

# Three New Species of the Family Eosentomidae (Protura) from the Nasu Imperial Villa, Central Japan

Osami Nakamura

Omaeda 2507–9, Fukaya-shi, Saitama 369–1246, Japan  
E-mail: osami@nakamura.email.ne.jp

(Received 8 September 2020; Accepted 25 February 2021)

<http://zoobank.org/A1208587-E61D-47C0-809D-54172EA24DD9>

Three new proturan species, *Eosentomon villare* sp. nov., *Pseudanisentomon nasuense* sp. nov., and *P. villaticum* sp. nov., collected from the Nasu Imperial Villa, Tochigi Prefecture, central Japan are described. *Eosentomon villare* sp. nov. is characterized by the absence of foretarsal sensillum  $b'1$ , a long empodium on the hind tarsus, four pairs of anterior setae on abdominal tergite VII ( $A1, 2, 4$ , and  $5$ ), two anterior and seven posterior setae on sternite VIII, and six setae on sternites IX–X. Both *P. nasuense* sp. nov. and *P. villaticum* sp. nov. also lack foretarsal sensillum  $b'1$ . *Pseudanisentomon nasuense* sp. nov. has long empodia on the middle and hind tarsus and five pairs of anterior setae on abdominal tergite IV. *Pseudanisentomon villaticum* sp. nov. is distinguished from its congeners by the number of anterior setae on abdominal tergite VII (three pairs:  $A2, 4$ , and  $5$ ), the absence of foretarsal sensillum  $c'$  and seta  $x$ , and rudimentary setae 1 and 2 on tergite XI. In addition to descriptions of these new species, an updated key to species of *Pseudanisentomon* Zhang and Yin, 1984 is provided.

**Key Words:** *Eosentomon*, *Pseudanisentomon*, key, chaetotaxy, taxonomy.

## Introduction

The Nasu Imperial Villa (area: ca. 660 ha) is located at the southeastern foot of Mt. Chausu-dake in Nasu-machi, Tochigi Prefecture, central Japan. Part of the area was once used as pastureland; however, the grassland landscape had previously been lost due to the cessation of grazing and the establishment of forest. In December 2011, the Garden Division of the Imperial Household Agency cut down trees to re-grass the area. In conjunction with re-grassing, soil fauna surveys were conducted from 2011 to 2015 in an initiative by the Tochigi Prefectural Museum. During these surveys, 2914 proturan specimens were collected including 19 determined species belonging to nine genera in three families. Undetermined eosentomid specimens also were obtained (Nakamura 2019); these were closely examined and three species new to science were identified. One new species of *Eosentomon* Berlese, 1908 and two new species of *Pseudanisentomon* Zhang and Yin, 1984 are described below. In addition, an updated key to the species of *Pseudanisentomon* is provided.

## Materials and Methods

Substrate was collected from four sites of secondary forest dominated by *Quercus crispula* Blume and *Pinus densiflora* Siebold and Zucc. in the Nasu Imperial Villa. Protura were extracted from litter and soils using Tullgren funnels and then preserved in 95% ethanol. Subsequently, specimens were individually mounted in polyvinyl lactophenol medium. They were manipulated into position with a pin embedded in a

wooden stick and then covered with a coverslip. These slides were dried for four days in an oven at 60°C. Morphological characters were observed using differential interference microscopy (Olympus BHS-N) and specimens were drawn with the aid of a drawing tube (Olympus BH2-DA).

Most terms and designations used here are after Tuxen (1964) and Imadaté (1974). However, descriptions of some characteristics, e.g., chaetotaxy of the head and hind tarsus, and the structure of some elements of the mouthparts, are after Bernard (1990).

In the following descriptions, the holotype measurement is given first followed by the range of paratype measurements in parentheses. Holotypes and some of the paratypes are deposited in the collection of the National Museum of Nature and Science (NSMT), and some of the paratypes are in the collections of Tochigi Prefectural Museum (TPM) and Saitama Museum of Natural History (SMNH).

## Taxonomy

Family *Eosentomidae* Berlese, 1909

Genus *Eosentomon* Berlese, 1908

*Eosentomon villare* sp. nov.

(Figs 1, 2; Table 1)

*Eosentomon* sp. NIV: Nakamura 2019: 18.

**Diagnosis.** Labral setae present; cephalic anterior additional setae absent; foretarsal sensilla  $b'1$  and  $c'$  absent; long empodium on hind tarsus; abdominal tergites V–VII with four pairs of anterior setae ( $A1, 2, 4, 5$ ),  $P1a$  on VII short at

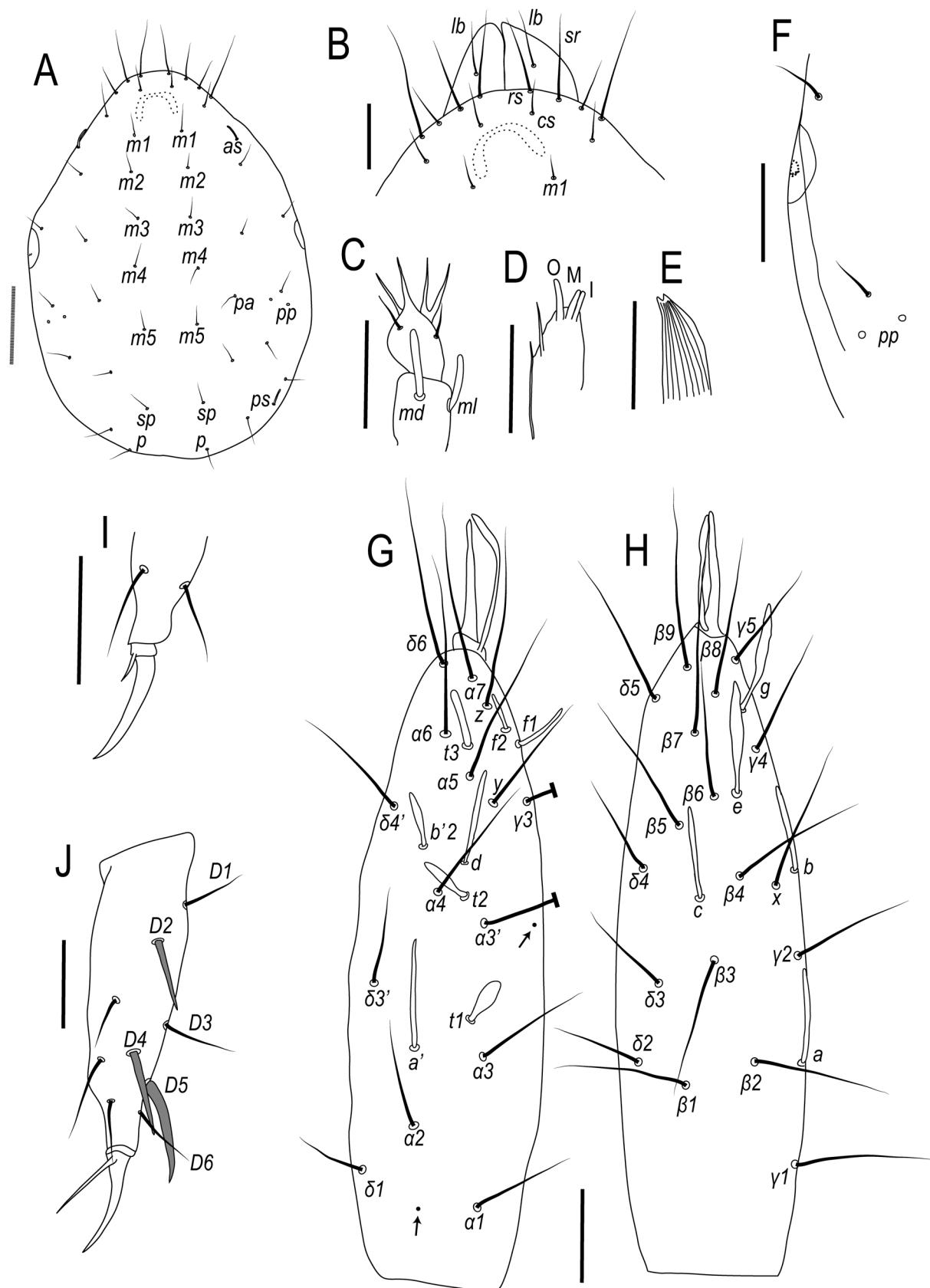


Fig.1. *Eosentomon villare* sp. nov., holotype, female (NSMT-Ap 539). A, Dorsal view of the head; B, labrum and rostral region; C, maxillary palpus; D, galea; E, mandible; F, pseudoculus; G, interior view of the foretarsus; H, exterior view of the foretarsus; I, distal part of the middle tarsus; J, dorsal view of the hind tarsus. Abbreviations: *as*, anterior sensillum; *cs*, clypeal seta; *I*, inner digit; *lb*, labral seta; M, median digit; *md*, dorsal sensillum; *ml*, lateral sensillum; O, outer digit; *p*, median posterior seta; *pa*, posterior additional seta; *pp*, a pair of sensilla posterior to pseudoculus; *ps*, posterior sensillum; *rs*, rostral seta; *sp*, median subposterior seta; *sr*, subrostral seta. Arrows show pores. Scale bars: 10 µm.

