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SYMBIOTIC RELATIONSHIPS BETWEEN PSEUDOSCORPIONS (ARACHNIDA) AND PACKRATS (RODENTIA)

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ABSTRACT. Thirty-two species of pseudoscorpions have been found co-existing with nine packrat (or woodrat) species of the genus *Neotoma*, and this association has been referred to as phoresy. Phoresy is a term for passive dispersal when an animal literally hitches a ride on another to reach a new habitat. The pseudoscorpions reported above live in or on the nests of the packrats and do not ride on the rats themselves, eliminating a truly phoretic association. All life-history stages of the small arachnids have been found in packrat nests, indicating at least a commensalistic relationship exists, whereby the pseudoscorpion benefits from shelter and food found in the nests, and reproduces there as well. Two pseudoscorpion species have been reported feeding on packrat ectoparasites, specifically larval and adult fleas, and thus a mutualistic relationship beneficial to both "guest" and "host" exists.

RESUMEN. Treinta y dos especies de pseudoescorpión han sido halladas en los nidos de ratas del género *Neotoma*, y esta asociación ha sido llamada foresis. Foresis, sin embargo, es un término específico para dispersión pasiva donde un animal viaja sobre otro para llegar a un nuevo habitat. Los pseudoescorpiones viven en los nidos de las ratas y no han sido encontrados sobre las ratas mismas, descartando una verdadera asociación foretica entre ellos. En los nidos de las ratas se han encontrado todos los estadíos del ciclo de vida de los pseudoescorpiones, indicando que existe una asociación comensalistica donde los pequeños arácnidos se benefician de la protección y el sustento que reciben en el nido, e incluso se reproducen en él. Se han reportado dos especies de pseudoescorpión alimentandose de los ectoparasitos de las ratas, específicamente de pulgas larvales y adultas, resultando en una asociación mutualistica donde ambos el "huesped" y el "hospedero" se benefician.

Keywords: Packrats, *Neotoma*, phoresy, commensalism, mutualism

The presence of pseudoscorpions in rodent nests has been known for a long time (e. g., see Beier 1948; Weygoldt 1969). Noteworthy are the interactions between these arachnids and packrats (also known as woodrats) of the genus *Neotoma* Say and Ord, 1825; to date, 20 genera and 32 species of pseudoscorpions have been registered from the nests of 9 species of packrats. A number of these reports came from faunistic surveys of the nest inhabitants (e. g., Walters & Roth 1950; Beck et al. 1953; Fitch & Rainey 1956; Cudmore 1986; and Alvarez et al. 1988), which merely list the arthropods found on or inside the packrat nests. A number of other reports originate from taxonomic works describing the often-new species of pseudoscorpions retrieved from those nests (Chamberlin 1952; Hoff & Clawson 1952; and Hoff 1956a, b, c), paying little attention to the possible interactions between "host" and "guest".

Symbiosis has been defined by Wilson (1975) as the intimate, relatively protracted, and dependent relationship of members of one species with those of another. He further recognized three kinds of such interactions: parasitism, commensalism and mutualism. Phoresy is defined as "A symbiotic relationship, especially among arthropods and some fishes, in which one organism transports another organism of a different species" (http://www.yourdictionary.com/). Vachon (1940) provided the first comprehensive review of the topic of phoresy in pseudoscorpions. He noted that many different species had been reported clinging to the appendages of other arthropods, primarily flies (Diptera), presumably for dispersal to new habitats, and termed it active phoresis. Other pseudoscorpions have been found as "residents" under the wing-covers or elytra of beetles (Coleoptera), presumably feeding on mites (ectoparasitic and/or ectocommensalistic) and not readily engaged in dispersal activities, and he termed this passive phoresis. He also noted that some pseudoscorpions had been retrieved from the plumage of birds, and presumed that they were feeding on feather mites (Acari), and thus also fell under his category of passive phoresis. In light of the various definitions given above, active phoresis is an example of commensalism where the pseudoscorpion benefits from being dispersed, and the fly is neither harmed nor benefited. Passive phoresy however could be either an example of ectocommensalism where the pseudoscorpion benefits both from the protection afforded by the elytra of the beetle and from the nourishment on non-parasitic mites while there, and the beetle gets no benefits; or an example of mutualism if the pseudoscorpion feeds on parasitic mites thus benefiting the beetle by their removal.

