

Ecological and evolutionary pathways of social behavior in Pseudoscorpions (Arachnida: Pseudoscorpiones)

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Received: 25 September 2008 / Revised: 5 February 2009 / Accepted: 26 February 2009 / Published online: 10 March 2009
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Abstract Despite the great biodiversity in the Arachnida, some taxa are still now poorly known, mainly in terms of biology, ecology, and behavior. Pseudoscorpions are small arachnids (2–8 mm) that live in cryptic environments, being in general solitary predators of other invertebrates. The most studied Pseudoscorpion species are those from temperate areas, which revealed that Pseudoscorpiones present some level of sociality based on maternal care. Most developed sociality is seen in tropical species. Here, we reviewed this issue, presented examples of social behavior, and suggested the steps involved in the evolution of permanent sociality in the Neotropical Atemnidae genus, *Paratemnoides*. We discussed that the extended parental care, division of labor, cooperative breeding and feeding, and the tolerance among members dividing the same share could be considered enough to characterize a true social life, same in invertebrates.

Keywords Arachnida · Cooperation · Evolution · Bark Fauna · Neotropics · Cerrado

Introduction

For centuries, social behavior has caused fascination among researchers of natural sciences. It occurs specially due to its rarity in the major part of taxonomic groups and peculiar selective and evolutionary process. Nowadays, there is an enormous quantity of papers related to general aspects of social life, which includes classification models, origins, and evolution (e.g., Wilson 1971). Considering invertebrates, the major part of known social life is restricted to insects, mainly Hymenoptera. It is not common in Arachnida, where spiders, in particular, compound a group recognized as solitary, intolerant, and sometimes territorial and cannibalistic animals (D'Andrea 1987; Gonzaga 2007; Lubin and Bilde 2007). However, one can be surprised with notable examples of huge spider colonies able to produce permanent aggregations maintained by a cooperation system (D'Andrea 1987; Gonzaga 2007; Lubin and Bilde 2007). Nevertheless, the differences among insects and spiders (e.g., Wilson 1971; Darchen and Delage-Darchen 1986; Avilés 1997; Plateaux-Quénu 1997; Choe and Crespi 1997; Costa 2006) are obvious and well discussed. In Arachnida, the most complex models of cooperative societies occur in Araneae, for example *Anelosimus eximius* and *Stegodyphus dumicola*, among others (Avilés 1997; Gonzaga 2007; Lubin and Bilde 2007). In Arachnida, only Pseudoscorpions can present social life as developed as spiders (Tizo-Pedroso and Del-Claro 2007).

Recently, a well-done analysis revealed important similarities among insects' and spiders' social life (Choe and Crespi 1997; Costa 2006), but the universality of social stages classification is also a matter of question (Wilson 1971; Darchen and Delage-Darchen 1986; Avilés 1997; Plateaux-Quénu et al. 1997; Wcislo 1997; Costa 2006). Indeed, the three basic attributes for a species to be

Communicated by R. F. Oliveira

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considered eusocial (Table 1), based on insects (Michener 1974), are not totally applied to other invertebrates. Depending on the ecological factors, non-insect species can fill up the attributes of eusociality in a specific moment but not in other circumstances (Costa 2006). In the existent systems, it is difficult to point out where Pseudoscorpions could be placed. Thus, we will use the model proposed to social spiders by Kullmann (1972) to classify the known Pseudoscorpions species and discuss the main characteristics and evolutionary process related to Pseudoscorpions social behavior.

The Pseudoscorpiones order

Pseudoscorpions are small arachnids (2–8 mm) that live in cryptic environments such as leaf litter, rock crevices, under stones and barks of live trees, and or rotten trunks, among others (Weygoldt 1969; Harvey 1986). In Europe and North America, there is a species very common inside old and missed books, *Chelifer cancroides* (Linnaeus 1758; Cheliferidae), which has scared through time several librarians, being popularly known as book scorpions (Levi 1953). These animals, also named false scorpions, resemble scorpions in morphological aspects like shape and presence of chelated pedipalps, but differ strongly in size, being smaller and by the absence of the elongated metasoma with the sting in distal portion (Weygoldt 1969; Harvey 1986). Pseudoscorpions occur in almost all terrestrial environments, including islands, where they arrive through phoresy associated to birds for example, wherein an exception are polar regions (Harvey 1986 and references therein).

