Zoological Studies **63**:42 (2024)
doi:10.6620/ZS.2024.63-42

Zoological Studies

Open Access

The Cryptic Diversity of the Terrestrial Microarthropods, *Ptenothrix* Börner (Collembola: Dicyrtomidae) from Taiwan: New Species Plus the Lectotype Designation for *Ptenothrix denticulata* (Folsom, 1899)

Hsin-Ju Cheng[1,§], Bruno Cavalcante Bellini[2,§], Frans Janssens[3], Taizo Nakamori[4], and Chih-Han Chang[1,5,*]

[1]*Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617, Taiwan.*
**Correspondence: E-mail: chihhanchang@ntu.edu.tw, chihhanchang.ntu@gmail.com (Chang)*
E-mail: hsinjucheng.tw@gmail.com (Cheng)
[2]*Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte (UFRN), Natal 59072-970, RN, Brazil.*
E-mail: entobellini@gmail.com (Bellini)
[3]*Evolutionary Ecology, Department of Biology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerpen, Belgium.*
E-mail: frans.janssens@collembola.org (Janssens)
[4]*Department of Environment and Natural Sciences, Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama 240-8501, Japan. E-mail: nakamori-taizo-gc@ynu.ac.jp (Nakamori)*
[5]*Department of Life Science, National Taiwan University, Taipei 10617, Taiwan*

lsid:zoobank.org:pub:16537856-6A02-48A7-928B-C8EB5353C0C4
[§]HJC and BCB contributed equally to this work.
Received 3 May 2024 / Accepted 19 July 2024 / Published 12 November 2024
Communicated by John Wang

This is the first taxonomic study of Collembola in Taiwan integrating morphological and molecular evidence to investigate the Taiwanese species in the genus *Ptenothrix* Börner. We discovered that specimens previously identified as *Ptenothrix denticulata* (Folsom, 1899) actually consist of several cryptic species, of which we described two species new to science. Our data revealed that, although these species are remarkably similar to each other, they can be distinguished by color patterns, chaetotaxic characters and DNA barcoding (*COI*). We also designated one of the syntypes of *Ptenothrix denticulata* (Folsom, 1899) as its lectotype, and treated *Dicyrtoma denticulata* (Salmon 1964) as a synonym of *Ptenothrix denticulata* (Salmon 1964) (syn. nov.). Lastly, our study suggests that the diversity of Collembola in Taiwan is still poorly understood, with a high potential for new studies focusing on these microarthropods.

Key words: Soil fauna, Systematics, Genetic diversity, Phylogeny, Ptenothricinae

BACKGROUND

Collembola are one of the most abundant groups of terrestrial microarthropods that live in various habitats, including leaf litter, soil, plant surfaces, fungal sporocarps, decaying wood, etc (Bellinger et al. 1996–2024). Within the litter-soil habitat, they are recognized as one of the most prevalent organisms, often attaining densities of up to 40,000 individuals per square meter in temperate grasslands or forests (Orgiazzi et al. 2016). To date, approximately 9,500 extant Collembola species have been described globally, with estimates

Citation: Cheng HJ, Bellini BC, Janssens F, Nakamoriv T, Chang CH. 2024. The cryptic diversity of the terrestrial microarthropods, *Ptenothrix* Börner (Collembola: Dicyrtomidae) from Taiwan: new species plus the lectotype designation for *Ptenothrix denticulata* (Folsom, 1899). Zool Stud **63**:42. doi:10.6620/ZS.2024.63-42.

suggesting that the group species richness may actually reach 50,000 or even more (Hopkin 1997; Bellinger et al. 1996–2024). In spite of past endeavors, a large amount of the Collembola diversity is still unknown, particularly in countries that lack a history of taxonomic research of these taxa, such as Taiwan.

Dicyrtomidae Börner, 1906 (*sensu* Deharveng 2004) is a family of springtails from the order Symphypleona, and its species are mostly atmobiotic (Bretfeld 1999), inhabiting plant leaf and litter surfaces. Their body is about 1 to 3 millimeters long and pigmented (some species show very distinct color patterns), and they have long limbs and a full set of eight ocelli per side of the head. The main features that separate the Dicyrtomidae from other Symphypleona families are aspects of the antennae, which have an antennomere IV shorter than half of III, and antennae elbowed between antennomeres II and III (Bretfeld 1999). Currently, Dicyrtomidae comprises two subfamilies: Ptenothricinae Richards, 1968, which features the presence of bothriotrichum D in adults, and Dicyrtominae Richards, 1968, which lacks this characteristic (Bretfeld 1999).

Although Dicyrtomidae are colorful and have relatively large body sizes, not many in-depth studies have applied integrative and modern methods to explore the diversity of this family. The lack of fundamental studies has significantly hindered our understanding on the biology and ecology of dicyrtomids, for instance, the underlying mechanisms of their coloration polymorphism.

In Asia, studies related to Dicyrtomidae have not seen much progress after the 1970s (*e.g.*, Yosii 1970; Yosii and Lee 1963). These past studies were mainly based on morphology and focused on taxonomy. After this, little molecular and other complementary evidence has been used to study this fauna (*e.g.*, Cheng et al. 2022). This lack of effort has greatly underestimated the Dicyrtomidae species diversity, especially when cryptic species exist. In addition, morphological polymorphism, *e.g.*, color pattern variations, could be misleading since species identification is only based on morphological characteristics, and previous studies of dicyrtomids lack other useful diagnostic details applied in the current taxonomy of Symphypleona (Mateos 2008; Katz et al. 2015; Potapov et al. 2018). In Taiwan, only seven species of Dicyrtomidae have been recorded so far (Cheng et al. 2022). However, the diversity of Taiwanese Dicyrtomidae clearly surpasses the existing records (H.-J. Cheng, pers. obs.), and more research is needed to better circumscribe this family.

Ptenothrix is the most species-rich genus in Dicyrtomidae, with about 80 described extant species (Bellinger et al. 1996–2024). Compared to other Dicyrtomidae, the main diagnostic characteristics of the genus include: (1) head dorsally with prominent spine-like chaetae; (2) large abdomen without protuberance, but with the full set of bothriotricha (A–D), and posteriorly dorsally covered by rows of small spine-like chaetae; (3) neosminthuroid chaetae absent from the parafurcal area; (4) posterior side of hind tibiotarsus with 2 (rarely 3) modified serrated chaetae; (5) claws usually without a tunica; (6) tenaculum with 4+4 teeth; and (7) outer and inner chaetae of dens often coarsely serrated (Yosii and Lee 1963; Yosii 1970; Bretfeld 1999; Fjellberg 2007; Oliveira et al. 2020; Jo and Park 2023). So far, only three species of *Ptenothrix* have been documented in Taiwan: *Ptenothrix denticulata* (Folsom, 1899), *Ptenothrix corynophora* Börner, 1909, and *Ptenothrix monochroma* Yosii & Lee, 1963 (Cheng et al. 2022). The number of described *Ptenothrix* spp. in Taiwan is fewer than those of neighboring countries; for example, at least 17 exist in Japan (Ito et al. 2012) and seven in Korea (Jo and Park 2023). Apparently, the diversity of *Ptenothrix* in Taiwan is poorly understood. Furthermore, many Asiatic species of the genus are remarkably similar to each other in overall chaetotaxy and even in color pattern (Folsom 1899; Börner 1909; Yosii and Lee 1963; Lin and Xia 1985a b), a condition that raises doubts about the validity of some of these species, or contrarily, supports the presence of cryptic diversity within the genus.

This study aims to investigate the cryptic diversity of *Ptenothrix* in Taiwan. We hypothesize that specific color patterns can be reliable diagnostic characteristics of morphologically similar species in the genus. The differences of color pattern on the head vertex of specimens in Taiwan made us hypothesize that they are not the recorded *Ptenothrix denticulata* (Folsom, 1899), but are actually two new and distinct species.

MATERIALS AND METHODS

Specimen collection

Specimens of *Ptenothrix* were collected throughout Taiwan during 2021–2023 (Fig. 1). The collection methods included beating vegetation and aspirating from grass blades of *Miscanthus*, leaves of Bambusoideae, dead leaves of understory vegetation, and rotten wood (Fig. 2), as well as setting Malaise traps. Specimens were preserved in 85% ethanol and stored at 4°C until morphological examination and molecular analysis. In order to confirm the identities of the sampled specimens, two type specimens of *Ptenothrix denticulata* (Folsom, 1899) deposited at the Smithsonian National Museum of Natural History

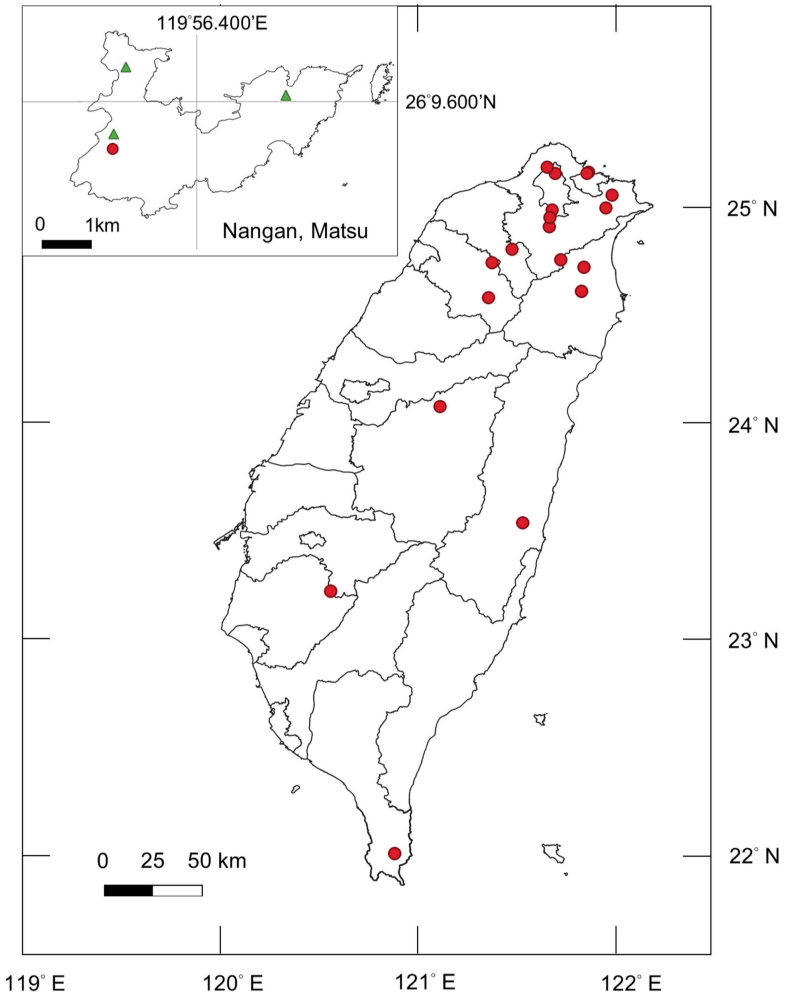

Fig. 1. Sampling localities of the two new species in Taiwan. Red dots represent *Ptenothrix taiwanensis* sp. nov. sampling sites, mainly distributed in north and central Taiwan and one locality in Nangan Island in Matsu, which could be due to recent human intervention. Green triangles represent *Ptenothrix matsuensis* sp. nov., with known distribution only in Nangan Island, Matsu.

Fig. 2. *In situ* images of specimens of *Ptenothrix taiwanensis* sp. nov., indicating that rotten wood and algae-covered surface are two of their preferred habitats.

(NMNH), Washington, USA (USNMENT01747048) and the Museum of Comparative Zoology in Harvard University (MCZ 14770) were examined (Fig. 3). Additionally, we attempted to collect topotype specimens of *Ptenothrix denticulata* (Folsom, 1899) in its type locality in Japan (Komaba, Tokyo). Specimens that were newly collected and analyzed in this study were deposited at the NTU Insect Museum, Department of Entomology, National Taiwan University (NTUE), and the National Museum of Natural Science in Taichung, Taiwan (NMNS).

Molecular analysis

For molecular phylogenetic analysis, DNA was extracted from entire specimens using the QIAamp DNA Micro Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. The specimens were subjected to an overnight incubation at 56°C subsequent to the addition of ATL buffer containing proteinase K. After this, 1 µl of carrier RNA was introduced into buffer AL. The resultant DNA-containing buffer was transferred into a fresh column. Simultaneously, the voucher specimens were preserved in a solution of 75% ethanol after DNA extraction so as to link morphology with genetic data. After extraction, the DNA was eluted in a 50 µl buffer and subsequently stored at -20°C. The mitochondrial marker cytochrome *c* oxidase subunit 1 (*COI*) was chosen for phylogenetic analysis. Polymerase chain reactions (PCRs) were conducted using primers

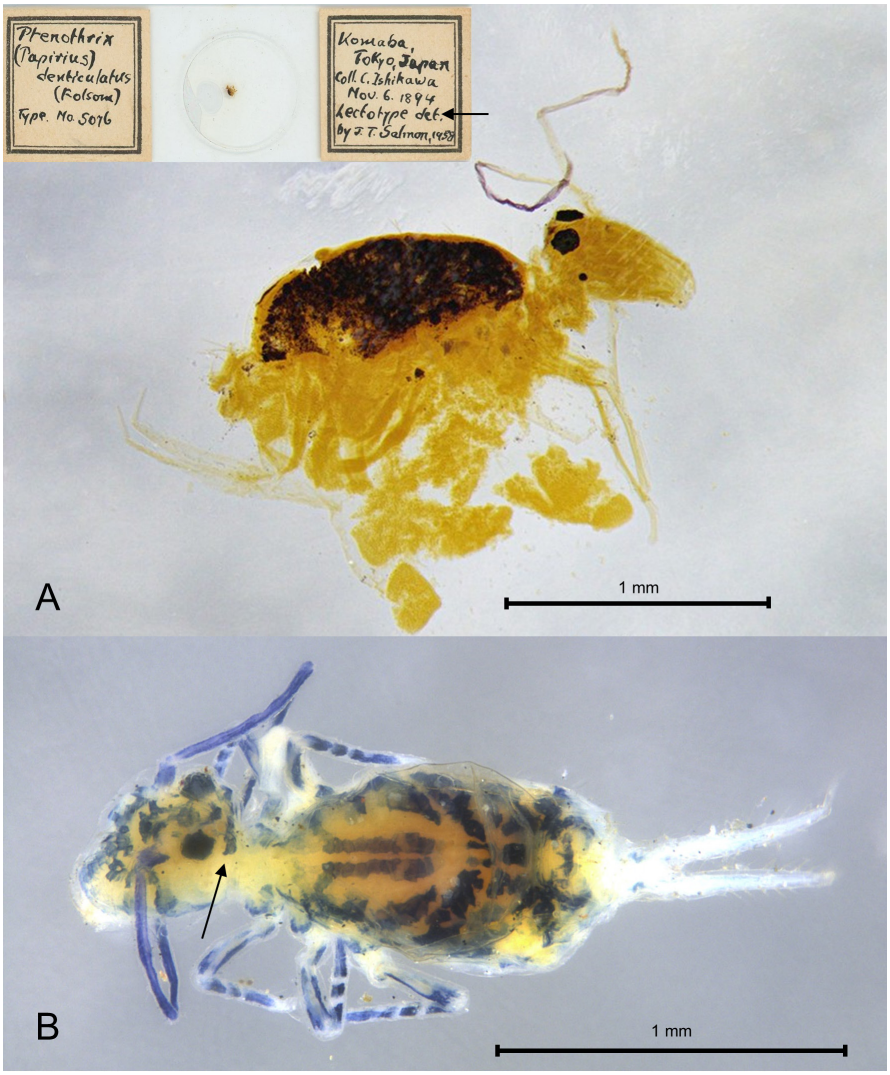

Fig. 3. Syntypes of *Ptenothrix denticulata*. (A) Slide specimen USNMENT01747048 from the Smithsonian National Museum of Natural History; arrow indicates that Salmon intended to designate it as the lectotype. (B) Ethanol specimen MCZ 14770 from the Museum of Comparative Zoology at Harvard University (the picture was provided by the museum); the arrow indicates the presence of a transversal band of pigment on the head vertex.

