

Meteorona kishinouyei, a new family, genus and species (Cnidaria, Cubozoa, Chiroadropida) from Japanese Waters

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Academic editor: *L. van Olfvegen* | Received 1 December 2014 | Accepted 17 April 2015 | Published 11 May 2015

<http://zoobank.org/7690E036-F8BD-4B62-A7BB-EF9DD1D6DE87>

Citation: Toshino S, Miyake H, Shibata H (2015) *Meteorona kishinouyei*, a new family, genus and species (Cnidaria, Cubozoa, Chiroadropida) from Japanese Waters. ZooKeys 503: 1–21. doi: 10.3897/zookeys.503.9047

Abstract

A new family, genus and species of cubozoan box jellyfish belonging to the order Chiroadropida is reported from the eastern Japan. *Meteorona kishinouyei* **gen. et sp. n.** possesses the following unique morphological characters with respect to other known species in the Chiroadropida: having one tentacle per scalpel-like unbranched pedaliu and slightly raised unbranched gastric saccules. A comparative table of the primary diagnostic characters of genus and order in the Chiroadropida is given. The order Chiroadropida is redefined. The family Chiropsellidae is established. Discussion is provided on the implications for these findings on our current understanding of Cubozoan systematics.

Keywords

Box jellyfish, Chiropsellidae, Japan, taxonomy

Introduction

The order Chiroadropida currently comprises 13 species in two families, Chiroadropidae and Chiropsalmidae (Gershwin 2006a; Cornelius et al. 2005; Lewis and Bentlage 2009; Bentlage 2013). Chiroadropids are characterized by having multiple tentacles extending from a single branching pedaliu on each corner of the swimming bell. The first

identified species of Chirodropida, *Chiropsalmus quadrumanus* (Müller, 1859) was described by Müller (1859) (as *Tamoya quadrumana*). Agassiz (1862) erected the genus, *Chiropsalmus* Agassiz (1862) and *T. quadrumana* was subsequently moved to that genus by Haeckel (1880) when he erected the order Chirodropida (as Chirodropidae) as part of Cubomedusae (formerly of the class Scyphozoa). Thiel (1936) erected the family Chiropsalmidae to replace the family Chirodropidae, when at the time it was classified as a monotypic family in the order Cubomedusae. Werner (1973) elevated Cubomedusae to the class Cubozoa that included Chirodropidae and Carybdeidae. Subsequently, Gershwin (2006a) elevated the family Chirodropidae to the order Chirodropida, and resurrected the family Chiropsalmidae. Recent molecular phylogenetic analyses and taxonomic investigations suggested that Chirodropida is a monophyletic order thought to include the paraphyletic Chiropsalmidae (Collins et al. 2006; Collins 2009; Bentlage et al. 2010).

Chirodropids have been reported from a range of tropical, sub-tropical, and mild temperature localities in the Pacific and Atlantic (Gershwin 2006a; Cornelius et al. 2005; Lewis and Bentlage 2009; Bentlage 2013). This group is infamous and well known by local fishermen, divers and bathers as dangerous box jellyfish due to their potentially lethal sting. In particular, envenomation by *Chironex yamaguchii* poses a serious problem to public health and tourism in Japan, with 100 to 200 stings reported per year, and a total of three fatalities following envenomation in Okinawa, southern Japan (Yamaguchi 1980; Okinawa Prefectural Institute for Health and Environment 1999). Currently, part of the life cycle of only one chirodropid is known: *C. fleckeri* (Yamaguchi and Hartwick 1980; Hartwick 1991). In an attempt to focus on counter-measures against envenomations, some workers have looked at diurnal migration and seasonal occurrence of Chirodropid medusae, and the potential habitat of polyps has been investigated using light traps (Iwanaga et al. 2005).

Five species of Japanese cubozoans have been reported, *Carybdea brevipedalia* Kishinouye, 1891, *Copula sivickisi* (Stiasny, 1926), *Tripedalia cystophora* Conant, 1897, *Morbakka virulenta* (Kishinouye, 1910), and *Chironex yamaguchii* Lewis & Bentlage, 2009 (Uchida 1929; 1970; Yamaguchi 1982; Lewis and Bentlage 2009; Bentlage et al. 2010; Bentlage and Lewis 2012; Akiyama et al. 2013) (Table 1). In this study, five specimens of an unknown cubozoan species were collected from eastern Japan. Our morphological and molecular phylogenetic analyses suggest that the cubozoan should be regarded as new family, genus and species within the order Chirodropida.

Table 1. List of Japanese Cubozoa. **a** Uchida (1929); **b** Uchida (1970); **c** Bentlage et al. 2010; **d** Akiyama et al. (2013); **e** Bentlage and Lewis (2012); **f** Yamaguchi (1982); **g** Lewis and Bentlage (2009).

Current name	Former name	Japanese name	Reference
<i>Carybdea brevipedalia</i> Kishinouye, 1891	<i>Carybdea rastonii</i>	Andon-kurage	a, b, c
<i>Copula sivickisi</i> (Stiasny, 1926)	<i>Carybdea sivickisi</i>	Himeandon-kurage	a, b, c
<i>Tripedalia cystophora</i> Conant, 1897	<i>Tripedalia cystophora</i>	Mitsuderippo-kurage	b, d
<i>Morbakka virulenta</i> (Kishinouye, 1910)	<i>Tamoya haplonema</i>	Hi-kurage	a, b, c, e
<i>Chironex yamaguchii</i> Lewis & Bentlage, 2009	<i>Chiropsalmus quadrigatus</i>	Habu-kurage	f, g

Methods

Specimens were collected using a scoop, 170 mm in diameter, at Souma, Onahama and Fujisawa, eastern Japan between 24 August 2011 and 18 October 2013 (Fig. 1). The medusae were fixed in 5% formalin in seawater, and deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT). Prior to fixation, a tentacle subsample of each specimen was preserved in 99.5 % ethanol for DNA extraction.

Taxonomic observation and measurements were made on preserved specimens. Measurements were made with digital calipers (CD-20CPX, Mitsutoyo Corporation, Japan) to the nearest 0.01 mm. The following measurements were made according to Gershwin 2005 (Fig. 2): bell height (BH), diagonal bell width (DBW), interhopal width (IRW), pedial width (PW), pedial canal width (PCW), outer keel width (OKW), inner keel width (IKW), tentacle base width (TBW), velarial width (VW). Sex was determined by examining gonadal tissue under a light microscope. In this study, some of new measurements were added as below: Diagonal exumbrella width (DEW) and diagonal subumbrella width (DSW) were both measured across diagonal base of outer keel or inner keel of pedalia, respectively, on a flattened specimen. Outer keel

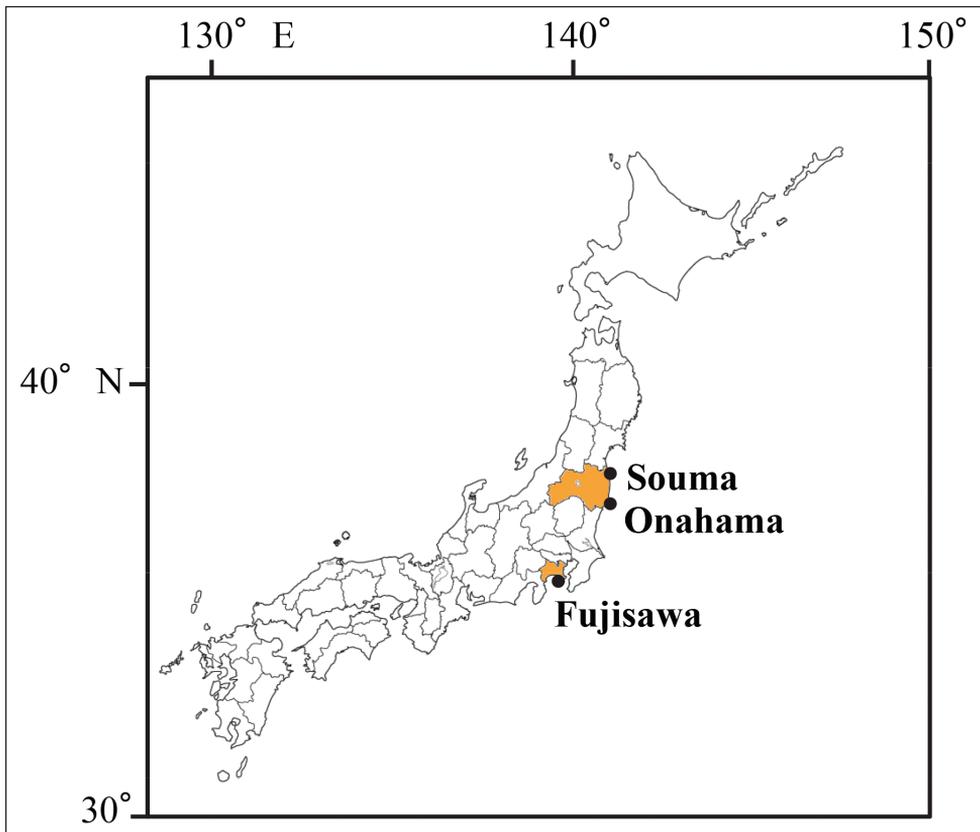


Figure 1. Map of the sampling sites.

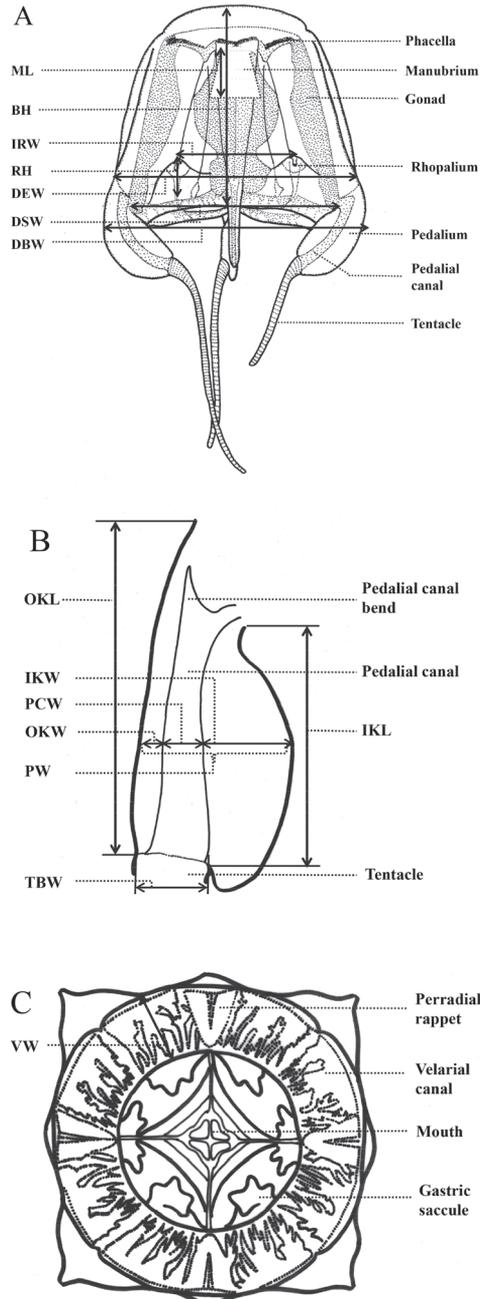


Figure 2. Key characters for identification and measurement of parts of the Cubozoa. **A** lateral view **B** pedalium **C** oral view. BH = bell height; DBW = diagonal bell width; DEW = diagonal exumbrella width; DSW = diagonal subumbrella width; IKL = inner keel length; IKW = inner keel width; IRW = interrhopalial width; ML = manubrium length; OKL = outer keel length; OKW = outer keel width; PCW = pedalial canal width; PW = pedalial width; RH = rhopalium height; TBW = tentacle base width; VW = velarial width.

length (OKL) and inner keel length (IKL) were both measured from the exumbrella lamella or subumbrellar lamella, respectively, to the tentacle insertion. Rhopalial height (RH) was measured from the base of rhopalial stalk to velarial turnover. Manubrium length (ML) was measured from the base of manubrium to mouth.

For nematocyst identification in the medusae, squashes prepared from fresh tissues were examined under a compound microscope. Nematocysts were identified according to Mariscal (1971), Östmann (2000) and Gershwin (2006b). For determination of the abundance of nematocyst types in medusae, roughly 500 nematocysts were identified, measured and counted from two specimens, NSMT-Co1569 and NSMT-Co 1571.

Near complete sequences of the nuclear 18S rDNA genes (approximately 1800 bp) were used for molecular phylogenetic analysis. Genomic DNA was extracted from the 99.5 % ethanol preserved subsampled tentacle tissue of NSMT-Co1569, NSMT-Co1571 and NSMT-Co1572 using the DNeasy Blood and Tissue Kits (Qiagen, Germany) following the manufacturers protocol. 18S rDNA was PCR amplified and sequenced using primers and protocols outlined in Collins et al. (2008). The new sequences were aligned using MEGA 6.06 with built in ClustalW. Phylogenetic analysis and pairwise distance measurements were determined using the maximum likelihood method with 1000 bootstrap replications in MEGA 6.06. All of these sequences have been deposited in DDBJ under accession numbers LC033478-LC033480 for the new species (Table 2).

Table 2. Taxa included in the phylogenetic analyses and GenBank accession numbers for sequences. Sequences obtained in this study are in **bold**.

Species	GenBank No.	Reference
<i>Alatina moseri</i> (Australia)	GQ849082 (as <i>Alatina mordens</i>)	Bentlage et al. 2010
<i>Carybdea branchi</i> (South Africa)	GQ849089	Bentlage et al. 2010
<i>Carybdea brevipedalia</i> (Japan)	GQ849092 (as <i>Carybdea mora</i>)	Bentlage et al. 2010
<i>Carybdea marsupialis</i>	AF358106	Bentlage et al. 2010
<i>Carybdea rastonii</i>	AF358108	Collins et al. 2002
<i>Carybdea xaymacana</i>	AF358109	Collins et al. 2002
<i>Carybdea xaymacana</i> (Panama)	GQ849090	Bentlage et al. 2010
<i>Carukia barnesi</i>	AF358107	Collins et al. 2002
<i>Copula sivickisi</i>	AF358110 (as <i>Carybdea sivickisi</i>)	Collins et al. 2002
<i>Gerongia rifkinae</i>	AF358105 (as <i>Darwin carybdeid</i>)	Collins et al. 2002
<i>Meteorona kishinouyei</i> (Fujisawa)	LC033478	this study
<i>Meteorona kishinouyei</i> (Onahama)	LC033479	this study
<i>Meteorona kishinouyei</i> (Souma)	LC033480	this study
<i>Morbakka virulenta</i> (Japan)	GQ849083	Bentlage et al. 2010
<i>Malo maxima</i> (Australia)	GQ849084 (as <i>Malo kingi</i>)	Bentlage et al. 2010
<i>Tripedalia cystophora</i> (Indonesia)	GQ849088	Bentlage et al. 2010
<i>Chironex fleckeri</i> (Australia)	GQ849073	Bentlage et al. 2010
<i>Chironex yamaguchii</i> (Japan)	GQ849076	Bentlage et al. 2010
<i>Chiropsalmus quadrumanus</i> (Brazil)	GQ849078	Bentlage et al. 2010
<i>Chiropsella bronzie</i>	AF358103 (as <i>Chiropsalmus</i> sp.)	Collins et al. 2002

Results

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Peterson, 1979

Class Cubozoa Werner, 1973

Order Chiropodida Haeckel, 1880

Family Chiropsellidae fam. n.

<http://zoobank.org/7690E036-F8BD-4B62-A7BB-EF9DD1D6DE87>

Family diagnosis. Chiropodida with unbranched gastric saccules. Gastric phacellae V-shaped or horseshoe shaped. Sensory niches U-shaped, with medial flap on upper rhopalial scale. Pedalial canal bend slight volcano or knee-shaped. Pedalia four, branched with 5 to 11 tentacles or unbranched with one tentacle.

Type genus. *Chiropsella* Gershwin, 2006.

Chiropsella bronzie Gershwin, 2006: 25–36, pl. 4–6.

Chiropsella bart Gershwin & Alderslade, 2006: 15–21, figs 1–4.

Chiropsella rudloei Bentlage, 2013: 1–7, figs 1–3.

Genus *Meteorona* gen. n.

<http://zoobank.org/E3AA7CD7-8DE7-4BEE-9151-2D6EAAD54793>

Genus diagnosis. Chiropsellidae with smooth, unbranched, slightly raised gastric saccules. Gonads leaf-shaped. Gastric phacellae horseshoe-shaped. Sensory niches U-shaped, with medial tongue-shape flap on upper rhopalial scale. Pedalia four, unbranched, scalpel-like with one tentacle per pedalium.

Type species. *Meteorona kishinouyei* sp. n. here designated.

Etymology. The genus name comes from the meteor-like appearance of the jellyfish shooting through the sea while swimming. The name *Meteorona* is taken from the Latin ‘Meteoron’, with the suffix -a. Gender is feminine.

***Meteorona kishinouyei* sp. n.**

<http://zoobank.org/02513932-6CFC-4A34-87AD-863677521769>

New Japanese name: Ryusei-kurage

Figures 3–12

Material examined. Holotype: NSMT-Co1572. Eastern Japan, Fukushima Prefecture, Souma, Matsukawa-ura, 37°48'39.3"N, 140°58'3.3"E, 14 October 2013, collector: Ko Tomikawa, one adult male. Paratypes. NSMT-Co1568, 1569, 1570. Eastern Japan, Kanagawa Prefecture, Fujisawa, Enoshima, Shonan Port, 35°18'4.75"N, 139°28'61.0"E,

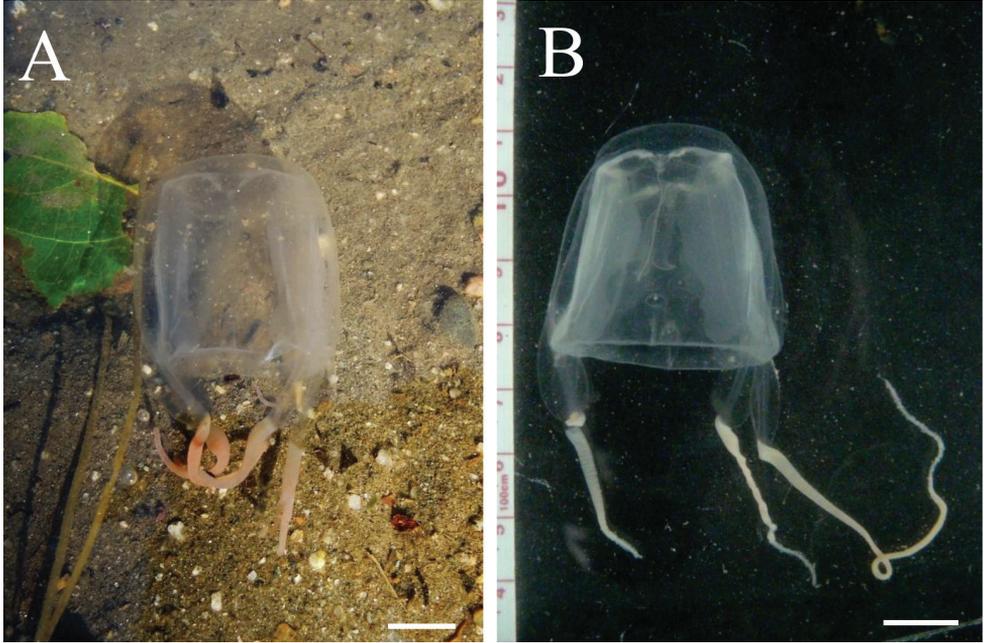


Figure 3. *Meteorona kishinouyei* sp. n., holotype, live, lateral view. **A** in situ, photo courtesy of Ko Tomikawa **B** in laboratory, photo courtesy of Yusuke Kondo. All scale bars represent 1 cm.

Table 3. Size (mm) of *Meteorona kishinouyei*. *: The holotype. Nos. Co1568-1571 are paratypes. BH = bell height; DBW = diagonal bell width; DEW = diagonal exumbrella width; DSW = diagonal subumbrella width; ML = manubrium length; IKL = inner keel length; IKW = inner keel width; IRW = interrhopalial width; OKL = outer keel length; OKW = outer keel width; RH = rhopalium height; PCW = pedalial canal width; PW = pedalial width; TBW = tentacle base width; VW = velarial width. All bars represent unavailable due to dissection.

Specimen No.	BH	DBW	DEW	DSW	IRW	PW	PCW	OKW
NSMT-Co1568	34,3	49,5	44,0	41,3	22,6	7,3	1,5	2,8
NSMT-Co1569	28,7	41,7	–	–	19,6	6,8	1,2	2,6
NSMT-Co1570	15,3	19,6	18,9	15,5	9,2	3,7	1,0	1,1
NSMT-Co1571	23,7	28,3	25,5	22,6	15,4	6,7	1,5	2,9
NSMT-Co1572*	34,6	46,5	42,9	39,6	22,0	6,9	1,8	3,1
Specimen No.	IKW	OKL	IKL	TBW	RH	VW	ML	SEX
NSMT-Co1568	3,0	17,2	11,2	2,6	5,6	5,5	15,2	Male
NSMT-Co1569	3,2	13,7	7,1	2,1	4,4	5,4	11,9	Female
NSMT-Co1570	1,3	7,5	4,9	0,9	2,3	2,8	3,6	Female
NSMT-Co1571	2,3	16,4	11,1	2,0	4,5	4,3	10,0	Female
NSMT-Co1572*	2,1	17,7	11,1	2,7	5,1	6,0	12,5	Female

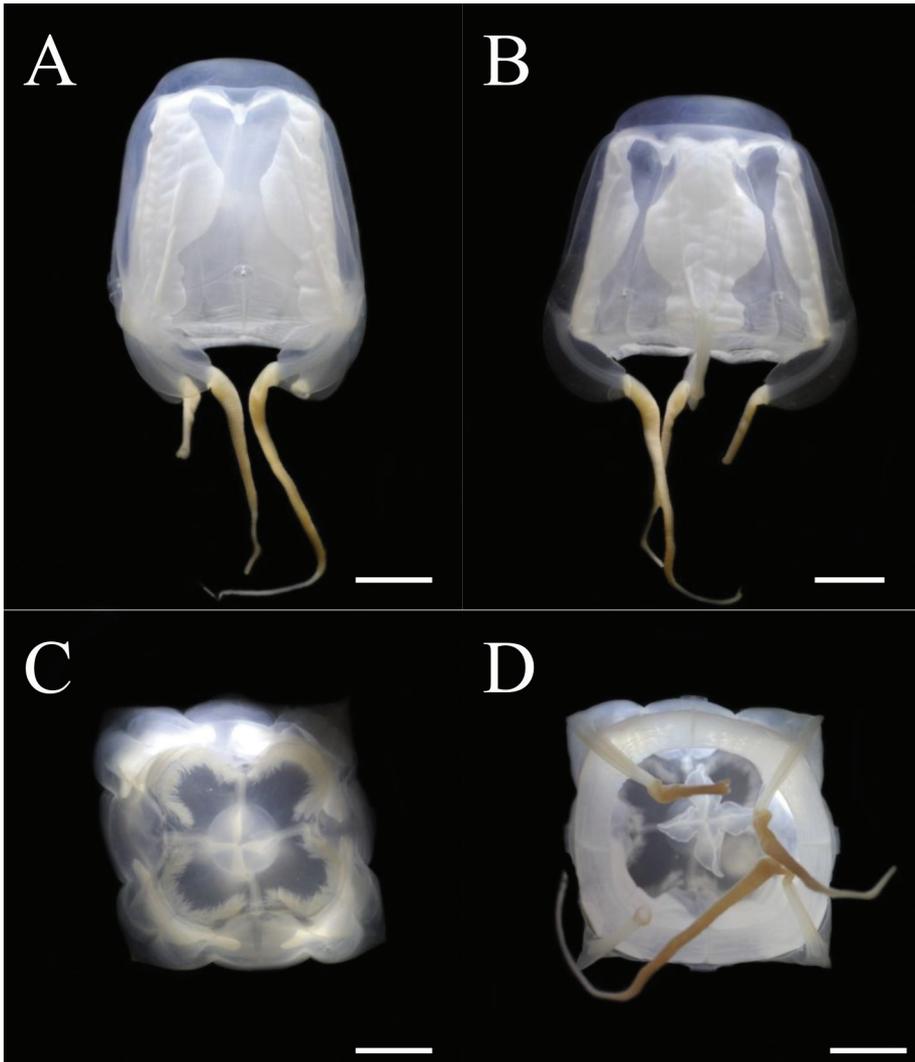


Figure 4. *Meteorona kishinouyei* sp. n., holotype. **A, B** lateral view **C** apical view **D** oral view. All scale bars represent 1 cm.

23 August 2011, collector: Haruka Shibata, one adult female. NSMT-Co1571. Eastern Japan, Fukushima Prefecture, Iwaki, Onahama Port, 36°56'29.1"N, 140°54'.32.9"E, 18 October 2013, collector: Shun Ishikawa, one adult female.

Description. Adult medusae with smooth exumbrella, with evenly thick mesoglea of rigid consistency (Fig. 3, Fig. 4, Fig. 5). BH about 35 mm and DBW about 50 mm (Table 3). Interradius thickened throughout bell height, with deep median furrow spanning height of bell. Adradial furrows spanning lower two thirds of bell. Coronal indentation shallow just below apex. Exumbrella lacking nematocyst warts or freckles. Gonads attached along entire length of interradial septa, leaf-shaped, not overlapping

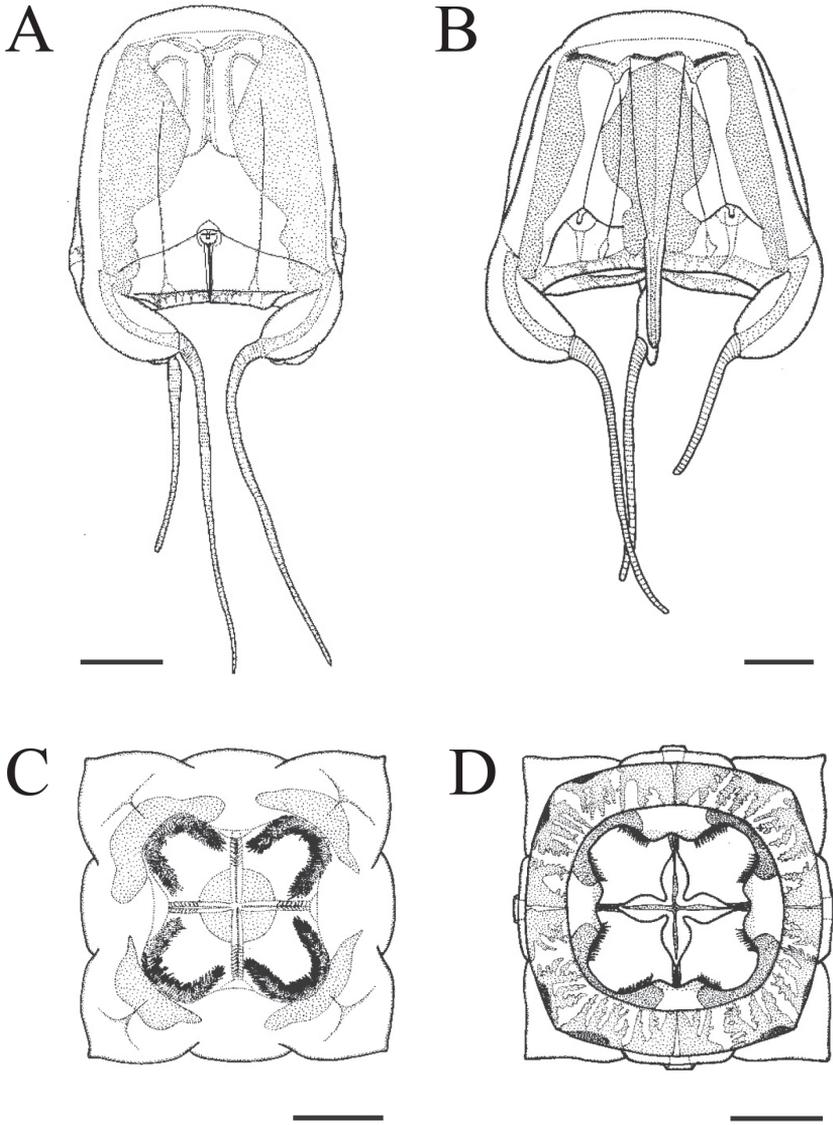


Figure 5. Illustration of *Meteorona kishinouyei* sp. n., holotype. **A, B** lateral view **C** apical view **D** oral view. All scale bars represent 1 cm.

along the interradius (Fig. 6A, 7A). Manubrium length about 40% of bell height. Manubrium cruciform with four narrow, lanceolate lips (Fig. 6B).

Gastric saccules unbranched, slightly raised and opaque (Fig. 5D, 6C, 7B). Gastric phacellae horseshoe-shaped in each corner of stomach (Fig. 6D, 7C). Gastric cirri simple and unbranched (Fig. 6E, 7D). Sensory niches four, perradial, U-shaped, with one shallow covering scale above and no lower scale, upper scale with central tongue-shaped flap partially shielding rhopalium, located approximately 1/6 of bell height from velarial

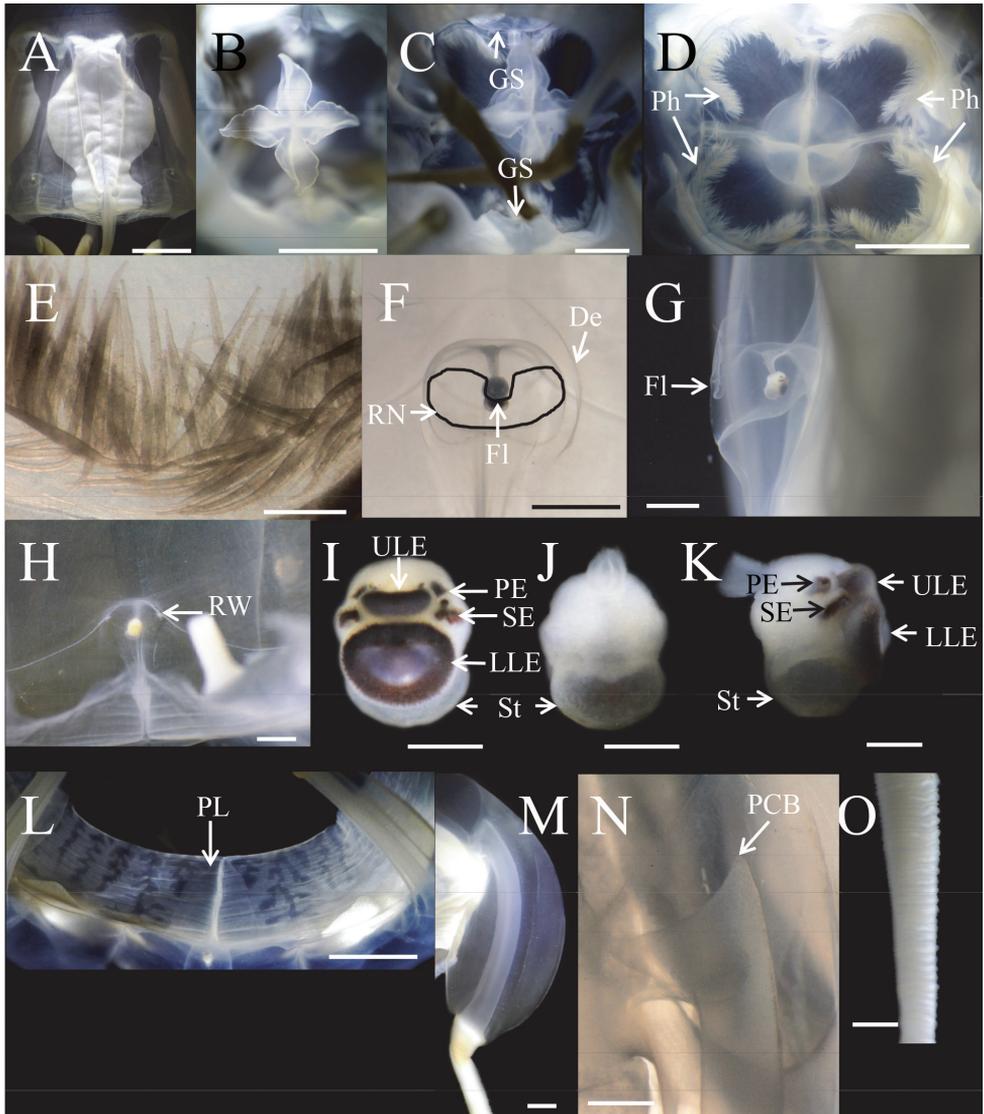


Figure 6. *Meteorona kishinouyei* sp. n., holotype. **A** gonad **B** mouth oral lips **C** gastric saccules **D** phacellae **E** gastric filaments **F** rhopalial niche ostia, front view **G** rhopalial niche ostia, side view **H** rhopalial window **I** rhopalium, front view **J** rhopalium, rear view **K** rhopalium, side view **L** velarium; **M** pedaliar canal bend **N** pedaliar canal bend **O** tentacle. De: depression; Fl: flap; GS: gastric saccule; LLE: lower lens eye; PCB: pedaliar canal bend; PE: pit eye; Ph: phacella; PL: perradial lappet; RN: rhopalial niche ostia; RW: rhopalial window; SE: slit eye; St: statolith; ULE: upper lens eye. Scale bars: 1 cm (**A–E, L**), 5 mm (**C**), 2 mm (**F–H, M–O**), 1 mm (**E**), 0.5 mm (**I–K**).

turnover (Fig. 6F, G, 7E, F). The rhopalial niche located in a triangular shaped depression of exumbrella (Fig. 6F, 7E). Subumbrellar rhopalial windows flat (Fig. 6H). Each of the four rhopalia bearing a set of six eyes, with the two median possessing prominent

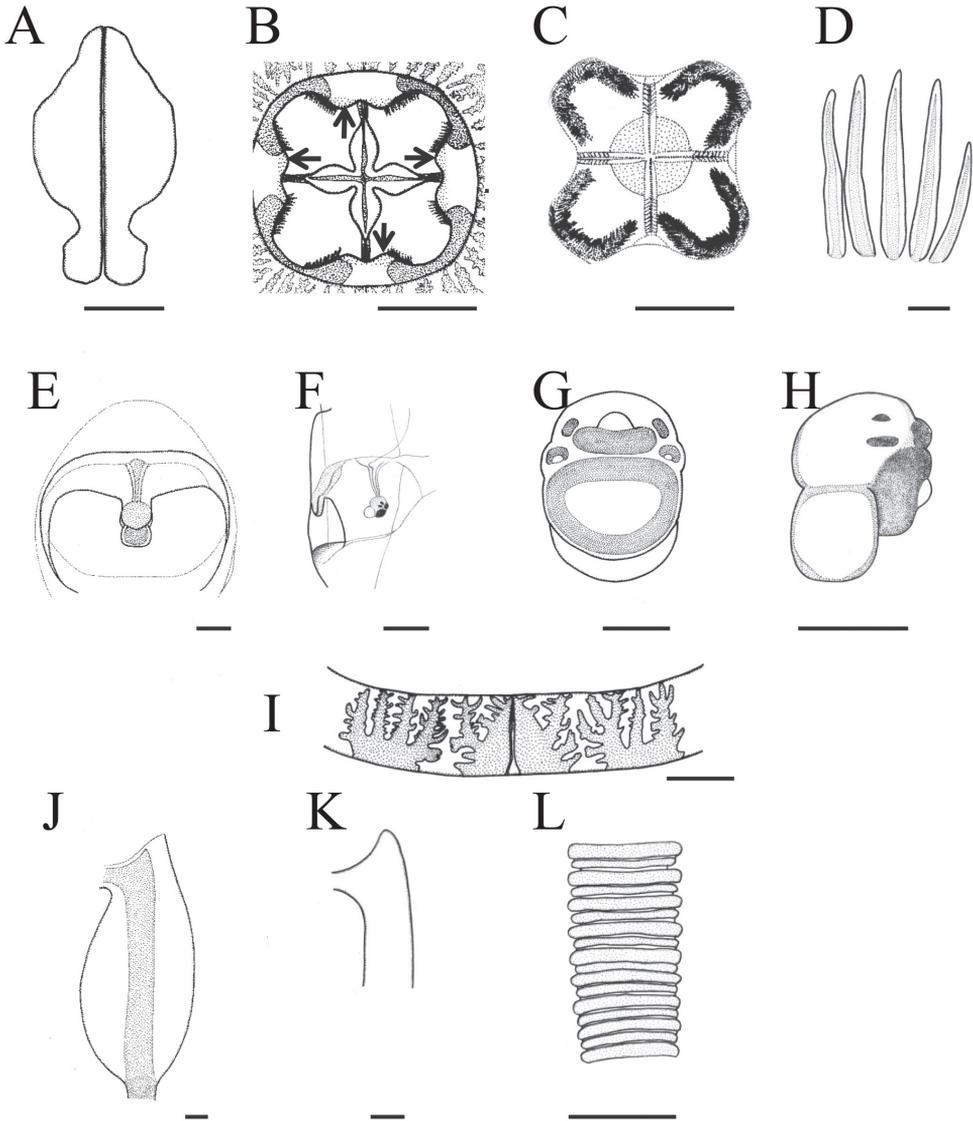


Figure 7. Illustration of *Meteorona kishinouyei* sp. n., holotype. **A** gonad **B** gastric saccule **C** phacellae **D** gastric filaments **E** rhopalium niche ostia and opening, front view **F** rhopalium niche ostia and opening, side view **G** rhopalium, front view **H** rhopalium, side view **I** velarium **J** pedalius **K** pedalial canal bend **L** tentacle. Allows indicate gastric saccule. Scale bars: 1 cm (**A–C**, **I**), 2 mm (**D**, **J–L**), 1 mm (**E–F**, **H**), 0.5 mm (**G**).

lenses and the four lateral ones adjacent to the lens eyes being pigment pits and slit (Fig. 6I–K, Fig. 7G, H). A single broad bean shaped statolith located behind each complex eye (Fig. 6I–K). Velarial canals one per octant, dendritic, with only the tips defined along the velarial margin (Fig. 6L, Fig. 7I). Frenulum a single solid, gelatinous struc-

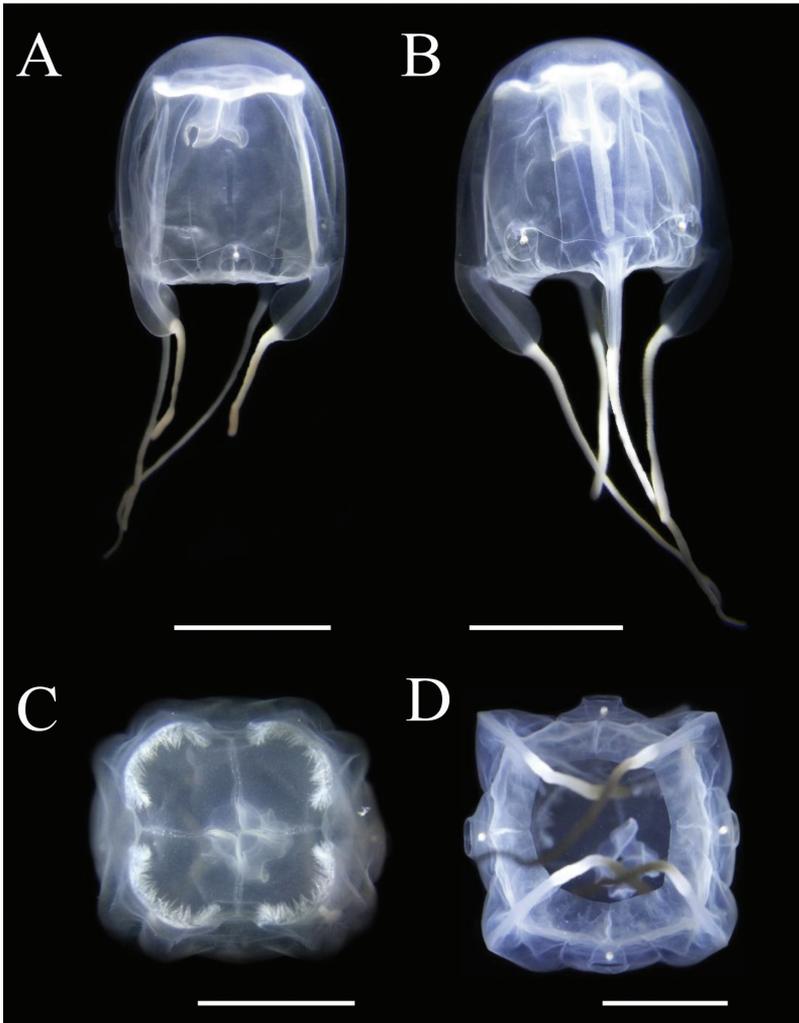


Figure 8. *Meteorona kishinouyei* sp. n., young medusa, paratype NSMT-Co1570. **A, B** lateral view **C** apical view **D** oral view. All bars represent 1 cm.

ture, extending to near velarial margin (Fig. 6L). Velarial width about 20% of DSW. Pedalia scalpel-like, each bearing one tentacle (Fig. 6M, Fig. 7J). Pedalia about half of bell height, inner keel rounded, about two times the width of pedalial canal. Outer keel width approximately twice that of pedalial canal, inner keel width and outer keel width almost equal. Proximal pedalial canal bend slight volcano-shaped (Fig. 6N, Fig. 7K). Tentacles four, with one per pedalium, base width up to 2.7 mm thick, round in cross section, with nematocyst rings alternate thick and thin in preserved specimens (Fig. 6O, 7L). Color and length of tentacles in living specimens was light brownish (Fig. 3A, B).

