Description and immature stages of *Hirtodrosophila batracida* sp. n. (Diptera: Drosophilidae), a predator of frog embryos

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The unique biology of a drosophilid whose larvae are predators of the Central American glass frog, *Centrolenella fleischmanni* (Boettger), was presented in detail by Villa. Here, the correct assignment of the species is made to the genus *Hirtodrosophila* Duda (previously identified as a species of *Zygothrica* Wiedemann), the species is described, and fine morphological features of the larvae are described. The species is described from specimens from Nicaragua, although there are other unconfirmed records from throughout Central America. Relationships of *H. batracida*, n.sp. with several other species in the genus are briefly discussed. *Hirtodrosophila* are only known to be mycophagous; the only conceivable host shift was from fungi to frog's eggs.

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Introduction

Among the slightly more than 3000 species of drosophilid flies in the world, there are some with truly bizarre life histories. Perhaps 99% of the species whose breeding sites are known have been found associated with decaying fruit and leaves, fungi, as well as living and decaying flowers. Ashburner (1981) provides a particularly interesting review of the 'entomophagous and other bizarre drosophilids.' Larvae of some species of *Cacoxenus* Loew are cleptoparasites of bee nest provisions (Juillard 1947), larvae of *Cladochaeta* Coquillett (and an African species of *Leucophenga* Mik) are ectoparasites of cercopid nymphs (Grimaldi 1994, in press), and in Hawaii larvae of *Titanochaeta* Knab predate embryos of spiders in their silken egg sacs (Swezey 1929). A group of related steganine genera (*Acletoxenus* Frauenfeld, *Hyalistata* (Wheeler), *Mayagueza* Wheeler, *Pseudiastata* Coquillett, and *Rhinoleucophenga* Hendel) are larval predators on sessile Homoptera. Certainly, among the most bizarre habits of all is a small African group in *Drosophila* Fallén, the *simulivora* group, whose larvae are predators on larvae of simuliids, aquatic chironomids, and even the jelly-like egg masses of a dragonfly (Tsacas & LeGrand 1979). Akin to this last habit is a Central American species of *Hirtodrosophila*, described here, whose larvae are predators on embryos of certain land-breeding frogs. Clearly, drosophilids have among the most varied habits in the Cyclorrhapha, probably equal to the diversity of chloropid ecologies.

Review of life history

Our knowledge of the habits and hosts of *Hirtodrosophila batracida* sp. n. is due entirely to the comprehensive work of Villa (1977; 1978; 1980; 1984), from which this brief review is drawn. In Villa's 1977-paper, the 'frogfly' is identified as a *Drosophila* sp.; later it was referred to as *'Zygothricha* sp. [sic] (near *pleurostrigata*)' (Villa 1980) and as *Zygothrica* sp. (Ashburner 1981; Villa 1984). The species *pleurostrigata* Burla, 1956 was transferred from *Zygothrica* to *Hirtodrosophila* by Grimaldi (1987). Lastly, *Hirtodrosophila* was removed as a subgenus of *Drosophila* and erected as a genus, related to *Zygothrica* (Grimaldi 1990).

The 'frogfly' lays its eggs on the jelly mass containing the frog eggs. It preferentially oviposits on the egg masses of certain land-breeding frogs, particularly *Centrolenella fleishmanni* (Boettger) (Centrolenellidae). This tiny glass frog occurs com-

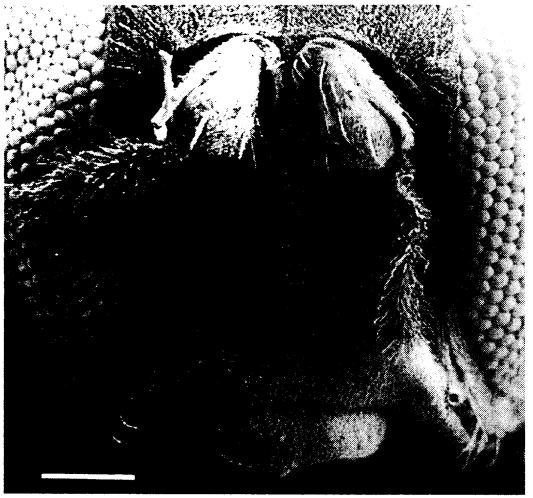


Fig. 1. SEM (frontal view) of face and antenna of *Hirtodrosophila batracida* sp. n. Scale bar: 100 μm.

