

Convergent fighting behavior in two species of Neotropical harvestmen (Opiliones): insights on the evolution of maternal care and resource defense polygyny

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Abstract. Males of several harvestman species fight for the possession of oviposition sites. Usually, males use spines and elongated appendages as weapons in these fights. Although males of many cranaiids have spines that could be used as weapons, there is no report of male-male fights in this family. Here we describe the first case of a male-male fight in cranaiids. Males of *Phareicranus* aff. *spinulatus* face each other, extend their second pair of legs laterally, and use them to hit the second legs of the opponent. Pedipalps are kept above the chelicerae and not used to strike the opponent. The fighting behavior is remarkably similar to that described for Goniosomatinae (Gonyleptidae). We interpret morphological and behavioral similarities between cranaiids and goniosomatines as convergences. Moreover, we suggest that body/egg size and predation pressure may have influenced the evolution of parental care and resource defense polygyny in these two harvestman clades.

Keywords: Cranaiidae, egg-attendance, Goniosomatinae, mating system, body size

Males of several harvestman species fight each other for the possession of oviposition sites used by egg-bearing females (reviewed in Buzatto & Machado 2014). Different parts of the males' body may be modified and used as weapons in intrasexual fights. Among some species of Neopilionidae (suborder Eupnoi), for instance, males have enlarged chelicerae that are used to hit and grab the rivals (Painting et al. 2015). Among many species of the family Gonyleptidae (suborder Laniatores), males use spines on the fourth pair of legs (mainly on the coxa, trochanter, and femur) to pinch the opponent (Willemart et al. 2009; Buzatto et al. 2014). In some gonyleptid species belonging to the subfamily Goniosomatinae, males fight using their elongated second pair of legs. Fights begin with males facing each other, holding their elongated second pair of legs laterally extended, the first pair of legs retracted above the dorsal scute, and the pedipalps raised or extended forward (Fig. 1A, B). In this position, males hit each other on the tip of their second legs several times and intercalate these sequences of hits with periods of immobility. Males may also attack the opponent's first pair of legs with rapid pedipalp strikes. In most of the fights, one male runs away after some rounds of hits and the winner holds the territory, where females oviposit and remain attending the eggs (Buzatto & Machado 2008).

Although many species of Cranaiidae (Laniatores) show marked sexual dimorphism (Pinto-da-Rocha & Kury 2007), and males have many spines and tubercles that could be used as weapons, there is no report of male-male fights in this family. Several cranaiid species also show maternal egg attendance (García-Hernández & Machado 2017), and in some of them egg-tending females are found close to each other, suggesting the existence of harems, which are likely to be defended by territorial males (S. García-Hernández & G. Machado unpublished data). Here we describe for the first time intrasexual fights between males of an undescribed cranaiid species, the Colombian *Phareicranus* aff. *spinulatus* (Cranainae). The fighting behavior is remarkably similar to that described for goniosomatine harvestmen, and male-male

fights also seem to be related to the possession of territories where females lay eggs. Considering that cranaiids and goniosomatines are not closely related taxa (Pinto-da-Rocha et al. 2014; see also Fernández et al. 2017), we interpret the similarities as convergences between these two clades of Neotropical harvestmen, and discuss the selective pressures that may have favored the evolution of a mating system based on territory defense.

On December 11, 2011, we conducted a field trip to the rural zone of Santa Rita, municipality of Carmen de Viboral, Antioquia, Colombia (5°53'48.40"N, 75°12'44.96"W, 1743 m altitude). The site has high precipitation levels throughout the year (nearly 100 mm of rain per month), and is covered by pristine cloud forest. Close to the entrance of an artificial cave formerly used as a gold mining site, we found two males of *P.* aff. *spinulatus* approaching each other. We filmed and photographed the interaction between them and the descriptions we provide below are based mostly on the footage (Supplementary Material 1, available online at <http://dx.doi.org/10.1636/JoA-S-17-070.s1>). On July 20, 2013, we conducted a second field trip to the same site, aiming at recording other fights and gathering additional behavioral information. Although we did not find any male-male interactions in this second trip, we gathered behavioral information on female egg attendance, which is also provided here. We deposited two males of *P.* aff. *spinulatus* as voucher specimens at the Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ 4283).

