# Pseudoscorpions of the family Feaellidae (Pseudoscorpiones : Feaelloidea) from the Pilbara region of Western Australia show extreme short-range endemism 

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#### Abstract

The phylogenetic relationships of the Australian species of Feaellidae are assessed with a molecular analysis using mitochondrial (CO1) and nuclear (ITS2) data. These results confirm the morphological analysis that three previously undescribed species occur in the Pilbara bioregion, which are named and described: Feaella (Tetrafeaella) callani, sp. nov., $F$. (T.) linetteae, sp. nov. and $F$. (T.) tealei, sp. nov. The males of these three species, as well as males of $F$. anderseni Harvey and other unnamed species from the Kimberley region of north-western Australia, have a pair of enlarged, thick-walled bursa that are not found in other feaellids. Despite numerous environmental impact surveys for short-range endemic invertebrates in the Pilbara, very few specimens have been collected, presumably due to their relictual distributions, restricted habitat preferences and low densities.


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## Introduction

With only a handful of named species, the Feaellidae are one of the smallest pseudoscorpion families, surpassed only by Pseudogarypidae with seven recent species and the monotypic Parahyidae (Harvey 2013). Feaellids have arguably the most unusual body shape of any pseudoscorpion, with short raptorial pedipalps and a highly thickened femur, a strongly rounded abdomen and deeply lobed anterior margin of the carapace (Figs 7, 18, 32, 33). Along with Pseudogarypidae, they belong to the superfamily Feaelloidea (e.g. Chamberlin 1931; Harvey 1992). Opinions on the relationships of the feaelloids have varied since they were first described, and they have been placed between the Garypidae and Cheliferidae in the Panctenodactyli by With (1906), as a member of the suborder Monosphyronida by Chamberlin (1931) and in the suborder

Neobisiinea (roughly equivalent with Chamberlin's Diplosphyronida) by Beier (1932). Weygoldt (1969: 129) summarised the dilemma posed by some of the morphological features found in feaellids, stating 'it seems that they are an old family that originated either close to the Heterosphyronida or somewhere between Heterosphyronida and Diplosphyronida. They should be considered, perhaps, as a separate suborder, but further taxonomic work is necessary before this question can be settled'. Harvey (1992) found feaelloids to group with the superfamily Chthonioidea, which together formed the suborder Epiocheirata, whereas in molecular analyses using three mitochondrial and nuclear genes, Murienne et al. (2008) recovered feaelloids as the sister-group to all other pseudoscorpions, and Arabi et al. (2012) found them to be sister to Iocheirata.

Since its inception (Ellingsen 1906), the Feaellidae has comprised a single genus, Feaella Ellingsen, 1906, but an unpublished Ph.D. thesis (Judson 1992) proposed a novel generic arrangement that divided Feaella into several separate genera. More recently, new genera have been recognised in south-east Asian caves (M. S. Harvey, unpubl. data) and from the Atlantic Forest biome in southern Brazil (Harvey et al. 2016). The genus Feaella is most speciose in Africa with nine species, plus individual species from the Seychelles, the Indian region and north-western Australia (Harvey 2013), and a single species from Eocene Baltic amber deposits (Henderickx and Boone 2014). The sole recognised Australian species, F. anderseni Harvey, 1989 was described from specimens collected in the rainforest thickets in the Kimberley region of north-western Australia (Harvey 1989). This species was placed in the subgenus Feaella (Tetrafeaella) Beier, 1955 by Harvey (1989) due to the presence of four lobes on the anterior carapaceal margin, but Judson (1992) found that it had sufficient differences from other feaellids to suggest that it should be placed in a new genus.

This study focuses on feaellid specimens that have been collected from the Pilbara region of Western Australia, some 1600 km south-west of the known distribution of $F$. anderseni. The epigean terrestrial invertebrate fauna of the Pilbara region is highly diverse, with numerous short-range endemic species (e.g. Johnson et al. 2004; Durrant et al. 2010; Volschenk et al. 2010; Harvey et al. 2012a; Smith et al. 2012; Harms and Framenau 2013; Castalanelli et al. 2014).

To aid in the discrimination of Feaella species in the Pilbara we also obtained mitochondrial and nuclear sequence data from each population and compared them to sequence data of $F$. anderseni. The combined data suggest the presence of three
species in the Pilbara, each of which is morphologically and genetically distinct from $F$. anderseni.

## Materials and methods

## Morphological techniques

The material examined for this study is lodged in the Western Australian Museum, Perth (WAM). The specimens were studied using temporary slide mounts prepared by immersing the specimens in lactic acid at room temperature for several hours to days, and mounting them on microscope slides with 10 - or $12-\mathrm{mm}$ coverslips supported by small sections of $0.25,0.35$ or 0.5 mm diameter nylon fishing line. After being studied, the specimens were rinsed and returned to $75 \%$ ethanol with the dissected portions placed in $12 \times 3 \mathrm{~mm}$ glass genitalia microvials (BioQuip Products, Rancho Dominguez, CA, USA). Specimens were examined with a Leica MZ16A dissecting microscope, and an Olympus BH2 (Shinjuku, Tokyo) or a Leica DM2500 (Wetzlar, Germany) compound microscope, the latter fitted with interference contrast, and illustrated with the aid of a drawing tube attached to the compound microscope. Measurements were taken at the highest possible magnification using an ocular graticule.

Terminology and mensuration mostly follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey 1992), chelicera (Judson 2007) and faces of the appendages (Harvey et al. 2012b). Length and breadth (or height) of segments are depicted above and below a slash ( / ). The following abbreviations are used: chelal trichobothria: fixed finger: $e b$, externo-basal trichobothrium; esb, externo-sub-basal trichobothrium; est, externo-subterminal


Fig. 1. A living adult male of Feaella (Tetrafeaella) linetteae, sp. nov., from George River, Millstream-Chichester National Park.
Table 1. Specimens used in the molecular analysis, with GenBank accession numbers

