An ancient Antarctic endemic genus restored: morphological and molecular support for *Gomphiocephalus hodgsoni* (Collembola: Hypogastruridae)

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Abstract. *Gomphiocephalus hodgsoni* Carpenter was only the second collembolon[†] to be described from the Antarctic continent. It was collected first in 1902 from Granite Harbour, southern Victoria Land, Eastern Antarctica, by the British National Antarctic Expedition (1901–1904). Since then several studies have investigated the distribution, ecology, ecophysiology and molecular composition of the species. Despite two morphological redescriptions and an absence of detailed evolutionary phylogenetic studies, the genus *Gomphiocephalus* was recently reduced to a subgenus of *Schoettella* Sch¨affer. Here, we redescribe the species in detail and use morphological and molecular (cytochrome *c* oxidase subunit I and *28S*) data to indicate its generic relationships within Hypogastruridae. Characters of *Gomphiocephalus* do not conform with those of any extant genus in the family, including *Schoettella*. In addition, the only *Schoettella* species described from the southern hemisphere, *Schoettella subcorta* Salmon, is shown here to belong in the genus *Xenylla*. Furthermore, molecular data indicates the genus has no close relationship to any other in Poduromorpha, and in particular Hypogastruridae. Therefore, we restore *Gomphiocephalus* to generic status. Our results reinforce the already recognized high level of endemism in the Antarctic fauna at both species and generic levels, and emphasise the necessity of using both morphological and molecular data in determining the systematics and evolutionary relationships of the fauna.

Introduction Adams *et al.*, 2006; Stevens & Hogg, 2006a; Stevens *et al.*, 2006a, b). A recent focus has been on whether Collembola Continental Antarctic Collembola have been the subject of (and other terrestrial invertebrates) persisted in Antarctica throughout glacial advances, or whether they are recent

numerous entomological studies for over 100 years, ever since colonizers (Stevens *et al.*, 2006b; Convey & Stevens, 2007; the Southern Cross British Antarctic Expedition, 1898–1900

Convey *et al.*, 2008, 2009; Cranston *et al.*, 2010). Stevens (Janetschek, 1967; Wise, 1967, 1971; Greenslade, 1995; & Hogg (2006b) and Stevens *et al.* (2006b) consider that Collembola, like most terrestrial invertebrates (Adams *et al.*,

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2006) in this region, are likely to be relicts that have survived

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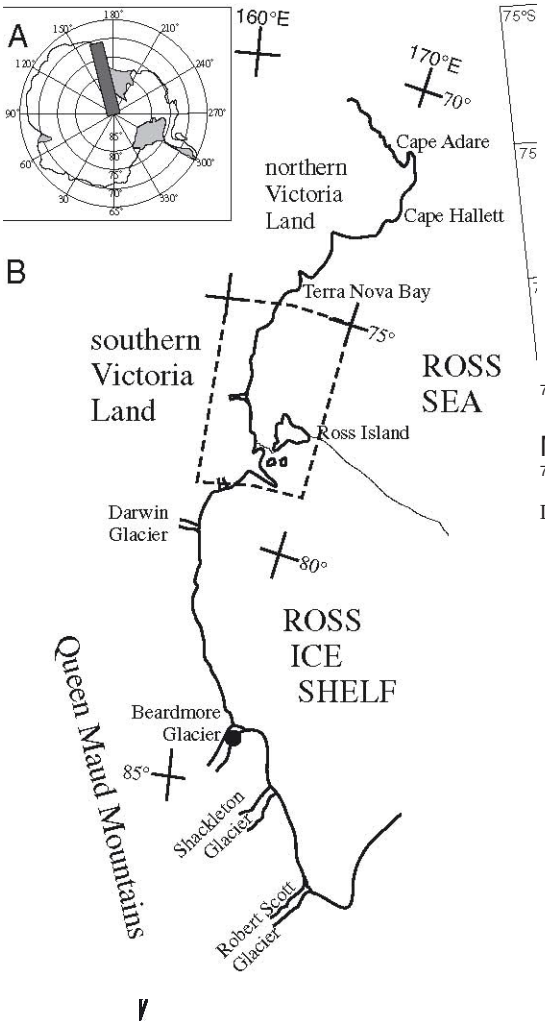
†The name Collembolon, erected by Sir John Lubbock over 100 years ago, is a Greek singular noun and the plural therefore is Collembola. The adjective is collembolan (with a lower case c).

glaciation in refugia. Support for this hypothesis has been dominated by the high faunal endemicity described from small ice-free regions of eastern Antarctica, where most of the continental fauna is found. For instance, 60% (6/10) of collembolon genera and 90% (9/10) of species are endemic (Wise, 1967, 1971; Sinclair & Stevens, 2006), and recent



C David Gl.

N 50 km
75 30'S

°

Mt. George Murray Ross

76 30'S°

Depot I. Tripp
Granite
Harbour

McKay Gl.

77 S°

Dorsal	a	—	6	6	7	5	6
	m	2*b*	4 + s*c*	4 + s*d*	2	2	2

76 S

°

Sea Mawson Gl.

Marble Pt.
Victoria V

Ross I.

Wright V.
C. Royds
77 30'S

°

Taylor V. C. Evans

Taylor Gl.
Garwood V Miers V.

°

78 S Ross Black I. Ice Lake Mt. Discovery Shelf

Penny Minna Bluff
78 30'S

°

164 E° 166E168E

° °

162 E

°

160 E

°

Fig. 1. A, location of the Transantarctic Mountains in eastern Antarctica; B, sampling locality for *Biscoia sudpolaris* (Beardmore Glacier, solid circle) and location of southern Victoria Land; C, southern Victoria Land inset reveals the entire species distribution for *Gomphiocephalus hodgsoni* (black squares, localities of specimens; grey square, type locality of Granite Harbour).

B

SOUTH POLE

molecular evidence indicates that all ten species are endemic (Torricelli *et al.*, 2010).

Of the ten species of Collembola found in eastern Antarctica, only two, *Biscoia sudpolaris* Salmon and *Gomphiocephalus hodgsoni* Carpenter belong to the family Hypogastruridae, and both are type species for monobasic genera (Fig. 1). The genus *Gomphiocephalus* was erected by Carpenter in 1908 for the new species *G. hodgsoni* (Carpenter, 1908), first collected in 1902 at Granite Harbour, southern Victoria Land, Antarctica, by the British National Antarctic Expedition (1901–1904). *Gomphiocephalus hodgsoni* was only the second collembolon described from the Antarctic continent. Since that time studies have established its distribution (known to be endemic to southern Victoria Land; Fig. 1), and various aspects of its ecology, ecophysiology and molecular properties have been documented (Janetschek, 1967; Smith, 1970; Peterson, 1971; Wise, 1971; Duncan, 1979; Davidson & Broady, 1996; Stevens & Hogg, 2002, 2003, 2006b; Meyer-Rochow *et al.*, 2005; McGaughran *et al.*, 2008, 2009a, b, 2010a).

affer, 1896). Clarification of the relationships of Antarctic genera will improve our understanding of the palaeogeography and

affer on the basis of a single character state: the absence of an empodial appendage (see also Sch¨

More recently, *G. hodgsoni* has been redescribed (Carpenter, 1921; Salmon, 1962), with details of the immature and adult dorsal and ventral chaetotaxy of abdomen V provided by Peterson (1971), and Meyer-Rochow *et al.* (2005) described the ultrastructure of the ocelli. However, the full chaetotaxy has never been described, making it difficult to determine the correct systematic relationships of the genus within the family. *Gomphiocephalus* remained as a monobasic genus until Thibaud *et al.* (2004) reduced it to a subgenus of C*Schoettella* Sch¨

evolutionary history of the region, and of Collembola in general (Stevens & Hogg, 2006b; Stevens *et al.*, 2006b; Convey *et al.*, 2009; McGaughran *et al.*, 2010b). Thus, we redescribe *G. hodgsoni* providing a full chaetotaxy and comparison of the morphology of the genus with closely related genera within the Hypogastruridae. We examine the phylogeny of the species within the Poduromorpha with a focus on Hypogastruridae using both mitochondrial (cytochrome c oxidase subunit I, COI) and nuclear (D1, D2 and D3 regions of *28S*) markers. Based on both molecular and morphological data, we refute its close relationship with *Schoettella*, as proposed by Thibaud *et al.* (2004), and restore *Gomphiocephalus* as a monobasic genus.

Material and methods

Sequence data

Molecular data were gathered for the D1, D2 and D3 regions of *28S* and *COI* for 76 taxa (Table S1). We selected two families (Isotomidae and Tomoceridae) within Entomobryomorpha as outgroup taxa. *Tomocerus* was used because the superfamily Tomoceroidea has been found to be the sister group of Poduromorpha (D'Haese, 2002; Xiong *et al.*, 2008). The ingroup includes all the major existing families within Poduromorpha: Hypogastruridae, Odontellidae, Onychiuridae, Tullbergiidae, Brachystomellidae, Neanuridae and Poduridae (Gulgastruridae, Pachytullbergiidae and Isotogastruridae are not represented, but are of doubtful status and comprise only a few species in the Northern Hemisphere). A special emphasis has been given to the Hypogastruridae with 57 taxa (some species with several specimens) representing all the major lineages relevant to the present study (D'Haese, 2002, 2003b): *Triacanthella*, *Hypogastrura*, *Ceratophysella*, *Xenylla*, *Paraxenylla*, *Microgastrura*, *Schoettella*, *Biscoia* and *Gomphiocephalus*.

