

Onychiuridae of China: species versus generic diversity along a latitudinal gradient

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Abstract

Our knowledge of Chinese Onychiuridae (sensu Deharveng 2004) accelerated during the five last years. From 2008, we have recorded 29 species and six genera of Onychiuridae new for China, reflecting an increase of 64 % in the number of species and 46 % in the number of genera for the country. Twenty-one of these species were new to science. Today, there are 45 described species belonging to 13 genera of Onychiuridae in China. Their diversity pattern exhibits a remarkable gradient in genus versus species diversity from southwestern China (14 species in four genera) to northeastern China (18 species in 10 genera). A checklist and a key to genera of Chinese Onychiuridae are given. Because huge regions of China remain unsampled or undersampled, and because species have narrow distribution, an increase in species number is likely to continue at the same pace in the coming years.

Keywords Collembola | distribution | biodiversity patterns | checklist | identification key | taxonomy

1. Introduction

The family Onychiuridae (sensu Deharveng 2004) was recorded for the first time from China by Denis (1929a,b), on the basis of material collected by Silvestri, with two species: *Onychiurus fimetarius* (Linnaeus, 1758) from Beijing and *Onychiurus conjungens* (Börner, 1909) from Yunnan. In 1954, Stach described the new species *Onychiurus sinensis* from Hebei and in 1964 the new species *O. hangchowensis* from Zhejiang, and *O. kowalskii* and *O. orientalis* from Jiangsu. During the following thirty years, five additional species only were cited for this family, namely *Onychiurus foliatus* Rusek, 1967, *Onychiurus shanghaiensis* Rusek, 1971, *Pseudonychiurus shanghaiensis* Lin, 1980 and *Onychiurus armatus* (Tullberg, 1869) from Shanghai, and *Onychiurus dinghuensis* Lin & Xia, 1985 from Guangdong. In 1997, Zhao et al. gave a list

of Chinese Onychiuridae, which mentioned 13 species of *Onychiurus* (having hastily put in synonymy the two species *Onychiurus shanghaiensis* and *Pseudonychiurus shanghaiensis*), and two other species that are now placed in the family Tullbergiidae sensu Deharveng, 2004. In the following years, three new species were described (*Onychiurus tamurai* Yue & Yin, 2000, *Thalassaphorura qixiaensis* Yan, Shi & Chen, 2006 and *Psyllaphorura jiangsuensis* Yan, Huang & Chen, 2007).

When we began our investigations in 2008, 17 species were therefore known from China, including *Pseudonychiurus shanghaiensis*, a species both *incertae sedis* and of dubious status (cf. below), all members of the subfamily Onychiurinae. Most of these species were assigned at this time to *Onychiurus*, but they actually correspond to seven valid genera according to modern systematics: *Allonychiurus* with three species, *Heteraphorura* with one species, *Onychiurus*

with two species, *Orthonychiurus* with three species, *Protaphorura* with one species, *Psyllaphorura* with one species and *Thalassaphorura* with five species.

Before 2008, Onychiuridae were recorded from only eight of the 34 Chinese provinces: Beijing (north), Hebei (north), Jiangsu (east), Shanghai (east), Zhejiang (east), Taiwan (southeast), Guangdong (southeast) and Yunnan (southwest). At this time, much smaller surrounding countries such as Japan and Korea (South and North) had more species of Onychiuridae than China, respectively 26 and 21 species recorded in 11 and 9 genera. Therefore, Onychiuridae of China appeared to be very poorly known taxonomically.

2. Results

During our investigations beginning in 2008, we collected and checked many specimens from the south, east and northeast of China. In total, we added 29 species, i.e. an increase of 64% in the number of Chinese species, including 21 species new for science. To date, 45 species belonging to 14 genera have been recorded from China. A checklist of species currently reported from China and a key to genera are given in this paper, as well as comments on the distribution patterns of Onychiuridae biodiversity in the country.