| Species | Depository and registration number | Type status | Locality | CO1 | ITS | 18 S | 28S |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Pseudogarypidae <br> Neopseudogarypus scutellatus Morris, 1948 | WAM T129596 |  | Tasmania: Launceston, Cataract Gorge, Cataract Lookout Track, $41^{\circ} 26^{\prime} 46^{\prime \prime} \mathrm{S}, 147^{\circ} 06^{\prime} 59^{\prime \prime} \mathrm{E}$ | KU696432 | KU696468 | - | KU696443 |
| Feaellidae <br> Feaella (Tetrafeaella) anderseni Harvey, 1989 | WAM T63158 |  | Western Australia: Bonaparte Archipelago, Steep Head Island, $14^{\circ} 26^{\prime} 48^{\prime \prime} \mathrm{S}, 125^{\circ} 59^{\prime} 40^{\prime \prime} \mathrm{E}$ | EU559500 | - | EU559355 | - |
| Feaella (Tetrafeaella) PSE101 | WAM T82526 |  | Western Australia: North Maret Island, $14^{\circ} 24^{\prime} 08.1^{\prime \prime} \mathrm{S}, 124^{\circ} 58^{\prime} 55.2^{\prime \prime} \mathrm{E}$ | KU696440 | - | - | - |
| Feaella (Tetrafeaella) PSE102 | WAM T66774 |  | Western Australia: Berthier Island, $14^{\circ} 31^{\prime} 07.3^{\prime \prime} \mathrm{S}, 124^{\circ} 59^{\prime} 10.2^{\prime \prime} \mathrm{E}$ | KU696441 | KU696469 | KU696456 | KU696444 |
|  | WAM T133407 |  | Western Australia: Berthier Island, $14^{\circ} 31^{\prime} 07.3^{\prime \prime} \mathrm{S}, 124^{\circ} 59^{\prime} 10.2^{\prime \prime} \mathrm{E}$ | KU696442 | KU696470 | KU696467 | KU696445 |
| Feaella (Tetrafeaella) callani, sp. nov. | WAM T131028 | Holotype male | Western Australia: Orebody $24, \sim 7 \mathrm{~km} \mathrm{~N}$ of Newman, $23^{\circ} 16^{\prime} 57.11^{\prime \prime} \mathrm{S}, 119^{\circ} 44^{\prime} 58.86^{\prime \prime} \mathrm{E}$ | KU696433 | - | KU696462 | KU696446 |
|  | WAM T131838 | Paratype tritonymph | Western Australia: Orebody $24, \sim 7 \mathrm{~km} \mathrm{~N}$ of Newman, $23^{\circ} 16^{\prime} 57.11^{\prime \prime} \mathrm{S}, 119^{\circ} 44^{\prime} 58.86^{\prime \prime} \mathrm{E}$ | KU696434 | KU696473 | KU696458 | KU696447 |
|  | WAM T131839 | Paratype tritonymph | Western Australia: Orebody $24, \sim 7 \mathrm{~km} \mathrm{~N}$ of Newman, $23^{\circ} 16^{\prime} 57.11^{\prime \prime} \mathrm{S}, 119^{\circ} 44^{\prime} 58.86^{\prime \prime} \mathrm{E}$ | KU696435 | KU696471 | KU696459 | KU696448 |
|  | WAM T131841 | Paratype tritonymph | Western Australia: Orebody 24, $\sim 7 \mathrm{~km} \mathrm{~N}$ of Newman, $23^{\circ} 16^{\prime} 57.11^{\prime \prime} \mathrm{S}, 119^{\circ} 44^{\prime} 58.86^{\prime \prime} \mathrm{E}$ | KU696436 | KU696472 | KU696460 | KU696449 |
| Feaella (Tetrafeaella) linetteae, sp. nov. | WAM T135841 | Holotype male | Western Australia: Millstream-Chichester National Park, George River, 2.2 km SE of Mt Montagu, $21^{\circ} 23^{\prime} 38^{\prime \prime} \mathrm{S}, 117^{\circ} 19^{\prime} 46^{\prime \prime} \mathrm{E}$ | - | KU696475 | KU696461 | KU696451 |
|  | WAM T135732 | Paratype deutonymph | Western Australia: Millstream-Chichester National Park, George River, 2.2 km SE of Mt Montagu, $21^{\circ} 23^{\prime} 38^{\prime \prime} \mathrm{S}, 117^{\circ} 19^{\prime} 46^{\prime \prime} \mathrm{E}$ | - | KU696474 | KU696463 | KU696450 |
| Feaella (Tetrafeaella) tealei, sp. nov. | WAM T63963 | Holotype male | Western Australia: Sulfur Springs, $21^{\circ} 08^{\prime} 17^{\prime \prime} \mathrm{S}, 119^{\circ} 11^{\prime} 49^{\prime \prime} \mathrm{E}$ | - | KU696476 | - | - |
|  | WAM T78157 | Paratype female | Western Australia: Sulfur Springs, $21^{\circ} 08^{\prime} 17^{\prime \prime} \mathrm{S}, 119^{\circ} 11^{\prime} 49^{\prime \prime} \mathrm{E}$ | - | KU696477 | KU696457 | KU696454 |
|  | WAM T133719 | Female | Western Australia: Corunna Station, $\sim 160 \mathrm{~km} \mathrm{SE}$ of Port Headland, $21^{\circ} 23^{\prime} 19.40^{\prime \prime} \mathrm{S}$, $119^{\circ} 37^{\prime} 06.50^{\prime \prime} \mathrm{E}$ | - | KU696480 | KU696466 | KU696455 |
|  | WAM T113769 (specimen lost after DNA extraction) | Unknown | Western Australia: $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site, $21^{\circ} 27^{\prime} 01.2^{\prime \prime} \mathrm{S}, 119^{\circ} 03^{\prime} 53.8^{\prime \prime} \mathrm{E}$ | KU696437 | KU696478 | KU696464 | KU696452 |
|  | WAM T113773 (specimen lost after DNA extraction) | Unknown | Western Australia: $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site, $21^{\circ} 27^{\prime} 01.2^{\prime \prime} \mathrm{S}, 119^{\circ} 03^{\prime} 53.8^{\prime \prime} \mathrm{E}$ | KU696439 | - | - | - |
|  | WAM T113774 | Tritonymph | Western Australia: $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site, $21^{\circ} 27^{\prime} 01.2^{\prime \prime} \mathrm{S}, 119^{\circ} 03^{\prime} 53.8^{\prime \prime} \mathrm{E}$ | KU696438 | KU696479 | KU696465 | KU696453 |


trichobothrium; et, externo-terminal trichobothrium; ib, internobasal trichobothrium; isb, interno-sub-basal trichobothrium; ist, interno-subterminal trichobothrium; it, interno-terminal trichobothrium; movable finger: $b$, basal trichobothrium; $s b$, sub-basal trichobothrium; st, subterminal trichobothrium; $t$, terminal trichobothrium; cheliceral setae: ebs, externobasal seta; es, external seta; gs, galeal seta; is, interior seta; $l s$, laminal seta; $s b s$, sub-basal seta; others: cs, coxal spines; pd, patellar depression; ss, specialised setae. The species are treated in alphabetical order.

## Molecular methods

For this study, tissue samples were taken from 15 specimens of Australian Feaellidae, including three specimens of Feaella from the Kimberley region and 12 specimens from the Pilbara region (Table 1). Legs were taken from one side of the specimen for DNA extraction. For all but two specimens, whole genomic DNA was extracted from tissue samples using DNeasy blood and tissue kits (Qiagen, Chadstone, Vic., Australia) following the manufacturer's instructions and eluting in $50 \mu \mathrm{~L}$ of elution buffer. For two specimens (WAMT113774 and WAMT113773), the ANDE method of genomic DNA extraction was used (Castalanelli et al. 2010). For each specimen, four gene regions were targeted for sequencing: cytochrome $c$ oxidase 1 (CO1) and three nuclear genes, 18 S rRNA, 28 S rRNA and the internal transcribed spacer subunit 2 (ITS2).

Amplification of CO1 used the primers LCO1490 and HCO2198 (Folmer et al. 1994). Amplifications were carried out in $25-\mu \mathrm{L}$ reactions, which included $2 \mu \mathrm{~L}$ of template DNA, $0.2 \mu \mathrm{M}$ of each primer, 1 mM dNTPs and 3 mM $\mathrm{MgCl}_{2} 1 \times$ buffer and one unit of taq (MyTaq). The reactions were run on a 'touch-up' program: $95^{\circ} \mathrm{C}$ for 5 min ; then seven cycles of $95^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 40^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for 60 s ; then 35 cycles of $95^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 50^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for 60 s ; with a final extension at $72^{\circ} \mathrm{C}$ for 10 min . Amplification of the complete 18 S rRNA ( $\sim 1.8 \mathrm{~kb}$ ) was carried out in three fragments, using the primer pairs $1 \mathrm{~F} / 5 \mathrm{R}, 3 \mathrm{~F} / 18 \mathrm{Sbi}$ and 18Sa2.0/9R (Giribet et al. 1996; Whiting et al. 1997). Amplification of 28 S rRNA used the primers 28 Sa (Nunn et al. 1996) and 28SpsR1 (Murienne et al. 2008). For 18S and 28 S amplifications the same sample reaction concentrations were used as for CO1, but with the relevant primer pair. All amplifications were run on the same protocol: $95^{\circ} \mathrm{C}$ for 5 min ; then 35 cycles of $95^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 49^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for 60 s ; with a final extension at $72^{\circ} \mathrm{C}$ for 10 min . Amplification of ITS2 used the primers 5.8S and 28S (Rix et al. 2010) with the same sample reaction concentrations as above.

Products were visualised on the eGel Electrophoresis system (Life Technologies, Scoresby, Vic., Australia), on 2\% agarose gels with ethidium bromide. Bidirectional sequencing was carried out at the Australian Genome Research Facility. For the newly prepared specimens, sequences and workflows were

Figs 2-5. Collecting sites of Pilbara Feaella species: 2, rocky gorge north of Newman, the type locality of $F$. (Tetrafeaella) callani, sp. nov.; 3, 4, rocky hillside near George River, Millstream-Chichester National Park, the type locality of $F$. (Tetrafeaella) linetteae, sp. nov.; 5, rocky outcrop near Sulfur Springs, the type locality of $F$. (Tetrafeaella) tealei, sp. nov. (Fig. 2 courtesy of Shae Callan, other images by M. Harvey.)
managed in the Geneious software package (version 7.1.5) (Kearse et al. 2012) using the LIMS Biocode plug-in (http:// www.mooreabiocode.org). Editing and alignment also occurred in Geneious.

The tree was rooted on the pseudogarypid Neopseudogarypus scutellatus Morris, 1948 of the family Pseudogarypidae, which is the only other family included in the superfamily Feaelloidea (e.g. Chamberlin 1931; Harvey 1992; Murienne et al. 2008). DNA extraction, amplification and sequencing of this specimen were carried out in this study. We also included previously published sequence data for a specimen of Feaella anderseni (Table 1) that were originally published by Murienne et al. (2008).

The datasets were aligned separately for each gene using the MUSCLE plug-in in Geneious, with default settings (Edgar 2004). The CO1 alignment was translated to ensure the absence of stop codons. Due to the phylogenetic breadth of the dataset, the ribosomal gene alignments had many regions that were difficult to align. As such, the program gBlocks was used to remove phylogenetically uninformative sites (Castresana 2000; Talavera and Castresana 2007). Smaller final blocks and gaps were allowed in the final alignment. Initially, the 28 S and ITS2 alignments were 1122 bp and 425 bp , respectively. After removing uninformative sites, the alignments were 1090 bp and 407 bp , respectively. Both alignments were compared and no differences in topology or confidence were observed in the final trees. The final trees shown here are from the datasets that have had non-informative sites removed using gBlocks.