When we approached the cave entrance in our first field trip, we found two males of *P.* aff. *spinulatus* close together (ca. 10 cm) and facing each other on a rock wall. The males approached each other and stopped with the frontal part of their bodies nearly 2–3 cm apart (Fig. 1C, D). In this position, the first pair of legs of both males was retracted above the dorsal scute (Fig. 1C). The second pair of legs was widely extended laterally and, during most part of the interaction, both males performed fast frontward-backward movements with these legs (Figs. 1C, D). With the fast movements, the tips

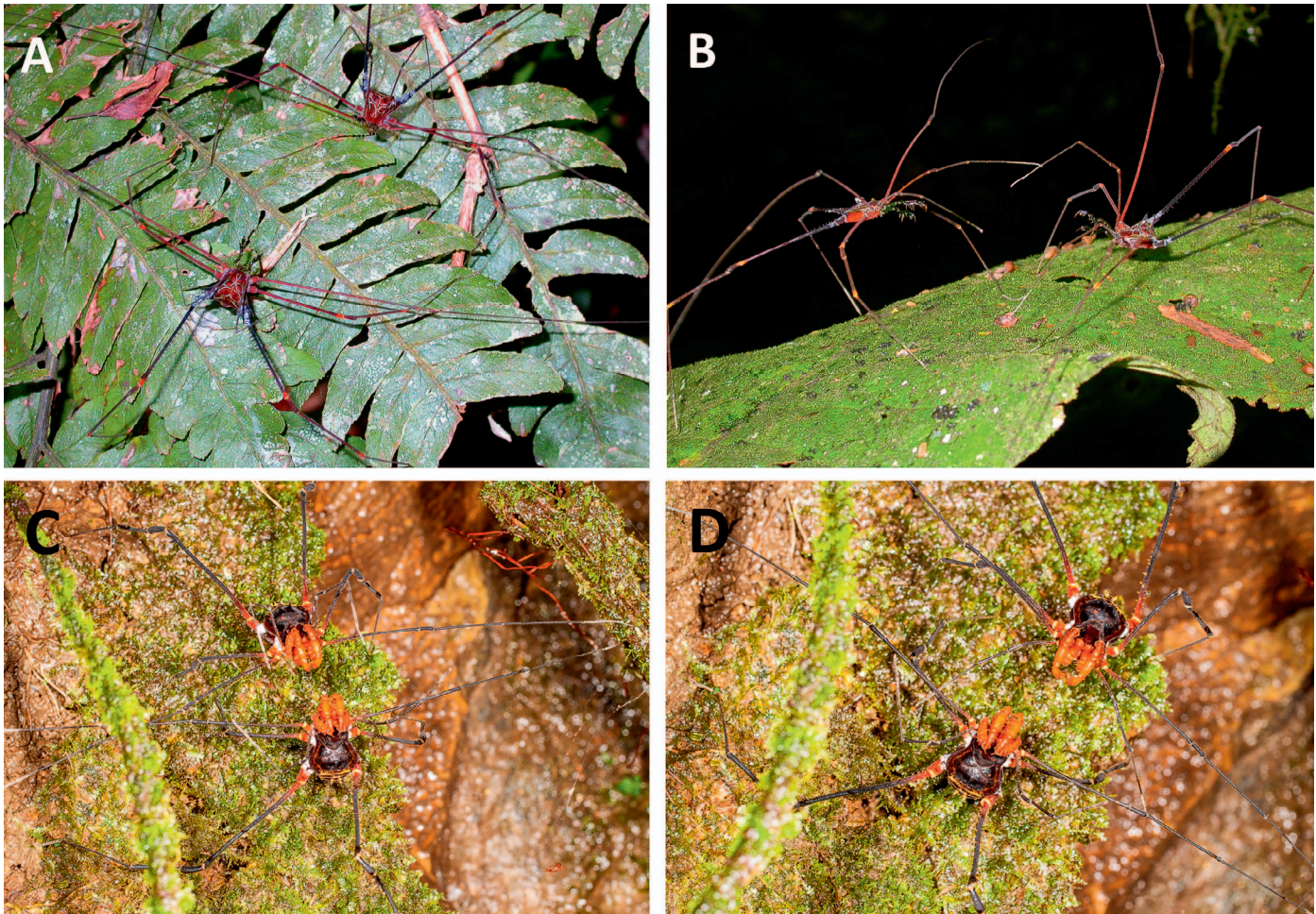


Figure 1.—(A & B) Males of the harvestman *Serracutisoma proximum* (Gonyleptidae: Goniosomatinae) fighting on the vegetation in the Atlantic Forest, São Paulo, Brazil (photos: Bruno A. Buzatto). During the fight, the males face each other, keep their second pair of legs extended laterally, and use these legs to hit the legs of the opponent. Note that in (A) the first pair of legs of both males is retracted above the dorsal scute and in (B) these legs are gently touching each other. During the fight, males rarely use these legs to touch each other, but their pedipalps are stretched frontwards and occasionally used to strike the front legs of the opponent. (C & D) Males of the harvestman *Phareicranaus* aff. *spinulatus* (Cranaiidae) fighting on a rock in a Colombian cloud forest (photos: Sebastián Vieira-Urbe). The general posture and the behavior of the fighting males is remarkably similar to those described for *S. proximum*. The main differences are that pedipalps are not stretched frontwards (C & D), and the first pair of legs is not retracted above the dorsal scute in *P.* aff. *spinulatus* — instead, these legs are used to touch and tap the pedipalps and front legs of the opponent (D).

