Molecular and morphological systematics of hypogean schizomids (Schizomida : Hubbardiidae) in semi-arid Australia

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*Abstract***.** We used molecular and morphological techniques to study troglobitic schizomids inhabiting a variety of subterranean landforms in semi-arid Western Australia. The study was designed to explore the taxonomic and phylogenetic status of newly discovered populations of subterranean schizomids. Molecular sequences of the mitochondrial DNA (mtDNA) Cytochrome Oxidase subunit 1 (COI) and small subunit ribosomal RNA (12S) were obtained from a total of 73 schizomid specimens. Populations sampled from boreholes within mesa landforms in the Robe Valley were highly genetically distinct from species of *Draculoides* found elsewhere in the Pilbara (Cape Range and Barrow Island). Pronounced genetic structuring was also evident at a fine spatial scale within the Robe Valley, with populations from each of the mesas examined exhibiting unique and highly divergent mtDNA lineages. These molecular data were generally supported by small but significant morphological features, usually in the secondary male structures, but some species were represented only by female specimens which possessed more conservative morphologies. The molecular data defined two major in-group clades, which were supported by morphological differences. One clade was widespread and included the type species of

Draculoides, *D. vinei* (Harvey), along with *D. bramstokeri* Harvey and Humphreys, *D. brooksi* Harvey, *D. julianneae* Harvey, *D. mesozeirus*, sp. nov. and *D. neoanthropus*, sp. nov. The second clade was restricted to the Robe Valley and deemed to represent a new genus, *Paradraculoides*, which included four new species *P. anachoretus*, sp. nov., *P. bythius*, sp. nov., *P. gnophicola*, sp. nov. and *P. kryptus*, sp. nov. (type species).

Introduction

Arid and semi-arid biotopes have traditionally been considered poor prospects for subterranean fauna as the chances of moisture-dependent organisms finding suitable subterranean microclimates sustained over the course of millions of years of surface aridification being considered too remote (e.g. Peck 1980; Howarth 1988). However, the arid zone of Western Australia has forced these views to be substantially reviewed with the discovery of multiple separate lineages of both troglobites – organisms residing in air-filled voids – and stygobites – organisms residing in water-filled voids – including numerous invertebrates, but predominately arachnids, myriapods, crustaceans and insects (e.g. see reviews of Harvey *et al.* 1993; Humphreys 1999, 2000, 2001b, 2001a; Eberhard *et al.* 2005; Humphreys 2006). These subterranean organisms are thought to have evolved *in situ* from a time prior to the aridification of the region during the mid-Tertiary (late Miocene-Pliocene) when the surface environment was largely forested and mesic (Truswell 1990), supporting many lineages of sub-tropical fauna which no longer occur in the area (e.g. Humphreys 2000).

Amongst the many different arthropod assemblages now known to be present in the area, members of the arachnid order Schizomida are amongst the best studied (Harvey 1988; Humphreys *et al.* 1989; Humphreys 1990; Humphreys and Collis 1990; Humphreys 1991; Harvey 1992; Adams and Humphreys 1993; Harvey and Humphreys 1995; Humphreys 2000; Harvey 2001b). Indeed, the discovery (Main 1980) and subsequent description of *Schizomus vinei* Harvey, 1988 twenty years ago (Harvey 1988) was one of the first descriptions of a troglobitic organism from the Cape Range region, which is now known to be amongst the richest sites for hypogean diversity in the world (Humphreys 2000). *Schizomus vinei* was later transferred to the genus *Draculoides* Harvey, 1992 (Harvey 1992) and found to occur in numerous caves within the Cape Range peninsula (Harvey 1992; Harvey and Humphreys 1995; Harvey 2001b). The genus *Draculoides* was later augmented with three additional species, *D. bramstokeri* Harvey and Humphreys, 1995 from caves and bores on Barrow Island and the north-eastern tip of the Cape Range peninsula (Harvey and Humphreys 1995), *D.*

julianneae Harvey, 2001 from a cave situated on the western side of Cape Range (Harvey 2001b), and *D. brooksi* Harvey, 2001 from a borehole on the northern end of Cape Range (Harvey 2001b). Such fine-scale distributions are not unusual for schizomids and similar patterns have been documented in other regions of the world, in particular the south-western U.S.A. and Mexico (e.g. Rowland and Reddell 1979a, 1979b, 1980, 1981; Reddell and Cokendolpher 1991), and Cuba (e.g. Armas 1989; Teruel 2000; Armas 2002a, 2002b; Teruel and Armas 2002; Teruel 2003; Armas 2004; Teruel 2004; Armas 2005). It seems probable that most species of Schizomida have highly restricted and localised distributions which reflects their narrow environmental tolerances and low dispersal capabilities (Vine *et al.* 1988; Humphreys *et al.* 1989), fitting the definition of short-range endemics as defined by Harvey (2002). The only exceptions appear to be *Zomus bagnallii* (Jackson, 1908) and *Stenochrus portoricensis* Chamberlin, 1922 that have very wide distributions (e.g. Rowland and Reddell 1980; Martín and Oromí 1984; e.g. Reddell and Cokendolpher 1995; Harvey 2001a, 2003) and may have been inadvertently dispersed via human transport systems.

The apparent predilection for short-range endemism displayed by Australian schizomids (Harvey 2002) promises exciting discoveries regarding the evolutionary consequences of the late Miocene aridification in northern Australia. The present study was conceived to understand the relationships amongst schizomid specimens that were recovered from within seven pisolite mesas, or channel iron deposits (Ramanaidou *et al.* 2003; MacPhail and Stone 2004) in the Robe River Valley (Fig. 10). These landforms were created by the erosion of a linear body of iron-rich alluvial material that collected in palaeoriver channels during the early-mid Miocene (ca. 24-10 mya), at a time when surface environments were wetter than at present (MacPhail and Stone 2004). They contain many small fissures and cavities, and support a small but complex array of troglobitic invertebrates such as spiders, mites, pseudoscorpions, springtails, silverfish, diplurans and cockroaches (Humphreys, G., unpublished data). In many cases these fauna appear to represent descendents of forest-dwelling surface forms that retreated below the surface after the onset of aridity in the region approximately 10 mya (BMR Palaeogeographic Group 1990; Humphreys 1993b). The hypogean schizomids studied here are restricted to the Pilbara bioregion which covers an area of 179,287 km^2. The western Robe Valley mesas fall within the Chichester sub-bioregion, which is described as "Archaean granite and basalt plains supporting shrub steppe" (Thackway and Cresswell 1995). Cape Range belongs to the Carnarvon bioregion: "Quaternary alluvial, Aeolian and marine sediments overlying Cretaceous strata" (Thackway and Cresswell 1995).

The resulting molecular and morphological analyses have found that each mesa – the largest only some 989 hectares – contains its own endemic schizomid species. In addition, we were able to include molecular and morphological data for some of the previously named species of *Draculoides* from Cape Range peninsula and Barrow Island, as well as morphological data for a single male specimen recovered from near the Pilbara town of Newman, while sampling a borehole for stygofauna.

Examination of the morphological features of the Pilbara specimens allowed us to recognise several putative morphologies consistent with in-situ speciation events and to detect two divergent clades. In addition to the morphological data, we also make use of DNA sequence data to diagnose these new schizomid species based on unique combinations of nucleotide substitutions (Bond and Sierwald 2003). This combined data approach was necessary because of the difficulty in obtaining adult specimens that bear the mature reproductive organs usually used for the diagnosis of schizomid species (e.g. Rowland and Reddell 1979a, 1979b, 1980, 1981; e.g. Harvey 1992; Reddell and Cokendolpher 1995), which is a common problem for studies of subterranean invertebrates (Paquin and Hedin 2004). Following Bond and Sierwald (2003), we use unique combinations of nucleotide substitutions to diagnose species. In doing so our diagnoses are explicitly made within the framework of the phylogenetic species concept (Nixon and Wheeler 1990).

Materials and Methods

Specimen sampling

The material utilised in this study was obtained using two different methods. Some specimens were hand collected from within caves in the Cape Range area. Schizomids and other troglofauna from the Robe Valley and Barrow Island were sampled by means of custom-built litter traps suspended within boreholes in each of the various study areas. Drill logs were reviewed, where available, to identify areas where fracture zones or cavities occurred in the profile. Traps were suspended within each hole sampled to align with these more prospective zones. Traps were constructed from 60 mm internal diameter PVC storm-water pipe cut to a length of 120 mm. The external diameter of the completed trap was such that it fit closely against the interior of the sampled bore once installed, facilitating fauna entry into the trap. Both ends were sealed with 10 mm spacing aviary mesh after the tubing was filled with wet leaf litter. Leaf litter material was gathered locally from the ground surface on the island, particularly from the bases of *Acacia* shrubs. The collected litter was soaked in water and irradiated in a microwave oven on maximum power setting (to kill any

surface invertebrates present and assist in break-down). Litter was added to the traps wet and kept in sealed containers until immediately prior to insertion into the boreholes. After the installation of each trap, the opening of each borehole was sealed to maintain humidity and to minimize the input of surface fauna into the traps. Traps were left in the ground for approximately six weeks to allow sufficient time for troglofauna colonization. Traps were then recovered and stored in labeled zip-lock bags for return for sorting in the laboratory.

The specimen recovered from near the town of Newman was found during sampling for stygofauna. It was collected from a borehole using a plankton net.

The maps were produced with the computer program ArcView 3.2 (ESRI Inc., Redlands, CA) after the relevant locality data were stored in an Access database. Coordinates were obtained from global positioning system (GPS) coordinates taken *in situ* at the time of collection.

DNA extraction, polymerase chain reaction and characterisation of mtDNA sequences

DNA was extracted from whole animals or 1-2 individual legs with a Qiagen DNeasy kit (Hilden, Germany) with final elution on 60uL AE buffer. Where the entire specimen was utilized no voucher specimen exists. However, such individuals were chosen from samples containing multiple specimens and those specimens form the morphological vouchers for each putative taxon.

Sequences from the mitochondrial Cytochrome Oxidase subunit I (COI) and small subunit ribosomal RNA (12S) were obtained from a total of 73 schizomid specimens from the Robe Valley, Barrow Island and Cape Range (Table 1). These sequences consisted of 696 nucleotides (nt) and 428 nt from COI and 12S respectively, and were PCR amplified with the primers schiz–COI-115F (CAGCCCACGCTTTTGTAATAA), schiz-COI-863R (GGCTGCTGTAAAATAAGCTCGT), and 12SR-J-14199 (Kambhampati and Smith 1995), 12SAI (Kocher *et al.* 1989) respectively. Typical 25 µL PCR reactions consisted of PCR Buffer (160mM $(NH_4)_2SO_4$, 670mM Tris-HCl pH 8.0, 0.1% Tween-20; Bioline, UK), 2.5mM $MgCl_2$, 0.2mM each dNTP, 1.5 U Taq (Bioline RedTaq), primers (both 0.4µM), and 2.5 µL DNA template. The reaction was cycled through 94°C 2 minutes, (94°C 30 seconds, $T_{annealing}$ °C 20 seconds, 72°C 15 seconds) x 35, 72°C 2 minutes. Annealing temperature was 48˚C for COI and 40˚C for 12S. PCR products were purified using a MoBio PCR cleanup kit and sequenced using the ABI BigDye chemistry.

Molecular phylogenetic analysis

Sequences were checked by eye and edited using SEQUENCHER software (GENECODES). Alignment was performed with CLUSTAL W (Higgins *et al.* 1994) with default parameters. Phylogenetic relationships among haplotypes were determined by maximum likelihood analysis (ML) and maximum parsimony (MP) analysis implemented in the program PAUP* version 4.0b10 (Swofford 1998). Analysis was conducted on the combined COI and 12s sequence because analysis of each gene separately produced highly congruent trees (results not shown). Prior to ML analysis we determined the model of sequence evolution that best fitted the data according to the Aikaike Information Criteria (AICc) with MODELTEST 3.6 (Posada and Crandall 1998), and used these parameter estimates as input for PAUP*. ML analysis was conducted using a heuristic search with tree-bisection and reconnection (TBR) branch swapping and 10 random addition sequences per search. Support for clades was evaluated with non-parametric bootstrapping incorporating 100 pseudoreplicates with TBR and three random addition sequences per search. For MP analysis gaps were treated as a fifth state, and heuristic searches consisted of 500 random sequence additions with a maximum of 100 trees retained per replicate and rearranged using TBR branch swapping. Support for clades was evaluated with non-parametric bootstrapping, incorporating 500 pseudoreplicates with 100 trees retained at each step and rearranged using TBR branch swapping.

Molecular diagnosis of species

Combinations of nucleotide substitutions that were unique and therefore diagnostic for each species were determined using the trace all characters function of the MESQUITE program (Maddison and Maddison 2005). To do so we created a strict consensus tree from the six best trees identified in the MP analysis, all with 1165 steps, and plotted the nucleotide substitutions that diagnosed each clade onto this tree. Following the methods of Bond and Sierwald (2003), we report for each species the character state (nucleotide) followed by the nucleotide position number in brackets. The nucleotide position number refers to the position in the aligned data set. For the COI sequence these numbers correspond to positions 1684-2379 of the *Drosophila yakuba* Burla reference sequence [NC_001322; (Clary and Wolstenholme 1985)]. Alignment of the 12S sequence to a reference sequence is more problematic because of the presence of insertions and deletions.

Morphological examination

All specimens utilised in this study are lodged in the Western Australian Museum, Perth (WAM). Apart from the in-group specimens listed below as part of the taxonomic review, we also utilized specimens of two other Australian schizomids as out-group taxa in the molecular and morphological analyses (Table 1).

Terminology of the morphological structures follow Harvey (1992) and Reddell and Cokendolpher (1995). The following abbreviations were used for the setae of the flagellum: dm1, 4 (dorso-median 1, 4), dl1, 3 (dorso-lateral 1, 3), vm1, 2, 4, 5 (ventro-median 1, 2, 4, 5), vl1, 2 (ventro-lateral 1, 2).

The specimens were examined with a Leica MZ16 microscope (Leica Microsystems Ltd, Heerbrugg, Switzerland). The whole-body images were composed using the software program AutoMontage Pro Version 5.02 (p) (Syncroscopy; Cambridge, UK) utilizing multiple images taken with a Micropublisher 5.0 digital camera, manufactured by Q-Imaging (Surrey, BC, Canada), attached to the Leica microscope. Temporary slide mounts of dissected structures were prepared by immersion of specimens in concentrated lactic acid at room temperature for several hours, and mounting them on microscope slides with 10 or 12 mm cover-slips supported by small sections of 0.25 mm diameter nylon fishing line. These slide-mounts were studied with an Olympus BH-2 compound microscope (www.olympusmicro.com, verified August 2007) and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 x 3 mm glass genitalia microvials (BioQuip Products, Inc.; Rancho Dominguez, CA).

Phylogenetic analysis based on morphology

Phylogenetic analyses based upon morphology were performed through the examination of specimens of all species of *Draculoides* and *Paradraculoides*, plus two out-group species of the subfamily Hubbardiinae, *Bamazomus* sp. and *Brignolizomus woodwardi* (Harvey, 1992) (Table 1). Each species included in this study was examined for characters that could be used in a morphological analysis. The data were collated and managed in Nexus Data Editor version 0.5.0 (Page, 2001). A total of 12 characters were included in the analysis. All characters were treated as unordered and despite the invocations by some authors to remove uniformative (autapomorphic) characters from analyses (see Bryant 1992; see Yeates 1992; Prendini 2000), two autapomorphic characters were retained in the analysis so that a full

range of characters was treated. The data were analysed with the programs Winclada version 1.00.04 (Nixon 2002) and NONA version 2.0 (Goloboff 1993). The data were analysed under equal weights using the heuristics function in NONA with the parameters set to "Maximum trees to keep = 1,000,000", "Number of replications (mult*N) = 1,000", "Starting trees per rep (hold/) = 1,000", and "Multiple TBR + TBR (mult*max*)". Each of the trees produced using NONA and Winclada were viewed after the function "hard collapse unsupported nodes in ALL trees" was invoked. Support for individual nodes was measured by jackknifing (Farris *et al.* 1996), which examines the effect of randomly removing characters; it was implemented within Winclada and NONA.

Character states

Character 1. Pedipalp, trochanter, mesal spur: 0, present; 1, absent.

The pedipalpal trochanter of most hubbardiids bears a small but distinct median spur (e.g. Harvey, 1992; Reddell and Cokendolpher, 1995). This spur is absent in all species of *Draculoides* and *Paradraculoides*.

Character 2. Abdomen, tergite II, number of setae: 0, 2 setae + 3 pairs of microsetae; 1, 3 setae + 3 pairs of microsetae

Tergite II of most hubbardiids possess 2 setae (in addition to the 3 pairs of microsetae situated in the anterior half) (Fig. 11). All species of *Paradraculoides* possess 3 setae (Fig. 12), a unique feature within the family. The only other hubbariids with more than 2 setae are species of *Clavizomus* Reddell & Cokendolpher, 1995 from south-east Asia and *Mayazomus* Reddell & Cokendolpher, 1995 from central America which possess more than 3 setae (Reddell and Cokendolpher, 1995).

Character 3. Size: 0, small (e.g. propeltidium length less than 1.6 mm); 1, large (e.g. propeltidium length greater than 1.65 mm).

Two species of the group included in this analysis are substantially larger than the others. *Draculoides vinei* and *D. julianneae* have a female propeltidium length of 1.66-2.23 mm, whereas the others are less than 1.6 mm with the largest being *D. brooksi* (1.51 mm) and the smallest being *P. kryptus* (0.93-1.26 mm).

Character 4. Gonopod, female: 0, present; 1, absent.

The female genital region of most hubbardiids bears one or more pairs of spermathecae and usually a median gonopod (e.g. Reddell and Cokendolpher, 1995). *Draculoides vinei* is the only Australian hubbardiid that lacks a gonopod (Harvey, 1988, 1992).

Character 5. Flagellum, male, lateral compression: 0, not laterally compressed; 1, laterally compressed.

The male flagellum of species of *Draculoides* is laterally compressed such that it is much higher than wide (Figs 13-17, 22-24, 29-31). In nearly all other hubbardiids, the male flagellum is dorso-ventrally flattened (e.g. Figs 36-38, 47-49) or, at most, somewhat globular.

Character 6. Flagellum, male, distal constriction: 0, absent; 1, present.

The tip of the male flagellum of *D. vinei* and *D. julianneae* is constricted in the region of seta dl1 (Figs 22, 23; Harvey, 1992), rather than evenly tapering to the end (e.g. Figs 14, 15, 29-31).

Character 7. Flagellum, male, seta dm4, position: 0, situated distally; 1, situated medially.

Seta dm4 of the male flagellum is distally placed in many different Australian hubbardiids (e.g. Figs 36, 38, 47, 49), but is situated medially in most species of *Draculoides* (Figs 14, 16, 22, 24, 29, 31), with the exception of *D. vinei* (Fig. 13).

Character 8. Flagellum, male, seta dl1, size: 0, not reduced; 1, reduced.

Seta dl1 of the male flagellum of most hubbardiids is approximately the same size as other setae on the flagellum (Figs 38, 49). Seta dl1 of the three species of *Draculoides* found on Cape Range, *D. vinei*, *D. julianneae* and *D. brooksi*, is much smaller than the other setae (e.g. Figs 13, 24).

Character 9. Flagellum, male, seta vl1, position: 0, situated laterally; 1, situated ventrolaterally.