Pseudoscorpiones is a diversified order that represents more than 3% of all known arachnids, the fourth most diverse group in this class. They are distributed in 25 families, 470 genera, and around 3,400 described species (see Harvey 2002, 2007 for recent statement of systematic). If we consider the small number of taxonomists in this peculiar group, the cryptic habit of the major part of known species, and lack of precise information about tropical invertebrate diversity, we can speculate that these numbers could be, in fact, bigger. Fossil proofs demonstrated that

these animals have walk about on Earth since early Devonian, 380 millions of years, and present very few morphological modifications in relation to the extant species (Shear et al. 1989). These ancestors, related to Chthonioidea, already had pedipalps, chelicerae, galea (structure used to produce silk), and trichobothria to perceive vibrations. Due to its similarities, in size, morphological aspects, and suggested habitats by fossil records, some researchers believe that the biological and behavioral features could have been maintained (Shear et al. 1989; Poinar et al. 1998).

Life history

Microhabitat

Pseudoscorpions, in the Old and the New World, are predominantly solitary animals that can live in the ground substratum, in the vegetation, or in both; they use one or other ways to find a better ecological resource. In spite that the most common species lives in the leaf litter, rock crevices, or bark trees, there are also species that inhabit unexpected places like rosettes of Bromeliaceae (Weygoldt 1969; Aguiar and Bührnheim 2003) and other vegetation in coast (Gabbutt 1970), bat guano (Andrade and Gnaspini 2002), ant and bee nests (Cole et al. 1995; Gonzalez et al. 2007), and the body of birds and mammals (Francke and Villegas-Guzman 2006). Regardless that the lifetime of adults is poorly known (Levi 1948, 1953), literature data suggest that their lifetime is too variable just as their habitat preferences. *C. cancroides* (Cheliferidae) for example, can live several years, including three post-embryonic stages that can delay 1 or 2 years. To other species, Weygoldt (1969) pointed out that the post-embryonic development can delay more than 1 year, but also without present reliable information about adult lifetime. We have been studying a Neotropical species, *Paratemnoides nidificator* (Atemnidae), and our data regarded in laboratory conditions showed that the whole lifetime of this species is around 4 years in laboratory ($X \pm SD = 46 \pm 14$ months; $N = 34$ individuals, 17 males and 17 females).

Table 1 The basic features of eusocial Hymenoptera (adapted from Wilson 1971) applied to cooperative spiders and Pseudoscorpions

Social features	Eusocial insects	Cooperative spiders	Cooperative Pseudoscorpions
Cooperative breeding ^a	+	+	+
Overlapping generations ^a	+	+	+
Reproductive caste ^a	+	–	–
Cooperative forage	+	+	+
Haplodiploid system	+	–	–

^a Attributes most commonly used by most authors to consider a species as eusocial

Diet

Springtails, book lice, beetles, and other insect larvae, mites, and other small invertebrates constitute the food items of these active predators (e.g., Gilbert 1951; Weygoldt 1969; Harvey 1986). Both adults and juveniles are able to hunt, and in general, juveniles feed with higher frequency (Levi 1948; Weygoldt 1969). In the hunting behavior, the pedipalps are important weapons for prey capture (Schlegel and Bauer 1994). There is a poison gland associated to one or both pedipalps' fingers (or can be absent in some families) to subdue and paralyze the prey (Harvey 1992). In fact, the toxin is inoculated through a more developed tooth present in the distal portion of the chelae that is also used to grasp the prey's body to its pedipalps (Gilbert 1951; Schlegel and Bauer 1994). In Epiocheirata, there is no poison gland, which is an important taxonomic aspect (Harvey 1992). Solitary species present some prey specificity, for example, *C. cancroides* is a predator of book lice and other small insects (Levi 1948, 1953); in caves of South America, *Maxcheres iporangae* (Mahnert and Andrade 1998; Chernetidae) feeds on small invertebrates that lives on bat feces (Andrade and Gnaspini 2002). On the other hand, recent studies have showed that social species can be generalist and that it is probably related to the major needs of food supply to satisfy an entire colony. Tizo-Pedroso and Del-Claro (2007) studied the forage ecology and social life of *P. nidificator* (Atemnidae) in the Brazilian savannas and documented the use of more than 60 distinct prey items (15 taxonomic groups), which included dangerous preys like ants and spiders (Fig. 1). Pseudoscorpions can also present cannibalism, a charac-

teristic of solitary species that also can occur among individuals of different colonies in the social species (Weygoldt 1969; Tizo-Pedroso and Del-Claro 2007).

