



An enigmatic lineage of mites from Baltic amber shows a unique, possibly female-controlled, mating

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It is generally assumed that male control over mating and a lack of precopulatory female choice are prevalent in many animals and in astigmatan mites in particular. We show that several morphological structures of females of some astigmatan mites are indicative of precopulatory female choice: (1) copulatory tubes acting like intromittent organs; (2) specialized structures assisting male–female attachment and possibly allowing indirect mate selection in immature females; and (3) a unique, pad-like terminal opisthosomal organ used to cling to the male during copulation in *Glaesacarus rhombeus* (= *Acarus rhombeus* Koch et Berendt, 1854) belonging to an extinct family, Glaesacaridae, from the Upper Eocene Baltic amber. An exceptionally well-preserved copulating pair from amber provides insight into the function of this organ and reproductive behaviour in this mite. Female control over mating may reduce the timing of insemination, harassment by males, and damage caused by copulation. As a consequence, this can lessen male–male aggression, select against precopulatory guarding, and reduce the risk of predation. By contrast to extant taxa, males of *G. rhombeus* do not have any apparent specialized structures aiding clinging to the female during copulation, suggesting that this mating system is either an earlier step in the evolution of the female-dominated mating system and/or a remarkable example of imbalanced female counteradaptations against the male's reproductive interest that may occur during an arms race between the two sexes. We offer an approach that can falsify the hypothesis assuming precopulatory female choice and discuss an alternative hypothesis suggesting that these female structures evolved in response to the need to reduce damage associated with mating or precopulatory guarding. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 102, 661–668.

ADDITIONAL KEYWORDS: *Acarus rhombeus* – Astigmata – *Glaesacarus rhombeus* – precopulatory female choice.

INTRODUCTION

Male control over mating is prevalent in many animals in which sperm is transferred directly via intromission (Brown, Crespi & Choe, 1997; Walter & Proctor, 1999). In astigmatan mites, males can monopolize females through pre- and postcopulatory guarding, defending females from other males via fighting, and, possibly, through harassing females and thereby coercing them into mating. A recent review of mite biology noted that female choice has not been demonstrated in mites (Walter & Proctor, 1999). However, there is evidence from scattered mor-

phological studies indicating the possibility of active precopulatory mate choice by females: copulatory tubes acting like intromittent organs in adult females (Atyeo, 1992; Gaud & Atyeo, 1996) and specialized organs in immature females that assist male–female attachment (Popp, 1967; Fain, 1971; Witaliński, 1999). The particular focus of the present study is a unique, pad-like terminal organ in females of *Glaesacarus rhombeus* (= *Acarus rhombeus* Koch et Berendt, 1854), the oldest known fossil Astigmata, belonging to an enigmatic family of mites from the Upper Eocene Baltic amber (approximately 40 Mya). Until recently (Sidorchuk & Klimov, 2011), this mite species was known from a brief and schematic original description allowing for broad interpretations

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of its diagnostic characters, including the terminal pad-like organ. The detailed structure of this organ was not clear, nor was it clear in which sex this organ occurs. The use of a novel amber polishing technique allowed a description of the detailed morphology of this unusual structure, as well as an exceptionally well-preserved copulating pair found in amber, with the male still attached to the female terminal attachment organ, and his aedeagus still inserted in the female copulatory opening. On the basis of this evidence, we discuss a possible role of the terminal female organ in reproductive behaviour. We also review the functional morphology of analogous structures of recent species of astigmatan mites and their possible indication of precopulatory female choice.

MATERIAL AND METHODS

Acarus rhombeus represents an enigmatic lineage of mites historically placed in five different families of astigmatan and non-astigmatan mites. It cannot be assigned any known superfamily of Astigmata; however, it may be distantly related to modern Lemanniellidae and Heterocoptidae. A detailed taxonomic treatment of *A. rhombeus* based on material (including types) deposited in four museums is available elsewhere (Sidorchuk & Klimov, in press).

Amber with mite inclusions was trimmed and polished to obtain small (approximately 1 mm), six-sided pieces. Polished and trimmed samples were then stored in aqueous thymol solution (one or two drops of saturated solution per 1 mL of water). Images were made from dry samples to maximize the visibility of external structures. For the examination, water was removed by placing samples in a zip-locked bag with silica gel (desiccant) for several days. Light microscopy (Leica, $\times 100$ – 1000) with combined dissecting and reflected cold lighting was used. The sample was fixed using a polyethylene strip with a small hole to expose the inclusion. The strip was fixed with a double-sided sticky tape and immersion oil applied on the amber. After examination, the oil was removed with a soft cloth. Images were obtained using a Scope Tec DCM 500 camera at different focal points and then combined using FOCUS PRO, version 5.0 (HelconSoft).

