

The bizarre male of *Spalangia dozieri* (Hymenoptera: Pteromalidae): adaptations for male phoresy or the result of sexual selection?

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Abstract—*Spalangia dozieri* Burks is newly recorded as a gregarious parasitoid in the puparia of *Chrysomya albiceps* (Wiedemann), *C. putoria* (Wiedemann), *Lucilia eximia* (Wiedemann), and *L. sericata* (Meigen) (Diptera: Calliphoridae), and represents the first report of gregariousness in *Spalangia* Latreille. The previously unknown males of *S. dozieri* are described and compared with females. Males have highly modified legs and several other sexually dimorphic features that differ from those of other *Spalangia* species. Most of the unusual features are hypothesized to be adaptations for grasping and holding and it is suggested that males either are phoretic on adults of their dipteran hosts or, possibly, that males exhibit aggressive or other atypical behaviour toward siblings that is correlated with being gregarious. Barbados, Brazil, Dominica, St. Lucia, St. Vincent, and Trinidad are recorded as new country distribution records for *S. dozieri*.

Résumé—*Spalangia dozieri* Burks est signalé pour la première fois comme parasitoïde grégaire des pupariums de *Chrysomya albiceps* (Wiedemann), *C. putoria* (Wiedemann), *Lucilia eximia* (Wiedemann) et *L. sericata* (Meigen) (Diptera: Calliphoridae); c'est la première mention de grégarisme chez *Spalangia* Latreille. Nous décrivons les mâles, jusqu'à maintenant inconnus, de *S. dozieri* et les comparons aux femelles. Les mâles possèdent des pattes fortement modifiées et plusieurs autres caractères à dimorphisme sexuel qui les distinguent des autres *Spalangia*. Nous posons l'hypothèse selon laquelle la plupart de ces caractères inusités sont des adaptations pour s'accrocher et se tenir; nous pensons que les mâles pourraient être phorétiques sur les adultes des diptères qui leur servent d'hôtes ou qu'ils pourraient montrer des comportements agressifs ou autrement atypiques avec les individus de même fratrie en relation avec leur grégarisme. La Barbade, le Brésil, la Dominique, Sainte-Lucie, Saint-Vincent et Trinidad représentent de nouveaux pays qui s'ajoutent à l'aire de répartition connue de *S. dozieri*.

[Traduit par la Rédaction]

Introduction

The subfamily Spalangiinae (Hymenoptera: Chalcidoidea: Pteromalidae) is composed of the monotypic genus *Playaspalangia* Yoshimoto known only from Mexico, and the cosmopolitan genus *Spalangia* Latreille. All species whose biology is reliably known are primary parasitoids of the puparia of cyclorhaphous Diptera or, much more rarely,

hyperparasitoids of Hymenoptera or Lepidoptera through Tachinidae (Diptera) primary hosts (see references in Noyes 2003). Species of *Spalangia* are considered to be solitary parasitoids, although King (2006) reported that in rare instances two individuals of *S. endius* Walker can develop in a single puparium.

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Noyes (2003) lists 51 valid world species of *Spalangia*, of which almost one quarter have been described since Bouček (1963) reviewed the world species. Bouček (1963) provided a detailed genus description for *Spalangia*, but individuals are easily recognized by a very few features. Specimens are mostly black, lacking the metallic green luster of many Pteromalidae, and are usually quite shiny except often for umbilicate setiferous punctures on the head and mesosoma. Furthermore, the antennae are inserted, wide apart, at the extreme anterior margin of the head; each antenna is only 10-segmented, the flagellum lacking a basal ring segment (anellus) and consisting of just 7 funicular segments and an undivided club. *Spalangia* is one of the most easily recognizable of the almost 600 genera described in Pteromalidae because it has such a distinctive and uniform body habitus, and it or Spalanginae is usually differentiated within the first few choices of relevant keys (e.g., Graham 1969; Dzhankmen 1978; Farooqi and Subba Rao 1985; Bouček and Rasplus 1991; Bouček and Heydon 1997). Species within *Spalangia* are differentiated primarily by sculptural features of the head and mesosoma plus forewing and petiolar setal patterns and differences in the relative proportions of various body parts. In addition to the presence or absence of an ovipositor, the sexes are usually easily distinguished by antennal structure. Females have a clavate flagellum with the first funicular segment at most as long as the pedicel, whereas males have a longer, more filiform flagellum with the first funicular segment usually distinctly longer than the pedicel. Within species, males and females are usually readily associated because of the limited sexual dimorphism.

In 2006 the junior author reared several species of Chalcidoidea as pupal parasitoids of Calliphoridae (Diptera) from São Paulo State, Brazil. Included was a species of *Spalangia* that not only was reared as a gregarious parasitoid but also had males with conspicuously modified legs and several other features unlike those of other known members of the genus. After comparison with type material, the senior author determined that associated females were conspecific with *Spalangia dozieri* Burks. This species was described originally from 1 female collected in Cuba and 18 females from Puerto Rico. Burks (1969, p. 3) stated that the holotype and 17 of the paratypes were reared from “the pupa” of *Sarcodexia lambens* (Wiedemann) (= *Sarcodexia sternodontis* Townsend

(Diptera: Sarcophagidae). Examination of the unidentified *Spalangia* collection in the United States National Museum of Natural History revealed seven other broken females plus three identically labelled males that Burks did not include as paratypes or mention in the original description of *S. dozieri*. One of the males has a handwritten label with “prob. not the ♂ of this sp”., which likely explains why he did not mention the males. Less understandable is why Burks described the females rather than the males as a new species, because the females are quite normal representatives of *Spalangia*, whereas the males exhibit the same bizarre modifications as those we reared as gregarious parasitoids in Brazil. None of the specimens reared from *S. lambens* are associated with host puparia, but based on label data, all were reared the same day. This and Burks’ (1969) use of “pupa” rather than “pupae” suggests that they too emerged from a single puparium, although he did not state explicitly whether the species was solitary or gregarious. The purpose of the present study is to describe the males of *S. dozieri* relative to females and to discuss the possible functional significance of their unusual features.

