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Mating behavior of *Dactylochelifer latreillii latreillii* (Pseudoscorpiones: Cheliferidae): A quantitative study

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Abstract. The arachnid order Pseudoscorpiones is characterized by a huge number of different mating strategies. Cheliferidae, for instance, have developed complex mating dances, including the use of the curious ram's horn organs of males. The present study provides a detailed description of the mating behavior of *Dactylochelifer latreillii latreillii* (Leach, 1817), including first quantitative data for each behavioral unit, based on the analysis of laboratory video captures of individual mating ceremonies. Previous studies on mating in cheliferids have been purely qualitative, including a description of mating in a distinct subspecies of *D. latreillii*, *D. l. septentrionalis* Beier, 1932. Qualitatively, our data on *Dactylochelifer l. latreillii* is roughly consistent with these older observations except for some differences in the vibrating behavior of males.

Keywords: Mating dance, courtship, ram's horn organs, spermatophore

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Sperm transfer in animals is either realized as direct transfer, also known as copulation, where males place the sperm in receptive structures of the female, or indirect transfer, where the sperm mass is deposited in the environment. In the Arthropoda, indirect sperm transfer via spermatophores is widely distributed. Many soil-dwelling arthropods, including Collembola, some Myriapoda and Arachnida rely mainly on this mode of reproduction. Within arachnids, indirect sperm transfer, including the production of freestanding spermatophores, occurs in the Scorpiones, Pseudoscorpiones, Amblypygi, Uropygi, Schizomida and in some Acari (Proctor 1998).

Particularly in the Pseudoscorpiones, major variability occurs with respect to the mating behavior prior to spermatophore deposition as well as regarding spermatophore morphology. Males of some families (e.g., Chthoniidae and Neobisiidae) deposit their spermatophores independently of the presence of females (Weygoldt 1969). Based on our current understanding of the pseudoscorpion tree of life (Harvey 1992; Murienne et al. 2008; Benavides et al. 2019), this strategy may be considered plesiotypic in the order and is observed in early-derivative taxa. More derived taxa need the presence of a female for spermatophore deposition and have developed distinct courtship behaviors. The performance of a mating dance has been documented for species of the superfamily Cheliferoidea (Weygoldt 1969, 1970; Harvey 1992). Spermatophore deposition in the presence of a female, as happens in species with a mating dance, potentially reduces the risk of spermatophore desiccation, thus offering the opportunity to colonize drier habitats. Other arguments in favor of mating in presence of a partner are the certainty of paternity and decreased sperm wastage, as summarized by Stam & Hoogendoorn (1999).

In contrast to other cheliferoid families, male Cheliferidae use specific structures called ram's horn organs (RHOs) during the mating process. RHOs are present in most species of cheliferids and are only missing in a few genera, where they are considered to be secondarily reduced (Harvey 1992). These organs are paired evaginations of the posterior ventral diverticulum. Usually hidden under the posterior genital operculum, they are extruded during courtship (Legg 1974b). The function of the RHOs is still enigmatic; however, some authors speculate that they function as carriers of a chemical cue (Vachon 1938; Weygoldt 1966, 1969).

In the past decades, publications on mating behavior of pseudoscorpions were almost exclusively dedicated to species of the cheliferoid family Chernetidae (Zeh & Zeh 1992, 1997; Andrade & Gnaspini 2003; Palen-Pietri et al. 2019), whereas mating in Cheliferidae has not been studied recently. Quantitative studies on mating, as already available for some other arachnid groups (e.g., Girard et al. 2011; Fowler-Finn et al. 2019), are scarce for pseudoscorpions (Palen-Pietri et al. 2019) and particularly missing in Cheliferidae. Although some authors try to give a comparative overview on mating phase duration of certain pseudoscorpion groups (Weygoldt 1966, 1969, 1970; Andrade & Gnaspini 2003), the majority of data is restricted to scattered time indications for behavioral steps without any remarks on sample size and data range (Kew 1912; Vachon 1938; Weygoldt 1966, 1969, 1970; Boissin 1973). In order to improve comparability of pseudoscorpion mating behavior, especially concerning closely related taxa, standardized and detailed quantitative studies are urgently needed.