We included D1 and D2 sequences from D'Haese (2002) along with additional new specimens: most of the D3 and *COI* sequences were obtained for the present work from ethanol-preserved specimens. Included are sequences from Dell'Ampio *et al.* (2009: *28S* for one *Gomphiocephalus* specimen), Giribet *et al.* (2004: *COI* for *Folsomia*, *Neanura*, *Onychiurus* and *Tetrodontophora*) and Stevens & Hogg (2006b: *COI* for *Biscoia*). Extractions were carried out using Qiagen DNeasy extraction kit. Amplification was carried out in a 25 μL volume reaction using Amersham Bioscience puReTaq Ready-To-Go PCR Beads. The PCR programme for *28S* fragments consisted of an initial denaturing step at 94°C for 1 min, 40 amplification cycles (94°C for 30 s, 52°C for 45 s, 72°C for 1.5 min), and a final step at 72°C for 5 min. D1, D2 and D3 regions of 28S were amplified using the following LCO1490 and HCO2198 primers (Folmer *et al.*, 1994) or primers designed specifically for Collembola in the BoEM Lab: LCO1490col (5'-WYTCDACWAAYCRYAARGAYATYGG-3') and HCO2198col (5'-TANACYTCNGGRTGNCCRAARAA TCA-3'), with an initial denaturing step at 94°C for 1 min, five amplification cycles (94°C for 40 s, 45°C for 40 s, 72°C for 1 min), followed by 35 cycles with an annealing temperature of 51°C and a final step at 72°C for 5 min. Chromatograms obtained from the automated sequencer (ABI 3730) were visually checked for errors using SEQUENCHER v4.8 (Gene Codes Corporation). Complete *COI* fragments were 658 bp long; complete D1, D2 and D3 fragments are 375–379, 406–435 and 523–541 bp long, respectively. There is a 16-bp sequence between the D2 and D3 regions that is completely conserved across all Collembola (CCCGTCTTGAAACACG) that was not amplified in D'Haese (2002), Giribet *et al.* (2004) and Tully *et al.* (2006), and was therefore not used here. All new sequences are deposited in GenBank (National Center for Biotechnology Information NCBI), and accession numbers are listed in Table S1.

Phylogenetic analyses

Data sets were analysed using parsimony in a dynamic homology context through direct optimization (Wheeler, 1996, 2001; Agolin & D'Haese, 2009) implemented in POY4 v4.1.2 (Varon *et al.*, 2010). Each locus (*28S* regions D1, D2 and D3 and *COI*) was analysed separately and in combination for the complete taxon sampling of 76 taxa (with 13 missing entries for *COI*, three for D3, and one for D1 and D2; see Table S1). The influence of gap, transition and transversion costs was explored through sensitivity analysis (Wheeler, 1995) to avoid an arbitrary choice of parameters. Three indel : transversion cost ratios (1, 2 and 4), with extension gaps weighted as half the cost of opening gaps, and three transversion : transition cost ratios (1, 2 and 4), resulted in 45 individual analyses. The results are reported in noninterpolated cartesian graphs of areas of the parameter space. The areas of the graphs show the strict consensus results whether the groups are monophyletic, para-phyletic or polyphyletic (e.g. Janies, 2001; D'Haese, 2002), and are reported on the nodes as 'Navajo rugs' (*sensu* Giribet, 2003), and here we use Navajo rugs on nodes to illustrate the monophyly or nonmonophyly under all nine explored parameter sets. Character congruence is used as an optimality criterion to choose the parameter set that maximizes congruence among the loci. Congruence was measured by the incongruence length difference test (ILD) metrics (Mickevich & Farris, 1981). This value is calculated by dividing the difference between the overall tree length and the sum of its data components: ILD =

(length combined – length individual sets)/length combined. The tree with 28SrD1.2a (5'-CCCSSGTAATTTAAGCATATTA-3') and

primer pairs, respectively: 28SC1′–28SC2; 28SC2p–28SD2 (D'Haese, 2002); 28SA–28SBOUT (Giribet *et al.*, 2004; Tully *et al.*, 2006). The three fragments were amplified

logeny (Table S2). These data sets were also analysed using 28SBOUT. *COI* sequences were amplified with either maximum likelihood (ML) implemented in the programme

from the analysis that minimizes character conflict among all the data is taken as the best overall explanation of character variation, and thus the best estimate of the phy-

RAxML v7.0.4 (Stamatakis *et al.*, 2006) under default settings
(i.e. GTRCAT).

All analyses were performed on a parallel computing LINUX cluster [USM2700; 112 central processing units (CPUs) in 27 nodes, 6 GB random-access memory (RAM) per node]. Parsimony analyses were performed with the following two-step strategy: the data was submitted to 100 random-addition sequence replicates, and the resulting topologies were swapped with tree–bisection–reconnection (TBR). The trees obtained were fused by tree fusing (Goloboff, 1999). The optimal trees were then submitted to TBR branch swapping, including all trees found within 10% of the cost. Then, for the second step, trees resulting from the different weighting schemes were concatenated and submitted as input trees to further refine the result using tree fusing with TBR branch swapping (e.g. D'Haese, 2003c). Support for individual nodes were calculated using Bremer support values and bootstrap (parsimony and ML), with 500 replicates.

Results

Sequence variability

The mtDNA (*COI*) alignment after editing was 658 bp (219 codons) (Appendix S1). Among the 63 taxa no insertions, deletions or stop codons were detected. The 28S rRNA included the D1, D2 and D3 regions (Appendix S1). Some sequences varied in length, which was neither species-nor genus-specific, and relates to the variable length of loops in the gene. The sequences used here include all sites for 75 taxa for D1 (385 bp), 75 taxa for D2 (515 bp) and 73 taxa for D3 (577 bp).

Phylogenetic relationships

The gap:tv:ts = 4 : 2 : 1 weighting scheme yielded the lowest ILD value (0.027; see Table S2), and therefore minimized the incongruence among the data sets. The 421 weighting analysis resulted in three most parsimonious cladograms of 7855 steps (Appendix S1), and we include the cladogram consistent with the strict consensus tree here (Fig. 2). The topology shown in Fig. 2 agrees with the ML analyses, unless noted below (Fig. S1). We also examined which groups were found to be monophyletic according to the different weighting schemes. The cartesian graphs in Fig. 2 show the strict consensus results (Navajo rugs), and illustrate the monophyly or non-monophyly under all nine explored parameter sets (note that the 421 weighting analysis is shown in the central model). Our analyses recovered Poduromorpha as monophyletic (in all models except 821), compared with the Entomobryomorpha out-groups. Nonmonophyly of Hypogastruridae is consistent with the results from D'Haese (2002), and may reflect incomplete taxon and/or gene sampling (despite a greater volume of sequence data used here) to sufficiently resolve these lineages.

Within Poduromorpha, Hypogastruridae (except *Triacanthella*) + Poduridae + Brachystomellidae + Neanuridae are monophyletic under all nine models. Within Hypogastruridae, *Hypogastrura* and *Ceratophysella* each form monophyletic clades (except *Willemia* is included within *Hypogastrura*). The remaining clade, also monophyletic, includes Hypogastruridae

Brachystomellidae + Neanuridae + Poduridae, again this is consistent with previous studies (D'Haese, 2002). Within this clade, *Schoettella* is the sister group (in eight of nine models) to a clade including *Gomphiocephalus* + Poduridae + *Xenylla* + *Paraxenylla* +*Biscoia* + *Microgastrura* + Brachystomellidae

Neanuridae, which was monophyletic in all nine analyses. *Gomphiocephalus* is always sister group to Brachystomellidae + Neanuridae, except in the 1641 analysis (Appendix S1), where *Gomphiocephalus* is the sister group of Brachystomellidae + Neanuridae + *Biscoia* + *Microgastrura*.

Some minor differences were found comparing the tree topologies between maximum parsimony (MP) and ML analyses, and these generally occurred on weakly supported nodes in both analyses (see Figs 2, S1). It is worth noting that Fig. 2 is consistent with strict consensus, and that the alternative relationships observed in the ML analysis were consistent with a number of MP trees obtained for different Sankoff matrices (Appendix S1). The only differences observed were seen in the ML analysis showing Odontellidae + Tullbergiidae, whereas the MP analysis has Tullbergiidae + Onychiuridae (*Triacanthella* being at the 'base' in both cases), and these three families being monophyletic in the ML analysis (Fig. 2); *Hypogastrura* and *Ceratophysella* are monophyletic in the ML (sister groups in the MP analysis); and *Paraxenylla*/*Xenylla* + Poduridae + *Biscoia* + *Microgastrura* are monophyletic in the MP analysis (sister group to *Gomphiocephalus* + Brachystomellidae + Neanuridae), whereas in the ML *Paraxenylla*/*Xenylla* are sister to Poduridae + *Biscoia* + *Microgastrura* + *Gomphiocephalus* + Brachystomellidae + Neanuridae (Appendix S1; Fig. 2).