Beier (1948) elaborated upon Vachon's review; he restricted phoresy to mean Vachon's active phoresy and coined the term phagophilia (= "love to eat") for his passive phoresy based on the assumption that the pseudoscorpions "ride" their hosts to feed upon the commensals and ectoparasites. The terms ectocommensalism and ectoparasitism are currently favored over phagophilia. In the same paper Beier also discussed four other kinds of associations between pseudoscorpions and other animals: (a) species found in the nests of social insects, (b) species found in bird nests, (c) species found in the nests of small mammals or on such mammals, and (d) species found in human habitations. This was an unfortunate classification, because given the title of Beier's paper, ever since then the interaction between pseudoscorpions and packrats has been regarded as phoretic in nature and not given further consideration, even though the pseudoscorpions are not riding on the rats for dispersal purposes.

Finally, Muchmore (1971) updated Beier's work, providing additional records primarily from the New World and from his own observations. In this work he followed Beier's classification, and made a remark that further detracted from establishing the true nature of the interactions between pseudoscorpions and packrats: "Because all of the species listed above (of pseudoscorpion) belong to genera whose members typically inhabit soil and ground litter, it is reasonable to believe that their associations with mammals come about by chance." Chamberlin (1952) described three new species, from three different genera, then known only from *Neotoma* nests. Hoff & Clawson (1952) described five new species in four different genera, from *Neotoma* nests. Hoff (1956b) described one new genus and four new species from *Neotoma* nests. Are these discoveries the result of "fortuitous" associations? Could Knudsen's (1956) findings of 1 to 44 pseudoscorpions in 109 out of 153 (71%) nests sampled come about by "chance"? Does the diversity of pseudoscorpion taxa found *in* the nests of several different species of *Neotoma*, not *on* the rat itself, support the notion of phoresy? In this contribution we review the existing information on pseudoscorpion-packrat associations and propose that they are commensalistic and/or mutualistic rather than phoretic in nature.

MATERIALS AND METHODS

A typical packrat nest has four separate components (Álvarez et al. 1988). (1) The cover (= "the hut", "the house" or "the midden") which consists of sticks, prickly-pear pads and other assorted objects (bones, plastic toys, etc.) topping the nest. (2) The green chamber (= "feeding chamber") where the rat stores and eats its food, consisting primarily of fresh vegetable matter, fungi, fruits and seeds. (3) The resting chamber(s) (= "nest cups" or "the inner nest") consisting primarily of dried grass and fur. (4) The passages that interconnect the other components. The exact composition, size and quality of the materials used in the various parts of the nest vary among individuals and also between species (e. g., see Villegas-Guzman, 2003). Each component offers a different environment for small arthropods and differs in its accessibility to them from the surrounding areas.

Two recent contributions have actually searched for pseudoscorpions in different parts of the packrat nests (Montiel-Parra & Villegas-Guzman, 1997; and Villegas-Guzman 2003). These two studies reveal trends of frequency (i. e., percentage of nests of a given species of packrat occupied by a given species of pseudoscorpion), density (i.e., number of individuals of a given species of pseudoscorpion, including different life history stages found in a given nest), and diversity (i. e., number of species of packrats whose nests are inhabited by the same species of pseudoscorpion). In addition, knowledge of the location of the pseudoscorpion on or in the nest provides some insight into the possible interactions between "host" and "guest".

A single specimen of leaf-litter or bark inhabiting pseudoscorpion found on the cover of a packrat nest suggests nothing more than accidental transportation on a stick carried by the rat to build-up and maintain its nest—this is an incidental association due to chance. One or more pseudoscorpions of the same species, in the green chamber of several nests of the same species of packrat would indicate that they actively seek, and remain in, this habitat to feed upon scavengers and detritivores (mostly mites)—this is commensalism. Finding many pseudoscorpions, including all or most life-history stages (depending on the season of sampling) inside the nest implies a more intimate association, and if the pseudoscorpions are feeding on fleas (both larvae and adults) or parasitic mites found in the resting chamber, then we have mutualism.

