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A new member of the genus *Isotomurus* from the Kuril Islands (Collembola: Isotomidae): returning to the problem of “colour pattern species”

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Abstract

Colour pattern is the most common character to identify species in several large genera of Collembola. Its use often raises problems due to various and poorly investigated extent of chromatic variability among species. *Isotomurus festus* **sp. nov.** is here described from Kunashir Isl. (the Kuriles, the Far East of Russia). The species, a member of the ‘*antennalis*’ group, is characterized by the lack of trichobothria and slender claws, but is greatly variable in coloration. DNA barcoding (COI) results supports that all the colour forms encountered belong to the same species. While colour pattern has been shown to be the most reliable character for species identification in several Entomobryidae genera, it might not be the case in *Isotomurus* Börner, 1903, the sole large Isotomidae genus where colour pattern is routinely used for taxonomy.

Key words: the Far East, hydrophilic, colour pattern, barcoding, taxonomy, polymorphism

Introduction

The term “colour pattern species” was proposed by Yoshii (1989) for species that can be separated only by colour pattern of the body. This concept resulted from the study of the “forms” of the Paronellidae subgenus *Pseudoparonella* (*Oceaniella)* Yoshii, 1989 in New Caledonia, in which all morphological characters were the same, including macrochaetotaxy of the body, while their very distinct colour patterns indicated several valid species. According to Yoshii the term was just a temporary one reflecting the state of Collembolan taxonomy at that time. In the history of taxonomy of Collembola, the value of colour was used and examined many times. It is a central character in the taxonomy of three large genera of Entomobryidae: *Seira* Lubbock, 1869 (Christiansen & Bellinger 2000, Mari Mutt 1986), *Entomobrya* Rondani, 1861 and *Orchesella* Templeton in Templeton & Westwood, 1836. Paclt (1959), for instance, considered the various colour pattern of South African *Seira* as polymorphism within the boundaries of a single species, while previous and subsequent workers recognized more than 20 different species in the country, each with a more or less characteristic pattern (Womersley 1934, Yosii 1959, Janion-Scheepers *et al*. 2015). In *Entomobrya* or *Orchesella,* colour pattern has long been the only character for species discrimination, and it remains the easiest one for identifying most species. In the course of modern taxonomy development, the value of colour has been however challenged. For instance, in *Entomobrya*, Jordana & Baquero (2005) recently proposed a new setae notation system, which aimed to, as far as possible, “avoid the use of colour pattern”. In the monograph on Palearctic Capbryinae and Entomobryini Jordana (2012), nevertheless, provided two keys to identify species of *Entomobrya*, one "partly by colour and morphology" and another by chaetotaxy. In the whole Entomobryoidea, beyond problems of colour variations in some species, the validity of “colour pattern species” was clearly supported in several cases by molecular and morphological data, i.e. several species differing only in colour pattern were validated, in particular among Lepidocyrtinae (Soto-Adames 2002, Mateos Frias 2012) and Entomobryinae (Zhang *et al*. 2011).

A recent paper by Katz *et al.* (2015) combining colour pattern and molecular approaches brings additional insight into this question for *Entomobrya*, showing both the taxonomic interest of colour pattern and its limitation: in some cases, a same colour pattern was shown to be associated to different Molecular Operational Taxonomic Units (MOTUs)—considered as "species" by the authors. This study also shows that chaetotaxy is affected by variability, as expected for plurichaetotic species, and that its use may be no more reliable than colour pattern in *Entomobrya*. The main conclusion of this paper is that colour pattern is a species-specific issue, in other words that its value as a taxonomic character has to be established for each species through the study of polymorphism.

The use of colour remains a challenge to taxonomists in Entomobryomorpha and Symphypleona. Taxonomy of other groups is less dependent on this character though similar questions may arise also in Poduromorpha, for example when using pattern in banded species of Pseudachorutinae (Oliveira & Deharveng 1984, Hisamatsu & Tamura 1998, Weiner & Najt 1998) or in some groups of Lobellini (Cassagnau & Deharveng 1984). The character was also examined in taxa consisting of superficially very similar species, such as Tomoceridae where delicate differences in small pale spots and iridescence of scales covering were shown to be indicators of specific status (Felderhoff *et al.* 2010).

