

A Review of the Genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an Inquiline Fig Wasp with Brachypterous Males, With Descriptions of Two New Species,

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Abstract.—Biological observations and a description of two new species of the braconid genus *Psenobolus* are presented. These wasps were reared from the syconia (figs) of *Ficus (Urostigma)* spp. in San Jose, Costa Rica where they appear to develop as inquilines with chalcid fig wasps. No indication of parasitism was found. The sexes of the new species are dimorphic: the females are typical braconids; the males, however, are brachypterous with many characters in common with males of the chalcidoid *Idarnes*, also found in the figs.

INTRODUCTION

The braconid genus *Psenobolus* was described by Reinhard in 1885 from wasps reared from a fig fruit collected in St. Catharina, Brazil. Reinhard's description included normal winged females and males. No biological information was given.

In 1965, the senior author (Ramirez) sent to the late C. F. W. Muesebeck at the U. S. National Museum, Washington, DC, specimens of winged females and brachypterous males of a braconid wasp reared from the figs of *Ficus (Urostigma) velutina* Willd. in Costa Rica which he thought were parasitizing *Blastophaga torresi* Grandi (presently in the genus *Pegoscapus*). The females were identified as a new species of *Psenobolus*. Muesebeck stated that there were "no braconid males in the sample" adding that the "males present were some species of *Idarninae* (Chalcidoidea), which presumably developed as an inquiline." Ramirez continued to collect and rear *Psenobolus* from *F. (U.) velutina* and other *F. (Urostigma)* species and the females were always associated with extremely dimorphic brachypterous males. In 1991, he sent more specimens to

the junior author (Marsh) at the U. S. National Museum who also identified the females as a new species of *Psenobolus* but considered the brachypterous males to be bethylids or tiphiids if not idarnine chalcids. Even Marsh's colleagues in the Hymenoptera Unit could not identify these unusual males. Undauntedly, in 1993 Ramirez sent another sample to Marsh that contained females and brachypterous males as before. However, one male was actually gynandromorphic: the head and metasoma were typical male but the mesosoma had one side with male brachypterous wings and swollen femora while the opposite side was female with normal wings and legs! This was convincing evidence that the brachypterous males did belong to the females and that the species was possibly developing in the figs as an inquiline with the males being highly modified similar to the idarnine chalcids also present (see below). Further evidence that these males are those of the female braconid is that the males of the type species, *P. pygmaeus* Reinhard, and males of another species in the U. S. National Museum are fully winged but have similar

antennae and swollen femora to those of the brachypterous males.

Many of the chalcidoid wasps that develop in the syconia (figs) of *Ficus* are brachypterous or wingless: the males of Agaoninae are completely wingless while those of other agaonids (non-pollinators) are brachypterous or wingless. Hamilton (1979) observed that of the more than 18 species of fig wasps found in two Brazilian *Urostigma* fig species, many had wingless males and several showed extreme sexual dimorphism. He also found that there was lethal combat among several types of these wingless males. Additionally, Murray (1989) found 25 species with flightless males among the fig wasps he collected.

BIOLOGY OF *PSENOBOLUS* IN FIGS

(Biological information presented below based primarily on study of *P. ficarius* n. sp.)

Species of *Psenobolus* appear to be inquiline wasps that develop in the syconia of the genus *Ficus* subgenus *Urostigma* section *Americana* only. The female probably pierces the fig wall with her long ovipositor and lays the eggs in the female flowers of the figs ("gall flowers") which were recently oviposited into and pollinated by the symbiotic agaonid wasps. The larval and pupal stage occur inside the gall flowers. The adult brachypterous males emerge from the galls before the females but simultaneously with the agaonid and *Idarnes* males. The *Psenobolus* males apparently then mate with the "inactive" females while they are still inside the galls, although this was not observed. This is similar to other New World fig inquiline wasps such as the genera *Idarnes* and *Critogaster*. According to Hamilton (1979), "the great majority of male fig wasps are wingless" and this, along with precocious mating, has been well documented. After mating, the females emerge from the galls and escape from the syconia through the

exit holes in the fig wall made by males of the agaonid pollinators. *Idarnes* females also depend on the agaonid males for escape from the syconia. The sex ratio of *Psenobolus* was found to be 1:1.