The smallest young medusa (NSMT-Co 1570) had a BH of about 15 mm, DBW of about 20 mm (Fig. 8, 9). Mesoglea was thin and softer than that of adults. Adradial

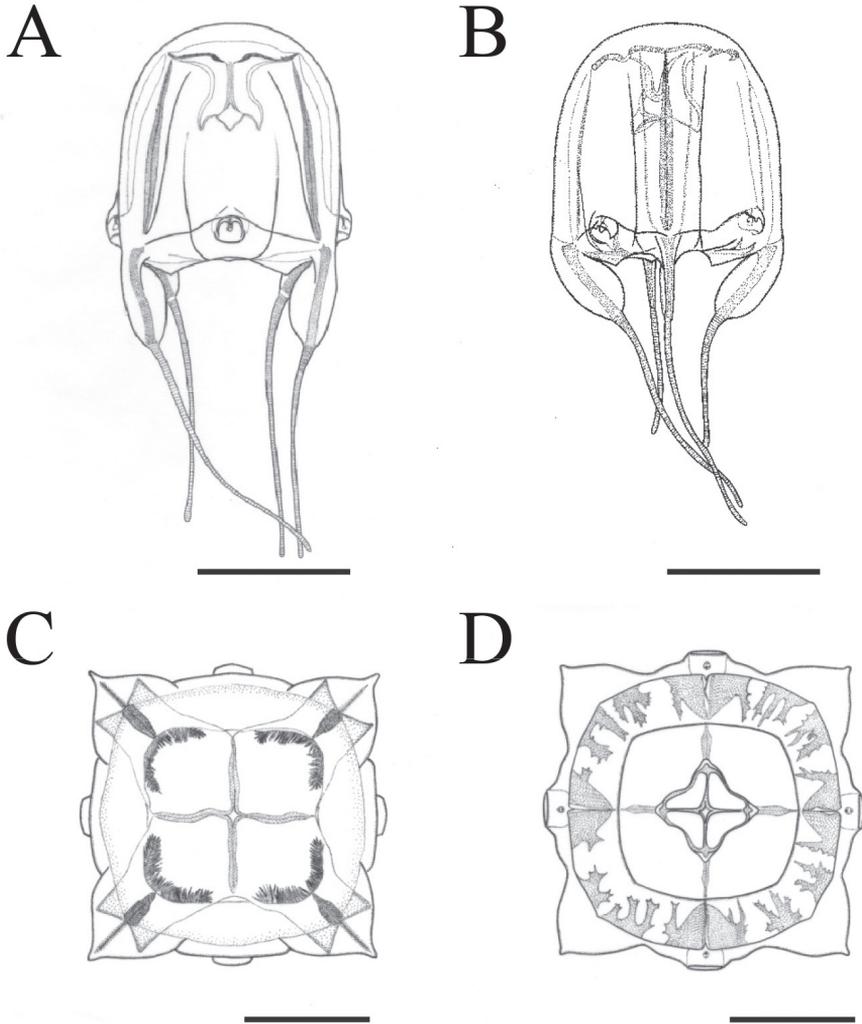


Figure 9. Illustration of *Meteorona kishinouyei* sp. n., young medusa, paratype NSMT-Co1570. **A, B** lateral view **C** apical view **D** oral view. All bars represent 1 cm.

furrows spanning half of the bell height (Fig. 8A, 9A). Interradial furrows spanning the entire height of the bell (Fig. 8B, 9B). Coronal indentation shallow and exumbrella nematocyst freckles absent. Gonads attached along entire length of interradial septa, leaf-shaped, not overlapping along the interradius (Fig. 10A). Manubrium length about 20% of bell height. Gastric saccules not developed. Gastric phacellae four-leaf clover shaped in each corner of stomach (Figs 8C, 9C, 10B). Depression of exumbrella not developed. Upper medial rhopalial scale flap shorter than in adults (Fig. 10C, D). Velarial canals one per octant, dendritic but with minor branching (Fig. 10E). Pedalium scalpel-like (Fig. 10F). Volcano-shaped pedalial canal bend smoother than in adults (Fig. 10G). Tentacle with nematocyst rings alternate thick and thin in preserved specimens (Fig. 10H).



Figure 10. *Meteorona kishinouyei* sp. n., young medusa, paratype NSMT-Co1570. **A** gonad **B** phacella **C** rhopaliar niche ostia, front view **D** rhopaliar niche ostia, side view **E** velarium **F** pedalius **G** pedial canal bend **H** tentacle. Fl: Flap; PCB: Pedial canal bend Scale bars: 2 mm (**A**, **E–F**), 1 mm (**C–D**, **G–H**), 0.5 mm (**B**).

Cnidome. Six different nematocyst types identified and measured in the paratype specimen (NSMT-Co1571) (Table 4, Fig. 11). Tentacle: Large microbasic *p*-rhopaloids, banana-shaped *p*-mastigophores, small oval beehive isorhizas, rod-shaped isorhizas, small sub-spherical *p*-rhopaloids. Manubrium: Tiny microbasic euryteles, small sub-spherical *p*-rhopaloids. Phacellae: Tiny microbasic euryteles, small sub-spherical *p*-rhopaloids. Exumbrella lacking nematocysts.

Molecular phylogenetics. In the resulting ML tree (Fig. 12), three major monophyletic clades were formed in the order Chirodropida: 1) Chirodropidae (*Chironex*

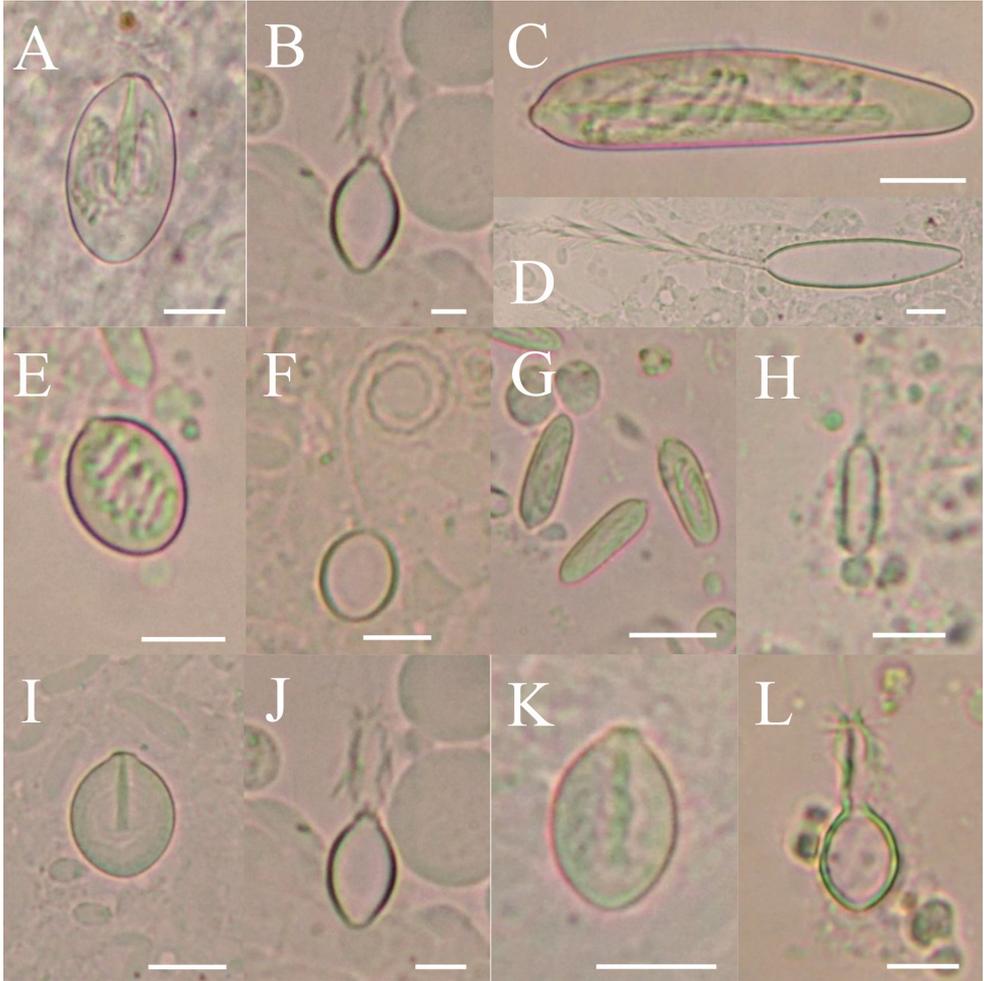


Figure 11. Nematocysts of *Meteorona kishinouyei*, paratype NSMT-Co1571. **A, B** Large microbasic *p*-rhopaloids. Intact (**A**), discharged (**B**) **C, D** Banana-shaped *p*-mastigophores. Intact (**C**), discharged (**D**) **E, F** Small oval beehive isorhizas. Intact (**E**), discharged (**F**) **G, H** Rod-shaped isorhizas. Intact (**G**), discharged (**H**) **I, J** Small sub-spherical *p*-rhopaloids. Intact (**I**), discharged (**J**) **K, L** Tiny microbasic euryteles. Intact (**K**), discharged (**L**). All bars represent 10 μ m.

fleckeri and *C. yamaguchii*); 2) Chiropsalmidae (*Chiropsalmus quadrumanus*); 3) A third group (*Meteorona kishinouyei* and *Chiropsella bronzie*). The monophyly of the third group was evident in the 18S phylogenetic tree with high bootstrap values, well supporting the validity of the new family.

Habitat and ecology. Holotype specimen of *Meteorona kishinouyei* was collected near shore in shallow waters of the Matsukawa-ura lagoon, Fukushima prefecture, eastern Japan. Until March 2011, the north part of the lagoon extended to the sea via a man-made channel. However, the channel was destroyed and considerable sea water

Table 4. Cnidomes of *Meteorona kishinouyei*, paratype (NSMT-Co1571). D, L represent capsule diameter and length, respectively, in μm .

Part	Type		Min	Max	Mean	SD	N
Tentacle	banana-shaped microbasic <i>p</i> -mastigophore	D	11,58	15,49	13,62	1,06	21
		L	58,22	67,85	62,60	2,54	21
	large microbasic <i>p</i> -rhopaloid	D	15,64	20,61	17,64	1,21	30
		L	26,05	33,02	29,27	1,65	30
	small sub-spherical <i>p</i> -rhopaloid	D	11,63	15,49	13,57	1,08	25
		L	15,09	19,96	17,37	1,31	25
	small oval beehive isorhiza	D	9,77	11,86	10,67	0,56	30
		L	12,36	15,12	13,38	0,72	30
	rod-shaped isorhiza	D	3,38	5,92	4,56	0,62	30
		L	9,92	18,31	15,11	1,45	30
Exumbrella	N/A	D	–	–	–	–	–
		L	–	–	–	–	–
Manubrium	small sub-spherical <i>p</i> -rhopaloid	D	12,45	16,67	14,50	0,97	30
		L	16,15	19,35	17,79	0,90	30
	tiny microbasic eurytele	D	9,80	12,19	11,06	0,61	30
		L	14,29	18,69	16,22	0,98	30
Phacella	small sub-spherical <i>p</i> -rhopaloid	D	11,73	14,39	13,27	0,63	30
		L	14,03	18,42	16,37	1,00	30
	tiny microbasic eurytele	D	9,63	12,49	10,82	0,83	15
		L	12,56	19,79	15,82	1,91	15

flowed into the lagoon as a result of the 2011 Tohoku earthquake and tsunami. *M. kishinouyei* medusae may have been brought into the lagoon on the high waves. Moreover, *M. kishinouyei* may be a neritic species. Young medusae appeared during August, while adult medusae appeared between August and November. *Carybdea brevipedalia* was collected together with *M. kishinouyei* along at Onahama port and Shonan at the water surface in a shallow area (water depth 3–10 m) port during daytime. Polyps of *M. kishinouyei* may metamorphose into young medusae during summer. However, the polyp stage and life history are unknown.

Etymology. The species is named *kishinouyei* (noun in apposition) to honor Professor Kamakichi Kishinouye, zoologist and fishery scientist. Kishinouye's meticulous studies and observations have led to many important contributions in the description of cubozoan zoology

Differential diagnosis. A comparison of key features of the species of Chirodropida is presented in Table 5. *Meteorona kishinouyei* can be distinguished from all other chirodropid species by shape of pedalium, gastric saccules and rhopaliar niche. All of the species in the order Chirodropida have branching pedalia, each bearing multiple tentacles. *M. kishinouyei* has one tentacle per unbranching pedalium like species of the order Carybdeida. Shape of gastric saccules are cock's-comb shaped/grape-cluster-like (*Chironex*), elongate, tapered, with numerous axial processes, or absent (*Chirodropus*)

Table 5. Morphology of chirodropida medusae in previous and the present studies. All bars represent lacking data.

Family	Genus	Nematocysts on exumbrella	Gastric saccule shape	Gastric phacella shape	Rhopalial covering scale	Number of tentacles	Pedialial branching pattern	Pedialial canal	Pedialial canal bend
Chiropsellidae fam. n.	<i>Meteorona</i> gen. n.	–	Slightly raised	Horseshoe shaped	Tongue	1	Unbranching	Undivided	Slight volcano
	<i>Chiropsella</i>	–	Solid and spherical, sessile	V-shaped Horseshoe shaped	Cigar/Banana/ Tongue/Squarish to rounded	5–11	Usually but always opposite	Divided	Knee-shaped/ Slight volcano
Chirodropidae	<i>Chirodropus</i>	–	Elongate, tapered, with numerous axial processes, or absent	V-shaped	–	9–21	Bilateral with reduced 'palm'	Unknown	Spike
	<i>Chirodactis</i>	–	–	Arranged vertically along stomach wall	–	9–11	Bilateral with reduced 'palm'	Unknown	Spike
	<i>Chironex</i>	–	cock's-comb shaped/grape-cluster-like	V-shaped	–	7–15	Alternate	Divided	Spike/volcano
Chiropsalmidae	<i>Chiropsalmus</i>	Fine warts	Finger-like and short	Horseshoe shaped	–	2–9	Opposite	Undivided	Slight volcano
	<i>Chiropsoides</i>	–	Finger-like and long	V-shaped	–	4–11	Unilateral	Undivided	Spike

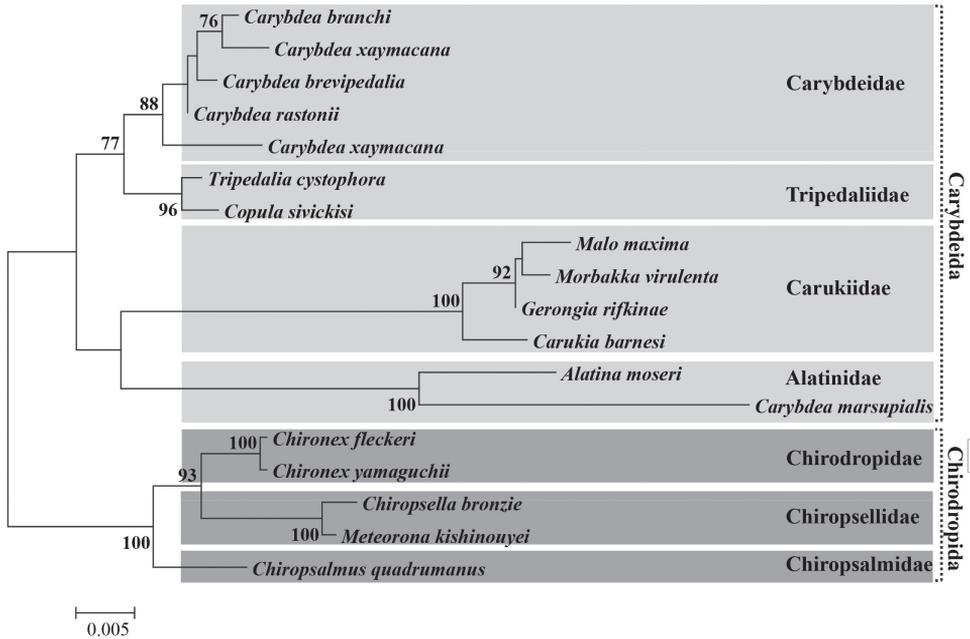


Figure 12. Maximum-likelihood tree for 18 cubozoan taxa based on the nuclear 18S rDNA data set. Scale bars indicate branch length in substitutions per site. Nodal support values are presented as the ML bootstrap value; only values >50% are shown.

in Chirodropidae, finger-like in Chiropsalmidae, spherical in *Chiropsella*. *M. kishinouyei* were slightly raised. All chirodropids have sensory niches located in a triangular shaped depression of the exumbrella. However, only *M. kishinouyei* and *Chiropsella* have a central flap hanging down from the upper scale of the rhopalial niche. Exumbrella nematocysts are lacking in all chirodropid species except *Chiropsalmus*.

Discussion and conclusions

Meteorona kishinouyei is most likely to be confused with the carybdeid *Carybdea brevipedalia* from eastern and northern Japan. Kishinouye (1891) described two cubozoan species, *C. brevipedalia* and *Carybdea latigenitalia*, collected from Shima (Mie prefecture, western Japan) and Hitachi (Ibaraki prefecture, eastern Japan) respectively. Box jellyfish with similar descriptions have been reported as *Carybdea rastonii* or *Carybdea mora* (Kramp 1961; Gershwin and Gibbons 2009). However, recent molecular phylogenetic analyses and taxonomic investigations suggest that *C. rastonii* reports from Japan should be regarded as *C. brevipedalia* (Bentlage et al. 2010; Bentlage and Lewis 2012). However, the account and drawing of *C. latigenitalia* in the original description agree well with *M. kishinouyei*: dendritic velarial canals, well developed mouth lips,

half-moon shaped phacellae, very wide gonads and one tentacle per unbranching long pedalum (Kishinouye 1891). However, Uchida (1929) suggest that *C. latigenitalia* should be regarded as *C. rastonii*. Unfortunately, it is likely that the material investigated for the original description of *C. latigenitalia* was lost. Additionally, as the name has not been in common usage, and it no longer fits the description of a species of the genus *Carybdea*, there is no justification for/obligation to resurrect the species name (ICZN 1999).

Two families, Chiropodidae and Chiropsalmidae are currently classified in the order Chiropodida (Gershwin 2006a) defined by Gershwin (2006a) as: Cubozoa with branched pedalia bearing numerous tentacles; with or without gastric saccules. However, *M. kishinouyei* has one tentacle per unbranched pedalia and leaf-like gonads. We therefore propose emending the order Chiropodida as follows:

Order Chiropodida Haeckel, 1880, sens. emend.

Diagnosis. Cubozoa with or without gastric saccules; with branched or unbranched pedalum; with a triangular shaped depression of exumbrella surrounded rhopaliar niche; with a triangular shaped perradial lappet and highly divergent branching velarial canals.

Based on our maximum likelihood study, *M. kishinouyei* and *Chiropsella bronzie* appear to be the closest relatives in the currently understood cubozoan phylogenetic relationships. Moreover, *Meteorona* and *Chiropsella* have some common morphological characters such as the unbranched gastric saccule, rhopaliar flap and slight volcano-shaped pedalial canal bend. However, the shape of pedalum and number of tentacles differs between the two species.

Chiropsella has been classified as a genus in the family Chiropsalmidae (Gershwin 2006a, b, Gershwin and Alderslade 2006, Bentlage 2013). Family Chiropsalmidae defined as follows by Gershwin (2006a): Chiropodida with smooth, unbranched, finger-like gastric saccules, lacking gastric filaments. However, *Chiropsella* has gastric filaments in its stomach (Gershwin 2006a, b, Gershwin and Alderslade 2006, Bentlage 2013). Therefore, the establishment of the family Chiropsellidae is proposed that includes *Chiropsella* and *Meteorona*.

Acknowledgements

We would like to express our sincere thanks to Ko Tomikawa, Yusuke Kondo (Hiroshima University) and Shun Ishikawa (Kitasato University) for providing the specimens and photos. The manuscript was greatly improved by the constructive comments Shin Kubota (Kyoto University) and Cheryl Lewis (National Museum of Natural History, Smithsonian Institution). The research was financially supported by the Sasakawa Scientific Research Grant from The Japan Science Society and the Research Institute of Marine Invertebrates Foundation by Research Institute of Marine Invertebrates.

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Description of a new species of *Potamonautes* MacLeay, 1838, from the iSimangaliso Wetland Park, South Africa

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Academic editor: S. De Grave | Received 5 March 2015 | Accepted 27 April 2015 | Published 11 May 2015

<http://zoobank.org/305BDD0E-C8EA-4D4B-A280-4AF2CD7348F5>

Citation: Peer N, Perissinotto R, Gouws G, Miranda NAF (2015) Description of a new species of *Potamonautes* MacLeay, 1838, from the iSimangaliso Wetland Park, South Africa. *ZooKeys* 503: 23–43. doi: 10.3897/zookeys.503.9532

Abstract

A new species of freshwater crab, *Potamonautes isimangaliso* **sp. n.**, is described from the western shores of False Bay, Hluhluwe, within the iSimangaliso Wetland Park, South Africa. While bearing a superficial resemblance to *P. lividus*, the new species has been found to be genetically distinct, diverging from the former by 7.4–7.8% in mtDNA. *Potamonautes isimangaliso* most closely resembles *P. lividus*, but is distinguished by a unique suite of carapace characters, colouration, and size. The new species also lives in close association with oxygen-poor, fresh ephemeral pans, while the habitat of *P. lividus* is well above the surface water line of the closest water body. An updated identification key for the *Potamonautes* species of South Africa is provided.

Keywords

Brachyura, freshwater, *Potamonautes*, taxonomy, ephemeral pans, sand forest, iSimangaliso Wetland Park

Introduction

Freshwater crabs play a key role in ecosystems by serving as an important food source for larger taxa, and recycling nutrients through detritivorous feeding habits (Cumberlidge 2009). They link terrestrial and aquatic habitats by moving between the two systems, and are considered bioindicator species of environmental change in some habitats (Schuwerack et al. 2001). *Potamonautes* is the only genus of primary freshwater crab (Yeo et al. 2014) in South Africa, with 16 described species occurring in the country, two having been described in recent years (Daniels and Bayliss 2012; Phiri and Daniels 2014).

The iSimangaliso Wetland Park forms the southernmost region of the Maputaland centre of endemism and constitutes the focus of biodiversity conservation in the region (Smith et al. 2008). Recent ecological and biodiversity surveys of Lake St Lucia have been conducted in an attempt to update local taxonomic records, identify undescribed species, highlight the change in diversity over time, and provide illustrated and annotated checklists to use as identification tools (Nel et al. 2012; Peer et al. 2014; Perissinotto et al. 2014). Surveys have revealed the existence of an undescribed species of *Potamonautes* along the western shores of False Bay (Fig. 1) that most closely resembles *P. lividus* Gouws, Stewart & Reavell, 2001 in morphological appearance, exhibiting a rounded vaulted carapace and the potential ability to spend a large amount of time out of water. However, genetic analysis showing a 7.4–7.8% difference across the combined 16S rDNA and COI gene fragments in comparison to *P. lividus* (G. Gouws unpubl.) and morphological analysis (present study) indicate that the two species are indeed distinct.

In this paper we describe *Potamonautes isimangaliso* sp. n. from the sand forests of the iSimangaliso Wetland Park. NP and GG wrote the taxonomic part of this study, including the description of the new species, while the contribution of the other authors dealt with natural history and ecological observations.

Materials and methods

Collection of crabs

Crabs were collected from four localities (Fig. 1) using a sweep net in pans or by active hand capture. The unidentified species was found in 2012–2013 during routine surveys in the area as part of an ongoing project on the biodiversity of Lake St Lucia, supported by the iSimangaliso Park Authority and the provincial conservation authority, Ezemvelo KZN Wildlife, and subsequently during a dedicated survey undertaken in February 2015. Specimens were preserved in 10% formalin or 70% ethanol, once photographs were taken using a Canon Powershot G12.

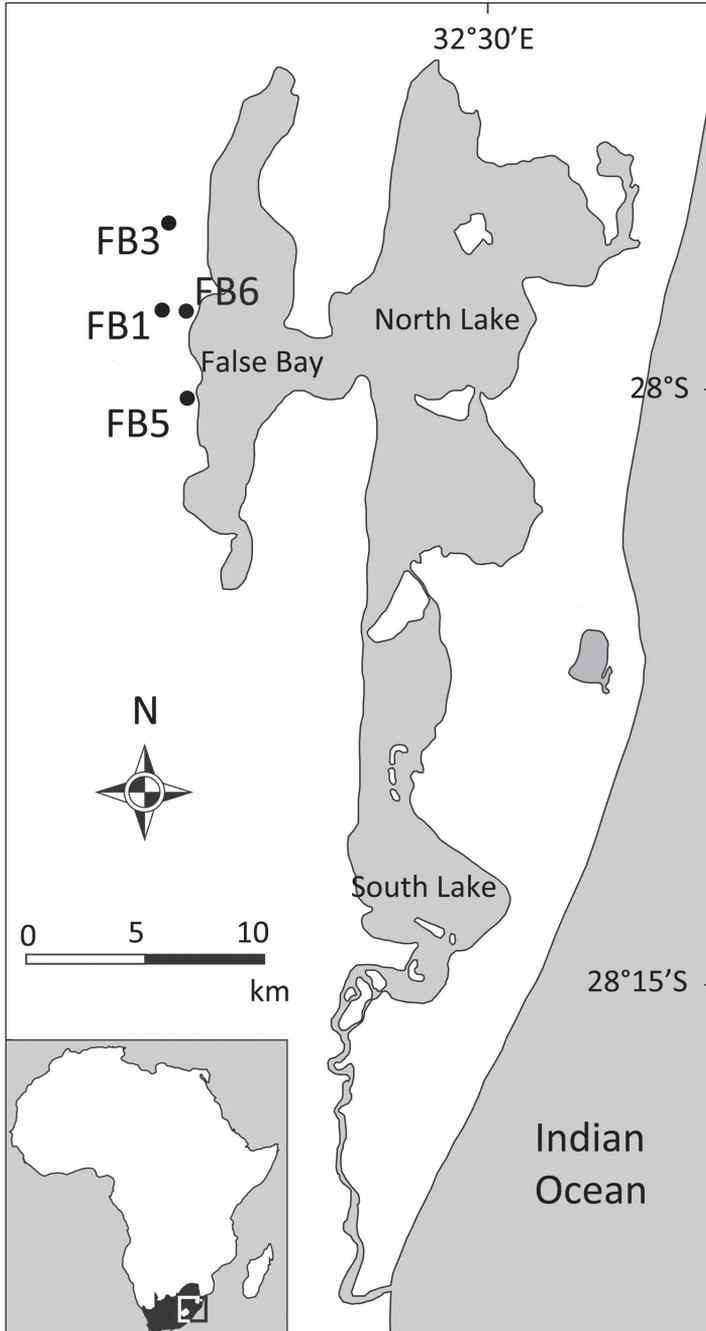


Figure 1. Map of Lake St Lucia on the east coast of South Africa. Collection localities, indicated by black dots and labelled with codes, are all restricted to the western shore of False Bay, within the False Bay Park. FB1 = Main Road Pan; FB3 = Mpophomeni Pan; FB5 = Dukandlovu Pan; FB6 = Sandy Point Pan.

Morphological and morphometric analyses

In the laboratory, a pair of Vernier callipers was used to measure morphological variables. A Nikon SMZ25 microscope fitted with a Nikon Digital Sight DS-Fi2 camera was used for macro-examination and to take photos of gonopods and mouthparts.

Abbreviations for depositories and provinces:

ISAM	Iziko South African Museum, Cape Town, South Africa
NMMU	Nelson Mandela Metropolitan University Collection.
EC	Eastern Cape
WC	Western Cape
KZN	KwaZulu–Natal

Abbreviations for all morphological and morphometric characters (Gouws et al. 2001)

CL	Carapace length
CWW	Carapace widest width
CWP	Carapace posterior width
PFC	Distance between postfrontal crest and anterior margin
ED	Distance between orbits
CWA	Distance between exorbital teeth
CH	Carapace height
AW6	Width of sixth abdominal segment
MCPL	Major cheliped propodus length
MCPH	Major cheliped propodus height
P2ML	Pereopod 2, merus length
P2MH	Pereopod 2, merus height
s2/s3	First sternal groove (suture between the second and third sulci)
s3/s4	Second sternal groove (suture between the third and fourth sulci)
CRDL	Right cheliped, dactyl length
CLDL	Left cheliped, dactyl length
CRPL	Right cheliped, propodus length
CLPL	Left cheliped, propodus length
CRPW	Right cheliped, propodus width
CLPW	Left cheliped, propodus width
ML	Merus length
MW	Merus width

For the morphometric analyses, eight variables (CL, PFC, CWP, ED, CH, AW6, CRPL and CRPW) were log transformed and used to run a stepwise discriminant function analysis in STATISTICA v 12.5 (Statsoft 2004). Data for *Potamonautes lividus* were obtained from G. Gouws and represent the specimens used for the de-

scription of *P. lividus* (Gouws et al. 2001). Classification functions were calculated and individuals were then reassigned to groups based on a priori probabilities. Canonical scores were plotted for both species on a frequency histogram to support distinction between the two forms. Lastly, a linear regression analysis was used to examine variation for specific variables.

Genetic analysis

DNA was extracted from each specimen and amplification of the mitochondrial cytochrome c oxidase subunit I (COI) and 16S ribosomal DNA genes were carried out following protocols outlined by G. Gouws (unpubl.). Amplifications were confirmed by electrophoresis in 1% agarose gels with an ethidium bromide stain. The product was then viewed on an ultraviolet transilluminator. Sequences were generated from a representative of the new species, using approaches described elsewhere (Daniels et al. 2002; Phiri and Daniels 2014; G. Gouws (unpubl.)).

Results

Morphometric analysis

The new species (*Potamonautes isimangaliso* sp. n.) was distinguished from *P. lividus* by its larger size, flatter carapace and more rounded posterior. The carapace variables CL, CH and CWP contributed the most to distinguishing between the two forms in the discriminant analysis. Fig. 2 highlights the morphometric distinction between the two species.

The classification function was calculated for both species as follows:

$$Y(P. isimangaliso) = 926.798(\text{LogCL}) - 602.076(\text{LogCH}) - 7.966(\text{LogCWP}) - 178.319$$

and

$$Y(P. lividus) = 1428.33(\text{LogCL}) - 743.234(\text{LogCH}) - 321.805(\text{LogCWP}) - 296.179$$

Individuals were reassigned to groups based on a priori probabilities using these classification functions. 100% of both forms were correctly classified with no individuals being reassigned. Three variables (CWP, PFCD and CH) were regressed over CL and a significant difference was seen between the two species as follows: CWP/CL – SS = 0.1, df = 2, F = 2.29, p < 0.001; PFCD/CL – SS = 0.1, df = 2, F = 2.29, p < 0.001; CH/CL – SS = 0.1, df = 2, F = 5.99, p < 0.001 (Fig. 3a, b, c)

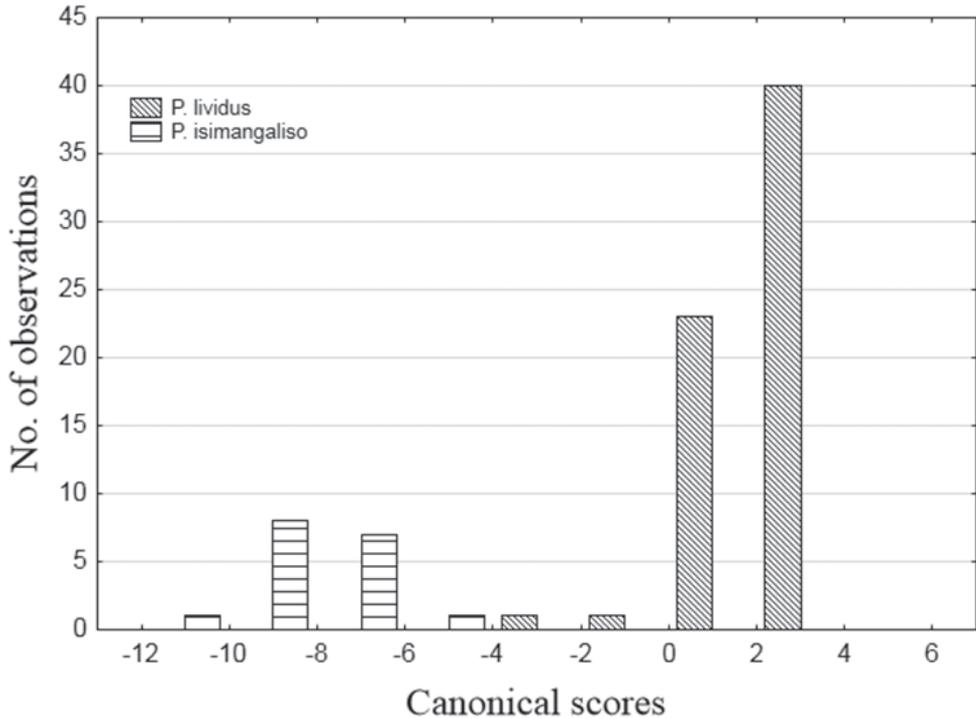


Figure 2. Histogram of canonical scores for *P. isimangalis* and *P. lividus* calculated from a discriminant function analysis.

Taxonomic description

Potamonautes isimangalis Peer & Gouws, sp. n.

<http://zoobank.org/4D5E76D6-BFEB-41CE-BF3D-EBD2AA3820D7>

Type series. Holotype: male, CL = 37 mm, ephemeral pan 200 m away from the western fence of False Bay Park (FB3), iSimangaliso Wetland Park (27°57'31.33"S, 32°21'42.15"E; elevation 62 m), 2 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy and L. Clennell legit (ISAM A78908).

Allotype: female, CL = 27 mm, ephemeral pan, next to road leading from Dukandlovu campsite to False Bay Park entrance gate (FB5), 5 km south of Lister's Point, iSimangaliso Wetland Park (28°0'51.70"S, 32°21'55.36"E; elevation 10 m), 1 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy and L. Clennell legit (ISAM A78909).

Paratypes: one male, one female, collection data same as per holotype (NMMU); one male, ephemeral pan along the main road of False Bay Park (FB1), iSimangaliso Wetland Park (27°58'32.02"S, 32°21'51.62"E; elevation 42 m), 1 February 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy, and L. Clennell

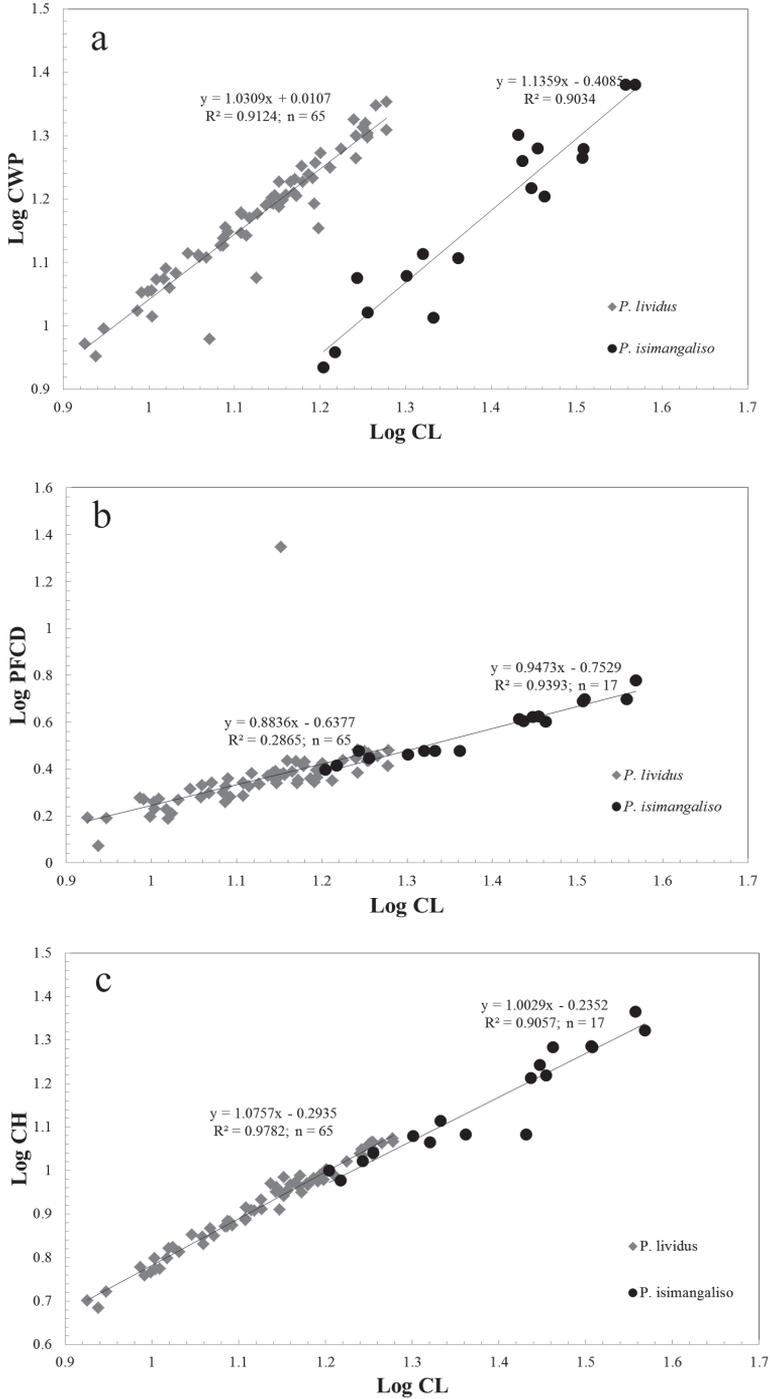


Figure 3. Regressions of **a** LogCWP over LogCL **b** LogPFCD over LogCL and **c** LogCH over LogCL between the two species *P. isimangaliso* and *P. lividus*. All differences between regressions were statistically significant ($p < 0.001$).

Table 1. Morphometric variables (mm) of *Potamonautes isimangalis* sp. n. holotype and paratype specimens.

Variable	Holotype	Males (n=8)	Females (n=7)
CL	37	13.2–36.1	18–27
CWW	55.1	18–53	26–40.1
CPW	24	9–24	10.5–20
PFC	6	2–5	2.8–4.1
ED	15.6	5–16	8.5–12.8
CWA	34	14.1–40.5	21.5–32
CH	21	7–23.2	11–12.1
AW6	12	3.1–11	7–23.4
MCPL	49.3	11.5–44.5	17.2–29.2
MCPH	21.9	4.1–20.1	7–13.7
P2ML	21.3	6.5–18.9	8.9–13.8
P2MH	6.5	2–6.1	3–5

legit (ISAM A78910); one male, ephemeral pan, collection data same as per allotype (ISAM A78911); two males, two females, ephemeral pan along the main road of False Bay Park (FB1), iSimangalis Wetland Park (27°58'32.02"S, 32°21'51.62"E; elevation 42 m), 31 January 2015, R. Perissinotto, R.H. Taylor, D. Bilton, M.S. Bird, S.J. du Plooy, and L. Clennell legit (ISAM A78912); two females, collection data same as per holotype, 26 November 2013, R. Perissinotto, R.H. Taylor, N. Peer, N.A.F. Miranda, M.S. Bird, J.L. Raw and L. Clennell legit (NMMU); one male, one female, ephemeral pan near Sandy Point in False Bay Park (FB 6), iSimangalis Wetland Park (27°58'36.0"S, 32°22'17.0"E; elevation 12 m), 25 November 2013, R. Perissinotto, R.H. Taylor, N. Peer, N.A.F. Miranda, M.S. Bird, J.L. Raw and L. Clennell legit (ISAM A78913); two males, ephemeral pan, collection data same as per allotype, 5 December 2012, R. Perissinotto, N.A.F. Miranda, N. Peer, J.L. Raw legit (ISAM A78914).

Diagnosis. Main distinguishing features of *P. isimangalis* from *P. lividus* Gouws, Stewart & Reavell, 2001 as follows: slightly granulated, horizontal anterolateral margin more rounded than in *P. lividus*; downward projection of postfrontal crest at exorbital edges; uniform colouration of dark purplish brown with lighter or orange coloured joints, cheliped tips and pereopods tips. *Potamonautes isimangalis* is larger than *P. lividus*, with a maximum size of 37 mm CL recorded in males.

Description. Carapace (Fig. 4a, c). Cephalothorax somewhat vaulted (CH/CL = 0.57), wide (CWW/CL = 1.49) and ovoid in general. Branchial region extremely rounded, forming a quarter of a circle with anterolateral margin. Anterior margin straight, lying on same horizontal plane as anterolateral margin; anterolateral margin slightly granulated. Urogastric grooves well-defined; cardiac and cervical grooves well-defined where attached to the urogastric groove, but then becoming poorly defined and shallow towards edge of carapace. Epigastric lobes well-defined above postfrontal crest by two indentations forked from midpoint of postfrontal crest. Postfrontal crest slightly granulated, curving forward medially. Postfrontal crest indistinct medi-



Figure 4. *Potamonautes ismangaliso* sp. n. male holotype CWW 55.1 mm (ISAM A78908). **a** dorsal view **b** ventral view and **c** cephalothorax, frontal aspect. Scale bar: 10 mm. Photos: Nasreen Peer.

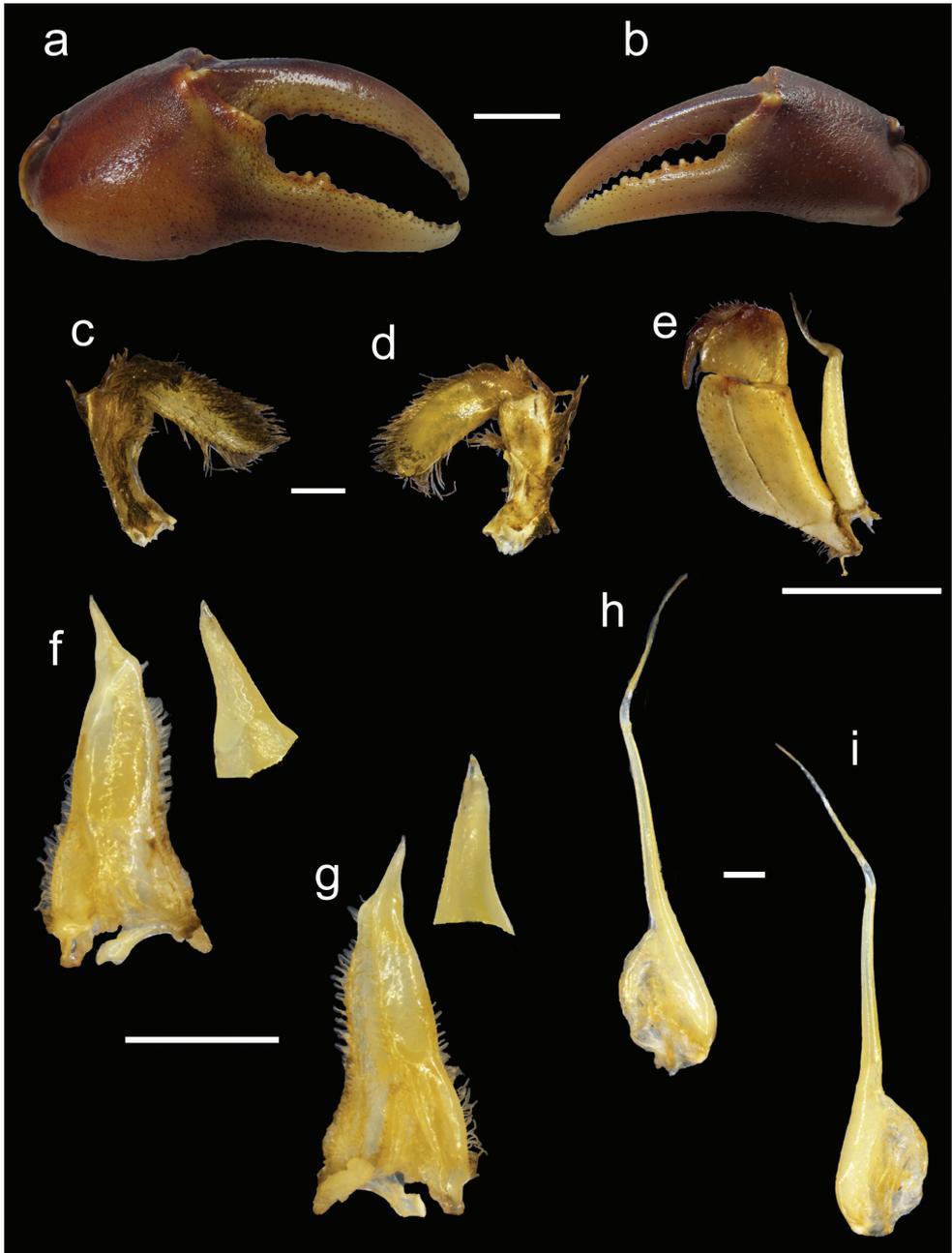


Figure 5. *Potamonautes isimangaliso* sp. n. male holotype CWW 55.1 mm (ISAM A78908). **a** major cheliped **b** minor cheliped **c** right mandibular palp posterior view **d** right mandibular palp anterior view **e** 3rd maxilliped **f** left gonopod 1 anterior view with enlarged terminal segment **g** left gonopod 1 posterior view with enlarged terminal segment **h** left gonopod 2 anterior view and **i** left gonopod 2 posterior view. Scale bars: 10 mm (**a, b**), 1 mm (**c, d**), 10 mm (**e**), 5 mm (**f, g**), 1 mm (**h, i**). Photos: Nasreen Peer.

ally but pronounced posterior to orbital margins, curving prominently downwards at epibranchial region. Moderate presence of small exorbital teeth, but complete absence of epibranchial teeth. Flank of carapace smooth, with clear horizontal (epimeral) suture separating pterygostomial region from subhepatic and suborbital regions; vertical (pleural) groove dividing subhepatic region from suborbital region.

