

# A systematic revision of the South African Pettalidae (Arachnida : Opiliones : Cyphophthalmi) based on a combined analysis of discrete and continuous morphological characters with the description of seven new species

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**Abstract.** The cyphophthalmid family Pettalidae in South Africa is revised and seven new species are described from museum material collected between 1939 and 1985. Two of these are placed in the genus *Purcellia* and five in *Parapurcellia*, bringing the total number of described South African cyphophthalmids to 15. In addition, *Purcellia peregrinator* is transferred to the genus *Parapurcellia*. Phylogenetic analyses of discrete morphological and continuous morphometric characters, both separately and in combination, support the generic assignments and contribute towards a more detailed understanding of the systematics of the group in South Africa. In order to assess the stability of our phylogenetic results, the different morphological datasets were analysed under equal and implied weighting, as well as under several weighting schemes that varied the respective contribution to tree length of the discrete and continuous data partitions. These variations generated two phylogenetic hypotheses: (1) monophyly of the South African pettalids + *Austropurcellia* from north-eastern Australia as a derived clade within Pettalidae; and (2) polyphyly of the South African pettalids with *Parapurcellia* basal within Pettalidae. The latter hypothesis is congruent with previous molecular phylogenies of Cyphophthalmi, and has moderate bootstrap support. The sisterhood of *Purcellia griseoldi*, sp. nov. and *P. lawrencei*, sp. nov. receives high nodal support across analytic methods. New combination: *Parapurcellia peregrinator* (Lawrence, 1963).

**Additional keywords:** Afromontane forests, Gondwanan biogeography, morphometrics, South Africa.

## Introduction

The opilionid order Cyphophthalmi (often referred to as mite harvestmen) is represented by 17 species in Africa (Giribet 2000; Giribet and Prieto 2003). These include members in the tropical families Neogoveidae (three described species in the genus *Parogovia* Hansen, 1921), represented in western equatorial and western sub-Saharan Africa (Sierra Leone, Ivory Coast, Cameroon, Equatorial Guinea and Gabon; Hansen 1921; Juberthie 1969; Legg 1990; Giribet 2000; authors' unpubl. data), and Ogoveidae (three described species in the genus *Ogovea* Roewer, 1923), represented in western equatorial Africa (Cameroon, Equatorial Guinea and Gabon; Hansen and Sørensen 1904; Hansen 1921; Giribet 2000; Giribet and Prieto 2003), plus a species of uncertain affinity from Kenya, *Marwe coarctata* Shear, 1985 (Shear 1985; Giribet and Boyer 2002). Within the territories of the former temperate Gondwana, the family Pettalidae is represented in South Africa by three genera, the monotypic *Speleosiro* Lawrence, 1931, and seven species in the genera *Purcellia* Hansen & Sørensen, 1904 and *Parapurcellia* Rosas Costa, 1950, plus a species in the

monotypic genus *Manangotria* Shear & Gruber, 1996 in Madagascar. A second monotypic genus, *Ankaratra* Shear & Gruber, 1996, remains untested phylogenetically and is so far considered *incertae sedis* (Shear and Gruber 1996; Giribet 2000).

Pettalidae contains eleven genera distributed across the continental fragments of temperate Gondwana (Boyer and Giribet 2007; Giribet and Boyer 2007): *Chileogovea* Roewer, 1961 (Chile) – *Aoraki* Boyer & Giribet, 2007, *Rakaia* Hirst, 1925 and *Neopurcellia* Forster, 1948 (New Zealand) – *Austropurcellia* Juberthie, 1988 (Queensland, Australia) – *Karripurcellia* Giribet, 2003 (Western Australia) – *Pettalus* Thorell, 1876 (Sri Lanka) – and the above mentioned African genera. Each genus is restricted to a single landmass, despite prior hypotheses of trans-Tasman distributions in *Rakaia* and *Neopurcellia* reported from New Zealand and Australia (see Boyer and Giribet 2007).

There is considerable molecular and morphological support for the monophyly of many family-level clades within the Cyphophthalmi (Giribet and Boyer 2002; Boyer *et al.* 2007a), but the intergeneric relationships, especially within the family Pettalidae, are less resolved (e.g. Giribet 2003; Boyer and Giribet

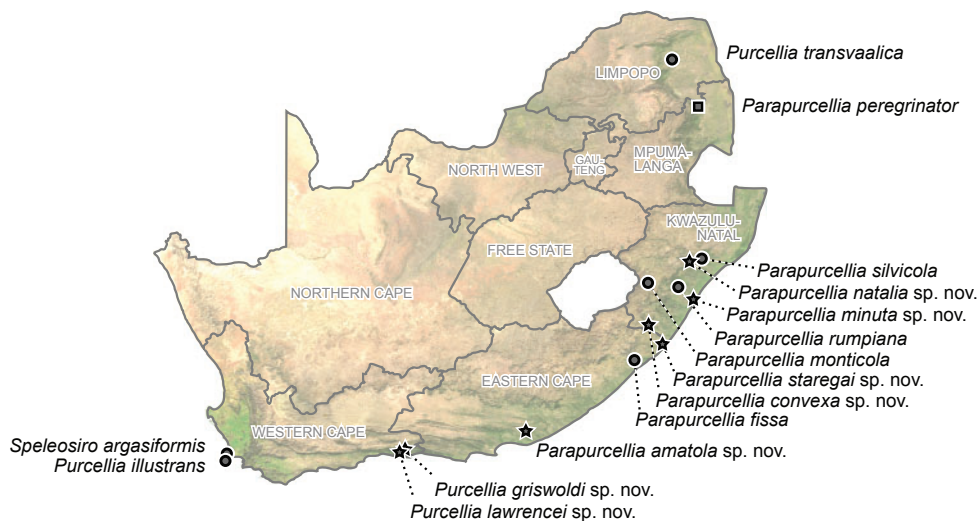
2007, 2009; de Bivort *et al.* 2010). Molecular evidence favours the monophyly of all genera as currently defined, although only a few (*Aoraki*, *Rakaia*, *Pettalus*) have been thoroughly sampled in molecular studies (Boyer and Giribet 2007; Boyer *et al.* 2007a, 2007b). In these studies, the African pettalids were restricted to representatives of only three species, one in the genus *Purcellia* and two in the genus *Parapurcellia*, and South Africa was paraphyletic with respect to other landmasses.

The described South African pettalid fauna is currently distributed in two geographic regions (Fig. 1). Two species are found in the Western Cape province, specifically in and around Table Mountain. *Purcellia illustrans* Hansen & Sørensen, 1904 has been collected in forests surrounding Table Mountain. *Speleosiro argasiformis* Lawrence, 1931 is a large (5 mm) cyphophthalmid found in the Wynberg cave system in Table Mountain (Juberthie 1970). The former species is a medium-sized cyphophthalmid with morphological characteristics typical of other members of South African pettalids, such as relatively unmodified opisthosomal posterior tergites in males and females, second palp articles that are less than half ornamented and bilobed anal plates in males. For illustrations of these and other cyphophthalmid morphological terms, see de Bivort *et al.* (2010). One conspicuous feature of *P. illustrans* is the position of its anal plate, which is shifted anteriorly onto the ventral surface of the animal compared with other pettalids. *Speleosiro argasiformis* has conspicuous troglomorphic modifications, such as elongated appendages.

While *Speleosiro* is monotypic, *Purcellia* is currently represented by two additional species found in eastern South Africa. *Purcellia transvaalica* Lawrence, 1963 is found in the Hanglip forest of the Limpopo Province and has an appearance typical of other *Purcellia* species. *Purcellia peregrinator* Lawrence, 1963, found in Mariepskop Forest, Mpumalanga Province, has characteristics more typical of the genus *Parapurcellia*, which has a distribution in the Natal Drakensberg and Natal–Zululand Coast of the Eastern Cape and

Kwazulu–Natal Provinces. In fact, Lawrence (1963: 279) stated that ‘This species resembles [*Parapurcellia*] *silvicola* from Zululand in the shape of the tarsus IV.’ In particular, it has ozophores oriented at 45° off the lateral margin, rather than dorsal ozophores, projections of the anterior gonostome wall, a small (~2.5 mm) body length, and no evidence of functional eyes under light microscopy – unlike *Purcellia*, which has lensless eyes situated in the bases of the ozophores. Based on these characters, as well as several others discussed below, and consistent placement of *Purcellia peregrinator* within *Parapurcellia* in our phylogenetic analyses, we reassign *Purcellia peregrinator* to *Parapurcellia*, establishing the new combination *Parapurcellia peregrinator* (Lawrence, 1963), leaving the number of described species in *Parapurcellia* at five. *Parapurcellia fissa* (Lawrence, 1939) and *Parapurcellia silvicola* (Lawrence, 1939) are distinctive due to their deeply lobed posterior tergites. In the remaining two species, *Parapurcellia monticola* (Lawrence, 1939) and *Parapurcellia rumpiana* (Lawrence, 1933), the posterior tergites are relatively unmodified, and their morphologies are typical of small pettalids, although the former species is distinguishable from the other South African species by its tall profile.

The Natal Museum of South Africa (NMSA) kindly provided us with undescribed cyphophthalmid specimens collected by several arachnologists between 1939 and 1985. We identified two distinct morphospecies, collected in the Knysna forest that straddles the border of the Eastern and Western Cape Provinces, which appear to belong in *Purcellia*. An additional four morphospecies from localities in the Eastern Cape and Kwazulu–Natal Provinces, segregated years ago by W. Starega, who assigned tentative names to some of the species, appear to belong in *Parapurcellia*. We have chosen to use his names as much as possible to honour his early recognition of the different morphologies. These are described as new species below, and our placement of them into their respective genera is supported by morphological phylogenetic analysis.



**Fig. 1.** Map of pettalid type collection localities in South Africa. Circles indicate localities of species described before this work. Stars indicate new species described herein. Square indicates *Parapurcellia peregrinator* (Lawrence, 1963) **new comb.**, whose genus is reassigned herein.

The NMSA collections, along with most collections of previously described species, were made before the era of molecular phylogenetics. Their long-term storage in 70% ethanol has precluded the possibility of analysing the species-level relationships of the South African pettalids using molecular

sequences. In order to investigate the phylogenetic relationships of the South African material, we chose to perform a phylogenetic analysis under the parsimony criterion using all available morphological data. Attempts at 'total evidence' analysis have proved successful in past analyses of the Cyphophthalmi

**Table 1. Discrete character matrix**  
Character codings are explained in Appendix 2

Taxa	Characters							
	000000000	111111111	222222222	333333333	444444444	555555555	666	
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012
<i>Parapurcellia staregai</i> , sp. nov.	032200011	0311?01100	011001?100	00-00?0100	0112000100	1130100100	0??	
<i>Parapurcellia amatolae</i> , sp. nov.	032200011	0311?00100	1101011000	00-0020100	0112000100	1130100100	0??	
<i>Parapurcellia convexa</i> , sp. nov.	032200011	0311?00100	0101011100	00-0020100	0112000110	1120100101	0??	
<i>Parapurcellia natalia</i> , sp. nov.	032200011	0310?00100	011101?100	00-00?0100	0112000110	1130100100	0??	
<i>Parapurcellia minuta</i> , sp. nov.	032200011	0311?01100	0101011000	00-0020110	0112000110	10-0100100	0??	
<i>Parapurcellia peregrinator</i>	032200011	0211?00100	111101?110	00-0030?00	0112000110	1120100100	0??	
<i>Parapurcellia silvicola</i>	032200011	0311?00000	0101011100	00-0020100	011?000110	0100100101	0??	
<i>Parapurcellia monticola</i>	032200011	0211?00000	0101011100	00-0020100	011?000110	1130100100	0??	
<i>Parapurcellia rumpiana</i>	032200011	0210?01100	0101?11101	?0-??30100	011?000110	110?100100	0??	
<i>Parapurcellia fissa</i>	032200011	0311?00100	0101?1?10?	?????30100	01?000110	?130100100	0??	
<i>Purcellia transvaalica</i>	222200011	0201?01100	110101?100	00-002??00	0112100100	1140110100	0??	
<i>Purcellia illustrans</i>	222200011	0001?00000	1101011101	00-0020100	0112100100	0140110100	001	
<i>Purcellia griswoldi</i> , sp. nov.	222200010	0201?00100	1001011100	00-0020100	0112100100	1140110100	011	
<i>Purcellia lawrencei</i> , sp. nov.	222200011	0301?00100	110101?100	00-0020100	0112100100	1140110100	0??	
<i>Speleosiro argasiformis</i>	022200011	0001?00000	1100011101	?0-0020100	0111000100	0140110100	0??	
<i>Rakaia isolata</i>	232200011	0001?01000	110101?100	00-0020000	01?000110	0100101101	0??	
<i>Rakaia lindsayi</i>	232200011	0001?00000	1100010210	00-0020000	011?000110	0100100101	0??	
<i>Rakaia magna australis</i>	232200011	0001?01000	1100011200	00-0020000	011?000110	0100100100	0??	
<i>Rakaia media</i>	232200011	0001?00000	1101011200	00-0020000	0112?00110	0100100100	0??	
<i>Rakaia solitaria</i>	132200011	0001?00000	1101011200	00-0020000	011?000110	0100101100	0??	
<i>Rakaia sorenseni digitata</i>	232200011	0001?00000	1101011100	00-0020050	010--00110	00-01-1000	0??	
<i>Aoraki crypta</i>	232200011	0001?00000	1110010101	00-0020000	0112?00110	01311-0000	0??	
<i>Aoraki denticula</i>	232200011	0001?00000	1110010201	00-0021000	0112?00110	01301-0001	0??	
<i>Aoraki inerma</i>	232200011	0001?00000	1110010201	00-0020000	0112?00110	01311-0000	0??	
<i>Aoraki longitarsa</i>	232200011	0001?00000	1110010201	00-0021000	01?000110	0100100101	1??	
<i>Aoraki tumidata</i>	232200011	0001?01000	?11001011?	?0-??2???	?112100111	10-0101101	0??	
<i>Karripurcellia harveyi</i>	232200011	0001?00010	1110010210	00-0020000	010--10100	00-00-0000	0??	
<i>Karripurcellia peckorum</i>	232200011	0001?01010	1110010210	00-0020000	010--10100	00-00-0000	001	
<i>Karripurcellia sierwaldae</i>	232200011	0001?01010	1100011200	00-0020000	010--10100	00-00-0000	0??	
<i>Austropurcellia scoparia</i>	232200011	0001?00000	1101011101	00-0030100	0114000110	01101-0000	11?	
<i>Austropurcellia woodwardi</i>	232200011	0201?00000	?1??11101	00-0030100	011?000110	0130100100	1??	
<i>Chileogovea jocasta</i>	132200011	0011?00000	1110010101	00-1140000	0112100100	00-00-0000	0??	
<i>Chileogovea oedipus</i>	132100011	0011?00000	1110010211	00-1141000	0112100101	10-00-0000	01?	
<i>Pettalus lampetides</i>	122200011	0011?00010	1110110001	00-0041001	010--02100	00-01-1000	01?	
<i>Pettalus cimiciformis</i>	122100011	0031?0001?	1110010101	00-??4100?	010--02100	00-01-1000	0??	
<i>Troglosiro aelleni</i>	010210011	0010?00000	2110000201	0110030000	0010?03-00	00-00-0000	0??	
<i>Troglosiro longifossa</i>	010210011	00100100100	2110000101	0110030000	0010?03-00	00-00-0010	0??	
<i>Troglosiro ninqua</i>	010210011	0010100000	2110000000	0110030000	0010?03-00	00-00-0010	0??	
<i>Huitaca ventralis</i>	010200101	111-100010	2110010201	0110030001	0010?03-00	00-00-0000	00?	
<i>Neogovea</i> sp.	010200111	1310101010	?11?01000?	??????0??	?0??03-00	00-00-0000	0??	
<i>Metagovea philipi</i>	010200111	121?1000?0	2110000101	0110030001	0010?03-00	00-00-0000	001	
<i>Cyphophthalmus duricorius</i>	010211011	0020000101	0000010100	00-0010000	0011?03-01	10-00-0000	011	
<i>Parasiro coiffaiti</i>	000201010	0010000101	0100010000	0111120000	000--01000	00-00-0000	010	
<i>Siro acaroides</i>	010211010	0010000100	0000000000	00-1110000	0011103-00	10-01-0000	011	
<i>Siro rubens</i>	010211011	0020000100	0000020100	00-0010000	0011103-01	00-00-0000	011	
<i>Suzukielus sauteri</i>	012200011	0010?00100	0000020100	1101120100	0013000101	00-00-0000	011	
<i>Stylocellus rambalae</i>	111200101	0000?10001	01101102?1	00-0151010	020--00000	00-00-0000	0??	
<i>Stylocellus tambusisi</i>	111200100	1210?10001	01100102??	00-00?1010	020--00000	10-00-0000	0??	
<i>Fangensis cavernarum</i>	011200100	0010?10101	0100010210	00-0051010	1211?00000	00-00-0000	001	
<i>Fangensis spelaeus</i>	011200100	0010?10101	0100010210	00-0051010	1211?00000	00-00-0000	001	

Table 2. Continuous character matrix as it appears in the 1:1 weighted combined analysis  
Character definitions are given in Appendix 3

Table with 39 columns and 100 rows of species names and their corresponding character state values.



combining morphological and molecular data partitions (Boyer and Giribet 2007; Clouse *et al.* 2009). Recently, morphometric data were shown to carry significant phylogenetic signal in Cyphophthalmi (Clouse *et al.* 2009; de Bivort *et al.* 2010) and Pettalidae specifically (de Bivort *et al.* 2010). Therefore, we performed phylogenetic analyses of the South African pettalids, as well as 15 outgroup species, using both traditional discrete morphological data and morphometric data (separately and in combination). Two phylogenetic hypotheses emerge from these analyses, one in which the South African pettalids form a derived clade within Pettalidae (on their own or in conjunction with the Australian genus *Austropurcellia*), and the other in which *Parapurcellia* is basal within Pettalidae and the group of South African species is polyphyletic. The latter hypothesis bears some similarities to earlier molecular studies, but they had sparser taxon sampling with respect to the South African pettalid fauna (Boyer and Giribet 2007, 2009; Boyer *et al.* 2007b).

### Methods and abbreviations

Specimens used in this study were provided by the following institutions.

AMNH	American Museum of Natural History, New York (USA)
BMNH	The Natural History Museum, London (UK)
CM	Canterbury Museum, Christchurch (New Zealand)
FMNH	Field Museum of Natural History, Chicago (USA)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge (USA)
MHNG	Muséum d'histoire naturelle, Genève (Switzerland)
MNHN	Musée National d'Histoire Naturelle, Paris (France)
MNZ	Te Papa Tongarewa/Museum of New Zealand, Wellington (New Zealand)
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo (Brazil)
NMSA	Natal Museum of South Africa, Pietermaritzburg (South Africa)
QM	Queensland Museum, Brisbane (Australia)
SAM	South African Museum, Cape Town (South Africa)
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (Germany)
USNM	USA National Museum (Smithsonian Institution), Washington, DC (USA)
WAM	Western Australian Museum, Perth (Australia)
ZMH	Zoological Museum of Hamburg, Hamburg (Germany)
ZMB	Museum für Naturkunde, Berlin (Germany)
ZMUC	Zoologisk Museum, University of Copenhagen, Copenhagen (Denmark)

### Specimen handling and illustration

In total, 35 pettalid and 15 outgroup cyphophthalmid taxa were analysed. Animals from our collection and specimens on loan were preserved in ethanol (typically 95% in recently collected specimens, 70% otherwise), and imaged using scanning electron microscopy (SEM) and focus-stacked light micrographs according to the methods detailed in Clouse and Giribet (2007). For all descriptions, the holotype male was

photographed under light microscopy; when available and with the lending institution's permission, paratype males were imaged by SEM and preserved on mounting stubs. Tracings of the dorsal, ventral and lateral body views, and lateral appendage views were generated by directly tracing over specimen micrographs using Adobe Illustrator (Adobe Systems Inc., San Jose, CA). One male and one female paratype of *Purcellia griswoldi*, sp. nov. were dissected in ethanol and their genitalia mounted temporarily in glycerol for imaging by compound microscopy.

### Character coding

Conspicuous discrete characters, such as the position of the ozophores, were scored from our database of images. The states of more subtle characters, such as the ornamentation of particular appendage segments, were confirmed by examination under light or scanning electron microscopy. The discrete characters used are described in Appendix 2 and enumerated in Table 1. Continuous characters were scored from digital images of the dorsal, ventral and lateral views of the animals using the software, ImageJ (Research Services Branch, NIMH, NIH, Bethesda, MD) as detailed in de Bivort *et al.* (2010). Raw measurements and scaled shape descriptor characters were analysed for pair-wise independence and, when found to be dependent, collapsed using principal components analysis based on an independence cutoff of 1.31, which was previously found (de Bivort *et al.* 2010) to yield the trees most consistent with previous studies. These methods were performed using custom scripts in MATLAB (Mathworks Inc., Natick, MA) and yielded the 78 simple and complex continuous characters detailed in Table 2 and Appendix 3.

### Phylogenetic analyses

The discrete character matrix was analysed in the phylogenetic program Tree analysis with New Technology (TNT) (Goloboff *et al.* 2008). For the parsimony analysis under equal weighting, heuristic searches were performed using the 'New Technology' option and 1000 random addition sequences. In all tree searching, the Sectorial Search (Goloboff 1999), Ratchet (Nixon 1999), Drift (Goloboff 1999) and Tree Fusing (Goloboff 1999) options were enabled. Under implied weighting (Goloboff 1993) for  $k$  ranging from 1 to 6, 300 random addition replicates were used. Bootstrapping was done over 100 replicates, each using 300 random addition sequences, and the absolute node frequencies were recorded. The parameters used for the continuous dataset were identical, with the exception of the bootstrap analysis, in which only 100 random addition sequences were used because the continuous search runs were considerably slower. All resulting trees were rooted with Stylocellidae as an outgroup following Boyer *et al.* (2007b).

The relative weighting of data partitions in combined analyses can influence tree topology. Precise relative weighting could be achieved by iteratively weighting a partition, solving for trees with that dataset, determining the length of the tree contributed by the weighted characters, adjusting their weight by their new length contribution, etc., until the tree and data partition weights converged. Alternatively, approximate relative weighting (Clouse *et al.* 2009) can be accomplished by multiplying the

continuous partition of the combined dataset (in its original form) by the factor  $a \times L_D/L_C$ , where  $a$  is the final desired contribution of the continuous data portion compared to the discrete portion (i.e. 1/8th, 1/4th, etc.),  $L_C$  is the length of the tree inferred from the continuous data in their original form, and  $L_D$  is the length of the tree inferred from the discrete data.

