

# Sexually dimorphic claws predict courtship and mating sequence in the intertidal oribatid mite *Fortuynia atlantica* (Acari, Oribatida)

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## Short note

### ABSTRACT

*Fortuynia atlantica*, is a sexually dimorphic oribatid mite and although observations are lacking, direct sperm transfer is assumed. We found an additional sexual dimorphism in claw morphology, with females showing relatively smaller and more curved claws, which may point to a possible direct contact during reproduction. Males possess lateral notogastral projections and these could be used as ‘handles’ by the females in the course of some kind of mating. The claws of the females are large enough to embrace the male’s lateral projections and the females’ first legs are long enough to attach to the males’ body from behind without hampering its movement with the rest of the legs. Based on these indications, we propose a hypothetical mating scenario where the male attracts females via pheromones, the female approaches from behind and clasps with the claws of the leg I the ‘handles’ of the male. This stimulates the male to deposit a stalkless spermatophore and in a final step the male leads the still attached female over the spermatophore to absorb it. Observation of living specimens is ultimately necessary to verify the existence of the proposed or any other mating behaviour.

**Keywords** spermatophore; pheromone; intertidal; geometric morphometrics

## Introduction


In most species of oribatid mites, dissociated sperm transfer via stalked spermatophores is the common mode of reproduction, and the gender of adults cannot be determined without examining the genitalia which are usually hidden in the genital vestibule (Behan-Pelletier 2015). Only one percent of brachypyline Oribatida are known to show a distinct sexual dimorphism and although proximal or associative mating is assumed for most species of this minority, such a behaviour has been observed only in a handful of them (Behan-Pelletier 2015). Grandjean (1956, 1966b) observed a courtship dance, which he called ‘promenade à deux’, in *Erogalumna zeucta* Grandjean, 1966 and *Centroribates mucronatus* (G. & R. Canestrini, 1882), where the male holds on to the gastronomic region of the female with its first pair of legs and then they walk in a chain. Similar observations were made in the non-brachypyline genus *Collohmanna*, where males and females also walk in a chain, but after this courtship dance, the male secretes a nuptial gift onto specialized structures of the genu-tibia of its fourth pair of legs and then offers it to the female (Schuster 1962; Norton and Sidorchuk 2014). Physical contact in combination with a transfer of a nuptial gift was also reported in an undescribed *Mochloribatula* species from Brazil (Oliveira *et al.* 2007). However, in all these cases direct sperm transfer following courtship was only assumed to occur. The only observation of such a transfer in an oribatid mites was in a non-dimorphic species of *Pilogalumna* that exhibits no courtship behaviour;

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instead, the male forcefully attaches a stalkless spermatophore close to the genital plate of the female (Estrada-Venegas *et al.* 1996).

Distinct sexual dimorphism is thought to have evolved in oribatid mites as a response to intermittent dryness, aquatic habitats and spatially discrete habitats (Norton and Alberti 1997, Behan-Pelletier 2015). The littoral environment represents an intermittently dry habitat and consequently the number of sexually dimorphic species is relatively high there (see Behan-Pelletier 2015 and Pfingstl 2015; for details). *Fortuynia atlantica* Krisper & Schuster, 2008, an intertidal oribatid mite from Bermuda and the Caribbean, represents one of the most striking cases of sexual dimorphism. The males show enlarged porose areas at the bases of most notogastral setae, two of these setae (*la*, *lm*) are very long with leaf shaped tips, and there is a pair of strongly protruding and overhanging lateral projections on a level with setae *h*<sub>3</sub>, in the posterior half of the gastronomic area (Krisper and Schuster 2008). This strong dimorphism was suggested to be involved in some kind of mating behaviour, allowing rapid sperm transfer during low tide (Pfingstl 2013). No such behaviour has been observed, but *F. atlantica* successfully reproduced in the laboratory despite the documented absence of stalked spermatophores that would have indicated typical indirect sperm transfer (Pfingstl 2013).

Herein, we report yet another dimorphic trait in this species—differences in claw morphology—and test with morphometric means if the form of the female claw is appropriate for holding the notogastral protrusions of the male. We then predict the eventual discovery of courtship sequence that encompasses all dimorphic features of males and females.