The brachypterous males of these species of *Psenobolus* from Costa Rica are soldier males. With their prognathous heads and large mandibles they have been observed to fight to the death with other males of their own species. Many specimens we have seen have lost most of their antennae apparently from this fighting activity as well as while searching for females, gnawing through the galls and mating. Only a few authors have reported fighting in other fig wasps. Joseph (1958) observed fighting in *Philotrypesis* and Murray (1989) described intensive fighting in *Philotrypesis* and *Apocrypta bakeri*. The extreme dimorphism and dwarfing of male fig wasps may be partially attributable to fighting. According to Hamilton (1979), apart from the large heads and mandibles and perhaps the shield-like head and pronotum, the other modifications, such as winglessness, are probably not connected with selection for fighting. We feel, however, that many characters of the fig wasp males are, in fact, associated with fighting, such as brachyptery or winglessness, reduction in number of antennal segments and mating inside the galls.

The polymorphism and dwarfing of male *Psenobolus*, absent in the female, is probably associated with the amount of "vegetable food" left by the agaonid larva in each gall as suggested by Joseph (1984) rather than caused by a supergene (or a switched set of genes) that controls size and morphology as suggested by Hamilton (1979). According to Joseph (1984), male fig wasps survive as dwarf individuals, increasing the proportion of males.

THE "AGAONIDIZATION" OF *PSENOBOLUS*

The brachypterous males of *Psenobolus* have many characters in common with

males of *Idarnes* (Torymidae in the sense of Gordh 1975 or Agaonidae in the sense of Boucek 1988) which also develop as inquilines in New World *Ficus* (*Urostigma*) figs. The common morphological and biological characters are listed below. We compared the brachypterous *Psenobolus* males with the description of *Idarnes* presented by Gordh (1975).

Morphological characters shared between brachypterous *Psenobolus* and *Idarnes* males:

Head

- Extreme polymorphism, soldier type males
- Prognathous heavily sclerotized heads
- Head wider or as wide as long
- Reduced eyes
- Ocelli absent
- Reduced antennae, large scape
- Large mandibles, articulated in horizontal plane

Mesosoma

- Dorsoventrally compressed
- Large pronotum
- Short legs with swollen femora

Biological characters shared between *Psenobolus* and *Idarnes*:

Males

- Polymorphic
- Non flying
- Emerge before females
- Lethal fighting between males
- Mating with inactive females
- Do not abandon fig in which they developed
- Probably do not feed as adults (not observed)

Females

- Ovipositors longer than body
- Oviposit after pollination of syconium
- Oviposit through syconial wall
- Mated while inside gall and inactive
- Abandon gall after mating

Depend on agaonid males to escape from fig

Similar fig hosts—*Ficus* (*Urostigma*) section *Americana*

Occur only in New World.

The most significant similarities are that both groups are inquilines in *Ficus* (*Urostigma*) section *Americana* figs and that the males are often extremely polymorphic and flightless with depressed bodies. Although these are remarkable similarities between these two unrelated groups of wasps, there are differences which make it easy to distinguish *Psenobolus* and *Idarnes*. Males of *Psenobolus* have a two-segmented trochanter, typical for braconids, whereas *Idarnes* males have a one-segmented trochanter fused to the femur. The antenna of male *Psenobolus* has 9–12 distinct antennomeres with a swollen scape and pedicel (Fig. 8); *Idarnes* antenna has 4–5 antennomeres, a swollen scape and a distal club formed by the fusion of the last three antennomeres. The *Idarnes* males do not have a developed labiomaxillary complex indicating that they do not feed, whereas the *Psenobolus* males have distinct mouth parts although they also probably do not feed. Wing reduction in fig wasps may be related to fighting and mating inside the syconial cavity or inside the galls. According to Hamilton (1979), "wing reduction (in some fig wasps) is probably partly in the interest of redirection of growth into greater sperm production and (sometimes) into fighting adaptations, and partly simply because wings are an encumbrance for the male activities inside the figs." He also felt that the coincidence of winglessness, fighting and dimorphism is not accidental.

We suspect that the genus *Psenobolus* is still in a process of adaptation to development in the gall flowers of figs because the type species, *P. pygmaeus*, and several winged males of an unknown species from Trinidad, have winged males with modified antennae and swollen femora

similar to the brachypterous males. Much more study needs to be done on the biology of these unusual braconids to establish their exact biological relationship with the other wasps in figs. An interesting study would be to revisit near the type locality of *P. pygmaeus* in Brazil to study the biology of the more normal males.

