Recent advances and synthesis in biodiversity and biogeography of arenicolous Collembola

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Abstract. Synthesis and new data on interstitial Collembola-fauna in littoral and continental sand sediments. Collembola biodiversity in supralitoral and inland sands can not be compared to the biodiversity developed in mineral soils or leaf litter, and Collembola biodiversity in intertidal sands is lower. The problem of the dispersial of these littoral sand Collembola is considered. A number of species appear have a trans-oceanic dispersal on considerable distances on or in sea water.

Résumé. **Données récentes et synthèse sur la biodiversité et la biogéographie des Collemboles des sables.** Nouvelles données et synthèse sur la faune des Collemboles interstitiels des sables littoraux et continentaux. Les biodiversités des Collemboles des zones sableuses supralittorales et continentales ne peuvent être comparées à celles des sols et des litières ; la biodiversité de ceux de la zone sableuse intertidale est encore plus basse. Le problème de la dispersion des Collemboles des sables littoraux est discuté. Un certain nombre de ces espèces semblent avoir une disperssion trans-océanique sur des distances considérables.

Keywords: Collembola; Sand; Intertidal; Supralittoral; Biodiversity; Dispersal.

Interstitial Collembola inhabit fine-grained loose sediments, predominantly sand, of some biotopes like "dry" sands (supralittoral and inland zones), and "humid" sands (intertidal zone). These habitats have been overlooked until recently and, in 1985, we began to work on this populations (Massoud & Thibaud). In 1997, Thibaud & Christian published a global review of arenicolous interstitial Collembola including 168 species recorded from supralittoral and inland sand, and 56 species from marine intertidal sand. Here, we publish new data on 43 species, from which 22 are new species for thescience and we focus on this interstitial sand Collembola.

Materials and methods

In all these studies, the specimens from "dry" sands were collected from sand of beaches or dunes and, for extraction of specimens, flotation technic was used (Christian & Thibaud 1988). The specimens from "humid" sands were collected, for superficial zone, by "hole Chappuis" method (Chappuis 1946) or, for more deep zone, by "pumping" method (Delamare Debouteville 1954). The collected specimens were preserved in alcohol and mounted in a Marc André II solution (André 1946).

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Results

The results are summarized in the table 1 and in the appendix.

In interstitial Collembola from "dry" sands (supralittoral and inland) a total of 228 species (about 40%) seem to be restricted to sandy habitats and may be considered as"psammobiotic". The others can be classified as "edaphic-psammophilic".

The most common genera are: *Willemia, Xenyllogastrura, Axenyllodes, Friesea, Micranurida, Doutnacia, Mesaphorura, Onychiurus, Protaphorura, Scaphaphorura, Tullbergia, Isotogastrura, Archisotoma, Folsomia, Folsomides, Folsomina* and *Isotomodes,* all Poduromorpha or Entomobryomorpha Isotomidae.

186 species have been recorded from supralittoral sands, in beaches or dunes. About 45% are endemic, about 23% are European and/or Mediterranean, 10% holarctic, 10% neo- or pantropical and 12% cosmopolitan or with a wide distribution. However, in numerous cases endemism may be biased by the small number of sampling sites, especially in extra-European regions.

63 species have been recorded from inland sands. About 16% are endemic, 37% European and/or Mediterranean, 13% holarctic, 5% neo- or pantropical and 29% cosmopolitan or with a wide distribution. The relatively smaller proportion of endemic species in inland sands may be a consequence of extensive

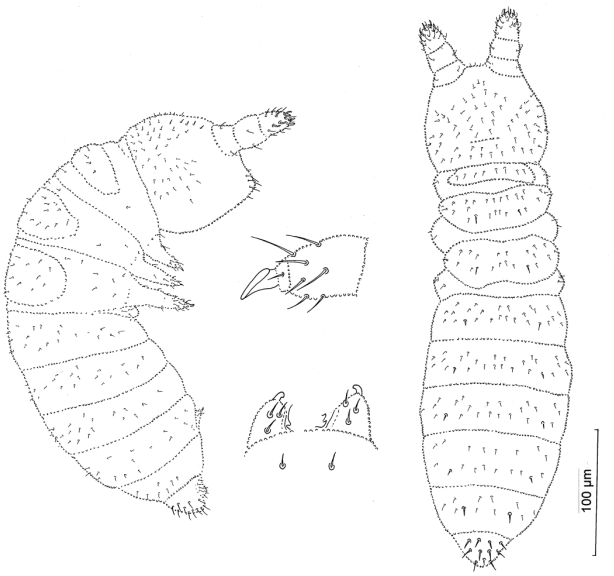

Figure 1
Friesea anophthalma Thibaud & Weiner 1997, habitus in dorsal view and side-face, with tibiotarsi and claw, and regressed furca. It is an interstitial species from littoral sands, endemic of New-Caledonia.

samplings in Europe, the best investigated region with respect to Collembolan faunas.