The alignments were run through jmodeltest 2.1.4 (Darriba et al. 2012) to choose the most appropriate model of evolution, which was GTR + G for all alignments. Trees were built for each alignment separately, using the RaxML plug-in (version 7.2.8) (Stamatakis 2006) in Geneious using the default settings with 1000 bootstrap replicates. A concatenated alignment was also built and analysed using RaxML, with partitions relating to the different gene regions.

## Results and discussion

## Molecular analysis

The 18 S gene region showed only a single variable site, for one specimen, and so was not analysed any further. The CO1 gene region failed to amplify for five of the 15 ingroup specimens (Table 1), including both specimens of $F$. linetteae, necessitating the inclusion of the ITS2 region to supplement the CO1 data. The internal transcribed spacer region has been shown to be a useful species level marker in other arachnids (e.g. Schwendinger and Giribet 2005; Ben-David et al. 2007; Harvey et al. 2008; Agnarsson 2010; Rix et al. 2010; McHugh et al. 2014; Bragagnolo et al. 2015). It successfully amplified in all species, for 13 specimens, and was highly variable, providing another line of evidence supporting the morphological conclusions. The 28 S rRNA region also amplified in 12 of 15 specimens, and was variable. Divergences among the specimens at CO1 are shown in Table 2, and show that the two Pilbara Feaella that were sequenced ( $F$. tealei and $F$. callani) were $18.5 \%$ divergent. Due to gaps in the alignments, even after uninformative sites were removed using gBlocks, genetic distance (p-distance) was not calculated for ITS2 and 28 S.
Table 2. Pairwise divergence values (p-distance) for CO1

| Species | Specimen | Feaella tealei <br> WAM <br> T113769 | $\begin{gathered} \text { Feaella } \\ \text { tealei } \\ \text { WAM } \\ \text { T113773 } \end{gathered}$ | Feaella <br> tealei <br> WAM <br> T113774 | Feaella callani <br> WAM <br> T131028 | Feaella callani <br> WAM <br> T131838 | Feaella callani <br> WAM <br> T131839 | Feaella callani <br> WAM <br> T131841 | $\begin{gathered} \text { Feaella } \\ \text { PSE102 } \\ \text { WAM } \\ \text { T133407 } \end{gathered}$ | Feaella anderseni <br> WAM <br> T63158 | Feaella <br> PSE102 <br> WAM <br> T66774 | Feaella <br> PSE101 <br> WAM <br> T82526 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Feaella tealei | WAM T113773 | 0.0000 |  |  |  |  |  |  |  |  |  |  |
| Feaella tealei | WAM T113774 | 0.0000 | 0.0000 |  |  |  |  |  |  |  |  |  |
| Feaella callani | WAM T131028 | 0.1853 | 0.1853 | 0.1853 |  |  |  |  |  |  |  |  |
| Feaella callani | WAM T131838 | 0.1853 | 0.1853 | 0.1853 | 0.0000 |  |  |  |  |  |  |  |
| Feaella callani | WAM T131839 | 0.1853 | 0.1853 | 0.1853 | 0.0000 | 0.0000 |  |  |  |  |  |  |
| Feaella callani | WAM T131841 | 0.1853 | 0.1853 | 0.1853 | 0.0000 | 0.0000 | 0.0000 |  |  |  |  |  |
| Feaella PSE102 | WAM T133407 | 0.1836 | 0.1836 | 0.1836 | 0.2087 | 0.2087 | 0.2087 | 0.2087 |  |  |  |  |
| Feaella anderseni | WAM T63158 | 0.1953 | 0.1953 | 0.1953 | 0.2053 | 0.2053 | 0.2053 | 0.2053 | 0.1770 |  |  |  |
| Feaella PSE102 | WAM T66774 | 0.1853 | 0.1853 | 0.1853 | 0.2087 | 0.2087 | 0.2087 | 0.2087 | 0.0033 | 0.1770 |  |  |
| Feaella PSE101 | WAM T82526 | 0.1770 | 0.1770 | 0.1770 | 0.2104 | 0.2104 | 0.2104 | 0.2104 | 0.1336 | 0.1903 | 0.1302 |  |
| Neopseudogarypus scutellatus | WAM T129596 | 0.2471 | 0.2471 | 0.2471 | 0.2554 | 0.2554 | 0.2554 | 0.2554 | 0.2638 | 0.2771 | 0.2621 | 0.2855 |

All three single-gene gene trees supported the independent evolutionary history of the three new species (Figs S1-S3); however, the relationships among species differed between genes. The concatenated alignment gene tree provided strong support for the three new species, and supported the monophyly of the Pilbara species (Fig. 6). However, only 28S strongly supported the monophyly of the Pilbara species (Fig. S3).

The specimens originally identified as $F$. anderseni were sourced from three separate locations in the Kimberley region and showed deep divergences, suggesting the presence of three distinct species. At CO1, these specimens were between $13 \%$ and $20 \%$ divergent (Table 2). We could find no significant morphological differences between the population from Steep Head Island and the holotype of $F$. anderseni (type locality Cape Bougainville), some 35 km away. The other populations, from North Maret Island and Berthier Island, are here termed Feaella PSE101 and $F$. PSE102, respectively.

## Systematics

Family FEAELLIDAE Ellingsen
Genus Feaella Ellingsen
Feaella Ellingsen, 1906: 260.
Type species: Feaella mirabilis Ellingsen, 1906, by monotypy.

## Remarks

Pending the proposed reclassification of the genus Feaella into multiple genera (Judson 1992), the Australian species are
here described in Feaella and the subgenus Tetrafeaella, following the most recent taxonomic publications of the family. Feaella (Tetrafeaella) is easily distinguished from most other feaellid genera and subgenera by the presence of four protuberances on the anterior margin of the carapace, whereas Feaella (Difeaella) Beier, 1964 and Iporangella Harvey, Andrade \& Pinto-da-Rocha, in press, have only two such protuberances, and Feaella (Feaella) has six (e.g. Ellingsen 1906; Beier 1955, 1964; Harvey et al. in press). Feaella (Tetrafeaella) differs from the only other named feaellid taxon with four anterior lobes, Scaleniella Harvey, in press, by the lack of any modifications to coxae II and III, and by the enlarged pleural sclerites (Harvey submitted).

The number of blades in the rallum of the chelicera varies within the Feaelloidea. All species of Pseudogarypidae bear two blades (e.g. Morris 1948; Benedict and Malcolm 1978; Muchmore 1981), as do both species of the genus Scaleniella from south-east Asia (Harvey submitted). Ellingsen (1906) claimed that the rallum was absent in F. mirabilis, but With (1908) found one of Ellingsen's specimens to have a singlebladed rallum. Heurtault-Rossi and Jézéquel (1965) noted that the specimens from Cote d'Ivoire that they identified as F. mirabilis (but which actually belong to an undescribed species, see Judson (1992)) lacked a rallum. A single-bladed rallum was also found in F. anderseni (Harvey 1989) and Iporangella orchama Harvey, Andrade, Pinto-da-Rocha, 2016 from Brazil (Harvey et al. in press). The published descriptions of all other species fail to mention the number of blades. All three species described here from the Pilbara also lack a rallum, which


Fig. 6. Maximum likelihood phylogeny of Australian Feaellidae, using the concatenated dataset of CO1 and ITS2. Bootstrap values are presented for all nodes. See 'Materials and methods' for more details.
is a significantly different morphology from the single-bladed rallum found in $F$. anderseni.

## Subgenus Feaella (Tetrafeaella) Beier

Feaella (Tetrafeaella) Beier, 1955: 546.
Type species: Feaella mucronata Tullgren, 1907, by subsequent designation of Harvey (1991: 231).

## Feaella (Tetrafeaella) anderseni species-group

## Diagnosis

Species of the Feaella (Tetrafeaella) anderseni species-group differ from all other feaellids by the pair of enlarged, thick-walled bursa in the male genitalia (Fig. 17).

## Description

Adult
Most setae short, inconspicuous, slightly curved and acuminate.

Chelicera (Figs 14, 29, 40). Hand with four large and several small setae; is and $l s$ adjacent to each other; movable finger with one subdistal seta; with two dorsal and one ventral lyrifissures; rallum absent; lamina exterior absent; movable finger short.

Pedipalp (Figs 9, 24, 36). Trochanter with prolateral conical protuberance, femur with prolateral process, chela tubular. Fixed chelal finger and hand with eight trichobothria, movable chelal finger with four trichobothria (Figs 10, 25, 36): esb and est situated midway on retrolateral face; ib, isb and ist situated basally in straight row; $e b$ and it situated subdistally, very close to each other; et situated distally, much closer to diploid trichobothrium ( $d t$ ) than to $i t$; $d t$ situated distally; st situated sub-basally; $t$ adjacent to $s b$; movable chelal finger with several specialised, lanceolate setae distal to $b$. Venom apparatus absent. Chelal teeth large and diastemodentate.

Carapace (Figs 7, 21, 34, 35). Anterior margin with four equal-sized lobes; with two pairs of eyes situated on tubercles away from anterior carapaceal margin; all eyes with tapetum; with posterior furrow; without postero-lateral processes.

