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An extreme case of epitoky in an Australian Collembolon: *Isotopenola perterrens* sp.n. (Hexapoda: Collembola: Isotomidae)

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> Abstract

Isotopenola perterrens **sp.n**. is described from a 40 year old *Eucalyptus* plantation in Victoria, Australia, and its occurrence in an adjacent site of remnant native vegetation is reported. Fully adult males are armed with numerous strong spine-like macrochaetae on lateral parts of head and body tergites and with fields of long bristles on latero-ventral and ventral areas of abdomen. Antennae of epitokous males are of normal shape but bear thickened chaetae. This is the second and most extreme case of epitoky recorded in the genus. The occurrence of sexual dimorphism, of which epitoky is a subset, is summarised for Australian Collembola. Environmental factors that appear to facilitate successful recolonisation of native fauna onto revegetated sites in Australia are proposed.

> Key words

Sexual dimorphism, revegetation, cyclomorphosis, ecomorphosis, reproductive cycle.

1. Introduction

The collembolan genus *Isotopenola* Potapov et al. (Isotomidae-Anurophorinae) was erected for a group of species from southern regions with habitus and some characters similar to the Eurasian genus *Subisotoma* Stach (Potapov et al. 2009) and of similar size of up to 2 mm. It was differentiated from *Subisotoma* by the presence of secondary granulation on the sterna and two ventral setaceous fields, one on each side of the mid line of the sternum of the third abdominal segment (sf-III). *Isotopenola* is known only from the Southern Hemisphere. Four species were included by Potapov et al. (2009) in the genus. Of these, three were from Australia, *loftyensis* (Womersley, 1934), *australis* (Womersley, 1934) and *delicata* Potapov et al., 2009; one was from southern India (Nilgiri Hills, 300 km SW Bangalore); and several probable species from New Zealand are not yet confirmed. One of these species, *I. australis*, exhibits sexual dimorphism.

Species of *Isotopenola* are found widely in subhumid and humid temperate climatic zones of Australia from the Eyre and York Peninsulas in South Australia to the Mt Lofty Ranges, across south eastern Australia, Tasmania and north as far as Atherton Tableland in Queensland as well as a single record from arid regions (MacDonnell Ranges, Northern Territory). It is most frequent in *Eucalyptus* forest leaf litter, moss and native *Poa* grasslands in temperate climates. On even more humid, cooler sites, it is sometimes replaced by species of *Cryptopygus* Willem (Isotomidae-Anurophorinae). For example, on Mt Lamington, Queensland, a species of *Isotopenola* is most abundant at 900 m while a species of *Cryptopygus* is only found at the summit of 1100 m (Greenslade & Kitching 2011).

Here we describe a new species of *Isotopenola*, *I. perterrens*, from a forty year old *Eucalyptus* plantation in southern Victoria and a nearby site of remnant native vegetation. This species exhibits extreme epitoky in fully adult males. The term epitoky, first described by Cassagnau (1952, 1955, 1956, 1958), was coined for species in which certain specimens show marked morphological and some internal changes with season and/or weather, realised during moulting.

2. Abbreviations and terminology

Institutes

MSPU	Moscow State Pedagogical University
SAMA	South Australian Museum Adelaide

Morphology

A–E (Fig. 4)	papillae on labial palp
A–H (Fig. 5)	ocelli
Abd.I–VI	abdominal segments I–VI
Ant.1–4	antennal segments 1–4
AO	antennal organ on third antennal segment
bms	basal microsensillum / -sensilla
d	dens
gen	genital opening
LM	lateral macrochaetae
lp	lateral process
LS	large spines
man	manubrium
ms	microsensillum / -sensilla
mu	mucro
PAO	postantennal organ
s	sensillum / sensilla
SS	small spines
sf-III	ventral setaceous field
t.ch.	tenent tibiotarsal chaetae
Th.I–III	thoracic segments I–III
u	unguiculus
U	unguis

Terminology for chaetotaxy used here is as follows: Ordinary chaetae are short, fine setae; they can be developed into short spines. Macrochaetae are longer chaetae and can be developed into bristles which are stronger and thicker, or further developed into strong spines also long. Sensilla (s) may be microsensilla and are constant and are fine, thin-walled setae.

3. Results

3.1. Description

Isotopenola perterrens n.sp.

