

REVISION OF *FOLSOMINA* DENIS  
(COLLEMBOLA: ISOTOMIDAE) WITH A DESCRIPTION  
OF A NEW SPECIES FROM SOUTHEAST ASIA AND  
THE PACIFIC REGION AND COMMENTS ON ECOLOGY

Penelope Greenslade

*Division of Entomology, CSIRO, GPO Box 1700, Canberra, ACT 2601, Australia.*

**ABSTRACT.** - The four described species of the pantropical and Australasian genus *Folsomina*, *F. yosii* Lawrence, 1969, *F. onychiurina* Denis, 1931, *F. yongxingensis* Chen, 1987 and *F. wuyanensis* Zhao and Tamura, 1992, are reviewed. *Folsomina yosii* Lawrence, 1969, is a junior synonym of *F. onychiurina* Denis, 1931, and *F. onychiurina* Denis sensu Lawrence, 1969, is a different species here named *F. lawrencei*. A new species, *F. infelicia*, is described and recorded from Malaysia, Thailand, Sumatra and Fiji. A key is given to species in the genus and notes on species distribution and on biology are included. All species appear to be parthenogenetic and show progressive adaptations towards soil living.

**KEY WORDS.** - *Folsomina*, new species, Isotomidae, Collembola, Malaysia.

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INTRODUCTION

Adaptations to a euedaphic way of life are commonly seen among collembolan taxa as many species in the Class are soil-living. The morphological features associated with this way of life are progressive loss of pigment, regression of ocelli, reduction in length and sometimes loss of some setae and appendages, small body size, vermiform body shape, and development of the chemosensory system of S setae on the antennae. Life history characteristics of deep-soil-living Collembola have been documented (Petersen, 1980) and include an extended duration of development from egg to adult, fewer but larger eggs and progeny, aseasonal reproduction, a lower metabolic activity and parthenogenetic reproduction.

*Folsomina* Denis, 1931, is an example of a soil-inhabiting genus in which all species appear to be parthenogenetic and show different degrees of morphological adaptation to soil living. The genus was proposed for a species of Isotomidae from Costa Rica, *Folsomina onychiurina* Denis, 1931. The genus is clearly distinct from others in the family in its lack of postantennal

organ and ocelli, fusion of the distal three abdominal segments and the form of the sensory organ on antennal segment IV. Additions to the description were given by Denis (1933) based on additional material from Costa Rica. *Folsomina onychiurina* has been recorded from North, Central and South America, Africa, India, Asia, Oceania, Australia and New Zealand (Winter, 1963a,b; Salmon, 1964; Lee, 1977; Maeda & Tanaka, 1982; Suhardjono, 1989). Gisin (1960) and Christiansen & Bellinger (1980) treated *Folsomina* as a subgenus of *Folsomia* Willem although the latter authors stated that they did so as a "matter of convenience" and later (Christiansen & Bellinger, 1992) accepted its generic status. The only new species described in the genus since 1931 have been *Folsomina yosii* Lawrence, 1969 from the Solomon Islands, *Folsomina yongxingensis* Chen, 1987, and *Folsomina wuyanensis* Zhao & Tamura, 1992, both from China. As well as *F. yosii*, Lawrence (1969) recorded *F. onychiurina* from the Solomon Islands, which he redescribed from material collected at a number of localities in the islands.

As originally described, *Denisia falcata* Folsom, 1932, from Hawaii, the only member of the monobasic genus *Denisia* Folsom, 1932, has some similarities to *Folsomina*, but seemed to belong in a different genus since it has a postantennal organ. After examining syntypes, Lawrence (1969) concluded that *D. falcata* was based on a composite of two specimens belonging to different species in the genera *Isotomiella* and *Folsomina*, and he designated as lectotype a specimen of *Isotomiella minor* (Schäffer, 1896) from the type series to "prevent further confusion" (Lawrence, 1969).

Christiansen and Bellinger (1992) noted that *F. onychiurina* is almost certainly the same species as that described by Lawrence (1969) as *F. yosii* and that the *F. "onychiurina"* redescribed by Lawrence (1969) in the same paper appears to be another species. Examination of Denis' and Lawrence's descriptions and figures confirmed these ideas (Greenslade 1994) and *F. onychiurina* sensu Lawrence, 1969, is here proposed as *Folsomina lawrencei*. The holotypes of both species have now been examined as well as Solomon Islands material determined as *F. onychiurina* by Lawrence. A new species of *Folsomina* is recognised in collections from Malaysia, Thailand and Fiji, which is intermediate between *F. lawrencei* and *F. onychiurina* in morphological adaptations to life in the soil, and is described here. Bedos (1994) noted that this undescribed species also occurs in Sumatra. Comments are made on the distribution and biology of these species and the validity of genera consisting only of parthenogenetic forms.

Abbreviations for repositories: ANIC: Australian National Insect Collection, Canberra, Australia; BMNH: The Natural History Museum, London; MNH: Muséum National d'Histoire Naturelle, Paris; SAMA: The South Australian Museum, Adelaide, South Australia.

## TAXONOMY

### *Folsomina* Denis, 1931

*Type species.* - *Folsomina onychiurina* Denis, 1931: 128, by monotypy.

*Description.* - White; elongate body, abdomen IV, V and VI fused; clothing of smooth, pointed setae, upright macrosetae fairly well differentiated from ordinary setae, becoming

longer posteriorly, thorax II to abdomen IV-VI with 1 1/2, 3, 3, 10 pairs respectively; number, type and position of S setae constant for all species known, with thorax II to abdomen IV-VI, 4, 3/2, 2, 3, 5 pairs respectively including a large pair of cylindrical S setae (sl) dorsolaterally on abdomen V; abdomen VI with 4-6 very fine short setae (gl of Deharveng and Oliveira 1990); cuticle with fine rectangular granules, no pseudopores or epicuticular canals visible.

