

## Breathing adaptations of males in fig gall flowers (Hymenoptera: Agaonidae)

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**Abstract:** *Apocryptophagus* and *Sycophaga* wasps (Sycophaginae, *sensu* Boucek 1989) develop in the syconia of *Sycocarpus* and *Sycomorus* figs. The syconia are full of a liquid when the males eclose from their galls. The males have terminal abdominal filaments that are extensions of the peritremes. These filaments are used to anchor the posterior part of the abdomen inside the fig galls, and to maintain the abdominal spiracles inside them. Earlier authors suspected a breathing function. In this position some males spend up to 20 minutes probably using the air present inside the galls while they are searching for the dispersed female-containing galls for mating inside. By migrating from gall to gall, the males are able to breath and displace themselves along and around all the inundated syconial cavity without drowning. In this paper, new observations and structures associated with breathing are presented and illustrated with photographs. *Apocryptophagus* and *Sycophaga* males also possess very enlarged longitudinal tracheal trunks which probably function as air or gas reserves. *Apocrypta* fig wasps (Sycophaginae) also develop in syconia with inundated cavities and the males seem also to use for breathing the air present in the galls. The females of these genera eclose from their galls after mating and after the liquid of the syconial cavity has been absorbed. Contrary to suggestions by other authors, who supposed the filaments of the male *Apocryptophagus* and *Sycophaga* were breathing structures or temporary air stores themselves, evidence shows that they help to anchor the end of the gaster inside the galls and that gas exchange occurs thorough spiracles in the gaster.

**Key words:** Male, respiration, adaptations, Hymenoptera, Sycophaginae, fig wasps.

The larvae of all sycophilous wasps develop inside modified female fig flowers ("gall flowers") where they get the nourishment and air for respiration. Several authors have explained the functions of the large or filamentous peritremes of some males of the subfamily Sycophaginae. For example, Williams (1928) suggested that the filaments allowed the males of *Sycophaga nota* (= *Apocryptophagus* ?) to remain submerged [in the liquid of the syconial cavity] for some time or were used as floating devices. He also noted (without explaining why) that the male had a little difficulty in withdrawing the diverging lamellae [or filaments] from the galls. Wiebes (1982) noted that the males of *Eukoebelea* [probably *Apocrypaphagus*] are among the first to appear in the humid interior of the receptacle and that

they have "gills", *i.e.*, long filaments on the spiracular peritremes. Murray (1990) noted that *Eukoebelea* males (= *Apocryptophagus*) use the forked tip of the abdomens as an anchor, and that the *Apocrypta bakeri* male sometimes will anchor himself to a gall by lodging the expanded tip of the abdomen on the inside of a narrow entrance hole. Godfray (1988) noted that *Apocryptophagus* sp. males partially emerged from the gall after mating, keeping the rear part of the body anchored in the original gall. Ramírez (1987) postulated that the large peritremes and protruding breathing structures found in some fig wasps were adaptations to the humid environments in which they live during part of their life cycle. Compton and McLaren (1989) concluded that the peritremes of fig wasps studied by them "act as respiratory

siphons and perhaps also as temporary gas stores" for the insects.

According to Compton and McLaren (1989), the hydrofuge hairs on the peritremes of some fig wasps are associated with syconia having liquid-filled lumens. These hairs were found to be capable of repelling liquids and perhaps also serving as temporary air stores.

Both the male and female syconia of the *Meomorpha*, *Sycocarpus* and subgenus *Sycomor* *figs*, where Old World Sycophaginae wasps develop, are pollinated by *Ceratosolen* wasps (Wiebes 1963) and become filled with a transparent liquid or "liquour" after being oviposited or pollinated (Cunningham 1889, Baker 1913, Williams 1928, Murray 1987). This phenomenon has also been observed by the author for several other species of the subgenus *Sycomor* (*sensu* Ramírez 1977), for *Ficus minahassae* (Teysm. et Vr.) Miq. (sect. *Sycidium*, ser. *Phaeopilosae*) and *Ficus pseudopalma* Blanco (sect. *Pseudopalmeae*) of subgenus *Ficus* which are also pollinated by *Ceratosolen* wasps. Compton and McLaren (1989) also mentioned the presence of liquid in the lumens of *Sycomor* and *Sycocarpus* figs.

This article rather proposes the indirect associated respiratory functions of the tail-like appendages on some Sycophagini males, as well as of the large peritremes of Apocryptini males (Sycophaginae).

