

New insight into the systematics of the *Willowsia* complex (Collembola: Entomobryidae)

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Abstract. The three closely related genera *Willowsia* Shoebottom 1917 with 22 species, *Janetschekbrya* Yosii 1971 with 2 species and *Americabrya* Mari-Mutt & Palacios-Vargas 1987 with 3 species (the “*Willowsia* complex”) are examined in the light of a phylogenetic analysis and a re-evaluation of their original differential characters. A hypothesis based on 56 morphological characters is proposed for 15 *Willowsia* species and *Americabrya arida* Christiansen & Bellinger 1980. With *Drepanosira hussi* Neuherz 1976 as outgroup, three major clades are recovered: the species *Willowsia samarkandica*, a clade with 4 species, and a large clade with 10 species and *Americabrya arida* in a terminal position. Conversely, if *Americabrya* is used as outgroup with the *Willowsia* species as ingroup, all *Willowsia* including *W. samarkandica* constitute a monophyletic clade. Biogeographically, we show that the *Willowsia* complex exhibits a remarkable distribution pattern. Beside four species of *Willowsia* largely distributed across continents, all species of the complex are restricted to two areas: the Neotropics, with the three species of *Americabrya* and the *Willowsia* species closest to this genus (*W. mexicana*); and the temperate and subtropical region of Asia, with all other species of *Willowsia* and the two species of *Janetschekbrya*. Using characters of scale morphology, the genera *Americabrya*, *Janetschekbrya* and *Willowsia* are redefined. Four types of scale morphology are disclosed in the genus *Willowsia*. The strong similarities between the scales of *W. mexicana* and those of *Americabrya* on one hand, and between those of *Janetschekbrya* and the chaetae of the unscaled genus *Himalanura* on the other hand, suggest that *Willowsia* in its current definition is probably paraphyletic. A key to the 27 recognizable species of the *Willowsia* complex is provided. *W. samarkandica* is redescribed. Complements to descriptions, mostly dorsal chaetotaxy, are given for *W. buski*, *W. japonica*, *W. nigromaculata* and *W. platani*. Three species new to science are described: *W. yiningensis* **sp. nov.**, *W. qui* **sp. nov.** and *W. potapovi* **sp. nov.** Two species are synonymized: *W. kahlertae* **syn. nov.** of *W. japonica*, and *W. mesothoraxa* **syn. nov.** of *W. jacobsoni*. Three species considered as *Willowsia* in the literature are placed as *incertae sedis* because data on the presence of scales on dentes are unavailable. Two species are removed from *Willowsia* and assigned to *Lepidosira* for having scales on dentes.

Résumé. Nouvel aperçu de la systématique du complexe *Willowsia* (Collembola : Entomobryidae). Les trois genres étroitement apparentés *Willowsia* Shoebottom 1917 avec 22 espèces, *Janetschekbrya* Yosii 1971 avec 2 espèces et *Americabrya* Mari-Mutt & Palacios-Vargas 1987 avec 3 espèces (“complexe *Willowsia*”) sont reconsidérés à la lumière d’une analyse phylogénétique et d’une ré-évaluation de leurs caractères différentiels originaux. Une hypothèse basée sur 56 caractères morphologiques est proposée pour 15 espèces de *Willowsia* et *Americabrya arida* Christiansen & Bellinger 1980. Avec *Drepanosira hussi* Neuherz 1976 comme groupe externe, trois clades majeurs sont mis en évidence : l’espèce *Willowsia samarkandica*, un clade de 4 espèces, et un clade de 11 espèces avec *Americabrya arida* en position terminale. Par contre, si *Americabrya* est utilisé comme groupe externe avec les espèces de *Willowsia* comme groupe interne, tous les *Willowsia* y compris *W. samarkandica* constituent un clade monophylétique. Du point de vue biogéographique, nous montrons que le complexe *Willowsia* présente un patron de distribution remarquable. En dehors de 4 espèces de *Willowsia* à large distribution intercontinentale, toutes les espèces du complexe sont limitées à deux régions : la région néotropicale, avec les trois espèces d’*Americabrya* et la *Willowsia* la plus proche de ce genre (*W. mexicana*), et l’Asie tempérée et subtropicale, avec toutes les autres espèces de *Willowsia* et les deux espèces de *Janetschekbrya*. Sur la base de la morphologie des écailles, les genres *Americabrya*, *Janetschekbrya* et *Willowsia* sont redéfinis. Quatre types morphologiques d’écailles sont reconnues dans le genre *Willowsia*. Les fortes similarités entre les écailles de *W. mexicana* et celles d’*Americabrya* d’une part, et entre celles de *Janetschekbrya* et les soies du genre *Himalanura* dépourvu d’écailles d’autre part, suggèrent que le genre *Willowsia* dans son actuelle définition est probablement paraphylétique. Une clé des 27 espèces reconnaissables du complexe *Willowsia* est fournie. *W. samarkandica* est redécrite. Des compléments aux descriptions,

principalement la chétotaxie dorsale, sont donnés pour *W. buski*, *W. japonica*, *W. nigromaculata* et *W. platani*. Trois espèces nouvelles pour la science sont décrites: *W. yiningensis* **sp. nov.**, *W. qui* **sp. nov.** and *W. potapovi* **sp. nov.** Deux espèces sont mises en synonymie: *W. kahlertae* **syn. nov.** de *W. japonica*, et *W. mesothoraxa* **syn. nov.** de *W. jacobsoni*. Trois espèces considérées comme *Willowsia* dans la littérature sont placées en *incertae sedis*. Deux espèces sont retirées du genre *Willowsia* et placées dans le genre *Lepidosira* du fait de la présence d'écaillés sur la dens.

Keywords: Phylogeny, biogeography, macrochaetotaxy, *Americabrya*, *Janetschekbrya*.

Supraspecific taxonomic categories among scaled Entomobryinae remain poorly delimited as soon as extra-European fauna is considered. This is the case for the group of three genera called here for practicality the *Willowsia* complex (*Willowsia*, *Americabrya* and *Janetschekbrya*). This group, which includes several of the most widespread species of Collembola in the world, exhibits potential relationships with various other Entomobryidae, in relation with the evolutionary process of scale differentiation. We investigate here the systematics of this group with special emphasis on scale morphology and macrochaetotaxy.

Shoebottom (1917) established the genus *Willowsia* for *Seira nigromaculata* Lubbock 1873, based on its pointed scales. Later, this character was replaced by the absence of scales on dentes (Bonet 1930; Denis 1941); simultaneously, some authors, including the previous two, often used *Sira* (unjustified emendation of *Seira* Lubbock 1869 by Tullberg 1872), instead of *Willowsia*, which was validated again by Salmon (1945). Yoshii and Suhardjono (1989) considered that this genus was polyphyletic.

Yosii (1971) erected the genus *Janetschekbrya* for the new Himalayan species *J. himalica*, characterized by narrow scales, those of the posterior row of each tergite strongly elongate. He transferred *W. brahamides*

Denis 1936 from the Himalaya (Yosii 1971) and *W. yamashitai* Uchida 1969 from Japan (Yosii 1977) into this genus. Later, three American species (*arida* Christiansen & Bellinger 1980, *matthewsi* Snider 1981 and *epiphyta* Loring 1984) were described as *Janetschekbrya*; in 1987, Mari-Mutt and Palacios-Vargas transferred them to the new genus *Americabrya* (type-species *A. arida*), distinct from the former by narrow scales with “two distinct longitudinal ribs”, but they did not compare it with *Willowsia*.

The present paper is an attempt to explore the taxonomic structure of the *Willowsia* complex through the detailed morphological analysis of macrochaetotaxy and scale morphology.

Material and Methods

Morphological study

After clearing in lactic acid, specimens were mounted under a coverslip in Marc André II solution, and were studied under a Leica DMLB microscope. Photographs were taken under a Leica DMR microscope using a mounted Leica DFC420 digital camera, and were enhanced with Photoshop CS2 (Adobe Inc.).

Cephalic chaetae are named after Jordana & Baquero (2005), interocular chaetae after Mari-Mutt (1986), and dorsal body chaetotaxy follows the nomenclature of Szeptycki (1979).

Type material deposit

Specimens examined are deposited in the following institutions: Department of Biological Science and Technology, Nanjing University, Nanjing, China (NJU); Museum National d'Histoire Naturelle, Paris, France (MNHN); Moscow State Pedagogical University, Moscow, Russia (MSPU).

Phylogenetic analyses

Phylogenetic analyses were performed on a matrix comprising 56 morphological characters, mainly drawn from dorsal chaetotaxy in adult (Appendix 1), and 17 taxa (Appendix 2), with the method of outgroup polarization (*Drepanosira hussi* Neuherz 1976, and *Americabrya arida*). Characters were drawn from literature and checked from direct examination of all species (including an undescribed *Willowsia* from southern Tibet). All characters were equally weighted, and all 3 multistate characters were treated as unordered. Character states were scored as question marks (?) if ambiguous or missing. Heuristic searches were performed with the program PAUP* v4.0b10 (Swofford 2002), using tree bisection–reconnection (TBR) branch swapping and 1000 random-addition replicates.

Table 1. Synapomorphies and homoplastic changes at the nodes of the strict consensus tree of fig. 1A.

Nodes	Synapomorphies	Homoplastic changes
19		11.1, 17.1, 20.1
20		27.1, 28.1, 29.1, 40.1, 41.1
21	6.0	7.0, 8.0, 25.1
22	33.1, 36.1	16.1, 28.1, 29.1
23	14.1	15.1, 20.1, 26.0, 42.1, 48.1
24	34.1, 46.1	13.1, 27.1, 30.1, 44.1
25		35.1, 40.1, 41.1, 45.1
26	9.0, 53.1, 56.1	17.1
27		48.0
28	12.0	31.1
29	21.1	23.1, 26.1
30	22.1, 37.1, 43.1, 55.1	4.3, 18.1
31	10.1, 54.1	50.1

Implicit enumeration option was used in TNT (Goloboff *et al.* 2008). The support of nodes was assessed in TNT with non-parametric bootstrap (Felsenstein 1985) procedures (1000 pseudoreplicates, 10 random-addition replicates) and the Decay index (Bremer 1994).

Results

Phylogeny

Using *Drepanosira hussi* as outgroup and (*Willowsia* spp. + *Americabrya arida*) as ingroup, the heuristic parsimony analysis of the data matrix (Appendix 2) yielded two most parsimonious trees of 113 steps [consistency index (CI), 0.51; retention index (RI), 0.76] in PAUP, and the same two trees were produced with implicit enumeration algorithm in TNT. The strict consensus tree (fig. 1A) has a length of 115 steps

with CI = 0.50 and RI = 0.75. The synapomorphies and the homoplastic changes at the nodes are shown in tab. 1.

We have three major monophyletic clades in the strict consensus tree. The first clade includes the single species *W. samarkandica* Martynova 1972. The second clade (node 21) is supported by one synapomorphy: scales numerous with very short and subequal spinules (6.0), and three homoplasies: scales present on antennae (7.0) and scales present on the ventral side of manubrium (8.0), macrochaeta p5 absent on Th. II (25.1). It groups Chinese and Vietnamese *Willowsia*. The third clade (node 26), is supported by three synapomorphies: accessory chaetae of bothriotrichal complex unmodified (9.0), macrochaeta B3 absent on Abd. IV (53.1), and macrochaeta A2p absent on Abd. IV (56.1), and one homoplasy: macrochaeta m2i