Materials and methods

The junior author reared specimens of *S. dozieri* by placing 150 third-instar larvae of *Chrysomya albiceps* (Wiedemann), *C. megacephala* (Fabricius), *C. putoria* (Wiedemann), *Cochliomyia macellaria* (Fabricius), *Lucilia eximia* (Wiedemann), or *L. sericata* (Meigen) (Diptera: Calliphoridae) into containers with ground beef as food and wood shavings as a pupating medium for the larvae. Each container had a 6 cm diameter hole in the top that was covered with mesh to permit parasitoid entrance and two mesh-covered holes in the bottom to allow rain to drain. The containers were hung in trees (Fig. 1) approximately 2 m high in urban, wild, and farm (close to a sheep farm) localities in the vicinity of Botucatu (22°55'S, 48°30'W), São Paulo State, Brazil, in 2006 and 2007. After 7 days all puparia in the containers were separated individually in gelatin capsules and laboratory-reared for up to 35 days. Puparia were examined daily and, in an attempt to establish parasitoid colonies, any parasitoids emerged from a single puparium were released into an experimental container that contained separate cotton swabs soaked with water or honey plus white puparia of the same species

Fig. 1. Carrion traps hung in a tree near a sheep farm, Edgardia Farm, Botucatu, São Paulo State, Brazil.



from which the parasitoids had been reared. Unparasitized adult blow flies emerged within 4 days, therefore mature puparia were removed from the experimental containers after 3 days, reared individually, and replaced with new white puparia until all the initial parasitoids had died. The puparia from which parasitoids emerged were not retained and attributes of behaviour were not studied.

Specimens discussed are in the following four institutions: Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada (CNC); Zoology Museum, University of São Paulo, São Paulo, São Paulo State, Brazil (ZMUSP); Natural History Museum, London, England (BMNH); and United States National Museum of Natural History, Washington, D.C., United States of America (USNM). The description of female *S. dozieri* is intended primarily to illustrate the typical structure of the genus for comparison with males of the species, but diagnostic features are given to differentiate females from other New World species of *Spalangia*. Terms for structures follow Gibson (1997). Specimens were photographed with a Leica DC500 digital camera attached to a Leica Z16 APO microscope and serial images obtained were combined using AutoMontage. These and the scanning electron microphotographs obtained from uncoated specimens using a Philips XL30 environmental scanning electron microscope were digitally retouched using Adobe Photoshop to enhance clarity.

Spalangia dozieri Burks

Spalangia dozieri Burks, 1969: 3–4; Figures 1, 2. Holotype ♀ (USNM 69872, examined). Type data: Mayaguez, Puerto Rico, 26 August 1936, H.L. Dozier, from pupa of *Sarcodexia sternodontis* Townsend.

Diagnosis (female)

Pronotal collar without crenulate sulcus paralleling posterior margin but with distinct median sulcus and with well-separated circular setiferous punctures (Fig. 13); propodeum with median, posteriorly tapered rugulose–reticulate region (Fig. 17); petiole with several setae laterally (Figs. 17, 19).

Remarks

Spalangia dozieri is not included in any key to species, but females are differentiated from those of all other New World *Spalangia* species by the combination of the three features given in the diagnosis. Males of *S. dozieri* are readily differentiated from those of other *Spalangia* species by several features, including their unique leg structure, described below.