Dispersal behaviors

Due to its small size, Pseudoscorpions present restrictions to disperse or to migrate to other environments. The most common way to explore a new site is, indeed, to walk from one place to another. It enables Pseudoscorpions to occupy a new piece of a bark tree a few meters distant from the original position in the same tree or in a neighbor tree, for example. However, Pseudoscorpions can present an unexpected way of dispersion. They can be phoretic, attaching itself to the body parts of a larger flyer insect as a vehicle or they can ride the vector (Poinar et al. 1998; Zeh and Zeh 1992a, b). Phoresy is a common way of dispersion also observed in other arachnids like mites and also insects that use the body of birds and mammals. To Pseudoscorpions, it is barely discussed and has already been evidenced in 11 of the 25 families (Poinar et al. 1998). Some authors believe that it can represent an important way to the foundation of new colonies in social species (Fig. 2; Tizo-Pedroso and Del-Claro 2007). This field work is promising because there are some incredible cases of phoresy in Pseudoscorpions, like that of *Cordylochernes scorpioides* (Linnaeus 1758; Chernetidae, Zeh and Zeh 1992c, d). This animal uses the body of Harlequin giant beetles (*Acrocinus longimanus*, Cerambicidae) as a vehicle, and males dispute the vector. Additionally, the copulation and sperm transfer in this species can occur on the beetle's dorsum (Zeh and Zeh 1997).

Fig. 1 Invertebrate taxonomic groups used as food item by *P. nidificator* in Brazilian Cerrado. Numbers above columns represent the total of morph species in the groups (adapted from Tizo-Pedroso and Del-Claro 2008)

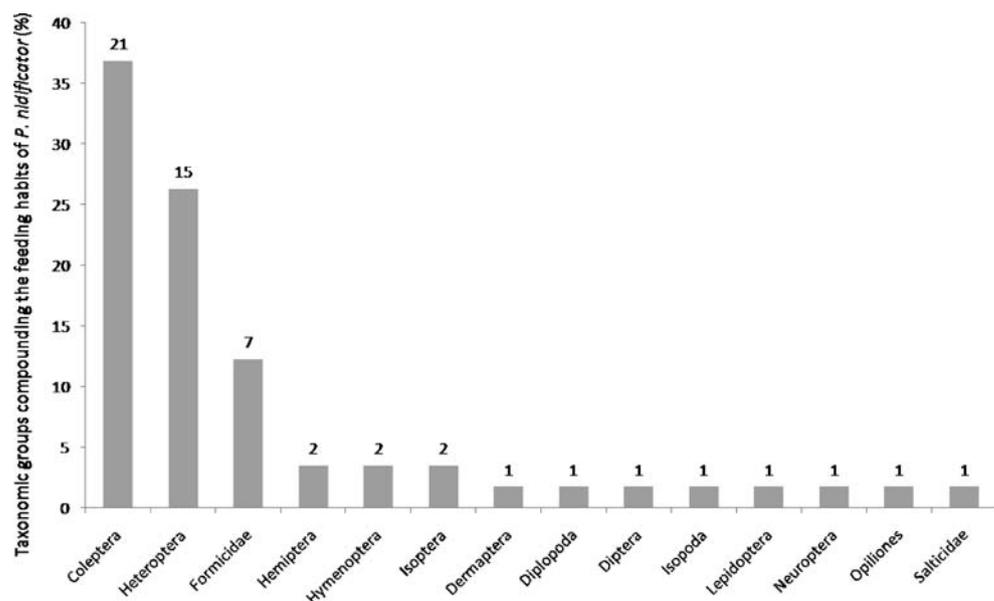




Fig. 2 Multiple phoresy behavior. Several individuals of *P. nidificator* attach themselves on the vector appendices (in this case a hemipteran predator) to disperse to new environments

Reproduction

The reproductive behavior of Pseudoscorpions is known only in 13 of the 25 families (Zeh and Zeh 1997). They are dioic animals, with internal fecundation and indirect sperm transfer, through a spermatophore. This structure, the spermatophore, a package full of sperm, is deposited on the ground in the courtship (“pairing behavior”), or this “bag” is simply abandoned in a common way to be found by the females (Weygoldt 1969). When there is pairing behavior, the spermatophore is more complex in its structure, and it presents some triggers that enable attachment to the female's genital opening (Weygoldt 1969). These animals, in general, reproduce once a year, but it can be different in social species, which might present successive reproduction events through the year, mainly in summer and spring (Tizo-Pedroso and Del-Claro 2007). Unfortunately, there are few data about the reproductive system such as information about ecology, natural history, and behavior of these animals. In fact, in some cases, there is no direct contact between male and females, thus so, there is no pairing behavior (Zeh and Zeh 1997).