In five years, the number of species reported from China more than doubled (Fig. 1), and many new species are currently under study (Fig. 2). Most described species are only recorded from a single locality, with more than 60% not known outside China. Most of the Chinese territory, including the largest regions like Tibet or Xinjiang, is still unexplored regarding Onychiuridae (Fig. 3). It can be

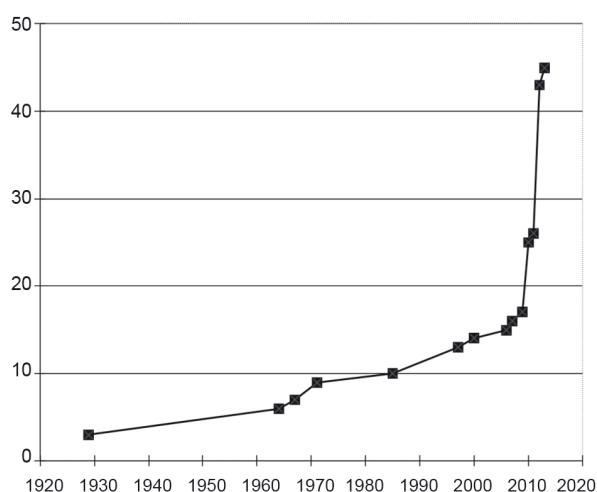


Figure 1. Accumulation curve of the number of Onychiuridae species reported from China with time (*Pseudonychiurus shanghaiensis* Lin, 1980, *incertae sedis*, not included).

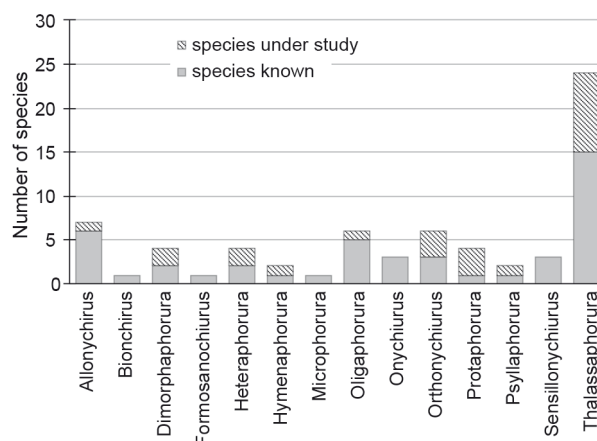


Figure 2. Species of Onychiuridae already known versus under study by the authors (updated in December 2012; *Pseudonychiurus shanghaiensis* Lin, 1980, *incertae sedis*, not included).

therefore safely assumed that most of the Chinese Onychiuridae biodiversity remain to be discovered and described.

In addition, barcode analysis of *Thalassaphorura* (unpublished data) reveals that a significant fraction of biodiversity is escaping traditional taxonomic investigations, because several populations not differentiated by morphology were found to reach a level of genetic divergence similar to that observed between species. In contrast to this high species diversity, the absence of genera new to science in our samples is puzzling. Our findings even suggest that several taxa established from the western palaearctic fauna might have to be synonymized in the future, as discussed in Sun et al. (2010) for *Thalassaphorurini* and *Onychiurini*.

2.1. Checklist of Chinese Onychiuridae

The following checklist includes 45 species of Onychiuridae in 14 genera (Fig. 4), of which two are reported for the first time in China. Names given in the list are updated names according to current taxonomy of the family. Species names used in the cited records are given when they differ from the current name.

1. *Allonychiurus antennalis* Sun, Chen & Deharveng, 2011 – Distribution: Jiangsu: Nanjing (Sun et al. 2011).
2. *Allonychiurus foliatus* (Rusek, 1967) – Distribution: Shanghai (Rusek 1967: 189, as *Onychiurus foliatus*).
3. *Allonychiurus hangchowensis* (Stach, 1964) – Distribution: Zhejiang: Hangzhou (Stach 1964: 8, as *Onychiurus hangchowensis*).
4. *Allonychiurus megasomus* Sun, Yan & Chen, 2009 – Distribution: Jiangsu: Nanjing (Sun et al. 2009).