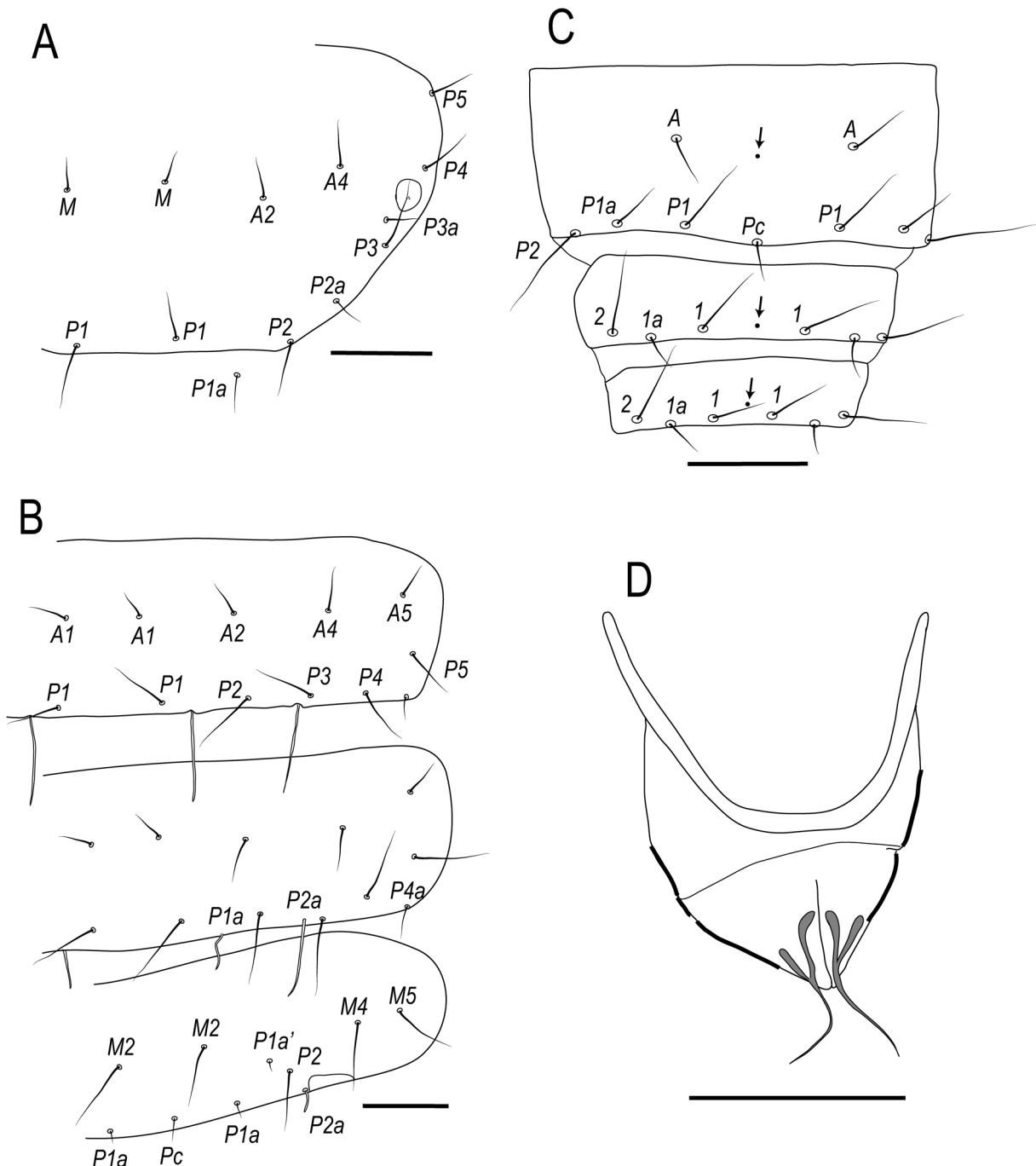


Fig. 2. *Eosentomon villare* sp. nov., holotype, female (NSMT-Ap 539). A, Dorsal view of thorax III, right side; B, dorsal view of abdomen VI-VIII, right side; C, ventral view of abdomen VIII-X; D, female squama genitalis. Arrows show pores. Scale bars: 20 µm.

posterior margin; sternite VIII with two anterior and seven posterior setae, IX-X with six setae.

**Specimens examined.** Holotype (NSMT-Ap 539): female, the Nasu Imperial Villa, Nasu-machi, Tochigi Prefecture, 37.1100°N, 140.0158°E, elev. 919 m, secondary forest dominated by *Q. crispula* and *P. densiflora*, 7 October 2011, K. Furuno et al. leg. Paratypes: two females (TPM-IV-14024; SMNH-Ap-36639), same data as for the holotype except sampling date, 15 October 2013.

**Description.** Body length. 663 (598–676) µm.

Head. 94 (91–94) µm long, 70 (71–73) µm wide. Posterior additional setae and seta *m*4 present, but anterior additional

seta absent, anterior and posterior sensilla present (Fig. 1A); median subposterior seta (*sp*) subequal to median posterior seta (*p*) in length, 8 (8) µm; one pair of sensilla (*pp*) posterior to pseudoculus rudimentary. Labral setae present (Fig. 1B). Rostral seta normal, about equal to subrostral seta, 13 (12–13) µm in length (Fig. 1B). On maxillary palpus (Fig. 1C), dorsal sensillum length 7 µm, longer than lateral sensillum, 5 µm. On galea (Fig. 1D), digit O slightly longer than M and I. Mandible with two teeth (Fig. 1E). Clypeal apodeme distinct (Fig. 1A, B). Pseudoculus with a central mark (Fig. 1F), 10 (10) µm long, PR=9 (9).

Legs. Foretarsus length (Fig. 1G, H) 68 (68–70) µm; claw

Table 1. Chaetotaxy of *Eosentomon villare* sp. nov.

		Dorsal		Ventral	
		Formula	Composition of setae	Formula	Composition of setae
Thorax	I	4	1, 2	6-2	A1, 2, 3, M
	II	6	A2, 4, M	6	P1, 2, 3
		16	P1, 1a, 2, 2a, 3, 3a, 4, 5	6	A1, 2, 3, M
	III	6	A2, 4, M	6-4	P1, 2, 3
		20	P1, 1a, 2, 2a, 3, 3a, 4, 5, 5a, 5a'	8	A1, 2, 3, M1, 2
					P1, 2, 3, 4
Abdomen	I	4	A1, 2	4	A1, 2
		12	P1, 1a, 2, 3, 3a, 3a'	4	P1, 2
	II-IV	10	A1, 2, 3, 4, 5	6	A1, 2, 3
		16	P1, 1a, 2, 2a, 3, 4, 4a, 5	4	P1, 2
	V-VII	8	A1, 2, 4, 5	6	A1, 2, 3
		16	P1, 1a, 2, 2a, 3, 4, 4a, 5	10	P1, 2, 2a, 2a', 3
	VIII	6	M2, 4, 5	2	A
		9	Pc, 1a, 1a', 2, 2a	7	Pc, 1, 1a, 2
	IX-X	8	1, 2, 3, 4	6	1, 1a, 2
	XI	8	1, 2, 3, 4	8	1, 2, 3, 4
	Telson	9		12	

12 (13–14) µm, TR=5.7 (4.9–5.3); empodium 11 (11) µm, EU=0.9 (0.8); sensillum *s* length 16 (14–16) µm, longer than claw. Sensillum *t1* nearer to  $\alpha_3$  than to  $\alpha_3'$ , BS=0.9 (0.8); *t2* small, narrowly spatulate; *t3* slightly broadened, reaching base of  $\alpha_7$ ; *a* linear, not reaching base of *y2*; *b* linear, reaching base of *y3*; *c* linear, surpassing base of  $\beta_5$ ; *d* linear, reaching base of  $\alpha_5$ ; *e* and *g* rounded spatulate and large; *f1* and *f2* thin, *f2* shorter than *f1*; *a'* linear; *b'1* absent; *b'2* same as *t2*, small, narrowly spatulate; *c'* absent. A pore between  $\alpha_1$  and  $\delta_1$ , and between *b* and  $\alpha_3'$ . Length of middle tarsus 29 (28–33) µm, length of claw 10 (11) µm; empodium short and about 1/4 of claw in length (Fig. 1I), 3 (3) µm long; hind tarsus 36 (36–39) µm, claw 11 (12) µm; empodium longer than 2/3 of claw in length (Fig. 1J), 8 (8) µm long; on hind tarsus (Fig. 1J), *D2* and *D4* spine-like, more slender than *D5*.

**Chaetotaxy.** Chaetotaxy as in Table 1 and Fig. 2A–C. On thoracic tergites II–III (Fig. 2A), *P1a* and *P2a* seta-like, but shorter than *P1*; *P1a* posterior to *P1-P2*; *P2a* slightly closer to *P2* than to *P3*; *P1a*, 7 (7–9) µm long, subequal or slightly longer than *P2a*, 7 (6–7) µm long. Abdominal tergites II–IV with five pairs of anterior setae (*A1* to 5), V–VII with four pairs (*A1*, 2, 4, 5); *P1a* on tergite I, and *P1a* and *P2a* on II–VI delicate, longer than *P1*; *P1a* on VII short, about 1/2 of *P1* in length, 9 (9) µm long, at hind margin; *P2a* on VII subequal to *P1* in length (Fig. 2B); *P1a* on I–VI nearer to *P1* than to *P2*; *P2a* on II–VII nearer to *P3* than to *P2*; on VIII (Fig. 2B) *P1a'* normal and slightly anterior to *P2*, *P2a'* short, linear. Setae on thoracic and abdominal sternites all seta-like; sternite VIII with two anterior and seven posterior setae; sternites IX–X with six setae (Fig. 2C).

**Porotaxy.** Abdominal tergites IX–X with a pair of pores near seta 1. Abdominal sternites I–XI with one medial pore (Fig. 2C). Telson with two dorsal medial pores and one ventral medial pore.

**Female squama genitalis** (Fig. 2D). Caput processus blunt,

slightly curved against median edge of stylus, corpus processus reduced except for well-developed alae processus; filum processus long and slender; proximo-lateral sclerotization present; stylus apex narrowly rounded.

**Chaetotoxic variation.** *P4a* on abdominal tergites III–IV and *P2a* on abdominal sternites VI–VII asymmetrically absent and asymmetrically present in one paratype female.

**Remarks.** The genus *Eosentomon* contains more than 280 species and is common in most areas of the world. Within this genus, the new species is similar to *E. sociale* Bernard, 1975, *E. erwini* Copeland, 1978 and *E. quapawense* Tipping and Allen, 1994 from the USA, and to *E. notiale* Tuxen and Imadaté, 1975 from the Solomon Islands, according to a combination of important features such as the absence of foretarsal sensillum *b'1*, the long empodium on the hind tarsus, and two anterior and seven posterior setae on sternite VIII (Bernard 1975; Tuxen and Imadaté 1975; Copeland 1978; Tipping and Allen 1994). This new species differs from these four established species, however, by the anterior setae on abdominal tergite VII (six setae in the four established species), the setae on abdominal sternites IX–X (four setae in the four established species but six on IX in *E. quapawense*), and the structure of the female squama genitalis.

