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Acarologia is under free license and distributed under the terms of the Creative Commons-BY-NC-ND which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author and source are credited.
BIOLOGY AND DESCRIPTION OF A NEW PYGMEPHORID MITE (ACARINA : TARSONEMIDA) ASSOCIATED WITH THE SOIL-NESTING BEE AGAPOSTEMON NASUTUS (HYMENOPTERA : HALICTIDAE)

BY G. RACK 1 and G. C. EICKWORT 2

ABSTRACT

The new species Parapygmephorus (Sicilipes) costaricanus (Pygmephoridae : Neopygmephorinae) is described from adult females, males, and larvae, and distinguished from P. (S.) halictinis. Adult females are phoretic on adult Agapostemon nasutus and detach from female bees when the bees construct or provision nest cells. The mites oviposit when the mature bee larvae defecate and the mite larvae feed upon some component or contaminant of the bee feces. Adult male mites carry pharate females with their enlarged hind legs and the mites copulate before their hosts moult into adults. Adult female mites attach to the emerging adult bees.

These mites are evidently commensals of bees and their life cycles are closely synchronized with those of their hosts. The biology of these mite species associated with bees previously has not been described. This species occurs not only in Costa Rica but also in Mexico, according to E. A. Cross.

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INTRODUCTION

Adult females of species of Parapygmephorus s. str. and Parapygmephorus (Sicilipes) have been collected on bees (Cross, 1965; Mahunka, 1974; Rack and Delfinado, in preparation). These hosts include the halictid genera Crinoglossa, Nomia, Agapostemon, Augochlora Augochlorrella, Dialictus, and Evylaeus (Cross, 1965; Eickwort and Eickwort, 1971, 1972, 1973; Bohart and Youssef, 1976). There have been no previous accounts of the biology of these bee associates. We describe below all stages of a new species of Parapygmephorus (Sicilipes) that is associated with the neotropical "sweat bee" Agapostemon nasutus, and the life cycle of the mite in the nest cells of its host. This new species is closely related to Parapygmephorus (Sicilipes) halictinis Cross, 1965, the type species of the subgenus, a species associated with Agapostemon virescens.

METHODS

Mites were collected during a study of the nesting biology of Agapostemon nasutus during July and August 1965 near Turrialba, Cartago Province, Costa Rica. The biology of the host bee and the techniques for excavating nests and rearing immature bees were described by Eickwort and Eickwort (1969). In order to correlate the development of the mite and its host, 79 cells from 9 nests were each placed in a screw-top vial in the field and brought to the laboratory for microscopic examination. Each vial contained the immature host, provisions or feces if present, and part but not all of the cell wall and surrounding soil (cells could only be located by breaking open the cell walls). After examination, most mites were preserved in 95% ethanol. An attempt was made to rear mites in 6 petri dishes provided with moistened cotton, bee feces, and bee pupae. Mold quickly infested these dishes and data were only obtained on hatching of eggs. Mites were also noted on 22 bee pupae from other cells and their development was recorded daily along with the development of their hosts. The presence and distribution of mites were also noted on 30 adult female bees from nest burrows and cells.

Observations on the mites' development and interactions with their hosts were by GCE. GR prepared the descriptions and illustrations of the instars and is responsible for the systematic conclusions.

1. SYSTEMATIC ACCOUNT

Parapygmephorus (Sicilipes) costaricanus sp. n.

(Figs. 1-11)

FEMALE: Length (without gnathosoma) 160-230 μm, holotype 220 μm (mean of 25 specimens 200 μm); width 90-145 μm, holotype 140 μm (mean of 25 specimens 125 μm), broadly conical, yellowish white (pinkish to brownish in life).

