Feaella (Tetrafeaella) obscura sp. nov. – a new pseudoscorpion species from the Maldives (Arachnida, Pseudoscorpiones), and an updated identification key to the subgenus Feaella (Tetrafeaella)

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Abstract

The Feaellidae Ellingsen, 1906 is a small but ancient family of pseudoscorpions with 20 extant species across the Southern Hemisphere, and fossils from the Lower Cretaceous of Myanmar and the Eocene of Europe. Here, we describe and illustrate Feaella (Tetrafeaella) obscura sp. nov. as a new species from the Maldives archipelago in the Indian Ocean. This is the first record of Feaella from a young oceanic island and may indicate a potential for long-distance dispersal in this lineage. We also elevate Feaella (T.) capensis nana Beier, 1966 to full species rank as F. (T.) nana Beier, 1966 and provide an identification key to the members of the subgenus Feaella (Tetrafeaella), thereby facilitating the identification of species.

Key Words

biogeography, dispersal, endemism, false scorpion, taxonomy

Introduction

Pseudoscorpions belonging to the family Feaellidae Ellingsen, 1906 are amongst the most unusual arachnids and have a spectacular morphology that includes a carapace with multiple frontal lobes, a dorsoventrally flattened and heavily sclerotised body, and pedipalps that are stout, heavily armed and without a venom gland in both fingers (Harvey et al. 2016b; Judson 2017). The family has a Pangaean distribution and amber fossils are known from the Lower Cretaceous of Myanmar (Henderickx and Boone 2016) and Baltic amber in Europe (Hendrickx and Boone 2014; Harms and Dunlop 2017), whereas twenty extant species are found in tropical and subtropical regions in central and southern Africa, north-western Australia, tropical India and Sri Lanka, the Seychelles, Madagascar, and Brazil (Fig. 1) (Harvey 2013, 2018; Harvey et al. 2016a, b; Judson 2017).

Their strange morphology aside, feaellids are also of fundamental importance in understanding the evolution of character systems in pseudoscorpions (Benavides et al. 2019). According to the most recent transcriptomic analysis (Benavides et al. 2019), Feaellidae and its sister-family Pseudogarypidae Chamberlin, 1923 are the sister group to all pseudoscorpions with venom glands in the pedipalp fingers and placed within their own sub-order Atoposphyronida Harvey, 2019. The present-day distribution of the family and the fossil record (Harms and Dunlop 2017) suggests that this is a remnant lineage that may have survived in relictual habitats across the Southern Hemisphere.

Feaellidae are grouped into two subfamilies, Feaellinae (Ellingsen, 1906) and Cybellinae Judson, 2017 (Judson, 2017). Feaellinae comprises two genera, Feaella Ellingsen, 1906 from Africa, India, Madagascar-
The species were found during an inventory in the collections of the Hungarian Natural History Museum (HNHM) and stored in 70% ethanol. They were cleared in a 3:1 mixture of lactic acid and gelatine to be examined with a Zeiss Stemi 2000-c stereomicroscope and a Zeiss Axioskop 2 light compound microscope. Drawings and measurements were made with the aid of the Zeiss Axioskop 2 microscope. Measurements were taken using a custom-made BK Plus Lab System by Dun, Inc. with integrated Canon EOS 7D Mark II, microscopic lens (5× and 10× magnification) and the Zerene stacker version 1.04 software. Scanned electron images were taken from temporarily dried specimens mounted on copper wire, using a Hitachi TM4000 Plus scanning electron micrograph (SEM). Mensuration follows the reference points in Chamberlin (1931) as does the terminology, except for modifications for the pedipalps and chelal trichobothria (Harvey 1992), the chelicera (Judson 2007), and the faces of the appendages (Harvey et al. 2012).