Among the Japanese *Eosentomon* species, the new species is similar to *E. udagawai* Imadaté, 1961, *E. dubium* Nakamura, 2010, and *E. inconditum* Nakamura, 2010 in having a long empodium on the hind tarsus and two anterior and seven posterior setae on sternite VIII (Imadaté 1974; Nakamura 2010). However, the new species differs from these three established species by the absence of foretarsal sensillum *b'1* (present in the three established species) and the structure of the female squama genitalis (duck's head-type caput processus in the three established species). Moreover, this new species is distinguished from *E. udagawai* by the labral setae (absent in *E. udagawai*) and the length of the empodium on the middle tarsus (about one-third of the

claw length in *E. udagawai*), from *E. dubium* by the anterior setae on abdominal tergites V–VII (ten setae on V–VI and six on VII in *E. dubium*), and from *E. inconditum* by the anterior setae on abdominal tergite VII (six setae in *E. inconditum*). The following eight Japanese *Eosentomon* species also lack foretarsal sensillum *b'1*: *E. kumei* Imadaté and Yosii, 1959, *E. topochi* Imadaté, 1964, *E.toi* Imadaté, 1964, *E. brachychaetum* Nakamura, 2010, *E. kantoense* Nakamura, 2010, *E. spatulatum* Nakamura, 2010, *E. calvum* Nakamura, 2010, and *E. hiroshianum* Nakamura, 2010; however, the new species is easily distinguishable from these as they have a short empodium on the hind tarsus (Imadaté 1974; Nakamura 2010).

**Distribution.** Japan, known only from the type locality.

**Etymology.** The specific name is derived from the Nasu Imperial Villa, the type locality.

Genus *Pseudanisentomon* Zhang and Yin, 1984

*Pseudanisentomon nasuense* sp. nov.

(Figs 3, 4; Table 2)

*Pseudanisentomon* sp.: Nakamura 2019: 18 (partim).

**Diagnosis.** Foretarsal sensillum *b'1* absent, *d* fairly broad, and *t3* long, reaching base of tarsal claw; long empodia on both middle and hind tarsi; abdominal tergites II–IV with five pairs of anterior setae, V–VII with four pairs of anterior setae (*A1, 2, 4, 5*); sternites IX–X with six setae.

**Specimens examined.** Holotype (NSMT-Ap 540): female, the Nasu Imperial Villa, Nasu-machi, Tochigi Prefecture, 37.1102°N, 140.0152°E, elev. 928 m, secondary forest dominated by *Q. crispula* and *P. densiflora*, 5 September 2012, K. Furuno et al. leg. Paratypes (n=21): one female (NSMT-Ap 541), same data as for the holotype; same locality as for the holotype, two males (NSMT-Ap 542, 543), 11 June 2012, one male and one female (NSMT-Ap 544, 545), 7 November 2012, one male and one female (NSMT-Ap 546, 547), 15 October 2013, K. Furuno et al. leg.; 37.1105°N, 140.0150°E, elev. 929 m, one male and one female (NSMT-Ap 548, 549), 11 June 2012, one male (NSMT-Ap 550), 7 November 2012, K. Furuno et al. leg.; 37.1102°N, 140.0161°E, elev. 918 m, one male and three females (TPM-IV-14025–14028), 11 June 2012, one male (TPM-IV-14029), 15 October 2013, one male (TPM-IV-14030), 27 October 2015, K. Furuno et al. leg.; 37.1100°N, 140.0158°E, elev. 919 m, one female (SMNH-Ap-36640), 7 October 2011, one female (SMNH-Ap-36641), 11 June 2012, one female (SMNH-Ap-36642), 7 November 2012, two males (SMNH-Ap-36643, 36644), 15 October 2013, K. Furuno et al. leg.

**Other material examined** (n=17): same locality as for the holotype, one female, 7 November 2012, one male and one female, 15 October 2013, one female and one matusus junior, 27 October 2015; 37.1105°N, 140.0150°E, elev. 929 m, one male and one female, 7 October 2011, one male and one female, 11 June 2012, one matusus junior, 7 November 2012, one matusus junior, 15 October 2013; 37.1102°N, 140.0161°E, elev. 918 m, two males, one female and one matusus junior; 37.1100°N, 140.0158°E, elev. 919 m, one male,

7 November 2012, one female, 27 October 2015.

**Description.** Body length. 722 (592–780) µm.

**Head.** 99 (95–100) µm long, 67 (66–74) µm wide. Posterior additional setae and seta *m4* present, anterior additional seta absent; anterior and posterior sensilla present (Fig. 3A); median subposterior seta length 8 (7–9) µm, 1.1 times longer than median posterior seta, 7 (6–8) µm; a pair of rudimentary sensilla posterior to pseudoculus rudimentary. Labral setae present (Fig. 3B). Rostral seta length 11 (10–12) µm, tapering, subequal to subrostral seta, 11 (10–14) µm in length (Fig. 3B). On maxillary palpus (Fig. 3C) dorsal sensillum length 6 (5–7) µm, longer than lateral sensillum, 4 (4–6) µm. On galea (Fig. 3D), digit O longer than M and I. Mandible with two teeth (Fig. 3E). Clypeal apodeme distinct (Fig. 3B). Pseudoculus with three lines, central one long and other two short (Fig. 3F), 7 (7–9) µm long, PR=15 (12–15).

**Legs.** Foretarsus length (Fig. 3G, H) 64 (61–67) µm; claw 12 (11–13) µm, TR=5.0 (4.7–5.5); empodium 12 (11–13) µm, EU=1.0 (0.9–1.1); sensillum *s* length about equal to claw, 11 (11–13) µm. Sensillum *t1* nearer to *α3* than to *α3'*, BS=0.9 (0.9–1.0); *t2* thin; *t3* broad, reaching base of tarsal claw; *a* linear; *b* linear, reaching base of *β6*; *c* linear, reaching base of *γ3*; *d* fairy broad, reaching base of *α5*; *e* absent; *f1* narrowly spatulate; *f2* linear; *g* rounded spatulate and large; *a'* linear; *b'1* absent; *b'2* and *c'* thin, almost same length. A pore posterior to seta *y*. Length of middle tarsus 27 (26–30) µm, length of claw 10 (8–11) µm; hind tarsus 33 (33–37) µm, claw 11 (8–10) µm; both empodia long, about 2/3 of claw length on middle tarsus, 7 (5–8) µm long (Fig. 3I); empodium longer than 2/3 of claw length on hind tarsus (Fig. 3J), 9 (7–9) µm long; on hind tarsus (Fig. 3J), *D2* seta-like; *D4* spine-like, but more slender than *D5*.

**Chaetotaxy.** Chaetotaxy as in Table 2 and Fig. 4A–D. On thoracic tergites II–III (Fig. 4A), *P1a* and *P2a* seta-like; *P1a* posterior to *P1–P2*; *P2a* on II slightly nearer to *P2* than to *P3*; *P2a* on III halfway between *P2* and *P3*; *P1a* and *P2a* on II–III shorter than *P1*; on II *P1a* 8 (7–10) µm, slightly longer than *P2a*, 7 (5–7) µm; on III *P1a* 7 (9–11) µm, length subequal to or slightly longer than *P2a*, 7 (7–9) µm. Abdominal tergites II–IV with five pairs of anterior setae (*A1* to *5*), V–VII with four pairs (*A1, 2, 4, 5*); *P1a* on I, *P1a* and *P2a* on II–VI and *P2a* on VII delicate, longer than *P1*; *P1a* on VII short, about 1/3 of *P1* in length, 5 (4–7) µm long, at hind margin (Fig. 4B); on VIII (Fig. 4C) *P1a'* with basal dilatation and slightly anterior to *P2*, *P2a'* falcate. Setae on thoracic and abdominal sternites all seta-like; VIII with two anterior and seven posterior setae; IX–X with six setae (Fig. 4D).

**Porotaxy.** Abdominal tergites I–V with posterosubmedial pore between *A2* and *P2*; IX–X with one medial pore (Fig. 4C). Abdominal sternites VIII–X with one medial pore (Fig. 4D). Telson with one dorsal medial pore and two ventral medial pores.

**Genitalia.** Female squama genitalis (Fig. 4E), with caput processus shaped like a duck's head, filum processus short; proximo-lateral sclerotization present; posterior sclerotization of stylus apex present. Male squama genitalis with short basiperiphallar setae (Fig. 4F).