Dorsum (fig. 1): Propodosoma broad, with 2 pairs of setae. Mediolateral prodorsal setae (ptl) short, moderately plumose. Posterior prodorsal setae (pi) long, slightly but distinctly plumose. Sensillus with long pedicel and a club, covered with short branches. Stigmata roundish. Surface of hysterosoma with jagged, shingled sculpturing that is clearest on the first segment, scarcely visible on the fourth segment. The sculpturing of the 4 segments is very variable. Length of setae c₄ nearly twice c₁, both shortly but distinctly plumose. Setae d₁ shorter than c₂, plumose. Setae c₂ 2/3 c₁, both plumose. Setae f₁ nearly as long as f₂. Setae c₂ are the longest dorsal setae.
Figs. 1-5: *Parapygmephorus (Sicilipes) costaricanus* sp. n., holotype female.
1) dorsal; 2) ventral; 3) right leg I, dorsal; 4) right leg II, dorsal; 5) right leg IV, dorsal.
Venter (fig. 2): All apodemes present but scarcely visible. Epimeres I with 2 pairs of weakly plumose setae, never forked. Epimeres II with 2 pairs of nearly smooth setae. Of the epimeric setae 3, pair 3b are the longest and insert nearest to each other and on apodeme IV. Epimeric setae 4b are the longest ventral setae; distance between 4a shorter than distance between 4b. Setae $h_1$ inserting apical to $h_3$ and $h_5$. All ventral setae of hysterosoma smooth.

Leg I (fig. 3): As broad as leg II but tibiotarsus somewhat broader. Femur with 3 setae, seta c hooked. Genu dorsally with 2 plumose, ventrally with 2 smooth setae. Tibiotarsus distally with a strong claw and an immovable counterpart. Tibial solenidia small, nearly equal. Of the tarsal solenidia, only one is large and the other very reduced, scarcely visible. Tibiotarsus dorsally with circular, mediolateral sclerotised plate. Leg II (fig. 4): Tibia proximally with a small solenidion; tarsus proximally with a thicker solenidion, distally with 2 claws and a pulvillus. Leg III: Tibia proximally with a small solenidion; tarsus distally with 2 claws and a pulvillus. Leg IV (fig. 5): Proximal edge of trochanter nearly straight, not bulbous; ventrally with 1 seta. Femur with 2 setae; genu ventrolaterally with 1 seta; tibia proximally with a tiny solenidion and 4 shortly plumose setae; tarsus with 6 setae, 2 claws and a pulvillus.

Fig. 6: Parapygmeophorus (Stellipes) costaricanus sp. n., paratype male, dorsal, legs I-III not shown.

Male: Length (without gnathosoma) 200-310 $\mu$m (mean of 20 specimens 256 $\mu$m); width 130-185 $\mu$m (mean of 20 specimens 170 $\mu$m). Yellowish white (pinkish in life). Legs I-III especially long and slender, leg IV very robust. Gnathosoma extremely reduced, much smaller than in other families and genera. The proportion of the length of gnathosoma to length of
Parapygmehorus (Sicilipes) costaricanus sp. n., paratype male.
7) ventral; 8) right leg I, dorsal; 9) right leg IV, dorsal.
eg I is $1:22$ ($Scolarurus$ fragilis, $1:4$; $Bakeriana$ exigua, $1:5$). Such a proportion has not been previously found in the superfamily Pygmaphoroidea.

*Dorsum* (fig. 6): Propodosoma with 3 pairs of smooth setae, pi much longer than the others, which insert in a transverse row, pi with very fine, smooth tip. On the hysterosoma, setae $c_1$, $c_2$ and $d_1$ insert on the same tergum; $c_2$ extremely long, nearly smooth, with fine tip. $e_1$ more than 3 times longer than $c_2$. Genital capsule large, with many rings. Penis short, not reaching tergum $e$.

*Venter* (fig. 7): Apodemata well developed. Epimeres I and II with 2 pairs of setae, epimeres III and IV with 3 pairs of setae. All setae short and smooth.

*Leg I* (fig. 8): Tibia and tarsus separated. Tibia with only 1 solenidion. Tarsus with 2 solenidia, distally with a single claw. *Leg IV* (fig. 9): Lateral setae of all 20 examined males were broken off, the only unbroken one is short and acute. Tibia with a long, slender solenidion. Tarsus with 4 setae and 1 thorn, the longest seta inserting ventrally.