## Taxonomy

Order **OPILIONES** Sundevall

Suborder **CYPHOPHTHALMI** Simon

Family **PETTALIDAE** Simon

Genus ***Speleosiro*** Lawrence, 1931

### Diagnosis

Ozophores in a completely dorsal position. Eyes and eye lenses absent. Male coxae IV endites lacking anterior projections. Dentition of the mobile digit of the chelicerae non-uniform with the largest tooth in a central position. Male anal plate bilobed with a large central depression spanning roughly half the area of the anal plate. Scopulae originating on the anterior ventral surface of the anal plate, along the edges of the raised lateral portions. Anal gland on tergite VIII.

### Type species

*Speleosiro argasiformis* Lawrence, 1931.

### Species included

*Speleosiro argasiformis* Lawrence, 1931.

### Distribution

South Africa: only known from the type locality, Wynberg Caves in Table Mountain, Cape Peninsula, Western Cape Province.

### Remarks

This genus is monotypic and nests within the genus *Purcellia* in some of our phylogenetic analyses (see below), consistent with its type locality falling within the range of that genus. Morphologically, however, it exhibits strong troglomorphic modifications to both limbs and body that justify its retention as a separate genus in the absence of consistent phylogenetic placement within *Purcellia*. Analysis of molecular data for this species in the future may help resolve its specific phylogenetic placement.

Genus ***Purcellia*** Hansen & Sørensen, 1904

### Diagnosis

Ozophores in a completely dorsal position. Eyes present, incorporated into the base of the ozophores without lenses. Male coxae IV endites lacking anterior projections (as in Fig. 2J). Dentition of the mobile digit of the chelicerae non-uniform with the largest tooth in a central position (as in Fig. 2N).

Male anal plate bilobed with a large central depression spanning roughly half the area of the anal plate (as in Fig. 2K, L). Scopulae originating on the anterior ventral surface of the anal plate, along the edges of the raised lateral portions. Anal gland on tergite IX with its opening oriented ventrally (as in Fig. 2L).

### Type species

*Purcellia illustrans* Hansen & Sørensen, 1904.

### Species included

*Purcellia illustrans* Hansen & Sørensen, 1904; *Purcellia transvaalica* Lawrence, 1963; *Purcellia griswoldi*, sp. nov.; *Purcellia lawrencei*, sp. nov.

### Distribution

South Africa: Limpopo, Eastern Cape, and Western Cape Provinces.

### Remarks

This genus includes most members of the genus *Purcellia* after Rosas Costa (1950; Giribet 2000) except *Parapurcellia peregrinator*, new. comb., which is here transferred to *Parapurcellia*. The species of *Purcellia* have large depressions on the male anal plate and no projections in the gonostome wall and are distributed in southern South Africa, with the exception of *Purcellia transvaalica*, found in north-eastern South Africa.

### ***Purcellia griswoldi***, sp. nov.

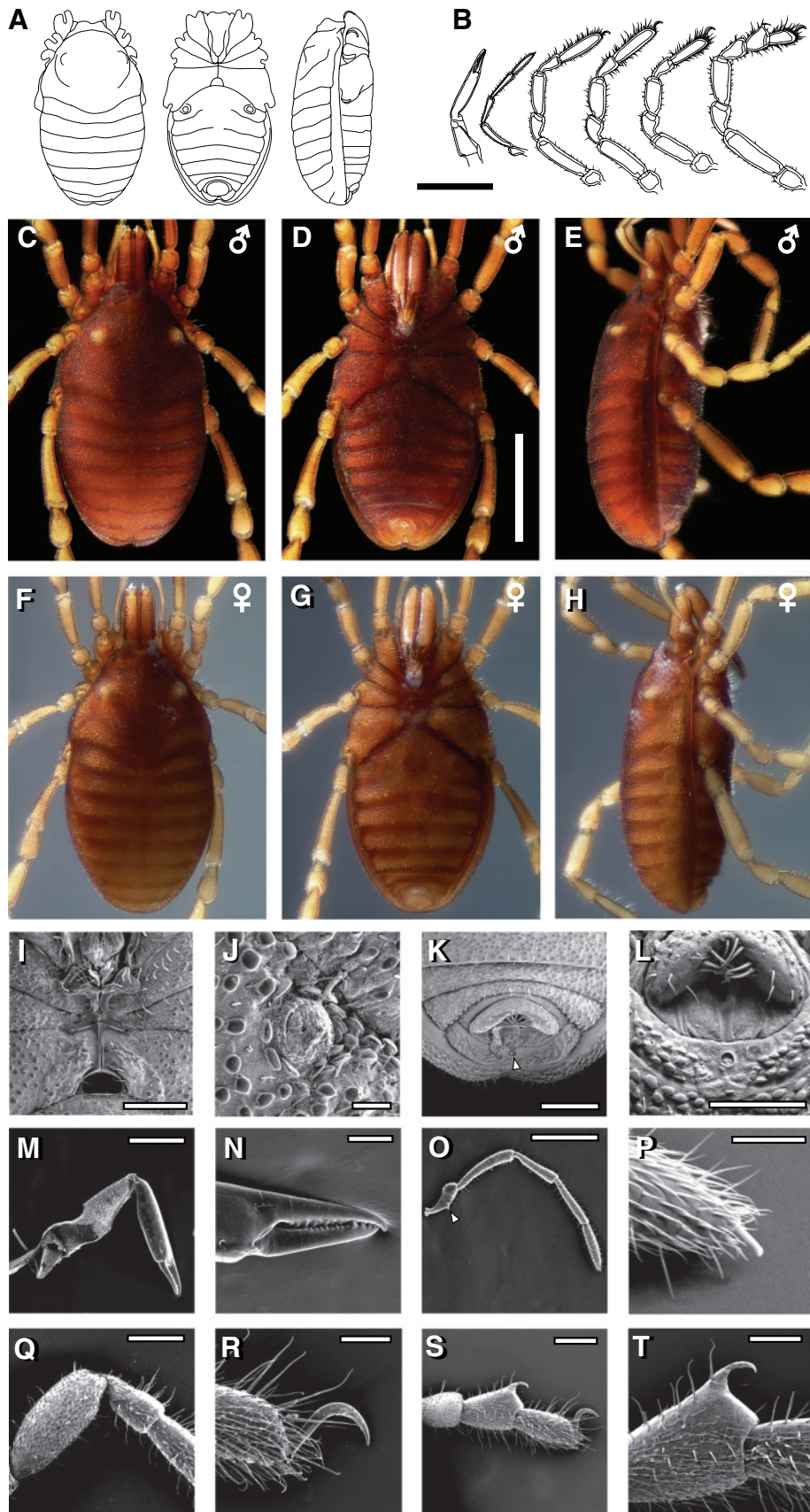
(Figs 2, 3, Table 3)

### Material examined

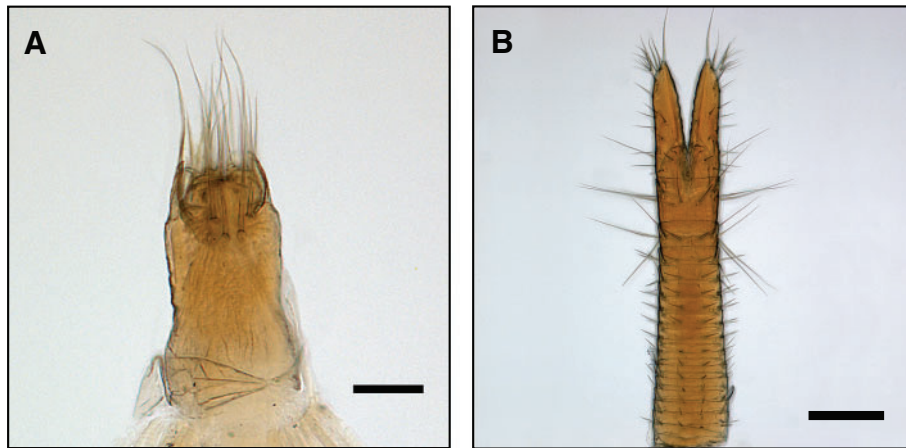
*Holotype*. ♂ (NMSA) from indigenous forest in Diepwalle For. Sta. (33°57'S 23°10'E, 548 m [1, 800 ft]), 22 km NE of Knysna, Cape Province, South Africa; leg. C. Griswold, J. Doyen, T. M. Griswold; 11–13.xi.1985.

*Paratypes*. 3 ♂, 5 ♀ (NMSA), same collecting data as holotype; 1 ♂ (MCZ) mounted for SEM; 1 ♂, 1 ♀ (AMNH #158), same locality as holotype, leg. S. Peck, J. Peck, 12.xii.1981; 8 ♂, 9 ♀ (FMNH #81–604) from forest litter, same locality as holotype, leg. S. Peck, 13.xii.1981; 1 ♂ (AMNH #177) from Berlese funnel of forest and log litter from Stormsrivier State Forest, near Goesabos, Eastern Cape Province, South Africa, leg. S. Peck, J. Peck, 20.xii.1981; 2 ♂, 2 ♀ (AMNH #192) from Berlese funnel of forest and log litter from Goudveld forest, near Knysna, Cape Province, South Africa, leg. S. Peck, J. Peck, 28.xii.1981; 21 ♂, 26 ♀ (FMNH #81–621) from forest litter from Tzitzikama Forest National Park, Eastern Cape Province, South Africa, leg. S. Peck, 20.xii.1981.

*Additional material examined*. **South Africa, Cape Province:** 3 juveniles (NMSA), same collecting data as holotype; 2 ♂, 1 juvenile (FMNH #81–603) from elephant dung, same locality as holotype, leg. S. Peck, 12.xii.1981; 13 juveniles (FMNH #81–604) from forest litter, same locality as holotype, leg. S. Peck, 13.xii.1981; 1 juvenile (AMNH #192) from Berlese funnel of forest and log litter from Goudveld forest, near Knysna, leg. S. Peck, J. Peck, 28.xii.1981; 19 ♂, 9 ♀, 3 juveniles (AMNH) from Berlese funnel of forest litter from Tzitzikama Forest National Park, Eastern Cape Province, leg. S. Peck, J. Peck, 20.xii.1981; 21 ♂, 16 ♀, 59 juveniles (FMNH #81–621) from forest litter from Tzitzikama Forest National Park, Eastern Cape Province, leg. S. Peck, 20.xii.1981; 48 juveniles (FMNH #81–621) from forest litter from Tzitzikama Forest National Park, Eastern Cape Province, leg. S. Peck, 20.xii.1981; 1 juvenile (FMNH #81–732) from forest litter from Goudveld forest, near Knysna, leg. S. Peck, 28.xii.1981.







**Fig. 3.** *Purcellia griswoldi*, sp. nov. (A) Spermatopositor of male paratype. Scale bar 0.1 mm. (B) Ovipositor of female paratype. Scale bar 0.2 mm.

### Diagnosis

With a relatively short, unenlarged tergite IX. Anterior margin of dorsal prosoma at the site of cheliceral articulation not projecting laterally. Lateral margins of coxae IV visible along almost their entire length in the dorsal view.

### Description

#### Male

Total length 2.43 mm, width across ozophores 0.83 mm, greatest width 1.49 mm, in the opisthosoma; nearly as wide in the prosoma, behind the ozophores; greatest height 1.05 mm, length–width ratio 1.75. Body reddish-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly triangular. Eyes present, visible as a white mass under ozophores, lenses absent. Dorsal, vertical-facing ozophores with circular opening; ornamentation uniform and non-directional (Fig. 2A, C). Transverse prosomal sulcus present but inconspicuous. Transverse opisthosomal sulci visible. Mid-dorsal, longitudinal opisthosomal sulcus present but inconspicuous. Coxae IV wide, with lateral margins entirely visible beyond the lateral prosomal margin in the dorsal view. Dorsal scutum flat; maximum width and height at opisthosomal area.

Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites. Coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 2A, D, I) near each other. Anterior margin of coxae II endites enlarged, curving laterally and posteriorly to form an m-shaped ridge. Endites of coxae III not running along the margin between coxae II and III; coxae IV

endites running parallel to coxae IV midline suture for a distance slightly longer than the gonostome. Coxal endites forming smooth sternal plate with greatest width 0.34 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites without projections. Gonostome roundly semi-circular, 0.091 mm long and 0.15 mm wide, delimited by coxae IV everywhere except posterior margin. Lateral walls formed by very slightly elevated endites of coxae IV (Fig. 2I). Coxae IV with granulated ridges flanking gonopore and coxae IV endites.

Spiracles circular, slightly open to the lateral posterior, with maximum diameter 0.11 mm (Fig. 2J). Sternal opisthosomal glands absent. Sternite 8 and posterior margin of sternite 7 curved anteriorly through the midline. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 2D, K). Tergite IX uniform in length, bilobed, with a single central opening of the anal gland oriented ventrally; tergite VIII lacking opening of the anal glands. Anal plate measuring 0.21 × 0.30 mm, with wide anterior-pointing v-shaped depression and scopulae originating in the central ventral surface along the margins of the raised lateral portions of the anal plate (Fig. 2D, L). Cuticle with tubercular–microgranulate morphology (Murphree 1988) in all ventral areas including coxae and anal plate, except on coxal and palpal endites, margin of ventral surface between the sternites and tergites and the depression of the anal plate (Fig. 2D, I–L).

Chelicerae relatively elongate, with few setae, first article with microgranulation on dorsal and lateral surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article without prominent dorsal and ventral processes (Fig. 2M). Second article sub-cylindrical, its widest portion near middle of article but closer to articulation with mobile digit, bearing a longitudinal apodeme on the lateral

**Fig. 2.** *Purcellia griswoldi*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicer, palp and legs I, II, III and IV. (C–E) Automontage photographs of holotype male in dorsal, ventral and lateral views. (F–H) Automontage photographs of paratype female in dorsal, ventral and lateral views. (I–T) Scanning electron micrographs (SEMs) of male paratype: (I) ventral gonostome complex; (J) spiracle; (K) anal region, arrowhead indicates opening of the anal gland; (L) magnified view of anal region; (M) chelicer; (N) chelicer dentition; (O) palp, arrowhead indicates ventral process on trochanter; (P) palpal claw; (Q) tibia and metatarsus of leg II; (R) leg II claw; (S) leg IV tarsus; (T) magnified view of leg IV tarsus showing adenostyle. Scale bars: A, B 1 mm; C–H 1 mm; I 0.2 mm; J 0.05 mm; K, L 0.2 mm; M 0.5 mm; N 0.1 mm; O 0.5 mm; P 0.05 mm; Q 0.2 mm; R 0.1 mm; S 0.2 mm; T 0.1 mm.

**Table 3. Lengths of the segments of the legs and palps of the new species described herein**Lengths/widths of legs (L) and palps (P) in  $\mu\text{m}$ . Parentheses indicate length-to-width ratio. Tarsus II indicates the portion of the tarsus distal to the dividing suture

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Tarsus II	Sum
<i>Parapurcellia amatolae</i>								
P	237/101 (2.35)	351/95 (3.69)	266/82 (3.24)	293/79 (3.71)		337/79 (4.27)		1484
LI	186/169 (1.10)	596/193 (3.08)	313/172 (1.82)	405/168 (2.41)	269/141 (1.90)	480/153 (3.14)		2248
LII	191/155 (1.23)	497/162 (3.07)	280/174 (1.60)	341/173 (1.97)	245/135 (1.81)	427/149 (2.86)		1979
LIII	189/156 (1.21)	356/159 (2.24)	267/170 (1.57)	297/166 (1.79)	241/120 (2.00)	323/117 (2.76)		1673
LIV	262/158 (1.66)	535/166 (3.22)	307/183 (1.68)	333/171 (1.95)	259/132 (1.96)	395/164 (2.41)	197/124 (1.59)	2092
<i>Parapurcellia staregai</i>								
P	191/94 (2.03)	305/81 (3.77)	229/83 (2.76)	247/65 (3.80)		283/76 (3.72)		1255
LI	162/131 (1.23)	487/139 (3.50)	256/142 (1.80)	327/139 (2.36)	230/128 (1.81)	396/147 (2.70)		1858
LII	163/131 (1.24)	404/135 (3.00)	230/140 (1.65)	272/136 (2.01)	201/129 (1.56)	355/133 (2.67)		1626
LIII	166/125 (1.33)	327/125 (2.62)	210/142 (1.48)	223/134 (1.67)	185/99 (1.87)	285/102 (2.80)		1397
LIV	236/126 (1.87)	441/143 (3.07)	235/144 (1.64)	297/139 (2.13)	197/118 (1.66)	350/131 (2.67)	151/96 (1.58)	1756
<i>Parapurcellia convexa</i>								
P	241/75 (3.21)	343/91 (3.77)	226/85 (2.66)	255/75 (3.40)		272/76 (3.58)		1337
LI	159/149 (1.07)	500/158 (3.16)	261/155 (1.68)	324/155 (2.09)	185/127 (1.45)	381/159 (2.40)		1810
LII	153/127 (1.21)	415/141 (2.94)	203/150 (1.35)	267/151 (1.77)	174/120 (1.45)	302/136 (2.22)		1514
LIII	150/138 (1.08)	323/141 (2.29)	199/142 (1.40)	237/142 (1.67)	201/105 (1.92)	282/105 (2.67)		1392
LIV	245/135 (1.82)	394/149 (2.64)	244/153 (1.60)	288/168 (1.71)	189/134 (1.41)	336/175 (1.92)	165/110 (1.50)	1696
<i>Parapurcellia natalia</i>								
P	153/98 (1.56)	367/86 (4.27)	239/75 (3.19)	298/78 (3.82)		300/74 (4.05)		1357
LI	160/156 (1.03)	504/149 (3.39)	244/147 (1.66)	338/142 (2.39)	238/132 (1.81)	434/146 (2.98)		1918
LII	170/138 (1.23)	427/130 (3.28)	224/134 (1.67)	279/141 (1.97)	208/116 (1.80)	375/123 (3.04)		1683
LIII	169/138 (1.22)	347/134 (2.59)	199/142 (1.40)	252/134 (1.88)	198/102 (1.95)	307/91 (3.39)		1472
LIV	232/137 (1.70)	423/144 (2.94)	216/152 (1.43)	289/157 (1.84)	210/117 (1.80)	352/128 (2.75)	166/97 (1.72)	1722
<i>Parapurcellia minuta</i>								
P	187/70 (2.67)	282/67 (4.21)	198/63 (3.14)	214/53 (4.04)		219/56 (3.91)		1100
LI	130/102 (1.27)	417/119 (3.51)	195/124 (1.57)	244/117 (2.08)	170/99 (1.71)	317/111 (2.84)		1473
LII	145/101 (1.43)	323/111 (2.92)	156/127 (1.23)	208/118 (1.76)	145/98 (1.48)	262/110 (2.37)		1238
LIII	128/104 (1.24)	262/99 (2.64)	124/104 (1.19)	175/106 (1.65)	139/80 (1.74)	221/76 (2.91)		1050
LIV	160/106 (1.51)	353/114 (3.08)	196/135 (1.45)	217/118 (1.83)	158/101 (1.56)	261/115 (2.26)	113/78 (1.44)	1344
<i>Purcellia griswoldii</i>								
P	272/120 (2.27)	510/98 (5.20)	378/95 (3.98)	413/80 (5.16)		385/92 (4.18)		1958
LI	215/237 (0.91)	779/202 (3.86)	371/200 (1.86)	544/185 (2.95)	304/165 (1.85)	633/175 (3.61)		2848
LII	241/268 (0.90)	766/230 (3.33)	376/242 (1.56)	527/240 (2.19)	329/171 (1.92)	639/162 (3.96)		2878
LIII	198/220 (0.90)	503/180 (2.80)	273/190 (1.43)	380/190 (2.00)	236/141 (1.67)	455/120 (3.78)		2046
LIV	286/220 (1.30)	736/217 (3.40)	331/214 (1.55)	487/216 (2.26)	264/192 (1.37)	534/209 (2.56)	294/139 (2.12)	2637
<i>Purcellia lawrencei</i>								
P	281/120 (2.34)	486/109 (4.46)	373/95 (3.93)	393/88 (4.47)		405/92 (4.40)		1938
LI	214/203 (1.06)	738/200 (3.69)	345/192 (1.79)	552/188 (2.93)	303/153 (1.98)	626/179 (3.51)		2777
LII	204/201 (1.02)	590/188 (3.14)	270/190 (1.42)	448/191 (2.35)	242/148 (1.64)	519/157 (3.31)		2273
LIII	165/205 (0.81)	536/184 (2.91)	283/194 (1.46)	416/191 (2.18)	252/137 (1.84)	478/143 (3.35)		2132
LIV	281/201 (1.40)	718/231 (3.11)	374/206 (1.81)	493/224 (2.20)	330/193 (1.71)	583/227 (2.57)	306/145 (2.11)	2779

side. Proximal article 0.59 mm long, 0.24 mm wide, second article 0.85 mm long, 0.15 mm wide, moveable finger 0.27 mm long, 0.052 mm wide. Dentition on mobile digit non-uniform, with eight small denticles on the proximal portion of the digit and five larger distal denticles. Fixed digit with 13 uniform denticles (Fig. 2N).

Palp with club-shaped trochanter, narrowing posteriorly, bearing a small ventral process (Fig. 2O). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.041 mm long.

Legs (Fig. 2B, Table 3) with all claws smooth, long and hook-like, without lateral ornamentation (Fig. 2R, S). Surfaces of all

trochanters, femurs, patellae, tibiae, and metatarsi of legs III and IV entirely ornamented. Metatarsi of legs I and II ornamented proximally and smooth distally. All tarsi appearing smooth by light microscopy, ornamented sparsely by brown granules. Tarsus of leg I lacking distinct solea. Tarsus IV bisegmented (Fig. 2S, T), carrying a lamelliform adenostyle towards the middle of the proximal segment; approximate length of adenostyle 0.14 mm, bearing no setae (Fig. 2T); distal margin at 44% of tarsal length.