of the second pair of legs (mostly the tibia, tarsus, and metatarsus) of both males whipped each other. The hitting with the second pair of legs was intercalated with brief periods of immobility. Occasionally, the first pair of legs was extended forward and used to touch or quickly tap the pedipalps, first and second pair of legs of the opponent (Fig. 1D). During the entire interaction, the pedipalps of both males were kept retracted above the chelicerae, and were not used to strike the opponent (Fig. 1C, D). The interaction lasted 15 min, from 15:50 h to 16:05 h, after which the males were probably disturbed by the light of our flashes and left the place. We found no females close to the place where we observed the two males fighting, but there was another conspecific male nearly 0.5 m from the fighting males.

In our second field trip, we did not find males fighting each other, but found two females of *P.* aff. *spinulatus* attending their eggs in a damp pocket of a roadside bank (Fig. 2A). They

were both prostrated on a clutch of eggs, in the typical egg-tending posture observed in many species of Laniatores (Machado & Macías-Ordóñez 2007). Eggs were laid in a single layer on the substrate, and in both clutches, the eggs had a small amount of debris attached to their surface (Fig. 2B). The mean egg diameter was 2.75 mm (SD = 0.08 mm; $n = 8$), representing 24% of the female's dorsal scute length (Fig. 2B). The number of eggs in one of the clutches was 22, and the distance between the two egg-tending females was nearly 2 m (Fig. 2A). The other clutch was inside a crack, so that it was not possible to count the eggs. In between the two egg-tending females, we found an adult male. In this trip, we also found another adult male in a similar damp pocket several meters away in another roadside bank. No female or egg clutch was found close to this male.