Initial descriptions of cheliferid mating include observations on *Dactylochelifer latreillii* (Leach, 1817) by Kew (1912) and Weygoldt (1966). In both publications, the authors refer to animals from coastline habitats. We therefore assume that the individuals belonged to the subspecies *D. latreillii septentrionalis* Beier, 1932, which is restricted to coastal areas (van den Tooren 2005), rather than to the inland-dwelling and herein studied nominate subspecies, *D. latreillii latreillii* (Leach, 1817). A film showing the mating behavior of the cheliferid *Hysterochelifer meridianus* (L. Koch, 1873) was taken by Boissin (1967); however, we do not know whether this film still exists.

In the present study, the mating behavior of *Dactylochelifer latreillii latreillii* was qualitatively and quantitatively analyzed in detail. Particular behavioral sequences were identified, described, quantified with respect to duration and summarized in a flowchart ethogram. Data presented are supported by a

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Table 1.—Identification and description of the main behavioral units of the mating ceremony of *Dactylochelifer latreillii latreillii*.

Phase	Behavioral unit	Description
I: Initial contact	Grasping one palp	The male grasps one pedipalp of the female with both of his pedipalps. Usually one of his palps holds the chela and the other a proximal segment of the females pedipalp; the female shows resistance and eventually grasps the male with her free pedipalp.
II: Mating dance	Holding both palpal chelae	The male grasps the free pedipalp of the female and now holds both palpal chelae with his own pedipalps and starts the extrusion of his RHOs, locomoting forwards and back; the female is still reluctant, but participates passively at the end of this behavioral unit.
II: Mating dance	Holding one palpal chela	The male releases one palp of the female, changes between holding either the left or the right palp after a while, moves forward with RHOs extruded, occasionally pushing back the female with his free pedipalp, afterwards moving backwards; the female acts passively and starts following the movement of the male, occasionally showing resistance again.
II: Mating dance	Both palps released	The male releases both palps of the female, starting to push back the female with his pedipalps after extruding RHOs; the female increasingly approaches the male while his RHOs are extruded.
III: Sperm transfer	Spermatophore deposition	The male moves forward, pushing back the female once again, presses his genital operculum to the ground accompanied by fast shaking movements, lifts up his body upwards and back, releasing the stalk of the spermatophore with a drop of fluid, after remaining in this position for a few seconds, he moves backwards, releasing the sperm package on top of the spermatophore, RHOs are continuously extruded until he retreats; the female stays closely in front of the male.
III: Sperm transfer	Waiting behind spermatophore	The male retreats and then waits behind the spermatophore with RHOs continuously extruded, until the sperm mass is transferred; the female moves forwards over the spermatophore.
III: Sperm transfer	Grasping both palpal femora	The male grasps and holds the femora of both palps of the female, the drop of fluid on the stalk of the spermatophore gets transferred to the genital operculum of the female by contact. The male straightens his modified first pair of legs and grasps the genital operculum of the female, pulling it first in his direction and pushing it afterwards back on top of the spermatophore. The male continues to hold the females palps and genital operculum and starts pushing forward and back, until the female shows resistance which leads to the separation of the mates.

supplementary video (available online at https://doi.org/10.1636/JoA-S-20-057.s1) of specific behavioral steps.

METHODS

Individuals of *Dactylochelifer latreillii latreillii* were collected in Burgenland, Austria (47.7691300°N, 16.7670890°E) between 08–14 July 2019 by sifting leaf litter; voucher specimens are deposited at the Institute of Biology, University of Graz (Voucher #: Dact01-39). Single individuals were kept in small plastic containers (40 mm diameter x 40 mm height) with a moistened plaster layer (10 mm) at the bottom. Species confirmation and sex determination was carried out using an Olympus SZX12 (Tokyo, Japan) Stereomicroscope. Specimens were fed with adult, flightless *Drosophila melanogaster* Meigen, 1830 once a week.

Mating was induced by bringing together random male-female pairs on a glass plate covered with a small, clear plastic dish (40 mm diameter x 4 mm height) and subsequent mating dances were observed with a Wild M8 (Heerbrugg, Germany) Stereomicroscope under daylight conditions (between 14:00–19:00) at room temperature of 23 °C. Mating was documented via video recording with a JVC TK-C1381 camera (Yokohama, Japan) attached to the stereomicroscope.

