Sexual behaviour of mygalomorph spiders: when simplicity becomes complex; an update of the last 21 years

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Summary

A generally common impression seems to be that the mygalomorphs have simple repertoires of behaviours, but many authors have concluded that this traditional portrayal of mygalomorph behaviours is misleading. An increasing number of studies of reproductive behaviour of mygalomorphs have revealed intricate and complex mechanisms of communication employed by this group. Our objective was to provide a synthetic treatment of the literature published in the last 21 years about sexual behaviour of mygalomorph spiders, in order to contribute in improving our understanding on the widespread and unique behaviours they exhibit. We provide a brief introduction to reproductive behaviour of mygalomorph spiders, and then examine some of the general patterns of courtship and mating behaviours known on some mygalomorph families.

Introduction

Courtship can be defined as those ritualized behavioural patterns that are preparatory to mating and also to influence cryptic female choice during copulation (Eberhard 1991, 1994; Peretti & Eberhard 2009; Foelix 2011). In a traditional view, courtship among spiders is considered to have three main functions: i) partner recognition (species and sex); ii) orientation of individuals and synchronization of mating; and iii) suppression of non-reproductive behavioural patterns (e. g. prey-capture behaviour) (Barth 1993; Foelix 2011). The male copulatory courtship over female is common in spiders, inducing the female to favour him in reproductive decisions which occur after intromission and which can affect his reproductive success (Eberhard 1994, 1996).

Intraspecific interactions of araneomorph spiders have received considerable attention, but there are few detailed studies on intraspecific interactions of mygalomorph spiders (see Jackson & Pollard 1990; Costa & Pérez-Miles 2002 for a review). Most studies of mygalomorph courtship and mating have been conducted in the laboratory (Minch

1979; Jackson & Pollard 1990; Costa & Pérez-Miles 2002; Bertani *et al*. 2008; Ferretti *et al*. 2011, 2012). A general common impression seems to be that the mygalomorphs have simple repertoires of behaviours (Gerhardt 1929; Platnick 1971) or for example, that courtship in tarantulas is not so conspicuous (Baerg 1928; Gerhardt 1929). However, as these spiders have plesiomorphic features, studies on them can provide important perspectives to formulate evolutionary hypotheses. Moreover, Jackson & Pollard (1990) concluded that the traditional portrayal of mygalomorph display behaviour as simple is misleading.

An increasing number of studies of reproductive behaviour of mygalomorphs have revealed intricate and complex mechanisms of communication employed by this group (Coyle 1986; Coyle & O'Shields 1990; Jackson & Pollard 1990; Costa & Pérez-Miles 1998), and particularly on Theraphosidae (Baerg 1958; Minch 1979; Costa & Pérez-Miles 1992; Pérez-Miles & Costa 1992; Prentice 1992, 1997; Shillington & Verrel 1997; Punzo & Henderson 1999; Yánez *et al*. 1999, Costa & Pérez-Miles 2002; Quirici & Costa 2005). A synthetic treatment of the literature published in the last 21 years about sexual behaviour of mygalomorph spiders will contribute to improve our understanding on the widespread/ unique behaviours exhibited by them, the behavioural characteristics among families, and homologous behaviours (named differently by authors in most cases).

The purpose of this paper is, first, to provide a brief introduction to reproductive behaviour of mygalomorph spiders, and then to examine some of the general patterns of courtship and mating behaviour known on some mygalomorph families from the studies reported in the last 21 years. Jackson & Pollard (1990) published a literature review on courtship and mating function in Mygalomorphae prior to the 1990s. There are four groups to consider based on a recent phylogenetic classification of Mygalomorphae (Bond *et al*. 2012): Mecicobothriidae and Antrodiaetidae (sheet-web mygalomorph spiders), Dipluridae (funnel-web mygalomorph spiders), Theraphosidae (tarantulas), and Nemesiidae and Microstigmatidae (tube-trapdoor mygalomorph spiders).

Courtship and mating in mygalomorph spiders

With some exceptions, mating in mygalomorph spiders usually takes place during warm months, mainly in spring and summer (Coyle & Icenogle 1994; Costa & Pérez-Miles 2002; Pérez-Miles *et al*. 2005). Sperm induction, in which the male transfers sperm from the genital opening under the abdomen to the secondary sexual organs on the pedipalps, is performed early by males after maturation and they could recharge their palpal organs several times (e. g. Baerg 1958 reported more than 17 sperm inductions in six weeks). This is achieved by depositing sperm onto a small sperm web (Baerg 1958; Costa & Pérez-Miles 2002). The sperm is then absorbed by the palpal organ, in which it is stored until mating. Adult males then change their sedentary life-style to become wanderers in search of females.

To ensure recognition by the female, the male uses various techniques to approach her. In most species, the male has an intricate courtship ritual that is species specific

(Postiglioni & Costa 2006). However, in other burrowing species, the male just carefully approaches the female. Arguably, from the available literature many spider species show differences in their courtship behavioural patterns; thus it is hardly possible to make valid general statements about this behaviour. However, chemical communication during courtship seems to be widespread in mygalomorphs (Costa & Pérez-Miles 2002; Pérez-Miles *et al.* 2007; Copperi *et al.* 2012). Frequently, males reveal their presence to females by tapping rhythmically near their burrow or over the silk mat. It has been postulated that seismic signals are the main communicatory channel used by burrowing mygalomorphs during courtship (Quirici & Costa 2005, 2007).