Coxal region (Figs 12, 27, 39). Median maxillary lyrifissure situated basally near clivus; posterior maxillary lyrifissure absent. Coxa I without depression, with 3-4 stout nonalveolate processes (coxal spines) posteriorly (Figs 13, 28, 39); coxa II without coxal spines.

Legs (Figs 15, 30, 41, 43). Patellae of all legs with shallow dorsal depression (Figs 16, 42); femora III and IV shorter than patellae III and IV; femora III and IV not solidly fused with patellae III and IV, respectively; metatarsi and tarsi fused; subterminal tarsal setae acuminate; sub-ungual spine present; arolium slightly shorter than claws.

Abdomen (Figs 7, 23, 32, 33). Ovoid; tergite XI and sternite XI fused; tergite XII and sternite XII (anal sclerites) strongly sclerotised; tergite XII with two setae or with setae absent; anal region with raised circular rim. Sternite II of female absent (Fig. 45); sternite III of male and female slender (Figs 17, 31, 44). Pleural membrane with numerous sclerotised
pleural platelets in two rows (Figs 7, 8, 20, 23, 32, 33), most platelets with a single seta.

Genitalia. Male with a pair of enlarged, thick-walled bursa (Fig. 17); median genital sac ovoid. Female with large gonosac, covered with scattered pores.

## Tritonymph

Pedipalp. Fixed chelal finger with seven major trichobothria, plus diploid trichobothria ( $d t$ ), movable chelal finger with three trichobothria (Figs 11, 38); isb and $s b$ absent; $e s b$ and est situated midway on retrolateral face; $i b$ and ist situated basally; eb and it situated medially; et situated closer to diploid trichobothrium ( $d t$ ) than to $i t$; $d t$ situated distally; $t$ situated closer to $s t$ than to $b$, or midway between st than to $b$; movable chelal finger with several specialised, lanceolate setae distal to $b$.

Carapace. Four anterior lobes; two pairs of eyes.

## Deutonymph

Pedipalp. Fixed chelal finger with six major trichobothria, plus diploid trichobothria $(d t)$, movable chelal finger with three trichobothria (Fig. 26); esb, isb, sb and st absent; est situated midway on retrolateral face; ib and ist situated basally; $e b$ and it situated medially; et situated closer to diploid trichobothrium ( $d t$ ) than to $i t ; d t$ situated distally; movable chelal finger with several specialised, lanceolate setae distal to $b$.

Carapace. Four anterior lobes; two pairs of eyes.

## Remarks

The three new species described below are morphologically very similar to each other and form a monophyletic group based on molecular sequence data (Fig. 6). The pair of enlarged thickwalled bursa in the male genitalia (Fig. 17) is a highly unusual feature and is also shared by $F$. anderseni and other undescribed species from the Kimberley region of north-western Australia (M. S. Harvey, unpubl. data).

Feaella (Tetrafeaella) callani, sp. nov.
(Figs 8-17)
http://zoobank.org/urn:lsid:zoobank.org:act:030655B7-8655-4127-9949-E16AA8552CC5

## Material examined

Holotype. Western Australia: $\widehat{\jmath}$, Orebody 24, $\sim 7 \mathrm{~km} \mathrm{~N}$ of Newman, $23^{\circ} 16^{\prime} 57.11^{\prime \prime} \mathrm{S}, 119^{\circ} 44^{\prime} 58.86^{\prime \prime} \mathrm{E}, 29 . \mathrm{iv}-7 . v .2013$, under rocks, S. Callan (WAM T131028).

Paratypes. Western Australia: four tritonymphs, collected with holotype (WAM T131838-131841).

## Diagnosis

Feaella callani differs from the other species of the Feaella anderseni group as follows: from $F$. anderseni by the lack of a rallum on the chelicera; from $F$. linetteae and $F$. tealei by smaller size (e.g. chela (with pedicel) length 0.56 mm ( ${ }^{\top}$ ) compared with $0.635-0.665 \mathrm{~mm}\left(\delta^{\top}\right)$ and $0.62-0.645 \mathrm{~mm}$ ( $Q$ ) for the other species), less circular abdomen and the stouter tergites (e.g. half-tergite VI ( ${ }^{\top}$ ) $2.94 \times$ longer than broad, but $3.00-3.30\left({ }^{\top}\right)$


Figs 7, 8. Feaella (Tetrafealla) callani, sp. nov., male holotype (WAM T131028) (before dissection): 7, dorsal; 8, ventral.
and $\left.3.10-3.13 \mathrm{~mm}()^{( }\right)$in the other two species); and from $F$. linetteae by the position of trichobothrium $s b$, which is situated slightly basally to $t$ (Fig. 10), whereas it is situated opposite $t$ in $F$. linetteae (Fig. 25).

## Description

## Adult male

Colour. All sclerotised portions deep red-brown (Figs 7, 8). All sclerotised portions coarsely tuberculate.

Setae. Most setae short, inconspicuous, slightly curved and acuminate.

Cerotegument. Most surfaces covered with very thin cerotegument.

Chelicera (Fig. 14). Hand with four large and four small setae; is and $l s$ adjacent to each other; setae es and $s b s$ with single denticle, others acicular; movable finger with one subdistal seta; galea very thick, without rami; fingers without teeth; rallum absent; serrula exterior with $\sim 16$ blades; lamina exterior absent.

Pedipalp (Fig. 9). Trochanter with prolateral conical protuberance, $2.12 \times$ longer than broad, femur very robust with pronounced triangular process on prolateral corner near base, $1.77 \times$, patella conical $2.87 \times$, chela tubular, chela (with pedicel) $4.31 \times$, chela (without pedicel) $3.88 \times$, hand (without pedicel) $0.58 \times$ longer than broad. Fixed chelal finger and hand with eight major trichobothria, plus diploid trichobothrium $(d t)$, movable chelal finger with four trichobothria (Fig. 10): $e s b$ and est situated midway on retrolateral face; $i b$, isb and ist situated basally in straight row; eb and it situated subdistally;
et situated closer to diploid trichobothrium ( $d t$ ) than to $i t ; d t$ situated distally; $s b$ situated slightly basally to $t ; b$ situated closer to $t$ than to finger tip. Venom apparatus absent. Chelal hand very small; retrolateral condyle small and rounded; with dorsal protuberance at base of finger. Chelal teeth large, retrorse and diastemodentate: fixed finger with eight curved, marginal teeth and 11 prolateral teeth; movable finger with 11 curved, marginal teeth and 10 prolateral teeth. Movable chelal finger with several specialised, lanceolate setae distal to $b$ (Fig. 10).

Carapace (Fig. 7). Anterior margin with four lobes, median pair same size as lateral pair; with two lobes between eyes; lateral margins nearly parallel, slightly widened medially; $1.36 \times$ longer than broad; with two pairs of eyes situated on tubercles away from anterior carapaceal margin; all eyes with tapetum; with numerous inconspicuous setae; with a pair of postero-lateral processes; shallow posterior furrow present.

Coxal region (Figs 12, 13). Pedipalpal coxa with small basal lateral processes; with numerous small setae; without medial depression or coxal spines; median maxillary lyrifissure basal, situated near clivus; posterior maxillary lyrifissure absent. Coxa I without depression, with 3-4 stout non-alveolate processes (coxal spines) posteriorly; coxa II without coxal spines.

Legs (Fig. 15). Patellae I and II shorter than femora I and II, each patella with shallow dorsal depression (Fig. 16); femora III and IV much shorter than patellae III and IV; femora III and IV not solidly fused with patellae III and IV, respectively; metatarsi and tarsi fused; tarsi long and slender, without tactile seta; subterminal tarsal setae acuminate; sub-ungual spine present; claws smooth; arolium much shorter than claws, with fimbriate distal margin.


Figs 9-17. Feaella (Tetrafeaella) callani, sp. nov., male holotype (WAM T131028) unless stated otherwise: 9, left pedipalp, dorsal; 10, right chela, lateral; 11, left chela, lateral, tritonymph paratype (WAM T131838); 12, right coxae I-IV, ventral; 13, coxae I showing coxal spines, ventral; 14 , left chelicera, dorsal; 15 , left leg IV, lateral; 16 , left patella IV, lateral; 17 , male genitalia, ventral. Scale bars $=0.1 \mathrm{~mm}($ Figs 13,14$)$, 0.2 mm (Figs 10, 12, 17), 0.25 mm (Figs 9, 11, 15).

Abdomen (Figs 7, 8). Longer than broad, somewhat ovoid; tergites II-IX and sternites IV-X with distinct median suture lines; half-tergite VI $2.94 \times$ longer than broad; tergite XI and sternite XI fused; tergite XII and sternite XII (anal sclerites) strongly sclerotised; most segments with numerous setae, generally arranged in a single irregular row along posterior margin of sclerite; tergite XII and sternite XII each with two setae; anal region with raised circular rim. Most setae very small and inconspicuous; setae of sternites II and III longer. Pleural membrane with 16 pairs of sclerotised pleural platelets in two rows. First pair of spiracles connected to anterior margin of sternite IV; second pair of spiracles connected to anterior margin of sternite V .