**Matusus junior** (n=4). Body length 580–618 µm. Head

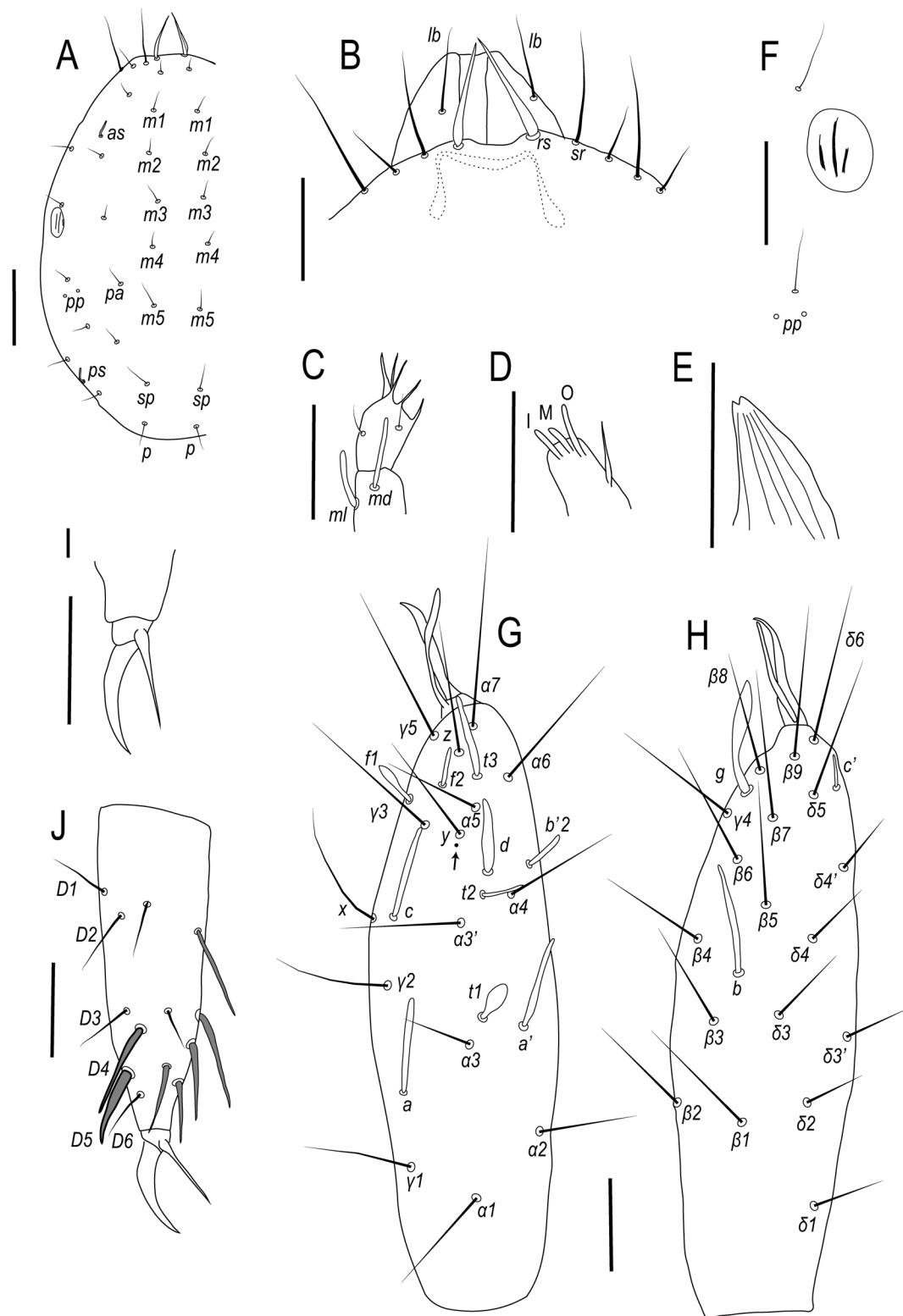


Fig. 3. *Pseudanisentomon nasuense* sp. nov., holotype, female (NSMT-Ap 540). A, Dorsal view of the head; B, labrum and rostral region; C, maxillary palpus; D, galea; E, mandible; F, pseudoculus; G, interior view of foretarsus; H, exterior view of the foretarsus; I, distal part of the middle tarsus; J, dorsal view of the hind tarsus. Abbreviations: *as*, anterior sensillum; *I*, inner digit; *lb*, labral seta; *M*, median digit; *md*, dorsal sensillum; *ml*, lateral sensillum; *O*, outer digit; *p*, median posterior seta; *pa*, posterior additional seta; *pp*, a pair of sensilla posterior to pseudoculus; *ps*, posterior sensillum; *rs*, rostral seta; *sp*, median subposterior seta; *sr*, subrostral seta. Arrow shows pore. Scale bars: 20 µm in A; 10 µm for all other images.

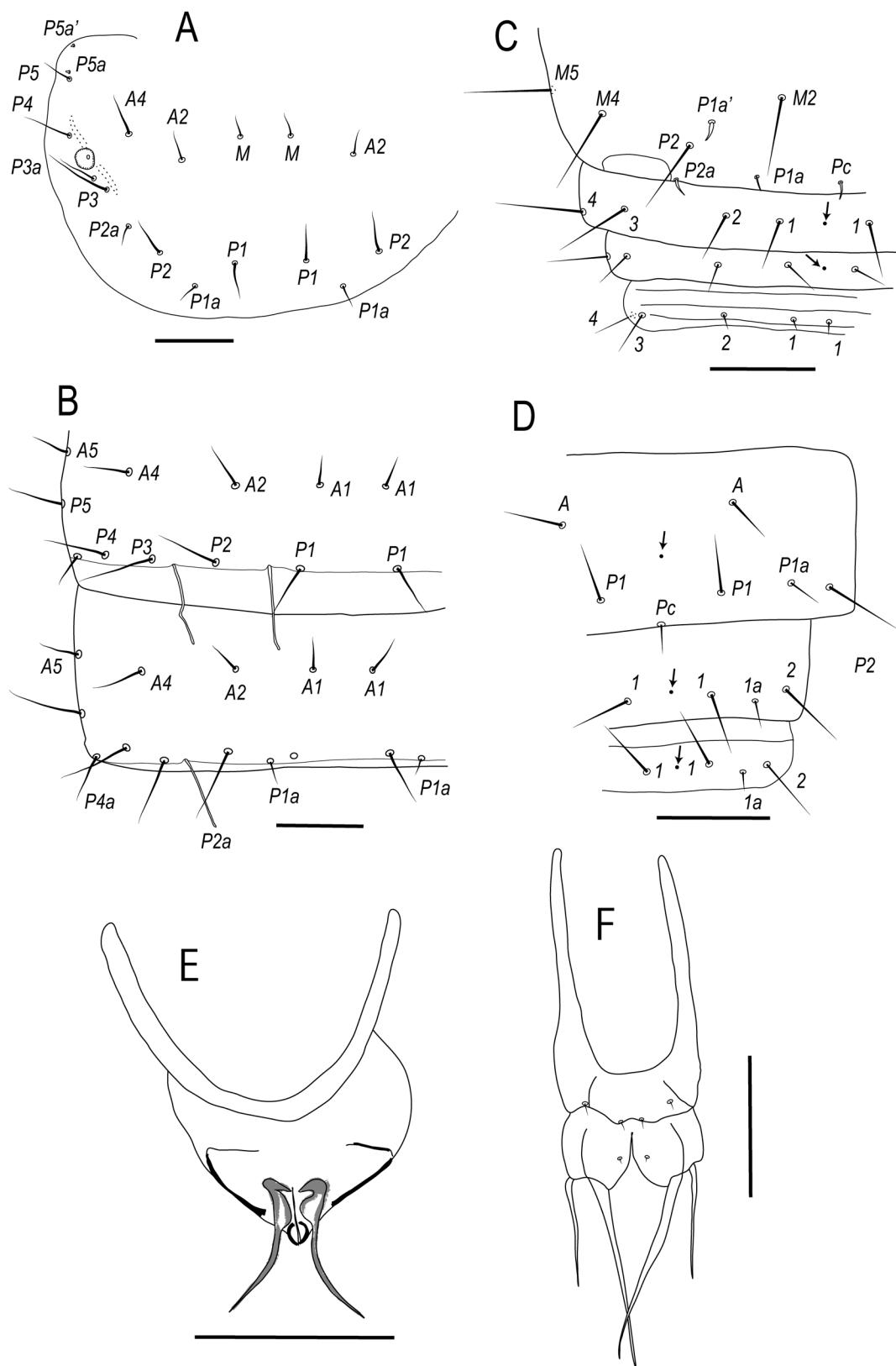


Fig. 4. *Pseudanisentomon nasuense* sp. nov. A, Dorsal view of thorax III, right side; B, dorsal view of abdomen VI–VII, left side; C, dorsal view of abdomen VIII–XI, left side; D, ventral view of abdomen VIII–X, right side; E, female squama genitalis; F, male squama genitalis. Arrows show pores. A–D, Holotype, female (NSMT-Ap 539); E, paratype, male (SMNH-Ap-36643). Scale bars: 20 µm.

Table 2. Chaetotaxy of *Pseudanisentomon nasuense* sp. nov.

		Maturus junior		Imago	
		Formula	Composition of setae	Formula	Complementary setae
<b>(Dorsal)</b>					
Thorax	I	4	1, 2	4	
	II	6	A2, 4, M	6	
		16	P1, 1a, 2, 2a, 3, 3a, 4, 5	16	
	III	6	A2, 4, M	6	
		20	P1, 1a, 2, 2a, 3, 3a, 4, 5, 5a, 5a'	20	
Abdomen	I	4	A1, 2	4	
		12	P1, 1a, 2, 3, 3a, 3a'	12	
	II-IV	10	A1, 2, 3, 4, 5	10	
		16	P1, 1a, 2, 2a, 3, 4, 4a, 5	16	
	V-VII	8	A1, 2, 4, 5	8	
		16	P1, 1a, 2, 2a, 3, 4, 4a, 5	16	
	VIII	6	M2, 4, 5	6	
		9	Pc, 1a, 1a', 2, 2a	9	
	IX-XI	8	1, 2, 3, 4	8	
	Telson	9		9	
<b>(Ventral)</b>					
Thorax	I-II	6-2	A1, 2, 3, M	6-2	
		6	P1, 2, 3	6	
	III	6-4	A1, 2, 3, M1, 2	6-4	
		8	P1, 2, 3, 4	8	
Abdomen	I	4	A1, 2	4	
		4	P1, 2	4	
	II-III	6	A1, 2, 3	6	
		4	P1, 2	4	
	IV-VII	6	A1, 2, 3	6	
		10	P1, 2, 2a, 2a', 3	10	
	VIII	2	A	2	
		7	Pc, 1, 1a, 2	7	
	IX	6	1, 1a, 2	6	
	X	4	1, 2	6	1a
	XI	4	1, 3	8	2, 4
	Telson	12		12	

91–94 µm long, 63–74 µm wide; pseudoculus 7–8 µm long, PR=11–14. Foretarsus length 56–59 µm; claw 10–11 µm, TR=5.0–5.6; empodium 9–10 µm, EU=0.8–1.0; sensillum *s* 9–11 µm; shape and position of foretarsal sensilla same as those of imago, BS=0.8–0.9. Length of middle tarsus 27 µm, length of claw 8–10 µm, empodium 5–6 µm; hind tarsus 29–33 µm, claw 10–11 µm, empodium 7–10 µm. Chaetotaxy as in imago, but lacking *P1a* on abdominal sternite IX and 2 and 4 on sternite XI.