Systematics

We follow Fjellberg (1998) and D'Haese (2003a, b) for the nomenclature of setae. Additional comparisons for Hypogastruridae used da Gama (1969, 1988), Thibaud *et al.* (2004), Yosii (1960) and Jordana *et al.* (1997).

***Gomphiocephalus* Carpenter, 1908 stat.n.**
(Figs 3–8)

Type species. Gomphiocephalus hodgsoni Carpenter, 1908

dial appendage absent. Furcula present, reduced, mucro small,

Diagnosis of genus. Habitus of *Hypogastrura* and *Xenylla*. Length up to 1.6 mm (Figs 3, 4). Body pigmented, black. Postantennal organ (PAO) generally circular, 8 + 8 ocelli (Fig. 5). Mouthparts normal as for family, but some maxillary lamellae slightly reduced. Maxillary palp simple with two sublobals. Labium with five e guards. Labrum reduced,

two sublobals. Labium with five e guards. Labrum reduced, with 5, 4 setae only. Antenna IV with five thickened sensilla (Figs 6, 7). Apical bulb large and subdivided (Fig. 6). Empo-

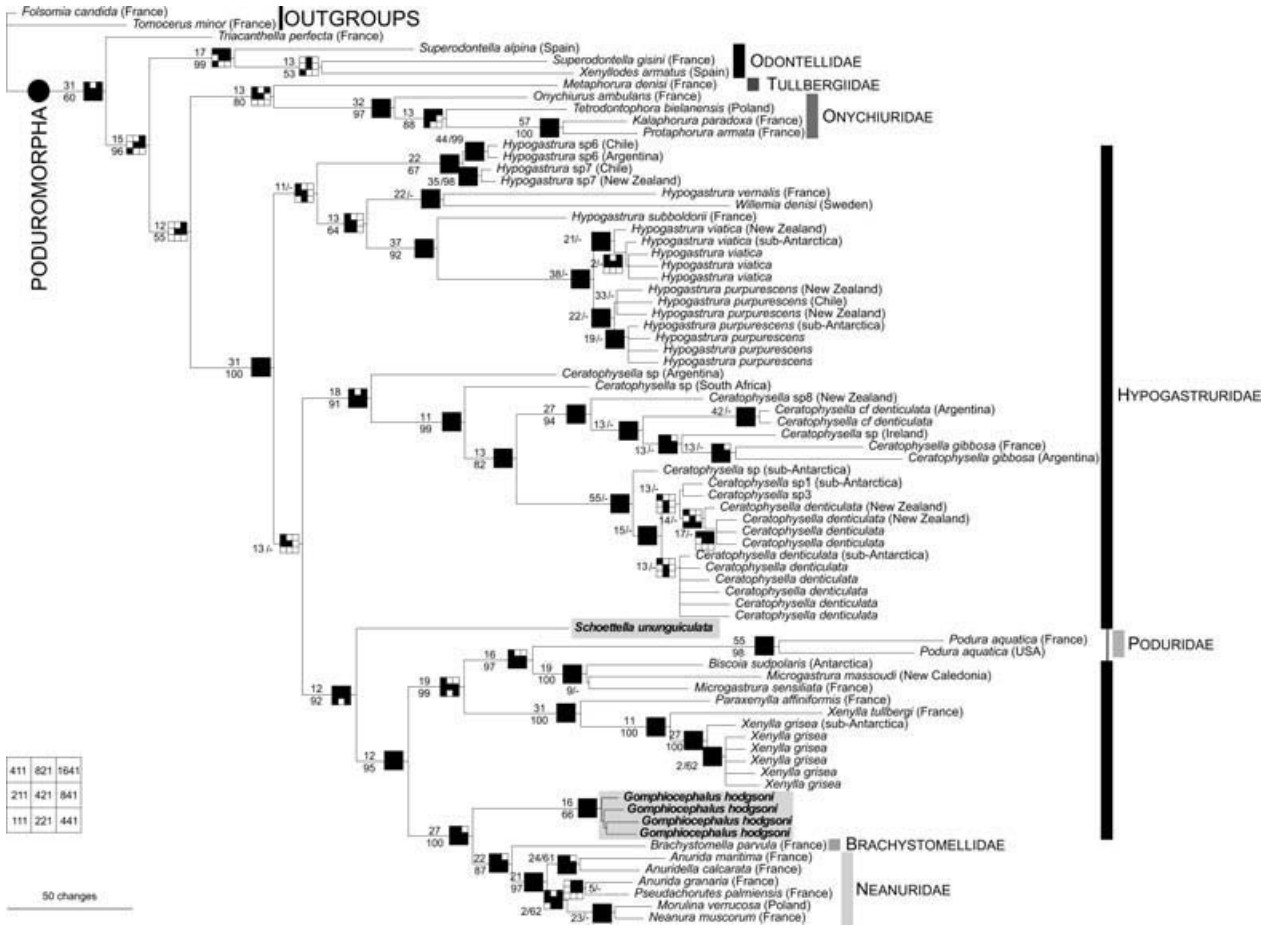


Fig. 2. Phylogenetic (maximum parsimony) relationships within Poduromorpha, with emphasis on the position of *Gomphiocephalus hogdsoni* ;the genera *Folsomina* (Isotomidae) and *Tomocerus* (Tomoceridae), both within Entomobryomorpha, were used as out-group taxa. Most parsimonious tree (7855; consistent with the strict consensus) for regions D1, D2 and D3 of *28S* ribosomal DNA and *COI* mitochondrial DNA, analysed simultaneously for the optimal parameter set gap : tv : ts = 4 : 2 : 1, with extension gaps weighted as half of the opening gaps. Bremer and bootstrap (<50%) support above and below (or after) branches, respectively. Navajo rugs on the node illustrate the monophyly (black squares) or non-monophyly (white squares) under the nine explored parameter sets. The locations of taxa are shown in parentheses, unless immediately below a taxon from the same location. See Figure S1 for maximum-likelihood analysis.

fused to dens (Fig. 4). Dens with three or four setae. Tenaculum with two plus two teeth, no setae. Anus subterminal. Two short anal spines present (Fig. 8).

***Gomphiocephalus hodgsoni* Carpenter stat.n.**
(Figs 9–28)

Schoettella (*Gomphiocephalus*) *hodgsoni* (Carpenter); Thibaud *et al*. (2004).

Type locality. Granite Harbour, Antarctica (77°00′30″S, 162°34′00″E).

Material examined (all SAMA). ANTARCTICA: 5♀ ,3♂ , Granite Harbour, Cape Geology (77°00.863′S, 162°36.086′E), Island (Frati, Carapelli); 16 specimens, Ross Island, Cape Bird (76°55.906′S, 166°54.808′E), on cinder under moss (*Bryum* sp.), 15 December 1975 (Horning); 2♀ , Taylor Valley, Borns Glacier (77°45.833′S, 162°02.240′E), 29 December 2000 (Stevens). (Note: see comment below for information on type