LCO1490 and HCO2198 (Folmer et al. 1994), and the PCR cycles followed Cheng et al. (2022).

The obtained sequences were assembled using Geneious (Biomatters Ltd., Auckland, New Zealand), double-checked by eye, and aligned employing ClustalX 2.0 (Larkin et al. 2007). Recorded species of Dicyrtomidae in Taiwan and neighboring regions, including *Ptenothrix corynophora* Börner, 1909, *Ptenothrix monochroma* Yosii & Lee, 1963, *Ptenothrix huangshanensis* Chen & Christiansen, 1996, *Papirioides jacobsoni* Folsom, 1924, and *Papirioides caishijiensis* Wu & Chen, 1996, were included in the phylogenetic analyses because they are the only species that have reliable *COI* sequences on GenBank. *Sminthurus viridis* (Linnaeus, 1758) (Sminthuridae, Symphypleona) was used as the outgroup. Kimura's two-parameter distances of the aligned sequences were calculated with MEGA X (Kumar et al. 2018). Maximum Likelihood analysis was performed employing IQ-TREE (Nguyen et al. 2015). The selection of optimal partitioning schemes and molecular evolution models for the phylogenetic analyses was conducted using PartitionFinder (Lanfear et al. 2016). Clades exhibiting *p*-distances of *COI* exceeding 8% were tentatively designated as potential species following the approach outlined by Katz et al. (2015). These findings were subsequently integrated with morphological characters to facilitate species delimitation.

Examining slide specimens

The ethanol-preserved specimens were clarified with Nesbitt's fluid (chloral hydrate 40 g, distilled water 25 ml, concentrated hydrochloric acid 2.5 ml), cleaned with Arlé's fluid (chloral hydrate 9 g, 85% lactic acid 9 ml, glycerin 9 g, 9 drops of formalin) and mounted in Hoyer's medium (gum arabic 6 g, chloral hydrate 40 g, glycerin 4 ml, distilled water 10 ml) (Arlé and Mendonça 1982; Bellinger et al. 1996–2024). Slide and ethanol-preserved specimens were examined using a Nikon SMZ800N stereomicroscope equipped with a plan Apo 1× objective lens and a Nikon ECLIPSE E200 compound microscope and photographed using a TOUPCAM MTR3CMOS07100KPA digital camera.

For the chaetal terminology, we followed: Betsch and Waller (1994) for the head and large abdomen chaetotaxy; Fjellberg (1999) for the labial palp; Cipola et al. (2014) for the labral chaetotaxy; Betsch (1997) for the small abdomen, also using the labels provided by Yosii and Lee (1963), as an alternative description for comparison between the new species and other described ones; and Bretfeld (2001) for dorsal chaetae of the dens. Chaetae labels are marked in bold in the text. Abbreviations used in descriptions are: Ant—antennal segment(s), Abd—abdominal segment(s), Th—thoracic segment(s). Body and appendages covered by different types of chaetae are represented in figure 4.

Examining specimens with SEM

For scanning electron microscopy (SEM), specimens were dehydrated (Schneeberg et al. 2017) and dried at critical point using a Hitachi HCP-2 Critical Point Dryer. Dried specimens were glued on a carbon conductive tape, sputter coated with platinum, and mounted on a specimen holder. Finally, images were captured using a Hitachi Tabletop TM-3000 scanning electron microscope under Hitachi TM3000 software.

RESULTS

Examination of the archived types of *Ptenothrix denticulata* suggests that in 1899, Folsom described the species based on three type specimens without designating a holotype (Folsom 1899). Therefore, in accordance with ICZN Article 73.2, all three specimens of the type series can be automatically considered syntypes. According to Salmon (1964: 634 as *Dicyrtoma* and p. 642 as *Ptenothrix*), the specimens of the type series have been preserved: one as holotype and as *Dicyrtoma* in the Museum of Comparative Zoology in Harvard University, USA (now missing), and two as paratypes, one in the Smithsonian

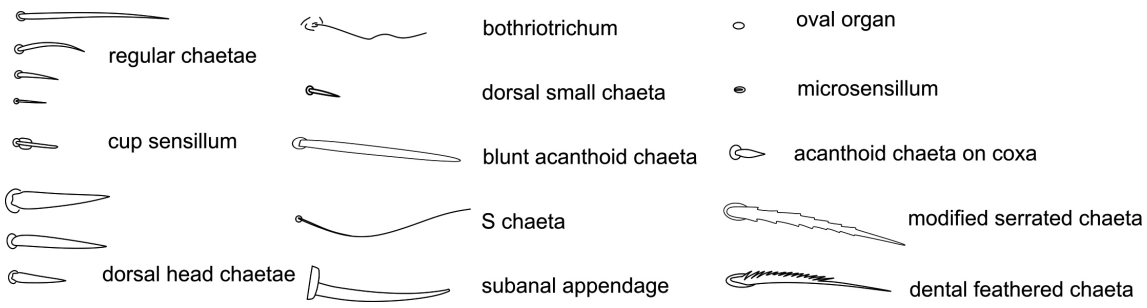

Fig. 4. Chaetae symbols used in the morphological descriptions of the new species.

National Museum of Natural History, Washington, USA (USNMENT01747048; Fig. 3A) and another in the Museum of Comparative Zoology in Harvard University, USA (MCZ14770; Fig. 3B). The slide specimen USNMENT01747048 is not in ideal condition and the gut contents greatly decrease the visibility of its chaetotaxy, making it impossible to verify its morphology in detail. Using the images of the ethanol specimen MCZ14770 provided by the Museum of Comparative Zoology at Harvard University, we were able to confirm that there is a continuous transverse stripe behind the eyes, which is consistent with the figures in the original description (Folsom 1899). However, this specimen is severely deformed, and it is impossible to examine further characteristics in detail. Therefore, although the two specimens of the type series exist, it is not possible to study their morphology in detail to redescribe the species. A redescription based on more recent materials from the type locality is urgently needed.

Fourteen *Ptenothrix* specimens from the type locality of *Ptenothrix denticulata* (Folsom, 1899) in Japan (Komaba, Tokyo) were examined, and all specimens have a discontinuous transverse stripe on the vertex of the head, consistent with the original description of *P. denticulata* var. *catenata* Börner, 1909. However, according to the original description and the type specimen deposited at Harvard University, *Ptenothrix denticulata* has a continuous transverse stripe on the head vertex. Thus, the specimens collected from the type locality were identified as *P. denticulata* var. *catenata*. According to Article 45.6.4 of ICZN, since *Ptenothrix denticulata* var. *catenata* was published before 1961, and the author explicitly used the term "var.", it is now a subspecies: *Ptenothrix denticulata catenata* Börner, 1909.

Among the 67 specimens collected throughout Taiwan, we recognized two morphospecies that are morphologically similar to *Ptenothrix denticulata* (Fig. 5A–F). However, we were unable to find any *P. denticulata* topotypes in the type locality in Japan after several attempts. Based on the original description and re-description of *P. denticulata* (Folsom, 1899; Yosii and Lee 1963), we discovered that the two morphospecies differ considerably from *P. denticulata* in the dorsal head patterns and the number of teeth on the basal unguiculus. The mean interspecific K2P distance between the two morphospecies was 16.7%, comparable to the interspecific genetic variations of the analyzed *Ptenothrix* specimens (14.0–17.5%; Table 1). Additionally, both morphospecies were recovered as independent monophyletic lineages in the maximum likelihood analysis (Fig. 6). Thus, based on both morphological and molecular results, we concluded that the two morphospecies are indeed two species new to science, namely *Ptenothrix taiwanensis* sp. nov. and *Ptenothrix matsuensis* sp. nov. *Ptenothrix taiwanensis* sp. nov. was mainly found in the low elevations in north and central Taiwan, whereas *P. matsuensis* sp. nov. was collected from Nangan Island in Matsu during the wet season (Table S1). The two new species are described below.

Order Symphypleona Börner, 1901 *sensu* Bretfeld, 1986
Suborder Appendiciphora Bretfeld, 1986
Superfamily Dicyrtomoidea Börner, 1906 *sensu* Bretfeld, 1994
Family Dicyrtomidae Börner, 1906
Subfamily Ptenothricinae Richards, 1968 *sensu* Bretfeld, 1999

Genus *Ptenothrix* Börner, 1906

Genus diagnosis: Large abdomen without protuberance. Head, large abdomen anteriorly, and Abd VI with large spines (blunt acanthoid chaetae). Large abdomen posteriorly with longitudinal rows of short spines. Bothriotrichia A and D present on adults. Neosminthuroid chaetae missing on the parafurcal area. Dorsal valve of small abdomen dorsally with 5 chaetae arranged in two transverse rows; anterior with 3 chaetae and posterior with 2 robust, large and apically rounded chaetae (blunt acanthoid chaetae). Tibiotarsus III posteriorly with 2 (or rarely 3) modified serrated chaetae. Claws mostly without a tunica. Retinaculum with 4+4 teeth. Outer and inner dorsal chaetae of dens often serrated (based on Yosii and Lee 1963; Yosii 1970; Bretfeld 1999; Fjellberg 2007; Oliveira et al. 2020; Jo and Park 2023).

Type species: *Podura atra* Linnaeus, 1758.

Ptenothrix taiwanensis sp. nov.

(Figs. 5A–C, 7–11, 12A, 12C, 13, Table 2)
urn:lsid:zoobank.org:act:DC999C0A-A464-458B-99F0-0E65B70FD2CB

Ptenothrix denticulata (Folsom, 1899): Cheng et al. 2022, p. 137–138 (text-fig. 4A).

Type material: TAIWAN: Holotype ♀ on slide: Taiwan, New Taipei City, Xindian Dist., Changfu Temple (24.91491, 121.53243), 7, May. 2022. by searching rotten wood, HJ Cheng, DY Cheng, JK Cheng leg. (NTUE13100001). 4 paratypes on slides: 3♀1♂, same data as holotype (1♀1♂ in NTUE: ♀ NTUE13100002, ♂ NTUE13100003; 2♀in NMNS: 8848-1, 8848-2). 3 paratypes in ethanol: 2♀1 sex undetermined (DNA voucher), same data as holotype

(1♀1 sex undetermined in NTUE: ♀ NTUE13100004, sex undetermined NTUE13100005; 1♀ in NMNS: 8848-3).

Other analyzed slide specimens: TAIWAN: 1♀, Keelung City, Anle Dist., Lover's Lake Park (25.159123, 121.704894), 23. September. 2022, by searching rotten wood, leg. HJ Cheng, ZJ Chang (NTUE13300001); 1♀, Yilan County, Datong Township (24.619015, 121.679917), 1. October. 2022, by beating vegetation, leg. HJ Cheng, ML Fu (NMNS: 8848-4); 2♂, Pingtung County, Manzhou Township, 31. June to 4. July. 2009, leg. ML Jeng (NMNS: 8848-5, 8848-6); 3♀1♂, Hualien County, Da Nong Da Fu Forest Park, 18. November to 12. December. 2018, flight interception

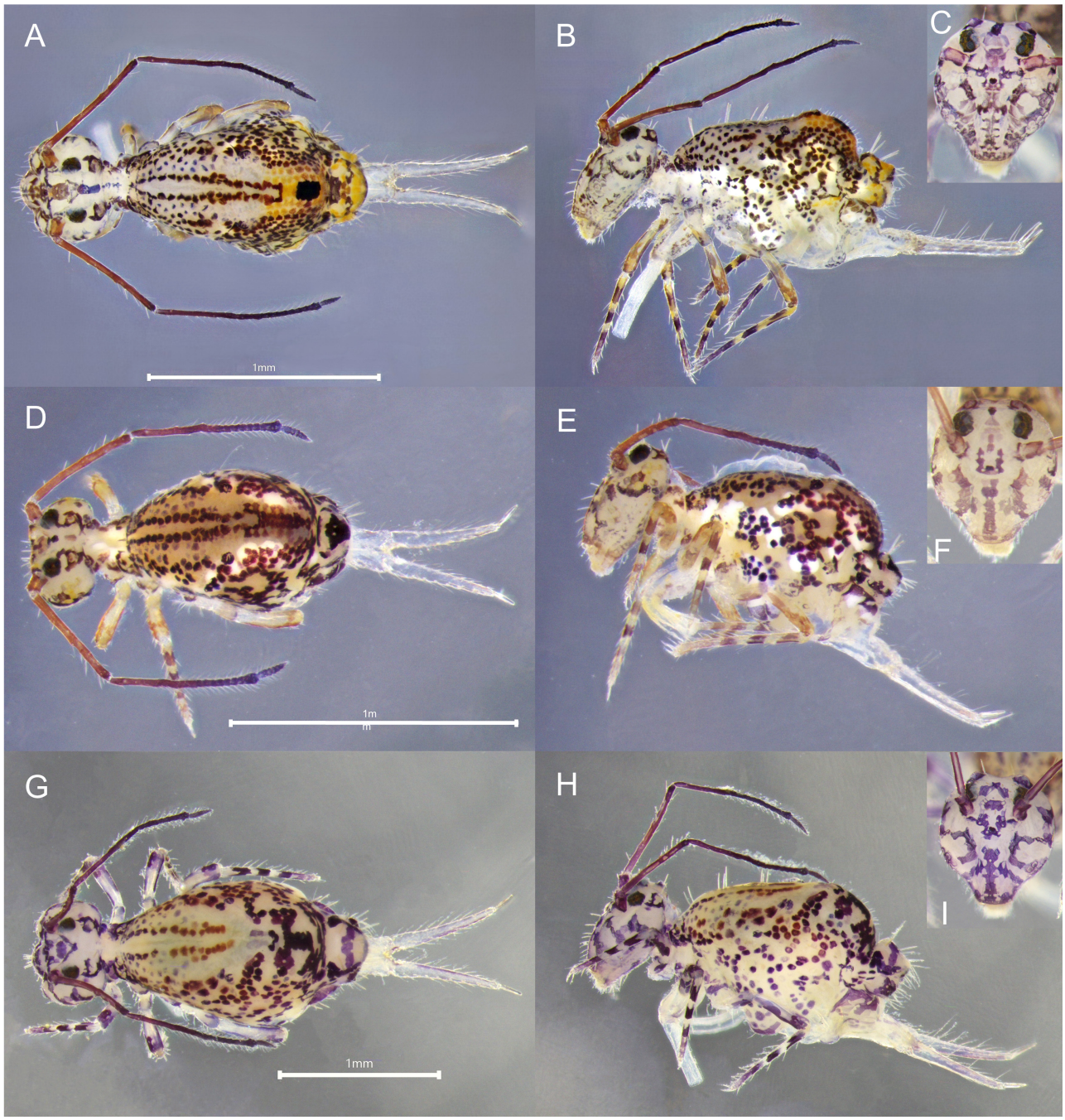

Fig. 5. Habitus of the two new species and subspecies *catenata* of the *P. denticulata* group : (A, B, C) Dorsal, lateral, and facial views of *Ptenothirx taiwanensis* sp. nov., respectively; (D, E, F) Dorsal, lateral, and facial views of *Ptenothrix matsuensis* sp. nov., respectively; (G, H, I) Dorsal, lateral, and facial of *Ptenothrix denticulata catenata* Börner, 1909, respectively.