In Isotomidae, the pattern of dark spots and bands on the body is mainly used in modern taxonomy for two large genera, *Isotoma* Bourlet, 1839 and *Isotomurus* Börner, 1903. The latter genus is one of the most abundant arthropods in temperate wet habitats and exhibits a great diversity of colour patterns. However, the species identification in *Isotomurus* remains one of the most "problematic" task in the family, in spite of considerable contribution of the taxonomists (Deharveng & Lek 1993; Carapelli *et al.* 2005; Fjellberg 2007). In the past *Isotomurus* colour forms were often considered as intraspecific variability (Folsom, 1937; Stach, 1947; Gisin 1960, Poinsot-Balaguer 1976). Conversely, Cassagnau (1987) considered that colour pattern had been often neglected or inaccurately analyzed, while it could be a useful character if its fluctuation range is studied on a large number of specimens. Further molecular analysis and ecological observations confirmed that "colour forms" often corresponded to valid species (Carapelli *et al.* 1995a, 1995b, 2001, 2005). Other morphological characters (details of chaetotaxy) partly supported the value of colour pattern, which, however, remained the leading if not the only diagnostic character, as summarized by Carapelli *et al.* (2001): "The habit of considering the different pigmentation patterns as one of the most useful discriminating features at the species level is confirmed". Two problems remained in *Isotomurus*: one is that several species can be characterized by similar colour patterns; another one is that intra-specific variability of the pattern exists in many species, making the determination of deviated individuals hardly possible (Carapelli *et al.* 2001; Fjellberg 2007).

In the course of our study of Collembola from the Far East of Russia we found an interesting material of abundant and highly variable new species of *Isotomurus*, the description of which is given below. The lack of taxonomic significance of its colour forms is supported by genetic data (COI 5' 'barcoding fragment').

Material and methods

Species description. Vocabulary and setal notation follows mostly Potapov (2001). The following abbreviations are used: Abd.—abdominal segment; Ant.—antennal segment; AO—antennal organ; *ms*—micro *s*-seta(e) or *ms*-setae (=microsensillum(a) auct.); PAO—post-antennal organ; *s* in the text and figures—macro *s*-setae or *s*-setae (=sensillum(a) auct.); Th.—thoracic segment.

DNA barcoding and sampling. Twelve specimens of *I. festus* **sp. nov.**, including 3 pale and 9 banded, as well as specimens of three other *Isotomurus* species were barcoded (Table 1).

Molecular analyses. DNA was extracted from entire specimens in 30µl of lysis buffer (http://www.ccdb.ca/docs/CCDB_DNA_Extraction.pdf) and proteinase K incubated at 56°C overnight. DNA extraction followed a standard automated protocol using 96-well glass fibre plates (Ivanova *et al.* 2006). Specimens were recovered after DNA extraction using a specially designed work flow allowing their morphological examination (Porco *et al.* 2010). The 5' region of COI used as a standard DNA barcode was amplified using M13 tailed primers LCO1490 and HCO2198 (Folmer *et al.* 1994). Samples that failed to generate an amplicon were subsequently amplified with a pair of internal primers combined with full length ones (C_LepFolF/C_LepFolR) (Ivanova—published on www.boldsystems.org). The standard PCR reaction protocol of the Canadian Center for DNA Barcoding was used for amplifications (http://www.dnabarcodes2011.org/conference/preconference/CCDB-Amplification-animals.pdf), and products were checked on a 2% E-gel 96Agarose (Invitrogen). Unpurified PCR amplicons were sequenced in both directions using M13 tailed primers, with products subsequently purified using Agencourt CleanSEQ protocol and processed using BigDye version 3.1 on an ABI 3730 DNA Analyzer (Applied Biosystems). Sequences were assembled and edited with Sequencher 4.5 (GeneCode Corporation, Ann Arbor, MI, USA). The alignment was obtained using BIOEDIT version 7.0.5.3 (Hall 1999). Sequences are publicly available on BOLD in the dataset [DS-ISOKU] accessible via through the following DOI (dx.doi.org/10.5883/DS-ISOKU) and on GenBank (GU656452-GU656455, GU656457, KY829286-KY829308).

Data analyses. Distance analyses were performed with MEGA6 (Tamura *et al.* 2013), utilizing a Neighbor-Joining (Saitou & Nei 1987) algorithm with the Kimura-2 parameter model (Kimura 1980) to estimate genetic distances. The robustness of nodes was evaluated through bootstrap re-analysis of 1000 pseudoreplicates. The tree was replotted using the online utility iTOL (Letunic & Bork 2007).

TABLE 1. List of barcoded specimens.