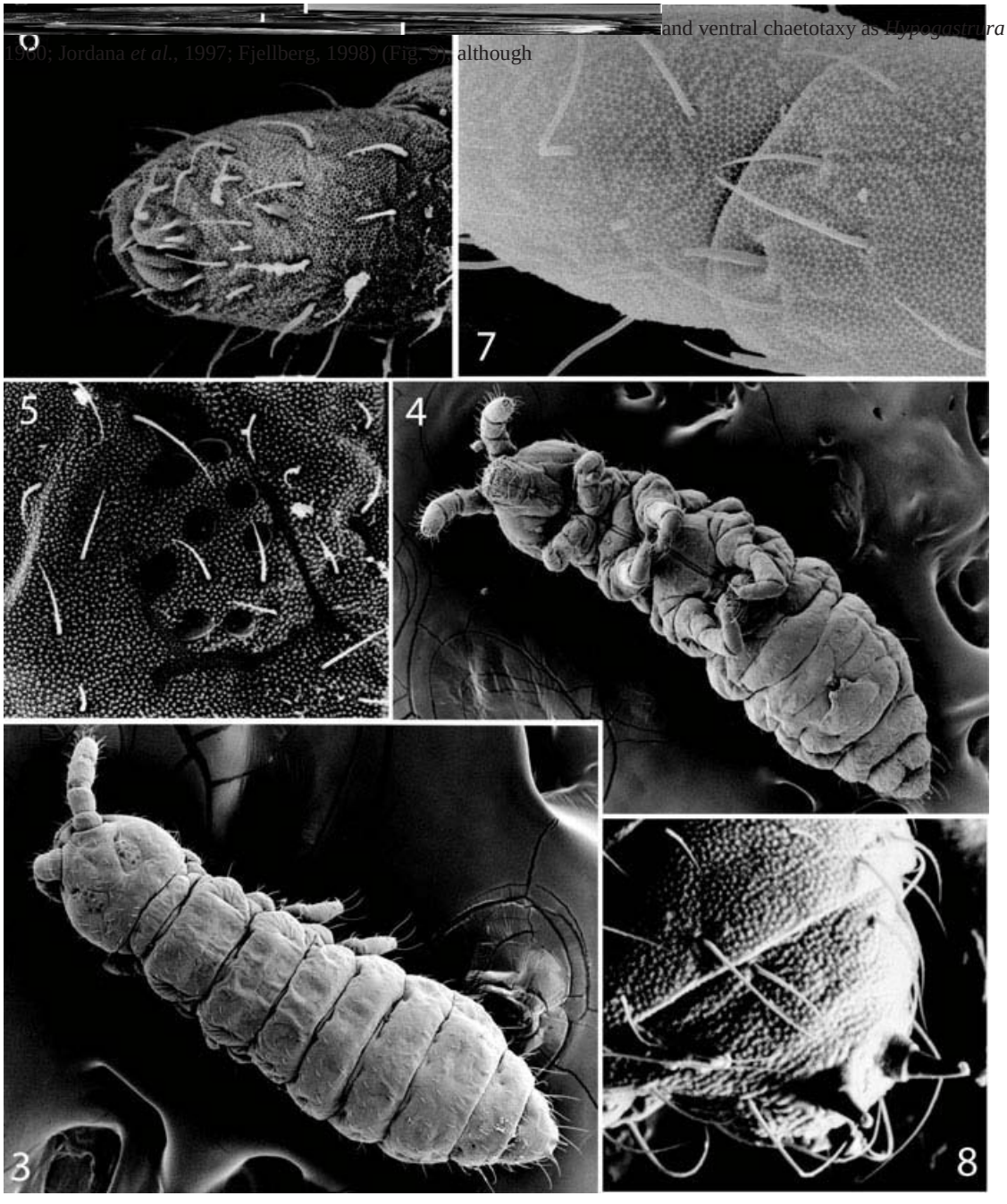
material.)

Mean size. Males always slightly smaller than females, and mean lengths of individuals vary with locality. ♀ 1.53, ♂ 1.39 mm, (Cape Bird, Ross Island); ♀ 1.39, ♂ 1.26 (Depot Island) and ♀ 1.29, ♂ 1.18 (Granite Harbour).

Colour. Dark black, slight reddish tinge.

Cuticle. Small, primitive primary granules only on append

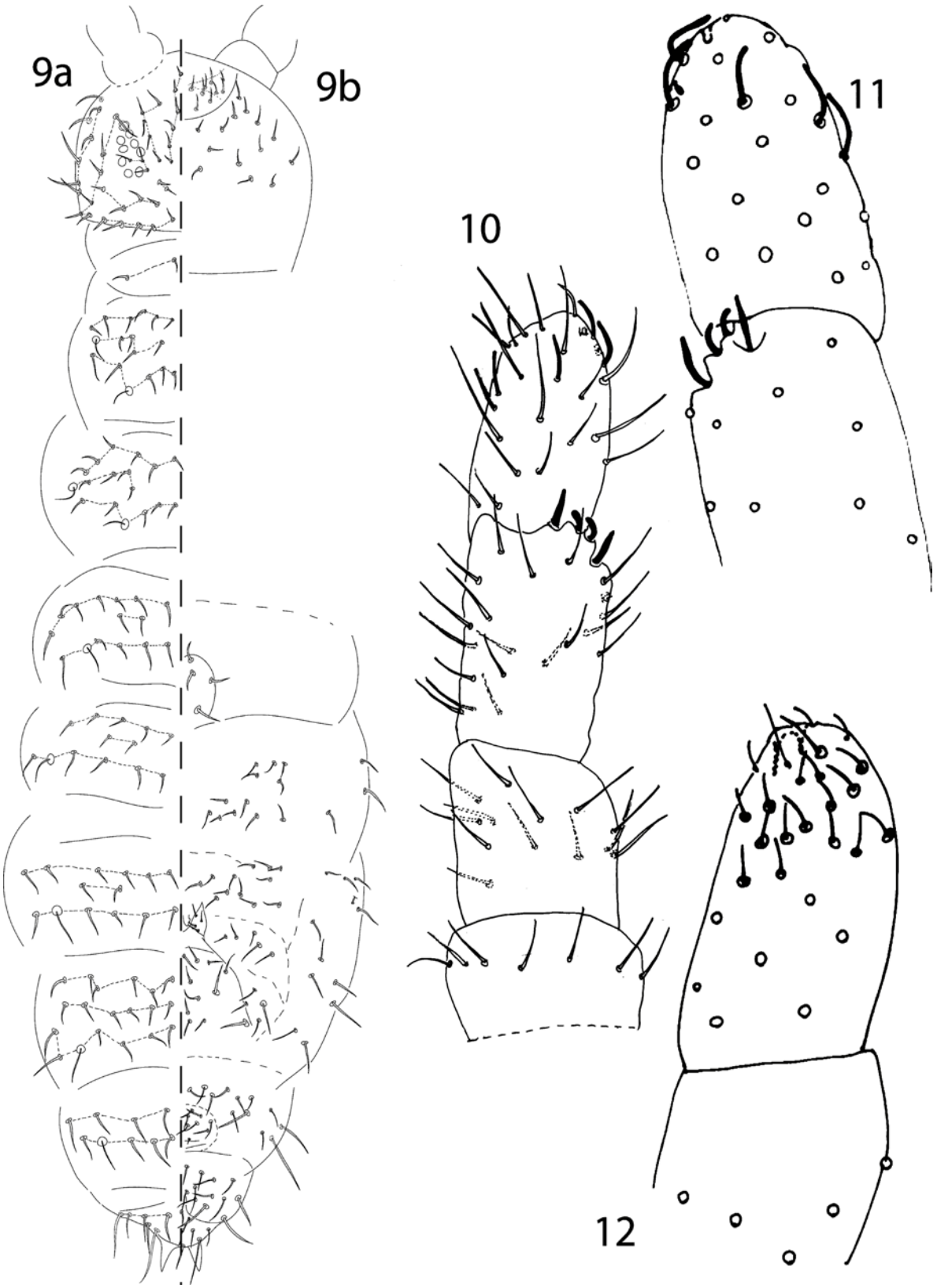
and ventral chaetotaxy as *Hypogastrura* basic plan (Yosii, 1960; Jordana *et al.*, 1997; Fjellberg, 1998) (Fig. 9), although



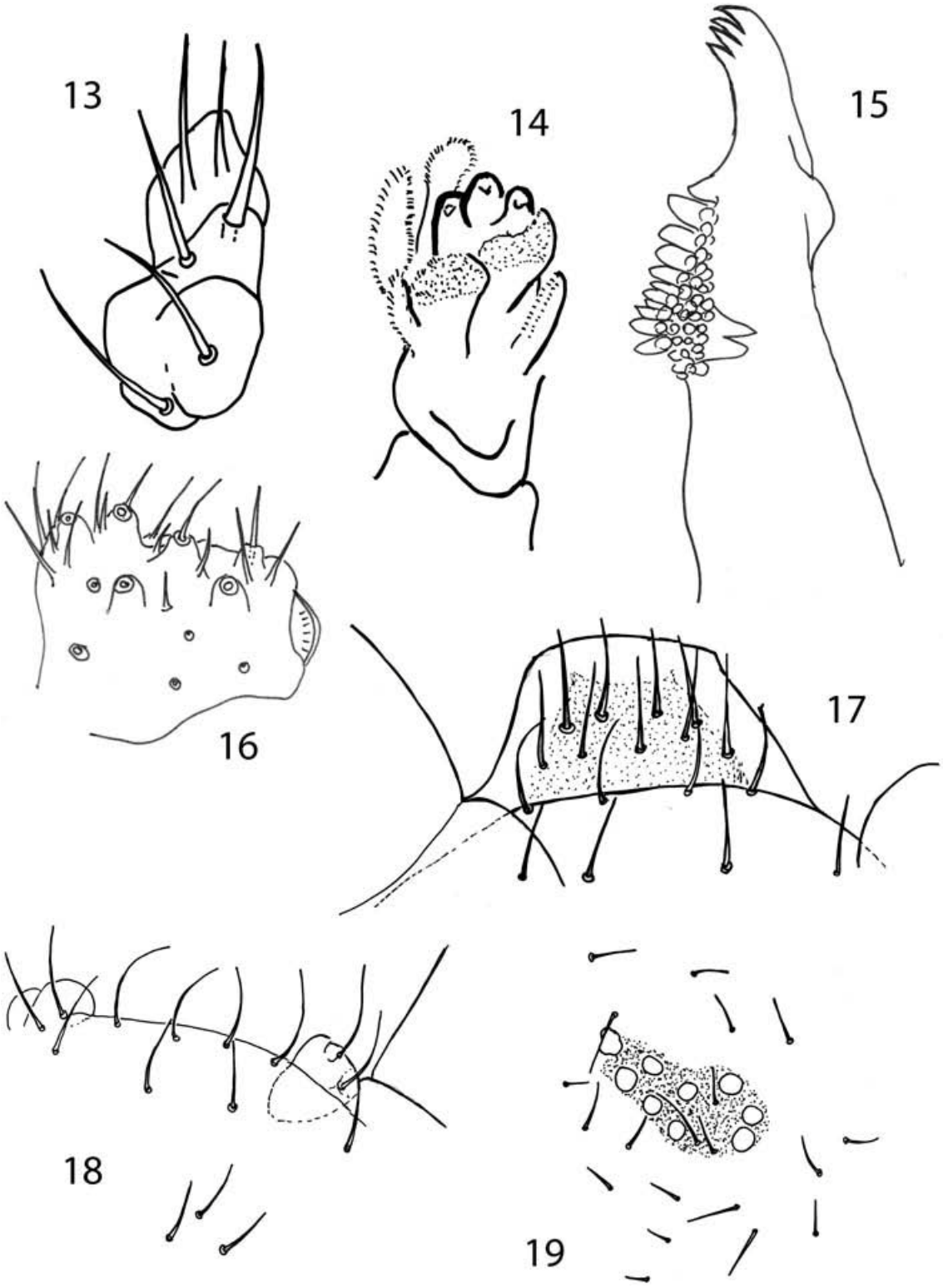
Figs 3–8. *Gomphiocephalus hodgsoni*, scanning electron micrographs: 3, whole animal, dorsal view; 4, whole animal, ventral view; 5, ocelli patch and postantennal organ (PAO); 6, antennal segment IV, dorsal view; 7, antennal segment III organ; 8, abdominal segments V and VI, dorsal view.
Note: Figs 3 and 4 are from the Cape Bird population.