Couples were observed for at least 15 minutes or until mating was finished. Of 46 couples, brought together for observations, 29 had contact and in 9 cases, a spermatophore was produced. Video files of successful mating were analyzed with the software EthoWatcher® (ver. 1.0, online at https://ethowatcher.paginas.ufsc.br/; Crispim Junior et al. 2012). Descriptive statistical analysis was done in Excel (Microsoft Office Professional Plus 2019); box-plots and statistical testing (One-way ANOVA) were performed using PAST (ver. 3.19, Hammer et al. 2001).

The term "behavioral unit" was used, similarly to other recent publications (Stanley et al. 2016; Palen-Pietri et al. 2019) on arachnid mating behavior. Major behavioral units were named according to existing terms from Weygoldt (1969); the terminology of genital structures follows Legg (1974a, b).

For scanning electron microscopy, specimens preserved in pure ethanol were air-dried and subsequently mounted on aluminum stubs using adhesive carbon discs prior to sputter coating with gold (AGAR sputter coater, Gröpl, Tulln, Austria). Scanning electron microscopic (SEM) images were taken with a Philips XL30 ESEM (Philips/FEI, Vienna, Austria) at high vacuum mode and 20 kV.

RESULTS

The mating behavior of *Dactylochelifer latreillii latreillii* can be divided into three main phases: initial contact (phase I), mating dance (phase II) and sperm transfer (phase III). The behavioral units of the mating ceremony are listed and described in Table 1, and time measurements are given in Table 2. Transitions from one behavioral unit to the next are displayed in a flowchart (Fig. 1).

Phase I started with the male grasping one pedipalp of the female. The female usually responded with resistance which

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Table 2.—Time measurements in successful mating events ($n = 9$) including mean duration, standard deviation (SD), coefficient of variation (CV) and data range (Min., Max.).

Phase	Behavioral unit	Mean (sec)	SD (sec)	CV (%)	Min. (sec)	Max. (sec)
Phase I (total)	Grasping one palp	7	5	68	3	19
Phase II	Holding both palpal chelae	460	316	69	36	1025
Phase II	Holding one palpal chela	664	374	56	160	1359
Phase II	Both palps released	97	70	71	23	222
Phase II (total)		1220	534	44	484	1917
Phase III	Spermatophore deposition	24	5	20	18	31
Phase III	Waiting behind spermatophore	9	3	38	5	14
Phase III	Grasping both palpal femora	137	38	28	92	195
Phase III (total)		170	43	25	116	232
Total mating		1397	567	41	631	2026

varied in intensity between individuals. Phase I, with a mean of only 7 seconds, was the shortest of the three phases.

Phase II (mating dance), represents the main courtship behavior and is the longest phase, with a duration of about 20 min. During this phase, RHOs of the male were repeatedly extruded and presented to the courted female. A single extrusion of the RHOs lasted for a mean of 5.8 ± 2.0 seconds (Fig. 3), and the mean extrusion-frequency per minute was 6.6 ± 1.3 RHOs/min. In successful courtships, defined as those in which the female accepted the spermatophore, females showed a transition from resistance towards passive participation. In many cases, especially when not successful, males returned to the preceding behavioral unit of the mating dance (Fig. 1). The beginning of the mating dance was marked by male grasping of the other pedipalp of the female and holding her on both of her chelae. Next, the male released one pedipalp of the female. In most cases, the male changed from holding one pedipalp of the female to the other pedipalp after 2.64 ± 1.57 minutes on average, with pedipalp-changes happening up to 10 times (mean = 5 ± 2.7). After having displayed the RHOs, the male started to push back the female with the free pedipalp, while the female became more active and approached the male during the next extrusion of the RHOs. Finally, the male released both pedipalps of the female for a short period and continued with pushing back the female and extruding the RHOs.