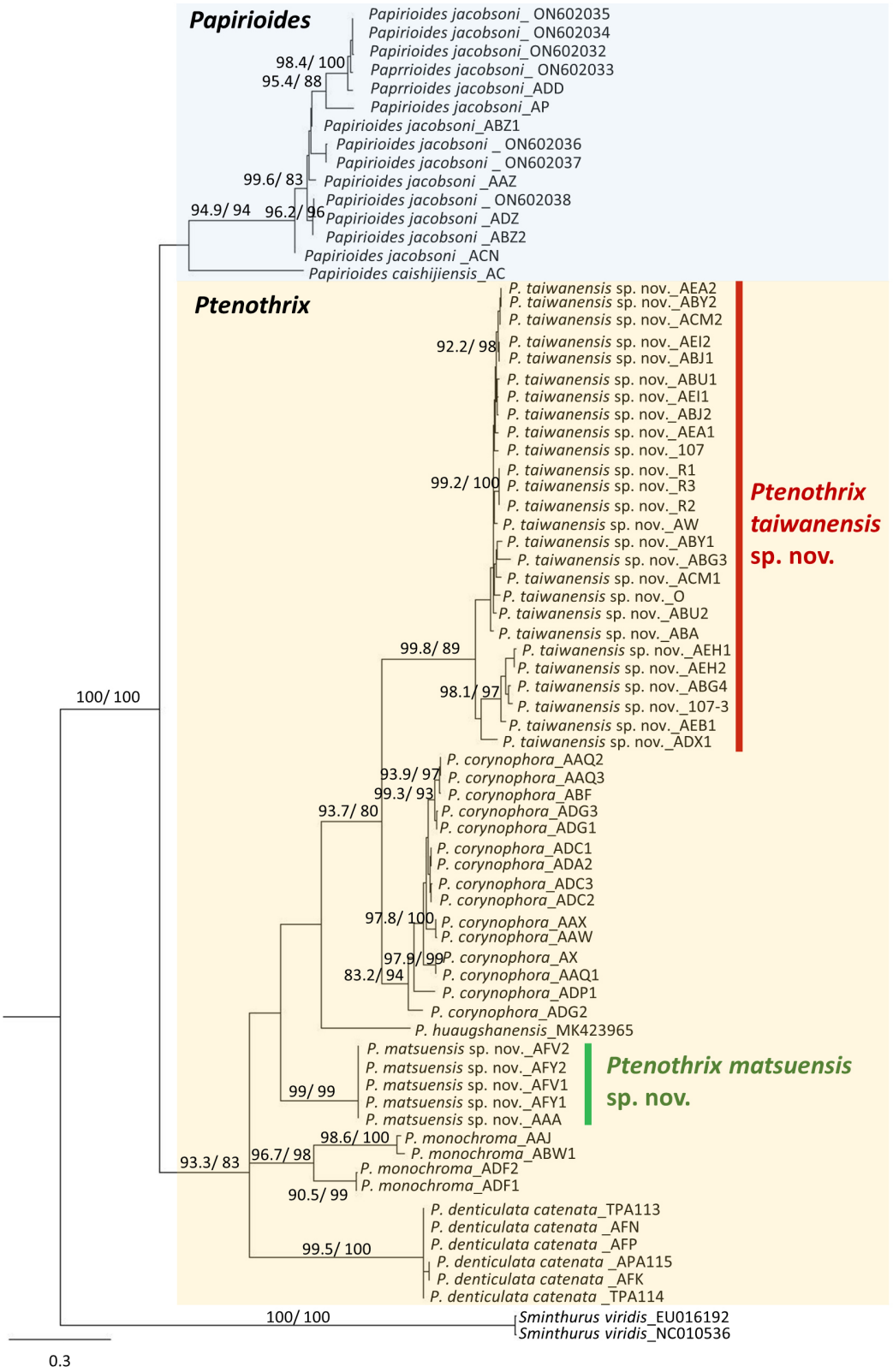

Fig. 6. Maximum Likelihood tree based on *COI* sequences of Dicyrtomidae species in Taiwan. Genera *Papirioides* Folsom, 1924 and *Ptenothirx* are labeled with blue and yellow backgrounds, respectively. The red bar indicates the clade of *Ptenothrix taiwanensis* sp. nov.; the green bar indicates the clade of *Ptenothrix matsuensis* sp. nov.. Node values represent the ultrafast bootstrap support (≥ 90%) and SH-aLRT test (≥ 80%) values, respectively. *Sminthurus viridis* (Sminthuridae, Symphypleona) represents the outgroup.

trap, leg. YH Ho (NMNS: ♀8848-7, ♀8848-8, ♀8848-9, ♂8848-10); 1♀3♂, Tainan City, Dongshan Dist., Shihe Mountain, 27. August to 7. October. 2021, Malaise trap, leg. ML Jeng, YH Ho, WT Yang (NMNS: ♀8848-11, ♂8848-12, ♂8848-13, ♂8848-14); 2♀1♂ New Taipei City, Fushan Botanical Garden (24.7634, 121.5849), 14. September to 2. October. 2021, flight interception trap, leg. YH Ho, CT Hsu (NMNS: ♀8848-15, ♀8848-16, ♂8848-17); 1♀, Hsinchu County, Syakaro National Trail, 18. May. 2022, leg. LH Chen (NTUE13300002).

Etymology: The name *taiwanensis*, an adjective meaning "Taiwanese", is given to this species with reference to its type locality, Taiwan.

Diagnosis: Head vertex with a median longitudinal stripe of dark pigment between the eyes, each eyepatch with a posterior dark spot (Fig. 5A, C), dorsal large abdomen with a posterior dark spot, small abdomen without any large spot of pigment (Fig. 5A). Ant II with 3 (Fig. 7B), Ant III with 10 cup sensilla, distal Ant III partially divided into about 8 pseudo-subsegments (Fig. 7C), Ant IV with 4 subsegments (Fig. 7D). Head frontal area with 6+6 spines, D line central spines shorter than the lateral ones, clypeal area with 2 large blunt unpaired central acanthoid chaetae and 2 less thick midfacial unpaired chaetae, b, c, e and f lines with 2 cup sensilla each (Fig. 8A). Large abdomen anterior Th. II m line with 1+1 or 2+2 large blunt acanthoid chaetae, dorso-posterior region with 4 longitudinal lines of short spines, with 6, 5, 14, 14 spines from the more lateral to the more dorsal line, respectively (Fig. 9A). Parafurcal area with two cup sensilla, without any serrated chaetae. Dorsal anal valve of small abdomen with as1–2, ms2, ms4 and mps4 as blunt acanthoid chaetae in both sexes; ventral anal valve aai1 of the female and mi1 of both sexes as blunt acanthoid chaetae, 3 chaetae between aai1 and ai6 in males and females; female subanal appendage smooth, blunt and thick (Fig. 9B, C). Tibiotarsus III with 2 modified serrated chaetae, 1 microsensillum in a cavity (oval organ), 5 cup sensilla, and 4 oval organs (without inner sensilla) (Fig. 10F). Ungues with pseudonychia and lacking tunica, with 2 dorsal, 2 internal and 2+2 lateral teeth each, unguiculi with one internal tooth each, apical filaments acuminate or slightly knobbed, surpassing the ungues tip on all legs (Fig. 11A–C). Manubrium with 8–10 dorsal chaetae on each side. Dens dorsally (posteriorly) with 24 chaetae, 15 of them feathered (Fig. 11F), dens ventral (anterior) formula from the apex to the basis: 3, 2, 1, 1… 1 (Fig. 11G).

Description: Average body (head + trunk) length of type series: 2.4 mm in females and 1.77 mm in males, holotype with 2.3 mm. Habitus typical of the genus. Body and appendages with different types of chaetae as presented in figure 4. Specimens in ethanol with background color white to pale yellow, with mottled brown symmetrical longitudinal stripes upon the anterior 4/5 of the dorsum, connected by a stripe and scattered around lateral sides of the body. A dark almost square patch on the bulge of the dorso-posterior large abdomen, small abdomen without any large spot of pigment, head with irregular patterns of pigment, vertex with a longitudinal stripe of dark pigment between eyes, each eyepatch with a posterior dark spot. Ant I red-purple, Ant II basally pale red, apically dark purple, Ant III–IV dark purple. Legs yellowish, banded with three purple stripes on tibiotarsus. Furca pale (Fig. 5A, B). Most body chaetae smooth (not denticulate).

Head (Figs. 7–8): Antennae shorter than body, 1.7 mm in holotype. Holotype antennal segment ratio of Ant I:II:III:IV as 1:6.26:8.28:1.57. Ant I with 7 regular chaetae, two of them ventral (Fig. 7A), Ant II with 20 regular chaetae plus 3 cup sensilla (Fig. 7B), Ant III distally partially divided into about 8 distal pseudo-subsegments, with 80 regular chaetae, 10 cup sensilla and 1 microsensillum, apical organ typical, with 2 sense rods inside a single shallow invagination (Fig. 7C), Ant IV with 4 subsegments and about 61

Table 1. Mean interspecific and intraspecific (grey background) K2P distances of *COI* sequences of the Dicyrtomidae and Sminthuridae species in the phylogenetic analysis

	1	2	3	4	5	6	7	8	9
1. *Ptenothrix taiwanensis* sp. nov.	5% (*n* = 26)								
2. *Ptenothrix matsuensis* sp. nov.	16.7%	0% (*n* = 5)							
3. *Ptenothrix denticulata catenata*	16.7%	16.0%	1% (*n* = 6)						
4. *Ptenothrix corynophora*	13.3%	14.0%	16.3%	5% (*n* = 15)					
5. *Ptenothrix monochroma*	17.5%	14.1%	16.9%	14.8%	7% (*n* = 4)				
6. *Ptenothrix huangshanensis*	16.3%	14.2%	16.5%	14.7%	15.0%	0% (*n* = 1)			
7. *Papirioides jacobsoni*	20.9%	19.9%	19.9%	20.6%	18.9%	20.3%	7% (*n* = 14)		
8. *Papirioides caishijiensis*	19.2%	19.0%	18.4%	17.2%	17.3%	20.0%	18.7%	0% (*n* = 1)	
9. *Sminthurus viridis*	26.4%	28.5%	24.5%	28.7%	29.0%	28.2%	27.6%	28.3%	0% (*n* = 2)

regular chaetae (Fig. 7D). Head length (along the longitudinal aspect of the body) 306.81 µm in a female paratype (holotype unclear due to position), head height (from mouth to vertex) 560 µm in holotype. Eyes 8+8 with black pigment (Fig. 13G), eyepatches with 2 interocular spine-like chaetae, the internal larger than the external (Fig. 8A). Head frontal area with only A, D, E lines, with 2/3/1 spines, respectively (6+6 spines

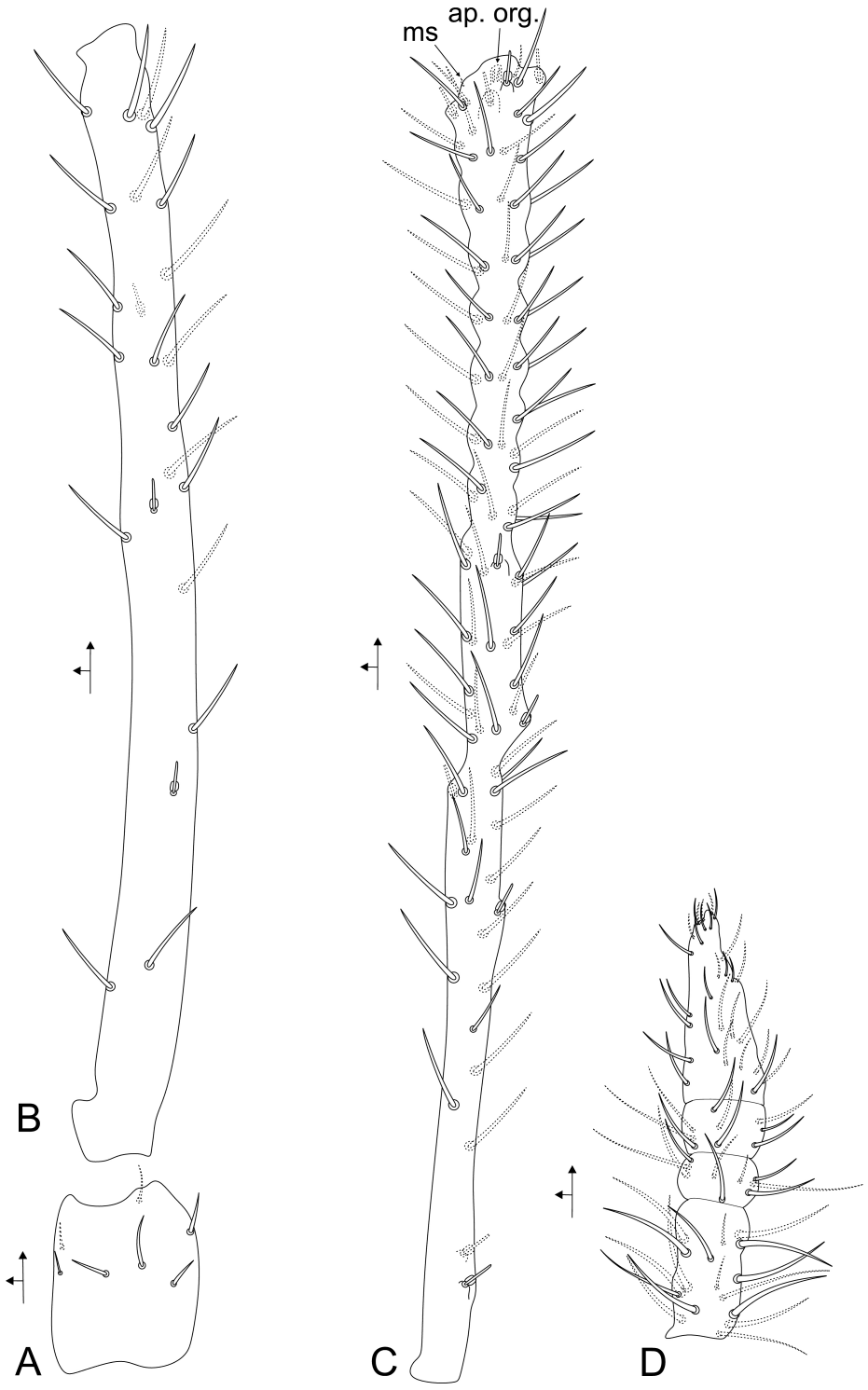

Fig. 7. *Ptenothrix taiwanensis* sp. nov. left antennal segments, dorsal view: (A) Ant I; (B) Ant II; (C) Ant III with the apical organ (ap. org.), surrounding cup sensilla and a microsensillum (ms); (D) Ant IV with four subdivisions.

