ASSOCIATION BETWEEN NEOTROPICAL BURROWING SPIDERS (ARANEAE: NEMESIIDAE) AND MITES (ACARI: HETEROSTIGMATA, SCUTACARIDAE)[1]

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SPIDER-MITE ASSOCIATIONS
SPIDER BIOLOGY
PHORESY
SCUTACARIDAE

SUMMARY: Whilst collecting burrowing spiders of the family Nemesiidae from 16 localities in Argentina, phoretic mites were found on *Stenoterommata iguazu*, *Stenoterommata platense* and *Stenoterommata uruguai*. These mites are described here: *Scutacarus (S.) araneophilus* n. sp. and *Scutacarus (S.) adgregatus* n. sp. Associations between spiders and scutacarids were not previously known. Aspects of the biology of the spiders and the interactions between mites and spiders are reported and discussed.

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RESUMEN : Durante colectas de arañas cavadoras de la familia Nemesiidae en 16 localidades de Argentina, se encontraron ácaros foréticos sobre *Stenoterommata iguazu*, *S. platense*, and *S. uruguai*. Se describe aquí a estos ácaros, como *Scutacarus (S.) araneophilus* n. sp. and *Scutacarus (S.) adgregatus* n.sp. Ninguna asociación entre arañas y escutacaridos se conocía previamente. Se discute la interacción entre los ácaros y las arañas, tomando en cuenta los datos conocidos de la biología de ambos.

For many species of the terrestrial mite family Scutacaridae phoresy is a more or less essential part of their life-cycle (DELFINADO 1976, BINNS 1979, EBERMANN 1991). Terrestrial arthropods are almost exclusively used as transporters by the phoretomorphic females of these mites. Such phoretic hosts are known from many insect orders (CROSS & BOHART 1992). For example, all social insects have known associations with scutacarids, mainly with representatives of the most species-rich genera, *Imparipes* and *Scutacarus* (EICKWORT 1990). However, associations of scutacarids with other species of Arachnida are rare, and associations with spiders were so far unknown.

During intense collecting of burrowing spiders (Mygalomorphae, Nemesiidae) from some Argentinian provinces by one of the authors (P.A.G.), many specimens of phoretic scutacarids were detected. These mites, and the first known associations between spiders and scutacarids, are described here.

MATERIAL

While mite infestation was not a bias for the choice of specimens collected, larger spiders were preferred due to their value in systematic research. All specimens of *Stenoterommata platense* were examined for

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mites by G. C. EICKWORT (†) under a stereomicroscope. The location of mites on the infested spiders was noted, but the total number of phoretic mites on a single spider was not determined. Only a few mites were removed from each infested spider and slide-mounted in HOYER's or SWAN's medium by G. C. EICKWORT and E. E. . The remaining material was alcohol-preserved. Therefore, the numbers of mites given below reflect only the number of microscopic slides produced.

Localities of collected *Stenoterommata* specimens respectively phoretic mites

Unless otherwise noted the spiders were collected by P. A. G. at different localities in Argentina. The corresponding codes ("GCE") for single mites/ microscopic slides are given in brackets.

Prov. Misiones:

(1) Ruta Provincial 19 and Arroyo Uruzú, 2-6 Feb. 1988, from *S. platense*, 43 mites from 2 spiders, (GCE 90-0405-1).

(2) Salto del Urugua-í, 25 Nov. 1981, from *S. uruguai*, 12 mites from 6 spiders, (GCE 90-0405-3).

(3) Ruta Provincial 19 and Arroyo Uruzú, Parque Provincial Urugua-í, 2-7 Feb. 1988, from *S. platense*, 9 mites from 1 spider (5 *S. araneophilus* n. sp., 4 *S. adgregatus* n. sp.) (GCE 90-0405-4).

(4) Ruta Provincial 101, Arroyo Santo Domingo, Parque Nacional Iguazú, 30 Jan. 1988, Goloboff & Szumik coll., from *S. iguazu*, 7 mites from 3 spiders (GCE 91-0108-13a, b, c).

(5) Wanda, July 1983, from *S. iguazu*, 3 mites from 1 spider (GCE 91-0108-7a, b, c).

(6) Parque Nacional Iguazú, Nov. 1981, from *S. iguazu*, 1 mite (GCE 91-0108-4a).

(7) Parque Nacional Iguazú, July 1983, from *S. iguazu*, 1 mite (GCE 91-0108-10a).