The beginning of sperm transfer (phase III) is indicated by deposition of the spermatophore. Before releasing the sperm package, the male stopped in his movement, accompanied by an alignment of legs III and IV to the opisthosoma in posterior direction, well visible in dorsal view. During this behavioral unit, RHOs were continuously left extruded for 27.7 ± 4.5 seconds mean (Fig. 3). Then the male stepped backwards and the sperm package appeared. The male waited behind the spermatophore with RHOs continuously left extruded for 46.6 ± 7.4 seconds mean (Fig. 3). Means of RHOs extrusion duration during mating dance, spermatophore deposition and waiting behind spermatophore are significantly different from each other (One-way ANOVA, $F = 99.06$, $P < 0.001$). Subsequently, the female moved forward over the spermatophore until the drop of fluid on the stalk of the spermatophore contacted her genital operculum. Meanwhile the male grasped the female at both palpal femora, straightened his modified first pair of legs and attached both legs to the genital plate of the female with the tarsal claws (Fig. 2). Then, he pulled her towards him, placing her genital operculum with a single pushing movement over the tip of the spermatophore, where the sperm package is located. As a consequence, the inclined stalk of the spermatophore reached a more upright position. The claws of the modified tarsi of the male's leg I (Fig. 4) remained attached to the genital operculum of the female with the terminal part of the spermatophore fitting in between the distal exterior sinus of the tarsal segments. The male continued with pushing movements, whereas the female remained motionless for a few seconds, until she started to move again and finally separated from the male, terminating the mating event. Males often continued to perform pushing movements for a while even without a female. In one of the cases studied, sperm transfer was not successful because the female left, although the male had already deposited a spermatophore. In this case, the male remained in a waiting position for a while and went off too after some time.

On average, the whole ceremony (= all behavioral phases together) took about 23 minutes.

DISCUSSION

We here describe the mating behavior of *D. latreillii latreillii* for the first time. Our data add to observations on mating in *D. latreillii septentrionalis* (Kew 1912; Weygoldt 1966, 1969). The entire mating ceremony in *D. latreillii septentrionalis* takes 10–30 min and almost half a minute for the construction of the spermatophore (Weygoldt 1966) which is in good agreement with our measurements. In contrast to Weygoldt (1966, 1969), we did not observe vibrating body movements in male *D. latreillii latreillii*, except for slight jerky movements at the end of the RHO's display. Interestingly, differences in vibrating intensity are also reported from the congeneric cheliferid species *Hysterochelifer tuberculatus* (Lucas, 1849) and *H. meridianus* (Weygoldt 1970).

Some authors describe mating in Cheliferidae generally as a mating dance without body contact (e.g., Proctor 1998). While this is true for the few Cheliferini studied like the book scorpion *Chelifer cancroides* (Linnaeus, 1758) and *Hysterochelifer* Chamberlin, 1932 this is obviously not the case in species of *Dactylochelifer* Beier, 1932 (Vachon 1938; Weygoldt 1966; Boissin 1973). Males of *Dactylochelifer* hold the female firmly at the beginning of the mating dance, but always release her before spermatophore deposition. Later, after she has