In the first study, Montiel-Parra & Villegas-Guzman (1997) excavated five nests of the packrat *N. albigula* Hartley, in a pine forest in Durango, Mexico.

In the second study Villegas-Guzman (2003) sampled the following packrat nests: ten nests of *N. albigula*, five in Tamaulipas and five in San Luis Potosi, Mexico, in dry xerophytic scrubland; seven nests of *N. palatina* in Zacatecas, Mexico, in low deciduous forest; five nests of *N. goldmani* in San Luis Potosi, Mexico, associated with prickly-pear plants (*Opuntia* sp.) in dry scrubland; five nests of *N. mexicana* in mixed oak-pine forest in Durango, Mexico; and five nests of *N. micropus* in thorn bush in Tamaulipas, Mexico. In each study the various components from each nest were collected into separate plastic bags, and returned to the laboratory for processing. The samples were initially weighed and hand-sorted in search of arthropods; and subsequently placed individually in Berlese funnels for one week to extract the fauna therein. The remaining nest materials were hand-sorted a second time to ensure thorough collections. The pseudoscorpions obtained were processed following Hoff's (1949) method, with the modifications recommended by Wirth & Marston (1968). The specimens are deposited in the Colección Nacional de Arácnidos (CNAN) of the Instituto de Biología, Univ. Nacional Autonoma de México. Further details are given in Villegas-Guzman & Perez (2005).

RESULTS

Walters & Roth (1950) used Berlese funnels to sample the fauna of the "inner nest" (n=30) of *N. fuscipes monochroura* Rhoads near Corvallis, Oregon, and reported that ". . . pseudoscorpions . . . were found commonly in all the nests," but no further details on density and abundance were given, and the species was subsequently described as *Dinocheirus serratus* (Moles 1914). In the description of *D. sicarius* Chamberlin 1952 (Chamberlin 1952) [the records in the literature appear as *D. sicarius* but Muchmore (1997) synonymized this name under *D. serratus*] are listed five males from a nest of *N. fuscipes* found in Berkeley, California; and the following are listed from three nests (both "nest house" and "midden" reported separately) of *Neotoma* sp. from Monterey, California [nest 646: 6 ♀♀, 28 NN (=nymphs); nest 647: 1 ♂, 8 ♀♀, 20 NN; nest 649: 1 N]. Here we have the first evidence that the pseudoscorpions are apparently not only living in, but also reproducing inside the packrat nests.

Beck et al. (1953) sampled the "inner nest" of two species of packrat in Utah. In three out of 16 nests surveyed of *N. cinerea* (Ord) they reported seven specimens of *Archeolarca rotunda* Hoff & Clawson 1952; although in the original description of that species the authors provide records from five different nests, as follows: (a) March 1951: 2 ♂♂, 3 ♀♀, 1 T (=tritonymph); (b) March 1951: 1 ♀, 1 D (=deutonymph); (c) Oct.: 1 D; (d) Nov. 1951: 1 ♀; (e) Nov. 1951: 1 ♂, 3 ♀♀, 1 D. Here we have further evidence that the pseudoscorpions are actually living and reproducing inside the packrat nests. Beck et al. (1953) also reported finding 31 specimens of an "undetermined family" in 8 out of 35 nests of *N. lepida* Thomas sampled. This is presumably

Hesperochernes utahensis Hoff & Clawson 1952, and in the original description (1952) the authors report it from both *N. lepida* [April 1951: 1 ♂, 2 ♀♀, 2 TT, 1 D, 2 PP (=protonymph)] and *N. cinerea* (April 1949: 1 ♂, 2 ♀♀, 4 NN).