Mygalomorphs mate face to face with bodies tilted up and males extending their pedipalps under the females (Baerg 1928; Costa & Pérez-Miles 2002; Ferretti & Ferrero 2008; Ferretti *et al.* 2011, 2012). Mygalomorph males often have special structures on their forelegs or second leg pair which are known in some species to clasp (but in others they do not have this function) the female during mating (Eberhard 1985). Although the anatomical details differ between species, all these structures are known as claspers or spurs. The area of the female clasped, grasped, or contacted also varies from species to species. In most mygalomorphs, claspers or spurs on the male first leg pair serve to lock or hold the female fangs, probably as a precaution against cannibalistic tendencies in the female and prevents her from attacking during mating (Jackson & Pollard 1990). Moreover, these species-specific male morphological structures that contact females during copulation may also deliver important stimuli that induce female cooperation (Coyle 1985). Prior to the 1990s, research on mygalomorphs focused on mating posture and clasping (Baerg 1928; Coyle 1971; Coyle & Shear 1981; Coyle 1985; Raven 1988). More recently, the mechanism of sexual communication and behavioural characteristics of male and female during courtship and mating have been the focus of attention (Quirici & Costa 2005; Postiglioni & Costa 2006; Pérez-Miles *et al.* 2007; Bertani *et al.* 2008; Ferretti *et al.* 2011; Copperi *et al.* 2012; Ferretti *et al.* 2012).

Characteristic mating behaviour of the mygalomorph spiders involves the male approaching the female from the front, the female raising her prosoma, and the male inserting one or both palps into the female's genital opening. Afterwards, both spiders separate cautiously (Baerg 1928; Coyle 1971; Coyle & Shear 1981; Raven 1988; Coyle 1985; Pérez-Miles & Costa 1992; Costa & Pérez-Miles 2002; Pérez-Miles *et al.* 2007; Ferretti *et al.* 2012).

Sheet-web and turret mygalomorph spiders

Mecicobothriidae is a relatively small family containing nine species placed among four genera (Platnick 2013). They are mostly small spiders that live close to the soil in crevices, under rocks, pieces of wood, and are often found quite deep in organic ground litter (Costa & Pérez-Miles 1998). Although they are active animals, they spend most of their lives within the confines of a sheet web (Gertsch & Platnick 1979; Costa & Pérez-Miles 1998). Unfortunately, sheet web builders of the family Mecicobothriidae are both

rare in nature and difficult to breed in the laboratory, so their reproductive biology is little known. However, Costa & Pérez-Miles (1998) described the reproductive biology of *Mecicobothrium thorelli* Holmberg, 1882. Male courtship patterns are elicited by the silk threads of female webs. The behavioural characteristics displayed during courtship are listed in Table 1. These courtship characteristics suggest that vibrations transmitted through the silk threads are the primary means of communication (Costa & Pérez-Miles 1998). Females remain immobile in the presence of courting males.

The clasping demonstrated in this species is unique regarding the cheliceral apophyses of males. The male usually spreads apart his chelicerae when pushing the female, and then the female opens her chelicerae and bites into the male's cheliceral groove lying between the two cheliceral apophyses. Based on these observations, Costa & Pérez-Miles (1998) proposed that clasping might have evolved from a frontal aggressive encounter with full contact of chelicerae, common in agonistic encounters. Cheliceral clasping and the long structure of male palps contribute to a non-elevated copulation position achieved by females. The palpal insertion pattern is complex and the embolus reaches a perpendicular position with respect to the dorsum of the palp, but turns slightly back to be inserted. The embolus insertion and withdrawal movements are repeated numerous times. Costa & Pérez-Miles (1998) suggested that they must overcome a mechanical resistance. Moreover, the right embolus can enter the right receptacle (and the same for left organs) according to the complementary spiral orientation of embolus and spermathecae (Costa & Pérez-Miles 1998). Arguably, the palpal insertions may cause intense genitalic stimulation which could determine sexual selection by cryptic female choice, following Eberhard's hypothesis (Eberhard 1985). This species exhibits post copulatory activities including: male leg-tapping, violent pushes with outspread chelicerae, and conspicuous body vibrations when males pursue females. In response to these male behaviours, females flex their legs against the body and remain immobile. It is remarkable that males of *M. thorelli* stay together with the females for at least 30 min., attacking the next courting males, thus considering this behaviour as mate guarding, an uncommon behaviour in Mygalomorphae.

