ILLUSTRATED KEY TO *PSEUDACTEON* DECAPITATING FLIES (DIPTERA: PHORIDAE) THAT ATTACK *SOLENOPSIS SAEVISSIMA* COMPLEX FIRE ANTS IN SOUTH AMERICA

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ABSTRACT

This paper provides an illustrated key in English and Portuguese to 18 South American species of *Pseudacteon* decapitating flies that attack *Solenopsis* fire ants in the *saevissima* complex. The taxonomic history and current status of species in the genus *Pseudacteon* are discussed. *Pseudacteon* flies are of interest because of their unusual life history and potential value as classical fire ant biocontrol agents.

Key Words: biocontrol, taxonomy, ovipositor, parasitoid, Brazil, Argentina

RESUMO

Este trabalho fornece uma chave ilustrada em inglês e português para 18 espécies sul āmericanas de *Pseudacteon* que atacam formigas lava-pés *Solenopsis* do complexo *saevissima*. A história taxonômica e a posição atual das espécies no gênero *Pseudacteon* são discutidas. As pequenas moscas *Pseudacteon* são de interesse devido a sua ciclo de vida incomum e potencial valor como agentes de biocontrole clássico das formigas lava-pés.

Phorid flies in the genus *Pseudacteon* are of particular interest because of: 1) their potential use as classical biocontrol agents for imported fire ants in the United States and other parts of the world (Porter 1998) and 2) their unusual life history (Porter et al. 1995a). *Pseudacteon* flies appear to be promising biocontrol agents because fire ants utilize a suite of highly specific defenses against attacking flies (Orr et al. 1995; Porter et al. 1995b; Morrison 1999). These defenses could only have evolved and be maintained if *Pseudacteon* flies were having evolutionary impacts on fire ant populations or the production of sexuals.

Pseudacteon flies are the kind of parasitoids that give science fiction writers fodder for their stories. Adult females dive in and inject their torpedo-shaped eggs into the bodies of ant workers in only a fraction of a second. Their highly sclerotized external ovipositors (Figs. 1-19) appear to function in a lock-and-key fashion, allowing an egg to be rapidly and precisely inserted into specific locations of the ant thorax. The newly hatched maggot moves into the head of its host where it develops for 2-3 weeks (Pesquero et al. 1995; Porter et al. 1995a). Just prior to pupation, the maggot apparently releases a chemical that causes the intersegmental membranes of its host to dissolve. Within hours, the host worker is decapitated leaving the body still twitching. The maggot consumes everything in the head and pupates inside the empty head capsule, using it as a pupal case (Porter et al. 1995a). Surprisingly, the sex of developing flies appears to be determined by the size of their host rather than by their genes (Morrison et al. 1999).

The genus *Pseudacteon* was described by Coquillett (1907). Female *Pseudacteon* flies are characterized by having fully developed wings, large eyes with hundreds of ommatidia, a subquadrate frons with a median furrow, more than 4 bristles on the frons, unforked wing veins, hind tibia with a dorsal hair palisade, and a symmetrical highly sclerotized ovipositor (Coquillett 1907; Disney 1994). See Borgmeier (1963) for a more complete diagnosis of the genus. Like other phorids, *Pseudacteon* flies have shortened costal and radial veins and a ball-and-socket articulation between the greatly enlarged third antennal segment and the conus of the second antennal segment (Disney 1994).

Twenty-seven species of *Pseudacteon* flies are known to attack fire ants in the genus *Solenopsis* (Porter 1998). About a dozen additional species are known to attack ants in other genera including: *Dorymyrmex, Linepithema, Crematogaster, Lasius, Liometopum, Myrmica,* and *Pseudolasius* (Disney 1994; Brown & Feener 1998). *Pseudacteon* flies have been collected from the following regions: South America, North America, Europe, Asia, Australia, and Indonesia (Borgmeier 1963;

Disney 1994; Brown & Feener 1998; Disney & Michailovskaya 2000).