*LARVA* (figs. 10, 11): A total of 13 larvae were measured: 4 larvae with pharate adult females (length without gnathosoma 225, 225, 240, 255 $\mu m$; width 127, 140, 140, 140 $\mu m$); 3 larvae with pharate adult males (length without gnathosoma 310, 315, 320 $\mu m$; width 210, 210, 225 $\mu m$); and 6 larvae without pharate adults (length without gnathosoma 225, 240, 250, 255, 270, 270 $\mu m$; width 125, 140, 140, 152, 160, 160 $\mu m$).

Figs. 10-11: *Parapygmaphorus* (Siellipes) costaricanus sp. n., paratype larvae. 10) dorsal; 11) physogastric larva, dorsal.
Body oval, nearly white. Gnathosoma elongate, dorsally with 2 conical thorns. Propodosoma with 3 pairs of setae on a weakly defined shield, first seta minute, third longest. Hysterosomal shields also poorly defined. Setae $c_1$ and $c_2$ nearly of equal length, $d_1$ somewhat longer and thicker, $e_1$ nearly twice as long as $e_2$. Segment $f$ distinctly separated and acute. Setae $f_1$ nearly 3 times longer than $f_2$, with long, very thin tip. All dorsal setae barbed.

_Venter_: Epimeres I and II each with 2 short, thin, smooth, needle-shaped setae. Epimeres III each with 2 setae. Otherwise, hysterosoma with only 3 pairs of tiny, smooth setae inserting around the terminal anus.

_Leg I_: Femur with 3 setae. Tibia and tarsus each with 1 solenidion, tarsus with 2 claws, without pulvillus. _Leg II_: Tibia and tarsus each with a small solenidion, tarsus with 2 claws and pulvillus. _Leg III_: Tibia with a tiny solenidion, tarsus with 2 claws and pulvillus.

Male and female larvae can only be distinguished by size, because when the adults appear as pharate, morphological details of the larvae are difficult to recognize. Larvae without pharate adults do not show distinct sexual differences.


**Paratypes.** 24 females, 20 males, 13 larvae with same locality as holotype, July and August 1965, deposited in the United States National Museum; the collection of Earle A. Cross, Department of Entomology, University of Alabama, Tuscaloosa, Alabama, USA; Snow Entomological Collection, The University of Kansas, Lawrence, Kansas, USA; Cornell University Insect Collection, Ithaca, New York, USA; Zoologisches Museum Hamburg, West Germany; Hungarian National Museum, Budapest, Hungary.

**Other specimens examined.** Additional material (females, males, larvae) with same data as paratypes is deposited in Cornell University and Zoologisches Museum Hamburg.

The new species occurs not only in Costa Rica, but also in Mexico where the host, _Agapostemon nasutus_, is also found. Dr. EARLE A. CROSS kindly loaned us a female which was collected in Moctezuma, Chihuahua, Mexico, July 23, 1953, on _Agapostemon_ sp. (probably _A. nasutus_, which is common in Mexico). He had recognized that this mite belonged to a new species.

**Discussion**

_Parapygmephorus_ (Sicilibes) _costaricanus_ is closely related to _P. (S.) halictinis_ Cross, 1965. In contrast with _halictinis_, setae $e_1$ are longer than $e_2$, setae $4a$ insert farther apart, setae $2c$ are shorter and thinner, setae $h_1$ insert farther apart, and the shingled sculpturing on the hysterosomal dorsum is more jagged in _costaricanus_.

Males and larvae of other species and subgenera of _Parapygmephorus_ have not yet been described. Comparing our males with the few described males in other genera of Pygmephoroidea, they are more closely related to _Bakerdania_ and _Scutacarus_ than to _Siteroptes_ and _Pedicilaster_, whose males and larvae have 4 pairs of setae on the propodosomal shield. In contrast to the known males in _Bakerdania_, males of _P. costaricanus_ have an extremely short gnathosoma, long legs I, no second solenidion on tibia I, a short penis, and a larger overall size than females.

