for posterior margin of mandibular cardo in ventral view (Figure 5d).

Gnathochilarium: A pointed triangular plate, with anterior incision, creating two apical areas (remnants of stipites?), which are not fully divided from remaining gnathochilarium. Apically with two pairs of small setae (rudimental palps?). The gnathochilarium is covered by few setae, especially well developed at its lateral margins (Figure 5d).

Antennae: Antennae stout ca. twice as long as head, with 7 antennomeres, covered by setae arranged in rows. Antennomeres 1–5 and 7 wider than long, antennomere 6 longest, ca. as wide as long (Figure 5e). Apical margin of antennomere 5 and 6 with a row of sensilla basiconica, 3 or 4 on 5th, 5 on 6th. Apical (7th) antennomere with a marginal row of 12 sensilla, which are swollen in their middle. Apical disc with 4 sensory cones (Figure 5f, g).

Collum: Collum large, concealing posterior part of head and posterior pair of ommatidia from above, ca. twice as long as following body-ring. Posterior margin nearly straight in dorsal view, only slightly rounded. Covered by setae (Figures 4b, 5a).

Body-rings: Up to 43 tergites + preanal ring. Body-rings semi-circular in cross section, tergites well separated from pleurites and sternites. Tergites with distinct transverse division into pro- and metazonite, few longitudinal short striae on metazonite along division. Prozonite length ca. 1/3 of body-ring, anterior margin with net-like ornamentation. Metazonite with three more or less regular transverse rows of setae (Figure 6a). Metazonite mesally at anterior margin with small demarcated rectangular area, which flattens out posteriorly (Figure 6b). Ozopores starting from body-ring 5 on metazonite in some distance from lateral margin of tergite, surrounded by an inconspicuous rim (Figure 6a, c). Sternites carrying tracheal opening lateral of legs from leg-pair 3 onwards, slightly

elevated (Figure 6c), tracheal opening also present lateral of the gonopods. Last body-ring anterior of preanal ring apodous, pleurites overlapping (Figure 6c, d).

Preanal ring: Preanal ring narrow cylindrical, forming completely fused ring around paraprocts (anal valves). Covered by 3 rows of particularly long setae. Paraprocts free of setae (Figure 6c, d).

Legs: Up to 78 leg pairs (female). Leg 1 and 2 with 6 podomeres, from leg 3 onwards 7 podomeres (with short trochanter) (Figure 6e). 1st leg pair slightly smaller than following legs. Coxa carrying eversible sacs (coxal pouches) from leg pair 3 onwards, except for ultimate leg pairs. Tarsus long narrow with apical claw and cylindrical paronychium, paronychium longer than claw (Figure 6f).

Male sexual characters: Male gonopore positioned on coxa of leg pair 2, on an elongated lobe (gonapophysis or pseudopenis) (Figure 7a). Leg pairs 9 and 10 modified to well-developed leg-like gonopods (Figure 7b–f).

Anterior gonopod consisting of 6 podomeres (segmentation not visible in all views). Podomere 3 largest, ca. as long as podomere 4 + 5. Podomeres 1–5 with few setae (Figure 7b–d). Apical podomere (6) strongly modified, apically divided into two lobes, an outer lobe and an inner lobe. The outer lobe is triangular in shape and carries laterally a long pointed spine, which bends inwards towards the inner lobe. At base of outer lobe a group of 4 setae. Inner lobe apically and mesally rounded, lateral margin straight (Figure 7e, f). Inner side of apical podomere incised by groove/fold, extending along its whole length and along inner margin of inner lobe. Within fold lies apical portion of posterior gonopod's apical podomere, engulfed by anterior gonopod (Figure 7d). Inner side of apical podomere base with a group of prominent setae, posterior of mesal groove/fold. Sternite carrying anterior gonopod with a pair of swellings medially of gonopods, each carrying a group of setae.

Posterior gonopod leg-like, consisting of 6 podomeres. Podomeres 1 and 2 minute, ca. half as long as podomere 4. Podomere 3 as long as podomere 4 + 5. Podomere 6 longest, ca. 1.5 times as long as remaining posterior gonopod. Apical podomere (6) elongated and narrows anteriorly, tip hollow. Apical podomere lies within fold formed by anterior gonopod, surpassing anterior gonopod. Posterior gonopod devoid of setae (Figure 7c, d).

Female sexual character: Coxae of second leg pair free, not touching each other. Female gonopores on coxae of second leg pair, small circular, no division visible.

Remarks: Very similar to NZAC03038958 (Figure 8) from Poor Knights Islands. Shares with *Siphonethus enotatus* Chamberlin, 1920 a pointed acuminate head, cylindrical long antennae, moderately long and dense setae on the body.

Siphonethus aff. *dudleycookeorum* sp. nov.

Figures 8 & 9

Material examined: 7 males, 2 females, 5 juveniles (NZAC03038958), NEW ZEALAND, Poor Knights Island, Tawhiti Rahi, 5.xii.1980, leg. G. Kuschel. Sifted decayed wood & litter on plateau 80/136.

Remarks: These specimens resemble *Siphonethus dudleycookeorum* sp. nov. from Great Britain in their shape of the head (Figures 8a, b, 9a), the sculpture of the labrum (Figure 8c), in setation (Figures 8–9d, e, 9a), and in the structure and shape of the gonopods (Figure 8 g). The specimens differ slightly from *S. dudleycookeorum* sp. nov. in the proportions of the anterior gonopod's apical lobes, although little is known about intraspecific variation within Colobognatha. Furthermore, some of the specimens from New Zealand show darker longitudinal lateral stripes

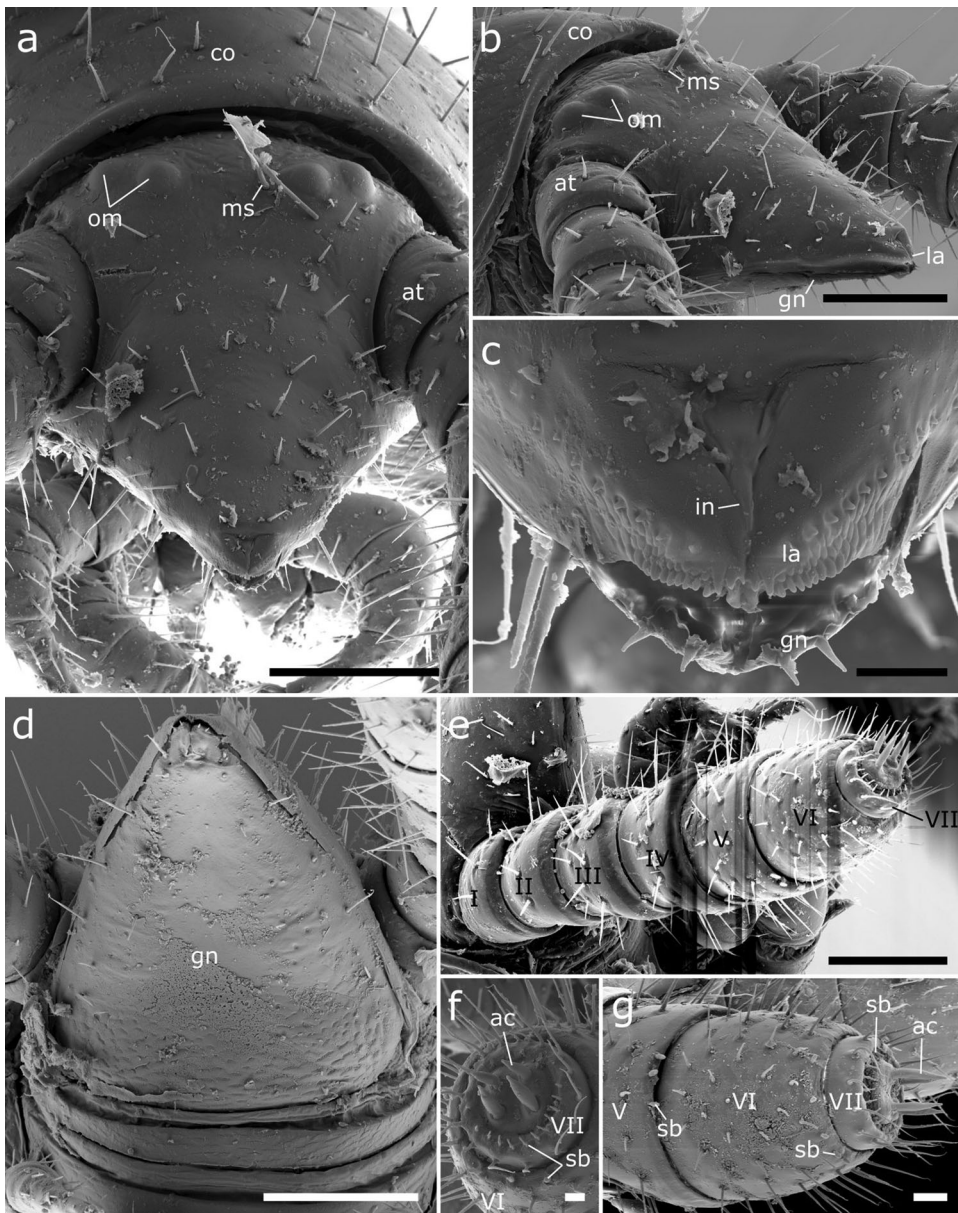


Figure 5. *Siphonethus dudleycookeorum* sp. nov., male holotype (ZFMK-MYR11376) from Great Britain, head, SEM images. **(a)** Head, frontal view. **(b)** Head, lateral view. **(c)** Detail of labrum. **(d)** Gnathochilarium. **(e)** Antennae, overview. **(f)** Antennae apical antennomeres, apical view. **(g)** Antennae apical antennomeres, lateral view. **Scale:** a, b, d, e = 100 μ m, c, f = 10 μ m, g = 20 μ m. **Abbreviations:** I-VII = antennomere 1-7, ac = apical cones, at = antennae; co = collum, gn = gnathochilarium, in = incision of labrum, la = labrum, ms = macrosetae, om = ommatidia, sb = sensilla basiconica.

differing from the colour pattern of *S. dudleycookeorum* sp. nov., although this might be the results of colour fading in ethanol. However, no genetic barcodes could be obtained and taxonomic characters as well as inter- and intraspecific variations are only poorly understood for the Siphonotidae. Therefore, we currently hesitate to view these specimens as identical to *S. dudleycookeorum* sp. nov..