monly from southern Mexico to Surinam, at sea level to about 2000 feet elevation. It lays a clutch of 18-21 eggs under a broad leaf (such as ginger lilly, *Hedychium*, or *Coix*) that hangs over a small stream. About 25 larvae per clutch were found, but there must be considerable competition, since 2-4 embryos are needed to sustain one larva. There are seasonal trends in infestation rates on the frog eggs; in the rainy season, 50% of the clutches were partially consumed, 20% of them were entirely consumed, so this species has a major impact on the population biology of the frog. The frog embryos that are not devoured by the larvae drop into the water and complete their metamorphosis in the sediments of the stream margin. Fly larvae do not subsist well on dead frog embryos, so they are obligate predators. Typical of most insects, oviposition site preference (OSP) of the female fly seems to be restricting the host use. Villa transferred fly eggs to egg masses of various frogs (*Agalychnis*, *Hyla*, other *Centrolenella*, even *Rana*) and found that the fly larvae readily feed.

Hirtodrosophila batracida is not the only fly to breed in frog eggs; another kind of Cyclorrhaphan are several species of *Gastrops* Williston (Ephydridae), a New World genus. *Gastrops* also appear to be obligate predators of the frog embryos, and are about as abundant as *Hirtodrosophila batracida*. I have netted the adults of *Gastrops* fairly often around the shores of forest streams in Costa Rica.

Taxonomy

Genus *Hirtodrosophila* Duda

Hirtodrosophila Duda, 1923: 41; Grimaldi (1990).
Drosophila (*Hirtodrosophila*): Sturtevant (1942); Wheeler (1981); Vilela & Bächli (1990).

A revised diagnosis for the genus is provided in Grimaldi (1990), which includes the following characters. Carina absent or, if present, always very short and narrow; flagellomere I usually with long setulae; ventral margin of cercus with tuft of fine, short setulae; male with comb of long, fine setae on ventral lobe of epandrium; oviscapt with several pegs on the dorsal margin, usually separated by a gap from the other, apical and ventral pegs.

The new species possesses just some of these features: it lacks the long setulae on flagellomere I (the pilosity is standard with most other drosophilids); ventral margin of the cercus (male) is without a tuft of fine setulae, but it does possess a pair of lobes seen in several other *Hirtodrosophila* (see Discussion below); also, the ventral lobe of the epandrium is stout and the group of setae are not arranged in a row or comb.