**Material and Methods:** Gall syconia from a single tree in early male phase of a gyno-dioecious *F. nota* (Blanco) Merr., (for developmental phases, see Galil and Eisikowitch 1968) were collected on the campus of the University of Philippines at Los Baños (UPBL) in November, 1989. The syconia were found to have emerging males of *Apocryptophagus nota* (Baker).

The syconia of *F. sur* Forssk. (monoecious) were also obtained from a single tree in early male phase at the Botanical Garden of Rhodes University, Grahamstown, South Africa (November, 1990), when the *Sycophaga cyclostigma* and *Apocrypta* sp. males were eclosing from the galls. The liquid of the syconial cavity in both species had not been absorbed and the cavity was completely inundated. The syconia were transversely cut near the ostium to preserve the maximum volume of fluid. Many nematodes were swimming in the liquid at the time the syconia were opened.

Observations were made using a dissecting microscope while the males of *Apocryptophagus nota*, (Baker) *Sycophaga cyclostigma* Waterston and *Apocrypta* sp. (probably *A. guineensis* Grandi) were eclosing from the galls and mating. The males did not appear to be disturbed by the microscope light and manipulations after the syconia were opened and they continued searching and mating.

## RESULTS

The terminal filaments of *Apocryptophagus* and *Sycophaga* (Figs. b-c, Fil) are extensions of the peritremes of the two abdominal spiracles with the small spiracles located at their bases. They are covered with small bristles (Fig. C) or hairs as noted by Ansari (1967). The hairs are bent over at their tips (Compton & McLaren 1989). *Apocrypta* males have wide plate-like (not prong-like) large and conspicuous spiracular peritremes covered with bristles or sensilla (Ulemberg 1985).

When early male phase syconia of both species of fig studied were opened, the *Apocryptophagus* and *Sycophaga* males had cut, with their mandibles, a narrow slit from inside the gall flowers where they developed. They partially emerged, head first, leaving the end of the abdomen with the filaments and spiracles inside the gall (Fig. a). While still anchored with the rear part of the abdomen and filaments inside the galls, the males stretched out the abdomen (like an elastic ribbon) inside the inundated syconial cavity and appeared to search in the liquid for galls containing females of their own species. Abdomen stretching allowed the males to find female-containing galls a distance of about six galls. Once the anchored males of both genera found a gall containing a female, with the mandibles they cut a narrow slit in the upper surface of the gall, introducing the narrow flat head and thorax. Immediately they liberated the end of the abdomen and the filaments from the gall in which they developed, contracted the body rapidly and penetrated completely into the gall, probably mating there. Shortly after the abdomen disappeared, the male head started emerging through the exit (see also Williams 1928), suggesting that mating was brief, as noted by Godfray 1988 for *Apocrypta* sp.,