Sternites (Fig. 4b). Sternites 1 and 2 fused; first sulcus absent as a result; second sulcus s2/s3 prominent, running completely across sternum; third sulcus s3/s4 projecting downwards medially towards abdominopelvic region. Sulci and episternal sulci thereafter well-defined but shallow.

Third maxillipeds (Figs 4c, 5e). Filling entire buccal frame except transversely oval respiratory openings at top lateral corners. Ischium slightly scabrous, with pronounced groove running vertically. Flagellum on exopod of third maxilliped fairly long, curving upward at distal ends.

Mandibular palp (Fig. 5c, d). Consisting of two segments; terminal segment undivided and smooth, with dense tuft of setae protruding from base; hirsute margins; light covering of setae on posterior surface; subterminal segment enlarged distally where it joins with terminal segment.

Pereopods (Figs 4a, b, 5a, b). General right-handedness and prominent inequality of chelae where CRDL/CLDL = 1.32. Dactyl of major chela moderately arched; large interspace formed in major cheliped when fingers are closed, long slim interspace formed by closing of fingers in minor cheliped. Twenty four cutting teeth present on the dactyl of major cheliped and 29 on dactyl of minor cheliped; 3 larger and more prominent than the rest. Propodus fairly inflated; right propodus larger (CRPL/CLPL = 1.41) and wider (CRPW/CLPW = 1.75) than left. Left pollex with 25 cutting teeth and right propodus with 18. Carpus on either side containing one prominent tooth followed by one smaller tooth. Meri strongly granulated around margins; slender pereopods (pereopod 2: ML/MW = 3.28; pereopods 5: ML/MW = 2.17), pereopod 3 is longest and pereopod 5 shortest; ventral margins of meri smooth; ventral margins of propodi slightly serrated; dorsal margins of meri and propodi bearing fine sharp bristles; dactyli serrated and ending in sharp points.

Pleon (Fig. 4b). First five segments broad and short, with segments 6 and 7 longer; segments 1–6 four sided, with triangular distally-rounded terminal segment (telson).

Pleopods (Fig. 5f, g, h, i). Gonopod 1 bearing short terminal segment only 0.23 times the length of the subterminal segment. Terminal segment curving slightly away from midline when viewed posteriorly. Gonopod widest at base, with both subterminal and terminal segments tapering and ending in sharp point. Inner lateral margin of subterminal segment irregular; outer lateral margin curving in a concave manner towards middle of gonopod; both margins hirsute. Groove extending almost through entire length of gonopod, visible on posterior surface, lined with setae. Distal margin of subterminal segment irregularly curved. Gonopod 2 consisting of two segments; terminal segment relatively long (0.47 times length of subterminal segment), very slim; subterminal segment wide at base, sharply becoming very narrow around 0.4 of length at which point narrow process forms, leading up to terminal segment. Small tuft of

setae present on outer margin of base of subterminal segment. Gonopod 2 curved, moving outwards away from medial line of gonopod proximally, curving back towards medial line distally.

Variation. The major cheliped does not always display a pronounced interspace when fingers are closed. In juveniles and in the female allotype this was less prominent. The arching of chelipeds varies too, with some (particularly the minor chelipeds) bearing straight dactyli while others are fairly rounded. All collected specimens display a pronounced heterochely and all appear to be right-handed.

Live colouration. Colouration of carapace may vary between light brown, maroon, purplish-brown and almost black. Similarly, tips of dactyli may be either orange, bright yellow or a dull yellow.

Distribution. Currently only known from the False Bay region of the iSimangaliso Wetland Park on the north-east coast of South Africa.

Type locality. South Africa, KwaZulu-Natal, iSimangaliso Wetland Park, False Bay - Western Shores: Mpophomeni Pan (27°57'31.33"S, 32°21'42.15"E); Dukandlovu Pan (28°0'51.70"S, 32°21'55.36"E); Main Road Pan (27°58'32.02"S, 32°21'51.62"E); Sandy Point Pan (27°58'36.0"S, 32°22'17.0"E).

Etymology. The species is named after the iSimangaliso Wetland Park, located in northern KwaZulu-Natal, where it is currently thought to be micro-endemic. This is significant as the iSimangaliso Wetland Park falls within the Maputaland centre of endemism (Smith et al. 2008), highlighting the importance of this park as a global biodiversity hotspot. The Park is a UNESCO World Heritage Site and contains three Ramsar Wetlands of International Importance.

Remarks. *Potamonautes isimangaliso* sp. n. is easily distinguishable from most other *Potamonautes* spp. found in South Africa. *Potamonautes dentatus* Stewart, Coke & Cook, 1995, *P. parvispina* Stewart, 1997, *P. unispinus* Stewart & Cook, 1998, *P. warreni* Calman, 1918 and *P. calcaratus* (Gordon, 1929) all bear dentate anterolateral margins or epibranchial corners, while *P. isimangaliso* has a rounded epibranchial corner and mildly granular anterolateral margin.

Potamonautes perlatus (H. Milne Edwards, 1837), *P. granularis* Daniels, Stewart & Gibbons, 1998, *P. sidneyi* Rathbun, 1904, *P. barbarai* Phiri & Daniels, 2014 and *P. barnardi* Phiri & Daniels, 2014 all have sharply-defined scabrous or granular epibranchial corners and prominent postfrontal crest, while *P. isimangaliso* has a heavily rounded smooth epibranchial corner and poorly-defined postfrontal crest. *Potamonautes parvicorpus* Daniels, Stewart & Burmeister, 2001 also displays a finely granulated anterolateral margin and rounded epibranchial corners, but the resemblance to *P. isimangaliso* is superficial, as it differs in the indentation of its anterior margin where *P. parvicorpus* bears a slightly indented anterior margin while that of *P. isimangaliso* lies straight. Further differences are seen in locality as the habitat of *P. parvicorpus* is restricted to high mountain streams in the Western Cape (Daniels et al. 2001).

Potamonautes clarus Gouws, Stewart & Coke, 2000, *P. depressus* (Krauss, 1843), *P. brincki* (Bott, 1960), *P. flavusjo* Daniels, Phiri & Bayliss, 2014 and *P. lividus* Gouws, Stewart & Reavell, 2001 all have smooth anterolateral margins and rounded smooth

epibranchial corners but bear differences compared to *P. isimangaliso*. One of the diagnostic characters of *P. depressus* is the dorsally flattened carapace, where $CL/CH = 2.3\text{--}2.6$. *Potamonautes isimangaliso* has a more vaulted carapace with a CL/CH ratio of 1.6–1.8. *Potamonautes brincki* and *P. clarus* are smaller crabs (max CL = 27 mm in males for both species), preferring fast-flowing mountain stream habitats. *Potamonautes flavusjo* is ecologically distinct from *P. isimangaliso* and can be found in the Mpumalanga Highveld. In addition to this, the species is smaller and has flattened chelipeds, not adapted for burrowing (Daniels et al. 2014). Light yellow chelipeds and ventral surfaces of pereopods characterise *P. flavusjo*.

Potamonautes lividus shares a similar distribution, outward appearance and preference for air-breathing with *P. isimangaliso*. However various differences exist between the two species. The level and angle of anterolateral margin differ, where *P. isimangaliso* bears an anterolateral margin lying on the same horizontal plane as the anterior margin. Conversely, *P. lividus* has an anterolateral margin which angles downward to join the anterior margin and thus sits higher than the anterior margin. The downward angle of postfrontal crest at exorbital edges is seen in *P. isimangaliso* but not in *P. lividus*. Carapace flatness is indicated by the CL/CH ratio which equates to 1.5 for *P. lividus* and 1.8 for *P. isimangaliso* holotypes. The maximum size (37 mm CL in *P. isimangaliso* and 25.5 mm CL in *P. lividus*), colouration (dark blue carapace with bright orange chelipeds in *P. lividus* and dark brown/purple carapace with brown or dull yellow cheliped in *P. isimangaliso*), inflation of chela with gap between propodus and dactyl (dactyl of *P. lividus* is more arched than that of *P. isimangaliso*) and the number of poorly-developed teeth on carpus (*P. lividus* containing one prominent and three rudimentary teeth; *P. isimangaliso* containing one prominent and one rudimentary tooth) further distinguish the two species. Gonopods of both species are very similar with the only difference being the tuft of setae found at the base of pleopod 2 in *P. isimangaliso*. Specimens resembling *P. lividus* were found in the Dwesa Forest, Eastern Cape and appear to be genetically nearly identical to *P. lividus* (Daniels et al. 2014). This further substantiates the genetic distinctiveness of *P. isimangaliso*. The smallest mature male of *P. isimangaliso* recorded had a CL of 13.2 mm whilst all females recorded were mature (min CL = 18 mm).

Preliminary sequence data for two mitochondrial gene regions (16S: GenBank accession number KR137640; COI: KR137642) generated from a representative of the new species, using approaches described elsewhere (Daniels et al. 2002; Phiri and Daniels 2014; G. Gouws unpubl.), were notably divergent (7.3% and 7.9%, respectively) from published 16S (AY042248; Daniels et al. 2002) and COI (AF510879; Daniels et al. 2002) sequences of *Potamonautes lividus* from KwaZulu-Natal.

Habitat and ecology. *Potamonautes isimangaliso* sp. n. inhabits freshwater ephemeral pans (maximum salinity recorded: 0.75) which fill up with fresh, oxygen-deprived water after rainfall events, mainly during the summer wet season. These pans are located along the western shores of False Bay, Lake St Lucia (Fig. 6a–d) in clearings of the sand forest biome of False Bay and are generally partially shaded. *Potamonautes isimangaliso* and *P. lividus* are found in close proximity although *P. lividus* has not



Figure 6. Sampling localities of *Potamonautes isimangalis* sp. n.: **a** Main Road Pan (FB1) **b** Mpophomeni Pan (FB3) **c** Dukandlovu Pan (FB5) and **d** Sandy Point Pan (FB6), completely dry during Feb 2015. Photos: **a–c** Lynette Clennell; **d** Nasreen Peer.

been found in False Bay Park and *P. isimangalis* has not been found outside of the park. Furthermore, a difference in habitat type between *P. isimangalis* and *P. lividus* Gouws, Stewart & Reavell, 2001 is seen, where the latter is known to inhabit burrows well above the surface water line in *Ficus* and *Barringtonia* swamps (Gouws et al. 2001), while the new species was found in close association with ephemeral pans in sand forest habitat with burrows extending below the surface waterline. Vegetation types include the dominant canopy species *Cleisthantus schlechteri*, *Hymenocardia ulmoides*, *Psydrax fragrantissima*, *Croton pseudopulchellus* and *Drypetes arguta* (Kirkwood & Midgley, 1999), as well as various *Acacia* spp. (Moll 1980). Grass species such as *Paspalum vaginatum* and *Eleocharis* sp. are also closely associated with this environment (Moll 1980). Aquatic plants associated with the ephemeral pans include the reed *Typha capensis*, the sedge *Juncus kraussii*, the mangrove fern *Acrostichum aureum* and the duckweed *Lemna* sp. (Howard-Williams 1980).

Potamonautes isimangalis adults form burrows on the banks of these pans (Fig. 7a), while juveniles are found either in burrows or free-crawling in shallow water (2–50 cm). The species lives sympatrically with *P. sidneyi* but is separated by habitat

Table 2. Physico-chemical parameters of sampling localities †.

	Main Road Pan (FB1)	Mpophomeni Stream (FB2)	Mpophomeni Pan (FB3)	Dukandlovu Pan (FB5)
Temperature (°C)	26.1	20.4	22.03	26.73
Salinity	0.15	8.36	0.29	0.75
Maximum depth (mm)	80	500	700	250
pH	7.2	7.03	7.42	6.9
Turbidity (NTU)	1310.5	14	151	306.3
Dissolved oxygen (% sat.)	19.8	90.1	22.4	69.6

† No data is included for Sandy Point Pan (FB6) as the site was dry at the time of sampling.

type, with *P. sidneyi* inhabiting flowing streams and able to withstand higher salinities of up to 9 (18 May 2013, Mpophomeni Stream, 27°57'7.17"S, 32°22'37.21"E). Oxygen levels in the pans inhabited by *P. isimangaliso* are quite low compared to flowing streams (Table 2).

Although the species appears to be more closely associated with water than its morphologically closest congener, *P. lividus* (Gouws et al. 2001), the low levels of oxygen characteristic of the pans along with the ephemeral nature of the waterbodies indicate a greater affinity for a terrestrial lifestyle, as it may be more effective to obtain oxygen through air-breathing. This has been recorded previously in various African freshwater brachyuran genera and a high-vaulted carapace may be indicative of this change, where periods of dryness favour the evolution of burrowing semi-terrestrial, air-breathing tendencies (Cumberlidge 1999; Cumberlidge 2009). Specimens of *P. isimangaliso* have been observed in deep burrows (30–50 cm) around desiccated pools. Because the rainy season in this area is generally restricted to the period November–April (late Austral spring to early Autumn), much of the population hibernates deep in the mud, where traces of moisture persist throughout the dry season. Crabs return to the surface only after major rainfall events have filled up the ephemeral pools. The summer of 2014–2015 had been particularly dry in the area, with substantial rain falling in the False Bay area starting only in the middle of January (69 mm during 15–17 Jan, 54 mm during 28–30 Jan 2015; False Bay Park Meteo Station). Numerous adult and sub-adult crabs were observed from 31 Jan to 3 Feb in the newly filled ephemeral pools but hardly any young juvenile, indicating that the previous drought conditions had not allowed spawning to happen yet.

The feeding ecology of the species is largely unknown, although *Potamonautes* crabs are generally thought to shift from a diet of aquatic invertebrates to a more herbivorous or opportunistic diet with age (Hill and O'Keeffe 1992). The chelar dentition is serrate and the larger crusher chela lacks rounded or molariform occlusive geometry in the proximal region, probably due to wearing down over time. The dentition of the chela is indicative of an opportunistic omnivorous diet (Yamada and Boulding 1998).



Figure 7. A Burrows of *Potamonantes isimangalis* sp. n. are typically found on the banks of ephemeral pans and are even maintained when pans are completely dry **B** *Potamonantes isimangalis* sp. n. in its natural habitat. Photos: Lynette Clennell.

Updated key for the identification of the *Potamonautes* species of South Africa**Based on Day et al. (2001)**

- 1 Anterolateral margin bearing one tooth or many distinct teeth 2
 – Anterolateral margin smooth tooth, sometimes serrated or granulated 6
- 2 Anterolateral margin bearing two or more distinct teeth 3
 – Anterolateral margin bearing one distinct tooth at epibranchial corner 4
- 3 Postfrontal crest complete to anterolateral margin; epibranchial sinus absent..
 *Potamonautes warreni* Calman, 1918
 – Postfrontal crest interrupted at exorbital teeth; epibranchial sinus present
 *P. dentatus* Stewart, Coke & Cook, 1995
- 4 Postfrontal crest not continuous posterior to exorbital teeth; merus of chelipeds bearing a spine on both antero- and posterior-inferior granulate margins *P. calcaratus* (Gordon, 1992)
 – Postfrontal crest complete; no spine on merus of cheliped 5
- 5 Postfrontal crest not sloping backwards towards anterolateral margin; epibranchial sinus absent *P. unispinus* Stewart & Cook, 1998
 – Postfrontal crest sloping backwards to meet anterolateral margin; epibranchial sinus present *P. parvispina* Stewart, 1997
- 6 Anterolateral margin granulated, forming distinct angle with postfrontal crest at epibranchial corner; epibranchial region usually scabrous or granulated 7
 – Anterolateral margin rounded and smooth, meeting postfrontal crest at rounded epibranchial corner; epibranchial region usually without scabrosity or granulation 10
- 7 Carapace and postfrontal crest strongly granulated, with pronounced scabrosity in epibranchial region 8
 – Carapace and postfrontal crest moderately granulated, with relatively smooth epibranchial region 9
- 8 Carapace anterior relatively narrow and curved moderately over the branchial region; inward-extending lobe absent from short terminal segment of gonopod 2; confined to the Olifants River system in the Cape Fold Mountains below the Bulshoek dam wall (WC)
 *P. granularis* Daniels, Stewart & Gibbons, 1998
 – Carapace anterior relatively wide and curved slightly over the branchial region; long slender S-shaped terminal segment of gonopod 2 is formed by inward extending lobe; not occurring in the Western Cape *P. sidneyi* Rathbun, 1904
- 9 Occurring largely in the Western Cape, also extending further north and east; found in western flowing drainage systems including the Olifants River, where it occurs above the Bulshoek dam wall
 *P. perlatus* (H. Milne Edwards, 1837)
 – Restricted to southern flowing drainages in the Western Cape (Gamtoos River and Gourits River) *P. barbarai* Phiri & Daniels, 2014

- Restricted to the Berg River and tributaries of the Breede River (WC).....
..... ***P. barnardi* Phiri & Daniels, 2014**
- 10 Carapace depressed and dorso-ventrally flattened; ratio of carapace length to height between 2.1 and 2.6..... **11**
- Carapace vaulted and arched; ratio of carapace length to height between 1.5 and 2.2 **12**
- 11 Carapace flatter, with a ratio of carapace length to carapace height between 2.3 and 2.6; postfrontal crest often directed forward near anterolateral margin; dark yellow-brown or green-brown in colour***P. depressus* (Krauss, 1843)**
- Carapace more vaulted, with ratio of carapace length to carapace height between 2.1 and 2.3; postfrontal crest straight near the anterolateral margin; orange in colour..... ***P. clarus* Gouws, Stewart & Coke, 1995**
- 12 Dactyli of chelipeds flattened; postfrontal crest, pereopods and chelipeds bright yellow; occurring in the Mpumalanga Highveld.....
..... ***P. flavusjo* Daniels, Phiri & Bayliss, 2014**
- Dactyl of chelipeds moderately or highly arched **13**
- 13 Anterolateral margin curving inward over carapace surface in the branchial region; occurring in KZN **14**
- Anterolateral margin not curving inward over carapace surface in the branchial region; occurring in the WC **15**
- 14 Bearing one prominent tooth and three rudimentary teeth on carpus of cheliped; tuft of setae absent from base of pleopod 2; carapace dark with distinctive blue sheen; chelipeds and pereopods bright orange
..... ***P. lividus* Gouws, Stewart & Reavell, 2001**
- Bearing one prominent tooth and one rudimentary tooth on carpus of cheliped; tuft of setae present at base of pleopod 2; carapace uniformly purplish brown with similar coloured or slightly brighter chelipeds and pereopods.....
..... ***P. isimangaliso* sp. n.**
- 15 Flange present on terminal segment of mandibular palp... ***P. brincki* (Bott, 1960)**
- Flange absent from terminal segment of mandibular palp
..... ***P. parvicorpus* Daniels, Stewart & Burmeister, 2001**

Acknowledgements

The authors are grateful to R.H. Taylor, L. Clennell, D. Bilton, M.S. Bird, S.J. du Plooy and J.L. Raw for assistance with collections. L. Clennell is acknowledged for photography. P-P. Steyn and J.B Adams are thanked for their help with plant identification. The iSimangaliso Wetland Park Authority and Ezemvelo KZN Wildlife are also gratefully acknowledged for providing logistical assistance and permits for this project. We are grateful to Thobile Ndlovu for providing rainfall data for the area. This work is based on the research supported by the South African Research

Chairs Initiative of the Department of Science and Technology (DST) and National Research Foundation (NRF) of South Africa. Any opinion, finding and conclusion or recommendation expressed in this material is that of the author(s) and the NRF does not accept any liability in this regard.

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Two new species of *Edmockfordia* García Aldrete (Psocodea, 'Psocoptera', Epipsocidae), from Valle del Cauca, Colombia, and description of the female *E. chiquibulensis* García Aldrete

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Academic editor: *K. Yoshizawa* | Received 14 April 2015 | Accepted 24 April 2015 | Published 11 May 2015

<http://zoobank.org/8D0B1108-BDCD-4268-8549-27A3F3445546>

Citation: Nieto JAM, Obando RG, Aldrete ANG (2015) Two new species of *Edmockfordia* García Aldrete (Psocodea, 'Psocoptera', Epipsocidae), from Valle del Cauca, Colombia, and description of the female *E. chiquibulensis* García Aldrete. ZooKeys 503: 45–54. doi: 10.3897/zookeys.503.9789

Abstract

Two new species of *Edmockfordia* García Aldrete, from Valle del Cauca, Colombia, and the female of *E. chiquibulensis* García Aldrete, are described and illustrated. A key to the species of *Edmockfordia* is included; the genus was previously known only from Belize. The genus is re-diagnosed to include female characters. The distribution of the genus is considerably widened, from Belize to northeastern South America.

Keywords

Neotropics, Belize, South America, Epipsocetae, taxonomy

Introduction

The genus *Edmockfordia* was described by García Aldrete (2009) on the basis of three male specimens collected with Malaise traps at the Chiquibul Forest Reserve, Belize; numerous additional specimens from the same locality have become available since, including females of *E. chiquibulensis*. Two male specimens, representing each a

different, undescribed species, were recently collected in Valle del Cauca, Colombia; the purpose of this work is to describe those two species and to re-diagnose the genus, to include female characters, besides, the distribution of the genus is extended from Belize to northern South America.

Material and methods

The Colombian specimens available for study were collected with led light traps, at the Pericos Natural Reserve and El Danubio, in Buenaventura, Valle del Cauca, Colombia. The Belizean specimens were collected in flight interception traps, at the Chiquibul Forest Reserve, Cayo District, Belize. The specimens for microscopic examination were dissected in ethanol 80%, and their parts (head, right wings and legs, and genitals) were mounted on slides in Canada balsam, following the procedure in González et al. (2011). The whole specimens, before dissection, were placed in 80% ethanol and observed with a Nikon SMZ 645 microscope, for color description. Standard measurements were taken on the slides, utilizing a Nikon E200 microscope; the measurements are given in μm , and the abbreviations of parts measured are the following: FW, HW: lengths of right fore- and hind- wings, F, T, t1, t2: lengths of femur, tibia, and tarsomeres 1 and 2 of right hind leg, ctt1: number of ctenidobothria on t1 of right hind leg, fl...fn: lengths of flagellomeres 1...n of right antenna, IO, D, d: minimum distance between compound eyes, antero-posterior diameter and transverse diameter, respectively, of right compound eye, all in dorsal view of head, PO: d/D. The Colombian specimens are deposited in the Entomology Museum, Universidad del Valle (MUSENUV), Santiago de Cali, Colombia. The Belizean specimens are deposited in the Mexican National Insect Collection (CNIN), Instituto de Biología, UNAM, Mexico City.

Taxonomy

Edmockfordia calderonae sp. n.

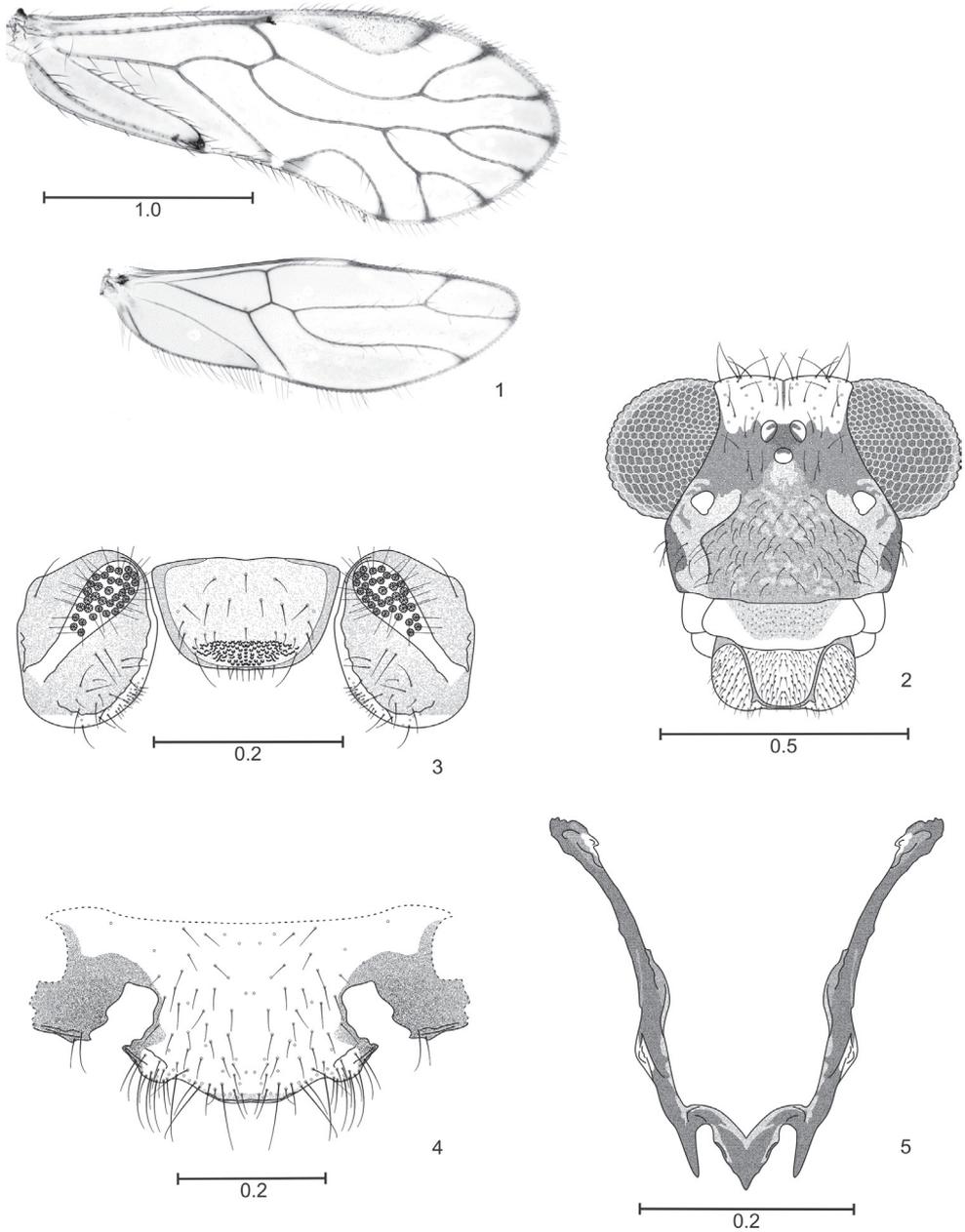
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Figures 1–5

Type locality. COLOMBIA. Valle del Cauca. Buenaventura. Vereda El Salto. Pericos Natural Reserve, 350 m., 3°56'N, 76°47'W.

Type material. Holotype male, 9–11.VIII.2013. light trap, O. Saenz, N. Calderón. Deposited in the Entomology Museum, Universidad del Valle, Santiago de Cali, Colombia (MUSENUV slide No. 25775).

Etymology. It is our pleasure to dedicate this species to Nadia Calderón, a graduate student at the Universidad del Valle, who, together with Oscar Saenz Manchola, collected the specimens of the two species of *Edmockfordia* here described.



Figures 1–5. *Edmockfordia calderonae* sp. n. Male. **1** Forewing and hindwing **2** Front view of head **3** Epiproct and paraprocts **4** Hypandrium **5** Phallosome. Scales in mm.

Diagnosis. Phallosome with three posterior projections, with posterior end broadly W shaped; external parameres short, little developed; aedeagal arch slightly projected posteriorly; epiproct broadly rounded posteriorly.

Color (in 80% ethanol). Body mostly pale brown, with creamy areas, as indicated below, pronotum, propleura and metapleura brown, upper half of mesopleura brown, lower half creamy; meso- and metanotal lobes creamy, bordered with brown. Abdomen creamy, clunium brown. Head (Fig. 2), with a brown transverse band between compound eyes enclosing the ocellar triangle; vertex creamy; genae brown; ocelli hyaline, with dark brown centripetal crescents; postclypeus brown, anteclypeus centrally brown, sides creamy; labrum pale brown anteriorly, fading towards the posterior margin. Antennae with scape and pedicel brown, flagella pale brown. Maxillary palpomeres 1–4 brown. Legs: front coxa, and trochanters of all legs creamy; coxae of mid and hind leg with a dark brown spot on outer border; femora mostly creamy, with a brown spot on proximal and distal ends; tibiae and tarsi pale brown. Forewings hyaline, pterostigma with a brown spot distally, and a brown band proximally; veins brown, each with a brown spot distally, at wing margin; a brown spot at nodulus. Hindwings hyaline, veins pale brown, with brown spots distally, at wing margin. Epiproct and paraprocts creamy. Hypandrium creamy, with postero-lateral corners brown.

Morphology. As in diagnosis, plus the following: outer cusp of lacinial tip broad, with eight denticles; compound eyes with interommatidial setae, mostly dorsally. Forewings (Fig. 1) symmetric, pterostigma elongate, rounded, widest in the middle; Rs with two branches, M dichotomously branched, resulting in four branches; areola postica low, apically rounded. Hindwings symmetric (Fig. 1), Rs of two branches, M simple. Coxae of hind leg without Pearman's organ; trochanters of all legs dorsally with two long setae, tarsi of front legs without ctenidobothria, mid legs with 21 ctenidobothria on t1, t2 with two ctenidobothria. Hypandrium (Fig. 4): symmetric, setose, posterior border convex. Phallosome (Fig. 5): open anteriorly, side struts long, slender, sclerotized, external parameres short; aedeagal arch slightly projected posteriorly in the middle; endophallus membranous, without sclerites. Paraprocts (Fig. 3): elongate, ovoid, with short setae and a field of microsetae along inner margin, sensory fields with 22–23 trichobothria on basal rosettes. Epiproct (Fig. 3): trapeziform, broadly rounded posteriorly, setose, with a field of microsetae along posterior border; a field of papillae mesally, next to posterior border.

Measurements. FW: 2675, HW: 2000, F: 625, T: 1125, t_1 : 500, t_2 : 120, ctt_1 : 30, f_1 : 550, f_2 : 440, IO: 260, D: 240, d: 300, IO/d: 0.86, PO: 1.25.

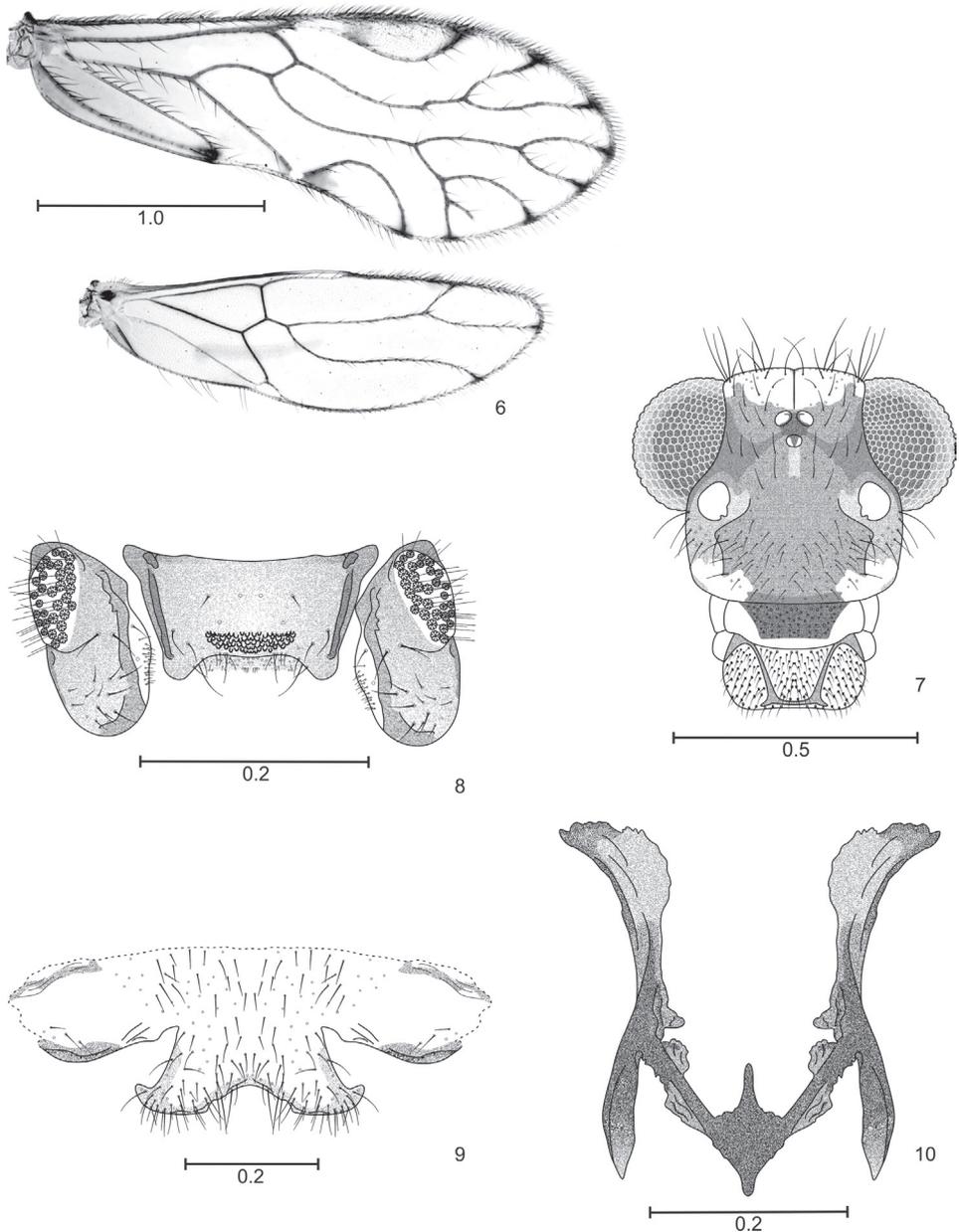
***Edmockfordia saenzi* sp. n.**

<http://zoobank.org/E827F942-11AA-4E20-93BB-F82C4B9DECB0>

Figures 6–10

Type locality. COLOMBIA. Valle del Cauca. Buenaventura. Vereda El Salto. Pericos Natural Reserve, 350 m., 3°56'N, 76°47'W.

Type material. **Holotype** male, 28–29.III.2013. Light trap, O. Saenz, N. Calderón. Deposited in the Entomology Museum, Universidad del Valle, Santiago de Cali, Colombia (MUSENUV, slide code No. 25774).



Figures 6–10. *Edmockfordia saenzi* sp. n. Male. **6** Forewing and hindwing **7** Front view of head **8** Epiproct and paraprocts **9** Hypandrium **10** Phallosome. Scales in mm.

Paratypes. 2 male, **COLOMBIA.** Valle del Cauca. Buenaventura. Vereda El Danubio, 340 m., 3°36'58.8"N, 76°53'59.5"W. 28–29.VIII.2014. Light trap. R. González, O. Saenz, N. Calderón. Paratypes deposited in the Entomology Museum, Universidad del Valle, Santiago de Cali, Colombia (MUSENUV, slide code No. 26135–26136).

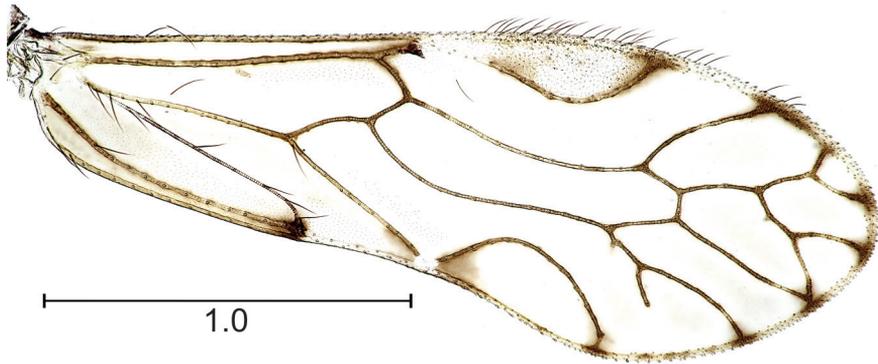


Figure 11. Anomalous forewing venation in *E. saenzi* sp. n. Scale in mm.

Etymology. We take pleasure to dedicate this species to Oscar Saenz Manchola, one of its collectors, a graduate student at the Universidad del Valle, Santiago de Cali, Colombia.

Diagnosis. Differing from *E. calderonae* and from *E. chiquibulensis* in having the phallosome aedeagal arch apically rhomboid, in having the external parameres extremely long, falcate, reaching the level of the aedeagal apex, and in having the postero-lateral corners of the epiproct rounded, protuberant.

Color (in 80% ethanol). Body mostly brown, with creamy areas, as indicated below, pronotum and propleura brown; meso- and metanotal lobes creamy, bordered with brown, upper halves of meso- and metapleura brown, lower halves creamy. Abdomen creamy. Head (Fig. 7), with a broad, transverse, dark brown band between compound eyes, enclosing the ocellar group; vertex creamy; genae proximally creamy, distally brown; ocelli hyaline, with ochre centripetal crescents; postclypeus brown, anteclypeus brown in the center, creamy on the sides; labrum creamy. Antennae with scape and pedicel brown, flagella pale brown. Maxillary palpomeres 1–4 brown. Legs: coxae and trochanters creamy; femora mostly creamy, with a brown spot on proximal and distal ends; tibiae and tarsi pale brown. Forewings hyaline, pterostigma with a brown spot at the apex, and a brown band proximally, veins pale brown, each with a brown spot distally, at wing margin, a brown spot at confluence of Cu_2 and A. Hindwings hyaline, veins pale brown, each with a brown spot distally, at wing margin. Clunium brown, epiproct pale brown, with sides dark brown; paraprocts pale brown, hypandrium almost unpigmented.

Morphology. As in diagnosis, plus the following: outer cusp of lacinial tip broad, with seven denticles; compound eyes with inter-ommatidial setae, mostly dorsally. Forewings (Fig. 6) asymmetric, pterostigma elongate, rounded, widest in the middle; R_s two branched; M dichotomously forked, resulting in four branches, right wing with M_4 incompletely forked; areola postica low, apically rounded; left wing with open areola postica, vein $Cu1A$ arising from M . Hindwings (Fig. 6) symmetric: R_s of two branches, M simple. Coxae of hind leg without Pearman organ, trochanters of all legs dorsally with two long setae; tarsi of front legs without ctenidobothria, $t1$ of mid legs

with 11 ctenidobothria, t_2 without ctenidobothria. Hypandrium (Fig. 9), symmetric, setose, with posterior border obtusely concave. Phallosome (Fig. 10): open anteriorly, V-shaped, side struts broad, dilated proximally and curved outwards. Paraprocts (Fig. 8): elongate, ovoid, with short setae, and a field of microsetae along the inner border, sensory fields with 30–31 trichobothria on basal rosettes. Epiproct (Fig. 8): broad, trapeziform, with field of short setae and a field of microsetae along posterior border; a field of papillae mesally, next to posterior border.

Remarks. Of the two paratypes for this species, one of them presents a forewing vein pattern with a four branched M, as described for the genus, however, a second specimen present the distal third of the forewing reticulated (Fig. 11) (e. g. R4+5 and M1 connected by a cross vein, R4+5 distally forked, a vein arising from the middle of R4+5 forked at wing margin, with the second branch fused at wing margin with M1, forming a closed cell, M1 absent, and M3 branched, with the branch near the areola postica incomplete.

Measurements. FW: 2700, HW: 2025, F: 675, T: 1150, t_1 : 500, t_2 : 140, ctt_1 : 26, f_1 : 540, f_2 : 470, IO: 280, D: 180, d: 280, IO/d: 1, PO: 1.5.

Edmockfordia chiquibulensis García Aldrete, 2009

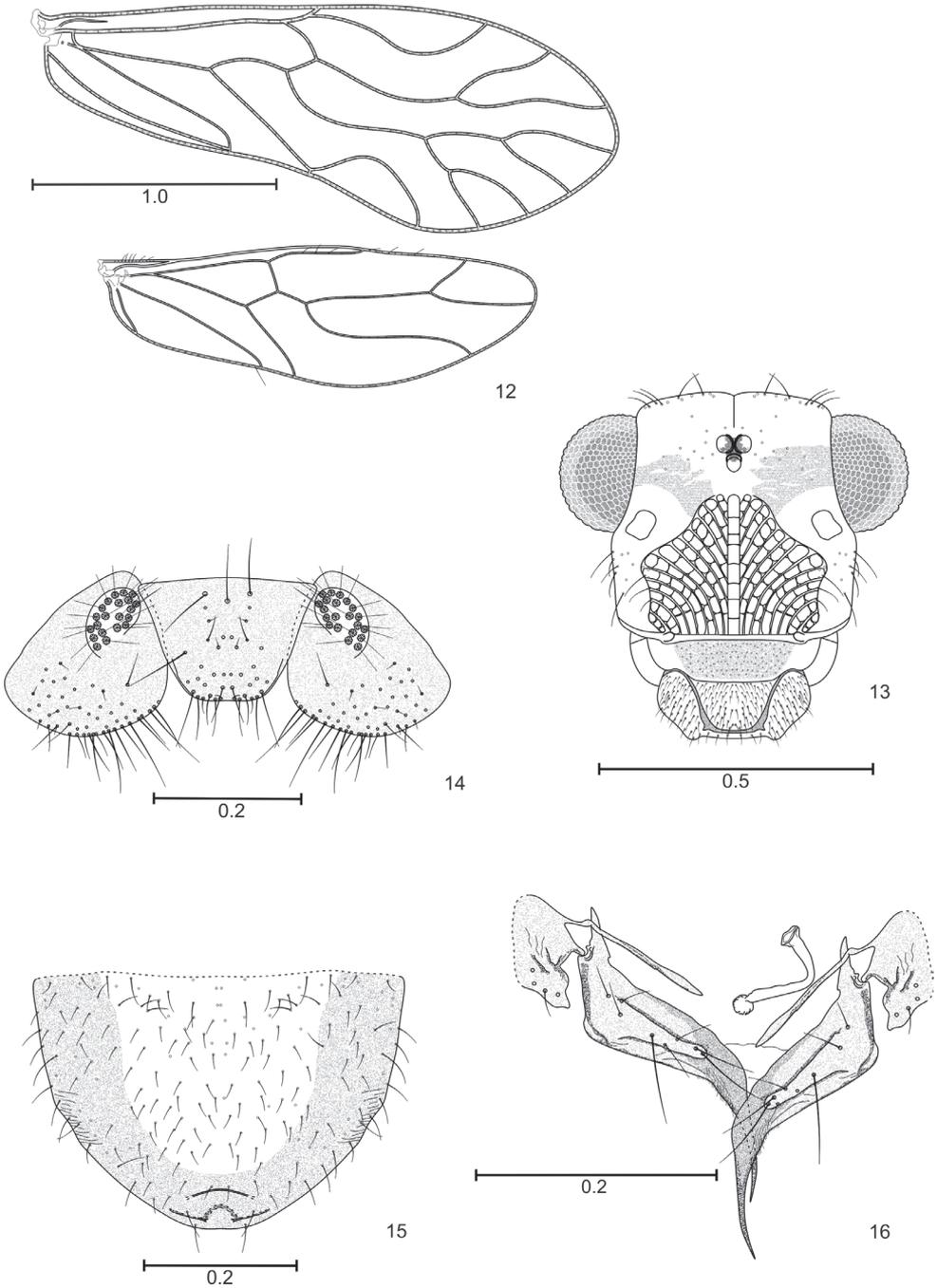
Figures 12–16

Color (19 years, three months in 80% ethanol). Essentially as in the male (see García Aldrete 2009). Scape and pedicel brown, flagella pale brown. Legs pale brown.