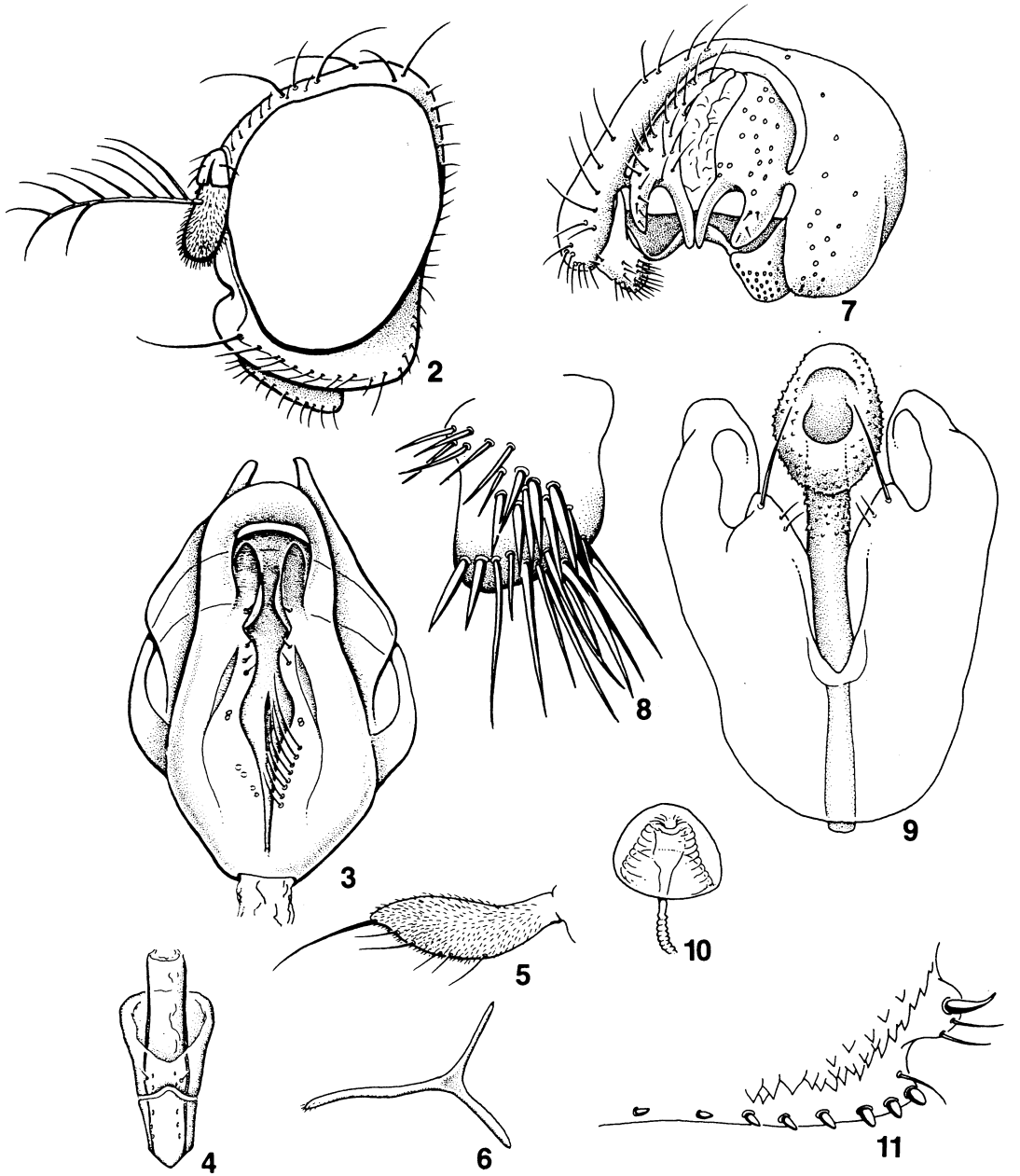
Features that the new species has that are typical of *Hirtodrosophila* and related genera (*Hirtodrosophila* Genus Complex, sensu Grimaldi 1990) are the following: arista with single ventral branch; carina narrow and small; clypeus narrow and deep; ventral lobes present on cercus; floor of cibarium with sclerotized, anterior bulb and few sensilla; cardo-stipital element of lacinia with long, thin dorsal and ventral arms.

Hirtodrosophila batracida sp. n.

Type material. - Holotype, ♂, NICARAGUA: Matagalpa, IX/9/75, J. Villa, reared from egg masses of *Centrolenella fleischmanni*; not dissected; in the American Museum of Natural History, New York [AMNH]. Paratypes: Series of 15 ♂, 22 ♀, and critical-point dried larvae, with same collection data, also in AMNH. Villa (1978) mentioned additional localities, from Oaxaca, Mexico and San José province, Costa Rica, but I have not seen adult material from these localities.

Etymology. - 'Frog killer,' from the Greek, batrachos (frog), and the Latin suffix -cida (pertaining to killing).