Abbreviations

Chelicer trichobothriotaxy: $bs =$ basal seta; $sbs =$ sub-basal seta; $is =$ interior seta; $es =$ exerior seta; $ls =$ laminal seta; $ge =$ galeal seta. Chelal trichobothriotaxy: $eb =$ externo-basal; $esb =$ externo-subbasal; $est =$ exter-no-subterminal; $et =$ externo-terminal; $ib =$ interno-basal; $isb =$ interno-subbasal; $ist =$ interno-subterminal; $it =$ in-erno-terminal; $t =$ terminal; $st =$ subterminal; $sb =$ sub-basal; $b =$ basal; $dt =$ duplex trichobothrium.

Figure 1. Known distribution of the family Feaellidae. Circle colours: blue = Recent records; green = fossil records; and red = $F.(T.)$ obscura sp. nov.
Results

Taxonomy

Superfamily Feaelloidae Ellingsen, 1906
Family Feaellidae Ellingsen, 1906
Subfamily Feaellinae Ellingsen, 1906

Remarks. The genus Feaella is divided into three subgenera: Feaella (Feaella), Feaella (Difeaella), and Feaella (Tetrafeaella) based on the number of frontal lobes on the carapace (Mahnert 1982). Our new species has four lobes and is assigned to Tetrafeaella, hence the diagnosis is against similar species with four protuberances. The species can also be diagnosed against the east Asian genus Cybella Judson, 2017 which lacks pleural sclerites on the abdomen which are obvious in our species.

Feaella (Tetrafeaella) obscura sp. nov.

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Figs 2A–F, 3A–H, 4A–F, 5A–G

Type material. Holotype female from the Maldives, Kabudu Island (might refer to Kaudu [0°17’N, 73°1’E] or Kandudu Islands [2°19’N, 72°55’E]), June 1984, leg: Győző Horváth. [On the label: Maldives, Kabudu sz., 1984.VII. leg.: Győző Horváth] (HNHM Pseud-2009). Paratypes: 1 male (HNHM Pseud-2010) and 1 female (ZMH-A0003101); all same data as holotype.

Etymology. The name of the species refers to the obscure evolutionary and geographic origins of the species that is unlikely to have evolved on the young island that is the locus typicus.

Distribution. Maldive Islands (Fig. 1).

Diagnosis. A typical Feaella (Tetrafeaella) habitus (Figs 2A, B, 3A) that differs from all the other species of the subgenus by the following combination of characters: with the anteromedian lobes of carapace being closer to each other than to the anterolateral ones; anterolateral pair approximately as broad as anteromedian pair, anteromedian lobes longer. Palpal trochanter with prolateral pair approximately as broad as anteromedian pair, anteromedian lobes longer than to the anterolateral ones; anterolateral teromedian lobes are closer to each other than to the posterior one-fourth of carapace on each side, and posterior one-fourth of carapace nearly parallel, slightly widened medially; all eyes with tape-tum; with numerous inconspicuous setae; with a pair of posterior-lateral processes; shallow anterior and posterior furrows present. Three slit-like lyrifissures at the level of posterior one-fourth of carapace on each side, and two near posterior base.
Coxal region (Figs 2E, 3B): pedipalpal coxa with strong basal lateral processes; with numerous small setae and 3 acuminate apical setae. Coxa I with medioposterior depression (coxal pit), a single primary coxal spine posteriorly; coxa II with 9 secondary spines in male and 8–11 in females (Fig. 3C). Pedipalpal coxa somewhat longer as combined length of leg coxae I–IV.

Legs (Fig. 5D, E): claws simple, arolium shorter than claws. Metatarsi and tarsi fused. Each patella with a shallow dorsal depression. Tarsi without tactile setae, vestitural setae short and acuminate. Patellae I and II slightly shorter than femora I and II; patellae III and IV nearly twice as long as femora III and IV.

Abdomen: longer than broad, somewhat ovoid; tergites II–IX and sternites IV–X with distinct median suture lines; tergite XI and sternite XI fused; tergite XII and sternite XII (anal sclerites) strongly sclerotised; most segments with numerous setae; tergite XII and sternite XII with two setae; anal region with raised circular rim (Fig. 3D). Setae of sternites II and III longer than vestitural setae. Pleural membrane with a dorsal row of 15 and a ventral row of 14 sclerotised pleural platelets.