Ocelli and postantennal organ absent; antenna IV with a pair of large oval, retractable, sensory vesicles with three ribs on dorsal surface inserted in a pit surrounded by 3 well developed S setae distally on antenna IV, organite (or) and so setae present with about five thin cylindrical blunt "soies mousses" more basally; apical bulb and pin seta absent; antenna III organ with two small pegs, short guard seta and a ventral S seta similar in size to dorsal pegs; antenna II with 18 ordinary setae, one S seta and 3 microsetae; antenna I with 13 ordinary setae, 2 microsetae and 2 S setae; 4 preclypeal setae; anterior margin of labrum with 4 setal-tipped teeth and 4, 5, 5 setae of which the most anterior one or two rows arise from tubercles; mouthparts well sclerotised; maxillary palp bifurcate with 3 sublobes; maxilla with 3 strong teeth; head with 3 + 3 setae ventrally along mid line.

Ventral (sternal) setae absent; tibiotarsi with 21 - 27 setae; clavate tenent hairs absent; empodial appendage with two narrow lamellae and no apical setae; claw without teeth; ventral tube with 1 + 1 anterior setae, 4 + 4 distal setae and 3-4 posterior setae; rami tenaculum with 4 + 4 teeth and one seta; manubrium with 1 + 1 anterior distal setae and 9 - 13 posterior setae; dens with a few slight crenellations medially; mucro with 1 - 3 teeth and no seta. Males not observed.

\* In their generic diagnosis Christiansen and Bellinger (1992) quote the mucro as being sickle-shaped but this is only true for *F. onychiurina*.

**Distribution.** - Pantropical and southeastern Australia.

**Remarks.** - *Folsomina* is a member of the subfamily Anurophorinae as indicated by the absence of a postantennal organ, the possession of anterior spinose setae on the labrum and of 6 S setae on antenna IV. It differs from all other isotomid genera in the possession of large, oval, retractable, ribbed vesicles on antenna IV. From their position, these vesicles appear to have arisen by enlargement of two distal S seta. *Isotomiella* Bagnall also possesses six enlarged S setae distally on antenna IV, and *Folsomina* is similar to *Isotomiella* also in lacking ocelli but differs from it in the fusion of abdomen IV and V, in the arrangement of S setae on the body and the lack of ciliated setae.

The S setae on the body are of three types; cylindrical, dagger-shaped or fine and pointed and were figured by Lawrence (1969, Fig. 12 p. 551; Fig. 20 p. 553) for both *F. onychiurina* and *F. yosiii* sensu Lawrence now *F. lawrencei*. The relative lengths of the S setae compared to the ordinary setae are constant within species but differ between species although the cylindrical setae on abdomen V vary slightly in length and thickness within a species. The revised nomenclature for S setae (Oliveira & Deharveng, 1990, Deharveng & Oliveira, 1990) is adopted here and their disposition and form for all body segments is given in Table 1. Specific differences lie in the number of ordinary setae between the S setae on each segment.

Table 1: Number, position, type and distribution of S setae on species of *Folsomina* per half tergite.

Sensory seta	spe	sl	sv
Thorax II	1	3	
Thorax III	1	2	
Abdomen I	1	1	
Abdomen II	1	1	
Abdomen III	1	1	1
Abdomen IV			
Abdomen V	2	1	2

*Folsomina infelicia*, new species

(Figs. 1-7, Table 2)

**Material examined.** - Holotype - slide mounted: WEST MALAYSIA: Negri Sembilan, Labu Oil Palm Estate, soil, 1977-78 (Vythilingan) (SAMA 22618).

Paratypes - 7 specimens, slide mounted, same data as holotype (SAMA).