RESULTS

STRUCTURES INDICATIVE OF FEMALE-CONTROLLED MATING

Opisthosomal pad-like protrusion in females of Glaesacarus

An unusual feature of the fossil, free-living mite (Larsson, 1978) *G. rhombeus*, is the female adaptation

to attach to the male during mating using a terminal opisthosomal pad-like protrusion (Fig. 1D, E). The structure has a whorl of tiny setae (Fig. 1D), which surrounds the area coming into immediate contact with the male body (Fig. 2C). The female's copulatory opening is situated ventroterminally on this protrusion (Fig. 1E). The mating is retroconjugate (Fig. 2A, B). When in a copulatory position, the female attachment organ fits the posterior portion of the male opisthosoma at a distance that allows the male aedeagus to be inserted into the female copulatory opening (Fig. 2B, C). The shape of the female attachment organ suggests that it uses surface adhesive forces to cling to the male rather than negative pressure. Probably, the geometry of the female–male joint and the presence of the surrounding setae facilitate the adhesion (Fig. 2C, D). At this point, the female attachment organ is analogous to posterior opisthosomal plates developed in males of some astigmatan mites [e.g. Heterocoptidae, *Paulacarellus*, *Histiogaster*, *Reckiacarus*, *Thyreophagus* (Acaridae)], which are used to attach to the female during copulation or precopulatory guarding.

Female copulatory tubes functioning as intromittent organs

Some astigmatan females have a flexible copulatory tube (terminal projection with a copulative opening at the end) acting as intromittent organs (Fig. 1A) that penetrate the genital opening of the male (Fig. 1B) to achieve insemination (Echimyopodidae, Crypturoptidae) (Gaud, Atyeo & Berla, 1973; van Bronswijk, De Cock & Oshima, 1973). In other females (Thoracosathesidae), the terminal projection is sclerotized and less flexible (Atyeo, 1992), resembling even more the true aedeagus. Female copulatory tubes are also found in some Rosensteiniidae, some Glycyphagidae, some Chaetodactylidae (e.g. *Sennertia vaga*), some Eustathiidae (e.g. *Echineustathia*, *Neochauliacia*), some Freyanidae (*Halleria*), Trouessartiidae (some *Trouessartia*), Pterolichidae (*Heliaspis*, *Cyrtonyxobius*, *Oxygnurus*, *Musophagobius*, *Phasidolichus*, and *Pelargolichus*), Avenzoariidae (*Bdellorhynchus*), and Caudiferidae (*Caudifera* and *Semicaudifera*) (Gaud & Mouchet, 1958; OConnor & Reisen, 1978; Peterson, Atyeo & Moss, 1980; Atyeo, 1992; Gaud & Atyeo, 1996; Mironov, 1999; Klimov & OConnor, 2008; OConnor, 2009). A very short copulatory tube was described in some Aeroglyphidae (*Glycycometus*) (Fain, 1976). Apparently, these tubes evolved independently in several astigmatan lineages, at least once in the superfamilies Glycyphagoidea and Analgoidea, and probably several times in the superfamily Pterolichoidea.