Morphology. Wings (Fig. 12), distal labral sensilla and pretarsal claws as in the male (see García Aldrete 2009). Outer cusp of lacinial tip with seven denticles. Labral sclerites joined distally by a sclerotized band (Fig. 13). Subgenital plate (Fig. 15) broad, with field of short setae; pigmented area deeply concave anteriorly; posterior border rounded, a strongly sclerotized, concave band next apex, and a transverse crease anterior to it. Gonapophyses (Fig. 16) complete, v_1 slender, about half the length of v_2+3 , joined to clunium by a membranous band. v_2+3 wide based proximally, with a short, pointed “heel”; v_3 a well defined, long slender lobe on side of v_2 , bearing eight setae; distal process almost straight, acuminate, with a field of microsetae proximally. Paraprocts (Fig. 14) broadly semicircular, with setae as illustrated, and a field of microsetae next distal border. Sensory fields elliptic, with 21 trichobothria on basal rosettes. Epiproct (Fig. 14) trapeziform, with field of setae on distal half, and three mesal macrosetae next anterior border.

Measurements. FW: 2434, HW: 1784, F: 555, T: 998, t_1 : 449, t_2 : 113, ctt_1 : 27, f_1 : 608, f_2 : 493, IO: 343, D: 227, d: 159, Mx_4 : 184, IO/d: 2.15, PO: 0.46.

Specimens studied. Belize. Cayo District. Chiquibul Forest Reserve. New María, 24.III.1995, 640 m. Malaise trap, paratype female. 17–20.I.1995, flight interception trap, female paratype. San Pastor, 560–580 m. 23–26.III.1995, paratype female. All specimens collected by T. King & A. Howe.



Figures 12–16. *Edmockfordia chiquibulensis* Female. **12** Forewing and hindwing **13** Front view of head **14** Epiproct and paraprocts **15** Subgenital plate **16** Gonapophyses and IX sternum. Scales in mm.

A new diagnosis of *Edmockfordia* García Aldrete

Belonging in the Epipsocidae. Five distal labral sensilla, one central placoid, flanked at a distance by a pair trichoid-placoid. Without row of cuticular cones on setal bases of fore- femora. Forewings Rs 2 branched, M dichotomously branched, resulting in 4 M veins, Hindwings Rs 2 branched, M unbranched. Phallosome open anteriorly, broadly V-shaped, with side struts stout, proximally curved outwards; external parameres well developed. Aedeagal arch projected posteriorly, or rhomboid in the middle. Endophallus membranous, without sclerites. Paraprocts with a sclerotized marginal band, next inner border. Epiproct trapeziform, with a field of papillae mesally, next posterior border. Female subgenital plate with a concave sclerotized band next apex. Gonapophyses complete, v1 short, slender, v2+3 with a proximal heel.

Key to the species of *Edmockfordia*

- 1 Phallosome with one posterior projection, external parameres long, well developed (Fig. 10).....**2**
- Phallosome with three posterior projections, external parameres short, little developed (Fig. 5) ***E. calderonae* sp. n.**
- 2 Posterior projection of phallosome triangular, external parameres not reaching the posterior level of the aedeagal arch.....***E. chiquibulensis* García Aldrete**
- Posterior projection of phallosome rhomboid, external parameres long, reaching the posterior level of the aedeagal arch (Fig. 10).....***E. saenzi* sp. n.**

Discussion

The species here dealt with extend the distribution of *Edmockfordia* from the Chiquibul Forest Reserve, in Belize, to Valle del Cauca, Colombia, all across Central America to northern South America. The two new species confirm the diagnosis of the genus: vein M in forewing dichotomously branched, side struts of phallosome stout, curved anteriorly, external parameres conspicuous, aedeagal arch projected posteriorly, paraprocts with a sclerotized band along inner border, and epiproct trapeziform, bearing a field of papillae mesally, next to the posterior border. The three species known in the genus differ in genitalic details, as indicated in the key above.

Acknowledgments

We thank Oscar Saenz Manchola and Nadia Rocío Calderón, for the donation of the Colombian specimens here studied. JAM and RGO thank the Biology Department, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Santiago de Cali,

Colombia. JAM thanks particularly the scholarship program “Young Researcher”, of COLCIENCIAS, and the Research Vicerectory, Universidad del Valle, for academic support. ANGA thanks Instituto de Biología, Universidad Nacional Autónoma de México, for continuous research support.

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Updated list of Collembola species currently recorded from South Africa

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Academic editor: *W. Weiner* | Received 18 November 2014 | Accepted 5 April 2015 | Published 11 May 2015

<http://zoobank.org/C0DA02DC-49B0-43C4-A012-5377CAA94629>

Citation: Janion-Scheepers C, Deharveng L, Bedos A, Chown SL (2015) Updated list of Collembola species currently recorded from South Africa. *ZooKeys* 503: 55–88. doi: 10.3897/zookeys.503.8966

Abstract

Understanding the abundance and richness of species is one of the most fundamental steps in effecting their conservation. Despite global recognition of the significance of the below-ground component of diversity for ecosystem functioning, the soil remains a poorly studied terrestrial ecosystem. In South Africa, knowledge is increasing for a variety of soil faunal groups, but many still remain poorly understood. We have started to address this gap in the knowledge of South African soil biodiversity by focusing on the Collembola in an integrated project that encompasses systematics, barcoding and ecological assessments. Here we provide an updated list of the Collembola species from South Africa. A total of 124 species from 61 genera and 17 families has been recorded, of which 75 are considered endemic, 24 widespread, and 25 introduced. This total number of species excludes the 36 species we consider to be dubious. From the published data, Collembola species richness is high compared to other African countries, but low compared to European countries. This is largely a consequence of poor sampling in the African region, as our discovery of many new species in South Africa demonstrates. Our analyses also show that much ongoing work will be required before a reasonably comprehensive and spatially explicit picture of South Africa's springtail fauna can be provided, which may well exceed 1000 species. Such work will be necessary to help South Africa meet its commitments to biodiversity conservation, especially in the context of the 2020 Aichi targets of the Convention on Biological Diversity.

Keywords

Biodiversity, endemism, soil fauna, introduced species, taxonomy

Introduction

The documentation of biodiversity is an essential first step for its conservation. A major barrier to so doing for invertebrates is a lack of taxonomic information on various groups. This taxonomic impediment and its implications for biodiversity studies have been widely discussed (Godfray 2002, Samper 2004). Despite these challenges, taxonomic knowledge continues to increase globally (Nilsson-Örtman and Nilsson 2010, Joppa et al. 2011, Platnick 2014, van Noort 2014). Nonetheless, given rapid environmental change and its effects on biodiversity (Butchart et al. 2010), it is unclear what the rate of extinction is for many groups (Pimm et al. 2010, Costello et al. 2013), complicating conservation efforts and assessments of their efficacy, thus underscoring the urgency to further document global biodiversity (Dirzo and Raven 2003, Bacher 2012).

This situation is as true for southern Africa as it is elsewhere. Knowledge of the South African fauna is increasing rapidly, especially in the case of a wide range of invertebrate groups (Foord et al. 2002, Robertson 2000, 2002, Parr et al. 2003, Dippenaar-Schoeman et al. 2006, Dippenaar-Schoeman and González Reyes 2006, Haddad and Dippenaar-Schoeman 2006, Hlavac 2007, Rouse and van Noort 2013). Nonetheless, many groups still remain relatively poorly studied, especially soil-dwelling taxa, which are essential for both above- and below-ground ecosystem functioning (Wardle et al. 2004, Hugo-Coetzee and Avenant 2011, Janion et al. 2011a). At the same time, considerable impacts on biodiversity continue to be documented as a consequence of habitat modification for agriculture and urban development, biological invasions, pollution, and climate change (Erasmus et al. 2002, Rouget et al. 2003, Biggs et al. 2008, Chown 2010, Pryke and Samways 2010, Huntley and Barnard 2012, Liu et al. 2012). In consequence, much need exists for documenting and understanding biodiversity and the processes underlying its variation across a wide range of groups, and especially the soil fauna.

Collembola are amongst the most widespread and abundant soil arthropods (Petersen and Luxton 1982, Hopkin 1997). Despite their obvious significance in soil systems, their utility as bioindicators (Lawrence 1953, Hopkin 1997, van Straalen 1998), their significance in the alien species faunas of many areas (Roques et al. 2009, Terauds et al. 2011), and the current growth in both morphological (Deharveng 2004) and molecular (Hogg and Hebert 2004, Rougerie et al. 2009) means to assess their diversity, they remain poorly known in South Africa. Indeed, by comparison with other regions of the world (Deharveng 2004), and other invertebrate taxa in the country (Scholtz and Chown 1995, Robertson 2000, Foord et al. 2011, Dippenaar-Schoeman 2014), knowledge of the group can be considered scanty.

The first attempt to collate all taxonomic information on the Collembola of South Africa was undertaken by Paclt (1959), listing *ca.* 65 species. Subsequently, an unpublished list entitled “Aquatic Collembola of South Africa” was made available online (P. Greenslade, no date), while Thibaud (2013) listed most publications until 2013. To date there are 38 publications on Collembola recorded or described from South Africa, the earliest by Börner (1908). Most notably, comprehensive descriptions were made by

Yosii (1959), Paclt (1959, 1964, 1965, 1967), Coates (1968a, 1968b, 1969), Weiner and Najt (1991, 1998, 1999), and later Barra (1994, 1995, 1997, 1999, 2001, 2002, Barra and Weiner 2009). However, little other work has been done and the current list of species for the country is clearly an underestimate, with an incomplete understanding of which species might be introduced and thus might have substantial impacts, despite the fact that such impacts have been suggested for the country (Annecke and Moran 1982, Liu et al. 2012).

To address this substantial gap in the knowledge of soil biodiversity, a collaborative project was established in 2008 (Janion et al. 2011a, Bengtsson et al. 2011, 2012). Besides large-scale sampling and systematic assessments, which have resulted in new discoveries and species descriptions (Janion et al. 2011b, Potapov et al. 2011, Janion et al. 2012, 2013), a major component of the project has comprised the compilation of all currently available information on Collembola recorded from South Africa. Here we present this compilation as an updated checklist. It will provide a starting point for understanding the diversity of this group, as has been done for other geopolitical regions (e.g. Culik and Zeppelini 2003, Abrantes et al. 2010, 2012), and will assist South Africa to meet its obligations under the Convention on Biological Diversity (see for example Aichi Target 9 on identifying invasive alien species, and Aichi Target 17 on a national biodiversity strategy, <http://www.cbd.int/sp/targets>).

Methods

All publications on Collembola species described or recorded from South Africa were collated from Salmon (1964) and Thibaud (2013). The list was checked and completed using the website “Checklist of the Collembola of the World” (Bellinger et al. 2014), the bi-annual bibliographical lists issued by the Museum National d’Histoire Naturelle (Paris, France), Zoological Record, Web of Science™ (full date range of 1900 to 2014), and genus or species revisions from taxonomic journals sourced from the references identified using the original search methods. Nomenclature follows Bellinger et al. (2014), as it may have changed for certain taxonomic groups since the original description of the species. All published papers and webpages were examined and the following information was recorded when available: collection details including date, collector, province, place, nearest town, habitat type, and collection method, type locality and accession number if given. Only species with full species names were included in the species list of Table 2, thus excluding morphospecies identified to genus or to suspected species (e.g. *Seira* sp. or *Isotomurus* cf. *maculatus*). However, every record from the literature is listed in the Supplementary material (Suppl. material 1). The species were assigned a South African province from the locality recorded. From these points a species richness map was produced in ArcMap V10.2 (ESRI 2014).

The species were also divided into the following categories based on their distribution: 1) endemic if they were described from South Africa and have not been recorded elsewhere, 2) introduced if there is evidence from the literature that the species was

introduced from another place, 3) widespread if the species is also present outside of South Africa but its origin is unknown, thus not considered introduced, or 4) dubious, when the species name given in the literature is considered a misidentification based on current taxonomic knowledge or if subsequent taxonomic work suggested this is the case (see Suppl. material 1).

To make an estimate of expected species richness, we used data collected from extensive sampling in the Western Cape Province of South Africa, which has been the main focus of much work on the group. The dataset comprises a total of 217 samples we obtained using several sampling techniques (see below) in as many localities and different microhabitats as possible throughout the Western Cape, including Afromontane forest, different fynbos vegetation types (see Mucina and Rutherford 2006), intertidal habitats, caves, and disturbed areas such as gardens and agricultural areas. Leaf litter, moss, rotten wood and soil samples were taken at different sampling sites over the duration of the project (2008–2012), and occasionally sieving and pit-fall traps were also used. Typically, samples were extracted using a Berlese-Tullgren approach for five to seven days, or until dry (Berlese 1905, Tullgren 1918, Hopkin 1997). In addition, active searching was done in the field. Riparian soil was washed for water-dependent species, which were collected with a fine brush on the surface of water. Fine sand such as sea sand was washed in the laboratory and animals were also collected with a brush. Vegetation such as branches from bushes, fynbos shrubs, and grasses was beaten over a tray and animals were collected by means of an aspirator. All samples are stored in 96–99% ethanol at the Centre for Invasion Biology (C.I.B) Stellenbosch, or the Museum National d’Histoire Naturelle (MNHN) Paris. As identifications and species descriptions are still ongoing, we only used confirmed morphospecies for the purpose of calculating the number of species expected for the Western Cape.

Sampled-based rarefaction curves were plotted to estimate the number of species for the Western Cape, using Chao1 and Jackknife 2 in EstimateS V8.2.0 (Colwell 2009). Jackknife 2 does not require data to be normally distributed and provides conservative, but accurate estimates (Magurran 2004). Sampling is considered adequate when the rarefaction curves and the estimators converge at the highest observed values (Longino et al. 2002).

Results

According to the literature, a total of 160 species from 61 genera and 17 families have been recorded from South Africa (Table 1), with a relatively steady increase in descriptions since the first records in the early 1900s (Fig. 1). Of the recorded species, 36 are considered dubious, most of them misidentified records from Paclt (1959, 1967). Of the other species, 75 are endemic, 25 are thought to be alien species introduced to the country by human activity, and 24 have a widespread distribution, at least so far as current sampling indicates (Table 2). The majority of species have been recorded from

Table 1. A summary of the Collembola species recorded from South Africa based on the literature.

	Number of species recorded from literature	Number of species accepted from literature	Introduced	Endemic	Widespread
PODUROMORPHA					
Hypogastruridae	19	11	4	5	2
Brachystomellidae	6	6	1	5	0
Neanuridae	16	15	2	10	3
Odontellidae	3	2	0	1	1
Onychiuridae	5	1	0	1	0
Tullbergiidae	8	7	1	3	3
TOTAL	57	42	8	25	9
ENTOMOBRYOMORPHA					
Isotomidae	23	19	5	8	6
Entomobryidae	49	36	8	25	3
Cyphoderidae	10	9	0	8	1
Paronellidae	1	1	0	0	1
Tomoceridae	1	1	0	1	0
TOTAL	84	66	13	42	11
NEELIPLLEONA					
Neelidae	1	1	0	0	1
TOTAL	1	1	0	0	1
SYMPHYPLEONA					
Sminthuridae	2	1	0	0	1
Katiannidae	5	4	1	1	2
Dicyrtomidae	2	2	1	1	0
Bourletiellidae	7	7	1	6	0
Sminthuridae	2	1	1	0	0
TOTAL	18	15	4	8	3
TOTAL	160	124	25	75	24

the Western Cape (67 species), Kwazulu-Natal (46 species) and the Eastern Cape (20 species) (Fig. 2). Records from the other provinces are sparse (1–10 species), with the North West Province and Limpopo having the lowest recorded richness (three and one species, respectively). Although many authors did not indicate the habitat type where collections took place (Supplementary Material Suppl. material 1), the majority mentioned were from sites that are within the forest biome (see Mucina and Rutherford 2006 for full details of South Africa's biomes and vegetation types). However, other vegetation types mentioned include those of the grassland biome and disturbed areas such as gardens, orchards and plantations.

The sample-based species rarefaction curve for the Western Cape did not reach an asymptote (Fig. 3). The two richness estimators (Jackknife2: 348 species, Chao1 with 95% Confidence Intervals: 323, lower CI: 270, upper CI: 416) suggest that at least 6–7 times more than the number of species currently recorded from the literature will be found in the province, given the steep slope of the non-asymptotic curve.

Table 2. Collembola species recorded from South Africa, with “Current species name” as confirmed name (Bellinger et al. 2014), and “Name published in source” as name used in the original source when different from current species name. Abbreviations used: South Africa (SA), Western Cape (WC), Eastern Cape (EC), Kwazulu-Natal (KZN), Gauteng (G), Limpopo (L), Free State (FS), Northern Cape (NC), Mpumalanga (MP), North West Province (NWP), Lesotho (Les), endemic (E), introduced (I), dubious record (D) or widespread (W), species present outside of South Africa but not considered introduced). Genera endemic to South Africa are indicated by an asterisk (*). See Suppl. material 1: Table S1 for full collection and citation details.

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
PODUROMORPHA						
Hypogastruridae						
<i>Acheronticella thibaudii</i> Barra, 1994	Barra 1994	KZN	W	Beach sand		South Africa and several tropical regions of East Africa and Southeast Asia (Thibaud 2010)
<i>Austrogastrura lobata</i> (Yosii, 1959)	Yosii 1959	WC	E		<i>Choreutinula lobata</i> Yosii, 1959	
<i>Ceratophysella armata</i> (Nicolet, 1842)	Womersley 1934, Paclt 1959, 1967, Coates 1970	WC, KZN, EC, FS, G, NC	D	Damp soil, moss, litter	<i>Hypogastrura armata</i> Nicolet, 1842	Western palaeartic distribution.
<i>Ceratophysella armata trispina</i> (Womersley, 1934)	Womersley 1934	WC	D		<i>Hypogastrura armata</i> var. <i>trispina</i> Womersley, 1934	Described from a single specimen with three anal spines, could also have been <i>Triacanthella</i> sp.
<i>Ceratophysella longispina</i> (Tullberg, 1876)	Womersley 1934	NC, KZN,	D		<i>Hypogastrura longispina</i> Tullberg, 1876	Northern hemisphere circumpolar distribution (Fjellberg 1998)
<i>Hypogastrura manubrialis</i> (Tullberg, 1876)	Womersley 1934, Paclt 1959, 1967	NC, KZN, WC	I	Wet habitat		Distributed worldwide, considered introduced in the Southern hemisphere
<i>Hypogastrura manubrialis neglectus</i> (Börner, 1901)	Womersley 1934	WC	D		<i>Hypogastrura manubrialis</i> var. <i>neglectus</i> (Börner, 1901)	Dubious: lacks two anal spines, no more information provided.
<i>Hypogastrura purpurescens</i> (Lubbock, 1868)	Womersley 1934, Paclt 1959, 1967	WC	I	Wet leaves	<i>Hypogastrura pseudopurpurescens</i> Womersley, 1928 in Womersley 1934 <i>Hypogastrura (Hypogastrura) purpurescens</i> (Lubbock, 1868) in Paclt 1959, 1967	The species can be considered as introduced from Northern hemisphere, as has recently been confirmed for Australia (Greenslade et al. 2014).
<i>Hypogastrura sahlibergi</i> (Reuter, 1895)	Paclt 1959	WC	D	Near stream		Dubious record: holarctic distribution (Bellinger et al. 1996–2014).
<i>Hypogastrura sahlibergi rosea</i> (Reuter, 1895)	Womersley 1934	WC	D	Damp rocks	<i>Hypogastrura sahlibergi</i> var. <i>rosea</i> (Reuter, 1895)	Agrees with <i>sahlibergi</i> s. str. except for colour. <i>Species inquirenda</i> .

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Hypogastrura viatica</i> (Tullberg, 1872)	Womersley 1934, Paclt 1959	WC	I	Littoral		Nordic countries and Arctic, considered introduced in southern hemisphere (Greenslade 2002).
<i>Mesogastrana libyca</i> (Caroli, 1914)	Paclt 1959	WC	D	Forest litter	<i>Choreutimula libyca</i> Caroli, 1914	Probably <i>Austrogastrana lobata</i> (Yosii, 1959), present in the same locality.
<i>Triacanthella madlba</i> Janion, D'Haese & Deharveng, 2012	Janion et al. 2012	WC	E	Cave guano		
<i>Willemia trilobata</i> Barra, 1995	Barra 1995	KZN	E	Beach sand		
<i>Xenylla capensis</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Xenylla mauritima</i> Tullberg, 1869	Paclt 1959, 1967	WC, EC, KZN, NWP	I	Wet habitat, forest		Cosmopolitan distribution (Fjellberg 1998), probably introduced in the Southern hemisphere
<i>Xenylla rhodesiensis</i> Womersley, 1929	Coates 1970	MP	E	Wet habitat		
<i>Xenylla schilleri</i> Börner, 1903	Paclt 1959	Les	D	At stream		Only recorded from Europe, while the collection locality in South Africa is very isolated and at a high altitude
<i>Xenylla yucatanana</i> Mills, 1938	Barra 1995	KZN	W	Forest soil		Pan-tropical distribution (Deharveng et al. 2011)
Brachystomellidae						
<i>Brachystomella africana</i> Yosii, 1959	Yosii 1959	WC	E		<i>Brachystomella parvula africana</i> Yosii, 1959	
<i>Brachystomella coatesi</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Brachystomella georgensis</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Brachystomella parvula</i> (Schäffer, 1896)	Womersley 1934, Paclt 1959, 1967, Coates 1970	MP, WC, KZN, EC, FS	I	Wet litter		Cosmopolitan distribution (Fjellberg 1998)
<i>Probachystomellides nicolaii</i> Weiner & Najt, 1991*	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Setanodosa capitata</i> (Womersley, 1934)	Womersley 1934	WC	E		<i>Brachystomella capitata</i> Womersley, 1934	
Neanuridae						

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Aethiopella capensis</i> (Womersley, 1934)	Womersley 1934, Paclt 1959	WC, KZN	E	Stony stream	<i>Centrimeria flavoanternatus</i> var. <i>capensis</i> Womersley, 1934	Described and previously only known from Ethiopia (Massoud 1967)
<i>Aethiopella handschini</i> (Denis, 1924)	Paclt 1959	Les, WC	D	Under stone, litter		Cosmopolitan distribution (Fjellberg 1998)
<i>Anurida maritima</i> (Guérin-Méneville, 1836)	Womersley 1934, Paclt 1959, Yossi 1959, Lawrence 1953	WC, KZN	W	Littoral		
<i>Ectonura barnai</i> Janion, Bedos & Deharveng, 2011	Janion et al. 2011b	WC	E	Forest leaf litter		
<i>Ectonura coatesi</i> Barra, 1994	Barra 1994	KZN	E	Litter on dunes		
<i>Ectonura monochaeta</i> Janion, Bedos & Deharveng, 2011	Janion et al. 2011b	WC	E	Forest leaf litter		
<i>Ectonura natalensis</i> (Womersley, 934)	Womersley 1934, Paclt 1959	KZN, WC, EC	E	Litter	<i>Achorutes natalensis</i> Womersley, 1934 <i>Neamura natalensis</i> (Womersley, 1934)	
<i>Ectonura oribiensis</i> (Coates, 1968)	Coates 1968	KZN	E	Soil, litter	<i>Neamura oribiensis</i> Coates, 1968	Cosmopolitan, possibly introduced in the southern hemisphere
<i>Friesea claviveta</i> Axelson, 1900	Womersley 1934	KZN, WC	I	Litter		Recorded from South Africa and Madagascar (Thibaud 2008)
<i>Friesea versabilis</i> Barra, 1995	Barra 1995	KZN	W	Under vegetation		
<i>Najaffrica riebi</i> (Barra, 1994)*	Barra 1994	KZN	E	Dune litter	<i>Sachorutes riebi</i> Barra, 1994	
<i>Neamura muscorum</i> (Templeton, 1835)	Coates 1968a	EC	I	Litter		Sub-cosmopolitan, introduced in the southern hemisphere. All other species of the genus are in Europe.
<i>Pseudachorutella africana</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Pseudachorutes alluaudi</i> (Delamare Debutteville, 1946)	Paclt 1959	KZN	W	Forest leaf litter	<i>Centrimeria alluaudi</i> Delamare Debutteville, 1946	Described and only known so far from Eastern Africa (Massoud 1967).
<i>Pseudachorutes univescatus</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		
<i>Vitronuna joanna</i> (Coates, 1968)	Coates 1968a	NWP	E	Soil	<i>Neamura joanna</i> Coates, 1968	
Odontellidae						

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Odontella sylvatica</i> Weiner & Najt, 1991	Weiner and Najt 1991	WC	E	Forest leaf litter		Recorded from South Africa and Madagascar (Thibaud 2008)
<i>Odontella deharvengi</i> Barra, 1995	Barra 1995	KZN	W	Soil		Dubious identification, European distribution
<i>Superodontella empodialis</i> (Stach, 1934)	Paclt 1959	KZN	D		<i>Odontella empodialis</i> Stach, 1934	
Onychiuridae						
<i>Deutaphorura inermis</i> (Tullberg, 1869)	Womersley 1934, Paclt 1959	WC	D	Under stones	<i>Onychiurus fimearius</i> (Linné, Lubbock) (sic) in Womersley 1934 <i>Onychiurus pseudinermis</i> Börner, Börner 1903 in Paclt 1959	Given the confusion around the species <i>fimearius</i> , <i>inermis</i> and <i>pseudinermis</i> , and the age of the specimen slides, the identification given by authors (following Bellinger et al. 1996-2014) is uncertain. The Schött description is insufficient to recognize the species.
<i>Orthonychiurus camerunensis</i> (Schött, 1926)	Paclt 1967	G	D	Soil	<i>Onychiurus camerunensis</i> Schött, 1926	
<i>Orthonychiurus saasveldensis</i> (Weiner & Najt, 1991)	Weiner and Najt 1991	WC	E	Forest, on bark	<i>Onychiurus saasveldensis</i> Weiner & Najt, 1991	
<i>Protaphorura armata</i> (Tullberg, 1869)	Lawrence 1953	?	D		<i>Onychiurus armatus</i>	A holarctic distribution. Southern records of <i>Protaphorura</i> are usually <i>Thalassaphorura</i> species, or possible introductions.
<i>Protaphorura matsumotoi</i> (Kinoshita, 1923)	Paclt 1959	FS	D	Soil	<i>Onychiurus matsumotoi</i> Kinoshita, 1923	A species <i>inquirenda</i> after Yosii (1977), only recorded so far from Japan.
Tullbergiidae						
<i>Delanarephorura capensis</i> Janion, Weiner & Deharveng, 2013	Janion et al. 2013	WC	E	Soil		
<i>Delanarephorura septyckii</i> Barra & Weiner, 2009	Barra and Weiner 2009	EC	E	Dry grassland		
<i>Fissunaphorura miscellanea</i> Barra, 1995	Barra 1995	KZN	E	Soil		
<i>Mecaphorura krausbaueri</i> (Börner, 1901)	Womersley 1934, Paclt 1959	WC, EC, FS	D	Soil, under stones	<i>Tullbergia krausbaueri</i> Börner, 1901	Dubious identification, most <i>Mecaphorura</i> have been identified as <i>M. krausbaueri</i> before the split of this species by Rusek (1971). Older records are not reliable (Fjellberg 1998).

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Mesophoruma yosii</i> (Rusek, 1967)	Barra 1995	KZN	W			Cosmopolitan distribution
<i>Panathullbergia callipygos</i> (Börner, 1902)	Womersley 1934	WC	I		<i>Tullbergia callipygos</i> Börner, 1902	Holarctic distribution
<i>Tullbergia meridionalis</i> Cassagnau & Rapoport, 1962	Barra 1995	KZN	W	Dune sand		Described from Argentina and later recorded from South Africa.
<i>Tullbergia kilimanjarica</i> (Delamare Deboutteville, 1953)	Pact 1959, 1967, Coates 1970	WC, KZN, MP	W	Forest leaf litter, garden soil	<i>Mesophoruma kilimanjarica</i> Delamare Deboutteville, 1953	Described from Tanzania and later recorded from South Africa.
ENTOMOBRYOMORPHA						
Isotomidae						
<i>Archisotoma sabulosa</i> Barra, 1997	Barra 1997	KZN	E	Littoral dune sand		
<i>Arlea tridens</i> Barra, 1997	Barra 1997	KZN	E	Dune litter		
<i>Bullistrana schoetti</i> (Dalla Torre, 1895)	Womersley 1934, Yosii 1959, Pact 1959, 1967	WC, EC	I	Vegetation, rain pools	<i>Proisotoma schoetti</i> (Dalla Torre, 1895) in Womersley 1934 and Pact 1959, 1967	Cosmopolitan distribution
<i>Clavisotoma africana</i> (Womersley, 1934)	Womersley 1934, Pact 1959	WC	E	Wet leaves, rain pools	<i>Proisotoma africana</i> (Womersley, 1934)	
<i>Folsomides americanus</i> Denis, 1931	Pact 1959, Barra 1997	KZN	W	From dry leaves		Cosmopolitan distribution
<i>Folsomina onychiarina</i> Denis, 1931	Barra 1997	KZN	W			Pantropical distribution
<i>Hemisotoma thernophila</i> (Axelson, 1900)	Womersley 1934, Pact 1959, Coates 1970	KZN, WC	W	Under rotting leaves	<i>Isotoma bituberculata</i> Wählgren, 1906 in Womersley 1934 and in Pact 1959 <i>Isotomina thernophila</i> (Axelson, 1900) in Coates 1970	Cosmopolitan distribution. <i>Isotoma bituberculata</i> is proposed as a synonym of either <i>Hemisotoma thernophila</i> or <i>H. orientalis</i> (Stach, 1947) in Potapov (2001). We provisionally consider it as a synonym of <i>H. thernophila</i> , the most widespread species of the genus <i>Hemisotoma</i> .
<i>Isotoma fruitima</i> Scherbakov, 1899	Pact 1959	KZN	D		<i>Sorensia fruitima</i> (Scherbakov, 1899)	The species is described without PAO, but body pigment is present; as such, it does not fit any known genus (Potapov 2001). Species inquirenda.

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Isotoma mauretania</i> Handschin, 1926	Womersley 1934	WC	D			<i>Species inquirenda</i> . Stach (1947) considered this Algerian species as a possible member of the genus <i>Isotomurus</i> , but the description is too brief to support such a statement. See also <i>Isotomurus palustris</i> .
<i>Isotomiella sodwana</i> Barra, 1997	Barra 1997	KZN	E	Litter and humus on sand dunes		
<i>Isotomodes productus</i> (Axelson, 1906)	Womersley 1934	WC	I	Under stones		Subcosmopolitan, records from southern hemisphere scattered.
<i>Isotomurus balteatus</i> (Reuter, 1876)	Womersley 1934	WC	D		<i>Isotomurus palustris</i> var. <i>balteata</i> (Reuter, 1876).	<i>I. balteatus</i> is a species of Europe recognizable by its transversal stripes on tergites. We have seen such a colour pattern in South African Isotomidae of an undetermined genus which is not <i>Isotomurus</i> . The record of this species for South Africa is therefore dubious.
<i>Isotomurus palustris</i> (Müller, 1776)	Womersley 1934, Paet 1959, 1967	WC, EC, G, KZN	I			Specimens of <i>Isotoma mauretania</i> Handschin, 1926 recorded in Womersley 1934 were re-identified as <i>I. palustris</i> by Paet (1959). This change is probably wrong, as Paet states that specimens lack bothriotrichia.
<i>Isotomurus tricuspis</i> Börner, 1906	Paet 1959, 1967	WC	D	Damp moss		Specimens of <i>Isotomurus palustris</i> var. <i>balteata</i> cited by Womersley (1934) are considered as <i>I. tricuspis</i> by Paet (1959), based on similar pattern of transversal stripes on tergites. However, these South African forms need to be examined morphologically to confirm their congeneric status with <i>I. tricuspis</i> from Java.
<i>Micranuroporus musci</i> Bernard, 1977	Barra 1997	KZN	W	Humid sand 20 cm under pioneer vegetation		Subcosmopolitan interstitial species.

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Microsomia caeca</i> (Wahlgren, 1906)	Paclt 1959	KZN, WC	W	From wet debris	<i>Cryptopygus caecus</i> Wahlgren, 1906	Current name after Potapov (2001).
<i>Parisotoma mossopi</i> (Womersley, 1934)	Paclt 1959	FS	E	From soil containing organic material	<i>Isotoma notabilis</i> ssp. <i>mossopi</i> Womersley, 1934	
<i>Parisotoma notabilis</i> (Schäffer, 1896)	Paclt 1959, 1967	WC	I	Wet leaves, leaf litter;	<i>Isotoma notabilis</i> Schäffer, 1896 in Paclt 1959, 1967	
<i>Parisotoma obscuracellata</i> Potapov, Janion & Deharveng, 2011	Potapov et al. 2011	WC	E	Litter under plants, coastal		
<i>Parisotoma sexsetosa</i> Potapov, Janion & Deharveng, 2011	Potapov et al. 2011	WC	E	Forest leaf litter		
<i>Pauropygus causanelli</i> (Thibaud, 1996)	Barra 1997	KZN	W	Littoral sand	<i>Cryptopygus niebi</i> Barra, 1997	Synonymy after Potapov, Gao and Deharveng 2013. On the coasts of Indian and Atlantic Oceans
<i>Proisotoma davidi</i> Barra, 2001	Barra 2001	EC	E	Grassland soil		
<i>Proisotoma minuta</i> (Tullberg, 1871)	Paclt 1959, 1967	WC, KZN, FS, EC	I	Litter		Cosmopolitan species.
Entomobryidae						
<i>Capbrya marshalli</i> Barra, 1999*	Barra 1999	EC	E	Grassland		
<i>Capbrya themeda</i> Barra, 1999*	Barra 1999	EC	E	Grassland		
<i>Coecobrya caeca</i> (Schött, 1896)	Goto 1953	WC	D	In cave	<i>Sinella caeca</i> (Schött, 1896)	<i>C. caeca</i> is restricted to northern America according to Chen and Christiansen (1997), and unlikely to have been introduced in South African caves. The South African species might be the cosmopolitan <i>C. tenebricosa</i> (Folsom, 1902) (Zhang et al. 2009)
<i>Coecobrya hoeffti</i> (Schäffer, 1896)	Paclt 1959	WC	D	In cave		Extra-European records are dubious (Jordana 2012). The Paclt specimens, from the same locality as the Goto (1953) specimens, may rather belong to the cosmopolitan species <i>C. tenebricosa</i> (Zhang et al. 2009)

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Entomobrya atrocincta</i> Schött, 1897	Paclt 1967	WC	I?	Litter		The large distribution of the species makes it difficult to determine from which region it may have been introduced. In addition, most colour patterns described in the literature do not fit the original and clear description of Schött (1897).
<i>Entomobrya decemfasciata</i> (Packard, 1873)	Womersley 1934	WC	D			Contrary to the claim of Womersley, <i>E. decemfasciata</i> does not occur in "most temperate parts of the world, including Europe". Reliable records are restricted to North America. The colour pattern given by Womersley is different from that given by Christiansen and Bellingier (1998) for specimens of the USA.
<i>Entomobrya lanuginosa</i> (Nicolet, 1842)	Womersley 1934	WC	I?		<i>Entomobrya nivalis</i> Linnaeus, 1758 f. <i>immaculata</i> Schäffer, 1896	The cited form is tentatively reported to <i>E. lanuginosa</i> . In that case it would be an introduced species.
<i>Entomobrya minima</i> Brown, 1926	Brown 1926	KZN	E	Under stone		
<i>Entomobrya multifasciata</i> (Tullberg, 1871)	Paclt 1967	WC, NC, G	I	Litter, next to stream		Widespread in the holarctic region.
<i>Entomobrya nicoleti</i> (Lubbock, 1876)	Womersley 1934	WC	I?		<i>Entomobrya nivalis</i> f. <i>maculata</i> Schäffer, 1896	The cited form is tentatively reported to <i>E. nicoleti</i> . In that case it would be an introduced species.
<i>Entomobrya nivalis</i> (Linnaeus, 1758)	Paclt 1959, 1967, Coates 1970	WC, EC, FS, KZN	I	Litter, rainwater pool		Cosmopolitan distribution, but most reliable records are in the holarctic region.
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871	Paclt 1959	KZN, EC	I?	Dry leaves, damp soil		Cosmopolitan distribution, but considered introduced in southern hemisphere where other related species are absent.
<i>Lepidocyrtus ferrugineus</i> (Schött, 1893)	Paclt 1959	KZN	D	Dry leaves		Described from Africa, the species needs a modern redescription to be recognizable.
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)	Womersley 1934, Paclt 1967	WC	D	Litter		Records of this species from the southern hemisphere need to be checked.