It has to be noted that 21 species are reported also from supralittoral sands.

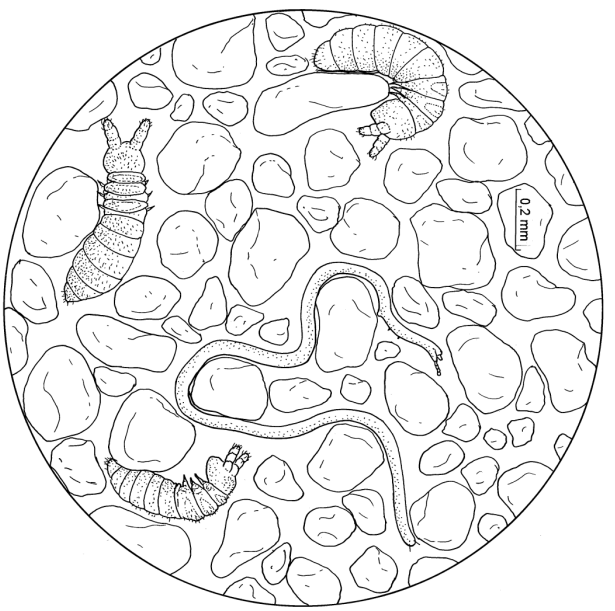

Figure 2
Littoral sand, under binocular-lens, of New-Caledonia, with three specimens of Collembola *Friesea anophthalma* Thibaud & Weiner 1997, and one specimen of the Acarina Nematalycidae *Gordialycus* sp.

In these "dry" sands, between 1 to 12 species (average 3,5 ± 1), and between 1 to 180 individuals (average 24 ± 5) per positive standard sample (2000 cm^3) are found. Numerous juvenile specimens are present in most samples.

Within the interstitial Collembola from "humid" sands (intertidal), a total of 57 species, only about 20% seem to be considered as "psammobiotic". The other can be classified as "thalassobionts".

The most common genera are: *Friesea, Anurida, Archisotoma, Cryptopygus* and *Psammisotoma*.

About 40% are endemic, about 30% are European and/or Mediterranean, 7% holarctic, 3% neo- or pantropical and 20% cosmopolitan.

In these "humid" sands, between one to four species (average 1,5 ± 0,4), and between one to 130 individuals (average 9 ± 3) per positive sample are found.

Discussion

As Thibaud & Christian, wrote in 1997, considering the low number of sampling sites and the scarcity of evaluable studies (about 40 in 1997, 70 more in 2006), all statements are still a hypothesis.

Nevertheless we can now make some conclusions concerning these interstitials populations of Collembola: Psammobiotic and most of edaphic-psammophilic Collembola species are small (body length of mature specimens: 0.2–0.7 mm), narrow and characterised by depigmentation, microphthalmy or anophthalmy, short antennae and legs, short or completely reduced furca (Fig. 1). These morphological characters cause arenicolous interstitial Collembola to look like typical euedaphic species, but flexible and slender enough to be able to move between sand grains of small size without changing pore architecture. The pore structure is comparatively uniform, especially in fine sands with homogenous granulometry, offering live space only for microorganisms and a certain life-form of minute invertebrates which constitute the terrestrial mesopsammon (Fig. 2). The percentage of morphologically adapted Collembola increases with decreasing grain-size down to 200–180 µm.