Name	spcms	sample
Isotomurus cassagnaui Deharveng & Lek, 1993	4	France: Haute-Garonne: Izaut-de-l'Hôtel, 27.vii.10, Sun Xin leg (31–249)
Isotomurus palustris f.*catalana* (Cassagnau, 1987)	4	France: Pyrénées-Orientales: Argelès-sur-Mer, 03.vi.13, L. Deharveng leg (66–1235)
Isotomurus gallicus Carapelli *et al*., 2001	3	France: Tarn: Larroque, 11.ii.14, L. Deharveng and S. Zon leg. (81–105)
Isotomurus festus **sp. nov.** "banded" form	9	Russia: Kurilsky Reserve, 1.vi.11, Matalin A. leg (RU-MP11-01)
Isotomurus festus **sp. nov.** "pale" form	3	Russia: Kurilsky Reserve, 1.vi.11, Matalin A. leg (RU-MP11-01)
Isotomurus unifasciatus (Börner, 1901)	4	Belgium: Bruges, 07.xii.08, L. Deharveng and A. Bedos leg. (BEL-031)

Taxonomy

Isotomurus festus sp. nov.

Figs 1–26.

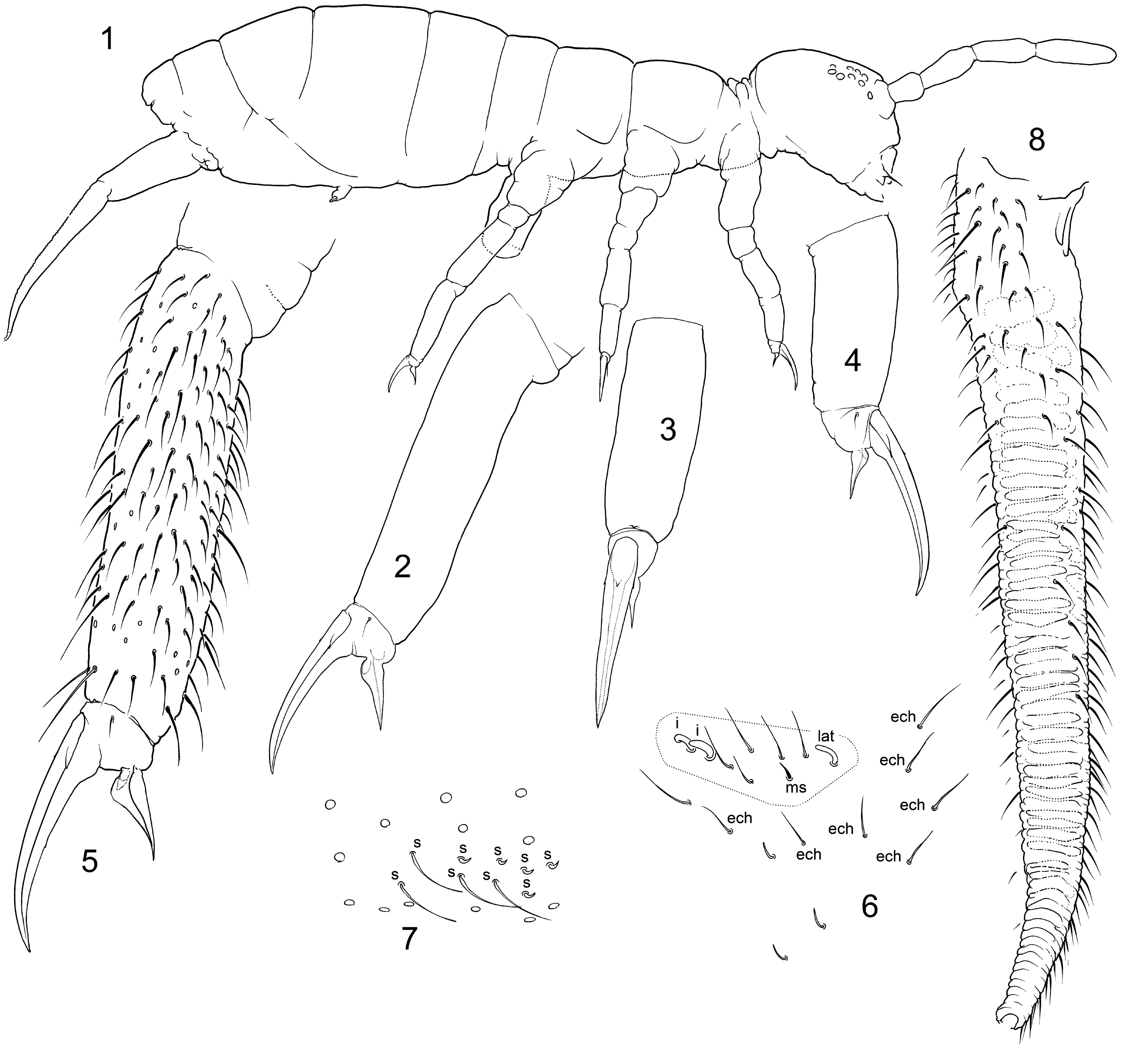
Type material: Holotype, Russian Far East, the Kuril Islands, Kunashir Isl., Kurilsky Reserve, vicinity of Alekhinskaya outpost, behind Sernaya Bay, bank of spring, in moss sprinkled with water, 1.vi.2011. A. Matalin leg**.** Many paratypes in the same locality.