**Chaetotaxic variation.** *Pc* on abdominal sternite VIII absent in one female; *A2* on abdominal tergite III asymmetrically absent in one male; *P2a'* on abdominal sternites VI and VII absent and asymmetrically absent in one maturus junior, respectively.

**Remarks.** The genus *Pseudanisentomon* is distributed in China and Japan, and consists of 22 species, of which 18 are from China and four are from Japan (Yin 1999; Nakamura 2010; Bu et al. 2020). The new species resembles *P. songkiangensis* (Yin, 1977), *P. guangxiensis* (Yin and Zhang, 1982), *P. huichouense* Zhang and Yin, 1984, and *P. jiangxiensis* Yin, 1987 from China by the absence of foretarsal sensillum

*b'* 1 and long empodia on both the middle and hind tarsus. However, the new species differs from *P. songkiangensis*, *P. huichouense*, and *P. jiangxiensis* by the five pairs of anterior setae on abdominal tergite IV (four pairs of anterior setae in the three established species), and from *P. guangxiensis* and *P. huichouense* by having six setae on abdominal sternites IX–X (four setae in these two established species). Moreover, the new species is distinguished from *P. songkiangensis* by having five pairs of anterior setae on abdominal tergites II–III (four pairs of anterior setae in *P. songkiangensis*), from *P. jiangxiensis* by the length of foretarsal sensilla *a* and *c* (short in *P. jiangxiensis*), from *P. guangxiensis* by the length of sensilla *t2* and *f2* on the foretarsus (not short in *P. guangxiensis*), and from *P. huichouense* by the shape and length of foretarsal sensillum *t3* (not broad and short in *P. huichouense*).

**Distribution.** Japan, known only from the Nasu Imperial Villa.

**Etymology.** The specific name is derived from the name of the district, Nasu-machi, where Nasu Imperial Villa of the type locality is located.

***Pseudanisentomon villaticum* sp. nov.**  
(Figs 5–8; Table 3)

*Pseudanisentomon* sp.: Nakamura 2019: 18 (partim).

**Diagnosis.** Foretarsal sensilla  $b'1$ ,  $c'$  and seta  $x$  absent,  $a$  nearer to  $y1$  than to  $y2$ ,  $f1$  broad and long; long empodium on hind tarsus; abdominal tergite VII with three pairs of anterior setae ( $A2$ ,  $4$ ,  $5$ ), 1 and 2 rudimentary on X; sternites IX–X with six setae.

**Specimens examined.** Holotype: female (NSMT-Ap 551), the Nasu Imperial Villa, Nasu-machi, Tochigi Prefecture, 37.1100°N, 140.0158°E, elev. 919 m, secondary forest dominated by *Q. crispula* and *P. densiflora*, 15 October 2013, K. Furuno et al. leg. Paratypes (n=10): one female (NSMT-Ap 552), same data as for the holotype; same locality as for the holotype, two males (NSMT-Ap 553, 554), 7 October 2011, one female (NSMT-Ap 555), 11 June 2012, one male, one female (TPM-IV-14031, 14032), 7 December 2012, one male (TPM-IV-14033), 27 October 2015, K. Furuno et al. leg.; 37.1102°N, 140.0152°E, elev. 928 m, one male (SMNH-Ap-36645), 27 October 2015, K. Furuno et al. leg.; 37.1105°N, 140.0150°E, elev. 929 m, one male (SMNH-Ap-36646), 15 October 2013, K. Furuno et al. leg.;

37.1102°N, 140.0161°E, elev. 918 m, one female (SMNH-Ap-36647), 15 October 2013, K. Furuno et al. leg.

Other material examined (n=18): one female and one larva II, same data as for the holotype; same locality as for the holotype, one female and one larva II, 7 October 2011, one larva II and one larva I, 5 September 2012, one larva II, 7 November 2012, one female and one larva II, 15 October 2013, one larva II, 17 October 2015; 37.1102°N, 140.0152°E, elev. 928 m, one male, 27 October 2015; 37.1105°N, 140.0150°E, elev. 929 m, one male and one larva II, 11 December 2011, one female, 7 November 2013; 37.1102°N, 140.0161°E, elev. 918 m, one male, 11 December 2011, one female, 15 October 2013, two females, 27 October 2015.

**Description. Body length.** 663 (592–715) µm.

**Head.** 102 (96–104) µm long, 68 (69–72) µm wide. Anterior and posterior additional setae, and seta  $m4$  present; anterior and posterior sensilla present (Fig. 5A); median subposterior seta length, 8 (7–9) µm, 1.2 times longer than median posterior seta, 7 (7) µm; a pair of rudimentary sensilla posterior to pseudoculus rudimentary. Labral setae present (Fig. 5B). Rostral seta length 13 (11–13) µm, longer than subrostral seta, 11 (10–12) µm, (Fig. 5B). On maxillary palpus (Fig. 5C) dorsal sensillum ( $md$ ), 6 (5–6) µm, longer than lateral sensillum ( $ml$ ), 4 (4–5) µm. On galea (Fig. 5D), all digits similar in

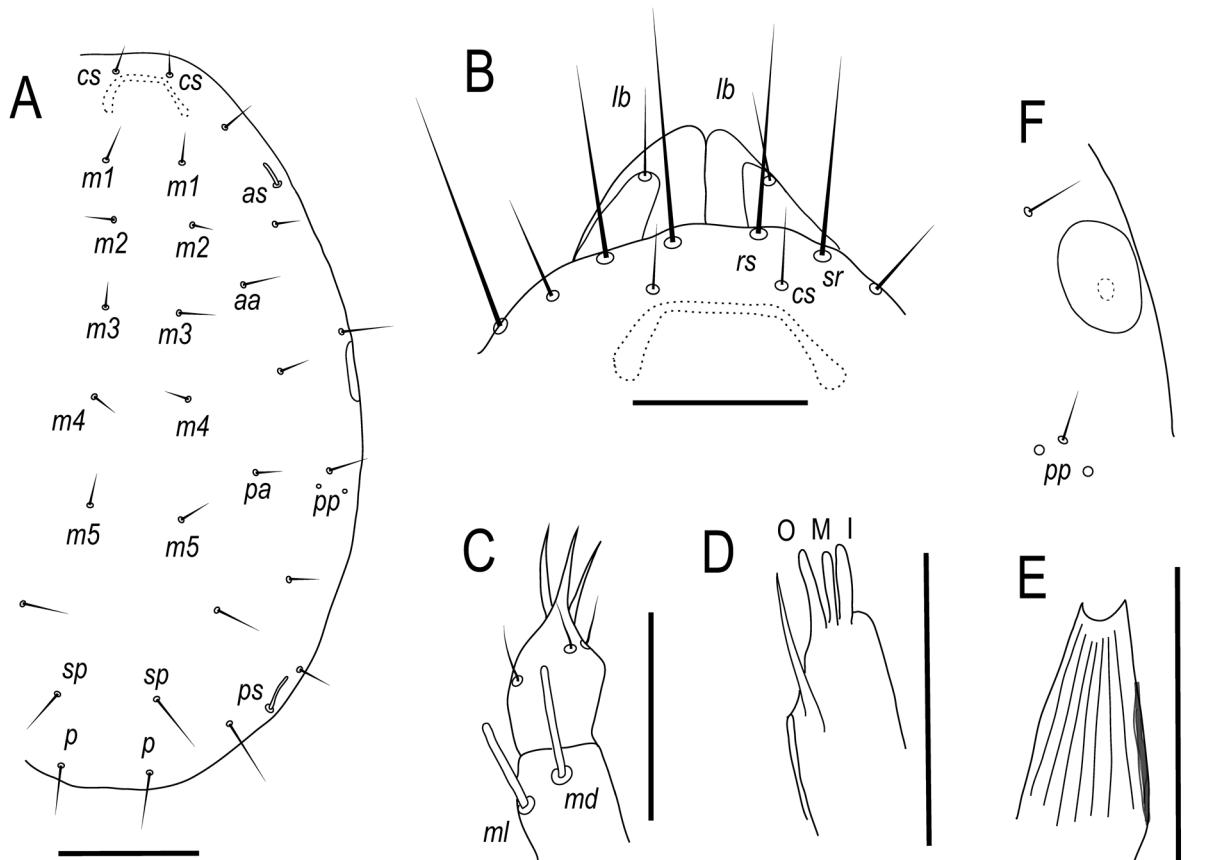


Fig. 5. *Pseudanisentomon villaticum* sp. nov. A, Dorsal view of the head; B, labrum and rostral region; C, maxillary palpus; D, galea; E, mandible; F, pseudoculus. A–C, F, Holotype, female (NSMT-Ap 551); D and E, paratype, female (NSMT-Ap 555); F, paratype, female (SMNH-Ap-36647). Abbreviations: aa, anterior additional seta; as, anterior sensillum; cs, clypeal seta; I, inner digit; lb, labral seta; M, median digit; md, dorsal sensillum; ml, lateral sensillum; O, outer digit; p, median posterior seta; pa, posterior additional seta; pp, a pair of sensilla posterior to pseudoculus; ps, posterior sensillum; rs, rostral seta; sr, subrostral seta. Scale bars: 20 µm in A; 10 µm for all other images.