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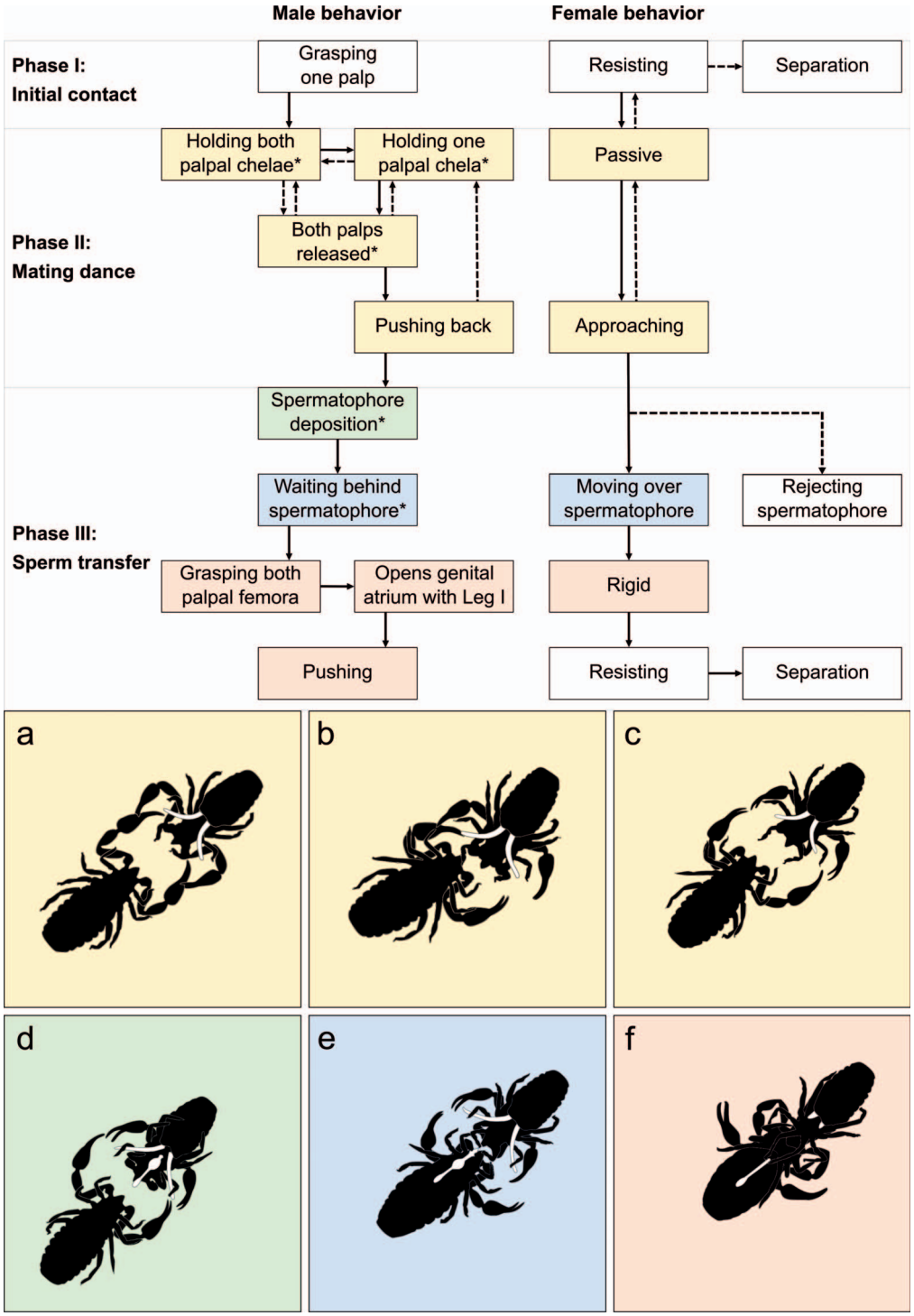


Figure 1.—Flowchart of the mating behavior of males and females of *Dactylochelifer latreillii latreillii*. Arrows with solid lines guide through the sequence of behavioral units resulting in successful mating; arrows with dashed lines show occasionally occurring alternative paths (returning to previous units or pretransfer termination of mating). Asterisks indicate units with RHOs extrusions. Pictograms (a-f) of a pair (male upper right, female lower left corner) from ventral view in black, RHOs and spermatophore in white. a: Holding both palpal chelae; b: Holding one palpal chela; c: Both palps released; d: Spermatophore deposition; e: Waiting behind spermatophore; f: Grasping both palpal femora. a-c: Centered to the pair; d-f: Centered to the fixed spermatophore. Background colors in the ethogram and in the pictograms are corresponding.

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Figure 2.—Mating of *Dactylochelifer latreillii* documented in the field. The female (on the left) with palpal femora grasped by the male (on the right) during sperm transfer phase (Photo: M. Schröer).

