

# A new species of *Friesea* (Collembola: Neanuridae) from Hebei Province, North China and a cladistic analysis

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**Abstract:** *Friesea incognita* sp. nov. is described from China. This new species is characterized by the combination of: 2 + 2 eyes, no capitate tenent hairs on tibiotarsi, three anal spines, furcula without mucro and dens with 3 setae. Total dorsal and ventral chaetotaxy of the new species is given. A revised key for identification of the species of this genus with 2 + 2 eyes is given. Forty-seven characters of antennal sensilla, eyes and body chaetotaxy are chosen for the cladistic analysis performed for 18 species of this genus, including 12 with 2+2 eyes. Results indicate the new species *F. incognita* seems to be related to *F. nauimetzli* from Mexico. The phylogenetic relationships of the species are not well resolved due to the presence of many homoplasies among different species that adapt to a similar soil habitat.

**Key words:** springtails; chaetotaxy; eye; furcula; cladistic analysis; taxonomy

## 中国河北省奇刺蚧属一新种及支系分析（弹尾纲：疣蚧科）

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**摘要:** 记述河北省奇刺蚧属 1 新种: 迷奇刺蚧 *Friesea incognita* sp. nov.。迷奇刺蚧的主要特征是头部有 2+2 眼, 足胫跗节无粘毛, 腹部末端具 3 根臀刺, 弹器端节退化不见, 齿节具有 3 根刚毛。详尽描述了新种身体背面和腹面的毛序。修订更新奇刺蚧属具有 2+2 眼种类的检索表。选取触角感器、眼、体表毛序等 47 个形态特征, 对该属 18 个物种进行了支序分析, 包括 12 种具有 2+2 眼的物种, 结果发现新种 *F. incognita* 与墨西哥分布的 *F. nauimetzli* 较为相近。由于适应类似的地下生存环境导致许多趋同特征的出现, 本研究未能完全解析各物种之间的系统发育关系。

**关键词:** 跳虫; 毛序; 眼; 弹器; 支序分析; 分类

## Introduction

The genus *Friesea* Dalla Torre, 1895 is the fifth most speciose genus of Collembola, with more than 180 named species (Bellinger *et al.* 2019). It has a cosmopolitan distribution and its

Accepted 24 September 2019. Published 25 December 2019. Published online 12 December 2019.

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members live in many different habitats: soil, litter, moss, lichens, epiphytic plants, bark of trees, marine littoral environments, sand and even caves. Their feeding habits are diverse; many can prey on rotifers, tardigrades and even other microarthropods (Palacios-Vargas & Vidal Acosta 1994; Castaño-Meneses *et al.* 2004). There is a strong intraspecific variability of morphology that may be a reason for the large number of species in this genus.

The body of a *Friesea* species is covered by setae either smooth and acuminate or barbate and clavate. This is more obvious on the abdominal segment VI, where setae and anal spines are important characters for the separation of species. There is a variation in the degree of transformation of setae to spines. They can be separated as follows: if the ratio of width measured at base / length is 1/4 or more, it is a true spine; when it is between 1/4 and 1/10 it is a spiniform seta; but if it is less than 1/10, then it is a regular seta (Palacios-Vargas 1986).

The furcula development in many species varies and is correlated with the tenaculum form (Cassagnau 1958); often both are missing (state 5). Many species lack a mucro, but still have dens with 2 or 3 setae on a furcal vestige (states 4 and 3 respectively). Sometimes the mucro is hook-like and fused to the dens (state 2). Very rarely, the dens and mucro are well separated (state 1). At most there are three dental setae present.

Nine species of *Friesea* have been cited from China (Gao 2007): *F. daliensis* Tamura and Yue, 1998 (Yunnan), *F. japonica* Yosii, 1954 (Japan and China: Zhejiang, Shanghai), *F. lijiangensis* Tamura and Yue, 1998 (Yunnan), *F. mirabilis* Tullberg, 1871 (Zhejiang, Fujian); *F. sublimis* Macnamara, 1921 (wide distribution, including China), *F. truncatopilosa* Rusek, 1971 (Guangdong), *F. quadrispiensis* Gao and Yin, 2006 (Shaanxi) and *F. shaanxiensis* Gao and Yin, 2006 (Shaanxi). The most recent contribution to this genus was by Gao and Palacios-Vargas (2010) who described *F. buyuni* from Ningxia.

During the study of collembolan collections from the Liaoheyuan Natural Reserve of Hebei Province, North China, one new species of the genus *Friesea* was identified and is described in below.

## Material and methods

Specimens were collected by Tullgren funnels and preserved in 80% ethanol. The material was mounted under slides in Hoyer's solution and dried in an oven at 50°C before identification. Line drawings were made using a drawing tube on a phase contrast microscope. Plates were made using the program Adobe Illustrator. Specimens are deposited in the Shanghai Natural History Museum (SNHM) and the Universidad Nacional Autónoma de México (UNAM). For the sensilla of antenna we follow the system of Deharveng (1981), and for the body chaetotaxy, mainly Dányi *et al.* (2010).

Abbreviations. Ant. — antennal segment; Asp. — anal spine; s. s. — sensillum, sensilla, sensorial setae; Th. — thoracic segment; Abd. — abdominal segment; a — anterior row setae; m — medial row setae; ms — microsensillum; p — posterior row setae; sgd. — dorsal guard sensillum; sgv. — ventral guard sensillum; X — lack of a seta.

## Taxonomy

### Family Neanuridae Börner, 1901

### Subfamily Frieseinae Massoud, 1967

### Genus *Friesea* Dalla Torre, 1895

*Triaena* Tullberg, 1871: 155. Type species: *Friesea mirabilis* (Tullberg, 1871).