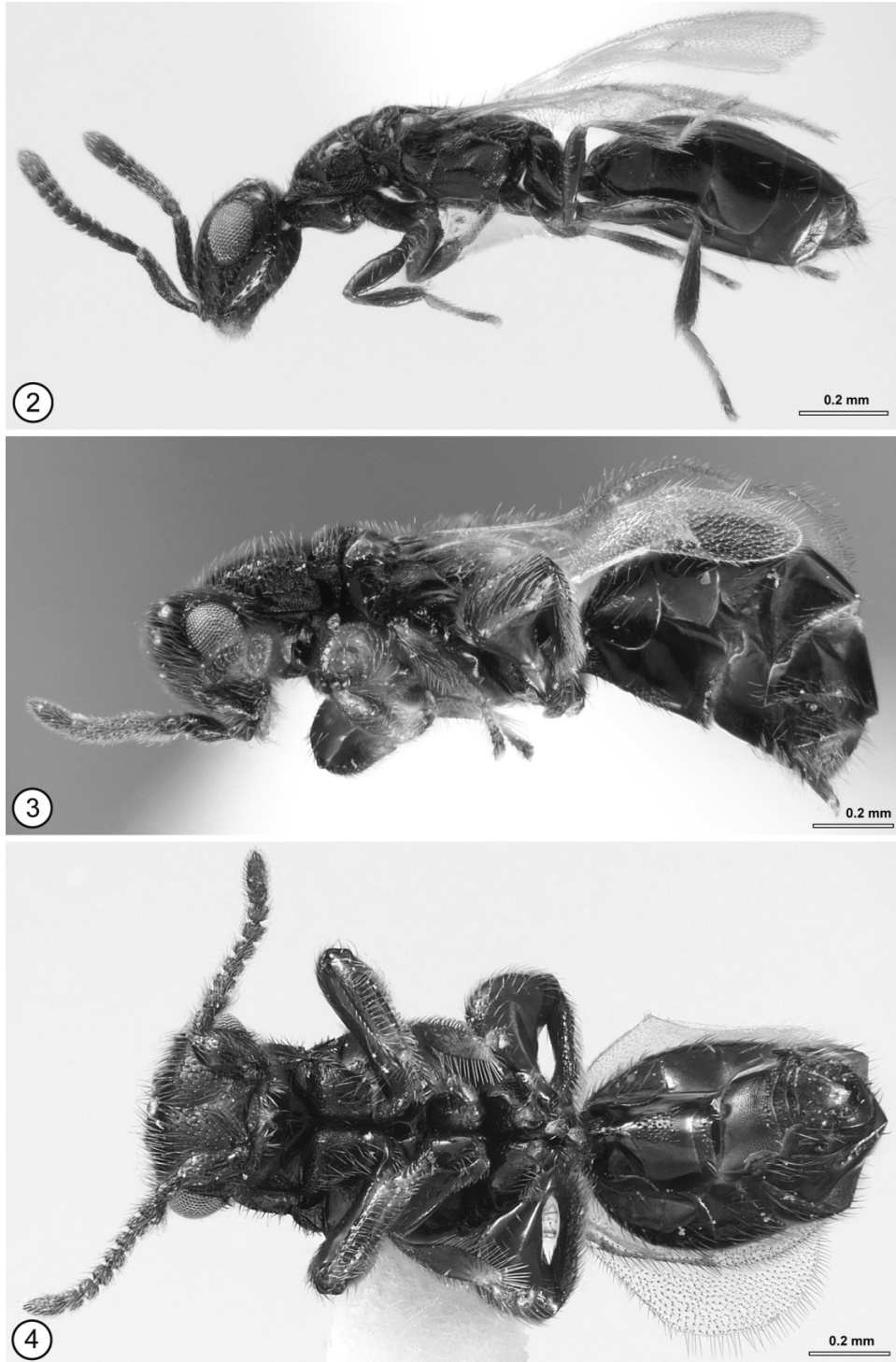
Description

Female

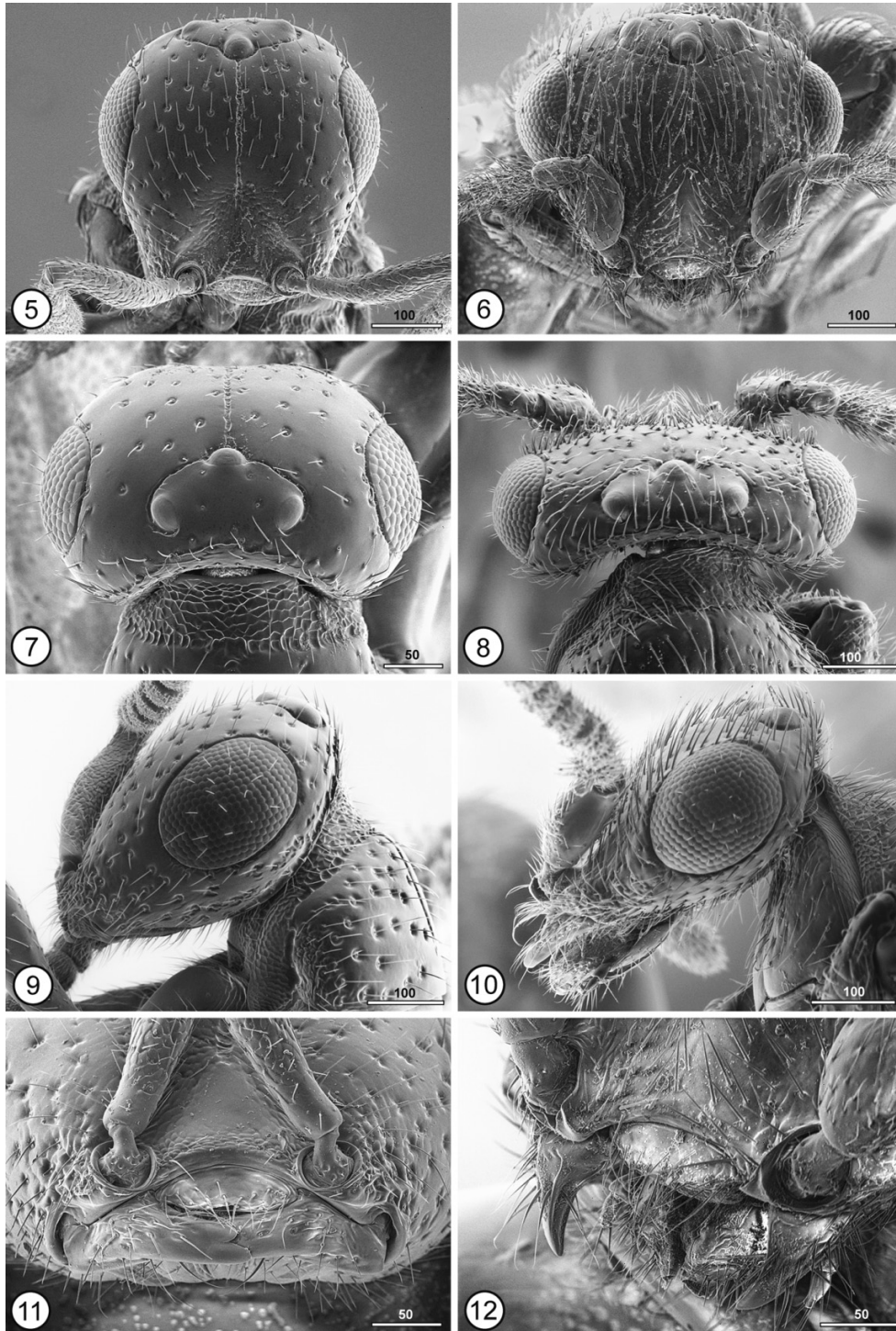
Body 1.2–2.4 mm long (Fig. 2). Head in frontal view (Fig. 5) about as high as wide; interantennal region without setae (Figs. 5, 11) and parascrobal region and frontovertex sparsely setose, the setae originating from distinct circular punctures (Figs. 5, 7, 9); in dorsal view (Fig. 7) about 1.5–2× as wide as long and in lateral view ovoid (Fig. 9). Mandible bidentate (Fig. 11). Antenna (Fig. 15) with scape spindle-shaped and, excluding radicle, about 5× as long as greatest width; pedicel elongate-triangular, about 2× as long as apical width; flagellum clavate; funicle with first segment about 0.3–0.4× as long as pedicel and at least slightly transverse, and subsequent segments distinctly transverse; funicular segments and clava uniformly setose with short setae.