(8) Parque Nacional Iguazú, July 1983, from *S. platense*, 2 mites from 1 spider (GCE 91-0108-5a, b).

(9) Arroyo Piñalito, 2 km below Ruta Provincial 101, 11 Jan. 1988, Goloboff & Szumik coll., from *Stenoterommata iguazu* or *S. uruguai* (both spider species were collected together in this locality, and hosts were not individualized), 3 mites from 2 spiders, (GCE 91-0108-14a, b, c).

(10) Ruta Provincial 17, 33 km E Eldorado, 20 Sep. 1992, Goloboff & Szumik coll., from *S. platense*, 10 mites from 1 spider (3 *S. araneophilus* n. sp., 7 *S. adgregatus* n. sp.) (no GCE number) = Locus typicus of *S. adgregatus* n. sp. .

Prov. Buenos Aires:

(11) Hudson, 8 Aug. 1982, from *S. platense*, 7 mites from 2 spiders (GCE 90-0405-2).

(12) 17 km S Magdalena, April 1983, from *S. platense*, 14 mites from 8 spiders, (GCE 90-0405-6, a) = Locus typicus of *S. araneophilus* n. sp. .

(13) Punta Indio, 13 March 1983, from *S. platense*, 7 mites from 1 spider (GCE 89-0921-1, b-i).

(14) Belén de Escobar, Estancia "El Cazador", 22 Sept. 1979, from *S. platense*, 6 mites from 3 spiders (GCE 91-0108-2, 3, 9).

Prov. Santa Fe:

(15) Arroyo del Medio, in front of San Nicolas, 1 Feb. 1983, Rosas coll., from *S. platense*, 1 mite (GCE 91-0108-8a).

Prov. Entre Rios:

(16) Parque Nacional El Palmar, 12-16 Feb. 1981, from *S. platense*, 1 mite (GCE 91-0108-1).

METHODS

The spiders were determined by P. A. G. to species, sex and developmental stage. Younger stages in mygalomorphs show, in general, a more rounded sternum and palpal coxae, and fewer trichobothria, maxillary cuspules and setae. Although some studies on the size and number of trichobothria per instar in nemesiids exist (*Nemesia caementaria* (Latr.): BUCHLI 1970; *Acanthogonatus pissii* (Simon): CALDERÓN 1983), no comparable studies exist for any *Stenoterommata*, and the instars of *S. platense* are uncharacterized (even their number is unknown). Females were considered "adults" if they were as large or larger than the smallest conspecific females observed with egg-sacs or eggs maturing in the abdomen.

The descriptions of the new mite species were prepared by E. E.; the interactions of the new mites and spiders are described by P. A. G. .

RESULTS

Descriptions of the new mites

Nomenclature: Notation of the body setae and legs is modified after Lindquist (1977).

Abbreviations: *ap* = apodeme, *Fe* = femur, *Ge* = Genu, *n* = number of measurements, *pstpl* = posterior sternal plate, *sol* = solenidion, *solTi* = tibial solenidion, *solTa* = tarsal solenidion, *solTiTa* = tibiotarsal solenidion, *Ta* = tarsus, *Ti* = tibia, *TiTa* = tibiotarsus, *Tr* = trochanter, *wpstpl* = width of posterior sternal plate, *x* = average value, ≅: about the same length, < = shorter than, > = longer than.

Body dimensions: For the body length, the distance between outer edge of segments C and PS was taken; and for the body width, the width of the anterior edge of the posterior sternal plate. All the measurements in this paper are given in µm.

Scutacarus (S.) araneophilus new species, female (Figs. 1-2)

Body dimensions (values for individual sites):

Prov. Misiones: (GCE 90-0405-1): length 146-197, x = 170 (n=42); wpstpl 63-84, x = 75 (n=42). (GCE 90-0405-3): length 170-204, x = 178 (n=12); wpstpl 75-87, x = 81 (n=12). (GCE 90-0405-4): length 158-211, x = 187 (n=4); wpstpl 69-86, x = 80 (n=4). (GCE 91-0108-13a, b, c): length 161-190, x = 181 (n=7); wpstpl 76 (n=7). (GCE 91-0108-7a, b, c): length 185-187 (n=2); wpstpl 73-79 (n=2). (GCE 91-0108-4a): length 190 (n=1); wpstpl 82 (n=1). (GCE 91-0108-10a): length 194 (n=1); wpstpl — (GCE 91-0108-5a, b): length 175 (n=2); wpstpl 73-76 (n=2). (GCE 91-0108-14a, b, c): length 168-178 (n=2); wpstpl 79 (n=1). Ruta Provincial 17, 33 km E Eldorado (no GCE number): length 170-204, x = 187 (n=3); wpstpl 75-85, x = 82 (n=3).