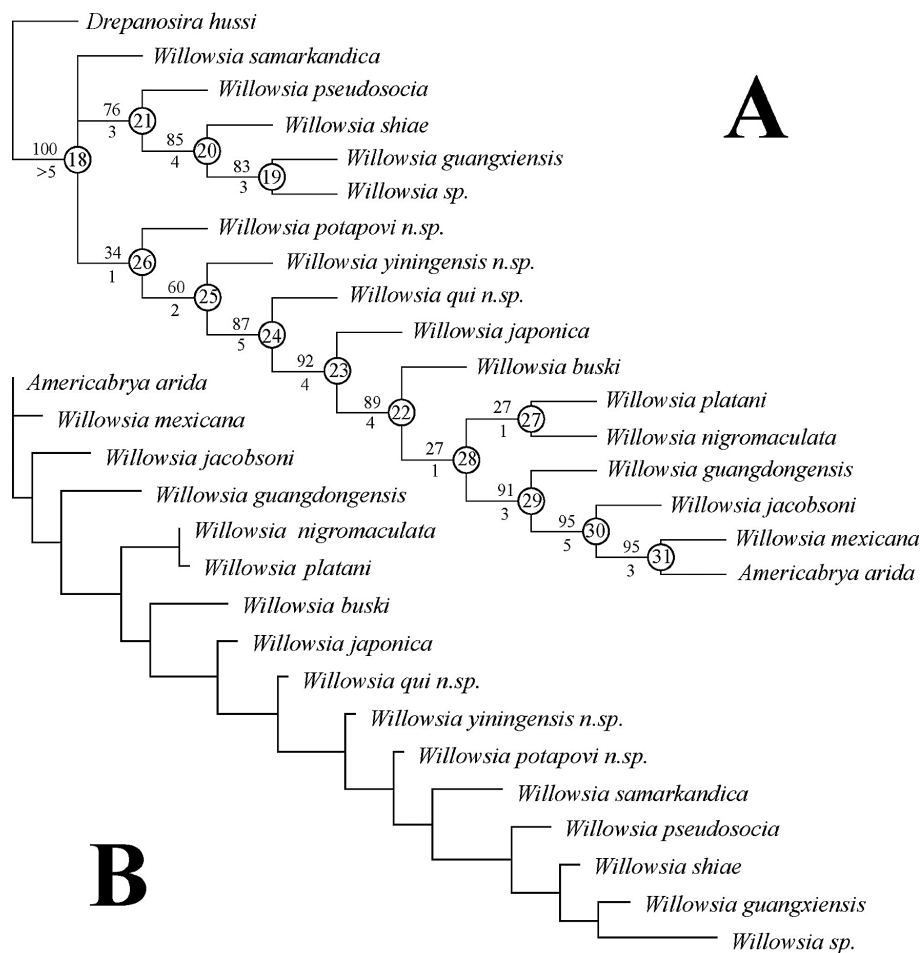


Figure 1

Phylogenetic analyses. **A**, *Drepanosira hussi* as outgroup and (*Willowsia* + *Americabrya arida*) as ingroup. Strict consensus of two equally parsimonious trees with 115 steps (CI = 0.50, RI = 0.75). The bootstrap values and Bremer indices are given above and below branches respectively; nodes numbers are framed. **B**, *Americabrya arida* as outgroup, *Willowsia* as ingroup.

absent on Th. II (17.1). The node 29 (four tropical species including *A. arida*), with high bootstrap and Bremer values, is supported by one synapomorphy: macrochaeta p1 absent on Th. II (21.1), and two homoplasies: macrochaeta p4 absent on Th. II (23.1) and macrochaeta p5pi absent on Th. II (26.1). According to this topology, *Americabrya* appears as an extreme evolution of *Willowsia* in terms of scale morphology and chaetal reduction, and the genus *Willowsia* is not monophyletic. *W. samarkandica* is an isolated taxon.

We performed a second analysis restricted to the 15 species of *Willowsia* and using *Americabrya arida* as outgroup. It yielded a unique tree, strongly different from the previous one, with two clades: a clade restricted to *W. mexicana* and a well supported clade grouping all other *Willowsia* species including *W. samarkandica* (fig. 1B). The genus *Willowsia* is monophyletic in this topology, if *W. mexicana* is excluded.

Of the 56 characters used for analyses, 44 are presence/absence of macrochaetae. Actually, the differences between the two trees might reflect the level of pluri- or paurochaetosis of the species selected as outgroups, which are at the opposite: *Drepanosira hussi* has the highest number of diagnostic macrochaetae of all studied species (40), *Americabrya* the lowest number (4).

One of the striking results of the analyses is the ladder-like topology of the largest clade, reflecting a progressive reduction (or increase) in the number of dorsal macrochaetae. This seems to be a major trend in the evolution of the *Willowsia* complex, as already suggested by Szeptycki (1979) on a small subset of species. Its evolutionary significance and its translation at taxonomic level require more exhaustive analyses, including a wider selection of outgroups from related genera (*Lepidosira* Schoett 1925, *Janetschkebrya* and *Himalanura* Yosii 1971), for which detailed information is currently lacking.

Taxonomy

The *Willowsia* complex

Among scaled Entomobryinae sensu Szeptycki (1979) (*Willowsiini* sensu Soto-Adames *et al.* 2008), the *Willowsia* complex as understood here includes three closely related genera having in common a bidentate mucro, no scales on dens and claw with one or two unpaired inner teeth. They include 27 species in total (tab. 2): 3 *Americabrya*, 2 *Janetschkebrya* and 22 *Willowsia*. Three additional species are incertae sedis, and belong either to *Willowsia*, or to *Lepidosira*.

Americabrya was erected for *Janetschkebrya arida*,

for having “non-ciliated scales with two distinct longitudinal ribs” (Mari-Mutt & Palacios-Vargas 1987), contrary to *Janetschkebrya* where scales are covered with numerous short ribs. The authors however did not compare it to *Willowsia*. Actually, the scale edge of the two *Americabrya* species other than *A. arida* is ciliated like in most *Willowsia*. Scale narrowness was later used to define *Americabrya* (Bellinger *et al.* 2009). However, some of the scales are narrow as well in some *Willowsia* like *W. japonica* (Folsom 1897) and *W. potapovi* **sp. nov.** (fig. 8M). Actually, scales of *Americabrya* can be characterized by their two longitudinal ribs which run laterally from basis to nearly the tip of the scale, all scales having this morphology. By comparison, ribs are more than two, and are either interrupted (at least some of them) or short to very short in other *Willowsia* and in *Janetschkebrya*. The uninterrupted ribs figured by Folsom (1932) for *Willowsia jacobsoni* from Hawaii, have not been retrieved by further authors (Mari-Mutt 1981, and here). Whether *Americabrya* represents a basal clade within the *Willowsia* complex or an extreme stage of scale and chaetotaxy evolution within the genus *Willowsia* is still pending.

Janetschkebrya was isolated from *Willowsia* on the ground of its narrower scales “with those marginal scales along the posterior border of each tergite ... strongly elongated” (Yosii 1971). The diagnosis was later extended to include species now grouped in the genus *Americabrya* (Christiansen & Bellinger 1980) on the ground of scale narrowness. However, scale sculpture (numerous short ribs in *Janetschkebrya* versus two long ribs in *Americabrya*) and chaetotaxy (plurichaetotic in *Janetschkebrya* versus oligochaetotic in *Americabrya*) are completely different, suggesting that the two genera are probably only remotely related, as suspected by Christiansen and Bellinger themselves (1980). Here, we come back to the original diagnosis, limiting the genus *Janetschkebrya* to its two Himalayan species (*himalica*, *brahamides*). In 1977, Yosii transferred *W. yamashitai* in *Janetschkebrya* without explanation, but probably on the ground that tergite scales are fusiform-elongate and very narrow in this species. However in the absence of information about the relative length of scales in the posterior row of tergites, we still keep it provisionally among *Willowsia*, its original genus. *Janetschkebrya brahamides* (Denis) redescribed by Yosii in 1971 on material from eastern Nepal, is likely to concern a species different from the *Sira brahamides* of Denis, described from Ladakh in India. Types were not retrieved, and original description is insufficient, but slight difference in claw structure and coloration, as well as geographical distribution give support to this proposal.

In several species of *Willowsia*, like in *Janetschekbrya*, scales of the posterior row of tergites are much larger than the others but never as elongate as in the former genus. The thin elongated scales of *Janetschekbrya* actually exhibit obvious similarity with the tergal "scaly setae" figured and described by Yosii (1971) as characteristic of *Himalanura*, a non-scaled Entomobryidae which is also mostly diversified in the Himalayan region.

The idea that *Janetschekbrya* and some *Willowsia* may directly derive from *Himalanura*-like species (Yosii 1971) needs to be explored further.

The 22 remaining species belong to the large genus *Willowsia* (tab. 2). It differs from *Janetschekbrya* by scales of the posterior row not much more elongate than others on tergites, and from *Americabrya* by more-than-2-ribs scales always dominant dorsally, and ribs of

Table 2. Species of the *Willowsia* complex.

Valid species	Original genus	Current genus	After	Type locality
<i>arida</i> Christiansen & Bellinger 1980	<i>Janetschekbrya</i>	<i>Americabrya</i>	Mari-Mutt & Palacios-Vargas 1987	USA, Arizona, Chiricahua Mts
<i>epiphyta</i> Loring 1984	<i>Janetschekbrya</i>	<i>Americabrya</i>	Mari-Mutt & Palacios-Vargas 1987	Peru, Madre de Dios, Puerto Maldonado
<i>matthewsi</i> Snider 1981	<i>Janetschekbrya</i>	<i>Americabrya</i>	Mari-Mutt & Palacios-Vargas 1987	Costa Rica, Puntarenas, Osa Peninsula
<i>brahamides</i> Denis 1936	<i>Sira</i>	<i>Janetschekbrya</i>	Yosii 1971	India, Ladakh, Pangong Lake
<i>himalica</i> Yosii 1971	<i>Janetschekbrya</i>	<i>Janetschekbrya</i>		Nepal, Khumbu Himal, Pangpoche
<i>abrupta</i> Schött 1917	<i>Sira</i>	<i>Willowsia</i>	Greenslade 1994	Australia, Queensland, Ravenshoe (= Cedar Creek)
<i>bartkei</i> Stach 1965	<i>Willowsia</i>	<i>Willowsia</i>		Vietnam, Lao Cai, Sa Pa
<i>buski</i> Lubbock 1869	<i>Seira</i>	<i>Willowsia</i>	Schoebotham 1917	Great Britain
<i>formosana</i> Denis 1929	<i>Sira</i>	<i>Willowsia</i>	Yosii 1956	China, Taiwan, Taioku
<i>fuscana</i> Uchida 1944	<i>Sira</i>	<i>Willowsia</i>	Shi & Chen 2004	Mariana Islands, Pagan
<i>guangdongensis</i> Zhang, Xu & Chen 2007	<i>Willowsia</i>	<i>Willowsia</i>		China, Guangdong, Heshan
<i>guangxiensis</i> Shi & Chen 2004	<i>Willowsia</i>	<i>Willowsia</i>		China, Guangxi, Tianlin
<i>hyalina</i> Handschin 1928	<i>Sira</i>	<i>Willowsia</i>	Yosii 1966	Indonesia, Java, Cibodas
<i>ieti</i> Yosii 1971	<i>Willowsia</i>	<i>Willowsia</i>		Nepal, Khumbu Himal, Pangpoche
<i>jacobsoni</i> Börner 1913	<i>Sira</i>	<i>Willowsia</i>	Stach 1965	Indonesia, Java, Semarang
<i>japonica</i> Folsom 1897	<i>Seira</i>	<i>Willowsia</i>	Yosii 1955	Japan, Honshu, Tokyo
<i>mekila</i> Christiansen & Bellinger 1992	<i>Willowsia</i>	<i>Willowsia</i>		Hawaii, Oahu
<i>mexicana</i> Zhang, Palacios-Vargas & Chen 2007	<i>Willowsia</i>	<i>Willowsia</i>		Mexico, Oaxaca, Oaxaca city
<i>nigromaculata</i> Lubbock 1873	<i>Seira</i>	<i>Willowsia</i>	Schoebotham 1917	Great Britain
<i>nivalis</i> Yosii 1971*	<i>Willowsia</i>	<i>Willowsia</i>		Nepal, Khumbu Himal, Thata
<i>platani</i> Nicolet 1842	<i>Degeeria</i>	<i>Willowsia</i>	Denis 1924	Europe
<i>potapovi</i> sp. nov.	<i>Willowsia</i>	<i>Willowsia</i>		Azerbaijan, Girkan Reserve
<i>pseudosocia</i> Stach 1965	<i>Willowsia</i>	<i>Willowsia</i>		Vietnam, Lao Cai, Sa Pa
<i>qui</i> sp. nov.	<i>Willowsia</i>	<i>Willowsia</i>		China, Zhejiang, Taishun
<i>samarkandica</i> Martynova 1972	<i>Willowsia</i>	<i>Willowsia</i>		Uzbekistan, Samarkand
<i>shiae</i> Pan, Zhang & Chen 2006	<i>Willowsia</i>	<i>Willowsia</i>		China, Tibet, Yadong
<i>yamashitai</i> Uchida 1969	<i>Willowsia</i>	<i>Willowsia</i>	Yosii 1971	Japan, Honshu, Odawara
<i>yiningensis</i> sp. nov.	<i>Willowsia</i>	<i>Willowsia</i>		China, Xinjiang, Yining
Species <i>incertae sedis</i> (no data on the presence of scales on dens)				
<i>brahma</i> Imms 1912	<i>Seira</i>	<i>Willowsia</i>	Shi & Chen 2004	India, Uttar Pradesh, Allahabad
<i>intermedia</i> Schött 1921	<i>Sira</i>	<i>Willowsia</i>	Shi & Chen 2004	Chile, Juan Fernandez island
Species described as <i>Willowsia</i> , transferred to <i>Lepidosira</i> (scales present on dens)				
<i>alba</i> Nguyen 2005	<i>Willowsia</i>	<i>Lepidosira</i>	this work	Vietnam, Vinh Phuc
<i>nigropunctata</i> Nguyen 2005	<i>Willowsia</i>	<i>Lepidosira</i>	this work	Vietnam, Son La

* Ut *W. brahmides* in Yosii 1966b

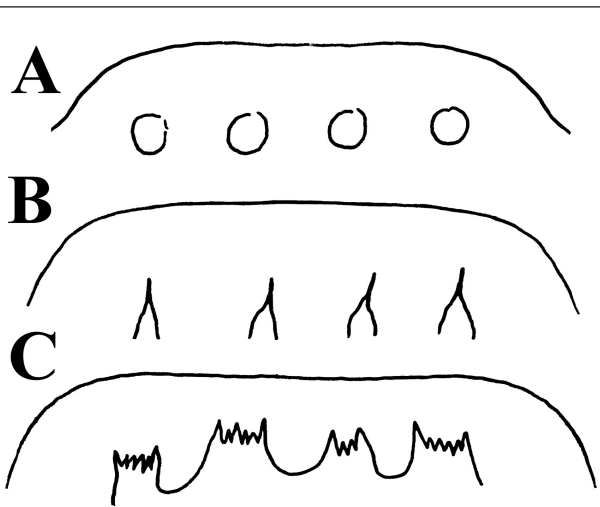


Figure 2
Labral papillae. **A**, rounded, *Willowsia nivalis*, redrawn from Yosii (1971); **B**, conical, *Willowsia platani* (Nicolet 1842); **C**, each with more than 2 denticles, *Willowsia jacobsoni*, redrawn from Mari-Mutt (1981).

various length, usually not running along the whole scale. *Willowsia* is actually loosely characterized, and exhibit a surprising diversity of scale morphologies. Scale tip is typically pointed apically in most case (but rounded for some of the scales in a few species), scale width is narrow to very broad (with a large range of width in some species), scale size is short to very large (with sometimes intermediates in a same species), and scale sculpture ranges from numerous regularly arranged minute spinules to ribs of various length.