On the other hand, supralitoral and inland "dry" sand biotopes have 21 species in common (±8%), whilst "humid" intertidal and "dry" littoral sands are faunistically more distinct; only nine (±4%) of intertidal Collembola species are also reported in littoral sands. Collembola biodiversity in supralitoral and inland "dry" sands is much lower than the biodiversity developed in mineral soils or leaf litter. Besides the spatial conditions mentioned above, oligotrophy and highly variable humidity and temperature harshen

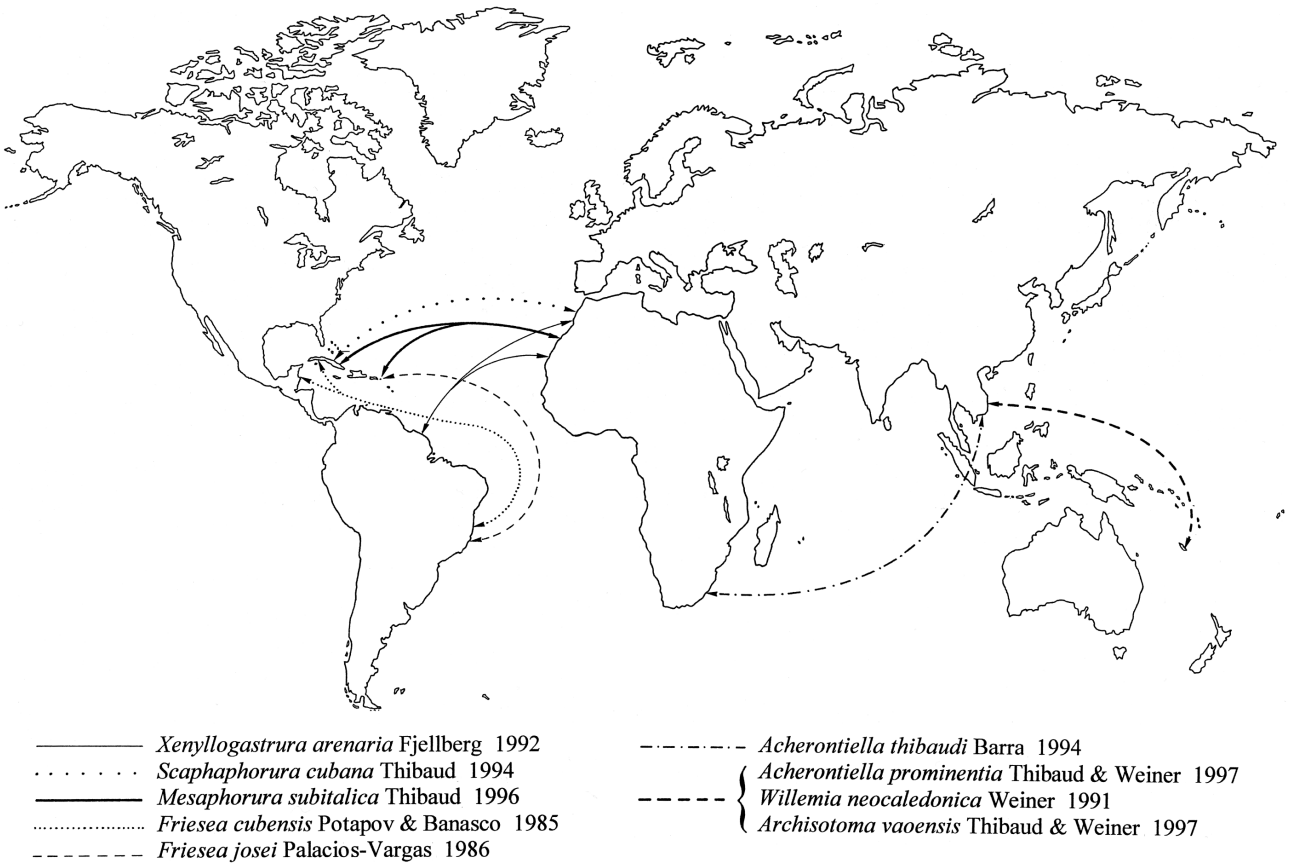

Figure 3
Trans-oceanic repartition of some species of interstitial sand Collembola.

this "extreme" biotope. Collembolan biodiversity in intertidal "humid" sands is lower than that in supralitoral and inland sands. The limited flood resistance of many Collembola species and the low salt tolerance provide a plausible explanation. For the distribution of thalassobiotic species, salinity is obviously of greater influence than the grain-size composition of the littoral substrate. With the exception of typical rock-dwellers, the majority of intertidal Collembola show no distinct substrate preference; they colonize sand as well as gravel and to some extent, loamy sediments.