Diagnosis. Neanuridae with conical antennae and antennal IV subapical bulb simple or trilobed, 5–6 dorsal sensilla; from 8 to zero eyes each side. Postantennal organ lacking. Cephalic seta d0 present. Three ocular setae always present. Maxilla capitulum triangular with two toothed lamellae, one large with several teeth and one small with 2–3 teeth. Mandible with about 7 teeth but no molar surface. Tibiotarsi with or without tenent hairs. Furcula from well-developed to completely lacking, correlated with tenaculum development. Abdominal segment VI with dorsal spines, spiniform setae or simple setae.

Distribution. Cosmopolitan.

### *Friesea incognita* Bu & Palacios-Vargas sp. nov. (Figs. 1–12)

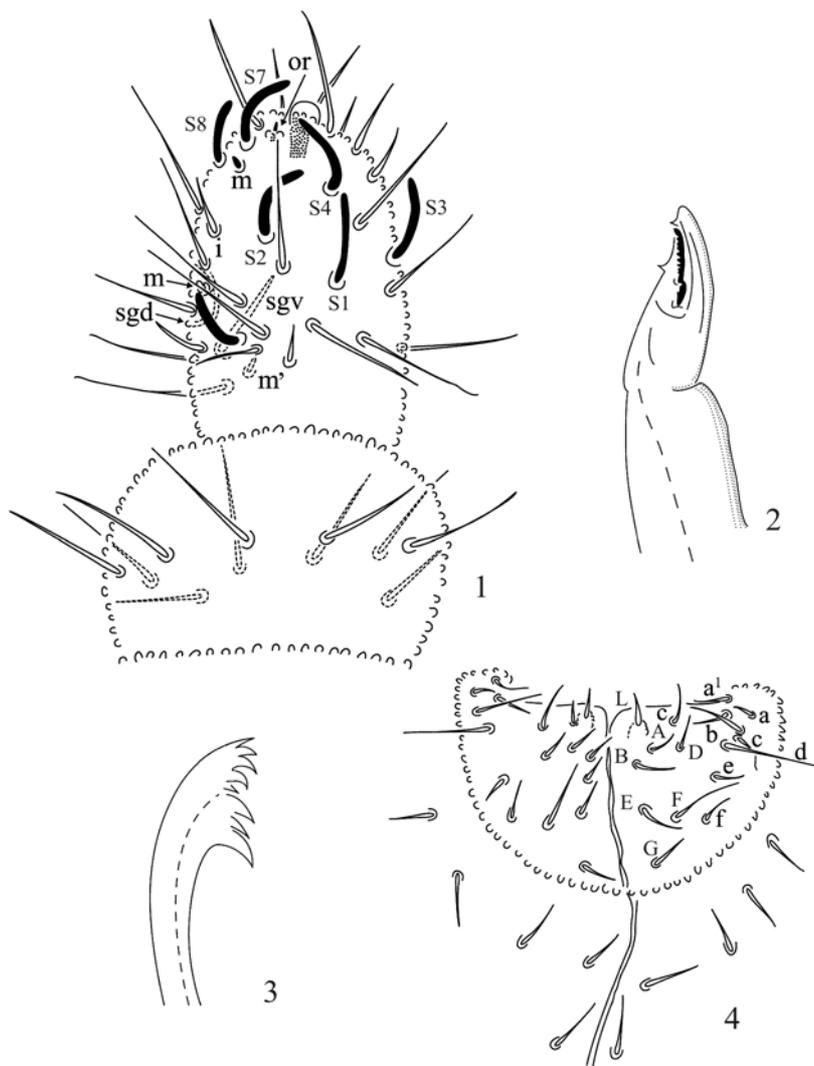
Description. Adult body averaging 790 µm long (730–860 µm,  $n = 10$ ), body colour white, eyes with black colour on granular patch. Setae smooth, short and acuminate, from 10–13 µm (head seta 0) to 30–36 µm on posterior abdominal segments, those of Abd. V (27–36 µm, and ss 26–28 µm), and Abd. VI with anal spines a1 18–25 µm and the unpaired spine p0 only 13–15 µm.

Ant. I with 7 setae, Ant. II with 12–13, Ant. III organ with sgd curved, sgv straight, one microsensillum, and two short cylindrical microsensilla under a cuticular fold. Ant. IV with 4 thick (S2, S4, S7 and S8) and two thin sensilla (S1 and S3), apical bulb simple, one microsensillum and one small subapical organite (Fig. 1). Length ratio Ant. I : II ; III + IV = 1 : 1; 1.6–1.7.

Labrum with 2/5, 5, 4 setae. Labium with complete chaetotaxy including papillate setae L. Labial palp with 4 small setae and long seta “d”. Two pairs of postlabial setae (Fig. 4). 2 + 2 eyes separated by 3–4 cuticular granulations, posterior one smaller than anterior (Figs. 5, 6). Mandible with two fused lamellae, with total of 7–8 teeth (Fig. 3). Maxillary capitulum with one internal subapical tooth, and one median; two lamella, one larger with 7 teeth and one smaller with 2–3 teeth (Fig. 2).

Head and thoracic chaetotaxy as in Fig. 5, Th. I with 4 + 4 dorsal setae and one lateral. Leg chaetotaxy from I to III: subcoxae 2 with 0, 2, 2; coxae, 3, 7, 7; trochanters 5, 5, 5; femora 11, 11, 10, tibiotarsi 18, 18, 17 setae. Two distal-ventral setae on tibiotarsus smaller and thinner than others. No capitate tenent hairs. Unguis (16–17 µm) without teeth. Pretarsus with 1 seta on each side.