Genitalia (Fig. 17). Pair of enlarged, thick-walled bursa; median genital sac long and ovoid, extending to sternite V .

Dimensions (mm). Male: holotype: body length 2.11; abdomen breadth (without pleura) 0.95. Pedipalp: trochanter $0.275 / 0.13$, femur $0.575 / 0.325$, patella $0.43 / 0.15$, chela (with pedicel) $0.56 / 0.13$, chela (without pedicel) 0.505 , hand (without pedicel) length 0.075 , movable finger length 0.37 . Chelicera $0.22 / 0.13$; movable finger 0.095 . Carapace $0.58 / 0.425$; anterior eye diameter 0.10 , posterior eye diameter 0.07 . Leg I: femur $0.23 / 0.08$, patella $0.205 / 0.0 .85$, tibia $0.175 / 0.065$, tarsus $0.285 / 0.055$. Leg IV: femur $0.205 / 0.09$, patella $0.31 / 0.11$, tibia $0.36 / 0.065$, tarsus $0.39 / 0.055$.

## Tritonymph

Pedipalp. Femur $1.89 \times$ longer than broad, patella $2.79 \times$, chela (with pedicel) $4.25 \times$, chela (without pedicel) $4.08 \times$, hand $0.71 \times$ longer than broad. Fixed chelal finger with seven major trichobothria, plus diploid trichobothrium $(d t)$, movable chelal finger with three trichobothria (Fig. 11); isb and $s b$ absent; $e s b$ and est situated midway on retrolateral face; ib and ist situated basally on prolateral face; eb and it situated subdistally; et situated closer to diploid trichobothrium (dt) than to $i t ; d t$ situated distally; st situated sub-basally, $t$ and $b$ situated subdistally (Fig. 11).

Carapace. $1.19 \times$ longer than broad; with four anterior lobes; with two pairs of eyes.

Coxal region. Coxa I without depression, with 2-3 stout non-alveolate processes (coxal spines) posteriorly; coxa II without coxal spines.

Legs. Much as in adult.
Dimensions (mm), WAM T113838. Body length 2.00. Pedipalp: femur $0.54 / 0.285$, patella $0.39 / 0.14$, chela (with pedicel) $0.51 / 0.12$, chela (without pedicel) 0.49 , hand length 0.085 , movable finger length 0.365 . Carapace $0.47 / 0.395$.

## Remarks

Feaella callani has been found at a single locality in the southeastern Pilbara region, near the town of Newman (Fig. 46).

## Etymology

This species is named for Shae Callan, collector of the specimens.
Feaella (Tetrafeaella) linetteae, sp. nov.
(Figs 1, 18-31)
http://zoobank.org/urn:lsid:zoobank.org:act:1C8CF991-7611-49B2-8B1
D-7B7BA175D884

## Material examined

Holotype. Western Australia: $\widehat{0}$, Millstream-Chichester National Park, George River, 2.2 km SE of Mt Montagu, $21^{\circ} 23^{\prime} 38^{\prime \prime} \mathrm{S}, 117^{\circ} 19^{\prime} 46^{\prime \prime} \mathrm{E}, 1181 \mathrm{~m}$, under rock, 26.iii.2015, M.S. Harvey, J. Huey (WAM T135841).

Paratype. Western Australia: 1 deutonymph, same data as holotype expect 23.iii.2015, L. Umbrello (WAM T135732).

## Diagnosis

Feaella linetteae differs from the other species of the Feaella anderseni group by the position of trichobothrium $s b$, which is opposite $t$ (Fig. 25), whereas it is situated between st and $t$ in other species (Figs 10, 37). It further differs from them as follows: from $F$. anderseni by the lack of a rallum on the chelicera; and from $F$. callani by its larger size (e.g. chela (with pedicel) length 0.635 mm ( $\widehat{o}^{\top}$ ), compared with 0.56 mm ( ${ }^{\top}$ ) in F. callani); slightly more rounded abdomen (Fig. 23), and the narrower tergites (e.g. half-tergite VI $3.30 \times\left(\mathrm{o}^{\mathrm{o}}\right)$ longer than broad, but $2.94 \times$ ( ${ }^{*}$ ) in $F$. callani).

## Description

## Adult female

Colour. All sclerotised portions deep red-brown (Figs 18-23). All sclerotised portions coarsely tuberculate.

Setae. Most setae short, inconspicuous, slightly curved and acuminate.

Cerotegument. Most surfaces covered with very thin cerotegument.

Chelicera (Fig. 29). Hand with four large and five small setae; is and $l s$ adjacent to each other; seta $s b s$ with single denticle, others acicular; movable finger with one subdistal seta; galea very thick, without rami; fingers without teeth; rallum absent; serrula exterior with $\sim 16$ blades; lamina exterior absent.

Pedipalp (Fig. 24). Trochanter with large blunt protuberance, femur very robust with pronounced triangular process on prolateral corner near base, $2.06 \times$ longer than broad, patella conical, $3.09 \times$, chela tubular, chela (with pedicel) $4.54 \times$, chela (without pedicel) $4.29 \times$, hand (without pedicel) $0.61 \times$ longer than broad. Fixed chelal finger and hand with eight major trichobothria, plus diploid trichobothrium ( $d t$ ), movable chelal finger with four trichobothria (Fig. 25): esb and est situated midway on retrolateral face; ib, isb and ist situated basally in straight row; eb, it and et situated subdistally; $e t$ situated closer to diploid trichobothrium $(d t)$ than to $i t ; d t$ situated distally; sb opposite $t ; b$ situated slightly closer to $t$ and $s b$ than to finger tip. Venom apparatus absent. Chelal hand very small; retrolateral condyle small and rounded; with dorsal protuberance at base of finger. Chelal teeth large, retrorse and diastemodentate: fixed finger with 12 curved, marginal teeth and 16 prolateral teeth; movable finger with 22 curved, marginal teeth and 11 prolateral teeth. Movable chelal finger with $\sim 6$ specialised, lanceolate setae distal to $b$ (Fig. 25).

Carapace (Fig. 21). Anterior margin with four lobes, median pair same size as lateral pair; with two lobes between eyes; lateral margins nearly parallel, slightly widened medially; $1.38 \times$ longer than broad; with two pairs of eyes situated on


Figs 18-23. Feaella (Tetrafealla) linetteae, sp. nov., male holotype (WAM T135841) (before dissection): 18, dorsal; 19, ventral; 20, lateral; 21, cephalothorax, dorsal; 22, cephalothorax, ventral; 23, abdomen, dorsal.
tubercles away from anterior carapaceal margin; all eyes with tapetum; with numerous inconspicuous setae; without posterolateral processes; shallow posterior furrow present.

Coxal region (Figs 22, 27). Pedipalpal coxa: with small basal lateral processes; with numerous small setae; without medial depression or coxal spines; median maxillary lyrifissure basal, situated near clivus; posterior maxillary lyrifissure absent. Coxa I without depression, with three stout non-alveolate processes (coxal spines) posteriorly (Fig. 28); coxa II without coxal spines.

Legs (Fig. 30). Patellae I and II shorter than femora I and II, each patella with shallow dorsal depression; femora III and IV much shorter than patellae III and IV; femora III and IV not solidly fused with patellae III and IV, respectively; metatarsi and tarsi fused; tarsi long and slender, without tactile seta; subterminal
tarsal setae acuminate; sub-ungual spine present; claws smooth; arolium much shorter than claws, with fimbriate distal margin.

Abdomen (Fig. 23). Longer than broad, somewhat ovoid; tergites II-IX and sternites IV-X with distinct median suture lines; half-tergite VI $3.30 \times$ longer than broad; tergite XI and sternite XI fused; tergite XII and sternite XII (anal sclerites) strongly sclerotised; most segments with numerous setae, generally arranged in a single irregular row along posterior margin of sclerite; tergite XII and sternite XII each with two setae; anal region with raised circular rim. Most setae very small and inconspicuous; setae of sternite III longer (Fig. 31). Pleural membrane with 16 pairs of sclerotised pleural platelets in two rows (Fig. 20). First pair of spiracles connected to anterior margin of sternite IV; second pair of spiracles connected to anterior margin of sternite V .


Figs 24-31. Feaella (Tetrafeaella) linetteae, sp. nov., male holotype (WAM T135841) unless stated otherwise: 24, left pedipalp, dorsal; 25, left chela, lateral; 26, left chela, lateral, deutonymph paratype (WAM T135732); 27, right coxae I-IV, ventral; 28, coxae I showing coxal spines, ventral; 29, left chelicera, dorsal; 30 , right leg IV, lateral; 31, genital sternites, ventral. Scale bars $=0.1 \mathrm{~mm}$ (Figs 28, 29); 0.2 mm (Figs 25, 26, 31); 0.25 mm (Figs 24, 27, 30).