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Lepidolergeria meyerne</i> Coates, 1969*	Coates 1969	MP	E	Dead leaves		
<i>Orcheella hefyasciata</i> (Harvey, 1896)	Paclt 1959	FS, G	D	Litter	<i>Entomobrya hefyasciata</i> Harvey, 1896	Assigned to the genus <i>Entomobrya</i> by Paclt (1959), today considered as an <i>Orcheella</i> (Christiansen and Bellingr 1998). All reliable records are from the USA.
<i>Pseudosinella alba</i> (Packard, 1873)	Paclt 1959	WC, EC	I	Litter		Cosmopolitan distribution, but most reliable records are in the holarctic region.
<i>Pseudosinella biguttata</i> Barra 1997	Barra 1997	KZN	E	Sand forest litter		
<i>Pseudosinella immaculata</i> (Lie-Petersen, 1897)	Paclt 1959	KZN	D			All reliable records of this species are from Western Europe (Gisin and Da Gama 1972), following major taxonomic changes in species delimitations introduced in the 60'
<i>Pseudosinella octopunctata</i> Börner, 1901	Paclt 1959	WC, FS	I?	Wet litter		Subcosmopolitan distribution, but most tropical and southern hemisphere records need confirmation.
<i>Seira addoensis</i> Coates, 1968	Coates 1968	EC	E	Soil and vegetation		
<i>Seira amela</i> Coates, 1968	Coates 1968, 1970	EC, WC	E	Shore vegetation		
<i>Seira annulicornis</i> (Börner, 1903)	Yosii 1959, Coates 1968, 1970	WC, MP, G, FS, KZN,	W		<i>Seira (Lepidocyrtinus) annulicornis</i> (Börner, 1903) in Yosii 1959	African distribution
<i>Seira annulipes</i> (Handschin, 1929)	Womersley 1934	KZN, WC	W	On vegetation	<i>Lepidocyrtinus annulipes</i> , misspelling for <i>Lepidocyrtinus annulipes</i> Handsch., 1929	African distribution. Redescription needed on modern standards.
<i>Seira annulosa</i> (Wahlgren, 1906)	Womersley 1934	WC	D	Shore vegetation	<i>Lepidocyrtinus flavovirens</i> var. <i>annulosa</i> Wahlgren, 1906	Species previously known from Sudan; morphological features given by Wahlgren and Womersley do not allow reliable identification.
<i>Seira barnardi</i> (Womersley, 1934)	Womersley 1934, Yosii 1959, Paclt 1959, 1967, Coates 1968, 1970	WC, NWP	E	Wet leaves	<i>Lepidocyrtinus cooperi</i> var. <i>barnardi</i> Womersley, 1934 <i>Seira (Lepidocyrtinus) barnardi</i> (Womersley, 1933) (sic)	

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Seina capensis</i> (Womersley, 1934)	Womersley 1934, Yosii 1959, Coates 1968	WC, EC	E	On vegetation	<i>Lepidocyrtinus capensis</i> Womersley, 1934 <i>Seina (Seina) capensis</i> (Womersley, 1934) in Yosii 1959	
<i>Seina damerella</i> Coates, 1968	Coates 1968, 1970	L, MP	E	Litter	<i>Seina (Lepidocyrtinus) dany</i> Yosii, 1959	
<i>Seina dany</i> Yosii, 1959	Yosii 1959, Coates 1968	WC	E			Also recorded from Mozambique by Coates (1968) and from Yemen by Barra (2004)
<i>Seina eleana</i> Coates, 1968	Coates 1968, 1970	MP	W	From dry vegetation		
<i>Seina flavovirens</i> (Börner, 1903)	Womersley 1934, Yosii 1959, Coates 1968	WC	D		<i>Lepidocyrtinus flavovirens</i> Börner, 1903 in Womersley 1934; author should be (Börner, 1903) <i>Seina (Seina) flavovirens</i> (Börner, 1903) in Yosii 1959	May correspond to several whitish species of <i>Seina</i> .
<i>Seina grisea</i> (Womersley, 1934)	Womersley 1934, Coates 1968	WC	E	From vegetation	<i>Pseudosina grisea</i> Womersley, 1934	Possibly a synonym of <i>Seina flavovirens</i> according to Yosii (1959)
<i>Seina grisea annulata</i> (Womersley, 1934)	Womersley 1934	WC	D		<i>Pseudosina grisea</i> var. <i>annulata</i> Womersley, 1934	The taxonomic value of this form is uncertain. This variety might be synonym of <i>S. flavovirens</i> after Yosii (1959).
<i>Seina incerta</i> (Handschin, 1926)	Womersley 1934	WC	D	Estuary	<i>Lepidocyrtinus incertus</i> Handschin, 1926	The species has a characteristic colouration, but is only known from the Mediterranean region where it is uncommon, so unlikely to have been introduced to South Africa.
<i>Seina laeta</i> (Börner, 1908)	Börner 1908	NC	E		<i>Pseudosina (Mesina) laeta</i> Börner, 1908	
<i>Seina lindai</i> Coates, 1968	Coates 1968	EC, WC	E	Wet litter		
<i>Seina muerephila</i> Coates, 1968	Coates 1968	EC, WC	E	Litter		
<i>Seina matheusi</i> Coates, 1968	Coates 1968, 1970	EC, WC	E	From vegetation		
<i>Seina metala</i> Coates, 1968	Coates 1968	WC	E	Litter		
<i>Seina metarivosa</i> Coates, 1968	Coates 1968	FS, NC	E	From grass		
<i>Seina munnui</i> (Paclt, 1959)	Paclt 1959	NC	E	In ants' nest	<i>Diamantimum munnui</i> Paclt, 1959	Transferred to <i>Seina</i> by Salmon (1964)
<i>Seina nagatai</i> Yosii, 1959	Yosii 1959	WC	E		<i>Seina (Seina) nagatai</i> Yosii, 1959	
<i>Seina pollens</i> (Börner, 1908)	Börner 1908	NC	E		<i>Pseudosina nyassica</i> var. <i>pollens</i> Börner, 1908	

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Seira pseudocoverulea</i> (Denis, 1924)	Womersley 1934, Yosii 1959	WC	D	Estuary	<i>Lepidocyrtinus pseudocoveruleus</i> (Denis, 1924) in Womersley 1934	African species. A study of the chaetotaxy of Ethiopian specimens would be however necessary to confirm identification (Yosii 1959).
<i>Seira rowani</i> Yosii, 1959	Yosii 1959, Coates 1968, 1970	WC	E	On vegetation	<i>Seira (Afrosetina) rowani</i> Yosii, 1959	
<i>Seira rykeri</i> Coates, 1968	Coates 1968	WC	E	On vegetation		
<i>Seira squamoornata</i> (Scherbakov, 1898)	Paclt 1959, 1967	KZN, WC, FS, G, NC	D	Soil and vegetation		The numerous records of this species by Paclt are all dubious, and concern various endemic species of the genus. <i>S. squamoornata</i> is today considered to be limited to the Palearctic region.
<i>Seira tsikama</i> Coates, 1968	Coates 1968, 1970	WC	E	Forest leaf litter		
<i>Seira uaeedeni</i> Coates, 1968	Coates 1968	KZN	E	From shrub and grass		
Cyphoderidae						
<i>Calobatimus rhadinopus</i> (Börner, 1913)	Börner 1913, Paclt 1967	KZN, G	E	Termite nest	<i>Calobatella rhadinopus</i> Börner, 1913	
<i>Cyphoda colura</i> (Börner, 1908)	Börner 1908	NC	E	Termite nest	<i>Cyphoderus colurus</i> Börner, 1908	
<i>Cyphoda limboxiphia</i> (Börner, 1913)	Börner 1913, Paclt 1967	KZN, G	E?	Termite nest	<i>Cyphoderus limboxiphus</i> Börner, 1913	
<i>Cyphoda natalensis</i> (Börner, 1913)	Börner 1913, Womersley 1934	KZN, WC	E	Termite nest	<i>Cyphoderus natalensis</i> Börner, 1913	
<i>Cyphoderus assimilis</i> (Börner, 1906)	Paclt 1959	KZN	W	Ant nest		Cosmopolitan distribution
<i>Cyphoderus bidenticulatus</i> Parona, 1888	Börner 1913	KZN	E	Termite nest		
<i>Cyphoderus omeris</i> Delamare Deboutville, 1945	Paclt 1959, Womersley 1934	WC	D	In cave	<i>Cyphoderus arriatus</i> var. <i>aethiopicus</i> Hanschin, 1929 in Womersley 1934,	Wrong identification of Womersley after Paclt (1959)
<i>Cyphoderus squamidives</i> Silvestri, 1918	Silvestri 1918, Paclt 1959, 1967	KZN, WC, G	E?	Termite nest	<i>Cyphoderus arriatus</i> var. <i>squamidives</i> in Silvestri 1918	
<i>Cyphoderus trinervis</i> Paclt, 1965	Paclt 1965	G	E	Termite nest		
<i>Pseudocyphoderus wasmanni</i> Börner, 1913	Börner 1913, Paclt 1967	KZN, G	E	Termite nest		

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
Paronellidae						
<i>Dicranocentriga nigromaculata</i> (Schött, 1903)	Paclt 1959	KZN	W		<i>Paronella nigromaculata</i> Schött, 1903 in Paclt 1959	African species. The generic name <i>Dicranocentriga</i> Wray, 1953 was reactivated by Mitra (2002)
Tomoceridae						
<i>Neopohorella dubia</i> Womersley, 1934*	Womersley 1934	WC	E			
NEELIPLEONA						
Neelidae						
<i>Megalobothrax minimus</i> (Willem, 1900)	Paclt 1967	WC	W	Damp soil, moss		Cosmopolitan species, currently in course of splitting. South Africa specimens will have to be re-examined.
SYMPHYPLEONA						
Sminthurididae						
<i>Denisiella serroseta</i> (Börner, 1908)	Börner 1908, Paclt 1959	NC	W		<i>Sminthurides (Stenacidia) serroseta</i> in Börner 1908; <i>Sminthurides (Denisiella) serroseta</i> in Paclt 1959	African species
<i>Sphaeridia minima</i> (Schött, 1893)	Paclt 1959, 1967	FS, WC	D	From soil	<i>Sminthurides (Sphaeridia) minimus</i> (Schött, 1893)	<i>S. minima</i> is distributed in western Africa. It is very similar, if not identical, to the cosmopolitan species <i>S. pumilis</i> Krausbauer, 1898. Bretfeld (1999) considers that the Paclt specimens may belong to <i>S. pumilis</i> , but that those from Cameroon may represent distinct species. A revision of these tropical <i>Sphaeridia</i> is clearly needed.
Katiannidae						
<i>Katianna kerguelensis</i> Denis, 1947	Paclt 1959	KZN	D			The South African records of this sub-Antarctic species need confirmation.
<i>Sminthurinus mime</i> (Börner, 1907)	Womersley 1931, Paclt 1959, Paclt 1967	WC	W	Beneath vegetation	<i>Sminthurinus terrestris</i> Womersley, 1931	the two species, that are nevertheless synonymized by Greenslade (1994). Widely distributed in the southern hemisphere and in tropical Asia.

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Sminthurinus niger</i> (Lubbock, 1873)	Womersley 1931, Paclt 1959	WC	I	Under loose bark		Mostly holarctic. Tropical and Australian records may be the result of introductions. The synonymy of <i>S. pallidus</i> Womersley 1931 with <i>S. terrestris</i> proposed by Paclt (1959) is based on unsufficient ground and not accepted here.
<i>Sminthurinus pallidus</i> Womersley, 1931	Womersley 1931, Paclt 1959	WC	E	Beneath vegetation	<i>Sminthurinus terrestris</i> Womersley, 1931 in Paclt 1959	
<i>Stenognathellus stenognathus</i> (Börner, 1907)	Paclt 1959	WC, KZN	W	Litter	<i>Sminthurinus stenognathus</i> (Börner, 1907)	Africa and Argentina.
Dicyrtomidae						
<i>Dicyrtomina africana</i> Womersley, 1931	Womersley 1931	WC	E	On vegetation	<i>Dicyrtomina minuta</i> form <i>africana</i> Womersley, 1931	The validity of this form needs confirmation.
<i>Dicyrtomina minuta</i> (O. Fabricius, 1783)	Paclt 1959, 1967	WC	I	At stream, on vegetation		Northern hemisphere, probably introduced in southern regions. Paclt considered <i>Dicyrtoma minuta</i> f. <i>africana</i> as identical with <i>D. minuta</i> .
Bourletiellidae						
<i>Bourletiella arvalis</i> (Fitch, 1863)	Paclt 1959	WC	I	Lucerne pasture	<i>Bourletiella (Bourletiella) arvalis</i> (Fitch, 1863)	Northern hemisphere, with local occurrence in southern hemisphere where it has been probably introduced.
<i>Pronastriopes barnardi</i> (Womersley, 1931)	Womersley 1931, Paclt 1959	WC	E	Amongst grass	<i>Deuterosminthurus marmoratus</i> var. <i>barnardi</i> Womersley, 1931	A colour form of <i>P. marmoratus</i> . Paclt (1959) synonymized this form with <i>R. schultzei</i> on insufficient evidence.
<i>Pronastriopes marmoratus</i> (Womersley, 1931)	Womersley 1931, Paclt 1959	WC	E	Rainwater pools	<i>Deuterosminthurus marmoratus</i> Womersley, 1931	Paclt (1959) synonymized this species with <i>R. schultzei</i> on insufficient evidence. Generic assignation after Betsch (1980).
<i>Pronastriopes schultzei</i> (Börner, 1908)	Börner 1908	WC, G, NC	E	Among vegetation, wet habitat	<i>Bourletiella schultzei</i> in Börner, 1908	Paclt (1959) proposes to synonymize <i>P. marmoratus</i> , <i>P. barnardi</i> and <i>P. schultzei</i> , with <i>R. lineata</i> on weak morphological evidence as all these species are too briefly described. The same author considers in 1967 that his previous citation of <i>schultzei</i> (in Paclt 1959) as <i>Rastriopes lineatus</i> (here <i>R. lineata</i>).

Current species name	Source	Province recorded from in SA	Status	Habitat if given in source	Name published in source if different from the current one	Comments
<i>Ponastriopes webbi</i> Paclt, 1964	Paclt 1964, Coates 1970	KZN, MP, EC	E	On vegetation, litter		
<i>Rasstriopes lineata</i> Womersley, 1931	Womersley 1931, Paclt 1959, 1967	WC, NC, G	E	Under a fallen twig and on rainwater pool (Womersley 1931), on vegetation (Paclt 1959), moss and rotten leaves, grass on river banks (Paclt 1967)	<i>Rasstriopes schultzei</i> in Paclt 1959	Paclt (1959) synonymized this species with <i>R. schultzei</i> , but in 1967 considered that the specimen he identified as <i>schultzei</i> in Paclt (1959) was in fact <i>R. lineata</i> , bona species.
<i>Tritosminthurus schuhi</i> Snider, 1988*	Snider 1988	WC	E			
Sminthuridae						
<i>Papirinus prodigosum</i> Yosii, 1954	Paclt 1959	KZN	D		<i>Sphynotheca prodigiosa</i> (Yosii, 1954)	The genus <i>Papirinus</i> , placed among Katiannidae in Breffeld (1999), is considered here as closer to Sminthuridae. This species is only known from Japan. Other species exist in Madagascar, Sumatra, Thailand and Congo. The South African species is probably new (Betsch 1980).
<i>Sminthurus viridis</i> (Linnaeus, 1758)	Lawrence 1953, Paclt 1959	WC	I	On vegetation		Mainly holarctic species, thought to have been introduced from Europe (via Australia) as eggs in soil through the importation of clover seed (Wallace 1968, Wallace and Walters 1974).

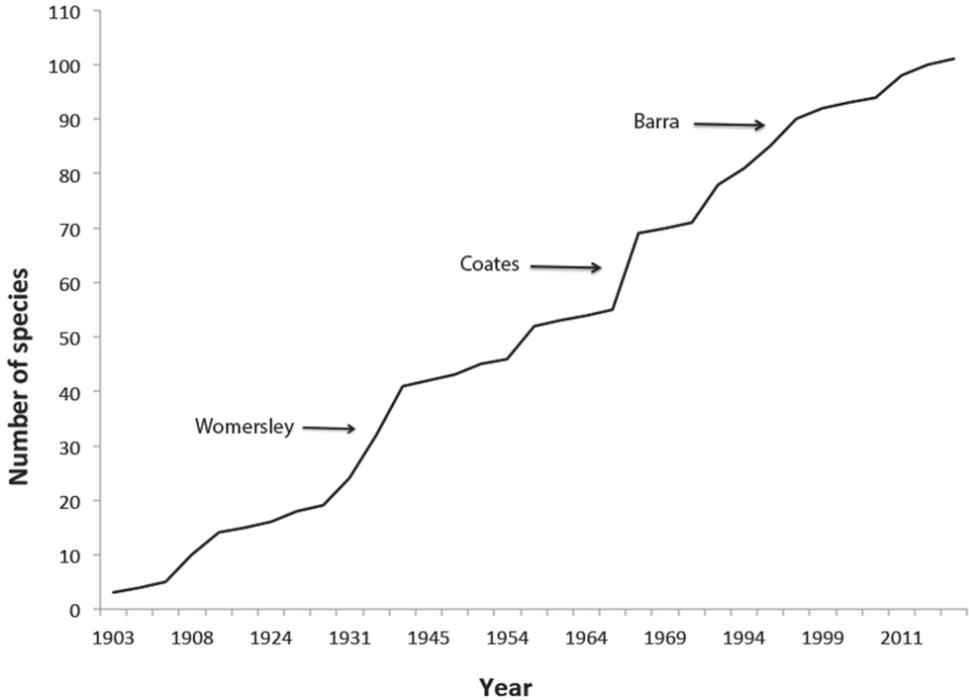


Figure 1. The cumulative number of Collembola species described from South Africa. The three major increases in described species are indicated by the author names (Womersley, Coates and Barra).

Discussion

The number of Collembola species recorded for South Africa is low compared to well-studied regions such as Europe (Deharveng 2007), but is the highest of all African countries south of Sahara (Thibaud 2013). Low sampling intensity in Africa seems to be the main reason for this pattern. Based on new records and species discovered during recent systematic sampling in the Western Cape Province alone (Janion et al. 2011a, b, Potapov et al. 2011, Janion et al. 2012, Liu et al. 2012, Janion et al. 2013), it is clear that many species remain to be recorded and described for this province. Given low richness documented elsewhere in South Africa the same situation is likely to be the case both there and in other African countries. The spatial distribution of species richness records also suggests that incomplete sampling coverage lies at the heart of the current diversity patterns. Most records to date have come from those provinces where taxonomists were either based or hosted such as in Cape Town of the Western Cape Province (Womersley 1934, Paclt 1959, Yosii 1959), and in Pretoria of the Gauteng Province (Coates 1969), reflecting a recurrent bias in geographic patterns of diversity of poorly known groups (Deharveng et al. 2000). Although Collembola do generally prefer moist environments (Hopkin 1997), which may mean lower diversity in arid provinces such as the Northern Cape and North-West Provinces (see Mucina and Rutherford 2006),

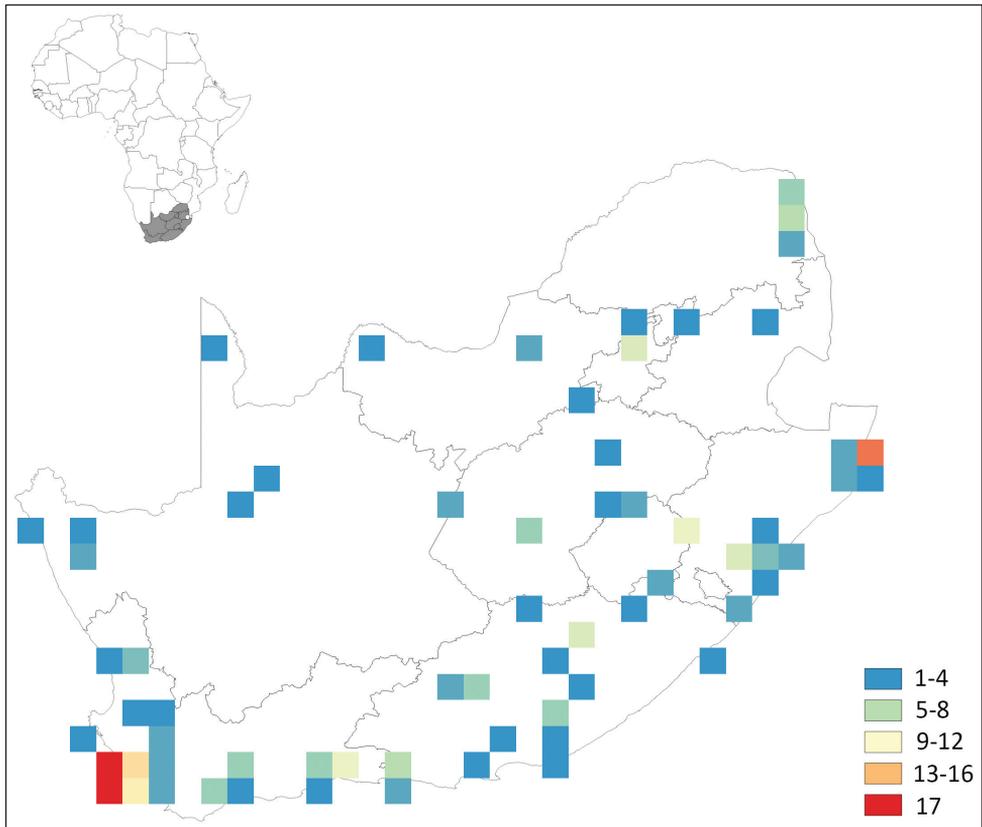


Figure 2. Number of Collembola species recorded for each degree square grid in South Africa.

low species richness in provinces such as Limpopo and Kwazulu-Natal is at odds with most other groups in the country (see e.g. Davis 1997 for dung beetles, Erasmus et al. 2000 for antlions, Foord et al. 2002 for spiders, Evans et al. 2006 for amphibians and birds, Schoeman and Foord 2012 for ants). The only exception to the poor knowledge of the fauna is for the sub-Antarctic Prince Edward Island group (consisting of Marion Island and the smaller Prince Edward Island), which is geopolitically a part of South Africa, and for which the fauna has been thoroughly investigated (Table 3, Gabriel et al. 2001, Hugo et al. 2006, Chown and Froneman 2008). Such a general situation of poor knowledge is typical for the Collembola in many parts of the world (e.g. Cicconardi et al. 2013), and will hamper efforts both to conserve this diversity (Cardoso et al. 2011) and to understand which components of it are non-indigenous and may be having impacts on the indigenous fauna (see discussion in Roques et al. 2009).

With the caveat in mind of undersampling, both in many parts of Africa and country-wide, it is worth considering what the current information on species in the country suggests. It appears that endemism is likely to be high (currently 65%). This value is similar to that found for other invertebrate groups and plants in South Africa, with

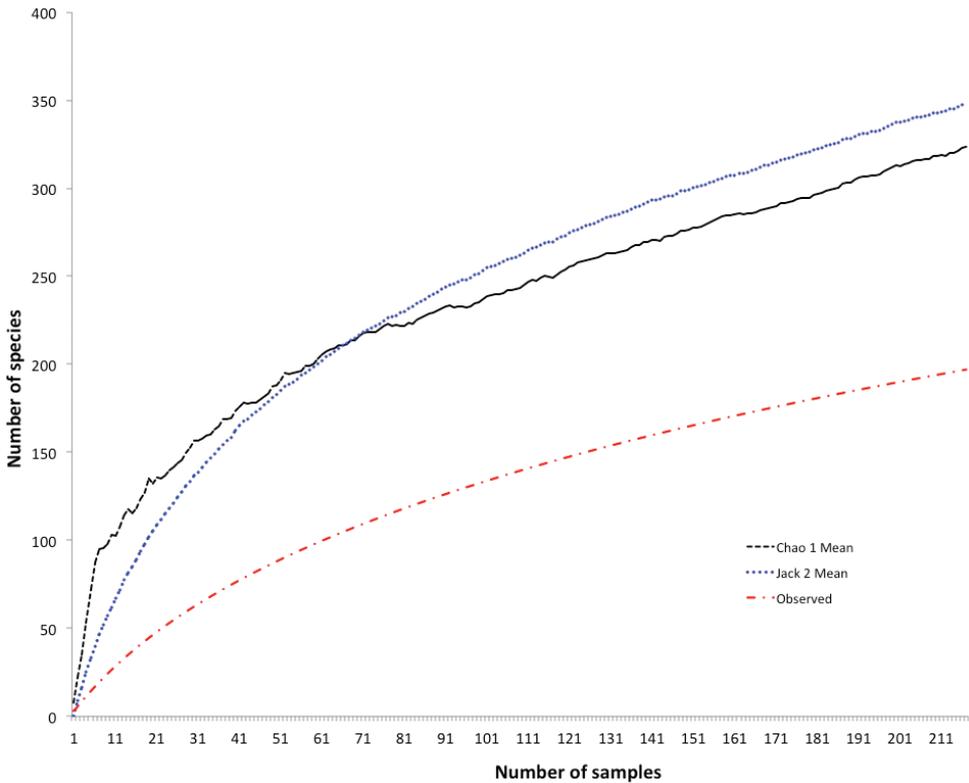


Figure 3. A sample-based rarefaction curve for the Western Cape, for observed species richness, and the Chao1 and Jackknife2 Estimators.

an extraordinary high number of endemic species found in the south-western Cape (see Colville et al. 2002, Goldblatt and Manning 2002, Herbert and Kilburn 2004, Rebelo et al. 2006, Pryke and Samways 2010). Endemicity is expected to increase with local sampling, but will likely decline if sampling is undertaken in neighbouring countries where information on the group is similarly low (e.g. Namibia, see Thibaud and Massoud 1988). Currently, sampling in the southern part of Africa mostly concerns sites within South Africa, generating a rapid increase in species richness and endemicity, as many additional endemic species have been obtained from samples as little as a few kilometres from already well sampled areas (Janion-Scheepers, Bedos and Deharveng unpublished results).

Currently, six genera are thought to be endemic to South Africa: *Najtafrica* Barra, 2002 (one species, Pseudachorutinae), *Probrachystomellides* Weiner & Najt, 1991 (one species, Brachystomellidae), *Capbrya* Barra, 1999 (two species, Entomobryidae), *Lepidokrugeria* Coates, 1969 (one species, Lepidocyrtinae), *Neophorella* Womersley, 1934 (one species, Tomoceridae) and *Tritosminthurus* Snider, 1988 (one species, Bourletielidae). *Neophorella dubia* was described from a single specimen by Womersley (1934) and is the only endemic species of the family Tomoceridae to occur in South Africa.

Table 3. Species recorded from the Prince Edward Islands, an island group geopolitically part of South Africa. Abbreviations used: E = endemic to Marion Island, S = sub-Antarctic distribution, I = introduced, D = dubious.

Current species name	Source	Status	Name in source and comments
PODUROMORPHA			
Hypogastruridae			
<i>Ceratophysella denticulata</i> (Bagnall, 1941)	Deharveng (1981)	I	<i>Ceratophysella</i> cf. <i>denticulata</i> (Bagnall, 1941)
<i>Hypogastrura viatica</i> (Tullberg, 1872)	Deharveng (1981)	D	Not found again since 1981, possible contamination (CJS pers. obs.)
Neanuridae			
<i>Friesea tilbrookii</i> Wise, 1970	Deharveng (1981)	S	<i>Friesea viennei</i> Deharveng, 1981 (syn Greenslade 1986)
Tullbergiidae			
<i>Tullbergia bisetosa</i> Börner, 1902	Deharveng (1981)	S	
ENTOMOBRYOMORPHA			
Isotomidae			
<i>Cryptopygus antarcticus travei</i> Deharveng, 1981	Deharveng (1981)	E	
<i>Cryptopygus dubius</i> Deharveng, 1981	Deharveng (1981)	S	
<i>Cryptopygus tricuspis</i> Enderlein, 1909	Deharveng (1981)	S	
<i>Folsomotoma marionensis</i> (Deharveng, 1981)	Deharveng (1981)	E	<i>Isotoma (Sorensia) marionensis</i> Deharveng, 1981
<i>Isotomurus maculatus</i> Müller, 1876	Deharveng (1981)	I	<i>Isotomurus</i> cf. <i>palustris</i> , confirmed as <i>I. maculatus</i> by Greenslade (2010)
<i>Mucrosomia caeca</i> (Wahlgren, 1906)	Deharveng (1981)	S	<i>Cryptopygus caecus</i> Wahlgren, 1906 (new comb. after Potapov 2001)
<i>Parisotoma notabilis</i> (Schäffer, 1896)	Deharveng (1981)	I	<i>Isotoma (Parisotoma) notabilis</i>
Tomoceridae			
<i>Pogonognathbellus flavescens</i> (Tullberg, 1871)	Gabriel et al. (2001)	I	
NEELIPLEONA			
Neelidae			
<i>Megalothorax minimus</i> Willem, 1900	Deharveng (1981)	I	<i>Megalothorax</i> cf. <i>minimus</i> Willem, 1900, identification confirmed by C. Schneider (pers. comm.)
SYMPHYPLEONA			
Katiannidae			
<i>Sminthurinus granulosus</i> Enderlein, 1909	Deharveng (1981)	S	<i>Sminthurinus</i> cf. <i>granulosus</i> Enderlein, 1909 in Deharveng (1981)
<i>Sminthurinus tuberculatus</i> Delamare Deboutteville & Massoud, 1963	Gabriel et al. (2001)	S	<i>Sminthurinus</i> cf. <i>kerquelenensis</i> Salmon, 1964 in Deharveng (1981)
<i>Katianna</i> sp.	Chown and Froneman (2008)	E	

Paclt (1959) mentioned that besides the single holotype specimen, this species was not found again and he synonymised it with the Paronellidae *Dicranocentruca nigromaculata* (Schött, 1903). Ireson and Greenslade (1990) re-examined the type specimen and re-assigned the species to Tomoceridae, stressing however its similarity with Isotomidae

(Skaife 1954). In spite of intensive sampling in its type locality of Table Mountain (Janion-Scheepers, Bedos and Deharveng unpublished results), the species was not retrieved in any of our samples, and is considered here as a *species inquirenda*.

The current information also suggests that approximately 20% of the Collembola species found in South Africa may have been introduced by humans to the region and should therefore be considered alien (see Pyšek et al. 2004 for terminology). Understanding what the proportion of introduced species in the fauna actually is will depend on additional comprehensive sampling, and on further consideration of species currently thought to be alien. Thus, several species resembling well-known European taxa had previously been mistakenly assigned to these taxa. For example, *Seira squamoornata*, which was originally described from the Ukraine, was thought to be a common polymorphic species in South Africa after Paclt (1959). However, Yosii (1959) did not even include this species in his list, while Coates (1968b) found that specimens labelled as one species (*S. squamoornata*) by Paclt (1959), could actually be identified as several endemic species described by Yosii (1959) or Coates (1968b), and concluded that this European species does not occur in South Africa. Indeed, to date 25 indigenous species of *Seira* have been described from South Africa (Yosii 1959, Coates 1968b), and the richness of the genus is likely much larger.

Nonetheless, that several alien species are present, especially of European origin, is not surprising given the close historical links between South Africa and Europe (Gillio-mee and Mbenga 2007). Most of the invasive species were collected in disturbed environments, in gardens or close to human settlements (Supplementary Material Suppl. material 1) bearing out findings for a range of other groups that disturbance may favour alien species establishment (Chytrý et al. 2005, MacDougall and Turkington 2005, Richardson and Pyšek 2006). Perhaps the best known of the alien species is *Sminthurus viridis*, also known as the Lucerne flea (Wallace 1964, Wallace and Walters 1974), which received considerable attention in South Africa during the late 1960s due to its pest status. It is thought to have arrived from Australia as eggs in soil through the importation of clover seed (Walters 1968, Wallace and Walters 1974). It was first collected in 1951 near Somerset West and by 1959 over 50 000 hectares of Lucerne were infested (Wallace and Walters 1974). The problem now appears largely to have been resolved, although the species is still listed as a pest of Lucerne (Annecke and Moran 1982).

In conclusion, based on published knowledge only, the Collembola species richness of South Africa is high compared with other African countries (Thibaud 2013), but low compared with non-African countries (Deharveng 2007) and with the richness of other invertebrate groups in the South African region (Scholtz and Chown 1995). This is likely due to undersampling, as recent discoveries (e.g. Janion et al. 2011b, Potapov et al. 2011, Janion et al. 2012, 2013) have indicated. Owing to a recent, large and comprehensive ecological and systematic study, accompanied by DNA Barcoding (Porco et al. 2012) largely focused on the country's Western Cape Province (Bengtsson et al. 2010, Janion et al. 2011a, Liu et al. 2012), a substantial increase in the number of species is expected. With 67 species recognised for the Western Cape from the recorded literature, the richness estimates indicating at least 6–7 times that

number being present, and based on experience in other undersampled countries such as Thailand (Bedos 1994), we expect that species richness for the country will exceed 1000. Improvement of systematic knowledge through studies such as these, and improvements in ecological understanding of the impacts of both landscape change and invasive species on the springtail fauna (e.g. Gabriel et al. 2001, Liu et al. 2012), will help South Africa meet its commitments to biodiversity conservation especially as set out in the 2020 Aichi Biodiversity Targets.

Acknowledgements

Grant Duffy assisted with the production of the map. Clement Schneider identified the *Megalothorax minimus* from Marion Island. We are grateful for support from the South Africa–France bilateral grants (PROTEA I and II), and the DST-NRF Centre of Excellence for Invasion Biology. SLC is supported by ARC DP140102815.

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Supplementary material I**Table S1**

Authors: Charlene Janion-Scheepers, Louis Deharveng, Anne Bedos, Steven L. Chown

Data type: occurrence

Explanation note: Collection details of Collembola recorded from continental South Africa.

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Alpha taxonomy of the genus *Kessleria* Nowicki, 1864, revisited in light of DNA-barcoding (Lepidoptera, Yponomeutidae)

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Academic editor: E. van Nieuwerkerken | Received 16 March 2015 | Accepted 27 April 2015 | Published 11 May 2015

<http://zoobank.org/25D68B1C-6ACF-47D4-BD77-9C3CCEDC0E86>

Citation: Huemer P, Mutanen M (2015) Alpha taxonomy of the genus *Kessleria* Nowicki, 1864, revisited in light of DNA-barcoding (Lepidoptera, Yponomeutidae). *ZooKeys* 503: 89–133. doi: 10.3897/zookeys.503.9590

Abstract

The taxonomy of *Kessleria*, a highly specialized montane genus of Yponomeutidae with larval host restriction to Saxifragaceae and Celastraceae (*Saxifraga* spp. – subgenus *Kessleria*; *Saxifraga* spp. and *Parnassia* spp. – subgenus *Hofmannia*), is revised based on external morphology, genitalia and DNA barcodes. An integrative taxonomic approach supports the existence of 29 species in Europe (the two known species from Asia and North America are not treated herein). A full 658 bp fragment of COI was obtained from 135 specimens representing 24 species, a further seven sequences are >560 bp. Five new species are described: *Kessleria cottiensis* sp. n. (Prov. Torino, Italy; Dep. Hautes Alpes, France), *Kessleria dimorpha* sp. n. (Dep. Alpes-de-Haute-Provence, France), *Kessleria alpmaritimae* sp. n. (Dep. Alpes-Maritimes, France), *Kessleria apenninica* sp. n. (Prov. Rieti, Prov. L'Aquila, Italy), and *Kessleria orobiae* sp. n. (Prov. Bergamo, Italy).

Keywords

Lepidoptera, Yponomeutidae, *Kessleria*, new species, integrative taxonomy, DNA barcode, morphology, cryptic diversity, European mountains

Introduction

The genus *Kessleria* Nowicki, 1864 is one of the striking examples of long underestimated or neglected diversity in the generally well known fauna of European Lepidoptera. This deficiency of knowledge is reflected in the fact that only 9 out of the 29 European species were described before 1960, and 18 species, or two-thirds of the fauna, after 1990 (Friese 1960, Huemer and Tarmann 1992, 1993). The genus is exceptional in Lepidoptera due to its highly specialized host-plant relationship with the Saxifragaceae, a habit shared e.g. by a section of the Curculionidae genus *Dichotrachelus* (Merigalli et al. 2013). Whereby the large majority of species is restricted to *Saxifraga*, two species feed on the herbaceous Celastraceae genus *Parnassia*, long considered as Saxifragaceae (The Angiosperm Phylogeny Group 2009). Through these host-plant relationships, *Kessleria* is a genus characteristic of mountain regions in the northern hemisphere, reaching high altitudes of about 3000 m in the European Alps and only exceptionally occurring below 600 m. In such alpine environments adult morphology may be adapted to rough climatic conditions with female brachyptery observed in several families of Lepidoptera (Sattler 1991), including minimum five species of *Kessleria*. Two major revisions (Friese 1960, Huemer and Tarmann 1992) are primarily based on external and internal morphology of adults, supplemented by ecological data. These authors established a stable and undisputed alpha taxonomy of *Kessleria*, which has been in use for the last two decades. Recently discovered suspected morphospecies led to the implementation of molecular methods as an additional tool in species delimitation. Sequences of the COI barcode region (Hebert et al. 2003, 2009) confirmed the species status of the vast majority of previously described taxa, and helped in resolving suspected cryptic species-complexes and in delimiting five species new to science.

Material and methods

Extensive descriptions and diagnoses of previously described European species of *Kessleria* including keys to males and females, colour figures of adults, black-and-white figures of male and female genitalia, last abdominal segments, illustrations of wing venation and figures of larval habits and habitats have been published by Huemer and Tarmann (1992, 1993) and are not repeated here.

Our study was initially based on morphology of the extensive material published in detail by Huemer and Tarmann (1992), and about 100 additional specimens, with DNA barcode sequences as an additional tool for delimitation of cryptic species. Most of the material was set and dried according to standard practice, some were spread, and a few only pinned. Genitalia preparations followed standard techniques for microlepidoptera (Robinson 1976), adapted for *Kessleria* e.g. by the manual eversion of cornuti (Huemer and Tarmann 1992). Wing venation was not considered for new species de-

scriptions as it proved irrelevant for alpha taxonomy in the genus in the earlier revision by Huemer and Tarmann (1992).

We tried to obtain DNA barcode sequences, a 658 base-pair long segment of the 5' terminus of the mitochondrial COI gene (*cytochrome c oxidase I*), from 150 specimens, three from LMK and ZMUO respectively, and 144 from TLMF. DNA samples (from a single dried leg) were prepared according to the accepted standards. Legs from 150 specimens of *Kessleria* were processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) using their standard high-throughput protocol described in deWaard et al. (2008). Successfully sequenced voucher specimens are listed in Suppl. material 1 together with species names, sample-IDs, process-IDs, BINs, COI-5P sequence length, and trace counts. Sequences were submitted to GenBank during printing stage; GenBank accession numbers further details including complete voucher data and images can be accessed in the public dataset "Lepidoptera of Europe - *Kessleria*" <http://dx.doi.org/10.5883/DS-LEAKE> in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007). Degrees of intra- and interspecific variation in the DNA barcode fragment were calculated under the Kimura 2-parameter (K2P) model of nucleotide substitution using analytical tools in BOLD systems v3.0. (<http://www.boldsystems.org>). A neighbor-joining tree of DNA barcode data of European taxa was constructed using Mega 5 (Tamura et al. 2011) under the K2P model for nucleotide substitutions. In taxonomic delimitation, we applied principles of integrative taxonomy (Padial et al. 2010) and considered a barcode divergence of roughly 2% supported by at least one morphological character indicating species distinctiveness. We acknowledge that any threshold value of genetic distinctiveness is artificial and should not alone be used as indicating species status (cf. Collins and Cruickshank 2013), for which reason we considered 2% genetic difference associated with at least one morphological character indicating species integrity in the sense of e.g. General Lineage Species Concept (deQueiroz 1998) and Phylogenetic (diagnostic) Species Concept (Cracraft 1989), which both are applicable in delimiting also allopatric populations.

Photographs of the adults were taken with an Olympus SZX 10 binocular microscope and an Olympus E 3 digital camera, and processed using the software Helicon Focus 4.3 and Adobe Photoshop CS4 and Lightroom 2.3. Genitalia photographs were taken with an Olympus E1 Digital Camera from Olympus BH2 microscope.

Measurements were taken with a micrometer eyepiece.

Abbreviations of institutional collections

- BMNH** Natural History Museum (British Museum, Natural History) London, United Kingdom
LMK Landesmuseum Kärnten, Klagenfurt, Austria

MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHU	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
NHMV	Naturhistorisches Museum, Vienna, Austria
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
ZMUO	Zoological Museum, University of Oulu, Finland
ZMUC	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, München, Germany

Results

The checklist of European *Kessleria* largely follows Huemer and Tarmann (1992). The proposed tentative structure into species groups is based on morphology and as far as available DNA barcode data, but a well-grounded phylogenetic analysis will require further data, particularly from nuclear markers.

Checklist of European *Kessleria*

Kessleria Nowicki, 1864

Subgenus *Kessleria* Nowicki, 1864

Kessleria alpicella-group

K. alpicella (Stainton, 1851)

= *K. alpicella* (Herrich-Schäffer, 1855), Homonym

K. mixta Huemer & Tarmann, 1992

Kessleria alternans-group

K. alternans (Staudinger, 1871)

K. cottiensis sp. n.

K. dimorpha sp. n.

K. wehrlii Huemer & Tarmann, 1992

K. alpmaritimae sp. n.

Kessleria petrobiella-group

K. nivescens Burmann, 1980

K. petrobiella (Zeller, 1868)

Kessleria albanica-group

K. macedonica Huemer & Tarmann, 1992

K. albanica Friese, 1960

K. burmanni Huemer & Tarmann, 1992

K. insubrica Huemer & Tarmann, 1993

K. hauderi Huemer & Tarmann, 1992

Kessleria apenninica-group

K. apenninica sp. n.

K. diabolica Huemer & Tarmann, 1992

K. brevicornuta Huemer & Tarmann, 1992

K. pyrenaea Friese, 1960

K. brachypterella Huemer & Tarmann, 1992

Kessleria zimmermanni-group

K. zimmermanni Nowicki, 1864

= *K. tatica* Friese, 1960

K. albomaculata Huemer & Tarmann, 1992

K. caflischiella (Frey, 1880)

Kessleria albescens-group

K. klimeschi Huemer & Tarmann, 1992

K. helvetica Huemer & Tarmann, 1992

K. inexpectata Huemer & Tarmann, 1992

K. orobiae sp. n.

K. albescens (Rebel, 1899)

Subgenus *Hofmannia* Heinemann & Wocke, 1877

K. saxifragae (Stainton, 1868)

K. fasciapennella (Stainton, 1849)

= *K. longipennella* Friese, 1960

Molecular analysis

Sequencing resulted in a full barcode fragment of 658 bp for 135 specimens, covering 24 species. A further seven sequences that were longer than 560 bp were included in the analysis. A single short sequence of 307 bp was not considered, and sequencing failed for seven voucher specimens. Mean intraspecific divergence is 0.61%. It ranges from 0–4.27%, exceeding 2% only in three species, which, however, may include further cryptic diversity (e.g. *K. alpicella*, *K. albanica* and *K. inexpectata*) and should be tested accordingly with more material (Table 1, Fig. 1). On the contrary, interspecific divergence in the genus is much higher with a mean divergence of 10.38% and maximum of 16.22%. Interspecific divergence to the nearest neighbour ranges from 1.86–9.29%, with the only exception being *K. inexpectata* and *K. helvetica*, which overlap in DNA barcode (Table 1, Fig. 1).

From sequence analysis of 20 *Kessleria* species based on at least three sequences, 17 species are delimited by a minimum of one to a maximum of 10 diagnostic characters whereas *K. inexpectata*, *K. cottiensis* and *K. alpmaritimae* have no diagnostic character (Table 1).

Table 1. Intraspecific distance and interspecific divergence to the nearest neighbour in the genus *Kessleria*. Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

Species	# sequ	Mean intra	Max intra	Nearest neighbour	Nearest species	Nearest species	Diagnostic characters
<i>Kessleria albanica</i>	5	2.05	2.98	PHLAB1059-10	<i>Kessleria burmanni</i>	9.29	8
<i>Kessleria albescens</i>	3	0	0	PHLAD145-11	<i>Kessleria orobiae</i>	2.66	3
<i>Kessleria albomaculata</i>	1	N/A	N/A	PHLAD138-11	<i>Kessleria petrobiella</i>	6.76	-
<i>Kessleria alpicella</i>	12	1.52	4.27	PHLAD119-11	<i>Kessleria wehrlii</i>	6.9	6
<i>Kessleria alpmaritimae</i>	6	0	0	PHLAD119-11	<i>Kessleria wehrlii</i>	1.87	0
<i>Kessleria alternans</i>	10	0.12	0.31	PHLAD122-11	<i>Kessleria cottiensis</i>	2.65	3
<i>Kessleria apenninica</i>	4	1.06	1.71	PHLAI438-13	<i>Kessleria pyrenaea</i>	5.47	3
<i>Kessleria burmanni</i>	6	0	0	PHLAD140-11	<i>Kessleria hauderi</i>	7.61	6
<i>Kessleria caftischiella</i>	8	0.04	0.15	PHLAD118-11	<i>Kessleria alpmaritimae</i>	6.39	6
<i>Kessleria cottiensis</i>	5	0	0	PHLAB957-10	<i>Kessleria dimorpha</i>	1.86	0
<i>Kessleria dimorpha</i>	4	0.08	0.15	PHLAD122-11	<i>Kessleria cottiensis</i>	1.86	1
<i>Kessleria fasciapennella</i>	8	0.04	0.15	PHLAI063-12	<i>Kessleria saxifragae</i>	7.21	8
<i>Kessleria hauderi</i>	2	0	0	PHLAB1059-10	<i>Kessleria burmanni</i>	7.61	-
<i>Kessleria helvetica</i>	1	N/A	N/A	PHLAB1065-10	<i>Kessleria inexpectata</i>	0.31	-
<i>Kessleria inexpectata</i>	7	1.4	2.18	LASTS544-14	<i>Kessleria helvetica</i>	0.31	0
<i>Kessleria insubrica</i>	4	0.08	0.15	PHLAB1059-10	<i>Kessleria burmanni</i>	8.95	9
<i>Kessleria klimeschi</i>	5	0.06	0.15	PHLAB1065-10	<i>Kessleria inexpectata</i>	8.83	10
<i>Kessleria nivescens</i>	14	1.09	2.5	PHLAD138-11	<i>Kessleria petrobiella</i>	3.29	4
<i>Kessleria orobiae</i>	5	0.31	0.46	PHLAB1067-10	<i>Kessleria albescens</i>	2.66	1
<i>Kessleria petrobiella</i>	4	0	0	PHLAD132-11	<i>Kessleria nivescens</i>	3.29	1
<i>Kessleria pyrenaea</i>	1	N/A	N/A	PHLAB861-10	<i>Kessleria apenninica</i>	5.47	-
<i>Kessleria saxifragae</i>	20	0.44	1.29	LEFIB126-10	<i>Kessleria fasciapennella</i>	7.21	9
<i>Kessleria wehrlii</i>	4	0	0	PHLAD118-11	<i>Kessleria alpmaritimae</i>	1.87	1
<i>Kessleria zimmermanni</i>	5	0	0	PHLAD138-11	<i>Kessleria petrobiella</i>	5.73	6

Taxonomy

New species of *Kessleria*

Kessleria alternans-group

The *K. alternans*-group is characterized by strong sexual dichroism and to a lesser extent dimorphism, with females being smaller and lighter, but not strongly brachypterous (Figs 2–11). The genitalia are characterized by the strong reticulate sculpture of the apical part of the phallus (Figs 12–21) and the ductus bursae, which is extended into the corpus bursae (Figs 22–26). Larval host-plants, as far as known, belong to the small-leaved *Saxifraga* spp., particularly the *S. oppositifolia*-complex, and to broad-leaved congeners such as *S. paniculata*. Five species belong to this group: *K. alternans*, *K. wehrlii* and the new taxa *K. cottiensis*, *K. dimorpha* and *K. alpmaritimae*.