Pronotal collar convex with median sulcus and distinct, well-separated circular setiferous punctures (Fig. 13). Mesoscutal median lobe smooth and shiny both anteriorly (region often overridden by pronotal collar) and posteriorly, but finely coriaceous medially, with transverse band of irregular sculpture delineating posterior margin of coriaceous region and with sparse setiferous punctures toward notauli (Fig. 13);

Figs. 2–4. *Spalangia dozieri*, habitus: 2, ♀, lateral view; 3, ♂, lateral view; 4, ♂, ventral view.



Figs. 5–12. *Spalangia dozieri*: 5, ♀ head, frontal view; 6, ♂ head, frontal view; 7, ♀ head, dorsal view; 8, ♂ head, dorsal view; 9, ♀ head, lateral view; 10, ♂ head, lateral view; 11, ♀ mandibles; 12, ♂ mandibles. Scale bars are in micrometres.



lateral lobes shiny and smooth except for sparse inconspicuous setiferous punctures (Fig. 13). Scutellar–axillar complex (Fig. 13) shiny and smooth except for a few setae originating from minute punctures on axilla and laterally on scutellum; scutellum with complete crenulate furrow delimiting frenum, the furrow sometimes tapered and becoming shallower or narrowly interrupted medially (Figs. 13, 17). Legs normal, with elongate, slender, and comparatively inconspicuously setose femora and tibiae (Fig. 2). Tarsi slender, at least $0.75\times$ as long as respective tibia, with basitarsi obviously elongate, about as long as combined lengths of subsequent three or four segments (Fig. 23; Burks 1969, fig. 1). Tarsal claws long and curved (Fig. 20; Burks 1969, fig. 2). Forewing bare behind submarginal vein except for a few setae distally in basal cell. Propodeum (Fig. 17) with broadly lanceolate to somewhat heart-shaped posteriorly tapered rugulose–reticulate median region; callus uniformly rugose. Petiole rugulose–reticulate dorsally and with several setae along sides (Fig. 17).

Male

Body 1.1–1.9 mm long (Figs. 3, 4). Head in frontal view (Fig. 6) obviously transverse, about $1.3\times$ wider than high; interantennal region, parascrobal region, and frontovertex densely and conspicuously setose (Figs. 4, 6, 12), the setae originating mostly from minute punctures or tiny bumps; strongly transverse in dorsal view (Fig. 8), about $2.75\times$ as wide as long, and comparatively thin and somewhat wedge-shaped in lateral view (Fig. 10). Mandible unidentate, tapered to apex (Fig. 12). Antenna (Fig. 16) with scape compressed, ovate, and, excluding radicle, only about $1.75\times$ as long as greatest width; pedicel only about $1.5\times$ as long as wide; flagellum filiform; funicle with first segment about as long as pedicel and about as long as wide, but widened distally, and subsequent segments slightly transverse to quadrate but distinctly pedunculate; funicular segments and clava with comparatively long, curved setae, and first funicular segment with obviously longer, distally curved setae ventrally (Fig. 16, insert).

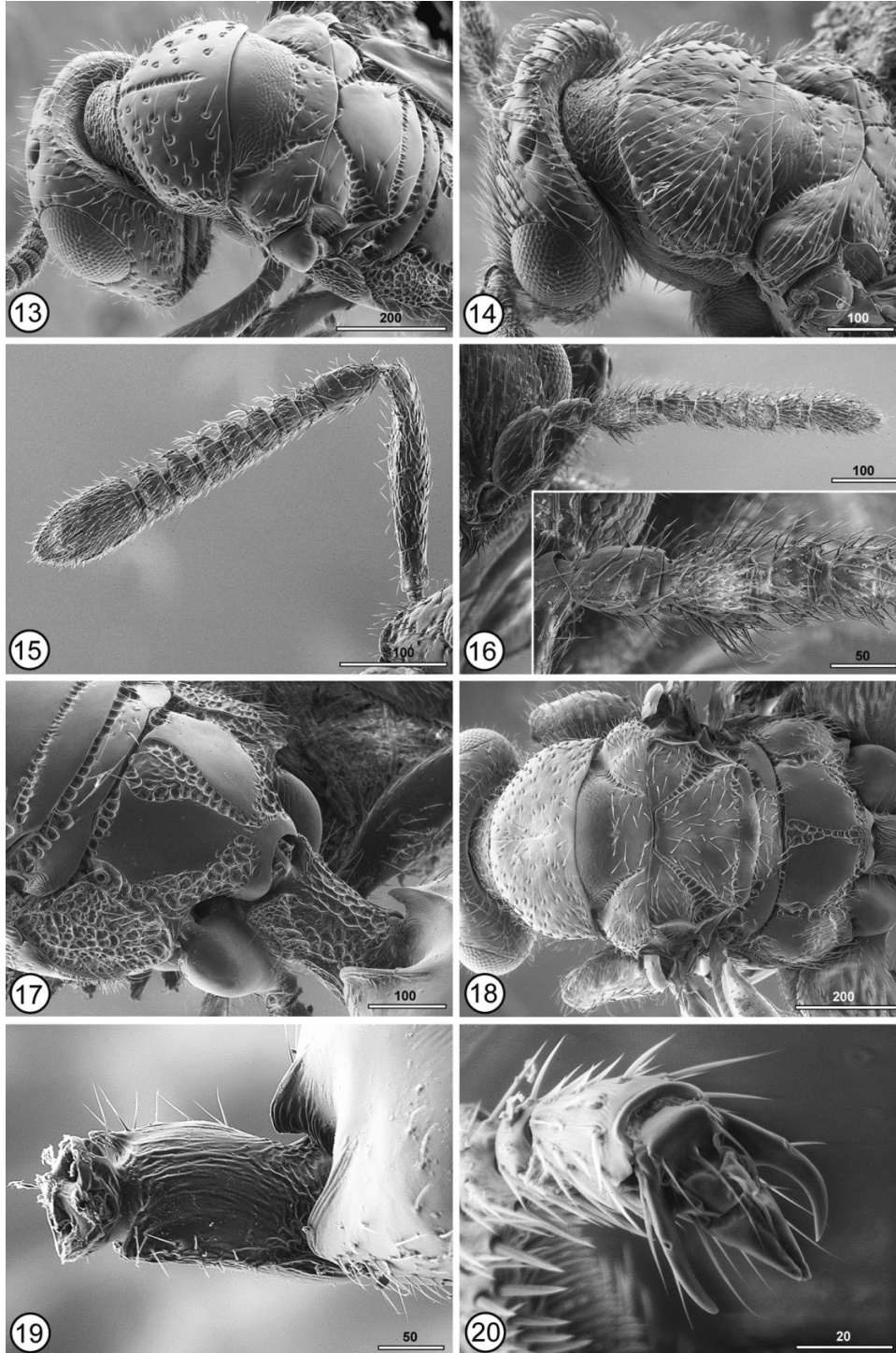
Pronotal collar with median sulcus but flattened dorsally, and with more crowded, smaller and less distinct, mostly minute setiferous punctures than female (*cf.* Figs. 13, 14, 18). Mesoscutum similar to that of female but more densely setose, particularly lateral lobes, with