Genitalia. Pair of enlarged, thick-walled bursa; median genital sac extending to segment IV.

Dimensions (mm). Holotype male: body length 2.13; abdomen breadth (without pleura) 1.08. Pedipalp: trochanter $0.39 / 0.245$, femur $0.66 / 0.32$, patella $0.495 / 0.16$, chela (with
pedicel) $0.635 / 0.14$, chela (without pedicel) 0.60 , hand (without pedicel) length 0.085 , movable finger length 0.47 . Chelicera $0.265 / 0.17$; movable finger 0.11 . Carapace $0.60 / 0.435$; anterior eye diameter 0.055 , posterior eye diameter 0.06 . Leg I: femur $0.27 / 0.08$, patella $0.24 / 0.085$, tibia $0.21 / 0.07$, tarsus $0.33 / 0.05$.

Leg IV: femur 0.25/0.09, patella $0.345 / 0.105$, tibia $0.435 / 0.065$, tarsus 0.415/0.06.

## Deutonymph

Pedipalp. Femur $1.84 \times$ longer than broad, patella $2.63 \times$, chela (with pedicel) $4.32 \times$, chela (without pedicel) $4.05 \times$, hand $0.68 \times$ longer than broad. Fixed chelal finger with six major trichobothria, plus diploid trichobothrium ( $d t$ ), movable chelal finger with two trichobothria (Fig. 26); esb, isb, st and $s b$ absent; $e s b$ and est situated midway on retrolateral face; $i b$ and ist situated basally on prolateral face; eb, it and et situated subdistally; et situated closer to $d t$ than to $i t ; d t$ situated distally; $t$ and $b$ present (Fig. 26); two lanceolate setae situated distal to $b$.

Carapace. $1.19 \times$ longer than broad; with four anterior lobes; with two pairs of eyes.

Coxal region. Coxa I without depression, with three stout non-alveolate processes (coxal spines) posteriorly; coxa II without coxal spines.

Legs. Much as in adult.
Dimensions (mm), paratype. Body length 1.60. Pedipalp: femur $0.405 / 0.22$, patella $0.315 / 0.12$, chela (with pedicel) $0.475 /$ 0.11 , chela (without pedicel) 0.445 , hand length 0.075 , movable finger length 0.325 . Carapace $0.41 / 0.345$.

## Remarks

Feaella linetteae has been found at a single site in the Pilbara region of Western Australia. The first specimen collected, a deutonymph, was found on the underside of a rock on a rocky hillside in Millstream-Chichester National Park by one member of a group of people searching for small invertebrates. Further searching that day by the entire party was unsuccessful. Several hours searching three days later by MSH and JAH uncovered the second specimen, an adult female, which was found under a rock that was positioned in the permanent shade of a larger rock forming a relatively cool environment. It is possible that feaellids in the Pilbara secrete themselves deep within the rock piles, making them difficult to locate.

## Etymology

This species is named for Linette Umbrello who collected the first specimen.

Feaella (Tetrafeaella) tealei, sp. nov.
(Figs 32-45)
http://zoobank.org/urn:lsid:zoobank.org:act:0A200319-D719-4F98-A4E 5-3874929AA068

## Material examined

Holotype. Western Australia: $0^{\wedge}$, Sulfur Springs, $21^{\circ} 08^{\prime} 17^{\prime \prime} \mathrm{S}$, $119^{\circ} 11^{\prime} 49^{\prime \prime}$ E, 4.ix.2006, under rocks, R. Teale, P. Runham, M. Greenham (WAM T63963).

Paratype. Western Australia: 1 \&, collected with holotype (WAM T78157).

Other material. Western Australia: $1+$, Corunna Station, $\sim 160 \mathrm{~km}$ SE. Port Headland, $21^{\circ} 23^{\prime} 19.40^{\prime \prime} \mathrm{S}, 119^{\circ} 37^{\prime} 06.50^{\prime \prime}$ E, 24.ii.2014, B. Parsons (WAM T133719); 1 tritonymph, $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site, gully, $21^{\circ} 27^{\prime} 01.2^{\prime \prime} \mathrm{S}, 119^{\circ} 03^{\prime} 53.8^{\prime \prime} \mathrm{E}$, tullgren funnel, 30.iii.2011, A. Slabber(WAM T113774).

## Diagnosis

Feaella tealei differs from the other species of the Feaella anderseni group as follows: from $F$. anderseni by the lack of a rallum; from $F$. callani by its larger size (e.g. chela (with pedicel) length $0.665 \mathrm{~mm}\left({ }^{( }\right)$and $0.62 \mathrm{~mm}(\%) \mathrm{mm}$ compared with 0.56 mm ( ${ }^{1}$ ) in $F$. callani); slightly more rounded abdomen (Figs 32, 33), and narrower tergites (e.g. half-tergite VI $3.00 \times$ $\left(\mathrm{O}^{1}\right)$ and $3.10-3.13 \times(\mathrm{O})$ longer than broad, but $2.94 \times\left(\mathrm{O}^{1}\right)$ in $F$. callani); and from $F$. linetteae by the position of trichobothrium $s b$, which is situated slightly basally to $t$ (Fig. 37), whereas it is situated opposite $t$ in $F$. linetteae (Fig. 25).

## Description

## Adult

Colour. All sclerotised portions deep red-brown (Figs 32, 33). All sclerotised portions coarsely tuberculate.

Setae. Most setae short, inconspicuous, slightly curved and acuminate.

Cerotegument. Most surfaces covered with very thin cerotegument.

Chelicera (Fig. 40). Hand with four large and five small setae; is and $l s$ adjacent to each other; seta $s b s$ with single denticle, others acicular; movable finger with one subdistal seta; galea very thick, without rami; fingers without teeth; rallum absent; serrula exterior with $\sim 13\left(\widehat{o}^{\wedge}, ~\right.$ ㅇ) blades; lamina exterior absent.

Pedipalp (Fig. 36). Trochanter with prolateral conical protuberance, $0.60 \times\left(\mathrm{O}^{\top}\right)$, ? (damaged) ( O ), femur very robust with pronounced triangular process on prolateral corner near base, $1.73 \times\left(\delta^{1}\right)$ and $1.75-1.79 \times($ ( $)$ ) longer than broad, patella conical $3.13 \times\left(\mathrm{O}^{1}\right)$ and $3.03-3.28 \times($ ( $)$, chela tubular, chela (with pedicel) $4.27 \times\left(\delta^{\top}\right)$ and $4.16-4.28 \times(\%)$, chela (without pedicel) $3.85 \times\left(\mathrm{o}^{1}\right)$ and $3.87-4.00 \times(\mathrm{q})$, hand (without pedicel) $0.77 \times\left(\mathrm{o}^{1}\right)$ and $0.65-0.69 \times(q)$ longer than broad. Fixed chelal finger and hand with eight major trichobothria, plus diploid trichobothrium ( $d t$ ), movable chelal finger with four trichobothria (Fig. 37): esb and est situated midway on retrolateral face; ib, isb and ist situated basally in straight row; eb, it and et situated subdistally; et situated closer to diploid trichobothrium ( $d t$ ) than to $i t$; $d t$ situated distally; $s b$ situated between st and $t ; b$ situated closer to $t$ than to finger tip. Venom apparatus absent. Chelal hand very small; retrolateral condyle small and rounded; with dorsal protuberance at base of finger. Chelal teeth large, retrorse and diastemodentate: fixed finger with 14 (o) and 16 ( O ) curved, marginal teeth and 12 ( $\delta^{\top}$ ) and 14 ( $(f)$ prolateral teeth; movable finger with $11\left(\delta^{\top}\right)$ and $12(Q)$ curved, marginal teeth and $12\left(\delta^{1}\right)$ and 14 (q) prolateral teeth. Movable chelal finger with several specialised, lanceolate setae distal to $b$ (Fig. 37).

Carapace (Figs 34, 35). Anterior margin with four lobes, median pair same size as lateral pair; with two lobes between eyes; lateral margins nearly parallel, slightly widened medially; $1.55 \times\left({ }^{\top}\right)$ and $1.55 \times($ ( $)$ ) longer than broad; with two pairs of eyes situated on tubercles away from anterior carapaceal margin; all eyes with tapetum; with numerous inconspicuous setae; with a pair of postero-lateral processes; shallow posterior furrow present.

Coxal region (Fig. 39). Pedipalpal coxa: blunt lateral processes situated basally; with numerous small setae; without


Figs 32-35. Feaella (Tetrafealla) tealei, sp. nov.: 32, 34, male holotype (WAM T63963) (before dissection): 32, dorsal; 34, cephalothorax and pedipalp, dorsal. 33, 35, female paratype (WAM T78157) (before dissection): 33, dorsal; 35, cephalothorax and pedipalp, dorsal.
medial depression or coxal spines; median maxillary lyrifissure basal, situated near clivus; posterior maxillary lyrifissure absent. Coxa I without depression, with $2-3$ stout non-alveolate processes (coxal spines) posteriorly (Fig. 39); coxa II without coxal spines.