TAXONOMY OF NEW WORLD

PSENOBOLUS

Genus *Psenobolus* Reinhard

Psenobolus Reinhard, 1885, in Mayr, Verh. Zool.-Bot. Ges. Wien 35:246. Type species: *Psenobolus pygmaeus* Reinhard (monotypic).

Diagnosis.—A cyclostome braconid in subfamily Doryctinae; female normal, occipital carina present, fore tibia with row of short stout spines on anterior edge, fore wing with three submarginal cells, first subdiscal cell open at apex, vein 2-1A absent or indistinct at apex, hind wing with vein

M+CU about equal to length of 1M, vein m-cu slightly curved toward wing apex, hind coxa rounded at base without tubercle, ovipositor usually much longer than body; male either similar to female but with basal flagellomeres stalked and scape and femora swollen, or often extremely dimorphic, brachypterous (see description below).

Comments.—Females of this genus can be identified by using the key to Western Hemisphere Doryctinae presented by Marsh (1993). Reinhard included a single species in the genus; subsequently Enderlein (1912) and Szépligeti (1902) added four species but these have all been transferred to the genus *Notiospathius* (see Shenefelt and Marsh 1976). In addition to the two new species described below the junior author has seen several new species from the Neotropical Region and these will be dealt with in a future revision of the genus now in preparation.

KEY TO NEW WORLD SPECIES OF *PSENOBOLUS*

Females

- 1. First metasomal tergum wider at apex than at base, not parallel sided . . . *pygmaeus* Reinhard
- First metasomal tergum as wide at apex as at base, parallel sided (Fig. 5) 2
- 2. Flagellum entirely brown; propodeum brown *ficarius* new species
- Flagellum yellow on basal half; propodeum yellow *parapygmaeus* new species

Males

- 1. Winged, similar to female *pygmaeus* Reinhard
- Brachypterous, extremely dimorphic (Figs. 6-9) 2
- 2. Head wider than long in dorsal view (Fig. 7); 9-10 antennomeres, scape and pedicel very large and swollen (Fig. 8) *ficarius* new species
- Head about as wide as long; 12 antennomeres; scape and pedicel less swollen
- *parapygmaeus* new species

Psenobolus pygmaeus Reinhard

Psenobolus pygmaeus Reinhard, 1885, in Mayr, Verh. Zool. Bot. Ges. Wien 35:247. Lectotype female, "St.Catharina in Brasilien," deposited in Zoological Museum, Humboldt University, Berlin, Germany.

Diagnosis.—Female: body color honey yellow, propodeum dorsally, first meta-

somal segment and median-basal spot on second metasomal tergum brown, scape, pedicel and first 3-4 flagellomeres yellow, remainder light brown; 20-antennomeres; head cubical, wider than high in anterior view; eyes large, malar space shorter than basal width of mandible; ocelli small, ocellular distance about four times diameter of lateral ocellus; frons excavated; vertex,

frons and temple smooth, face smooth medially, rugulose laterally; mesosoma flattened dorsoventrally, smooth except propodeum weakly rugulose dorsally; notauli shallow, weakly crenulate anteriorly, absent before scutellum, not meeting; sternaulus smooth, about as long as mesopleuron; metasoma petiolate, first tergum narrow at base, suddenly widened at apex, apical width about twice basal width, carinate rugose, rugulose at base; remainder of terga smooth except second tergum in middle at base carinate, groove between second and third terga very weak and smooth; ovipositor about $1\frac{1}{2}$ times longer than body; fore wing with three submarginal cells, stigma nearly as broad as long, vein m-cu interstitial with 2RS, vein 1cu-a slightly beyond 1M, second subdiscal cell open at apex, vein 2-1A absent at apex; hind wing with vein M+Cu nearly equal to 1M, vein m-cu weakly curved toward wing apex; fore tibia with row of 4-5 short stout spines on anterior edge, hind coxa without basal tubercle, femora at least 4 times as long as wide.