Prov. Buenos Aires: (GCE 90-0405-2): length 170-206, x = 192 (n=7); wpstpl 75-87, x = 81 (n= 7). (GCE 90-0405-6, a) = Locus typicus: length 163-223 (holotype 204), x = 192, (n=13); wpstpl 77-93 (holotype 92), x = 86, (n=12). (GCE 89-0921-1, b - i): length 156-209, x = 187 (n=6); wpstpl 77-84, x = 80 (n=6). (GCE 91-0108-2, 3, 9) : length 175-211, x = 191 (n=5); wpstpl 76-85, x = 80 (n=5).

Prov. Santa Fe: (GCE 91-0108-8a): length 187 (n=1); wpstpl 85 (n=1).

Prov. Entre Rios: (GCE 91-0108-1): length 158 (n=1); wpstpl 76 (n=1).

The entire surface of the body stippled with fine pores; free edge of tergite C with fine radial stripes. Cupulae ia small, rounded with central porus, ip has not been found.

Body setation: Length of setae may vary, i.e. identical setae on the left and the right side of the body may differ considerably in length.

Dorsum (Fig. 1a): All setae very long, thin, sparsely barbed. Fine tips of c1, c2, d, h1 and h2 in most cases broken. c1 > c2; c1 < d or c1 ≅ d or c1 > d (rarely); e < f, e < h2 or e ≅ h2 or e > h2 (rarely); d > f (most commonly) or d ≅ f; f > h1, h1 with only one exception (holotype !) shorter than half the length of f, length relation of f to h1 = 1: 0.25 – 0.53, holotype 1: 0.34/0. 53 (left and right side of body), x = 1: 0.34 (n = 71).

Venter (Fig. 1b): ap1 well developed, ap2 and ap3 present, weakly sclerotized, ap4 does not reach half the width of pstpl, ap5 reduced. Setae sparsely barbed or smooth. 1a > 1b < 2a > 2b, 2b dagger-shaped, smooth; 3a > 3b > 3c; 4a before 4b, 4a < 4b > 4c; ps1 > ps2 or ps1 ≅ ps2 (only 1 specimen of 116), ps3 half the length of ps2 or shorter.

Trichobothrium scl (Fig. 2a) club-shaped, thin-stemmed, with fine scales distally, v2 > v1.

Legs (the number of the solenidia is given in parentheses):

Leg I (Fig. 2b): Setal formula: Tr 1, Fe 3, Ge 4, TiTa 16 (4 sol); TiTa slender, powerful claw with