Seta vl1 is usually situated laterally on the male flagellum in hubbardiids. This seta appears to have been relocated slightly ventrally in several species, including all species of *Draculoides* and *Paradraculoides* (Figs 16, 31) except for *D. julianneae* (Fig. 24) and in *P. kryptus* (Fig. 49).

Character 10. Flagellum, male, seta dl3, position: 0, situated on same level as vl2; 1, situated posterior to vl2.

Seta dl3 of the male flagellum is usually situated on the same level as seta vl2 (Figs 16, 31, 49). In *D. julianneae*, *D. vinei* and *P. bythius*, dl3 is situated posterior to seta vl2 (Figs 13, 24, 38).

Character 11. Flagellum, male, seta vm1: 0, situated on same level as vm2 or slightly posterior to vm2; 1, situated anterior to vm2.

Seta vm1 of the male flagellum is situated adjacent to vm2 or slightly posterior to vm2 in most of the species included in this study (e.g. Figs 13, 23, 37, 48). In *D. bramstokeri* and

D. neoanthropus seta vm1 is situated anterior to vm2 (Figs 15, 30).

12. Flagellum, female, microseta: 0, situated dorsal to seta vm4; 1, situated near seta vm2

A pair of small microsetae is present on the female flagellum, either dorsal to seta vm4 (Figs 20, 27, 34, 45), or situated near seta vm2. Amongst the taxa included in this study, only *P. bythius* possesses the latter morphology (Figs 41, 52).

Results

A total of 1119 nucleotides were sequenced, and these consisted of 436 (39%) variable sites of which 355 (32%) were parsimony informative. Base frequencies were unequal (A = 35.8%, T = 37.5%, C = 14.9%, G = 11.8%). No stop codons were identified in the protein coding COI gene indicating that the sequence was of mitochondrial origin. Overall 56 haplotypes were recovered, including 34 from the Robe Valley. These sequences have been deposited in Genbank under accession numbers EU272675 - EU272786, and are available as an alignment file on the Entrez database.

The substitution model identified by the AICc as most appropriate for the combined dataset was a GTR + I + G with the proportion of invariant sites estimated to be 0.5117, and the gamma shape parameter estimated to be 1.7716. The maximum likelihood and parsimony analysis of the molecular data produced identical tree topologies, and identified five strongly supported clades from the Robe Valley (Fig. 4). Each clade is restricted to an individual mesa, except in the case of clade B/C, which is shared by Mesas B and C (Fig. 4). Each of these clades is differentiated by a unique combination of nucleotide substitutions, which are summarized in Table 2. The clades A, B/C, G, K, and MR exhibit 7, 15, 7, 21, and 54 unique nucleotide substitutions. In addition, strongly supported clades that corresponded to *D. bramstokeri* (Barrow Island), *D. vinei*, *D. julianneae* (both Cape Range) were identified. These exhibited 24, 11, and six unique nucleotides substitutions, respectively.

The morphological analysis using NONA and Winclada produced three trees of 16 steps and three trees of 17-18 steps. The three shortest trees were retained, and each had a Consistency Index of 0.75 and a Retention Index of 0.80. Two of these trees recovered both *Draculoides* and *Paradraculoides* as monophyletic clades, with the remaining tree recovering a monophyletic *Paradraculoides* and a paraphyletic *Draculoides*. The paraphyly of *Draculoides* is driven by the position of *D. mesozeirus*, which was placed as the sister to *Paradraculoides* plus the remaining *Draculoides*; the ambiguous placement for *D. mesozeirus* is due to the lack of male specimens. In all three trees *D. vinei* and *D. julianneae* are

recovered as sister-species, as are *D. bramstokeri* + *D. neoanthropus*, although in one tree, D. mesozeirus is placed with *D. bramstokeri* + *D. neoanthropus* as a trichotomy. The strict consensus tree (length 20 steps, Consistency Index 0.60 and Retention Index 0.60) found a monophyletic *Paradraculoides* but rendered *Draculoides* as a flat comb (Fig. 5), even though the clade *D. vinei* + *D. julianneae* was supported.

Whilst the general structure of the trees produced in the morphological analysis mimic those found in the molecular analysis, the latter analysis, unsurprisingly, detected higher resolution within each genus and within individual species. The trees were identical whether *Brignolizomus woodwardi* or *Bamazomus* sp. was selected as the outgroup.

The morphological analysis suffered from the lack of males for *D. mesozeirus, P. anachoretus* and *P. gnophicola*, and the lack of females for *D. neoanthropus*, producing numerous missing entries. The removal of these four species, followed by a similar analysis using NONA and Winclada with identical search parameters, produced a single most parsimonious tree of 16 steps, a Consistency Index of 0.75 and a Retention Index of 0.75. This tree (Fig. 6) found complete support for the monophyly of both *Draculoides* and *Paradraculoides*.

Discussion

The combination of molecular and morphological analyses employed in this study unambiguously defines multiple species restricted to several different landforms in arid Western Australia. The likelihood of further species occurring in other subterranean habitats within the Pilbara and adjacent regions cannot be discounted; indeed the extremely rapid rate of discovery of new troglofauna and stygofauna within the region suggests that further discoveries of hypogean schizomids are inevitable. The presence of *Draculoides neoanthropus* within alluvial deposits in the Newman region some 420 km away from its nearest relative (Fig. 7) is a case in point. Despite knowledge of the presence of stygofauna in the Newman area for several years (e.g. Bradbury 2000), detailed searches for troglofauna have not yet been undertaken.

The Australian schizomid fauna is represented by several hypogean species located in the Pilbara and Kimberley of Western Australia, Cutta Cutta caves, Northern Territory, and the Chillagoe caves, Queensland (Harvey 1988; Harvey and Humphreys 1995; Harvey 2000a, 2001b). The remaining species are found in rainforest biotopes across northern Australia, extending as far south as south-eastern Queensland (Harvey 1992, 2000b) and northern New South Wales (Harvey, unpublished data). This strongly suggests that the semi-arid species nowadays confined to subterranean biotopes are derived from rainforest dwelling ancestors

(Humphreys 1993b). The onset of aridification throughout inland Australia, which began during the Late Miocene and Early Pliocene, is suggested to have brought about the loss of mesic forest systems (Truswell 1990). Certain invertebrate assemblages are hypothesized to have colonized subterranean spaces, accumulating troglomorphic morphological features (Humphreys 1993b). The lack of any epigean schizomids throughout the Pilbara suggests that the aridification process has culminated in the entire modern schizomid fauna being represented by subterranean relicts.

Although the subterranean schizomid fauna of Western Australian contains representatives of several genera (Harvey 1992; Harvey and Humphreys 1995; this study; Harvey 2001b), we have been able to obtain molecular data for representatives of *Draculoides* and *Paradraculoides*. Members of these two genera share a significant morphological character, the lack of a mesal spur on the pedipalpal trochanter. This spur is present in the vast majority of hubbardiid genera, including most Australian species, and the lack of a spur has been used to define the genus *Draculoides* (Harvey 1992; Reddell and Cokendolpher 1995). Thus, unless the spur has been lost more than once, it seems that parsimonious to assume that all of the Pilbara species lacking the spur form a monophyletic group. In our analysis, which admittedly is limited in scope, this character (Character 1) served to unambiguously unite *Draculoides* and *Paradraculoides* in a single clade. Within this clade, our study identified two major groups with *Draculoides* including *D. vinei*, *D. julianneae*, *D. bramstokeri* and *D. mesozeirus*, and *Paradraculoides* containing *P. anachoretus*, *P. bythius*, *P. gnophicola*, *P. kryptus* and *P*. sp. (Warramboo). Support for the *Paradraculoides* clades was strong under the molecular analysis, whereas support for the *Draculoides* clade was weaker (Fig. 4). The morphological analysis supported both clades but only when adults of both sexes were available for study (Fig. 6). Regrettably, adult males were unavailable for *P. anachoretus*, *P. gnophicola* and *P*. sp. (Warramboo), adult females were not available for *D. neoanthropus* and *P*. sp. (Warramboo). Our analysis was further hampered by the absence of sequence data for *D. brooksi* and *D. neoanthropus*. Further examination of morphological and molecular data – including more slowly evolving genes – as well as additional taxa, may help to sort the relationships of these organisms within the region.

The sampling regime adopted in this study concentrated on the fauna found within the pisolitic mesas in the Robe River valley and the limestone karst on Barrow Island, with less emphasis on the Cape Range fauna. Thus we were unable to test the genetic provinces detected within *D. vinei* by Adams and Humphreys (1993).

All of the species included in the present study are short-range endemics as defined by Harvey (2002). The most wide-ranging species, *D. vinei* and *D. bramstokeri*, occur over an area

of 87 and 148 km^2 on Cape Range peninsula and Barrow Island, respectively, in limestone karsts. The other eight species of *Draculoides* and *Paradraculoides* have very small ranges. Six of the mesas along the Robe River Valley each contain endemic species of schizomids: *D. mesozeirus* within Middle Robe; *P. anachoretus* within Mesa A; *P. bythius* within Mesa B and Mesa C; *P. gnophicola* within Mesa G; *P. kryptus* within Mesa K; and *P.* sp. within Warramboo. The latter species is readily diagnosed using molecular sequence data (Fig. 4) but is not named in this study due to the lack of adult specimens. Each of these mesas have been separated from each other due to geological uplift and erosion events along the river valley, isolating troglofauna within each mesa and restricting gene flow such that subsequent speciation has occurred. Each mesa has been highly eroded internally such that small fissures and voids permeate the substrate.

The four species named above in the new genus *Paradraculoides*, along with a fifth species that is not named due to the lack of adult material (*P.* sp. Warramboo), are restricted to the western deposits in the Robe Valley, Mesas A, B, C, G, K and Warramboo. The only species of *Draculoides* in the Robe Valley, *D. mesozeirus* from Middle Robe, is genetically (Fig. 4) and morphologically (Fig. 5) more similar to the other species of the genus and indeed, was found to be the sister-species to *D. bramstokeri* from Barrow Island (Fig. 4), despite poor branch support and long branch lengths. The male flagellum of *Draculoides bramstokeri* (Figs 14-17) shows strong similarities to that of *D. neoanthropus* from the Newman region of the Pilbara (Fig. 29-31) which is not reflected in the morphological analysis (Fig. 5). The lack of molecular sequence data for *D. neoanthropus* and the lack of adult male specimens of *D. mesozeirus* ensure that any resolution between the two data sets will remain speculative.

Each of the Robe Valley mesas contains other troglofauna, some of which have been taxonomically studied, including blind, troglobitic pseudoscorpions of the families Chthoniidae (Edward and Harvey in press) and Syarinidae (Harvey and Edward 2007), and a blind oonopid spider (Harvey and Edward in press). Further searches for troglofauna, including schizomids, should be conducted especially in areas likely to be affected by resource development in the Pilbara and adjacent areas. The findings of this study indicate that the relictual distributions of these short-range endemic subterranean invertebrates may coincide with channel iron deposit formations in topographically inverted landscapes in the Pilbara region (Ramanaidou *et al.* 2003; Twidale 2003). This in turn suggests that future major mining developments may adversely affect populations of these Tertiary relicts.

Systematics

Family **Hubbardiidae** Cook

Subfamily **Hubbardiinae** Cook

Genus ***Draculoides*** Harvey

Draculoides Harvey, 1992: 82-83; Harvey and Humphreys, 1995: 183-184; Reddell and Cokendolpher, 1995: 69.

Type species

Schizomus vinei Harvey, 1988, by original designation.

Diagnosis

Draculoides is very similar to *Paradraculoides* as they both lack a mesal spur on the pedipalpal trochanter, a exhibited by few other hubbardiids. *Draculoides* differs from *Paradraculoides* by the laterally compressed male flagellum, and the presence of only 2 setae on tergite II. *Paradraculoides* has a dorso-ventrally compressed male flagellum and has 3 setae on tergite II.

Description

Body without clavate setae. Anterior process of propeltidium with pair of setae followed by single seta; corneate eyes and eye spots absent; metapeltidium divided. Pedipalp not sexually dimorphic and without armature; trochanteral mesal spur absent; male pedipalps probably not dimorphic. Moveable cheliceral finger with 1 or 2 accessory tooth and guard tooth at end of serrula. Anterodorsal margin of femur IV produced at about a 90° angle. Abdominal tergite II with 2 macrosetae; male abdomen not elongated; male with slight development of posterodorsal process on abdominal segment XII. Male flagellum laterally compressed; female flagellum with three segments. Spermathecae consisting of two pairs of short, uniramous lobes, not strongly connected to each other basally, without nodules, short gonopod present in most species, but absent in *D. vinei*.

Remarks

As noted above the genus *Draculoides* is currently represented by four named species from Cape Range Peninsula and Barrow Island (*D. vinei*, *D. bramstokeri*, *D. julianneae* and *D. brooksi*) (Figs 7-9). We here add a further two species from the Pilbara region, one from a pisolitic mesa near Pannawonica (Fig. 10), and the other from alluvial deposits near Newman

(Fig. 7). All known populations of the genus are troglobitic and are restricted to subterranean cave or fissure environments in a variety of karstic systems.

Key to species of *Draculoides*

1. Males (those of *D. mesozeirus* not known).....2
   Females (those of *D. neoanthropus* not known).....6
2. Flagellum very deep, rounded in lateral view; flagellar seta dl1 not reduced in size; flagellar seta vm1 anterior to vm2 3
   Flagellum less deep, not especially rounded in lateral view; flagellar seta dl1 very small; flagellar seta vm1 on same level as vm2.....4
3. Flagellum terminally pointed..... *D. neoanthropus*
   Flagellum terminally rounded..... *D. bramstokeri*
4. Flagellum not constricted posteriorly in dorsal and ventral views.....*D. brooksi*
   Flagellum constricted posteriorly in dorsal and ventral views 5
5. Flagellum terminally pointed.....*D. vinei*
   Flagellum terminally rounded.....*D. julianneae*
6. Gonopod absent.....*Draculoides vinei*
   Gonopod present 7
7. Propeltidium greater than 1.90 mm in length .....*D. julianneae*
   Propeltidium less than 1.80 mm in length 8
8. Flagellar seta dl1 distal to level of vl1 9
   Flagellar seta dl1 quite close to level of vl1.....*D. mesozeirus*
9. Flagellar seta dm1 on same level as vm2 .....*D. brooksi*
   Flagellar seta dm1 situated slightly posterior to vm2 ..... *D. bramstokeri*

Draculoides vinei (Harvey)

(Figs 8, 13)

Schizomus vinei Harvey, 1988: 16-19, figs 1-9; Vine, Knott and Humphreys, 1988: 21-32, figs 1-3; Humphreys, Adams and Vine, 1989: 177-197, figs 2-5; Humphreys, 1990: 181-185, figs 2-5; Humphreys and Collis, 1990: 102-107, figs 1-4; Humphreys, 1991: 610, 615-619.

Draculoides vinei (Harvey): Harvey, 1992: 83-85, figs 1, 3, 7-11; Adams and Humphreys, 1993: 151-153; Harvey, Gray, Hunt and Lee, 1993: 130, 131; Humphreys, 1993: 166, 167; Georgescu, 1994: 239; Harvey and Humphreys, 1995: 184-185, figs 1-2; Morton, Short and Barker, 1995: 21; Reddell and Cokendolpher, 1995: 69-70, figs 17, 51-54; Humphreys, 1998: 25; Harvey, Shear and Hoch, 2000: fig. 4.2e; Harvey, 2003: 108.

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Shot Pot Cave, C-106, Cape Range [22°04'S,114°01'E], 30.v.1983, M. Newton, B. Alden (WAM 87/987).

Paratypes. **Australia:** *Western Australia:* l ♂, same data as holotype (WAM 87/988); 3 ♀, 14 juveniles, same data except 21.ix.1983, J. Lowry (WAM 84/182-188, 85/1229-1238); 1 ♀, 1 juvenile (without abdomen), Dry Swallet Cave, C18, Cape Range [22°05'S, 114°00'E], 20.v.1983, B. Vine, M. Griffiths, A. Vine, B. Knott (WAM 87/989-990); 1 ♀, same data (Museum of Victoria K-746), not examined for this study; 1 juvenile, 'Spiral Cave', Cape Range, viii.1962, P. Cawthorn (WAM 87/991).

Other material. **Australia:** *Western Australia:* Cape Range: 1 ♀, Anomaly Cave, cave C-96, 22°15'S, 113°57'E (WAM T42239); 1 juvenile, Bell Cave, cave C-29, 22°06'S, 114°01'E (WAM T46832); 1 ♂, 2 juveniles, cave C-102, 22°07'56"S, 113°59'03"E (WAM T40719, T40776); 2 ♂, 2 ♀, cave C-107, 22°07'00"S, 113°59'54"E (WAM T40725, T40726, T40727, T40728); 2 ♂, 13 ♀, 55 juveniles, cave C-118, 22°09'41"S, 113°59'41"E (WAM T98/1560, T98/1563, T40729, T40730, T40731, T40732, T40733, T40734, T40735, T40736, T40737, T40738, T40739, T40740, T40779, T40780, T40781, T40782, T40783, T40784, T40785, T40786, T40787, T40788, T40789, T40790, T40791, T40792, T40793, T40794, T40795, T40796, T40797, T40798, T40799, T40800, T40801, T65508, T65509, T65510, T65511); 1 ♂, 8 ♀, 10 juvenile, cave C-126, 22°08'49"S, 113°59'55"E (WAM T98/1561, T40741, T40742, T40743, T40744, T40745); 2 juveniles, cave C-142, 22°08'30"S, 113°59'09"E (WAM T40802, T40803); 3 juveniles, cave C-154, 22°09'13"S, 113°58'46"E (WAM T40804, T40805, T40806); 1 ♂, cave C-160, 22°12'34"S, 113°58'17"E (WAM T40746); 2 ♂, 1 ♀, 12 juveniles, cave C-167, 22°09'16"S, 113°59'45"E (WAM T98/1562, T40754, T40755, T40756, T40823, T40824, T40825); 2 juveniles, cave C-188, 22°07'S, 114°00'E (WAM T98/1573, T98/1574); 1 juvenile, cave C-203, 22°26'14"S, 113°54'39"E (WAM T40826); 1 juvenile, cave C-227, 22°02'49"S, 114°00'30"E (WAM T40828); 2 juveniles, cave C-247, 22°15'41"S, 113°57'46"E (WAM T40829); 1 ♀, 2 juveniles, cave C-250, 22°16'33"S, 113°58'52"E (WAM T40758); 3 ♂, 7 juveniles, cave C-254, 22°02'16"S,