Figs. 1–12

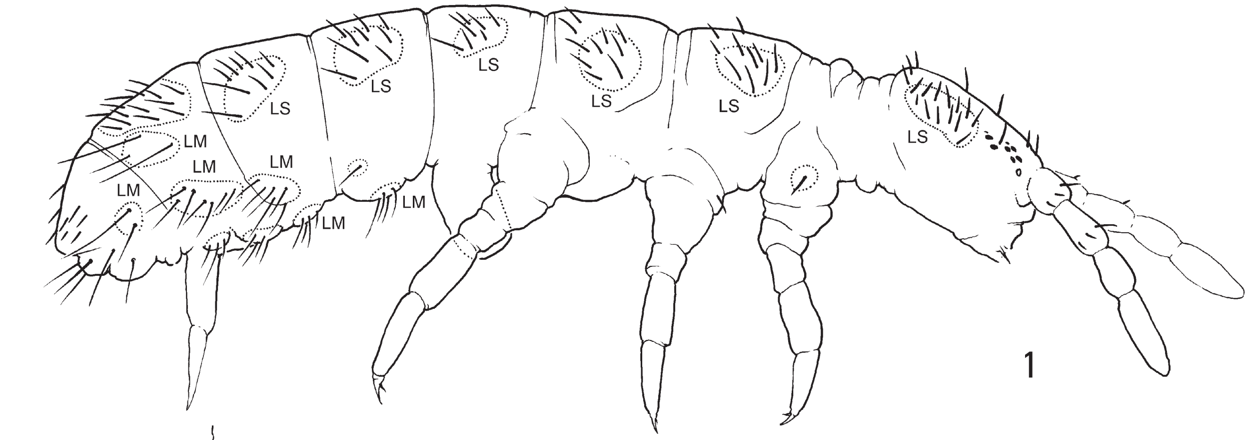
Type material. Holotype, epitokous male: Australia, Victoria, Mt Helen, 40 year old *Eucalyptus* plantation, leaf litter, sticks, bark, moss, leg. P. Greenslade, 6.xii.2009, 37°38.840′S 143°53.451′E, asl 502 m. – Paratypes: 8 specimens with same locality and date as holotype (3 epitokous); 7 specimens from the same locality, vii.2010, 37°37.810′S 143°53.45′E (none epitokous). – Deposition of holotype and 7 paratypes at SAMA, 8 paratypes at MSPU.

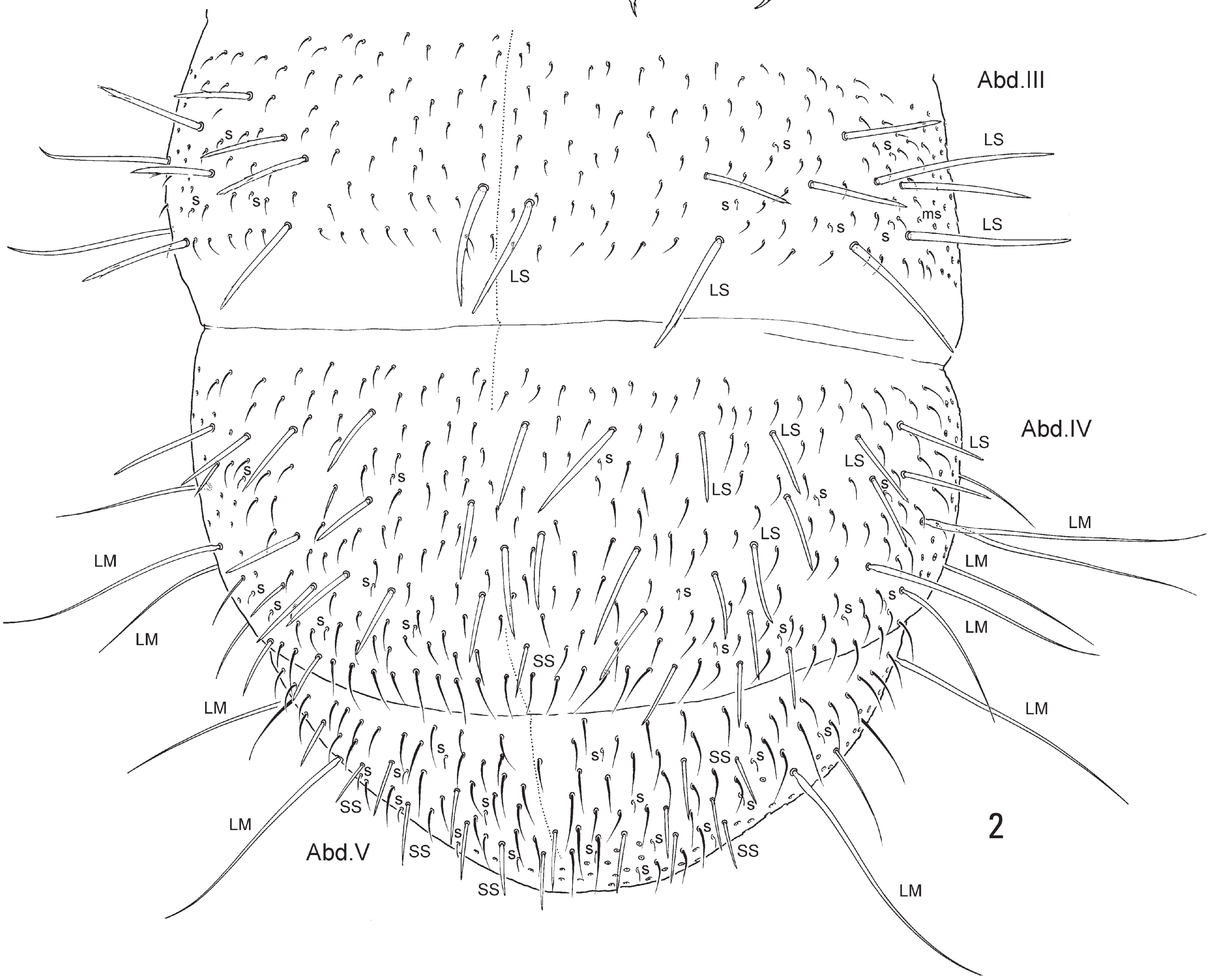
Type locality. Mt Helen, Ballarat, Victoria Australia.