Dorsal chaetotaxy of thorax and abdomen in Figs. 5, 8 and 10. Abd. V with setae row p longer than row a. Abd. VI with 3 spines, two longer in position a1, and one smaller in position p0 (Fig. 10). Furcula (state 3 of Cassagnau 1958), manubrium with 5 pairs ventro-internal setae, dens with 3 setae each and no mucro. Tenaculum with two teeth on each ramus and no setae. Ventral chaetotaxy is shown in Fig. 9. Ventral tube with 4 + 4 setae. Female with 3 pairs of pregenital setae, 9–12 circumgenital setae and 2 eugenital (Fig. 11); male with 3 pairs of pregenital setae, about 24 circumgenital and 4 + 4 eugenital setae (Fig. 12).



Figures 1–4. *Friesea incognita* sp. nov. 1. Ant. II–IV, dorsal view; 2. Maxilla; 3. Mandible; 4. Labium.

**Variation.** Four specimens with 4–5 setae on ventral tube, other with 4 + 3; one with 2 + 3 dental setae, one male with a very small mucro on right dens. One specimen with 1 + 2 eyes, another one with 1 + 0, other two without eyes. The eye position can vary and may correspond to A and D (Fig. 6) or to A and E (Fig. 7). One pre-adult male lacks one right spine a1 and has the spine p0. One specimen has 2 + 1 postlabial setae. Dorsal and mainly ventral chaetotaxy also shows some variation as seen by Grow & Christiansen (1974) for American species.

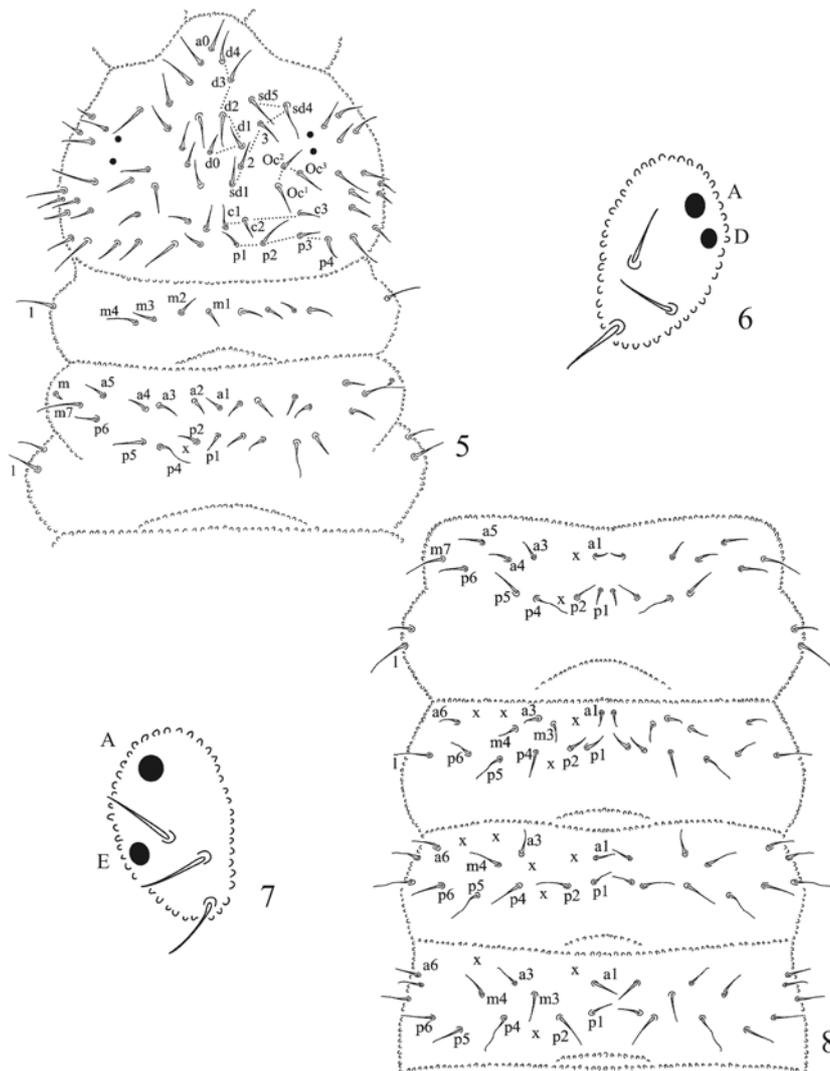
**Holotype.** ♀, (Slide no. HB-C2016035) (SNHM), **China**, Hebei Province, Chengde, Pingquan County, Liaoheyuan Natural Reserve, extracted from soil samples, 41°32'N, 118°44'E, elev. 1230–1500 m, 13-VII-2016, collected Yun BU. **Paratypes.** 4♀2♂ (slides nos. HB-C2016048, HB-C2016051–HB-C2016054) (SNHM), 2♀, 1 pre-adult ♂ (slide no. HB-C2016034) (UNAM), same data as holotype.

**Diagnosis.** *Friesea incognita* sp. nov. is characterized by the combination of: presence of

2 + 2 eyes, no capitate tenent hairs on tibiotarsi, three anal spines, furcula without mucro and dens with 3 setae.