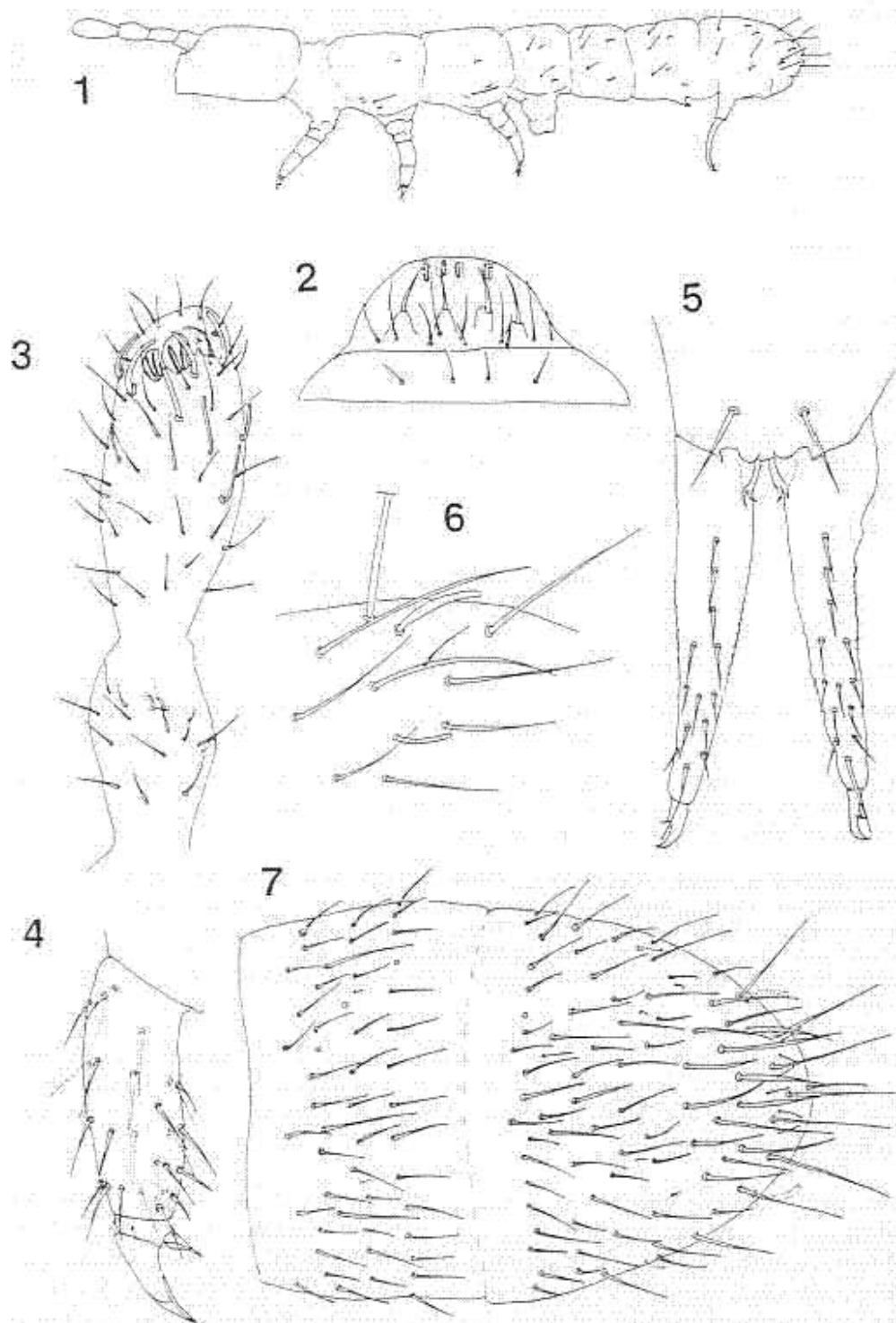
**Other material examined.** - FIJI: sample 1 (preadult) soil, 1977 (Edwards) (SAMA); THAILAND: Doi Inthanon, leaf litter, 1989 (Bedos & Deharveng CM44) (SAMA); INDONESIA, Sumatra, Rantau Pandan, primary forest, 1991 (Bedos & Deharveng).

**Description of adult Female.** - Size up to 0.75 mm; cylindrical body; clothing of fine smooth setae with macrochaetae fairly well developed, over twice the length of an ordinary seta on abdomen VI, arranged as follows from thorax II to abdomen IV-VI, 1,1/2,3,3,10; S setae very short, less than one third the length of ordinary setae on thorax II, type as in Table 2; number of setae between S setae from thorax II to abdomen IV - VI 6,8/2,2,2,4 ordinary setae between spe setae; axial setae from thorax II to abdomen IV-VI 6,5/3,3,3,5 + 111 unpaired on fused abd IV,V and VI.

The two antenna IV sensory vesicles oval in shape, external surface with three strong ribs; 6 well developed S setae on antenna IV, four thick, two rather thinner; labrum with 2 inner setal-tipped teeth and 2 large lateral teeth; anterior row of labral setae arising from tubercles, two of the teeth on the maxilla of equal size.

Tibiotarsi I, II, III with 21, 21, 25 setae; furcal base with 3,4 or rarely 5 setae; posterior surface of manubrium with 11 setae; dens slightly longer than the manubrium, with 4 posterior setae and 12 or 13 (rarely 11) anterior setae, most distal seta nearly reaching to tip of mucro; mucro with two teeth; abdomen V with 1 large and 1 small fine seta between two large cylindrical sl and sv setae; abdomen V and VI with two or three pairs of dorsal setae thick and spine like; abdomen VI with 7 very fine, short, medial setae dorsally, a, very short, m, a macrochaeta and p, an ordinary seta; genital aperture of female crescent-shaped with slightly sclerotised borders.

**Ratios.** - Antennae:head diagonal = 1:1; thorax II S setae:ordinary setae = 1:3.4; manubrium:dens:mucro = 5:6:1; abdomen VI spe seta: fine (gl) setae:ordinary setae:macrochaetae = 1:2:4:7; abdomen VI a,m,p, = 1:4.5:2.



Figs. 1-7. *Folsomia infelicia*, new species. 1, whole animal showing position and number of macrochaetae and S setae; 2, labrum and preclypal setae; 3, antenna III-IV; 4, tibiotarsus III; 5, anterior view of dens and distal portion of manubrium; 6, sl and sv setae of abdomen V-VI; 7, dorsal view of abdomen III-VI.

Table 2. Sensory clothing of *Folsomina infelicia* new species per half tergite.

Types of S setae	Thorax II	Thorax III	Abdomen I	Abdomen II	Abdomen III	Abdomen IV-VI
Cylindrical, short	1 spe <sup>*</sup>	1 spe <sup>*</sup> 2d	1spe <sup>*</sup> 1d	1spe <sup>*</sup>	1spe <sup>*</sup> 1sv	2spe <sup>*</sup>
Cylindrical, medium	1d					2d
Cylindrical, large				1sv		1sv
Thin, fine, short, pointed	1d					
Micro S seta, dagger-shaped	1d				1d	

\*1. In row anterior to p row.