Antrodiaetidae are Holarctic in distribution, and currently comprises three genera composed of 48 nominal species (Bond *et al.* 2012; Platnick 2013). These spiders usually build cryptic, silk-lined subterranean burrows that are concealed by a collapsible turret or collar during daylight hours (Hendrixson & Bond 2005). Coyle & Icenogle (1994) made observations on reproductive behaviour on the species of *Aliatypus* (Antrodiaetidae). Males detect female position by sexual pheromones associated with the female silk in the burrow. When males contact the burrow, they paw with their pedipalps and front legs (Table 1). Although Coyle & Icenogle (1994) did not observe mating behaviour in *Aliatypus*, the authors suggested that it could be similar to that of *Atypoides* and *Antrodiaetus* (Coyle 1971, 1986). Males possibly copulate by contacting the female only lightly with the first legs, and use their long pedipalps to reach her genital opening. Coyle & Icenogle (1994) proposed

Behaviour	Brief description	Equivalency among Authors	Families
Male Courtship Behaviours			
Palpal drumming	Up and down alternating movements of pedipalps.	*tapping* (Coyle & O'Shields 1990) *paw* (Coyle & Icenogle 1994) *pedipalp drumming* (Stradling 1994; Yañez *et al.* 1999) *palpate* (Ferretti & Ferrero 2008).	Antrodiaetidae, Mecicobothriidae, Dipluridae, Theraphosidae
Leg tapping	Vigorous hits with legs I and sometimes with legs II or both against the substrate, the female´s silk mat or the female´s body.	*tapping* (Coyle & O'Shields 1990; Shillington & Verrel 1997; Punzo & Henderson 1999) *paw front legs* (Coyle & Icenogle 1994) *leg drumming* (Yañez *et al.* 1999) *beating* (Ferretti *et al.* 2011).	Antrodiaetidae, Mecicobothriidae, Dipluridae, Nemesiidae, Theraphosidae, Microstigmatidae
Leg beating	Quick upward and downward movements of the legs, with tibia, metatarsi, with extended tarsi and beating and scraping female coxae.	Ferretti *et al.* (2012)	Microstigmatidae
Scratching	Extending legs I or pedipalps, touching the substrate, and then moving the leg backward over the substrate, removing the soil and piling it.	Bertani *et al.* (2008), Ferretti *et al.* (2011)	Nemesiidae, Theraphosidae
Stretching	Legs I upward and downward to contact the web, flexing reaching an angle of 45° between femur-patellae.	*quiver* (Ferretti *et al.* 2012).	Microstigmatidae, Nemesiidae
Body vibrations	High-frequency movement of the body or legs usually caused by the inward contractions of legs III with femorae positioned almost vertically.	*twitching/quivering/body jerking* (Coyle & O'Shields 1990) *vibratory movements* (Stradling 1994) *quiver* (Shillington & Verrel 1997) *stridulating behaviour* (Prentice 1992) *shaking body* (Punzo & Henderson 1999) *shaking* (Yañez *et al.* 1999).	Mecicobothriidae, Dipluridae, Theraphosidae
Spasmodic beats	Extending legs II or III and making vigorous backward and forward movements, reaching the legs of female.	Pérez-Miles & Costa (1992), Costa & Pérez-Miles (2002), Quirici & Costa (2005), Pérez-Miles *et al.* (2007), Ferretti & Ferrero (2008).	Theraphosidae Nemesiidae
Brushing	Raising, flexing and extending legs I, II and pedipalps and scratching against those of the female.	*leg fencing* (Coyle & O'Shields 1990, Shillington & Verrel 1997) *gentle movements* (Ferretti *et al.* 2011).	Dipluridae, Nemesiidae, Theraphosidae
Female Courtship Behaviours			
Body vibrations	Quick (high-frequency) vibratory movements of the entire body or legs.	*twitching/quivering/body jerking* (Coyle & O'Shields 1990) *vibratory movements* (Stradling 1994) *shaking* (Yañez *et al.* 1999) *body jerks* (Ferretti *et al.* 2011).	Dipluridae, Theraphosidae
Leg tapping	Leg flexing, lifting and lowering, contacting the ground.	*drumming forelegs* (Prentice 1992) *active female display* (Costa & Pérez-Miles 2002) *faint tapping* (Bertani *et al.* 2008)	Theraphosidae
Male Mating Behaviours			
Clasping	The male use claspers on his legs I to clasp the female's fangs, pedipalps or legs when she raise her body up.	Coyle & Icenogle (1994), Costa & Pérez-Miles (1998, 2002), Coyle & O'Shields (1990), Ferretti *et al.* (2011), Ferretti *et al.* (2012)	Antrodiaetidae, Mecicobothriidae, Dipluridae, Nemesiidae, Microstigmatidae, Theraphosidae
Palpal boxing	Alternating up and down movement of pedipalps, contacting the female's sternum.	*pedipalp boxing* (Yañez et al. 1999) *palpal movements* (Costa & Pérez-Miles 2002)	Theraphosidae, Nemesiidae, Microstigmatidae
Biting fangs	Male and female interweave forelegs and open chelicerae and fangs; then the male presses the female fangs with his own.	Postiglioni & Costa (2006)	Theraphosidae
Female Mating Behaviours			
Catalepsis	An immobile state during and after mating, in which females turn quiescent and let a male push and pull her around.	*cataleptic state* (Coyle & O'Shields 1990) *quiescence* (Pérez-Miles *et al.* 2007) *passive state* (Costa & Pérez-Miles 1998) *unmoving* (Shillington & Verrel 1997)	Mecicobothriidae, Dipluridae, Theraphosidae, Microstigmatidae
Body jerks	High-amplitude twitching of all legs and pedipalps.	*quivers* (Coyle & O'Shields 1990)	Nemesiidae, Dipluridae

Table 1: Common sexual behaviours of Mygalomorphae: brief description, equivalencies of terms across authors, and families.

that these trap-door species lacking tibial apophyses that aid lifting the front of the female (a behaviour widespread between mygalomorphs) may copulate within the burrow and thereby reduce the chance of being detected by predators.

