Importance and evolution of sexual dimorphism in different families of Collembola (Hexapoda)

José Guadalupe Palacios-Vargas[1] and Gabriela Castaño-Meneses[1,2]

[1]Universidad Nacional Autónoma de Mexico (UNAM), Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Ecología y Sistemática de Microartrópodos, Ciudad Universitaria 04510, México, D.F. E-mail: jgpv@hp.fciencias.unam.mx [2]UNAM, Facultad de Ciencias, Unidad Multidisciplinaria de Docencia e Investigación, Campus Juriquilla, Boulevard Juriquilla 3001, CP 76230, Querétaro, México. E-mail: gcm@hp.fciencias.unam.mx

Abstract – A bibliographic revision of sexual dimorphism in different families of Collembola was performed in order to determine the most common patterns in each group. We list several examples of the sexual dimorphism in different families of Collembola, which illustrate from some of the smallest differences between males and females to major differences between both sexes in some families. We show different cases of sexual dimorphism in *Spinactaletes*, *Sminthurides*, and the remarkable morphology of *Guthriella muskegis*. It seems that most of the cases of strong sexual dimorphism are related to aquatic habitats or behaviour still not fully understood. Species belonging to primarily aquatic families (fresh water or marine water) have the most evolved morphology, where males have clasping antennae to attach the females in order to avoid loosing them with the movement of the water.

Index terms: *Guthriella muskegis*, morphological variations, secondary sexual characters.

Importância e evolução do dimorfismo sexual em diferentes famílias de Collembola (Hexapoda)

Resumo – Uma revisão bibliográfica do dimorfismo sexual em diferentes famílias de Collembola foi feita para determinar os padrões morfológicos mais comuns em cada grupo. Foram listados diversos exemplos de dimorfismo sexual em diferentes famílias de Collembola, que ilustram desde as menores diferenças entre machos e fêmeas até as grandes diferenças entre os sexos em algumas famílias. Foi mostrado o dimorfismo sexual em *Spinactaletes e Sminthurides*, e a morfologia marcante de *Guthriella muskegis* foi documentada. É provável que a maioria dos exemplos mais evidentes de dimorfismo sexual estejam relacionados ao habitat aquático ou a padrões de comportamento ainda não compreendidos. As espécies que pertencem às famílias aquáticas primárias (água doce ou água marinha) são as que têm morfologia mais evoluída. Os machos têm antenas preênseis, para agarrar as fêmeas e evitar que se desprendam com o movimento da água.

Termos para indexação: *Guthriella muskegis*, variações morfológicas, caracteres sexuais secundários.

Introduction

Guaranteeing the transference of genetic information to subsequent generations is a fundamental task in all living beings. The success of this process is related to differences in the access to mating, or sexual selection (Darwin, 1871). On mating, competition appears generally between males to be selected by females. The sexual dimorphism in males of Hexapoda appears in different groups, showing complex patterns that include particular behavior for mating. Nevertheless, even in groups in which there is no copulation, in which the males do not have much contact with females, and the transfer of sperm is done by other mechanisms, there is still some kind of sexual dimorphism.

In Collembola, fecundation is through the transfer of spermatophore, which in some cases is direct, with complex behavior of both sexes (Kozlowski & Aoxiang, 2006), and some species have several modified structures to be able to accomplish that function. Most of these records in Collembola belong to the members of Symphypleona

(Bretfeld, 1971), mainly in *Deuterosminthurus* and in many members of the Sminthurididae (v. gr. *Denisiella*). Nevertheless, there are records of sexual dimorphism in other groups as Isotomidae: *Folsomia* (Ding et al., 2006), *Vertagopus* (Denis, 1928; Goto, 1972; Goloshchapova et al., 2006), *Proisotoma* (Goloshchapova et al., 2006); *Najtia vicaria* (Arlé & Mendonça, 1986); and even in some Entomobryidae: *Seira* (Zeppelini & Bellini, 2006), *Willowsia* (Mari-Mutt, 1981; Zhang et al., 2007), *Orchesella* (Ernsting & Isaaks, 2002) and *Entomobrya* (Ramel et al., 2008); and in the genera *Arrhopalites* (Christiansen & Bellinger, 1996) and *Cyphoderus* (Yoshii, 1990). In *Schoettella* (Hypogastruridae), important differences in the cuticular lipids have been found in each sex (Porco et al., 2004).