114°01’31”E (WAM T98/1565, T40759, T40760, T40830, T40831, T40832, T40833, T40834, T40835); 9 juveniles, cave C-256, 22°01’15”S, 114°02’39”E (WAM T40836, T40837, T40838, T40839, T40840); 2 juveniles, cave C-260, 22°04’24”S, 113°58’59”E (WAM T40841, T40842); 1 ♀, 2 juveniles, cave C-263, 22°01’00”S, 114°02’37”E (WAM T40761, T40843); 2 juveniles, cave C-277, 22°04’09”S, 113°59’01”E (WAM T40844); 2 specimens, cave C-29, 22°06’S, 114°01’E (WAM T98/1580, T98/1581); 1 juvenile, cave C-291, 22°16’01”S, 113°57’53”E (WAM T40845); 3 juveniles, cave C-300, 22°16’36”S, 113°57’25”E (WAM T40846); 1 specimen, cave C-312, 22°03’S, 114°01’E (WAM T98/1586); 2 ♀, 6 juveniles, cave C-62, 22°09’55”S, 113°59’18”E (WAM T98/1570, T40769, T40770, T40717, T40771, T40772, T40773, T40774); 1 ♂, 1 ♀, 3 juveniles, cave C-65, 22°05’42”S, 114°00’03”E (WAM T98/1584, T40718); 1 juvenile, cave C-658, 22°05’24”S, 113°59’00”E (WAM T42201); 1 juvenile, cave C-79, 22°05’33”S, 114°00’08”E (WAM T45925); 1 specimen, cave C-91, 22°05’S, 113°59’E (WAM T98/1579); 1 ♀, 3 juveniles, Cork-screw Cave, C-56, 22°06’21”S, 114°00’11”E (WAM T40716, T40766, T40767, T40768); 1 juvenile, Dog Cave, C-113, 22°10’50”S, 113°59’00”E (WAM T40778); 1 ♂, 2 ♀, 11 juveniles, 3 specimens, Dry Swallet Cave, C-18, 22°05’24”S, 113°59’30”E (WAM T40715, T40764, T40765, T46831, T48331, T65501, T65502, T65503, T65504); 1 ♀, 4 juveniles, Gullet Cave, C-159, 22°07’23”S, 114°00’18”E (WAM T98/1564, T40812, T40813, T40814); 1 juvenile, inside Bell Cave, C-29, 22°06’S, 114°01’E (WAM T57445); 1 ♂, 3 ♀, 5 juveniles, 2 specimens, Papillon Cave, C-15, 22°12’48”S, 113°58’32”E (WAM T98/1566, T98/1567, T98/1575, T98/1582, T98/1583T40714, T40763, T42200, T42237, T42238, T57446); 1 specimen, Pattys Posthole Cave, C-402, 22°12’S, 113°59’E (WAM T40762); 9 ♀, 19 juveniles, 3 specimens, Rock Bench Cave, C-162, 22°09’00”S, 113°59’51”E (WAM T40747, T40748, T40749, T40750, T40751, T40752, T40753, T40817, T40818, T40819, T40820, T40821, T40822, T95/747, T98/1568, T98/1569, T98/1571, T98/1572); 5 juveniles, Root Cellar Cave, C-156, 22°07’16”S, 113°59’45”E (WAM T40807, T40808, T40809, T40810, T40811); 1 juvenile, Shot-hole Tunnel, cave C-64, 22°02’39”S, 114°01’06”E (WAM T40775); 1 ♂, 2 ♀, 5 juveniles, Shotpot Cave, C-106, 22°04’21”S, 114°00’39”E (WAM T40722, T40723, T40724, T40777); 1 juvenile, ‘Spiral’ Cave, C-167, 22°09’09”S, 113°59’44”E (WAM T62595); 2 juveniles, The Star Chamber, cave C-161, 22°12’33”S, 113°58’14”E (WAM T40815); T40816); 2 ♀, Trionomo Cave, C-103, 22°07’26”S, 113°59’18”E (WAM T40720, T40721); 1 ♂, 1 juvenile, Two Hundred Cave, C-207, 22°12’14”S, 113°59’16”E (WAM T40757).

Diagnosis

Draculoides vinei is included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II and the laterally compressed male flagellum. It strongly resembles *D. julianneae* as the males of both species possess a posteriorly constricted flagellum. *Draculoides vinei* possesses a pointed tip to the male flagellum, whereas *D. julianneae* has a small, rounded tip, and females lack a gonopod in the genitalia, whereas females of *D. julianneae* possess a gonopod. This species can be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: C(56), A(164), G(356), C(554), T(627), G(718), A(719), G(789), C(799), A(821), C(907).

Remarks

Draculoides vinei is restricted to caves situated within Tulki limestone along the central elevated section of the Cape Range peninsula. Using morphological (Figs 5, 6) and molecular techniques (Fig. 4), *D. vinei* is consistently most similar to *D. julianneae* which occurs within coastal limestone on the western side of the Cape Range peninsula (Fig. 8).

Draculoides bramstokeri Harvey and Humphreys
(Figs 9, 14-17)

Draculoides bramstokeri Harvey and Humphreys, 1995: 185-187, figs 1-11 (in part, Barrow Island populations only); Reddell and Cokendolpher, 1995: 69; Humphreys, 2001: 114, 121; Harvey, 2003: 108.

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Barrow Island, Ledge Cave (Cave B-1), 20°48’S, 115°20’E, 6.ix.1991, W.F. Humphreys, B. Vine (WAM 93/2094).

Paratypes. **Australia:** *Western Australia:* 1 ♂, 1 ♀, Barrow Island, Cave B-1, 20°48’S, 115°20’E, 10.ix.1991, W.F. Humphreys, B. Vine, D. Goodgame (WAM 93/2096-2097); 2 ♂, 3 juveniles, Barrow Island, Cave B-1, 20°48’S, 115°20’E, 25/04/1992, W.F. Humphreys, B. Vine (WAM 93/2098-93/2102); 1 ♀, Barrow Island, Ledge Cave (Cave B-1), 20°48’S, 115°20’E, 06/09/1991, W.F. Humphreys, B. Vine (WAM 93/2095).

Other material examined. **Australia:** *Western Australia:* Barrow Island: 1 juvenile, 1.3 km NW. of Chevron Texaco Camp, 20°49’12”S, 115°26’04”E (WAM T76924); 3 juveniles, 3.0 km N. of Chevron Texaco Camp, 20°48’04”S, 115°26’44”E (WAM T76923, T66016,

T66017); 1 ♀, 1 juvenile, 3.4 km NNW. of Chevron Texaco Camp, 20°47’54”S, 115°26’05”E (WAM T76936, T66015); 2 juveniles, 3.9 km NW. of Chevron Texaco Camp, 20°47’34”S, 115°26’50”E (WAM T76930); 3 juveniles, 4.0 km N. of Chevron Texaco Camp, 20°47’32”S, 115°27’03”E (WAM T76925, T66001, T66004); 1 ♂, 3 ♀, 4 juveniles, 4.2 km N. of Chevron Texaco Camp, 20°47’26”S, 115°26’57”E (WAM T76933, T66002, T66003); 1 juvenile, 4.3 km N. of Chevron Texaco Camp, 20°47’25”S, 115°27’10”E (WAM 76935); 2 juveniles, 4.4 km N. of Chevron Texaco Camp, 20°47’19”S, 115°26’48”E (WAM T76926, T76931); 1 ♀, 4.5 km N. of Chevron Texaco Camp, 20°47’14”S, 115°26’41”E (WAM T66011); 2 juveniles, 4.6 km N. of Chevron Texaco Camp, 20°47’12”S, 115°26’41”E (WAM T76934, T75209); 2 juveniles, 4.9 km N. of Chevron Texaco Camp, 20°47’27”S, 115°27’14”E (WAM T76928, T75208); 1 ♂, 2 ♀, 5 juvenile, 5.8 km N. of Chevron Texaco Camp, 20°46’33”S, 115°26’53”E (WAM T76927, T76937, T76932, T66012, T66014, T66013, T75204, T75214); 2 juveniles, 6.3 km W. of Chevron Texaco Camp, 20°49’07”S, 115°23’04”E (WAM T75207, T66008); 5 juveniles, 7.0 km NW. of Chevron Texaco Camp, 20°47’04”S, 115°23’41”E (WAM T75206, T66009, T66010); 1 ♂, 1 ♀, 11 juveniles, 7.1 km NW. of Chevron Texaco Camp, 20°47’02”S, 115°23’39”E (WAM T71967, T76929, T 66005, T66006, T66007, T75210, T75205); 1 juvenile, 2 macerated specimens, Bore WB2, 20°51’36”S, 115°21’17”E (WAM T93/2109-93/2110, T42198); 2 ♂, Cave B-1, 5 juveniles, 1 macerated specimen, 20°47’53”S, 115°19’53”E (WAM T93/2103-93/2108, T42197); 2 ♂, 1 juvenile, Cave B-10, 20°49’S, 115°23’E (WAM T93/2112-T93/2115); 1 juvenile, Cave B-6, 20°51’S, 115°23’E (WAM T93/2111); 1 juvenile, old L4 anode well, 20°48’22”S, 115°23’21”E (WAM T42199); 6 juveniles, old WB2 anode well, 20°51’36”S, 115°21’17”E (WAM T42195); 1 juvenile, old WF7 anode well, 20°51’01”S, 115°22’43”E (WAM T42196); 1 juvenile, site WB.2, 20°46’S, 115°24’E (WAM T60181); 1 juvenile, site WL4, 20°46’S, 115°24’E (WAM T 60180).

Diagnosis

Draculoides bramstokeri is included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II and the laterally compressed male flagellum. Males differ from all other species of the genus except *D. neoanthropus* by the very deep, rounded flagellum, the flagellar seta dl1 not reduced in size and flagellar seta vm1 situated anterior to vm2. It differs from *D. neoanthropus* by the small, rounded terminal flagellar tip which is drawn to a distinct point in *D. neoanthropus*. This species can be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: T(36), A(50), T(98), C(120), C(170), A(173), G(246), T(254), C(315), C(316), T(419), G(468), A(548),

C(850), A(877), C(906), T(910), C(913), A(918), T(1000), T(1046), T(1080), T(1087), C(1098), A(1100).

Description

See Harvey and Humphreys (1995).

Remarks

Draculoides bramstokeri was described by Harvey and Humphreys (1995) primarily based upon specimens from Barrow Island, situated off the coast of Western Australia. Harvey and Humphreys (1995) also attributed several specimens to this species from the Exmouth region of Cape Range peninsula. As outlined below, the Exmouth material is now considered to represent specimens of *D. brooksi*, and thus *D. bramstokeri* is endemic to Barrow Island (Fig. 9), and *D. brooksi* is restricted to the north-eastern region of Cape Range peninsula (Fig. 8).

Draculoides brooksi Harvey

(Figs 8, 11, 18-21)

Draculoides bramstokeri Harvey and Humphreys, 1995: 184-187 (in part, Exmouth populations only).

Draculoides brooksi Harvey, 2001: 174-175, figs 2, 4-6; Harvey, 2003: 108.

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Cape Range area, Ampolex A borehole, 21°53'S, 114°06'E, 28.iv.1996, litter trap in base of borehole, W.F. Humphreys, R.D. Brooks (WAM T40640).

Other material examined. **Australia:** *Western Australia:* 3 juveniles, Cape Range area, Ampolex A borehole, 21°53'S, 114°06'E, 28.iv.1996, litter trap in base of borehole, W.F. Humphreys, R.D. Brooks (WAM T40641); 1 juvenile, Camerons Cave (C-452), 21°58'S, 114°07'E, 26.x.1994, R.D. Brooks (WAM T60178); 1 ♀, Camerons Cave, cave C-452, 21°57'56"S, 114°07'23"E, 26.v.1994, W.F. Humphreys, K. Cameron (WAM 94/1862); 1 ♂, 1 ♀, Camerons Cave, cave C-452, 21°58'S, 114°07'E, 11.viii.1992, W.F. Humphreys, R.D. Brooks (WAM 93/2116-2117); 2 ♀, cave C-452, Camerons Cave, 21°58'S, 114°07'E, 11.i.1994, R.D. Brooks (WAM 94/42-43); 1 ♂, 3 ♀, Camerons Cave, cave C-452,

21°57’56”S, 114°07’23”E, 12.iv.1994, R.D. Brooks (WAM 94/1858-1861); 1 ♀, Exmouth Limestone Lease, bore #RC2, 15 m deep, 22°00’08”S, 114°04’54”E, 20.i.2001, R.D. Brooks (WAM T45927); 1 ♂, 1 ♀, Exmouth Limestone Lease, bore #DDH2, 40 m deep, 22°00’02”S, 114°04’40”E, 22.i.2001, R.D. Brooks (WAM T45928); 1 juvenile, Exmouth Limestone Lease, bore #N8, 27 m deep, 21°59’55”S, 114°04’35”E, 15.i.2001, R.D. Brooks (WAM T45929); 1 juvenile, Cape Range, Bore E2, 21°56’S, 114°07’E, 24.vi.1993, in bore, W.F. Humphreys, R.D. Brooks (WAM 93/2118); 2 juveniles, Cape Range, Bore E2, 21°56’S, 114°07’E, 3.viii.1993, R.D. Brooks, W.F. Humphreys (WAM 93/2119-2120); 3 juveniles, Cape Range, Bore E2, 21°56’S, 114°07’E, 17.vi.1993, R.D. Brooks, W.F. Humphreys (WAM 93/2121-2123); 1 juvenile, Exmouth, town bore E2, 21°56’S, 114°07’E, 14.v.1995, R.D. Brooks (WAM T60179).

Diagnosis

Draculoides brooksi is included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II and the laterally compressed male flagellum. Like *D. vinei* and *D. julianneae*, the male and female flagellar seta dl1 is reduced in size, and seta vm1 is situated on the same level as vm2. It differs from *D. vinei* and *D. julianneae* by the lack of a constricted distal portion of the male flagellum.

Description

Adult female (WAM 93/2117)

Colour: yellow-brown.

Cephalothorax: propeltidium with 9 setae, arranged 2 (in row): 1: 2: 2: 2 anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 13 setae, including 2 sternapophysial setae; posterior sternum triangular, with 6 setae.

Chelicera: fixed finger with 2 large teeth plus 4 smaller teeth between these, basal and distal teeth each with 1 very small, blunt, lateral tooth; brush at base of fixed finger composed of 6 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 4 short whip-like setae, small serrations present on one side of broad part of setae; movable finger file composed of 17 long lamellae, blunt guard tooth present subdistally, 1 large accessory tooth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, without mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.54 length of tarsus.

Legs: tarsus I with 6 segments; femur IV 3.48 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 + 4 (4 microsetae diagonal): 2 + 6 (6 microsetae in column): 2: 2: 2: 2: 2: 4: 4, segment XII with very small dorsal process.

Flagellum: 3 segmented (Figs 18-20), first segment slightly longer than second, third longest, 4.60 times longer than broad, 1 pair of microsetae positioned anterior end of third segment, additional microsetae present between vm4 and vm5, and close to vl2, seta dm1 situated dorso-medially only slightly posterior to vm2, seta dl1 situated anterior to dm4, dm4 situated sub-distally, dl3 situated at posterior margin, slightly posterior to vl2, vm1 situated ventral to vm2, vm4 situated midway between vm1 and vm5, vm5 situated slightly closer to vm4 than vl2, vl1 situated posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of spermathecae, each pair connected basally before connection with bursa, distally round and smooth (Fig. 21); sparsely covered with small pores; gonopod short, slightly bifurcate distally.

Dimensions (mm): ♀ (WAM 93/2117): Body length 5.22. Propeltidium 1.51/0.87. Chelicera 1.00. Flagellum 0.48/0.10. Pedipalp: trochanter 0.77, femur 0.78, patella 0.85, tibia 0.78, tarsus 0.39, claw 0.21, total excluding claw 3.57. Leg I: trochanter 0.54, femur 1.87, patella 2.43, tibia 1.87, metatarsus 0.52, tarsus 0.80, total 8.03. Leg IV: trochanter 0.45, femur 1.76/0.51, patella 0.77, tibia 1.21, metatarsus 1.10, tarsus 0.68, total 5.97.

Remarks

Harvey (2001b) described this species from an adult male and three juveniles taken from a borehole situated on the northern edge of Cape Range peninsula. Subsequent examination of the specimens attributed to *D. bramstokeri* by Harvey and Humphreys (1995) from caves in the Exmouth region of Cape Range peninsula revealed that they were incorrectly identified and are in fact referable to *D. brooksi*. Thus *D. bramstokeri* is endemic to Barrow Island (Fig. 9) and *D. brooksi* is restricted to the north-eastern portion of Cape Range peninsula (Fig. 8).

Draculoides julianneae Harvey

(Figs 8, 22-24)

Draculoides julianneae Harvey, 2001: 173-174, figs 2, 3; Harvey, 2003: 108.

Material examined

Holotype. **Australia:** *Western Australia:* ♀, cave C-215, Cape Range peninsula, 22°02'S, 113°56'E, 19.v.1995, B. Vine, J.M. Waldock (WAM 98/1553).

Paratypes. **Australia:** *Western Australia:* 4 ♀, same data as holotype (WAM 98/1549-1552); 1 ♀, same data as holotype (WAM 98/1585).

Other material. **Australia:** *Western Australia:* 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°55'55"E, 25.vi.1999, R.D. Brooks (WAM T42202); 1 ♂, 1 ♀, 6 juveniles, Cape Range, cave C-215, 22°01'40"S, 113°55'55"E, 20.iii.2002, P.G. Kendrick, D. Rosencranz, W.F. Humphreys (WAM T45838); 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°55'55"E, 4.vii.2002, central root area, on sediment bank, J. Anderson, *et al*. (WAM T57444); 1 female, 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°56'56"E, 29.vi.2004, deep zone, R.D. Brooks (WAM T62596); 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°56'56"E, late 2004, R.D. Brooks (WAM T65512); 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°56'56"E, late 2004, R.D. Brooks (WAM T65513); 1 juvenile, Cape Range, cave C-215, 22°01'40"S, 113°56'56"E, late 2004, R.D. Brooks (WAM T65514); 1 juvenile, Cape Range, cave C-111, 21°55'08"S, 114°00'17"E, late 2004, R.D. Brooks (WAM T65505); 1 juvenile, Cape Range, cave C-111, 21°55'08"S, 114°00'17"E, late 2004, R.D. Brooks (WAM T65506); 1 juvenile, Cape Range, cave C-111, 21°55'08"S, 114°00'17"E, late 2004, R.D. Brooks (WAM T65507).

Diagnosis

Draculoides julianneae is included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II and the laterally compressed male flagellum. It is very similar to *D. vinei* as the males of both species possess a posteriorly constricted flagellum. *Draculoides vinei* possesses a pointed tip to the male flagellum, whereas *D. julianneae* has a small, rounded tip. This species can be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: C(623), C(751), C(787), T(790), G(990), A(1061).

Description

Adult male (WAM T45838)

Colour: yellow-brown.

Cephalothorax: propeltidium with 9 setae, arranged 2 (in row): 1: 2: 2: 2 anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 12 setae, including 2 sternapophysial setae; posterior sternum triangular, with 7 setae.

Chelicera: fixed finger with 2 large teeth plus 5 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 9 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 5 short whip-like setae, small serrations present on one side of broad part of setae; movable finger file composed of 21 long lamellae, blunt guard tooth present subdistally, 1 large accessory tooth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.50 length of tarsus.

Legs: tarsus I with 6 segments; femur IV 4.06 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 + 4 (4 microsetae diagonal): 2 + 6 (6 microsetae in column): 2: 2: 2: 2: 2: 4: 4; segment XII with very small dorsal process.

Flagellum: very narrow, higher than broad, abruptly tapering posteriorly, 4.44 times longer than broad (Figs 22-24); seta dm1 situated dorso-medially, seta dl1 very small, situated within lateral sulcus, posterior to vl1 and ventral to dm4, dm4 situated at beginning of lateral sulci, dl3 situated at posterior margin, vm1 situated slightly posterior to vm2, vm4 situated midway between vm1 and vm5, vm5 ventral to vl1, vl2 situated sub-distally, additional microsetae present near vm2, vl1, vl2 and dl3.