**Etymology.** The species name indicates the unknown taxonomic status of this new species when it was found.

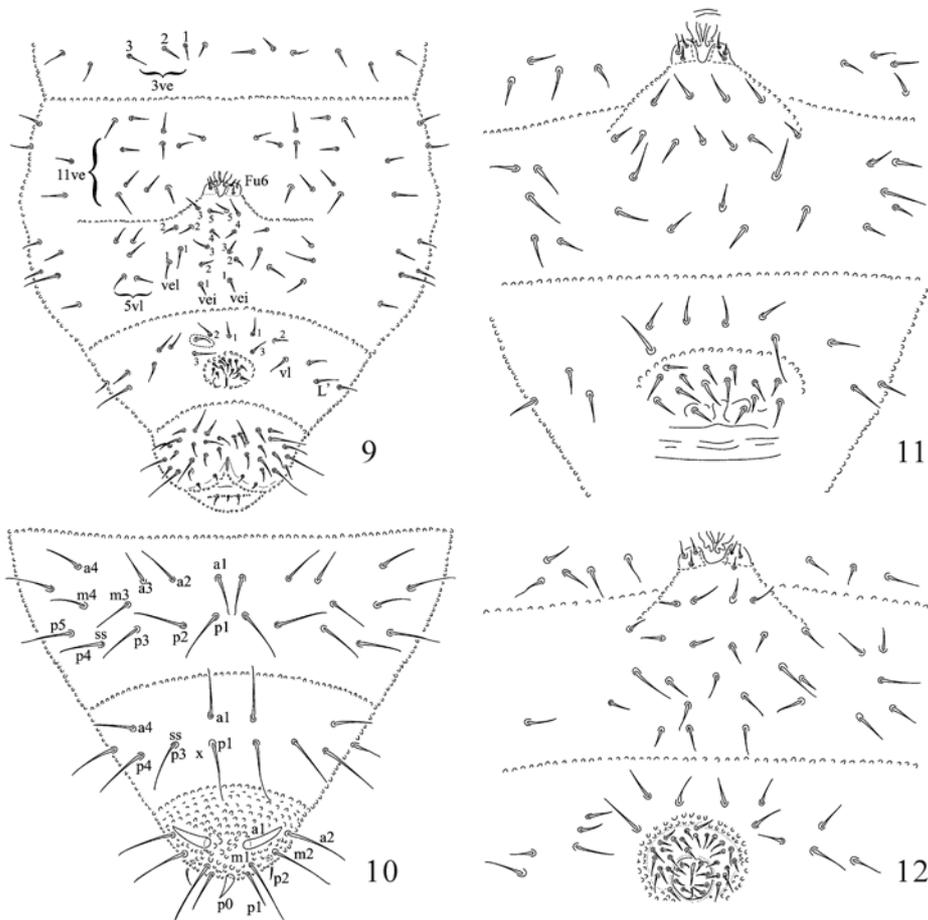
**Distribution.** China (Hebei).



Figures 5–8. *Friesea incognita* sp. nov. 5. Head and Th. I–II, dorsal view; 6. Right ocular area of one paratype; 7. Left ocular area of another paratype; 8. Th. III and Abd. I–III, dorsal view.

**Remarks.** *Friesea incognita* sp. nov. shares the presence of 2 + 2 eyes with 16 species which are distributed in Mexico, United States of America, Africa, Australia, Europe and Asia, which includes 3 Asian species, *F. arnei* Weiner & Najt, 1985 from North Korea, *F. microphthalmala* Deharveng & Bedos, 1991 from Thailand and *F. buyuni* Gao & Palacios-Vargas,

2010 from China. This new species is similar to *F. arnei* in the presence of a reduced furcula without mucro, and 3 setae on each dens, but differs in the position of the eyes (more separated in *F. arnei*) and, most remarkable, is the presence of 4 anal spiniform setae in position a1 and m1, while the new species has three true spines with two of them in position a1 and one in p0. *Friesea incognita* sp. nov. and *F. buyuni* have the same head chaetotaxy and 2 + 2 eyes, but they are in different positions; in addition *F. buyuni* has 2 additional setae on row m of Th. II and III and Abd. VI has six barbulate spinose setae (a1, a2, and m1) but no true spines. Ventrally Abd. IV has only 3 pairs of ventro-internal setae, while the new species has 5 pairs. *Friesea microphthalmalma* also has very similar chaetotaxy, three anal spines in the same position as the new species and 2 + 2 eyes, but in different positions. The most important difference is that *F. microphthalmalma* has seta p2 on Abd. V, the mucrodens has a small mucro and the ventral-internal setae on Abd. IV with only four setae.



Figures 9–12. *Friesea incognita* sp. nov. 9. Abd. II to VI, ventral view; 10. Abd. III to VI, dorsal view; 11. Genital plate of female and ventral of Abd IV; 12. Genital plate of male and ventral of Abd. IV.

This new species is also similar to *Friesea stachi* Kseneman, 1936 from the Czech Republic. The original description was short and general (only two drawings were given), but

the similar characters are: tibiotarsi without tenent hairs, tenaculum with 2 + 2 teeth, and the presence of 3 anal spines. The description mentioned that there are 5 sensilla, the body size being more of 0.4 mm and having a small furcula with mucro. Simón (2005) and Massoud (1976) add that the dens has only two setae. The main difference is the presence of 3 dental setae and larger size in *Friesea incognita* sp. nov. (0.8 mm). It seems that there is variation in the number of eyes in *F. stachi*, with three forms according to Cassagnau (1958).

Discussion of Chaetotaxy. Although chaetotaxy is of great importance in Collembola taxonomy, it is only useful, if the intraspecific variability is known (Grow & Christiansen 1974). For the genus *Friesea*, Grow and Christiansen (1974) investigated this topic in detail for some North American representatives. Subsequently, variability was found in other species as mentioned in works by Hamra-Kroua *et al.* (2009), Palacios-Vargas (2005), and Smolis and Skarżyński (2006).