5. *Allonychiurus shanghaiensis* (Rusek, 1971) – Distribution: Shanghai (Rusek 1971: 117, as *Onychiurus shanghaiensis*).
6. *Allonychiurus songi* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (north and south) and Changchun; Heilongjiang: Honghe National Nature Reserve (Sun & Wu 2012e).
7. *Bionychiurus changbaiensis* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (north and south) (Sun & Wu 2012c); Liaoning: Dandong; Heilongjiang: Shuangyashan (unpublished data, new record).
8. *Dimorphaphorura jingyueensis* Sun & Wu, 2012 – Distribution: Jilin: Changchun (Sun & Wu 2012f).
9. *Dimorphaphorura sanjiangensis* Sun & Wu, 2012 – Distribution: Heilongjiang: Honghe National Nature Reserve (Sun & Wu 2012a); Jilin: Changbai Mountain (north) (Sun & Wu 2012d).
10. *Formosanochiurus formosanus* (Denis, 1929) – Distribution: Taiwan (Denis 1929b: 307, as *Onychiurus formosanus*), Shanghai (Lin 1980: 189, as *Onychiurus formosanus*). – Distribution outside China: Japan.
11. *Heteraphorura conjungens* (Boerner, 1909) – Distribution: Yunnan (Denis 1929a: 167, as *Onychiurus conjungens*).
12. *Heteraphorura seolagensis* (Lee, 1974) – Distribution: Heilongjiang: Shuangyashan; Jilin: Changbai Mountain (south) (unpublished data, new records for China) – Distribution outside China: Korea.
13. *Hymenaphorura nearctica* Pomorski, 2001 – Distribution: Jilin: Changbai Mountain (south) (unpublished data, new record for China) – Distribution outside China: North America.