Intertidal sands are thus extreme in various respects, allowing the colonization of only a small number of both morphologically and physiologically adapted specialists. Since permanent humidity rarely coincides with high salinity in littoral or continental sand, the interstitial collembolan fauna of these terrestrial biotopes rarely overlaps the intertidal fauna. The spatial separation of habitat types does not provide a satisfactory explanation for this faunistic difference: on the one hand, there is frequently a sharp difference from intertidal to supralittoral sands; on the other hand, a species such as *Scaphaphorura arenaria* - which occurs in supralittoral as well as in remote continental sand accumulations - shows the remarkable dispersal capability of interstitial Collembola.

At least, we can remark that some species from interstitial littoral sands, in Palaeotropical zone, have all a trans-oceanic distribution (Fig. 3), like *Acherontiella thibaudi* Barra 1994 (Natal in South Africa Republic and Vietnam), *Acherontiella prominentia* Thibaud & Weiner 1997, *Willemia neocaledonica* Weiner 1991 and *Archisotoma vaoensis* Thibaud & Weiner 1997 (all of them from New Caledonia and Vietnam), and, in Africa and Neotropical zones, like *Xenyllogastrura arenaria* Fjellberg 1992 (Canary Islands, Mauritania, Marocco and French Guyana), *Scaphaphorura cubana* Thibaud 1994 (Cuba and Marocco), *Mesaphorura subitalica* Thibaud 1996 (Mauritania and Antilla, Mexico), *Friesea cubensis* Potapov & Banasco 1985 (Cuba, Mexico and Brazil), *Friesea josei* Palacios-Vargas 1986 (Puerto Rico and Brazil), *Paraxenylla piloua* Thibaud & Weiner 1997

Table 1. Classification of arenicolous habitats and types of the inhabitants

"humid" sands Intertidal zone	**"dry" sands Supralittoral & Inland zones**	
57 spp. 20% psammobiotic 80% thallasobiont	228 spp. 40% psammobiotic 60% edaphic-psammophilic	
Intertidal	**Supralittoral**	**Inland**
57 spp. 40% endemic 30% European-Med. 20% cosmopolitan 7% holarctic	186 spp. 45% endemic 23% European-Med. 12% cosmopolitan 10% holarctic 10% neo-pantropical	63 spp. 16% endemic 37% European-Med. 29% cosmopolitan 13% holarctic 5% neo-pantropical
(positiv sample) in 2000 cm3 =		
1-4 spp. average 1,5 ± 0,5 spp. 1-131 individuals average 9 ± 3 individuals	1-12 spp. average 3,5 ± 1 spp. 1-188 individuals average 25 ± 5 individuals	

(New Caledonia and Senegal), and *Psammisotoma kingae* Greenslade & Deharveng 1986 (Australia, New Guinea, Indonesia and Senegal).

I have bred some Collembola species "under water" (Thibaud 1970). These Collembola, from families Hypogastruridae (*Ceratophysella, Hypogastrura, Schaefferia* and *Typhlogastrura*), or Onychiuridae (*Onychiurus*), or Isotomidae (*Folsomia* and *Isotomurus*), can undergo embryonic and post-embryonic development, and adult life, under water and on water. I can therefore consider them as "sub-aquatic" animals (Thibaud 1970). This was confirmed recently by Coulson *et al.* (2002): five species of Collembola (in the genera: *Hypogastrura, Onychiurus, Folsomia* and *Tetracanthella*) were exposed on the surface film of sea water. These species survived for over fourteen days. One species (*Tetracanthella arctica*) survived submersion in sea water for longer than two weeks. We can conclude that, probably, a number of species of Collembola – and other microarthropods – have a trans-oceanic dispersal, over considerable distances, on sea water. Keeping in mind the possibility of air dispersal (Berland 1937), these possibilities must be taken into account in the study of Collembola distribution in the world.