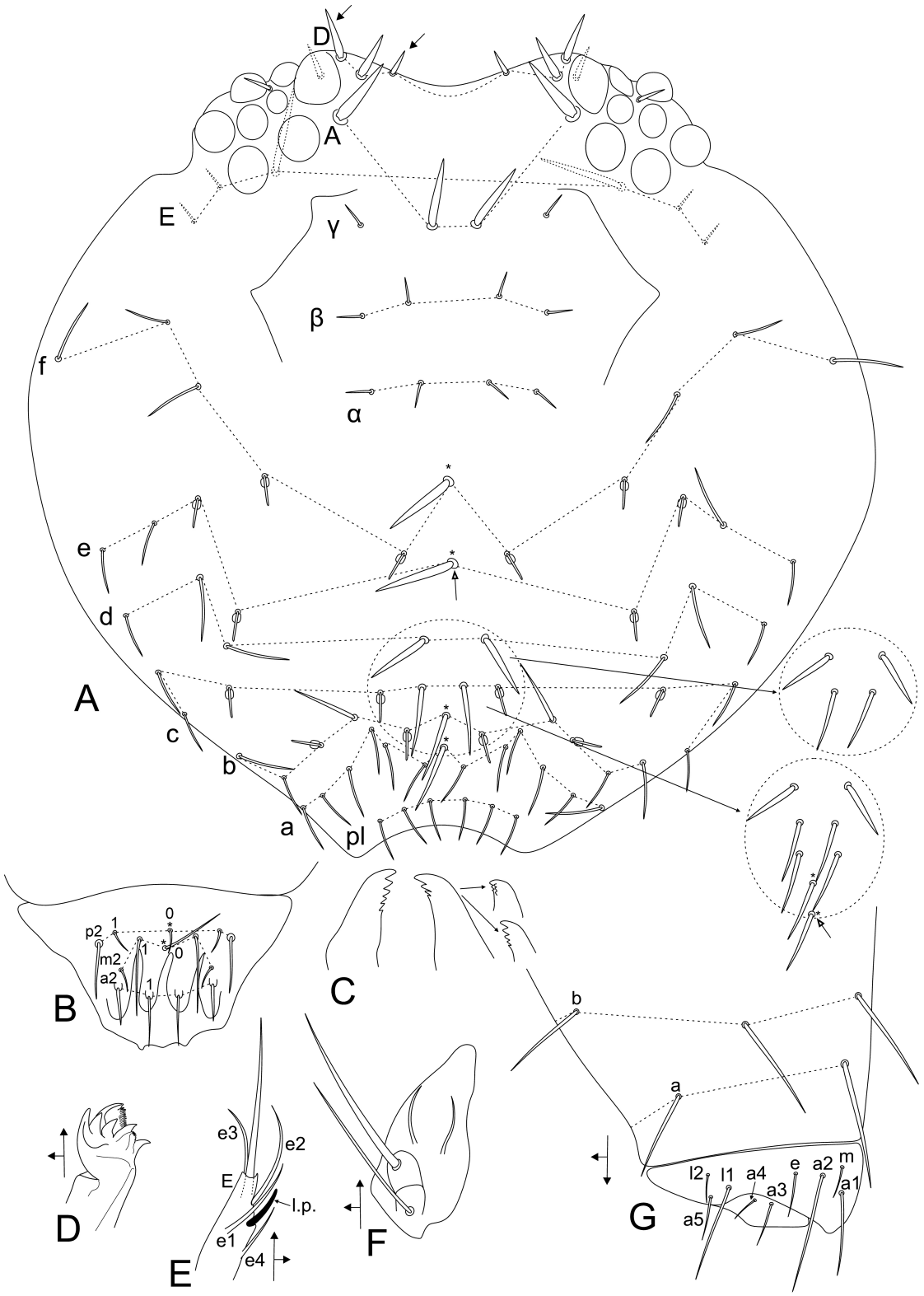

Fig. 8. *Ptenothrix taiwanensis* sp. nov. head: (A) Chaetotaxy of head at frontal view, asterisks indicate unpaired chaetae, black arrows highlight the differences between the lateral and internal chaetae of D line; white arrow indicates a chaeta present or absent, in detail the dotted circles indicate variations of midfacial chaetotaxy; (B) Labral chaetotaxy; (C) Mandible apexes, teeth structure and number vary following the detail at the left; (D) Left maxilla capitulum; (E) Labial palp papilla E (right side); (F) Left maxillary outer lobe and sublobal plate; (G) Left ventral head chaetotaxy including the basal labium (basomedian and basolateral fields).

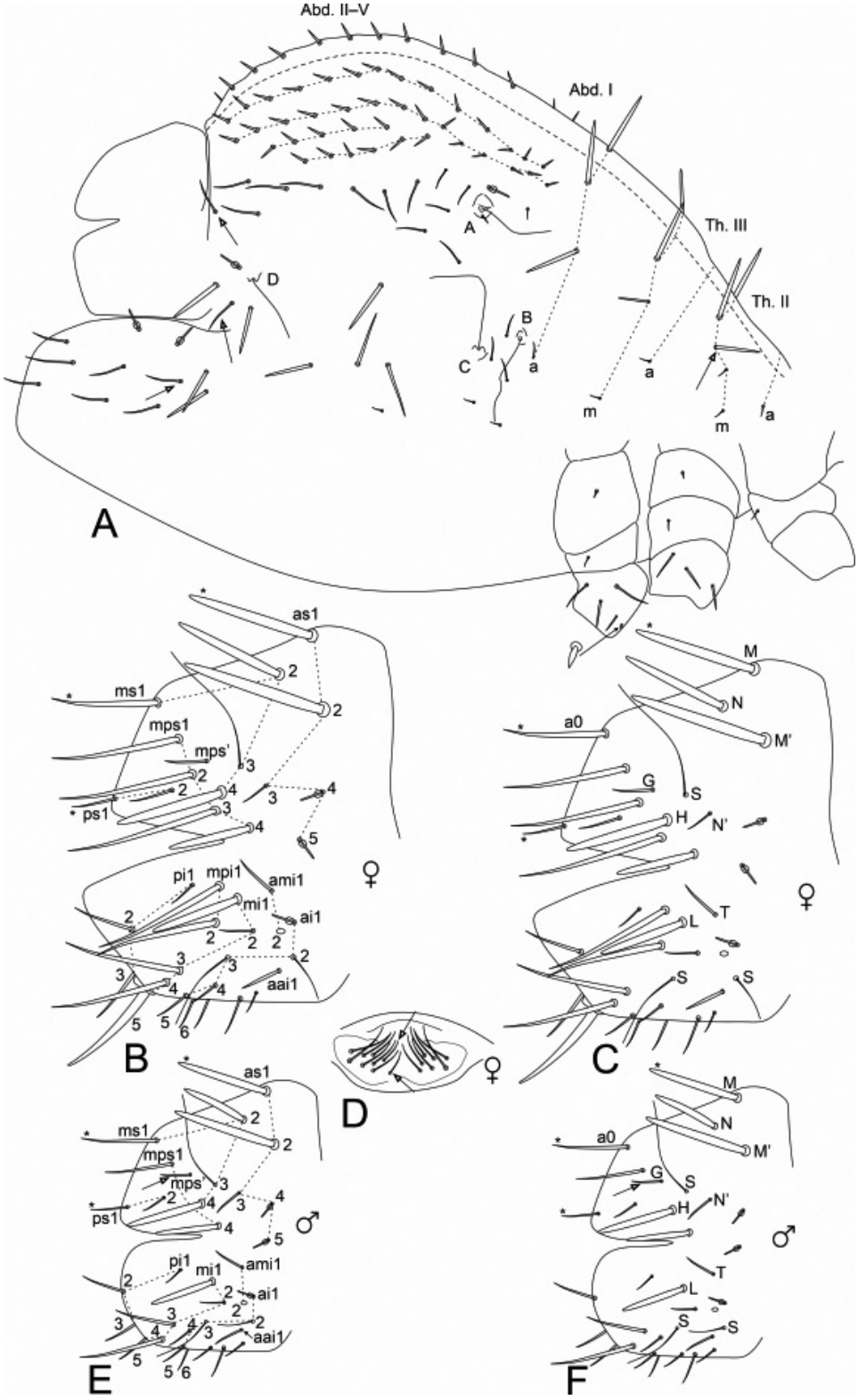

Fig. 9. *Ptenothrix taiwanensis* sp. nov. large and small abdomen: (A) Large abdomen chaetotaxy of a female (lateral view), white arrows indicate chaetae presence or absence, the detail under the figure points to coxa III with a short acanthoid chaeta; (B) Small abdomen of female (lateral view) (labels following Betsch 1997); (C) Small abdomen of female (lateral view) (labels following Yosii and Lee 1963); (D) Genital plate of female; (E) Small abdomen of male (lateral view) (labels following Betsch 1997); (F) Small abdomen of male (lateral view) (labels following Yosii and Lee 1963).

in total), D line central spines shorter than the lateral ones (Fig. 12A). Interantennal area α, β and γ lines with 2/2/1 short chaetae, respectively; clypeal area a–f lines (dorsal and ventral areas combined) in most specimens with 8(+1)/8(+1)/5/4/4(+1)/5(+1) chaetae respectively; b, c, e and f lines with 2 cup sensilla each; few specimens with chaetae a1, b1 or e1 absent or with extra chaetae between c and b lines (Fig. 8A). Distal margin of the clypeus with 3 prelabral chaetae, chaetotaxy of labral with 2(+1) p, 2(+1) m + 2 a

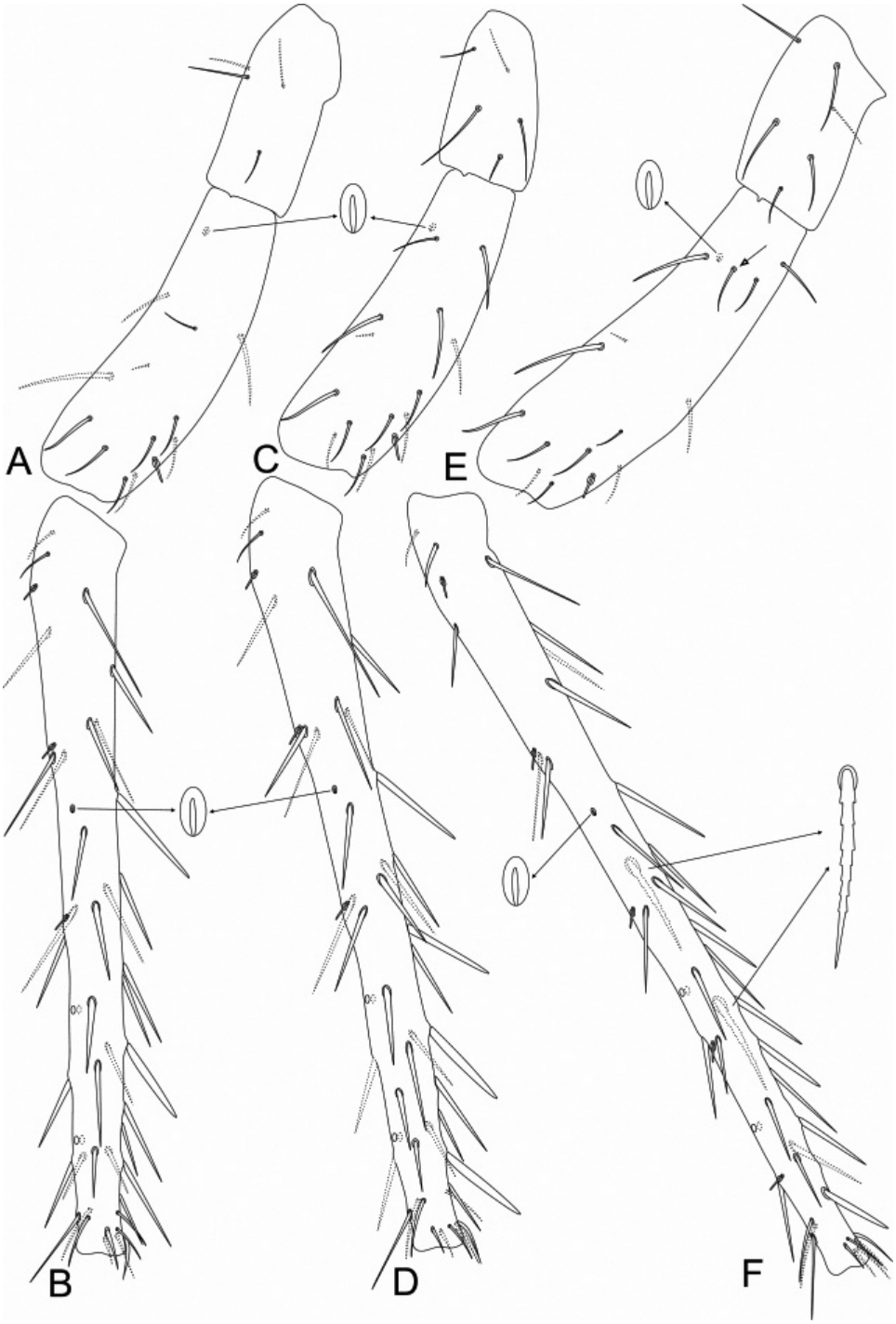

Fig. 10. *Ptenothrix taiwanensis* sp. nov. legs: (A, C, E) Trochanters and femora I, II, III, respectively (anterior view), each with 1 basal microsensillum, white arrow indicates a present or absent chaeta on femur III; (B, D, F) Tibiotarsi I, II, III, each with 1 microsensillum and 2 pairs of oval organs, tibiotarsus III with two modified serrated chaetae at the anterior side.