CROSS (1965) described the genus _Parapygmephorus_ with 3 subgenera: _Parapygmephorus_, _Petalomium_ and _Sicilibes_. Description of the latter subgenus was based on 3 undescribed species.
which were phoretic on halictid bees. In the same paper he described the species *halictinis*, the type species of the subgenus *Sicilipes*. Mahunka (1970 a) synonymized *Parapygmephorus* with *Bakerdania*, elevated *Petalomium* to genus, and (1970 b) placed *Sicilipes* as a subgenus of *Bakerdania*. Later (1974) he re-established *Parapygmephorus* as a genus. We prefer to retain *Sicilipes* as a subgenus of *Parapygmephorus* because the species in the subgenera *Parapygmephorus* s. str. and *Sicilipes* seem to be specialized associates of bees and resemble each other closely. They are readily distinguishable from *Petalomium*, most of whose species are inquilines of ants. The species of the large genus *Bakerdania* seldom occur on insects but often are in nests of small mammals, in detritus and in litter. Future examinations of extensive material (Rack and Delfinado in preparation) will show whether *Sicilipes* should be elevated to generic rank like *Petalomium*.

2. Biological Account

*Summary of life history of Agapostemon nasutus in Turrialba, Costa Rica.* Agapostemon nasutus nested in a nearly vertical bank of alluvial sandy silt. Up to 15 female bees occurred in each communal nest. All females were inseminated and had well developed ovaries; presumably all made and provisioned their own cells. Nest burrows extended inwards and downwards to a depth of about 1 m. Cells were constructed at the ends of 1.7 to 8.0 cm long lateral burrows extending horizontally from the main burrows. Each cell was lined with a waterproof glandular secretion and provisioned with a mixture of pollen and nectar in the shape of a slightly flattened ball. A single egg was laid on top of the provision mass and the cell was then closed and the lateral burrow filled with soil. Presumably no further contact took place between adult nest bees and the developing immature stages until the latter reached maturity. The egg hatched in 2 or more days and the larva consumed the provision mass, presumably in 4 to 5 days as does *Agapostemon texanus* (Roberts, 1969). The fully fed, mature larva rested on its dorsum for up to 5 days and then began defecating, plastering the feces on the upper posterior portion of the cell wall. Defecation took 1 1/2 to 2 days and then the postdefecating larva (prepupa) rested on its dorsum for up to 7 days before undergoing ecysis to the pupa. (Duration of mature larval and prepupal stages were based on laboratory rearings and may have been unnaturally long.) The pupal stadium lasted 21 to 22 days in the laboratory and could be timed by color changes of the developing pharate adult. The adult rested in the cell for a day or more following ecysis while its cuticle hardened, then presumably dug its way to the open main burrow through the soil filling the lateral burrow. Adult males quickly left the nests and did not re-enter them. They flew rapidly about the nest site and nearby plants and mating occurred outside of the nests. Adult females remained in their natal nests, joined other nests, or started new nests. Developmental stages were not synchronized in the nests and the species was multivoltine in Turrialba.

*Development of P. (Sicilipes) costaricanus in the nests of Agapostemon nasutus.* Adult female mites were located in 2 of 8 empty cells just excavated by female bees. Up to 10 adult female mites were also found in each of 10 of 13 cells containing provision masses and host eggs. All but 1 of these mites were on the cell walls or in the soil surrounding the cells; the other mite was on a provision mass. Similarly, up to 15 adult female mites were found on cell walls or in soil surrounding each of 5 of 9 cells containing feeding bee larvae; only 1 mite was on a provision mass. Mites were located in only 1 of 7 cells containing mature, predefecating bee larvae;
these adult female mites were on the cell walls and in the surrounding soil. All 5 cells containing postdefecating bee larvae (prepupae) contained mites. These adult female mites were avoid rather than flattened and all but 1 were on the surface of the bees’ feces. Mite eggs were also present on the feces.