Adult and subadult males and females of the same size, 1.5–1.8 mm. Colour blackish-blue, appendages paler. Body plump, with cryptopygy. Cuticle with small pits regularly scattered all over body. Lateral parts of head and thorax, intersegmental areas, the most part of venter with secondary granulation (Fig. 5). 8 ocelli[1] per side, G and H much smaller (half as long as others) and hardly visible. PAO widely elliptical, without constriction, 1.2–1.8 × as long as ocellus diameter and 0.4–0.7 × as long as Claw 3. Maxillary palp simple, 4 sublobal chaetae present. Labrum with 2/554 chaetae. Labial palp with all papillae A–E present, papilla A with 1, B with 3–4 (variable), D with 4, E with 4 guard chaetae, proximal chaetae 3 (Fig. 4). Basomedial field of labium with 4 chaetae. Ventral side of head with 4+4 post labial chaetae along ventral line (more rarely 5 or 6 on one side). Ant.1 with 16–21 (normally 19–20) common chaetae, 2 bms (dorsal and ventral) and 2 ventral sensilla (s), Ant.2 with 3 bms and 1 distal s, Ant.3 without bms and with 5 distal s, including one lateral in AO. Inner sensillum of AO clearly broadened, a little shorter than outer ones, additional sensilla absent. Ant.4 with numerous thin, differentiated sensilla, subapical organite very small, sometimes fully hidden in cuticular burrow, subapical microsensillum present.

All terga with dense cover of uniform, long or short ordinary chaetae (Figs. 2, 5, 8, 9), macrochaetae absent except on epitokous males with uniformly short ordinary chaetae and macrochaetae, non-epitokous

[1] In Collembola this term does not refer to the median eyes as is common usage for other Arthropoda, but to groups of fused ommatidia of the modified compound eyes; see Hopkin (1997).