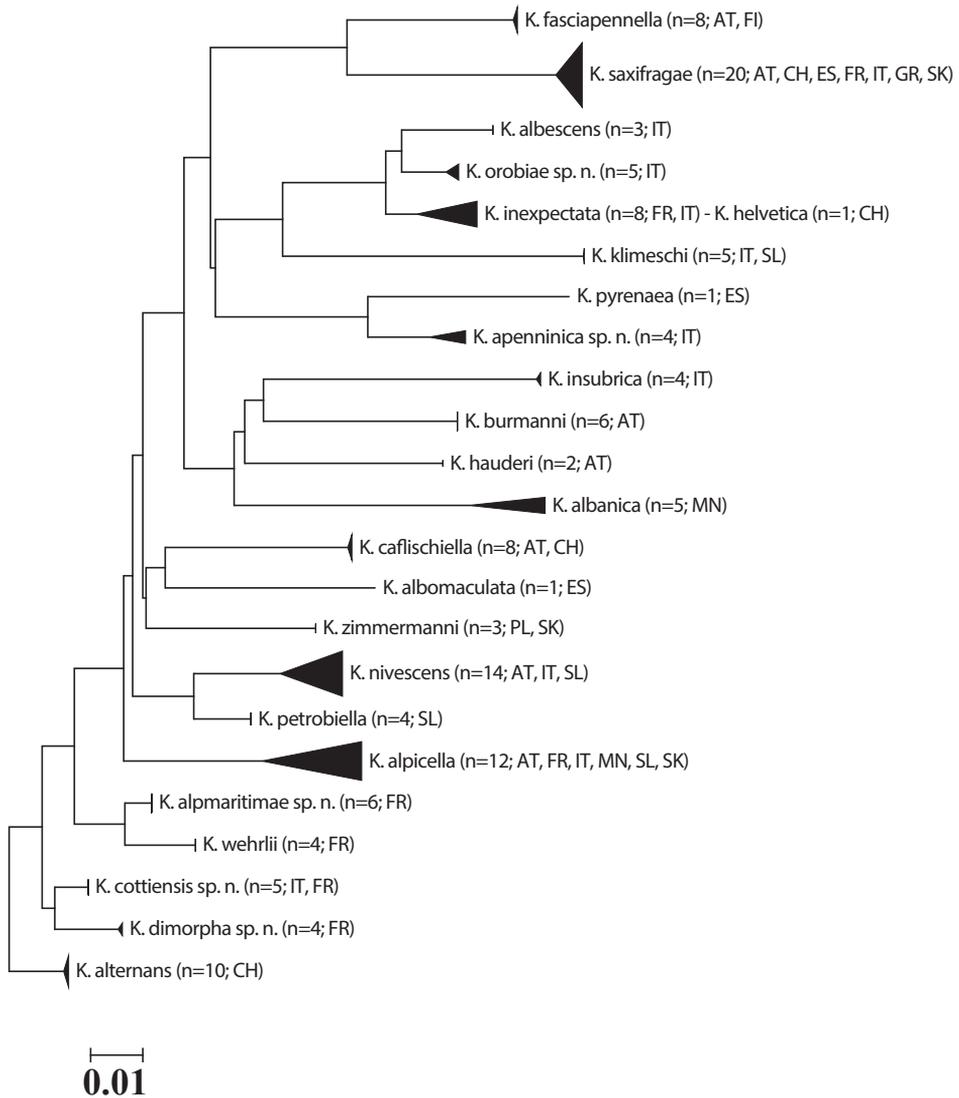
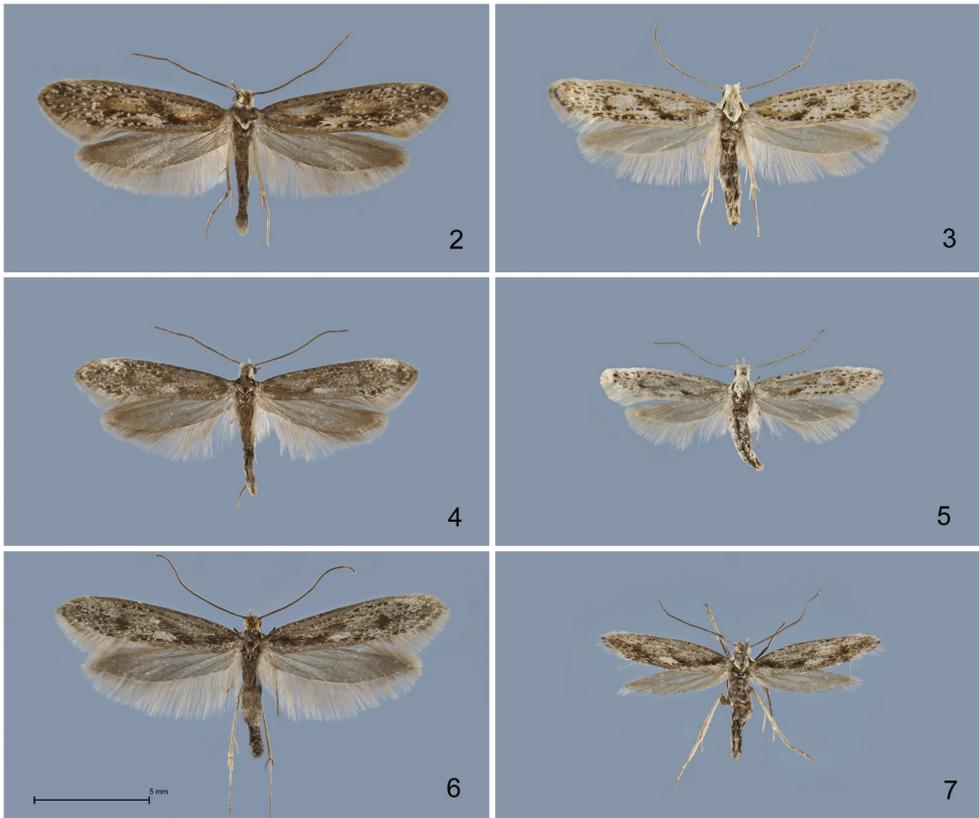


Figure 1. Neighbour-joining tree (Kimura 2 parameter, built with MEGA 5; cf. Tamura et al. 2011). Note: the scale bar only applies to internal branches between species. The width of the triangles represents the sample size, and the depth the relative genetic variation within the cluster ($2 \times$ scale bar). Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

***Kessleria cottiensis* sp. n.**

<http://zoobank.org/21EBBA7D-08EE-4713-B958-F67F00B0CEE5>

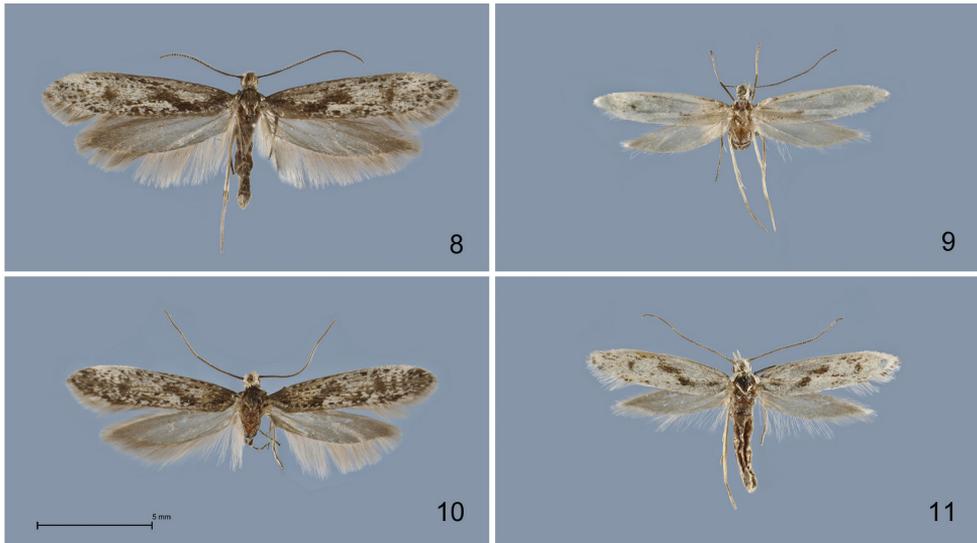
Type material. Holotype. ♂, „ITALIA, Prov. Torino Alpi Cozie, 2150 m Colle delle Finestre 27.7.1990 leg. Huemer & Tarmann“ „YPO 58 ♂ P. Huemer“ (TLMF).



Figures 2–7. *Kessleria* adults in dorsal view. **2** *K. alternans*, ♂, Switzerland, Graubünden, SE Sils-Maria, 1820–1870 m, 13.7.1989, leg. Huemer, Karsholt & Tarmann (TLMF) **3** *K. alternans*, ♀, same data (TLMF) **4** *K. cottiensis* sp. n., ♂, paratype, Italy, Prov. Torino, Alpi Cozie, V. delle Finestre, 1700 m, 27.7.1990, leg. Huemer & Tarmann (TLMF) **5** *K. cottiensis* sp. n., ♀, paratype, same data (TLMF) **6** *K. dimorpha* sp. n., ♂, paratype, France, Dep. Hautes-Alpes, Col Agnel, 2770 m, 4.8.2010, leg. Huemer (TLMF) **7** *K. dimorpha* sp. n., ♀, paratype, same data (TLMF).

Paratypes. Italy: 13 ♂, 7 ♀, same data, genitalia slides YPO 59 ♂ P. Huemer, YPO 77 ♂ P. Huemer, DNA barcode IDs TLMF Lep 03106, TLMF Lep 03107, TLMF Lep 03108 (TLMF); 3 ♂, 6 ♀, same data, but V. delle Finestre, 1700 m, genitalia slides YPO 66 ♂ P. Huemer, YPO 67 ♀ P. Huemer (TLMF). **France:** 1 ♂, Dep. Hautes-Alpes, Nevache, 1950m, 31.7.2001, leg. Nel, genitalia slide 12937 J. Nel, DNA barcode ID TLMF Lep 03144 (TLMF); 1 ♂, Dep. Hautes-Alpes, Vallee de la Claree, 2000 m, 3.7.2002, leg. Nel, genitalia slide 14644 J. Nel, DNA barcode ID TLMF Lep 03142 (TLMF).

Diagnosis. *K. cottiensis* resembles other taxa of the *K. alternans*-group in wing markings and colour (Figs 2–11), but the male differs in the on average smallest forewing length of 7.59 mm (n=14) vs. 8.75 mm (n=13) in *K. wehrlii*, 8.55 mm (n=26) in *K. alternans*, 8.05 mm (n=6) in *K. alpmaritimae* and 8.25 mm (n=6) in *K. dimorpha*.



Figures 8–11. *Kessleria* adults in dorsal view. **8** *K. wehrlii*, ♂, paratype, France, Dep. Alpes Maritimes, Mont Gelas Massiv, Mont Colomb W, 2450 m, 24.7.1990, leg. Huemer & Tarmann (DNA barcode ID TLMF Lep 01857) (TLMF) **9** *K. wehrlii*, ♀, paratype, same data (TLMF) **10** *K. alpmaritimae* sp. n., ♂, paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 18.–19.7.1991, leg. Huemer & Tarmann (TLMF) **11** *K. alpmaritimae* sp. n., ♀, paratype, same data (DNA barcode ID TLMF Lep 01851) (TLMF).

Compared to *K. wehrlii* and *K. alpmaritimae*, the whitish suffusion of the forewing is largely reduced. The ochre-brown markings, which are well present in *K. alternans*, are almost completely absent. The female of *K. cottiensis* is also distinctly smaller than *K. alternans*, with a forewing length of 6.13 mm (n=8) on average *vs.* 7.58 mm (n=11), whereas females of *K. cottiensis* and *K. alpmaritimae* are indistinguishable. *K. wehrlii* is insufficiently known from only a single worn female specimen. Compared to the genetically nearest neighbour *K. dimorpha*, which is similar in forewing length (6.0 mm, n=4), the hindwings are slightly less reduced and the ground colour of the forewing is much lighter. Diagnostic characters in genitalia are generally weak. The male genitalia differ from *K. alpmaritimae* by the medially strongly widened valva, from *K. alternans* by the more slender cornuti, from *K. wehrlii* by three instead of four cornuti, and from the nearest neighbour *K. dimorpha* by the distinctly longer phallus (1.65–1.70 mm *vs.* 1.32–1.36 mm) (Figs 12–21). The female genitalia show no diagnostic characters to related species of the *K. alternans*-group (Figs 22–31).

Description. Male (Fig. 4). Head covered with erected whitish hair-like scales; antennae dark grey-brown, indistinctly lighter ringed; thorax and tegulae dark grey-brown. Forewing length 7.0–8.8 mm (Ø 7.59 mm; n=14); ground colour dark grey-brown, mottled with whitish scales, particularly in distal half, forming indistinct patches in fold and on costa at about 4/5; irregular black dots on veins and few brown scales in medial part of wing; oblique blackish fascia at about 1/3 to 1/2 indistinct;



Figures 12–17. *Kessleria* male genitalia. **12** *K. alternans*, Switzerland, Graubünden, SE Sils-Maria, 1820–1870 m, 13.7.1989, leg. Huemer, Karsholt & Tarmann, gen. slide YPO 22 (TLMF) **13** idem, distal part of phallus enlarged **14** *K. cottiensis* sp. n., paratype, Italy, Prov. Torino, Alpi Cozie, V. delle Finestre, 1700 m, 27.7.1990, leg. Huemer & Tarmann, gen. slide YPO 66 (TLMF) **15** idem, distal part of phallus enlarged **16** *K. dimorpha* sp. n., paratype, France, Dep. Hautes-Alpes, Col Agnel, 2770 m, 4.8.2010, leg. Huemer gen. slide YPO 149 (TLMF) **17** idem, holotype, gen. slide YPO 158, distal part of phallus enlarged.

termen mixed whitish-grey, dark grey-brown in apical part; fringes light grey, darker in apical area. Hindwing dark grey, fringes with dark grey base, distal part light grey.

Female (Fig. 5). Head covered with erected whitish hair-like scales; antennae grey-brown, distinctly ringed whitish; thorax and tegulae whitish. Forewing length 5.8–6.3 mm ($\bar{\text{O}}$ 6.13 mm; $n=8$); ground colour whitish, mottled with black scales, particularly along veins and in tornal part, patches of brown scales in medial part of wing from base to end of cell; oblique blackish fascia at about 1/3 to 1/2 indistinct, separated into larger dash-like patch and reduced dot; termen whitish with some dark grey-brown mottling in apical part; fringes greyish-white, darker in apical area.

Male genitalia (Figs 14–15). Socii long and slender, with apical spine; anterior margin of tegumen with medial process; gnathos broadly tongue-shaped, smooth; valva moderately slender, length 0.66–0.70 mm, medially distinctly widened, maximum width of about 0.24–0.26 mm, densely covered with long hairs in medial part and short setae on ventromedial margin, ventromedial part weakly convex, distal part slender with ventrally convex and dorsally projected apex, costa strongly sclerotized with some distal dentation; sacculus oval, weakly confined, densely covered with strong setae; saccus sizeable in length, about 0.38–0.42 mm, stout, about same width throughout, apex rounded; phallus ca. 1.65–1.70 mm long and slender, straight, apically with distinct reticulate sculpture, uneverted vesica with ca. 0.76–0.80 mm long sclerotized part, three prominent needle-shaped, one single, the other basally connected, cornuti of about 0.46–0.51 mm in length.

Female genitalia (Figs 23, 28). Genitalia ca. 4.9 mm in length; papilla analis large, densely covered with long setae; apophysis posterior rod like, ca. 0.70 mm, about length of apophysis anterior; apophysis anterior rod like; posterior part bifurcated with straight dorsal and inwardly curved ventral branch; lamella postvaginalis with large sclerotized mediolateral patches, covered with microtrichia, medial area less sclerotized, posteriolateral part with hump, covered with some long setae; ostium bursae membranous; antrum weakly sclerotized, funnel-shaped; ductus bursae very long, about 2.8 mm, from entrance of ductus seminalis to transition into corpus bursae covered with finely granulous sculpture, particularly in posterior and anterior part, ductus bursae extended into posterior part of corpus bursae, entrance to corpus bursae weakly widened; corpus bursae well delimited, about 1.2 mm in length, ovoid, with small plate-like signum.

Molecular data. The average intraspecific divergence of the barcode region is 0.0% ($n=5$). The minimum distance to the nearest neighbour *K. dimorpha* is 1.86%, whereas the minimum divergence to *K. alternans*, *K. alpmaritimae* and *K. wehrlii* ranges from 2.65% and 2.98% to 3.63%, respectively.

Etymology. The species name refers to the type locality in the Cottian Alps (Alpi Cozie, Alpes cottiennes).

Distribution (Fig. 32). Only known from a small area in the southwestern Alps (Cottian Alps) of Italy and France. An alleged *K. alternans* from the Graian Alps (Huemmer and Tarmann 1992) likely refers to *K. cottiensis*, but the specimen in question could not be re-examined.

Ecology. Host-plant and early stages unknown. The adults were collected in late July. The flight period can most likely be further prolonged, depending on snow coverage and elevation. A specimen collected earlier during the summer, on June 9th, by Jäckh in Valle delle Finestre (Huemer and Tarmann 1992) probably belongs to *K. cottiensis*. The adults were collected during the day, flying freely in the morning hours and flushed out from their resting places with a bee-smoker. The species occurs in alpine grassland interspersed with calcareous rocks. Vertical distribution: from about 1700 m to 2150 m.

Remarks. *K. cottiensis* described here was already suspected to be distinctive from *K. alternans* by Huemer and Tarmann (1992), who illustrated adults (Figs 6–7) and cornuti of male genitalia (Fig. 105).

***Kessleria dimorpha* sp. n.**

<http://zoobank.org/B77D97D9-D8B3-4829-A8B6-4A7C13D5434A>

Type material. Holotype. ♂, „Frankreich Dep. Hautes-Alpes Col Agnel, 2770 m 6°59'02"E, 44°41'10"N 4.8.2010, leg. Huemer TLMF 2011-010“ „BC TLMF Lep 01756“ „YPO 158 ♂ P. Huemer“ (TLMF).

Paratypes. France: 7 ♂, 5 ♀, same data, genitalia slides YPO 149 ♂ P. Huemer, YPO 159 ♀ P. Huemer, DNA barcode IDs TLMF Lep 01757, TLMF Lep 01758, TLMF Lep 01759 (TLMF); 4 ♂, 1 ♀, same data, leg. Wieser (LMK).

Diagnosis. *K. dimorpha* resembles other taxa of the *K. alternans*-group in wing markings and colour (Figs 2–11), but the male differs from the genetically nearest neighbour *K. cottiensis* by the on average distinctly larger forewing length of 8.25 mm (n=6) *vs.* 7.59 mm (n=14). Larger species are *K. wehrlii* with forewing length 8.75 mm (n=13) and *K. alternans* with 8.55 mm (n=26), whereas *K. alpmaritimae* with 8.05 mm (n=6) is of similar size. Furthermore, *K. wehrlii* and *K. alpmaritimae* have a much more prominent whitish suffusion on the forewing, whereas the ochre-brown markings of *K. dimorpha* rather resemble *K. alternans*. The female of *K. dimorpha* reflects a tendency to reinforced brachyptery and is distinctly smaller than *K. alternans* with a forewing length of only 6.0 mm (n=4) on average *vs.* 7.58 mm (n=11), whereas females of *K. cottiensis* and *K. alpmaritimae* are strongly suffused with whitish scales. *K. wehrlii* is insufficiently known from only a single worn female specimen. The male genitalia differ from all other taxa of the *K. alternans*-group by the distinctly shorter phallus with <1.40 mm *vs.* a minimum of 1.50 mm in other species (Figs 12–21). The female genitalia show no diagnostic characters to related species of the *K. alternans*-group (Figs 22–31).

Description. Male (Fig. 6). Head covered with ochre-brown hair-like scales; antennae almost unicolorous dark grey-brown; thorax and tegulae mixed dark grey-brown and ochre-brown. Forewing length 8.0–8.4 mm (Ø 8.25 mm; n=6); ground colour dark grey, intensively mottled with light grey, ochre-brown and whitish scales, white medial patch in fold; black dots particularly on costal and subcostal veins; black patch near base and at end of cell, oblique blackish fascia at about 1/3 to 1/2 reduced

to large patch in fold; termen mixed dark and light grey; fringes basally dark grey, distal part whitish-grey, darker in apical area. Hindwing dark grey, fringes with dark grey base, distal part whitish-grey.

Female (Fig. 7). Head covered with erected whitish hair-like scales; antennae grey-brown, indistinctly lighter ringed; thorax and tegulae whitish. Forewing length 6.0 mm (\emptyset 6.0 mm; n=4); ground colour whitish, mottled with dark grey and black, particularly along fold and in tornal part, few black dots along costal and subcostal vein, small patches of ochre-brown scales in medial part of wing particularly in fold and at end of cell; oblique blackish fascia at about 1/3 to 1/2 indistinct, separated into larger dash-like patch and reduced dot; termen mixed whitish and dark grey; fringes whitish-grey, with dark grey basal part near apex. Hindwing grey, fringes whitish-grey with darker basal part.

Male genitalia (Figs 16–17). Socii long and slender, with apical spine; anterior margin of tegumen with medial process; gnathos broadly tongue-shaped, smooth; valva moderately slender, length 0.71–0.72 mm, medially weakly widened, maximum width of about 0.26–0.28 mm, densely covered with long hairs in medial part and short setae on ventromedial margin, ventromedial part weakly convex, distal part moderately slender with ventrally convex and dorsally projected apex, costa strongly sclerotized with weak distal dentation; sacculus oval, weakly confined, densely covered with strong setae; saccus short, about 0.32 mm, stout, about same width throughout, apex rounded; phallus ca. 1.32–1.36 mm long and slender, straight, apically with distinct reticulate sculpture, uneverted vesica with ca. 0.58–0.60 mm long sclerotized part, three to four prominent needle-shaped cornuti of about 0.38–0.40 mm in length.

Female genitalia (Figs 24, 29). Genitalia ca. 4.9 mm in length; papilla analis large, densely covered with long setae; apophysis posterior rod like, ca. 0.72 mm, about length of apophysis anterior; apophysis anterior rod like; posterior part bifurcated with straight dorsal and inwardly curved ventral branch; lamella postvaginalis with large sclerotized mediolateral patches, covered with microtrichia, medial area less sclerotized, posterolateral part with hump, covered with some long setae; ostium bursae membranous; antrum weakly sclerotized, funnel-shaped; ductus bursae long, ca. 2.3 mm, posterior part from entrance of ductus seminalis anterior and anterior part covered with finely granulous sculpture, medial part with weak and hardly discernible sculpture, ductus bursae extended into posterior part of corpus bursae, entrance to corpus bursae weakly widened; corpus bursae well delimited, about 1.4 mm in length, ovoid, with small plate-like signum.

Molecular data. The average intraspecific divergence of the barcode region is low with 0.08%, ranging from a minimum of 0% to a maximum of 0.15% (n=4). The minimum distance to the nearest neighbour *K. cottiensis* is 1.86%, whereas the minimum divergence to *K. alternans*, *K. alpmaritima* and *K. wehrlii* ranges from 3.15% and 3.64% to 4.3%, respectively.

Etymology. The species name refers to the remarkable sexual dimorphism.

Distribution (Fig. 32). Only known from the type locality, the French side of Col Agnel (Cottian Alps), close to the Italian border.

Bionomics. Host-plant and early stages unknown. Based on the type locality, the host-plant is most likely *Saxifraga* cf. *oppositifolia*. The adults have been collected in early August during the early morning hours from about 7–10a.m. at low temperatures between 2–5 °C. Males were flying actively during this period in search for females. Both sexes were later found in copula, often sitting on cushions of their suspected host-plant. A single female was found at light, attracted from its nearby habitat and crawling upwards to the light tower, but unable to fly actively. From personal observations of PH, it is likely that the slightly reinforced brachyptery of *K. dimorpha* is combined with flightlessness. The species occurs in rocky habitat on siliceous soil. Vertical distribution: about 2800 m.

Remark. Fringes of the examined females seem partially lost and thus may lead to a biased impression of the extent of wing reduction.

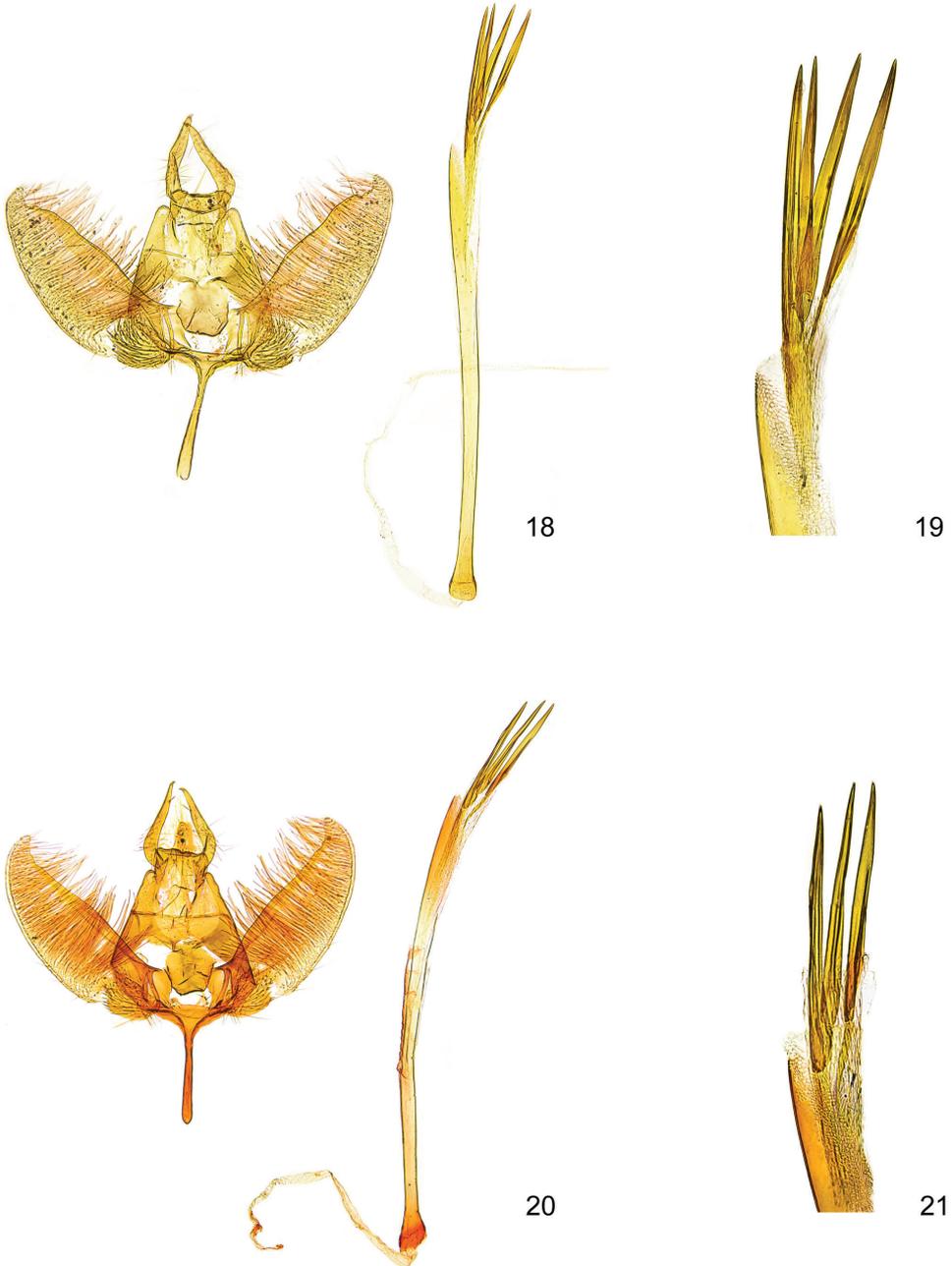
***Kessleria alpmaritimae* sp. n.**

<http://zoobank.org/03637C4C-2AA3-489F-948E-A14CB72DD121>

Type material. Holotype. ♂, „FRANKREICH Dep. Alpes Maritimes Marguareis W-Hang Navela 2100–2200 m 21.–23.7.1990“, leg. Huemer, Tarmann“, „YPO 79 ♂ P. Huemer“ (TLMF).

Paratypes. France: 9 ♂, 5 ♀, same data, genitalia slide YPO 55 ♂ P. Huemer (TLMF); 7 ♂, 2 ♀, same data, but 18.–19.7.1991, DNA barcode IDs TLMF Lep 01850, TLMF Lep 01851, TLMF Lep 03100, TLMF Lep 03101, TLMF Lep 03102, TLMF Lep 03103 (TLMF); 3 ♂, 5 ♀, same data, but 23.7.1990 (TLMF); 1 ♂, same data, but Punta Marguareis, 2450–2650 m, 23.7.1990 (TLMF).

Diagnosis. *K. alpmaritimae* resembles other taxa of *K. alternans*-group in wing markings and colour (Figs 2–11), but the male with average forewing length of only 8.05 mm (n=6) is distinctly smaller than *K. wehrlii* with 8.75 mm (n=13) and *K. alternans* with 8.55 mm (n=26) and larger than *K. cottiensis* with only 7.59 mm (n=14). *K. dimorpha* with an average forewing length of 8.25 mm (n=6) is similar in size, but clearly differs by the largely reduced whitish suffusion of the forewing, a character stage which also applies to *K. cottiensis* and *K. alternans*, whereas *K. wehrlii* is intensely mottled whitish. The female with forewing length of only 6.06 mm (n=3) is distinctly smaller than that of *K. alternans* with 7.58 mm (n=11), but hardly separable from other species in size. Compared to the genetically nearest neighbour *K. dimorpha*, the hindwings are less reduced and the ground colour of the forewing is much lighter. The female of *K. wehrlii* is insufficiently described due to limited material, and the females of *K. cottiensis* and *K. alpmaritimae* are indistinguishable. The male genitalia differ from *K. cottiensis* by the medially weakly widened valva, from *K. alternans* by the more slender cornuti, from the nearest neighbour *K. wehrlii* by three instead of four cornuti, and from *K. dimorpha* by the distinctly longer phallus (1.52–1.58 mm vs. 1.32–1.36 mm) (Figs 12–21).



Figures 18–21. *Kessleria* male genitalia. **18** *K. wehrlii*, paratype, France, Dep. Alpes Maritimes, Mont Gelas Massiv, Mont Colomb W, 2450 m, 24.7.1990, leg. Huemer & Tarmann (DNA barcode ID TLMF Lep 01857), gen. slide YPO 64 (TLMF) **19** idem, distal part of phallus enlarged **20** *K. alpmaritimae* sp. n., paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 18.-19.7.1991, leg. Huemer & Tarmann, gen. slide YPO 55 (TLMF) **21** idem, distal part of phallus enlarged.

The female genitalia show no diagnostic characters to related species of the *K. alternans*-group (Figs 22–31).

Description. Male (Fig. 10). Head covered with erected whitish hair-like scales; antennae dark grey-brown, indistinctly lighter ringed; thorax and tegulae dark grey-brown. Forewing length 7.0–8.5 mm ($\bar{\text{O}}$ 8.05 mm; n=6); ground colour blackish to dark grey-brown, intensely mottled with whitish scales, particularly from basal fifth to 4/5; veins with distinct black dots, particularly along costa, subcosta, cubital and anal veins, medial and radial veins with indistinct brown lines; oblique blackish fascia at about 1/3 to 1/2 indistinct; termen dark grey-brown; fringes light grey, with slightly darker base and indistinct fringe line. Hindwing dark grey, fringes light greyish-white with slightly darker base.

Female (Fig. 11). Head covered with erected whitish hair-like scales; antennae grey-brown, indistinctly ringed whitish; thorax and tegulae whitish. Forewing length 5.9–6.3 mm ($\bar{\text{O}}$ 6.06 mm; n=3); ground colour whitish, mottled with few black scales, particularly along veins, patches of black scales near base and at distal end of cell; oblique blackish fascia at about 1/3 to 1/2 distinct, separated into two dashes; termen whitish with some blackish dots in apical part; fringes white. Hindwing grey, fringes whitish-grey.

Male genitalia (Figs 20–21). Socii long and slender, with apical spine; anterior margin of tegumen with medial process; gnathos broadly tongue-shaped, smooth; valva moderately slender, length 0.72–0.76 mm, medially weakly widened, maximum width of about 0.26–0.27 mm, densely covered with long hairs in medial part and short setae on ventromedial margin, ventromedial part weakly convex, distal part slender with ventrally convex and dorsally projected apex, costa strongly sclerotized with weak distal dentation; sacculus oval, weakly confined, densely covered with strong setae; saccus short, about 0.32–0.33 mm, stout, about same width throughout, apex rounded; phallus ca. 1.52–1.58 mm long and slender, straight, apically with distinct reticulate sculpture, uneverted vesica with ca. 0.62–0.66 mm long sclerotized part, three prominent needle-shaped, one single, the other basally connected, cornuti of about 0.42–0.44 mm in length.

Female genitalia (Figs 26, 31). Genitalia ca. 4.9 mm in length; papilla analis large, densely covered with long setae; apophysis posterior rod like, ca. 0.76 mm, about length of apophysis anterior; apophysis anterior rod like; posterior part bifurcated with straight dorsal and inwardly curved ventral branch; lamella postvaginalis with large sclerotized mediolateral patches, covered with microtrichia, medial area less sclerotized, posterolateral part with hump, covered with some long setae; ostium bursae membranous; antrum weakly sclerotized, funnel-shaped; ductus bursae very long, ca. 2.4 mm, from entrance of ductus seminalis to transition into corpus bursae covered with finely granulous sculpture, particularly in posterior and anterior part, ductus bursae extended into posterior part of corpus bursae, entrance to corpus bursae weakly widened; corpus bursae well delimited, about 1.2 mm in length, ovoid, with largely reduced plate-like signum.

Molecular data. The average intraspecific divergence of the barcode region is 0.0% (n=6). The minimum distance to the nearest neighbour *K. wehrlii* is 1.87%,



22

23

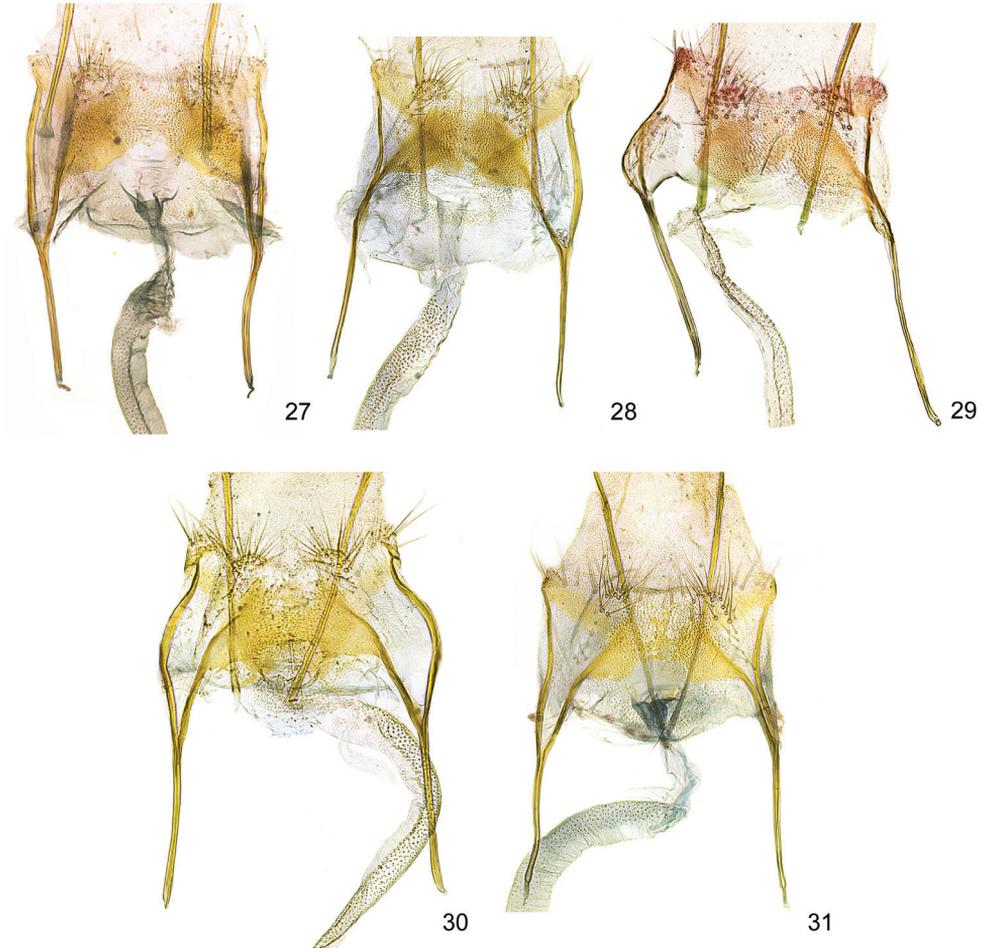
Figures 22–23. *Kessleria* female genitalia. **22** *K. alternans*, Switzerland, Graubünden, SE Sils-Maria, 1820–1870 m, 13.7.1989, leg. Huemer, Karsholt & Tarmann, gen. slide YPO 6 (TLMF) **23** *K. cottiensis* sp. n., paratype, Italy, Prov. Torino, Alpi Cozie, V. delle Finestre, 1700 m, 27.7.1990, leg. Huemer & Tarmann, gen. slide YPO 67 (TLMF).



Figures 24–26. *Kessleria* female genitalia. **24** *K. dimorpha* sp. n., paratype, France, Dep. Hautes-Alpes, Col Agnel, 2770 m, 4.8.2010, leg. Huemer, gen. slide YPO 159 (TLMF) **25** *K. wehrlii*, paratype, France, Dep. Alpes Maritimes, Mont Gelas Massiv, Mont Colomb W, 2450 m, 24.7.1990, leg. Huemer & Tarmann, gen. slide YPO 69 (TLMF) **26** *K. alpmaritimae* sp. n., paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 18.-19.7.1991, leg. Huemer & Tarmann (TLMF).

whereas the minimum divergence to *K. cottiensis*, *K. dimorpha* and *K. alternans* ranges from 2.98% and 3.64% to 3.75%, respectively.

Etymology. The species name is a made-up word which refers to the area of the type locality, the Alpes Maritimes.



Figures 27–31. *Kessleria* female genitalia, details of VIII abdominal segment enlarged. **27** *K. alternans*, Switzerland, Graubünden, SE Sils-Maria, 1820–1870 m, 13.7.1989, leg. Huemer, Karsholt & Tarmann, gen. slide YPO 6 (TLMF) **28** *K. cottiensis* sp. n., paratype, Italy, Prov. Torino, Alpi Cozie, V. delle Finestre, 1700 m, 27.7.1990, leg. Huemer & Tarmann, gen. slide YPO 67 (TLMF) **29** *K. dimorpha* sp. n., paratype, France, Dep. Hautes-Alpes, Col Agnel, 2770 m, 4.8.2010, leg. Huemer, gen. slide YPO 159 (TLMF) **30** *K. wehrlii*, paratype, France, Dep. Alpes Maritimes, Mont Gelas Massiv, Mont Colomb W, 2450 m, 24.7.1990, leg. Huemer & Tarmann, gen. slide YPO 69 (TLMF) **31** *K. alparitima* sp. n., paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 18.–19.7.1991, leg. Huemer & Tarmann (TLMF).

Distribution (Fig. 32). Only known from the type locality, the Marguareis Massif, in the French Alpes Maritimes.

Ecology. Host-plant and early stages unknown. The adults have been collected in the last third of July during the day, flying freely in the morning hours and flushed out from their resting places with a bee-smoker. The species occurs in rocky habitat on calcareous soil. Vertical distribution: from about 2100 m to 2650 m.

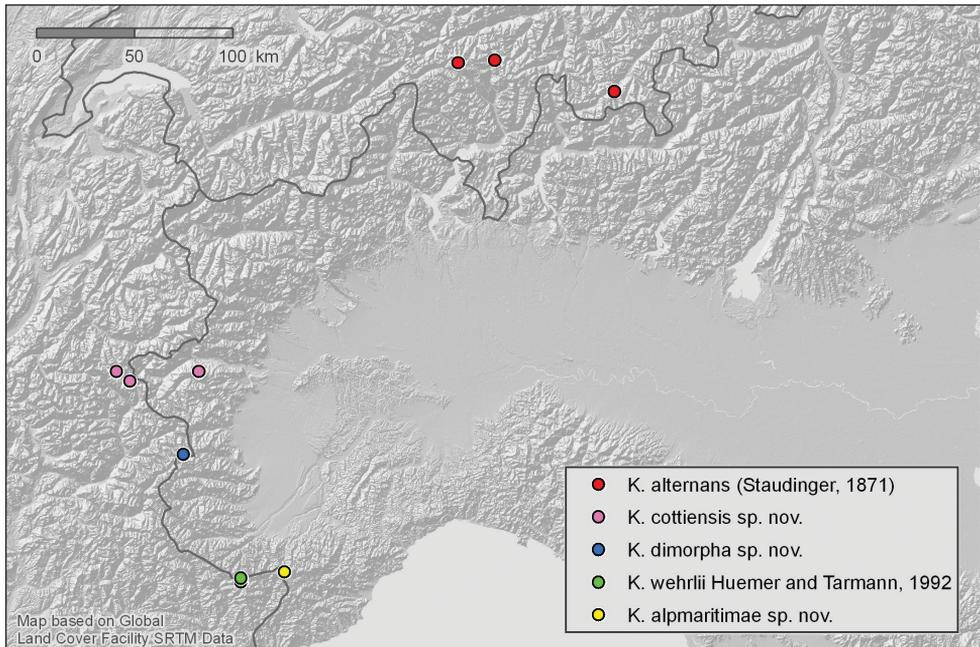


Figure 32. Distribution pattern of the *Kessleria alternans*-group from examined material.

Remarks. *K. alpmaritimae* described here was already suspected to be distinctive from *K. alternans* by Huemer and Tarmann (1992), who illustrated adults (Figs 8–9).

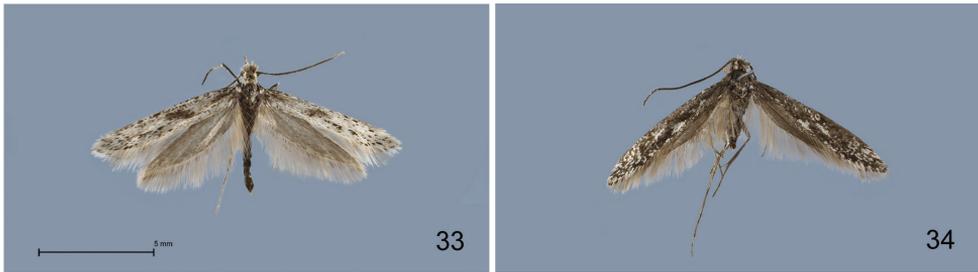
Kessleria apenninica-group

The *K. apenninica*-group s.str. only includes the new species *K. apenninica* which is characterized e.g. by slender forewings. From characters of the male genitalia, such as the short cornuti, closer relatives are likely to be the Iberian *K. diabolica*, *K. brevicornuta*, *K. brachypterella* and *K. pyrenaea*, which all differ in adult morphology (see Figs 33–38, and Huemer and Tarmann 1992). These species together with *K. apenninica* may form a larger species-group, but at present material is scarce and supporting molecular data are lacking. The nearest neighbour of the new species with a full DNA barcode is tentatively attached to *K. pyrenaea* and considered for the differential diagnosis.