This paper provides an illustrated key to the 18 described species of *Pseudacteon* flies that are known to attack *Solenopsis saevissima* complex fire ants. Previous keys to these species are impractical to use because they do not include all known species and rely on characters that are either difficult to see or too variable to be effective (Borgmeier 1925, 1969). Fire ants in the *saevissima* complex inhabit regions of South America from the Amazon Basin of Brazil, west to the Andes and south through the Province of Buenos Aires in Argentina (Trager 1991). Most of the *Pseudacteon* species in South America were described by Borgmeier (1925, 1926, 1938, 1962, Borgmeier & Prado 1975). Additional South American species were named by Schmitz (1914, 1923), and Pesquero (2000). The host species of *Pseudacteon conicornis* Borgmeier was previously unknown (Borgmeier 1962), but it is included in this key because it was recently collected attacking *Solenopsis saevissima* ants near Rio de Janeiro (Brown 2000). We also included *P. convexicauda* in this key because it has occasionally been collected over *Solenopsis* fire ants (Borgmeier 1962; Porter 1998); nevertheless, this is very rare and recent collections indicate that it is probably a parasitoid of *Paratrechina* ants (M. A. P., unpubl. data).

Materials and Methods

Photographs of fly ovipositors (Figs. 1-20) were obtained using scanning electron microscopes in the University of Florida Departments of Entomology and Zoology and the Universidade de São Paulo, Intsituto de Fisica in São Carlos. Flies were prepared using standard dehydration techniques and their abdomens were mounted on stubs for gold coating. We used NIH Image (1.62) public domain software (http://rsb.info.nih.gov/nih-image/) to improve the contrast and orientation of the photos. CorelDRAW 6 was used to assemble the plates.

Material Examined

This paper is based primarily on collections made by the authors and inspection of type material from T. Borgmeier in the Muzeu de Zoologia da USP, São Paulo, Brazil. C. R. F. Brandão (Muzeu de Zoologia da USP), B.V. Brown (Los Angeles Co. Museum), L. E. Gilbert (Univ. of Texas at Austin), and P. J. Folgarait (Universidad Nacional de Quilmes, Buenos Aires, Argentina) supplied additional specimens for use with the electron microscope.

Location data for flies illustrated in Figs. 1-19 are as follows: Fig. 1, near Desengano, RJ, Brazil; Fig 2, Rio Claro, SP, Brazil; Fig. 3, Pindamonhangaba, SP, Brazil; Fig. 4, Rio Claro, SP, Brazil; Fig. 5a, Buenos Aires Province, Argentina; Fig. 5b, Rio Claro, SP, Brazil; Fig. 6a, Jundiai, SP, Brazil; Fig. 6b, Goiânia, GO, Brazil; Fig. 7, São Carlos, SP, Brazil; Fig. 8a, Hurlingham, BA, Argentina; Fig. 8b, Goiânia, GO, Brazil; Fig. 9, Rio Claro, SP, Brazil, Fig. 10, São Carlos, SP, Brazil; Fig. 11, Goiânia, GO, Brazil; Fig. 12, Rio Claro, SP, Brazil; Fig. 13, San Ignacio, MS, Argentina; Fig. 14, Rio de Janeiro, RJ, Brazil; Fig. 15, Goiânia, GO, Brazil; Fig. 16, Rio Claro, SP, Brazil; Fig. 17a, Viçosa, MG, Brazil; Fig. 17b, Goiânia, GO, Brazil; Fig. 18, Goiânia, GO, Brazil; Fig. 19a, São Paulo State, Brazil; Fig. 19b, Buenos Aires Province, Argentina.

Results and Discussion

Variation

Several species illustrated in our key exhibit regional variability. Some cases may be intraspecific clinal variation while other cases may be true sibling species isolated by geography or host preferences.

In the case of *Pseudacteon curvatus* Borgmeier, individuals from around São Paulo, Brazil have a more sharply curved ovipositor (Fig. 5b) than those from near Buenos Aires, Argentina (Fig. 5a). The ventral tooth is also sharper in specimens from Brazil (Fig. 5b) and this tooth lacks the medial reinforcement ridge seen in Fig. 5a.

The ovipositor of *Pseudacteon nudicornis* Borgmeier from Jundiai (Fig. 6a) is proportionally wider than that of the specimen from Goiânia (Fig. 6b). Also, the inner margin of the upper plate of the lateral lobes is convex compared to concave for the specimen from Goiânia.

For *Pseudacteon cultellatus* Borgmeier, the terminus of central extension of the ovipositor has a strong lateral extension for specimens collected near Buenos Aires (Fig. 8a), but only a slight extension for specimens collected from Goiânia (Fig. 8b).

The ovipositor of *Pseudacteon affinis* Borgmeier collected from Goiânia (Fig. 17b) is much narrower than it is for flies collected near Viçosa (Fig. 17a).