The presence of six dorsal sensilla on Ant. IV is normal for the genus and corresponds to S1–S4 and S7–S8. Some authors have given alphabetical letters to these sensilla, but that makes comparison with other Neanuridae problematic. The apical bulb is usually simple and in a few cases, it is trilobated as in *F. quadrispina* Cassagnau & Rapoport, 1962 and *F. lobulata* Palacios-Vargas & Díaz, 1986. Ant. III may have from 11 to 13 simple setae in this genus. Ant. I always has 7 simple setae. Head chaetotaxy is very constant in most species. The setae a0 and d0, can be present or not, but there are 5 subdorsal setae (from sd1 to sd5) in most species, as well as 4 dorsal cephalic setae (d1 to d4), although they can be longer than other setae of the same group. Ocular setae are always three, Oc1–Oc3. Cervical setae are always present, but c3 is displaced to a lateral position (except in *Friesea neocaledonica* Palacios-Vargas, 1988). There are always 4 posterior cephalic setae (p1–p4). The labium always has the same setae in all species, the tuberculate setae “L”, and from A to G, as well as the same setae on the labial palp. On Th. I there can be from 2 + 2 to 4 + 4 dorsal setae which corresponds to row m, plus one lateral seta on each side.

One single chaetotaxic system for the body of *Friesea* was proposed by Deharveng & Bedos (1991) but that system is more suitable to the subfamily Neanurinae, no homologies were made with the other relevant antennae sensorial structures. For Frieseinae, it is more convenient to use the system of Yosii (1961) which allows an easier comparison with other species in the genus.

The sensorial chaetotaxy (body sensorial setae, s.s.) on Th. II and III is at position p3, but it corresponds to p4, as p3 has disappeared on thoracic segments as pointed out by Gama (1964, 1959) in her descriptions of *Friesea maritima* Gama, 1964 and *F. landeiroi* Gama 1959 and by Simón (1975) in *Friesea steineri*. The s.s. on Abd. II to IV is p4 and on Abd. V as p3 but it has been named as p2 in Jordana *et al.* (1997). The position of s.s. always remains the same as is usually observed in *F. neocaledonica* Palacios-Vargas, 1988 where all the setae have become clearly capitate except for the sensorial setae.

The number of clavate tenent hairs on tibiotarsi is useful and has low intraspecific variation. Clavate setae on Abd. VI are sometimes present and are usually better developed on posterior segments of body.

Important observations were made recently by Dányi *et al.* (2010) for *F. handschini* on the variability observed in the setal number on the dens, pointed out also before by Cassagnau (1958) and Massoud (1967). According to Dányi *et al.*, most of the *F. handschini* specimens

showed 3 + 3 setae on dens in contradiction to 2 + 2 of the original description. Grow and Christiansen (1974) also found intraspecific variability of this character in North American *Friesea* species, as did Jordana *et al.* (1997) in *Friesea albida* Stach, 1949.

We can conclude that because of the morphological, ecological and genomic plasticity of this genus, it belongs to an old lineage with very wide distribution. It is interesting to note that this genus is very specious and has a variety of feeding habits. It is surprisingly a huge genus and living in many biotypes, when compared with *Halofriesea*, which has only two marine species, or *Gisinea* or *Tremoisea*, which have only a Holarctic distribution.

### Key for the species of *Friesea* with two pairs of eyes

1. Abd. VI with 3 true thick anal spines ..... 5
  - . With only spine-like setae on Abd. VI or none ..... 2
2. Without tenaculum and furcula, body length (0.6 mm); Abd. VI with slightly barbulate setae .....
  - F. jaliscoensis*
  - . With tenaculum with 2 teeth on each ramus and reduced furcula ..... 3
3. With 2 dental setae ..... *F. geminioculata*
  - . With 3 dental setae ..... 4
4. Abd. VI with 6 clavate setae, mucro completely lacking ..... *F. nauimeztli*
  - . Abd. VI without clavate setae ..... 16
5. Without any spike-like setae on Abd. VI, no tenaculum, no furcula ..... *F. vtorovi*
  - . With several spike-line setae on Abd. VI ..... 6
6. With 7 spine-like setae on Abd. VI, length 1.6–1.9 mm, apical bulb on Ant. IV trilobed, hypertrichosis, some setae on head, thorax and mainly on abdomen with very long setae ..... *F. neptunia*
  - . With 8 or fewer than 7 spine-like setae on Abd. VI, small species, 1 mm or less ..... 7
7. With 8 spine-like setae on Abd. VI ..... *F. kardosia*
  - . With 6 or fewer anal spines ..... 8
8. With mucro well developed ..... *F. danica*
  - . Without mucro ..... 9
9. Without dens, only vestige of furcula with 6 setae, no tenaculum ..... *F. buyuni*
  - . Dens with setae, tenaculum with teeth ..... 10
10. With 4 anal spine-like setae ..... 11
  - . With 6 or fewer than 4 anal spines ..... 12
11. With 2 tenacular teeth ..... *F. arnei*
  - . With no tenacular teeth ..... *F. subterranea*
12. With 6 anal spines and 3 dental setae ..... 13
  - . With fewer than 6 anal spines ..... 14
13. With 2 tenacular teeth, 1 mm length ..... *F. alaskella*
  - . With only one tenacular tooth ..... 15
14. With 3 anal spines and 2 tenacular teeth ..... *F. stachi*
  - . With 2 anal spines and one tenacular tooth ..... *F. wilkeyi*
15. With setae a2 on Abd IV ..... *F. deharvengi*
  - . Without setae a2 on Abd. IV ..... *F. judithae*
16. Mucro very small fused to dens ..... *F. microphthalma*
  - . Mucro absent, dens with 3 setae ..... *F. incognita* **sp. nov.**

Cladistic Analysis. Taxon sampling and morphological data. There are 17 *Friesea* species

which have two eyes per side, including the new one described in this study; but only 12 are included in this analysis. *F. danica* Fjellberg, 1998, *F. kardosia* (Wray, 1952), *F. stachi* Kseneman, 1936, *F. geminioculata* Loksa, 1964, *F. wilkeyi* Christiansen & Bellinger, 1973 were excluded because their descriptions were very brief.