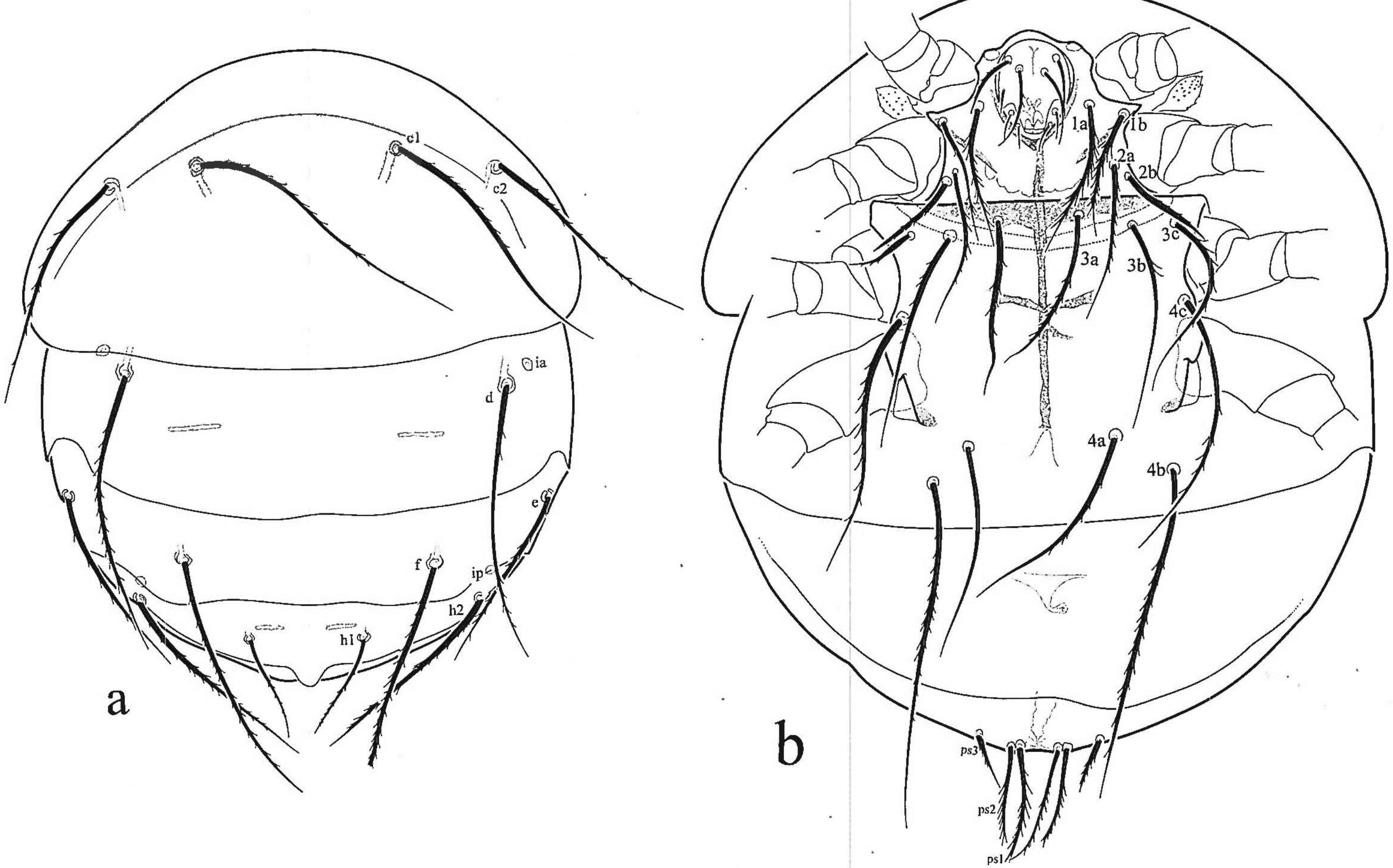

FIG. 1: *Scutacarus araneophilus* n. sp. female (holotype). — a) Dorsum, b) Venter; body length 204 μm.

FIG. 2: *Scutacarus araneophilus* n. sp. female. — a) Trichobothrium, b) leg I; separate drawned solenidia somewhat enlarged, c) leg II, d) leg III, e) leg IV.

sharp tip; length of sol $\omega2 < \omega1 > \varphi2 > \varphi1$ or $\varphi2 \cong \varphi1$ or $\varphi2 < \varphi1$; $\omega2 \cong \varphi1$, slender; $\omega1$ thickened, finger-shaped, $\varphi1$ thin stemmed, club-shaped, pointed distally.

Leg II (FIG. 2c): Tr 1, Fe 3, Ge 3, Ti 4 (1sol), Ta 6 (1 sol), solTi shorter and thicker than solTa; Ta with two claws and empodium.

Leg III (FIG. 2d): Tr 1, Fe 2, Ge 2, Ti 4 (1 sol), Ta 6; solTi small; Ta with two claws and empodium.

Leg IV (FIG. 2e): Tr 1, Fe 2, Ge 1, TiTa 7; dTi the longest tibiotarsal seta, dTi > tc′ > pv″ > tc″; all setae barbed.

Material examined: 116 females from 16 localities (No. 1–16).

LOCUS TYPICUS: Locality No. 12.

TYPE MATERIAL: Deposition of holotype and 65 paratypes in the Museo Argentino de Ciencias Naturales, Buenos Aires; 10 paratypes in the Fundación e Instituto Miguel Lillo, S. M. de Tucumán, Argentina; 10 paratypes and additional alcohol preserved material in the Cornell University Insect Collection, Ithaca, New York; 10 paratypes in the Zoologisches Institut und Zoologisches Museum, University of Hamburg; 10 paratypes in the Musée d'Histoire Naturelle, Geneva; 10 paratypes in the Hungarian Natural History Museum, Budapest.

ETYMOLOGY: The name 'araneophilus' refers to the new species habit of using spiders as phoretic hosts.