The holotype and 15 paratypes are deposited in the collection of the Department of Zoology & Ecology, Moscow State Pedagogical University. 17 paratypes including 12 vouchers of barcoded specimens are deposited in the collection of the Museum national d'Histoire naturelle (MNHN) in Paris.

Description. Body size 1.9–2.3 mm. Body shape as common for the genus, with rather prognathous head (Fig. 1). Brightly orange when alive (probably true only for colour forms with light background, see below). In alcohol background pale yellowish. Eye areas black, connected by broad band on anterior part of head, bases of antennae paler. Posterior part of head with large black medial spot. Antennae and foots diffusely dark, furca paler. Other characteristics of colour pattern of body varies (see below).

8+8 ommatidia of subequal size in typical position. PAO broad elliptical, as long as nearest ommatidium. Maxillary outer lobe with 4 sublobal hairs and bifurcate palp (Fig. 11). Labrum with 4 prelabral setae, labral edge as common for the genus, with four sharp ridges and ventro-apical ciliation. Frontoclypeal area with many setae. Labial palp with all usual papillae and complete set (16) of guards, ~ 9 proximal, 5–6 basomedian and 5 basolateral setae present (Fig. 12). Ventral side of head with 5–9+5–9 postlabial setae (Fig. 12). Maxillary head with lamella 1 slender, not expanded, with one row of stronger cilia along edge, other lamellae with fields of thin denticulation. (Figs 9–10). Antennae about 1.4–1.7 as long as head diagonal. With rather few s-setae on three first antennal segments. Ant. 1 with 5–9 s-setae: 5–3 short and thick ("spine-like") and 2–4 long (Fig. 7), Ant. 3 with few s-setae, “AO area” with two thick inner s-setae, group of slender s-setae in more lateral position, ms-seta and one thick lateral s-seta, with several erect s-setae around (Fig. 6). Ant. 4 with minute secondary branch present on subapical pin-seta (bifurcate pin-seta).

Body with cover of finely ciliated setae unequal in length (Fig. 23), ciliation often visible only under highest magnification. Neither trichobothria nor true macrosetae differentiated. Ratio longest setae to length of Abd. V as 0.3–0.4. The s-setae short (Fig. 22), longer on posterior part of trunk (Fig. 23). Number of s-setae in full grown specimens as 4,4/4,5–7,>14,>15,>14 (Fig. 21), first instar juveniles with somewhat fewer s-setae on posterior tergites (Fig. 24). The ms-setae 1,1/1,1,1 in number. Accp-s-setae in front of p-row in grown specimens, Abd. III–V with asymmetrical arrangement and number of s-setae with some in medial position (unpaired). On Abd. IV and V considerable part of dorsal area covered with as-s-setae (Fig. 21).



FIGURES 1–8. *Isotomurus festus* **sp. nov.**: 1, habitus; 2–4, distal part of leg 3,2, and 1; 5, distal part of leg 3; 6, s of Ant.3 (area of AO); 7, s of Ant.1; 8, dens, posterior view. *s*—s-seta, *ms*—ms-setae, *lat*—lateral s-setae of AO, *i*—inner s-seta of AO, *ech*—erect s-seta.

Legs with slender and long claws, ratio tibiotarsus : outer edge of claw as 0.8–1.0 on Leg 1 and 1.5–2.0 on Leg 3 (Figs 2–4). Claw with a pair of small lateral tooth, an outer one, and rudimentary inner tooth (often invisible)

(Fig. 5). Empodial appendage without inner tooth. Tibiotarsi in juvenile specimens and first instar with 8 distal setae. Retinaculum with 4+4 teeth and 10–15 setae. Ventral tube with 3+3 laterodistal, 0–5+0–5 anterior and 16–20 posterior setae. Manubrium densely covered by setae. Manubrial thickening simple, without teeth in medial part. Dens rather slender, continuously narrowed, with rather few short setae on posterior side which cover only its basal part (ca 1/5 of its length). One of posterior setae in basal part slightly longer than others. Posterior side of dens crenulated, wrinkles regular in distal half and more disordered in basal half (Fig. 8). Mucro with four teeth (Fig. 13–16) and a seta on outer side. "Apical" tooth large (as large as subapical). Subapical tooth with two lamellae running to mucro base. Middle tooth scoop-like with two lamellae running back, outer lamella wider. Outer proximal tooth of common shape. Ratio manubrium : dens : mucro as 6.8–9.7 : 10.5–16.5 : 1. Ratio mucro : outer edge of claw III as 0.25–0.34. First instar juveniles without ventroapical manubrial setae and seta on mucro. Males are sporadic and thus the population consists mostly of females. Fully adult males have not been seen by us and so presence of modified setae on Abd. III–IV remains to be studied.