Dimensions (mm): ♂ (WAM T45838): Body length 6.99. Propeltidium 1.88/0.89. Chelicera 1.31. Flagellum 0.69/0.16. Pedipalp: trochanter 0.94, femur 1.04, patella 1.04, tibia 0.97, tarsus 0.50, claw 0.25, total excluding claw 4.49. Leg I: trochanter 0.77, femur 3.04, patella 4.03, tibia 3.25, metatarsus 0.83, tarsus 1.12, total 13.04. Leg IV: trochanter 0.62, femur 2.52/0.62, patella 1.06, tibia 1.98, metatarsus 1.69, tarsus 0.93, total 8.8.

Remarks

Harvey (2001b) named this species from several females and juveniles collected within cave C-215 on the western edge of Cape Range peninsula (Harvey 2001b, fig. 2). Additional specimens including two males have since been taken from the same cave, which is described here. The morphology of the male flagellum indicates that it is distinct from all other members of

the genus, but is most similar to *D. vinei.* A population of *Draculoides* from C-111, represented in the collections by juvenile specimens is referred to *D. julianneae* based upon the morphology of the flagellum and the results of the molecular analysis. The sequence data places them with *D. julianneae* with fairly high support (Fig. 4); although they are somewhat distinct, it is less than the level of divergence associated with clades afforded specific status in this study.

Draculoides mesozeirus, sp. nov.

(Figs 10, 25-28)

Material examined

Holotype. **Australia:** *Western Australia:* ♀, Middle Robe (Borehole M2ERC027, trap 1), 23.5 km E. of Pannawonica, 21°41'54"S, 116°32'27"E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T63329).

Paratypes. **Australia:** *Western Australia:* all from Middle Robe: 1 ♀ (trap 2) same data as holotype (WAM T63330); 1 ♀, Borehole M2ERC034 (trap 2), 23.3 km E. of Pannawonica, 21°41'49"S, 116°32'21"E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T63328).

Other material examined. **Australia:** *Western Australia:* all from Middle Robe: 1 juvenile, same data as holotype (WAM T63337); 2 juveniles, Borehole M2ERC0063 (trap 1, 3), 22 km E. of Pannawonica, 21°41'47"S, 116°31'34"E, 1.vi.2005, L. Mould (WAM T63374, T63373); 2 juveniles, Borehole M2ERC0034, 23.3 km E. of Pannawonica, 21°41'49"S, 116°32'21"E, 26.v.2005, L. Mould (WAM T63334); 1 juvenile, Borehole M2ERC0026, 23.5 km E. of Pannawonica, 21°41'54"S, 116°32'28"E, 27.v.2005, L. Mould (WAM T63333); 1 juvenile, Borehole M2ERC0029 (trap 1), 23.4 km E. of Pannawonica, 21°41'50"S, 116°32'26"E, 27.v.2005, L. Mould (WAM T63335).

Diagnosis

Draculoides mesozeirus is tentatively included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II. Females of this species are relatively small, with a propeltidium length of 1.17-1.29 mm. Flagellar seta dl1 quite close to level of vl1. This species can be further distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: T(38), T(62), C(107), C(125), A(135), T(158), C(176), C(216), C(286), C(289), T(299), C(302), T(305), G(308), T(369), A(371), T(380), T(383), A(389), T(461), C(473), C(483), T(590), C(593), C(668), C(716), A(722), T(725),

C(728), T(742), C(749), C(752), T(772), T(773), A(774), C(798), A(806), T(808), T(810), A(811), T(831), C(842), T(855), T(929), C(987), T(993), G(994), C(1000), T(1006), T(1076), A(1092), A(1099), C(1100), C(1101).

Description

Adult females

Colour: yellow-brown.

Cephalothorax: propeltidium with 9 setae, arranged 2 (in row): 1: 2: 2: 2; anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 13-15 setae, including 2 sternapophysial setae; posterior sternum triangular, with 6 setae.

Chelicera: fixed finger with 2 large teeth plus 4 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 9 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 5 short whip-like setae; movable finger file composed of 15 long lamellae, blunt guard tooth present subdistally, 1 large and 1 small accessory teeth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.59 length of tarsus.

Legs: tarsus I with 6 segments; femur IV 2.88 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 macrosetae + 4 microsetae (microsetae diagonal): 2 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4-5; segment XII without dorsal process.

Flagellum: 3 segmented, first segment slightly longer than second, third longest, 4.5 times longer than broad, 1 pair of microsetae positioned on same level as vm4 on third segment, additional pair of microsetae present between dl3 and vl2, seta dm1 situated dorso-medially on same level as vm2, seta dl1 small, situated slightly posterior to vl1, dm4 situated sub-distally, closer to dl1 than dl3, dl3 situated at posterior margin slightly posterior to vl2, vm1 situated ventral to vm2, vm4 situated closer to vm1 than to vm5, vm5 situated ventral to dm4, vl1 situated posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of small spermathecae, each pair connected basally before connection with bursa (Fig. 28); receptacula with numerous external microtubule-bearing pores; gonopod short, not distally bifurcate.

Dimensions (mm): holotype ♀ (WAM T63329): Body length 4.06. Propeltidium 1.17/0.64. Chelicera 0.84. Flagellum 0.36/0.08. Pedipalp: trochanter 0.51, femur 0.54, patella 0.58, tibia 0.53, tarsus 0.27, claw 0.16, total excluding claw 2.43. Leg I: trochanter 0.40, femur 1.25, patella 1.56, tibia 1.25, metatarsus 0.39, tarsus 0.63, total 5.48. Leg IV: trochanter 0.34, femur 1.24/0.43, patella 0.57, tibia 0.91, metatarsus 0.77, tarsus 0.52, total 4.35.

Variation: propeltidium length 1.17-1.29 mm (n = 3).

Remarks

Without male specimens, this species is only tentatively included within *Draculoides*, as the molecular data do not consistently cluster *D. mesozeirus* with other members of the genus. It is easily distinguished from *Paradraculoides* by the presence of only 2 macrosetae on tergite II, and the sequence data (Fig. 4, Table 2).

Draculoides mesozeirus is restricted to the Middle Robe mesa situated east of Pannawonica in the Pilbara region of Western Australia (Fig. 7), and is the only schizomid species thus far found in the Robe River Valley that does not belong to *Paradraculoides*.

Etymology

The specific epithet refers Middle Robe, the only known location from which this species has been collected (*mesos*, Greek, middle; and *zeira*, Greek, robe).

Draculoides neoanthropus, sp. nov.

(Figs 7, 29-31)

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Ore Body 25 (borehole WO57, 9 m depth), 6.5 km ENE. of Newman, 23°20’25”S, 119°47’29”E, 3.v.2006, L. Mould, J. Lynas (WAM T75215).

Diagnosis

Draculoides neoanthropus is included in the genus *Draculoides* by the presence of 2 macrosetae on tergite II and the laterally compressed male flagellum. Males differ from all other

species of the genus except *D. bramstokeri* by the very deep, rounded flagellum, the flagellar seta dl1 not reduced in size and flagellar seta vm1 situated anterior to vm2. It differs from *D. bramstokeri* by the distinctive pointed flagellar tip which is small and rounded in *D. bramstokeri*.

Description

Adult male (holotype)

Colour: light yellow-brown.

Cephalothorax: propeltidium with 9 setae, arranged 2: 1: 2: 2: 2 anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 13 setae, including 2 sternapophysial setae; posterior sternum triangular, with 7 setae.

Chelicera: fixed finger with 2 large teeth plus 5 smaller teeth between these, basal tooth with 2 small lateral teeth, and distal tooth with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 8 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 6 short whip-like setae, no serrations visible; movable finger file composed of 16 long lamellae, blunt guard tooth present subdistally, 1 large and 1 small accessory teeth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.51 length of tarsus.

Legs: tarsus I with missing segments; femur IV 2.57 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 macrosetae + 4 microsetae (microsetae diagonal): 2 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4; segment XII of male with small dorsal process.

Flagellum: laterally compressed (Figs 29-31), 4.66 times longer than broad; seta dm1 situated dorso-medially, seta dl1 situated midway between vl1 and dl3, dm4 situated sub-distally between dl3 and dm1, dl3 situated at posterior margin above vl2, vm1 situated anterior to vm2, vm2 situated closer to vm1 than to vm4, vm5 situated midway between vm4 and vl2, 1 pair of microsetae positioned laterally on anterior end, additional microsetae present near vl1, and between vl2 and vm5.

Dimensions (mm): holotype ♂: Body length 4.53. Propeltidium 1.30/0.707. Chelicera 0.982. Flagellum 0.499/0.107. Pedipalp: trochanter 0.676, femur 0.702, patella 0.728, tibia 0.686,

tarsus 0.354, claw 0.182, total excluding claw 3.146. Leg I: trochanter 0.520, femur 1.789, rest missing. Leg IV: trochanter 0.447, femur 1.498/0.582, patella 0.676, tibia 1.206, metatarsus 1.009, tarsus 0.582, total 5.418.

Remarks

Draculoides neoanthropus has only been found from a single ore body situated near the town of Newman in the south-eastern Pilbara (Fig. 7). The specimen was collected from a borehole using a plankton net whilst sampling for stygofauna within the water table at 9 m depth. The specimen shows slight signs of decomposition and was probably lying dead on the surface of the water table prior to collection. Hence, the collection of DNA sequence data was not attempted.

Etymology

The species epithet is derived from the town of Newman (*neo*, Greek, new; *anthropos*, Greek, man).

Genus ***Paradraculoides*** gen. nov.

Type species

Paradraculoides kryptus, sp. nov.

Diagnosis

Paradraculoides differs from all other hubbardiid genera by the presence of 3 macrosetae on tergite II; most hubbardiids possess 2 macrosetae, whereas species of *Clavizomus* and *Mayazomus* possess more than 3 setae. The lack of a mesal spur on the pedipalpal trochanter – also found in species of *Draculoides* – is found in very few other hubbardiid genera (see *Remarks*, below).

Description

Body without clavate setae. Anterior process of propeltidium with pair of setae followed by single seta; corneate eyes and eye spots absent; metapeltidium divided. Pedipalp not sexually dimorphic and without armature; trochanteral mesal spur absent; male pedipalps probably not dimorphic. Moveable cheliceral finger with 1 or 2 accessory teeth, and guard tooth at end of serrula. Anterodorsal margin of femur IV produced at about a 90° angle. Abdominal tergite II

with 3 posterior setae; male abdomen not elongated; male with slight development of posterodorsal process on abdominal segment XII. Male flagellum somewhat rounded and dorso-ventrally flattened; female flagellum with three segments. Spermathecae consisting of two pairs of short, uniramous lobes, not strongly connected to each other basally, without nodules, gonopod present, short and slightly bifurcate terminally.

Remarks

Paradraculoides bears a very strong resemblance to *Draculoides* and it is highly probable that they represent sister-taxa. Species of both genera share a striking apomorphic feature, the lack of a small mesal spur on the pedipalpal trochanter. This spur is found on all other Australian schizomids (Harvey 1992; Harvey and Humphreys 1995; Harvey 2000a, 2000b, 2001b) and on most other hubbardiid genera (Reddell and Cokendolpher 1995). The only hubbardiids that lack a spur, besides the two Western Australian genera, are members the Asian genera *Clavizomus* Reddell and Cokedolpher 1995, *Neozomus* Reddell and Cokedolpher 1995, *Oculozomus* Reddell and Cokedolpher 1995 and *Trithyreus* Kraepelin 1899 (Reddell and Cokendolpher 1995). It should be noted that only the male morphs of *Neozomus tikaderi* (Cokendolpher, Sissom and Bastawade 1988) and *Oculozomus biocellatus* (Sissom 1980) with elongate pedipalps lack the spur whereas those males with 'normal' pedipalps possess the spur (Reddell and Cokendolpher 1995). It is not known whether the females of these species possess a spur, as this feature was not explicitly stated in the descriptions (Sissom 1980; Cokendolpher *et al.* 1988; Reddell and Cokendolpher 1995).

The formal recognition and naming of *Paradraculoides*, despite its apparent close relationship with *Draculoides*, is in keeping with the relatively narrow generic diagnoses operating nowadays (Harvey 1992; Reddell and Cokendolpher 1995; Harvey 2000a, 2001a; e.g. Armas 2002a; Armas and Teruel 2002; Teruel and Armas 2002; Teruel 2003) for hubbardiine genera.

Etymology

This genus is named for its close resemblance to species of the genus *Draculoides*. Like *Draculoides* it is to be treated as masculine in gender.

Key to species of *Paradraculoides*

1. Males (those of *P. anachoretus* and *P. gnophicola* not known).....2

Females.....3

2. Flagellar seta vl2 situated slightly away from distal margin of flagellum .....*P. bythius*

Flagellar seta vl2 situated on distal margin of flagellum..... *P. kryptus*

3. Flagellum with 1 pair of microsetae present on segment 2 .....*P. bythius*

Flagellum with 1 pair of microsetae present on segment 3 4

4. Flagellar seta dm4 situated closer to dl3 than to dl1..... *P. kryptus*

Flagellar seta dm4 situated closer to dl3 than to dl1.....5

5. Flagellar seta dl3 on approximately same level as vl2 ..... *P. anachoretus*

Flagellar seta dl3 situated slightly distal to vl2.....*P. gnophicola*

Paradraculoides anachoretus, sp. nov.

(Figs 10, 32-35)

Material examined

Holotype. **Australia:** *Western Australia:* ♀, Mesa A (Borehole 2497, trap 3), 45.2 km W. of Pannawonica, 21°40’11”S, 115°53’13”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T63327).

Paratypes. **Australia:** *Western Australia:* all from Mesa A: 1 ♀, Borehole 2501 (trap 1), 44.5 km W. of Pannawonica, 21°39’57”S, 115°53’36”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T63331); 1 ♀, Borehole 2501 (trap 2), 44.5 km W. of Pannawonica, 21°39’57”S, 115°53’36”E, 21.xii.2004, G. Humphreys, M. Greenham (WAM T63311); 1 ♀, Borehole 3073 (trap 2), 21°40’43”S, 115°52’23”E, 25.vii.-8.ix.2005, G. Humphreys et al. (WAM T66235).

Other material examined. **Australia:** *Western Australia:* all from Mesa A: 1 juvenile, Borehole 3188 (trap 1), 46.5 km W. of Pannawonica, 21°40’36”S, 115°52’30”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65756); 1 juvenile, Borehole 2582 (trap 4), 44.0 km W. of Pannawonica, 21°39’19”S, 115°53’51”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65757).

Diagnosis

Paradraculoides anachoretus is included in the genus *Paradraculoides* by the presence of 3 macrosetae on tergite II. Females of this species differ from *P. bythius* by the position of microsetae on the third flagellar segment (situated on the second segment in *P. bythius*), and from *P. kryptus* by the position of setae dm4, which is closer to dl1 in *P. anachoretus* and

closer to dl3 in *P. kryptus*. Setae dl3 is parallel with vl2 in females of this species compared with dl3 positioned posterior to vl2 in *P. gnophicola*. This species can be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: A(230), T(263), C(348), G(659), C(824), C(963), T(1119).

Description

Adult females

Colour: yellow-brown.

Cephalothorax: propeltidium with 9 -10 setae, arranged 2 (in row): 1: 2: 1-2: 2: 0-2 anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 13-14 setae, including 2 sternapophysial setae; posterior sternum triangular, with 6-7 setae.

Chelicera: fixed finger with 2 large teeth plus 4 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 9 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 5 short whip-like setae; movable finger file composed of 15 long lamellae, blunt guard tooth present subdistally, 1 large accessory tooth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, without mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.48 length of tarsus.

Legs: tarsus I with 6 segments; femur IV 3.07 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 macrosetae + 4 microsetae (microsetae diagonal): 3 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4-5; segment XII without dorsal process. Flagellum (Figs 32-34) 3 segmented, first segment slightly longer than second, third longest, 4.25 times longer than broad, 1 pair of microsetae positioned anterior end of third segment, additional pair of microsetae present between dl3 and vl2, seta dm1 situated dorso-medially posterior to vm2, seta dl1 situated anterior to dm4, dm4 situated sub-distally, dl3 situated at posterior margin directly above vl2, vm1 situated ventral to vm2, vm4 situated midway between vm1 and vm5, vm5 situated midway between vm4 and vl2, vl1 situated posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of spermathecae, each pair connected basally before connection with bursa (Fig. 35), distally round and smooth; sparsely covered with small pores; gonopod short, not distally bifurcate.

Dimensions (mm): holotype ♀ (WAM T63327): Body length 4.39. Propeltidium 1.21/0.68. Chelicera 0.86. Flagellum 0.34/0.08. Pedipalp: trochanter 0.54, femur 0.57, patella 0.62, tibia 0.58, tarsus 0.31, claw 0.15, total excluding claw 2.62. Leg I: trochanter 0.41, femur 1.35, patella 1.66, tibia 1.33, metatarsus 0.43, tarsus 0.62, total 5.80. Leg IV: trochanter 0.35, femur 1.26/0.41, patella 0.58, tibia 0.96, metatarsus 0.86, tarsus 0.51, total 4.52.

Variation: propeltidium length 1.09-1.39 mm (n = 4).

Remarks

Paradraculoides anachoretus is restricted to Mesa A situated east of Pannawonica in the Pilbara region of Western Australia (Fig. 10).

Etymology

The specific epithet refers to the subterranean existence of this species within Mesa A (*anachoretes*, Greek, hermit, recluse).

Paradraculoides bythius, sp. nov.

(Figs 1-3, 10, 36-42)

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Mesa B (Borehole 0016, trap 3), 37.9 km W. of Pannawonica, 21°39’49”S, 115°57’27”E, 1.vi.2005, M. Greenham, D. Kamien and L. Mould (WAM T63364).

Paratypes. **Australia:** *Western Australia:* 1 ♀ (trap 1) same data as holotype (WAM T63365); 1 ♂, Mesa B, Borehole 0014 (trap 3), 37.9 km W. of Pannawonica, 21°39’58”S, 115°57’27”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65759); 2 ♀, Mesa B, Borehole 0021 (trap 2), 38.1 km W. of Pannawonica, 21°39’36”S, 115°57’20”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T63340, T66070).

Other material examined. **Australia:** *Western Australia:* 1 juvenile (trap 1) same data as holotype (WAM T63367); 1 juvenile, Mesa B, Borehole 0023 (trap 2), 38.1 km W. of Pannawonica, 21°39’49”S, 115°57’20”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65758); 3 juveniles, Mesa C, Borehole 0012 (trap 3, 4, 2), 37.7 km W. of Pannawonica,

21°41’30”S, 115°57’47”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65760-65762).

Diagnosis

Paradraculoides bythius is included in the genus *Paradraculoides* by the presence of 3 macrosetae on tergite II and the dorso-ventrally compressed male flagellum. The male flagellum differs from that of *P. kryptus* by the lateral position of setae vl1, dl3 posterior to vl2, and distal end of flagellum tapering to a point. Females of this species differ from all other females by the position of microsetae between the two most anterior segments of the flagellum. This species can also be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: T(21), C(65), C(113), A(128), T(281), C(371), C(372), C(428), C(524), T(594), A(596), C(605), A(644), G(1082), A(1091).

Description

Adults

Colour: ranging from yellow-brown to dark orange-brown.

Cephalothorax: propeltidium with 6-9 setae, arranged 2-3 (in row): 1-2: 2: 2: 0-2 anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 12-14 (♂), 13-16 (♀) setae, including 2 sternapophysial setae; posterior sternum triangular, with 6-8 (♂), 7-8 (♀) setae.