Spermatopositor short (0.35 mm), typical of pettalids (Fig. 3A). Setal formula 4, 6, 4/4. Dorsal side of penis with a group of four long microtrichiae on each side, with bases arranged

in a V and not fused. Distal margin of medium lobe of the spermatopositor bilobed, with three short apical microtrichiae on each lobe. Ventral side with two long microtrichiae on each side, the bases arranged as a parallelogram, not fused at the base. Gonopore complex with two short movable fingers in the shape of curved hooks, slightly surpassing the edge of the spermatopositor.

#### Female

Similar to male in non-sexual characters (Fig. 2F–H). Female paratype slightly larger than male holotype. Total length 2.55 mm, width across ozophores 0.83 mm, greatest width 1.40 mm, in the opisthosoma; nearly as wide (1.35 mm) in the prosoma, behind the ozophores; greatest height 1.05 mm, length-width ratio 1.83. Anal plate in a terminal position compared with male, though not visible from the dorsal view, without a bilobed elevated anterior margin. Tergite VIII not bilobed. Tarsus IV thin, longer than in males, not bisegmented. Gonostome area typical of pettalids with coxae of leg IV not meeting in the midline.

Ovipositor not sheathed at base, longer than 1 mm when not extended, with bilobed terminal segment (Fig. 3B). Each segment with a row of six setae. Those in the second and third to last segments more than twice as long as the remainder. Apical lobes elongated with numerous short setae, each lobe with a single long apical seta and a subapical, lateral, multibranching sensory process.

#### Remarks

This species is likely sympatric with *Purcellia lawrencei* and has been found abundantly at several locations, being, along with *P. illustrans*, one of the most broadly distributed South African pettalids. This is unusual within South African Cyphophthalmi, most species of which are found at few, if any, localities beyond the type locality.

#### Distribution

Known from the Eastern and Western Cape Provinces of South Africa, from Goudveld Forest in the west to Tzitzikama Forest in the east.

#### Habitat

Specimens have been collected using Berlese funnelling of forest and log litter and directly off elephant dung in the Knysna subtropical moist broadleaf forest.

#### Etymology

This species is named after Charles E. Griswold, an arachnologist colleague who collected the type specimens and who has contributed enormously to the knowledge of Afrotropical arachnids.

#### *Purcellia lawrencei*, sp. nov.

(Fig. 4, Table 3)

#### Material examined

*Holotype*. ♂ (NMSA). Original label is difficult to read, marked as follows: '1875-Knysna W.G.R Jan 1939'. Records at the NMSA indicate the

following: collected near Knysna (34°02'S 23°02'E), Western Cape Province, South Africa, leg. W. G. Rump, i.1939.

*Paratype*. 1 ♀ (NMSA), same collecting data as holotype.

#### Diagnosis

Lacking a longitudinally expanded tergite IX. Anterior margin of dorsal prosoma at the site of cheliceral articulation not projecting laterally. Prosoma wider than opisthosoma. None of the lateral margin of coxae IV visible beyond the lateral margins of the prosoma in dorsal view.

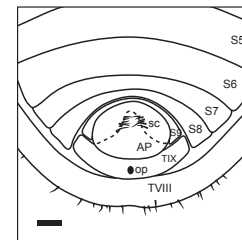
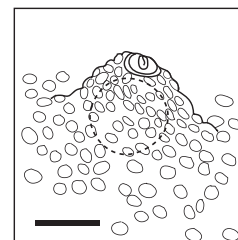
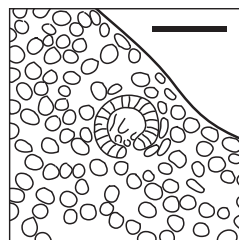
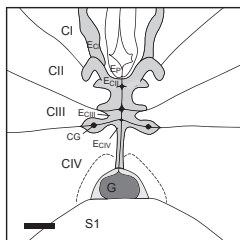
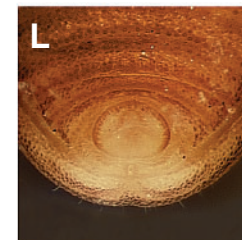
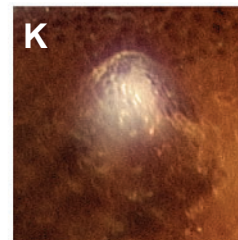
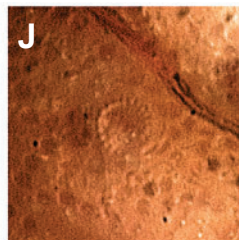
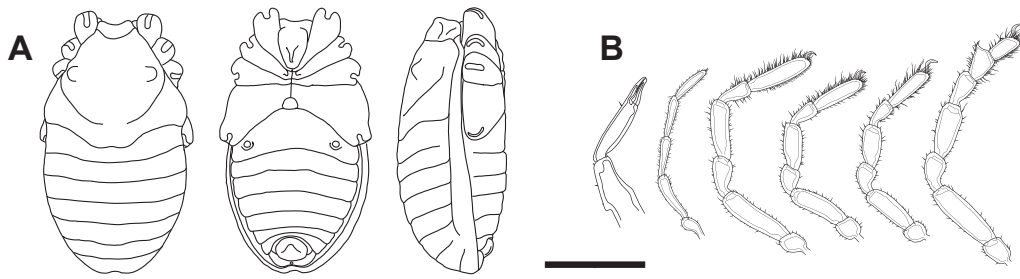
#### Description

##### Male

Total length 2.43 mm, width across ozophores 0.85 mm, greatest width 1.39 mm, in the prosoma, behind the ozophores, greatest height 1.04 mm, length-width ratio 1.75. Body orange-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly triangular. Eyes present, visible as a white mass under ozophores, lenses absent. Dorsal, vertical-facing ozophores with circular opening; ornamentation uniform and non-directional (Fig. 4A, C, K). Transverse prosomal sulcus present but inconspicuous (Fig. 4A, C). Transverse opisthosomal sulci visible. Mid-dorsal, longitudinal opisthosomal sulcus present but inconspicuous (Fig. 4C). Dorsal scutum flat; maximum width in prosoma, maximum height at opisthosomal area.

Coxae of legs I, II and III free. Ventral prosomal complex with coxae I not meeting at the midline, separated by the palpal endites. Coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 4A, D, I) near each other. Anterior margin of coxae II endites enlarged, curving laterally and posteriorly to form an m-shaped ridge. Endites of coxae II and III running along their sutures giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance slightly longer than the gonostome. Coxal endites forming a smooth sternal plate with greatest width 0.28 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites without projections. Gonostome round to semi-circular, 0.083 mm long and 0.13 mm wide, delimited by coxae IV everywhere except posterior margin. Lateral walls formed by very slightly elevated endites of coxae IV (Fig. 4I). Coxae IV with ornamented ridges flanking gonopore and coxae IV endites.

Spiracles circular, slightly open to the posterior, with maximum diameter 0.096 mm (Fig. 4J). Sternal opisthosomal glands absent. Sternite 8 and posterior margin of sternite 7 curved anteriorly through the midline. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 4A, L). Tergite IX uniform in length, not bilobed, with a single central opening of the anal gland oriented ventrally, tergite VIII lacking opening of the anal glands. Anal plate measuring 0.23 × 0.31 mm, with wide anterior-pointing v-shaped depression and scopulae originating in the central ventral surface along the margins of the raised lateral portions of the anal plate (Fig. 4). Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites,



margin of ventral surface between the sternites and tergites, and the depression of the anal plate (Fig. 4C, D, I–L).

Chelicerae relatively robust, with few setae, first article with microornamentation on dorsal and lateral surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article with small dorsal process, lacking ventral processes (Fig. 4B). Second article sub-cylindrical, its widest portion through middle of article, bearing a longitudinal apodeme on the lateral side. Proximal article 0.69 mm long, 0.30 mm wide, second article 0.95 mm long, 0.18 mm wide, moveable finger 0.28 mm long, 0.075 mm wide. Dentition on mobile digit non-uniform, with 8 small denticles on the proximal portion of the digit and 4 larger distal denticles.

Palp with club-shaped trochanter, narrowing posteriorly (Fig. 4B). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.035 mm long.

Legs (Fig. 4B, Table 3) with all claws smooth, long and hook-like, without lateral ornamentation. Surfaces of all trochanters, femurs, patellae, tibiae, and metatarsi of legs III and IV entirely ornamented. Metatarsi of legs I and II ornamented proximally and smooth distally. Tarsi of legs I and II ornamented by sparse brown granules. Tarsi of legs III and IV appearing smooth by light microscopy. Tarsus of leg I lacking distinct solea. Tarsus IV bisegmented (Fig. 4B), carrying a lamelliform adenostyle towards the middle of the proximal segment; approximate length of adenostyle 0.096 mm, bearing no setae; distal margin at 43% of tarsal length.

Spermatopositor not studied, due to the single male specimen available (the holotype).

#### Female

Similar to male in non-sexual characters (Fig. 4F–H). Female paratype slightly larger and longer than male holotype. Total length 2.60 mm, width across ozophores 0.81 mm, greatest width 1.41 mm, in the opisthosoma; nearly as wide (1.35 mm) in the prosoma, behind the ozophores; greatest height 1.08 mm, length-width ratio 1.93. Anal plate in a terminal position compared to male, though not visible from the dorsal view, without a bilobed elevated anterior margin. Tergite VIII not bilobed. Tarsus IV thin, longer than in males, not bisegmented. Gonostome area typical of pettalids with coxae of leg IV not meeting in the midline.

#### Remarks

This species is likely sympatric with *Purcellia griswoldi*.

#### Distribution

Only known from the type locality, near Knysna, Western Cape Province, South Africa.

#### Habitat

No further information is available beyond the collection locality, which is within the Knysna subtropical moist broadleaf forest.

#### Etymology

The species is named after Reginald Frederick Lawrence, a prolific South African zoologist who published more than 200 articles mostly focusing on South African arthropods.

Genus *Parapurcellia* Rosas Costa, 1950

#### Diagnosis

Ozophores slightly elevated above carapace, facing 45° (as in Fig. 5E). Eyes and eye lenses absent. Male coxae IV endites bearing anterior projections in the gonostome wall (as in Fig. 5F). Dentition of the mobile digit of the chelicerae uniform (except in the case of *Parapurcellia peregrinator* (Lawrence, 1963) **new combination**). Male anal plate bilobed with a small central depression spanning less than one third the area of the anal plate (as in Fig. 5J). Scopulae absent, or originating on the central ventral surface or posterior margin of the anal plate, typically along the edges of the raised lateral portions. Anal gland on tergite IX with its opening oriented posteriorly (as in Fig. 5L).

#### Type species

*Parapurcellia fissa* (Lawrence, 1939).

#### Species included

*Parapurcellia fissa* (Lawrence, 1939); *Parapurcellia monticola* (Lawrence, 1939); *Parapurcellia rumpiana* (Lawrence, 1933); *Parapurcellia silvicola* (Lawrence, 1939); *Parapurcellia peregrinator* (Lawrence, 1963), **new combination**; *Parapurcellia amatola*, sp. nov.; *Parapurcellia convexa*, sp. nov.; *Parapurcellia minuta*, sp. nov.; *Parapurcellia natalia*, sp. nov.; *Parapurcellia staregai*, sp. nov.

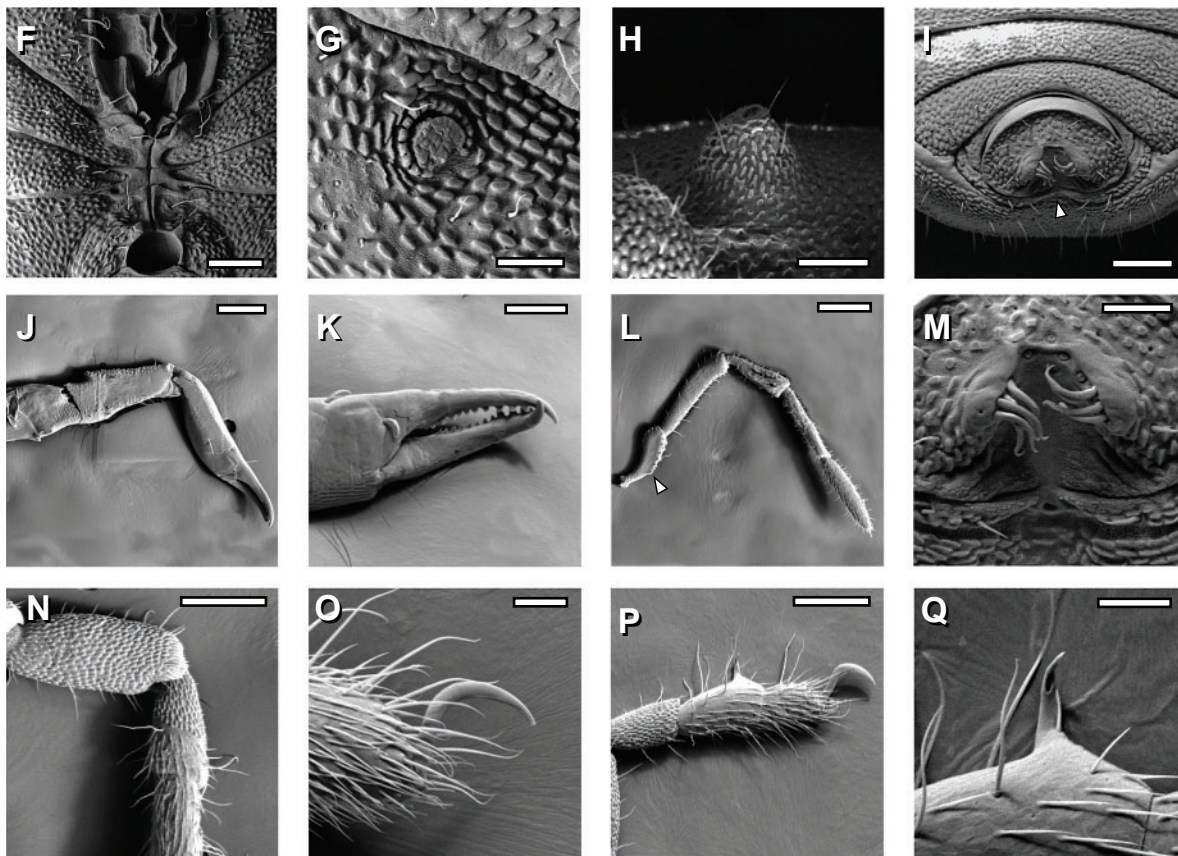
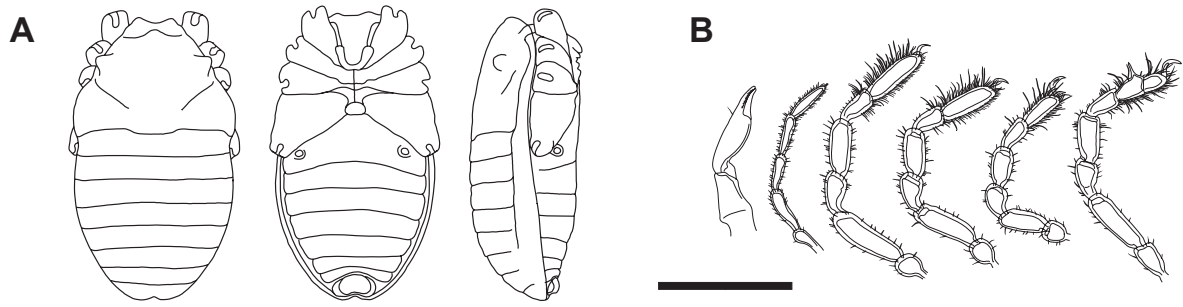
#### Distribution

South Africa: Eastern Cape, Kwazulu-Natal, and Mpumalanga Provinces.

#### Remarks

This genus includes all members of the old genus *Parapurcellia* (*sensu* Rosas Costa 1950; Giribet 2000) plus *Purcellia peregrinator* Lawrence, 1963, all animals with small depressions on the male anal plate and anterior projections in the gonostome wall. They are distributed from southern to eastern South Africa.

**Fig. 4.** *Purcellia lawrencei*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicera, palp and legs I, II, III and IV. (C–E) Automontage photographs of holotype male in dorsal, ventral and lateral views. (F–H) Automontage photographs of paratype female in dorsal, ventral and lateral views. (I–L) Automontage photographs of various holotype body parts. For all species in which there were insufficient specimens to SEM paratypes, automontage photographs of the holotype are provided, along with annotated tracings (below) to clarify their details. Specific morphological features are as follows: (I) Ventral gonostome complex. CI–CIV and E<sub>CI</sub>–E<sub>CIV</sub> indicate the coxae and coxal endites of legs I–IV respectively. E<sub>p</sub> is the palpal endite, CG coxal gland, G gonostome, and S1 sternite 1. (J) Spiracle. (K) Ozophore. Dashed line indicates eye incorporated into base of ozophore. (L) Anal region. S5–9 indicate sternites 5–9, AP anal plate, SC scopulae on anal plate, TIX tergite IX, TVIII tergite VIII, and OP opening of the anal gland. Dashed line indicates posterior margin of raised anal plate lobes. Scale bars: A, B 1 mm; C–H 1 mm; I–L 0.1 mm.



***Parapurcellia amatola*, sp. nov.**

(Fig. 5, Table 3)

*Material examined*

*Holotype.* ♂ (NMSA) from Amatola Mountains, near Hogsback, Eastern Cape Province, South Africa, leg. D. Brothers, iv.1965.

*Paratypes.* 2 ♂ (NMSA), same collecting data as holotype.

*Additional material examined.* 1 juvenile (NMSA), same collecting data as holotype.

*Diagnosis*

Tergite VII entirely convex. Tergite VIII not prominently lobed. Anterior margin of gonopore rounded. Mid-dorsal longitudinal opisthosomal sulcus absent. Margins between coxae III and IV meeting in an acute angle at the midline.

*Description**Male*

Total length 2.09 mm, width across ozophores 0.86 mm, greatest width 1.20, in the prosoma, behind the ozophores, greatest height 0.79 mm, length-width ratio 1.74. Body pale yellowish-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly trapezoidal. Eyes absent. Ozophores conical, dorsal, facing 45°, with terminal ozopore with circular opening; ornamentation uniform and non-directional (Fig. 5A, C, H). Transverse prosomal sulcus present but inconspicuous, most prominent laterally (Fig. 5A, C). Transverse opisthosomal sulci inconspicuous. Mid-dorsal, longitudinal opisthosomal sulcus absent. Dorsal scutum flat; maximum width and height in prosoma.

Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites; coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV reaching the midline (Fig. 5A, D, F). Endites of coxae II and III running along their margins giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance longer than the gonostome. Coxal endites forming smooth sternal plate with greatest width 0.43 mm between coxae III and IV. Pores of coxal glands visible at inner margin between coxae III and IV. Sternum absent. Coxae IV endites with horn-like projections on anterior margin of gonostome. Gonostome elliptical, 0.058 mm long and 0.12 mm wide, and delimited anteriorly by coxae IV. Lateral walls formed by elevated endites of coxae IV (Fig. 5F).

Spiracles nearly circular, open laterally, with maximum diameter 0.057 mm (Fig. 5G). Sternal opisthosomal glands absent. Sternites 7 and 8 narrow, curved anteriorly through the midline, posterior margin of sternite 6 similarly curved. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 5I).

Tergite IX and posterior margin of tergite VIII curving to the anterior at the mid-line, appearing w-shaped. Tergite VIII lacking anal glands; tergite IX with a single central opening of the anal gland oriented posteriorly. Anal plate measuring 0.16 × 0.25 mm, with an ungranulated anterior-pointing v-shaped depression and scopulae originating in the central ventral surface (Fig. 5J). Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites, and depression of anal plate (Fig. 5F-I).

Chelicerae relatively robust, with few setae, first article with microgranulation on dorsal and lateral surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article with prominent dorsal crest, lacking ventral processes (Fig. 5B, J). Second article robust, sub-cylindrical, its widest portion near articulation with mobile digit, bearing a longitudinal apodeme on the lateral side. Proximal article 0.54 mm long, 0.25 mm wide, second article 0.73 mm long, 0.19 mm wide, moveable finger 0.19 mm long, 0.058 mm wide. Dentition on mobile digit non-uniform, with 6 small denticles on the proximal portion and 4 larger distal denticles. 11 uniform denticles on fixed digit.

Palp with club-shaped trochanter, narrowing posteriorly (Fig. 5B). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.39 mm long.

Legs (Fig. 5B, N-Q, Table 3) with all claws smooth long and hook-like, lacking lateral pegs or other ornamentation (Fig. 5O, P). Surfaces of all trochanters, femurs, patellae, and tibiae entirely ornamented; metatarsi partially ornamented (Fig. 5N). Tarsus of leg I lacking a distinct solea. All tarsi appearing smooth by light microscopy. Tarsus IV bisegmented (Fig. 5B, P, Q), carrying a lamelliform adenostyle towards the middle of the proximal segment; approximate length of adenostyle 0.10 mm, bearing no setae (Fig. 5Q); distal margin at 49% of tarsal length.

Spermatopositor not studied.

*Female*

Unknown.

*Distribution*

Only known from the type locality in the Amatola Mountains, near Hogsback, Eastern Cape Province.