Colour forms. Type population consists of several colour forms mixed together. Pale variant is almost without pigmentation on corpus apart from weak diffuse spots on lateral parts of body and bases of legs, dark spot is also often seen on front part of mesothorax (Fig. 18). Most individuals have a broad mid-dorsal band interrupted in intersegmental areas and running from thorax to last abdominal segment. The size of spots forming the band become narrow towards posterior, the spots are much weaker or absent at the end of abdomen (Fig 17). Lateral parts of Th. II–Abd. II have dark irregular spots. In some individuals the main colour pattern is masked by darker background and therefore medial band is hardly visible (Fig. 20). Some specimens are, in fact, with homogeneous diffuse and rather pale colouration (Fig. 19). Colour photos of the described forms and their variability (apart from diffusely dark one) are shown in Figs 25–26. Association of colour pattern with size of the individuals or sex has not been detected.

In the subsequent molecular analysis, the variants with clear medial band were named “banded” (Figs 17, 20), while all others, without such a band, were called “pale” (Figs 18–19).

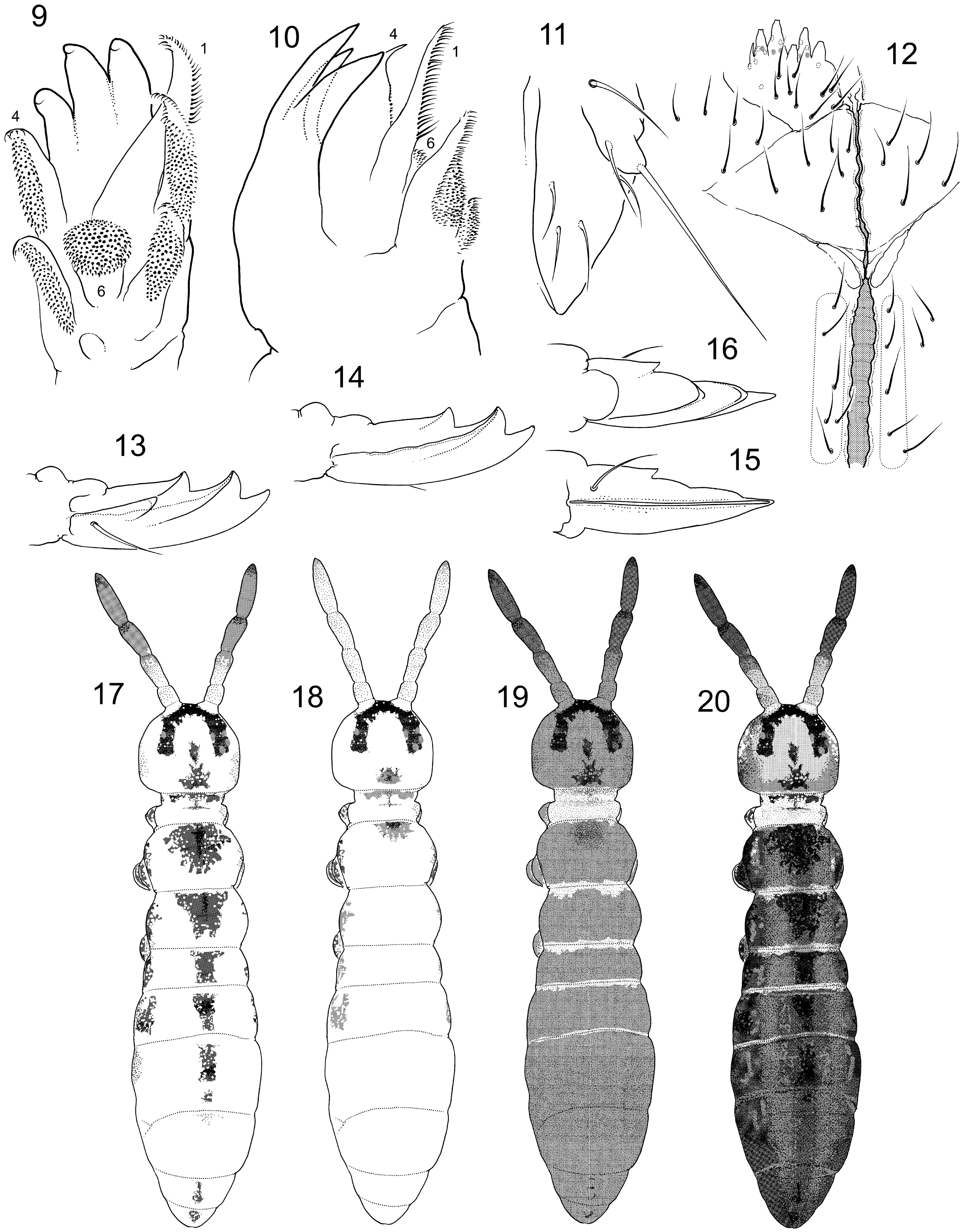
Name derivation. The name reflects bright (festal) colour of alive specimens.