Habitus. Head slightly triangular; abdomen elongate, tapering slightly, narrowest at thoracic segment VI, then gradually broadening to abdominal segments II and III; broadest at abdominal segments II and IV; abdominal segments V and VI fairly long; abdominal segment VI with one pair of moderately long, slightly curved spines on large papillae; anus subterminal, abdominal segment VI at angle of about 30° to horizontal; ratios of lengths of abdominal segments III : IV : V:VI = 1.3:1.4:1.3 : 1 (Fig. 9).

and pointed setae. No indication of plurichaetosis. The dorsal

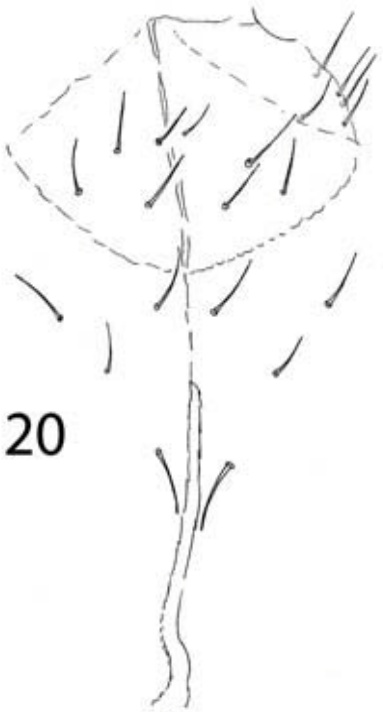


Figs 9–antenna chaetotaxy; 11, antennal segment IV ventral chaetotaxy; 12, antennal segment IV dorsal chaetotaxy. Note: Fig. 9 was digitally prepared using Adobe ILLUSTRATOR CS2 with a digital pen and a WACOM Intuos4 digitizer board.



Figs 13–19. *Gomphiocephalus hodgsoni*, line drawings: 13, maxillary outer lobe; 14, maxilla; 15, mandible; 16, labium; 17, labrum; 18, clypeus; 19, chaetotaxy of and around eye patch.

illa; 15, mandible; 16, labium; 17, labrum; 18, clypeus;



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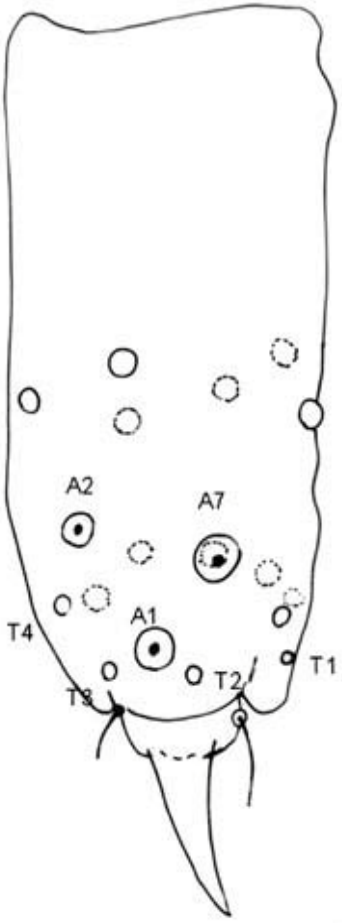

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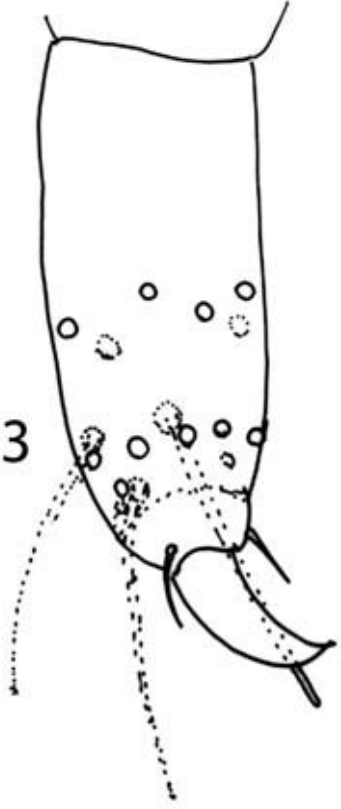

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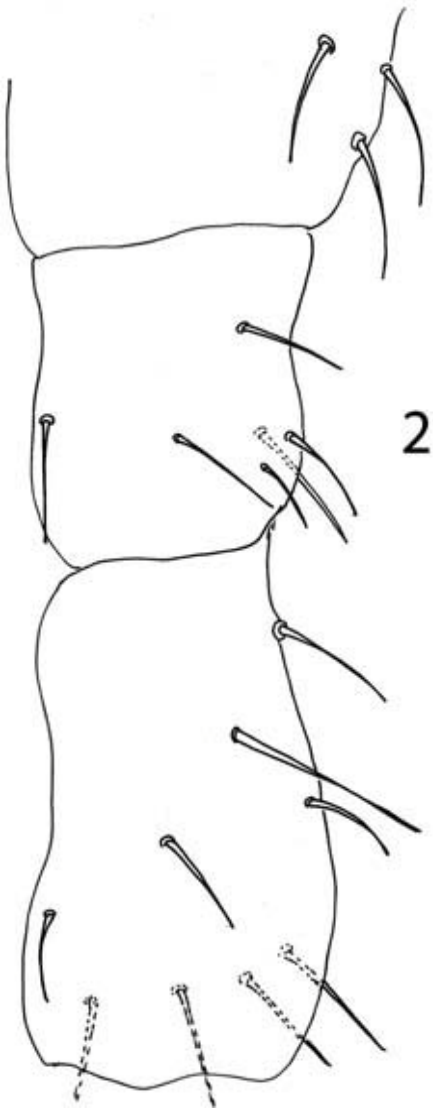