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Appendix

Species exclusively found in sand since 1997

1. Ukrainia (Thibaud & Taraschuk 1997)

Axenyllodes ukrainus Thibaud & Taraschuk 1997 (Ukrainia)
Micraphorura irinae Thibaud & Taraschuk 1997 (Ukrainia)

2. Latvia (Fjellberg & Jucevica 2000)

Archisotoma martae Fjellberg & Jucevica 2000 (Latvia)

3. Denmark (Fjellberg 1998)

Doutnacia mols Fjellberg 1998 (Denmark)

4. Denmark and Sweden (Fjellberg 1998)

Micranurida balta Fjellberg 1998 (Denmark and Sweden)

5. Germany (Sterzynska & Ehrnsberger 1998)

Mesaphorura petterdassi (Fjellberg 1988) (Norway and North Sea, Germany)

6. Republic South Africa (Barra 1997 and 2002)

Najtafrica riebi (Barra 1994) (Prov. Natal in South Africa Republic)
Cryptopygus riebi Barra 1997 (Prov. Natal)
Archisotoma sabulosa Barra 1997 (Prov. Natal)

7. Venezuela (Thibaud & Diaz 1998)

Xenyllogastrura venezueliensis Thibaud & Diaz 1998 (Venezuela)

8. Brazil (Thibaud & Palacios-Vargas 1999)

Isotomodes carioca Thibaud & Palacios-Vargas 1999 (Brazil)

9. Mexico (Palacios-Vargas & Thibaud 1998; Thibaud & Palacios-Vargas 2000, 2001; Palacios-Vargas & Thibaud 2001)

Willemia psammophila Palacios-Vargas & Thibaud 2001 (Mexico)
Brachystomella baconaoensis Gruia 1983 (Cuba, Mexico)
Stachorutes maya Thibaud & Palacios-Vargas 2000 (Mexico)
Mesaphorura matilei Thibaud & Palacios-Vargas 2000 (Mexico)
Cryptopygus axayacalt Palacios-Vargas & Thibaud 2001 (Mexico)
Isotogastrura ahuizotli Palacios-Vargas & Thibaud 1998 (Mexico)
Isotogastrura veracruzana Palacios-Vargas & Thibaud 1998 (Mexico)
Isotogastrura atuberculata Palacios-Vargas & Thibaud 2001 (Mexico)

10. Vietnam (Thibaud 2002)

Mesaphorura mani Thibaud 2002 (littoral sand sp.; Vietnam)
Stenaphorura marionae Thibaud 2002 (Vietnam)
Spicatella bedosae Thibaud 2002 (Vietnam)

11. Morocco (Potapov & Thibaud 2003; Thibaud & Boumezzough 2006)

Xenyllogastrura arenaria Fjellberg 1992 (Canary Islands, Mauritania, Marocco)
Mesaphorura schembrii Thibaud & Christian 1989 (Malta, Albania, Marocco)
Mesaphorura subitalica Thibaud 1996 (Mauritania, Antilla, Marocco)
Scaphaphorura cubana Thibaud 1994 (Cuba, Marocco)
Folsomides arenus Potapov & Thibaud 2003 (Marocco)
Folsomides croci Potapov & Thibaud 2003 (Marocco)
Isotogastrura coronata Fjellberg 1995 (Canaria Island, Albania, Marocco)
Archisotoma subtheae Thibaud & Boumezzough 2006 (Marocco)
Cryptopygus caussanelli Thibaud 1996 (Mauritania, Senegal)

12. French Guyana (Thibaud 2004)

Xenyllogastrura arenaria Fjellberg 1992 (Canary Islands, Mauritania, Marocco, French Guyana)
Mesaphorura guyana Thibaud 2004 (French Guyana)

13. Senegal (Thibaud & N'Diaye 2006)

Paraxenylla piloua Thibaud & Weiner 1997 (New Caledonia, Senegal)
Xenyllogastrura arenaria Fjellberg 1992 (Canary Islands, Mauritania, Marocco, French Guyana, Senegal)
Mesaphorura subitalica Thibaud 1996 (Mauritania, Antilla, Marocco, Senegal)
Sensilatullbergia senegalensis Thibaud & Ndiaye 2006 (Senegal)
Archisotoma bothrilongaequalis Thibaud & Ndaye 2006 (Senegal)
Archisotoma senegalensis Thibaud & Ndaye 2006 (Senegal)
Cryptopygus caussaneli Thibaud 1996 (Mauritania, Senegal)
Psammisotoma kingae Greenslade & Deharveng 1986 (Australia, Papouasia-New Guinea, Indonesia, Senegal)