In order to determinate the most common patterns in each group, we illustrate the sexual dimorphism found in members of different families in diverse habitats: *Pseudachorutes* (Neanuridae), *Spinactaletes* (Spinactaletidae), *Coenaletes* (Coenaletidae), *Denisiella* (Sminthurididae) and *Guthriella muskegis* (Guthrie) (Isotomidae).

Sexual dimorphism determination

Specimens from different habitats were evaluated in order to determine sexual dimorphism: terrestrial (*Pseudachorutes:* Neanuridae; *Guthriella muskegis:* Isotomidae; *Denisiella:* Sminthurididae); primary fresh water (*Sminthurides:* Sminthurididae), littoral (*Spinactaletes:* Spinactaletidae); and associated with hermit crabs (*Actaletes*: Actaletidae). These belonged to the collection of the authors, deposited at the Universidad Nacional Autónoma de México.

Sexual dimorphism in Collembola families

According to the literature reviewed, there are sexual dimorphism records in ten of the 33 families of Collembola. Secondary sexual characters have been recorded in 28 genera. The main examples of sexual dimorphism, found in different families of Collembola, are shown in Table 1.

In the Symphypleona, sexual dimorphism is more evident, and this character affects head and antennae and the success of spermatophore transfer to the females, regardless of the environment (these modifications occur in edaphic habitats, as well as in aquatic, freshwater or marine littoral). In the case of the terrestrial *Pseudachorutes* (Neanuridae), two ventral organs were observed in the male (Gao & Palacios-Vargas, 2008), and interpreted as sexual dimorphism, which is very clearly symmetrical for both sides of the body. This kind of sexual dimorphism has been observed in other members of the Poduromorpha (as Onychiuridae), and might be common in other families.

In the case of the Isotomidae, the most extraordinary modifications in *Guthriella muskegis* are in the end of the body, in particular the presence of spines and modifications of the setae. Males present ornamentation similar to the patterns found in other groups of Arthropoda, as the Insecta, in order to attract females. These characteristics may only emerge when males are in the reproductive condition and males very similar to females can be found, even in the adult phase, without modifications. In modified males, the setae look like leaves and they develop abdominal spines, which are not present in the females; even the antennae are modified (Figure 1). There are also records of modifications of the antennae in other species of Isotomidae, their function are still unknown. The specimens of *G. muskegis* are from Cerro Fábrega, Bocas del Toro, Panama.

For the Entomobryidae, the main sexual differences are in the color patterns, and in the modification of mucro and genital aperture.

In the case of the species members of the littoral, *Spinactaletes* spp. (Spinactaletidae), the modifications are the presence of a spur in the tibiotarsus III and also clasping antennae in the males.

For the peculiar case of *Coenaletes caribaeus* Bellinger (Coenaletidae), which lives between the shell and the hermit crab, we studied the differences of males and females (Palacios-Vargas et al., 2000). The modifications include the presence of clasping antennae with spines and also some spines on thorax and abdomen, although their function are still unknown.

Table 1. Sexual dimorphism among Collembola.