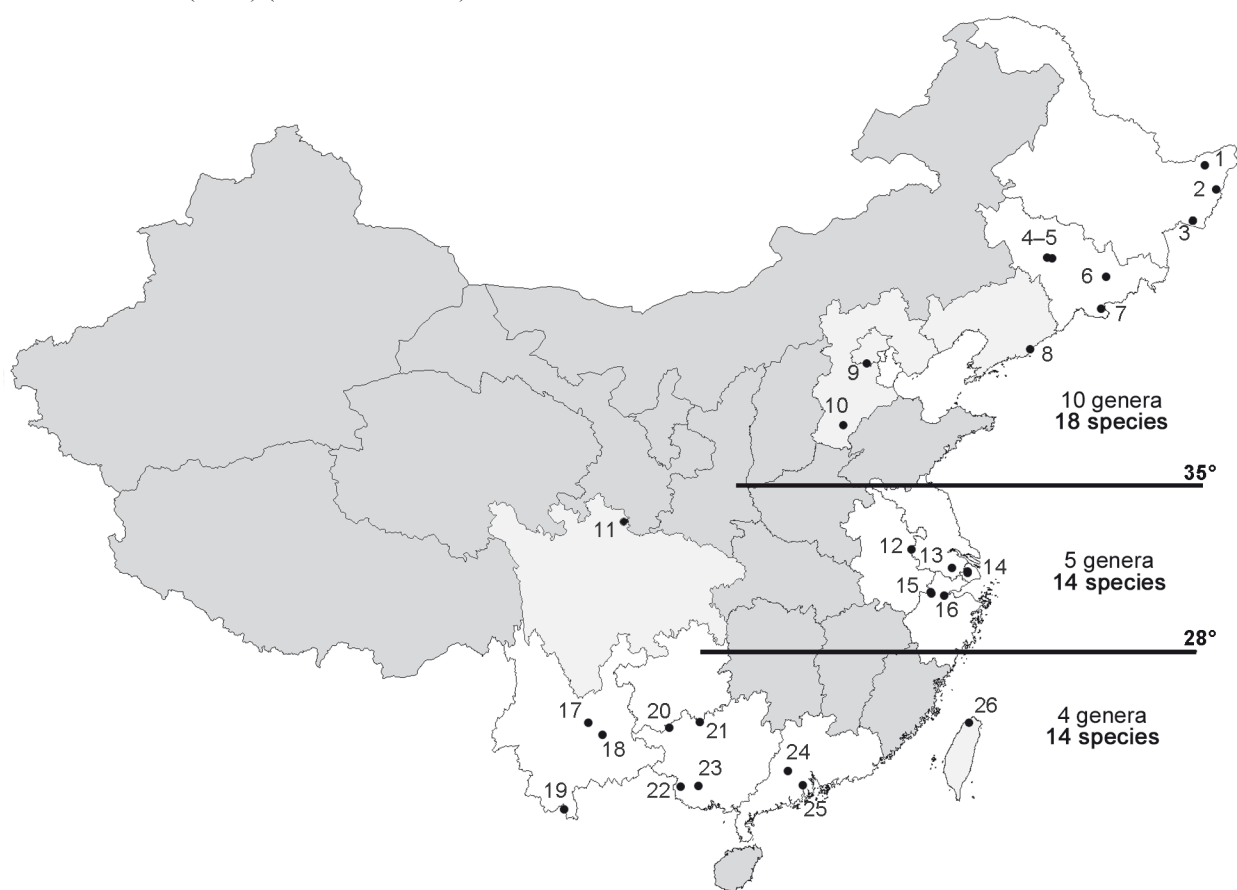


Figure 3. Distribution of Onychiuridae in China. Grey: provinces without record; pale grey: provinces with a single species recorded; white: provinces with several species recorded (not included in the count: *Pseudonychiurus shanghaiensis*, *incertae sedis* and dubious records of two species: *Onychiurus fimetarius* and *Protaphorura armata*).

(1) Heilongjiang: Honghe National Nature Reserve, (2) Heilongjiang: Shuangyashan, (3) Heilongjiang: Lake Khanka, (4) Jilin: Changchun: park of Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, (5) Jilin: Changchun: Jingyuetan National Forest Park, (6) Jilin: Changbai Mountain (north), (7) Jilin: Changbai Mountain (south), (8) Liaoning: Dandong, (9) Beijing, (10) Hebei: Kwantsunghsien (Guangzong), (11) Sichuan: Jiuzhaigou Valley, (12) Jiangsu: Nanjing, (13) Jiangsu: Suzhou, (14) Shanghai: The People's Park, (15) Zhejiang: Lin'an, (16) Zhejiang: Hangzhou, (17) Yunnan: Kunming, (18) Yunnan: Yi-leang (Yiliang), (19) Yunnan: Xishuangbanna, (20) Guangxi: Yachang, (21) Guangxi: Mulun, (22) Guangxi: Nonggang, (23) Guangxi: Bapen, (24) Guangdong: Dinghushan, (25) Guangdong: Xinhui, (26) Taiwan: Taibei.