DIFFERENTIATION FROM RELATED SPECIES: *Scutacarus araneophilus* n. sp. shows morphological similarity with *Scutacarus uncinatus* Mahunka, 1968 from Chile. Both species share the unusually long dorsal setae c1-c2, d and f and position and length of setae 4a-4b. *Scutacarus araneophilus* n. sp. differs from *S. uncinatus* in the following characters: In *araneophilus* the length of h1 is significantly less than half the length of f, in *uncinatus* it is clearly longer than half the length. In *araneophilus* ps3 reaches half the length of ps2 or is shorter, in *uncinatus* ps2 and ps3 are equally long. In *araneophilus* ps1 and ps2 are always barbed, and smooth in *uncinatus*. In *araneophilus* dTiIV > tc′, in *uncinatus* dTiIV < tc′. The setation of legs I-III could not be compared, as these characters were not considered in the description of *uncinatus*.

Male and larva: Unknown.

Scutacarus (S.) adgregatus new species, female

(Figs. 3-4)

Body dimensions (values for individual sites):

Prov. Misiones: Ruta Provincial 17, 33 km E Eldorado (Locus typicus) (no GCE number): length 144-211 (holotype 197), x = 182 (n = 6); wpstpl 69-81 (holotype 72), x = 77 (n = 6). (GCE 90-0405-4): length 173-185, x = 179 (n = 4); wpstpl 72-76, x = 74 (n = 4).

The entire surface of the body stippled with fine pores; free edge of tergite C with fine radial stripes. Cupulae ia and ip small, rounded.

BODY SETATION: In the present species the length of setae is variable. Not only do setae differ between individuals, but so do equivalent setae of the two body halves of an individual.

DORSUM (FIG. 3a): Setae sparsely barbed. c1 > c2 or c1 ≅ c2 (only on one body side of one specimen); c1 < d or c1 > d (only on one body side of one specimen) or c1 = d; e > f; e > h2 or e < h2 (only on one body side of one specimen) or e ≅ h2; d < f or d ≅ f (only on one body side of one specimen); f > h1, h1 longer than half the lenght of f, length relation of f to h1 = 1: 0.55 – 0.84, holotype 1: 0.76/0.84 (left and right side of body), x = 1: 0.68 (n=17; measurement on one or both body sides; 10 specimens).

VENTER (FIG. 3b): ap1 well developed, ap2 and ap3 present, weakly sclerotized, ap4 does not reach half the width of pstpl, ap5 reduced. Setae with exception of 2b barbed. 1a > 1b or 1a ≅ 1b, 1b ≅ 2a > 2b, 2b dagger-shaped, smooth; 3a < 3b > 3c; 3a ≅ 3c; 4a slightly before 4b, 4a < 4b > 4c; ps1 ≅ ps2 > ps3.

Trichobothrium scl (FIG. 4a) club-shaped, thin-stemmed, with fine scales distally, v2 ≅ v1.

Leg I (FIG. 4b): Setal formula: Tr 1, Fe 3, Ge 4, TiTa 16 (4 sol); TiTa somewhat thickened, claw weakly developed with sharp tip; length of sol $\omega2 \cong \omega1 > \varphi2 < \varphi1$; $\omega2$, $\varphi2$ slender, $\omega1$ thickened, finger-shaped, $\varphi1$ thin-stemmed, club-shaped, pointed distally.

Leg II (FIG. 4c): Tr 1, Fe 3, Ge 3, Ti 4 (1sol), Ta 6 (1 sol), solTa longer and thicker than solTi; Ta with two claws and empodium.

Leg III (FIG. 4d): Tr 1, Fe 2, Ge 2, Ti 4 (1 sol), Ta 6; solTi small; Ta with two claws and empodium.