The three genera of the *Willowsia* complex may be separated as follows:

1. Scales narrow, chaeta-like, finely sculpted with all ribs short and regularly arranged (fig. 3A), much longer, elongate and narrow in the posterior row of tergites *Janetschekbrya*
- Scales variously sculpted, not chaeta-like and not much longer in the posterior row of tergites 2
2. All scales narrow, with 2 uninterrupted lateral ribs; macrochaetotaxy reduced *Americabrya*
- Scales (or most scales in *Willowsia mexicana*) different, with various types of sculpture, from very short spinules to long ribs *Willowsia*

The genus *Willowsia* Shoebotam 1917

Type species. *Seira nigromaculata* Lubbock 1873

Type locality. Great Britain

Diagnosis. 4-segmented antennae. 8+8 eyes. Bidentate mucro. Presence of one or two unpaired teeth on claw. Scales mostly pointed, with rough sculpture of very short spinules to long ribs.

Morphological characters for taxonomy. Characters most classically used for separating *Willowsia* species include color pattern, dorsal chaetotaxy, scale morphology and distribution, tenent hair length and capitation, unguiculus morphology, length of distal smooth part of dens, mucronal spine length and labral papillae morphology. Only scale morphology was found useful for species grouping, but labral papillae (Fig. 2), for which data are too scarce, may provide interesting clues as well in the future.

Types of scales and species groups. The extreme diversity of scale morphology (sculpture and outlines) in *Willowsia* led authors to use it as a major character, together with macrochaetotaxy and colour pattern, for defining species of the genus. Shi & Chen 2004 defined two kinds of scale sculpture in *Willowsia* (spinulate and striate), and Zhang *et al.* (2007) added

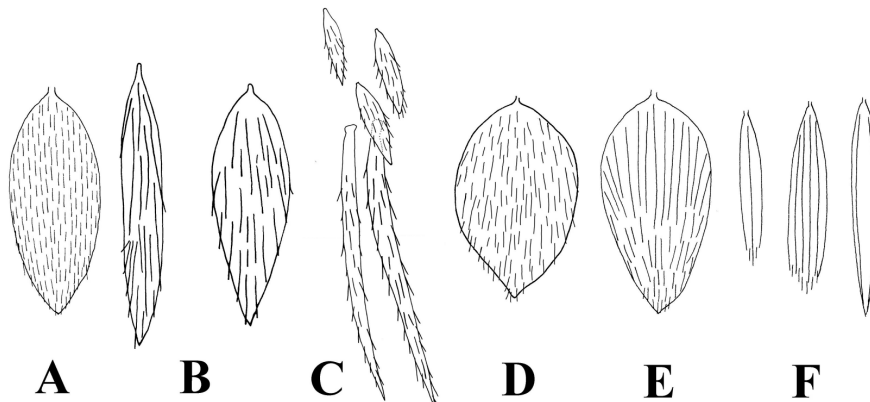


Figure 3
Scale sculpture. **A**, spinulate type, *Willowsia* sp. from Tibet; **B**, short rib type, narrow scales, *W. japonica* redrawn from Yoshii (1992); **C**, *Janetschekbrya brahamides*, redrawn from Yosii (1971); **D**, short rib type, broad scales, *W. ieti*, redrawn from Yosii (1971); **E**, long basal rib type, *W. platani* (Nicolet 1842) (specimen from Fleurance, Gers, France); **F**, uninterrupted rib type, *W. mexicana*, redrawn from Zhang *et al.* (2007).

a third type (ribbed). Here, we recognize four types of scales. The short rib type and the long basal rib type roughly match the Shi & Chen' striate type.

The **spinulate type** (fig. 3A): scales broad with numerous very short and equal spinules, regularly sparsed (*bartkei*, *guangxiensis*, *pseudosocia*, *shiae*, sp. (Tibet)). Each spinule is progressively thickened distally. In species with this scale type, accessory chaetae of bothriotrichal complex of Abd. IV are broadly or scaly modified (Fig. 4B).

The **short rib type** (fig. 3B and 3D): scales more or less elongate-fusiform, often narrow, usually pointed, with all ribs moderately short (longer than in the spinulate type) and irregular in length (*hyalina*, *ieti*, *japonica*, *nivalis*, "*platani*" sensu Uchida 1969, and *yamashitai*). Among the listed forms, *japonica* (fig. 3B), "*platani*" sensu Uchida 1969 and *yamashitai* have most scales narrow, fusiform scales at least 3 times longer than wide, with relatively long ribs similar to those of *Janetschekbrya* (fig. 3C). In that case, ribs on the scales clearly derive from cilia of the ordinary chaetae. In a second group (*hyalina*, *ieti* and *nivalis*), the scales are at most 2.6 times longer than wide, with relatively shorter ribs. This type is intermediate with the spinulate type.

The **long basal rib type** (*buski*, *formosana*, *guangdongensis*, *jacobsoni* (personal observation), *mekila*, *nigromaculata*, *platani*, *potapovi* sp. nov., *qui* sp. nov., *samarkandica* and *yiningensis* sp. nov.): scales usually broad and pointed (narrow in *potapovi*), with ribs of various length converging distally, those starting from the basis of the scale longer, replaced distally by shorter ones (fig. 3E). In species with this scale type, accessory chaetae of bothriotrichal complex of Abd. IV are unmodified when described (Fig. 4A).

The **uninterrupted ribbed type**, with all ribs parallel, running straight from basis to tip of the scale; the scale is narrow, not pointed when more than 3 ribs are developed. This kind of scale is characteristic of the single species *W. mexicana*. It has obvious similarities with *Americabrya*, with scale ribs uninterrupted and few in number (1–10, fig. 3F versus 2 ribs in *Americabrya*), and reduced chaetotaxy. Moreover, its distribution matches that of the genus *Americabrya*, with which it constitutes an entirely neotropical group, while all other *Willowsia* except the cosmopolitan ones are absent from America. Ecologically, *W. mexicana* is associated with *A. arida*, and both may dominate certain Collembolan communities in Mexico (Cutz-Pool *et al.* 2008).

Illustrations of scale sculpture are not available or insufficient in several descriptions of the literature. In that case, scales cannot be assigned to a type. The scales of *W. formosana*, considered of the uninterrupted ribbed type in Zhang *et al.* (2007), are here placed in the long basal rib type, because ribs are briefly interrupted

and / or slightly shift at middle-course, according to the original figure of Denis (1929). Redescription of the species is needed in any case, as ribs are not distally convergent in these drawings. In *W. jacobsoni*, the illustrations given in the literature differ: scale ribs are uninterrupted but more or less distally convergent after Folsom's drawing (1932); they are of the short rib type after Mari-Mutt (1981); they clearly match the long basal rib type in specimens recently collected in southern Sulawesi. In several species, lateral scales differ from the dorsal ones in size and outlines, but they are usually of the same type. We refer in this paper to scales of the dorsal side of the body.

Scale morphology and size across the different tergites and the different areas of a tergite may therefore follow interesting specific patterns that remain largely undocumented. The different scale types recognized here are likely to correspond at least in part to actual lineages, but the presence of intermediate morphologies, the poor description of most ancient species, and the complexity of chaetotaxic pattern would make taxonomic decision premature at this stage.

Ecology and biogeography

The *Willowsia* complex has a wide latitudinal distribution, from arctic regions (*W. buski* and *W. nigromaculata*, Babenko & Fjellberg 2006) to tropical areas, with relatively narrow ecological requirements for all known species. Most live in the vegetation, and are typically found under barks of standing trees at least in Europe.

Species of the *Willowsia* complex are not present worldwide. Two areas of diversification can be recognized: subtropical Asia, and to a lesser degree tropical to subtropical America (fig. 5). In addition,

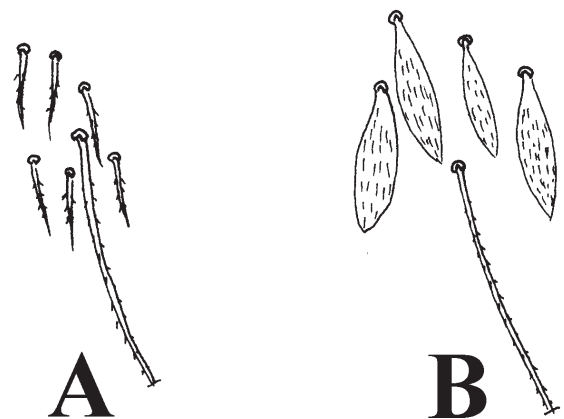


Figure 4
Accessory chaetae of bothriotrichal complex on Abd. IV. **A**, unmodified, *Willowsia platani* (Nicolet 1842); **B**, scale-like, *Willowsia* sp. from Tibet.

a few species have colonized several continents. Except these subcosmopolitan elements, species of the *Willowsia* complex have not been recorded from Africa, Europe, most of north America and most of the Australasian region.

Four species are subcosmopolitan, possibly following human introductions across different continents. All exhibit the long basal rib type of scale. Three of them (*W. buski*, *W. nigromaculata* and *W. platani*) are widespread in northern temperate and subtropical region, and are the only species of the complex present in Europe. *W. jacobsoni* is pan-tropical (Africa, Asia and America). None of the temperate species is in a basal position in the phylogenetic reconstructions, but *W. jacobsoni* is branched basally on the tree when *Americabrya arida* is used as outgroup.

Four species are neotropical, including the three known species of the genus *Americabrya*, and *W. mexicana*, the species of *Willowsia* most closely related to *Americabrya*.

Temperate and subtropical Asia have the largest diversity of species. Most non-subcosmopolitan species of *Willowsia* are limited to this region (except *W. mexicana*), as well as the two species of *Janetschekbrya*. Distribution ranges are restricted to type locality or relatively narrow, except *W. japonica* present from western China to Japan and Hawaii. There is an interesting geographical structuration (fig. 5): the two species of *Janetschekbrya* are Himalayan, *Willowsia* with narrow scales of the short rib type are Japanese, and the

Willowsia with scales of the spinulate type are restricted to a small area including northern Vietnam and south western China (Tibet and western Guangxi).

Key to species of the *Willowsia* complex

Three species are not included in the key because of insufficient descriptions: *W. brahma* Imms 1912, "*Sira*" *fusca* Uchida 1944, and "*S.*" *intermedia* Schoett 1921. A fourth one (*W. mesothoraxaca* Nguyen 2001) is synonymised with *W. jacobsoni*.

Willowsia brahma is placed in *Willowsia* by Shi & Chen (2004). The original description does not even mention the presence of scales, and no further indication of the species is found in the literature. The species is here considered as *incertae sedis*.

Sira intermedia is placed in *Seira* by Mari-Mutt & Bellinger (1990), and in *Willowsia* by Shi & Chen (2004). However, the morphology of scales as well as their distribution on the body is unknown. It could be a *Willowsia* or a *Lepidosira*. The species is considered as *incertae sedis*.