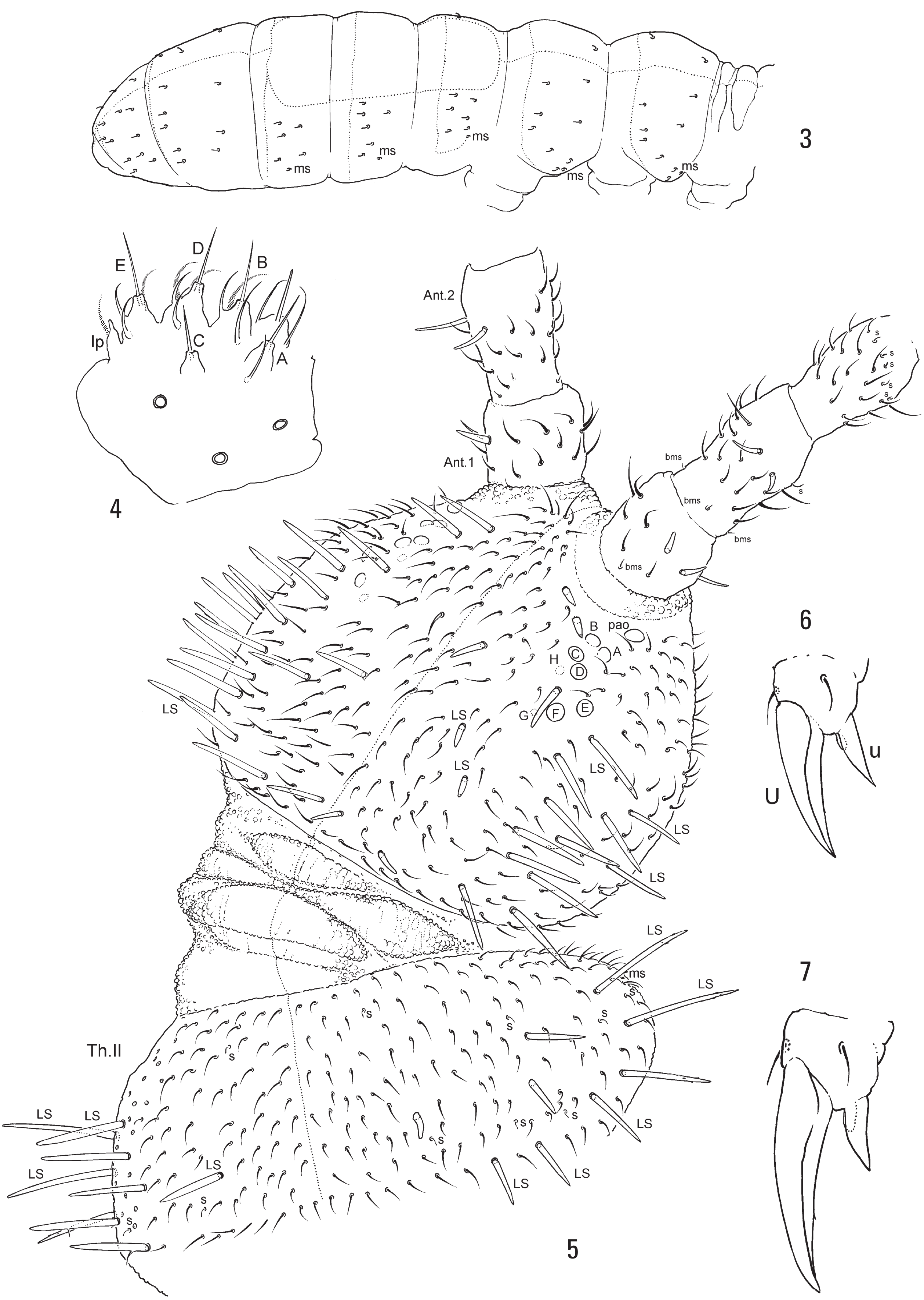




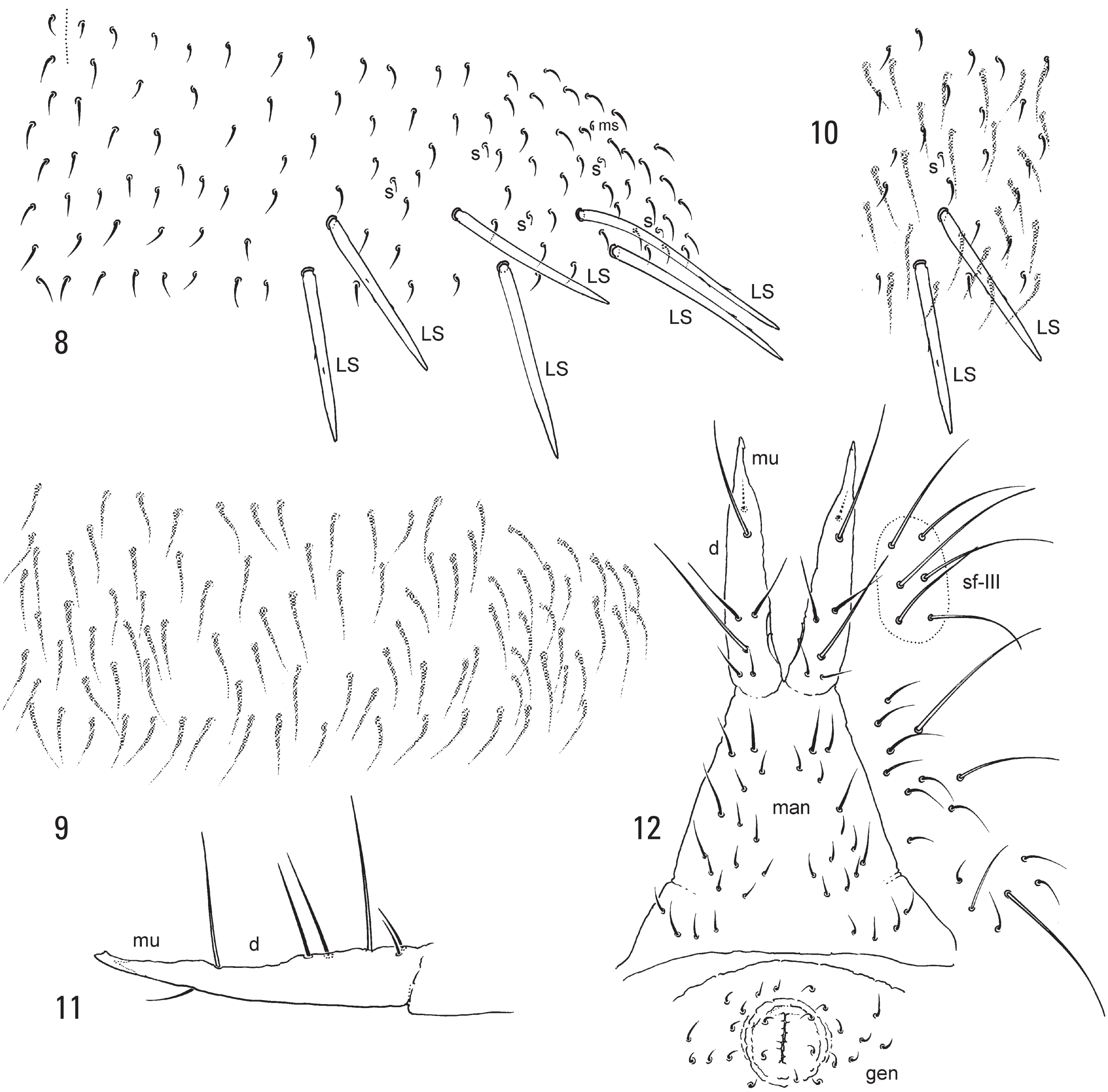
Figs. 1, 2. *Isotopenola* sp.n., epitokous male. **1**: Distribution of spines and macrochaetae on body (groups of lateral spines = LS and lateral and ventral macrochaetae = LM are marked). **2**: Dorsal chaetotaxy of Abd.III–V (the last segment is hidden under Abd.V).