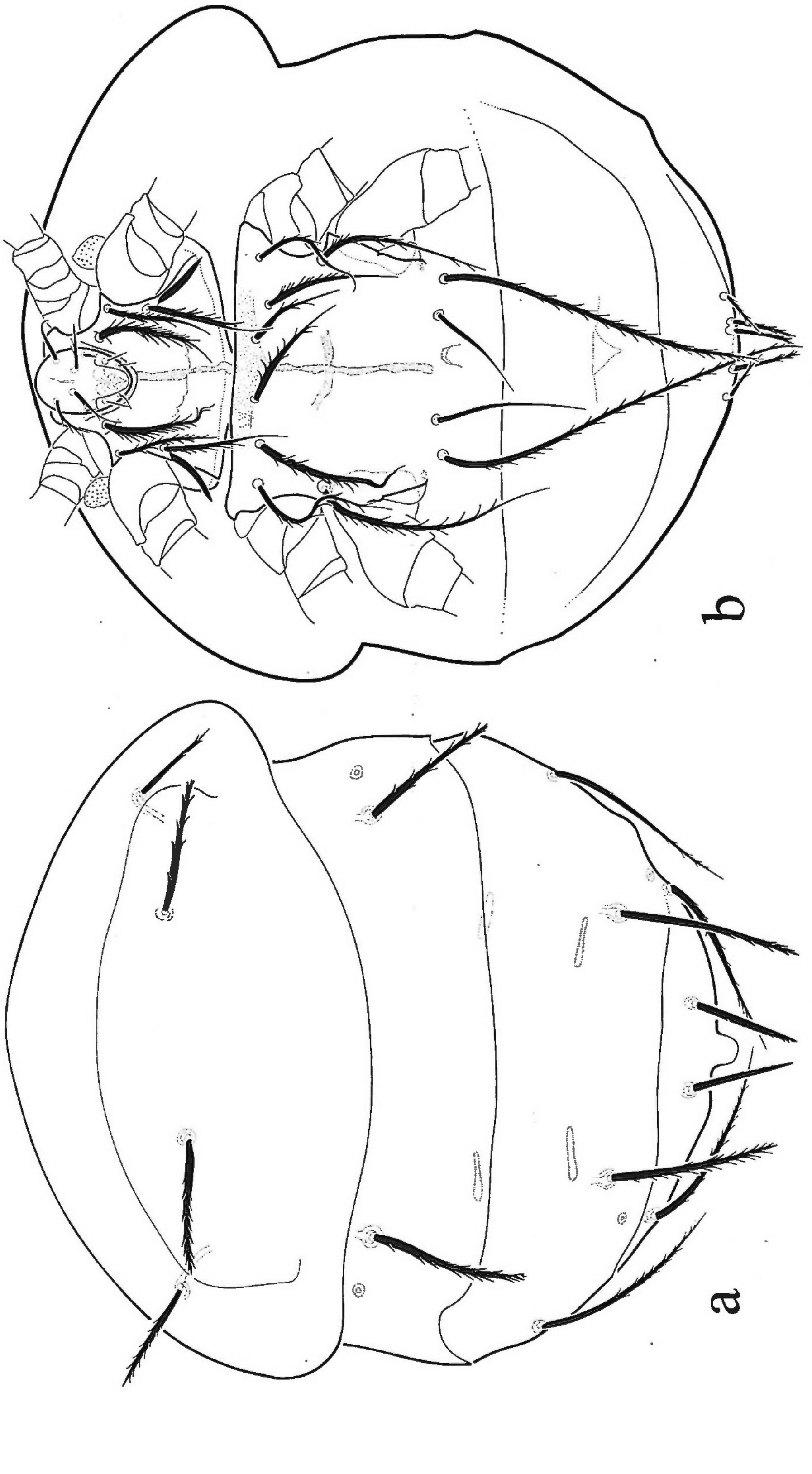

FIG. 3: *Scutacarus adgregatus* n. sp. female (holotype). — a) Dorsum, b) Venter; body length 197 μm.

FIG. 4: *Scutacarus adgregatus* n. sp. female. — a) Trichobothrium, b) leg I; separate drawned solenidia somewhat enlarged, c) leg II, d) leg III, e) leg IV.

Leg IV (FIG. 4e): Tr 1, Fe 2, Ge 1, TiTa 7; dTi the longest tibiotarsal seta, dTi > tc′ > pv″ > tc″; all setae barbed.

Material examined: 11 females from 2 localities (No. 3, 10).

LOCUS TYPICUS: Locality No. 10.

TYPE MATERIAL: Deposition of holotype and 2 paratypes in the Museo Argentino de Ciencias Naturales, Buenos Aires; 2 paratypes in the Fundación e Instituto Miguel Lillo, S. M. de Tucumán, Argentina; 2 paratypes in the Cornell University Insect Collection, Ithaca, New York; 2 paratypes in the Zoologisches Institut und Zoologisches Museum, University of Hamburg; 1 paratype in the Musée d'Histoire Naturelle, Geneva; 1 paratype in the Hungarian Natural History Museum, Budapest.