Funnel-web mygalomorphs

Diplurids comprise 24 genera and 179 species that are characterized by the extremely long lateral spinnerets which are used to build conspicuous, perennial capture webs (Coyle & O'Shields 1990; Platnick 2013). Diplurids use well-defined sheet webs with a funnel-like retreat to detect and capture prey in trees or from under stones, soil crevices, logs or moss mats, or above ground in protected spots at the base of plants (Coyle & O'Shields 1990, Dippenaar-Schoeman 2002). Before the 1990s, there were observations on courtship and/or mating for four species included in the Dipluridae. Coyle & O'Shields (1990) published a remarkable study on courtship and mating of the diplurid *Thelechoris striatipes* (Simon, 1889) (formerly *T. karschi* Bösenberg & Lenz, 1895). The courtship of males of *T. striatipes* consists of an early non-contact phase of vibratory signalling. During this phase, a courting male often advances and begins low amplitude twitching which gradually increases in frequency and amplitude to become high amplitude quivering (Table 1). The possible functions and origins of the courtship behaviour patterns in this species suggest that male quivers and advances are probably distinct enough from prey struggles to generate vibrations that inhibit the predatory response of receptive females.

Females also show courtship behaviour in response to courting males performing quivers, silk walking, and advances towards males (Table 1). This female response appears to encourage the male to continue courting. Then, a contact phase begins between the spiders. In this phase, the spiders face one another and lower and raise and flex and extend their first and second pairs of legs. During this phase, the body is often raised and lowered and the fangs are extended. This behaviour appears to be ritualized agonistic behaviour and may play a role in assessment of male fitness. Then, males begin the clasping process: raising and extending their first legs; the apophysis at the end of the male's first tibia engages the prolateral face of chelicerae of female.

During mating, the angle between male and female cephalothoraxes is 80–100° and the female pedicel is flexed upwards so that the cephalothorax-abdomen angle is 40–80°. The female appears to be cataleptic except for occasional quivering of her legs and pedipalps. During some copulation attempts, Coyle & O'Shields (1990) observed that the female's genital area is distended and more exposed than usual. Mating of this diplurid species is characterized by numerous bouts of unsuccessful palpal insertion attempts, relatively few successful insertions, and a tendency for re-mating with different females. The courtship and mating behaviour units in *T. striatipes* are similar in form, context and function to behaviours observed in one or more of the four other diplurid taxa whose courtship and

mating behaviours have been described (Coyle 1985, 1986; Raven 1988; Raven & Schwedinger 1989).

Tarantulas

Theraphosids are the largest and longest-lived spiders in the world and currently comprise 124 genera and 946 species (Costa & Pérez-Miles 2002; Platnick 2013). The subfamily Theraphosinae is endemic to the New World and has the highest species richness of the family. In recent years, more and more research has been carried out on the courtship and mating behaviour of the Theraphosidae (Costa & Pérez-Miles 2002; Quirici & Costa 2005; Bertani *et al*. 2008; Ferretti & Ferrero 2008; Copperi *et al*. 2012). The available literature has increased considerably in relation to other families of Mygalomorphae. This could be due to the greater popularity of these spiders as pets worldwide.

Regarding the courtship of theraphosid males, they are capable of detecting female pheromones associated with female silk threads that trigger male sexual behaviour and facilitate the sexual encounter and species recognition (Costa & Pérez-Miles 1992; Pérez-Miles & Costa 1992; Costa & Pérez-Miles 2002; Postiglioni & Costa 2006; Pérez-Miles *et al*. 2007; Ferretti & Ferrero 2008). The sexual behaviour is characterized by the alternation of periods of activity and inactivity (Quirici & Costa 2005) and the common behavioural patterns are shown in Table 1. The most widespread behaviours in theraphosids are palpal drumming, that seems to act as a short-distance communication, maybe because it is usually displayed near the female burrow or female position (Pérez-Miles *et al*. 2007; Ferretti & Ferrero 2008); and body vibrations (the third pair of legs would be responsible of the vibrations) that transmit the species-specific signals through the ground, alerting the female of male presence even up to 1. 2 m distance on a heterogeneous susbstrate (Prentice 1992; Costa & Pérez-Miles 1992; Prentice 1997; Costa & Pérez-Miles 2002; Quirici & Costa 2005; Ferretti & Ferrero 2008; Copperi *et al*. 2012). *Grammostola vachoni* Schiapelli & Gerschman, 1961 and *Aphonopelma hentzi* (Girard, 1852) males perform body vibrations subsequent to palpal drumming (Punzo & Henderson 1999; Ferretti & Ferrero 2008).