Diagnosis. - Oral margin of face and notopleural area darker brown than rest of body; cheek shallow; flagellomere I without long setulae; oviscapt with single apical peg largest, slightly hooked; cerci (male) with sclerotized, medial pair of thin lobes and broader lateral pair. Prensisetae (on surstylus)

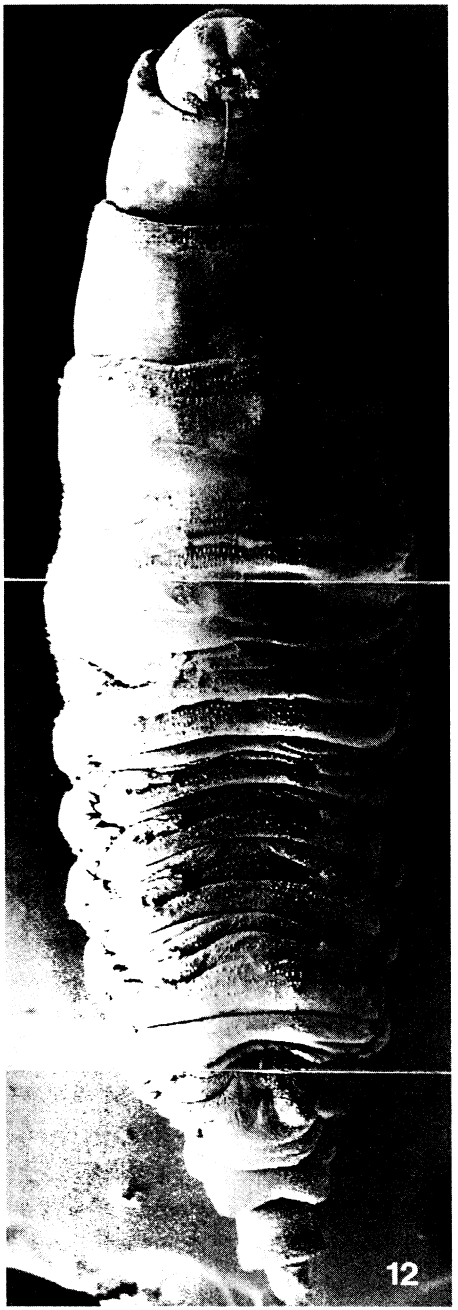


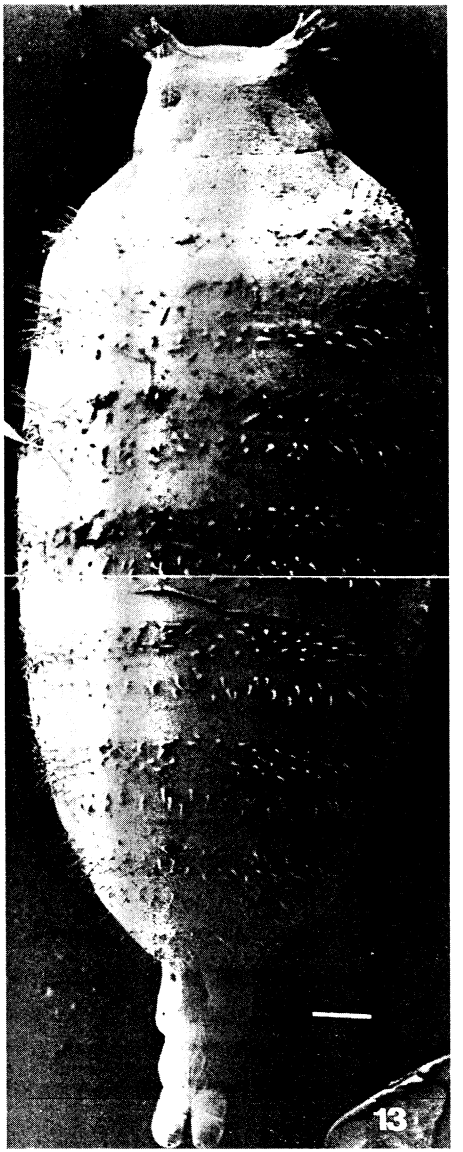
Figs 2-11. *Hirtodrosophila batracida* sp. n., adult features: (2) head, lateral view; (3) cibarial floor and bulb, with sensilla; (4) labrum; (5) palp; (6) cardo-stipital element of lacina; (7) epandrium; (8) surstylus; (9) aedeagus and hypandrium; (10) spermathecal capsule; (11) oviscapt.

not peg-like, but stiff, stout setae; distiphallus bulbous, with numerous minute scales.