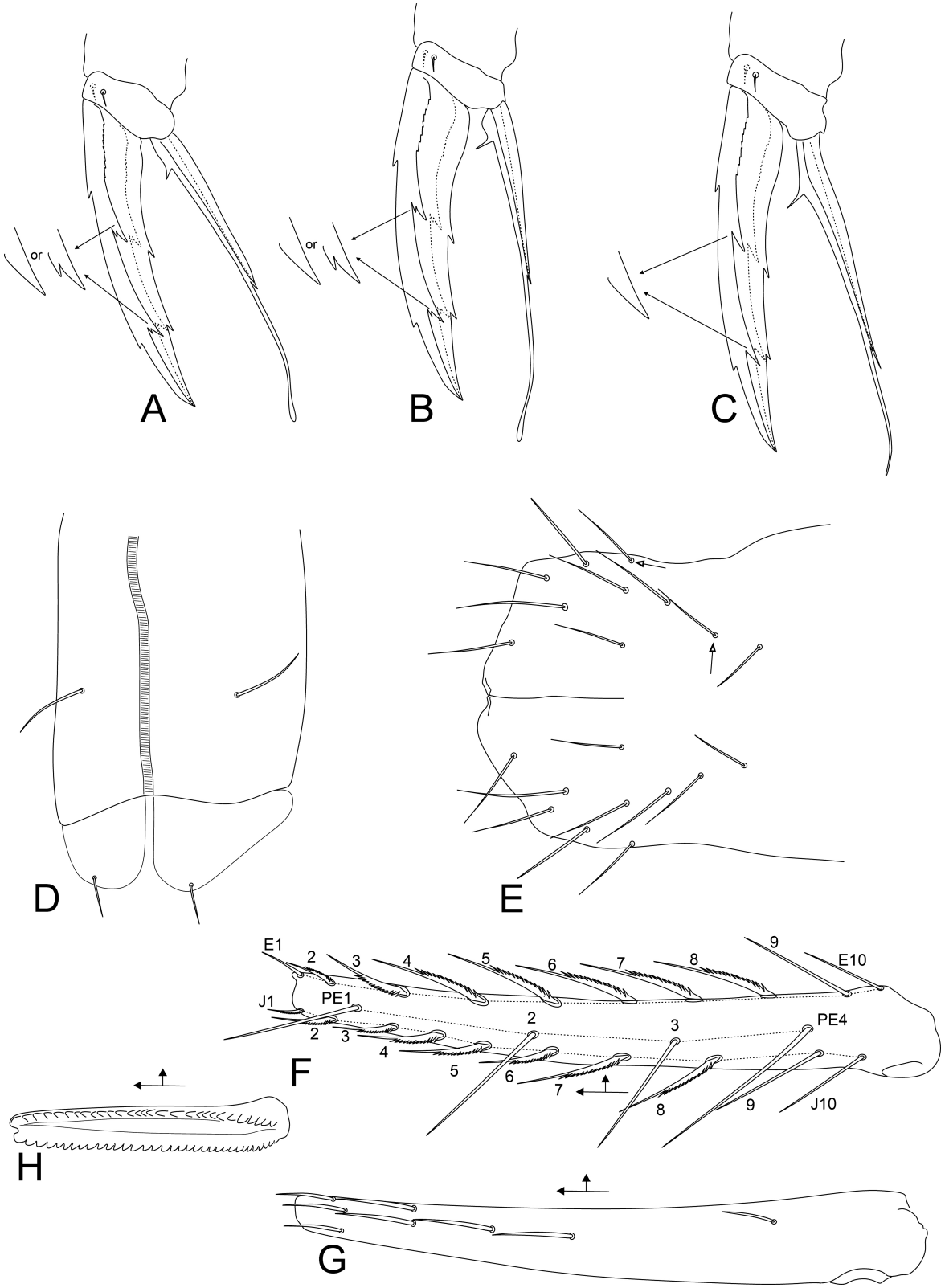

Fig. 11. *Ptenothrix taiwanensis* sp. nov. empodial complexes, collophore, and furca: (A–C) Empodial complexes I–III, respectively, lateral lamella of some specimens with a basal extra smaller tooth in the fore and mid legs; (D) Collophore anterior view and lateral flaps; (E) Manubrium dorsal (posterior) chaetotaxy, white arrows indicate present or absent chaetae; (F) Dens dorsal (posterior) chaetotaxy; (G) Dens ventral (anterior) chaetotaxy; (H) Mucro (posterior/dorsal view).

chaetae, a2 thicker than the others, p0 and p1 chaetae reduced; labrum without clearly formed papillae (Fig. 8B). Mandibles asymmetrical with 4–6 apical incisive teeth (left with 4–6 teeth, right with 4 teeth) (Fig. 8C); maxilla capitulum globular, with 6 lamellae, 3 smooth and 3 fringed, without any clear modification (Fig. 8D); Labial papilla E with 4 guard chaetae, lateral process finger-shaped, almost reaching the apex of the papilla (Fig. 8E); details of other labial papillae not clearly observable. Maxillary outer lobe with 2 chaetae subequal in length, apical one thicker than the basal one, sublobal plate with 2 chaetae-like appendages (Fig. 8F). Ventral groove with 1 and 1 surrounding chaetae from lines a and b, respectively, labium basal fields with 4 central (a2 longer than the others) and 5 lateral chaetae (Fig. 8G).

Trunk (large and small abdomens) (Fig. 9): Trunk length of the holotype 1.54 mm. Large abdomen (Fig. 9A): thorax continuous with abdomen, without any visible segmentation or constrictions. Chaetotaxy similar between males and females, Th II with 1 a and 3 to 4 m chaetae, 1+1 or 2+2 of them as large blunt acanthoid chaetae; Th III with 1 a and 3 m chaetae; Abd I with 3 a chaetae; bothriotricha A (Fig. 13A), B, C present and misaligned, A posteriorly to B–C and on a large papilla with a surrounding cup sensillum, B and C with 4 surrounding chaetae between them, each inside a small papilla; dorso-posterior region with 4 longitudinal lines of spine-like chaetae, with 6/5/14/14 chaetae for the more lateral to the more dorsal line, respectively. Parafurcal area (furca basis) without neosminthuroid chaetae, with 2 cup sensilla, 2 large blunt acanthoid chaetae and 6 to 7 regular chaetae. Bothriothricum D in the large abdomen, in a small papilla. Small abdomen of the female (Fig. 9B): dorsal anal valve with as1–5, ms1–4, mps1–4, mps' and ps1–2 chaetae, as1, ms1 and ps1 unpaired; as4–5 as cup sensilla, as1–2, ms2, ms4 and mps4 as blunt acanthoid chaetae, ms3 as a S chaeta; ventral anal valves each with aai1, ai1–6, ami1–2, mi1–5, mpi1–2 and pi1–3 chaetae, ami2 as an oval organ; ai1 as a cup sensillum, ai2–3 as S chaetae, aai1 and mi1 as a blunt acanthoid chaetae, mi5 as the subanal appendage, smooth, blunt and thick. Another interpretation of the small abdomen chaetotaxy following Yosii and Lee (1963) in fig. 9C. Genital plate of the female lacking dorsal chaetae, ventral area with 7 to 9 chaetae on each side (Fig. 9D). Small abdomen of male (Fig. 9E): dorsal anal valve with as1–5, ms1–4, mps1, mps4, mps' (present or absent), and ps1–2 chaetae, as1, ms1, ps1 unpaired, as4–5 as cup sensilla, as1–2, ms2, ms4, mps4 as blunt acanthoid chaetae, ms3 as a S chaeta; ventral anal valves each with aai1, ai1–6, ami1–2, mi1–5 and pi1–3 chaetae, ai1 as a cup sensillum, ai2–3 as S chaetae, ami2 as an oval organ, mi1 as a blunt acanthoid chaeta; 3 chaetae between aai1 and ai6 in males (Figs 9B, E and 12C) and females. Another interpretation of the small abdomen chaetotaxy following Yosii & Lee (1963) in fig. 9F. Genital plate of male densely covered by chaetae, number unclear.

Large abdomen appendages (Figs. 9A, 10, 11): Epicoxa, subcoxa and coxa I with 0, 1, 0 chaetae, respectively (Fig. 9A); trochanter I with 4 regular chaetae; femur I with 12 regular chaetae plus 1 microsensillum in a cavity (oval organ) (Fig. 13E) and 1 cup sensillum (Figs. 10A, 13B); tibiotarsus I with 40 regular chaetae plus 1 microsensillum in a cavity (oval organ), 3 cup sensilla and 4 oval organs (Fig. 13D, without inner sensilla), distal whorl with 8 chaetae (Fig. 10B). Epicoxa, subcoxa and coxa II with 1, 1, 3 chaetae, respectively (Fig. 9A); trochanter II with 5 regular chaetae; femur II with 14 regular chaetae plus 1 microsensillum in a cavity (oval organ) and 1 cup sensillum (Fig. 10C); tibiotarsus II with 41 regular chaetae plus 1 microsensillum in a cavity (oval organ), 3 cup sensilla and 4 oval organs (without inner sensilla), distal whorl with 9 chaetae (Fig. 10D). Epicoxa, subcoxa and coxa III with 1, 1, 5 chaetae (including one apical small acanthoid chaetae), respectively (Fig. 9A); trochanter III with 6 regular chaetae; femur III with 14 regular chaetae plus 1 microsensillum in a cavity (oval organ) and 1 cup sensillum (Fig. 10E); tibiotarsus III with 37 regular chaetae plus 2 modified serrated chaetae (Fig. 13F), 1 microsensillum in a cavity (oval organ), 5 cup sensillum, and 4 oval organs (without inner sensilla), distal whorl with 9 chaetae (Fig. 10F), number of teeth on modified serrated chaetae variable, from 4 to 7. Tibiotarsus I with an apical sinusoid chaeta bending across the unguiculus. Inner apical macrochaeta spiky in tibiotarsus I (Fig. 10B), and blunt in tibiotarsi II–III (Fig. 10D, F). Foot complexes I–III with 2 small pretarsal chaetae each, 1 anterior and 1 posterior; ungues with 2 unpaired inner teeth subequal in size, lateral lamellae with 2+2 teeth (Fig. 13K, some specimens with an extra basal smaller tooth in the fore and mid legs), pseudonychia present (Fig. 13L), merged to the dorsal face with 2 unpaired dorsal teeth, the proximal one smaller, with lateral margins irregularly serrate. Unguiculi with 1 basal tooth and 1 axial filament surpassing the tip of the ungues, apical filaments acuminate or slightly knobbed (Fig. 11A–C). Collophore with 1+1 chaetae on corpus plus 1+1 distal chaetae on lateral flaps, with a pair of long and warty sacs as typically seen in Dicyrtomidae (Fig. 13H, I). Tenaculum typically with a quadridentate ramus, corpus with 4 apical chaetae (Fig. 13J). Furcal size length in holotype as manubrium = 168.48 μm; dens = 556.21 μm; and mucro = 176.94 μm. Manubrium with 8 to 10 dorsal (posterior) chaetae on each side

(Fig. 11E); dens dorsally (posteriorly) with 24 chaetae: 10 on the dorso-external (E1–10), 10 on the dorso-internal (J1–10) and 4 dorso-central (PE1–4) chaetae, respectively, external and internal chaetae feathered (Fig. 13C), except for the chaetae near the manubrium and an apical-external one (Fig. 11F); dens ventrally (anteriorly) with 8 chaetae, with the following formula from the apex to the basis: 3, 2, 1, 1… 1 (Fig. 11G); mucro with a narrow apex, with both edges serrated, with about 33 (inner) and 28 (outer) serrations on each edge, with an apical notch (Fig. 11H). Ratio mucro: dens: manubrium in holotype 1: 3.3: 1.05.

Distribution: Low elevation of Taiwan (mainly the northern and central region), and one locality in Nangan Island, Matsu (public toilet of Mt. Yuntai).

Habitat: Most Dicyrtomidae, including *Ptenothrix taiwanensis* sp. nov. are atmobiotic (Bretfeld 1999). Specimens of the new species generally inhabit wet rotten wood and dead leaves of tree ferns and *Miscanthus* bushes. Some specimens were also found associated with the leaf litter layer, especially juveniles. Sampling localities of *Ptenothrix taiwanensis* sp. nov. are presented as orange dots in figure 1.

Remarks: *Ptenothrix taiwanensis* sp. nov. specimens were identified as *Ptenothrix denticulata* (Folsom, 1899) in Cheng et al. (2022), which is now proven to be a misidentification (see Fig. 6 and Table 2). *Ptenothrix taiwanensis* sp. nov. is remarkably similar

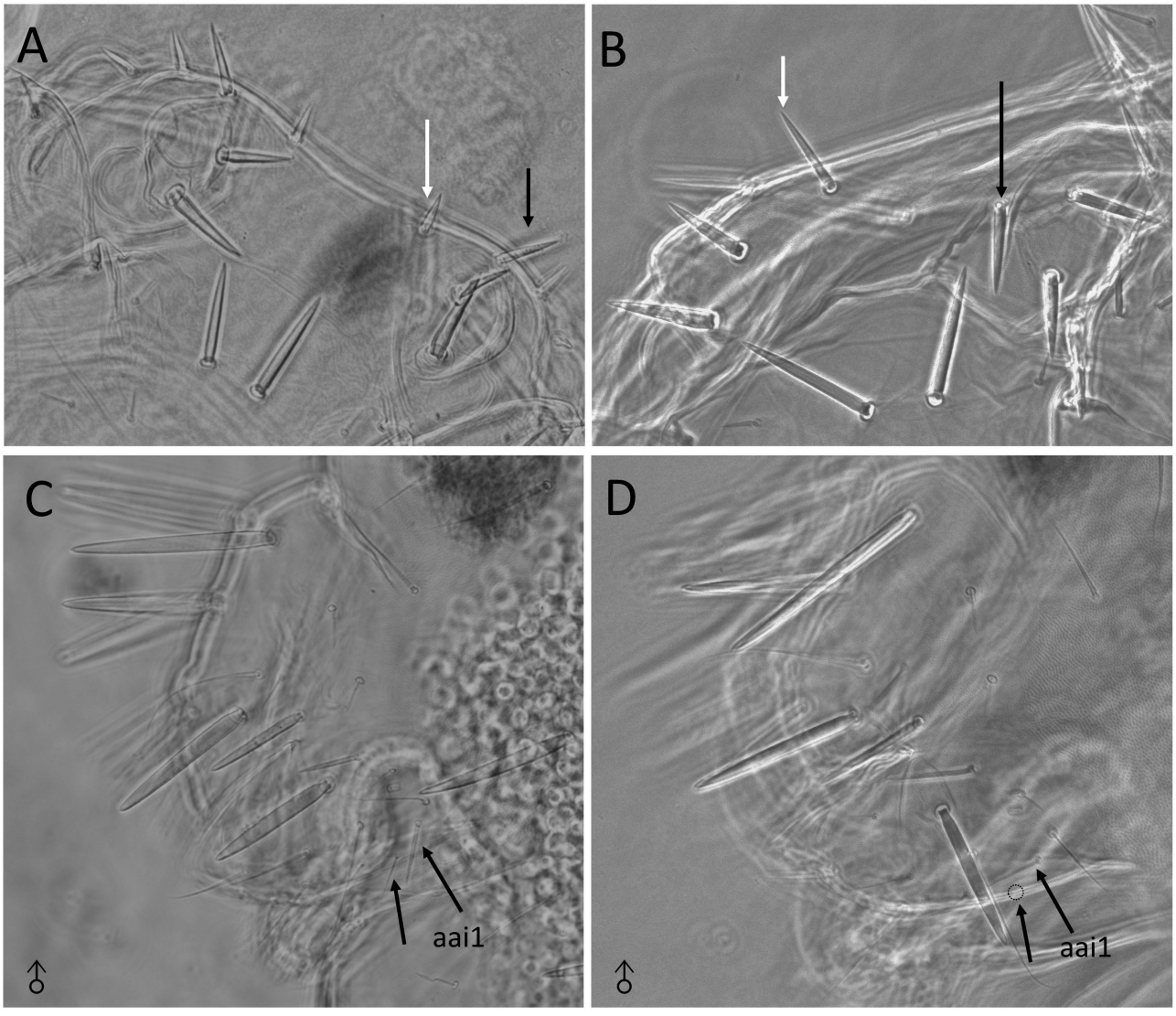

Fig. 12. Morphological comparison of the two new species. Frontal spines on line D of: (A) *Ptenothrix taiwanensis* sp. nov.; and (B) *Ptenothrix matsuensis* sp. nov. (white arrows mark the central spines, black arrows mark the lateral spines near the eyes). Small abdomen of a male of: (C) *Ptenothrix taiwanensis* sp. nov.; and (D) *Ptenothrix matsuensis* sp. nov. The latter species lacks one chaeta between aai1 and ai6 (marked with a dotted circle in panel D) compared to the former one.