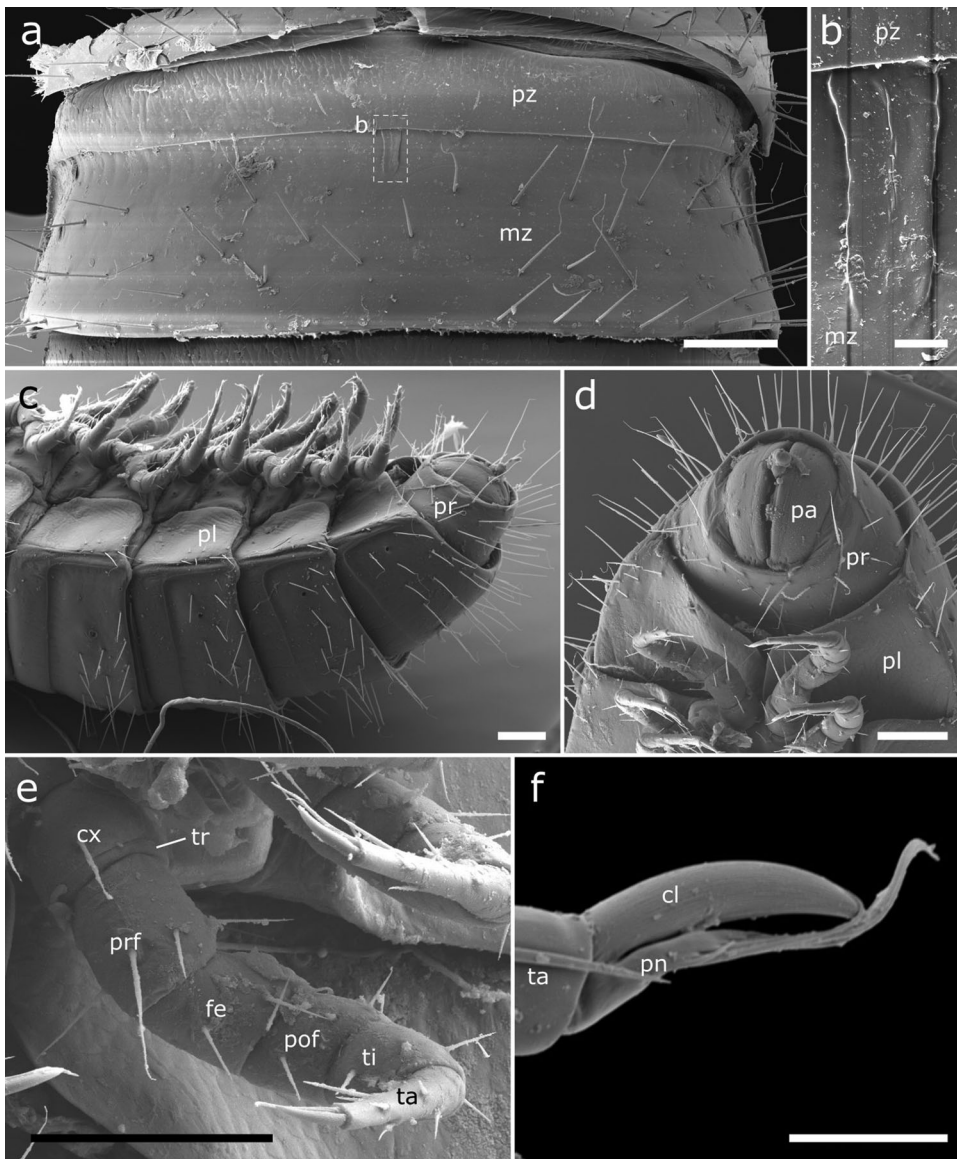


Figure 6. *Siphonethus dudleycookeorum* sp. nov., female paratype (ZFMK-MYR10094; a-e) and male holotype (ZFMK-MYR11376; f) from Great Britain, body-rings and legs, SEM images. **(a)** Body-ring, dorsal view. **(b)** Details (mesal rectangular structure) of (a). **(c)** Posterior body-rings and preanal ring, lateral view. **(d)** Posterior body-rings and preanal ring, ventral view. **(e)** Ultimate walking leg. **(f)** Detail of claw with paronychium. **Scale:** a, c-e = 100 μ m, b = 10 μ m, f = 20 μ m. **Abbreviations:** cl = claw, cx = coxa, fe = femur, mz = metauonite, oz = ozopore, pa = paraprost, pof = postfemur, pl = pleurite, pn = paronychium, pr = preanal ring, prf = prefemur, ta = tarsus, ti = tibia, tr = trochanter.

Siphonethus coxaespinosus sp. nov.

Figures 10–13

Material examined: Holotype: Male (NZAC03038955), NEW ZEALAND, Poor Knights Is., Tawhiti Rahi, Shag Bay, 30 m, 12.ix.1980, leg. J.C. Watt, Litter 80/72. Paratypes: 22 females, 16 males, 18 juveniles, same data as holotype.

Paratypes: 5 males, 7 immature males, 1 female, 12 juveniles (NZAC03038954), NEW ZEALAND, Poor Knights Island, Tawhiti Rahi, Shag Bay, 40 m, 12.ix.1980, leg. J.C. Watt, Litter 80/73.

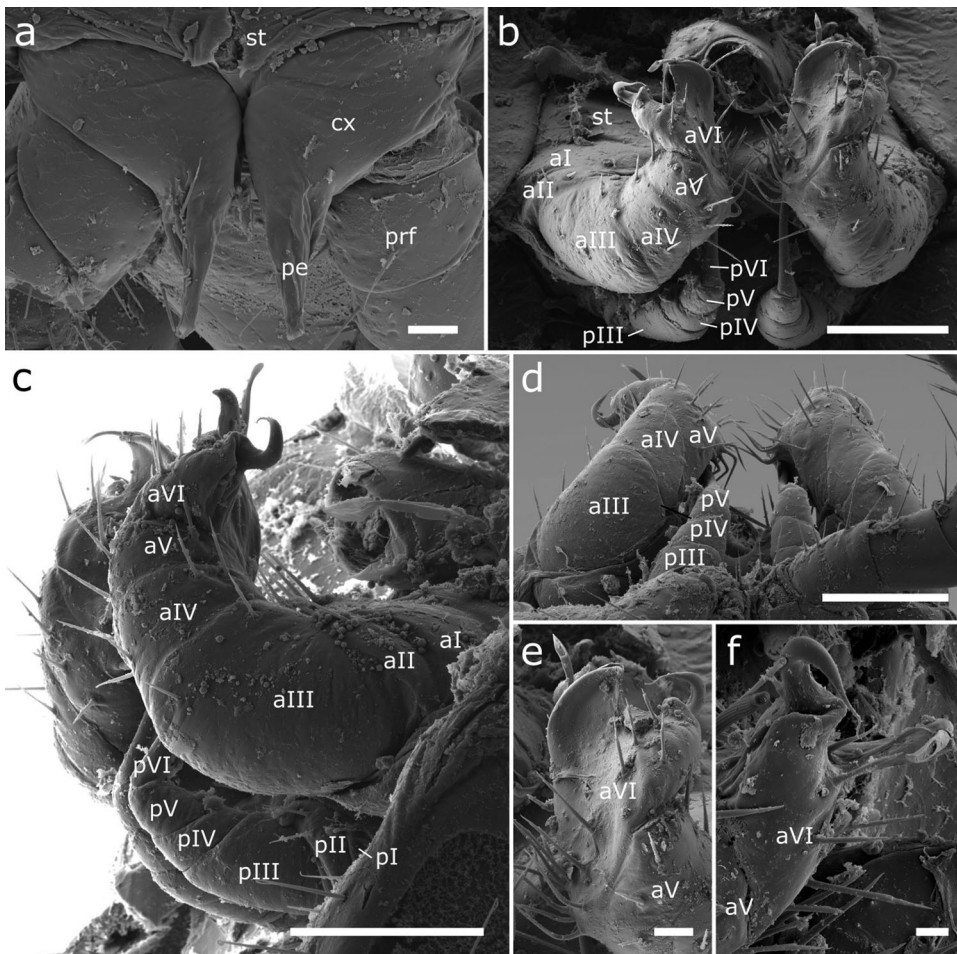


Figure 7. *Siphonethus dudleycookeorum* sp. nov., male holotype (ZFMK-MYR11376) from Great Britain, male sexual characters, SEM images. **(a)** Leg pair 2 with penes. **(b)** Gonopods, ventral view. **(c)** Gonopods, lateral view. **(d)** Gonopods posterior view. **(e & f)** detail of anterior gonopod apical podomeres. **Scale:** a = 20 μ m, b-d = 100 μ m, e = 20, f = 10 μ m. **Abbreviations:** al-aVI = podomeres of anterior gonopod, cx = coxa, pe = penis, pl-pVI = podomeres of posterior gonopod, prf = prefemur, st = sternite.

Etymology: The species name *coxae-spinosus* is derived from the latin *coxae* = hips and *spinose* = thorny, and refers to the characteristic spine on the coxae of the male specimens. Noun in apposition.

Diagnoses: In *S. coxae-spinosus* sp. nov. two pairs of ommatidia and mesal rectangular structure on anterior margin of metazonite are present similar to *S. dudleycookeorum* sp. nov. and *S. obtusus* sp. nov.. Differs from *Siphonethus dudleycookeorum* sp. nov. and *S. obtusus* sp. nov. by the shorter setation on the body-rings and head. Shares with *S. obtusus* sp. nov. a single marginal row of setae on the pleurites, a head, which is stouter than in *S. dudleycookeorum* sp. nov., a labrum lacking sculpture, and the position of the macrosetae between the ommatidia (opposed to anterior of ommatidia). The apical podomere of the anterior gonopod differs from *S. dudleycookeorum* sp. nov. in its shape, it is not divided into two lobes, and by the absence of the lateral curved spine. *S. coxae-spinosus* sp. nov. differs from *S. dudleycookeorum* sp. nov. and *S. obtusus* sp. nov. by the presence of setae which carry apically a brush of spines on the anterior gonopods, the presence

of well-developed paired protuberances on the anterior gonopod's sternite, and by the presence of coxal projections in males, as well as flattened paronychchia on the anterior legs. In females coxae of leg-pair 2 fused and sternite fused to syncoxosternite, vulvae opening behind syncoxosternite.

Description

Colouration in ethanol: Specimens are pale, whitish and no colour pattern could be observed (Figure 10).