Chelicera: fixed finger with 2 large teeth plus 4 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 9 (♂), 8-9 (♀) setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 4-5 short whip-like setae, no serrations visible; movable finger file composed of 20 (♂), 20 (♀) long lamellae, blunt guard tooth present subdistally, 1 large and 1 small accessory teeth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.46 (♂), 0.44 (♀) length of tarsus.

Legs: tarsus I with 6 segments; femur IV 3.32 (♂), 3.08 (♀) times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 macrosetae + 4 microsetae (microsetae diagonal): 3 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4 (♂, ♀); segment XII of male with small dorsal process, of female without dorsal process.

Flagellum: male: broad, gently tapering posteriorly, 2.23 times longer than broad (Figs 36-38); seta dm1 situated dorso-medially, seta dl1 small, situated midway between vl1 and dl3, dm4 very small, situated distally between dl3, dl3 situated at posterior margin, vm1 situated slightly posterior to vm2, vm4 situated between vm1 and vm5, vm5 slightly posterior to vl1, vl2 situated sub-distally, additional microsetae present near dl1, vl1, vl2, vm5, and lateral to vm2 and vm4. Female: 3 segmented (Figs 39-41), first segment slightly longer than second, third longest, curving upwards posteriorly, 4.44 times longer than broad, 1 pair of microsetae positioned laterally on anterior end of second segment, additional microsetae present near vl2 and dl3, seta dm1 situated dorso-medially, seta dl1 large, situated dorso-laterally between dm1 and dm4, dm4 situated sub-distally, closer to dl3 than to dl1, dl3 situated at posterior margin slightly posterior to vl2, vm1 situated ventral to vm2, vm4 situated midway between vm1 and vm5, vm5 angled posteriorly, situated slightly closer to vm4 than to vl2, vl1 posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of spermathecae, each pair connected basally before connection with bursa, distally round and smooth (Fig. 42); evenly covered with small pores; gonopod short, distally bifurcate.

Dimensions (mm): holotype ♂ (paratype ♀, WAM T63340): Body length 4.76 (4.87). Propeltidium 1.32/0.73 (1.37/0.81). Chelicera 0.91 (1.06). Flagellum 0.49/0.22 (0.40/0.09). Pedipalp: trochanter 0.61 (0.66), femur 0.62 (0.76), patella 0.74 (0.84), tibia 0.67 (0.75), tarsus 0.35 (0.39), claw 0.16 (0.17), total excluding claw 2.99 (3.40). Leg I: trochanter 0.55 (0.50), femur 2.00 (1.80), patella 2.62 (2.22), tibia 2.14 (1.79), metatarsus 0.61 (0.53), tarsus 0.82 (0.74), total 8.74 (7.58). Leg IV: trochanter 0.45 (0.45), femur 1.66/0.50 (1.54/0.50), patella 0.70 (0.68), tibia 1.26 (1.21), metatarsus 1.11 (1.04), tarsus 0.65 (0.62), total 5.83 (5.54).

Variation: propeltidium length 1.22-1.37 mm (n = 5).

Remarks

Paradraculoides bythius is found in Mesas B and C situated west of Pannawonica in the Pilbara region of Western Australia (Fig. 10).

Etymology

The specific epithet refers to the subterranean existence of this species within Mesas B and C (*bythios*, Greek, of the deep).

Paradraculoides gnophicola, sp. nov.

(Figs 10, 43-46)

Material examined

Holotype. **Australia:** *Western Australia:* ♀, Mesa G (Borehole 0159A, trap 4), 22.4 km SW. of Pannawonica, 21°44’20”S, 116°08’06”E, iii.-v.2005, M. Greenham, D. Kamien and L. Mould (WAM T65763).

Paratypes. **Australia:** *Western Australia:* 1 ♀, Mesa G, Borehole 0014A (trap 2), 21°43’57”S, 116°07’01”E; 1 ♀ (trap 1), 21.xii.2004, G. Humphreys, M. Greenham (WAM T63312); 1 ♀, Mesa G, Borehole 0057A (trap 4), 21.xii.2004, G. Humphreys, M. Greenham (WAM T63316).

Other material examined. **Australia:** *Western Australia:* 3 juveniles, same data as holotype except (traps 4, 3) (WAM T65764, T65803)

Diagnosis

Paradraculoides gnophicola is included in the genus *Paradraculoides* by the presence of 3 macrosetae on tergite II. Females of this species differ from other females by the position of microsetae between the two most posterior segments of the flagellum, the position of setae dm4, which is closer to dl1 than to dl3, and the position of setae dl3, which is posterior to vl2. This species can also be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: C(32), T(152), C(287), A(359), C(683), A(874), T(1101).

Description

Adult females

Colour: variable ranging from pale to dark yellow-brown.

Cephalothorax: propeltidium with 9-11 setae, arranged 2 (in row): 1: 2: 2: 2: 2: 0-2; anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 13-15 setae, including 2 sternapophysial setae; posterior sternum triangular, with 6 setae.

Chelicera: fixed finger with 2 large teeth plus 5 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 10 setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 5 short whip-like setae; movable finger file composed of 21 long lamellae, blunt guard tooth present subdistally, 1 large accessory tooth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.47 length of tarsus.

Legs: tarsus I with 6 segments; femur IV 3.08 times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Abdomen: chaetotaxy of tergites I-IX: 2 macrosetae + 4 microsetae (microsetae diagonal): 3 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4-5; segment XII without dorsal process.

Flagellum: 3 segmented, first segment slightly longer than second, third longest, curving upwards posteriorly, 4.1 times longer than broad, 1 pair of microsetae positioned laterally on anterior end of third segment, additional pair of microsetae present anterior to vl2, seta dm1 situated dorso-medially, seta dl1 large, situated anterior to dm4, dm4 situated anterior to dl3 and close to dl1, dl3 situated at posterior margin dorsal to vl2, vm1 situated ventral to vm2, vm4 situated midway between vm1 and vm5, vm5 situated slightly closer to vm4 than to vl2, vl1 posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of elongate spermathecae, each pair connected basally before connection with bursa (Fig. 46), distally round and smooth; sparsely covered with small pores; gonopod short, not distally bifurcate.

Dimensions (mm): holotype ♀ (WAM T65763): Body length 5.55. Propeltidium 1.43/0.84. Chelicera 1.07. Flagellum 0.41/0.10. Pedipalp: trochanter 0.70, femur 0.68, patella 0.75, tibia 0.69, tarsus 0.34, claw 0.16, total excluding claw 3.16. Leg I: trochanter 0.49, femur 1.64, patella 1.99, tibia 1.66, metatarsus 0.50, tarsus 0.67, total 6.95. Leg IV: trochanter 0.42, femur 1.54/0.50, patella 0.70, tibia 1.19, metatarsus 1.04, tarsus 0.61, total 5.50.

Variation: propeltidium length 1.00-1.43 mm (n = 3).

Remarks

Paradraculoides gnophicola is found within Mesa G situated 22 km SW. of Pannawonica in the Pilbara region of Western Australia (Fig. 10).

Etymology

The specific epithet refers to the subterranean existence of this species within Mesa G (*gnophos*, Greek, darkness; and -*cola*, Latin, dweller).

Paradraculoides kryptus, sp. nov.

(Figs 10, 12, 47-53)

Material examined

Holotype. **Australia:** *Western Australia:* ♂, Mesa K (Borehole 1685 trap 1), S. of Pannawonica, 21°43’06”S, 116°15’36”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65801).

Paratypes. **Australia:** *Western Australia:* 1 ♂, Mesa K, Borehole 1721 (trap 3), S. of Pannawonica, 21°42’56”S, 116°15’57”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65795); 1 ♂, Mesa K, Borehole 1728 (trap 1), S. of Pannawonica, 21°43’01”S, 116°15’53”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65796); 2 ♀ (trap 2) same data as holotype (WAM T65802, T65998); 2 ♀, Mesa K, Borehole 1694 (traps 1, 2), S. of Pannawonica, 21°43’09”S, 116°15’52”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65798, T65997).

Other material examined. **Australia:** *Western Australia:* all from Mesa K: 1 juvenile, same data as holotype (WAM T65800); 1 juvenile, Borehole 1689 (trap 2), S. of Pannawonica, 21°43’07”S, 116°15’53”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65797); 1 juvenile, Borehole 1694 (trap 2), S. of Pannawonica, 21°43’09”S, 116°15’52”E, 12.vii.2005, M. Greenham, D. Kamien and L. Mould (WAM T65799).

Diagnosis

Paradraculoides kryptus is included in the genus *Paradraculoides* by the presence of 3 macrosetae on tergite II and the dorso-ventrally compressed male flagellum. The male flagellum differs from that of *P. bythius* by the ventrolateral position of setae vl1, position of dl3 parallel to vl2, and blunt distal end of flagellum. Females of this species differ from *P. bythius* by the position of microsetae between the two most posterior segments of the flagellum. In this species, setae dm4 is closer to dl3 than dl1, setae dl3 is parallel with vl2, and setae dm1 is parallel with vm2. This species can also be distinguished from the others considered here by the following combination of unique mtDNA (COI and 12S) gene nucleotide substitutions: T(12), C(101), T(177), C(182), C(221), T(368), C(386), C(401), C(440), C(443), C(476), C(635), C(638), T(771), G(772), C(786), A(876), T(965), C(1027), C(1092), T(1097).

Description

Adults

Colour: yellow-brown.

Cephalothorax: propeltidium with 9-11 setae, arranged 2 (in row): 1-2: 2: 2: 2: 0-2; anterior margin drawn to a sharply downturned point between chelicerae; eye spots absent. Mesopeltidia widely separated. Metapeltidium divided. Anterior sternum with 12-15 setae, including 2 sternapophysial setae; posterior sternum triangular, with 6-8 setae.

Abdomen: chaetotaxy of tergites I-IX: ♂, 2 macrosetae + 4 microsetae (microsetae diagonal): 3 macrosetae (Fig. 12) + 6 microsetae (microsetae in column): 2: 2-3: 2: 2: 2: 4: 4; ♀, 2 macrosetae + 4 microsetae (microsetae diagonal): 3 macrosetae + 6 microsetae (microsetae in column): 2: 2: 2: 2: 2: 4: 4; segment XII of male with small dorsal process, of female without dorsal process.

Flagellum: male: broad, gently tapering posteriorly, 1.90 times longer than broad (Figs 47-49); seta dm1 situated dorso-medially, seta dl1 small, situated midway between vl1 and dl3, dm4 very small, situated distally between dl3, dl3 situated at posterior margin dorsal to vl2, vm1 situated slightly posterior to vm2, vm4 situated between vm1 and vl2 on edge of ventral protuberance, vm5 slightly posterior to vl1, additional microsetae present between vm5 and vl2, and lateral to dm1. Female: 3 segmented (Fig. 50-52), first segment slightly longer than second, third longest, 4.13 times longer than broad, 1 pair of microsetae positioned on anterior end of third segment, additional pair of microsetae present anterior to dl3 and vl2, seta dm1 situated dorso-medially on same level as vm2, seta dl1 very small, situated dorsal to vm5, dm4 situated sub-distally, closer to dl3 than dl1, dl3 situated at posterior margin dorsal to vl2, vm1 situated ventral to vm2, vm4 situated closer to vm1 than to vm5, vm5 situated closer to vm4 than to vl2, vl1 situated posterior to vm4 and anterior to dl1.

Female genitalia: 2 pairs of large spermathecae, each pair connected basally before connection with bursa, distally round and smooth (Fig. 53); evenly covered with small pores; gonopod short, slightly bifurcate distally.

Chelicera: Male: fixed finger with 2 large teeth plus 5 smaller teeth between these, basal and distal teeth each with 1 small, blunt, lateral tooth; female fixed finger with 2 large teeth plus 4 smaller teeth between these, basal tooth with 1 small, blunt, lateral tooth; brush at base of fixed finger composed of 7 (♂), 9 (♀) setae, each densely pilose in distal half; lateral surface with 3 large, lanceolate, terminally pilose setae; internal face of chelicera with 4 short whip-like setae; movable finger file composed of 18 (♂), 18 (♀) long lamellae, blunt guard tooth present subdistally, 1 large accessory tooth present near middle of file.

Pedipalp: without apophyses; trochanter with sharply produced distal extension, ventral margin with stout setae, with mesal spur; tibia and tarsus lacking spines; tarsus with spurs; claw 0.48 (♂), 0.52 (♀) length of tarsus.

Legs: tarsus I with 6 segments; femur IV 3.27 (♂), 2.79 (♀) times longer than wide; anterodorsal margin of femur IV produced at about a 90° angle.

Dimensions (mm): holotype ♂ (paratype ♀, WAM T65798): Body length 4.60 (4.04). Propeltidium 1.18/0.67 (1.18/0.59). Chelicera 0.81 (0.80). Flagellum 0.40/0.21 (0.33/0.08). Pedipalp: trochanter 0.54 (0.50), femur 0.54 (0.52), patella 0.57 (0.56), tibia 0.52 (0.50), tarsus 0.29 (0.27), claw 0.14 (0.14), total excluding claw 2.46 (2.35). Leg I: trochanter 0.46 (0.40), femur 1.62 (1.25), patella 2.04 (1.54), tibia 1.66 (1.24), metatarsus 0.49 (0.40), tarsus 0.72 (0.62), total 6.99 (5.45). Leg IV: trochanter 0.39 (0.35), femur 1.44/0.44 (1.20/0.43), patella 0.62 (0.56), tibia 1.07 (0.88), metatarsus 0.91 (0.76), tarsus 0.63 (0.53), total 5.06 (4.28).

Variation: propeltidium length 0.93-1.26 mm (n = 7).

Remarks

Paradraculoides kryptus is found within Mesa K situated south of Pannawonica in the Pilbara region of Western Australia (Fig. 10).

Etymology

The specific epithet refers to the subterranean existence of this species within Mesa K (*kryptos*, Greek, hidden).

Paradraculoides sp.

(Fig. 10)

Material examined

Australia: *Western Australia:* 4 juveniles, Warramboo (MEADC2381, T2-3), 21°39’45”S, 115°49’33”E, 25.vii.-8.ix.2005, litter trap, G. Humphreys *et al*. (WAM T66234).

Remarks

Four juvenile specimens of a species of *Paradraculoides* were recovered from Warramboo, an area that lacks the mesa formation but represents the western extension of pisolitic geology present within Mesa A. Molecular sequence data (Fig. 4) suggests that no gene flow occurs between this population and *P. anachoretus* and that species status is probably warranted. The lack of adult specimens precludes any assessment of any potential morphological characteristics that would support the molecular data, and we therefore refrain from describing and naming this species until appropriate specimens become available.

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Table 1. Specimens of Hubbardiidae used in the molecular analysis. Locations for which voucher specimens were not retained are denoted with †.

Genus	Species	State	Site	Latitude	Longitude	WA Museum registration number	GenBank accession numbers (COI, 12S)
Bamazomus	sp.	Qld	Fitzroy Island	16°56’S	145°59’E	T65530	EU272676, EU272732
Brignolizomus	*woodwardi*	Qld	Whites Hill Reserve	27°30’S	153°05’E	T65515	EU272675, EU272731
Draculoides	*bramstokeri*	W.A.	Barrow Island	20°47’26”S	115°26’57”E	T66002	EU272678, EU272734
Draculoides	*bramstokeri*	W.A.	Barrow Island	20°46’33”S	115°26’53”E	T66012	EU272680, EU272736
Draculoides	*bramstokeri*	W.A.	Barrow Island	20°48’47”S	115°25’18”E	T66017	EU272682, EU272738
Draculoides	*bramstokeri*	W.A.	Barrow Island	20°47’05”S	115°23’40”E	†	EU272683, EU272739
Draculoides	*bramstokeri*	W.A.	Barrow Island	20°49’07”S	115°23’08”E	†	EU272684, EU272740
Draculoides	*bramstokeri*	W.A.	Barrow Island (S4)	20°47’37”S	115°25’38”E	†	EU272681, EU272737
Draculoides	*bramstokeri*	W.A.	Barrow Island (B27)	20°47’49”S	115°26’53”E	†	EU272679, EU272735
Draculoides	*bramstokeri*	W.A.	Barrow Island (B11)	20°47’19”S	115°27’04”E	†	EU272677, EU272733
Draculoides	*julianneae*	W.A.	Cape Range, cave C-215	22°01’40”S	113°55’55”E	T45838	EU272688, EU272744
Draculoides	*julianneae*	W.A.	Cape Range, cave C-111, Breakdown Maze	21°55’08”S	114°00’17”E	T65505	EU272695, EU272751
Draculoides	*julianneae*	W.A.	Cape Range, cave C-111, Breakdown Maze	21°55’08”S	114°00’17”E	T65506	EU272696, EU272752
Draculoides	*julianneae*	W.A.	Cape Range, cave C-215	22°01’40”S	113°55’55”E	T65512	EU272685, EU272741
Draculoides	*julianneae*	W.A.	Cape Range, cave C-215	22°01’40”S	113°55’55”E	T65513	EU272686, EU272742
Draculoides	*julianneae*	W.A.	Cape Range, cave C-215	22°01’40”S	113°55’55”E	T65514	EU272687, EU272743
Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’54”S	116°32’28”E	T63333	EU272725, EU272781
Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’49”S	116°32’21”E	T63334	EU272726, EU272782
Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’50”S	116°32’26”E	T63335	EU272727, EU272783
Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’54”S	116°32’27”E	T63337	EU272728, EU272784
Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’47”S	116°31’34”E	T63373	EU272729, EU272785

Draculoides	*mesozeirus*	W.A.	Middle Robe	21°41’47”S	116°31’34”E	T63374	EU272730, EU272786
Draculoides	*vinei*	W.A.	Cape Range, Dry Swallett Cave, C-18	22°05’24”S	113°59’30”E	T65501	EU272689, EU272745
Draculoides	*vinei*	W.A.	Cape Range, Dry Swallett Cave, C-18	22°05’24”S	113°59’30”E	T65502	EU272690, EU272746
Draculoides	*vinei*	W.A.	Cape Range, Dry Swallett Cave, C-18	22°05’24”S	113°59’30”E	T65503	EU272691, EU272747
Draculoides	*vinei*	W.A.	Cape Range, cave C-118	22°09’41”S	113°59’41”E	T65508	EU272692, EU272748
Draculoides	*vinei*	W.A.	Cape Range, cave C-118	22°09’41”S	113°59’41”E	T65509	EU272693, EU272749
Draculoides	*vinei*	W.A.	Cape Range, cave C-118	22°09’41”S	113°59’41”E	T65510	EU272694, EU272750
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°39’57”S	115°53’36”E	T63323	EU272698, EU272754
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’31”S	115°52’24”E	T63325	EU272699, EU272755
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’30”S	115°53’13”E	T63332	EU272700, EU272756
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’31”S	115°52’24”E	T63336	EU272701, EU272757
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’30”S	115°53’13”E	T63339	EU272702, EU272758
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’47”S	115°52’46”E	T66228	EU272706, EU272762
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°41’11”S	115°53’02”E	T66232	EU272705, EU272761
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’41”S	115°52’14”E	T66233	EU272707, EU272763
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’43”S	115°52’23”E	T66235	EU272708, EU272764
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’25”S	115°52’17”E	T66236	EU272709, EU272765
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°39’33”S	115°54’25”E	T66315	EU272703, EU272759
Paradraculoides	*anachoretus*	W.A.	Mesa A	21°40’02”S	115°53’52”E	T66316	EU272704, EU272760
Paradraculoides	*bythius*	W.A.	Mesa B	21°39’36”S	115°57’20”E	T63341	EU272710, EU272766
Paradraculoides	*bythius*	W.A.	Mesa B	21°39’52”S	115°57’27”E	T63366	EU272711, EU272767
Paradraculoides	*bythius*	W.A.	Mesa B	21°39’49”S	115°57’27”E	T63367	EU272712, EU272768
Paradraculoides	*bythius*	W.A.	Mesa B	21°39’49”S	115°57’27”E	T63367(3)	EU272713, EU272769
Paradraculoides	*bythius*	W.A.	Mesa C	21°40’37”S	115°57’48”E	T63343	EU272714, EU272770
Paradraculoides	*bythius*	W.A.	Mesa C	21°40’37”S	115°57’48”E	T63344	EU272715, EU272771
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°43’57”S	116°07’01”E	T63313	EU272718, EU272774
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°43’57”S	116°07’01”E	T63314	EU272719, EU272775
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°44’21”S	116°06’21”E	T63315	EU272720, EU272776
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°44’03”S	116°07’52”E	T63345	EU272721, EU272777
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°44’20”S	116°08’06”E	T63371	EU272716, EU272772
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°44’20”S	116°08’06”E	T63371(3)	EU272722, EU272778
Paradraculoides	*gnophicola*	W.A.	Mesa G	21°44’20”S	116°08’06”E	T63372	EU272717, EU272773

Paradraculoides	*kryptus*	W.A.	Mesa K	21°43’07”S	116°15’53”E	T65797	EU272723, EU272779
Paradraculoides	*kryptus*	W.A.	Mesa K	21°43’06”S	116°15’36”E	T65802	EU272724, EU272780
Paradraculoides	sp.	W.A.	Warramboo	21°39’45”S	115°49’33”E	T66234	EU272697, EU272753

Table 2. Diagnostic nucleotide substitutions for schizomid species from the Pilbara and neighbouring regions, Western Australia. Numbers indicate nucleotide position and black boxes identify diagnostic nucleotides.