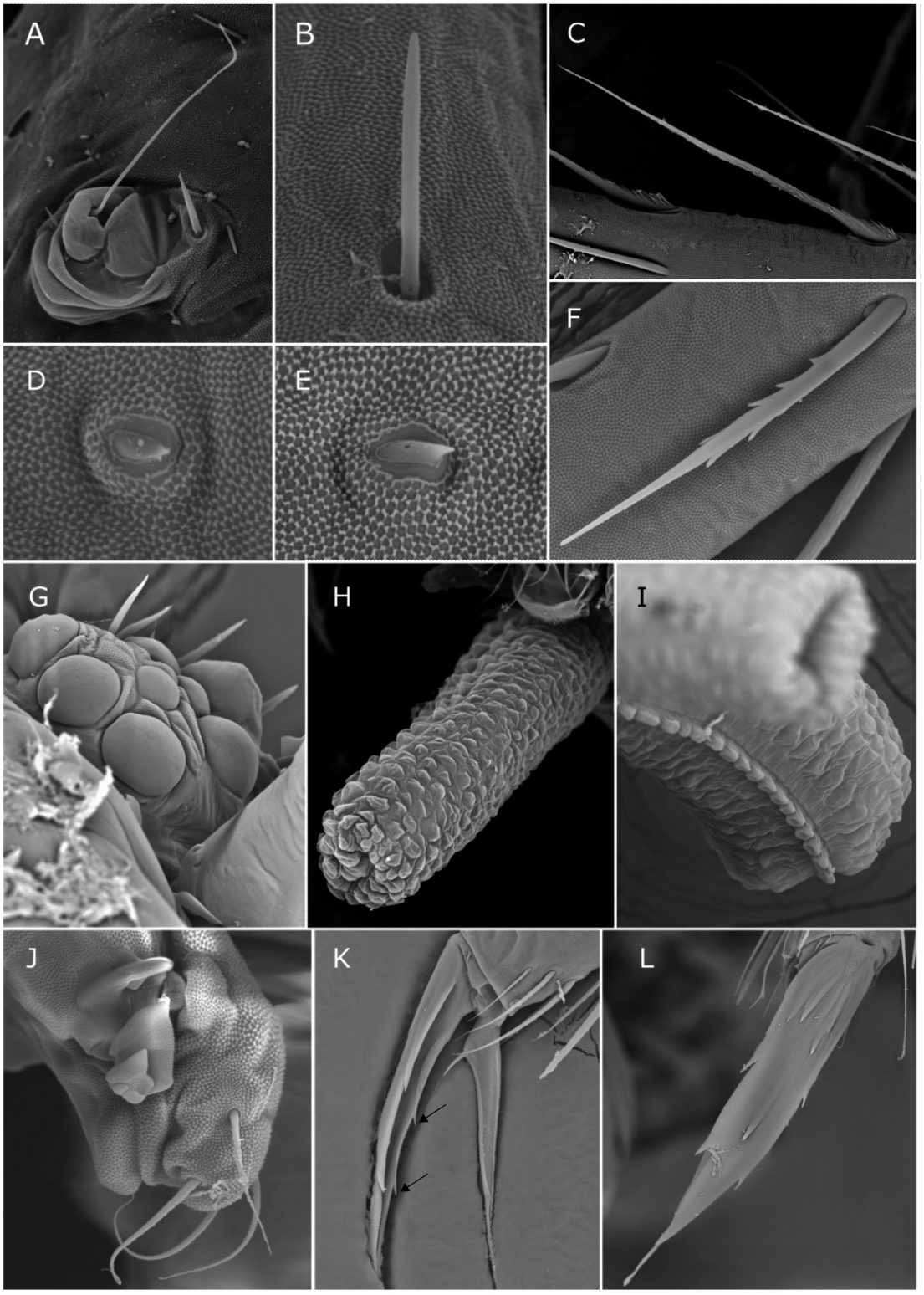

Fig. 13. *Ptenothrix taiwanensis* sp. nov. SEM (scanning electronic microscope) images: (A) Bothriotrichum A of the large abdomen; (B) Cup sensillum on tibiotarsus; (C) Serrated dental chaetae; (D) Oval organ on tibiotarsus; (E) Microsensillum on tibiotarsus; (F) Modified serrated chaeta on tibiotarsus III; (G) Right eyepatch, dorsal view; (H) Collophore vesicle with warty sacs; (I) Collophore sacs with warty vesicles at ventral view; (J) Tenaculum, lateral view; (K) Lateral view of the empodial complex I, unguis with 2 unpaired inner (black arrows) and 2 lateral teeth; (L) Dorsal view of unguis I, showing the pseudonychia merged with the dorsal unguis, at the apex there is the unguiculus elongated axial filament, slightly knobbed at the tip.

to *Ptenothrix matsuensis* sp. nov., described in the next section. We consider both to be cryptic species due to their strong resemblance in color pattern and overall chaetotaxy. In addition to Taiwan Island, *P. taiwanensis* was also collected on the tile wall in a public toilet in Nangan Island in Matsu, but was not found in any other localities in Matsu. This made us presume that the record in Matsu could be due to recent human intervention.

Compared with other *Ptenothrix* species found in the vicinities specimen collection, such as Taiwan and South China, Japan, and the type locality of *P. denticulata* (Table 2), the two new species differ from the others by: frontal head A internal spines as long as lateral ones (shorter than the lateral ones in *P. denticulata* (Folsom, 1899) and longer in *P. denticulata catenata* Börner, 1909, *P. corynophora* Börner, 1909 *P. gigantisetae* Lin & Xia, 1985, and *P. huangshanensis* Chen & Christiansen, 1996), Ant IV with 4 subdivisions (2–4 in *P. denticulata*, 2–3 in *P. corynophora*, 5 in *P. huangshanensis*, and 7 in *P. gaoligonshanensis* Itoh & Zhao, 2000), and dorsal dens with 10 inner chaetae (9 in *P. annulatus*, *P. dinghuensis*, *P. gigantisetae*, *P. palmisetacea*, and *P. sinensis*). Further comparisons are listed in table 2.

Table 2. Main differences between the *Ptenothrix* species found in Taiwan, Japan, and South China

Species	Head vertex color pattern	Ant IV subdivisions	Ant III subdivisions	Frontal head A internal spines compared to the lateral ones	Frontal head D internal spines compared to the lateral ones	Total n° of large abdomen dorsal spines
P. taiwanensis sp. nov.	A patch behind each eye, a central longitudinal stripe	4	± 8	=	<	39
P. matsuensis sp. nov.	A patch behind each eye, an indistinct central patch (sometimes absent)	4	± 8	=	=	34–39
P. denticulata	A transverse band	4[1]; 2–3[2]	At least 9[1]; 5–6[2]	<[2]	<[2]	11?
P. denticulata catenata	A patch behind each eye[3]	4[4]	± 8[4]	>[4]	<[4]	?
P. corynophora	No patch[6]	2[5], 3[6]	6[5]; 7[6]	>	=[6]	?
P. monochroma	No patch	4	?	?	?	?
P. annulatus	Numerous yellow round patches	unclear	5	?	?	?
P. dinghuensis	?	4	6	?	<	?
P. gigantisetae	No patch	4	7	>	>	?
P. huangshanensis	Head with a quadrilateral hollow spot posterior to each eyepatch	5	8	>	=	34
P. palmisetacea	?	4	7	?	?	?
P. yunnanus	A broad median streak on the vertex	4	7	>	<	?
P. gaoligonshanensis	?	7	7	=	<	?
P. sinensis	?	4	7	?	?	?

Species	Unguiculus III teeth	Manubrial dorsal chaetae	Inner chaetae row of dorsal dens	Outer chaetae row of dorsal dens	N° of outer teeth of mucro	N° of inner teeth of mucro	References
P. taiwanensis sp. nov.	1	8–10	10	10	28	33	This study
P. matsuensis sp. nov.	1	7	10	10	34	46	This study
P. denticulata	2[1], 1[2]	?	10[2]	10[2]	31[2]	38[2]	[1]Folsom 1899; [2]Yosii and Lee 1963
P. denticulata catenata	1	7[4]	10[4]	10[4]	?	?	[3]Börner 1909; [4]This study
P. corynophora	1[6]	> 7 (10?)[6]	?	?	26	42	[5]Börner 1909; [6]Yosii and Lee 1963
P. monochroma	1	9	?	?	47	36	Yosii and Lee 1963
P. annulatus	1	?	9	9	36	45	Lin and Xia 1985a
P. dinghuensis	0	?	9	10	22	26	Lin and Xia 1985a
P. gigantisetae	1	?	9	9	21	24	Lin and Xia 1985b
P. huangshanensis	1	8	10	10	21–29	28–31	Chen and Christiansen 1996
P. palmisetacea	1	?	9	10	18–20	18–20	Lin and Xia 1985a
P. yunnanus	1	8	?	?	26	22	Itoh and Zhao 2000
P. gaoligonshanensis	1	8	10	10	42	30	Itoh and Zhao 2000
P. sinensis	1	?	9	10	32	26	Lin and Xia 1985a

***Ptenothrix matsuensis* sp. nov.**

(Figs. 5D–F, 12B,12D, 14, Table 2)
urn:lsid:zoobank.org:act:B784F1E5-234C-4B42-8F29-F6B96A9AE17A

Type materials: TAIWAN: Holotype ♀ on slide, Lienchiang County, Nangan Township, Shengtian Park (26.154204, 119.916068), 25. May. 2023, by beating vegetation, leg. HJ Cheng, YH Ho (NTUE13100006). 4 paratypes on slides: 2♀2♂, same data as holotype (1♂1♀ in NTUE: ♂ NTUE13100008, ♀ NTUE13100007, 1♂1♀ in NMNS: ♂ 8848-18, ♀8848-19). 2 paratypes in ethanol: 1♂1 sex undetermined (DNA voucher), Lienchiang County, Nangan Township, Motianling (Skyscraper Ridge) Trail (26.161192, 119.953177), 25. May. 2023, by beating vegetation, leg. HJ Cheng, YH Ho (1♂1 sex undetermined in NTUE: ♂ NTUE13100009, sex undetermined NTUE13100010).

Other analyzed slide specimens: TAIWAN: 3♀ on slide, Lienchiang County, Nangan Township, Siwei Rd. (26.173417, 119.917225), 25. May. 2023, leg. HJ Cheng, YH Ho (2 in NTUE: NTUE13300003 and NTUE13300004; 1 in NMNS: 8848-20). 3♂ on slide, Lienchiang County, Nangan Township, Motianling (Skyscraper Ridge Trail) (26.161192, 119.953177), 25. May. 2023, leg. HJ Cheng, YH Ho (1 in NTUE: NTUE13300005; 2 in NMNS: 8848-21, 8848-22).

Etymology: The new species was named after its type locality, Matsu Islands.

Diagnosis: Head vertex without a longitudinal stripe of dark pigment between eyes, each eyepatch with a posterior dark spot (Fig. 5D), dorsal large abdomen lacking any dark spot, dorsal small abdomen almost entirely covered by a large patch of dark pigment (Fig 5D). Ant II with 3, Ant III with 10 cup sensilla, distal Ant III partially divided into about 8 pseudo-subsegments, Ant IV with 4 subsegments. Head frontal area with 6+6 spines, D line central spines as long as the lateral ones (Figs. 12B, 14A), clypeal area with 2 large blunt unpaired central acanthoid chaetae and 2 less thick midfacial unpaired chaetae, b, c, e and f lines with 2 cup sensilla each. Large abdomen Th. II anterior m line with 1+1 large blunt acanthoid chaetae, dorso-posterior region with 4 longitudinal lines of short spines, with 5–6/ 5/ 12–14/ 12–14 spines from the more lateral to the more dorsal line, respectively (Fig. 14B). Parafurcal area with two cup sensilla, without any serrated chaetae. Dorsal anal valve of small abdomen with as1–2, ms2, ms4 and mps4 as blunt acanthoid chaetae in both sexes; ventral anal valve aai1 of the female and mi1 of both sexes as a blunt acanthoid chaetae, 3 chaetae between aai1 and ai6 in females, only 2 in males (Figs. 12D, 14C); female subanal appendage smooth, blunt and thick. Tibiotarsus III with 2 modified serrated chaetae, 1 microsensillum in a cavity (oval organ), 5 cup sensilla, and 4 oval organs (without inner sensilla) (as in Fig. 10F). Ungues with pseudonychia and lacking tunica, with 2 dorsal, 2 internal and 2+2 lateral teeth each, unguiculi with one internal tooth each, apical filaments acuminate or slightly knobbed, surpassing the ungues tip in all legs (as in Fig. 10A–C). Manubrium with 7 dorsal chaetae on each side (Fig. 14D). Dens dorsally (posteriorly) with 24 chaetae, 15 of them feathered (as in Fig. 11F), dens ventral (anterior) formula from the apex to the basis: 3, 2, 1, 1… 1 (as in Fig. 11G).