Sira fusca, given by Uchida (1944) as lacking scales on antennae, furcula and legs, and having scale ribs of various length [long basal rib type], is rightly placed in *Willowsia* by Shi & Chen (2004). However, the remaining information provided by Uchida is insufficient to include it in the present key.

W. mesothoraxa is here considered as a synonym of *W. jacobsoni*: the male has exactly the colour pattern of *W. jacobsoni lipostropha* Börner 1913, and the female exactly the colour pattern of the main form (Mari-Mutt 1981); the labral margin has 4 tubercles with 3 teeth by tubercle, as in *W. jacobsoni*; scales have the same morphology and sculpture as those of *W. jacobsoni*. The only difference is the chaetotaxy, that is insufficiently described in *W. mesothoraxa*.

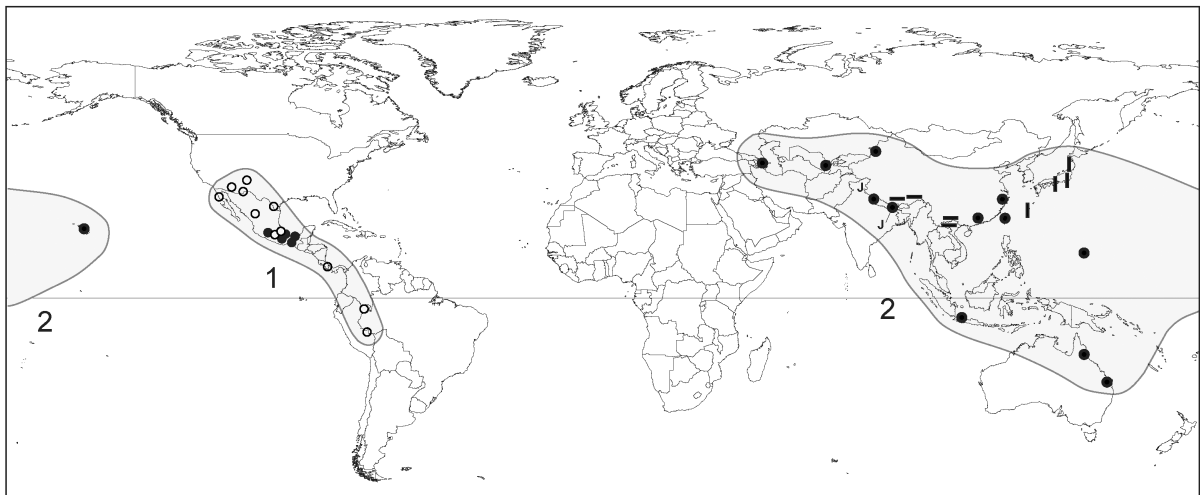


Figure 5

Geographical distribution of *Willowsia*, *Janetschekbrya* and *Americanura*, excluding the subcosmopolitan species *W. buski*, *W. jacobsoni*, *W. nigromaculata* and *W. platani*. **1**, the American area of diversification; **empty circles**, genus *Americabrya* (3 species); **full circles**, *Willowsia mexicana*. **2**, the Asiatic area of diversification (19 species); **vertical bar**, *Willowsia* with narrow scales of the short rib type; **horizontal bar**, *Willowsia* with scales of the spinulate type; **full circles**, other *Willowsia*; **J**, *Janetschekbrya*.

1. Scales with only two distinct longitudinal ribs **2** (*Americabrya*)
 - Scales, or most of the scales in *W. mexicana*, different, usually with many ribs or spinules **4**
2. Abd. III with 1+1 central macrochaetae *A. matthewsi*
 - Abd. III with 2+2 central macrochaetae **3**
3. Abd. IV with 4+4 central macrochaetae *A. arida*
 - Abd. IV with 3+3 central macrochaetae *A. epiphyta*
4. Scales narrow and fusiform with short ribs, those of the posterior row much longer than others and similar to enlarged macrochaetae **5** (*Janetschekbrya*)
 - Scales different **6** (*Willowsia*)
5. No colour pattern on tergites. Abd. II with 5+5 macrochaetae *J. brahamides*
 - A distinct colour pattern of various patches on tergites. Abd. II with 7+7 macrochaetae *J. himalica*
6. Scales broad with many very short spinules regularly arranged (spinulate type) **7**
 - Scales with ribs of various length, none as very short spinules **11**
7. Abd. II-III without pigment **8**
 - Abd. II-III with dark blue pigment, at least partly **9**
8. A median patch of pigment on Abd. V. No pigment behind eye patches and on Th. II-Abd. I *W. nivalis*
 - Two small symmetrical patches of pigment on Abd. V. A longitudinal band of pigment behind each eye patch running postero-laterally up to Abd. I *W. pseudosocia*
9. Scales absent on legs and manubrium. Abd. II-III entirely dark blue pigmented *W. bartkei*
 - Scales present on manubrium **10**
10. Scales absent on legs. Pigment present on all tergites as large irregular patches *W. shiae*
 - Scales present on legs. Abd. II-III entirely dark blue pigmented *W. guangxiensis*
11. Mucron with subapical tooth much smaller than apical one and basal spine long reaching midway between the subapical and apical teeth *W. samarkandica*
 - Mucron with teeth subequal and basal spine short, reaching the apex of subapical tooth **12**
12. Ordinary scales of tergites very narrow, more than 6 times longer than wide *W. yamashitai*
 - Ordinary scales of tergites at most 4 times longer than wide **13**
13. Unguiculus truncate **14**
 - Unguiculus lanceolate **16**
14. Tenent hair 2 times as long as unguis *W. formosana*
 - Tenent hair less than 1.5 times as long as unguis **15**
15. Pigment absent on tergites *W. hyalina*
 - A pair of lateral patches on Abd. IV *W. ieti*
16. All segments with scattered pigment *W. buski*
 - Pigment not uniformly distributed on each segment ... **17**
17. Transverse bands present only on Th. III and Abd. III and irregular patches present on lateral side of Th. II, Abd. I, II and IV *W. abrupta*
 - Pattern different **18**
18. Antennae and ventral side of manubrium scaled *W. guangdongensis*
 - Antennae and ventral side of manubrium unscaled **19**
19. Labral papillae with at least 2 denticles **20**
 - Labral papillae conical **21**
20. Scale ribs as long as the scale itself. Abd. IV with 4+4 central macrochaetae *W. mexicana*
 - Scale ribs variable in size, but not as long as the scale itself. Abd. IV with 5+5 central macrochaetae *W. jacobsoni*
21. Abd. I with 7+7 macrochaetae *W. potapovi* **sp. nov.**
 - Abd. I with at most 4+4 macrochaetae **22**
22. Abd. II with 5+5 central macrochaetae *W. yiningensis* **sp. nov.**
 - Abd. II with at most 4+4 central macrochaetae **23**
23. Abd. II with 4+4 central macrochaetae *W. mekila*
 - Abd. II with 3+3 central macrochaetae **24**
24. Abd. I with 4+4 macrochaetae *W. qui* **sp. nov.**
 - Abd. I with at most 3+3 macrochaetae **25**
25. Abd. III with 2+2 central macrochaetae *W. japonica*
 - Abd. III with 3+3 central macrochaetae **26**
26. Irregular and small strips of pigment mainly present laterally on tergites *W. nigromaculata*
 - Large dark transverse bands at least on Th. III and Abd. II-IV *W. platani*

Species descriptions

Willowsia qui sp. nov. (fig. 6)

Type material. Holotype: ♀ on slide, China, Zhejiang Province, Taishun, Wuyanling, Shuang Keng Kou, altitude 600 m, 27°37'N 119°46'E, 4.VIII.2005, collection number 9279, collected by Chen Jian-Xiu team. Paratypes: 2 ♀♀ on slide and 4 in alcohol, same as holotype. One paratype on slide deposited in MNHN and others in NJU.

Description. **Body length** up to 1.8 mm. **Colour pattern.** Ground colour pale yellow in alcohol. Eye patches dark blue and one lighter strip between two eyes. Whole antenna gradually darker towards tip. Irregular strips and patches present on lateral thorax, Abd. III, median and posterior Abd. IV, Abd. V-VI (fig. 6A). **Head.** Eyes 8+8, eyes G & H smaller than others. Antenna about 1.8 times as long as cephalic diagonal. Antennal segment ratio as I:II:III:IV = 1:1.6–2.0:2.2–2.3:2.7–3.0. Antennal apical bulb unilobed. Labral margin with four conical papillae. Labral formula 4/ 5, 5, 4; prelabrals ciliate (fig. 6B). Lateral process of labial palp straight, thick as normal chaetae, with tip just reaching apex of same labial papilla (fig. 6C). Subapical chaeta of maxillary outer lobe subequal to apical one, 3 smooth sublobal hairs on sublobal plate (fig. 6D). Labial base chaetae as MREL₁L₂, all finely ciliate (fig. 6E). Cephalic dorsal chaetotaxy as 4 antennal (An), 4 median (M) and 3 sutural macrochaetae; S₀ and Ps₂ present; S₁ absent; interocular chaetae

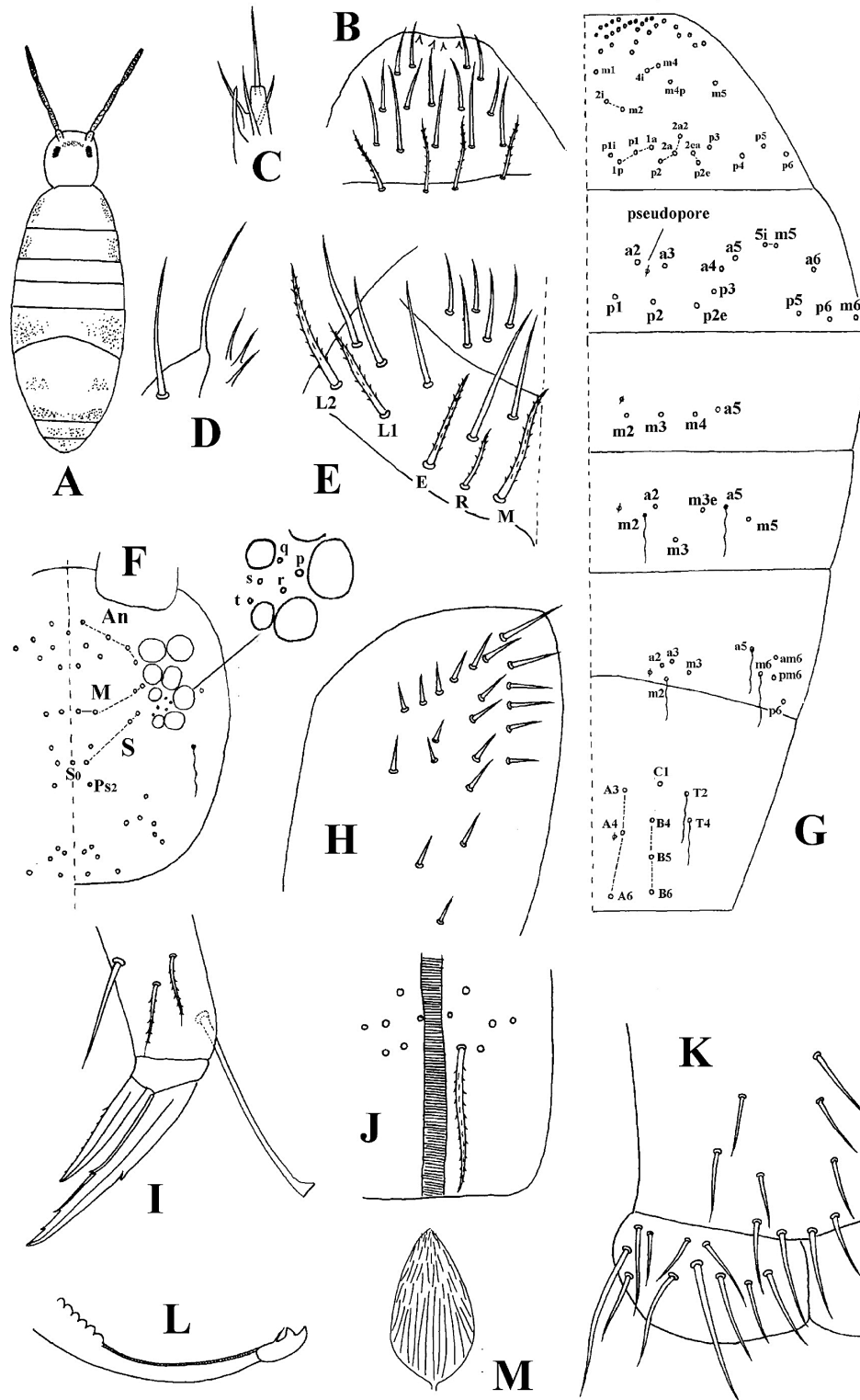


Figure 6
Willowsia qui sp. nov. **A**, colour pattern; **B**, labrum; **C**, lateral process of labial palp; **D**, maxillary outer lobe; **E**, chaetae on labial base; **F**, cephalic dorsal chaetotaxy and interocular chaetae; **G**, body dorsal chaetotaxy; **H**, trochanteral organ; **I**, hind foot complex; **J**, anterior face of ventral tube and lateral flap; **L**, mucro; **M**, body scale.