Genital region: Female (Figs 3F, 5F): 10 acuminate microsetae on each plate. Male (Fig. 5G): 40–45 acuminate microsetae on genital plate. Inner genital structures could not be clearly seen.

Measurements (in mm, ratios in parentheses): Male paratype. Body 1.83. Carapace 0.51/0.41 (1.24×). Chelicera 0.19/0.10 (1.9×), movable finger 0.085. Palpal femur 0.51/0.29 (1.76×), patella 0.41/0.14 (2.93×), chela (with pedicel) 0.53/0.13 (4.08×), chela (without pedicel) 0.50, hand (with pedicel) 0.15, hand (without pedicel) 0.12, movable finger 0.37. Leg I. trochanter 0.12/0.19
Females (holotype, followed by paratype in parentheses and then the ratios also in parentheses). Body 2.16 (2.46). Carapace 0.61/0.48 (0.64/0.50) (1.27–1.28×). Chelicera 0.20/0.12 (0.21/0.12) (1.67–1.75×), movable finger 0.095 (0.10). Palpal femur 0.63/0.37 (0.69/0.40) (1.70–1.73×),

Figure 3. Feaella (Tetrafeella) obscura sp. nov, female holotype (HNHM Pseud-2009): SEM images. A. Body, dorsal view; B. Coxal region; C. Coxae I and II with medioposterior depression and coxal spines (primary coxal spines of coxae I highlighted in purple); D. Anal region; E. Carapace, dorsal view; F. Female genital region with pedal coxae IV; G. Right chelal tip, dorsal view; H. Specialised, lanceolate setae (marked with arrow) midway between t and finger tip.
patella 0.51/0.18 (0.54/0.19) (2.83–2.84×), chela (with pedicel) 0.60/0.16 (0.61/0.16) (3.75–3.81×), chela (without pedicel) 0.57 (0.57), hand (with pedicel) 0.16 (0.17), hand (without pedicel) 0.12 (0.10), movable finger 0.40 (0.41). Leg I. trochanter 0.15/0.11 (0.16/0.12) (1.33–1.36×), femur 0.24/0.07 (0.27/0.08) (3.38–3.43×), patella 0.22/0.08 (0.21/0.09) (2.33–2.75×), tibia 0.20/0.07 (0.22/0.07) (2.85–3.14×), tarsus 0.22/0.05 (0.22/0.05) (4.4×). Leg IV. trochanter 0.26/0.14 (0.27/14) (1.86–1.93×), femur 0.18/0.10 (0.19/10) (1.8–1.9×), patella 0.36/0.11 (0.37/0.12) (3.08–3.27×), tibia 0.42/0.06 (0.44/0.07) (6.29–7.00×), tarsus 0.36/0.05 (0.38/0.06) (6.33–7.20×).

**Differential diagnosis.** Aside from *Feaella (T.) obscura* there are twelve species of *Feaella (Tetrafeaella): F. (T.) affinis* Hirst, 1911 (Seychelles); *F. (T.) capensis* Beier, 1955; *F. (T.) macronata* Tullgren, 1907 and *F. (T.) parva* Beier, 1947 (all South Africa), *F. (T.) indica* Chamberlin, 1931 (India and Sri Lanka), *F. (T.) leleupi* Beier, 1959.

**Figure 4.** *Feaella (Tetrafeaella) obscura* sp. nov, female holotype (HNHM Pseud-2009): SEM images. A. Left chela, retrolateral view; B. Left chela, dorsomedial view; C. Left chela, ventral view. Male paratype (HNHM Pseud-2010): SEM images. D. Left chela, retrolateral view; E. Left chela, ventral view; F. Left chela, medial view.
(Congo), *F. (T.) nana* Beier, 1966 comb. nov. (previously treated as a subspecies of *capensis* but see below), *F. (T.) perreti* Mahnert, 1982 (Kenya) and the western Australian species *F. (T.) anderseni* Harvey, 1989, *F. (T.) callani* Harvey et al., 2016, *F. (T.) linetteae* Harvey et al., 2016 and *F. (T.) tealei* Harvey et al., 2016.