Pseudacteon obtusus Borgmeier flies from the region around the city of São Paulo are generally small flies (Morrison & Gilbert 1999) that lack aristae on the antennae, but *P. obtusus* collected in western and southern parts of their range are commonly large flies with aristae on the antennae. The absence of aristae is typically a male trait. Male *Pseudacteon* flies are usually smaller than female flies so the absence of aristae in small females may be an allometric trait associated with small size. Large- and small-sized *P. obtusus* have been collected at the same site in northern Argentina, but it is unknown whether large individuals are from a genetically distinct population or merely the facultative result of development in larger hosts.

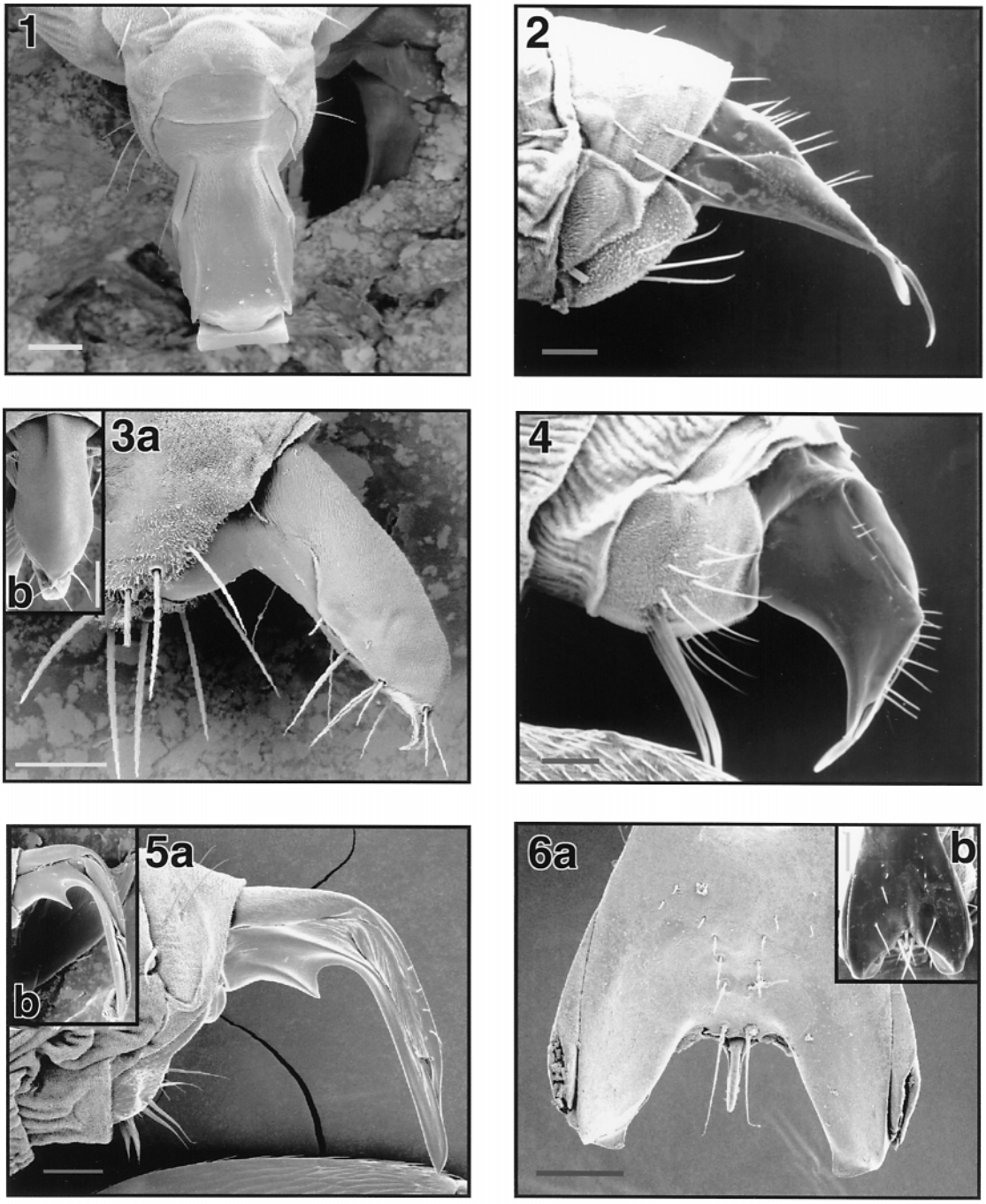


Fig. 1. Dorsal posterior view of *P. conicornis* external ovipositor. Fig. 2. Lateral view of *P. solenopsidis* ovipositor. Fig. 3. *P. convexicauda*; a) lateral view; b) dorsal posterior view. Fig. 4. *P. borgmeieri,* lateral view. Fig. 5. *P. curvatus,* lateral view; a) from Buenos Aires Province, Argentina; b) from São Paulo State, Brazil. Fig. 6. Dorsal-posterior view of *P. nudicornis*; a) from São Paulo State, Brazil, b) from Goiás, Brazil. Bars in figures indicate 50 μm.