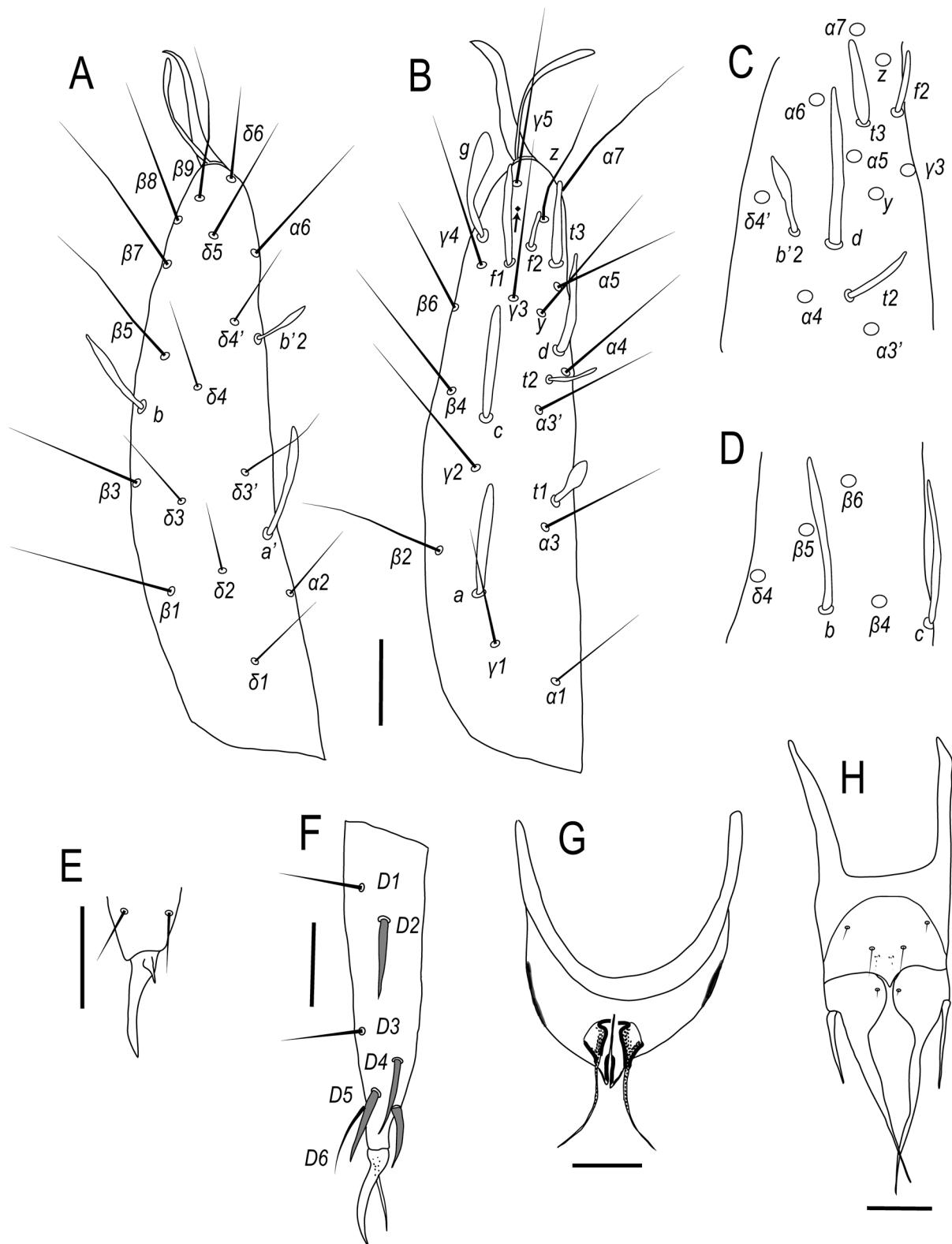


Fig. 6. *Pseudanisentomon vallaticum* sp. nov. A, Exterior view of the foretarsus; B, interior view of the foretarsus; C, distal part of the interior view of the foretarsus; D, central part of the exterior view of the foretarsus; E, distal part of the middle tarsus; F, dorsal view of the hind tarsus; G, female squama genitalis; H, male squama genitalis. Arrow shows pore. A, B, and E-G, Holotype, female (NSMT-Ap 551); C and D, paratype, male (NSMT-Ap 554); H, paratype, male (NSMT-Ap 553). Scale bars: 10  $\mu$ m.

shape and length. Mandible with two teeth (Fig. 5E). Clypeal apodeme distinct (Fig. 5A, B). Pseudoculus with a weak central mark (Fig. 5F), 9 (8-11)  $\mu$ m long, PR=12 (10-13).

Legs. Foretarsus length (Fig. 6A-D) 68 (63-68)  $\mu$ m; claw

12 (12-13)  $\mu$ m, TR=5.8 (4.9-5.7); empodium 12 (12-13)  $\mu$ m, EU=1.0 (0.9-1.0); sensillum  $s$  longer than claw, 15 (14-16)  $\mu$ m. Sensillum  $t_1$  nearer to  $\alpha_3$  than to  $\alpha_3'$ , BS=0.9 (0.8-0.9);  $t_2$  thin;  $t_3$  broad, surpassing base of  $\alpha_7$ ;  $a$  broad,

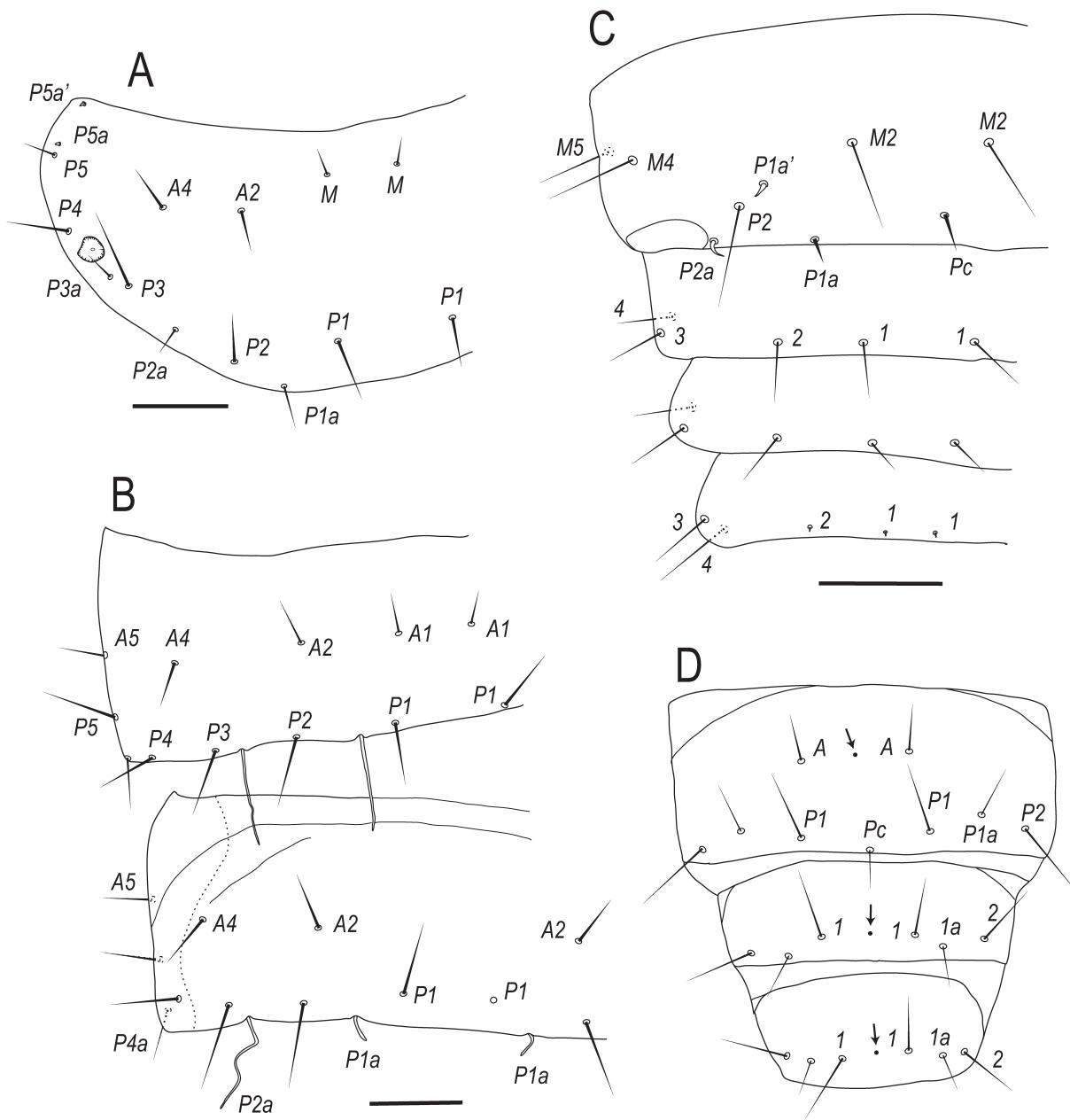


Fig. 7. *Pseudanisentomon villaticum* sp. nov., holotype, female (NSMT-Ap 551). A, Dorsal view of thorax III; B, dorsal view of abdomen VI–VII; C, dorsal view of abdomen VIII–XI; D, ventral view of abdomen VIII–X. Arrows show pores. Scale bars: 20 µm.

slightly closer to  $\gamma_1$  than to  $\gamma_2$ ; b narrowly spatulate, surpassing base of  $\beta_6$ ; c broad, almost reaching base of  $\gamma_3$ ; d broad, reaching base of  $t_3$ ; e absent; g rounded spatulate and large; f1 broad, surpassing base of  $\gamma_5$ ; f2 thin; a' slightly broad; b'1 absent; b'2 small, narrowly spatulate; c' absent; seta x absent. A pore posterior to  $\gamma_5$ . Length of middle tarsus 32 (31–33) µm, length of claw 10 (10–11) µm, empodium short, about 1/5 of claw length, 2 (2) µm (Fig. 6E); hind tarsus 39 (37–39) µm, claw 11 (10–11) µm; empodium longer than 2/3 of claw length (Fig. 6F), 7 (7–9) µm long; on hind tarsus (Fig. 6F), D2 and D4 spine-like.