All cells with bee pupae contained mites. In 4 cells with white-eyed pupae (0-3 days after pupation), small mite larvae were numerous on the surface of the bees’ feces and on their larval exuviae. This was also true in 4 cells with light-brown-eyed pupae (4-5 days after pupation), with mite larvae also crawling on the bee pupae. Swollen mite larvae (pharate adults) were seen in 1 cell and adult female mites and eggs were seen in 2 cells, indicating that oviposition was still occurring. In 8 cells with medium-brown- to dark-brown-eyed pupae (6-15 days after pupation), all postembryonic stages of the mites occurred although small larvae were less frequent. Swollen, inactive larvae (pharate adults) were found on cell surfaces, in indentations of the bee pupae (especially of the abdomens), and on the bees’ feces and larval exuviae.

Male mites appeared to develop faster than females and adult males walked actively on all surfaces, including the bee pupae. A male walked on 3 pairs of legs with his fourth pair held upwards. When he encountered any other mite with his fore legs, he immediately bent forwards in a “head stand” so his hind pair of legs encountered the mite and picked it up. Adult males and females, apparently in copulo, had the apices of their opisthosomas in contact, the male holding the female above him and facing in the opposite direction. Adult males also frequently carried inactive pharate adults about, holding them aloft with their hind legs. When 2 males contacted each other, they both reared up to clasp each other with their hind legs, but quickly released their hold.

In the 6 cells with bee pupae whose heads and thoraces were darkening (16-18 days after pupation), the mites were mostly adult females and occurred on the bees’ feces, the cell walls, and the bee pupae. In the 3 cells with bee pupae ready to ecdyse into adults (19-22 days after pupation), the adult female mites were concentrated on the surfaces of the pupae, with few mites on the feces and cell walls.

Supplementary data were obtained from 6 bee pupae collected in the dark-eye stage that were observed daily as they developed into fully colored pupae. The mites on these pupae were predominantly pharate adults plus a few active adult males that sometimes carried pharate adults, until 1 to 2 days before the pupal head and thorax darkened (14-15 days after pupation). At that time ecdysis to the adult female instar occurred and the adult female mites moved readily over both the bee pupae and the vials that enclosed them. On the 7 bee pupae that were observed daily through adult emergence, adult female mites were concentrated on the pupae (and not on the vial surfaces) just before emergence.

In the 2 cells that contained freshly emerged adult male bees, adult female mites were concentrated on the cell walls and not on the bees. Similarly, on the 7 adult bees (both male and female) that were observed daily in their development from pupae, the mites left the adult bees shortly after ecdysis and occurred on the vial surfaces and pupal exuviae. On 2 male bees observed during ec dysis, the mites remained on the bees during the process. Of those freshly emerged adult bees captured in cells (without examination of cell walls), 2 males lacked mites and 2 males and 1 female bore mites. Apparently at least some mites transferred to adult bees before the latter dug their way out of their natal cells.

Three adult female bees were captured in burrows soon after emergence and before they began reproduction, judging from their unworn condition, extensive fat deposits, lack of sperm in their spermathecae, and undeveloped ovaries. All of these bore large numbers of inactive adult female mites attached to metasomal (gastral) ter gum I and the propodeum. Of 27 older
female bees that were presumably provisioning cells, judging by their worn, inseminated condition and well-developed ovaries, 12 carried adult female mites. These mites clung to the bees' hairs with their fore tarsal claws and appeared flattened.

Mites were fewer and more scattered on male bees. Males of *A. nasutus* do not re-enter nests and copulation lasts 10 seconds or less in *Agapostemon* (Bohart, 1950; Abrams, 1977), thereby making transfer of mites between mating hosts improbable. It is unlikely that mites attached to male *A. nasutus* are able to reproduce.