\*2. In fourth row of setae, 6 setae apart, and each seta of the pair, 1 setae apart laterally.

Comment: Specimens from Sumatra are rather larger than those from Fiji and Malaysia and in addition to the 4 basal posterior setae on the dens possessing two further very fine, short setae more distally, the length of these microsetae being variable.

### *Folsomina lawrencei*, new species

(Fig. 8, Table 3)

*Folsomina onychiurina* sensu Lawrence, 1969 (p. 551 figs 12-19) (nec Denis, 1931).

**Material examined.** - Holotype - slide mounted: SOLOMON ISLANDS: Guadalcanal, Mt Ausien, leaf litter and soil, rainforest, 10 Aug.1966 (Greenslade) (21811) (BMNH).

Paratypes - same locality, habitat data and collector as holotype but 13 Oct.1963 (11342) (BMNH), Feb.1966, (21121) (BMNH), 7 Mar.1966 (21312) (BMNH), (22312) (BMNH), Mar.1966 2 specimens (21354) (SAMA), 28 Mar.1966 (22469) (BMNH), 10 Mar.1966 (21804) (SAMA).

**Other material examined.** - SOLOMON ISLANDS: Malatoha, Honiara, Guadalcanal; Dala, Malaita; Small Malaita; Tatamba, Buala, Ysabel; Yandina, Russel Is.; Wagina, Choiseul; Rendova, Munda, New Georgia (all BMNH). AUSTRALIA: Torres Strait, Murray Is, litter vines and bamboo forest, 17 Jul.1974, (Cameron) (SAMA). NEW HEBRIDES: Erromanga, ca 2 km NNE of Nuangkau River bridge, 18° 53'S, 169° 12'E, 200 m, mixed mesophyll evergreen vine forest, soil 4-8 cms, 3 Aug.1971, (Lee NH 33) (SAMA).

The holotype was chosen from slide specimens mounted by Lawrence and labelled *Folsomina* sp. cf. *F. onychiurina*. The specimen most closely resembling his figures (Lawrence, 1969: Figs. 12-19) and the description was chosen as holotype. Only specimens examined in the current study are listed here.

**Description of adult female.** - As in Lawrence (1969) for '*F. onychiurina*' adult with additional mensural and sensorial features as given below. Size up to 1 mm in length, body elongate, cylindrical; clothing of smooth pointed ordinary setae, macrochaetae not well developed, arranged as follows from thorax II to abdomen IV-VI, 1,1/1,2,2,10; S setae on body and antennae fairly long and slender from two thirds length of ordinary setae on thorax II and slightly longer on abdomen V; number of setae between S setae from thorax II to abdomen III as follows: 8,8/8(7),8,9; axial setae from thorax II to abdomen IV-VI 6(7),4/4,4,3,10 (1 unpaired).

Table 3. Sensory clothing of *Folsomina lawrencei*, new species per half tergite

Segments	Thorax II	Thorax III	Abdomen I	Abdomen II	Abdomen III	Abdomen IV-VI
Types of S setae						
Cylindrical, medium, long	1sl	1sl	1sl	1sl	1sv	
Cylindrical, long, thick						1sl 1sv
Thin, pointed, medium long	1spe	1spe	1spe <sup>2</sup>	1spe	1spe	2spe <sup>2</sup>
Short, thin, pointed	1sl	1sl				
Dagger-shaped	1sl					

\*1. Positioned in 4th row of setae.

\*2. Positioned in middle row, 8 seta between s<sup>+</sup> setae.

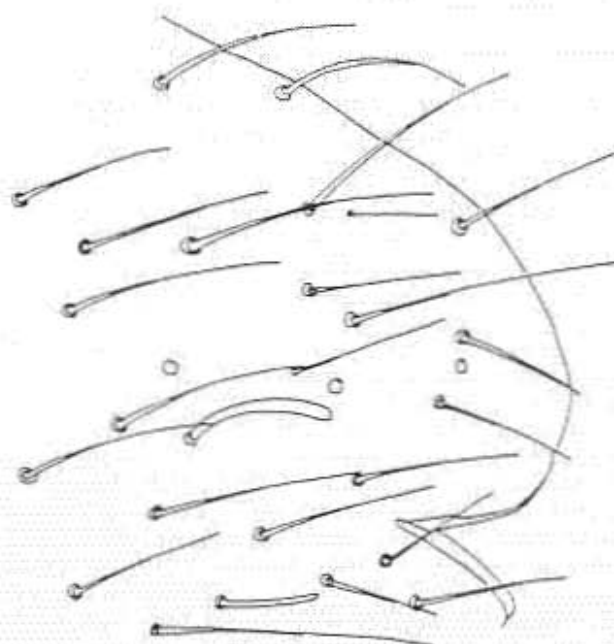


Fig. 8. *Folsomina lawrencei*, new species sl and sv and distal medial fine setae of abdomen IV-VI.

Antenna IV sensory vesicles slightly more elongated than in other species, oval and with three ribs; S setae fairly slender; labrum very well developed with 4 strong, nearly equal teeth on anterior margin, and spine-like setae in rows a and m (Fig. 10); mouthparts heavily sclerotised, maxilla with three teeth of different sizes.

Tibiotarsi I, II, III with 21, 21, 25 setae; furca inserted ventrally to abdomen IV; furcal base with 3/3(2) setae; posterior surface of manubrium with 13 setae; dens equal or less than one and a half times length of manubrium and with 7 anterior and four posterior setae, most distal of these longer and stronger than others, extending to halfway along mucro; most basal posterior setae of dens 2.5 times longer than the adjacent seta; mucro with 2 teeth; abdomen V sl seta long and cylindrical; the two setae between the two cylindrical sl and sv setae on abdomen V of equal size; abdomen VI with 2 + 2 very fine, long, medial setae; abdomen VI with a<sub>and m</sub> seta apparently absent in specimens examined.