**Chaetotaxy.** Chaerotaxy as in Table 3 and Fig. 7A–D. On thoracic tergites II–III (Fig. 7A),  $P1a$  and  $P2a$  seta-like;  $P1a$  posterior to  $P1$ – $P2$ ;  $P2a$  on II slightly nearer to  $P2$  than to  $P3$ ;  $P2a$  on III halfway between  $P2$  and  $P3$  or slightly nearer to

$P2$  than to  $P3$ ; on II  $P1a$  length 9 (8–10) µm, shorter than  $P1$ , 11 (10–11) µm; on III  $P1a$  length 9 (9–10) µm, subequal to  $P1$ , 11 (10–11) µm;  $P2a$  on II–III 7 (5–7) and 8 (6–8) µm, respectively, shorter than  $P1a$ . Abdominal tergites II–IV with five pairs of anterior setae ( $A1$ – $5$ ), V–VI with four pairs ( $A1$ , 2, 4, 5); VII with three pairs (A2, 4, 5); IX–X with 4 setae, but 1 and 2 on X rudimentary (Fig. 7C).  $P1a$  on abdominal sternite I,  $P1a$  and  $P2a$  on II–VI and  $P2a$  on VII delicate and longer than  $P1$ , but  $P2a$  on VII subequal to  $P1$  in length;  $P1a$  on VII short, 1/3–1/4 of  $P1$  in length, 5 (5–6) µm long, at hind margin (Fig. 7B); on VIII (Fig. 7C),  $P1a'$  falcate and slightly anterior to  $P2$ ,  $P2a'$  falcate. Setae on thoracic and abdominal sternites all normal; VIII with two anterior and seven posterior setae; IX–X with six setae (Fig. 7D).

**Porotaxy.** Abdominal sternites VIII–X with one medial

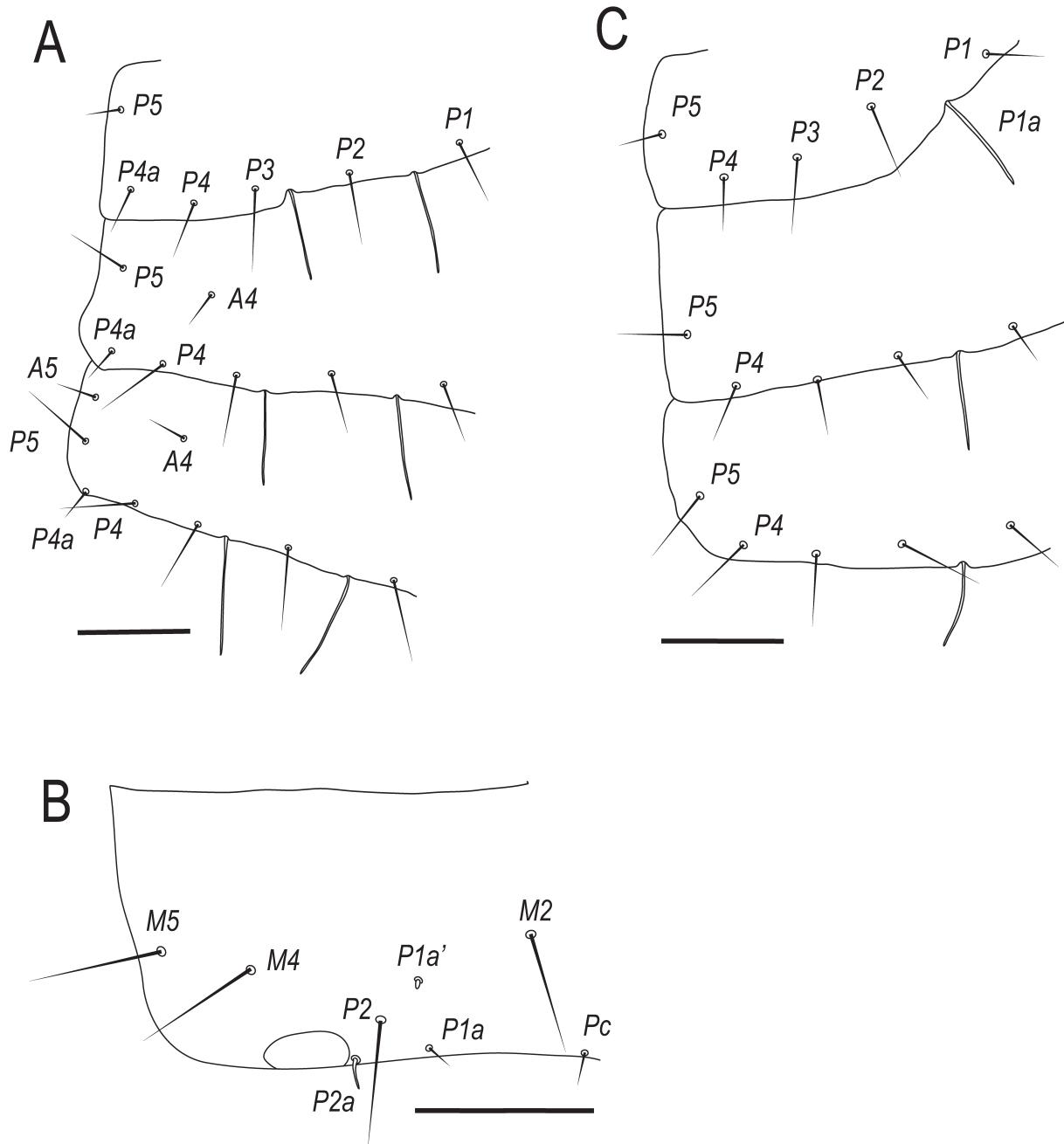


Fig. 8. Larval chaetotaxy of *Pseudanisentomon villaticum* sp. nov. A, Dorsal view of abdomen II-IV of Larva II; B, dorsal view of abdomen VIII of Larva II; C, dorsal view of abdomen II-IV of Larva I. Scale bars: 20  $\mu$ m.

pore (Fig. 7D). Telson with one ventral medial pore.

**Genitalia.** On female squama genitalis (Fig. 6G) caput processus bent against the median edge of stylus in a sharp angle, outer and inner edges of corpus processus sclerotized; filum processus long; proximo-lateral sclerotization present; median sclerotization at posterior part of stylus. Male squama genitalis with short basiperiphallar setae (Fig. 6H).

**Larva II** (n=7). Body length 488–559  $\mu$ m. Head length 85–95  $\mu$ m; pseudoculus 8–9  $\mu$ m long, PR=11. Foretarsus length 59–60  $\mu$ m; claw 11–12  $\mu$ m, TR=4.5–5.0; empodium 10–12  $\mu$ m, EU=0.9–1.0; sensillum s 14  $\mu$ m; shape and position of foretarsal sensilla same as those of imago; BS=0.8–0.9. Length of middle tarsus 25–26  $\mu$ m, length of claw 9  $\mu$ m,

empodium 2  $\mu$ m long; hind tarsus 31–33  $\mu$ m, claw 9–10  $\mu$ m, empodium 5–8  $\mu$ m. P5 on abdominal tergites II and III displaced anteriorly and at same level with A4 on III (Fig. 8A). P1a on abdominal tergite VIII distal to P2 (Fig. 8B).

**Larva I** (n=1). Body length 462  $\mu$ m. Head 91  $\mu$ m long; pseudoculus indistinct. Foretarsus length 54  $\mu$ m; claw 11  $\mu$ m, TR=4.9; empodium 11  $\mu$ m, EU=1.0; sensillum s 13  $\mu$ m; shape and position of foretarsal sensilla same as those of preceding stages. Length of middle tarsus 23  $\mu$ m, length of claw 9  $\mu$ m, empodium 2  $\mu$ m long; hind tarsus 28  $\mu$ m, claw 10  $\mu$ m, empodium 7  $\mu$ m.

**Remarks.** This new species differs from all its congeners by the three pairs of anterior setae on abdominal tergite VII

Table 3. Chaetotaxy of *Pseudanisentomon villaticum* sp. nov.

	Larva I			Larva II		Imago	
	Formula	Primary setae	Formula	Secondary setae	Formula	Tertiary and complementary setae	
<b>(Dorsal)</b>							
Thorax	I	2	1	4	2	4	
	II	4	A2, M	6	A4	6	
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 3a	16	
	III	4	A2, M	6	A4	6	
		12	P1, 1a, 2, 3, 4, 5	20	P2a, 3a, 5a, 5a'	20	
Abdomen	I	0	0	4	A1, 2	4	
		12	P1, 1a, 2, 3, 3a, 3a'	12		12	
	II	0		0		10	A1, 2, 3, 4, 5
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 4a	16	
	III	0		2	A4	10	A1, 2, 3, 5
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 4a	16	
	IV	0		4	A4, 5	10	A1, 2, 3
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 4a	16	
V-VI	0			4	A4, 5	8	A1, 2
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 4a	16	
VII	0			4	A4, 5	6	A2
		12	P1, 1a, 2, 3, 4, 5	16	P2a, 4a	16	
VIII	6	M2, 4, 5	6			6	
	7	Pc, 1a, 2, 2a	9	P1a'		9	
IX				8	1, 2, 3, 4	8	
X-XI						8	1, 2, 3, 4
Telson	9		9			9	
<b>(Ventral)</b>							
Thorax	I-II	4-2	A1, 2, M	6-2	A3	6-2	
		2	P2	6	P1, 3	6	
	III	4-2	A1, 2, M1	6-2	A3	6-4	M2
		2	P2	6	P1, 3	8	P4
Abdomen	I	4	A1, 2	4		4	
		4	P1, 2	4		4	
	II-III	2	A1	4	A2	6	A3
		4	P1, 2	4		4	
	IV-VII	2	A1	4	A2	6	A3
		6	P1, 2, 3	8	P2a	10	P2a'
	VIII	0		0		2	A
		5	Pc, 1, 2	7	P1a	7	
IX				4	1, 2	6	1a
X						6	1, 1a, 2
XI						8	1, 2, 3, 4
Telson	12		12			12	

(four pairs in other species). Nakamura (2010; table 2) incorrectly described tergite VII as having three pairs of anterior setae (A2, 4, and 5) in for *P. donan* Nakamura, 2010; however, it actually has four pairs of setae (A1, 2, 4, and 5), as shown in the following figure: Nakamura (2010: fig. 6D). Aside from this feature, this new species resembles *P. songkiangensis* by lacking foretarsal sensilla *b'1* and *c'* and by *a* being situated nearer to *y1*; however, it is discriminated from *P. songkiangensis* by the length of the empodium on the middle tarsus (longer in *P. songkiangensis*) and the lengths of foretarsal sensilla *t3, d*, and *f1* (shorter in *P. songkiangensis*).