Outgroups include *Gisinea dehelzi* Massoud, 1965, *Gisinea tiliae* Babenko, 1998, *Halofriesea kai* (Christiansen & Bellinger, 1992), *Oudemansia* ca. *esakii* from China, *Tremoisea israelica* and *Tremoisea enigmatica* Cassagnau, 1973. We also included the following species *F. australica* Greenslade & Deharveng, 1997, *F. capensis*, *F. curupira*, *F. handschini*, *F. hnaeu* and *F. najtae* to represent in the data matrix a bigger morphological diversity within the genus.

A total of 47 characters were used in this analysis (nine were non-informative and were not considered), 31 binary characters and 16 multistate characters (Appendix 1). All characters were treated as unordered and equally weighted (Wilkinson 1992). With the data of the four genera of the Frieseinae and one of Neanurinae, a matrix with a total of 24 species was constructed (Appendix 2).

Phylogenetic relationships. Parsimony analyses were carried out using the programs Winclada (Nixon 1999) and NONA 1.6 (Goloboff 1993) using the heuristic strategy search and the settings hold = 10000, multit\*n = 1000 and hold/ = 10000, followed by TBR (treebisection-reconnection) branch swapping as the search strategy. Bootstrap values were obtained using NONA with 1000 replications, multit\*n = 50 and hold/ = 50.

Results of the analysis are shown in Fig. 13, which is the one of strict consensus. The length is 192, the Ci is 0.40, the Ri is 0.45 and there are 9 non-informative characters (Fig. 13).

In the cladogram, *Halofriesea* is very clearly separate from the group of *Friesea* species and closer to *Tremoisea* and *Gisinea* than to *Friesea*. Other genera in the subfamily Frieseinae are more closely related. The genus *Oudemansia* (Neanurinae) is closer related to *Friesea* and more precisely to *Friesea najtae*, and this may be due the homoplasies of body chaetotaxy.

There are several species of *Friesea* which can clearly be isolated as *Friesea neptunia* who have as autapomorphy the shape of setae p1 on Abd. VI which is spiniform and not a true spine (Character 41 in Appendix 2). The rest of the species are grouped by the presence of real spines. *Friesea curupira* has 1 + 1 eyes as an autopomorphy, a character which separates it from the others in the group. Divided into two groups, one of them has the most species and shares the presence of the shape of real anal spines a1 on Abd. VI (Fig. 13).

Most of these species fall in the group where the synapomorphy is the state of reduction of the tenaculum, but it is difficult to separate them because of the large amount of homoplasies present. All share a small size and reduction of eye number, and these might be an adaptation to soil life. As for character 5, even it is one homoplasy with the presence of cephalic setae d0, it seems that is responsible for the formation of the unresolved clade. *Friesea arnei* from Asia and *F. buyuni* are very closely related and share many characters, but *Friesea incognita* sp. nov. would appear to be related to *F. nauimetzli* from Mexico, which seems unlikely (Fig. 13). Perhaps the only way to resolve the relationships of these species might be with the help of molecular biology.