The social life of Pseudoscorpions

As previously mentioned, Pseudoscorpions are primarily solitary animals. However, these solitary species present parental care, a common characteristic expected in all known species (e.g., Weygoldt 1969). In Chthonioidea, a classical example, the female produces a brood pouch that is maintained and attached to its genital opening. It is similar to a sac full of fluids and embryos inside. The mother sometimes can build a silk chamber, but it depends on the species. When the female does not produce the silk

chamber, it remains with the pouch until the nymphs hatch, and in 1 or 2 days, the dispersion occurs. When the chamber is produced, the female stays inside the chamber until the protonymphs hatch. Also, 1 or 2 days later, the dispersion occurs (e.g., Weygoldt 1969). To all known species, females produce a nutritive fluid that feeds embryos and nymphs in development.

The major part of Cheliferoidea is solitary but its embryonic sac is different, which is a membranous and well-defined structure that results in a clear separation of each embryo. In this case, the structure is named brood sac (Fig. 3). This superfamily is divided into Chernetidae, Atemnidae, Cheliferidae, and Withiidae. The existence of some degree of sociality in members of the Cheliferidae, Chernetidae, Atemnidae, and also in Neobisiidae was identified. These families could represent the first steps in the development way of social behavior in this animal group: gregarity. Levi (1948, 1953) reported the founded aggregations of *C. cancroides* (Cheliferidae), a species recognized to be solitary and sometimes territorial (Levi 1953; Weygoldt 1969). Gregarity was evidenced through simple observation of groups of individuals together in the soil at the basis of plants. In Neobisiidae were evidenced cases of aggregations in one species from the litoranean zone, *Neobisium maritimum* (Leach 1817). This European species lives insides crevices of rocks, and two or three reproductive females can build reproductive chambers side by side (Gabbutt 1966; 1970). However, it is only an anecdotal observation since there are no data about any cooperation, only a suggestion. Weygoldt (1969) in his extensive studies in Pseudoscorpion biology described females of *Neobisium muscorum* (Leach 1817) that build cooperatively their reproductive silk chamber. Another extraordinary example was presented by Orghidan and



Fig. 3 Female of *Americhernes bethanae* (Mahnert 1978) in its reproductive silk chamber. The embryos develop in the brood sac attached in the mother's genital opening

Dumitrescu (1964), that reported aggregations of dozens of adults and their silk chambers in the Cheliferidae *Hysterochelifer meridianus* (Linnaeus 1758) and in the Cheridiidae *Apocheiridium ferum* (Simon 1879). Turk (1953) described a small Chernetidae from Argentina, *Sphenochernes schulzi* (Turk 1953), that appears to have some degree of cooperation like capture of large prey (ants) or collective dispersion. Another form of sociality occurs in Atemnidae, in this case based on more elaborated maternal care. In this case, females of *Atemnus politus* (Simon 1878) are able to provide maternal care up to the brood dispersion. The more elaborated cases of sociality in Pseudoscorpions are seen in *Paratemnoides* genus (Table 2).

The *Paratemnoides* case

The *Paratemnoides* genus (Harvey 1992) encloses an important number of species known in Atemnidae (Chamberlin 1931). Nowadays, 33 species are recognized and widely distributed through Americas, Africa, and Asia (Harvey 2008). In contrast to the great richness of this genus, the literature provides very few data about its natural history,

ecology, or behavior. The few information available report two social species in the Americas: *P. nidificator* (Balzan 1888) and *Paratemnus elongatus* (Banks 1895). Recently, *Paratemnus minor* (Balzan 1892) was recognized as a synonym of *P. nidificator*. For a review in statement of *Paratemnoides*, see Klausen (2005). Brach (1978) was the first to call attention to aspects of the cooperative life in Pseudoscorpions. The author observed colonies of *P. elongatus* in the bark of *Pinus elliotti* at Florida, and he reported a series of communal behaviors like the group life, multiple phoresy, and the existence of silk chambers, built side by side inside the colonies. The forage behavior of this species was investigated in more details by Zeh and Zeh (1990) that observed groups of *P. elongatus* capturing preys up to 30 times heavier than an individual hunter. After that, natural history aspects, with details of group life and post-embryonic development, were reported also to *P. minor* in Brazil (Hahn and Matthiesen 1993a, b). However, the extreme sociality in Pseudoscorpions was revealed only in recent days in a series of papers by Tizo-Pedroso and Del-Claro (2005, 2007, 2008) with *P. nidificator*.