as pqrst (fig. 6F). **Thorax and legs.** Dorsal chaetotaxy shown in fig. 6G. Th. II with 3 (m1, m2, m2i) medio-medial, 4 (m4, m4i, m4p, m5) medio-lateral and 13–14 posterior macrochaetae; p4–6 as macrochaetae. Th. III with 13–14 macrochaetae on each side; macrochaetae a1 and a6i absent. Trochanteral organ with 20–22 smooth spiny chaetae; among them, 12 in arms, 10–12 between arms (fig. 6H). Tibiotarsus with inner differentiated chaetae ciliate, the most distal one on hind legs smooth. Unguis with 2 small lateral and 4 inner teeth, all tiny; lateral ones 0.5 distance from base, inner pair with tip

reaching 0.48 internal length of claw, median one at 0.76 and distal one at 0.88 distance from base. Unguiculus slender and acuminate with outer edge slightly serrate. Tenent hair slender and clavate, subequal to unguis (fig. 6I). **Abdomen.** Abd. IV 2.1–3.0 times as Abd. III in length along dorsal midline. Abd. I with 4+4 (m2–4, a5) macrochaetae; Abd. II with 3 (a2, m3, m3e) central and 1 (m5) lateral macrochaetae; Abd. III with 3 (a2, a3, m3) central and 3 (am6, pm6, p6) lateral macrochaetae; Abd. IV with 7 (A3–4, A6, B4–6, C1) central macrochaetae on each side. Tenaculum with 4 + 4 teeth and 1 large striate

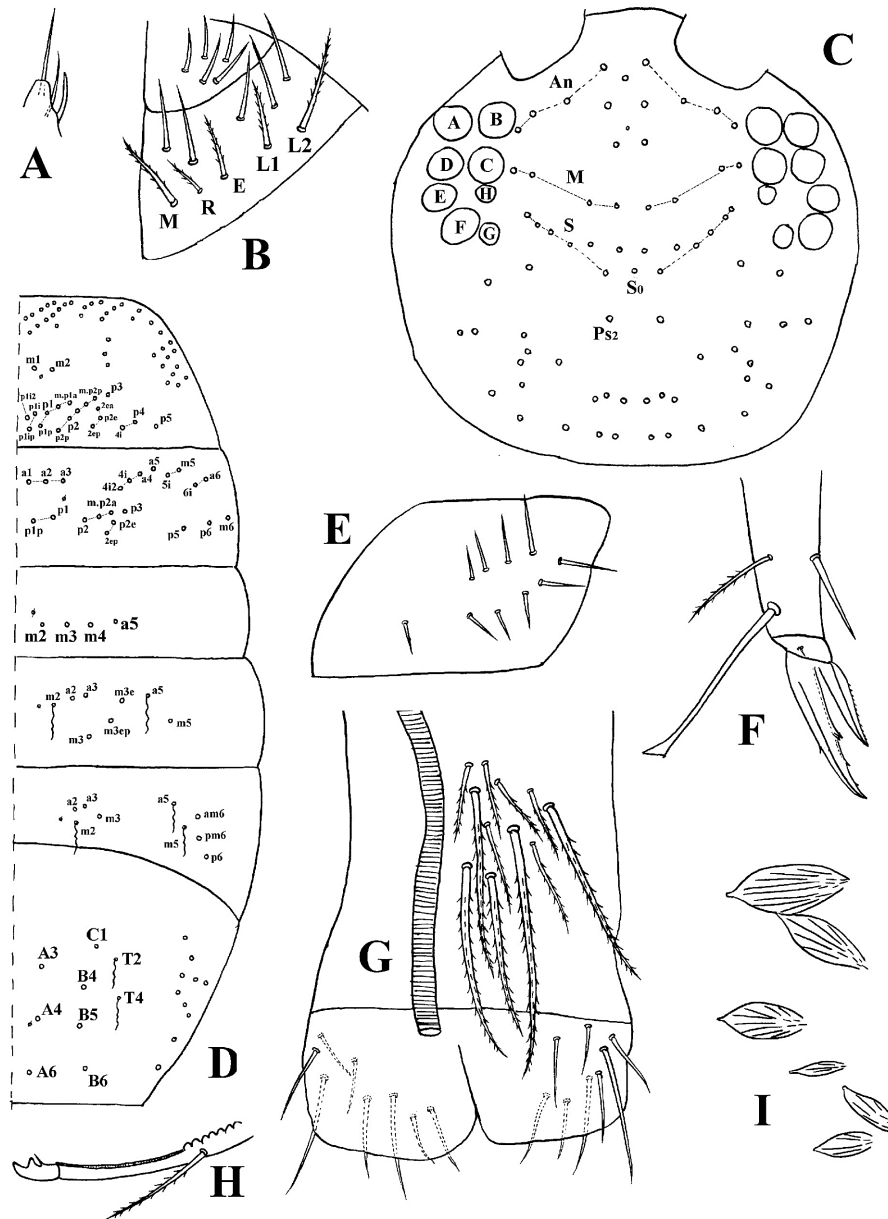


Figure 7

Willowsia yiningensis sp. nov. **A**, lateral process of labial palp; **B**, chaetae on labial base; **C**, cephalic dorsal chaetotaxy; **D**, body dorsal chaetotaxy; **E**, trochanteral organ; **F**, hind foot complex; **G**, anterior face of ventral tube and lateral flaps; **H**, mucro; **I**, body scale.

chaeta. Ventral tube anteriorly with about 5 large and many ciliate chaetae (fig. 6J); posteriorly with 4 apical smooth chaetae and 6 smooth chaetae; each lateral flap with 11 smooth chaetae (fig. 6K). Smooth part of dens 2.2 times mucro in length. Mucro bidentate with basal spine short with tip reaching apex of subapical tooth (fig. 6L). **Body scales.** Scales of the long basal rib type, heavily sculpted and leaf-like with tip pointed (fig. 6M). Scales absent on antennae, legs, manubrium and dentes.

Etymology. Named after J.-Q. Qu, who helped to classify this species.

Ecology. Found in litter, debris and rotten logs of evergreen broad-leaved forest.

Remarks. This new species is similar to *W. japonica* in conical labral papillae, dorsal chaetotaxy of posterior part of Th. II, Abd. II and Abd. IV, trochanteral organ and ventral tube; it differs from it in 3 sutural chaetae on head (5 in *japonica* according to Yoshii 1992), presence of macrochaetae m1, m2i, m4i and m4p on Th. II, p2e on Th. III, a5 on Abd. I and a3 on Abd. III, and different body scales.

Willowsia yiningensis sp. nov. (fig. 7)

Type material. Holotype: ♀ on slide, China, Xinjiang Province, Yining, Hebin Garden, 43°54'N 81°19'E, 7.VIII.2000,

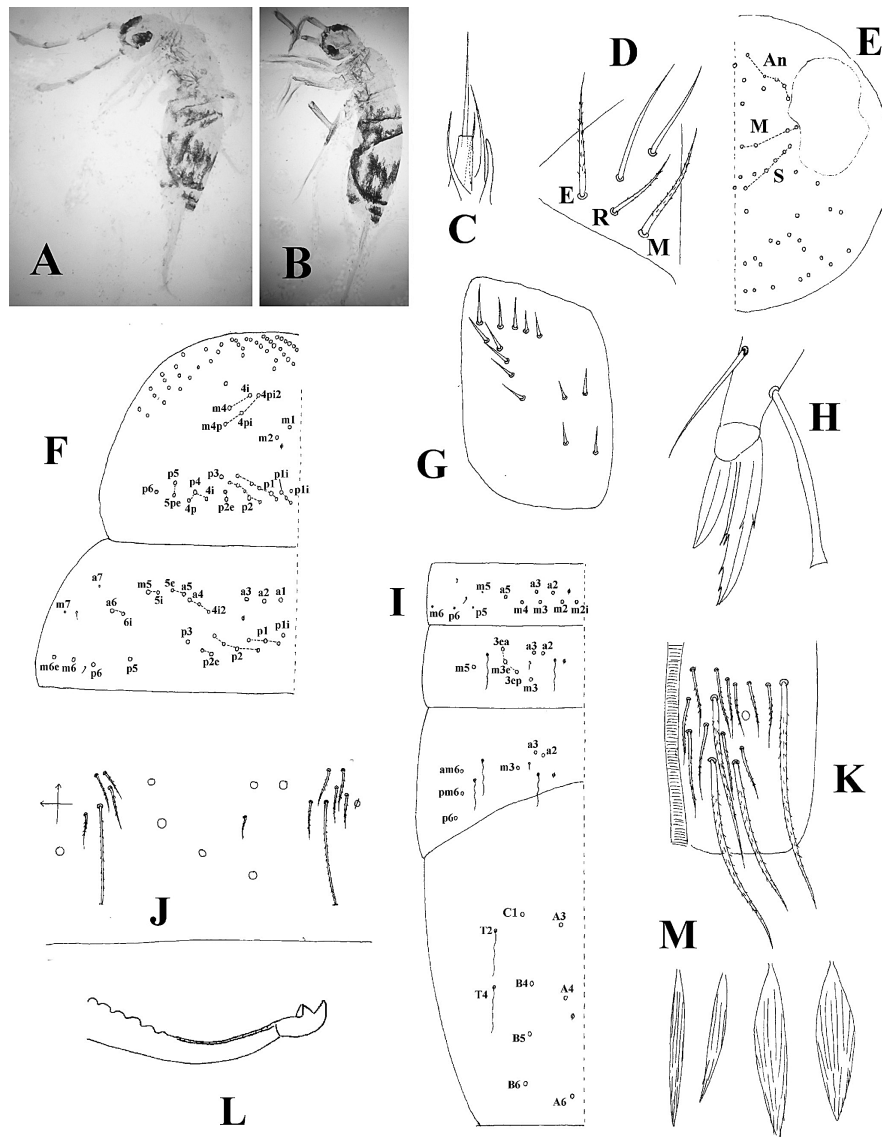


Figure 8

Willowsia potapovi sp. nov. A & B, colour pattern; C, lateral process of labial palp; D, chaetae on labial base; E, cephalic dorsal chaetotaxy; F, thoracic chaetotaxy; G, trochanteral organ; H, hind foot complex; I, abdominal chaetotaxy; J, accessory microchaetae of bothriotrichal complexes on Abd. II; K, anterior face of ventral tube; L, mucro; M, body scales.

collected by Chen Jian-Xiu. Paratypes: 3 ♀♀ on slide, same data as holotype. One paratype on slide deposited in MNHN and others in NJU.

Description. **Body length** up to 1.8 mm. **Colour pattern** not clear, ground colour pale yellow in alcohol. **Head.** Eyes 8+8, G & H much smaller than others. Antenna 1.75 times as long as cephalic diagonal. Antennal segment ratio as I:II:III:IV = 1:1.6:1.6:2.0. Antennal apical bulb unilobed. Labral margin with four conical papillae. Labral formula 4/5, 5, 4; prelabrals ciliate. Lateral process of labial palp slightly curved, as thick as normal chaetae, with tip apparently exceeding apex of same labial papilla (fig. 7A). Labial base chaetae as MREL₁L₂, all finely ciliate; chaeta R 0.4–0.5 times M in length (fig. 7B). Cephalic dorsal chaetotaxy (fig. 7C) as 4 antennal, 4 median and 5 sutural macrochaetae; S₀, S₁ and Ps₂ present. **Thorax and legs.** Dorsal chaetotaxy shown in fig. 7D. Th. II with 2 (m1, m2) medio-medial, 2 (m4, m4p) medio-lateral and about 19 posterior macrochaetae; p4-5 and p4i as macrochaetae. Th. III with 22 macrochaetae on each side; m5i and a6i as macrochaetae. Trochanteral organ with 8–10 smooth chaetae; among them, 7–9 in arms and 1 between arms (fig. 7E). Tibiotarsus with inner differentiated chaetae ciliate, the most distal one on hind legs smooth. Unguis with 2 lateral and 4 inner teeth, all tiny; lateral ones at 0.5 distance from base; inner pair with tip reaching 0.50–0.53 internal length of claw, median one at 0.69–0.74 and distal one at 0.88–0.91 distance from base. Unguiculus acuminate with outer edge serrate. Tenent hair slender and clavate, apparently longer than unguiculus and subequal to unguis (fig. 7F). **Abdomen.** Abd. IV 4–5 times as Abd. III in length along dorsal midline. Abd. I with 4 + 4 (m2-4, a5) macrochaetae; Abd. II with 5 (a2, a3, m3, m3e, m3ep) central and 1 (m5) lateral macrochaetae; Abd. III with 3 (a2, a3, m3) central and 3 lateral macrochaetae; Abd. IV with 7 (A3-4, A6, B4-6, C1) central and 11 lateral macrochaetae on each side. Abd. IV with 7 (A3-4, A6, B4-6, C1) central and 11 lateral macrochaetae on each side. Accessory chaetae of bothriotrichal complex on Abd. IV unmodified. Tenaculum with 4 + 4 teeth and 1 large striate chaeta. Ventral tube anteriorly with 5 + 5 large and about 6 small ciliate chaetae; each lateral flap with 8 smooth chaetae (fig. 7G). Smooth part of dens 2.5–3.1 times mucro in length. Mucro bidentate with basal spine short with tip reaching apex of subapical tooth (fig. 7H). **Body scales.** Scales of the long basal rib type, pointed and heavily sculpted (fig. 7I). Scales absent on antennae, legs, manubrium and dentes.