**Ratios.** - Antennae:head diagonal = 7:9; thorax II: spe setae:ordinary setae = 1:1.5; manubrium:dens:muco = 3.5:3.7:1; abdomen VI: spe seta: fine median setae:ordinary setae:macrochaetae = 2:1:3:5

*Folsomina onychiurina*, Denis

(Fig. 9, Table 4)

*Folsomina onychiurina*, Denis 1931: 128.

*Folsomina yosii* Lawrence, 1969: 552 (syn. Greenslade, 1994: 74).

**Material examined.** - Holotype - 1, slide mounted: COSTA RICA: Orizuaço, Dec. 1911, Mat Sub 1930 Tf (MNH).

Paratypes - 20 slide mounted specimens, COSTA RICA: Aparicán, Aug. 1931 C.R. 1932 No. 6 (MNH).

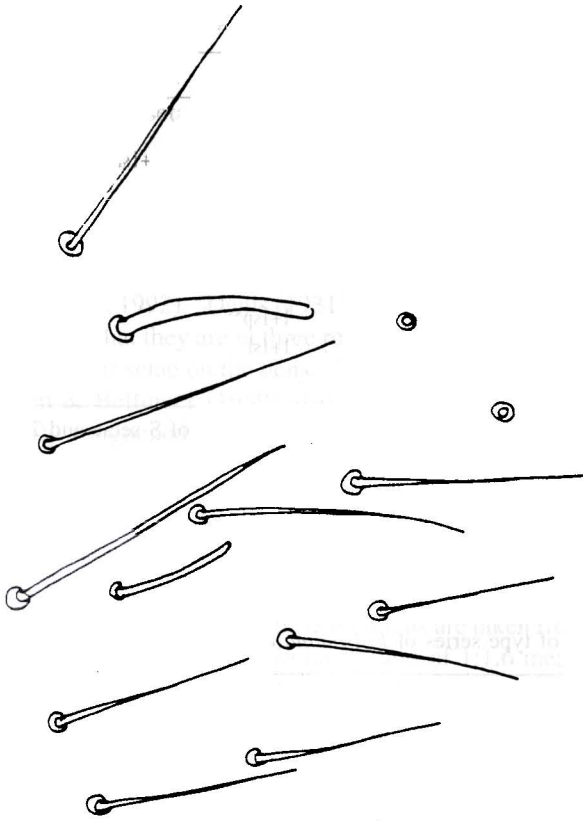
**Other material examined.** - labelled "cf. *Folsomina yosii*, SOLOMON ISLANDS: Guadalcanal, nr Honiara, Lungu, 28 Jun. 1965., (Lawrence) Roy. Soc. Exped., BM 1966-1 (BMNH). NEW HEBRIDES: soil core sample 33.0-4 cms 34.0-4 cms x 2, 4-8 cms, 35.0-4 cms, 36.0-4 cms, 4-8 cms. (Butterfield) (SAMA). PACIFIC IS: Niue, Vaupapau, 19 Jul. 1977 (Edwards) (SAMA); Ellis Is, Tivalu, banana silen, 8 Aug. 1977 (Edwards) (SAMA); Samoa, Alofar, cabbage, 22 Jul. 1977, Tiavi, cabbage, (Edwards) (SAMA). AUSTRALIA: Queensland, Great Barrier Reef, Swain's Reef (SAMA); Riversong West (SAMA); Frigate Cay (SAMA); One Tree Is. *Pisonia* leaf litter, soil (King) (SAMA); Cooloola, Warrawonga, leaf litter (Greenslade) (SAMA); Northern Territory, 3 k NE Jabiru (Morton) (SAMA); Manbulloo, site 8 1a, soil core, unburnt site (Mott) (SAMA); soil core, site 8 1b, soil core (Mott) (SAMA); Kunoth Paddock, ungroved mulga, leaf litter (Greenslade) (SAMA); Victoria, Walpeup, soil under wheat, (Longstaff) (ANIC); South Australia, Kangaroo Island, Rocky River, sandy mallee (Greenslade) (SAMA); Narracoorte Caves Reserve, leaf litter (Greenslade) (SAMA); Robe, leaf litter under *Leucopogon* (Greenslade) (SAMA); Robe, dune slope pitfalls, (Greenslade) (SAMA); Western Australia, Weelawadji, (SAMA); Dwelling Up, soil, (Postle) (SAMA); Gnaragar, Victoria, Healesville, Cooranderk Reserve, (Hardy) (SAMA); New South Wales, 1.6km S of Coolac, Berlesate ANIC 252, river-bank woodland (Mitchell), (ANIC); Urbenville, tall wet Eucalyptus woodland, (Greenslade) (SAMA); Norfolk Is, Moo'oo litter (Greenslade) (SAMA), Philip Island, above Moo'oo stone, (Greenslade); Dorrigo, Bellingen, leaf litter (Weir) (SAMA); Legume 20 k E, high altitude rainforest leaf litter, (Greenslade) (SAMA); Cordeaux, open forest, (Molton) (SAMA); SE Kyogle, Firdon's Creek, leaf litter, rainforest (Greenslade) (SAMA); Narrabri, ACIAR cotton fields (Lyton Hitchins) (ANIC), Harden, wheat paddock, soil cores, 1994-96, Cowra, wheat paddock, soil cores. SULAWESI: nr Kotamobagu, Lolak, mangroves, Sept. 1985 (Greenslade) (SAMA). MALAYSIA: Negri Sembilan, Labu Oil Palm Estate, soil, 1977-78, (Vythilingan) (SAMA).