Distribution and ecology. Known only from the type locality. It was found in mass population forming orange layer in wet mosses sprinkled with running water of mountain spring (Fig. 27).

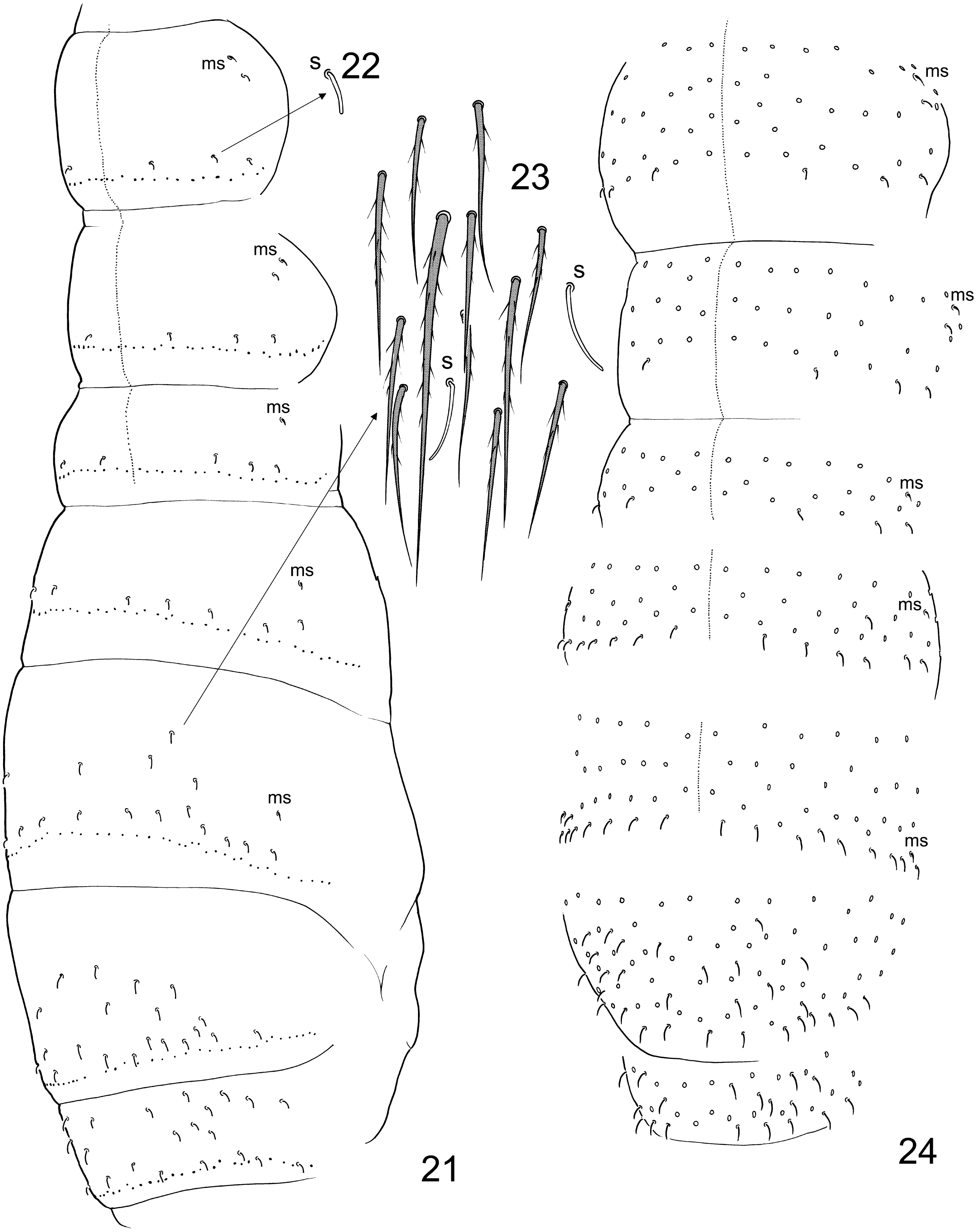
Discussion. Three species, i.e. *I. festus* **sp. nov.**, *I. chaos* Potapov & Babenko, 2011 and *I. antennalis* Bagnall, 1940, combine in a compact group which probably deserves the rank of supra-specific taxon. So far we named it as the ‘antennalis’ group (Potapov 2001) which is defined by the lack of trichobothria and macrosetae on the abdominal segments. S-chaetotaxy is disproportionate in all mentioned species: tergites of thorax and anterior half of abdomen have few s-setae while posterior half of abdomen possesses many such setae. Thus both *I. festus* **sp. nov.** (Fig. 17) and *I. chaos* (Fig. 1 in Potapov & Babenko 2011) have only 3 accp-s-setae on Th. II, III, and Abd. I and many irregularly scattered s-setae on the last abdominal segments. *Isotomurus antennalis* is also characterized by a similar s-pattern on body (Fjellberg, pers. comm.). The new species differs from the other two members of the group by a combination of very slender claws, large apical tooth of mucro and weak setal covering of posterior side of the dens. All three characters are uncommon within the genus *Isotomurus*: slender claws are shared with *I. alticolus* (Carl, 1899) (Europe) and *I. takahashii* (Yosii, 1940) (Japan), large apical tooth with *I. annectens* Yosii, 1963 (Japan). *Isotomurus takahashii* was described as a member of *Isotoma,* the genus having no trichobothria. Afterwards Yosii (1963) wrote that "*setae sensuales* [=trichobothria, authors' note] were previously overlooked, but they are rather short, filiform and ciliated on all sides" and moved accordingly *I. takahashii* to the genus *Isotomurus.* The species belongs to group other than ‘antennalis’. *Isotomurus annectens* differs from *I. festus* **sp. nov.** by normal shape of claw and presence of trichobothria.