Knudsen (1956), in a remarkable contribution that has received little attention in the pseudoscorpion ecology literature, reported the presence of the pseudoscorpion *D. serratus* in 71% of 153 packrat nests surveyed in Los Angeles Co., California, and he found from one to 44 "guests" per nest. The pseudoscorpions fed on larval and adult fleas (Siphonaptera), as well as mites and other arthropods. During the summer months Knudsen found an average of 18 fleas in nests without pseudoscorpions, and only 12 fleas in nests with them. He also reports a ratio of 5 adult fleas to 3 pseudoscorpions, so we can estimate he found an average of 7 pseudoscorpions per nest. In laboratory experiments the pseudoscorpions fed readily on larval fleas (94 out of 100 tested), adult fleas (88 of 100) and mites (90 out of 100); when offered a choice between larval and adult fleas, 66% chose the former; between larval fleas and mites the choices were 70 versus 30%; and between adult fleas and mites, the fleas were taken 69% of the time.

Cudmore (1986) also used Berlese funnels to sample 10 nests of *N. floridana* (Ord) in Indiana. He found only one specimen of *Chthonius* (*Ephippiochthonius*) *tetrachelatus* (Preyssler 1790), and eight specimens of *Hesperochernes canadensis* Hoff 1945 in four separate nests. In those 10 nests he found 16,380 mites, belonging to 20 different species of both parasitic and non-parasitic habits.

Montiel-Parra et al. (2001) found 144 specimens of *Tychochernes inflatus* Hoff 1956: 11 ♂♂, 5 ♀♀ (two carrying 12 and 13 eggs, respectively), 15 TT, 75 DD and 38 PP from five nests of *N. albigula* in Durango. Also in one of the five nests they found seven specimens (3 ♂♂, 4 ♀♀) of *Cheiridium insperatum* Hoff & Clawson 1952. This pseudoscorpion species was apparently originally discovered by Beck et al. (1953) in Utah, who reported two specimens as "new genus & new species" from two nests of *N. cinerea*; whereas Hoff & Clawson in the original description (1952) detail specimens from two nests, as follows: (a) Aug.: 3 ♀♀, 3 ♂♂, 2 TT; and (b) Sept.: 10 ♂♂, 7 ♀♀, 5 TT, 1 D, 1 P. Montiel-Parra & Villegas-Guzman (1997) found 7,427 arthropods in the five nests sampled, ranging from 2906 to 266 per nest ($\bar{x}$ = 1495); and their breakdown in the nest components was: 5,342 in the resting chamber (71%), 941 in the passageways (13%), 783 in the green chamber(s) (11%) and only 361 (5%) on the cover. Among the pseudoscorpions the seven specimens of *Ch. insperatum* were found in the green chamber; whereas for *T. inflatus* 110 were in the resting chambers (75%), 20 in the green chambers (14%), 10 on the cover (7%) and 6 (4%) in the passageways. They found 374 fleas (Pulicidae and Ceratophyllidae), mostly in the resting chambers. This distribution inside the nest suggests that *Ch. insperatum* probably feeds on scavengers and that *T. inflatus* feeds on ectoparasites, especially the fleas, just as *D. serratus* does in the nests of *N. fuscipes* in California and Oregon.

Finally, Villegas-Guzman (2003) found 159 pseudoscorpions belonging to 11 different species in the 32 nests of five different species of packrats studied; some nests had single specimens, others had numerous specimens. Their distribution inside the nests was as follows: 64 in the resting chamber (40%), 53 on the cover (33%), 30 in the green chamber (19%), and 12 in the passageways (8%). Additional details can be found in Villegas-Guzman & Perez (in press). Six of the eleven species recorded by Villegas-Guzman (2003) can be regarded as incidentals, having been carried to the nest by the rat with some food or nest material, unknown to both the pseudoscorpion and the rat. One female of *Lustrochernes grossus* (Banks 1893) was found in the resting chamber of a *N. albigula* nest. One female *Paraliochthonius* sp. was found on the cover of a *N. mexicana* nest. One female of *Serianus dolosus* Hoff 1956 was found in the green chamber of a *N. albigula* nest. Two deutonymphs of *Chelifer cancroides* (L. 1758) were found on the cover of a *N. micropus* nest. Three deutonymphs of *Dinocheirus* sp. were also found on the cover of a *N. palatina* nest. Finally, *Juxtachelifer fructuosus* Hoff 1956 was found in nests of two species of rats: (a) one deutonymph in the resting chamber of a *N. albigula* nest; and (b) and three females—two in the cover and one in the green chamber—of a *N. mexicana* nest. Most likely these pseudoscorpions were brought in during the foraging forays of the residents.