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Figure 5. *Feaella* (*Tetrafeaella*) *obscura* sp. nov. A. Right chelicera, dorsal view – female holotype (HNHM Pseud-2009); B. Right pedipalp, dorsal view – female holotype; C. Left chela, retrolateral view – female holotype; D. Leg I, lateral view – female paratype (ZMH-A0003101); E. Leg IV, lateral view – female paratype; F. Female genital region – female holotype; G. Male genital region – male paratype (HNHM Pseud-2010).
Feaella (T.) obscura is most similar in general habitus of carapace and pedipalps and in most characters (see in the key below) to the following species from Africa, India and the Seychelles.

It differs from F. (T.) capensis in having a pronounced and triangular dorsomedial process on the prolateral corner of palpal femur near its base (absent in F. (T.) capensis), conical shape of the frontal carapace lobes (long and triangular), pleural membrane with a dorsal row of 15 and ventral row of 14 platelets (15 and 15 in F. (T.) capensis) (Beier 1955).

Feaella (T.) obscura differs from F. (T.) nana in having a pronounced and triangular dorsomedial process on the prolateral corner of the palpal femur near its base (absent in F. (T.) nana). Furthermore, in having pleural membrane with a dorsal row of 15 and a ventral row of 14 sclerotised pleural platelets (in F. (T.) nana the number of these are 14 and 14). In Feaella (T.) obscura on fixed chelal finger isb much closer to ib than to ist and these three trichobothria do not form a straight row, and trichobothrium eb situated clearly closer to the fingertip than to ist (in F. (T.) nana isb, ib and ist are equally placed and form a straight row, and eb is situated midway between ist and the finger tip) (Beier 1966).

The new species differs from F. (T.) indica in having a pronounced and triangular dorsomedial process on the prolateral corner of palpal femur near its base (in F. (T.) indica this process is absent). The chelae of F. (T.) obscura are as long as the palpal femora (in F. (T.) indica these are distinctly shorter than the palpal femora). Furthermore, the palpal femur length/width ratio of F. (T.) obscura is 1.70–1.76× (this value is 1.90× in F. (T.) indica) (Chamberlin 1931; Beier 1932).

In the case of F. (T.) affinis Hirst, 1911 trichobothria sb and st of movable chelal finger are closer to b than t (in the new species sb and st are situated midway between b and t). Furthermore, in F. (T.) affinis trichobothrium ist of fixed chelal finger is at the level of esb and est is placed distal to them (in F. (T.) obscura, ist is equidistant from est and esb) (Mahnert 1978).

Remarks on locality

The specimens were found in soil samples of the Hungarian Natural History Museum and collected by Mr. Győző Horváth who was a friend of Dr. Sándor Mahunka (former director of HNHM, Department of Zoology) and occasionally collected soil samples for the museum. The collecting label clearly points to the Maldives, however, the island name Kaudu [0°17’N, 73°1’E] or Kandudu islands [2°19’N, 72°55’E]. Mr. Horváth passed away some years ago and no further data are available.

Biogeography

The present-day distribution of Feaelidae has been interpreted as a prime example of continental vicariance (Harvey 1989) although this hypothesis is based on distributional data only and requires further testing. One observation that may lend support to this hypothesis is that all species records come from old and stable landmasses (continents or ancient islands such as Madagascar and the Seychelles), with the exception of the Bonaparte Archipelago in north-western Australia which, however, is geologically part of the mainland (Henderson and Johnson 2016). This is a distributional pattern to be expected for poor dispersers with a long evolutionary history.