setae originating from minute punctures (Figs. 14, 18). Scutellar–axillar complex almost uniformly setose except for bare frenum (Fig. 18). Femora strongly, bulbously enlarged (Figs. 3, 4), the profemur (Fig. 25) and metafemur (Figs. 29, 30) most conspicuously so; mesofemur (Fig. 26) and metafemur (Fig. 30) with anterior surface bare except dorsally; metafemur with ventral margin concave (Figs. 29, 30). Protibia (Fig. 25) robust, thickened and comparatively broad, ventroapically flat with long, distally curved setae, the dorsally convex surface also with long setae; mesotibia strongly compressed with anterior (lower) surface concave and almost bare except for very short, sparse, inconspicuous setae (Figs. 26, 28), but posterior (upper) surface convex and setose, most densely so toward dorsal (anterior) margin (Fig. 27), and with a row of increasingly long, distally curved setae along ventral (posterior) margin and distal lobe (Figs. 27, 28); metatibia robust-tubular, ventral surface flattened and slightly concave so as to leave ovate space between tibia and concave margin of femur when tibia and femur appressed (Figs. 4, 29, 30), and ventral surface with very short inconspicuous setae but other surfaces much more densely setose–spinose. Tarsi robust, short, less than half as long as respective tibia, with basitarsi much shorter than combined lengths of subsequent three, distinctly transverse, tarsomeres (Figs. 4, 25, 30), and at least distal tarsomere quite broad in dorsal view (Fig. 22). Tarsal claws short, lobular (Fig. 21). Forewing with basal cell completely setose. Propodeum (Fig. 18) with posteriorly tapered median region less distinctly sculptured and sometimes narrower than for female; callus with about anterior half smooth and shiny. Petiole similar to that of female except with finer longitudinal striae dorsally (Fig. 19).

Biology

Burks (1969) previously reported the sarcophagid *S. lambens* as a host. We newly reared *S. dozieri* as a gregarious pupal parasitoid of four of six reared species of Calliphoridae — *C. albiceps*, *C. putoria*, *L. eximia*, and *L. sericata*. Puparia with *S. dozieri* were obtained only from sites near a sheep farm. From nine rearing events, 1–17 females but at most only 1 male were obtained from individual puparia (Table 1). Subsequent parasitism of the same host species of blow fly in the laboratory by the reared parasitoids occurred four times, but the sex ratio and number of emerged parasitoids

Fig. 13–20. *Spalangia dozieri*: 13, ♀ head and thorax, dorsolateral view; 14, ♂ head, pronotum, and mesoscutum, dorsolateral view; 15, ♀ antenna; 16, ♂ antenna (insert: pedicel and basal three funicular segments); 17, ♀ scutellar frenum to base of gaster; 18, ♂ mesosoma, dorsal view; 19, ♂ petiole; 20, ♀ tarsal claws and arolium. Scale bars are in micrometres.



Figs. 21–30. *Spalangia dozieri*: 21, ♂ tarsal claws and arolium; 22, ♂ mesotarsus, dorsal view; 23, ♀ metatarsus, lateral view; 24, ♂ mesotarsus, lateral view; 25, ♂ front leg; 26, ♂ middle leg; 27, ♂ mesotibia (posterior view) and mesotarsus (dorsal view); 28, ♂ mesotibia (anterior view) and mesotarsus (ventral view); 29, ♂ hind leg, posterior view; 30, ♂ hind leg, anterior view. Scale bars are in micrometres.