Females of *Avicularia avicularia* Linnaeus, 1758, *Eupalaestrus weijenberghi* (Thorell, 1894), *Acanthoscurria suina* Pocock, 1903, *Aphonopelma paloma* Prentice, 1993, *Grammostola vachoni* and *Sickius longibulbi* (Soares & Camargo, 1948) respond to male courtship signals, but it is not a widespread behaviour in the family. The typical pattern for a female response is to tap their front legs or palps in answer to male courtship (Table 1). This response is usually displayed after male palpal drumming, and indicates a sexually receptive state (Stradling 1994, Quirici & Costa 2005; Copperi *et al*. 2012). Prentice (1992, 1997) observed that the percussion or vibration could be audible to humans. Recently, Copperi *et al*. (2012) proposed that the female response could orient the male towards her location from long distances in species that inhabit crevices and under stones.

When spiders contact one another, they adopt an elevated position with the characteristic position front to front. In

most species studied to date (Costa & Perez-Miles 1992, 2002; Pérez-Miles & Costa 1992; Shillington & Verrell 1997; Punzo & Henderson 1999; Yañez *et al*. 1999; Quirici & Costa 2005; Postiglioni & Costa 2006), the male positions himself in front of the female when mating, with both bodies tilted up and with the male extending his palps under the female and inserting them in an alternating phase into her genital opening. Males of *Grammostola* species perform spasmodic beats with the second pair of legs immediately after contacting the female; its function could be the relaxation of female fangs, taking into account that this behaviour is displayed during clasping and unclasping (Costa & Pérez-Miles 2002; Postiglioni & Costa 2006; Ferretti & Ferrero 2008). It is well known that most male theraphosids have specialized tibial spurs that clasp the female's fangs or the female fang following the inner curvature of his palp, and its tip comes to rest within the area between the base of the spur and the tibia during mating. One curious case is that reported for males of the Brazilian theraphosid *Sickius longibulbi* which clasp the female on her first pair of legs (Bertani *et al*. 2008).

The mating position achieved for most theraphosid species is characteristic: males push up the female's body, and raise her to reach a position that forms an angle of 60–80° between carapace and abdomen; females usually enter an immobile state (Table 1). One exception to this is again shown in *S. longibulbi*. Males of this species try to knock the females down by pushing the female's body until she is lying on her back and males can position themselves at an angle of 90° with the reclining female (Bertani *et al*. 2008). During mating, theraphosid males usually make from one to five palpal insertions and the copulation is of short duration (Costa & Perez-Miles 1992; Pérez-Miles & Costa 1992; Punzo & Henderson 1999; Ferretti & Ferrero 2008). Costa & Pérez-Miles (2002) observed that a high number of failed palpal insertions are frequent in some species, and this increases the duration of copulation.

Regarding the mating system of theraphosids, it has been reported that males mate multiple times with different females and, also, females accept various males per reproductive season. The case of the species *Eupalaestrus weijenberghi* is paradigmatic, with monandry and polygyny, and males that make only one palpal insertion during copulation (Pérez-Miles *et al*. 2007). After mating, males escape safely, and aggression and cannibalism are only circumstantial (Shillington & Verrel 1997; Costa & Pérez-Miles 2002; Ferretti & Ferrero 2008). Females usually remain immobile and quiescent for some minutes after mating with their first pair of legs and palps elevated in a threat position (Table 1). Although some publications have noted the sexual cannibalism of theraphosid species (Brazil & Vellard 1926; Punzo & Henderson 1999), the absence of sexual cannibalism seems to be the rule for theraphosids, with only occasional post-copulatory female attacks towards males (Prentice 1997; Shillington & Verrel 1997; Yañez *et al*. 1999; Costa & Pérez-Miles 2002; Postiglioni & Costa 2006; Pérez-Miles *et al*. 2007; Bertani *et al*. 2008; Ferretti & Ferrero 2008).

Tube-trapdoor mygalomorphs

The family Nemesiidae has 43 genera and 364 described species (Platnick 2013). Nemesiids are relatively large, brown, elongated spiders with robust legs. Most species live in silk-lined burrows that vary in shape from a simple, deep burrow, to a Y-shaped burrow, to burrows with side passages or chambers made under rocks; some species finish these with a hinged door, and other species construct tunnel-webs with short burrows (Goloboff 1995, Dippenaar-Schoeman 2002; Ferretti *et al*. 2011). Little is known about the behaviour of the nemesiids. To date, the reproductive behaviour of only two species of the genus *Acanthogonatus* is known: *A. tacuariensis* (Pérez-Miles & Capocasale, 1982) and *A. centralis* Goloboff, 1995 (Ferretti *et al*. 2011). Usually, courtship of nemesiid males is initiated before or after contacting silk threads of females at the burrow entrance and comprise scratching and leg tapping over the substrate with the first legs (Table 1). Ferretti *et al*. (2011) observed that these behaviours in *A. centralis* may serve as a long-distance communication because they are displayed mainly away from the female's position or tunnel-web. When males contact the female's silk threads, they start to stretch the web by slowly extending legs I downwards to contact the web, and then flexing them, reaching an angle of 45° between the male femur-patellae. Additionally, males can display palpal drumming over the silk threads of the female's web (Pérez-Miles & Capocasale 1982; Ferretti *et al*. 2011).