Female *Pseudacteon tricuspis* Borgmeier flies collected from São Paulo, Brazil west to Mato Grosso do Sul and south to Santa Fe, Argentina look like Fig. 19a. South and east of Santa Fe through the province of Buenos Aires they look like Fig. 19b. The major differences are that the

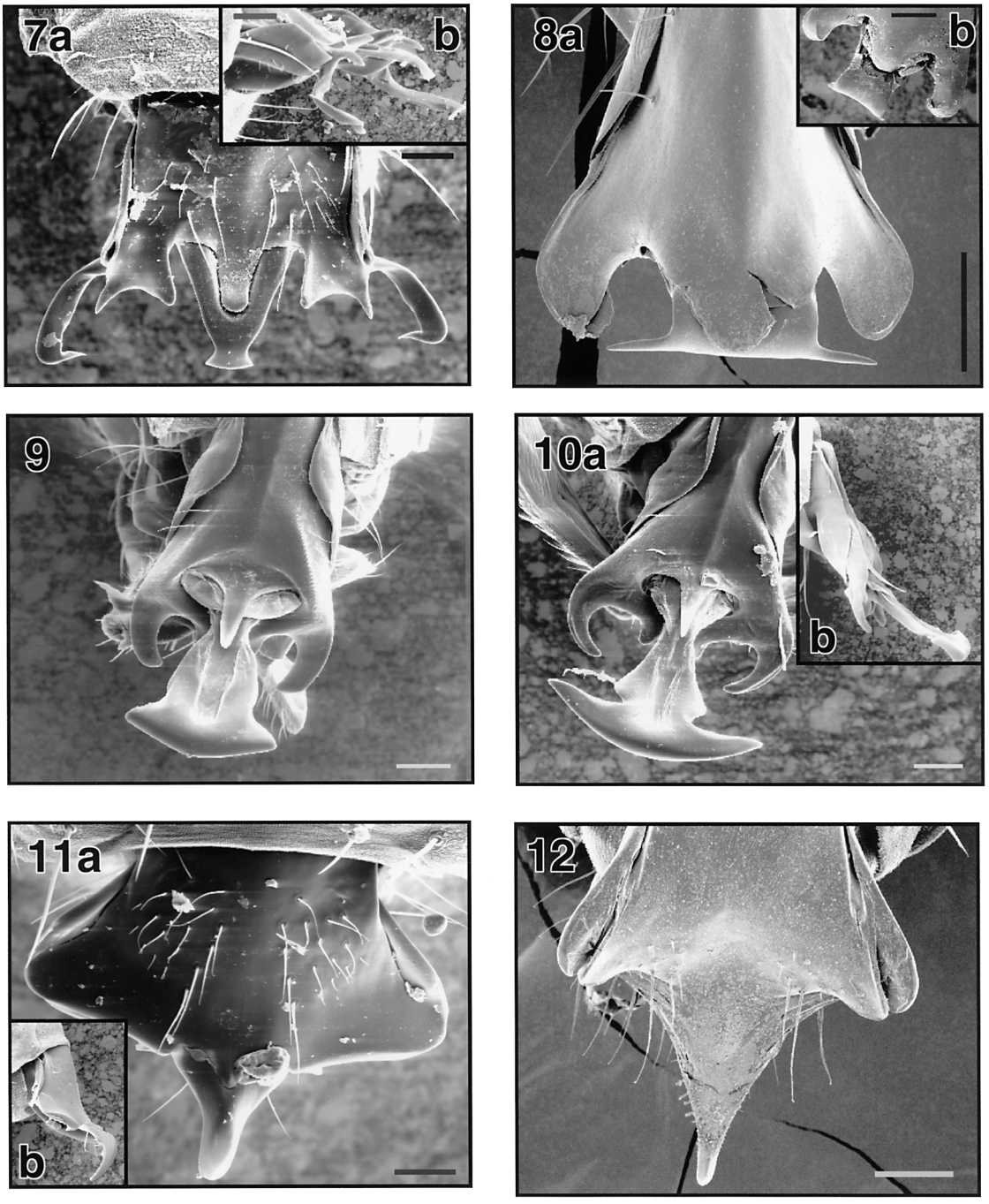


Fig. 7. Ovipositor of *P. fowleri*, b) lateral view. Fig. 8. *P. cultellatus*, a) from Buenos Aires Province, Argentina, b) from Goiás, Brazil. Fig. 9. *P. pradei*. Fig. 10. *P. disneyi*, b) lateral view. Fig. 11. *P. lenkoi*, b) lateral view. Fig. 12. *P. litoralis*. Figures show ovipositors in dorsal-posterior view unless specified otherwise. Bars in figures indicate 50 μm.