Etymology. Named after the type locality.

Ecology. Found in litter, debris and rotten logs in garden.

Remarks. This new species is close to *W. qui* sp. nov. in conical labral papillae, claw structure (outer edge of unguiculus serrate) and chaetotaxy of Abd. I, III and IV; however, it differs from it in 5 sutural chaetae on head, absence of m2i and m4i on Th. II, presence of a6i on Th. III, a3 and m3ep on Abd. II and reduced trochanteral organ.

Willowsia potapovi sp. nov. (fig. 8)

Type material. **Holotype:** ♀ on slide, Caucasus, Azerbaijan, Girkan Reserve, 38°38'N 48°43'E, in moss on bark of oak-tree, 30.I.1982. Paratypes: 6 ♀♀ on slide, locality same as holotype, 31.I.1982; 9 ♀♀ and 1 ♂ on slide, locality same as holotype, 3.II.1982. All collected by M. Potapov. Six paratypes deposited in NJU, 2 in MNHN and others including holotype in MSPU.

Additional material. 4 ♀♀ on slide, Caucasus, Georgia, Borzhomi area, Ahaldaba, ravine of Nedzura River, 42°4'N 44°1'E, under bark of trees, 27.I.1983, collected by E. Samoderzenkov; ♀, Caucasus, Georgia, Adzhamet Reserve, in litter of oak forest, 28.I.1983, collected by M. Potapov.

Description. **Body length** up to 2.18 mm. **Colour pattern.** Ground colour pale yellow in alcohol. Eye patches dark blue. Each antennal segment weakly pigmented and each tip darker. Transverse dark blue band present just behind antennal bases. Body dorsum with scattered blue pigment along lateral margins from thorax to Abd. I. Transverse irregular blue patches present from Abd. II to Abd. VI. Each leg with light blue pigment scattered (figs 8A & B). **Head.** Eyes 8+8. Antenna 3.0 times as long as cephalic diagonal. Antennal segment ratio as I:II:III:IV = 1:1.5:1.2:1.6. Antennal apical bulb distinct and unilobed. Labral margin with 4 conical papillae. Labral formula 4/5, 5, 4; prelabrals ciliate. Lateral process of labial palp slightly curved, as thick as normal chaetae, with tip nearly reaching apex of labial papilla (fig. 8C). Labial base chaetae as MREL₁L₂; all finely ciliate; chaeta R 0.7 times M in length (fig. 8D). Cephalic dorsal chaetotaxy (fig. 8E) with 5 antennal (An), 4 median (M) and 5 sutural (S) macrochaetae; S₀, S₁ and Ps₂ present. **Thorax and legs.** Dorsal macrochaetae shown in fig. 8F. Th. II with 2 medio-medial (m1, m2), 5 medio-lateral (m4, m4i, m4p, m4pi) and about 23 posterior macrochaetae on each side; p4-6 as macrochaetae; p1i2 and p4p sometimes absent. Th. III with 27 macrochaetae on each side; m5i and a6i present. Trochanteral organ with about 14 smooth spiny chaetae (fig. 8G). Unguis with 2 lateral and 4 inner teeth; lateral one at 0.50 distance from base, inner pair with tip reaching 0.50 internal length of claw, median one at 0.75 and distal one 0.90 distance from base. Unguiculus slender and acuminate. Tenent hair clavate and thick, subequal to unguis (fig. 8H). **Abdomen.** Abd. IV 6 times as Abd. III in length along dorsal midline. Dorsal macrochaetae shown in fig. 8I. Abd. I with 7 macrochaetae on each side; Abd. II with 6 central (a2, a3, m3, m3e, m3ea, m3ep) and 1 lateral (m5) macrochaetae; Abd. III with 3 central (a2, a3, m3) and 3 lateral (am6, pm6, p6) macrochaetae; Abd. IV with 7 central macrochaetae (A3-4, A6, B4-6, C1) on each side. Accessory microchaetae of bothriotrichal complexes on Abd. II–IV ciliate and unmodified (fig. 8J). Tenaculum with 4 + 4 teeth and one large striate chaeta. Ventral tube anteriorly with 5 larger ciliate chaetae and about 10 ciliate chaetae on each side (fig. 8K); posterior side not clear; each lateral flap with about 12 smooth chaetae. Smooth part of dens 1.8 times mucro in length. Mucro bidentate, apical tooth subequal to subapical one; basal spine short with tip reaching apex of subapical tooth (fig. 8L). Male genital plate not clearly seen. **Body scales.** Scales of the long basal rib type, narrow, pointed, subequal in length, proximally with more or less faint rather long ribs, distally heavily sculpted with short ribs (fig. 8M). Scales absent on antennae, legs, manubrium and dens.

Ecology. Found in moss on bark of oak-tree and litter of oak forest.

Etymology. Named after M. Potapov, who collected most specimens studied here.

Remarks. This new species is similar to *W. samarkandica* in long inner teeth on unguis, trochanteral organ, chaetotaxy of Th. III and Abd. III. It differs from it in longer tenent hair, large subapical tooth on mucro, narrower scales with longer ribs, unmodified accessory microchaetae of bothriotrichal complexes, absence of m1i and m2i on Th. II, presence of m2i on Abd. I and m3ea on Abd. II, more reduced chaetotaxy on Abd. IV.

***Willowsia samarkandica* Martynova 1972 (fig. 9)**

Type material (examined). Holotype ♀, Uzbekistan, Samarkand, Southwest part of Karakum Desert, well Uchkuduk, 42°7'N 63°40'E, 25.IX.1962.

Additional material examined: 6 ♀♀ on slide, Turkmenistan, Karakum Desert, Repetek, Kuyun-Kuyu, 38°34'N 63°10'E, small mammal hole, 19.X.1982, collected by D. Krivokhatski; 11 ♀♀ on slide, Turkmenistan, Karakum Desert, Repetek, 16–26.V.1979, collected by D. Krivokhatski. Holotype in Zoological Institute (S.-Petersburg), Russia, 5 specimens deposited in MSPU, 2 in MNHN and others in NJU.

Redescription. **Body length** up to 2.2 mm. **Colour pattern.** Light bluish pigment on body and nearly light in alcohol. Eye patches dark. **Head.** Eyes 8+8. Antenna 3.0 times as long as cephalic diagonal. Antennal segment ratio as I : II : III : IV = 1 : 2.0 : 1.8 : 2.5. Antennal apical bulb distinct and unilobed. Ant. III organ with 2 rods (fig. 9A). Labral margin with 4 papillae; each one with 2–3 denticles. Labral formula 4/ 5, 5, 4; prelabrals ciliate. Lateral process of labial palp as thick as normal chaetae, with tip nearly reaching apex of labial papilla (fig. 9B). Labial base chaetae as MREL₂; all finely ciliate, chaeta R 0.6 times M in length (fig. 9C). Cephalic dorsal chaetotaxy (fig. 9D) with

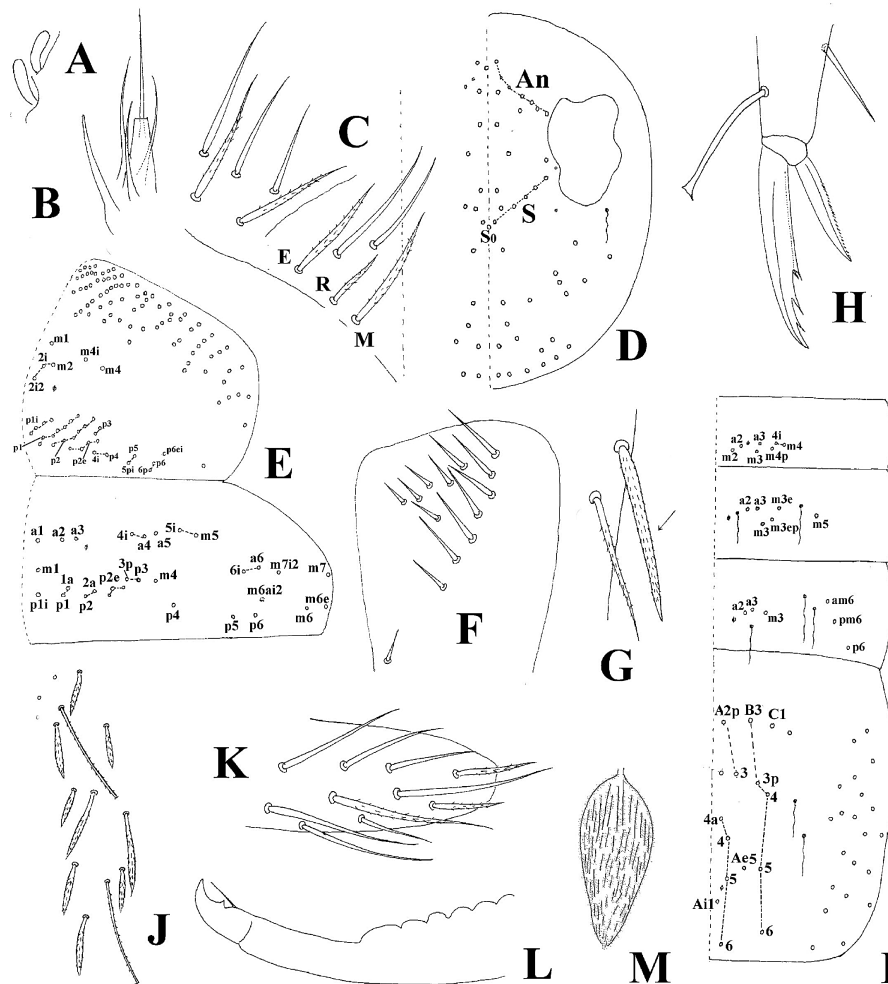


Figure 9

Willowsia samarkandica Martynova 1972. **A**, Ant. III organ; **B**, lateral process of labial palp; **C**, chaetae on labial base; **D**, dorsal cephalic chaetotaxy; **E**, thoracic macrochaetae; **F**, trochanteral organ; **G**, tibiotarsal inner differentiated chaetae; **H**, hind foot complex; **I**, abdominal chaetotaxy; **J**, accessory microchaetae of bothriotrichal complexes on Abd. IV; **K**, lateral flap of ventral tube; **L**, mucro; **M**, body scale.

about 7 antennal (An) and 5 sutural (S) macrochaetae; S_0 and Ps_2 present and S_1 absent. **Thorax and legs.** Dorsal macrochaetae shown in fig. 9E. Th. II with 4 medio-medial (m1, m2, m2i and m2i2), 2 medio-lateral (m4, m4i) and 31 posterior macrochaetae on each side; p5, p5pi, p6, p6pi and p6pi2 as macrochaetae. Th. III with 28 macrochaetae on each side; m4, p4, m7i2 as macrochaetae; m6ai2 rarely as macrochaeta. Trochanteral organ with 12–14 smooth spiny chaetae; among them, 11–12 in arms, 1–2 between arms (fig. 9F). Tibiotarsus with inner differentiated chaetae finely ciliate, the most distal one smooth (fig. 9G). Unguis with 4 inner teeth; inner pair with tip reaching 0.6 internal length of claw, median one at 0.75 and distal one 0.88 distance from base. Unguiculus slender and acuminate with outer edge finely serrate. Tenent hair with tip clavate, obvious shorter than unguis (fig. 9H). **Abdomen.** Abd. IV 4 times as Abd. III in length along dorsal midline. Dorsal

macrochaetae shown in fig. 9I. Abd. I with 6–7 macrochaetae; a5i sometimes absent; m2i absent. Abd. II with 5 central (a2, a3, m3, m3e, m3ep) and 1 lateral (m5) macrochaetae. Abd. III with 3 central (a2, a3, m3) and 3 lateral (am6, pm6, p6) macrochaetae. Abd. IV with about 16 central and 20–21 lateral macrochaetae on each side. Accessory macrochaetae of bothriotrichal complexes on Abd. II–IV ciliate and broadly modified (fig. 9J). Ventral tube anteriorly with 3 large ciliate chaetae and many ciliate chaetae on each side; posteriorly with two apical smooth chaetae and some ciliate chaetae; each lateral flap with 7 smooth and 3 ciliate chaetae (fig. 9K). Smooth part of dens 1.6 times mucro in length. Mucro bidentate, apical tooth much larger than subapical one; basal spine long with tip beyond apex of subapical tooth (fig. 9L). **Body scales.** Scales of the long basal rib type, hyaline, coarsely sculpted and leaf-like with tip pointed (fig. 9M). Scales absent on antennae and legs.