Four of the species reported by Villegas-Guzman (2003) can be considered commensalistic because of their ubiquitousness in packrat nests. First, 25 specimens of *Ch. insperatum* were found in five of the seven nests of *N. palatina* sampled; all life stages were retrieved from the nests; and individuals were found in the four separate nest components, although primarily (20) on the cover. This species was previously recorded from *N. albigula* nests from Durango by Montiel-Parra et al. (2001). Second, 16 specimens of *Illinichernes distinctus* Hoff 1949 were collected from two of the five nests of *N. mexicana*; all life stages were obtained from all the separate nests components. Third is *Larca chamberlini* Malcolm & Benedict 1978, where 18 specimens were retrieved from two nests of *N. mexicana* in Durango; all life stages except protonymphs were present (and their absence from the samples is probably correlated with the species life cycle and the season of sampling), and individuals were found in all parts of the nests. Finally, *Tychochernes inflatus* was collected from the nests of three different species of rats: (a) 22 specimens from four nests of *N. albigula* from San Luis Potosi, all life stages, mostly from the resting chambers; (b) 29 specimens from five nests of *N. goldmani*, also from San Luis Potosi; all life stages represented, mostly from the resting chambers; and (c) 10 specimens from one nest of *N. mexicana*, from Durango; only adults, but also mostly from the resting chamber. It is noteworthy to recall that 144 specimens of *T. inflatus* were also recovered from five nests of *N. albigula* from Durango; all life stages represented, and also primarily from the resting chambers (Montiel-Parra et al. 2001).

Lastly, the specific nature of the symbiotic relationship between *Pachychernes* sp. and *N. micropus* is more difficult to ascertain. This undescribed species is known only from 23 specimens (1 ♂, 3 ♀♀, 11 TT, 5 DD, 3 PP) collected in four of the five nests sampled; however, all specimens were on the "cover" of the nests except for one tritonymph found in the "green chamber". The nesting habits of this packrat differ from other species in usually lacking passageways and green chambers; the nests have a well defined resting chamber (occasionally 2), and the materials usually associated with the green chamber, such as mesquite pods and seeds, were mixed with the lower half of the cover (moist and rotting sticks). Their absence in the resting chamber strongly suggests that they do not feed on the rats' ectoparasites, and thus they should be considered as strict commensals.

All the available records of pseudoscorpion-on-packrat coexistence are listed in Table 1, and the most important conclusions are summarized below. A total of 32 species of pseudoscorpion have been found coexisting with nine packrat species, and of these, 8 species are known only from those nests! The rat hosting the greatest number of pseudoscorpion species is *N. albigula* with eight species, followed by *N. mexicana* and *N. micropus* with five species each. The pseudoscorpion with the most "hosts" is *Tychochernes inflatus*, found in nests of four different packrats, followed by *Archeolarca rotunda*, *Ch. insperatum* and *Hesperochernes molestus* Hoff 1956, each found coexisting with three *Neotoma* species. Pseudoscorpions of the genus *Dinocheirus*, belonging presumably to seven different species (the two unidentified specific records were found coexisting with different species of packrat than the five identified species), coexist with packrats, as do four different species in the genus *Hesperochernes*.

There are 17 taxa which have been reported only once, from a single nest. Of these, 10 are represented by single specimens, even though on some of them more than one nest was sampled: *Chthonius tetrachelatus*, one specimen from 10 nests; and *Lustrochernes grossus*, *Paraliochthonius* sp. and *Serianus dolosus*, one specimen in five nests each. Two pseudoscorpion species are represented by two individuals, and for one of these, five "host" nests were sampled; two additional species are known from three specimens, one of them also from multiple nest sampling; and one species is represented by four specimens from a single nest. These occurrences we accept as due to chance, and consider the "coexistence" to be merely incidental. However, there are two other single-nest records that indicate another type of interspecific interaction: for *D. imperiosus* Hoff 1956, 14 specimens were found in one nest, and for *D. venustus* Hoff & Clawson 1952, 61 specimens in a single nest!