ETYMOLOGY: The name 'adgregatus' refers to the unexpected finding of a further phoretic species of Scutacaridae on mygalomorph-spiders.

DIFFERENTIATION FROM RELATED SPECIES: *Scutacarus adgregatus* shows similar positioning and form of dorsal setae and setae 4a-4b to the species *Scutacarus topali* Mahunka, 1963 from Argentina and *Scutacarus hoplopes* Mahunka, 1969 from Bolivia. In *S. adgregatus* and *S. topali* ap4 does not reach half the width of pstpl; in *S. hoplopes* ap4 reaches the lateral edge of pstpl. Leg IV of *S. adgregatus*: dTi > tc′ > pv″ > tc″, in *S. topali* and *S. hoplopes*: dTi < tc′ > pv″ < tc″ (tc′ > tc″ > dTi > pv″).

Male and larva: Unknown.

BIOLOGY OF THE SPIDERS

For a better understanding of the association between spiders and mites, some knowledge of the biology of the spiders is essential. In this context, new information on the biology of the *Stenoterommata* species is given. (field observations by P. A. G.). As with many other mygalomorph spiders, this genus is long-lived, with females undergoing several post-maturation moults. The spiders live in open burrows in the soil. Their burrows are about 15 cm long, with the walls covered by silk, providing a stable environment. In drier seasons the spiders may seal the burrow mouth with silk or lay more silk along the burrow walls, helping to maintain a moist environment (as has been described by COYLE (1971), for spiders in the family Antrodiaetidae). Prey remnants and exuviae are usually deposited in the bottom of the burrow. When hunting, spiders await prey at the entrance of their burrow, with anterior legs lying on the substrate, in a position similar to that of *Nemesia* (BUCHLI 1969). The mother maintains her eggs in the burrow until hatching. Juveniles remain in the maternal burrow for a short time and then disperse, apparently establishing burrows close to their mother's burrow. Burrows are enlarged with successive instars of the spiders. Juveniles and adult females never leave their burrows. The only interactions among individuals of *Stenoterommata* occur when juveniles are still living in their mother's burrow and when the spiders are mating. Males abandon their burrows, shortly after maturation, in order to search for female burrows. They do not again establish their own burrows (they are often found under logs and stones). Two matings of *S. platense* were observed in captivity; one took place at the entrance of a female's burrow and the other within. In both cases the male escaped without harm after mating (the mating at the burrow entrance ended when the male jumped backwards, apparently disturbed by some signal the observer could not detect). It is not known whether males survive to mate again in nature.

INFESTATION OF THE SPIDERS WITH MITES

Three species of *Stenoterommata* bore female scutacarid mites: *S. platense* Holmberg, 1881, *S. uruguai* Goloboff, 1995 and *S. iguazu* Goloboff, 1995. Of 110 spiders examined, 35 were infested. Of the 41 adult (large) female *Stenoterommata* examined, 27 (65.9%) bore scutacarids, and 2 of the 3 (66.7%) adult male spiders bore scutacarids. Of the 60 juvenile spiders examined, 6 (10.0%) bore scutacarids; this is significantly different from the infestation rate for adult spiders ($\chi^2 = 35.54$, $p = 0.001$). Among the mediumsized juvenile spiders, 5 of 20 (25.0%) females and 1 of 19 (5.3%) males bore scutacarids. None of the 27 smaller juveniles (which could not be sexed; presumably no important differences in ecology or behavior between sexes exist at this point in development) bore scutacarid mites.

Of the 35 infested spiders, 33 bore only mites of the species *Scutacarus araneophilus*; *Scutacarus adgregatus* on the other hand could only be found on 2 spiders (*S. platense*), always associated with *araneophilus*.

Without exception specimens of *S. araneophilus* n. sp. were located only in the mid-ventral membranous area between the fourth pair of coxae, where they were arranged gnathosoma-downwards. Only one spider also bore scutacarid mites on the dorsal surfaces of coxae IV. This spider was one of the two specimens which carried both new scutacarid species. The two host-spiders infested with both new species of scutacarids (localities 3 and 10), were also the only ones found to carry phoretic pygmephorids in their thoracic foveae. Four adult female *S. platense* that carried *Scutacarus araneophilus* n. sp. also carried deutonymphs of an acarid mite. These deutonymphs were attached to the surfaces of the basal podits of the legs.