(Dates and habitats available from author for Australian material. Also not included are the Solomon Islands records given in Lawrence (1969).

**Description of adult female.** - As in Lawrence (1969), except for the following additions, emendations and mensural characters. Body size up to 0.65 mm long, cylindrical, distally slightly broadened, abdomen distally rounded; clothed in simple setae with distinctly longer macrochaeta, thorax II to abdomen IV-VI with 2 + pairs on each segment. Cuticle consisting of densely arranged rectangular granules over all body.

Antenna IV sensory vesicles rounder and smaller than those of *F. infelicia*; ss of antenna IV as in Fig. 10, antenna III with range of ventral blunt cylindrical setae laterally; labrum narrow with 2 small spine-like internal teeth and two external broad teeth; 3 sublobal hairs; S setae moderately long, just under half the length of ordinary setae on thorax II and abdomen IV; tibiotarsus with 21, 21, 27 setae; abdomen V with 1 large and 1 small fine seta between two large cylindrical S setae; manubrium with 13 setae; dens much longer than manubrium;





Figs. 9. *Folsomina onychiurina* Denis. 12, S setae of abdomen IV-VI.

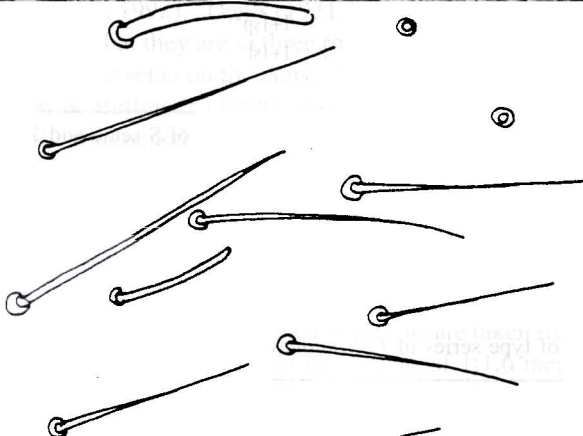
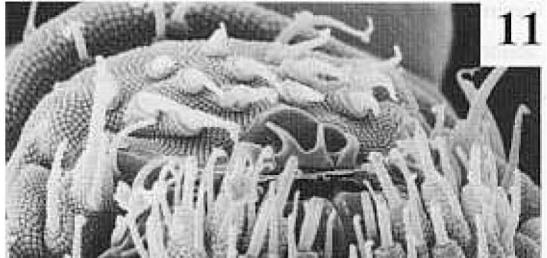
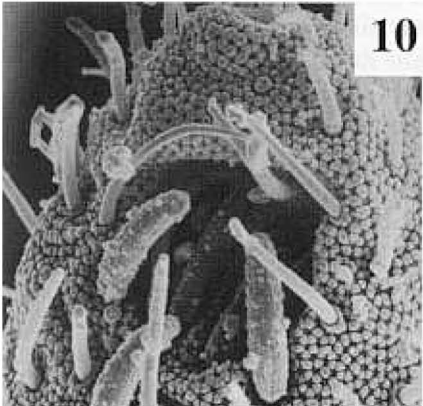


Table 4. Sensory clothing of *Folsomina onychiurina* Denis per half tergite.

Segments	Thorax II	Thorax III	Abdomen I	Abdomen II	Abdomen III	Abdomen IV-VI
Types of S setae						
Cylindrical, short	1+1sl			1+1sl <sup>*1</sup>		1+1sp
Cylindrical, fat, medium						1+1sp
Cylindrical, thin						2+2sa <sup>*2</sup>
Thin, pointed				1+1 <sup>*3</sup>	1+1sa <sup>*4</sup>	
Long, thin, pointed	1+1sp <sup>*1</sup> 1+1sl	1+1sp <sup>*2</sup> 1+1sl	1+1sp <sup>*3</sup> 1+1sl			
Dagger-shaped	1+1ms					1+1sl

\*1 Positioned in row 4, 5-6 setae between the medial pair of S setae and 2+2 setae between lateral and medial S setae.

\*2 Positioned in row 2, 6 setae between each S<sup>1</sup> seta.

\*3 Positioned in anterior row of seta, 4 setae between each S seta.

\*4 Positioned in middle row, 6 setae between each S seta.

Table 5. Comparison of type series of *Folsomina onychiurina* Denis and *F. yosii* Lawrence.

	Holotype BSIP <i>yosii</i> Lawrence	Holotype CR <i>onychiurina</i> Denis	6 Paratypes CR <i>onychiurina</i> Denis
Units of length			
manubrium	40 (lateral) 30 (ventral)	35	40,43,35,40,40,47
dens	65 lat	80 dorsal	70,80,85,85,90,85
micro	5	5	5-6
abdomen IV-VI	105,100	95,100	85,95,95,100
ordinary setae (midant)	18, 15	15,18,20	13,16,22,25,17
macrochaetae	30 - 35	41,42	36,39,35
abdomen III	60	52	60,75
Numbers of setae			
antenna I	13 + 2s + 1ss	13 + 2s + 1ss	not seen
furcal base	5/6, 5/5or6	5/?	6/? ,6/8
rami tenculum	1	?	1
dental setae	18,19 PNL 21-22	18,17?	21,18,20,22,20,2 1

furcal base with 6/7 setae; dens with 6 posterior setae and 17-22 anterior setae; micro with one tooth.