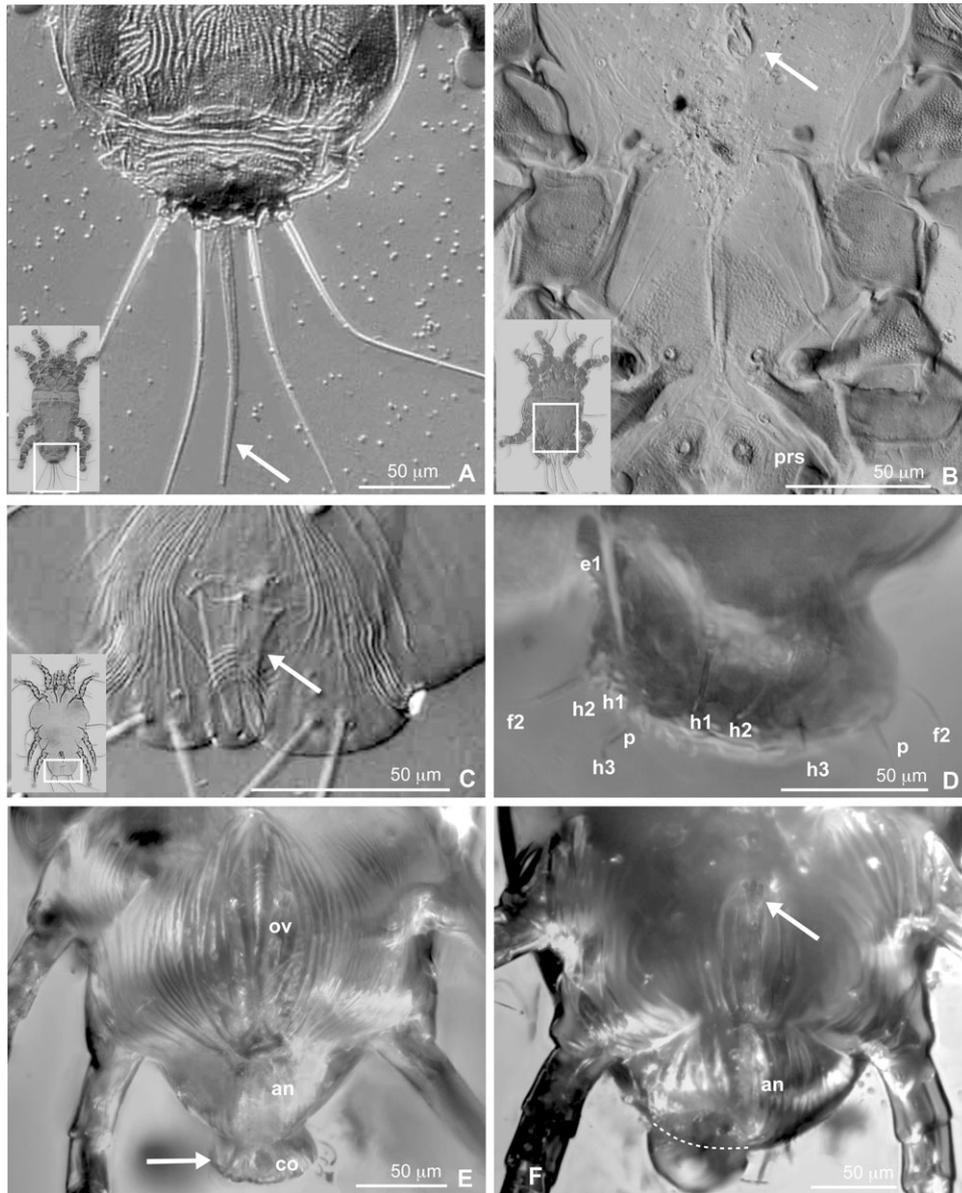


Figure 1. Structures indicative of female-controlled mating. A, female copulatory tube (arrow), *Crypturoptes dentatus* (Crypturoptidae). B, male aedeagus (arrow), *C. dentatus*. C, 'docking' papillae (arrow), tritonymph of *Proctophylloides* aff. *musicus* (Proctophylloidae). D, terminal opisthosomal pad-like projection of female, *Glaesacarus rhombeus*, dorso-lateral view, setal notations are indicated. E, F, female and male ventral hysterosoma of *G. rhombeus*, with the terminal projection and aedeagus indicated by arrows, respectively (dashed line marks the posterior outline, which is partially hidden by artefact in amber). an, anal opening; co, copulatory opening of female; ov, oviporus; prs, para-anal suckers.

'Docking' structures in immature females

In several taxa, immature females develop special structures complementary to the male attachment organs, facilitating precopulatory guarding and possibly increasing the level of female choice in this system. Examples are the smooth plates around striated cuticle allowing attachment of

the male suckers (Canestriniidae, many feather mites); 'docking' papillae (Fig. 1C) fitting to the deep male suckers (e.g. Chirodiscidae, *Proctophylloides*, *Psoroptes*); and concavities interlocking the mushroom-like male sucker-derived protrusions (*Pterophagus*) (Popp, 1967; Fain, 1971; Witaliński, 1999).