Table 2 Available knowledge about social behavior in Pseudoscorpions

Species	Family	Distribution ^a	Social level	Classification ^b	Author(s) and publication year
<i>Paratemnoides nidificator</i>	Atemnidae	Central and South America	Permanent and cooperative life form	Non-territorial permanent social	Hahn and Matthiesen (1993a, b); Tizo-Pedroso and Del-Claro (2005, 2007, 2008)
<i>Paratemnoides elongatus</i>	Atemnidae	Central and South America and south of North America	Permanent and cooperative life form	Non-territorial permanent social	Brach (1978); Zeh and Zeh (1990)
<i>Atemnus politus</i>	Atemnidae	Europe and north of Africa	Extended maternal care	Subsocial	Weygoldt (1969)
<i>Apocheiridium ferum</i>	Cheiridiidae	Europe	Large aggregations of adults and silk chamber	Temporary social	Orghidan and Dumitrescu (1964)
<i>Chelifer cancrroides</i>	Cheliferidae	Cosmopolitan	Facultative aggregations	Temporary social	Levi (1948, 1953)
<i>Hysterochelifer meridianus</i>	Cheliferidae	Europe and north of Africa	Large aggregations of adults and silk chamber	Temporary social	Orghidan and Dumitrescu (1964)
<i>Sphenochernes schulzi</i>	Chernetidae	South America: Argentina	Some level of cooperation and group dispersion	No sufficient information for classify	Turk (1953)
<i>Neobisium maritimum</i>	Neobisiidae	France, Ireland; Portugal; United Kingdom	Two or three females can build silk reproductive chambers side-by-side in rock crevices	Non-territorial temporary social	Gabbutt (1962, 1966)
<i>Neobisium muscorum</i>	Neobisiidae	Europe	Facultative cooperation in brood silk chamber by females in laboratory	Non-territorial temporary social	Weygoldt (1969)

^a Additional information was obtained in Harvey's online catalog of Pseudoscorpiones (Harvey 2008)

^b Based on Kullmann (1972)

P. nidificator is a common species that lives in communal nests under barks of Cerrado (the Brazilian tropical savanna) trees. Nests are composed of adults (sex ratio 2:3, males and females, respectively) and nymphs, sometimes more than 200 individuals (Tizo-Pedroso and Del-Claro 2007). Inside each nest, we can find several molt (minimum of three to up to 40 units) and brood chambers (less than seven units). The differences between the two types of chambers help us to understand the development of social life in this species. The silk molt chambers (Fig. 4a) are built exclusively by nymphs, in cooperation, and are used in the process of ecdysis. These chambers also act as a shelter against climatic disturbance, protection against natural enemies, and a place where nymphs and adults can interact. Brach (1978) suggested that when inside of the chambers, adults can thermoregulate, which could maintain warm during the coldest hours. In the Cerrado, which is very dry and hot during the day but the temperature falls ten or more Celsius degrees at the night, we speculate that chambers can also help in the maintenance of humidity. Experimental manipulation revealed that the development of *P. nidificator* nymphs without the molt chamber can be interrupted by the attack of fungus, which kills them. Additionally, nymphs alone are unable to finish the chamber until the torpor phases of ecdysis needing help of their colony mates (unpublished data). The brood chamber is also built with the silk (Fig. 4b), this time produced by a reproductive female, which does the entire job alone. The female remains inside the chamber until the nymphs arise and pull off the brood sac. Then, the mother and the nymphs will leave the chamber only to feed on preys captured by other adults. So, males and other non-reproductive females allow the young individuals to feed freely on the prey they captured. Thus, this species exhibit not only nest cohabitation and food share but cooperation levels reaches cooperative parental care. Maternal care in

this species shows another distinct feature. If a mother, for instance, is alone in the bark of a tree without help of coespecifics to get a prey and time is passing, it and its brood will be hungry. Tizo-Pedroso and Del-Claro (2005) showed that reproductive females of *P. nidificator* can offer themselves as food to brood in a process known as matrophagy. These authors suggested that in this case, by reducing the chances of cannibalism and increasing the individual tolerance, matrophagy should be considered an important step in the evolution of permanent sociality in this particular species.