Taxa	Characteristics	References
Neanuridae		
Pronura pomorskii Smolis & Deharveng	Fore legs structure	Smolis & Deharveng (2006)
Hypogastruridae		
Hypogastrura assimilis (Krasbauer)	Body length	Folker-Hansen et al. (1996)
Schoettella ununguiculata (Tullberg)	Cuticular lipids	Porco et al. (2004)
Isotomidae		
Agrenia spp.	Male antenna elongated with more developed 2nd and 3rd segments.	Strenzke (1958)
Anurophorus serratus Deharveng	Curved sensilla occur on the ventromedial side of the three last antennal segments of males.	Deharveng (1976)
Archisotoma besselsi (Pack.)	Male antenna elongated with more developed 2nd and 3rd segments. Abdominal shortened macrosetae forming a "brush".	Denis (1928)
Axelsonia tubifera Strenzke	Male antenna elongated and broadened with more developed 2nd and 3rd segments.	Fjellberg (1986)
Dimorphotoma porcella Ellis	Male antenna elongated and broadened with more developed 2nd and 3rd segments. Male abdominal setae longer and thicker than in females.	Ellis (1976)
Folsomia fimetaria (L.)	Body length	Folker-Hansen et al. (1996)
Jestella siva Najt	Male antenna elongated and broadened with more developed 2nd and 3rd segments. Male abdominal setae longer and thicker than in females.	Najt (1977)
Najtia vicaria (Arlé)	Male antenna elongated, Ant. IV horn-like curved, lateral cephalic macrosetae, Abd. IV with crowbar-like structures.	Arlé & Mendonça (1986)
Rhodanella minos (Denis)	Presence of a pair of very long, out-standing, curved horn-like setae, one on either side of the head, and by the presence of stouter antennae and modified setae on some of the abdominal segments.	Goto (1972)
Vertagopus pseudocinereus Fjellberg	Males 2nd antennal segment curved and with slightly serrated setae. Shortened macrosetae forming a "brush".	Goloshchapova et al. (2006)
Actaletidae		
Spinactaletes spp.	Length of male antenna, form of Ant. IV, chaetotaxie of Ant. II, III and IV, wide of Ant. I. Prefemoral and protibiotarsal chaetotaxie of males.	Soto-Adames (1988)
Entomobryidae		
Entomobrya atrocincta Schött	Body color pattern	Ramel et al. (2008)
Seira mantis Zeppelini & Bellini	Modifications in the fore legs	Zeppelini & Bellini (2006)
S. raptora Zeppelini & Bellini	Modifications in the fore legs	Zeppelini & Bellini (2006)
Orchesella cincta (L.)	Body color pattern	Mari-Mutt (1981)
Willowsia jacobsoni (Börner)	Body color pattern and body length	Mari-Mutt (1981)
Paronellidae		
Cyphoderus albinus Nicolet	Females with bidentate mucro	Yoshii (1990)
Coenaletidae		
Coenaletes caribaeus Bellinger	Fourth antennal segment in male with 2 subapical organs in separate minute pegs and 8th thin, uniform blunt setae in apical half.	Palacios-Vargas et al. (2000)
Sminthurididae	Antenna of males modified as clasping organ	
Denisiella diomedesi Palacios-Vargas	Second and third antennal segment highly modified as clasping organ in males.	Palacios-Vargas (2007)
Debouttevillea marina Murphy	Males second antennal segment modified in a clasping organ.	Massoud & Betsch (1972), Eberhard (2004)
Jeannenotia stachi Jeannenot	Males second antennal segment modified in a clasping organ.	Massoud & Betsch (1972)
Sminthuridia sphaeridioides (Murphy)	Males second antennal segment modified in a clasping organ.	Massoud & Betsch (1972), Eberhard (2004)
Yosiides himachal (Yosii)	Males second antennal segment modified in a clasping organ.	Massoud & Betsch (1972), Eberhard (2004)
Arrhopalitidae		
Arrhopalites jay Christiansen & Bellinger	Presence of a tunica and an unguicular filament on the posterior foot of female	Christiansen & Bellinger (1996)
Arrhopalites lacuna Christiansen & Bellinger	Number of antennal subsegments and the fact that the male seta e3 differs strikingly from the female	Christiansen & Bellinger (1996)
Bourletiellidae		
Bovicornia greensladei Massoud & Delamare Deboutteville	Males second antennal segment modified as clasping organ	Eberhard (2004)
Deuterosminthurus spp.	Body and head length, longer antennae in males. Female with subanal appendages	Palacios-Vargas & González (1995)