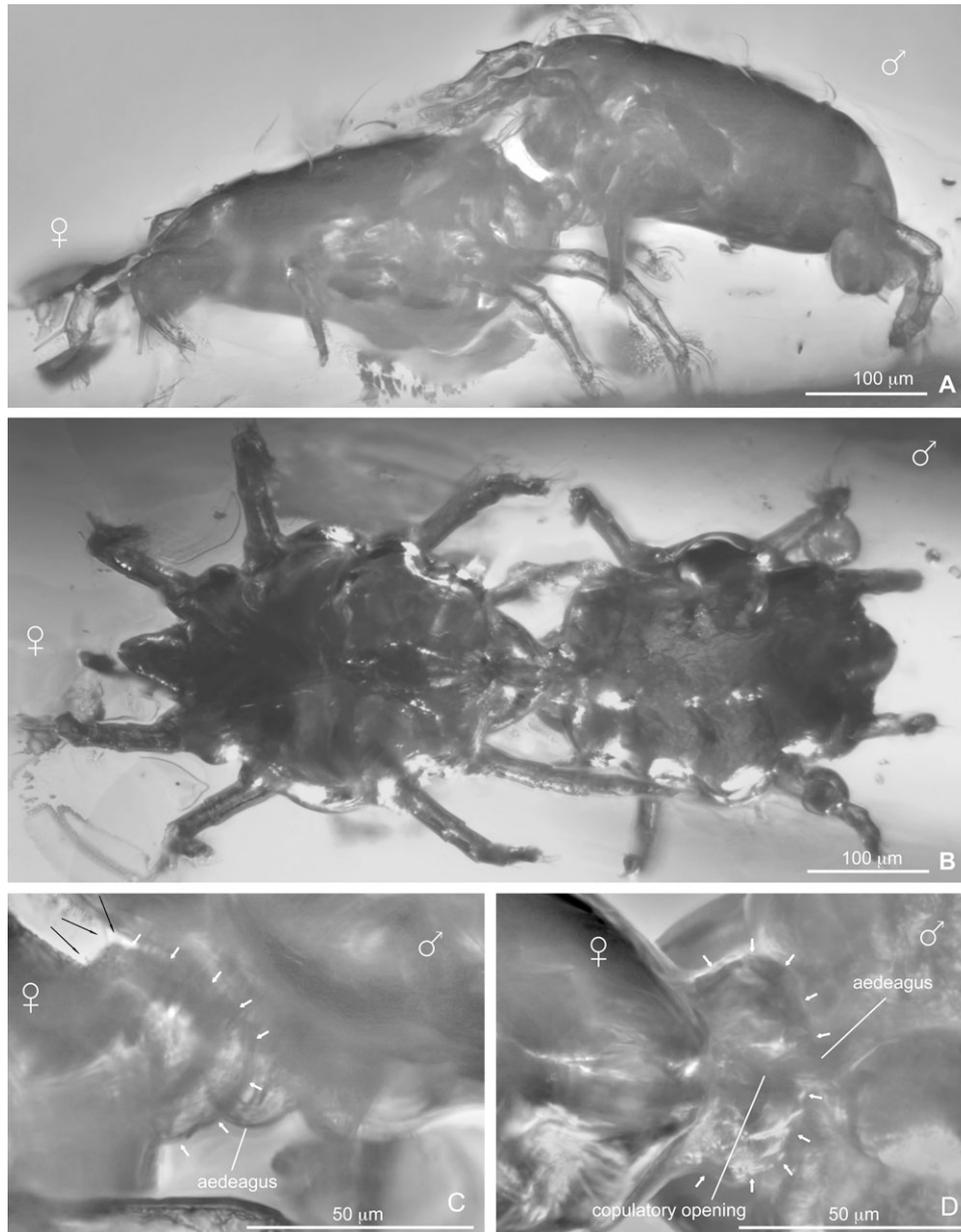


Figure 2. Mating of *Glaesacarus rhombeus*, lateral (A) and ventral (B) view; same genital regions, lateral (C) and ventral (D) view. Short arrows indicate the outlines of the female terminal opisthosomal projection and long arrows show the marginal setae of this projection.

DISCUSSION

MATING AND REPRODUCTIVE BEHAVIOUR IN ASTIGMATA

Astigmatan mites perform direct insemination. The male has a strongly sclerotized aedeagus that delivers sperm or endospermatophores to the female's spermatheca during copulation. If an endospermatophore is present, then it is injected in liquid form and solidifies inside the spermatheca (Griffiths & Boczek,

1977). There are two mating positions: proconjugate or parallel (the male is above and facing the same direction as the female) and retroconjugate or reverse (the male is above and facing away). Histiostomatoidea, Hemisarcoptoidea, Glycyphagidae, Aero-glyphidae, Rosensteiniidae employ proconjugate mating, whereas Canestriniidae, Chortoglyphidae, Echimyopodidae, Acaroidea, Hypoderatoidea, Hetero-coptidae, Lemanniellidae, and Psoroptidia are characterized by retroconjugate mating (O'Connor, 2009).