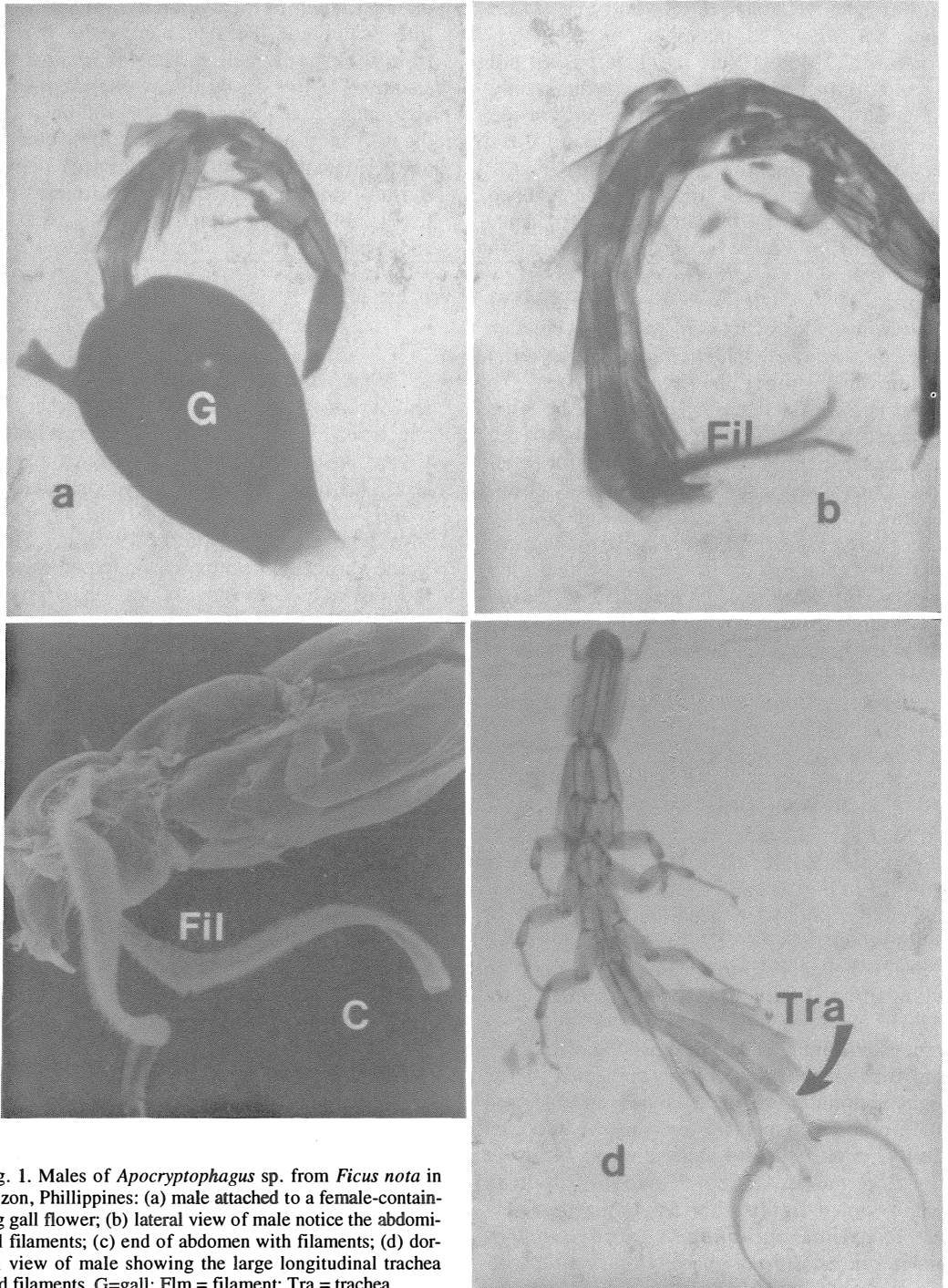


Fig. 1. Males of *Apocryptophagus* sp. from *Ficus nota* in Luzon, Philippines: (a) male attached to a female-containing gall flower; (b) lateral view of male notice the abdominal filaments; (c) end of abdomen with filaments; (d) dorsal view of male showing the large longitudinal trachea and filaments. G=gall; Flm = filament; Tra = trachea.

probably *A. mega* Ulemberg and *Apocryptophagus* sp. males inhabiting *F. hispidioides* S. Moore. Then, the male pushed out the anterior part of the body, leaving again only the end of the abdomen and filaments inside the gall, and the process was repeated. By sequentially using the gall of the last mated female as a stationary "respiratory tank" each male could cover all the cavity. Less frequently, the galls left empty by other males, (e.g., an empty gall of a *Ceratosolen* male, as noted by Godfray 1988), galls with mated females, or those with males of its own species, were also used. *Sycophaga cyclostigma* males have an abdominal morphology similar to *Apocryptophagus* males, they also become anchored with the filaments, and probably use the gases present in the galls of *F. sur* for respiration; one male seemed to actively search for 22 min while anchored from one gall. Both *Apocryptophagus* and *Sycophaga* males possess very enlarged tracheal trunks along their bodies (Fig. d, Tra.), as also illustrated by Compton and McLaren (1989, Fig. 1) which probably function as air sacs or air reserves. Other sycophilous wasps do not have enlarged trachea; e.g., *Philotrypesis caricae* (L.) as illustrated by Joseph (1958, Figs. 15-17).

Several *Apocryptophagus* males (N=12) were experimentally dislodged from the galls and left in the fig cavity. They would reach an open gall and enter it; otherwise, they became inactive or died. Males (N=12) anchored to their galls (as in Fig. a) and extracted from the syconial cavity, were introduced into a 70% alcohol solution and survived for  $\leq 8$  min, while those (N=12) that were introduced without contact with galls (as in Fig. d) died almost immediately. These observations provide indirect evidence that anchored males used gall oxygen and that they used only the spiracles of the eight abdominal segment. When an anchored male met a conspecific male in the syconial cavity, it pushed him aside and no biting or fighting was observed. However, Godfray (1988) noted fighting for an *Apocryptophagus* sp. The *Apocryptophagus* and *Sycophaga* males studied did not guard females after mating or spend much time within female galls, in contrast with Murray's observations (1990) on *Apocrypta bakeri* (Joseph).