Results of barcode analysis and general comments concerning the colour forms of *Isotomurus*

The DNA barcoding results support the specific status for the population described here as *I. festus* **sp. nov.**: no genetic difference was detected between its colour forms (Fig. 28). The genetic divergence between the new species and the other species of the genus (ranging from 18.74% to 21.18%: Table 2) is comparable to the divergence found among these described species (ranging from 22.07% to 24.82%: Table 2). Intraspecific divergences were also found similar (ranging from 0% to 1.52%: Table 2).



FIGURES 9–20. *Isotomurus festus* **sp. nov.**: 9–10, maxillary head, inner (9) and ventral (10) views (1,4,6 – lamellae); 11, maxillary outer lobe; 12, labium (labial guards not shown) and postlabial area (encircled); 13–16, mucro, outer (13), inner (14), ventral (15), and dorsal (16) views; 17–20, contrasting variants of colour pattern: banded (17), pale (18), diffusely dark (19) dark and banded (20).



FIGURES 21–24. *Isotomurus festus* **sp. nov.**, chaetotaxy of body: 21, sensillar chaetotaxy in adult individual; 22, s-seta of Th. II, 23, setae and s-setae of dorsal area of Abd. III, 24, chaetotaxy in first instar (common setae shown as dots). *ms*—micro-s-seta, *s*—s-seta.

FIGURES 25–27. Photos of banded and pale specimens in dorsal (25) and lateral (26) views; and the type biotope (27) of *I. festus* **sp. nov.**

TABLE 2. Intraspecific and interspecific genetic divergences among species (based on K2p distances percentages for COI)

species	Intraspecific divergence	Interspecific divergence				
		I. palustris f.*catalana*	*I. cassagnaui*	*I. festus* **sp. nov.**	*I. gallicus*	*I. unifasciatus*
I. palustris f.*catalana*	0.15					
I. cassagnaui	1.08	22.07				
I. festus **sp. nov.**	1.52	18.74	19.68			
I. gallicus	0.31	22.35	24.82	21.18		
I. unifasciatus	0.00	22.38	23.09	20.50	22.37	