## Material and methods

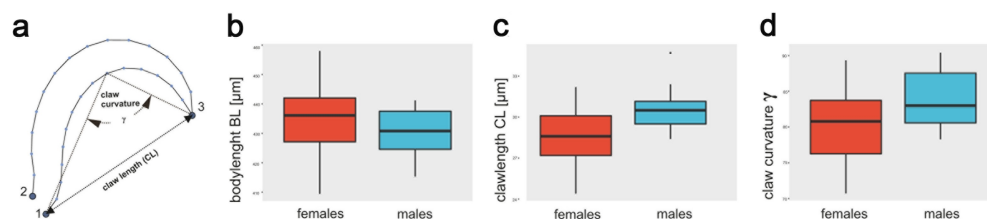
All investigated material is stored in the personal collection of one of the authors (TP; it comprises 141 adult specimens of 8 different littoral mite species). For the target species *Fortuynia atlantica*, we compared the shape of the first leg claw of 11 males and 15 females. Geometric morphometric data analyzed in this study is from Pfingstl *et al.* (2020) and Kerschbaumer and Pfingstl (2021) and is stored at Dryad; methods are given in the respective publication. Data analysis was done in Rstudio vers. 1.3.1093 (R Core Team 2020).

## Results and discussion

### Differences in claw shape and their possible role

Among eight investigated littoral species (given in supplementary Figure S1) only *F. atlantica* is known to show distinct sexually dimorphic characters (apart from claws), and it was also the only species showing a considerable difference between male and female claws of the first leg. Despite having larger bodies, claws of the first leg of *F. atlantica* females are significantly smaller and more curved than those of males (Fig. 1). *Fortuynia atlantica* females still show the typical ‘rock-shape’ claws (Pfingstl *et al.* 2020), but nonetheless differ from females of other species, living in the same habitat (see supplementary Figure S1). The claws of the other legs are also smaller in females but their dimorphic character is not as distinct as in leg I.

This dimorphism indicates that female claws might be somehow involved in some kind of physical contact during mating. In *Collohmanna gigantea* Sellnick, 1922 and *E. zeucta*, where the male holds on to the flanks of the female for a ‘chain walk’, paraxial tarsal setae of the attaching leg are shaped like long ribbon noodles or long feathers, which are thought to facilitate maintaining physical contact with the female’s smooth notogastral cuticle (Grandjean 1966a, b). Interestingly, *Collohmanna johnstoni* Norton & Sidorchuk, 2014 shows the same ‘chain walk’ without having modified setae on male tarsus I. However, if no such additional adhesive structures exist, strong attachment could be achieved by hooking the claws to a morphological structure of the partner. There are no known examples of claws used for maintaining contact during a courtship or mating in oribatid mites yet, but there are at least two



**Figure 1** (a) schematic drawing with landmarks and obtained measurements on first leg claw. (b-d) box-plots showing the differences in body length, claw length and claw curvature between males and females of *F. atlantica*. The line in the middle of each box represents the median for each group examined.

reports of sexual claw dimorphism (Grandjean 1955, Fernandez 1984). Males of the marine associated *Podacarus auberti* Grandjean, 1955 possess distinctly larger claws than females and males of the aquatic *Hydrozetes ringueleti* Fernandez, 1984 show a large ventral tooth on the claw of leg III. The latter species additionally shows a modified femur II shape and a large spine on femur IV (Fernandez 1984), which suggests that the legs might be used to clasp the female. However, if claws can hook on to a morphological structure like a cuticular projection, the contact between partners will be steadier. Cuticular notogastral protuberances are shown by males of several dimorphic species but in nearly all cases they are unpaired and equipped with large porose areas (Behan-Pelletier 2015), consequently they might primarily serve to attract females via some kind of secretion rather than being an anchor for claws. Krisper and Schuster (2008) also reported porose areas on the lateral projections of male *F. atlantica*, but we were not able to confirm their presence and thus an excretory role for these ‘handles’ is questionable. The lyrifissure *ih*, on the other hand, is located directly on the projections and thus gives sensory feedback if anything touches these lateral structures. Therefore, we think that the lateral projections of the males are used as anchors for the claws of the females.