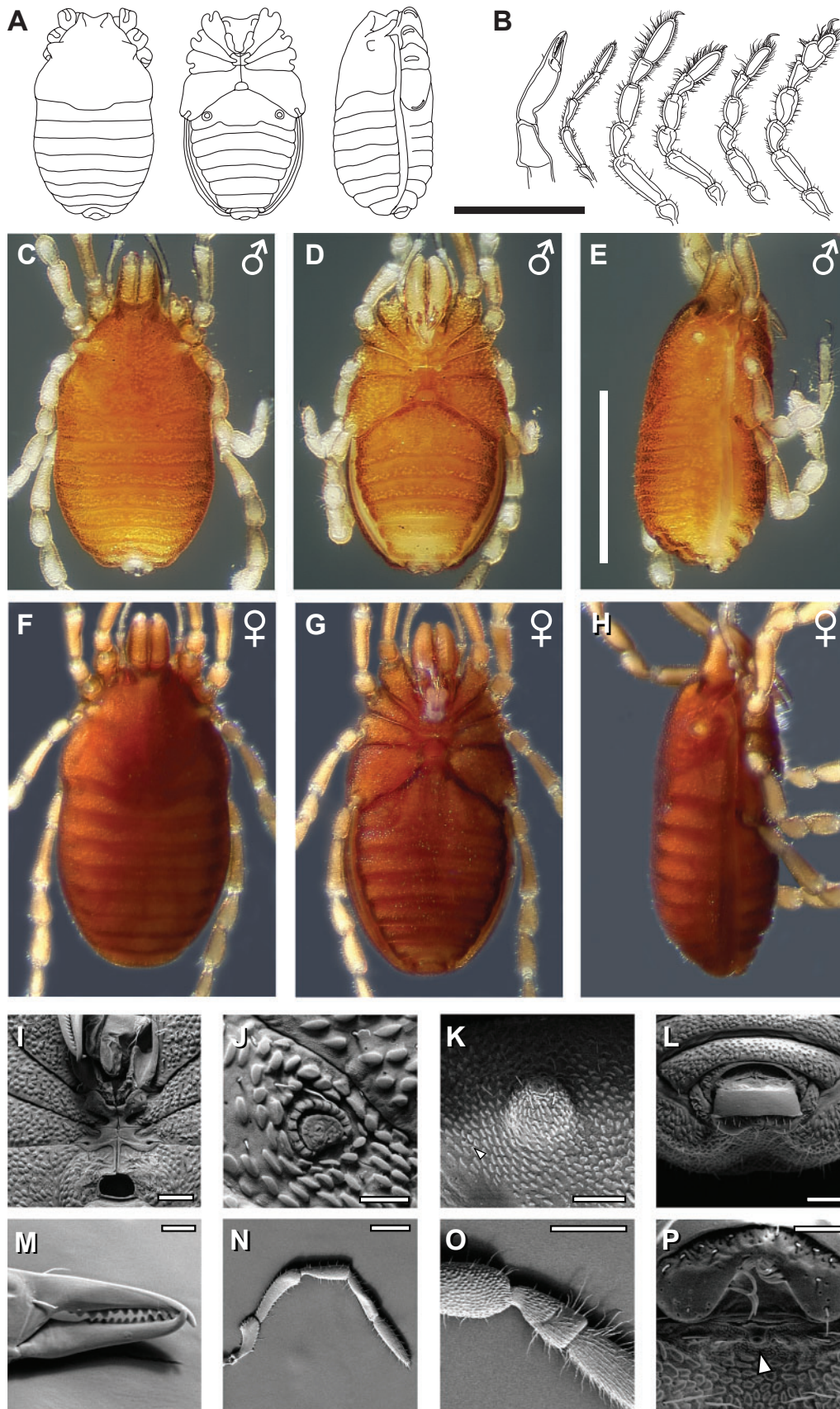
*Habitat*

No further information is available beyond the collection locality, which is within the Amatola subtropical moist broadleaf forest.

*Etymology*

*Amatola*, a noun in apposition, after its collection locality, the Amatola forest.

**Fig. 5.** *Parapurcellia amatola*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicera, palp and legs I, II, III and IV. (C-E) Automontage photographs of holotype male in dorsal, ventral and lateral views. (F-Q) SEMs of male paratype: (F) ventral gonostome complex; (G) spiracle; (H) ozophore; (I) anal region, arrowhead indicates opening of the anal gland; (J) chelicera; (K) chelicera dentition; (L) palp, arrowhead indicates ventral process on trochanter; (M) magnified view of anal region; (N) tibia and metatarsus of leg II; (O) leg II claw; (P) leg IV tarsus; (Q) magnified view of leg IV tarsus showing adenostyle. Scale bars: A, B 1 mm; C-E 1 mm; F 0.1 mm; G 0.05 mm; H 0.05 mm; I 0.1 mm; J 0.2 mm; K 0.1 mm; L 0.2 mm; M 0.05 mm; N 0.2 mm; O 0.05 mm; P 0.2 mm; Q 0.05 mm.





***Parapurcellia convexa***, sp. nov.

(Fig. 6, Table 3)

*Material examined*

*Holotype*. ♂ (NMSA) from *Podocarpus* forest litter from Weza State Forest near Stafford's Post (30°31'S, 29°45'E), 30 km from E. Kokstad, KwaZulu Natal Province, South Africa, leg. P. M. Croeser, W. Starega, 26.v.1985.

*Paratypes*. 3 ♂, 1 ♀ (NMSA), same collecting data as holotype.

*Diagnosis*

Dorsal scutum robustly convex, higher in the opisthosoma than the dorsal width across the ozophores. Tergite VIII deeply lobed. Scopulae of anal plate visible in dorsal view. Single opening of the anal gland on tergite IX. Tergites IV–VI concave. Chelicerae tightly articulated.

*Description**Male*

Total length 1.73 mm, width across ozophores 0.76 mm, greatest width 1.02 mm, in the opisthosomal area, greatest height 0.82 mm, length-width ratio 1.70. Body light reddish-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly triangular. Eyes absent. Ozophores conical, dorsal, facing 45°, with terminal ozopore with circular opening; ornamentation uniform and non-directional (Fig. 6E, K). Transverse prosomal sulcus present but very inconspicuous (Fig. 6C). Transverse opisthosomal sulci distinct, particularly in the posterior. Mid-dorsal, longitudinal opisthosomal sulcus absent. Dorsal scutum convex, flattened medially, but otherwise ovoid; maximum width and height at tergites III and IV respectively.

Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites, coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 6A, D, I) near each other. Anterior margin of coxae II endites enlarged, curving laterally and posteriorly to form an m-shaped ridge. Endites of coxae II and III running along their sutures for a short distance giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance longer than the gonostome. Coxal endites forming smooth sternal plate with greatest width 0.22 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites with horn-like projections on anterior margin of gonostome. Gonostome elliptical, 0.065 mm long and 0.096 mm wide, with straight posterior margin, and delimited by coxae IV everywhere except posterior margin. Lateral walls formed by slightly elevated endites of coxae IV (Fig. 6I).

Spiracles nearly circular, open laterally, with maximum diameter 0.066 mm (Fig. 6J). Sternal opisthosomal glands absent. Sternite 8 rectangular. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 6L). Tergite IX with a single central opening of the anal gland oriented posteriorly; tergite VIII lacking anal glands. Anal plate measuring 0.11 × 0.25 mm, deeply bilobed by an anterior-pointing u-shaped depression bearing scopulae along the margin of the depression from the posterior margin of the anal plate to the central ventral surface (Fig. 6P). Tergites III through VIII curving anteriorly through the midline, with tergite VIII deeply so, appearing bilobed. Tergite IX and anal plate visible in the dorsal view, lateral margins of tergite VII visible in the ventral view. Tergite VIII with setae along its posterior margin. Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites, margin of ventral surface between the sternites and tergites, and anterior portions of distended tergites (Fig. 6C–E, I–L). Granules more widely spaced than in most other members of *Parapurcellia*, typically separated by distances comparable to the widths of individual granules.

Chelicerae robust, with few setae. Proximal article with microgranulation on dorsal and lateral surfaces, with a dorsal process, but lacking ventral processes (Fig. 6B). Second article sub-cylindrical, its widest portion closer to articulation with mobile digit than proximal margin, appearing without conspicuous ornamentation under light microscopy, and bearing a longitudinal apodeme on the lateral side. Proximal article 0.55 mm long, 0.26 mm wide, second article 0.73 mm long, 0.20 mm wide, moveable finger 0.25 mm long, 0.055 mm wide. Dentition uniform and similar on both cheliceral fingers, with 12 denticles on each (Fig. 6M).

Palp with club-shaped trochanter, widest in the anterior (Fig. 6B, N). Dimensions of palpal articles of male given in Table 3. Palpal claw 0.045 mm long.

Legs (Fig. 6B, O, Table 3) with all claws smooth, long and hook-like, without lateral ornamentation. Surfaces of all trochanters, femurs, patellae, and tibiae entirely ornamented; metatarsi partially ornamented. All tarsi appearing with ornamentation on proximal dorsal surfaces and smooth elsewhere by light microscopy. Tarsus of leg I lacking distinct solea. Tarsus IV bisegmented (Fig. 6B), carrying a lamelliform adenostyle towards the middle of the proximal segment, approximate length of adenostyle 0.050 mm, bearing no setae; distal margin at 45% of tarsal length.

Spermatopositor not studied.

*Female*

Similar to male in non-sexual characters (Fig. 6F–H). Female paratype slightly larger and longer than male holotype. Total length 1.78 mm, width across ozophores 0.75 mm, greatest width 1.02 mm, in the opisthosoma; nearly as wide (1.01 mm) in the prosoma, behind the ozophores; greatest height 0.75 mm, length-

**Fig. 6.** *Parapurcellia convexa*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicera, palp and legs I, II, III and IV. (C–E) Automontage photographs of holotype male in dorsal, ventral and lateral views. (F–H) Automontage photographs of paratype female in dorsal, ventral and lateral views. (I–P) SEMs of male paratype: (I) ventral gonostome complex; (J) spiracle; (K) ozophore; (L) anal region; (M) chelicera dentition; (N) palp; (O) tibia and metatarsus of leg II; (P) magnified view of anal region, arrowhead indicates opening of the anal gland. Scale bars: A, B 1 mm; C–H 1 mm; I 0.1 mm; J 0.05 mm; K 0.1 mm; L 0.1 mm; M 0.05 mm; N 0.2 mm; O 0.2 mm; P 0.05 mm.

width ratio 1.75. Anal plate in a terminal position, not visible in the dorsal view, without a bilobed elevated anterior margin. No tergites bilobed. Tarsus IV thin, longer than in males, not bisegmented. Gonostome area typical of pettalids with coxae of leg IV not meeting in the midline.

#### Distribution

Only known from the type locality: Weza State Forest, KwaZulu Natal Province, South Africa

#### Habitat

Specimens were collected in *Podocarpus* litter.

#### Etymology

From Latin, *convexus*, the species is named for the shape of its opisthosoma in the lateral view, which is considerably more convex than in other members of this genus.

### *Parapurcellia minuta*, sp. nov.

(Fig. 7, Table 3)

#### Material examined

*Holotype*. ♂ (NMSA). Original label is difficult to read, marked as follows: '2820—Durban Aug. '40 W.G.R.' Records at the NMSA indicate the following: collected near Durban, KwaZulu Natal Province, South Africa, leg. W.G. Rump, viii.1940.

*Paratypes*. 1 ♂, 2 ♀ (NMSA), same collecting data as holotype.

#### Diagnosis

Small animal. Tergite VII concave. Chelicerae loosely articulated with the anterior prosomal margin. Scutum length–width ratio nearly exactly 2.0. Sternal plate formed by the coxae III and IV endite narrow (0.16 mm).

#### Description

##### Male

Total length 1.52 mm, width across ozophores 0.62 mm, greatest width 0.76 mm, in the prosoma, behind the ozophores, the opisthosoma nearly as wide, greatest height 0.61 mm, length–width ratio 1.99. Body pale yellowish-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly triangular. Eyes absent. Ozophores conical, dorsal, facing 45°, with terminal ozopore with circular opening; ornamentation uniform and non-directional (Fig. 7A, C, E). Transverse prosomal sulcus present but inconspicuous (Fig. 7C). Transverse opisthosomal sulci inconspicuous. Mid-dorsal, longitudinal opisthosomal sulcus absent. Dorsal scutum flat; maximum width and height in prosoma.

Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites, coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 7A, D, J) near each other. Anterior margin of coxae II endites enlarged, curving laterally and posteriorly to form an m-shaped ridge. Endites of coxae II and III running along their sutures giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance slightly longer than the gonostome. Coxal endites forming small smooth sternal plate with greatest width 0.16 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites with horn-like projections on anterior margin of gonostome. Gonostome elliptical, 0.056 mm long and 0.081 mm wide, delimited by coxae IV everywhere except posterior margin. Lateral walls formed by slightly elevated endites of coxae IV (Fig. 7I).

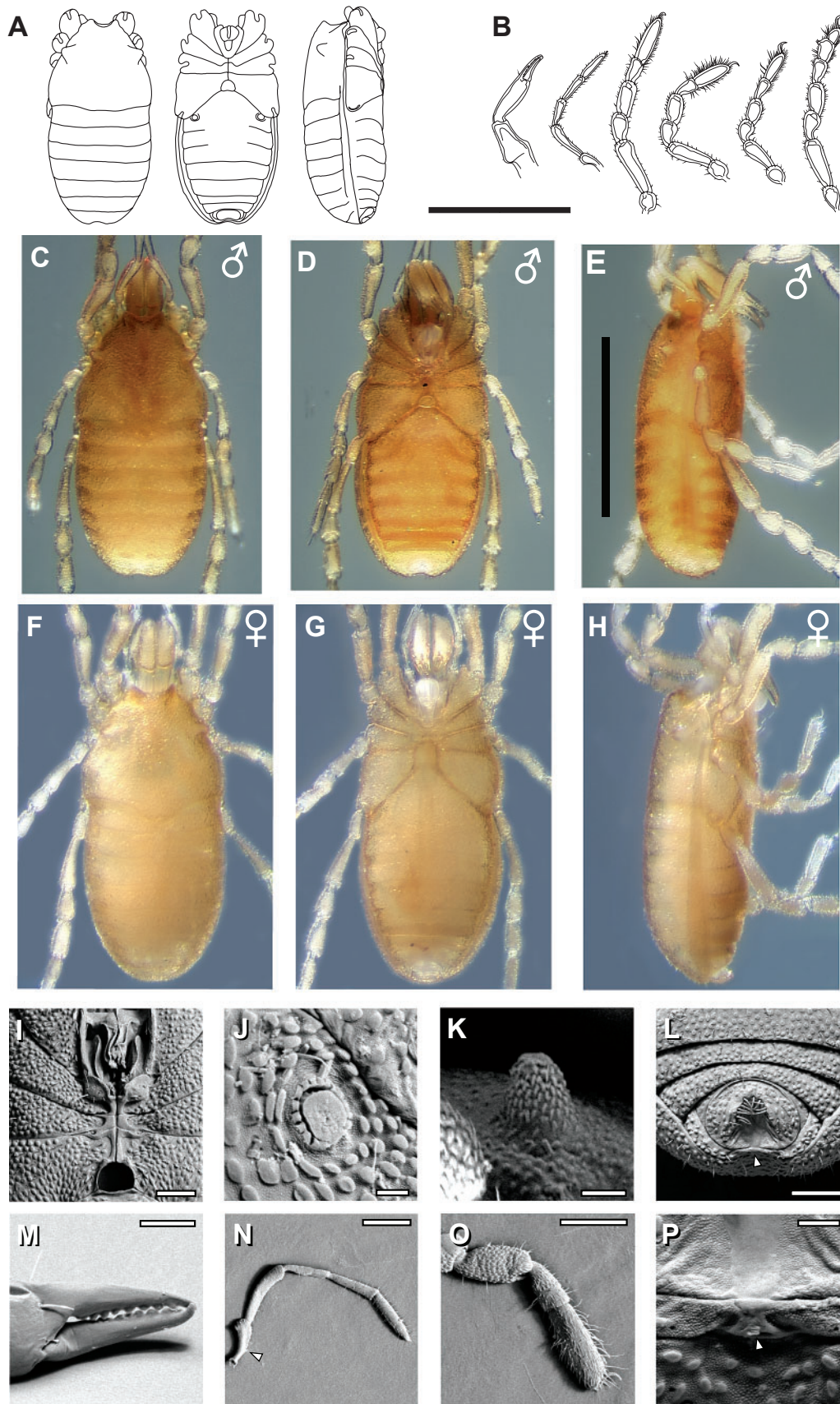
Spiracles nearly circular, open laterally, with maximum diameter 0.053 mm (Fig. 7J). Sternal opisthosomal glands absent. Posterior margin of sternite 8 curved anteriorly through the midline, sternite 7 trapezoidal. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 7A, D, L). Tergite IX curving to the anterior at the mid-line, appearing w-shaped. Tergite IX with a single central opening of the anal gland oriented posteriorly; tergite VIII lacking opening of the anal glands. Anal plate measuring 0.072 × 0.18 mm, with an anterior-pointing v-shaped depression and scopulae originating in the central ventral surface along the margins of the raised lateral portions of the anal plate (Fig. 7L). Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites, and margin of ventral surface between the sternites and tergites (Fig. 7C–E, I–L, P).

Chelicerae relatively robust, with few setae, first article with microgranulation on dorsal and lateral surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article with a dorsal process, lacking ventral processes (Fig. 7B). Second article sub-cylindrical, its widest portion near middle of article but closer to articulation with mobile digit, bearing a longitudinal apodeme on the lateral side. Proximal article 0.43 mm long, 0.21 mm wide, second article 0.57 mm long, 0.12 mm wide, moveable finger 0.21 mm long, 0.037 mm wide. Dentition uniform and similar on both cheliceral fingers, with 10 denticles on each (Fig. 7M).

Palp with club-shaped trochanter, narrowing posteriorly, bearing a small ventral process (Fig. 7B, N). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.032 mm long.

Legs (Fig. 7B, O, Table 3) with all claws smooth, long and hook-like, without lateral ornamentation (Fig. 7O). Surfaces of all trochanters, femurs, patellae, and tibiae entirely ornamented;

**Fig. 7.** *Parapurcellia minuta*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicer, palp and legs I, II, III and IV. (C–E) Automontage photographs of holotype male in dorsal, ventral and lateral views. (F–H) Automontage photographs of paratype female in dorsal, ventral and lateral views. (I–P) SEMs of male paratype: (I) ventral gonostome complex; (J) spiracle; (K) ozophore; (L) anal region, arrowhead indicates opening of the anal gland; (M) chelicer dentition; (N) palp, arrowhead indicates ventral process on trochanter; (O) tibia and metatarsus of leg II; (P) magnified view of anal region, arrowhead indicates opening of the anal gland. Scale bars: A, B 1 mm; C–H 1 mm; I 0.1 mm; J 0.02 mm; K 0.05 mm; L 0.1 mm; M 0.05 mm; N 0.2 mm; O 0.2 mm; P 0.02 mm.



metatarsi partially ornamented. All tarsi appearing smooth by light microscopy, tarsi of leg I ornamented by a few sparse brown granules. Tarsus of leg I lacking distinct solea (Fig. 7B). Tarsus IV bisegmented, carrying a small adenostyle towards the middle of the proximal segment, terminating in a tuft of ~5 setae; approximate length of adenostyle 0.034 mm; distal margin at 47% of tarsal length.

Spermatopositor not studied.

#### Female

Similar to male in non-sexual characters. Female paratype slightly larger and longer than male holotype. Total length 1.64 mm, width across ozophores 0.60 mm, greatest width 0.80 mm, in the opisthosoma; nearly as wide (0.79 mm) in the prosoma, behind the ozophores; greatest height 0.61 mm, length-width ratio 2.06. Anal plate in a similar position as the male, without a bilobed elevated anterior margin. Tergite VIII not bilobed. Tarsus IV thin, longer than in males, not bisegmented. Gonostome area typical of pettalids with coxae of leg IV not meeting in the midline.

#### Distribution

Only known from the type locality, which is itself not precisely known, but is recorded as near Durban, KwaZulu Natal Province, South Africa.

#### Habitat

No further information is available beyond the collection locality, which has a mild subtropical climate.

#### Etymology

From Latin *minutus* meaning 'lessened', past participle of *minuere*, the species is named for its small size, with a body measuring only 1.5 mm in length.

### *Parapurcellia natalia*, sp. nov.

(Fig. 8, Table 3)

#### Material examined

*Holotype*. ♂ (NMSA). Original label is incomplete, marked as follows: '2841 – Mazongwa... Fa... Nov 40 R.F.L.' Records at the NMSA indicate the following: collected near Krantzkop, Mazongwana Forest, 20 miles N.E. of Greytown, KwaZulu Natal Province, South Africa, leg. R.F. Lawrence, xi.1940.

#### Diagnosis

Small animal, widest in prosoma. Bearing inconspicuous mid-dorsal longitudinal opisthosomal sulcus. Chelicerae tightly articulated with anterior prosomal margin.

#### Description

##### Male

Total length 1.58 mm, width across ozophores 0.68 mm, greatest width 0.88 mm, in the prosoma, behind the ozophores, greatest height 0.57 mm, length-width ratio 1.79. Body pale yellowish-brown, legs off-white (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without

lateral projections; prosoma roundly triangular. Eyes absent. Ozophores conical, dorsal, facing 45°, with terminal ozopore with circular opening; ornamentation uniform and non-directional (Fig. 8A, C, E, H). Transverse prosomal sulcus present but inconspicuous (Fig. 8A, C). Transverse opisthosomal sulci visible. Mid-dorsal, longitudinal opisthosomal sulcus inconspicuous (Fig. 8C). Dorsal scutum flat; maximum width and height in prosoma.