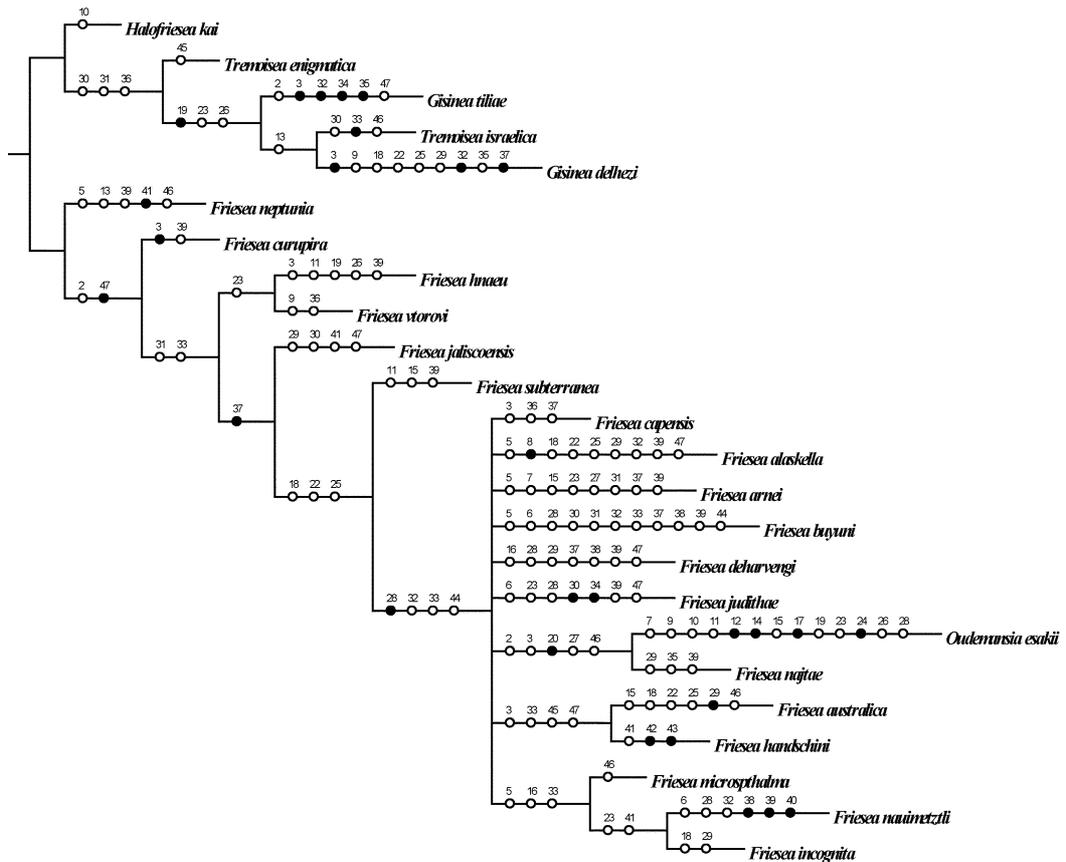


Figure 13. Strict consensus tree (length: 192, CI: 0.40, RI: 0.45).

## Acknowledgements

Thanks are given to Prof. Guodong REN and Dr. Zhao PAN from Hebei University and all staff from Liaoheyuan Nature Reserve for their generous help during the collection of specimens. We also thank María MARTÍNEZ for her help in preparation of the final plates. This study was supported by the National Natural Science Foundation of China (31772509) and the Natural Science Foundation of Shanghai (17ZR1418700). The field work was partly supported by the Forest Pest Investigation Project of Hebei Province hosted by Professor Guodong REN.

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**Appendix 1: List of characters, state definition and coding.****HEAD**

- 1 Number of sensilla on Ant. IV: 6 (0), 5 (1)
- 2 Subapical vesicle on Ant. IV: simple (0), trilobed (1)
- 3 Ocelli number: 8+8 (0), 2+2 (1), 1+1 (2), 0+0 (3)
- 4 Setae sd number: 5 (0), 4(1), 3(2), 2(3), 1(4)
- 5 Setae d0: present (0), absent (1)
- 6 Setae d number: 4 (0), 3 (1), 2 (2), 1 (3)
- 7 Setae a0: present (0), absent (1)
- 8 Ocular setae number: 3 (0), 2(1), 1 (2)
- 9 Setae number of c row: 4–3 (0), 2–0 (1)
- 10 Setae number of p row: 4,7 (0), 2–3 (1)

**THORAX I**

- 11 Setae number of m row: 4–6 (0), 1–3 (1)

**THORAX II**

- 12 Setae number of a row: 4–6 (0), 1–3 (1)
- 13 Setae number of m row: 4–5 (0), 1–3 (1)
- 14 Setae number of p row: 4–5 (0), 1–3 (1)

**THORAX III**

- 15 Setae number of a row: 4–5 (0), 1–3 (1)
- 16 Setae number of m row: 5–7 (0), 2–4 (1), 0–1 (2)
- 17 Setae number of p row: 4–6 (0), 1–3 (1)

**ABDOMEN I**

- 18 Setae number of a row: 4–6 (0), 2–3 (1), 0–1 (2)
- 19 Setae number of m row: 4–5 (0), 2–3 (1), 0–1 (2)
- 20 Setae number of p row: 5–7 (0), 2–4 (1), 0–1 (2)
- 21 Number of setae of ventral tube: 5–11 (0), 3–4 (1)

**ABDOMEN II**

- 22 Setae number of a row: 4–6 (0), 2–3 (1), 0–1 (2)
- 23 Setae number of m row: 4–5 (0), 2–3 (1), 0–1(2)
- 24 Setae number of p row: 4–6 (0), 2–4 (1), 0–1 (2)

**ABDOMEN III**

- 25 Setae number of a row: 4–6 (0), 1–3 (1)
- 26 Setae number of m row: 4–5 (0), 1–3 (1)
- 27 Setae number of p row: 5–7 (0), 3–4 (1), 1–2 (2)
- 28 Tenaculum: present (0), absent (1)

**ABDOMEN IV**

- 29 Setae number of a row: 4–6 (0), 2–3 (1), 0–1 (2)
- 30 Setae number of m row: 4–5 (0), 2–3 (1), 0–1(2)
- 31 Setae number of p row: 6–7 (0), 3–5 (1)

**ABDOMEN V**

- 32 Setae number of a row: 5–6 (0), 3–4 (1), 1–2 (2)
- 33 Setae number of m row: 3–4 (0), 2–3 (1), 0–1(2)
- 34 Setae number of p row: 5–6 (0), 3–4 (1)

**ABDOMEN VI**

- 35 Number of spines on Abd. VI: 5–6 (0), 3–4(1), 1–2(2), spines absent (3)
- 36 Setae a1: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 37 Setae a2: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 38 Setae m1: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 39 Setae m2: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 40 Setae p0: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 41 Setae p1: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 42 Setae p2: without modification (normal setae) (0), capitated setae (1), spiniform setae (2), spine (3)
- 43 Number of setae on dens: 6 (0), 5 (1), 4 (2), 3 (3), 2 (4), absent (5)
- 44 Furcula: present (0), absent (1)

**LEGS**

- 45 Tenent hairs on tibiotarsi: present (0), absent (1)
- 46 Tooth on claw: present (0), absent (1)
- 47 Size of the organism: 0.46–0.60 mm (0), 0.61–0.75 mm (1), 0.76–0.90 mm (2), 0.91–1.3 mm (3), 1.4–2.8 mm (4)