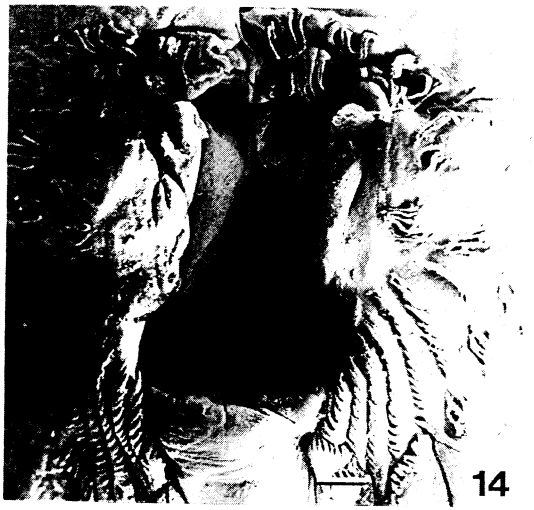
Description. – Body mostly light brown; oral margin on face and notopleural area slightly darker brown.

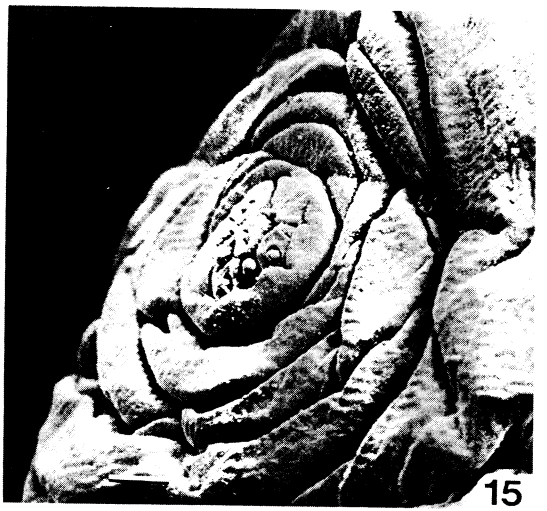
Head: Face narrow; with narrow, short carina (Fig. 1). Eye with sparse, short interfacetal setulae.

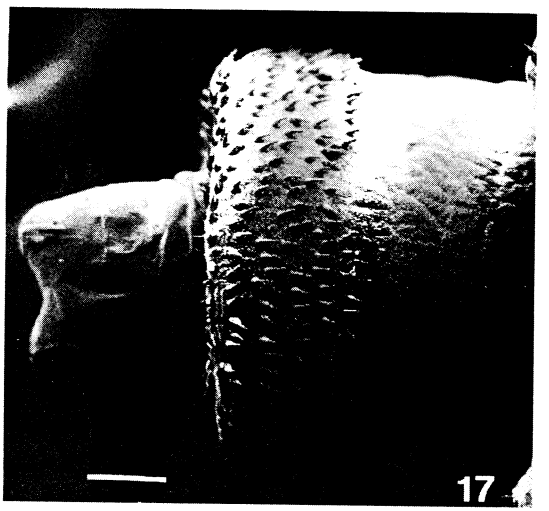




Figs 12, 13. SEM of immature stages of *Hirtodrosophila batracida* sp. n.: (12) ventral view of 3rd instar larva; (13) puparium (anterior spiracles are retracted). Scale bar: 200 μm.