Legs (Figs 41, 43). Patellae I and II shorter than femora I and II, each patella with shallow dorsal depression (Fig. 42); femora III and IV much shorter than patellae III and IV; femora III and IV not solidly fused with patellae III and IV, respectively; metatarsi and tarsi fused; tarsi long and slender, without tactile seta; subterminal tarsal setae acuminate; sub-ungual spine present; claws smooth; arolium much shorter than claws, with fimbriate distal margin.

Abdomen (Figs 32, 33). Longer than broad, somewhat ovoid; tergites II-IX and sternites IV-X with distinct median suture lines, and sternite III of female with posterior indentation; half-tergite VI $3.00 \times\left(\delta^{*}\right)$ and $\left.3.10-3.13 \times()^{( }\right)$longer than broad; tergite XI and sternite XI fused; tergite XII and sternite XII (anal sclerites) strongly sclerotised; most segments with numerous setae, generally arranged in a single irregular row along posterior margin of sclerite; tergite XII without setae and sternite XII with two setae; anal region with raised circular rim. Most setae very small and inconspicuous; setae of male sternites II and III longer (Fig. 44). Pleural membrane with 16 pairs of sclerotised pleural platelets in two rows. First pair of spiracles connected to anterior margin of sternite IV; second pair


Figs 36-46. Feaella (Tetrafeaella) tealei, sp. nov., male holotype(WAM T63963) unless stated otherwise: 36, right pedipalp, dorsal; 37, right chelicera, dorsal; 38 , right coxae I and II showing coxal spines, ventral; 39, left chela, lateral; 40, left chela, lateral, tritonymph (WAMT113774); 41, left chela, lateral, deutonymph (WAM T113773); 42, right leg I, lateral; 43, right patella I, lateral; 44, right leg IV, lateral; 45, male genital sternites, ventral; 46, female genital sternites, ventral, female paratype (WAM T78157). Scale lines $=0.05 \mathrm{~mm}$ (Fig. 37); 0.1 mm (Figs 41, 43); 0.2 mm (Figs 38-40, 45, 40); 0.25 mm (Figs 36, 42, 44).


Fig. 47. Map of the Pilbara region of Western Australia showing known distribution of Feaella species: Feaella (Tetrafeaella) callani, sp. nov. (■); F. (T.) linetteae, sp. nov. (■); F. (T.) tealei, sp. nov. (©).
of spiracles connected to anterior margin of sternite V. Sternite II of female absent (Fig. 45).

Genitalia. Male with a pair of enlarged, thick-walled bursa; median genital sac long and ovoid, extending to sternite V. Female with large gonosac, covered with scattered pores.

Dimensions (mm). Males: holotype: body length 2.22; abdomen breadth (without pleura) 1.07. Pedipalp: trochanter $0.13 / 0.215$, femur $0.665 / 0.385$, patella $0.47 / 0.155$, chela (with pedicel) $0.555 / 0.13$, chela (without pedicel) 0.50 , hand (without pedicel) length 0.10 , movable finger length 0.365 . Chelicera $0.205 / 0.135$; movable finger 0.095 . Carapace $0.59 / 0.38$; anterior eye diameter 0.055 , posterior eye diameter 0.05 . Leg I: femur $0.26 / 0.17$, patella $0.22 / 0.085$, tibia $0.19 / 0.065$, tarsus 0.27/0.05. Leg IV: femur 0.23/0.10, patella $0.33 / 0.12$, tibia $0.375 /$ 0.065 , tarsus $0.39 / 0.055$.

Females. Paratype WAM T78157 followed by one other female (when measured): body length 2.59 (2.40). Pedipalps: trochanter ? (damaged), femur 0.71/0.38 (0.68/0.38), patella $0.515 / 0.17$ ( $0.59 / 0.18$ ), chela (with pedicel) $0.62 / 0.145$ ( $0.645 /$ 0.155 ), chela (without pedicel) 0.58 ( 0.60 ), hand length 0.10 ( 0.10 ), movable finger length 0.43 ( 0.445 ). Carapace $0.68 / 0.44$ ( $0.675 / 0.465$ ); anterior eye diameter 0.05 , posterior eye diameter 0.055. Leg I: femur $0.27 / 0.08$, patella $0.21 / 0.085$, tibia $0.205 /$ 0.065 , tarsus $0.305 / 0.055$. Leg IV: femur $0.245 / 0.095$, patella $0.355 / 0.12$, tibia $0.42 / 0.07$, tarsus $0.415 / 0.06$.

## Tritonymph

Only some details are visible, as the specimen is in very poor condition. Pedipalp: chela (with pedicel) $4.22 \times$ longer than
broad, chela (without pedicel) $3.91 \times$, hand $0.78 \times$ longer than broad. Fixed chelal finger with seven major trichobothria, plus diploid trichobothrium $(d t)$, movable chelal finger with three trichobothria (Fig. 38); isb and sb absent; esb and est situated midway on retrolateral face; ib and ist situated basally on prolateral face; eb, it and et situated subdistally; et situated closer to diploid trichobothrium ( $d t$ ) than to $i t$; $d t$ situated distally; st situated sub-basally, $t$ closer to $s t$ than to $b$ (Fig. 38).

Carapace. Four anterior lobes; two pairs of eyes.
Coxal region. Coxa I without depression, with three stout non-alveolate processes (coxal spines) posteriorly; coxa II without coxal spines.

Legs. Much as in adult.
Dimensions (mm), WAM T113774. Pedipalp: chela (with pedicel) $0.485 / 0.115$, chela (without pedicel) 0.45 , hand length 0.09 , movable finger length 0.34 .

## Remarks

Feaella tealei has been collected from three locations in the northern Pilbara of Western Australia, separated by at most 58 km (Fig. 46). Adult specimens are not available from the site $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site, but the sequence data conclusively demonstrate that this population is conspecific with those from Sulfur Springs and Corunna Station (Figs 6, S1-S3). Apart from the four specimens listed above, two other specimens from $\sim 50 \mathrm{~km}$ SE of Wodgina Mine Site (WAM T113769 and T113773) were included in the molecular analysis (Table 1). Unfortunately the specimens were lost after the DNA extraction process.

The first two specimens to be collected came from a patch of shale along an intermittently dry creek line in September 2006. A search for further specimens at the locality and other likely nearby sites over several days in October 2008 by R. Teale and MSH was unsuccessful. Other specimens of this species have been collected from 50 km SE of Wodgina Mine Site, but a visit to this site in 2011 by MSH failed to yield any further specimens. A female was later collected from Corunna Station.

## Etymology

This species is named for Roy Teale, one of the collectors of the type specimens, in recognition of his contributions to Australian biodiversity and conservation.

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## References

Agnarsson, I. (2010). The utility of ITS2 in spider phylogenetics: notes on prior work and an example from Anelosimus. The Journal of Arachnology 38, 377-382. doi:10.1636/B10-01.1
Arabi, J., Judson, M. L., Deharveng, L., Lourenco, W. R., Cruaud, C., and Hassanin, A. (2012). Nucleotide composition of CO1 sequences in Chelicerata (Arthropoda): detecting new mitogenomic rearrangements. Journal of Molecular Evolution 74, 81-95. doi:10.1007/s00239-012-9490-7
Beier, M. (1932). Pseudoscorpionidea II. Subord. C. Cheliferinea. Das Tierreich 58, i-xxi, 1-294.
Beier, M. (1955). Pseudoscorpionidea, gesammelt während der schwedischen Expeditionen nach Ostafrika 1937-38 und 1948. Arkiv för Zoologi, Ser. 2 7, 527-558.
Beier, M. (1964). Weiteres zur Kenntnis der Pseudoscorpioniden-Fauna des südlichen Afrika. Annals of the Natal Museum 16, 30-90.
Ben-David, T., Melamed, S., Gerson, U., and Morin, S. (2007). ITS2 sequences as barcodes for identifying and analyzing spider mites (Acari: Tetranychidae). Experimental \& Applied Acarology 41, 169-181. doi:10.1007/s10493-007-9058-1
Benedict, E. M., and Malcolm, D. R. (1978). The family Pseudogarypidae (Pseudoscorpionida) in North America with comments on the genus Neopseudogarypus Morris from Tasmania. The Journal of Arachnology 6, 81-104.
Bragagnolo, C., Pinto-da-Rocha, R., Antunes, M., and Clouse, R. M. (2015). Phylogenetics and phylogeography of a long-legged harvestman (Arachnida: Opiliones) in the Brazilian Atlantic Rain Forest reveals poor dispersal, low diversity and extensive mitochondrial introgression. Invertebrate Systematics 29, 386-404. doi:10.1071/IS15009
Castalanelli, M. A., Severtson, D. L., Brumley, C. J., Szito, A., Foottit, R. G., Grimm, M., Munyard, K., and Groth, D. M. (2010). A rapid nondestructive DNA extraction method for insects and other arthropods.