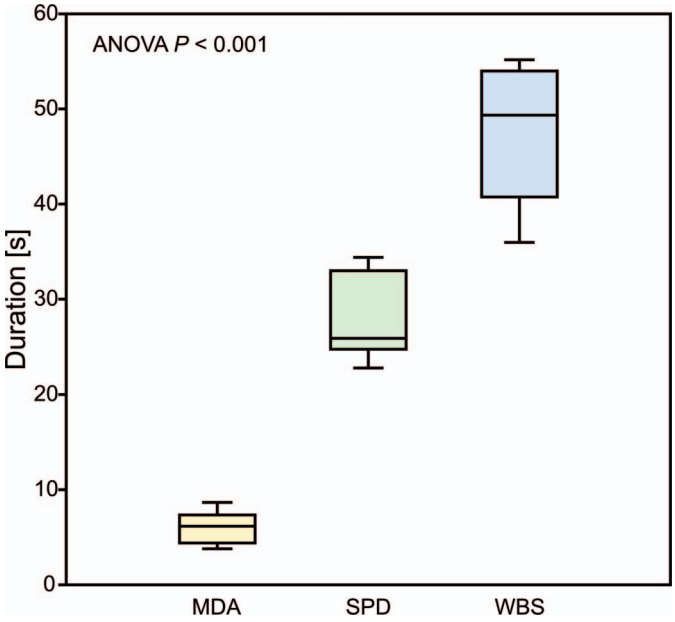


Figure 3.—Duration of single RHOs extrusions in the mating dance phase (MDA) and the final two extrusions starting in the subsequent behavioral units of spermatophore deposition (SPD) and waiting behind spermatophore (WBS) in successful mating events ($n = 9$). Note that RHOs were repeatedly extruded throughout the mating dance, but only once in the two following units.

approached the spermatophore on her own, the male grasps her again. This step of releasing the female appears to be critical for successful mating, since females are able to decide whether they accept or reject the spermatophore.

Variation in the duration of behavioral units, indicated by the coefficient of variation in Table 2, is relatively high in the initial contact and mating dance phase. By contrast, the variation in sperm transfer phase is low. High individual variation may be explained by courting pairs that often return to a preceding behavioral unit, thus repeating parts of the ceremonial. This was the case if the female did not show response to a certain step of the mating dance. Some couples finished the mating dance phase after a few minutes while in others, the dance took about half an hour before the spermatophore was produced. The duration for spermatophore deposition itself was very constant in this study and takes about half a minute in other Cheliferidae too (Vachon 1938; Weygoldt 1966). This may be due to the time that is needed for the fixation of the spermatophore in the required position.

The spermatophore morphology of the subspecies studied resembles the description and illustration by Weygoldt (1966, 1969) for the species. The drop of fluid on the stalk of the spermatophore which touches the female's genital operculum first, is supposed to initiate a swelling process of the sperm mass (Weygoldt 1966, 1970).

Males of the Dactylocheliferini are characterized by a huge diversity in tarsal morphology of leg I, which makes the tarsus an important character in species identification (e.g., Schawaller 1987). The distally concave and proximally thickened shape of the exterior tarsal margin in male *D. l. latreillii* (Figs. 4 a, d), together with this exterior tarsal margin facing towards the stalk of the spermatophore during transfer, is interpreted as a structure used to border and stabilize the spermatophore. If this is the case, this adds an explanation for the functional morphology of the characteristic shape of the tarsus in this species.

In our observations, as well as in former studies, the ram's horn organs are displayed frequently during the mating dance. Upon initial display of RHOs, females react with decreased resistance towards the mating attempts of the male and even start to approach the male during the extrusion of RHOs later. We observed that the extrusion of RHOs is not uniform in *D. l. latreillii*, but changes from frequent short extrusions during mating dance to single long extrusions twice during sperm transfer phase. Males terminate the use of these organs as soon as the female has walked over the spermatophore. The biological significance of the observed changes in the duration of RHOs extrusion is not clear yet, as the precise function of the ram's horn organs of male cheliferids is still enigmatic. Their histological structure was documented by Vachon (1938) and Boissin et al. (1970). There is no doubt that the development of these large structures with a complex folding mechanism comes with evolutionary costs and therefore RHOs must be of high benefit to the males. In *Chelifer* Geoffroy, 1762 and *Hysterochelifer*, the receptive females place themselves motionless in front of the male, that apparently "arrests" the female solely with his RHOs and not by forced body contact (Vachon 1938; Weygoldt 1966, 1969). A potential function of these organs as a carrier of pheromones during mating has already been proposed by Vachon (1938) and later by Weygoldt (1966, 1969). This assumption has still not been supported by sufficient scientific evidence but is subject of current research by the authors.