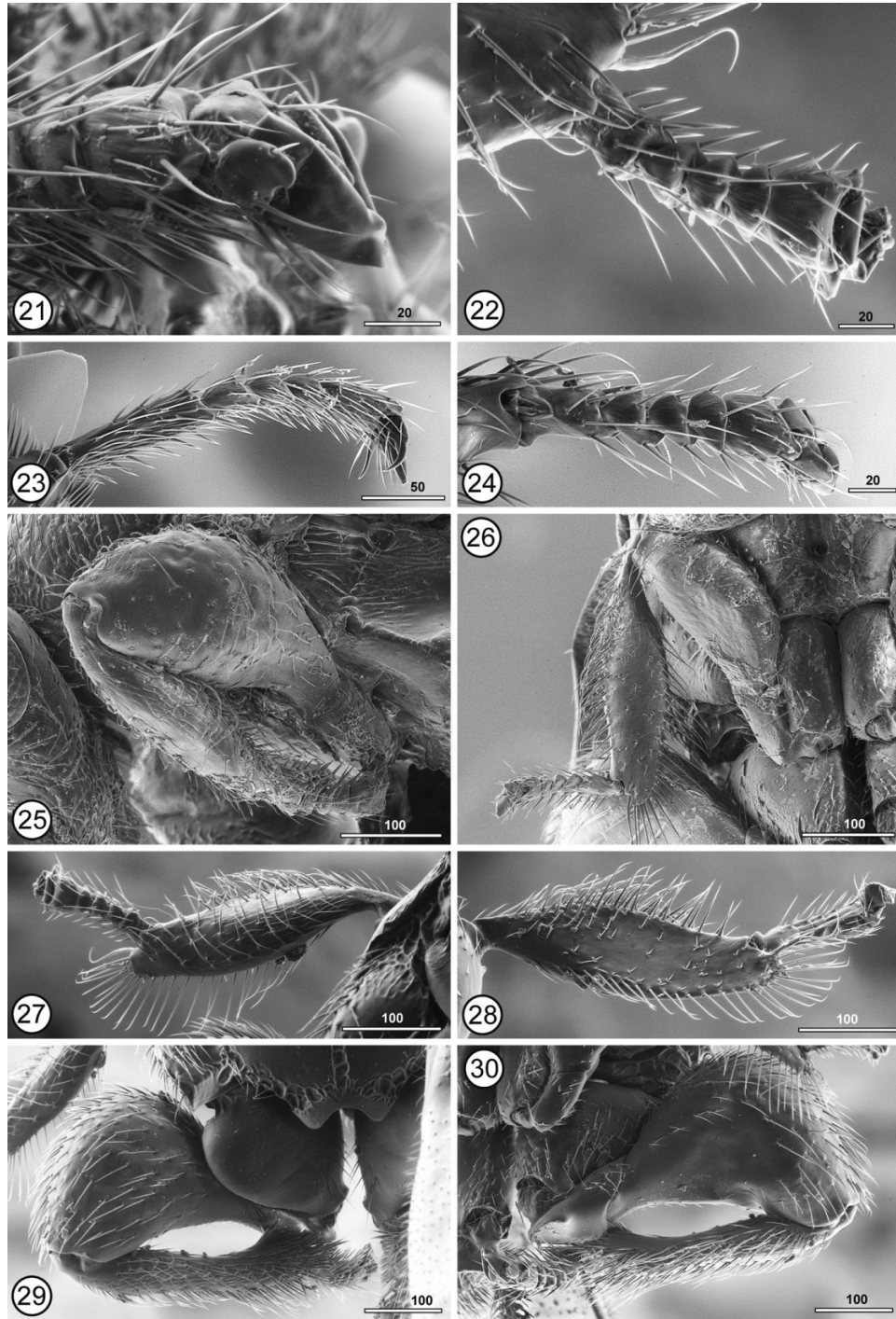


Table 1. Numbers of *Spalangia dozieri* emerged from individual blow fly (Calliphoridae) puparia reared from carrion traps in São Paulo State, Brazil, in 2006 and 2007.

Date	Host	No. of parasitoids per puparium	No. of females	No. of males
16–23.ii.2006	<i>Lucilia eximia</i>	10	9	1
16–23.ii.2006	<i>Lucilia eximia</i>	7	6	1
16–23.ii.2006	<i>Lucilia sericata</i>	5	5	0
13–20.iv.2006	<i>Lucilia sericata</i>	18	17	1
13–20.iv.2006	<i>Lucilia sericata</i>	5	4	1
13–20.iv.2006	<i>Lucilia eximia</i>	3	2	1
15–22.ii.2007	<i>Lucilia sericata</i>	1	1	0
9–16.iii.2007	<i>Chrysomya albiceps</i>	11	10	1
16–23.iii.2007	<i>Chrysomya putoria</i>	12	12	0
Total		72	66	6

were not determined because some adult parasitoids escaped from the containers. Adult parasitoids typically emerged from a single hole chewed in the puparium.

Distribution

In addition to the type material from Cuba and Puerto Rico (USNM, 1♀ BMNH) listed in Burks (1969), we saw specimens from the following Neotropical localities: **BARBADOS.** Turner Hall Woods, 21.ii.79, S. Peck, dung trap (2♀ CNC). **BRAZIL. São Paulo State:** Botucatu, Edgardia Farm, C. Reigada, 16–23.ii.06, ex *L. eximia* (1♀, 2♂), 13–20.iv.06, ex *L. sericata* (21♀, 2♂), 9–16.iii.07, ex *C. albiceps* (5♀), 16–23.ii.06, ex *C. putoria* (7♀) (CNC, ZMUSP). **DOMINICA.** St. Mark Parish, Scott's Headpoint, 2.xii.94, L. Masner, grassland (2♀ CNC). **ST. LUCIA.** Praslin, 13°52.9'N, 60°53.9'W, 50 m., 11–28.vii.07, lowland woodland ravine, flight-intercept trap (38♀ CNC). **ST. VINCENT.** St. David, Richmond Beach, 10.vii.76, J.S. Noyes (1♂ BMNH). **TRINIDAD.** Caroni Brasso, 17.vii.76, J.S. Noyes (1♀ BMNH).

Discussion

Some of the sexual dimorphism exhibited by *S. dozieri*, such as the difference in forewing setal pattern between the sexes and the generally finer body sculpture, filiform and more conspicuously setose flagellum, and shorter scape and more globular pedicel in males, is also characteristic of some other species of *Spalangia*. Males of *S. impunctata* Howard have a comparatively short first funicular segment similar to that of *S. dozieri*, but the conspicuously longer setae and somewhat distally