central extension of the ovipositor of flies collected south of Santa Fe is broader (about as long as wide) and the membranous filaments are parallel with the central extension and hooked downward at their terminus (Fig. 19b) rather than gently curved and congruent with the lateral lobes (Fig. 19a). These differences correspond to a switch in hosts from *Solenopsis invicta* Buren/ *Solenopsis saevissima* F. Smith to *Solenopsis richteri* Forel. A third variety of *P. tricuspis* from

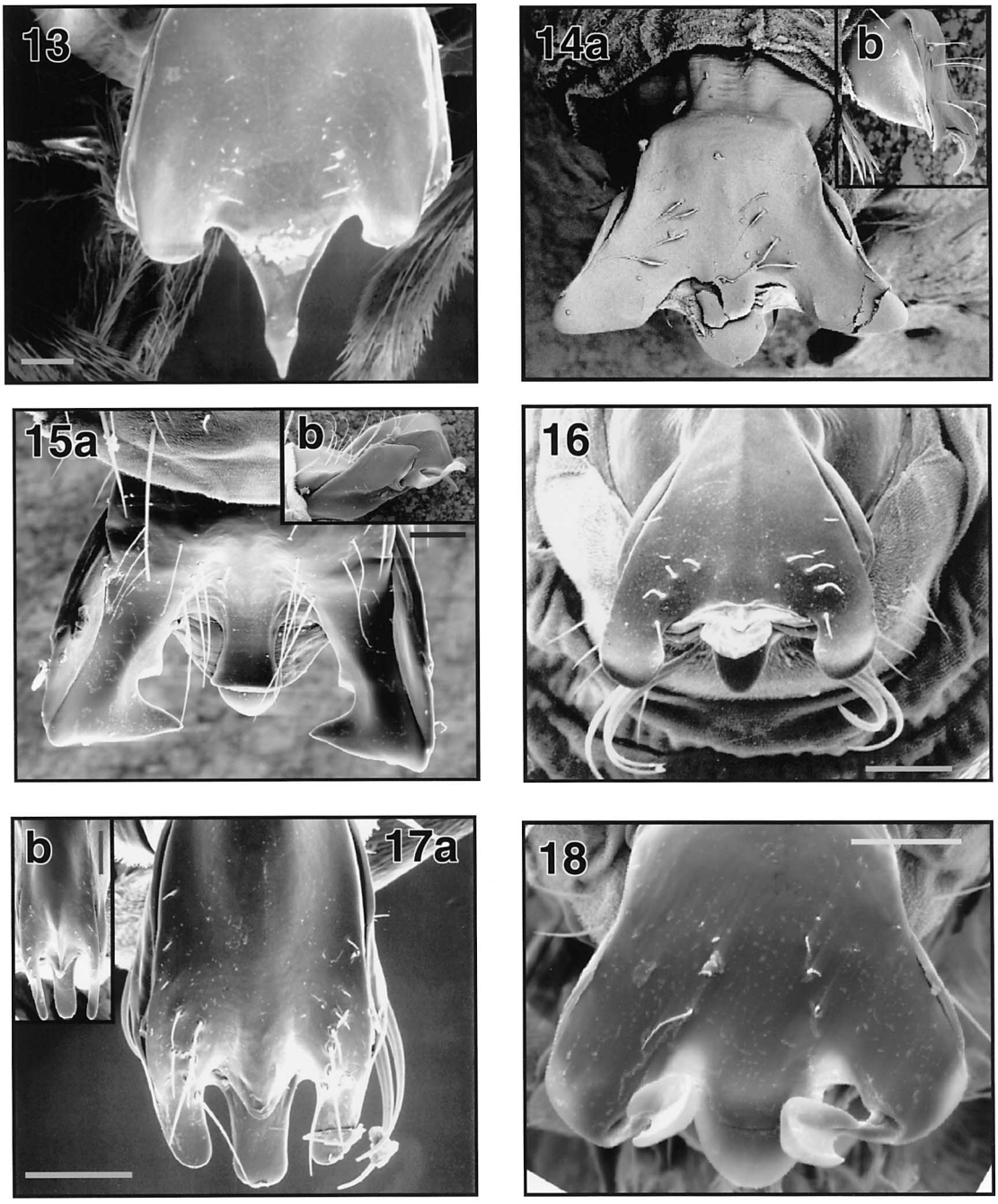
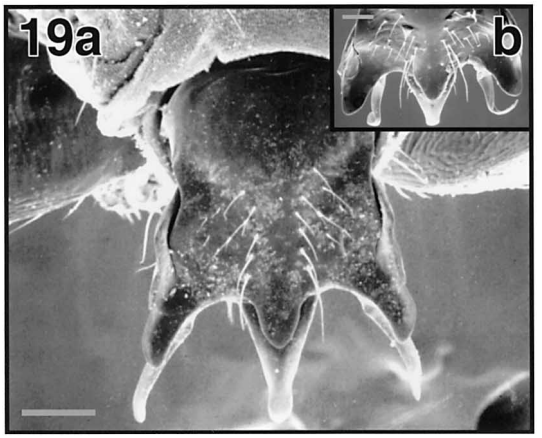