Table 1.—Pseudoscorpions recorded from packrat nests, including number of nests sampled, number of nests in which pseudoscorpions were found, life stages present (MM = males, FF = females, TT = tritonymphs, DD = deutonymphs, PP = protonymphs), total numbers retrieved from the nests, and the citation for each record (including multiple records for either guest or host species). *Species found exclusively in *Neotoma* nests.

Pseudoscorpion species	*Neotoma* host	Nests sampled	Nests having pseudo-scorpions	MM	FF	TT	D	PP	Total found	Authors
*Aglaochitra rex** Chamberlin 1952	sp.	?	1		1				1	Chamberlin, 1952
Archeolarca rotunda	*cinerea*	?	5	3	8	1	3		20	Hoff & Clawson, 1952
	cinerea	?	3						7	Beck et al., 1953
	albigula	?	1		4	2			6	Hoff, 1956c
	sp.	?	?	2	3	3 nymphs			8	Muchmore, 1971
Atemnidae	sp.	?	1		1	2 nymphs			3	Muchmore, 1971
*Cheiridium insperatum**	*cinerea*	?	2	4	10	7	1	1	23	Hoff & Clawson, 1952
	albigula	5	1	3	4				7	Montiel-Parra et al., 2001
	albigula	5	1	3	5				8	Villegas-Guzmán, 2003
	palatina	7	5	7	9	4	4	1	25	Villegas-Guzmán, 2003
Chelifer cancroides	*micropus*	5	1				2		2	Villegas-Guzmán, 2003
Chthonius tetrachelatus	*floridana*	10	1						1	Cudmore, 1986
Dinocheirus astutus Hoff 1956	*albigula*	?	19	17	28	65 nymphs			110	Hoff, 1956a
	sp.	?	1	1	1				2	Hoff, 1956a
*Dinocheirus imperiosus**	sp.	?	1			13 nymphs			14	Hoff, 1956a
Dinocheirus texanus Hoff & Clawson 1952	*micropus*	?	2	5		5 nymphs			10+	Hoff & Clawson, 1952
Dinocheirus serratus	*fuscipes*	30	all						many	Walters & Roth, 1952
	fuscipes	?	?	5					5	Chamberlin, 1952
	fuscipes	153	109	1 to 44 per nest					many	Knudsen, 1956
	sp.	?	1	1	3				4	Muchmore, 1971
	sp.	1	1	6	9	6 nymphs				Muchmore, 1997
	sp.	1	1	1						Muchmore, 1997
	sp.	1	1	1	3	4 nymphs				Muchmore, 1997
	sp.	1	1	7	5	4 nymphs				Muchmore, 1997
Dinocheirus venustus	sp.	?	1	8	33	20 nymphs			61	Hoff & Clawson, 1952
Dinocheirus sp.	*cinerea*	?	1						1	Beck et al., 1953
Dinocheirus sp	*palatina*	5	1				3		3	Villegas-Guzmán, 2003
Hesperochernes canadensis	*floridana*	10	4						8	Cudmore, 1986
*Hesperochernes molestus**	sp.	?	1	3	1	14 nymphs			18	Hoff, 1956a
	albigula	?	1	1					1	Hoff, 1956a

Table 1.—Continued.