Measurements: Length: 8 mm, Width: 0.5 mm. Up to 41 tergites + preanal ring and 75 leg-pairs (18 juv (10–16 T), 22f (18–26 T), 16 m (18–28 T); Up to 41 tergites and 75 leg pairs (5M (24, 31, 36, 41, 41 T), 1F (25 T). Several juveniles and immature males with 10–18 tergites (Figure 10a).

Head: Head conical, stout (Figure 11a, b). Labrum rounded, split longitudinally with triangular field. Margin of labrum not sculptured, lined by a row of setae (Figure 11c). Two pairs of ommatidia. One pair of macrosetae mesally of ommatidia. Head covered by few setae anterior of ommatidia. Mandibles not visible externally (Figure 11b).

Gnathochilarium: Stout triangular plate, which is longitudinally incised anteriorly. Apically with two pairs of setae (rudimentary palps?). Covered by few setae, longest along margin (Figure 11d).

Antennae: Antennae consisting of 7 antennomeres, covered by setae arranged in row. Antennomeres wider than long, antennomere 6 longest, antennomere 4 and 5 widest. Sensilla basiconica in row on antennomere 5-7. Apical disc with 4 sensory cones (Figure 11e).

Collum: Collum large, saddle shaped, concealing posterior part of head, reaching to posterior ommatidia. Ca. twice as long and as wide as following tergites. Covered by setae (Figure 11a).

Body-rings: Up to 41 tergites + preanal ring. Body-rings semicircular, tergites well separated from pleurites and sternites. Tergites divided into prozonite and metazonite with distinct margin. Metazonite with faint longitudinal lines on anterior margin (Figure 12a) and mesal rectangular structure (Figure 12b). Metazonite with short setae arranged in 3 more or less regular rows. Ozopores starting on body-ring 5, laterally on metazonite with inconspicuous rim, not elevated (Figure 12a). Pleurites almost rectangular, with lateral marginal row of setae. Sternites carrying tracheal openings lateral of legs from leg 3 onwards, slightly elevated, tracheal opening also present lateral of the gonopods. Last body-ring anterior of preanal ring apodous, pleurites overlapping (Figure 12c).

Preanal ring: Preanal ring narrow cylindrical, forming completely fused ring around paraprocts. Paraprocts surrounded by row of setae, longer setae dorsally, shorter setae ventrally. Paraprocts free of setae (Figure 12c).

Legs: Up to 75 leg pairs. Leg 1 and 2 with 6 podomeres, from leg 3 onwards 7 podomeres (with short trochanter). 1st leg slightly smaller than following. Coxa carrying eversible sacs (coxal pouches) from leg pair 3 onwards, except for ultimate leg pairs (Figures 11–12c–e). Coxa with anteriad projection, most conspicuous on coxa of 2nd leg in males (Figures 12–13), not visible on posterior leg-pairs (Figures 12c). Tarsus long narrow with apical claw and paronychium, which is longer than the claw. Paronychium of anterior legs flattened (spatulate?) (Figure 12d), paronychium of posterior legs cylindrical (Figure 12e).

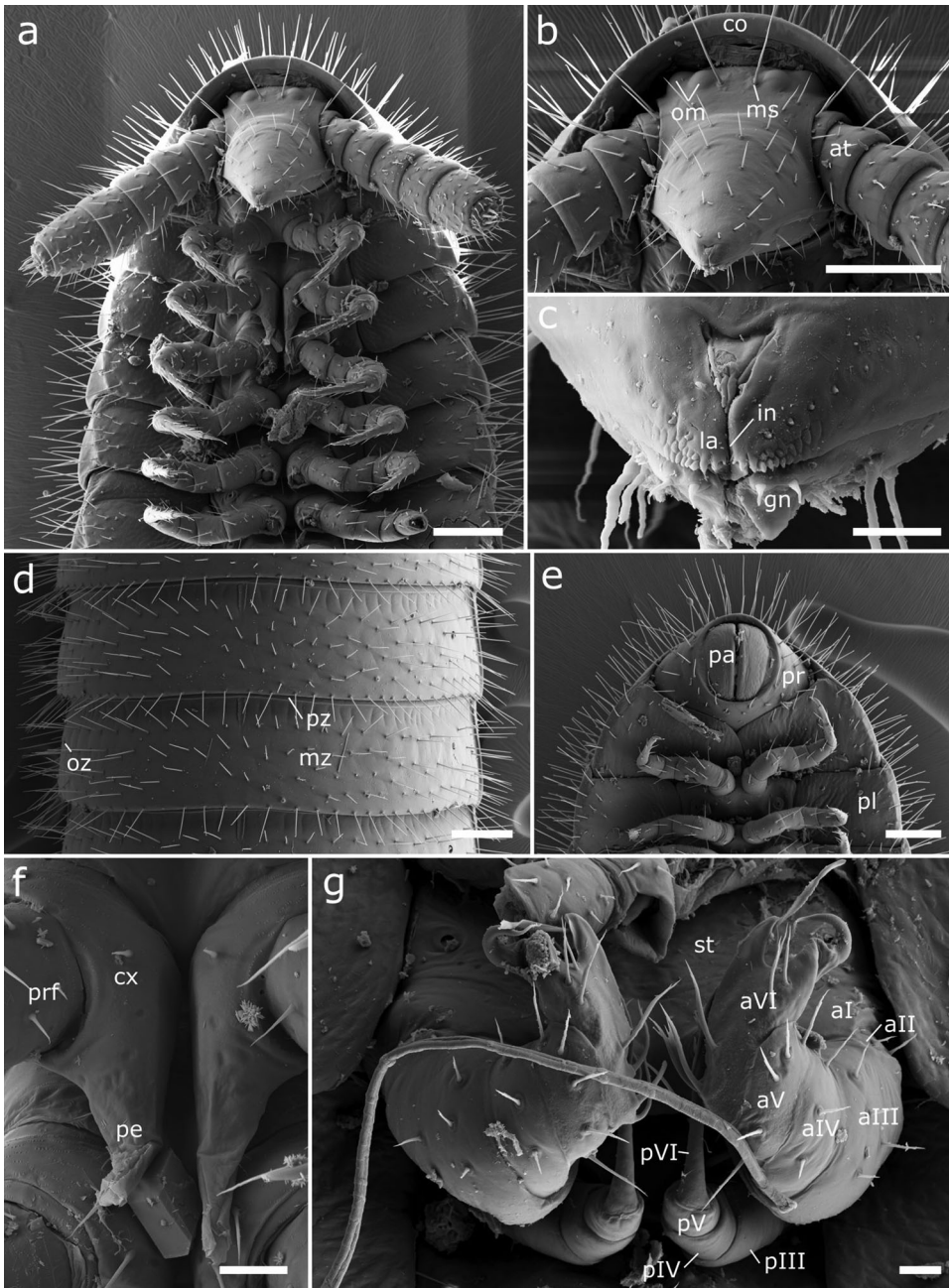


Figure 8. *Siphonethus* aff. *dudleycookeorum* sp. nov. (NZAC03038958), male, from New Zealand, SEM images. (a) Anterior body, ventral view. (b) Head, frontal view. (c) Detail of labrum. (d) Mid body-ring, dorsal view. (e) Posterior body-rings and preanal ring, ventral view. (f) Leg pair 2 with penes, ventral view. (g) Gonopods, ventral view. **Scale:** a, b, d, e = 100 μ m, c = 10 μ m, f, g = 20 μ m. **Abbreviations:** al-aVI = podomeres of anterior gonopod, at = antennae, co = collum, cx = coxa, gn = gnathochilarium, in = incision of labrum, la = labrum, ms = macrosetae, mz = metazonite, om = ommatidia, oz = ozopore, pa = paraproct, pe = penis, pl-pVI = podomeres of posterior gonopod, pl = pleurite, pr = preanal ring, pz = prozonite.

Male sexual characters: Male gonopore positioned on coxa of leg pair 2, on an elongated laterally flattened lobe (gonapophysis or pseudopenis). Coxa 2 carries a conspicuous projection anterior of penis (Figure 13a). Leg pairs 9 and 10 modified into well-developed gonopods (Figure 13b-e).

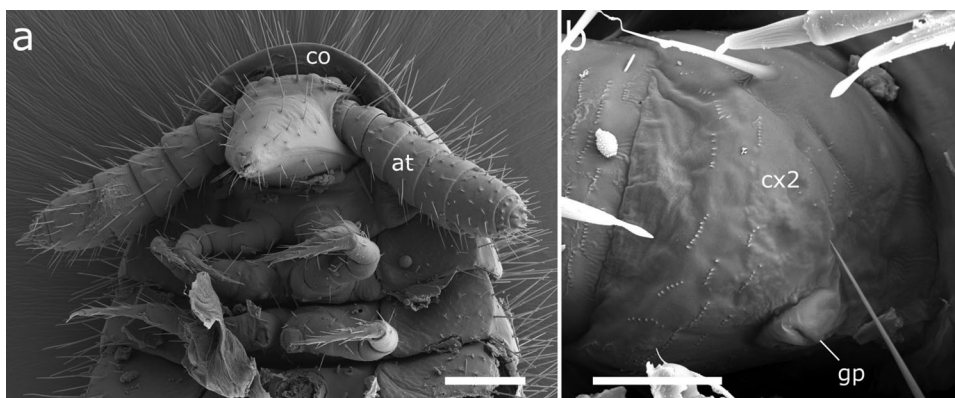


Figure 9. *Siphonethus* aff. *dudleycookeorum* sp. nov. (NZAC03038958), female, from New Zealand, SEM images. **(a)** Anterior body, ventral view. **(b)** Coxa of leg 2 with gonopore. **Scale:** a = 100 μ m, b = 20 μ m. **Abbreviations:** at = antennae, co = collum, cx = coxa, gp = gonopore.

Anterior gonopod consisting of 5 podomeres (segmentation barely visible even in SEM images), covered by setae. Podomere 3 and 4 with apical row of setae (Figures 13b–d). Podomere 5 extends in apical lobe, in which apical podomere of posterior gonopod rest. Base of lobe with 13–15 long setae, carrying spines, which form a brush- or cone-like structure terminally on outer setae, in apical third on inner setae (Figure 13e).

Posterior gonopod leg-like, consisting of 6 podomeres, apical podomere (6) extending into long, flattened and twisted flagellum, which rests in lobe of anterior gonopod and extends beyond it (Figure 13b, c).

Sternites anterior of anterior gonopod carry paired conspicuous projections, covered by spines and almost as large as anterior gonopod (Figure 13d).