In a recent molecular phylogeny, the family Cranaiidae appears within the family Gonyleptidae, as the sister group to



Figure 2.—(A) Damp pocket in a roadside bank where we found two egg-tending females (F) and a large adult male (M) of *Phareicranaus* aff. *spinulatus*. Only one female is visible in the photo (circle); the other female and the male were inside a rock crack and below roots and vines, respectively, but their positions are indicated by arrows (photo: Sebastián Vieira-Urbe). Scale bar = 0.5 m. (B) Egg-tending female of *P. aff. spinulatus* prostrated on a clutch containing 22 large eggs in early stages of embryonic development. Note that the eggs are covered by debris, which is probably attached to the egg surface by the egg-tending female (photo: Sebastián Vieira-Urbe).

the subfamily Ampycinae, and closely related to the clade K92 and the subfamily Manaosiinae (Pinto-da-Rocha et al. 2014). The subfamily Goniosomatinae is located far from the clade including the Cranidae (Pinto-da-Rocha et al. 2014). Although the phylogenetic position of the Cranidae as a clade within the Gonyleptidae still deserves further investigation, cranids and goniosomatines clearly do not share a recent common ancestor. Moreover, whereas cranids occur mostly in the northern region of South America, along the Andes and Amazon Basin up to Panama (Pinto-da-Rocha & Kury 2007), goniosomatines are restricted to the Atlantic forest, from southern to northeastern Brazil (DaSilva & Gnaspini 2009). Despite the distant phylogenetic relationship between cranids and goniosomatines, it is remarkable that they show so many convergences. Pinto-da-Rocha & Kury (2003) were the first to point out some morphological convergences between them, including large body size, stout and long legs bearing few spines, and robust and heavily armed pedipalps. Three years later, Machado & Warfel (2006) added other convergent traits related to behavior, such as maternal egg attendance of large eggs laid mostly on rock walls and damp pockets in roadside banks. The findings reported here extend the number of behavioral convergences to several traits of the mating system, which will be discussed below.

The general fighting behavior of *P. aff. spinulatus* is very similar to that described for the goniosomatine *Serracutisoma proximum* (Mello-Leitão, 1922) (Buzatto & Machado 2008; Fig. 1A, B), and has no parallel with other harvestmen for which fights have already been described (see Buzatto & Machado 2008 and Painting et al. 2015). Males of both species face each other, keep their first pair of legs retracted above the body, and hit the second pair of legs of the opponent using their own second pair of legs (see video in Supplementary Material 1, online at <http://dx.doi.org/10.1636/JoA-S-17-070.s1>). One difference is that males of *S. proximum* use their

pedipalps to strike the opponent and grasp his pedipalps or first pair of legs. After that, the grasped appendage may be chewed on and amputated by the chelicerae of the attacking male (Buzatto & Machado 2008). In *P. aff. spinulatus*, males keep the pedipalps retracted above the chelicerae during the entire fight, and they did not extend them frontwards or use them to grasp the opponent (compare pedipalpal posture between Fig. 1A, B and 1C-D). Probably as a consequence of the pedipalpal strikes, the first pair of legs in *S. proximum* is rarely used to touch the first pair of legs of the opponent (e.g., Fig. 1B). In *P. aff. spinulatus*, however, the first pair of legs is frequently used to touch and tap the opponent (Supplementary Material 1) — perhaps to acquire information on his posture and/or strength because cranids, like most harvestman species, are unable to form visual images (Acosta & Machado 2007).

Male-male fights in *P. aff. spinulatus* are probably related to the possession of a territory that is used by females as oviposition site. Our suggestion is based mainly on the fact that males were fighting without any conspecific female around. This is a pattern typically observed in resource defense polygynies, a mating system in which males defend territories that attract females due to the presence of food, shelter or oviposition sites (Ostfeld 1987). The presence of an adult male close to egg-tending females is also a pattern commonly reported for many other harvestman species exhibiting a resource defense mating system (Machado et al. 2015). As it occurs with all goniosomatines studied so far (Machado 2002), females of *P. aff. spinulatus* seem to attend eggs inside the males' territories, and the putative harem we found had two egg-tending females. In some harem-defending harvestman species, there are two male morphs with different mating tactics. Large and heavily-armed males (majors) usually defend territories and guard their mates for as much as two days after mating, whereas small and poorly-armed males (minors) rely mostly on harem invasion, sneak copulations, and very rarely

exhibit mate guarding (Buzatto & Machado 2014). This is the case of *S. proximum*, in which majors have a second pair of legs almost twice as long as those of minors and females, probably because these legs are used as weapons in territorial fights and only majors fight for territory possession (Buzatto et al. 2011). Unfortunately, we do not have many individuals of *P. aff. spinulatus* deposited in museums to test whether their second pair of legs is also sexually and intra-sexually dimorphic. Though, according to our view, the existence of two male morphs with different mating tactics in *P. aff. spinulatus* would not be surprising.