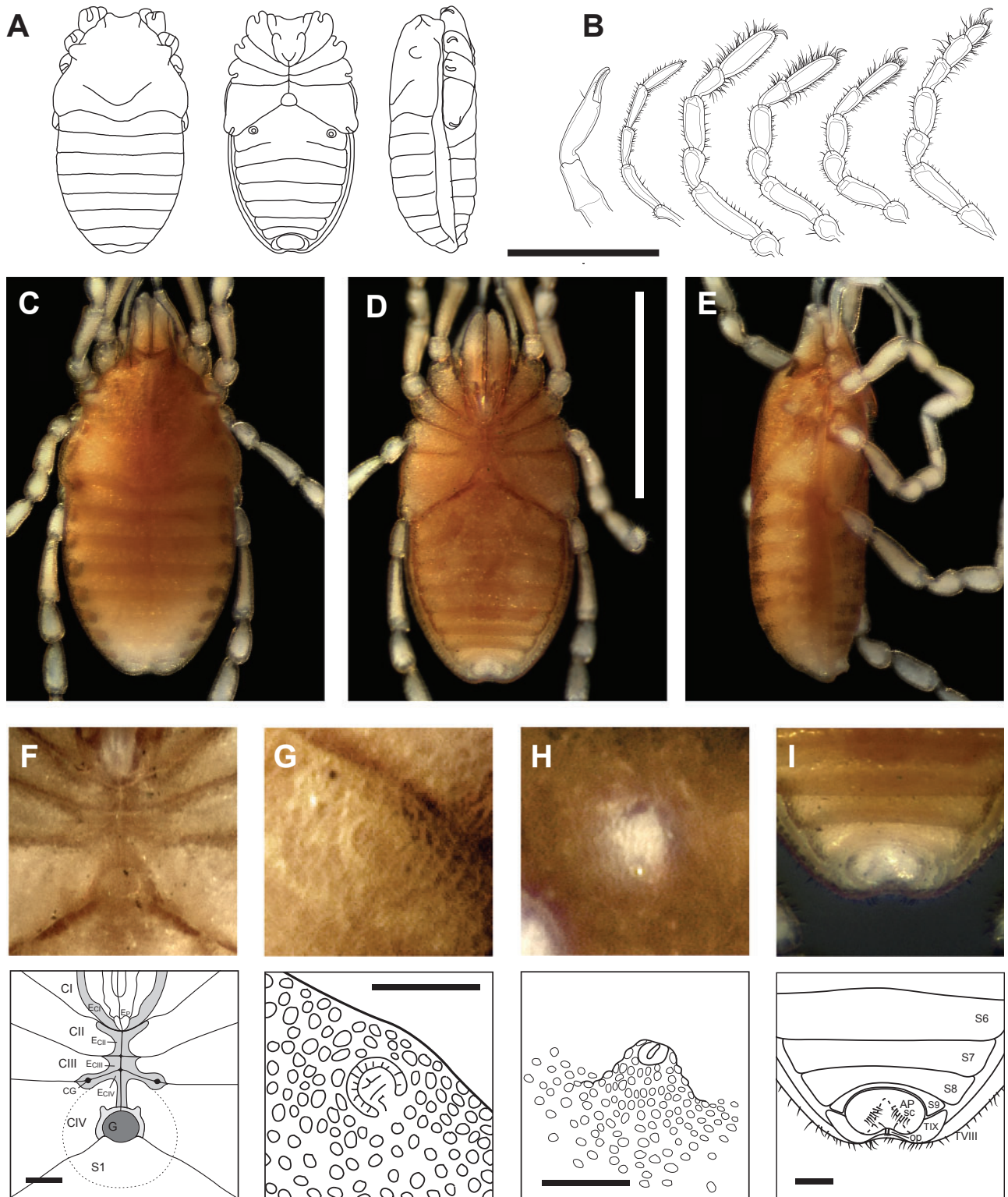
Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites, coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 8A, D, F). Endites of coxae II and III running along their sutures giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance slightly less than the gonostome. Coxal endites forming smooth sternal plate with greatest width 0.28 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites with horn-like projections on anterior margin of gonostome. Gonostome nearly elliptical, 0.080 mm long and 0.093 mm wide, and delimited by coxae IV everywhere except posterior margin. Lateral walls formed by elevated endites of coxae IV (Fig. 8F).

Spiracles nearly circular, open on the posterior half of its lateral side, with maximum diameter 0.053 mm (Fig. 8G). Sternal opisthosomal glands absent. Posterior margin of sternite 8 and sternite 9 curved anteriorly through the midline, sternite 7 trapezoidal. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 8D, I). Anterior margin of tergite IX curving to the anterior at the mid-line, appearing deeply bilobed. Tergite IX with a single central opening of the anal gland, oriented posteriorly, surrounded by a region of small setae. Tergite VIII lacking anal glands. Anal plate measuring 0.12 × 0.22 mm, with an anterior-pointing v-shaped depression and scopulae originating in the central ventral surface (Fig. 8I). Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites, margin of ventral surface between the sternites and tergites, and depression of anal plate (Fig. 8C–I).

Chelicerae robust, with few setae, first article with microgranulation on lateral and proximal-dorsal surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article with a dorsal process and weak ventral process most prominent laterally (Fig. 8B), articulating tightly with anterior margin of prosoma. Second article sub-cylindrical, its widest portion near articulation with mobile digit, bearing a longitudinal apodeme on the lateral side. Proximal article 0.47 mm long, 0.21 mm wide, second article 0.68 mm long, 0.15 mm wide, moveable finger 0.19 mm long, 0.039 mm wide. Dentition uniform and similar on both cheliceral fingers, with 11 denticles on each.

Palp with club-shaped trochanter, narrowing posteriorly (Fig. 8B). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.036 mm long.

Legs (Fig. 8B, Table 3) with all claws appearing smooth, long and hook-like, without lateral ornamentation under light microscopy. Surfaces of all leg trochanters, femurs, patellae, tibiae, and metatarsi entirely ornamented. All tarsi appearing



**Fig. 8.** *Parapurcellia natalia*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicer, palp, and legs I, II, III and IV. (C–E) Automontage photographs of holotype in dorsal, ventral and lateral views. (F–I) Automontage photographs of various holotype body parts, with annotated tracings: (F) ventral gonostome complex. CI–CIV and E<sub>CI</sub>–E<sub>CIV</sub> indicate the coxae and coxal endites of legs I–IV respectively. E<sub>P</sub> is the palpal endite, CG coxal gland, G gonostome, and S1 sternite 1. (G) Spiracle. (H) Ozophore. (I) Anal region. S6–9 indicate sternites 6–9, AP anal plate, SC scopulae on anal plate, TIX tergite IX, TVIII tergite VIII, and OP opening of the anal gland. Dashed line indicates posterior margin of raised anal plate lobes. Scale bars: A, B 1 mm; C–E 1 mm; F–I 0.1 mm.

smooth by light microscopy. Tarsus of leg I lacking distinct solea. Tarsus IV bisegmented (Fig. 8B), carrying a lamelliform adenostyle towards the middle of the proximal segment; approximate length of adenostyle 0.069 mm, bearing no setae; distal margin at 39% of tarsal length.

Spermatopositor not studied, as only the holotype was available.

#### Female

Unknown.

#### Distribution

Only known from the type locality: 20 miles NE of Greytown, KwaZulu Natal Province, South Africa.

#### Habitat

No further information is available beyond the collection locality, which has a subtropical moist savannah climate.

#### Etymology

*Natalia*, a Latinized adjective in the female gender, refers to the Natal region of South Africa, where the species was collected.

### ***Parapurcellia staregai*, sp. nov.**

(Fig. 9, Table 3)

#### Material examined

*Holotype*. ♂ (NMSA). Original label is largely illegible, marked as follows: '8452 - Tra[illegible]W IX-64 R.F.L[illegible]'. Records at the NMSA indicate the following: collected in or near Trafalgar, Cape Province, South Africa, leg. R.F. Lawrence, ix.1964.

#### Diagnosis

Small animal. Chelicerae loosely articulated with anterior prosomal margin. Tergite VIII not deeply convex; anal plate not visible in dorsal view. Dorsal scutum length-width ratio approximately 1.8. Sternite 9 not appearing bilobed.

#### Description

##### Male

Total length 1.72 mm, width across ozophores 0.74 mm, greatest width 1.00 mm, in prosoma, behind ozophores, greatest height 0.68 mm, length-width ratio 1.71. Body pale yellowish-brown (when preserved in 70% ethanol). Anterior margin of dorsal scutum concave without lateral projections; prosoma roundly triangular. Eyes absent. Ozophores conical, dorsal, facing 45°, with terminal ozopore with circular opening; ornamentation uniform and non-directional (Fig. 9A, C, E, H). Transverse prosomal sulcus present but inconspicuous (Fig. 9C). Transverse opisthosomal sulci inconspicuous. Mid-dorsal, longitudinal opisthosomal sulcus inconspicuous. Dorsal scutum flat; maximum width and height in prosoma.

Coxae of legs I, II and III free. Ventral prosomal complex with left and right coxae I not meeting at the midline, instead separated by the palpal endites, coxae II, III and IV meeting at the midline, margin between coxae II and III, and margin between coxae III and IV both reaching the midline (Fig. 9A, D, F) near each other.

Anterior margin of coxae II endites enlarged, curving laterally and posteriorly to form an m-shaped ridge. Endites of coxae II and III running along their sutures giving coxae III endites a v-shaped appearance; coxae IV endites running parallel to coxae IV midline suture for a distance slightly longer than the gonostome. Coxal endites forming smooth sternal plate with greatest width 0.34 mm between coxae III and IV. Pores of coxal glands visible at inner margins between coxae III and IV. Sternum absent. Coxae IV endites with horn-like projections on anterior margin of gonostome. Gonostome semicircular, 0.081 mm long and 0.12 mm wide, with straight posterior margin, and delimited by coxae IV everywhere except posterior margin. Lateral walls formed by elevated endites of coxae IV (Fig. 9F).

Spiracles nearly circular, open laterally, with maximum diameter 0.057 mm (Fig. 9G). Sternal opisthosomal glands absent. Sternite 8 curved anteriorly through the midline, posterior margin of sternite 7 similarly curved. Sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 9D, J). Anterior margin of tergite IX curving to the anterior at the midline, appearing w-shaped. Tergite IX with a single central opening of the anal gland oriented posteriorly; tergite VIII lacking opening of the anal glands. Anal plate measuring 0.11 × 0.21 mm, with an anterior-pointing v-shaped depression and scopulae originating in the central ventral surface (Fig. 9I). Cuticle with tubercular-microgranulate morphology in all ventral areas including coxae and anal plate, except on coxal and palpal endites, margin of ventral surface between the sternites and tergites, and depression of anal plate (Fig. C-I).

Chelicerae relatively robust, with few setae, first article with microgranulation on dorsal and lateral surfaces, second article appearing without conspicuous ornamentation under light microscopy. Proximal article with a dorsal process and weak ventral process most prominent laterally (Fig. 9B). Second article sub-cylindrical, its widest portion near middle of article but closer to articulation with mobile digit; ornamented by small scale-like projections, and lacking apodemes. Proximal article 0.47 mm long, 0.22 mm wide, second article 0.65 mm long, 0.14 mm wide, moveable finger 0.18 mm long, 0.045 mm wide. Dentition uniform and similar on both cheliceral fingers, with 12 denticles on each.

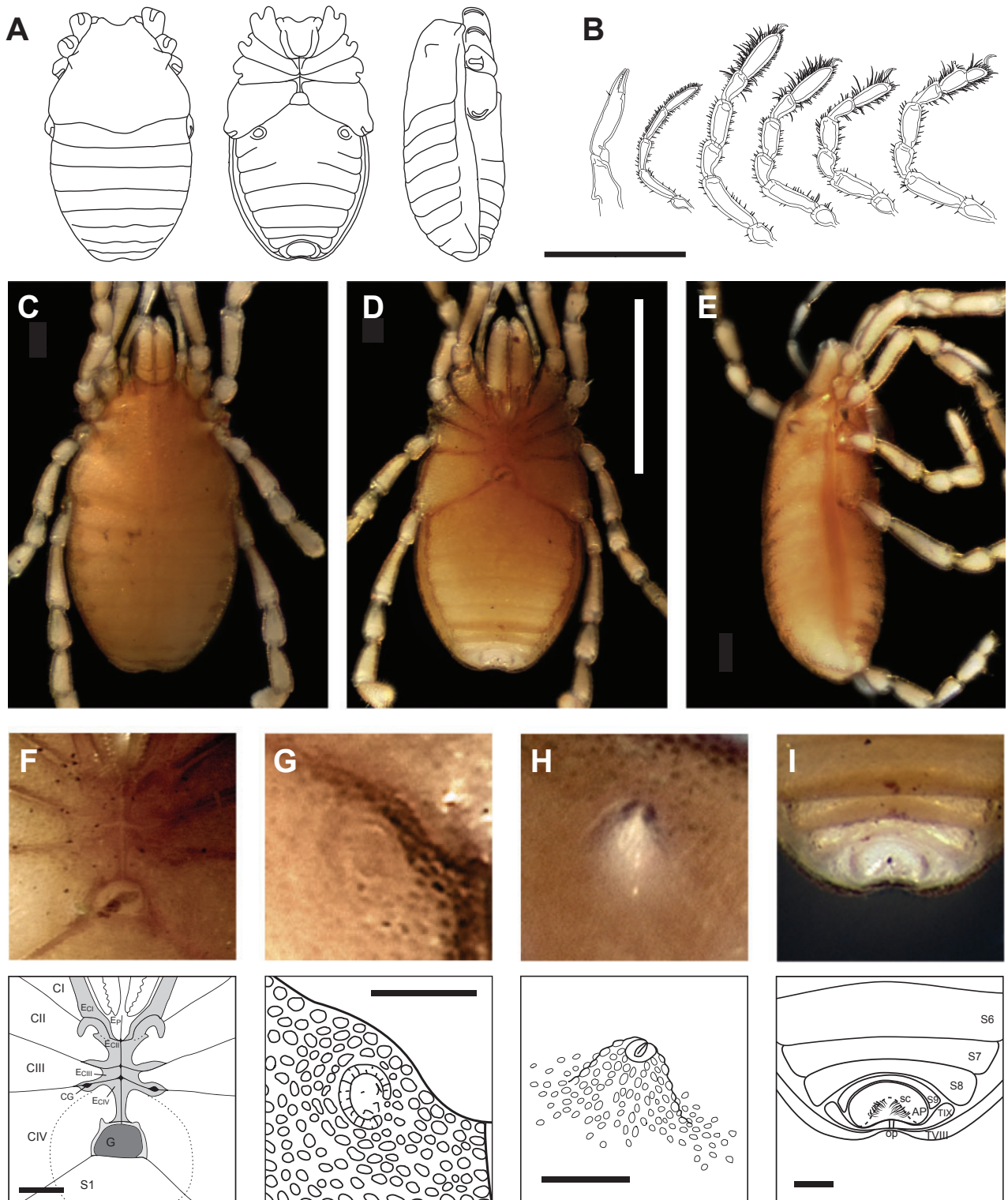
Palp with club-shaped trochanter, narrowing posteriorly (Fig. 9B). Dimensions of palpal articles from trochanter to tarsus of male given in Table 3. Palpal claw 0.033 mm long.

Legs (Fig. 9B, Table 3) with all claws appearing smooth, long and hook-like, without lateral ornamentation under light microscopy. Surfaces of all trochanters, femurs, patellae, tibiae, and metatarsi entirely ornamented. Metatarsi of legs I and II partially divided by a radial groove at ~55% of metatarsal length. All tarsi appearing smooth by light microscopy. Tarsus of leg I lacking distinct solea. Tarsus IV bisegmented, carrying a lamelliform adenostyle towards the middle of the proximal segment, approximate length 0.058 mm bearing no setae; distal margin at 48% of tarsal length.

Spermatopositor not studied, as only the holotype was available.

#### Female

Unknown.



**Fig. 9.** *Parapurcellia staregai*, sp. nov. (A) Illustrations of holotype body in dorsal, ventral and lateral views. (B) Illustrations of chelicer, palp and legs I, II, III and IV. (C–E) Automontage photographs of holotype in dorsal, ventral and lateral views. (F–I) Automontage photographs of various holotype body parts, with annotated tracings: (F) Ventral gonostome complex. CI–CIV and E<sub>CI</sub>–E<sub>CIV</sub> indicate the coxae and coxal endites of legs I–IV respectively. E<sub>P</sub> is the palpal endite, CG coxal gland, G gonostome, and S1 sternite 1. (G) Spiracle. (H) Ozophore. (I) Anal region. S6–9 indicate sternites 6–9, AP anal plate, SC scopulae on anal plate, TIX tergite IX, TVIII tergite VIII, and OP opening of the anal gland. Dashed line indicates posterior margin of raised anal plate lobes. Scale bars: A, B 1 mm; C–E 1 mm; F–I 0.1 mm.

### Distribution

Only known from the type locality: in or near Trafalgar, Eastern Cape Province, South Africa.

### Habitat

No further information is available beyond the collection locality, which has a subtropical moist savannah climate.

### Etymology

Species is named after colleague arachnologist Wojciech Starega, who devoted an important part of his career to the study of African Opiliones and who curated and identified the Cyphophthalmi collection of the Natal Museum, segregating most of the species described in this paper.

## Results and discussion

The mite harvestmen of South Africa currently belong to three genera in the family Pettalidae: *Purcellia* Hansen & Sørensen, 1904 (north-eastern South Africa and Cape Peninsula), *Speleosiro* Lawrence, 1931 (Cape Peninsula), and *Parapurcellia* Rosas Costa, 1950 (south to eastern South Africa). The phylogenetic analyses below predominantly associate *Purcellia peregrinator* with *Parapurcellia* rather than other species in its current genus. A suite of morphological characters unequivocally justifies the transfer of *Purcellia peregrinator* to the genus *Parapurcellia*, and forms the basis of rediagnoses of the three South African pettalid genera provided above.

In our phylogenetic analyses, *Fangensis spelaeus* was chosen as the outgroup during heuristic searches, but trees were re-rooted to have the family Stylocellidae as the sister group of the remaining Cyphophthalmi. This relationship was found in earlier molecular studies (Giribet and Boyer 2002), particularly when using maximum likelihood as optimality criterion (Boyer *et al.* 2007b). These studies also offer support, under other parameters, to the hypothesis that the Pettalidae are sister to the remaining Cyphophthalmi, as shown in a recent more inclusive analysis of the order Opiliones (Giribet *et al.* 2010). The alternative rooting has no effect on the internal phylogeny of Pettalidae.

### Equally weighted analysis of each data partition

We analysed the discrete and continuous morphology datasets using parsimony as the optimality criterion under equal character weighting. Generally, fewer than 50 random addition sequences were required to find the shortest trees with the discrete dataset. For the discrete data the number of most parsimonious trees is large (in the thousands), so we decided to use a driven search until hitting minimum tree length 1000 times (see Giribet 2005, 2007). This yielded 2757 trees of 228 steps, which after TBR collapsing resulted in 295 trees. The strict consensus of these trees (Fig. 10A) has all the families of Cyphophthalmi monophyletic, except for Sironidae, which is unresolved with respect to Pettalidae and (Troglósironidae + Neogoveidae). The monophyly of these families and the polyphyly of Sironidae are results consistent with several previous molecular and discrete morphological

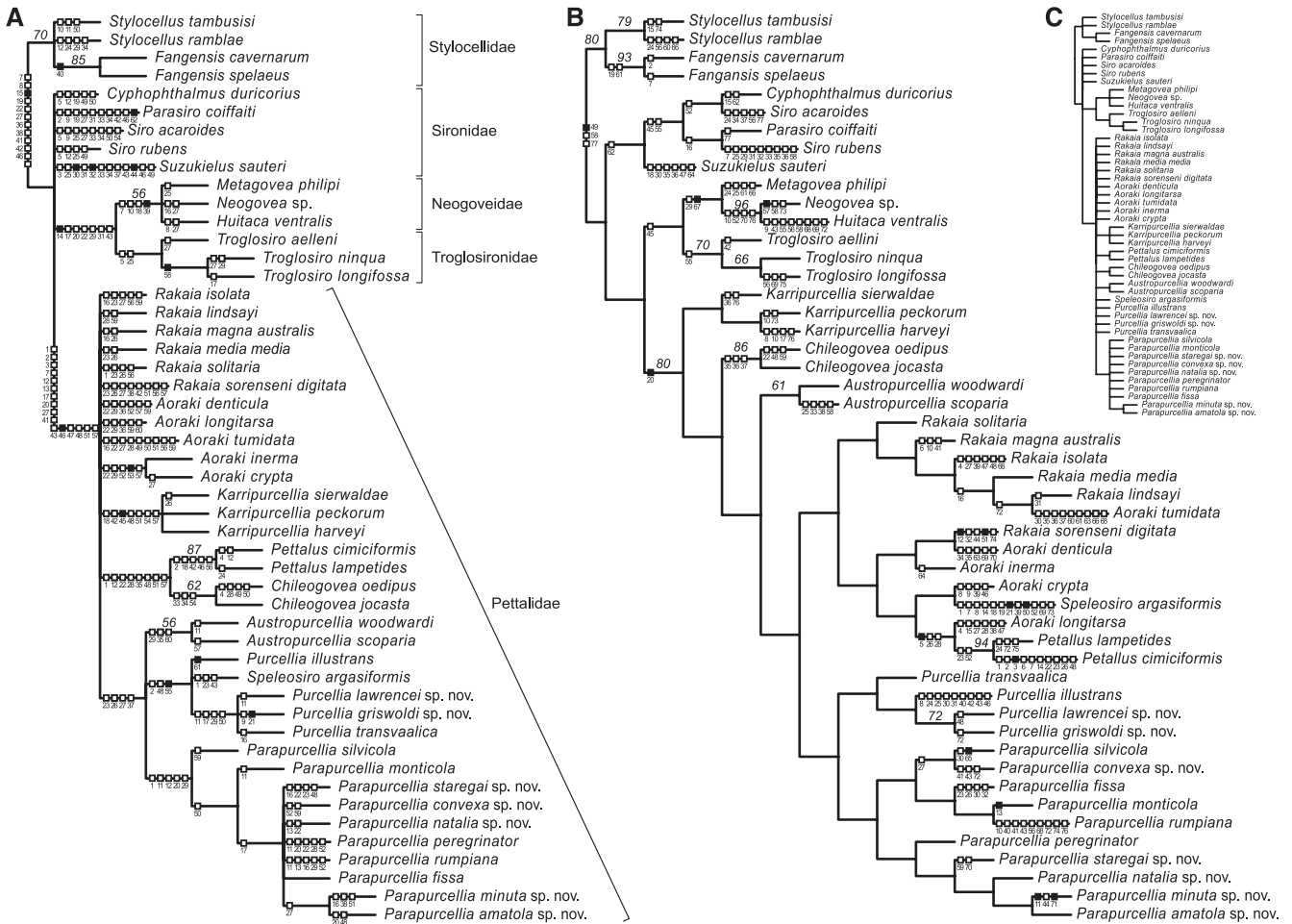
studies (Giribet and Boyer 2002; Giribet 2003; de Bivort and Giribet 2004; Boyer *et al.* 2007b; Giribet *et al.* 2010).

Optimisation of the characters onto this tree reveals many character state changes supporting deep, family-level relationships (e.g. 11 state changes separate Stylocellidae from the other families, 16 optimise at the base of Pettalidae, and 7 at the base of (Troglósironidae + Neogoveidae)). However, most character changes are ambiguously optimised, changing along multiple nodes on the tree. Notable unambiguous character state changes include the presence of Rambla's organ in *Fangensis* (Schwendinger and Giribet 2005), the presence of a sternum in Stylocellidae, the presence of a oral lappet in (Troglósironidae + Neogoveidae), the presence of free sternites 8 and 9 and tergite IX in Pettalidae, the presence of a v-shaped modification of sternites 6–8 in *Karripurcellia* (Giribet 2003), and the presence of a large anal plate depression in males uniting *Purcellia* and *Speleosiro*.