males and females with uniformly long ordinary chaetae. Dorsal axial chaetotaxy of Th.II–Abd.IV as 7–10, 10–11/8–9,7–8,8–9,11–14. Tergal sensilla distinctly different from ordinary chaetae, short and slender, arranged in two irregular transverse rows, anterior and posterior (excluding lateral parts of Th.II, Th.III, and Abd.V), position and number variable. Total number of sensilla on Th.II–Abd.V 7–8,6–8/4–5(6),4–5(6),4–6,7–9,ca.9–10 (Fig. 3). The number of tergal microsensilla 11/111. Sternum of Th.III without chaetae.

Unguis with or without small tooth (Figs. 6, 7). Unguiculus shorter than unguis (unguiculus : unguis = 0.40–0.55). Tibiotarsi 1–3 with many proximal chaetae, tibiotarsus 1 with 24–26, tibiotarsus 2 with 26–28, tibiotarsus 3 with 33–37. Tibiotarsal tenent chaetae (t.ch.) 1, 2, 2, slightly clavate, longer than inner edge of unguis (Claw 3 : t.ch. = 0.7–0.8). Ven-



Figs. 3–7. *Isotopenola* sp.n., epitokous male. **3**: Distribution of (macro)sensilla and microsensilla on body (area on abdomen devoid of sensilla is marked). **4**: Labial palp (A–E – labial papillae). **5**: Dorsal chaetotaxy of head (A–H – ocelli) and Th.I–II (sensillum positioned most laterally on Th.II is not shown). **6, 7**: Apical part of leg 3 in female (6) and adult epitokous male (7).



Figs. 8–12. *Isotopenola* sp.n. **8–10**: Abd.I in epitokous male in ecdysis: old cuticle (8), new cuticle (9), area of tergite with "double" cuticle (10). **11**: Mucrodens, lateral view. **12**: Ventral chaetotaxy of Abd.III–V in epitokous male and furca (tenaculum not shown, submedial setaceous field marked).

tral tube with 4+4 lateral and 4–7 posterior chaetae, normally 4 in distal transversal row. Tenaculum with 4+4 teeth and one chaeta. Submedial fields on Abd. III sternum with 6–12 chaetae (sfIII), anterior part of furcal subcoxa with 9–15 chaetae (Fig. 12), posterior part with 14–18 chaetae. Manubrium without anterior chaetae, posterior face (Fig. 12) with 4–6+4–6 chaetae on laterobasal lobes. Dens with 1 anterior and 6 posterior chaetae in position common for the genus. 1 small basal posterior chaeta sometimes absent on one side. Mucro long, with 2 teeth (Fig. 11). Ratio of manubrium : dens : mucro = 4.1–5.9 : 3.1–4.6 : 1.

Fully adult males that have a conspicuous ejaculatory duct are strongly modified, mainly with regard to chaetotaxy. They are covered with numerous short chaetae as is normal but also armed with spines and bristles (Figs. 2, 5, 8). Straight spines are scattered all over the body with two types distinguished, large (LS) and small (SS). Large spines predominate and are arranged mainly in lateral parts of head, Th.II, Th.III, and Abd.I–III, where they are grouped into dorsolateral "brushes" (Fig. 1). The spines positioned more laterally in brushes may be longer and slightly curved (Fig. 2). Abd.IV is more regularly and densely covered with these spines. Abd.V and posterior edge of Abd.IV bear small spines. Single small spines are sometimes present among the large ones on all other tergites and head. One specimen with small spines distributed on