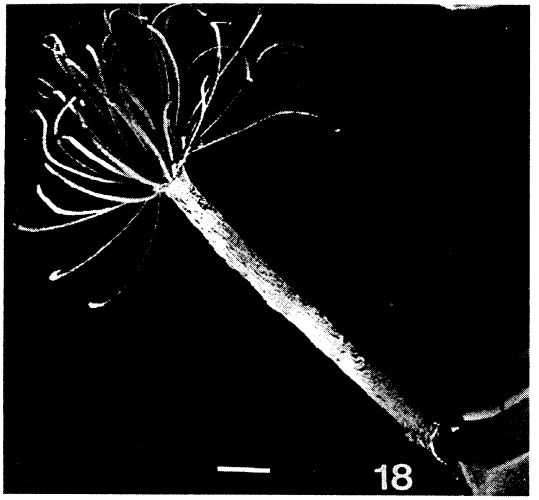


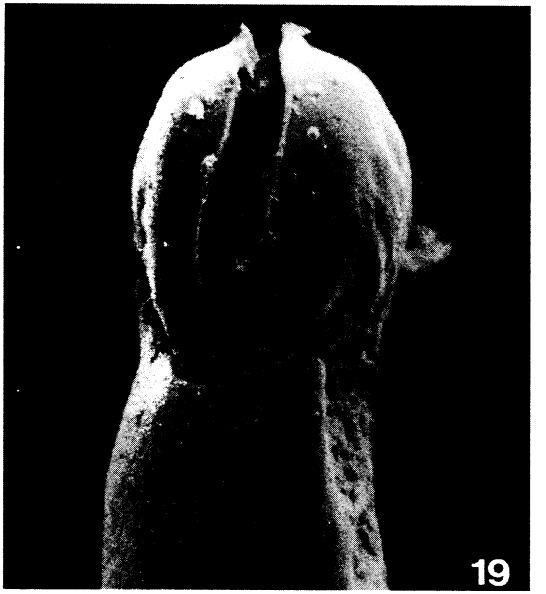


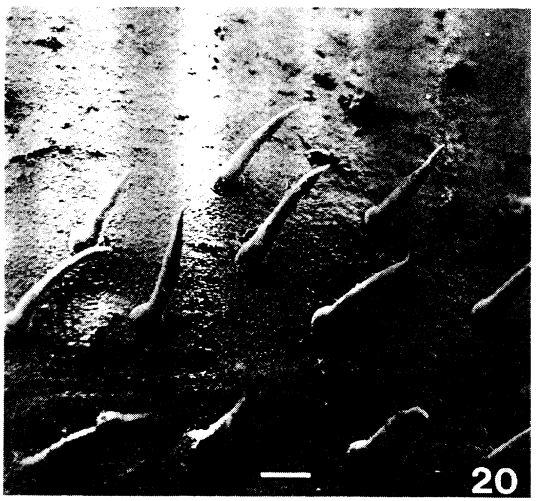


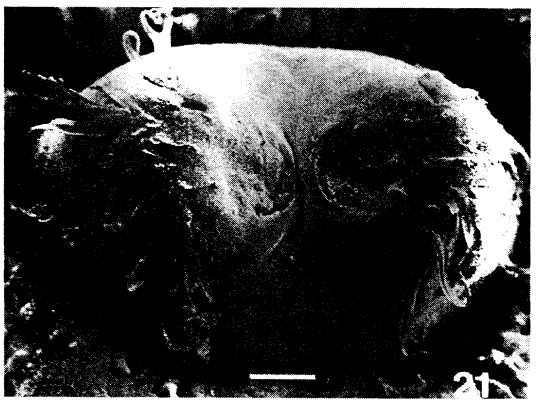
Figs 14-17. SEM of 3rd instar larva of *Hirtodrosophila batracida* sp. n.: (14) head, frontal view, showing oral cavity, oral ridges, and mouthooks; (15) maxillary palp; (16) creeping welt spinules, segment 3; (17) apex of posterior end (lateral view), showing posterior spiracle. Scale bars: 14, 20 μm; 15, 5 μm; 16 and 17, 50 μm.

Oral margin darker brown than rest of face. Clypeus deep, but width is narrow (Fig. 1). Oral cavity large, with proboscis barely protruding. Palp with apex pointed, having single long apical seta nearly equal to length of palp (Fig. 5). Cardo-stipital element of lacinia with long, thin dorsal and ventral arms (Fig. 6). Labrum short (Fig. 4). Floor of cibarium with heavily sclerotized anterior bulb; row of 4-9 long posterior sensilla, 2-3 short anterior sensilla (Fig. 3). Single pair of vibrissae present; cheek shallow; eye deep (Fig. 2). Antenna: pedicel with standard array of setae and complete dorsal seam (Fig. 1); flagellomere I without long setulae; arista with generally 5 dorsal branches, 1 ventral branch, and long apical fork (Fig. 2). Frontal-orbital setae: proclinates and posterior reclinates approximately equal in length, anterior reclinate slightly smaller; anterior reclinate slightly closer to proclinate than to posterior reclinate. Bases of ocellar setae in ocellar triangle. Postocellars small, ca.