Kessleria apenninica sp. n.

<http://zoobank.org/F2B3CFD4-6A60-414F-9CB3-DC7E54424C45>

Type material. Holotype. ♂, „Italia Prov. Rieti Monte Terminillo 13°00,6'E, 42°29,0'N 1730–1780 m, 16.7.2010 leg. Huemer TLMF 2010-020“ „YPO 147 ♂ P. Huemer“ „TLMF Lep 01662“ (TLMF).



Figures 33–34. *Kessleria* adults in dorsal view. **33** *K. apenninica* sp. n., ♂, holotype, Italy, L’Aquila, NP Gran Sasso, ex Miniera di Lignite, 1750 m, 14.-15.7.2010, leg. Huemer (DNA barcode ID TLMF Lep 01663) (TLMF) **34** *K. pyrenaica*, ♂, Spain, Aragon, Parzan (Bielsa) env. Pico de la Rubinera, 2700–3005 m, 10.-11.7.2010, leg. Cesanek (DNA barcode ID TLMF Lep 08933) (TLMF) (coll. Tokár).

Paratypes. Italy: 1 ♂, same data, DNA barcode ID TLMF Lep 01661 (TLMF); 2 ♂, Prov. L’Aquila, NP Gran Sasso, ex Miniera di Lignite, 13°42,8'E, 42°25,6'N, 1750 m, 14.-15.7.2010, leg. Huemer, genitalia slide YPO 148 ♂ P. Huemer, DNA barcode IDs TLMF Lep 01663, TLMF Lep 01664 (TLMF).

Diagnosis. *K. apenninica* is characterized by unusually slender forewings and a pure white colour with black pattern. Species from the *K. apenninica*-group are externally unmistakably distinguishable from one another both by wing pattern and colour (Figs 33–34, and Huemer and Tarmann 1992), but the genitalia of males are similar (Figs 35–38). However, in *K. apenninica* the saccus is distinctly shorter than in all other species with 0.23 *vs.* minimum 0.29 mm.

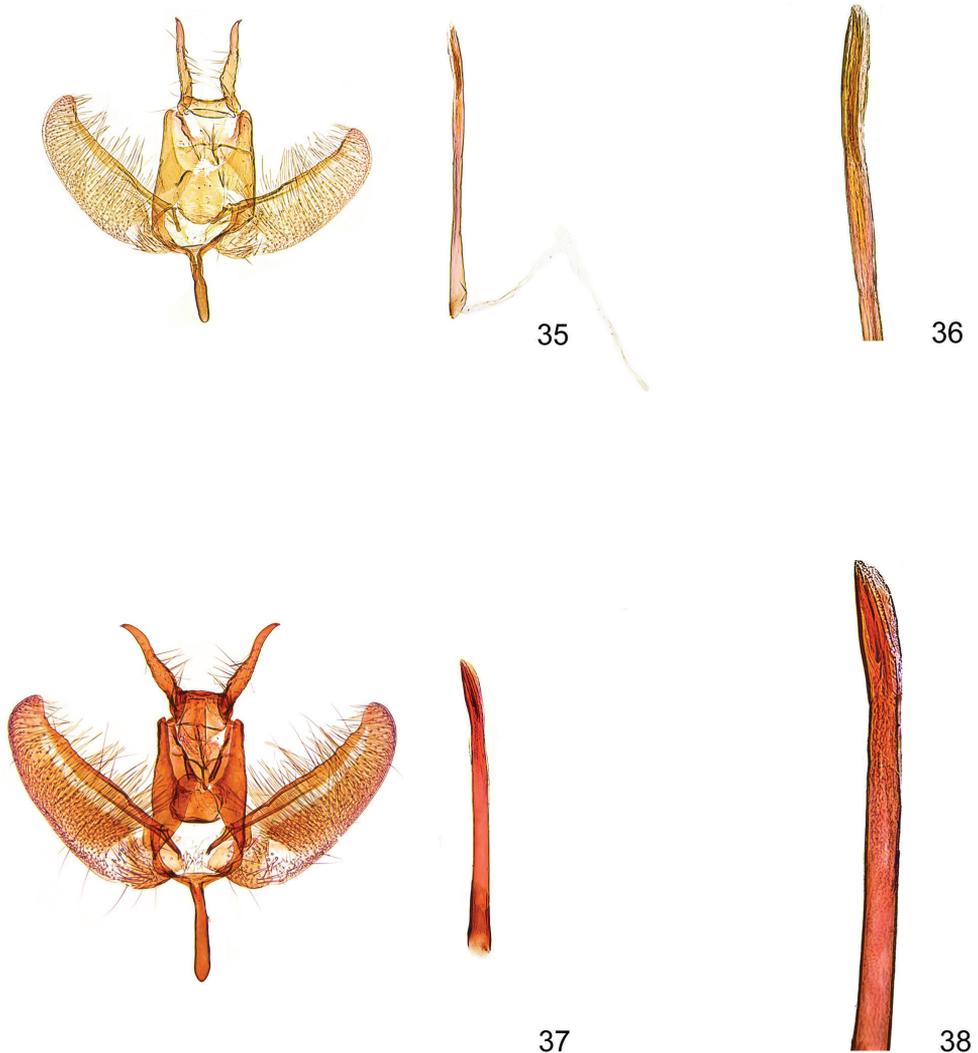
Description. Male (Fig. 33). Head covered with whitish hair-like scales; antennae almost unicolorous dark grey with light grey apex; thorax and tegulae mixed dark grey and whitish. Forewing length 5.8–6.9 mm ($\bar{\text{O}}$ 6.4 mm; n=4); forewing slender; ground colour white, mottled with black; black dots on veins and in terminal area; black patch near base and oblique blackish fascia at about 1/3 to 1/2; fringes white with indistinct dark grey fringe line. Hindwing dark grey, fringes with dark grey base, distal part white.

Female. Unknown.

Male genitalia (Figs 35–36). Socii long and slender, with apical spine; anterior margin of tegumen with medial process; gnathos broadly tongue-shaped, smooth; valva slender, length 0.61 mm, max width 0.19 mm; densely covered with long hairs in medial part and short setae on ventromedial margin, ventromedial part weakly convex, distal part with ventrally convex and dorsally projected apex, costa strongly sclerotized with indistinct distal dentation; sacculus oval, weakly confined, densely covered with strong setae; saccus short, about 0.24 mm, slender, about same width throughout, apex rounded; phallus 0.95 mm long, slender, uneverted vesica with ca. 0.35 mm long sclerotized apical part, including 3 short cornuti of about 0.22 mm length [hardly discernible in situ].

Female genitalia. Unknown.

Molecular data. *K. apenninica* splits into two geographically separated haplogroups, which in our examination – based on limited material – did not reveal any



Figures 35–38. *Kessleria* male genitalia. **35** *K. apenninica* sp. n., ♂, holotype, Italy, L’Aquila, NP Gran Sasso, ex Miniera di Lignite, 1750 m, 14.-15.7.2010, leg. Huemer gen. slide YPO 147 (DNA barcode ID TLMF Lep 01663) (TLMF) **36** idem, distal part of phallus enlarged **37** *K. pyrenaea*, ♂, Spain, Aragon, Parzan (Bielsa) env. Pico de la Rubinera, 2700–3005 m, 10.–11.7.2010, leg. Cesanek, gen. slide 15/1391 P.Huemer (DNA barcode ID TLMF Lep 08933) (coll. Tokár) **38** idem, distal part of phallus enlarged.

morphological differences. The average intraspecific divergence of the barcode region is considerable with 1.05%, ranging from a minimum of 0% to a maximum of 1.69% (n=4). The minimum distance to the nearest neighbour *K. pyrenaea* is 5.47%.

Etymology. The species name refers to the Apennines where all type specimens have been collected.

Distribution. Only known from the Apennines in Central Italy.

Ecology. Host-plant and early stages unknown, but the species probably feeds on an unidentified broad-leaved *Saxifraga* species growing on steep rocks. The adults have been collected in the last third of July from light. The species occurs in rocky habitat on calcareous soil. Vertical distribution: from about 2100 m to 2200 m.

Kessleria albescens-group

The *K. albescens*-group is characterized by small and predominantly whitish-coloured species without obvious sexual dichroism or dimorphism (Figs 39–48). The male genitalia are recognizable by the strongly spinous sacculus, the long and stout saccus, and particularly the phallus with two long cornuti with bases of similar length (Figs 49–58). The female genitalia are characterized by the curved entrance of the ductus bursae and the finely granulated sculpture of the entire ductus bursae (Figs 59–66). Larval host-plants, as far as is known, belong to broad-leaved *Saxifraga* spp., e.g. *S. paniculata* and *S. incrustata*. Five species are known: *K. albescens*, *K. inexpectata*, *K. helvetica*, *K. klimeschi* and the new species *K. orobiae*.

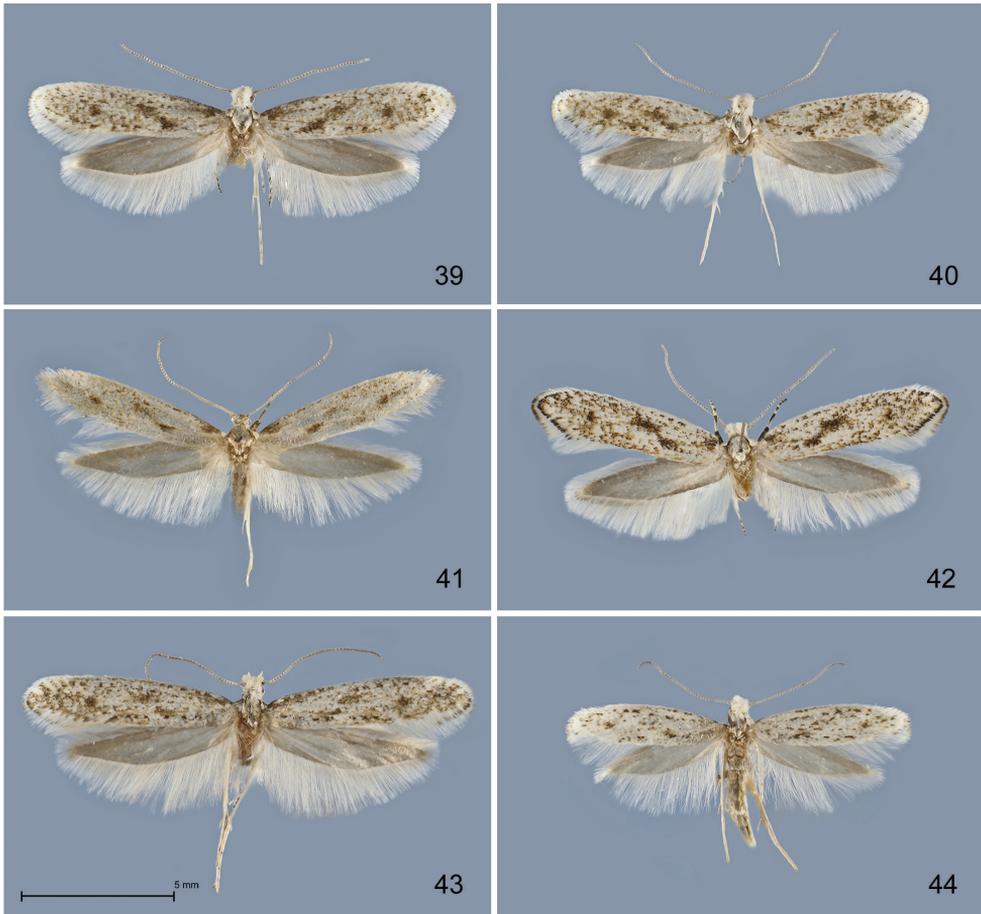
Kessleria orobiae sp. n.

<http://zoobank.org/86461879-486E-49A4-9004-D35885EAED96>

Type material. Holotype. ♂, „ITALIA sept. Prov. Bergamo, Alpi Orobie Zambra Alta – Plassa 9°47'48"E, 45°54'12"N 1160 m, 24.6.2013 leg. Huemer“ „DNA Barcode TLMF Lep 09972“ „YPO 160 ♂ P. Huemer“ (TLMF).

Paratypes. Italy: 6 ♂, 6 ♀, same data, DNA barcode IDs TLMF Lep 09971, TLMF Lep 09973 (TLMF); 1 ♂, 1 ♀, same data, but e.l. 11.7.2013 (TLMF); 7 ♂, 2 ♀, same data, but leg. Mayr (coll. Mayr, Feldkirch); 1 ♂, Prov. Bergamo, Alpi Orobie, Val d'Arera, 2000 m, 14.–15.8.1992, leg. Huemer (TLMF); 1 ♀, Prov. Bergamo, Alpi Orobie, W. Ca. San Marco, 2100 m, e.l. 31.7.1992, leg. Huemer & Tarmann, DNA barcode ID TLMF Lep 03175 (TLMF).

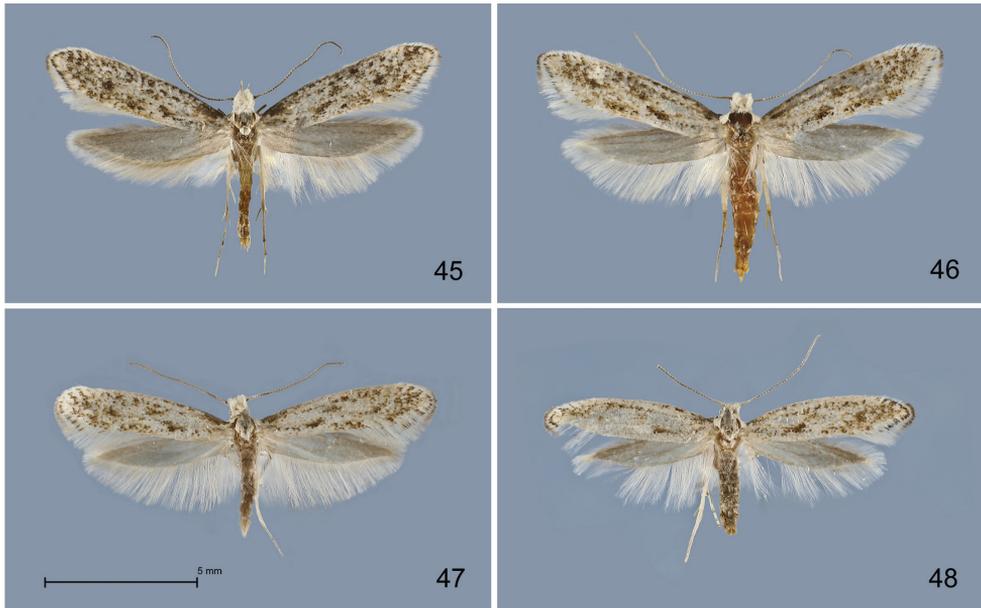
Diagnosis. *K. orobiae* largely resembles other taxa of the *K. albescens*-group in wing markings and colour, and cannot be unambiguously separated (Figs 39–48). Similarly, female genitalia exhibit no significant diagnostic characters for discrimination at species level (Figs 59–66, and Huemer and Tarmann 1992). The most reliable diagnostic characters in the species-group are found in the male genitalia (Figs 49–58). *K. orobiae* differs from *K. klimeschi*, *K. albescens* and *K. helvetica* by a much shorter saccus (0.32 mm *vs.* minimum 0.38–0.58 mm) which is only about half the length of the valva compared to the minimum 0.75 times the length of the valva in the other species. In *K. inexpectata* the saccus is slightly longer and furthermore without the apical widening of *K. orobiae*, *K. albescens* and *K. helvetica*. The two needle-shaped cornuti are similar in all species, with the exception of *K. klimeschi* with only one needle-shaped and one sub-ovate cornutus, and *K. helvetica* with cornuti of about 0.50 mm in length.



Figures 39–44. *Kessleria* adults in dorsal view. **39** *K. klimeschi*, ♂, holotype, Italy, Prov. Udine, Montasio, Malga Pecol, 1600 m, 24.6.1989 e.l., leg. Huemer & Tarmann (TLMF) **40** *K. klimeschi*, ♀, paratype, same data, but 3.7.1989 e.l. (TLMF) **41** *K. helvetica*, ♂, holotype, Switzerland, Wallis, Zermatt, 1850 m, 10.8.1980, leg. Whitebread (DNA barcode ID TLMF Lep 01868) (TLMF) **42** *K. helvetica*, ♀, Switzerland, Wallis, Zermatt, Triftschlucht, 1820 m, 10.6.2014 e.l., leg. Schmid (DNA barcode ID TLMF Lep 14996) (TLMF) **43** *K. inexpectata*, ♂, paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 21.–23.7.1990, leg. Huemer & Tarmann (TLMF) **44** *K. inexpectata*, ♀, paratype, same data (TLMF).

The female genitalia largely resemble other species of the *K. albescens*-group with only quantitative differences, such as a longer ductus bursae than in *K. albescens* (1.6 mm *vs.* 1.3–1.4 mm), and the overall length of genitalia which exceeds *K. klimeschi* (4.2 mm *vs.* 3.5 mm).

Description. Male (Fig. 45). Head covered with white hair-like scales; antennae ringed dark grey and whitish; thorax and tegulae mixed dark grey and white, distally predominantly white, particularly tegulae. Forewing length 6.7–7.3 mm (Ø 7.03 mm; n=6); ground colour whitish-grey, intensively mottled with blackish-grey spots all over



Figures 45–48. *Kessleria* adults in dorsal view. **45** *K. orobiae* sp. n., ♂, paratype, Zambla Alta – Plassa, 1160 m, 24.6.2013 leg. Mayr (coll. Mayr) **46** *K. orobiae* sp. n., ♀, paratype, same data (coll. Mayr) **47** *K. albescens*, ♂, Italy, Monte Baldo, Bocca di Navene, 14.7.1987, leg. Huemer & Tarmann (DNA barcode ID TLMF Lep 03131) (TLMF) **48** *K. albescens* ♀, same data, but 10.9.1987 e.l. (DNA barcode ID TLMF Lep 01866) (TLMF).

wing, few ochre-brown scales in dorsal part; blackish-grey patches at base of costa and at end of cell, oblique blackish-grey fascia at about 1/3 to 1/2 narrow and indistinct, medially separated; termen whitish-grey; fringes white, basally with distinct blackish-grey cilia line, apex with small dark grey tip. Hindwing dark grey, fringes with dark grey base, distal part white.

Female (Fig. 46). As male. Head covered with white hair-like scales; antennae ringed dark grey and whitish; thorax and tegulae mixed dark grey and white, distally predominantly white, particularly tegulae. Forewing length 5.9–6.6 mm ($\bar{\text{O}}$ 8.18 mm; $n=5$); ground colour whitish-grey, intensively mottled with blackish-grey spots all over wing, few ochre-brown scales in dorsal part; blackish-grey patches at base of costa and at end of cell, oblique blackish-grey fascia at about 1/3 to 1/2 narrow and indistinct, medially separated; termen whitish-grey; fringes white, basally with distinct blackish-grey cilia line, apex with small dark grey tip. Hindwing dark grey, fringes with dark grey base, distal part white.

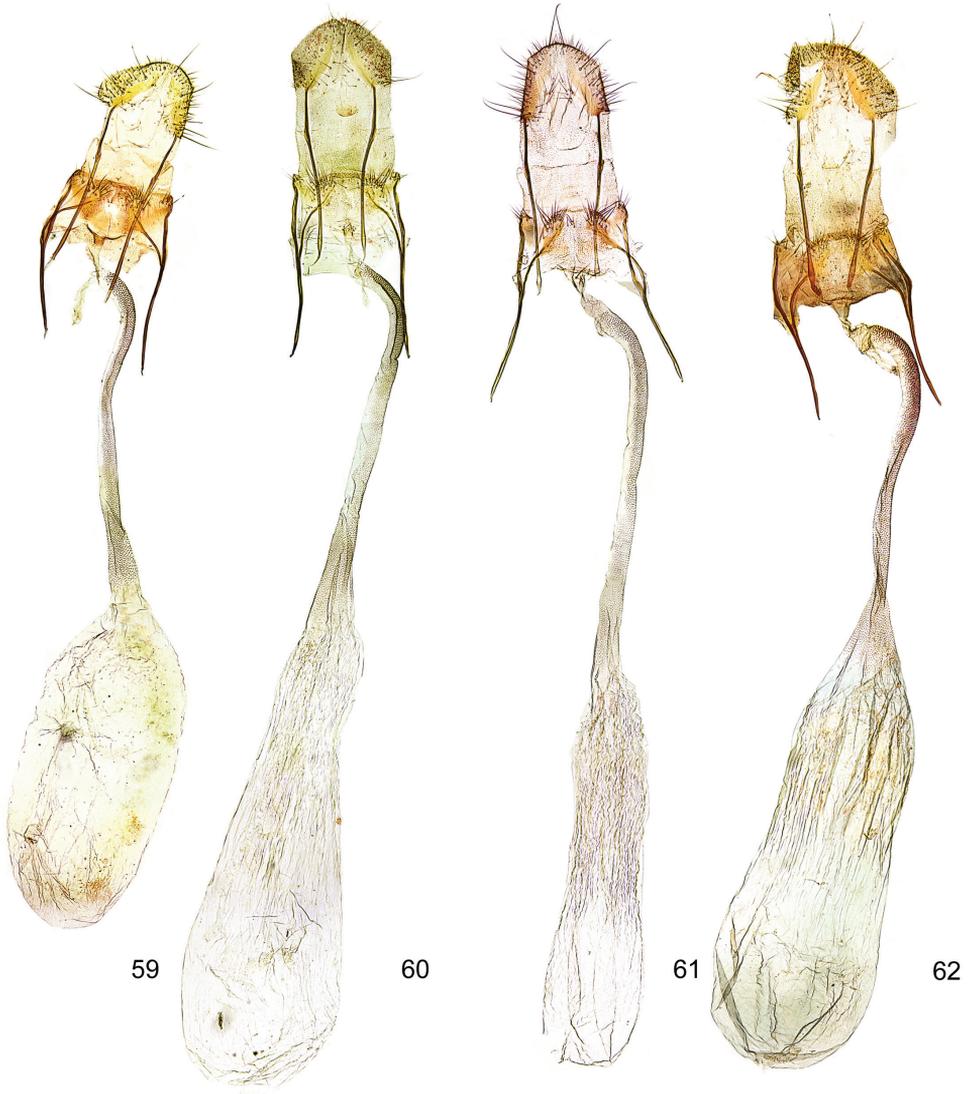
Male genitalia (Figs 55–56). Socii long and slender, with apical spine; anterior margin of tegumen with medial process; gnathos broadly tongue-shaped, smooth; valva slender, length 0.60 mm, maximum width 0.18 mm; densely covered with long hairs in medial part and short setae on ventromedial margin, apical part ventrally convex, costa strongly sclerotized without dentation; sacculus oval, weakly confined,



Figures 49–54. *Kessleria* male genitalia. **49** *K. klimeschi*, holotype, Italy, Prov. Udine, Montasio, Malga Pecol, 1600 m, 24.6.1989 e.l., leg. Huemer & Tarmann, genitalia slide YPO 17 (TLMF) **50** idem, cornuti enlarged **51** *K. helvetica*, holotype, Switzerland, Wallis, Zermatt, 1850 m, 10.8.1980, leg. Whitebread, gen. slide 350 Whitebread (DNA barcode ID TLMF Lep 01868) (TLMF) **52** idem, distal part of phallus enlarged **53** *K. inexpectata*, paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 21.–23.7.1990, leg. Huemer & Tarmann, gen. slide YPO 63 (TLMF) **54** idem, distal part of phallus enlarged.

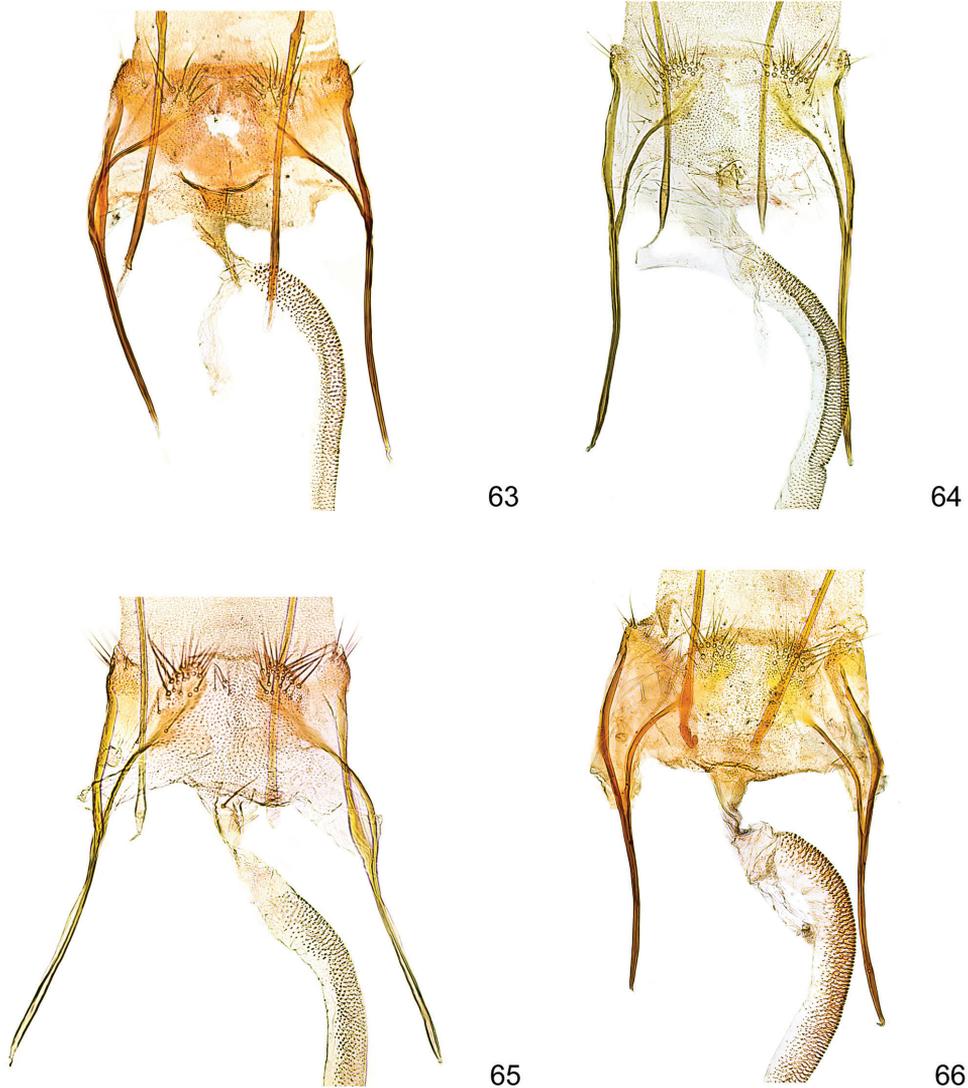


Figures 55–58. *Kessleria* male genitalia. **55** *K. orobiae* sp. n., holotype, Zambla Alta – Plassa, 1160 m, 24.6.2013 leg. Huemer, gen. slide YPO 160 (TLMF) **56** idem, distal part of phallus enlarged **57** *K. albescens*, ♂, Italy, Monte Baldo, Bocca di Navene, 14.7.1987, leg. Huemer & Tarmann, gen. slide YPO 19 (DNA barcode ID TLMF Lep 03131) (TLMF) **58** idem, distal part of phallus enlarged.



Figures 59–62. *Kessleria* female genitalia. **59** *K. klimeschi*, paratype, Italy, Prov. Udine, Montasio, Malga Pecol, 1600 m, 24.6.1989 e.l., leg. Huemer & Tarmann, gen. slide YPO 76 (TLMF) **60** *K. inexpectata*, paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 21.–23.7.1990, leg. Huemer & Tarmann, gen. slide YPO 74 (TLMF) **61** *K. orobiae* sp. n., paratype, Zambla Alta – Plassa, 1160 m, 24.6.2013, leg. Huemer, gen. slide YPO 161 (TLMF) **62** *K. albescens*, Italy, Monte Baldo, Bocca di Navene, 14.7.1987, leg. Huemer & Tarmann (TLMF).

densely covered with strong setae; saccus moderate in length, about 0.32 mm, stout, distally widened with rounded apex; phallus 1.34 mm long, slender, uneverted vesica with ca. 0.70 mm long sclerotized apical part, including two prominent needle-shaped cornuti of about 0.40 mm length.



Figures 63–66. *Kessleria* female genitalia, details of VIII abdominal segment enlarged. **63** *K. klimeschi*, paratype, Italy, Prov. Udine, Montasio, Malga Pecol, 1600 m, 24.6.1989 e.l., leg. Huemer & Tarmann, gen. slide YPO 76 (TLMF) **64** *K. inexpectata*, paratype, France, Dep. Alpes Maritimes, Marguareis W-Hang, Navela, 2100–2200 m, 21.-23.7.1990, leg. Huemer & Tarmann, gen. slide YPO 74 (TLMF) **65** *K. orobiae* sp. n., paratype, Zambla Alta – Plassa, 1160 m, 24.6.2013, leg. Huemer, gen. slide YPO 161 (TLMF) **66** *K. albescens*, Italy, Monte Baldo, Bocca di Navene, 14.7.1987, leg. Huemer & Tarmann (TLMF).

Female genitalia (Figs 61, 65). Genitalia ca. 4.2 mm in length; papilla analis large, densely covered with long setae; apophysis posterior rod like, ca. 0.70 mm, about length of apophysis anterior; apophysis anterior rod like; posterior part bi-

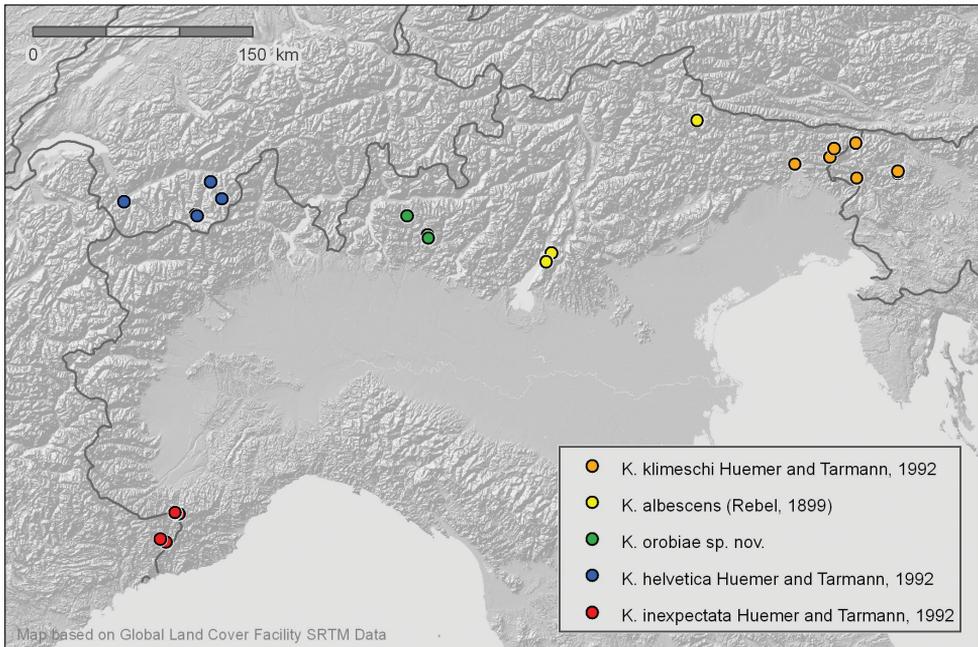


Figure 67. Distribution pattern of the *Kessleria albescens*-group from examined material.

furcated with straight dorsal and inwardly curved ventral branch; ventral branch descending into patch like sclerite; lamella postvaginalis with sclerotized lateral patches, covered with microtrichia, medially membranous, posterolaterally with hump, covered with some long setae; ostium bursae membranous; antrum weakly developed, ring-like; ductus bursae long, about 1.6 mm, weakly curved in posterior part, from entrance of ductus seminalis to almost transition to corpus bursae densely covered with finely granulous sculpture; sculpture in posterior part nearly bacillary, distally increasingly granulous, entrance to corpus bursae widened, without sculpture; corpus bursae about 1.7 mm in length, saccate, posterior part folded, without signum.

Molecular data. The average intraspecific divergence of the barcode region is low with 0.31%, ranging from a minimum of 0.15% to a maximum of 0.46% (n=5). The minimum distance to the nearest neighbour *K. albescens* is 2.66%, whereas the minimum divergence to *K. inexpectata*, *K. helvetica* and *K. klimeschi* ranges from 3.14% and 3.46% to 9.53%, respectively.

Etymology. The species name refers to the Orobian Alps (Alpi Orobie) in northern Italy, where the type locality is situated.

Distribution (Fig. 67). Only known from Zambla Alta – Plassa and few nearby localities in the Orobian Alps (Prov. Bergamo, Italy).

Ecology. The larval habits are insufficiently known, but based on our observations, the larva lives in the shoots and as a leaf-miner in basal leaves of *Saxifraga*

paniculata and *Saxifraga* sp. Mined leaves are partially spun together and covered with a fine silken web. The adults have been collected from the *Saxifraga*-cushions or nearby rock during the day. In the first few hours of the night they have been observed with a head-lamp flying actively around the larval habitat or sitting near the host-plant. The adult is on the wing from late June to mid-August, depending on altitude and snow coverage. Bred specimens date from mid to late July. *K. orobiae* occurs in rocky habitat both on calcareous and siliceous soil. Vertical distribution: from about 1100 m to 2100 m.

Established European species of *Kessleria*

A brief overview of established species lists including original description, type locality, type material, references of published images of adults and images of genitalia, and hitherto unpublished molecular data. For extensive generic and species descriptions and diagnoses, see Huemer and Tarmann (1992).

Genus *Kessleria* Nowicki, 1864

Kessleria Nowicki 1864: 12. Type species: *Kessleria zimmermanni* Nowicki, 1864 by monotypy and original designation.

Subgenus *Kessleria* Nowicki, 1864

Kessleria alpicella (Stainton, 1851)

Tinea (*Oecophora*!) *alpicella* [Fischer von Röslerstamm, Mann in litt.] Stainton 1851: 17. Type locality: Europe [?Austria]. Type material: Lectotype (designated by Huemer and Tarmann 1992: 16) (BMNH) [examined].

Swammerdamia alpicella Herrich-Schäffer 1855: 272. Type locality: Austria, Niederösterreich, Schneeberg. Type material: Syntypes [not traced]. Homonym and synonym.

Redescription and diagnosis see Huemer and Tarmann 1992: 16–18, figs 1–2 (adult), figs 85–93 (male genitalia), figs 220–221 (female genitalia).

Molecular data. *K. alpicella* splits into three geographically separate haplogroups, indicating potential cryptic diversity. The average intraspecific divergence of the barcode region is high with 1.52%, ranging from a minimum of 0% to a maximum of 4.27% (n=12). The minimum distance to the nearest neighbour *K. wehrlii* is 6.9%.

***Kessleria mixta* Huemer & Tarmann, 1992**

Kessleria mixta Huemer and Tarmann 1992: 18. Type locality: Albania, Korab. Type material: Holotype (designated by Huemer and Tarmann 1992: 19) (NHMV) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 18–19, Fig. 3 (adult), figs 94–96 (male genitalia).

Molecular data. Unavailable.

Remarks. Female unknown.

***Kessleria alternans* (Staudinger, 1871)**

Kessleria alternans Staudinger 1871: 291. Type locality: Switzerland, Graubünden, Sils-Maria. Type material: Lectotype (designated by Friese 1960: 75) (MNHU) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 19–22, figs 4–6 (adult), figs 97–102 (male genitalia), figs 223–224 [misidentified figures depicting newly described species in this paper are not listed].

Molecular data. The intraspecific divergence of the barcode region is low, ranging from a minimum of 0% to a maximum of 0.32% (mean 0.12%) (n=10). The minimum distance to the nearest neighbour *K. cottiensis* is 2.65%.

Remarks. Huemer and Tarmann (1992) already recognized and described a remarkable amount of individual and geographical variation. At that time, this variation was considered as intraspecific, and the authors hesitated to describe further species.

***Kessleria wehrlii* Huemer & Tarmann, 1992**

Kessleria wehrlii Huemer and Tarmann 1992: 22. Type locality: France, Dep. Alpes-Maritimes, Mont Colomb. Type material: Holotype (designated by Huemer and Tarmann 1992: 23) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 22–23, figs 11–12 (adult), figs 109–111 (male genitalia), fig. 211 (8th abdominal segment), fig. 222 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is 0.0% (n=4). The minimum distance to the nearest neighbour *K. alpmaritimae* is 1.87%.

***Kessleria nivescens* Burmann, 1980**

Kessleria nivescens Burmann 1980: 105. Type locality: Italy, Prov. Verona, Monte Baldo. Type material: Holotype (designated by Burmann 1980: 107) (SMNK) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 23–26, figs 13–17 (adult), figs 115–120 (male genitalia), fig. 219 (female genitalia).

Molecular data. *K. nivescens* splits into three geographically separate haplogroups. The intraspecific divergence of the barcode region is high, ranging from a minimum of 0% to a maximum of 2.5% (mean 1.09%) (n=14). The minimum distance to the nearest neighbour *K. petrobiella* is 3.29% (mean 4.52%, max. 4.92%).

Remarks. Huemer and Tarmann (1992) already recognized and described a considerable amount of individual and geographical variation, particularly in phenotypic appearance, but the authors hesitated to describe further species due to the lack of diagnostic genitalia characters. Molecular data suggest possible cryptic diversity, but further investigations are required.

***Kessleria petrobiella* (Zeller, 1868)**

Scythropia petrobiella Zeller 1868: 607. Type locality: Slovenia, [Log Pod Mangrtom]. Type material: Lectotype (designated by Huemer and Tarmann 1992: 37) (BMNH) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 37–39, figs 32–33 (adult), figs 156–161 (male genitalia), fig. 229 (female genitalia).

Molecular data. The intraspecific divergence of the barcode region is 0% (n=4). The minimum distance to the nearest neighbour *K. nivescens* is 3.29%.

***Kessleria macedonica* Huemer & Tarmann, 1992**

Kessleria macedonica Huemer and Tarmann 1992: 26. Type locality: Kosovo/Macedonia, Shar Planina, Crni vrh. Type material: Holotype (designated by Huemer and Tarmann 1992: 26) (ZSM) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 26–27, fig. 18 (adult), figs 121–123 (male genitalia).

Molecular data. Unavailable.

Remarks. Female unknown.

***Kessleria albanica* Friese, 1960**

Kessleria albanica Friese 1960: 68. Type locality: Albania, Nikai. Type material: Holotype (designated by Friese 1960: 68) (ZSM) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 27–28, fig. 19 (adult), figs 124–125 (male genitalia).

Molecular data. *K. albanica* splits into three geographically separate haplogroups, indicating potential cryptic diversity. The average intraspecific divergence of the barcode region is high with 2.08%, ranging from a minimum of 0% to a maximum of 3.12% (n=5). The minimum distance to the nearest neighbour *K. burmanni* is 9.29%.

Remarks. Female unknown.

***Kessleria burmanni* Huemer & Tarmann, 1992**

Kessleria burmanni Huemer and Tarmann 1992: 28. Type locality: Austria, Nordtirol, Nordkette. Type material: Holotype (designated by Huemer and Tarmann 1992: 30) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 28–30, figs 20–22 (adult), figs 126–131 (male genitalia), fig. 225 (female genitalia), figs 63–65 (SEM egg structures).

Molecular data. The average intraspecific divergence of the barcode region is 0.0% (n=6). The minimum distance to the nearest neighbour *K. hauderi* is 7.61%.

***Kessleria insubrica* Huemer & Tarmann, 1993**

Kessleria insubrica Huemer and Tarmann 1993: 41. Type locality: Italy, Prov. Bergamo, Val d'Arera. Type material: Holotype (designated by Huemer and Tarmann 1993: 45) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1993: 41–46, fig. 1 (adult), figs 5–6 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is low with 0.08%, ranging from a minimum of 0% to a maximum of 0.15% (n=4). The minimum distance to the nearest neighbour *K. burmanni* is 8.95%.

Remarks. Male unknown.

***Kessleria hauderi* Huemer & Tarmann, 1992**

Kessleria hauderi Huemer and Tarmann 1992: 31. Type locality: Austria, Steiermark, Eisenerzer Reichenstein. Type material: Holotype (designated by Huemer and Tarmann 1992: 32) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 21–33, figs 23–24 (adult), figs 132–137 (male genitalia), fig. 227 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is 0% (n=2). The minimum distance to the nearest neighbour *K. burmanni* is 7.61%.

***Kessleria diabolica* Huemer & Tarmann, 1992**

Kessleria diabolica Huemer and Tarmann 1992: 33. Type locality: Spain, Prov. Avila, Sierra de Gredos. Type material: Holotype (designated by Huemer and Tarmann 1992: 33) (ZMUC) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 33, fig. 25 (adult), figs 138–140 (male genitalia).

Molecular data. Unavailable.

Remarks. Female unknown.

***Kessleria brevicornuta* Huemer & Tarmann, 1992**

Kessleria brevicornuta Huemer and Tarmann 1992: 34. Type locality: Spain, Prov. Avila, Sierra de Gredos. Type material: Holotype (designated by Huemer and Tarmann 1992: 34) (coll. Arenberger, Vienna) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 34–35, figs 26–27 (adult), figs 141–143 (male genitalia), fig. 235 (female genitalia).

Molecular data. Unavailable.

***Kessleria pyrenaea* Friese, 1960**

Kessleria pyrenaea Friese 1960: 76. Type locality: France, Dép. Pyrénées-Orientales, Mt. Canigou. Type material: Holotype (designated by Friese 1960: 76) (NHMV) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 35, fig. 28 (adult), figs 144–146 (male genitalia).

Molecular data. The intraspecific divergence of the barcode region is unknown (n=1). The minimum distance to the nearest neighbour *K. apenninica* is 5.47%.

Remarks. Female unknown. The identity of the sequenced specimen is doubtful.

***Kessleria brachypterella* Huemer & Tarmann, 1992**

Kessleria brachypterella Huemer and Tarmann 1992: 36. Type locality: France, Dép. Hautes-Pyrénées, Pic du Midi de Bigorre. Type material: Holotype (designated by Huemer and Tarmann 1992: 34) (BMNH) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 36–37, figs 29–30 (adult), figs 147–149 (male genitalia), fig. 228 (female genitalia).

Molecular data. Unavailable.

***Kessleria zimmermanni* Nowicki, 1864**

Kessleria zimmermanni Nowicki 1864: 13. Type locality: Poland, Tatra mts., ?Kopa Magury. Type material: Lectotype (designated by Huemer and Tarmann 1992: 39) (SDEI) [examined].