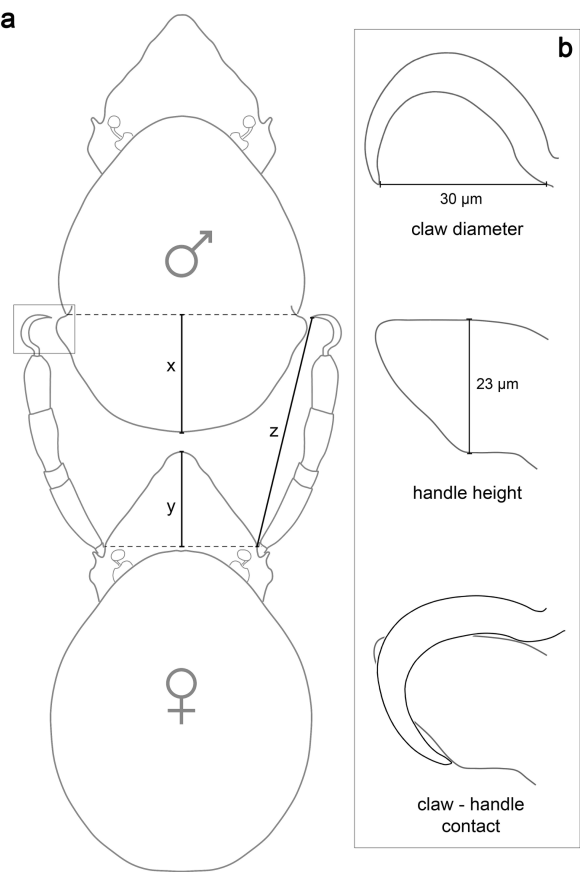
### Morphological conditions for a claw–handle contact

A physical contact between female claws I and notogastral handles is only possible if the following conditions are met: (1) the legs I of the females should be long enough to reach both ‘handles’ simultaneously (they need to bridge the distances from the ‘handles’ to the posterior end of the male notogaster and the distance from the female rostrum to the insertions of leg I) (Fig. 2a)  $\rightarrow z > x + y$ ; (2) the claw diameter of female leg I should be larger than the diameter or size of the ‘handle’ (Fig. 2b). Of course, small but sharp claws could still somehow cling to the projections and shorter legs may still be able to reach both handles when the female mounts the notogaster of the male, but we tested optimal conditions, i.e. claws can clasp most effectively and the female can still walk unhindered with the rest of their legs when the first pair is still attached.

Measurements of the distances to bridge were made in nine specimens of each gender and resulted in the values given in Table 1. The mean distance to bridge is 203  $\mu\text{m}$  and the mean leg length of the females is 252  $\mu\text{m}$  and thus females can easily reach the ‘handles’ simultaneously. Measurements of the claws of 15 females resulted in a mean claw diameter of 28.5  $\mu\text{m}$  and in a mean ‘handle’ height of 23  $\mu\text{m}$  in nine investigated males and thus the second condition is also met.

### Hypothetical mode of sperm transfer

The unique dimorphism in claw and the given physical conditions do not necessarily confirm that *F. atlantica* females indeed clasp the ‘handles’ of the males to perform some kind of ‘chain walk’. But based on these morphological features and the absence of stalked spermatophores,