**Distribution.** Japan, known only from the Nasu Imperial Villa.

**Etymology.** The specific name is derived from the Nasu Imperial Villa, the type locality.

## Discussion

The posterior setae *P5* on abdominal tergites II-III are anteriorly displaced in the larva II of *P. villaticum* sp. nov. The anterior displacement of *P5*, however, is not observed in larva I (Fig. 8C) and adults. The same phenomenon is observed in larva II of some *Eosentomon* species (Nakamura 1997, 2010; Nakamura and Likhitrakarn 2009). The anterior setae *A4* and *A5* appear in larva II, but *A5* is not present on abdominal ter-

gites II and III. All anterior setae occur in matus junior. On the other hand, the same anterior displacement has been observed in adults of *E. kimum* Imadaté, 1964, *E. nupri* Nakamura, 1983, and *E. rishir* Nakamura, 2004, which lack A5 on their abdominal tergites (Nakamura 1983, 2004). The anterior displacement of P5 is probably a compensatory effect due to the absence of A5. It is likely that this is a common phenomenon in larvae II of the family Eosentomidae.

### Key to species of *Pseudanisentomon*

1. Abdominal sternite VIII with single row of seven posterior setae ... *P. dolichempodium* (Yin and Zhang, 1982)
- Abdominal sternite VIII with double rows of two anterior and seven posterior setae ..... 2
2. Abdominal sternites IX–X with six setae ..... 3
- Abdominal sternites IX–X with four setae ..... 15
3. Abdominal tergite VII with three pairs of anterior setae (A2, 4, and 5); foretarsal seta x absent .....  
..... *P. villaticum* sp. nov.
- Abdominal tergite VII with four pairs of anterior setae (A1, 2, 4, and 5); foretarsal seta x present ..... 4
4. Abdominal tergites II–III with four pairs of anterior setae (A1, 2, 4, and 5) ..... 5
- Abdominal tergites II–III with five pairs of anterior setae (A1, 2, 3, 4, and 5) ..... 6
5. Foretarsal sensillum b'1 absent; empodium of middle and hind tarsus long ..... *P. songkiangensis* (Yin, 1977)
- Foretarsal sensillum b'1 present; empodium of middle and hind tarsus short ..... *P. trilinum* (Zhang and Yin, 1981)
6. Abdominal tergite IV with four pairs of anterior setae (A1, 2, 4, and 5) ..... 7
- Abdominal tergite IV with five pairs of anterior setae (A1, 2, 3, 4, and 5) ..... 8
7. Pseudoculus with striae and two beads; foretarsal sensillum b'1 absent ... *P. sininotialis* Zhang and Yin, 1984
- Pseudoculus with striae but without beads; foretarsal sensillum b'1 present ..... *P. jiangxiensis* Yin, 1987
8. Foretarsal sensillum b'1 absent .... *P. nasuense* sp. nov.
- Foretarsal sensillum b'1 present ..... 9
9. Foretarsal sensillum b'1 nearer to δ3' than to δ4' ..... 10
- Foretarsal sensillum b'1 halfway between δ3' and δ4' ..... 14
10. Labral setae absent; empodium on the middle tarsus less than 1/5 of claw length ..... *P. donan* Nakamura, 2010
- Labral setae present; empodium on the middle tarsus longer than 1/3 of claw length ..... 11
11. Foretarsus less than 70 μm ..... 12
- Foretarsus longer than 90 μm ..... 13
12. Pseudoculus without striae; foretarsal sensillum c' longer than t3 ..... *P. parvum* Nakamura, 2010
- Pseudoculus with striae; foretarsal sensillum c' shorter than t3 ..... *P. minystignum* (Yin, 1979)
13. Pseudoculus with two or five striae; foretarsal sensillum a halfway between γ1 and γ2 ..... *P. meihwa* (Yin, 1965)
- Pseudoculus with five striae and three beads; foretarsal sensillum a nearer to γ1 than to γ2 .....  
..... *P. wanense* Zhang, 1987
14. Labral setae present; empodium on the middle tarsus about 1/5 of claw length ..... *P. ishii* Nakamura, 1996
- Labral setae absent; empodium on the middle tarsus about 1/3 of claw length ..... *P. babai* (Imadaté, 1964)
15. Empodia of middle and hind tarsus longer than 1/3 of claw length ..... 16
- Empodia of middle and hind tarsus less than 1/5 of claw length ..... 20
16. Foretarsal sensillum b'1 absent ..... 17
- Foretarsal sensillum b'1 present ..... 18
17. Pseudoculus simple; abdominal tergite IV with five pairs of anterior setae (A1, 2, 3, 4, and 5) .....  
..... *P. guangxiensis* (Yin and Zhang, 1982)
- Pseudoculus with three striae; abdominal tergite IV with four pairs of anterior setae (A1, 2, 4, and 5) .....  
..... *P. huichouense* Zhang and Yin, 1984
18. Foretarsal sensillum c' present; abdominal tergite II with four pairs of anterior setae (A1, 2, 4, and 5) .....  
..... *P. sheshanensis* (Yin, 1965)
- Foretarsal sensillum c' absent; abdominal tergite II with five pairs of anterior setae (A1, 2, 3, 4, and 5) ... 19
19. Pseudoculus simple; foretarsal sensillum c' present....  
..... *P. molykos* Zhang and Yin, 1984
- Pseudoculus with three striae; foretarsal sensillum c' absent ... *P. cangshanense* Imadaté, Yin, and Xie, 1995
20. Abdominal tergite III with five pairs of anterior setae (A1, 2, 3, 4, and 5) ..... 21
- Abdominal tergite III with four pairs of anterior setae (A1, 2, 4, and 5) ..... 22
21. Pseudoculus simple; foretarsal sensillum b'1 absent ...  
..... *P. paurophthalmum* Zhang and Yin, 1984
- Pseudoculus with three long and two short striae; foretarsal sensillum b'1 present .....  
..... *P. lishuiensis* Bu, Gao, and Luan, 2020
22. Pseudoculus without inner structure; abdominal tergite II with four pairs of anterior setae (A1, 2, 4, and 5) ....  
..... *P. pedanempodium* (Zhang and Yin, 1981)
- Pseudoculus with inner structure; abdominal tergite II with five pairs of anterior setae (A1, 2, 3, 4, and 5) ... 23
23. Pseudoculus with “#” like striae; foretarsal sensillum c' absent ..... *P. yongxingense* Yin, 1988
- Pseudoculus with a central bead; foretarsal sensillum c' present ..... *P. yaoshanensis* Zhang and Yin, 1984

### Acknowledgements

I am indebted to His Majesty the Emperor Emeritus for providing the opportunity to conduct research and study in this area. I am grateful to the Imperial Household Agency staff for their assistance and cooperation in the survey, and to Mr. K. Furuno, Dr. K. Ishii, the late H. Sakayori, Mr. Y. Takahashi, Mr. T. Shinkawa, and Dr. Y. Minamiya for providing specimens. I would like to thank two anonymous reviewers for their constructive comments and invaluable suggestions on the manuscript, and Enago ([www.enago.jp](http://www.enago.jp)) for the English language review.

## References

- Berlese, A. 1908. Nuovi Acerentomidi. *Redia* 5: 16–19.
- Berlese, A. 1909. Monografia dei Myriomata. *Redia* 6: 1–182.
- Bernard, E. C. 1975. A new genus, six new species, and records of Protura from Michigan. *The Great Lakes Entomologist* 8: 157–181.
- Bernard, E. C. 1990. New species, clarifications, and changes in status within *Eosentomon* Berlese (Hexapoda: Protura: Eosentomidae) from the United States. *Proceedings of the Biological Society of Washington* 103: 861–890.
- Bu, Y., Gao, Y., and Luan, Y. 2020. Two new species of Protura (Arthropoda: Hexapoda) from Zhejiang, East China. *Entomotaxonomia* 42: 163–177.
- Copeland, T. P. 1978. A new genus and two new species of Eosentomoidae (Protura: Eosentomidae). *Proceedings of the Entomological Society of Washington* 80: 473–484.
- Imadaté, G. 1974. *Fauna Japonica. Protura (Insecta)*. Keigaku Publishing Company, Ltd., Tokyo, 351 pp.
- Nakamura, O. 1983. *Eosentomon nupri* sp. nov. from Hokkaido (Protura, Eosentomidae). *Kontyû*, Tokyo 51: 596–600.
- Nakamura, O. 1997. Protura from Taiwan. *Edaphologia* 5: 17–53.
- Nakamura, O. 2004. A new species of the genus *Eosentomon* (Insecta: Protura: Eosentomidae) from Rishiri Island, Hokkaido, Northern Japan. *Species Diversity* 9: 359–366.
- Nakamura, O. 2010. Taxonomic revision of the family Eosentomidae (Hexapoda: Protura) from Japan. *Zootaxa* 2701: 1–109.
- Nakamura, O. 2019. Protura from the Chōku-tei bower in the Nasu Imperial Villa, Nasu-machi, Tochigi Prefecture, central Japan. *Bulletin of Tochigi Prefectural Museum* 36: 15–19. [In Japanese with English abstract]
- Nakamura, O. and Likhitrakarn, N. 2009. Protura (Hexapoda) from DoiSuthep-Pui National Park, Chiang Mai, Thailand. *Zootaxa* 2121: 1–16.
- Tipping, C. and Allen, R. T. 1994. Description of two new species of *Eosentomon* from Ouachita Mountains of Arkansas (Protura, Eosentomidae). *Journal of the Kansas Entomological Society* 67: 253–266.
- Tuxen, S. L. 1964. *The Protura. A Revision of the Species of the World with Keys for Determination*. Hermann, Paris, 360 pp.
- Tuxen, S. L. and Imadaté, G. 1975. The Protura of the Bismarck Archipelago and Solomon Islands. *Bulletin of the British Museum (Natural History). Entomology* 31: 331–375.
- Yin, W. Y. 1999. *Protura, Fauna Sinica, Arthropoda*. Science Press, Beijing, China, 510 pp., 8 pls. [In Chinese with English summary]
- Zhang, Z. and Yin, W. Y. 1984. A revision of the species and genera of the subfamily Anisentominae (Protura: Eosentomidae). *Entomotaxonomia* 6: 59–76.