Whitehouse and Lubin (2005), based on the functions of spiders society, proposed a new way to evaluate how social behavior evolved in Araneae. These authors suggested that colonies can have a protective, reproductive, or forage function. To the cooperative spiders, the authors suggest that the main function is to improve reproduction. Whitehouse and Lubin (2005) do not discard the possibility of overlap between functions. Social structure among Pseudoscorpions and cooperative spiders is similar, which suggest that the main function of sociality in Pseudoscorpions could also be reproductive. In social spiders, hunt cooperation is suggested to be more of a consequence than cause of group life (Whitehouse and Lubin 2005). In Pseudoscorpions, it is different. Although the reproductive function of group life be present and strong in *P. nidificator* (Tizo-Pedroso and Del-Claro 2007), the cooperative hunting is also fundamental. In colonies without hunt cooperation, the individuals disperse or die. Thus, we suggest that in social Pseudoscorpions, the positive result of a combination of distinct functions (reproduction, forage, and defense) could have favored the group life.

Non-territorial permanent sociality (sensu Avilés 1997) is considered the highest level of social organization in arachnids. To be a permanent social, the species has to present: group life, overlapping generations, common nest,

Fig. 4 Silk chambers in *P. nidificator*. **a** Molt silk chambers; **b** reproductive silk chamber



and cooperative behavior. In the case of *P. nidificator*, we suggest that this species goes beyond this classification. In fact, the nymph activities (mainly built of molt chambers that can be used by adults, see above) differ strongly from non-reproductive adult activities (hunt and defense) and from the reproductive female. Thus so, could it be considered division of labor, resembling social hymenopterans? Could this species be classified as *quasisocial* like several hymenopterans wasps? To us, extensive parental care, division of labor, cooperative breeding and feeding, and the tolerance among members that shares the same nest sounds enough to characterize a true social life seen in other invertebrates.

Sociality and Pseudoscorpiones phylogeny

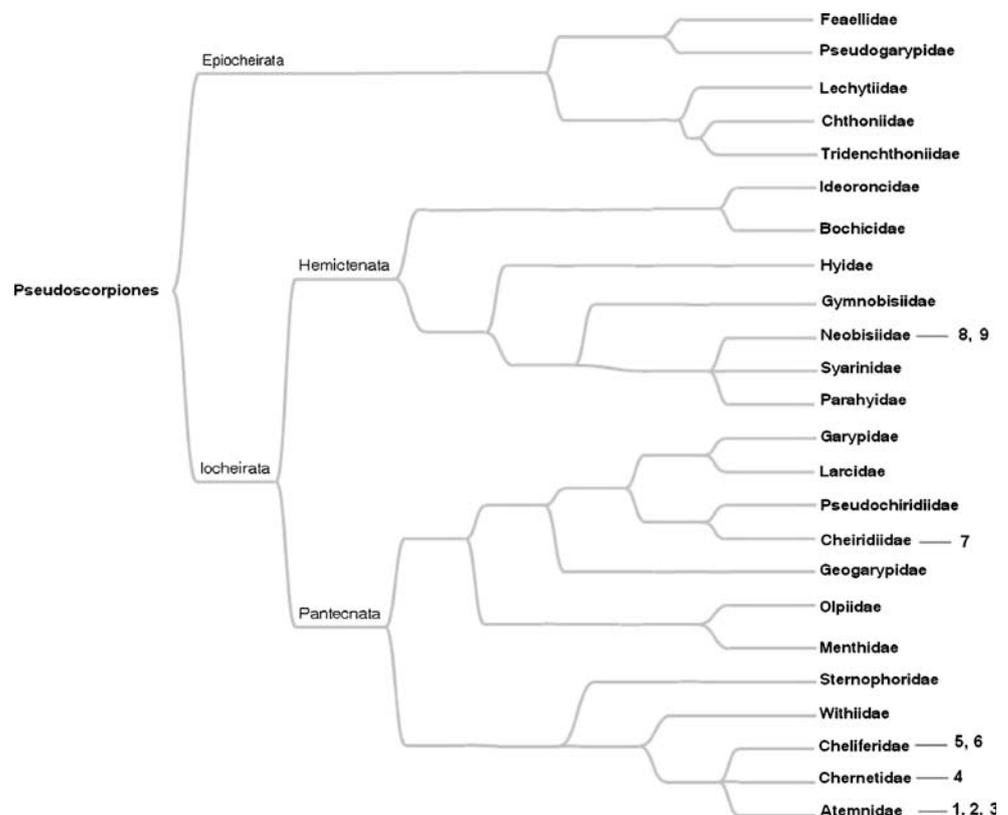
The phylogenetic relationships between species that present some level of sociality could provide a better understanding of how social behavior evolved in Pseudoscorpiones. Still, nowadays, available information is not enough to map and analyze phylogenetically the social strategies in this group. Murienne et al. (2008) proposed a general phylogeny to Pseudoscorpiones based on molecular data, and their results do not corroborate the previous ones of Harvey (1992) that used traditional morphological analysis. The main difference is that to Murienne et al. (2008), superfamilies