Fig. 13. *P. nocens* ovipositor. Fig. 14a. *P. comatus*, b) lateral view. Fig. 15a. *P. dentiger*, b) lateral view. Fig. 16. *P. wasmanni*. Fig. 17. *P. affinis*, a) from Minas Gerais, Brazil, b) from Goiás, Brazil. Fig. 18. *P. obtusus*. Figures show ovipositors in dorsal-posterior view unless specified otherwise. Bars in figures indicate 50 μm.

Goiânia (not illustrated) is much smaller and has the membranous filaments extending off the lateral lobes at a joint part way up the lobe.

The significance of regional variation is largely unknown; however, different biotypes of the same species or sibling species can be specialized to attack different fire ant hosts. For example, *P. curvatus* from Argentina clearly prefers the native black fire ant (*S. richteri*) over the red fire ant (*S. invicta*) found further to the north (Porter & Briano 2000). Similarly, *P. tricuspis* females from around Buenos Aires strongly prefer *S. rich-*



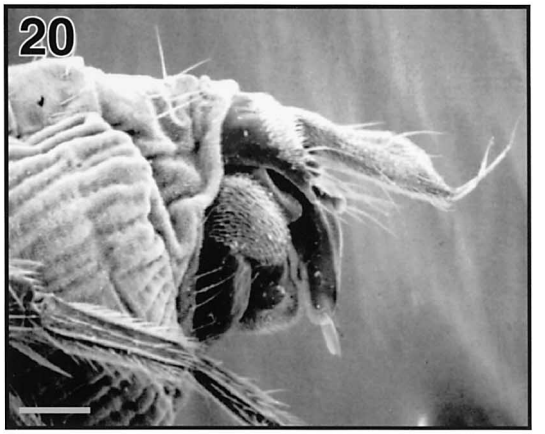


Fig. 19. *P. tricuspis* ovipositor in dorsal posterior view, a) from São Paulo State, Brazil, b) from Buenos Aires Province, Argentina. Fig. 20. Lateral view of *P. tricuspis* male hypopygium, from Brazil. The anal tube extends out prominently with two stout hairs at its terminus. The penis and hypandrium are tucked in below. Males of other known *Pseudacteon* species are very similar in general appearance (Disney 1991) and much more difficult to distinguish than females. Bars in figures indicate 50 μm.

teri fire ants while *P. tricuspis* females from near São Paulo prefer *S. invicta* fire ants (S. D. P., unpubl. data). Matching appropriate *Pseudacteon* biotypes to imported fire ants in the United States is likely to be important in their success as biocontrol agents.

Illustrated Key [Chave Ilustrada]

This illustrated key is for females of *Pseudacteon* species that parasitize *Solenopsis saevissima* complex fire ants in South America. It is based primarily on characteristics of the external ovipositor. [Esta chave ilustrada é para fêmeas de espécies de *Pseudacteon* parasitóides de formigas do complexo *Solenopsis saevissima* na América do Sul. Chave baseada em características dos últimos segmentos esclerotizados do abdome (ovipositor).]