The present finding is the first record of the Feaelidae from an oceanic island other than the Seychelles which, in contrast to the Maldives, are geologically old and known to support ancient Gondwanan fauna (Gerlach and Marusik 2010). The atolls of the Maldives emerged as recently as 5500–4500 years ago as lagoon sediments were exposed by shoreline changes (Kench et al. 2005), although volcanic activity in the Maldives has also shaped this region for as long as 60 million years and many of the atolls have underlying volcanic basalt (Droxler 1992). We cannot exclude the hypotheses that the presence of Tetraefaella here is a result of vicariance and long-term persistence in an island landscape that changed dynamically over time but dispersal is equally likely, in particular since many islands drowned and re-emerged as sea levels changed. We are not sure where F. (T.) obscura originates but we have checked the new species carefully against congeners from India and Sri Lanka, which are the most promising candidates for a source population. Our new species is clearly different from F. indica but also from several undescribed species from Madagascar. So, if F. (T.) obscura originated elsewhere it must be from a region where the genus is presently undescribed. Dispersal modes are also not clear and passive oceanic drift is as likely as anthropogenic dispersal. The Maldives is a popular tourist destination and timber as well as soil samples are imported regularly from other regions to support the local industry. The evolutionary origins of F. (T.) obscura remain enigmatic until fresh samples are being collected for genetic studies.

The status of Feaella (T.) capensis nana Beier, 1966

While our focus is the description of a new species, the study of relevant literature also reveals inconsistencies in the description of F. (T.) capensis from South Africa. The species was originally described from Cape Point in the Western Cape but Beier (1966) also recorded this species from Kruger National Park in Limpopo Province, almost 1700 km apart. There are several differences in morphology between both populations, including body size (females from Cape Point: 2.6 mm in body length; 1.7 mm from Kruger) and chelal length (females from Cape Point: 0.68 mm; 0.40–0.50 mm from Kruger) but Beier preferred to treat the Kruger populations as a subspecies, F. (T.) capensis nana, next to the nominate form Feaella (T.) capensis capensis. Our perception of range sizes in Feaella has changed drastically since then and recently molec-
Identification key to the species of the subgenus Feaella (Tetrafeaella)

Since Chamberlin’s first key to the family (Chamberlin 1931) which included four species only, several keys were published for the African fauna (Beier 1955, Mahnert 1982). To better diagnose F. (T.) obscura from species with a similar morphology, we provide the following identification key which is constructed based on our new data and the literature (Tullgren 1907; Hirst 1911; Chamberlin 1931; Beier 1932, 1947, 1955, 1959, 1966; Mahnert 1978, 1982; Harvey 1989; Harvey et al. 2016a). The proportions are given for both sexes whenever possible.