**Ratios.** - Setae on thorax II: S setae:ordinary setae = 1:2; abdomen V: S seta:ordinary setae:macrochaetae = 1:2:3.5.

**Remarks.** - The Costa Rican and Solomon Islands specimens are compared in Table 5. As noted by Lawrence (1969) and other authors there is some variation in the number of setae on the dens from 17 to 22 (16 - 20 according to Christiansen & Bellinger, 1980, "of about 20" Christiansen & Bellinger, 1992). Denis (1931) stated that there are many anterior setae on the dens and later (1933) that they are in three rows although Lawrence (1969) noted that Denis recorded 10-12 anterior setae on the dens. The lectotype has 17 and 18 setae in this position. Christiansen & Bellinger (1980) also mentioned that the macrochaetae of *F. onychiurina* are slightly roughened but this feature was not observed in the specimens examined here.

Lawrence (1969) noted considerable variation in the manubrium:dens:micro ratio in the published records of *F. onychiurina* and suggested that this was too great for the records to be of only a single species. The ratio measured on specimens from Costa Rica was from 1:1.75 to 1:2.8 depending on the whether the measurements are taken from a dorsal or lateral position. The Solomons holotype of *F. yosiii* has a ratio of 1:1.6 measured laterally. In all other respects the descriptions given by Denis and Lawrence are similar.

Other differences were observed between the Costa Rican and Solomon Island specimens. The type of *F. yosiii* is slightly smaller than specimens from Costa Rica and the setae are shorter. The macrochaetae are longer on the Costa Rican specimens but their relative length, compared to ordinary setae, is about the same; ratio of ordinary setae:macrosetae:length of abdomen IV-VI = 1:1.9:5 for the holotype of *F. yosiii* and 1:2:4 for the holotype of *F. onychiurina*. These differences are all within the range of variation shown by material of the species from different sites in Australia (Table 6) where larger specimens with longer setae seem to be associated with sites with higher rainfall. This species is capable of penetrating deep into the soil as shown by individuals being taken at depths of 30-45 cm under wheat fields in the Victorian mallee of Australia.

Table 6. Characters distinguishing *Folsomina onychiurina* Denis, *F. infelicia*, new species and *F. lawrencei*, new species.

Character	<i>onychiurina</i>	<i>lawrencei</i>	<i>infelicia</i>
Tibiotarsal setae	21,21,27	21,21,25	21,21,25
Antenna IV's vesicle	short round	long oval	median tripartite
Abdomen IV s': ord. setae	half ord. seta 0.5:1	two thirds ord. seta 0.66:1	a quarter ord. seta 0.25:1
Anterior dental setae	17-22	7	11-13
Post dental seta	6	4	4
Antenna III organ	1 ord. seta from guard s'	1 ord. seta from guard s'	adjacent guard s'
Abdomen VI fine setae	2 + 2	2 + 2	3 + 3
Teeth micro	1	2-3	2

*Folsomina wuyanensis* Zhao & Tamura, 1992

This species was described from the Zhejiang Province, China. The written description and figures do not allow differentiation of this species from *F. onychiurina*, but the authors state that *F. wuyanensis* differs from *F. onychiurina* in that the dentes have 3 dorsal and 2 ventral setae of which the ventrodorsal one is single and the longest; the ventral tube has 4 setae on each lateral flap. These are all characters also present on *F. onychiurina*, apart from the posterior (dorsal) setae of the dens, of which there are 6 in *F. onychiurina*. However the two most distal setae are often small and difficult to distinguish. A number of critical characters were not included in the original published description of this species and it has not been possible to borrow types. Consequently the status of this species is left unchanged, although it is possible that *F. wuyanensis* is a synonym of *F. onychiurina*.

*Folsomina yongxingensis* Chen, 1987

As noted by Bedos (1994), this species, described from the Xisha islands, China, is close to the species described by Lawrence as *F. onychiurina*, here described as *F. lawrencei* n. sp., apparently differing only in the number of posterior setae on the dens and in the development of macrochaetae on the abdomen, the formula for which is given as 1,1/3,3,4, (with those on abdomen IV-VI not figured) in *F. yongxingensis* according to Chen's figures, compared to 1,1/1,2,2,10 in *F. lawrencei*. A number of characters were not described in the original publication of this species and it has not been possible to borrow types for examination. Consequently the status of this species is left unchanged here.

## DISCUSSION

Although the number, position and type of S setae are constant in this genus, species differ in the relative length of the S setae on antennal segments III and IV and in the number of ordinary setae between the S setae on abdominal segments IV-VI. Other specific differences, listed in Table 7, are the number of mucronal teeth, the relative lengths of manubrium, dens and micro, the number of setae on the dens and the elongation of the body. There are also differences in the degree of sclerotisation of the mouthparts and in the robustness of the labrum. These are all adaptations to soil dwelling, and three of the *Folsomina* species illustrate possible progressive adaptation to life in deep soil, with *F. onychiurina* being the least adapted, *F. lawrencei*, the most adapted and *F. infelicia* intermediate. The centre of radiation of the genus is likely to be southeast Asia/western Pacific region, as all five named species occur there.

*Folsomina* species appear to be at least facultatively parthenogenetic as males are rare. A preadult male was detected among specimens of *Folsomina infelicia* but no males were found in material of the other two species. Species concepts in parthenogenetic forms differ from those of sexually reproducing species, because the character of parthenogenesis itself is likely to be a parallelism and not a synapomorphy, unless one assumes that each species arose from an existing parthenogenetic species. The most popular definitions of biological species in current usage are restricted to sexually reproducing, biparental organisms with potential for gene exchange between populations or with populations of each species fixed in entire, reproductively cohesive units. Using these definitions, *Folsomina* species could be

paraphyletic clones of an unknown sexual species or alternatively they may have arisen from different, unknown, sexually reproducing ancestors.