Female sexual characters: Second coxae and sternite fused to syncoxosternite. Female gonopore (vulva) positioned behind syncoxosternite behind leg 2, cone-shaped, divided by furrow. Second leg consisting of 5 podomeres. Apical podomere of leg-pair 2 a third as long as tarsi on remaining legs, lacking a claw (Figure 13f).

Siphonethus obtusus sp. nov.

Figure 14–17

Material examined: Holotype: Male (NZAC03038954), NEW ZEALAND, Poor Knights Island, Tawhiti Rahi, Shag Bay, 40 m, 12.ix.1980, leg. J.C. Watt, Litter 80/73. Paratypes: 3 males, 1 female.

Etymology: The species name *obtusus* is derived from the Latin word *obtusus* = obtuse/blunt, and refers to the obtuse head of the species compared to the pointed head of many other Siphonotidae. Noun in apposition.

Diagnoses: *S. obtusus* sp. nov. differs from *S. dudleycookeorum* sp. nov. and *S. coxaespinosus* sp. nov. by the presence of elevated ozopores. Differs from *S. dudleycookeorum* sp. nov. by a stouter head, which lacks a sculptured labrum, as in *S. coxaespinosus* sp. nov.. *S. obtusus* sp. nov. differs from *S. dudleycookeorum* sp. nov. and *S. coxaespinosus* sp. nov. by the shape of the apical podomere of the anterior gonopod, this carries a mesal lobe covered by spines on the apical podomere. Differs from *S. coxaespinosus* sp. nov. by the absence of sternal protuberances behind the gonopods, the absence of special setae on the apical podomeres of the anterior gonopod and the absence of coxal protuberances.

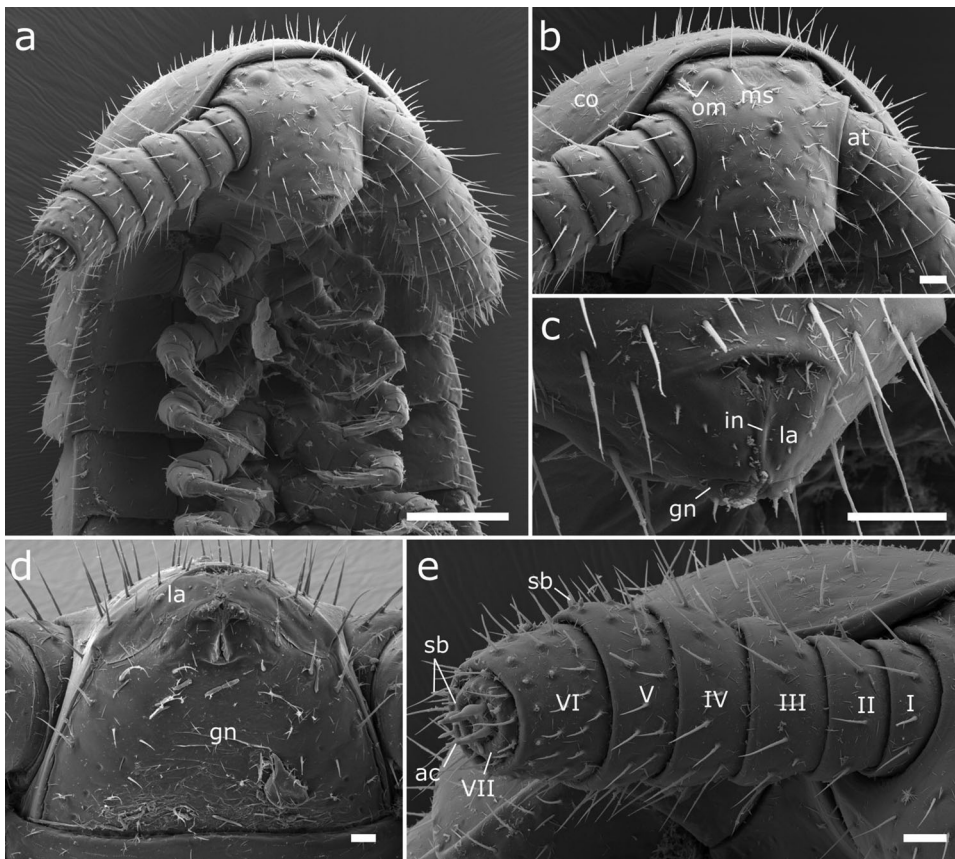


Figure 11. *Siphonethus coxaespinosus* sp. nov. (NZAC03038955) from New Zealand, male, SEM images. (a) Anterior body, ventral view. (b) Head, frontal view. (c) Detail of labrum. (d) Gnathochilarium, ventral view. (e) Antennae. **Scale:** a = 100 μm , b, c, e = 20 μm , d = 10 μm . **Abbreviations:** I-VII = antennomere 1-7, ac = apical cones, at = antennae; co = collum, gn = gnathochilarium, in = incision of labrum, la = labrum, ms = macrosetae, om = ommatidia sb = sensilla basiconica.

Body-rings: Up to 28 tergites + preanal ring. Body-rings semicircular, tergites well separated from pleurites and sternites. Tergites divided into prozonite and metazonite with distinct margin. Metazonite with faint longitudinal lines on anterior margin (Figure 16a) and mesal rectangular structure (Figure 16b). Metazonite with long setae arranged in 5 irregular rows. Ozopores starting on body-ring 5, laterally on metazonite, slightly elevated (Figure 16a). Pleurites almost rectangular, with lateral marginal row of setae (Figures 15a, 16c). Sternites carrying tracheal openings lateral of legs, also present lateral of the gonopods. Last body-ring anterior of anal ring apodous, pleurites overlapping.

Preanal ring: Preanal ring narrow cylindrical, forming completely fused ring around paraprocts. Covered by long setae, setae shorter ventrally of paraproct. Paraproct devoid of setae (Figure 16c).

Legs: Up to 46 leg pairs. Leg 1 and 2 with 6 podomeres, from leg 3 onwards 7 podomeres (with trochanter). 1st leg pair slightly smaller than following legs, but not reduced in segmentation. Coxa carrying eversible sacs (coxal pouches) from leg pair 3 onwards (Figure 15a), except for ultimate leg pairs. Tarsus long and narrow with apical claw and paronychium, paronychium ca. twice as long as claw (Figure 16d).

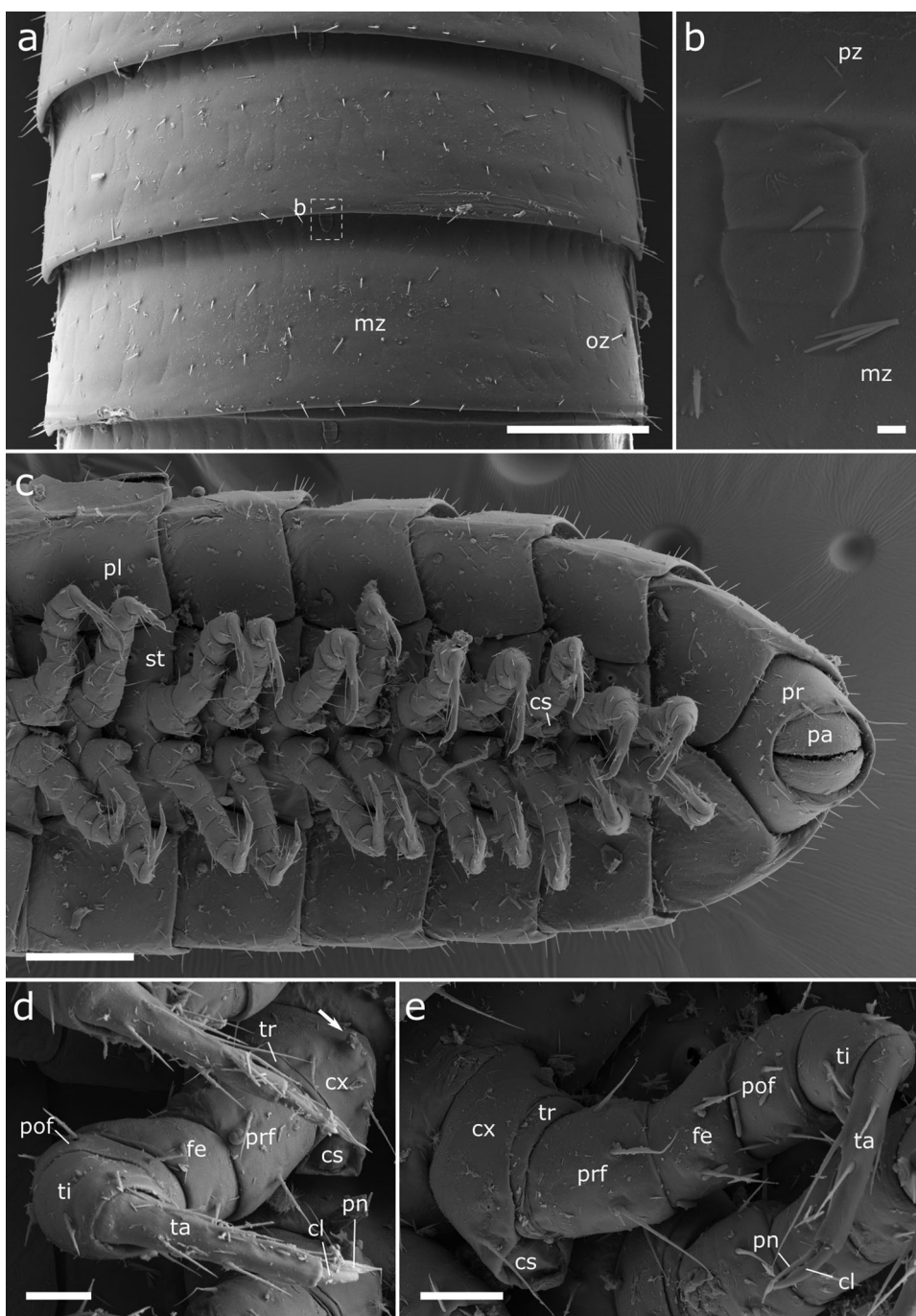


Figure 12. Body-rings and legs of *Siphonethus coxaespinosus* sp. nov. (NZAC03038955) from New Zealand, male, SEM images. **(a)** Body-ring, dorsal view. **(b)** Details (mesal rectangular structure) of (a). **(c)** Posterior body-rings and preanal ring, ventral view. **(d)** Anterior leg. **(e)** Posterior leg. **Scale:** a, c = 100 μ m, b = 2 μ m, d, e = 20 μ m. **Abbreviations:** cl = claw, cs = coxal sacs, cx = coxa, fe = femur, mz = metaonite, oz = ozopore, pa = paraproct, pof = postfemur, pl = pleurite, pn = paronychium, pr = preanal ring, prf = prefemur, ta = tarsus, ti = tibia, tr = trochanter.