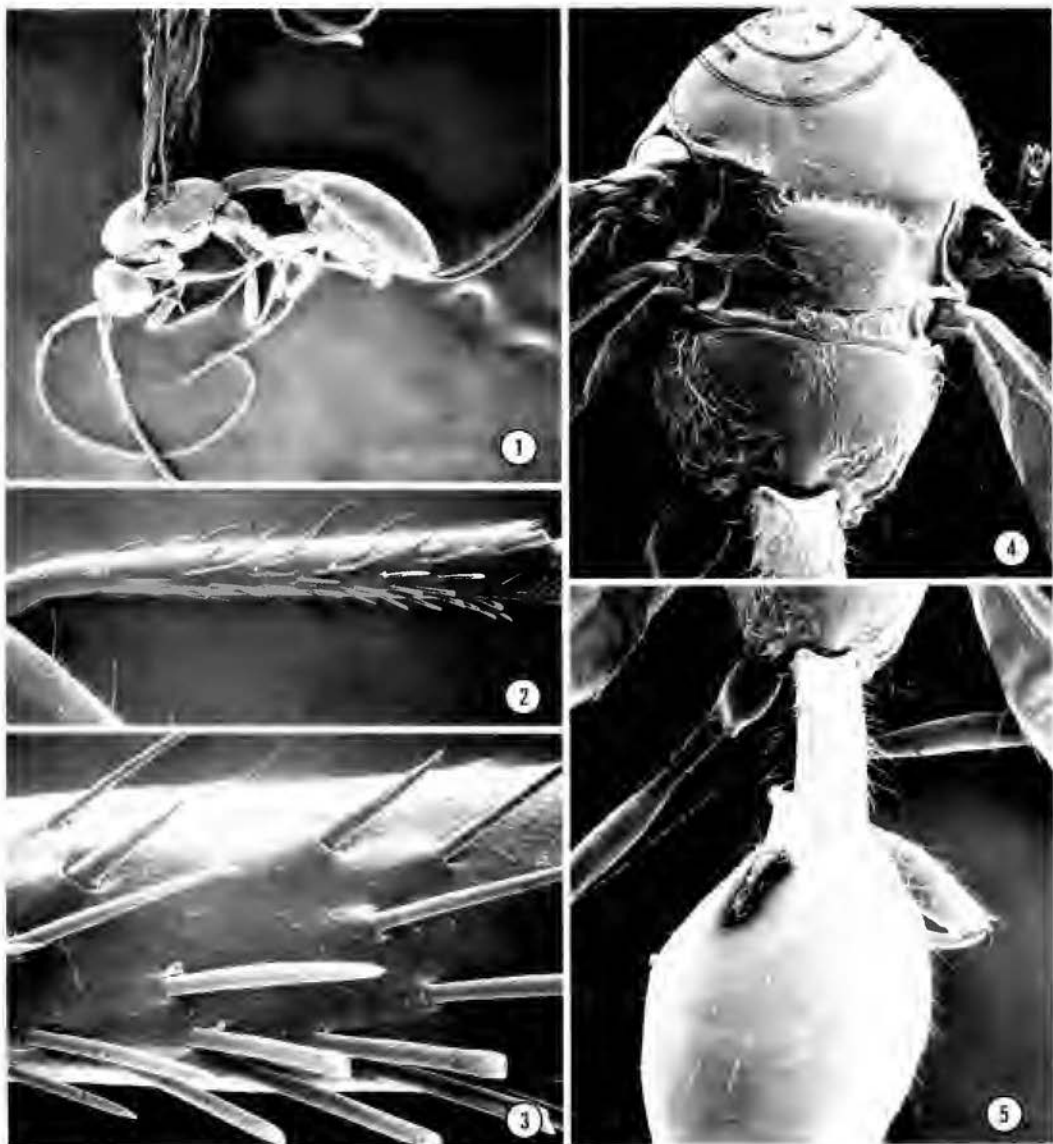
Male: similar to female except as follows; flagellomeres 1-4 stalked at base, swollen at apex; all femora swollen, about 2 times as long as wide.

Comments.—This species differs from the two new species described below by having the first metasomal tergum of the female wider at apex than long and by having winged males. It is presently known only from Brazil. The type series was reared from "Feigenfrüchten" but no indication of which genus or species of figs.