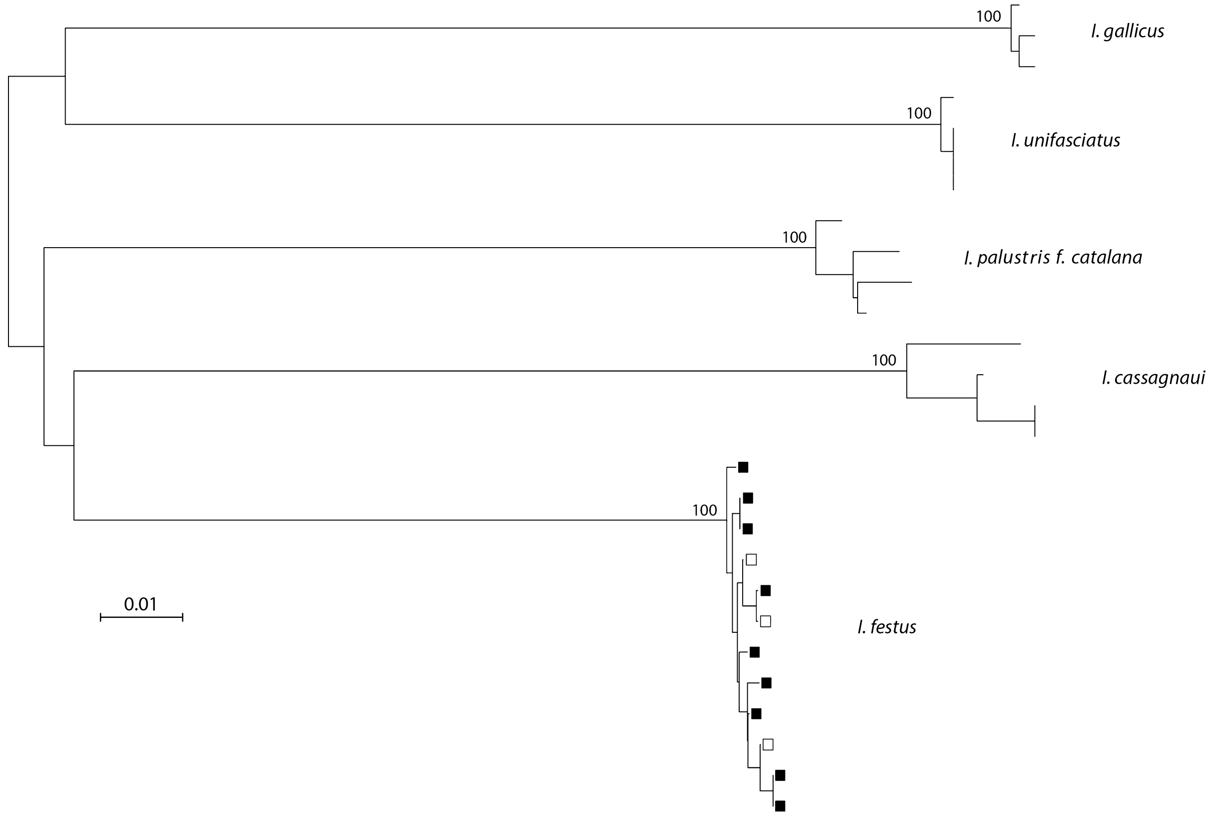


FIGURE 28. Neighbour-joining trees (K2P) based on COI for the four *Isotomurus* species and one colour form. 100% bootstrap support values are shown on branches. For *I. festus* **sp. nov.** black squares stand for 'banded' specimens and white squares for 'pales' ones.

Further study based on a larger taxonomic sampling and additional genes less prone to signal saturation than COI will be necessary to understand the relations between *I. festus* **sp. nov.**, the members of the '*antennalis'* group and morphologically similar taxa such as the two 'austral' forms, *Chionobora* Greenslade & Potapov, 2015 (Tasmania) and *Kaylathalia* Stevens & d'Haese, 2016 (Antarctic), which share several essential characters with the *'antennalis'* group of *Isotomurus* (Greenslade & Potapov, 2015, Stevens & d'Haese, 2016) and make the situation even more complex.

Regarding polychromatism, our molecular results support unambiguously that the two contrasting colour patterns of *I. festus* **sp. nov.** represent only a polymorphism within a single species. After analysing several *Entomobrya* species with contrasted patterns, Katz *et al.* (2015), concluded that "genetic divergence did not always correlate with colour pattern variation" and so that the diagnostic value of this character was species dependent, requiring its evaluation in each species. The result of the present study leads us to similar conclusions for the genus *Isotomurus:* colour pattern variations may either correspond to intra-specific polychromatism as in *I. festus* **sp.**

nov., or represent real diagnostic characters among closely related species as shown by Carapelli *et al.* (1995) who established the taxonomic value of colour patterns in several species of the genus based on genetic markers.

Given the large number of *Isotomurus* colour forms described in the first half of the XXth century and many synonymies subsequently proposed without any analysis of polymorphism in colour patterns (Gisin 1960, summarized in Potapov 2001), as well as the frequent co-occurrence of different colour forms in a same habitat (Carapelli *et al.* 1995b), the re-assessment of the taxonomy of the genus is unavoidable. Such a task might prove to be a long run one and molecular taxonomy can certainly help achieving it.

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