	12	21	32	36	38	50	56	62	65	98	101	107	113	120	125	128	135	152	158	164	170	173	176	177	182	216	221	230	246	254	263	281	286	287	289	299	302	305	308	315	316	348	359	365	368	369
D. bramstokeri	A	A	T	T	A	A	T	A	T	T	T	A	T	C	T	T	G	A	A	T	C	A	A	C	A	T	T	T	G	T	A	A	T	T	A	A	A	A	A	C	C	T	T	T	A	C
D. julianneae	A	A	T	C	A	C	T	A	T	A	T	T	T	T	T	T	G	A	A	T	T	T	A	C	A	T	T	T	A	A	A	A	T	T	G	A	A	A	A	T	T	T	T	A	A	C
D. vinei	A	A	T	C	A	C	C	A	T	A	T	T	T	T	T	T	G	A	A	A	T	T	A	C	A	T	T	C	A	A	A	A	T	T	G	A	A	A	A	T	T	T	C	G	A	C
D. mesozeirus	A	A	T	C	T	C	T	T	T	A	T	C	T	T	C	C	A	A	T	T	T	C	C	C	A	C	T	T	A	A	A	A	C	T	C	T	C	T	G	T	T	T	T	T	A	T
P. anachoretus	A	A	T	C	A	Y	T	A	T	A	T	A	T	A	T	C	G	A	A	T	T	T	A	C	T	A	T	A	A	A	T	A	T	T	G	A	A	A	A	A	T	C	C	A	A	C
P. bythius	A	T	T	C	A	C	T	A	C	A	T	A	C	A	T	A	G	A	A	T	T	T	T	C	T	A	T	C	A	A	A	T	T	T	G	A	A	A	A	A	T	T	C	A	A	C
P. gnophicola	A	A	C	C	A	Y	T	A	T	A	T	A	T	A	T	T	G	T	A	T	T	T	T	C	A	A	T	C	A	A	A	A	A	T	C	G	A	A	A	A	A	T	T	A	T	A	C
P. kryptus	T	A	T	C	A	T	T	A	T	A	C	A	T	A	T	T	G	A	A	T	T	C	T	T	C	A	C	C	A	A	A	A	A	T	T	G	A	A	A	A	A	T	T	C	T	T	C

	371	372	380	383	386	389	401	419	428	440	443	461	468	473	476	483	524	548	554	590	593	594	596	605	623	627	635	638	644	659	668	683	716	718	719	722	725	728	742	749	751	752	771	772	773	774	786
D. bramstokeri	T	T	A	A	T	T	T	T	T	T	T	A	G	T	T	T	T	A	T	A	T	C	T	T	T	C	T	T	T	A	A	T	T	A	G	T	A	T	A	T	T	T	A	A	C	C	T
D. julianneae	T	T	A	A	A	T	T	C	T	T	T	A	A	T	T	T	T	C	T	A	T	C	T	T	C	C	T	T	Y	A	T	T	T	A	G	T	A	T	A	T	C	T	A	A	C	C	T
D. vinei	T	T	A	A	W	T	T	C	T	T	T	A	A	A	T	T	T	T	C	A	T	C	T	T	T	T	T	T	C	A	T	T	T	G	A	T	A	A	A	T	T	T	A	A	C	C	T
D. mesozeirus	A	T	T	T	T	A	T	C	T	T	T	T	A	C	T	C	T	C	T	T	C	C	T	T	T	C	T	T	T	A	C	T	C	A	G	A	T	C	T	C	T	C	A	T	T	A	T
P. anachoretus	T	T	A	A	T	T	T	C	T	T	T	A	A	A	T	T	T	T	T	A	A	C	T	T	T	C	A	T	T	G	A	T	T	A	G	T	A	T	A	A	T	T	A	A	C	C	T
P. bythius	C	C	A	A	T	T	T	C	C	T	T	A	A	A	T	T	C	T	T	A	A	T	A	C	T	C	T	T	A	A	A	T	T	A	G	T	A	T	A	A	T	T	A	A	C	C	T
P. gnophicola	T	T	A	A	A	T	T	C	T	T	T	A	A	A	T	T	T	C	T	A	A	C	T	T	T	C	A	T	T	A	A	C	T	A	G	T	A	T	A	A	T	T	A	A	C	C	T
P. kryptus	T	T	A	A	C	T	C	C	T	C	C	A	A	A	C	T	T	C	T	A	A	C	T	T	T	C	C	C	C	A	A	T	T	A	G	T	A	T	A	A	T	T	T	G	C	C	C

	787	789	790	798	799	806	808	810	811	821	824	831	842	850	855	874	876	877	906	907	910	913	918	929	963	965	987	990	993	994	1000	1006	1027	1046	1061	1076	1080	1082	1087	1091	1092	1097	1098	1099	1100	1101	1119
D. bramstokeri	T	A	A	A	T	T	A	A	G	T	A	A	T	C	A	C	Y	A	C	T	T	C	A	A	T	A	A	T	A	A	T	A	T	T	T	A	T	T	T	T	T	A	C	T	A	A	A
D. julianneae	C	A	T	A	T	T	A	A	G	T	A	A	T	T	A	T	C	T	A	T	C	T	T	A	A	A	A	G	A	A	A	A	T	C	A	A	C	T	A	T	T	C	A	T	T	A	A
D. vinei	T	G	A	A	C	T	A	A	G	A	A	A	T	T	A	T	T	T	A	C	C	T	T	A	A	A	A	A	A	A	A	A	T	C	C,T	A	C	T	A	T	T	C	A	T	T	A	A
D. mesozeirus	T	A	A	C	T	A	T	T	A	T	A	T	C	T	T	T	C	T	T	T	C	T	T	T	A	A	C	T	T	G	C	T	T	C	T	T	C	T	A	T	A	A	A	A	C	C	A
P. anachoretus	T	A	A	A	T	T	A	A	G	T	C	C	T	T	A	C	C	T	A	T	A	T	T	A	C	A	A	A	A	T	A	A	T	C	T	A	C	T	A	C	T	C	T	T	T	A	T
P. bythius	T	A	A	A	T	T	A	A	G	T	A	C	T	T	A	C	C	T	A	T	A	T	T	A	T	A	A	A	A	T	A	A	T	C	C	A	C	G	A	A	T	A	T	T	T	A	A
P. gnophicola	T	A	A	A	T	T	A	A	G	T	A	C	T	T	A	A	T	T	A	T	A	T	T	A	T	A	A	A	A	T	A	A	T	C	T	A	C	T	A	C	T	A	T	T	T	T	A

P. kryptus T A A A T T A A G T A C T T A C A T A T A T T A T T A A A A A A C C T A C T A T C T T T T A A

Table 3. Morphological character matrix used in the phylogenetic analysis; see text for character states.

Taxon	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
Brignolizomus woodwardi	0	0	0	0	0	0	1	0	0	0	0	1
Bamazomus sp.	0	0	0	0	0	0	1	0	1	0	0	1
Draculoides bramstokeri	1	0	0	0	1	0	0	0	1	0	1	1
Draculoides brooksi	1	0	0	0	1	0	0	1	1	0	0	1
Draculoides julianneae	1	0	1	0	1	1	0	1	0	1	0	1
Draculoides mesozeirus	1	0	0	0	?	?	?	?	?	?	?	1
Draculoides neoanthropus	1	0	0	?	1	0	0	?	1	0	1	?
Draculoides vinei	1	0	1	1	1	1	1	1	0	1	0	1
Paradraculoides anachoretus	1	1	0	0	?	?	?	?	?	?	?	1
Paradraculoides bythius	1	1	0	0	0	0	1	0	0	1	0	0
Paradraculoides gnophicola	1	1	0	0	?	?	?	?	?	?	?	1
Paradraculoides kryptus	1	1	0	0	0	0	1	0	1	0	0	1

FIGURE LEGENDS

Figs 1-3. *Paradraculoides bythius*, sp. nov.: *1*, *2*, paratype ♂ (WAM T65759), dorsal and lateral views, respectively; *3*, paratype ♀ (WAM T63340), lateral view.

Fig. 4. Maximum likelihood phylogram for schizomid specimens used in this study and based on the combined COI and 12S molecular data (-Ln likelihood = 6723.04). The strict consensus of the six best trees (1165 steps each) determined by Maximum Parsimony identified an identical topology. Numbers at nodes represent bootstrap support for that node (Maximum Likelihood/Maximum Parsimony). * indicates values ≥ 95. Where nodes were not recovered with > 50% bootstrap support in both trees, the Maximum Parsimony support is denoted with -.

Fig. 5-6. Cladograms depicting relationships within species of *Draculoides* and *Paradraculoides*, and two outgroups, character numbers appear above and character states below characters (see Table 1); only unambiguous character states are depicted: *5*, parsimony analysis of 12 characters scored for 12 taxa (Table 3) using equal weights. The analysis resulted in three equally parsimonious trees (length = 20, *CI* = 0.60, and *RI* = 0.60); the resulting consensus tree is shown here. Jack-knife branch supports greater than 50% are depicted below branches. 6, parsimony analysis with *D. mesozeirus*, *P. anachoretus*, *P. gnophicola* and *D. neoanthropus* removed (due to each species known from only one sex). The analysis produced only a single most parsimonious tree (length = 16, *CI* = 0.75, and *RI* 0.75.

Figs 7-10. Maps showing known records of *Draculoides* and *Paradraculoides* species in mid-Western Australia: *7*, records of *Draculoides* spp. (●) and *Paradraculoides* spp. (○); *8*, Cape Range Peninsula showing records of *D. vinei* (●), *D. julianneae* (○) and *D. brooksi* (⊙); *9*, *Draculoides bramstokeri* (●); *10*, Robe River Valley showing records of *P. anachoretus* (○), *P. bythius* (□), *P. gnophicola* (⊡), *P. kryptus* (△), *P.* sp. (⊙), and *D. mesozeirus* (●).

Fig. 11-12. Tergites I-III showing setation patterns: *11*, *Draculoides brooksi* Harvey, ♀ (WAM 93/2116); *12*, *Paradraculoides kryptus*, sp. nov., paratype ♂ (WAM T76906).

Fig. 13. *Draculoides vinei* (Harvey), holotype ♂ (WAM 87/987), flagellum, lateral. See Materials and Methods for setal abbreviations.

Figs 14-17. *Draculoides bramstokeri* Harvey and Humphreys, ♂ (WAM T66002), unless stated otherrwise: *14*, flagellum, dorsal; *15*, flagellum, ventral; *16*, flagellum, lateral; *17*, flagellum, lateral, holotype ♂ (WAM 93/2094). See Materials and Methods for setal abbreviations.

Figs 18-21. *Draculoides brooksi* Harvey, ♀ (WAM 93/2117): *18*, flagellum, dorsal; *19*, flagellum, ventral; *20*, flagellum, lateral; *21*, genitalia, dorsal. See Materials and Methods for setal abbreviations.

Figs 22-24. *Draculoides julianneae* Harvey, ♂ (WAM T45838): *22*, flagellum, dorsal; *23*, flagellum, ventral; *24*, flagellum, lateral. See Materials and Methods for setal abbreviations.

Figs 25-28. *Draculoides mesozeirus*, sp. nov., holotype ♀ (WAM T63329): *25*, flagellum, dorsal; *26*, flagellum, ventral; *27*, flagellum, lateral; *28*, genitalia, dorsal. See Materials and Methods for setal abbreviations.

Figs 29-31. *Draculoides neoanthropus*, sp. nov., holotype ♂ (WAM T75215): *29*, flagellum, dorsal; *30*, flagellum, ventral; *31*, flagellum, lateral. See Materials and Methods for setal abbreviations.

Figs 32-35. *Paradraculoides anachoretus*, sp. nov., holotype ♀ (WAM T63327): *32*, flagellum, dorsal; *33*, flagellum, ventral; *34*, flagellum, lateral; *35*, genitalia, dorsal. See Materials and Methods for setal abbreviations.

Figs 36-42. *Paradraculoides bythius*, sp. nov.: *36-38*, holotype ♂ (WAM T63364): *36*, flagellum, dorsal; *37*, flagellum, ventral; *38*, flagellum, lateral; *39-42*, paratype ♀ (WAM T63340): *39*, flagellum, dorsal; *40*, flagellum, ventral; *41*, flagellum, lateral; *42*, genitalia, dorsal. See Materials and Methods for setal abbreviations.

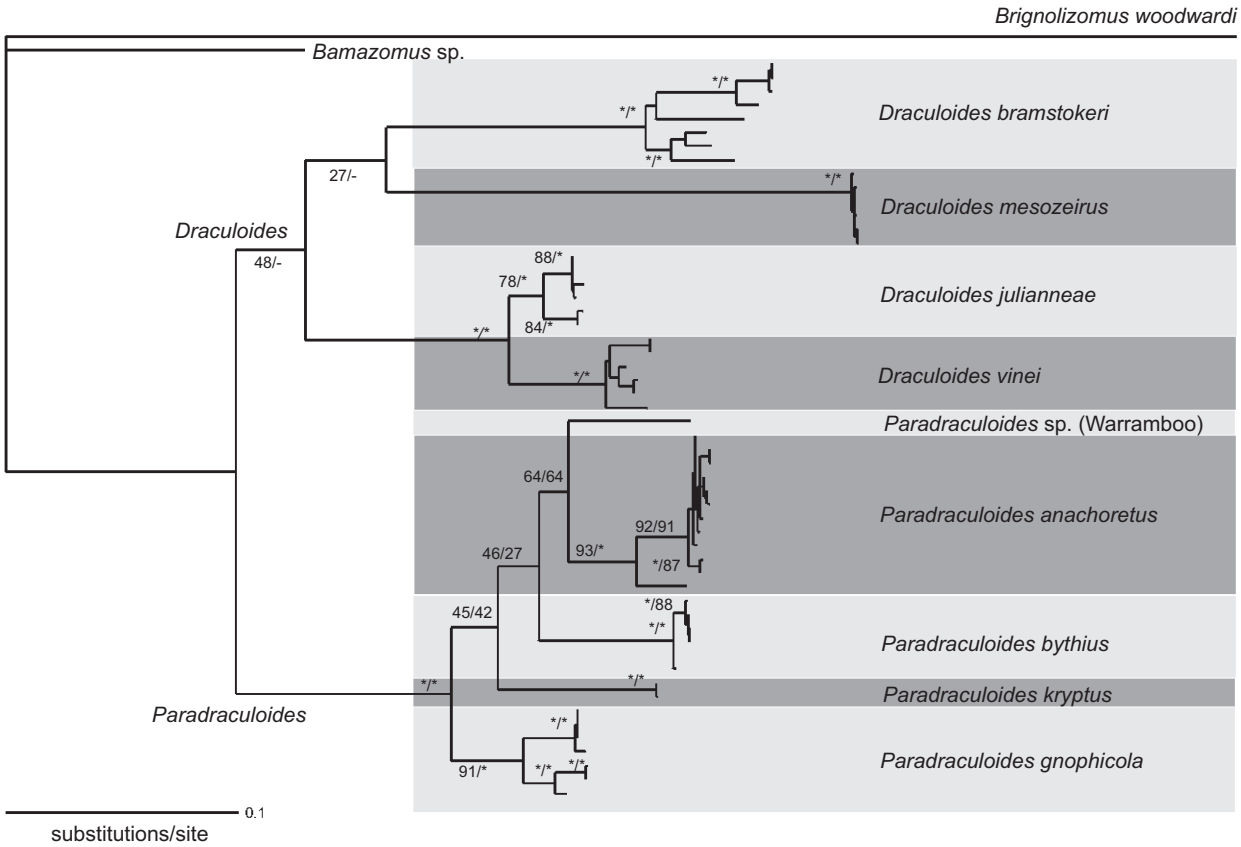
Figs 43-46. *Paradraculoides gnophicola*, sp. nov., holotype ♀ (WAM T65763): *43*, flagellum, dorsal; *44*, flagellum, ventral; *45*, flagellum, lateral; *46*, genitalia, dorsal. See Materials and Methods for setal abbreviations.

Figs 47-53. *Paradraculoides kryptus*, sp. nov.: *47-49*, holotype ♂ (WAM T65801): *47*, flagellum, dorsal; *48*, flagellum, ventral; *49*, flagellum, lateral; *50-53*, paratype ♀ (WAM T65798): *50*, flagellum, dorsal; *51*, flagellum, ventral; *52*, flagellum, lateral; *53*, genitalia, dorsal. See Materials and Methods for setal abbreviations.