Several genera within Pettalidae appear monophyletic in our analyses under equal weighting (*Karripurcellia*, *Pettalus*, *Chileogovea*, *Austropurcellia* and *Parapurcellia*) but their position with respect to one another is unstable or receives low support, with the exception of *Pettalus* + *Chileogovea* and a South African clade. The New Zealand genera *Aoraki* and *Rakaia*, each monophyletic with high support in all published molecular studies (Boyer and Giribet 2007, 2009; Giribet *et al.* 2010), are not monophyletic with this dataset. In the discrete-character analysis of Boyer and Giribet (2007) both genera are monophyletic but they are supported by a single ambiguous character change, and the genera are not recovered in the continuous-character analysis of de Bivort *et al.* (2010). *Speleosiro* appears nested within the genus *Purcellia* forming a trichotomy with *Purcellia illustrans* and the remaining *Purcellia*, which form an unresolved clade of animals primarily from western South Africa. *Parapurcellia* is monophyletic with *P. silvicola* and *P. monticola* basal to the remaining species, and *P. amatola* and *P. minuta* are sister species. The South African pettalids form an unresolved clade with *Austropurcellia*, an association found in previous molecular and morphological studies (Giribet and Boyer 2002; Boyer *et al.* 2007b; Boyer and Giribet 2009; Giribet *et al.* 2010), although these studies sometimes find *Purcellia* and *Austropurcellia* to be basal to the rest of Pettalidae.

Using the continuous morphological character dataset, we found one tree of length 1878.5 (Fig. 10B) that predominantly agrees with the discrete morphological tree. The data in this character matrix underwent independence analysis and collapse of non-independent characters before analysis using an independence cutoff value of 1.31, which was previously found (de Bivort *et al.* 2010) to recover the most family-level groups with strong support. Thus, while it was not surprising that the continuous morphological dataset supported all the family-level relationships found in the discrete morphological tree, it should be noted that a broad range of independence cutoff values support those clades (de Bivort *et al.* 2010). In contrast to the discrete analysis, the continuous analysis found Sironidae as monophyletic, with *Suzukielus* sister to all the other species. Because the family-level relationships found in the discrete tree are reiterated in the continuous tree, and continuous trees, by their very nature tend to be fully resolved, the strict consensus





**Fig. 10.** (A) Strict consensus of thousands of trees, each of length 228, obtained under parsimony analysis of the discrete character dataset under equal weighting. Labels on the right indicate families. Hollow boxes indicate changes in ambiguous characters – defined as characters that change more than once in the tree. Filled boxes indicate unambiguous characters. Small numbers are the number of the character changing. Italicised numbers on branches indicate the bootstrap support value. (B) Shortest tree (length 1878.5) obtained under parsimony analysis of the continuous character dataset. Since most continuous character change to some degree on all branches, marks indicate those character changes of magnitude greater than 1.5 standard deviations of the character's values across all taxa. Markings are otherwise the same as on the discrete tree. (C) Strict consensus of trees A and B.

of the single continuous tree and the discrete trees (Fig. 10C) looks quite similar to the consensus discrete tree.

The concept of optimised character states changing (or not) on particular branches of a tree does not carry over especially well from discrete to continuous analyses, since the degree to which a character changes on a branch can vary continuously. Therefore, we chose to annotate the continuous character tree with 'large' character changes (Fig. 10B) defined (arbitrarily) as at least a change of 1.5 times the standard deviation of the value of the character across taxa. Unlike the changes in the discrete tree, deep family-level branches of the tree were not associated with large changes in values of the continuous characters. Large changes to characters that occurred only once on the tree include the widening of the spiracle opening in Stylocellidae, the widening of bilateral features of the scutum (such as the ozophores and the terminal posterior lobes) in Pettalidae, and the increased concavity of tergite VI in *Aoraki longitarsa* + *Pettalus*.

The internal relationships of the pettalid genera supported by the continuous tree differ from those few intergeneric relationships supported by the discrete tree. For example, *Chileogovea*, sister to *Pettalus* in the discrete tree is found, along with *Karripurcellia*, in a grade at the base of Pettalidae. And while *Aoraki* and *Rakaia* were unresolved in the discrete tree, in the continuous tree they cluster in a clade that also includes *Pettalus* (from Sri Lanka) and *Speleosiro* (from South Africa), a relationship that is unlikely given the geologic history of Gondwana, the low vagility in these animals, molecular evidence in favour of the monophyly of each of the New Zealand pettalid genera (Boyer and Giribet 2007), and morphological evidence for the monophyly of *Purcellia* plus *Speleosiro* (Giribet 2003). Nevertheless, the continuous tree agrees with the discrete tree about several relationships within Pettalidae, including the monophyly of *Parapurcellia*, the association of *Parapurcellia monticola* and *P. silvicola*,

*P. minuta* and *P. amatola* as sister species, and the positioning of the South African pettalids as derived within the family – a relationship typically supported by morphological (Giribet and Boyer 2002), but not molecular data (Boyer *et al.* 2007b).

#### *Implied weighting analysis of each data partition*

Analysis of either the discrete or morphological datasets under implied weighting using a variety of concavity values ( $k$ ) yielded trees with a variety of topologies. Therefore the consensus of implied weighting trees, which reveals groups with robust support in the dataset, for each dataset (Fig. 11) was largely unresolved, particularly the consensus tree generated from continuous morphological data only.

The consensus of all most parsimonious trees derived from the discrete dataset (Fig. 11A) with  $k$  ranging from 1 to 6 (trees for  $k > 6$  were essentially identical to the equally weighted tree) had all families as monophyletic with the exception of Sironidae, which was polyphyletic by the placement of *Suzukielus* as the sister group of *Pettalidae*. This relationship is not unprecedented in discrete datasets (de Bivort and Giribet 2004) and the position of *Suzukielus* varies between trees with different optimisation criteria in analyses of combined molecular and discrete datasets (Boyer *et al.* 2007b). The relationships between genera within *Pettalidae* were nearly entirely unresolved within this tree, although *Speleosiro* was found as sister to *Purcellia illustrans* and *Purcellia* was sister to *Parapurcellia peregrinator*. This latter relationship is notable because this species was originally described in the genus *Purcellia* — as were all the South African species described by R.F. Lawrence, even after J.A. Rosas Costa erected the genus *Parapurcellia* in 1950) — and was re-assigned above. Among all the trees presented herein, only this one supports *Parapurcellia peregrinator* as more closely allied with *Purcellia* than *Parapurcellia*.

For values of  $k$  ranging from 3 to 6, the consensus of trees derived from the discrete dataset (Fig. 11B) is considerably more resolved, providing some support for *Chileogovea* as sister to the rest of *Pettalidae*, with *Pettalus* + *Karripurcellia* as the next most basal group. *Austropurcellia* was found as the sister group of the South African pettalids, in which *Purcellia* is found nested within *Parapurcellia*.

Under implied weighting with  $k$  ranging from 1 to 6, the continuous dataset yielded trees whose strict consensus (Fig. 11C) is nearly entirely unresolved, supporting only Stylocellidae, *Austropurcellia*, *Parapurcellia amatola* + *P. natalia* + *P. minuta*, and the highly improbable group Troglisironidae + *Siro acaroides* + *Cyphophthalmus duricorius*. The consensus of trees with  $k$  ranging only from 4 to 6 (Fig. 11D) reveals support for a few plausible groups such as *Purcellia*, *Austropurcellia*, *Karripurcellia* and *Pettalus*. Because the continuous dataset was prepared using independence analysis and collapse of dependent characters, all the characters used in the analysis contain unique phylogenetic information – i.e. there is minimal redundancy between characters. Perhaps the low quality of the trees generated with continuous data and implied weighting is due to down-weighting of non-redundant phylogenetic information by the implied weighting algorithm. Indeed, the continuous dataset was highly sensitive to implied

weighting and only yielded trees similar to those from the equally weighted analysis for  $k > 30$ .

#### *Analysis of combined data under equal and implied weighting*

The most parsimonious trees generated using either discrete or continuous data under equal weighting, and discrete data under implied weighting support numerous family-level relationships (Figs 10, 11). Moreover, both continuous and discrete datasets under equal weighting support several specific relationships within *Pettalidae* (such as *Parapurcellia amatola* and *P. minuta* being sister species) (Fig. 10). Because both datasets support several evolutionary relationships, we performed phylogenetic analyses on datasets combining these two data partitions under weightings designed to vary their respective contributions to the final tree length (see Methods section). These analyses were done by allowing the characters to be differentially weighted in two different ways simultaneously. First, the discrete and continuous data partitions were weighted relative to each other (in terms of their approximate final respective contributions to tree length – see Methods) as follows: 8 : 1, 4 : 1, 2 : 1, 1 : 1, 1 : 2, 1 : 4, and 1 : 8. Second, for each of those partition weightings, TNT analyses were done under equal weighting and implied weighting for  $k = 1–6$ . This yielded 49 different trees. The status of many groups of interest across these parameter conditions is shown in Fig. 12A. The supported phylogenetic groups tend to be robust to the relative weighting of the continuous and discrete data partitions, but sensitive to the concavity parameter of the implied weighting analysis ( $k$ ).

Many plausible groups are found to be monophyletic under all values of  $k$  and all relative weightings between the continuous and discrete data partitions – the families *Pettalidae*, *Stylocellidae*, *Neogoveidae*, and *Troglisironidae*; the clade *Neogoveidae* + *Troglisironidae*; the genera *Karripurcellia*, *Austropurcellia*, *Chileogovea*, and *Pettalus*; and the sister relationship of *Purcellia griswoldi* and *P. lawrencei*. With respect to *Pettalidae*, *Suzukielus* is found as its sister group in all implied weighting analyses, consistent with the implied weighting analysis of the discrete data alone (Fig. 11A, B). In all equal weighting analyses, *Suzukielus* is found within *Sironidae*. The position of *Suzukielus* has been contentious. In previous morphological analyses of discrete data *Suzukielus* was allied to *Pettalidae* (Giribet and Boyer 2002; Giribet 2003; de Bivort and Giribet 2004), but it was placed with *Sironidae* in the analysis of continuous character data of de Bivort *et al.* (2010). In all analyses here presented, there is an affinity between *Pettalidae* and *Sironidae*, with the two families forming a grade in most analyses that includes *Troglisironidae* + *Neogoveidae*, and a clade for high  $k$  values and datasets in which the discrete partition is weighted highly.

Within *Pettalidae*, the genera *Aoraki* and *Rakaia*, which are respectively monophyletic in molecular studies (Boyer and Giribet 2007, 2009; Boyer *et al.* 2007b), were not found to be monophyletic, although in most analyses in which  $k$  is not equal to 1, the two genera form a grade. *Karripurcellia* and *Pettalus* are sister genera in 27 of 49 cases, with little relation to  $k$  or the partition weighting. The South African genus *Parapurcellia* was always found as either a non-monophyletic grade at the

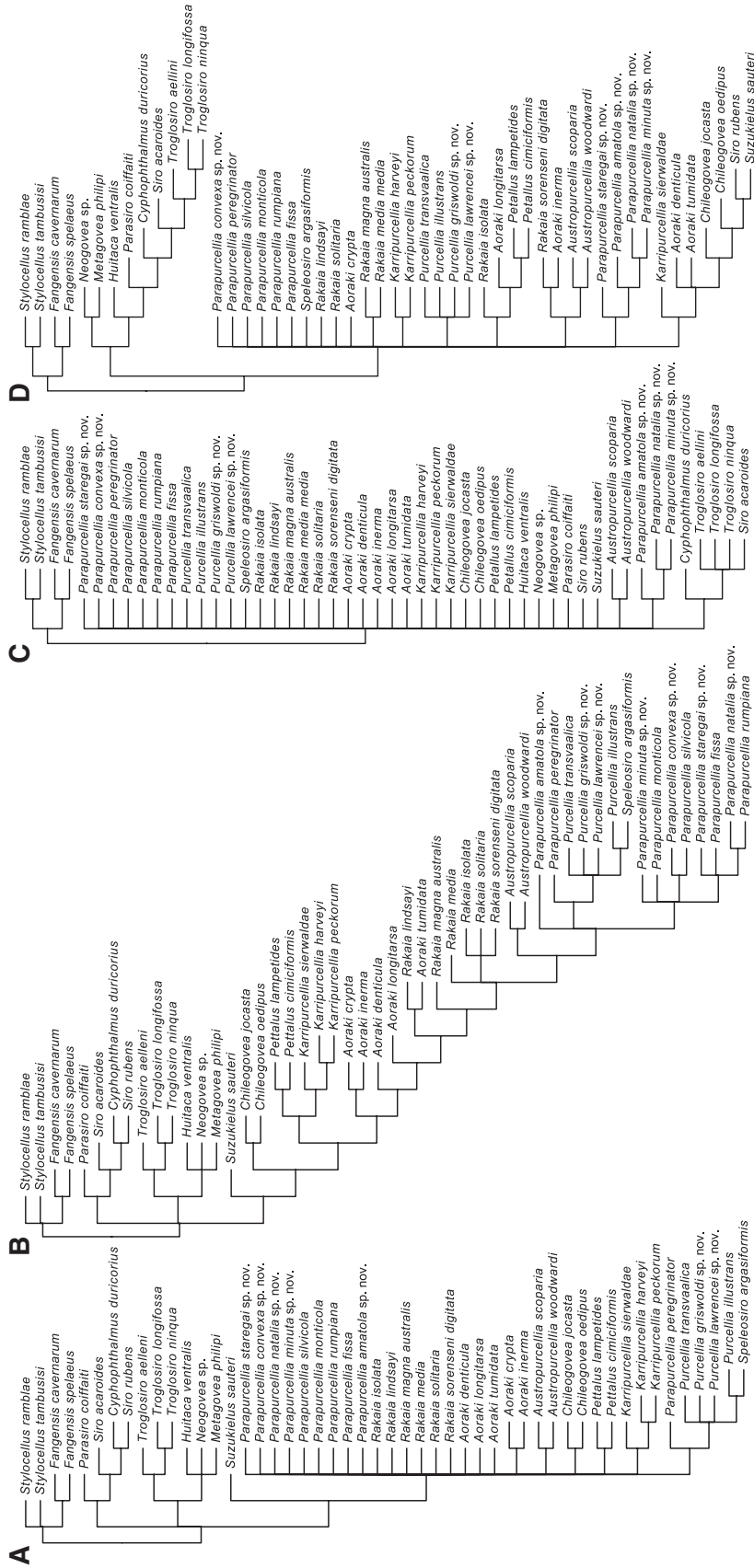
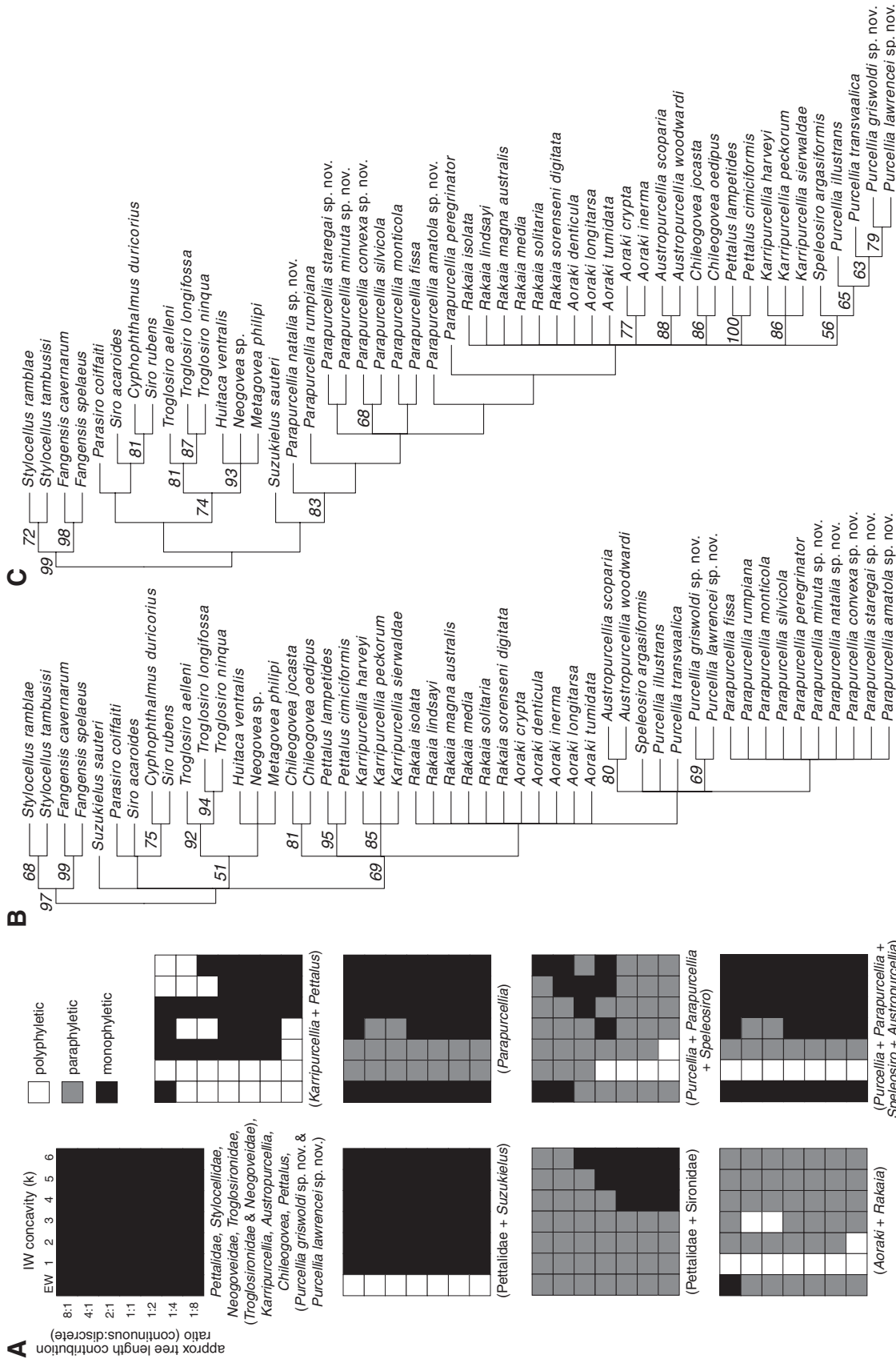


Fig. 11. (A) Strict consensus of trees obtained under parsimony analysis of the discrete dataset under implied weights for *k* values ranging from 1 to 6. (B) As in A, but only for *k* ranging from 3 to 6. (C) Strict consensus of trees obtained under parsimony analysis of the continuous dataset under implied weights for *k* values ranging from 1 to 6. (D) As in C, but only for *k* ranging from 4 to 6.



**Fig. 12.** (A) Navajo rugs summarising results for clades of interest analysed under parsimony, using combined discrete and continuous data. The search conditions varied across equal weights (EW) and implied weights with *k* values ranging from 1 to 6, and the relative weight of the continuous dataset to the discrete dataset ranging from 8 : 1 to 1 : 8. (B) Strict consensus of all trees found in which the genus *Parapurcellia* is found to be a derived group within the Petalidae (and monophyletic). This corresponds to all trees under EW, *k* = 4, *k* = 5 and *k* = 6, and *k* = 3 for data partition weighting ratios of 8 : 1, 1 : 1, 1 : 2, 1 : 4 and 1 : 8. (C) Strict consensus of all trees in which the genus *Parapurcellia* is found to be basal within the Petalidae (and paraphyletic). This corresponds to all trees under *k* = 1 and *k* = 2, and *k* = 3 for data partition weighting ratios of 4 : 1 and 2 : 1. Numbers on the branches of trees in B and C indicate the bootstrap support values derived from analyses of the 1 : 1 weighted combined dataset under EW, *k* = 1, and *k* = 6 respectively.

base of Pettalidae (for  $k=1$ , 2 and sometimes 3), or a clade. This distinction can be used to establish two alternative hypotheses for the phylogenetic relationships within Pettalidae (Fig. 12B, C).

The strict consensus of all trees in which *Parapurcellia* was found to be monophyletic (Fig. 12B), places the South African pettalids in a derived, internally unresolved clade that also includes *Austropurcellia*. The affinity of *Austropurcellia* and the South African pettalids was also found in the molecular study Boyer *et al.* (2007b), although they also found a consistent association between the South African genera and the South American genus *Chileogovea* that was absent in our results. The strict consensus of all remaining trees (Fig. 12C) is consistent with Boyer *et al.* (2007b) in that *Purcellia* and *Speleosiro* form a clade which is in turn found in an unresolved group containing the remaining pettalid genera. Both of these evolutionary hypotheses have respective consistencies with previous molecular studies, thus it is hard for us to favour one over the other, on the basis of phylogenetic relationships found in earlier studies.

We performed bootstrap analysis on the dataset with 1:1 weighting between the partitions, for  $k=1$  and  $k=6$  which respectively correspond to the derived (Fig. 12B) and basal (Fig. 12C) hypotheses for the position of *Parapurcellia*. Both analyses yielded support values  $>50$  for Stylocellidae, Troglosironidae, Pettalidae, Troglosironidae+Neogoveidae, six pettalid genera, *Cyphophthalmus*+*Siro rubens*, and *Purcellia griswoldi*+*P. lawrencei*. However (for these parameters) there is greater support for several other clades in the basal *Parapurcellia* hypothesis; Neogoveidae, *Parapurcellia convexa*+*P. silvicola*, *Aoraki crypta*+*A. inerma* (Boyer *et al.* 2007b), *Speleosiro*+*Purcellia*, *Purcellia*, and *P. illustrans*+the remaining *Purcellia*. This may provide some evidence in favour of the hypothesis that places *Parapurcellia* basal within Pettalidae.

#### Position of *Parapurcellia peregrinator*

Our reassignment of *Purcellia peregrinator* to *Parapurcellia peregrinator* is supported by numerous discrete morphological character differences between these genera, e.g. the presence/absence of anterior projections of the gonostome wall, the posterior/ventral orientation of the anal gland opening, and the absence/presence of a large anal plate depression. While there were no large magnitude changes in the value of continuous characters between *Purcellia* and *Parapurcellia*, this species nevertheless falls well within *Parapurcellia* in the continuous data analyses.