widened structure of the first funicular segment (Figs. 4, 16) are unique to males of *S. dozieri*. Furthermore, even though males of other species of *Spalangia* often have somewhat finer body sculpture than females, which is typically correlated with a somewhat smaller body, males of *S. dozieri* are unique in having much denser and more conspicuous setation on the head (Figs. 6, 8, 10, 14), dorsal surface of the thorax (Figs. 14, 18; cf. Figs. 2, 3), and legs (Figs. 25–30). The obviously more transverse and thinner head in males than in females of *S. dozieri* (cf. Figs. 7–10) is also atypical, as is the flatter pronotum (cf. Figs. 13, 14). Within *Spalangia*, males of *S. dozieri* are unique in having unidentate mandibles (Fig. 12). Females of *S. dozieri* have bidentate mandibles (Fig. 11) similar to those of both sexes of other species of *Spalangia*. Much more conspicuously different from *S. dozieri* females and other species of *Spalangia* are the modified legs of *S. dozieri* males. The hind legs resemble those of Chalcididae or some Torymidae (Chalcidoidea), with a greatly enlarged metafemur; however, in contrast to members of these two families, the ventral surfaces of both the metatibia and the metafemur are concave so that an ovate space remains between them when they are appressed (Figs. 4, 29, 30). This space, the greatly enlarged metafemur, and the unusually robust-tubular metatibia all suggest that the hind leg is modified to hold something securely between the femur and tibia. The combination of an enlarged profemur and enlarged, ventroapically broad, flattened, and strongly setose protibia (Figs. 3, 4, 25) also suggests that the front leg is modified for grabbing and holding something between the femur and tibia, though possibly not in a pincerlike fashion as suggested for the hind leg. All the

Fig. 31. Superimposed images of *Lucilia sericata* and ♂ *Spalangia dozieri* at the same relative magnification.



coxae (Figs. 4, 26, 29) are also larger than those of the female. Although the difference is difficult to quantify, the prothorax of the male also appears proportionally larger than that of the female (*cf.* Figs. 2, 3, 13, 14). The comparatively large prothorax, procoxae, and profemora all indicate larger and more powerful muscles to manipulate the front legs. Unlike the front and hind legs, the middle legs do not appear to be modified for providing greatly increased strength. The mesofemur is the least conspicuously enlarged of the femora, and in contrast to the tubelike pro- (Fig. 25) and meta-tibiae (Figs. 29–30) the mesotibia (Figs. 4, 26–28) resembles the corbícula of some bees; that is, it is compressed, with long setae extending from its edges to form a large surface area. Finally, the tarsi of all the legs are very short and robust (Figs. 24–30) compared with those of the female (*cf.* Figs. 23, 24), and appear to be modified to increase rigidity and thus strength. Although the tarsal claws of the male are much shorter and less

strongly curved and pointed than those of the female (*cf.* Figs. 20, 21), the distal tarsomere is broad in dorsal view (Fig. 22) and the male may therefore have a larger arolium than the female.

Figure 31 illustrates the size difference between a male *S. dozieri* and an adult of one of its known hosts, *L. eximia*. We suggest that this size difference is sufficiently large that the fly could carry a male *S. dozieri* in flight, and that most of the sexual dimorphism and atypical features of *S. dozieri* males could be modifications to enable phoresy. Adults of other solitary *Spalangia* species use their bidentate mandibles to chew an exit hole in the host puparium for escape. The unidentate mandibles of males (Fig. 12) could have a similar function, but because they are uniquely modified they are probably also adapted for some other function, such as piercing or “pinching” the cuticle or intersegmental membrane between two sclerites of a host fly. Many other phoretic parasitoids are

known to use their mandibles, at least in part, to attach to their host carrier (Clausen 1976). The flatter head (*cf.* Figs. 7–10) and somewhat flatter pronotum (*cf.* Figs. 13, 14) of the male than of the female also suggest that the male, if phoretic, attaches between two body surfaces, perhaps at the base of the wings between these and the body. The much denser setae on the head and dorsal surface of the thorax of the male (*cf.* Figs. 5–10, 13, 14, 18) could interdigitate with setae or pubescence of the fly. The comparatively large prothorax (Fig. 14), greatly enlarged pro- and meta-femora, robust-tubular pro- and meta-tibiae (Figs. 4, 25, 29, 30), and short, robust tarsi of all the legs (Figs. 24–30) are apparently modified to increase strength and are therefore possibly used to hold onto a host fly. The front legs may be stretched out to grasp the fly, with the ventroapically flattened and strongly setose protibia being appressed to the body surface, whereas the hind legs are likely used to hold some body part pincerlike between the femur and tibia. The comparatively dense and strong setae of the pro- and meta-tibiae could interdigitate with setae on the fly or be appressed to some pubescent or roughened surface. The middle legs, however, are more likely held out on either side of the body, with the enlarged, concave, almost smooth lower surface of each mesotibia (Figs. 26, 28) appressed to some comparatively smooth and bare region of the fly cuticle, and the long, distally curved setae along its edges and anterodorsally on the tibia (Figs. 26–28) interdigitating with setae on the fly. If males of *S. dozieri* are phoretic, the atypical modifications discussed above are likely necessary to prevent the male being removed during grooming of the fly. Although the longer, more strongly curved, and acutely pointed tarsal claws of females (Fig. 20) might be considered better adapted for grasping a rough surface, some known phoretic parasitoids have an enlarged arolium that is used for attachment to the host carrier (Clausen 1976; Orr *et al.* 1986; Naumann and Reid 1990). For phoretic species of *Brachista* Walker (Chalcidoidea: Trichogrammatidae), Pinto (1994) hypothesized that the strongly decurved structure of their tarsal claws was to remove them from the surface of the robber fly (Diptera: Asilidae) host to permit more intimate contact by the arolium. The reduced size of the tarsal claws of *S. dozieri* males (Fig. 21) may serve the same function; that is, it enables a larger surface area of the arolium for adhesion. It is possible that the muscle mass of

the very short, ovoid scape of males (Figs. 4, 16) enhances their ability to control the setose flagellum, which might be used to grasp or interdigitate with some body part of the fly. However, the use of the antennae by males in courtship displays or otherwise in mating is typical of chalcids (Assem 1974; Assem *et al.* 1982), and not all the atypical features of *S. dozieri* males may be adaptations for the same purpose.