1 Ovipositor simple, without lateral lobes; [Ovipositor simples, sem lobos laterais]; Figs. 1-5 . . . . . **2**

— Ovipositor with lateral lobes in dorsal-posterior view; [Ovipositor com lobos laterais em vista dorsoposterior]; Figs. 6-19 . . . . . **6**

2 (1) Antennae with aristae, ovipositor not flattened dorsoventrally; [Antena com arista, ovipositor não achatado dorsoventralmente] **3**

— Antennae without aristae, ovipositor somewhat flattened dorsoventrally with a small spatulate extension on the end; [Antena sem arista, ovipositor algo achatado dorsoventralmente com um pequeno prolongamento em forma de espátula no final]; Fig. 1 . . . . . ***P. conicornis* Borgmeier**

3 (2) Ovipositor approximately linear in lateral view; [Ovipositor aproximadamente retilineo em vista lateral]; Figs. 2-3 . . . . . **4**

— Ovipositor angled or curved in lateral view; [Ovipositor angulado ou curvado em vista lateral]; Figs. 4-5. . **5**

4 (3) Ovipositor lanceolate with a small membranous extension near terminus; four medium hairs or setae under abdomen just before ovipositor; [Ovipositor lanceolado com pequena peça membranosa no fim; quatro pelos médios sob o abdome pouco antes do ovipositor]; Fig. 2. . . . . ***P. solenopsidis* Schmitz**

— Ovipositor blunt, broadly rounded on dorsum; flat or somewhat concave on ventral surface; eight stout socketed hairs under abdomen before ovipositor, about ½ the length of the ovipositor (probably accidental over *Solenopsis* ants); [Ovipositor em forma de bastão com a superfície ventral plana e dorsal convexa; oito pelos robustos encaixados sob o abdome pouco antes do ovipositor, com aproximadamente metade do comprimento do ovipositor]; Fig. 3 . . . . . ***P. convexicauda* Borgmeier**

5 (3) Ovipositor short with the dorsal surface truncated and directed downward; with several stout hairs extending out under ovipositor, almost as long as the ovipositor; [Ovipositor curto com o dorso da região terminal truncado e ápice direcionado para baixo; vários pelos robustos quase tão longos quanto o ovipositor extendendo sob o ovipositor]; Fig. 4 . . . . . ***P. borgmeieri* Schmitz**

— Ovipositor long, curved downward, with a large ventral tooth near base; hairs on last abdominal segment not unusually long; [Ovipositor longo, curvado para baixo e com um dente grande na região ventral da base; pelos sob o último segmento abdominal não longos]; Fig. 5 . . . . . ***P. curvatus* Borgmeier**

6 (1) Ovipositor bilobed with a small central projection; [Ovipositor bilobado com uma pequena projeção central]; Fig. 6. . . . . ***P. nudicornis* Borgmeier**

— Ovipositor trilobed or not bilobed; [Ovipositor trilobado ou não bilobado]; Figs. 7-19. . . . . **7**

7(6) Two teeth on each lateral lobe separated by a shallow concavity; under each lobe, there is a long sclerotized ice tong-like appendix, curved and pointed at the end; the central piece of the ovipositor is in the form of a "Y"; [Lobos laterais com dois dentes separados por superfície levemente côncava; sob cada lobo há um longo apêndice esclerotizado com ápice curvado e pontiagudo; peça central em forma de "Y"]; Fig. 7. . . . . ***P. fowleri* Pesquero**

— Not as above; [Não como acima] **8**

8 (7) Central extension of ovipositor expanded laterally at end; antenna without arista; [Peça central expandida lateralmente no fim; antena sem arista]; Figs. 8-10 . . . . . **9**

— Central extension not expanded laterally at terminus; antenna with or without an arista; [Peça central não expandida lateralmente no fim; antena com ou sem arista]; Figs. 11-19 . . . . . **11**

9 (8) Central extension of ovipositor broadly rounded at end; [Peça central amplamente arredondada no fim]; Fig. 9-10 . . . . . **10**

— Central extension truncated at end; [Peça central truncada no fim]; Fig. 8. . . . ***P. cultellatus* Borgmeier**

10 (9) Central extension of ovipositor in the form of a bell; [Peça central em forma de sino]; Fig. 9. . . . . ***P. pradei* Borgmeier**

— Central extension in the form of an anchor; [Peça central em forma de âncora]; Fig. 10 ***P. disneyi* Pesquero**

11 (8) Central extension of ovipositor much longer (posteriorly) than the lateral lobes; [Peça central muito mais longa posteriormente do que os lobos laterais]; Figs. 11-13 . . . . . **12**