When the spiders contact, the males touch the females with weak movements of their front legs over the female's cephalothorax (brushing). While in contact, males make spasmodic beats with the second or third pair of legs. The main function of this behaviour seems to be to relax the female fangs, since they are displayed during the clasping and unclasping of female's fangs. Also, males display palpal boxing near the female genital opening.

Males clasp the females' fangs with the tibial apophyses of legs I. During copulation, the male pushes the female back onto her back legs and, still standing with the first pair of legs between the chelicerae and the distal portion of the coxa of the pedipalps, raises her. For mating, an angle of 90–100º exists between the male and female cephalothoraxes. The female's pedicel is flexed upward, reaching a cephalothorax-abdomen angle of 60–80°. From this position, the male inserts his embolus into the female's genital opening. In some copulation attempts, the female's genital zone is distended, with the genital lips protruding, thus resulting in a more exposed genital opening than usual. It is remarkable that females of *A. centralis* display body jerks during mating, made by the high amplitude twitching of all legs and palps. These female body jerks could possibly act as a stimulus to start male palpal insertions.

The far less diverse and somewhat enigmatic family Microstigmatidae contains only seven genera and 16 species. These spiders, in particular, have long been overlooked, both because of their rarity in collections and their extremely small size (adult males are 1–3 mm in total length). The spiders are not known to construct burrows or retreats and are supposed to make minimal use of silk. Recently, Ferretti *et al*. (2012) described for the first time
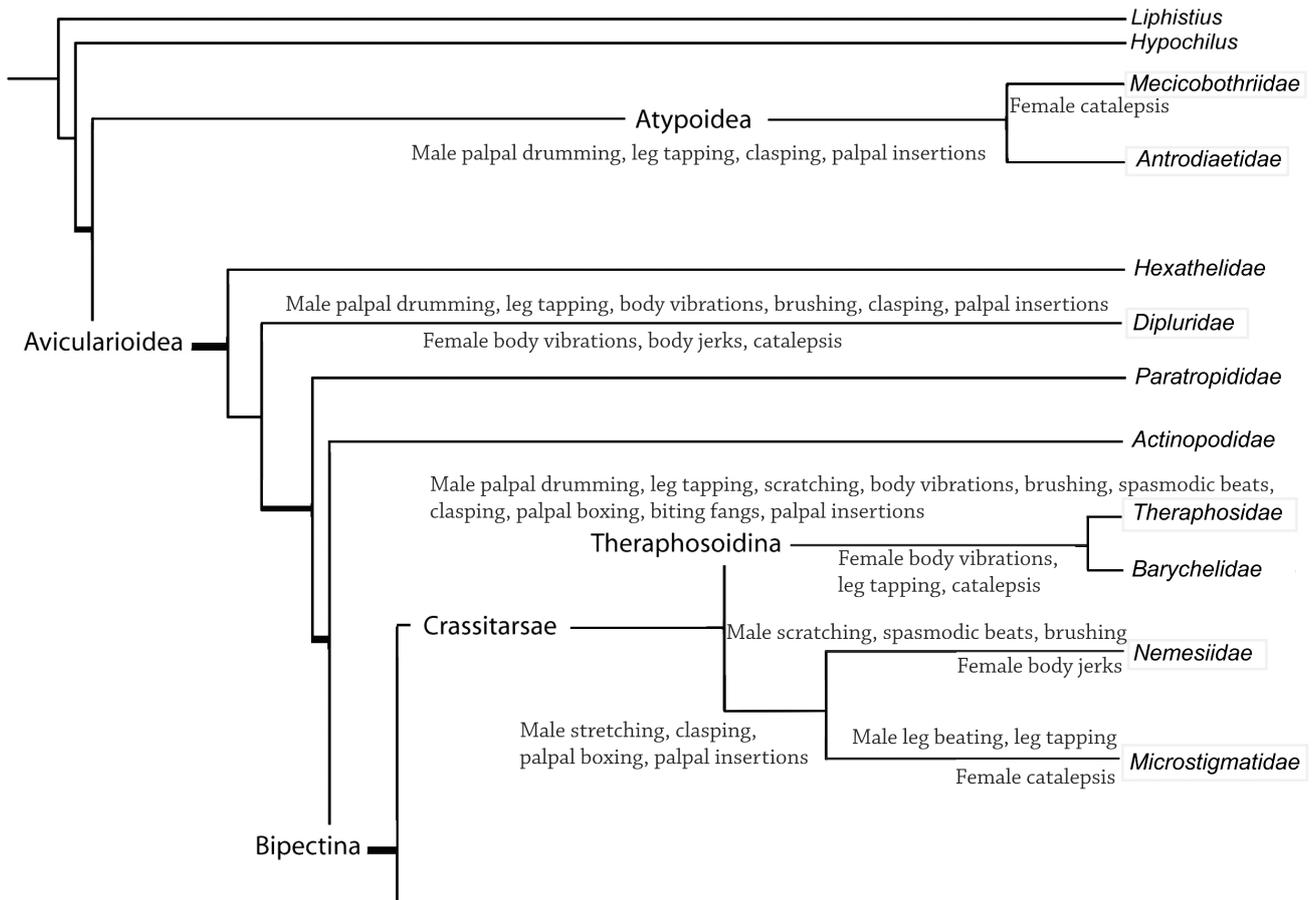
Fig. 1: Phylogenetic hypothesis for Mygalomorphae and characteristic sexual behaviour of families. Only the section with the families treated in this review (grey rectangles) is shown. Modified from Bond *et al.* (2012).

the sexual behaviour of *Xenonemesia platensis* Goloboff, 1989.