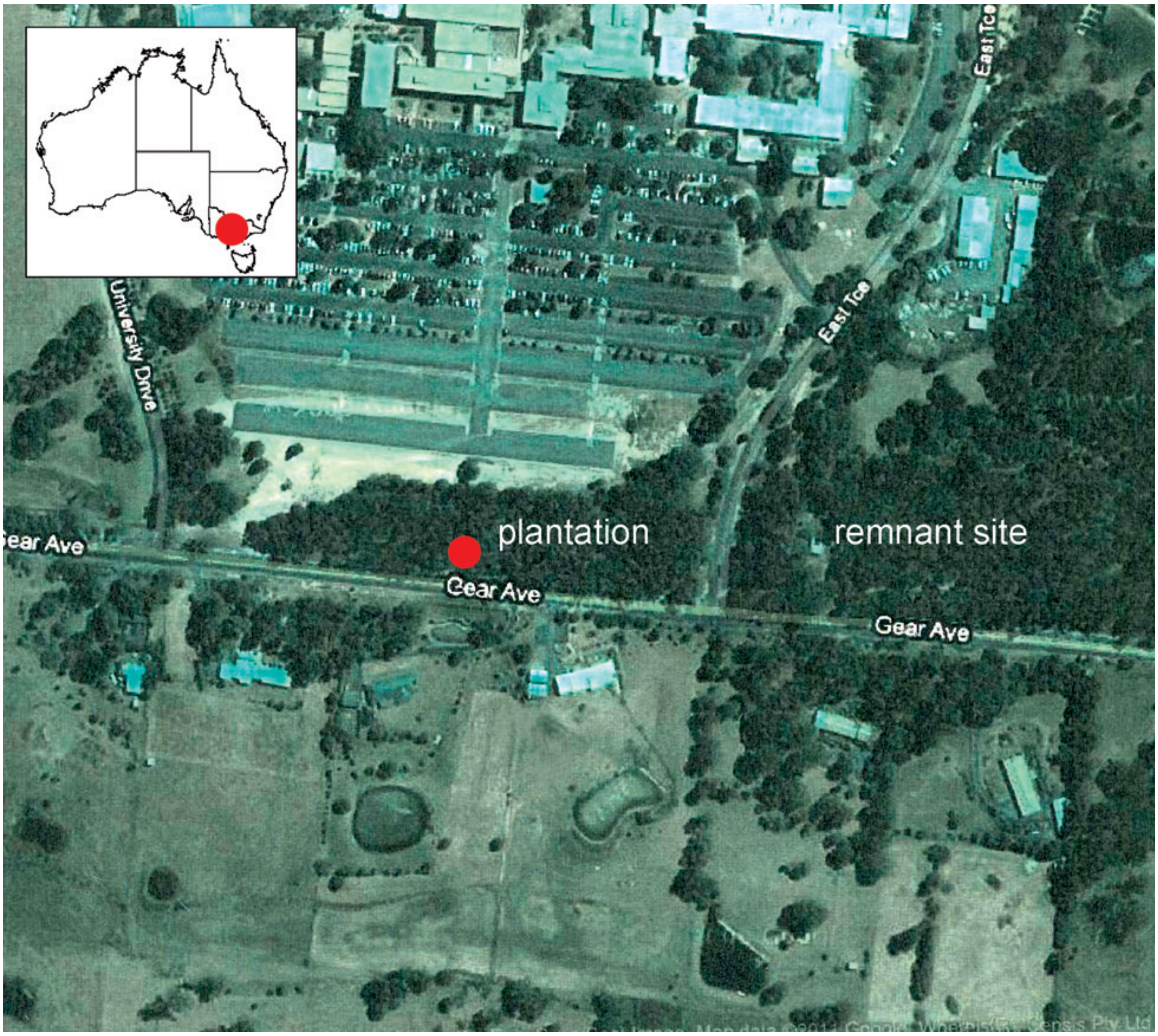


Fig. 13. Map showing location of type locality (plantation) and adjacent patch of remnant vegetation at Mt Helen.

posterior half of Abd.IV was observed. Depending on specimen, the position and number of spines vary (often asymmetrically) but they maintain the general pattern of distribution described above. Ordinary chaetae of the body are short resulting in the chaetotaxy of epitokous males being strongly differentiated into thick, straight, large spines and short chaetae (Fig. 8). This contrast is more striking on the thorax and anterior half of the abdomen. Lateral parts of Abd. IV and latero-ventral and ventral parts of Abd.II – VI bear long bristles arranged in groups (Figs. 1, 2). As these chaetae extend laterally the habitus of epitokous males appears to be more dorsoventrally flattened than in non-reproductive individuals. The unguiculus in epitokous males is somewhat shorter, i.e. ratio unguiculus : unguis = 0.37 – 0.44 in epitokous males and 0.5 – 0.54 in females and non-reproductive males (Figs. 6, 7). Chaetotaxy of females and non reproductive males is unmodified with numerous, both short and long, chaetae (as in fig. 97 in POTAPOV et al. 2009) as is common for the genus.

One male was observed in ecdysis from reproductive to non-reproductive instar exhibiting the transformation of strongly differentiated chaetotaxy with heavy spines to non-spiny, homogeneous "female" chaetotaxy (Figs. 8 – 10). This suggests that epitokous (reproductive) and non-epitokous (non-reproductive) stages are likely to alternate in the life cycle of the species. Modified males were found in December (summer), while non-reproductive females and males were observed in July (winter).

An additional character that differs between the sexes is the presence of two thickened, apically truncate spurs on the third pair of legs in males. Truncate spurs are present on legs of many species of Anurophorinae; however, they are always less well developed and similar in both sexes, so not a sexually dimorphic character.

Figs. 14 – 20. Photographs of habitats at Ballarat where *Isotopenola perterrens* were found. **14 – 16**: Type locality (plantation). **17 – 20**: Source area of remnant vegetation and part of the ground cover.