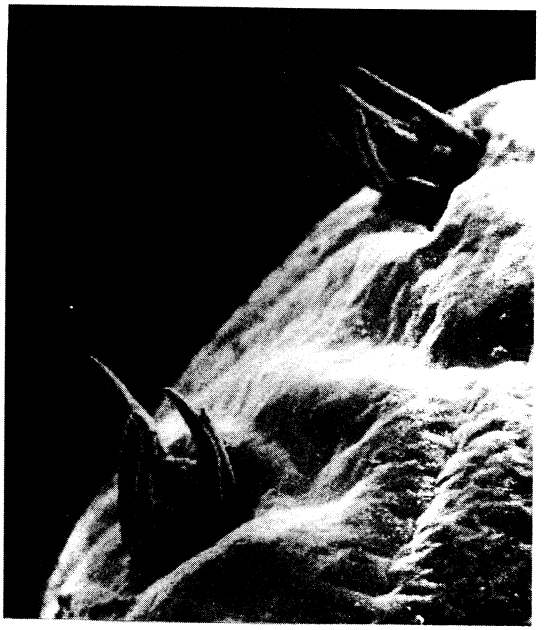


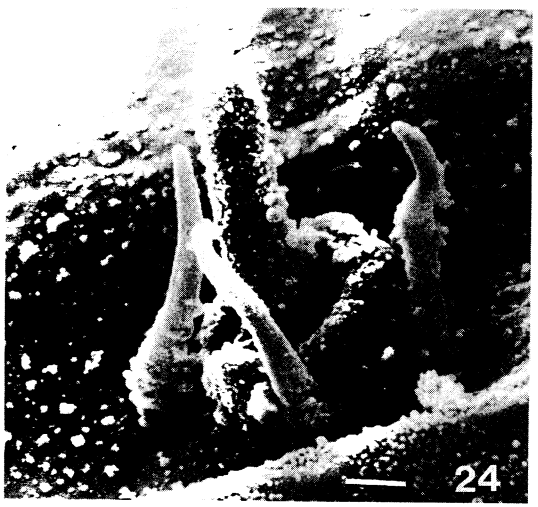
Figs 18-21. SEM of puparium of *Hirtodrosophila batracida* sp. n.: (18) fully everted anterior spiracle, showing numerous spiracular filaments; (19) spiracular opening at apex of filament; (20) creeping welt spinules, segment 5; (21) posterior spiracles with spiracular hairs. Scale bars: 18, 200 μm; 20 and 21, 20 μm.

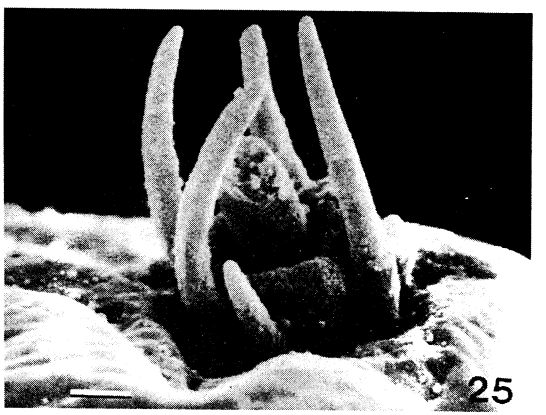
0.5 length of ocellars, cruciate for about 0.5x their length.

Thorax: Mesonotum and scutellum unicolorous light brown. Acrostichal setulae in 6-8 uneven rows between anterior dorsocentral setae. No presutural setae present. Anterior dorsocentral seta ca. 0.7x length of post. dorsocentral. Postpronotal lobe with 2 large setae. Notopleural area with 2 large setae. Katepisternum with 1 very long seta, shorter and thinner one slightly dorsad. Dorsal half of pleuron darker brown; ventral half very light, almost yellow. Wing without markings. Halters yellow. Legs yellow to light brown. Hind tarsi with ventral 'hair seam' along entire length, with row of fine ctenidial combs parallel to seam.