Males begin the courtship when they directly contact the female's body. During this initial contact, females remain largely motionless. The male does not start courtship when he contacts female silk, but does so only after contacting the female herself. After initial contact, the male stretches on the female's silk mat. The female raises her body up to an angle of almost 60° relative to the substrate and the male makes palpal boxing and leg tapping over the female's body.

The male clasps the female's palps and chelicerae between his first pair of legs. The distal portion of each male tibia, without tibial apophyses or megaspines, is placed against the prolateral surface of each female pedipalp base. During copulation, the male positions himself under the female, facing her sternum. The female's pedicel is flexed upwards so that the cephalothorax-abdomen angle is 30–50°. In palpal insertion attempts, the male continues performing leg tapping and stretching. Ferretti *et al.* (2012) observed that males of *X. platensis* court females while mating by intense leg beating.

Conclusions

Chemical sexual communication in mygalomorphs has been described by many authors (Costa & Pérez-Miles 2002; Ferretti & Ferrero 2008; Ferretti *et al.* 2011), thereby discrediting previous hypotheses about the absence of chemical cues in these spiders (Petrunkevitch 1911; Baerg 1928; Platnick 1971). Males of mygalomorphs use chemical or tactile cues from silk spun around the female's burrow entrance or the silk from sheet webs that prime a short-range male-searching behaviour. All families treated here, with the exception of the Microstigmatidae, are capable of detecting female sexual pheromones associated with silk threads. The exception in Microstigmatidae could be attributed to the low number of observations or to the absence of female silk due to the minimal use of silk that characterize these spiders (Griswold 1985; Ferretti *et al.* 2012). Pheromones on female silk facilitate sexual encounter and species recognition. Coyle & Shear (1981) provided the first strong evidence of a contact sex pheromones being the prime courtship releaser of courtship and mating in a mygalomorph spider, *Sphodros abboti* Walckenaer, 1835 (Atypidae). The wide distribution in several families of Mygalomorphae (Antrodiaetidae, Dipluridae, Mecicobothriidae, Nemesiidae and Theraphosidae), and in Mesothelae (Haupt 1977), of female sex pheromone release indicates that tactochemical sexual communication is an early acquisition in spiders.

Courtship behaviour patterns in mygalomorph spiders serve a number of functions, including the recognition of species and sexual recognition, the correct positioning of the sexes with respect to one another in order to ensure insemination, and the reduction or elimination of aggressive behaviour (Jackson & Pollard 1990; Punzo & Henderson 1999; Costa & Pérez-Miles 2002).

Mygalomorphs have simple eyes and likely lack acute vision (Land 1985, Dippenaar-Schoeman 2002). Their courtship displays provide vibrational, substrate-borne stimuli when partners are apart, and tactile and chemotactic stimuli when spiders are in direct contact. Courtship characteristics of mygalomorph spiders suggest that vibrations transmitted through the silk threads or substrate are the primary means as communication before direct contact, and the seismic signals are the main communicatory channel used by burrowing mygalomorphs during courtship. The most widespread behavioural units of courtship of males between mygalomorph families are palpal drumming and leg tapping. Considering that mecicobothriids and antrodiaetids are the sister group of the Avicularioidea (Bond *et al.* 2012), an early acquisition of these behaviours is suggested (Fig. 1). The possible function of these behaviours could involve acoustic/vibratory signals as a communication mechanism in burrowing and sheet-web builder families. Body vibrations, also a widespread behaviour between mygalomorph families, are caused by leg III movements and may serve as distant seismic communication (Quirici & Costa 2005, Pérez-Miles *et al.* 2007).

Female responses (body vibrations and leg tapping) to male courtship have been reported for Dipluridae and Theraphosidae. These female behaviours indicate her receptive condition, attractiveness, and location (Costa & Pérez-Miles 2002; Quirici & Costa 2005; Copperi *et al.* 2012). The scarce records on female responses to male courtship could be due to difficulties in observing female behaviour in the field or in the laboratory because these behaviours are displayed mainly inside their burrows.

After contact, brushing, leg beating, and spasmodic beats are common behaviours displayed by mygalomorph males over female's bodies. Costa & Pérez-Miles (2002) proposed that spasmodic beats with legs II could be a synapomorphy of the genus *Grammostola*, but nemesiids also display this behaviour during courtship (Fig. 1) (Ferretti *et al.* 2011). Their function seems to be the relaxation of female fangs, taking into account that it is mainly displayed during clasping and unclasping. All these movements cause the female to assume a threat posture with open fangs, a necessary condition for the male to clasp. Threatening behaviour of females functions primarily as an antipredator defence (Jackson & Pollard 1990).