1 All four anterior lobes of carapace with approximately equal width, and placed equidistantly from each other. Presence of a pair of enlarged, thick-walled bursa in male genitalia (Australia) ...................... 2 [F. (T.) anderseni species-group]
- Clear differences in length and/or in width of anteromedian and anterolateral lobes of the carapace, and/or in the distance between them ................................. 5
2 Cheliceral rallum present. Pedipalpal femur 1.78–1.91× longer than broad (female); chela with pedicel 0.510–0.580 mm (female) ......................................................... F. (T.) anderseni
- Cheliceral rallum absent ......................................................... 3
3 Trichobothrium ℓ situated distal to sb on movable chelal finger. Pedipalpal femur 1.73× (male) and 1.75–1.79× (female) longer than broad; chela with pedicel 0.555 (male) and 0.645 mm (female) and palp pal femur 0.600–0.640 mm (female) ......................................................... F. (T.) tealei
- Trichobothria sb and ℓ on movable chelal finger approximately at the same level (same distance from the finger basis) ....4
4 Trichobothrium sb is situated basally to ℓ on movable chelal finger, on fixed finger isb much closer to ℓ than to ist. Pedipalpal femur 1.77× longer than broad (male). Smaller species, chela with pedicel 0.560 mm (male) and palp pal femur 0.575 mm (male) ......................................................... F. (T.) callani
- Trichobothrium sb is situated opposite to ℓ on movable chelal finger, on fixed finger isb equally distant from ℓ and ist. Pedipalpal femur 2.06× (male) longer than broad. Larger species, chela with pedicel 0.635 mm (male) and palp pal femur 0.660 mm (male) ......................................................... F. (T.) linetetteae
5 All four anterior lobes of carapace with the same width ................................................................................. 6
- Anterior lobes of carapace with unequal width .................................................................................. 10
6 Anterior lobes of carapace have approximately equal length. Anteromedian lobes much closer to anterolateral ones than to each other. Pedipalpal femur 1.78× longer than broad (South Africa, Swaziland) ......................................................... F. (T.) mucronata
- Anteromedian lobes clearly longer than the anterolateral ones .......................................................... 7
7 On fixed chelal finger isb, ℓ and ist are equally placed and form a straight row. Trichobothrium eb is situated midway between ist and the fingertip ....................................................... 8
- On fixed chelal finger isb much closer to ℓ than to ist and these three trichobothria do not form a straight row. Trichobothrium eb situated closer to the finger tip than to ist ..................................................... 9
8 All four anterior lobes of the carapace rather conical, the anteromedian lobes somewhat longer than the anterolaterals. Pedipalpal femur robust, 1.77× (female). Pleural membrane with a dorsal and a ventral row of 14–14 sclerotised pleural platelets. (South Africa) ......................................................... F. (T.) nana comb. nov.
- Anterior lobes of carapace clearly more robust, the anteromedian ones rather triangular, the anterolateral ones conical. The two anteromedian lobes much longer than the anterolateral ones. Pedipalpal femur unusually attenuated, 2.06× (male) longer than broad. Pleural membrane with a dorsal row of 10 and a ventral row of 11 sclerotised pleural platelets. (South Africa) ......................................................... F. (T.) parva
9 Pronounced and triangular dorsomedial process on prolateral corner of palpal femur near its base is absent. All four anterior lobes of the carapace long and triangular, the anteromedian ones somewhat longer than the anterolaterals. Pedipalpal femur 1.66× (female) longer than broad. Pleural membrane with a dorsal and a ventral row of 15–15 sclerotised pleural platelets. (South Africa) ......................................................... F. (T.) capensis
- A pronounced and triangular dorsomedial process on the prolateral corner of palpal femur near its base is present. All four anterior lobes of the carapace robust and rather conical, the anteromedian ones somewhat longer than the antero-

sector.
lateral. Palpal femur length/width ratio is 1.70–1.73× (female) and 1.76× (male). Pleural membrane with a dorsal row of 15 and a ventral row of 14 sclerotised pleural platelets. (Maldives) ................................................................. F. (T.) obscura sp. nov.

10 Anteromedian lobes are approximately two times wider than the anterolateral ones. Dorsal line of chela concave, approximately at the middle of fixed finger a strong protuberance is present. Pedipalpal femur 1.77–1.86× (female) and 1.80–1.89× (male) longer than broad. (Kenya)................................................................................................................. F. (T.) perreti

– Anterolateral lobes are clearly wider than the anteromedian ones ................................................................. 11

11 Anterolateral lobes at least two times broader than anteromedian ones and are flattened at their apical part. Pedipalpal femur 1.80× (female) and 1.61× (male) longer than broad (Democratic Republic of Congo) ................................................................. F. (T.) leleupi

– Anterolateral lobes less than two times broader than anteromedian ones and are triangular or at least rounded at their apical part ................................................................................................................................. 12

12 All four anterior lobes of carapace are placed equidistant from each other. Chelae are approximately as long as the palpal femora. Pedipalpal femur 1.72–1.90× longer than broad. Trichobothrium sb is closer to st than to b on movable chelal finger (Seychelles). ................................................................................................................................. F. (T.) affinis

– Anteromedian lobes are closer to each other than the anterolateral ones. Chelae are distinctly shorter than palpal femora. Palpal femur length/width ratio is 1.90× (female). Trichobothrium sb is situated equidistantly between st and b on movable chelal finger (Bangladesh, India, Sri Lanka) ................................................................................................................................. F. (T.) indica

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