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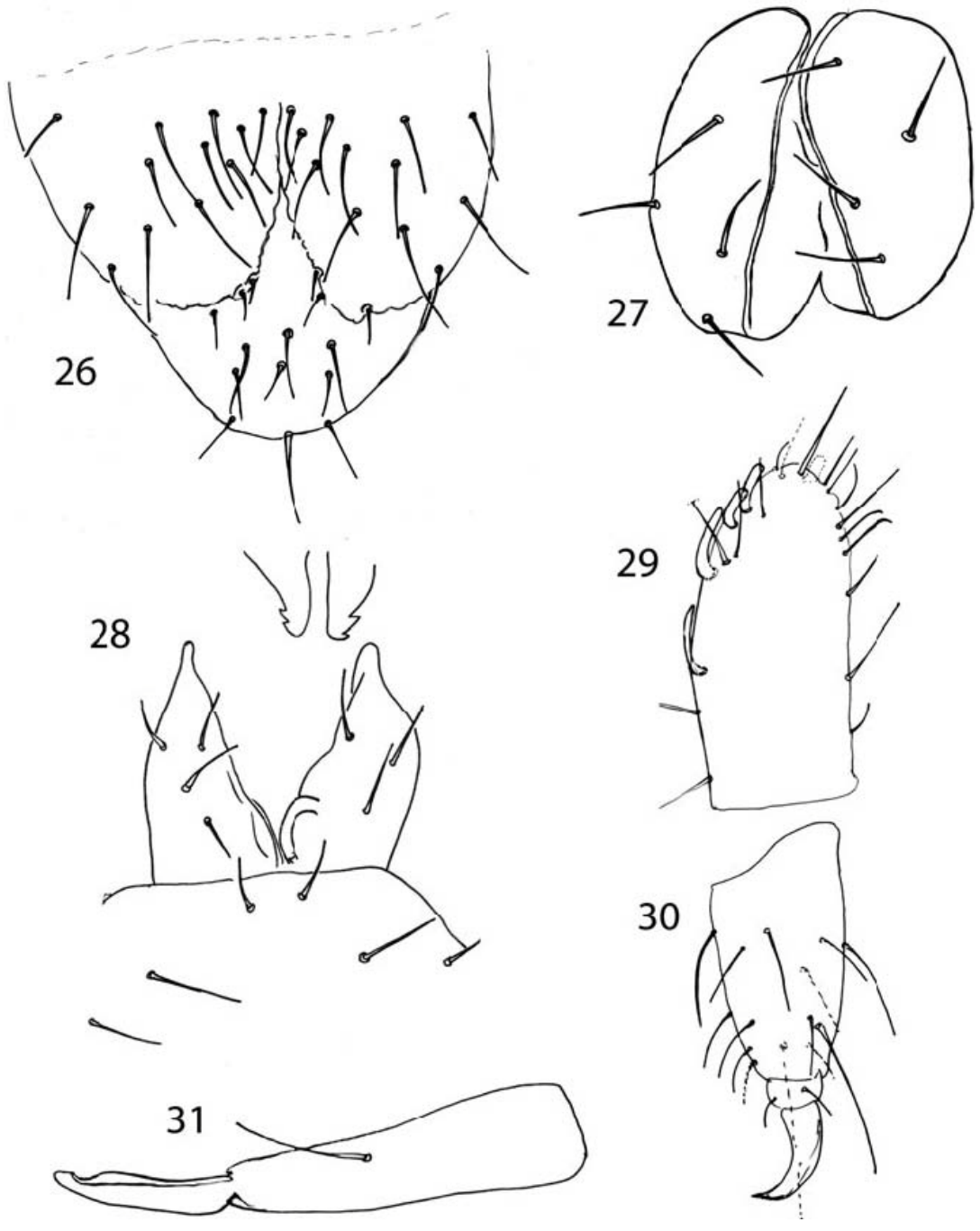

Figs 26–31. *Gomphiocephalus hodgsoni*, line drawings: 26, ventral chaetotaxy of anal lobes; 27, ventral tube; 28, furca and tenaculum. *Xenylla subcorta* line drawings: 29, antennal segment IV, lateral view; 30, claw and tibiotarsus furca; 31, tenaculum.

oc4 on head absent and c1 missing (Fig. 9a) in nearly S setae on abdomen as p5 (abdominal segments I–IV) and all specimens (present as setulae in 7% of specimens); p1 p4 (abdominal segment V) (Fig. 9). Microsensillum not seen. displaced anteriorly (similar to 50% of the *Xenylla* species Labile setae for 29 individuals summarized in Table 1. examined that possessed c1 with p1 absent). Other absent setae relative to the hypogastrurid basic plan in Table 1 (note sd2 *Head.* Antennae short, boundary between segments III and

3, 3/2, 2, 2, IV oblique ventrally; antennal segment IV wit
segments II and III as p4 and m7. sion containing expande

lamella 4 broad with a tooth, lamella 5 narrow and lamella 6 short, rounded and broad; postantennal organ simple, round

Coxa	3	7
Trochanter	6	6 on head;

total ventral head chaetotaxy (14 + 14) follows the *Xenylla* basic plan (Jordana *et al.*, 1997) (Fig. 20; Table 1). Cuticle of ventral groove smooth, not tubercular.

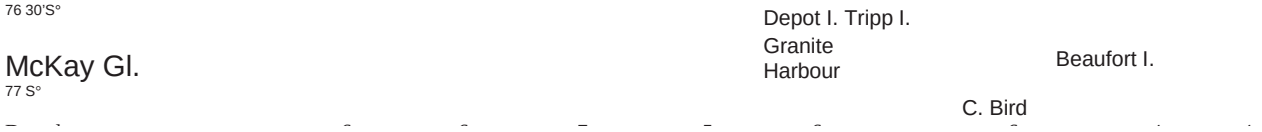

Table 1. Dorsal chaetotaxy for *Gomphiocephalus hodgsoni*, following the basal pattern described for *Hypogastrura* in Fjellberg (1998), and ventral chaetotaxy following D'Haese (2003a), unless stated otherwise (see also Fig. 9).

Thorax Abdomen[a]

Position I II III I II III IV V

Dorsal variability: [a] abdominal segments I and II, Cape Bird specimens conform with *Hypogastrura*, with ss at p5, but with m row absent; abdominal segment IV, Granite Harbour, additional p seta (right side only in some specimens); a3 and p4 absent and m2 present in some individuals (one side); abdominal segment III, a2, m3, m4 and p4 missing in Cape Bird specimens; abdominal segment IV, m1 and m2 missing (m1, m2 present and m3, m4 absent on one side in one specimen), in Cape Bird specimens m1–m3 missing; a4 missing on one specimen from Depot Island; additional m seta present on one side in one Depot Island specimen; abdominal segment V, m row missing (as in *Xenylla*), additional p seta present such that ss at p4 in Depot Island and Granite Harbour (Hypogastruridae generally have ss at p3), but p3 setae missing in Cape Bird specimens, such that ss at p3 (except for one Cape Bird specimen which has ss at p4); a2 absent on one side in one specimen (Depot Island); m0 present in one, and m1 present in another Cape Bird specimen; abdominal segment VI, p1 absent (present in one Cape Bird specimen, but p0 absent in same specimen); m0 present in two Granite Harbour specimens. [b] m2 missing (one specimen with 3 + 2). [c] m1 absent, ss m7, m3 displaced posteriorly. [d] m1 and m2 absent (m5 absent on one specimen, m4 on another), ss m7. [e] ss p4. [f] ss p4 (p3 absent on one side in one specimen). Ventral variability: [g] Setae arrangement as in *Xenylla welchi* (da Gama, 1969: pg 4), one seta absent (possibly p5) on one Depot Island specimen. [h] Arrangement similar to *Xenylla* (da Gama, 1969), but *Gomphiocephalus* with more setae (da Gama, 1969). [i] Anterior sternum 12 + 12, furcal scx2 5 + 5, scx1 5 + 5, manubrium 10 + 10, dens 3 + 3. [j] 10 + 10 (excl. genital plate); genital plate, ♀ 8 + 8(♂ 15 + 15), anterior anal lobes 12 + 12, posterior anal lobe 5 + 5 (2 are m0, p0).

bi-or trilobed (see Figs 3, 4, 6, 7); antennal segment IV with around 42 setae altogether, five unequal thickened sensilla, two (S7, 8 or A, B) curved, broad, distal and subdistal respectively, another three (E, F, D) thinner and others not detected; subapical organ and s microchaeta present; ventral surface of antennal segment IV with 11–13 shortish, parallel sided, slightly pointed setae, three of which are at base of antennal segment IV bulb; antennal segment III with 20 setae, antennal segment III organ consisting of two inner short curved thick pegs, two stout outer longer thick blunt sensilla, ventral sensillum present, minute; antennal segment II with 13 setae; antennal segment I with seven setae and no microchaetae (Figs 10–12); four long curved prelabral setae and four frontoclypeal setae; labral setae reduced, 4, 5, with p row absent, anterior row stronger, indication of four small teeth on the anterior margin of the labrum. Maxillary outer lobe simple with two sublobals.

Ratio of antennal segments I–IV = 1.3:1:2:2; ratio of antennae : head diagonal = 1.1:1.
and posterior (see Fig. 5), not lateral to antennal base, with slight tendency to divide into
three or four parts; ocelli eight plus eight (Fig. 17); two plus two postlabial setae ventrally

Mouthparts (Figs 13–16) with four-toothed mandible, possessing a strongly toothed and ridged grinding mandibular plate; maxilla with three subequal teeth and lamella 1 weak, with toothed field and few ciliations; lamella 2 with short fringe, slightly longer than teeth, lamella 3 short and thin, lamella 4 broad with a tooth, lamella 5 narrow and lamella 6
Ratio of PAO : ocellus A = 7:6.

Thorax. Thoracic segment I without setae ventrally, two plus two setae dorsally; thoracic segment II with one plus one ventral setae, 17 + 17 (m1, m2 or m3 usually missing) setae dorsally; thoracic segment III with one plus one ventral setae, 17 + 17 (m1, m2, p4 usually missing) setae dorsally (Fig. 9a); chaetotaxy of legs normal, as for family (Figs 21–23; Table 2). Empodial appendage absent, claw long and narrow, with one minute internal tooth in distal–mid position, sometimes absent; two, three and three long clavate tenent hairs on legs I, II and III, respectively, two of them are A1 and A7, and the other, slightly more basal in position, is A2. M displaced towards whorl A. Linea ventralis normal for family.

Table 2. Chaetotaxy (numbers of setae) on legs of adult specimens of *Gomphiocephalus hodgsoni*.