Typically, mating in mygalomorph spiders involves a face to face position, with males clasping female chelicerae with forelegs and elevating females to reach the genital area with palps. When this position is achieved, they initiate palpal insertions. If the posture of mygalomorphs generally tends to be with the female leaning up, and if mygalomorph females often become immobile while mating, then mygalomorph males often need to hold females in position. Clasping, a male mating behaviour widespread among mygalomorph taxa, may serve to protect the male, to position and steady the mating pair for more effective sperm transfer, and to convince the female to permit palpal insertions (Eberhard 1985; Coyle 1986; Coyle & O'Shields 1990). Clasping the female's fangs, for example, may function in holding the female in place. It may also function in warding off attacks, but not necessarily. Just because fangs are weapons, this does not imply that the function of clasping fangs must be to ward off attacks. Perhaps some features peculiar to mygalomorph biology enhance selection for such male-specific leg claspers that reduce the risk of mate-inflicted injury. Coyle (1985) suggested that signals from male clasping behaviour may be significant in intersexual connection and that the female may be able to discriminate between male claspers of different geometries. The widely documented and remarkable longevity of adult female mygalomorphs may create a relatively high adult female/adult male ratio and, consequently, increased mating opportunities for any male. This may, in turn, increase the selection pressure for male traits (like claspers) which would enhance his chances of surviving a mating. The cheliceral clasping in Mecicobothriidae, also reported for an antrodiaetid species (Coyle 1971), is a *sine qua non* condition for a successful copulation, and female biting appears to cancel the aggressive and/or predatory impulse and consequently inhibit further attacks (Costa & Pérez-Miles 1998).

Males of some species of Mygalomorphae court females during mating, and this suggests that females might be testing the copulatory abilities of males. The number of palpal insertions is variable, involving failed insertions, and making longer mating durations and requiring more effort from males to perform sperm transfer. Usually, females remain immobile during mating and males escape safely after mating. Palpal insertions attempts that do not lead to successful insertion could be consistent with Eberhard's hypothesis that sexual selection by female choice commonly occurs during copulation attempts (Eberhard 1996). It is possible that the female, even though largely cataleptic, may be providing mechanical challenges to the male's copulatory ability, monitoring his performance, and adjusting her behaviour and/or physiology to maximize her fitness. On the other hand, failed insertion attempts occur in other spiders and maybe to mechanical fit (Huber 1993; Prenter *et al.* 1994; Eberhard 1996), however, it has not been established whether improper male morphology or improper positioning of the male genitalia prior to insertion (or both) are responsible for this phenomenon.

The risk of sexual cannibalism may be a hazard for male mygalomorphs and they have apparently evolved behavioural traits to reduce this risk; for example, swift retreat after mating (Jackson & Pollard 1990; Shillington & Verrel 1997). It is clear that watching mygalomorph mating can create an expectation of great violence and the notion that a male is protecting himself from a female attack can be compelling. But how real and immediate is the danger to a male? Interpreting clasping as a male's effort at physically restraining a predatory female is complicated by another apparently prevalent feature of mating mygalomorph females. Females of many species go into an immobile state. This state is known as catalepsis: a female goes immobile, quiescent, and lets the male push and pull her around. Within the scope of this paper, this female behaviour was reported for Mecicobothriidae, Dipluridae, Theraphosidae and Microstigmatidae (Fig. 1). The exception is Nemesiidae, in which females remain active during mating, making body jerks. Perhaps a male clasps a female as an additional (backup) protection in case she suddenly comes out from her immobile state or in the case of active females during mating (Nemesiidae).

The notion that male clasps can physically restrain lethal females just does not appear compatible with females being immobile. It seems, instead, that a male's clasping behaviour (as palpal boxing, brushing, and spasmodic beats) provide a stimulus to which a female responds by going immobile. This alternative to a hypothesis of simple physical restraint might still be compatible with the notion that males are protecting themselves from cannibalistic females, but the relationship between clasping behaviour, female passivity, and the potential for cannibalism is unclear. Moreover, although males of Nemesiidae perform palpal boxing and spasmodic beats towards females, they open their fangs and allow male clasping by males, but females never reach an immobile state during mating.

The present state of information clearly implies that although, traditionally, mygalomorph spiders are considered relatively simple regarding their genitalia and sexual coupling behaviour, they exhibit intricate mechanisms of communication and sexual behaviours (such as copulatory courtship and complex palpal insertion patterns) that open an exciting field for future research. From our understanding, the classic portrayal of the behaviour of mygalomorphs as simple is changing, not because spiders behave in different ways, but now the focus of attention during mygalomorph interactions lies in female behaviour (usually not observed in previous studies), male and female behaviour during and after mating, or meticulous male courtship behaviour. From the results of this new set of data, we can argue that the behaviours are far from simple, being very complex in some species, even with new questions to formulate about possible interpretations.

Finally, we will make the following recommendations for future studies of sexual behaviour in Mygalomorphae: 1) observations should include the male behaviour before contacting with female, in order to determine the presence of pheromones associated with the silk threads of females; 2) females should be kept in as natural an environment as possible; for example, the construction of an artificial burrow not only allows observations of female behaviour, but elicits behavioural responses to male courtship, as was observed for many theraphosids; 3) note whether individuals perform behavioural patterns during mating that could be interpreted as courtship in copula; 4) direct observations should be complemented by video-recording to detect precise behavioural characteristics; and 5) studies should include several pairs and, preferably, more than one population.

Acknowledgements

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