Based on their structural modifications, it is hypothesized that *S. dozieri* males are phoretic, and this could be supported by the fact that 48 females but no males were collected in the flight-intercept trap. However, the collection of a single male in St. Vincent shows that males emerge from the puparium and, at least sometimes, occur free in the environment. Furthermore, the hypothesis of male phoresy is not supported by our knowledge of the biology of other phoretic Hymenoptera. Among parasitoid Hymenoptera, adult phoresy is most common in Scelioninae (Platygastridae: Platygastridae) and Trichogrammatidae, although a few instances of adult phoresy have also been reported for Eulophidae, Eupelmidae, Pteromalidae, and Torymidae (Podagrionini) (Chalcidoidea) (Askew 1971; Clausen 1976). In all but one instance the phoretic species is an egg parasitoid, but it is always the female that exhibits phoresy, which enables it to be carried to and locate the oviposition site of its host. Naumann and Reid (1990, figs. 1, 2) illustrated a male of *Ausasaphes shiralee* Naumann and Reid (Pteromalidae: Asaphinae) as phoretic on the pronotum and elytra of species of *Chalcolampra* Blanchard (Coleoptera: Chrysomelidae), although they stated that only four females were discovered as phoretic in the field. Females of *A. shiralee* parasitize the eggs of species of *Chalcolampra* (Naumann and Reid 1990). *Pteromalus puparum* (L.) (Pteromalidae: Pteromalinae) is the only example of a phoretic parasitoid that is not an egg parasitoid. Females of *P. puparum* parasitize the pupae of large Lepidoptera, and they have been reported as riding on large caterpillars. Females cannot oviposit through the hard cuticle of mature pupae, and their phoresy presumably allows them to stay with a caterpillar, once it is located, and wait for it to pupate, as a young pupa with a soft cuticle is a potential host (Askew 1971; Naumann and Reid 1990). The phoretic adults of both *A. shiralee* and *P. puparum* move freely on the host carrier, and although *A. shiralee* has quite a large arolium (Naumann and Reid 1990,

fig. 7), neither species is conspicuously modified to facilitate attachment.

The collection of numerous *S. dozieri* females in a flight-intercept trap and the similar body sizes of the sexes suggest that males do not grasp females and carry them like male Tiphidae (Hymenoptera: Vespoidea) do, and we can offer no hypothesis concerning the adaptive advantage of phoresy for males of a pupal parasitoid such as *S. dozieri*. It is therefore possible that the structural modifications of *S. dozieri* males are correlated with behaviours related to sex, such as male combat, courtship, or mating. Within the genus *Spalangia*, *S. dozieri* is uniquely gregarious. Sexual dimorphism correlated with sex is known for some gregarious species in Chalcidoidea, although extreme dimorphism is characteristic only of those species in which males not only are far fewer in number than females but also compete for females and normally do not emerge from the host. This includes males of species of *Melittobia* Westwood (Eulophidae) in the cocoons or puparia of their Aculeata (Hymenoptera) hosts and dipteran parasites (Assem 1975; Matthews *et al.* 2008), and males of pollinating Agaonidae and other non-pollinating chalcid taxa that are intimately associated with the syconia of figs (*Ficus* L., Moraceae) (Weiblen 2002; Greeff *et al.* 2003). Unlike *S. dozieri* males, the males of these two groups are usually less pigmented than the females, are brachypterous or apterous, and have vestigial eyes and often large mandibles (Assem *et al.* 1980; Weiblen 2002). Male fig wasps do have enlarged femora and robust tibiae and tarsi that are somewhat similar to those of male *S. dozieri*, but these are apparently associated with burrowing out of the fig to provide an escape route for females (Weiblen 2002). The modified front and hind legs and uniquely structured mesotibiae of *S. dozieri* males are definitely not adapted for such a purpose. It is possible that the 3 males in the original type material of *S. dozieri* emerged along with 22 females from a single puparium, but we reared at most 1 male with different numbers of females in all instances where multiple individuals were reared from a single puparium. The sex ratio suggests that sib-mating may be common in *S. dozieri*, unlike such solitary species as *S. cameroni* Perkins (King 1990), but does not support the atypical features of males being modifications for male *versus* male aggression. Also, there is no obvious aggression between the sexes of solitary species of *Spalangia* (King 2006, 2008). In

S. endius, courtship display includes wing fanning by the male as he approaches the female and, after mounting, rapid up and down vibration of his body and tapping of the female's sides with his middle legs (King and Fischer 2005; King 2008). There is almost no difference between postmounting courtship and mating positions in solitary *Spalangia* species. A male mounts the posterior end of a female positioned such that his head is over her mesosoma, his front legs are on her mesosoma or gaster, and his hind legs extend under her gaster (Assem *et al.* 1980, fig. 6; King and Dickerson 2008). Males of many other Pteromalidae have a more anterior postmounting courting position than in *S. endius* or other *Spalangia* species for which this is known, and this necessitates the male backing up to mate when the female signals receptivity (Assem 1974). Assem *et al.* (1980) suggested that the more posterior courtship position in *Spalangia* species prevents other males from clasping the female's gaster after she opens her genital orifice and inseminating her before the courting male does. We did not observe courtship or mating events. Males of *Spalangia* species remate readily, but females rarely do so (King *et al.* 2005). Because of the greater number of females available for mating with a single *S. dozieri* male, it is possible that males of this species mate with females more aggressively than in other *Spalangia* species, either within the puparium before the females emerge or as they emerge but before they can disperse. The front and hind legs could be used to grasp a female securely, whereas the middle legs could be used for some sort of tactile courtship. However, the female must still open her genital orifice to permit insemination, and aggressive mating does not explain the generally much more setose body, flatter head and pronotum, or, likely, the unidentate mandibles of males, or such anomalous features as an anteriorly smooth propodeal callus.

Based on male morphology we suspect that male phoresy is the most likely explanation for the bizarre sexual dimorphism that characterizes *S. dozieri*, although none of the hypotheses offered above for the atypical structure of males are supported by direct observation or biological attributes. We hope that our report will lead to further studies of *S. dozieri* and its dipteran hosts and ultimately to an answer to this enigma.

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