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

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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 behavior 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.

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 determine 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.

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<tr>
<th>Taxa</th>
<th>Characteristics</th>
<th>References</th>
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| Neanuridae  
Procura pomorskii Smolis & Deharveng | Fore legs structure | Smolis & Deharveng (2006) |
| Hypogastruridae  
Hypogastrura assimilis (Krasbauer)  
Schoettella ununguiculata (Tullberg) | Body length  
Cuticular lips | Folker-Hansen et al. (1996)  
Porco et al. (2004) |
| Isotomidae  
Agraria spp. | Male antenna elongated with more developed 2<sup>nd</sup> and 3<sup>rd</sup> segments. | Strenzke (1958) |
| Anurophorus serratus Deharveng | Curved sensilla occur on the ventromedial side of the three last antennal segments of males. | Deharveng (1976) |
| Archisotoma bessleri (Pack.) | Male antenna elongated with more developed 2<sup>nd</sup> and 3<sup>rd</sup> segments. Abdominal shortened macrosetae forming a “brush”. | Denis (1928) |
| Axelsonia tubifera Strenzke | Male antenna elongated and broadened with more developed 2<sup>nd</sup> and 3<sup>rd</sup> segments. | Fjellberg (1986) |
| Dimorphophoma porcella Ellis | Male antenna elongated and broadened with more developed 2<sup>nd</sup> and 3<sup>rd</sup> segments. Male abdominal setae longer and thicker than in females. | Ellis (1976) |
| Folsomia fimetaria (L.)  
Jestella siva Najf | Body length  
Male antenna elongated and broadened with more developed 2<sup>nd</sup> and 3<sup>rd</sup> segments. Male abdominal setae longer and thicker than in females. | Folker-Hansen et al. (1996)  
Najf (1977) |
| Najia vicaria (Arlé) | Male antenna elongated, Ant. IV horn-like curved, lateral cephalic macrosetae, Abd. IV with crowbar-like structures. 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. | Arlé & Mendoza (1986)  
Goto (1972) |
| Rhodanella minos (Denis) | Male antenna elongated, Ant. IV horn-like curved, lateral cephalic macrosetae, Abd. IV with crowbar-like structures. 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. | Arlé & Mendoza (1986)  
Goto (1972) |
| Vertagopus pseudocinererus Fjellberg | Male antenna elongated and with slightly serrated setae. Shortened macrosetae forming a “brush”. | Goloshchepova et al. (2006) |
| Actaelidae  
| Entomobryidae  
Entomobrya atrocinct Schött  
Seira manis Zeppelini & Bellini  
S. raptora Zeppelini & Bellini  
Orechessella cincta (L.)  
Willowsia jacobsoni (Börner) | Body color pattern  
Modifications in the fore legs  
Modifications in the fore legs  
Body color pattern  
Body color pattern and body length | Ramel et al. (2008)  
Zeppelini & Bellini (2006)  
Zeppelini & Bellini (2006)  
Mari-Mutt (1981)  
Mari-Mutt (1981) |
| Paronellidae  
Cyphoderus albinus Nicolet | Females with bidentate macro | Yoshii (1990) |
| Coenaleidae  
Coenales caribaeus Bellinger | Fourth antennal segment in male with 2 subapical organs in separate minute pegs and 8<sup>th</sup> thin, uniform blunt setae in apical half. | Palacios-Vargas et al. (2000) |
| Sminthurididae  
Denisiella diomodesi Palacios-Vargas  
Deboutvillea marina Murphy  
Jeannenotia stachy jeannenot  
Smithuridia sphaeroides (Murphy)  
Yosides himachal (Yossi) | Antenna of males modified as clapping organ  
Second and third antennal segment highly modified as clapping organ in males.  
Males second antennal segment modified in a clapping organ.  
Males second antennal segment modified in a clapping organ.  
Males second antennal segment modified in a clapping organ.  
Males second antennal segment modified in a clapping organ. | Palacios-Vargas (2007)  
Massoud & Betsch (1972)  
Massoud & Betsch (1972)  
| Arrhopaliidae  
Arrhopalites jay Christiansen & Bellinger  
Arrhopalites lacuna Christiansen & Bellinger | Presence of a tunica and an unguicular filament on the posterior foot of female  
Number of antennal subsegments and the fact that the male seta e3 differs strikingly from the female | Christiansen & Bellinger (1996)  
Christiansen & Bellinger (1996) |
| Bourletellidae  
Bovicornia greensiadei Massoud & Delamare Deboutville  
Deuteromincinus spp. | Males second antennal segment modified as clapping organ  
Body and head length, longer antennae in males. Female with subanal appendages | Eberhard (2004)  
Palacios-Vargas & González (1995) |
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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References