Description: Average body (head + trunk) length of type series: 1.82 mm in females and 1.38 mm in males, holotype with 1.9 mm. Habitus typical of the genus. Overall chaetotaxy similar to *Ptenothrix taiwanensis* sp. nov. Head vertex without a longitudinal stripe of dark pigment between eyes, each eyepatch with a posterior dark spot (Fig. 5D), dorsal large abdomen lacking any dark spot, dorsal small abdomen almost entirely covered by a large patch of dark pigment. Ant I red-purple, Ant II basally pale red, apically dark purple, Ant III–IV dark purple. Legs yellowish, banded with three purple stripes on tibiotarsus. Furca pale. Most body chaetae smooth (not denticulate).

Head: Antennae shorter than body, 1.27 mm in holotype. Holotype antennal segments ratio of Ant I:II:III:IV as 1:6.73:7.7:1.8. Antennal chaetotaxy as in *Ptenothrix taiwanensis* sp. nov., with no observable differences between the two species, Ant I with 7 regular chaetae, two of them ventral (as in Fig. 7A), Ant II with 20 regular chaetae plus 3 cup sensilla (as in Fig. 7B), Ant III distally partially divided into about 8 distal pseudo-subsegments, with 80 regular chaetae, 10 cup sensilla and 1 microsensillum, apical organ typical, with 2 sense rods inside a single shallow invagination (as in Fig. 7C), Ant IV with 4 subsegments and about 61 regular chaetae (as in Fig. 7D). Head length (along the longitudinal of the body) 243.5 μm in a female paratype (holotype unclear due to position), head height (from mouth to vertex) 613.97 μm in holotype. Head chaetotaxy mostly similar to *Ptenothrix taiwanensis* sp. nov. Eyes 8+8 with black pigment, eyepatches with 2 interocular spine-like chaetae, the internal larger than the external one (Fig. 14A). Head frontal area with only A, D, E lines, with 2/3/1 spines, respectively (6+6 spines in total), D line central spines sharp and as long as the lateral ones (Figs. 12B, 14A). Interantennal area α, β and γ lines with 2/2/1 short chaetae, respectively (as in Fig. 8A); clypeal area a–f lines (dorsal and ventral areas combined) with 8(+1)/8(+1)/5/4/4(+1)/5(+1) chaetae respectively; b, c, e and f lines with 2 cup sensilla each. Distal margin of the clypeus with 3 prelabral chaetae, chaetotaxy of labral with 2(+1) p, 2(+1) m + 2

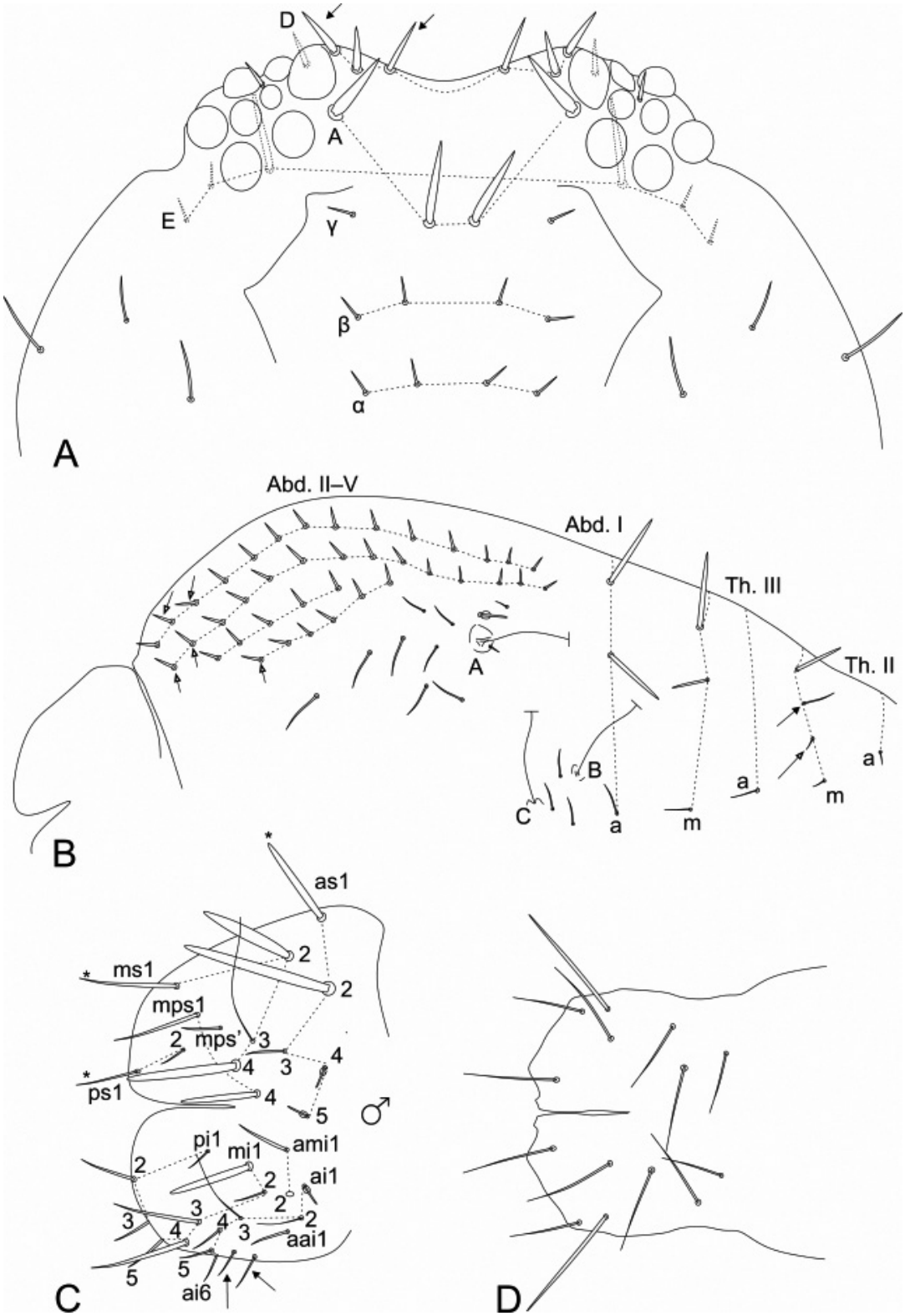

Fig. 14. *Ptenothrix matsuensis* sp. nov. main chaetotaxic diagnostic features compared to *P. taiwanensis* sp. nov.: (A) Head interocular, frontal and interantennal chaetotaxy, black arrows highlight the similar lengths of the lateral and internal chaetae of D line; (B) Large abdomen chaetotaxy (partially represented), white arrows mark chaetae/spines present or absent, the black arrow points to a regular chaeta which is blunt acanthoid in *P. taiwanensis* sp. nov.; (C) Small abdomen of male (labels following Betsch 1997), black arrows point to two chaetae between aai1 and ai6; (D) Manubrium dorsal (posterior) chaetotaxy, with 7+7 chaetae.

a chaetae, a2 thicker than the others, p0 and p1 chaetae reduced; labrum without clear formed papillae (as in Fig. 8B). Mandibles asymmetrical with 4–6 apical incisive teeth (left with 6 teeth, right with 4 teeth); maxilla capitulum globular, with 6 lamellae, 3 smooth and 3 fringed, without any clear modification (as in Fig. 8C and D). Labial papilla E with 4 guard chaetae, lateral process finger-shaped, almost reaching the apex of the papilla (as in Fig. 8E). Maxillary outer lobe with 2 chaetae subequal in length, apical one thicker than the basal one, sublobal plate with 2 chaetae-like appendages (as in Fig. 8F). Ventral groove with 1 and 1 surrounding chaetae from lines a and b, respectively, labium basal fields with 4 central (a2 longer than the others) and 5 lateral chaetae (as in Fig. 8G).

Trunk (large and small abdomens): Trunk length of holotype 1.31 mm. Large abdomen: thorax continuous with abdomen, without any visible segmentation or constrictions. Chaetotaxy similar between males and females, and almost identical to *Ptenothrix taiwanensis* sp. nov. Th II with 1 a and 3 to 4 m chaetae, none as large blunt acanthoid chaetae; Th III with 1 a and 3 m chaetae; Abd I with 3 a chaetae; bothriotricha A, B, C present and misaligned, A posteriorly to B–C and on a large papilla with a surrounding cup sensillum, B and C with 4 surrounding chaetae between them, each inside a small papilla; dorso-posterior region with 4 longitudinal lines of spine-like chaetae, with about 5–6/5/12–14/12–14 chaetae for the more lateral to the more dorsal line, respectively (Fig. 14B). Parafurcal area (furca basis) without neosminthuroid chaetae, with 2 cup sensilla, 2 large blunt chaetae and 7 regular chaetae. Bothriothricum D in the large abdomen, in a small papilla (as in Fig. 9A). Small abdomen of the female: dorsal anal valve with as1–5, ms1–4, mps1–4, mps' and ps1–2 chaetae, as1, ms1 and ps1 unpaired; as4–5 as cup sensilla, as1–2, ms2, ms4 and mps4 as blunt acanthoid chaetae, ms3 as a S chaeta; ventral anal valves each with aai1, ai1–6, ami1–2, mi1–5, mpi1–2 and pi1–3 chaetae, ami2 as an oval organ; ai1 as a cup sensillum, ai2–3 as S chaetae, aai1 and mi1 as a blunt acanthoid chaetae, mi5 as the subanal appendage, smooth, blunt and thick; 3 chaetae present between aai1 and ai6 (as in Fig. 9B). Small abdomen of male: dorsal anal valve with as1–5, ms1–4, mps1, mps4, mps', and ps1–2 chaetae, as1, ms1, ps1 unpaired, as4–5 as cup sensilla, as1–2, ms2, ms4, mps4 as blunt acanthoid chaetae, ms3 as S chaeta; ventral anal valves each with aai1, ai1–6, ami1–2, mi1–5 and pi1–3 chaetae, ai1 as a cup sensillum, ai2–3 as S chaetae, ami2 as an oval organ, mi1 as a blunt acanthoid chaeta; 2 chaetae present between aai1 and ai6 (Figs. 12D, 14C). Genital plates of female and male unclear.

Large abdomen appendages: overall chaetotaxy of legs, ventral tube, tenaculum and furca as described to *Ptenothrix taiwanensis* sp. nov. Epicoxa, subcoxa and coxa I with 0, 0, 1 chaeta, respectively; trochanter I with 4 regular chaetae (as in Fig. 9A); femur I with 12 regular chaetae plus 1 microsensillum in a cavity (oval organ) and 1 cup sensillum (as in Fig. 10A); tibiotarsus I with 40 regular chaetae plus 1 microsensillum in a cavity (oval organ), 3 cup sensilla and 4 oval organs (without inner sensilla), distal whorl with 8 chaetae (as in Fig. 10B). Epicoxa, subcoxa and coxa II with 1, 1, 3 chaetae, respectively (as in Fig. 9A); trochanter II with 5 regular chaetae; femur II with 14 regular chaetae plus 1 microsensillum in a cavity (oval organ) and 1 cup sensillum (as in Fig. 10C); tibiotarsus II with 41 regular chaetae plus 1 microsensillum in a cavity (oval organ), 3 cup sensilla and 4 oval organs (without inner sensilla), distal whorl with 9 chaetae (as in Fig. 10D). Epicoxa, subcoxa and coxa III with 1, 1, 5 chaetae (including one apical small acanthoid chaetae), respectively (as in Fig. 9A); trochanter III with 6 regular chaetae; femur III with 14 regular chaetae plus 1 microsensillum in a cavity (oval organ) and 1 cup sensillum (as in Fig. 10E); tibiotarsus III with 37 regular chaetae plus 2 modified serrated chaetae, 1 microsensillum in a cavity (oval organ), 5cup sensillum, and 4 oval organs (without inner sensilla), distal whorl with 9 chaetae, number of teeth on modified serrated chaetae variable, from 4 to 7 (as in Fig. 10F). Tibiotarsus I lacking any apical bent sinusoid chaeta. Inner apical macrochaeta spiky in tibiotarsus I and blunt in tibiotarsi II–III (as in Fig. 10B, D and F). Foot complexes I–III similar to *Ptenothrix taiwanensis* sp. nov., with 2 small pretarsal chaetae each, 1 anterior and 1 posterior; ungues with 2 unpaired inner teeth subequal in size, lateral lamellae with 2+2 teeth, duplicate teeth not seen, pseudonychia present, merged to the dorsal face with 2 unpaired dorsal teeth, the proximal one smaller, with lateral margins irregularly serrate. Unguiculi with 1 basal tooth and 1 axial filament surpassing the tip of the ungues, apical filaments acuminate or slightly knobbed (as in Fig. 11A–C). Collophore with 1+1 chaetae on corpus plus 1+1 distal chaetae on lateral flaps (as in Fig. 11D), with a pair of long and warty sacs. Tenaculum with a quadridentate ramus, corpus with 4 apical chaetae. Furcal size length in holotype as manubrium = 153.62 μm; dens = 421.74 μm; and mucro = 149.07 μm. Manubrium with 7 dorsal (posterior) chaetae on each side (Fig. 14D); dens dorsally (posteriorly) with 24 chaetae: 10 on the dorso-external (E1–10), 10 on the dorso-internal (J1–10) and 4 dorso-central (PE1–4) chaetae, respectively, external and internal chaetae feathered, except for the chaetae near the manubrium and an apical-external one (as in Fig. 11F); dens ventrally (anteriorly) with 8 chaetae, with the following formula from the apex to the basis: 3, 2, 1, 1… 1; mucro with a narrow apex, with both edges

serrated, with about 46 (inner) and 34 (outer) serrations on each edge, with an apical notch. Ratio mucro: dens: manubrium in holotype 1: 2.83: 1.03.

Distribution: Nangan Island, Matsu, Taiwan. Habitat: Specimens of *Ptenothrix matsuensis* sp. nov. were found on dead leaves of tree ferns and *Miscanthus* bushes, similarly to *Ptenothrix taiwanensis* sp. nov. Sampling localities are presented as green triangles in figure 1. It is noteworthy that *Ptenothrix matsuensis* sp. nov. was only found during the wet season in Nangan Island, while no specimens were collected during the dry season, a condition that could be related to the life history of the species.

Remarks: *Ptenothrix matsuensis* sp. nov. is remarkably similar to *P. taiwanensis* sp. nov. in overall morphology (Fig. 5), but they appeared as distinct taxa in our analyses of *COI* phylogeny (Fig. 6) and K2P distances (Table 1). Even so, *P. matsuensis* sp. nov. can be objectively distinguished from *P. taiwanensis* sp. nov. by: head vertex with an unclear or absent central longitudinal pigment (with a central longitudinal stripe of dark pigment in the latter), frontal head D internal spines as long as the lateral ones (shorter than the lateral ones in *P. taiwanensis* sp. nov.), manubrium with 7 dorsal chaetae (*vs.* 8–10 in *P. taiwanensis* sp. nov.), and only 2 chaetae present between aai1 and ai6 in the small abdomen of the male of *P. matsuensis* sp. nov. (3 chaetae present in the male of *P. taiwanensis* sp. nov.) (Fig. 12). For further comparisons between similar species of *Ptenothrix* from Taiwan, South China and Japan, see table 2.