Pseudoscorpion species	*Neotoma* host	Nests sampled	Nests having pseudo-scorpions	MM	FF	TT	D	PP	Total found	Authors
	micropus	?	1		1				1	Hoff, 1956a
Hesperochernes unicolor (Blanks 1908)	*micropus*	?	1	1	1				2	Hoff & Clawson, 1952
Hesperochernes utahensis	*cinerea*	?	1	2	2	4 nymphs			7	Hoff & Clawson, 1952
	lepida	?	1	1	2	2	1	2	8	Hoff & Clawson, 1952
Illinichernes distinctus	*mexicana*	5	2	5	4	1	6		16	Villegas-Guzmán, 2003
*Juxtachelifer fructuosus**	*albigula*	5	1				1		1	Villegas-Guzmán, 2003
	mexicana	5	1	1	2				3	Villegas-Guzmán, 2003
	albigula	18		19	22	50 nymphs			91	Hoff, 1956b
Larca chamberlini	*mexicana*	5	2	4	5	8	1		18	Villegas-Guzmán, 2003
Lechytia hoffi Muchmore 1975	*lepida*	?	1						1	Beck et al., 1953
	lepida	?		1					1	Hoff & Clawson, 1952
	albigula	?		4	2				6	Hoff, 1956c
Lustrochernes grossus	*albigula*	5	1		1				1	Villegas-Guzmán, 2003
Microbisium parvulum (Banks 1895)	sp.	?	1		1				1	Muchmore, 1971
*Globocreagris nigrescens** (Chamberlin 1952)	sp.	?	2	3	2				5	Chamberlin, 1952
Micocreagris sp.	sp.	?	1	1					1	Muchmore, 1971
n. gen. & n. sp.	*cinerea*	?	2						2	Beck et al., 1953
Paraliochthonius sp.	*mexicana*	5	1		1				1	Villegas-Guzmán, 2003
Pachychernes sp.*	*micropus*	5	4	1	3	11	5	3	23	Villegas-Guzmán, 2003
Pseudogarypinus frontalis (Banks 1909)	sp.	?	1	1					1	Muchmore, 1971
Pseudozaona sp.	sp.	?	1		1	3 nymphs			4	Muchmore, 1971
	sp.	?	1	1					1	Muchmore, 1971
Serianus dolosus	*albigula*	5	1		1				1	Villegas-Guzmán, 2003
*Tychochernes inflatus**	sp.	?	1	1					1	Hoff, 1956a
	albigula	5	5	11	5	15	75	38	144	Montiel-Parra et al., 2001
	albigula	5	5	13	22	13	66	30	144	Villegas-Guzmán, 2003
	albigula	5	4	3	1	6	11	1	22	Villegas-Guzmán, 2003
	goldmani	5	5	4	5	12	7	1	29	Villegas-Guzmán, 2003
	mexicana	5	1	4	2	?	?	?	6	Villegas-Guzmán, 2003

DISCUSSION

First, it is important to note that there are no reports of pseudoscorpions on packrats, ruling out phoresy as the primary association between these organisms. It is not only possible, but also quite probable, that the pseudoscorpions engaged in a commensalistic/mutualistic association with packrats use phoresy as a means of dispersal between host nests. There are reports of pseudoscorpions on other mammals and those specific instances mostly are indeed phoresy, although in the case of *Epichernes aztecus* Hentschel (in Muchmore & Hentschel 1982), a more intricate interaction seems to be going on (see below).

The presence of those pseudoscorpion species found in more than one nest, coexisting with more than one packrat species, or represented by adults and nymphs inside the nests cannot be due to chance alone. We consider that the interaction between packrats and pseudoscorpions is clearly mutualistic in the case of *D. serratus*, which is not only known to feed on adult and larval fleas, but also caused an important reduction in flea numbers inside the hosts' nests (from an average of 18 to an average of 12; Knudsen 1956); and possibly so in the case of *Tychochernes inflatus* because of its prevalence in the resting chambers of the nests, the diversity of packrat species it coexists with, and the single observation of an adult feeding on a flea larva (Montiel-Parra et al. 2001). All the other species, for the time being, are here considered commensalistic due to lack of information regarding their feeding habits—if they are shown to feed, even occasionally, on the rats' ectoparasites (mites and fleas primarily) then they would become mutualists. In either case, the benefits of this association to the pseudoscorpions are multiple: (a) the nests provide protection from the weather; (b) they also provide a more benign microclimate, especially in the arid and semiarid regions inhabited by packrats; and (c) due to the packrats' habits of feeding inside the nest, a community based on scavengers and detritivores develops on which the pseudoscorpions prey [see Montiel-Parra and Villegas-Guzman (1997), for an analysis of the trophic structure of a nests' arthropod community].