Psenobolus ficarius Ramirez and Marsh,
new species
(Figs. 1-10)

Female.—**Body color:** honey yellow except flagellum, ocellar triangle, propodeum, first metasomal segment and basomedial spot on second tergum which are dark brown, propodeum occasionally light brown; wings hyaline, veins light

brown but becoming clear yellow toward base and apex of wing, stigma brown with small yellow area at extreme base and apex; ovipositor sheaths brown. **Body length:** 2.5-3.0 mm. **Head:** entirely smooth; frons excavated, with short carina between antennae; face broader than high; hypoclypeal depression small and oval, diameter slightly greater than malar space; malar space short, about $\frac{1}{6}$ eye height; temple narrow, about $\frac{1}{2}$ eye width; occipital carina complete; ocelli very small, ocellular distance about 5 times diameter of lateral ocellus, ocellar triangle isocles-shaped; 21-25 antennomeres, all flagellomeres longer than scape and pedicel. **Mesosoma** (Fig. 4): pronotum smooth and polished, with deep longitudinal smooth groove laterally; mesonotum and scutellum smooth and polished, notauli complete and finely impressed, scutellum flattened; mesopleuron smooth and polished, sternaulus smooth, about $\frac{3}{4}$ length of mesopleuron; propodeum without carinae, with two basal lateral semicircular smooth and polished areas, rugulose medially, apically and laterally. **Metasoma** (Fig. 5): petiolate; tergum 1 rugulose carinate, slender, parallel sided, apical and basal widths equal, basal width about $\frac{1}{2}$ width of propodeum; remainder of terga smooth and shining except a small basal medial rugose area on tergum 2, terga 2-5 each with sparse row of long white setae at apex, tergum 2 with sparse area of long white setae at base; ovipositor very long, at least as long as entire body and usually about twice as long. **Legs:** fore tibia with row of 4-6 short stout spines on anterior edge (Figs. 2-3); hind coxa round at base without distinct tooth; inner spine at apex of hind tibia strongly curved. **Wings:** fore wing (Fig. 10) with stigma short and broad, breadth greater than length of vein r, vein r-m present, thus three submarginal cells present, vein r about $\frac{3}{4}$ as long as 3RSa, vein m-cu interstitial with 2RS, second subdiscal cell open at apex, vein 2-1A weak or absent apically; hind wing with



Figs. 1-5. *Psenobolus ficarius* new species. 1, habitus; 2, fore tibia showing chaetobothria; 3, same, enlarged; 4, mesosoma, dorsal view; 5, metasoma, dorsal view.

vein M+Cu about $\frac{3}{4}$ length of 1M, vein m-cu curved toward wing apex.

Male.—**Body color:** honey yellow except mandibles, scape, pedicel, trochanters and base of tibiae brown. **Body length:** 2.0–2.5 mm. **Head:** prognathous, wider than long in dorsal view, smooth and shining (Figs. 7, 9); 9–10 antennomeres, scape and pedicel large and swollen, width of scape

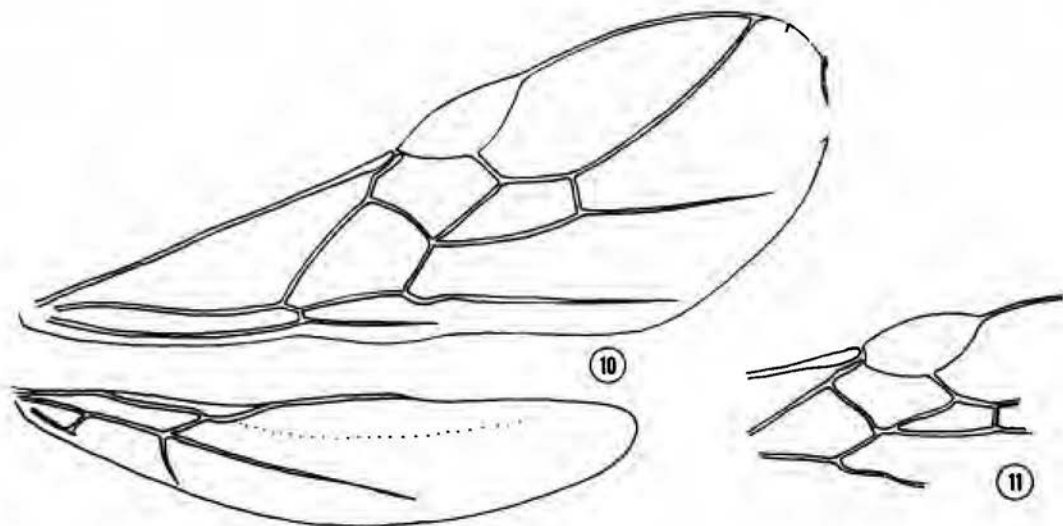
greater than diameter of eye, flagellomeres 1–5 stalked, very narrow at base and wide at apex (Fig. 8); mandibles large, tips crossing when closed (Fig. 8); clypeus very narrow, concave; hypostomal depression oval; labrum concave; eyes small, temple behind eye about 5 times length of eye; ocelli absent; occipital carina absent. **Mesosoma** (Figs. 7, 9): smooth and polished,