Lectotype designation of *Ptenothrix denticulata* (Folsom, 1899)

The type material of *Papirius denticulatus* Folsom, 1899 in NMNH is a slide-mounted specimen, and is labeled as "*Ptenothrix* (*Papirius*) *denticulatus*(sic) (Folsom) Type No 5076" and "Komaba, Tokyo, Japan. Coll. C. Ishikawa. Nov. 6. 1894. Lectotype det. by J. T. Salmon, 1938". Although the specimen is labeled as "lectotype" on the slide, the lectotype designation was never formally published, rendering it an invalid type designation under ICZN Art. 74. In 1938, while planning to write a monograph on Collembola of the world, Salmon visited the museums as part of a tour in various institutions in Europe, Great Britain, and the United States to examine and re-describe poorly described Collembola type specimens. Nevertheless, the monograph was never finished. In 1974, the author published the drawings he had completed in the Zoology Publications from Victoria University of Wellington (Salmon 1974), but *Ptenothrix denticulata* was not included in this article (Dana M. De Roche, personal communication, January. 12. 2023). As a result, we herein designate the specimen of *Papirius denticulatus* Folsom, 1899 in the Smithsonian Institution National Museum of Natural History, Washington, USA (catalog no. USNMENT01747048) as the lectotype for *Ptenothrix denticulata* (Folsom 1899).

DISCUSSION

Folsom (1899) originally described three specimens of *Papirius denticulatus* without designating a holotype. In 1938, Salmon examined these specimens and classified them as two different species: *Dicyrtoma denticulata* (Salmon, 1964:634), with a type specimen deposited in the Museum of Comparative Zoology, Harvard, USA and *Ptenothrix denticulata* (Salmon, 1964:642), with two type specimens, one deposited in the Museum of Comparative Zoology, Harvard, USA, and the other in the Smithsonian National Museum of Natural History, Washington, USA. Salmon differentiated *Dicyrtoma* from *Ptenothrix* based on the presence or absence of annulations on Ant. III and Ant. IV, with *Dicyrtoma* lacking these distinct annulations and *Ptenothrix* having them.

Subsequent research by Betsch (1980) demonstrated that annulations on Ant. III are ontogenetic, being absent or indistinct in juveniles and becoming distinct in adults. Following Betsch's findings, we can reasonably conclude that the specimen classified as *Dicyrtoma denticulata* by Salmon (1964), which is now missing, is a juvenile form of *Ptenothrix denticulata*. Therefore, all three specimens originally described by Folsom (1899) belong to a single species, *Ptenothrix denticulata*. Our re-evaluation shows that *Dicyrtoma denticulata* (Salmon, 1964:634) is synonymous with *Ptenothrix denticulata* (Folsom, 1899), specifically a juvenile form. Consequently, the specimens should be referred to as *Ptenothrix denticulata* (Folsom 1899), with *Dicyrtoma denticulata* (Salmon, 1964:634) as a synonym of *Ptenothrix denticulata* (Salmon, 1964:642) (syn. nov.).

Color patterns and their variations are commonly regarded as useful diagnostic characters that should not be overlooked, especially when there is a constant variation of these features between species of the same genus (Soto-Adames 2002; Ding et al. 2019). As a result, the detailed depiction of color patterns should not be omitted in morphological descriptions, since they are helpful for further taxonomic comparisons. Our finding that specimens previously identified as *Ptenothrix denticulata* (Folsom, 1899) in Cheng et al. (2022) that have slightly different color patterns actually belong to two new species adds another piece of evidence

supporting the importance of carefully studying this feature in different taxa, as well as indicating that the diversity of Collembola in Taiwan is still underexplored (Cheng et al. 2022). In addition to Taiwan and Japan, based on image records curated in http://www.collembola.org, specimens that look superficially similar to the *Ptenothrix* species investigated in this study have also been found in Massachusetts, USA (Bellinger et al. 1996–2024). While the identities of the imaged animals are unclear, as well as whether they are native or introduced, the presence of a species potentially related to Asiatic taxa on the other side of the Pacific Ocean highlights the need for further research. Accordingly, clarifying the taxonomic identities of *Ptenothrix denticulata* and *Ptenothrix denticulata catenata* with redescriptions and molecular data is critical for the taxonomic foundations of Asiatic *Ptenothrix*. Taxonomic studies of *Ptenothrix* and other springtails in Taiwan are fundamental and critical for a better understanding of the real species richness of the country, dispersal mechanisms and taxa distribution, all important data which can be used to outline strategies for the conservation of Taiwanese soil fauna.

When we surveyed the original descriptions of *Ptenothrix* species found in Taiwan, South China, and Japan, we found that many taxa only have oversimplified morphological descriptions. Many details of most species are still unknown, such as the chaetotaxy of antennae and legs, and the number and distribution of dorsal spines on the large abdomen. This made it difficult not only to understand the morphologies of these species, but also to look for appropriate characteristics for interspecific comparisons. Hence, more comprehensive descriptions, incorporating molecular information whenever possible, will help to resolve potential taxonomic issues as well as facilitate further integrative studies.

CONCLUSIONS

Ptenothrix taiwanensis sp. nov. and *P. matsuensis* sp. nov. are described and illustrated in this study. Morphology of the *Ptenothrix* species distributed in Taiwan, Japan, and South China are compared. Interspecific and intraspecific genetic distances and phylogenetic analysis are used to support that the two species of *Ptenothrix* are new to science. In addition, we designate the lectotype of *P. denticulata* (Folsom, 1899). The discoveries of the present study suggest that further surveys are required to fully understand the diversity of Collembola in Taiwan.

Acknowledgments: We are grateful to two anonymous reviewers for their constructive comments on an earlier version of this article. We thank Dr. Crystal A. Maier (curator) Whit Farnum (imager) in the Museum of Comparative Zoology at Harvard University, USA, and Dana De Roche, the curator of the Smithsonian National Museum of Natural History, Washington D.C., USA, for providing access to the museum collections. We appreciate Dr. Hui-Yun Tseng in the NTU Insect Museum, Department of Entomology, National Taiwan University, Taiwan, and Dr. Jing-Fu Tsai, Dr. Mei-Ling Chan, and Bao-Cheng Lai at the National Museum of Natural Science, Taiwan for helping archive the specimens newly collected in this study. We also thank Dr. Yu-Feng Hsu for providing helpful advice about ICZN related issues. We are thankful to the following people who provided important samples for this study: Yu-Hsiang Ho, Tzu-Po Lin, Hou-Feng Li, Hsiang-Yun Lin, BingJhih Liou, Wei-tsen Liu, Chieh Kao, Li-Hung Chen, Tsai-Wen Hsu. We are also thankful to the staff of Komabano Park, Meguro-ku, Tokyo, Japan for allowing samples collection in the park. We are grateful to the staff of Technology Commons, College of Life Science, NTU for assistance with scanning electron microscopy. This study was supported by the National Science and Technology Council, Taiwan (MOST 108-2621-B-002-001-MY3 and MOST 111-2621-B-002-005-MY3) and the Ministry of Education, Taiwan (Yushan Fellow Program) to C.-H. Chang, the National Science and Technology Council, Taiwan to H.-J. Cheng (112-2927-I-002-527), and the Brazilian National Council for Scientific and Technological Development (CNPq), grant number 309114/2021-7, to B.C. Bellini.

Authors' contributions: HJC, FJ, and CHC initiated the study. HJC and TN conducted the sampling. HJC and BCB conducted the drawing and morphological descriptions. HJC and CHC performed molecular analysis and drafted the manuscript.

Competing interests: HJC, BCB, FJ, TN and CHC declare they have no conflicts of interest.

Availability of data and materials: DNA sequences newly acquired in this study are deposited in GenBank. Specimens are deposited at the NTU Insect Museum, National Taiwan University (NTUE), Taipei, Taiwan and the National Museum of Natural Science (NMNS), Taichung, Taiwan.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Arlé R, Mendonça C. 1982. Estudo preliminar das espécies de *Dicranocentrus* Schött, 1893, ocorrentes no Parque Nacional da Tijuca, Rio de Janeiro (Collembola). Revista Brasileira de Biologia **42:**41–49.

Bellinger PF, Christiansen KA, Janssens F. 1996–2024. Checklist of the Collembola of the World. Available at: http://www.collembola.org.

Betsch JM. 1980. Éléments pour une monographie des Collemboles Symphypléones (Hexapodes, Aptérygotes). Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série, Série A, Zoologie **116:**1–227.

Betsch JM. 1997. An ontogenetically focused chaetotaxial scheme in Symphypleona (Collembolan). Pedobiologia **41:**13–18.

Betsch JM, Waller A. 1994. Chaetotaxic nomenclature of the head, thorax and abdomen in Symphypleona (Insecta, Collembola). Acta Zoologica Fennica **195:**5–12.

Börner C. 1909. Japans Collembolenfauna. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin **2:**99–135.

Bretfeld G. 1999. Synopses on Palaearctic Collembola: Symphypleona (Vol. 2). Abhandlungen und Berichte des Naturkundemuseums Gorlitz **71:**1–318.

Bretfeld G. 2001. Symphypleona from Northwest and West Africa, collected in the years 1979–1986 by Johan MERTENS, Gent (Insecta, Collembola). Senckenbergiana Biologica **81:**87–131.

Chen JX, Christiansen K. 1996. A new species of *Ptenothrix* from China (Collembola: Dicyrtomidae). Florida Entomologist **79:**586–591. doi:10.2307/3496072.

Cheng HJ, Janssens F, Chang CH. 2022. An updated checklist of Collembola in Taiwan, with DNA barcoding of *Papirioides jacobsoni* Folsom, 1924 (Symphypleona, Dicyrtomidae). ZooKeys **1123:**123–146. doi:10.3897/zookeys.1123.90202.

Cipola NG, Morais, JWD, Bellini BC. 2014. A new species of *Seira* (Collembola: Entomobryidae: Seirini) from Northern Brazil, with the addition of new chaetotaxic characters. Zoologia **31:**489–495. doi:10.1590/S1984-46702014000500009.

Ding YH, Yu DY, Guo WB, Li JN, Zhang F. 2019. Molecular phylogeny of *Entomobrya* (Collembola: Entomobryidae) from China: Color pattern groups and multiple origins. Insect Science **26:**587–597. doi:10.1111/1744-7917.12559.

Fjellberg A. 1999. The Labial Palp in Collembola. Zoologischer Anzeiger **237:**309–330.

Fjellberg A. 2007. The Collembola of Fennoscandia and Denmark, part II: Entomobryomorpha and Symphypleona. Fauna Entomologica Scandinavica **42:**1–264.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol Marine Biol Biotech **3:**294–299.

Folsom JW. 1899. Japanese Collembola. Part II. Proceedings of the American Academy of Arts and Sciences **34:**261–274.

Hopkin SP. 1997. Biology of the springtails: (Insecta: Collembola). Oxford University Press, New York, 330 pp.

Ito R, Hasegawa M, Ichisawa K, Furuno K, Suma Y, Tanaka S, Hasegawa M, Keiko N. 2012. Classification of the Suborder Neelipleona Massoud, 1971 and Symphypleona Borner, 1901 (Hexapoda: Entognatha: Collembola) from Japan. Edaphologia **91:**99–156.

Itoh R, Zhao LJ. 2000. Five new species of the family Sminthuridae (Collembola) from Yunnan, Southwest China. Taxonomical Studies on the Soil Fauna of Yunnan Province in Southwest China, pp. 147–162.

Jo SH, Park KH. 2023. A new species of *Ptenothrix* Börner, 1906 (Collembola, Symphypleona, Dicyrtomidae) from South Korea. Zootaxa **5301:**124–136. doi:10.11646/zootaxa.5301.1.6.

Katz AD, Giordano R, Soto-Adames FN. 2015. Operational criteria for cryptic species delimitation when evidence is limited, as exemplified by North American *Entomobrya* (Collembola: Entomobryidae). Zool J Linn Soc-Lond **173:**818–840. doi:10.1111/zoj.12220.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol **35:**1547–1549. doi:10.1093/molbev/msy096.

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2016. PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol Biol Evol **34:**772–773. doi:10.1093/molbev/msw260.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG. 2007. Clustal W and Clustal X version 2.0. Bioinformatics **23:**2947–2948. doi:10.1093/bioinformatics/btm404.

Lin S, Xia F. 1985a. Four new species of *Ptenothrix* from Dinghu Mountain, Guangdong (Collembola: Dicyrtomidae). Entomotaxonomia **7:**61–67.

Lin S, Xia F. 1985b. Two new species of Dicyrtomidae (Collembola: Symphypleona). Acta Entomologica Sinica **28:**206–209.

Mateos E. 2008. The European *Lepidocyrtus* Bourlet, 1839 (Collembola: Entomobryidae). Zootaxa **1769:**35–59. doi:10.11646/zootaxa.1769.1.2.

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution **32(1):**268–274. doi:10.1093/molbev/msu300.

Oliveira JVLC, Ferreira AS, Zeppelini D. 2020. Two new species of Collembola (Arthropoda: Hexapoda) from Minas Gerais, Brazil. Neotrop Entomol **49:**420–434. doi:10.1007/s13744-020-00769-8.

Orgiazzi A, Bardgett RD, Barrios E et al. (Eds.) 2016. Global soil biodiversity atlas. European Commission, Publications Office of the European Union, Luxembourg, 176 pp.

Potapov M, Porco D, Deharveng L. 2018. A new member of the genus *Isotomurus* from the Kuril Islands (Collembola: Isotomidae): returning to the problem of "colour pattern species". Zootaxa **4394:**383–394. doi:10.11646/zootaxa.4394.3.4.

Richards WR. 1968. Generic classification, evolution, and biogeography of the Sminthuridae of the world (Collembola). Mem Entomol Soc Can **53:**1–54. doi:10.4039/entm10053fv.

Salmon JT. 1964. An index to the Collembola. Royal Society of New Zealand Bulletin **7:**1–651.

Salmon JT. 1974. Notes and drawings from type material of Collembola. Zoology Publications from Victoria University of Wellington **66:**1–41.

Schneeberg K, Bauernfeind R, Pohl H. 2017. Comparison of cleaning methods for delicate insect specimens for scanning electron microscopy. Microsc Res Techniq **80:**1199–1204. doi:10.1002/jemt.22917.

Soto-Adames FN. 2002. Molecular phylogeny of the Puerto Rican *Lepidocyrtus* and *Pseudosinella* (Hexapoda: Collembola), a validation of Yoshii's "color pattern species". Mol Phylogenet Evol **25:**27–42. doi:10.1016/S1055-7903(02)00250-6.

Yosii R. 1970. On Some Collembola of Japan and adjacent Countries II. Contributions from the Biological Laboratory, Kyoto University **23:**1–32.

Yosii R, Lee CE. 1963. On some Collembola of Korea, with notes on the genus *Ptenothrix*. Contributions from the Biological Laboratory, Kyoto University **15:**1–37.

Supplementary materials

Table S1. Specimens with *COI* sequences analyzed and their GenBank accession numbers. (download)