Neobisioidea, Garypoidea, and Cheliferoidea are not monophyletic groups. Here, we pointed and discussed the position of social species in the group (Fig. 5) based on Harvey (1992).

The Cheliferoidea superfamily groups six of nine known social species of Pseudoscorpiones (Fig. 5) that are distributed in three families: Chernetidae (one species), Cheliferidae (two species), and Atemnidae (three species). These three families can be considered sister groups; however, according to Harvey (1992), they are not a monophyletic clade (but see also Proctor 1993). The other social species are in Neobisiidae and Cheiridiidae, groups that are very distant (Fig. 5).

Behavioral characteristics reveal that in Neobisiidae, the two social species, in fact, are gregarious with a very simple cooperation system. The Cheiridiidae species also present a very simple social behavior and huge aggregations without any cooperation. The major problem to understand social behavior in a phylogenetic perspective in Cheliferoidea is that the species present so different levels and mechanisms of sociality that it is difficult to suggest a common origin to this subgroup. For example, could it be that Cheliferidae followed a parasocial rote (sensu Wilson 1971) while Atemnidae followed a subsocial rote (sensu Wilson 1971)? The data about Chernetidae are so few that we can affirm nothing about it.

Fig. 5 The Pseudoscorpiones phylogeny (adapted from Harvey, 1992), with the social species. 1 *P. nidificator*; 2 *P. elongatus*; 3 *A. politus*; 4 *S. schulzi*; 5 *H. meridianus*; 6 *C. cancroides*; 7 *A. ferum*; 8 *N. maritimum*; 9 *N. muscorum*



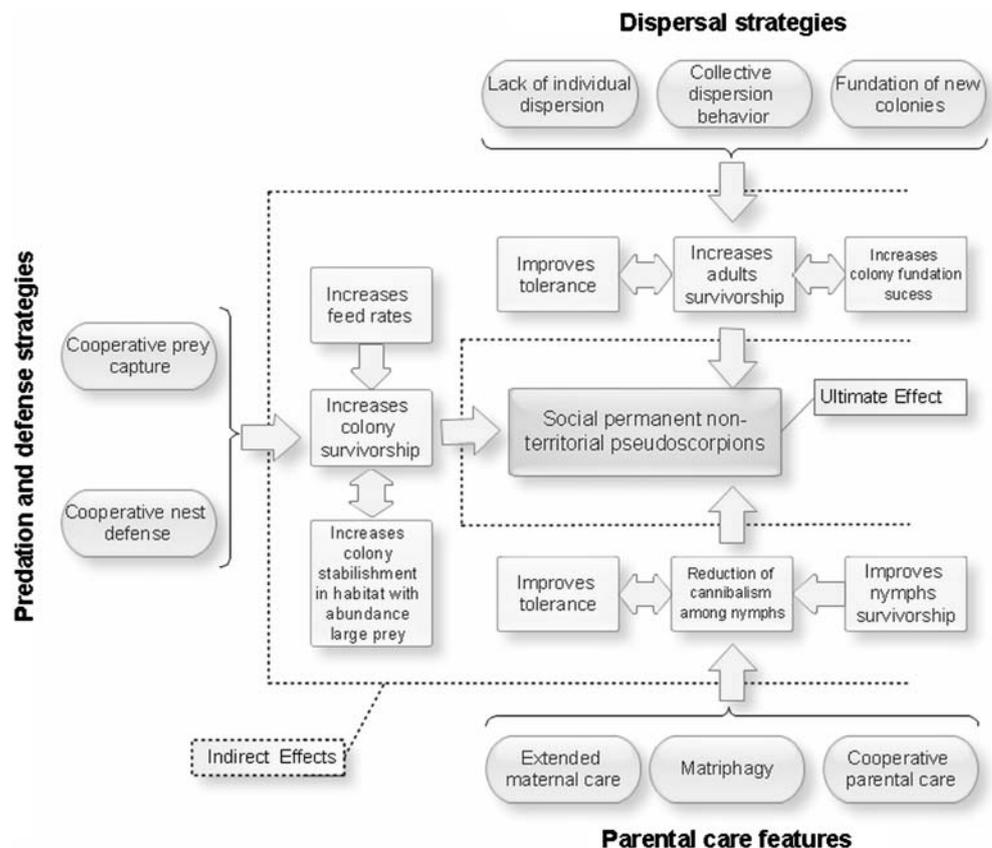
Steps in evolution of social behavior in *Paratemnoides*