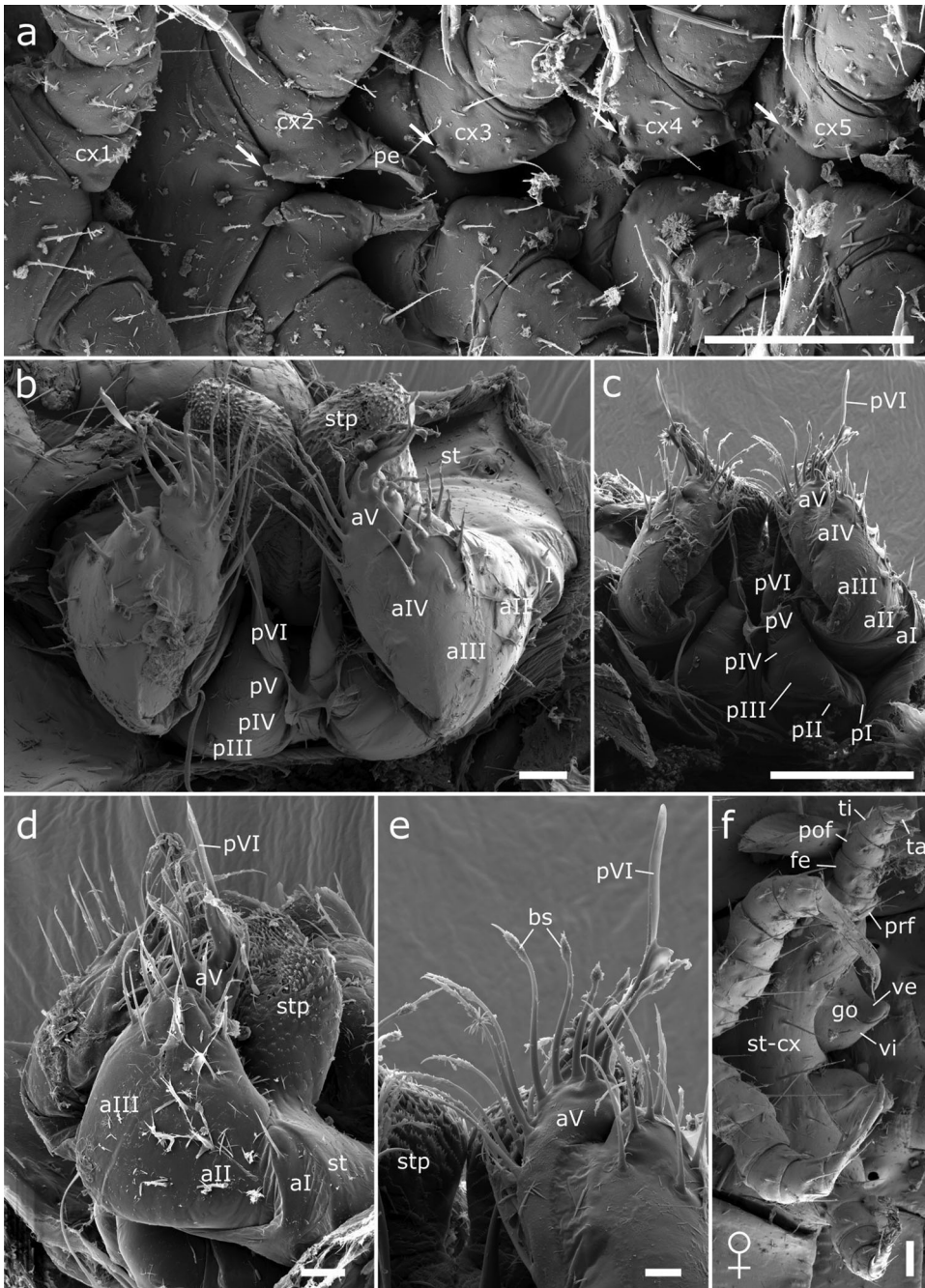


Figure 13. Male (a-e) and female (f) sexual characters of *Siphonethus coxaespinosus* sp. nov. from New Zealand, male, SEM images. (a) Anterior coxae of male (NZAC03038954), ventral view. (b-f) Gonopods of NAZAC03038955. (b) Ventral view. (c) Posterior view. (d) Lateral view. (e & f) Detail of apical podomere of anterior gonopod. (e) Ventral view. (f) Gonopore and 2nd leg pair of female, ventral view. **Scale:** a, c = 100 μ m, b, d-f = 20 μ m. **Abbreviations:** al-aV = podomeres of anterior gonopod, bs = brush-like setae, cx = coxa, go = gonopore, pe = penis, pl-pVI = podomeres of posterior gonopod, prf = prefemur, st = sternite, stp = sternal projection, ve = external valve of vulva, vi = internal valve of vulva.



Figure 14. *Siphonethus obtusus* sp. nov. (NZAC03038954) from New Zealand. (a) Three male specimens. (b) Male, habitus, lateral.

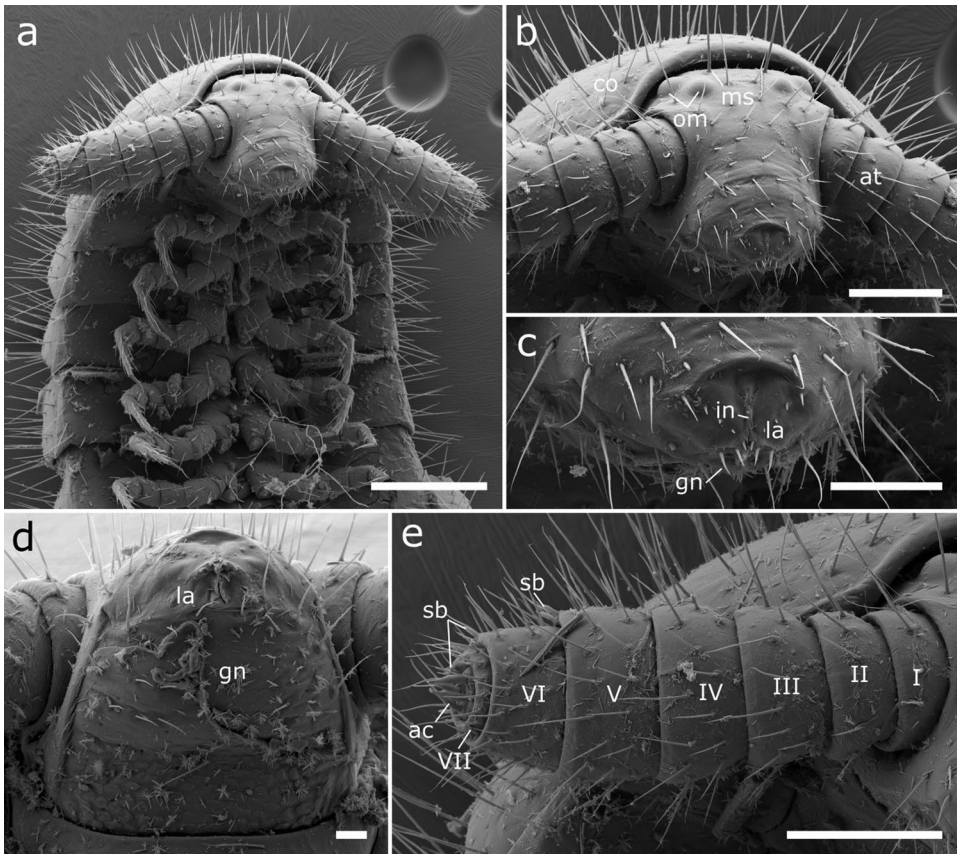


Figure 15. Head of *Siphonethus obtusus* sp. nov. (NZAC03038954) from New Zealand, male, SEM images. (a) Anterior body, ventral view. (b) Head, frontal view. (c) Detail of labrum. (d) Gnathochilarium, ventral view. (e) Antennae. **Scale:** a = 200 μ m, b, c, e = 100 μ m, d = 20 μ m. **Abbreviations:** I-VII = antennomere 1-7, ac = apical cones, at = antennae; co = collum, gn = gnathochilarium, in = incision of labrum, la = labrum, ms = macrosetae, om = ommatidia, sb = sensilla basiconica.

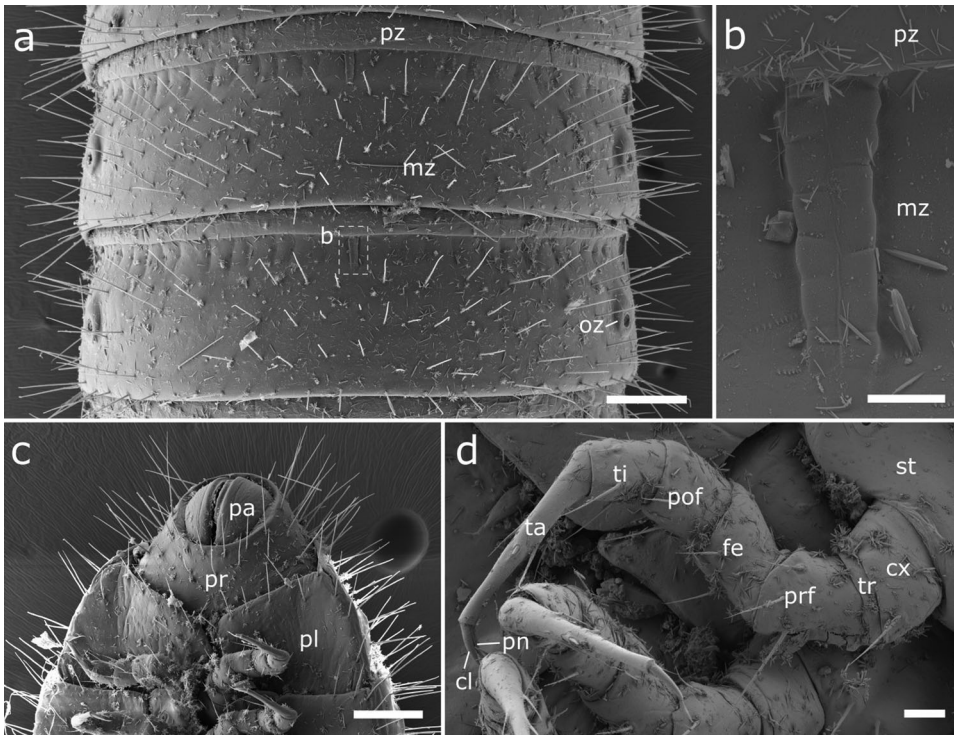


Figure 16. Body-rings and legs of *Siphonethus obtusus* sp. nov. (NZAC03038954) from New Zealand, male, SEM images. **(a)** Body-ring, dorsal view. **(b)** Details (mesal rectangular structure) of (a). **(c)** Posterior body-rings and preanal ring, ventral view. **(d)** Posterior leg. **Scale:** a, c = 100 μ m, b = 10 μ m, d = 20 μ m. **Abbreviations:** cl = claw, cs = coxal sacs, cx = coxa, fe = femur, mz = metaonite, oz = ozopore, pa = paraproct, pof = postfemur, pl = pleurite, pn = paronychium, pr = preanal ring, prf = prefemur, ta = tarsus, ti = tibia, tr = trochanter.