The diversity of mammalian nests inhabited by pseudoscorpions goes beyond packrats and has been reported from several continents (Weygoldt 1969; Muchmore 1971); if those mammals do not feed in their nests, then the pseudoscorpions are most likely feeding on ectoparasites, thus establishing a mutualistic relationship. The number of pseudoscorpion species known exclusively or primarily from packrat nests keeps increasing as these microhabitats are adequately sampled, and this attests to the suitability of the nests as an environment conducive to reproductive success. We predict that additional pseudoscorpion species will be discovered as more mammalian nests are sampled adequately.

From an evolutionary perspective it is not difficult to envision how these associations develop. First, a rodent brings material into its nest, be it food or bedding material (e.g., straw) and accidentally transports the pseudoscorpion along. Finding a suitable environment and an adequate food supply the pseudoscorpions have no pressing need to leave and stay as commensals. If necessary, the pseudoscorpions can leave the nests either actively, by walking out, or passively, by riding on the rodent during one of its foraging expeditions (= phoresy). How do the pseudoscorpions colonize new nests? Accidentally, as in the opening scenario, or by hitching a ride directly to their new home when offspring rodents disperse from the maternal nest (again = phoresy). It is well documented that rodents, and rodent nests, have arthropod ectoparasites that are suitable pseudoscorpion prey, and thus the transformation from commensal to mutualist is uneventful and evolutionarily rather simple to achieve.

Some pseudoscorpions are apparently obligate rodent-nest inhabitants, but it is not presently known whether they have a commensalistic or a mutualistic relationship with their host(s), as is the case of the European *Lasiochernes pilosus* (Ellingsen 1910), which is known only from vole (*Microtus* spp.) and mole (*Thomomys* spp.) nests and has never been found in leaf-litter, under tree bark or under stones (Weygoldt pers. comm.). It is quite difficult to ascertain if some of the pseudoscorpion-packrat associations are obligatory or not: although some species (n = 8) such as *Pachychernes* sp. from Tamaulipas are at present known only from packrat nests, no serious efforts to collect them elsewhere have been made and thus their presence outside the nests cannot be ruled out. Pseudoscorpion species found in nests of more than one packrat species, such as *Tychochernes inflatus*, or those with wide geographical distributions, indicate dispersal activities (active or passive) contrary to an obligatory symbiotic association.

There are, however, pseudoscorpions that are found exclusively on their rodent hosts, as is the case of the genus *Epichernes* Muchmore, which has three species known only from rodents: *E. aztecus* on the volcano mouse *Neotomodon alstoni alstoni* Merriam in the vicinity of Mexico City (Muchmore & Hentschel 1982); *E. navarroi* Muchmore 1990 on the forest spiny pocket mouse *Heteromys gaumeri* Allen & Chapman, and on the white-footed mouse *Peromyscus yucatanicus* Allen & Chapman, in Quintana Roo, Mexico (Muchmore 1990); and *E. guanacastensis* Muchmore 1992 on the spiny pocket mouse *Liomys salvini* (Thomas) in Costa Rica (Muchmore 1992). Muchmore & Hentschel (1982) reported 766 specimens of *E. aztecus* combed from the fur of live-trapped mice, and the pseudoscorpions apparently feed primarily upon the ectocommensal mites which also occur on the volcano mice in large numbers. The evolutionary step from nest commensal/mutualist to mouse commensal/mutualist is small indeed, and this relationship certainly is not simple phoresy. Interestingly, *Neotomodon*, as the name implies, is closely related to *Neotoma*; and *Epichernes* is closely related to *Cheiridium*, a well-known rodent nest inhabitant, suggesting an interesting co-evolutionary scenario that deserves further investigation, and which definitely indicates that pseudoscorpion-rodent interactions are not casual or accidental.

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