There is no clear pattern in the distribution of these mating systems at the base of Asigmatan tree. Early derivative astigmatan lineages may utilize either pro- (Histiostromatoidea) or retroconjugate (Heteroceptidae, Lemanniellidae, Canestriniidae) mating.

Free-living astigmatan mites often live in large groups, allowing frequent mating. For those species studied, females usually can mate as often as several times a day (Radwan, 2007). Peculiar morphology of the female seminal receptacle favours the sperm of the last mating male, particularly if the time between consecutive copulations is short (Radwan & Witaliński, 1991; Witaliński, 1999). However, it is unclear if last-male sperm precedence can be generalized to all Astigmata. The easy availability of the female for mating in large groups creates a strong sexual conflict between the reproductive success of the individual male and female promiscuity (which may decrease the fitness of the female but increase the fitness of her daughters; Radwan, 2007) or, alternatively, the need to reduce harassment and loss of fitness caused by frequent copulations. As the two sexes have conflicting optimal reproductive strategies, an arms race between males and females emerges as a powerful evolutionary force. It results in a spectacular array of behavioural and morphological adaptations exhibited by males and, to a lesser extent, by females.

Males usually maximize their chances to pass their genetic material by monopolizing mates either by physically isolating adult females or female nymphs from other males or by fighting rival males. An example of the former is the precopulatory guarding characteristic to some free-living and, especially, vertebrate-associated Astigmata (Witaliński, Dabert & Walzl, 1992; Liana, 2005). The male holds on to the female nymph using modified legs, suckers, pad-like protrusions or flattened setae, and copulates with her as soon as she reaches adulthood. In Chirodiscidae, the immature female lacks functional legs and is attached to the male for the entire duration of her development (Fain, 1971). As indicated above, in several taxa, immature females develop special structures complementary to the male attachment organs, facilitating precopulatory guarding and possibly increasing the level of female choice. Astigmata also display postcopulatory guarding behaviour, where the partners form a post-insemination association that prevents the female from re-mating and, as a consequence, protects the male sperm investment (Radwan & Siva-Jothy, 1996; Fashing, 2001). *Roubukia* (Chaetodactylidae) has large filamentous endospermaotophores that can block the female copulatory opening from further intromissions (Klimov & OConnor, 2008). Male-to-male combat is another way to increase indirectly the fertilization success and

paternity. In some Acaridae, males use legs III for fighting, with the winning male impaling his rival with the strongly pointing ends of the enlarged legs. Males of *Bdellorhynchus* (Avenzoariidae) use monstrously enlarged chelicerae to combat rival males. Males with the largest chelicerae can defend an entire flight feather on a duck host and monopolize all females inhabiting this feather (OConnor, 2009).

There is a variety of sexually dimorphic structures in the males, developed in response to the need to maintain position during copulation, pre- and post-copulatory mate guarding, and agonistic behaviour toward other males: para-anal, midventral, tarsal, and pretarsal suckers; enlarged and modified legs and chelicerae; and an array of posterior opisthosomal plates, lobes, protrusions, and enlarged and flattened terminal setae (Guillot & Wright, 1983; Witaliński *et al.*, 1992; Dabert & Ehrnsberger, 1998; Dabert & Mironov, 1999; Fashing, 2001; Wirth, 2005; Klimov & OConnor, 2008; OConnor, 2009). However, males of *Glaesaccarus* do not have any suckers, or setal or opisthosomal modifications. Para-anal suckers use negative pressure as the coupling force (Witaliński *et al.*, 1992), whereas other structures rely on adhesive surface forces occurring at the contact between the male/female surfaces. Usually, males with retroconjugate mating exhibit the most pronounced sexual dimorphism, with para-anal and tarsal suckers present in many taxa (OConnor, 2009).

FEMALE-CONTROLLED MATING

The term 'female choice' describes a process whereby females differentially mate with some males among a pool of potential mates (Holland & Rice, 1997). Astigmatid mites have several sex pheromones in both males and females, and a relatively elaborate male courtship and mounting to female, which involves female cooperation (Levinson, Levinson & Oelker, 1989). Although there are no rigorous experimental data, it is plausible that astigmatid females may react differently to complex chemical and behavioural stimuli offered by males before mating (e.g. males producing more sex pheromones or performing better during the mounting may be preferred). It is generally considered that copulating mites are characterized by a remarkable lack of precopulatory female choice of male mates in many cases (Walter & Proctor, 1999: 83). Nevertheless, several morphological features present in females indicate at least the possibility of this. In the case of species exhibiting female copulatory tubes (Fig. 1A), males have evolved different mechanisms for the reception of the tube into the male genital apparatus (e.g. short and/or internalized aedeagi) (Fig. 1B). However, in most of these examples, the process of pairing and sperm transfer