3.2. Distribution

Currently known only from the type locality and from a nearby remnant vegetation site (50 m apart) in Victoria (Australia) (Fig. 13). However, there are possible records from southern Victoria; these are unconfirmed as epitokous males were absent. Collections came from three sites carrying remnant vegetation in south eastern Victoria, all within 200 km of Ballarat, and were also made in autumn (March) but additionally in spring (August) (Greenslade et al. 2011).

3.3. Diagnosis

The new species belongs to the genus *Isotopenola* in having distinct secondary granulation on sterna and submedial setaceous fields ventrally on Abd.III.

Many characters of the post labial area, labial palp, tibiotarsi (with abundant chaetae), first antennal segment and body tergites are shared with *I. loftyensis*, which is known from a range of sites in the southern Mt Lofty Ranges of South Australia (Potapov et al. 2009). The new species differs from the latter species in having fewer sensilla on body with half to two thirds fewer depending on tergite. Epitoky is unknown in *I. loftyensis* but fully adult males have not been collected.

The second species of the genus with strongly modified reproductive males, *I. australis*, has a different type of epitoky. In this species the spines in males are weaker, denser and of subequal size. Reproductive females are also modified but less so; they also bear spines, but fewer and smaller ones (Potapov et al. 2009). The extent of epitoky in the genus *Isotopenola* is not yet understood and, as the phenomenon appears to be seasonally linked; collections throughout the year of other Australian and New Zealand species are needed.

3.4. Ecology

The plantation site at Mt Helen, south western Victoria (Fig. 13, 14 – 16), has a temperate climate with maximum temperatures of 21 – 24°C in summer and 9 – 12°C in winter. Rainfall averages just over 700 mm p.a., mainly falling in winter, but prior to the collection of epitokous males in 2009, rainfall in five of the six previous years had been lower than the average. However, the drought had partially broken with a heavy rainfall in late spring of 2009 (November), two weeks before the collections of epitokous males of *Isotopenola perterrens* were made. Soils are poor, being ancient sea floor of Ordovician age. Prior to 1970, when the university moved to the site, the land had been grazed but not cropped and, in the early 1970s, a grove of *Eucalyptus viminalis* and *Eucalyptus botryoides*, both native to Victoria, was planted between the road and the university car park; several species of *Acacia*, some not local, were included as a fast growing overstorey. The plantation has never been harvested (Fig. 14). The *Acacia* shrubs have almost completely died out with the closure of the canopy. The ground cover consists of a thick layer of leaf litter, bark and other rotting timber; some patches of mosses are also present (Figs. 14 – 16). Management is minimal and consists of spot spraying of weeds such as gorse, and cool, fuel reduction burning every 10 years in a mosaic pattern. The size of the plantation is 50 m by 200 m.

Adjacent to the plantation type locality (50 m upslope), is a large patch of remnant native vegetation (Fig. 13, 17 – 20), 300 m by 200 m, with a native grassy understorey carrying mainly the local *Eucalyptus obliqua*. In early March 2012 (i.e. after acceptance of this manuscript for publication) epitokous *I. perterrens* were found in leaf litter of this site. It is most likely the source area for the *I. perterrens* population in the nearby plantation.

Epitokous males were only found in summer (on the plantation: December) and in autumn (on the nearby remnant site: March) at Mt Helen. This is the same season as Chimitova & Potapov (2011) found epitokous males of *Subisotoma stepposa* in Russia, another species showing extreme modifications of sexually active and neutral males.

In a survey of 20 revegetated, untreated or remnant vegetation sites in Victoria in 2010, unconfirmed *I. perterrens* were found in autumn (March) in soil cores from three of the eight remnant vegetation sites, whereas none were found on the six revegetated and on the six untreated sites. No epitokous males were observed. The mean density of this species on the three remnant sites was 17,000/m^2. The revegetated sites were narrow, on average 10 m wide, only 8 – 12 years old and isolated from any areas of remnant vegetation (Greenslade et al. 2011). It is significant that the older and larger Mt Helen plantation, adjacent to a remnant site harbouring the same species (a likely source area), was able to support an abundant population of *I. perterrens* as did only remnant sites in the wider survey although some exotic Collembola were present there (*Hypogastrura* sp.).

Considerable funds have been spent in Australia in revegetating degraded lands in an attempt to promote native biodiversity (Greenslade et al. 2011). Although native soil invertebrates have not been shown to be able to colonise the young revegetated sites sampled in our survey, the presence of *I. perterrens* on this larger, older plantation site shows that given enough time, location near a source area, revegetated sites can support large, reproducing populations of at least some native species.