14. *Micraptorura changbaiensis* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (south) (Sun & Wu 2012d).
15. *Oligaptorura chankaensis* Sun & Wu, 2012 – Distribution: Heilongjiang: Lake Khanka (Sun & Wu 2012f).
16. *Oligaptorura judithae* (Weiner, 1994) – Distribution: Jilin: Changbai Mountain (north) (Sun & Wu 2012d) – Distribution outside China: North Korea.
17. *Oligaptorura koreana* (Weiner, 1994) – Distribution: Jilin: Changbai Mountain (south and north) (Sun & Wu 2012d) – Distribution outside China: North Korea.
18. *Oligaptorura pseudomontana* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (north) (Sun & Wu 2012d).
19. *Oligaptorura ursi* Fjellberg, 1984 – Distribution Heilongjiang: Honghe National Nature Reserve (Sun & Wu 2012a); Jilin: Changbai Mountain (north) (Sun & Wu 2012d) – Distribution outside China: Northern Holarctic.
20. *Onychiurus antennalis* Sun & Zhang, 2012 – Distribution: Zhejiang: Lin'an (Sun & Zhang 2012).
21. *Onychiurus fimetarius* (Linnaeus, 1758) – Distribution: Beijing (Denis 1929a), Shanghai (Lin 1980), Yunnan: Yi-Leang (Denis 1929b), dubious records. – Distribution outside China: Europe.
22. *Onychiurus gulinensis* Sun & Zhang, 2012 – Distribution: Jiangsu: Nanjing (Sun & Zhang 2012).
23. *Orthonychiurus kowalskii* (Stach, 1964) – Distribution: Jiangsu: Nanjing (Stach 1964: 12, as *Onychiurus kowalskii*); Guangdong: Xinhui, and Shanghai (Rusek 1971: 116, as *Onychiurus kowalskii*).
24. *Orthonychiurus folsomi* (Schaffer, 1900) – Distribution: Hebei: Kwantsunghsien (Stach 1954: 65, as *Onychiurus sinensis*); Zhejiang (Zhao 1992: 418, as *Onychiurus folsomi*) – Distribution outside China: North America, Australia, Germany, Japan.
25. *Orthonychiurus himalayensis* (Choudhuri, 1958) – Distribution: Yunnan: Kunming (Tamura & Zhao 1997: 47, as *Onychiurus himalayensis*); Sichuan: Jiuzhaigou Valley; Jiangsu: Suzhou (unpublished data, new records) – Distribution outside China: Nepal.
26. *Protaptorura armata* (Tullberg, 1869) – Distribution: Shanghai (Rusek 1971: 116, and Lin 1980: 189, both as *Onychiurus armatus*, dubious records) – Distribution outside China: Northern Hemisphere and Australia (Bellinger, Christiansen & Janssens 1996–2013).
27. *Psyllaptorura jiangsuensis* Yan, Huang & Chen, 2007 – Distribution: Jiangsu: Nanjing (Yan et al. 2007).
28. *Sensillonychiurus changchunensis* Sun & Wu, 2012 – Distribution: Jilin: Changchun (Sun & Wu 2012b).
29. *Sensillonychiurus pseudoreducta* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (south) (Sun & Wu 2012g).
30. *Sensillonychiurus reducta* Sun & Wu, 2012 – Distribution: Jilin: Changbai Mountain (south) (Sun & Wu 2012g).
31. *Thalassaptorura bapen* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Bapen (Sun et al. 2010).
32. *Thalassaptorura dinghuensis* (Lin & Xia, 1985) – Distribution: Guangdong: Dinghushan (Lin & Xia 1985: 80, as *Onychiurus dinghuensis*).
33. *Thalassaptorura encarpata* (Denis, 1931) – Distribution: Guangxi: Mulun (Sun et al. 2010); Jilin: Changchun (unpublished data, new record) – Distribution outside China: cosmopolitan.
34. *Thalassaptorura grandis* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Mulun, Yachang and Nonggang (Sun et al. 2010).
35. *Thalassaptorura lifouensis* (Thibaud & Weiner, 1997) – Distribution: Jilin: Changchun (Sun & Wu 2012e) – Distribution outside China: New Caledonia.
36. *Thalassaptorura macrospinata* Sun & Wu, 2012 – Distribution: Jilin: Changchun (Sun & Wu 2012b).
37. *Thalassaptorura orientalis* (Stach, 1964) – Distribution: Jiangsu: Nanjing (Stach 1964: 9, as *Onychiurus orientalis*).
38. *Thalassaptorura petaloides* (Rusek, 1981) – Distribution: Guangxi: Mulun, Nonggang and Bapen (Sun et al. 2010) – Distribution outside China: Iraq, New Caledonia, Hawaii.
39. *Thalassaptorura pomorskii* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Mulun, Yachang (Sun et al. 2010).
40. *Thalassaptorura qixiaensis* Yan, Shi & Chen, 2006 – Distribution: Jiangsu: Nanjing (Yan et al. 2006).
41. *Thalassaptorura reducta* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Bapen, Nonggang (Sun et al. 2010).
42. *Thalassaptorura tamurai* (Yue & Yin, 2000) – Distribution: Shanghai (Yue & Yin 2000: 44, as *Onychiurus tamurai*).
43. *Thalassaptorura tiani* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Bapen (Sun et al. 2010).