Male sexual characters: Male gonopore positioned on coxa 2, on an elongated flattened/fan-shaped lobe (gonapophysis or penis) (Figure 17a). Leg pairs 9 and 10 modified to well-developed gonopods (Figure 17b–d).

Anterior gonopod consisting of 5 podomeres (segmentation mainly visible in posterior view), podomere 2 largest, podomere 2–4 each with single row of long setae. Podomere 5, basally with group of larger setae, apically with large plate-like outer lobe and small spoon shaped inner lobe, covered by small spines. Sternite with mesal pair of setae.

Posterior gonopod leg-like with 6 podomeres, devoid of setae. Apical podomere longest, draw out into long flagellum, ca as long as podomere 1–5 combined (Figure 17b–d).

Female sexual characters: Coxae of second leg pair free, not touching. Gonopores (vulvae) on coxae of second leg pair, bulged, no division visible (Figure 17e).

Siphonethus sp. 1

Material examined: DNA-Vouchers from Drummond et al. (2015): Female (NZAC03011232) (Figure 18a–c), NEW ZEALAND, Little Barrier Island, xii.2010, Plot 9 L (CM30C30), litter. Juvenile, (NZAC03012795) (Figure 18d, e), NEW ZEALAND, Little Barrier Island, xii.2010, Plot 3 N, litter.

Remarks: The DNA-Voucher NZAC03011232 is a female with 35 tergites + preanal ring and is ca. 7 mm in length. The specimen is of uniform pale whitish colour, with partly transparent cuticle (Figure 18a), which is probably the result of the lysis for DNA extraction (see Drummond et al.

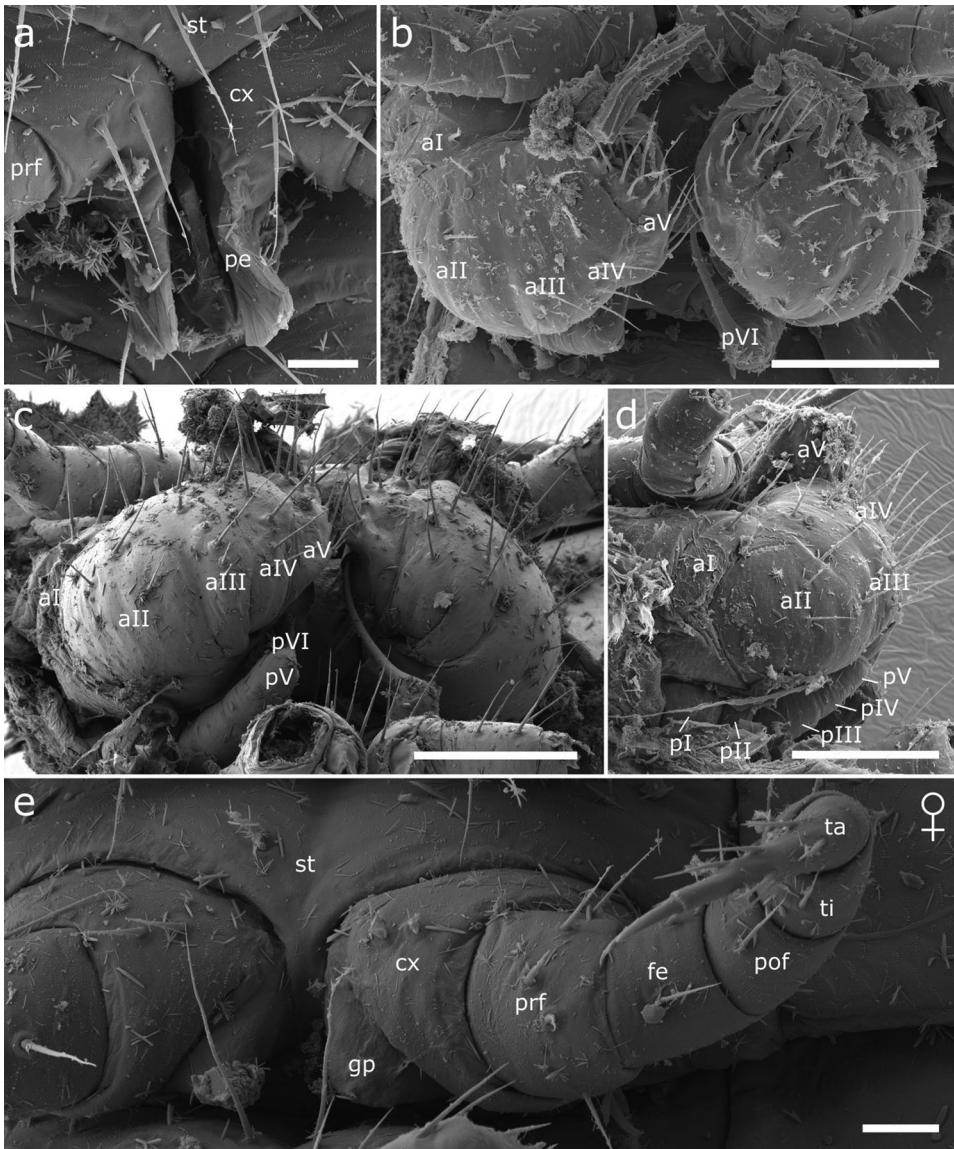


Figure 17. Male (a-d) and female (e) sexual characters of *Siphonethus obtusus* sp. nov. (NZAC03038954) from New Zealand, male, SEM images. **(a)** Coxa of leg pair 2 with gonopore, ventral view. **(b-d)** Gonopods. **(b)** Ventral view. **(c)** Posterior view. **(d)** Lateral view. **(e)** Female, second leg pair with gonopore, ventral view. **Scale:** a, e = 20 μ m, b-d = 100 μ m. **Abbreviations:** al-aV = podomeres of anterior gonopod, cx = coxa, fe = femur, gp = gonopore, pe = penis, pl-pVI = podomeres of posterior gonopod, pof = postfemur, prf = prefemur, st = sternite, ta = tarsus, ti = tibia.

2015). The head is pointed and slightly constricted anterior of the antennae as in *Siphonethus dudleycookeorum* sp. nov.. The specimen has two pairs of ommatidia and long macrosetae on the head (Figure 18b). The body is densely covered by long setae. The anterior margin of the metazonite carries a median rectangular structure, as well as fine longitudinal striae as in *S. dudleycookeorum* sp. nov.. As the specimen is a valuable DNA-Voucher it was not dissected for further examination.

The DNA-Voucher NZAC03012795 is a small juvenile with 6 tergites and 6 leg pairs. The animal is hollow and the cuticle transparent (Figure 18d) as a result of lysis for DNA extraction. The body is densely covered by setae and the head is pointed as in the female specimen.

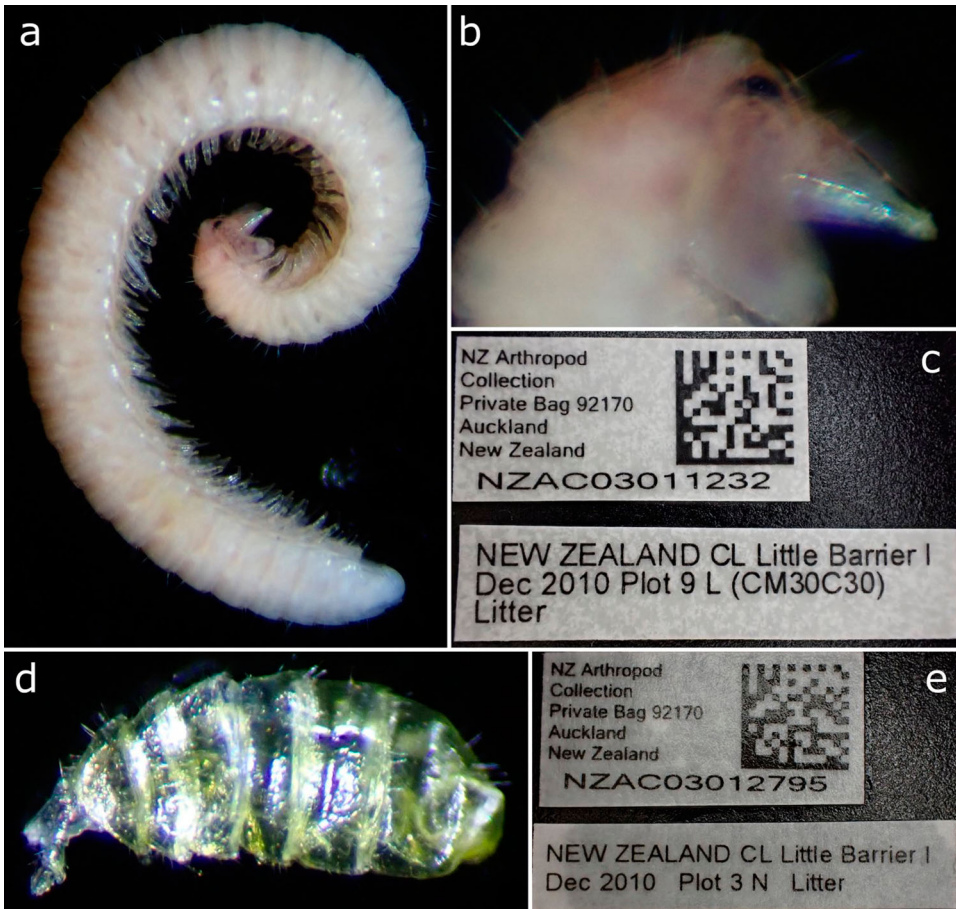


Figure 18. *Siphonethus* sp., specimens sequenced by Drummond et al (2015). **(a-c)** Female (NZAC03011232). **(a)** Habitus, lateral. **(b)** Details of head. **(c)** Label. **(d & e)** Juvenile (NZAC03012795). **(d)** Habitus, dorsal. **(e)** Label.