4. Sexual dimorphism in Australian Collembola

Several phenomena have been described in Collembola where morphologically different forms are present in adult individuals, some of which are reversible (Fjellberg 1976a,b, 1985). These are sexual dimorphism, epitoky, ecomorphosis and cyclomorphosis but the terms have not always been defined unambiguously and the difference between them has not always been stated unambiguously. Each phenomenon is initiated by a different stimulus, has a different duration and is experienced by different life stages and sexes. Sexual dimorphism describes any external morphological difference between males and females at any stage but usually only in adults (apart from differences in the genitalia). As a subset of sexual dimorphism, epitoky describes a morphologically different form displayed by males when they are in the reproductive but non-feeding stage. Cassagnau (1952, 1955, 1956, 1958) was the first to record the phenomen of epitoky, under which term he included ecomorphosis. This author also (Cassagnau 1986a,b) recorded 15 species of Isotomidae and 5 species of Hypogastruridae that exhibited ecomorphosis in southern France and described the phenology of the different forms.

In Australia, epitoky in Collembola is likely to be more widespread than current records suggest. For instance the phenomenon has been observed in a species of *Cryptopygus* Willem from Tasmania (P. Greenslade, unpublished observations). Moreover, males of all *Isotopenola* species could be epitokous. The phenomenon may be density dependent: Chimitova & Potapov (2011) showed that the presence of epitokous males of *Scutisotoma stepposa* (Martynova) is linked to population density and so one hypothesis is that epitoky could give an advantage in competition between males when population density is high. Ecomorphosis includes some morphologies similar to epitoky, in which development of spines is involved, but also other structures. However, it is initiated instead by a change in weather from the cool, moist, conditions to dryer, hotter conditions. All stages of a species respond, males, females and immatures. Alternatively, cyclomorphosis is instigated by the regular change in seasons to the cold, often arid, conditions of winter from more favourable summer conditions and vice versa (Fjellberg 1976a,b). There have been cases observed where species appear to permanently retain the cyclomorphological form after permanent changes in climate to continuously cold or continuously warm.

Palacios-Vargas & Castaňo-Meneses (2009) in a review of sexual dimorphism in Collembola only listed a selection of examples. None were Australian although sexual dimorphism *per se* in Australia is common in epigaeic Symphypleona, particularly Bourletiellidae, such as in the genus *Corynephoria* Absolon, where males are normally smaller and with a different, usually a darker, colour. In *Bourletides wallacei* Betsch & Massoud, 1972, the males have modified antennae as well as a protruding tubercle dorsally on the head. The males of each of the four species of *Nasosminthurus* Stach (Bourletiellidae) possess quite different morphological peculiarities: either exceptionally long antennae (*N. nigridorsalis* (Womersley, 1932)), or spines on the antennae (*N. sigmoides* (Womersley, 1933)), or a nasal organ similar to that of *Pseudobourletiella spinata* (MacGillivray, 1893) (*N. dimorphus* (Womersley, 1932)), or a field of dense, long, fine chaetae laterally ('cheeks') on the head (*N. analis* (Womersley, 1939)). The world wide *P. spinata* has been found sporadically in Australia on still fresh water lagoons along the River Murray in South Australia (Kingston Common, Banrock wetlands) and in New South Wales (reed swamp, Lemma, Georges River). It possesses several other morphological similarities with the Australian endemic genus, *Nasosminthurus* (P. Greenslade, unpublished results).

As recorded in detail by Palacios-Vargas & Castaňo-Meneses (2009) and included references, the males of aquatic and terrestrial Sminthurididae invariably possess a complex arrangement of spines and lobes on the antennae. An extreme form is displayed in the males of the rare *Pygicornides horridus* Betsch, 1969, which have not only an elaborate array of spines and tubercles on the antennae, but also a pair of dorsal thoracic vesicles and long tentacles arising from abdomen VI. This species is found in hot dry regions in north west Western Australia but only appears after a heavy rainfall event. Species of marine littoral Neanuridae, such as *Pseudanurida* Schött, and Isotomidae, such as *Archisotoma* Linnaniemi and *Psammisotoma* Greenslade & Deharveng, have less extreme morphological modifications such as an elongated tip of abdomen, or feathered spines on tibiotarsal III (Strenzke 1955; Murphy 1971; Thibaud 1993; Fjellberg 2007).

One form of sexual dimorphism not commonly encountered is that of the extreme elongation of abdomen VI in females of canopy inhabiting *Epimetrura* spp. such as *E. rostrata* (Greenslade & Sutrisno) (Entomobryidae) in southern Queensland, presumably associated with egg laying into bark (Greenslade & Sutrisno 1994). Among Orchesellinae (Entomobryidae), all males in the Australian endemic genus *Australotomurus* Stach possess spines and/or clubs on the antennae and sometimes also on the labium. Australian Poduromorpha do not exhibit conspicuous sexual dimorphism. In the males of a few undescribed species of Odontellidae, there are fields of small spines ventrally on abdomen II; sometimes a small pocket or slit is present (P. Greenslade, unpublished results). A similar type of sexual dimorphism is seen in males of some Onychiuridae, such as the introduced *Orthonychiurus folsomi* (Schäffer).

It is important to be aware of these numerous examples of polymorphism among Collembola when describing or identifying individuals to species in order to guard against new taxa being erected to encompass what might be considered new forms.

5. Acknowledgments

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