Leg I Leg II Leg III

SubcoxaI 1 2 2

Subcoxa II 0 3 3 8 6

Femur 11 11 10 Tibiotarsus 8/11 8/11 7/11

Ratio claw : anal spine = 1.6 : 1 ; ratio tenent hair : claw = 1.7:1.

Abdomen. Ventral tube with four plus four lateral setae (Table 1); rami of tenaculum very small, without setae but with two plus two teeth; manubrium with between ten and 12 setae; dens reduced, short and squat, with 3(4) setae, without enlarged cuticle granulations; mucro small, triangular, fused to dens (Figs 9b, 28). Male plate with a mean of 35 (range 24–40) setae on slightly raised tubercle (Fig. 24). Female plate with a mean of 20 setae (range 11–24) (Fig. 25). Setae on anal valves variable, 12–16 each side, plus three plus three hr setae (Figs 26, 27).

Ratio mucro : dens : manubrium = 1: 2: 15.

Comment. Carpenter noted that his description was based on a few damaged fragments, which was the only material available to him, and that type material was deposited in the Natural History Museum, London (Carpenter, 1908). Four slides were located: three at the Natural History Museum, London, each registered as slide number 1908.225 and labelled 'Gomphiocephalus hodgsoni Carp, Granite Harbour, S. Victoria Land, "Discovery" '; two of these slides were labelled originally as 'Types' by Carpenter, but all three are now labelled as 'Type'; the fourth slide was an unregistered slide found in the National Museum of Ireland, mounted in Canada balsam and labelled 'Gomphiocephalus hodgsoni Carpenter; S. Victoria Land, "Discovery", Granite Harb[our]', and marked later as a syntype by
P.N. Lawrence of the Natural History Museum, London, who examined it in 1983. Unfortunately, the fragments in these slides are poorly preserved and are no longer useful to identify the necessary taxonomic characters.

Although Carpenter (1908) described 'head spines' as present, he later stated that he had misinterpreted the mandibular bases as head spines (Carpenter, 1921). In 1921 he also drew the dorsal and ventral chaetotaxy of adults in detail, but his depiction has been found to be somewhat imaginative. For instance, he shows thoracic segments II and III with two rows of setae instead of three, and abdominal segments I, III and V with three rows instead of two; consequently, his figures cannot be relied on. Salmon (1962) did not illustrate body chaetotaxy in his redescription, and shows only two setae on the dens.

All specimens examined showed considerable asymmetry, and individuals varied in which setae were lost and which were present, particularly on the dorsal sections of the m row on thoracic segments II and III, abdominal segments I–IV, the apex of the head and on the labrum. We hypothesize that this could be a response to stress caused by the Antarctic climate. It was difficult to establish what was the most common chaetotaxy for the species (see Table 1). We compared in detail the chaetotaxy of three populations of *G. hodgsoni*. There were differences between the three populations in the mean length of individuals and the extent of asymmetry and variation in chaetotaxy. The extent of asymmetry varied with locality, with the most climatically severe site showing the greatest variation (Table 1): greatest in the Granite Harbour individuals and least in Cape Bird individuals. Depot Island was intermediate, and there were too few specimens from Taylor Valley to compare. Fluctuating asymmetry has been suggested to indicate stress in populations (Hogg *et al.*, 2001; Trotta *et al.*, 2005), and these Antarctic populations may support this hypothesis.
Stevens & Hogg (2003, 2006b) and McGaughran *et al.* (2008, 2010a) recorded very little within-population genetic variability, but found the greatest genetic differences between populations from the Dry Valleys, including Taylor Valley, and other populations. We found no obvious morphological differences between the two Taylor Valley specimens available, compared with the specimens from the other populations, apart from a high variability in chaetotaxy (including asymmetry within specimens).

***Xenylla subcorta* (Salmon) comb.n.**
(Figs 29–31)

Schoettella subcorta Salmon

Type locality. Lake Te Anau, South Island, New Zealand.

Material examined. Holotype and single specimen, male: Lake Te Anau, under bark of rimu (*Dacrydium cupressinum*) tree, 5 Januray 1940. Slide 3/341, Te Papa Museum, Wellington, New Zealand. J.T. Salmon. On slide in euparol.
The holotype is a dark, uncleared specimen, and many characters, including much of the chaetotaxy, cannot be determined.

Colour. Black to dark grey.

Length. Body as mounted strongly concave, distally curved upwards. Length 0.8 mm.

Chaetotaxy. Short fine setae on body. S setae very long and upstanding, much longer than ordinary setae, especially laterally on thorax, being nearly four times longer.

Head. Antennal length: body length = 0.24. Antennal segment IV with at least four S setae, A and B broad, blunt, C slightly thinner and longer, D more so (Fig. 29), basally with three very long setae. Four lenses on ocelli patch seen. No PAO seen.

Thorax. Claw without teeth, both pretarsal setae present. Two long, clavate tenent hairs on each leg present, both in row A (A1 and A7) (Fig. 30). Empodial appendage absent. All T setae

on tibiotarsi short. Empodial appendage absent, but both pretarsal setae present.
Ratio of inner length of claw : tenent hair length = 0.75.

Abdomen. Ventral tube with four fairly long setae. Furca tapering, short but elongate (Fig. 31). Dens slightly tapering, with only one seta. Mucro elongate, mainly fused with dens,

slightly tapering and with upturned tip, with very narrow lamella starting just behind tip and extending to one-third of distance from base. Two small anal spines present dorsally on abdominal segment VI.

Ratio mucro : dens = 1:2.

Male genital opening bulbous, with eight setae on one side in inner row and eight in outer.

Comment. Salmon (1941) noted as characters of this species that a 'rudimentary empodial appendage' was represented by a 'small bristle', also eight plus eight ocelli and a PAO equal to an ocellus in width, with four elliptical lobes. However, he states that the PAO was very indistinctly defined. Salmon also observed five 'sense rods' on antennal segment IV. The holotype clearly has no empodial appendages on any leg. Salmon must have mistaken a pretarsal seta for the empodial appendage. As the holotype is uncleared, it would not have been possible for Salmon to distinguish the ocelli and PAO clearly, nor see five 'sense knobs', as only setae on the 'edges' of antennal segment IV, as mounted, are obvious.

In his key to the genus *Schoettella*, Stach (1949) lists only the characters given by Salmon (1941), where the only one that is not consistent with *Xenylla* is the apparent 'bristlelike empodial appendage' already noted above as being an observational error.

Fjellberg (1998) provides a comprehensive diagnosis for the genus *Xenylla* Tullberg. The characters that can be observed on the type of *Schoettella subcorta* are: antennal segment IV with four (should be six) sensilla, with A–C lateroapical, D dorsal, and E and F on inner side of antenna; furca with never more than two setae on dens; two anal spines present shorter than claw; tibiotarsal setae A1 and A7 elongated, clavate. Fjellberg's (1998) figures for *Xenylla* species show the length of the lateral S on thoracic segment II compared with ordinary setae to be from three to five times longer, whereas for *Schoettella ununguiculata*, it is only twice as long. As there are no characters on *subcorta* that do not conform with *Xenylla*, and several that do not conform with *Schoettella*, we assign the species to *Xenylla* (Fig. S2).

There are only two *Xenylla* species recorded from New Zealand, *Xenylla maritima* Tullberg and *Xenylla atrata* Salmon. *Xenylla subcorta* is neither of these species, *X. atrata* has no furca and the furca of *X. maritima* is shorter and of a different shape (da Gama & Greenslade, 1981). The dens and mucro of *Xenylla subcorta* are similar to those of *Xenylla greensladeae* da Gama from Australia (da Gama, 1974), but the mucro is completely fused to the dens and is much shorter, and no distal narrow lamella is present in that species. The ratio of claw length to dens + mucro in *X. greensladeae* is 1 : 1.5, which in *X. subcorta* is 1 : 3. *Xenylla subcorta* is considered here to be endemic to New Zealand.

Discussion

Hypogastruridae has been considered to be the most 'basal' family of Collembola, mainly because they possess a primitive chaetotaxic pattern (Yosii, 1960), although current evidence suggests that Tomoceridae and Isotomidae (outgroups in Fig. 2) represent an earlier branching than the subclass Poduromorpha, based on fossil evidence (Greenslade & Whalley, 1986). The morphology and phylogeny of *Gomphiocephalus*, as revealed here, shows that it is a reduced form and derived within the family. As one of only two endemic hypogastrurid genera in eastern continental Antarctica, it is considered relictual (present in Antarctica since glaciation completed by 12–23 Mya), along with the remaining species of this region (see also Stevens *et al.*, 2006a, b, 2007; Stevens & Hogg, 2006b; Torricelli *et al.*, 2010).