### KEY TO SPECIES OF *FOLSOMINA*

1. Mucro with one tooth: dens with 17-22 anterior setae, twice as long as manubrium; furcal base with 6/7 setae ..... 4
- Mucro with two to three teeth; dens with fewer than 14 anterior setae, less than twice as long as manubrium; furcal base with less than 5/5 setae ..... 2
2. Dens with 7 anterior setae, about the same length as manubrium ..... 3
- Dens with 11 - 13 anterior setae, about half as long again as manubrium .....  
..... *F. infelicia*, new species
3. Dens posteriorly with 4-5 setae; abdominal macrochaeta 3,3,3,6 ..... *F. yongxingensis* Chen
- Dens posteriorly with 3 setae; abdominal macrochaetae 1,2,2,10 ..... *F. lawrencei*, new species
4. Dens with 6 posterior (ventral) setae ..... *F. onychiurina* Denis
- Dens with 3 posterior (ventral) setae ..... *F. wuyanensis* Zhao & Tamura

### BIOLOGY

Winter (1963b) recorded *F. onychiurina* in leaf litter and humus from three Peruvian tropical vegetation types, lowland, montane and cloud forest, but not from above 3800m nor from the coast, thereby implying some ecological restrictions to the distribution of this widespread species. Greenslade (1969) noted that *F. onychiurina* (as *F. new species*) was present in montane and coastal samples from the Solomon Islands but absent from lowland rainforest, while *F. lawrencei* (as *F. onychiurina*) was present in lowland and coastal habitats but absent from montane collections, indicating that its range may be limited by low temperatures. In support of this hypothesis, in Australia *F. lawrencei* apparently does not occur further south than the Torres Strait Islands, while *F. onychiurina* is much more widely distributed and occurs as far south as Kangaroo Island in both eucalypt forest and in other more xeric vegetation types. It is a common cave species in south-east Asia (L. Deharverg, pers. comm). The two species are sympatric at some localities and *F. onychiurina* appears to coexist with *F. infelicia*, but *F. lawrencei* and *F. infelicia* have not yet been found at the same localities.

In Australia *F. onychiurina* appears largely restricted to warmer, humid parts of the continent. Maeda & Tanaka (1982) noted that it migrates vertically according to season, retreating lower into the soil profile in winter. In Australia *F. onychiurina* has been found at depths of 45 cm in soil in a wheat field in the semiarid region of Victoria. In wheat fields in central New South Wales under humid conditions, it was collected at depths of between 0 and 10 cms and at densities of 500 to 2000/m<sup>2</sup>. Populations were significantly increased by the incorporation of stubble (SI) once a year before planting ( $p < 0.001$ ) (Longstaff et al., 1998), the increase being significantly greater on direct-drilled (DD) compared to traditionally tilled fields (TT) (Fig. 12). *Folsomina onychiurina* therefore appears relatively tolerant of disturbance, being able to retreat deeper into the soil under adverse conditions.

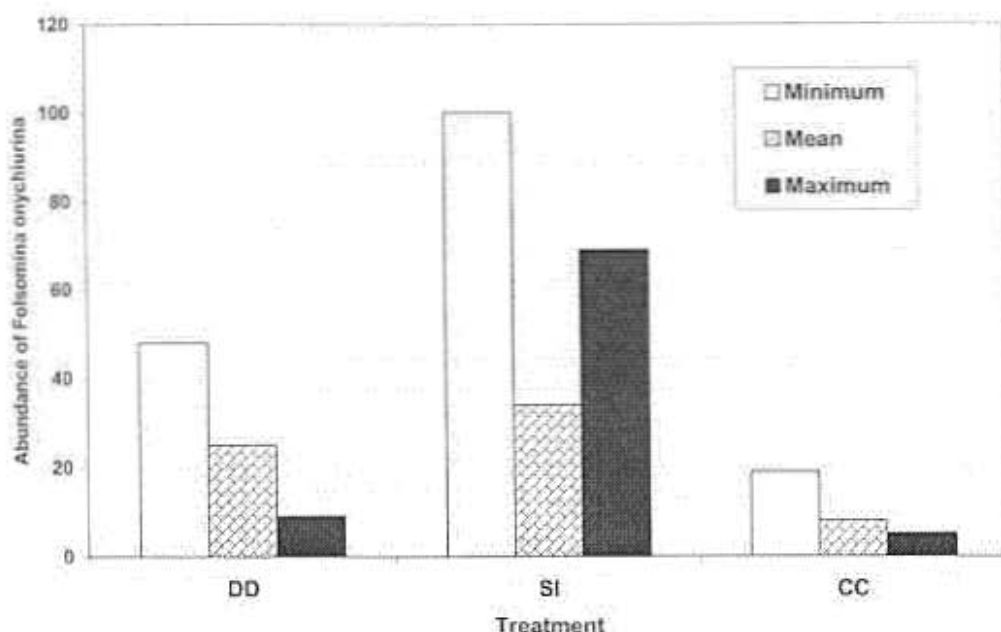


Fig. 12. Abundance of *Folsomina onychiurina* Denis in wheat fields at Cowra, Australia, under different tillage regimes (CC, conventional cultivation, DD, direct drilling, SI, stubble incorporation) and three levels of disturbance (minimum, mean and maximum).

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