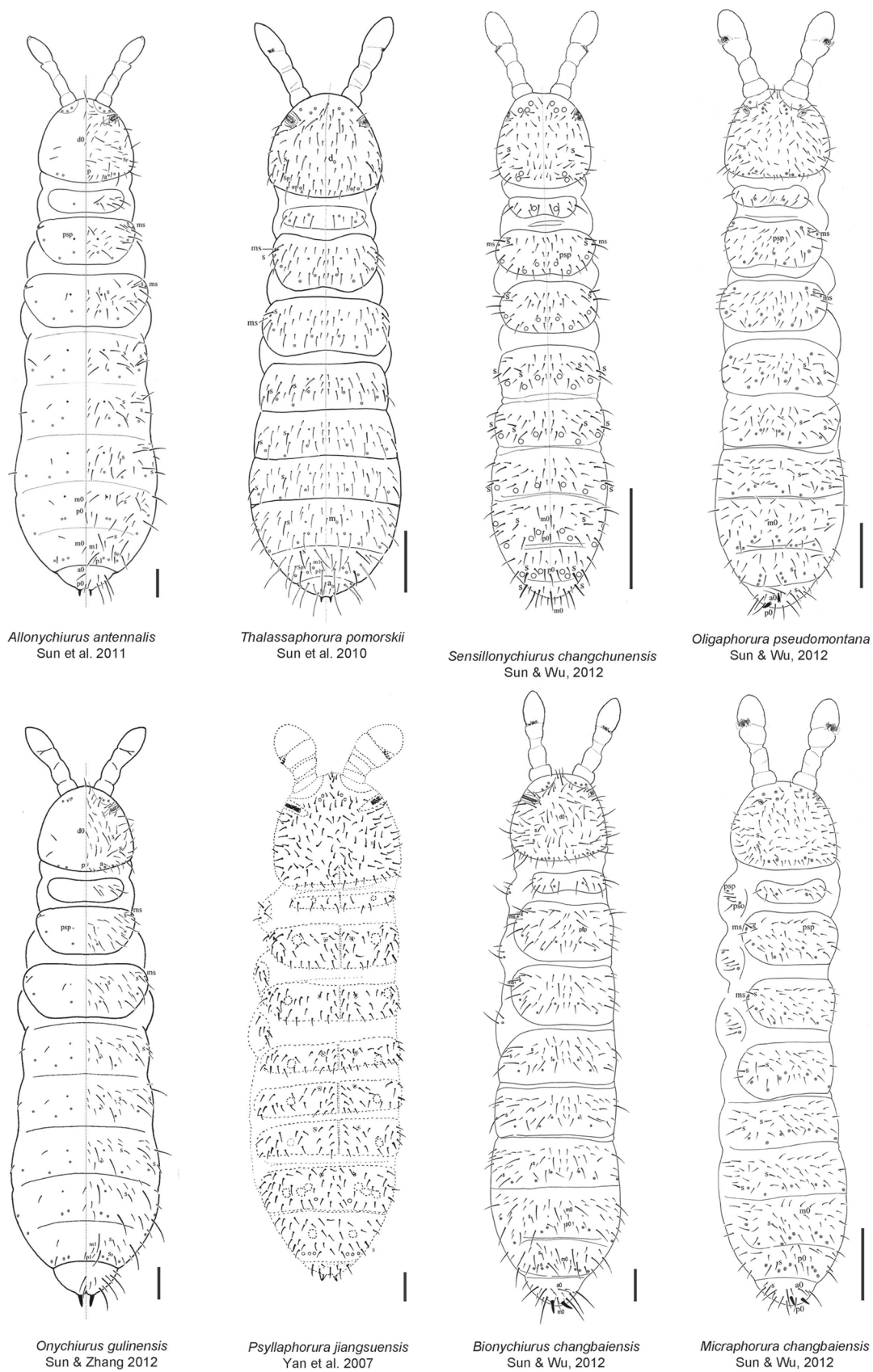


Figure 4. Habitus of Chinese genera of Onychiuridae (Scale bars = 0.1 mm).

44. *Thalassaphorura tibiotarsalis* Sun, Chen & Deharveng, 2010 – Distribution: Guangxi: Bapen and Nonggang (Sun et al. 2010).
45. *Thalassaphorura yodai* (Yosii, 1966) – Distribution: Yunnan: Xishuangbanna (Tamura & Zhao 1997: 47, as *Onychiurus yodai*) – Distribution outside China: Nepal, Japan.

Incertae sedis. The genus *Pseudonychiurus* Lin, 1980 based on the species *Pseudonychiurus shanghaiensis* Lin, 1980 from Shanghai is invalid as preoccupied by *Pseudonychiurus* Bagnall, 1948 (type *Aphorura dentata* Folsom, 1902) (Ellis & Bellinger 1984). Its type and unique species (*P. shanghaiensis* Lin, 1980: 188) is described from molting specimens, for which the author erected the subfamily Pseudonychiurinae. The species *P. shanghaiensis* Lin is placed in *Onychiurus* by Zhao et al (1997) as they consider it a synonym of *Onychiurus shanghaiensis* Rusek, 1971. The genus *Pseudonychiurus* Lin is considered a synonym of *Allonychiurus* Yoshii, 1995 by Weiner (1996: 182); its species would be in this case a junior homonym of *Allonychiurus shanghaiensis* (Rusek, 1971). Actually, neither the generic placement of *shanghaiensis* Lin nor the synonymy of *Pseudonychiurus* Lin with *Allonychiurus* have been justified on morphological grounds. We therefore consider here *Pseudonychiurus shanghaiensis* Lin, 1980 as *incertae sedis*. We do not use it in the statistics on Chinese Onychiuridae.