Only in the analysis of the discrete data alone, under implied weighting, does *Parapurcellia peregrinator* occur outside *Parapurcellia*, in this case as the sister group to *Purcellia*+*Speleosiro*. This does not imply that *P. peregrinator* belongs within *Purcellia*, since *Parapurcellia* is rendered paraphyletic with respect to *Purcellia*+*Speleosiro* in this tree. Lastly, in the analysis of the combined discrete and continuous datasets, *P. peregrinator* nests within *Parapurcellia* whether the genus is found as a derived clade within, or at the base of Pettalidae. In the phylogenetic hypothesis in which *Parapurcellia* is basal,

*P. peregrinator* is found as the sister group to the remaining non-*Parapurcellia* pettalids (Fig. 12C). From these observations, we conclude that *Parapurcellia peregrinator* is clearly not a member of *Purcellia* and instead belongs in the reassigned genus, though it appears in a few instances to be an intermediate taxon between the rest of *Parapurcellia* and either *Purcellia* or the rest of the family Pettalidae.

#### Biogeography of the South African pettalids

In a cladistic biogeographic analysis of the distributions of spiders across Afrotropical regions, Griswold (1991) found that the Knysna and Table Mountain areas of endemism are sister regions, while the eastern regions are more closely related to other regions outside of South Africa, namely a clade formed by the ((Eastern Africa Volcanoes+Eastern Arc Mountains)+Madagascar). The eastern regions show a sister relationship between the Natal Drakensberg and the Transkei-Natal Midlands, while the Transvaal Drakensberg is more closely related to the Africa Volcanoes+Eastern Arc Mountains+Madagascar clade. We found that *Purcellia* and *Speleosiro* form a clade, supporting in part the relationships of the Knysna and Table Mountain areas of endemism, but *P. transvaalica* is found in Griswold's Transvaal Drakensberg area of endemism, which is more closely related to the ((Africa Volcanoes+Eastern Arc Mountains)+Madagascar) clade. The distribution of *Parapurcellia* corresponds with Griswold's Natal-Zululand Coast, Transkei-Natal Midlands and Natal Drakensberg areas of endemism, but our phylogenetic conclusions are too tenuous to derive meaningful comparisons.

One can compare the distribution of pettalids with the distributions of other terrestrial invertebrates with likely similar dispersal rates and ecological requirements (Harvey 1996). Among Opiliones, several groups show similar distribution patterns, but perhaps most striking is that of the genera *Graemontia* Lawrence, 1931, as recently summarised by Kury (2006), and *Monomontia* Lawrence, 1931 (see Kauri 1961). Phylogenetic analyses of these genera would be necessary before concluding whether their biogeographic patterns are also similar. Another matching distribution is that of the onychophoran genus *Peripatopsis* (Hamer *et al.* 1997), but in this case it seems that there are several basal lineages in the Western Cape province (Table Mountain and Knysna Forest areas of endemism) and from there the clade has extended its range towards the Eastern Cape and Kwazulu-Natal provinces (Daniels *et al.* 2009).

#### Note added in proof

During the course of this study, a new South African species, *Purcellia leleupi* Starega, 2008, was described in the *Polish Journal of Entomology* 77(1), 51–56. We were not aware of this species until our study was completed. Its description and illustrations do not allow clear diagnosis of the species, but it seems that the apical tarsal segment length–width ratio ( $\sim 3.0$ ) distinguishes it from *P. griswoldi* and *P. lawrencei*, and sternite 8 looks very different, being completely divided and triangular on each side, although this could be an inaccuracy of the description.

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## References

- Boyer, S. L., and Giribet, G. (2007). A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. *Cladistics* **23**, 337–361. doi:10.1111/j.1096-0031.2007.00149.x
- Boyer, S. L., and Giribet, G. (2009). Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography* **36**, 1084–1099. doi:10.1111/j.1365-2699.2009.02092.x
- Boyer, S. L., Baker, J. M., and Giribet, G. (2007a). Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread 'mite harvestman' defies DNA taxonomy. *Molecular Ecology* **16**, 4999–5016. doi:10.1111/j.1365-294X.2007.03555.x
- Boyer, S. L., Clouse, R. M., Benavides, L. R., Sharma, P., Schwendinger, P. J., Karunaratna, I., and Giribet, G. (2007b). Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography* **34**, 2070–2085. doi:10.1111/j.1365-2699.2007.01755.x
- Clouse, R. M., and Giribet, G. (2007). Across Lydekker's line—first report of mite harvestmen (Opiliones: Cyphophthalmi: Stylocellidae) from New Guinea. *Invertebrate Systematics* **21**, 207–228. doi:10.1071/IS06046
- Clouse, R. M., de Bivort, B. L., and Giribet, G. (2009). A phylogenetic analysis for the south-east Asian mite harvestman family Stylocellidae (Opiliones: Cyphophthalmi) – a combined analysis using morphometric and molecular data. *Invertebrate Systematics* **23**, 515–529. doi:10.1071/IS09044
- Daniels, S. R., Picker, M. D., Cowlin, R. M., and Hamer, M. L. (2009). Unravelling evolutionary lineages among South African velvet worms (Onychophora: *Peripatopsis*) provides evidence for widespread cryptic speciation. *Biological Journal of the Linnean Society. Linnean Society of London* **97**, 200–216. doi:10.1111/j.1095-8312.2009.01205.x
- de Bivort, B., and Giribet, G. (2004). A new genus of cyphophthalmid from the Iberian peninsula with a phylogenetic analysis of the Sironidae (Arachnida: Opiliones: Cyphophthalmi) and a SEM database of external morphology. *Invertebrate Systematics* **18**, 7–52. doi:10.1071/IS03029
- de Bivort, B. L., Clouse, R. M., and Giribet, G. (2010). A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae). *Journal of Zoological Systematics and Evolutionary Research* **48**, 294–309. doi:10.1111/j.1439-0469.2009.00562.x
- Ewing, H. E. (1923). *Holosiro acaroides*, new genus and species, the only new world representative of the mite-like phalangids of the suborder Cyphophthalmi. *Annals of the Entomological Society of America* **16**, 387–391.
- Forster, R. R. (1948). The sub-order Cyphophthalmi Simon in New Zealand. *Dominion Museum Records in Entomology* **1**, 79–119.
- Forster, R. R. (1952). Supplement to the sub-order Cyphophthalmi. *Dominion Museum Records in Entomology* **1**, 179–211.
- Forster, R. R. (1955). Further Australian harvestmen (Arachnida: Opiliones). *Australian Journal of Zoology* **3**, 354–411. doi:10.1071/ZO9550354
- Giribet, G. (2000). Catalogue of the Cyphophthalmi of the world (Arachnida, Opiliones). *Revista Ibérica de Aracnología* **2**, 49–76.
- Giribet, G. (2002). *Stylocellus ramblae*, a new stylocellid (Opiliones, Cyphophthalmi) from Singapore, with a discussion of the family Stylocellidae. *The Journal of Arachnology* **30**, 1–9. doi:10.1636/0161-8202(2002)030[0001:SRANSO]2.0.CO;2
- Giribet, G. (2003). *Karripurcellia*, a new pettalid genus (Arachnida: Opiliones: Cyphophthalmi) from Western Australia, with a cladistic analysis of the family Pettalidae. *Invertebrate Systematics* **17**, 387–406. doi:10.1071/IS02014
- Giribet, G. (2005). Book reviews: TNT: tree analysis using new technology. *Systematic Biology* **54**, 176–178. doi:10.1080/10635150590905830
- Giribet, G. (2007). Efficient tree searches with available algorithms. *Evolutionary Bioinformatics* **3**, 1–16.
- Giribet, G., and Boyer, S. L. (2002). A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). *The Journal of Arachnology* **30**, 110–128. doi:10.1636/0161-8202(2002)030[0110:ACAOTC]2.0.CO;2
- Giribet, G., and Boyer, S. L. (2007). Pettalidae Shear, 1980. In 'Harvestmen: The Biology of Opiliones'. (Eds R. Pinto-da-Rocha, G. Machado and G. Giribet.) pp. 99–101. (Harvard University Press: Cambridge, MA.)
- Giribet, G., and Prieto, C. E. (2003). A new Afrotropical *Ogovea* (Opiliones, Cyphophthalmi) from Cameroon, with a discussion on the taxonomic characters in the family Ogoveidae. *Zootaxa* **329**, 1–18.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P., and Kury, A. B. (2010). A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* **26**, 408–437. doi:10.1111/j.1096-0031.2009.00296.x
- Goloboff, P. A. (1993). Estimating character weights during tree search. *Cladistics* **9**, 83–91. doi:10.1111/j.1096-0031.1993.tb00209.x
- Goloboff, P. A. (1999). Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* **15**, 415–428. doi:10.1111/j.1096-0031.1999.tb00278.x
- Goloboff, P. A., Farris, J. S., and Nixon, K. C. (2008). TNT, a free program for phylogenetic analyses. *Cladistics* **24**, 774–786. doi:10.1111/j.1096-0031.2008.00217.x
- Goodnight, C. J., and Goodnight, M. L. (1980). *Metagovea philipi*, n. sp., a new cyphophthalmid (Arachnida) from Ecuador. *Transactions of the American Microscopical Society* **99**, 128–131. doi:10.2307/3226087
- Griswold, C. E. (1991). Cladistic biogeography of Afrotropical spiders. *Australian Systematic Botany* **4**, 73–89. doi:10.1071/SB9910073
- Hamer, M. L., Samways, M. J., and Ruhberg, H. (1997). A review of the Onychophora of South Africa, with discussion of their conservation. *Annals of the Natal Museum* **38**, 283–312.
- Hansen, H. J. (1921). 'Studies on Arthropoda I. The Pedipalpi, Ricinulei, and Opiliones (exc. Op. Laniatores) collected by Mr. Leonardo Fea in tropical West Africa and adjacent Islands.' (Gyldendalske Boghandel: Copenhagen.)
- Hansen, H. J., and Sørensen, W. (1904). 'On two orders of Arachnida: Especially the Suborder Cyphophthalmi, and Ricinulei, Namely the Family Cryptostemmatoidae.' (Cambridge University Press: Cambridge, UK.)
- Harvey, M. S. (1996). Small arachnids and their value in Gondwanan biogeographic studies. In 'Gondwanan Heritage: Past, Present and Future of Western Australian Biota'. (Ed. S. D. Hopper.) pp. 155–162. (Surrey Beatty & Sons: Sydney.)
- Hirst, S. (1925). On some new genera and species of Arachnida. *Proceedings of the Zoological Society of London* **1925**, 1271–1280.

- Joseph, G. (1868). *Cyphophthalmus duricorius*, eine neue Arachniden-Gattung aus einer neuen Familie der Arthrogastren-Ordnung entdeckt in der Luëger Grotte in Krain. *Berliner Entomologische Zeitung* **12**, 241–250. doi:10.1002/mmnd.18680120208
- Juberthie, C. (1956). Une nouvelle espèce d'Opilions Sironidae de France et d'Espagne: *Parasiro coiffaiti* n. sp. *Bulletin du Muséum national d'histoire naturelle, Paris* **28**, 394–400.
- Juberthie, C. (1969). Sur les opilions cyphophthalmes Stylocellinae du Gabon. *Biologia Gabonica* **5**, 79–92.
- Juberthie, C. (1970). Les opilions cyphophthalmes cavernicoles. Notes sur *Speleosiro argasiformis* Lawrence. *Bulletin du Muséum National d'Histoire Naturelle* **42**, 864–871.
- Juberthie, C. (1979). Un cyphophthalmes nouveau d'une grotte de Nouvelle-Calédonie: *Troglosiro aelleni* n. gen., n. sp. (Opilions, Sironinae). *Revue Suisse de Zoologie* **86**, 221–231.
- Juberthie, C. (1988). Un nouvel opilion cyphophthalmes aveugle d'Australie: *Austropurcellia* gen. nov., *scoparia* n. sp. *Memoires de Biospeologie* **15**, 133–140.
- Kauri, H. (1961). Opiliones. In 'South African Animal Life. Results of the Lund University Expedition in 1950–1951'. (Eds B. Hanström, P. Brinck and G. Rudebeck.) pp. 9–197. (Almqvist & Wiksell: Uppsala.)
- Kury, A. B. (2006). A new species of *Graemontia* Lawrence, 1931, from the Western Cape, South Africa, with notes on the relationships of the genus (Opiliones: Laniatores: Triaenonychidae). *African Zoology* **41**, 45–50. doi:10.3377/1562-7020(2006)41[45:ANSOGL]2.0.CO;2
- Latreille, P. A. (1804). 'Histoire naturelle, generale et particuliere des Crustacés et des Insectes.' (F. Duart: Paris.)
- Lawrence, R. F. (1931). The harvest-spiders (Opiliones) of South Africa. *Annals of the South African Museum* **29**, 341–508.
- Lawrence, R. F. (1933). The harvest-spiders (Opiliones) of Natal. *Annals of the Natal Museum* **7**, 211–241.
- Lawrence, R. F. (1939). A contribution to the opilionid fauna of Natal and Zululand. *Annals of the Natal Museum* **9**, 225–243.
- Lawrence, R. F. (1963). The Opiliones of the Transvaal. *Annals of the Transvaal Museum* **24**, 275–304.
- Legg, G. (1990). *Parogovia pabsgarnoni*, sp. n. (Arachnida, Opiliones, Cyphophthalmi) from Sierra Leone, with notes on other African species of *Parogovia*. *Bulletin of the British Arachnological Society* **8**, 113–121.
- Murphree, C. S. (1988). Morphology of the dorsal integument of ten opilionid species (Arachnida, Opiliones). *The Journal of Arachnology* **16**, 237–252.
- Nixon, K. C. (1999). The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**, 407–414. doi:10.1111/j.1096-0031.1999.tb00277.x
- Pickard-Cambridge, O. (1875). On three new and curious forms of Arachnida. *Annals and Magazine of Natural History. Series* **4**, 383–390.
- Roewer, C. F. (1916). 7 neue Opilioniden des Zoolog. Museums in Berlin. *Archiv für Naturgeschichte* **81**, 6–13.
- Roewer, C. F. (1923). 'Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones.' (Verlag von Gustav Fisher: Jena.)
- Roewer, C. F. (1961). Opiliones aus Sud-Chile. *Senckenbergiana Biologica* **42**, 99–105.
- Rosas Costa, J. A. (1950). Sinopsis de los géneros de Sironinae, con la descripción de dos géneros y una especie nuevos (Opiliones, Cyphophthalmi). *Arthropoda* **1**, 127–151.
- Schwendinger, P. J., and Giribet, G. (2005). The systematics of the south-east Asian genus *Fangensis* Rambla (Opiliones: Cyphophthalmi: Stylocellidae). *Invertebrate Systematics* **19**, 297–323. doi:10.1071/IS05023
- Sharma, P., and Giribet, G. (2005). A new *Troglosiro* species (Opiliones, Cyphophthalmi, Troglosironidae) from New Caledonia. *Zootaxa* **1053**, 47–60.
- Sharma, P., and Giribet, G. (2006). A new *Pettalus* species (Opiliones, Cyphophthalmi, Pettalidae) from Sri Lanka with a discussion on the evolution of eyes in Cyphophthalmi. *The Journal of Arachnology* **34**, 331–341. doi:10.1636/H05-33.1
- Shear, W. A. (1979). *Huitaca ventralis*, n. gen., n. sp., with a description of a gland complex new to cyphophthalmids (Opiliones: Cyphophthalmi). *The Journal of Arachnology* **7**, 237–242.
- Shear, W. A. (1985). *Marwe coarctata*, a remarkable new cyphophthalmid from a limestone cave in Kenya (Arachnida, Opiliones). *American Museum Novitates* **2830**, 1–6.
- Shear, W. A. (1993a). The genus *Chileogovea* (Opiliones, Cyphophthalmi, Pettalidae). *The Journal of Arachnology* **21**, 73–78.
- Shear, W. A. (1993b). The genus *Troglosiro* and the new family Troglosironidae (Opiliones, Cyphophthalmi). *The Journal of Arachnology* **21**, 81–90.
- Shear, W. A. (1993c). New species in the opilionid genus *Stylocellus* from Malaysia, Indonesia and the Philippines (Opiliones, Cyphophthalmi, Stylocellidae). *Bulletin of the British Arachnological Society* **9**, 174–188.
- Shear, W. A., and Gruber, J. (1996). Cyphophthalmid opilionids new to Madagascar: two new genera (Opiliones, Cyphophthalmi, Pettalidae). *Bulletin of the British Arachnological Society* **10**, 181–186.
- Starega, W. (2008). The second species of *Purcellia* Hansen et Sørensen, 1904 (Arachnida: Opiliones: Pettalidae) from South Africa. *Polish Journal of Entomology* **77**, 51–56.
- Thorell, T. (1876). Sopra alcuni Opilioni (Phalangidea) d'Europa e dell'Asia occidentale, con un quadro dei generi europei de quest'Ordine. *Annali Museo civico Storia naturale Giacomo Doria* **8**, 452–508.

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**Appendix 1. List of material examined by light microscopy to generate the continuous data set**


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- Parapurcellia peregrinator* (Lawrence, 1963) – holotype ♂ (NMSA ZA.8) from Mariepskop Forest, Pilgrim's Rest, Mpumalanga, South Africa.  
*Parapurcellia silvicola* (Lawrence, 1939) – syntype ♂ (NMSA) from Nkandhla Forest Reserve and Ngoye Forest, Kwazulu-Natal, South Africa.  
*Parapurcellia monticola* (Lawrence, 1939) – syntype ♂ (NMSA 1838) from Drakensberg Mountains, Kwazulu-Natal Province, South Africa.  
*Parapurcellia rumpiana* (Lawrence, 1933) – syntype ♂ (NMSA) from Pietermaritzburg, Kwazulu-Natal Province, South Africa.  
*Parapurcellia fissa* (Lawrence, 1939) – syntype ♂ (NMSA 1119) from Port St. Johns, Eastern Cape Province, South Africa.  
*Purcellia transvaalica* Lawrence, 1963 – syntype ♂ (NMSA) from Hanglip Forest (near Louis Trichardt), North Transvaal Province, South Africa.  
*Purcellia illustrans* Hansen & Sørensen, 1904 – ♂♂ (ZMUC, MCZ) from Table Mountain, Western Cape Province, South Africa.  
*Speleosiro argasiformis* Lawrence, 1931 – holotype ♂ (SAM ENW B001473) from Wynberg Caves, Table Mountain, Western Cape Province, South Africa.  
*Rakaia isolata* Forster, 1952 – holotype ♂ (CM A. 14) from North Canterbury, South Island, New Zealand.  
*Rakaia lindsayi* Forster, 1952 – holotype ♂ (MNZ DM 2/160) from Stewart Island, South Africa.  
*Rakaia magna australis* Forster, 1952 – holotype ♂ (CM A. 12) from Lewis Pass, South Island, New Zealand.  
*Rakaia media* Forster, 1948 – holotype ♂ (MNZ DM 2/101) from Bay of Plenty, North Island, New Zealand.  
*Rakaia solitaria* Forster, 1948 – holotype ♂ (MNZ DM 2/107) from Opouawa Gully, West Wairarapa, North Island, New Zealand.  
*Rakaia sorenseni digitata* Forster, 1952 – holotype ♂ (CM A. 19) from Chaslands, Otago, South Island, New Zealand.  
*Aoraki crypta* (Forster, 1948) – holotype ♂ (MNZ DM 2/385) from Coromandel and Bay of Plenty, North Island, New Zealand.  
*Aoraki denticula* (Forster, 1948) – holotype ♂ (MNZ DM 2/53) from Nelson, Marlborough, and Buller, South Island, New Zealand.  
*Aoraki inerma* (Forster, 1948) – holotype ♂ (MNZ DM 2/45) from Te Aroha Mountain, Waikato, North Island, New Zealand.  
*Aoraki longitarsa* (Forster, 1952) – holotype ♂ (MNZ DM 2/796) from Mount Cook, Canterbury, South Island, New Zealand.  
*Aoraki tumidata* (Forster, 1948) – holotype ♂ (MNZ DM 2/50) from Cuvier Island, Coromandel, North Island, New Zealand.  
*Karripurcellia harveyi* Giribet, 2003 – holotype ♂ (WAM T42519) from Crowea, Western Australia, Australia.  
*Karripurcellia peckorum* Giribet, 2003 – holotype ♂ (WAM T47011) from Warren National Park, Western Australia, Australia.  
*Karripurcellia sierwaldae* Giribet, 2003 – holotype ♂ (WAM T47013) from Warren National Park, Western Australia, Australia.  
*Austropurcellia scoparia* Juberthie, 1988 – holotype ♂ (MNHN) from north-eastern Queensland, Australia.  
*Austropurcellia woodwardi* (Forster, 1955) – holotype ♂ (QM) from Great Dividing Range, Queensland, Australia.  
*Chileogovea jocasta* (Shear, 1993a) – holotype ♂ (AMNH) from Pata de Gallina, Region de Bío-bío, Chile.  
*Chileogovea oedipus* (Roewer, 1961) – holotype ♂ (ZMH) from Isla de Chiloé, Región de Los Lagos, Chile.  
*Pettalus lampetides* Sharma & Giribet, 2006 – holotype ♂ (MHNG) from Diyaluma Falls, Province of Uva, Sri Lanka.  
*Pettalus cimiciformis* (Pickard-Cambridge, 1875) – holotype ♂ (BMNH) from unspecified locality, Sri Lanka.  
*Troglosiro aelleni* Juberthie, 1979 – holotype ♂ (MHNG) from d'Adio Cave, Mount Adio, New Caledonia.  
*Troglosiro longifossa* Sharma & Giribet, 2005 – holotype ♂ (MNHN) from Gîte Kanua, Port Boisé, New Caledonia.  
*Troglosiro ninqua* Shear, 1993b – holotype ♂ (MNHN) from Mount Ninqua, New Caledonia.  
*Huitaca ventralis* Shear, 1979 – holotype ♂ (MCZ 14835) from 30 Km South of Chinácota, Provincia Norte de Santander, Colombia.  
*Neogovea* sp. – undescribed ♂ (MZUSP) from Turuma Mirim, State of Amazonas, Brazil.  
*Metagovea philipi* Goodnight & Goodnight, 1980 – holotype ♂ (AMNH) from Los Taxos Cave, Morona Santiago Province, Ecuador.  
*Cyphophthalmus duricorius* Joseph, 1868 – syntype ♂ (ZMB 4189) from cave, Predjama, Slovenia.  
*Parasiro coiffaiti* Juberthie, 1956 – syntype ♂ (MNHN) from Girona, Spain.  
*Siro acaroides* (Ewing, 1923) – syntype ♂ (USNM) from Coast Range Mountains, Benton County, Oregon (USA).  
*Siro rubens* Latreille, 1804 – syntype ♂ (MNHN) from Massif Central, France.  
*Suzukiellus sauteri* (Roewer, 1916) – lectotype ♂ (SMF RI/1280) from Yamanaka, Suruga, Japan.  
*Stylocellus ramblae* Giribet, 2002 – holotype ♂ (FMNH) from Botanical Gardens of Singapore, Singapore.  
*Stylocellus tambusisi* Shear, 1993c – holotype ♂ (BMNH [E] 1999.174) from Tambusisi Mountains, Sulawesi Tengah, Sulawesi, Indonesia.  
*Fangensis cavernarum* Schwendinger & Giribet, 2005 – holotype ♂ (MHNG) from Tham Nam Phrathat, Si Sawat District, Kanchanaburi Province, Thailand.  
*Fangensis spelaeus* Schwendinger & Giribet, 2005 – holotype ♂ (MHNG) from Kaeng Lawa Cave in western Thailand.
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### Appendix 2. Discrete morphological characters used in the phylogenetic analyses and discussion