1


2


3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Bamazomus sp.
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Draculoides mesozeirus
Draculoides julianneae
Draculoides vinei
Paradraculoides sp. (Warramboo)
Paradraculoides anachoretus
Paradraculoides bythius
Paradraculoides kryptus
Paradraculoides gnophicola
Draculoides
Paradraculoides
27/-
48/-
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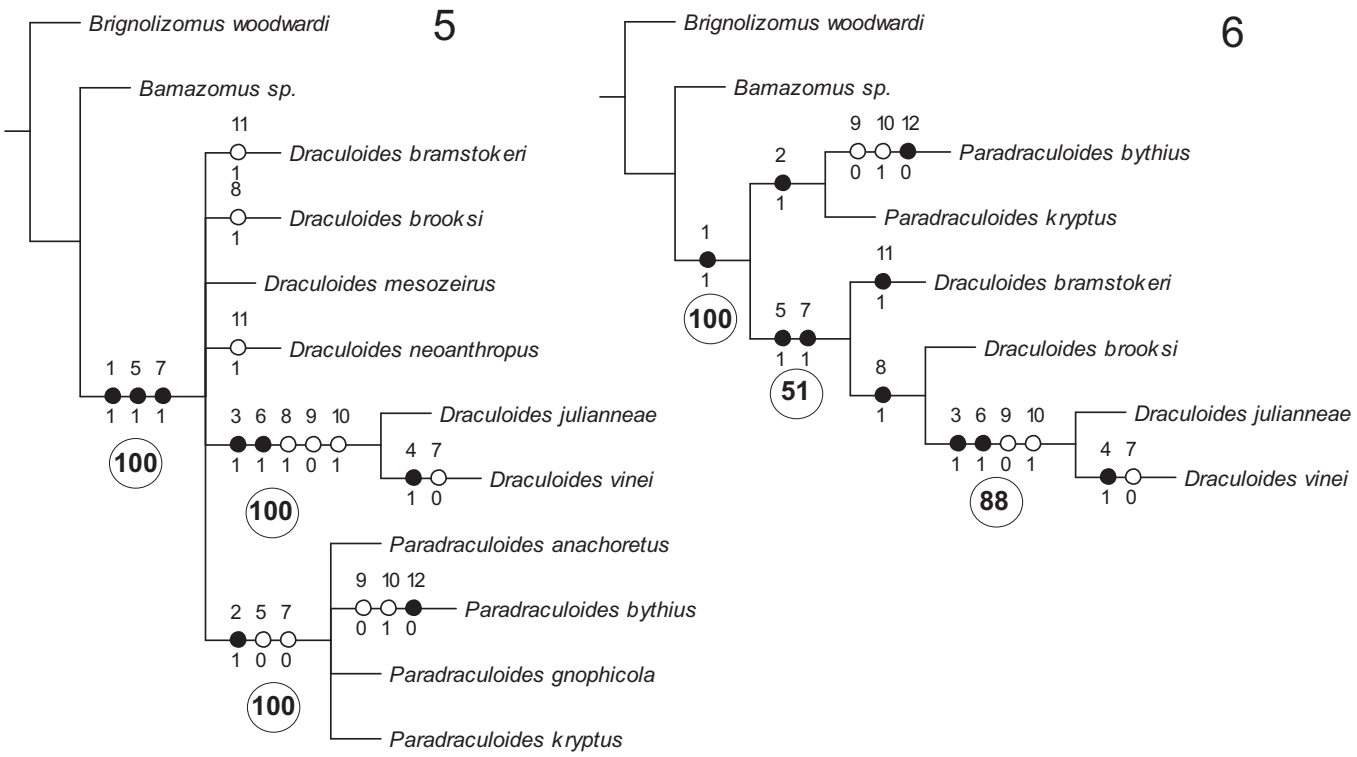
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Bamazomus sp.
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Draculoides bramstokeri
8
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Draculoides brooksi
Draculoides mesozeirus
11
1
Draculoides neoanthropus
1 5 7
1 1 1
100
3 6 8 9 10
1 1 1 0 1
Draculoides julianneae
4 7
1 0
Draculoides vinei
100
Paradraculoides anachoretus
9 10 12
0 1 0
Paradraculoides bythius
2 5 7
1 0 0
Paradraculoides gnophicola
100
Paradraculoides kryptus
6
Brignolizomus woodwardi
Bamazomus sp.
9 10 12
0 1 0
Paradraculoides bythius
2
1
Paradraculoides kryptus
1
1
100
11
1
Draculoides bramstokeri
5 7
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1 1 0 1
Draculoides julianneae
4 7
1 0
Draculoides vinei
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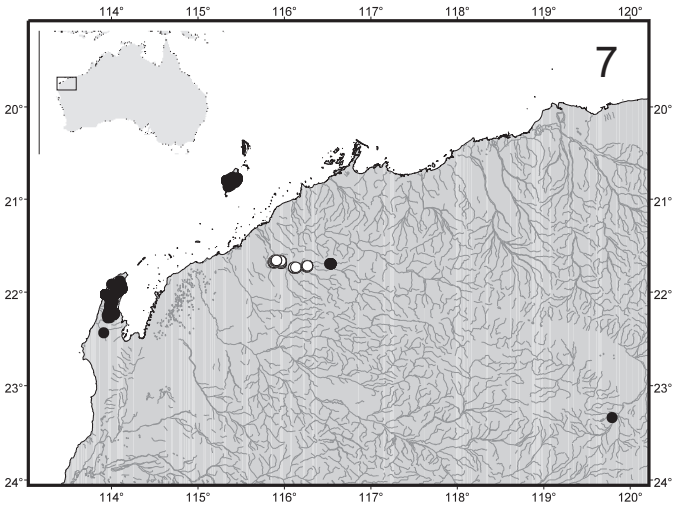
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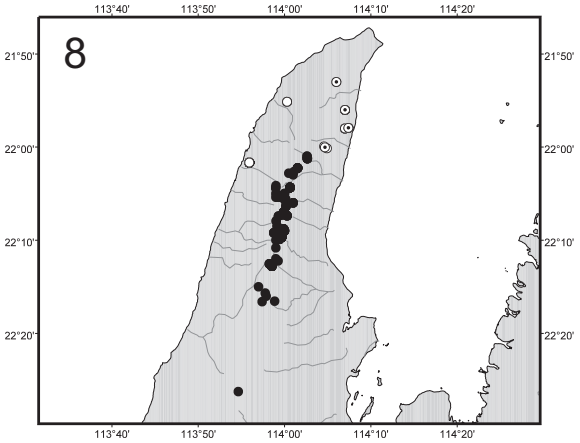
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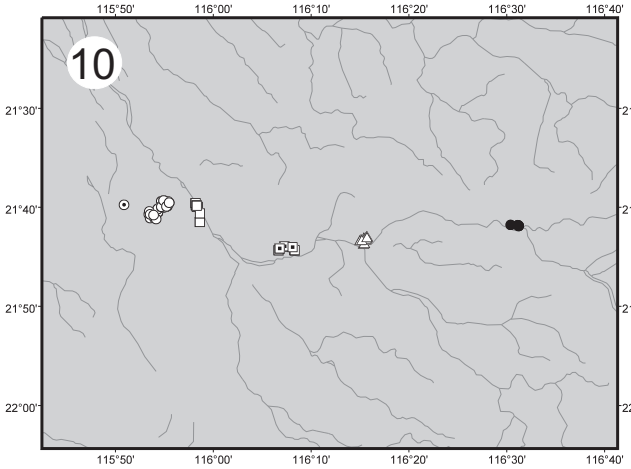
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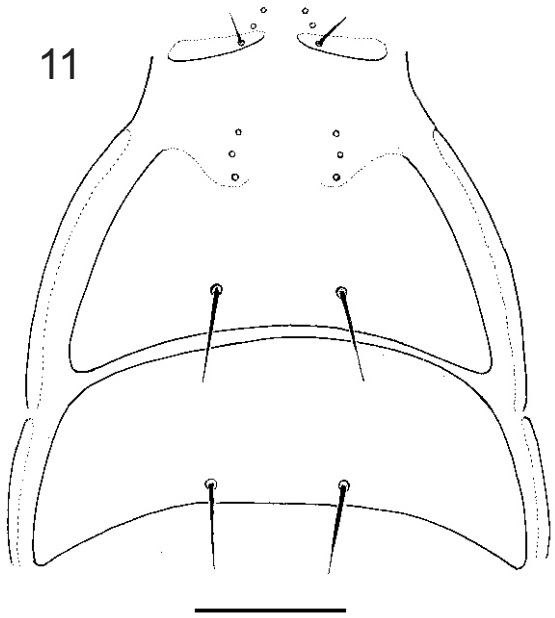
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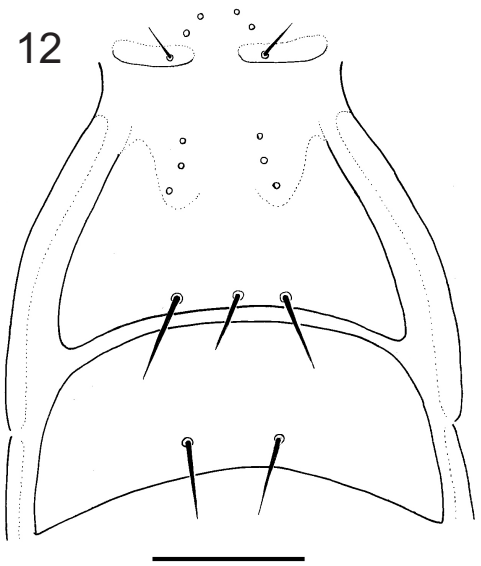
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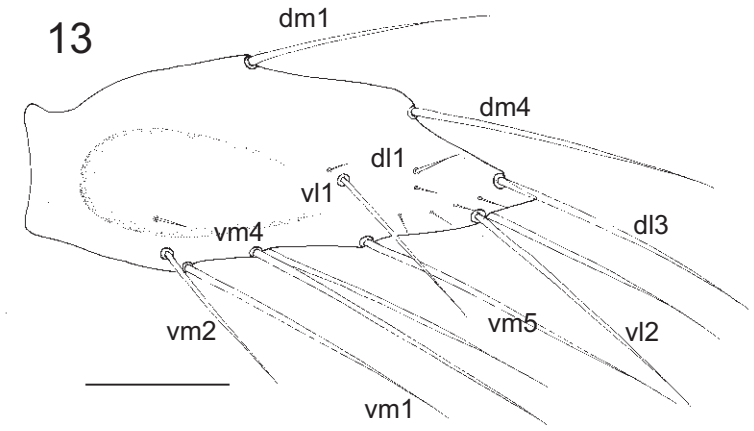
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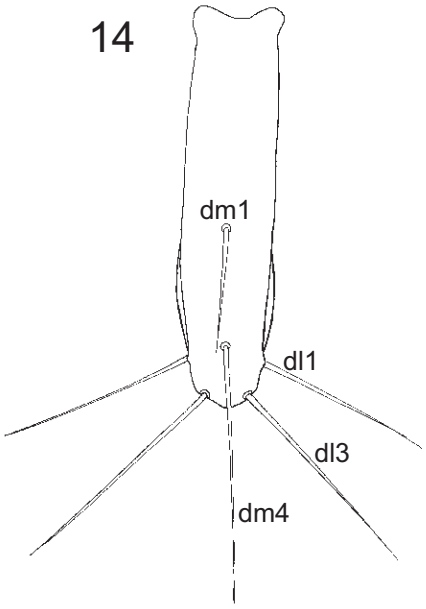
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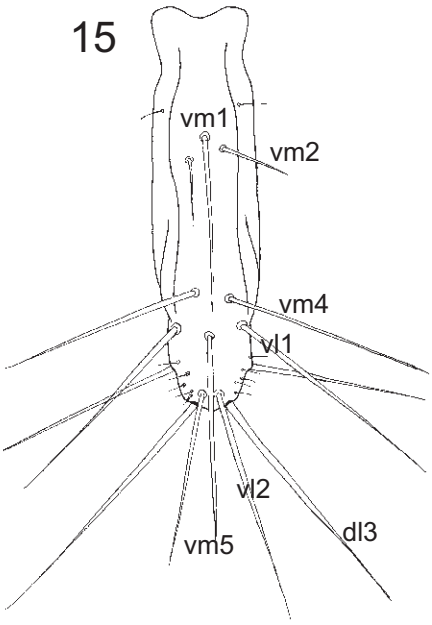
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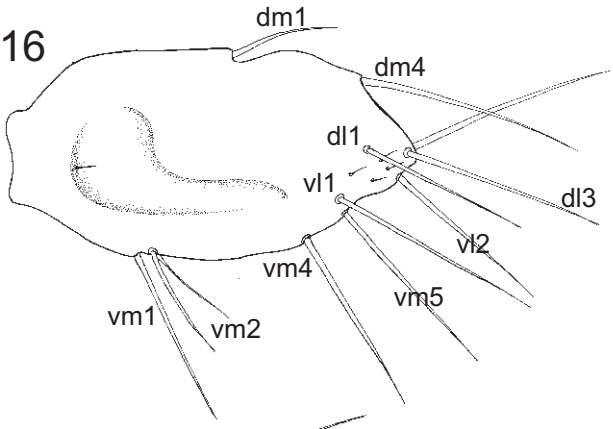
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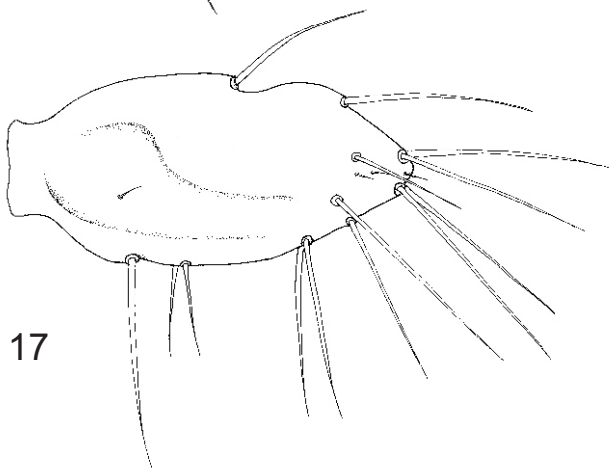