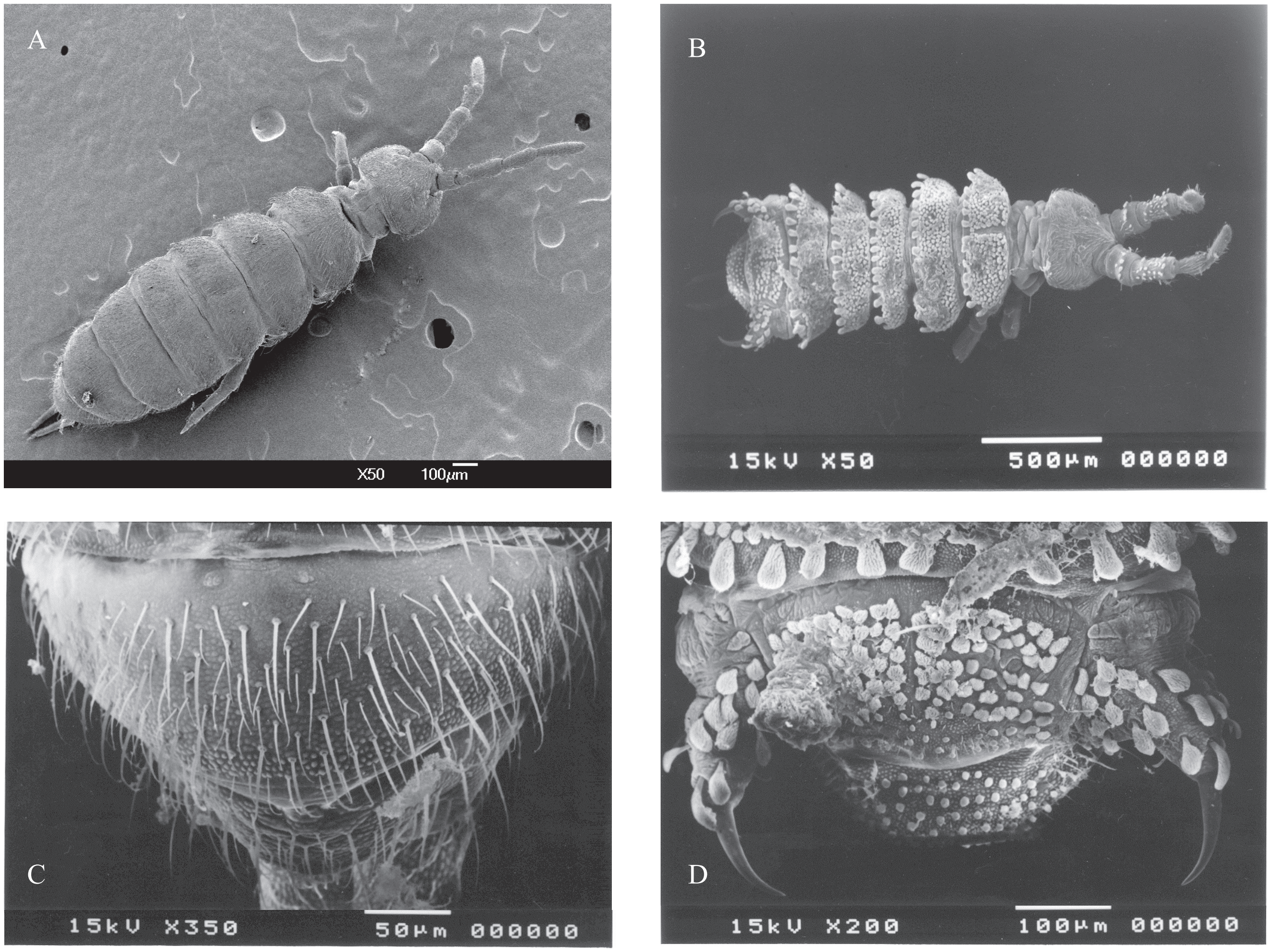

Figure 1. Female and male of *Guthriella muskegis*. Dorsal view of female (A), dorsal view of male (B), last abdominal segments in female (C), and last abdominal segments in male (D).

Conclusions

1. The habitat can be a very important factor determining the presence of several sexual characters.
2. Fresh water and marine littoral springtails present more important morphological modifications to facilitate sperm transfer from the male to the female.
3. In terrestrial species, the most extraordinary case is that of *G. muskegis* which ornamentation is similar to the patterns found in other groups of Arthropoda.

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