Figs. 6-9. *Psenobolus ficarius* new species, males. 6, ventral view; 7, dorsal view; 8, head, ventral view; 9, lateral view.

flattened dorsoventrally; mesonotum sharply declivous to pronotum; notauli and scutellum absent; propodeum without any carinae; mesopleuron small, sternaulus absent. **Metasoma:** all terga smooth and polished; tergum 1 short,

broad, oval shaped, dorsoventrally flattened (Fig. 7); remainder of terga similar to female. **Legs** (Fig. 9): all femora short and swollen; all tibiae narrow basally, swollen apically; fore and middle tarsi with tarsomeres 1-4 extremely short, api-



Figs. 10–11. Wings of *Psenobolus* species. 10, *P. ficarius* new species; 11, *P. parapygmaeus* new species.

cal tarsomere longer than tarsomeres 1–4 combined, claws large and simple; hind tarsomeres 1 and 5 equal in length and equal to length of 2–4 combined. **Wings:** brachypterous with few short veins near base (Figs. 7, 9).

Holotype female.—COSTA RICA, San Jose, El Tornillal, San Geronimo de Moravia, February 18, 1983, W. Ramirez. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica.

Paratypes.—COSTA RICA: 1 female, 11 males, 1 gyandromorph, same data as holotype; 6 females, 11 males, same data as holotype with date February 28, 1983, ex *Ficus velutina* Willd.; 5 females, 45 males, same data as holotype with date February 29, 1993, from fig; 14 females, 11 males, same data as holotype with date December 30, 1992; 3 females, La Canada, Cartago, January 31, 1964, W. Ramirez, ex *Blastophaga torresi* Gir. in *Ficus velutina*; 3 females, San Jose, Zurqui de Moravia, 1600 m, August 1994 and March 1992, col. Paul Hanson. Deposited in: Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica; U. S. National Museum, Washington, DC; Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie, WY; Canadian

National Collection, Ottawa, Canada; Natural History Museum, Leiden, The Netherlands.

Comments.—The above host record of *Blastophaga torresi* is in error as mentioned in the introduction and biology sections. The original assumption when these wasps were first collected in 1964 was that they were parasitoids of fig wasps which has since been disproved.

Etymology.—The species name is Latin for “of figs” in reference to the biology of the species.

***Psenobolus parapygmaeus* Ramirez and Marsh, new species**
(Fig. 11)

Female.—Differs from *ficarius* as follows: basal 4–5 flagellomeres yellow, remainder gradually becoming brown to apex, propodeum yellow, second metasomal tergum entirely yellow; fore wing with vein m-cu meeting RS+M before 2RS (Fig. 11).

Male.—Differs from *ficarius* as follows: head as wide as long in dorsal view; 12 antennomeres, scape not as swollen as in *ficarius*, width about equal to eye diameter.

Holotype female.—COSTA RICA: Route to La Suize, Turrialba, August 29, 1973, Fi-

cus (Urostigma) sp., one fruit, coll. W. Ramirez. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica.

Paratypes.—COSTA RICA: 3 females, 1 male, same data as holotype. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica; U. S. National Museum, Washington, DC.

Etymology.—The species name is from the Greek *para* meaning "near" in reference to the similarities of this species to *pygmaeus*.

Other *Psenobolus* Species

The U. S. National Museum contains one female from Panama, one male from Mexico collected in wild figs and two males from Trinidad. The three males are fully winged and have stalked antennae and swollen femora as in *pygmaeus*. The junior author has also seen females of several apparently undescribed species from Mexico, Central America and northern South America which indicates that the genus is probably wide spread throughout the Neotropics where figs are growing. A revision of the entire genus is in preparation.

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