In the province of Misiones another species of Nemesiidae, *Rachias timbo* Goloboff, 1995, is relatively common; this species was not found to host mites. The burrows of *Rachias* differ from those of other nemesiids in lacking a silk lining (see GOLOBOFF 1995: 57); the environmental conditions inside those burrows are likely to be quite different. Some specimens of this species differ from *Stenoterommata platense*, *S. iguazu* and *S. uruguai* in having modified, short blunt setae (not easily grasped by mites) on the membranes between the fourth coxae. Three smaller species of *Stenoterommata* occur in Entre Ríos and northern Buenos Aires (*S. crassistylus* Goloboff, 1995, *S. tenuistylus* Goloboff, 1995 and *S. palmar* Goloboff, 1995); none of these has been observed to host mites.

DISCUSSION

In phoretic scutacarids, transport host specifity can sometimes be fairly strict. Phoretomorphic females of *Archidispus* clearly prefer carabids to any other arthropods, but a preference for certain species could not be observed (KARAFIAT 1959). In this case phoretic hosts are chosen randomly and play — apart from the phoretic transport — no further role in the life-cycle of the mites. On the other hand, the phoretic association can be part of a co-existence of two species extending beyond simply transportation. Good examples are found in the wide range of ant-associated arthropods. Many of these myrmecophile arthropods, which live in ants' nests and benefit from all the advantages of co-habitation (HÖLLDOBLER 1990), are tolerated, others are not even registered by their hosts (belonging to this group, called 'Synoeketes', are many representatives of mite families, including the scutacarids). Many of these use their co-habitants also as phoretic hosts. The main advantage for the establishment of such a co-habitation is the availability of food, usually in the form of detritus overgrown by fungi, or the foraging remains of the ants. In all breeding experiments with scutacarids, fungivory — larvae and females sucking the liquid contents of the fungi's hyphae — was observed. The males have reduced mouth-parts and do not feed in their adult stage (among others NORTON & IDE 1974; BINNS 1979; EBERMANN 1981, 1982, 1991; SCHOUSBOE 1986). Observations of this kind, and the clearly non-accidental transport association between the spiders and their phoretic scutacarids, suggests the two new species of scutacarids also co-habit with their spiders. The larval development of *Scutacarus araneophilus* and *S. adgregatus* probably takes place in the burrows of *Stenoterommata*, where the females and larvae would find enough detritus overgrown with fungi to feed on. Some species of scutacarids living in underground nests of bees exhibit parallels with those associated with spiders. These mites feed on the fungus that infests the decaying brood or provision mass, and can develop in cells in which living brood occurs. The mites feed on the fungus that infests the bee faeces. Furthermore, the bees are used as phoretic hosts. (CROSS & BOHART 1992; EICKWORT 1994).

The higher rate of infestation of adult spiders may indicate either that mites preferentially attach to adults, or simply that there are more adult female mites in the older burrows of the adult spiders. There are several possible ways in which adult female mites could reach a spider burrow. The well-developed phoresy, with mites highly localized on their hosts, suggests that dispersal via spiders is important. If this is really the case, there are two possibilities. First, the mites may be phoretic on the juvenile spiders when the latter leave their maternal burrows to start their own burrows. These juveniles, only a few millimeters long, were not collected in our study. Second, the mites may also disperse using the adult male spiders, entering female burrows when the spiders mate. If mites can be carried by dispersing juveniles, unmated males will host mites; if they cannot, only already mated males should host mites. That some mites occurred on juvenile spiders, and that some males collected in their burrows (therefore unmated) carried mites, indicate that dispersal by repeated matings of adult male spiders cannot be the only means of infestation of new burrows.

Associations (parasitic and non-parasitic ones) between spiders and mites are extremely rare compared with those between insects and mites (VINCENT & RACK 1983). Phoretic associations between scutacarids and spiders were previously unknown, and associations with other arachnids are rare. The scutacarid mite *Imparipes (I.) tocatlphilus* Ebermann & Palacios-Vargas, 1988, described from Mexico, is phoretic on the ricinuleid species *Cryptocellus boneti* (EBERMANN & PALACIOS-VARGAS 1988). *Scutacarus (S.) acarorum* Goeze, 1780 and *S. (S.) deserticolus* Mahunka, 1969 live preferentially in nests of Holarctic bumble-bees and are transported on both the bumble-bees and co-habiting mesostigmatic mites, within and outside the bumble-bees' nest (CHMIELEWSKI 1971; EBERMANN 1991; 1992).

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