Figure 19. *Siphonethus* sp. **(a & b)** NZAC03038956. **(a)** Habitus, lateral. **(b)** Label. **(c & d)** NZAC03038957. **(c)** Habitus, lateral. **(d)** Label.

Siphonethus sp. 2

Material examined: Female (NZAC03038956) (Figure 19a, b), NEW ZEALAND, Poor Knights Island, Tawhiti Rahi, 10 Dec. 1980. G. Kuschel, sifted litter from dry water channel 80/148.

Remarks: Body uniform pale, with 48 tergites + preanal ring, ca. 9 mm in length. Head pointed, tapering anterior of antennae and with two ommatidia (Figure 19a) as in *Siphonethus dudleycookeorum* sp. nov.. Body densely covered by long setae and metazonite with median rectangular structure and fine striae on anterior margin as in *S. dudleycookeorum* sp. nov.. As only a single female is present we hesitate to assign it to *Siphonethus dudleycookeorum* sp. nov.. The vial also includes a single Polyxenida specimen.

Siphonethus sp. 3

Material examined: Female (NZAC03038957) (Figure 19c, d), NEW ZEALAND, Poor Knights Island, Tawhiti Rahi, ix.1980, pit trap 80/75

Remarks: Body uniform pale, with 25 tergites + preanal ring, ca. 5 mm in length. Head stout and with two pairs of ommatidia (Figure 19c) as in *Siphonethus coxaespinosus* sp. nov. and *Siphonethus obtusus* sp. nov.. Body sparsely covered by short setae as in *S. coxaespinosus* sp. nov.. As only a single female is present we hesitate to assign it to *Siphonethus coxaespinosus* sp. nov..

Genetic analyses

Our distance analyses including all available COI barcodes for the Polyzoniida, showed a p-distance from the New Zealand specimens of 14.3% (NZAC 03012795) and 13.9% (NZAC 03011232) to *Siphonethus dudleycookeorum* sp. nov. (ZFMK MYR10095) from Great Britain. The genetic distance between the two specimens from New Zealand (KP421302.1; KP421754.1) was 0.2%. The genetic p-distance of *S. dudleycookeorum* sp. nov. to the only other members of the Siphonotidae for which sequence data are available, viz. *Rhinotus purpureus* and *Eumillipes persephone* was between 27.7% and 28%. The genetic distance to representatives of the families Hirudisomatidae and Polyzoniidae was comparatively high, 28% (*Polyzonium germanicum*, ZFMK-MYR1351, ZSM-MYR00428) and 31.1% (Hirudisomatidae sp., BIOUG32547-D08) (Table 3). Phylogenetic reconstruction (Figure 20) retrieved *S. dudleycookeorum* sp. nov. from Great Britain as a sister-group to the two unidentified specimens from New Zealand with a high bootstrap support (100%). A monophyletic Siphonotidae was retrieved with the three specimens from New Zealand as the sister-group to a clade comprising *Eumillipes persephone* and the two *Rhinotus purpureus*. Siphonotidae was supported by a bootstrap of 100%, *Eumillipes persephone* + *Rhinotus purpureus* was supported by a bootstrap of 98%. While Polyzoniida + Hirudisomatidae and a monophyletic Hirudisomatidae were supported by a bootstrap of 100%, a monophyletic Polyzoniidae only retrieved low support (44%).

Discussion

Siphonethus Chamberlin, 1920

The family Siphonotidae comprises 12 genera and ca. 30 species, of which the majority is in need of revisionary work, as genus specific characters are only poorly understood, and their taxonomy and classification is rather chaotic. Even the diagnostic characters of the family seem not fully clear as discussed by Shear (2016). Problems arise from the poor quality of descriptions, and the rarity and small size of the Polyzoniida (Verhoeff 1924; Hoffman 1977). Most species descriptions are rather short, lacking detailed accounts on the species-specific gonopods and

Table 3. Distance matrix. Numbers in parenthesis indicate the GenBank accession number and the voucher number.

<i>Polyzonium germanicum</i> (KJ408479.1; ZFMK-MYR-1351)																						
<i>Polyzonium germanicum</i> (KJ408478.1; ZFMK-MYR_1351)	0.000																					
<i>Polyzonium germanicum</i> (JQ350463.1; BC ZSM-MYR-00428)	0.003	0.003																				
<i>Angarozonium aduncum</i> (MN232230.1; MPE03458)	0.166	0.166	0.166																			
Polyzoniidae sp. (MG313496.1; BIOUG16675-B07)	0.189	0.189	0.192	0.198																		
Polyzoniidae sp. (MF749827.1; BIOUG12147-H08)	0.183	0.183	0.186	0.196	0.006																	
Polyzoniidae sp. (MF749315.1; BIOUG20666-C09)	0.192	0.192	0.192	0.196	0.004	0.000																
Polyzoniidae sp. (MF748857.1; BIOUG08056-A01)	0.186	0.186	0.189	0.196	0.002	0.008	0.006															
Polyzoniidae sp. (MF748772.1; BIOUG08056-A02)	0.186	0.186	0.189	0.196	0.002	0.008	0.006	0.000														
Polyzoniidae sp. (MF747063.1; BIOUG12147-H09)	0.184	0.184	0.187	0.196	0.008	0.002	0.000	0.009	0.009													
Polyzoniidae sp. (MF747336.1; BIOUG20657-F12)	0.195	0.195	0.195	0.198	0.000	0.005	0.004	0.002	0.002	0.007												
Hirudisomatidae sp. (MG321144.1; BIOUG32547-D08)	0.240	0.240	0.240	0.210	0.207	0.204	0.206	0.209	0.209	0.205	0.207											
Hirudisomatidae sp. (MG320829.1; BIOUG32546-G09)	0.237	0.237	0.237	0.205	0.204	0.200	0.203	0.206	0.206	0.202	0.204	0.000										
Hirudisomatidae sp. (MG313136.1; BIOUG24236-C02)	0.236	0.236	0.236	0.210	0.206	0.204	0.205	0.209	0.209	0.205	0.204	0.000	0.000									
Hirudisomatidae sp. (MG310535.1; BIOUG24236-C01)	0.236	0.236	0.236	0.210	0.206	0.204	0.205	0.209	0.209	0.205	0.204	0.000	0.000	0.000								
Hirudisomatidae sp. (MF748655.1; BIOUG08056-C03)	0.236	0.236	0.236	0.210	0.206	0.204	0.205	0.209	0.209	0.205	0.204	0.000	0.000	0.000	0.000							
Hirudisomatidae sp. (MF748591.1; BIOUG08056-C07)	0.236	0.236	0.236	0.210	0.206	0.204	0.205	0.209	0.209	0.205	0.204	0.000	0.000	0.000	0.000	0.000						
Pancrustacea sp. (KP421754.1; NZAC_03012795)	0.294	0.294	0.294	0.340	0.284	0.284	0.295	0.286	0.286	0.284	0.288	0.328	0.340	0.313	0.313	0.313	0.313					
Mandibulata sp. (KP421302.1; NZAC_03011232)	0.286	0.286	0.286	0.340	0.278	0.278	0.295	0.280	0.280	0.278	0.288	0.328	0.340	0.307	0.307	0.307	0.307	0.002				
<i>Siphonethus dudleycookeorum</i> sp. nov. (ON023662; ZFMK-MYR10094)	0.280	0.280	0.280	0.318	0.297	0.295	0.297	0.298	0.298	0.295	0.300	0.312	0.320	0.298	0.298	0.298	0.298	0.143	0.139			
<i>Rhinotus purpureus</i> (ON023660)	0.312	0.312	0.315	0.354	0.322	0.318	0.318	0.323	0.323	0.318	0.332	0.326	0.334	0.321	0.321	0.321	0.321	0.292	0.286	0.278		
<i>Rhinotus purpureus</i> (ON023661; ZFMK MYR10127)	0.310	0.310	0.313	0.354	0.322	0.318	0.318	0.323	0.323	0.317	0.330	0.326	0.334	0.320	0.320	0.320	0.320	0.292	0.286	0.277	0.006	
<i>Eumillipes persephone</i> (OK602741.1; T147101-MPE5068)	0.321	0.321	0.321	0.362	0.327	0.323	0.331	0.324	0.324	0.321	0.337	0.361	0.371	0.352	0.352	0.352	0.352	0.284	0.275	0.280	0.257	0.255