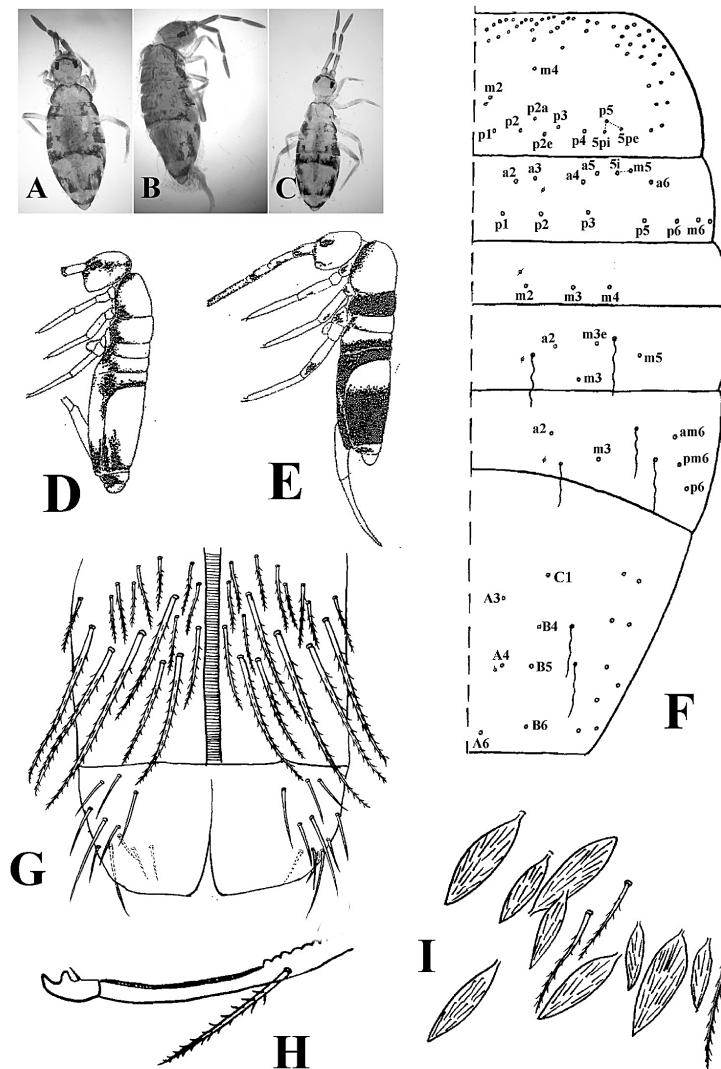


Figure 10

Willowsia japonica (Folsom 1897). A-E, colour pattern. A-C, female forms from the same population. D-E, female and male after Yoshii (1992). F, dorsal body chaetotaxy; G, anterior face of ventral tube and lateral flaps; H, mucro. I, body scales.

Remarks. The scales as figured in original description correspond to the short rib type, but in original material they exhibit relatively long basal rib. *W. samarkandica* is characterized by smaller subapical tooth on mucro, thin unguis, shorter tenent hair and unique thoracic chaetotaxy. It is the only species with reduced subapical tooth on mucro in this genus, and pseudopore on Abd. I external to a2 macrochaeta while it is internal to m2 in other species.

The reduced mucronal subapical tooth and several features of *W. samarkandica* (scale sculpture, modified accessory setae of bothriotrichal complex, abundant dorsal macrochaetae, strong inner teeth on dens, as well as its occurrence in central Asia) suggest affinities with the genus *Drepanosira*; however, we keep it in *Willowsia* due to bidentate mucro and absence of scales on antennae and ventral side of manubrium. Because of its very distinctive features, *W. samarkandica* could deserve generic status on its own.

Willowsia japonica (Folsom 1897) (fig. 10)

Sira japonica Folsom 1897

Sira japonica in Yosii 1942

Prenura bimaculata Börner 1909

Sira bimaculata in Yosii 1942

Willowsia kahlertae Christiansen & Bellinger 1992 new syn.

Type locality. Tokyo, Japan.

Specimens examined. Hawaii: 1 ♀ paratype on slide, Kukuihaele, 20°6'N 155°33'W, 14.XII.1961. China: 1 ♀ on slide, China, Xinjiang Province: Tianshan, altitude 1980m, 43°52'N 120°5'E, 2.VIII.2000, collected by Chen Jian-Xiu; 5 ♀♀ on slide, Hubei Province, Yichang: Sanxia University, 30°32'N 111°29'E, 5.X.2001, collected by Wang Fang; 3 ♀♀ on slide, Jiangsu Province, Agricultural Academy of Sciences, 32°3'N 118°47'E, 20.IX.2001, collected by Song Jindi; 3 ♀♀ on slide and 17 in alcohol, Zhejiang Province, Taizhou, Linhai, 28°50'N

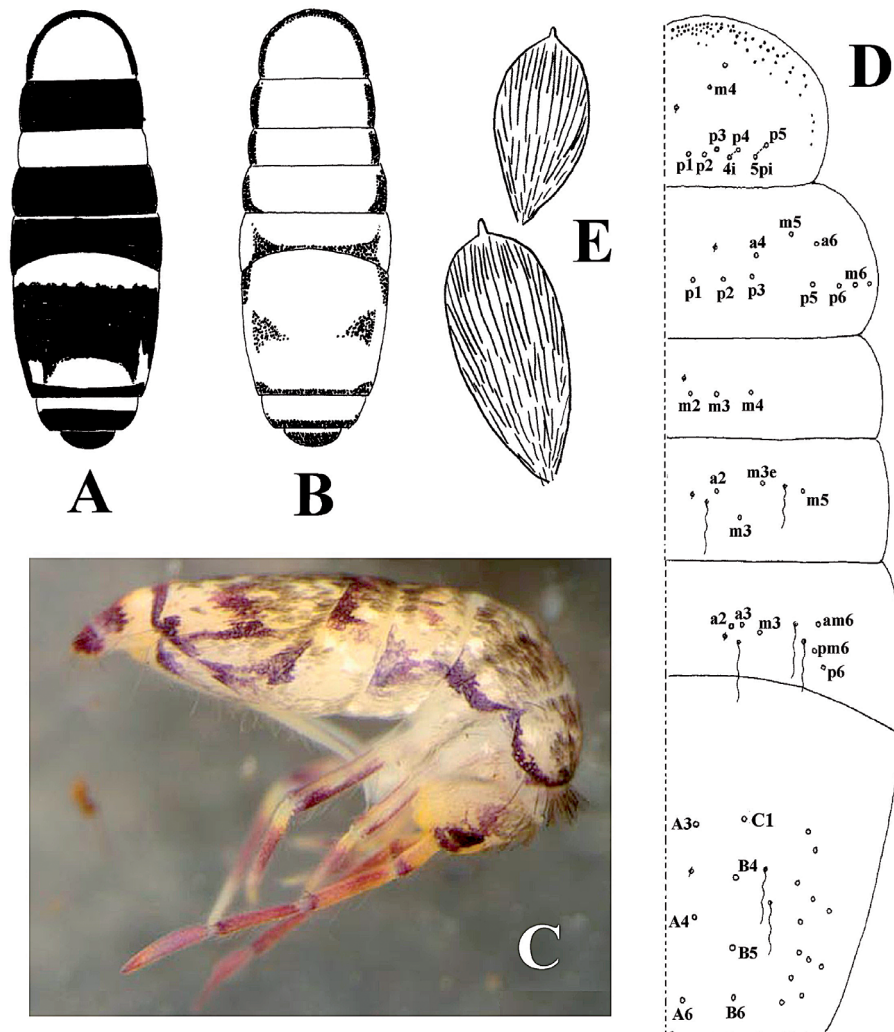


Figure 11

Willowsia platani (Nicolet 1842) and *Willowsia nigromaculata* (Lubbock 1873). A-C, colour pattern. A, *W. platani*. B-C, *W. nigromaculata*; D, *W. nigromaculata*, body dorsal chaetotaxy; E, *W. nigromaculata*, body scales.

121°7'E, 10.VII.2008, collected by Pan Zhixiang.

Complement to description. Females with lateral patches on Thorax, Abd. I, II and IV, usually a pair of small patches present on dorsal Th. III and Abd. II, and transverse bands on posterior Abd. III and Abd. V (figs 10A–D). Males with lateral strips on Th. II and Abd. I, and transverse bands on Th. III, Abd. II–IV (fig. 10E). Dorsal macrochaetae shown in fig. 10F. Th. II with 1 (m2) medio-medial, 1 (m4) medio-lateral and 11 on posterior part; p5pi and p5pe often absent. Th. III with 13–14 macrochaetae on each side; a3 often absent; m5i as macrochaeta. Abd. I with 3 (m2–4) macrochaetae; Abd. II with 3 (a2, m3, m3e) central and 1 (m5) lateral macrochaetae; Abd. III with 2 (a2, m3) central and 3 lateral macrochaetae; Abd. IV with 7 (A3–4, A6, B4–6, C1) central macrochaetae on each side. Ventral tube anteriorly with 6+6 large and many small ciliate chaetae; each lateral flap with 11 smooth chaetae (fig. 10G). Smooth part of dens 2.2–2.9 times mucro in length. Mucro bidentate, apical tooth subequal to subapical one; basal spine short with tip reaching apex of subapical tooth (fig. 10H). Body scales of the short rib type, narrow and heavily sculpted with tip pointed (fig. 10I). Scales absent on antennae, legs, manubrium and dentes.

Ecology and distribution. Under flowerpot, stones and bricks. Widely distributed in China, Japan and Hawaii.

Remarks. Yoshii (1992) synonymized *W. japonica* and *W. bimaculata*, and identified them as male and female forms, respectively. We examined paratypes of *W. kablertae* from Hawaii, and found that they shared the same features as our *W. japonica* specimens from China, including colour pattern and dorsal chaetotaxy. We did not observe males in our Chinese specimens, so we cannot confirm the sexual dimorphism reported by Yoshii.

Willowsia platani (Nicolet 1842) (fig. 11 A)

Degeeria platani Nicolet 1842

Seira platani in Lubbock 1873

Type locality. Not given in original description, but probably Europe.

Specimens examined. France: 6 ♀♀ on slide, France, Gers, Fleurance, 43°50'N 0°39'E, moss on tree, 20.IV.1965, collected by P. Cassagnau. Georgia: 2 ♀♀ on slide, Caucasus, Adzhamet Reserve, under bark of zelkova (*Plataner carpinifolia*) in *Carpinus* forest, 26.I.1983, collected by M. Potapov; 4 ♀♀ on slide, Caucasus, ca 10 km W Kutaisi, 42°15'N 42°42'E, under bark of *Eucalyptus*, 30.I.1983, collected by M. Potapov.

Complement to description. Dark transverse bands present on Th. III, Abd. II–IV, Abd. V posteriorly and Abd. VI (fig. 11A). Dorsal chaetotaxy as in *W. nigromaculata* (fig. 11D). Th. II with 1 (m4) medio-lateral, 7 posterior macrochaetae; p4i and p5pi as macrochaetae. Th. III with 10 macrochaetae on each side; macrochaetae a5, m5i and a6i absent. Abd. I with 2 or 3 macrochaetae, m2 sometimes as microchaeta; Abd. II with 3 (a2, m3, m3e) central and 1 (m5) lateral macrochaetae; Abd. III with 3 (a2, a3, m3) central and 3 lateral macrochaetae; Abd. IV with 7 (A3–4, A6, B4–6, C1) central and 12 lateral macrochaetae on each side. Accessory chaetae of bothriotrichal complex on Abd. IV unmodified (fig. 4A). Scales of the long basal rib type, heavily sculpted with tip pointed; absent on antennae, legs, manubrium and dentes (like in *W. nigromaculata*, fig. 11E).

Ecology. Found mostly under bark of trees, never on stones.

Remarks. This species, widely distributed across Europe and

Asia, has characteristic transverse bands on Th. II and Abd. II–IV. Chaeta m2 of Abd. I always develops as a microchaeta in Caucasus specimens, the same case also occurring in *W. nigromaculata* from Caucasus area. See also *W. nigromaculata* remarks.

Willowsia nigromaculata (Lubbock 1873) (figs 11 B–E)

Seira nigromaculata Lubbock 1873

Type locality. Great Britain.