has not been observed in living mites. The existence of female copulatory tubes, correlated with the compensatory changes in the male genital apparatus, suggests that (1) sexually antagonistic coevolution (Arnqvist & Rowe, 2002) may occur in these mating systems and (2) females may assume the active role during mating and have partial or complete control over copulation. Similarly, there are correlated changes between the 'docking' papillae of immature females (Fig. 1C) and the male suckers (Witaliński *et al.*, 1992). The existence of these papillae in the female nymph indicates both the adaptive value of precopulatory guarding to the immature females, as well as ongoing coevolution between the interlocking organs in the two sexes. In the fossil mite *G. rhombeus*, the female uses a unique terminal pad-like protrusion to attach to the male during mating (Figs 1D, E, 2C, D), and probably, this is indicative of female control over mating. However, unlike the cases involving extant mites with female copulatory tubes and 'docking' papillae, the male of *G. rhombeus* does not have any apparent specialized structures aiding attachment to the female during copulation (e.g. opisthosomal modifications, and para-anal and tarsal suckers) (Fig. 1F). We hypothesize that *G. rhombeus* may display either an earlier step in the evolution of the female-dominated mating system and/or represent a remarkable example of imbalanced female counteradaptations against the male's reproductive interest that may occur during an arms race between the two sexes (Arnqvist & Rowe, 2002).

The evolutionary significance of possible precopulatory female choice and associated morphological structures is not clear because of the lack of experimental data. These structures may help females to actively select among males by directly controlling insemination, and therefore sperm acceptance. They may act as barriers that favour some males over others, resulting in indirect choice, as in the case of immature females having structures assisting in the male–female attachment. Female control over mating may reduce the timing of insemination, damage caused by copulation, and harassment. As side effects, this can lessen male-to-male aggression (Brown *et al.*, 1997), reduce the risk of predation, and select against precopulatory guarding. Another possibility is that female control can act as a sorting process that increases the likelihood that females will use the sperm of males of superior competitive ability, as opposed to male phenotypes that simply practice forced copulation or are extremely adept in securing mating to achieve reproductive success (Dickinson, 1997). This hypothesis assumes that male coercive ability is not correlated with his quality as a mate.

The hypothesis assuming precopulatory female choice at the level of adult females (e.g. species with

female copulatory tubes and *Glaesacarus*) predicts that precopulatory guarding will be strongly selected against in this system. In feather mites (where the absence can not be attributed to phylogenetic constraints), *Trouessartia* and other taxa listed in the section 'Structures indicative of female-controlled mating' do display the absence of precopulatory guarding (B. M. O'Connor, pers. comm.), seemingly supporting this hypothesis. However, some taxa (e.g. Crypturoptidae, Thoracosathesidae) require more detailed observations. Finding taxa combing precopulatory guarding and the presence of female copulatory tubes or attachment organs will falsify the hypothesis of female precopulatory choice.

An alternative to the above hypothesis assuming precopulatory female choice is the need for reduction of potential damage associated with mating (Morrow & Arnqvist, 2003) or precopulatory guarding. There is experimental evidence suggesting that multiple matings correlate with reduction of the female life span and fecundity (Radwan & Rysinska, 1999). However, direct physical damage to adult or nymphal females by males has not been observed, and females of free-living species, such as *Sancassania*, apparently cooperate with their mates despite the high costs of multiple matings (Radwan & Rysinska, 1999). Furthermore, in cases where precopulatory guarding is present, damaging the female, which presumably mates only once (Witaliński *et al.*, 1992), will result in the direct loss of fitness of the male offspring and should be selected against by natural selection (unless there is a substantial risk of not finding mates by the male).

Investigation of extant species (e.g. with female copulatory tubes) may help to select among these hypotheses and provide insight on the adaptive value of these organs. Unfortunately, feather mites, where structures associated with possible precopulatory female choice are most conspicuous, cannot complete their life cycle outside their hosts. A reliable method to maintain them in laboratory conditions over their entire life cycle should be developed first. Furthermore, taxa with female intromittent organs are associated with rare tropical birds and difficult to obtain. Because experimentation with these organisms is extremely difficult, we hope that inferential data presented in our paper will motivate researchers to conduct further investigations.

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