Appendix 2. Morphological matrix with 24 taxa and 47 characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Oudemansia eskii</i>	?	1	0	0	1	0	1	0	1	1	1	1	1	1	1	2	1	1	2	1	?	1	2	1
<i>Friesea curupira</i>	0	0	2	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0
<i>Friesea hnaeu</i>	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	2	0	1	0	2	0
<i>Friesea najtae</i>	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0
<i>Friesea australica</i>	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0
<i>Friesea handschini</i>	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0
<i>Friesea capensis</i>	0	0	3	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0
<i>Friesea alaskella</i>	0	0	1	0	0	0	0	3	0	0	0	0	1	0	0	?	0	0	1	0	1	0	1	0
<i>Friesea arnei</i>	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	1	0	1	1	2	0
<i>Friesea buyuni</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0
<i>Friesea delharvengi</i>	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	1	1	1	0
<i>Friesea judithae</i>	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0
<i>Friesea microsphalima</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	1	0	1	1	1	0
<i>Friesea nauimetzli</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	2	0	1	1	0	1	1	2	0
<i>Friesea neptunia</i>	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0
<i>Friesea subterranea</i>	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Friesea vitorovi</i>	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	?	0	2	0
<i>Friesea jaliscoensis</i>	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0
<i>Friesea incognita</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	0	1	1	2	0
<i>Halofriesea kai</i>	?	?	?	0	1	0	1	0	0	1	1	0	1	0	0	1	0	0	1	0	?	0	2	0
<i>Tremoisea enigmatica</i>	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	?	?	0	1	0	1	0	2	0
<i>Tremoisea israelica</i>	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gisinea delhezi</i>	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	?	1	0	0
<i>Gisinea tiliae</i>	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0

## Continued Appendix 2.

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	
<i>Oudemansia esakii</i>	1	0	1	0	1	1	1	3	1	1	1	2	3	3	0	0	0	0	0	0	0	1	0	0
<i>Friesea curupira</i>	0	1	0	3	1	1	0	5	1	1	1	2	0	0	3	0	0	0	0	0	1	1	1	0
<i>Friesea hnaeu</i>	0	0	0	3	1	1	1	5	2	1	1	2	0	0	3	0	0	0	0	0	1	1	1	4
<i>Friesea najtae</i>	1	1	1	0	1	1	1	3	1	1	0	1	3	3	3	0	0	0	0	0	0	1	0	2
<i>Friesea australica</i>	0	1	0	1	2	1	1	3	2	1	1	2	3	3	0	0	0	0	0	0	0	0	0	2
<i>Friesea handschini</i>	1	1	0	1	1	1	1	3	2	1	1	0	3	3	0	0	3	3	3	0	0	0	1	0
<i>Friesea capensis</i>	1	1	0	1	1	1	1	3	1	1	1	3	0	0	0	0	0	0	0	0	0	1	1	3
<i>Friesea ataskella</i>	0	1	0	1	0	1	1	4	1	1	1	1	3	3	3	0	0	0	0	0	?	?	?	0
<i>Friesea arnei</i>	1	1	1	1	1	1	0	3	1	1	1	2	2	0	2	0	0	0	0	0	0	1	1	0
<i>Friesea buyuni</i>	1	1	0	3	1	0	0	5	2	1	1	1	2	2	2	0	0	0	0	0	1	1	1	1
<i>Friesea deharvengi</i>	1	1	0	2	0	1	1	3	1	1	1	1	2	2	2	0	0	0	0	0	0	1	1	1
<i>Friesea judithae</i>	1	1	0	2	1	2	1	3	1	2	1	1	3	3	3	0	0	0	0	0	0	1	1	0
<i>Friesea microsphalma</i>	1	1	0	1	1	1	1	3	2	1	1	2	3	0	0	?	0	?	?	0	0	1	0	1
<i>Friesea nauimetzli</i>	1	1	0	2	1	1	1	4	2	1	1	2	3	1	1	1	3	0	0	0	0	1	1	4
<i>Friesea neptunia</i>	0	1	0	3	0	1	0	5	1	1	1	?	2	2	2	0	2	0	0	1	1	0	0	0
<i>Friesea subterranea</i>	1	1	0	3	1	1	1	5	2	1	1	2	3	0	3	0	0	0	0	0	1	1	1	0
<i>Friesea vitorovi</i>	0	1	0	?	1	1	1	?	2	1	1	3	0	0	0	0	0	0	0	?	?	?	?	1
<i>Friesea jaliscoensis</i>	0	1	0	3	0	0	1	5	2	1	1	2	3	0	0	0	3	0	0	1	1	1	2	2
<i>Friesea incognita</i>	1	1	0	1	0	1	1	3	2	1	1	2	3	0	0	0	3	0	0	0	0	1	1	4
<i>Halofriesea kai</i>	0	1	0	?	1	1	0	3	1	0	0	2	2	2	0	0	0	0	0	0	0	1	?	4
<i>Tremoisea enigmatica</i>	0	1	0	0	0	0	1	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	1	4
<i>Tremoisea israelica</i>	0	0	0	0	0	1	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	4
<i>Gisinea delhezi</i>	1	0	0	?	1	0	1	2	1	0	1	?	7	?	?	?	?	?	?	?	?	1	1	3
<i>Gisinea tiliiae</i>	0	0	0	0	0	0	1	1	1	3	2	3	0	0	0	0	0	0	0	0	0	1	?	3