Characters new to this analysis will be discussed in some detail; characters used in previous studies are referenced as follows: *GB* indicates character number from the matrix analysed in Giribet and Boyer (2002). *G* indicates Giribet (2003). *DG* indicates de Bivort and Giribet (2004). *BG* indicates Boyer and Giribet (2007)

1. Eyes – (0) absent; (1) present with lens; (2) present, incorporated into ozophore (GB 2; DG 1; BG 1).
2. Ozophore position – (0) type 1; (1) type 2; (2) type 3; (3) dorsal, facing 45° (GB 2; G 1; DG 2; BG 2).
3. Ozophore opening type – (0) subterminal; (1) infolded; (2) terminal, with circular opening; (3) labial; (4) disc-shaped (DG 3; BG 3).
4. Ozophore ornamentation – (0) absent; (1) ornamented on approximately half of its surface; (2) entirely ornamented; (3) ornamented on less than half of its surface. The surface of the ozophores of most species is entirely covered in tubercular micro-granulate ornamentation (*sensu* Murphree, 1988) of varying density. However in some species in this study (*Chileogovea oedipus* and *Pettalus cimiciformis*) roughly half of the surface of the ozophore lacks ornamentation.
5. Spiral ornamentation of the ozophore – (0) absent; (1) present (DG 4; BG 4).
6. Proximal end of coxae I meeting along the midline – (0) absent; (1) present (DG 24; BG 23).
7. Second coxae – (0) free; (1) fused to coxae of legs III (GB 11; G 8; DG 25; BG 24).
8. Proximal end of male coxae III meeting along the midline – (0) absent; (1) present (DG 26; BG 25).
9. Coxae II and III endites with processes running along their suture – (0) absent; (1) present (DG 27; BG 26).
10. Gonostome of male in anterior position – (0) absent; (1) present (DG 29; BG 27).
11. Shape of the gonostome – (0) semicircular-trapezoidal; (1) subhexagonal; (2) semicircular; (3) oval; (4) circular. Previous uses of this character (de Bivort and Giribet, 2004; Boyer and Giribet, 2007) have used just two states: semicircular-trapezoidal and subhexagonal. Here, we recognise that there is substantial diversity in the shape of the gonostome, adding the latter three states. Most cyphophthalmids possess semicircular-trapezoidal gonostomes, although with the greater specificity afforded by this extended character state list, some species (e.g. *Austropurcellia woodwardi*, *Metagovea philipi* and *Stylocellus tambusisi*) have been recoded as having semicircular gonostomes. The only species in this analysis with a different coding under the original scheme was *Huitaca ventralis*, with its subhexagonal gonostome. Among the South African pettalids, all have either oval or semicircular gonostomes except *Purcellia illustrans*, the gonostome of which is semicircular-trapezoidal. Generally, oval gonostomes are found on the smaller South African pettalids, particularly those in the genus *Parapurcellia*.
12. Anterior projections of male coxae IV endite – (0) no projections; (1) projections in gonostome wall; (2) projections adjacent to coxal pore; (3) projections along suture of coxae IV (BG 29).
13. Endites of coxae IV running adjacent to midline suture for a length longer than gonostome – (0) absent; (1) present (DG 32; BG 30).
14. Oral lappet – (0) absent; (1) present. An oral lappet in the posterior end of the stomotheca is present in Troglósironidae and Neogoveidae but absent or unevaluated in all other taxa in this study.
15. Sternum – (0) absent; (1) present (G 17; DG 28).
16. Protruding chelicerae – (0) absent; (1) present (G 21; BG 5).
17. Widest part of cheliceral distal article – (0) near base; (1) near articulation with mobile digit (DG 5; BG 6). See next character for discussion.
18. Attenuate chelicerae – (0) absent; (1) present (GB 3; G 3). Animals, often troglomorphic, with dramatically tapering second cheliceral segments, e.g. *Huitaca ventralis* were originally coded (Giribet and Boyer, 2002; Giribet, 2003) as having ‘attenuate’ chelicerae. Later (de Bivort and Giribet, 2004; Boyer and Giribet, 2007) this character state was redefined as the second segment of the chelicerae having its widest part near the base of the article or near the articulation with the mobile digit (character 17, above). All animals with attenuate chelicerae were then coded as having the widest part of the second segment of their chelicerae near that article’s base. Here, we recognise that the second segment of the chelicerae of many species is widest near its base, but does not have the elongate, gracile quality originally intended by ‘attenuate’ (e.g. *Chileogovea jocasta*). Therefore, these two characters have been coded separately. Within the South African Pettalidae, no species have attenuate chelicerae, and all but *Parapurcellia silvicola*, *Parapurcellia monticola*, and *Purcellia illustrans* have chelicerae with the widest part of the second article near the articulation with the mobile digit.
19. Distal segment of chelicerae ornamented – (0) absent; (1) present (GB 4; DG 6; BG 7).
20. Dentition of the mobile digit of the chelicerae – (0) uniform; (1) dentition non-uniform with largest tooth occurring in the centre of the row of teeth; (2) jagged or bilobed with smaller lobe distal (GB 6; DG 7; BG 8).
21. Basal article of chelicerae with dorsal crest – (0) absent; (1) present (GB 7; G 5; DG 8; BG 9).
22. Basal article of chelicerae with ventral process – (0) absent; (1) present (GB 8; G 6; DG 9; BG 10).
23. Apodeme on chelicerae – (0) absent; (1) present (BG 11).
24. Basal article of chelicerae with a second ventral process – (0) absent; (1) present. In nearly all species, the first article of the chelicerae has no, or a single, ventral process. *Pettalus lampetides* and *Stylocellus ramblae* have a second ventral process on the basal article of their chelicerae.
25. Ornamentation of the basal cheliceral segment – (0) sparsely ornamented; (1) densely ornamented throughout most of its length; (2) densely ornamented centrally. The first segment of the chelicerae are densely ornamented in most cyphophthalmids, except for, in this dataset, *Troglosiro*, *Metagovea philipi*, and *Siro acaroides*, which are sparsely ornamented, and *Siro rubens* and *Suzukielus sauteri* which are densely ornamented centrally.
26. Palp trochanter with ventral process – (0) absent; (1) present (GB 10; G 7; DG 11; BG 12).
27. Ornamentation of second palp article – (0) absent; (1) less than half ornamented; (2) more than half ornamented. The degree of ornamentation on the second palp article shows considerable variation across and within the cyphophthalmid families. In the South African pettalids, the second palp article is less than half ornamented, except in the small species *Parapurcellia amatola* and *P. minuta* which have no ornamentation on the third palp article.
28. Ornamentation of third palp article – (0) absent; (1) present. Most cyphophthalmids have no ornamentation on the third palp article. Within Pettalidae, *Parapurcellia peregrinator*, *Rakaia lindsayi*, *Aoraki tumidata*, *Karripurcellia harveyi*, *K. peckorum*, and *Chileogovea oedipus* have ornamented third palp articles.
29. Solea in tarsus I – (0) absent; (1) present (GB 12; G 9; DG 13; BG 13).
30. Claw of leg I with modifications – (0) absent; (1) present. In a small number of cyphophthalmids, the claw of leg I is modified with lateral pegs or ridges. In this dataset, only *Suzukielus sauteri* has modifications to the claw of leg I; therefore this character is uninformative with respect to our phylogenetic analyses, but is retained in the matrix for reference.
31. Claw of leg II with modifications – (0) absent; (1) present (DG 16; BG 15).

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## Appendix 2. (continued)

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32. Claw of leg II with special row of teeth forming a comb – (0) absent; (1) present (DG 17; BG 16).
33. Claw of leg III with modifications – (0) absent; (1) present (DG 18; BG 17).
34. Claw of leg IV with modifications – (0) absent; (1) present (DG 19; BG 18).
35. Leg II ornamentation – (0) all segments smooth; (1) metatarsus and tarsus smooth; (2) metatarsus partially ornamented and tarsus smooth; (3) metatarsus ornamented and tarsus smooth; (4) metatarsus and dorso-basal part of the tarsus ornamented; (5) metatarsus ornamented and tarsus almost entirely ornamented (BG 14).
36. Ornamentation of tarsi III and IV – (0) absent; (1) present (DG 23; BG 22).
37. Male tarsus IV – (0) entire; (1) bisegmented; (2) bisegmented dorsally only (GB 15; G 11; DG 21; BG 19).
38. Adenostyle – (0) lamelliform; (1) ending in a tuft of setae; (2) fimbriate; (3) triangular and heavily sclerotized; (4) plumose; (5) digitiform; (6) bilobed tip (GB 16; G 12; DG 21; BG 20).
39. Adenostyle in the most-basal region of the tarsus – (0) absent; (1) present (DG 22; BG 21).
40. Rambla's organ – (0) absent; (1) present. In males of *Fangensis* (and some other stylocellids), the cuticle of tarsus IV is modified retrolaterally to form some sort of sensorial structure (Schwendinger and Giribet, 2005; Clouse *et al.*, 2009).
41. Spiracle shape – (0) circular; (1) open circle; (2) 'C' shaped (GB 21; G 14; DG 33; BG 31).
42. Exocrine glands on opisthosoma – (0) absent; (1) present (BG 32).
43. Position of opisthosomal exocrine glands – (0) on anterior sternal region; (1) on tergite VIII; (2) on tergite IX; (3) on tergites VIII and IX; (4) on tergite IX and anal plate (BG 33).
44. Orientation of anal gland opening – (0) posterior; (1) ventral. In cyphophthalmids with anal glands, the opening can be oriented either ventrally, so that it is fully visible in the ventral view of the animal, or posteriorly, so that it is visible in the posterior view, and only obliquely or tangentially in the ventral view. This character is best assessed by SEM. Within the Pettalidae, *Parapurcellia*, *Speleosiro*, *Austropurcellia* have posterior-oriented anal gland openings. *Purcellia*, *Chileogovea*, and *Aoraki tumidata* have ventral-oriented anal gland openings.
45. V-shape modification of sternites 6–8 – (0) absent; (1) present (G 15; DG 36; BG 34).
46. Sternite 8, 9, and tergite IX – (0) all free; (1) sternites 8 and 9 medially fused; (2) sternite 9 and tergite IX fused, but sternite 8 free; (3) all fused into corona analis; (4) sternites 8 and 9 completely fused, tergite IX free (GB 24; G 16; DG 37; BG 35).
47. Relative position of sternite 9 and tergite IX – (0) stylocellid type; (1) pettalid type (GB 25; DG 38; BG 26).
48. Male tergite IX – (0) entire; (1) bilobed (GB 26; G 17).
49. Longitudinal carina in male anal plate – (0) absent; (1) present (G 18; DG 39; BG 38).
50. Ornamentation in midline of male anal plate – (0) present; (1) absent (DG 40; BG 39).
51. Scopulae on anal plate – (0) absent; (1) present (GB 27; G 20; BG 40).
52. Position of origin of anal scopulae – (0) posterior margin; (1) anterior margin; (2) posterior ventral surface; (3) central ventral surface; (4) anterior ventral surface (BG 41).
53. Scopulae on male tergite IX – (0) absent; (1) present (BG 42).
54. Male tergite VIII bilobed – (0) absent; (1) present (GB 28; G 21; BG 44).
55. Large depression on midline of male anal plate – (0) absent (depression absent or small); (1) present. In animals with a depressed central region of the male anal plate, this region is either large, taking up approximately half or more of the area of the anal plate (*Purcellia* and *Speleosiro*) or small, taking up roughly a third of the area of the anal plate (*Parapurcellia*, *Rakaia*, *Aoraki longitarsa*, *A. tumidata*, and *Austropurcellia woodwardi*).
56. Two scopulae originating from each inner margin of tergite VIII – (0) absent; (1) present (G 22; BG 45).
57. Bilobed male anal plate – (0) absent; (1) present. In most pettalids, the male anal plate is depressed in the middle, or raised on the lateral posterior margins, appearing bilobed. This characteristic is absent, and the anal plate is entire, in *Pettalus*, *Chileogovea*, *Karripurcellia*, *Aoraki crypta*, *A. denticula*, *A. inerma*, *Austropurcellia scoparia*, and in the members of all other families.
58. Anterior opisthosomal sternites of male concave – (0) absent; (1) present. Most cyphophthalmids do not have concave anterior opisthosomal sternites. However, this character is present in *Troglosiro longifossa* and *T. ninqua*.
59. Male tergite VII bilobed – (0) absent; (1) present. In animals with deeply divided dorsal posterior regions, tergite VII can appear bilobed in the dorsal view. This is absent in most cyphophthalmids, but present in *Parapurcellia convexa*, *P. silvicola*, *Rakaia isolata*, *R. lindsayi*, *Aoraki denticula*, *A. longitarsa* and *A. tumidata*.
60. Extension of the scopulae – (0) absent; (1) present. In *Aoraki longitarsa*, and *Austropurcellia* the scopulae of the anal plate region are greatly extended, appearing as a tail.
61. Movable fingers of spermatopositor – (0) absent; (1) present (DG 45).
62. Ovipositor with sense organs – (0) absent; (1) present (GB 32; DG 46).
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### Appendix 3. Continuous morphological characters used in the phylogenetic analyses

Continuous characters used in our analysis are either 'simple' characters (a single morphometric ratio or direct measurement) or 'complex' characters comprising the first principal component of two or more simple characters across all taxa. Simple characters were collapsed into a single complex character when independence analysis indicated that they were correlated without any outlying examples across all taxa (see methods section). For diagrams of the measurements taken see de Bivort *et al.* (2010)

1. 'Overall size' – complex character encoding 49 different raw measurements see de Bivort *et al.*, 2010 for full list.
2. Width between posterior points if the posterior of the animal is bilobed, otherwise 0.
3. 'Prominence of tergite VIII' – complex character encoding the length and concavity of tergite VIII.
4. Anterior-to-posterior distance from the most posterior to the most anterior points of the posterior margin of tergite VII (tergite VII 'concavity').
5. Concavity of tergite VI.
6. Distance that the anal plate rises dorsally above the lateral-ventral margin of the posterior tergites, in lateral view.
7. Distance that the anal plate protrudes distally from the sternites surrounding it, in lateral view.
8. Concavity of sternite 6.
9. Anterior scutum margin concavity.
10. Distance from the anterior margin of the scutum to the highest dorsal point (dorsal crest) on the first segment of the chelicer.
11. Length-to-maximum width ratio of the prosoma + opisthosoma.
12. 'Bottom-heaviness' – complex character encoding the fractional distance from the anterior to the posterior at which the maximal prosomal width and maximal opisthosomal width are found.
13. Fractional distance from the anterior to the posterior of the maximal body thickness.
14. Fractional distance from the anterior to the posterior of the maximal tergite thickness.
15. Fractional distance from the anterior to the posterior of the maximal sternite thickness.
16. Maximal sternite thickness divided by the maximal body thickness.
17. Maximal tergite thickness divided by the maximal body thickness.
18. Ratio of the maximal prosomal width to the maximal opisthosomal width.
19. Minimal width of first tergite divided by the maximal opisthosomal width.
20. 'Laterality of projections of the scutum' – complex character encoding the distance from the midline to (one of) the most posterior point(s) divided by the maximal opisthosomal width, the height of the tip of the ozophore divided by the local thickness of the tergite, the distance from the prosomal margin to the ozophore tips divided by the prosomal width, and the distance from the prosomal margin to the ozophore lateral margins divided by the prosomal width.
21. Distance from the anterior prosomal margin to the ozophores, along the anterior-posterior axis.
22. Tergite VIII width divided by the width of the opisthosoma.
23. Maximal length of tergite VIII divided by the length of the scutum.
24. Maximal length of tergite VII divided by the length of the scutum.
25. Maximal length of tergite VI divided by the length of the scutum.
26. Concavity of tergite VIII divided by the length of the scutum.
27. Concavity of tergite VII divided by the length of the scutum.
28. Concavity of tergite VI divided by the length of the scutum.
29. Distance that the anal plate rises dorsally above the lateral-ventral margin of the posterior tergites, divided by the maximal body thickness.
30. Width of the anal plate divided by the maximal opisthosomal width.
31. Length of the anal plate divided by the total scutum length.
32. Thickness of the anal plate divided by the total thickness of the scutum.
33. Length-to-width ratio of the anal plate.
34. 'Size of the anal plate depression' – complex character encoding the width of the central depression of the anal plate divided by the width of the anal plate, the length of the depression divided by the length of the anal plate, the width of the unornamented central region of the anal plate divided by the width of the anal plate, and the fractional area of the anal plate that is modified compared to surrounding (typical) cuticle; 0 if these features are absent.
35. Width of the anal plate carina divided by the width of the anal plate, 0 if carina is absent.
36. Length of the anal plate carina divided by the length of the anal plate, 0 if carina is absent.
37. Length of the unornamented central region of the anal plate divided by the length of the anal plate, 0 if the anal plate is completely ornamented.
38. Length of the setae on the posterior margin of the anal plate divided by the length of the prosoma.
39. Length of the setae on the posterior margin of tergite IX divided by the length of the prosoma.
40. 'Anal plate anterior displacement' – complex character encoding the maximal length of tergite IX divided by the length of the scutum and the concavities of sternites 9, 8 and 7 each divided by the total length of the scutum.
41. Maximal length of sternite 9 divided by the length of the scutum.
42. Maximal length of sternite 8 divided by the length of the scutum.
43. Maximal length of sternite 7 divided by the length of the scutum.
44. Maximal length of sternite 6 divided by the length of the scutum.
45. Width of the fused suture between sternites 8 and 9 divided by the maximal width of the scutum, 0 if the sternites are free.
46. Concavity of sternite 6 divided by the length of the scutum.
47. Width of the spiracle divided by the maximal width of the scutum.
48. Distance between the spiracles divided by the maximal width of the scutum.
49. Degrees of the open portion of the spiracle, 0 if the spiracle is circular.
50. Width of the gonostome divided by the maximal width of the scutum.
51. Length of the gonostome divided by the length of the scutum.

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**Appendix 3.** (continued)

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52. Length-to-width ratio of the gonostome.
  53. 'Size of the sternal region' – complex character encoding the distance from the anterior margin of the scutum to the centre of the gonostome, divided by the length of the scutum, the distance from the anterior margin of the gonostome to the posterior margin of the palpal endites/mouthparts divided by the length of the scutum, and the length of the suture between the left and right coxae IV endites at the midline divided by the length of the scutum.
  54. Distance along the anterior-posterior axis from the centre of the gonostome to the lateral margin of sternite 1 divided by the length of the scutum.
  55. Length of the suture between the left and right coxae I endites at the midline divided by the length of the scutum.
  56. Length of the suture between the left and right coxae II endites at the midline divided by the length of the scutum.
  57. Length of the suture between the left and right coxae III endites at the midline divided by the length of the scutum.
  58. Length of the suture between the coxae II and III endites divided by the width of the prosoma.
  59. Maximal width across the coxal endites divided by the width of the prosoma.
  60. 'Length of anterior coxae' – complex character encoding the length of coxa I measured from the its most medial point of its endite to its most distal point ('radial length' of coxae I) divided by the width of the prosoma, and the radial length of coxae II divided by the width of the prosoma.
  61. 'Length of posterior coxae' – complex character encoding the radial length of coxae III divided by the width of the prosoma and the radial length of coxae IV divided by the width of the prosoma.
  62. Distance between the tips of coxa I and II divided by the length of the scutum.
  63. Distance between the tips of coxa II and III divided by the length of the scutum.
  64. Distance between the tips of coxa III and IV divided by the length of the scutum.
  65. Thickness of coxae IV divided by the maximal thickness of the body.
  66. Distance between the lateral margins of coxae IV divided by the width of the prosoma.
  67. Distance along the anterior-posterior axis from the most anterior point of the prosoma to the margin of the prosoma at the midline divided by the length of the scutum.
  68. Length of the first segment of the chelicer divided by the length of the scutum.
  69. Length of the second segment of the chelicer divided by the length of the scutum.
  70. 'Length of the mobile digit of the chelicer' – complex character encoding the length of the mobile digit of the chelicer divided by the length of the scutum, and the length of the mobile digit of the chelicer divided by the length of the second segment of the chelicer.
  71. Maximal width of the first segment of the chelicer divided by the width of the prosoma.
  72. Maximal width of the second segment of the chelicer divided by the width of the prosoma.
  73. 'First segment of the chelicer thickness' – complex character encoding the maximal thickness of the first segment of the chelicer divided by the maximal thickness of the body, and the minimum thickness of the first segment of the chelicer just proximal to the dorsal crest, divided by the maximal thickness of the body.
  74. Height of dorsal crest above the point proximal to the dorsal crest where the first segment of the chelicer attains its minimal thickness, divided the maximal thickness of the first segment of the chelicer.
  75. Distance from the proximal end of the first segment of the chelicer to the highest point of the dorsal crest divided by the length of the first segment of the chelicer.
  76. P to D position of maximal width of cheliceral segment 2.
  77. Distance along the midline from the anterior margin of the scutum to the dorsal crests divided by the length of the scutum.
  78. Length over which the second segment of the chelicer is ornamented divided by the length of the second segment of the chelicer, 0 if the second segment of the chelicer is unornamented.
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