The food source of *P. costaricanus* could not be defined. Neither the adult nor the larval mites fed on the developing or adult bees. The pollen-nectar provisions intended for the bee larvae also were not a food source for the mites. No mites occurred in 7 cells containing moldy provisions and the mites in rearing dishes did not appear to feed on fungus that infested the pollen. The food source for the mite larvae apparently occurred in the fecal deposits of the bee larvae, either the feces themselves or some contaminant thereof. The adult female mites apparently did not feed between their emergence as adults and when they left their phoretic bee hosts in new cells. However, some feeding probably occurred before they oviposited; the food source is unknown.

Based on the above data, the life cycle of a typical *P. costaricanus* is as follows. The adult female attaches to the hairs of an adult female bee before the latter digs her way out of her natal cell. The mite detaches from her phoretic host without feeding when the bee constructs or provisions her cell. The mite remains on the cell walls (or possibly in the surrounding soil) while the bee larva consumes its provisions. When the mature bee larva defecates on the cell wall, the mite moves onto the feces and oviposits. The mite larvae feed on some component or contaminant of the feces and swell greatly. The inactive pharate adult females occur on the bee's feces, larval exuvium, cell walls, and on the bee itself, which had pupated at least 6 days earlier. Adult male mites emerge before females and frequently carry about pharate adults with their enlarged hind legs; they copulate with adult females (and possibly with pharate adult females). Adult females emerge 1 or 2 days before the bee pupa darkens and move freely about the cell walls, larval bee feces, and on the pupa itself. Just before the bee ecldyes to the adult, the adult female mites concentrate on the pupal surface and they may stay there during ecldysis. However, soon afterwards the mites apparently leave the newly emerged adult bee, only to attach to it again before it leaves the cell. Mites develop equally well in cells containing male and female bees, but attach less frequently to male bees and probably are unable to reach new nests when phoretic upon them.

**Discussion**

All or nearly all cells in nests of an aggregation of *Agapostemon nasutus* were infested with *P. (Sicilipes) costaricanus*, judging from contents of pupal cells. There was no indication of any harm done to the developing bees by the mites and the mite-bee relationship is commensal. The mite appears to be an obligatory associate of groundnesting bees and its life cycle is closely synchronized with that of its host: mite larvae hatch just when food provided by the bee's larval feces becomes available, and adult female mites emerge in time to attach to their phoretic host before the adult bee leaves its natal cell.

Collections of other species of Neopygmeghorinae (to be described in subsequent papers by GR and Mercedes Delfinado) in cells of groundnesting halictine bees by GCE suggest that the commensal relationship described for *P. costaricanus* and *A. nasutus* is characteristic of those Neopygmeghorinae that are associated with bees.
Two other Pygmephoridae associated with halictine bees have been investigated biologically. MOHAMED and SOLIMAN (1974) observed "Siteroptes cerealium" (non Kirchner) feeding on fungus that infested provision masses in cells in which the immature bees had died. They also observed feeding on bee eggs in the laboratory, but halictine eggs are very difficult to maintain in the laboratory and the mites may have fed upon already dead eggs. Trochometridium tribulatum, originally described as predaceous upon larval bees (Cross, 1965), has also been reared on fungus found in nest cells (Cross and MOSER, 1971). In contrast to P. costaricanus, both of these species have physogastric adult females. Adults emerge directly from eggs in "S. cerealium" while a quiescent larva is present in T. tribulatum. Morphological as well as biological resemblances of Trochometridium to Pyemotes suggest that the former genus should be transferred from the Pygmephoroidea back into the Pyemotoidea.

Our observations suggest that there is considerable inbreeding in P. costaricanus since mating takes place only among mites reared in the same cell. There is a discrepancy, however, in the fact that fewer than half the adult female bees in the nests bore mites with which to infest cells, but all of the pupal cells had mites. There are two possible sources for mites in cells constructed by mite-free bees: more than one female bee may enter a cell prior to its closure, or adult female mites may move through the soil or nest burrows to enter cells before or during defecation by the larval bees. The second hypothesis is supported by similar dispersal behavior by adult females of T. tribulatum (Cross, 1965; Cross and BOHART, 1969) and "S. cerealium" (MOHAMED and SOLIMAN, 1974). Both hypotheses allow for some outbreeding in P. costaricanus.

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