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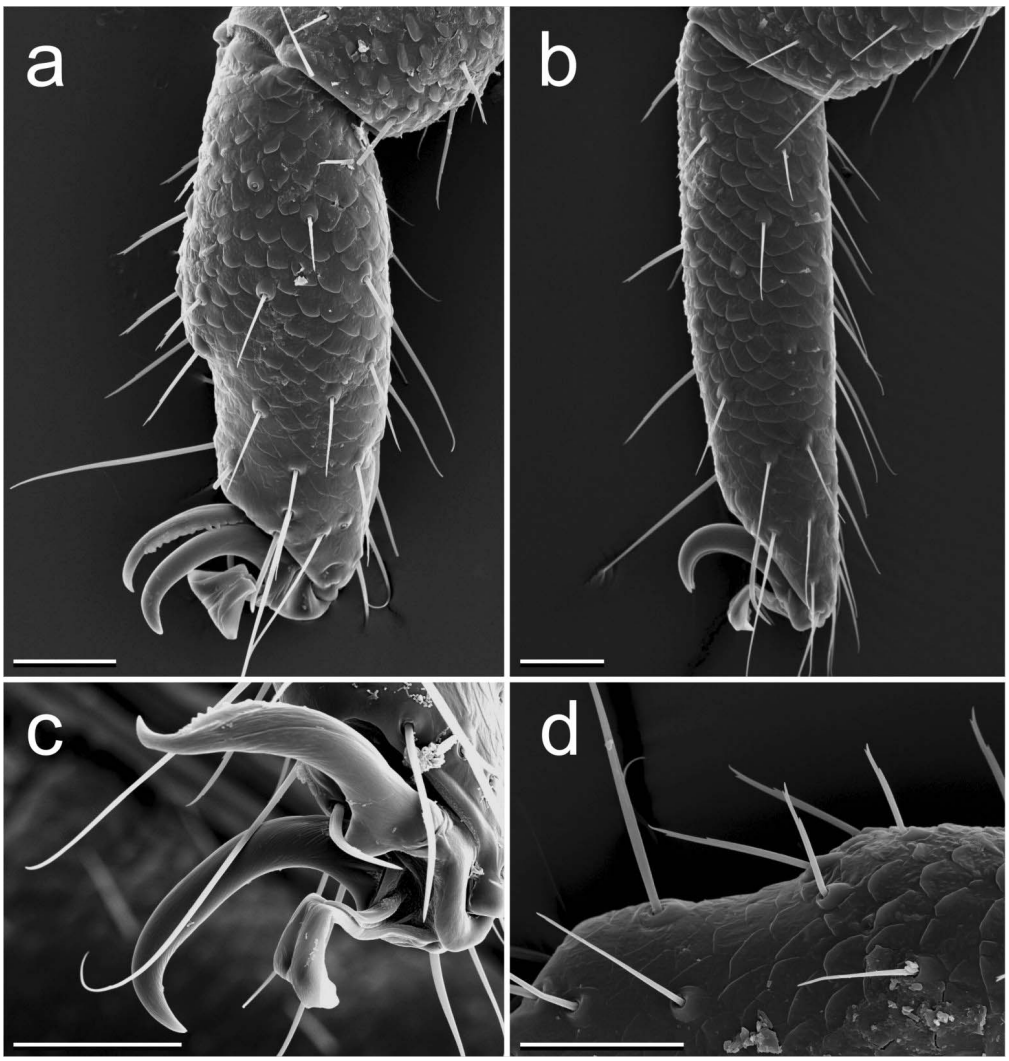


Figure 4.—SEM images of tarsus of Leg I of *D. latreillii latreillii*. a: Male; b: Female; c: Detail of the modified claws of the male; d: Detail of the modified tarsus of the male. Scale bars = 50 μm.

tium) of the University of Graz, Austria. We are very thankful to Edith Stabentheiner (Institute of Biology, Plant Physiology, University of Graz) for access to and help with the scanning electron microscope, to Moritz Schröer for the provided photo (Fig. 2) and to our colleagues David Fröhlich and Maximilian Wagner for assistance with figure layout. We finally thank two anonymous reviewers for their useful comments that substantially improved this work.

SUPPLEMENTAL MATERIALS

Supplementary Video S1.—Mating of *Dactylochelifer latreillii latreillii* recorded from ventral view under lab conditions. Note that phases were cut for this video; 45Mb mp4 file. Online at https://doi.org/10.1636/JoA-S-20-057.s1

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