Why are there so many morphological and behavioral convergences between cranaids and goniosomatines? Whereas goniosomatines are relatively well-studied harvestmen, the same is not true for cranaids, and this lack of basic biological knowledge hampers a strongly supported answer for this question. However, it is reasonable to say that species of these two clades are ecological equivalents, defined as non-closely related taxa that occupy similar habitats, belong to the same guild, and perform similar ecological functions in different biomes (Pianka 1974; Gitay et al. 1996). Cranaid and goniosomatine species live mostly in tropical forests, where they are found foraging mainly on the vegetation at night (e.g., Acosta & Machado 2007; Proud et al. 2012; Caetano & Machado 2013; Colmenares & Tourinho 2014). Moreover, both in the Atlantic and in the Amazon forest, species of these two clades are the largest representatives of the harvestmen community, feeding mostly on large prey, such as cockroaches, moths, beetles, and even frogs (Table S1 in Supplementary Material 2, available online at <http://dx.doi.org/10.1636/JoA-S-17-070.s2>, and Figure S1 in Supplementary Material 3, available online at <http://dx.doi.org/10.1636/JoA-S-17-070.s3>). Some species of the two clades can also be found inside caves, where they also feed mostly on large prey, including earthworms, cave crickets, and wandering spiders (Table S1 in Supplementary Material 2). Considering that the sister groups to both cranaids and goniosomatines are composed mostly of small-bodied, short-legged, and ground-dwelling species (Pinto-da-Rocha et al. 2014), we argue that three morphological traits found in these two clades, namely large body size, long legs, and heavily armed pedipalps, evolved convergently under selection for the use of large prey and/or a greater spectrum of prey sizes living on the vegetation (see further discussion on leg length and vegetation use in Curtis & Machado 2007 and Caetano & Machado 2013).

In a comparative study with insects, a positive relationship has been found between female and egg sizes (Gilbert & Manica 2010). Another comparative study with frogs found an association between parental care and large egg size, and showed that the evolution of large egg size precedes the evolution of parental care (Summers et al. 2006). Based on these life-history patterns found for terrestrial ectotherms, we propose a hypothetical evolutionary scenario that accounts for many behavioral convergences between cranaids and goniosomatines. First, natural selection favoring large body size in species of both clades may have promoted a side effect: large females tend to lay large eggs, which have proportionately lower respiratory and metabolic rates, and slower development rate (Sargent et al. 1987). Assuming that instantaneous egg mortality is constant throughout embryonic development,

the longer the development, the higher is offspring mortality. If parental presence reduces mortality risk of eggs with slow development (as it is the case in harvestmen, see review in Santos et al. 2017), theory predicts that parental care should evolve (Klug & Bonsall 2009). Once parental care has evolved, the next step should be the evolution of oviposition site selection, because inadequate sites may expose both the eggs and the parents to unfavorable biotic and abiotic conditions (Mousseau & Fox 1998). Females of several predatory species living on the vegetation and exhibiting maternal care indeed select oviposition sites (Osses et al. 2008 and references therein). Finally, whenever the preferred oviposition sites can be economically defended by males, we should expect the evolution of a resource defense polygyny mating system (Emlen & Oring 1977). This evolutionary scenario explains why cranaids and goniosomatines are so large, lay large eggs, exhibit maternal egg attendance, and have a mating system based on resource defense, in which males fight for the possession of oviposition sites. Our hypothetical scenario also proposes a series of evolutionary transitions that could be formally tested when the availability of basic information on the biology of a larger set of cranaid and gonyleptid species allows comprehensive comparative studies.

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