— Central extension of ovipositor, at maximum, a little longer than the lateral lobes; [Peça central, no máximo, pouco mais longa do que os lobos laterais]; Figs. 14-19. . . . . **14**

12 (11) Central extension hooked downward (Fig. 11b); lateral lobes broadly joined with central extension; the angle formed between a lateral lobe and the central extension is >90°; [Peça central curvada para baixo no ápice (Fig. 11b); lobos laterais fundidos com a peça central; ângulo formado entre um lobo lateral e a peça central é >90°]; Fig. 11. . . . . ***P. lenkoi* Borgmeier & Prado**

— Central extension not hooked downward; angle formed between a lateral lobe and the central lobe is <90°; [Peça central não curvada para baixo; ângulo formado entre um lobo lateral e a peça central é <90°]; Figs. 12-13. . . . . **13**

13 (12) Lateral lobes rounded and extend out diagonally; central extension cylindrical; [Lobos laterais arredondados e direcionados diagonalmente; peça central cilíndrica]; Fig. 12 . . . ***P. litoralis* Borgmeier**

— Lateral lobes truncate and directed posteriorly; central extension flattened; [Lobos laterais truncados e direcionados posteriormente; peça central achatada]; Fig. 13 . . . . . ***P. nocens* Borgmeier**

14 (11) Lateral lobes truncated at ends; [Lobos laterais truncados posteriormente]; Figs. 14-15 . . . . . **15**

— Lateral lobes rounded or pointed at ends; [Lobos laterais arredondados ou ponteagudos]; Figs. 16-19 . **16**

15 (14) Lateral lobes and central lobe of similar length, separated by a small oblique incision; [Lobos laterais simples, separados da peça central por uma pequena incisão oblíqua; lobos laterais e peça central de comprimentos semelhantes]; Fig. 14 . . . . . ***P. comatus* Borgmeier**

— lateral lobes complex, each with a tooth directed medially (Fig. 15); a membranous filament also extends off internal border (Fig. 15b); [Lobos laterais complexos com um dente dirigido para a linha mediana (Fig. 15); na borda interna há um filamento membranoso (Fig. 15b)]. . . . . ***P. dentiger* Borgmeier**

16 (14) Abdomen with several stout hairs extending out under ovipositor, hairs are almost as long as the ovipositor; lateral lobes without membranous appendages; [Último segmento do abdome com vários pelos robustos direcionados sob o ovipositor, esses pelos são quase tão longos quanto o ovipositor; lobos laterais sem apêndices membranosos]; Figs. 16-17 . . . . . **17**

— Without long stout hairs under ovipositor; lateral lobes with membranous extensions; [Sem pelos longos e robustos; lobos laterais com apêndices membranosos]; Figs. 18-19 . . . . . **18**

17 (16) Lateral lobes of ovipositor diverge diagonally; ovipositor about as long as wide; [Placa dorsal do ovipositor com bordas que divergem anteroposteriormente; ovipositor quase tão longo quanto largo]; Fig. 16 . . . . . ***P. wasmanni* Schmitz**

— Lateral lobes of ovipositor subparallel; ovipositor much longer than wide; [Placa dorsal do ovipositor com bordas sub-paralelas; ovipositor muito mais longo do que largo]; Fig. 17 . . . . . ***P. affinis* Borgmeier**

18 (16) Lateral lobes broadly rounded, each with a membranous extension off their inner borders directed medially; membranous extension in the shape of a stocking; [Lobos laterais amplamente arredondados; apêndice membranoso em forma de botina saindo da borda interna dos lobos laterais]; Fig. 18 . . . . . ***P. obtusus* Borgmeier**

— Lateral and central lobes pointed, in form of a trident; membranous filament under each lateral lobe; [Ovipositor em forma de tridente; filamento membranoso vermiforme saindo sob os lobos laterais]; Fig. 19 . . . . . ***P. tricuspis* Borgmeier**

A key to male *Pseudacteon* flies is not provided because most males are undescribed and unknown to science because they are not attracted to fire ant workers. Unlike most South American species, large numbers of *P. tricuspis* males (Fig. 20) are commonly collected in the field because they are attracted to fire ants and attempt to mate with ovipositing females (Porter 1998). *P. curvatus* flies mate away from fire ant mounds shortly after emerging from the pupae (Wuellner & Porter, unpubl. data). The mating behavior of the other 16 species of *Pseudacteon* flies that attack *saevissima* complex fire ants is unknown.

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