Journal of Asia-Pacific Entomology 13, 243-248. doi:10.1016/j.aspen. 2010.04.003

Castalanelli, M. A., Teale, R., Rix, M. G., Kennington, J. W., and Harvey, M. S. (2014). Barcoding of mygalomorph spiders (Araneae: Mygalomorphae) in the Pilbara bioregion of Western Australia reveals a highly diverse biota. Invertebrate Systematics 28, 375-385.
Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17, 540-552. doi:10.1093/oxfordjournals.molbev.a026 334
Chamberlin, J. C. (1931). The arachnid order Chelonethida. Stanford University Publications, Biological Sciences 7(1), 1-284.
Darriba, D., Taboada, G. L., Doallo, R., and Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9, 772. doi:10.1038/nmeth. 2109
Durrant, B. J., Harvey, M. S., Framenau, V. W., Ott, R., and Waldock, J. M. (2010). Patterns in the composition of ground-dwelling spider communities in the Pilbara bioregion, Western Australia. Records of the Western Australian Museum 78(Suppl.), 185-204. doi:10.18195/ issn.0313-122x.78(1).2010.185-204
Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32, 1792-1797. doi:10.1093/nar/gkh340
Ellingsen, E. (1906). Report on the pseudoscorpions of the Guinea Coast (Africa) collected by Leonardo Fea. Annali del Museo Civico di Storia Naturale di Genova, Ser. 3 2, 243-265.
Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. C. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3, 294-299.
Giribet, G., Carranza, S., Baguñà, J., Riutort, M., and Ribera, C. (1996). First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Molecular Biology and Evolution 13, 76-84. doi:10.1093/oxfordjournals. molbev.a025573
Harms, D., and Framenau, V. W. (2013). New species of mouse spiders (Araneae: Mygalomorphae: Actinopodidae: Missulena) from the Pilbara region, Western Australia. Zootaxa 3637, 521-540.
Harvey, M. S. (1989). A new species of Feaella Ellingsen from north-western Australia (Pseudoscorpionida: Feaellidae). Bulletin of the British Arachnological Society 8, 41-44.
Harvey, M. S. (1991). 'Catalogue of the Pseudoscorpionida.' (Manchester University Press: Manchester, UK.)
Harvey, M. S. (1992). The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invertebrate Taxonomy 6, 1373-1435. doi:10.1071/IT9921373
Harvey, M. S. (2013). Pseudoscorpions of the World, version 3.0. Western Australian Museum, Perth. Available at http://museum.wa.gov.au/catalo gues-beta/pseudoscorpions [Accessed 4 February 2016].
Harvey, M. S., Berry, O., Edward, K. L., and Humphreys, G. (2008). Molecular and morphological systematics of hypogean schizomids (Schizomida: Hubbardiidae) in semi-arid Australia. Invertebrate Systematics 22, 167-194. doi:10.1071/IS07026
Harvey, F. S. B., Framenau, V. W., Wojcieszek, J. M., Rix, M. G., and Harvey, M. S. (2012a). Molecular and morphological characterisation of new species in the trapdoor spider genus Aname (Araneae: Mygalomorphae: Nemesiidae) from the Pilbara bioregion of Western Australia. Zootaxa 3383, 15-38. doi:10.11646/zootaxa.3383.1.3
Harvey, M. S., Ratnaweera, P. B., Udagama, P. V., and Wijesinghe, M. R. (2012b). A new species of the pseudoscorpion genus Megachernes (Pseudoscorpiones: Chernetidae) associated with a threatened Sri Lankan rainforest rodent, with a review of host associations of Megachernes. Journal of Natural History 46, 2519-2535. doi:10.1080/ 00222933.2012 .707251

Harvey, M. S., Andrade, R., and Pinto-da-Rocha, R. (2016). The first New World species of the pseudoscorpion family Feaellidae
(Pseudoscorpiones: Feaelloidea), from the Mata Atlântica biome. Journal of Arachnology 44, 227-234.
Henderickx, H., and Boone, M. (2014). The first fossil Feaella Ellingsen, 1906, representing an unexpected pseudoscorpion family in Baltic Amber (Pseudoscorpiones, Feaellidae). Entomo-Info 25, 5-11.
Heurtault-Rossi, J., and Jézéquel, J. F. (1965). Observations sur Feaella mirabilis Ell. (Arachnide, Pseudoscorpion). Les chélicères et les pattesmâchoires des nymphes et des adultes. Description de l'appareil reproducteur. Bulletin du Muséum National d'Histoire Naturelle, Ser. 237, 450-461.
Johnson, M. S., Hamilton, Z. R., Murphy, C. E., MacLeay, C. A., Roberts, B., and Kendrick, P. G. (2004). Evolutionary genetics of island and mainland species of Rhagada (Gastropoda: Pulmonata) in the Pilbara region, Western Australia. Australian Journal of Zoology 52, 341-355. doi:10. 1071/ZO04027
Judson, M. L. I. (1992). African Chelonethi. Studies on the systematics, biogeography and natural history of African pseudoscorpions (Arachnida). (University of Leeds: Leeds, UK.)
Judson, M. L. I. (2007). A new and endangered species of the pseudoscorpion genus Lagynochthonius from a cave in Vietnam, with notes on chelal morphology and the composition of the Tyrannochthoniini (Arachnida, Chelonethi, Chthoniidae). Zootaxa 1627, 53-68.
Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., and Drummond, A. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12), 1647-1649. doi:10. 1093/bioinformatics/bts199
McHugh, A., Yablonsky, C., Binford, G., and Agnarsson, I. (2014). Molecular phylogenetics of Caribbean Micrathena (Araneae: Araneidae) suggests multiple colonisation events and single island endemism. Invertebrate Systematics 28, 337-349.
Morris, J. C. H. (1948). A new genus of pseudogarypin pseudoscorpions possessing pleural plates. Papers and Proceedings of the Royal Society of Tasmania 1947, 43-47.
Muchmore, W. B. (1981). Cavernicolous species of Larca, Archeolarca and Pseudogarypus with notes on the genera (Pseudoscorpionida, Garypidae and Pseudogarypidae). The Journal of Arachnology 9, 47-60.
Murienne, J., Harvey, M. S., and Giribet, G. (2008). First molecular phylogeny of the major clades of Pseudoscorpiones (Arthropoda: Chelicerata). Molecular Phylogenetics and Evolution 49, 170-184. doi:10.1016/j.ym pev.2008.06.002
Nunn, G. B., Theisen, B. F., Christensen, B., and Arctander, P. (1996). Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3
expansion segment in the crustacean order Isopoda. Journal of Molecular Evolution 42, 211-223. doi:10.1007/BF02198847
Rix, M. G., Harvey, M. S., and Roberts, J. D. (2010). A revision of the textricellin spider genus Raveniella (Araneae: Araneoidea: Micropholcommatidae): exploring patterns of phylogeny and biogeography in an Australian biodiversity hotspot. Invertebrate Systematics 24, 209-237. doi:10.1071/IS09048
Schwendinger, P. J., and Giribet, G. (2005). The systematics of the southeast Asian genus Fangensis Rambla (Opiliones: Cyphophthalmi: Stylocellidae). Invertebrate Systematics 19, 297-323. doi:10.1071/ IS05023
Smith, G. B., Eberhard, S. M., Perina, G., and Finston, T. (2012). New species of short range endemic troglobitic silverfish (Zygentoma: Nicoletiidae) from subterranean habitats in Western Australia's semi-arid Pilbara region. Records of the Western Australian Museum 27, 101-116.
Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688-2690. doi:10.1093/bioinformatics/bt1446
Talavera, G., and Castresana, J. (2007). Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Systematic Biology 56, 564-577. doi:10.1080/ 10635150701472164
Volschenk, E. S., Burbidge, A. H., Durrant, B. J., and Harvey, M. S. (2010). Spatial distribution patterns of scorpions (Scorpiones) in the arid Pilbara region of Western Australia. Records of the Western Australian Museum 78(Suppl.), 271-283. doi:10.18195/issn.0313-122x.78(1).2010.271-284
Weygoldt, P. (1969). ‘The Biology of Pseudoscorpions.' (Harvard University Press: Cambridge, MA.)
Whiting, M. F., Carpenter, J. M., Wheeler, Q. D., and Wheeler, W. C. (1997). The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18 S and 28 S ribosomal DNA sequences and morphology. Systematic Biology 46, 1-68.
With, C. J. (1906). The Danish expedition to Siam 1899-1900. III. Chelonethi. An account of the Indian false-scorpions together with studies on the anatomy and classification of the order. Oversigt over det Konigelige Danske Videnskabernes Selskabs Forhandlinger, Ser. 7 3, 1-214.
With, C. J. (1908). Remarks on the Chelonethi. Videnskabelige Meddelelser fra den Naturhistorisk Forening i Kjøbenhavn, Ser. 6 10, 1-25.

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