To establish and discuss similarities between social Pseudoscorpions and other social Arthropods is difficult, mainly due to the fact that they belong to groups phylogenetically distant, as for example Apidae (Hymenoptera), Theridiidae (Araneae), and Atemnidae (Pseudoscorpiones). Despite this fact, Pseudoscorpiones are still now poorly known in all aspects compared with other arthropods. There are few details in the major part of papers that describes social behavior and also lack known cases that could be considered intermediate steps in the evolution of sociality in this group. Any proposal about the evolutionary steps that conducted Pseudoscorpions to sociality is only a speculation. In the specific case of *P. nidificator*, the extreme parental care, matrophagy (Tizo-Pedroso and Del-Claro 2005), is very suggestive. Matrophagy can reduce chance of cannibalism and increases tolerance among nymphs. Thus, individual tolerance in *P. nidificator* possibly resulted of matrophagy (Tizo-Pedroso and Del-Claro 2005) and could have also increased the chances of cooperative breeding and hunting among individuals, which progressively resulted in a more elaborate strategy of social life (Fig. 6). In cooperative spiders, the individual tolerance is also indicated as an

initial step (Avilés 1997), followed by the life in a common nest (Lubin and Bilde 2007), cooperative hunting, and breeding (Lubin and Bilde 2007). Despite the fact that Pseudoscorpions and spiders have several biological differences, the similarities in social attributes suggest a convergent evolution. However, up to this moment, there is no enough information in the literature to support a linear hypothesis as proposed in the pioneer evolutionary studies of spider sociality (Kullmann 1972; D'Andrea 1987; Plateaux-Quénu et al. 1997).

Indeed, social life is rare among arachnids, and social *Paratemnoides* genus is a peculiar and unique example of permanent sociality (sensu Avilés 1997) in Pseudoscorpions. These animals call our attention to other relevant questions related to the evolution of the ecological scenery that allowed its derivation, like: Are we underestimating the occurrence of social behavior in this group? Is there any other social species in the Brazilian savannas and, also, in the almost unknown invertebrate fauna of the Amazonian forest? Could we find more examples in other similar tropical systems? Where are the intermediate Pseudoscorpion species that represents the step between the simple parental care present in all of them and the complex sociality observed in *Paratemnoides*? There is a lot of work to be done.

Fig. 6 Suggestive steps that conducted to the evolution of social behavior in *P. nidificator* (Pseudoscorpiones: Atemnidae). All Pseudoscorpions present parental care (basic feature). Matrophagy could increment it, reducing chances of cannibalism and enlarging tolerance and cooperative behaviors related to feeding, defense, and dispersal. Possibly, the sum of different adaptative features more probably resulted in a social permanent non-territorial species (sensu Avilés 1997) than a strong isolated aspect



Acknowledgments We thank Dr. Rui Oliveira for inviting us to write this review, Marina F. Mineo and Pietro K. M. Mendonça and two anonymous referees for suggestions and English review, and to Plamen Mitov for sending us copy of old papers about Pseudoscorpions. K. Del-Claro thanks the financial support from the CNPq (PQ) and the Fapemig. E. Tizo-Pedroso is supported by the Fapemig.

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