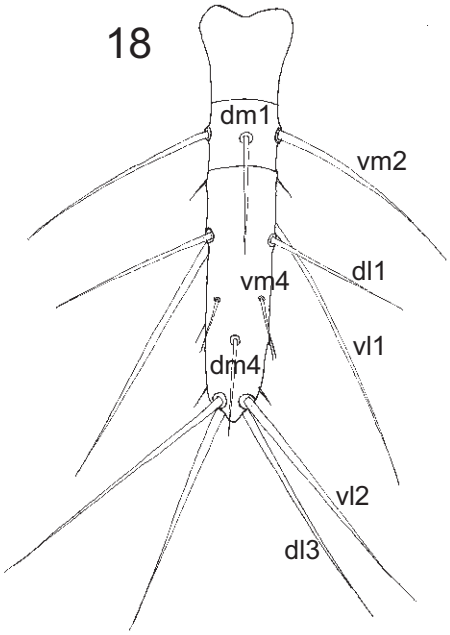
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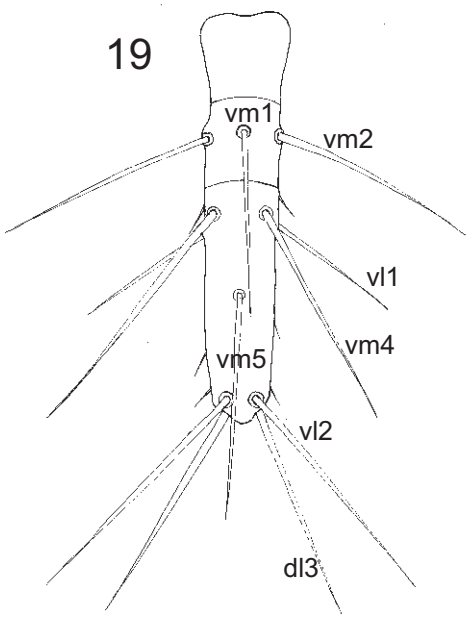
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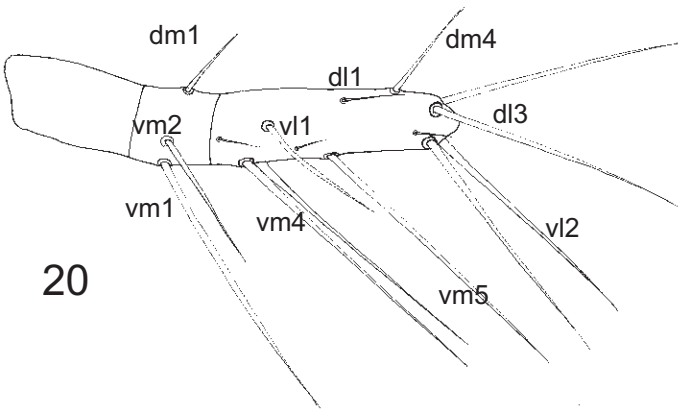
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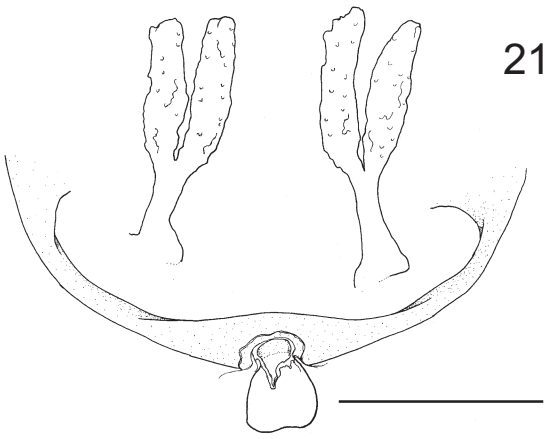
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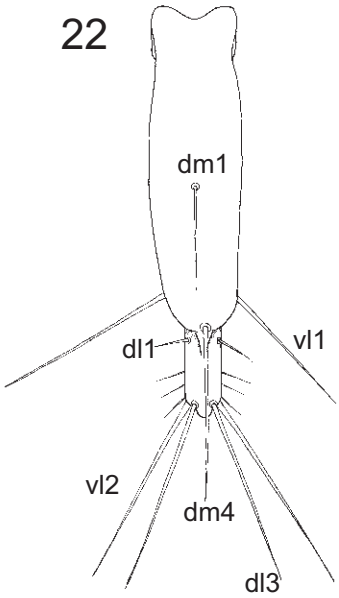
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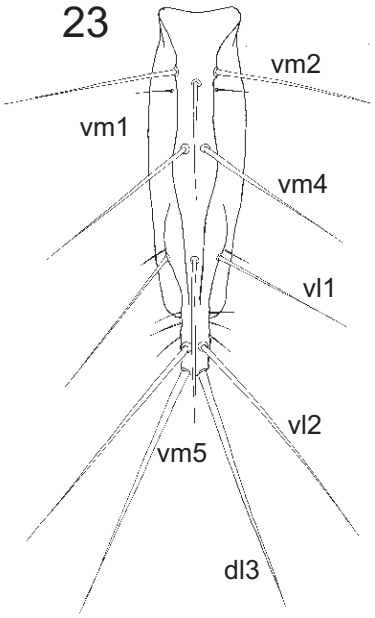
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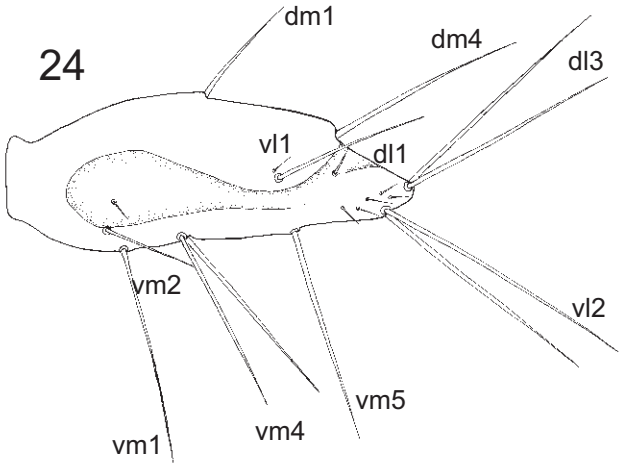
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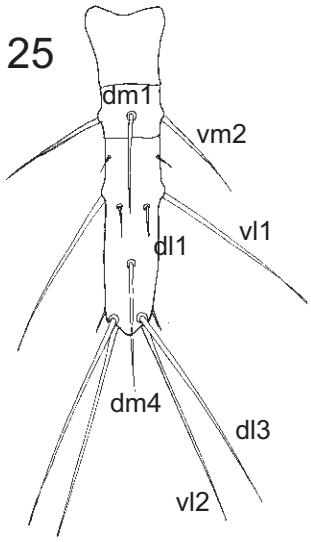
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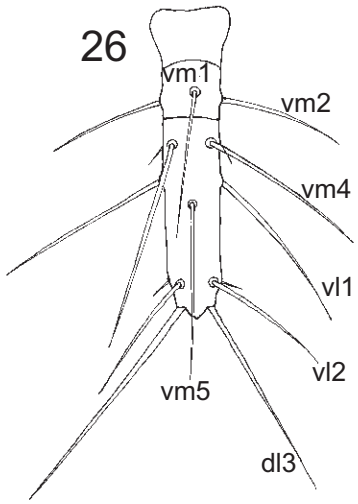
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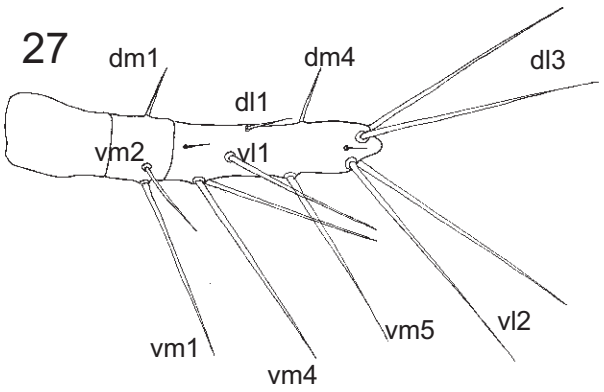
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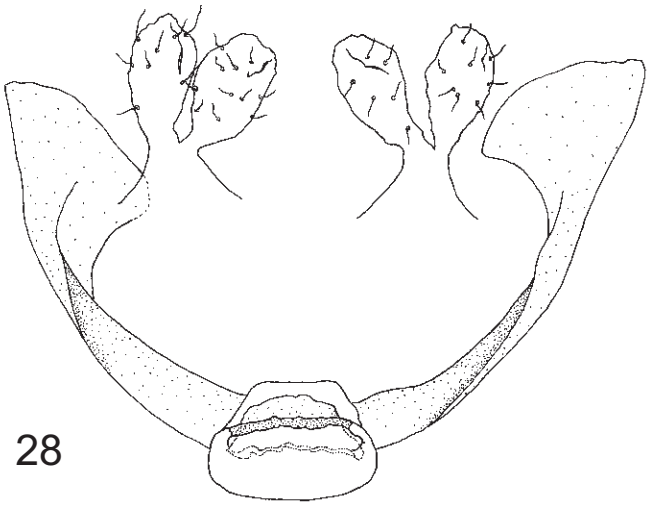
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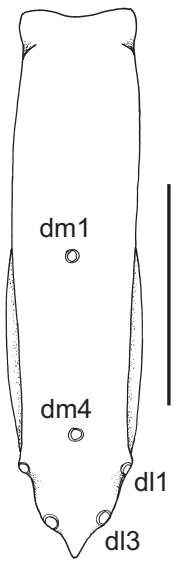
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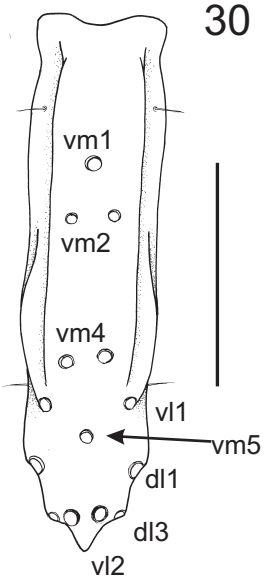
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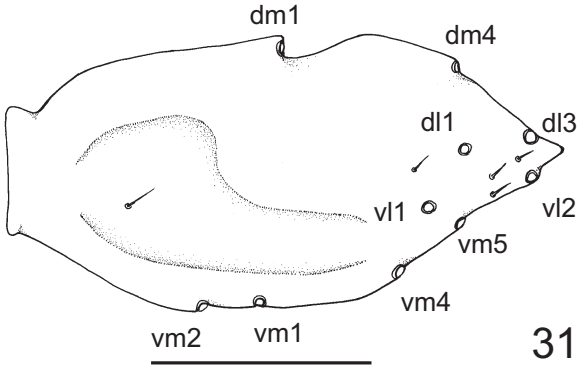
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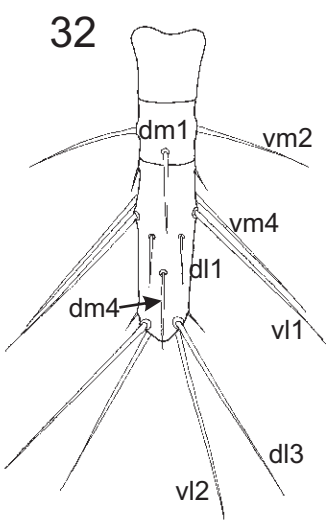
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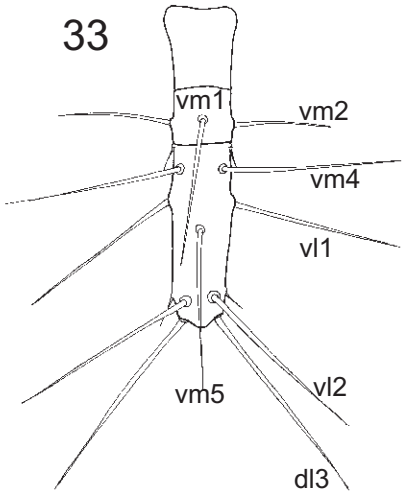
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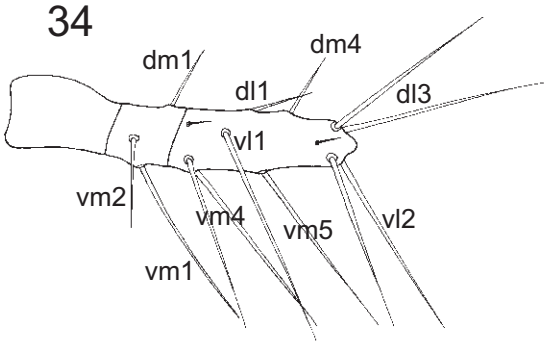
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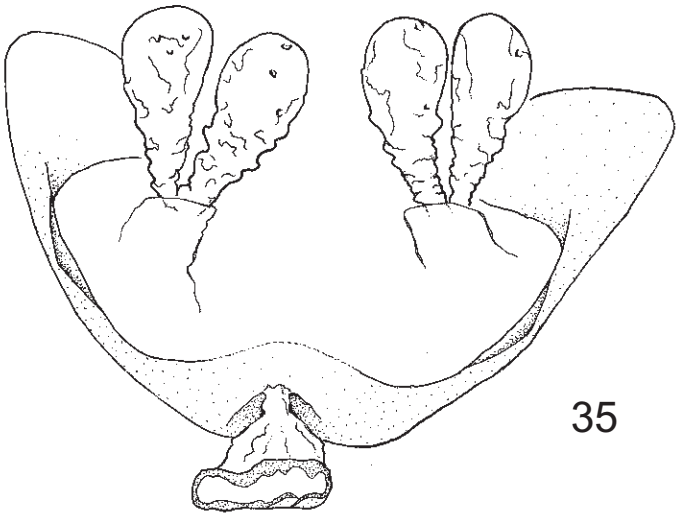
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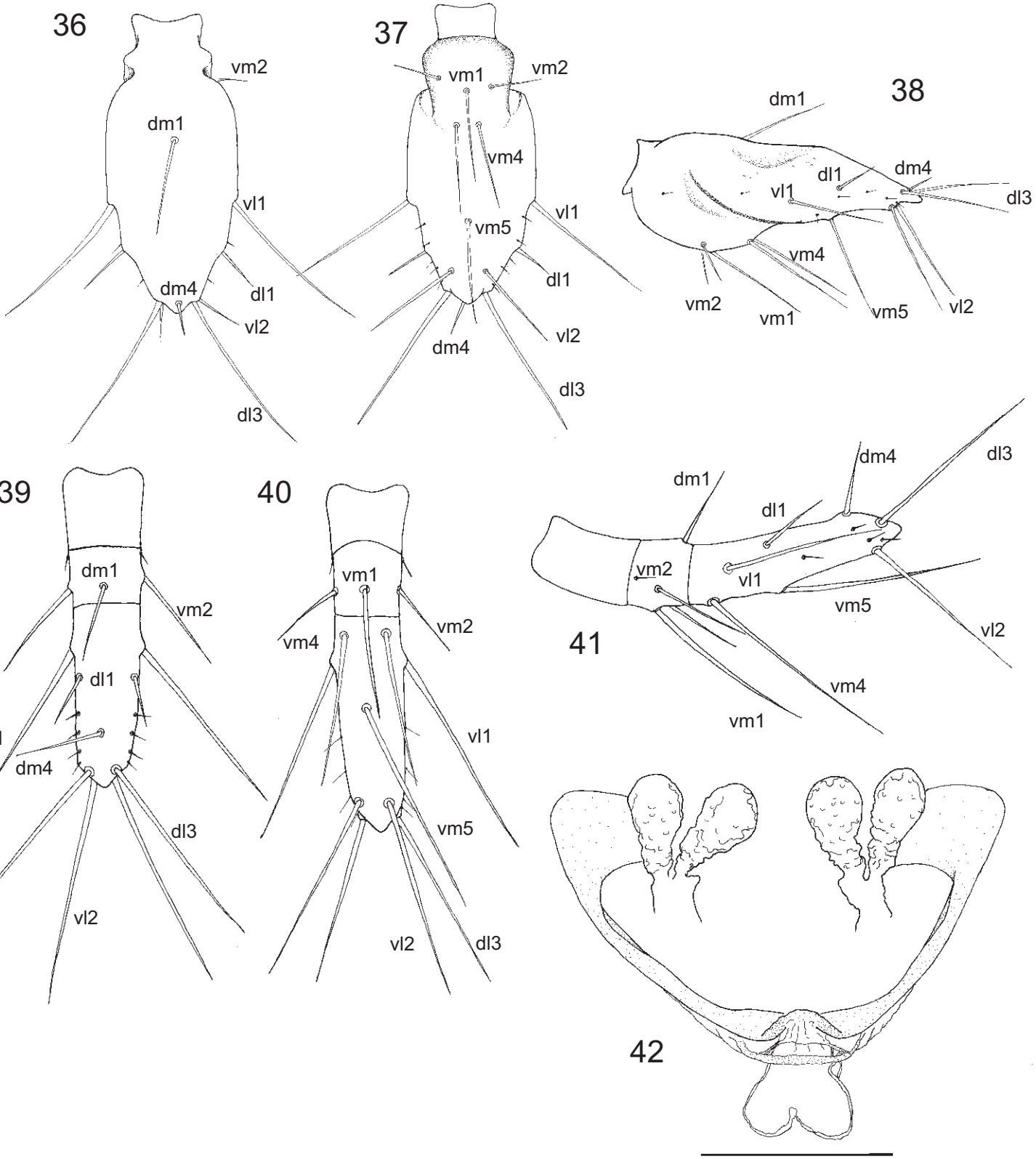
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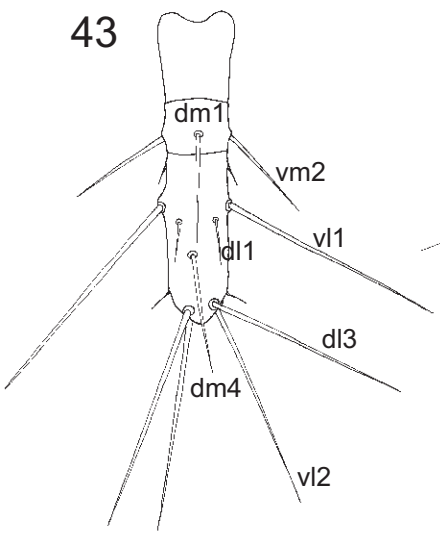
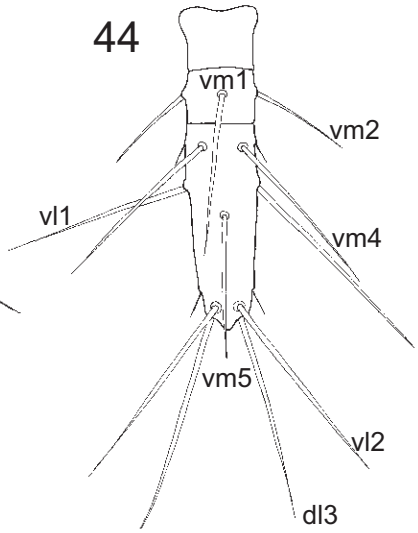
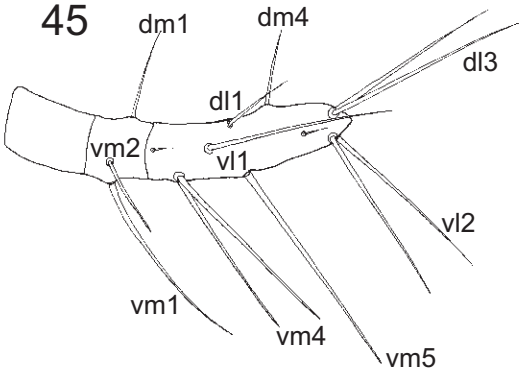
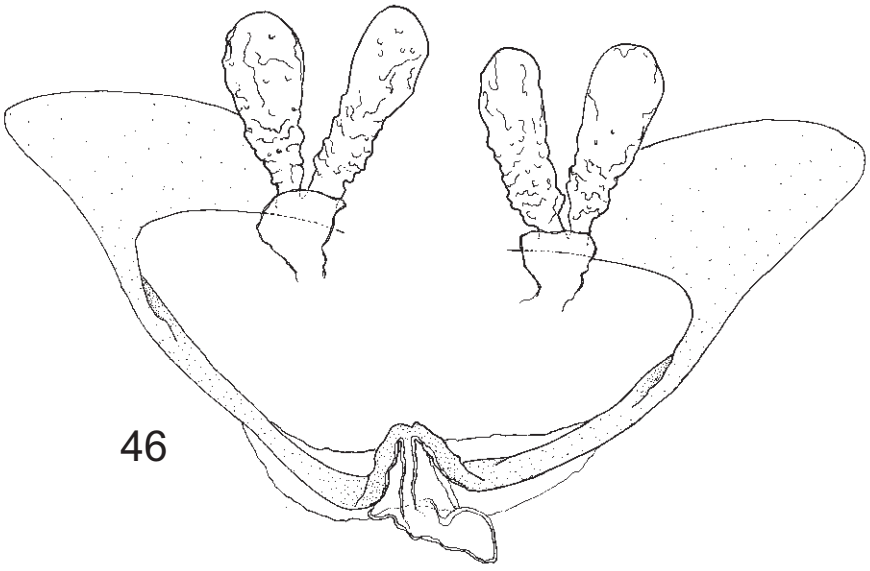
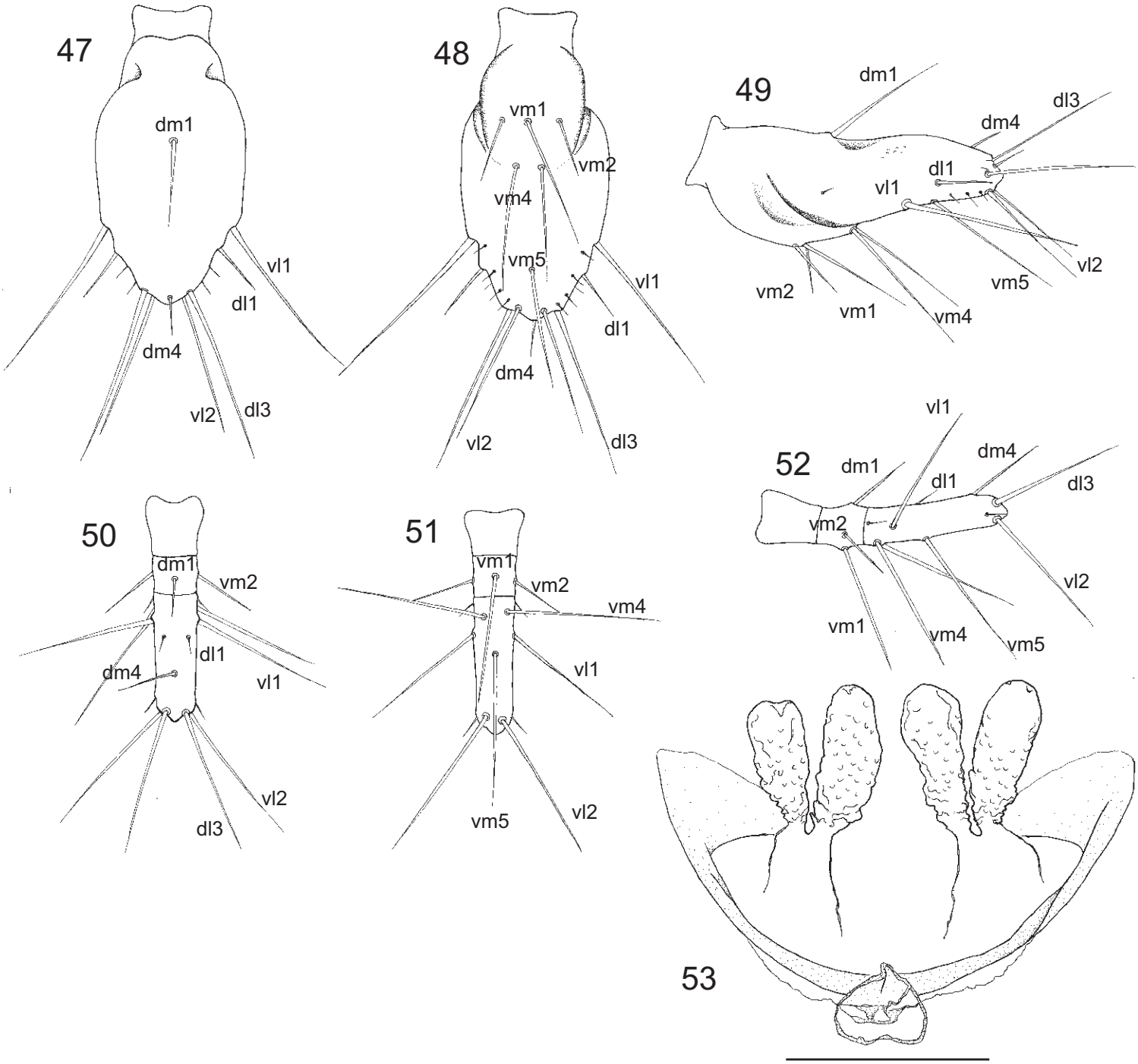
vm1
42


43
dm1
vm2
vl1
dl1
dl3
dm4
vl2


44
vm1
vm2
vl1
vm4
vm5
vl2
dl3


45
dm1
dm4
dl3
dl1
vm2
vl1
vl2
vm1
vm4
vm5


46


47
dm1
vl1
dl1
dm4
vl2
dl3
48
vm1
vm2
vm4
vm5
vl1
dl1
dm4
vl2
dl3
49
dm1
dl3
dm4
dl1
vl1
vl2
vm2
vm5
vm1
vm4
50
dm1
vm2
dl1
dm4
vl1
vl2
dl3
51
vm1
vm2
vm4
vl1
vm5
vl2
52
vl1
dm1
dm4
dl1
dl3
vm2
vl2
vm1
vm4
vm5
53