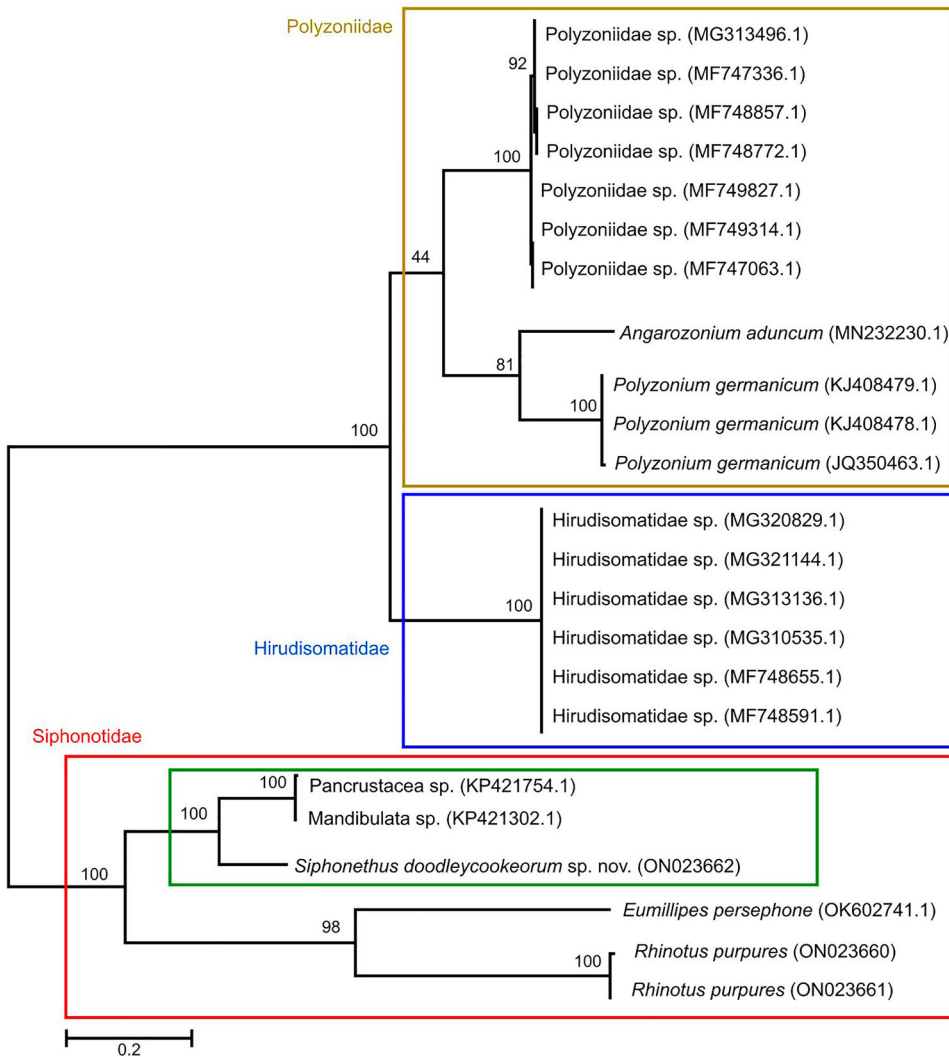


Figure 20. Maximum likelihood tree of Polyzoniida based on the COI sequence after 1000 bootstrap replicates analyzed with the Hasegawa Kinshino Yano Model. Numbers on branches indicate bootstrap support. Codon positions included were 1st+2nd+3rd. All positions with less than 5% site coverage were eliminated. The tree is drawn to scale, with branch length indicating genetic distance. Specimens from New Zealand in green box.

illustrations. As stated by Shear (2016) future research on the Siphonotidae needs to include examinations of males of all nominal genera. We provisionally place the new species in *Siphonethus* Chamberlin, 1920, the only genus known from New Zealand, to avoid creating further chaos in the current classification of the Siphonotidae. The genus *Siphonethus* is a 'source of considerable difficulty' (Hoffman 1977: 431), as it might be a senior or a junior synonym of another siphonotid genus.

We suggest that the species currently classified as *Siphonethus* Chamberlin, 1920 constitute two distinct genera, with *S. enotatus* Chamberlin 1920 as the type species for *Siphonethus*. But detailed examinations of *S. enotatus* and *S. bellus* are needed for clarification. From the available data we conclude that *Siphonethus enotatus* Chamberlin, 1920 and *Siphonethus dudleycookeorum* sp. nov. may belong to a group with the following characters: head pointed and tapering anterior of antennae; antennae long, cylindrical, widening distally; head excavated at insertion of antennae, with

transverse depression. The second group comprises *S. bellus* Chamberlin, 1920, *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov. and is characterised by the following characters: head stout, anteriorly rounded; antennae stout, moderately clavate. Setation and colouration seems to be variable, and the latter is probably impacted by the preservation and storage. Furthermore, *S. dudleycookeorum* sp. nov. has an anterior gonopod consisting of six podomeres, while in *S. coxaespinosus* sp. nov. and *S. obtusus* the anterior gonopod consists of five podomeres, and the state is unknown for *S. enotatus* and *S. bellus* (both are only known from females). While the shape and position of the male gonopore is used to distinguish polyzoniid families (Hoffman 1982; Enghoff et al. 2015), the female gonopore (vulva) remains largely unstudied and only view studies (e.g. Kurnik & Thaler 1989) use it as a diagnostic character. The shape and position of the female gonopore varies greatly between the studied specimens, although it has to be taken into account that it is unknown how the structure of the vulva changes during development. More detailed studies of the female gonopore might yield more taxonomically relevant characters to distinguish species, genera or even families.

Siphonethus dudleycookeorum sp. nov., *S. coxaespinosus* sp. nov. and *S. obtusus* sp. nov. share characters with the genus *Siphonotus* Brandt, 1837 as the metazonite mesally carries a demarcated rectangular area at its anterior margin. However, this character has only been described for *Siphonotus brasiliensis* Brandt, 1837 (Hoffman 1977) and it is unknown if it is present in all *Siphonotus* species, or even common among the Siphonotidae in general. A similar structure has been described from the posterior margin of tergites 1–4 of *Siphonotus latus* Verhoeff, 1924 (fig. 97) from Australia. All species described here differ from undescribed species from the South Island of New Zealand, which will be described at a later date, by the absence of the rectangular structure on the anterior margin of the metazonite.

Diversity of the Polyzoniida on New Zealand

The genus *Siphonethus* Chamberlin, 1920 has previously been known from the two species *Siphonethus enotatus* Chamberlin, 1920 and *Siphonethus bellus* Chamberlin, 1920, both from the North Island of New Zealand. Not a single species has currently been described from the South Island. The siphonotid *Rhinotus bivitattus* (Pocock, 1894), which is also known from New Caledonia and the Loyalty Islands, is recorded from Tauranga, New Zealand (Carl 1926). However, Dawson (1958) argues that the species might be introduced to the islands. It is also likely that the single female specimen, which was collected from New Zealand (leg. Dr. Thilenius) and was subsequently lost (Dawson 1958), was actually a representative of a different genus and/or species.

It can be expected that the assessment of natural history collections from New Zealand and Oceania, as well as more sampling efforts in the area, will lead to the discovery and description of numerous siphonotid species new to science. Fundamental for such an effort would be the detailed redescription of *S. enotatus* and *S. bellus* based on type material and freshly collected material (preferably males) from the type localities, including molecular analyses. We were able to study specimens from the South Island of New Zealand, which are distinct and clearly differ in somatic and gonopod characters from the species described here. These specimens await description. For Australia it is known that a great variety of siphonotid millipedes await description (Marek et al. 2021).

Six siphonotid species from Australia, placed in the three genera *Siphonotus* Brandt, 1837, *Rhinotus* Cook, 1896 and *Eumillipes* Marek, 2021 are described: *Siphonotus brevicornis* Pocock, 1903, *Siphonotus flavimarginatus* Attems, 1911, *Siphonotus latus* Verhoeff, 1924, *Rhinotus michaelsoni* (Attems, 1911), *Rhinotus mjöbergi* Verhoeff, 1924, *Eumillipes persephone* Marek, 2021. However, in unpublished works, several more species and siphonotid genera, which await description, have been recorded (Shear 2016; Marek et al. 2021) and an unpublished revision of the Australian Polyzoniida has been undertaken (Black 1997). These Oceanian millipedes can be found mainly in wet forests (Black 1997). We suggest that especially the wet forests of Oceania and less accessible

habitats, such as deeper soil layers (Marek et al. 2021), will harbour a great variety of unknown polyzoniidan species.

Introduction of *Siphonethus dudleycookeorum* sp. nov. to Great Britain

Reports of alien species introduced into New Zealand are frequent with over 2,200 species of alien invertebrates alone, which cause considerable damage (Barlow & Goldson 2002). The opposite, the introduction of New Zealand species to other parts of the world, are rare. *Siphonethus dudleycookeorum* sp. nov. was probably transported to Great Britain by the transportation of plants from New Zealand. Hence, the specimens were encountered between tree ferns from New Zealand and Australia in Lamorran House Gardens. The blast search of the genetic barcode recovered unidentified Panarthropoda and Mandibulata from Little Barrier Island in New Zealand (Drummond et al. 2015) as closest match, and the species is morphologically highly similar to specimens from Tawhiti Rahi (Poor Knights Island, New Zealand). However, it seems unlikely that *Siphonethus dudleycookeorum* sp. nov. has been directly introduced from Tawhiti Rahi, a small island, to which the access is highly restricted due to nature conservation efforts (Coulston 2002). We suggest rather that *Siphonethus dudleycookeorum* sp. nov. was introduced from the mainland of New Zealand to Great Britain and to Tawhiti Rahi as well, as the island was extensively cultivated over a long period, which has heavily impacted the native flora and fauna (Hayward 1993). The introduction of *Siphonethus dudleycookeorum* sp. nov. is probably facilitated by the similar mild, maritime climate in northern New Zealand and the southern part of the British Isles. The unique climatic conditions of Lamorran House Gardens, without frost since 1987, allow the growth of many subtropical and southern hemisphere flora (Lamorran House Gardens).

Another example of an alien soil invertebrates introduced by human activity from New Zealand to the British Isles is the New Zealand flatworm (*Arthurdendyus triangulatus* (Dendy, 1894)). As a predator of earthworms this flatworm has a negative effect on earthworm populations across its introduced range, and thereby on the nutrient cycle and also on native predators of earthworms (Murchie & Gordon 2013). As a non-predatory millipede, which is probably highly specialized to feed on more or less liquid food (Moritz et al. 2022), *Siphonethus dudleycookeorum* sp. nov. is unlikely to cause severe problems. The preferred food source of *Siphonethus dudleycookeorum* sp. nov. is unknown but for other Polyzoniida it is assumed that they feed on algae, bacterially degraded substances and fungal hyphae (Dunger 1993). Therefore, *Siphonethus dudleycookeorum* sp. nov. might be in competition with other species that graze on algae, bacteria and fungi. Unlike *Arthurdendyus triangulatus*, *S. dudleycookeorum* sp. nov. has not been recorded outside the botanical garden, as is also the case for *Rhinotus purpureus* and other alien millipedes, centipedes, and woodlice, which are only known from greenhouses in Europe (Decker et al. 2014; Stoev et al. 2010; Gregory & Lugg 2020).

Genetic analyses

As only very few COI sequences are available for Polyzoniida, with a total of 20 sequences from GenBank plus 3 sequences from this study covering 8 putative species, and as the COI sequence is only of limited value for inferring phylogenetic relationship, the phylogenetic hypothesis presented here has to be taken with caution. Based on the low genetic distance of 0.2% we suggest that the two unidentified Polyzoniida from Little Barrier Island, New Zealand (NZAC03012795 and NZAC03011232) are representatives of the same species, while the moderate genetic distance of 13.9% between these two specimens and *Siphonethus dudleycookeorum* sp. nov. suggests that the two species are congeneric. This is also supported by morphological data, as they share several somatic characters like the shape of the pointed head, which narrows anterior of the antennae, the presence of two ommatidia, the long and dense setation of the body and the rectangular

structure and striation on the metazonites. We hesitate to describe the species from Little Barrier Island, as males are unavailable and a detailed examination with dissection of the valuable voucher specimens is not possible.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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