Abdomen: Tergites dark brown. Female genitalia: Oviscapt bearing 1 large, sharp apical peg; small notch separating apical peg with row of ventral ones; row of 8-9 smaller pegs along ventral margin (Fig. 11). Spermathecal capsule wider than high; not round, slightly tapered apicad; introvert annulated (Fig. 10). Male genitalia: Epandrium connect-







Figs 22-25. SEM of 3rd instar larva, features of posterior end, of *Hirtodrosophila batracida* sp. n.: (22) rectal pad; (23) pair of sensilla organs on last segment; (24) detail of sensilla organ on penultimate segment; (25) sensilla organ on last segment (detail). Scale bars: 22, 20 μm; 24 and 25, 2 μm.

ed to cerci by very narrow bridge. Cerci with sclerotized pair of narrow, thin lobes medially; thicker pair laterally (bearing 4-5 minute setulae). Epandrium with ventral lobes stout, setose, but setae not arranged in rows nor especially long (Fig. 7). Surstylus with prensisetae not peg-like; but long, stiff, and bristle-like (Fig. 8). Hypandrium simple; anterior margin rounded, approximately near apex of aedeagal apodeme. Aedeagus with bulbous apex; bulb and collar bearing numerous minute scales. Each paraphysis with single long seta and medially with 2 small setulae (Fig. 9).

Larva (third instar) and pupa. – Basic body form a standard, apodous, Cyclorrhaphan type (Fig. 12). Mandibles heavily sclerotized, thick and blunt. Oral lamellae not well developed, with only 6 short rows bordering mouth; numerous groups of 5-8 fine filaments each surrounding dorsal margin of mouth (Fig. 14). Maxillary palp with standard array

of sensilla, surrounded by numerous folds (Fig. 15). Anterior spiracles long (when seen fully everted); with ca. 40 long, fine spiracular filaments (Fig. 18); spiracular openings at tips of filaments slit-like (Fig. 19). Creeping welt spinules in larva stout and strongly hooked, in 5-6 rows per segment; longer, thinner, and erect on puparium (Fig. 20, cf. 16). Perianal pads of larva large (Fig. 22); 2 segments posterior to it each with unique sensory organs; composed of thick central scolopidium, surrounded by 5 thinner sensilla (Figs 23-25). Penultimate segment with 1 sensory organ directly behind each perianal pad (Fig. 24); posterior-most segment with pair of sensory organs behind each pad (Figs 23, 25). Posterior spiracles telescopic, sheath ringed completely by 6-7 irregular rows of creeping welt spinules (Fig. 17). Posterior spiracular openings standard for Cyclorrhapha: spiracular slits flanked laterally by ribbon-like, branched spiracular hairs (Fig. 21).

Discussion

The species is unequivocally placed in the genus *Hirtodrosophila*, based on features discussed above. In fact, it appears closely related to a group of species that possess the ventromedial and ventrolateral pair of lobes on the cerci (male) and a bulbous distiphallus with small scales. This group includes *clypeata* Wheeler, *clypeora* Wheeler, *mexicoa* Wheeler, and *thoracis* Williston. Definitive statements on species relationships, however, must await a revision of at least the New World species of *Hirtodrosophila*. There are 24 described species in this genus for the New World, but I have collected in one site alone in Panama nearly 30 species, all swarming on fungi, and most of which are undescribed. Perhaps as many as 200 New World species exist.

Until the work of Jaime Villa, all species of *Hirtodrosophila* were only known to be mycophagous. In the Neotropics, as probably elsewhere, some species are rather specific to particular pliant, fibrous polypore fungi; and others have tastes for numerous kinds of fleshy fungi. Given this set of relationships, the only scenario possible is a transition from fungi to frog eggs. One conceivable intermediate step between mushroom-breeders and the frogfly is found in some species of *Hirtodrosophila* that breed in jelly fungus (among other hosts), like *Auricularia* (Auriculariaceae). Whatever the exact transition from fungi to frog's eggs, *H. batracida* represents a quantum leap in the evolution of host use.

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