The *Apocrypta* males (probably *A. guineensis*) of about 10 syconia of *F. sur*, eclosed from

their galls while the syconial cavity was still filled with liquid. They cut narrow slits to eclose from their galls, and stayed for a short time anchored to the slit by the swollen rear of the abdomen. Next they pulled the abdomen from the gall, carrying two air bubbles in the abdominal peritremata, swam and "searched" between the galls until they found one containing a female, where they cut a narrow slit, penetrated and apparently mated, for a few seconds.

## DISCUSSION

The males of *Apocryptophagus*, *Apocrypta* and *Sycophaga* emerge from the gall where they developed before the males of other species (e.g. *Ceratosolen*, *Philotrypesis*, *Sycoryctes* and others). This probably prevents overcrowding and avoids damage by males of fighting species ("soldier males" of Murray 1989 and 1990). These observations support the hypothesis that, in order to breath inside the inundated syconial cavities, the Sycophagini males and probably *Apocrypta*, use the oxygen present inside the gall flowers which contrary to the syconial cavity do not have liquid. The ribbon-like extensible abdomens of *Apocryptophagus* and *Sycophaga* males allow them to search and to find the female-containing galls, which are dispersed inside the syconial cavity while they are still anchored to a gall. The large non-projecting broad concave peritremes of *Apocrypta* males probably allow them to breath inside the female-containing galls, as well as to obtain air bubbles from the gall which are carried on the peritremes, while freely traveling along the inundated syconial cavity.

The function of the liquid found in the syconial lumen is uncertain (Compton & McLaren 1989). Janzen (1979) suggested (with no supporting evidence) a defensive function, stating "that the liquid without doubt contains antibiotic compounds". McLaren and Compton (in preparation) have failed to confirm that the liquid of *F. sur* has either anti-fungal or anti-bacterial properties. The liquid of the syconial cavity is secreted by the figs after the primary sycophilous wasps have oviposited or fertilized the fig flowers and this probably avoids the penetration of supernumerary pollinators, as suggested by Baker (1913), and of supernumerary *Sycophaga* colonizers.

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## RESUMEN

Las avispas de los higos *Apocryptophagus* y *Sycophaga* (Sycophaginae) se desarrollan en siconos de *Sycocarpus* y *Sycomorus*. Los siconos de los higos hospederos están llenos de un líquido cuando los machos eclosionan de sus agallas. Los machos tienen filamentos terminales en el abdomen que son extensiones de los peritremas, los cuales se usan para sostener y anclar la sección posterior del abdomen dentro de las agallas, mantener los espiráculos abdominales adentro y respirar el aire presente en ellas. Autores anteriores supusieron una función respiratoria. En esta posición los machos pueden respirar hasta por 20 minutos mientras buscan las agallas con hembras para fecundar. Migrando de agalla a agalla y copulando con las hembras inactivas que se encuentran en ellas, los machos respiran y se desplazan alrededor de la cavidad siconal inundada sin ahogarse. Los machos de *Apocryptophagus* y *Sycophaga* poseen troncos traqueales longitudinales muy grandes que probablemente funcionan como reservas de aire o gas. En este trabajo se presentan nuevas observaciones e ilustra con fotografías las estructuras asociadas con la respiración de los machos dentro de las agallas. Las avispas *Apocrypta* (Sycophaginae) también se desarrollan en los siconos de *Sycocarpus* y *Sycomorus* con cavidades inundadas y los

machos usan el aire de las agallas para respirar aunque no poseen filamentos terminales. Las hembras de los géneros mencionados son fertilizadas dentro de las agallas y eclosionan de éstas cuando el líquido del sicono ha sido absorbido. Contrariamente a las sugerencias de otros autores que creyeron que los filamentos de los machos *Apocryptophagus* y *Sycophaga* eran estructuras respiratorias o reservas de aire, la evidencia demuestra que los filamentos abdominales sirven para anclar la parte caudal del abdomen dentro de las agallas y que intercambio de gas ocurre a través de los espiráculos abdominales.

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