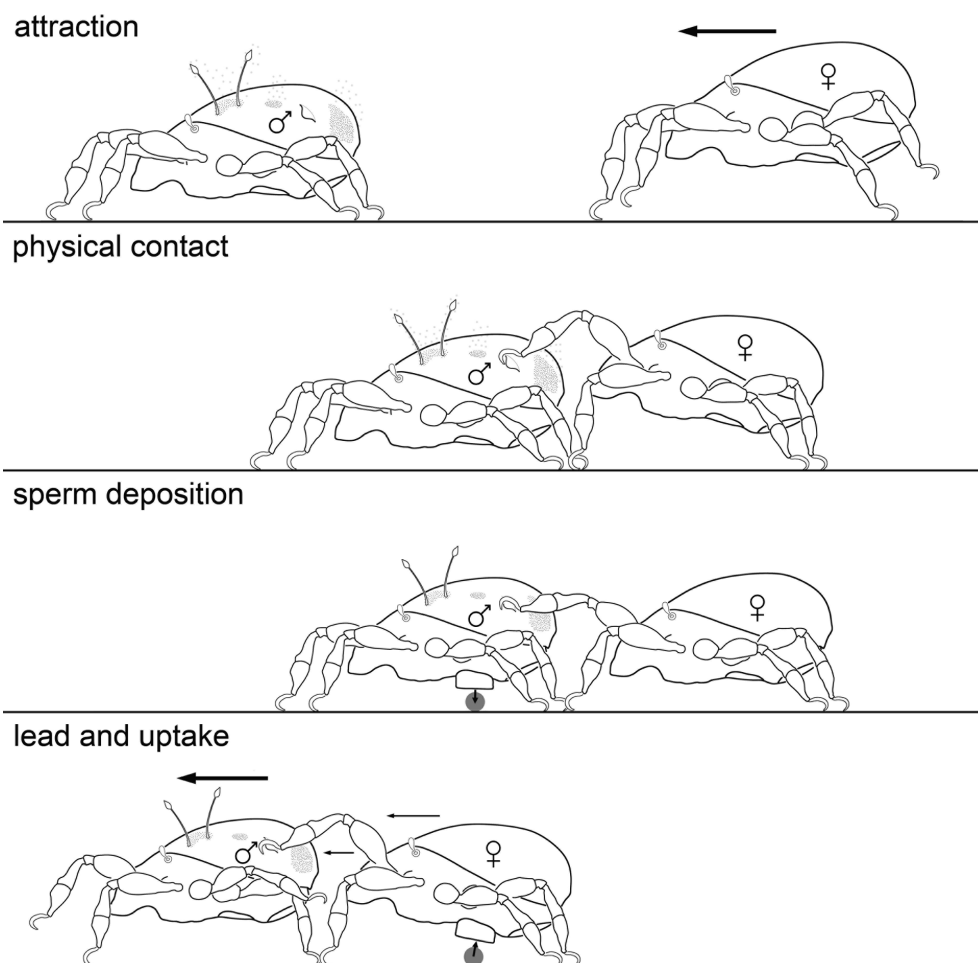


**Figure 2** Graphical depiction (dorsal view) of measured morphological features. (a) distance to bridge, when clasping both handles simultaneously; x - distance from line of 'handles' to the posterior end of the male, y - distance from rostrum to insertion first leg, z - length of leg I. If  $x+y > z$  no physical contact with both legs possible, if  $x+y < z$  physical contact and 'lead behaviour' possible. (b) claw diameter and handle height allowing steady grip.

**Table 1** Measured distances (depicted in Fig. 2) of nine *F. atlantica* males and females in μm. x - distance from line of 'handles' to the posterior end of the male, y - distance from rostrum to insertion first leg, z - length of leg I. min – minimum, max – maximum.

	Males	Females	
	x	y	z
1	117	82	262
2	111	86	246
3	92	102	267
4	99	108	246
5	105	102	243
6	99	92	252
7	108	92	237
8	132	92	250
9	119	92	262
min	92	82	237
max	132	108	267
mean	109	94	252

we hypothesize that a courtship and/or mating behaviour, enabling quick sperm transfer when mites are active during low tide, is shown in this species. The sperm transfer could happen as follows: In a first step ('attraction'), the male needs to attract a willing female, and as sexually



**Figure 3** Hypothetical process of courtship and sperm transfer in *Fortuynia atlantica*. 1) ‘attraction’: male attracts female with pheromones; (2) ‘physical contact’: female attaches to the lateral notogastral projections of male with claws of first leg; (3) ‘sperm deposition’: male deposits an unstalked spermatophore; (4) ‘lead and uptake’: male leads female over spermatophore which is then absorbed by female with its genital opening.

dimorphic porose organs are suggested to be secretory organs possibly producing pheromones (Norton and Alberti 1997), the male may secrete pheromones via the enlarged notogastral porose areas at the base of setae *la* and *lm*. These long and leaf shaped setae may facilitate pheromone dispersion allowing a transmission over larger distances in air. The female detects the attractant and approaches the male from behind (Fig. 3). The next step is ‘physical contact’; guided by pheromones, the female raises the first pair of legs and clasps the ‘love handles’ (lateral notogastral projections) of the male with the claws. When the female is properly hooked to the male, the next phase begins with the male depositing a stalkless spermatophore (Fig. 3, ‘sperm deposition’). In a final step (‘lead and uptake’), the male pulls the female over the spermatophore and then the female inserts it into the genital opening.

## Conclusions

Direct sperm transfer by a courtship or mating behaviour has never been observed in *F. atlantica* but sexual dimorphism suggests it exists, and the newly-discovered difference in claw morphology points to a possible scenario. As with other sexually dimorphic oribatid mites,

proof will require direct observations of living mites. These are time consuming and difficult to perform, though they are much more needed in acarological research. This short note could be a motivation for acarologists to do so.

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