Table 3 compares the key morphological characters that differ between genera of Hypogastruridae found commonly in southern regions. It shows that *Gomphiocephalus* is most similar to *Xenylla* in the reduction of chaetotaxy and furca, and loss of empodial appendage, but differs from it in having eight ocelli, not five, and also in the presence of a PAO (da Gama, 1969, 1988) (Table 3). It is similar to *Mesogastrura* in the structure of the PAO, but this genus has no anal spines, among other differing characters. The genus *Schoettella* lacks an empodial appendage, as does *Gomphiocephalus*, but differs from it in several key characters: loss of one full row of labral setae (*Schoettella* possesses the full complement); head with c1 absent (present in *Schoettella*); antennal segment IV with five sensilla (not six as in *Schoettella*); three clavate tenent hairs (A1, A2 and A7), and not four (A1, A2, A7 and T2) as in *Schoettella*; thoracic segment II with two plus two ventral setae (not three plus three as in *Schoettella*); presence of ventral setae on the abdomen (versus none in *Schoettella*); abdominal segment V s seta p4 (not p3 as in *Schoettella*); and rami tenaculum with two plus two teeth (not three plus three, as in *Schoettella*) (Table 3). The morphology of *Gomphiocephalus* is also similar to *Choreutinula* Paclt in the lack of empodial appendage, reduced furca and chaetotaxy, number of ocelli and form of PAO, but it differs from it in having two anal spines, a more reduced furca and reduced labral chaetotaxy.

The importance of taxon sampling was essential to adequately appraise *Gomphiocephalus* in the context of all relevant hypogastrurid genera currently recognized, and it was also critical in resolving the phylogenetic relationships. For example, Stevens & Hogg (2006b) found *Biscoia* and *Xenylla* forming a clade, based on a much smaller data set (mitochondrial DNA *COI*), whereas in the present study we found strong support (all nine MP models and ML) for a close relationship between *Biscoia* and *Microgastrura*, but taxonomic knowledge for *Biscoia* is lacking, and precludes further comment (see Table 3). This placement with *Biscoia* differs from *Microgastrura* + Neanuridae (based on 28S data only) in the earlier study by D'Haese (2002). Although we have made considerable effort to include the many relevant genera, *Gomphiocephalus* is a sister group to Neanuridae and Brachystomellidae. This is potentially analogous to the *Microgastrura* example above, and more extensive sampling throughout the Southern Hemisphere may reveal more closely related genera to *Gomphiocephalus*: currently we know of none.

Table 3. Comparison of morphological characters between *Gomphiocephalus* and *Schoettella*.

	Thibaudyllaa	*Gomphiocephalus*	*Hallus*	*Schoettella*	*Hypogastrura*	*Ceratophysella*	*Xenylla*	*Parraxe*	*nylla*	Najt & *Bisciola*	*Triacanthella*[a]	*Mesogastrura*	Genus C	arpenter	*Sch*¨*affer*	Bourlet	B¨ornner	Tullberg	Murphy	Weiner	Sa

limon

Schaffer

Bonet

Antennal 777–87777?7

segment III) Empodial Absent

Absent Present Present Absent Absent Absent Present Present

as Present, but appendage rudiment or small, hair absent l

ike Tenent hairs 2, 3, 3; mostly 3, 4, 4; Pointed or Pointed

(n als on maxillary l
ot outer lobe a
cl Labralsetae v
ea 5,4reduced 5,5,4a
rly 5,5,4 5,5,4 5,5,4 t
4 5,5,4or 5,5,4 ? e
(n 4,5,4 5,5,4 5, 4,
ot 4or 5, 3, 4 Ocellic
cl 8 + 88 + 88 + 8 l
ea normally 28 + 85 a+
r) 55 + 55 + 58 + 88
se + 8or 6 + 62 + a
ns 2to5 + 5 t
ill Postantennal e
a Round slight ,
on 4small 4 lobes 4+
dif lobes Absent 1
fer Absent Absent –
en Absent Four 4
ti- external Round, 1
an lobe organ c
te tendency to lobes l
nn lobes division a
al into 4 Head Oc4 v
at Absent Absent a
ed Absent Present t
) Absent Absent e
se Absent Absent
g Absent Absent c
m Head p1, c1 p1 l
en present, c1 a
t Present Present v
IV Present Present a
N Present Present ? t
u Usually c1 e
m absent, p1 absent
be present present c
ro Head v1/v2 l
f 2 Present Present a
2 Present v1 v
2 Present, v1 absent
1(v2 and v1 v2 t
2) absent ? Present e
1– Present o
3 sometimes absent
1o absent Thoracic 2
segment r0 + 23 + 32 + 2or3
I, setae 0 + 32 + 2or3 + 33
Number ? + 3 3(4) 3 + 3? 5
of 5 6 3? + 5to 7 + 72 + 2
Up to 10 2 segment I no. of
4–8 (4) su setae Mi s on

Absent Present Present Present Absent Absent ? ? Not seen Present 0, 1, 1 None None None 1 + 1or None None ? 0, 1, 2 or None –III absent 0, 1, 2 m7, p4 (p3 m7, p4 (p3 m7 (m5 absent), m7, p4 m7, p4 m7, p4 m4, p4 ? p5?, m7 m7, p4 II/III present) absent) p4 (p3 thoracic ss

6 4 5 At bl thoracic c
least 4 8 ob

Table 3. Continued

hibaudylla Gomphiocephalus Schoettella Hypogastrura

Ceratophysella Xenylla Paraxenylla Najt & *Biscoia Triacanth*

ella[a] *Mesogastrura* Genus

Carpenter *Sch¨affer* Bourlet B¨orner Tullberg Murphy Weiner Salmon Sch¨affer Bonet

none Position of anus Subterminal Terminal Terminal Terminal Ventral Terminal Ventral Terminal Terminal Terminal Anal spines 2 (equal to 2 (one-2 2 (two-thirds 2 Absent Absent or Absent 3 (2 + dentical) Absent

Fused with Long[b], Long, separate L

ong, Separate Pointed, Long, Separate Long or

short, *T* Long separate dens pointed, separate (f

used separate or separate separate separate or

short with absent) lamella Rami tenaculum 2 +

or
none
(no
None
? p2
or p3
None
segment V p
macro
)
macro
chaeta

Abdominal p5 p5 p5 p5 p5 p5 or p4 p5 ? p5 p4

Abdominal p2 p1 or p2 ? p1 p1 None A1

segment IV ss

Abdominal p4 p3 p3 p3 p2, p3 or p2, 3, o

or 2 + 23 + 3 teeth

r 4 p2–3 ? p3 or p4 p4 segment V ss p4

Small
Mesochaeta
Sometimes
Macrochaeta
Mesochaeta
Mesochaeta
Mesochaeta ?
Macroseta
Mesochaeta
segments I macrochaeta macrochaeta (macrochaetae) and II length of p2

Furca

Reduced
Normal
Normal
Normal
Reduced
Reduced
Reduced
Normal
Normal
Normal
Mucr
o

Abdominal p5 (some p6) p5 p5 p5 p6 p5 p5 ? p5 p5 segments I–III ss

Abdominal

T | nal segments I length | nal segments | ss | nal segment IV | nal segment V | nal segment V chaeta | maculu | of an | nes

+ 44 + 44 + 4 Reduced 1 + 14 + 4 ? 7–10 + 7–10 4 + 4 or 2, 3 or 4

4 + 44 + 44

[a] Most species in this genus are highly poly-and pluricha etose, so it is difficult to establish homologies of setae. [b] 'Long' is approximately equal to half or a third dens in length. Other genera are included within Hypogastruridae, which are morphological candidates with a focus on Australasian and Antarctic representatives. Character information sourced from da Gama (1969), Fjellberg (1990, 1998, 2010), Palacios–Vargas & Janssens (2006), Thibaud *et al.* (2004), Queiroz & Deharveng (2008), Wu & Yin (2007), Najt & Weiner (1997) and Salmon (1962).

claw) third to length of setiform one-fif

th claw) length of claw)

On the basis of these characters of generic status, and the most current phylogeny using both mitochondrial and nuclear markers, and including both *Schoettella* and *Gomphiocephalus*, there is no support for maintaining *Gomphiocephalus* as a subgenus of *Schoettella*. The morphological and molecular relationships reported here indicate that it is not closely related to any other genus in the family. As we build on robust molecular phylogenies (taxon sampling and sequence data), we move a step closer to a greater understanding of the relationships of Antarctic genera, and the palaeogeography and evolutionary history of the region. Here, our morphological and molecular evidence unequivocally supports restoring an ancient Antarctic endemic genus. Rather than molecular data replacing morphology (Packer *et al.*, 2009; Bybee *et al.*, 2010; Cook *et al.*, 2010), we suggest that it is now normal practice in taxonomy and systematics to indulge in both approaches.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2010.00553.x

Table S1. List of taxon names, locations and molecular data (showing GenBank accession numbers) for the D1, D2 and D3 regions of *28S* and *COI* for 76 taxa.

Table S2. Cladogram lengths and incongruence values (ILD metrics) for separate and combined analyses for each of the nine explored parameter sets.

Appendix S1. Nexus files containing the *COI*,D1,D2 and D3 alignments from *28S* and all trees generated from all analyses.

Figure S4. Maximum likelihood analysis with bootstrap support shown at nodes (500 replicates), all other notation as in Fig. 2.

Figure S5. Diagnostic generic characters between *Schoettella*, *Xenylla* and *subcorta*.

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