2.2. Patterns of Onychiuridae diversity along a north-south latitudinal gradient

The diversity of the family exhibits a dramatic gradient from southwestern to northeastern China with increasing generic diversity, while species diversity remains stable (Fig. 3). In the south, an exceptional species diversity of the genus *Thalassaphorura* was encountered in the karsts of Guangxi, where eight species, of which six were new to science, were recognized (Sun et al. 2010). Each of the four sites surveyed in Guangxi yielded two to five species (Sun et al. 2010), not including several still undescribed species. In contrast, in the north, 12 Onychiuridae species were found in the Changbai Mountain Range, but in eight different genera (Fig. 5).

An increase in generic diversity from tropical/Mediterranean to temperate/boreal climates, though never formally documented in the literature for Onychiuridae or other Collembola, is obvious when published revisions and checklists across the northern hemisphere are compared. It is the case for America, where a complete dataset is available in Christiansen

& Bellinger (1998) for the Nearctic and in Mari-Mutt & Bellinger (1990, 1996) for the Neotropics. Chinese Onychiuridae clearly illustrates this gradient across the Eastern Palaearctic. What was not expected, however, is the radiation we discovered in the genus *Thalassaphorura* in southern China, which compensates the loss of generic diversity along the gradient by a higher diversification of this genus in southern regions. *Thalassaphorura* is widely distributed in the Holarctic, but only in southern China (and possibly in northern Vietnam from unpublished observations) has it diversified to such an extent. A variety of mechanisms underlying biodiversity patterns have been debated in the literature (Willig et al. 2003, Ricklefs 2004). In the present case, a working hypothesis would be that three different mechanisms are involved. The first one is the distance to the area of evolutionary diversification of Onychiuridae, which is clearly the temperate and boreal zone of northern hemisphere (Weiner 1996); the strong decrease in genus number from northern to southern China illustrates this gradient. Second, the radiation of *Thalassaphorura* would reflect the general trend to increasing local endemism among non-parthenogenetic lineages of Collembola from boreal to southern regions of the world (for instance see Deharveng & Suhardjono 1994 for *Isotomiella* Bagnall, 1939), *Thalassaphorura* being one of the few genera of Onychiuridae that reached the tropics. At least, the frequent co-occurrence of four species of *Thalassaphorura* in a single sample of soil suggests that local environment, possibly species interactions, also contribute to the pattern, through unknown pathways; no other similar case has been reported so far for any other genus of Onychiuridae in the area of diversification of the family.

In a more general scope, as far as we know, the gradient of biodiversity documented here seems to be unique among soil fauna. In this respect, it deserves further investigations, in particular regarding life traits and evolutionary relationships of co-occurring parthenogenetic and bisexual species of *Thalassaphorura*.