Specimens examined. France: 2 ♂♂ on slide, many in alcohol, Massy near Paris, under bark of plane tree, 26.VII.2009, collected by A. Bedos & L. Deharveng (sample 91-021). Russia: 1 ♀ on slide, Moscow, 55°45'N 37°37'E, in house, IV.1983, collected by M. Potapov; 21 ♀♀ on slide, Moscow area, in garden, between wood boards, 28.VIII.1985, collected by M. Potapov. Armenia: 30 ♀♀ on slide, Caucasus, Erevan, 40°9'N 44°30'E, Botanic Garden, under bark, 31.X.1987, collected by M. Potapov. China: 4 ♀♀ and 1 ♂, Xinjiang, Yining, altitude 1500–1600m, 43°54'N 81°19'E, 12.VIII.2000, collected by Chen Jian-Xiu.

Complement to description. Irregular patches and strips of dark pigment mainly present on lateral sides of body; narrow transverse bands on posterior part of Abd. III–IV; Abd V–VI dark blue-violet (figs 11B–C). Dorsal chaetotaxy shown in fig. 11D. Scales of the long basal rib type, dark grey, heavily sculpted with tip pointed like in *W. platani* (fig. 11E).

Ecology. Found in a variety of habitats, on bark of trees, bricks, stones, and sometimes in house.

Remarks. The macrochaetotaxy described here is in agreement with the detailed chaetotaxic patterns given by Szeptycki (1979) for specimens from Poland, except in some details. Whether this reflects individual variability or geographical variations remains to be established. As a worldwide distributed species, *W. nigromaculata* was once considered as a variety of *W. platani*; the two forms share most morphological characters, including dorsal chaetotaxy, in support to this conception. However, we maintain *W. nigromaculata* as a distinct species for its different colour patterns, much lighter with limited dark patches. This pattern is extremely stable in the examined populations. Interestingly, it is very similar to the colour pattern of *W. japonica*, the most common species in eastern Palearctic region. Smooth part of dens appeared longer in *nigromaculata* than in *platani*, a difference which has to be checked on larger populations. Sexual dimorphism was not observed in our specimens, where females were largely dominant.

Willowsia buski (Lubbock 1869) (fig. 12)

Seira buski Lubbock 1869

Type locality. Britain.

Specimens examined. Azerbaijan: 15 ♀♀ on slide, Caucasus, Girkan Reserve, 38°38'N 48°43'E, under the bark of oak-tree, 30.I.1982 and 3.II.1982, collected by M. Potapov.

Ukraine: 4 ♀♀ on slide, Crimea, Demerdzi Mt., 44°56'N 34°6'E, beech forest, under bark, 2.V.1983, collected by A. Babenko. Russia: 5 ♀♀ on slide, North European part, Arkhangel'sk area, near Ramen'ye, 64°32'N 40°33'E, organic debris in hollow of old birch-tree. VIII.1981, collected by M. Potapov.

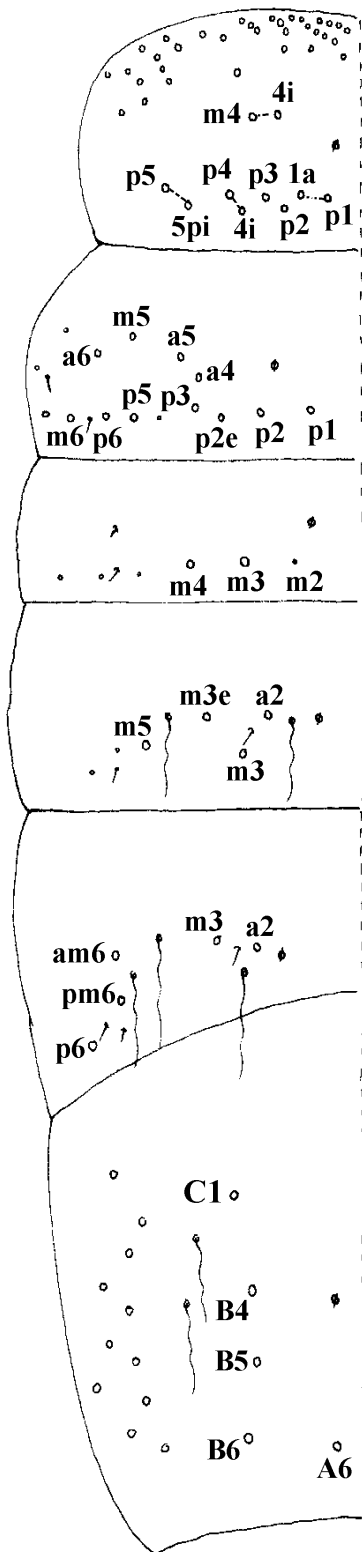


Figure 12
Willowsia buski (Lubbock 1869). Body dorsal chaetotaxy.

Complement to description. Dorsal chaetotaxy shown in fig. 12. Scales of the long basal rib type. Labial base chaetae as MREL₁L₂.

Ecology. Under bark of trees or in vegetal debris.

Remarks. *W. buski* is most close to *W. platani* and *W. nigromaculata*, both widespread species, in scale morphology, unilobed Ant. IV apical bulb, 4 conical papillae on labral margin, claw structure, chaetotaxy of Th. II, Th. III (laterally) and Abd. I-II (fig. 12). It differs from these species in 3 sutural macrochaetae on head, presence of p1a on Th. II and p2e and a5 on Th. III, absence of a3 on Abd. III and A3-4 on Abd. IV, and scattered dark pigment on body. Compared to the first instar chaetotaxy of the species based on specimens from Poland (Szeptycki 1979) the adult chaetotaxy described here exhibits considerable changes in the size (particularly on Abd. IV) and position of chaetae and macrochaetae, pointing to the need of using adult specimens in taxonomic description of *Willowsia*.

Comments on colour pattern and sexual dimorphism

Colour pattern has been considered as a useful taxonomical tool in most groups for long time, particularly before chaetotaxy was widely used. It is usually stable in *Willowsia* species although limited variability often occurs in a population or with age. Sexual dimorphism in coloration was firstly described in *W. jacobsoni* Börner by Mari-Mutt (1981), and later reported in *W. japonica* by Yoshii (1992) and in *W. mesothoraxa* (here considered as a synonym of *W. jacobsoni*) by Nguyen (2001). Yoshii (1992) mentioned that *W. platani* and *W. nigromaculata* may be sexually dimorphic in colour, and this was not retrieved in our own study (both forms were mostly female, and the few males had the same color pattern). We didn't find males in our Chinese collection of *W. japonica* as well. In absence of further evidence, *nigromaculata* and *platani* are considered here as separate species differing only by colour pattern.

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Appendix 1. Characters and character state descriptions

- Length ratio of smooth part of dens to mucro: (0) ≤ 1.5 ; (1) > 1.5 .
- Ant. IV apical bulb: (0) unilobed; (1) bilobed.
- Labral chaetae: (0) ciliate; (1) smooth.
- Labral papillae : (0) absent; (1) rounded (fig. 2A); (2) conical (fig. 2B); (3) each with more than 2 denticles (fig. 2C).
- Mucro: (0) bidentate with two teeth subequal; (1) subapical tooth reduced.
- Sculpture of scales: (0) covered of very short and subequal spinules (fig. 3A); (1) with unequal ribs, those of the basal part long to rather long (fig. 3B-C); (2) with only two longitudinal ribs laterally (fig. 3D).
- Scales on antennae: (0) present; (1) absent.
- Scales on the ventral side of manubrium: (0) present; (1) absent.
- Accessory chaetae of bothriotrichal complex of Abd. IV: (0) unmodified (fig. 4A); (1) broadly or scaly modified (fig. 4B).
- Labial chaeta R: (0) present; (1) absent.
- Labial chaeta M_2 : (0) present; (1) absent.
- Macrochaeta S_0 on head: (0) present; (1) absent.
- Macrochaeta S_1 on head: (0) present; (1) absent.

14. Macrochaeta Ps₂ on head: (0) present; (1) absent.
 15. Macrochaeta m1 on Th. II: (0) present; (1) absent.
 16. Macrochaeta m2 on Th. II: (0) present; (1) absent.
 17. Macrochaeta m2i on Th. II: (0) present; (1) absent.
 18. Macrochaeta m4 on Th. II: (0) present; (1) absent.
 19. Macrochaeta m4i on Th. II: (0) present; (1) absent.
 20. Macrochaeta m4p on Th. II: (0) present; (1) absent.
 21. Macrochaeta p1 on Th. II: (0) present; (1) absent.
 22. Macrochaeta p2 on Th. II: (0) present; (1) absent.
 23. Macrochaeta p4 on Th. II: (0) present; (1) absent.
 24. Macrochaeta p4i on Th. II: (0) present; (1) absent.
 25. Macrochaeta p5 on Th. II: (0) present; (1) absent.
 26. Macrochaeta p5pi on Th. II: (0) present; (1) absent.
 27. Macrochaeta a1 on Th. III: (0) present; (1) absent.
 28. Macrochaeta a2 on Th. III: (0) present; (1) absent.
 29. Macrochaeta a3 on Th. III: (0) present; (1) absent.
 30. Macrochaeta a4i on Th. III: (0) present; (1) absent.
 31. Macrochaeta a5 on Th. III: (0) present; (1) absent.
 32. Macrochaeta a5e on Th. III: (0) present; (1) absent.
 33. Macrochaeta m5i on Th. III: (0) present; (1) absent.
 34. Macrochaeta a6i on Th. III: (0) present; (1) absent.
 35. Macrochaeta m2i on Abd. I: (0) present; (1) absent.
 36. Macrochaeta m2 on Abd. I: (0) present; (1) absent.
 37. Macrochaeta m3 on Abd. I: (0) present; (1) absent.
 38. Macrochaeta m4i on Abd. I: (0) present; (1) absent.
 39. Macrochaeta m4p on Abd. I: (0) present; (1) absent.
 40. Macrochaeta a2 on Abd. I: (0) present; (1) absent.
 41. Macrochaeta a3 on Abd. I: (0) present; (1) absent.
 42. Macrochaeta a5 on Abd. I: (0) present; (1) absent.
 43. Macrochaeta a2 on Abd. II: (0) present; (1) absent.
 44. Macrochaeta a3 on Abd. II: (0) present; (1) absent.
 45. Macrochaeta m3ea on Abd. II: (0) present; (1) absent.
 46. Macrochaeta m3ep on Abd. II: (0) present; (1) absent.
 47. Macrochaeta m3ei on Abd. II: (0) present; (1) absent.
 48. Macrochaeta a3 on Abd. III: (0) present; (1) absent.
 49. Macrochaeta m7 on Abd. III: (0) present; (1) absent.
 50. Macrochaeta A3 on Abd. IV: (0) present; (1) absent.
 51. Macrochaeta A4 on Abd. IV: (0) present; (1) absent.
 52. Macrochaeta A5 on Abd. IV: (0) present; (1) absent.
 53. Macrochaeta B3 on Abd. IV: (0) present; (1) absent.
 54. Macrochaeta C1 on Abd. IV: (0) present; (1) absent.
 55. Macrochaeta B4 on Abd. IV: (0) present; (1) absent.
 56. Macrochaeta A2p on Abd. IV: (0) present; (1) absent.

Appendix 2. Morphological data matrix

species	1	11	21	31	41	51
<i>Drepanosira hussi</i>	00021	11110	01000	00000	00000	10000
<i>Willowsia buski</i>	00020	11100	01111	11001	00000	01111
<i>Willowsia guangdongensis</i>	10120	10000	00111	11011	10110	11111
<i>Willowsia guangxiensis</i>	01020	00010	11000	01001	00001	11110
<i>Willowsia jacobsoni</i>	10030	11100	10111	11111	11110	11111
<i>Willowsia japonica</i>	11020	11100	01111	01011	00010	01001
<i>Willowsia mexicana</i>	10130	11101	00111	11111	11010	11111
<i>Willowsia nigromaculata</i>	10020	11100	00111	11011	00000	01111
<i>Willowsia platani</i>	00020	11100	00111	11011	00000	01111
<i>Willowsia pseudosocia</i>	0?010	00010	01000	00000	00001	10000
<i>Willowsia samarkandica</i>	10031	11110	01100	00001	00000	00000
<i>Willowsia shiae</i>	01020	00010	01000	00000	00001	11110
<i>Willowsia yiningensis</i> sp. nov.	10020	11100	01000	01010	00000	10000
<i>Willowsia qui</i> sp. nov.	10020	11100	01100	00000	00010	11001
<i>Willowsia potapovi</i> sp. nov.	10020	11100	01000	01000	00000	00000
<i>Willowsia</i> sp.	01030	00010	11001	11111	00000	01111
<i>Americabrya arida</i>	00130	21101	00111	11111	11110	11111