Kessleria tatrica Friese 1960: 71. Type locality: [?Poland], Tatra mts. Type material: Holotype (designated by Friese 1960: 71) (NHMV).

Redescription and diagnosis see Huemer and Tarmann 1992: 39–42, figs 32–33 (adult), figs 162–167 (male genitalia), fig. 217 (8th abdominal segment), fig. 226 (female genitalia).

Molecular data. The intraspecific divergence of the barcode region is 0% (n=3). The minimum distance to the nearest neighbour *K. petrobiella* is 5.73%.

***Kessleria albomaculata* Huemer & Tarmann, 1992**

Kessleria albomaculata Huemer and Tarmann 1992: 42. Type locality: France, Dép. Hautes-Pyrénées, Cauterets. Type material: Holotype (designated by Huemer and Tarmann 1992: 42) (MNCN) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 42–43, fig. 36 (adult), figs 153–155 (male genitalia), fig. 216 (8th abdominal segment).

Molecular data. The intraspecific divergence of the barcode region is unknown (n=1). The minimum distance to the nearest neighbour *K. petrobiella* is 6.76%.

Remarks. Female unknown.

***Kessleria caflischiella* (Frey, 1880)**

Swammerdamia caflischiella Frey 1880: 344. Type locality: Switzerland, Wallis, ?Gamsen.
Type material: Holotype (designated by Frey 1880: 344) (BMNH) [examined].

Redescription and diagnosis see Huemer and Tarmann 1992: 49–51, figs 45–46 (adult), figs 191–196 (male genitalia), fig. 229 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is low with 0.04%, ranging from a minimum of 0% to a maximum of 0.15% (n=8). The minimum distance to the nearest neighbour *K. alpmaritimae* is 6.39%.

***Kessleria klimeschi* Huemer & Tarmann, 1992**

Kessleria klimeschi Huemer and Tarmann 1992: 47. Type locality: Italy, Prov. Udine. Montasio, Malga Pecol. Type material: Holotype (designated by Huemer and Tarmann 1992: 48) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 47–49, figs 43–44 (adult), figs 185–190 (male genitalia), fig. 218 (8th abdominal segment), fig. 233 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is low with 0.06%, ranging from a minimum of 0% to a maximum of 0.15% (n=5). The minimum distance to the nearest neighbour *K. inexpectata* is 8.83%.

***Kessleria helvetica* Huemer & Tarmann, 1992**

Kessleria helvetica Huemer and Tarmann 1992: 46. Type locality: Switzerland, Wallis, Zermatt. Type material: Holotype (designated by Huemer and Tarmann 1992: 47) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 46–47, figs 41–42 (adult), Figs 179–184 (male genitalia), fig. 232 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is unknown (n=1). *K. helvetica* overlaps in the barcode with a haplogroup of topotypical *K. inexpectata*, but diagnostic morphological characters indicate species status. The minimum distance to a further haplogroup of *K. inexpectata* is 1.77%.

***Kessleria inexpectata* Huemer & Tarmann, 1992**

Kessleria inexpectata Huemer and Tarmann 1992: 45. Type locality: France, Dep. Alpes Maritimes, Marguareis. Type material: Holotype (designated by Huemer and Tarmann 1992: 46) (TLMF) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 45–46, figs 39–40 (adult), figs 173–178 (male genitalia), fig. 231 (female genitalia).

Molecular data. *K. inexpectata* splits into two major haplogroups. The average intraspecific divergence of the barcode region within the haplogroup of topotypical specimens is low with 0.16%, ranging from a minimum of 0% to a maximum of 0.32% (n=4) whereas the average intraspecific variation within the second haplogroup is considerable with 0.84% (maximum 1.68%). The mean intraspecific divergence of the entire sample is 1.42% (maximum 2.18%). The haplogroup of the topotypical population overlaps with *K. helvetica*. The minimum distance to *K. orobiae* is 3.14%.

***Kessleria albescens* (Rebel, 1899)**

Hofmannia albescens Rebel 1899: 177. Type locality: Italy, South Tyrol, Bozen. Type material: Lectotype (designated by Friese 1960: 72) (NHMV) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 43–44, figs 37–38 (adult), figs 168–172 (male genitalia), fig. 230 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is 0% (n=3). The minimum distance to the nearest neighbour *K. orobiae* is 2.66%.

Subgenus *Hofmannia* Heinemann & Wocke, 1877***Kessleria saxifragae* (Stainton, 1868)**

Zelleria saxifragae Stainton 1868: 139. Type locality: Austria, Nordtirol, Kaisergebirge. Type material: ?Syntypes (examined by Huemer and Tarmann 1992: 53) (BMNH) [examined].

Description and diagnosis see Huemer and Tarmann 1992: 51–54, figs 47–50 (adult), figs 197–202 (male genitalia), fig. 236 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is low with 0.43%, ranging from a minimum of 0% to a considerable maximum of 1.28% (n=20). The minimum distance to the nearest neighbour *Zelleria celastrusella* Kearfott, 1903, from North America is 6.22%, and the minimum distance to the congeneric *K. fasciapennella* is 7.21%.

***Kessleria fasciapennella* (Stainton, 1849)**

Zelleria fasciapennella Stainton 1849: 80. Type locality: GB, Scotland, Edinburgh, Pentland hills. Type material: Lectotype (designated by Huemer and Tarmann 1992: 54) (BMNH) [examined].

Kessleria longipennella Friese 1960: 83. Type locality: Russia, Karelia, S Petrosawodsk. Type material. Holotype (designated by Friese 1960: 83) (SDEI).

Description and diagnosis see Huemer and Tarmann 1992: 54–56, figs 52–54 (adult), figs 203–208 (male genitalia), fig. 237 (female genitalia).

Molecular data. The average intraspecific divergence of the barcode region is low with 0.04%, ranging from a minimum of 0% to a maximum of 0.15% (n=8). The minimum distance to the nearest neighbour *Zelleria celastrusella* Kearfott, 1903, from North America is 6.58%, and the minimum distance to the congeneric *K. saxifragae* is 7.21%.

Discussion

Our study proves the advantage of an integrative taxonomic approach, initially based on morphology, with molecular data supplemented as an additional tool for delimitation of cryptic species. Even within genera of European Lepidoptera which had been considered as well explored, cryptic diversity seems much more widespread than hitherto estimated. Recent molecular studies have proven the existence of a remarkable amount of cryptic species in several genera or species-groups, e.g. *Callisto* (Kirichenko et al. 2015), *Stigmella* (Nieuwerkerken et al. 2012), *Olethreutes* (Seeger et al. 2010), *Ela-chista* (Mutanen et al. 2013), *Eulamprotes* (Huemer et al. 2013), *Sattleria* (Huemer and Hebert 2011, Huemer and Timossi 2014), *Caryocolum* (Huemer et al. 2014) and *Coleophora* (Baldizzone et al. 2014, Tabell and Baldizzone 2014). Similarly, the proportion of unnamed species in *Kessleria* is high, adding about 20% to the hitherto described species diversity, not including several further yet unresolved possible candidates of cryptic diversity. We expect to find such additional overlooked taxa in e.g. *K. alpicella* and *K. albanica*, but additional material is needed to resolve this. Outside Europe, the species diversity of *Kessleria* cannot even be estimated at the present time, with the Chinese *K. nivosa* (Meyrick, 1938) as the only known congeneric species from Asia, and *K. parnassiae* (Braun, 1940), a close relative of *K. fasciapennella*, from North America. Particularly the Asian fauna of *Kessleria* may prove diverse, e.g. indicative of which is an extraordinary diversity of potential *Kessleria* host-plants in China with 216 out of about 450 worldwide known species of *Saxifraga* (139 endemic) and 63 out of 70 *Parnassia* spp. (49 endemic) (Jintang et al. 2001).

Most of the newly described species belong to complexes of closely related species with strictly allopatric distribution patterns. *K. cottiensis*, *K. dimorpha* and *K. alpmaritimae* are morphologically and genetically most similar to *K. alternans* and

K. wehrlii, forming a separate species group in *Kessleria* (Fig. 32). Similarly, *K. orobiae* along with *K. albescens*, *K. klimeschi*, *K. helvetica* and *K. inexpectata* belong to a species-group of cryptic allopatric taxa (Fig. 67). All these taxa are extremely similar in external and internal morphology. This is a phenomenon well known from the related genus *Yponomeuta*, namely the *Y. cagnagellus* species-complex which includes morphologically virtually indistinguishable species (Bakker et al. 2008), which furthermore often share DNA barcodes. Evolution and reproductive isolation in this genus was likely driven by specific host-plant associations and sex pheromones (Menken 1981, Menken et al. 1992, Menken 1996, Löfstedt 1991, Turner et al. 2010). Unlike *Yponomeuta*, barcode sharing seems to be a rare exception in *Kessleria*, only observed in *K. helvetica* and *K. inexpectata* so far, and indicating possible introgression or recent speciation. DNA barcode divergence to the nearest neighbour is considerable in *Kessleria* with roughly 2–3% distance in sister species, rising to about 6–9% between morphologically well separated taxa (Table 1, Fig. 1). If reflected by at least one supplementing morphological character stage we consider barcode divergence of roughly 2% as taxonomically relevant. These taxa are described as cryptic species and not subspecies, although such decisions are prone to subjectivity (Hausmann and Huemer 2011, Huemer and Mayr in press, Mutanen et al. 2012).

A similar extent of interspecific divergence in allopatric sister species is also known from other Lepidoptera with geographically restricted alpine distribution patterns, e.g. *Sattleria* (Huemer and Hebert 2011) and *Sciadia* (Huemer and Hausmann 2009). The timing of radiation of these and *Kessleria* is unknown, but estimations of substitution rates of COI indicate that divergences of 1.0–2.5% correspond to divergence times of roughly one million years (Kandul et al. 2004, Hausmann et al. 2011). Even though such estimations should be considered with caution, they indicate that several well separated species of *Kessleria* may have diverged already in the lower Pliocene (5.3 mya–1.8 mya) while others, such as four out of five newly described species, are possibly of younger origin. Speciation in these taxa was likely reinforced by climatic oscillations in the late Pliocene and during the Pleistocene, with unglaciated but highly isolated refugial areas, particularly in the southern Alps, an area well documented as a hotspot for endemic Lepidoptera (Huemer 1998). The widespread female flightlessness may have been crucial for reducing dispersal and interrupting gene flow, particularly in maternally inherited mitochondrial DNA, thereby expediting the speciation processes. Host-plant relationship itself seems of limited importance for speciation processes in *Kessleria* as host specificity is moderately pronounced and host-plants are regularly much more widespread than their consumers. E.g. *Saxifraga paniculata* as one of the major host-plants of species of the *K. albescens*-group is widely distributed in the Alps and other European mountain systems, but the *Kessleria* spp. are allopatrically distributed in a small section of the southern Alps. Summing up, further in-depth phylogenetic studies will be necessary to finally identify drivers of speciation in *Kessleria*.

Acknowledgments

We are particularly grateful to Paul Hebert and his team at the Canadian Centre for DNA Barcoding (Guelph, Canada), whose sequencing work was enabled by funding from the Government of Canada to Genome Canada through the Ontario Genomics Institute. We are also grateful to the Ontario Ministry of Research and Innovation and to NSERC for their support of the BOLD informatics platform.

Stefan Heim (TLMF) is acknowledged for his kind assistance with photographic work. Toni Mayr (Feldkirch, Austria), Jürg Schmid (Illanz, Switzerland), Zdenko Tokár (Michalovce, Slovakia) and Christian Wieser (Klagenfurt, Austria) provided material for our examination. Furthermore, we thank all the institutions and private persons who supported earlier work on the genus, and in this context particularly PH's former co-author Gerhard Tarmann (Innsbruck, Austria) for various kinds of help.

PH is particularly indebted to the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano - South Tyrol for helping to fund the project "Genetic biodiversity archive - DNA barcoding of Lepidoptera of the central Alpine region (South, East and North Tyrol)", and to the Austrian Federal Ministry of Science, Research and Economics for funds received in the framework of ABOL (Austrian Barcode of Life).

We thank two anonymous reviewers and the subject editor Erik van Nieuwerkerken for several helpful comments on the manuscript. Last, but not least, we thank Marianna Teräväinen (Helsinki, Finland) for linguistic improvement of the manuscript.

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Supplementary material I

Sample information for specimens used in this study.

Authors: Peter Huemer, Marko Mutanen

Data type: Species data

Explanation note: Details of collecting data, images, sequences, and trace files for the barcoded specimens are available in the public BOLD dataset “DS-LEAKE”, accessed at <http://dx.doi.org/10.5883/DS-LEAKE>

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Taxonomic status and redescription of *Magneptychia nebulosa* (Butler, 1867) (Lepidoptera, Nymphalidae, Satyrinae) with a lectotype designation

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Academic editor: Carlos Peña | Received 17 December 2014 | Accepted 16 April 2015 | Published 14 May 2015

<http://zoobank.org/E2BD558E-F4D8-4615-938D-5F3326679333>

Citation: Nakahara S, Marín MA, Ríos-Málaver C (2015) Taxonomic status and redescription of *Magneptychia nebulosa* (Butler, 1867) (Lepidoptera, Nymphalidae, Satyrinae) with a lectotype designation. ZooKeys 503: 135–147. doi: 10.3897/zookeys.503.9156

Abstract

A redescription of *Magneptychia nebulosa* (Butler, 1867), a poorly known euptychiine butterfly, is given here, and accurate distributional data are provided for the first time. Taxonomic status of this taxon has been discussed by comparing its morphology against its possible congeners. In addition, lectotype designation for *M. nebulosa* is provided in order to objectively establish the identity of this taxon and consequently stabilize the nomenclature.

Resumen

Se presenta una redescrípción de *Magneptychia nebulosa* (Butler, 1867), una mariposa euptychina poco conocida y se brinda por primera vez datos de su distribución. Se discute el estatus taxonómico de este taxón por comparación de su morfología con la de posibles congéneres. En adición, se provee un lectotipo para *M. nebulosa*, en búsqueda de establecer objetivamente la identidad de este taxa y consecuentemente estabilizar su nomenclatura.

Keywords

Euptychiina, Neotropical, Taxonomy, Venezuela, Morphology

Palabras claves

Euptychiina, Neotropical, Taxonomía, Venezuela, Morfología

Introduction

Magneuptychia Forster, 1964 is one of the most diverse genera in the subtribe Euptychiina (Lepidoptera: Nymphalidae: Satyrinae: Satyrini), containing 32 described species and many undescribed species (Lamas 2004, Brévignon 2005, Brévignon and Benmesbah 2012). When Forster (1964) established the genus *Magneuptychia*, he simultaneously established the closely related genus *Argyreuptychia* Forster, 1964, which was subsequently synonymized under *Cissia* Doubleday, 1848 by Miller (1968). *Magneuptychia* is distinguished from *Cissia* by the former's larger and more robust wingspan, its complete absence of an eyespot on the upper wing surface, and its more developed uncus (Forster 1964). However, species of both genera are poorly known, so precise character states are uncertain and not ideal for diagnoses (Forster 1964). Recent phylogenetic studies indicate that some species of *Cissia* and *Splendeuptychia* Forster, 1964 are closely related to *Magneuptychia* (Peña et al. 2010), and did not recover *Magneuptychia* as a monophyletic group, indicating that species composition between these genera must be revised thoroughly. In order to achieve this, it is necessary to reestablish the identity of those species currently placed in these genera using concrete diagnostic characters.

This paper focuses on the scarce and poorly known species *Magneuptychia nebulosa* (Butler, 1867). This specific epithet was previously found to have been misapplied to other taxa and almost no accurate information was available regarding the species' taxonomy, biology, and distribution. Therefore, a redescription of *M. nebulosa* based on a morphological analysis is provided, enabling future researchers to confidently identify this taxon. Two related taxa, *Magneuptychia mimas* (Godman, 1905) and *Magneuptychia alcinoe* (C. & R. Felder, 1867) were also studied in details and directly compared to *M. nebulosa*. The first accurate locality data for *M. nebulosa* is also provided. During our examination of *Magneuptychia* specimens, we found that the *M. nebulosa* type label was misapplied. Consequently, a lectotype designation for *M. nebulosa* is included in order to objectively establish the identity of this taxon and stabilize the nomenclature.

Materials and methods

Morphology. Male and female genitalia were dissected using the methods of Peña and Lamas (2005), except the female genitalia were stained for 30–60 seconds in dilute chlo-

razol black before being stored in 100% glycerin. Genitalia and external morphological characters were studied using a stereomicroscope and photographed by Canon EOS 50D. The terminology for genital and abdominal structures follows Klots (1956), except for the term brachia and aedeagus, which follows Muschamp (1915) and Peña and Lamas (2005) respectively. Forewing length was measured from the base to the tip of the wing using Vernier calipers. Nomenclature for wing venation follows the Comstock-Needham system as described by Miller (1970), and nomenclature for the areas and elements of the wing pattern follows Peña and Lamas (2005) and Neild (1996). All examined specimens, including type specimens, were examined from the following collections:

AN	Andrew Neild collection, London, UK
BMNH	The Natural History Museum, London, UK
IVIC	The Venezuelan Institute for Scientific Research, Miranda, Venezuela
MGCL	McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Florida, USA

Photographs of additional specimens (Warren et al. 2014) were also examined, as well as one dissection prepared at the Museo Entomológico Francisco Luis Gallego (MEFLG), Universidad Nacional de Colombia, Medellín, Colombia.

Primary type specimen data

Magneptychia nebulosa: LECTOTYPE: Male (Fig. 1c): /Venezuela/Venezuela Pur. from Dyson 47-9/ (BMNH)

Magneptychia mimas: SYNTYPE: Male (Fig. 1e): Type H.T./M#/Type of Species./ Coroico. 6500ft., Bolivia. Garlepp./B.M. TYPE No. Rh3225. *Euptychia mimas*, Godm./BMNH(E) #983007/B.M.(N.H) Rhopalocera Slide No. 16843./T.G.H. 1953. 16./ Godman-Salvin Coll. 1904.-1. *Euptychia mimas*, Godm./ (BMNH)

Magneptychia alcinoe: SYNTYPE: Female (Fig. 1d): Type/FELDER COLLN./Alcinoe /Rothschild Bequest B.M. 1939-1./Type of N. alcinoe Feld? = E. benedicta, Butl. of w it may be a good local form Comp w type E. benedicta Butler/ ECUADOR, Sarayacu. C. Buckley B.M. Type No. Rh3224. (BMNH)

Genitalic dissections for *M. alcinoe*

Magneptychia alcinoe: Male, Ecuador: Tungurahua Prov., Rio Machay, 1700m July 4–5 1993 J. P. W. Hall & K. R. Willmott (MGCL) KW-13-05; Male, Ecuador: Pichincha Prov., Rio Toachi, Union del Toachi 800m June 30 1993 J. P. W. Hall & K. R. Willmott (MGCL) KW-13-06; Colombia: Antioquia, Municipio de Amalfi, bosque Picardia N6°47'33", W75°06'36", 1050msnm October 12 2007 09:30:00 borde de bosque A. M. Velez (MEFLG); Male, Ecuador: Tandapi, Rio Pilaton,

Pichincha 1500m August 10 1993 J. P. W. Hall & K. R. Willmott (MGCL) SN-14-57; Female, Ecuador: Esmeraldas Prov. Rd. Lita-Alto Tambo km.16. 850m June 6 1994 J. P. W. Hall & K. R. Willmott (MGCL) SN-14-60; Female, Colombia: Valle, Bitaco, 1700m Jan 7 1985 J. B. Sullivan (MGCL) SN-14-107.

Results

Magneptychia nebulosa (Butler, 1867)

Figs 1, 2 and 4

Euptychia nebulosa Butler (1867: 479)

Redescription. MALE: forewing length 19.6–21.5 mm (n=4).

Wing shape. Forewing with costa slightly convex, inner margin straight, outer margin almost straight, medium section slightly concave, anterior slightly convex, angular. Hind wing rounded, slightly angular, base of costa convex, inner margin convex beyond vein 3A, tornus rounded, outer margin slightly undulating, apex slightly angular.

Wing venation. Forewing recurrent vein absent; hindwing humeral vein present.

Dorsal surface. Forewing ground color brown, submarginal band dark brown, undulating, extending from apex towards tornus, delimiting the slightly darker area, marginal band dark brown, extending from apex towards tornus, fringe greyish brown.

Hindwing color brown, submarginal band dark brown, undulating, extending from apex towards tornus, convex in each cell; marginal band dark brown extending from apex towards tornus; postmarginal and tornal areas pale ocher, fringe greyish brown.

Ventral surface. Forewing ground color chestnut brown, paler along inner margin; discal band thin, straight, reddish brown, extending from radial vein to just beyond vein 2A; postdiscal band reddish brown, weakly undulating, slightly wider than discal band, extending from radial vein and traversing towards inner margin until vein 2A, curved basally in cell Cu2-2A, approximately 2/3 distance from wing base to apex; faint band between postdiscal and submarginal bands dark brown, broad, extending from radial vein to just beyond vein Cu2; submarginal band dark brown, undulating, extending from apex to tornus, becoming less undulating towards the tornus, parallel to postdiscal band; marginal band dark brown, darker than submarginal band, almost straight, extending from apex towards tornus; narrow band distal to marginal band, dark brown, traversing outer margin, delimiting remaining area and fringe; submarginal ocellus in cell M1-M2 black with two white pupils and orange ring; fringe brown.

Hindwing ground color same as forewing, overlaid with subtle whitish pearly cast along inner margin and basal area; discal band reddish brown, slightly distally curved, extending from costal margin to inner margin, approximately 1/3 distance from wing base to apex; undulating postdiscal band color and width same as discal band, weakly undulating, traversing from costal margin towards inner margin, slightly bent basally in discal cell, curved distally in cell Cu1-Cu2 and curved inwards towards the anal mar-

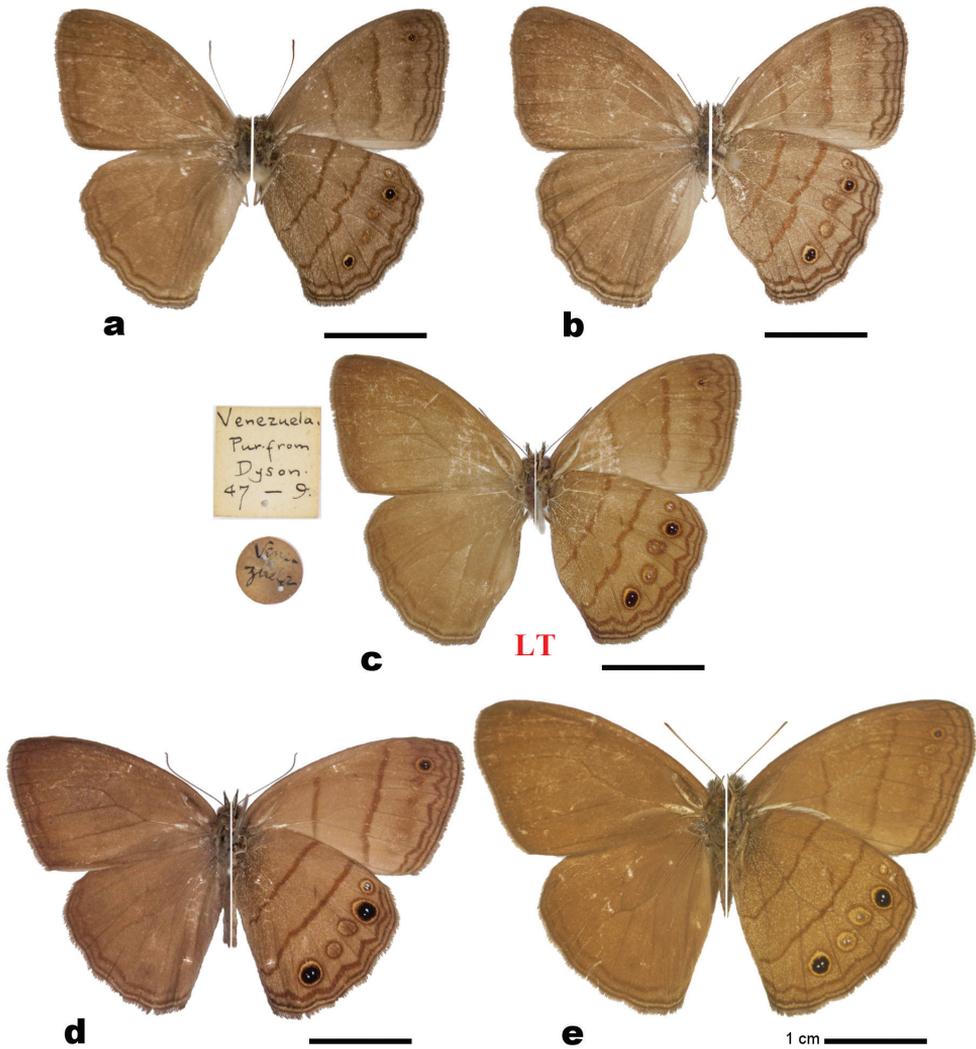


Figure 1. *Magneptychia* adults (dorsal view on left, ventral view on right): **a** Male *M. nebulosa* from Miranda, Venezuela **b** Female *M. nebulosa* from Miranda, Venezuela **c** Lectotype of *M. nebulosa* (photo credit: Trustees of the Natural History Museum, London) **d** Syntype of *M. alcinoe* (photo credit: Trustees of the Natural History Museum, London) **e** Syntype of *M. mimas* (photo credit: Trustees of the Natural History Museum, London).

gin below vein 2A, approximately 2/3 distance from wing base to apex; submarginal band dark brown, extending from apex towards tornus, curved basally in each cell; dark brown marginal band traversing along marginal line from apex towards tornus; narrow band distal to marginal band, band dark brown, traversing along outer margin, delimiting remaining area and fringe; five submarginal ocelli present, cells Rs-M1 and M1-M2 each with black, orange-ringed ocellus with two white pupils, M1-M2 ocellus relatively large (compared to ocellus in cell Rs-M1), cells M2-M3 and M3-Cu1 each with orang-

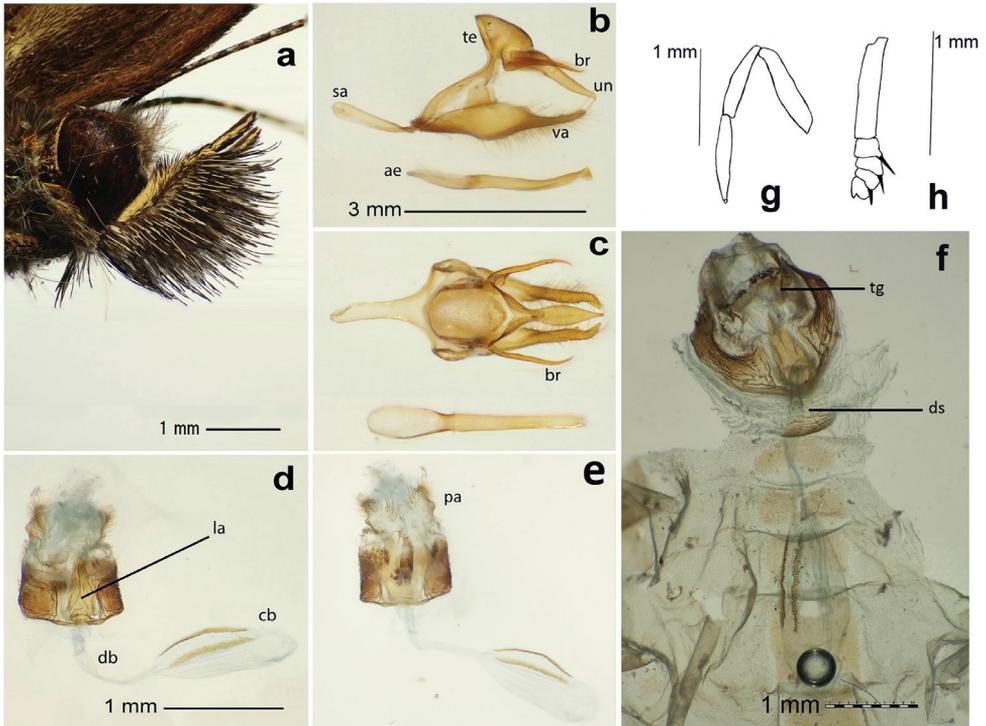


Figure 2. *Magneuptychia nebulosa*: **a** head in lateral view **b** male genitalia (SN-14-35) in lateral view **c** male genitalia in dorsal view **d** female genitalia (SN-14-59) in ventral view **e** female genitalia (SN-14-59) in dorsal view **f** female genitalia (SN-15-44) in dorsal view including sternites **g** male foreleg (tarsus, tibia and femur) **h** female foretarsus. Abbreviations: **ae**, aedeagus; **br**, brachia; **cb**, corpus bursae; **db**, ductus bursae; **la**, lamella antivaginalis; **pa**, papillae analis; **sa**, saccus; **ds**, ductus seminalis; **te**, tegumen; **tg**, tergite; **un**, uncus.

ish relatively small ocellus, sometimes indistinct, Cu1-Cu2 with black, orange-ringed ocellus with two white pupils, similar in size to M1-M2 ocellus; fringe greyish brown.

Head. (Fig. 2a) Eyes entirely brown, sparsely hairy; frons golden-brown, with whitish scales at base; labial palpi approximately 4 mm long, covered with brown and white scales, 2nd segment densely covered in long black and white hairs ventrally, about 3–4 times as long as segment width, 3rd segment about 40 % of 2nd segment in length; antennae 8 mm long, approximately 40% of forewing length, scape and pedicel white, flagellum reddish brown dorsally, grey ventrally.

Legs. Tarsal segments reduced, foretarsus and tibia equal in length, femur slightly longer (Fig. 2g); midleg and hindleg covered with cream greyish scales, tarsus and tibia adorned with spines ventrally, a pair of tibial spurs present at distal end of tibia.

Abdomen. Eighth tergite and sternite reduced.

Genitalia. (Fig. 2b, c) Uncus elongate, slightly curved downward, with hooked apex, appears nearly elliptical in dorsal view, brachia hooked, pointed upward, positioned at approximately 45° angle, curved dorsally at middle of dorsal posterior mar-

gin, about 2/3 length of uncus; tegumen expanded dorsally, flattened ventrally; appendices angulares present; vinculum fused to posterior margin of tegumen, divided medially; saccus narrow and evenly wide in lateral view; costal margin of valvae slightly broadened medially, apex narrow, slightly curved towards uncus; aedeagus straight, broadening anteriorly.

FEMALE: Similar to male except as follows: Wings wider and rounder; forewing length 19.6–21.0 mm (n=8); dorsal ground color slightly paler; ventral ground color pale ocher, discal and postdiscal bands orange-brown; foretarsus divided into 5 segments (Fig. 2h); weakly sclerotized region between 7th and 8th sternite present in intersegmental membrane. **Female genitalia.** (Fig. 2d–f) Eighth tergite sclerotized, dorso-posterior area apparently weakly sclerotized; lamella antevaginalis sclerotized, sub-triangular in ventral view; 8th segment heavily sclerotized laterally; ductus bursae unsclerotized, origin of ductus seminalis located approximately one third distance from ostium bursae to corpus bursae, corpus bursae equally long as ductus bursae, with two brownish signa.

Distribution. (Fig. 3) All known specimens of *M. nebulosa* are from the slope of Serranía del Litoral in the Cordillera de la Costa: A huge mountainous district in northern Venezuela. However, one male specimen in the BMNH has a label that says 'Colum', implying it may have actually been collected in Columbia. On the other hand, it may be a misinterpretation of 'Colonia [Tovar]' (popular collecting site near Caracas) rewritten from an original label by BMNH staff. This label also says 'Dys', indicating the specimen was collected by Dyson, who had a lot of northern Venezuelan specimens and may have accidentally attached a Venezuelan label to this specimen (A. Neild, pers. comm.). A valid record from Colombia is needed to confirm its occurrence, as it is possible that this is a mislabeled Venezuelan specimen. The specimens in the BMNH bear no locality information other than the country of collection. However, *M. nebulosa* specimens found in other collections have more accurate locality data: 4 males, VENEZUELA, Miranda, Altos de Pipe, 24 March 1973. J.B. Sullivan (MGCL) (3 dissection vials prepared: SN-14-33; SN-14-34; SN-14-35; 1 without label); 4 females, same data as males; Female, Venezuela: Miranda, Altos de Pipe J.B. Sullivan (MGCL) (1 dissection vial prepared: SN-14-59); 1 female, VENEZUELA, Miranda, Altos de Pipe, 17 March 1973. J.B. Sullivan (MGCL); 1 female, VENEZUELA, Miranda, Altos de Pipe, 24 July 1979. J.B. Sullivan (MGCL) (dissection vial without label); 1 female, VENEZUELA, Miranda, Altos de Pipe (IVIC site), above km11 turn off to Caracas to Los Teques rd, 1550-1650m, 13 Oct 2002 (AN). 1 female, VENEZUELA, Miranda, Cumbre Azul, 2km. NW of Los Teques, 11-0-1200m, 23.vii 1981 Lee D Miller (MGCL). 1 female, VENEZUELA, Dist. Federal Massif du Naiguta, 3 July 1957. R. Lichy (MGCL) (1 dissection vial prepared: SN-14-106); 1 female, VENEZUELA, Dist. Federal Massif du Naiguta, 1 September 1948. R. Lichy (MGCL) (dissection vial prepared: SN-15-44). In addition, the third author has recorded *M. nebulosa* many times from Quebrada Honda (Fig. 4), El Jarillo (Miranda, Venezuela) and Altos de Pipe, see Suppl. material 1 for these data.

The female specimen in the AN collection is from a humid lower montane forest isolated on a ridge line along the southern slope of Cordillera de la Costa. The vegeta-



Figure 3. Map showing known localities for *M. nebulosa*: blue dot = Quebrada Honda, El Jarillo; orange dot = Cerro Azul, Los Teques; red dot = Altos Pipe; green dot = Massif du Naiguata.

tion here has trees with a canopy over 15 m high, such as *Miconia* sp. (Melastomataceae), *Palicourea* sp. (Rubiaceae), *Clusia* sp. (Clusiaceae), and *Chusquea* sp. (Poaceae) (pers. obs.). Several true cloud forest inhabitants (e.g. *Evenus coronata* (Hewitson, 1865) (Lycaenidae), *Corades enyo enyo* (Hewitson, 1849) (Nymphalidae) and *Epiphile epicaste epicaste* (Hewitson, 1857) (Nymphalidae) are also recorded here (pers. obs.). Thus, it is reasonable to expect that *M. nebulosa* can also be found in lower cloud forests on the slopes of the Cordillera de la Costa.

Godman and Salvin (1880) reported a record of *M. nebulosa* from Chiriquí, Panama. However, his illustration is morphologically different from the lectotype, suggesting that this record is invalid. The ventral hindwing postdiscal band is not wavy as in *M. nebulosa*. Three of the ocelli differ in both size and color, and the large apical ocellus has one pupil instead of two. The ventral forewing submarginal area lacks an obvious brown undulating band, and the ventral forewing discal band is much more curved. Forster (1964: p.104, figure 105, as *Ypthimoides nebulosa*) figured a male genitalia of *M. nebulosa* based on a specimen from Bolivia. Although this genitalia appears to resemble those of *M. nebulosa*, to judge from the curved ventral margin of tegumen and the developed cucullus, we believe this is not *M. nebulosa* and this Bolivian record is invalid.

Diagnosis. Phenotypically, *M. nebulosa* most closely resembles *M. alcinoe* and *M. mimas*. These species can be distinguished from *M. nebulosa* by size and wing pattern. *Magneptychia nebulosa* is relatively small and possesses a wavy, somewhat irregular postdiscal band (slightly bent basally in discal cell, curved distally in cell Cu1-Cu2) of the ventral hind wing, whereas *M. alcinoe* and *M. mimas* are larger and have a straight hindwing postdiscal band. This straight ventral hindwing postdiscal band is also present in all other *Magneptychia*. However, some of the members of *Parypthimoides* (e.g. *P. poltys*



Figure 4. *Magneptychia nebulosa* photographed in Quebrada Honda (photo by Cristóbal Ríos).

(Prittwitz, 1865)) also exhibits this curved postdiscal band. *Magneptychia nebulosa* possesses a rather reddish discal and post discal bands. The number of white pupils in the five ventral hindwing subapical ocelli varies within *M. alcinoe* and is thus occasionally diagnostic; some specimens of *M. alcinoe* have only one pupil in one of the ocellus (K. Willmott, pers. comm.), whereas *M. nebulosa* always have two pupils in four ocelli, and one pupil in the larger, fifth ocellus. In addition, *M. nebulosa* may be confused with a variation of *M. modesta* (Butler, 1867), which is a species that seems to be very variable and is perhaps a complex of several species. However, *M. nebulosa* differs from this taxon by the combination of the undulating ventral hindwing postdiscal band and double-pupilled ocelli in ventral hindwing cell M1-M2 (usually one in *M. modesta*).

Lectotype designation for *Magneptychia nebulosa* (Butler, 1867)

Magneptychia nebulosa was described from Venezuelan specimens. The type series was originally deposited in the Dyson collection and subsequently purchased by the BMNH in 1847 (G. Lamas, pers. comm.), where it is now deposited. The extant type series consists of one male (Fig. 1c) with two labels (/Venezuela/Venezuela Pur. from Dyson 47-9/) and one female that is currently labeled as the type (/Type/Venezuela/Venezuela Pur.

from Dyson 47-9/Type/ B.M. Type No. Rh3223. *Euptychia nebulosa* Butl/). However, Butler's description omits both the sex and the number of specimens examined, therefore, any "type" specimens ought to be syntypes. Because of the similarity of so many *Magneuptychia* species, it is important to select a lectotype to fix the name.

Butler provides a precise forewing measurement of 1.55 inches (39.37 mm). This theoretically makes it possible to deduce which specimen was the subject of Butler's description, though the male and female syntypes have nearly identical forewing lengths of 39 mm and 40 mm, respectively. Butler's description also clearly refers to five ocelli, three of which are relatively small with two pupils. Male ocelli have two pupils, but female ocelli only have one. Therefore, we designate the male specimen as the lectotype of *M. nebulosa*. This is important because: (a) this male specimen most closely agrees with the original description, (b) it is in better condition than the female specimen, and (c) the male genitalia of euptychiine species are better known and are more commonly figured than female genitalia, and therefore have more scope to delimit species. The specific epithet *nebulosa* has been incorrectly applied to different taxa in Forster (1964) and D'Abrera (1988), as well as in the BMNH and other public collections (pers. obs.). This lectotype designation will remove doubt about the true identity of *M. nebulosa*. The female specimen is consequently designated as a paralectotype. Note that this lectotype and paralectotype have a slightly different wing coloration probably because it faded over time.

List of selected citations for *M. nebulosa* being misapplied

Godman and Salvin (1880): p.86 (text); pl. 8 (ventral surface)

Weymer (1911): p.209 (text); pl. 48 (ventral surface)

Forster (1964): p.104 (male genitalia illustration, as *Ypthimoides nebulosa*)

Brown and Mielke (1967): p.91 (as *Ypthimoides nebulosa*)

D'Abrera (1988): p.776 (male dorsal and ventral surface)

Discussion

The male and female genitalia of *M. nebulosa* are extremely similar to those of *M. alcinoe*. Despite dissecting several specimens per species, we could not find any convincing species-level differences except for their overall size, which appears to correlate to the differences in overall body size. However, the male genitalia exhibit some variation of the costal region and cucullus of the valvae, as well as variation in patterns of the cornuti. Further examination of these structures could provide diagnostic characters for male specimens of these taxa.

In general, most euptychiine species are distinguishable from their congeners by characters of the male and female genitalia, so the genitalic similarity would ordinarily suggest that *M. nebulosa* and *M. alcinoe* are conspecific. However, the small adult size

of *M. nebulosa*, its rather reddish bands, its curved ventral hindwing post discal band, and its rather small ocelli are all consistent and appear to be reliable characters to distinguish it from *M. alcinoe*. We were not able to find records or specimens of *M. alcinoe* from Cordillera de la Costa, nor *M. nebulosa* from an area inhabited by *M. alcinoe*, suggesting that the two species are allopatric. Cordillera de la Costa is isolated from the adjacent Sierra de Turimiquire and Cordillera de la Mérida by flat and scrubby lowlands, namely the depression of Yaracuy and the depression of Unare, respectively (see Fig. 3). However, we believe the evidence to support conspecificity (similar genitalia, no known area of sympatry) is weaker than the evidence supporting treatment as two different species (adult size, wing pattern, geographic isolation reinforced by specialized habitat preference). Therefore, we would settle the matter in favor of two species, and therefore treat *M. nebulosa* as a valid species, presumably close to *M. alcinoe*. Since *M. nebulosa* was originally described as a species and never treated as a synonym, this treatment maintains the status quo. Although some might argue that it is not a reasonable decision to treat a Neotropical butterfly taxon known only from the Cordillera de la Costa as a valid species, we have two similar examples of montane cloud forest nymphalid species, *Memphis maria* Pycrz & Neild, 1996 and *Diaethria panthalis* (Honrath, 1884), which are also currently also known only from this mountain range (Neild 1996). On the other hand, it is true that there are many end-of-distribution-subspecies known from Cordillera de la Costa (e.g. *Pedaliodes manis ivica* Vilorio & Pycrz, 2010), indicating that this kind of judgment is somewhat subjective.

Although the status of *M. nebulosa* is currently resolved, other uncertainties about *Magneptychia* remain. For example, the type of *M. mimas* closely resembles that of *M. alcinoe*, leading some to suggest that these taxa are conspecific, with the former merely being a Bolivian population of the latter. Conversely, these similarities may instead suggest the need for an “*alcinoe*” species group to distinguish these very similar taxa from other *Magneptychia*. The relationships between *M. nebulosa* and its congeners are still not fully understood; a revision of the genus is crucial to facilitate identification of euptychiine species in museum collections. Once we have a better understanding of Euptychiina and can reliably identify them, they can be used in broader, higher-impact studies of conservation and biogeography.

Acknowledgements

We thank Andrew Neild (UK) for discussion and for providing photos and valuable comments on the manuscript. Thanks are also due to Gerardo Lamas (Peru) for valuable discussion throughout the course of preparing this article; to David Lees (BMNH) and Blanca Huertas (BMNH) for kindly dissecting specimens at BMNH and for their help; to BMNH for allowing us to use photos, and to David Plotkin (MGCL) for correcting English and for providing comments on the manuscript. We are also grateful to Colciencias (grant No. 1118-521-28378) and the National Science Foundation (grant No. DEB-1256742).

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Supplementary material I

Records for *M. nebulosa* from Quebrada Honda, El Jarrillo, Miranda, Venezuela

Authors: Shinichi Nakahara, Mario Alejandro Marín, Cristóbal Ríos-Málaver

Data type: Adobe PDF file

Explanation note: Records for *M. nebulosa* from Quebrada Honda, El Jarrillo, Miranda, Venezuela; Altos de Pipe, Instituto venezolano de Investigaciones Científicas, Miranda, Venezuela: Cristóbal Ríos Málaver Leg: These following specimens are deposited in the reference collection of the Venezuelan Institute of Scientific Research IVIC, Altos de Pipe, Miranda, Venezuela.

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