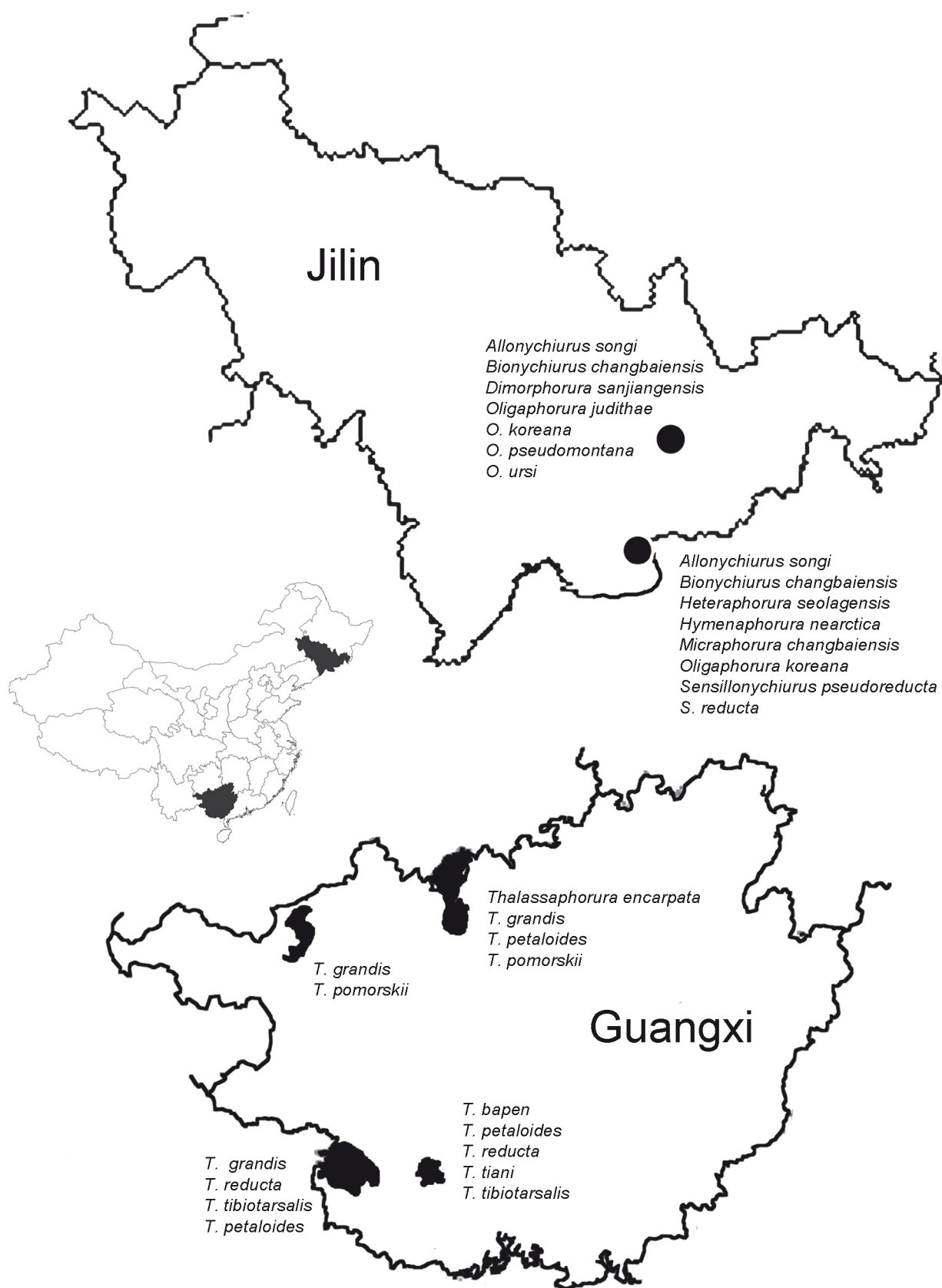


Figure 5. Contrasted composition of Onychiuridae biodiversity in two provinces of China: Guangxi in the south (with four collection sites) and Jilin in the northeast (with two collection sites in Changbai mountain).

2.3. Key to genera of Chinese Onychiuridae

1. Posterior pseudocelli on the head absent 2
Posterior pseudocelli on the head present 4
2. Furca reduced to two knobs with chaetae on it *Psyllaphorura*
Furca reduced to finely granulated area with chaetae posteriorly 3
3. Dorsal pseudocelli on Abd. III absent, chaetae on unpaired anal lobe thickened, labium with papilla E *Heteraphorura*
Dorsal pseudocelli on Abd. III present, chaetae on unpaired anal lobe not thickened, labium without papilla E *Hymenaphorura*
4. Postantennal organ with a 3–5 lobed vesicle 5
Postantennal organ with more numerous vesicles 7
5. Furca reduced to a finely granulated area *Dimorphaphorura*
Furca reduced to a small cuticular fold or cuticular pocket 6
6. Furca with cuticular pocket and 1+1 dental chaetae posteriorly *Micraphorura*
Furca with cuticular fold and 2+2 dental chaetae in two rows posteriorly *Oligaphorura*
7. Postantennal organ with simple vesicles 8
Postantennal organ with compound vesicles 9
8. Dorsal cephalic chaeta d_0 absent *Protaphorura*
Dorsal cephalic chaeta d_0 present *Thalassaphorura*
9. Furca reduced to finely granulated area with 2+2 chaetae posteriorly arranged in two rows 10
Furca reduced to finely granulated area (rarely reduced to cuticular pocket) with 1+1 or 2+2 chaetae posteriorly arranged in one row 11
10. Chaeta d_0 absent on head, furcal rudiment adjacent to the border of Abd. III-IV sterna *Sensillonychiurus*
Chaeta d_0 present on head, furcal rudiment situated behind the border of Abd. III-IV sterna *Allonychiurus*
11. Furcula reduced to a cuticular fold *Bionychiurus*
Furcula reduced to a finely granulated area 12
12. Anal spines absent *Orthonychiurus*
Anal spines present *Onychiurus*

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